

Jennifer Vonk  
Todd K. Shackelford  
*Editors*

# Encyclopedia of Animal Cognition and Behavior



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# Encyclopedia of Animal Cognition and Behavior

With 1102 Figures and 130 Tables

 Springer

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## Preface

At its core, the study of animal cognition and behavior is interdisciplinary, drawing on the work of biologists, zoologists, psychologists, and anthropologists, to name a few key fields. With these diverse perspectives, a certain lack of convergence of definitions of key constructs is inevitable. This is especially true with the study of animal cognition because it necessitates the inference of underlying processes that cannot be directly observed or experienced. It is therefore essential to carefully operationalize those underlying constructs from a swath of behaviors that can be directly observed. This volume covers the behaviors of species that differ as immensely as, for example, the honeybee from the beluga whale. Thus, behaviors that serve similar underlying functions and motivations may appear vastly different across species. Established researchers and novice investigators alike might struggle to reconcile and synthesize the vast research on a rapidly expanding array of study species. It is the goal of this *Encyclopedia of Animal Cognition and Behavior* to bring some clarity to the ever-changing views and topics explored by the many researchers that contribute to knowledge of animal behavior and to celebrate the similarities and differences among species afforded by evolutionary processes.

We hope that interested readers, as both novel entrants into the research community and more senior investigators looking for concise reviews of the latest consensus on a topic, will find this volume to be a valuable resource. This *Encyclopedia of Animal Cognition and Behavior* is the culmination of an intense and laborious undertaking that relied upon the expertise and talents of International contributors, section editors, and editorial/production staff at Springer for whom we are sincerely grateful.

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Jennifer Vonk  
Todd K. Shackelford  
Editors

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## About the Editors



**Jennifer Vonk** received her Ph.D. in comparative psychology from York University, Canada, in 2002 and previously held a faculty position at the University of Southern Mississippi before joining Oakland University in 2011 where she is a professor of psychology. She examines the mechanisms underlying cognition and behavior in diverse species (including amphibians, reptiles, birds, mammals, human children and adults) with the goal of better understanding the evolutionary factors giving rise to cognitive capacities. She also conducts research that contributes to improving the welfare of captive species. She has published over 100 empirical papers, book chapters, commentaries, and edited volumes and has held several editorial positions including co-editor-in-chief for *Animal Behavior and Cognition* and section editor for *PeerJ*. She is a fellow of the Society for Behavioral Neuroscience and Comparative Psychology/Division 6 of the American Psychological Association.



**Todd K. Shackelford** received his Ph.D. in evolutionary psychology in 1997 from the University of Texas at Austin. Since 2010, he is professor and chair of the Department of Psychology at Oakland University (<http://www.oakland.edu/psychology>) in Rochester, Michigan, where he is co-director of the Evolutionary Psychology Lab ([www.ToddKShackelford.com](http://www.ToddKShackelford.com)). In 2016, he was appointed Distinguished Professor by the Oakland University Board of Trustees. He led the founding of new Ph.D. and M.S. programs (<http://www.oakland.edu/psychology/grad/>), which launched in 2012. Shackelford has published around

300 journal articles and his work has been cited over 27,000 times. Much of Shackelford's research addresses sexual conflict between men and women, with a special focus on men's physical, emotional, and sexual violence against their intimate partners. Since 2006, Shackelford has served as editor of the journal *Evolutionary Psychology* ([www.epjournal.net](http://www.epjournal.net)) and in 2014 founded the journal *Evolutionary Psychological Science* (<http://www.springer.com/psychology/personality+%26+social+psychology/journal/40806>) as editor-in-chief. Shackelford is an elected fellow of the Association for Psychological Science and the American Psychological Association.

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# A

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## 11 $\beta$ ,21-Dihydroxy-4-pregnene-3,20-dione

► [Corticosterone](#)

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## 11 $\beta$ ,21-Dihydroxyprogesterone

► [Corticosterone](#)

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## 2AFC

► [Two-Alternative Forced-Choice Paradigm, The](#)

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## 4-Pregnene-11 $\beta$ ,21-diol-3,20-dione

► [Corticosterone](#)

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## 4-Pregnene-3,20-dione

► [Progesterone](#)

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## Aardvark

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## Synonyms

[Ant bear](#); [Anteater](#); [Earth pig](#)

## Introduction

The aardvark (*Orycteropus afer*) is a burrowing quadruped nocturnal mammal that can be found across sub-Saharan Africa. People often mistakenly identify aardvarks as anteaters, and while ants are a primary part of their diet, aardvarks are a different taxonomic grouping and the only extant species in the order Tubulidentata. Aardvarks are an extremely reclusive species and are rarely observed in the wild. African folklore states that sighting an aardvark twice in your lifetime will lead to a long and happy existence (Knothig 2005).

The name aardvark originates from “aarde” meaning earth and “vark” meaning pig. The name is derived from the Afrikaans language, a language derived from Dutch. The scientific name

*Orycteropus afer* is derived from Greek and can roughly be translated to “digger foot of Africa.”

### Description

Aardvarks have large bodies with elongated heads and very small necks. They are nocturnal animals that live in dug burrows and come out at night to forage for insects. Their snouts end in a flat nose that has small hairs to keep dirt and insects out of their nostrils. They are covered in coarse fur on most of their bodies except their tail and part of their head. They are naturally a yellowish-gray color but often appear brown or red due to their fur retaining soil from their burrowing activity. It is thought that fur in this mammal is not necessarily to help regulate temperature like with most mammals, but rather to help prevent ants and termites from biting their thick skin during their foraging forays. Due to being a nocturnal species, their skin can burn if they are in the sun for an extended period. This can be problematic for aardvarks kept in captivity, and zookeepers will frequently cover aardvarks in sunscreen to prevent sunburn. A difference that has been noted between male and female aardvarks is that females have lighter colored heads and the tip of the female's tail is white. While the purpose of this is unknown, it is theorized that it is to help an aardvark cub follow their mother.

Aardvarks are able to independently move their large cylinder-shaped ears and close their nostrils on demand when digging to prevent dirt and insects from entering their ears and nostrils. As is the case with most nocturnal vertebrates, aardvarks are color-blind and have poor vision and rely on their keen sense of hearing and smell to navigate their surroundings. An aardvark's teeth are very different from the teeth of most other animals and are not meant specifically for grinding or tearing (Brewer 2003). Their teeth are a unique cylinder shape that lacks a root or enamel. The tooth is made of multiple smaller cylinders that are fused together to create the individual teeth. Aardvarks use their highly adapted teeth to break the exoskeleton of the insects it licks with its tongue. One theory on the evolution of the unique shape of their teeth is that it is caused by a symbiotic relationship they

have developed with the aardvark cucumber. (*Cucumis humifructus*) (Knothig 2005). The cucumber is a subterranean fruit that gets its namesake from only animal known to dig them up and eat them – the aardvark. The seeds are then released in the feces, which the aardvark bury. Their large spoon-like claws are good for digging into the hard earth and breaking open cement-like termite mounds. An aardvark's tail acts as a weight to allow them to stand on their hind legs and grip an insect mound with their forelimbs. This standing position helps provide the grip necessary to break open hard termite mounds with their claws. Once an aardvark is fully grown, they are about 6 ft long (1.83 m) from snout to tail and can weigh between 80 and 150 pounds (36.29 kg and 68.04 kg, respectively) on average.

### Habitat

In the wild an aardvark's habitat consists mostly of open woodland, scrub, and grassland. They generally avoid dense forests, deserts, and mountainous terrain due to being ill-equipped to live in those areas. They prefer to burrow in areas where the soil is loose and easy to dig into and that is within a reasonable distance from their foraging area (Knothig 2005). Aardvarks can largely be found roaming throughout sub-Saharan Africa but are unevenly distributed due to ill-suited terrain and human interference. It is unclear if aardvarks are truly territorial due to lack of empirical studies and their solitary, nocturnal behavior. Some evidence shows aardvark will maintain multiple burrows over a large home range, sometimes even miles apart, each of which will have a specific purpose (Knothig 2005). Some dens may be used as a temporary resting place after a night of foraging forays, and others may exist only to be used for hiding from predators. Aardvarks also construct more permanent dens that are mainly used by females with cubs. However, they generally have several dens in several areas, as well as several tunnels, or tunnels that are made specifically to hide from predators within a home range. Aardvarks are primarily nomadic, with the main exception being for females caring for cubs, which generally stay in one area for safety of her

offspring. Their burrows can be quite large – as much as 10–13 m (33–43 ft) long – and generally have several entrances and chambers used for sleeping and rearing offspring. The burrows are built to retain moisture and regulate temperature, making it cool during the day and warm at night. Once aardvarks abandon a burrow to move to a new area, the abandoned burrow can provide an environmental service by trapping seeds of plants in the entrance area where they cannot be destroyed by other factors in the environment. Abandoned burrows also provide an important keystone habitat function for other animal species, some of which are on the International Union for the Conservation of Nature (IUCN) threatened species list (Whittington-Jones et al. 2011). An example of one such group of species would be pangolin (*Phataginus* spp.) in areas where ranges overlap. Services provided by aardvarks can also extend beyond occupation of abandoned burrows. Some species, such as the aardwolf (*Proteles cristata*) and the bat-eared fox (*Otocyon megalotis*), will take advantage of termite mounds opened by an aardvark to eat the stray termites in disturbed mounds.

### Diet

An aardvark's diet mainly consists of ants and termites but can include aardvark cucumber, beetles, and insect larvae. Throughout the year ants are their primary food source, but during the winter months they will switch to prey that is more readily available, such as termites and other insects due to lack of available ants in the environment. An aardvark is willing to walk 10–20 miles per night during foraging forays. They forage in a zigzag pattern until they detect and begin to follow signs of food (Melton 2008). Aardvarks capture their prey using a combination of their long prehensile tongue, their adhesive saliva, and large claws. All of these features together make the aardvark well-suited for accessing ant and termite mounds, some of which can be as hard as concrete. As they eat, their tongues also collect dirt and small rocks which help an aardvark to digest the insects it consumes. Aardvark disturbance at mounds

compounds with consecutive night forays. They will start disturbing the mound slowly, inflicting only minor damage; however, after several nights of consecutive visits, they can dig entirely into the ant and termite mounds such that their whole body can fit inside the hole they have created. In captivity an aardvark can be fed a mixture of fruits and vegetables, rice, vitamins, and several other ingredients to replace their natural diet. However, they can be difficult to care for in captivity due to their nocturnal nature as well as their dietary and habitat needs. For the food to be edible, it must be blended into a fluid consistency due to an aardvark's teeth not adapted for chewing solids.

### Vulnerabilities

Even though aardvarks are primarily nocturnal, they are still hunted by animals such as lions (*Panthera leo*), African leopards (*Panthera pardus pardus*), hyenas (*Hyaenidae*), and large snakes (mainly pythons). Warthogs (*Phacochoerus africanus*) have also been known to attack young aardvarks. Aardvarks are a very cautious and systematic animal. They will complete a specific series of events every time they prepare to leave their burrow. They spend substantial time listening for potential predators prior to departure from their burrow. If they unintentionally make noise that may attract the attention of predators, they will stop and listen again until perceived predation risk is diminished. This hypervigilant behavior continues within a few feet of their burrow such that they may bolt back to the burrow if necessary. Fleeing to a burrow is a primary means of defense in this species. Aardvarks digging unfinished burrows are more vulnerable as they are forced to exit their den backward and do not yet have appropriate escape cover. They also have been shown to use their powerful hind legs and large claws to ward off predators during agonistic interactions. The predominant danger to the aardvark's habitat and way of life is encroachment by humans. They are regularly killed by farmers for damaging roads, fences, and dams. Aardvarks are hunted for bushmeat and use in traditional medicine. Climate change poses a formidable risk to sustainability of aardvark populations as they may not be able to

adapt to minor changes in temperature and are at risk for reduced food availability if prey items are vulnerable to temperature changes.

### Life Cycle

Aardvarks have been known to live for about 20 years in captivity, but their life span in the wild is unknown. Aardvarks are solitary in nature and only come together during mating season where nomadic males will spend several weeks with a female mate before moving on in an attempt to find another female to mate with. Gestation for a female aardvark is about 7 months in duration, and they usually produce a single cub per pregnancy. Newborn cubs are small, pink, hairless, and blind and only weigh about 2 kg. An aardvark cub is almost entirely dependent on its mother during the first 2 weeks post-parturition. During this time the cubs use their hearing and sense of smell in order to navigate their environment. Cubs will remain in the burrow during that 2-week period before being able to venture out on short forays at night with their mother; however, they will not be weaned until approximately 3 months of age. Cubs will begin to create their own burrows just outside of their mother's burrow at about 6 months of age but will not completely leave their mother's burrow until around the time they are able to mate. They become capable of reproduction at about 2 years of age.

More facts about aardvarks:

- Much of the aardvark's fame is because it is the first animal to appear alphabetically in an English encyclopedia making it largely unknown in countries where English is not the primary language spoken.
- Aardvarks are commonly called anteaters, but they are not related at all. The reason for the incorrect comparison is due to both being myrmecophagous species, meaning they eat ants and termites primarily.
- Very little is known about aardvarks due to being reclusive in their natural habitat, and very few are found in captivity.
- Their powerful legs, feet, and claws are so strong they are able to shift about 2 ft of soil in about 15 s. That is more than a team of men with shovels can do.
- The aardvark is the only member of the order Tubulidentata, which is a reference to its unique tube-shaped teeth, that is known to still be alive at this point in time.
- In 1869 the first aardvark to be placed in a zoo was brought to London from South Africa (Goldman 2007).

### Cross-References

- ▶ Agonistic Behavior
- ▶ Feeding
- ▶ Foraging
- ▶ Home Range
- ▶ Life History
- ▶ Mating
- ▶ Omnivore
- ▶ Pangolin
- ▶ Predation Risk
- ▶ Predator Defense
- ▶ Prey
- ▶ Sex Differences
- ▶ Sexual Dimorphism

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## Abandonment

- [Anaclitic Depression](#)
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## Ablactation

- [Weaning](#)
- 

## Absolute Number Discrimination

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Number plays a continuous role in humans' everyday interactions – for many, our early morning routine may involve checking the temperature outside to know whether to grab a jacket on our way out the door, or checking our pockets for correct change to grab a coffee. Likewise, number is also an important function for nonhuman animals in their daily existence – knowing how much food is available, how many offspring one has, or how many predators are approaching are all useful survival skills that may be assessed through the use of numerical discrimination.

Counting in humans is defined as a formal process of enumeration in which each item in an array must be given a unique tag (Piaget 1952). When counting is referred to colloquially in research with nonhuman animals, it is generally referring instead to simple numerical discrimination, as opposed to formal number systems or mathematical ability (the exception to this are studies which explicitly study whether animals are able to discriminate absolute discrete number; however, results from these studies as a whole are inconclusive). Arithmetic is the product of human language and culture, and is generally considered a uniquely human construct. Interestingly, however, two human tribes (the Pirahã and the Mundurukú)

have been shown to exist with no formal system or language to represent number (Everett et al. 2005; Sheffler 1978). The Mundurukú have number words up to only five, although each word is not as definite in meaning as number words in English; the Pirahã, on the other hand, do not have words for precise numbers, but rather concepts for small amounts versus larger amounts. Interestingly, in both cases, the lexical limitation is no obstacle to the ability of these individuals to discriminate between larger quantities of items (Gordon 2004; Pica et al. 2004). Likewise, preverbal human infants are able to discriminate quantities, despite lacking linguistic ability to express their choices (Wynn 1992; Xu and Spelke 2000).

Adult humans, nonhuman animals, and preverbal infants are all able to discriminate basic quantities due to an evolutionarily primitive system of numerical discrimination, known as the approximate number system (ANS; Merritt et al. 2012). According to the ANS, number is represented internally on a continuous number line, which allows both humans and nonhuman animals to discriminate approximate magnitudes. Number only takes on a discrete representation in human language when number symbols become mapped onto these approximate magnitudes through learning during childhood language acquisition and subsequent mathematics training. It is from this shared and primitive system that number symbols and the more precise use of number that is typical of adult humans has presumably risen.

A key element of the approximate number system is that it obeys Weber's law. Weber's law states that the change in stimulus intensity needed for an organism to detect a change is a constant proportion of the original stimulus intensity, rather than a constant amount. Two effects that are seen as a result of this are the *distance* effect and the *magnitude* effect. The distance effect maintains that the greater the distance between two numbers, the easier they will be to discriminate (for example, 9 vs. 1 will be easier to discriminate than 3 vs. 1). The magnitude effect is the common finding that when distance is held constant, larger numbers are harder to discriminate

than smaller numbers (for example, 2 vs. 1 is easier to discriminate than 9 vs. 8).

Ratio effects in accordance with Weber's law have clearly been demonstrated in many species. The most intensive early work in this area was conducted by Otto Köehler, with a variety of bird species (Köehler 1951). Subjects were presented with containers covered with lids showing different numbers of pieces of grain glued to the lid. The birds were rewarded for pecking at the lid with fewer pieces of grain, and punished for choosing an incorrect lid (punishment in this case ranged from being shooed away from the container by the experimenter, to having the incorrect lid thrown up into the air by a device known as the "frightening springboard" upon selection). Birds learned to choose the lid with fewer items; however, there are several alternate ways in which they could have solved this problem. If comparing, for example, a lid with 2 pieces of grain to a lid with 5 pieces of grain, the 2 pieces of grain will take up less space than the 5 pieces of grain, making it possible for the birds to solve this problem based on a judgment of surface area, rather than number. With enough trials, the birds could also simply learn to recognize the lid with two items as the correct response, without actually making a judgment based on relative numerosity. While it is not known if Köehler took any measures to eliminate these potential confounds, current studies of number in animals typically control for these issues by manipulating the size of stimuli such that it cannot be used as a reliable source of information. Animals are also typically trained with one set of ratios, and then tested with a new set of ratios. If an animal has simply memorized correct responses, then their performance should fall to chance when given new ratios. If, on the other hand, they understand numerosity they should apply the rule "choose the smaller number of items," making it possible for the animal to choose correctly when given a ratio they have never seen before (it is worth noting that Köehler taught animals to choose the smaller number of items, whereas most studies typically teach animals to choose the larger number of items).

Number has also been studied through the use of the operant conditioning chamber. Roberts

(2010) showed pigeons three different combinations of red and green light flashes, using ratios of 2 versus 1, 3 versus 2, and 4 versus 2. The use of these particular ratios was important because the distance between numbers is 1 for 2 versus 1 and 3 versus 2, but increases to 2 for 4 versus 2. The ratio between numbers, on the other hand, was equal for 2 versus 1 and 4 versus 2, but smaller for 3 versus 2. If distance was controlling the performance of the pigeons, then it should have been found that 4 versus 2 was most easily discriminated, while 2 versus 1 and 3 versus 2 were harder but equally discriminable. Instead, it was found that 2 versus 1 and 4 versus 2 were equally discriminable, while 3 versus 2 was significantly more difficult to discriminate. This finding suggests that ratio, not distance, was controlling the performance of the birds.

Number takes three forms – cardinal, ordinal, and nominal numbers. Cardinality refers to the elements of a set, and essentially asks the question "how many." Ordinality refers to the rank of an item (e.g., third place). Nominality concerns assigned numbers (e.g., zip codes in the United States) used for labeling purposes only, and is therefore a uniquely human practice. Studies of numerosity in nonhuman animals are thus concerned exclusively with cardinal and ordinal number. When animals choose between two discrete numbers (e.g., 2 vs. 4), this constitutes a study of cardinality. Ordinality, however, has also been assessed in nonhuman animals. In a landmark study, Brannon and Terrace (1998) trained two monkeys to respond to displays containing 1–4 items in an ascending numerical order. As a control for non-numerical cues, exemplars were varied with respect to size, shape, and color, such that the correct response could only reliably be obtained through the use of number. The monkeys were later tested, without reward, on their ability to order stimulus pairs composed of the novel displays of 5–9 items. Both monkeys were found to correctly order the novel items. In another study, Cantlon and Brannon (2006) trained monkeys to order pairs of numerical stimuli with the values of 1–9. Once the monkeys learned to order these values, they were introduced to pairs of novel displays of 10, 15,



20, and 30 items. Once again, monkeys were able to spontaneously order the novel values, suggesting that there is no known upper limit on the numerical capacity of these animals.

A number of different procedures have been used in studying number in nonhuman animals. Often, these paradigms have been borrowed from developmental psychology studies of human infants, as in both cases procedures need to be nonverbal. In one study (West and Young 2002), a version of the preferential looking technique that had previously been used with infants (Wynn 1992) and monkeys (Flombaum et al. 2005) was adapted for use with dogs. In this task, dogs watched as food items were placed, one at a time, behind a screen and out of their view. The screen was then lifted so that the dog could see the resulting number of items. In one condition, dogs saw a simple, correct calculation ( $1 + 1 = 2$ ). In two other conditions, however, dogs either saw an unexpected outcome in which fewer objects were present when the screen was lifted than should be expected ( $1 + 1 = 1$ ), or saw an outcome in which more objects resulted than should be expected ( $1 + 1 = 3$ ). When an expected outcome was used, dogs spent as much time looking at the outcome as they did looking at the initial presentation of items, but when a result was unexpected, dogs spent significantly longer looking at the resulting amount of food. This suggests that, like infants and monkeys, dogs may have been anticipating the outcome of the calculations, which would require them to employ some form of numerical system.

While the majority of numerical experiments with nonhuman animals take place in a laboratory setting (where arguments could be made that numerical ability is the result of thousands of trials in an artificial scenario), animals have also been shown to be sensitive to number in the wild. In one study using playback recordings of lioness roars, defending adult female lions were found to be more likely to approach the location of the recordings if they heard the roar of a single female lion, than if they heard the roars of three female lions (McComb et al. 1994). Avoiding the costs of engaging in territory fights with larger groups of assailants presents one of many selective

advantages presented by the use of numerical information in the wild.

There is substantial support for the existence of the ANS, meaning that numbers are represented internally in an indiscrete fashion on a number line. The mathematical formulation of this number line, however, has been debated. Some researchers (Whalen et al. 1999) have proposed that this number line uses scalar variability. In this case, the numbers on the number line are equally spread, with variability that increases across numbers, making discrimination more difficult. Proponents of the logarithmic model (Nieder and Dehaene 2009), on the other hand, maintain that variability is fixed, while numbers themselves are numerically compressed as magnitude increases across the number line. Predictions made by both of the models, however, are quite similar.

While the ANS remains the most dominant explanation for numerical processing, arguments have also been made for a secondary number system, often referred to as the object file system (Brannon 2006; Carey 1998; Feigenson et al. 2004). While the analogue magnitude system is generally an accepted account of numerical representation, the object file system is more controversial. The object file system (sometimes referred to as “subitizing”) deals only with small numbers, specifically numbers 1–4. These numbers are thought to be mapped discretely in a one-to-one representation, making them instantly accessible. For example, if subjects are shown four dots on a screen, they do not need to systematically count the dots because they will immediately recognize that there are four dots.

In support of the object file system, Hauser et al. (2000) found that wild, untrained monkeys were able to discriminate and successfully choose a larger number of food items over a smaller number of food items. Over 200 semi-free-ranging rhesus monkeys watched as experimenters placed pieces of apple into each of two containers. The experimenters then walked away so that the monkeys could approach the containers. When the containers contained ratios of 1 versus 2, 2 versus 3, 3 versus 4, or 3 versus 5 slices of apple, the monkeys chose the container

with the greater quantity of food. Interestingly, however, when the ratios exceeded the number four (4 vs. 5, 4 vs. 6, 4 vs. 8, or 3 vs. 8) the monkeys were unable to reliably choose the container with the most food. Hauser et al. suggested that the breakdown in performance of the monkeys when the number exceeded four items is evidence that the monkeys were using a spontaneous number system (i.e., the object file system) as opposed to an analogue magnitude system in order to solve the problem. In subsequent laboratory studies, (Beran 2001; Beran and Beran 2004), however, experiments analogous to those of Hauser et al. (2000) were conducted, in which chimps watched as an experimenter sequentially dropped pieces of food (M&Ms. or pieces of fruit), one-by-one, into each of two bowls. The chimp was then allowed to choose one of the two bowls and consume its contents. In this laboratory task, chimps discriminated magnitude well beyond 4 items, and up to 10 items.

The most persuasive argument against the use of an object file system is that even with numbers 1–4, both humans and nonhuman animals have been shown to demonstrate the ratio-effects that are the signature of the ANS (Beran and Rumbaugh 2001). If the one-to-one representation suggested by the object file system were in fact being used, then these ratio effects should not be seen for the numbers 1–4. As a result, some researchers question the evolutionary need for this secondary system. An alternate explanation for the extremely rapid processing of numbers 1–4 would be that the ANS is simply very quick in discriminating such small quantities, because of their lesser magnitude.

Rapid advances in the development of functional magnetic resonance imaging (fMRI) technology has provided further insight into the understanding of numerical cognition, implicating the intraparietal sulcus (IPS) as the primary brain structure involved in numerical processing (Nieder 2005). Although it was originally thought that the IPS might contain a specified number module, evidence now suggests that the IPS serves a “patchwork” of different functions (Ansari 2008). The prefrontal cortex (PFC) is also involved in numerical processing; however,

response latencies are faster in the IPS than in the PFC, suggesting that the IPS extracts numerical information and subsequently sends the information to the PFC for processing (Nieder and Dehaene 2009).

Single cell recordings have also proven to be a great asset in understanding numerical processing. In a delayed matching to sample task (Nieder and Miller 2004), monkeys were shown an array of 1–5 items and subsequently had to decide if a sample array matched this number. Single-cell recordings showed that the monkeys had number-selective neurons, which fired preferentially to particular numerical values and thus appeared to be “tuned” for specific numbers. These tuning curves are imprecise, such that a neuron with a “preference” for 6 may also fire for 5 and 7. The resulting tuning curves help explain the distance and magnitude effects associated with the analogue magnitude system. When two numbers are farther apart, their respective tuning curves will overlap less, creating less “noise” around the number and making them easier to discriminate. Tuning curves, however, get wider and less precise as numerical magnitude increases. Thus, while 1 versus 2 will have narrower tuning curves that are more precise, 8 versus 9 will have broader tuning curves that overlap more with surrounding numbers, making discrimination more difficult.

The question of numerical processing in animals can be traced back as far as the misadventures of Clever Hans (Pfungst 1911). While it was proven that Hans was not able to perform any type of arithmetic, we know today through the comparative study of number that many nonhuman species are sensitive to numerosity, and can make decisions based on this information. Advances in technology through the use of both fMRI and single cell recordings have also thoroughly increased our understanding of numerical processing, allowing researchers not only to pinpoint regions of the brain associated with number, but also to identify number selective neurons, which elegantly explain behavioral data in terms of Weber’s law and the ANS. To date, there is little information as to what the upper limit of numbers that can be discriminated may be in nonhuman

animals. Additionally, further comparative investigation may be useful in understanding species-related differences in numerical discrimination, and how they may be related to memory systems. For example, although both chimps and monkeys have been successful in numerical tasks with sequential presentation of items (Beran 2001; Beran and Beran 2004), there is evidence that monkeys more easily discriminate numerosity in tasks that use simultaneous presentation of items (Nieder et al. 2006). Furthermore, in a study with dogs (Macpherson and Roberts 2013), subjects were found to be incapable of discriminating number in several variations of a sequential task, yet discriminated number easily when stimuli were presented simultaneously. This apparent difficulty in discriminating sequentially presented items may reflect a limitation in working memory, as subjects in these experiments must mentally keep track of how many items they have seen presented to them. Further studies are needed to more fully understand any cognitive or physiological differences in processing number across species.

## Cross-References

- [Approximate Number System \(ANS\)](#)
- [Arabic Numerals](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Numerosity](#)

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## Absolute Pitch

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## Synonyms

[Perfect pitch](#)

## Definition

In humans, the ability to name or vocally produce any musical note without using a reference note. More broadly, the ability to accurately remember auditory pitch not just in terms of the relationships among pitches.

## Introduction

If you ask a musician for an example of a musical talent or gift, one of the most common answers would be absolute pitch (AP), and for good reason. Typically defined as the ability to name or produce musical notes without the need for a

starting reference, AP is thought to be exceedingly rare, with an estimated incidence of occurrence of around 1 in 10,000 people (Bachem 1955). While this number may vary substantially across cultures (Miyazaki et al. 2012), it is clear that AP is disproportionately present in top music conservatories across the world (cf. Deutsch et al. 2006), and moreover, a number of well-known composers and musicians, from Mozart to Mariah Carey, have reportedly possessed AP. Yet, despite over a century of empirical research, the origins and nature of AP are still an open scientific question, situated within a broader question about the origin and nature of listening skills and expertise.

## The Etiology of AP

Perhaps the most fundamental debate in the study of AP is how the ability develops. An influential theory of AP development is the *critical period theory*, which posits that AP depends entirely on musical training acquired early in life, during a critical period of development. A number of studies have reported that AP and early musical training are associated, assessed both by self-report (Bachem 1940; Levitin and Rogers 2005; Vitouch 2003) and tests of pitch identification (Deutsch et al. 2006; Lee and Lee 2011). Other early-life experiences that affect attention to pitch and that covary with AP, such as tonal language experience (e.g., Mandarin Chinese, Deutsch et al. 2004) and congenital or early-onset blindness (Hamilton et al. 2004), have also been used to support the *critical period* theory. Recently, the *critical period theory* was supported by a study demonstrating that a drug treatment, thought to “reopen” the critical period in mice (Yang et al. 2012), potentiates acquisition of AP in adult human listeners (Gervain et al. 2013), although in this study, AP performance was well below the performance that is criterial of AP listeners.

The *genetic theory* of AP asserts that development depends on a specific genetic endowment, requiring relatively minimal environmental shaping. The fact that AP tends to run in families supports this (Theusch et al. 2009), but it is difficult to differentiate genetic from environmental

factors, given that early musical training also runs in families (Baharloo et al. 2000). The rate of AP concordance among identical twins is significantly higher than the rate among fraternal twins (Theusch and Gitschier 2011). However, the “equal environment assumption” of twin studies may not be tenable, as identical twins tend to be treated as more similar than fraternal twins (Joseph 2002). Overall, despite several investigations, the putative genes for AP have not been identified, and it is clear that if there is a genetic basis to AP, it is not inherited in simple Mendelian fashion (Theusch and Gitschier 2011).

Given there has been some support for both the *critical period* and *genetic theories*, a third theory integrates these in a *hybrid theory* (Zatorre 2003). This *hybrid theory* states that early musical training within a critical period is necessary, but not sufficient, for AP to develop. Rather, early musical training must be accompanied by some genetic predisposition.

The *practice theory* conceptualizes AP as a listening skill, able to be learned at any time in life through perceptual training along with the appropriate general cognitive mechanisms for effective learning (e.g., effective attention control, sufficient working memory). Until recently, this theory has not been considered seriously because prior AP training studies have produced only modest improvements in absolute pitch identification (Takeuchi and Hulse 1993), and retention of this modest learning has been assumed to be short-term, although it has not been generally tested after a substantial retention interval. But there have been some studies that reported pitch identification performance comparable to “genuine” AP possessors after training (Rush 1989), with trained performance persisting for several months (Brady 1970). More recently, adult training of AP was shown to be statistically associated with individual differences in auditory working memory, which actually mediated the relationship between early musical training and AP learning in adults (Van Hedger et al. 2015a). These findings suggest that AP acquisition in adults may be better understood as a listening skill rather than an ability endowed at birth or crystallized within a critical period. This treats the skill of AP as

similar to other perceptual skills, given that working memory has been implicated in a variety of other perceptual category-learning tasks (Lewandowsky et al. 2012).

## Describing AP

Many of the controversies surrounding the origins of AP could be seen as rooted in a simple question that has no simple answer: *How should AP be measured?* The conventional definition (being able to name or produce a musical note without the aid of a reference note) is broad and does not address issues that arise when considering the actual variability in AP performance based on a number of factors, some of which are outlined below. This variability is important because, contrary to the simple definition, systematic and idiosyncratic variability in AP performance suggests the conception of the process of AP is neither monolithic nor exactly the same across people or time, which has implications for understanding how AP arises and operates.

**Variability in Note Identification:** The instrumental timbre and octave register of the to-be-identified note can influence categorization accuracy (Bahr et al. 2005). Individuals tend to have better AP memory for their primary instruments, sometimes to such an extent that AP ability does not manifest for other instruments (Ward and Burns 1982). There are also systematic differences in AP accuracy based on instrumental timbre, as timbres such as pure tones (Lockhead and Byrd 1981) and the human voice (Vanzella and Schellenberg 2010) tend to be harder to identify compared to timbres such as piano and violin. Even among highly familiar instrumental timbres and octave registers, AP possessors display reduced performance when making judgments about notes that randomly switch between timbre and octave, suggesting that these attributes are an integral part of their category representations (Van Hedger et al. 2015b). Given that many tests of AP ability only present participants with one or two timbres (e.g., Athos et al. 2007), results of many AP assessments may not fully capture the diversity of AP.



Particular notes may also relate to difficulty of AP categorization. Specifically, “black-key” notes tend to be less accurately and more slowly identified compared to “white-key notes,” with the notes “C” and “G” being easiest to identify (Miyazaki 1990). While this effect was initially described using a critical period framework – as white keys are generally learned at the youngest age and before black keys on a keyboard – the current prevailing view is that these note class differences stem from distributional differences in the listening environment. For example, Deutsch et al. (2011) were able to explain about 65% of the variance in note categorization accuracy with the estimated frequency of occurrence of each note in the listening environment.

The listening environment also appears to be essential in holding note categories in place. Both past and present environmental factors are important in the development and maintenance of AP (Wilson et al. 2012), with recent musical activity able to “tune up” AP ability (Dohn et al. 2014). Moreover, the “present” environment can be operationalized at a rapid timescale – within a single experimental session. When presented with music that was flattened by a fraction of a semitone, AP possessors reoriented their sense of what is “in tune” versus “out of tune” based on this listening experience (Hedger et al. 2013; Van Hedger et al. 2018).

On top of environmental influences, AP ability has been documented to shift with age, though the mechanisms for this change are not well understood. These age-related shifts have been reported as early as 40 years old and can progress to the point where individuals are two or three semitones removed from the “correct” note (Ward 1999). However, some individuals demonstrate no age-related shift, and thus more work is needed to understand the physiological and cognitive components of this effect. Given that these shifts would result in an individual consistently misclassifying a note by a fixed amount, some researchers have given partial or full credit for semitone errors (e.g., Athos et al. 2007) or assessed AP ability by the relative deviation of a

response to the “correct” answer (e.g., Bermudez and Zatorre 2009).

AP as Dichotomous Versus Continuous: By this point, it should be clear that an individual’s past and present experiences indelibly shape their AP “fingerprint,” and thus AP is not synonymous with the perfect identification of any pitched sound. This variability in AP identification, however, means that the empirical study of AP requires establishing performance thresholds that can appropriately differentiate “AP possessors” from “non-AP possessors.” Yet, the question of whether individuals can be cleanly binned into categories of “AP possessor” and “non-AP possessor” has been controversial since the earliest days of empirical research on the topic (Bachem 1937).

Support for AP as a dichotomous versus continuous ability appears to depend on the way in which it is tested. Often, tests of AP involve making a *timed* note category judgment (generally within 3–5 s). The logic for this “timeout window” is that AP should involve the *rapid* identification of a pitched sound. Indeed, when adopting this testing format, performance appears to be binned into relatively discrete populations of individuals near chance versus individuals near ceiling accuracy (Athos et al. 2007). However, allowing for longer periods to respond can reveal a more variable distribution, with many individuals falling between chance and ceiling performance (Bermudez and Zatorre 2009). As such, timed tests may exaggerate the dichotomous nature of AP.

Another factor in the consideration of AP as dichotomous versus continuous is that of *implicit absolute pitch*. While implicit AP is measured in several ways, the fundamental idea is that most individuals, regardless of explicit AP or musical training, have some long-term memory for absolute pitch based on pitch regularities in the listening environment, even if they are not able to assign cultural labels (e.g., note names) to isolated pitches. For example, individuals can differentiate popular melodies (Schellenberg and Trehub 2003), single iconic pitches such as the censer “bleep” (Van Hedger et al. 2016b), and even

isolated in-tune from out-of-tune notes (Van Hedger et al. 2016a) based on absolute pitch information. These examples illustrate that the listening environment shapes long-term memory for absolute pitch across *all* individuals, not just those who can explicitly label isolated notes.

AP in Nonhuman Animals: When conceptualizing absolute pitch in broader terms – not tied to associating pitches with culturally specific labels – it becomes possible to discuss how absolute pitch manifests in nonhuman animals. For example, in an operant conditioning paradigm that has been used across species, listeners are rewarded for responding to some ranges of tones but not others, and moreover the rewarded tone ranges are interleaved with the non-rewarded tone ranges (Weisman et al. 2012). In this paradigm, most rats (*Rattus norvegicus*) and humans showed successful learning with three, but not eight, tone ranges. In contrast, pigeons demonstrate some success at the eight tone-range task, and many vocal-learning birds displayed high levels of accuracy on both three and eight tone-range tasks (Friedrich et al. 2007). From these results, it is perhaps tempting to conclude that avian species – in particular, vocal-learning avian species – have better absolute pitch abilities than mammals. However, it should be noted that humans with absolute pitch are able to perform at levels that approach vocal-learning birds, though their pattern of errors suggests that they potentially engage in different strategies (Weisman et al. 2010). Overall, comparative work is valuable for understanding the nature of absolute pitch abilities across species, though it is important to consider how absolute pitch is operationalized before claiming that particular species do or do not “possess” absolute pitch.

## Conclusion

Absolute pitch has fascinated musicians, scholars, and the general population since it was first formally described, largely because of its conceptualization as a rare and mysterious expertise. In part, this idea of AP has been bolstered by

oversimplifying the description of AP, and not considering just how much variability exists in AP performance across and within listeners. While there are still many unanswered questions surrounding its development, it has become clear that AP is best conceptualized as a kind of listening expertise rather than an endowed special ability. Moreover, given that implicit, long-term memory for absolute pitch appears to be present in almost everyone, as well as several nonhuman animal species, it is possible that what makes AP special is the learning by which listeners develop the musical knowledge to understand and categorize absolute pitch in the context of a culturally developed system of music.

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Auditory Processing and Perception](#)
- ▶ [Auditory Signals](#)
- ▶ [Cognition](#)
- ▶ [Critical Period for Song Learning](#)
- ▶ [Critical Periods](#)
- ▶ [Culture](#)
- ▶ [Dual-Store Model](#)
- ▶ [Equal Environments Assumption](#)
- ▶ [Learning](#)
- ▶ [Pattern Learning](#)
- ▶ [Sensory Judgment](#)

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## Accessor

► Receiver

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## Accessory Nipple

► Supernumerary Nipple

## Accidental/Intentional Experiment

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### Synonyms

[Intentionality test](#); [Theory of mind](#); [Unintentional and intentional experiment](#)

### Definition and Description

An experiment in which subject responses to purposeful (intentional) and unplanned (accidental) actions by an experimenter are measured as a means to identify whether an individual (human or nonhuman) understands the intentional actions of others. The intentional and accidental experiment is relevant to the topic of theory of mind, as it tests whether subjects understand intentional behaviors, one of the requisite components to understanding that others have thoughts and beliefs similar or separate to their own.

Two common variations of the accidental/intentional experiment use “accidental” and “intentional” actions of experimenters while indicating the location of rewards and “clumsy” and “competent” experimenters responsible for delivery of rewards. The basic premise of the experiment is that the subject must discriminate between the actions of the experimenter that will result in successful delivery of the reward and those that will not result in delivery of the reward.

In an initial study, subjects were trained to identify or request an item (usually food reward) hidden under an opaque container that has been identified with a marker placed on top of it, signaling the location of the food (Call and Tomasello 1998). During the subsequent testing phase, the marker was either intentionally placed on top of the container or accidentally dropped onto one of the other containers. In this procedure, the container was said to have been marked intentionally or

accidentally. The subject was presumed to have recognized the intentions of others if the intentionally marked container was selected over the accidentally marked container (Call and Tomasello 1998).

In another variation of the task developed by Povinelli et al. (1998), during the training phase, subjects were exposed to a “clumsy” experimenter who accidentally dropped the reward, a “competent” experimenter who successfully delivered the reward, and a “negligent” (and in some cases “aggressive”) experimenter who intentionally dropped the reward. During the subsequent testing phase, the subject was to be given the chance to select the reward from one of the three experimenters. In this procedure, the subject was said to have recognized the intentions of others if the “competent” experimenter was selected over the “clumsy” and “negligent” experimenters (Povinelli et al. 1998).

In the intentional and accidental action experiment, the actions are often signaled by experimenters with eye gaze (toward or away from a location), intentional or accidental dropping or misplacing of the food reward, failure to deliver a food reward, and verbal cues such as “oops,” “oh no,” “okay,” and “there.”

## Human Studies

Research on the ability of children to recognize intentions has primarily focused on young children, and the comparative framework for comparing humans and nonhumans involves studies with young, preverbal children (infant to 2 years). In these studies, researchers have relied on nonverbal measures such as eye gaze (Phillips et al. 1992), habituation-dishabituation (head turn) (Gergely et al. 1995), imitation (Meltzoff 1995; Carpenter et al. 1998; Olineck and Poulin-Dubois 2005), and reaching/grabbing (Behne et al. 2005) in order to identify whether or not children are able to recognize the intentions of others. Research using each of these measures suggests that by the end of their first year, children are able to identify the intentions of others.

Many of the studies that examine the ability of children to recognize intention and accidental actions incorporate verbal indicators or cues to signal the intentional and accidental actions. For example, Carpenter et al. (1998; replicated by Olineck and Poulin-Dubois 2005) examined the ability of young children (14–18 months) to reproduce or imitate intentional and accidental actions modeled by an adult. These actions were indicated by the experimenter as intentional or accidental with the words “there!” (intentional action) and “woops!” (accidental action). Research using verbal cues to signal intentional and accidental actions indicates that young children, 16–18 months of age, imitated significantly more intentional than accidental actions modeled by an adult. Additionally, in studies that require the child to imitate an adult model as a measure of understanding, the intentional and accidental actions were signaled by the modeler/experimenter by failing to complete the task, negative facial expression (frown), dropping the object, or refusing to offer the object to the child (Meltzoff 1995; Behne et al. 2005). Results of these studies indicate that children as young as 9 months of age are able to differentiate the intention of others by observing the modeler/experimenter’s actions and facial expression (Behne et al. 2005).

## Nonhuman Studies

The bulk of research employing the use of intentional and accidental experiment methodology to test intentionality is found in research with primates, specifically the great apes. Two examples from research on chimpanzees and orangutans are presented below.

Call and Tomasello (1998) investigated the ability of human children, chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*) to identify the intentions of others. The procedures for eliciting responses to intentional and accidental behaviors of the models consisted of a training and a testing phase. In the training phase, the authors trained the subjects to select a “correct” box containing a food reward using a three-phase delayed stimulus discrimination task. Phase one

consisted of introducing the subjects to the concept that a food reward could be found under one of the three boxes. Training subjects included partially hiding the food reward under the boxes. Visibility of the food rewards was slowly decreased on each subsequent trial until fully hidden. Phase two consisted of the introduction of a marker that “marked” the box containing the food (stimulus discrimination phase). In this phase, the subject was trained to select the box with the marker in order to obtain the hidden food reward within. The subjects learned to associate the marked box with the location of the food reward. Phase three consisted of a delayed-response procedure. In this phase, the marker was placed on the box containing the food reward but was then removed. The subject was then allowed to select the box with the food reward after a delay. Responses of the subject were delayed 1 s, increasing in successive trials to 10 s and then to 20 s (delayed discrimination task).

During the testing phase, the experimenter baited the boxes out of view of the subjects and then allowed the subjects to view the boxes without the presence of the markers. Two intentional actions and two accidental actions were then performed. The order of the presentation of the intentional and accidental actions, as well as the location of the hidden food, was counterbalanced. The two intentional actions consisted of (1) the experimenter picking up the marker and placing it on the top of the box while looking at the box and (2) the experimenter picking up the marker and dropping it on the box while looking at the box. In both intentional action types, the marker was left on the box for 3 s and was then removed. The boxes were then pushed toward the subject to allow the subject to select the box containing the food reward.

The two accidental actions consisted of placing the marker on a ledge behind the boxes and (1) the experimenter moving the ledge resulting in the marker being dislodged and falling on to one of the boxes and (2) the experimenter knocking the marker off of the ledge on to the box. While performing the accidental actions, the experimenter did not look at the boxes. After the accidental placement of the marker, the experimenter left the marker in place for 3 s, then removed the

marker, and allowed the subjects to select the box containing the food reward. A verbal prompt “oops” was used for two of the chimpanzee subjects in order to investigate the potential benefit of a verbal prompt on performance. Each trial consisted of one intentional action and one accidental action. The intentional and accidental placement of the marker may or may not have corresponded to the correct location of the reward. In other words, the marker may or may not have signaled the actual location of the reward. The authors hypothesized that when presented with the choice of these two marked locations, the intentionally marked location should be selected over the unintentionally or accidentally marked location, indicating the individual understands the intention of the experimenter. The subjects (both chimpanzees and orangutans) tended to select the intentionally marked boxes more than the accidentally marked boxes at the beginning of the experiment, and subsequently accuracy of their selections decreased as the experiment progressed. With regard to the decreased accuracy, the authors concluded that “...[this] could be interpreted as an indication that accidental actions became less plausible after accidents occurred in each trial” (Call and Tomasello 1998, p. 202).

Povinelli et al. (1998) used a procedure in which young chimpanzees were trained to point to unfamiliar actors in order to receive rewards (cups of juice). During the training phase of this experiment, the subjects were exposed to actors who handed cups of juice to experimenters who then offered the juice to the chimpanzees. The chimpanzees were then presented with actors who (1) “accidentally” dropped the juice on the floor before handing it to the experimenter, (2) “intentionally” poured the juice on the floor, or (3) “aggressively” threw the juice on the floor. The chimpanzees were then tested to see which actor they selected for delivery of the juice as indicated by pointing to the actors. The authors hypothesized that the actors who accidentally dropped the juice on the floor should be selected over those who intentionally or aggressively dropped the juice. The results showed nonsignificant effects of the three conditions, indicating that the chimpanzees did not show a preference

for which actor delivered the juice, leading the authors to conclude that chimpanzees are not able to tell the difference between intentional and accidental actions of human experimenters (Povinelli et al. 1998, p. 215).

In a second experiment, Povinelli et al. (1998) addressed some methodological issues such as the possibility that the chimpanzees preferred interacting with certain human actors over others. In this experiment, the actors were counterbalanced across three conditions for each chimpanzee; the same actors played one of the three roles for the same chimpanzee but switched roles for different chimpanzees. In this experiment, a neutral actor, victim actor, and intentional actor were used to deliver (or not deliver) a food reward. Each session contained two combinations of actor scenarios. The neutral actor picked up the food reward and handed it to the experimenter who then handed it to the chimpanzee. The victim actor delivered the food reward to the experimenter who then ate the food reward intended for the chimpanzee. The intentional actor always ate the food reward intended for the chimpanzee rather than handing it to the experimenter. After a training session in which the chimpanzees were exposed to each actor multiple times, counterbalancing for action and location (left or right side), the chimpanzees were tested for preference of human actors by exposing the chimpanzees to combinations of actors as (1) intentional actor versus victim, (2) victim versus neutral actor, and (3) intentional actor versus neutral actor. Results indicated that the chimpanzees did not prefer one actor over another, regardless of their behavior toward the experimenter. Similar to the first experiment by Povinelli et al. (1998), results from this modified procedure indicated that chimpanzees do not recognize the intentions of human experimenters.

## Limitations

As suggested by Call and Tomasello (1998), the accidental and intentional action studies used with nonhuman subjects may allow us to investigate whether nonhumans are able to differentiate between the subtle behavioral (and in some cases

verbal) cues that accompany intentional and accidental actions made by humans. However, just as errors occur in the ability to recognize intentional or accidental acts in human-to-human interaction (e.g., sarcasm, deception, threats, displays of emotion, etc.), we would also expect similar errors in nonhuman subjects, and, similarly, failure should not necessarily be an indication of inability.

Other limitations suggested by Povinelli et al. (1998) point to the developmental stage of the subjects tested. In their study, the chimpanzees (5–7 years old) were unable to distinguish between the accidental and intentional acts presented by the unfamiliar actors. Povinelli et al. suggest that this may have been due to the lack of cognitive development of their subjects. The authors also suggest that their subjects may not have perceived the difference between the types of actions “. . .because the severity of the outcome was too mild” (p. 215). Povinelli et al. seem to suggest that the consequences of the actor’s actions were of little significance to the subjects possibly due to the low or diminished value of the food reward.

Perhaps the most obvious limitation of the accidental and intentional action experiment is the use of linguistic cues employed by many researchers. Exclamations of “whoops” to indicate accidental action or “okay” to indicate intentional action may carry little to no meaning for the nonhuman subjects in these experiments. Call and Tomasello (1998) found that the two nonhuman subjects that were exposed to verbal cues did not performed any better than did subjects that were not exposed to verbal cues. Whether or not an individual recognizes an exclamation of “whoops” or “okay” to indicate accident or intention, the linguistic cue may simply serve to draw the attention of the subject to a desired reward, resulting in negative results. For example, inadvertently dropping a delicious treat on the floor may, for many test subjects in a laboratory environment, signal a rare opportunity for acquiring the delicious treat regardless of the intention of the actor. The verbal cues used to indicate accident or intention simply indicate the availability of the food reward.

Consideration must be given to the early rearing environment and the role this may play in the ability to understand the accidental or intentional acts of others. Call and Tomasello found that the orangutan Chantek performed much better than the other subjects in their study of accidental and intentional actions. Chantek's early rearing experience resembled that of a young child from the age of 9 months to 9 years. Chantek acquired the signs of American Sign Language and spent most of his waking hours with human caregivers (Miles 1986). Call and Tomasello attributed Chantek's superior performance to these early rearing experiences and human enculturation. In addition to the individual's environment, knowledge of the materials used in these tests as well as the familiarity of the animals to the experimenter/caregivers may yield contradictory results (although see Pitman and Shumaker 2009, refuting differences in early rearing conditions).

The social behavior of the different primate species tested must also be taken into account when assessing the ability to recognize the intentions of others. For example animals in the wild likely reap the rewards brought about by the actions of others, regardless of the intention of the act. The inadvertent (or possibly intentional) dropping of a highly coveted food item by a dominant individual may be recovered by a subordinate individual. Knowledge of whether the dominant individual meant to drop the food item may be irrelevant, if even knowable; the opportunity to recover the food and avoidance of repercussion from the dominant individual are paramount and perhaps necessary for survival. Another example of the behavioral differences between human and nonhuman primates was suggested by Call and Tomasello (1998). The authors stated that the type of action that resulted in the subjects selecting the location of the hidden food reward was the dropping of the marker on the box and not the intentional placement of the marker on the box. The authors hypothesized that the subjects identified this action (dropping) as an indicator of the hidden food reward because this pattern of behavior is more common (dropping of food) in

chimpanzees and orangutans than actual sharing of food by handing food or placing of food in another's hand.

Although the results of the accidental and intentional experiment may yield contrasting results across, and in some cases within, human and nonhuman populations with regard to evidence of theory of mind, the experimental procedure provides some insight into the cognitive capacities of these species. Age, social behavior, and methodological considerations however must be considered when comparing populations and making conclusions regarding the capacity to identify the intentional and accidental actions of others.

## Cross-References

- [Josep Call](#)
- [Michael Tomasello](#)
- [Theory of Mind](#)

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## Accipiters

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## Synonyms

[Accipitridae](#); [Goshawk](#); [Hawk](#); [Sparrowhawk](#); [True hawks](#)

## Definition

A genus of the Family Accipitridae considered to be “true” hawks including 48 different species, many of which are goshawks and “sparrowhawks.”

## Introduction

Accipiters, or “true” hawks, have a variety of characteristics that separate them from other genera within the Family Accipitridae. There are 48 different species within the genus and include Cooper’s hawks (*Accipiter cooperii*), Sharp-shinned hawks (*Accipiter striatus*), Northern

goshawks (*Accipiter gentilis*), Eurasian sparrowhawks (*Accipiter nisus*), and many others. Though empirical studies of Accipiter hawks are limited, previous research has shown fascinating morphological and behavioral characteristics that maximize survival and fitness in this group of species.

## Habitat and Populations of Accipiters

The three common Accipiters of North America include Northern Goshawks, Cooper’s hawks, and Sharp-shinned hawks. Northern Goshawks are listed by the US Department of Agriculture Forest Service as a “sensitive species” and a “management indicator” due to their acute sensitivity to changes in their environment (Lawler and Schumaker 2004). Accipiters typically inhabit mature, closed-canopy forested areas but can be found in riparian areas, open landscapes, or isolated clumps of trees as well. These hawks prefer stands of trees with higher canopy volume and structure, and/or tree height variations.

Though Accipiter habitats can be affected by wildfires, timber harvest, and diseases, they are most drastically affected by urbanization. While many Accipiters are found in unaltered or “natural” habitats, they also occupy suburban and urban areas throughout North America. Landscape change due to urbanization alters the composition of bird communities; however, it is uncertain the degree to which the urban footprint is harmful or beneficial to Accipiter hawk species.

## Color Morphs and Sexual Dimorphism

Many raptors come in different morphs, or colorations. Plumage polymorphism is defined as variation in feather plumage coloration within the same age or sex of a population. This polymorphism is rare across avian taxa, and only occurs in around 3.5% of bird species. Within Accipiter species plumage polymorphism is typically exhibited by a dark morph and a light morph; however, frequency of polymorphism in a population may represent a response to environmental



circumstances or founder effect (i.e., reduced genetic diversity in a population due to a small number of ancestors) (Amar et al. 2013). Many Accipiter hawks also follow a unique form of sexual dimorphism: females are generally around 40% larger than males in most species. There are many hypotheses that have been proposed to explain the difference in size from hunting behaviors to female dominance in the species, but a definitive explanation has not yet been confirmed.

## Migration Behavior and Flight

Many Accipiters are considered migratory species. Cooper's hawks in California can be migratory or nonmigratory based on their geographic location, with populations in northern California exhibiting migratory behavior, and southern California populations exhibiting year-round residency (Bloom et al. 2017). This is assumed to be the effect of different climates and overwintering conditions across the migration range of these Accipiter populations.

Flight behavior in hawks is significantly affected by weather conditions during migration. Wind direction is the most significant driver in the flight height of migrating Accipiters. For example, Sharp-shinned hawks at Cape May, New Jersey, will fly lower in western winds, presumably to avoid being displaced over the Atlantic Ocean (Woltmann and Cimprich 2003). Alternatively, hawks have been shown to fly at higher altitudes in winds that are blowing in the direction of migration.

Accipiters also stagger migration initiation based on age and sex. First-year or younger birds precede adults by an average of 2 weeks, whereas females precede males by 1 week on average. However, there is evidence that some Accipiter species are shifting timing of migration compared to previous years, presumably due to increasing global temperatures. Autumn migration departures in sharp-shinned hawks are around 4 days later now than those in 1974 (Rosenfield et al. 2011). This could indicate climate change creating warmer, more-ideal environments for prey species.

## Pair Bonds

Many Accipiter species are thought to have ephemeral pair bonds – or bonds that are formed and only last through the breeding season. Female Accipiters usually have a larger home range than their male counterparts because males are the territory holders and more restricted in their movements than females. Females typically desert their breeding territories (which includes their mate), but males retain their breeding territory year-round. This separation among males and females results from limited resources in the breeding territory during the nonbreeding period. However, Accipiters of both sexes tend to remain year-round in urbanized areas, because of increased resource availability. For example, Cooper's Hawks in Tucson, Arizona maintained pair bonds outside of their breeding season creating perennial pair bonds (Boggie et al. 2015). This year-round interaction with a mate increases nest site defense, may prevent loss of a breeding site to competitors, and may solidify a mating-pair bond which could strengthen their partnership and improve breeding efficiency.

## Nesting

Accipiter nests can typically be found in large, tall trees in areas with limited groundcover. Nests built by raptors tend to be very large in comparison to the body size of the builder, with larger nests at reduced risk of damage or loss during weather events. For example, goshawk nests may reach more than 600 kg compared to their body weights of only around 1 kg. Nest size is not only affected by the size of the Accipiter species that built it but also environmental factors and age. Many Accipiters refurbish their old nests, year after year; however, this does not necessarily contribute to increases in nest size over time due to compaction. Larger nests can also indicate a greater number of eggs laid in a clutch and may improve reproductive success of an individual. Temperature – and, in turn, climate change – can affect nest size (warmer weather equates to a decrease in nest size). Nest size also correlates

with age of the individual and will begin to decrease as the bird begins to age. Thus, nest size is not only an indicator of clutch size but also builder condition (i.e., age) and potentially effects of climate change (Møller and Nielsen 2015).

Males will also build nests periodically. The purpose of these alternative nests is unclear, but it is inferred that these structures could be displayed for mate attraction and allow males to prepare a quality nest for a future reproductive year. A male Cooper's Hawk was observed in Oshkosh, Wisconsin, building a nest in the absence of a female mate; however, that nest was utilized later that year for a clutch of eggs (Rosenfield and Sobolik 2017).

### Food Delivery and Brood Maturation

In most Accipiter species, the female incubates her brood while the male hunts and delivers food to the nest. Once the nestlings become more independent, the female will usually resume hunting to help the male in provisioning food. While these delivery methods and contributions may differ slightly between individual species, males typically exhibit greater food delivery rates, up to 80% of deliveries on average (Eldegard et al. 2003).

Accipiter nestlings spend around 40 days in the nest. Eurasian Sparrowhawks specifically have a 4-week nesting period, followed by a fledgling period that lasts around 3–4 weeks. Fledglings are dependent upon food delivery for a period of time after fledging and can depend on food provisioning from parents for weeks or months.

During the nesting period, the female rarely leaves the nest, except to retrieve food deliveries from the male. The female responds to male vocalizations during prey deliveries with a wail, and then she flies out to meet him and to retrieve the food. Direct nest deliveries by males are uncommon. It is believed that the female's wail may mimic that of the begging behavior in nestlings, which may encourage males to find and deliver more food.

A new behavior recently recorded by Rosenfield (2014) shows fledgling Cooper's hawks "proning." This activity notes that flighted fledglings will lie with their bodies flat against tree limbs or even on the ground. The purpose of this fledgling behavior is unknown, but some have hypothesized that it could be a variation of camouflage to help hide young birds as they continue to develop their flying skills and move further from their nest. This activity has been recorded across North America and is not specific to one individual group of Accipiters.

### Predation Behavior

Accipiter species all feed on different forms of prey, and prey preferences are driven by body size, location, and other factors. Eurasian sparrowhawks have been recorded to prey on over 120 bird species. Some Accipiters will even feed on other Accipiters; for example, goshawks have been known to prey upon the smaller sparrowhawks. While avian species provide the most biomass of most Accipiter diets, many – like Cooper's hawks – are opportunistic predators. They can feed on a variety of birds, mammals, and even lizards; but typically size of prey is relative to the raptor's body size.

Though often opportunistic in prey choices, Accipiters are known hunt strategically. Accipiters show limited association with prey "hotspots" (e.g., bird feeders, nesting areas that contain high volumes of predictable prey) and instead follow time and space unpredictability which gives prey little warning on if/when they could be attacked (Roth and Lima 2007a). While unpredictability in their hunting movement seems random, hawks possess a well-developed sense of direction and location within their home ranges. Movements may be strategically unpredictable, whereby individuals distribute hunting activity evenly over the landscape to reduce likelihood of predator avoidance behavior in their prey.

Hawks also have specific temporal patterns in hunting based on their prey's activity patterns.



Hunting during midday heat is energetically expensive and can deter the movements of prey species as well as the Accipiter species that hunt them. Roth and Lima (2007b), recorded a lack of early morning hunting by sharp-shinned hawks that could also indicate an avoidance of owls – a common predator of this Accipiter species. Cooper’s hawks were also shown to avoid hunting activity in early morning hours.

## Conclusion

Accipiters, or “true” hawks, are unique in their behaviors and genera-specific characteristics. Their nests are found in a variety of ecosystems and their size and construction depends on multiple factors in their environment. Accipiters have a specific sexual dimorphism and unique color morphs. Pair bonds can either be ephemeral or perennial depending on their environmental circumstances, and mating rituals can even include a male building a nest to “impress” a female. Food delivery during brood maturation is performed by the male, young linger near their nests even after fledging, and a newly documented “proning” behavior has recently been documented in some species. These hawks also have very distinct temporal predation and migration patterns and behaviors. Overall, Accipiters are complex birds of prey with complex behaviors and qualities that separate them from other genera in the Family Accipitridae.

## Cross-References

- [Biparental Care](#)
- [Brooding](#)
- [Camouflage](#)
- [Clutch](#)
- [Feeding](#)
- [Hatching](#)
- [Home Range](#)
- [Hunting](#)
- [Pair Bond](#)

- [Predator](#)
- [Prey](#)
- [Sex Differences](#)
- [Sexual Dimorphism](#)

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## Accipitridae

### ► Accipiters

## Accipitriformes Sensory Systems

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### Synonyms

Hearing; Magnetoreception; Mechanosensation; Olfaction; Taste; Vision

### Definition

The order Accipitriformes include the families Pandionidae (the ospreys, *Pandion haliaetus* and *P. cristatus*), Sagittariidae (the secretary bird, *Sagittarius serpentarius*), and about 250 species in the family Accipitridae, which has been diverging, since about 34 million years ago, into hawks, eagles, kites, harriers, buzzards as well as Old World vultures (Mindell et al., 2018). The order had earlier been included in Falconiformes but is now recognized as separate order of raptorial birds more closely related to owls (Strigiformes) and New World vultures (Cathartiformes) than to falcons and caracaras (Falconiformes). Accipitriformes are carnivorous birds with sharply hooked bills and curved talons that occur on all continents except Antarctica, with the largest diversity in Africa. They range in size from the pearl kite (*Gampsonyx swainsonii*) and the little sparrowhawk (*Tachyspiza minullus*) weighing 100 g or less to the cinereous griffon (*Aegypion monachus*) and the Himalayan griffon (*Gyps himalayensis*) weighing more than 10 kg.

Sensory systems allow animals to extract relevant information from the environment, adapted to animals' lifestyle and habitat; in birds, the

ability to fly and the feeding habits are most important for the evolution of sensory systems such as vision, olfaction, gustation, hearing, as well as the magnetic sense and somatosensory system (Martin, 2017). These senses allow the birds to navigate and perceive information about conspecifics, predators, food sources, and retreats.

### Introduction

Accipitriform raptors are apex predators and with the exception of vultures and the unusual fruit-feeding palm-nut vulture (*Gypohierax barbatus*), these hunt for prey. While many of them are opportunistic, most have a preferred type of prey, often small mammals or birds, and some are more specialized. The snail kite (*Rostrhamus sociabilis*), for instance, predominately feeds on snails, the bat hawk (*Macheiramphus alcinus*) on bats (Black et al., 1979), and honey buzzards (of the genus *Pernis*) on social insects and honey. Ospreys are cosmopolitan fish-eating birds, and the secretary bird is mostly terrestrial, hunting its prey – including insects, small mammals, birds, lizards, crabs, and snakes – on foot.

A considerable number of accipitriform raptors are long-distance migrators, moving between their breeding grounds in the northern hemisphere and more southerly wintering areas (Nagy et al., 2017). Most accipitriforms are active during daylight but some species can fly during twilight, and few even at night. Some vultures can be observed feeding at night on carrion, but they most likely have arrived at the carcass before dusk. Red-tailed hawks (*Buteo jamaicensis*), African goshawks (*Accipiter tachiro*), and Wahlberg's eagles (*Aquila wahlbergi*) can hunt bats at dusk but not after sunset (see Mitkus et al., 2018), while the bat hawk hunts bats both at dusk and in moonlit nights (Black et al., 1979). The second nocturnal species is the letter-winged kite (*Elanus scriptus*), which hunts bats and nocturnal desert rodents at night (see Mitkus et al., 2018). Raptors that can use powered flapping flight to migrate at night, especially when crossing the sea, include the osprey (*Pandion haliaetus*), honey buzzards, and

the northern harrier (*Circus cyaneus*, see Mitkus et al., 2018).

Little is known about intraspecific communication. Accipitriform raptors are usually brown, with some black, grey, and white. UV reflection from the cere is common, as are yellow to red legs and bills. Most obvious in color is the Egyptian vulture with bright yellow face, and species flushing facial skin color such as the secretary bird, African harrier-hawk (*Polyboroides typus*), and some Old World vultures. Raptors are not usually sexually dichromatic in their plumage, except in a few species including the harriers (*Circus* spp.), and the sparrowhawks (*Accipiter* spp.). The use of adventitious coloration, derived from bathing in mud pools rich in iron oxides, occurs in two species, the bearded vulture (*Gypaetus barbatus*) and the Egyptian vulture (*Neophron percnopterus*; Sarasola et al., 2018).

Courtship flights with male feeding, occasionally in air, require acute vision, while courtship vocalizations (Jurisevic, 1998; Penteriani, 2001) and acoustic communication between parents and their brood rely on good hearing.

## Vision

Accipitriform raptors are famous for their outstanding eyesight but differences are large, both depending on size and between actively hunting species and scavengers such as the vultures. The largest species have two to three times the spatial resolution of humans and thus can see details at two to three times the distance as ourselves. The wedge-tailed eagle (*Aquila audax*), for instance, can resolve gratings of 140 cycles/degree visual angle, and the Indian vulture (*Gyps indicus*) of up to 135 cycles/degree, while the resolution of smaller species is similar or even lower than that of humans (Harris's hawk, *Parabuteo unicinctus* up to 60 cycles/degree; black kite, *Milvus migrans* up to 32 cycles/degree; for references see Potier et al., 2020b). This high spatial resolution is reached only under good viewing conditions in bright light and decreases dramatically in dim light. Even under optimal light conditions, Accipitriformes require relatively high-intensity

contrasts of 10% or more to be able and resolve patterns (see Potier et al., 2020b).

Scavengers tend to have relatively smaller eyes (Potier, 2020) and have only one central fovea – a tiny pit in the retina, in which retinal neurons are displaced while photoreceptors are packed densely allowing for the reported high spatial acuity. In contrast to the human fovea, the central fovea of raptors does not look forward, but sideways. Actively hunting species have a second fovea located in the temporal region of the retina, thus looking forward into the binocular visual field (Potier et al., 2017). This second fovea is probably used to control the talons during prey capture and handling.

Differences between scavengers and hunters are also found in the visual fields. Actively hunting species, such as the short-toed snake eagle (*Circaetus gallicus*), have large monocular visual fields (139 degrees) and wide cyclopean visual fields (259 degrees) with narrow binocular visual fields (20 degrees wide) and large blind sectors behind and above the head (Martin & Katzir, 2000). Scavenging species like vultures, by contrast, tend to have larger binocular visual fields and narrower blind sectors above the head (Potier, 2020).

Like the majority of birds, most Accipitriformes have tetrachromatic color vision, based on four spectral types of single-cone photoreceptors. In Accipitriformes, these are sensitive to violet, blue, green, and red light. Sensitivity to ultraviolet light is low in most species because the ocular lens absorbs most light of wavelengths below 380 nm. Of nine investigated species, the lens of the red kite (*Milvus milvus*) transmits least and that of the marsh harrier (*Circus aeruginosus*) most ultraviolet (Lind et al., 2014; Potier et al., 2020b). In the scavenging cinereous vulture (*Aegypius monachus*) and the nocturnally/crepuscularly active black-winged kite (*Elanus caeruleus*), sensitivity to ultraviolet light is further reduced because the violet-sensitive visual pigment has been lost (Wu et al., 2016), leaving the birds with trichromatic color vision. In addition to the single cones, raptors, like all birds, also have double cones in the retina – two closely intertwined cones with a broader spectral

sensitivity to light of long wavelengths. The function of these double cones is not yet understood, but they are assumed to contribute to the perception of self-motion from optic flow – the movement of the visual image during flight. In Accipitriformes, like in other diurnal birds, rod photoreceptors adapted to see well in dim light are accounting for only about 20–25% of all photoreceptors. Rods and double cones are absent from the central fovea, an additional adaptation to high-resolution color vision (Mitkus et al., 2017; Potier et al., 2018).

Visual information is carried to the brain via the axons of the retinal ganglion cells. Birds have a complete optic nerve crossing and three parallel pathways, the tectofugal pathway to the optic tectum, the thalamofugal pathway to the thalamic nuclei and further the visual Wulst, and the accessory optic system that is thought to contribute to visual flight control.

Accipitriform raptors have slightly faster vision than humans, but only in very bright light conditions, where the Harris's hawk can resolve light flickering with a temporal frequency of up to 78 Hz, which is slower than falconiforms and some passerines (Potier et al., 2020a).

## Hearing

Raptors can use acoustic information for communication (e.g., northern goshawk *Accipiter gentilis*, Penteriani, 2001; black-shouldered kite *Elanus notatus*, and letter-winged kite *Elanus scriptus*, Jurisevic, 1998), to detect concealed prey (*E. scriptus*, *E. notatus*, Jurisevic & Sanderson, 1998), and, in some species, potentially also predators (Sergio & Hiraldo, 2008).

The outer ear of birds is a tube positioned just behind and below the eye, usually covered by feathers but openly visible in vultures (Martin, 2017). Unlike most raptors, harriers (of the genus *Circus*) have an owl-like facial mask improving their directional hearing abilities. The middle ear of birds consists of only two elements, the bony columella and the cartilaginous extracolumella. In the inner ear, the basilar membrane with the sensory hair cells is positioned in the

lagena, a short, slightly curved bony tube. Sound frequency and location of a sound source are coded in the avian auditory midbrain nucleus (Calford et al., 1985).

Hen harriers (*Circus cyaneus*) can locate prey acoustically almost as well as owls from a distance of 3–4 m, and with a resolution of 2 degrees in the horizontal and the vertical plane. This is more accurate than red-tailed hawks (*Buteo jamaicensis*), which have thresholds of 8–12 degrees in the horizontal plane, and much higher in the vertical plane (Rice, 1982). The absolute sensitivity of hearing has been investigated in red-tailed hawks, Eurasian sparrowhawks (*Accipiter nisus*), brown goshawks (*Accipiter fasciatus*), and bald eagles (*Haliaeetus leucocephalus*). All of these have their highest sensitivity to sounds around 2000 Hz, and a broad sensitivity band ranging over 4 octaves. The cutoff at high frequencies was determined as 5700 Hz for the eagles and 8000 Hz for the red-tailed hawks, and low-frequency cutoff lower than 200 Hz. Thus, hearing is similarly sensitive in accipitriform raptors as in songbirds and parrots, but less sensitive than in owls (McGee et al., 2019).

## Chemical Senses: Taste and Olfaction

The birds' sense of smell has long been considered poor, and only recently been investigated in more detail. While birds lack the vomeronasal organ known from many other vertebrates, the olfactory system of many species is well developed, and the number of functional olfactory receptor genes generally quite high (Steiger et al., 2008).

The use of olfaction for finding dead carcasses has been established for New World vultures (Cathartiformes), but little is known about olfaction in Accipitriformes (for a review see Potier, 2019).

Air inhaled through the nostrils passes through three chambers or conchae (Roper, 1999), the first two of which filter out small particles and warm the air, while the third is lined with olfactory epithelium. Similar to falconiform raptors, the golden eagle (*Aquila chrysaetus*) has relatively few olfactory receptor genes but estimations

suggest close to 300 in the oriental honey buzzard (*Pernis orientalis*; Yang et al., 2015). Accordingly, the honey buzzard can detect pollen, important in the species' diet, by olfaction. Anecdotal observations indicate that several species of Old World vultures (of the genera *Gyps* and *Sarcogyps*) may be able to find buried carcasses, likely by olfaction (see Potier, 2019).

It is well known that many birds use preen oil secreted by the uropygial gland for chemical communication, the chemical composition of these secretions have been analyzed only in one species of Accipitriformes, the black kite *Milvus migrans* (Potier et al., 2018). In this species, composition varies between individuals and seasons and during the breeding season, reflects genetic relatedness.

The sense of taste – allowing for the detection and discrimination of chemical and nutrients in food – is even less studied in accipitriform birds. The taste buds of birds are distributed in the oral cavity and tend to be more frequent on the palate, the pharyngeal floor, and the lower mandible than on the tongue. They are often not associated with papillae and connected with the surface by a taste canal (Rowland et al., 2015). Whereas birds have lost of the G-protein-coupled taste receptor that mediates the perception of sweet (Baldwin et al., 2014), they have two genes for bitter receptors (Wang & Zhao, 2015). Sour and salt reception is based on channels rather than G-protein-coupled receptors, and present in Accipitriformes, as in other birds.

## Somatic and Magnetic Senses

Other sensory modalities found in other birds, such as the somatosensory system and a magnetic sense, have barely been studied in Accipitriformes (Martin, 2017). The somatosensory system is based on receptors distributed over the body that allow the birds to detect thermal, noxious, and mechanic stimuli such as vibration, pressure, or air flow (Gottschaldt, 1985). The two types of somatosensory receptors found in the dermis are Herbst (lamellar) corpuscles that are sensitive to vibration and Grandry corpuscles that are sensitive to fast movements (Gottschaldt, 1985). None

of these have been studied in Accipitriformes specifically, even though they must play important roles for behavioral control of flight, feeding, and other tasks.

A magnetic sense has been proven for birds such as passerines and pigeons, in which it contributes to the ability to navigate on large foraging trips and during migration, but the anatomical and physiological basis of this sensory modality has not yet been discovered (Wiltshko & Wiltshko, 2019). While many species of Accipitriformes are also long-distance migrants (Nagy et al., 2017), it has not been investigated whether they also have the ability to sense the magnetic field of the earth.

## Conclusions

Accipitriformes include fast-flying predators, many of which also migrate between over long distances, opportunists and scavengers, which can cover long distances when searching for carcasses. While hunting for prey is largely based on vision, hearing and olfaction may play larger roles than presently acknowledged for raptors. Vision has been studied to some degree, but the other senses are barely understood, and how these fascinating birds navigate during long-distance migration between breeding and wintering areas is largely unknown.

## Cross-References

- ▶ [Accipiters](#)
- ▶ [Auditory Processing and Perception](#)
- ▶ [Carnivore \(Diet\)](#)
- ▶ [Diurnality](#)
- ▶ [Ecology](#)
- ▶ [Falconiformes Cognition](#)
- ▶ [Falconiformes Locomotion](#)
- ▶ [Falconiformes Sensory Systems](#)
- ▶ [Navigation](#)
- ▶ [Olfactory Discrimination](#)
- ▶ [Optic Flow](#)
- ▶ [Predator](#)
- ▶ [Vertebrate Nervous System](#)
- ▶ [Visual Search](#)



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## Acclimation

### ► Acclimatization

## Acclimatization

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## Synonyms

Acclimation; Acclimatization; Adaptation; Conditioning; Habituation

## Definition

Acclimatization is the process of physiological adaptation by animals or plants due to changes in climatic or environmental conditions.

The process of adjustment of cells or organisms in new environmental conditions including temperature, humidity, photoperiod, and other climatic conditions is called Acclimatization. In order to sustain themselves, during this process, organisms tend to adjust their morphological and biochemical properties in response to new environmental conditions. Depending on the natural characteristics and types of adaptation, the time taken for Acclimatization shows a lot of variation in different organisms ranging from hours to months in some to over a lifetime in others.

Acclimatization is a well-coordinated phenotypic response against environmental stresses that gradually diminishes or lessens relatively upon removal of stressors. Acclimatization occurs in two different phases; i.e., acute stress response and chronic stress response. The acute phase Acclimatization response is under homeostatic regulation and is also known as short-term response. On the contrary, chronic phase response is under homeorhetic regulation and also known as long-term response. When chronic stress persists over several generations, response due to Acclimatization becomes genetically stable and the animal is adapted to the new environmental conditions (Collier et al. 2018). Acclimatization in humans depends on various environmental conditions such as exposure to heat and other climatic conditions. Survival of humans requires significant and increased reliance on these mechanisms (Hanna and Tait 2015).

Climate change is a fundamental challenge for organisms as it deeply and pervasively affects the way they live in their habitats. Climate change not only affects reproduction but also plays a significant role in limiting adaptation activities. Biochemical and physiological changes happening during adaptation are regulated by the change in temperature and gene expression. During Acclimatization in the cold environment, cellular and metabolic changes are observed, which include increased formation of excessive amount of sugars, soluble proteins, organic acids, new protein variants, and change in lipid composition of membranes (Hughes and Dunn 1990). The increase in temperature beyond the average for a number of days changes the adaptation capabilities. Heat waves strongly affect human activities as well as the health and productivity of animals (Pasqui and Di Giuseppe 2019).

Transportation and induction of animals from their adopted conditions to new and unfamiliar conditions are stressful events that result in adverse effects in the general health of animals. The adaptation against these stressful conditions causes several biochemical changes in the animals that allow animals to stabilize in new

environmental conditions in terms of physiological and nutritional changes.

Plants are constantly exposed to biotic and abiotic stresses that reduce their productivity. Plant responses to these stresses are complex in nature and involve physiological and cellular adaptations. It is pertinent to mention that biotic and abiotic stresses also play a significant and positive effect on plant performance in terms of growth, cellular metabolic activity, and adaptability by reducing the susceptibility to stress to a limited extent (Rejeb et al. 2014). Interaction between low temperature and other environmental conditions, e.g., photoperiod and availability of water play a significant role in the Acclimatization of organisms (Pan et al. 1994). Low temperature exposure may alter the growth, habit, and germination of the plants. Acclimatization of plants due to freezing stress is a complex process and the inheritance of frost tolerance is mutagenic in nature (Hughes and Dunn 1996).

## Cross-References

- [Acclimation](#)
- [Adaptation](#)

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## Accumbens Nucleus

- [Nucleus Accumbens](#)

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## Acoustic Communication

- [Mustelid Communication](#)

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## Acoustic Signals

- [Auditory Signals](#)

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## Acquisition

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## Definition

Gradual development of an association between events that are encountered together.

## Introduction

Events that have biological relevance to the organism can elicit reflexive responses (e.g., food can elicit salivation). Through a similar



process, organisms may produce responses in order to bring forth or prevent the occurrence of a consequence (e.g., following a command to obtain a food reward). In either situation, a link or association between the two events develops, and responses consistent with this association are observed. These responses have the important function of preparing the organism for an impending biologically relevant event or better suiting the organism to maximize reward and minimize punishment in its environment. The process by which paired events become associated is known as *acquisition*.

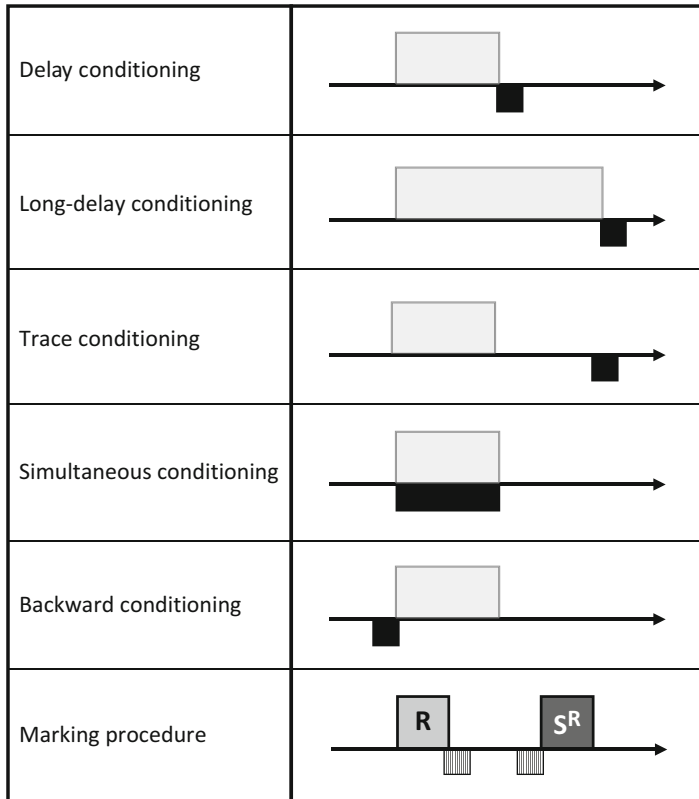
### What Relationships Are Acquired?

Learning about environmental events can be broadly classified as occurring through classical conditioning or instrumental conditioning. In *classical conditioning*, an environmental event (e.g., a tone) consistently signals the occurrence of a (usually) biologically significant event that naturally produces a response. Consequently, the environmental event also comes to elicit a response (Pavlov 1927). For example, food is an unconditioned stimulus (US) that produces an unconditioned response (salivation). Through repeated pairings, an association between the tone and food is *acquired*, and the tone begins to elicit a salivation response conditional on having been paired with the US. Thus, the tone becomes a conditioned stimulus (CS) that produces a conditioned response (CR) of salivation. Instrumental conditioning is a related process but, in this situation, the association that is *acquired* is between a response (R) produced by the subject and the consequence of that response (reinforcement or punishment;  $S^R$ ; cf. Skinner 1938). For example, a child who cries (R) at the grocery store and receives a lollipop to comfort her ( $S^R$ ) may *acquire* an association between crying and obtaining candy, which will reinforce (increase the likelihood of observing in the future) the response of crying.

### Parameters That Affect Acquisition of an Association

**Contiguity.** Associations are more easily acquired among events that occur in close proximity than among events that are distant from each other. Events that occur close in time to each other are *temporally contiguous*, and events that occur close in space to each other are *spatially contiguous*. For example, touching a doorknob and immediately receiving a static electricity shock would make someone fear touching doorknobs much more likely than if she received the shock a minute afterward. Similarly, if a dog sits and receives a treat immediately upon completing the behavior the likelihood of associating the behavior of sitting and receiving the treat would be much higher than if she received the treat long after sitting on command. When events are not contiguous, it is possible that other events take place between the stimulus and the outcome (e.g., the doorknob-static electricity shock; classical conditioning) or between the response and the outcome (sitting response-treat; instrumental conditioning), and those “other” events may become associated to the outcome. However, it is possible to “mark” the event that is paired with the outcome to “bridge” the gap between the two. Thus, a dog may be presented with a clicker when producing a response, and the clicker again used when the outcome is delivered; the presence of the clicker can act as a bridge between the two events favoring the acquisition of a hierarchical association between the two (see *acquisition of higher-order and hierarchical associations* below). Figure 1 presents different contiguity arrangements between a stimulus and an outcome, as well as an example of a marking procedure.

**Contingency.** *Contingency* refers to the likelihood that two events will occur together as opposed to apart (Rescorla 1968). Some stimulus-outcome or response-outcome pairs are encountered together more often than apart, that is, they have a *positive contingency*. For example, it is very likely that a fall will result in pain, that is, falling and experiencing pain have a strong positive contingency. In contrast, it is very unlikely



**Acquisition, Fig. 1** Common stimulus arrangements with various degrees of contiguity. *Arrows* represent the time line. *Light gray rectangles* above the time line represent CSs, *small black squares* under the timeline represent USs. In delay conditioning, the CS terminates immediately before or slightly overlaps with US delivery. A similar arrangement takes place in long delay conditioning, except that the CS is of long duration. In the trace conditioning situation, there is a gap between CS termination and US

onset during which a memory “trace” is expected to link the two events. In simultaneous and backward conditioning, the CS overlaps with the US or follows US termination, respectively; thus, no *anticipatory* response is observed. The marking procedure is a way to bridge the gap between two events; in this case, the response (R) is “marked” by an event that is repeated immediately prior to delivering the outcome ( $S^R$ ). The mark serves to bridge the gap between the two events

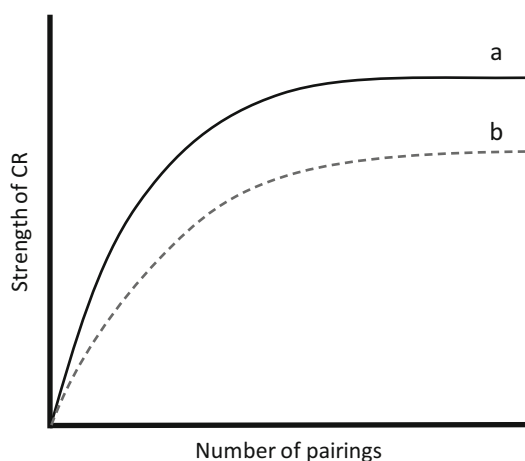
that a fall will result in receiving a static electricity shock; thus, falling and experiencing a shock have a very weak (or near zero) positive contingency. Not surprisingly, we are more likely to acquire an association between falls and pain than between falls and shocks. Responses and outcomes also share some level of contingency. For example, if a child is ignored (outcome) every time she throws a temper tantrum (response), the strong positive contingency between the two events will make it more likely that an association between them is acquired than if they shared a weak positive contingency (e.g., if the child was only occasionally ignored when throwing a tantrum). It is also

possible that events occur more often apart than together. For example, it is very unlikely that a fall will result in muscles becoming relaxed. Thus, there is a strong *negative contingency* between falling and experiencing relaxation. In this case, an association is also acquired, but between the occurrence of a stimulus (or response) and the omission of the outcome. Although there may be some controversy as to whether associations can be acquired to omitted events, some theorists assume that unfulfilled expectations can act as outcomes (e.g., Rescorla and Wagner 1972).

**Stimulus duration.** In general, long antecedents (stimuli or responses) and/or long outcomes

reduce the strength of the response that their association produces. This is not to say that long events do not result in the acquisition of associations, but it is possible that only the portions of those long events that are temporally contiguous to each other become associated. For example, in *inhibition of delay* (or *long-delay conditioning*; Fig. 1) a long stimulus predicts an outcome in its final stages. Usually, subjects come to respond to the final segment of the stimulus, suggesting that they acquire information about stimulus duration and outcome timing. This suggests that “stimuli” and “responses” can be viewed as a sequence of events rather than a single, discrete event (see *Discrete vs. real-time acquisition* below).

**Number of pairings.** The more two events occur together, the stronger the associations that develop among them. As a general rule, the first few pairings result in the greatest behavioral change consistent with acquisition of the association; as pairings continue, the association is presumed to increase in strength but behavioral change becomes less pronounced (see Fig. 2).

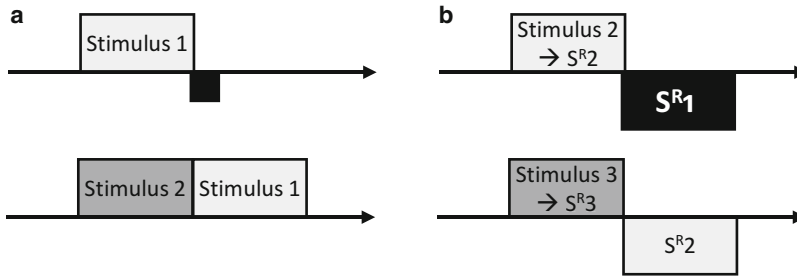


**Acquisition, Fig. 2** Schematic response acquisition curve. As the number of pairings between events increases, the response observed as a result of the learning situation is also observed to increase. The curve is said to be *negatively accelerated* because more behavior change (a steeper slope) is observed in the early than the late pairings. Curves *a* and *b* represent differences between two acquisition situations in which the paired events differed in salience, with a steeper slope and a higher level of responding observed to the more salient pair (*a*) than the less salient pair (*b*).

**Stimulus salience and relevance.** In general, stimuli that are more salient or intense acquire associations to their outcomes faster than stimuli that are less salient or intense. In turn, more salient outcomes result in stronger responses than less salient outcomes (see Fig. 2). Operant responses cannot be assessed in terms of salience, but the extent to which they “belong” with the outcome can determine the strength of the association developed between response and outcome (e.g., Breland and Breland 1961). For example, a pigeon will be much faster to learn to peck to obtain food (the response of pecking has high “belongingness” with the outcome of food) than it is to coo in order to obtain food (the cooing response has low “belongingness” with the outcome of food).

## Acquisition of Higher-Order and Hierarchical Associations

Associations can be acquired even in the absence of an outcome of high biological relevance. These associations are often known as *higher order associations*, and they can be viewed as instances in which links among multiple associations are acquired, such that behavior is controlled by a chain of associations rather than a single association. For example, Stimulus 1 may be paired with an outcome and an association acquired among them. If Stimulus 2 acquires associations to Stimulus 1, Stimulus 2 may develop a higher-order association to the outcome and acquire the same capacity to control behavior as Stimulus 1. Fears and phobias are common instances in which higher-order associations develop. An individual who encountered a dog (Stimulus 1) and received a bite (outcome) may come to fear dogs. This individual may also come to fear a park near her house (Stimulus 2) because dogs frequent that park, even if she has never had a negative experience in the park. Money is a general form of a higher order association, in which a reinforcer (e.g., food items;  $S^R1$ ) acquires an association to paper money ( $S^R2$ ), which in turn becomes associated with other forms of currency (e.g., credit cards;  $S^R3$ ).  $S^R1$ ,  $S^R2$ , and  $S^R3$  are known as



**Acquisition, Fig. 3** Schematic representation of higher-order acquisition. *Panel A* presents a higher-order conditioning situation. The *top* represents pairings between a CS (Stimulus 1) and the US (black square under the timeline). The *bottom* represents the higher-order situation, in which a second stimulus (Stimulus 2) is paired with Stimulus 1. As a result of the Stimulus 1-US pairings, Stimulus 1 should elicit a CR; as a result of the Stimulus

2-Stimulus 1 pairings, Stimulus 2 is also likely to elicit a CR when presented by itself. *Panel B* presents a conditioned reinforcement situation. If a Stimulus (Stimulus 2) is paired with a reinforce ( $S^R1$ ), Stimulus 2 may come to acquire reinforcing properties of its own and become a conditioned reinforcer ( $S^R2$ ). Other stimuli that acquire associations to  $S^R2$  (e.g., Stimulus 3) may also become conditioned reinforcers

*conditioned reinforcers*, and they acquire hedonic properties that make them act as effective reinforcers (see Fig. 3 for a schematic representation).

## Acquisition Versus Performance

It may be apparent from the previous section that *acquisition* of an association is not equivalent to *behavioral performance* based on that association. The examples described above presented a direct association between acquisition and performance: A tone paired with food came to produce a salivation response or a dog performed a sitting response to obtain a treat. However, there are also many situations in which there appears to be little relationship between acquisition and performance. For example, an individual on his way to work may often encounter a woman walking her dog. There may be no overt behavior to either woman or dog, but an association may be acquired between the woman and her dog. This association may become evident if, later on, the man develops a phobia of dogs and has a strong emotional reaction when encountering the woman by herself (this is known as *sensory preconditioning* because subjects can acquire associations between sensory events *prior* to conditioning; Brogden 1939). Thus, despite the fact that there was no overt behavior to demonstrate it, there was an

association acquired between two sensory stimuli that were experienced together (the woman and dog). Furthermore, there are also situations in which there appears to be an inverse relationship between acquisition and performance. Situations characterized by a negative contingency between the stimulus or response and outcome may *prevent* a response (this is known as *conditioned inhibition*; Savastano et al. 1999). Thus, even if acquisition has taken place, behavioral performance based on that acquisition may not reflect the nature or strength of the association that was acquired (Miller and Escobar 2001).

## Discrete Versus Real-Time Acquisition

At the theoretical level, there are many different views of acquisition. Some theories suggest that acquisition can be modeled as associations that acquire set amounts of strength in each trial. For example, Rescorla and Wagner (1972) suggested that acquisition is a function of the extent to which the outcome is still surprising (i.e., “how much” of the outcome is not yet predicted by the stimulus). Changes in predictability of the outcome (or *associative strength*) are presumed to reflect acquisition of the association. This approach is simple and predicts many phenomena, but it assumes that acquisition and performance have a

direct relationship, which does not allow the model to explain situations in which an association may exist but it may not be observed in behavior (e.g., sensory preconditioning). Furthermore, a discrete-trials approach ignores the fact that time is a continuum and acquisition could be taking place each instant an event is experienced. Indeed, *real-time* approaches assume that all events can be divided into microelements, each of which can acquire different associations to other microelements within and across events (e.g., Wagner and Brandon 2001). Although these approaches are clearly more realistic, they are also extremely complex and have their own difficulties, such as which time units should be used to determine the duration of the microelements.

### How Does Acquisition Take Place in the Brain?

Acquisition is the basic process that underlies learning and memory. When two events (e.g., a cue and outcome) are paired, their neural signature is activated together and this activity leads to the formation of new synapses and/or strengthening of existing synapses. Classic studies conducted by Eric Kandel in the 1960s with the sea slug *Aplysia californica* confirmed that experience not only results in changes in behavior but also results in cellular changes that can be correlated to the acquisition of new behavior. Experience with paired events can also potentiate synaptic transmission, making it more effective. Thus, subsequent experience of the events can activate the synapses more effectively (a process known as *long-term potentiation*; e.g., Rogan et al. 1997). This increased synaptic effectiveness parallels acquisition of the response, suggesting that the two processes (response acquisition and synaptic strengthening) are closely related.

### Conclusion

Acquisition is a fundamental process that allows organisms to incorporate information about the

environment and use it at a later time to adapt their behavior to the current situation. Many properties of the events that enter into associations determine the rate and extent of acquisition of the association. Associations will be stronger among events that occur in high temporal and spatial proximity (high contiguity), reliably occur together (high contingency), occur together many times (high number of pairings), and which naturally “belong” together (high relevance). Events that are absent can also enter into associations if one of their associates is present in a learning situation, creating higher-order associative links. How acquired associations translate into actual behavior is still a matter of debate because what was learned (acquisition) may not map directly onto behavior (performance). Modeling acquisition is a complicated endeavor because, although acquisition is often represented as resulting in discrete changes in behavior, organisms perceive and use information in real time. Acquisition results in changes in effectiveness of the synapses involved in detecting the relationship between events, suggesting that acquisition is a psychological process with clear physiological implications.

### Cross-References

- ▶ [Associative Learning](#)
- ▶ [Conditioned Inhibition](#)
- ▶ [Contingency](#)
- ▶ [Inhibition of Delay](#)
- ▶ [Instrumental Learning](#)
- ▶ [Long-Term Potentiation](#)
- ▶ [Operant Conditioning](#)
- ▶ [Pavlovian Conditioning](#)
- ▶ [Reinforcement](#)

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33,500 extant species. The most ancient fossils known of the group are scales from the Late Silurian. The fossil record of the group is more diverse, and the fossils are more complete in deposits of the Devonian and Carboniferous (Choo 2015; Nelson et al. 2016).

Along this 400 million years, the ray-finned fishes evolved reaching almost every aquatic environment in both salt and freshwater, from deep abyssal areas to the highest river basins. Throughout the evolution of these fishes, almost every kind of aquatic habitat has been reached, so that they are found in areas with large differences in temperature, elevation, pressure, salinity, pH, turbidity, luminosity, and availability of oxygen. This diversity of environments reflects the adaptations of the sensory organs and behavior found in the ray-finned fishes species (Helfman et al. 2009). In this entry, we will see more about the structures and senses of the Actinopterygians and how they are adapted to the habitats occupied by these species.

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## Acquisition of Knowledge About Spatial Location

### ► Rodentia Navigation

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## Actinopterygii (Bony Fish)

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### Synonyms

Ray-finned fishes

### Introduction

Actinopterygii is the most diverse group of Chordata, with about 470 families and more than

## Anatomy

### Skeleton

The anterior portion of the skeleton on every Actinopterygii is the cranium, where the brain and most sensorial organs are found. This complex structure is divided in **Neurocranium** and **Branchiocranium**. The neurocranium is divided in two portions, each one derived from a different embryonic tissue, **Chondrocranium** and **Dermatocranium**. The chondrocranium is formed from endochondral bones, meaning that the brain case is originally cartilaginous, which is later replaced by bones during the ontogenetic development. The dermatocranium develops from dermal bones, which are derived from groups of scales that change into bones. The histology of both kinds of bones is very similar; however, the embryonic development is completely different. The neurocranium is usually divided in four areas, each one associated with a different sense organ: (1) ethmoid region (related to the olfactory nasal capsule); (2) orbital region (around the eyes); (3) optic region (encompassing



the ear chamber); and (4) basicranial region (connecting the brain to the spinal cord).

The branchiocranium, also known as visceral cranium, is composed of the bones present in jaws, branchial, opercular, pharyngeal, and ventral orbital regions of the cranium. This portion is derived from dermal bones. It is in the branchiocranium where the teeth are usually found among the species of Actinopterygii. The teeth are found not only in the jaws, but they also may occur in branchial and pharyngeal bones. There is a great diversity of teeth forms among ray-finned fishes: (1) caniniform (tooth is slender and conical); (2) cardiform (thin teeth ordered in a series of rows); (3) molariform (robust teeth used to smash food); and (4) villiform (short and pointed teeth). Other patterns found in Actinopterygii include: (1) teeth fused in a plate; (2) triangular arrowhead shaped teeth; and (3) species with no teeth in the jaws but only in pharyngeal bones.

In the vertebral column, each vertebra develops from cartilaginous structures named arcualia. The formation of vertebrae may occur in two different ways: (1) monospondylus, when there is only a single vertebra for each arcualia, and (2) diplospondylous, when two vertebrae are formed from each arcualia. Among Actinopterygii, the diplospondylous condition is only found in the monotypic order Amiiformes. Two kinds of vertebrae are recognized in each species of Actinopterygii: (1) precaudal vertebrae, present from the anterior portion of the column to the end of the body cavity, and (2) caudal vertebrae, in the posterior portion of the body. The caudal vertebrae feature a closed hemal canal and a completed hemal spine ventrally. The dorsal portion of both caudal and precaudal vertebrae is similar, presenting a neural spine supported by the neural arches.

Ribs and intramuscular bones are found next to precaudal vertebrae. Most of Actinopterygii have the pleural ribs distributed between the third and the last precaudal vertebrae, and these structures are positioned around the visceral cavity protecting the organs. Other intramuscular bones found in Actinopterygii are epineurals, epicentrals, and epipleurals.

The final portion of the Actinopterygians body is the caudal fin, which is a complex structure composed of vertebral centrum, vertebral accessories, and also fin rays. Over the different Actinopterygii lineages, the caudal fin has been modified, adapting to each environment reached by the ray-finned fishes. The classification of caudal fins is based on dorsal-ventral symmetry and the internal morphology of the fin. In Actinopterygii, there are two kinds of fins found: heterocercal and homocercal. Species with heterocercal pattern present the column extending to the superior portion of the tail, in the dorsal lobe. This type of fin is observed in the plesiomorphic orders Acipenseriformes (sturgeons and paddlefishes), Lepisosteiformes (gars) and Polypteriformes (bichirs and reedfish). The second pattern found in Actinopterygii is the homocercal, in which the caudal fin is symmetric externally and internally. This internal symmetry is possible due to a series of bones named hypurals, positioned after the last vertebra. The external symmetry comes from the disposition of the caudal-fin rays connecting with the hypurals. Only one species presents the caudal fin externally symmetric but not internally, *Amia calva*, the Bowfin (Amiiformes). This intermediate pattern is named hemihomocercal.

Three kinds of unpaired fins may be found in Actinopterygians: dorsal fin, anal fin, and adipose fin. These fins are always aligned with the sagittal plane of the body, with the dorsal and adipose fins positioned dorsally and anal fin ventrally. The dorsal and anal fins are externally supported by lepidotrichia, small bones derived from scales. Internally these fins are held by radials, which are named interneural bones in the dorsal fin and interhemal bones in the anal fin.

Plesiomorphic lineages of Actinopterygii have only one dorsal fin with soft rays. In Teleostei, an anterior dorsal fin with spines is found; in species with two dorsal fins, the first is always composed of spines and the second by soft rays. The primary function of the dorsal fin was related to making the swim more stable, but this function has been modified along the evolution of different lineages. Some of the most abrupt

changes are found in remoras (Echeneidae), in which the dorsal fin is modified into a suction disk allowing these fishes to attach themselves to larger animals, and in anglerfishes (Lophiiformes), the dorsal fin spine is modified in a structure named illicium and is used as a fishing rod to capture preys.

Unlike the dorsal fin, few lineages show diversification in the anal fin. In some families of the order Cyprinodontiformes, males have the anal fin modified as a reproductive structure, the gonopodium. A similar modification may be found in the genus *Zenarchopterus* (Beloniformes), where the anal fin is modified in an andropodium. In some lineages, as Gymnotiformes and Notopteridae (Osteoglossiformes), the anal fin is used as the main locomotory structure.

The adipose fin is an extra fin found in some lineages of Teleostei, positioned posterior to the dorsal fin. Despite the name, this fin is not usually composed of adipose tissue. Lepidotrichia and bones of support are generally absent in this fin. The adipose fin has evolved independently in different lineages, yet, the function of this fin is still unknown.

Ray-finned fishes present two pairs of paired fins, the pectoral and pelvic fins. The pectoral fin is positioned in the anterior portion of the flank. The pectoral-fin rays are supported by radials attached to the pectoral girdle. In tetrapods this girdle is connected with the vertebral column. However, in Actinopterygii, the pectoral girdle is connected to the posterior portion of the neurocranium. The pelvic fin is positioned in the ventral portion of the body, anterior to the anal fin. Plesiomorphic groups present the pelvic fin in an abdominal position; however, along the evolution of the ray-finned fishes, this fin became anteriorly positioned in the thorax or even assuming a jugular position. Pelvic fins in jugular position may be found even anteriorly to the pectoral fins. The pelvic girdle of tetrapods is connected to the vertebral column. In ray-finned fishes, the pelvic girdle usually has no connection with other structures, except for the species with jugular pelvic fins, that are generally connected with the pectoral girdle.

## Scales

Scales are found covering the body of almost every species of Actinopterygii. In this clade there are two basic kinds of scales: (1) the ganoids and (2) the cycloids and ctenoids (Roberts 1993). Ganoid scales are found in Polypteriformes, Acipenseriformes, and Lepisosteiformes. This scale generally presents spots of connection and articulation. Sturgeons and Paddlefishes (Acipenseriformes) show the most modified ganoid scales, which are featured as large plates letting most of the body naked, covered only by the skin. Cycloids and ctenoids scales are found in Teleostei and have two main layers. The first one is composed of salts (mostly calcium carbonate and hydroxyapatite) distributed in an organic matrix. The second layer is more internal and mainly composed of collagen fibers. These scales are aligned overlapping the next scale, giving much more flexibility to the individual than ganoid scales. Cycloids and ctenoids scales differ from each other due to the absence of ctenii (spinules on posterior margin) in cycloid scales. There are three kinds of ctenoid scales: (1) crenates, with spines only in the margin of the scale; (2) spinoids, when the ctenii reach the main body of the scale; and (3) ctenoids, with the spinules found as ossifications separated from the scale. During the ontogenetic process, the development of the scales begins on the caudal peduncle in the lateral line. After this, the scales advance in dorsal and ventral rows parallel to the lateral line, propagating to the anterior portion of the body. When the progress of the scales is finished, their number remains unchanged during the life of the individual.

## Cardiovascular System

This system is responsible for the distribution of nutrients, excretory metabolites, and respiratory gases, making the cardiovascular system also important for osmoregulation, excretion, and respiration. In Actinopterygii, the basic pattern of the blood flow starts in the heart, proceeds to the gill arches, and one part goes to the head and another part to the body, and then back to the



heart. The pericardial cavity shelters the heart, and this cavity is positioned posteriorly and ventrally to the gill arches. The heart of Actinopterygians is divided into four sequential chambers: sinus venosus, atrium, ventricle, and bulbus arteriosus (Farrell and Jones 1992). The last chamber is a nonmuscular bulbus, which stabilizes the pressure of the blood coming from the ventricle. When compared with tetrapods, the heart of ray-finned fishes shows a very small weight relative to the body weight. Lethargic species present a proportion of less than 0.1% between heart weight and body weight. More active species have heavier hearts, but never reaching more than 0.25% of the body weight.

## Respiratory System

Aquatic breathing demands more energy than aerial breathing. While the oxygen composes about 20% of the atmosphere, in water environments this gas may be diluted in less than 1%. Thus, the respiratory system of the Actinopterygians needs to extract as much oxygen as possible from the water (Graham and Lee 2004). The organs responsible for gas exchange are the gills. They have an osteologic structure supporting the secondary lamellae (thin membranes well-vascularized with a large surface).

Oxygen is absorbed and carbon dioxide is released by diffusion, and to optimize this process the blood in the secondary lamellae flows in countercurrent with the water passing through the gills. This opposite flow is necessary for the correct function of the gills. To ensure this countercurrent flow, two strategies are used by the Actinopterygii species. The process most commonly used is to alternate the size of the oral and opercular chambers, increasing and decreasing the volumes. The water flows from the mouth to operculum keeping the correct direction and the respiratory cycle. The second process is named ram ventilation, where the individuals simply swim with the mouth slightly opened, keeping the water flow through the gills. Ram ventilation is used by pelagic high-speed species and it saves

energy, since only the swim muscles are used to breathe, in opposition to the previous pattern of ventilation.

In some species the oxygen may also be acquired from the atmosphere. Gills usually need to be in an aquatic environment to keep the correct shape, since when exposed to an aerial habitat the gills collapse and stick together, making gas exchange impossible. Therefore, species with this ability to breathe atmospheric air also present morphological adaptations in some structures to enable them to utilize the atmospheric air. Those modifications are divided into three categories: (1) species with air-breathing organs derived from the alimentary tract, as gas bladder, stomach or intestines; (2) modifications in the head, such as gills modified to work properly in atmospheric environments; and (3) a well vascularized skin allowing the cutaneous gas exchange (Graham 1997).

## Swim Bladder

The bladder is filled with oxygen, nitrogen, and carbon dioxide, being also known as gas bladder. The function of this organ has changed through the Actinopterygii evolution, as probably the original function of the gas bladder was similar to the one of a lung. In extant species this bladder is used mainly for hydrostatic and buoyancy control, although in some species the swim bladder is also used for breathing and in sound perception or production. In some deep-sea or benthic species, this bladder is lost. The most internal layer of the swim bladder, the bladder epithelium, has a different origin than the other layers, as this epithelium has an endodermic origin, while the other tissues are derived from the mesoderm.

Two kinds of swim bladder are found in adults of Actinopterygii: physostomous and physoclistous. In physostomous species, the acquisition and release of gas occurs by a connection between the swim bladder and the alimentary tract, called the pneumatic duct. The physostomous pattern is plesiomorphic among the ray-finned fishes, and species

with adults presenting the physoclistous pattern, juveniles present a physostomous swim bladder.

In physoclistous species there is no duct connecting the bladder with other organs, and the addition of gas is performed by the gas gland. This gland transfers gas dissolved on the blood, by diffusion, to the air bladder. The gas is released by a modified area of the swim bladder, called the oval. This structure transfers the air to the blood, and the excess gas is carried to the gills and released in the environment.

## Nervous System

In Actinopterygii, the nervous system is divided into cerebrospinal, encompassing the central nervous system and peripheral nervous system, and the autonomic systems, with sympathetic and parasympathetic ganglia.

The central nervous system contains the brain and spinal cord. Anatomically the brain is divided into five portions: telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon. Each portion has a different function, processing information of different parts of the body. The telencephalon is responsible for the perception of the olfactory system; this part of the brain is homologous to the brain of tetrapods. The diencephalon function is to connect the information arriving and departing related to the endocrine system and homeostasis. In the dorsal portion of the diencephalon there is a well-vascularized structure named pineal body. The function of this structure is associated with color change, seasonal cycles, and circadian clock. Despite being a structure of the brain, the pineal body has light-sensitive cells, similar to the retinal cones. The mesencephalon is connected with the optic nerve, and all the information received by the eyes is processed by this portion of the brain. The next portion of the brain is the metencephalon, which comprises the cerebellum, responsible for the equilibrium of the swim, eye muscles, and muscular tonus. The last portion of the brain is the myelencephalon, controlling osmoregulation, breathing, and transmitting the information of each sensory systems,

with the exception of the olfactory and visual systems. The myelencephalon also connects the brain to the spinal cord.

## Sensory Systems

An important step to understand the sensory systems of Actinopterygians is to be aware that the perception of stimuli in aquatic environments differs from that in aerial environments. Taste and smell, that are very different from each other for land organisms, are very similar in water. Some wavelengths of light begin to fade according to the depth, and the sound travels faster and further than through the air. The perception of the environment may also change along the ontogeny of some species, when adults and juveniles are found in different niches (Poling and Fuiman 1998; Braun et al. 2002).

### Mechanoreception

In Actinopterygii, this sense perceives the vibration of the water. These stimuli are received by sensory hair cells, featuring cilia (Schellart and Wubbels 1997). Modifications on the vibration of the water change the frequency of nerve impulses emitted by the sensory cell to the brain. Two main mechanosensory systems are found in ray-finned fishes: the lateral line (receiving stimuli of turbulence around the fish, helping in hunting, positioning in school, and avoiding obstacles) and the inner ear (helping in hearing and equilibrium).

Among the Actinopterygii the lateral line system is a plesiomorphic feature, found even in Silurian fossil jawless fishes. The sensitive hair cells of this system are found clustering together with a gelatinous dome covering the cells, in a structure named neuromast. The function of the gelatinous cupula is to protect the hair cells from background noise, thus only stronger vibrations will be detected by the neuromasts. In the lateral line system, the neuromasts may be found in two possible conformations: (1) free neuromasts over the skin, or (2) in channels under the skin and scales (in the trunk) or dermal bones (in the head).

In the early ontogenetic stages of ray-finned fishes, all neuromasts are superficial and mostly disposed on the head. Along the development the distribution of the neuromasts extends to the trunk and the channels are formed encompassing them, under the skin. Those channels have pores, allowing the water to enter and interact with the neuromasts. The protection provided by the channels helps to avoid the permanent background noise of the water around the fish, making those neuromasts very sensitive to modifications on the water flow or high frequency vibrations (20–100 Hz). This kind of neuromasts is usually well-developed in species inhabiting turbulent waters habitats or in fast swimmers. Superficial neuromasts are more sensible to movements in environments of slow currents and low frequencies (below 20 Hz), making them very useful to detect preys and predators. Free neuromasts are more abundant in species inhabiting slow current environments and sedentary species.

Hair cells are also responsible for equilibrium and balance of ray-finned fishes. In the pars superior of the inner ear, there are three semicircular canals, that contain endolymph, and the terminal ampulla, connected with the semicircular canals, containing sensory hair cells. This portion of the inner ear receives the stimuli related to equilibrium and balance. The movement of the fish is reflected in the endolymph and changes in the posture, orientation, or speed are perceived by the hair cells. These cells send this information to the brain, which analyzes and corrects the balance and equilibrium of the individual.

The cavities of inner ear named saccule and lagena (in pars inferior) and utricle (in pars superior) are the portions responsible by hearing. Each cavity holds an otolith (structures of the inner ear made from calcium carbonate), which is surrounded by the otolithic membrane. This membrane connects the otolith with the tissue of the cavity. The tissue of each cavity is composed of sensorial hair cells that send to the brain the information from mechanic stimuli related to the sound. Otoliths react to the vibration due to their density. Most structures of the ray-finned fishes body have the same density as water, not interacting with its vibration. However, the

vibration of the water may interact with spaces filled with gas inside the body of the fish, such as the gas bladder. Some species have adaptations that connect the gas bladder to the inner ear, improving their hearing. Better hearing species include cods, in which the anterior portion of the bladder is positioned very closely to the inner ear; sardines, in which the gas bladder is in contact with the inner ear; African mormyrids, which present independent gas bladders close to the inner ears, and the Othophysi species. In the species of Othophysi, small bones connect the gas bladder to the inner ear. This adaptation is derived from the modified anterior vertebrae, and this structure is named Weberian ossicles. Thus, the vibration of the gas bladder is directly transmitted to the inner ear, making the hearing of Othophysi the most complex and accurate among the Actinopterygii.

### Chemoreception

In aerial environments the difference among olfaction, the sense of molecules dissolved in air, and gustation, the perception of chemicals dissolved in water, is very clear. However, for species inhabiting aquatic environments, those limits are not so clear, and chemoreceptors may be found in different structures than just mouth and nostrils. Several kinds of molecules dilute in water and the capacity of noticing these molecules allow the ray-finned fishes to locate shelter, to communicate with other individuals, to find food, and to evade predators. In Actinopterygii, the chemoreceptors related to the perception of the environment are usually associated with the olfaction, whereas the receptors related to the identification of the food are generally linked to the gustation (Hara 1986).

The chemoreceptors of the ray-finned fishes are mainly concentrated in the paired olfactory chambers. These structures are invaginations usually on the anterior portion of the head. Inside the chambers there is the olfactory epithelium usually organized in rosettes. The stimuli received by this tissue are transferred to the olfactory lobes of the brain. Inside the chamber there are cells with cilia generating the movement of the water through the sensitive cells. This water flux allows the

animal to continuously perceive the molecules around. Among the ray-finned fishes the olfaction is mainly used to find partners, receiving stimuli of sex steroids, of pheromones, and of alarm substances. Thus, this sense is extremely important to avoid predators and to reproduction. Damages in those receptors may affect the behavior of the individual, disturbing the social interactions of the specimen.

The sense of taste in Actinopterygians is mainly used to recognize what may be eaten. Sensory cells responsible for the gustation may be found isolated or grouped in taste buds. Isolated cells may be very abundant, with up to 4000 per mm<sup>2</sup>. The taste buds contain a smaller number of cells, usually between 30 and 100. Those chemoreceptors are found inside the mouth but also in structures around the mouth, as lips and barbels, or even in trunk and fins.

### Vision

In aquatic environments the intensity of light and the wavelength available differ according to the depth and to what chemical substances are dissolved in the water, as salts and organic matter. These differences among the habitats lead to distinct adaptations related to ray-finned fishes vision organs. Wavelengths closer to the red end (lower frequencies) are the firsts to disappear with the increasing depth, while those closer to the violet end (higher frequencies) reach deeper into water. Despite that, ultraviolet light does not reach very deep in the water (Guthrie and Muntz 1993).

The morphology of the ray-finned fishes' eyes is very similar to the other vertebrates. The most external layer is a thin transparent cornea, followed by the pupil. Unlike tetrapods, in which the pupil diameter is variable according to the light available, in Actinopterygii the pupil size is fixed. The next structure found in the eye is a spherical lens, contrasting with the eyes of tetrapods, which have a convex and less dense lens. The center of the eye is a cavity filled with liquid, the posterior portion of which is composed of the layers of the retina, where the light stimuli are received by the photosensory cells and sent to the brain. In Actinopterygians, the focus of the image inside the eye is obtained by moving the lens to anterior or posterior portion of the eye,

adjusting according to the distance between the fish and the object (Hawryshyn 1998).

Two kinds of photosensory cells are found in the retina of Actinopterygii species: cones and rods. Rods are the most sensitive to the light, allowing to see even with low light. However, these cells generate images with low resolution. The rods are more numerous in species occupying niches with low light, as deep sea, nocturnal, or crepuscular species. Cones have a lower sensitivity to light, and therefore more light is necessary to stimulate it, but these cells can generate images with higher resolution than rods. These cells are sensitive to different wavelengths, depending on which kind of opsin, the photoreceptive glycoproteins, is present in each cell. Cones with porphyropsins perceive longer wavelengths, or colors between red and yellow. These cells are usually found in species living near the water surface. Photosensory cells with rhodopsin are sensitive to wavelengths of the colors between green and blue; thus, these cells are more common in species living in habitats somewhat deeper. In species inhabiting deep sea areas, the most usual opsin found in the cones is the chrysopsin, and these cells detect colors from blue to violet, which reach deeper in the water. In some species inhabiting areas near the surface or shallow habitats, an opsin sensible to ultraviolet light also may be present.

As the light intensity may vary according to each habitat, the Actinopterygii species feature three types of cones, with a few species featuring more than three or only two types. The arrangement of the photosensory cells may vary according to the habitat of the species and also along the ontogenetic development. In some species in which juveniles and adults occupy different niches, not only the distribution of the cells may be modified, but even the opsin expressed by each cell may be modified. Despite the variety of light wavelengths that can be detected by Actinopterygians, reaching even ultraviolet light, some species are also able to see polarized light.

In most species of ray-finned fishes there is a U-shaped choroid gland around the optic nerve. The function of this gland is to provide oxygen to the retina because of its high need for the gas. The last part of the eye is the sclera, a layer

to protect those delicate internal structures. In Actinopterygii, the sclera is usually found as sclerotic bones, while in Myxiniiformes and Petromyzontiformes the sclera is fibrous, and in Chondrichthyes this structure is presented as cartilaginous plates.

Between the retina and the protective sclera there is a well-vascularized layer named choroid. In a few species of Actinopterygii the choroid may present a tapetum lucidum. This is a structure made by guanine crystals that reflect back to the eye the light that passed through the retina and was not absorbed by it. This adaptation increases the visual perception in conditions of low light.

### Electroreception

In Actinopterygii, few groups have the capacity to feel electric fields. This sense is perceived by electroreceptor organs that only have evolved in some lineages. The cells that compose this organ are derived from mechanoreceptor hair cells during the ontogeny (Whitehead and Collin 2004). In ray-finned fishes, there are two kinds of electroreceptor organs: ampullary receptors and tuberous receptors.

Ampullary receptors are found in invaginations of the skins. Externally there is a pore, connecting the receptors to the environment. This pore leads to a canal containing a conductive gel, and to the receptor. This kind of organ detects stimuli of low frequency electric fields, between less than 0.1 and 25 Hz, perceiving electrical signals coming from other animals. In this organ the perception of electricity is due to differences in electric potential between the apical and basal membranes.

Tuberous receptors are placed over the skin, covered by a layer of epithelial cells. These receptors are sensitive to electric fields of higher frequency, between 50 and 2000 Hz, and are used for electrolocation, detecting electric pulses of the individual itself. Thus, only species with electric organ discharge have tuberous receptors. These receptors may be divided into two main kinds according with which stimuli are detected: the frequency of the pulses or their amplitude. With those receptors the individual is able to detect any kind of object passing through the coverage area of the electric field. Electric organs

are composed of modified muscle cells named electrocytes (Von der Emde 1998). These cells usually have a disk-like shape and are arranged in rows. The electric pulse is generated by an ion flux over the membrane of the electrocytes. Each cell generates a small electric current, but because they are aligned in rows and the electric discharge is simultaneous, the effect is additive, amplifying the discharge, as little batteries in a row.

### Reproduction

Several kinds of reproductive patterns are found among Actinopterygii species, the differences range from the number of mating partners along the life of the individual, to the existence or not of parental care. For most species of the group the sex of the individual is defined in early life stages and kept along the lifetime (Bone and Moore 2008). Nevertheless, in some species both gametes are produced, and this species are divided into two categories: simultaneous hermaphrodites and sequential hermaphrodites. Species considered simultaneous hermaphrodites are very rare, and the individuals are able to produce fertilized eggs, or sperm and eggs in one spawning. Sequential hermaphrodites change the gender along the lifetime, and all the reproductive structures correspondent to the present sex become functional. Species in which individuals are born as females and become males throughout development are named protogynous, and species where the first stage is male and the second female are named protoandrous (Emlen and Oring 1977).

Most of the ray-finned fishes' species have more than one opportunity to reproduce in their lifetime, and these species are named iteroparous. However, in a few species only one single spawning event occurs in life. These species are known as semelparous, and they are usually diadromous or perform a great migration. Diadromous species are divided into two kinds: (1) anadromous (the individuals are born in freshwater, migrate and grow in the sea, and then migrate back to freshwater to reproduce) and (2) catadromous (the individuals are born in the sea, migrating to freshwater to grow, and then migrate to the sea to reproduce). A well-known example of

semelparous species is the salmon, living most part of the life in the sea but going up rivers to spawn.

The number of reproductive partners also varies in the different species of the group, and may be divided into three main patterns. (1) Promiscuous species, when the partner is chosen with little or no degree of selection. In those species multiple individuals of both sexes spawn together at the same time or in a short time. (2) Monogamous species, in which the individuals remain breeding exclusively with the same partner. In this case, the couple not necessarily stays together after the mating season. (3) Polygamous species, in which individuals of only one sex have many partners. When the female presents several partners it is named polyandry, and when the male has different partners it is called polygyny, which is more common. Among the polygynous strategies the formation of harems may also be found. In this case a group of females stay with one male and only reproduces with him, who protects the whole group. Another strategy comprised by the polygamous pattern is the formation of leks, in which many males concentrate in a specific area only to display to females.

Most of the ray-finned fishes' species leaves the eggs after spawning, not presenting any kind of parental care. However, this behavior is found in several lineages of Actinopterygii, in different levels and time periods. The first stage of parental care includes to build a nest. In some species the eggs are buried in the nest after the spawning and the parents leave the eggs. Other species stay with the nest until the birth of the offspring, protecting the eggs from predators, cleaning the nest, removing sediments, unviable eggs, and keeping a water flux to maintain the eggs oxygenized. In other species the eggs are eventually carried in the mouth to provide a better protection to the offspring. In some species the development of the eggs is internal, and this kind of bearing is divided in ovoviviparous (when the eggs are kept inside the mother and embryos feed on the yolk present in the egg) or viviparous (when there is a specialized tissue responsible for feeding the embryos and performing gas

exchange). In a few species, after the birth, the adults also may produce mucus to feed the juveniles or help them to obtain food.

## Cross-References

- [Circulatory System](#)
- [Fertility](#)
- [Morphology](#)
- [Nervous System, The](#)
- [Olfactory Perception](#)
- [Parental Investment](#)
- [Photoreceptors](#)
- [Polyandry](#)
- [Polygamy](#)
- [Polygyny](#)
- [Sensory Receptors](#)
- [Vertebrate Nervous System](#)
- [Vertebrates \(Chordata\)](#)
- [Zoology](#)

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## Action Perception

### ► Embodied Perception

## Action Potentials

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## Synonyms

Neural impulse

## Definition

An action potential is a brief event that occurs when there is a change in the membrane potential, or electrical activity, of a neuron.

## Introduction

Action potentials play an integral part of communication between neurons and are involved in many processes within the central nervous system, neuromuscular junctions, and cardiac functions. They occur in response to a stimulus, such as sensory input or neurotransmitters, usually through the dendrites of the neuron. These stimuli cause small excitations in the dendrites or cell body called graded potentials. Graded potentials are summated and must be strong enough to trigger the impulse. At rest, the inside of a neuron is negative relative to the outside. Once it is stimulated, the intracellular environment becomes positive relative to the outside of the cell, thus allowing ion channels to open and sodium ( $\text{Na}^+$ ) to move into the axon. Most neurons have a protein called myelin that surrounds segments of the axon and insulates them from extracellular electrical activity. Small sections that remain unmyelinated are referred to as nodes of Ranvier. These nodes contain many ion channels that help the action potential regenerate as it travels down the axon. Myelin allows for the action potential to quickly travel from node to node, as it promotes low resistance for the conduction of positive ions. This action of jumping from node to node is called saltatory conduction. Once the action potential travels down the axon, there is a positive spike in the membrane potential that causes a release of neurotransmitters into the synapse through the neuron's terminal buttons.

## All-or-None Principle

A neuron is connected to thousands of other neurons; therefore it can receive numerous stimuli at one point in time. The strength of the stimuli does not affect the amplitude, or intensity, of an action potential. In addition, an action potential is only generated if there is sufficient stimulation. These properties make up the all-or-none principle. In other words, an action potential will have the same intensity of firing regardless of the intensity of a stimulus. While the strength of the stimulus does not affect the intensity of the action potential,

it does affect the frequency of firing (Barnett and Larkman 2007).

## Measurement of an Action Potential

An action potential can be measured by recording the electrical potential of the cell membrane using electrodes. Electrical activity is most commonly measured using two points, one as a reference and another to record changes in potential, relative to the reference point. The extracellular environment is used as the reference point for recording electrical changes in a neuron. When the recording electrode is inserted into the axon, a negative potential is measured. This indicates that, at rest, the inside of the neuron is more negative than the extracellular environment.

Each ion involved in the action potential has a concentration gradient due to the permeability of the membrane. The potential for each ion can be measured by the Nernst equation:  $E_i = \frac{RT}{zF} \ln \frac{[C]_o}{[C]_i}$ . In this equation  $E_i$  indicates the equilibrium of a single ion,  $R$  is the Universal Gas constant,  $T$  is temperature,  $z$  is the charge of the ion,  $F$  is Faraday's constant,  $C_o$  is the concentration of the ion outside the cell, and  $C_i$  is the concentration of the ion inside the cell (Hille 2001). Outside of the cell, there is a high concentration of sodium, calcium, and other ions, while the inside has a high concentration of potassium ( $K^+$ ). Each of these ions has an equilibrium potential ( $E_i$ ) as a result of the concentration gradient.  $Na^+$  has a positive equilibrium potential ( $E_{Na^+}$ ) of about +55 mV.  $K^+$  has a negative equilibrium potential ( $E_K$ ) of about -75 mV (Barnett and Larkman 2007). The resting potential of the cell is at about -60 mV. As ions move across the membrane, the membrane voltage ( $V_m$ ) and permeability change. In order to calculate the membrane potential of a cell, the Goldman equation is used:  $V_m = 58 \log \frac{P_K[K]_o + P_{Na}[Na]_o + P_{Cl}[Cl]_i}{P_K[K]_i + P_{Na}[Na]_i + P_{Cl}[Cl]_o}$ , where  $P$  indicates the permeability of the cell (Purves et al. 2001a).

During an action potential (Fig. 1), the  $Na^+$  channels open and  $V_m$  increases or depolarizes, toward  $E_{Na^+}$ . As more  $Na^+$  rush into the cell, a

positive feedback loop occurs.  $Na^+$  increases  $V_m$ , which opens more voltage-gated ion channels, allowing more  $Na^+$  into the cell, further increasing  $V_m$  toward  $E_{Na^+}$ . The loop repeats until all the  $Na^+$  channels open and the cell reaches the peak voltage of the action potential, meaning the concentration of  $Na^+$  is equal on both sides of the membrane. This point is known as the absolute refractory period. During this period, no more  $Na^+$  can enter the cell to create another action potential. The high  $V_m$  then inactivates the  $Na^+$  channels and opens the voltage-gated  $K^+$  channels. As this occurs,  $K^+$  rush out of the cell and  $V_m$  decreases or repolarizes, toward  $E_{K^+}$ . During this period, action potentials are unlikely but possible only in response to strong stimuli. This is known as the relative refractory period. Since  $E_K$  is lower than -60 mV,  $V_m$  falls under the resting potential resulting in hyperpolarization (Purves et al. 2001a). The cell then repolarizes back to resting potential via the sodium-potassium pump.

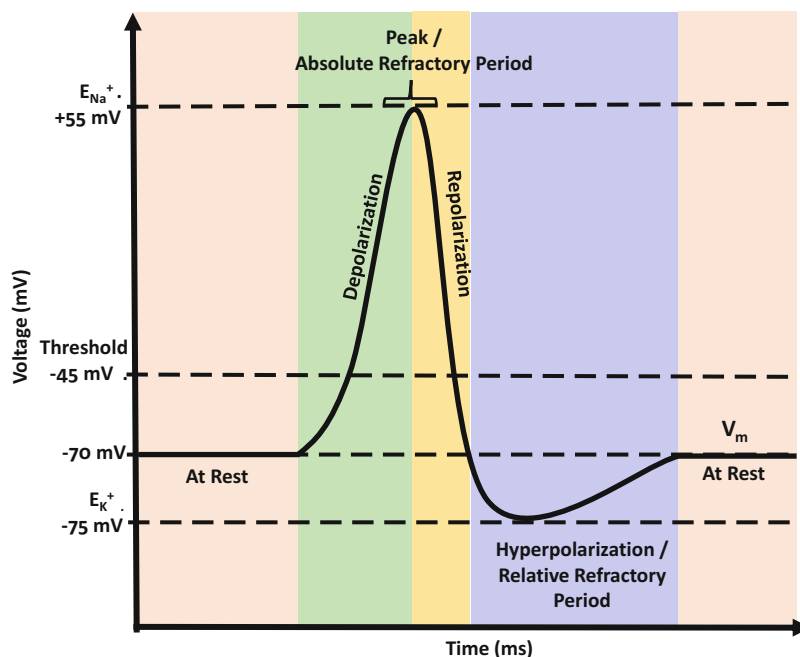
## Sodium-Potassium Pump

A neuron maintains a resting potential around -60 mV due to an electrochemical gradient created by the active transport of the sodium-potassium pump ( $Na^+/K^+$  pump). This transporter works by pumping three  $Na^+$  ions out and two  $K^+$  ions into the cell. At rest, the extracellular environment has a higher concentration of  $Na^+$ , while the intracellular environment has a higher concentration of  $K^+$ . The  $Na^+/K^+$  pump requires ATP as energy because it moves the ions against their concentration gradients. This action results in a deficit of positive ions inside the cell making it negative relative to the extracellular environment (Glitsch 2001).

## Initiation

There are three steps to the occurrence of an action potential: initiation, propagation, and termination. Initiation of the action potential begins with a stimulus that causes ion channels to open, usually on the dendrites or cell body. A stimulus can be excitatory or inhibitory. When a neurotransmitter binds





A

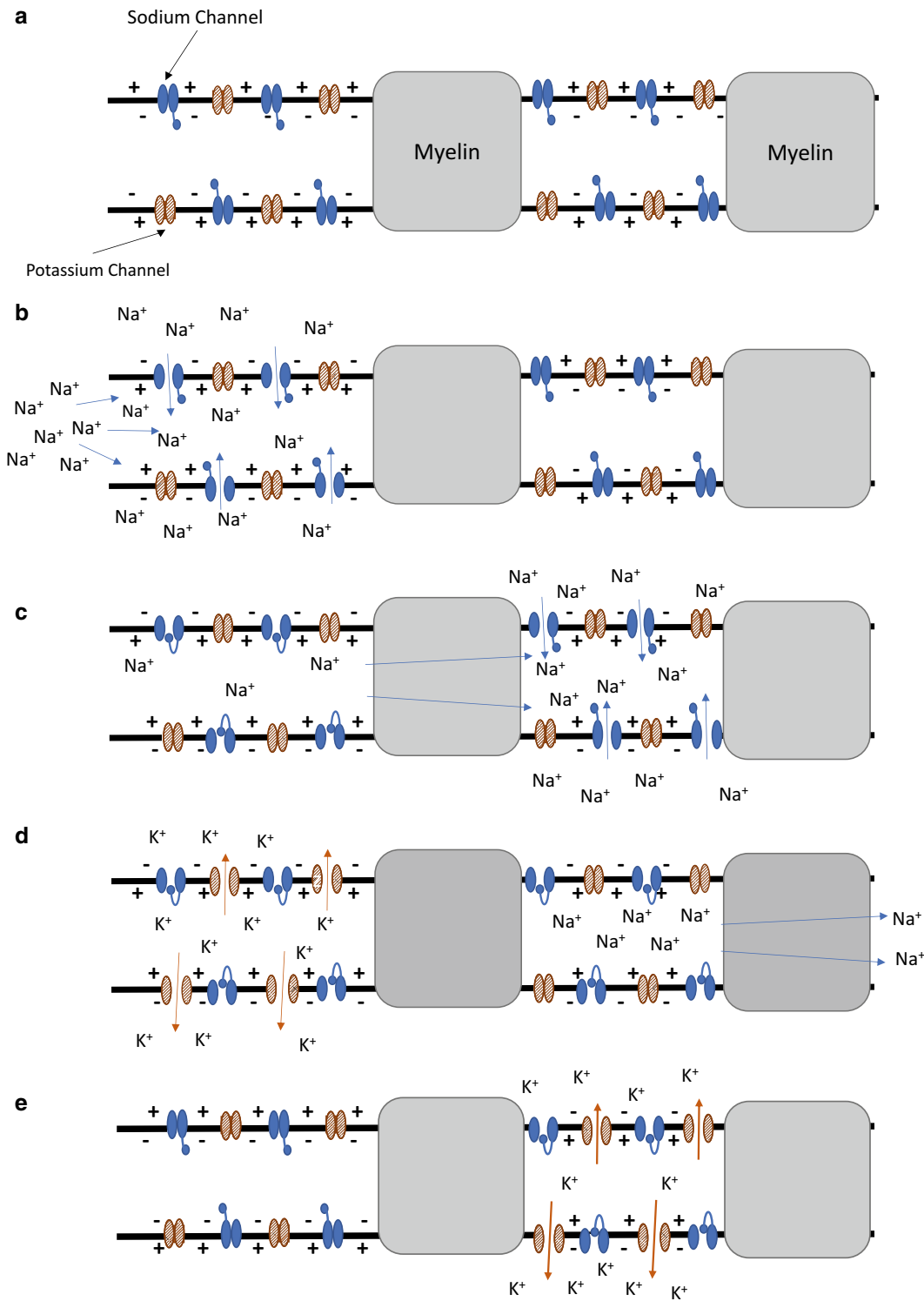
**Action Potentials, Fig. 1** Stages of action potential. Membrane potential starts at rest at  $-70$  mV. Once threshold is reached at  $-45$  mV, the membrane potential depolarizes toward the  $\text{Na}^+$  potential at  $+55$  mV. At this point, known as the absolute refractory period, another action potential cannot occur because no more  $\text{Na}^+$  can enter the

cell. The membrane then repolarizes to the equilibrium potential of potassium at  $-75$  mV. During this stage, the relative refractory period, only strong stimuli can elicit another action potential. The membrane then goes back to resting potential by action of the sodium-potassium pump

to a receptor that increases the probability for depolarization, it is called an excitatory postsynaptic potential (EPSP). When a neurotransmitter binds to a receptor to increase the chance for hyperpolarization, it is called an inhibitory postsynaptic potential (IPSP) (Purves et al. 2001b). EPSPs and IPSPs alter the permeability of the membrane by affecting the ion channels (Krnjevik 1987). Positive or negative ions enter the cell body and work their way along the membrane toward the axon hillock, where they are collected and summated. This movement across the membrane causes small variations in electrical potential of the cell, known as graded potentials. The graded potentials must sufficiently depolarize the cell and bring the membrane potential to a threshold, usually  $-40$  mV, in order for an action potential to occur. Once the membrane potential reaches the threshold, the axon hillock experiences a reversal in charge, where it becomes positive relative to the outside of the cell (Palmer and Stuart 2006).

## Propagation

Once the action potential is initiated, the positive charge in the axon hillock is propagated to the adjacent, unmyelinated segment of the axon (Palmer and Stuart 2006). As the flow of positive ions moves into adjacent segments,  $\text{Na}^+$  and  $\text{K}^+$  voltage-gated ion channels are activated.  $\text{Na}^+$  channels open first, allowing the positive ions to rush into the cell (Fig. 2b). Once the inside of the axon becomes positive, the channels deactivate via a ball and chain mechanism in which a ball blocks the channel, preventing further  $\text{Na}^+$  from entering the cell (Fig. 2c). This systematic deactivation is called the refractory period and prevents the action potential from moving backward. Furthermore, the negative electrostatic charge in the following segment pulls the positive ions forward. As the  $\text{Na}^+$  channels inactivate, voltage-gated  $\text{K}^+$  channels open and allow  $\text{K}^+$  to move out of the cell, following their concentration gradient



Action Potentials, Fig. 2 (continued)

(Fig. 2d). This is known as repolarization. The  $K^+$  channels are slow to deactivate and bring the segment below resting potential, hyperpolarizing it (Fig. 2e) (Barnett and Larkman 2007). The action of the  $Na^+/K^+$  pump brings each segment back to resting potential from the hyperpolarized state.

## Termination

### Chemical

Termination takes place when neurotransmitters are released into the synapse through the neuron's terminal buttons. When an action potential reaches these buttons, the positive charge opens voltage-gated calcium ( $Ca^{++}$ ) channels.  $Ca^{++}$  rush into the cell following their concentration gradient. The  $Ca^{++}$  bind to proteins that attach neurotransmitter-containing vesicles to the membrane of the terminal button. A conformational change occurs in the proteins so that they pull and fuse the vesicles to the membrane, allowing neurotransmitters to be released into the synaptic cleft. This process is known as exocytosis (Llinas et al. 1981).

### Neuromuscular

Termination of an action potential can also have different physiological effects. In a neuromuscular junction, the action potential of a motor neuron will elicit the contraction of a muscle fiber. In this case, the neurotransmitter released by the presynaptic cell is acetylcholine, or Ach. The muscle cell contains sodium and calcium ion channels that have an Ach receptor. When it binds, these channels open causing the ions to rush into the cell. Inside the cell, the calcium binds to receptors in the sarcoplasmic reticulum, which contains a

large supply of calcium ions. This action causes the release of the ions which spread from cell to cell and fiber to fiber causing the muscle to contract (Lodish et al. 2000).

## Cross-References

- Axon
- Dendrites
- Myelination
- Nervous System
- Neuron
- Neurotransmitters

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**Action Potentials, Fig. 2** Propagation of action potential down the first and second segment of an axon. (a) Neuron membrane at rest with no stimulus. (b) Sodium channels on membrane open as a response to the positive charge of the axon hillock, and  $Na^+$  rushes into the cell as reversal of charge occurs. (c) Sodium channels in the first segment inactivate.  $Na^+$  are pulled down the myelinated portion of the axon to the second segment, and the sodium channels

open. (d) Potassium channels open in the first segment, and  $K^+$  rush out of the cell. In the second segment, sodium channels inactivate and  $Na^+$  are pulled down the myelinated axon to the third segment (not shown). (e) Potassium channels close, sodium channels close, and the cell returns to resting potential in the first segment. Potassium channels open, and  $K^+$  rush out of the cell in the second segment. This process continues down the segments of the axons

Purves, D., Augustine, G. J., Fitzpatrick, D., Katz, L. C., LaMantia, A. S., McNamara, J. O., & Williams, S. M. (2001b). Excitatory and inhibitory postsynaptic potentials. In *Neuroscience* (2nd ed.). Sunderland: Sinauer Associates.

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## Active Choice Judgment

### ► Judgment Bias

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## Active Memory

### ► Short-Term Memory

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## Activity Anorexia

### ► Activity-Based Anorexia

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## Activity Budget

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## Synonyms

Time budget

## Definition

A tool used to quantify what an animal does during the period of observation.

## Introduction

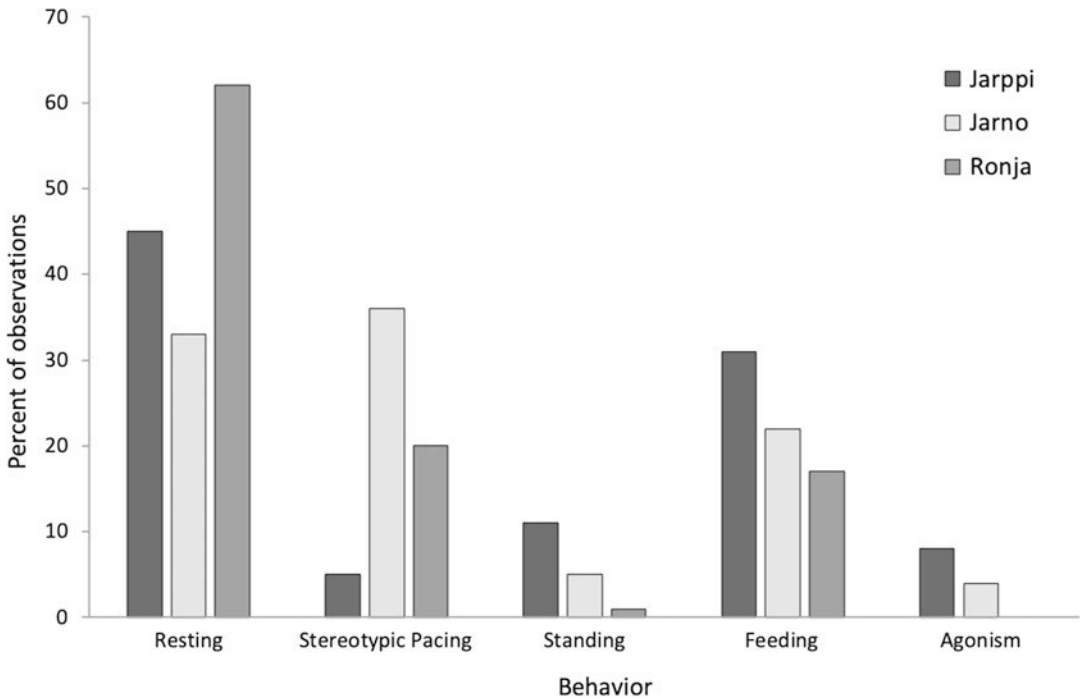
An important component of studying animal behavior is to establish an activity budget for the

species of interest. An activity (or time) budget quantifies what an animal does during the period of observation. It is typically constructed either by recording the duration of an animal's various behaviors for a set amount of time or by sampling at regular intervals what an animal or a group of animals is doing over a longer period of time. The method chosen is determined by the question the researcher wants to answer and the type of behaviors that are to be observed. Comparison of activity budgets within a species can reveal the effects of many different factors including age, sex, seasonal effects, and anthropogenic disturbances. Activity budgets can also be compared between captive and wild animals to help determine how behavior is affected by captivity. Changes in the distribution of behaviors or the occurrence of behaviors not seen in the wild can serve as important indicators about the health and welfare of captive animals. Activity budgets are a useful tool for conservation management.

## Constructing an Activity Budget

Activity budgets have been created for a variety of species representing invertebrates and all five vertebrate groups, amphibians, birds, fish, mammals, and reptiles. They are established in conjunction with an ethogram that describes the behaviors to be recorded and whether those behaviors are best classified as events (generally less than a few seconds in duration, such as a sneeze) or states (often persisting for minutes or hours, such as feeding or resting). A hypothetical activity budget is illustrated in Fig. 1.

Activity budgets conducted in the wild may vary substantially in the level of detail that can be recorded. The simplest type of budget is dichotomous, recording if the animal is moving or not. These types of budgets are generally compiled using technology to track free-ranging animals that move quickly through thick brush, treetops, or water which would be a challenge for researchers to follow on foot or with binoculars. In these cases, advances in technology using radio telemetry or GPS tracking collars equipped with accelerometers can yield binary information



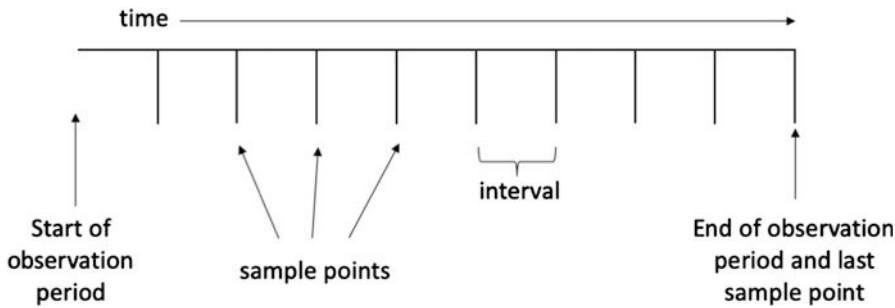
**Activity Budget, Fig. 1** A hypothetical activity budget for three reindeer (*Rangifer tarandus*), Jarppi, Jarno, and Ronja. After data are collected, the percent of sample points that each behavior was observed can be calculated. For each individual animal, the scores across all of the behaviors should sum to 100%. In this example, individual

differences can be seen in the behavioral activities. Furthermore, these data reveal sex differences. The female, Ronja, was observed resting more often than the males and the males were more often observed standing and feeding. Only the males were observed engaged in agonism

about whether or not the subject is moving. For animals in captivity and those in the wild that can be more easily observed and tracked on foot, researchers are more likely to record a variety of behaviors. This can be done manually on paper, on a laptop or by voice recording, or by using devices such as smartphones and video cameras to record behavior continuously for subsequent analysis. Researchers log which behaviors are occurring using one of several standard sampling procedures.

Three sampling methods have been described in the literature (see Altmann 1974; Lehner 1998; Martin and Bateson 2007). In continuous (all-occurrences) sampling, the researcher records when a behavioral event occurred or the start and end time of a behavioral state. This method provides a largely unbiased representation of the frequency, latency, and duration of what an animal is doing throughout the observation period, although

it may underestimate the duration of long behavioral states that continue past the observation period. It is useful for studying sequences of behaviors but is not always practical because of constraints on the human observer. In fixed interval time point or instantaneous sampling, the observation period is divided into intervals of fixed duration (e.g., every 30 s or every 5 min; see Fig. 2). At the end of each sample interval (the sample point), the researcher records what the animal is doing. This procedure is less demanding on the researcher than continuous sampling but has the downside of underestimating the frequency of extremely rare or very brief behaviors. Conspicuous behaviors may also be overestimated because of a researcher's natural tendency to record such behaviors if they occur just before or just after the sample point. In one-zero sampling, the researcher simply records if a target behavior occurred at any point during the sample interval. This method may be acceptable



**Activity Budget, Fig. 2** A schematic of a fixed interval time point or instantaneous sampling procedure. The observation period is divided into intervals of equal duration. At the end of each interval (including the end of the observation period), there is a sample point. At each

sample point, the observer records the activity of the animal. The frequency that a behavior is observed with this sampling method is considered a good proxy for the time spent actually engaged in that behavior

for recording intermittent behaviors of short duration such as play. Researchers sometimes use multiple sampling methods in the same study in order to optimize accurate activity profiles.

### Activity Budgets in the Wild

Activity budgets are commonly used by researchers as part of their documentation of the natural history of a species and to answer questions about ecological and social influences on the behavior of a species. They have been important for showing that the time spent in different activities can vary both diurnally and seasonally within groups, between males and females, as a function of social rank and age, and between groups in different habitats. The impact of these variables on activity budgets can shed light on how animals maintain energy budgets. For example, food resources often fluctuate with seasonal variations requiring an adaptive response. King colobus (*Colobus polykomos*) monkeys appear to adopt an energy conservation strategy, spending more time resting and less time feeding when preferred seeds are not available. On the other hand, Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) appear to adopt an energy-maximizing strategy, foraging more in the resource-poor season.

Numerous studies have reported diurnal and seasonal effects on activity. Beltramino et al. (2019) inferred activity budgets for the sedentary

Argentine sea bass (*Acanthistius patachonicus*) using algorithms to parse information from accelerometer data loggers. They found that active behaviors in the sea bass in the northern Patagonian gulfs of Argentina were on average 50% higher during the warm water season (16–18 °C) than during the cold water season (8–10 °C). In a study of a group of François' langurs (*Trachypithecus francoisi*) at the Nonggang Nature Reserve, Guangxi Province, China, diurnal activity revealed morning and afternoon peaks in feeding behavior with a midday resting peak (Zhou et al. 2007). Using instantaneous sampling (15 min fixed interval), the researchers also found seasonal effects on feeding activity with two significant peaks (morning and afternoon) in the dry season but only the afternoon peak in the rainy season. This difference may be related to seasonal variations in food sources and temperature although the authors do not rule out a measurement artifact that obscured a morning feeding peak in the rainy season. Age differences were also observed in this study with adults spending more time resting, feeding, and grooming and immatures spending more time playing.

The effects of sex, age class, and social rank on activity budgets have also been widely examined. One study used radio telemetry to record daily activity budgets of 26 South Georgia shags (*Phalacrocorax georgianus*) during the chick-rearing period at Bird Island, South Georgia. Two sexually distinguishable foraging patterns

were observed; males spent more time flying and on the sea and, in 93% of the pairs, the female was the first to leave the nest each day to search for food. Another study compared activity budgets for parent, nonparent, and juvenile wintering common cranes (*Grus grus*). In the period following arrival at the wintering grounds when still dependent on their parents, juveniles spent more time feeding and less time alert and preening than adult birds. This difference later disappeared when most of the juveniles reached parental independence. This study also compared parents and nonparents to determine potential costs and benefits of parental care. Although parents were more vigilant (higher rates of scanning) and spent less time feeding and resting than nonparents, there was no apparent cost as their net and absolute food intake rates were higher than those of nonparent adults. The effect of social rank on vigilance behavior in rutting ungulates has yielded discrepant findings. A study of territorial male impala (*Aepyceros melampus*) found they allocated more time to vigilance against intruding rivals. However, a study of elk (*Cervus elaphus*) found that rutting bulls engaged in courtship spent little time being vigilant. This pattern suggests that, in ungulates, variations in vigilance during rutting may reflect an interaction between social rank and species-specific mating systems rather than social rank per se.

Isbell and Young (1993) used activity budgets to examine the effects of sex, rank, habitat, and group size in six groups of vervet monkeys (*Cercopithecus aethiops*) living in Amboseli National Park, Kenya. Over a period of 20 months between June 1986 and January 1988, they calculated the average time that monkeys spent on feeding, moving, resting, scanning, allogrooming, or other (social and nonsocial) activities. Overall, males scanned more than females and dominants scanned more than subordinates. Scanning may be used to monitor for predators or to check on potential competitors for food or mates. Habitat effects were observed on two behaviors. Briefly, vervet monkeys spent more time moving and allogrooming in the *Acacia xanthophloea* habitat than the monkeys in the *A. tortilis* habitat. The difference in moving is consistent with differences in

resource distribution and food abundance between the two habitats. The researchers suggested that the influence of habitat on allogrooming might reflect differences either in ectoparasite density or in group size. The groups in *A. xanthophloea* were larger than the groups in *A. tortilis*, and allogrooming was positively correlated with group size.

### Activity Budgets in Captivity

Activity budgets are frequently used to assess animal welfare in captive settings. Captive environments are often designed to elicit natural behavior or behavior that resembles that of the animal's wild counterparts. Animals in the wild spend much of their activity budget on survival needs, like finding food and mates. These needs are often not present for captive animals, where food is provisioned and mating is controlled. Given that many animals have adaptations to help serve these needs, and not performing them can impact both the mental and physical health of the animals, there is great interest in understanding how closely captive animals' activity budgets resemble their wild counterparts.

Historically this was done by a direct comparison – constructing an activity budget in a captive species and comparing it to that same species in the wild. For example, Veasey et al. (1996) compared the activity budget of giraffes (*Giraffa camelopardalis*) in four zoos to those found in the wild. They found significant differences in the amount of time the giraffes spent feeding, ruminating, standing, and engaging in stereotypical behavior. Interestingly, although occurring at significantly lower rates, stereotypical behavior was not absent in the wild giraffes, showing that it may not be an abnormal manifestation of life in captivity. However, the authors suggest that the differences in the activity budgets did not arise from behavioral restriction in captivity but rather from observation methods. Despite taking care to closely replicate the same methods in captivity and the wild, they noted that the presence of observers had a larger impact on giraffe behavior in the wild versus in captivity, and certain



behaviors like stereotypies might be more visible with the closer distances and unobstructed viewing allowed by captivity. Furthermore, they noted that the four different methods they used to observe the giraffes in the wild (ranging from following them in a four-wheel drive vehicle to approaching them on foot) resulted in dramatically different activity budgets, suggesting that a wild study using a single method might not be representative of the species' full behavioral repertoire.

In general, there are numerous differences in data collection methods that can impact the comparability of field and captive data. With the advent of new accelerometer technology that can be used across settings and reduce the need for observers to collect data in person, there is potential for more accurate comparisons. However, differences in behavior observed from captive to wild would still require critical interpretation. In the giraffe study, the giraffes with the best enclosure, a large, grassy paddock, spent the most time grazing and lying down (Veasey et al. 1996). These two behaviors are less possible in wild giraffes, since the dry season limits grazing and lying down increases predation risk. In other words, when they have the choice, giraffes choose to rest more, suggesting that the decreased activity seen in captivity may not reflect a welfare problem.

In recent years, a desire to better understand the impact of activity on captive animal welfare has led to a different approach, using activity budgets to study behavioral diversity, which is a measure of the number of different behaviors an animal performs (the richness of their behavior) combined with the frequency of different types of behavior (Miller et al. 2020). It is thought that if an animal exhibits high behavioral diversity, they are using more of their natural adaptations and are appropriately mentally stimulated. This inference is supported by data across species showing that as behavioral diversity increases, stress hormones, such as glucocorticoids, decrease.

Behavioral diversity can be assessed by constructing an activity budget and examining both the number of different behaviors exhibited by an individual and the frequency with which they perform those different behaviors. Behaviors

included in this analysis should only consist of those relating to positive welfare (Miller et al. 2020). Although certain behaviors such as stereotypical behaviors or aggression are certainly part of an animal's activity budget, and large amounts of time spent in these behaviors should elicit concern, it is helpful to understand how much of an animal's time is devoted to positive behaviors. The activity budget data can also be used to calculate a behavioral diversity index, the most famous of which is the Shannon-Weiner index. These indices combine all of the different types of behavior into an overall value that reflects the variety and frequency of behaviors an individual is performing. Behavioral diversity indices can be useful for comparing activity budgets across individuals and different institutions.

## Conclusion and Future Directions

Activity budgets have long been used to better understand the activity patterns of animals in the wild and how those patterns are influenced by ecological and social factors. Such information has proven crucial for assessing the potential impact of anthropogenic disturbances and for conservation management of endangered and threatened species. In a study of the North Atlantic population of minke whales (*Balaenoptera acutorostrata*), a mysticete, on one of their feeding grounds (Faxaflói Bay, Iceland), Christiansen et al. (2013) used a biologically based modeling approach to construct activity budgets to demonstrate that whale watching boat interactions resulted in a 42% decrease in overall feeding activity. Such short-term behavioral disruptions warrant further analysis as they may have a cumulative impact on vital rate measures (survival, growth, and reproduction) that could influence species fitness. In another study, continuous recording of the Sri Lankan endemic shrub frog *Pseudophilautus popularis* in a wetland-home garden setting in an urban area revealed that the height at which male frogs perch on leaves and branches to call gradually increases from about 15 cm around dusk to a maximum of 180 cm above ground level by 2300 h and then, after



about 2 h, gradually decreases toward dawn (Dayananda and Wickramasinghe 2014). These findings underscore the importance of biodiversity in vegetation stratification to maintain a habitat that will support the conservation of this species.

Activity budgets can also be used to assess changes to a captive animal's environment and the impact of welfare interventions. For example, a review of 28 studies revealed that in 78.6% of them, behavioral diversity increased following the provision of enrichment or some other enhancement to the enclosure (Miller et al. 2020). Likewise, a decrease in behavioral diversity, or increase in abnormal behaviors or inactivity, could signal a welfare problem that needs attention. Regular monitoring of captive animals' activity budgets is crucial to their well-being. This can be a challenge not only in terms of cost and labor but in sustaining unbiased and consistent observations. The use of automated electronic surveillance systems and behavioral recognition software may well help alleviate such problems.

Recent advances in technology have played an important role in improving the quality and accuracy of activity budgets for both wild and captive animals. Hertz et al. (1988) suggested that the perplexing problem of why taxonomically diverse reptiles do not routinely use their maximal capacities for locomotion might well be solved by attaching accelerometers to lizards for long-term monitoring of activity in response to rare events. The use of increasingly sophisticated accelerometer devices coupled with machine learning algorithms and visual authentication of behavior are only likely to strengthen the unbiased comparisons that can be made between wild and captive activity budgets. Finally, for both wild and captive animals, changes in activity budgets must be assessed before and after human interactions or interventions, to better understand and manage the impacts humans are having on other species.

## Cross-References

- [Agonism and Social Status](#)
- [Allogrooming](#)

- [Animal Welfare](#)
- [Captivity](#)
- [Conservation](#)
- [Ethogram](#)
- [Focal Animal Sampling](#)
- [Hormones and Behavior](#)
- [Observational Methods](#)
- [Play Behavior](#)
- [Predation Risk](#)
- [Predator Defense](#)
- [Rutting](#)
- [Vigilance](#)

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## Activity-Based Anorexia

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 (UNED), Madrid, Spain

## Synonyms

Activity anorexia; Activity-induced anorexia;  
 Self-starvation; Semi-starvation-induced hyper-  
 activity (SIH)

## Definition

Activity-based anorexia (ABA) is a robust phenomenon that takes place in many animal species in which excessive physical activity is developed to a deleterious level when access to food intake is restricted to a short period of time a day (e.g., 1–2 h), resulting in reduced eating and substantial body weight loss. Paradoxically, the increment in locomotor activity takes place when energetic balance is negative, so that continued exposition of an animal (usually rats or mice) to intermittent food delivery plus almost permanent access to exercise could drive the animal to die if it is not withdrawn from the procedure. ABA constitutes the most recognized animal model of anorexia nervosa disease in humans due to the similarities between the behavior observed when animals are submitted in the laboratory to the above conditions and the characteristics of clinical patients suffering the disorder.

## Historical Background

The first scientific observations of the effect of long periods of starvation on different species of birds, reptiles, and mammals in the mid-nineteenth century by Charles Chossat (1843) reflected that, during much of the process, the animals remained to a greater or lesser extent in a state of agitation that lasted until the moments near before their death. Although those studies, which would hardly meet current ethical standards, detailed the physiological processes that took place in the animals, no significant importance was conferred to the high physical activity developed. It was not until the early twentieth century when the work of Richter (1922), sponsored under the direction of J.B. Watson, delved into the biological basis of spontaneous activity in laboratory rats, bringing to experimental study the locomotive behavior developed by the animals in constant conditions of light and temperature and introducing the use of boxes and running wheels to make precise measurements of the activity developed. In those experiments, it was revealed the existence of circadian rhythms in the activity of the subjects, as well as the concentration of this activity around the meal period when it was supplied once a day, among other observations of the factors that influence the level of activity and that are still valid today, such as the sex of the animal or the ambient temperature.

However, the systematization of studies on the failure of maintaining stable weight in rats living in activity wheels under a food deprivation schedule has its milestone in the work of Routtenberg and Kuznesof (1967), who named the phenomenon “self-starvation.” Those authors introduced a control group, with the same food schedule but without access to the running wheel, that ate more and stabilized its loss in weight compared with the activity group who “self-starved” and died.

In the 1980s of the twentieth century, the influential work of Epling, Pierce, and Stefan (1983) highlighted the importance of locomotor activity in times of food shortage in the phylogeny of species as a form of survival, relating the behavior observed in the laboratory animals with that developed in many cases of anorexia nervosa in

humans. These instances were called activity-based anorexia, linking since then the study of its causes and the development of treatments for this disorder to a valid animal model given that it reproduces many of the characteristics present in the anorexic patients.

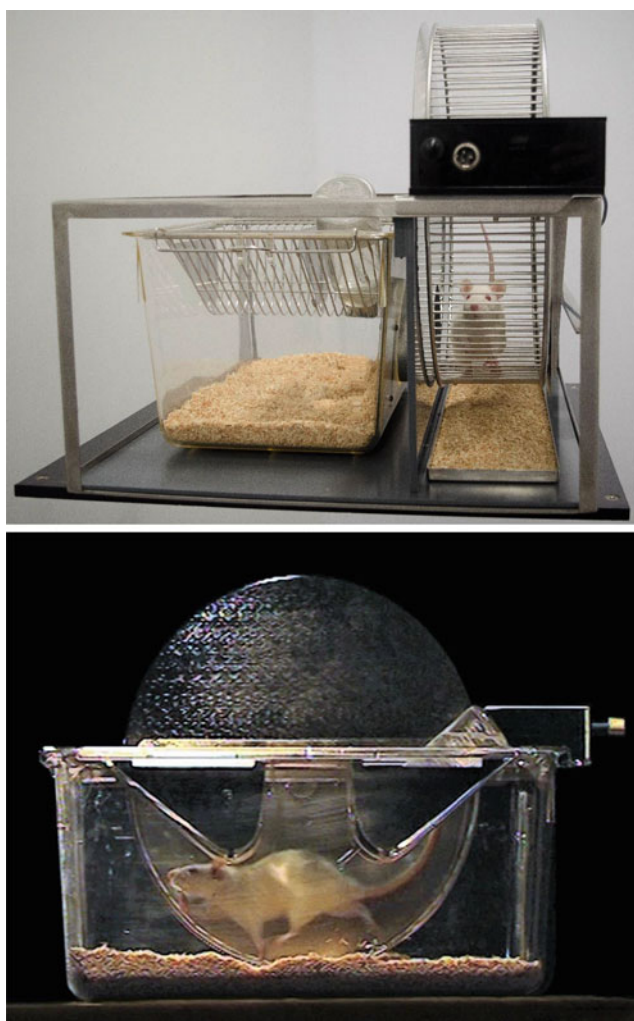
## Experimental Protocol

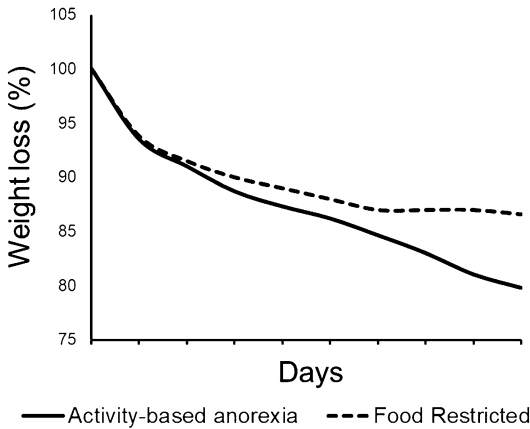
The basic ABA protocol includes the use of two groups of animals, usually named Active and Sedentary, or simply ABA and FR (food restricted). The procedure in the ABA (Active) group starts with the removal of food and

allowance of free access to a running wheel for 23 h before the next meal opportunity (see Fig. 1). This day is known as day 0, and the weight data obtained prior to food restriction is the initial weight against which its loss is calculated the remainder days. Animals in the ABA group usually have 1–2 h food exposition and 22–23 h of wheel access each subsequent day until the end of the procedure. In order to prevent death and reduce animal suffering, each subject is removed from the procedure when reaching 20–25% of weight loss for two consecutive days. Animals in FR (Sedentary) group are subjected to the same food restriction schedule but without access to the running wheel. All animals

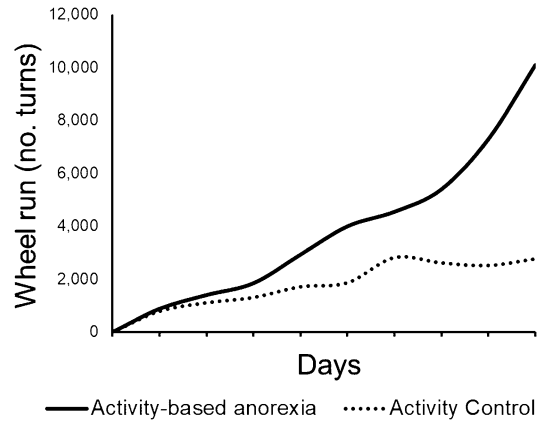
### Activity-Based Anorexia,

**Fig. 1** Images showing a home cage with attached activity wheel that can be used to run the activity-based anorexia (ABA) procedure in the laboratory with rats





**Activity-Based Anorexia, Fig. 2** Expected results in weight loss during ABA procedure



**Activity-Based Anorexia, Fig. 3** Expected results in wheel running during ABA procedure

in both groups are weighed each day before the meal period. As seen in Fig. 2, FR animals (dotted line) show initial reduction in body weight and then stabilization around 85% of their free-feeding weights. However, ABA animals (straight line) fail to maintain their weights and progress with a dramatic reduction. Accompanying weight loss, ABA animals show a gradual increase of running along the days in the procedure (Fig. 3, straight line). Comparing both groups, it can be suggested that weight loss relates to the increased activity expressed in ABA animals. It can be added an optional extra control group for activity (unrestricted); here animals are maintained in ad libitum food schedule and have the same time access to a running wheel than ABA animals. In this case, animals do not show the excessiveness in activity observed in the ABA group (Fig. 3, dotted line). These results suggest that the increase in activity relates to the food schedule. See Carrera, Fraga, Pellón, and Gutiérrez (2014) for an extensive description of the protocol.

## Main Interpretations

Regarding the hypotheses to explain ABA, they can be grouped in two: those that focus on food

consumption and those that suggest a central role for activity.

Within the first group, authors (e.g., Kanarek and Collier 1983) suggest that running interferes with the adaptation to the meal schedule preventing ABA animals from maintaining their weights, while the subjects in the control group with same food exposition but with lack of access to a running wheel can maintain their weights. Results have shown that prior exposure to the food schedule causes retardation in the development of ABA, but it does not prevent it (Lett et al. 2001).

Within the group of authors that give a crucial role to activity, there are theories that suggest that wheel running is linked to foraging behavior. Animals increase their activity during shortages of food as a natural selection mechanism to search for alternative sources, activity being possibly induced by the intermittency of food occurrence (Epling et al. 1983). The fact that the intensity of wheel running frequently increases in anticipation to food when it is given periodically (Bolles and Moot 1973) suggests that running is maintained by its consequences as it is explicitly operant running or another schedule-induced behavior. It is well documented that ABA animals distribute their running in two peaks around food occurrence, just before and immediately after meal, according to the control exerted by food availability.

## Influencing Factors

There are some factors that are involved in the vulnerability or resistance to ABA. As commented before, prior exposure to the feeding schedule retards the development of ABA. On the contrary, prior exposure to a running wheel facilitates its development. It is known that high ambient temperature prevents the phenomenon. Regarding individual variables, older and heavier rats are more resistant than young and light rats to develop ABA. In the case of sex differences, there are conflicting results, but data seems to point a greater vulnerability to ABA of female rats. Factors that could increase stress, such as social isolation or early maternal separation, contribute to a greater vulnerability; however, environmental isolation (e.g., sound of other animals running) can prevent excessive activity. Early handling experience also reduces the vulnerability to ABA. Some studies have found that ABA can be developed with only 2–4 h of wheel running access per day, mainly those in proximity to next food availability (a phenomenon known as food-anticipatory activity – FAA). Other modulating factors are related to the type of food used (e.g., its dryness or quality).

## Neurobiological Basis

The ABA model has not only been applied for the analysis of environmental and individual variables that influence the phenomenon and/or the study of the functional relationships established between starvation and hyperactivity during its development. In recent decades, it has been used to try to unravel neurobiological and physiological aspects involved, as well as possible vulnerabilities. The ABA protocol allows the control of psychosocial variables that are difficult to isolate in studies of this sort carried out with clinical patients. In these experiments there have been used different strains of rats and mice with specific phenotypic characteristics or genetically modified for a gene that encodes both central and peripheral substances, or receptors, that regulate feeding and/or physical activity. These subjects are

submitted to the ABA conditions (i.e., restricted food delivery and free access to a running wheel) allowing the identification and understanding of the biological substrates and processes that drive behavioral characteristics exhibited along the procedure under tightly controlled conditions.

Research has pointed out the involvement of the gut-brain axis in reduced food consumption and development of overactivity in ABA. Peripheral orexinergic signal of ghrelin gut hormone, that induces appetite, and the circulating level of leptin, as a satiety signal informing about adipose tissue reserves, are detected in the brain level through the brain stem afferences to hypothalamus, considered a central regulator of feeding behavior. These hormones influence two populations of neurons located in the arcuate nucleus (Arc), the effects of which are antagonistic respect feeding behavior. While the orexinergic group of neurons are activated by ghrelin and promote ingestion, proopiomelanocortin (POMC) system neurons are activated by leptin, secreting anorexigenic substances that inhibit food consumption. Both leptin and ghrelin are implicated in the development of excessive physical activity during starvation, while ghrelin has been specifically associated with anticipatory activity developed when food is supplied under fixed interval schedules. An imbalance of these peptides along the progression of ABA, and their interaction with dopamine projections in the mesolimbic reward pathway, could account for the aberrant rewarding properties of food and physical activity and contribute to the development and maintenance of the process (see Adan and Kaye 2011, for a review). Drugs that exert control over dopamine, key neurotransmitter in reward and motivational systems, and regulatory central neurotransmitter serotonin, mainly antidepressants and antipsychotics, also have been profusely investigated as targets of possible pharmacological treatments.

Other structures and pathways that have been studied as associated with the hallmarks of ABA are cortico-striatal neuro-circuitry, hypothalamic-pituitary-adrenal (HPA) axis, other structures in the limbic system, as hippocampus or amygdala, or the endocannabinoid system (Schalla and Stengel 2019).



## Conclusion

Activity-based anorexia is a good animal model of human anorexia nervosa, and the investigation of the behavioral and neurobiological mechanisms involved will help in better understanding the disorder and the development of more efficacious interventions.

## Cross-References

- Adolescence
- Animal Models
- Animal Psychopathology
- Circadian Rhythms
- Classical Conditioning
- Comparative Psychology
- Contingency
- Day/Night Cycle
- Environmental Influences
- Exploratory Behavior
- Foraging
- Hormones and Behavior
- John B. Watson
- Laboratory Research
- Learning
- Light/Dark Cycle
- Neurotransmitters
- Operant Conditioning
- Parsimony
- Polygenic Inheritance
- Positive Reinforcement
- Reinforcement
- Rodentia Diet
- Schedule-Induced Behavior
- Schedules of Reinforcement
- Serotonin
- Sexual Dimorphism
- Thermoregulation

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## Activity-Induced Anorexia

- Activity-Based Anorexia

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## Ad Hoc Sampling

- Anecdote

## Adam Miklosi

Ádám Miklósi

Eötvös Loránd University, Budapest, Hungary

**Ádám Miklósi, PhD**, is a Professor of Ethology at the Eötvös Loránd University in Budapest. He participates in editorial boards of several journals including *Animal Cognition*, *Applied Animal Behavior Science*, and *Frontiers of Psychology*. His interests are in animal cognition with particular focus on communication and social learning. More recently he became interested in animal-robot interaction and started an interdisciplinary new approach called ethorobotics.

### Early Life and Educational Background

Dr. Miklósi was born September 25, 1962, in Budapest, Hungary. Adam grew up in Budapest, the capital city of Hungary, and was determined to become a biologist already by the end of the elementary school. He started undergraduate studies in 1981 following 4 years in a secondary school and 1 year spent at the Hungarian Defense Force in obligatory service. He graduated in 1986 from the Eötvös Loránd University as a biologist

### Professional Career

Adam Miklósi received a fellowship from the Hungarian Academy of Sciences for 3 years during which he started his research carrier at the Laboratory of Behaviour Genetics at Eötvös Loránd University. Subsequently, he became an associate professor at the newly formed Department of Ethology at the same university. He received his PhD in 1995 for studying the learning mechanisms of predator avoidance in the paradise fish. Starting in 1997, he spent 2.5 years in England at Sussex University supported

by a Royal Society Research Grant and a fellowship from the Wellcome Trust (Barth et al. 2005). After returning to Hungary he became reader, and in 2006, he was appointed as a head of department. He defended his thesis and received the degree of “Doctor of Sciences” in 2006 by the Hungarian Academy of Sciences. In 2011 he was promoted to full professor and was elected a corresponding member of Hungarian Academy of Sciences.

In 2003, he received a Frank A. Beach Comparative Psychology Award (best paper of the year) and, in 2010, the Distinguished Scholar Award from the International Association of Human-Animal Interaction Organisations (IAHAIO). For his outstanding contribution to teaching, the Eötvös Loránd University awarded him the Medal for the Scientific Education of Biology Students, and the Juhász-Nagy Pál Prize for assisting in biology student competitions. In 2015, the Hungarian Academy of Sciences honored him with the Prize of the Hungarian Academy for research achievements. He is a member of the Hungarian Biological Society (from 1988) and the Hungarian Ethological Society (from 1991). He is also a member of the board of trustees of the Dogs for Humans charity. This organization facilitates the education of dog handlers and also trains dogs for the disabled.

He participated in several large-scale international research consortiums supported by the European Union. One of these studied the evolution of referential communication, the other investigated possibilities of human-robot interaction from an ethological point of view. From 2008 to 2012, he was chair of an ESF (European Science Foundation) Research Networking Program titled “The Evolution of Social Cognition: Comparisons and integration across a wide range of human and non-human animal species.” This program coordinated the work of 28 different research organizations working in the field of comparative cognition.

As of 2017 he is the author of 166 papers published in scientific peer-reviewed journals, his Hirsch index is 38.

## Research Interests

Miklósi is the co-founder and leader of the *Family Dog Project* (<http://familydogproject.elte.hu>), which aims to study human-dog interaction from an ethological perspective. The process of domestication put dogs into a unique relationship with humans because they gained skills that allow specific behavioral adjustments in the human social environment (Gácsi et al. 2009; Lakatos et al. 2009; Miklósi and Topál 2013; Topál et al. 2009a, b). Miklósi and his collaborators showed that dogs develop specific attachment relationships with their owners, dogs are able to communicate with humans using a range of fine-tuned visual and acoustic signals (Lakatos et al. 2009; Téglás et al. 2012), and dogs are also able to learn via observation and utilize such knowledge for their own benefit. In recent years, he became interested also in the automatization of measuring dog behavior and looking at ways to study the neural and genetic aspects of dog behavior using non-invasive methods (Andics et al. 2014, 2016; Héjjas et al. 2009; Kis et al. 2014).

Miklósi and his team worked out the concept of ethorobotics – an area at the cross road of robotic engineering and ethology – the main goal of which is to build functionally relevant robots that fit in the anthropogenic environment and are able to interact socially with humans similarly as other animal species. He is also studying animal-robot interaction in order to find out what kind of challenges should a robot overcome to become a social partner of animals, and also to use the robot as a stimulus to study the mental representation of the “other” in animals, especially dogs.

Over more than 20 years The *Family Dog Project* published more than 150 scientific papers, and organized several conferences. In 2008 researchers and experts gathered for the first time in Budapest and started the conferences series of Canine Science Forum (<http://csf2008.elte.hu>) to share their results and insights on dogs and their relationship with humans.

In 2014 he published the second edition of an academic volume entitled *Dog Behavior, Evolution and Cognition* by Oxford University Press

that summarizes the most recent status on dog-oriented research (Miklósi 2007).

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## Adaptation

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## Synonyms

Behavioral adaptations; Environment; Evolution;  
Fitness; Physiological adaptations; Structural  
adaptations; Survival

## Definition

Adaptation can be defined as alterations/changes in physiological, behavioral, and structural characters of an individual in response to their environment.

## Introduction

Adaptation consists of Latin words *ad* (“toward”) plus *aptus* (“fit for some role”); any structural, physiological, or behavioral character that increases organism’s survival fitness as well as their reproduction ability in existing environment. In other words, adaptation is the ability of any living organism to survive and reproduce successfully under the existing environment.

Adapted organisms are more fit because they are (1) able to secure food and nutrients; (2) able to obtain air and water; (3) secure spaces in niche; (4) cope with physical conditions such as temperature, light, and heat; (5) defend themselves from their predators; (6) reproduce and rear offspring; and (7) quickly respond to changed environment.

## Historical Background

Up until the middle of eighteenth century, scientists generally believed that various living forms have existed in this universe without undergoing any change and will remain unchanged in future also. Many features of living organisms like the bee’s sting, the vertebrate (an animal with a backbone), and the human brain have been created by a supernatural power to serve their specific purpose. A philosophy known as “theory of special creation or creationism.”

But at end of the eighteenth century, the scientific community started noticing the morphological similarities occur in plants and animals of different periods in earth, existence of many connecting links between species of different periods, increasing complexity of structure in both plants and animals through geological periods, and prompted a new idea that living organisms on earth developed gradually and unevenly from simple to advanced organisms. New species develop due to modifications in preexisting forms. Such modification occurs in any species due to changed environmental conditions, and organisms need to adapt themselves according to its new environment to survive.

## Factors Affecting Adaptation

Most organisms have different dimensions of adaptation and should interact to different aspects of their environments simultaneously. Adaptation involves coping with both physical/abiotic environmental factors (light, dark, temperature, water, and wind) and complex biotic environmental factors (other organisms such as mates, competitors, parasites, predators, and escape tactics of prey). Adaptation mainly occurs due to changes in the environmental conditions, life cycle pattern, or relationship with organisms. All changes in environmental conditions and human activities may cause shifting of organisms in a new niche or in environmental stresses or pressures. In such conditions, those organisms survive successfully that develop suitable characteristics according to the new situation. Organisms that are not suitably

adapted to new environment will either have to move out or die, sometimes result in the disappearance of entire species. This is known as “Natural Selection” (Pianka 2000).

In 1859, Charles Darwin (1809–1882), the great English naturalist, published his famous book *The Origin of Species by Means of Natural Selection*. In this book, Darwin discusses adaptation of organisms as the product of natural selection. Natural selection implies that – when forced to compete for limited resources such as food – those organisms best adapted to their specific environment are most likely to survive, reproduce, and transmit their traits to offspring.

Adaptation and acclimation (acclimatization) are entirely different phenomenon. Adaptation is a phenomenon that occurs in population. The process of developing adaptations occurs over many generations, generally a slow process. Acclimation or acclimatization, on the other hand, generally involves single lifetime or develops instantly and deals with issues that are less threatening. For example, when we move to a higher altitude, respiration and physical exertion will become a problem due to low O<sub>2</sub> pressure. However, after spending a period of time under the high altitude conditions, one may acclimatize to the reduced O<sub>2</sub> pressure (Shukla and Chandel 1996).

## Types of Adaptations

All organisms including plants, animals, and microbes live in different environments like drier, hotter, colder, more acidic, saline, darker, sunnier, etc. Different genetic methods, such as mutation and genetic recombination, are helpful in the survival of these organisms, when any type of modifications/changes occurs in these habitats. These changes pass down to offsprings and become prevalent in the population as an adaptation. The three basic types of adaptations, based on how the genetic changes are expressed, are structural, physiological, and behavioral adaptations. Most organisms have combinations of all these types.

## Structural Adaptations

All adaptations that involve some part of plant/animal, such as the size or shape of the teeth, which is covered by the animal’s body, are known as structural adaptations.

### Type of Teeth

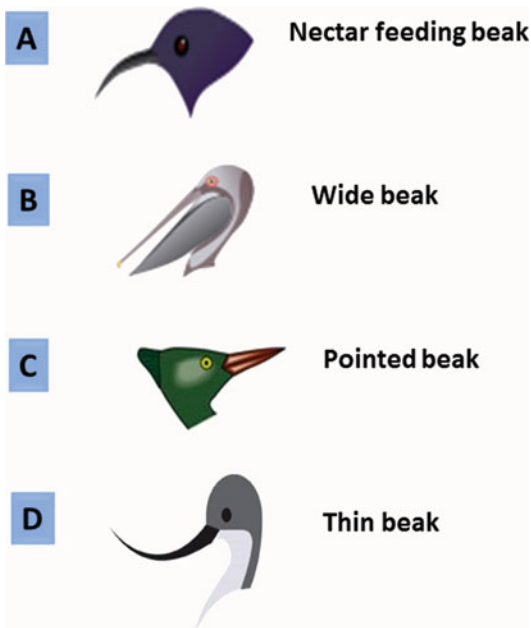
The number, size, shape, and location of teeth and the movement of the jaw differ in mammals according to the type of food they eat. The number and type of teeth also reveal about diet and feeding methods of animals. For example, carnivore (like cougar) has long canines that are used to bite and tear the prey. On other hand, herbivore (like beaver) lacks canines and uses its long incisors to strip bark and gnaw wood.

For example, variations in structural features of bird beaks are an important adaptation which greatly depends on type of the food and how it is obtained. For example, woodpeckers have long, tough, pointed beaks, along with a very robust skull that allows them to hammer holes in trees in search of food. Hooked beaks can be used for biting and stripping (similar to mammal’s incisors), whereas long slender beaks can be used to gather nectar from flowers, as in humming birds. Thin beaks are generally useful for manipulating prey, like caterpillars. Wide beaks are useful for catching flying prey, like mosquitoes. Other variations observed in beaks include serrated edges for holding prey (like fish) (Fig. 1).

### Body Coverings

Hair, scales, spines, and feathers grow from the skin. All of these parts help animals survive in their environments.

For example animals living in a hot dry environment like the chaparral biome manage their internal temperature with large areas of exposed skin with little internal volume such as tails, legs, or ears. The black-tailed jackrabbit has extremely large ears, approximately one third of its body in length. Dozens of small blood vessels present in large ears which expand when the animal is hot, allowing more quantities of blood to flow through the ears and be exposed to the external environment, cooling the blood as it moves. When



**Adaptation, Fig. 1** Types of beaks

external environment is cool, the blood vessels constrict, lessening the amount of blood that passes through the ears. Jackrabbit can very efficiently maintain its internal body temperature with this adaptation (Schmidt-Nielsen 1972). Other desert mammals, such as foxes, rabbits, mice, and rodents, also possess this adaptation (<https://chaparralbiomedexter.weebly.com>).

Another example is an ostrich (animal with a specialized coat) which has no feathers on its head, neck, and legs but a fluffy coat of feathers on its back and abdomen. The lack of feathers allows heat to more efficiently escape and the thick coat of feathers protects the ostrich's back from the sun.

Plants adapt themselves to hot climates in a number of ways. Plants maintain their water levels and minimize water loss mostly through structural adaptations such as small waxy leaves with a thick cuticle, the reduced size allows for less sun exposure, and the waxy layer over a thick cuticle ensures little water escapes through transpiration. Leaves of these plants typically possess few stomata or leaves reduced to spines and stem is the

main photosynthetic organ because the leaves are unable to perform photosynthesis, e.g., *Opuntia*. Many xerophytic plants (desert and arid plants) are adapted to capture and store water. During the rare rains in the desert, they absorb as much of water as possible and store, e.g., *Cacti*, *Opuntia*, *Agaves*, and *Euphorbias* (cactus-like plants). These plants will store water in their stems, leaves, or trunks, known as “succulent” (Fig. 2).

The sand lizard (*Moloch*) and horned toad (*Phrynosoma*) have hygroscopic skin to absorb moisture. Desert animals prevent water loss from their body by different mechanism like making skin impermeable by thickening and hardening as well as through the presence of scales and spines (*Phrynosoma*, *Moloch*), reducing the number of sweat glands in mammals and becoming active at night (nocturnal). Animals like polar bears, penguins, Arctic fox, etc. living in coldest habitats on earth like Antarctica, Arctic, and Alpine regions have thick fur, and layer of fat skin helps in insulation and to keep warm. Also they have well-curved and sharp claws that support them in walking on ice (Fig. 3).

#### Camouflage/Mimicry

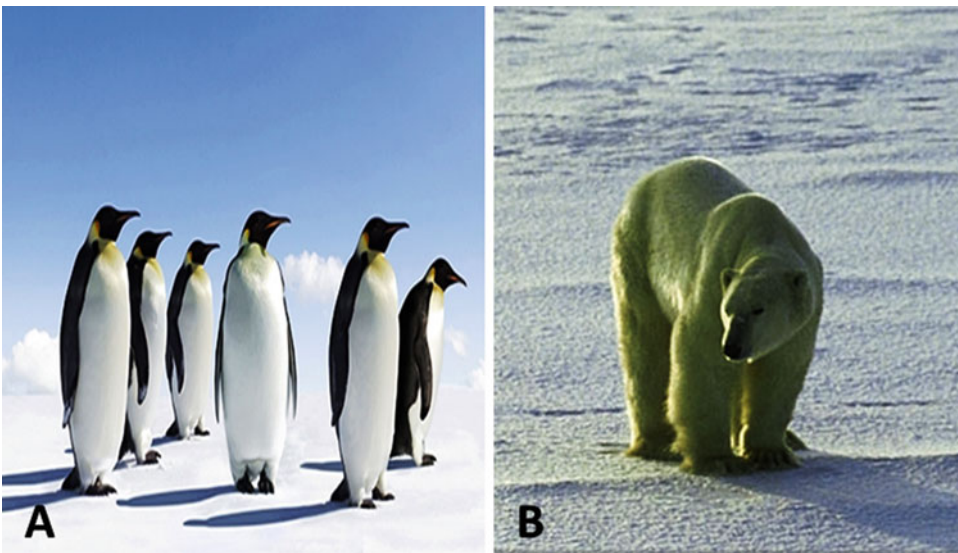
Many animals have the ability to blend with surrounding environment in order to avoid a predator, e.g., scorpion fish and leaf frogs can change their appearance to match their surroundings. Polar bears, penguins, Arctic fox, etc. have snowy white fur to camouflage them and protect from predators. Many forest animals have striped or spotted appearance similar to leaves, and desert animals may be sandy colored. The chameleon has the ability to change its colors according to the color of the surroundings as it has several layers and varieties of chromatophores.

#### Physiological Adaptations

Physiological adaptations are related to changes in the chemistry and metabolism of different organisms and are usually not visible. Animals in the desert like kangaroo rats have very concentrated urine which means little to no water is wasted and the liquids can be reabsorbed back into the body of the animal.



**Adaptation, Fig. 2** Succulent plants (A: *Opuntia* B: *Euphorbia* sp.)

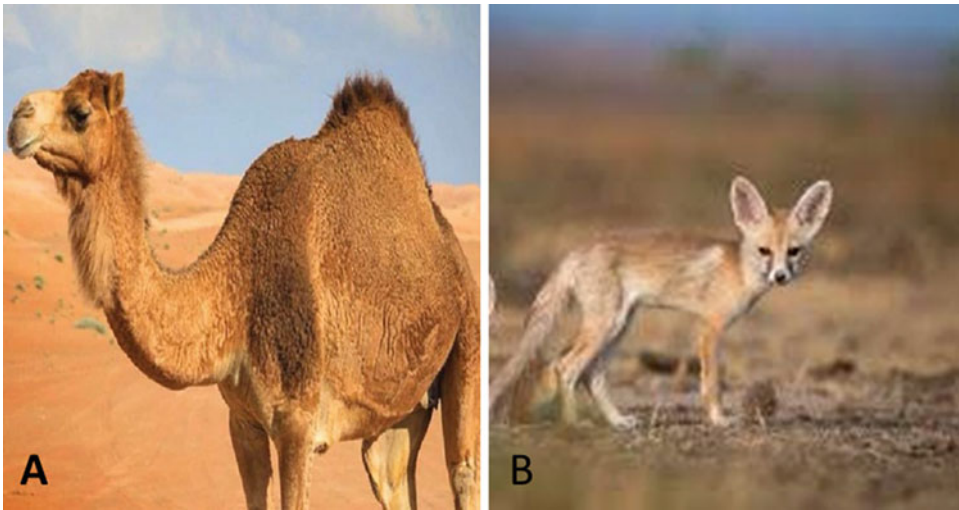


**Adaptation, Fig. 3** Cold habitat animal (A: Emperor penguin B: Polar bear)

Deserts are the dry and hot regions; plants and animals have different adaptations like, they can save water in the form of body fat in structures like hump (e.g., camels) or have short body structure like ear and tails to maintain the body temperature and to reduce water loss (e.g., fox) (Fig. 4). In hot and dry climates, an alternative

pathway, i.e., Crassulacean acid metabolism (CAM) for photosynthesis is operated where water loss is reduced by keeping the stomata closed during the day. During night,  $\text{CO}_2$  absorbed and stored in vacuoles through open stomata and converted to energy by photosynthesis during the day.





A

**Adaptation, Fig. 4** Desert animals (A: Camel B: Fennec fox)

### Behavioral Adaptations

Any adaptation that affects an animal's actions are called behavioral adaptations. These may include what an animal can eat, how they mate, or how they protect themselves.

#### Hibernation

Hibernation is one of the several ways for survival of animals in extreme cold winters. Hibernation involves certain changes in animals such as decrease in body temperature, slow breathing, and reduced metabolic rate. Squirrels, woodchucks, and chipmunks are able to hibernate for up to 12 months. Several other animals that hibernate are bears, bats, skunks, bees, snakes, and groundhogs.

#### Movement/Migration

It is a behavioral adaptation that involves an animal or group of animals moving from one place to another and then back again. Animals move for the following reasons: (a) to get more suitable environment; (b) to get food; (c) to get safe place to mate and raise their offsprings.

#### Nest Parasitism

Some birds like cuckoo prefer to lay their eggs in the nests of other species, who then feed and take care for the cuckoos' orphaned offspring. This feature is known as nest parasitism (<http://www.animalplanet.com/wild-animals>).

### Current Approaches to Adaptation

Charles Darwin was the first to postulate the central role of adaptation in evolution. There is a big gap in our understanding about adaptive traits and their underlying molecular bases. Ronald Fisher was the first to explain this topic theoretically by his "geometric model" of phenotypic change and adaptation (Fisher 1930). According to Fisher, probability of a mutation to be adaptive is nearly 50% for mutations of infinitesimally small effects and approximately zero for mutations of very large effects. Fisher also mentions that minor effect mutations are more likely to be beneficial compared to major effect mutations, but less likely to fix in a population.

Recent models of genetic basis of adaptation are mainly focused on DNA or protein sequence evolution. These studies have provided evidence for a small number of sequence changes occurring during the adaptive evolution of a gene (Gillespie 1991), as well as support for large relative fitness increases after the substitution of a beneficial mutation (Orr 1998). These studies also suggest that major effect mutations may be important to adaptive evolution.

Some researchers make a distinction between current use and the historical origin of adaptive traits. This distinction has led some researchers

(Stephen Jay Gould and Elisabeth Vrba) to suggest a different term “exaptation” to describe traits that were originally intended to perform different functions in an organism. For example, white coat of snowshoe hare helps them to camouflage in the snow and does not provide information about the origin of the species of white fur. It may have evolved for its improved heating properties and only by chance proved to be advantageous as camouflage. Therefore, sometimes the features we treat them as adaptive are really only secondary uses of traits that originally arose for other reasons.

## Conclusion/Summary

Living organisms inhabit in different ecosystems or natural environments which present a variety of biotic and abiotic stresses. (1) Adaptation is an evolutionary process through which a species becomes more fit to live in challenging environments. (2) Every adapted species possess some unique adaptive character that may be structural, behavioral, and physiological or can involve life-history parameters.

Structural adaptations involve some morphological features of an organism (e.g., size or shape of the teeth). Behavioral adaptations affect animal's actions to increase its survival and reproduction fitness (e.g., unique lekking behavior in different morphs of male ruff allows them to increased access to females for mating). Physiological adaptation comprises of the response of a species to a particular stimulus (e.g., many xerophytes has sunken stomata to reduce water loss by transpiration). Adaptive evolution is driven by natural selection and is one of the important processes that explain the diversity of life.

## Cross-References

- [Acclimatization](#)
- [Adaptedness of Behavior](#)

- [Behavioral Adaptations](#)
- [Environmental Influences](#)
- [Fitness](#)
- [Genetic Variation](#)
- [Natural Selection](#)
- [Serotonin](#)
- [Structural Adaptations](#)
- [Survival](#)

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## Adaptation Studies

- [Selection Study](#)

## Adaptations

- [Semi-aquatic](#)

## Adaptedness of Behavior

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### Synonyms

Adaptation; Adaptive behavior; Behavioral accommodation; Behavioral plasticity; Fitness

### Definition

The adaptedness of behavior depends on the effects behavior has on individual fitness, i.e., how it influences survival and reproductive success. This hinges in turn on how well suited to environmental conditions the behaviors are.

### Introduction

Behavior is a major determinant of fitness. It influences foraging success, the ability to avoid predators, success in the competition for resources, and reproductive success. Similarly to other traits, behavior evolves through natural selection; individuals with behaviors that allow them to produce more viable offspring than other individuals pass more copies of their genes onto the next generations, and thereby also the genes for their behaviors, which then increase in frequency in the population.

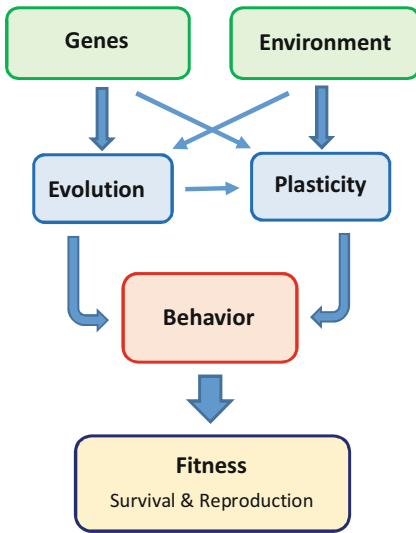
Evolution consequently gradually changes the behavior of individuals so that they become better and better adapted to local environmental conditions; lions have evolved a hunting strategy that is efficient in the catching of prey on the savannah, while their prey have evolved escape strategies that increase their possibility of escape in the same habitat. This dependency on environmental conditions implies that changes in the environment can reduce the adaptive value of behaviors (Candolin and Wong 2012; Wong and

Candolin 2015). For instance, newly hatched sea turtles use the moonlight reflecting off the ocean to find their way from the beach to the sea. However, artificial lighting from roads and cities is currently disorienting the turtles, which, instead of heading toward the sea, are drawn toward the land. Here, dangerous roads take their toll, and land predators, such as foxes, dogs, and birds, further decimate the population, while the hatchlings that escape these hazards may eventually die from dehydration. Thus, the behaviors that have evolved under past, natural conditions are maladaptive in human-altered environments.

The degree to which behaviors are sensitive to changes in the environment, and the extent to which they remain adaptive or not, depends on their plasticity (or robustness) and on the possibility of evolutionary changes. In the following, I will discuss why behaviors are sensitive to environmental conditions, how they can be altered through plastic responses and evolutionary changes to become better suited to prevailing conditions, and why individuals in a population often differ in their behaviors.

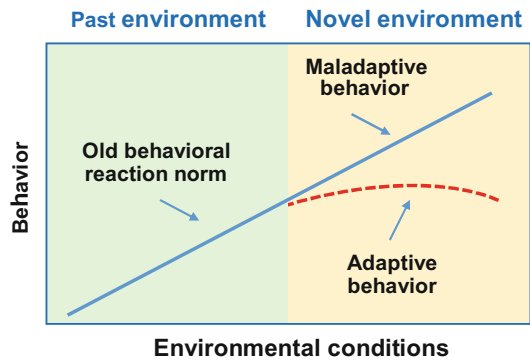
### Dependence on Environmental Conditions

The behavior that an animal adopts in a particular environment depends on its behavioral reaction norm (or response curve), in other words, on the behaviors that a particular genotype expresses across a range of environments (Tuomainen and Candolin 2011; Sih 2013). For instance, the behavioral reaction norm of an animal can induce it to increase its food intake when temperature rises or to spend less time searching for food when it rains. Thus, reaction norms determine how animals adjust their behavior to variation in the environment. The norms have been shaped by past evolutionary processes and have a genetic basis. They can evolve across generations, similarly to other traits, as well as change during the life span through environmental and epigenetic effects, including parental effects (Fig. 1).



**Adaptedness of Behavior, Fig. 1** Behaviors are determined by both genes and the environment. These determine the evolution of behavior and its degree of plasticity, which then influence the survival and reproductive success of individuals and, hence, their fitness

Because behavioral reaction norms have evolved in the past, under the conditions that then prevailed, they can be maladaptive under altered conditions. Thus, species that encounter conditions that they have not encountered in their recent evolutionary past may not have reaction norms suited to the altered conditions (Fig. 2). For instance, many animals have evolved migration strategies that are timed so that reproduction coincides with the peak availability of critical food resources for offspring. However, climate change is currently altering the phenology of food organisms, which is disrupting the timing between arrival at breeding grounds and food availability. An example is the long-distance migratory pied flycatcher (*Ficedula hypoleuca*) that migrates from overwintering sites in Africa to breeding grounds in Europe. The species rely on a short burst of caterpillar availability each spring to feed its young. However, the caterpillars have been emerging earlier as temperature in spring has risen. Because the flycatchers use their endogenous timing mechanisms to determine when to migrate, they have not been able to advance their arrival date to the same extent as spring has advanced at the breeding grounds. This



**Adaptedness of Behavior, Fig. 2** When the environment changes, animals respond to the changes according to their behavioral reaction norms, which have evolved under past environmental conditions. However, these may not be adaptive under the altered conditions but result in maladaptive behaviors. Evolutionary changes of behavioral reaction norms may be needed for individuals to behave adaptively in the new environment

has resulted in a phenological mismatch between the hatching of the nestlings and the availability of caterpillars (Both and Visser 2001).

When animals decide on the behavior to adopt in a given situation or environment, they generally use various cues to evaluate the environmental conditions. For instance, many animals in seasonal habitats use day length as a cue for when to start reproductive activities, such as defending a territory, building a nest, or attracting mates. These cues are usually reliable indicators of current conditions. However, when the environment suddenly changes, either naturally or because of human activities, the cues may become unreliable indicators of environmental conditions. For instance, artificial lighting along beaches does not indicate the position of the sea to newly hatched sea turtles. The earlier evolved behavioral strategy then becomes maladaptive and causes an “evolutionary traps,” with sea turtles orienting toward the artificial light on land. Other examples of evolutionary trap are aquatic insects laying their eggs upon asphalt or glass because these reflect polarized light in the same manner as the water surface and jewel beetles copulating with discarded beer bottles because the surface of the bottles resembles that of females (Robertson et al. 2013).



Maladaptive behaviors in altered environments can cause the decline of populations. In the worst case scenario, this can result in their eventual extinction of the population and perhaps even of the species. A population decline is especially likely when the environmental change is rapid and there is not enough time for evolutionary adaptation. For instance, juvenile African penguins (*Spheniscus demersus*) use cold surface water with high chlorophyll levels as a cue of high fish abundance. However, overfishing by humans has drastically decreased fish stocks in areas where these conditions apply, while climate change has caused remaining fish to move southward. This has resulted in the penguins now selecting feeding areas where forage fish are scarce. They are thus caught in an ecological trap, which is decimating the population (Sherley et al. 2017).

Species that are especially likely to show maladaptive behaviors in changing environments are species from habitats that have been highly stable in the past. These species are usually less plastic and less able to phenotypically adjust to altered conditions. This is because plasticity has not been needed in the past environment and, hence, has not evolved. Similarly, species that encounter novel conditions, which they have not encountered in their recent evolutionary past, may lack reaction norms that are adaptive under the altered conditions. Genetic adaptation and the evolution of behaviors suited to altered conditions are in turn less likely in species with longer generation time, as these may evolve too slowly to keep track with the changes. Small populations may again lack the genetic variation needed to genetically adapt to changing environments.

## Plasticity of Behavior

The degree of behavioral plasticity that an individual expresses depends on its reaction norms for the behaviors, as well as on how these norms have been molded by environmental factors, parental effects, and learning during the life span (Tuomainen and Candolin 2011). Thus, both

genes and experiences during development influence behavioral responses and their plasticity.

Behavioral responses to environmental change can largely be divided into three different forms: (1) The behavioral response may be more or less fixed so that an animal always responds in a particular way to the stimuli, such as attacking a prey when detecting it. (2) The behavioral response may be plastic, and the animal adjusts its behavior to the exact nature of the stimuli, according to its reaction norm. For instance, a predator may adjust its attack behavior to the size or escape ability of the prey. (3) The behavioral response may change during the life span, depending on the conditions that the individual encounters during its lifetime, as well as on its ability to learn new behaviors or improve its skills. For instance, a predator may acquire more advanced hunting skills with age and, hence, attempt to catch prey it would not have aimed at when younger and more inexperienced.

The degree and form of behavioral plasticity are generally adaptive in the natural, undisturbed environment, within the constraints that arise because of other traits (discussed in more detail later). This is because selection across generations has promoted the evolution of behavioral plasticity that maximizes fitness in a particular habitat or context.

## Early Life Experience and Development

Experiences during early development can have persistent effects on behavior into adulthood, through parental effects as well as through direct effects of the environment on the developing individuals. Parental effects arise when the conditions that the parents encounter during their lifetime affect the offspring. This can be through the quality of parental care; the transfer of hormones and nutrients via egg yolk, placenta, and milk; or through transgenerational epigenetic effects that alter the expression of the genes encoding for behavior. Parental effects usually improve offspring fitness and are adaptive. This is because improved offspring fitness increases also the fitness of the parent, which selects for beneficial parental effects. For instance, breeding western bluebirds (*Sialia mexicana*) influence the

aggression and dispersal behavior of their offspring by biasing the birth order of the offspring by sex. When population density increases and the availability of resources declines, females produce more aggressive, dispersive sons. These disperse and colonize new areas where competition for resources is lower and conditions are more favorable (Duckworth et al. 2015).

The conditions that the offspring encounter during development can similarly influence behaviors expressed in later life (Sachser et al. 2013). For example, western black widow spiders (*Latrodectus hesperus*) experiencing poor food conditions during development mature at a smaller size and are more aggressive than well-fed spiders (DiRienzo and Montiglio 2016). These small, aggressive spiders build webs that differ in structure from those of well-fed spider; they are lighter and more efficient in catching prey but less safe. The lower safety implies that poor condition spiders take higher risks in favor of larger food intake. This is probably an adaptive adjustment as the impact of foraging on fitness increases with deteriorating body condition, while the investment into avoiding predators may not improve fitness when body condition endangers survival. Interestingly, if the body condition of the spiders improves in later life, the spiders start building denser and safer webs. However, the webs are still less safe than those of spiders well-fed during development, which indicates that the web-building behavior cannot be fully adjusted to changes in body condition later in life – some degree of maladaptation may still occur.

The influence of environmental conditions on behaviors is often mediated by effects on the development of morphological and physiological characteristics, such as body size or the functioning of the endocrine system. Poor environmental conditions usually result in a small body size, which in turn can impinge on behaviors such as aggression and reproductive behavior. For instance, the larvae diet of dung beetles determines their body size and horn size as adults and, hence, their reproductive tactic. Well-fed males of *Onthophagus acuminatus* develop large horns that they use in the fight for females. Small males, on the other hand, who have experienced

poorer food conditions, develop tiny horns, or no horns at all, and attempt to steal fertilizations by sneaking on pairs of mating beetles (Emlen 1994).

The timing of maturity can influence the mating tactic adopted, as it determines the size of the individual during reproduction. In the coho salmon (*Oncorhynchus kisutch*), males that mature precociously at a small size become “jacks” that sneak on the spawning grounds, while males that mature at an older age when larger become “hooknoses” that fight for females (Gross 1985). A further possibility is that the behavioral tactic adopted changes over the life span of the individual as it grows. In the Azorean rock-pool blenny (*Parablennius parvicornis*), males adopt a sneaking or satellite tactic when small and switch to a nesting, courting tactic when larger (Oliveira et al. 2001). Satellite males are males that are attached to the territory of a nest-holder and help this in defending the territory in exchange for occasional matings.

The adoption of different reproductive tactics is generally adaptive in the natural environment; it maximizes the fitness of individuals that differ in condition and in prerequisites for various fitness-linked behaviors (Gross 1996). However, if conditions change, the adaptedness of the different tactics may change as well.

### Population Characteristics

The density and structure of the population can influence the behavior of the individuals in the population. The impact may be mediated through competition for resources and mates. For example, elks (*Cervus canadensis manitobensis*) adopt a more generalist habitat selection strategy when population density increases; they choose their preferred habitat – mixed forests – less often when density is high, and their home ranges are smaller (van Beest et al. 2016). These changes are likely to be adaptive, as generalist strategies usually yield the greatest fitness return at high densities, while specialist strategies are more favorable when density is low and the competition for preferred resources is weak. Thus elks appear to be able to adaptively alter their habitat choice in response to changes in population density.

Changes in the operational sex ratio (OSR) – the ratio of fertilizable females to sexually active males – can alter the intensity of competition for mates and, hence, mating behavior. For example, male guppies (*Poecilia reticulata*) decrease their courtship activity when the OSR becomes more male biased and fewer females are available to mate with. Instead males start interfering with the courtship behavior of other males, with the aim to disrupt their mating attempts and, in so doing, make the females available as mates. This may increase the mating success of dominant males in relation to subdominant males. Female guppies, in turn, are more selective when more males are available to choose among; they show a stronger preference for colorful males, as the color generally indicates male quality (Jirotkul 1999). Thus, changes in the OSR in guppy populations influence both male-male competition and female choice.

Changes in population size or structure can influence the degree to which individuals help and support each other and, hence, their social behavior. Change in relatedness (kinship) among individuals is particularly likely to influence cooperation. This is because individuals are expected to favor close relatives to gain inclusive fitness benefits; helping relatives with shared genes to reproduce can increase the number of copies of their own genes (or alleles) that are passed on to the next generations. Cooperation is therefore most beneficial among related individuals. If the degree of kinship changes, cooperative behaviors may change as well. For instance, flocks of long-tailed tits (*Aegithalos caudatus*) show more helping behavior during breeding when the flock contains closer related individuals (Napper and Hatchwell 2016).

## Learning

The ability of animals to learn new behaviors, or modify existing ones, can increase the adaptive value of their behavioral repertoire. Learning occurs as a result of an individual's experience and practice. The ability varies among species as well as within species, depending on genetically determined capacities, as well as on environmental and parental effects. Learning requires that the

individual can perceive its behaviors and change them. The changes may occur through habituation to the conditions, such as the presence of humans that pose no predation risk in urban areas or by adopting new behaviors, such as learning to capitalize on the food found in garbage cans.

New behaviors may be adopted through associative learning, such as through trial and error or by imitating other individuals. Young zebra finches (*Taeniopygia guttata*), for instance, learn how to build nests by observing nest building by familiar conspecifics (Guillette et al. 2016). Interestingly, the finches don't learn new skills if observing unfamiliar conspecifics. This indicates that the use of social information depends on familiarity. Such group-dependent learning of new behaviors can promote the cultural transmission of information within a social group.

However, learning is not always adaptive. For instance, the imitation of the behavior of others may not benefit imitators that differ in other characteristics. An individual in poor condition that copies the behavior of an individual in good condition may expend more energy on the behavior than it can afford, or the behavior may expose it to increased risk of predation or attacks from other individuals. Thus, learning is under selection and can evolve as other traits.

## Optimal Behavior: Trade-Offs and Constraints

Trade-offs among behaviors limit plasticity. For example, the need to watch out for predators restricts the rate at which an individual can forage, while the opportunity to mate can reduce vigilance for predators. The optimal balancing of investments among various behaviors depends on their fitness benefits. Because being killed by a predator has a larger impact on fitness than a slight reduction in food intake, animals may forgo foraging opportunities for safety. Similarly, the possibility to reproduce may surpass the benefit of prolonging life by evading predators, particularly in animals with only a few possibilities to mate during their lifetime.

The fitness benefits of behaviors can vary depending on life history stage, body condition, and environmental factors and influence the investment into them. A young animal may invest

in safety rather than in reproduction if more reproductive opportunities are available at an older age when larger and more experienced. An old individual, on the other hand, that nears the end of its life span and, hence, has few future reproductive opportunities, may invest in current reproduction rather than in safety and in extending its life span. For example, male threespine stickleback (*Gasterosteus aculeatus*) takes larger risks toward the end of their single breeding season: they are more likely to engage in conspicuous reproductive activities in the presence of predators and develop more bright nuptial coloration that attracts predators as well as females (Candolin 1998, 2000).

Changes in environmental conditions that alter the costs and benefits of behaviors can similarly influence the investment into them. For example, the hunting of top predators that reduces their abundance decreases predation risk for smaller species. These may then spend less time watching out for predators and instead increase their foraging rate. Such behavioral adjustments are usually adaptive and improve fitness. However, adjustments can be maladaptive when novel environmental conditions are encountered and the behaviors have not been shaped by evolution to suit these. The adaptedness of behavioral adjustments depends on the ability of the animal to perceive the changes as well as to respond adaptively to these. Species may fail to perceive the changes, or they may lack reaction norms for responding adaptively to these. For instance, many species reduce their normal activities when encountering humans, although the humans pose no risk (Frid and Dill 2002). For instance, birds are less likely to establish breeding territories and reproduce in forests where they are disturbed by walking humans (Botsch et al. 2017).

Various constraints may further limit the degree to which behaviors are expressed. For instance, an animal may not be able to increase its foraging rate because of its hunting tactic, long handling time, or slow metabolism. For instance, butterflies that feed on nectar from deep-tubed flowers cannot increase their suction time by developing longer proboscides (elongated mouthparts). This is because the length is constrained by

manipulation times per flower; the longer the proboscis, the more time the butterfly has to spend handling the flower, and this functional cost limits elongation and nectar intake (Bauder et al. 2015). In addition, the perpetual coevolution between interacting species can prevent behaviors from reaching maximal optimality. For instance, predators continually evolve traits that make it more difficult for prey to detect them, while prey evolve counteradaptations that improve their ability to detect the predators, such as improved hearing or smelling. This eternal coevolution may result in neither species behaving completely optimally at any time.

Because of various trade-offs and constraints, most behaviors are not maximally expressed or expressed in the most profitable way. They are instead expected to evolve toward an optimal state under prevailing conditions, considering the various constraints and the trade-offs that limit their expression. Foraging rate, for example, is a compromise among hunger level, body condition, the necessity to avoid predators, and the constraints imposed by morphological and physiological characteristics. Changes in environmental conditions that disrupt the behaviors from their optimal state may require the animals to adjust their behaviors accordingly to maintain their high fitness. If plastic adjustments are not possible, because of various constraints and the lack of adaptive reaction norms, selection for evolutionary alterations in behaviors will strengthen. In the following section, I will discuss the likelihood that animals can evolve better adapted behaviors when phenotypic plasticity is not enough.

## Evolution of Behavior

The evolution of behavior depends on the strength of selection and on the existence of genetic variation in the direction of selection, as well as on the influence of epigenetic effects on the expression of genetic variation. When the environmental change is gradual, as is usually the case during natural changes, animals may gradually adapt their behavior to the new conditions. The evolution may occur through beneficial mutations

spreading in the population, i.e., through selective sweeps, as well as through immigrants bringing new genetic material into the population, i.e., through gene flow. Moreover, hybridization between species can incorporate new genetic material into their gene pools. Such gradual changes are usually adaptive, with natural selection favoring genes and alleles that improve the fitness of individuals. Increased fitness of individual may in turn increase the viability of the population.

Behaviors can change also through random evolutionary changes – genetic drift – particularly in small populations or when a new population is founded by only a few individuals with limited genetic variation (founder effect). Thus, the split of a population into smaller subpopulations because of habitat fragmentation can result in the subpopulations evolving in random directions. For instance, the small and relict population of brown bears in the Italian Apennine Mountains differs in aggressiveness from other bear populations because of random genetic drift. It became separated from other populations by farming and forest burning in Neolithic times and developed reduced aggressiveness through high inbreeding and random fixation of alleles (Benazzo et al. 2017). Such random changes may not necessarily be adaptive. However, populations with maladaptive behaviors are expected to be quickly wiped out. In the case of the Apennine brown bear, the population has survived despite reduced aggressiveness, as the number of competitors has decreased and also because the less aggressive temperament allows coexistence with humans.

When only a few individuals survive to a change in environmental conditions, a population bottleneck occurs that can drastically decrease the amount of genetic variation in behavior. The bottleneck can either increase or decrease the fitness of the population, depending on the stability of the environment after the bottleneck. Bottlenecks can increase population viability by selecting individuals best adapted to current conditions, as only the best fit individuals, with behaviors well suited to the conditions, are expected to survive. On the other hand, bottlenecks can decrease population viability by impeding adaptation to further

changes in the environment, as genetic variation is lost.

In general, the ability of a population to evolve behaviors better suited to altered environmental conditions depends on the rapidity of the change in relation to the generation time of the individuals and on population size and the magnitude and direction of genetic variation. Species with longer generation time, typical for larger top predators, are less likely to adapt their behavior to rapid environmental changes. Small populations, or populations that have not encountered similar conditions in the past, may again lack the genetic variation needed to adapt. In addition, mutations may be too slow to arise to rescue small populations, and immigration of individuals with beneficial alleles may be unlikely if rarer species. When populations are not able to adapt by evolving behaviors better suited to altered conditions, the populations may decline and eventually go extinct (Reed 1999).

When the requirements for evolution are fulfilled, in terms of suitable genetic variation and ample time for evolutionary changes, evolution may still not occur because of various constraints. Trade-offs among traits are particularly common causes of restricted evolution. For instance, a population that has the genetic variation needed to evolve a foraging tactic that reduces predation risk may not evolve the tactic because it would have negative effects on foraging rate. Similarly, various morphological and physiological constraints may limit evolution, such as the evolution of faster escape speed, as this is limited by physiological, energetic, and biomechanical factors. Thus, the evolution of behaviors is constrained by correlations with other traits and by various genotypic and phenotypic limitations.

## Interaction Between Plasticity and Evolution

Phenotypic plasticity – the ability of an individual to alter its characteristics in response to changes in the environment – can influence the evolution of behaviors, by either facilitating or constraining evolutionary changes. Plasticity in behavior can

facilitate evolution by promoting the persistence of a population in a changing environment, as this allows more time for selection to act on heritable variation. Plasticity can also reveal hidden genetic variation that selection can act on and thereby also facilitate evolution. Alternatively, plasticity can constrain evolution by hiding genetic variation.

Whether plasticity reveals or hides genetic variation depends on how it influences the distribution of phenotypes in relation to genotypes in the population. If plasticity results in different genotypes producing the same phenotype, this hides genetic variation, which constrains evolution. On the other hand, if plasticity increases phenotypic differences among genotypes (while maintaining the correlation between phenotype and genotype), this improves the detectability of genetic variation, which can facilitate evolution. An example of behavioral plasticity constraining evolution by hiding genetic variation is the response of the reef fish *Acanthochromis polyacanthus* to elevated CO<sub>2</sub> levels. Chronic exposure of juveniles to high CO<sub>2</sub> reduces their variation in behavioral response to chemical alarm cues of predators (Welch and Munday 2017). This masks genetic variation in antipredator behavior, which reduces its heritability. Reduced heritability decreases in turn the potential of the species to genetically adapt to elevated CO<sub>2</sub> levels. Because the plastic responses are maladaptive – the fish become less responsive to chemical alarm cues – the species may not be able to adaptively adjust to rising CO<sub>2</sub> levels in the ocean, neither through plasticity nor through evolutionary changes.

Behavioral plasticity can influence evolution also by moving the phenotypes in the same or opposite direction to selection, depending on whether plasticity is adaptive or maladaptive. If the phenotypes are moved in the same direction as selection (adaptive plasticity), so that the phenotypes come closer to the optimum phenotype, selection will relax, which constrains evolution. If plasticity is maladaptive and moves the phenotypes further from the optimum, in the opposite direction to selection, selection will strengthen, which can promote evolution. However, whether maladaptive plasticity promotes evolution

depends also on its effects on genetic variation. In the above example with reef fishes responding to elevated CO<sub>2</sub> levels, the maladaptive plastic responses hide genetic variation, which constrains evolution.

Phenotypic plasticity can be lost over evolutionary time through genetic accommodation or assimilation. The phenotype originally produced through plasticity then becomes genetically encoded via natural selection. It is then fixed and can no longer change with environmental conditions. For instance, the production of alternative, diet-induced, larval ecomorphs of spadefoot toads is replaced by the production of only one ecomorph when several species compete for food. When the species occur separately, in allopatry, they produce two ecomorphs: omnivores that eat detritus and carnivores that specialize on shrimp and other tadpoles. When two species are brought together and occur in sympatry and, hence, have to compete for detritus, one of the species loses the plasticity and becomes nearly fixed for producing carnivores only. The loss of plasticity occurs through genetic accommodations, whereby the ecomorph becomes genetically canalized. The loss of plasticity is caused by changes in the regulation of gene expression (Levis et al. 2017).

## Variation Among Individuals

Within a population, there is often large variation among individuals in their behavior. This within-species variation can be adaptive and improve individual fitness or, alternatively, be maladaptive if some individuals are not able to behave adaptively because of various constraints or past experiences or evolutionary processes (the ghost of selection past). The variation in behavior can be genetically determined or the results of phenotypic plasticity or a combination. Most often the variation is a combination of the two, with environmental conditions and intrinsic properties of individuals modifying genetically determined behavioral reaction norms. For instance, during invasions into new areas, individuals at expanding



range edges often differ in their behavior from individuals in the range core: they are often bolder and more exploratory and aggressive. These differences in behavior can have a genetic basis but also be modified by experience. For example, cane toads (*Rhinella marina*) at invasion fronts are bolder and take more risks than toads in range cores. These individual differences have a genetic basis but can be modified by individual experiences of environmental and demographic conditions (Gruber et al. 2017).

Within-population variation in social and reproductive behaviors is often adaptive and promoted by selection. For instance, individual great tits (*Parus major*) follow alternative social strategies depending on their behavioral characteristics. Proactive great tits – which are fast-exploring individuals – form weak associations with a great number of conspecifics and move between foraging flocks, while reactive tits, which are slow-exploring birds, form stronger and more stable relationships with a few conspecifics (Aplin et al. 2013). These social strategies are adaptive and maximize individual fitness as well as the social organization of the population.

Adaptive, alternative reproductive behaviors are common in species where individuals attempt to monopolize mates. Individuals in poor condition, who are not able to acquire mates through the dominant tactic, such as by establishing a territory and courting females, may adopt an alternative mating tactic, such as sneaking. The alternative behavior is then a conditional strategy that improves the fitness of the individual compared to attempting to reproduce through the dominant strategy. Alternative reproductive behaviors can be also genetically determined and have equal fitness that is maintained through frequency-dependent selection. In the lek-breeding ruff (*Philomachus pugnax*), three genetically determined reproductive tactics occur: territorial “independent” males with dark plumage that defend courts on leks, white satellite males that join the territorial males on courts and compete for matings by co-displaying to attract females, and small, female-mimicking faeders that visit the courts of territorial males and attempt rapid

copulations when females solicit matings from displaying males (Jukema and Piersma 2006).

Maladaptive behaviors are especially common when individuals are not adapted to prevailing environmental conditions. In particular, when conditions are changing rapidly because of human activities, some individuals may behave maladaptively because their reaction norms are not suited to the novel conditions. Such individuals will eventually be wiped out from the population. However, if the environment continues to change, the population may never be composed of mostly well-adapted individuals and, hence, never become well adapted to local conditions.

## Conclusion

The behavior that an animal expresses in different situations is a major determinant of its fitness. It influences foraging success, predator avoidance, social interactions, dispersal, and reproductive success. Behaviors are determined by genetically determined reaction norms, which can be influenced by environmental factors, early life experiences, and learning. Behaviors are usually more or less adaptive in the natural environment. However, sudden environmental changes, particularly those induced by human activities, can seriously disrupt their adaptive value. Because behavioral responses are usually the first response to altered environmental conditions, they can have a decisive impact on the success of populations in disturbed environments.

The influence that behavioral responses have on populations in changing environments is an emerging research field. Considering the rate at which humans are altering environments and the fact that biodiversity is seriously declining in many areas of the world, more information is needed on the factors that influence population viability in disturbed environments. Important topics in need of more attention are the degree to which behaviors contribute to the decline or growth of populations and how behaviors can be considered in conservation and management practices to improve population viability.

## Cross-References

- Behavioral Flexibility
- Behavioral Variation
- Heritability of Behavior
- Kin Selection
- Natural Selection

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## Adaptive Behavior

- [Adaptedness of Behavior](#)
- [Plantae](#)

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## Adaptive Diversification

- [Adaptive Radiation](#)

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## Adaptive Memory

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## Synonyms

[Fitness relevance](#); [Mnemonic](#); [Selection pressures](#); [Survival processing](#)

## Definition

A memory advantage for information processed in a fitness-relevant domain (e.g., animacy, mortality salience, mate selection)

## Introduction

The adaptive memory literature describes a memory benefit for information processed for its fitness value. Early iterations of this finding, first reported by Nairne, Thompson, and Pandeirada (2007), showed participants' incidental recall was greatest after they had rated a set of words according to how well they would assist them “find[ing] steady supplies of food and water and protect[ing themselves] from predators” (p. 264). This “survival advantage” has been widely replicated across various laboratories, research designs, tasks, stimuli, languages, age groups, and other manipulations and factors (Kazanas and Altarriba 2015; Schwartz et al. 2014). Following these replications and extended research, Nairne and Pandeirada (2016) proposed a functionalist explanation: a general survival optimization system flexible enough to account for the now, far-reaching literature. They described an ultimate mechanism for this effect, with a highly flexible system of resources humans use to detect and respond to threats and related cues from the environment. This flexibility can account for survival processing advantages observed for scenarios describing various environments, eras, predators, and more. Recently, researchers have begun to explore whether these memory advantages extend to other fitness-relevant domains – described as the field of “adaptive memory” – such as those pertaining to animacy and mortality salience (Altarriba and Kazanas 2019). Additional domains, including contamination, cheater detection, and mate selection, have also been explored for their mnemonic value. Findings from these various domains show some are more strongly linked to memory than others, perhaps the result of more focused attention, increased arousal, and

so on. The noted discrepancies across domains suggest some differences in the processes and mechanisms involved in these tasks, though each reflect the selection pressures theorized to have shaped human evolution, including its cognitive development.

## Animacy

One of these domains of research investigates the relationship between animacy and memory. VanArsdall, Nairne, Pandeirada, and Blunt (2013) tested memory for nonwords presented with either a living property (*dislikes tomatoes*) or a nonliving property (*requiring a key*). Both recognition (Experiment 1) and recall (Experiment 2) were higher for nonwords presented with living properties. Similar designs with children as young as 4 years old show similar results (Aslan and John 2016), suggesting some innate prioritization of living things.

Nairne, VanArsdall, Pandeirada, Cogdill, and LeBreton (2013) then reexamined results originally presented by Rubin and Friendly (1986), asking what lexical characteristics best contribute to memory. Rubin and Friendly had originally reported the significance of imagery, availability, and emotionality, though they had not considered recall attributed to animacy. Nairne et al. (2013) collected new ratings showing animacy may be the strongest predictor of recall. For example, the positive correlation between animacy ratings and recall was twice that of imagery. Next, they tested intentional learning for animate and inanimate words, matching the two word types on nearly a dozen lexical variables. Recall was again higher for the animate words, extending the earlier findings they had reported with nonwords (VanArsdall et al. 2013).

Additional support for this animacy advantage comes from a series of experiments conducted by Bonin, Gelin, and Bugaiska (2014). In their first two experiments, participants categorized words (Experiment 1) or pictures (Experiment 2) as either animate or inanimate. In both experiments, their participants categorized animate stimuli faster than inanimate stimuli. In addition, recall

was higher for animate stimuli. Experiment 3 included a remember-know recognition task, with participants indicating whether they remembered, knew, or guessed when responding. Overall, animate words were recognized faster, with participants also more confident they remembered the animate words. Their final experiment tested whether semantic richness factors into animacy effects. Although the words had been originally matched on imagery ratings, Bonin et al. collected a new set of independent ratings pertaining to sensory experience (e.g., taste, touch, sight). These ratings were equivalent for animate and inanimate words, reducing the likelihood differences in memory are a function of sensory experiences.

Bonin, Gelin, Laroche, Méot, and Bugaiska (2015) investigated additional explanations for these animacy effects, including the role of richness/elaborative encoding and interactive imagery. Two of their experiments showed greater recall with animate words, despite a cognitively demanding categorization task during encoding. The authors replicated the animacy effect again, even with a dual-task procedure. These results suggest animacy advantages are largely independent of cognitive resources, such as attention, and they do not rely on richness or elaborative encoding, unlike the survival advantage (Kroneisen et al. 2013). In one additional experiment, Bonin et al. (2015) asked participants to create interactive situations for animate and inanimate words. Animate words were again more memorable, though the interactive imagery task did not add to this effect. Leding (2018) explored a related hypothesis, testing whether deeper processing underlies animacy effects. In one experiment, participants processed animate and inanimate words either shallowly (*whether each word contained an "e"*) or deeply (*according to its pleasantness*). In both conditions, participants recalled significantly more animate words than inanimate words, reducing the likelihood deeper processing promotes these animacy effects. Perhaps participants do not need any explicit tasks or encoding instructions to attend to animacy.

Recently, Meinhardt, Bell, Buchner, and Röer (2020) have argued otherwise, citing evidence

richness of encoding could be a proximate mechanism of these animacy effects. In their experiments, they showed memory advantages for animate words were mediated by participants' generated ideas for those animate words. Experiments with Nairne et al.'s (2013) word list, along with additional experiments using a new word list, resulted in similar findings: Participants generated a greater number of ideas for animate words than for inanimate words; this was followed by their recalling a significantly greater proportion of animate words. These findings encourage additional research, exploring whether this richness arises automatically or whether it drains cognitive resources, as would be the case with sustained attention (though they note it is not likely due to mental arousal, Meinhardt et al. 2018).

Threat or *perceived threat* appears to be unrelated to these memory advantages. Across a series of experiments, Leding (2019a, b) has shown animacy effects persist even after factoring in the role of threat. After norming a new set of words to compare animacy and threat effects separately, she tested recall of the combined word types: animate (both threatening and nonthreatening) and inanimate (both threatening and nonthreatening). Independent main effects of both animacy and threat – without a significant interaction – strongly suggest threat does not contribute to the animacy effect (see also Leding 2020). Importantly, these findings replicated under both intentional learning and divided attention conditions (Leding 2019a) and with online data collection (Leding 2019b). Findings from the divided attention condition support previous work showing the automaticity of these effects, as animacy processing cannot be too demanding of a task if it persists under these complex conditions (e.g., Bonin et al. 2015).

Gelin and colleagues have examined the generalizability of animacy effects to various encoding instructions (Gelin et al. 2017) and types of contextual information (Gelin et al. 2018). They replicated the animacy effect across scenarios including Nairne et al.'s (2007) survival and moving scenarios, a novel tour guide scenario, and a pleasantness-rating task. These results show reliable recall advantages across four

scenarios and their encoding instructions. Additional experiments found animacy advantages for a word's spatial information (its location on a computer screen) and temporal information (its presentation at the beginning, middle, or end of a list). These results highlight the generalizability of animate word memory to other aspects of the study design.

One set of studies has provided some counter-intuitive results for the animacy literature. Studies with cued recall tasks are not as consistently in favor of animacy advantages, with some even showing *reverse animacy effects*. VanArsdall, Nairne, Pandeirada, and Cogdill (2015) used animate and inanimate Swahili-English word pairs to test animacy effects in paired-associate learning (i.e., learning a second language). Memory for both animals and people was greater than memory for furniture and general objects. Meanwhile, Popp and Serra (2016) found a reverse animacy effect with their word pairs, as their results showed better memory for object-object word pairs, relative to animal-animal word pairs. They replicated this finding in a second experiment, with additional results showing null effects between Swahili-English and English-Swahili animal- and object-based word pairs. Finally, in their last experiment, recall was higher for object-object word pairs than for animal-animal word pairs, as well as for mixed word pair types (animal-object and object-animal). Popp and Serra's (2016) results suggest attentional capture underlies these results with cued recall, as participants' attention is drawn to processing the individual animate words from each pair, rather than encoding both words from the word pair. Notably, a similar argument for attentional capture has been made for other tasks, with Leding (2020) finding lower discriminability for both animate and threatening items during recognition.

Kazanas, Altarriba, and O'Brien (2020) continued this line of research, testing animacy with cued recall following survival, moving, and pleasantness-rating encoding instructions. All participants learned a set of English-Spanish animate and inanimate word pairs. Word pairs were presented visually and auditorily, paired with a black and white image, and were then tested

with sentence-completion, picture-naming, and matching tasks. The authors found reliable reverse animacy effects across all conditions and tasks: In each one, participants' memory for inanimate word pairs was significantly greater than their memory for animate word pairs. Findings across free and cued recall do appear to differ, with researchers surmising the animate word of each word pair pulls attention from the other word, preventing successful paired-associate learning. This is likely to be an automatic feature of animate word processing, as animacy effects tend to replicate in designs with cognitively demanding features and additional tasks (e.g., Bonin et al. 2015; Leding 2018). Thus, future work is needed to better understand the proximate mechanisms underlying the animacy effect, as they do not appear to be elaborative encoding (Bonin et al. 2015) or mental arousal (Popp and Serra 2018), nor can they be attributed to semantic richness (Bonin et al. 2014).

## Mortality Salience

In another aspect of adaptive memory, the mortality salience literature tests whether the notion of death underlies memory advantages like those found following survival processing. Death processing, or mortality salience, involves thinking about one's own death, the circumstances that might bring about death, and the afterlife. Differing from the animacy literature, these findings are a bit more variable, with some finding mortality salience – and the memory benefit from information processed for its mortality salience – could share some of the mechanisms underlying the survival advantage or rely on another set of mechanisms entirely (Hart and Burns 2012).

The “predator” described in Nairne et al.'s (2007) survival scenario represents one of the elements that may heighten a participant's sense of mortality. Soderstrom and McCabe (2011) investigated scenario eras (comparing ancestral and modern survival processing), as well as various predators, for their effect on the survival advantage. They included five conditions in their

study: the standard survival scenario (Nairne et al. 2007), a survival scenario with a zombie predator, a modern (city) survival scenario with attackers, a modern (city) survival scenario with zombies, and a pleasantness-rating control condition. In what was initially described as a controversial finding, recall with the zombie predator scenarios was greater than recall with the predator and attacker scenarios, across both ancestral and modern scenarios. These findings challenged the idea that ancestral priorities underlie the survival advantage, given the low likelihood of encountering a supernatural predator. Similarly, using a demon predator – replacing *predator* with *demon* in the survival scenario – Kazanas and Altarriba (2017) showed participants recalled more words than the standard predator version of the scenario. Wanting to examine the predator's function in enhancing memory, they tested whether more dominant predators, such as a demon, could produce larger memory advantages. Predators were pilot-tested, with demons rated significantly more negative than zombies and other creatures, though they still possess traits consistent with actual, living predators. Despite these differences, the magnitude of the survival advantage, relative to pleasantness ratings, was equivalent across the demon and predator scenarios.

However, these seemingly controversial findings may actually support the general survival optimization system proposed by Nairne and Pandeirada (2016). Zombies and demons could represent *super predators* that activate self-preservation mechanisms and boost recall (Nairne 2014). Presenting a survival scenario describing a super predator may activate a stronger, more automatic response, lending itself to the most focused attention and encoding for later retrieval (Kazanas and Altarriba 2018).

Hart and Burns (2012) considered whether the results described by Soderstrom and McCabe (2011) might be a function of mortality salience, meaning the complexity we attribute to death could motivate various cognitive processes. Thus, considering one's own death will enhance encoding and long-term retention. Hart and Burns (2012) and Burns, Hart, and Kramer (2014a) have investigated this “dying to remember” hypothesis

(Burns and Hart 2014) with a series of related experiments.

In one of these experiments, Hart and Burns (2012) assessed recall following a priming phase, instead of the typical word rating task. Participants were asked to describe their emotions as they considered either their own death or watching television. They also completed the Positive and Negative Affect Schedule (PANAS; Watson et al. 1988), to assess the impact of various mood states on performance. Finally, participants rated a list of words on their pleasantness. Recall for these words was greater following the mortality salience prime than the television prime. Importantly, recall was not mediated by either the PANAS score or pleasantness ratings for the list of words, suggesting a mortality salience effect not influenced by these factors.

Later, Burns et al. (2014a) asked whether there is a functional connection between the survival advantage and the mortality salience effect. The authors created mortality salience and survival scenarios emphasizing participants' need to prepare emotionally, mentally, and physically for their death or survival. The authors found similar recall rates across the survival and mortality salience conditions (both significantly greater than pleasantness ratings), replicating this pattern across three experiments, even after refining the mortality salience scenario to better match the survival scenario, and using a larger, online sample and a new set of words. To test whether self-referential processing was responsible for this memory advantage over pleasantness ratings, they replaced the pleasantness control condition with the television-watching scenario used by Hart and Burns (2012). Recall was again significantly greater in the survival and mortality salience conditions, relative to the control condition. These findings suggest the advantage cannot be attributed to self-reference alone. Additionally, with similar recall rates following these manipulations, they reduced the likelihood these conditions rely on different mechanisms (see also Zhao et al. 2018). In fact, Burns, Hart, Kramer, and Burns (2014b) argue mortality salience and survival advantages both rely on item-specific processing, with some of their recall data indicating

they also rely on relational processing. Their mechanisms may not only overlap, but they also may activate the same cognitive processes.

Other work has suggested different mechanisms underlie survival and mortality salience advantages (Bell et al. 2013; Klein 2012), finding differences in the magnitude of memory advantages across survival and mortality salience processing. In one example, Klein (2012) created similarly worded conditions but found recall from the mortality salience condition did not differ from the pleasantness-rating condition and these recall rates were significantly *lower* than survival processing. Ratings collected from participants indicated they generated significantly more thoughts of planning while engaging in survival processing, relative to mortality processing, suggesting some role of planning in the survival advantage, but not in mortality salience effects. Considering these differences, Klein (2012) concluded survival and death relevance may actually rely on different mental processes and cognitive activities.

Research into mortality salience has been mixed, with some studies finding lower recall rates than survival processing (Bell et al. 2013; Klein 2012) and others finding similar recall between the two scenarios (Burns et al. 2014b). These mixed findings lead researchers to question whether these scenarios promote and rely on different cognitive mechanisms. As some others suggest survival and death processing do not completely overlap, future research should determine the proximate mechanisms they share, as well as those defining them. Future research will also benefit from a new set of normative data, constructed by Alonso, Díez, and Fernandez (2021). Their norms include 750 Spanish concrete nouns, all rated for their relevance to situations described as "avoiding death by protecting from predators and other kinds of harm" (p. 157). Researchers will find these useful when wanting to control for these dimensions; perhaps they might also test for differences in language acquisition, such as advantages in acquiring words pertaining to one's mortality, or specific biases and attention on one's mortality, related to various psychopathology.



## Contamination

Adaptive memory may also extend to scenarios involving contamination, with researchers testing hypotheses grounded in the human Behavioral Immune System (BIS; Schaller 2006): a system coordinating detect-and-avoid processes, such as those protecting humans from various contaminants, pathogens, and more. Previous work has demonstrated meaningful memory advantages for this notion of “contamination processing.” For example, Chapman, Johannes, Poppenk, Moscovitch, and Anderson (2013) showed participants disgusting, fearful, and neutral images, either concurrently with a line-discrimination task or alone. The participants then completed a remember-know recognition task, following a delay of either 10 min, 45 min, or 1 week. Advantages in memory for the disgusting images were observed after just 10 min; these advantages increased over time, with better recognition performance at the longer retention intervals. This was the case across all participants, including those multitasking with the line-discrimination task. Disgusting imagery also slowed reaction time, suggesting these advantages may be the result of disgust narrowing participants’ attention (see also Bell and Buchner 2010). Important to this discussion, disgust appeared to be a more motivating force than did fear, with the researchers wondering if emphasizing specific subcategories of disgust (e.g., food, injuries) might further increase these effects.

Fernandes, Pandeirada, Soares, and Nairne (2017) tested whether the Behavioral Immune System also extends to memory for contaminated items. Their participants read scenarios describing how items had been touched by either sick or healthy individuals. Items were paired with verbal descriptions (e.g., a person with a constant cough) and faces with varying physical appearances. Across these manipulations, participants remembered more items when they had initially appeared with descriptions or faces suggesting a sick person had touched them. They also observed better source memory for those items. Importantly, this effect disappeared when participants were told the actors had applied makeup merely to *appear* sick.

Thus, an imminent threat would engage true survival processing, as their appearance alone did not motivate some disgust or fear mechanism.

Gretz and Huff (2019) noted similar advantages in source memory and item recognition. Their participants viewed videos showing items touched by individuals described as contagious (a person diagnosed with influenza, sneezing in the video), noncontagious (a person diagnosed with cancer), or healthy. Their results showed a specific contamination advantage, with greater memory for those items touched by the contagious individuals. This was particularly the case for those scoring high on the “germ aversion” subscale of the Perceived Vulnerability to Disease scale (PVD; Duncan et al. 2009), suggesting an applied individual differences variable. Gretz and Huff recommend additional research determining the underlying mechanisms of this effect, as they note the specificity of their findings – that touching an item is not enough to engage Behavioral Immune System mechanisms – to items touched by contagious individuals, *only*.

Critically, contamination processing does not always promote memory advantages. One such example was described by Bonin, Thiebaut, Prokop, and Méot (2019a), who also investigated disgust and fear mechanisms for the contamination effect. One of their experiments asked participants to engage in survival processing when the predator was described as a zombie: either disgusting in appearance or presented as an attacker. Recall following survival processing was equivalent across these two scenarios, though both produced superior recall to a pleasantness control condition. These findings suggest previous results by Soderstrom and McCabe (2011), also involving scenarios describing a zombie predator, were not motivated by disgust. These results also suggest contamination, by way of disgust, is not as effective of a mnemonic as others investigated in the adaptive memory literature.

Contamination does appear to motivate memory in most cases, though, presumably once participants reach some threshold for feeling threatened. Bonin, Thiebaut, Witt, and Méot (2019b) recommend researchers present faces to their participants, with faces providing more

critical cues than scenarios describing touched items. Across their numerous studies, memory advantages involving contamination were limited to those specific cases when they presented faces of infected individuals along with the items they had touched. This effect also extended to source memory for the items, as well as the faces. No memory advantages were observed if these scenarios were merely described to participants, without the presented faces. Thus, the faces were particularly helpful in activating participants' Behavioral Immune System responses.

Contamination studies extend the adaptive memory literature via the Behavioral Immune System. This system is hypothesized to provide the various resources needed to enhance information processing for contaminated items and their sources (e.g., Bonin et al. 2019a; Fernandes et al. 2017; Gretz and Huff 2019). These resources are particularly employed when faces are presented to participants, signaling their poor health (Bonin et al. 2019a), and for the more "germ-averse" participants (Gretz and Huff 2019). Future research will be needed to determine whether memory advantages for contamination are a function of disgust or fear (or perhaps both), as these results remain mixed (Bonin et al. 2019b; Chapman et al. 2013).

### Additional Fitness-Relevant Domains

In addition to animacy, mortality salience, and contamination, researchers have tested several other fitness-relevant problems for their mnemonic value, many of which – like contamination – test the memorability of individuals described in scenarios. Early examples of these studies suggested some limitations of the survival advantage, for example, Savine, Scullin, and Roediger (2011) showed memory advantages did not appear to extend to faces, including real or computer-generated faces, or descriptions of those faces (*he is very good at reading maps*), even when the scenarios involved hostile threats. Similarly, Hou and Liu's (2019) participants showed little differences in their memory for faces rated either trustworthy or untrustworthy, though survival

processing generally promoted face memory relative to a non-survival hunting contest.

As a result, researchers began to study more specific domains, rather than test general memory for faces. Cheater detection is one such domain extending the survival processing literature. Buchner, Bell, Mehl, and Musch (2009) assessed source memory for faces, asking whether participants would better remember a face if it was described as trustworthy than if it was described as a cheater. Buchner et al. (2009) randomly combined faces with cheating, neutral, or trustworthy descriptions. Participants had the best memory for faces paired with cheating descriptions, while memory for trustworthy and neutral faces did not differ. In addition, participants later rated the cheaters as less attractive (Experiment 1) and less likeable (Experiments 2–4). This memory advantage also impressively persisted following a 1-week retention interval (Experiment 3). Importantly, Buchner et al. (2009) showed memory for cheaters was not dependent upon the specific nature of the offense or the cheater's social status. Their subsequent work suggests participants' heightened emotional reactions to the described cheating behavior may account for these effects (Bell and Buchner 2011). They further surmised social contract theory explains these findings; ancestral violations of social exchange would have created a significant burden on their small groups. Perhaps, even small cheating offenses – with direct, negative consequences for the victim – would be remembered, and group members would likely limit future interactions with that individual.

Reproduction and individuals' mate value can also drive memory processing. Derringer, Scofield, and Kostic (2017) tested variants of the survival scenario, such as rating adjectives (*happy*; *secretive*) needed to find a mate or detect sexual/emotional infidelity or rating gifts to bring on a romantic date. In some cases, participants' memory supported adaptive memory advantages, with better memory for adjectives helping participants find a mate, relative to evaluating a co-worker. Other comparisons did not significantly differ, for example, participants did not recall more gifts they would bring on a romantic

date, relative to a housewarming party. These mixed results suggest only some of these manipulations tap into fitness-relevant memory benefits.

Mate selection may provide a more fruitful route for further research. Pandeirada, Fernandes, Vasoncelos, and Nairne (2017) asked female participants to assess male faces and descriptions (*is an honest person; is envious*) for their desirability as a long-term mate or co-worker. Somewhat more conclusively than Derringer et al. (2017), they showed better face recognition and source memory following the long-term mate condition, though participants in the long-term co-worker condition recalled more descriptions. They reasoned the faces likely held participants' attention more so than the verbal descriptions, and, it is likely faces are considered more important for mating contexts than working contexts. Results from these related studies suggest some support for mate selection as a fitness-relevant problem with associated memory advantages.

Together, studies from the cheater-detection and mate-selection literatures provide some indication memory advantages extend to other fitness-relevant domains. However, not all issues attributed to fitness/survival carry these benefits. Sandry, Trafimow, Marks, and Rice (2013) conducted a large study comparing memory across participants who engaged in survival processing to those engaged in rating tasks describing incest avoidance, jealousy, status, and more. They replicated the survival advantage, with better memory relative to the pleasantness control condition, but found no significant differences between the remaining conditions and pleasantness ratings. Their mate-selection and cheater-detection scenarios fared similarly, though some of the more recent studies have reported differing results (e.g., Derringer et al. 2017). Sandry et al. suggest participants directly instructed to consider their survival will be the most motivated to encode (and retrieve) the provided materials.

## Conclusions

From a functionalist perspective, survival memory advantages indicate human memory prioritizes the

encoding and retrieval of fitness-relevant information. Researchers recently began to test the mnemonic value of other fitness-relevant domains, such as those pertaining to the more broad "adaptive memory" literature, including animacy, mortality salience, contamination, cheater detection, and mate selection. Each domain has provided promising results, with memory in several cases equating or surpassing that of various control conditions. Importantly, these memory advantages replicate across numerous tasks, including recall and recognition of words and faces, source memory, and more. An important aim for future research will be to discern the various mechanisms explaining these memory advantages, for example, whether they share or differ from those explaining survival memory advantages.

## Cross-References

- [Adaptation](#)
- [Animacy](#)
- [Arousal](#)
- [Attention Bias](#)
- [Cognition](#)
- [Death](#)
- [Evolutionary Psychology](#)
- [Fear Response](#)
- [Functionalism](#)
- [Laboratory Research](#)
- [Planning](#)
- [Predator](#)
- [Predator Defense](#)
- [Predator Detection](#)
- [Recall](#)
- [Survival Processing](#)

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## Adaptive Radiation

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## Synonyms

[Adaptive diversification](#); [Divergent evolution](#); [Evolutionary radiation](#)

## Definition

Adaptive radiation can be defined as a type of evolutionary process in which organisms show diversification in physical and anatomical structure from their ancestral species for better adaptations to the changing environment (Schluter 2000).

## Introduction

According to Charles Darwin's book *Origin of Species*, various processes have played an important role in the evolution of spectacular biological diversity on Earth. Among all, adaptive radiation has been considered as the most crucial factor for maintaining this diversity. It is comprised of two main features: speciation (formation of new

species driven by certain ecological conditions) and phenotypic adaptation resulting in the emergence of an array of new species showing distinct morphological and physiological characters. This phenomenon was first put forward by Darwin during his voyage to the Galápagos Islands (Grant 1999) and relies on the notion of ecological opportunity that is described as an abundance of evolutionarily accessible resources underutilized by competing taxa (Schluter 2000).

### Ecological Opportunity: A Prerequisite for Adaptive Radiation

Ecological opportunity is a necessary phenomenon for adaptive radiation to occur. Simpson (1953) proposed that ecological opportunity could become accessible for organisms in four ways:

- (i) Appearance of new resources: Ecological opportunity can prompt adaptive radiation if new resources appear in the given area. In other words, evolutionary diversification of a clade may prove beneficial for other species. For example, the evolution of grasses presented an opportunity for the primitive species of horses to exploit and evolve under changing environmental conditions.
- (ii) Geographic colonization: Geographic colonization has undoubtedly accounted for the majority of adaptive radiations on remote islands like the Hawaiian archipelago, Galápagos Islands, Caribbean islands, etc. One of the main reasons behind this is the absence of species competing for the available resources on islands which were otherwise present on the mainland. Furthermore, the absence of predators may also permit the use of habitats which were earlier inaccessible, thereby facilitating adaptive diversification.
- (iii) Mass extinctions: Mass extinction events leading to the removal of complete or large proportions of ecologically dominant species support the hypothesis of ecological opportunity. After such events, surviving species are released from competitive and

predatory pressure, and are left with plenty of resources that pave the path for their evolutionary diversification. For example, many clades of birds and placental mammals showed explosive radiation after cretaceous-paleogene mass extinction of the dinosaurs (Erwin 2015).

- (iv) Key innovations: Key innovations can be basically defined as evolution of novel features or traits that provides the capability for species to take advantage of available resources which they could not utilize previously and thus promotes adaptive radiation (Rabosky 2014). Examples of key innovations include the evolution of adhesive toepads in anoles and geckos, evolution of wings in birds and bats, and the evolution of pharyngeal jaws in labrid fishes. All these cases of key innovations have opened new opportunities for evolutionary radiation within the existing environmental milieu (Stroud and Losos 2016).

### Classical Examples of Adaptive Radiation

**Darwin's finches:** Darwin's finches are members of tanager bird family Thraupidae and represent the most symbolic example of adaptive radiation inhabiting the patchy and diverse landscape of Galápagos Island. To date, approximately 15 species of Darwin's finches have been identified. These species arose from a single ancestor that probably migrated to Galápagos from the mainland of South America 3 billion years ago. All such species differ from each other in several aspects of ecology, morphology, and songs (Grant 1999). One of the major difference occurred in the shape and size of finches' beak which are specialized according to the primary source of nutrition available to them. For example, the largest ground finch (*Geospiza magnirostris*) has developed the thickest beak, which allows it to break open the hardest seeds. Likewise, the smallest ground finch (*Geospiza fuliginosa*) has evolved a smaller beak, which allows it to specialize on small seeds and the medium ground finch (*Geospiza fortis*) has a medium-sized beak, which facilitates consumption of intermediary sized seeds (Weiner 1994).

**Caribbean *Anolis* lizards:** *Anolis* lizards are another fascinating example of adaptive radiation. There are about 400 species of *Anolis* which are widely distributed in the West Indies as well as mainland Central and South America. These *Anolis* lizards provide an insight to determine how adaptive radiation varies in mainland and island condition. Divergence of *Anolis* on mainland has essentially been attributed to the process of speciation and is not adaptive to any substantial extent. However, *Anolis* on the islands like Cuba, Jamaica, and Puerto Rico have evolved in such a convergent way that each species can be grouped in one of six “ecomorphs” named as trunk-ground, trunk-crown, grass-bush, crown-giant, twig, and trunk depending upon the microhabitat they colonize (Irschick et al. 1997).

**African cichlids:** Cichlids fishes of east African great lakes also show adaptive radiation. There are around 2,000 species of cichlids inhabiting different lakes such as Lake Tanganyika, Lake Malawi, and Lake Victoria. Each species has distinct morphology in terms of habitat, diet, sexually selected traits, and perform various ecological roles including those of scavengers, predators, and herbivores, etc. For example, *Lethrinops furcifer* commonly resides in sandy area nearby beaches whereas *Hemitilapia oxyrhynchus* lives in shallow vegetated environment in Lake Malawi (Konings 2016).

**Hawaiian honeycreepers:** Hawaiian honeycreepers belonging to the family Fringillidae have specific beaks which are well adapted according to their dietary requirements. For example, lower mandible of *Hemignathus wilsoni* is short and sharp for scraping tree bark while its upper mandible is long and curvy for searching out insects underneath the wood. However, *Telespiza cantans* has evolved a thick beak for eating tough seeds. Presently, 17 species are known to exist in the Hawaiian Islands (Olson 2004).

## Conclusion

Adaptive radiation is a remarkable and complex route for evolutionary divergence and is governed by several different parameters such as ecological, genetical, developmental, geographical, etc.

When coupled with ecological opportunity, adaptive radiation resulted in the burst of new species from preexisting species through a process known as rapid speciation. Ever since the publication of the Darwin’s work, this process has managed to amaze and motivate ecologists as well as the public. However, the exact mechanism by which radiation takes place under diverse environmental backgrounds and why it varies among different taxa are still an area of active research. In this regard, more information related to genes and genomes along with detailed knowledge of natural selection will enhance our understanding of adaptive diversification.

## Cross-References

- [Allopatric Speciation](#)
- [Charles Darwin](#)
- [Competition](#)
- [Divergent Evolution](#)
- [Evolution](#)
- [Extinction in Learning](#)
- [Niche Divergence](#)
- [Paleobiology of Dinosauria](#)
- [Predator](#)
- [Speciation](#)

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## Adaptive Specialization

► Susan D Healy

## Adaptive Superiority

► Inversion Effects

## Addition

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The study of arithmetical reasoning and numerical understanding has been a topic of interest for cognitive, developmental, and comparative psychologists for many decades. Questions of whether mathematical processes are innate and how they develop has led to many studies on children's numerical capabilities, including studies designed to help outline the relationships between understanding quantities and numbers and the arithmetical transformations that can change those representations. One well-studied aspect of arithmetical competence in children is the process of addition (e.g., Carpenter et al. 1982). Addition is defined as the process or skill of calculating the total of two or more numbers or amounts. At a young age, children have already gained a simple understanding of the concept of

“more” and “less” (Brush 1978), and then they learn to count. But, it is not until they get older that they come to appreciate addition, subtraction, and other operations. Studies with infants have produced mixed findings regarding sensitivity to addition operations (e.g., McCrick and Wynn 2004), suggesting that, at best, infants make imprecise judgments by recognizing that a numerical change must take place when an additive or subtractive operation occurs but with no implication of the magnitude or direction change from that operation (Wakeley et al. 2000). The ability of young children to grasp only basic properties of numerical transformations and contradictory results with infants provides incomplete evidence for the idea of innate numerical proficiency. However, studies with nonhuman animals provide additional evidence of an evolutionary basis for humans' adeptness with numbers and the mathematical reasoning that underlies addition.

For example, in one compelling case, Boysen and Berntson (1989) trained a chimpanzee named Sheba to enumerate sets of items, and then label those sets with an Arabic numeral by pointing to the correct numeral. After learning to do this, Sheba could then move to separate locations, see multiple sets of items, and provide the label for the total number of items, presumably by adding the sets together. However, it was not clear whether Sheba did this by adding two represented sets (e.g., 2 plus 2 equals 4) or by “counting-on” from the first set to the second (e.g., “1, 2” and then “3, 4”). In either case, the results clearly showed that Sheba could combine spatially discontinuous sets and label them accordingly. Other work with chimpanzees presented a “summation” test in which chimpanzees could select between two arrays of food items. In the early versions, there were two sets, each of a differing number of items, and chimpanzees were highly successful in choosing the larger set. Subsequent experiments showed that those chimpanzees could combine pairs of sets in separate locations into two choice sets, and then choose the larger combined amount of food from the choice sets after summing the items in each pair (Rumbaugh et al. 1987). This was true even when the single-largest set of items was not part of the summed set that had more total food in it.



Other research showed that nonhuman primates could sum symbols for quantity such as Arabic numerals. Olthof et al. (1997) presented squirrel monkeys with Arabic numerals to choose from, and they gave the monkeys a number of food rewards equal to the selected numeral. After monkeys became good at that test, they presented pairs of numerals to be combined to determine the greatest amount of food that could be obtained, and the monkeys learned to do this, even when the single largest numeral was part of the pair that was less overall (similar to Rumbaugh et al. 1987). In some cases, the squirrel monkeys even performed well when three numerals had to be added together to generate the overall number of food items in that choice set. Thus, monkeys summed the values of Arabic numerals in this test.

Such performances are not limited to nonhuman primates. A parrot named Alex also showed evidence of performing addition when presented with sequential sets of items that he had to label with a verbal Arabic numeral (e.g., Pepperberg 2006). Alex was asked, “How many total X?” before he was shown two sets of items such as jelly beans or nuts. The sets were presented sequentially, so he could never see all items at once. Instead, he had to combine the sets in order to label them properly. He performed well in most cases, also suggesting a parallel to the ability of young children to begin to be able to add sets. This ability to accommodate different arithmetic operations may emerge very early in the lives of animals as well, with newborn chicks showing some capacity for accommodating addition and subtraction operations on sets of items they see move behind an occluder (e.g., Rugani et al. 2009).

The basis for nonhuman animal arithmetic competencies such as those described above comes from their ability to represent quantity, albeit inexactly. Gallistel and Gelman (1992) suggested that a preverbal counting model may account for numerical understanding in the absence of language and that this mechanism is used both by young children and by nonhuman primates. This *accumulator* model, originally developed by Meck and Church (1983), posits that “pulses” are passed, regulated by a gate, with one-for-one correspondence to the objects

or events being counted to an *accumulator* which sums the value and sends it to memory to allow for comparison to other values. Such a mechanism could allow an animal to add sets of items to its representation of the summed total of a set, and some studies have shown that animals seemingly do combine item-by-item serially presented sets into a summed total. For example, Beran (2004) adapted the “summation” test of Rumbaugh et al. (1987) to present chimpanzees with an item-by-item summation task in which each item was added to a nonvisible final set quantity varying in both set size and difference between sets. Chimpanzees were adept at choosing the larger number of summed items in this type of discrimination (also see Hanus and Call 2007). These results offered support for the *accumulator* model, due to a decrease in performance when the difference between sets was small and when overall magnitudes were larger compared to when they were smaller.

Addition by animals also can be approached in other ways, such as by assessing whether nonhuman primates can sum two sets presented in full (rather than one-by-one) on a computer screen. Such approaches are appealing because they can be used comparably across species, and they can control many stimulus features that are confounded with number of items, such as density, total area, and others. For example, Cantlon and Brannon (2007) presented monkeys and college students with trials in which the participants first saw arrays of dots in succession that they had to combine even though they never saw all items at once. Then, they had to choose from two options the array that most closely approximated the sum of the previous arrays. This required them to view two smaller sets, combine them into a representation of the total, and then match that total. Monkeys’ performance closely mirrored that of the human participants, and these results suggested that nonhuman primates are capable of numerical computation in the absence of symbolic representation and that monkeys share similar arithmetic-processing mechanisms with humans.

The study of addition in children and nonhuman animals offers many avenues to answer questions about the development of more

advanced human mathematical abilities. A comparative approach, with nonhuman primates and other animals, also offers potential answers regarding the origins and mechanisms behind arithmetic fluency and the understanding of operations such as addition. A complete understanding of addition, structurally, behaviorally, and developmentally, serves to improve interventions for mathematical education and for aiding those that struggle with learning arithmetic and other mathematical operations.

## Cross-References

- ▶ Alex the parrot
- ▶ Approximate Number System (ANS)
- ▶ Arabic Numerals
- ▶ Counting
- ▶ Duane Rumbaugh
- ▶ Irene M. Pepperberg, PhD
- ▶ Josep Call
- ▶ Michael J. Beran
- ▶ Numerosity
- ▶ Sarah “Sally” Boysen
- ▶ Sarah, Lana, Sherman, and Austin
- ▶ Sue Savage-Rumbaugh
- ▶ William Roberts

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## Additive Genetic Variance

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## Definition

Additive variation is the total effect on a trait stemming from one or more gene loci. Each locus contributes to the trait in a measurable way.

## Introduction

Within a population, there are numerous potential sources of phenotypic variations. Each of these sources signifies a distinctive underlying origin.

These sources of phenotypic variations decide whether that trait has an evolutionary potential and holds an ability to respond to natural/artificial selection or whether it can respond to environmental variations. A large number of investigators across the world are engaged in determining the significance of both the genetic and environmental factors in regulating the phenotypic expression of a particular trait. These types of information will help them in predicting the evolutionary dynamics of a whole population with reference to a particular trait (Waldmann 2001; Fisher et al. 2004; Byers 2008; Saastamoinen 2008).

### Phenotypic Variance

Phenotypic variability ( $V_P$ ) within a population occurs because of two major components which are additive. These are genetic variance ( $V_G$ ) and environmental variance ( $V_E$ ). This relationship is summarized as (Falconer and Mackay 1981; Lynch and Walsh 1998; Byers 2008):

$$V_P = V_G + V_E$$

However, recently with the evolution of epigenetics, the equation is modified as:

$$V_P = V_G + V_E + V_{GE}$$

where  $V_{GE}$  stands for variance associated with the interaction of genetic and environmental factors.

The genetic variance ( $V_G$ ) can be further subdivided into three types, i.e., (1) additive genetic variance, (2) dominance variance, and (3) epistatic variance.

Additive genetic variance occurs due to genes which show an additive effect on the quantitative trait. This results in deviance from the mean phenotype due to inheritance of a particular allele and its relative effect on phenotype. It measures the magnitude to which individual phenotype differences can be prophesied due to additive effects of allelic substitutions.

Dominance genetic variance, on the other hand, is associated with dominant gene actions which cover the influence of the recessive alleles at the particular locus. Epistatic genetic variance

occurs due to statistical interaction among loci, i.e., gene-by-gene interaction. The genetic basis of this variance is epistasis, and it is called the **interaction genetic variance** ( $V_I$ ).

### Heritability

Heritability refers to the proportion of phenotypic variance due to additive genetic variance among individuals. It is often measured as a fraction of the total variance for the trait that is genetic.

The equation can be given as:

$$H = V_G/V_P$$

where **H** stands for heritability.

It should be noted that here H does not define the fraction that is genetically determined but the fraction of the variability that is genetic. It is worth noticing that in the absence of genetic variation (every individual with the same genotype),  $V_G = 0$ , and hence **H** = 0. Contrariwise, if there is no environmental variability (everyone is subjected to same environmental effects), then  $V_E = 0$  or  $V_G = V_P$  and, therefore, **H** = 1. These values are the theoretical parameters for the H. However, for a polygenic trait, H value would lie somewhere between 0 and 1.

For example, if two inbred lines of beans are intercrossed, in the F1, the variance in bean weight is measured as 1.5. The F1 is self-crossed; in the F2, the variance in bean weight comes out to be 6.1. If we have to estimate the broad sense heritability of bean weight in the F2 population, it can be calculated as:

As the variance in F1 is all environmental and variance in F2 is environmental and genetic, therefore:

$$V_E = 1.5, V_P = 6.1; \text{ therefore, } V_G = 6.1 - 1.5 = 4.6.$$

And heritability of bean weight can be calculated as **H** =  $V_G/V_P$ , i.e.,  $4.6/6.1 = 0.754$ .

### Cross-References

- [Dominance](#)
- [Epistasis](#)



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## Adjunctive Behavior

### ► Schedule-Induced Behavior

## Adolescence

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## Synonyms

Juvenile period; Pubescence

## Definition

The stage in human and nonhuman animal development through which a juvenile becomes a reproductively and behaviorally mature adult.

## Introduction

Adolescence is a developmental stage in an animal's life history that is characterized by both reproductive and behavioral maturation. The terms “puberty” and “adolescence” are often used interchangeably as synonyms. However, it is more accurate to consider adolescence as the period in which an animal transitions into an adult that is reproductively, socially, and cognitively mature (Sisk and Foster 2004), encompassing puberty, which more precisely is the process through which an individual becomes reproductively mature. Specialists in this area argue that reproductive (gonadal) development and behavioral development are distinct processes, driven by separate neurobiological mechanisms, that are linked by interactions between gonadal steroid hormones and the nervous system (Sisk and Foster 2004).

Adolescence is a period that is typically associated with marked changes in cognition and social behavior that include a weakened ability to regulate affect and behavior, increased reactivity to stressors, an increase in risk-taking behavior, and a greater social awareness (Crone 2009; Spear 2009; Steinberg 2005). These changes in behavior and cognition could be thought of as forming two distinct categories, primary and secondary. Primary changes contribute directly toward maturation, such as improvements in executive function, and development of sexual behavior. The reorganization of neural circuitry and increase in gonadal steroid hormones required to enact the primary changes lead to temporary secondary changes associated with psychological vulnerability such as increased sensitivity to stressors, increased risk-taking behavior, and weaker regulatory control of behavior and affect (Schulz and Sisk 2016; Steinberg 2005).

Although all vertebrate species undergo a period of transition to become reproductively and behaviorally mature (Ball and Wade 2013), mammalian species, particularly primates and rodents, are the dominant focus in scientific literature on this period of development.

## The Role of Hormones in the Onset of Puberty

In primates and sheep, the hypothalamic-pituitary-gonadal (HPG) axis (comprising the hypothalamus, anterior pituitary, and gonads) is active during prenatal life and infancy, is suppressed during a prepubertal period of development, and then reactivates and matures throughout puberty resulting in reproductive maturation (Delemarre-Van De Waal 2002; Plant 2015; Plant and Zorub 1982). The HPG axis reactivates when gonadotropin-releasing hormone (GnRH) is secreted by the hypothalamus following stimulation by the neuropeptide kisspeptin (Clarke et al. 2015; Irwig et al. 2004). GnRH is released into the blood stream in pulses and stimulates the secretion of two gonadotrophins, luteinizing hormone (LH) and follicle stimulating hormone (FSH), from the anterior pituitary gland. Gonadal development is triggered by this release of LH and FSH, which stimulates ovarian follicles to produce estrogens and progesterone, as well as stimulating the Leydig cells in the testis to produce testosterone.

In contrast to primates and sheep, which experience an extended window of prepubertal development and reactivation of the HPG, spermatogenesis in rats and hamsters begins shortly after birth at days 5 and 9, respectively (van Haaster and de Rooij 1993), and the rise in pubertal hypothalamic activity in rodents is not thought to be part of a reactivation of the HPG axis (Plant 2015).

While puberty is associated with clear physiological markers, adolescence is a period of gradual change, and there are no distinct physiological markers that indicate its beginning and end. In rats, the window within which adolescence occurs is widely considered to be days 28–42 after birth, with adulthood being reached by day 60, while some use a less conservative classification and consider adolescence to occur between days 21 (the typical onset of weaning) to 59 (McCormick and Mathews 2010). Although adolescence in humans is typically thought of as occurring during the teenage years, hormonal and organizational brain changes begin between 9 and

10 years in females and 10 and 12 years in males (Peper and Dahl 2013). The visible signs of puberty typically thought to signal its onset (such as onset of menarche in females, pubic hair growth, and sexually dimorphic physical changes) actually occur toward the final stages of puberty. If we define human adolescence as beginning and ending according to the maturation of the brain, then this period of human development could be considered to begin around the age of 10 and cease in the mid to early 20s (Sisk and Zehr 2005).

## Neurological Development in Adolescence

Steroid hormones have two methods of action in the nervous system: activational or organizational. The activational effect of steroid hormones is temporary and typically associated with the adult response to its presence or absence (Sisk and Zehr 2005). Of most relevance to adolescence is the organizational effect that steroid hormones play in reorganizing the nervous system, which is a permanent change. There is a large body of evidence indicating that neurological development continues throughout adolescence. In both human and nonhuman animals, reorganization of neural circuitry occurs during adolescence, using many of the same processes involved in the original formation of the nervous system, including programmed cell death (apoptosis), neurogenesis, dendritic pruning, and sexual differentiation (Schulz and Sisk 2016). The structural changes associated with this adolescent neural reorganization are sex and brain region specific (Sisk and Zehr 2005).

In addition to reorganization and activation of the neural circuits associated with reproductive behavior, regions of the mammalian brain associated with emotional regulation, behavioral inhibition, and risk/reward judgments are especially impacted by changes in brain structure and function (Steinberg 2005). Areas of the medial and dorsal prefrontal cortex and the ventral prefrontal cortex are integral to cognitive regulation of goal-directed behavior and affective response

(Nelson et al. 2005). Adolescent developmental changes in these areas involve pruning and increased myelination of synaptic networks responsible for social cognition and appear to be driven by gonadal-independent development (Nelson et al. 2005). The regions of the brain associated with affective responses to rewards and punishers include the nucleus accumbens, amygdala, and hypothalamus, and in contrast to those brain regions responsible for cognitive regulation, these regions are heavily imbued with gonadal steroid receptors which moderate considerable reorganization during puberty as a result of gonadal development (Nelson et al. 2005). However, adolescent reorganization of the regions necessary for the expression of reproductive behavior is activated both by gonadal steroid hormones and unknown gonadal steroid-independent mechanisms (Sisk and Foster 2004).

That some aspects of neurological remodeling of the adolescent brain can occur independently of gonadal maturation highlights the fact that reproductive and behavioral maturation are distinct, though entwined, processes (Sisk and Foster 2004). For example, the ability to express reproductive behavior in hamsters is reliant upon both gonadal maturation and steroid-independent adolescent maturation, as copulatory behavior can be artificially triggered by testosterone in castrated hamsters after puberty (Schulz et al. 2004), but not before (Romeo et al. 2002). Indeed, that puberty and adolescence are linked but not the same thing has considerable consequences for long-term behavioral outcomes of hormone-brain interactions when the timing of pubertal and non-pubertal changes during adolescence differ.

The timing of gonadal maturation in mammals can be impacted by a number of extrinsic factors, including calorie intake, calcium levels, extreme exercise, and even the quality of the infant-parent relationship and familial stress (Belsky et al. 2010). A mismatch in the timing of gonadal maturation and adolescent brain reorganization could have considerable effects on individual differences and risk of psychopathologies in adulthood (Sisk and Zehr 2005), and further research on the behavioral outcomes of hormone-brain

interactions during puberty and adolescence is warranted (Sisk and Foster 2004). In human females, early gonadal maturation has been consistently associated with greater risks of clinical depression and eating disorders, in addition to problems with substance use (Golub et al. 2008); however, these results are confounded by problems of study design and are associations, not causation, so may be caused by correlations with unaccounted for confounding variables such as familial stress.

### **Differences in Cognition and Behavior During Adolescence**

Adolescence triggers the emergence of considerable behavioral changes as the juvenile animal develops into the adult. Some of these changes are associated only with the adolescent phase, while others are permanent. Some of the most distinct changes are the emergence of reproductive behavior, agonistic and impulsive behavior and stress reactivity.

In rodents, the emergence of reproductive behavior occurs 1–2 weeks after pubertal testosterone increases in males and 1–2 weeks after vaginal opening in females (Sisk and Zehr 2005). To elicit reproductive behavior, the maturation of the gonadal axis alone isn't enough. Steroid-independent and steroid-dependent organizational changes in the brain are required during adolescence to enable these behaviors to be activated by gonadal steroid hormones and to function without impairment. Indeed, if gonadal hormones are absent during adolescent neurological development, it can cause long-lasting impairments to reproductive behavior (Sisk and Zehr 2005). Examples of typical reproductive behaviors in mammals that are activated by the presence of gonadal hormones after adolescent remodeling include mounting and lordosis (presenting to indicate sexual receptivity). The influence of pubertal gonadal hormones on the reproductive behavior of an animal depends on the species, sex, and timing of exposure.

Development of other adult behavioral patterns, in addition to reproductive behavior, also

relies on the organizational effect of gonadal hormones. A traditional behavioral test for measuring anxiety is the open-field test, in which lower levels of activity are interpreted as reflecting greater levels of anxiety. Adult male rats are typically less active in an open-field test than adult females, and they display less social behavior in novel environments. These differences emerge during puberty and can be prevented by castration and reinstated by replacement of testosterone during puberty. Such findings clearly demonstrate the organizational effect of gonadal hormones on these anxiety-related behaviors (Schulz et al. 2009). Comparatively, gonadal hormones expressed during puberty have also been shown to have a significant organizational impact on the development of spatial cognition via studies of people with naturally occurring disorders of the HPG axis (Sisk and Zehr 2005). Specifically, the lack of gonadal hormone expression during the normative puberty age window leads to impairments in spatial cognition in adults that cannot be repaired by administration of gonadal hormone treatments after the age of 20. Flank rubbing in Syrian hamsters and territorial scent marking in tree shrews during male-male interactions are further examples of behavior that emerges during adolescence due to gonadal hormone-dependent reorganization (Sisk and Zehr 2005).

Adolescent rats show distinct adolescent-phase differences from adults in learning and memory that stem from extensive changes to the neural circuitry that mediate these processes during adolescence (McCormick and Mathews 2010). The regions of the brain that mediate the majority of learning and memory are the medial prefrontal cortex, amygdala, and hippocampus, all of which have dense corticosteroid receptors and are influenced by glucocorticoids. An example of the differences between adolescent and adult rats is the higher thresholds for tolerating aversive motivational learning exhibited by adolescent rats when compared to adults (Pautassi et al. 2008). Differences have also been demonstrated in the responses of adolescent rats to fear conditioning that imply ongoing development of the amygdala and hippocampus (McCormick and Mathews

2010). At least part of these differences in learning and memory in adolescents can be attributed to differences in the experience of stress by adolescents, impacting performance on tasks involving a stress component.

Prepubertal rats exhibit activation in response to anxiogenic drugs in the nucleus accumbens, part of the ventral striatum, while postpubertal rats exhibited activation predominantly in the prefrontal cortex (Lyss et al. 1999). It is therefore not surprising that stress-related behavior in rats differs significantly between adolescents and adults, given the developmental processes occurring in the limbic and prefrontal areas (Spear 2009). Further discussion of differences in stress response of adolescents will be described below in reference to adolescence as a sensitive period of development.

### **Adolescence as a Sensitive Period of Development**

As stated previously, adolescence involves considerable reorganization of the brain's neural circuitry that can occur independently of gonadal reproductive maturation during puberty. Because the organizational effects of gonadal hormones on adult behavior are only possible during the adolescent period of development, adolescence is considered to be a sensitive period for neurological development. However, even if these changes occur at the correct times, the changes themselves are associated with additional psychological vulnerability in adolescents such as increased risk-taking behavior, weaker regulatory control of behavior and affect, and increased sensitivity to stressors (Schulz and Sisk 2016; Steinberg 2005).

Spear (2000) proposed a hypothesis that the organizational changes associated with adolescent neurological remodeling lead to increased stressor reactivity via the hypothalamic-pituitary-adrenal (HPA) axis, which in turn increases the risk of developing psychopathologies in vulnerable individuals. In order to evaluate this hypothesis, it is vital to understand the role of adolescence in

normally developing children, to determine whether changes in stress physiology and emotional reactivity are indeed characteristic of the transition from childhood to adolescence (Spear 2009). A set of seminal experiments published in a special edition of *Developmental Psychology* in 2009 focused on stress reactivity and emotional sensitivity during the transition into adolescence provide just such evidence.

Gunnar et al. (2009) examined 82 children between the ages of 9 and 15 years, recording baseline and stressor levels of salivary cortisol as a marker of HPA activation, pubertal development status, self-reported stress, and cardiac measures of sympathetic and parasympathetic activity (Gunnar et al. 2009). The results of their study indicate clear changes in the activity of the HPA axis as children transition into adolescents, observing developmental increases in cortisol under both baseline and stressor conditions. The increase in basal cortisol observed by Gunnar and colleagues was found to be associated with puberty, as opposed to simply being age-related. Their findings were strikingly similar to those of Stroud et al. (2009), who using similar psychophysiological methods were also able to provide evidence for puberty-related hyperresponsiveness to stressors (Stroud et al. 2009). Differences in baseline cortisol levels due to maturation in adolescents highlight the importance of ascertaining pre-challenge baselines of any measures being used prior to implementing challenges in behavioral tests.

It has been suggested that, in humans, this normative developmental increase in reactivity in the HPA axis and autonomic nervous system could promote a shift toward dysregulation of the stress response in at-risk individuals, leading to the development of clinical psychopathologies such as depression (Spear 2009; Stroud et al. 2009). This hypothesis promotes the consideration of adolescence as a sensitive period in which experiences during this time can have long-term impacts on an individual's behavior and cognition. Evidence for just such an effect can be found in studies using animal models, such as the work of Chaby and colleagues

(Chaby et al. 2013) who tested the impact of chronic unpredictable stress experienced by adolescent rats on their long-term cognitive bias, decision-making, coping response, and exploratory behavior. Their results showed that unpredictable stress experienced during adolescence has lasting effects on cognition and behavior of rats, which exhibited greater sensitivity to reward loss and a negative cognitive bias lasting into adulthood. Such results support the notion that chronic unpredictable stress experienced during adolescence can induce long-term negative affective states, which is likely in turn to impact upon a suite of differences as adults in cognition and executive function inducing biases in decision-making, attention toward negative stimuli, judgment, and memory (e.g. Paul et al. 2005; Shields et al. 2016). Such negative cognitive biases could have adaptive ecological significance, if, for example, an animal inhabits an area with high-predation levels (Chaby et al. 2013); however, for humans and captive/companion animals that live outside of typical ecological niches, these stress-induced alterations could have long-term detrimental impacts on their emotional and behavioral well-being.

## Conclusion

Adolescence is a period of dramatic neurological development that is organized by both gonadal and non-gonadal hormone pathways. This period encompasses puberty, with adolescent changes typically beginning long before physiological signs of puberty are apparent and ending long after reproductive maturity is reached. Significant remodeling of the brain's neural circuitry during this period has both short-term and long-term impacts on behavior and cognition that characterize adolescence as a sensitive period in development. Studies involving adolescent animals should take into account possible normative differences in basal levels for all response variables and consider the potential long-term impacts of testing on individual differences. Furthermore,

attention should be paid to this period of development by pet owners, as chronic stress experienced during adolescence could shape stress reactivity later in life.

## Cross-References

- Endocrine System
- Executive Function
- Hormones and Behavior
- Insect Locomotion
- Life History
- Puberty

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## Adrenalin

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## Synonyms

Epinephrine

## Definition

Adrenalin is a hormone and neurotransmitter which is secreted by the adrenal glands and certain neurons in response to panic, threat, or fear (fight or flight response). Stress is another stimulus for secretion of this hormone.

## Adrenal Glands

The paired glands located superior to each kidney in the retroperitoneal space are called adrenal (suprarenal) glands. The adrenal glands divided into two structurally and functionally distinct regions which are as follows:

- Adrenal cortex, which comprises 89–90% of the gland and located peripherally.
- Adrenal medulla, which is small and centrally located.

A connective tissue capsule covers the gland. The adrenal glands are richly supplied with the blood flow. Steroid hormones are produced by the adrenal cortex which is essential for maintaining electrolyte balance in the body. Complete loss of adrenocortical hormones lead to death due to dehydration and electrolyte imbalance in a few days to week which can be treated only by hormonal therapy. The adrenal medulla produces three catecholamine hormones – norepinephrine

(noradrenaline), epinephrine (adrenalin), and a small amount of dopamine.

## Adrenal Cortex

The adrenal cortex is subdivided into three zones which are as follows:

*Zona glomerulosa*: This outer zone lies deep to the connective tissue capsule and composed of cells which are closely packed and arranged in spherical clusters. These cells secrete hormones called mineralocorticoids because they affect mineral homeostasis.

*Zona fasciculata*: It is the middle zone and widest of the three zones and consists of cells arranged in long and straight columns. Glucocorticoids are mainly secreted by these cells and maintain glucose homeostasis.

*Zona reticularis*: This is the inner zone and consists of cells which are arranged in branching cords and synthesize small amounts of weak androgens having masculinizing effects.

## Adrenal Medulla

This is the inner part of the adrenal gland which is a modified sympathetic ganglion of the autonomic nervous system (ANS). It develops from the same embryonic tissue as all other sympathetic ganglia, but its cells lack axons. The cells of the adrenal medulla which secrete hormones are called as chromaffin cells.

The two major hormones synthesized by the adrenal medulla are epinephrine and norepinephrine (NE), also called as adrenaline and noradrenaline, respectively.

## Physiological Effects

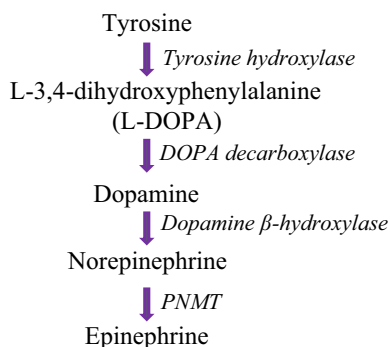
It acts by binding to different adrenergic receptors ( $\alpha_1$ ,  $\alpha_2$ ,  $\beta_1$ ,  $\beta_2$ , and  $\beta_3$ ) of the sympathetic nervous system. Cannon (1931) proposed the idea of involvement of adrenal medulla and sympathetic nervous system in fight, flight, and fright

response. The responses to adrenalin stimulation are as follows:

- Stimulation of  $\alpha$ -adrenergic receptors leads to increased glycogenolysis (Arnal et al. 1986) in the liver and muscle, and glycolysis in muscle.
- Stimulation of  $\beta$ -adrenergic receptors leads to enhanced lipolysis in adipose tissue, adrenocorticotrophic hormone (ACTH) secretion from the pituitary gland, and increased cardiac output.

## Biosynthesis

It is synthesised in the adrenal medulla in an enzymatic pathway shown in Fig. 1. Precursor molecule of adrenalin is tyrosine which further oxidized to L-3, 4-dihydroxyphenylalanine (L-DOPA). Decarboxylation of L-DOPA gives dopamine which is converted to norepinephrine by dopamine  $\beta$ -hydroxylase. The last step is the methylation of the primary amine of norepinephrine, catalyzed by the enzyme phenylethanolamine N-aminotransferase (PNMT). S-adenosylmethionine (SAME) acts as the methyl donor. PNMT is mainly found in the chromaffin cells and in brain, but in very small amounts. In 1953, Coupland suggested that the adrenal cortex secreted a “methylation factor” that influenced the N-methylation of norepinephrine to form epinephrine. In 1959, Kirshner identified the adrenomedullary enzyme, PNMT (phenylethanolamine N-methyltransferase),



**Adrenalin, Fig. 1** The enzymatic pathway for synthesis of epinephrine (adrenalin)



responsible for the synthesis of epinephrine from norepinephrine.

## Regulation

The expression of PNMT is dependent on high concentrations of adrenocortical glucocorticoids (Wurtman and Axelrod 1965) which are released from the adrenal cortex that reach the medulla via an intra-adrenal portal vascular system. In the adrenal medulla, these glucocorticoids regulate PNMT in two ways, transcriptionally and post-translationally, by regulating the stability of the protein (Wong 2003). The levels of PNMT consequently affect the synthesis of adrenalin. In addition, epinephrine biosynthesis is activated by neural stimuli through the splanchnic innervation of the gland.

PNMT expression along with glucocorticoid levels were thought to be an important factor in defining the fate of undifferentiated cells as chromaffin cells but not as neurons. Recently, it has been observed that glucocorticoids receptor-deficient mice develop normal numbers of chromaffin cells, indicating that glucocorticoid signaling is not essential for forming the neuroendocrine phenotype in chromaffin cells and suggesting involvement of other factors (Huber et al. 2002).

Stress is also considered to be another stimulus for production of adrenalin. The main components of the stress system are hypothalamic CRH, as well as locus cereleus-norepinephrine and autonomic systems and their peripheral effectors. Thus, response of the endocrine system to stress is characterized by activation of the HPA axis and the sympathetic adrenomedullary system, which is associated with hypersecretion of adrenal hormones, particularly glucocorticoids and epinephrine (Pervanidou and Chrousos 2007). Production of adrenalin is stimulated by increasing the activity of tyrosine hydroxylase and dopamine  $\beta$ -hydroxylase which are key enzymes involved in catecholamine synthesis.

The reaction of the adrenal gland to stress has been studied in different animal models, using, for example, immobilization stress or cold stress where the release of catecholamines is stimulated

by the splanchnic innervation of the gland (Ehrhart and Bornstein 2008).

In stress conditions, adrenal cortex is stimulated by ACTH to release cortisol which consequently increases the expression of PNMT enzyme in chromaffin cells.

Chromaffin cells also possess nicotinic acetylcholine receptors which bind to acetylcholine resulting in depolarization of the cell and influx of calcium through voltage-gated calcium channels. Increased levels of calcium in the cells trigger the exocytosis of chromaffin granules, hence increasing the level of adrenalin in the bloodstream.

Adrenalin does not exert negative feedback regulation unlike other hormones. Its action is terminated with reuptake into nerve terminal endings, some minute dilution, and metabolism by monoamine oxidase and catechol-*O*-methyl transferase.

## Conclusion

Adrenalin is a key hormone playing role in flight or fight response. When brain senses some danger, adrenalin levels are elevated in bloodstream which is termed as adrenalin rush because its effects are executed very fast and once the danger is gone it may last up to an hour. To combat this hormone rush, “rest and digestive system” has to be activated which allows body to rest. There are medical conditions which results in overproduction of adrenaline such as surreptitious epinephrine administration, pheochromocytoma, and other tumors of the sympathetic ganglia.

## Cross-References

- [Androgens](#)
- [Death](#)
- [Medulla Oblongata](#)
- [Nervous System](#)
- [Phenotype](#)
- [Pituitary Gland](#)
- [Protein](#)

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## Adulthood

- [Insect Locomotion](#)
- [Puberty](#)

## Adventitious Reinforcement

- [Superstition Experiment \(Staddon and Simmelhag 1971\)](#)

## Affect

- [Animal Emotion in Farmed Animal Welfare Assessment](#)

## Afferent and Efferent Impulses

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## Synonyms

[Sensory and motor impulses](#)

## Definition

Neural impulses which travel from sensory organs/receptors to the central nervous system (CNS) are known as afferent impulses, whereas those which travel from the CNS to the organs/glands are known as the efferent impulses.

## Introduction

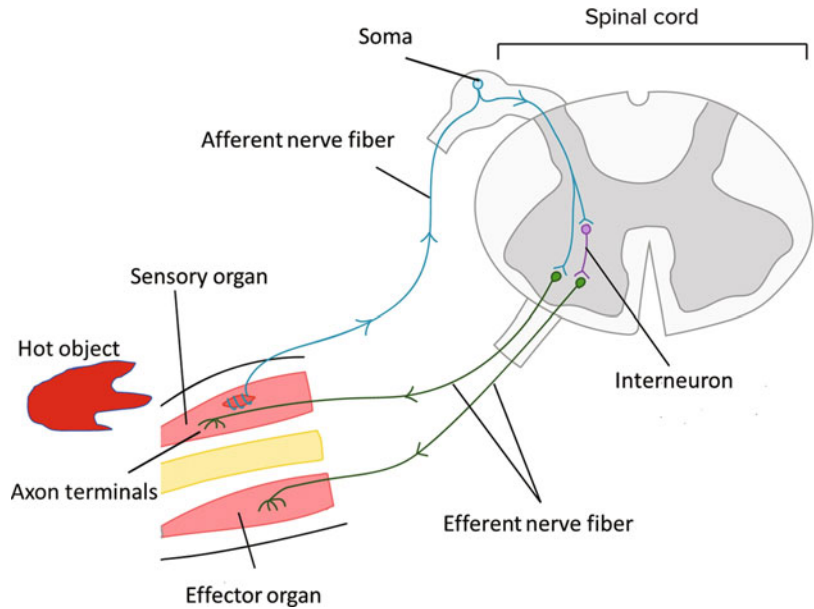
Those nerve cells which help in communication of action potentials (neural impulses) between the central nervous system and other body organs form the part of peripheral nervous system (PNS) (Baars and Gage, 2010). Depending upon the direction of this signal, neural impulses can be divided into two:

- (a) Afferent: neural impulse carries signals from sensory receptors or organs to the brain or spinal cord (CNS) for their further processing/analysis and
- (b) Efferent: neural impulse carries signals from brain or spinal cord (CNS) to the organs (like limbs, muscle, glands, etc.) for displaying proper reaction.

Due to their function, nerve fibers which carry afferent impulses are known as afferent nerves or sensory nerves, and those nerve fibers which carry efferent impulses are known as efferent nerves or

### Afferent and Efferent Impulses, Fig. 1

Afferent and efferent nerve fiber  
(Image adapted from:  
<https://www.khanacademy.org/science/biology/human-biology/neuron-nervous-system/a/overview-of-neuron-structure-and-function>. This image is licensed under a CC BY-SA 4.0 license)



motor nerves. On the other hand, the neurons which connect sensory nerves and motor nerves are known as interneurons or association nerve cells (Fig. 1).

### General Description

Both afferent and efferent terms have been derived from French. Afferent from *ad ferens* (Latin *ad* literally means **to** and verb *ferre* means **bring**) = **bring towards**, and efferent from *ex ferens* (Latin *ex* means **from** and verb *ferre* means **carry**) = **carrying away**.

The PNS gathers information from the environment and directs it towards the CNS; the CNS processes this information and directs it back to the PNS for suitable reaction. For example, when you accidentally touch a hot iron-press, the heat sensation is transmitted by the peripheral nerve to the spinal cord (afferent impulse), upon which spinal cord sends back signals through the nerves to the limb to initiate some motor action like to withdraw your limb or to push away the iron-press (efferent impulse). (Ganong, 2005) In former case, sensory neurons are involved; whereas in

latter case, motor neurons execute the desired actions. The sensory neurons receive a wide variety of stimuli such as taste, smell, light, pain, etc. through different senses and sends these signals upwards through the nerves to reach in the CNS. Hence, these are also known as afferent or ascending pathways. The motor neurons form the efferent or descending pathways as they pass the signals along the nerves to the effector organ, which are primarily the muscles and glands (Fig. 1).

As evident from fig. 1, there is structural difference between afferent and efferent neurons. Afferent impulses are transmitted by pseudo-unipolar nerve cell, that is, it contains a soma with long axon that splits into two branches; one branch runs to the periphery and the other toward the spinal cord. Therefore, no dendrites are present in this case. The soma of efferent neuron is satellite shaped and consists of several shorter dendrites projecting out of it along with a long axon. This axon generally forms a neuromuscular junction with the effectors. (Dharani, 2015) The motor neuron is present in the grey matter of the spinal cord and medulla oblongata and forms an electrochemical pathway to the effector organ or muscle.

Cross-References

- [Action Potentials](#)
- [Axon](#)
- [Nerve Cells](#)
- [Neural Impulse](#)
- [Neuron](#)

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Affiliative Behaviors

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Synonyms

[Affiliative bond](#); [Affiliative interaction](#); [Social behavior](#)

Definitions

|                         |                                                                                                                                                                              |
|-------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Social behavior         | Behavior that occurs among individuals of the same or different species when they interact with each other and usually provides mutual benefits to all individuals involved. |
| Affiliative interaction | Friendly and peaceful interactions exchanged among individuals with the function of developing,                                                                              |

|                  |                                                                                                                              |
|------------------|------------------------------------------------------------------------------------------------------------------------------|
|                  | maintaining, or strengthening social bonds.                                                                                  |
| Affiliative bond | Long-term relationships established among individuals and characterized by high rates of friendly and peaceful interactions. |

Introduction

Animals engage in social activities that can be affected by the simple presence of other individuals around them. In some cases, the presence of others may facilitate positive social interactions – also called affiliative behaviors – but in other cases, may constrain them perhaps by increasing aggressive behaviors. The way that individuals interact affiliatively with others is based on several factors like age, sex, kinship, and ecological conditions. Affiliative behaviors are important in maintaining group cohesion and increasing individual fitness in different animal species. The particular functions of affiliative behaviors vary among species, type of behavior, age, and sex.

Affiliative Behaviors

Through affiliative behaviors, animals can display a wide range of interactions, either intra- or interspecifically. An affiliative behavior is often defined as friendly and peaceful acts exchanged among individuals. Affiliative behaviors occur across a wide variety of taxa, but are particularly common among birds and mammals, and are often found within the category of social interaction. In the order Primates, for example, individuals dedicated less than 10% of their activity budget to social activities (60 primate species from 28 genera), and affiliative behaviors account for more than 80% of all social interactions (Sussman et al. 2005). The types of affiliative behaviors vary between species. For example, in mammals, affiliative behaviors are classified as grooming (either cleaning skin and hair among individuals or engaging in gestures related to cleaning); spatial proximity (referring to the

distance among individuals); approaching (individual approaches to one or more other individuals); social play (two or more individuals exchange in a suite of behaviors that may be practiced for more costly behaviors such as mating, fighting, or fleeing for a certain period of time); touching (any body part of individuals are in contact briefly); hugging (individual places its arms around the body of the receiver); and food sharing (transfer of food among individuals). Other taxon-specific affiliative behaviors in mammals are exhibited like synchronous swimming and contact behaviors in dolphins (Clegg et al. 2017) or greet (sniff or touch noses) and head on neck or back (head resting on the neck or back of other animals) in the wild ass (Asa et al. 2012). Birds also interact affiliatively to each other through allopreening behaviors that correspond to allogrooming (mutual grooming) in mammals and consist of involved individuals cleaning body parts that cannot be cleaned by self-preening. Other affiliative behaviors that have been reported for birds are sitting within reaching distance, social play, and invite preening (Braun et al. 2012).

The study of affiliative behaviors allows determining the degree of affiliation, affiliative relationship, sociality index, and the establishment of social bonds among members of the group (see affiliative bond). Before estimating any measure of affiliation between individuals, it is necessary to collect behavioral data from the studied animal. Martin and Bateson (2007) provide different recording methods that can be used in the study of affiliative behaviors like ad libitum sampling, focal animal sampling, and scan sampling. Affiliative behaviors can be recorded as the duration or frequency that individuals were in contact, huddling, grooming, or engaged in any other affiliative behavior.

## Factors That Influence Affiliative Behaviors

The expression of affiliative behaviors among individuals depends on several factors such as

biological (age, sex), social (hierarchical rank, kinship), hormonal, and ecological conditions. It is hypothesized that individuals may interact affiliatively with other individuals of similar age-sex class such as immature with immatures, female with females, and male with males. In some species, females are more likely to engage in affiliative behaviors to form alliances and gain support during harassment (such as by high-ranking individuals) and during competition or infant care (Connor et al. 2006). In species with female-biased dispersal, males exchange affiliative behaviors (e.g., approach, embrace, arm wrap, and groom) with one another more than with females. Males form strong bonds with one another through affiliative behaviors for inter-community territorial display, boundary patrols, and raids into the neighboring territory to defend or gain access to females (Slater et al. 2009).

On the other hand, members of different age-sex classes can engage in affiliative behaviors. For example, in primates, adult males interact affiliatively with younger individuals maybe to reduce physiological stress (Bardi et al. 2017), to increase mating opportunities (developing affiliative relations with females), or to enhance greater spatial centrality in the group and, consequently, enhance predator protection (Gould 1997). However, immatures can benefit from affiliation with adult males to enhance predator detection, alloparental care, and opportunities to develop social skills (Gould 1997). Females and males can also engage in affiliative behaviors as seen in birds; males engaged more in allopreening behavior with females than with other males. Allopreening between females and males has been associated with strengthening and maintenance of pair bonds between breeding partners as well as with parental cooperation over offspring care (Kenny et al. 2017).

Social aspects such as hierarchical rank also influence affiliative behaviors among individuals. In species characterized by a dominance hierarchy, individuals of the same dominance rank tend to engage more in affiliative behaviors compared to individuals of differing ranks. For

instance, high-ranking individuals are more often in proximity and engage more in grooming between each other than low-ranking individuals. However, this pattern is not always consistent since some subordinates tend to interact affiliatively with high-ranking individuals presumably to obtain benefits like gaining access to food resources that are monopolized and support in agonistic interactions (Seyfarth and Cheney 2012; Smith et al. 2007). In hyenas, the social rank of males and females influences the association between them. Both high- and middle-ranking males associated most closely with high-ranking females (Szykman et al. 2001).

Genetic relatedness between group members is also a critical parameter that influences affiliative behavior. Kin-directed affiliative behavior is prevalent in social animals, and kin selection theory suggests that individuals enhance inclusive fitness benefits by biasing affiliative behavior toward relatives (Hamilton 1964). In particular, animals with high genetic relatedness engage affiliative behaviors more frequently than those with less genetic relatedness or nonrelatives (Smith 2014). The effect of kinship has been studied in birds in which preening bouts toward siblings are more frequent and of longer duration than toward non-siblings (Ju and Lee 2016). In species with female philopatry (an organism remains in its birthplace), like baboons, ground squirrels, and elephants, affiliative behaviors predominate between females compared to males (Lawson Handley and Perrin 2007). The establishment of social bonds with kin females, through affiliative behaviors, can reduce levels of aggression among them, increase levels of care for dependent young, decrease the cost of maternal investment, and reduce the risk of infanticide or predation (Silk 2007). In species with male philopatry (e.g., chimpanzees and dolphins), affiliative behaviors predominate among males compared to females, allowing them to increase access to territory and opportunities of mating (Lawson Handley and Perrin 2007).

Kin selection also provides an explanation of cooperative breeding and associated affiliative

behaviors between relatives. Cooperative breeding is widely recognized in social insects, birds, mammals, and fish. Under the cooperative breeding context, helper individuals preferentially provide care to close kin enhancing the fitness of all individuals involved. These actions that benefit other individuals, like helping behaviors toward others, sharing resources, and cooperating, are called prosocial behaviors. The prosocial behavioral repertoire is diverse, involving various forms of affiliative behaviors, and it can be seen across different animal species (Dugatkin 2013; Rault 2019). Kin selection theory explains prosocial behavior toward kin. Additional examples of this behavior between relatives involve self-sacrifice by parents to benefit their offspring or help close kin. However, prosocial behavior cannot be explained entirely by kinship because several animals that are not genetic relatives cooperate with each other in many contexts. For example, vampire bats share part of their blood meal to hungry conspecific, or female elephants help raise the offspring of other group mates (Dugatkin 2013). Reciprocal altruism theory (Trivers 1971) explains why an individual tends to behave cooperatively with nonkin. This theory suggests that individuals who cooperate and help others would increase the possibility of being helped in return.

Hormone levels are also important for affiliative behaviors. Oxytocin and vasopressin (vasotocin for nonmammalian vertebrates) are two neuropeptide hormones that modulate affiliative behaviors across vertebrate taxa. For instance, the hormone oxytocin promotes affiliative behaviors important in the formation and maintenance of cooperation, social bonds, and group cohesion (De Dreu 2012). Thus, individuals exposed to oxytocin increase food sharing and allogrooming in vampire bats (Carter and Wilkinson 2015) and social play in domestic dogs (Romero et al. 2015). Vasotocin is a hormone found in nonmammalian vertebrates, and it is a homologue of vasopressin in mammals. The hormone vasotocin plays an important role in the social development in birds. Chicks exposed to



this hormone increase affiliative interest (e.g., proximity, vocal communication, and contact behaviors) in parents through development, and males increase time spent in proximity with opposite sex conspecifics as they mature (Baran et al. 2016).

The ecological conditions in which individuals live impact the quantity and quality of the affiliative behaviors. In particular, habitat quality, space availability, food availability, resource distribution, or risks influence this behavior. For example, in poor-quality habitats with low food availability, individuals decrease affiliative behaviors like social play as an energy-saving strategy or due to a constrained activity budget under this condition (Nunes et al. 1999; Stone 2008). Similarly, grooming has been linked to variations in food availability; individuals groom more when food resources are abundant but diminish when food is limited (Defler 1995). Under space reduction of crowding conditions, some animal species adopt a conflict-avoidance strategy. This strategy consists of minimizing affiliative behaviors (e.g., social play and grooming) to decrease social interactions and the possibility for conflict due to forced proximity among individuals and limited escape opportunities (Judge 2000). On the other hand, there are cases in which animals increase affiliative behaviors (e.g., grooming) as a tension-reduction strategy. This strategy is used as a way to mitigate increased tension and reduce the likelihood of aggression when spatial density increases (Judge 2000). Finally, the risk that faces individuals in their habitats also regulates affiliative behaviors. For instance, animals engage in grooming under a situation of lower predation risk (Cords 1995) or decrease play in risky habitats in terms of injuries for individuals (Berger 1980).

## The Benefits of Affiliative Behaviors

Animals engage in affiliative behaviors because these provide them with several benefits. The benefits vary as a function of the type of affiliative

behavior that individuals perform as well as in function of the species, sex, and age of the partners. For example, grooming serves to remove dirt, flakes of dry skin, and parasites. Furthermore, grooming may help to establish and maintain affiliative relationships between individuals, which serve to protect them against competition with other group members. Additionally, individuals can use grooming as a currency to have access to resources or tolerance at feeding sites, reduce tension, or restore relationships after conflicts (Clutton-Brock 2016).

Social play is an important affiliative behavior in the development of young individuals. Through playing, individuals can acquire short-term and long-term motor and social benefits needed in adult life (Palagi 2018). Regarding social benefits, immatures, by playing, can acquire social skills like the ability to manage interactions with conspecifics, build social relationships, enlarge their social networks, and strengthen social bonds (Palagi 2018). In many species of animals, play continues in adulthood. Adults can use play in solving or preventing disputes, anticipating and buffering periods of social tension between unfamiliar partners, and increasing social tolerance (Palagi 2018).

Food sharing is considered affiliative behavior and is widespread in animals, including insects, birds, cetaceans, vampire bats, and primates. Some examples of food sharing include blood donations in vampire bats, sharing of meat and plant material in chimpanzees, and sharing food between adult lion tamarins, young ravens, and juvenile jackdaws. Food sharing is an important behavior because it helps to increase foraging efficiency, reduce predation risk or individuals may exchange food for grooming or support in a dominance conflict, and maintain coalitions (Stevens and Gilby 2004).

Coalitions between individuals are important in the establishment of communal signaling. Communal signaling is a form of communication in which males and females collaborate to produce visual and acoustic displays. In birds, females and males form coalitions that help to

establish communal signaling between them, which is important to defend home ranges, foraging territories, as well as positions in partnership of groups (Tobias et al. 2016).

## Conclusion

Affiliative behavior is present across a multitude of animal taxa. In general, affiliative behaviors in various forms provide several social benefits to manipulate situations, including formation of bonds that increase individual fitness. These kinds of social behaviors exist between relatives, mates, and nonrelatives and even among different species. Affiliative behaviors play an important role in the formation of bonds and alliances among individuals, favoring social integration, and are essential for maintaining complex social systems.

## Cross-References

- [Affiliative Bond](#)
- [Agonistic Behavior](#)
- [Allogrooming](#)
- [Alloparental Care](#)
- [Dominance Hierarchy](#)
- [Grooming](#)
- [Kinship](#)
- [Philopatry](#)
- [Play](#)
- [Pro-social Behavior](#)

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## Affiliative Bond

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## Synonyms

[Affiliative relationships](#); [Pair-bonding](#); [Social bonds](#); [Social bonding](#)

## Definition

Long-term relationships of individuals, characterized by a high degree of proximity and high rates of friendly interactions, are termed affiliative or social “bonds.” The process by which such relationships are established and maintained is termed “social bonding.”

## Adaptive Significance

Evolutionarily, the oldest bond is probably that between mother and offspring, and emerged when postnatal maternal care became crucial for offspring survival. Mother-infant bonds are particularly important in species where offspring's dependence on the mother is a prolonged and energetically costly process, as in some birds and especially in mammals. In the latter, bonds between the mother and infant emerge during the earliest stages of ontogenetic development to facilitate nursing, and often, as in humans, extend well beyond the lactation period to ensure offspring's survival into reproductive age. In animals where successful rearing of the offspring depends on the investment of both sexes, as commonly seen in many bird species and some mammals, social bonds (termed “pair-bonds”) develop between a male and a female. Ensuring paternity, the need of joint provisioning of the offspring,

coordinated territorial defense, or protection of offspring against infanticidal males (i.e., males that kill other males' offspring) may ultimately be the reasons why males form long-lasting dyadic relationships with females in these animals.

Stable and long-lasting affiliative relationships also occur beyond reproductive units and are often forged between members of the same sex. Human social bonds are an example of such relationships, which are believed to be the basis of human hyper-cooperative nature most likely responsible for the biological success of our species. However, bonded relationships outside the context of reproduction also characterize other animals living in complex societies, such as dolphins, elephants, or nonhuman primates (hereafter: primates) (reviewed in Seyfarth and Cheney 2012). In primates, for example, groups consist of a relatively stable number of individuals, who rarely migrate. This allows group members to develop complex relationships with each other through frequent and repeated interactions. These interactions can be agonistic, generating dominance relationships, or affiliative resulting in bonded relationships. Both types of relationships serve primarily to cope with challenges associated with group living. In primates, an animal's behavior toward another individual often depends on the relationship of that individual with third parties, making the process of bond formation in these animals particularly intricate.

The adaptive benefits of social bonds in group-living animals have been explored to a considerable extent in baboons. In these primates, females remain in their natal group upon reaching sexual maturity and associate closely with related females mainly (e.g., with daughters and sisters) forming matriline. Interactions within and between matriline are influenced by clear dominance relationships, with lower ranking females being aggressed or displaced by more powerful females more often than vice versa. Female baboons form strong and durable bonds with few other females. It has been shown that females that form such relationships are characterized by increased longevity and offspring survival (Silk et al. 2010). This is likely because social bonds in

baboons mitigate the costs of group living in a species with a high degree of agonistic interactions between conspecifics. For example, by enhancing prospect of gaining coalition partners or tolerance from other individuals, affiliative bonds may provide protection from social conflict, or reduce stress associated with it, ultimately leading to higher longevity or offspring survival (Silk et al. 2010). These benefits of social bonds identified in baboons parallel those found in humans, where social support is positively associated with wellbeing, while social isolation is linked to impaired mental health and mortality. Studies on baboons reveal, therefore, that human social bonding is deeply rooted in the evolutionary past.

In some male-philopatric species, competition between males for social status and the associated reproductive benefits seem to be the main drivers for establishing male-male social bonds. In chimpanzees, for example, long-lasting bonded relationships between males are crucial for achieving and maintaining social status, which in turn is vital for gaining sexual access to fertile females (Muller and Mitani 2005). In contrast to female baboons, male chimpanzees often form durable bonds with unrelated group members. As in male chimpanzees, long-lasting social bonds found in dolphins also facilitate coalition formation between males to gain sexual access to females (reviewed in Seyfarth and Cheney 2012). Social bonds thus substantially contribute to reproductive success in group-living animals, by providing a supportive environment and/or by enhancing competitive potential of individuals forming them.

## Proximate Mechanisms

Social bonds have a strong physiological component, with endocrine system playing an especially important role in mediating them. Hormones, such as vasopressin, and neurotransmitters, such as endorphin, have been linked to mammalian social bonding. However, the neuropeptide oxytocin has received most scientific attention in this respect (reviewed in Crockford et al. 2014).

Oxytocin, which is produced in hypothalamus and released by the posterior pituitary into the blood, plays a vital role in stimulating birth and lactation. Facilitating nursing is an important function of mother-offspring bonds. There is hence no coincidence that a hormone involved in lactation also plays a crucial role in mediating mother-infant social bonds. Oxytocin released into the blood at birth, for example, facilitates olfactory infant recognition and triggers the onset of maternal care. Studies on several mammal species showed that infusion of this hormone facilitates, while blockage hampers, maternal behavior. This evolutionary ancient role of oxytocin in mediating mother-infant bonds was extended to facilitating other types of bonds in mammals. Most notably, oxytocin plays a pivotal role in social bonding between a male and a female. In mammals that form long-term male-female bonds, such as prairie voles or humans, the production of this hormone can be triggered by sexual intercourse or tactile contact and increases tolerance and rates of affiliative behavior between the two sexes. Importantly, oxytocin mediates social bonds between non-kin in group-living animals – evolutionarily the most recent type of bonds. In humans, for example, the administration of this hormone increases trust toward strangers. In chimpanzees, its production is elevated after grooming with a bonded partner or during between-group conflict to facilitate within-group affiliation – a pattern also observed in humans (Samuni et al. 2017). Thus, the effect of this hormone on social bonding extends well beyond reproductive units.

Oxytocin release has a number of socio-positive psychological effects, including increased social attention, social recognition, and social memory. Oxytocin also reduces social anxiety and stress. All these effects facilitate social interactions and, in turn, bond formation with conspecifics. Oxytocin receptors are found in reward centers in the brain, suggesting that this hormone reinforces affiliative interactions by facilitating their occurrence in the future.

Social experience during early development, such as attachment style with the mother, has important consequences for social bonding (reviewed in Crockford et al. 2014). For example,

in humans and macaques mothering styles are impaired, showing abusiveness or overprotection, if the mother experienced early separation during development, and in vervet monkeys mothering styles of mothers and daughters are correlated. In both human and nonhuman primates, individuals that experienced trauma during early development have impaired social functioning as adults. There is evidence that early social experience affects the development of oxytocin-related physiological mechanisms, pointing again on the pivotal role of this hormone in social bonding.

## Bond Maintenance

This complex proximate machinery regulates the formation and maintenance of social bonds by influencing behavior toward the partner. How social bonds are expressed in animal behavior often depends on the species, but it is generally recognized that mutual tolerance, reflected by a close spatial proximity, is a good indicator of bonds across animal taxa (reviewed in Dunbar and Shultz 2010). Maintaining close proximity with affiliated individuals allows monitoring their activities and therefore is crucial for various benefits associated with affiliative bonds, ranging from antipredator protection of the offspring to mutual support in agonistic interactions with conspecifics. Coordinating activities with the partner has also been recognized as an important component of a bonded relationship, especially in pair-bonding animals where coordinating activities with the partner is crucial for effective rearing of the offspring.

Although social bonds can be long lasting, they require constant re-evaluating or re-affirming to ensure their maintenance, with many animals exhibiting signaling behaviors that function specifically in this way. By duetting, for example, pair-bonding birds and other animals test each other's attention to the partner's actions and, in turn, the bond between them (e.g., Smith 1994). A similar function can be attributed to synchronous swimming or surfacing in dolphins or dancing in humans. In most primates, reciprocally balanced grooming seems to be the main bonding

behavior, which explains why this activity consumes considerably more time than required by its original hygienic function. By routinely producing these affiliative signals animals reinforce the bond between them, which in turn facilitates mutually beneficial forms of social support such as tolerance or aid in agonistic interactions.

## Bond Flexibility

Since maintaining social bonds is a costly process especially in terms of time devoted to it, their formation must be favored by specific conditions. Exploring factors mediating bond formation, especially in group-living species, is therefore an especially interesting research avenue. One study showed, for example, that in periods of social instability, female baboons limit their grooming interactions to a smaller number of individuals consisting of core social partners that are more likely to provide support (Wittig et al. 2008). This suggests that social bonds are not inflexible but swiftly adjusted to the current social situation. Since social bonds are often linked to within-group competition, it is likely that its degree, reflected by the intensity of agonistic interactions or dominance relationships, is another factor influencing patterns of social bonding with specific individuals. Investigating social factors affecting social bonds, therefore, has the potential to expose selection pressures driving their evolution in group-living animals.

While the adaptive importance of strong, long-term bonds in group-living species has been widely recognized, the role of more flexible, temporary affiliations should not be underestimated. Forming such short-term social bonds or coalitions with individuals that are not necessarily affiliated on a long-term basis might be particularly important in animals, such as chimpanzees or humans, where grouping patterns are often unpredictable due to animals forming temporary subgroups which size and composition frequently change. In such fission-fusion societies, preferred long-term social partners are not always available. Perhaps to cope with this challenge, male chimpanzees use flexible and time-efficient signals

such as chorusing to facilitate short-term coalitions with both long-term preferred and neutral social partners (Fedurek et al. 2013). Similarly, while it has been shown that strong social bonds in baboons bring about clear adaptive benefits, in some baboon populations the number of weak (i.e., temporary) rather than strong or long-term social relationships predict offspring survival and longevity (McFarland et al. 2017). It is possible that strong and weak social bonds complement each other (Fedurek et al. 2013) and that the relative importance or prevalence of these two types of bonds depends on specific social and ecological conditions characterizing a given population (McFarland et al. 2017) – a topic that should be explored in more detail by future studies.

## Cross-References

- ▶ [Affiliative Behaviors](#)
- ▶ [Alloparental Care](#)
- ▶ [Attachment](#)
- ▶ [Group Living](#)
- ▶ [Maternal Behavior](#)
- ▶ [Monogamy](#)
- ▶ [Oxytocin](#)
- ▶ [Parenting](#)

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## Affiliative Interaction

- [Affiliative Behaviors](#)

## Affiliative Relationships

- [Affiliative Bond](#)

## Affordance

- [Plantae](#)
- [Social Affordance](#)

## Affordances

- [Perception-Action Theory](#)

## African Grey Parrot

- [Language Research: Parrots](#)

## African Manatee

- [Sirenia Diet](#)

## Agamogenesis

- [Asexual Reproduction](#)

## Age of Mammals

- [Cenozoic Era](#)

## Age-Graded

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## Synonyms

[Age-related](#)

## Definition

An ordering pattern for animals or conditions that is based on age. Often the “value” of different age-grades is thought to increase with age, also referred to as age-positive or positive age-graded pattern. Or the value first increases and then decreases with age, referred to as inverted U-shaped or J-shaped pattern. The latter can turn into an age-inversed pattern, also called negative age-graded.

## Introduction

In its most general form, the term “age-graded” refers to an age pattern underlying a particular

condition or a change (i) in an organizational social characteristic; (ii) of an anatomical, physiological, or cognitive feature; or (iii) of a behavior or a behavioral syndrome. Specifically, in the social sciences, the term “age grade” is used to describe an organizational pattern in a society. In developmental biology and individual life histories, age-gradedness is common, because an organism undergoes predictable, age-related changes, for example in hormonal status. Such age-related changes also occur during cognitive and behavioral development.

In behavioral studies, the term is most commonly used in studies describing the patterns of dominance relationships and the structure of dominance hierarchies. Here, the way in which age relates to or affects dominance rank leads to several distinct patterns, which vary across species and sexes. Often these patterns can be explained through variation in fighting abilities over the lifetime of an individual. At the same time, additional variables need to be taken into account, such as presence of kin, resource value, coalitions, winner-loser effects, etc., to fully explain the emerging patterns.

### Age, Fighting Ability, and Rank

When animals compete over access to limited resources, such as food, mates, etc., the outcome of an interaction is often determined by the fighting abilities of the contestants also referred to as resource holding potential or resource holding power (RHP; Parker 1974). Based on repeated interactions with consistent outcome, a dominance rank (or rank for short) can be assigned to an individual relative to other individuals, either in a group or a population. Generally, assuming that all other things are equal, the fighting ability of an individual determines its rank (see also “basic rank”), and age-graded patterns of rank emerge depending on the relationship between RHP and age.

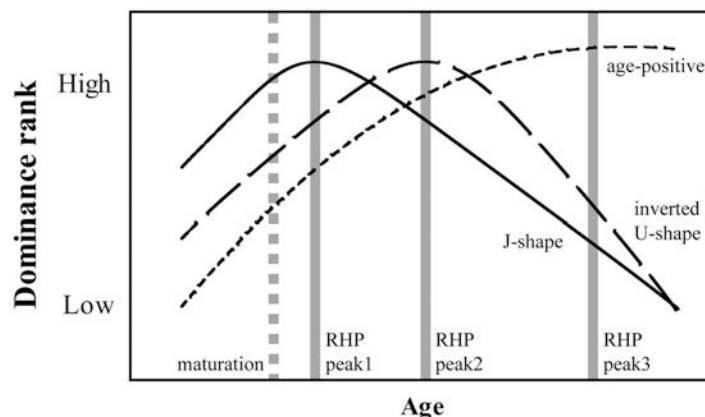
Initially, individual fighting ability increases with age, because size, strength, and weaponry

increase during ontogeny and maturation. After maturation, the further development of RHP varies across species (Clutton-Brock 2016). If an individual reaches its peak strength soon after maturation, the rank trajectory will be “J-shaped” (Fig. 1, RHP peak 1). More specifically, as individuals grow and mature they challenge older and weaker individuals, enter the hierarchy, and rise in rank. They reach their peak in rank when they reach their peak strength. Thereafter, they lose to younger and stronger individuals and drop in rank. The situation is similar in species, in which peak strength is reached later after maturation, but the increase in rank is slower and the trajectory resembles an “inverted U-shape” (Packer 1979; Fig. 1, RHP peak 2). Examples for these rank trajectories can be found among some male primates, red deer stags, and female horses. Notably, rank trajectories of individuals may depart from this pattern through coalitions or other factors affecting the relationship between age and RHP (Alberts et al. 2003).

In some invertebrates and vertebrates, individuals never cease to grow (called indeterminate growth), while in others, body mass (but not structural size) increases or weaponry continues to develop after maturity. If size, mass, or weaponry are decisive in competitive interactions, the average rank trajectory should follow the trajectory of RHP, that is, the youngest individuals should be at the bottom and the oldest individuals at the top of the hierarchy. This pattern is frequently referred to as age-graded, although the more precise term would be “age-positive” or “positive age-graded” (Fig. 1, RHP peak 3).

In the typical case, an individual matures in a group or a population or an individual immigrates into a new group. This individual, if it is the youngest with the lowest RHP, takes the lowest slot in the hierarchy. Over time new individuals cue at the bottom while older, higher ranking individuals die and the aging members of the cue become higher ranking. Positive age-graded patterns are common, for example, in ungulates and elephants as well as male hyenas, female dolphins, and a few female primates such as





**Age-Graded, Fig. 1** Average trajectories for dominance ranks following age-related changes in RHP under three conditions (RHP peak 1: shortly after maturation; RHP peak 2: several years after maturation; RHP peak 3: late in life) leading to J-shaped, inverted U-shaped, and age-

positive patterns. Under all three conditions, an individual occupies the highest ranks during the time it reaches its peak RHP. Other factors affecting rank play a negligible role

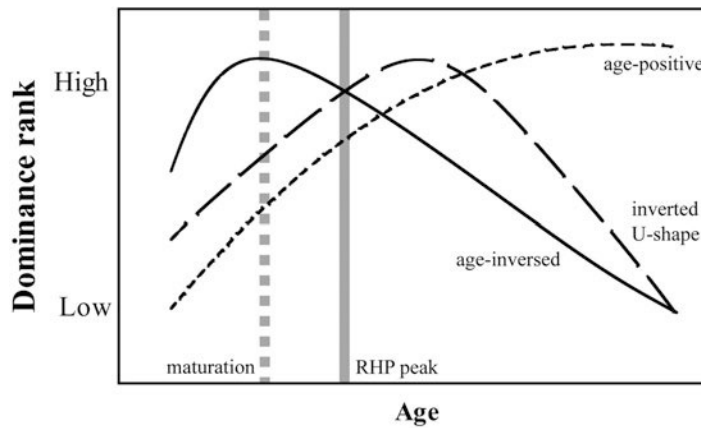
gorillas and chimpanzees (Clutton-Brock 2016). Clearly, such a system will not always be perfectly age-related. For example, the position at entry into a hierarchy is variable and can depend not only on an individual's fighting abilities but also on the presence of kin and other factors as has been documented for female chimpanzees (Foerster et al. 2016). Similarly, if individuals survive long enough they can become weak and senile such that the oldest individuals in a population or group drop in rank.

Importantly, while age-related trajectories can be driven by fighting abilities as outlined above, factors other than RHP can influence rank as well (see also "dependent rank"). Under such conditions, age-related trajectories can emerge, in which the peak rank does not coincide with peak RHP.

An extreme variation of J-shaped trajectories occurs in some female primates such as mantled howler monkeys, gray langurs, and Phayre's leaf monkeys (Lu et al. 2013), which exhibit "age-inversed" or "negative age-graded" hierarchies (Fig. 2). The key difference is here that individuals occupy the highest ranks that are not yet adult and clearly before their peak in RHP (Hrdy and Hrdy 1976). The emergence of this pattern is still

unexplained, but has been theoretically linked, among other things, to age-related changes in resource value (Broom et al. 2009).

In yet other cases, the rank trajectory follows an inverted U-shape; however, the highest ranks are occupied by individuals that are several years beyond peak RHP (Fig. 2). In the extreme case, old and weak individuals occupy the highest ranks (Fig. 2; age-positive). Because older but weaker individuals occupy the top ranks, these patterns indicate that factors other than RHP allow these individuals to outrank younger, stronger ones. One explanation for these two patterns is so-called winner-loser effects (Dugatkin 2014). Here, individuals entering a hierarchy are beaten by stronger (older) individuals. This initial win will increase the likelihood of winning in the future. Similarly, the initial loss will increase the likelihood of losing in the future. Over time the winner is more likely to win and the loser is more likely to lose, even if the RHPs of the contestants should reverse with time. This mechanism is a potential explanation for the age-positive nature of female chimpanzee hierarchies (Foerster et al. 2016). Another mechanism is the formation of coalitions by older individuals to outcompete younger and stronger individuals as has been



**Age-Graded, Fig. 2** Average trajectories for dominance ranks following age-inversed, inverted U-shaped, and age-positive patterns. All three trajectories are “independent” of the peak RHP. In an age-inversed pattern, individuals

occupy the highest ranks before peak RHP. In an inverted U-shape and an age-positive pattern they occupy the highest ranks after they reached peak RHP. For mechanisms maintaining these patterns see text

observed, for example, among Barbary macaque males (*Macaca sylvanus*). The extreme cases are some human societies such as the Samburu people. In their gerontocracy, the oldest members maintain their power through social values, ritual practices, and punishment (Spencer 2004).

- [Resource Holding Potential](#)
- [Resource Holding Power](#)

## Conclusion

The term “age-graded” is often indiscriminately applied to all kinds of age-related patterns. Often it is used to describe an “age-positive” pattern. But other patterns are possible, making it necessary to clearly describe the trajectory (age-inversed, J-shaped, inverted U-shape, age-positive) more precisely. These patterns are the result of changes in fighting ability over the lifetime of an individual, but additional factors can modify the relationships between age, RHP, and rank.

## Cross-References

- [Agonism and Social Status](#)
- [Agonistic Behavior](#)
- [Basic Rank](#)
- [Dominance](#)
- [Dominance Hierarchy](#)
- [Rank](#)

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## Agent-Based Modelling

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### Synonyms

[Individual-based modelling](#); [Individual-orientated modelling](#); [Multi-agent systems](#) (has other meanings, occasionally used as synonym.)

### Definition

Agent-based models are a type of model based on computer simulation, where the behavior of a system is determined by the activities of autonomous individuals and their interaction with and through an environment.

### Introduction

Agent-based modelling (ABM) is a research method for understanding the collective effects of individual action selection. More generally, ABM allows the examination of macrolevel effects from microlevel behavior. Science requires understanding how an observed characteristic of a system (e.g., a solid) can be accounted for by its components (e.g., molecules). In ABM, we build models of both the components and the environment in which they exist, and then observe whether the over-all system-level behavior of the model matches that of the target (or *subject*) system. Constructing agent-based models (ABMs) can be seen as a form of theory building. The consequence of expressing a theory as a simulation is that many aspects of the coherence and explanatory power of the theory can be checked by examining the simulation outputs.

Typical elements of an agent-based model are the attributes and behaviors of agents, the

relationships between agents and their interactions, the environment, and how the agents interact with and through the environment (Macal and North 2010).

ABM is still a sufficiently new research methodology that there is still some controversy in its use, and still some unevenness in its application and description in scientific papers. ABMs can be very sensitive to initial conditions and can produce complex behavior which can be difficult and computationally intensive to analyze and understand. Without sufficiently established methodological practice, it can sometimes be difficult to incorporate ABM results into true scientific discourse. However, the practice is becoming more widespread and ABMs are frequently included as one form of evidence in many high-profile scientific articles.

In this article, we review ABM and the techniques for its analysis. In the section “[History](#),” we discuss the history of ABM and give some examples of where it has been used. In the section “[Designing and Running ABMs](#),” we discuss the considerations to be taken into account when designing and running ABMs, and popular platforms for constructing them. In the section “[Analyzing ABMs](#),” we discuss the analysis of ABMs and how this can be used in theory building. Finally in the section “[Example: Flocking Behavior](#)” a simple and well-known ABM is described – that of the flocking behavior of birds by Reynolds (1987).

### History

Agent-based models emerged from work on cellular automata (CA), the first of which was created by John von Neumann and Stanislaw Ulam in the 1940s. Their idea was to try to build a machine that could autonomously reproduce itself, and the solution was a complicated set of rules on a grid. In 1970, John Conway simplified this idea in his Game of Life (1970). This game involves a grid of cells in which every cell interacts with its eight neighboring cells according to four basic rules which decide whether the cell will live or die. These basic rules create many different emergent

and complex patterns including one which copies itself in the process of destroying itself.

In the 1970s, one of the first ABMs was developed. This model was developed by Schelling and was used to study segregation (Schelling 1971). This model was implemented by physically placing dimes and pennies on a piece of graph paper, where a coin moves location if it has a majority of immediate neighbors of the other coin type. After a number of these moves, the emergence of segregation of pennies and dimes can be seen. Thus, in this model agents (the coins) make decisions and interact with one another in an environment (the grid) – contrasting with CA models where it is only the environment that is considered.

After Schelling's physical implementation of an agent-based model, ABMs began to be programmed using computers. This meant they could be more complicated and run for many more iterations. Thus, ABM became a more useful tool and work using them truly began. Robert Axelrod was a key player in the first work using computer based agent-based models. Axelrod's early work focused on using ABM to study the best solutions to the iterated prisoner's dilemma – a game theoretical model of cooperative behaviors (Axelrod 1984). Axelrod remains one of the area's main advocates.

Other early applications of ABM were in biology. Hamilton (1971) and Hogeweg and Hesper (1979) used early modelling techniques to establish basic principles of animal sociality. In the 1980s, ABMs also started to be used to study specific animal behaviors, such as the social interaction structure and ontogeny of bumble bees (Hogeweg and Hesper 1983) and the flocking behavior of birds (Reynolds 1987). After these initial developments and progressively powerful computational power, ABMs have become an increasingly popular tool in animal behavior, ecology, the social sciences, the life sciences, and economics.

A notably large early agent-based model was the simulation of whole artificial societies in the Sugarscape model by Epstein and Axtell (1996). This model looks at a simple grid environment where sugar is distributed unevenly and agents move from cell to cell and use the sugar as a

resource (whether it be for food or a trading material). By adding more rules, the model can be interpreted to show complex social behavior including disease transmission, inheritance, trade networks, economic inequality, and combat.

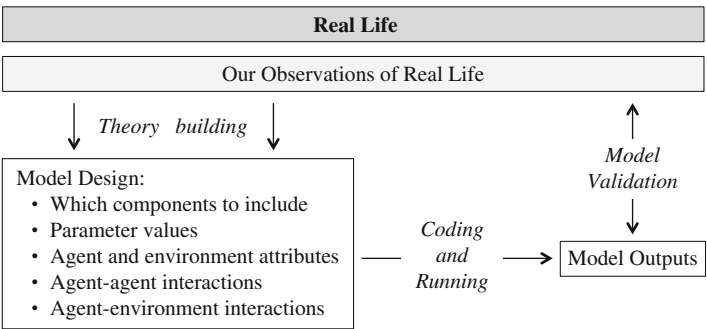
Research using ABMs has also included how culture changes and spreads (Axelrod 1997a), the evolution of cooperation (Axelrod 1997b), the societal collapse of the Anasazi people (Dean et al. 2000), social behavior in primates (Hemelrijk 2000), the study of agricultural economics (Berger 2001), the spread of cancer (Preziosi 2003), land use (Brown et al. 2005), predator-prey relationships between killer whales and other marine mammals (Mock and Testa 2007), sharing information (Čače and Bryson 2007), crowd behavior during emergency evacuation (Pan et al. 2007), and the adaptive immune system (Folcik et al. 2007). They have become an established method used broadly in high-impact publications in the social and biological sciences, including studies of political party policy dynamics in Ireland (Laver 2005), schisms in religion (Whitehouse et al. 2012), the impact of naive individuals on consensus formation (Couzin et al. 2011), the appearance of modern human behavior (Powell et al. 2009), and the origins of war (Choi and Bowles 2007).

Agent-based models can therefore now be accepted as widely used. They are able to demonstrate interesting, unexpected, and complex behaviors even from very basic rules, sometimes of extreme scientific importance. However, without properly analyzing and validating the results found from an agent-based model, the work can be as ungrounded as a computer game, rather than demonstrating real scientific progress. We address this issue in the section “[Analyzing ABMs](#).”

## Designing and Running ABMs

Designing a model involves knowledge and assumptions about the system being modelled. Models are abstractions of reality, and therefore they do not have to contain every single factor to do with the system. Because of this, decisions on which important components to include in the

**Agent-Based Modelling, Fig. 1** A flow diagram of key steps in the modelling process. It is important to note that the observed data which are used to inform on the model’s design should not also be used in the model-validation step



model, and those which do not need to be included, need to be made. These decisions can be based on which dynamics are of particular interest, the aspects of the system for which data are available, and more subjective or literature-based decisions about which factors are believed to be theoretically important.

There are several platforms for implementing agent-based models, including NetLogo (Wilensky 1999), Repast (North et al. 2013), MASON, and Swarm. A comparison of these is given by Railsback et al. (2006). However, the use of a platform is not mandatory and an agent-based model can be coded relatively easily in an ordinary programming language, particularly languages that are object oriented. However, many platforms provide tools for visualization and analysis that model authors find useful.

Often there will be stochastic elements to ABMs. Due to this, every time a model is run the results will be somewhat different, just as in many experiments with the physical world or living animals. In these cases, models should be run multiple times in order to know that the results found are representative. By running the ABM many times the user can get an idea for how variable the results are, and what kind of general model results occur. If the results of different runs of the model vary more largely than is predicted by theory, it could be a sign that the model has not been implemented properly and there may be a bug in the code, or equally that the theory is incorrect. Determining which is the problem is also a matter of analysis.

After designing, building, and running the model, it should then be verified and validated.

These will be discussed in the next section. Key steps in the modelling process are shown in Fig. 1.

### Analyzing ABMs

After running an ABM, the next step is to analyze the resulting outcomes. Analyzing results is done by observing what happens in the model after a certain number of iterations, or over a number of runs. Different experimental runs may use either the same parameters, in order to discover the range of possible results due only to the effects of random variation; or use systematically varying parameter values, to test the significance of each parameter set or *condition* (parameter sensitivity analysis). In-depth analysis of these observations can aid in understanding how the ABM is working and how sensitive it may be to different parameter values.

In order for ABM (or any model) to be useful to science, it must provide both a means of explanation and a mechanism for improving that explanation. The explanatory force of the model is the extent to which an observed meta-level phenomena can be accounted for by the behavior of its microlevel actors (Bryson et al. 2007). Thus, in model validation, the explanatory force of the model is analyzed. Models that do not perfectly match real-world data can be improved by postulating additional characteristics of the model; those that do meet requirements may possibly be improved or made more general by simplification – that is by discovering whether any aspects of the model are not necessary to the outcome and can be removed.

### Parameter Sensitivity Analysis

Sensitivity analysis is used to investigate how input parameters affect the outcomes of the model. If there is uncertainty in the value for the input parameters, then this analysis will give some idea of the degree to which this impacts the results from the model. Unless a particular range of parameter values is specified in the theory behind the model, over-dependence on specific values can be seen as fragility in the model, though they may also serve as a prediction coming from the model concerning what values the parameter correlates may be expected to hold in the target system the model describes.

A commonly used type of parameter sensitivity analysis is investigating the effect of varying one parameter while keeping all the others at their default values (the “fix-all-but-one” method). With increasing model complexity, the effects parameters have on the outcomes of a model can become exponentially more difficult to analyze. Varying one parameter at a time reduces this complexity, but relies on having a default value to set the other parameters to. Where such values are not known, e.g., when there are insufficient data available, an ill-considered default value may be chosen and an important range of model outcomes overlooked. However, if there are data which suggest that only a small range of values are realistic, then the complexity of the search may be reduced even where no exact value is known.

A more thorough type of parameter sensitivity analysis is to vary all parameters randomly within a predefined range of realistic values. By doing this for many runs of the model, the parameter set space can be investigated more comprehensively, and there is less chance of overlooking important model outcomes because of ill-defined default parameter values. However, since this approach investigates multiple parameter changes at the same time, the results are more challenging to analyze than those using the fix-all-but-one approach. Cluster analysis can be used to distinguish the types of model output that occur when

the model is run many times with random parameters, and then the parameter value distributions for each cluster can be determined (Gallagher 2017, p. 162).

### Model Verification and Validation

As ABM has become more prevalent, there has been an increasing emphasis on developing methods of verification and validation (Balci 1998; Kennedy et al. 2005). *Verification* is the process of making certain a model runs as designed. In science, this is roughly equivalent to ensuring that good experimental practice has been followed. This can be done by debugging and peer-reviewing the code to make sure that all components of the system act as expected. *Validation* is the process of making certain the model actually models the target system. When ABMs are used for sciences such as biology, validation is equivalent to hypothesis testing (Bryson et al. 2007). Model validation may be seen as one mechanism of model verification, provided that successfully replicating the behavior of the target system is unlikely to occur by chance.

There are only two important criteria for validating an ABM. These are the same as for validating any behavioral model:

1. Does the behavior of the ABM match the behavior of the target system within the standard metrics of hypothesis evaluation?
2. Do all the attributes of the agents and their environment have plausible correlates in the target system being modelled?

Regarding the “standard metrics,” these depend largely on the success of previous explanatory efforts. If the literature contains no prior explanation or model, then it may be sufficient to show a qualitative similarity between the model and the target system. The model is now a theory explaining the data, and as the first one it is necessarily the best. However, if there is another competing model, then we need either to use standard statistical

hypothesis testing to decide which will be the better match, or possibly to argue one model is more parsimonious, though such arguments can be problematic (Myung et al. 2000). For the second criterion, the issue is whether the modeler has given the artificial agents any capacities that real subjects could not or arguably would not possess.

There is a common perception that ABMs are so complex (i.e., have so many parameters) that they can be made to easily match any data or predict any outcome, but that having done so the system will have no capacity for generalization and therefore no predictive power. In practice, however, building and debugging ABMs is a difficult skill, and matching datasets is not easy. While it is true that ultimately most datasets can be matched, the principle value of the model is expressing what aspects need to be changed in order to generate these various outcomes. Again, a working model is best understood as a theory of the system, and any parameters and parameter values required for that model to work that were not a part of the original theory are predictions derived from that theory.

If a model is built first to a set of justified assumptions and *subsequently* matches a dataset with minimal adjustment, then it can be considered to be at least partially validated. Of course, the more datasets it matches, the better-validated the model becomes. As this notion of *better-validated* implies, validation is not simply a state that either holds or does not hold for a model. Rather a model, like any scientific hypothesis, becomes more *probable* (given the data) the more it is validated. But a model never becomes perfectly certain (Box 1979). Indeed, the purpose of any theory is to abstract from the real world and that process of abstraction necessarily entails losing detail and precision. The only exception is if a model becomes understood to such an extent that it can be *proven* correct in a logical or formal analytic sense.

This observation returns us to the matter of verification. Verification is most pernicious in purely formal systems, where validation cannot

be grounded in real-world data. A proof can only be judged by human reasoning and is only as good as its premises (Bundy et al. 2005; Edmonds and Bryson 2004). Formal systems are used in mathematics and similar disciplines as a mechanism of knowledge *discovery*, and therefore, verification is both more critical and more difficult. Again, when validation is performed via hypothesis testing against real-world data, validation itself serves as a form of verification. To the extent a computational model reliably matches and predicts a target system's performance, then it *is* a model, in the formal sense of the word.

### ABMs as Scientific Hypotheses

The scientific method is a process of “systematic observation and experimentation, inductive and deductive reasoning, and the formation and testing of hypotheses and theories” (Andersen and Hepburn 2016). In this way, hypotheses can be continuously improved by refinement or rejection. As stated above, ABMs may be viewed as a scientific theory about how the real-life system behaves, and as such model validation is a form of hypothesis testing (Bryson et al. 2007). Hence, every time we validate a model, we can learn something new about how the real-life system might work and then refine hypotheses about this system accordingly. Thus, in the next version of modelling a particular system we may have even more robust ideas about parameter values or relationships within the model and its target system.

The analysis of an existing agent-based model can be done as a three-phase process (Bryson et al. 2007). The first phase is a *replication* of the model. This may not seem (or even be) strictly necessary in the case where the model is publicly available – the results in that case can be checked just by rerunning the original model on another computer. However, reimplementing the model from its description in the literature can be a valuable exercise. Reimplementation may uncover important aspects of the model that the model's original authors either took for granted,

overlooked, or even forgot about during the course of their research (King 1995; Axtell et al. 1996). ABMs may be valid without actually having been fully verified or understood. This is true of any scientific hypothesis; part of the scientific method is improving this understanding of a theory as a community.

Once the critical attributes of the model are well understood, we can enter the second phase of the analysis, *model understanding*. Here, we carefully consider what the implied or the explicit correlates of those attributes are. Again, just as in any science, we go through a process of finding testable predictions and implications that result from our hypothesis. The third and final phase is *testing* these predictions and implications, looking first into the extant literature, and then (if necessary) to proposing and executing new experiments or measures on the target system.

With regard to the second phase, two similar methods can be used to predict what parameter values in the model give the most realistic results and thus help us to make inferences about the real-life system. These methods are fitting to idealized outcomes (FIO) (Gallagher et al. 2015) and approximate Bayesian computation (ABC) (Beaumont 2010). Both approaches have three steps:

1. The model is run many times with random parameter values.
2. Observed data, whether rich in detail (in the case of ABC) or imprecise (in the case of FIO), are compared to every run of the model. Model runs that give the closest match to the observed data are then separated out.
3. The parameter value combinations which were used in these closest-match model runs are interpreted as potentially being most realistic. Where the model includes stochastic elements, it is wise to check that the fit holds for repeated runs.

As mentioned in the section “[Parameter Sensitivity Analysis](#),” step 1 allows trends between the parameters and the outcomes to be seen, as well

as studying parameter interdependencies and sensitivity.

Step 2 is where ABC and FIO differ. In ABC summary statistic(s) from observed data are compared to the same summary statistic(s) from the modeled data. Thus, in ABC the comparison of the simulation and observed data is much more robust, and thus ABC can be used to validate complex models. However, to do this ABC relies on having detailed observed data, which is not always possible. Thus, if observed data are not rich enough to allow ABC, but some general outcome either is known or is of interest, FIO can still be used in model validation.

In step 3 the two methods allow a prediction of what parameter values are likely to cause observed data and which parameter values are not. And thus using these methods we can make new and informed predictions about the real-life system, which should then be tested in the third phase of analysis.

## Example: Flocking Behavior

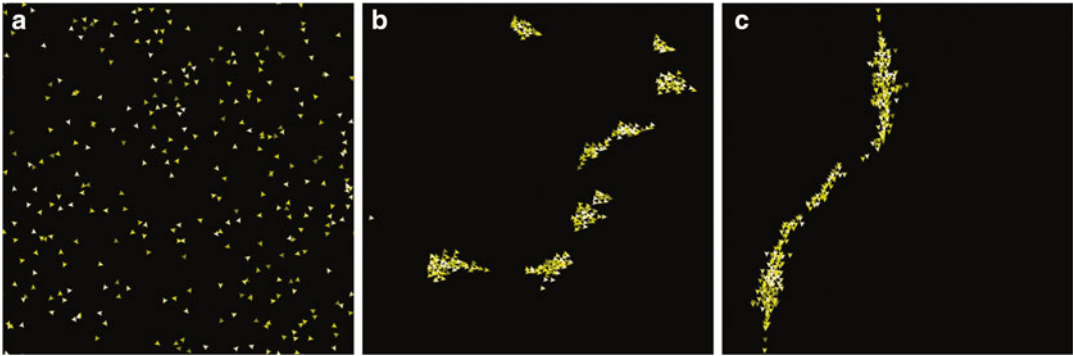
A popular and early example of ABM is the model of coordinated animal movement posited by Craig Reynolds (1987). This model, called Boids, has proven extremely fertile in biology (Couzin et al. 2011; Hemelrijk 2000).

The Boids model has three basic rules which determine how each agent (or “boid”) moves:

1. Separation: if another agent is too close, then steer to avoid it.
2. Alignment: calculate the average direction of the surrounding agents and steer to move in this same direction.
3. Cohesion: steer to move toward the average position of nearby agents (but do not get too close).

Depending on various parameter values chosen in this model (e.g., the minimum distance apart and the maximum distance an agent can observe around itself) and how long the model is run, different macrolevel behavior can





A

**Agent-Based Modelling, Fig. 2** Positions of agents in the Boid agent-based model by Reynolds (1987). Implemented in the “Flocking” model example in NetLogo 5.1.0 (Wilensky 1999). (a) shows the starting positions of agents, (b) shows the positions of agents after 100 iterations

of the model when agents can see moderately far around them, and (c) shows the positions of agents after 100 iterations of the model when agents can see very far around them

emerge. For example, if the agents can be quite close together and see moderately far around them then here might be multiple flocks of agents, but if they can see very far around them then a single flock of agents can emerge. Examples of these flocking behaviors can be seen in Fig. 2.

The initial locations and directions of agents are randomly chosen every time the model is run, and thus even with the same parameters each run of the model can look very different.

As an entirely fictitious example for purpose of illustrating the process of making predictions from this model, let's assume that the average number of birds in a real-life flock is 20, for some species and set of circumstances. We can run the model many times while varying the parameter which accounts for how far around it each agent can observe other agents. Every time the model is run, we record the mean number of agents in each flock. By selecting the runs of the model which gave average flock sizes of 20, we can then find which parameter value was used in these runs. Thus, from this we can make a prediction of the distance birds can observe the direction of travel and positions of other birds.

A real-world example of an analysis of a very similar model to boids posited to explain primate social hierarchies is presented by Bryson et al. (2007).

## Conclusion

Since the 1980s, agent-based modeling has become an increasingly popular tool in animal behavior studies, social sciences, economics, and life sciences. ABM focuses on modelling the microlevel behaviors of the system and examining the macrolevel effects these can have. To be useful to theory building, ABMs need to be validated by comparison to the real-life system which is being modelled. In this way, new insights, sharper intuitions, and predictions can be made.

## Cross-References

- [Behavioral Variation](#)
- [Effect Size](#)
- [Exemplar Theory](#)
- [Intervening Variables](#)
- [Linkage Analysis](#)
- [Model Fitting](#)
- [Motivational State](#)
- [Neural Network](#)
- [Parsimony](#)
- [Social Network Analysis](#)
- [Turing Test](#)
- [Virtual Reality Experiments](#)

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## Age-Related

### ► Age-Graded

## Age-Related Decline

### ► Senescence

## Aggregation

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## Definition

An aggregation refers to both the process of grouping and the resulting spatial gathering of animals.

## Introduction

Animal aggregations are the most basic form of social life, on top of which more elaborated social behaviors, such as cooperation and division of labor, have evolved. Aggregations are observed across the animal kingdom, from insects all the way to humans. Depending on the developmental stages of animals and the environmental conditions, aggregations can take various forms. They can count just a few individuals or several millions, involve physical contacts or only spatial proximity, be spatially stable or move, and last a few seconds or persist for a long time. Additionally, aggregations can have a stable composition or show a regular turnover of individuals.

## Passive Versus Active Aggregations

Two broad types of aggregations are generally considered (Parrish and Edelstein-Keshet 1999). Passive aggregations refer to groups that develop in response to environmental heterogeneities (e.g., shelters, light, food sources, marine

currents, or wind), while active aggregations result from inter-individual attraction (e.g., social interactions). In this case, group formation is mediated by social stimuli that are actively emitted (signals), for instance, when animals need to recruit others to a target (e.g., pheromones), or passively displayed cues (e.g., footprints). While passive aggregations always develop around environmental heterogeneities, active aggregations can also be observed in homogeneous environments (e.g., empty arena).

## Mechanisms of Grouping

The mechanisms of group formation and disruption have been extensively studied since the 1980s, with the development of self-organization theory and experimental approaches combining behavioral observations, simulations of

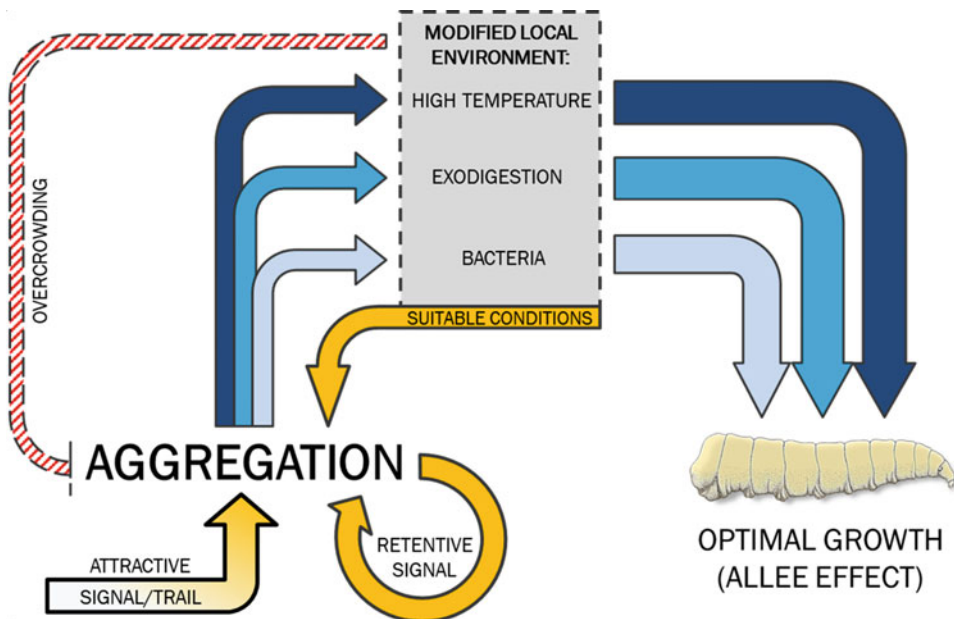
computational models, and implementation in autonomous robots (Camazine et al. 2003).

## Group Formation

Aggregations develop based on feedback loops that influence an individual's tendency to join others and stay grouped in response to aggregation stimuli (e.g., Lihoreau et al. 2016). Long-range stimuli (e.g., volatile pheromones or visual displays) often have an attractive effect, whereas short-range stimuli (e.g., nonvolatile pheromones or contacts) tend to be retentive. These attractive and retentive effects can be additive, for example, in active aggregations of blowfly larvae where the larger the group the higher the probability that individuals join and stay (Fig. 1).

## Collective Movements

Once an active aggregation is formed, various patterns of collective motion can emerge from



**Aggregation, Fig. 1** Mechanisms of group formation and fitness consequences in necrophagous blowfly larvae (Diptera: Calliphoridae). Positive feedbacks are represented by orange arrows. Negative feedbacks are represented in red. Larvae leave a chemical trail as they move on the substrate. These cuticular cues, along with thigmotaxis, maintain larvae densely aggregated, which results in deep modifications of the environment. First, the metabolic heat emitted by larvae increases temperature up

to 45 °C in large maggot-masses. Second, the exodigestive enzymes and the mechanical action of the hundreds of mouth-hooks break muscular fibers and liquefy flesh, while highly efficient antimicrobial compounds control the growth of yeast, fungi, and bacteria. The combination of these effects favors the fast development of larvae (Allee effect). In case of overcrowding (e.g., food depletion or overheating), larvae move to the periphery, resulting in a self-regulation of the aggregation

attraction, repulsion, and alignment forces between individuals (Couzin et al. 2005). Animals can collectively rotate around an empty core (e.g., schooling fishes), dig the food substrate (e.g., drosophila larvae), or migrate to a new favorable environment (e.g., marching locusts). A general feature of these collective movements is their density-dependence. During population outbreaks of desert locusts, nymphs form marching bands that can extend over kilometers. When high densities of nymphs are reached, individuals start to align their displacements, reduce collective changes in direction, and ultimately move together in the same direction (Buhl et al. 2006).

### Group Disruption

In most cases groups erode from the independent leaving events of individuals (e.g., animals on a food source become satiated and leave). However, quick synchronized dispersion can also result from social interactions, for instance, in response to a stressing event (e.g., predators). In fruit fly aggregations, the number of immobile individuals has an inhibitory effect on the probability of leaving. But following exposure to an aversive odor (e.g., CO<sub>2</sub>), contacts between moving individuals that start fleeing and stationary individuals that did not yet respond to danger trigger collective escape behaviors (Ramdya et al. 2015).

### Costs and Benefits of Grouping

Aggregations provide a range of fitness benefits to individuals that typically increase with population density and peak at a critical density. This pattern is known as the “Allee effect.”

### Predation Risks

Aggregations can reduce predation risks through several mechanisms (Krause and Ruxton 2002). At the most basic level, for any one predator attack, the larger the group of prey animals, the lower the chance that any particular individual will be the victim (i.e., dilution effect). Grouping can also augment the efficiency of vigilance

behaviors through information transfer (i.e., many-eyes effect) or distract predators that have more difficulties to focus and catch any single prey (i.e., confusion effect). In conditions of overcrowding, however, aggregations may attract more predators and parasitoids, as well as favor the spreading of diseases and pathogens among group members.

### Modifications of Local Conditions

The group itself can have an effect on local conditions and help individuals to cope with natural variations of the environment. Some animals protect themselves from cold by rising temperature above ambient. For moving aggregations, grouping can also reduce energetic expenditure during flight or swim, a benefit resulting from particular group structures (e.g., V formation in birds) that improve the aero- or hydrodynamism of individuals (Weimerskirch et al. 2001). Other animals, such as necrophagous blowfly larvae, modify their food resource by releasing metabolic heat and accumulating exodigestive enzymes that speed up food liquefaction and create favorable conditions for larval development (Fig. 1). At high densities, however, these group effects can become deleterious, leading to self-pollution (e.g., waste accumulation) or thermic stress.

### Information Transfer

Grouping may enables individuals to obtain important information about the environment that would otherwise be costly to acquire (Sumpter 2010). In active aggregations, information transfer can lead to collective decision-making whereby individuals agree on an option to take among other alternatives (e.g., a food source, a shelter, a direction). When some individuals detect a suitable option, their change of behavior is perceived by the others that tend to follow their choice. The probability of an individual to follow can depend on a quorum, i.e., a threshold in the number of individuals displaying the behavior. Through this process, large groups have lower probabilities to reproduce “mistakes” (i.e., non-adaptive behaviors) expressed by a single or few individuals. Such collective responses

often improve the speed and accuracy of decision-making.

## Mixed Species Aggregations

Although less studied, several animals form inter-specific aggregations (Boulay et al. 2017). This is the case in birds, where “follower” species can join “leader” species. In such mixed-species flocks, followers can benefit from the anti-predator vigilance of leaders, and thus re-allocate their energy to foraging. If resources are sufficiently abundant for limiting interspecific competition, benefits can be equally distributed between species (e.g., dolphins, seabirds, and sharks aggregating to concentrate large amount of preys), suggesting that the benefits of grouping can also drive the evolution of mutualistic associations.

## Conclusion

The benefits of aggregations, their emergent patterns, and their ubiquity among animal species have made them the subject of numerous studies in past and recent decades. While most research has focused on describing the general mechanisms leading to group formation and maintenance across a wide diversity of species, still little is known about the evolutionary processes that drive gregarious behaviors. Future developments in comparative quantitative research and evolutionary modeling are promising avenues to fill this gap.

## Cross-References

- ▶ [Assemblage](#)
- ▶ [Chemical Cues](#)
- ▶ [Costs of Group Living](#)
- ▶ [Group Living](#)
- ▶ [Huddling](#)
- ▶ [Optimal Group Size](#)
- ▶ [Social Behavior](#)

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## Aggression

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## Synonyms

[Agonistic behavior](#); [Animal combat](#); [Animal conflict](#); [Competitive behavior](#); [Dominant/subordinate relationship](#); [Hostile behavior](#); [Offensive behavior](#)

## Definition

Conspecific aggression is an offensive behavioral strategy directed towards a competing member of the same species that is adapted to secure some resource at minimal cost.

## Introduction

Aggression, from the Latin *aggressio* for attack, is frequently used synonymously for agonistic behavior which include threats, displays, retreats, placation, and conciliation. Psychologists define aggression as a behavior intended to harm another individual, which is less fitting for animals as they need not act with intent. Furthermore, while aggression is symptomatic for numerous psychiatric disorders, it is not necessarily an aberrant behavior, and it is considered to be adaptive for evolution and survival of animals and humans alike. Even so, there are still differing schools of thought on the origin and cause of human aggression (Bushman and O'Brien 2017). This contribution, however, summarizes insights into mechanisms controlling aggression in animals – specifically that between animals of the same species (conspecific aggression, as opposed to interspecific aggression, e.g., between predator and prey). A main focus is on cognitive processes. Traditionally, cognition basically refers to the capacity of the human mind to control what it does (Domingo, this volume). In animals, it encompasses the neuronal processes of perception, learning, memory, and decision-making that enable animals to perceive, process, and retain information about the world and decide to act on it (Rößler and Auersperg, this volume). Put simply, this article outlines how animals make the decision to fight or flee in agonistic encounters with conspecific rivals.

## Conspecific Aggression in Animals

Conspecific aggression is known in members of all major animal groups, from simple sea anemones to the great apes. Darwin recognized that this widespread occurrence reflects the fact that the

“struggle for existence” is “most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers.” Animal aggression hence serves primarily to obtain or defend some resource. Their contests typically follow a stereotyped sequence of behaviors, starting with threats and escalating to physical engagement with use of “weapons” (mandibles, horns, teeth, claws) that can inflict injury and even kill. Even so, animals tend to fight with “gloved fists” and resolve disputes before serious injuries occur. This seemingly selfless or altruistic behavior was once thought to have a “species preserving” function. Later, application of Game Theory to contests between hypothetical animals with different fighting strategies (Maynard Smith and Price 1973) led to the recognition that restrained aggression is an Evolutionary Stable Strategy that maximizes individual fitness by avoiding costs of self-injury (see Dawkins 1976 on Kin Selection and Selfish Gene Concept, as opposed to Group Selection). Conspecific aggression can therefore be defined as an offensive behavioral strategy directed towards a competing member of the same species that is adapted to secure some resource at minimal cost. Animals must, therefore, perform a cost-benefit analysis in order to decide when best to fight or flee. To do this, they are thought to assess information from agonistic signals exchanged during fighting to determine individual Resource Holding Potential (RHP), or put simply win chances (see, e.g., Arnott and Elwood 2009). An individual’s RHP depends largely on physical factors (size, strength, weaponry, energy reserves), but also on aggressive motivation, i.e., the tendency to invest energy in fighting. Fight motivation is mostly promoted by the presence and value of resources, previous wins, and physical exertion, but suppressed mainly by previous defeats. But what are the underlying proximal mechanisms? How is aggressive motivation represented in the animal brain, how do experiences influence it? How is information gained from agonistic signals used for assessing win chances? Just how do animals appear to know when best to fight or flee?

## Neural Control of Aggression

The neural circuits controlling aggression in mammals are embedded within the “social behavior network” that regulates other social behaviors and are dauntingly complex (Nelson and Trainor 2007). Functionality in neuronal circuits is determined to a great extent by chemical messengers released from the synapses that connect the neurons and include locally acting neurotransmitters and neuromodulators with wider spread actions that can bias the output of entire circuits. Neurochemicals controlling aggression (de Boer and Koolhaas 2017) have been identified by measuring behaviorally correlated changes in their levels, and from the effect of selective drugs (receptor agonists and antagonists, inhibitors of transmitter synthesis, release, degradation, and re-uptake), and genetic engineering (“knock out” or disruption of genes controlling synthesis and functioning of transmitters and their receptors). They include the amine neuromodulators serotonin (5-hydroxytryptamine: 5HT), dopamine (DA), adrenaline (AD), noradrenaline (NA also termed norepinephrine), octopamine (OA, the invertebrate analogue of NA), the inhibitory amino acid neurotransmitter  $\gamma$ -aminobutyric acid (GABA), neuromodulator peptides such as vasopressin and oxytocin and androgens like testosterone. Their functions in aggression vary depending on their release site in the brain, and the receptor type activated. Manipulating these messenger systems have even more varied effects that depend on the age, sex, and social status of the animal, and its previous experiences and momentary mental state or specific behavioral context. Despite a wealth of information on their actions, insights into the natural behavioral functions of neurotransmitters in controlling the decision to fight or flee are only just beginning to emerge.

## Controlling the Decision to Fight

**Initiation:** Attack is typically initiated by specific releasing stimuli (web vibration in spiders,

red plumage in robins, male song in female crickets, male scent in lobsters and mice). In mammals, selected regions of the social behavioral network (ventromedial hypothalamus) elicit attack (Falkner et al. 2016). Multiple transmitters participate (Nelson and Trainor 2007; de Boer and Koolhaas 2017). AD/NA are generally accredited with preparing the animal to fight or flee, while brain NA facilitates aggression, but consistent relationships have not been found. DA, in the mesocorticolimbic system, also seems required for aggression, but its precise role is unclear. Testosterone promotes aggression, and lowering testosterone production by castration reduces aggressiveness in males. Oxytocin and vasopressin, which are released into the blood to regulate parturition and lactation, respectively, salt and water balance, are also released into the brain’s social behavior network. In rodents, vasopressin facilitates offensive aggression, as does its homologue arginine vasotocin in fish, whereas oxytocin generally has antiaggressive effects (Caldwell 2017). In crustaceans, 5HT induces the animals to adopt an aggressive posture and engage in fighting (see Huber 2005), whereas in insects OA promotes fighting behavior (reviews: Stevenson and Rillich 2016, on crickets; Hoopfer 2016; Asahina 2017, on fruit flies). In male crickets, antennal contact to another male is the natural aggression releasing stimulus and has both a mechanical and male-specific pheromone component. Although male antennal contact elevates OA levels, OA is not actually necessary for initiating aggression (Rillich and Stevenson 2015). In fruit flies, a male aggression-promoting contact pheromone has been identified along with responsive gustatory receptors that connect to OA neurons (Andrews et al. 2014), which then relay to recently identified neurons that control aggression (Watanabe et al. 2017). It seems that specific male and female pheromones act on different subsets of neurons that release OA as a neuromodulator to control the decision to fight contacted males, but court females. Furthermore, the presence of females elevates male-



male aggression, but not if the males had previous female contact. Apparently female pheromone inhibits aggression via the action of GABA (Yuan et al. 2014).

**Experience dependent promotion of escalation and persistence:** In mammals, many experiences influence neurotransmitter systems with consequences for aggression. Physical exertion can promote or suppress it, whereas resources and winning an encounter increases subsequent aggressiveness and win chances (Hsu et al. 2006). In humans, winners at sport have elevated levels of the androgen testosterone compared to losers. In fish the winner effect is actually mediated by androgens, and mice winners show an increased expression of androgen receptors (Oliveira et al. 2009; Fuxjager et al. 2010). In crickets, male antennal contact, the physical exertion of flying, and the act of fighting all lead to elevated levels of OA (Adamo et al. 1995). Furthermore, each of these experiences, as well as resource possession (residency in a shelter), increases a cricket's tendency to escalate and persist in fighting specifically via the action of OA (Stevenson and Rillich 2016). The neuromodulator OA thus represents the motivational component of aggression in insects by acting at numerous levels to increase the tendency to start and persist at fighting.

### Controlling the Decision to Flee

It is generally accepted that agonistic signals (threat displays and calls, physical force) exchanged during fighting serve as cues to assess win chances (or RHP) for the decision to fight or flee (see Arnott and Elwood 2009). Theoretically, this decision could be based on average differences in signal quality (Sequential Assessment Model), the sum of own actions (Energetic War of Attrition Model), or the sum of opponent actions (Cumulative Assessment Model), but there are few examples where the strategy is known. First insights into the basic underlying mechanism are known for crickets. Manipulating agonistic signaling and perception revealed that

crickets conform to the Cumulative Assessment Model in that they stop fighting and flee when the accumulated sum of their adversary's agonistic actions surpasses a threshold, which varies with aggressive motivation (Rillich et al. 2007). Put simply, crickets enter a fight prepared to receive a set amount of aversive stimuli (threats and knocks) and flee when the limit is reached. Later experiments revealed that the impact of the opponent's agonistic signals activates the NO signaling pathway which then induces retreat. Blocking this pathway causes crickets to persist exceptionally long, while activation causes them to give up earlier (Stevenson and Rillich 2015). Similarly, in male mice, genetic deletion of the enzyme for NO synthesis induces persistent fighting. This effect seems to result from influences on testosterone and 5HT signaling (Bedrosian and Nelson 2014). In mammals, 5HT is known mainly for its suppressing effect on aggression, although it also has promoting effects and complex interactions with arginine vasopressin (review: Morrison and Melloni 2014). The role of 5HT in insect aggression is presently unclear. As in mammals, 5HT can promote or suppress aggression in insects depending on the receptor subtype activated (Johnson et al. 2009).

### The Loser Effect

Losing an aggressive contest against a conspecific (social defeat) is followed by a period of reduced aggressiveness in most animals that can last for hours or days (Hsu et al. 2006). This loser effect is accompanied by changes in transmitter systems, but their role in loser depression is unclear (de Boer et al. 2016). In mice, approach or avoidance decisions after social defeat are biased by the 5-HT system under the control of GABA-releasing neurons in the dorsal raphe nucleus. Silencing these neurons prevents the acquisition of social avoidance in response to social threat (Challis et al. 2013). In crickets, the loser effect results from activation of the NO-signaling pathway at defeat (Stevenson and Rillich 2015) and can also be induced in crickets by applying an

aggression priming stimulus (antennal stimulation with another male's antenna) followed by a potentially aversive stimulus (wind stimulation of the cerci). As for the decision to flee, this context-dependent effect of aversive stimulation requires NO (Rillich and Stevenson 2017). Physical exertion (flying) and resource possession can each induce recovery of aggression after defeat via the action of OA (review Stevenson and Rillich 2016). However, DA but not OA is necessary for natural spontaneous recovery. In these territorial animals, recovery from social defeat is responsible for increased aggressiveness after social isolation (Stevenson and Rillich 2013).

### Chronic Social Defeat Stress

In mammals, social defeat is a major stressor that induces depression like symptoms that become severe following multiple defeats (chronic social defeat, Hammels et al. 2015; Yu et al. 2016). While 5HT plays some role, it is unclear whether it does so normally, or only under extreme pathological conditions (Olivier 2015). Chronic social defeat also induces long-term depression of aggression in fruit flies and crickets (Trannoy and Kravitz 2017; Rose et al. 2017) with possible lifelong consequences for future behavior. Aggression may thus determine behavioral differences between conspecifics (animal "personality" Briffa and Sneddon 2016).

### Genes and Aggression

Individual difference in behavior results from both the genetic background (nature) and social experience (nurture), but in varying degrees depending on the trait (Polderman et al. 2015). The impact of genes on aggression is evidenced by animals bred for hyper-aggressiveness, but the relationship is complex and poorly understood. Although individual genes affecting aggression have been identified in mice and fruit flies (Anholt and Mackay 2012; Hoopfer 2016), large numbers of pleiotropic and epistatically

interacting genes are associated with this complex behavior (Zwarts et al. 2012).

### Conclusions

The neurochemical systems involved in controlling aggression and the influences of various experiences on its expression are similar in many respects in widely different animals and imply a common evolutionary root. Indeed, some of the molecular mechanisms underlying this complex behavior in fruit flies show remarkable similarities to those in mice and even humans (Thomas et al. 2015). Even so, the complex social structures of "higher" animals call for a more flexible and precise control of aggressive behavior and associated emotions. "Lower" animals, such as invertebrates, have not only simpler nervous systems, they lack beyond reasonable doubt the complexity of emotions (fear, anger) and rely on instinct rather than rational for their decisions, which is a clear investigational advantage. Their social interactions, particularly in insects, are nonetheless intricate and flexible. Despite this, the seemingly complex cognitive task of deciding when best to fight or flee can be controlled reasonably simply, using neuromodulators to differentially adjust behavioral thresholds. So perhaps the control of aggressive behavior in "higher" organisms is an extension with variations on this theme.

### Cross-References

- ▶ [Adaptedness of Behavior](#)
- ▶ [Agonistic Behavior](#)
- ▶ [Altruism](#)
- ▶ [Charles Darwin](#)
- ▶ [Cognition](#)
- ▶ [Comparative Cognition](#)
- ▶ [Decision-Making](#)
- ▶ [Dominance](#)
- ▶ [Evolutionarily Stable Strategies](#)
- ▶ [Game Theory](#)
- ▶ [Hormones and Behavior](#)
- ▶ [Innate Releasing Mechanism](#)



- ▶ Kin Selection
- ▶ Konrad Lorenz
- ▶ Martin Daly and Margo Wilson
- ▶ Motivation
- ▶ Nature Versus Nurture
- ▶ Neural Control of Behavior
- ▶ Neurotransmitters
- ▶ Personality in Animals
- ▶ Psychopharmacology of Sex Steroids
- ▶ Resource Holding Potential
- ▶ Richard Dawkins
- ▶ Serotonin
- ▶ Stress
- ▶ Territoriality
- ▶ Territory Defense

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## Aggressive Mimicry

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## Definition of “Aggressive Mimicry”

This is a term used when predators make signals that indirectly manipulate the behavior of their prey. Aggressive mimicry can be thought of as being a type of communication, as it involves two individuals (i.e., a sender and a receiver) and a signal, but in this instance the sender does not communicate to share information with the receiver in a reciprocal way. Instead, the sender uses specific signals to play mind games with the receiver, with the response elicited being detrimental to the receiver but beneficial to the sender. This type of communication is manipulative in an indirect way because, instead of being based on the sender physically forcing the receiver to do something in particular, it is based on assisting the sender with gaining indirect control of the receiver’s behavior (Jackson and Cross 2013).

## Mimicking Potential Prey

One of the most well-known examples of a predator indirectly manipulating the behavior of its prey comes from anglerfish, these being large deep-water fish species that prey on smaller predatory fish which, in turn, prey on small invertebrates. To communicate with their prey, anglerfish twitch fleshy spines extending in front of their mouths in ways that appear to resemble the stimulus the smaller predatory fish normally get from their own prey. When the smaller fish inspect the source of the signal, they are attacked and eaten by the anglerfish (Wilson 1937).

There is still much to be learned about how and why the anglerfish’s signals work, but more is known about caudal luring, a predatory strategy

used by snakes to exploit the prey identification systems of their prey, often lizards. When luring its prey, a snake may move its tail in characteristic ways that resemble the wriggling of caterpillars and other worm-like insect larvae that the lizards eat. However, puff adders also deploy lingual luring by moving their tongues in characteristic ways that lure amphibian prey (Glaudas and Alexander 2017).

Other important insights into how predators communicate with their prey come from considering invertebrates that specialize at preying on spiders. In these scenarios, having specialized strategies is essential because the tables can turn at any moment, with the hunter becoming the hunted. For example, when *Stenolemus bituberus*, an assassin bug reaches the edge of a spider's web, it lures the resident to within striking range by plucking the silk strands in ways that appear to mimic the movements made by a struggling insect (Wignall and Taylor 2011). Such a strategy is feasible because many spiders see poorly and rely on using their webs as an extension of their sensory systems. This means that, by stepping on to a web, a predator can directly manipulate a part of its prey's sensory apparatus (Jackson and Cross 2013).

There are, however, some spiders that are known to have excellent eyesight and actively hunt for their prey. *Portia* is a genus of jumping spiders (family Salticidae) from Africa, Asia, and Australia that specializes at preying on other spiders, and part of what it means to say that *Portia* is "specialized" is that this predator uses flexible strategies for communicating with its prey. After reaching the edge of another spider's web, *Portia* makes web signals by using any one or any combination of its eight legs and two pedipalps (Tarsitano et al. 2000), and it varies these signals according to the type of prey encountered. For example, *Portia* has an innate predisposition to use particular signaling routines when encountering some of its more common prey, but it relies on using trial-and-error during encounters with other prey (Jackson and Wilcox 1993). It also flexibly adjusts its signals according to feedback from the prey, such as by using trial and error to make signals that slowly lure in a more dangerous spider (Tarsitano et al. 2000).

## Mimicking Potential Mates

Some predators also succeed in prey capture by resembling the potential mates of their prey. For example, male *Photuris* and *Photinus* fireflies use species-specific flashing signals for finding mates, with the intervals elapsing between the male's flashing signal and the female's flashing reply usually being species-specific. However, once a *Photuris* female has mated, she starts answering the flashing signals from *Photinus* males and starts adopting the inter-flash interval characteristic of *Photinus* females rather than the inter-flash interval of her own species. In this way, she lures in the *Photinus* male close enough to attack, kill and eat him (Lloyd 1975).

In another example, females of *Euryattus*, a salticid species from Queensland, Australia, use dead rolled-up leaves for nests which they suspend from vegetation or from rock ledges using heavy silk guy lines. When a *Euryattus* male courts a potential mate, he walks down a guy line, positions himself on the leaf, and then shakes the leaf by suddenly flexing all his legs at the same time. The female cannot see the male while she is inside her leaf nest, and she emerges either to mate or to drive the male away. However, a spider-eating salticid from the same habitat, *Portia fimbriata*, will also walk down a guy line, position itself on the leaf, and then make leaf-shaking signals that resemble those made by *Euryattus* males. In these instances, when the female emerges from her nest, she is greeted by a predator instead of by a potential mate (Jackson and Wilcox 1990).

These examples show how aggressive mimicry strategies can become entangled with mating strategies, but the predator and prey can also be conspecific individuals. For instance, salticid courtship displays are often highly visual and, when a subadult (i.e., a juvenile that is one molt short of maturity) female of *Portia labiata* encounters a conspecific male, she displays in ways that resemble a mature female. However, as a subadult, this female is physically incapable of mating. When an adult male courts and attempts to mate with her, she makes a predatory attack on the male (Jackson and Hallas 1986).

## Chemical Mimicry

Although many examples of aggressive mimicry are visual, bolas spiders deploy chemical aggressive mimicry to capture male moths. These spiders emit from their bodies a particular blend of compounds that match the pheromones used by the females of their prey. When a male moth approaches, the spider whirls its bolas (a single line of silk with a drop of sticky glue at the end) to capture and reel in its prey.

Bolas spiders can attract more than one species of male moth, with *Mastophora cornigera* attracting as many as 19 different moth species. Another bolas spider, *Mastophora hutchinsoni*, mainly eats two moth species, *Tetanolita mynesalis* and *Lacinipolia renigera*. These two moths differ in their activity periods, with *L. renigera* being more active earlier in the night and with *T. mynesalis* being more active later in the night. To capture both species in a single night, *M. hutchinsoni* releases analogues of both moth species' pheromones, but it reduces its emission of the *L. renigera* pheromone blend as the night progresses. In doing so, *M. hutchinsoni* can capture *T. mynesalis* during later evening hours without reducing its capture rate of *L. renigera* during earlier evening hours (Haynes et al. 2002).

## Conclusion

The examples presented here are all of predators providing stimuli that indirectly manipulate the behavior of their prey. In all of these instances, the word “information” can be substituted with “misinformation,” as the elicited response to a given stimulus is advantageous to the sender and disadvantageous to the receiver. The sender can be thought of as behaving like a wolf in sheep's clothing, and yet there are differences in how taxonomically precise the sender's stimulus may be in “mimicking” a particular model. The anglerfish and snakes, for example, send signals that may mimic prey, but not particular species. Predators that mimic potential mates may be more

precise, as they send signals that are relevant in particular male-female interactions. However, for understanding what a predator is “mimicking,” it is especially important to consider the prey's own classification system rather than formal scientific taxonomy (see discussion in Jackson and Cross 2013). Often, a taxonomically precise model may not be necessary when eliciting a response that is favorable to the predator.

In the context of cognition, predators that raid webs can give us particularly important insights. The outcome of an aggressive mimic's “misinformation” can have life-or-death consequences for both the predator and the prey and, in these instances, having a rigid routine is potentially fatal for the predator. Instead, successful outcomes may often depend on the predator being flexible, which means that the predator needs to have the capacity to make decisions and to use trial-and-error for tailoring a particular signal to a particular kind of prey. In other words, although aggressive mimicry is usually considered in the context of animal communication, flexibility and deception are important expressions of animal cognition as well.

## Cross-References

- [Arthropod Cognition](#)
- [Bear Sensory Systems](#)
- [Communication](#)
- [Deception](#)
- [Mimicry](#)
- [Pheromone](#)
- [Predator](#)
- [Predator Detection](#)
- [Prey](#)
- [Signaller](#)
- [Visual Recognition of Prey and Predators](#)

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## Aggressiveness

- [Benefits for Aggression in Humans](#)

## Aging

- [Senescence](#)

## Aging Rate

- [Lifetime Expectancy](#)

## Agnosopsia

- [Blindsight](#)

## Agonism

- [Agonistic Behavior](#)

## Agonism and Social Status

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## Definitions

Agonism is the collective term for social behaviors related to fighting (e.g., physical combat, displays, threats) and connected to resource competition or social status. An individual's social status may be determined by myriad factors, like dyadic interactions. Often, individuals that successfully utilize agonistic behaviors obtain high status within their social group, although high social status may also be gained via more pacifistic means (e.g., by forming positive social bonds or alliances) or inherited.

## Agonism

Agonistic behavior includes a range of defensive and aggressive behaviors that promote individual



survival and fitness. They fall under three main categories of behaviors: display/threat, aggression, and submission/avoidance.

Displays and threat behaviors are intended to make a competitor appear more physically capable, stronger, or larger than another (Manning and Dawkins 1998). Displays take the place of direct fighting, and animals who convey their strength through gestures reduce the cost of physical aggression. Frill-necked lizards (*Chlamydosaurus kingii*), for example, communicate their size by fanning out neck skin, making their heads look larger and flashing bright red and orange scales at opponents. This display is usually accompanied by head-bobbing, arm-, and tail-waving. Frilling is often seen in ritualized disputes during mating season (Shine 1990).

Direct aggression is most often seen when competing individuals are of similar size. Usually these fights do not escalate to the point of causing extreme injury, although possible, particularly if they are between members of different groups. In black mambas (*Dendroaspis polyepis*), fights consist of wrestling bouts, where one male attempts to pin another's head to the ground in order to win mating rights (Fogden 2000).

Submission is when one individual attempts to avoid injury from a dominant conspecific through a series of conciliatory displays. These often involve the submitting animal presenting a vulnerable part of its body to a dominant individual, sometimes incorporating behaviors derived from infant dependency or sexual solicitation. While some are simple, such as when dogs or wolves (*Canis sp.*) cower to dominant individuals (Schenkel 1967), some involve elaborate gestures, like bearded dragon (*Pogona vitticeps*) arm-waving (often seen in adolescents submitting to adults) (Grenard 2007). Similar to submissive behaviors, avoidance behaviors are inherently self-preserving; they reduce energy expenditure and risk of injury as animals typically avoid outright combat. If the costs to an animal are too high, avoiding a fight is the preferred option.

## Influences on Agonism

Agonistic behavior can begin in the brain, endocrine system, or genes. Within the brain, neocortical and subcortical structures control aggression (Purves et al. 2001). The amygdala is a structure with great power over agonism. When stimulated, it can increase aggression and when damaged, it can suppress associated dominance behaviors. The presence and concentration of androgens (specifically testosterone) can also significantly influence agonism in individuals. Levels of androgens may be influenced by an individual's age, rank, sex, and/or breeding status. Glucocorticoids (GCs), hormones associated with stress, are also responsible for agonism in animals. In cichlid teleost fish (*Aequidens pulcher*), cortisol notably increases the performance of submissive behaviors in agonistic interactions, which indirectly increases aggression (Munro and Pitcher 1985). A high prevalence of glucocorticoids may promote agonism, thus further facilitating the development of social hierarchies, which will be discussed in the following sections.

## Social Status

In social species, group members often have differential ranks, meaning individuals or kin groups are dominant over others, defining their social status. An individual's social status determines access to resources, reproductive opportunities, and, in some cases, ability to control part or all of the group.

Depending on the animal society in question, status may play a greater or lesser role among the species' social system. Some societies, such as hyena (*Crocuta sp.*), exhibit a linear dominance hierarchy, or pecking order, in which each individual within a group is either dominant or submissive relative to another member of the group (Watts and Holekamp 2007). Other species, like gorillas (*Gorilla sp.*), maintain a despotic social system, in which all members are equally submissive to one leader (in this case, the silverback male). African painted dogs (*Lycaon pictus*) and

meerkats (*Suricata suricatta*) are other despotic species (Alcock 2005). Still other species are egalitarian in their social relationships, where rank plays a minimal, if any, role in intrasexual interactions (e.g., northern muriqui (*Brachyteles hyppochanthus*) (Mitani et al. 2012).

A variant of ranking exists in eusocial species, where group members are a part of a caste system and belong to a certain role or occupation, determined at birth. Examples of eusocial animals include honey ants (*Myrmecocystus mexicanus*), naked mole rats (*Heterocephalus glaber*), and honey bees (*Apis* sp.) (Andersson 1984). In a caste system, reproductive rights and resource access are divided according to “duty.” In other words, those that perform a “lower” kind of work will not have the same opportunities as those in more elevated positions, despite working cooperatively as a whole unit. Yet, unlike the other forms of social structure discussed above, individuals of a certain caste generally lose behaviors or characteristics that are often found in other castes.

## Influences on Status

Social status may be heavily influenced by the social environment, particularly an individual’s involvement in dyadic interactions (typically intrasexual) with other members of its group, as well as relatedness to others and group tenure. The quality and outcome of these interactions provide a method for better understanding an individual’s place in their respective society. After an animal’s “place” is established, they do not need to fight for resources each time they meet. Huntingford (1984) identified three overarching types of interactions that can determine status: resource-holding potential, investment in the resource, and “ownership” of the resource (i.e., home-territory advantage). Ultimately, those who value a given resource more than their competitor are predicted to achieve dominance over that competitor.

In addition to the social environment, an individual’s intrinsic characteristics may also

influence their social status. For example, social status has been linked to cognitive function, in that socially dominant individuals display greater accuracy on cognitive tasks and vice versa (i.e., causality is unclear). This is seen in pheasants (*Phasianus colchicus*): chicks that perform well on cognitive tasks are also more likely to obtain higher rank among conspecifics (Langley et al. 2018). It may also be the case that inherent personality traits influence status, as shown in rainbowfish (*Melanotaenia duboulayi*) (Colleter and Brown 2011).

Social status has also been connected to physiological and genetic mechanisms. In some species, animals inherit status, in the form of ordinal rank, from their parent(s). Many monkey species, like rhesus macaques (*Macaca mulatta*), inherit rank from their mother (Vandeleest et al. 2016), while male Canada goose (*Branta canadensis*) chicks’ rank is based on the rank of their collective family (Raveling 1970). Other studies have noted the interconnectedness of status, agonistic interactions, and GC levels. In wolf (*Canis lupus*) populations at Yellowstone National Park, high-ranking individuals exhibited higher GC levels, posited to be associated with their need for readiness to preserve their rank. Additionally, high GC levels coincide with rank stability, not necessarily rank order (Sands and Creel 2004).

## The Intersection of Agonism and Social Status

Animals of low rank not only experience reduced access to resources but also exhibit reductions in health and well-being. Animals that are more willing and able to initiate disputes with group members are more likely to defend territory, mates, or other resources, and consequently gain and maintain elevated status. High-ranking individuals typically use agonism to keep group members “in check,” presenting the opportunity for lower-ranking individuals to receive extensive and possibly unprovoked displacement aggression. In a study of red junglefowl (*Gallus spadiceus*), lower-ranking individuals were most often pecked

by higher-ranking group members, in spite of the lower-ranked individual initiating allopreening (i.e., grooming) (Vestergaard et al. 1993). Such prolonged aggression can have direct and indirect consequences on subordinates' health and wellbeing (e.g., Snyder-Mackeler et al. 2016). Increased aggression between group members and/or in connection to social status appear to be a problem also for managed wildlife (e.g., Sands and Creel 2004). In contrast, for some species, stability in status, rather than relative rank and status, contributes to enhanced welfare and health (e.g., *M. mulatta*, Vandeleeest et al. 2016).

Animals of low rank who receive more agonistic attention from peers may also experience the suppression of neuroendocrine function. Stress inhibits the parasympathetic nervous system, subsequently halting hormone production that aids in digestion, reproduction, and growth. Stress responses like this are adaptive in situations where "fight-or-flight" is necessary to maintain internal homeostasis. However, a chronic stress response can lead to the acquisition of disease and other dysregulation. The energy expelled following a stressor is not stored, causing organs and physiological functions to work overtime, wearing them down. Long-term, chronic stress, and wasted energy can lead to muscle atrophy, hypertension, and fatigue, among other issues that may lead to an overall compromised wellness (Sapolsky 2004).

## Comparisons with Humans

Among humans, status persists in nearly every social group. Even as young children, our interactions with others begin to determine our rank within classrooms, friend groups, and future interactions (Garandean et al. 2014). This can influence our emotional states, which could then affect future interactions with others. Particularly in children, social hierarchies may promote the victimization of and aggression toward low-status individuals (Garandean et al. 2014). It has been argued that socioeconomic status among adults is the closest approximation to a true dominance hierarchy in our species. This argument is

bolstered by evidence that socioeconomic status influences individual health due to access to resources like medical insurance (Sapolsky 2004). As seen in animals, humans can experience reduced quality of life and well-being dependent on their social status.

## Conclusion

Across species, agonistic interactions lie at the heart of social status, and both act upon one another to shape the lives of gregarious animals. While agonistic interactions may help individuals assert themselves as leaders among other members of their species conferring benefits, the maintenance of elevated rank is also not without cost. It is also important to remember that, for many species, social status is an emergent property: and individual's rank is depending on their social environment and is thus dynamic, with the potential to change over time.

## Cross-References

- [Aggression](#)
- [Agonistic Behavior](#)
- [Basic Rank](#)
- [Caste](#)
- [Conspecifics](#)
- [Dominance](#)
- [Dominance Hierarchy](#)
- [Fear Response](#)
- [Homeostasis](#)
- [Hormones and Behavior](#)
- [Troop](#)

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## Agonistic Behavior

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## Synonyms

Aggression; Agonism; Dominance

## Definition

Agonistic behavior is any social interaction or engagement, which involves threatening behavior, aggression, fighting, or submission.

## Overview

Agonistic behavior is commonplace across the animal kingdom. It can be described as a suite of social behaviors related to any form of aggressive or fighting actions, which occur between two or more individuals of the same species and therefore exclude predator-prey interactions. Agonistic behaviors play an important role in shaping both an individual's life history in solitary species and group structure in gregarious animals. These behaviors can be categorized into three main components: threat, aggression, and submission. All three are interrelated and can occur in combination or alone. The most common agonistic behaviors occur over access to a certain resource, such as food, shelter, and territory, or access to a mating partner. These agonistic behaviors can range from very mild, such as fleeing another individual, to severe physical fighting which can even lead to death (Maynard Smith 1974). Many animal

species have developed ritualized displays so that an escalation of contest between two individuals is not always necessary and two opponents can decide on their likelihood of victory beforehand. An agonistic interaction is only likely to occur if the disputed resource is of sufficient magnitude to induce competition. If a resource is common, evenly distributed, or of low value, it is unlikely that agonism will transpire. The rates at which agonistic behaviors occur within a given species, population, community, or social group can depend on many factors ranging from spatial position of individuals, to the number of individuals present, to the distribution of the resource and the condition of the individuals involved. A suite of sex steroid hormones, including androgens, mainly regulates agonistic behavior.

### Threat Behavior

Threat behavior may be exhibited by one individual to another in order to show their intent to be aggressive. Threat behaviors include but are not limited to vocalizations, facial threats, physical movements toward an opponent, and posturing to show ones physical attributes. Threat behaviors do not include physical contact. Threat behaviors are a method to show ones discontent without resulting in full escalation of a contest into physical aggression. Threat behaviors should lead to the target of the behavior to back down (show submission) and leave the contest before it escalates, or if not then potentially costly physical aggression will most likely occur. These threats are often displays of intimidation where an individual will try to emphasize their size or weaponry to attempt to make their opponent show submission. The extent to which outcome is likely to escalate depends on the motivation of the two opponents and the resource in question.

Threat behaviors include ritualized displays within the animal kingdom, in which individuals can convey multimodal information to others. In terms of agonistic aggression, this can be a low-cost method for individuals to decipher the size and strength of an opponent. These displays can range from body size or weaponry (e.g., size of

antlers in ungulates or canine size in nonhuman primates; Clutton-Brock 2009) to stereotyped signals. Visual signals can range from facial threats in primate species to colorful displays of fish and cephalopods. Furthermore, chemical signaling such as scent marking or information contained in urinary secretions in fish can also act as a means to convey an individual's prowess. Individuals can assess their opponent from at a distance and decide if physical contest is required. Depending on the signal strength and quality, the opponent may not be necessarily present, for example, vocalizations, scent marking, or urinary secretions can all advertise information for one individual to another without the advertiser being visually present. These threat behavioral cues can therefore also advertise a territory and allow weaker individuals to avoid areas where they know stronger conspecifics are residing. Such behavior can be valuable in two ways: firstly, it can save individuals' time as they do not need to constantly engage in aggressive contest with every opponent they come across, and secondly it can save individuals' energy and potential risk of injury. These ritualized displays can be used as a proxy for overall strength and reduce the possibility of escalation into a full fight which could cause major injury to one or both of the contestants. For example, many male songbirds produce complex vocalizations to mark their territory with louder calls showing greater strength, and other males in the area can decide if they wish to engage in an aggressive conflict after hearing the song, and insects use vocalizations to defend resources (Wingfield et al. 1987).

### Aggressive Behavior

Aggression is a term which can be defined and interpreted in various ways. Here, aggression is referred to as an act or behavior by one individual, which inflicts physical harm to another. Historically, studies investigating aggression in males have focused on a sexual context, either aggression between males to gain mating access to females or territory defense, as males aim to fertilize as many females as possible to maximize

reproductive success (Clutton-Brock 2009; Trivers 1972). Whereas research into female-female aggression has focused on access to resources, such as access to clumped food resources, access to males, or territory defense, as females generally invest more heavily in fewer offspring (Clutton-Brock 2009; van Schaik 1989). Males have been considered to be more aggressive than females in the historical literature as males must outcompete one another to access a non-divisible resource (estrous females). However, females can be equally aggressive and have been shown to compete for access to resources even to a lethal level. Fights between female matrilineal social groups can lead to severe injury or death of several individuals in nonhuman primates. Access to food resources is considered one of the main drivers of female reproductive success and as a result is one of the main contexts under which female conflict occurs. Several socioecological models state that within-group feeding competition between females shapes their group structure. Depending on the rate at which resources can be depleted and the level to which resources can be monopolized determines the severity and frequency of conflict within the social group (Clutton-Brock 2009; van Schaik 1989). Male reproductive success is generally driven by competition for access to estrous females, and as a result direct competition between males is the main form of conflict observed (Clutton-Brock 2009; Trivers 1972). The intensity can vary depending on if the species in question are seasonal or nonseasonal breeders. Seasonal breeding species have a defined window within which all females will be in estrous, and so male-male competition is high during these mating seasons. This leads to periods of high and low intensity and frequency of conflict between males. Whereas for nonseasonal breeding species, females can be in estrous at any time of the year, and so male competition for access to females is more unpredictable.

Aggression also occurs between males and females. Due to direct male-male competition, there is often large sexual dimorphism in many species, where males show greater physical attributes (such as body size and weaponry). This

means males are often able to win agonistic contests against females. However, depending on the motivation and context of the situation, females do win contests against males. For example, in some nonhuman primate species and spotted hyenas (*Crocuta crocuta*), females frequently win fights against males and are dominant over some or all of males in their social groups (East et al. 2003; Kappeler 1993; Young et al. 2017). Females can reject mating opportunities with males in some species and can use aggressive contests to protect their offspring and avoid infanticide (Clutton-Brock 2009). Aggression can occur between social groups to maintain their territory and in extreme circumstances can even lead to lethal aggression between groups, such as in chimpanzees (*Pan troglodytes*, Watts et al. 2006).

Dominance refers to the chance of one individual winning a fight over another and usually occurs over a limited resource (such as food, mating opportunities, or territory). Dominance can occur between solitary and group living individuals and even between groups. A dominance hierarchy or rank structure occurs after repeated interactions between two individuals over time, whereby the winner and loser of the contests can be ordered. The majority of agonistic aggression observed occurs between two individuals and is thus dyadic agonistic contest (Drews 1993). Overall, dominance within groups acts to allow individuals a priority of access to certain resources or commodities. This can include food, shelter, mates, or the spatial position within a social group for predator avoidance. Therefore, individuals in gregarious species strive to achieve as high a social status (position in the dominance hierarchy) as possible to infer such benefits. It is worth noting that physical attributes and weaponry alone are not always the deciding factors in dominance rank acquisition. Several other factors such as social alliances can play a large role. In some species, including several primate species, several additional factors such as strong social relationships with other group members (males and females) can improve an individual's rank position (Smith et al. 2010). Forming strong bonds with other group members can lead to coalitionary

alliances where individuals come to each other's aid during aggressive contest. This is known as agonistic or coalitionary support. As females are often the philopatric sex in primate species, females often support kin within social groups (Chapais 1995). This can be against other females or against males within their social group. Males are also observed to form coalitions; these can be with females against other males or between males. Male coalition formation can range from opportunistic support where a male joins an ongoing dyadic contest between two opponents or can be coordinated where two individuals target a specific opponent. These coalitions can occur in two main contexts: firstly, "leveling" coalitions whereby individuals break up male female consorts or mating opportunities to level the mating skew in a group and secondly "revolutionary" or rank related coalitions, whereby individuals join forces to usurp a higher-ranked individual (van Schaik et al. 2006; Young et al. 2014).

As conflict can be commonplace in group living animals, conflict resolutions have been observed in various forms in order to restore or repair relationships after a conflict has occurred. It is thought that such behaviors can act to appease the negative impacts of aggression from one individual to another and maintain group cohesion and stability. This is particularly common among related individuals within a social group to repair the damage of an aggressive interaction (Aureli et al. 2002). Individuals may also attempt to redirect an aggressive act; under such circumstances an individual who has received aggression will redirect such aggression to another group member who is close by. This is most often a subordinate group member, and it acts to reduce the chance of further aggression to them and moves the attention of the aggression to another individual.

### Submissive Behavior

Generally submissive behavior goes hand in hand with aggressive behavior and is a clear signal given by the loser of an agonistic contest to their opponent that they no longer wish to carry on the contest. These signals can be very clear such as

fleeing from an opponent to avoid the conflict altogether or to avoid further escalation of an ongoing conflict. However, submissive behavior can be much more subtle, for example, one individual can approach another and merely displace it from a given resource, such as a feeding patch. During such interactions the "aggressor" need not show any actual aggressive behavior, but their mere presence alone and approach toward the other individual is enough for them to give up their resource and move away. Such interactions show a clear understanding of an individual's relative strength and knowledge. Avoidance behavior can be beneficial, as it does not allow a fight over a resource to break out which could lead to serious injury. By giving clear submissive signals, weaker or lower-ranked individuals can avoid conflict with more powerful opponents.

### Agonistic Behavior and Hormones

Aggressive behavior is physiologically regulated by a suite of different steroid hormones; these include a range of sex hormones (such as androgens and estradiol) which can increase aggressive behavior and serotonin which acts to decrease aggressive behavior. In particular testosterone has been shown to play a major role in promoting aggressive behavior in a range of species. This was first shown in experimental studies by Berthold in 1849 on roosters (male chicken, *Gallus gallus domesticus*; for a full description, see Soma 2006), where castrated roosters showed low aggression rates, little interest in mating, and a decrease in secondary sexual characteristics compared to non-castrated roosters. In territorial bird species, increases in display behavior at the start of spring (start of the breeding season) are linked with increases in luteinizing hormone and testosterone above baseline levels (Wingfield et al. 1987). These increases in hormonal output increase male competitive behaviors and as a result aid them in competing for a mate and then guarding their nest and mate against other male intruders. However, some bird species show high levels of agonistic behavior outside of the breeding season when testosterone levels are low; here

it has been shown that estradiol is the steroid which mediates agonistic interactions in birds (Soma 2006). Further research is required to see if this is the case for other species too. Indeed the link between testosterone and aggression in both human and nonhuman primates remains ambiguous and also requires further research.

The challenge hypothesis states that in periods of social instability, testosterone and aggression are correlated (Wingfield et al. 1990). In seasonal breeding species, for example, the challenge hypothesis posits a link between testosterone secretion and aggression. Seasonal patterns of testosterone secretion are observed in males where testosterone increases before the breeding season (or when a female is in estrous) in order to increase the competitive ability of the individual for mating competition. However, the challenge hypothesis suggests that due to competition between males for females, testosterone secretion will increase to maximum levels which in turn will increase the tendency for males to aggress one another. This heightening of aggressive contest due to rising testosterone only occurs in a mating contest, and outside of such times, male relationships are maintained via other means such as recognition of other individuals' attributes and the dominance hierarchy. Research in chimpanzees (who breed all year round) also showed support for the challenge hypothesis with aggression rates and testosterone levels increasing whenever a female was in estrous. This suggests that the challenge hypothesis is not just applicable to seasonal breeders (Muller and Wrangham 2004).

## Conclusion

Agonistic behaviors occur across almost every taxa of the animal kingdom. These behaviors can range from subtle threat behaviors to full physical contest and even lead to death. The extent to which an agonistic contest will escalate depends on the value of the resource being contested, the motivation of the competitors, and the level of similarity in attributes between the opponents. As physical contest is costly both temporally and energetically, many species have evolved

ritualized behaviors in which to assess an opponent before engaging in physical contest. This also reduces the risk of physical injury or death. Overall, agonistic behaviors play an important role in shaping individual life histories for solitary living species through gregarious social species and ultimately shape the wide range of social and mating systems observed today.

## Cross-References

- ▶ [Aggression](#)
- ▶ [Agonism and Social Status](#)
- ▶ [Alpha](#)
- ▶ [Androgens](#)
- ▶ [Basic Rank](#)
- ▶ [Costs of Group Living](#)
- ▶ [Dominance](#)
- ▶ [Dominance Hierarchy](#)
- ▶ [Group Living](#)
- ▶ [Post-conflict Resolution](#)
- ▶ [Tolerance](#)

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## Aha Moment

- [Insight in Pigeons](#)
- [Insight in Rats](#)

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## "a-ha Moment"

### ► [Insight](#)

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## Ai (Chimpanzee)

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Ai is a female chimpanzee who has been the research partner of Prof. Tetsuro Matsuzawa of Kyoto University, Japan, for more than four decades. Ai has participated in many different cognitive tasks over the years, allowing researchers to compare her performance to that of human subjects, under the umbrella of comparative cognitive science.

Ai is a West African chimpanzee (*Pan troglodytes verus*), a subspecies distributed across several countries including Guinea, Ivory Coast, Liberia, and Sierra Leone. She is thought to have been born somewhere in West Africa around November 1976. She was likely separated from her mother and shipped by an animal dealer from Monrovia, Liberia, to Japan. Japan only ratified CITES, the convention prohibiting the international trade of endangered species, in 1980; thus in the 1970s, it was still legal to import chimpanzees from the wild. Nonetheless, this does not diminish the distressing history of wild chimpanzees being caught and sold to zoos and biomedical facilities across North America, Europe, and Japan for decades.

Based on her pattern of dental eruption, researchers estimated Ai's age as approximately 1 year when she arrived at the Primate Research Institute of Kyoto University on November 10, 1977. This date marks the official start of the "Ai project." Initially, the Ai project was conceived as the Japanese answer to the "ape-language" studies popular in the USA at the time.

These studies, run predominantly by psychologists, aimed to elucidate the cognitive capabilities of young chimpanzees who were raised in

human environments. The best known subjects were the chimpanzees Vicky, Gua, Washoe, Sarah, Lana, and Nim, among others. Other apes included a gorilla named Koko, the bonobo Kanzi, and an orangutan named Chantek. Each of these apes was raised in a human environment and encouraged to interact with human partners. Communication and language were the central foci of ape-language projects. The media used for interactions between humans and apes included spoken language, gestural sign language, colored plastic chips, and specially designed pictograms called lexigrams.

When the Ai project started, we already had some understanding of apes' capability to learn rudimentary forms of human language. The Ai project was unique because it did not focus on communication but instead on the psychophysical measurement of perception, cognition, and memory. In other words, the key question was how the world was perceived by a chimpanzee. Importantly, using the same apparatus and following the same procedure, the performance of the chimpanzee participants could be compared directly with that of human subjects.

Ai first learned the names of eight familiar objects: pencil, toothbrush, wooden block, glove, bowl, paper, lock, and key. The names she learnt were lexigrams, i.e., geometric figures, built from nine basic elements: horizontal line, orthogonal line, wave, vertical wave, small solid circle, small solid lozenge, large open circle, large open lozenge, and open square. Each lexigram, constructed by combining two or three of these basic elements, corresponded to one of the objects. Besides Ai, two other young chimpanzees – Akira and Mari – also participated in the acquisition of object names. The procedure involved a so-called symbolic match-to-sample task: when a specific object was presented to the chimpanzees, they had to choose the corresponding lexigram from a keyboard in order to name it.

On April 15, 1978, Ai pressed a key on the keyboard for the first time. She mastered the symbolic match-to-sample task for all 8 objects in 57 daily sessions over a period of 2.5 months. Akira took 83 sessions, and Mari took 104 sessions.

Thus, it became clear that there were pronounced individual differences among our students.

The three young chimpanzees mastered color names too. They were taught 11 different colors: red, orange, yellow, green, blue, purple, pink, brown, white, gray, and black. The names were again lexigrams. For example, the color red was represented by a lexigram combining an open lozenge and a horizontal line, while blue was a large open circle combined with a small solid circle. By asking the chimpanzee Ai to name a variety of different colors – the 224 color chips of the Munsell color system representing different hues, brightnesses, and saturation – using her “vocabulary” of color lexigrams, her color perception was shown to be very similar to that of humans. Chips from color boundaries, such as reddish pink or bluish green, elicited longer response times from both humans and Ai. In sum, the basic color categorization system found in humans is shared with chimpanzees.

Ai also learned the 26 letters of the alphabet. These were used to measure her visual acuity, determining the threshold by changing the size of a given letter placed at a distance of 3 m. Ai's binocular visual acuity was about 1.5, comparable to that of human subjects. Once she was able to discriminate the letters, she was taught to use specific ones as labels for familiar chimpanzees and humans. Asking Ai to name individuals from photographs by choosing the corresponding letters revealed that it was easier for Ai to discriminate chimpanzees than humans (much like it is easier for humans to discriminate other humans than chimpanzees).

Ai was also the first chimpanzee who mastered the skill of using Arabic numerals to label numbers of items. For example, when six pencils were shown in a display window to Ai, she would correctly choose the numeral 6 on the keyboard. Even more, she combined her naming skills to describe the number, color, and identity of a sample of objects at the same time. Suppose that five red pencils were shown to Ai: she pressed three keys, “5,” “red,” and “pencil,” consecutively. Interestingly, this led to a unique finding in the form of spontaneously preferred “word order.” Ai was free to press the three keys in any order, yet

her preference was to choose either the object name or the color name first and always choose the number last. This spontaneous tendency is reminiscent of a rudimentary grammatical rule.

Thanks to collaborators such as Masaki Tomonaga, Kazuo Fujita, and Shozo Kojima, Ai also participated in many other computer-based tasks exploring topics such as visual search, mental rotation, face inversion effect, delayed memory, metacognition, auditory threshold, visual-auditory synergy effect, understanding tempo, and so on. Touch-sensitive monitors were used not only to record single responses but also to shape touch-and-drag behavior allowing line drawing and the sorting of objects into multiple categories. Other input media, such as a drag ball, were later introduced, and even a piano keyboard was used for cognitive tests.

The original Ai project is centered on a paradigm in which a single chimpanzee faces a single computer monitor. However, in subsequent stages of the project, researchers became interested in social aspects of intelligence and in tasks that involved real-life objects and individuals. Thus the laboratory shifted away from using single booths for testing to using dual booths, then to triple booths, and even to testing chimpanzees in the outdoor compound where they lived with their groupmates. Masako Myowa-Yamakoshi studied imitation and discovered that chimpanzees found it difficult to reproduce simple actions if these did not involve objects. Shinya Yamamoto studied collaboration and discovered that chimpanzees found it difficult to help out a partner in the neighboring booth.

This paradigm shift from single subject to social setting may have been driven by researchers of the laboratory being encouraged to visit chimpanzee field sites in Africa to observe the real lives of these apes in their natural habitat. Many of them went to Bossou, Guinea, West Africa, where Prof. Matsuzawa has established his field studies. Bossou chimpanzees are known to have a unique culture that includes the use of a pair of stones as hammer and anvil to crack open oil palm nuts. Chimpanzee society in the wild is structured around a rich social network, within

which the strong mother-infant bond is especially important. In such communities, chimpanzees pass on skills, techniques, and values from one generation to the next. The process through which such knowledge is acquired via observational learning has been described as “Education by master apprenticeship.”

In 2000, when Ai was 23.5 years old, she gave birth to a son named Ayumu on April 24. In the same year, two more female chimpanzees at the Primate Research Institute gave birth: Chloe to a daughter named Cleo, and Pan to a daughter named Pal. With these births, the focus of the Ai project changed once again, now to the three mother-infant pairs. The new focus is best described as comparative cognitive developmental science (CoCoDev science). The 3 pairs were members of a group of 14 chimpanzees of 3 different generations, including 3 adult males, 8 adult females, and 3 baby chimpanzees. They lived in an enriched environment, a large outdoor compound with many trees, shrubs, and grasses, and 15-m-high climbing frames built in 1998. Two huge, 16-m-high cages were connected to the outdoor compound in 2012. This complex habitat afforded the chimpanzees two kinds of fundamental freedom: the freedom to move and the freedom to eat. They split into small parties and freely visited different parts of their habitat. This process simulates the fission-fusion grouping dynamics that is characteristic of chimpanzees in the wild.

From the time the three baby chimpanzees were born in 2000, the Ai project introduced the technique of participant observation. This is a unique way of the study that unites three components: a researcher, a mother, and a child. The researchers entered the chimpanzee testing rooms and interacted with the mothers and their infants – in a sense, they participated in the daily lives of the chimpanzees. Thanks to the long-term friendship between researchers and the mother chimpanzees, the researchers were able to ask the mothers to help them test their offspring. There were three such researcher-mother-offspring trios: Matsuzawa-Ai-Ayumu, Tomonaga-Chloe-Cleo, and Tanaka-Pan-Pal. Matsuzawa was able to participate in the testing of all three chimpanzee



pairs. Misato Hayashi also joined to test three children.

In the Western tradition, researchers frequently separated baby chimpanzees from their mothers. The isolated babies were then raised in a human home, and their cognitive development is studied. The logic was that by keeping the rearing conditions the same as that of a human infant, any differences observed could be attributed to innate species differences. However, chimpanzee babies isolated from their mothers often exhibited signs akin to depression. They were forced to adapt to a human environment. Not only was this a highly abnormal situation, but it is clearly unethical to separate a baby from its mother. As an alternative, the participant observation approach of the Ai project brought new insights into our understanding of the mother-infant relationship in chimpanzees.

Chimpanzee babies start to recognize their mother's face at around 1 month old. They show facial gestural imitation just like human babies. They start to understand pointing, even to distant targets behind them. Mothers share food with their offspring, although active sharing is rare: it is most often the offspring who initiate the sharing. Satoshi Hirata has focused on the acquisition of tool use. Observational learning of tool use, such as "fishing" for honey, mirrors the education by master-apprenticeship model that was originally postulated for chimpanzees in the wild. There is no active teaching from the mother, but the offspring have an intrinsic motivation to copy the adults' behavior. As the young grow, not only the mother but also other adults become important sources of information and skills for them. Claudia Sousa showed that Ayumu the son started to use tokens for the vending machine at 2 years old after observing the mother Ai's behavior after the birth. This age is somehow corresponding to the first onset of tool use in the wild such as use of leaves for drinking water.

Among the various cognitive capacities explored in the Ai project, the most impressive finding was the extraordinary working memory of young chimpanzees. Dora Biro, Nobuyuki Kawai, and Sana Inoue were involved in the

endeavor to characterize chimpanzees' unique memory. Ai was the first chimpanzee who mastered the so-called masking task to test her recall. In this task, a set of Arabic numerals between 1 and 9 appeared at random locations on the touch monitor. After the subject touched the smallest number, the other numerals were replaced by white rectangles. To solve the task, the subject had to touch the rectangles in the order that corresponded to the ascending sequence of the numerals originally displayed. The three young chimpanzees were excellent at this task, while adult chimpanzees, including Ai, were as good as adult humans. However, Ayumu, the best performer among the three young chimpanzees, was outstanding even with as many as nine numerals: he made the first touch to "1" in less than 0.5 s (that is, he needed only 0.5 s to memorize the entire sequence), and his accuracy was more than 80%. No human subjects can match Ayumu's accuracy at this latency.

Chimpanzees can outperform humans in a cognitive task. This message is important. So far, other studies have successfully demonstrated chimpanzee intelligence in several domains such as tool use, drawing, and gestural sign language. But those skills are also human skills. However, in the case of numerical memory, chimpanzees' performance was better than humans'. For the first time, chimpanzees were shown to be better than humans in an intellectual domain. This kind of finding may help us to abandon outdated notions of a human-animal dichotomy. Humans are part of the animal kingdom, and every species in the animal kingdom has developed its own unique set of cognitive capabilities.

The chimpanzee Ai is a sort of icon of the Ai project, a holistic approach to understanding our closest living relatives. The project unites field-work and laboratory work. It has also contributed to other scientific disciplines such as genomics: the first chimpanzee trio genome comes from three chimpanzees at the Primate Research Institute, Akira the father, Ai the mother, and Ayumu the son. Each of about 3 billion base pairs was analyzed and we found 46 SNPs in one generation. Among the SNPs, three-quarters originated

from father's side while one quarter came from the mother side.

As of July 2019, there are 305 chimpanzees housed at 48 facilities in Japan. All the apes in Japan have been registered by the Great Ape Information Network (GAIN) project. The database is open to the public, allowing anyone to access individual records any time from any place. The database is renewed in real time when an individual dies or when one is born. The system facilitates postmortem utilization of specimens, thus reducing the need for biomedical study on live chimpanzees.

Ai turns 43 in 2019. Chimpanzees can live for 50 years or longer. She will continue to be an invaluable research partner who can reveal to us hitherto unknown aspects of the chimpanzee mind. For further information, please visit the HP:

<http://langint.pri.kyoto-u.ac.jp/ai/>



Figure. Participant observation in the trio of researcher-mother-offspring, Matsuzawa-Ai-Ayumu.

## Aim

► [Goal](#)

## AL 288-1

► [Lucy](#)

## Alarm Calls

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## Synonyms

[Alarm signal](#); [Alarm vocalization](#); [Antipredator call](#); [Antipredator signal](#)

## Definition

A loud sound emitted during any stage of a predator/prey interaction.

## Introduction

Predation is one of the largest contributors to natural mortality for all animals, and the persistent threat of predation thus exerts a major influence on behavior in many species. Different species respond to predatory threats in different ways. Some species adopt cryptic strategies to reduce detection by predators, whereas others focus on strategies to better detect the predators themselves and then either elude or confront them. One of the most common behavioral responses to predators involves the production of loud, conspicuous vocalizations, or alarm calls by prey species. Such calls are produced by many species of mammals and birds when they encounter predators and they can function to alert conspecifics to the danger and prompt appropriate escape responses in them that improves their survival (Sherman 1980), or they may communicate to the predator itself that it has been detected and that the probability of a successful hunt is requisitely diminished (Caro 1995). The underlying factors which lead to the production of alarm calls may be due to changes in affect or motivation (Morton 1977), the type of predator that is encountered (Evans 1997), or the urgency of response that may be required (Owings and Leger 1980).

## The Functions of Alarm Calls

Alarm calls tend to be among the loudest and most conspicuous calls in species' vocal repertoires. As a result, they represent a potentially risky behavior, because producing loud calls when a predator is detected almost certainly draws the predator's attention towards the caller itself. Therefore, those who call (as opposed to those who might remain silent) almost certainly increase their own risk of being preyed upon. In fact, among Belding's ground squirrels, individuals that produced alarm calls (8%) were more likely to be attacked than those who did not produce calls (4%; Sherman 1977). Nevertheless, alarm calling is very common among birds and mammals; therefore, it seems there must be some important benefits to calling that compensate for these costs. It is critical to ask, then, "What does an individual gain by producing alarm calls?"

Individuals that live in groups composed primarily of closely related kin might acquire inclusive fitness benefits from warning and potentially protecting relatives from predators (Sherman 1980). If true, individuals with kin nearby should call more than those without. In fact, research on several mammalian species supports this prediction (Blumstein 2007; Wheeler 2008). For example, among 13-lined ground squirrels (*Spermophilus tridecemlineatus*), adult females with offspring and collateral kin nearby, produce more alarm calls to terrestrial predators than do adult males with fewer direct and collateral kin nearby. Importantly, alarm calling is correlated with increased survival of offspring and close relatives (Schwagmeyer 1980). Similar results have been reported in black-tailed prairie dogs (*Cynomys ludovicianus*) and Columbian ground squirrels (*Spermophilus columbianus*), where breeding females that are surrounded by kin produce alarm calls at higher rates than do males or breeding females (MacWhirter 1992).

Alarm calling to warn kin may occur more widely. For example, among nonhuman primates, vervet monkeys are noted for producing a variety of conspicuous alarm vocalizations when they detect predators nearby. Like female ground squirrels, female vervet monkeys are also the

philopatric sex; hence, groups of vervet monkeys are comprised of related females (and their offspring) and unrelated, immigrant males (Cheney and Seyfarth 1990). Female vervets also tend to maintain close social bonds with their female relatives, while males are socially peripheral and interact predominantly only with adult females in estrus and with their own offspring (Cheney and Seyfarth 1990). If the alarm calls of vervet monkeys function to warn kin, as they seem to do in ground squirrels, adult female vervet monkeys should produce calls at higher rates than do males. Results indicate that, in fact, there is no difference in the calling rates of males and females (Cheney and Seyfarth 1981). However, high-ranking females with more kin in the group produce more calls than lower-ranking females with fewer kin. Furthermore, high-ranking males with more offspring were also found to produce more calls than low-ranking males with fewer offspring (Cheney and Seyfarth 1981). Although these results indicate that alarm calls are produced by both males and females in vervet monkeys, they nevertheless suggest that the production of alarm calls during predator encounters may have evolved through the kin-selected benefits associated with warning relatives about potential dangers.

Warning kin is not the only possible selected benefit associated with producing alarm calls, however. When survival of a mate is important to an individual's fitness, individuals may call to warn mates (Krams et al. 2006; Witkin and Ficken 1979). For example, Carolina wrens form pair bonds throughout the year and these pair-bond relationships are critical in maintaining and defending a breeding territory (Morton and Shalter 1977). When a female loses a mate, she can no longer maintain the territory and is quickly driven out by another pair. Because a female cannot defend a territory alone, it might benefit her to protect her mate from potential predators by producing alarm calls. In fact, results using a tethered hawk confirmed that female Carolina wrens produce significantly more "chirt" calls than do males (Morton and Shalter 1977). In contrast, in great tits (*Parus major*), it seems to be the males who produce alarm calls to warn mates. Males produce

alarm calls both within and outside their breeding ranges if a female is nearby but do not call when alone. This pattern suggests that male alarm calls function to warn potential mates of predators (Krams et al. 2006).

Alarm signals can function as warnings to kin or mates, but it is also possible that these signals can function to manipulate and potentially deter predators themselves (e.g. Caro 1995). Somewhat counterintuitively, prey species sometimes produce vocal signals that actually draw a predator's attention towards them. For example, primates produce loud alarm calls that may function to deter predators, particularly those that rely on stealth (Zuberbühler et al. 1997, 1999). Research on six different species of monkey in the Tai forest, Ivory Coast, shows that the monkeys are more likely to produce conspicuous alarm calls to predators, like the leopard, that rely on stealth (or ambush) to capture prey, and remain silent when they detect a pursuit predator (e.g., chimpanzees) that are comparatively undeterred by having been detected and instead rely on outpacing their prey (Zuberbühler et al. 1997). Furthermore, through observations of a radio-collared leopard, Zuberbühler et al. (1999) have shown that the alarm calls of the monkeys do have an effect on the predator; following natural vocalizations by the monkeys, or experimental playback of their calls, a radio-collared leopard was more likely to give up its hunt and leave the area.

## The Mechanisms Underlying Alarm Calls

An additional important focus of research on alarm call behavior concerns the underlying mechanisms that motivate the production of these signals and the associated issue of the potential messages that alarm calls convey to listeners. Here, a long-standing view is that alarm vocalizations often reflect the underlying motivational state (e.g., fear) of the individual encountering a predator (Morton 1977, 1982). Morton (1977) developed this view into a broader theoretical framework that relates the detailed acoustic structure of signals given in a variety of circumstances – including encounters with predators –

to the different states of arousal or motivation that they reflect, what he termed “motivation-structural rules.” Morton (1977) predicted, for example, that harsh, low-frequency sounds indicate aggressive motivations, while tonal, high-frequency sounds indicate appeasement or fear. Additionally, if a signal rises in frequency, whether it is harsh or tonal, it represents a decrease in hostility and an increase in appeasement or fear, whereas a signal that decreases in frequency represents an increase in hostility. Morton (1977) also proposed that most calls are structurally graded and are used in a variety of circumstances such that the specific message content of any particular signal can be reliably interpreted only with the aid of additional contextual information (Morton 1982).

There is general support for these motivation-structural rules of vocal communication. However, at the same time, additional research has demonstrated that, at least for some species, alarm calls may also convey more specific details of predator encounters (Marler 1985). For example, the structurally distinct alarm signals produced by vervet monkeys appear to track the category of predator encountered (i.e., eagle, leopard, snake). Given their apparent predator-specificity, such calls have been labeled “referential” because they appear to function as rudimentary symbols of the predators themselves akin to our human words for these animals. In order for a vocalization to be considered a referential signal, it needs to meet two specific criteria (Evans 1997): (1) it must be produced only in particular contexts, such as in encounters with a specific category of predator; (2) its effect on listeners must be context-independent in that the call alone must allow listeners to engage in appropriate responses without the need for contextual information (Macedonia and Evans 1993).

A number of primate and other mammalian taxa have been reported to produce alarm signals that meet these criteria for functional reference (Digweed et al. 2005; Greene and Meagher 1998; Kirchlof and Hammerschmidt 2006). The best-documented example comes from the alarm calls of vervet monkeys (Cheney and Seyfarth 1990). Vervet monkeys are small-bodied

monkeys that tend to move both on the ground and in the trees and are thus exposed to a wide variety of predators, including large cats, raptorial birds, and snakes. Observational and experimental research has shown that vervet monkeys produce three acoustically distinct alarm calls to these three different classes of predator, and that each predator induces a distinct behavioral response that is appropriate to it (Seyfarth et al. 1980). For example, upon spotting a leopard, vervets give one type of alarm call and immediately scramble up a tree and out onto its terminal branches where leopards are too large to go. On spotting an aerial predator, the monkeys give a different alarm call and immediately drop out of the tree where they are most vulnerable. On encountering a snake, the monkeys give a third alarm call type and stand bipedally to scan the ground around them. Importantly, animals that hear an alarm call engage the appropriate response even if they themselves have not actually seen the predator. Hence, the calls seem to “refer to” the predators in a way at least crudely similar to our own words for these animals (Seyfarth et al. 1980).

Subsequent research has documented a similar system of acoustically distinct, predator-specific alarm calls in a handful of other primate species including ring-tailed lemurs, Diana monkeys, and Campbell’s monkeys (Macedonia 1990; Zuberbühler 2000, 2001). The word-like properties of such alarm calls appears to be shared by domestic chickens, who produce two distinct alarm calls, one for ground predators and one for aerial predators (Evans et al. 1993). Upon seeing an aerial predator, or hearing an aerial predator alarm call, a chicken will turn an eye to the sky and/or crouch and run for cover. In contrast, when they spot a ground predator (e.g., raccoon) or hear the ground predator alarm call, chickens assume an erect vigilant posture as the prelude to rapid escape (running or flying away). Systematic experiments revealed that caged chickens produce an aerial alarm call when videos of eagles are shown from monitors positioned above their cages and produce terrestrial alarm calls to videotape of raccoons on a monitor positioned at ground level (Evans et al. 1993). Playback experiments revealed that the same responses were

elicited by playback of the alarm calls in the absence of any associated predator or model of it, suggesting that the behavioral responses do not require additional contextual information (Evans et al. 1993).

However, further experiments revealed that when video of a raccoon was presented from a monitor above the cage, the chickens produced the aerial alarm call and crouched low to the ground, behavior more appropriate to raptors flying overhead (Evans and Marler 1995). Similarly, when video of an eagle was played from a monitor positioned on the ground, the chickens gave the terrestrial predator alarm call and stood erect and vigilant, behavior more appropriate to a terrestrial predators encountered on the ground (Evans and Marler 1995). These findings suggest that the alarm calls and associated behavioral responses of chickens might be driven more by the position of the predator (in the air or on the ground) than by the class of predator per se.

At the same time, research on other primate and mammal species suggests that alarm calls do not necessarily represent the predators at all but instead reflect the relative urgency of response that is required (Fichtel and Kappeler 2002; Le Roux et al. 2001; Randall and Rogovin 2002). One of the clearest documented examples of these types of calls comes from California ground squirrels, *Spermophilus beecheyi*. Ground squirrels were found to produce “whistle” vocalizations primarily in response to large raptors and “chatter” vocalizations primarily in response to terrestrial predators (Owings and Leger 1980). On the surface, then, the calls appeared to represent the different predator types much the way the alarm vocalizations of vervet monkeys represent the different predators they encounter. However, additional research on California ground squirrels revealed additional important variation.

Ground squirrels typically produce a broadband “chatter” vocalization when they detect terrestrial predators at a distance and then stand bipedally to monitor the predator’s movements to see if they need to escape to their burrows. In contrast, when they spot an aerial predator, typically only at close range and stooping, the squirrels produce a high-frequency, tonal “whistle” and



bolt immediately for their burrows (Owings and Virginia 1978; Owings and Leger 1980). However, when a terrestrial predator is detected only at the last minute and at close range, the ground squirrels emit the tonal whistle and run immediately for their burrows, whereas, when a raptor is spotted in the distance, they emit the chatter call and remain vigilant to see what the raptor will do. As a result, although the whistle and chatter alarm calls correlate with the distinction between aerial and terrestrial predators, this correlation seems to reflect a coincidence in how these different predators are typically encountered because, ultimately, the production of the calls is most sensitive to the immediacy of the risk and therefore the urgency of response that is required independent of the type of predator involved (Owings and Morton 1998).

Alarm call systems in other species appear to reflect neither strictly referential categorizations of predator types nor response urgency. For example, white-faced capuchin monkeys (*Cebus capucinus*) of Central America produce two subtly distinct alarm calls, one given relatively exclusively to aerial predators and the other given to terrestrial predators but also produced in a range of other circumstances as well (Digweed et al. 2005). The loud bark call used in terrestrial predator encounters is sometimes also given to non-predatory species and can be used in broader mobbing contexts, such as when confronting and surrounding potential food competitors or species on which the capuchins themselves prey. It appears then that capuchins have a mixed system of alarm calling, with one call given fairly specifically to aerial predators and a subtly different call given in a wider range of contexts that involve threat or aggression on the part of the monkeys (Digweed et al. 2005).

Such mixed alarm call systems are not without precedent in primates. Paralleling the capuchins, saddleback tamarins (*Saguinus fuscicollis*) use the same call that they produce to terrestrial predators in other assertive contexts such as intergroup encounters (Kirchlof and Hammerschmidt 2006). Similarly, white sifakas (*Propithecus verreauxi*), a prosimian primate from Madagascar,

also display a mixed alarm call system (Fichtel and Kappeler 2002). Like capuchins, sifaka produce one call specifically for aerial predators and another for terrestrial predators and in other situations of high arousal, including aggressive interactions with conspecifics.

These mixed systems of calling may highlight other important ecological or social distinctions among species. For example, both the white sifaka and saddleback tamarin are almost exclusively arboreal and so, by definition, may have a more limited range of escape options and thus a less focused need for multiple predator-specific alarm messages (Fichtel and Kappeler 2002; Kirchlof and Hammerschmidt 2006). White-faced capuchins are semiarboreal and semiterrestrial and so, like vervet monkeys, have a diversity of possible escape responses to the various predators that prey on them. However, unlike vervet monkeys, capuchins are, as a species, more assertive and pugnacious generally. They are known to prey on other small mammals (e.g., coati pups) and birds, and they aggressively confront other fruit competitors (e.g., peccary). They also sometimes confront and mob potential predators like tayra and some snake species. Hence, their approach to many species may be more confrontational generally. As a result, they may have evolved a mixed alarm call system that can alert conspecifics to some specific dangers (e.g., stooping raptor) but that can also function more generally to attract others attention to the source of a disturbance, whether it is a predator or competitor, or even a potential prey animal, to facilitate active engagement or mobbing (Digweed et al. 2005).

In sum, there are a variety of possible functions for the alarm calls produced by prey species encountering predators and a similar variety of possible underlying mechanisms that motivate calling, and there is, as yet, no clear framework for predicting which will apply in a given species.

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## Alarm Signal

### ► Alarm Calls

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## Alarm Vocalization

### ► Alarm Calls

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## Alert

### ► Arousal

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## Alex the Parrot

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## Synonyms

Animal “language”; Avian cognition; Comparative cognition; Nonhuman intelligence; Parrot cognition

Alex, a Grey parrot (*Psittacus erithacus*), was known for his extensive cognitive and communicative abilities. He was the subject of a 30-year research project to determine similarities and differences between his capacities and those of humans and various other nonhuman subjects. A description of his life and achievements follows.

## Early Life

Hand-raised by a Chicago area parrot breeder, Alex was sold to a local pet store at about 4 months of age, where he resided, in a large cage with other Grey parrots, until approximately 13 months of age. He was then chosen, at random by the store manager, to become a research subject. Random choice ensured that any experimental success was not a consequence of having been bred specifically for intelligence or vocal ability.

## Laboratory Environment

Although Alex was a research subject that lived in a laboratory setting at various universities (Purdue, Northwestern, University of Arizona, MIT, Brandeis), his environment was designed somewhat like that of a children’s preschool. He was caged only at night or if left alone temporarily during the day. He did not interact with other parrots during his first 14 years of research, but had constant human companionship. He was trained and tested at specific times; at other times he was simply treated as one might treat a young child: humans labeled objects with which he was interacting or foods he was eating, vocally noting their colors and shapes; humans asked him what he wanted or where he wished to go within the laboratory (options included his cage, a jungle gym, human shoulders, knees, etc.). He was never food- or water-deprived, although a delicacy might be withheld until he vocally labeled it.

## Training Techniques

Alex was trained by an interactive procedure, the Model/Rival (M/R) technique, based on methods developed by Bandura and Todt. Details and rationale for the procedure and full citations for these researchers are provided elsewhere (e.g., Pepperberg 1981, 1999). Briefly, the technique involves three-way *social* interactions among two humans and the parrot to demonstrate targeted vocal behaviors (Pepperberg 1981). The parrot watches and listens as one trainer presents objects and queries the other trainer about them (e.g., “What’s here?”, “What shape?”), giving praise and transferring the named object to the human partner to reward correct answers. Incorrect responses are punished by scolding and temporarily removing items from sight. Thus, the second human is both a model for the parrot’s responses and its rival for the trainer’s attention and illustrates consequences of errors. Eventually the parrot is included in interactions, being queried and rewarded for successive approximations to correct responses; training is adjusted to its performance level. The M/R technique exchanges



roles of trainer and model, so that the parrot learns that one person is never solely the questioner and the other the respondent, but that both individuals can undertake both parts in the interaction. Because the object is transferred upon its identification, as an intrinsic reinforcer, the bird experiences the direct link between object and label (Pepperberg 1981, 1983). Later, a bird is trained to state “I want X,” to separate requesting and labeling (Pepperberg 1988a) and to enable it to request preferred rewards while learning labels for items in which it has little interest.

## First Labels

Via M/R training, Alex first learned to vocally identify various materials and objects. After 26 months, his vocabulary consisted of nine nouns: paper, key, wood, hide (rawhide chips), peg wood (wooden clothes pins), cork, corn, nut, pasta (bow-tie macaroni); three color adjectives: rose (red), green, and blue; two shape phrases: three-corner (triangle) and four-corner (square); and functional use of the word “no” (Pepperberg 1981). He could identify materials and objects even if they differed from training exemplars (e.g., “wood” was identified correctly whatever the size, shape, or color). Given the various possible combinations of his labels, he could identify, spontaneously request, or refuse over 30 different items with an accuracy of ~80% (Pepperberg 1981). Of particular interest was that, without training, he transferred color and shape labels to items that constituted novel combinations of shape/color and material.

Alex also began acquiring labels without direct training. He learned something about the phonology of his labels – that new vocalizations to describe novel objects or those he particularly desired could be formed by recombining parts of existent utterances (e.g., “banerry” – banana/cherry – for an apple) or multiple labels (e.g., “grey nut” for a sunflower seed). For additional examples, see Pepperberg (1990b, 2009). He learned he could query trainers to acquire labels for novel items, colors, and materials, using phrases such as “What’s that?” or “What color?”

(Pepperberg 1990b). He engaged in considerable private vocal practice to refine such labels (Pepperberg et al. 1991). Details of such behavior can be found in the cited references and are summarized in Pepperberg (1999).

## Concept of Category

Such data led to an investigation of whether Alex could understand hierarchical concepts and their associated labels – that is, recognize not just what is or is not “green,” but that attributes such as “green” and “blue,” “3-corner” and “4-corner,” and “wood” and “paper” could be appropriately subsumed under specific, respective labels of “color,” “shape,” and “matter,” and that any object could be described in terms of any one or any combination of these attributes. For example, given a particular item, could he learn to respond “rose” to “What color?”, “4-corner” to “What shape?”, “wood” to “What matter?”, and “block” to “What toy?” (Pepperberg 1983). By this time, he had two more color labels (“yellow,” “grey” – charcoal to black) and two more shape labels (“2-corner,” “5-corner”). Initially, he successfully responded to color and shape queries, identifying different attributes of a single exemplar successively. Later, he learned to respond to “What matter/toy?” (Pepperberg 1999). Thus, he extracted the relevant category from a multivariant item, responding with the label for the one, correct instance of this category at better than 80% accuracy, even when combinations of color/shape/material were novel (Pepperberg 1983).

## Object Permanence

A subject, human or nonhuman, who understands object permanence knows objects do not cease to exist if they move out of view and that their physically distinct aspects are unaffected by movement (Piaget 1952). Although the concept seems so basic that no organism could exist without it, it develops over time and in several stages, each stage representing a different level of comprehension (Piaget 1952). Only after Piaget’s

writings were translated into English did researchers examine how nonhuman development might compare to that of humans, and, even then, most studies involved nonhuman primates (review in Doré and Dumas 1987).

The original object permanence study (Pepperberg and Kozak 1986) was based on the early experiments with nonhuman primates and children. Using those criteria, Alex succeeded on all stages. He could, for example, infer the transfer of a hidden object that could have been moved to any of three locations, and succeeded on a trick question in which the object's hiding place is not where it logically should be (Pepperberg and Kozak 1986). After researchers re-evaluated those earlier experiments, criteria for full Stage 6 object permanence became more stringent, but Alex, and later another Grey parrot, Griffin, succeeded on these additional tasks, including a variation of the carnival "shell game" (switching hiding places) and another ensuring that the subject was attending to the particular object being hidden by surreptitiously replacing it with a less-favored item (Pepperberg et al. 1997). Additional studies also confirmed that Grey parrots could not have been tracking olfactory cues or eye gaze (e.g., Pepperberg et al. 2013).

## Concepts of Same/Difference

Researchers once believed the concept of same/different could not be mastered by nonhumans other than primates (Premack 1983). Same/different involves not simply recognizing identity versus nonidentity, but rather understanding that any two items can have certain attributes in common (e.g., same color, shape) and others in which they differ (e.g., size, material), being able to designate these relationships via arbitrary symbols, and transferring this understanding to any novel exemplar set (Premack 1983). Demonstrating success by a nonprimate, non-mammalian subject would be an important scientific advance.

Alex already comprehended the concept of category; could he now use category labels in a

same/different task (Pepperberg 1987a) He learned, via M/R training, to answer queries of "What's same/different?" to a small subset of item pairs (sets that were red, green, or blue; triangular or square; and rawhide or wood) with the appropriate *category* label, "color," "shape," or "matter" (the latter pronounced "mah-mah"). To be correct, he had to (1) attend to multiple aspects of two different objects; (2) determine, from a vocal question, if his response should be based on similarity *or* difference; (3) determine, for the items shown, which categories were same and which were different (e.g., were both items triangular, or green, or of different material?); and (4) vocally encode the label for the targeted category. He was then tested on novel pairs, including objects whose attributes he could not label (e.g., a pink plastic elephant and a brown plastic toad). His accuracy averaged between 76% and 80% (Pepperberg 1987a). He responded equally well on "trick" questions, in which more than one attribute was either same or different; those trials ensured he was attending to the questions and not responding simply to the single odd attribute (Pepperberg 1987a).

## Concept of Absence

Experiments on the concept of nonexistence are difficult. Subjects generally respond to absence only when their expectation of presence is violated; furthermore, verbally encoding this situation (reacting in a specific manner) rather than, for example, simply avoiding stimuli that fail to provide rewards denotes a relatively advanced stage of cognitive development (Brown 1973). As of the early-1980s, only marine mammals (a sea lion, *Zalophus californianus*; a dolphin, *Tursiops truncatus*) and two chimpanzees (*Pan troglodytes*) had demonstrated such behavior (for full citations for these studies, see Pepperberg 1988b). What about a talking parrot?

Alex learned, using the M/R technique, to respond "none" to the *absence* of either similarity or difference between two objects (Pepperberg 1988b). As before, training occurred on a small

subset of items, and testing used novel items, usually involving attributes for which Alex had no labels. Accuracy averaged 80–84%, showing he was as knowledgeable as other nonhumans previously tested.

## Relational Concepts

The ability to respond to relational rather than absolute concepts is a frequently used metric for cross-species comparisons (see Premack 1983), because learning about relative concepts (e.g., “darker than”) is more difficult than learning about absolute concepts (e.g., “black”). Responding on a relative basis requires a subject to compare stimulus choices (e.g., grey is dark compared to white, light compared to black), then derive and use an underlying, more abstract, general concept; in contrast, learning an absolute stimulus value requires forming a single association (e.g., label “X” to designate x). Could Alex understand a relative concept?

Relative size was chosen (Pepperberg and Brezinsky 1991). Alex learned to respond to “What color bigger/smaller?” for a small subset of items. Using both queries meant that, as in previous tasks, he had to attend closely to the question and not simply respond based on, for example, “more.” Testing again involved many novel combinations of many novel items, for which he often had no labels. His accuracy was >77% (Pepperberg and Brezinsky 1991). Notably, without any training, he transferred use of “none” from absence of similarity/difference to an absence of a size differential, a totally distinct attribute: When first shown exemplars of the same size, he spontaneously responded “none.” He also, without training, correctly responded to “What *matter* bigger/smaller?” (Pepperberg and Brezinsky 1991).

## Comprehension Studies

Alex produced labels on demand and vocally requested information, but label comprehension had not formally been examined. Such testing was

necessary: Studies with apes had shown they could have good production skills without comprehension and vice versa (Savage-Rumbaugh 1986).

Without additional training, two experiments were performed. First, Alex saw groupings of multiple objects of various colors, shapes, and materials and was asked about a specific attribute (e.g., “What color is object-X?”, “What shape is object-Y?”, “What object is color-A?”, or “What object is shape-B?”). Accuracy was >80% for all queries (Pepperberg 1990a). Next, he was required to label the specific instance of one category of an item uniquely defined by the *conjunction* of two other categories (e.g., “What color is shape-A *and* object/material-B?”). Other items in the collection exemplified one, but not both, these defining categories. Accuracy was >76% (Pepperberg 1992). Given that he could succeed only if he understood the targets of all these questions, his data demonstrate equivalent comprehension and production abilities (for the implications of these findings, see Pepperberg 1999).

## Basic Number Concepts

Koehler’s earlier studies on Grey parrots (for a review, see Pepperberg 1999) demonstrated that these birds could perform complex match-to-sample tasks involving number, and had ruled out alternative explanations based on mass, contour, density, brightness, etc. But whether a non-human could actually *count*, in the same manner as young children (reviewed in Pepperberg and Carey 2012) was a different matter (see Pepperberg 2006a). Alex’s numerical experiments spanned the 1980s until his death in 2007.

Because Alex already knew the labels “three” and “four” (see above), M/R training began on collections of three and four objects, using a subset of items he could label; testing (i.e., “How many?”) involved a wide range of novel sets. He was subsequently trained on “two” and “five,” then “six” and “one.” When tested on novel sets for all numbers including sets of objects he could not label, placed in completely random arrays,

accuracy was 75–80%; tests controlled for all nonnumerical bases for his responses (Pepperberg 1987b). Notably, he represented quantities exactly – error patterns were random, not showing the peak near correct responses that would suggest only a general sense of quantity. The majority of errors were generic – labeling a set of keys as “key,” not “three key.” Such responses were not completely wrong, but Alex had not answered the question; thus, these responses were considered errors. Without training, he also labeled the quantity of a subset of objects within a grouping (e.g., Xs among Xs and Ys) with 70% accuracy, something young children find difficult (reviewed in Pepperberg 1999).

These data demonstrated that Alex could quantify sets, but did not specify the mechanism being used. Adult humans achieve similar numerical accuracy on such tasks either by subitizing or clumping – perceptual, not counting, mechanisms. Subitizing and clumping are used for small sets when sufficient time for counting is unavailable (see Pepperberg 1999). Thus, Alex was, without training, given an additional task involving heterogeneous sets, developed for humans, to separate counting from other mechanisms. He was asked about the quantity of a subset in a complex grouping – e.g., how many red blocks in a set of red and blue balls and blocks (Pepperberg 1994). On such a task, humans count, even when the answer involves a single item. Alex’s accuracy, >80%, matched that of humans, suggesting a counting strategy. However, avian perceptual capacities might be more advanced than those of humans. Thus, a noncounting mechanism could not be ruled out, but the decision was made to study other numerical abilities first.

Alex was also tested on comprehension of numerical labels. In a variant of the heterogeneous subset task, he saw collections involving random arrays of several numerical subsets of different colors (e.g., sets of keys, four red, five green, and six blue) or objects (e.g., all blue items, two key, three cork, five block) and, without any training, was asked to label the color of a particular number (e.g., respectively, “What color six?”, “What object three?”; Pepperberg and Gordon 2005). Accuracy was ~88%.

## A Zero-Like Concept

Unexpectedly, during the comprehension study, Alex spontaneously used “none” to represent absence of a set of a targeted quantity: a zero-like concept. Shown a set of two, three, and six objects, he was asked “What color three?” Instead of providing a color, he said “five.” He repeated “five” when asked twice more. He did not display disruptive behavior patterns that sometimes indicated a disinclination to work on a given task (e.g., Pepperberg and Gordon 2005), just continued replying “five.” The questioner, realizing something unusual, said “OK, Alex, tell me, what color five?”; he immediately responded “none” – thus, without training, transferring the concept from absence of an attribute (“same/different”) to absence of quantity (Pepperberg and Gordon 2005). Further testing demonstrated this was not a chance occurrence. He had, additionally, manipulated the trainer into asking the question he wished to answer, demonstrating some level of intentionality. His use of “none” was not equivalent to a human’s use of “zero,” but clearly an important step.

## Addition

Alex spontaneously showed an interest in addition, during training of the aforementioned Griffin on sequential auditory number processing (Pepperberg 2006a). True addition is complex and rare among nonhumans: For example, only one study, on an ape (chimpanzee), involved summation and required that the animal symbolically label the sum up to four (Boysen and Berntson 1989). Other studies purporting to test addition either did not require symbolic labeling or the subjects could be responding with respect to non-numeric bases (e.g., density, mass, contour; see Pepperberg 2006a). Thus, when Alex seemingly labeled the total number of clicks presented to Griffin over separate trials, the decision was made to investigate his abilities formally.

The study adapted the protocol of Boysen and Berntson (1989). Alex saw a tray with two upside down cups, under which trainers had earlier

hidden various quantities of differently sized items such as nut pieces, cracker bits, or jelly beans. Identical candy hearts were occasionally used to see if accuracy was higher when mass/contour cues were available. An experimenter brought the tray to Alex's face, lifted the left cup, showed what it hid for 2–3 s in initial trials, replaced the cup over the quantity, then replicated the procedure for the right cup (Pepperberg 2006a); Alex was asked "How many total?" On some trials, nothing was under both cups to see if he could transfer use of "none" to this situation; for other trials, sets contained from one to six items, in all possible combinations. Overall, accuracy was ~85%; however, as the data came in, it became clear that Alex seemed to have specific difficulty with trials involving five objects under one cup and nothing under the other, stating "six" (his largest number at the time). Such results suggested that, like humans, he might be subitizing – using a fast perceptual mechanism – when he did not have enough time actually to count. Thus, the time during which the sets were visible was increased; his accuracy on  $5 + 0$  went to 100% (Pepperberg 2006a). Data from these experiments not only demonstrated Alex's competence in addition, but also presented evidence for a counting-like strategy for the quantity five. Interestingly, he did not use "none" at a statistically significant level when it would have been appropriate, showing that his concept of zero, closely related to absence, was not as fully developed as that of humans (Pepperberg 2006a). However, he never stated "two" – the number of cups – for zero; thus, he realized what was to be enumerated. He often stated "one," somewhat like another chimpanzee, Ai (Biro and Matsuzawa 2001), also trained on numerical symbols, who confused "one" and "zero" and seemed to understand that both labels represented quantities at the lower end of the number line.

Later, two complex forms of summation were tested. First, Alex was required to sum over three object sets with a maximum total value of six (Pepperberg 2012). Three sets would likely require additional memory load, requiring two updates after seeing the first set rather than one update. His death precluded testing all possible

addends and sums, but he scored a statistically significant 8/10 on trials that were possible. Because he had by then (see below) learned the meanings of Arabic numerals and quantities to eight (Pepperberg and Carey 2012), a second experiment tested his ability to add two Arabic numerals to maximum value of eight. To be correct, he would have to understand the exact, not an approximate, meaning of the Arabic symbols. Again, his death precluded all possible combinations, but he achieved a statistically significant score of 9/12 (Pepperberg 2012). His data suggested abilities somewhat more advanced than those of chimpanzees (Boysen and Berntson 1989).

## Ordinality and Equivalence

Alex's "one"/"none" confusion when asked about absence of a set of objects would make sense if he grouped one/zero as quantifying the smallest amounts he could label; such grouping would also suggest some understanding of the order of his number labels. Were that the case, he would have made the inference on his own, because – as noted above – his numerical labels were not trained in order, as occurs for children (see Pepperberg and Carey 2012). Interestingly, apes, like those described above that symbolically label quantities, never inferred ordinality of all their numbers – that is, never inferred a full number line, in which each number is one more than the one before and one less than the one after. Unlike young children, they had to undergo extensive training to acquire such understanding (e.g., Biro and Matsuzawa 2001; Boysen et al. 1993; see discussion in Pepperberg 2006b). Might Alex have inferred ordinal relations among all his numerals on his own?

To test this possibility, he was first trained to label Arabic numerals in the absence of quantities to which they referred (Pepperberg 2006b). He saw trays of differently colored numerals, colors of each numeral varying among the trials, and via M/R training, learned to respond to, for example, "What color six?" or "What number blue?" He thereby acquired both production and



comprehension of the relationships between Arabic numerals and his vocal labels; he already comprehended and produced the same vocal labels in conjunction with object sets. If, based on the relationships between object sets and vocal labels, and vocal labels and numerals, he could infer equivalence relationships between the Arabic numerals and sets, testing on such inferences could provide information about ordinality: He could be given two Arabic numerals and, given his knowledge of bigger/smaller (Pepperberg and Brezinsky 1991), could be asked which was bigger or smaller. He could succeed only if he understood both the equivalence relationship and ordinality. To allow multiple queries on the same pairs without engaging in training, different colors of Arabic numerals were used; he was queried “What color number bigger/smaller?” (Pepperberg 2006b). Numerals of same value and physical size but different colors were also used to see if he replied “none”; numerals of the same value but different colors and physical sizes were used to see if he also replied “none”; and Arabic numerals were compared with sets of objects that were smaller or larger than the numeral’s value to evaluate the extent of his knowledge (Pepperberg 2006b). All such trials were intermixed.

He succeeded on every comparison involving two same-sized Arabic numerals, including those involving “none,” averaging 83–88%. For trials on Arabic numerals of the same value, but of different sizes, counting as correct either “none” or the color label of the targeted number (because the basis for his response was the issue of interest, either size or value would be correct), his accuracy was 100% (chance of 2/3: a color or “none”). Interestingly, he began these trials responding based on which numeral was physically bigger, but halfway through the study switched to saying “none,” likely transferring his understanding that the task was based on symbolic value from the other trials (Pepperberg 2006b).

For trials contrasting Arabic numerals with object sets, with one exception he was correct whether sets represented values greater or smaller than the numeral (e.g., given an orange Arabic 6 and three blue blocks and asked “What color

bigger?”, he responded “orange”). The sole exception was for sets containing *one* object and an Arabic numeral – then he consistently responded “none,” as though the question referred only to the number of objects and not symbolic values (Pepperberg 2006b).

Responses demonstrated that he inferred not only the equivalence of numerosity of Arabic numerals, vocal labels, and object sets, but also the ordinality of his numerical symbols. Thus, he responded more like children than other non-human subjects (see Pepperberg 2006b).

### Could Alex’s Number Sense Resemble Children’s Even Further?

Although these studies demonstrated numerical competence beyond that of other nonhumans, Alex still differed from children (reviewed in Pepperberg and Carey 2012). For example, children acquire an understanding of numbers below 4 by training and above 4 by inference: They learn cardinality (the value of numerical symbols) for very small numbers ( $<4$ ) and a general sense of “more versus less” while acquiring a meaningless, rote ordinal number series (much like they initially learn the alphabet, without understanding that “LMNOP” represents several letters), usually roughly between ages 2 and 4 years. At about 4 years, they associate knowledge of quantity in the small sets with this number sequence to form 1:1 correspondences that they extend to larger amounts for both cardinal and ordinal accuracy (reviewed in Pepperberg and Carey 2012). Children thereby generally deduce meaning for numerals “five” and above without any training. No nonhuman, including Alex, demonstrated this type of inference. But Alex had inferred ordinality; why not cardinality?

Some evidence suggested that Alex’s difficulty in acquiring new labels might depend more on learning how to physically produce their sounds than with learning their meanings (see Pepperberg 1999). To produce any given English utterance, he had to learn to coordinate his syrinx, tracheal muscles, glottis, larynx, tongue height and protrusion, beak opening, and even his esophagus

(reviewed in Pepperberg 1999). A plan was devised to separate issues of vocal production from those of numerical label comprehension (Pepperberg and Carey 2012).

The plan had several steps. First, Alex was tested on sets containing numbers of items beyond his current labeling ability: Would he use “six,” his largest current label, or somehow indicate that these sets did not correspond to number labels he could produce? He reacted as if the latter: He refused to answer unless badgered multiple times with the same question (Pepperberg and Carey 2012). He was also asked to identify the color of a set of six items on trays containing, for example, sets of four, seven, and eight items; here he replied “none,” again showing he did not label the color of the closest, but incorrect, set (Pepperberg and Carey 2012).

The labels 7 and 8 were trained in the absence of appropriate sets of objects. Alex had no knowledge that they were even numbers at this stage; thus, he was also trained that  $6 < 7 < 8$ . He was then tested as to whether he could infer the relationships among 7, 8, and his other Arabic symbols. He succeeded, but that did not yet show he understood exact meanings for 7, 8 – which could, for example, represent 10 and 20 items.

The final test involved presenting sets of seven and eight items and asking “How many?” to see if Alex would use his novel labels appropriately on first trials. As he had been trained on two novel labels, he could not simply infer a relation between a novel label and a novel set. But because his earlier labels had been taught in pairs that were one larger and one smaller than his current knowledge (i.e., training on “two” and “five” after testing “three” and “four”), and he already knew “none” was the only label to indicate something less than “one,” and “eight” was larger than “seven,” he likely had a good chance of success. He did succeed, showing he, like children, understood that, without specific training, “eight” was exactly one more than “seven,” which was exactly one more than “six”: that is, he could infer cardinality from ordinality (Pepperberg and Carey 2012). Thus, despite being phylogenetically much further from humans than are great apes, he responded more like children than did the apes.

## Optical Illusions

Alex was also evaluated on how he literally saw the world – how he processed the Müller-Lyer optical illusion, for which humans either underestimate or overestimate the length of a line with arrows attached, respectively, either inwardly  $< >$  or outwardly  $> <$  (Pepperberg et al. 2008). Using the Brentano version in which the two figures are fused (see figures in Pepperberg et al. 2008) and two differently colored lines, without training Alex was asked “What color bigger/smaller?” (Pepperberg and Brezinsky 1991). Perpendicular lines instead of arrows were used on some trials, to see if he would respond “none” (i.e., nothing bigger nor smaller) when humans would not see any illusion. Arrow angles more acute or obtuse, and central lines thicker or thinner than in the original stimuli, were used to see if Alex reacted as do humans when certain aspects of the figure are emphasized or de-emphasized. He reported the illusion in trials where human observers would have reported the classic illusion and he showed a lessened or absent illusion in trials where humans would not have reported the illusion or were less likely to do so because of variations in line width or arrow angle (Figs. 4 and 5 in Pepperberg et al. 2008). The data were particularly interesting in that tests did not use statistical averaging over hundreds of trials, nor did training involve related figures as was generally the case for other nonhumans; Alex’s vocal responses were simply recorded.

## Conclusion

Alex died September 6, 2007; he had lived for 31 years, spending 30 of them among humans dedicated to demonstrating the extent of his cognitive and communicative abilities. He was the first nonhuman, nonprimate, nonmammalian subject to acquire elements of a human communication system, and the only one to learn to do so via human speech. Use of symbolic representation enabled him to learn advanced concepts and be compared with other nonhumans with similar

capacities; his vocal abilities allowed him to be questioned the same way as young children, so direct comparisons could be made with humans. His data led to a breakthrough in understanding avian capacities and inspired studies on large numbers of psittacine and corvid species. Although his early demise meant his understanding of many other concepts were not tested, research has continued with several Grey parrots.

## Cross-References

- [Absolute Number Discrimination](#)
- [Addition](#)
- [Ai \(chimpanzee\)](#)
- [Arabic Numerals](#)
- [Cardinality](#)
- [Chunking](#)
- [Comparative Cognition](#)
- [Counting](#)
- [Language Research: Parrots](#)
- [Psittacine Cognition](#)
- [Zero Concept](#)

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## Algae

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### Definition

It is an assemblage of photosynthetic aquatic protists including seaweeds and other unicellular forms containing chlorophyll and lack stem roots and leaves.

### Introduction

The algae are photosynthetic thallophytes (plant lacking root stem and leaves) having chlorophyll as a primary photosynthetic pigment and lack a sterile covering of cells around the reproductive

cells. Together with the other land plants, in aquatic ecosystem the algae by photosynthesis play major role in the global primary production. The algae are found in enormous range of habitats, more commonly occur in water both in fresh and marine, from snowfields to the hot spring and from damp earth and plant leaves to sun baked desert soil. Some endolithic algae colonize in the cracks of rocks. It can also occur on shores and coasts, attached to the bottom or live suspended in the water itself. Algae play a very important role in carbon cycle as it is primary producer and the environment has free oxygen due to presence of algae and cyanobacteria. They help in living by producing oxygen in one way, but in other way, their enormous growth causes algal boom in water body that may be detrimental to other aquatic body like fishes. Algae are considered as a polyphyletic group because they do not have a common ancestor (Nabors 2004). They show a wide range of reproduction from simple asexual to complex sexual (Smithsonian 2010). Many structures that significantly present in the land plant like phyllids of bryophytes; roots, leaves, and other organs found in tracheophytes (vascular plants); and rhizoids in nonvascular plant are lacking in algae. Most of the algae are phototrophic and mixotrophic, i.e., deriving energy both from photosynthesis and uptake of organic carbon either by osmotrophy, myzotrophy, or phagotrophy. Some of the unicellular species of green algae, dinoflagellates, golden algae, and some others are heterotrophs or become parasites, relying entirely on external energy sources, and have limited or no photosynthetic apparatus (Figueroa-Martinez et al. 2015). The algae that have photosynthetic machinery is derived from cyanobacteria that produce oxygen as a by-product of photosynthesis, unlike other photosynthetic bacteria such as purple and green sulfur bacteria.

### Classification of Algae

The algae is classified in many ways

- Nuclear organization. It can be prokaryotic or eukaryotic. In prokaryotes there is only one class, i.e., cyanophyceae, whereas all other classes of algae come under eukaryote.
- Nature of cell wall components: The algal cell wall is generally made up of polysaccharide, lipid, and protein. The inner layer is made up of cellulose and the outer is pectin. In chlorophyceae, the cell wall is made up of cellulose. In phaeophyceae, cell wall contains alginic acid and fucinic acid. In rhodophyceae, the cell wall is made up of xylans and galactans.
- Pigmentation and photosynthetic apparatus: There are various pigments present in algae. Chlorophyll a is present in all algae, chlorophyll b is mainly present in chlorophyceae and eugleniacea, chlorophyll c is present in phaeophyceae and cryptophyceae, chlorophyll d is found in rhodophyceae, and chlorophyll e is found in xanthophyceae. Carotenoids are found in all classes of algae, and biliproteins are specially found in rhodophyceae and cyanophyceae.
- Nature of reserve food: Starch is the main reserve food in algae which is common in all classes. In rhodophyceae, the reserve food is floridean starch, in phaeophyceae the reserve food is laminarin.
- Flagellation: The number, types, and position of flagella also play important role for separation of different classes of algae. In cyanophyceae and rhodophyceae, the flagella are completely absent in vegetative and reproductive structure. All other classes have flagella in different orientation.
- Types of life cycle and reproduction: The presence and method of sexual reproduction are also important criteria for classification of algae.

F. E. Fritsch (1948) was the first to propose a most comprehensive and authoritative classification of algae. Fritsch has described in his book *The Structure and Reproduction of the Algae*.

### 1. Chlorophyceae

It is divided into nine orders

- (i) Volvocales, e.g., *Chlamydomonas*
  - (i) Chlorococcales, e.g., *Chlorella*, *Hydrodictyon*
  - (ii) Ulotrichales, e.g., *Ulothrix*
  - (iii) Cladophorales, e.g., *Cladophora*, *Pithophora*
  - (iv) Chaetophorales, e.g., *Ulvella*, *Coleochaete*
  - (v) Oedogoniales, e.g., *Oedogonium*
  - (vi) Conjugales, e.g., *Spirogyra*, *Zygnema*
  - (vii) Siphonales, e.g., *Vaucheria*
  - (viii) Charales, e.g., *Chara*, *Nitella*
2. **Xanthophyceae (Yellow green algae)**  
It is divided into four orders
- (i) Heterochloridales, e.g., *Heterochloris*
  - (ii) Heterococcales, e.g., *Myxochloris*
  - (iii) Heterotrichales, e.g., *Microspora*
  - (iv) Heterosiphonales, e.g., *Botrydium*
3. **Chrysophyceae**
- (ii) Chrysomonadales, e.g., *Crysodendron*
  - (iii) Chrysosphaerales, e.g., *Chrysosphaera*
  - (iv) Chrysotrichales, e.g., *Chrysoclonium*
4. **Bacillariophyceae (Diatom, yellow or golden brown algae)**
- (i) Centrales, e.g., *Chaetoceras*, *Cyclotella*
  - (ii) Pennales, e.g., *Pinnularia*, *Denticula*
5. **Cryptophyceae**
- (i) Cryptomonadales, e.g., *Cryptomonas*, *Cyanomonas*
  - (ii) Cryptococcales, e.g., *Tetragonidium*
6. **Dinophyceae**
- (i) Desmomonadales, e.g., *Desmocapsa*, *Desmomastrix*
  - (ii) Thecatales, e.g., *Prorocentrum*, *Exuviaella*
  - (iii) Dinophysiales, e.g., *Dinophysis*, *Phalacroma*
  - (iv) Dinoflagellata, e.g., *Elastodinium*, *Heterocapsa*
  - (v) Dinococcales, e.g., *Dinastridium*, *Dissodinium*
  - (vi) Dinotrichales, e.g., *Dinotrix*, *Dinoclonium*
7. **Chloromonadineae**
- (i) Chloromonadales, e.g., *Vacuolaria*, *Trentonia*
8. **Euglenoinaceae**
- (i) Euglenaceae, e.g., *Euglena*, *Ascoglena*

- (ii) Astasiaceae, e.g., *Astasia*, *Menoidium*
- (iii) Peranemaceae, e.g., *Petalomonas*, *Anisonema*

#### 9. Phaeophyceae

- (i) Ectocarpales, e.g., *Ectocarpus*, *Punctaria*
- (ii) Tilopteridales, e.g., *Tilopteris*
- (iii) Cuteriales, e.g., *Cutleria*
- (iv) Sporochneales, e.g., *Carpomitra*, *Sporochneus*
- (v) Desmarestiales, e.g., *Desmarestia*
- (vi) Laminariales, e.g., *Laminaria*, *Macrocystis*
- (vii) Sphacelariales, e.g., *Sphacelaria*
- (viii) Dictyotales, e.g., *Dictyota*, *Padina*
- (ix) Fucales, e.g., *Fucus*, *Sargassum*

#### 10. Rhodophyceae

- (i) Bangiales, e.g., *Bangia*, *Porphyra*
- (ii) Nemalionales, e.g., *Nemalion*, *Naccaria*
- (iii) Gelidiales, e.g., *Gelidium*
- (iv) Cryptonemiales, e.g., *Gloeopeltis*, *Dumontia*
- (v) Gigartinales, e.g., *Gigartina*, *Gracilaria*
- (vi) Rhodymeniales, e.g., *Rhodymenia*, *Champia*
- (vii) Ceramiales, e.g., *Polysiphonia*, *Ceramium*

#### 11. Myxophyceae

- (i) Chroococcales, e.g., *Gloeocapsa*, *Chroococcus*
- (ii) Chamaesiphonales, e.g., *Chamaesiphon*
- (iii) Pleurocapsales, e.g., *Pleurocapsa*
- (iv) Nostocales, e.g., *Nostoc*, *Oscillatoria*
- (v) Stigonematales, e.g., *Nostochopsis*, *Stigonema*

In 1989 Robert Edward Lee classified the algae into four distinct groups (Lee 2008).

**Group 1:** Prokaryotic algae – Cyanobacteria, chlorophyll *a*, phycobiliproteins.

**Group 2:** Eukaryotic algae with chloroplast surrounded by two membranes of the envelope.

**Glaucophyta:** It represents the intermediate position in the evolution of chloroplast.

**Rhodophyta:** No flagellated cells, floridean starch is storage product, chl *a*, phycobiliproteins.

**Chlorophyta:** Chlorophyll *a* and *b*, storage product is starch.

**Group 3:** Eukaryotic algae with chloroplast surrounded by one membrane of chloroplast endoplasmic reticulum.

Euglenophyta: Chlorophyll *a* and *b*, storage product is paramylon, characteristic type of cell division.

Dynophyta: (Dinoflagellates), mesokaryotic nucleus, chlorophyll *a* and *c<sub>1</sub>*, cell commonly divided into epicone and hypocone by a girdle, helical transverse flagellum.

Apicomplexa: Heterotrophic flagellates with colorless plastid.

**Group 4:** Eukaryotic algae with chloroplast surrounded by two membranes of chloroplast endoplasmic reticulum.

Cryptophyta: Nucleomorph present between inner and outer membrane of chloroplast endoplasmic reticulum, chlorophyll *a* and *c*, phycobiliprotein, periblast inside plasma membrane.

Heterokontophyta: Anterior tinsel and posterior whiplash type flagella, chlorophyll *a* and *c*, fucoxanthin, storage product is chrysolaminarin. The following classes have been identified (Anderson 2004).

Chrysophyceae (Golden brown algae): Chlorophylls *a*, *c<sub>1</sub>*, *c<sub>2</sub>* (Andersen and Mulkey 1983), two flagella perpendicular to each other.

Synurophyceae: Chlorophyll *a* and *c<sub>1</sub>*.

Eustigmatophyceae: Basal swelling of the tinsel flagellum adjacent to the eyespot, chlorophyll *a*.

Pinguiphyceae: Unusually high concentration of polyunsaturated acids, especially 20:5.

Dictyochophyceae: Tentacles or rhizopodial on basically amoeboid vegetative cells (Moestrup 1995; Preisig 1995).

Pelagophyceae: Unicellular algae.

Bolidophyceae is small order of flagellated marine picophytoplankton which is related to the diatoms and their cells have chlorophyll *a*, *c<sub>1</sub>*, *c<sub>2</sub>*, *c<sub>3</sub>*, beta-carotene, diatoxanthin, and fucoxanthin as do the diatoms.

Bacillariophyceae: Chlorophyll *a*, *c<sub>1</sub>*, and *c<sub>2</sub>* with the major carotenoid being the golden brown fucoxanthin.

**Raphidophyceae:** Chlorophyll *a* and *c*, two membranes of chloroplast endoplasmic reticulum, anterior flagellum is commonly tinsel, whereas the posterior flagellum is naked.

**Xanthophyceae:** Motile cells with a forwardly directed tinsel flagellum and a posteriorly directed whiplash flagellum, chlorophyll *a* and *c* (Sullivan et al. 1990).

**Phaeothamniophyceae:** Fucoxanthin and heteroxanthin occur together.

**Phaeophyceae:** Chlorophyll *a*, *c*<sub>1</sub>, and *c*<sub>2</sub>. Storage product is laminarin, exclusively found in marine habitat.

**Prymnesiophyta:** Uninucleate flagellate characterized by the presence of a haptonema between two smooth flagella.

## Algae and the Fossil Record

Fossilized filamentous algae from the Vindhya basin have been dated back to 1.6–1.7 billion years ago (Bengtson et al. 2009). The cyanobacteria in the form of stromatolites are the oldest group of algae dating back about 2700 million years. Earlier the atmosphere was devoid of oxygen and only composed of methane, ammonia, and other reduced compound. Photosynthesis by cyanobacteria started to build up the oxygen content of the atmosphere to what it is today. First eukaryotic algae appear was similar to Glaucophyta, with endosymbiotic cyanobacteria instead of chloroplasts.

## Symbiotic Algae

**Coral reefs** – These are deposition of calcareous exoskeleton of marine invertebrates of the order Sclerectinia. For cell building processes these cells metabolize sugar and oxygen and utilize the energy. The algal protists act as endosymbionts in the cells of the coral forming marine invertebrates and help them by generating sugar and oxygen available through photosynthesis using incident light and carbon dioxide produced by the host. Stony corals require endosymbiotic

algae from the genus *Symbiodinium* to be in a healthy condition (Taylor 1983).

**Sponges** – Some endosymbiotic algae live very close to the sponges like breadcrumb sponges (*Halichondria panicea*).

**Lichens** – It is the body structure formed by association of algae and fungi. The fungal symbiont belongs to ascomycotina or basidiomycotina, and the algal symbiont belongs to green algae and cyanobacteria. The association is termed a morphogenesis because the lichen has the form and capabilities not possessed by the symbiont species alone (they can be experimentally isolated).

## Algae and the Environment

**Toxic algae:** It can be toxic in two ways (Hallegraeff et al. 2003).

**Enormous populations in the aquatic environment:** Heavy growth of few algae, e.g., the diatom *Chaetoceros* or the prymnesiophyte *Chrysochromulina* can block the gills of fish and can be particularly a problem in aquaculture systems. Anoxxygenic condition created leads to killing of fish, at the end of blooms of other algae (e.g., green algae) as the algae die and decompose.

**Toxin production:** Some toxins produced by the algae kill other organisms that prey on these algae. Indeed, this probably was the reason that these algae were selected for in the evolutionary process since it reduced predation by grazers (Gilbert 1996). Filter-feeding shellfish can accumulate large quantities of these toxins as they filter the algae out of the water. Consumption of the shellfish by man, birds, and animals results in sickness and death. The algae that produce phycotoxins are:

### Cyanophyceae

**Neurotoxin and Saxitoxin:** It blocks the transmission of signal from neuron to neuron. These compounds bind to voltage activated Na<sup>+</sup> channels and block influx of Na<sup>+</sup>, thereby stopping the generation of an action potential (Shimizu 2000).

**Hepatotoxins:** Microcystin and nodularin are inhibitors of protein phosphatases.

## Chemical Defense Mechanisms of Algae

Loss of various micro- and macroalgal biomass occur by invertebrate predation and herbivore grazing. So, the algal population have evolved the chemical defense mechanism which can be constitutive or inducible. The toxic “red tide” dinoflagellates that have reduced grazing by copepods is the example of constitutive defense mechanism (Wolfe 2000). The increased production of phlorotannins by brown algae and the increased production of halogenated furones by red algae, on grazing by invertebrates, are examples of inducible defense mechanism (Pavia et al. 2003). Various types of defense chemicals are given below.

**Seriochemicals** – act between individual of the same species, e.g., pheromones

**Allelochemicals** – act between members of different species, e.g., kairomones and synomones (Cembella 2003)

**Bioremediation-** *Desmodesmus pleiomorphus* has been reported for biosorption of cadmium (Monteiro et al. 2010). *Fucus spiralis*, *Ascophyllum nodosum*, and *Chondrus crispus* are macroalgal species for copper sorption reported by Romera et al. (2007).

**Pollution control** – Some scientist found that 60–90% of nitrogen runoff and 70–100% phosphorus runoff is captured from manure effluents using a horizontal algae scrubber also known as algal turf scrubber (ATS). They found that cucumber and corn seedlings grew just as well using ATS organic fertilizer as they did with commercial fertilizers.

**Algal Sunscreen for ultraviolet damage** – Ozone depletion causes ultraviolet light to reach the earth that lead to hazardous consequences. Springtime ozone reductions up to 60% compared with values 30 years ago have been recorded (Karsten et al. 1999). This has resulted in increased amounts of UV-B reaching the surface of the earth. The production of ultraviolet sunscreen by algae is the one way the cells have evolved in dealing with damaging UV light. Most commonly used compound is Mycosporin like amino acid that absorbs between 310 and 360 nm (Karsten et al. 1999).

## Hydrogen Fuel Cells and Gas Production by Algae

Hydrogen fuel cells are clean energy source for vehicle nowadays and play a very important role in pollution control. The production of hydrogen gas in green algae has been extensively studied (Melis et al. 2000; Ghiradi et al. 2000). Nearly 40,000 algal species have been described, and this is likely only a small fraction of the total number of available species. The US Department of Energy’s Aquatic Species Program analyzed approximately 3000 different microalgae for their potential to produce biofuels (Kars et al. 2006).

## Conclusion

Algae is a group of morphologically diverse photosynthetic protists that live freely and in symbiotic relation with some organisms. It has various uses and applications including energy, biofuel production, and as various foods. Algae have some role in bioremediation and pollution control and also have chemical defense mechanism that protects them from invertebrate predation and herbivore grazing.

## Cross-References

- Evolution
- Herbivore

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## Alkaloid

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Alkaloids are cyclic compounds containing nitrogen in a negative oxidation state which is of limited distribution in a living organism. The term “alkaloid” marks its origin from the word “alkaline” which in Arabic means “ashes of plants.” They are generally known to be plant metabolites but are also produced by bacteria, fungi, and animals (Clark and Hufford 1992). Presently, more than 5,500 alkaloids are known and are highly placed with respect to their diversity, efficiency, and therapeutic significance. Research shows that almost 20% of the plants produce alkaloids and their major source in the flowering plants is the

angiosperm (Pelletier 1983). Being toxic in nature, their main role in plants is to defend them against the micro-organisms, insects, and herbivores.

Chemically, they are a class of natural compounds, majority of which contain nitrogen and a few of them being non-nitrogen heterocyclic organic amines. Mostly, basic in nature but these compounds can also range from being neutral to weakly acidic (McNaught and Wilkinson 1997). Apart from the usual carbon, hydrogen, and nitrogen, elements such as chlorine, oxygen, sulfur, phosphorous, and bromine might also exist in the alkaloids (Manske and Holmes 2014; Lewis 1998). Owing to their basic nature, they form alkaline solutions on dissolving in water and also form salts with acids. They are colorless, crystalline/liquid at room temperatures and have a bitter taste.

Attributable to the great structural diversity in the alkaloids, no fixed and uniform classification of the alkaloids exists. However, scientists most commonly divide the alkaloids into 5 classes:

- (a) **True alkaloids:** They owe their origin to the amino acids. The characteristic feature includes the presence of nitrogen in the heterocyclic ring. Some of the examples of this class include atropine, nicotine, and morphine (Plemenkov 2001).
- (b) **Protoalkaloids:** Like true alkaloids, protoalkaloids also originate from the amino acids but contain nitrogen which is not a part of the heterocyclic ring, e.g., mescaline, adrenaline, and ephedrine (Plemenkov 2001).
- (c) **Polyamine alkaloids:** Polyamine alkaloids are the derivatives of putrescine, spermidine, and spermine (Bienz et al. 2005).
- (d) **Cyclopeptide alkaloids:** They are macrocyclic compounds embodying ANSA (Ammonium N-phenyl-1-naphthylamine-8-sulfonate) structure. Further, they are most commonly present in Rhamnaceae family, e.g., mucronine and sativanine (Gournelis et al. 1997; Tuentner et al. 2017).
- (e) **Pseudoalkaloids:** They are pharmacologically active compounds which have not been derived from amino acids, e.g., caffeine and theobromine.

**Bioactivity of Alkaloids:** Alkaloids possess great chemical flexibility which brings about enormous biological activity. A single alkaloid can change its structure and play multiple functions depending upon the cellular conditions. This ability makes them a unique set of secondary metabolite compounds. Studies on the alkaloids produced by the *Amaryllidaceae* family shows that they function as analgesics, antivirals, anti-malarials, antineoplastics properties and also exhibit some effects on the central nervous system (Tadeusz 2007). Another, alkaloid fagaronine obtained from the *Fagara zanthoxyloides* Lam. (Rutaceae) has been known for the hemoglobi-nization of human leukemic cells (Dupont et al. 2005). Quinoline alkaloids obtained from the genus *Haplophyllum* A. Juss. (family Rutaceae) are associated with estrogenic effect (Nazrullaev et al. 2001). According to Caron et al. (1988), 34 quasi-dimeric indole alkaloids showed potent antibacterial activity against gram positive bacteria like *Staphylococcus aureus* and *Bacillus subtilis*. Other organisms which were found susceptible to 31 different alkaloids are *B. subtilis*, *S. aureus*, *Mycobacterium smegmatitis*, *Escherichia coli*, *Pseudomonas aeruginosa*, *Candida albicans*, and *Aspergillus niger*. An alkaloid allosecurinine was tested for the normal process spore germination of some saprophytic and pathogenic fungi, e.g., *Alternaria alternata*, *A. solani*, *A. brassicicola*, *A. brassicae*, *Curvularia lunata*, *C. pallescens*, *C. maculans*, *Curvularia species*, *Fusarium udum*, *Colletotrichum species*, *C. musae*, *C. gloeosporioides*, *Erysiphe pisi*, *Helminthosporium echinoclova*, *H. penniseti*, *H. spiciferum*, and *Heterosporium* sp. It has been noticed that it resisted mild spore germination of all the fungi tested whereas depicted high efficacy against *Curvularia lunata*, *Curvularia* sp., *Collectotrichum* sp., *C. musae* and *Heterosporium* sp. by complete inhibition of spore germination at very low concentrations (Singh et al. 2007). They also had extensive use in agriculture in the past where they were used as salts of nicotine and anabasine as insecticides (Matolcsy et al. 1988).

Thebaine, an alkaloid obtained from opium has been used to develop a new drug naloxone, which



is an opioid receptor antagonist (Dewick 2002). Many alkaloids like ajmaline, caffeine, atropine, colchicine, codamine, etc. are still used in medicines the form of their salts.

## Conclusion

Many alkaloids have been used for several hundreds of years in medicine and even today they are prominent sources of drugs. In most of the human history, alkaloids from plant extracts have been used as ingredients in liquid medicine and poisons. Ancient people used plant extracts containing alkaloids for treating a large number of ailments including: snakebite, fever, and insanity. Therefore, more research is required not only to completely understand the therapeutic potential of alkaloids but also to increase their production through tissue culture techniques.

## Cross-References

► [Plantae](#)

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## Allele Flow

► [Gene Flow](#)

## Allele Frequency

► [Gene Frequency](#)

## Allele Sharing

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## Synonyms

[Allele sharing methods; Identity by descent \(IBD\)](#)

## Definition

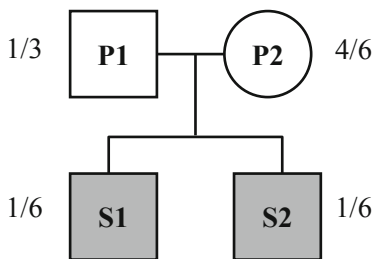
The sharing of alleles of certain genes and/or markers among siblings and related individuals.

## Introduction

The concept of allele sharing is derived from the Mendelian law of segregation of alleles. Two siblings (sibs) can exhibit allele sharing which is identity by descent (IBD) due to inheritance from a common parent. Sharing of allele can also be incidental when the reason for sharing is not known and is known as identity by state (IBS). According to Mendelian segregation rules, the probability that pair of siblings would share both marker alleles = 0.25, one marker allele = 0.5, and zero marker allele = 0.25. This follows the Mendelian expected ratio of 1:2:1.

## Allele Sharing Methods

These are popular nonparametric analytical methods used for the study of complex disorders. Affected sib-pair (ASP) analysis is one of the common and simplest of allele sharing methods (Fig. 1). If affected siblings or relatives share the



**Allele Sharing, Fig. 1** Affected sibpair analysis. Two affected sibs (S1, S2) and their parents (P1, P2) are represented. One affected son, S1 receives alleles 1/6 from her parents. Assuming Mendelian random segregation, his brother, S2, can either receive the same set of allele, IBD = 2 (as shown) with a probability of 0.25 or only one of them i.e., 1/6 or 3/6, IBD = 1, with a probability of 0.5 or receives a different set i.e. 3/4, IBD = 0, with a probability of 0.25 (zero sharing). If the marker is linked to the disease locus, the probability of the sharing of marker alleles will be increased in affected sibpairs (Drawn as interpreted from Lander and Schork (1994))

same alleles more often than chance, it may imply an association between allele and the disease. This might occur due to linkage between the marker alleles and the disease gene or candidate gene (Risch 1990; Lander and Schork 1994).

The classical parametric methods for linkage analysis rely on transmission disequilibrium test and are based on LOD scores. These methods therefore require the knowledge of inheritance mode of the loci, allele frequencies, number of loci affecting the disease phenotype, penetrance estimations, etc. Such methods are very successful in mapping genes or markers for Mendelian genetic disorders. However, in the case of complex disorders like diabetes, asthma, schizophrenia, and Alzheimer's, these methods might not prove helpful. Inheritance of complex disorders doesn't follow Mendelian genetics, and there are multiple loci influencing these disorders. Genotype-environment interaction also plays a big role in the manifestation of these disorders. It is often difficult to estimate mode of inheritance, allele frequencies, and penetrance expression in such cases.

Allele sharing method is a model-free non-parametric method and does not make any assumptions on mode of inheritance. It simply analyses whether the inheritance pattern of markers is consistent with Mendelian segregation. Sharing methods compare the actual sharing with the random probabilities, and a significant deviation indicates linkage. However, these methods usually involve studies on very large samples of sib pairs. Usually, such methods are used along with linkage analysis (Risch 1990; Whittemore and Halpern 1994; Kruglyak et al. 1996; Kong and Cox 1997). Allele sharing data is observed to increase the power and efficiency of disease – marker association studies – and helps in search for variants that predispose to complex disorders (Fingerlin et al. 2004). Allele sharing methods can be used for the analysis of qualitative as well as quantitative traits, whereas affected sib-pair method is used to investigate the possible sharing of maternal or paternal alleles by IBD. The analysis of quantitative traits by this method involves the understanding that siblings that share more alleles at a locus by IBD

should be phenotypically more similar than siblings that share fewer alleles. In a study carried out on 80 sib pairs affected with juvenile rheumatoid arthritis (JRA), excess sharing of two HLA-DR alleles was observed among ASPs with JRA (Prahalad et al. 2000). Similar studies for other complex genetic disorders like osteoarthritis (Callegaro et al. 2010) and venous thromboembolism (DeVisser et al. 2013) demonstrate the use of allele sharing methods for increased efficiency of linkage analysis.

## Conclusion

Allele sharing methods are important analytical tools for complex genetic disorders as they are nonparametric in nature and are therefore advantageous over parametric methods. However, studies need to be carried out on large samples of sib pairs or related individuals for effective interpretations, although determining the mode of inheritance of major susceptibility genes in a complex disorder may provide useful information to understand the disease.

## Cross-References

- [Allelic Association](#)
- [Mendel's Laws](#)
- [Pedigree](#)

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## Allele Sharing Methods

- [Allele Sharing](#)

## Alleles

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## Synonyms

[Allelomorph](#)

## Definition

Alleles are variant forms of a gene that differ in sequence information.

## What Are Alleles at Genetic Level?

The term allele refers to variant forms of a gene. A gene can be considered as any stretch of the DNA that gets transcribed, i.e., gets converted to RNA. So, a gene is basically a sequence of nucleotides that is characterized by its specific loci or position in the genome.

The nucleotide sequence information of a gene can have variants and each variant of the gene having a different sequence is referred to as an allelic form or allele of the gene.

A gene may have a single or multiple allelic forms.

## How Do Allelic Forms Arise?

Allelic variants arise due to mutations, i.e., changes in the sequence information (Watson 2014). Suppose a gene has a single allelic form having a particular sequence. In course of time, the sequence can get changed due to variety of factors, and the new form with the changed sequence is considered as a new allelic form of the same gene.

## How Do Alleles Function Differently?

It is the sequence information of the gene that determines the product that it is going to form. Alleles differ in sequence information and site of the variation determines the type of change observed:

- A change in the coding sequence may result in alteration in the amino acid sequence of the resultant protein. Such changes may or may not affect the structure and functionality of the protein.
- A change in splice sites may induce larger-scale changes with splice variants being formed.
- Changes in regulatory regions have the potential to alter the transcription rate and therefore the abundance of the product.

Changes in untranslated regions can alter the RNA stability and therefore the abundance of the product.

It is also possible that an allelic variant may not affect the protein functionality or abundance. But whenever there is a significant change in functionality or abundance of a gene product, it alters the overall cellular processes under its control and gives rise to an alternate phenotype.

## Example of Allelic Systems: Single, Two, Multiple

While a few genes may have single allelic forms, most of the genes are polymorphic, i.e., they have multiple allelic variants at the population level. Technically, a gene is defined as polymorphic if the rarer allele has an abundance of at least 1% at the population level (Futuyma 2006).

Historically, the most abundant allelic form of a gene in a population was referred to as the wild type allelic form, while the other rarer forms were considered as mutant types. Now it is known that most alleles are highly polymorphic and the population frequency of different allelic forms depends on the particular population under consideration. What is wild type in a particular population can be a rare form in another population.

It must be remembered that the maximum number of alleles an individual organism can have is equal to its ploidy, i.e., the number of haploid sets it possesses. For diploid organisms like humans, maximum two allelic variants are possible in a single organism. Likewise, haploid organisms have single allelic forms, while tetraploids may have as many as four allelic variants in one individual. If an organism possesses the same allelic form of a gene in each of its homologous chromosomes, then it is considered as homozygous for that gene. If the allelic forms are different, then it is considered as heterozygous for that locus.

Therefore, the maximum number of allelic variants that an organism can possess is limited by

the number of haploid sets. Polymorphism exists at the level of population and not individual.

For example, human AB blood group has three major allelic forms, A, B, and O at population level, but an individual may only have maximum of two allelic forms.

Major histocompatibility complex genes, which form a crucial element of our immune system, have hundreds of allelic variants.

**Dominant and Recessive Alleles**

Alleles can be either dominant or recessive in terms of their expression (Snustad and Simmons 2003). If an allelic form can express its phenotype in heterozygous configuration, i.e., when other allelic forms are also present in the organism, then its expression is said to dominate over the expression of the other alleles, and such alleles are considered as dominant alleles. The allele whose expression is suppressed by the dominant counterpart is considered as the recessive allele. Such recessive alleles require homozygous condition to express their phenotype.

It must be understood that dominance and recessiveness are relative phenomenon. Consider three allelic forms for fruit color: A1 (red), A2 (pink), and A3 (white). Allele A2 may be recessive to allele A1 such that a genotype A1A2 would show phenotype of A1 (red). But the same recessive allele A2 may be dominant to allele A3 in a way that A2A3 shows phenotype of A2 (pink). In the first case, A1A2, allele A2 is recessive, while in the second case, A2A3, the same allele A2 is dominant. So the dominance hierarchy is as follows for these three alleles

$A1 > A2 > A3$ . It is evident that the dominance or recessiveness of an allelic form depends on the other allelic form it is paired with and thus it is a relative phenomenon. Dominance is the relationship between two alleles of a gene and their associated phenotypes (Table 1).

Dominance and recessiveness are only applicable in heterozygous context.

Sometimes, the resultant phenotype may be a mixed expression of the two participating alleles. For example, flower color allele B1 (red) and allele B2 (yellow) in heterozygous condition B1B2 would produce a mixed orange color phenotype. In such a configuration, allele B1 and B2 are considered to be incompletely dominant over each other.

Alleles can also be codominant where both allelic forms express at the same time. ABO blood group is a prime example where individuals with AB genotype show simultaneous expression of A as well as B form of the glycoprotein on their red blood cell surface.

**Determination of Allelic and Genotype Frequencies in a Population**

For populations following the assumptions of Hardy–Weinberg equilibrium, the allelic and corresponding genotype frequencies can be calculated from each other by simple mathematical relations.

Hardy–Weinberg equilibrium assumes the following (Hartl and Clark 2007):

- 1. Organisms are diploid.
- 2. Sexual reproduction is the sole mode of reproduction.

**Alleles, Table 1** Table showing dominance hierarchy between multiple allelic forms of a gene

| Genotype | Allele 1 | Allele 2 | Phenotype of allele 1 | Phenotype of allele 2 | Phenotype of organism | Dominance status of allele 1 | Dominance status of allele 2 |
|----------|----------|----------|-----------------------|-----------------------|-----------------------|------------------------------|------------------------------|
| A1A1     | A1       | A1       | Red                   | Red                   | Red                   | Homozygous                   | Homozygous                   |
| A2A2     | A2       | A2       | Pink                  | Pink                  | Pink                  | Homozygous                   | Homozygous                   |
| A3A3     | A3       | A3       | White                 | White                 | White                 | Homozygous                   | Homozygous                   |
| A1A2     | A1       | A2       | Red                   | Pink                  | Red                   | Dominant                     | Recessive                    |
| A2A3     | A2       | A3       | Pink                  | White                 | Pink                  | Dominant                     | Recessive                    |
| A1A3     | A1       | A3       | Red                   | White                 | Red                   | Dominant                     | Recessive                    |

- 3. Mating is random.
- 4. Population is infinitely large.
- 5. Generations are nonoverlapping.
- 6. Allele frequencies are same in both sexes.
- 7. No selection pressure is operative.
- 8. Mutation is not taking place.
- 9. No genetic drift or migration of organisms.

For a two allele system, the relation is as follows:

$$p + q = 1 \text{ and } p^2 + 2pq + q^2 = 1$$

where,

- p = frequency of allele p
- q = frequency of allele q
- p<sup>2</sup> = frequency of genotype pp
- q<sup>2</sup> = frequency of genotype qq
- 2pq = frequency of genotype pq

**Allelic Variants Contributing to Genetic Disorders**

As allelic variants alter the function of the gene product, it is understandable that a number of variants can contribute to genetic disorders.

Many genetic disorders are caused by recessive alleles, where the heterozygotes act as “carriers” of the trait. The phenotype of the disorder is only evident in the homozygous individuals possessing two copies of the mutant allele. Lethal genetic disorders are mostly recessive in nature because otherwise the dominant lethal allele would prevent the deleterious allele from being passed on to next generation. Dominant lethal alleles can arise by spontaneous mutations but they are rarely propagated. Sometimes dominant lethal alleles may propagate if the onset of the disease is after the attainment of reproductive age (Table 2).

**Implications at Population Level**

At the population level, selection pressure determines the prevalence of any allelic form of a gene (Hartl 2012). If the prevailing conditions would

**Alleles, Table 2** Genetic disorders seen in humans and nature of the causative alleles. X-linked, Y linked, and autosomal mean that the corresponding gene loci are on X-chromosome, Y-chromosome, and autosomal chromosome, respectively

|                     |                                                                   |
|---------------------|-------------------------------------------------------------------|
| Autosomal dominant  | 1. Huntington’s disease<br>2. Familial hypercholesterolemia       |
| Autosomal recessive | 1. Sickle cell anemia<br>2. Cystic fibrosis<br>3. Phenylketonuria |
| X-linked dominant   | 1. X-linked hypophosphatemia<br>2. Rett syndrome                  |
| X-linked recessive  | 1. Duchenne muscular dystrophy<br>2. Red-green color blindness    |
| Y-linked            | 1. Azoospermia<br>2. Swyer syndrome                               |

favor a certain allelic variant, the frequency of that allele would keep increasing as long as the selection pressure is operative.

Consider this hypothetical example. Gene C controls body color of an insect X. Allele C1 produces green body color while allele C2 produces red. The insects live in lush green vegetation. Crows prey on these insects. Which allelic form would benefit the insects? Obviously allele C1 as it would allow better camouflage on the backdrop of the lush green vegetation. Therefore, as long as the crows are preying on the insects (selection pressure), the frequency of allele C1 would keep increasing. Insects having allele C2 will be preyed upon and eliminated.

Another very well-known real-life example is of the sickle cell anemia. Sickle cell anemia is caused by a mutant allelic form of hemoglobin. This mutant form is prone to polymerization and distorts the normal shape of RBCs, making them prone to breakage. In homozygous state, this mutation leads to deleterious condition sickle cell anemia. Normally this trait provides no advantage on the normal human physiology and heterozygous individuals show minor physiological problems.

Interestingly, in areas where Plasmodium malaria is prevalent, this mutant allelic form is much more and occurs at a much higher



frequency. Plasmodium needs RBCs to complete their life cycle. Mutant hemoglobin allele makes the RBCs prone to degradation and unsuitable for Plasmodium life cycle. Hence this mutant form is selected in heterozygous condition to make individuals resistant to Plasmodium malaria. This phenomenon is known as heterozygote superiority. This is a very elegant example of how varying selection pressure can alter the abundance of different allelic forms among populations.

In a situation where natural selection does not favor any particular allelic form, the abundance of different alleles would remain constant through generations.

In summary, alleles are the underlying factor which has made possible the amazing diversity we see in this world. Crossing over, random distribution of chromosomes, and other factors contributing to diversity are all dependent on the presence of allelic variants in the first place.

## Cross-References

- [Allele Sharing](#)
- [Allelic Association](#)
- [Autosome](#)
- [Balanced Polymorphism](#)
- [Carrier](#)
- [Chromosomes](#)
- [Directional Selection](#)
- [DNA](#)
- [Genes](#)
- [Genetic Variation](#)
- [Heredity](#)
- [Heterozygote Superiority](#)
- [Homozygosity](#)
- [Recessive](#)

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## Allelic Association

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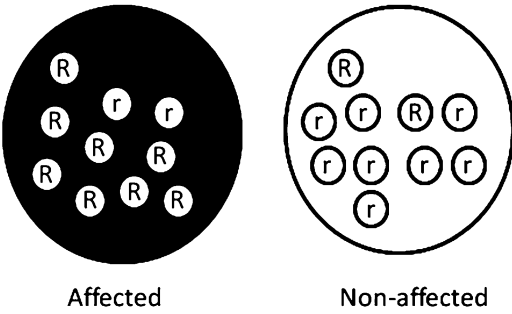
## Definition

Allelic association refers to the statistical association between an allele and the observed phenotype. It measures the frequency of co-occurrence of the allele and observed phenotype in a population, which is more than expected and nonrandom (i.e., not by chance). It is a population-specific characteristic, hence varies among populations and doesn't require observation of parental transmission of gametes carrying alleles.

## Introduction

Allelic association is an important parameter in population genetics to investigate genetic etiology of complex traits or diseases (Lowe and Reddy 2015). An allele is each of the two or more alternative forms of a gene present at a single locus on a chromosome. Allelic association refers to the statistical association of an allele to an observed phenotype, or a trait, in a population which is more than expected and nonrandom (i.e., not by chance). In simpler terms, it is an observation that how much





**Allelic Association, Fig. 1** Allelic association of a complex disease. (In affected group frequency of allele “R” is significantly more than allele “r” indicating its association with the observed complex disease in the studied population)

the variations in genotype correlate to the phenotypic variations. Let us take an example; assume that Fig. 1 indicates occurrence of a complex disease in a population. In genetic analysis, it is found that frequency of allele “R” is significantly higher than allele “r” in affected than nonaffected group; which gives a deduction that it has an allelic association with the observed complex disease.

A closely related but distinct concept is “linkage disequilibrium (LD)” or “gametic disequilibrium.” LD denotes random associations of alleles across loci located on the same chromosome, i.e., LD is an inter-allelic association rather than between an allele and a phenotype. LD arises due to faults of crossing over during meiosis in a gametic phase and its effect diminishes with time in the process of evolution due to recombination events in innumerable meiotic divisions which would shift loci and break inter-allelic linkage. The term “linkage disequilibrium” and “allelic association” should not be used interchangeably. Salient differences between allelic association and LD have been provided in Table 1.

Types

Allelic association to a trait may be direct – showing a cause-effect relationship, or indirect – through intermediary markers. A third type of association may be spurious, where apparent association is not linked to the genetic etiology.

**Allelic Association, Table 1** Allelic association versus linkage disequilibrium (LD)

| Allelic association                                                             | Linkage disequilibrium (LD)                                           |
|---------------------------------------------------------------------------------|-----------------------------------------------------------------------|
| Unrelated subjects can be studied; knowing the family pedigree is not essential | Subjects should be in genetic relation; family pedigree must be known |
| Allele should be at or near the gene affected                                   | Loci can be far away from the gene affected                           |
| Allelic heterogeneity affects the power                                         | Allelic heterogeneity does not affect the power                       |
| Applicable for common traits                                                    | Applicable for rare traits                                            |

Allelic Association Mapping Using Single Nucleotide Polymorphs (SNPs)

An allelic association can be studied searching single nucleotide polymorphs (SNPs) in candidate regions (Collins et al. 2001), or in genome-wide association studies (GWAS) (Bush and Moore 2012). A SNP arises from a single base-pair change at any locus in the DNA sequence, which occurs with high frequency in animal genome. SNPs are the chief source of genetic variations and play an important role in etiology of several complex and multifactorial diseases. Susceptibility or protection to a particular disease has been found well correlated with several polymorphisms. Association mapping studies identify functional polymorphisms (polymorphism producing an effect in gene function) that predispose to complex diseases. Population-based approaches are concerned with exploiting allelic associations between the SNPs and disease-predisposing loci (Collins et al. 2001). The 1000 Genomes Project Consortium provides an extensive online database of SNPs across worldwide populations, a highly valuable source for studying genetic etiology of common diseases (The 1000 Genomes Project Consortium 2015). Computational technology has revolutionized the statistical analysis of allelic association. ALLASS is publicly available software for mapping a disease locus by allelic association (Collins and Morton 1998).

## Allelic Association Versus Linkage

Allelic association denotes that frequency of a single or group of alleles at a gene locus is correlating with the observed phenotypic outcome. In comparison, linkage gives an indication that a particular region of a chromosome which is showing enhanced linkage signaling for the used probe markers for a phenotypic outcome contains the causative alleles. Hence, allelic association analysis is a high-resolution study which would point to a gene locus or a particular allele (which would be a few base pair long), and linkage is a low-resolution study which only indicates to a specific segment of a chromosome (a segment is limited by breaking sites of a chromosome during meiosis event for recombination and each may contain few thousands of base pairs). In this sense, a prior linkage analysis for a phenotypic outcome narrows down the search in the whole genome (which contains about 3 billion base pairs) to a particular chromosomal segment (containing a few thousands of base pairs) where a causative allele should be searched for.

## Allelic Association Analysis

There are two designs commonly used for studying allelic association, one is population based (or proper case-control study) and another is family based. In a population-based study, a difference of the allelic frequency at particular loci is measured between the case – in which observed phenotype is present and a control – in which observed phenotype is absent. As the allelic frequency may naturally vary between different populations and in the sections of a single population, so a population-based study may be confounded by naturally occurring allelic variations in subsections of a population, a concept which is called “population stratification” (Wang et al. 2006). The family-based designs take care of the natural variation of allelic frequency in segments of the population, in which comparison is made between participants from the same family. Allelic frequency variation is measured in parents who

bear the allele and phenotype is expressed in the offspring (case) and compared with the other parents belonging to the same family who bears the allele but the phenotypic effect is not transferred to the offspring (control).

The science of investigating causal genes or alleles or a DNA segment for a phenotypic variance is called “reverse genetics” (Griffiths et al. 2000). The identification of a particular gene or allele responsible for the observed phenotypic variance can be done by “positional cloning” (a common method used in reverse genetics) which involves three steps: (i) “meiotic mapping” which allows identifying DNA segments containing causal gene or allele (Lodish et al. 2000), (ii) physical mapping which includes sequencing of the marked DNA segment (O’Rourke 2014), and (iii) finding mutation in the decoded sequence and verifying its functional role. The intermediary marker alleles (which are showing increased frequency with the observed phenotype but not create a cause-effect relationship) can be also used to locate a causative allele or gene which can be further reached by sequencing of the DNA segments in proximity. Any significant difference in allelic frequency between the genetically unrelated case and control (population-based study) can be tested by the classical Pearson’s  $\chi^2$  test. If case and control are genetically related (family-based study), transmission disequilibrium test (TDT) can be applied which is based on allele transmission rate between genetically related individuals (Ewens and Spielman 2004).

## Cross-References

- ▶ [Alleles](#)
- ▶ [Base Pair](#)
- ▶ [Crossover](#)
- ▶ [DNA Marker](#)
- ▶ [Gene](#)
- ▶ [Gene Frequency](#)
- ▶ [Gene Map](#)
- ▶ [Indirect Association](#)

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## Allelomorph

- [Alleles](#)

## Alligator Locomotion

- [Crocodilia Locomotion](#)

## Allocare

- [Alloparental Care](#)

## Allogrooming

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## Synonyms

[Grooming](#); [Social grooming](#)

## Introduction

Allogrooming is a form of caregiving through physical contact, typically where one animal uses its hands, mouth, or other part of its body to touch another animal (Dunbar 2010; Newton-Fisher and Kaburu 2017; Spruijt et al. 1992). The mechanical motion of grooming resembles scratching, picking, stroking, or rubbing (in some animals licking and nibbling) and is directed towards the outer body surface, whether that surface is fur, feathers, or bare skin (Dunbar 2010; Pellis and Pellis 2010; Spruijt et al. 1992). Grooming is widely studied in primates (Dunbar 2010; Newton-Fisher and Kaburu 2017; Schino and Aureli 2010; Spruijt et al. 1992), but it occurs in a wide variety of other animals too, including arthropods, birds, and other mammals such as ungulates and rodents (Pellis and Pellis 2010; Spruijt et al. 1992). The word “allogrooming” means “grooming another” and usually refers to same-species grooming. The functions of allogrooming (why it exists and what the benefits are) are many and varied (Spruijt et al. 1992), but there are two main functions: (1) allogrooming provides a cleaning service, and (2) it confers a social benefit.

## Hygiene

Cleaning is the primary function of allogrooming across all animals who do it (Spruijt et al. 1992). For example, in many insect species, allogrooming plays a very important role in disease control. Insects have been observed to remove pathogens from each other's bodies through allogrooming (Zhukovskaya et al. 2013). Among birds, the definition of grooming overlaps with the definition of "preening," and hence the term "allopreening" is used (Spruijt et al. 1992). Allopreening has been shown to have an important cleaning function in birds. For example, in a study of pigeons, the incidence of allopreening in test pairs was found to have an inverse relationship to the number of lice found in the feathers of those pairs (Villa et al. 2016). The cleaning function is also well known in mammals, particularly primates (Spruijt et al. 1992). For example, in a study of allogrooming in baboons, those individuals who received more grooming had fewer ticks in their fur and were consequently healthier than those who received less grooming (Akinyi et al. 2013).

## Sociality

Beyond the cleaning function, allogrooming is integral in the social repertoire of many species (Dunbar 2010; Pellis and Pellis 2010; Spruijt et al. 1992). Allogrooming is a markedly intimate social pastime, requiring the focused concentration of the groomer and the sitting-still willingness of the groomee. Gupta and Sinha (2016), studying wild bonnet macaques, observed how attentively the groomer responded to gestures of the groomee. For example, if the groomee held out its tail while being groomed elsewhere on its body, the groomer switched its grooming attention to the tail. The same would happen if the groomee moved other parts of its body into the attentional gaze of the groomer: the groomer would switch to grooming the area that the groomee gestured towards. In fact, the investigators determined that groomers responded "appropriately" (switching grooming to the body part

indicated) to more than 94% of pertinent gestures, a result which illustrates the keen two-way sensitivity that constitutes allogrooming behavior. In the everyday lives of animals, allogrooming is often mixed in with other social bonding behaviors such as social play (Pellis and Pellis 2010). Social touching is a vital constituent of many animal societies (Dunbar 2010; Pellis and Pellis 2010; Spruijt et al. 1992). When two individuals engage in a grooming bout, it creates pleasure for the groomee because the tactile stimulation causes the release of endorphins in the groomee's body (see review in Dunbar 2010), which helps strengthen the social bond between the two animals (the groomee associates that groomer with pleasure) and it also reduces tension (Dunbar 2010; Russell and Phelps 2013).

## Grooming Markets

Allogrooming is therefore a valuable behavior: it cleans, it reduces tension, it is a social bonding mechanism, and it feels pleasurable to receive. Because of this value, scientists have studied allogrooming as a kind of natural version of money. For example, 10 min of grooming is a "parcel," a finite period during which the groomer is providing a service to the groomee. Hence, one can think of this parcel of grooming as a kind of payment, with a benefit to the receiver and (presumably) some cost for the giver (Russell and Phelps 2013). Using this idea of grooming as a currency, an animal society can be viewed as a "marketplace" wherein commodities (such as allogrooming) can be traded back and forth somewhat like money (see Dunbar 2010; Newton-Fisher and Kaburu 2017; Schino and Aureli 2010; Russell and Phelps 2013). In most primate species, grooming happens often (Dunbar 2010) and therefore scientists have devoted considerable attention to the issue of grooming *reciprocity*: where an "animal... makes a direct trade of 10 min of grooming for 10 min of being groomed" (Dunbar 2010, p. 263) (10 min is therefore a "parcel size"). In a meta-analysis of 14 primate species across 25 different datasets, Schino and Aureli (2010) tested whether reciprocity is an

important explanatory factor in a primate's decision to start grooming someone (i.e., groom those who have given you grooming in the past) – in contrast to the influence of kin selection (i.e., groom those who are members of your family group). They found that reciprocity played a larger role than kin selection in explaining allogrooming efforts, a result that demonstrated the importance of allogrooming as a tradeable currency in primate societies.

### Allogrooming as Chimpanzee Politics

Allogrooming is a decision. At a given time, an animal chooses to start grooming someone else. In a complex social setting, there might be various factors that influence that decision. As described above, a primate may choose to groom as a form of reciprocation (Schino and Aureli 2010). However, a social group often consists of more than two individuals. Imagine a group of three individuals. There, the decision becomes one of preference: you can only groom one at a time, so your decision about whom to groom depends on your preference. The decision becomes further complicated if the group has four, five, six, or more. This becomes the marketplace as described above: you have a commodity to give or to receive, and a number of individuals with whom you can choose to groom. Far beyond a simple cleaning task, a chance to bond socially or to pay back a favor – the grooming decision in a large group becomes political. One can look at the chimpanzee study of Newton-Fisher and Kaburu (2017) to illustrate the complexities of a grooming decision. Specifically, they investigated the influence of two other variables: *dominance* and *bystander effects* (both described below). Observing a large group of chimpanzees ( $N = 63$ ) at the Budongo Forest Reserve (Uganda), the investigators focused on the allogrooming of eight adult males. These males differed from each other in their dominance rank, which was calculated based on the outcome of aggressive interactions between the males: for each observed fight, a winner and a loser was determined – a male was recorded as being a loser if he was observed “screaming, cowering or

running away, or receiving but not returning physical violence and/or wounds” (Newton-Fisher and Kaburu 2017, p. 156). The dominance hierarchy was established by counting the wins and losses, and ranking the males accordingly (the alpha was the male with the most wins compared to losses). They then calculated “rank distance” by subtracting lower scores from higher scores. This means that, for each pair of males, they had a score of how far apart the males were on the dominance hierarchy (e.g., the first and fifth most dominant had greater rank distance than the first and second). The other important variable in the study – the bystander effect – referred to the effect of having other chimpanzees in the vicinity of an allogrooming event, but not participating in the focal grooming.

Based on their data, Newton-Fisher and Kaburu (2017) had a number of results that showed how grooming decisions in chimpanzee males were influenced by the interaction of rank distance and bystander effect. They had six main significant results. The first result concerned the beginning of a grooming bout, when a subordinate male approached a dominant male and started grooming. They measured “initial investment,” which referred to how long the subordinate male spent grooming the dominant before the dominant responded in any way (e.g., starting to groom back). In other words, the investment is the degree of grooming effort that a subordinate is willing to expend with no payoff. They compared a number of different grooming pairs, with varying extents of rank distance between pairs. They found that with greater rank distance, the initial investment was greater. This illustrates how subordinates were willing to invest substantial unreciprocated grooming effort depending on their position in the hierarchy. Clearly, allogrooming is a kind of strategy that subordinate males were using in response to dominance – and the degree of effort invested depended on rank distance. Other results obtained in this study involved bystanders and how dominant the bystanders were. They found that, if bystanders were high-ranking, the initial investment and the parcel size were lower than if the bystanders were not as high-ranking. This showed that the mere presence of a dominant male had an

effect on a chimpanzee's grooming decision, even though that dominant was not directly involved. A related analysis was the rank distance between the bystander and the groomee. They found that initial investment was lower commensurate with the rank distance. In other words, the groomer tended to invest less grooming to the groomee if the bystander outranked the groomee. Finally, the study had two results related to the reciprocation of grooming – specifically, whether the groomee would pay the grooming back while being groomed. They found that reciprocation was more likely if there were fewer bystanders. They also found that grooming was more likely to be reciprocated if there was a smaller rank distance between the two groomers. Overall, the results of Newton-Fisher and Kaburu (2017) illustrate how allogrooming is more than an isolated event between two individuals. Allogrooming is, for many animals, an essential protocol in their social politics.

## Cross-References

- [Affiliative Behaviors](#)
- [Aggression](#)
- [Agonistic Behavior](#)
- [Altruism](#)
- [Communication Networks, Eavesdropping, and Audience Effects](#)
- [Conspecifics](#)
- [Decision-Making](#)
- [Dominance](#)
- [Dominance Hierarchy](#)
- [Friendships in Animals](#)
- [Game Theory](#)
- [Grooming](#)
- [Helping Behavior](#)
- [Kin Selection](#)
- [Kinship](#)
- [Mutualism](#)
- [Primates](#)
- [Rank](#)
- [Social Affordance](#)
- [Social Behavior](#)
- [Social Grooming](#)

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## Allometry

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Allometry, in a broad sense, describes how phenotypic traits change with changes in overall body size. Biological variation in a large range of physiological, morphological, ecological, and life-history traits is highly correlated with variation



in organism size, and the concept of allometry represents important hypotheses for understanding this trait variation.

## The Allometric Model

Allometric scaling relationships are described by power functions, often referred to as allometric equations. They have the form  $Y = aX^b$ , where  $b$  is the scaling exponent that describes how the trait  $Y$  relates to changes in the overall size variable  $X$ . When  $b = 1$ , traits enlarge proportionally to overall size, a case which is referred to as isometry. The shape of the organism will not change with changes in overall size if traits scale isometrically. When  $b \neq 1$ , the size of the trait will change in different proportions to changes in overall size, and the shape of the organism will change with changes in overall size. Allometric relationships with an exponent smaller than 1 are referred to as negative allometry, while relationships where  $b > 1$  are referred to as positive allometry.

A power function yields a linear equation on a log-log scale,  $\log(Y) = a + b\log(X)$ , where  $b$  is the allometric scaling exponent. The conventional way of estimating the parameters in an allometric scaling relationship is to fit a least square regression on log-transformed trait and body size data. The log-transformation of the data is not to linearize the relationship but to analyze the data on a proportional scale, assuming errors are multiplicative rather than additive (Kerkhoff and Enquist 2009). The  $a$  parameter represents the intercept of the linear model and will equal the mean of the trait if the body size data are centered around zero before fitting the linear model.

Variation in body size exists at several levels and three different types of allometries have traditionally been recognized based on three different sources of variation in body size (Cheverud 1982). Two types of allometry are estimated using within-species data: Ontogenetic allometry refers to the scaling relationship between a trait and body size during the growth of individuals, while static allometry refers to the observed scaling relationship between a trait and body size

across individuals measured at a similar developmental stage. Evolutionary allometry refers to the scaling relationship observed among population or species means.

## Examples of Allometric Relationships

Allometric scaling relationships have been important for structuring knowledge of size variation of traits (Schmidt-Nielsen 1984). An example is the scaling relationship between brain mass and body mass, which has attracted interest for more than a century. Although empirical estimates of the allometric exponent ( $b$ ) in the relationship between brain and body mass among mammal species vary, it is always found to be less than 1. The negative allometric scaling relationship of brain size across species indicates that brain mass does not generally increase in equal proportion to increases in overall body size. In other words, given their smaller body size, shrews have a proportionally larger brain size than elephants. The allometric model also allows an assessment of which species having a smaller or bigger brain size than predicted by their body size. For example, according to a study by Boddy et al. (2012) who studied the allometric scaling relationship between brain mass and body mass in more than 600 species of mammals, baleen whales have brain sizes less than predicted by the allometric model given their body mass, while humans have a brain size much larger than the predicted value.

Allometric scaling relationships have also inspired hypotheses explaining how and why specific traits scale the way they do. For example, the positive allometry hypothesis claims secondary sexual traits almost universally exhibit positive static allometry ( $b > 1$ ) since a steep allometric exponent will evolve if an increased relative trait size yields increased fitness (see Bonduriansky 2007 for a review of the positive allometry hypothesis). Another popular hypothesis is the negative allometry ( $b < 1$ ) of genitalia in spiders and insects, often explained by the advantage of males having genital sizes that are appropriately adjusted to the most common size of internal genital structures in females (Eberhard 2009).



Although these hypotheses often hold, traits under natural selection show both positive and negative allometry, which suggests that steepness of the allometric exponent is not a reliable indicator of the type of selection that has operated on a trait (Voje 2016).

### Allometry Reflecting Adaptation or Constraint?

To what extent ontogenetic allometries are expected to predict static and evolutionary allometric relationships is debated. Hypotheses explaining evolutionary allometries fall in two broad categories: those based on developmental constraints and those based on functional adaptation between traits and overall size. Huxley (1932) showed that if two morphological traits grew in proportion to each other, variation in growth rate would necessarily produce a scaling pattern between them that follows a power relationship. If the growth relationship of a particular trait is more or less fixed among species, evolutionary changes are bound to follow trajectories imposed by ontogenetic or static allometries, meaning evolutionary allometries must be similar to these. Partially supporting the allometry as constraint hypothesis is the observation that ontogenetic and static allometries are found to be rather invariant and tend to predict evolutionary divergence below the species level, but less so on longer time scales (Voje et al. 2014). An alternative explanation of the low variability of static and ontogenetic slopes is that natural selection favors particular scaling relationships between traits and overall size. Attempts of changing the static slope in artificial selection experiments have indeed succeeded, but the changes have been very small, indicating a low evolvability of the allometric slope parameter (Bolstad et al. 2015).

### Cross-References

- [Adaptation](#)
- [Coevolution](#)
- [Ontogeny](#)

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### Allomother

- [Alloparental Care](#)

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### Allomothering

- [Alloparental Care](#)

## Alloparental Care

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### Synonyms

[Allocare](#); [Allomother](#); [Allomothering](#); [Aunting](#); [Auxiliary](#); [Helper](#)

### Definition

“Alloparental care” is care that is directed by an individual (an alloparent) toward dependent young that are not their offspring (Wilson 1975). The act of providing alloparental care is referred to as “alloparenting.”

### Types of Alloparental Care

Alloparental care has been reported widely across the animal kingdom, specifically in birds (Koenig and Dickinson 2004), fishes (Wisenden 1999), invertebrates (Wilson 1971), and mammals (Solomon and French 1997). Animals employ a variety of strategies to produce and rear their young, which influences the ways that alloparents can contribute care. Most birds, fishes, and invertebrates lay eggs, while all mammals (aside from monotremes) give birth to live young. In most mammals, milk is the sole medium of nutrient intake for young during the first stage of life. In other taxa, young immediately feed on similar materials to mature individuals, either with the assistance of foraging parents (or alloparents), as in birds, or independently, as in fishes. These differences in the ways that animals rear their young have led to the diversity of alloparental care expressed across the animal kingdom;

alloparental care encompasses a wide array of behaviors, including allonursing, food provisioning, grooming, nest building, territory defense, thermoregulation, and transport.

### Alloparental Care Across Breeding Systems

Alloparental care is exhibited by animals living across a range of social systems. These behaviours occurs mostly in group-living animals classified among three types of breeding systems: eusocial, cooperative, and communal. “Eusocial breeding” is when a dominant breeding pair is assisted by permanently nonbreeding alloparents to rear their offspring. Alloparents specialize in specific types of care, which can result in behavioral, morphological, and physiological differences between alloparents with different specializations, often referred to as castes. Eusocial breeding has been reported in invertebrates, such as ants, bees, termites, and wasps, as well as two mammalian species, the Damaraland mole rat (*Fukomys damarensis*) and the naked mole rat (*Heterocephalus glaber*). “Cooperative breeding” is when a dominant breeding pair is assisted by nonbreeding alloparents to rear their offspring, with more flexible parameters than eusocial breeding; alloparents need not specialize in one type of offspring care over their entire lives. In cooperative breeders, alloparents are often the dominant breeders’ offspring that have not yet dispersed from their natal territory. Cooperative breeding is relatively common among birds, while less so in mammals and fishes. “Communal breeding” is when offspring care is shared by multiple breeding individuals that can also be assisted by temporarily nonbreeding alloparents. Communal breeders do not necessarily need to breed at the same time, meaning that individuals can take turns breeding and providing care for one another’s offspring. Most social animals that are not eusocial or cooperative breeders can be considered communal breeders due to the more relaxed definition (i.e., cetaceans, bats, elephants, most primates, lions; Solomon and French 1997, pp. 1–10). While communal breeding is common

in mammals, it is relatively rare among birds and fishes.

In species that breed eusocially, cooperatively, or communally, alloparents and breeders live together and thus often have ongoing social interactions. Alloparental care is also exhibited by “solitary breeders,” which are common across the animal kingdom and include birds, fishes, insects, and mammals. Solitary breeding is when young are raised by one or two individuals, which can be either the genetic parent(s) and/or an alloparent. Alloparental care in these types of breeders can occur following the eviction, voluntary leave, or death of a genetic parent(s) and subsequent replacement by an individual that provides care for the young that were left behind (termed “adoption” in some species). Adoption can also occur when parents actively transfer (or farm out) their offspring to an alloparent that provides care for their young (Wisenden 1999).

### Misdirected Parental Care

Alloparental care can be misdirected parental care, when individuals are deceived into providing care for another individual’s offspring as a result of ineffective or absent kin recognition mechanisms. In these cases, an alloparent is unable to differentiate between young that they themselves produced and another individual’s young. In birds and fishes, this can occur when individuals lay their eggs in the nest of another breeder (termed “brood parasitism”). Some fish species may also covertly deposit their gametes at competing individuals’ spawning sites. In mammals, females have been observed to mate with multiple males to confuse paternity in an attempt to secure care from multiple males (termed “cuckoldry”). This may result in a male providing care for dependent young that are not his own offspring but that he believes to be his own based on past mating behavior. For the remainder of this entry, we will focus on alloparental care that is not a result of misdirected parental care. Below, we discuss the ultimate and proximate drivers of alloparental care, with selected examples from three vertebrate taxa: birds, fishes, and mammals.

## Evolution of Alloparental Care

### Fitness Benefits of Alloparental Care to Parents and Their Offspring

There is evidence in many species that alloparental care improves parents’ long-term survival, their future reproductive success, and/or the fitness of their current offspring (Tanaka et al. 2018; Russell et al. 2007; Brouwer et al. 2012). The distribution of fitness benefits among parents and their offspring depends on the ways that parents respond to alloparental care. Their responses can vary widely, with parents maintaining their care (termed “additive effects”) at one end of the spectrum and reducing their care to offset alloparental care (termed “load-lightening effects”) at the other end (Hatchwell 1999). For instance, in birds that exhibit additive effects, hatchlings will be provisioned with more food as the number of alloparents visiting the nest increases. Conversely, in birds that exhibit load-lightening effects, parents will reduce their provisioning rates as the number of alloparents increases and hatchlings will receive the same amount of food regardless of alloparental number. The way that parents respond to alloparental care varies across the animal kingdom, with some species showing additive effects, some showing load-lightening effects, and some showing an intermediate response (Hatchwell 1999). Load-lightening effects have also been documented in response to *expected* alloparental care through a reduction in prenatal parental investment. For instance, in some bird and fish species, mothers that anticipate assistance from alloparents based on group composition will reduce their offspring investment at the egg-laying stage, leading to smaller eggs and thus, smaller hatchlings (Dixit et al. 2017). Smaller hatchlings that are provided with additional care from alloparents exhibit “catch-up” growth and, ultimately, attain the same sizes that they would have if their mothers had laid larger eggs. The way that parents respond to alloparental care ultimately represents a trade-off between current and future offspring investment. Load-lightening effects tend to increase parents’ survival and future reproductive success, while additive effects tend to increase the fitness

of their current offspring. Across the animal kingdom, alloparental care influences the fitness of parents and/or their offspring in various ways, as shown in the next paragraph.

Alloparental care can shorten the amount of time that elapses between births and increase the size of the litter or brood in species where multiple offspring are produced at a time. For instance, alloparental care in mammals can increase mothers' energy balance because they are able to forage more often or more efficiently, or rest more while their offspring are cared for by alloparents. This can increase mothers' milk nutrient densities and improve the nutrient intake of offspring during nursing bouts. This leads to accelerated offspring growth and earlier weaning, which can allow mothers to return to estrous more quickly and, ultimately, increase their lifetime reproductive output (Solomon and French 1997, pp. 11–33; Mitani and Watts 1997). There is limited evidence that alloparental care impacts the long-term survival of parents; however, this has been shown in some species (i.e., superb fairywrens, *Malurus cyaneus*; Russell et al. 2008).

In many species, there is evidence that alloparental care improves the lifetime survival and/or reproductive success of offspring. This has been attributed to the fact that offspring that receive alloparental care tend to be heavier at independence. Heavier offspring are more likely to survive in the long-term, reproduce for the first time at a younger age, and/or be more attractive to the opposite sex (Hodge et al. 2009; Russell et al. 2007). Lastly, in some social species, affiliative interactions during infancy (the time from birth to the end of weaning) that occur between alloparents and young can be maintained throughout life. These social bonds can lead to life-long fitness benefits for both parties (Maestripieri 1994).

### Fitness Costs of Alloparental Care to Alloparents

There is compelling evidence across the animal kingdom that alloparental care can be costly to the alloparent (Heinsohn and Legge 1999). Alloparents will incur different costs depending on the type and frequency of support that they provide to young as well as their own developmental

stage. To provide care, alloparents often forego foraging time, which can lead to weight loss (or failure to gain weight). Alloparents across taxa may spend time babysitting other individuals' young to ensure that they are warm and safe from predators. This can have substantial costs for the alloparent. For instance, individuals that spend the day babysitting can lose body weight throughout the day, while those that forage with the group will gain weight (Clutton-Brock et al. 1998). In addition to lost feeding time, alloparental care can be costly if behaviors are energetically demanding. Two of the most energetically demanding forms of alloparental care are allonursing and transport (Solomon and French 1997, pp. 11–33). “Allonursing,” when females nurse young that are not their own offspring, is highly energetically demanding and has been reported in a wide variety of mammals, including primates, cetaceans, and canids (MacLeod and Lukas 2014). Transport is a behavior mostly reported in primate species, as young are transported with the rest of the group throughout the day immediately following birth until they can locomote independently (Fig. 1). In addition to incurring high-energy expenditure, transport likely reduces alloparents' feeding efficiency as well as their agility when moving through trees, which can have consequences when fleeing from predators (Solomon and French 1997, pp. 11–33). There are also many mouth-brooding fishes where



**Alloparental Care, Fig. 1** Female ursine colobus monkey (*Colobus vellerosus*) holding the infant of the female to her right. (Photo by Stephanie Fox)

alloparents transport other individual's young in their mouth, which impedes their ability to feed (Wisenden 1999). Provisioning young with food items can also be costly, although the costs of provisioning will depend on a species' foraging strategies. In contrast to birds and mammals, most fish species do not provision their young with food. This narrows the potential costs of alloparenting to elements of predator protection and burrow maintenance.

Weight loss (or failure to gain weight) can have substantial fitness impacts on alloparents in the long term, particularly in alloparents that are still developing into adults. As mentioned above, individuals that are heavier at independence often have higher reproductive success; thus, if alloparental care reduces individuals' ability to gain weight, it could have long-term fitness consequences (Lindström 1999). In species where alloparental care is provided by mature and/or postreproductive individuals, weight loss is likely less costly in the long term. There is compelling evidence across taxa that alloparents incur costs when providing care. Why then should animals engage in these behaviors, if they are not just cases of misdirected parental care? Despite the fitness costs associated with providing care to another individual's offspring, there are inclusive and direct fitness benefits that alloparents can accrue.

### **Inclusive Fitness Benefits of Alloparental Care to Alloparents**

Alloparents can increase their inclusive fitness (their own direct fitness and the direct fitness of their genetic relatives) if care is directed toward related individuals that benefit from the additional care ("kin selection" hypothesis, Hamilton 1964). Across the animal kingdom, there is limited evidence that alloparents adjust the amount of care provided to reflect their genetic relatedness to care recipients (Clutton-Brock 2002). In many cases, this can be explained by the membership and social dynamics of animal groups. For instance, there is clear evidence in many species that, when alloparents select care recipients, they discriminate between kin and non-kin. For example, alloparental care in primates and cetaceans may be

biased toward maternal female kin, especially among populations in which females live and reproduce in their natal group and matrilineal social bonds are maintained throughout life (Fedigan 1982). Older, postreproductive females can play key roles as alloparents in these species. For females of species with long life-histories, several of which experience menopause, it may be more beneficial for older individuals to help rear the offspring of their adult progeny, rather than to continue investing in their own reproduction ("grandmother hypothesis"; Hawkes and Coxworth 2013). Thus, in many species, alloparents do in fact discriminate when choosing their care recipients, and this is based on preferred social relationships that may reflect a shared kinship. Furthermore, in species where social groups comprise closely related individuals, mechanisms that allow alloparents to discriminate among care recipients based on genetic relatedness may be redundant. Nonetheless, there are still species where alloparental care is directed toward unrelated individuals or even where relatedness reduces the amount of care provided by alloparents; direct fitness benefits may better explain the evolution of alloparental care in these species.

### **Direct Fitness Benefits of Alloparental Care to Alloparents**

There are many ways that alloparents can accrue fitness benefits directly, regardless of their relatedness to care recipients. While inclusive fitness benefits are more generally applicable across taxa, direct fitness benefits will vary according to the species-specific ways that animals survive and reproduce. Below, we discuss the most commonly cited direct fitness benefits of providing alloparental care. First, alloparental care can afford immature individuals the opportunity to practice their parenting skills, which increases the likelihood that they will successfully rear their own offspring in the future ("skill" hypothesis; Selander 1964, p. 206). This is especially important in species in which offspring care involves a novel skill that, prior to parenthood, is not part of daily life. In birds, reproductive success tends to be lower in younger, less experienced breeders. This has been attributed to a lower reproductive



effort but also to less experience in providing care for dependent young. Immature individuals that are able to practice building a nest and caring for eggs and hatchlings will likely be more successful at rearing their own offspring. In primates, transport is an important element of offspring care, and a major source of infant mortality for arboreal primates is being dropped from trees. Thus, immatures who hold and carry other individuals' offspring may have more success as adults in carrying their first offspring. The "skills" hypothesis has been supported in a variety of other bird and mammal species, leading some researchers to declare this as a major driver of alloparental care in their study taxa. Second, alloparents could accrue direct fitness benefits if their contribution increases their social status among other group members ("social prestige" hypothesis; Zahavi 1995). For instance, alloparental care in many species can be a way for males to signal to potential mates that they are high-quality parents, increasing their mating opportunities. In many species, males that provide care for other individual's offspring are afforded more mating opportunities in the future, either with the offspring's mother or other females. Providing care can allow for alloparents to build or strengthen beneficial social relationships with parents and their offspring. These social bonds can have fitness benefits for alloparents in the long-term. For instance, in species showing dominance hierarchies, low-ranking individuals may benefit through coalitionary support, grooming, and tolerance while feeding, from high-ranking individuals following the contribution of alloparental care to the dominant individuals' offspring (Maestripietri 1994). Lastly, the "group augmentation" hypothesis posits that, if alloparents are better able to survive and/or reproduce in larger groups, they can benefit directly from contributing to the rearing of new group members, regardless of their relatedness (Kokko et al. 2001). There are many benefits associated with living in larger groups, including reduced predation risk through dilution and more alloparents to assist with rearing future offspring. In fish, alloparents can facilitate the survival of their own young by arranging other individual's young at the edge of

the brood to deflect predators from their own offspring. Furthermore, by adopting other individual's young that are smaller in size and more likely to be targeted by predators, they can improve the likelihood that their own offspring will survive (Wisenden 1999). In conclusion, we emphasize that these direct benefits are species-specific and thus, while we have provided evidence in some taxa, there is also evidence that these benefits do not occur in others. Furthermore, inclusive and direct fitness benefits of alloparental care are not mutually exclusive and thus, they could be collectively driving these behaviors.

## Proximate Drivers of Alloparental Care

### Role of the Parents

Parents in many species take an active role in alloparental care. As mentioned previously, alloparental care can be a result of misdirected parental care. In these cases, parents use behavioral tactics (i.e., cuckoldry in mammals, brood parasitism in fishes and birds) to ensure that their offspring are cared for by alloparents. Furthermore, some parents are able to use their dominant status to solicit alloparental care. For instance, subordinate individuals that provide more care are less likely to be evicted from their natal group by dominant breeders, securing access to communal resources and nepotistic benefits ("pay-to-stay" hypothesis; Gaston 1978). Alloparental care appears to compensate for the costs that subordinates impose on dominants by residing in their territory and/or social group (i.e., competition for limited resources). In some species, dominant breeders will even coerce subordinates into providing alloparental care, with evidence for this in some species (i.e., naked mole rats, *Heterocephalus glaber*; superb fairywrens, *Malurus cyaneus*; Lake Tanganyika cichlids, *Neolamprologus pulcher*) but not in others (i.e., meerkats, *Suricata suricatta*) (Santema and Clutton-Brock 2012).

On the other hand, parents in some species will actually reject alloparental care when there is potential for the offspring to be harmed. Parents may be less permissive of alloparents that are

inexperienced if the care entail risks. For instance, in primates, the inexperience of younger alloparents may lead to clumsy interactions and cause harm to the infants (i.e., falls from trees) (Maestriperi 1994). Additionally, in groups with strong dominance hierarchies, low-ranking primates may have difficulty retrieving their offspring from higher-ranking alloparents and thus be more resistant to relinquish their offspring to other individuals. A failure to retrieve one's own offspring can have detrimental consequences for the offspring, particularly if it is unable to obtain milk from the mother, a phenomenon referred as "aunting-to-death" (Maestriperi 1994). Thus, in some species, the extent to which alloparental care is exhibited may depend more on maternal permissiveness than on the motivation of alloparents.

### Alloparent Age, Sex, and Physical Condition

In the castes of eusocial insects, alloparents specialize in different types of care and individuals can develop behavioral, morphological, and physiological differences (Wilson 1971). This type of permanent specialization in alloparental care has not been confirmed in any species of bird, fishes, or mammal. Regardless, the tendency for alloparents to contribute care can still vary based on a variety of factors, including age, sex, and physical condition. This has been attributed to state-dependent costs and benefits of providing alloparental care (Cockburn 1998).

When there are sex differences in the amount of alloparental care contributed, it is the philopatric sex that tends to provide more care (Clutton-Brock et al. 2002). Individuals from the philopatric sex remain and breed in the group in which they were born. Thus, the philopatric sex is more likely to accrue direct fitness benefits from alloparental care (i.e., group augmentation, social bonds) than the dispersing sex, which explains why the philopatric sex tends to provide more alloparental care. Alloparents can also modify the amount of care that they provide based on the offspring's sex, often favoring the philopatric sex as these are the individuals that will remain in the social group in the long-term. The amount of alloparental care provided can also be influenced

by the age of the alloparents (Zöttl et al. 2016). When immature individuals provide alloparental care, the amount of care provided tends to decrease as alloparents prepare to disperse and/or invest in their own reproduction. As age and weight are often correlated, it can be difficult to disentangle the ways that these two factors impact alloparental care. There is, however, some evidence that, when accounting for age, heavier individuals are generally more likely to contribute alloparental care (Clutton-Brock et al. 2002).

### Cross-References

- [Cooperative Breeding](#)
- [Inclusive Fitness](#)

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## Allopatric Speciation

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## Etymology

From Greek *allo* meaning “other,” and *patric* meaning “home.”

## Synonyms

Geographic speciation

## Definition

Speciation caused by geographical isolation.

Speciation is the evolutionary process from which new species originate. There are three main recognized modes of speciation: allopatric, peripatric, and sympatric. Here, we will focus on allopatric speciation.

Allopatric speciation occurs when there is geographic isolation and consequently, no ► [gene flow](#) between separated populations, allowing these newly isolated populations to evolve separately. This is usually caused by some geographical barrier splitting the population into two (or more) subpopulations. These geographic barriers can vary and include mountains, rivers, islands, and others (see examples below). A few individuals may cross this barrier in some cases, but the gene flow remains reduced, maintaining the speciation process. Other events that affect populations of a species, such as local diseases, can also isolate populations, generating similar consequences as those of geographical barriers (Ridley 2009). Allopatric speciation would be considered a type of ecological speciation since ecological differences (as environment and niche) are directly involved in the speciation process, acting as barriers.

Because of the isolation, however caused, subpopulations no longer exchange genes, and their reproductive isolation (see definition below) begins to gradually increase as a result of ► [mutation](#), ► [genetic drift](#), and effects of ► [natural selection](#). In general, the environmental differences to which these subpopulations are exposed impose specific selective pressures, which, in turn, may select more adaptive individuals (Mayr 2001). Eventually, each subpopulation's genome begins to restructure and diverge from the rest of their ancestral population. The length of time that this geographic isolation persists culminate in the species' genetic differentiation (Dobzhansky 1951).

It is possible to discriminate two types of events that can cause geographical isolation: dichopatric (allopatric vicariance) and peripatric speciation. The primary difference between both types is the population size. Dichopatric

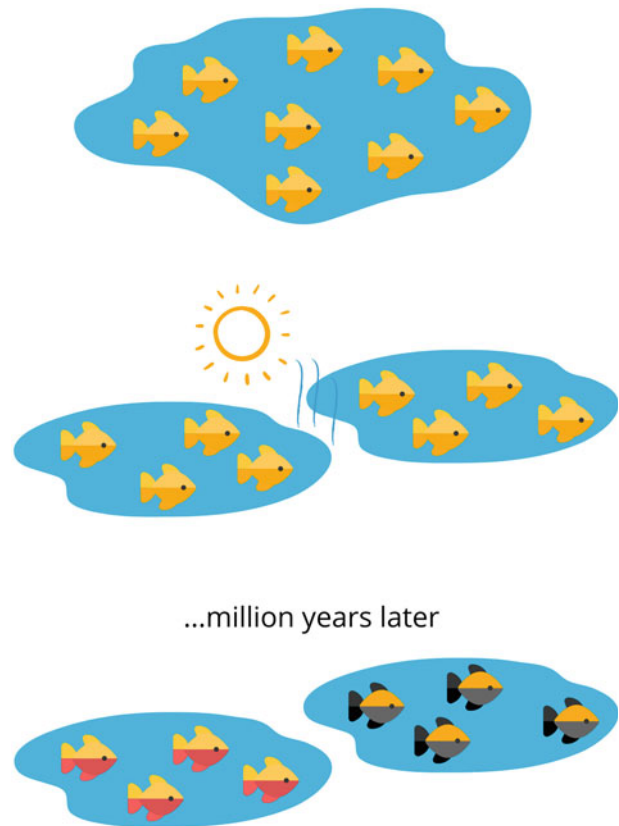
speciation events, which usually isolate large populations, are caused by the rise of a geographical barrier, such as the drying up of a stretch of a river splitting a previously contiguous population (as shown in Fig. 1), or the elevation of sea level, isolating part of a previously contiguous population on an island. In peripatric speciation, a small part of the ancestral population becomes geographically isolated by establishing a new territory on their distribution periphery. This isolation may occur either by the appearance of a new geographic barrier or by dispersion through an existing one. By colonizing new areas beyond the species distribution range, this population experiences founder effects and may pass through a genetic bottleneck (Fig. 2). Since usually only a few individuals colonize new regions, they carry only a small ► [gene pool](#) of their original population. As a result, these individuals may be potentially exposed to high selection pressure imposed by the new environment. This combination makes this population more prone to extinction, and at the same time facilitates their genotype restructuring, allowing it to differentiate from their ancestral population (for more details see Mayr 2001).

## Reproductive Isolation

Reproductive isolation occurs when members of two or more different populations cannot reproduce with each other or generate only nonviable descendants. In this case, a population is prevented from interbreeding with other populations due to geographical barriers or other mechanisms (e.g., physiological, morphological, and temporal barriers). This isolation can be caused by two different categories of barriers: pre-zygotic, which acts before mating or fertilization, such as a geographical barrier; and post-zygotic, which acts after fertilization, such as zygote abnormality. Post-zygotic mechanisms usually arise from accumulated mutations in each of the isolated populations, which, when united in a hybrid, cause loss of fitness. This phenomenon is called Dobzhansky-Muller incompatibility.

**Allopatric Speciation,**

**Fig. 1** Allopatric speciation caused by the rise of a geographical barrier (dichopatric)



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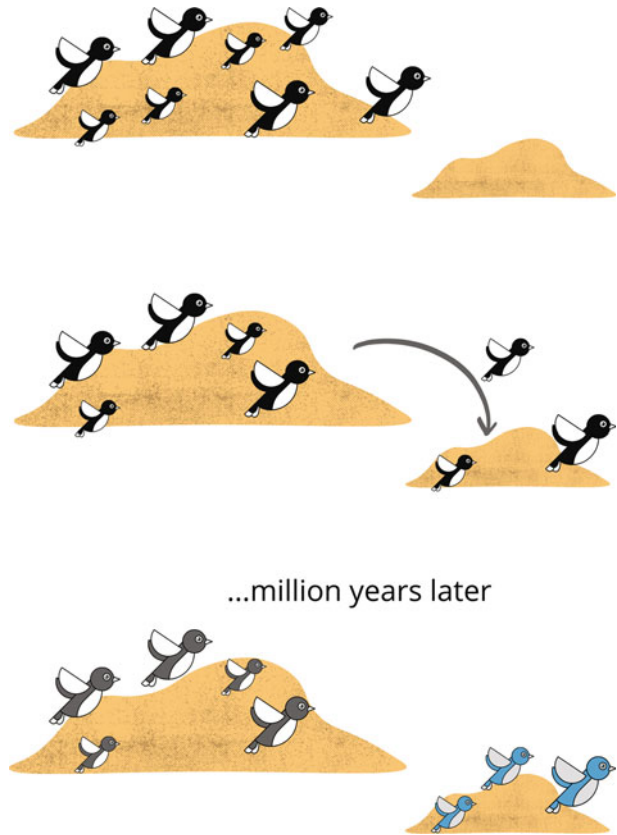
**Brief Historical Perspective**

Understanding the diversity of species and elucidating the mechanisms that generate them have always been of interest to evolutionary theorists and, in fact, are the main questions that motivated Darwin's studies. In 1835, the geologist Leopold Von Buch pointed out the importance of geographical barriers as demarcating different "genus" (following the Aristotelian genus sense). However, allopatric speciation was not documented until the 1940–1960s, by Ernst Mayr. Geographic isolation culminating in reproductive isolation was important to Mayr and his biological concept of species, reinforcing the genetic basis of speciation presented by Theodosius Dobzhansky in 1937. The concept of allopatric speciation was crucial for the understanding of the speciation phenomenon, and this geographical approach generated a subsequent

productive field of evolutionary studies, functioning as the basis of most species concepts currently recognized, as well as the unified concept of species (for details, see de-Queiroz 2007).

**A Classical and Current Example****Darwin's Finches**

Darwin's finches are one of the most classic examples of allopatric speciation and ► [adaptive radiation](#). Approximately 15 species of finches evolved from a single ancestor group that colonized Galapagos' archipelago islands in South America. Because geographic isolation prevented gene flow, each population evolved independently under the natural selection pressures imposed by each island. This evolution is evident when looking at birds' different beak shapes that vary according to each island's available food and

**Allopatric Speciation,****Fig. 2** Allopatric speciation caused by founder effects (peripatric)

consequently with the bird's feeding habit. For instance, some of the finches have beaks adapted to eat cactus flowers without getting scratched, while others are adapted to breaking hard nuts. These adaptations are clear examples of how natural selection and speciation can act over time, differentiating one species into two or more species, each adapted to their new environments.

**Sydney Octopus**

Until 2014, there were two recognized populations of the Sydney octopus *Octopus tetricus* in Australia: one from the far east, and another from the far west, which some authors considered as possibly being two different species. It is known that these two populations were isolated within the last 3.2–6.9 million years. This period coincides with the cooling of the previously tropical Miocene seas along the southern Australian coastline and the Bassian Isthmus's rising during the Pliocene era. For many

Australian species, the glacial-interglacial epochs during the early Pleistocene resulted in a northward progression of cooler waters, causing some species to retreat along the eastern and western coasts isolating populations, which allowed genetic differentiation among them (Amor et al. 2014). Recently, a study combining molecular and morphological data proposed a new taxonomy of *Octopus tetricus*, delineating *Octopus tetricus* into two species, which probably diverged by allopatric speciation (Amor et al. 2014).

Despite being an old concept, allopatric speciation is still part of a fruitful field in science. With the advent of molecular dating techniques, it is now possible to precisely identify which geographical barriers acted as insulators between taxonomic groups. This recent, but important, step has created new avenues to be explored by researchers from different fields, allowing a deeper understanding about the patterns and processes that are part of each lineages' history speciation.

## Cross-References

- [Adaptive Radiation](#)
- [Aristotle](#)
- [Bottleneck Effect](#)
- [Gene Flow](#)
- [Gene Pool](#)
- [Genetic Drift](#)
- [Mutations](#)
- [Natural Selection](#)
- [Speciation](#)

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## Alpha

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## Synonyms

[Dominant](#)

## Definition

In animals living with a hierarchical organization, alpha is the highest ranking individual, also called dominant.

## Introduction

Social animals frequently organize themselves in dominance hierarchies. In this hierarchical organization, individuals have different access to resources. The highest animal in the rank is the alpha and their position is maintained through agonistic interactions, so the alpha is the individual who wins fights over all others (Cafazzo et al. 2010). Male, female, or both (normally a reproductive couple) can be alphas, depending on the social organization of the specie.

Normally, alpha animal is the individual in the group that monopolizes most of the resources as food, mates, spatial location, and territory (see examples below). Alpha position can be attained through aggression and intimidation or collaborating and with the support of subordinates (Sapolsky 2005).

## Who Will Become the Alpha?

Social and physical characteristics will influence who will become the alpha individual, and this will vary a lot among species. However, older individuals normally dominate younger ones (Cafazzo et al. 2010; Creel 2001). Size is also a good predictor of dominance, with bigger individuals dominating smaller ones (Whiteman and Côté 2004).

## Why Is Good to Be the Alpha?

Dominance interactions denote competitive interactions about resources over which most group-living animal species compete, such as food, mates, spatial location, and territory. The extent to which resources are divided unequally among individuals varies as a function of the dominance style of different species (Sapolsky 2005). However, in most species the alpha has a higher portioning of resources.

In most cooperatively breeding birds and mammals, reproductive rates are higher for dominants and its common that the alpha is the only one that reproduces (Creel 2001).

Dominant orangutan males, for example, have more pronounced secondary sexual characteristics and, besides that, can suppress the development of subordinate individuals, making them appear “juvenile” (Sapolsky 2005).

Food partitioning is also observed in dogs, with alpha gaining access to food prevailing over the other in the group (Cafazzo et al. 2010). The alpha also has the privilege to steal food from other group members who often did not react (Cafazzo et al. 2010). Dominant may also have higher foraging rates, as for example in cleaning gobies (fish), because the alpha monopolizes areas with higher food density (Whiteman and Côté 2004). In experimental and controlled conditions, dominant fish eat more than subordinates in the dwarf cichlid *Apistogramma agassizii* (Kochhann et al. 2015).

Spatial centrality in the group for dominants has been described for many species (such as primates, spiders, fish, and birds) (Hemelrijk 2000).

## The Alpha Position and Stress

Although the dominant position has some privileges, it is not free of charge. Some characteristics of the social hierarchy can make the alpha position the most stressful of the rank. Dominants have elevated glucocorticoid, a response related to elevated stress when a hierarchy is unstable or in species in which dominants fight more often than do subordinates (Creel 2001).

Higher stress markers are also observed in alpha individuals where they have to repeatedly and physically reassert their rank; those that are cooperative breeders; and those with transient periods of major rank instability (Sapolsky 2005).

## Conclusion

Alpha is the highest rank individual in a dominance hierarchy. The alpha position is achieved through agonistic interactions and determines the individual that will have a privilege in accessing resources.

## Cross-References

- Beta
- Dominance
- Dominance Hierarchy

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## Alteration

- Recombination

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## Alterations

- Mutations

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## Alternative Mating Tactics

- Hermaphrodite



Alternative Reproductive Strategies

► Facultative Polyandry/Strategic Pluralism

Alternative Reproductive Tactics

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Definitions

|                                       |                                                                                                                                                                                                                                                          |
|---------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Strategy                              | A set of decision rules, which has a genetic basis, leading to a tactic.                                                                                                                                                                                 |
| Tactic                                | The behavioral phenotype, which results from a strategy. A strategy can have one, two, or several different tactics.                                                                                                                                     |
| Alternative reproductive tactics ARTs | Consistent variation in reproductive behaviors between males or females of one species.                                                                                                                                                                  |
| Alternative strategies                | Two (or more) genetically based strategies of one sex that lead to two (or more) alternative tactics.                                                                                                                                                    |
| Mixed strategy                        | One strategy that, depending on frequency depending selection, leads to two or more ARTs which have equal mean fitness.                                                                                                                                  |
| Conditional strategy                  | One strategy which determines that individuals follows a subordinate tactic with low reproductive success while they are small with low competitiveness, but switch to a dominant tactic with high reproductive success when increasing competitiveness. |

|                                    |                                                                                                                                                                                                                                                                                                                                 |
|------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Single strategy                    | One strategy with two or more alternative tactics. The environment determines which tactic an individual chooses and also whether ARTs have different or same mean fitness. The single strategy combines the mixed and the conditional strategy, emphasizing the importance of the environment in determining fitness outcomes. |
| Bourgeois tactic                   | The tactic with the highest possible fitness.                                                                                                                                                                                                                                                                                   |
| Best of a bad job                  | An individual follows a tactic with a lower fitness than an alternative tactic, because it is not competitive enough to successfully follow the bourgeois tactic.                                                                                                                                                               |
| Relative plasticity hypothesis RPH | The RPH is based on the assumption that differences between ARTs are similarly regulated via hormones as are the differences between the sexes.                                                                                                                                                                                 |

Introduction

Alternative reproductive tactics (ARTs) refer to the consistent use of different reproductive behaviors between conspecifics of the same sex in one population at the same time. Hereby the difference between individuals is discontinuous, such that one can put individuals into two or more categories. A tactic refers to the behavioral phenotype, which results from a strategy. A strategy can have different tactics, e.g., territorial male versus satellite male. If a strategy has only one tactic, then more than one strategy must be present in the population for ARTs to be present. It is typically tactics which are studied, not strategies.

Examples of ARTs in Males and in Females

ARTs are more common in males than in females, probably because reproductive success in males is more skewed than in females. For example, in



species in which a few competitive males monopolies the access to fertile females, smaller and less competitive males might develop best of a bad job tactics to mate with these females and gain at least some reproductive success before being big enough to be a dominant male. If more than one reproductive tactic occurs in a population, then ARTs occur. This is basically the case in every species where apart from bourgeois males (see below), another type of males occurs that are trying to fertilize females. In males, the following tactics have been described:

- **Bourgeois male:** These are males which follow the tactic with the highest mean fitness. Thus, these are the most competitive and most dominant males, which often defend a territory and/or a group of breeding females (harem).
- **Sneakers:** These are small males trying to sneak copulations with females defended by bourgeois males. Satellite males, roamers, and floaters are different types of sneaker males. Sometimes this term is used for roamers and floaters in reptiles, which means for subordinate males that are not (like satellite males) associated to a specific territory. Sneaker males occur in many lizard species such as marine iguana (*Amblyrhynchus cristatus*) and tree lizard (*Urosaurus ornatus*), and in cichlid fish such as *Lamprologus callipterus*.
- **Satellite males:** These males are associated to a specific territory but do not defend a territory themselves. They are typically less competitive and smaller than bourgeois males. They try to mate with females in the territory they are associated with. In some species like bluegills (*Lepomis macrochirus*), these males have female mimicry, meaning they look and behave like females, explaining why the bourgeois males do not chase them away. Satellite males occur in many lizard species such as marine iguana (*Amblyrhynchus cristatus*) and tree lizard (*Urosaurus ornatus*), in tree frogs and several species of crickets.
- **Roamers:** This term is usually only used for mammals. Roamers typically have a well-defined home range that is very large and

overlaps the home range of several bourgeois males but not defended as a territory. These males roam over a large area, trying to avoid the bourgeois males but to meet and to copulate with any females they encounter. Example: African striped mouse (*Rhabdomys pumilio*).

- **Floaters:** This term is used mainly for birds and mammals. Floaters are males that, in contrast to roamers, do not have a well-defined home range, but float through the population, trying to copulate with females defended by bourgeois males. Floaters occur in many bird species such as the red-winged blackbird (*Agelaius phoeniceus*).
- **Helpers:** Helpers are males that help a breeding pair to raise the pair's offspring i.e., they help to raise young that are not their own. In many species, helpers also try to fertilize eggs/females, either of the pair they are helping (cichlid *Neolamprologus pulcher*; pied kingfisher *Ceryle rudis*), or of neighboring groups (African striped mice, meerkats *Suricatta suricata*; superb fairy-wrens, *Malurus cyaneus*).

While ARTs have been mostly studied in males, female ARTs also occur. This is the case when the investment of other females such as maternal care can be exploited or when females monopolies the parental investment of males by forming one female-multiple male groups, mating polyandrously. As ARTs are alternative ways to gain fitness via reproduction, alternative mating tactics, such as monogamous versus polynadrous mating of females also represent ARTs, but such alternative mating tactics are difficult to measure and received little attention. In females, the following ARTs have been described:

- **Solitary versus communal breeding** in African striped mice, house mice, and probably many other small mammals.
- **In eusocial insects**, workers that are laying eggs in the nest dominated by a queen.
- **In some wasps**, females can either join the nest of another female (communal breeding) or start their own nest (single breeder).
- **Female dunnocks** can mate monogamously, polyandrously, or polygynandrously.

- Fire ants (*Solenopsis invicta*) females can form colonies with either one single monogynous queen or colonies with several breeding females.

### Species With and Without Morphological Differences Between ARTs

In some species, males following different tactics do not only differ in their behavior but also in their morphology. For example, in several lizard species with ARTs, the different tactics also differ in the coloration of their skin, such as the coloration of dewlaps in tree lizards. In species with genetically determined alternative strategies, males can differ dramatically in size, for example, in the cichlid fish *Lamprologus callipterus*, where bourgeois males are 10 cm long and weight 36 g, while dwarf males reach only 2.5 cm and 0.9 g. In some case, such as dwarf males parasitizing bourgeois males, the reason for the phenotypic difference is obvious. In contrast, why male lizards following ARTs differ in coloration is still not understood, and this question also received little scientific attention. Many studies on ARTs focused on such species where the different tactics can easily be distinguished, as obviously this makes it easier to study ARTs. However, in the huge majority of studies, individuals following ARTs differ mainly in behavior and often additionally to a small, not always (to the observer) obvious extent in body mass. Thus, species where ARTs are also phenotypically different are a special case.

### What Does Not Represent ARTs?

No examples of ARTs are interspecific brood-parasitism, sex change, simultaneous hermaphroditism, and infanticide (Taborsky 2008). In many species, each male might have different tactics to fertilize females, without these representing ARTs. For example, in most passerine birds, males are pair-living, copulating with their female partner, and additionally seeking to

copulate with neighboring females to gain extra-pair paternity. As all males follow this strategy, it does not represent ARTs, as there is no consistent variation between males. However, if it would be shown in one species that some males invest heavily in guarding their mate and not in extra-pair copulations, while other males don't invest in mate guarding but in extra-pair copulations, then this consistent variation would represent ARTs.

Alternative tactics can also occur in other behaviors than reproduction. For example, alternative dispersal tactics have been described in African striped mice (*Rhabdomys pumilio*), where the largest males disperse over short distances (less than 500 meters), intermediate males over large distances (several kms), and small males not at all (Solmsen et al. 2011). While these alternative dispersal tactics are correlated with ARTs (territorial male versus roaming male versus philopatric males), they do not represent ARTs themselves but rather a tactic of males of intermediate body mass to reach the high fitness tactic of territorial male in a distant subpopulation instead of becoming a roamer in the natal population. Similar alternative tactics that are not reproductive tactics can occur for different foraging strategies.

The occurrence of an alternative male (or female) morph that does not reproduce is not regarded as ARTs. Thus, traditionally cooperatively breeding species with nonbreeding helpers have not been considered as examples of ARTs. However, more detailed studies often found that helpers might breed when the opportunity arises, without changing their social status. Examples for this are female workers of many hymenopterans, male helpers in meerkats, in striped mice and in superb fairy-wrens, and helpers of both sexes in the cichlid *Neolamprologus pulcher*.

### Strategies Underlying ARTs

It is important to differentiate between the observed tactic and the underlying strategy (Gross 1996). A strategy refers to decision rules which determine which alternative tactic is

shown. A strategy has a strong genetic basic but is not totally genetically fixed, as there is variation between individuals, for example, when exactly to switch from one tactic to another. The strategy is determined by specific mechanisms which are a response to environmental cues. An example for a strategy might be the following decision rule: If you are larger than X, increase your testosterone level and become a territorial male, otherwise be a satellite male.

It has been stated that the differentiation between strategies and tactics is not useful as both relate to the same issue (Taborsky 2008). However, the differentiation between strategy and tactic can be very important, as it clearly indicates one shortcoming in our understanding of ARTs: Nearly all research has focused on the tactics themselves, i.e., the fitness consequences and the underlying endocrine mechanisms leading to ARTs (all the rest of the current article reviews this), while the underlying strategies have been ignored. Thus, for most species showing ARTs the underlying decision rules have never been estimated, tested, and validated. However, formulating these decisions rules can help us with coming up with better and more meaningful predictions, for example, about the expected fitness consequences of ARTs. On the other hand, if no clear set of decision rules (a strategy) can be formulated, this indicates a lack in our understanding of the ARTs of this specific species.

For male African striped mice, it has been proposed that they have one strategy, the decision rules of which determines which of the three possible ARTs a male follows, while the environment determines the fitness outcomes (Schradin and Lindholm 2011):

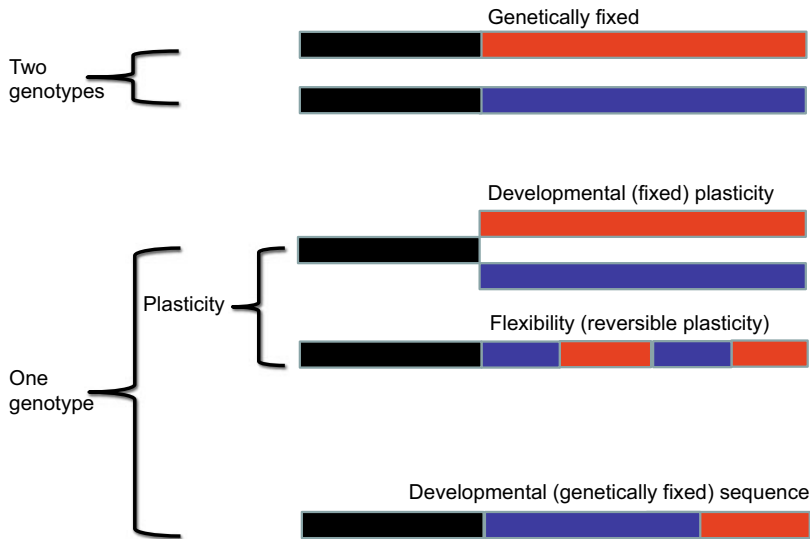
1. Decision: To remain philopatric to your natal group or to disperse?
  - (a) Remain a philopatric male if all females breed in communal groups defended by breeding males and your body mass is below the population mean and there are more sexually mature males than female groups in the population. Mate with any female from neighboring groups.
  - (b) Leave your natal group if:

- (i) At any time of the year, a breeding position becomes vacant in a neighboring group which you can fill.
  - (ii) At the beginning of the breeding season if population density is low and several single undefended females are present in the population which has a female biased sex ratio.
  - (iii) At the beginning of the breeding season if your body mass is above the mean of the population, independent of population density.
2. Decision: To become a roamer or try to become a territorial breeder?
  - (a) If all female breed solitarily then become a roaming male.
  - (b) If you find a group of communally breeding females that are not defended by a male that is larger than you then become the breeding male of this group, defend the territory of this group against other males, and try to copulate with all your females plus all females from neighboring groups.

This set of decision rules makes clear that being a roamer can be the result of two different processes: (1) an active choice, because many females breed solitarily and roaming is the best tactic or as good as being a territorial breeder. (2) Result of low competitive ability, i.e., the male chose to disperse and would choose to become a territorial breeder, but he cannot, because all communal female groups are defended by larger males. This is similar to the situation in stoplight parrotfish (*Sparisoma viridae*) where males start with the tactic of bachelor and the availability of free territories and their relative body size determines when they can switch to the territorial tactic (Cardwell and Liley 1991).

## Development and ARTs

The tactic an individual follows to have reproductive success develops during its life and can change during development (Fig. 1). Obviously, the time point when an individual reaches sexual



**Alternative Reproductive Tactics, Fig. 1** A simplified overview of the different pathways that can lead to ARTs, adapted from (Taborsky 2008). Top: ARTs can arise out of two (or more) different main genotypes determining which of the alternative tactics is expressed in each individual. Middle: One genotype can lead to ARTs via nonreversible developmental plasticity, where one out of two (or more) alternative pathways leading to ARTs is chosen. Empirical evidence for his mechanism leading to ARTs is missing. In contrast, most cases of ARTs are due to flexibility, i.e., reversible phenotypic plasticity, for example, many cases

where males follow either a best of a bad job or a bourgeois tactic, depending on their relative competitiveness. In some tree frogs, the biggest males are calling, smaller males are satellites, but when bigger males arrive/disappear, males can immediately switch their tactic, and later can switch again. Bottom: One main genotype can lead to ARTs when individuals follow different tactics during their development, for example, following a doing the best of a bad tactic as young small adults, and changing to the bourgeois tactic when older and more competitive

maturity is important for the expression of its reproductive tactic. In species where the reproductive tactic is genetically fixed, the tactic that an individual will follow throughout its life will then be expressed. If depending on the genotype two or more alternative tactics might be expressed, then we observe ARTs in this population (Fig. 1, top). In other species, it's the environment that determine which of two (or more) ARTs is expressed (Fig. 1, middle). However, especially in males, whether or not individuals can reproduce not only depends on when it reaches sexual maturity but also on its competitiveness, for which body mass is often a very good proxy. Large dominant males might reproduce, while small males, even though sexually mature, might have to wait and grow, possibly forming bachelor groups of nonbreeding males or remaining as nonbreeding subordinate males in a group.

There is strong selection pressure on individuals to reproduce, and accordingly in many species subordinate males are trying to mate with females, even when being small and dominated by larger males that try to monopolies access to receptive females. Such small males might follow a best of a bad job tactic, often called satellite or sneaker tactic, until they become larger and can follow the dominant bourgeois tactic (Fig. 1, bottom). In these species, which tactic is followed is mainly determined by growth after reaching adulthood, and as such determined by development during adulthood. While some authors do not regard such development dependent tactics as ARTs, they clearly are, as we need (1) ultimate explanations for the occurrence of such best of a bad job tactics which are (2) controlled by specific endocrine mechanisms, which evolved to maximize lifetime reproductive success.

Tactics can be genetically fixed or plastic (Fig. 1). Within the plastic tactics, developmental

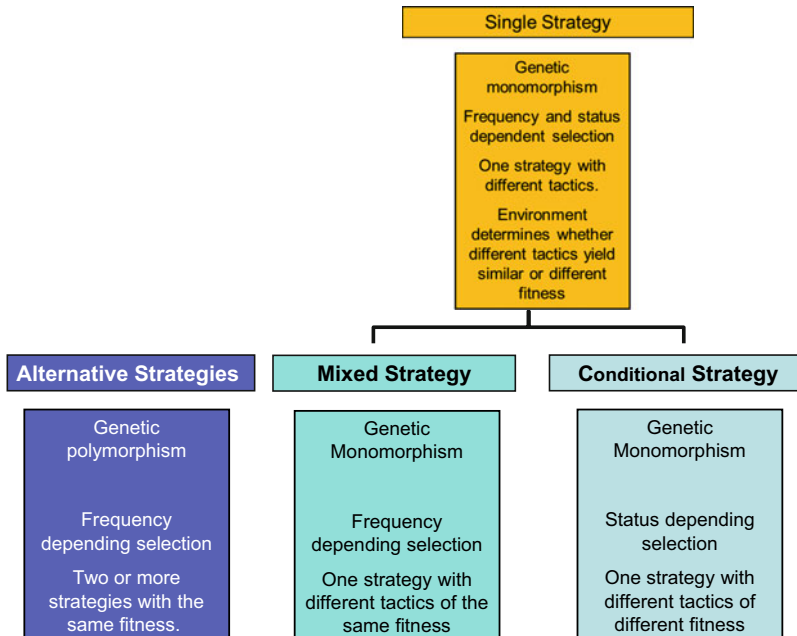
plasticity might lead permanently to one out of several alternative tactics, which the individual then cannot change anymore. The sequence of tactics might also be developmentally fixed, for example, from small sneaker to large bourgeois male, as described above. However, in many species, individuals can flexibly change their reproductive tactic repeatedly. This is also a form of plasticity, which in contrast to fixed developmental plasticity is called flexibility.

### Evolution of Strategies Underlying ARTs

The phenomenon of alternative reproductive tactics has been analyzed by game theory, where a tactic refers to a specific behavior resulting from individual decision rules, so-called strategies. Reproductive tactics have a strong influence on individual fitness and are thus under strong selection pressure. However, it is rather the underlying

strategies, i.e., developmental and cognitive decision rules that evolve and then produce the observed tactics. In a classical paper, Gross (1996) defined three categories of strategies (Fig. 2):

1. Alternative strategies: Genetically polymorphic, based on frequency-dependent selection. Different tactics yield the same average fitness. Examples are giant versus dwarf males of the cichlid fish *Lamprologus callipterus*. Alternative strategies are represented by genetically fixed tactics in Fig. 1.
2. Mixed strategies: Genetically monomorphic, based on frequency-dependent selection. Different tactics yield the same average fitness. No good empirical examples exist. Mixed strategies have also been characterized by a probabilistic basis, i.e., a probability  $x$  to play tactic  $X$  and probability  $1-x$  to play tactic  $Y$ . These represent developmental fixed plastic tactics in



**Alternative Reproductive Tactics, Fig. 2** Bottom: Traditional categorization of reproductive strategies (decision rules leading to tactics) by Gross (1996) and top modified by Schradin and Lindholm (2011). Differences between strategies refer to whether the shown tactic is genetically fixed (Alternative Strategies) or not (all other strategies).

While Gross (1996) further differentiated whether the fitness of ARTs is similar (Mixed Strategies) or different (Conditional Strategies), Schradin and Lindholm (2011), see the fitness outcome as variable depending on the current environmental conditions (Single Strategy)

Fig. 1, where tactics have the same average fitness and the chosen tactic then depends on the frequency of all tactics in the population.

3. Conditional strategies: Genetically monomorphic, based on status-dependent selection. Different tactics yield different fitness. The tactic that an individual chooses depends on its competitive abilities. The most competitive individuals follow the tactic that yields the highest fitness payoff, called the bourgeois tactic. Less competitive males (often called sneaker or satellite), that are smaller and younger than the bourgeois males, make the best of a bad job, following a tactic with lower fitness that is still better than no reproductive success at all. These males change to the bourgeois tactic when they grow larger. Many examples exist in both vertebrates and invertebrates. These represent flexible (reversible plasticity) and developmental sequenced tactics in Fig. 1.

Empirical studies on the African striped mouse revealed that fitness consequences of ARTs can be environment dependent. Male striped mice follow one of three ARTs: (1) Territorial breeding males defend a group of communally breeding females; (2) Solitary roaming males trying to copulate with any females they encounter; (3) Philopatric males that remain in their natal group and try to sneak copulations with females from neighboring groups. Under high population density, breeding males have 10 times higher reproductive success than roamers and 100 times higher reproductive success than philopatrics. However, under intermediate population density, breeding males and roamers have the same mean fitness, and no philopatrics occur (as all sexually mature males leave their natal group). Under very low population density, all males follow a roaming tactic, and some of these roamers have a very high reproductive success, higher than that of breeders under high population densities. These observations lead to the formulation of the single strategy, which contains both the mixed and the conditional strategy proposed by Gross (1996; Fig. 2).

The single strategy is a new term introduced by Schradin and Lindholm (2011) to replace the terms

mixed and conditional strategy, which differ mainly in the predicted fitness consequences (equal fitness for mixed versus different fitness payoffs for tactics arising from conditional strategies). Single strategies are not based on genetic polymorphisms, but all individuals follow the same or very similar decision rules when choosing a tactic. Individuals have flexible tactics, which means they can switch tactics, often repeatedly. Environmental conditions determine whether the different tactics yield similar or different fitness. By formulating the single strategy (=decision rules; see above) for striped mice, it became evident that fitness outcomes depend on the prevailing environment. To become a roamer can be the result of a male choosing to disperse and to roam, as the tactic yields high fitness. Alternatively, it can be the result of a male choosing to disperse and attempts to become a territorial breeder but not being competitive enough to do so. In the latter case, being a roamer would be a best of a bad job tactic.

The definitions by Gross (1996) have been criticized on theoretical grounds because of its focus on genetic polymorphism versus genetic monomorphism: even if different animals follow very similar decisions rules and show flexibility, i.e., they can change between tactics, they still might differ genetically, e.g., in their decision when to switch tactics (Shuster and Wade 2003). (Tomkins and Hazel 2007) further concluded that mathematical models can neither prove that fitness must be unequal (as was proposed by Gross 1996) nor that fitness must be equal (as was proposed by Shuster and Wade 2003).

## Endocrine Mechanisms of ARTs

The relative plasticity hypothesis (RPH) has been developed to explain the endocrine mechanisms underlying ARTs (Moore 1991). The RPH bases on the theoretical assumption that individuals of one sex that follow ARTs differ in their hormonal mechanisms in a similar way as is observed in primary sex differentiation between males and females (Moore 1991; Moore et al. 1998). Thus, in the same way as males and females differ hormonally, males of different reproductive tactics

are also expected to differ hormonally. Hormones can influence behavior via two main ways (Phoenix et al. 1959): (1) Early in life, hormones can have organizational effects that permanently change the central nervous system and as such adult behavior. Organizational effects are non-reversible. For example, male rodents that experience high levels of testosterone in utero will be more aggressive when being adult. (2) During adulthood, hormones have activational effects, acting on the central nervous system (which was formed via organizational effects during early development), making the expression of specific behaviors more likely. Activational effects are reversible, i.e., when the hormone secretion decrease, the behavior ceases. An example would be singing in song birds, which is activated by testosterone in spring and ceases in summer/autumn when testosterone levels decrease.

The RPH predicts that individuals following fixed ARTS differ in their hormone profiles early in development (organizational effects; Table 1). In contrast, when ARTs are sequential or flexible, individuals following different ARTs are predicted to differ in hormone profiles in adulthood (activational effects; Table 1). The main hormones involved in the regulation of male ARTs are androgens, such as testosterone. Bourgeois males typically have higher androgen levels than other males. Progesterone and glucocorticoids are other hormones that can be involved in the regulation of ARTs. While originally the RPH was formulated

for these steroid hormones only, it is now known that peptide hormones such as prolactin and neuropeptides (oxytocin and vasopressin) can also be involved. Figure 3 shows as an example of how hormone levels differ in male striped mice following ARTs. In this species, it has also been shown that males of the different tactics do not only differ in their endocrine profile but also that individual males change their hormone levels when switching tactics, and that experimental increase of testosterone might induce tactic change. Furthermore, this has consequences for their metabolism, as resting metabolic rate (metabolic rate to maintain basal functions only, measured as oxygen consumption when being at rest at thermo-neutrality) also differs between ARTs.

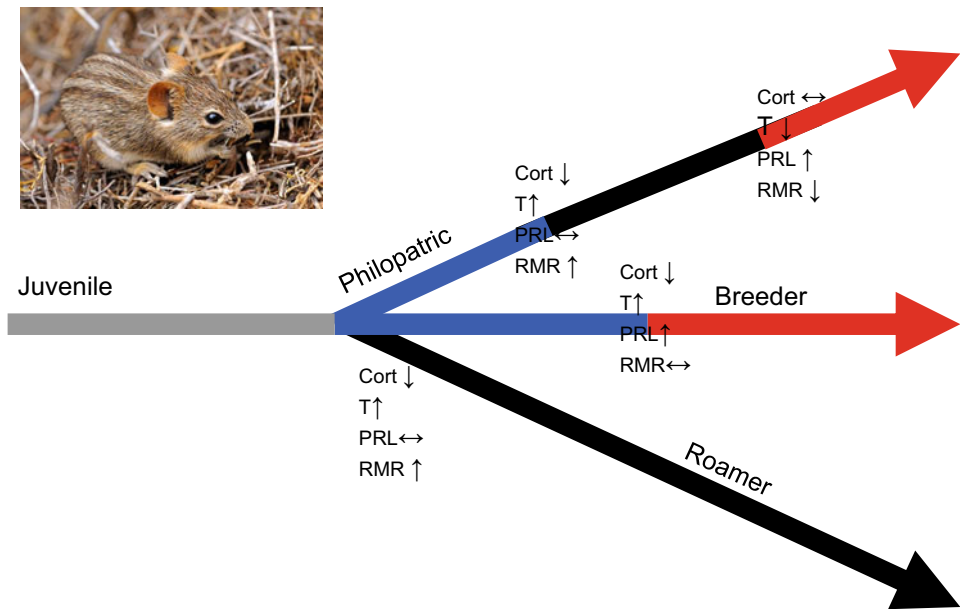
The endocrinology of ARTs has been investigated in more than 50 vertebrate species, especially in fish and reptiles, but also in birds and mammals, and a role of hormones in regulating ARTs has been reported in nearly every study (reviewed in Oliveira et al. 2008). However, the support for the predictions of the RPH has been low, both for correlative and experimental studies. Oliveira et al. (2008) concluded that the RPH fails to explain a large amount of the observed variation and thus reject the validity of the RPH. Specifically, the existence of hormonal differences in adults of species with fixed ARTs, and an effect of hormone manipulations in adults with fixed ARTs has led to a rejection of the RPH (Oliveira et al. 2008). However, these problems arise mainly

**Alternative Reproductive Tactics, Table 1** The hormone profile of males following ARTs as predicted by the RPH (Moore et al. 1998) and a revised version of the RPH which I suggest here. ACT: Activational effects leading to

different ARTs. ORG: Organizational effects leading to different ARTs. PHYS: Physiological effects resulting from different ARTs

| ART type          | Relative plasticity hypothesis by Moore 1998                                                                                               | Modified relative plasticity hypothesis                                                                                                                |
|-------------------|--------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Fixed</b>      | ORG: Hormonal differences in early development. Adults have similar hormone profiles, except when affected by different social experiences | ORG: Hormonal differences in early development.<br>PHYS: Hormonal differences between ARTs (adults) are similar to differences observed between sexes. |
| <b>Sequential</b> | ORG: Hormonal differences in adults when ARTs are formed. Otherwise hormone profiles are similar                                           | ORG: Hormonal differences during adulthood when ARTs are formed<br>PHYS: Hormone levels should differ between ARTs                                     |
| <b>Reversible</b> | ACT: Adult morphs will always differ in their hormone profile, but no differences in early development                                     | ACT: Hormone levels should differ between ARTs                                                                                                         |





A

**Alternative Reproductive Tactics, Fig. 3** Physiological change in male striped mice, which when reaching adulthood (not gray) can either remain as adult philopatric in their natal group (blue), become a solitary living roamer (black), or the breeding male of another group than their natal group (red). These switches in tactics are associated

with changes in physiology, and it has been shown that individual males change their physiological profile when changing tactic. *Cort* corticosterone, *PRL* prolactin, *RMR* resting metabolic rate, *T* testosterone, ↓ decrease, ↑ increase, = does not change

**Alternative Reproductive Tactics, Table 2** Predicted effects of experimental manipulations of hormones in males following ARTs as predicted by the RPH (Moore et al. 1998), and a revised version of the RPH which I suggest

here. ACT: Activational effects leading to different ARTs. ORG: Organizational effects leading to different ARTs. ARTI: Artificial effects that do not imply an evolved endocrine pathway that would occur under natural conditions

| ART type   | Relative plasticity hypothesis by Moore et al. 1998        | Modified relative plasticity hypothesis                                                                                                                                                                          |
|------------|------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Fixed      | ORG: Effective during early development, but not in adults | ORG: Effects in early development long-lasting and similar to effects observed in nature<br>ARTI ACT: Effects in adults short-lasting and similar or different to observed differences between ARTs              |
| Sequential | ORG: Effective in adults but not during early development  | ORG: Effective in adults when ARTs are formed, long-lasting and similar to effects observed in nature<br>ARTI ACT: Effects in final ART in adults short-lasting and similar to observed differences between ARTs |
| Reversible | ACT: Effective in adults but not during early development  | ACT: Effective in adults but not during early development                                                                                                                                                        |

from two facts that should be taken into account when considering the RPH (Table 2): (1) As the RPH is based on the comparison between the male and female sex, it does not predict that males of two fixed ARTs should only differ hormonally during development but not during adulthood. In

the same way, as males and females (fixed reproductive tactics in most vertebrates) differ in their hormonal profile, the same can be expected for two ARTs in one sex. (2) The prediction that hormone manipulations should have an effect in early development in species with fixed ARTs and

an effect in adults of species with plastic ARTs has been interpreted to mean it should otherwise have no effect. However, even in males of species with no ARTs, experimentally administering testosterone can have strong effects, such that the extracted conclusion it should not have an effect in species with fixed ARTs is not understandable. Further, some species with plastic ARTs cannot change their tactic at any stage, but only seasonally, for example, from one breeding season to the next (some blennies, a form of marine fish). Blennies with ARTs do not only show tactic specific behavior but also tactic specific morphology, which is difficult to change. Here, the effect of hormone manipulation might be dependent on the time of year, and experiments done during the breeding season (when the tactic for the season is already fixed) might be less meaningful than in the pre-breeding season. In sum, when taking into account physiological effects resulting from different ARTs and artificial effects that do not imply a natural mechanistic pathway, then the RPH is still highly valuable in understanding the endocrine control of ARTs.

I therefore suggest a modified version of the RPH, which takes two facts into account: (1) Physiological differences are expected in fixed ARTs in adulthood in the same way as hormonal differences are observed between males and females in most species (Table 1). (2) Experimental changes of hormones, potent mediators of physiology and behavior, can cause artificial effects on physiology and behavior that are not observed under natural conditions, as the imposed hormonal changes (for example, artificially high testosterone levels) also do not occur under natural conditions (Table 2).

In sum, the expression of fixed ARTs is regulated by permanent organizational effects during development which can then also lead to permanent differences of hormone profiles in adults. In species with plastic ARTs, the transition from one tactic to another tactic is associated with changes in the hormone profile, representing activational (reversible) endocrine effects. For example, androgen levels typically increase and glucocorticoid levels decrease when males switch from a sneaker to the bourgeois tactic.

## ARTs and Intraspecific Variation in Social Organization

Intraspecific variation in social organization (IVSO) occurs when a species shows two or more of the following forms of social organization: living solitarily, in pairs, one breeding male with several breeding females, one breeding female with several breeding males, or multi-male multi-female groups. Hereby, each form of social organization must be composed of breeding individuals, not only dispersing solitary individuals or bachelor groups. Thus, each sex must have the option to live under alternative forms of social organization. IVSO becomes obvious when individuals of both sexes change their reproductive tactics. In other words, if in one species both males and females can show ARTs, then this can lead to IVSO. For example, the house mouse (*Mus musculus*) can live solitarily, in pairs or in communal groups, with resource availability modifying the intensity of intrasexual aggression in males and female infanticide. In striped mice, both sexes show ARTs, and both sexes can live solitarily or in groups. Thus, solitary living or living in large communally breeding groups consisting of one male and two to four breeding females can occur. In sum, when both males and females show ARTs, both sexes can live in different forms of social organization, which is called intraspecific variation in social organization.

## Conclusion

When different individuals of one sex follow different tactics to reach reproductive success, this represents an interesting phenomenon for all students of animal behavior, both those interested in the evolution and those interested in the physiology and mechanisms of behavior. Such ARTs occur in both sexes though they seem to be more common in males and are clearly understudied in females. ARTs can evolve when either the alternative tactics yield the same average fitness, or if following a suboptimal tactic allows individuals to increase their lifetime reproductive success by having some, even if low, fitness when being

subordinate, waiting to grow and increase competitiveness before adopting the bourgeois tactic with the highest reproductive success. The expression of ARTs is regulated by the endocrine system. Permanent organizational effects (typically early in development) cause fixed tactics, reversible activational effects in adulthood cause switches in plastic tactics. If ARTs occur in both sexes, the social organization of an entire population can change, causing intraspecific variation in social organization. In sum, ARTs represent an interesting phenomenon that allows us to study the proximate causes and ultimate consequences of different behavioral (and sometimes also morphological) phenotypes within one single species.

## Cross-References

- [Adaptation](#)
- [Behavioral Flexibility](#)
- [Ecology](#)
- [Evolution](#)
- [Natural Selection](#)
- [Ontogeny](#)
- [Reproductive Fitness](#)
- [Social Behavior](#)
- [Ultimate Causation](#)

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## Alternative Splicing

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## Synonyms

[Differential splicing](#)

## Definition

Alternative splicing is the process in which multiple transcripts are generated from a single gene by different combinations of exons of the primary transcript.

## Introduction

In mammalian cells, a diverse array of proteins is generated by the regulation of gene expression at multiple levels including transcription, alternative

splicing, mRNA stability- decay, RNA editing, alternative polyadenylation, proteasomal degradation, and posttranslational modifications. These regulations determine the gene expression outcome. Splicing is the process in which noncoding introns are removed from the primary transcript and coding exons are joined to form functional mRNA. In alternative splicing, by using different splice sites, multiple mRNA and subsequently protein variants are generated from the same gene (Blencowe 2006). From RNA sequencing data, it is now revealed that around 95% of human genes undergo alternative splicing (Pan et al. 2008). The isoforms thus generated have structural variation as well as functional significance. Cells undergo alternative splicing to diversify number of proteins with a limited number of transcribed mRNA (Hartl 2011). About 38,016 distinct mRNA isoforms are generated by the alternative splicing in *Dscam* gene (*Down syndrome cell adhesion molecule*) of *Drosophila melanogaster* (Kalsotra and Cooper 2011; Nilsen and Graveley 2010). Alternative splicing explains the variance between the number of protein-coding genes in the human genome (~30,000) and the different types of proteins that are translated in the human body (~100,000) (Hartl 2011; Keren et al. 2010). Alternative splicing is very frequent in humans while rare in plants. There are many reports of tissue-specific alternative splicing in the case where particular isoform is required for that tissue only (Paterson et al. 2016). Alternative splicing has been postulated in many developmental pathways and disease conditions. Sometimes alternative splicing also leads to premature stop of translation by introducing a stop codon in the middle of the protein-coding mRNA.

## Splicing Machinery

Splicing is carried out by the splicing machinery, i.e., spliceosome which consists core splicing proteins, splicing regulatory factors (SRF), and snRNA (small nuclear RNA). The spliceosomes are directed toward the splice site by some specific

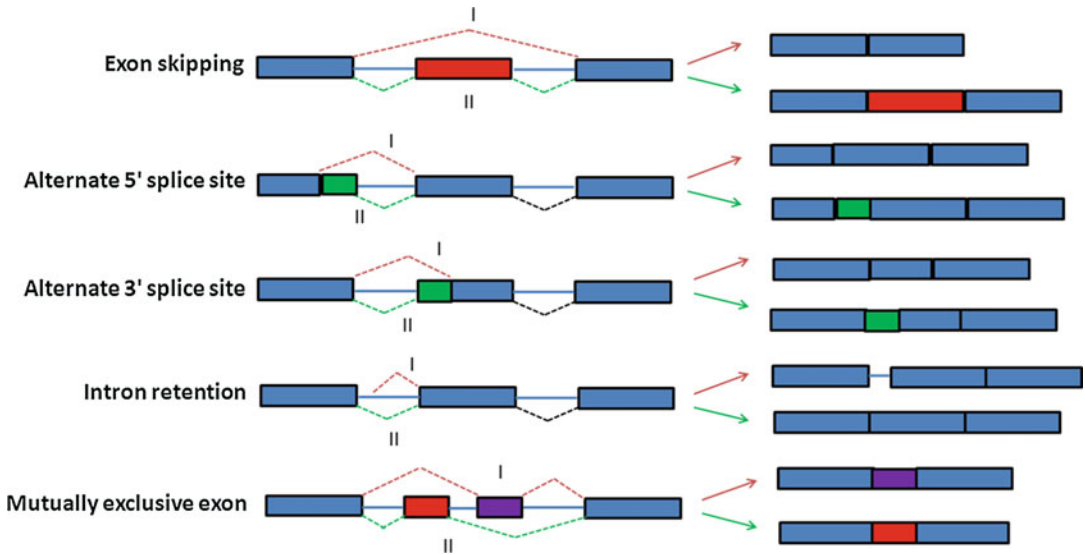
sequence at exon/intron boundaries which is less than 10 bp long. Multiple splice variants are generated by using different splice site in the pre-mRNA.

## Types of Alternative Splicing

There are five basic types of alternative splicing that vary among species (Fig. 1):

- (i) Exon skipping: An exon is either spliced out or retained from the primary transcript. Exon skipping is the most prevalent mode of alternative splicing in the mammalian system which accounts around 40% of alternative splicing event in higher eukaryotes.
- (ii) Alternate 3' splice site selection: When two or more splice sites are present in the downstream exon, only one is selected under specific condition.
- (iii) Alternate 5' splice site selection: When two or more splice sites are present in the upstream exon, only one is selected under a given condition. Splicing through alternate 3' splice site and alternate 5' splice site selection occur, respectively, around 18.4% and 7.9% of total splicing in higher eukaryotes (Keren et al. 2010). This type of splicing introduces little change in final coding sequences.
- (iv) Intron retention: An intron remains in the mature transcript altering the coding potential. It is a very rare event in the animal kingdom but prevalent in plants, fungi, and protozoa.
- (v) Mutually exclusive exons: Usage of the alternative exon in the final transcript.

**Functional Significance of Alternative Splicing:** The conservation of alternative splicing pattern throughout the evolution suggests their strong biological significance. Alternative splicing contributes for the proteome diversity in the cell. Alternative splicing has a central role in maintaining pluripotency of stem cells and also in developmental pathways. The core pluripotency factors



**Alternative Splicing, Fig. 1** Five different types of alternative splicing pattern. Blue, red, violet, and green boxes are exons, blue solid line is representing intron, dashed line

is corresponding to the splice sites. Splice isoform products after alternative splicing are shown on the right

undergo alternative splicing to produce multiple splice isoforms that have roles in the determination of cell state. Many anti- and proapoptotic factors as well as death receptors and caspases are generated through alternative splicing, each with prominent role in biological processes. Splice variants of certain apoptotic genes which are generated by the alternative splicing have the opposite functions. Alternative splicing at the 5' splice site in the first exon of BCL-X and APAF1 gene produces long and short isoforms with anti- and proapoptotic functions, respectively (Boise et al. 1993; Paronetto et al. 2016; Walke and Morgan 2000). The splice isoforms also affect the apoptosis process and immune cell homeostasis. Alternative splicing regulation by splicing regulatory proteins modulates the cell cycle progression along with apoptosis.

## Alternative Splicing and Human Diseases

Aberrant functioning of alternative splicing machinery is well reported in many human diseases as muscular dystrophy, hemophilia, neurodegenerative disorder, cancer, etc. Differential

splicing in the TP53 (tumor suppressor p53) is linked to many neurodegenerative diseases like Alzheimer's and amyotrophic lateral sclerosis (Paronetto et al. 2016). Point mutations in the hereditary diseases affect the alternative splicing and alternative polyadenylation. The deregulation in splicing of cancer-associated gene either by mutations in the splicing regulatory elements or by modulation in the activity of splicing factors implicated in its pathogenesis. The expression of many SR (splicing regulatory) proteins, viz., SRp20, SF2/ASF, and SC35, is upregulated in ovarian, colon, thyroid, kidney, and lung cancers. Regulation of alternative splicing of proto-oncogenes and tumor suppressors modulate their concentration and cellular activity with impact on cancer progression. Abnormal splicing leads to the formation of tumor inducing variants which affect the cell signaling and induce the cell proliferation. Alternative splicing in many cancers either generates active form of proto-oncogene or inactive form of tumor suppressor gene and thus draws the cells toward tumor development and progression. Modulation of splicing process is now a promising therapeutic approach to many human diseases.

## Conclusion

Each type of cell has its own regulatory mechanism of posttranscriptional regulation of gene expression to form the repertoire of proteins of their need in time- and context-specific manner. Metazoan transcriptome analysis uncovered the diversity in mRNA level generated by the alternative splicing. It is tightly regulated process in spatiotemporal manner. It is a means of gene expression regulation which enables a single gene to encode multiple mRNA/protein isoforms. There are five different modes of alternative splicing, viz., exon skipping, alternate 5' splice site, alternate 3' splice site, intron retention, and mutually exclusive exons. Alternative splicing is implicated in the development, pathological diseases, cell cycle, and many other cellular processes. The deregulation in this process and mutation in different splicing factor result in pathogenesis of many diseases.

## Cross-References

- [Exon](#)
- [Gene Expression](#)
- [Intron](#)

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## Altricial

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## Synonyms

[Nicolous](#)

## Definition

Animal young that are exceptionally helpless for a short period following birth and require extensive parental investment and care.

## Introduction

Both avian hatchlings and mammal offspring can be classified based on their developmental state at, and shortly following, birth. Young with limited motor functioning and a heavy reliance on parental care are often described as altricial young. In contrast, offspring that are born relatively independent and well-developed are labeled precocial young. These classifications first appeared in the early 1800s through the works of Carl Jakob Sundevall and Lorenz Oken (Starck and Ricklefs



1998). Since then, these labels have been widely adopted to identify the developmental state of avian and mammal offspring at birth, although recent research suggests that this dichotomous rating may not reflect the full range of development found in some families (Starck and Ricklefs 1998). However, within most avian and mammal orders, there are distinct characteristics that identify young as altricial.

### Altricial Aves Young

All birds produce offspring by laying eggs, which are then incubated outside the body. However, the level of embryonic development at which the young fully hatch from the egg can vary, causing both altricial and precocial young. For example, parrot chicks require parental care many months after hatching, while megapode hatchlings can fly within a day of hatching (Starck and Ricklefs 1998). The predominant developmental mode of ancestral birds is difficult to discern based on fossil records, but 8,890 of the 9,993 extant species of birds are classified as having altricial young (Scheiber et al. 2017). Altricial birds tend to be ectothermic for several days after hatching and have small brains, immature muscles, poorly ossified skeletons, a lack of plumage, closed eyes, and increased nest attendance. However, altricial birds make up for this initial immaturity through post-hatching rates of development that are, on average, three to four times faster than precocial bird species.

### Altricial Mammalia Young

It is presumed that ancestral nonhuman mammals produced altricial offspring (Derrickson 1992). However, over the years, nonhuman mammals have developed greater flexibility in developmental mode relative to avian orders. For example, the Carnivora and Rodentia both exhibit a full range of developmental modes, from extremely altricial to fully precocial (Starck and Ricklefs 1998). General characteristics of altricial nonhuman mammals include neonates born in litters, low

birth weight, a lack of body hair at birth, and eyes and ears closed at birth. In addition, altricial nonhuman mammals have gestational periods that are, on average, a third the length of precocial nonhuman mammals. The two developmental modes differ greatly in brain size at birth as well; adult altricial mammals typically have brains 7.5 times larger than their neonates, compared to precocial adults, which have brains only 2.5 times larger than precocial neonates (Martin 2007). To account for this variability in brain size at birth, rapid brain growth in altricial nonhuman mammals often continues for days or weeks after birth before stagnating. In contrast, rapid brain growth slows at or near the time of birth for precocial nonhuman mammals. It is within this aspect of postnatal growth that human infants, who continue to experience rapid brain growth for a year after birth, deviate from other mammals.

Humans are often classified as being secondarily altricial. That is to say that while human infants share many characteristics with their precocial relatives, they are also born quite helpless, like altricial young. It is believed that human ancestors initially gave birth to precocial young given that modern humans usually produce single, well-developed neonates with eyes and ears open after a lengthy 38-week gestation. For comparison, chimpanzees have an average gestation of 32 weeks, gorillas 37 weeks. In addition, the nutritional composition of human breast milk is remarkably similar to that of other precocial primates (Rosenberg and Trevathan 2002). Yet, human infants are born with their motor skills significantly underdeveloped and have the latest maturity patterns of any primate. As a result, human infants clearly rely heavily on their caretakers for survival and are therefore, also altricial.

### Selective Pressures for Altricial Young

The leading explanation for this paradox is described by the hypothesized obstetrical dilemma. Approximately 3 million years ago (mya), most likely within the genus *Australopithecus*, hominids developed bipedalism, or the ability to traverse on two rear limbs. The exact



selective pressures that resulted in this change are still unclear, but skeletal records indicate that the adjustment resulted in the development of a vertically oriented pelvis (Weiner et al. 2008). This transformation, in turn, significantly narrowed the human birth canal. This narrowing did not initially present a dilemma, as the average brain size was only 400 mL, compared to the present day 1,300–1,500 mL (Weiner et al. 2008). However, hominids eventually experienced encephalization around 2–2.5 mya, with brain size almost tripling between the *Australopithecus* and *Homo sapiens*. This extreme growth resulted in increasingly difficult birth scenarios, as infants struggled to fit through the narrowed birth canal. As such, strong selective pressures existed for infants to be born earlier in the prenatal period, while the brain is still relatively small and underdeveloped. These pressures came to fruition around 1.6–1.8 mya and resulted in a shortened gestational period within the *Homo erectus* species (Rosenberg and Trevathan 2002). Given that this change shortened prenatal growth, human infants were born rather physically underdeveloped relative to other primates. This modification has persisted since, resulting in the many altricial characteristics, as well as the unique postnatal rapid brain growth, we observe in modern human infants.

For nonhuman animals, the factors that inform the pace of infant development are somewhat less clear-cut. Generally speaking, the theory of evolution suggests that the success of an organism is measured by reproductive fitness. As such, traits are naturally selected for if they increase the number of offspring an organism is able to leave behind. Because all species have unique life histories based on habitat stability, mortality rate, etc., different traits can encourage drastically different effects across species. In other words, the same trait can increase reproductive fitness in one species, while lowering fitness in another. This variation in outcomes results in a pattern of differential selection for traits across species.

Selection for developmental states generally follows this same principle in birds and nonhuman mammals. If the offspring of a species is likely to reach sexual maturity, the species will usually have precocial young. Compared to altricial

young, precocial young requires less parental investment, requires less energy to develop and spend less time vulnerable to predation and adverse climate characteristics. However, a life history of increased mortality or a fluctuating environment may significantly decrease the probability that offspring reach sexual maturity. In these instances, selection pressures may bypass the advantages of having precocial young in an effort to increase reproductive rates via larger litters, shorter gestation, and shorter interbirth intervals (Pagel and Harvey 1988). Thus, some animals give birth to altricial young. For example, animals with unstable access to resources tend to favor giving birth to several altricial young, as this strategy increases the probability that at least one offspring will survive to reproductive age. Similarly, small mammals often favor high reproductive rates and altricial young, as they tend to have higher mortality rates relative to larger mammals. In the end, selection of developmental states results from a strenuous cost–benefit analysis that is unique to each species (Ricklefs 1969).

### Broader Impact of Altricial Young

Given that many environmental pressures shape whether a species has altricial or precocial young, it is not surprising that the developmental state of an infant can, in turn, impact other aspects of animal behavior. For instance, altricial young greatly increase the amount of maternal investment required and provide an opportunity for males to paternally invest in their offspring. For females, increased parental investment means a decrease in the ability to forage and provide for oneself after giving birth. As such, females with highly altricial young must rely on others to provide for them. This creates an opportunity for an infant's father to expand his paternal investment. With vulnerable, altricial young, offspring well-being is intrinsically tied to maternal well-being. As such, males may feel an increased pressure to provide for the mother of their offspring, so as to further the chances that their offspring will reach sexual maturity. These dual motivations, along with other factors such as concealed ovulation, ultimately encourage a shift towards

monogamous relationships; males do not want to invest in a mother if the offspring may not genetically be theirs, while females do not want to commit to raising a child if they will be abandoned. The best way to insure these respective desires is through sexual monogamy, and indeed, research suggests that mammals with monogamous mating systems tend to produce altricial offspring (Benshoof and Thornhill 1979).

Monogamy also requires some level of cooperation. Research suggests that approximately 1.8 mya, around the time changes in human gestation were believed to have occurred, hominid societies shifted from competition towards increased cooperation and sociality. It is likely that this shift can be partially attributed to the shared parental investment required to raise altricial young (Naccache 2012). Shared parental investment and monogamous relationships both require sustained collaborative interactions. As such, the introduction of altricial young may have served as a catalyst for the gradual increase in the complexity of social relationships found in many monogamous populations.

## Conclusion

Within the Mammalia and Aves classes, young come into the world with a vast range of abilities and competencies. The term altricial is used to describe young that fall on the underdeveloped end of this spectrum. These offspring are born with unique deficits that contribute to their helplessness and increase the need for parental care. While this care can be costly, some species may benefit from having altricial young when faced with certain environmental and biological pressures.

## Cross-References

- [Bipedalism](#)
- [Cooperation](#)
- [Encephalization](#)
- [Hatching](#)
- [Interbirth Interval](#)
- [Monogamy](#)

- [Ontogeny](#)
- [Parturition](#)
- [Parental Investment](#)
- [Parenting](#)
- [Paternal Behavior](#)
- [Precocial](#)
- [Reproductive Fitness](#)

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## Altruism

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## Origins of Altruism

The earliest conceptualization of altruism can be traced back to the Ancient Greeks and

forward to more contemporary behaviorists (Rushton and Sorrentino 1981 for review). The first view was from some of the writers of the old and new testaments and Freud who thought of human nature as essentially bad. A second view was popular among Socrates, Aristotle, and Carl Rogers, who thought of human nature as essentially moral and altruistic. The third view was commonly held by Plato, Locke, Watson, and Skinner who believed that human nature was neutral.

The term “altruism” was coined by French sociologist Auguste Comte (1858) in a description of his ethical doctrine indicating that individuals had a moral obligation to renounce self-interest and love for all others. Not long after Comte coined the term altruism, Darwin published his *Descent of Man* (1871), in which he proposed that humans are biologically disposed to behave socially, cooperatively, and helpful to one another. He speculated that it was “moral sense” that distinguished humans most from nonhuman animals, and it was composed of intellectual power and sociability. Interestingly, while Darwin described examples of altruism in nonhuman animal species, he identified a paradox in the way altruism evolved in natural selection. Specifically, he noted that, if the most altruistic members of a group were willing to die for others, sacrificing themselves, there would be fewer offspring of altruistic individuals to pass on the altruism trait.

Around the mid-1960s, in his book entitled *Animal Dispersion in Relation to Social Behavior*, Wynne-Edwards suggested that evolution occurred through group selection, at the level of the species (Wynne-Edwards 1962). He argued that many behaviors evolved for the good of the species as a whole, rather than at a lower level of organization. His arguments were strongly criticized by George C. Williams, an evolutionary biologist, in *Adaptation and Natural Selection* (Williams 1966), in which he argued on the basis of mathematical models that individuals would not altruistically sacrifice fitness for the sake of a group. He persuaded the majority of biologists that group

selection did not occur, other than in special situations such as the haplodiploid social insects like honeybees (Hymenoptera), where kin selection was possible. To support his stance, Williams used the popular lemming example, in which some lemmings take it upon themselves to commit suicide to relieve pressure on critical food resources. The classic scenario is one in which a population of lemmings is jumping off a cliff into treacherous water on a suicide mission but one individual wears a life preserver around its waist. In such a case, group selection would be said to favor the allele(s) for suicidal behavior. However, Williams argued that altruism could not have evolved through group selection because selection among individuals will usually have a stronger effect than group selection in shaping the genetic makeup of the population. Additionally, he argued that groups of altruists would have to prevail over groups of selfish individuals at a faster rate than the selfish individuals within the groups and group selection is much slower than individual selection.

## Types of Altruism

### Hamiltonian Altruism and Kin Selection

Charles Darwin discussed the concept of kin selection in his 1859 book, *The Origin of Species* in which he questions the altruistic behavior of sterile social insects, such as honeybees who leave reproduction to their mothers. He also describes how populations evolve across many generations through natural selection. Under natural selection, a gene encoding a trait that enhances the fitness of each individual carrying it, should increase in frequency within the population, and conversely, a gene that lowers the individual fitness of its carriers, should be eliminated. A gene that prompts behavior that enhances fitness of relatives but lowers the individual carrying it, should increase in frequency within a population because relatives often carry the same gene. The enhanced fitness of relatives would more than compensate for the fitness loss incurred by the individuals, making kin selection possible. In 1975, Harvard

biologist, E.O. Wilson published *Sociobiology*, which re-launched the debate about nurture versus nature and proposed that social behavior, such as altruism was often genetically programmed and that these genes were subject to natural selection. Relatively recently, Wilson recanted this explanation for altruism (discussed below and Nowak et al. 2010).

Maynard Smith (1964) coined the term “kin selection” to describe how helping relatives to reproduce resulted in indirect fitness benefits, the reproduction of nondescendent kin. Hamilton (1964) described kin selection more specifically stating that because genetically related individuals were likely to carry the copies of the same alleles, they would be more likely to help their kin to ensure that copies of their alleles were passed on. The prominent biologist, J. B. S. Haldane (1932) popularized the math involved in kin selection by stating that he was willing to lay down his life for two brothers or eight cousins. It was Hamilton who later expressed the conditions under which such altruism would evolve through the following equation:  $r \times b > c$  where  $r$  denotes the relatedness of the individuals,  $b$  denotes the benefit to the recipient of the altruistic act, and  $c$  denotes the cost to the altruist (Hamilton 1964). The equation predicts that altruistic behavior would more likely occur among individuals that are closely related kin. Cooperation is favored by natural selection if relatedness is greater than the cost to benefit ratio. Hamilton also coined the term “inclusive fitness” to refer to the total genetic success of an individual based on personal reproduction (direct fitness) and the effects on reproduction of nondescendent kin (indirect fitness). Inclusive fitness is a defining feature of kin selection.

#### Examples of Kin Selection

One popular example of kin selection is in the Polistes, paper wasp (Hamilton 1964). The female wasps mate with unrelated male wasps during the breeding season and then spend the winter hibernating in a shelter. In the spring, they emerge and start a nest that contains a single egg. Other females join the foundress

female and a hierarchy is established. The dominant female reproduces and the subordinates help rear the larvae and protect the nest against predators and parasites. The queen wasp uses sperm stored from last fall’s copulation to fertilize the eggs that were laid early in the season. These eggs are destined to become daughters. When it is adaptive to produce sons, she lays unfertilized eggs.

When the first females emerge, they help their mother raise more daughters (both full and half sister) rather than fly off and start their own colonies. The queen continues to produce more eggs. As summer progresses, some of the females that the queen produces, stop working and start taking food from their sisters. Later, males emerge for the first time and they also do nothing to help the colony. The latter females and males fly off together and mate, the males die, and the females hibernate through the winter to start the cycle all over again.

The daughters of the queen wasp serve in helper roles for life because they may not have the option to reproduce and by helping their sisters such that they increase their fitness indirectly. Females and males who do not take on the helper role may be acting to increase their fitness directly by increasing their personal chance of reproductive success.

Another example of kin selection is in the Belding’s ground squirrels. These squirrels produce a whistle-like alarm call when they see a terrestrial predator, such as a coyote or badger. Paul Sherman (1985) observed predators capture and kill alarm callers at a higher rate than non-calling, fleeing squirrels and investigated the mechanisms underlying the alarm calling. He found that the caller may serve to enhance its own personal chances of reproductive success by alerting its neighbors so that together they create a chaotic mass that confuses the predator and allows them to run away safely. But in addition, while the caller may reduce its chances for reproductive success, it increases its inclusive fitness by alerting its relatives. Females are more likely to give calls than males. They may be increasing the chances of survival of their offspring but also because females live with

many relatives compared to more solitary males, females could be increasing the survival of their relatives. Females with living relatives nearby call more frequently than females without living relatives as neighbors.

Evidence of gene bias in humans is suggested by the phenomenon of mother's brother (Alexander 1974). The phenomenon suggests that if a man lacks confidence in his paternity of his children, his nieces and nephews may become his closest relatives in the next generation. According to Alexander, lowered confidence in paternity may be caused by circumstances that involve husbands and wives living apart and/or long absences of husbands on hunting or military trips. Low confidence may lead to reduced paternal care by the mother's spouse, thus increasing the value of care given by the mother's brother. Mathematically, when a man can only estimate his paternity at 25% or lower, he becomes the most closely related male to the sister's offspring. Thus, in accordance with kin selection, preferential care may be given to those most genetically close to us but if the genetic components are questionable, the altruist may find the next closely related non-descendent kin to invest in. Evidence for the mother's brother's phenomenon is rare but is thought to occur in polygamous societies where confidence of paternity is relatively low.

Recent research on inclusive fitness and cooperation among kin shows that human kin selection may not only include genetic kin but also kin by marriage (in-laws) (Dyble et al. 2018). Unrelated kin and spouses may not necessarily share genes but they may have shared genetic interests in future reproduction, and therefore, may derive indirect fitness benefits through cooperating. For example, a mother may have an interest in the reproduction of her son's wife. Dyble and colleagues (2018) used a standard inclusive fitness theory to calculate a coefficient of shared reproductive interest that predicts altruism in both genetic kin and in-laws. The researchers concluded that "two-daughters-in-law or eight cousin's spouses" could be added to the inclusive fitness statement of saving two brothers and eight cousins.

## A Recent Debate about Kin Selection

For decades, many scientists have accepted the notion of kin selection which is based on inclusive fitness, genetic success based on personal reproduction (direct fitness), and effects on reproduction of nondescendent kin (indirect fitness). The prominent biologist E.O. Wilson was a strong proponent of kin selection, especially in explaining the behavior of social groups of animals such as bees, ants, and termites. Recently, E.O. Wilson, Martin Nowak, a Professor of mathematics, and Benjamin Allen, a Research Associate in mathematical biology, rejected this notion and have determined that the theory is mathematically flawed (Nowak et al. 2010). They point out that a large majority of the field data does not fit with the predictions of kin selection theory. They found that cooperation was common among many species where individuals were not genetically related and many instances where cooperation was not found within species, even though the mathematics of kin selection theory would predict it. Rather than kin selection, Wilson and colleagues (Nowak et al. 2010) suggest a mathematical model for the evolution of eusociality (sociality that involves cooperative brood care, overlapping generations within a colony, and a division of labor of reproductive and non-reproductive groups). The model does not require individuals to be related to others' offspring. There continue to be many defenders of the original kin selection theory.

## Reciprocal Altruism

In *The Evolution of Reciprocal Altruism*, Trivers (1971) discusses a different type of altruism than Hamilton suggested. In this entry, he describes how it pays off for individuals to render assistance to others when the cost is low and if, in doing so, it increases the probability of receiving help of greater value in the future. Trivers (1971) describes several conditions that favor the evolution of reciprocal altruism including: (1) a long life span of individuals of a species to maximize the chance for altruistic acts to occur, (2) low dispersal rate to increase the likelihood of interactions between the same

neighbors, and (3) interdependence of members of a species to keep individuals near each other. Trivers also mentions that while parental care, mutual dependence between parents and offspring, can be explained by Hamilton's model (Hamilton 1964), there is no reason that reciprocal altruism may not also operate between close kin. He also points out that these are broad conditions that favor reciprocal altruism but how many altruistic acts occur and the symmetry of those interactions are the most important parameters.

In his original description of reciprocal altruism, Trivers (1971) interpreted cooperative interactions between members of different species as reciprocal exchanges of assistance and pointed out their similarity to the Prisoner's Dilemma game (Axelrod and Hamilton 1981). In the Prisoner's dilemma, two individuals can each either cooperate or defect. No matter what the other does, defection yields a higher payoff than cooperation. If they both defect, both do worse than if both had cooperated. If the game is played long enough, it becomes an iterated version in which strategy can be used to determine the probability of cooperation and defection as a function of history. Among a huge number of reciprocal strategies, tit for tat is one of the most simplest ones. It is based on two simple rules: to cooperate in the first trial and, in the following, to do what the other player (opponent) did in the last trial. Under certain constraints, mutual cooperation appears to be the best strategy whenever reciprocity is maintained.

### Examples of Reciprocal Altruism

It has been suggested that altruistic acts performed between two individuals from different species may be the purest form of reciprocal altruism because there should not be any genetic enhancement from the altruistic act (Rothstein 1980). Some species interact with other species in a symbiotic relationship in which both groups have mutual dependency. For example, a large number of fish and shrimp are known to be cleaners of other larger species of fish (Feder 1966). Cleaner fish and shrimp rid host fish of ectoparasites by entering the gill or the mouth

of the host fish and ingesting the parasites. Cleaner fish and shrimp are distinctly colored and behave in distinct ways (i.e., dipping and rising movements) to attract host fish to be cleaned and inhibit other fish from eating them. According to Feder (1966), there is likely a strong selection for hosts not to harm their cleaners and, as predicted, there are species that mimic cleaners in similar colors and movements but then attempt to take a bite out of the fish approaching to be cleaned.

A host fish to be cleaned seems to perform several altruistic acts. First, it avoids eating the cleaner, even though natural selection should favor a cleaning followed by a good meal. Second, it signals to its cleaner when it is about to depart, and third, it may chase off other fish that pose a danger to the cleaner.

The behavior of the host fish may have resulted from natural selection because of the benefits of keeping the cleaner alive (Trivers 1971). To support the hypothesis that the host is repaid its initial altruism, Trivers (1971) presented several conditions favoring the evolution of reciprocal altruism. First, the host actually suffers from these parasites. Research has shown that the removal of all cleaner fish from a coral reef drastically reduces the number of larger fish within the next few days. Additionally, many of these territorial fish develop swellings, white fuzzy blotches and ulcerated sores. Secondly, finding a cleaner is difficult and dangerous. Observations show that if cleaners do not appear over one coral in about half a minute, host fish swim to another coral and wait. Thus, there may be several alternative cleaning stations to go to. In addition, it may be dangerous for some fish to be cleaned because they have to leave their protective environments. For example, moray eels do not normally leave their holes during the day time but they will in order to be cleaned. A third piece of evidence suggesting that the host is reciprocating its cleaner is that there is site specificity. Feder (1966) reviewed evidence for this, concluding that cleaner fish have regular stations to which fish wanting to be cleaned can go. This is especially evident of territorial recipients of the



cleaner. Fourth, the lifespan of the cleaner seems to be easily long enough for effective selection against cheaters. And lastly, it is been shown that hosts use the same cleaner repeatedly. All of this evidence suggests that the cleaner organisms and their hosts meet the conditions for the evolution of reciprocally altruistic behavior.

Another example examined by Trivers (1971) is the warning calls in birds. Warning calls in birds do not allow for the predator to easily determine the location of the call giver. However, giving a call may occasionally result in the death of the caller, either by the observing nearby predator or a second nearby predator. Trivers (1971) suggests that the calls are selected for because they aid the bird that gives the call. It is disadvantageous for an observer bird to have a predator eat a nearby conspecific or fellow bird because the predator may then be more likely to eat the observer bird. Thus, giving a warning call prevents predators from specializing on the caller's species which includes forming a specific search for the prey species, learning the habits of the species, and perfecting its catching techniques on it. Second, the warning call prevents predators from specializing on the species locality which includes frequenting the area where the birds live and learning useful information about the area in which the bird lives. According to Trivers (1971), it does not matter if the calling bird may be helping its non-neighbors more than it is helping itself. What counts is that it outcompetes conspecifics in areas where no one is calling. The noncalling neighbors will find themselves in an area without any caller and will be selected against relative to birds in an area with callers.

There is no evidence that the birds can discriminate against cheaters but there is also no evidence that the birds stop giving calls because their neighbors are not reciprocating. It seems that just the fact that the neighbor survives repays the caller of its own altruism.

In humans, sperm donation in the USA may be an example of reciprocal altruistic behavior. European and Australian investigators contend that sperm donation is primarily altruistic and

that financial motives are strictly secondary. Although in these communities, financial compensation is often withheld and yet recruitment remains successful. However, in the USA, the donor is usually paid for services rendered and without compensation, recruitment may be challenging. In a study by Rushton et al. (1981), 42 male sperm donors who were active in an insemination program were surveyed along with 50 male matched controls (note that the only difference is that they did not donate). Both donor and control groups opposed contact between offspring and donor and donors demonstrated little interest in meeting the recipients. Sixty-two percent of the donors surveyed said that money was the primary reason for participating. Thirty-six percent said that they would like to see the child and only 36% would inform their wife or partner. Two major differences in the motivation of donors versus controls were that controls were more in agreement than donors that donating sperm was altruistic. However, donors were in more agreement than controls that donating sperm was more like donating blood. In this survey, money was clearly the primary reason for donor participation. The majority of respondents would not participate if money was withheld. Furthermore, both donor and control groups favored financial compensation for participants. According to Rushton and colleagues (1981), sperm donors in the USA donate sperm based on reciprocal altruism.

A more recent study investigated the effect of reciprocity priming on organ donor registration intentions and behavior (O'Carroll et al. 2017). In Study 1, participants who were not currently registered organ donors took part either face-to-face or online and were randomly allocated to a reciprocity-prime or control condition. Primed participants were required to respond on a 7-point Likert scale from "*Strongly disagree*" to "*Strongly agree*," to the item "*I would accept an organ from a deceased donor in order to save my own life.*" The control item was "*Organ donation is important,*" and participants responded on the same 7-point scale. Following the manipulation, they were asked



to indicate, on either a paper or online questionnaire, their intention to join the organ donor register. Study 2 was similar to Study 1 but with the addition that after reporting intention, participants were then offered an organ donation information leaflet or the opportunity to click a link for further information (proxy behavioral measure). The results of both studies showed that reciprocity-primed participants reported greater intentions to register than controls. However, in the second study, there was no evidence of donation behavior. The findings showed that using reciprocity might be an effective tool to increase individuals' intentions of organ donor registration but this increase in intention may not translate into donation behavior.

### **Does Reciprocal Altruism Exist in Nonhuman Species?**

While there are numerous examples of what appears to be reciprocal altruism in nonhuman species, some scientists question whether cooperation among nonhuman species truly represents reciprocal altruism or whether it is limited to strategies that generate immediate fitness benefits (e.g., Clutton-Brock 2009). Although experimental studies with captive birds and mammals have shown that the probability that individuals will assist each other can be affected by the previous behavior of partners or other group members, very few attempts have been made to measure the net fitness benefits of reciprocal altruism between non-kin. Only a few of the studies commonly cited as examples of direct reciprocity in natural populations provide evidence that definitively excludes the possibility that cooperative behavior is maintained by immediate shared benefits, manipulative tactics, or kin selection.

Not only might there be alternative possible explanations for most examples of reciprocal altruism in nonhuman species but reciprocal exchanges can be costly, resources highly valuable, there can be considerable delays between giving, and extensive opportunities for cheating. Clutton-Brock (2009) suggests that reciprocal exchanges might also require some form of language to establish expectations and intentions,

to take into account the timing of exchanges, and to establish social norms to discourage cheating.

### **A Critique of Reciprocal and Genetic Altruism: Are They Really Separable?**

Reciprocal altruism and kin selection (genetic altruism) may not be clearly separable phenomena as they are currently defined. Reciprocal altruism is an exchange of favors between nonrelatives in which the giving and returning of favors occurs at different times and in which the cost of providing favors are lower than the benefits receiving them (Trivers 1971). Kin selection takes place when individuals increase their inclusive fitness by helping other individuals (usually closely related) who share the genes responsible for their aid giving behavior. Rothstein (1980) suggests that most examples of reciprocal altruism are special cases of kin selection. According to him, when conspecific reciprocal altruists exchange favors they are almost certainly doing so because they share at least some of genes responsible for their altruism. Therefore, the only type of reciprocal altruism that is distinguishable from kin selection is reciprocity between members of different species, such as the cleaner fish (Trivers 1971) described earlier. Because there are very few examples of interspecies cooperation, according to Rothstein (1980), there is generally always some genetic similarity among altruists and therefore, pure reciprocal altruism rarely exists and thus individuals who engage in reciprocal altruism are to some extent kin.

### **True Altruism and Ascetic Altruism**

#### **Conceptualizations**

There have been numerous attempts to conceptualize and explain true altruism. Simon's model (e.g., Simon 1990) suggests that, even if genes are the controlling sites of natural selection, people have the capacity to learn at the socioeconomic level which can lead to the selection of altruism. According to Simon (1990), docility is the basis for true altruism and true altruism

is a by-product of docility. Docility refers to the capacity for being instructed and the tendency to accept and believe those instructions. Docile individuals are those who are adept at social learning and who accept well the instruction society provides for them. These individuals tend to learn and believe what they perceive others in the society want them to learn and believe. Simon's model (1990) suggests that docile persons are more than compensated for their altruism by the knowledge and skills they acquire. A critical assumption of the model is that social organizations know better than individuals. That is, social organizations help structure the information that flows among individuals to improve their individual fitness. Thus, rather than function as independent individuals, there may be an accumulation of knowledge that gives each member of the group a fitness advantage.

Hoffman (1981) offers four kinds of behavioral evidence for biologically based altruism: (1) people frequently help others in society, (2) that a great deal of helping is performed by those whose needs for approval is not strong, (3) it often occurs almost immediately, and (4) that signs of relief in others appear to reinforce helping behaviors. Hoffman also suggests that natural selection requires a system that is reliable and yet also flexible and what therefore must have been acquired is a predisposition or a motive to help. And although this may be biologically based, it is nevertheless amenable to control by cognitive processes.

Another attempt at explaining true altruism has been to involve the construct of empathy. Aronfreed (1972) accounted for both the origin of empathy and the capacity of emphatic reactions to produce altruistic behavior. He observed that small children learn to feel bad when others feel bad and they learn to feel good when others feel good early in their lives because these conditions serve as conditioned stimuli, which through associations come to evoke similar affective responses. The motivation behind empathy is to relieve distress, which we supposedly feel when we see someone else suffering. Relieving one's own distress may appear to be a

selfish act but Hoffman (1981) argues that although the consequence of helping reduces the helper's distress, there is evidence that the conscious intention of helpers is to reduce the distress of another. In addition, he suggests that since motives are always accompanied by feelings of satisfaction, a feeling of satisfaction cannot be used to distinguish between egoist and altruistic motives.

Mary Maxwell discusses her conceptualization of true altruism in her book *Morality Among Nations: An Evolutionary View* (Maxwell 1990). In it, she proposes that reciprocal altruism led to the development of moral emotions (which she credits as Triver's idea). Moral emotions cause the development of notions of right and wrong. Notions of right and wrong result in the institutionalization of morality in human society. She believes it is faulty logic to state that natural selection requires altruism to be selfish and therefore all altruism is selfish. Rather, she contends that humans have entered into a "new human-created environment" in which mortality has different ways of controlling behavior and motives.

Joseph Lopreato defines true or ascetic altruism as behavior, conscious or unconscious which, guided by innate predispositions, potentially reduces the inclusive fitness of the benefactor while increasing that of the beneficiary (Lopreato 1981). In his article on *Genuine Altruism in Homo sapiens*, he attempts to search for and explain altruism as behavior that reduces the inclusive fitness of the giver while increasing that of the recipient. He refers to altruism as "ascetic altruism" because of the ambiguity with use of the term "altruism" and to include the concept of self-denial that is included in the concept of asceticism.

According to Lopreato (1984), true altruism evolved as a result of an increase in complexity of society or groups. Social pressures and demands of society (to help when needed) increased as the complexity of groups increased. However, as the selfish gene theory (Dawkins 1976) professes, we are internally driven to maximize our own genetic fitness. The drive to fulfill our social demands conflicts with our drive

for genetic fitness. This opposition causes dissonance that ultimately causes shame. In order to rid ourselves of this dissonance and shame, we gain souls or moralistic behavior. The soul allows us to be truly altruistic. As groups become more complex and increasingly demanding, the hierarchy of altruism would consist of true altruism at the top existing in groups with high socialization and complex interactions. At the bottom of the hierarchy would be genetic altruism existing in groups with very little social interaction and dependency. And reciprocal altruism should fall in the middle.

The evolution of the soul is a by-product of self-deception whose main effect was and may still be the maximization of inclusive fitness (Lopreato 1984). Self-deception may have evolved from increasing complexity of the reciprocal system and as a means of coping with flagrant cheating of an evolving dominance order. As long as self-deception and the idea of soul exist, a certain percentage of individuals are likely to fall victims to them.

### Does True Altruism Exist?

The ultimate question about true altruism is whether it exists such that people do things for each other without expecting something in return.

Several studies report physical and psychological benefits associated with altruistic behavior. For example, volunteerism is positively correlated with self-reported happiness, health, and well-being (see Filkowski et al. 2016 for review). People who regularly volunteer report greater satisfaction in life and exhibit reduced rates of depression and anxiety compared to those who do not volunteer. Similarly, engaging in acts of kindness has also been associated with increased well-being. These findings indicate that being aware of the kindness of others and of one's own acts of kindness is related to increased self-reported levels of well-being. In a study by Otake et al. (2006), participants were asked to count the number of acts of kindness they performed for 1 week. A control condition did not partake in the "counting kindness" task. Results indicated that counting acts

of kindness significantly increased self-report levels of happiness. Together, these studies suggest that altruistic behaviors not only benefit others but also have profound positive effects on the current and future physical and psychological well-being of the person performing the behavior.

Lopreato (1981) describes a discussion involving the sociobiologist E.O. Wilson, about whether Mother Theresa is an example of ascetic or true altruism. Mother Theresa was a member of the Missionaries of Charity and therefore nonreproductive. In Calcutta and elsewhere, she cared for poor, the forsaken, the sick, and the foundlings. She received international honor and recognition, including the 1979 Nobel Peace Prize. E.O. Wilson notes that even Mother Theresa is selfish, "for she seeks to save her soul" (cited in Lopreato 1981). Lopreato (1981) suggests that the sociobiology of altruism concerns the salvation of genes and not souls and therefore Mother Theresa is a true altruist and there may be others like her. She sacrificed her reproductive fitness in the service of countless individuals who are unrelated to her.

### Cross-References

- ▶ [Alarm calls](#)
- ▶ [Cheating](#)
- ▶ [Deception](#)
- ▶ [Decision-Making](#)
- ▶ [E.O. Wilson](#)
- ▶ [Genes](#)
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- ▶ [Reciprocity](#)
- ▶ [Reproductive Fitness](#)
- ▶ [Richard Dawkins](#)
- ▶ [Robert Trivers](#)
- ▶ [Origin of Species](#)

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## Amazonian Manatee

### ► Sirenia Diet

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## Ambiguous Cue Interpretation

### ► Judgment Bias

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## Amino Acid

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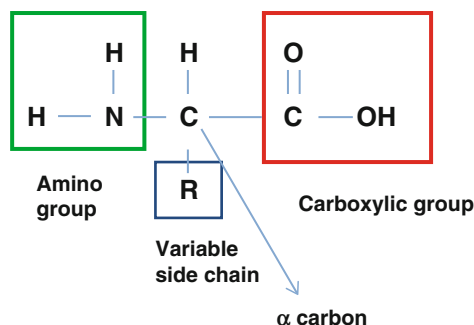
## Definition

Amino acids are compounds containing an amino group, a carboxyl group, a hydrogen atom, and a distinctive side chain, all bonded to a carbon atom, the  $\alpha$ -carbon.

## Introduction

Amino acids serve as monomer of proteins. Amino acid residues are covalently linked through peptide bond to form a protein. Twenty different amino acids are commonly found in proteins. The first discovered amino acid was asparagine. All amino acids have trivial or common names, in some cases derived from the source from which they were first isolated. Asparagine was first found in asparagus, hence the name asparagine (Vauquelin et al. 1806). All amino acids except glycine are optically active, i.e., they rotate the plane of polarized light.

In an amino acid, if the amino group and carboxylate groups are attached to the same carbon atom, which is called  $\alpha$ -carbon, then the amino acid is called  $\alpha$ -amino acid. Various  $\alpha$ -amino acids differ with respect to the side chain attached to their  $\alpha$ -carbon. The general structure of an amino acid is:



The R group or side chain attached to the  $\alpha$ -carbon is different in each amino acid.

Many naturally occurring amino acids which are not found in proteins have structures that differ from the  $\alpha$ -amino acids. In these compounds the amino group is attached to a carbon atom other than the  $\alpha$ -carbon atom, and they are called  $\beta$ -,  $\gamma$ -,  $\delta$ -, or  $\epsilon$ -amino acids depending upon the location of the C-atom to which amino group is attached. For example, GABA (gamma-amino-butyric acid) is a  $\gamma$ -amino acid, and  $\beta$ -alanine is a  $\beta$ -amino acid (Nelson et al. 2005).

Amino acids exist in solution as the dipolar ion or zwitterion. A zwitterion can act as either an acid or a base. Hence, an amino acid is an amphoteric molecule. Because amino acids contain ionizable

groups, the predominant ionic form of these molecules in solution depends on the pH. Titration of an amino acid illustrates the effect of pH on amino acid structure. The pH at which an amino acid has no net charge and is electrically neutral is called its isoelectric point (pI).

## Classification of Amino Acids

I. Classification based on nature of R group: This classification is based on the properties of R groups, in particular, their polarity or tendency to interact with water at biological pH.

1. *Nonpolar, aliphatic R groups*: glycine, alanine, proline, valine, leucine, isoleucine, methionine
2. *Aromatic R groups*: phenylalanine, tyrosine, tryptophan
3. *Polar, uncharged R groups*: serine, threonine, cysteine, asparagine, glutamine.
4. *Positively charged R groups*: lysine, histidine, arginine
5. *Negatively charged R groups*: aspartate, glutamate

II. *Classification based on dietary requirement of amino acids*: Living organisms differ in their capacity to synthesize the amino acids required for protein synthesis. Many microbes can produce all 20 standard amino acids from readily available precursors, but other organisms must obtain some preformed amino acids from their diet. Mammals and other animals can only synthesize a subset of these standard amino acids, known as the 12 nonessential amino acids. The remaining eight essential amino acids must be obtained from the diet:

1. *Essential amino acids*: isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, valine (arginine and histidine are essential for infants)
2. *Nonessential amino acids*: alanine, proline, asparagine, aspartate, cysteine, glutamate, glutamine, glycine, serine, tyrosine

## Standard and Nonstandard Amino Acids

More than 300 amino acids are present in cells; however, only 22 amino acids participate in protein synthesis ribosomically. Such amino acids are called proteinogenic or standard amino acids. Apart from the 22 standard amino acids, all other

amino acids which are not ribosomically incorporated into proteins are called nonstandard amino acids. In addition to the standard amino acids, some proteins may contain nonstandard amino acid residues formed by posttranslational modification of standard amino acid residues already incorporated into a polypeptide. These modifications are often essential for the function or regulation of a protein. Examples of such amino acids are 4-hydroxyproline, desmosine, and N-acetylserine (Ambrogelly et al. 2007).

## Cross-References

- [Codon](#)
- [Genetic Code](#)
- [Protein](#)
- [Ribosome](#)

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## Amniocentesis

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## Synonyms

[Amniotic fluid test \(AFT\)](#)

## Definition

Amniocentesis, also called as Amniotic Fluid Test (AFT), is an invasive prenatal medical procedure

carried out primarily to diagnose chromosomal abnormalities and/or infections by using fetal DNA from the cells collected from the amniotic fluid.

## Introduction

In 1956, American obstetrician Fritz Friedrich Fuchs and Danish gastroenterologist Polv Riis pioneered the technique of Amniocentesis by collecting samples to determine the fetal sex. Up until the 1970s amniotic fluid collection was done blind. In 1972, Jens Bang and Allen Northend reported that needle insertion for amniotic fluid collection could be done using ultrasound techniques.

Amniocentesis is usually reserved for those women considered at higher risk of carrying a fetus with a chromosomal or genetic abnormality. In most cases, the women are suggested to undergo amniocentesis only after genetic counseling to avoid miscarriage as a result of amniocentesis.

## General Description

The fetal programming hypothesis proposes that the in utero environment can impair fetal development, with a permanent effect on the phenotype. Amniocentesis is one of the techniques used to assess and predict the possible phenotypic or genotypic deformities. It is mainly of two types – early amniocentesis and second trimester amniocentesis, also called as late amniocentesis. The major difference between the two is the amount of amniotic fluid aspirated and the gestation period during which sampling is carried out. During early amniocentesis about 10–12 ml of fluid is collected from the amniotic sac, and sampling is done between 11–13 weeks of gestation whereas in late amniocentesis, which is carried out during 16th week of gestation period, up to 20 ml of sample can be extracted (A thumb rule suggests that not more than approximately 1 ml per week of gestation be extracted). Complications post procedure may include amniotic fluid leakage, pregnancy loss, preterm labor and delivery, respiratory distress, postural deformities, chorioamnionitis,



fetal trauma, and alloimmunization of the mother (rhesus disease). Some of the most common abnormalities detected are Down syndrome (trisomy 21), Edwards syndrome (trisomy 18), Patau syndrome (trisomy 13), and Turner syndrome (monosomy X) (Alfirevic et al. 2003; Ogilvie and Akolekar 2014).

The procedure is performed with uninterrupted ultrasound guidance under the influence of local anesthesia. A sterilized 22-gauge spinal needle is used to puncture the sac in an area away from the fetus. The needle is inserted through the maternal abdominal and uterine walls into the pocket of amniotic fluid within the amniotic sac. A total of 10–20 ml of fluid is aspirated. The fetal cells in the amniotic fluid and the fluid itself can be assessed for various infections, birth defects, or chromosomal abnormalities. The fetal cells can be further cultured and analyzed for a more detailed karyotyping (Alfirevic et al. 2003).

Prenatal exposure to elevated cortisol, heavy metals are known to impair cognitive abilities (Bergman et al. 2007) and have long-term effects on neurodevelopment and behavior, outcomes also include symptoms of Attention Deficit Hyperactivity Disorder (ADHD) and increased distress/anxiety (Bergman et al. 2010). The exposure of these can be assessed by analyzing the amniotic fluid collected during amniocentesis.

Advancement in technology allows for the use of certain molecular markers to assess the well-being of the fetus without having to opt for invasive techniques like amniocentesis. Comparative genomic hybridization (CGH) testing, next-generation sequencing (NGS)-based noninvasive prenatal test (NIPT), noninvasive biochemical tests like dual marker test, quadruple marker test are some of the tests that are suggested to be safer options than AFT.

## Cross-References

- [Embryo](#)
- [Fetus](#)
- [Heredity](#)

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## Amniotic Fluid Test (AFT)

- [Amniocentesis](#)

## Amodal Completion

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## Synonyms

[Perceptual completion](#); [Visual completion](#); [Visual interpolation](#)

## Definition

A perceptual phenomenon in which the observer recognizes portions of an object occluded by another object.

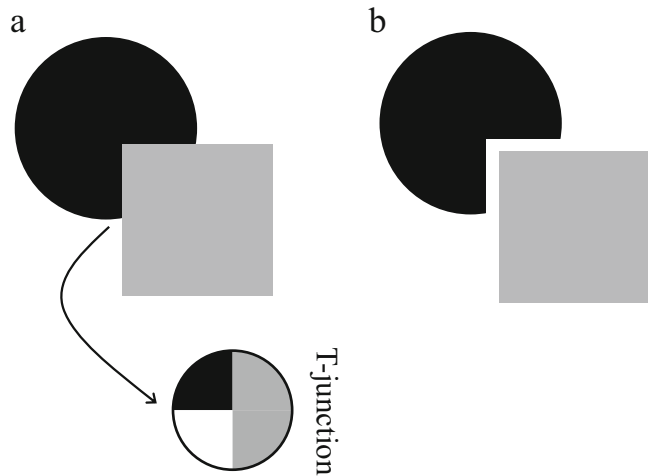
## Introduction

In the three-dimensional world, objects that are farther from the observer are often partly occluded by other objects that are closer to the observer.



**Amodal Completion,**

**Fig. 1** (a) An example of amodal completion containing a T-junction. (b) A case of no completion with a figure similar to (a)



Although the occluded portions of the farther objects cast no optical information on the observer's retina, they are recognized as if the occluded portions are completed, a phenomenon called amodal completion (Michotte et al. 1991). In Fig. 1a, the observer may perceive an intact disk "behind" a square by completing the portion "hidden" by the square, although the retinal image is merely a Pac-Man-like shape (three-quarters of a circle) placed adjacent to the square, with no gap between them. (If there is a gap between them, the Pac-Man-like shape will be perceived as it is, as in Fig. 1b.)

Some have proposed that completion of occluded portions of objects occurs at a high level of cognition, such as knowledge or belief. However, there are three lines of evidence that completion occurs in a more bottom-up fashion, or at an earlier level of our visual system: 1) Kellman and Spelke (1983) reported that 4-month-old infants perceptually complete occluded portions of objects. 2) When adult participants were required to find a truncated disk, search performance deteriorated when a square was placed adjacent to the truncated disk, suggesting that perceptual completion is an inevitable, automatic process that is difficult to submit to conscious control (Rauschenberger and Yantis 2001). 3) Electrophysiological studies have revealed that neurons in primary visual cortex (V1) in macaques respond to an occluded portion of an object (Sugita 1999). Similarly, a recent fMRI study has suggested that human V1 and V2 may

code occluded portions of an object (Ban et al. 2013).

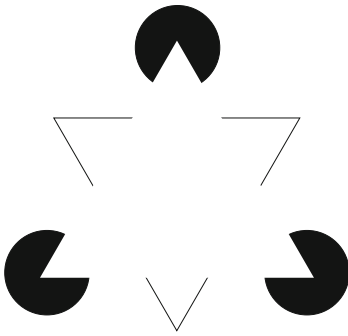
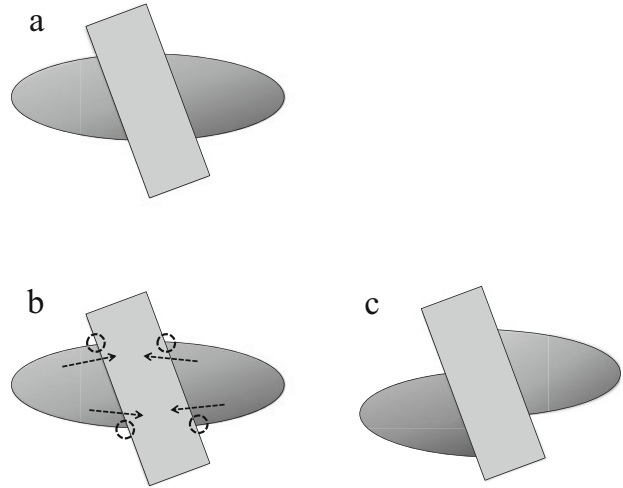
### Cues to Perceive Amodal Completion

One difference between Fig. 1a, b may be critical for amodal completion. In Fig. 1a, the contour of the disk meets the contour of the square, resulting in the formation of two T-junctions of contours, which our visual system may use to detect occlusion. When we look at Fig. 2a, an oval seems to be placed "behind" a rectangle; the center portion of the former appears to be occluded by the latter, suggesting that we perceptually complete the missing center part of the oval. Dotted circles in Fig. 2b show the four T-junctions. Kellman and Shipley (1991) have suggested that the relatability of contours is also important in completing occluded portions of figures, such that the hypothetical extension of a visible edge needs to be smoothly connected to the edge on the other side, as indicated by dotted arrows in Fig. 2b. Lack of contour relatability makes the two visible portions of the oval appear to be disconnected from each other, as in Fig. 2c.

According to Shipley and Kellman (1992), relatability is a common mechanism of amodal and modal completion. A famous example of modal completion is the well-known phenomenon of subjective contour, exemplified by the Kanizsa triangle (Fig. 3), in which we perceive a triangle

### Amodal Completion,

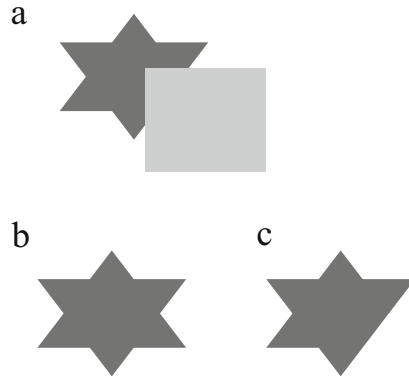
**Fig. 2** (a) Another example of amodal completion. (b) T-junctions and relatability. (c) Another case of no completion with a figure similar to (a)



**Amodal Completion, Fig. 3** An example of modal completion (Kanizsa illusion)

with visual attributes such as clear contours and a brighter surface “in front of” the white background. By contrast, in amodal completion, the occluded portion and contour of the occluded object can be recognized, but with no such visual attributes.

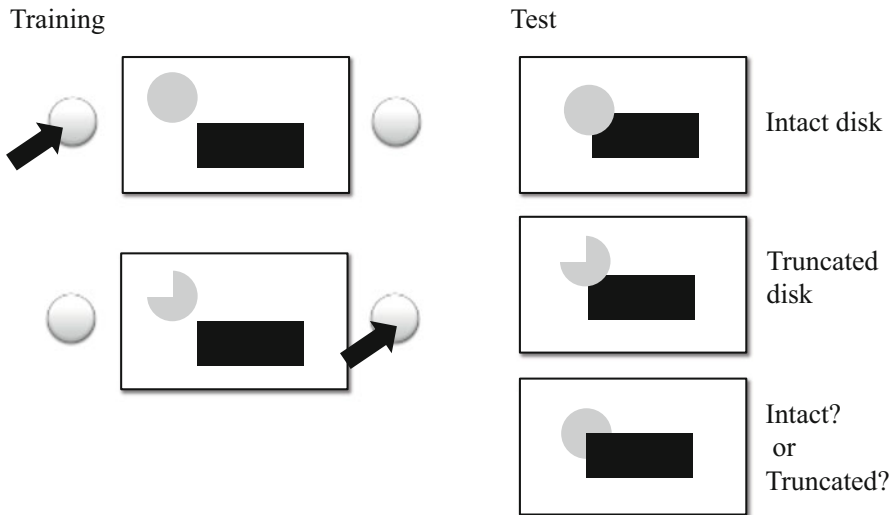
Although the mechanisms of amodal and modal completion are probably similar, modal and amodal percepts are unlikely to arise from identical processes. Determinants of the percept of an occluded portion include regularity of the overall figure (e.g., Sekuler 1994), as well as purely bottom-up cues such as T-junctions and relatability. For example, the figure of Fig. 4a may be perceived as the partly occluded hexagram in Fig. 4b, although an account solely based on relatability would predict that the completed figure must be like Fig. 4c.



**Amodal Completion, Fig. 4** (a) Another example of amodal completion. (b) Possible occluded figure in (a). (c) Possible occluded figure predicted by relatability account only

### Amodal Completion in Nonhuman Animals

Along with many other human visual functions, amodal completion may be shared with other species in the animal kingdom. A simple, non-verbal method can be used to investigate whether non-human animals do indeed experience amodal completion. As illustrated in Fig. 5, Sekuler et al. (1996) trained pigeons to select one choice stimulus when they were exposed to an intact disk and the other choice stimulus when they were exposed to a truncated disk. On each probe trial in the succeeding test phase, the pigeons were



**Amodal Completion, Fig. 5** An illustration of the procedure used by Sekuler et al. (1996)

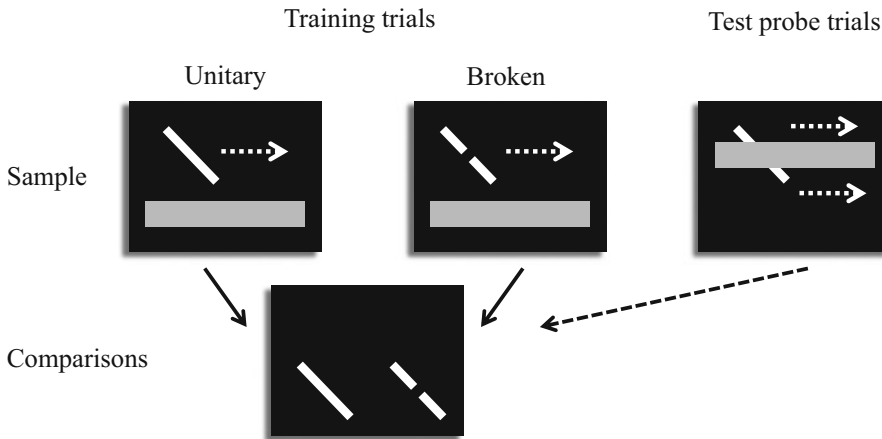
exposed to either A) an intact disk placed “on top of” a rectangle, B) a truncated disk placed “on top of” the rectangle, or C) a stimulus in which the rectangle was placed adjacent to the truncated portion of the disk. A choice of the stimulus corresponding to the intact disk on the probe trial in which the stimulus C was presented would have indicated that the animal experienced amodal completion, but the pigeons of Sekuler et al. made the other choice, indicating that they did not experience this completion.

Other procedures are also available to investigate amodal completion in nonhuman animals: yes/no or (symbolic) matching-to-sample, go/no-go (e.g., Cerella 1980), identical matching-to-sample (e.g., Ushitani et al. 2001), and visual search (e.g., Fujita and Ushitani 2005). Cerella (1980) trained pigeons to respond to a triangle and not to respond to other figures, such as circles or stars. After the accomplishment of the training, the pigeons were tested whether they would respond to partly occluded triangles. Pigeons did not frequently respond to partly occluded triangles, suggesting that they do not experience amodal completion. In an identity matching-to-sample task (See Fig. 6), Ushitani et al. (2001) trained pigeons to match a unitary bar and a similar but broken bar (i.e., there was a gap in the

middle of the bar) to each identical bar. In the test phase, when a bar with its middle portion being occluded by a rectangle was presented as sample, the pigeons selected the broken bar, suggesting that they did not complete the occluded portion of the bar.

Fujita and Ushitani (2005) instructed humans and trained pigeons to search for a partly truncated square among intact squares. In the test phase, the target (truncated square) was placed adjacent to another square with the truncated portion of the former being filled with the latter resulting in the formation of apparently-intact square as similarly to Fig. 1a. The reaction time and accuracy for humans to find the test target deteriorated due to the completion of the truncated portion of the target, whereas those for pigeons did not, suggesting that they did not experience amodal completion.

An animal’s natural responses can also be applied: Shimizu (1998) and Takahasi and Okanoya (2013) used courtship behavior in pigeons and Bengalese finches, respectively. Whereas pigeons showed courtship behaviors to movies of a conspecific, they stopped the behaviors to the same, but partly occluded movie, suggesting that they did not complete the occluded portions of the conspecific. In contrast,



A

**Amodal Completion, Fig. 6** An illustration of the procedure used by Ushitani et al. (2001)

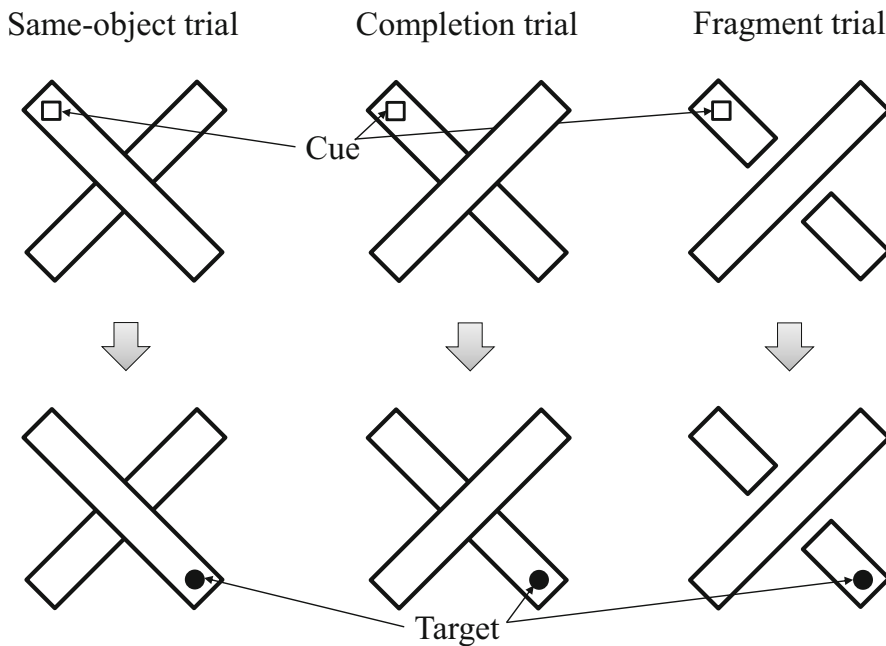
Bengalese fitches kept singing a courtship song to movies of a conspecific even when the movies were partly occluded, suggesting that they experience amodal completion. Lea et al. (1996) and Regolin and Vallortigara (1995) employed filial imprinting in domestic chickens. For example, Lea et al. presented newly hatched chicks with either a unitary bar, a broken bar, or a bar with its center occluded by a rectangle. Chicks imprinted on the unitary bar and the broken bar tended to approach each matching bar rather than the other. Chicks imprinted on the partly occluded bar preferred the unitary bar, suggesting that the chicks completed the occluded portion of the bar. The study by Regolin and Vallortigara resulted in the same conclusion.

Ushitani et al. (2010) demonstrated amodal completion in chimpanzees by taking advantages of object-based nature of their visual attention (Fig. 7). Ushitani et al. first demonstrated that chimpanzees' response latency to a target was shorter when the target appeared in the same rectangle in which a pre-cue had appeared than when it appeared in the other rectangle. Their response latency was also short when the pre-cue and the target separately appeared in two fragments but the fragments formed a unitary rectangle by amodal completion (Completion trial in Fig. 7). In contrast, response latency increased on the trials in which the two fragments formed no unitary figure (Fragment trial in Fig. 7). Note that no

discrimination was not required in this experiment; the chimpanzees just responded to the target.

Electrophysiology also provides us with a powerful method to investigate amodal completion in nonhuman animals. For example, Sugita (1999) recorded activities of orientation-selective cells of V1 in Japanese macaques that activated when a unitary bar was moving but not when a broken bar (i.e., a bar having a gap in the middle) was moving. The cells also activated when the gap of the broken bar was occluded by a patch, suggesting that they responded to a perceptually-unitary bar, i.e., the bar with its gap perceptually completed.

With the efforts of many research teams using the methods described above, various nonhuman animal species have been revealed to perceptually complete occluded portions of objects as humans do. Amodal completion has been demonstrated in a number of nonhuman primates, including chimpanzees (Sato et al. 1997; Ushitani et al. 2010), rhesus macaques (Fujita 2001), Japanese macaques (Sugita 1999), baboons (Deruelle et al. 2000; Fagot et al. 2006), and tufted capuchin monkeys (Fujita and Giersch 2005). Only one study has investigated whether a non-primate mammal species, the mouse, perceptually completes occluded portions of figures (Kanizsa et al. 1993). Although the choice pattern of the mice suggested that they did indeed complete the



**Amodal Completion, Fig. 7** A schematic illustration of the procedure used by Ushitani et al. (2010). Chimpanzee's response latency was short both on Same-object trial and on Completion trial whereas it was longer on Fragment trial

occluded portions, the results could also be interpreted as demonstrating a mere preference for a specific stimulus. A tentative conclusion of these studies is that amodal completion may be widely shared at least among primate species.

Results from studies of avian species have been mixed. Some research has suggested that amodal completion of occluded portions of objects does not occur in pigeons (Aust and Huber 2006; Cerella 1980; Fujita 2001; Fujita and Ushitani 2005; Sekuler et al. 1996; Shimizu 1998; Ushitani and Fujita 2005; Ushitani et al. 2001; Watanabe and Furuya 1997) and chickens (Nakamura et al. 2010, 2011). Other studies, however, have shown that special training or stimuli have enhanced amodal completion in these species (pigeons: Nagasaka et al. 2007; chickens: Forkman 1998). Because amodal completion of occluded portions requires 100–250 ms to be achieved (Rauschenberger and Yantis 2001), it appears to place a relatively heavy load on visual information processing. In terms of the ubiquitous trade-off between speed and accuracy in animal species, amodal completion may not be a default function, one that is automatic and always works,

but rather one that requires certain conditions to be triggered.

Recently, the study of amodal completion has extended to atypical species for psychological experiments. Among avian species, African grey parrots (Pepperberg and Nakayama 2016) and Bengalese finches (Takahasi and Okanoya 2013) have been revealed to complete occluded portions of figures. Studies of fish species has contributed to the literature on amodal completion, revealing that they perceptually complete occluded portions of visual objects (Darmaillacq et al. 2011; Sovrano and Bisazza 2008).

## Conclusion

Examination of more animal species would elucidate the evolution of amodal completion – when and why this cognitive function evolved. Furthermore, as shown in apparently inconsistent findings within the avian class that I have reviewed above, the investigation of species differences in the conditions under which amodal completion operates, rather than merely its existence or non-existence,

would provide additional insight on its mechanisms. More comparison between species and conditions would promisingly contribute to further understanding of amodal completion itself.

## Cross-References

- Depth Perception
- Gestalt
- Visual Perception

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## Amphibia

- [Caudata Cognition](#)

## Amphibious

- [Semi-aquatic](#)

## Amphisbaenians

- [Squamate Life History](#)

## Ampullae of Lorenzini

- [Electroreceptors](#)

## Amygdala

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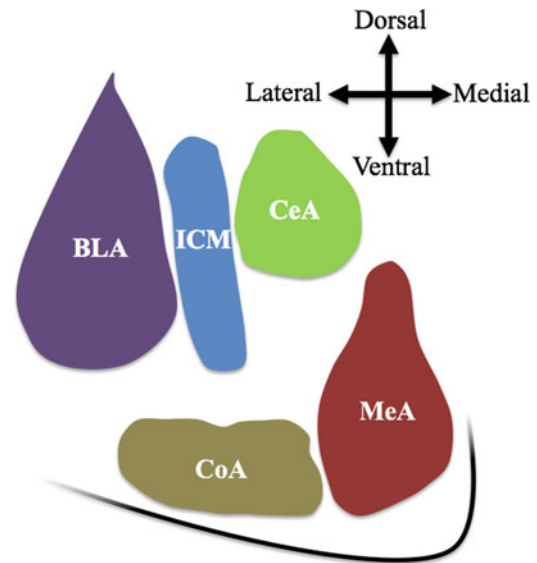
### Definition

The amygdala is a historically grouped complex of 13 nuclei in the brain, together receiving inputs from and projecting to nearly every part of the

central nervous system, supporting a wide variety of functions including associative learning, emotional learning, and responsivity, as well as ingestive, sexual, and social behavior.

### Introduction

The amygdala is a historically grouped complex of 13 nuclei in the brain, each differing in structure, connectivity, and function and together receiving inputs from and projecting to nearly every part of the central nervous system (Swanson and Petrovich 1998). Amygdala circuits support a wide variety of functions including associative learning, emotional learning, and responsivity, as well as ingestive, sexual, and social behavior (Aggleton 2000). Traditionally the amygdala has been divided into the basolateral (BLA), medial (MeA), central (CeA), and cortical (CoA) nuclei, and this will be the vastly oversimplified scheme used for the purposes of this entry (Fig. 1) (McDonald 1998). Amygdalar nuclei might potentially be grouped as structural extensions of the neocortex, claustrum, and striatum but can also be functionally separated into



**Amygdala, Fig. 1** A simplified representation of the basolateral (BLA), medial (MeA), central (CeA), and cortical (CoA) nuclei of the amygdala



four systems: main olfactory, accessory olfactory, autonomic, and frontotemporal cortical systems. While some argue that the historical category of “amygdala” ought to be eliminated, there are also advocates of the term “extended amygdala,” which states that central and medial amygdala form continuous structures with the lateral and medial divisions of the bed nucleus of the stria terminalis, and thus those regions should be included as members in the amygdaloid complex (Swanson and Petrovich 1998). Cats, rats, and monkeys each have cortical connectivity with the amygdala that relay visual, auditory, and somatosensory information. More direct connectivity from olfactory, gustatory, and visceral areas is also preserved across these species bypassing much of higher-level cortical processing (McDonald 1998).

Historically, the amygdala has been mischaracterized as the “fear center of the brain”; however, the fear response is only a subset of negative affective states resulting in withdrawal, escape, and avoidance responses that involve amygdalar function (LeDoux 2003; Paré and Quirk 2017). The amygdala is not limited to negative emotional states, as amygdalar nuclei also play an important role in positive emotional states resulting in attraction or approach response, and is thus better characterized as playing an important functional role in emotional learning more generally (Gallagher and Chiba 1996). In addition to emotional and associative learning, the amygdala plays a key role in the acquisition and consolidation of emotional memories by interacting with hormonal and neuromodulatory systems (McGaugh 2004).

## Historical Developments

In 1819, Burdach first described the collection of gray matter in the anterior portion of the medial temporal lobe, which appeared to form the shape of an almond, that he coined the “amygdala” (from the Greek for “almond,” Latin for “two tonsils”). In 1867, Meynert provided an anatomical description of the structure. By 1923, Johnston provided a rich anatomical description of the

“amygdaloid complex” which he dissociated into a set of phylogenetically older set of nuclei (the central, medial, and cortical nuclei) and a newer set of nuclei (the basal and lateral nuclei) associated with olfaction (Swanson and Petrovich 1998).

In 1888, Brown and Schafer were the first to describe a taming effect on monkeys after the removal of their temporal lobes. However, the amygdala was thought to be primarily associated with olfaction until Kluver and Bucy studied the effect of temporal lobe lesions in monkeys in 1939, where they observed a wide variety of changes in tameness, hyper- and hypo-emotionality, and hypersexuality that became known as Kluver-Bucy syndrome (Gallagher and Chiba 1996). In the late 1940s, MacClean developed a theory of the “visceral brain,” which included the amygdaloid complex as a more primitive and emotional “limbic system” (LeDoux 2003). In 1952, evidence was found that temporal lobe seizures were initiated with a primary neurological discharge originating from the amygdaloid region. Building on Hess’s discovery that stimulation of the hypothalamus could elicit a range of autonomic and stereotyped behavioral responses, along with similar studies of the brainstem, a series of stimulation experiments in cats, dogs, and primates strengthened the amygdala’s hypothesized role in generating these responses (Gloor 1955). By creating more targeted lesions of the amygdaloid complex, Weizkrantz demonstrated its role in emotional learning by giving neutral cues biological significance and by showing that amygdalar damage alone could account for the symptoms observed in Kluver-Bucy syndrome (Gallagher and Chiba 1996).

From the 1960s onward, the neuroscientific study of the amygdala progressively developed “tunnel vision,” driven by NIH funding treatment of anxiety disorders. Given the region’s robust responsivity to fearful stimuli, the neuroscientific community published a vast number of papers associating the amygdala specifically with fear (Paré and Quirk 2017). The first study highlighting the role of the amygdaloid complex in classical fear conditioning was published in 1963. In 1972, it was demonstrated that amygdalar lesions

led rats to exhibit reduced freezing responses to exposure to a natural predator (cat) and to a conditioned stimulus (CS) after being paired with a shock, suggesting a key role in defensive responsiveness (Aggleton in Aggleton 1992). Subsequent key contributions detailing the functional role of the amygdala in fear conditioning cemented fear research as the most dominant paradigm in amygdala research (LeDoux in Aggleton 1992; Davis in Aggleton 1992).

### **Functional Properties of Amygdalar Nuclei (BLA, CeA, MeA, CoA)**

The basolateral amygdala (BLA), often thought of as the sensory interface of the amygdala, receives primarily excitatory thalamic and cortical sensory projections and consists of the lateral (LA), basal, and accessory basal nuclei (LeDoux 2003; Paré and Quirk 2017). Lesions to the basolateral amygdala lead to impaired conditioning where a stimulus acquires biological value and results in impaired second-order Pavlovian conditioning. Lesions to the BLA also eliminate the unconditioned stimulus (US) devaluation effect. US devaluation occurs after training a CS-US pairing, and subsequently pairing that US with a different aversive CS, resulting in a diminished CR (Gallagher in Aggleton 1992). Connectivity between the BLA and prefrontal regions allows for top-down control (Paré and Quirk 2017). The BLA is also recruited for the consolidation of emotional memory, by mediating the memory-modulating effects of stress hormones (corticosterones and glucocorticoids such as cortisol) and affecting multiple neuromodulatory systems (norepinephrine, cholinergic) (McGaugh 2004).

The central amygdala (CeA) is often thought of as the amygdalar nucleus responsible for generating behavioral and autonomic responsivity in relation to the sensory stimuli relayed from the BLA and is the main output nucleus of the amygdala with projections to brainstem, hypothalamic, thalamic, and cortical regions (Pitkanen in Aggleton 1992). The central nucleus has the capability of triggering a wide variety of autonomic responses such as tachycardia, bradycardia, hypoalgesia, endocrine arousal, respiratory changes, and the

release of insulin. Lesions to the CeA result in deficits in appetitive conditioning. CeA damage also impairs conditioned bradycardia and abolishes the fear enhancement of the startle response (Gallagher in Aggleton 1992).

The medial amygdala (MeA), functionally associated with the accessory olfactory system which emphasizes inputs from the vomeronasal organ, plays a role in pheromone and odor processing, social recognition, predator identification, and sexual behavior. The MeA receives inputs from the accessory olfactory bulb and has projections to hypothalamic regions associated with defensive and reproductive behavior (Pitkanen in Aggleton 1992; Swanson and Petrovich 1998).

The cortical amygdala (CoA) is part of the main olfactory system and receives spatially distinct inputs from the glomeruli of olfactory bulb, which are responsible for representing specific types of odorants. The innate aversion and attraction to certain odors depend on the connections between the olfactory bulb and cortical amygdala, and these responses often reflect the evolutionary history of that species. For instance, if a rat is presented with odors prevalent in predator feces or urine, such as 2,5-dihydro-2,4,5-trimethylthiazoline (TMT), the cortical amygdala will trigger innate behavioral responses such as freezing or escape behaviors despite never having actually encountered the predator within its lifetime (Rosen et al. 2015).

### **Two Examples of Emotional Processing: Auditory and Context Fear Conditioning**

In classical fear conditioning, a neutral cue or sensory stimulus (CS) is paired with a noxious US until the CS elicits a fear response. Fear is generally expressed as freezing and startle responses coupled with autonomic changes in heart rate and respiration (Davis in Aggleton 1992). In the canonical fear circuit, during auditory fear conditioning, a tone CS enters the LA via the medial geniculate nucleus of the thalamus and cortical auditory projections (LeDoux 2003; Davis in Aggleton 1992). As the CS becomes associated with the US, a dorsal group of LA

cells induce plasticity (Chapman and Chattarji in Aggleton 1992). These neurons project to the CeA which generates the autonomic and defensive behaviors via the hypothalamus (sympathetic nervous system), periaqueductal gray (freezing), and neuromodulatory systems associated with arousal (LeDoux 2003).

It is now generally accepted that the canonical fear circuit is more complex than previously envisioned. It has been shown that amygdala-projecting auditory thalamic and cortical neurons also demonstrate CS responsiveness, suggesting that the LA is not the only site of plasticity in the canonical fear circuit (Paré and Quirk 2017). LA projections to CeA are hypothesized to be mediated by feedforward inhibition from the GABAergic cells in the intercalated cell mass. Lesion studies suggest that the intercalated cells are necessary for fear extinction; they are primarily GABAergic and are hypothesized to manage the inhibitory tone of the amygdala. The intercalated cell mass also receives inputs from medial frontal cortex which play an important role in maintaining the extinction of fear (Paré et al. 2004).

When fear conditioning takes place in a particular place or context, then the fear response can generalize to that context. Contextual information is relayed from hippocampal regions to the BLA (LeDoux 2003). The medial prefrontal cortex is also posited to play a role in the representation of emotion-sensitive contextual information for context fear. Stimulation of the hippocampal neurons which project to the BLA elicits an evoked field potential in BLA, and damage to this circuitry impairs freezing to the conditioned context (LeDoux 2003). Interestingly, if an animal is allowed to avoid the place where conditioning occurred or learns how to escape from the conditioned stimulus, then BLA lesioned rats indicate the retention of fear memory (McGaugh 2004).

## Future Directions

Future directions in the field include understanding how particular cell groups in specific subnuclei of the amygdala work with the hippocampus and the prefrontal cortex to regulate

the hypothalamic-pituitary-adrenocortical axis, which have consequences for a wide variety of hormonal and neuromodulatory systems related to system-wide arousal responses (McGaugh 2004). Fear researchers are seeking to generalize their findings to more ecologically and ethologically valid experimental paradigms than traditional Pavlovian conditioning paradigms. The frontier of amygdala research involves using advanced techniques (such as optogenetic activation, precise neural recordings, and viral tracing methods) to contextualize the function of each amygdalar nuclei and their cell types within the complex networks of neural systems in which they are embedded.

## Cross-References

- ▶ [Classical Conditioning](#)
- ▶ [Hippocampus](#)
- ▶ [Hypothalamus](#)
- ▶ [Neuron](#)
- ▶ [Neurotransmitters](#)

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## Anabolic Steroids

### ► Psychopharmacology of Sex Steroids

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## Anaclitic Depression

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### Synonyms

[Abandonment](#); [Depressive disorder](#); [Hospitalism](#); [Infant depression](#)

### Definition

The physical, social–emotional, and intellectual impairment of an infant’s development due to the separation from its mother or primary caregiver.

### Introduction

Anaclitic depression is a term used to describe the transient depressed state of infants after their separation from a mothering figure. This term has been used in research with human infants and animal infants, ranging from experiments with nonhuman primates to studies with guinea pigs and rats. Symptoms are similar but can vary slightly by species and by the individual mother–infant relationships pre-separation. While most studies agree that the effects of anaclitic depression are short-lived, disappearing after the

mother–infant reunion, few studies have examined potential long-term behavioral effects.

## Origins of Anaclitic Depression

Anaclitic depression was first described in a 1945 journal article titled “*Hospitalism*” by René Spitz. Spitz was a psychiatrist whose research was greatly influenced by the work of Sigmund Freud. Spitz studied child development within a psychoanalytic framework and investigated emotional deprivation in children (Blum 2011). In Spitz’s (1945) article on hospitalism, he coined the term “anaclitic depression” to convey the temporary depressed state of institutionalized infants (e.g., orphaned infants, infants removed from unfit mothers) who had been separated from their mothers for a limited period (typically less than 3 months). Spitz created this term in the context of a more extreme condition, “hospitalism” – the detrimental effects of confinement in a hospital environment – to refer to the deterioration of infants due to prolonged institutionalization. These syndromes were investigated as a result of the alarmingly high mortality rates in institutionalized infants before 1 year of age (Spitz 1945).

## Symptoms and Treatments in Human Infants

Anaclitic depression is most often associated with brief periods of emotional deprivation that occur during the first year of life, typically anywhere from 6 to 11 months of age. It appears to be triggered by the separation of the mother and infant, or as Spitz describes, the loss of a love object. Four to six weeks after the separation, the infant may begin showing striking changes in affect. Some of these symptoms can include apprehension, sadness, rejection of the environment (e.g., loss of interest in toys, people), decreased development, reduced reaction to stimuli, genital self-stimulation, slow movements, dejection, and refusal to eat. As the depression progresses the symptoms become more severe and include weepiness, withdrawal, stupor, loss

of appetite, and insomnia. Anaclitic depression appears to occur regardless of race, sex, developmental age, or intelligence (Spitz and Wolf 1946).

If deprivation last less than 3 months, then symptoms of depression may not progress to the severity of hospitalism. Spitz and Wolf (1946) offer three treatments for anaclitic depression: Prophylaxis – avoidance of infant separation from the love object (e.g., preventing mother–infant separation), restitution – restoration of the love object in the event it was deprived (e.g., returning the infant to the mother), or substitution – replacement of the love object (e.g., providing another caregiver to take the place of the mother – adoption).

### Anaclitic Depression in Nonhuman Primates

Although anaclitic depression was conventionally used to describe depression during the temporary institutionalization of human infants, it has since been generalized to other animal populations. Due to the unethical nature of experimentally inducing a state of anaclitic depression in human infants, animal models are necessary for studying this syndrome. Some of the first studies dealing with anaclitic depression in nonhuman primates took place at the University of Wisconsin Primate Laboratory in the early 1960s. During the next few decades, researchers separated mothers and infants for durations ranging from 5 min to 4 weeks to study the effects of anaclitic depression. Several of these studies also manipulated the social group that the infant was left in after separation. For example, while many of these studies kept the separated infants together in a group, one design took two infants away from their mothers and gave them each to the other mother (Jensen and Tolman 1962). In many of these cases, researchers found that the symptoms of separation paralleled those of Spitz's findings in the institutions.

A study by Seay and Harlow (1965) demonstrated the effects of separating infant rhesus monkeys (*Macaca mulatta*) from their mothers at about 7 months of age (about 30-weeks-old) for

a 3-week period. During the separation infants reacted immediately, violently protesting by screeching, running, climbing, and crying; however, soon after there was a marked decrease in infants' play activity and locomotion (Seay and Harlow 1965). In a similar study with infant pigtail monkeys (*Macaca nemestrina*), Kaufman and Rosenblum (1967) removed the pigtail mothers from their infants at an average of 6-months-old (about 26-weeks-old) for a 4-week period, leaving the infants within their original social group. The researchers found that infant pigtails reacted similarly to the rhesus monkeys, with screams of protest and struggles to reach the mother, shortly followed by agitation, pacing, searching, and lack of sleep. These symptoms lasted throughout the first day, while the following stage (24–36 h later) resulted in lethargy, genital self-stimulation, dejection, sadness, withdrawal from the environment, and slow or absent locomotion (Kaufman and Rosenblum 1967).

### Differences in Symptoms and Severity

There are notable individual differences in the severity of anaclitic depression after separation in both human and nonhuman primates. The severity of symptoms appears to be influenced by the mother–infant relationship pre-separation. For example, pigtail monkeys with more intense and insecure mother–infant relationships (infants spent less time exploring and more time in contact with their mothers, pre-separation), were associated with greater depressive symptoms in the infants; however, mother–infant relationships that were secure (infants showed more exploration and locomotion, pre-separation) were associated with little to no indicators of depression. Furthermore, pre-separation attachment is strongly associated with the mother's dominance rank within the social group. The more dominant females' infants were more securely attached, and the more submissive females' infants were less securely attached. Consequently, infants' severity of depression was negatively associated with the mothers' dominance rank; the most dominant female's infant never reached levels of

depression, while the more submissive females' infants displayed greater depressive behaviors (Kaufman and Rosenblum 1967).

Conversely, Spitz and Wolfe (1946) postulate the opposite effect in human infants. Based on his findings, he suggests that it is more difficult to replace a love object in which the infant is strongly attached. Although, his definition of attachment is unclear, denoted with categories of "good" and "bad" and ranging from "weak" to "intense," suggesting that the severity of symptoms is influenced most by the intensity of the relationship (e.g., more intense relationships associated with more depressive symptoms). Like human infants, monkey infants showed a decrease in their social interactions; however, unlike human infants, monkey infants' social contact began to recover as the separation period progressed, and almost reached pre-separation levels in the fourth and final week of the separation period. Infant monkeys also never lost interest in food, and were never considered ill, although, the pigtail infants had a sickly appearance (Kaufman and Rosenblum 1967).

These species' differences may be explained by the greater probability of survival of monkey infants without their mother compared to human infants without their mother. Monkey infants have greater locomotion abilities at this stage, and, therefore, can be more proactive in their social environment than human infants. Monkey infants can seek out a new source of comfort, increasing their likelihood of survival, while human infants are still dependent on older members of their social group, even as their locomotion ability increases (e.g., assistance walking, climbing stairs) (Kaufman and Rosenblum 1967).

Much like Spitz observed in human infants, Seay and Harlow (1965) observed that the separation appeared to have only a transient effect on the mother–infant relationship, giving further evidence that anaclitic depression is a temporary state. Kaufman and Rosenblum (1967) supplement this idea, concluding that the separation, at least in the short-term, created a closer relationship between mother and infant. These studies, however, are inconclusive regarding the long-term effects of anaclitic depression caused by the

brief separation of mothers and infants in both human and nonhuman primate infants.

To date, there are few studies with follow-up observations of human or animal infants (Zeanah et al. 2003). Some researchers suggest that separation during this period can have lasting effects. For example, Spencer-Booth and Hinde (1971) found that rhesus monkey infants separated from their mothers for only 6 days showed lasting effects documented up to 2 years after separation. Twelve months after separation and reunification, rhesus monkeys were observed to have more dependence on and greater proximity maintenance to their mothers, depressed locomotion, and more hesitation toward strange objects or situations than their nonseparated peers. These symptoms did decrease over time; however, they were still present 2-years post-separation (Spencer-Booth and Hinde 1971).

## Anaclitic Depression in Other Animals

While humans and nonhuman primates make up the majority of subjects in studies on anaclitic depression, this syndrome has been shown in other species. Albino Hartley guinea pigs (*Cavia porcellus*) who were separated from their mother for a short period, displayed increased vocalizations and crouched, lethargic states (Hennessy et al. 2017). Another study looked at these depressive behaviors in Wistar rat pups to examine separation behaviors in a species more distantly related to humans. The researchers found that rat pups showed greater activity and were less likely to sleep than their nonseparated peers. These behaviors were similar to the increased agitation and vocalizations observed in monkey infants (Hofer 1973), showing that this syndrome occurs across a wide variety of animals.

## Conclusions

Renee Spitz coined the term anaclitic depression to help explain the temporary depressive qualities of infants in institutionalized care. Anaclitic depression has since been generalized to many



other species, including nonhuman primates, as well as guinea pigs and rats. These animal models of anaclitic depression allow researchers to manipulate mother–infant separation when human experimentation becomes unethical. Further, the aforementioned animal studies help reinforce and expand upon Spitz’s original definition of anaclitic depression, providing additional evidence for anaclitic depression interventions.

It should be noted that even though the term “anaclitic depression” was created to describe the depressive state of temporarily institutionalized infants or infants experiencing loss of a love object; it is sometimes used to refer to adults who have intense attachments to relationships.

## Cross-References

- ▶ [Alloparental Care](#)
- ▶ [Attachment](#)
- ▶ [Coping Style](#)
- ▶ [Dominance Hierarchy](#)
- ▶ [Ethics](#)
- ▶ [Harry Harlow](#)
- ▶ [John Bowlby](#)
- ▶ [Maternal Behavior](#)
- ▶ [Nonhuman Primates](#)
- ▶ [Primate Locomotion](#)
- ▶ [Pro-social Behavior](#)
- ▶ [Primate Social Structure](#)
- ▶ [Stress](#)

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## Anagenesis

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In the general sense, evolution can be characterized by three distinct phenomena: (1) adaptation, the remarkable fit between an organism and its environment, (2) diversity, the great variety of extinct and extant organisms, and (3) complexity, the intricacy of the organization of internal and external structure and function (Muller and Olsson 2003). *Anagenesis* refers to the idea that there are directional trends in this complexity. In particular, a hierarchy of increasing levels of organization from the simple to the complex characterizes the diversification of species. As Dobzhansky et al. (1977, p. 236) put it in their classic text *Evolution*, anagenesis creates “organisms with novel characters and abilities beyond those of their ancestors.” In evolutionary biology, anagenesis refers to the progressive evolution of a species resulting in linear descent (phyletic



divergence); in contrast, cladogenesis refers to speciation by evolutionary splitting of a lineage (branching) to additional species.

The concept of anagenesis has also been used in comparative anatomy, comparative physiology, comparative endocrinology, as well as comparative psychology (Rensch 1959). Rensch identified several defining features of anagenesis, including: (1) increased complexity (differentiation), (2) centralization of structures and functions, (3) special complexity and centralization of the nervous system, (4) increased plasticity of structures and functions, and (5) increased independence from the environment and increasing command of environmental factors (progression of autonomy). Of course, independence from the environment is a relative concept, as no organism is ever free from its environment. When applied to the comparative study of behavior, anagenesis has typically referred to the progressive evolution of adaptive behavior, learning ability, or cognitive capacity that is often accompanied by the emergence of new psychological capacities (Gottlieb 1984).

The steps or units of anagenesis are typically referred to as “grades” or, in some cases, “levels” (Aronson 1984). A grade or level can be seen as an ascending series of improvements or increases in complexity of any structural or functional unit of analysis within animal groups that may or may not be closely related from a phylogenetic standpoint (Gottlieb 1984). Grades or levels thus address the ranking of behavioral organization (i.e., ability to exhibit various forms of learning, levels of exploratory behavior) relatively independent of strict evolutionary lineages (phylogenetic relationships). As a result, anagenetic analysis has been used most successfully to characterize grades or levels of behavioral complexity at the supraspecific level, that is, across genera, families, orders, or classes, rather than at the level of species. Examples include patterns of organization of the nervous system, increases in developmental plasticity, and improvements in behavioral versatility or adaptability to environmental change (Yarczower 1998). For example, within the order Chiroptera (bats), researchers have demonstrated that the relatively large brain observed in some bat species is associated with adaptations used

to feed on energy-rich foods that are often unpredictable in their spatial distribution (Eisenberg and Wilson 1978). Such descriptions of the specific fit between phenotypes and environments across genera provide a foundation for further studies of both adaptation and diversity.

Schneirla (1949) was among the first comparative psychologists to promote the importance of levels of psychological capacities to frame the comparative study of animal behavior. His anagenetic concept of levels (see Greenberg, this volume) emphasized the value of recognizing and assessing the range of differences in complexity, degree of development, and organization of behavior functions across different types of animal species. This type of approach has been termed “pheneticism” within evolutionary biology (Harvey and Pagel 1991), where grade or level is determined by similarity in phenotypic characters or traits rather than by phylogenetic relationships (common ancestry). For example, Tobach and Schneirla (1968) proposed a hierarchy of behavioral levels based on social and psychological organization: taxis, biotaxis, biosocial, psychotaxis, and psychosocial (see Greenberg, *Behavioral Levels*, this volume). Using this hierarchy, Greenberg (1995) noted that in the general sense, animals demonstrate less behavioral plasticity or versatility function at lower behavioral levels (i.e., taxis, biotaxis), whereas they demonstrate more behavioral plasticity or versatility function at higher behavioral levels at which psychological processes influence the course of behavioral development (i.e., psychotaxis, psychosocial). Importantly, increased behavioral plasticity is highly correlated with increasing nervous system size, complexity, and organization (Jerison 1973; Jerison and Barlow 1985). Gottlieb (1984) extended this approach to anagenesis by emphasizing that developmental plasticity and behavioral versatility are useful hallmarks of progressive behavioral evolution. He argued that application of this perspective allows a measure of anagenesis to be obtained by comparing different animals’ behavioral adaptability in response to experimentally altered ecological conditions or challenges. However, this ecologically based approach to testing anagenesis has received little research attention to date.

The concept of anagenesis and its use of grades or levels to compare behavioral evolution across animal species independent of strict evolutionary lineages have not been without criticism within comparative psychology (i.e., Capitanio and Leger 1979; Hodos and Campbell 1969, 1990). It is certainly the case that objective criteria for how to best distinguish successive grades or levels of developmental plasticity and behavioral versatility remain poorly defined. Hodos and Campbell (1969, 1990) see comparing evolutionary trends across groups of animals that are not closely related by way of common ancestry as overly subjective and even unscientific. They argue that most comparative psychologists do not base their work on strict evolutionary lineages (i.e., phylogenetic trees), which they view as the appropriate subject matter of a genuine comparative psychology. While such criticisms have been challenged (e.g., Gottlieb 1984; Greenberg 1995), it is clear that an objective description of the criteria used to identify differences in behavioral plasticity or versatility between higher and lower grades of animal species is crucial to the merit and usefulness of anagenetic analysis. Given that the comparative method has been the most general and effective technique for asking questions about the patterns of evolutionary change from Darwin to the present, comparisons of animal behavior and cognition using *both* evolutionary trends and evolutionary lineages will likely provide a deeper understanding of the phenomena of adaptation, diversity, and complexity.

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## Analogical Reasoning

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## Synonyms

Relational matching; Relational thinking

## Definition

A process of reasoning based on a similitude of relations which is perceived between the objects compared.

## Introduction

Reasoning by analogy is one of the most complex forms of abstract thinking in humans. Consider the following analogy: the fish is to water what the bird is to air. To understand this analogy, one must first determine the relation between a first set of stimuli (i.e., the fish is *in* the water) and subsequently search for that same functional relation between the second set of stimuli (e.g., the bird is *in* the air). In other words, this two-step process therefore requires that we first appreciate first-order relations (the fish:water and bird:air relations), and subsequently compare and judge the relation between these relations (second-order relation). This form of inferential process based on analogical reasoning is fundamental for a diversity of cognitive processes of considerable importance in humans, such as classification, transfer of learning in new contexts, problem solving, and creative thinking. The hypothesis has been repeatedly made that our exceptional abilities for analogical reasoning would be the major contributor to our high intelligence as a species (Hofstadter 2001; Gentner 2003).

One reason for which analogical reasoning is interesting is that it appears to be linked with human language. First, children with specific language impairment express difficulties in analogical tasks (Leroy et al. 2012). Second, although children already demonstrate rudiments of analogical reasoning at 2 years of age (Singer-Freeman 2005), their performance in analogy tasks at 3–4 years of age is fostered by their emerging capacity to represent abstract relations via linguistic labeling (Christie and Gentner 2013). Moreover, analogical reasoning does not approach adult-like performance until adolescence and the full growth of linguistic competencies (Richland et al. 2006).

## Analogical Reasoning in Nonhuman Animals

Comparative studies with nonhuman animals have questioned whether language is a prerequisite for complex forms of analogical reasoning. In this chapter, we will firstly document the fact that nonhuman animals have the capacity to process first-order relations. We will then document their ability for processing second-order relations, in other words, the relations between relations.

### Processing of First-Order Relations in Nonhuman Animals

Many animal species can judge relations between things. For instance, baboons can be trained to indicate if one object is above or below another object (Dépy et al. 1999). Particularly important for analogical reasoning is the abstract concept of sameness (identity). Using a wide variety of experimental tasks, researchers have shown that many animal species, including the chimpanzee, rhesus monkey, baboon, parrot, pigeon, rat, and even honeybee and bumblebee, have sufficient cognitive power to indicate if two things are identical or different (see review in Wasserman et al. 2017). In these experiments, the identity concept is presumed to be abstract, because the subjects express accurate same/different responses even when they must judge the relation between objects never seen before.

### Processing of Second-Order Relations in Language or Symbolic Competent Apes

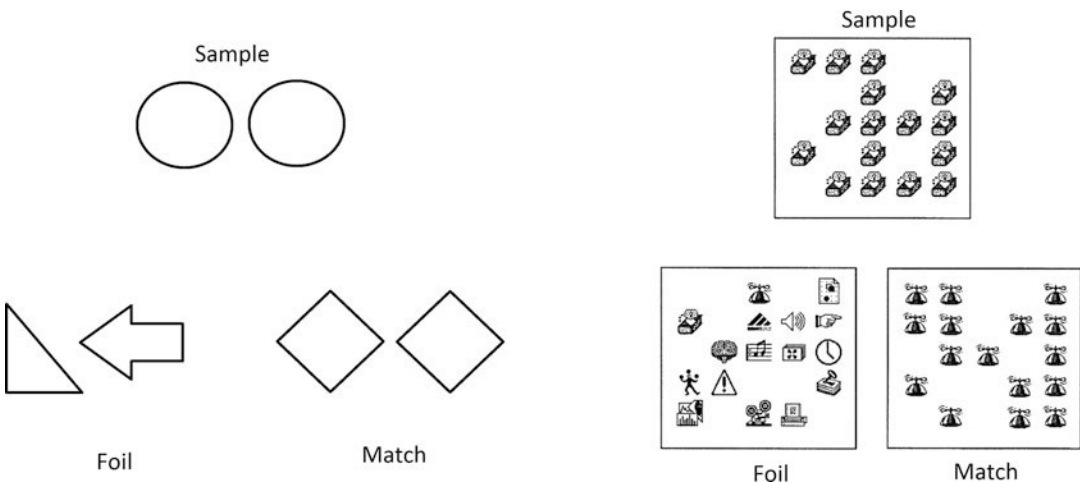
Gillan et al. (1981) published the first paper on second-order relational processing in animals. These authors tested an enculturated language-trained chimpanzee (*Pan troglodytes*) named Sarah, who had already learned the symbolic meaning of pieces of plastic and could use and combine these symbols as words in sentences to communicate with the experimenter. In one first test condition, Sarah saw a tray containing one pair of objects on one side, and one single object on the other side. Two other objects were shown below the tray, and Sarah had to indicate which of these two objects would complement the single object on the tray, so that the relations entertained

by these two objects is equivalent to the relations shown by the other stimulus pair. In another version of the task, Sarah was presented with two stimulus pairs, and she had to indicate if these two stimulus pairs showed the same or a different relation. She did so by selecting one piece of plastic symbolizing the same or different relations. Sarah was successful in these two versions of the task involving stimuli varying in shape, color, and marking. Moreover, she continued to be correct when the same tasks required the appreciation of functional relations between known household objects (e.g., closed lock and key vs. closed can and can opener). Considering Sarah's initial training with symbols, Premack (1983) logically considered that Sarah's success in the task of analogical reasoning can be explained by the cognitive competencies she developed via her "language" training.

The task used by Gillan et al. (1981) has never been replicated with other animal species. Later research on analogical reasoning in nonhuman animals has used instead the relational matching-to-sample task which is illustrated on the left side of Fig. 1. In this task, the subject first perceives one pair of objects that are either identical or different. Two other pairs are then presented, and the subject must select the pair exemplifying the

same (same or different) relation as the sample pair. One important feature of this task is that the items composing the sample are not used in the comparison pairs. Matching is therefore impossible of the sole basis of the individual items. Admittedly, the relational matching-to-sample task captures several features of analogical reasoning, because it requires the apprehension of the relation between pairs of items (first-order relation), and also the processing of the relation between relations (second-order relation).

Premack's (1983) conclusion that language training is required for analogical reasoning was questioned by Thompson et al. (1997). These authors tested five chimpanzees on a version of the relational matching-to-sample task using pairs of real objects or digitized images. One of the subjects was the language-trained chimpanzee Sarah cited above. Three other chimpanzees were language-naïve, but these subjects had previously learned the meaning of two different token shapes, each symbolizing the same or different relation. The last chimpanzee was both language- and symbol-naïve. Sarah and the three token-trained chimpanzees could successfully solve the relational matching-to-sample task, with no reliable difference among them. By contrast, the last chimpanzee who was both language-



**Analogical Reasoning, Fig. 1** Illustration of two different versions of the relational matching-to-sample task. In both versions, the subject must indicate which of the two comparison stimuli (i.e., the match) instantiate the same

relation as the sample stimuli. In the left-most version, the same different/relations are illustrated by pairs of stimuli. In the right-most version of the task, the same/different relations are shown by arrays of icons

and token-naïve failed miserably in the task. From their results, Thompson et al. (1997) concluded that the ability to process the relation between relations requires at least a form of symbolic/token training. This conclusion was however premature, as shown below.

### Processing of Second-Order Relations in Language-Naïve Primates and Birds

Most of the initial attempts to present the relational matching-to-sample task to language- or token-naïve animals were failures (see review in Thompson and Oden 1996, 2000). However, the picture began to change when researchers reasoned that relational matching could be facilitated if the relations are shown in arrays of multiple stimuli, rather than same/different stimulus pairs. Following this reasoning, Fagot et al. (2001) trained two Guinea baboons (*Papio papio*) in a version of the relational matching task using arrays of 16 (same or different) icons as sample and comparison stimuli. Figure 1 (right side) illustrates the kind of displays used in this task. The two baboons tested in Fagot et al. (2001) could achieve a high level of performance during the training phase. After training, they even continued to be above chance when a new set of icons was used to create each array, suggesting an ability to match relations between relations. The success of the baboons with arrays of icons prompted Cook and Wasserman (2007) to replicate that procedure with pigeons (*Columba livia*). These authors found that the birds could achieve 70% correct at the end of the training period. Much like baboons, the pigeons could also transfer their performance to new sets of stimuli. These findings were the first demonstrations that monkeys and pigeons have the capacity to match relations between relations.

A different approach to the problem was to capitalize on potential benefits of extensive training in the relational matching task. This procedural strategy was possible thanks to the most recent technological developments allowing the animals to be tested via an automated identification, with no need to remove them from their social group. Fagot and Thompson (2011) used this procedure with a group of 29 Guinea baboons (*Papio papio*) tested with a version of the

relational matching-to-sample task shown on the left of Fig. 1. Most of the baboons failed to learn the task, but five of them did. These five individuals could moreover maintain a high level of performance with stimuli never seen before. The fact that nonhuman primates can learn the relational matching-to-sample task with pairs of items is further confirmed in one capuchin (*Cebus apella*), among five, by Truppa et al. (2011). The training phase required approximately 17,000 trials in this study on capuchins, which is in the same range as for baboons (Fagot and Thompson, 2011).

In a more recent project, Smirnova et al. (2015) tested two hooded crows (*Corvus cornix*) which had already been trained on the identity concept. This study used pairs of shapes drawn on carton boards as stimuli in the relational matching-to-sample task. To obtain a bait, the crows had to lift the carton board showing the same relation as the sample board. The crows readily displayed high levels of relational responding in this task, and they did so in several versions of the task requiring an appreciation of the relations expressed by stimulus size, shape, and color. The authors explained this astonishing performance by the initial training that the birds have received on the identity concept. An earlier study on language-naïve orangutans (*Pongo pygmaeus*) and gorilla (*Gorilla gorilla*) had already shown that these animals can achieve a high level of performance in the relational matching task without extensive training (Vonk 2003).

### Are There Alternative Explanations to Relational Responding?

The possibility that nonhuman animals have sufficient cognitive capacities for second-order relational thinking remains a matter of hot debate, and researchers have examined alternative explanations that could explain their behavior in the relational matching-to-sample task. Penn et al. (2008) proposed that the nonhuman animals consider for responding the entropy of the displays in the relational matching-to-sample task, rather than the relations among the items present in the displays.



The concept of entropy has been introduced in this literature by Young and Wasserman (1997), and it corresponds to the degree of perceptual variability between the elements contained in each display. Following Penn et al.'s idea, the subjects would consider that an array containing different icons is more variable than an array containing identical items. This type of encoding would allow the matching of same or different arrays in the relational matching task on the sole basis of a global apprehension of the perceptual variability of the sample and comparison displays, rather than their relational properties. This hypothesis was directly tested by Flemming et al. (2013). Using arrays of icons containing only four items, they manipulated the entropy of the sample independently of their relation. They used sample stimuli which had the following possible structures: AAAA (all same icons, entropy = 0), AAAB (entropy = 0.81), AABB (entropy = 1.0) and AABC (entropy = 1.5), ABCD (all different icons, entropy = 2), with the location of each item randomized across trials. In a comparative perspective, these authors have also tested humans and baboons in this task. In the two species, results indicated that the relational structure of the sample arrays was the primary variable controlling subjects' choice performance. An effect of entropy was also revealed by the results, in both humans and baboons, but in both species this effect was secondary to the effect of the relations. This result is an additional confirmation that nonhuman animal species have the capacity to solve the relational matching task, and that their performance is controlled by the relational structure displays.

## Conclusions

Analogical reasoning is considered a hallmark of higher-order reasoning, and recent theoretical perspectives assert that this is a uniquely human cognitive trait (Penn et al. 2008). The close relationship found between the development of analogical reasoning and the emergence of language competence in children supports the conclusion that a linguistic mode of encoding is needed for

the emergence of complex forms of relational thinking. An initial study in a language-trained chimpanzee has supported this conclusion (Gillan et al. 1981; Premack 1983). However, more recent attempts to investigate the extent and limits of relational thinking in linguistic-naïve animals have shown that several species, including the pigeon, capuchin, baboon, chimpanzee, gorilla, and orangutan, can demonstrate second-order relational processing in the relational matching task (for an extensive review of this literature, see Wasserman et al. 2017). All these findings demonstrate that linguistic competences are not necessary for complex relational thinking, although a linguistic encoding of the task might of course help (e.g., Christie and Gentner 2013). One obvious limitation of this literature is that it probably focuses too much on the relational matching-to-sample task. Admittedly, this task cannot capture the full complexity of the processes involved in analogical thinking in humans, for instance, when we solve verbal analogies as complex as the well-known analogy which compares the solar system to the *Rutherford* atom model. The relational matching-to-sample task nevertheless contains some of the most basic features of analogical reasoning, among them the fact that the subjects must associate relation between relations. A close examination of the current comparative data suggests that nonhuman animals possess at least some of the cognitive antecedents of analogical reasoning in humans.

## Cross-References

- David Premack
- Inductive Reasoning
- Matching-to-Sample: Comparative Overview
- Means-End Reasoning

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## Anatomically Modern Humans (AMH)

### ► *Homo sapiens*

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## Anatomy

- Hominoidea Morphology
- Parahippocampal Cortex (PHC)
- Proboscidea Morphology



## Andrew Whiten

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### Biography

Andrew (Andy) Whiten is Emeritus Wardlaw Professor at the School of Psychology and Neuroscience, University of St Andrews, Scotland. He is an elected Fellow of the British Academy, the Royal Society of Edinburgh, and the International Cognitive Science Society. Whiten's research focuses on social learning and cultural transmission, providing insights into this "second inheritance system" and the role it plays in shaping behavior in concert with genetic inheritance and individual learning. Through his collaborations, Whiten has published papers on humans and non-human primates and has used experimental and observational techniques to answer questions about the social drivers of primate cognition.

Whiten joined the University of St Andrews as a Lecturer in 1975 after studying at the Universities of Sheffield, Bristol, and Oxford. He became Professor of Evolutionary and Developmental Psychology at the University of St Andrews in 1997 and was made Wardlaw Professor in 2001. In 2003, Whiten founded the Center for Social Learning and Cognitive Evolution and 5 years later established the Living Links to Human Evolution primate research center, housed at Edinburgh Zoo, providing a forum for public engagement with science in a zoo setting.

### Behavioral Ecology of Baboons

Whiten's early research focused on the behavioral ecology of chacma baboons (*Papio ursinus*) living in the Drakensberg mountains of South Africa and, later, olive baboons (*P. anubis*) in Kenya. This field research was conducted in collaboration with Richard Byrne, Peter Henzi, and Robert Barton.

### Machiavellian Intelligence

Initially inspired by their observations of "tactical deception" in wild baboons, in their 1988 book *Machiavellian Intelligence*, Andy Whiten and Richard Byrne highlighted links between the various aspects of primate intelligence in the social domain (Byrne and Whiten 1998). Framed against the earlier work of Nicholas Humphrey and Alison Jolly, Byrne and Whiten curated a volume of both new and previously published chapters that provided support for the "social intelligence hypothesis." Thirty years on, the ideas put forward in *Machiavellian Intelligence* still resonate and continue to be investigated in contemporary studies of primate cognition and behavior.

### Chimpanzee Culture

In the 1990s, Whiten led a consortium of primatologists to publish a report on chimpanzee behavior studied at long-term field sites across Africa (Whiten et al. 1999). In this seminal article, the authors compared the behavioral repertoires of chimpanzees living in seven different communities: Bossou (Guinea), Taï Forest (Ivory Coast), Gombe (Tanzania), Mahale M-group (Tanzania), Mahale K-group (Tanzania), Kibale Forest (Uganda), and Budongo Forest (Uganda). Through this collaborative effort, the authors identified 39 behaviors that were observed to be performed by chimpanzees in certain communities but not others. The authors proposed that the variance in behavioral patterns could be "seen to resemble those in human societies, in which differences between cultures are constituted by a multiplicity of variations in technology and social customs" (Whiten et al. 1999, p. 685), an idea that they crystalized as *Cultures in Chimpanzees*. This collaborative endeavor was expanded to include two additional sites (Lopé, in Gabon, and Assirik, in Senegal), and in a follow-up paper, the authors reviewed chimpanzee behaviors that were universals and others for which an environmental cause could be attributed, in addition to possible socially learned cultural behaviors (Whiten et al. 2001). When they published their original paper, Whiten

et al. (1999) recognized that behavioral traditions might not be unique to chimpanzees and such traditions have since been reported for a variety of other primate species, including orangutans, capuchin monkeys, and spider monkeys, as well as nonprimate animal species. While *Machiavellian Intelligence* called researchers to question behavioral theories of technical intelligence and instead to consider social influences on cognitive evolution, *Cultures in Chimpanzees* (Whiten et al. 1999) called us to question the uniqueness of human culture and the potential power of social learning in shaping animal behavior.

### Experimental Methods for Studying Social Learning

To gain a deeper understanding of the social and cognitive mechanisms that underlie primate social learning, Whiten has conducted numerous experimental studies with wild and captive nonhuman primate populations and also with human participants. Much of this research has incorporated a two-action task that can be solved in one of two arbitrary ways. The use of a two-action task allows the researcher to determine both if the naïve subject can learn a solution from observing an expert and also if they use the same method as the expert to do so. To increase the ecological validity of such tests, Whiten created tasks designed to mimic the actions required by wild primates to remove the tough casings of wild fruits or to obtain foods like honey or insects via extractive foraging techniques (Whiten et al. 1996). These tasks, dubbed “artificial fruits,” have ranged in their design and complexity, allowing researchers to test the fidelity of social learning (e.g., imitation versus emulation); hierarchical and serial imitation, and the ability of primates to make and use tools to extract food from these devices.

Whiten employed one such two-action task (the “pan-pipes”) in a groundbreaking study of captive chimpanzee social learning of tool use, run in collaboration with Victoria Horner and Frans de Waal (Whiten et al. 2005). Rather than

simply testing the transmission of information between two individuals as previous social learning tests had done, Whiten et al. (2005) exposed two entire groups of chimpanzees to a trained chimpanzee model in an “open diffusion” test design. Not only did this study show that the majority of observer chimpanzees were able to learn the task from observing the trained model, but also that they predominantly matched the specific method used by the model. Thus, the newly introduced behavior spread throughout each of the two social groups tested, mimicking culturally transmitted behavioral variation reported for wild chimpanzee communities (Whiten et al. 1999). Furthermore, the findings from this study challenged previous assumptions about primate social learning (i.e., it was restricted to enculturated individuals raised in human-centric environments or that social learning could only occur during the juvenile years). This open diffusion technique has subsequently been applied to study social learning in other nonhuman primate species and with human children. It has also been adapted to ask more nuanced questions about how, what, and when information is transmitted among primates (Kendal et al. 2015).

Whiten and colleagues have also run “diffusion chain” experiments, akin to the “telephone game,” that mimic vertical transmission down generations. This method provides more experimental control over what information is transmitted, as well as who has the opportunity to learn from whom. Whiten has applied this to chimpanzees, orangutans, and human children, revealing high-fidelity transmission of behavioral foraging techniques.

### Diversity in Studies of Social Cognition in Captive Primate Populations

The majority of Whiten’s research with captive primates has focused on social cognition, with an emphasis on social learning. His work with captive primates has encompassed a broad phylogenetic perspective, with studies being run with chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla gorilla*), orangutans (*Pongo abelii* and

*P. pygmaeus*), capuchin monkeys (*Cebus apella*), squirrel monkeys (*Saimiri sciureus*), and marmoset monkeys (*Callithrix jacchus*). This research has been run at a variety of facilities including sanctuaries (e.g., Ngamba Island Chimpanzee Sanctuary, Uganda), zoos (e.g., Zoo Atlanta, USA, and Edinburgh Zoo, UK), and laboratories (e.g., Yerkes National Primate Research Center, USA, and UT MD Anderson Cancer Center, USA). Beyond confirming the social diffusion of behaviors (Whiten et al. 2005), Whiten's work has attempted to tease apart social learning strategies ("who" do primates copy, e.g., Kendal et al. 2015) and mechanisms ("what" do primates copy, e.g., Hopper et al. 2015), as well as the social and environmental conditions that best support social learning (Caldwell and Whiten 2003).

### Studies with Wild Primate Populations

In recent years, Whiten has expanded his experimental studies of primate social learning to include field research, returning to South Africa, but now to study vervet monkeys (*Chlorocebus aethiops*). Working in collaboration with Erica van de Waal at her field site, as part of the Inkawu Vervet Project, Whiten has been involved in a number of field experiments on social learning (e.g., van de Waal et al. 2013). Through the use of artificial fruit tasks and the provision of novel foods, van de Waal, Whiten, and colleagues have revealed when and how information is transmitted among monkeys within a troop, as well as shedding light on how monkeys weigh their own personal experience against social information when they emigrate to a new group. These field experiments either reflect or have stimulated "sister" studies run with captive primates, allowing comparison between captivity and the field, as well as across species (e.g., Vale et al. 2017).

### Studies with Human Children

From early times Whiten's experimental work investigating primate social learning was

comparative, including both human and non-human primate subjects (Whiten et al. 1996). He has continued to provide a comparative perspective throughout his career. Just as with nonhuman primates, Whiten has tested human children with artificial fruit analogs, in dyadic, diffusion chain, and even open diffusion paradigms (Whiten and Flynn 2010). His work has revealed both the similarities and differences in how we learn new skills compared to our nonhuman cousins and has expanded to include work focused on other areas of social cognition (e.g., prosociality, Claidière et al. 2015). To better understand the relationship between children's theory of mind understanding and their capacity to learn from others, Whiten has also investigated the social learning capacities of children with autism (e.g., Williams et al. 2001).

### Public Engagement with Science

In addition to conducting research, Whiten has demonstrated an extensive commitment to public engagement with science, particularly evident in the design of the Living Links to Human Evolution research center at Edinburgh Zoo, of which Whiten was a founding director. At Living Links, visitors to the zoo can observe scientists running behavioral and cognitive research within two mixed-species communities of capuchins and squirrel monkeys. The dedication Whiten has shown to public understanding of science was recognized by the Royal Society of Edinburgh, who awarded him their Senior Prize and Medal for Public Engagement in 2014.

### Legacy

Whiten's impact on the field of comparative psychology, particularly on the study of primate social cognition, is far reaching. Both through his own research and that of his collaborators and former students, Whiten's theories and research findings continue to influence the field. His legacy is recognized both through the

continued relevance of his work and also through the awards he has received throughout his career that include the Osman Hill Medal, awarded by Primate Society of Great Britain in 2010, the Sir James Black Medal, awarded by the Royal Society of Edinburgh in 2013, and from honorary degrees bestowed by Heriot Watt University (2015), the University of Stirling (2016), and the University of Edinburgh (2017).

## Cross-References

- [Bennett G. Galef](#)
- [Bill McGrew](#)
- [Comparative Psychology](#)
- [Cooperation](#)
- [Copying](#)
- [Cultural Transmission](#)
- [Culture](#)
- [Cumulative Culture](#)
- [Deferred Imitation](#)
- [Diffusion](#)
- [Emulation](#)
- [Frans de Waal](#)
- [Ghost Control](#)
- [Goal-directed Behavior](#)
- [Imitation](#)
- [Learning](#)
- [Machiavellian Intelligence](#)
- [Mimicry](#)
- [Primate Cognition](#)
- [Primates](#)
- [Problem-solving](#)
- [Rational Imitation](#)
- [Richard Byrne](#)
- [Social Learning](#)
- [Stimulus and Local Enhancement](#)
- [Theory of Mind](#)
- [Trap-Tube Problem](#)
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## Androgen

- [Psychopharmacology of Sex Steroids](#)

## Androgens

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## Synonyms

Male hormone; Sex hormone; Testosterone

## Definition

Androgens are steroid hormones that play a determining role in the growth and perpetuation of male phenotype and reproductive functions.

## Introduction

Androgens are synthesized and secreted into blood stream abundantly in the form of testosterone (T) and regulates the reproduction, physiology, and metabolism of males. In majority of the cases, androgens are found to exert their effects by genomic pathways, which involve binding of androgens to the androgen receptor (AR) present in the nucleus; ultimately, this hormone receptor combo binds to the specific portions of DNA and bring out the response (Kang et al. 2003). In some cases, AR-induced nongenomic mechanisms have also been reported. Adequate amount of androgens is very necessary for successful reproduction and metabolism of males, and any alterations in the amount or improper signaling result in diseased conditions like androgen insensitivity syndrome (AIS), infertility, and prostate diseases. Nowadays, a large number of steroidal and nonsteroidal AR-ligands are used in the treatment of male hypogonadism (AR agonists) and prostate diseases (AR antagonists) and among other pathological conditions.

## Androgen Biosynthesis

The human testis is a complex organ made up of two different units: androgen producing Leydig cells of the interstitial compartment and sperm producing seminiferous tubule compartment which makes around 90% of the testis volume (Melmed et al. 2011). Testosterone (T) produced in the testis plays a critical role in sex development, sexual function, and reproduction.

Androgens are produced from cholesterol (C-27) by using a cascade of enzymes which are encoded by genes that are present in all steroid producing organs (Auchus and Auchus 2012). Cholesterol is stored in esterified form as lipid droplets in steroid producing Leydig cells. Trophic hormone initiates steroidogenesis by activating a chain of reaction that lead to hydrolysis of cholesterol esters into free cholesterol. The free cholesterol formed is transported into mitochondria by intracellular cholesterol transporters such as steroidogenic acute regulatory protein (StAR), sterol carrier protein 2 (SCP<sub>2</sub>), and peripheral benzodiazepine receptor (PBR). In the mitochondria, cholesterol is converted to pregnenolone (C-21) by the side chain cleavage enzyme complex that consist of *CYP11A1* (P450<sub>scc</sub>), ferredoxin (FDX1), and ferredoxin-reductase (FDR). In the classic pathway, pregnenolone is then converted through the  $\Delta 5$  pathway by *CYP17A1*(P450<sub>c17</sub>) to 17-hydroxypregnenolone (17OHPreg) and dehydroepiandrosterone (C-19) (DHEA) with the first reaction catalyzed by its 17 $\alpha$ -hydroxylase activity supported by P450 oxidoreductase (*POR*) and the second reaction by the 17,20 lyase activity supported by *POR* and cytochrome b5 (*CYB5*). Further, DHEA is converted to testosterone through androstenedione and the reaction is catalyzed by 3 $\beta$ -hydroxysteroid dehydrogenase type II and 17 $\beta$ -hydroxysteroid dehydrogenase 3. Testosterone may be converted to DHT which has about 10 times more affinity for the androgen receptor. This conversion is catalyzed by 5 $\alpha$ -reductase type II which is expressed in genital skin and the prostate. In humans, only little conversion to androstenedione occurs through the delta 4 pathway coming from progesterone (Prog) and 17-hydroxyprogesterone

(17OHP) because 17,20 lyase activity is poor on the substrate 17OHP compared to 17OHPreg (Flück et al. 2003).

## Androgens in Females

Quantitatively women secrete greater amount of androgen than estrogen. On the basis of maximum to minimum levels of steroids found in serum of women the sequence is dehydroepiandrosterone sulfate (DHEAS), dehydroepiandrosterone (DHEA), androstenedione (A), testosterone (T), and dihydrotestosterone (ref1). The overall effects of androgens in females are lower than estrogen because among all the androgens, receptors are only present for testosterone (T) and dihydrotestosterone. Remaining three androgen steroids are called pre-androgens. These androgens are produced from different zones of adrenal (zona reticularis and zona fasciculata) and ovaries (ovarian theca and ovarian stroma). Testosterone production does not get altered with age in females, but the levels of steroid hormones binding (SHBG) get decreased which lead to increase in the level of circulating testosterone in menopausal females (Burger 2002).

## Androgen Receptor Structure

Androgen receptor (AR) is a member of nuclear receptor family. These receptors function as a ligand inducible transcription factors. AR mediates the expression of target genes after binding to the androgens.

Androgen receptors are classical type of nuclear receptors. The androgen receptor (AR) (NR3C4, nuclear receptor subfamily 3, group C, gene 4) belongs to the steroid hormone group of nuclear receptors and having similarity with the estrogen receptor (ER), glucocorticoid receptor (GR), progesterone receptor (PR), and mineralocorticoid receptor (MR) (McKenna et al. 1999; Mangelsdorf et al. 1995). Male sexual development and differentiation is started via

binding of the AR to its native ligands testosterone and 5 $\alpha$ -dihydrotestosterone (DHT).

The human AR gene is located on X chromosome at position Xq11-q12 (Lubahn et al. 1988). Like other members of its family, the structure of AR is organized into functional domains, consisting of an N-terminal domain (NTD), a DNA-binding domain (DBD), and a C-terminal ligand-binding domain (LBD) (Kuiper et al. 1989). There is also a small hinge region between DBD and LBD. Whereas the DBD and LBD of the AR are highly conserved among species, the NTD displays the most sequence variability, which is important for differences in the homeostatic control and complexity of AR signaling (Li and Al-Azzawi 2009). The AR NTD is relatively long, representing almost half of the receptor coding sequence; it contains the major transactivation function domain of the AR, termed activation function 1 (AF1), which is responsible for almost all AR transcriptional activity (Simental et al. 1991). AF1 also interacts with transcriptional coregulators and members of the basal transcriptional machinery (Kumar and Litwack 2009). Another transcriptional activation domain AF-2 is situated in LBD portion (Kang et al. 2003). The mutation and deletion of this domain dramatically reduce the transcriptional activation of AR in responses to androgens.

Androgens such as testosterone are synthesized primarily by the Leydig cells in the testes, under the regulation of luteinizing hormone (LH) produced by the anterior pituitary gland. LH secretion is in turn regulated by gonadotropin-releasing hormone (GnRH). Male sexual differentiation fails to occur in the absence of androgens or without a functioning AR. A complete loss of AR function in males results in complete androgen insensitivity syndrome (Quigley et al. 1995). The role of the AR in the development and progression of prostate cancer has led to increasing interest in this nuclear receptor. Many studies have focused on providing new insights into the mechanisms of AR action in prostate cancer. The determination of the three-dimensional crystal structures of the AR DNA-binding domain (DBD) and ligand-binding



domain (LBD) has helped expand our understanding of this receptor by revealing fine molecular details.

### Mechanism of Androgen Action

Classically androgen show genomic actions via AR-mediated control of gene transcription. This mechanism usually requires at least 30–40 min to alter gene expression and hours to produce significant levels of newly expressed proteins. In the target cell, testosterone diffuses through the lipid bilayer of plasma membrane and interacts with AR bound by a multiprotein complex with heat shock proteins (HSP) and immunophilin chaperones, including HSP90, HSP70, HSP56, and p23. This multiprotein complex is present adjacent to the hormone-binding domain of the receptors and thought to keep the receptor in configuration that is favorable for binding to the hormones and incapable of binding through hormones (Heemers and Tindall 2007). After binding of androgen to the androgen receptor, it undergoes a conformational change, allowing its release from the multiprotein complex. This dissociation unmask AR NLS and dimerization motifs, allowing its increased phosphorylation, nuclear translocation, and homodimerization. In the nucleus, activated AR-ligand homodimer complex binds to specific recognition DNA sequences, the androgen response elements (AREs), localized in the promoter regions of androgen-regulated genes (Avellar et al. 1997; Goodman 2003).

### Nongenomic Action of Androgen

Classical action of androgen is performed via binding through androgen receptors in the nucleus, but some “nongenomic actions” have been also reported via activation of kinase signaling cascades. One well-known example of this action is elevated expression of “prostate specific antigen (PSA)” in prostate via stimulation through dihydrotestosterone. PSA causes cleavage of semenogelin and leads to the

liquefaction of the ejaculate and increases sperm mobility. Its abundance in plasma is widely used as a diagnostic marker of prostate cancer (Goodman 2003).

### Role of Androgens and Androgen Receptor in Sex Development

Androgen also plays a determining role in the development of sexual patterns in embryos during the gestational period. Embryos of both sexes have same developmental pattern till the sixth week of gestation. During this time period, formation of primitive gonads takes place by the migration of primordial germ cells from yolk sac enteroderm to the genital ridge. The primordial urogenital tract of both the sexes contains both Wolffian and Mullerian ducts. The primitive gonads start differentiating into testis at the onset of 6–7th week of gestation. This differentiation comprises of the formation of seminiferous cords and Leydig cells. Regression of Mullerian duct also takes place under the influence of Mullerian inhibiting substance (MIS) that inhibits the formation of female genital structures (Wilson and McPhaul 1996).

The initial differentiation of the testis is directed by SRY gene present on Y chromosome. Further, testosterone produced by primitive Leydig cells leads to the virilization of Wolffian duct structures, and formation of epididymis, vas deferens, and seminal vesicle takes place from 9th to 13th week of gestation. Wolffian duct differentiation requires testosterone and functional androgen receptors; thus, the development of internal ducts of male reproductive system is totally dependent upon testosterone availability in that critical time period of embryo development. On the other hand, development of external genitalia depends upon the availability of dihydrotestosterone (DHT) not on testosterone. Thus in few diseased conditions like “androgen insensitivity syndrome (AIS)” or “complete androgen insensitivity syndrome (CAIS),” the phenotype of the person is of females with normal feminine external genitalia and normal breast development



but internally testis with undeveloped Wolffian duct (Sinclair et al. 1990; Wilson et al. 1981).

## Nonreproductive Function of Androgen

Androgens play various nonreproductive roles also like bone and muscle development. Hypogonadism in male is associated with increased bone loss which is reversed after treatment with androgens (Kang et al. 2003). In skeletal muscle, androgen gets aromatized to estrogen and mediates its action via estrogen receptors. Testosterone also induces muscle growth by increasing satellite cell number along with a proportionate increase in myonuclear number. Eugonadal man, treated with different doses of testosterone, found to show muscular hypertrophy in a dose-dependent manner (Bhasin et al. 2003).

## Conclusions

Various information regarding the mechanism of action of androgens through AR via both genomic and nongenomic pathways are available now, but future investigations and researches are needed to fully elucidate the AR physiological function in male reproduction. More studies are also needed illustrating the roles of selective AR modulators (SARMs) and AR coregulator proteins not only in the more efficient pharmacological modulation of the AR in pathological conditions, such as male hypogonadism, diseases of the prostate, and osteoporosis, but also for the development of therapies for male contraception and treatment of male infertility. Other new approaches like analysis of AR knock-out mice and RNA interference will undoubtedly enhance our understanding of androgen effects on gene expression, especially in androgen target cells and organs.

## Cross-References

- Reproduction
- Reproductive Fitness
- Sex-Linked

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## Anecdote

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## Synonyms

[Ad hoc sampling](#); [Focal sampling](#); [Single subject](#)

Anecdotes are descriptions of events or phenomena, usually in narrative form. These descriptions can be true, false, or exaggerated, and anecdotes may be intended as accurate, humorous, engaging, or recountings of unexpected observations. In understanding human behavior and interaction, anecdotes are commonly used to delineate or illustrate character and motivations. In the study of history, anecdotes are used to illustrate events consistent with accepted understandings or to raise questions about these understandings (Gossman 2003). In western cultures, anecdotes about animals have an ancient lineage, with early Roman authors such as Aelian and Pliny the Elder describing intriguing instances (as well as accepted facts) about animal behavior, many

taken from earlier (often Greek) sources. Aelian (2nd–3rd century AD/1958) offers an instance of dolphins escorting a wounded dolphin away from its human captors after scaring them, positing that humans are much less helpful even to their kin (p. 295). Pliny the Elder (1st century AD/1983) describes a hunter who employs tame and wild ravens to capture game and a raven who, to secure rainwater in an urn, drops stones into it to raise the water level (p. 373). Such anecdotes continue to the present day. The medieval era offered anecdotes of animals' crimes and punishments (Evans 1987); anecdotes about animals were also used as allegories for human behavior. Much of the understanding of actual animals provided in anecdotes relied on the acceptance of ideas presented by master scholars such as Aristotle, as well as folk beliefs. However, some medieval scholars examined Aristotle's ideas critically. For example, Frederick of Hohenstaufen, writing in the thirteenth century, questioned Aristotle's knowledge of falconry:

on many points that he [Aristotle] cites in his book *On Animals* he reports that others have reported so, although he may not have seen it himself, nor had his informers seen it. For firm reliability is not produced by hearsay. (Translated in Beullens 2007, p. 146)

Montaigne (1580/1958), in his *Apology for Raymond Sebond*, provides numerous anecdotes about intelligent actions of animals to quell human self-admiration. He provides an example of a fox deliberating at water's edge, reasoning about the sounds of water it hears beneath an ice to determine whether it will support its weight. Although Descartes (1637/1971, pp. 42–43) later denied that examples like those of Montaigne showed anything comparable to reasoning and offered the explanation that animals' actions were instead comparable to actions of machines, his view was not generally accepted by scientists or others, who continued to provide anecdotes of animal intelligence (e.g., Guerrini 2007).

Anecdotes became a scientific problem in light of Darwin's (1871/1896) attempts to support his theory of evolution by natural selection by presenting stories of intelligent action by animals, suggesting a common psychology with humans

(Knoll 1997 in *AAA* (*AAA* refers to the Mitchell et al. (1997) reference, *Anthropomorphism, anecdotes, and animals*, from which are cited several chapters.)). For example, he describes a dog growling at a windblown parasol as indicating aggression derived from reasoning that the parasol was moved by an unseen agency (Darwin 1871/1896, p. 95). Darwin passed on his project of finding and evaluating evidence of animal intelligence to fellow scientist and friend Romanes (1882), who compiled enormous collections of animal anecdotes intended as evidence of mind or intelligence, as indicated by animals exhibiting choice and consciousness (p. 2). Romanes combed scientific and popular literature for facts about animal intelligence, loosely using three principles to determine what to accept as facts: they must be from an authority, the actions described must be distinctive and plausible in relation to the animal's goal (and not subject to an obvious alternative interpretation), and, if possible, they should be observed more than once in the type of animal described in the anecdote (pp. viii–ix). Adhering to these principles was difficult, and Romanes asked not only scientific colleagues but the general public for anecdotes and observations of animal intelligence (pp. x–xi). Although Romanes' anecdotes continue to delight, they lost their appeal for scientists when Morgan (1894, pp. 288–290) argued against their use by showing that what appeared to be intelligent action can derive from unintelligent trial and error. He describes his own dog Tony as, anecdotally, showing signs of intelligence when he lifts the latch of a gate to let himself out. But Morgan had observed the inception of this apparently intelligent action 3 weeks earlier, and the development to Tony's final action was a slow process not based on an understanding of the latch mechanism. Morgan (1894, p. 291) believed that "what we need is careful observation in place of anecdotal reporting"; with such careful observation "we shall acquire a better acquaintance with the psychological processes in animals than we could gain by a thousand anecdotes."

Morgan's claims were supported by Thorndike's (1898/1970) observations of the sequence of animals' attempts to escape when

placed in a "puzzle box": an animal had to perform a specific act to escape from the box and needed to repeat the act to escape when replaced in the box. Thorndike (1898/1970, p. 24) objected to the use of anecdotes, which "report only such facts as show the animal at his best":

Dogs get lost hundreds of times and no one ever notices it or sends an account of it to a scientific magazine. But let one find its way from Brooklyn to Yonkers and the fact immediately becomes a circulating anecdote. ... In short, the anecdotes give really the *abnormal* or *supernormal* psychology of animals.

Contrariwise, observations of individual animals could be used to deny complex cognition in an entire species, as when Pfungst (1911/1965) offered evidence that the horse Hans, who apparently understood how to count, solved problems in arithmetic, and read clocks, was not so clever but was instead responding to body movements of his owner when being questioned about his knowledge. "To remedy [the] defects" of anecdotes, Thorndike (1898/1970, p. 24) remarked, "experiment must be substituted for observation and the collection of anecdotes." Thorndike maintained an indifference to infrequent instances of apparent animal intelligence in his own work, as he never discussed data he presented showing that some cats in his puzzle box solved the problem on the first trial. The view that animals were without intelligence, which Thorndike's experiments promoted but did not always support, was strongly denounced by Mills (1899), who offered an imaginative anecdote to argue against Thorndike's view: he remarks that Thorndike "placed cats in boxes only 20x15x12 inches, and then expected them to act naturally. As well enclose a living man in a coffin, lower him, against his will, into the earth, and attempt to deduce normal psychology from his conduct" (Mills 1899, p. 266). Mills (p. 273) believed that accurate anecdotes were "not valueless" and that "there is no more reason to set aside reliable anecdotes of animals than of men" (1899, p. 262), yet he maintained that "Comparative psychology is advanced rather by systematic observations and experiments than by anecdotes" (p. 273). Washburn (1908, p. 5) delineated the

disadvantages of anecdotal evidence for comparative psychology:

1. The observer is not scientifically trained to distinguish what he sees from what he infers.
2. He is not intimately acquainted with the habits of the species to which the animal belongs.
3. He is not acquainted with the past experience of the individual animal concerned.
4. He has a personal affection for the animal concerned and a desire to show its superior intelligence.
5. He has the desire, common to all humanity, to tell a good story.

Washburn examined one of Romanes' anecdotes (1882, p. 91) which describes ants' burial of the dead in individual graves following a funeral procession; however, when some of the grave-digging ants attempted to escape, these ants were killed and all deposited in a single grave. "No funeral procession for them!" Washburn (1908, p. 9) remarks. According to Romanes (1882, p. 91), "The observation seems to have been one about which there could scarcely have been a mistake"; according to Washburn (1908, p. 9), "One is inclined to think it just possible that there was."

Among naturalists (who wrote for popular audiences, not scientists), anecdotes of observation were commonplace (see Lutts 1990). Burroughs and Muir, by writing of specific encounters with animals and the feelings these engendered, sought to bring out sympathy for animals. Seton and Roberts had observed animals in nature and wrote stories based on their knowledge and anecdotes of particular animals from the animals' perspective. These men often described animals as sharing similar emotional experiences with humans, elaborating the evidence for the emotions in the animals' behavior and context. Muir (1897) provided an extended anecdote of his adventures with the dog Stickeen, who followed him into a snowstorm in Alaska in 1879. As they were making their way back to camp amidst hazardous weather conditions, Muir and Stickeen leapt across many gorges, until one seemed too wide for Stickeen. Muir described

Stickeen's anxiety and refusal to follow him over the expanse, until finally the dog made the attempt and succeeded; Stickeen's joy at his success followed. Seton was a hunter and knowledgeable about animals but also relied on anecdotes he heard to create his stories. Like other naturalists at the turn of the century, Seton believed that anecdotes are valuable and sought evidence from everyday people about animal activities and published their responses. A great deal of the information provided in journals about birds, for example, was from untrained observers (Hayes 1904). Another naturalist, the Reverend William J. Long, wrote numerous books for children based on his own and (mostly) others' observations of wild animals. Long's anecdotes employed an anthropomorphic gloss to understand observations of animal behavior that many believed never happened (e.g., a bird making a cast for its leg injury when it put mud on an injury). Consequently, anecdotes came under scrutiny by other naturalists, particularly Burroughs and then US president, naturalist, and hunter Theodore Roosevelt, who called these naturalists "nature fakers" (see Lutts 1990). For these critics, the main problem was not the anecdote per se (as they were avid users of anecdotes) but rather the falsehoods presented. The same issues that Washburn listed a few years later as problems for scientific anecdotes were acknowledged. Concerns about naturalists' anecdotes appeared in *Science* in 1904. The first letter, by Wheeler (1904), deplored the fact that the public cannot distinguish sound natural history from "drivel in which animals are humanized beyond all recognition," claimed that Long's anecdotes indicated advanced knowledge animals could not possibly have, and noted the "lack of value, which serious students attach to anecdotes as evidences of rational endowment in animals" (p. 348). Others criticized Long as overly imaginative, jumping to conclusions from little evidence, and describing animal behaviors that no one else has observed. The final essay, by Hayes (1904), questioned Wheeler's (1904) analysis of Long's story of woodcock cast making. She claimed that it was Wheeler, not Long, who believed that cast making implies so much knowledge and understanding of theory and asserted

that Wheeler implied “that a man who blows on his fingers to warm them or on his tea to cool it has knowledge of the laws of thermodynamic and is ready to discuss entropy or an indicator diagram” (p. 625).

It is the merest commonplace fact that in order to avoid danger, to lessen pain, to save life, to gain pleasure, human beings are constantly performing acts the underlying principles of which they understand scarcely any better than a woodcock understands the principles of surgery. (p. 625)

Thus, the issues in relation to anecdotes are not only whether or not something happened but how it is to be interpreted if it happened. These issues continue to arise inside and outside scientific circles with people who live closely with animals (see Mitchell et al. 1997).

With the advent of behaviorism in American comparative psychology in the 1920s, concerns about anecdotes as too subjective were extended to all observations of animals, such that any descriptions must be as “objective” as possible, not referring to any mental processes of the animal (Watson 1924). Ethologists and Gestalt psychologists in Europe tended to be less concerned about subjective interpretation and overinterpretation and presumed that adequate description of animal activities required understanding their psychological processes (e.g., goals and emotions) as evident in their behavior (Ellis 1938; Köhler 1925; Mackenzie 1977). Researchers studying apes continued to use psychologically tainted (“anthropomorphic”) anecdotes to derive their understanding of their subjects; indeed, after denying the usefulness of anecdotes of ape behavior prior to behaviorism, primatologists “discovered” the same behaviors occurring among their apes, seemingly unaware that this was rediscovery (Mitchell 1999). Complex psychological terminology (“disgust,” “insight”) in relation to individual activities required not only specification of the animal’s behaviors that implicate the psychological description but also reference to prior related activities that substantiate this interpretation (Köhler 1925). In an attempt to assess the usefulness of anecdotal observations, Hebb (1946, p. 88) examined anthropomorphic observations of chimpanzee behaviors indicating friendliness,

aggression, and threat to determine that a completely “objective” categorization of chimpanzee behaviors led to “an almost endless series of specific acts in which no order or meaning could be found.” By contrast, “anthropomorphic” (i.e., psychological) descriptions of observed behaviors were much more useful as means for keepers and others to know how to interact safely with the chimpanzees.

Throughout much of the twentieth century, a general attitude against anecdotes remained among scientists, which was usually ignored when researchers desired to present anecdotal evidence consistent with current scientific views (usually about apes: e.g., Goodall 1986), but came to the fore when criticizing other researchers’ uses of anecdotes to support different views (e.g., see Mitchell 1993, 1999). Denigration (Keijzer 2013) or elevation (Swartz and Evans 1997 in *AAA*) of animal intelligence could be achieved via an anecdote about one animal that came to be viewed as evidence for the entire species. Initial field research in ethology, and especially in primatology, developed from a sometimes anecdotal methodology to more rigorous observational methods. When Altmann (1974) published her article detailing appropriate sampling methods for specific goals, ad libitum sampling (collecting observations of whatever happens) was viewed as useful only to develop further hypotheses and, perhaps, to learn about rare events. Field researchers in primatology began to use focal animal sampling more extensively, in part supported by sociobiological theory cognizing animals as agents, which led them to interact more directly with animals and, consequently, attempt to take on their perspective (Quiatt 1997 in *AAA*). Such were the attitudes when Griffin (1976) published *The question of animal awareness*, which challenged many accepted interpretations of animal behavior that denied intelligent action. Numerous scientists noted that, but rarely explicated why, anecdotalism was problematic for Griffin’s psychological interpretations of animals’ activities. Still, although scientists can and should find anecdotes about animals engaging, anecdotal descriptions cannot be used to discern the *psychological*



processes that allow for the behavior of apes or other animals (Heyes 1993; Mitchell commentary in Whiten and Byrne 1988, pp. 259–260). When Whiten and Byrne (1988) argued that anecdotes about animals observed by professional primatologists should be accepted as evidence of “tactical deception,” the response from other scientists was mixed, with some accepting anecdotes and others not. Although skepticism was deemed reasonable toward unique anecdotes, Whiten and Byrne (1988) argued that the anecdotes or ad lib observations reported by different observers could be compiled so as to provide multiple records of the same behavior. The term “anecdote” took on new meaning and was now used to refer to a narrative about an observation described by researchers with background and day-to-day knowledge of the nonhuman subjects of the observation (Whiten and Byrne 1988). This methodology only apparently answered many of the earlier criticisms of anecdotes as sources of knowledge about animals’ mental processes (Burghardt commentary in Whiten and Byrne 1988, pp. 248–249). It ignored the need (noted by Morgan (1894), e.g., in relation to his dog’s latch opening) for understanding the larger developmental context (prior behaviors) from which the behaviors described psychologically in the anecdote derive. (By contrast, many animal-language researchers and developmental psychologists, with their extensive knowledge of individual animals and children, contextualized behaviors developmentally for interpretation – see Miles 1997; Mitchell 1997; both in *AAA*; Piaget 1947/1972.) The belief that researchers’ extensive knowledge of animals would derail inaccurate psychological attributions remained unfounded. Whereas several critics remained skeptical that researchers employing anecdotes knew enough to distinguish between more and less complicated psychological explanations for behavior (Heyes 1993; Kummer et al. 1990; Mitchell commentary in Whiten and Byrne 1988, pp. 259–260; Mitchell 1997 in *AAA*), few field primatologists seemed concerned by the use of anecdotes of deception to infer mental state attribution in primates (see, e.g., commentaries following Whiten and Byrne 1988). But if we ignore the issue of whether or not one can attribute

mental states based on anecdotes or observations of nonhuman animals (and there are good reasons to indicate that one cannot: Lurz 2011; contrary to Bates and Byrne 2007), we are left with the fact that observing and naming behavioral patterns within and across species are essential to field studies and have been essential to ethology and comparative psychology from their beginnings (de Waal 1991). As Hobhouse (1901, pp. 89–90) had earlier noted:

In describing the behaviour of an animal, to use terms derived from human consciousness is often the only way of avoiding intolerable prolixity. Properly guarded and corrected by attention to points of difference as well as resemblance, such usage can lead to so little error that, even if we were ultimately to decide that all animals were automata, no change but that of names would be needed in our account. By “feeling” in an animal, then, we shall mean a state essentially similar in causation and function to that which we know as feeling in ourselves. Whether it is similar in other respects, is a question which we do not decide by merely using the term. And so with similar terms.

In our thinking about anecdotes, we seem consistently to rediscover what we already know.

Attempts to formulate a rationale for using anecdotes (observations presented in a narrative) as a source of evidence for an animal’s psychology remain problematic. One suggestion is that if an anecdote is deemed plausible in its description and psychological interpretation, it can count as evidence (Byrne 1997; Rollin 1997; both in *AAA*). But there are often multiple possible psychological interpretations of any given event, such that deciding which one is correct purely from observations is impossible (Lurz 2011; Mitchell 1997 in *AAA*). In addition, plausibility depends on what we currently know about an animal, such that using plausibility as a requirement for the acceptance of an anecdote’s veracity means that anecdotes cannot provide new information, however much they may suggest further research topics. Clearly we need to know the function or goal of an animal’s action if we are to understand it (Millikan 1997 in *AAA*), and anecdotes may provide novel hypotheses as to animals’ goals. Anecdotes are good for illustration of general findings, as in Goodall’s (1986) reframing of anecdotes as

“word pictures.” Summarizing the then recent state of thinking about anecdotes (see also Silverman 1997 in *AAA*), Mitchell (1997 in *AAA*, pp. 426–427) wrote:

Anecdotes by reliable observers can be accepted as believable evidence that specific *behaviors* occurred (this is, that *this* animal did *this* action and *that* animal did *that* action) when these behaviors can be accurately observed under the viewing conditions employed, anthropomorphic terminology can reasonably be used to label or entitle these behaviors, but the interpretation of these behaviors as scientific evidence for mental state attribution demands the same method used to evaluate the accuracy of anthropomorphism: data should be examined using multiple hypotheses varying in the sorts of mental states they propose (if any). As with any science, the accurate interpretation of evidence depends on the hypotheses and perspectives available; and the available evidence may support multiple hypotheses and perspectives. Note, however, that people concerned with ethics toward animals or control of animal behavior, or those just wanting to interact pleasantly with animals, might reasonably use anecdotes and ordinary common sense to fulfill purposes associated with these concerns and desires.

Almost all primate researchers note odd, unexpected, or apparently psychologically complex behaviors in their animal research subjects, perhaps in the hopes of someday understanding them, and sometimes these are reported. But we need to do the same for other species, about whom we are often less willing to construct complex psychological interpretations (Mitchell 1997 in *AAA*). Recent work focuses on whether or not behaviors described in anecdotes can be extended to other species members (e.g., Rutz et al. 2017). Proposed “new” requirements for the collection of anecdotes (Bates and Byrne 2007), where an anecdote is a record of behaviors made by knowledgeable observers soon after their observation, seem to be what researchers have been using all along: the observer must have experience with the animal, must record behavioral observations as soon as possible (and use this record rather than later reminiscences), and must observe multiple instances of the behavior. As noted earlier, this method assures one of the existence of the behavior but offers no reason to believe that individual behavioral observations

themselves, no matter how accurate, can be used to distinguish between complex and simpler psychological processes (Lurz 2011), however suggestive they may be.

## Cross-References

- [Anthropomorphism](#)
- [Language Research: Parrots](#)

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## Anger

### ► Benefits for Aggression in Humans

## Angiotensin

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## Synonyms

Angiotenin; Hypertensin

## Definition

Angiotensin (*angio* means “blood vessels” and *tensin* means “increase pressure”) is an oligopeptide hormone in blood plasma that increases blood pressure by vasoconstriction. It is a key hormone of the Renin–Angiotensin system (RAS) in human, which regulates blood pressure and body fluid balance.

In addition to hormone, angiotensin is a dipsogen (an agent that causes thirst) too. It also stimulates the secretion of aldosterone from zona glomerulosa of the adrenal cortex to increase sodium retention by the kidneys.

## Activation and Synthesis

The RAS can be activated in cases when there is loss of blood volume or reduced blood pressure sensed by baroreceptors in carotid sinus. In addition, reduced filtrate NaCl concentration or reduced filtrate flow also triggers RAS activation

by stimulating juxtaglomerular cells of kidney to release renin hormone.

Angiotensin is derived from the precursor molecule angiotensinogen (produced in the liver) under action of renin (kidney hormone) followed by angiotensin converting enzymes (ACE). It finally releases angiotensin in blood plasma for their downstream activity. This system together called Renin–Angiotensin system (Fig. 1).

Types of Angiotensin and Their Roles

Angiotensinogen, a precursor of angiotensin, is a serum globulin protein produced constitutively in liver and released to blood circulation. It is 452 amino acids long in human, where first 12 amino acids (1DRVYIHPFHLVI...452) are required for important biological activity. The first 12 amino acids of angiotensinogen are processed to produce different types of angiotensin.

Angiotensin I

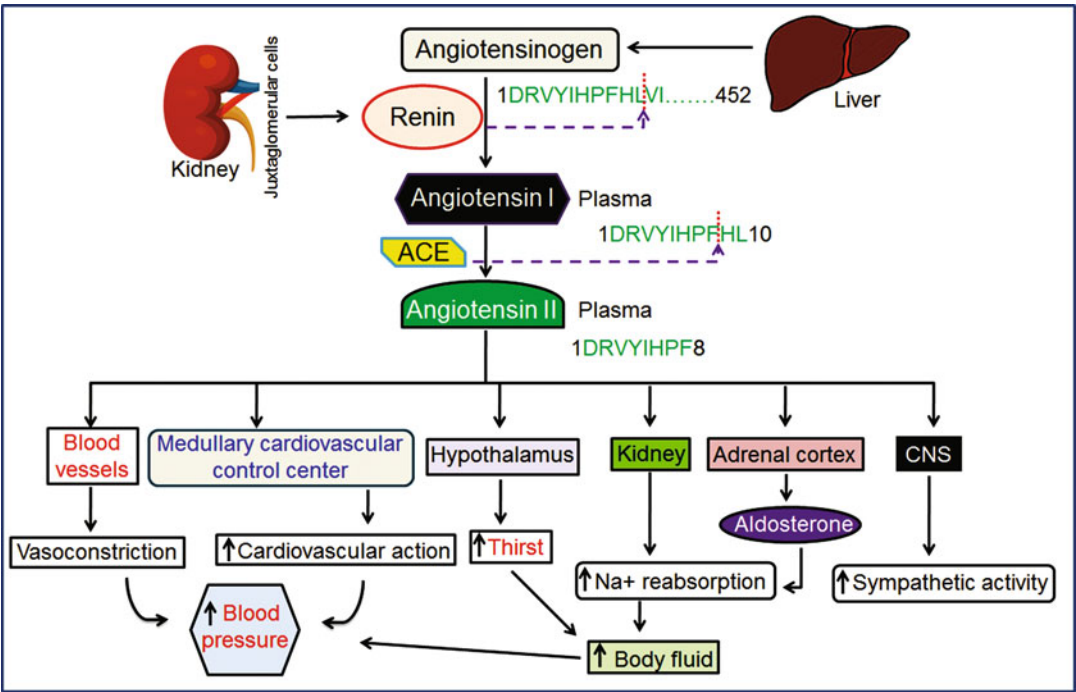
Angiotensin I, also called proangiotensin, is a decapeptide (DRVYIHPFHL) derived from angiotensinogen by the action of renin. Renin is produced in the kidneys in response to reduced blood pressure and NaCl concentration, and cleaves peptide bond between tenth position's leucine (L) and eleventh position's valine (V) of angiotensinogen (Fig. 1).

Roles

Angiotensin I has as such no direct biological activity but it works as a precursor of angiotensin II.

Angiotensin II

Angiotensin II, an octapeptide (DRVYIHPF), is a potent and biologically active form of angiotensin, which produced by removal of two C-terminal residues from angiotensin I via angiotensin-converting enzyme (ACE) (Fig. 1).



**Angiotensin, Fig. 1** Renin-Angiotensin system. The figure summarizes conversion of angiotensinogen (from liver) to angiotensin I and II by renin (from kidney) and

angiotensin converting enzyme (ACE), respectively. Different biological role of angiotensin II has been presented

### Roles

- (a). It acts on the central nervous system (CNS) to stimulate the production of vasopressin.
- (b). It works on smooth muscle of blood vessels to stimulate vasoconstriction (Kanaide et al. 2003).
- (c). Angiotensin II stimulates the secretion of aldosterone from adrenal cortex to retain  $\text{Na}^+$  and lose  $\text{K}^+$  in kidney.
- (d). Angiotensin II also acts on  $\text{Na}^+/\text{H}^+$  exchanger in the proximal tubule of the nephron in the kidney to stimulate reabsorption of sodium and excretion of proton. This also linked to bicarbonate reabsorption. It finally results in an increase in blood volume, pressure, and pH (Le 2012).
- (e). It acts on area postrema and subfornical organ of hypothalamic region in brain to increase thirst sensation (Johnson and Gross 1993).
- (f). It increases the secretion of ACTH from anterior pituitary gland, ADH from posterior pituitary gland (Johnson and Gross 1993), and norepinephrine by directly acting on postganglionic sympathetic fibers.
- (g). It upregulates lipogenesis and downregulates lipolysis (Yvan-Charvet and Quignard-Boulangé 2011).

### Angiotensin III

Angiotensin III, a Heptapeptide (RVYIHPF), is produced by N-terminal degradation of angiotensin II via aminopeptidase A. It shares some of its properties with angiotensin II.

### Roles

- (a). In brain, it acts within neural circuits of the CNS to regulate body fluid balance.
- (b). Like Angiotensin II, it also acts as a vasoconstrictor.
- (c). It stimulates the secretion of vasopressin to control volume homeostasis by reducing renal water loss and increasing blood pressure under conditions of hypovolemia (Reaux et al. 2001).
- (d). It also stimulates aldosterone production and increases mean arterial pressure.

### Angiotensin IV

Angiotensin IV, a hexapeptide (VYIHPF), is produced by N-terminal degradation of angiotensin III via aminopeptidase N. It plays important physiological role in CNS.

### Roles

- (a). Angiotensin IV can improve cognition through effects on acquisition, consolidation, and recall in learning and memory (Braszkowski et al. 1988; Gard 2008).
- (b). It plays role in vasodilation through NO (Mustafa et al. 2001).
- (c). It has shown mitogenic and trophic properties in different cell types (Mustafa et al. 2001).

### Conclusions

Homeostasis of body is required for adaptation in environment. There are many key biological molecules, which play important role in body homeostasis. Angiotensin, a key player of Renin–Angiotensin system, required for body homeostasis during reduced blood pressure or decreased  $\text{NaCl}$  concentration. It maintained blood pressure and  $\text{Na}^+$  in body fluid. Additionally, angiotensin also helps in learning and memory.

### Cross-References

- [Homeostasis](#)
- [Learning](#)
- [Memory](#)
- [Pituitary Gland](#)
- [Protein](#)

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## Angiotonin

### ► Angiotensin

## Animacy

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## Definition

The animacy effect in memory generally refers to better retention of animates (or information processed as animate) compared to inanimates (or information processed as inanimate).

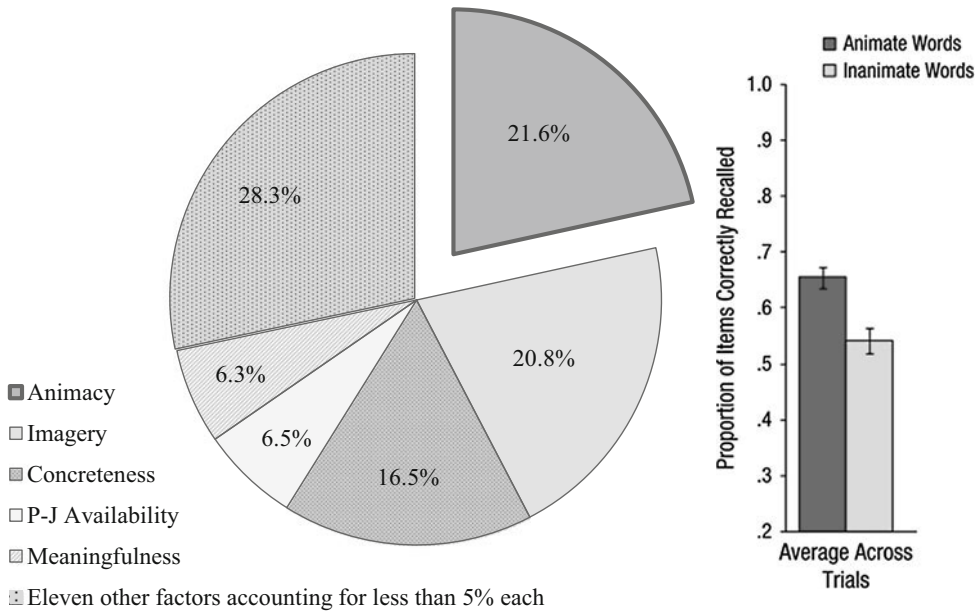
## Introduction

The adaptive memory framework proposes that memory is tuned to remember aspects of events that are relevant to fitness, that is, that enhance one's chances of survival and/or reproduction. Animates, such as animals and humans, are within the realm of such information because they can be potential prey, predators, mates, rivals, and partners for social interaction, among others (Nairne et al. 2017). Therefore, remembering animate items particularly well (as compared to inanimate items) should be an adaptive feature of our memory systems. Nairne and collaborators put this hypothesis to test a few years ago (Nairne et al. 2013), and various forms of empirical evidence have confirmed that, indeed, people remember animate entities better than inanimates, a phenomenon that has been termed the “animacy effect” (Nairne et al. 2017). In what follows we will briefly describe the experimental procedures that have been used to investigate this effect and some of the obtained results. We will also mention some of the potential proximate mechanisms that have been explored and future directions.

## How It Has Been Studied

Empirical evidence for the animacy effect has been collected using different experimental strategies that can simplistically be classified into item- and processing-based procedures.

*Item-based procedure.* In this line of research, the animacy dimension is determined at the item level, that is, memorability for animate items is compared directly to that of inanimate items. In the original work conducted by Nairne et al. (2013), the authors began by using a pre-existing word database that contained information on various word variables (e.g., imagery and emotionality) as well as on word recallability (Rubin and Friendly 1986). The authors classified those words on animacy, that is, whether each word clearly represented a nonliving thing (inanimate items) or a living thing (animate items). Then, using multiple regression analysis, they explored which word characteristics contributed the most in



**Animacy, Fig. 1** Results of the regression analyses denoting the recall predictors (Experiment 1, left side) and free recall results from Experiment 2 (right side; error bars represent standard errors of the mean) from Nairne et al. (2013)

predicting free recall. Their results revealed that animacy was one of the largest predictors of recall (see Fig. 1). In their second experiment, Nairne et al. preselected a set of animate and of inanimate words. Because words themselves can be characterized on various (other) mnemonic-relevant dimensions (e.g., frequency or imageability), care was taken to ensure that, on average, the two sets of words were equated on those dimensions. Then, participants were asked to memorize the words for a later memory test but were not informed about the animacy manipulation. The results revealed better memory performance for the animates than for the inanimates (see Fig. 1). Given the number of item characteristics that could potentially influence retention, however, item selection problems remained a concern. This led the authors to explore this phenomenon using a processing strategy.

*Processing strategy.* In this procedure, rather than comparing animate with inanimate words, participants are invited to think of new stimuli (e.g., nonwords) as corresponding either to living or to nonliving things (VanArsdall et al. 2013). For example, the nonword “BRUG” if presented

with the descriptor “has a busy schedule” would likely be considered to be a living thing, whereas the word “SMIG” presented with the sentence “needs a battery” would likely be considered to be a nonliving thing. In this procedure, each nonword is equally processed as an animate or inanimate across participants; therefore, the to-be-remembered information is the same in both conditions. What differs is the animacy status it becomes associated with. The animacy effect was replicated using this procedure when free recall or recognition was implemented.

### Evidence for the Mnemonic Animacy Effect

Most studies have used the item-based procedure described above. The animacy effect has been replicated across various laboratories, using different sets of items and in different languages (French: Bonin et al. 2014; European Portuguese: Félix et al. 2019; German: Meinhardt et al. 2018; English: Nairne et al. 2013; Popp and Serra 2018). The procedures have included intentional learning

tasks (i.e., participants are instructed to memorize the presented stimuli) as well as incidental learning conditions in which participants perform animacy-related tasks (e.g., classify the items on their animacy status; Bonin et al. 2015) or other encoding tasks (e.g., pleasantness rating task; Leding 2018); the effect holds under both learning conditions (Félix et al. 2019; Gelin et al. 2017). For the most part, the effect has been demonstrated using short retention intervals, but a recent study has revealed that it holds after a 48 h delay interval (Félix et al. 2019). The effect is also obtained when words and pictures are used as stimuli (Bonin et al. 2014) and when memory is tested in various forms: It remains significant in free recall (e.g., Bonin et al. 2015; Nairne et al. 2013; Popp and Serra 2016; Popp and Serra 2018), recognition (Bonin et al. 2014; Xiao et al. 2016), cued recall (VanArsdall et al. 2015; although see Popp and Serra 2016), spatial and temporal memory (Gelin et al. 2018), as well as metamemory judgments (Li et al. 2016).

### Proximate Mechanisms of the Animacy Effect

Researchers have actively investigated the mechanisms that potentially underlie the animacy effect (i.e., how it is produced). Several possibilities have been considered, including arousal, threat, interactive imagery, attention, or ease of information access. In the first two, it is hypothesized that animates could naturally be more emotionally arousing (Meinhardt et al. 2018; Popp and Serra 2018) or threatening (Leding 2018) than inanimates. However, when animate and inanimate sets of items are equated on arousal and threat, the animacy effect remains. Such dimensions can impact recall, but they cannot completely explain the animacy advantage. In the case of interactive imagery, it has been suggested that animates might naturally afford more imagery processes (as compared to inanimates). However, studies in which imaginative processing was induced, measured, or controlled for, have, as of this writing, also failed to account for the animacy effect (Bonin et al. 2015; Gelin et al. 2019). Other

authors have suggested the existence of an attention bias toward animates (New et al. 2007), which could mediate the memory advantage; however, no strong support for this idea has yet been found (e.g., Xiao et al. 2016). Finally, animates could simply belong to stronger and more accessible semantic categories (as compared to inanimates) facilitating their retrieval. Studies in which targets were masked by intermixing them with other non-related information, controlled for categorical aspects of the items being tested, or measured categorization strategies in the recalled output found no support for such hypothesis either (VanArsdall et al. 2017; see Xiao et al. 2016, for a somewhat related, but different, result). In sum, despite all the proposed explanations, the *how* of the animacy effect remains largely unexplained (Nairne et al. 2017).

### Conclusion

Animates have a privileged status in many aspects of our lives. Children from an early age distinguish animate from inanimate items (e.g., Opfer and Gelman 2011); animates seem to capture attention faster and hold it longer than inanimate items (e.g., Bugajska et al. 2018) and to activate the brain in different ways (Xiao et al. 2016), among others. They also assume a very special status in memory as animates are better retained and remembered than inanimates: the animacy effect. Furthermore, researchers have started to explore applied contexts in which we can take advantage of this mnemonic tuning to improve performance, such as the learning of a new language (Laurino and Kaczer 2019; VanArsdall et al. 2015).

In spite of the robustness of this effect, for the most part, it is still an uncontrolled variable in cognitive research (Nairne et al. 2017). Researchers rarely control for animacy in their selection of stimulus pools. Recently, investigators have been developing norming databases that include animacy (European Portuguese: Félix et al. *in press*; American English: VanArsdall 2016) in order to provide researchers with a useful tool to better select and manipulate animacy in



experiments. However, much more needs to be done to establish animacy as a relevant variable in the memory research field.

## Cross-References

- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Memory](#)
- [Biological Preparedness](#)
- [Evolution](#)
- [Evolutionary Psychology](#)
- [Memory](#)
- [Natural Selection](#)
- [Recall](#)
- [Survival Processing](#)

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## Animal "Language"

- [Alex the Parrot](#)

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## Animal Architecture

- [Nest Construction](#)

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## Animal Care

- [Husbandry](#)

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## Animal Combat

- [Aggression](#)

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## Animal Communication

- [Insect Communication](#)

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## Animal Conflict

- [Aggression](#)

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## Animal Defense

- [Primary Defenses](#)

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## Animal Emotion in Farmed Animal Welfare Assessment

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## Synonyms

[Affect](#); [Mood](#)

## Definitions

### Animal Welfare

Animal welfare has been defined in a multitude of ways. After Ruth Harrison's (1964) *Animal Machines* criticized confinement systems used in industrial animal agriculture, the Five Freedoms were created in order to define the needs of non-human animals (hereafter called animals), needs that if left unfulfilled would result in frustration. The Five Freedoms include freedom from hunger or thirst; discomfort; pain, injury, or disease; fear and distress; and freedom to express normal behaviors. Donald Broom, one of the founders of modern animal welfare science, later defined welfare more simply as an animal's state with regard to their attempts to cope with their environment (Broom 1988). David Mellor later took the definition further into the realm of positive welfare by advocating for provision of "a good life" and "a life worth living," whereby the balance of salient positive and negative experiences is positive (Mellor 2016). This definition of welfare, a culmination of decades of work, relies on understanding which experiences are experienced positively and which are experienced negatively, which leads one to ask how an animal is feeling about those experiences.

## Emotion

To assess whether experiences are positive or negative and hence whether an animal is living a “good life,” caretakers need to be able to assess whether an experience results in positive or negative emotion. Emotions are brief affective responses to an eliciting event and include an expressive component, a physiological component, and a subjective “feeling” experience (Désiré et al. 2002). In the study of human emotion, all three components can be studied, but in animals, the existence of feelings must be inferred based on the presence of behavioral and physiological responses to an event. The presence of emotions in animals is corroborated by research that demonstrates neural biology in different species as similar to that of humans (Désiré et al. 2002). Whereas emotion states are often described as brief, the consequences of those states can be long term with wider ranging welfare impacts, as has been demonstrated by modification of the corticotropic axis in depressive humans, calves, and pigs (Désiré et al. 2002). Historically, research into farmed animal emotion has focused largely on fear. This focus is likely the result of the skewed view of animal welfare generated by the Five Freedoms, which focus on alleviation of negative states, including fear, rather than provision of positive states. The closest the Five Freedoms come to providing experiences that could lead to positive welfare is the need to provide “freedom to express normal behavior.” While intensive animal agriculture often does not allow for even basic normal behaviors, like walking in hens or sows, there is no reason to believe that allowing hens or sows room to walk will provide enough positive experiences to shift the balance of positive vs. negative events in favor of positive. The recent shift in animal welfare science toward positive welfare has resulted in a shift toward measuring positive, in addition to negative, emotions in farmed animals.

## Introduction

Animal welfare assessment requires the collection of a variety of outcome-based measures designed

to assess an animal’s state with regard to health, affective state (i.e., emotion), and the ability to engage in natural behaviors. While all three types of indicators often are incorporated, albeit informally, into welfare assessments of small captive populations, like in zoos, assessment of farmed animal welfare is complicated by population numbers in the thousands or tens of thousands and high stocking densities that effectively obliterate the concept of a farmed animal existing as an individual. For this reason, and likely because the primary goals associated with raising animals for food are not to provide the animals with “lives worth living” but instead are efficiency and productivity, farmed animal welfare assessment techniques have historically focused largely on measures of health. The importance of emotion to accurate assessment of welfare has been clear for years among animal welfare scientists (Boissy et al. 2007) but has yet to be fully integrated in an objective way into farmed animal welfare assessment tools that can be easily and effectively implemented on farm. This article will review the range of emotions present in farmed animals, briefly explore the current state of animal welfare assessment in industrial animal agriculture, identify the extent to which emotion is measured, and assert the need that continues to be expressed among animal welfare scientists to utilize welfare assessments that include indicators of emotion (Wemelsfelder and Mullan 2014).

## Do Farmed Animals Experience Emotion?

The ability to feel emotions underlies the entire field of animal welfare science and thus is a necessary precursor to the development of ethical positions surrounding the exploitation of animals for human use. Investigation into the existence and development of emotionality in farmed animals began as early as the 1960s, when Candland et al. applied open-field testing, previously used to investigate emotions in rats, to explore fear in chickens (Candland et al. 1963). Animal emotion has largely been measured using a dimensional approach. The subjective component of emotion

has two independent dimensions: valence (positive/negative) and arousal or excitation (weak/strong) (Désiré et al. 2002; Vonk et al. 2021). Likely because humans are unable to fully understand the subjective component of emotion in animals, researchers have largely shied away from naming these dimensions using emotions found in humans (happiness, sadness, fear/surprise, and anger/disgust), let alone naming secondary self-conscious emotions in farmed animals (shame, embarrassment, guilt, pride, and envy). Given this, this entry will explore positively and negatively valenced emotions in farmed animals.

### Negative Valence: Fear

Fear, a negatively valenced emotion with high arousal, is the most well-studied emotion in farmed animals, likely because domestication requires a reduction in fear for animals to allow themselves to be in close enough contact with a potential predator (i.e., humans) that they can be subjected to stressful industry standard practices such as tail docking, castration, beak trimming, and disbudding. In addition, animal welfare scientists have sought over the past half century to reduce fear, in line with the Five Freedoms, as a way to improve welfare. Fear has been investigated in farmed animals using novel object tests to measure neophobia, human approach tests, food deprivation, social separation, tonic immobility tests, open field tests, and restraint tests. The expressive component of emotion can take at least three forms: behaviors, vocalizations, and postures/facial expressions.

Chickens have expressed fear through a variety of behaviors including vigilance, tonic immobility, escape attempts, flight from stressor, and distress calls (Baxter et al. 2019; Edgar et al. 2012; Hewlett and Nordquist 2019). Chickens exhibited increased head movements and reduced bouts of comfort behaviors in non-preferred environments, presumably while experiencing negative emotional states, as compared to when they are in preferred environments (Nicol et al. 2011). Physiologically, fearful chickens have been observed to have decreased peripheral temperatures, as compared to baseline

neutral state, as measured in the comb and the eye (Edgar et al. 2012).

The expressive component of fear in cattle has been displayed through immobility, avoidance of the stressor, changes in feeding behavior, and the amount of visible eye whites (Boissy et al. 1998; Bourguet et al. 2010; Sandem et al. 2004). Compared to stressed cows, nonstressed cows exhibited more frequent urination and defecation as well as increased immobility (Boissy et al. 1998). Fear appears to be communicated between individuals. Compared to heifers who were in the presence of a nonstressed conspecific, heifers in the presence of a conspecific who received electric shocks exhibited increased plasma cortisol and increased latency to feed and fed more slowly (Boissy et al. 1998). This study also found that conspecifics responded to the urine of stressed heifers more fearfully (i.e., increased latency to feed and explore, Boissy et al. 1998). Physiologically, compared to baseline levels 3 weeks prior to slaughter, cows at slaughter had increased heart rates and elevated plasma cortisol, urinary adrenaline, and noradrenaline (Bourguet et al. 2010).

Pigs have expressed fear through changes in locomotion levels, freezing, latency to explore novelty, vocalizations (including low-frequency grunts and high-pitched vocalizations), changes in urination and defecation, escape attempts, and attention to conspecifics who have experienced stress and by putting ears back and tail down (Carreras et al. 2016; Goumon and Špinka 2016; Leliveld et al. 2017; Reimert et al. 2017). Pigs who are experiencing negative emotions of low arousal (e.g., sadness) are likely to keep their tail tucked and motionless, whereas those who are experiencing negative emotions of high arousal (e.g., fear or anger) often suddenly tuck their tails (Camerlink and Ursinus 2020). Physiologically, compared to less fearful pigs, fearful pigs who took longer to approach a novel object had decreased dopamine in the prefrontal cortex (Carreras et al. 2016).

### Positive Valence: Happiness

Despite anecdotal behavioral evidence of happiness in farmed animals (e.g., calves frolicking through a field, piglets playing with one another,

etc.), research exploring positive emotion in farmed animals is scarce and is often studied concurrently with negative emotion. Despite the paucity of research devoted to understanding how farmed animals experience positive emotions, it is clear that farmed animals are capable of emotion states akin to happiness. Positive emotions in farmed animals have been assessed using a Pavlovian conditioning paradigm whereby animals learn to associate particular signals with positive (e.g., preferred foods), neutral (e.g., nothing), and negative (e.g., water spray) events; yoked control experiments involving the acquisition of an operant task combined with physiological measures; responses to positive events such as stroking, acquisition of a preferred food item, an enriched environment, or arrival of a conspecific; and observation of the expressive component during play.

The literature on positive emotions in chickens is scarce, which makes sense given that it is difficult for humans to understand emotions in individual chickens when an average chicken barn houses 30,000 chickens. Research has shown that when compared to anticipatory behavior seen prior to negative or neutral events, in anticipation of positive events (i.e., provision of mealworms), chickens expressed positively valenced emotions through comfort behaviors like preening and wing flapping (Zimmerman et al. 2011), standing still, walking slowly, and head bobbing (Moe et al. 2009).

Cattle who experienced success in learning increased locomotion, jumps, bucks, and kicks (Hagen and Broom 2004). Compared to when they were not being stroked, cattle who were stroked relaxed their ears backward or let them hang and decreased the amount of eye white that could be seen (Lange et al. 2020; Proctor and Carder 2015). Physiologically, compared to baseline, cattle presumably experiencing positive emotions had lower nasal temperatures and increased heart rates, but it is not yet clear whether those measures indicate valence or simply a change in valence (Hagen and Broom 2004; Lange et al. 2020; Proctor and Carder 2015).

Compared to pigs experiencing aversive conditions, pigs anticipating and experiencing

rewarding conditions (i.e., straw, peat, and raisins) expressed positive emotion through an increase in play behavior (Reimert et al. 2013). Research has found that pigs communicated positive emotions via shorter grunts with a lower frequency and less noise than pigs communicating negative emotions (Briefer et al. 2019). Piglets produced low-frequency, shorter grunts when they anticipated the arrival of a conspecific and produced higher-frequency, longer grunts when they anticipated the arrival of a human (Villain et al. 2020). Pigs can move their tails and ears, and the way they do so is influenced by the way they are feeling. Pigs who are playing and likely feeling positive emotions often wag their tails. In enriched environments, tails were most often curled up and ears directed forward. In general, a curled tail has been associated with positive emotions of high arousal (e.g., excitement), and a relaxed hanging but loosely wagging tail has been associated with positive emotions of low arousal (e.g., calm, Camerlink and Ursinus 2020). Physiologically, pigs experienced increased heart rate and changes in heart rate variability when they experienced a change in valence (Briefer et al. 2019).

Research on emotion in sheep and goats reveals that they too experience emotions, but a review of that literature is beyond the scope of this entry.

## Animal Welfare Assessment and the Regulatory Framework

While there is room for more research on emotion in farmed animals, there is no doubt that these species feel positively and negatively valenced emotions, likely including fear and happiness, but also potentially sadness, anger, and some secondary emotions. However, even if farmed animals are capable of feeling only positive and negative emotions, it is necessary to include assessments of emotion states when determining whether positive experiences outweigh negative experiences. Despite this knowledge, there are currently no federal laws to protect animals on farm in the United States. The two federal laws that apply to the treatment of farmed animals are

the Humane Methods of Slaughter Act, which exempts the vast majority of farmed animals (i.e., birds and fishes), and the 28-h law, which offers minimal protections for animals in transport. Given this regulatory framework, the animal agriculture industry in the United States is left to police itself with regard to farmed animal welfare, and hence, it should be noted that the following animal welfare assessment techniques are not mandated and may not be used on all farms. Animal welfare laws in the European Union are significantly stronger than those seen in the United States, and hence, these assessment techniques may be utilized more commonly in the EU.

### **Inputs Versus Outcome-Based Indicators of Welfare**

Before examining common welfare assessment techniques, it is necessary to understand the distinction between and importance of input versus outcome-based indicators of welfare. Welfare inputs include those factors that influence the welfare of an animal and include things like food, water, environmental factors, social groupings, stocking density, veterinary procedures, standard mutilations, and breeding programs. Outcome-based indicators of welfare include health measures, gait scores, body condition scores, behavioral measures including activity budgets and the presence of abnormal repetitive behaviors, and indicators of emotion state. It is important to examine both inputs and outcomes when assessing animal welfare. Animal welfare is an attribute of an individual, not a group, farm, or supply chain, and there are significant phenotypic and genotypic differences within breeds of the same species that lead to individual variation in response to those inputs. So while inputs are essential to ensure that the playing field is equal for all animals in a system and should be informed by animal welfare science, it is only through measurements of outcome-based welfare indicators, in at least a representative subsample of a group, that one can determine whether those inputs are providing for a positive welfare state.

### **Animal Welfare Assessment in the United States**

Welfare assessment on farm in the industrial animal agriculture system in the United States focuses largely on health. Whereas good health may indicate a lack of negative emotions associated with health status, it in and of itself does not translate into positive emotion, nor positive welfare. The National Chicken Council's Animal Welfare Guidelines include a variety of inputs designed to "minimize fear, pain, stress, and suffering," including but not limited to limits on stocking density, provision of 4 h of darkness per 24-h period, and environmental ammonia limits. The only on-farm, outcome-based welfare indicator found in the National Chicken Council's Animal Welfare Guidelines is the assessment of gait scores. The US pork industry has a similar set of voluntary guidelines laid out in the Common Swine Industry Audit-Pork Checkoff. Inputs include appropriate animal handling techniques, provision of "adequate space" to 90% of pigs, access to food and water, and whether less than 25% of pigs are electrically prodded during transport loading or unloading. Outcome-based welfare assessment involves daily recording of the number of pigs that have low body condition, severe lameness, tail-biting lesions, rectal and uterine prolapses, umbilical hernias, open wounds, and scratches. Similarly, the inputs included in the voluntary National Dairy FARM Program's Animal Care Version 4 include provision of food and water, protection from the elements, and daily exercise. The outcome-based welfare indicators include body condition scores, the presence of broken tails, hygiene scores, and assessment of lameness.

### **Animal Welfare Assessment in the European Union**

The regulatory framework that protects animals raised for food in the European Union (EU) is laid out in Council Directive 98/58/EC of 20 July 1998 concerning the protection of animals kept for farming purposes, with species-specific

regulations that ensure the welfare of pigs, calves, chickens raised for meat, chickens raised to lay eggs, and cattle. These regulations provide far more protections for animals on farm than are seen in the United States and have been informed by a large body of animal welfare research reviewed by the European Food Safety Authority's (EFSA) Panel on Animal Health and Welfare. Likely to ease enforcement, these regulations are largely input-based. However, reviews of the scientific literature have been commissioned by EFSA through the Animal Welfare Indicators Project (AWIN) regarding the use of animal-based welfare measures (outputs) in animal welfare assessment, and protocols that have come out of these projects do include some measures of emotion state, specifically through Qualitative Behavior Assessment (QBA) (Wemelsfelder 2007).

### Creating a Holistic Assessment of Welfare Through Inclusion of Indicators of Emotion

Negative emotions, which are often expressed in overt stereotypic behaviors, reduced health, and aggression, are already incorporated into routine welfare assessments, whether formally or informally, in animal agriculture (Bracke and Hopster 2006). However, alleviation of negative emotions does not necessarily result in the experience of positive emotions. For this reason, it is necessary to utilize welfare assessment tools like QBA in formal welfare audits and in routine farmer welfare assessments. Informal assessments of positive emotion can be conducted through behavioral observations that assess play behavior, affiliative behavior, self-grooming (although self-grooming can become stereotypical in nature), and the presence of positive vocalizations (Boissy et al. 2007). Assessments must seek to measure the frequency and magnitude of positive emotions and negative emotions; positive welfare results when the time spent in positive affective states exceeds that spent in negative affective states.

### Conclusion

Animals farmed for food experience both positively and negatively valenced emotions, communicated through behavior, ear and tail postures, facial expressions, and vocalizations. Physiologically, farmed animals experience emotion through changes in heart rate parameters, peripheral body temperatures, and hormonal changes. Despite literature confirming a complex emotional experience in these animals, and despite the knowledge that positive welfare is simply a state in which the balance of positive to negative states tips in favor of the positive, the vast majority of welfare assessment tools used in the animal agriculture industry focus primarily on output-based indicators of health, largely ignoring the presence of an inner emotional experience in these animals.

### Cross-References

- [Classical Conditioning](#)
- [Human Approach Test](#)
- [Neophobia](#)
- [Open-Field Test](#)
- [Restraint](#)
- [Tonic Immobility](#)

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## Animal Feed Industry

► [Feed Industry](#)

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## Animal Hypnosis

► [Tonic Immobility](#)

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## Animal Innovation

► [Innovation](#)

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## Animal Kingdom

► [Self-Decoration in Dolphins](#)

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## Animal Models

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## Introduction

In the neurosciences, animal models play a central role for experimentally investigating neurobehavioral (dys)functions and their underlying (patho)physiological mechanisms and processes. Almost always, when using animal models, one implicitly assumes that they simulate these mechanisms and processes in humans or a species other than the one investigated. These animal models thus focus on the homology/analogy of the behavior and underlying substrates with the final aim to learn about these behaviors and substrates in the species to be modeled. When developing a model or when selecting the most appropriate animal model for a research project, the most important selection criterion is its validity. Validity is the extent to which an animal model's underlying substrates and mechanisms, measurements, and the conclusions drawn from these measurements are well-grounded and represent the real world accurately.

The basic classes of validity, i.e., internal and external validity and face, construct, and

predictive validity, will be discussed, plus additional classes and subcriteria of validity that have been proposed as refinement and extension of criteria for evaluating animal models. Also, different types of animal models and a strategy to evaluate animal models systematically are described.

## Definition

“An animal model with biological and/or clinical relevance in the behavioral neurosciences is a living organism used to study brain-behavior relations under controlled conditions, with the final goal to gain insight into, and to enable predictions about, these relations in humans and/or a species other than the one studied, or in the same species under conditions different from those under which the study was performed” (van der Staay 2006, pp. 133–134).

This definition is followed throughout this entry and is basic to the model development and model evaluation process depicted in Fig. 1.

## Concepts, Mistaken for, and Concepts that Are Closely Related to “Animal Models”

The animal model literature is filled with conceptual confusions about the concepts test and model. They are categories of animal experimentation that have different purposes, different levels of validity, and different epistemic characteristics (see Table 1). Also, the literature sometimes fails to distinguish between a *model organism* and an *animal model*. A model organism is used to study biological phenomena in a target species, due to specific characteristics that include ease of manipulation and reproduction in the laboratory.

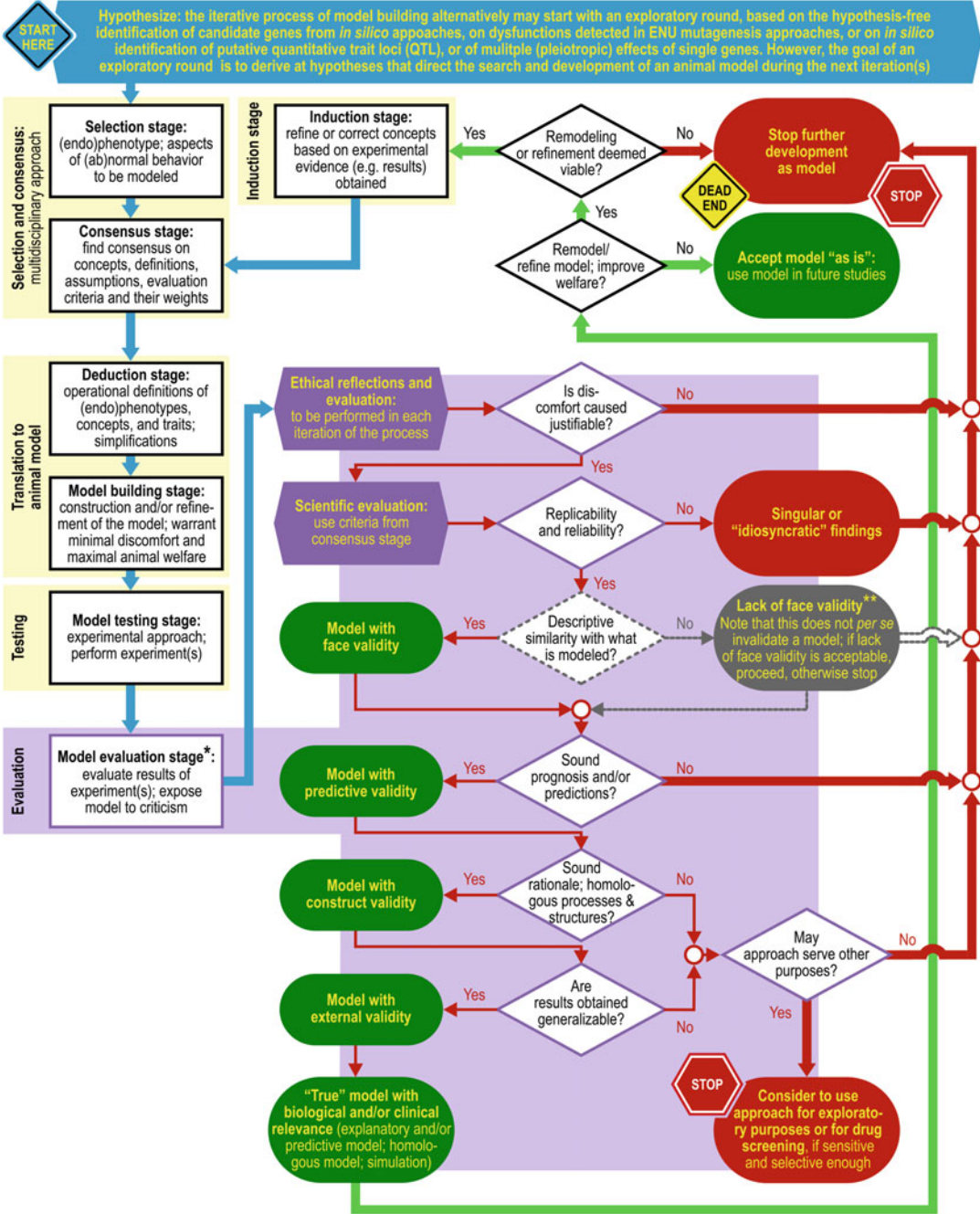
Willner (1991) discriminated three main types of animal experimentation in the behavioral sciences – screening tests, behavioral bioassays, and simulations – that are characterized by different uses. The first two fall under the category of **tests**.

## Screening Tests, Behavioral Bioassays, and Simulations

**Screening tests** are used to predict a desired drug activity from which novel candidates can be assessed. They can be further broken down into two subtypes: “First, some are categorized based on their ability to identify drug candidates with a specific type of clinical action. [...] Conversely, screening tests might also target a particular biochemical action or property in order to identify new drug candidates” (Wright 2002, p. 135). Screening tests have two main requirements: that they make exact and effective predictions about the biochemical action of the drug candidates and that they show that the candidates are efficacious in the target species or disorder (Willner 1991). Screening tests require only predictive validity, and the “relevance of the procedure [...] is not an issue, as long as the goal of correctly identifying drugs and drug effects is achieved” (Wright 2002, p. 135). The main use of a screening test is in pharmacological and pharmaceutical research.

**Behavioral bioassays** are used to study the physiological and neurobiological mechanisms that are associated with brain function, being associated with either the evaluation of specific physiological systems or neuronal circuits or measuring dysfunctions produced by experimental manipulations (Willner 1991). Given that behavioral bioassays do not simply seek to develop novel drugs, these types of animal experimentation can have increased explanatory power over screening tests.

**Simulations** generally attempt to model mental disorders based on comparative studies of the same states and conditions (Willner 1991). Simulations are more commonly used to study the pathophysiology and treatment of mental disorders, but they are also useful to produce insights into normal function. Simulations should require the use of animals with pathological organisms and therefore are highly dependent on the criteria and restrictions of validity (see below). *Only a simulation is a proper model, and both screening and behavioral bioassays should be considered “tests.”* While some behavioral bioassays use pathological organisms (e.g., the olfactory



**Animal Models, Fig. 1** The iterative process of model building and model evaluation. (Figure modified from van der Staay et al. 2014 with permission). \*: Here, face, predictive, and construct validities are used as criteria to evaluate a model. However, one may use other sets of validities instead. For examples of additional/alternative

types of validity that could be used to evaluate a model (see e.g., Belzung and Lemoine 2011, Ferreira et al. 2019, and Hoffman 2016). \*\*: If face validity is considered as crucial, failing to meet this criterion should end the model building and evaluation process

**Animal Models, Table 1** A classification of behavioral tests and models based on purpose, epistemic characteristics, and main use

| Category | Type, based on Willner (1991) | Purpose                                                                                                                                                                     | Epistemic characteristics                                                                                                                                                                                                                             | Main use                                                                               |
|----------|-------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------|
| Tests    | Screening tests               | Allows limited comprehension of an isolated aspect of a complex biological mechanism to be mapped<br>Limited predictive usefulness (e.g., predicting desired drug activity) | Underlying biological mechanism does not need to be similar<br>Not necessarily sensitive to, e.g., triggering factors<br>Not necessarily hypothesis-driven<br>Low construct validity; moderate predictive validity (pharmacological isomorphism only) | Drug discovery and screening                                                           |
|          | Behavioral bioassays          | Allows broader comprehension of a mechanism, without necessary causal analogy<br>Moderate predictive usefulness [e.g., studying neural bases of behavioral (dys)functions]  | Biological mechanism is similar, but not causally analogous<br>By definition, is sensitive to disturbances<br>High predictive validity, low to moderate construct validity                                                                            | Investigation of the physiological mechanisms that compose and organize brain function |
| Models   | Simulations                   | Can allow inferences and extrapolation to the human disorder, with high probability that the hypothesis thus generated is true                                              | Similar mechanisms with probable causal analogy<br>By definition, sensitive to disturbances<br>High face, predictive, and construct validity (considers the need to address theoretical constructs on the etiology, symptomatology, and treatment)    | Investigation of the neurobiological underpinnings of a disease                        |

bulbectomy test, in which ablation of the olfactory bulb produces learning deficits, hyper-reactivity, and glucocorticoid responses which are reversed by antidepressants or the stress-induced hyperthermia, in which transferring rats or mice to a novel environment increases body temperature in an anxiolytic drug-sensitive way), it is not *required* of them that the induction methods are analogs of etiological factors of the target disorder. Similar observations can be made for most research on transgenic organisms (e.g., knockout rodents). *Across this entry, “animal model” will be used interchangeably with “simulation.”* Table 2 provides a non-exhaustive overview over different types of model animals and of the dependent and independent variables in animal models.

## Biological and Clinical Relevance

An important criterion for using a behavioral model is biological and/or clinical relevance (van der Staay 2006). Relevance can be determined using many different criteria (van der Staay 2006), all of which depend on the purpose of the model, the information available for the evaluation, and the stage of development of the model (see Fig. 1). Thus, tests and models have different uses, which should be explicitly defined at the outset: “The explicit definition and designation of the specific purposes that an animal model should fulfill is basic as it allows to define a set of weighted criteria for evaluating the model” (van der Staay et al. 2009, p. 2). Many different uses of a model, and the differentiation between tests

**Animal Models, Table 2** Types of model animals and the independent and dependent variables in animal models. (Modified from van der Staay et al. 2009, p. 4. Table 1A, B). Part A lists different types of “model animals” for the

study of behavioral dysfunctions (inspired by Gamzu 1985). It focuses on the type of subject (independent variable) and is not concerned with the type of dependent variable measured

A: Types of “model animals” (note that the list of models is not exhaustive)

| “Normal” animals, i.e., animals without any observable behavioral deficit. (Studying behavior in “normal” animals provides the baseline data for identifying abnormal behavior)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | Animals with naturally occurring neuronal deviations, neuropathologies, or neurological/psychiatric (endo)phenotype(s)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      | Animals with experimentally induced behavioral dysfunctions or characteristic behavioral (endo)phenotype(s)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <p>Note: At first glance, normal animals are not model animals for the study of, for example, neurobehavioral disorders. Normal animals are used to:</p> <ul style="list-style-type: none"> <li>• Assess the safety/toxicology risk of a putative therapeutic;</li> <li>• Obtain an estimate of the putative abuse liability of a compound</li> <li>• Explore the neurobiological specificity of compounds and their molecular and cellular mechanisms of action</li> </ul> <p>Isogenic populations, for example:</p> <ul style="list-style-type: none"> <li>• Monozygotic twins or multiples</li> <li>• Clones</li> <li>• Inbred strains and variants; coisogenic strains (differing at one single locus); Coisogenic strains (differing by a mutation at a single locus); congenic strains, (differing at only one locus and a linked chromosomal segment); recombinant inbred strains (with a permanent set of recombinations between chromosomes from two or more inbred strains)</li> </ul> <p>Non-isogenic populations, for example:</p> <ul style="list-style-type: none"> <li>• Random bred and outbred strains; animals caught in the wild</li> </ul> | <p>Spontaneously and endogenously occurring psychiatric or neurological conditions; spontaneously occurring mutations; aging animals</p> <p>Genetic lines: Inbred strains and their crossings</p> <p>Selection lines, established through artificial selection favoring low and/or high values of a particular trait within a given population for a number of successive generations; preferentially including an unselected control line for comparison</p> <p>Selected extremes from a particular animal population, e.g., good vs. poor learners, dominant vs. subordinate animals, non-aggressive vs. aggressive animals; anxious vs. bold animals</p> | <p>Transgenic and knockout animals; isogenic or non-isogenic populations that express a neurobehavioral deficit or a neurological/psychiatric (endo)phenotype</p> <p>Animals from mutagenesis screens (after thorough phenotyping and validation)</p> <p>Selection lines resulting from selective breeding</p> <p>Environmental factors: e.g., animals experiencing acute or chronic stress, pain, or sleep deprivation</p> <p>Animals with disruptions induced by:</p> <ul style="list-style-type: none"> <li>• Dietary composition (e.g., tryptophan depletion)</li> <li>• Pharmacological compounds (e.g., scopolamine, MK-801), or</li> <li>• Electrically, or by hypoxia, or anoxia</li> </ul> <p>Animals with focal or global ischemic, embolic, or hemorrhagic cerebral stroke</p> <p>Animals with CNS-specific lesions, for example: neuro- or immunotoxic lesions; lesions induced by aspiration, ablation (knife cuts); radio-frequency lesions, cryogenic lesions</p> |

B: Independent and dependent variables

| Independent variable (in essence the model animals and their controls listed in part A)                                                                                     | Dependent variables and/or (endo)phenotypes                                                                                                                                                                  |                                                                                                                                                                |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                                                                                                                                             | Neuropathological changes                                                                                                                                                                                    | Behavioral changes                                                                                                                                             |
| E.g., genetically modified animals, aged animals, lesioned animals, ischemic animals, hypoxic animals, aged and lesioned animal, i.e., combination of deficits (see part A) | Damage or dysfunctions induced: Site and size of neuronal damage (neuropathology), effects on specific neuronal circuits or neurotransmitter systems, psychophysiological and/or biological (endo)phenotypes | Behavioral dysfunction or malfunction: Impaired cognitive performance, impaired sensorimotor functions, neuropsychiatric symptoms, behavioral (endo)phenotypes |
|                                                                                                                                                                             | Homology of damaged area(s) or neuropathological changes.                                                                                                                                                    | Homology of disrupted processes or impaired functions                                                                                                          |
|                                                                                                                                                                             | Operational definition(s) of the neuropathological (endo)phenotype(s)                                                                                                                                        | Operational definition(s) of the behavioral (endo)phenotype(s)                                                                                                 |



(screening, bioassays) and models (simulations), suggest that “(…) the value of an animal model is relative, not necessarily to the degree that it simulates the structural, functional, and behavioral correlates of [psychopathology], but to the degree that it comports with the specific tasks for which it is being used. The aims of neuropsychopharmacological research are heterogeneous, often being contextually calibrated to fit specific needs and questions of a wide variety of researchers. Consequently, acknowledging the proper roles and capacities of animal models, and not overgeneralizing or wresting them from their intended domains of application, is therefore a major step in arresting criticism pertaining to the legitimacy and logistics of animal modeling” (Wright 2002, p. 134).

An important consequence of that formulation is that “relevance” is always relative to the aims of the research and not an a priori property of the model. “Relevance reflects the meaningfulness and usefulness of results obtained with an animal model for a particular scientific and/or clinical purpose” (van der Staay 2006, p. 146). The purposes of a model are to enhance our understanding of the underlying substrates and mechanisms associated with the disorder and to assess the effects of drugs and treatments in a different system than the target population (e.g., the patient) (Maximino and van der Staay 2019; van der Staay 2006), allowing inferences and extrapolation to disorder in a certain target species, with high probability that the hypothesis that is generated by the model is true (Maximino and van der Staay 2019). However, a model may have a more limited applicability but still may be relevant for specific purposes (van der Staay et al. 2009).

While the concept of relevance is central to this formulation of behavioral models, it is sometimes confounded with the concepts of validity (see below). Thus, models possess relevance if they are valid and generalizable (van der Staay 2006). Since behavioral bioassays and screening tests do not require construct validity, their relevance lies in their sensitivity to find novel therapeutics (in vitro and in vivo) and/or in their capacity to generate novel hypotheses on normal and pathological brain functioning.

## Model Building as an Iterative Process

The aspects discussed so far draw attention to an implicit aspect of the use of animal models, viz., that model building is an iterative process. Therefore, it is sometimes difficult to judge whether a model is established (i.e., that it satisfies the preset validation criteria) or whether its developmental process is reaching a dead end because it fails to meet essential validation criteria (see Fig. 1). The central role of theory in construct validity (Maximino and van der Staay 2019), as well as the importance of the *zeitgeist* in the creation of a model, creates the necessity to make the theoretical basis of the model explicit. All model development begins with a hypothesis derived from data or theories (van der Staay 2006). Model building proceeds from this hypothesis-building stage to a **selection stage**, in which aspects of normal or abnormal behavior of the species to be modeled are selected. “This stage thus reflects the intended animal model and its first translation into testable behavior that is believed to be indicative for the behavioral (dys)function to be modeled.” (van der Staay 2006, p. 142). The next step in the model building process is a **consensus stage**, in which the criteria, definitions, and assumptions regarding the validity of the analogy are discussed and agreed upon. The following stage, the **deduction stage**, involves the decomposition of the endophenotypes under analysis and the verification of the translational relevance (i.e., whether the same endophenotype can be tested in both the model and the target) (Fig. 1). These steps are mostly theoretical and are followed by the **model building stage** per se (van der Staay 2006).

Probably the most important stage in this process is the **model evaluation stage** (Fig. 1), in which the results obtained with the model are evaluated (van der Staay et al. 2009). The many different proposals for evaluation strategies will be discussed in the next section. If the model is considered acceptable after this stage, the process enters an **induction stage**, in which knowledge gained from the experiments performed to develop and validate the model can be used to further refine or correct the concepts which sustain the model; otherwise, the researchers should

determine whether the failure was due to choosing inappropriate criteria to build the model or whether the criteria need to be refined.

Note that not all criteria can be evaluated in a single experiment. Testing replicability, for example, needs data from at least two experiments. For the time being, therefore, one may assume that a criterion is fulfilled, until enough evidence has been accumulated (i.e., after a number of experiments have been performed) to base the decision about whether a particular criterion is met, or whether the model fails to meet a criterion, on scientific evidence.

## Model Evaluation and Concepts of Validity

### Basic Classes of Validity

Concepts of validity are highly variable between model theorists (Belzung and Lemoine 2011; Ferreira et al. 2019; van der Staay 2006). While most follow the recommendation of using face, construct, and predictive validity as the main or essential criteria for evaluating a model, many other propositions appeared; Table 3 attempts to summarize these suggestions, which are detailed in what follows.

**Animal Models, Table 3** Concepts of validity, their definition, and their relations. (Adapted from Belzung and Lemoine 2011, Maximino et al. 2010, McOmish et al. 2014, and van der Staay et al. 2009)

| Validity concept    |                                                | Definition                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
|---------------------|------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Internal validity   | Replicability                                  | “The degree of accordance between the results of the same experiment performed independently in the same or different laboratories” (van der Staay et al. 2009, p. 3)                                                                                                                                                                                                                                                                                                   |
|                     | Reliability                                    | The overall consistency of measurements made using the model                                                                                                                                                                                                                                                                                                                                                                                                            |
| Face validity       | Ethological validity                           | Similarity of behaviors in normal and pathological organisms (Belzung and Lemoine 2011)                                                                                                                                                                                                                                                                                                                                                                                 |
|                     | Biomarker validity                             | Also an aspect of convergent validity; whether biomarkers associated with the disease also appear in the model (Belzung and Lemoine 2011)                                                                                                                                                                                                                                                                                                                               |
| Predictive validity | Pharmacological isomorphism/remission validity | A given drug effect being characteristic for a well-defined class of chemicals and indicative of a specific mode of action                                                                                                                                                                                                                                                                                                                                              |
|                     | Induction validity                             | “The action of the etiological factors on the observable effects of the model disease resemble its action on the observable effects of the human disease” (Belzung and Lemoine 2011, p. 9)                                                                                                                                                                                                                                                                              |
| Construct validity  | Homological validity                           | Whether the trait in question is homologous in humans and the species tested (Maximino et al. 2010)                                                                                                                                                                                                                                                                                                                                                                     |
|                     | Genetic validity                               | Similarity of the genetic or genomic basis for the endophenotype / disordered domain                                                                                                                                                                                                                                                                                                                                                                                    |
|                     | Environmental validity                         | Similarity of G x E interactions (McOmish et al. 2014)<br>Ontopathogenic validity: similarity of “early environmental factors whose interaction with the initial organism produces a vulnerable organism” (Belzung and Lemoine 2011, p. 7); triggering validity: “the similarity of triggering factors occurring during adulthood whose interactions with either a vulnerable or an initial organism produces a pathological organism” (Belzung and Lemoine 2011, p. 7) |
|                     | Mechanistic validity                           | Similarity of the mechanism one supposes or knows is working in the animal disease to the mechanisms that is presumed to be working in the human disease                                                                                                                                                                                                                                                                                                                |
|                     | Pathogenic validity                            | Similarity of the processes that lead to disease                                                                                                                                                                                                                                                                                                                                                                                                                        |
|                     | Inter-relational validity                      | Ability of the proposed model to target the interplay between various disordered domains (Stewart and Kalueff 2015)                                                                                                                                                                                                                                                                                                                                                     |
| External validity   | Convergent validity                            | Similarity of results from different methods                                                                                                                                                                                                                                                                                                                                                                                                                            |
|                     | Translational value                            | Ability of the proposed model to produce results which are translated to the target disorder                                                                                                                                                                                                                                                                                                                                                                            |



### Internal Validity and Reliability

Among the proposed methods for evaluating a model is the assessment of its reliability and replicability. **Reliability** is primarily a property of the method, while **replicability** is a property of the results obtained using a particular model. The first, then, indicates how consistent the method is or the extent to which the model yields consistent results each time that measurements are performed under the same conditions. In animal modeling, reliability refers to at least three different properties: the replicability of the model in different laboratories; the concordance of measures taken by different independent observers or by different methods (e.g., automated vs. manual data collection); and the evaluation of the temporal stability of the behavior measured. The concept is conflated with replicability, “the degree of accordance between the results of the same experiment performed independently in the same or different laboratories” (van der Staay et al. 2009, p. 3). Indeed, test theory identifies several classes of reliability estimates (inter-rater reliability, test-retest reliability, inter-method reliability, internal consistency reliability) which are sometimes related to replicability.

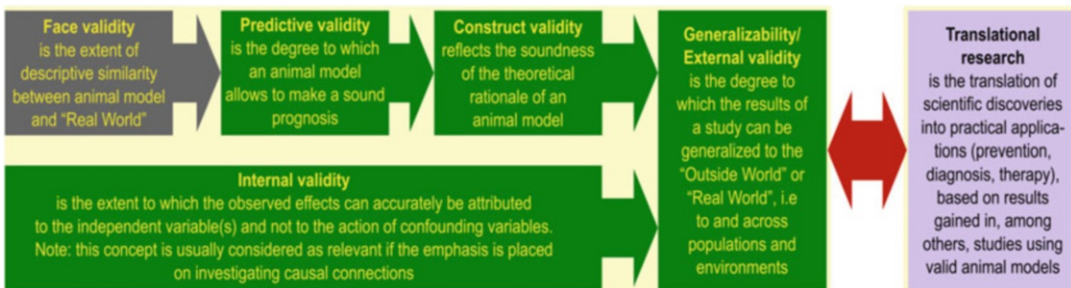
Both reliability and replicability are part of the **internal validity** of an experimental method (Table 3; Fig. 2), a characteristic of “how well a study was performed, how strictly putative confounding variables were controlled, and how confident one can be that the changes observed in the dependent variable(s) are *caused* by

experimentally manipulating the independent variable(s), and not by confounds” (van der Staay et al. 2009, p. 3). Internal validity refers mainly to the need to objectively, reliably, and replicably measure the phenomena being evaluated; therefore, it refers to the consistency of the experimental design (Belzung and Lemoine 2011) and the reduction of biases through randomization and blinding (Ferreira et al. 2019) as sine qua non conditions for external validity. Strictly speaking, internal validity is also about causality (van der Staay et al. 2009).

### Face Validity

**Face validity** refers to whether the test has a perceived resemblance to its target – whether it “looks like” its target. One important limitation to the attempt to establish face validity as a point-to-point correspondence between a disorder and an animal model is “the fact that there is no good reason to suppose that a given condition will manifest itself in identical ways in different species” (Maximino et al. 2010, p. 117). The presence of a symptom in itself has no value if it is not assumed to indicate the expression of an underlying pathological condition, and many authors consider face validity of lower significance for the evaluation of a model (McKinney and Bunney 1969; van der Staay et al. 2009).

Discarding direct references to symptomatology and focusing on neurobehavioral alterations that are distinctive of a given disorder increases face validity because it allows for the use of a



**Animal Models, Fig. 2** Face, predictive, construct, and external validities are the basis for animal model development and model evaluation (see also Fig. 1). In addition, in experimental approaches, two classes of validity may be distinguished: internal and external validity. The bidirectional and recursive relationship between animal models,

translation to applications, and reverse translation to animal models is indicated by the two-headed arrow to translational research. Insights gained in the translational stage may also feedback (reverse translation) to the model building and model evaluation process

given *endophenotype* that is observed in both species. For example, schizophrenic patients have deficits in working memory, attention, and sensorimotor gating that are not part of the diagnostic criteria; since sensorimotor gating can be assessed via measures of prepulse inhibition (PPI) of the startle reflex, decreases in PPI in nonhuman animals are often used as evidence for face validity (Gould and Gottesman 2006). This strategy shifts attention toward other variables, but the functional significance or the specificity of the endophenotype is not a requirement for its definition. For example, not all schizophrenic patients show PPI deficits, and PPI alterations can be found in other neuropsychiatric diseases.

Face validity is also increased by focusing on cross-species psychological processes, a strategy that “(…) requires prior extensive research on the biology and ethology of these species” (Belzung 2014, p. 1044), and is referred to as **ethological validity**. Ethologically valid models use endpoints that are functionally meaningful, serving the same *function* as the target behavior, domain, or endophenotype. Perhaps no field has focused so much on this as the field of anxiety research (Maximino et al. 2010).

Belzung and Lemoine (2011) proposed that face validity is associated with both ethological validity and **biomarker validity**: “The former is the similarity of behaviors related to the presumed pathological organism. Here again, the meaning matters more than the material similarity. Biomarker validity is the similarity of biological markers related to the presumed organism. What matters is the function of a marker, not its chemical composition” (Belzung and Lemoine 2011, p. 9).

### Predictive Validity

**Predictive validity** relates to the success of predictions derived from the model. Willner (1991) emphasized that predictive validity also includes McKinney’s and Bunney’s (McKinney and Bunney 1969) “similarity in treatment effectiveness”; in that sense, predictive validity reduces to *remission validity* or *pharmacological isomorphism*. While theoreticians for model building agree that predictive validity is less important than construct validity (van der Staay 2006; van der Staay et al. 2009), in

practice most researchers appear to consider pharmacological isomorphism as more important (Maximino et al. 2010). Pharmacological isomorphism also requires that drugs which are *not* effective in clinical settings do not affect the model (i.e., no errors of commission are present); for example, amphetamines are commonly used in pharmacological validation of anxiety models because they do not reduce anxiety, but can produce “false positives” by altering locomotion (Willner 1991). The appeal to pharmacological isomorphism, usually without reference to construct validity, weakens the operationality of the model and risks circularity in the definition; for example, defining an outcome in the EPM as anxiety-like because anxiolytic drugs decrease it, although a common practice, is circular definition.

Pharmacological isomorphism can be an important criterion for screening tests and behavioral bioassays, but it is not sufficient for a simulation (Willner 1991).

In addition to showing responses to clinically effective drugs, predictive validity of proper models requires that the model is responsive to drugs and treatments that exacerbate the same symptoms and that the model is responsive to all classes of drugs that are useful in treating the target disorder instead of being only sensitive to the effects of drugs with specific pharmacological characteristics (e.g., structure-activity studies) or show only narrow effects on specific neuronal functions (e.g., serotonin reuptake inhibitors). Also, predictive animal models should be sensitive to the relative potencies of different drugs corresponding with their potencies in clinical use (Ferreira et al. 2019). Moreover, simulations are less sensitive to false positives and false negatives than screening tests and behavioral bioassays: “False positives may be clinically effective at high doses, but go unnoticed due to the desire to stave off dire side effects. On the other hand, false negatives raise the possibility of clinical subgroups and populations with differing response patterns” (Wright 2002, p. 137).

### Construct Validity

Construct validity refers to the theoretical rationale behind a given model. The most influential

description of construct validity in animal modeling is that of Willner (1986), who proposed five subcriteria for a model to have construct validity: “[w]hether both the behavior in the model (1) and the features of [the disorder] being modeled (2) can be unambiguously interpreted, and are homologous (3), and whether the feature being modeled stands in an established empirical (4) and theoretical (5) relationship to [the target disorder]” (Willner 1984, p. 1).

### Subcriteria for Construct Validity

There is no consensus about what exactly Willner’s (1984) sub-criterion 5 entails. Atanasova (2015) suggests that construct validity “requires proper mapping between the hypothesized mechanisms underlying the human and the animal behaviors respectively” (Atanasova 2015, p. 172). Belzung and Lemoine (2011) argued that the theoretical relationship between model and target is understood in a polysemic sense, including theories about the nature of the disorder; the centrality of a dysfunctional process to the disorder (e.g., helplessness and anhedonia are central symptoms of depression, and fear generalization is a central aspect of PTSD, etc.); the dynamic of the disorder (time course, relationship to previous stress, etc.); and etiological aspects. Etiological aspects, in turn, include theories on the role of triggering events in causing the disorder in human patients and in animal models (e.g., stress may cause depressive-like symptoms in animal models and major depressive disorder in humans); the centrality of specific characteristics of these triggering events (e.g., stressor uncontrollability, intensity, or distance to threat); and the involvement of associated biological processes (e.g., dysfunctions in the brain reward system or the fear system).

Another important aspect of the theoretical grounding of construct validity is that properly developed theories can provide the model with stronger predictive and face validity (McNaughton and Zangrossi 2008). As a consequence, novel models generated directly from a theory can provide “a range of constructs from which a suitable model can be extracted by design” (McNaughton and Zangrossi 2008, p. 17).

The influence of the *zeitgeist* is especially important when considering the theoretical basis of construct validity. It has been argued that the theoretical choices that constrain model building should not be understood as homological – that is, “the choice for a model based on operant or respondent behavior, in a naturalistic situation or related to pharmacologic (sic) manipulation,” should not imply that the pathology that is modeled is reducible to these mechanisms (Gouveia and de Brito 2015, p. 308). Nonetheless, theoretical considerations are very important in model building: “Model-based science is an exercise in *theorizing* or speculating on unknown mechanisms and outcomes. Modeling is always an indirect type of theory-building practice” (Degeling and Johnson 2013, p. 95). A properly developed theory encapsulates a network of data and other theories, and by capturing the “essence” of this network, the construct is validated (McNaughton and Zangrossi 2008).

One central theoretical assumption of animal models is that of homology between model and target, in the evolutionary sense (Greek and Rice 2012). The (usually unspoken) assumption is that, since mental (and nonmental) disorders represent an extreme in a continuum, the trait/phenotype/domain of interest is conserved between healthy humans and other species. For example, it has been proposed that “normal” anxiety is an adaptive response that is part of the defensive repertoire of the animal. The obvious consequence is that the normal defensive repertoire of a given animal can be used to study “normal,” non-pathological anxiety (or at least some aspects of anxiety), as well as normal fear-like behavior. That is the concept of **ethological validity** proposed by Belzung and Lemoine (2011). Usually, however, the conservation is implied but never tested (Maximino et al. 2010). Moreover, which endpoint to choose cannot be so easily determined for other domains that are dysfunctional in several disorders, such as cognition.

### External Validity, Standardization, and Generalization of Tests and Models

In addition to the earlier described well-accepted criteria, other researchers have suggested the application of additional validity criteria to

improve the ability of animal models to identify novel drug targets (which is not the same as enhancing the analogy). Thus, genetic validity, environmental validity, and population validity have been proposed as important criteria (Hoffman 2016). These are special cases of **external validity**, which “involves an inference to the *robustness* of a causal relation outside the narrow circumstances in which it was observed and established in the first instance” (Guala 2003, pp 1198–1199, emphasis in the original). In that sense, external validity is a consequence of construct validity.

The establishment of the external validity of a given model is not straightforward; evaluation of generalizability is usually understood as the last step in the model evaluation stage (Fig. 1). While epistemological discussions on external validity usually rely on subject and laboratory conditions (Guala 2003), in the case of animal models, the tests for external validity rely on whether the model possesses validity across different housing conditions and laboratories or across different behavioral tests that are believed to measure the same underlying traits and whether the model enables insights and predictions to other species (van der Staay et al. 2009).

### Genetic and Environmental Validity

**Genetic validity**, as proposed by Kas and colleagues (2007), refers to whether there is an identical genetic basis for the endophenotype – that is, whether the genes that determine behavior in the model are also associated with the target disorder and shared between humans and the model organism. The use of behavioral domains (endpoints or endophenotypes representative of naturally occurring behavioral functions, such as social interaction, appetitive motivation, memory function, and emotionality) is similar to the “research domain criteria” (RDoC) approach proposed by the NIMH (Cuthbert 2014). In this case, the focus is not on altered (dysfunctional) endophenotypes, but instead on naturally occurring behavioral domains that are relevant to both animal behavior and human neuropsychiatric disorders. It is expected that “inter-species trait genetics rather than complex syndrome genetics will optimize genotype-phenotype relationships for

neuropsychiatric disorders and generate powerful new disease models that will facilitate the identification of biological substrates, their developmental consequences, and the environmental modulators underlying these disorders” (Kas et al. 2007, p. 324).

To increase the genetic validity, it is important to model a disordered domain across numerous species (Kas et al. 2007), largely based on the notion that behaviors and their genetic underpinnings are evolutionarily conserved across different species because of common adaptive mechanisms (Greek and Rice 2012). An important limitation of this approach is that genetic validity cannot be properly established for a wide variety of endophenotypes and genes. For example, some genes and behaviors do not correlate across species (LaPorte et al. 2008) – especially considering nonmammalian species, which show different number of genes encoding specific proteins. Moreover, the individual domains and endophenotypes which are analyzed may only incompletely model the target disorder, and in this case, genetic validity can only be established as an accessory argument after construct validity has been established. Finally, genetic analyses in animals usually demand isogenic lineages based on inbred strains, but the human population is genetically heterogeneous, and therefore using only inbred animals decreases external validity (see below) (Stewart et al. 2015).

**Environmental validity** adds a novel layer to the complexity of genetic validity in requiring that not only gene variants can be identified in both the model and the target disorder but that specific gene by environment interactions can be found for both cases (McOmish et al. 2014). In particular, behavioral models could benefit from “a complementary ‘enviromics’ approach, in which the ‘envirome’ contributing to the pathogenesis and progression of each disorder, and multiple disorder (‘environmental pleiotropy’), is systematically catalogued and computationally analysed” (McOmish et al. 2014, p. 4723).

The same critique made for the role of etiology in establishing validity can be made for both genetic and environmental validity, though, usually, it is precisely the genetic, genomic, or “enviromic” underpinning of the disorder that is

under study with the model, and therefore it is not known beforehand. A solution to this conundrum is assuming that both genetic and environmental validity are “accessories” in establishing external validity and are in fact practical consequences of using different species to test hypotheses. Indeed, the idea that gene by environment relations are important to the establishment of psychiatric disorders has a rich theoretical background that must be taken into consideration when assessing a model’s validity (van der Staay 2006).

Another approach to environmental validity is to consider whether standardized housing appropriately models the conditions in which target species (humans and nonhuman animals) usually live. What usually is referred to as “standard housing conditions for rodents” is in fact barren environments that produce animals that are metabolically morbid, and the environments in which animals are reared lack sensory, cognitive, and motor stimulation (Burrows et al. 2011). This, of course, contrasts with the majority of humans who receive a wide range of sensory, cognitive, and motor stimulation throughout their lifetimes: “The implicit argument here is that the conditions under which laboratory rodents are kept are well below what any wild animal in its natural environment might experience and, having observed the dramatic effects of marginally enriched environments upon the brain chemistry of these animals, we cannot ignore the possibility that a brain which enjoys even some basal level of stimulation (such as a mouse with even minimal levels of enrichment and/or the majority of humans, and thus the target population we are attempting to model) may be predisposed to respond differently to the therapeutics which are being tested preclinically than mice housed under standard conditions” (Burrows et al. 2011, p. 1380).

Important experimental confounds can be thus introduced, reducing the internal validity of the model; moreover, a model that is applied to animals reared in impoverished environments lacks construct validity (Burrows et al. 2011). While concerns on behavioral variability generated by environmental enrichment, as well as increases in cost and space needs, are common difficulties in most research settings, it has been proposed (Burrows et al. 2011; McOmish et al. 2014) that

a secondary screen is added to the set of experiments in order to test whether a given intervention that was shown to have efficacy under barren housing conditions also has effects in animals housed under enriched environments.

### Convergent Validity

One important aspect of external validity, in the case of animal models, is **convergent validity** (Atanasova 2015). This refers to the ability of results to converge (or at least be compatible) with results obtained with different methods that measure similar traits. Most guidelines for reporting or conducting in vivo animal research make recommendations regarding convergent validity, insisting on replication in different models of the same disease (e.g., different transgenics, strains, or lesion techniques); independent replication by different researchers or, ideally, research groups; and replication on different species. For example, in behavioral genetics it is common to demonstrate that knocking out a given gene produces alterations in more than one behavioral model. In behavioral models with several dependent variables, convergent validity is harder to establish, since the variables do not necessarily measure the same underlying construct (see above). In that case, a variety of multivariate statistical methods can be used to establish the underlying factors/traits that are shared by different dependent variables across tests. Factor-analytical, hierarchical clustering, multitrait-multimethod tests, animal model arrays, and multidimensional scales are useful in that direction (Maximino et al. 2014).

Perhaps more important than convergent validity is the need to increase translational value, the ability of a given model to produce results that are translated to the target condition/disorder. While drug development is not the only aim of animal modeling, the success rates for drugs which move in the production pipeline from preclinical to clinical research remain low, despite important advances in the use of high-throughput approaches to target identification. Belzung (2014) identified four “drawbacks” in current model research that decrease translational value: lack of homological validity; lack of pathogenic validity; lack of refinement of preclinical



situations; and predictions from animal models not taken into account when translating findings to the target disorder. In addition to these limitations, the inability to translate has been associated with differences in treatment modalities, when delays to start treatments that are unrealistic in the clinic are applied in the model; when the dose range used in the model is unfeasible in the clinic due to toxicity or reduced tolerability; or when differences in the timing of testing exist between animal studies and clinical trials (e.g., by using acute versus chronic treatment). Important factors for pharmacological research include treatment initiation time, duration, and frequency, as well as endpoint evaluation time (Stewart et al. 2015). The lack of pathogenic validity, for example, can occur due to the induction of the disease in animals that are healthy when the disorder occurs mainly as a comorbidity; to the use of homogeneous groups of animals, when the disorder affects a heterogeneous group of patients; or to the use of male animals when the disorder occurs mostly in female patients. Most of these recommendations rely on knowing aspects of the disorder that are relevant to the model and incorporate epidemiological data on the model. Thus, the external validity of a model will largely be determined by disorder-specific factors.

### External Validity and Standardization

Recently, the low external validity of animal models, particularly in pharmacological research, has been thoroughly discussed, and solutions to increase it have been proposed. The need to standardize procedures has also recently extensively been discussed. One criticism was that task variations sometimes are introduced to study specific aspects of the disordered domain, and therefore using standardized tasks can preclude these specific uses. Stewart et al. (2015) made methodological recommendations for anxiety research that can be applied to a wider field. They recommend focusing on multiple endophenotypes or endpoints, expanding beyond the usual breadth of tests which are common for a disorder. Stewart and co-workers (Stewart et al. 2015) also recommend including a panel of outbred strains to increase “population validity,” considering the genetic variability of human populations. They

also recommend using “smart” test batteries and considering a wider spectrum of drug regimens beyond the “classical” acute and chronic treatments, including the addition of intermittent treatment, subchronic treatment, and early or late treatment initiation times and the introduction of delayed response evaluations (e.g., assessing results several weeks after treatment initiation). Finally, they recommend clarifying and rethinking “inclusion/exclusion criteria” by including anomalous data (e.g., outliers) in the analysis or considering the potential stratification of these data on the population’s responses to drug treatments.

Denayer et al. (2014) proposed introducing “clinical trial features” in animal research. They suggest, in consonance with Stewart et al. (2015), that assessing and reporting “negative” effects (pain, discomfort, dyskinesia, and other side effects) in preclinical research can improve the rate with which potential candidates are discarded before they progress in the pipeline. They also advocate adding predictive biomarkers for treatment responsiveness, such as pharmacogenomic data or peripheral biomarkers, as classifiers in the screening. Finally, they suggest that “reverse translation” is as important as other strategies to refine the model, as biomarker and endophenotype research in patients can inform further iterations of the model building and evaluation processes. Notice that these recommendations point to a feedback between external validity and predictive validity.

A final recommendation regards not the alteration or refinement of animal models but the addition of “nontraditional” stages in clinical trials by testing drugs in an experimental setting in patients. For example, startle reactivity, carbon dioxide sensitivity, and fear generalization have been shown to be altered in anxiety and trauma and stress-related disorders and can be used, in addition to classical tests, to study drug and/or gene effects in rodents (Hoffman 2016). Importantly, they can be used in human patients to test drug effects (Hoffman 2016). Thus, drug candidates that normalize the activity of these “back-translated” variables in animal models would be tested in human subjects using analogous test paradigms in addition to the clinical settings.

## Hypothesis-Free Model Building?

The focus on construct validity, with a strong theoretical basis, represents an important epistemological contribution, but does not necessarily cover everything that the scientists that use models and tests do. High-throughput techniques in neuroscience and biomedical research have produced a plethora of genomic and proteomic data which were not driven by a specific hypothesis and are rather exploratory in nature. These “Big Data” approaches include genome-wide association studies in animals and humans, microarray and RNA-Seq studies in animals, and other next-generation sequencing techniques. These strategies analyze thousands of genes or transcripts at the same time, in a “shotgun” approach to attempt to find polymorphisms that are associated with a disorder or genes that are up- or down-regulated after a given treatment or experimental manipulation. As a result, many potential targets which were not predicted by theoretical accounts appear.

In spite of the excitement that these studies generate, the pathophysiology of mental disorders is unlikely to be related to a mutation in one single gene, but rather to the effects in complex biological pathways which involve multiple interacting gene products (Kas et al. 2011). As a result, mechanistic and translational approaches to link the hits obtained using these high-throughput genomic/transcriptomic approaches and genome-wide association studies with relevant endpoints are necessary, even when the candidates were generated with these hypotheses-free approaches. Tactical approaches include the integration of multiple datasets from human and animal studies to identify converging evidence for the role of a given gene or pathway in that disorder (Kas et al. 2011).

While high-throughput genomic/transcriptomic approaches and genome-wide association strategies can certainly increase throughput, they are not without problems. While genetic validity is starting to figure as an important aspect of model building, using it as a starting point to develop a model does not preclude other aspects – including knowledge about species differences and context-specificity of behavioral strategies

that are used in a given test (Kas et al. 2009). While using an endophenotype can increase external and face validity because these units are more easily translatable between humans and non-human animals, the choice of a behavioral endophenotype is still subject to other aspects of construct validity, especially homological validity, as well as aspects of face and predictive validity. For example, it is not clear whether the elevated plus-maze is an adequate test for panic attacks, although it can more properly model the hyperanxious aspect of panic disorder. In that sense, prioritizing genetic validity as a starting point is a useful strategy but should be approached carefully in order not to fetishize the gene and forget other aspects of behavioral modeling.

One important limitation of these approaches is that starting from the gene(s) instead of the disorder often creates the need for exploratory research on a plethora of models. This difficulty has already been established in relation to the needs imposed by phenotyping research in genetically engineered mice: “This vast murine factory line (...) is demanding ever-faster analysis. And the answers are sought now, ideally in the form of easily set-up, easy-to-follow, standardized protocols with high test-validity and secure intra- and inter-laboratory reliability” (Crabbe and Morris 2004, p. 1175). The authors exemplify, with the water maze, a task that is used to assess spatial memory. Pressures toward standardization and automation of data collection exist and are justified by the need to increase throughput; however, variations of the task allow for the analysis of different aspects of spatial learning and memory, and some of these variations are labor-intensive and preclude a high number of replications. Again, whether a standardized, automated, high-throughput version of the task is ideal depends on its use.

This use of automated tests is sometimes lauded as an advantage; however, besides risking missing important variables, “the suggestion that automation is *per se* a good thing seems to be driven by the belief that automatically recorded data escape the influence of the experimenter. There are scarce data to support this idea” (Crabbe and Morris 2004, p. 1177). The important factor here should not be throughput, but the



appropriate interpretation of behavioral data “that is crucial to their validity” (Crabbe and Morris 2004, p. 1177).

In addition, “hypothesis-free” approaches have increased after the application of computational power to quickly solve multivariate statistical analyses, often in an exploratory fashion. Computerized tracking also allows for the decomposition of animal movement in terms of linear and angular velocity, turning frequency, formation of “homebases,” etc. As a result, the number of endpoints derived from a single animal increased dramatically, and some authors exploit that to produce multivariate analyses. For example, Cachat et al. (2011) exploited the three-dimensional character of fish movement and analyzed zebrafish swimming in a novel environment. The combination of manual and automated decomposition of swimming patterns produced 15 endpoints; these were evaluated after “anxiogenic” (repeated morphine withdrawal, alarm pheromone exposure, caffeine, belonging to a highly anxious phenotype) or “anxiolytic” (chronic ethanol, chronic fluoxetine, chronic morphine, acute nicotine) treatments, and the results assessed with hierarchical clustering analysis. The authors revealed that all anxiogenic treatments cluster together, while all anxiolytic treatments cluster together, based on their behavioral effects. Moreover, they also revealed two main behavioral clusters. This exploratory analysis, however, was not followed by confirmatory techniques and therefore should not be interpreted as revealing the underlying structure of zebrafish responses to novelty; moreover, the hypothesis-free character of the approach makes it difficult to understand specifically what each cluster or sub-cluster means in behavioral terms.

## Conclusion

Animal models are used to gain insight into studying brain-behavior relations under controlled conditions and to enable predictions about these relations in humans and/or a species other than the one studied or in the same species under conditions different from those under which the study was performed (van der Staay 2006). Animal

models need to be thoroughly developed and validated, keeping in mind the intended use of the model. The purposes of the model determine the set of validation criteria that it must fulfill. Although a “classical” set of criteria has been proposed by Willner (Willner 1984, 1986, 1991), new approaches have suggested extended sets of validation criteria (Belzung and Lemoine 2011; Maximino et al. 2010; McOmish et al. 2014; van der Staay et al. 2009). These criteria may also be applied for selecting an (established) animal model for neurobehavioral research.

## Cross-References

- [Animal Psychopathology](#)
- [Animal Welfare](#)
- [Behavior Modification](#)
- [Transgenic](#)

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## Animal Models of Autism

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### List of Abbreviations

|       |                                |
|-------|--------------------------------|
| ASD   | Autism Spectrum Disorder       |
| CSF   | Cerebral Spinal Fluid          |
| GABA  | $\gamma$ -Aminobutyric Acid    |
| mTOR  | Rapamycin                      |
| NHP   | Nonhuman Primate               |
| OFC   | Orbitofrontal Cortex           |
| OT    | Oxytocin                       |
| TD    | Typically Developing           |
| TSC   | Tuberous Sclerosis             |
| USV   | Ultrasonic Vocalization        |
| vmPFC | Ventromedial Prefrontal Cortex |

### List of Genes

CNTNAP2  
FOXP2  
FMR1  
GRIN2B  
NLGN  
NRXN  
SHANK2/3

## Introduction

In 2016, the Center for Disease Control and Prevention estimated that about 1 in 68 children in the United States have been diagnosed with autism spectrum disorder (ASD), corresponding to approximately one million individuals under the age of 21. The prevalence of ASDs increased sharply since the 1990s, though it is unclear whether this increase can be fully explained by to a true increase in incidence, as opposed to greater diagnosis or broader diagnostic standards. One of the current criteria for diagnosis of ASDs is that the symptoms must compromise normal daily function, either in terms of occupation and school, or in the maintenance of social relationships. As such, ASDs have substantial social and financial costs, costing an estimate of \$250–300 billion annually in the United States.

Effective pharmacological treatments for ASDs have remained elusive. Pharmacological interventions are used to treat comorbid symptoms of autism, such as anxiety and attentional deficits, but there are no currently approved drugs that will treat the core symptoms. One of the reasons for this failure is the lack of good animal models for the disease. Animal models of disease are crucial to drug discovery and development, as well as for a better understanding of the molecular, cellular, and network changes underlying the disease. To date, some animal models have been used to shed light on the neurobiological etiology of ASDs, or on the neurobiology of social behavior more generally, whereas others appear to capture crucial behavioral similarities and show promise for future ASD research.

True animal models of any disorder are defined by formal criteria, typically face, construct, and predictive validity. To achieve face validity, the animal model must have behavioral or biological markers associated with the disease. Examples of altered biological markers include disruptions in molecular pathways, neuronal wiring or computation, or anatomy. To achieve construct (or etiological) validity, the method used to recreate the disorder in an animal model must resemble genetic, developmental, and/or environmental causes of the disorder. That is, the etiology, or biological cause, of the disease is the same in

both the model and the afflicted individuals. Finally, the achievement of predictive validity signifies that the animal model responds to clinical interventions, such as pharmacological agents, in a manner that recapitulates the response of individuals with the disease.

Construction of ASD animal models that achieve all three of these criteria will be challenging, though incremental progress is being made. There is no known biological marker universal for all cases of ASD, so achieving biological face validity in an animal model is impossible. However, there are established animal models with behavioral face validity that are characterized by distinctive neurobiological abnormalities (e.g., synaptic dysfunction), which lead to the converse challenge of determining whether in individuals with ASD have similar deficits. Challenges also exist for construct validity: Though it is known that ASDs have a genetic component, genetic predispositions typically have small effects, and many different genetic mutations can be attributed to the disorder. There are also several possible candidates for environmental causes of autism, such as prenatal stress or infection, advanced parental age, or exposure to air pollution, but none of these has been unambiguously confirmed. Similar to these difficulties in face and construct validity, predictive validity of ASD in an animal model is currently difficult to achieve, as there are no available drugs that improve ASDs core symptoms.

Thus, crucial to any animal model of ASD is the achievement of face validity in the behavioral sense. This, too, poses a unique set of challenges, because ASD is extremely heterogeneous. Two individuals, both diagnosed with ASDs, could have completely different symptoms, with no overlap except that they broadly involve social deficits and repetitive behavior. Moreover, interpretation of ASD-like behaviors in nonhuman animals depends on the species-typical expression of those behaviors. For example, rodents rely heavily on tactile and olfactory information, whereas primates are heavily visual; and different species, even those that are closely related evolutionarily (e.g., prairie voles and montane voles), may exhibit vastly different social behaviors.

## ASD: An Overview

To meet the diagnostic criteria for autism according to the DSM-V, individuals must show both deficits in social communication and restricted and repetitive behavior. Deficits in social communication can present as an inability to abide by the unwritten rules that guide typical human social behavior. For example, we expect language to be more formal when addressing an authority figure, such as a teacher, than when addressing a friend during casual conversation. Voice volume modulation is expected according to context, such as in a library. Often individuals with ASDs have trouble interpreting tone of voice, body language, or facial expressions when communicating. They may have trouble understanding metaphors, figures of speech, or sarcasm, or have difficulty taking turns during conversation or indicating interest and social engagement during conversation using nonverbal cues. Individuals with ASD also fail to initiate joint attention, in which they draw another party's attention to an object or event of interest. Social deficits may or may not be accompanied by active avoidance of social interaction. Avoidance of social interaction in ASD can result from disinterest or anxiety, but some people with ASD display a so-called "active-but-odd" phenotype, in which atypical social communication accompanies strong pro-social behavior. Regardless, the typical individual with ASD has difficulty initiating and maintaining relationships. In extreme cases of autism, spoken language and communicative facial expressions may be altogether absent. For any of these symptoms, the onset occurs during childhood.

The second diagnostic criterion is the presence of repetitive behaviors and/or restricted interests typically found in autism. These can be manifested as repetitive motor behaviors (e.g., hand flapping), speech behaviors (e.g., echolalia, or repeating overheard words), or repetitive object behaviors (e.g., lining up or flipping toys). Individuals with ASDs often have rigid, inflexible behavior, insisting on sameness or rituals, and have trouble with transitions. ASD diagnosis can

also include restricted interests, highly focused and intense interests for particular topics or objects, such as trains or baseball statistics. Sensory sensitivity or under-reactivity can also be a diagnostic symptom of ASD, such as adverse reactions to sounds or light, excessive smelling or touching of objects, or indifference to pain or extreme temperatures.

For a diagnosis of ASD, these two major classes of symptoms are required to have arisen during childhood, and must cause significant impairment in everyday functioning, such as interference in occupation, school, or social relationships. ASD may or may not be accompanied by intellectual disabilities (previously termed “mental retardation”).

The diagnosis for ASDs thus allows for substantial heterogeneity in both severity and in presentation. An individual with ASDs may have extreme intellectual disability, or s/he may be a savant, with remarkable capacity for memory or knowledge. S/he may be unable to speak or otherwise communicate, or s/he may be typical, or even eloquent, in speech but “socially awkward.” Some individuals learn strategies for coping with their diagnosis, such that they learn to mask their symptoms as they get older. Others are severely debilitated, and require resource-intensive services throughout their lives.

This heterogeneity in those clinically diagnosed with ASDs parallels the heterogeneity of subclinical presentations of these symptoms among the typical population. For example, it is not uncommon for TD children typically to display repetitive or ritualistic behavior. Some adults are passionate, almost single minded, about their hobby interests, such as model trains or bird watching. Many typical adults have difficulty perceiving the nuances of conversation or body language. Subclinical, “autistic-like” traits in TD individuals have been termed “endophenotypes,” and are overrepresented among close relations of individuals with ASD. The clinical term “autism spectrum” refers to the broad spectrum of symptomatic severity present in ASDs, and may in fact be part of a larger spectrum of behavioral variance present in the typical population.

## Animal Models of Repetitive Behaviors

Repetitive behaviors in animals are enhanced by captivity. Lab rodents and non-human primates (NHPs) as well as a plethora of zoo-kept species, are known to move in stereotypic patterns. Incessant pacing, flipping, bar-biting, auto-grooming (self-grooming), and self-injurious behavior have all been described, though there is substantial variation across individuals. This behavior is presumably caused by anxiety and “frustration” at the inability to express species-typical behaviors such as foraging, allogrooming, and territory patrol, and can often be alleviated by environmental enrichment. Similarly, repetitive behaviors in ASD appear to be a coping behavior, and ASD individuals with high levels of repetitive behaviors have lower cortisol levels than those with low levels (Gabriels et al. 2013). Antipsychotics such as aripiprazole and risperidone decrease repetitive movement in ASD individuals, an effect paralleled in some stereotypic animals.

Commonly assessed repetitive behaviors in rodent and nonhuman primate models of autism include stereotypic motor movements, pacing, and auto-grooming (Silverman et al. 2010). Another assessment of repetitive behavior in rodents is a marble burying assay. Defensive burying in rodents, in which they use their forepaws and heads to displace bedding in order to cover noxious objects, is part of their normal repertoire of behaviors. Small, discrete aversive objects, including electrified prods, noxious food objects, startling stimuli, and predators or predator odor, are all known to elicit this behavior, though mice will also attempt to bury larger threats, such as live scorpions. Rodents will also bury marbles, despite the fact that marbles are not aversive to mice based on avoidance assays. Marble burying behavior is also not correlated with performance on assays of anxiety, suggesting that repeated displays of this behavior reflects perseveration, rather than anxiety (Thomas et al. 2009).

Behavioral rigidity and resistance to change are also hallmarks of ASD, and there are established protocols for measuring resistance to change in animals. Most prominent of these are the reversal

learning paradigms, in which the animal must inhibit previously rewarded behavior. For example, a rat or mouse will be placed in a t-shaped maze in which either the left or right arm is baited with a food reward while the other arm remains empty. Once the rat learns to travel down the arm containing the reward, the reward contingency changes, such that the baited and unbaited arms are swapped. The rat learns to suppress the previously rewarded behavior in favor of the rewarded arm under these new circumstances, and the rate of this learning, or the number of errors, serves as an index for behavioral flexibility. The evolution of reversal learning in animals was likely driven by neural adaptations for foraging in fluctuating environments. Foraging animals use their spatial memory and reward history to return to locations in which they previously found food, but, to avoid forgone foraging opportunities and unnecessary energy expenditure, there would be strong selective pressure to evolve the ability to override previous foraging patterns once the food in a patch was gone.

In humans, rats, and rhesus macaques, orbitofrontal cortex and amygdala lesions increase perseveration of the incorrect choice after reward reversal, suggesting a crucial role for these structures in behavioral flexibility (Rudebeck and Murray 2008). Some researchers propose that a lack of self-control and inappropriate behavioral updating are fundamental cognitive deficits in ASD, stemming from abnormal development of an OFC-amygdala neural circuit. In some subtypes of ASD, deficits in the ability to flexibly update behavior may underlie both an insistence on sameness as well as an avoidance of social interaction, which tends to demand cognitive flexibility. Notably, however, though deficits in cognitive flexibility are inarguably present in day-to-day activities, the performance of ASD individuals on laboratory measures of cognitive flexibility, including reversal learning tasks, is mixed, leading some to suggest that better tasks in humans are required in order to isolate the cognitive constructs underlying inflexible behavior. This finding also reduces the face validity of reversal learning task deficits in animal models.

## Rodent Models of Social Dysfunction

Summarized below are the main assays used to measure social phenotypes in rodents:

- **Reciprocal social interactions** – Decreased interactions, including nose-to-nose sniffing, anogenital sniffing, play behavior in juveniles, and close physical contact between two or more mice may indicate lower sociality in rodent models.
- **Social approach task** – Mice are placed in the central chamber of a three-chambered apparatus, with the peripheral chambers containing a novel mouse or a novel object. The time spent in the chamber containing the mouse is a measure of social approach.
- **Social preference task** – Mice are placed in an apparatus identical to that used in the social approach task, but the peripheral chambers contain a novel mouse or a familiar mouse. Typically mice spend more time in the chamber containing the novel mouse.
- **Partition test** – Mice are placed in a cage divided in half by a perforated plastic partition, with a social partner placed on the opposite side. Social interest is measured as the amount of time spent at the partition.
- **Social transmission of food preference** – Rats will typically develop food preferences for a particular flavor (e.g., cocoa or cinnamon), after interacting with a social partner that has consumed that flavor. Rats sniff the face and whiskers of the demonstrator rat and the smell of the consumed flavor combined with volatile chemicals in the demonstrator's breath, will induce a bias toward that flavor in the target rat when subsequently presented with a flavor choice task.

## Animal Models of Vocal Communication

Most mammalian vocalizations are produced instinctively, relatively unshaped by social learning. This is demonstrated in part by experiments with squirrel monkeys and rhesus macaques, which, when cross fostered, deafened, or reared



in isolation, still have normal vocal development. Many mammalian vocalizations, including those of rats and rhesus macaques, appear to be associated with different emotional states. Rodents emit various types of ultrasonic vocalizations (USVs), and aberrations or decreases in these vocalizations have been demonstrated in some genetic models of ASD. Newborn pups will emit a 40-kHz USV when their temperature falls beneath a certain threshold, typically after they've wandered away from the nest. Their vocalizations trigger retrieval behavior in the mother rat. Juvenile rats will also emit "rat laughter" during play bouts with other individuals or when being "tickled" by a human investigator. This type of vocalization is clearly associated with positive affect, as rats will actively approach and pursue an experimenter's hand after a tickling bout, and tickling can be used as positive reinforcement to drive instrumental learning. Adult rats will also emit 22 kHz alarm cries in the context of inescapable aversive stimuli, including during male-male aggression and social defeat. Despite the association of these various USVs with different emotional states, it is unclear what communicative function, if any, these vocalizations serve.

Adult mouse USVs are emitted during social interaction, especially mating, but do not seem to reflect the affective state of the animal. USVs of adult mice consist of various syllables with distinctive acoustic properties that are emitted in nonrandom patterns, similar to birdsong, though the function of these vocalizations is unknown.

In contrast to the innate vocalizations of rodents and rhesus macaques, birdsong is a model of human language in that it emerges during a critical period early in development, requires social learning, and is reliant on specialized brain structures (Panaitof 2012). Juvenile songbirds will learn the song to which they are exposed, usually their father's song, after hatching. During this critical period of song learning, young songbirds "babble," stringing together "nonsense syllables" that eventually form into a coherent song. Once the critical period of learning closes, the song is "crystallized," and learning is severely limited. Interestingly, at least two autism susceptibility genes have been found to be

associated with aspects of song learning in birds. One of these, contactin-associated proteinlike 2 (*CNTNAP2*), encodes a neural cell adhesion molecule that serves as a target of the language and birdsong-related transcription factor FOXP2. *CNTNAP2* is related to brain sexual dimorphism in the songbird and has transcription specific to birdsong neural circuitry (Panaitof 2012). A second gene, *FMR1*, has dynamic transcription, leading to an increase in production during the beginning of the sensorimotor practice stage of song learning. *FMR1* is the cause of fragile X syndrome, which has a high comorbidity with ASD.

A few other species, like baboons, vervets, and prairie dogs, have "referential" vocalizations, in which various vocalizations map onto different types of predators. Vervets respond appropriately to the different alarm calls: in playback experiments, they look up into the sky and run into the bushes in response to "hawk" calls, and go up into the trees in response to "leopard" calls. Young vervets are more likely to give inappropriate calls, suggesting that the function, if not the structure, of these vocalizations require learning.

Marmosets, small, new-world primates that live in family groups, appear to have "conversations," in which they take turns vocalizing. As in humans, younger animals are more likely to interrupt conversations than older animals. Human vocal turn taking develops extremely early, typically between 4 and 7 months of age, before the infant has full speech development. Marmoset turn taking increases at the equivalent point in development (Takahashi et al. 2016). Conversational turn taking is often difficult for individuals with ASD. Better characterization of marmoset social behavior, combined with the potential for genetic manipulation in this species, may make this animal a more heavily used model of ASDs in the future.

## Genetic Models of ASD in Mice

Familial and twin studies of ASD have established beyond doubt that ASDs are influenced by genetics, and many mutations that are risk factors for



ASDs have been identified (Abrahams and Geschwind 2008). However, this genetic contribution is not straightforward: There is no single gene known to be associated with all cases of ASD; thus, ASDs are as genetically heterogeneous as they are behaviorally heterogeneous. Scientists have identified genetic mutations in about 20% of ASD cases, but each known mutation individually accounts for only 1% or less of ASD cases. With the advent of genomic manipulation, knock-in, knock-out, and transgenic mouse models relevant to ASD have been developed, allowing for the exploration of the behavior and etiology associated with ASD risk genes. As with nonpsychiatric diseases, mice can be engineered to replicate human mutations, so as to facilitate the study of the biological and neural changes that result from this genetic change. These genetic manipulations are typically performed on mice that are all of the same background, i.e., are essentially clones of one another, in order to avoid confounds that would arise from polymorphisms elsewhere in the genome.

The study of many ASD-associated genetic mutations in mice has begun to shed light on the common pathways and mechanisms affected by disparate mutations. Many genes are implicated in synaptic changes, such as *SHANK2*, *SHANK3*, *NLGN*, and *NRXN*, which code for proteins that govern synaptic adhesion. Other ASD-associated genes, e.g., *GRIN2B*, influence excitatory neurotransmission, and glutamatergic signaling, inhibitory signaling, and the balance of the two, may be another mechanism giving rise to altered connectivity and ASD-like deficits.

Some diseases that result from known genetic deficits, such as Fragile X Syndrome and Rett Syndrome, are highly comorbid with ASD. In some of these syndromes, the molecular pathways are relatively well defined, for example, the rapamycin (mTOR) signaling pathway in the case of tuberous sclerosis (TSC), and synaptic dysfunction in Rett Syndrome and Fragile X. TSC provides a good example of how mice containing a mutation for a syndrome known to be associated with ASD can shed light on the etiology of the disease. Tsc proteins regulate cell growth and axonal, dendritic, and synaptic

development and function. Individuals with TSC have the classical cortical tubers throughout the brain, as well as disorganized white matter tracts and aberrant synapse formation (Jeste and Geschwind 2014). Knockout mice with damage to the *TSC* genes have shown various cognitive deficits, including impairments in social interaction and repetitive behaviors and vocalization (Tsai et al. 2012). These mouse models provided the means by which to examine the larger molecular pathway influenced by *TSC* mutations, as well as the identification of a class of molecules that regulate the *TSC*-related pathways, mTOR inhibitors. mTOR inhibitors were found to rescue the cognitive and social impairments in knockout mice, and are now in clinical trials for patients with TSC.

## Environmental Models of ASD

Unlike syndromic cases of ASD, such as TSC, ASD is in many cases likely to result from an interaction between a genetic susceptibility and some environmental feature. The identification of environmental causes of ASD is still very much uncertain at the time of writing, but there is substantial evidence that most environmental insults leading to ASD occur prenatally. As a developmental disease, exposure to an environmental risk factor may have to overlap with a particular developmental stage, such as neural tube closure, in order to result in ASD. Potential environmental contributors to ASD include prenatal maternal stress, infection, and exposure to traffic-associated air pollutants.

### Valproic Acid

A useful environmental animal model of ASD is prenatal sodium valproate (VPA) exposure. VPA is an anti-epileptic and a mood stabilizer. If taken while pregnant, it triples the risk of having a child with ASD (Kazdoba et al. 2016). In mice and rats, in utero exposure to VPA causes altered social behavior in many assays of social behavior in mice and rats including decreased juvenile play and social exploration of a stranger (Kazdoba et al. 2016). Maternal VPA also induces repetitive

behaviors in the offspring, including increased motor behavior in the cage, stereotyped behavior, self-grooming, perseveration on a y-maze, increased marble burying, and decreased ultrasonic vocalizations. Interestingly, exposure to valproic acid transiently increases the transcription of Pax-6, a transcription factor implicated in the differentiation of glutamatergic cells, leading to increased expression of glutamatergic proteins. This observation is consistent with the ASD-like phenotypes observed during optogenetic interruptions in excitation/inhibition balance in mice (Yizhar et al. 2011), as well as with ASD risk genes associated with glutamatergic signaling (e.g., GRIN2B).

### Maternal Immune Activation

Epidemiological studies have linked maternal infections during pregnancy and ASD: Maternal infections of rodents induces ASD-related behavior in the offspring, including altered USV emission and impaired nest-seeking in pups, reduced social exploration in a three-chamber test, reduced social USV emission in adults, and a variety of repetitive behaviors, including self-grooming and marble burying. The effect of maternal infection seems to depend on the time of infection, with infections around the time of neural tube closing having the most reliable effects. Interestingly, the deficits seem not to be caused by the infection *per se*, but to the immune response to the infection. Introduction of nonpathogenic molecules such as poly-inosine:cytosine and lipopolysaccharide, which are nonpathogenic but evoke an immune response, are also effective in recreating ASD phenotypes in mice (Servadio et al. 2015).

### Neural Network Substrates of Social Behavior

Human interest in visual social information is adaptive, and the compromise of this social motivation and attention, as occurs in ASDs, is pathological. The kinds of adaptive social behaviors expressed by each species vary. In rodent models of ASD, rats and mice are assessed as having decreased social interest by exhibiting decreased reciprocal social interaction, such as sniffing and

following; lower exploration of another rat or mouse in a choice task; and/or decreased social play. In contrast, NHPs are primarily visual, rather than olfactory, and are capable of performing a large number of trials in highly controlled, visually guided choice tasks. A disproportionately large area of the primate brain performs visual computations, with over 30 dedicated regions devoted to visual processing. Many of these regions are specialized to process social information. Accordingly, primates also have specializations to send social information, including elaborate facial muscle specializations in the eyes, brow, cheeks, and lips with which to produce a wide range of facial expressions.

Based on patterns of cellular distribution and morphology, NHPs have subregions of frontal cortex that are orthologous to those in humans which are either absent or undifferentiated in rodents. The so-called “social brain” in humans is comprised of a network of areas highlighting the temporoparietal junction, anterior cingulate, fusiform face area, ventromedial prefrontal cortex, orbitofrontal cortex, and amygdala (Tremblay et al. 2017; Watson and Platt 2012a). Importantly, these regions have been found to be altered in fMRI studies of individuals of autism, as well as integral to social cognition in TD humans.

The face is a powerful social cue, and individuals with ASD fail to utilize this cue to its full extent. Both rhesus macaques and humans have face-selective regions required for face recognition in the temporal cortex, as identified by fMRI, and recording from rhesus macaques in these patches reveals that nearly 100% of the neurons in these regions are responsive to faces (Tsao et al. 2006). Individuals with ASD have deficits in their ability to remember and discriminate facial identities, and activate their amygdala and fusiform gyrus less than controls during facial emotion recognition tasks (Harms et al. 2010).

In particular, viewing others' eyes yields rich and dynamic social information. When presented with face images, TD individuals spend a disproportionate amount of time looking at the eye region. This is also true for NHPs including chimpanzees and rhesus macaques. In contrast, ASD

individuals avoid eye contact. Eye tracking studies show that individuals with ASD have fewer fixations in the eye regions; Infants who later develop ASDs exhibit declines in eye contact during 2–6 months of age; and performance of ASD individuals on the classic “reading emotion from the eyes” test, in which participants report the emotion being expressed based on images cropped to reveal only the eye regions, is compromised relative to TD individuals. This lack of a bias to look at the face and eyes deprives individuals of ASD of a rich source of social information.

Typically, TD individuals reflexively orient toward social information and attach value to this social information. That is, they find social information rewarding. One theory of autism is that social motivation deficits are at the root of social impairment (Chevallier et al. 2012). If children are not motivated to preferentially attend to social stimuli early in development, as are TD children, then they will not develop the expertise necessary for subsequent elaborations and refinement of various social skills (Chevallier et al. 2012). The social motivation network includes the orbitofrontal cortex (OFC), ventromedial prefrontal cortex (VMPC), striatum, and amygdala, structures which interact to compute the value of environmental stimuli and guide attention accordingly (Chevallier et al. 2012). Functional differences in this network correlate with individual difference in social motivation (Chevallier et al. 2012). Evidence for decreased social motivation in ASD include the core diagnostic criteria of early (<1 year) decreased orienting toward one’s name, social aloofness, and decreased eye contact, as well as eye tracking results showing fewer fixations on social vs. nonsocial objects when viewing images and movies. Moreover, ASD individuals have diminished preference and attention toward social sounds, including speech, vs. nonsocial sounds (Chevallier et al. 2012).

Electrophysiological studies in rhesus macaques shed some light on the role of cortical neurons in the processing of socially motivated behavior. Single cells in the OFC were recorded while monkeys performed a task designed to measure the NHP’s preference for various social

images and juice rewards. This revealed that neurons in the orbitofrontal cortex, which had previously been shown to encode subjective preference for various rewards, consists of spatially intercalated sets of individual neurons that respond preferentially to the receipt of social rewards or juice rewards (Watson and Platt 2012a). Recordings from other areas using the same behavioral paradigm exemplified the diversity of neural computation across the brain. In the lateral intraparietal region, neurons signaled the value of both social and juice rewards only when the assessment influenced the animal’s visual orienting decisions, thus establishing this region’s importance for motivated visual attention. Finally, neurons in the striatum signaled information about the type of reward, social vs. juice, without encoding the animal’s preferences for these rewards (Klein and Platt 2013).

Other experiments on NHPs that require the animals to make decisions that influence both itself and another animal are similarly revealing. Importantly, rhesus macaques were shown to derive reinforcement from the reinforcement of another animal, a phenomenon termed “vicarious reinforcement.” This is a type of emotional contagion, thought to be a precursor to empathy. Probing the frontal cortex in conjunction with the vicarious reinforcement task revealed that different subregions encoded different aspects of the task, with OFC encoding the amount of reward being delivered to one’s self, but not to another monkey, and with neurons in the anterior cingulate sulcus encoding forgone rewards, delivered to another monkey or to no-one, but not to one’s self. On the other hand, neurons in the anterior cingulate gyrus encoded rewards delivered to one’s self, to another monkey, or to both monkeys simultaneously, suggesting a shared role in vicarious and direct reinforcement (Chang et al. 2013).

## Multisensory Integration and ASD

Sensory processing dysfunction is common across the ASD spectrum, with 95% of children with ASD reporting sensory hyper- or hypo-responsiveness. These manifest as deficits in

unimodal sensory processing, including in the auditory, visual, and tactile domains, as well as in multisensory integration, in which multiple modalities are recruited simultaneously. Integration of information across modalities is particularly important for speech perception. Binding together auditory and visual information in a noisy environment, for example, while participating in adult conversation at child's birthday party, confers substantial increases in speech comprehension. The addition of visual information to auditory information during speech perception is equivalent to increasing the volume of the auditory information by 15 db. Impairments in multimodal integration, even if they stem from relatively low level sensory deficits, can potentially disrupt higher order cognitive processing, particularly social processing. For example, relative to TD individuals, children with ASD have decreased temporal binding of audiovisual speech cues, and the extent of this binding deficit in ASD individuals is predicted by the acuity of temporal binding during low-level, non-speech audiovisual stimuli (flashes and beeps) (Stevenson et al. 2014).

Audiovisual binding is represented in single neurons, as evidenced by studies in the rhesus macaque. When rhesus monkeys are shown videos of other monkeys making vocalizations, responses in primary auditory cortex neurons are enhanced when the visual information co-occurs with the auditory information within a certain time window, around 70–100 ms. In contrast, longer time intervals between the onset of visual and auditory information (around 200–330) leads to suppression of neuronal firing in the primary auditory cortex (Ghazanfar et al. 2005). The neural enhancement of integration seems to be specific to social stimuli, as pairing the vocalization with a movie of a black disk mimicking the dynamics of the mouth movement did not generate the same neural enhancement that occurred when viewing a movie of a monkey face vocalizing. This study demonstrates that neurons in the auditory cortex are capable of recruiting visual information during vocalization representation, and suggests that low-level sensory processing difficulties are likely to interfere

with speech-related brain signals in ASD. Far from being a property unique to primary sensory cortex, however, multisensory integration is a feature seen throughout the cortex. Therefore, a cellular or network change that interferes with global multisensory integration in ASD could account for a wide variety of ASD features.

## Oxytocin, Social Behavior, and Autism

Oxytocin is a neuropeptide that orchestrates mammalian behavior related to reproduction, parental care, and social affiliation. It is produced in the hypothalamus and circulated both throughout the brain and, via the pituitary, released in the body. In the brain, oxytocin binds to nerve cells through specialized receptors. Animal models are crucial to understanding the mechanisms of OT on behavior, as central OT release can only be measured invasively. Oxytocin regulates the so-called “ $\gamma$ -aminobutyric acid (GABA) switch,” in which neurotransmitter GABA shifts from excitatory to inhibitory around the time of birth. Several studies have identified genetic variations within the oxytocin pathway that are associated with autism and autism-related endophenotypes. Oxytocin is also under investigation as a biomarker for autism, as oxytocin plasma levels seem to correlate with either autism or with social impairments more generally. Manipulation of oxytocin has positive effects in many rodent models of ASD, either by correcting social deficits, restoring peripheral oxytocin levels, or reinstating the GABA switch (Peñagarikano 2017). These animal studies are corroborated by human studies that relate intranasal delivery of OT to ASD individuals to positive effects on social behavior, as measured by recognition of affective speech, Reading the Mind through the Eyes test, social cooperation and social selectivity in an online ball playing game, and enhancing attention to the eyes and face of others (reviewed in Stavropoulos and Carver 2013). However, many of these studies have been acute, single dose studies of OT, and the effect of long-term dosing of OT on individuals with ASD is currently under investigation as of 2018.

Early studies of oxytocin in sheep demonstrated the importance of this molecule in establishing a bond between parent and offspring. Sheep mothers strongly and selectively bond to their own offspring and reject foster offspring. The identity of their offspring is mediated by olfactory cues shortly after birth, and central infusion of oxytocin in absence of parturition is sufficient to cause a hormonally primed ewe adopt a foster lamb (Keverne and Kendrick 1992). Peripheral OT levels in human parents are associated with stronger bonding, greater contact, and higher synchrony between parent and child (Feldman and Bakermans-Kranenburg 2017).

In addition to being crucial to the establishment of the parent-child pair bond, oxytocin and the closely related neuropeptide vasopressin are also known to facilitate pair bonds between mates. Prairie voles, which are monogamous, and montane voles, which are promiscuous, are closely related rodent species. When housing captive mated pairs, prairie voles huddle in close proximity with their partner, whereas montane voles typically sit in opposite corners of the cage, maximizing the distance between individuals. As with mother/offspring bonding in sheep, a female prairie vole's attachment to her mating partner is mediated by oxytocin. When oxytocin is infused into the central nervous systems of female prairie voles, it creates a partner preference for male voles even in the absence of mating. The partner preference does not occur when the oxytocin infusion is paired with the delivery of an antagonist blocking the oxytocin receptor.

OT also appears to play a role in human romantic relationships. OT levels are higher in individuals in new romantic relationships than in singles, and OT levels correspond to overall relationship satisfaction. However, OT levels do not unambiguously correspond to relationship bliss in all contexts. For example, OT has also been associated with relationship stress and anxiety. It is clear that OT influences human pair bonds, but the way in which it does so is complex and not completely understood.

NHPs offer an important model to study the delivery, mechanisms, and behavioral effects of exogenous oxytocin. In male marmosets, a new

world monkey that exhibits biparental care, intracerebroventricular infusion of oxytocin reduces the rate of refusal to share food in response to juvenile offspring begging (Saito and Nakamura 2011). Exogenous oxytocin also seems to facilitate pair bond formation in marmosets, as intranasal oxytocin administration increases huddling behavior with their social partners (Smith et al. 2010).

Because peripheral applications of oxytocin probably do not reach the CNS, most clinical trials of OT for ASD rely on intranasal administration of OT. Studies on rhesus macaques show that intranasal applications delivered via nasal spray or nebulizer both influence cerebral spinal fluid (CSF) OT levels, whereas only nebulizer OT delivery alters plasma OT levels. Knowledge of the physiological differences arising from differences in OT delivery methods will be crucial for the development of an OT-based ASD intervention.

When combined with visual decision making tasks, the application of OT allows researchers to precisely assess how increases in central oxytocin levels affect the attention and preferences of NHPs with respect to social stimuli. For example, intranasal OT influenced behavior in a task that allowed a monkey to choose between targets that would deliver juice rewards to either himself, to another monkey, or to no one (an empty beaker). When the choice is between another monkey and an empty beaker, monkeys show enhanced rates of choosing to deliver reward to the other monkey after OT administration, as well as increased attention toward the other monkey (Chang et al. 2012). On the other hand, when choosing between juice delivery to another monkey and one's self, OT delivery increases the number of selfish choices. Oxytocin has also been shown to influence rhesus performance on a social attention task. As in humans, oxytocin in rhesus macaques increases the amount of attention to faces and eyes (Ebitz et al. 2013). It also increases vigilance for dominant individuals, a threatening social stimulus, though it does not change attention toward nonthreatening social stimuli, such as subordinate individuals or reproductive images (Ebitz et al. 2013).



Rhesus macaques also provide the opportunity to study the relationship of early life experiences and OT variations or manipulations with ASD related behaviors. Peer reared macaques that have been deprived of maternal care have lower CSF OT levels, and these are associated with reduced pro-social behavior, increased aggression, and increased stereotypic behavior (Winslow et al. 2003). Performance of male infant macaques on a face recognition task predicts endogenous central OT levels, but not peripheral OT levels, up to 5 years after the assessment (Madrid et al. 2017). Oxytocin application enhances working memory and social gaze tracking in male, but not female, infant macaques (Simpson et al. 2017).

### Advantages and Disadvantages of Different Models

Different animal species have different costs and benefits as models of ASD. First and foremost, mouse models offer superb genetic malleability. However, genetic techniques currently under development may soon make it easier to produce genetic models of ASD in other species, including NHPs such as marmosets and rhesus macaques. Other advantages of mice include their short developmental time courses, allowing for high throughput; their smaller size and less expensive housing and husbandry demands; and the relatively established assays for general health and intact sensory abilities, which are a prerequisite for testing downstream cognitive faculties. Many researchers argue that rodents have the key brain structures relevant to ASDs, including the amygdala and hippocampus, cerebellum, and basal ganglia. Finally, mice and rats, along with rhesus macaques have a long history of use as a biological model, resulting in a rich literature of the molecular and neurobiological substrates of their behavior and physiology. This literature is not as deep for less commonly used species, including birds and voles.

NHPs as animal models of ASDs are less practical than mice, but offer some important benefits (Watson and Platt 2012b). As noted above, rhesus

macaques can perform visual decision making tasks that allow researchers to rigorously determine the effects of social stimuli on the behavior of the animals. Importantly, these tasks can often be designed to be similar or identical to those employed in humans, offering unparalleled face validity. Many of these tasks rely heavily on the highly developed visual sense of primates, which is in contrast to the emphasis on olfaction found in most other mammals. NHPs display similarities to human social behaviors that most rodents lack, such as group living, dominance hierarchies, alliance and coalition formation, consortships, and intergroup warfare. Humans and NHPs share neural specializations common to the primate order, such as an expanded frontal cortex, that may be critical to the etiology of ASD. Rodents, lacking this fine differentiation of frontal cortex, may provide only part of the answer.

### Conclusion

Animal models reflect many ASD-related phenotypes relating to both social and repetitive behaviors. Genetic and environmental alterations in mice have revealed important hypotheses about the neurobiological underpinnings of ASD, such as excitation/inhibition balance and alterations in neural connectivity and synaptic structure. At the same time, studies in the rhesus macaque continue to yield a rich literature about the primate-specific neural circuits in the temporal and frontal lobes that are affected in ASD. Other species-specific cognitive specializations provide excellent models for domains of affected behavior in ASD, such as songbirds for language development, and marmosets for parenting and vocal turn-taking behaviors. Because ASD is heterogeneous in presentation and etiology, it will take many different animal models to understand, and ultimately treat, the disorder.

### Cross-References

- [Attachment](#)
- [Bennett G. Galef](#)

- Emotional Contagion
- Empathy
- Face-Selective Neurons: Comparative Perspectives
- Joint Attention
- Oxytocin
- Plathyrrhine Vocal Communication
- Primate Communication
- Roles of Medial Prefrontal Cortex Activity in Human and Animal Social Learning
- Social Learning

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## Animal Movement

### ► [Locomotion](#)

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## Animal Progression

### ► [Locomotion](#)

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## Animal Psychopathology

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## Synonyms

[Animal models](#); [Behavioral disorders](#); [Mental disorders](#); [Nonhuman](#)

## Introduction

Historically, there has been much debate surrounding whether animals can be used to study psychopathological syndromes that occur in humans. It has been argued that many mental illnesses are uniquely human and that it is not possible to study mental disorders in nonhumans due to their lack of ability to communicate through speech. However, it is now widely accepted that not only do animals experience various psychopathological syndromes similar to those observed in humans, but they can also be used as a model to study mental disorders in humans. For the past few decades, researchers have been able to use animal models to study disorders such as anxiety, depression, schizophrenia, and OCD. Analysis of animal behavior, neural circuitry, brain activity, and response to pharmacological compounds provides valuable information on these disorders, which may shed light on the disorder in humans. Given the subjective nature of many important symptoms of these disorders, however, it has proven very difficult to model human psychiatric disorders in animals. Perhaps the first person to study emotion in animals was Darwin, although his studies were limited solely to the expression of normal emotions (Walker 1991). Pavlov was the first scientist to propose that animals can be used to study psychiatric disorders that occur in humans. Pavlov's conditioning studies that demonstrated that dogs could learn to use a neutral cue to predict a biologically relevant event would eventually shed light on the development of PTSD and anxiety disorders in animals and humans (VanElzakker et al. 2014). Research on animal models of psychopathology increased drastically during the early-to-mid-twentieth century, and much of the work was concerned with schizophrenia and neurosis.

Much of the controversy surrounding the use of animals to model psychopathology in humans stems from the difficulty in proving these models as valid, due to the reliance on the *diagnostic and statistical manual of mental disorders* (DSM)/*International Classification of Diseases* (ICD) as a conceptual framework to diagnose

psychiatric disorders. Many of the symptoms used to diagnose psychiatric disorders in humans (e.g., delusions, hallucinations, thought patterns, obsessions) cannot be reliably ascertained in animals. Certain behavioral patterns can be observed, which may allow scientists to approximate these symptoms in animals, but this process is by no means exact. Many scientists have discussed the challenges surrounding the construction of valid animal models, and the majority of them have utilized a hierarchical list of criteria introduced by Paul Willner to assess the validity of animal models of depression (Kaffman and Krystal 2012). These criteria include face validity, predictive validity, and construct validity (Willner 1984). Face validity refers to the model's ability to demonstrate specific behavioral, biochemical, and anatomical features of the human disorder. Predictive validity refers to the ability of the model to behave similarly to humans in response to different clinical interventions. Construct validity refers to the model's ability to demonstrate some characteristics of the underlying pathophysiology. Perhaps the biggest challenge for establishing animal models with construct and predictive validities is the absence of reliable genetic markers or pathognomonic pathological lesions (Nestler and Hyman 2010).

Scientists have been able to generate animal models of psychiatric disorders using a variety of methods: genetic engineering, selective breeding, brain lesions, environmental manipulations, optogenetic manipulations, and administration of pharmacological compounds. When developing these disease models, particular biochemical pathways, proteins, or neural circuits may be altered, which presents a challenge to scientists in determining whether the disease model is simply a phenocopy, or whether it truly models a human disorder with useful implications for understanding the pathophysiology and developing treatments. The ultimate goal of an animal model should be to demonstrate similarities with humans in terms of the symptoms, etiology, therapy, and prevention of the disease. Often, it is not possible for the animal model to demonstrate similarities in each of these criteria, so the development of mini-models is a popular method to study a particular

aspect of a disorder (Book). Mini-models are behavioral phenomena studied in animals that may shed light on either the symptoms, etiology, therapy, or prevention of the disorder in humans. Mini-models usually do not account for all symptoms of a disorder, but may still prove useful in studying certain aspects of the disorder. The psychiatric disorders that have been most widely studied using animal models include depression, anxiety and related disorders, schizophrenia, and bipolar disorder.

### Animal Models of Depression

Although recent advances in technology have allowed for a deeper understanding of the disruption in neural circuitry, as well as the neuroendocrine and neurochemical disturbances underlying depression, none of these biomarkers have proven to be sufficient in diagnosing depression in humans nor in validating existing animal models (Krishnan and Nestler 2008). However, depression is often characterized by overstimulation of the hypothalamic-pituitary-adrenal (HPA) axis, and although this abnormality is not always observed in humans with diagnosed depression, it is useful in producing animal models of depression. In humans, the DSM is used to diagnose depression based on a cluster of highly variable symptoms, including irritability, guilt, suicidal thoughts, ruminations, and anhedonia. With the exception of homeostatic symptoms, anhedonia, and psychomotor behaviors, the majority of symptoms used to diagnose depression cannot be objectively measured in animals (Nestler and Hyman 2010). Because animal models cannot perfectly replicate human psychopathology, different models may prove more useful depending on the question being asked and the nature of the experiment (McKinney 1984). For example, scientists who are testing the clinical effects of a pharmacological compound, and scientists studying the behavioral and neurobiological components of depression, will likely use different models. In the case of testing the clinical effects of a new compound, the primary concern is the empirical validity of the model in predicting

the therapeutic efficacy of the drug, while the behavioral similarity of the animal model to humans becomes secondary.

Various methods are used to generate animal models of depression. It is known that stress and emotional losses are potent risk factors for depression, and different chronic stress paradigms have been utilized to produce a level of construct validity. One of the most common ways to administer chronic, unpredictable physical stress is to subject normal animals to repeated physical stressors over a period of weeks, or even months. These physical stressors may include electrical shocks, physical restraints, or extreme temperatures. Following periods of chronic physical stress, animals show anhedonia, which may be reversed by chronic administration of antidepressants (Willner 2005). Another way to model depression in animals is to subject them to chronic social defeat stress. When animals are subjected to repeated bouts of social subordination, they begin to display depressive symptoms such as anhedonia and social withdrawal, which may be reversed by chronic administration of antidepressants (Krishnan et al. 2007). Generating rodent models of depression through chronic social defeat stress may be advantageous to models generated through chronic physical stress. Chronic social defeat induces a metabolic syndrome in rodents which results in weight gain, as well as insulin and leptin resistance, which is consistent with homeostatic abnormalities seen in humans with depression (Chuang et al. 2010). Additionally, some rodents fail to develop symptoms of depression when exposed to chronic social defeat, which provides scientists for a model to study resilience to depression. Another model of depression that has shown a high amount of construct, face, and predictive validity is generated through early life stress. Rodents exposed to significant stressors early in their life, such as maternal separation, experience chronic neuroendocrine and behavioral abnormalities, some of which may be reduced through chronic administration of antidepressants (Meaney 2001). It has also been found that anhedonia can be induced in adult rodents which are socially isolated, and antidepressants can be effectively used to treat this effect (Wallace et al. 2009).

When analyzing the validity of different animal models of depression, it is very important to consider the means with which depressive symptoms are being induced. For example, the learned helplessness, forced swim, and tail suspension tests all involve exposing normal rodents to short-term stressors (Maier and Watkins 2005). This model may not provide useful information for translational studies, as depression in humans arises from a combination of underlying genetic vulnerability as well as exposure to chronic environmental stressors. Measuring certain depressive symptoms in rodents can be fairly straightforward. The two symptoms which are most commonly tested in order to measure the validity of an animal model of depression are anhedonia and homeostatic symptoms (Willner 2005). Anhedonia can be measured by observing the animal's interest in partaking in pleasure-inducing activities, such as engaging in social or sexual behaviors or showing a preference for a sucrose solution over plain water. However, with the sucrose preference test, there are a few issues to consider when designing the experiment. First, the concentration of sucrose should be taken into account, and if the concentration of sucrose is too high (>10%), rodents exposed to chronic stress may still prefer the sucrose solution over water. Also, there has been some concern over the use of sucrose as an alternative to water, as sucrose has a much higher caloric content and may be preferred by the rodents regardless of their exposure to stress. To address this issue, some researchers use saccharin as opposed to sucrose. While much progress has been made in the study of psychopathology and animal models of psychopathological syndromes, it is still far from an exact science, and there is still much progress to be made (Overstreet 2011).

## Animal Models of Anxiety

Fear and anxiety are emotions that have been evolutionarily selected for and which possess great adaptive value for organisms. Fear is an emotional response to a specific threat, while anxiety is an emotional response to a threat

that is unknown (Graeff and Guimarães 2012). Experiencing anxiety is normal and evolutionarily adaptive, but anxiety disorders can be quite pervasive and affect an individual's performance in everyday activities. As with animal models of all psychiatric disorders, animal models of anxiety do not replicate every aspect and symptom of anxiety disorder in humans. Rather, researchers attempt to generate a general state of anxiety in animals which may be related to anxiety disorder in humans (Lister 1990). In rodents, a state of anxiety may be produced by exposure to conflict situations generated by opposite motivational states which arise during approach-avoidance situations (Campos et al. 2013). For example, approach behaviors may be observed during conditioned responses in which a rodent is taught to seek or approach a certain object or location. It can also be observed when placing a rodent in a new environment, as rodents possess a general, unconditioned exploratory drive. Likewise, avoidance behaviors may be conditioned or unconditioned. Conditioned avoidance behaviors can be induced by pairing a neutral stimulus with a punished response such as an electrical shock. Examples of unconditioned avoidance behaviors include a rodent's aversion to brightly lit, open, and elevated locations. Animal models of anxiety that measure unconditioned conflicts are defined as ethological, while models that measure conditioned responses are defined as conditioned operant conflict tests.

The basic premise of ethological models is to study an animal's unconditioned behavioral responses when exposed to a new environment, which causes feelings of curiosity and fear. One of the most popular animal models of anxiety is the elevated plus maze (EPM). In this process, an elevated, plus-shaped apparatus with two open and two enclosed arms is raised aboveground level. This model is based on the rodent's general aversion to open spaces, as well as their natural curiosity and tendency to explore novel environments. This induces a behavior known as thigmotaxis, or remaining close to the edges of bounded spaces. This behavior results in the rodents remaining in the enclosed arms portion of the apparatus (Pellow et al. 1985). Confinement to

the enclosed portion of the apparatus in turn induces certain physiological responses characteristic of stress response, such as increased corticosteroid levels as well as increased defecation (Pellow and File 1986). However, administration of benzodiazepines alleviates these symptoms and results in the rodent's exploration of the rest of the apparatus. It is also important to note that several factors may affect the behavior of rodents in the EPM, such as prior exposure to stress, rodent species, lighting levels, familiarity with the maze, and the presence of the experimenter. Modified versions of the EPM exist which attempt to address these factors, among them including the elevated zero maze (EZM), the elevated T-maze (ETM), and the light-dark box.

The conditioned operant conflict test was developed by Geller and Seifter and demonstrates high predictive validity for classic anxiolytic drugs (Geller 1960). In this test, rodents are trained to press a lever to obtain a sugar-sweetened drink at variable intervals. They are deprived of food for 24 h, and during the test session, a signaling stimulus indicated that pressing the lever will now be accompanied with an electric shock, as well as the sugary drink. This induces an approach-avoidance conflict between receiving the sugary drink and getting shocked. The control rodents are observed to press the lever less often, whereas administration of an anxiolytic causes the rodents to press the lever more frequently. However, administration of opioid agonists such as morphine does not affect the frequency of lever-pressing, so it is clear that this effect is not due to antinociception (Millan and Brocco 2003). In 1971, John Vogel introduced a similar version of this conflict test, in which mice were deprived of water for a 24-h period and trained to locate a source of water in a box (Vogel et al. 1971). The following day, the mice were placed in the same box with a steel flooring which delivered an electrical shock to the mice every 20 licks of the water bottle. Administration of anxiolytic drugs results in the mice licking the water bottle with increased frequency. Both versions of this conflict test have high predictive validity for benzodiazepines and barbiturates, but Vogel's version of the conflict test also

responds to some non-anxiolytic drugs (Millan and Brocco 2003). Additionally, administration of antidepressants produces inconsistent results. For example, long-term administration of monoamine oxidase inhibitors and tricyclic antidepressants increases the frequency of punished responses, but administration of SSRI's such as fluoxetine does not (Scheffe et al. 1989). While both versions of the conflict test possess high predictive validity for anxiolytic drugs, Vogel's version of the test has the advantage of avoiding a prolonged training period.

Another animal model that scientists use to study anxiety disorders is the fear-conditioning model, which is a form of Pavlovian conditioning. Pavlovian conditioning describes an associative learning process in which a neutral stimulus (NS) is repeatedly paired with an unconditioned stimulus (US). After successful conditioning, the neutral stimulus alone can now elicit a biological response in the animal and is now known as the conditioned stimulus (CS). Fear conditioning involves the organism's association of a neutral stimulus, such as a flash of light or a sound, with an aversive stimulus, such as an electric shock. After repeated presentation of the NS with the aversive stimulus, the neutral stimulus alone can produce a fear response in the organism and is now known as the conditioned stimulus. Fear conditioning can be successfully performed in several organisms, including humans (LeDoux 2000). The organism's response to the conditioned stimulus during fear conditioning is usually characterized by freezing, increased heart rate, and increase release of stress-related hormones (Rudy et al. 2004). Animal models of anxiety produced through fear conditioning involve the animal undergoing psychological stress without any physical stimulus. As such, they are valuable models for studying anxiety-related disorders such as panic disorder and post-traumatic stress disorder (PTSD) (Mineka and Oehlberg 2008). Fear-conditioning models have high predictive validity when it comes to anxiolytics and antidepressants. Administration of benzodiazepines or SSRIs to rodents after acquisition reduces the amount of freezing when exposed to the conditioned stimulus, which agrees with clinical

findings that these drugs can be used to decrease symptoms of anxiety disorders (Takeshi et al. 2011). However, it was also observed that acute administration of SSRIs was also effective in this model, which is contrary to clinical findings (Oehrborg et al. 1995). Other animal models of anxiety include predator-encounter-based models, predator-exposure-based models for PTSD, neonatal isolation stress models, stress induced by circadian rhythm changes, stress induced by noisy stimulus, low temperature-induced stress, restraint and immobilization stress, social defeat stress, and chronic unpredictable stress (Campos et al. 2013). There are a significant number of animal models for anxiety and stress, so it is important for a scientist to carefully determine which model would be most appropriate given the question that is being asked and the methods being used to test the hypothesis.

## Animal Models of Schizophrenia

Schizophrenia is a severe mental disorder with a lifetime prevalence of about 0.4% worldwide (Saha et al. 2005). The typical onset of the disorder occurs between the late teen years and early 30s, and it is established that the disorder is highly influenced by genetics. Schizophrenia is a heterogeneous disorder characterized by cognitive dysfunction, positive symptoms, and negative symptoms. Examples of positive symptoms include delusions, hallucinations, and thought disorders. Examples of negative symptoms include social withdrawal, anhedonia, and catatonia. Several antipsychotic drugs are available which may help lessen the symptoms of schizophrenia, but they often result in serious side effects and have a low-response rate. The majority of antipsychotic drugs are somewhat effective in managing the positive symptoms of schizophrenia but have very little efficacy in managing negative and cognitive symptoms (Keefe et al. 2007). The current biochemical research into schizophrenia focuses on the implications of neurotransmitters such as dopamine, glutamate, 5-hydroxytryptamine (5-HT), gamma-aminobutyric acid (GABA), glycine, and

D-serine into the pathophysiology of the disease (Yang and Tsai 2017). Substantial progress has been made to develop valid rodent models that replicate the behaviors and brain pathologies associated with schizophrenia in humans, and it is vital to continue making progress in this area due to current limited knowledge of the biological basis of schizophrenia. The majority of research into the biological basis of schizophrenia focuses on certain neurobiological abnormalities, such as the thinning of the prefrontal and temporal regions of the cerebral cortex, reduced synthesis of GABA, and abnormal levels of dopamine in regions of the brain (Cannon et al. 2002). Developing valid animal models for schizophrenia is vital to improving current understanding of its development, as animal models allow for much more invasive studies on the structural and molecular abnormalities associated with schizophrenia which cannot be tested in human subjects.

Certain highly penetrant human mutations allow for the generation of animal models that replicate certain aspects of schizophrenia (Arguello et al. 2010). One example of such a mutation is the chromosome 22q11.2 micro-deletions, which is associated with symptoms of schizophrenia in about 30% of cases (Green et al. 2009). It is possible to generate mice with deletions in homologous regions of their genome; however, it is important to realize that humans with this mutation are not always diagnosed with schizophrenia. Some may be diagnosed with bipolar disorder or various other psychiatric illnesses, and there is still much work to be done in identifying which deletions are associated with schizophrenia-like behavioral abnormalities in mice. Another mutation associated with schizophrenia is the translocation that disrupts the gene disrupted in schizophrenia-1 (*Disc1*). The *Disc1* mutation was first identified in a Scottish family; however, even within this family, the mutation would not always result in schizophrenia. Other psychiatric illnesses such as bipolar disorder were also observed. Nonetheless, mice with the *Disc1* translocation have been generated, and many of them present with behavioral abnormalities similar to those seen with schizophrenia

(Pletnikov et al. 2008). The validity of these mice as models to study schizophrenia is still debated. Some cognitive deficits are associated with schizophrenia and can be used to attempt to validate animal models. For example, deficits in executive function, attention, and working memory are not specific to schizophrenia, but may assist in identifying whether a certain animal model displays behaviors reminiscent of schizophrenia (Simpson et al. 2010). Another useful behavior to observe is a deficit in prepulse inhibition (PPI), which is the phenomenon in which a weak initial stimulus inhibits the startle response evoked by the stronger stimulus. It is thought that a deficit in PPI represents the impaired sensorimotor gating, and PPI can be easily measured in animals.

## Future Directions

Developing animal models for human psychiatric illnesses is a challenging yet rewarding endeavor. The majority of psychiatric illnesses arise from a combination of environmental, genetic, and social factors. As such, it is not possible to perfectly reproduce a psychiatric illness in an animal model, so researchers must focus on producing and studying certain endophenotypes that mimic the illness in some way. For highly studied disorders such as depression, anxiety, schizophrenia, and bipolar, there may exist hundreds of different animal models that mimic the disorder in various ways. It is up to the scientist to determine which model would be most appropriate considering the nature of the experiment and question at hand. New animal models for psychiatric disorders are constantly being generated, and there has been a large focus in recent years on generating these models through genetic engineering. Many observations and conclusions are reached, while studying animal models are not relevant to the human counterpart of the illness, but nonetheless shed light on neurobiological and behavioral aspects of psychopathological syndromes in nonhuman subjects.



## Cross-References

- [Animal Models](#)
- [Animal Models of Autism](#)
- [Behavior Systems](#)
- [Learned Helplessness](#)
- [Pharmacogenetics](#)

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## Animal Response to Fire

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### Introduction

Fire has transformed terrestrial ecosystems since vascular plants colonized land. Many lifeforms have adapted to its recurrent and widespread impact. Understanding the complex interactions

in fire ecology becomes especially pressing with rapidly shifting fire regimes. An important but poorly recognized approach concerns the response of animals to fire, which can be categorized as avoidance, association, habituation, or interaction.

### Avoidance

Animals avoid fire and fire-modified landscapes. This pyrophobic response appears to be predominant. Many plants in fire-prone ecosystems have physical adaptations to mitigate fire damage. In contrast, terrestrial animals typically have the sensorimotor abilities to avoid fire (Engstrom 2010; Pausas and Parr 2018).

Fire can be detected by various senses, such as vision, olfaction, audition, and thermoreception (Engstrom 2010). For instance, captive shingleback lizards increase their activity and tongue flicking when exposed to light smoke without fire, which suggests that their escape behavior from wildfire is guided by olfaction alone (Mendyk et al. 2020). The ability to detect fire at a far distance or early stage is especially important for slower animals that need more time to flee or find shelter, compared to highly mobile animals such as birds. For example, some mammals rouse from torpor to escape, some amphibians flee to less flammable areas, some reptiles take cover in burrows, and some arthropods hide deep in soil or high in trees. The shells of tortoises and snails appear to offer some heat protection, but it is unclear to what extent fire influenced their evolution. In some fire-prone habitats, birds and eusocial insects protect their nests from fire by keeping the surrounding area clear from debris and vegetation (Engstrom 2010; Pausas and Parr 2018).

Many animals also avoid recently burned landscapes. Populations may crash when the availability of food, water, shelter, and nesting sites is decreased after fire. This effect can be reduced by relocating to adjacent unburned areas. For instance, the openness of burned landscapes makes it harder for lions to stalk prey, which is likely why they prefer to hunt in areas with more

undergrowth (Geary et al. 2020). Populations are generally more sensitive to these indirect habitat-level effects than direct individual-level mortality (Engstrom 2010; Geary et al. 2020; Pausas and Parr 2018).

## Association

Animals associate with fire-modified landscapes. They may still avoid fire but benefit from its aftermath. “Fire beetles” (*Melanophila*) possess both infrared and olfactory receptors to detect fire and smoke. These adaptations help them find recently burned trees – or even trees that are still burning – in which their larvae need to develop (Schütz et al. 1999). This provides the clearest case of fire adaptation in an animal. There are dozens of other pyrophilous insect species that are also attracted to recent burns for feeding, reproduction, or development. The darker color variants of pygmy grasshoppers become more common after fire, when this coloration offers better camouflage. Similarly, ground squirrels inhabiting burned landscapes are more often darker colored, and some African birds that breed in recently burned areas have darker eggs and chicks (Pausas and Parr 2018).

Many insectivorous animals associate with fire-modified landscapes when the abundance and accessibility of insects has increased (Engstrom 2010). Reptiles may be attracted to such open areas to bask (Geary et al. 2020). Animals that nest or seek shelter in dead trees benefit from fire increasing the availability of this rare resource. Burned areas may also incur health benefits because fire destroys parasites and pathogens. The increase in light and nutrients encourages seeds to germinate and surviving plants to sprout. This “greening phase” attracts pollinators and herbivores. Grassy ecosystems such as savannahs and prairies strongly depend on the rejuvenating effects of wildfire and grazing (Pausas and Parr 2018).

Burned landscapes also attract many predators. Wolves, for example, benefit from the greater abundance of prey and openness to hunt. However, population-level responses of vertebrate

predators are largely inconsistent and unclear based on current knowledge. Many factors play a role, such as species, location, habitat, competition, severity of fire, and time since fire. Behavioral flexibility alters predator-prey dynamics and buffers ecological impacts of fire. For instance, some predators shift strategy and focus on different species after fires, which mitigates the adverse effects that a specialist predator might experience (Geary et al. 2020).

Primates that inhabit fire-prone habitats often associate with burned landscapes, where they can experience more efficient foraging, traveling, and predator detection. Vervet monkeys significantly expanded their home range after a prescribed burn, mainly by incorporating burned habitat where they can feed on insects killed or stunned by smoke and fire. Another advantage of foraging in these areas is that wildfire occasionally “cooks” food, which kills pathogens and increases ease of chewing and digestion (Herzog et al. 2014). Savanna chimpanzees travel through burned areas, sometimes only minutes after the fire when the ash is still warm. The reduction in vegetation greatly improves visibility and ease of movement. Chimpanzees spend more time traveling and foraging, and less time resting and socializing, in burned compared to unburned areas (Pruetz and Herzog 2017).

## Habituation

Animals habituate to fire, responding appropriately and calmly. This response may optimize the tradeoff between potential harm and benefit of present fire. These animals typically also associate with post-burn landscapes. *Melanophila* fire beetles often meet and mate in burning trees (Pausas and Parr 2018; Schütz et al. 1999). Many birds of prey are attracted to wildfire (see Fig. 1). They likely improve their foraging success by hunting exhausted and disoriented prey fleeing the fire (Bonta et al. 2017; Geary et al. 2020). Other predatory animals also hunt near fire, but little is known about the importance of such fire foraging for their food intake (Pausas and Parr 2018). Crows and other corvids occasionally



**Animal Response to Fire, Fig. 1** Two black kites and a Torresian crow at a bushfire near Borroloola, Australia. (Photo courtesy of Robert Gosford)

engage in *anting*, which involves applying ants or substances to their feathers and skin, possibly to reduce discomfort. This may explain why some corvids have the peculiar habit to “fumigate” their plumage over chimney smoke, which also warms and dries them on wet days. Captive corvids sometimes bathe in smoke next to fire as well (Burton 1959).

Primates that associate with burned landscapes usually habituate to present wildfire. Savanna chimpanzees and vervet monkeys are accustomed to seasonal fire and calmly forage and travel next to it. Some vervets scanned the area when the smell and sound of approaching fire became perceivable to a human observer, and remained calm even when the fire was within 20 m distance (Herzog et al. 2014). In decreasing frequency, chimpanzees ignored, avoided, monitored, or navigated around wildfire. They sometimes rested and groomed in close proximity (<10 m) to fires that were small, which suggests their response is based on several factors, such as

experience, weather, flame height, and vegetation density. They were more careful and vigilant toward the end of the dry season, when fires are particularly fast and unpredictable (Pruetz and Herzog 2017).

## Interaction

Animals manipulate, transport, explore, investigate, or play with fire. Close interactions with fire are uncommon in nature but have been documented in captivity. The closest known interactions with wildfire come from northern Australian raptors – black kites in particular – that gather in large numbers near bushfires to hunt (see Fig. 1). A small fraction of these birds transports fire by picking up burning sticks in their talons or beaks and dropping them elsewhere. Spreading fire may increase their hunting success, but this curious behavior has not been investigated in detail (Bonta et al. 2017). Wild birds sometimes cause fires by incorporating hot cigarette butts in their nests. Several observers have reported how captive corvids *anted* with glowing embers and cigarettes by picking them up in their beaks and pressed them against their feathers. Some even learned to light matches by striking the heads with their beaks (Burton 1959).

During a time when zoo-housed chimpanzees were frequently supplied with cigarettes, they lit the correct end with burning matches or cigarettes, monitored the lit end, saved burning cigarettes in a way that prevented inadvertent extinguishment by cold surfaces, used fruit peels to safely handle hot residues, avoided combustible materials, carefully removed burning sacks, and ensured finished cigarettes were properly extinguished after dousing them in wet patches (Brink 1957). These observations suggest that, under the right conditions, large-brained animals such as chimpanzees and corvids can learn to safely and elaborately interact with fire and use smoldering objects as tools. Further studies on the complex and flexible behavior of animals toward fire will also illuminate how hominins likely came to use and control fire (Brink 1957; Herzog et al. 2014; Pruetz and Herzog 2017).

## Conclusion

The cascading effects in fire ecology are many and complex. The indirect population response to wildfire is described for many species, but the direct behavioral response of animals to present fire is poorly studied. Although the alteration of habitat affects animal communities more than direct mortality by fire, behavioral aspects should not be neglected because they explain how animals living in fire-prone areas mitigate the damage of fire – or even benefit from its effects – without apparent physical adaptations. Descriptions of animals' behavior toward fire are often vague or anecdotal, with a wide variety of responses caused by unclear factors and reported in only few species. Thus, the four response categories are based on limited literature and will surely prove to be too few and too unrefined. It is unfortunate that no clear conclusion can be drawn, not only because animal response to fire takes a central role in many ecosystems with human-caused shifts in fire regimes and resulting conservation concerns, but also because further examination of animal behavior toward fire will shed light on the cognitive capacities that kindled fire use in our own lineage.

## Cross-References

- [Corvids](#)
- [Play Behavior](#)
- [Predation Risk](#)
- [Primate Cognition](#)
- [Tool Use](#)

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## Animal Sexual Behavior

- [Sociosexual Behavior](#)

## Animal Social Relations

- [Friendships in Animals](#)

## Animal Society

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## Synonyms

- [Complex group](#)

## Definition

Cooperative group living.

## What Is an Animal Society?

Many animals form groups, either ephemerally or permanently, including schools of fish, colonies of seabirds, or herds of ungulates. However, many fewer species form more complex social groups that are often referred to as societies (Fig. 1). Defining a “society” is a difficult task because the term has different meanings to researchers in different fields. For example, the most advanced animal societies – eusocial insect societies – are defined by three criteria: (1) overlapping generations, (2) cooperative care of young, and (3) reproductive division of labor (i.e., many individuals in a group are temporarily or permanently sterile) (Wilson 1971). Yet, many cooperatively breeding vertebrate societies are also described by the same three criteria (Sherman et al. 1995). Despite many structural similarities, there are key differences between insect and vertebrate societies, the most important being that vertebrate societies lack permanently sterile individuals that aid in cooperative care of young and other tasks. Instead, nonbreeding “helpers” in most vertebrate species maintain the ability to reproduce, and often do so, later in life. In contrast, nonbreeding “workers” in most eusocial insects are not only sterile, but often morphologically and behaviorally distinct as well. Perhaps, then, the simplest definition of society, and one that encompasses vertebrates, insects, and other invertebrate species that form complex groups, is: cooperative group living (Rubenstein and Abbot 2017).

## The Evolution of Animal Society

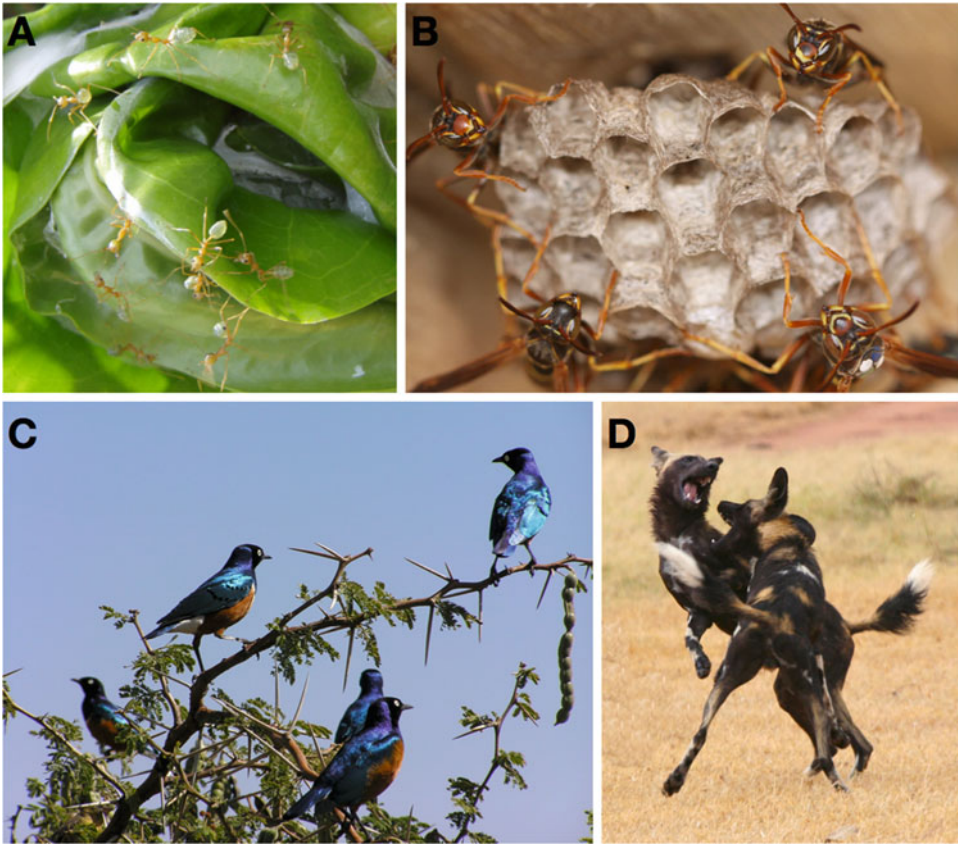
Whether in insects or vertebrates, animal societies are quite rare; less than 10% of birds, roughly 5% of mammals, and less than 2% of insects form societies. Most of these animal societies consist of kin (in other words, they are family groups), though this is not a prerequisite for

complex groups characterized by cooperation. However, interacting repeatedly with kin is important because it makes cooperation and altruism more likely to evolve. Indeed, William D. Hamilton’s classic work on inclusive fitness (both the direct fitness benefits of reproducing and the indirect fitness benefits of cooperating to raise relatives) and the evolution of altruism set the stage for studies of animal societies (Hamilton 1964). Inclusive fitness theory is an explicit framework that governs the evolution of social traits, irrespective of taxonomy (Bourke 2011). According to Hamilton’s Rule, a social action will be favored when its positive effect on indirect fitness is greater than its direct fitness cost:  $rb > c$ , or the product of the relatedness ( $r$ ) between two individuals and the fitness benefit ( $b$ ) an individual receives from the action valued against the fitness cost ( $c$ ) to the individual expressing the action.

Hamilton’s Rule has long formed the basis of how researchers approach studying animal societies and social evolution more broadly. Recognizing the importance of relatedness ( $r$ ) in Hamilton’s Rule, John Maynard Smith called the idea kin selection theory (Maynard Smith 1964). The central role of kin selection in promoting the evolution and maintenance of animal societies and cooperation more broadly has subsequently been demonstrated experimentally in numerous species of organisms ranging from wasps, to birds, to slime molds. Indeed, animal societies are most likely to form in species where the relatedness between parents and offspring is high because this ensures that the indirect genetic benefits gained by cooperating to raise kin are greater (Boomsma 2007). In other words, relatedness among group members (termed kin structure) is central to the formation of animal societies.

Although kin structure is important in the evolution of animal societies, relatedness is just one term in Hamilton’s rule. The ratio of the costs and benefits of cooperating to raise others’ young also influences whether altruism and animal societies will evolve. In most animal systems, the primary factor that influences the fitness costs and benefits of cooperative care of young is ecology. Ecology can constrain the ability of young to disperse and





A

**Animal Society, Fig. 1** A variety of insects (including the (a) ant *Oecophylla smaragdina* [© C. Moreau] and (b) wasp *Polistes fuscatus* [© E. Tibbetts]) and vertebrates (including the (c) superb starling *Lamprotornis superbus*

[© D. Rubenstein] and (d) African wild dog *Lycaon pictus* [© D. Rubenstein]) form societies characterized by cooperative group living. In these and many other species, groups are comprised of primarily related individuals.

attempt to breed independently, thus promoting the formation of family groups and the adoption of cooperative rearing of kin (Emlen 1982). Additionally, the costs of rearing young in harsh and unpredictable environments can favor the formation of animal societies because additional caregivers may be needed to successfully rear young when conditions are bad (Shen et al. 2017).

Thus, just as Hamilton pointed out (Hamilton 1964), to understand the evolution of animal societies, one must jointly consider the interaction between relatedness and the factors (typically ecological) that shape reproductive decisions and fitness outcomes. From an individual perspective, young must decide whether to disperse and attempt to breed independently, or remain at home and help raise others' (typically kin)

offspring. In vertebrates, these young individuals maintain the ability to reproduce no matter which decision they make. Even in some insect species like wasps (Fig. 1), individuals must make the decision to try and breed independently, or to remain at home and cooperate with relatives while sharing reproductive duties.

## Conclusion

Although species that form cooperative groups are quite rare, societies in a range of animal taxa share many characteristics, including overlapping generations, cooperative care of young, and reproductive division of labor, where many individuals in a group are temporarily or permanently sterile.

Indeed, societies in vertebrates and invertebrates are not only structurally similar, but they are also shaped by the same forces. Hamilton's Rule ( $rb > c$ ) describes how altruism, such as cooperative care of young and reproductive division of labor, could evolve within a society. Indeed, kin structure and relatedness between group mates, as well the role that ecology and the environment plays in shaping the reproductive costs and benefits associated with altruism, influence the formation of societies in insects and vertebrates alike.

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## Animal Structure

### ► Morphology

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## Animal Suffering

### ► Pain and Ethics of Animal Care and Use

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## Animal Tool Use

### ► Stone Tools

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## Animal Welfare

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## Synonyms

[Animal wellbeing](#)

## Definition

An explicit or tacit conceptual model or framework for understanding and assessing the overall good or poor state of an individual animal, with implications for ethical conduct in relation to that animal.

## Introduction

The desire to understand the welfare of animals springs from understanding animals as sentient beings that are able to suffer or enjoy experiences. Sentience (the ability to consciously sense and feel, including the capacity for suffering) is a morally significant state. As such, animal welfare typically includes consideration of an individual animal's subjective experiences, such as thoughts and emotions, which cannot be objectively and scientifically measured.

An assessment of an individual's welfare requires some process for making an overall judgment of a good or bad state based upon a variety of qualitatively different factors such as impairments, injuries, stresses, and inferred mental states that vary across time. Welfare assessments may be made relative to different



baselines or ideals, and with reference to different contexts, relationships, beliefs, and biases that vary between individual observers. Various conceptual models have been developed to attempt to resolve these interobserver differences as much as possible and develop a consensus around what constitutes good, bad or acceptable welfare.

The use of the specific term “animal welfare” is uncommon in published literature before 1920 and becomes commonplace only during the 1970s. The corresponding “animal welfare movement” occurs at different times in various countries. In the twentieth century, developments often arose initially in the United Kingdom before spreading to other countries, but more recent developments happened more or less simultaneously in a myriad of developed nations. The term “animal welfare” is still absent from many prominent dictionaries including the Cambridge and Merriam-Webster dictionaries, and definitions provided in other sources are conspicuously outdated in referring to animal welfare as a human duty rather than a state of the animal (e.g., Collins dictionary).

## Historical Context

An appreciation of the needs and experiences of animals goes far back in history. This includes religious prohibitions against overdriving animals, concern about animal cruelty as harmful to a person’s character, and promoting good care and husbandry of animals as a work ethic. Specific apparently cruel practices would be highlighted by commentators, but arguments against them were largely based in either encouraging the most effective techniques or the need for the people involved to display good moral character, rather than the suffering of the animals (e.g., the seventeenth century practice of attaching a plough to the horse’s tail rather than a harness; Blosch 2012). However, in order to endanger character, these practices must also have been considered cruel or at least demonstrative of insensitivity – even if animals were not generally considered to warrant moral consideration in their own right.

Attempts to understand and assess animal welfare in a formal ethical or scientific manner are usually traced to a brief statement made by Jeremy Bentham in the “Introduction to the Principles of Morals and Legislation” (1786, p. 311), where he argued that moral significance of an individual stems not from their intelligence or standing in society, but from their ability to suffer, specifically:

“The day may come when the rest of the animal creation may acquire those rights which never could have been withholden from them but by the hand of tyranny . . . The question is not, Can they reason? nor, Can they talk? but, Can they suffer?”

In the twentieth century, welfare went from being a purely moral consideration to a subject of scientific assessment with important implications for law, politics, and trade.

There are a great many specific historical events, which occur between the late eighteenth century and the present time, that are significant for the development of the concept of animal welfare and how individuals, institutions, and cultures engage with it. This history is largely one of issue-based public outrage and protest followed by the implementation of either a ban on the activity or its continuance governed by increasingly rigorous humane laws and regulations. However, the focus was increasingly on the ethical significance of the animal itself, as a victim of unnecessary or inappropriate suffering or death. For example, the criminalization of animal abuse began after protests about the mistreatment of working horses and livestock, and later the plight of stray dogs and cats. The actions of humane societies (e.g., Society for the Prevention of Cruelty to Animals 1824, American Humane Association 1877) led to the passage of laws distinguishing animals from insensate property by punishing the cruel treatment of animals, even if the perpetrator owned the animal. Legislation of this type passed in the United Kingdom in the 1820s and the United States beginning in the 1860s. National anticruelty regulations were gradually implemented in most countries although scope and enforcement varies (e.g., France 1850, India 1960), but such legislation still does not exist in some influential nations, including

China. Most countries that introduce anticruelty legislation continue to expand its scope over time to cover many species and a range of specific activities such as animal fighting, illegal forms of hunting, and fetish cruelty. However, tension continues to exist between the right of an animal to not be harmed or killed, and their status as property that is used in culturally significant activities that impair animal welfare and cause animal deaths. This is referred to as the sentient property problem (Favre 2004), or the caring/killing paradox (Arluke 1994).

The use of animals in research, and specifically vivisection, is a particularly contested subject. Research and teaching was initially unregulated. Models for requiring scientific and ethical justifications for these uses first developed in the United Kingdom after a series of protests in London referred to as the Brown Dog Affair (1903–1910). Since this period, animal-based research, testing, and teaching became increasingly regulated and overseen by ethical review committees that weigh the harm done to the animals against the projected benefits from carrying out the activity. It is now widely accepted that animal use that is harmful should be replaced whenever possible (Balls 1994). “Cruelty Free” products, that are not tested on animals, became popular in the 1970s; and many cosmetics companies committed to no longer testing on animals (e.g., Avon 1989; Revlon 1990). Animals also ceased to be used in crash tests, and nonanimal alternatives were developed for many routine medical tests such as pregnancy testing. However, animal testing remains central to biomedical research and safety testing where it continues to receive diminished, but majority, support in most countries.

The 1960s and 1970s saw the emergence of animal welfare as an important mainstream issue in many countries. Landmarks included the publication of Ruth Harrison’s book “Animal Machines” (Harrison 1964), which criticized intensive agricultural practices, and launched animal welfare as an important issue for consumers and industries including agriculture, manufacturing, and retailing. In the 1970s, several coherent philosophies were developed for the opposition of

most, if not all, animal use (a.k.a.: animal rights, abolitionism) specifically Peter Singer’s “Animal Liberation” (Singer 1973) and Tom Regan’s “The Case for Animal Rights” (1983). Animal rights activism became most distinct from animal welfare societies that aimed to ensure that animals were treated kindly but did not generally oppose their use for human purposes.

Many direct action groups focused their attentions on specific activities that harm the welfare of animals. For example, hunt saboteurs (e.g., Hunt Saboteurs Association 1963) in the United Kingdom disrupted the hunting of foxes with hounds, which was ultimately banned in 2004. Other groups targeted research using primates, whale hunting, bull fighting, the use of leghold traps, horse soring, battery cages for hens, or a myriad of other allegedly abusive practices. In some cases, more extreme groups liberated animals and harassed or even attacked people involved in these contested animal-based activities (e.g., Animal Liberation Front 1976; Stop Huntingdon Animal Cruelty 1999).

Direct action activism came to be increasingly balanced or even replaced with legal and political strategies throughout the 1980s and afterward. Organizations that focused on ending perceived abusive practices in particular locations were joined by more overarching entities aiming to change social norms and attitudes toward animals at the national or international level (e.g., Animal Legal Defense Fund 1979; PETA 1980). In the United States, the use of state-level ballot initiatives became popular as a method for creating pro-welfare laws without involving the usual slow and traditionally conservative political processes. Landmark events include the EU ban on gestation crates (2013) and passage of felony animal cruelty laws in 43 American states.

In the 2000s, property rights over some animals was further challenged by efforts to award certain “human” rights to animal groups (e.g., banning experimentation on primates, New Zealand 1999; Austria 2005). However, in general, the use of animals remains common, including activities that cause a loss of animal life, exposure to harm, or limitations on freedom of movement, reproduction, and other life

processes. Whereas the boundaries of acceptability have changed in most modern cultures, there remains a mainstream support for and legal protection for the use of animals for a myriad of human purposes including food, fiber, entertainment, and companionship.

These uses are increasingly regulated to ensure that animal welfare standards are followed in all animal-using industries including agriculture, research, entertainment, and the breeding and trade of pet animals. Trust in these standards is sometimes undermined by the release of video exposes and professional documentaries that show abusive treatment of animals in settings such as farms, circuses, and slaughterhouses. However, in an increasingly short media cycle, these investigations seem to be having a diminishing impact on public attitudes and often do not lead to tangible changes in practice.

Animal welfare is now a concept that most members of the public are familiar with and hold views about, including what kinds of animal use are justified, under what conditions, and on what ethical basis. Animal welfare is widely discussed and animal welfare issues are prominent in the media, proposed bills, and academic arena. People and organizations that use or handle animals are subject to critique and often have carefully formulated procedures based on explicit ethical principles and scientific information. The right to use animals, or to claim specific uses are humane or welfare-friendly, continued to be contested in lay and legal contexts.

## Prevailing Models

Animal welfare is a term that is predominantly used in utilitarian context where the goal is to reduce overall levels of suffering in a community or population. It is sometimes distinguished from “animal rights” (which asserts that an individual should not be exploited by another, Regan 1983) and “ethics of care” (where responsibilities are based on our relationship-based duties to others, Held 2006). However, in practice, these approaches and other sources of attitudes and beliefs are often all contributing

factors to any particular situation, rather than neatly separated.

Initially, animal care personnel within animal-based industries and professions tended to focus on the animal’s health and productivity, and assumed good animal welfare would be achieved as a result. This perspective continues to be expressed today by some industry users but is no longer widely accepted by the public who view animal welfare issues through a more direct, empathetic lens. Also, with the development of more extreme genotypes and intensive housing, it became increasingly apparent that the interests of the animal and the human-animal users are not always wholly aligned. Evolving technologies (stall and cage design, genetic manipulation, pharmaceuticals, etc.) allow people to more fully control and exploit animals, without requiring the animal’s cooperation. They also expand the levels of performance beyond the productivity limits of the ancestral or wild type. The extreme examples can be seen not only in relation to high producing agricultural animals, but also animal athletes, such as racehorses, and the extreme confirmations and associated congenital health problems experienced by some pedigree companion animals such as dogs.

Methods for formally assessing the state of animals were developed that emphasized new scientific discoveries and the developing public interest. For example, beginning with the work of Hans Selye popularized in the 1950s, it was appreciated that many adverse events accumulate in the form of stress, which impacts the hypothalamic-adrenal-pituitary axis and leads to a “general adaptation syndrome” (Selye 1950). Other executive processes that are intermediate between particular adverse events, and what the animal experiences or its overall state, contribute to many animal welfare models. In more recent times, this has led to advances in understanding the welfare implications of inflammatory processes, immunity and sickness behavior (Millman 2007), and of the conscious experience of an overall state of suffering or enjoyment, leading to the development of a pessimistic or optimistic outlook (a.k.a. “cognitive bias”). Some models of welfare focus on the quality of inputs to the

animals, but most relate to the overall experience or state of the animal and are based predominantly on outputs from the animals that directly reflect or correlate with that state. Summative states such as stress, suffering, or cognitive bias make up some greater or lesser portion of the overall welfare state. Concepts broader than animal, such as animal integrity or dignity, are also being increasingly recognized (Ortiz 2004).

In terms of specific academic models, Broom (1986) defines welfare as a measurable physical state of an animal in relation to its efforts to cope with its environment, with difficulty in coping and failure to cope resulting in impaired welfare. Dawkins (1990) emphasizes the role of suffering especially severe or chronic suffering as the most important aspect of an animal's welfare. Dawkins (1990) also emphasizes the animal's free choice as a method for determining which environments and other options will support favorable welfare states. Many theories developed after 1990 were more multidimensional in nature. For example, Fraser et al. (1997) suggest that considerations of an animal's welfare must include (1) its subjective state, (2) its biological health, and (3) its lifestyle in relation to what is natural for the animal or its "telos." Mellor and Beausoleil (2015) proposed a five Domains theory that includes nutrition, environment, health, and behavior all contributing toward the fifth domain of mental experience.

Particular conceptualizations of welfare have been adopted by important institutions and within certain industries. For example, the "Five Freedoms," which outlines negative experiences that animals should not have (broadly: hunger, discomfort, pain, fear, and restricted behavior) are widely adopted in the field of agriculture. The "3 Rs" (asserting that the use of animals should be refined, reduced, and replaced) is widely used in relation to animal-based research, teaching, and testing.

More overarching entities such as the OIE (World Organization for Animal Health) tend to have even more eclectic definitions that reference multiple different ideas. The following definition clearly refers to the work of Broom (Broom and Johnson 1993), freedom from suffering,

measuring different domains, and the connection to a human duty to avoid causing suffering:

"Animal welfare means how an animal is coping with the conditions in which it lives. An animal is in a good state of welfare if (as indicated by scientific evidence) it is healthy, comfortable, well nourished, safe, able to express innate behaviour, and if it is not suffering from unpleasant states such as pain, fear, and distress. Good animal welfare requires disease prevention and veterinary treatment, appropriate shelter, management, nutrition, humane handling and humane slaughter/killing. Animal welfare refers to the state of the animal; the treatment that an animal receives is covered by other terms such as animal care, animal husbandry, and humane treatment. (OIE 2010, p. 1)"

In the international arena, a Universal Declaration of Animal welfare has been proposed by the World Society for the Protection of Animals (WSPA). First launched in 2000, the most current (2014) text calls for signatories to recognize that animals are sentient and should be protected under the law. It references the OIE and the Five Freedoms and promotes the overall goal that states should "*prevent cruelty to animals and to reduce their suffering*" (Favre 2016). This declaration has not galvanized widespread international support. Earlier proposals with more of an animal rights-focus were also unsuccessful, including the Universal Declaration of Animal Rights (United Nations Educational, Scientific and Cultural Organization (1978), The Declaration of Animal Rights (Our Planet Theirs Too, 2011), and the Universal Charter of the Rights of Other Species (the Australian and New Zealand Federation of Animal Societies, 2000).

In summary, most current definitions of animal welfare describe it as a multidimensional state with subjective components. It is a state of the animal rather than a duty to the animal, and it is assessed based on measurements of how the animal is faring potentially including survival, health, immunocompetence, and behaviors – including abnormal behaviors such as stereotypy (Mason and Latham 2004). Increasingly, the focus of animal welfare has been shifting from only preventing negative states to providing "a life worth living" (Yeates 2011), which includes the animal experiencing positive welfare states

such as play and amicable social interactions (Yeates and Main 2008).

## Complicating Factors

### Subjectivity

Given that the animal's subjective states (e.g., emotions, cognition, pain) are typically considered an important part of its welfare, our inability to measure these states in a direct and objective manner is problematic. There is no simple solution to the problem of subjectivity in the science of animal experience, including human psychology. Attributing thoughts and feelings to nonhuman animals is often criticized as anthropomorphism; however, this critique is valid only when the attribution is made in error. A number of strategies have been used to resolve this problem. Ethically, there has been a move from assuming that animals do not have subjective experiences, to assuming that they do – based on equivalence to human experience or a precautionary principle. The argument being: it is less ethically problematic to allow for sentience or suffering where it is absent, than to permit suffering to occur simply due to lack of conclusive evidence. Methods for indirectly assessing subjective states have been developed and at least partially validated in many different areas. For example, physiological stress responses have been correlated to highly likely stressors. The animal's motivation to seek out or avoid experiences has been assessed (a.k.a. anticipatory states and conditioned place preference, Spruijt et al. 2001). And the ability of observers to intuitively judge animals' emotional states had been shown to closely match the emotion-provoking situations the animals were in (but that were hidden from the observer, see Wemelsfelder 2007).

### Time Factors

Animal Welfare, as described so far, is the state of an animal in a given moment or short period of time. However, individuals are in better or worse states across time and there is evidence that some periods of stress or adversity may actually be beneficial (e.g., Chamove and Moodie

1990). Assessing an animal's long-term or even lifetime welfare state is more difficult than making an assessment during a particular inspection or process. However, chronic welfare states are increasingly being addressed by research that assesses how animals interpret environments and develop their temperament and overall orientation to new experiences (i.e., optimism or pessimism; a.k.a. cognitive bias, Mendl et al. 2009).

### Groups

Many animals, especially domesticated species, naturally live in groups. It is also common to make decisions in relation to wildlife according to all of the animals in an area or of a species (e.g., conservation efforts). When assessing welfare in a group, any choice will affect the individuals of the group unevenly. For example, social housing is generally beneficial, but some animals in a group might be bullied and harassed by conspecifics, or relocating some wild animals might cause them stress and risk their lives but reduce the chances of species extinction (Dickens et al. 2010).

### The Role of Death

In the commonly used scientific and regulatory utilitarian framework, which emphasizes the avoidance of suffering, death is sometimes not treated as a significant issue other than in its role of terminating subjective states and eliminating the potential for future subjective states. However, in a more general context, death is considered highly significant, especially when the death is considered to have no purpose or utility. Existing frameworks of animal welfare typically do not capture the significance of death for the animal or for the average humane observer (Jensen 2016).

### Cultural Lenses

Acceptable compromises to animal welfare are distinguished from animal cruelty through a lens of activities that are socially acceptable versus unacceptable. For example: hunting versus thrill killing, or correcting an animal as part of training versus hitting it from frustration or anger. Within this social context, individuals will hold a diversity of views; however, the majority will tend to

align with what is historically acceptable and legal in the community. Academics within the Green Criminology tradition (where harms against animals or the environment are equated with harms against persons) challenge this approach and tend to suggest that all actions causing animal suffering should be considered unacceptable (Beirne and South 2013).

## Public Attitudes

Members of the general public often react to animal welfare scenarios on an intuitive or empathic manner rather than according to an explicit ethical framework. Activities that are common in the community might elicit little or no response even when they cause evident suffering. Any assessment of animal welfare has to, in some way, consider community standards, at least in the context of trying to implement changes in how animals are treated. Survey data also show that animal welfare is not treated as a distinct concept but overlaps with other terms such as free range or organic (Harper and Makatouni 2002). And, whereas an animal husbandry professional might equate cleanliness and hygiene with good animal welfare, the general public tends to put less emphasis on this factor and more on the naturalness of the animal's environment. For this reason, people using the term "animal welfare" may actually be speaking of quite distinct issues and priorities in relation to any particular animal or animal-related practice. One common example being the people directly involved in an activity who place a cultural value on the activity and feel they should be respected as experts, versus critics who may not understand why welfare-friendly practices are difficult or too expensive to immediately implement. For example, pigs as social animals theoretically benefit from social housing; however, the genetics of commercial pigs and their intensive housing mean that group housing can lead to high levels of aggression and injury (Rodenburg and Turner 2012). Thus, the ideal outcome of social housing will require many adjustments and may depend upon the

extent to which the public is willing to pay a higher price for options that better match their naturalistic preferences for animal raising.

## Selected Subtopics

Animal welfare as a global topic includes a great many areas of special interest. A few representative examples are given below:

### Analgesia

Historically, pain relief was considered unnecessary for many animals. For example, it was considered beneficial to not provide analgesia on the assumption that feeling pain would prevent an animal from moving around too much after surgery. With the development of concern for animal suffering and more sophisticated analgesics, pain relief is increasingly considered the norm at least for companion animals. Specifically, in most sectors, the use of multimodal pain relief is preferred, an approach to analgesia that addresses both the immediate pain from an event such as surgery and pain over subsequent days during the inflammatory response and beginning of healing. The provision of analgesia in other contexts, for example, during routine agricultural procedures such as dehorning and castration, remains challenging. However, the painfulness of these procedures is widely acknowledged (e.g., Sutherland and Tucker 2011) and research is underway to develop practical protocols for providing analgesia.

### Cosmetic Surgery

Historically, it had been considered acceptable to perform "utility surgeries" on animals to adapt them to the needs of human convenience. For examples, tail docking, dehorning, and debarking. With the acknowledgment of the significance of animal sentience, the public moved to endorsing only surgeries that are to the benefit of the animal; for example, tail docking of sheep to prevent fly-strike versus tail docking of dogs to meet breed standards. Traditionally acceptable "utility surgeries" are becoming unacceptable or are banned where they are deemed to be purely cosmetic (Hubrecht 1995).



### Environmental Enrichment

One of the great challenges of keeping animals in captivity is creating an environment that keeps them physically and mentally occupied in a manner that supports their health and welfare. Environmental enrichment is a term for features that are added to a habitat to overcome the harmful effects of barren or nonstimulating environments. Enrichment comes in many forms that can be summarized as sensory, structural, social, food-based, and cognitive. Environmental enrichment programs are common in laboratories, zoos, and aquariums, and increasing in agriculture and other settings as well (Young 2013).

### Extreme Confinement

Around the end of World War II, advances in hygiene, engineering, and nutrition supported the development of intensive housing for agriculture, research, breeding, and other settings. These systems, including ventilated laboratory animal caging, battery laying hen cages and gestation, and farrowing stalls for pigs, had many advantages in terms of protecting animals from hazards (i.e., predators and disease). However, it became apparent that barren conditions had serious consequences for natural behavior and mental states of animals. The idea developed that animals have not only physical needs such as food and warmth, but also spatial, behavioral, and psychological needs (Hughes and Duncan 1988). Although a middle ground is available in the form of enriched cages, the public seems to generally prefer cage-free options. These are challenging in terms of the use of resources and exposure of animals to the hazards of the environment.

### Low Stress Handling and Positive Training

Where interactions with humans are necessary or have the potential to be beneficial, there has been a strong shift from stressful experience and the use of force or punishment, and toward using gentle methods, rewards, and working with natural behavior. This paradigm shift is apparent in the replacement of old “dominance”-based approaches to training dogs and other animals toward developing a positive human-animal bond and obedience based on social rewards,

treats, and other positive outcomes. The use of positive motivation is also adopted in relation to livestock applications such as driving cattle and the design of slaughterhouses. Most notably the work of Temple Grandin in showing how understanding the animal’s point of view can lead to the development of handling and transportation systems that allow animals to move through a facility without feeling alarm or panic (Grandin 2007).

### Why Is Welfare Such a Source of Conflict?

Animal welfare is a state of the animal but it is ethically relevant to human culture and intersects with both human feelings (empathy) and social norms. A person’s beliefs about animal welfare are emotional and ethical and often deeply held. However, they are also often based on a complex combination of temperament, culture, and implicit and explicit conditioning. Currently, there are a number of unresolved cultural dissonances. For example, attitudes toward modern farming are increasingly negative; however, most people continue to consume the resulting products such as meat, milk, and eggs (Te Velde et al. 2002). When this ambiguity is combined with instantaneous communication between cultures around the world with unique histories and traditions, and intergenerational change, it leads to a great potential for disagreement about what is acceptable, appropriate, or admirable when it comes to human conduct in relation to animals.

### Conclusion

Animal welfare is the state of an individual animal on a valence scale from negative (suffering) to positive (good quality of life, enjoyment of life). An emphasis is often placed on the animal’s subjective experiences, but other factors relating to physical health and an ideal life for individuals of that species are also often considered relevant to the overall assessment of an individual’s welfare. Reference may also be made to contextual factors such as the duty of humans in relation to animals generally or in a specific context.



The precise model of welfare adopted by individuals and organizations is likely to vary according to their focus and goals. These definitions will also continue to change and evolve over time based on new technologies, information, and cultural imperatives. However, to be in accordance with sound science and ethics, the prevention of suffering and the goal of providing, whenever possible, a good life for the animal should always be included.

## Cross-References

- [Anthropomorphism](#)
- [Pain and Ethics of Animal Care and Use](#)
- [Stress](#)
- [Swine Cognition](#)

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## Animal Wellbeing

### ► Animal Welfare

## Animal-Assisted Intervention

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### Definition

Animal-assisted interventions are professionally facilitated interactions between an unfamiliar animal and a person or group used to improve individual health or well-being. Types of interventions include animal-assisted therapy, education, and activities.

### Introduction

Animal-assisted interventions (AAIs) are a subset of ► [human-animal interactions](#), a fundamental aspect of the human experience that captures the

mutual and dynamic exchanges between people and other animals. Distinguished from affiliative relationships (► [pets](#)), ► [service dogs](#), and emotional support animals, AAIs involve interactions facilitated by a trained professional or paraprofessional (e.g., handlers, researchers, teachers, therapists) where an unfamiliar animal serves to confer psychophysiological benefits to a person or group. Dogs are the most commonly used animals in AAIs, though many incorporate horses or other species. Interventions are diverse in delivery, environment, purpose, structure, and target-age demographic and have inspired scientific inquiry from a vast array of disciplines. As such, AAIs are partitioned into three types: animal-assisted therapy, education, and activities (AVMA 2019). Further, multidisciplinary interest has spurred a number of theories for understanding the effects of animal interventions, as well as a movement to prioritize animal welfare in interventions.

## Types of Animal-Assisted Interventions

AAIs' goal-directed, professional-facilitated, and time-bound nature distinguishes them from human-animal interactions involving pets and service animals. Types of AAIs – animal-assisted therapy, education, and activities – can be distinguished by their structure and goals.

### Animal-Assisted Therapy

Animal-assisted therapies (AATs) are interventions that incorporate an animal into a professionally developed and delivered treatment plan to improve human physical or psychological functioning (AVMA 2019). Professionals use AATs to achieve specific physical, psychological, or behavioral goals. For instance, animals in neurorehabilitation therapies for children and adults with conditions such as cerebral palsy, multiple sclerosis, and spinal cord injury facilitate physical activity and recreation while promoting well-being (Muñoz Lasa et al. 2015). Animals in psychological therapies confer emotional benefits, such as those shown to ease patients' distress in cognitive behavioral therapy (Hunt and Chizkov 2014). Animals also play integral

roles in behavioral therapies for children and adults, like promoting positive social interactions among individuals with autism spectrum disorder (Grandin et al. 2015).

### Animal-Assisted Education

Animal-assisted education (AAE) is an intervention directed or delivered by education professionals to meet educational goals (AVMA 2019). AAEs are implemented in classrooms for both typically developing students and those with special needs and range from primary classrooms to college campuses. Animal-assisted reading programs, for instance, are commonplace in primary classrooms to improve students' experience with reading and, thus, reading performance (Fung 2017). Animals are also used to promote motivation and concentration for students with special needs and, further, to improve their behavioral and emotional outcomes (Brelsford et al. 2017).

### Animal-Assisted Activities

Animal-assisted activities (AAAs) are loosely structured interventions facilitated by a professional or paraprofessional that center an animal as a motivational or social tool with the aim to improve individuals' quality of life (AVMA 2019). AAAs are rich in variety, lacking the rigid structure necessary in other interventions. For example, AAAs have been effectively used to decrease the stress of children during doctor and dentist visits, ease chemotherapy for oncology outpatients, and increase food intake among nursing home residents with dementia (Friedmann et al. 2010).

## Theories of Action

Multidisciplinary investigations of human-animal interactions have revealed an abundance of therapeutic effects, such as reducing physiological stress (e.g., heart rate, blood pressure; Vormbrock and Grossberg 1988), facilitating social interactions (e.g., individuals with autism spectrum disorder and dementia; Grandin et al. 2015; Muñoz Lasa et al. 2015), and improving

academic performance (e.g., reading literacy, motivation; Brelsford et al. 2017). Such diverse interest has given rise to many theories to explicate these therapeutic effects. Theories range from the neural level (e.g., activation of oxytocin system; Beetz et al. 2012) to the ecological level (e.g., biophilia; Wilson 1984). Researchers most commonly attribute the benefits of AAI to biophilia and social support theories (Fine and Beck 2015).

### Biophilia

Biophilia, or the *biophilia hypothesis*, postulates that humans have an innate tendency toward and affinity for life (Wilson 1984). This concept has been used as a building block to understand the therapeutic effects of natural environments (e.g., Ulrich 1983) and is now commonly extended to the similarly therapeutic potential of animal interactions (Friedmann et al. 2010; Beetz 2017). Experiences in natural environments and interactions with animals share the ability to reduce stress and anxiety. For example, the mere presence of an animal can decrease physiological reactions to short-term stressful situations (Demello 1999). Importantly, the biophilia hypothesis also acknowledges differences in the type and effect of animal species, both on an individual and cultural level (Wells 2019). Objections to biophilia, however, claim that empirical evidence of such affinity is both lacking and difficult to obtain (Herzog 2002; Joye 2011).

### Social Support

Animals provide social support to humans that alleviates the effects of challenging circumstances (Wells 2019). Social support from animals in AAIs has been primarily observed in two ways, where animals facilitate social interactions or serve as social mediators. For example, some individuals with autism spectrum disorder benefit from AAT because the animal can provide them with the support necessary to initiate social interactions (Grandin et al. 2015). Animals provide social support as mediators in reading programs, on the other hand, by fostering a more comfortable learning environment for students (Fung

2017). Further, animals can serve as alternatives to other humans, as demonstrated by animals that attenuated adults' physiological stress responses to a stressful situation more than did a friend (Polheber and Matchcock 2014).

## Animal Welfare

Affiliative and service animal interactions occur repeatedly between an exclusive human-animal pair and, though distinctive in purpose (i.e., bond and service, respectively), showcase evolved behaviors between humans and animals. Animal-assisted interventions, however, are comparatively novel. These interactions require animals to interact in an affiliative manner (i.e., peacefully attend to people and/or be petted) in a confined space with an unfamiliar human for an extended period of time (Butler 2013; Ng et al. 2015). AAIs are rapidly increasing across a variety of institutions, including airports, hospitals, and schools. The rising demand of AAIs underscores the need to prioritize and maintain the welfare of the animals. To prevent or mitigate any related distress, advocates have put forth three welfare tenets to uphold during any interaction (Fraser et al. 1997; Ng et al. 2015). First, animals' physical well-being must not be at risk, such that they are free from hunger, thirst, pain, and disease. Second, their affective well-being must be maintained by ensuring animals have freedom from discomfort, fatigue, and fear. Finally, they must be able to engage in behavior that is natural and appropriate in the present environment. Conveying the necessity to maintain both human and animal welfare to researchers and professionals affords animals ethical treatment as they serve humans in AAIs under these evolutionarily novel circumstances.

## Conclusion

Animal-assisted interventions are a promising supplement to conventional therapies and daily activities alike to improve the health and well-being of individuals. The therapeutic potential

of AAIs has sparked the interest of researchers across many scientific domains to better understand their mechanisms of action. That, in tandem with the ever-increasing presence of AAIs across schools, health-care systems, and other institutions, highlights a need to prioritize animal welfare during interventions. Further research efforts and stringent devotion to animal welfare will enable AAIs to continue their rapid growth across many aspects of the human experience.

## Cross-References

- [Human-Animal Interaction](#)
- [Pets](#)
- [Service Dogs](#)

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## Animal-Environment Mutuality

### ► Perception-Action Theory

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## Anisogamy

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## Synonyms

### Sexual reproduction

## Definition

Anisogamy can be defined as a mode of sexual reproduction in which fusing gametes, formed by participating parents, are dissimilar in size.



## Introduction

The most important event of an organism's life is to pass on genes to the next generation. Some organisms choose asexual mode, while some prefer more costly process, i.e., sexual reproduction (Barnard 2004). The sexual reproduction is considered as one of the greatest paradoxes of evolution as it applies twofold costs to its practitioners and still prevails in population as a major form of reproduction. The twofold cost of sexual reproduction is (I) cost of meiosis and (II) "fertility cost" of sex (Smith 1978). Whenever female reproduces sexually, she throws away half of her genotype, which foist 50% cost of meiosis. This loss is fulfilled by benefits of sexual reproduction. But this one is considered as misbelief aroused due to our thinking in terms of individual selection (Treisman and Dawkins 1976). The actual cost of sex lies in production of males whose parental investment is always lesser than females. A sexually reproducing female reduces her fertility to half by segregating her offspring into male and female, which are unable to reproduce independently (Lehtonen et al. 2012; Smith 1978, 1989). If there would be only costs of sexual reproduction, then at one time, the asexually reproducing organism should have outcompeted sexually reproducing organisms. But this has not happened, which means that we are also getting twofold advantage of sex which counterbalances costs of sex (Smith 1988, 1989).

Sexual reproduction can be classified into three types, i.e., isogamy, anisogamy, and oogamy, on

the basis of type of gametes produced by parents. Isogamy generally persists into unicellular organism (but not universal), while the anisogamy is found exclusively into multicellular plants and animals (Bulmer and Parker 2002).

## Isogamy

When the two sexually reproducing parents produce gametes of similar size, it termed as isogamy, and the organism is isogamous, e.g., *Chlamydomonas*, yeast, etc. In isogamy, there is generally no "male" or "female" sex, but the participating parents are called mating types like "+" and "-" parents (Fig. 1). In yeast, mating parents are known as "a and  $\alpha$ " cells.

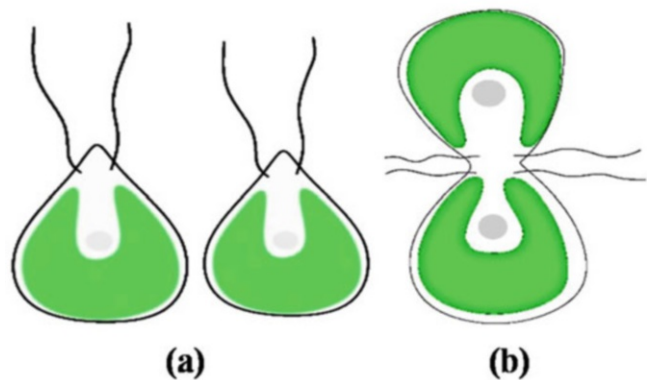
## Anisogamy

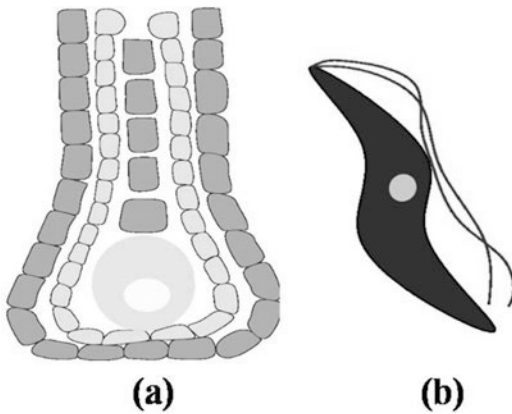
When two sexually reproducing parents produce gametes of different size, it is termed as anisogamy, and the organism is anisogamous. The sexes of parents are defined on the basis of gametes produced by them. Generally, the parent producing smaller gamete is "male," and the one producing larger gamete is "female" (Smith 1971). The both gametes can be motile or one of them can be motile and the other is immotile.

## Oogamy

This is the condition where fusion occurs between small, motile (male) and large, immotile gametes

**Anisogamy, Fig. 1** (a) Isogametes of *Chlamydomonas*, (b) fusion of both "+" and "-" gametes





**Anisogamy, Fig. 2** *Marchantia* sp., (a) archegonium-containing egg cell, (b) antherozoid

(female) like *Marchantia*, *Funaria*, etc. (Fig. 2). One more type of gamete differentiation has been suggested, known as pseudoanisogamy, where there are gametes of different size but there is no correlation between gamete size and fusion. This results in random fusion of gametes (Bell 1978; Birkhead et al. 2008; Bonsall 2006). Pseudoanisogamy is considered as an important event for evolution of anisogamy, but it was evolutionarily unstable due to which it has never been observed (Bell 1982; Bonsall 2006).

## Evolution of Anisogamy

Anisogamy is evolved from isogamy, and the most plausible explanation for its evolution is given by the disruptive selection of gametes (Parker et al. 1972; Bell 1978; Bonsall 2006). There are two major selection pressures acting on any species for determining optimum size of gametes. These selection pressures are numerical productivity (number of gametes produced by any parent in a given period of time) and zygote fitness (probability that the zygote will survive up to adulthood and will be able to reproduce, in as short time as possible) (Parker et al. 1972; Bell 1978). This is the conflict of productions vs. provisioning. Ancestral isogametic cells, like any other biological bodies, are likely to be varied slightly in size, and this variation was selectively

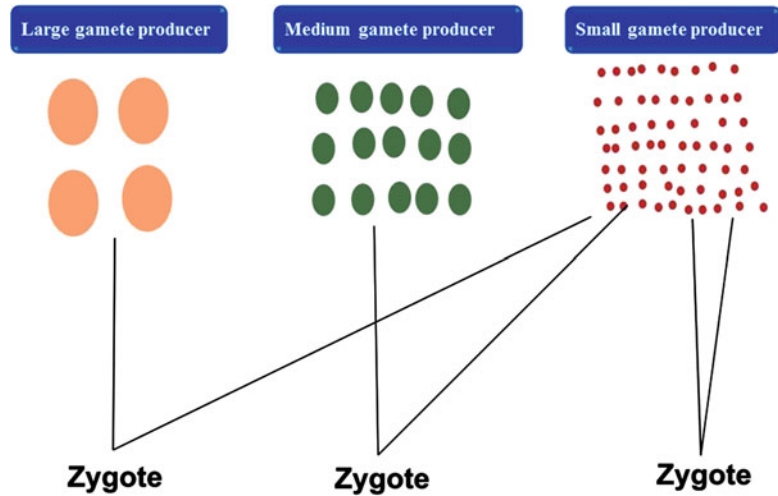
neutral (Parker et al. 1972). As suggested by Parker et al. (1972), the fusion between two larger gametes would be advantageous for species as it would provide better provisioning to resulting gametes. Fusion between two smaller gametes or one smaller and other intermediate gametes would have resulted into large number of zygotes, but since they have less cytoplasmic material, the resulting zygote would have poorer provisioning, and they would not survive till adulthood. So, better provisioning of larger-than-average gametes is exploited by smaller-than-average gametes. The smaller gametes have greater motility than larger gametes and are larger in numbers. Thus, before fusion of two large gametes, the smaller gametes will fuse with their larger counterparts owing to their great motility (Fig. 3). This triggered disruptive selection, i.e., selection of both extreme forms (only larger and smaller gametes). The intermediate gametes were not selected because neither they provide better provisioning nor they had greater motility (Barnard 2004).

## Role of Anisogamy in Animal Cognition and Behavior

The anisogamy plays an important role in behavior of organisms, mainly in animals. Different-sized gametes have resulted into different sexes, i.e., sexes are defined by the type of gametes they produce. Males generally produce numerous small and motile gametes (sperm or pollens), while females produce limited number of large and mostly non-motile gametes (egg or ovule). Different-sized gametes have put different selection pressure on male and female, thus giving rise to different sex roles (Knight 2002). Males are promiscuous, i.e., they are indiscriminate for sex and will mate at each opportunity, while females are choosy, i.e., they will mate with the best suitor (Darwin 1888; Knight 2002; Janicke et al. 2016). This promiscuous behavior of male was explained first by Bateman, which later becomes Bateman's principle. Bateman concluded that promiscuity pays off to males in terms of higher offspring compared to their monogamous competitors.



**Anisogamy, Fig. 3** The small gamete, due to high number and high motility will fuse with other type of gametes in population. But if zygote need high provisioning, then only those will be viable which involves fusion with larger gametes. This will result in selection of smaller and larger gametes producers, outcompeting intermediate gamete producers (Parker et al. 1972; Barnard 2004)



Also, promiscuity is not much beneficial for females as when their offspring were sired by more than one males, there reproductive output was reduced (Knight 2002; Bateman 1948). Thus, it would mean that male reproductive success is increased by mating as many as possible females, while for female reproductive success is increased by investing more into eggs and offspring (Bateman 1948; Barnard 2004). Bateman formulated his conclusion on the basis of energetic expenditures in the formation of gametes. He argued that male gametes (sperms or pollens) are tiny, and thus its production is energetically less costly for male, while the eggs are large in size and thus energetically costlier for females. Thus, male's reproductive success is not limited by the no. of gametes but is limited by the no. of successful mating, i.e., how much eggs he can fertilize. But in the case of females, her reproductive success is not limited by fertilization of eggs but is limited by the production of eggs (Bateman 1948; Trivers 1972; Knight 2002). An important modification in Bateman's principle was made by Trivers, where he explained it in terms of parental investment.

Trivers defined parental investment as "any investment made by parents in their offspring which will increase its chances of survival (thence their reproductive success), but, at the cost of their ability to invest in their next

offspring" (Trivers 1972). The sex that invests more in offspring becomes a limiting source for another which invests less, which will lead to intra-sexual competition for mating. Anisogamy has led to competition for limiting mating opportunities, mainly among male gametes and thus between males. As different-sized gametes evolved, sexual selection came into action (Astrid Kodric-Brown 1987). Since female gametes are limited as its production is costly for females in terms of energy, male competes with each other for mating, but in some cases female competition has also been seen. Once evolved, the anisogamy has been maintained in the population by gamete competition (Monro and Marshall 2016).

## Conclusion

Genetic recombination is a primitive condition found in single-celled organisms, higher plants, and animals. The purpose of genetic recombination is the production of new variation for adaptive evolutionary change in variable environments. Anisogamous gametes evolution is the base for the establishment of maleness and femaleness. It produces the asymmetry between the male and female sexes for the distribution of assets to mating. Always females distribute their

resources to progeny; the survival of several gametes (male) for each female consequences in sexual selection to distribute their assets to improve success in competition during fertilizations. The directional selection and stabilizing are the great response of males to constitute an evolutionary benefit to compensate the cost of their production.

## Cross-References

- ▶ Parental Investment
- ▶ Sex Role Reversal
- ▶ Sexual Reproduction
- ▶ Sperm Competition

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## Anne Pusey

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Anne Elizabeth Pusey is an accomplished scholar of animal behavior, with particular expertise in the behavior of lions (*Panthera leo*) and chimpanzees (*Pan troglodytes* spp.). Her primary research interests center on the evolution of social behavior, including patterns of competition, cooperation, and social bonds. Pusey was born in Oxford, England, in 1949 and completed her undergraduate degree in Zoology at Oxford University in 1970. Shortly thereafter, she became a field assistant for Dr. Jane Goodall's study of wild chimpanzees at Gombe National Park and went on to conduct her dissertation research on the Gombe chimpanzees in close collaboration with Goodall. Her doctoral degree, advised by Dr. David Hamburg, was awarded by Stanford University in 1978, and her dissertation focused on the physical and social development of wild adolescent chimpanzees. Chimpanzees have a prolonged period of post-weaning association with their mothers, and

Pusey's work was some of the first research to be published on the adolescent life stage (Pusey 1983, 1990). In particular, she documented the behavioral changes shown by females upon reaching sexual maturity and how these changes serve to prevent inbreeding (Pusey 1980). Pusey then turned her field research focus to lions and codirected the Serengeti Lion Project with Dr. Craig Packer from 1978 to 1989. Together, they published seminal research on cooperation and competition within coalitions of male lions (Packer and Pusey 1982), adaptations to avoid infanticide in female lions (Packer and Pusey 1983), non-offspring nursing in carnivores (Pusey and Packer 1994), and the evolution of sex-biased dispersal (Pusey and Packer 1987a). The study of dispersal patterns and inbreeding avoidance strategies are a consistent theme within Pusey's research program (Pusey and Packer 1987b; Pusey and Wolf 1996).

Pusey became a member of the faculty in the Department of Ecology, Evolution, and Behavior at the University of Minnesota in 1983. In late 1989, she began working in collaboration with Goodall to gather, archive, and digitize the long-term behavioral data collected as part of the Gombe chimpanzee study. The resultant database has become one of most important scientific resources in the study of primate behavior and is the basis of hundreds of peer-reviewed publications and numerous doctoral dissertations and masters theses. In particular, since chimpanzees are long-lived, the long-term dataset affords a much richer understanding of the complexities of chimpanzee behavior. For example, Pusey found that high dominance rank in female chimpanzees is correlated to increased reproductive success throughout the lifetime (Pusey et al. 1997). Her current research focuses on female social bonds and competition, the importance of male alliances, and primate life history. In addition, Pusey's students and collaborators have used the long-term database to investigate topics as diverse as the evolution of the hominid microbiome, mating strategies, chimpanzee hunting and tool use behavior, kin recognition, and the consequences of infectious disease. In 1999, she

was honored with the title of McKnight Distinguished University Professor at the University of Minnesota and in 2005; she was elected as a Fellow of the American Academy of Arts and Sciences. In 2010, Pusey became the Chair of Evolutionary Anthropology and a James B. Duke Professor at Duke University, where she established the Jane Goodall Institute Research Center. In recognition of her contributions to the field, she was elected as a Fellow of the Animal Behavior Society in 2013.

## Cross-References

- [Adolescence](#)
- [Dispersal Patterns](#)
- [Jane Goodall](#)
- [Primate Social Structure](#)

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## Anointing

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Anointing is a behavior in which an animal acquires substances on their bodies, either passively by absorbing chemicals from the environment or actively by rubbing against them or applying them by mouth (Weldon 2004). Fish, reptiles, birds, and mammals have all been recorded anointing, leading to a number of different terms depending on the specific nature of the behavior. In birds, passive and active anointing are seen in a wide range of species, often with formic acid-secreting ants, when it is referred to as “anting,” but also with a wide range of other invertebrates, citrus fruits, and flowers. Many birds also commonly use fine dirt, sand, or peat to cover their feathers, a behavior referred to as dusting, or peat-bathing (Hart 1997; Clayton et al. 2010), but also fitting the definition for anointing. Many mammals of several orders anoint, including carnivores, ungulates, insectivores, and primates, in which the behavior is referred to variously as anointing, scent rubbing, or fur rubbing (Weldon 2004).

There is no consensus on the function of anointing, and hypotheses are often specific to the anointing species, the materials used, and the context of use. The best studied examples of anointing are in birds, in which the behavior is generally thought to protect birds from lice or feather mites (Clayton et al. 2010). While the substances used by birds have consistently been shown to kill ectoparasites like mites and lice, as well as mold and microbes in vitro, experiments aiming to determine the effects of anointing by birds on ectoparasite abundance have failed to demonstrate parasite control.

In mammals, a wider range of hypotheses have been put forward to explain anointing, with olfactory or signaling hypotheses dominating. Carnivores’ anointing by rolling in carcasses or the feces of their prey may be explained by scent camouflage, increasing social attractiveness, or “group scent marking” to give animals a common scent. While often cited, these hypotheses lack empirical support. Frequent links between anointing and scent-marking behavior in carnivores suggests a role in intrasexual competition, possibly by “scent-matching,” in which anointing facilitates the process by which animals assess the status of competitors, or potential mates by comparing their odor with that of the surrounding area, or a defended resource (Gosling and McKay 1990). Hedgehogs have evolved a quite different form of anointing, for which various explanations have been proposed. Hedgehogs anoint by licking toxins from toads and other irritating substances, and transferring them to their spines (Brodie 1977). This process is thought to enhance defense from predators, by making the spines more effective. Although compelling, this hypothesis is not universally accepted, and explanations involving attracting mates and signaling presence have also been put forward (D’Havè et al. 2005).

Several species of primates have been recorded anointing including, black lemurs (*Eulemur macaco*), capuchin monkeys (*Cebus* and *Sapajus*), golden headed lion tamarins (*Leontopithecus chrysomelas*), owl monkeys (*Aotus* spp.), orangutans (*Pongo pygmaeus*), and black-handed spider monkeys (*Ateles geoffroyi*) (Alfaro et al. 2011). These species have been recorded anointing with a range of substances including several plant species, ants and millipedes in the wild, as well as some strong-smelling substances like detergent or cigarettes in captivity (Alfaro et al. 2011). Hypotheses for anointing in these species have been split between signaling and medicinal hypotheses. Olfactory communication is important in primates, and “group scent marking” has been put forward as a potential reason for the behavior. In some species, such as black-handed spider monkeys, the localization of anointing on specific body-parts and sexual differences in the frequency of the behavior suggest

olfactory communication (Campbell 2000), although it is not clear what is being signaled, or how existing olfactory signals might be enhanced.

Anointing in the primates is best-studied in capuchin monkeys (both of the *Cebus* and *Sapajus* genera.), which use plants such as *Piper* spp., onion (*Alium* spp.), and citrus (*Citrus* spp.), and invertebrates like ants and millipedes to elicit the behavior (see Alfaro et al. 2011 for a review). As well as anointing alone (individual anointing), capuchins also commonly anoint in groups rubbing against each other with the anointing materials (social anointing), in what appears to be a ritualized social activity. Hypotheses for the functional reasons for these different types of anointing range from medicinal to chemo-signaling and social bonding, but the prevailing hypotheses refer to chemical defense from ectoparasites and are similar to the explanations offered for anointing in birds.

The efficacy of many anointing materials used by primates in controlling ectoparasites under laboratory conditions has been convincingly established. Benzoquinone secretions from millipedes, oils from citrus peel, onion oils, and formic acid have all been shown to repel or kill ticks, millipede secretions also repel mosquitoes, onion oils also contain antimicrobial agents, and *Piper* plant leaves are used by people to treat skin conditions (Alfaro et al. 2011). Medicinal hypotheses are further supported in capuchins by behavioral studies of semi-free ranging groups that show an increase in anointing behaviors during the wet season when there are more flying insects and therefore potential for the spread of insect borne disease (Baker 1996). While the anti-parasitic effects of many of these substances are not in dispute, it is important to note that, as with anointing in birds, the effect of anointing on parasite abundance in living primates has not been demonstrated experimentally.

Anointing is a social activity in capuchins, and many individuals often come together to anoint, but the nature of the relationship between social behavior and anointing in these species is not clear. Experimentally, anointing has been shown variously to facilitate social interaction between individuals that typically avoid close contact in

wild groups, strengthen social bonds, and elicit aggression in captivity (Alfaro et al. 2011). Furthermore, anointing has been shown to improve the coverage of anointing materials, and coordinates the treatment of group mates, so can be explained without evoking a signaling hypothesis. As a result, experiments have failed to conclusively show whether individuals are engaging in this social activity purely in order to gain access to resources, suppressing aggressive interactions to do so, or whether further social and signaling benefits exist.

Clearly the benefits of anointing in animals are different across unrelated clades, and may even vary between related species. Many of the hypotheses are not mutually exclusive, and there may be multiple functions in any one species. It is easy to imagine how adaptive medicinal behaviors may become ritualized through natural selection and become social behaviors, just as social grooming has evolved a secondary social function in most primate species. Similarly, odors that are already attractive to a species because they relay medicinal benefits may secondarily evolve importance in signaling to potential mates or competitors as a symbol of status.

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## A-Not-B Problem

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## Synonyms

Perseveration; Perseverative error; Stage IV error

## Definition

The A-not-B error arises from the difficulty of switching an action directed toward one location toward a new location. The original set-up, called visible displacement, involves hiding a toy in location A while an infant is watching. The child is then allowed to search for it. If they retrieve the toy it is seen as an indication of object permanence – the understanding that objects continue to exist even if they are no longer perceived. After a number of repeats of this hide and seek procedure, the toy is then obviously hidden in a different location, B. Up to a certain developmental stage, infants persevere in searching in location A instead of B. This is called the A-not-B error. This behavior can be observed in reaching tasks, but also in larger spatial set-ups that require detours.

## Introduction

When Piaget published his theory of child development in 1937 (1954 in English), it quickly became absorbed by comparative psychologists because it offered a suitable framework for inter-species comparison. There are two reasons for this: first, Piaget was originally trained as a zoologist (the subject of his Ph.D. thesis was the snail), so his ideas are expressed within a broadly biological frame; and second, he denied that language develops prior to cognition, so his experimental tasks were designed to test cognition without relying on language. Much of his theorizing on early development was based on observable, nonverbal behavior, which makes it ideal for the study of animals (Pepperberg 2002).

According to Piaget, the A-not-B error occurs in Stage IV of the sensorimotor period (0–24 months) of human development. During stages I, II, and III infants acquire fundamental perceptual and motor abilities enabling them to perform search behavior. They are not yet able to search for an object that is no longer visible: it ceases to exist in the perceptual world of the infant and they therefore do not possess the concept of object permanence. Stage IV (from around 8 months) is defined by the ability of the infant to search for an object that has moved (or has been moved) out of sight. Here children are very likely to show the so-called A-not-B error, or Stage IV error, in which they continue to search at a previous hiding place (A) although the object was obviously hidden at a new place (B) (see Diamond 1990, for a review). A number of factors can affect the occurrence of the perseveration error, such as the delay between the hiding and retrieval, the number of possible hiding places, the motor requirements, and obviously the age of the infant (Markovitch and Zelazo 1999).

It was initially thought that children in Stage IV (approximately between 8 and 12 months) simply do not understand the concept of an object as continuing to exist out of sight, and in one place only. In certain set-ups, the error could be caused by associative learning as a repeated behavior is reinforced. At Stage V (from around 12 months), the A-not-B error no longer occurs.

## Comparative Studies

Piaget himself was the first to apply his theory to animal behavior, albeit at a theoretical level (Piaget 1971). The first published experimental Piagetian animal research was done in 1971 by Gruber, Girgus, and Banuazizi who investigated the development of object permanence in cats. And in addition to a large number of studies with primates, object permanence has been studied in dogs and wolves (Gagnon and Doré 1994), chicks (Etienne 1973), hamsters (Thinus-Blanc and Scardigli 1981), and magpies (Pollok et al. 2000). Vauclair (1996) gives a detailed account of published studies in this area, as do Cacchione and Rakoczy (2017).

This order of the developmental stages has been applied to animals as it provides a valid and reliable base for a comparison among species. Especially in the area of object permanence, animals can be grouped by the highest stage they can master.

Etienne (1973) stated that animals react in three different ways to the disappearance of objects: animals like insects, spiders, and some lower vertebrates apply special devices or stereotyped movements to find an object of immediate survival value; most birds and some mammals, like rabbits, possess either learned or unconditional responses they apply to find an object that has disappeared, but with no persistence; some mammalian carnivores, primates, and birds of the family Corvidae show spontaneous and active search behavior in response to the disappearance of an object. This third group's performance corresponds to at least Stage IV of Piaget's ranking of object permanence performance.

When considering the current literature on A-not-B errors in nonhuman animals, it has to be taken into account that the task set-up often varies from Piaget's original one. Most studies use variations of Uzgiris and Hunt's (1989) sequence of tests where the task for successive visible displacement involves the hiding of the target (treat or toy) out of sight in one location before it is moved by the experimenter in plain sight to a second location. In the original tests by Piaget,

the target was hidden and retrieved from location A several times before it is hidden in location B for another retrieval. A third, combined set-up was used by Amici et al. (2008). They hid the target in location A three times, then in the fourth trial they visibly moved it to location B after first hiding it at A. Zucca et al. (2007) repeated the hiding in location A twice before visibly hiding the target in location B. Most other current studies omit the repeating stage, such as Deppe et al. (2009) in their study with lemurs. These rather substantial differences in methodology need to be taken into account when considering and comparing findings. The method without the repeated retrieval excludes the explanation that the error is caused by motor memory. But it needs to be studied further whether errors in the visible displacement task with no repetition involve the same cognitive processes as the A-not-B error as initially investigated. Some authors suggest that social factors could explain the preference for the A location in certain species (Topál et al. 2008). Because the experimenter points to the location, interacts with it, and thereby teaches the animal where to look, it tends to focus on this location, instead of searching for the target independently. As seen in the history of animal cognition (Clever Hans – Pfungst 1911), every human involvement in an experiment can affect the outcome, especially in domesticated species such as dogs. This needs to be taken into account when designing and interpreting experiments, even if it does not apply to all species. Kis et al. (2012), for example, found that the “teaching” factor does not apply to common marmosets (*Callithrix jacchus*).

Table 1 provides a sample of studies across a range of species. For an overview of recent studies, see Cacchione and Rakoczy (2017).

Many species tested show the A-not-B error during their early development, but not when they are adults. Their developmental cognitive changes follow the same path as those of humans. The only exception so far are domestic dogs (*Canis lupus familiaris*) and cats (*Felis catus*). Neither puppies (Gagnon and Doré 1994) nor kittens show the perseveration error (Dumas and Dore 1991) whereas adult cats do (Dumas and Doré 1989). For adult dogs, the results are inconclusive as



**A-Not-B Problem, Table 1** Selected examples of studies reporting performance on successive visible displacement tasks

| Species                 |                               | References             | Show the A-not-B error? |
|-------------------------|-------------------------------|------------------------|-------------------------|
| Grey parrot             | <i>Psittacus erithacus</i>    | Pepperberg et al. 1997 | Yes                     |
| Yellow crowned parakeet | <i>Cyanoramphus auriceps</i>  | Funk and Matteson 2004 | Yes                     |
| Cat                     | <i>Felis catus</i>            | Dumas and Doré 1989    | Yes                     |
| Kitten                  | <i>Felis catus</i>            | Dumas and Dore 1991    | No                      |
| Wolf                    | <i>Canis lupus lupus</i>      | Fiset and Plourde 2013 | No                      |
| Puppy                   | <i>Canis lupus familiaris</i> | Gagnon and Doré 1994   | No                      |
| Goat                    | <i>Capra aegagrus hircus</i>  | Nawroth et al. 2015    | No                      |
| Carriion crow           | <i>Corvus corone</i>          | Hoffmann et al. 2011   | Yes                     |
| Eurasian jay            | <i>Garrulus glandarius</i>    | Zucca et al. 2007      | Yes                     |
| Gorilla                 | <i>Gorilla gorilla</i>        | Amici et al. 2008      | No                      |
| Chimpanzee              | <i>Pan troglodytes</i>        | Amici et al. 2008      | No                      |
| Bonobo                  | <i>Pan paniscus</i>           | Amici et al. 2008      | No                      |
| Orang-utan              | <i>Pongo pygmaeus</i>         | Amici et al. 2008      | Yes                     |
| Capuchin monkey         | <i>Cebus apella</i>           | Amici et al. 2008      | Yes                     |
| Long-tailed macaque     | <i>Macaca fascicularis</i>    | Amici et al. 2008      | Yes                     |

different set-ups have been used in different studies. The specific methodology of each study must be taken into account before any comparisons between species can be made.

### Spatial A-Not-B Errors

The A-not-B error involves the perseveration of a movement toward one location, and the inability to switch the movement away from it, despite the fact that the target was obviously moved toward a new location. The testing set-up for infants usually requires reaching for the target. But this behavior can also been seen on a larger scale, in detour tasks. The perseveration error occurs when participants attempt to use a previous route around a barrier despite a visible change in the correct path, thus rendering the attempted route impossible (McKenzie and Bigelow 1986). The basic set-up has the participant facing a straight barrier and they have to move around it through a gap at one end toward a target on the other side. The gap to walk through is in location A. After a few repeats, the barrier is moved so that the gap is now in location B, the other end of the barrier. There is no change in the size of the gap, or the difficulty in the task, only a change in location. This spatial set-up removes the experimenter input of touching or

indicating the target locations and therefore excludes social explanations for any errors. Perseveration cannot be explained by simple motor memory, as the detours take several seconds and involve far more complex movements than simple reaching, as in the original task. McKenzie and Bigelow (1986) explored this detour behavior in human infants and found the spatial equivalent of the A-not-B error in young infants (10-months old), but not in 14-month-old children. This indicates that the same cognitive development applies to both the searching and the detour behavior.

Several studies have shown that dogs will follow a previously learned path even if this no longer leads directly to the goal. Buytendijk and Fischel (1932) were the first to describe how dogs persevere with a detour path, even after changes in the set-up would make an alternative path much faster and easier. Clarke et al. (1951) found that 10-month-old puppies showed perseveration errors in detour tasks. Puppies persisted in following the wrong, but previously learned paths even if this resulted in falling from the end of a false ramp in an elevated detour test. These findings were confirmed for adult dogs reared in restricted environments by Thompson (1954).

More recently, the spatial A-not-B error has been explored in dogs (Osthaus et al. 2010) as well as horses, mules, and donkeys (Osthaus et al.

2013). The number of repetitions of the A trial varied and therefore allowed an exploration of the influence of repetition on perseveration. Unlike in the search set-up, adult dogs persevere in the detour task, even after one A trial. Horses perform comparably, whereas mules and donkeys had lower rates of spatial perseveration and showed fewer A-not-B errors. So far, equines have not yet been tested for A-not-B errors involving the search set-up. Further tests show the same error in cats, chickens, and sheep (Osthaus, unpublished data).

## Summary

The A-not-B reaching error has been shown to exist in most nonhuman species tested so far (Table 1). There are a few exceptions: apes (apart from orangutans), puppies, kittens, wolves, and goats. It must be taken into account that, although there is growing number of studies investigating object permanence in a wide range of species, most of them do not use specific tests to investigate the A-not-B error. In addition, the methodologies vary immensely between studies. Although many studies use the basic set of tests by Uzgiris and Hunt (1989) that explore successive visible displacements, the precise set-up varies between studies and makes comparisons near impossible. It is therefore difficult to compare species with regard to the A-not-B error until a standard test with a defined number of repetitions and movements between targets is implemented.

## Conclusion

The A-not-B error is a behavior observed across the animal kingdom and its causes remain undiscovered to date. Only with standardized tests will it be possible to investigate and identify the underlying cognitive processes.

## Cross-References

► [Visible Displacement](#)

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## Anseriformes

► [Waterfowl](#)

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## Ant bear

► [Aardvark](#)

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## Anteater

► [Aardvark](#)

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## Anthony (Tony) A. Wright

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Anthony A. Wright was born in Los Angeles, California, on January 4, 1943. Wright was raised in Glendora, a small bedroom community Southeast of Los Angeles founded by Wright’s paternal great grandfather. Wright’s father, Carlton Wright, continued the family tradition of being a Southern California citrus grower. Wright’s mother, Judith Wright, was an elementary school principal in the neighboring town of Covina. Wright spent much of his youth along the coast, surfing, sailing, and developing an affinity for fast cars. In 1965, Wright received a BA in Psychology from Stanford University (where he met his soon to be wife, Susan Briggs Wright). While at Stanford, Wright was greatly influenced by Gordon Bower, Richard Atkinson, Ernest Hilgard, and Karl Pribram. In 1970 he received an MA and in 1971 a PhD in Experimental Psychology both from Columbia University under the mentorship of Bill Cumming and Tony Nevin. Wright moved to Texas as an assistant professor at the University of Texas at Austin and was close to Janet Spence and Abe Amsel. From 1972 to 1994, he was a

faculty member in the Sensory Science Center of the University of Texas Health Science Center at Houston and since has been a professor in the Department of Neurobiology and Anatomy at the University of Texas McGovern Medical School at Houston.

The hallmark of Wright's research has been discovering functional relationships in comparative cognition. Functional relationships are revealed when one variable (independent) is manipulated along a continuum and its influence on another variable (dependent) is determined. This research strategy is at the core of Wright's major contributions to the study of animal cognition and behavior and began with his dissertation research. Wright's dissertation, "Psychometric and psychophysical hue discrimination functions for the pigeon," revealed hue-discrimination functions for pigeons via parametric manipulation and signal-detection theory analyses of small wavelength differences across the pigeon's visible spectrum and related these color discriminations to the pigeon's color categories derived from matching-to-sample color-naming functions. Following his contribution to color perception (Wright 1972; Wright and Cumming 1971), Wright began to focus on memory processing. Wright developed the first visual list memory procedures for nonhuman primates (Sands and Wright 1982). The defining feature of the visual list memory work was a recency-to-primacy shift in the serial position function as the delay increased between the presentation of a list of items and the probe (test) item. This functional relationship in the list-memory function over delay was discovered in all species tested: capuchin monkeys, rhesus monkeys, humans, and pigeons. These functions represented a qualitative similarity in memory processes across species and have been instrumental to understanding proactive and retroactive interference in nonhumans and humans (Wright 1998; Wright et al. 1985). More recently, Wright's interest in memory processes has focused on visual short-term memory. Wright developed a variant of the popular change detection procedure used with humans for nonhumans (Wright et al. 2010). By parametrically manipulating the number of items to be

discriminated, Wright has shown that like human memory, nonhuman memory functions are accounted for by the same variable-resource model of memory (e.g., Devkar et al. 2015). Wright has also made major contributions to abstract-concept learning in nonhumans. He challenged claims that nonhumans could not learn abstract concepts based on "failures to find." Wright has shown that a variety of species can learn abstract concepts if the conditions are right. As one example, he has shown that the training set size is critical to revealing clear evidence for abstract concepts. By systematically varying training set size, Wright has shown that abstract-concept learning increases with training set size until full concept learning occurs in all species tested (capuchin monkeys, rhesus monkeys, black-billed magpies, Clark's nutcrackers, and pigeons). Discovering the functional relationship between set size and accuracy revealed these species share the same qualitative ability to learn abstract concepts (Wright and Katz 2006; Wright et al. 2017).

Wright's passion for designing an apparatus has also been at the center of his research. He is a self-taught carpenter and machinist. He is driven by determining the best environment to test an animal while maintaining rigorous experimental control. As one example, he developed an operant chamber where pigeons peck at stimuli on the floor of the operant chamber, as opposed to the side of a wall (as seen in traditional chambers). Wright has also been a charismatic teacher at the UT Medical School for Medical Neuroscience and Problem-Based Learning. Inside and outside the laboratory, Wright was and remains a mentor to many of today's leading comparative psychologists. In 2012 the Comparative Cognition Society honored Wright with a special symposium and a series of articles, further showing his impact on animal cognition and behavior. These articles were published in *Behavioural Processes* along with Wright's retrospective feature article (Wright 2013).

## Cross-References

- [Change Detection](#)
- [Interference](#)

- List Memory Effects (Primacy and Recency)
- Matching-to-Sample
- Same/Different Learning

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## Anthropoid

- Haplorhini

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## Anthropology

- Napoleon Chagnon

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## Anthropomorphism

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Anthropomorphism has for most of the last century been considered a grievous sin in the study of animal behavior. Simply put, anthropomorphism is the attribution of human characteristics to non-human entities. It is often erroneously applied only to other animals using terms in describing and interpreting their behavior that derive from human psychology and behavior. Originally, however, it was applied by theologians and philosophers to viewing gods and other supernatural entities as possessing human-like emotions, thoughts, and motivations along with additional supernatural capabilities. The famous painting by Michelangelo in the Sistine Chapel of a white-haired Caucasian grandfather figure touching Adam epitomizes this approach, along with claims that God is jealous, gets angry, loves us as a parent, and so on. While many philosophers and theologians opposed such attributions to spiritual beings, their admonitions hold little sway with most religious people who want a personal god who will respond to them in psychologically familiar ways. Interestingly, the Judeo-Christian bible supports such anthropomorphism about both God and nonhuman animals (ants are industrious, snakes are both wise and vile, doves are innocent, etc.). This anthropomorphism is widespread in Hinduism, Judaism, Shinto, Norse, Greek, Roman, Australian aborigine, and many tribal religions. Supernatural agents have varying amounts of human attributes, famously enshrined in the Christian belief that Jesus was simultaneously divine and human. Furthermore, animals have themselves been models for numerous deities.

Outside of overtly religious sources, Aesop's fables and even the early compendia by Aristotle and Pliny from ancient Greece and Rome have numerous anthropomorphic descriptions. In many of these early writings, as well as folklore around the world, animals were used to provide moral lessons for humans. Pre-Darwinian writings by



early naturalists tried to be more careful, but often failed. An encyclopedic treatment mixed fine observations with human associations in sections with titles such as sympathy, joy, pain, envy, cruelty, jealousy, anger, revenge, hatred, gratitude, and generosity (Thompson 1851). Darwin's books comparing human and animal behavior (Darwin 1871, 1872) frequently used anthropomorphic attributions of animal mentality and emotion to support claims that rudiments of what we feel most distinctive about the human mind can be found in other species. Evolutionary approaches to mind and behavior have a long history of being similarly criticized for being too readily liable to seeing human attributes of thoughts, feelings, and emotions in nonhuman animals. For example, Romanes, Darwin's protégé on behavior, often resorted to anecdotes and anthropomorphic attributions (Romanes 1892) that we are quick to ridicule today as counter to good science (Galef 1996). For example, Galef wrote (p. 8) that "introspection, anecdote, and anthropomorphism all interfered with development of animal behavior as a scientific enterprise. Each had to be purged from discussions of animal behavior before the field could emerge as a science."

As scientists continue to look for the human in the "animal" and "animal nature" in much of our own behavior, emotions, and thought processes, it is difficult to come up with ways of talking that avoid anthropomorphic elements. Attempts to come up with completely behavioristic terminology have proved generally fruitless, even among their adherents, and thus the turn to cognitive approaches to mental processes that stray from mere behavioral descriptions. This is, however, more than a return to "folk psychology" and represents attempts to understand how cognitive and emotional mechanisms compare across taxa, including the human and nonhuman. The discussion of theology alongside ethology and comparative psychology is deliberate, as much discussion of animal behavior is actually motivated, although often unstated, by attempts to gain insights into human behavior and mental life and their evolution. That is, many are interested in the lessons we might learn from our evolutionary connections with other species involving decision making,

learning, culture, language, morality, ethics, how we treat other animals, and our obligations to the biosphere (Bekoff 1998; Griffin 1976). Indeed, a major reason for the modern reengagement with psychological similarities and differences across species were the critiques by animal rights and welfare movements that questioned many of our traditional ways of treating animals on farms, in laboratories, as pets, in zoo and aquariums, and even in the wild, such as hunting, fishing, and game and pest management practices. Thus, while vocal critics label much current animal behavior research as still unacceptably anthropomorphic (Wynne 2007), the need to develop useful and scientific ways of comparing psychological processes across species remains. Moreover, it must not be forgotten that many of the claims of early writers, albeit based on incomplete data and premature attributions of complex abilities to animals, have often been shown to be rather prescient (Burghardt 1985; Romanes 1883). While current discussions on inferences into the mental lives of other species utilize more accurate scientific methods and findings, behaviorist critiques are still ongoing, as seen in the views of Wynne and others, although these have been countered (Burghardt 2004, 2007). In large part the critics' main concern is that an unbridled mentalism has reemerged in animal behavior and psychology in general that has been abetted by relaxing the opposition to mentalistic approaches that marked both behaviorism and Tinbergen style ethology (Wynne 2007).

Although a thorough history of anthropomorphism in the study of animal behavior is not appropriate here, what is the status of anthropomorphism in animal behavior studies today? Probably the best source for accessing the literature on anthropomorphism is a book that brings together many authors and approaches to anthropomorphism (Mitchell et al. 1997). A treatment of all the often overlapping labels used for distinguishing "good" and "bad" anthropomorphism would be far too lengthy, but terms such as the following may be encountered. Listed in alphabetical order these include applied anthropomorphism, categorical anthropomorphism, critical anthropomorphism, folk psychology, generic anthropomorphism, global

anthropomorphism, heterophenomenology, inaccurate anthropomorphism, intentional stance, mental state attribution, mock anthropomorphism, neural analogical inference, phenomenological empathy, pragmatic anthropomorphism, reflective anthropomorphism, reflective ethology, situational anthropomorphism, subjective analogical inference, and subjective anthropomorphism. While the different subtypes of anthropomorphism and the labels used are often confusing, Robert Mitchell provides a pathway through the diversity (Mitchell 1997). Here I review a path that I have found useful.

Frans de Waal, who wrote the foreword to the Mitchell et al. (1997) volume, has revisited the field of comparative cognition and cognitive ethology in a historically situated and personal treatment that is both informative and interesting for students, general readers, and professionals alike (de Waal 2016). He criticizes not only the widespread anthropocentrism found in psychology and the social sciences and humanities, but argues that *anthropodenial*, a term he had coined, is often deployed as uncritically as is anthropomorphism. He deploys many examples on a diverse range of topics to argue that most researchers today in the field of comparative cognition are not equating human and animal mental states, emotions, or cognitive processes so much as to trying to establish the extent of the similarities and differences through empirical studies. Recent writers other than de Waal and primatologists have been at pains to argue that in studies of moral behavior to perceptual processes in non-human animals, we need to evaluate the abilities of other species on their own terms (Bekoff and Pierce 2009; Rivas and Burghardt 2002) a lesson going back to Jakob von Uexküll (1909), but still often forgotten in the world of anthropodenial (de Waal 2016). Indeed, studiously trying to avoid anthropomorphism can actually result in what can be termed *anthropomorphism by omission* (Rivas and Burghardt 2002).

Anthropomorphic descriptions are ubiquitous in our lives. We make inferences about the thoughts, emotions, and feelings, of other humans, even though, just like with animals, we have no direct conduit into their mental or personal worlds. Indeed, if we did not do this, normal

social life and interactions would be impossible. That we also make inferences about other animals is not surprising at all, as it has helped us in our dealings with domesticated and wild animals, even if errors are frequent and often dangerous, as when the behavior of strange dogs and wild bears is misinterpreted. We also extend our anthropomorphic reach to inanimate things, such as the weather, symbols, and animated movies. Anthropomorphism allows us to get deep pleasure from novels, plays, and poetry. Even young infants can interpret the actions of simple geometric objects moralistically (Bloom 2013). Radical behaviorists rarely describe the behavior of their pets, children, or colleagues without anthropomorphic language, and they would be viewed rather weirdly if they did. It is not just that professional jargon and daily language often differ, but that deeper issues are involved. An approach that works with and uses our anthropomorphic tendencies seems more useful than one of blanket denial. A way of doing this is *critical anthropomorphism*, which accepts that we are rather adept at making inferences about the mental lives and experiences of others based on our own experiences, experiences shaped by our evolutionary history that shares many recurrent life history demands with other species (Burghardt 1985, 1991). Given this, we can hypothesize how other species, as well as conspecifics, interact with their environment and experience events; but this must be based on using all the scientific information about the other species at our disposal such as their natural history, social system, sensory abilities, neural mechanisms, physiology, prior experiences, and so forth. Detailed explications of critical anthropomorphism are available (Burghardt 1991, 1998), but the main lesson seems to be that we should not ignore our own mental lives as we try to scientifically explore the behavior of other species and how they process their “private” experiences.

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## Anthropophagy (in Humans)

### ► Cannibalism

## Antipostatic Selection

### ► Frequency-Dependent Selection

## Anticipation of Future Events

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## Introduction

Humans routinely anticipate future events and organize current actions accordingly. This capacity has been termed “episodic foresight” (Suddendorf and Moore 2011) and is fundamental to enabling humans to control the future by planning, preparing for, and shaping events in desired ways. Adult humans tend to think more about the future than the past and even when thinking about past events, it is often done with a view toward influencing future outcomes (e.g., Baird et al. 2011; Baumeister et al. 2016). The human capacity to anticipate events has been argued to be unrivalled by any other animal species and considered a key adaptive strategy responsible for humans’ dominance on the planet (Gilbert and Wilson 2007; Suddendorf and Corballis 1997).

However, even if there is something uniquely human about episodic foresight, this is not to say that other species do not have sophisticated future-directed cognitive capacities. In fact, the

claim about human uniqueness has triggered a wealth of recent research on the prospective competences of other animals. From research on navigation to preparation, and from experimental studies on tool use to studies on choices with future consequences, this is now an extensive field in comparative psychology. Below recent findings from this domain are reviewed.

The future matters. In many situations, animals would benefit from some kind of capacity to anticipate significant potential future events. It is perhaps not surprising, then, that many species do indeed use cues to anticipate arising threats and opportunities. For instance, animals may take advantage of signs that predict future availability of resources, and those that do this more effectively than their competitors have a selective advantage (Alcaro and Panksepp 2011). Similarly, animals that can predict the approach of a threat can increase their chances of avoiding harm by taking pre-emptive action. These pressures have led to the evolution of quite sophisticated cognitive and perceptual strategies. For example, if chickens see a moving shadow on the ground, they tend to scan the sky in apparent search for a potential danger, such as a raptor. If they detect such a predator, they rapidly try to avoid falling prey, and their visual system links shadow and raptor to facilitate this process (Wilson and Lindstrom 2011). More generally, given that predator and prey species do not just fight, but also are in an evolutionary arms race pitting attack mechanisms and early warning mechanisms, there should be considerable selection pressure toward capacities to anticipate future events. The better a species can use cues to predict an opportunity or threat, the greater the chance to enhance fitness, for instance, through increased vigilance or appropriate approach or avoidance behavior (Bateson et al. 2011; Nettle and Bateson 2012). So, let us start with research on how animals learn to move toward potential positive and away from potential negative events.

## Spatial Cognition and the Future

There is a wealth of research documenting remarkable navigation capacities in diverse

species. For instance, animals such as rats (Tolman 1948) and bees (Menzel and Greggers 2015) construct something like a cognitive map to move efficiently through their environment. This allows them to increase their chance of escape in the face of a threat and their chance of obtaining the resources they need. Some monkeys, such as mantled howlers, for example, travel long distances in ways that seem to enhance the quantity of mature fruits they can consume (Hopkins 2016).

The neurocognitive basis of mammalian navigation likely involves fundamental homologies. In particular, the hippocampus has been identified as the neuronal foundation of cognitive maps (O'Keefe and Nadel 1978). Specific cells in the hippocampus respond to specific places in the environment. These place cells are part of a complex network of cells coding representations of space such as grid cells, border cells, and head-direction cells (Moser et al. 2015). The hippocampus is thus critical to representations of space and its affordances that enable a mammal to flexibly plot paths to reach a target even when confronted with novel obstacles.

Recent single cell recording in rats suggests that place cells in the hippocampus fire in particular sequences that can be reactivated at a later point, possibly indicating a mental replay of the past movement (Buhry et al. 2011). Such sequences have also been recorded prior to a rat taking a path, potentially indicating planning of the movement required to reach a goal (Dragoi and Tonegawa 2011; Gupta et al. 2010; Heyman 2007; Pfeiffer and Foster 2013). Unfortunately, it has remained uncertain how exactly such neural activation patterns relate to mental experience and foresight (Balter 2013). Indeed, it is not even entirely clear what, if anything, the function of these patterns are (Azizi et al. 2013; Bendor and Spiers 2016; Silva et al. 2015). Nonetheless, in the light of the established behavioral evidence indicating navigational competences, and given that the hippocampus is also critical to human episodic memory and foresight (Addis et al. 2007), it may seem likely that they do play a significant role.

Various research suggests that humans' closest surviving animal relatives have considerable route

planning capacities (Boesch and Boesch 1984). It has even been argued that adult male orangutans let others know where they are going to go next by emitting long calls in that direction (van Schaik et al. 2013), though it is difficult to disentangle any such intention from the leaner explanation that they tend to face both in the direction they are heading and in the direction they are calling. Common chimpanzees have been argued to strategically build nests to ensure that a desirable breakfast option is nearby (Janmaat et al. 2016), though again it is difficult to rule out alternative interpretations involving innate predispositions and/or associative learning. Behavioral tendencies that somehow result in future fitness benefits are common but they need not necessarily rely on explicit planning and intentions about future events (Suddendorf and Corballis 2007). Even bacteria demonstrate preparation ahead of arriving at a different environment. When *E. coli* travel through human digestive tracts, they switch on genes for maltose digestion even before reaching the maltose-rich regions (Mitchell et al. 2009). Natural selection can bring about such future-directed patterns when there are regularities the organisms encounter over many generations. Debate about what navigation and the neurological system underlying it tells us about animals' capacity to anticipate future events has thus continued (Corballis 2013a, b; Suddendorf 2013b). Next we turn to experimental behavioral studies that examine animals' capacity to take future consequences into account.

## Prudent Choices

A common way to examine choices that have distinct temporal consequences are paradigms in which subjects must pick one of the two options, often contrasting an immediate small reward and a larger reward that becomes available only after some time has passed. In these intertemporal choice tasks, animals and humans tend to lean toward selection of the immediate rewards, but in certain circumstances will pick the delayed option, such as when the reward on offer is very attractive and when the delay is quite short

(Cheke et al. 2011). Species differences have been reported in such paradigms. For example, pigeons and rats may pick delayed larger rewards when the delay is only a few seconds (Tobin and Logue 1994), but monkeys and apes sometimes pick larger rewards that entail waiting for over a minute (Rosati et al. 2007; Santos and Rosati 2015).

Chimpanzees appear to be particularly capable to delay. In one version of these tasks in which a small reward had to be kept for some time before it could be exchanged for a 40 times larger reward, chimpanzees even waited for up to 8 min (Dufour et al. 2007). In another paradigm involving gradual accumulation of small rewards, chimpanzees also postponed consumption for several minutes (Beran 2002; Beran and Evans 2006), and even appeared to deploy self-distraction while they waited (Beran et al. 2014; Evans and Beran 2007).

Although these tasks all seem to measure some capacity for prudent intertemporal choice, there is some concern that other factors may influence decision making. Indeed, there are various simple decision rules that could drive these choices even without anticipation of future events (Stevens 2011). In a selection task, for instance, an individual may simply approach the more attractive reward without any consideration of the entailed delay, turning the apparent intertemporal choice simply into a preference. One major recent critique of these paradigms has been that they typically involve many training and testing trials, and little consideration of the period of time between individual trials. If a choice of an immediate smaller reward shortens the time before the next trial, then it may well be most beneficial to continue choosing immediate rewards. When the salience of the intertrial delays is manipulated, the choices of animals change in accordance with this principle (Blanchard et al. 2013; Pearson et al. 2010).

Nonetheless, there is considerable consistency in the results to indicate animals such as rats, dogs, pigeons, and apes can choose to obtain a larger reward if it involves delaying gratification for relatively short periods of time (Anderson et al. 2010; Evans and Beran 2007; Leonardi et al. 2012; Osvath and Osvath 2008; Reynolds et al. 2002; Stevens et al. 2011). In some studies,

humans display similar response patterns when the rewards are foods (Rosati et al. 2007) and drinks (Jimura et al. 2009). However, this observation should not distract from the fact that in contrast to the evidence from nonhuman animals, humans frequently choose to put immediate gratification to one side to pursue rewards that are days or even years in the future. In fact, humans often deliberately manage and weigh their options by assessing the desirability and likelihoods of multiple possibilities. There are usually more than two options and more uncertain contingencies – both known and unknown – affecting a future outcome than is examined in intertemporal choice paradigms (Fawcett et al. 2012). Furthermore, it is not always delaying that is the most prudent option. Humans may choose to seek immediate gratification in one context, for instance where the likelihood of a better future payoff is judged insufficient, and choose to delay in others (Bulley et al. 2016). Little is known about animal capacities to make flexible choices between more than two options, and involving different probabilities and objectives.

Indeed, it is not even clear if nonhuman animals appreciate the basic fact that the future is uncertain and that it is often prudent to prepare for more than just one possible outcome of a future event. A simple paradigm developed to examine such a capacity involved dropping a desirable target into an upside down Y-shaped tube and giving subjects an opportunity to catch it (Redshaw and Suddendorf 2016). Two-year-old human children prepared for the drop by placing a hand under only one of the potential exits, and thus ended up missing out on the reward on half of the trials. Older children were increasingly more likely to prepare for both possibilities, with most 4-year olds spontaneously covering the two tube exits from trial one onward. By this age, then, children can consistently prepare for at least two mutually exclusive versions of an immediate future event. Some of the younger children eventually covered two exits but then subsequently regressed to covering one exit, implying a lack of insight into the uncertain nature of the future outcome. Interestingly, chimpanzees and

orangutans that were given this task performed similar to the youngest children, suggesting that they may not be capable of preparing for mutually exclusive events (also see Suddendorf et al. 2017). However, this is only an initial indication and replications with more animals are needed.

## Preparation

Humans can imagine any number of events and diverse outcomes – and prepare accordingly. Even in the absence of any present indicators of these potential futures, we can mentally entertain possibilities and practice responses. When we plan a holiday, for instance, we can ponder the anticipated pleasures and potential problems we may encounter. These thoughts, rather than external cues, may then prompt us to prepare for certain options (e.g., take the scuba license) and potential hazards (e.g., pack the seasick tablets). Though this may primarily reflect absence of evidence rather than evidence of absence, to our knowledge there is no indication that other animals engage in such deliberate preparations in the absence of external cues (Miloyan et al. 2015).

In the same vein, humans can prepare not only for anticipated external circumstances, but also for changes in their own internal states. Without being thirsty or cold in the present moment, we may set out to secure drinks and a way to keep warm at a later stage. The Bischof-Köhler hypothesis states that this capacity to imagine future motivational states, even when they conflict with one's current motivational state, is uniquely human (Bischof 1985; Bischof-Köhler 1985; Suddendorf and Corballis 1997). Other animals do, of course, act in ways that secure future needs, such as when they cache food or build a nest, but this need not necessarily be done with the future situation in mind (e.g., consider a young squirrel that stores nuts without ever having experienced winter). Nonetheless, this hypothesis has been challenged. For instance, two squirrel monkeys were argued to have anticipated their future thirst when they began to gradually prefer one piece of thirst-inducing date that was followed by water

delivered half an hour later, over the option of four pieces with water available only after 3 h (Naqshbandi and Roberts 2006; but also see Paxton and Hampton 2009). However, one may wonder why the monkeys, if they really were thinking about their future thirst, did not simply select the four pieces and wait until water was available before eating them (Suddendorf and Corballis 2010).

Other studies have exploited the fact that animals can lose their appetite for one particular food in comparison to other foods. Jays that were first fed to satiation with one type of food and then given the chance to cache either this same food or a different type seemed to store the currently undesirable food that would become desirable again in the future (Cheke and Clayton 2012; Correia et al. 2007). However, there are reasons to be cautious about a rich interpretation of these data (Suddendorf and Corballis 2008), for instance, because the behavior may reflect a cued present motivational state that incidentally happens to be no different from the future desire state (Redshaw 2014).

A common chimpanzee at a Zoo in Sweden has displayed an unusual behavior that has been claimed to run counter to Bischof-Köhler hypothesis. He placed stones and bits of concrete into piles and later used these as ammunition to hurl at zoo visitors (Osvath 2009; Osvath and Karvonen 2012). Because the piling up of the hard objects occurred in a calm state, it was argued that the chimpanzee may have anticipated and prepared for his need to hurl things as part of his excited display. Though there was a recent report of chimpanzees tossing stones into a tree cavity (Kühl et al. 2016), such preparation behavior has not been reported from other zoos nor in the wild. Experiments are needed to determine what has been driving this curious behavior and whether the chimpanzee displays other signs of foresight (Suddendorf 2013a).

Most experiments on preparation have given apes the opportunity to secure a tool for a future use. In one study, bonobos and orangutans were trained to obtain food with a tool and could then take that tool or distractor items out of the room

(Mulcahy and Call 2006). Perhaps unsurprisingly, the apes preferentially took the tool that was strongly associated with reward. More interestingly, on about half the trials they took the tool back into the testing room when given access an hour later and used it to obtain more of the reward. One bonobo and one orangutan, when the task was presented in the evening, even returned with the tool the next morning. In a similar study involving forced choices, three apes even showed preference for the target tool that was associated with a large reward, when one of the distractor options was an instant small food reward; they also showed a preference for novel tools that were similar in shape and function to previous tools that had solved the task (Osvath and Osvath 2008). However, both these studies have attracted methodological criticisms and systematic replications that rule out potential alternative explanations remain desirable (Redshaw 2014; Suddendorf 2006; Suddendorf and Corballis 2008). Furthermore, even if apes are capable of solving these tasks with some foresight, there is as yet no evidence to suggest that they can do so without first being cued by the immediate presence of the problem or the tool (Redshaw 2014).

One recent study examined great apes' capacity to prepare for multiple problems (Bräuer and Call 2015). By preparing several of the same tools, subjects could obtain a number of rewards. After they had learned to bite off and insert a piece of wood into a tube to get a reward, the experiments blocked access to the food apparatus and showed them how either none, one, or eight tubes were baited. The apes then had the opportunity to prepare before they were given an opportunity to gain the rewards. They made tools more often when rewards were available than when they were not, and they made more if there were eight rather than one reward available. So, this indicates some capacity for relevant preparation. However, instead of making eight tools to secure all rewards, they prepared less than two tools on average. So, the preparation was far from optimal, even though the apes had full visual access to the future problem during the tool preparation phase. It remains to be seen whether they would show a differential



performance across conditions if visual access were blocked and the future rewards had to be represented in working memory.

Another simple recent preparation task involved a series of paddles that subjects could turn so that a reward would fall where it could be retrieved. Bonobos and orangutans were able to rotate the paddles to direct the reward toward an open exit, but did poorly when a paddle below the paddle holding the reward had to be turned first so as to avoid the reward falling the wrong way (Tecwyn et al. 2013). Yet, in early studies, great apes could learn to work backward from a goal and select an appropriate initial choice – at least after extensive training and while the final reward was visible (Döhl 1968; Rensch and Döhl 1968).

In studies in which apes could not see the reward, performance was poor (Dufour and Sterck 2008). After having been trained that returning a token leads to a food reward, chimpanzees were given the opportunity to collect tokens or other objects and to bring them an hour later to a room in which they could exchange them for food rewards. The apes showed no sign of planning for the future exchange: they only rarely brought tokens and obtained rewards, and did not preferentially take tokens over distractors. In a similar study, three apes did show some preferential exchange of previously reinforced tokens, but unlike the previous study, the distractor items were not associated with food and so simple associative explanations cannot entirely be ruled out (Osvath and Persson 2013). Similarly, a study that reported some capacity to transport and exchange tokens in bonobos and orangutans is difficult to interpret as it did not involve any distractors (Bourjade et al. 2014). The results of these token-exchange paradigms indicate that some apes can select and transport relevant objects, but it remains possible that they may only do so because of learned associations with past rewards, and not because they have anticipated the specific future exchange events (Redshaw and Bulley 2017).

On a final note, there is as yet no evidence that any nonhuman animals can reflect on the *limits* of their prediction capacities and prepare

accordingly. Humans can prepare for multiple possible outcome of a single future event (cf. Redshaw and Suddendorf 2016) and may make complex contingency plans. Humans even predict their own future failure to remember and may prepare for that by creating alerts, writing lists, or leaving items in conspicuous locations (Risko and Gilbert 2016). Although a similar function can be observed in, for instance, the behavior of ants when they leave pheromone trails (Sterelny 2003), there is as yet no sign that animals flexibly anticipate their own prediction problems and therefore deploy reminders. However, this may reflect absence of evidence rather than evidence of absence. Future research might want to address this by, for example, presenting apes with search tasks in which they are given opportunities to mark relevant locations for future rewards.

## Conclusion

Although recent studies on navigation, choice, and preparation indicate some future-directed competences in nonhuman species, and therefore demonstrate some continuity in cognitive evolution, the complexity and flexibility of human foresight seems unrivalled. Furthermore, many of the described behaviors can be interpreted not only in a rich manner that attributes foresight, but also in leaner ways. The problem is that actions can be beneficial for one's future even when one was not aware of such contingencies. In other words, it is difficult to establish that an animal acted with the future in mind. How can we rule out associative learning, instincts, or mere chance as alternative explanations? Some quite conservative behavioral criteria have been proposed (Suddendorf and Corballis 2010): "(1) use of single trials to avoid repeated exposure to the same stimulus-responses relationships; (2) use of novel problems to avoid relevant learning histories; (3) use of different temporal/spatial contexts for the critical future-directed action to avoid cuing; (4) use of problems from different domains to avoid specific behavioral predispositions." Human children

demonstrate competence in tasks that meet these criteria relatively late, around age 4 (Redshaw and Suddendorf 2013; Suddendorf et al. 2011) at an age when purported critical mental component capacities, such as an ability to metarepresent, emerge (Suddendorf and Redshaw 2013). At present, there is no comparable evidence from non-human animals that meet these stringent criteria. But the future is uncertain – and it remains possible that future research may demonstrate more sophisticated animal capacities to anticipate future events.

## Cross-References

- Cognitive Map
- Declarative Memory
- Delayed Gratification
- Episodic Memory
- Goal
- Goal-Directed Behavior
- Innate Behaviors
- Intelligence
- Meta-Cognition
- Morgan's Canon
- Ockham's Razor
- Planning
- Primate Cognition
- Problem-Solving
- Prospective Memory

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## Antillian Manatee

- [Sirenia Diet](#)

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## Antipathy

- [Xenophobia](#)

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## Antipredator Call

- [Alarm Calls](#)

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## Anti-predator Defense

- [Primary Defenses](#)

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## Antipredator Signal

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## Antipredator Strategies

- [Predator Defense](#)

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## Anuran Gaits

- [Salientia Locomotion](#)

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## Anuran Locomotion

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## Anuran Movement

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## Anuran Navigation

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## Ape

- ▶ [Haplorhini](#)
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## Ape Cognition and Conservation Initiative (ACCI)

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### Definition

The Ape Cognition and Conservation Initiative (Ape Initiative) is the only dedicated research facility in North America to house and study bonobos. In a new era of great ape cognition and behavioral research, Ape Initiative is an international scientific destination with a focus on science, conservation, and civic engagement.

### Mission and Vision

The Ape Cognition and Conservation Initiative is dedicated to the conservation and protection of great apes worldwide, as well as responsible and sustainable research aimed at uncovering the evolutionary origins of human language, cognition, and behavior. The Ape Initiative aims to use the knowledge we gain from studies with great apes to better humanity by increasing public knowledge and understanding of our own species' origins, as well as our connection with the natural world. With a three-tiered mission of science, conservation, and civic engagement, the Ape Initiative aspires to become the leader in ape cognition research and conservation education.

### Science

Under the direction of Jared Taglialatela, PhD, and William Hopkins, PhD, the Ape Initiative's programs aim to enrich the lives of the bonobos and increase our understanding of great apes worldwide. By using lexigram keyboards to communicate with their caregivers, the bonobos are not only active participants in their own care, but are able to provide unprecedented insight into the mind of the species most closely related to humans.

### Conservation

The Ape Initiative continues to develop programmatic relationships with universities locally and globally to provide research and educational opportunities such as training programs in the behavioral sciences and internship programs for veterinary medicine. In time, the Ape Initiative hopes to train a new generation of scientists who can continue to learn from the apes in our care and increase our understanding of the evolutionary origins of our own species. It is the Ape Initiative's contention that understanding the behavior, ecology, and cognition of great apes is synonymous with conserving them.

### Civic Engagement

The Ape Initiative is a valuable resource for schools and organizations that share in the mission to educate individuals of all ages. One of the long-term goals of the Ape Initiative is to promote scientific literacy, conservation education, and environmental stewardship in the local community and beyond. The Ape Initiative works closely with educators to provide the facility and unique population of apes as a resource to supplement and expand existing primary and secondary school STEM initiatives.

The vision of the Ape Initiative is to be an internationally recognized research facility for the study of ape cognition and communication. Prior to the founding of the Ape Cognition and Conservation Initiative, the five bonobos were the responsibility of the Great Ape Trust where the focus moved away from serious scientific inquiry and the associated public and private sector

support for research. Since Hopkins and Taglialatela formed the Ape Initiative in December of 2013, the focus has been redirected to develop a comprehensive research program. This effort includes both a rigorous and sustained effort to secure programmatic funding from major governmental agencies and private foundations to support scientific research and the dissemination of the results of this research to the public by publishing these findings in high-impact, peer-reviewed journals.

## History

The bonobo ape-language project followed the LANA (Language Analogue) project, pioneered by Duane Rumbaugh and Ernst von Glasersfeld in 1971 at the Yerkes National Primate Research Center and later the Georgia State University Language Research Center in Atlanta, Georgia. A young female chimpanzee, Lana, was taught to communicate with researchers on a computerized keyboard using visual-graphic symbols, or lexigrams, created using simple grammatical structure (Rumbaugh 1977). Bonobos were included in the research in 1980 with the addition of Matata, a wild-born female. Matata did not successfully learn to communicate via lexigrams despite considerable formal instruction, but her adopted son, Kanzi, spontaneously began to not only use and understand these visual symbols to communicate with researchers but also acquired an advanced level of spoken English comprehension, through observation and exposure during his mother's training sessions (Savage-Rumbaugh et al. 1993).

In 2005, the project moved to Des Moines, IA, to a state-of-the-art custom-built facility with support provided by a single donor, a local philanthropist, Ted Townsend. Unfortunately, this resulted in a complete cessation of serious scientific research, with very limited data published in the scientific literature and few external grants awarded. Eventually, Mr. Townsend withdrew his financial support, resulting in the eventual collapse of the organization. In December of 2013, the Ape Cognition and Conservation

Initiative was formed with a new focus on understanding the two species most closely related to humans, chimpanzees and bonobos.

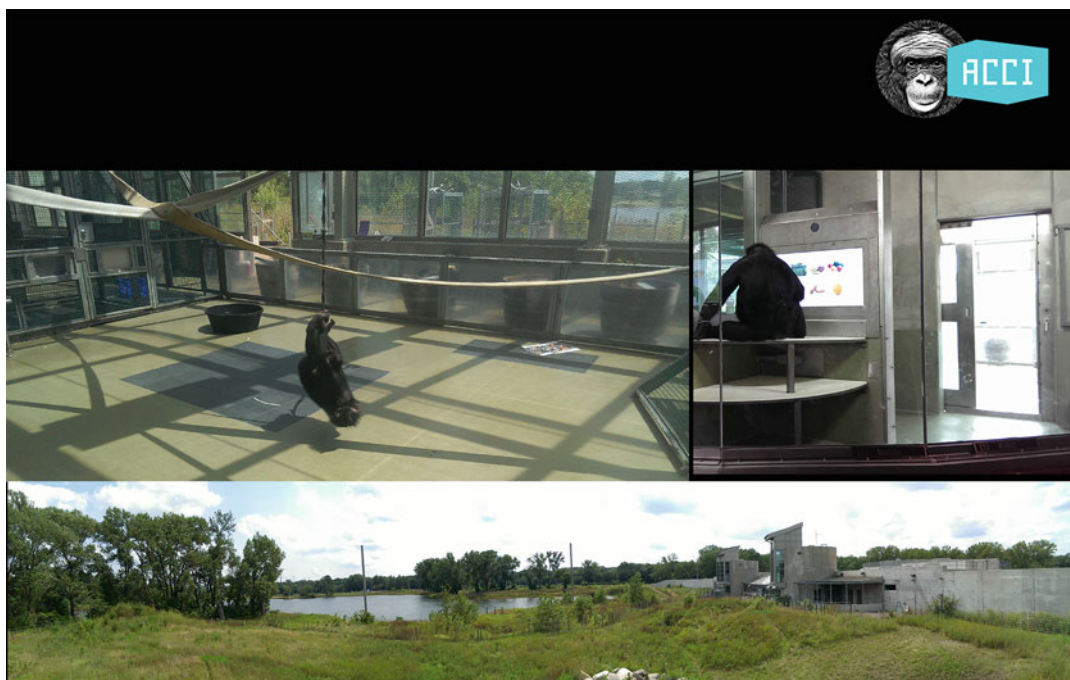
The Ape Initiative was formed through collaboration between two leading researchers in ape cognition, Jared Taglialatela (Kennesaw State University) and William Hopkins (Georgia State University). Collectively, they have over 50 years of research experience with bonobos, chimpanzees, and other great apes. In addition, they have more than 30 years of continuous NIH funding for research with chimpanzees and bonobos, publishing innovative, highly impactful, ethically sound research with direct translational value that has contributed meaningfully to science. Hopkins and Taglialatela were the first laboratory in the world to do noninvasive neuroanatomical and functional brain imaging in chimpanzees and the first to demonstrate voluntary control of vocalizations in bonobos and chimpanzees.

## Ape Initiative's Resources

Bonobos are a critically endangered species of great ape found exclusively along a relatively small section of the Congo River Valley in Central Africa. The name "bonobo" was believed to come from the misspelling of a village in the Congo called Bolobo. Chimpanzees and Bonobos have been recognized as distinct species since 1933. Bonobos have black faces with pink lips from birth, long black hair that is parted in the middle of the head, and hardly any chin hair, primarily eat fruit, travel on the ground during the day and nest in the trees at night, have a strong bond between mother and child that lasts until adulthood, and have a matriarchal society where the females play an integral role in the social structure. There are fewer than 200 bonobos in captivity outside of Africa.

The Ape Cognition and Conservation Initiative is situated on 230 acres in Des Moines, Iowa, in the Des Moines River Valley. The five bonobos currently living at the Ape Initiative are Kanzi, Elikya, Nyota, Maisha, and Teco. All of the bonobos participate in cognitive and behavioral research aimed at both enriching their lives and





**Ape Cognition and Conservation Initiative (ACCI), Fig. 1** Photograph shows indoor enclosure (top left), touchscreen workstation (top right), and aerial view of outdoor yards and facility (bottom). The Ape Initiative is

situated on 230 acres in Des Moines, Iowa. The apes have access and freedom to move through 6 acres of indoor and outdoor space. Photo from Jared Taglialatela, personal collection

helping researchers at the Ape Initiative uncover the evolutionary origins of human cognition and behavior (Fig. 1).

Kanzi (born in 1980) is internationally known for his English comprehension and symbol use. He is heralded as the first nonhuman primate to make stone tools and construct a fire. Kanzi can comprehend novel spoken English sentences (Savage-Rumbaugh et al. 1993). When he is introduced to a new object that he does not have a word for in his lexigram vocabulary, he combines symbols to describe the new item (Savage-Rumbaugh and Lewin 1994).

Nyota (born in 1998) is the son of Kanzi's late half sister, Panbanisha. Nyota appears to understand some spoken English and frequently uses the lexigrams to actively participate in his daily routine. His language skills remain scientifically unknown, but the Ape Initiative is currently experimentally evaluating both his lexigram symbol use and spoken English comprehension.

Maisha (born in 2000) is the last-born son of Matata. Maisha spends his days interacting with the rest of the bonobos in the Ape Initiative's care and foraging in over 6 acres of outdoor space at the Ape Initiative. Based on his parentage, Maisha has a diverse genetic makeup that is underrepresented in captive bonobo populations. He will play an important role in The Ape Initiative's conservation efforts.

Elikeya was born to Matata in 1997 and is Maisha's full sibling. She became the de facto matriarch of the Ape Initiative's bonobo group when Matata died in 2014. Elikeya showcases the importance of mother-son relationships in bonobos by spending a significant amount of time with her only offspring, Teco. Elikeya has not been tested on language comprehension but does participate in both touchscreen-based computer tasks and cognitive testing. Like Maisha, Elikeya will play an important role in bonobo conservation efforts.



Teco (born 2010) is the youngest of the bonobos at the Ape Initiative and the only bonobo born in the state of Iowa. Teco's behavior suggests that he does have some comprehension of the lexigrams and spoken English, but his linguistic capacity is currently unknown. Like his father, Nyota, the Ape Initiative is in the process of experimentally determining his linguistic competency.

The physical laboratory space at the Ape Initiative includes several strategically located touchscreen workstations to afford facile ape keyboard communication both within and between the subjects and researchers. Touchscreen workstations can also be configured to allow the apes to manipulate elements of their environment such as doors, remote cameras, and vending devices. In addition, the workstations allow researchers to administer computer-based tests to the subjects. Strategically placed IT connections allow for IP-based cameras, microphones, and other devices to be configured and reconfigured as research needs dictate the need for the collection of behavioral and communication data from the bonobos. The apes are also afforded control over major aspects of the building environment and may freely visit over 6 acres of outdoor areas (weather-permitting) with groves of trees and climbing structures around a lake providing researchers with unprecedented data collection opportunities.

## Future of Ape Initiative

In the future, the Ape Initiative aims to expand in terms of both the number of bonobos at the facility and the range of species available for scientific inquiry. The bonobo species survival program (SSP) and the Ape Initiative are currently working together to enhance the genetic diversity of the captive bonobo population by planning to add the five bonobos living at the Ape Initiative to the SSP. In addition to improving the viability of the captive population of this critically endangered great ape, this will allow the Ape Initiative to increase the number of subjects available for research. Additionally, the Ape Initiative is considering the addition of chimpanzees to its population of great apes to conduct comparative research with the two species that are most closely

related to humans. Achieving this goal would allow unprecedented comparative research. With the addition of chimpanzees, the Ape Initiative would be the only dedicated research facility in North America to house chimpanzees and bonobos and one of only two in the world.

The long-term research goal of the Ape Initiative is twofold. The Ape Initiative is working to expand our knowledge of the two species most closely related to humans and disseminating these findings via the publication of manuscripts in peer-reviewed scientific journals. Further, the Ape Initiative is working on disseminating findings to the public and educational organizations via formal training and community outreach. By continuing to conduct behavioral and cognitive research in a noninvasive and collaborative environment, the Ape Initiative's unique research can reach a broad audience both locally and internationally. The potential for international recognition and research funding through collaborative efforts cannot be overstated.

The Ape Initiative is working with the best and brightest investigators to carry out sophisticated and impactful research on great apes. By doing this, The Ape Initiative is becoming a premiere center for the study of comparative ape cognition. The Ape Initiative is using the results of behavioral and cognitive research to help improve the management and sustainability of captive populations as well as inform conservation efforts in range countries. The Ape Initiative is continuously developing education programs that aim to inform students of all ages about the two species most closely related to humans. During its relatively short history, The Ape Initiative has developed an internationally recognized research program that aims to not only gain unprecedented insight into the origins of our own species but also to gain knowledge that will help improve the welfare, and increase our understanding of, chimpanzees and bonobos.

## Cross-References

- [Duane Rumbaugh](#)
- [Kanzi](#)
- [Sue Savage-Rumbaugh](#)
- [William Hopkins](#)

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## Ape Gaits

- [Hominoidea Locomotion](#)

## Ape Locomotion

- [Hominoidea Locomotion](#)

## Apes

- [Catarrhine Cognition](#)
- [Catarrhine Communication](#)
- [Catarrhine Life History](#)
- [Hominoidea Sensory Systems](#)

## Aposematism

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## Synonyms

[Warning coloration](#); [Warning displays](#); [Warning signals](#)

## Definition

A characteristic that signals to potential predators that an animal is unprofitable as prey

## Introduction

Many animals are toxic, unpalatable, or otherwise unsuitable as prey items to potential predators. Such species often advertise their unprofitability to predators using warning signals, which is referred to as aposematism. This is generally advantageous to both predator and prey: the former avoids the costs of pursuing an unsuitable meal (ranging from wasted energy to illness or death) and the latter avoids a predation attempt. Aposematic signals contain two components: a secondary defense used upon attack by predators – such as chemical toxicity – that makes the prey unprofitable and a primary defense – such as a distinctive color or odor – that advertises this unprofitability and therefore functions to prevent attack. For instance, ladybird beetles are toxic to predators and advertise this with brightly colored (red, orange, or yellow) wings with black spots (Arenas et al. 2015). Aposematism is a well-studied topic within evolutionary biology, and aposematic signals have been found in many species across the animal kingdom. Extensive research has also been conducted documenting both learned and naïve predator responses to aposematic prey.

The concept of warning signals was originally proposed by Alfred Russel Wallace (1889) as an explanation for the bright colors often displayed by caterpillars, which at the time were seemingly at odds with the theory of natural selection. Wallace referred to the advertisement of noxious qualities as “warning coloration,” and the vast majority of early studies focused on colorful aposematic signals in the visual modality; however, warning signals have now been demonstrated in many sensory modalities and aposematic signals can include visual, acoustic, olfactory, gustatory, and behavioral components. The term “aposematism,” derived from the Greek *apo* (away) and *sema* (sign), was coined by Edward Poulton (1890) to describe Wallace’s concept of

warning coloration in his proposed nomenclature of antipredator defenses.

## Evolving Aposematism

Aposematism has been characterized as a paradoxical adaptation. Whereas there are clear benefits to advertising unpalatability to predators and aposematic signals have been documented in many species, the processes by which aposematic traits have originated are less straightforward. The effectiveness of aposematic signals increases with their density, yet aposematic species are also generally more conspicuous than their cryptic counterparts. How would the first individuals with mutations that increase conspicuousness survive long enough to facilitate predator learning and therefore gain a selective advantage?

Multiple hypotheses have been proposed to address this “rare conspicuous mutant” problem (reviewed by Mappes et al. 2005; Ruxton et al. 2004; Skelhorn et al. 2016). Some focus on stochastic events such as the temporary absence of predators, chance survival of mutants, or random shifts in prey population dynamics. If aposematism evolves by chance in one region, it can then spill over into neighboring populations. Species traits may also be important. A tendency for similar individuals to aggregate (potentially but not necessarily because they are closely related) could give rise to aposematism because the concentration of similar prey items aids in predator learning and dilutes the costs per individual, thus allowing even a small number of early aposematic individuals to give rise to predator avoidance. Similarly, better secondary defenses in conspicuous individuals can lead to increased survival rates from predation attempts and quicker predator learning. Characteristics of predator psychology and perceptual mechanisms may also be important. Predator characteristics such as neophobia (avoidance of novel items) and dietary conservatism (a preference for familiar food items) may explain the perpetuation of early mutants. Conspicuous aposematic signals may also interact with predator perceptual systems in

ways that facilitate rapid learning and retention. Predatory-prey dynamics may also play a role. For instance, the presence of more profitable prey species may ease selection for crypsis, and there is increasing evidence that strategic decision making by predators may be important. Multiple explanations can also be combined into more complex models of the evolution of aposematism, and modeling and simulation studies have demonstrated varying circumstances in which aposematism can arise and be maintained.

Another option is to circumvent the rare conspicuous mutant problem, postulating that aposematism can originate without an initial mutation event (reviewed by Ruxton et al. 2004). Aposematic signals could arise because they confer advantages in other contexts such as mating (i.e., via sexual selection), foraging, or thermoregulation, with evolution proceeding based on multiple selective pressures. Similarly, when prey are densely populated and the likelihood of detection by predators is high, relaxed selection on crypsis may allow for the evolution of aposematic signals. Aposematism could also develop following a rapid environmental change that causes a previously cryptic signal to become conspicuous. Finally, when defenses are visually apparent, such as sharp spines, increased conspicuousness may simply amplify the salience of an existing visual cue. It is important to note that these hypotheses are not mutually exclusive, and that aposematism, which has evolved multiple times across animal groups, may have done so via different routes in different species.

Phylogenetic analyses and reconstructions can be informative when studying trait evolution and can help to understand the context in which aposematism has arisen (reviewed by Härlin and Härlin 2003; Ruxton et al. 2004). For instance, in some animal groups aposematism is associated with prey aggregation, but aposematism appears to be the older trait, suggesting that prey aggregations were unlikely to have influenced its evolution. More research involving phylogenetic comparative analyses is likely to uncover other interesting trends.

## Signal Form

Why do aposematic signals look the way they do? A good warning signal should facilitate predator learning and long-term avoidance. Although aposematic signals are diverse, they also share many common characteristics that are related to their function.

Aposematic signals are generally conspicuous and include components such as bright colors or strong odors. There are a variety of (non-mutually-exclusive) reasons why conspicuous colors may be particularly suited to a warning signal (reviewed by Ruxton et al. 2004; Stevens and Ruxton 2012). Conspicuousness can facilitate detection by predators at a distance and may prevent cases of mistaken species identity. Conspicuous signals may also facilitate predator avoidance due to biases in predators' psychology. Conspicuous signals may enhance predator wariness, accelerate predator learning, decelerate forgetting, and increase prey recognition accuracy relative to other types of signals. They might also help to maintain an honest system (see next section) because the costs of conspicuousness without a backup secondary defense are too high for other species to pay. Whereas conspicuousness is often considered a defining trait of aposematism, the benefits of conspicuousness may saturate, however, leaving some aposematic species only moderately conspicuous. This may be caused by factors such as physiological costs to signal production, variability in predator behavior, trade-offs between various selective pressures, or viewing distance effects.

In addition to general conspicuousness, aposematic signals often include other similar elements (reviewed by Ruxton et al. 2004; Stevens and Ruxton 2012). Simple patterns with repeated elements are common. Simple patterns and redundant components may facilitate predator learning, and repeated elements may also increase contrast if they are rare in the environment. Aposematic signals also often involve similar colors, generally reds, yellows, and black. This could be because by using similar colors, aposematic species can reduce species-level learning costs when

predators learn (either individually or across evolutionary time) to generally avoid these commonly aposematic colors. In Müllerian mimicry (this volume), multiple aposematic species converge on a very similar phenotype, which is beneficial to all species involved. However, the common use of reds, yellows, and black may also be related to characteristics of the environment. Compared to other colors, reds and yellows contrast strongly against a green foliage background, remain distinctive in different lighting conditions, are distinctive in terms of both color and brightness, are distinctive from many other species, and may blend at a distance to create distance-dependent camouflage (i.e., the prey is camouflaged to avoid detection at a distance, but once a predator gets close they are conspicuous and advertise unprofitability) (Stevens and Ruxton 2012). This highlights the importance of considering ecology and species characteristics (e.g., different predators see colors differently) when studying aposematic signals.

Despite these general characteristics, aposematic signals remain variable both within species and between closely related species (Stevens and Ruxton 2012). This is somewhat puzzling because selection would be expected to favor close similarity between signals to facilitate predator learning. This diversity could be maintained by variation in the environment or predator community (e.g., across seasons or space), which could cause different morphs to be more successful in different times or areas. Additional selective pressures may also be involved, with phenotypes representing a trade-off between aposematism and other factors such as sexual selection.

## Signal Honesty

Do aposematic signals consistently reflect underlying qualities linked to prey unprofitability? Work on honest signaling has often focused on the handicap hypothesis (this issue), which posits that high costs associated with producing signals can prevent cheaters because low quality individuals cannot afford to pay. But aposematic signals

are not necessarily handicaps and the mechanisms of signal production and secondary defenses are not always linked (Guilford and Dawkins 1993; Ruxton et al. 2004). Conspicuous aposematic signals are often honest indicators of prey unprofitability in a qualitative sense because prey without secondary defenses such as toxicity are not able to pay the survival costs of being more noticeable to predators (reviewed by Summers et al. 2015). Without the secondary defense to back them up, the conspicuous signals associated with aposematism would lead to increased predation rates and lower fitness. The major exception is Batesian mimicry (this volume), in which an unprotected species mimics an aposematic species to gain the fitness advantages enjoyed by the latter without incurring the costs of defense. Batesian mimicry is well documented, but the local population density of mimics tends to be lower than that of the aposematic species they mimic because as the ratio of honest signalers to cheaters increases the degree of protection offered by the signal decreases.

Some aposematic species also exhibit quantitatively honest signals, where there is a positive correlation between the strength of aposematic signal and degree of unprofitability to predators (reviewed by Summers et al. 2015). This appears to be less common than qualitative honesty, although more research is needed. Quantitatively honest aposematic signals may be particularly likely when the signal is morphologically or physiologically linked to the method of defense.

## Conclusion

Aposematism has been a major research focus of biologists since the early days of evolutionary thinking. While the benefits of advertising unprofitability to predators seem straightforward at face value, some aspects of aposematism are perplexing, including aspects of its origin, the presence of intragroup variability, and less conspicuous aposematic signals. Aposematism remains a common interest in biology, and continued work in this area will likely contribute to our knowledge of the process of evolution and the

mechanisms that generate the incredible diversity of life on earth.

## Cross-References

- [Avoidance](#)
- [Batesian Mimicry](#)
- [Communication](#)
- [Foraging](#)
- [Honest Signaling](#)
- [Müllerian Mimicry](#)
- [Neophobia](#)
- [Predator Defense](#)
- [Primary Defenses](#)
- [Secondary Defenses](#)
- [Visual Recognition of Prey and Predators](#)
- [Warning](#)

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## Apparatus to Measure Spatial Learning and Memory

### ► Radial Arm Maze

## Apparent Death

### ► Tonic Immobility

## Appearance Reality Tests

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### Synonyms

Appearance versus reality; False perception; Visual illusions

### Definition

The ability to distinguish how an object perceptually appears from how it truly is.

### Introduction

Perception is not always veridical. Properties of objects, such as their shape, size, or color, can be perceived falsely due to factors such as illumination, refraction, and misleading contextual cues. Such perceptual mistakes are demonstrated by a wide variety of optical illusions (Palmer 1999). Misperception can also involve mistaking objects for other objects due to similarities in their surface features; for example, a fur coat thrown onto the floor may be mistaken for a dog. In some cases, the deceived individual is aware of falsely

perceiving the object, while maintaining knowledge of its true nature and further recognizing that the two are at odds. This demonstrates a capacity for appearance reality (AR) discrimination.

There are many examples in nature of appearance–reality disjunctions, including cases of camouflage in predators and prey, false eye spots on moth or butterfly wings, and simple cases of mistaken identity, such as misperceiving a stick as a snake. From an evolutionary point of view, the ability to distinguish the appearance of objects from their true nature provides clear adaptive advantages. Knowing true danger from apparent danger allows animals to protect themselves and their offspring while avoiding unnecessary expenditures of energy. When foraging for food, it is advantageous to distinguish edible from non-edible items, objectively larger from smaller food sources, and higher calorie items from lower calorie ones, regardless of any misleading appearances that occur. Even greater advantages can be gained by recognizing when other individuals are experiencing a false perception, and then using this knowledge to one's own advantage. A subordinate animal that recognizes when a competitor falsely perceives a nut as a stone, for instance, could wait until the competitor leaves the area before attempting to eat the nut. Indeed, the challenges of foraging, especially in competition with other individuals, are thought to have been one of the evolutionary forces driving expansions in brain size and increased intelligence in primates (Dunbar and Shultz 2007).

In addition to its evolutionary significance, AR discrimination may play an important role in social–cognitive development. Developmental researchers have found that children who pass tests requiring insight into their own mistaken perceptions of deceptive objects also expect others to be fooled by those same objects (Gopnik and Astington 1988; Moll and Meltzoff 2011). It has thus been suggested that AR discrimination could support the development of misrepresentation more generally. Becoming aware that objects can be falsely perceived by oneself, for example, could be a stepping stone to inferring false perceptions in others, which could in turn provide a basis for understanding false belief



states (Krachun et al. 2016; Lurz 2011). Given the evolutionary and developmental importance of AR discrimination, researchers have created a variety of tests to study this cognitive ability. The earliest tests were designed for preschool children, with later tests being developed to test AR discrimination in great apes. As the tests for apes were borrowed from the procedures designed for children, the children's tests are described first below, followed by the more recent tests for apes.

## AR Tests with Children

Empirical research on AR discrimination began with developmental research on human children. The primary goals of this research were to identify at which age this cognitive ability emerges, and to investigate its relationship to other cognitive abilities such as visual perspective taking and false belief understanding. The classic tests for children involve presenting them with an object whose appearance is at odds with its true identity, function, or properties. In the rock-sponge test (Flavell et al. 1986), for example, children are shown a sponge that looks convincingly like a rock, and they are then given the opportunity to handle the object and discover its true identity. To pass the test, children must correctly answer questions about what the object looks like and what it really is. The rock-sponge test makes use of what is called an "identity illusion" because the appearance of the object is misleading with regard to its true identity. Other AR tests for children use what are called "property illusions" because they create a contrast between the real and apparent perceptual properties of items. In one such test, for example, the experimenter places an object behind a transparent, colored filter and then questions children about the object's real and apparent color (Flavell et al. 1986). In other tests, children are asked to comment on the real and apparent size or shape of objects whose appearance is altered by various means; for example, a straight stick looks bent when placed in a glass of water, or an object looks bigger or smaller when placed behind a magnifying or minimizing lens (Braine and Shanks 1965; Taylor and Flavell 1984). Numerous studies

show that children begin to pass such tests reliably by 4–5 years of age. Younger children may also succeed when language demands are reduced, such as when children make nonverbal behavioral responses rather than verbally answering direct questions about the objects (Moll and Tomasello 2012; Sapp et al. 2000).

An important finding, with regard to the role of AR discrimination in cognitive development, is the similarity in children's performance on AR tests and their ability to attribute false perceptions and false beliefs to others. A comparable dramatic improvement in children's performance in all three types of test occurs in the 4–5 year age range. Additionally, for both verbal AR tests and false belief tests, there is evidence that younger children's difficulties may be due to misinterpreting the test questions (Deák 2006). Significant positive correlations in performance on AR tests and both false perception tests (Krachun and Lurz 2016) and false belief tests (Gopnik and Astington 1988) have also been observed. These parallels are thought to reflect the fact that all three tests rely upon a capacity for dual representation, the capacity to entertain two different representations of the same object (Flavell 1993; Perner et al. 1987).

## AR Tests with Great Apes

Given the boost to survival and reproductive success conferred by AR discrimination, it is reasonable to think the ability could be an evolved capacity across a range of species, not just humans. However, the extent to which non-human animals are capable of recognizing their own false perceptions and making AR discriminations is still largely unknown. The only direct investigations of AR discrimination in non-humans to date include a handful of studies with great apes, including chimpanzees (Karg et al. 2014; Krachun et al. 2009, 2016), as well as bonobos, gorillas, and orangutans (Karg et al. 2014). Unlike tests with humans, the goal has not been to determine when AR discrimination emerges during development but, rather, to determine whether apes possess this cognitive ability

at any age, even in adulthood. To this end, some juveniles but mostly adult apes have been tested, with the age of subjects ranging from 6–42 years old. The tests developed thus far use an object-choice format in which apes are allowed to choose between two items by pointing to the one they wish to receive from an experimenter. In these tests, researchers have taken advantage of apes' demonstrated strong preference for greater amounts of food over lesser amounts. When given a choice between a larger piece of food and a smaller piece of food, for example, almost all apes consistently choose the larger piece (e.g., see Krachun et al. 2009).

Capitalizing on these preferences, AR tests offer apes a choice between one item that perceptually *appears* to be the more desirable one but is actually the less desirable one, and vice versa. In order to obtain the truly more desirable item, the ape must point to the one that appears to be the less desirable item. A variety of illusion-producing stimuli have been used to create disjunctions between the appearance and the true nature of the choice items, including magnifying and minimizing lenses (Krachun et al. 2009, 2016), mirrors and color filters (Krachun et al. 2016), and boards that are used to partially occlude food items such that the truly longer item looks shorter and vice versa (Karg et al. 2014). The general procedure runs as follows: apes are first given the opportunity to view the food items in their natural state, and they then observe as an experimenter places the same items into their illusory context (e.g., behind the distorting lenses or occluding boards). Thus, the apes know about the true properties of the items, and they can see how placing the items into their illusory context causes their appearance to change. With the items displayed in their illusory context, the ape is then allowed to choose between the items. Apes that are not misled by the deceptive appearance of the items are expected to choose the apparently less desirable item in order to obtain the truly more desirable one. Repeated trials and sessions are administered (typically 12 trials per session over 2–8 sessions) with the location of the truly more desirable food item randomized across trials.

Results from tests using this procedure provide support for the idea that apes are capable of discriminating appearance from reality. Karg et al. (2014) found that across all four species of great ape, the truly more desirable food item was chosen in approximately 85% of trials. Krachun et al. (2009) did not find statistically significant results at the group level for the chimpanzees who participated in their AR test with distorting lenses; nevertheless, at the individual level, 57% of the chimpanzees chose the truly more desirable food item significantly more often than chance across all the trials administered. In Krachun et al. (2016), the percentage of chimpanzees doing so ranged from 50% to 100%, depending on the test. These combined results suggest that some, if not all, apes are capable of ignoring the misleading appearance of the items at the time of choice and choosing the apparently less desirable, but truly more desirable, item.

As with all tests investigating the cognitive abilities of nonhuman animals, efforts must be made to rule out explanations that appeal to lower-level cognitive processes than those being tested. In the case of the AR tests described above, Krachun et al. (2009) raised the possibility that apes could succeed by noting the initial location of the truly more desirable item and then simply choosing that location at the time of choice, without necessarily attending to the misleading appearance of the items in their illusory context. This strategy is made possible by the fact that the location of the truly more desirable item remains constant throughout the duration of each trial. In light of this, some AR studies (Krachun et al. 2009, 2016) have included a more challenging test that makes it impossible for apes to succeed using this simple method. This test differs from the simpler one in that once the experimenter has placed the items into their illusory context in full view of the ape, he/she then blocks the ape's view with a visual occluder, arranges the items on the table, then removes the visual occluder and allows the ape to choose between the two items. Thus, in this version of the AR test, although the ape sees the change in appearance of the items as they are placed into their illusory context, the final location of the truly more desirable item (e.g., the truly

larger one) is determined out of view of the ape. The only way that the ape can know the location of the truly more desirable item is to visually examine the items before making a choice, and to find and choose the item that *appears* to be the less desirable one. As this procedure makes it impossible for apes to simply track the location of the desired item throughout the trial, it is referred to as a “tracking” control test. Some apes that succeed with the simpler procedure are unable to pass this more challenging test, but other individuals continue to choose the truly more desirable food item significantly more often than chance under these conditions (Krachun et al. 2009, 2016). The reasons for these differences across individuals is unknown, but possibilities include differences in working memory, attention, motivation, and the ability to inhibit impulsive responding. Another possibility is that AR discrimination abilities may not be universally acquired in our closest ape relatives in the same way that they are by typically developing humans.

### The Reverse Contingency Argument

When interpreting the results of AR tests with apes, another possibility that must be considered is that successful apes could be using a “reverse contingency” rule to solve the problem. In an object-choice task, a reverse contingency rule means that obtaining the preferred reward is contingent upon choosing the nonpreferred reward. In a choice between a small and a large food reward, for example, the animal must point to the small reward in order to obtain the large reward from the experimenter. Similarly, if given a choice between two groups of food items, the animal must point to the group with fewer items in order to obtain the group with more items. In a series of studies using such reversed reward contingencies for both different-sized items and different numbers of items, Sally Boysen and her colleagues demonstrated that chimpanzees have an extremely difficult time with these tasks, often requiring hundreds of trials before they are able to master them (Boysen and Berntson 1995; Boysen et al. 2001). Their poor performance has been attributed to inadequate inhibition of an innate, evolved

impulse to reach for the greater amount of food, known as a prepotent response tendency. Apes’ consistently poor performance in reverse contingency tasks demonstrates that those that pass AR tests are unlikely to be doing so by learning a reverse contingency rule. This is because they are able to master AR tests in far fewer sessions than it typically takes them to master reverse contingency tasks. For example, Krachun et al. (2009) directly compared chimpanzees’ performance on an AR test with their performance on a matched reverse contingency task. The chimpanzees performed significantly better in the former than the latter, confirming that apes were not passing the AR test by using a reverse contingency rule.

### Related Cognitive Abilities and Tests

Although just a few studies have directly investigated AR discrimination in apes, a variety of other tests may tap into cognitive abilities that rely upon AR discrimination, or that share elements with AR tests. For example, “conservation” is the ability to recognize that the amount of a substance remains constant across changes in shape or arrangement that affect its appearance (Piaget and Inhelder 1974). In the classic liquid-conservation task for children, participants watch as the liquid from one of two identical containers is poured into another container with different proportions (e.g., taller and narrower than the original). Children are then asked whether the amount of liquid in the new container is the same as, or different from, the amount of liquid in the original container. Some investigators (e.g., Braine and Shanks 1965) have theorized that succeeding in conservation tests requires an understanding of the distinction between appearance and reality. Nonverbal conservation tests have been devised for apes, and these animals have had some success in these tests (Suda and Call 2004; Woodruff et al. 1978). However, it is unclear to what extent the apes relied upon strategies that involved discriminating appearance from reality. For example, they could have succeeded by tracking the larger amount of liquid through the transfer from one container to the

other, or by estimating the two quantities by visual inspection after the transfer was complete.

Another cognitive ability that shares features with AR discrimination (as well as with conservation) is “essentialism.” This is the understanding that the true identity or essence of an object remains unchanged despite changes in its superficial features. A common example used to illustrate essentialism is iron pyrite (fool’s gold): despite its superficial similarities to gold, iron pyrite is not the same kind of substance as gold. Cacchione et al. (2016) created a test for essentialism in chimpanzees that uses a standard object-choice paradigm. As in AR tests designed for apes, the choice in the essentialism test is between a preferred item and a nonpreferred item (e.g., slice of banana versus slice of carrot). Apes observe as an experimenter makes the items perceptually identical to one other, for example, by wrapping a banana peel around the outside of the carrot slice and painting the top of it yellow. Thus, the apes are faced with a choice between two items that look the same but are essentially different. Cacchione et al. (2016) found that when given a choice of this kind, the apes preferred the banana to the carrot, despite their identical appearance (provided the working memory demands of the task were sufficiently low and the ape’s motivation was sufficiently high). Thus, the apes chose according to the true identity of the objects, not according to their appearances. On this basis, the researchers suggest that apes may possess a basic form of essentialism that relies upon recognizing when the appearance of an object is incongruent with its true identity, which sounds very much like what children do in the identity-illusion AR tests described earlier. It should be noted, however, that these findings are subject to the same lower-level explanation given for apes’ success in the AR tests described above. A tracking control, similar to that devised for the AR tests, could rule out this alternative explanation.

## Extensions of AR Tests in Animals

Beyond testing for apes’ ability to tell real from apparent, AR tests for apes may also provide a novel way of testing other cognitive abilities, such

as metacognition. Metacognition is the ability to know about one’s own mental states and processes, such as knowing that you can remember someone’s name, or knowing how confident you are about a judgement you have made. In research with human children, AR discrimination is generally considered to be a form of metacognition (Flavell et al. 1986). This is because in order to answer correctly the questions posed to them in the standard verbal tests (e.g., “Does this look like a rock/sponge? Is it really a rock/sponge?”), children must be aware of their own perceptual states (i.e., how things perceptually appear to them), and such awareness is a form of metacognition. For over 20 years, researchers have been using a variety of experimental methods to investigate metacognition in nonhuman animals (Smith et al. 2012). As successful AR discrimination in children is considered a form of metacognition, it has been suggested that nonverbal AR discrimination tests could also be used to study metacognition in nonhuman animals (Call 2012). However, Call (2012) is cautious about this new approach, in part because nonverbal AR tests do not require subjects to report on how objects look to them, as verbal AR tests do. This raises the possibility that subjects could pass the nonverbal AR tests without being aware of their own perceptual states. Nevertheless, proper control procedures, such as tracking controls (above), may be able to rule out such nonmetacognitive explanations of successful performance on nonverbal AR tasks (Krachun et al. 2016).

Recently, developmental researchers have begun to apply methods from AR discrimination tests to test children’s ability to make inferences about others’ mental states, called “theory of mind.” Specifically, such tests have made use of illusory stimuli to investigate children’s understanding of others’ visual perspective (Moll and Meltzoff 2011), false perceptions (Krachun and Lurz 2016), and false beliefs (Buttelmann et al. 2015). To succeed in the tests, children must use their own experience with a visual illusion to infer that another individual will experience the illusion in the same way. It has been suggested (Krachun and Lurz 2016; Lurz 2009) that the “experience-projection” aspect of these tests makes them particularly useful for investigating theory of mind in

animals, because it removes the opportunity for animals to use behavioral or environmental cues to succeed. Given that the possible use of such cues (rather than inferences to mental states) by animals in theory of mind tests has been a controversial issue for decades (Povinelli and Vonk 2003), this is an important new direction in animal theory of mind research. In line with this new direction, Karg et al. (2016) used illusory stimuli in a task designed to test chimpanzees' understanding of mistaken perception in a naïve competitor. Although results did not show that chimpanzees understood the mistaken perceptions of the competitor, the study heralded in a new, innovative method for investigating theory of mind in animals.

## Cross-References

- Conservation
- Essentialism
- Experience Projection
- Meta-Cognition
- Mirror Self-Recognition
- Object-Choice Test
- Perception
- Representation
- Self-Awareness
- Theory of Mind
- Visual Illusions

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## Appearance Versus Reality

### ► Appearance Reality Tests

## Appendicular Skeleton

### ► Skeletal System

## Appetitive Response

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## Synonyms

Approach Behavior; Goal-directed Behavior; Preparatory Response

## Defining and Characterizing Appetitive Responding

Early components of a behavioral sequence may be referred to as appetitive, and late components may be referred to as consummatory. Appetitive responses have been characterized as variable, plastic, and purposive, whereas consummatory responses have been characterized as rigid, simple, and “automatically discharged” (Eibl-Eibesfeldt 1970; Tinbergen 1951).

Understanding the concept of appetitive responding requires attention to both appetitive and consummatory responding and their origination. Early concepts of appetitive and consummatory behaviors were first elaborated on by Craig (1918). Craig (1918) originally characterized appetitive responses as restless, varied forms of activity that served to orient an animal toward an object. Consummatory responses were innate responses consisting of what he referred to as “species-specific constancy.” Traditional ethological views (e.g., Tinbergen 1951) described species-typical behavior as consisting of sequences of appetitive responses and consummatory responses. Responses at the beginning of behavior sequences were referred to as appetitive, whereas the terminal responses at the end of behavior sequences were referred to as consummatory. Appetitive responses have been viewed as variable, plastic, and purposive, whereas consummatory responses have been characterized as rigid, simple, and “automatically discharged.” This perspective implies that appetitive components of behavior may be more susceptible to modification by conditioning than consummatory responses. However, there are numerous published examples suggesting a great deal of plasticity to what were once thought of as rigid and fixed consummatory behaviors.

Pavlov's classic method of studying what is learned about a conditioned stimulus (CS) that predicts an unconditioned stimulus (US) also illustrates a dichotomy of appetitive and consummatory responding. For example, a rodent is presented with a lever (CS) paired with a food pellet (US). After repeated pairings of the CS and US, the lever becomes a conditioned stimulus and may evoke motivation on its own. During



conditioning, the CS may elicit appetitive responses such as orientation to the CS as well as consummatory responses similar to those predictive of the US (i.e., licking, biting, and sniffing of the CS). An animal that directs responses toward the CS during conditioning is considered to be “sign tracking” as opposed to making responses toward the US (“goal tracking”). Goal trackers use the CS to signal impending food. Therefore, during presentation of the CS, they move toward the US. Sign tracking behavior involves an animal perseverating toward the CS rather than toward the US, which reduces the likelihood they will gain access to reward. Numerous drug studies have demonstrated that animals that have a high propensity to sign track attribute greater motivational value to the cues (CSs) associated with a drug (US) and are therefore more sensitive to the drug cues (see Robinson et al. 2014 for review). This sensitivity to drug cues may later result in drug-seeking behavior that might ultimately lead to relapse. Thus, appetitive sign tracking behavior has implications for vulnerability to drug abuse.

Appetitive responding also has roots in operant conditioning procedures. In Skinner’s classic experiment Skinner (1948) involving superstitious behavior in pigeons, food was presented at regular intervals and no behavior was required. Skinner reported that pigeons developed behaviors such as turning counterclockwise about the cage or thrusting its head into one of the upper corners of the cage just prior to food delivery. The pigeons were exhibiting the same behaviors that they were engaging in when the food first became available. Timberlake and Lucas (1985) referred to these behaviors as classically conditioned appetitive responding.

Investigators of animal behavior in laboratory paradigms have also distinguished between “early” and “late” response components when studying more complex behaviors. For example, Konorski (1967) viewed feeding behavior in terms of preparatory and consummatory responses. Preparatory responses involved the elicitation of hunger and searching behavior, whereas consummatory responses involved reflexes beginning with the arrival of food in the mouth. According to Konorski’s model, when a

cue was paired with the opportunity to eat, the conditioned response (CR) that resulted depended on the nature of the cue and when it was introduced during conditioning (i.e., as conditioning became better established, consummatory CRs replaced appetitive hunger CRs). This idea has been elaborated on more recently by Timberlake and his associates as the behavior systems theory (Timberlake and Lucas 1989). Behavior systems theory invokes a hierarchy of control mechanisms consisting of a series of modules organized in a temporal-spatial sequence, with general search and focal search behaviors at one end of the continuum and consummatory behaviors at the other end. Behavior systems theory was developed in an attempt to combine concerns about control of functional behavior with concerns of the role of learning in eliciting new responses and stimulus control.

## The Nature of Appetitive Responses

### Food

Early experiments using animal models typically studied consumption to assess many aspects of food reward but did not account for appetitive behavior. Hodos (1961) was the first to establish a reliable animal model to measure the strength or motivational value of a food stimulus using an appetitive behavior paradigm. Rats reliably pressed a lever for a sweet milk reinforcement, and the amount of effort they were willing to expend was a metric of reward strength. The degree of effort expended to obtain sucrose was tightly correlated with preference for and consumption of the same concentration. More recent animal models have studied appetitive behavior to examine the reward strength or motivational value of food.

### Sex

Frank Beach was among the first researchers to make a distinction between arousal and performance components (appetitive and consummatory, respectively) in male rats. Subsequent lesion studies further dichotomized appetitive and consummatory sexual behavior demonstrating that lesions to the medial preoptic area

(mPOA) eliminated copulatory behavior but not appetitive behaviors (e.g., Meisel and Sachs 1994). Thus, studies of male sexual behavior distinguish sexual motivation (i.e., “libido”) from the performance of copulatory acts. Similarly, studies in male Japanese quail that have utilized both pharmacological manipulations and lesions provide further functional evidence for the appetitive-consummatory distinction.

## Drugs of Abuse

Numerous drugs of abuse, in particular, psychostimulants, elicit appetitive responses that occur in the absence of drug administration. In animals, these appetitive responses typically take the form of compulsive drug-seeking behavior, and they may mimic various aspects of drug relapse in humans (e.g., Weiss et al. 2001). For example, environmental cues that become associated with the subjective effects of a drug may later evoke drug craving. Animal models demonstrate craving via drug-seeking behaviors by showing a preference for a place where they experienced the drug (i.e., a conditioned place preference) or by working for a drug (i.e., lever pressing).

## Neural Substrates of Appetitive Behaviors

Appetitive behaviors are primarily driven by the nature of the reward (e.g., sex, drug, food). Numerous structures are involved in reward-related processing including the hippocampus, prefrontal cortex, and ventral pallidum. However, the majority of research on appetitive behaviors implicates the involvement of the ventral tegmental area (VTA) and nucleus accumbens (NAc). These areas comprise the mesolimbic and mesocortical pathways that make up the reward circuits in the brain via dopaminergic neurons.

The VTA primarily consists of dopamine (DA) neurons and is implicated in many conditioned appetitive responses, specifically those responses associated with processing reward stimuli that motivate an appetitive response (Fields et al. 2007). Additionally, the NAc has both

afferent and efferent DA projections to and from the VTA, and it has long been viewed as the prominent “reward” center of the brain. For this reason, there is a plethora of information about the role of the NAc in appetitive behavior. The NAc has been shown to be involved with approach behaviors for reward-predicting stimuli, and blocking dopamine (DA) transmission in the NAc decreases approach to predictive stimuli in rodents.

## Conclusion

Historically, appetitive responses have been identified and studied as separate from consummatory responses, and observations of animal behavior reinforce the validity of this distinction. There are a variety of appetitive responses that have been investigated in numerous paradigms, including food, sex, and drug studies. Studies of appetitive responding typically have a motivational component such that an animal may seek out a particular stimulus. Appetitive responding is also often tested in learning experiments, and recent studies on substance abuse are focused on appetitive responding and how to extinguish those responses. Several brain structures and neural pathways have been associated with appetitive responding. However, future studies are needed to identify pathways and neural circuitry that are specific to particular types of appetitive responding.

## Cross-References

- ▶ [Adaptedness of Behavior](#)
- ▶ [Associative Learning](#)
- ▶ [Behavior Systems](#)
- ▶ [Classical Conditioning](#)
- ▶ [Ejaculate](#)
- ▶ [Feeding](#)
- ▶ [Goal-Directed Behavior](#)
- ▶ [Ivan Pavlov](#)
- ▶ [Learning](#)
- ▶ [Motivation](#)
- ▶ [Nucleus Accumbens](#)
- ▶ [Sign Tracking](#)

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## Applied Behavior Analysis

### ► Appetitive Response

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## Apprehension of Relations

### ► Insight

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## Approach Behavior

### ► Appetitive Response

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## Approach Test

### ► Human Approach Test

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## Approach/Withdrawal Theory

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T(h)eodore. C. Schneirla (July 23, 1902–August 20, 1968) was among the preeminent comparative psychologists of the twentieth century. An ardent antireductionist, he framed the study of animal behavior and comparative psychology as a holistic, integrative research program (Tobach and Aronson 1970) using both analysis and synthesis (Maier and Schneirla 1935, enlarged in 1964). This program influenced some of the most important comparative psychologists of the twentieth century (e.g., see Aronson et al. 1970). Although those influenced by Schneirla is today a relatively small group (one of the last remaining scientists trained by Schneirla, Ethel Tobach, passed away in 2015 (Greenberg 2015; see also Greenberg, Ethel Tobach, this volume)). Schneirla's ideas continue to influence the thinking of a great many contemporary scientists. Many adhere to his proposal that both psychology and biology are in essence developmental sciences. I also adhere to Schneirla's approach to the study of behavior, an orientation embracing both processes of evolution and development from an epigenetic framework (Lerner and Overton 2013; Michel and Moore 1995; Overton and Lerner 2014).

The focus of this essay is Schneirla's concept of approach/withdrawal which he first introduced in 1939 at a meeting of the American

Psychological Association: “This conception envisages negative-positive responses as fundamentally attributable to differential arousal of excitation-reaction systems which function as though they possessed distinctly different activation thresholds. Through natural selection, we may hypothecate the evolution of such mechanisms along adaptive lines. This view has utility as a hypothetical basis for understanding approach-withdrawal behavior in man” (p. 295). In developing this concept Schneirla (1959, 1965) acknowledged being influenced by others including Wundt, Darwin, Jennings, Pillsbury, and his own teacher, J. F. Shepard (Greenberg 1995). Whereas Schneirla identified this concept as a “theory,” it is at best a “pragmatic hypothesis” (Bunge 1980, p. 22) although its apparent universal application points to its lawlike character (Greenberg et al. 1991). It is useful to point out that in our still youthful history, psychology can point to no real laws (with the possible exception of the law of effect), and although we use the term theory often, we definitely have none that operate as do those in the older sciences. I direct readers to Uttal’s (2005) discussion of what theory is in science and why psychology has none.

Schneirla proposed the A/W concept as a way of understanding the origins of complex behavior in terms of simpler biphasic processes directly related to the quantitative characteristics of stimuli. “At first, he conceptualized the biphasic processes of approach and withdrawal as related to the state of the organism and the intensity of the effective stimuli, and as critical in the initiation and maintenance of activity. This concept of the biphasic approach-withdrawal concept was expanded later by considering it to be a fundamental feature both in the behavior of simple animals such as protozoa and in early stages of behavioral development of the more complex animal forms” (Tobach and Aronson 1970, p. xvi). Some examples discussed by Schneirla include the consistent lunging forward of many fishes, amphibians, and reptiles to “moving stimuli of small area [and the] snapping responses of toads depend upon quantitative properties of the stimulus” (1959, pp. 311–312); and, “An elementary type of orientation is that in which an animal

approaches a low-energy stimulus source, as a neonate kitten nears the abdomen of its mother through crudely directionalized responses to thermal and tactual stimuli from her” (1959, p. 313).

The fundamental premise behind the approach/withdrawal concept is that these response patterns underlie all complex adaptive responses and is a synthesis of several organizing concepts and principles. In their summary of the A/W theory, Raines and Greenberg (1998) described its essential elements: biphasic processes, stimulus intensity, levels of organization, plasticity and epigenesis, and maturation and experience.

*Biphasic processes* (i.e., approach and withdrawal): are characteristic of *all* animals at *all* phyletic levels and are traced to the evolution of adaptive sensory-motor systems – quite simple in lower animals, such as the light-sensitive single cells in earthworms, and complex in vertebrates mediated by the two branches of the autonomic nervous system.

*Stimulus intensity*: low-intensity stimuli elicit approach responses and high-intensity stimuli elicit withdrawal responses. This difference is true throughout the life histories of simple organisms and in the earliest developmental stages of more complex animals. Stimulus intensity refers not only to properties of the external stimulus but also accompanying internal organismic variables, which affect the perception of stimulus intensity resulting in the dimension of “effective stimulus intensity” (e.g., Helson’s 1964 adaptation level theory).

*Levels of organization* (see Greenberg, Behavioral Levels, this volume): Schneirla’s emphasis on this central organizing principle in science leads to a “psychological way” of understanding behavior in much the same way biologists (e.g., Woodger 1929) invoked the concept to develop a uniquely biological way of thinking. In this way, psychological events are not reducible to biology and physiology. Coupling this idea within the A/W concept provides a basis for identifying the lowest level of organization for adaptive functioning. McGuire and Turkewitz (1979) provided an account of the relationship of Schneirla’s concepts of *effective stimulus intensity* and *levels*.

*Plasticity and epigenesis:* species are increasingly behaviorally plastic at higher phyletic levels, as permitted by increasingly complex nervous systems. Schneirla's rejection of reductionism and biological determinism enables this increasing behavioral plasticity. Kuo (1967) referred to this as his principle of behavioral potentials, according to which organisms at each behavioral level have the potential to develop species-typical behaviors, although the realization of this potential is the result of the organism's experiential history and not from their biological endowments (i.e., genes). This rejection of biological reductionism in favor of developmental processes emphasizes that genetic expression is not determined or guaranteed but is probabilistic (e.g., Gottlieb 1970).

*Maturation and experience:* during maturation (i.e., growth and differentiation) the organism is exposed to experiences (all stimulative effects), and it is the *fused* system of maturation and experience (not their interaction) that directs the organism's behavioral development (Schneirla 1959, 1965). It is, of course, now clear that prenatal endogenous and exogenous stimulation affects behavioral development (Kuo 1967). Gottlieb (2001, p. 2) referred to these types of stimulation as nonobvious experiences. "As for nonobvious experiences, who would have dreamed that squirrel monkeys' innate fear of snakes derives from their earlier experience with live insects...? Or that chicks perceiving meal worms as edible morsels is dependent on their having seen their own toes move...?"

Which of these biphasic processes is activated in an organism depends on the stimulus and its intensity. Of course, even identifying just what a stimulus is can be difficult "We often naively assume that 'the stimulus' we present to an organism is 'the same stimulus' it responds to" (Greenberg et al. 1991, p. 41). As an example, Tronick (1967) showed that a radially decreasing shadow is an effective imprinting stimulus, a result predicted by A/W theory. However, Tronick pointed out that such a stimulus was one that increased in intensity – a decrease in the area of a shadow resulting in a brighter visual intensity. Clearly, the crucial dimension of stimulus

intensity depends a great deal on understanding the state of the perceiving organism. McGuire and Turkewitz (1979) distinguished between the objective (physical characteristics) and effective (organismic variables) intensities of a given stimulus. Stimulus intensity is a complex construct and not readily identified in a single modality or by a single physical characteristic. It has been defined in dynamogenic terms (Grice and Hunter 1964) as a dimension dependent on an organism's adaptation level (Helson 1964). Helson's mathematical analysis of a stimulus includes its physical characteristics, the state of the organism (including its degree of maturation and developmental level), and other contextual factors, a crucial dimension that Lerner (1989) has termed developmental contextualism. In the phenomenon of imprinting, Moltz (1963) invoked the A/W idea and hypothesized that chicks would imprint to withdrawing objects and not to those which approached. Whereas his data did not support this idea, Bengtson's (1983) analysis of the complexity of visual stimuli offers an explanation of Moltz's failure. Bengtson showed that, in imprinting, the intensity of the visual stimulus is a complex function of its angular speed and distance from the eye. Large imprinting objects, then, are not necessarily more intense than smaller ones. What was large or small to Moltz may not have been so to his chicks. Schneirla (1959, 1965) discussed A/W responses in many species and to many types of stimuli. For example, his 1959 paper "cited the apparent approach to moonlight reflecting from the surf by newly hatched loggerhead turtles at night, the proneness of certain lizards to approach green as opposed to other spectral hues and to approach figures with smooth outlines rather than others with broken outlines" (Greenberg and Haraway 2002, p. 64). Greenberg and Haraway's discussion of A/W shows it is still an important critical idea in comparative psychology.

## A/W Theory Today

With a single exception – Wolfgang Schleidt's (Schleidt et al. 2011) continued rejection of



Schneirla's interpretation and his continued support of the Lorenzian ethological interpretation of the Hawk-Goose phenomenon (that young birds flee from a hawk like figure because of an innate recognition of its predatory nature, rather than Schneirla's (1965) analysis that the shape of a looming predator is a more intense visual stimulus than is the shape of a looming non predator such as a goose) – it is a curious twist of history that the A/W concept has absolutely vanished from use in the animal behavior literature. Of course, Schleidt himself is an ethologist. However, despite a cautionary comment made by the influential developmentalist John Bowlby (1969) soon after Schneirla's (1965) last extended statement of the A/W concept, that "the extent of its applicability remains unknown" (p. 149), interest in the idea has persisted among developmentalists of all stripes (Hood et al. 1995). While many invoke the concept few acknowledge Schneirla's influence, as noted by Turkewitz (1987):

By the time his [Schneirla's] viewpoint had penetrated the realm of developmental psychology it had become, arguably, the dominant position in developmental psychobiology. As such, it tended to be treated by developmental psychologists as a product of the *zeitgeist* or as part of general lore, thus, not requiring attribution. (p.369)

A sampling of contemporary developmentalists working with A/W as formulated by Schneirla are:

**Margaret Sullivan:** work from her research group (e.g., Lewis et al. 2015) has often focused on aspects of emotional behaviors – anger, for example, as expressed by infants in response to blocked goals. This phenomenon is understood to be an approach-related affect. Their work is consistent with "Darwin's observation that anger leads to behaviors in overcoming obstacles to regain a goal while sadness is a withdrawal emotion as measured related to movement away from the goal. These differential action tendencies are supported by facial behaviors, body activity, and physiological responses such as heart rate and cortisol increases..." (Lewis et al. 2015, p. 1553). Schneirla (1959, 1965), too, indicated that A/W responses apply to the entire organism,

from its overt behavior to its covert physiology and neurology.

**Nathan Fox:** Fox's prolific group often focuses on physiological correlates of temperament (e.g., Helfinstein et al. 2012). Citing earlier work on several animal species they note that biphasic "tendencies across many species suggests that there may be neural circuitry common to many species that is involved in these behaviors...[M]ore recent work has extended these findings on approach by focusing on the neural architecture moderating approach-related behavior. Most recently, this work has mapped the relations between individual differences in human temperament and individual differences in neural circuitry function" (p. 818).

Much contemporary work in development, emotion, and temperament frequently refers not to "withdrawal," as in the Schneirla A/W formulation, but rather to "avoidance." This focus is the case in the Helfinstein article cited above and others such as Blair et al. (2004), who do not cite Schneirla, although they purport to study approach/withdrawal in preschoolers. They use *avoidance* and *withdrawal* interchangeably. Schneirla was quite clear that his use of *approach* is not the opposite of *avoid*: "Confusion is indicated when the term 'approach' is combined with 'avoid,' avoid' as if these were opposite concepts for motivation. ... Seeking and avoidance are of a higher evolutionary and developmental order than approach and withdrawal, and these terms should not be mismated" (Schneirla 1959, p. 298).

Another example of this point is Eliot (2006) who does cite Schneirla and thus, presumably, intends to be studying A/W. The term "withdrawal" never appears in his paper and it is clear that he is equating it with "avoidance." Citing Schneirla (1959), he comments that some have characterized "approach avoidance behavioral decisions as the most critical adaptive judgments that organisms have had to make in the evolutionary past, and it is likely that this adaptive function is the reason that approach-avoidance process are witnessed across animate forms of life..." (p. 113).

Lerner (1989) maintains that when Schneirla and his colleagues articulated the concept of



probabilistic epigenesis, they were laying the groundwork for modern developmental theories including the life span perspective in general. This essay is my attempt to outline the essentials of what is surely the most ambitious theoretical endeavor in comparative psychology, past and present. Schneirla began his theory building process in the early stages of his writing. Indeed, his now classic book, *Principles of animal psychology*, co-written with N. R. F. Maier (1934), contains the seeds of the theoretical ideas described in this essay. The principles are postulated to be universal, applying equally to humans and non-humans alike. The “theory,” incomplete as it is, has influenced many researchers across numerous spheres of psychology. Although he was a comparative psychologist, the persistence of his ideas in developmental psychology attests to its enormous significance.

## Cross-References

- [Behavioral Levels](#)
- [Comparative Psychology](#)
- [Development](#)
- [Ethel Tobach](#)
- [Evolution](#)

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## Approximate Number System (ANS)

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## Synonyms

Core number system; Numerical cognition; Numerosity

## Definition

The approximate number system (ANS) is a core cognitive system of numerical processing that governs animal and human nonsymbolic numerical representations. Weber’s law underlies the ANS, in which performance in discriminating set sizes increases as the ratio between sets also increases.

## Introduction

The ability to perceive, discriminate, store, and represent numerical information supports a host of everyday human behaviors and makes possible engineering feats that drive many of our technological innovations. Of relevance to the current chapter, engineers, astronauts, banking institutions, store clerks, and elementary math students base their simplest and more complicated calculations and numerical processing on a core system of number that is shared among human individuals as well as across a wide range of nonhuman species. Nonhuman animals (hereafter animals) also are sensitive to the quantitative and numerical nature of stimuli in their natural world, although they lack the more advanced forms of numerical

and quantitative processing that constitute a formal system of mathematics. But, even their more limited sensitivity to numerosity is important to many aspects of survival (e.g., foraging, predation, reproduction). To give an example from foraging behavior, discrimination of the largest amount of food from multiple options likely contributes to increased fitness, placing a premium on the ability to discriminate based upon quantity and perhaps even numerosity.

## The Approximate Number System

The core system of number processing is commonly referred to as the approximate number system (ANS) and has been proposed to govern animal and human nonsymbolic numerical representations (see Brannon and Roitman 2003; Cantlon et al. 2009; Gallistel and Gelman 2000, for reviews). A central feature of the ANS is that it follows Weber's law, which states that the degree of discriminability of stimuli is consistent provided the *relative difference* of the stimuli remains the same even as their absolute magnitudes change. The approximate, rather than exact, representational fidelity of true sensory experiences is another feature. Thus, quantities are represented inexactly, and the ability to discriminate any two quantities is a function of the ratio of those quantities to each other, rather than a function of the absolute sizes, numbers, or amounts (see Gallistel and Gelman 2000). Two important behavioral signatures of the ANS are the distance effect and the magnitude effect, both of which combine to generate what is often called the ratio effect. The distance effect reflects that the ability to discriminate between two sets or arrays varies as a function of the absolute difference between sets (e.g., it is easier to tell 10 coins from 5 than telling 10 coins from 8). The magnitude effect reflects that, in general, larger magnitudes or quantities are harder to distinguish from each other than are smaller magnitudes even if the difference is the same (e.g., it is harder to tell 10 coins from 9 compared to telling 4 coins from 3). The ratio effect therefore reflects Weber's law in showing that at a constant ratio, there is a constant degree of

discriminability (e.g., one will be as good at telling 4 coins from 5 as they are at telling 8 coins from 10, assuming the ANS is engaged in estimating the numbers of coins). For an example relevant to animal foraging, a ratio of 2:1 (8 berries vs. 4 berries) is easier to discriminate (i.e., reflected in higher accuracy and faster response times) than a 3:2 ratio (12 berries vs. 8 berries), despite the fact that the absolute difference in each array is the same – 4 berries.

## Behavioral Evidence for the ANS: Quantity Judgments

Comparative tests of numerical cognition often are assessed through relative quantity judgment tasks that present an individual animal with two or more arrays that vary in quantity (size, numerosness, or volume), quality (relative degree of preference), or sometimes both. When food stimuli are used, little to no training is required, and stable response patterns in terms of subjective food preferences as well as objective measures of quantity discrimination abilities are established. For example, when a female chimpanzee named Lana was presented with two quantities of cereal, she reliably chose the larger quantity of each comparison. And, in accordance with the signature size effect of the ANS, Lana's performance decreased when both sets were close to the upper limit of the total possible number of cereal pieces (10) and when the ratio between sets was closer to one (e.g., 8:9 was more difficult than 6:9; Dooley and Gill 1977). Tests of relative food quantity discrimination have now been given to a wide range of animal species, underscoring the adaptive value of quantity discrimination capacities, and in many cases ratio effects are evident.

Animals also have demonstrated proficiency in similar quantity discrimination tasks presenting only one food array at a given time. For example, orangutans (Call 2000), chimpanzees (Beran 2001, 2004), and capuchin monkeys (Evans et al. 2009) excelled at selecting the larger of two food quantities even when only one quantity was visible at a given time (either by presenting the subject with one entire array prior to the other

or by sequentially adding food items to one array at a time). Performance patterns revealed ratio effects characteristic of the ANS, and importantly, these results suggested that primates could represent numerical information similar to human adults in addition to the use of perceptual mechanisms. Similar performance patterns are evident in work with a variety of nonhuman primate species (e.g., Addessi et al. 2008; Hanus and Call 2007).

### **Behavioral Evidence for the ANS: Numerosity Judgments**

Relative numerosness tasks, unlike relative quantity judgment tasks, specifically control for nonnumeric cues that may lead an animal to respond based upon some other quantity dimension separate from number (e.g., size). These tasks are unique in that only true numerical (i.e., cardinal) properties can be used to guide responding rather than other nonnumeric cues (e.g., surface area, total volume, presentation speed, auditory cues, etc.). In perhaps the clearest example of such a task, Brannon and Terrace (2000) presented rhesus macaques with a computerized experiment depicting randomly generated stimulus arrays and trained the monkeys to sequence the numerosities 1 to 4 in ascending order while controlling for size, shape, and color of the items within arrays. In unreinforced transfer trials, monkeys responded to the numerosities 5 to 9 in ascending order. Importantly, performance patterns including accuracy and latency matched those of human adults in terms of distance and size effects of the ANS for both sets of numbers, even in the novel transfer trials. In a similar study, pigeons learned to sequence visual arrays of items in the numerical range of 1 to 7, with smaller numbers (and larger distances between the numbers) leading to higher performance rates in line with the predictions of the ANS (Emmerton et al. 1997). Subsequent research based on this task with other species including capuchin monkeys (Judge et al. 2005), a baboon and squirrel monkey (Smith et al. 2003), and lemurs (Merritt et al. 2011) revealed similar performance patterns governed by ratio effects.

As demonstrated above, carefully controlled numerosity tasks afford an advantage over food choice paradigms in that a variety of nonnumeric cues can be carefully controlled, and one is not faced with the concern that animals may find total amount of food more salient than the larger number of food items. Thus, efforts to automate and control sequential presentation tasks also have been developed. For example, Beran (2007) presented a computer task with two digital “containers” to rhesus monkeys into which digital items were “dropped” with the task objective to choose the container that received a greater number of items. The monkeys tracked and selected the larger of the two numerosities despite the fact that presentation duration (i.e., how quickly the items were added to the containers) and surface area (i.e., size of the falling items) were controlled. Monkeys showed clear evidence of ratio effects in all tests.

How do these comparative results stack up to human adult performance? The evidence indicates that the ANS is at play similarly in both human and nonhuman primate numerosity judgments, and direct comparisons of monkey and adult performance on similar tasks provide further support. For example, when human adults are prevented from counting via speeded presentation of stimuli or by use of articulatory suppression (e.g., Agrillo et al. 2016; Whalen et al. 1999), they demonstrated similar performance patterns to nonhuman primates in terms of the degree to which they respond on the basis of the ratio between sets. Cantlon and Brannon (2007) presented rhesus macaques and human adults with a computerized nonverbal addition task with the objective of adding together two dot arrays. These arrays were sequentially presented and subjects then selected between a dot array that represented the correct numerical sum and a foil dot array with the wrong answer. Although humans outperformed monkeys on the addition task, both adult and monkey performance was ratio dependent. As the ratio between the numerical sum and the foil approached one, performance in terms of accuracy decreased. These direct comparisons of animal to adult performance using identical methodology lend further support for continuity

in numerical processing devoid of human-unique experiences, culture, and linguistic processing and specifically a system that relies upon analog-numerical representations.

### Controversy: One Number System or Two?

There is little controversy surrounding the existence of the ANS as a core system of number. Although the ANS and its effects are well understood and accepted in the numerical cognition literature, there is also a claim for the existence of a second system for representing numerosity that is size-limited (typically described as four items or less) but that precisely represents small sets of discrete items. This second system, often referred to as the object file system (OFS), is described as a parallel individuation system that is limited in its ability to discriminate and estimate sets greater than four due to demands on attention and working memory (Feigenson and Carey 2005). Evidence for the OFS emerged from the developmental literature with young children and infants who demonstrated elevated performance patterns in response to small sets in comparison to large sets (containing more than four stimuli; e.g., Feigenson et al. 2002). However, other reports suggest that the ANS appears to be the main system underlying discrimination performance with little evidence for the OFS (e.g., Cantlon et al. 2010).

Comparative studies provide some support for elevated performance with small sets of less than four stimuli (fish: Agrillo et al. 2014; birds: Garland et al. 2012; amphibians: Krusche et al. 2010; primates: Hauser et al. 2000). For example, Hauser et al. (2000) presented semi-free ranging macaques with a two-choice discrimination task in which apple pieces were added to two buckets and the monkeys then selected the desired bucket (and presumably larger quantity of food). Monkeys successfully discriminated comparisons with small numerosities (1 vs. 2, 2 vs. 3, 3 vs. 4, 3 vs. 5) but failed at comparisons containing sets

with a larger number of items (4 vs. 5, 4 vs. 6, 4 vs. 8, 3 vs. 8). These results stand in contrast to a large number of primate studies demonstrating evidence of ratio effects with no evidence of a super-precision with small sets (e.g., Barnard et al. 2013; Beran 2001, 2004, 2007; Cantlon and Brannon 2007; Hanus and Call 2007; Nieder and Miller 2004).

In a recent comparative study, Beran and Parrish (2016) adopted a procedure used with human adults to assess the object file system in capuchin monkeys. In the original human study by Choo and Franconeri (2014), adults were presented with a computerized relative discrimination task comparing two sets of dots to one another followed by a same/different task in which they had to designate two sets as containing an identical number of dots or not. Both sets were either small (3 dots against 1, 2, 4, or 5 dots) or large (30 dots against 10, 20, 40, or 50 dots). Adults demonstrated faster response times when comparing the small sets versus when comparing the large sets despite the identical ratios. Capuchin monkeys did not show the same “super-precision” with small sets compared to large sets, with performance instead dictated by the ratio between dot arrays (Beran and Parrish 2016). A key feature of the comparative task was that it was the first formal study of numerical cognition given to these monkeys, and thus they had not received extensive training or former experience making these types of numerical judgments (see Bisazza et al. (2014) for a greater discussion on how training may lead to an overreliance on the ANS).

The debate regarding the existence of two core systems of number or one is ongoing, but comparative research definitively indicates that the ANS underlies much of our own numerical discrimination abilities as well as those of other animal species. It is also possible that a system equipped to deal with small sets with super-precision may be a result of human-unique learning experiences (e.g., Hyde 2011) or a necessary feature for tracking small sets of moving objects (Franconeri et al. 2007). Such a size-limited



system as the OFS for processing small numbers may be used by some species under certain conditions.

## Summary

The ANS is a hallmark feature of animal cognition. It underlies nearly all reported instances of numerical or quantitative judgments by species ranging across the spectrum of those that have ever been tested by comparative psychologists. The ANS is evident across sensory modalities (visual, auditory, etc.), and for discrete and continuous quantities, although its primary empirical assessment has been with discrete, visual stimuli. Behavioral studies such as those outlined in this article suggest an ontogenetic and phylogenetic continuity in numerical and quantitative processing. A consensus has emerged that the ANS supports and perhaps underlies advanced mathematical and numerical representations that emerge in human development and with formal education.

## Cross-References

- [Absolute Number Discrimination](#)
- [Arabic Numerals](#)
- [Duane Rumbaugh](#)
- [Michael J. Beran](#)
- [Numerosity](#)
- [Relative Numerosity](#)
- [Sarah “Sally” Boysen](#)

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## Arabic Numerals

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Nonhuman animals are implicitly sensitive to numerosity that does not require symbolic verbal representation of the numbers and does not require a counting repertoire (e.g., an analog magnitude system). In addition, with training, animals can demonstrate sensitivity to numerosity in a more precise manner that is aided by symbolic representation of numbers – such as Arabic numerals. Animals' use of numerals indicates a sense of “cardinality” regarding numerosity, and is a central feature of more advanced mathematical cognition. Comparative numerical cognition research has focused on whether animals can use Arabic numerals in a similar way to how humans use numerals, and what that may tell us about the basic cognitive processes that underlie the symbolic understanding of numerosity.

One approach to evaluating whether animals can represent numerosity symbolically is to have them appropriately match a numeral to some number of items (i.e., provide a cardinal label such as a numeral or other symbol for the perceived number). For example, Boysen and Berntson (1989) reported that a chimpanzee could identify the number of objects in her environment and point to the corresponding Arabic numeral. She also spontaneously demonstrated numerical representation through addition by correctly identifying the number of objects arranged in different locations and summing their numerosity before pointing to the numeral that indicated the summed total. Matsuzawa (1985) also showed that a chimpanzee could apply Arabic numerals as labels for sets of one to six items even when those items varied across trials. Pepperberg (1987) similarly demonstrated that the parrot Alex could report Arabic numerals vocally as the labels for sets of items and accurately report the summation of two sets.

Alternatively, animals can demonstrate the understanding of number cardinality by having them identify or collect an appropriate number of items to match a given Arabic numeral. This kind of task has come to be called “constructive” enumeration, because subjects need to use the numeral to guide subsequent collection efforts, presumably while enumerating items that have been collected and tracking whether that enumeration matches the Arabic numeral value. Rumbaugh et al. (1989), for example, demonstrated that the chimpanzee Lana could learn through successive training stages to see an Arabic numeral on a computer screen, and then use a cursor to collect boxes onscreen one at a time, until she had collected a set equal to that represented by the numeral. Lana and another chimpanzee, Mercury, learned to do this for up to the numeral 7 (Beran and Rumbaugh 2001). Xia et al. (2000) showed that pigeons could make the same collection responses by pecking a key an equivalent number of times to the Arabic numeral-like symbol presented on it. Like chimpanzees, pigeons were successful up to the numeral 6. However, in all of these cases, an interesting pattern emerged whereby larger set sizes were more difficult for subjects to match in their collections or pecks, a result that aligns with the idea that numerosity is represented inexactly by nonhuman species, with increased variability in those representations that follows Weber’s law. Specifically, Weber’s law states that stimuli must differ by the same proportion for individuals to maintain the same level of discrimination performance (e.g., discriminating three from six items is the same level of difficulty as discriminating five from ten items).

Experiments requiring the matching of numerals to sets-of-items and sets-of-items to numerals provide evidence that animals can establish symbolic recognition of a number’s cardinal value. Further research has established that animals can also symbolically recognize numbers’ relative values (i.e., their ordinal value). Washburn and Rumbaugh (1991) demonstrated that rhesus monkeys (*Macaca mulatta*) would choose the larger numeral in a set of numerals where the number of pellets earned matched the value of the numeral, even in probe trials with a novel set of numeral arrangements that had never been presented

before. Harris et al. (2010) expanded upon this to show that when facing a novel pairing of an array of dots to a numeral, macaques would spontaneously choose the higher valued option in either form. Olthof et al. (1997) presented squirrel monkeys with Arabic numerals in a manual task that involved the numerals indicating how many food items were hidden underneath the cards on which they were written. After the monkeys learned to choose the larger numeral values, they were presented with combinations of numerals to see if they could sum those values to determine the larger overall food amount from the two sets of numerals (in these tests, the monkeys could be shown 2 numbers vs. 2 numbers, 1 number vs. 2 numbers, and 3 numbers vs. 3 numbers). The monkeys generally selected the largest total amount of food given the combinations of numerals they saw in the response options, even when they sometimes had to choose a set with more overall food but not with the individually largest-value numeral. For example, they chose  $3 + 3$  over the numeral 5 in some cases. These results suggest that monkeys and pigeons can map numerals to a set amount and that this symbolic representation includes a generalized understanding of the relative ordinal numeral value. However, this transfer of ordinal recognition of numerical value did not generalize to the number “0” (i.e., cardinally the absence of an item or ordinally the value below 1) in chimpanzees (Biro and Matsuzawa 2001). The parrot Alex also failed to spontaneously recognize 0 in its ordinal position, although the parrot did recognize that 0 corresponded with “none” (Pepperberg 2006).

Arabic numerals also can be used by animals as information symbols for things that they must do. For example, Harris and Washburn (2005) showed the monkeys learned that Arabic numerals found inside a computerized maze indicated how many times that arm of the maze should be investigated because the numeral represented the number of rewarded runs of that arm of the maze. Comparative interest in number symbols such as Arabic numerals also goes beyond the desire to understand the processes underlying sensitivity to numerosity. The utility of such numeral knowledge can aid in research into other cognitive

processes such as executive functioning and planning strategies in animals. Washburn (1994), for example, demonstrated that an array of numerals can produce a Stroop-like interference effect. Washburn trained macaques to select the larger of two arrays of items onscreen. In baseline trials, the stimuli making up each set were nonnumerals, and thus monkeys faced no possible interference. However, when numerals were used, they either operated to aid the discrimination (congruent trials) because the set with more stimuli also consisted of the larger numeral items (e.g., an array of four numeral 3s vs. an array of two numeral 2s) or they operated to create potential interference (e.g., an array of four numeral 2s vs. an array of two numeral 3s). Washburn showed that performance was better when the number of numerals was congruent with the symbolic value of the numerals than when it was incongruent, a result that nicely suggested Stroop-like interference. In another approach to using numerals to assess broader cognitive capacities, Kawai and Matsuzawa (2000) studied planning abilities in chimpanzees when they had to sequence numerals. In that task, the chimpanzees had to select Arabic numerals in ascending order on a computer screen, with the key manipulation being that the numerals did not stay onscreen but were covered after being presented only briefly. Given this brief presentation, the chimpanzees had to rapidly discern where each of the numerals was located and then remember the necessary sequence to touch them all even after they were occluded. Thus, the sequencing of Arabic numerals allowed an assessment of working memory span and planning in chimpanzees.

To summarize, the use of Arabic numerals as discriminative stimuli has contributed many interesting findings in the comparative literature, both for “formal” studies of numerical cognition and for other areas of cognitive processing and behavioral discrimination. These findings are robust in that they have been observed in a variety of species and across a variety of tasks. Furthermore, these comparative data are often in agreement with results found in humans, particularly younger children in the case of numerical cognition research. Such results suggest a shared evolutionary mechanism that mediates symbolic discrimination across species, perhaps especially for

magnitude and quantitative information. Arabic numerals acquire meaning for animals, and can be used as important tools for understanding symbolic representation in other species.

## Cross-References

- [Addition](#)
- [Ai \(Chimpanzee\)](#)
- [Alex the Parrot](#)
- [Approximate Number System \(ANS\)](#)
- [Counting](#)
- [David Washburn](#)
- [Duane Rumbaugh](#)
- [Irene M. Pepperberg, PhD](#)
- [Michael J. Beran](#)
- [Numerosity](#)
- [Relative Numerosity](#)
- [Sarah “Sally” Boysen](#)
- [Sarah, Lana, Sherman, and Austin](#)
- [Stroop Effect](#)

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## Arachnids

### ► Arthropod Cognition

## Arbitrariness

### ► Cognition

## Arbitrary Stimuli

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## Synonyms

Generic; Neutral; Ubiquitously selected stimuli

## Definition

An arbitrary stimulus is an arbitrarily chosen cue paired with a biologically significant event (e.g., Unconditioned stimulus (US)). It does not have to share any inherent relationship with the US.

## Introduction

Definitions of Pavlovian conditioning from the general process view often pertain to forming associations between initially unrelated events. Usually, a cue that is neutral or arbitrary in relation to the US is paired repeatedly with the US in a certain temporal proximity. As a result, the cue alone comes to elicit conditioned responding. Conditioning is then identified by an increase or decrease in potential of responding to the conditioned stimulus (CS). The main premise of general process approaches to conditioning and learning is that all forms of learning could be explained in terms of a relatively modest number of general principles, and this popular description of Pavlovian conditioning reflects some of the important principles of how conditioning occurs. For sure, the search for general principles is one of the most important aspects of any scientific venture, and the general process view of Pavlovian conditioning has provided a great deal of knowledge about the principle mechanisms of conditioning and learning. Pavlov (1927) identified some of the major behavioral phenomena such as delayed conditioning, inhibition of delay, extinction, and spontaneous recovery in his laboratory. He noted that intense stimuli made more effective CSs than less intense ones. In addition to the stimulus intensity, he emphasized the role of CS modality in conditioning. For instance, tactile and auditory stimuli were more effective CSs than visual or thermal stimuli in the case of salivary conditioning with dogs. Thorndike (1911) had already dared to propose the Law of Effect to formulate the mechanism of instrumental behavior when Skinner (1938) characterized his own general process of learning based on schedules of reinforcement and shaping. According to Skinner, any arbitrary associative link could be formed between a response and the outcome with the same ease. These early efforts to establish general laws or principles of learning were followed by more recent researchers. Each of them contributed towards the betterment of the general theories of learning by revising or reformulating the previous ones. Kamin's (1969) demonstration of blocking effect is a turning point in the endeavor; his work indicated that the temporal contiguity accounts of

Pavlovian learning for the acquisition of conditioned responses were insufficient, in fact the paradigm might be more about contingency rather than contiguity. In other words, what a CS tells about the occurrence of the US should be more important than whether they are in temporal proximity. According to Kamin (1969), when we come to the second phase of the blocking procedure, the US has already become fully associated with the CS, thus in the presence of the same CS, the US is ineffective. Because the US is highly expected and no longer surprising now, there will be no more room for further increase in associative strength for another CS in spite of its temporal contiguity with the US. Thus, “the necessary and sufficient conditions” for the establishment of CS–US association needed to be investigated.

Rescorla and Wagner (1972) formulated an acquisition theory of learning focusing on the circumstances producing Pavlovian conditioning. The theory was able to offer an explanation for how a neutral stimulus gains associative strength from one trial to the next as the function of US expectancy by considering the summed associative strength of all cues present during that trial. Moreover, it was compatible with various learning phenomena such as blocking, overshadowing, overexpectation, and contextual conditioning. In the model, although CSs do not have to be purely neutral, they are always something arbitrary. The model grants the differences among CSs in terms of differences in their salience; however, in the original version of the model, the salience of a CS is constant and does not change during training. Although later on Wagner and Rescorla (1972) allowed that the effectiveness of CS could vary by factors other than its intensity, they did not use it any further than to explain the CS-pre-exposure effect. The attention-based models of conditioning (e.g., Mackintosh 1975; Pearce and Hall 1980) predominantly focused on the effectiveness of a CS in terms of the amount of attention it governs. For example, Mackintosh (1975) suggested if a CS predicts the occurrence of the US better than other stimuli present in the situation, its associability, and hence its effectiveness as a CS, will increase. Therefore, the effectiveness of a CS is the measure of its relative predictive strength in

regard to the other CSs present. The model is based on the change in associability of the CS through experience. These and other following models such as the SOP and AESOP models (Wagner 1981; Wagner and Brandon 1989), the comparator hypothesis (Stout and Miller 2007), the temporal coding hypothesis (Savastano and Miller 1998), and Rate Expectancy Theory (Gallistel and Gibbon 2000) treated a CS as an arbitrary stimulus.

Traditional accounts of conditioning included parameters such as stimulus salience, intensity, and discriminability in their analyses; however, they implicitly or explicitly agree with the notion of stimulus equivalency (Johnston 1981). According to the principle of stimulus equivalency, stimuli are generic events; hence, any two events could be associated with equal ease. Therefore, conditioned responses would develop regardless of the preexisting relations between the conditioned stimulus (CS) and unconditioned stimulus (US). Also, according to traditional general process views, the specific biological constraints experienced by species from different ecological niches that arose via evolution were insignificant in the analysis of behavior. This view calls forth the idea that the CS, by definition, is “neutral,” and it has no inherent effect on conditioning. Thus, the CS may be chosen arbitrarily with respect to the US. As Pavlov once assumed, any cue an animal could sense could be used as a conditioned stimulus for every response (Lakoff and Johnson 1999). The general process-based view of conditioning and learning made remarkable contributions to our understanding of the mechanisms of various learning phenomena. However, it has not said much about functional roles that conditioning plays in the lives of animals (Domjan 2005). This mechanistic-associative view has changed as behaviorist principles have undergone significant revision, particularly in light of findings from functional perspectives on learning.

In their long evolutionary histories, species have evolved necessary machinery to associate the co-occurrence of naturally occurring CSs and USs. In contrast to arbitrarily chosen cues, ecologically relevant cues are readily associated with their



resulting counterparts. Such examples shed light on the ultimate causes of learning mechanisms. For example, rats were able to associate audiovisual cues with a foot shock but not so with the illness; moreover, they were able to associate taste cues with illness but not so with the foot shock (Garcia and Koelling 1966). Similarly, Foree and LoLordo (1973) found that pigeons predominantly use auditory cues as discriminative stimuli for avoidance behavior as opposed to visual cues. What if an arbitrary CS reliably precedes the biologically significant US? Animals indeed learn to associate an arbitrarily chosen CS with the US. According to the Behavior Systems Approach (Timberlake and Lucas 1989), a conditioned stimulus (CS), even though it may be an arbitrary CS, is integrated into the behavior system that is activated by the US through the conditioning process. For example, an unpleasant US such as presentation of a brief foot shock activates a defense behavior system which generally includes unconditioned species typical defense reactions (e.g., jump). An arbitrary CS, which may be a brief tone or a light presented in the experimental chamber, is paired with the aversive US repeatedly until it reliably signals occurrence of the US. The CS-alone tests trials evince, by an increase in animal's immobility (e.g. freezing), that the CS acquired conditioned properties and became an integral part of the animal's defense behavior system. The nature of the resultant CR is determined by the behavior system relevant to the US involved. For that reason, the CR is not jumping but rather a freezing response. The ease of learning a particular task depends on the extent to which the conditioned stimulus is relevant to the behavior system that is activated by the US. In natural circumstances, ecologically relevant CSs which are already parts of the relevant behavior system reliably precede the occurrence of USs. Thus, Timberlake's (1994) pursuit to integrate stimulus and response factors into a general theory of learning has been well received by the scientific community. In line with the rise of functional approaches to learning, there has been growing interest in examining the ecological relevance of Pavlovian conditioning. For example, Domjan et al. (2004) applied functional approaches to better understand how Pavlovian conditioning interacts

with the preexisting organization of behavior in an animal model of sexual conditioning.

In conclusion, the general process theorists held that there is a set of general principles applicable to all learning; also, they believed that all examples of learning are manifestations of an underlying general process. This focus on searching for general mechanisms responsible for conditioned behavior surely advanced our understanding about various learning phenomena such as acquisition, extinction, external inhibition, recovery from extinction, stimulus generalization, stimulus discrimination, latent inhibition, conditioned suppression, conditioned inhibition, and blocking. The majority of these phenomena have been observed in laboratory settings by employing stimuli that are arbitrary with respect to what animals might experience in their natural environment. A complementary approach, which has yielded important additional insights into how conditioning works, focuses on functional and ecological relationships between animals and how they learn (Domjan et al. 2004).

## Cross-References

- [Associative Learning](#)
- [Behavior Systems](#)
- [Biological Preparedness](#)
- [Classical Conditioning](#)
- [Naturalistic Stimuli](#)

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## Arboreality

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## Introduction

Arboreality simply means living in the trees. There are numerous species that live in trees for all or part of their lives, including a wide range of rodent species, monkeys and great apes, koalas, sloths, many species of birds (such as parrots), and lizards like chameleons and geckos. Some animals live both on the forest floor and in tree crowns, whereas others, like Sumatran orangutans, are almost exclusively arboreal, rarely descending from the tree canopy. Arboreality imposes unique cognitive demands on animals because of the physical structure of the environment: trees and their branches form a discrete and discontinuous surface on which animals can move, and the risk of falling means that animals need to choose safe supports that can bear their weight in order to travel safely. In addition, food may be patchily and unpredictably distributed in three-dimensional space, so the cognitive demands of finding and processing food and of creating safe and comfortable places to sleep are greatly enhanced in arboreal compared to terrestrial habitats. Finally, forest environments (particularly those in the tropics) are often highly dynamic environments, with rapid growth and decay of trees, so that the physical environment may change in structure within an individual's lifespan. However, the cognitive challenges of arboreal life will vary among different taxa, according to their body size, mode of locomotion, and the part of the forest canopy that they need to access and move around.

Many animals that exploit both the forest floor and forest canopy need to climb, sometimes large distances, to get into the forest canopy, which requires them to oppose gravity. This is highly physically demanding, but is probably not cognitively demanding because the supports are not

compliant (flexible) – either because they are large (like tree trunks) or because the weight of the animal stabilizes the support (e.g., when chimpanzees climb thin vines or humans climb ropes). This allows the animals to rely on stereotyped, preprogrammed movements, which are cognitively simple and relatively easy to learn (Hunt 2004). Similarly, since forest-living bird species such as the scarlet macaw (*Ara macao*) can fly, they face fewer challenges accessing the forest canopy than arboreal mammals. In contrast traveling within tree crowns for mammals and birds can be both physically and cognitively demanding because forest canopy consists of a three-dimensional mesh of branches and vines that vary in their connectedness, flexibility, and continuity (Thorpe et al. 2009). For small-bodied animals, the gaps between branches can be very large in proportion to their body size, requiring large leaps to progress. For large-bodied animals, not all of the available supports will be strong enough to support their weight, leading to a risk of falling and potential injury or death. Many of the available weight-bearing supports may also deflect underneath their weight, making it difficult for them to predict how the support will behave when they load their weight onto it and requiring them to adjust their movement moment-by-moment as supports are found to be more or less compliant than estimated (Hunt 2004). These issues mean that large-bodied arboreal animals need to choose the supports they use carefully and therefore raise interesting questions about how much arboreal animals understand about the physical properties of their environment.

For many animals, the most challenging part of the forest canopy is called the “terminal branch niche.” This refers to the highly flexible branches at the periphery of tree crowns which bend substantially under the animal’s weight and vary enormously in their properties, making simple learning strategies ineffective. Despite the increased risks of falling in the terminal branch niche, it is one of the most desirable parts of the forest canopy for arboreal animals because it is where fruits tend to be abundant and where the narrowest gaps between tree crowns exist for animals that travel at height. Being able to predict

how flexible branches and lianas will behave under their weight is critical for the animal to ensure its safety and to minimize its path length to optimize the ratio between its daily energetic cost of locomotion and the energy it is able to consume. This becomes particularly cognitively challenging during long-distance arboreal travel where the animals ideally need to plan routes at least several steps ahead, to ensure they will not have to retrace their steps or take lengthy detours when they find gaps they cannot cross or supports that are not strong enough to take their weight.

### Cognitive Challenges of Arboreal Environments

We have outlined some of the challenges that arboreal environments pose for the animals that inhabit them. However, why might these challenges require specifically *cognitive* solutions, rather than the evolution of other kinds of behavioral adaptations, such as instinctive behavior or forms of associative learning? While there is considerable debate about the precise definition of the term “cognition,” there is reasonable consensus that it involves collecting, processing, and making decisions on the basis of information from the environment (see Shettleworth 2010). The key feature of cognition is therefore that it is flexible, allowing the animal to respond appropriately, even in novel situations. This is important in arboreal environments, because they tend to be complex and dynamic, showing substantial variability over both time and space. This means that a fixed or limited repertoire of responses is unlikely to be adequate, as the “appropriate” response is likely to change frequently (Chappell et al. 2012).

For many years, it was argued that ecological factors were likely to have driven cognitive development in primates, either because of the demands of locating unpredictable, spatially distributed food resources in tropical forests (Milton 1981) or because of the demands of dealing with a complex physical habitat (the “Technical Intelligence Hypothesis”: Byrne 1997). Subsequently, the research focus has shifted to social drivers of primate intelligence (the “Social Brain

Hypothesis”: Dunbar 1998). However, a recent, large, and robust meta-analysis of data on a range of primate species has suggested that brain size (and therefore, it is assumed, intelligence, but see Healy and Rowe (2007) for a critique) in primates is associated with diet, not sociality (DeCasien et al. 2017). Certainly, a variety of ecological factors associated with the complexity of arboreal life are likely to have been important for many arboreal animals, not just primates. Nevertheless, some of the largest animals to rely on forest canopy are the great apes: orangutans (*Pongo* sp.) are almost exclusively arboreal, and chimpanzees (*Pan* sp.) and gorillas (*Gorilla* sp.) exploit forest canopy extensively, particularly during the fruiting season. Their size means that they need to select supports for locomotion and nest building very carefully in order to avoid potentially lethal falls. This means that they may benefit from representing problems in a more abstract way, so that they can potentially evaluate the outcome of alternative actions mentally rather than physically, possibly planning such actions more than one step ahead. However, the behavioral adaptations of great apes and other arboreal species include elements of instinctive and learned behavior, alongside more cognitive elements. Untangling these inputs is difficult, but we can focus on flexible and contextually appropriate behavior, in which animals respond to the particular suite of problems with which they are faced.

In this contribution, we flesh out these possibilities in relation to great apes and also explore whether other species that live in arboreal habitats might also have evolved advanced cognitive abilities linked to their environment. We predict (**P**) that some arboreal animals, particularly the large-bodied ones that use the terminal branch niche or travel at height, can (**P1**) detect and reason about the properties, physical behavior, and affordances of arboreal supports and (**P2**) also about the predictable physical effects of their own actions. We suggest they might be able to (**P3**) evaluate routes in advance of movement and (**P4**) detect new risks or opportunities if supports confound their expectations and exploit these appropriately. We consider these predictions in relation to the cognitive demands of three key components of arboreal life:

nest building, locomotion, and remembering the location of arboreal resources. We then relate these findings to the cognitive needs of intelligent, arboreal species in captivity.

## Arboreal Nest Building

Nests can provide safe arboreal resting spaces for animals, protection from terrestrial predators, thermoregulatory advantages, and/or freedom from biting insects found at lower levels (Koops et al. 2012). For birds, nests have a crucial function in the incubation of eggs and sheltering altricial chicks before fledging. Building a safe, structurally sound nest is a complex task, involving selection of an appropriate site and choice of suitable materials. The nest maker then needs to manipulate the materials in relation to each other and the nest substrate to create a nest with enough structural integrity to support its occupants and to withstand movement of the tree and nest in the wind.

All great apes build arboreal nests, both for night-time sleep and for resting during the day (Stewart 2011). Orangutans build nests exclusively in the trees and chimpanzees predominantly do, while western lowland gorillas show the most variable nesting behavior, utilizing unconstructed ground nests as well as fully constructed ground or tree nests (Tutin et al. 1995). Because of the conserved nature of nest construction in great apes, it has been suggested that it evolved in a common great ape ancestor in the Miocene period and is thus likely to have contributed to the origins of great ape intelligence. Although there is likely an innate component to nest building in great apes, it is not an entirely instinctive behavior. Orangutans and chimpanzees are selective about the trees in which they choose to build nests, and research suggests that this relates to the innate flexibility of the wood of different tree species and perhaps to an understanding of the requirement for branches that will exhibit “greenstick” fractures, whereby the end of the branch fractures but does not detach completely (van Casteren et al. 2012). This phenomenon allows strength and rigidity to be built

into the nest by weaving larger branches over a framework of more solid limbs to form a platform, and then smaller twigs are folded over to form a raised rim (van Casteren et al. 2012). In some cases, leafy material is detached and added to the nest bowl to form a sleeping surface (Stewart et al. 2007; van Casteren et al. 2012). These nest types therefore require the ape to have an understanding of the physical properties of different tree species and the effect of their own actions on the branch, meeting predictions **P1** and **P2** above. They also need to organize their behavior in the correct sequence to construct a supportive nest that can bear their weight safely, which indicates an element of planning (**P3**). It has been shown that immature individuals build nests more efficiently and of a higher quality when exposed to nest-building adults which also indicates a role for learning and innovation in the building of nests.

Analogy with arboreal nest building in great apes suggests that some of the nest building behaviors of birds also reflect technical knowledge of the properties and mechanics of the materials they can use to build nests. Arboreal birds' nests vary enormously in their size, location, and structure and in the materials used to construct them (Breen et al. 2016). They can be made from a wide variety of both natural and man-made materials, often with several distinct materials used in one nest, each serving a different function. For example, while the outer part of a nest may be composed of relatively rigid twigs and sticks to provide structural strength, the nest cup may be lined with feathers, mosses, or other soft materials. The use of soft lining materials suggests that, like great apes (Samson and Hunt 2012), the birds have a concept of thermoregulatory needs and/or comfort. Birds' nests also vary widely in complexity, from an untidy pile of material to an intricately interwoven structure. Birds must make a myriad of important decisions, from selecting an appropriate location for their nest, choosing and manipulating appropriate materials, and constructing a secure, structurally sound nest, sometimes coordinating with their mate's construction activity (Healy et al. 2008).

Despite a long history of assumption that nest building by birds is instinctive, evidence is

growing that learning is an important component of nest construction behavior. Breen et al. (2016) have collated a myriad of examples from field-based observations and lab experiments to show that birds modify their behavior in nest site selection as a result of previous breeding success (avoiding previously unsuccessful nest sites but returning to those where they have raised young successfully) and that they vary the materials used according to the nature and risk of predation. Other studies suggest that some bird species may be sensitive to the structural properties of the materials they use. Biomechanical analysis of deconstructed nests showed that female blackbirds *Turdus merula* used significantly stronger and more rigid materials in the outer part of the nest structure compared to the inner part, as appropriate to their differing structural roles (Biddle et al. 2015). Furthermore, in a laboratory setting, male zebra finches *Taeniopygia guttata* preferentially selected nesting material on the basis of its structural properties, as a result of experience of building with different (man-made) materials (Bailey et al. 2014). This sensitivity to context and flexible, appropriate use of materials may fulfil predictions **P1** and **P2**. Although there is currently a lack of research on what guides behavior at each stage of the nest building process, it is possible that there may be an element of planning (**P3**) involved in the order of construction of different components of the nest (Healy et al. 2008).

Since tool use in birds involves similar behaviors (and often similar materials), nest building and tool use may share similar neural foundations (Breen et al. 2016) and represent cognitive abilities on the part of birds to learn (via individual or social learning) about the basic mechanics of the available materials and nest structures and to make decisions about those based on environmental variability. Such a relationship might also apply to nest building and tool use in great apes (Byrne 1997; van Casteren et al. 2012).

## Arboreal Locomotion

Chevalier-Skolnikoff et al. (1982, p. 650) suggested that, at least for orangutans, locomotor

demands were “the single major function for which the advanced cognitive abilities... evolved.” Povinelli and Cant (1995) subsequently suggested that self-concept in orangutans evolved to enable these large-bodied apes to negotiate thin, flexible branches during suspensory locomotion (like arm swinging and brachiation), particularly when crossing gaps in the canopy. They hypothesized that the unpredictable response of compliant weight-bearing structures when weight is transferred onto them, the need for several such structures to support the weight of a single individual, and the erratic orientation of supports together require that orangutans and perhaps other great apes must be able to step outside themselves and imagine how their body and its movements will affect fragile, easily deformable branches and twigs, in advance of movement (Povinelli and Cant 1995; Hunt 2004).

Hunt (2004) tested this theory by comparing the postural and locomotor repertoires of great apes, gibbons and siamangs, and baboons. Nearly 60% of orangutan locomotion relies exclusively on supports that are less than 10 cm in diameter and therefore likely to bend under their body weight (Thorpe et al. 2007), and Hunt found that overall orangutans showed the strongest evidence for positional behavior (posture and locomotion) repertoires likely to elicit a concept of self; however there was also some evidence for lowland gorillas. Although gorillas have long been considered to be largely terrestrial, it is increasingly apparent that they can be highly arboreal (Remis 1999) and that their locomotion is more similar to orangutans than to chimpanzees (Thorpe and Crompton 2006). In contrast chimpanzee positional behavior was far less likely to elicit self-concept, yet they have been one of the most successful in mirror self-recognition tests of self-concept (Gallup 1970; Povinelli et al. 1997). This indicates that the two measures of self-concept might not be causally connected or that self-concept might simply be related to body size rather than the complexity of locomotor and postural interactions between animals and their habitat (Hunt 2004).

Other aspects of arboreal locomotion also seem to require advanced cognitive skills. Tree sway is

a behavior where large-bodied animals, mostly orangutans and gorillas, sway tree trunk or vines back and forth with increasing magnitude to cross a gap in the forest canopy. In a comparison of the mechanical work involved in different types of gap crossing by orangutans, tree sway was found to be less than half as costly as jumping, and an order of magnitude less costly than descending the tree, and crossing the gap terrestrially, indicating that elastic compliance in arboreal supports can be used to reduce the energetic cost of gap crossing (Thorpe et al. 2007).

In order to sway trees to utilize the elastic energy within them, apes must have an understanding of the flexibility of the given tree trunk relative to the size of the gap to be crossed. Juvenile orangutans regularly practice this behavior, and one of us (SKT) has observed both their frustration and perseverance when it doesn't work out. But failure seems to be a very rare result in adult locomotion. Given the unique set of materials and conditions for each tree sway/gap crossing event, this behavior supports the first three of our cognitive predictions above. Anecdotal observations of tree sway reported in Thorpe et al. (2007) suggest that orangutans can also detect new positive and negative affordances if tree sway supports confound their expectations and exploit these appropriately (P4). For example, when a female orangutan traveling with her adolescent son failed to oscillate a tree trunk to sufficient magnitude to cross a gap, the son moved to a higher bough in the tree. This increased the effective mass of the tree trunk about the point of oscillation, and both were able to cross the gap. The fact that this positional adjustment worked first time suggests they had a fairly nuanced understanding of how to modify the mechanical behavior of the tree trunk.

Although monkeys regularly bounce on branches and occasionally seem to pump horizontal branches up and down before leaping into the next tree, they never seem to do so in a way that allows them to utilize the elastic recoil of the branch. Indeed they often pause after they have pumped the branch for the oscillations to reduce and do not leap at the point of the recoil at which they could benefit from energy return (SKT, pers. obs.).

## Arboreal Cognitive Maps

Foraging for arboreal animals (particularly frugivores or insectivores) is a complex task. Animals must locate food sources that might be widely spread throughout a forest and which are often either ephemeral or intermittently available, so they must also track phenology (Garber and Porter 2014). Furthermore, they must balance efficiency of travel between these resources, energy gain and nutrient balance, while minimizing predation risk and avoiding missing out on ephemeral foraging opportunities away from their route. To make the task more challenging still, the physical structure of the forest often prevents the animal from seeing the goal it is heading for (or any of the landscape features associated with it) from a distance. Thus, the ability to store, recall, and integrate detailed spatial information (e.g., Di Fiore and Suarez 2007; Garber and Porter 2014) and potentially to plan routes efficiently in advance of travel (Janson 2014) is likely to play a critical role in foraging success.

This constraint on visibility is reflected in the way in which researchers conceptualize different scales of navigation in forests: “small-scale” space is defined by the space in which an animal can gain different viewpoints or perspectives of a set of landscape features associated with feeding sites or the feeding sites themselves. In contrast, “large-scale” space is an area in which multiple viewpoints are not possible (Garber and Dolins 2014). The physical size of each area will vary substantially depending on the type of forest environment and the location of the animal within the vertical structure, for example, within or below the canopy. Two main strategies have been proposed for navigating within these spatial scales. Animals may construct a network or route-based (topological) mental map by storing the locations of salient landmarks (the nodes or orientation points), which are linked by familiar and reused routes on which the animals travel (Dolins and Mitchell 2010; Garber and Dolins 2014). Alternatively, animals may use a coordinate-based system, in which they store the coordinates of salient resources directly, providing the flexibility to visit the points in a different sequence and make novel shortcuts between them. A coordinate-

based system has been hypothesized to be possible only in small-scale space (Garber and Dolins 2014), and accordingly among primates, evidence is currently limited to chimpanzees traveling terrestrially within forested landscapes (Normand and Boesch 2009). Since forest canopy blocks many of the visual cues available to help animals navigate using landmarks, it is less clear whether chimpanzees or any other species are able to employ this strategy within this large-scale space. In theory, the use of a coordinate-based system (and to a more restricted extent, a route-based system) would allow animals to plan their routes several steps in advance, optimizing their path between foraging resources, fulfilling prediction **P3**. However, current evidence does not provide support a multi-step planning ability (e.g., Noser and Byrne 2014; Janson 2014), at least in somewhat artificial foraging experiments.

Our understanding of the cognitive maps of animals is confounded however by the fact that in any foraging decision, multiple ecological drivers will be at play, particularly in forest canopy. This is nicely demonstrated by Garber and Porter’s (2014) study that examined the arboreal foraging strategies of wild saddleback tamarins (*Saguinus fuscicollis weddelli*). They present data on daily travel routes, the direction of travel, the relationship between the distance actually traveled and the straight-line distance, and identification of the locations at which they changed direction to revisit feeding sites. They found that saddleback tamarin foraging behavior was most consistent with having a route-based mental map. However, they also showed that by not traveling in a straight line to revisit nearby feeding sites, the tamarins were able to update ecological information on resource availability and distribution. Thus the costs of not taking the most efficient path appear to be offset by the benefits of using multiple spatial strategies and travel patterns to more effectively locate and monitor new feeding sites.

## Caring for Arboreal Animals in Zoos

The cognitive demands of life in the forest canopy have important implications for our ability to



provide for the welfare of arboreal animals in zoos and sanctuaries. Forest is a complex and changeable environment in which large-bodied arboreal species clearly have to constantly think about their environment – how supports will behave under their weight as they move, where to rest, which food resource they should exploit next, and what route they should take to reach feeding and sleep sites. Dealing cognitively and physically with complexity and change is a fundamental aspect of their daily lives and is central to their ability to adapt to variable environments and to cope with adverse conditions. Without doubt this needs to be built into the enclosures of captive arboreal species.

## Conclusion

The study of the cognitive demands of arboreality falls into a broader area of research that investigates what animals understand about the properties of their physical environment and how they deal with complex and dynamic environments. Our results suggest that, as the largest-bodied arboreal species, orangutans meet most of the predictions we made about the cognitive abilities that would be required to thrive in forest canopy. They clearly understand and can reason about the physical behavior and affordances of arboreal supports and the physical effects of their own actions. They can also detect new positive and negative affordances if supports confound their expectations and exploit these appropriately. There is less evidence currently available that they can evaluate routes well in advance of movement or plan arboreal routes using coordinate-based maps. There is much less information available for other arboreal species, which provides scope for lots of exciting research projects to test the extent to which other arboreal animals have evolved advanced cognitive abilities as a consequence of the challenges of life in the forest canopy.

## Cross-References

- [Ape Cognition and Conservation Initiative \(ACCI\)](#)
- [Cativity](#)

- [Catarrhine Locomotion](#)
- [Catarrhine Navigation](#)
- [Clambering](#)
- [Nest Construction](#)
- [Primate Cognition](#)
- [Primate Locomotion](#)
- [Technical Intelligence Hypothesis](#)
- [Zoo](#)

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## Archaea

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## Definition

Archaeobacteria are group of microorganisms that are anaerobic autotrophs, come under a separate domain, and live under extremely hostile condition.

## Introduction

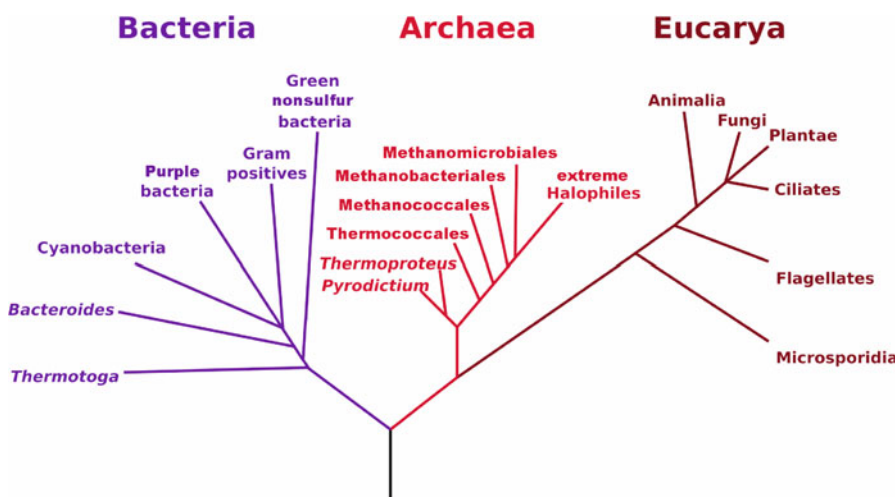
Archea have inhabited Earth for nearly 4 billion of its 4.6 billion years in existence, making them possibly the oldest living life form (Schopf 1983). Early time the earth is thought to have very less oxygen, but ample carbon dioxide. Earlier the bacteria and archaea did not require oxygen, but utilize carbon dioxide. In two billion years, they have covered the ocean floors, forming strong, collective mats. However, around 2.4 billion years ago global oxygen levels increased that may be due to release of oxygen from the Earth's crust (Rowland 2010). Like eukarya and bacteria the archaea is also diverse in nature both morphologically and physiologically. Morphologically they may be rod shaped, spherical, cuboidal, spiral, plate shaped, and irregular. Some are single celled and some are filamentous or aggregates. Their diameter range is from 0.2 to over 15  $\mu\text{m}$ . Some filament can grow up to 200  $\mu\text{m}$  in length.

They can be either gram positive or negative, but the cell wall is unique in archaea containing ether linkage in lipids while in bacteria the lipids in cell wall have ester linkage. They can multiply by binary, multiple fission or by fragmentation. They are found as anaerobic, aerobic, and as facultative anaerobes. They range from chemolithoautotrophs to organotrophs. They include psychrophiles, mesophiles, and hyperthermophiles that can grow above 100 °C (Willey et al. 2011). Archaea today have a wide variety of unique metabolisms that allow them to live in the most conducive places on Earth. They can eat iron, sulfur, carbon dioxide, hydrogen, ammonia, uranium, and all sorts of toxic compounds, and from their utilization they can produce methane, hydrogen sulfide gas, iron, or sulfur. They have the potential to turn inorganic material into organic matter, like turning metal to meat. This unique potential paved the way for their survival in oxygen-free habitats, boiling sulfuric acid pools near volcanoes, sulfur hot springs, glacial ice, methane seeps, rock four miles into the Earth, desert sands, acid mines, oil leaks, polluted waters, and toxic waste dumps (Rowland 2010). Recently, a species of archaea is reported as the Archeal Richmond Mine acidophilic nanoorganisms (ARMAN) comprising Microarchaeota and Parvarchaeota discovered in 2006 (Baker et al. 2006). With the advancement

in technology in 1990s, for the first time Woese's group sequenced the entire genome of an archaea, *Methanococcus jannaschii*, in 1996. *M. jannaschii* lives in hydrothermal vents on the ocean floor under extremely high pressures and proclaimed as a representative of the third domain (Rowland 2010). Whenever you see a hot, muddy, acidic spring, you are probably seeing the results of a thriving community of archaeal cells called *Sulfolobus*. This is the archaea most often isolated and most well-known by scientists. In sulfuric hydrothermal areas, it oxidizes sulfur into sulfuric acid, which helps to dissolve the rocks into mud (Yellowstone NPS).

### Phylogenetic and Metabolic Diversity of Archaea

Haeckel in 1866 challenged the formally proposed plant animal system classification system and wanted to separate the protists from plant and animal (Haeckel 1866). Later, Copeland further modified and placed bacteria in separate branch and Whittaker created fifth for fungi (Copeland 1938). Later, Carl Woese, by molecular level study, divided the living world into three distinct groups, i.e., Eubacteria, Eukarya, and Archaea (Fig. 1).



**Archaea, Fig. 1** Universal phylogenetic tree in rooted form, showing the three domains (Woese 1994)

Small subunit of ribosomes provides an excellent example as one structural feature in the small subunit of ribosomal RNA by which the eubacteria is distinguished from Archaeobacteria and eukarya (Gupta 1998). Based on the physiological and morphological differences the archaea is divided into five major groups, i.e., methanogenic archaea, archaeal sulfate reducer, extremely halophilic archaea, cell wall-less archaea, and extremely thermophilic sulfate reducer (Table 1). However, based on the phylogenetic evidences, the Bergey's manual has divided the archaea into two major phyla euryarchaeota (Eurus – wide, archiose – primitive) and crenarchaeota (Cren – spring). The euryarchaeota is versatile in their ecological niches and metabolic pattern. Methanogens, extremohalophile, sulfate reducer, many extreme thermophile with sulfur-dependent metabolism come under this phyla. The crearchaeotes resemble to the ancestors of archaea and all the species that belong to this group are thermophile and hyperthermophile.

Based on the 16S rRNA nucleotide sequence, recently a new phyla is gaining acceptance which is named as Korarchaeota (from the Greek word “Young man”). Yet the fourth phyla has also been suggested by the discovery of hyperthermophilic archeon *Nanoarchaeum aquitans* from submarine vent. *N. equitans* live symbiotically with the other genus *Ignococcus* that belong to Crenarchaeota, an autotrophic sulfur-reducing

bacteria. It has not been cultured so its physiology is hard to study. Both genus vary in their size so the cells can be studied for genome analysis. So, there are two accepted phyla of archaea that are reported till date. Later, by the use of advanced techniques and phylogenetic-based study many phyla have been generated, but they are not well accepted. Archaea mainly include the species that carry out the chemolithotropic and chemoorganotrophic metabolisms. They do not have a chlorophyll pigment but a unique form of energy generation occurs in some of the halophilic species.

Energy metabolism process is unique in some archaeal group like methanogens where the methane is produced by anaerobic process where carbon dioxide is the electron acceptor and hydrogen is the donor, or by catabolism of some organic compounds. Chemoorganotrophy and anaerobic fermentation are well studied in certain species of archaea. Halophiles and some thermoacidophiles are found to be aerobic, while anaerobic respiration in which the elemental sulfur is used as an electron acceptor is widespread in *Crenarchaeota*. Autotrophy is largely distributed in archaea. It is concluded that many catabolic pathways in the archaea are found that are very similar to bacteria, a good reminder that metabolism has a long evolutionary history. With this background and the phylogeny of Archaea firmly in mind, we now consider the organismal diversity of this fascinating domain of life.

**Archaea, Table 1** Groups of archaea based on morphological and physiological differences

| Group                                             | General characteristics                                                                                               | Representative genera                                      |
|---------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------|
| Methanogenic archaea                              | Strict anaerobes. Methane is the major metabolic end product                                                          | Methanobacterium<br>Methanococcus<br>Methanomicrobium      |
| Archaeal sulfate reducer                          | Irregular gram negative, autotrophic growth with thiosulfate and H <sub>2</sub> , trace                               | Archeoglobus                                               |
| Extremely halophilic archaea                      | Rods, cocci, or irregular shaped cell, primarily chemoorganoheterotrophs                                              | Halobacterium<br>Halococcus                                |
| Cell wall-less archaea                            | Thermoacidophilic, chemoorganotrophic, facultative anaerobe                                                           | Thermoplasma                                               |
| Extremely thermophilic S <sub>0</sub> metabolizer | Gram negative, filaments or cocci, obligately thermophilic, acidophilic or neutrophilic, autotrophic or heterotrophic | Desulfurococcus<br>Pyrodictium<br>Pyrococcus<br>Sulfobolus |

## Archaeal Cell Wall and Membrane

Archaeal cell ranges from 0.1  $\mu\text{m}$  to over 15  $\mu\text{m}$  diameter, and it occurs in many shapes more commonly as sphere, rod, spiral, and plates (Krieg 2005). Archaea can stain either gram positive and gram negative though they lack muramic acid and D amino acid that make up peptidoglycan (Esko et al. 2009). Some species form aggregates and filament of cells up to 200  $\mu\text{m}$  long. The nature of membrane lipid of the archaea is the distinctive feature. It differs from bacteria and eukarya in two ways. The first one is they contain hydrocarbon derived from isoprene units – five carbon branched molecules. The second is the hydrocarbon that is attached to glycerol by ether links rather than ester links (Fig. 2). When the two hydrocarbon chains are linked by glycerol, they are known as diether. Cells of the archaea can adjust the length by cyclizing the chains to form pentane ring that is more densely packed in the membrane, making them more stable at high temperature. It is also reported that the archaea increase the number of cyclopentane ring as the growth temperature increases. Seventy to 90 percent of the archaeal lipids are polar and remaining are nonpolar and are usually derivatives of squalene. Although there is significant difference in membrane lipids, the basic structure and design of archaea is similar to bacteria and eukarya like there are two hydrophilic surfaces and hydrophobic core. It is expected that from their need for stability, the membranes of extreme thermophiles such as *Thermoplasma* and *Sulfobolus*, that grow

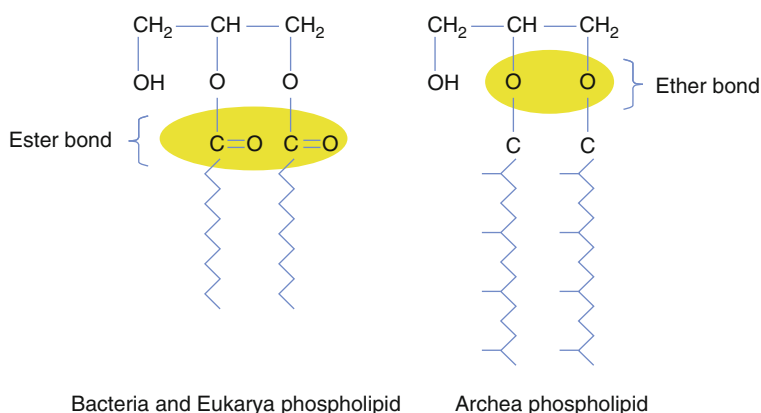
best at temperature over 85  $^{\circ}\text{C}$ , are almost completely tetraether monolayer. Archaea living in moderately hot environments have membrane containing some region with monolayer and some with bilayers. Without the constraints of the conserved molecule peptidoglycan, archaeal cell walls can be quite diverse. For instance, some methanogenic archaea have pseudomurein (a peptidoglycan-like polymer that is cross-linked with L-amino acids), while others contain a complex polysaccharide similar to the chondroitin sulfate of animal connective tissue. Interestingly, some hyperthermophilic archaea and methanogens have protein walls.

## Genetics and Molecular Biology of Archaeobacteria

Many genomic features of archaea are similar to bacteria and eukarya. Generally the genomic size of archaea is smaller than the bacterial genome. *Bacillus subtilis* genome size is 4.20 Mb while *Pyrobaculum aerophilum* genome size is 2.22 Mb and that of *Methanothermobacter thermautotrophicus* is 1.75 Mb. The largest genome size of Archaea is reported in *Methanosarcina acetivorans* with 5,751,492 base pairs (Galagan et al. 2002). Variation in G+C content (from about 21% to 68%) is the sign of archaeal diversity. The complete genome sequenced Archaea is found to have similarity with bacteria and eukarya. About 30% of all genes of archaea encoding proteins involved in transcription,

### Archaea,

**Fig. 2** Phospholipid membrane of archaea, bacteria, and eukarya





translation, or DNA metabolism shared similarity with eukarya. In contrast, a large number of the genes shared only between *bacteria* and *Archaea* are involved in metabolic pathways. In addition, evidence exists for horizontal gene transfer between these two domains, especially between thermophilic bacteria and archaea. Archaea have single circular chromosome and replication is bidirectional like bacteria. However, in sequenced archaea it is reported that the replication origin is flanked by genes encoding the eukaryotic-like initiation protein Cdc6/Orc1 and few archaea have multiple origin. Further, the genome analysis revealed that some of the replication proteins are similar to bacteria and others are unique to those of archaea. Some archaea have still dissimilarity with bacteria in having eukaryotic-like histone protein that binds to DNA and forms nucleosome-like structure. Transcription in archaea is more similar to eukarya than bacteria with Archaeal RNA polymerase being very close to its contemporary in eukaryotes (Allers and Meverch 2005). Archaea have only one type of RNA polymerase and its structure and function is close to that of eukaryotic RNA polymerase II with similar protein assemblies that help in the binding of the RNA polymerase to gene's promoter, but other factors are close to bacterial transcription factor.

## Genetic Exchange and Gene Transfer

Archaea reproduce asexually but DNA transfer and homologous recombination between closely related individuals occur frequently in the populations and have a key role in the formation of archaeal species. Moreover, the horizontal gene transfer (HGT) between the distantly related species can transfer novel functions and features and ignore the need for de novo evolution in the recipient (Cadillo-Quiroz et al. 2012). Recently 134 archaeal genomes are analyzed and it was found that many contained signatures of horizontally transferred DNA from bacteria, especially the methanogens, and the majority of the transferred genes were presumed to be functional (Nelson-Sathi et al. 2015). Chromosomal and

plasmid DNA exchange in halophilic archaea occurs by cell fusion-based manner (Naor et al. 2012). Moreover, a recent study reported the first archaea-specific DNA transport system seems to have a crucial role, especially under conditions of DNA damage (Van Volferen et al. 2016). The genes that are transferred horizontally in archaea mostly originate from bacteria, while the remaining genes are transferred from archaea or in some cases from eukaryotes (Brochier-Armanet et al. 2011). High rates of interdomain horizontal gene transfer is revealed by phylogenetic analysis in Marine Thaumarchaeota and Euryarchaeota that acquired 24% and 30% of their genes from bacteria, respectively (Brochier-Armanet et al. 2011).

## Thermostability in Archaea

The archaea have a special feature that helps to tolerate a very high temperature and now it is a burning issue for research. At high temperature, the protein of mesophilic microorganism got denatured by changing the state into unfolded form. In thermophilic archaea, these proteins remain normal and work properly. There are some structural strategy used by thermophiles that include increased hydrophobicity of protein core, an elevated number of ionic interactions on the protein surface, increased atomic packing density, additional hydrogen bonds, and shorter surface loop structures. It is found that the thermostable proteins have relatively higher number of valine, glutamate, lysine, and a fewer glutamine and valine residues. In addition to this, the thermophiles also have some chaperones that assist in refolding of the partially denatured proteins. They have a reverse DNA gyrase that induces positive rather than negative supercoils into DNA. Positive supercoiling increases the DNA thermostability (Presscott) (Willey et al. 2011).

## Phylum Crenarchaeota

This phylum has one class *Thermoprotei* divided into four orders and six families. Order



**Archaea, Table 2** Comparison between archaea and other domains (Willey)

| Features                       | Prokaryotes                                                              | Archaeobacteria                                | Eukaryotes                                         |
|--------------------------------|--------------------------------------------------------------------------|------------------------------------------------|----------------------------------------------------|
| <b>Genomic structure</b>       | Circular chromosome                                                      | Circular chromosome                            | Multiple linear chromosome                         |
| <b>Cell membrane</b>           | Ester linked lipid<br>Peptidoglycan                                      | Ether linked lipid<br>Pseudopeptidoglycan      | Ester linked lipid                                 |
| <b>Internal cell structure</b> | No membrane bound organelle                                              | No membrane bound organelle                    | Membrane bound organelle                           |
| <b>Metabolism</b>              | Phototrophy, autotrophy, aerobic and anaerobic respiration, fermentation | Methanogenesis is unique in archaea            | Photosynthesis, cellular respiration, fermentation |
| <b>Reproduction</b>            | Asexual reproduction, horizontal gene transfer                           | Asexual reproduction, horizontal gene transfer | Asexual and sexual reproduction                    |

*Thermoproteales* contains gram negative anaerobic to facultative and, hyperthermophilic rod shaped. Order *Sulfolobales* are coccus shaped thermoacidophiles and *Desulfurococcales* are coccoid or disk-shaped hyperthermophiles. *Caldisphaerales* are thermoacidophilic, aerobic, heterotrophic cocci. Many of these thermophiles are sulfur dependent. It may be used as either an electron acceptor in anaerobic respiration or an electron donor by lithotrops. They live in the place of geothermally heated soil or water that has abundant elemental sulfur.

**Phylum Euryarchaeota**

It is very diverse phylum with many genera methanogen. Five major physiologic groups within the euryarchaeotes are methanogens – They are considered as strict anaerobe and get the energy by converting CO<sub>2</sub>, H<sub>2</sub>, formate, methanol, and acetate into methane or methane and CO<sub>2</sub>. They are the largest group of cultured archaea. Halobacteria – They are other euryarchaeal groups which are aerobic chemoorganotrophs with respiratory metabolism. Extreme halophiles demonstrate a wide variety of nutritional capabilities. Thermoplasma – They are thermoacidophiles that lack cell walls. They grow in refuse piles of coal mines. They contain large amount of iron pyrites that is oxidized to sulfuric acid by chemolithotrophic bacteria. Extremely thermophilic sulfur reducer – This group have the class Thermococci with one order Thermococcales. They are strictly anaerobic

and can reduce sulfur to sulfide. Sulfate-reducing euryarchaeota – They are represented by the class Archaeoglobi. It can extract the electron from hydrogen, lactate, and glucose, and reduce sulfate, sulfite, or thiosulfate to sulfide. It is extremely thermophilic and is isolated from marine hydrothermal vents (Table 2).

**Conclusion**

Archaea can be aerobic, anaerobic, and facultative anaerobe occurring in extreme conditions and phylogenetically more close to eukarya than bacteria. It is multiplied by binary, multiple, or fragmentation. They can survive in extreme situation so they have the enzyme system that are utilized for further industrial application and molecular level study of organisms.

**Cross-References**

- [Phylogeny](#)
- [Woese’s Three Domains of Cellular Life](#)

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## Archaeology

### ► Stone Tools

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## Architecture

### ► Canine Morphology

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## Area

### ► Population

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## Arguments

### ► Referential Communication

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## Aristotle

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## Intellectual Biography

Aristotle was born in Stagira, Chalcidice, in 384 BCE to Phaestis of Chalcis and Nicomachus,

a physician at the court of King Amyntas II of Macedonia. While it is likely that Nicomachus died when Aristotle was young and Proxenus, a citizen of Atarneus, raised him. Aristotle's medical legacy may have spurred his enthusiasm for biology. His focus on systematic research, dissection, and the sheer size of the biological writings in the corpus are indications of early medical training. At the age of 17, Aristotle entered Plato's Academy and remained a scholar there until the death of Plato around 347 BCE. In his later ethical writings, Aristotle delineates the highest type of friendship from that of pleasure and utility. Plato's Academy was a community of just this kind of friendship: one grounded in a life of contemplation and virtue, a life that can only be sought in the development of the intellect and the pursuit of the good in political life. Legend has it that Plato remarked that his school consisted of two parts: the body of students and "The Mind" of Aristotle, the first of Aristotle's nicknames (Edel 1982). Plato also called him "The Foal" meaning that Aristotle kicked his teachers the way a foal kicks its dam (Natali 2013). His peers named him "The Reader," a jibe referring to the servant who read aloud to the students, the common way of engaging texts in ancient times (Edel 1982). Aristotle did his *own* reading and would famously read so late into the evening that he held a rock over a tin pan to wake him if he dozed off (Edel 1982; Natali 2013).

At the Academy, Aristotle's education included dialectical discussions and scientific activity including research into astronomy and the natural sciences. We can imagine, and have some evidence for, members of the Academy rigorously debating Plato's theory of the forms: the ontological notion that reality is distinguished by what is material (ephemeral, corporeal, particular objects) and what is formal (eternal, incorporeal, universal objects). Material objects are perceived with the senses but strict knowledge of them is not possible. For Plato, scientific understanding (strict knowledge) amounts to logical demonstration, that is, deduction from what is necessary. Knowledge consists of a set of universal, necessary, eternal, and true propositions. As

such, knowledge corresponds to that segment of reality that is eternal and universal. These "ideas" (*ideas*—another term Plato uses for the forms—*eidos*) are the objects of knowledge and, because knowledge is of what is real for Plato, constitute reality. Material objects constitute a secondary level of reality at best or are mere illusion at worst. This ontological and epistemological theory must have been at odds with the empirical predilections of a member of the cult of Asclepius because Aristotle famously argues that understanding begins with sensual *perception* in his *Posterior Analytics*. The basis of human knowledge is the ability to retain and revive these assorted sensory percepts, what he calls *memory*, and from *experience* humans notice symmetry (regularity) and asymmetry between and among properties. Experience is the basis of *intuition*, which is the first step in logical *demonstration*, the form that scientific propositions take according to Aristotle. In other words, it is through the experience of what humans perceive, i.e., particular objects, that they can ultimately gain understanding of what is eternal, universal, and necessary, i.e., the form. Aristotle's theory of knowledge is grounded in his theory of reality wherein the form's existence is dependent upon and concomitant to the matter's existence. The empirical basis for his epistemology and his argument, contra Plato, that form is embedded in matter are why he is commonly referred to as a naturalist and considered to have developed a new school of thought.

However, we interpret Aristotle's theories in relation to those of Plato, there is little doubt that Aristotle revered his master. He studied with Plato for nearly 20 years and famously elegized him as:

...the man whom it is not lawful for bad men even  
to praise,  
Who alone or first of mortals clearly revealed,  
By his own life and by the methods of his words,  
That a man becomes good and happy at the  
same time.  
Now no one can ever attain to these things  
again. (Jaeger 1934, p.107)

Plato's nephew, Spseusippus, succeeded him as head of the Academy. Some scholars intimate professional jealousy and Aristotle's biological

emphasis in philosophy, as opposed to that of Speusippus who leaned toward the mathematical, as the reasons for his departure from Athens. However, some regard his departure not as secession but an attempt to spread the political philosophy of the Academy. Aristotle and Xenocrates were invited by Hermias, then ruler of Assos, possibly to serve as political advisors but there is also evidence that there was a branch of the Academy there welcomed by Hermias. What appears clear is that anti-Macedonian sentiment fueled by the great Athenian orator Demosthenes influenced Aristotle's emigration. At Assos, Aristotle met and married a young woman named Pythia, who was Hermias' niece or perhaps his daughter, and they had two children, Pythia and Nicomachus. Aristotle's famous work on ethics, the *Nicomachean Ethics*, was named after their son and they also raised Proxenus' son, Nicanor, who became a general under Alexander. Much of Aristotle's research on the life of animals appears to have been done between 347–335 BCE at Assos, Atarneus, Lesbos, and Macedonia because the particular species he observes are indigenous to these regions and he consistently mentions places especially in and around Mitylene, Lesbos, in the biological writings (Natali 2013). Aristotle took his bride to Lesbos in 345 BCE. There he met his closest collaborator and eventual heir to his school, Tyrtamos of Eresos, whom Aristotle would rename Theophrastus, which means "divine speech." While Aristotle would establish in his *Historia animalium* (*Inquiry into Animals*) the founding document of biology, Theophrastus would do the same for botany in his *Historia plantarum* (*Inquiry into Plants*) (Fortenbaugh and Sharples 1988).

In 343–342 BCE, Aristotle accepted the invitation of Philip of Macedon to tutor his son Alexander. While there is much conjecture about the content of Alexander's education, some scholars suggest that Aristotle's relationship to the future leader of the known world proved beneficial to his own scholarship. Aristotle returned to Athens in 335 BCE to establish his own school at a grove sacred to the god Apollo Lyceus. At the Lyceum, Aristotle would discuss

with his students and write about a number of exotic species that scholars argue were actually observed in detail by his nephew, Callisthenes, who accompanied Alexander and wrote of his eastward conquests. Aristotle focused on the systematic collection of research material and established the first library at the Lyceum. He was also the first thinker to devise a system of logic. His greatest contribution to the field was the syllogism but he may also be credited with numerous metalogical theses such as the principle of excluded middle, and the laws of bivalence and non-contradiction. Aristotle "walked about" with his students in the morning discussing philosophy, earning them the name "Peripatetic." He carried on his work at the Lyceum organizing and writing most of the corpus until the death of Alexander in 323 BCE. Athens revolted, anti-Macedonian sentiment rose yet again, and Aristotle was charged with impiety in part for the hymn he had written for Hermias praising him as a god (Natali 2013). Aristotle decided not to face trial and retreated to Chalcis. He explains in a letter to Antipater, Macedonian general, and executor of Aristotle's will, that he would not let Athens sin twice against philosophy referring to the trial of Socrates. Antipater crushed the Athenian revolt and Demosthenes drank poison in order to avoid capture. Aristotle passed a year later from a stomach ailment. He had created the first major library, invented logic and biology, tutored the greatest ruler of the ancient world, and would influence the thought of several cultures for millennia to come.

## Scientific Method and Observation

Aristotle is the first major thinker to dedicate a special branch of knowledge to the systematic study of animal life. Of all the sciences he considers, he writes the most about biology. His research on animals constitutes roughly 25% of the extant corpus. *Inquiry into Animals*, *Parts of Animals*, *Generation of Animals*, *On the Psyche* (*De Anima*), *Movement of Animals*, *Progression of Animals*, *Parva naturalia* (a number of short essays on natural functions), and the last book of

the *Meteorology*, all contain discussions of animal life. Aristotle's method begins with (a) an inquiry grasping the differences between and the attributes of various animals and proceeds with an (b) investigation into their causes. The method of investigating the reasons why certain animals have particular attributes (b) Aristotle spells out in some detail at the opening of his *Parts of Animals*. Why it is that the elephant has an elongated trunk or the dolphin snores is the result of natural processes that are not random for Aristotle. Animals develop in specific ways in order to perform the functions that constitute their particular ways of living. They are unities of matter and form and he considers the ability to sufficiently explain the natural processes that result in animals developing in the ways they do the primary role of the natural philosopher.

In his various works concerning animal life, Aristotle presents descriptions of the attributes of over 200 different species. The *Inquiry into Animals* especially centers on these varied attributes and provides the first systematic classification of animals. Modern biological taxonomy is credited to Carolus Linnaeus' publication of the tenth edition of *Systema naturae* in 1758 with its tidy, hierarchical categorization of class, order, genus, and species (Leroi 2014). Many of Aristotle's kinds (*genê*) and greatest kinds (*megista gene*) correspond to modern classes, orders, genus, and species, but his classification lacks the range and coherence of modern taxonomy (Lennox 2001). This is due to his aim: Aristotle seeks to discover the nature of living things. For him, this amounts to demonstrating how it is that the attributes of an animal serve its purpose as a living being. His ordering of animal life is, therefore, teleological. It takes into account the genesis of animals, the material that serves as the locus for their development, the form or structural organization of their developing matter, and the purpose or final end of their development. Aristotle's *Generation of Animals* provides an explanation for the causal relation between form and matter in the early development of animals reflective of his patriarchal culture. He argues throughout that the female is the material cause of generation because she provides the passive

matter out of which the embryo is formed. The male, on the other hand, is the efficient cause of generation because his semen provides both the form of the embryo and the catalyst for its development (Connel 2016; Cooper 1988; Mayhew 2004).

The obvious problems with this and some of this other theories may, in part, be attributed to the way in which he gathered information. His method of acquiring data, what he calls examination of "*phainomena*," involves direct observation in some instances. However, there were many exotic species that Aristotle did not directly examine but were meticulously described to him (see Callisthenes' contribution above), and he considers analysis of informed and sometimes uninformed opinions (*doxa*) of animal anatomy and behavior as grist for the mill (Leroi 2014). These opinions could be those of other great thinkers including mythmakers and natural philosophers, people living adjacent to specific fauna, hunters, fishermen, etc. They sometimes led Aristotle to err; for instance, he infamously contends that the bison can defend itself from assailants by repeatedly projecting its excrement over long distances, excrement so pungent that it can burn the fur off hunting dogs and is only of this nature when the animal is alarmed (630a19–630b18). He also believes that spontaneous generation occurs in some animals, such as testaceans, anemones, grey mullets, and eels because he finds no evidence of their reproduction. But some fishermen's tales also led him to keen observations; Aristotle collectively names dogfish, rays, torpedo fish, and sharks *selakhe*, noting their cartilage where most fish have bone, but he specifically notes the unique reproductive structures of the smooth dogfish, *Mustelus mustelus*. Smooth dogfish are born live and are connected to their mother's uterus by an umbilical cord and placenta, features thought exclusive to mammals. Pierre Belon and Guillaume Rondelet confirm Aristotle's findings in the sixteenth century and Johannes Muller discovered it again in 1839 in his *Über den glatten Hai des Aristoteles* (*On Aristotle's Smooth Shark*) (Leroi 2014). Further, Aristotle comments that a tentacle of certain male octopi (*Argonauta argo*) is involved in



coitus. This tentacle was thought to be a parasite, because it commonly broke off and was discovered inside the female, until the mid-nineteenth century when it was confirmed a penis-tentacle.

One of Aristotle's most famous fish tales involves the paternal instincts of the Macedonian catfish. His description of the catfish's breeding habits is precise, including external fertilization, the resulting egg envelope, the development of embryonic eyes, and the slow growth of the larvae. But the observations he makes of the male protecting the young are particularly keen:

Of river-fish, the male of the catfish is remarkably attentive to the young. The female after parturition goes away; the male stays and keeps on guard where the spawn is most abundant, contenting himself with keeping off all other little fishes that might steal the spawn, and this he does for 40 or 50 days, until the young are sufficiently grown to make away from the other fishes for themselves. The fishermen can tell where he is on guard; for, in warding off the little fishes, he makes a rush in the water and gives utterance to a kind of muttering noise. He is so earnest in the performance of his parental duties that the fishermen at times, if the eggs be attached to the roots of water-plants deep in the water, drag them into as shallow a place as possible; the male fish will still keep by the eggs, and, if it is young, will be caught by the hook when snapping at the little fish that come by; it, however, he be sensible by experience of the danger of the hook, he will still keep by his charge, and with his extremely strong teeth will bite the hook in pieces. (621a20-b1)

Failing to recognize this extravagant paternal behavior in other European catfish, Louis Agassiz doubted Aristotle's account until he received some Macedonian fish from the physician to the Greek king confirming Aristotle's detailed observations. His assistant Samuel Garman named this novel species *Silurus aristotelis* in 1890, noting the four barbels on its chin in contrast to the six barbels of *Silurus glanis* (Leroi 2014).

## Animal Intellect and Teleology

Aristotle characterizes deer as possessing preeminent practical intelligence (*phronêsis*) in comparison to other quadrupeds. This is because of their effectiveness at avoiding threats in their environment. For example, stags when fattening up in the

fall shun their usual haunts in order to evade detection by predators. They also hide when shedding their antlers so that their vulnerability is inconspicuous. A doe will give birth at roadsides in the hope that human traffic will scare off predators. She will then swallow the afterbirth and lead the faun to a lair of precipitous rock with only one entrance in order to better protect her offspring. Aristotle thinks other animals display intelligence in safeguarding too. He cites cranes setting lookouts for protection while sleeping. He believes deer, dogs, goats, panthers, and tortoises use medications to counteract poisons and alleviate pain (Foster 1997). He contends that all animals perceive weather changes and, according to their natures, either migrate before the frost bites or make other provisions. Finally, he notes birds and insects exhibiting technical proficiency (*technê*) in constructing nests and other protective environs.

All of this amounts to the possibility that animals possess intellect (*vous*) or reason (*logos*), a possibility that, oddly enough, Aristotle denies. What Aristotle does grant animals is sense perception and the cognitive ability to mentally represent percepts (a process he refers to as *phantasia*). Humans can *willingly* recollect these percepts and, in the process, stimulate the desire to pursue or avoid the objects represented. They can further signify these percepts linguistically and consider whether their pursuit or avoidance is conducive to their long-term good. These capacities (intentional memory, language formation, and consideration of future welfare) Aristotle considers unique to humans. However, he also believes nature proceeds according to a rational design because it is teleological. Thus plants and animals may not possess reason but their behavior can be exhibitively of reason. Plants seek out nutrition and grow but do not do so consciously. Animals seek nourishment and do so with the aid of sensation and appetite. They perceive what is painful as harmful and what is pleasurable as beneficial aiding in their ability to survive. They can recall past sense impressions in order to aid in this process, but they cannot do so willingly. Consideration of future welfare appears difficult, if not impossible, according to this



schema. But Aristotle's extraordinary examples of animals' capacities to protect and ward off future harms are for him exhibitiv of the rationality of the cosmos rather than that of individual beings.

## Cross-References

- [Biological Motion](#)
- [Means-End Reasoning](#)
- [Origin of Species](#)
- [Rationality](#)
- [Richard Dawkins](#)

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## Arm-Foot Hanging

- [Primate Suspensory Behavior](#)

## Arm-Hanging

- [Primate Suspensory Behavior](#)

## Armored Fish

- [Placoderm Life Histories](#)
- [Placodermi Diet](#)

## Armored Fish Locomotion

- [Placodermi Locomotion](#)

## Armoured Fish

- [Placoderm Morphology](#)

## Arousal

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## Synonyms

[Alert](#); [Attentive](#); [Behavioral response](#); [Emotional arousal](#)

## Definition

A heightened physiological response or behavior to a stimulus (e.g., sweaty palms, increased heart rate, focused attention).

## Introduction

Arousal is a state that keeps us attentive or in some instances, makes us aware of our surroundings. For example, biologically, arousal can help us survive because we become aware and attentive to the current environment. Studies have found

arousal is part of the adrenergic system, with Pribram and McGuinness (1975) defining arousal as a physiological response to input, centered in the amygdala (see also Sharot and Phelps 2004; Styliadis et al. 2018). Arousal is a key component to survival in nature because it can cue the flight-or-flight system protecting us when we might be at risk. Arousal brings attention to what is going on around us, so studies might refer to arousal as a level of activation. Pribram and McGuinness (1975) discuss how activation can result in heightened defense responses. We see this when our heart starts beating a bit faster, and we begin to plan how we will approach the situation. This mechanism can be observed across the animal kingdom, for example, when animals hunt for food or sense they are about to be attacked. In humans, arousal can help us learn, memorize, and recall. Arousal can also play a role in our decision-making (Sanbonmatsu and Kardes 1988). We also see arousal as part of emotion processing, particularly the calm-exciting dimension of processing emotional stimuli. However, it is possible *too much* arousal can impair memory when we experience or process traumatic or obscene memories, which can be emotionally charged (Bradley et al. 1992). For these varied reasons, it is important to further research the mechanisms and effects surrounding arousal.

## Measuring Arousal

Since arousal is a heightened state, our bodies have physiological responses to the heightened state (e.g., increased heart rate, sweaty palms). Researchers have used physiological measurements to measure arousal during their studies. One physiological response researchers use to measure arousal is galvanic skin response (GSR) or skin conductance response (SCR). These measurements use the conductivity of human skin to measure changes in the sympathetic nervous system (Shi et al. 2007). Arousal can influence the flight-or-flight system, which is part of the sympathetic nervous system. Once the flight-or-flight system is activated, biological responses like sweaty palms occur, which are often observed in arousal studies. Similarly, pupil dilations, head

movement, pricking of the ears, respiration, and blood flow can be signs of arousal (Pribram and McGuinness 1975). In another example, Libkuman et al. (1999) used exercise tasks to measure physiological arousal by having participants ride on bikes at certain paces. Arousal can also be measured neurologically using machines like magnetoencephalography (MEG) or functional magnetic resonance imaging (fMRI). Another neurological measurement commonly used in arousal studies are event-related potentials (ERPs).

While physiological and neurological responses might be considered objective measurements, researchers must also consider the validity of the materials they use to induce arousal. For example, psychological studies might use pictures, events, and other materials to ensure participants are in an aroused state. Pilot studies are often used to ensure these materials induce arousal in participants during their experiments, or researchers might rely on previous research to locate materials that will induce arousal. For example, Vogt et al. (2008) used emotional pictures from the International Affective Picture System, and these pictures relate to varying arousal states (none, low, moderate, and high) (see also Mather et al. 2009). These pictures were previously piloted to show they can induce different arousal states. Words varying in arousal are also commonly used when studies want to research and measure arousal. Similar to researchers' use of pictures varying in arousal (e.g., high arousal, low arousal), words are selected from previous studies or published normative data testing these words.

Finally, self-report measures are also used to measure arousal, though they introduce more subjectivity to the dataset. One scale used to measure self-report is the Affect Grid. Russell et al. (1989) describe this scale as a grid-type scale where participants place a single mark on a grid according to how they feel. Pleasure-displeasure is placed on the horizontal dimension, while arousal-sleepiness is placed on the vertical dimension. This scale was later tested for validity by Killgore (1998). Another scale used to measure self-report is the How I Feel scale, which is typically used for children ages 8–12 (Walden et al.

2003). For the How I Feel scale, there are 30 statements (e.g., *I was mad very often*) and participants are asked to rate these statements on a scale of one to five, one being not at all true of me and five being very true of me. Of course, self-report is a more subjective measurement than an objective measurement. The more objective measures of arousal – those pertaining to physiological and neurological measures – are likely more valid and reliable than subjective, self-report measures, though the latter do have advantages with easier to collect data.

## Main Findings

Arousal is a well-researched concept among psychologists. An early study by Kleinsmith and Kaplan (1963) examined a hypothesis of preservative consolidation, predicting a pattern perceived under high arousal should show stronger memory and weaker immediate memory. To examine arousal, the researchers measured skin resistance while participants learned paired-associates. These paired-associates were composed of word-number pairs (i.e., three-kiss eight-love). Their results showed low arousal words were remembered more than high arousal words when immediate recall was required. However, in delayed recall, high arousal words were remembered more often than low arousal words, which they classified as a reminiscence effect (i.e., high permanent memory).

In a more recent study, Sharot and Phelps (2004) found similar results. For their study, they examined recognition for neutral and arousing words at two points in time (immediate and 1 day later). Their three experiments showed arousal can facilitate slower forgetting, like Kleinsmith and Kaplan (1963) had found. Sharot and Phelps (2004) found during delayed recall, arousing words were remembered more often than non-arousing words. Their results also showed poorer recognition of neutral words over time, whereas memory for arousing words remained the same or showed improvement over time. Similar findings with animal subjects have been noted (e.g., Cahill and Alkire 2003; Cahill et al. 2003).

These studies show arousal promotes a kind of buffering, in that arousing information (e.g., pictures, events) is preserved over time.

Researchers have also examined arousal as it pertains to encoding. In one example, Bradley et al. (1992) examined memory retrieval after participants rated slides according to their actual emotional reaction (pleasantness or unpleasantness). Arousal, valence, and dominance were rated after each slide using the Self-Assessment Manikin (SAM; Bradley and Lang 1994) rating system. Participants were divided into immediate recall and delayed recall conditions. In immediate recall, slides rated as pleasant promoted higher arousal, which resulted in better recall. However, the delayed recall condition performed in a different way. The slides rated as unpleasant were recalled more often than pleasant slides, and the unpleasant slides brought higher arousal. Their results suggested high arousal assists with memory performance, when memory for the event's occurrence is probed (Bradley et al. 1992).

Some researchers have noted particular differences between physiological arousal (i.e., running, biking) and emotional arousal (i.e., watching an emotionally charged movie). In a study by Libkuman et al. (1999), the researchers examined the influence of physiological and emotional arousal on recognition memory of central, background, and peripheral parts of an event. Libkuman et al. (1999) found physiological arousal had little impact on memory while emotional arousal helped improve memory for both central and background information. Their results supported previous findings of arousal being an important determinant of an event's memorability (Christianson 1992). Mather et al. (2006) also examined detailed aspects of memory. They were interested in examining how the emotional content of pictures affects participants' ability to remember where it appeared, while also assessing their brain activity while performing the memory tasks. They found poorer short-term memory for the location of highly arousing pictures than lower arousing pictures. In the fMRI results, they found emotionally arousing pictures recruited more attention, which was observed in activation in visual processing areas. Their results supported

previous findings that arousing pictures generate greater attention than neutral pictures. Our attention is interrupted by arousing information as Libkuman et al. (1999) and Mather et al. (2006) found. Similar results were reported by Kleinsmith and Kaplan (1963) and Sharot and Phelps (2004), who showed reduced immediate memory for arousing stimuli (and the reverse effect for long-term memory).

When arousing stimuli catch our attention, researchers have found it can be difficult for participants to disengage from them. Vogt et al. (2008) found these results during their study, where they examined valence and arousal of emotional stimuli, along with their influences on the allocation of spatial attention. Their results showed delayed disengagement of attention from highly arousing pictures, independent of their valence (i.e., across both positive and negative pictures). Additionally, emotionally arousing stimuli can pull attention from other sources. Mather and Sutherland (2011) hypothesize our attention is immediately focused toward emotionally arousing stimuli. They describe emotional arousal as having a “winner-takes-more” effect, in that, when processing information, arousal influences the competition between different stimuli. One important application of their work is the *weapons focus effect*, in which high arousal images – in both laboratory and real-world settings – capture and main attention to such a degree that other information from the environment goes largely ignored (Loftus et al. 1987). One additional application lies in working with trauma and other domains of clinical psychology; research shows mental illness (e.g., depression, PTSD) impairs an individual’s ability to disengage from negative stimuli (e.g., Levens and Gotlib 2010; Vythilingam et al. 2007). Difficulties disengaging from negative stimuli might be due to hyper-responsiveness to threat-related/negative stimuli (Vythilingam et al. 2007). Additionally, disengaging from negative stimuli might be difficult for these individuals because of an insensitivity to positive stimuli (Levens and Gotlib 2010).

These effects can also be observed with non-clinical samples. Delaney-Busch et al. (2016) examined valence and arousal influences on

different states of emotional word processing. They found when emotion is not relevant to the task the participants are performing, the arousal property of emotional words captures attention and brings sustained evaluative processing. An implication of these studies is in eyewitness testimonies. Brown (2003) examined how arousal influences eyewitness memory of an event and how it interacts with contextual reinstatement: a method used to have witnesses recreate a past event. To test their hypothesis, participants viewed slides of different contexts that contained one person or object in the center of the slide. Arousal was measured by asking participants to self-report their arousal for the specific slide. Their results supported context reinstatement procedures enhance recognition memory for non-arousing and unusual events but not arousing events. The results supported previous research showing peripheral information is not remembered as well in an arousing event (Christianson and Loftus 1991). This experiment also replicated enhanced memory for central information in arousing events. The arousal manipulation increased recognition rates for the central position, while decreasing false alarms. Their results supported that narrowing of attention during arousing events affects encoding for other peripheral or contextual information. These results are important to consider because when we find ourselves in an arousing situation, it can be challenging to later recall what happened.

While arousal is often described in terms of its beneficial properties, researchers have found arousal can also present limitations to attention and memory. For example, some have found high arousal can impair memory (e.g., Brown 2003; Mather et al. 2009; Mather et al. 2006; Mather and Sutherland 2011). Since arousal is typically focused on central information, the background and peripheral information can be missed and not encoded for memory. Mather et al. (2009) examined how arousal can limit memory on nearby information. Their results showed arousing pictures impaired memory for background information – a kind of perceptual suppression – though it did not impair memory for any foreground information (see also Brown

2003). Similar to the overstimulation of information during an arousing situation, arousal can have effects on our decision-making. Sanbonmatsu and Kardes (1988) found participants' decision-making was impaired when they were highly aroused, measured in their reduced processing. These results show how arousal pulls cognitive resources to such a degree, that the minimal, remaining resources cannot engage or complete other tasks.

## Conclusion

Arousal has been defined as a heightened state with physiological and behavioral responses to stimuli in our environment. Arousal has been linked to the amygdala, which is part of our sympathetic nervous system. This system plays a part in flight-or-fight responses when we sense danger. Arousal is similarly helpful in maintaining focus and helping us prepare an appropriate response. This focus can also extend to learning, memorizing, and recalling, as arousing stimuli tend to focus our attention (while also limiting our ability to attend to other, background, and peripheral stimuli).

On the other hand, as arousal exists on a continuum, one must also consider the adverse effects of high levels of arousal. Bradley et al. (1992) note too much arousal can impair memory when we experience or process traumatic or obscene memories. This is also important to consider when evaluating an eyewitness's recall. Additional limitations pertain to decision-making and other aspects of complex cognition, in which attention and focus are greatly needed. When we are highly aroused, we can only minimally process additional information, which can impair other tasks. Mather et al. note a need to explore exactly how arousal limits our attention. Individual differences should also be explored, as well as how they interact with participants' mood while processing emotional stimuli. Finally, we ought to delve deeper into the clinical applications of these findings, particularly how these findings relate to trauma. Together, future research can help gain more knowledge on how arousal functions – in

both helpful, survival contexts and those impairing other functioning.

## Cross-References

- ▶ [Accidental/Intentional Experiment](#)
- ▶ [Adaptive Memory](#)
- ▶ [Aggression](#)
- ▶ [Amygdala](#)
- ▶ [Attention Bias](#)
- ▶ [Cognition](#)
- ▶ [Cognitive Bias](#)
- ▶ [Decision-Making](#)
- ▶ [Encoding](#)
- ▶ [Event-Related Potentials \(ERPs\)](#)
- ▶ [Fear Response](#)
- ▶ [Information Processing](#)
- ▶ [Laboratory Research](#)
- ▶ [Predator Defense](#)
- ▶ [Predator Detection](#)
- ▶ [Stress](#)
- ▶ [Survival Processing](#)

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## Arousal Regulation

### ► Attachment

## Arthropod Cognition

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## Synonyms

[Arachnids](#); [Crustaceans](#); [Insects](#); [Intelligence](#); [Invertebrates](#); [Learning](#); [Memory](#)

## Definition

The perceiving, learning, and utilizing of information exhibited in the invertebrate animal phylum, Arthropoda.

## Introduction

Arthropods are a widely studied animal group, inspiring interest across a broad range of scientific disciplines due to the diversity of the environments they inhabit and their broad range of ecology. This group’s versatility has resulted in arthropods being the most successful animal group on the planet, with their membership including spiders, insects,



and crustaceans. Arthropods are characterized as a group by their segmented bodies, appendages with joints, a hard external exoskeleton, and a lack of internal bone structures. To the layman, the behaviors of these “lower order” organisms might appear as inflexible or hardwired and reflect the appearance of only limited cognitive abilities when compared to the cognition of vertebrates. However, there exists a wealth of scientific evidence that paints a picture of arthropods as organisms that exhibit large flexible behavioral repertoires, including the ability to perform complex cognitive functions despite their small brain size and limited neuron numbers. The cognitive processes exhibited by arthropods can be as simple as associative learning between a stimulus and a food reward or as complex as navigation using memorized visual cues or the sophisticated communication of the honeybee dance. Within this chapter, we discuss four broad topics concerning the cognitive abilities of arthropods: associative learning, spatial cognition, social cognition, and, finally, distributed cognition. Such an overview is not meant to be exhaustive but rather present an impression of the diverse range of cognitive abilities exhibited by the group.

## Associative Learning

Arthropods show a surprising capacity for learning a wide range of sensory cues that may predict either reward or punishment. These learned cues can be stored over the short or long term for further use. A large portion of the research exploring the learning and memory capabilities of arthropods has focused on associative learning, a cognitive process in which an organism learns through experience to associate certain behaviors with stimuli. This type of learning includes both classical conditioning and operant conditioning and has been widely used in arthropod research to showcase an array of cognitive skills.

## Classical Conditioning

Classical conditioning is a learning process in which an organism learns to associate a biologically neutral stimulus with a potent, biologically

relevant stimulus leading to a behavioral response when the neutral stimulus is presented alone. In the classic learning experiments conducted by Ivan Petrovich Pavlov, dogs learned to associate previously neutral sounds such as the ticking sound of a metronome with the presentation of food. Dogs originally only salivated when the food is present, but over a number of pairings, individuals would begin to salivate at the ticking sound even in the absence of food.

Insects are commonly used subjects in classical conditioning research. For instance, during olfactory learning experiments in honeybees, a restrained bee is presented with a neutral odor, the conditioned stimulus. As this odor is presented to the bee, the unconditioned stimulus, here a small amount of sucrose solution delivered to the bee’s antennae, is also presented. The bee’s unconditioned response to the sucrose is to extend its proboscis, a long tubular portion of the bee’s mouth, which it uses to feed (Fig. 1). After multiple exposures to the odor, followed by the sucrose solution, the bee will begin exhibiting a conditioned response to the odor alone, extending its proboscis when only the odor is presented. Olfactory memories in honeybees can be retained over long time periods when the subject is exposed to repeated presentations, whereas conditioning after only a single pairing will decay over the next 24-h period. Repeated pairings of the odor and sucrose can produce memories of the association that can last over 7 days (Menzel 1999; Giurfa and Sandoz 2012).

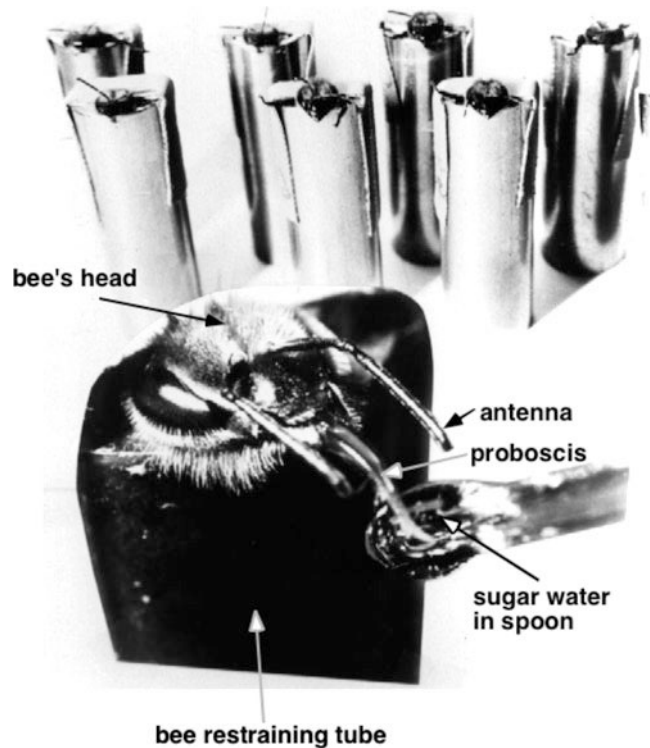
Evidence of this associative learning using both olfactory and visual stimuli is present across the arthropod phylum. The Pavlovian salivation response can be replicated by olfactory pairing in cockroaches (Watanabe and Mizunami 2007). Cockroaches were presented with a neutral odor and then a small amount of a sucrose solution. Just as in dogs, the unconditioned response measured was the saliva production in the cockroach’s mouth. After training, conditioned cockroaches increased salivation when presented with the conditioned odor alone but not when presented neutral odor types.

Associative learning can also encompass associations beyond those revolving around attaining food rewards. In a form of classical conditioning

**Arthropod Cognition,**

**Fig. 1** Images of proboscis extension response testing in restrained honeybees.

Individual bees are immobilized inside of metal restraining tubes where only the head, mouth (proboscis), and antennae are free. During classical conditioning testing, the bee is presented a conditioned stimuli (typically a neutral odor) and then a small amount of sugar water (unconditioned stimulus) is delivered to the antennae and proboscis via a small spoon. After multiple pairings of these stimuli, the bee will extend its proboscis when the odor is presented alone. (Image printed with permission from Dr. Randolph Menzel)



A

called aversive conditioning, the unconditioned stimulus presented to the animal is negative, such as an electric shock. After pairing the shock with a previously neutral stimulus, subjects will respond by avoiding this neutral stimulus in future tests. *Drosophila* fruit flies have been shown to readily learn these associations between different odors and electric shock, actively avoiding odors that have been previously paired with the aversive stimulus (Tully and Quinn 1985; Busto et al. 2010). Beyond insects, spiders and crabs show similar cognitive abilities, quickly learning associations between stimuli and visual cues. Hermit crabs are more likely to abandon a home shell for a new shell after experiencing an electric shock within the original. These crabs will also spend less time inspecting a new shell before deciding to swap (Elwood and Appel 2009).

Associative learning can be a strong driver of behavior, to the point where it can lead animals to override instinctive behavior. Certain crab species have an instinctive preference for darker environments due to predation pressures. This preference can be extinguished when bright light is paired

with food rewards. Instinctive behaviors can also be paired with adverse stimuli to decrease their prevalence. Crabs can also learn to avoid dark habitats when these dark environments are paired with aversive stimuli such as electrical shocks. Crabs and crayfish will learn this association and exhibit increased avoidance behaviors such as running responses or fleeing out of the area when darkened habitats are linked with electrical shock (Barr et al. 2008; Magee and Elwood 2013).

**Operant Conditioning**

Operant conditioning is a learning process that involves the frequency of a behavior being controlled by the behavior's outcome. Unlike classical conditioning, during operant conditioning, behaviors are not elicited by a stimulus but instead are shaped by the behavior's subsequent result, which can either be a reward or a punishment. Arthropods are adept at associative learning paradigms. This has made member species, the honeybee and *Drosophila* flies in particular, excellent models for use in learning experiments that test a number of learning parameters. Operant

conditioning in honeybees has been the subject of extensive study over the last century, pioneered by work using free-flying target discrimination tasks (von Frisch 1914). In these tests, free-flying bees are usually given a choice between two visual targets, one of which is associated with a food reward, in an experimental design that mirrors the honeybee's natural foraging behavior. In this experimental structure, the bee chooses where to land. This behavioral action determines if it receives a food reinforcer. Such tests have allowed researchers to discover a wealth of information regarding honeybee cognition and perception, including the use of visual and olfactory stimuli, image matching, color learning, numerical cognition, and time-linked learning (Giurfa 2015).

*Drosophila* flies are also commonly used in operant conditioning experiments to study a myriad of cognitive and genetic questions. An experimental instrument called a heat box is commonly used with this species (Putz 2002). The instrument's chamber is split, where half the area is punished and half is not. Whenever the test fly enters the punished portion of the chamber, the temperature of the space is heated. When the fly leaves this area, the temperature in the box returns to normal. Flies quickly learn this association and restrict their movement to the non-punished side of the chamber. This association has been shown to be stored in long-term memory, as trained flies will still avoid the punished portions of the heat box hours after training. Experiments have produced similar results in jumping spiders (Peckmezian and Taylor 2016), where specific areas of a chamber are linked to electrical shock. In jumping spiders, stimuli are typically associated with visual cues due to their high visual acuity. When electrical shocks are paired with either a black or white stimulus, spiders will respond similarly to *Drosophila* by subsequently avoiding those areas in the future (Putz 2002; Peckmezian and Taylor 2016).

## Spatial Cognition

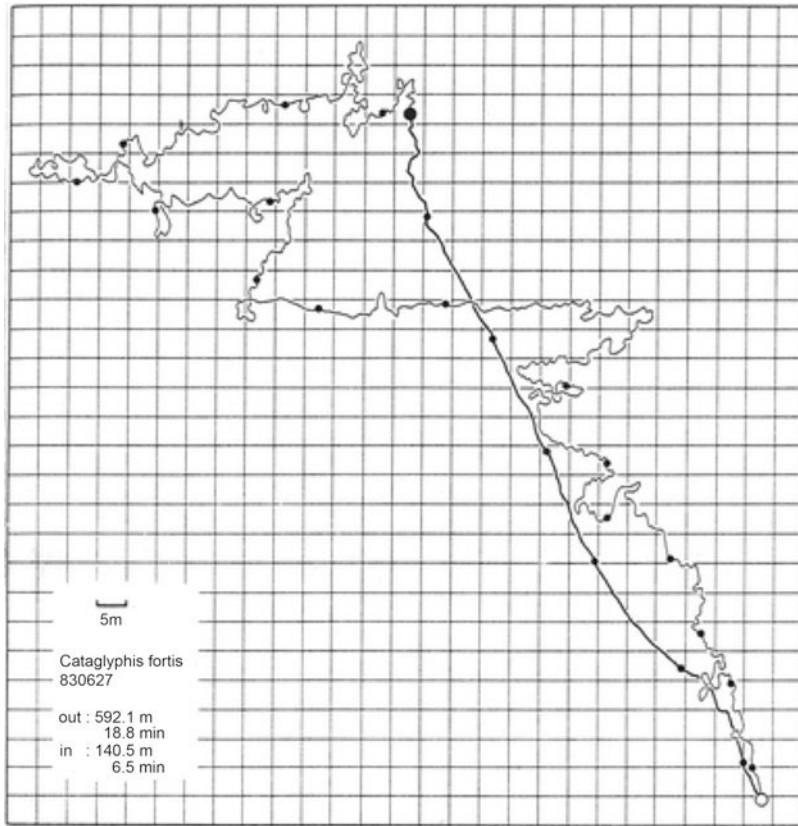
Animals that move through their environment need to be able to steer and find certain locations, be that a food source or the quickest path back to

their nest. Survival can often depend on the animal's ability to navigate accurately, especially when their environment is harsh and prolonged exposure to the elements could mean death. Navigation requires the acquisition and application of information in the environment that can indicate the direction and/or distance of a goal location. Often, animal navigators will collect environmental cues from multiple sources. Multiple information streams provide a further cognitive challenge: the navigator must integrate these signals before making a decision on where to go.

In the Tunisian desert, specialized foraging ants wander through the scorching and featureless terrain searching for food. These ants are active during the hottest parts of the day when they scavenge for other invertebrates that have fallen victim to the intense heat. These searching ants can travel hundreds of meters from the nest in long meandering paths before finding food. Once found, however, a forager will travel in a straight line back to the nest, a small inconspicuous hole (Fig. 2). How does this solitary ant find their nest in a featureless landscape when the intense heat makes chemical trails quickly evaporate? They accomplish this task using a navigational tool called path integration.

## Path Integration

Path integration is a cognitive process where the foraging ant acquires and combines both distance and directional cues for navigation during their search for food. When these two measurements are combined they allow the ant to keep track of their position relative to the nest's location during their trip. This is called their home vector. To measure the direction the foraging ant is facing, the ant has a sky compass that is based on cues such as the sun's location and the pattern of polarized light in the sky. In walking animals such as ants, distance estimates are collected through a step counter. These two measurements are collected, integrated, and stored during the winding outbound path until the foraging ant finds food and needs to return home. This allows the ant to constantly track the nest's location while out foraging. It then uses this collected information to accurately travel the correct distance and direction home (Fig. 2; Wehner and Wehner 1990).



**Arthropod Cognition, Fig. 2** An example of a complete foraging trip in the Tunisian desert ant, *Cataglyphis fortis*, which inhabits a salt pan environment with few landmarks. The forager's journey begins at the nest location in the bottom right corner, represented by an open circle. The thin line extending from the nest location represents the winding outbound path of the forager as she searches for food, with the small black circles marking her location at 60-s intervals. The large black circle indicates the location at which the forager found food. The thick line represents the

straight line inbound route back to the nest. The forager kept track of both its distance and direction from the nest during the outbound route through path integration, allowing for an efficient return to the nest entrance. (Image reprinted from *Insect navigation: use of maps or Ariadne's thread*, Wehner and Wehner (1990) (Fig. 4), published in *Ethology, Ecology & Evolution* by Taylor & Francis and reprinted with the publisher's permission (Taylor & Francis Ltd, <http://www.tandfonline.com>))

Honeybees are also known to use path integration to return to their nest after foraging, though the honeybee forager needs a different solution in order to estimate how far it has traveled, as counting steps is not very useful to a flying insect. To estimate flown distances, the honeybee forager records their traveled distance using optic flow. Optic flow is a visual cue resulting from the motion of objects and surfaces across the honeybee's visual field. As the honeybee moves through its environment, objects move or "flow" past their visual field. The honeybee can then use this information to estimate how far it has traveled and

combine it with the same sky-based directional cues as the ant in order to path integrate.

Even nonsocial arthropods use path integration to get to goal locations. Fiddler crabs need to defend home burrows and must remain vigilant for intruders even when they leave the burrow to feed on the open beach. If the burrow owner sees another fiddler crab trying to move into its burrow, it scurries back in a straight line to stop the intruder (Zeil and Layne 2002). The wolf spider also maintains a home burrow for safety and, additionally, to ambush prey. These spiders have shown the same distance and direction estimation

when returning to their burrows as ants and honeybees, indicating their use of path integration (Ortega-Escobar 2006).

The use of path integration is generally studied as a form of working memory, a memory type involving the short-term storing of information currently in use. The distance and direction components are compiled to give the animal a continuously updated location of its position relative to their nest, both during the outbound and inbound portions of their trip. As the animal reaches and enters its nest, the path integrator is reset to zero. Yet, work in both ants and honeybees has shown that these animals can also retain long-term memories of path integration information from previous foraging trips, allowing them to use path integration cues from these trips to return to an area if there is an abundance of food or to return to the nest from a known location after long delays (Beugnon et al. 2005).

### Landmarks and the Panorama

Path integration is merely one of the strategies in the navigational toolkits of arthropods. Individuals can also retain long-term memories of terrestrial cues in order to navigate. Research on terrestrial cues likely brings to mind the use of landmarks, but it is now believed that animals use the configuration of multiple objects in their visual field to navigate. There is now mounting evidence that these animals use the complete landmark makeup of the 360° visual scene, termed the panorama, to navigate rather than specific elements in the scene. The predominant theory on how insects and other arthropods use the panorama for navigation is by a view-based matching strategy (Collett 2010; Zeil et al. 2014). Here, stored images of the panorama are compared to the animal's current view while away from the goal location. To orient correctly to the goal, the navigator will attempt to match its current view with views it had previously stored. The resulting best visual match between the stored view and the current view gives the navigator the correct direction to their goal location.

View-based matching first requires that a navigator learn the panorama around its nest or other goal location. Nest panorama acquisition is

accomplished in honeybees and wasps through a behavior called learning flights. Before a forager first leaves the nest area, the forager slowly flies in looping arcs while facing the nest from multiple directions. Ants and spiders exhibit very similar behaviors, called learning walks, on the ground around the nest or burrow. When first leaving their nest or burrow, they will perform multiple pre-foraging trips within the nest area in looping paths that occasionally look back toward the nest direction. It is believed that during these learning flights or walks, views of the panorama around the nest are being stored for future use. Once the panorama at the nest site is learned, foragers leave the nest area, occasionally turning back to face the nest. By turning back to the nest the individuals can learn and store multiple views of the outbound route, as well as changes in the panorama for use when they need to find their way back. These stored memories are robust, allowing foragers to navigate home even after long delays.

Certain arthropod species living in environments with access to both the sky compass and terrestrial cues have shown an additional cognitive ability called cue integration, where individuals integrate information from multiple directional cues while navigating. As sky compass cues such as the sun's position are independent of the terrestrial panorama, they will not always match, leading to a cue conflict that must be resolved before a navigating animal decides which direction to go. Ants and honeybees displaced off their foraging route have been shown to average these two directional cues and choose a compromise direction between the two directions indicated by the sky compass and the panorama. This averaging ability appears to happen dynamically, as foraging ants will change how much weight they assign each cue depending on a number of factors, such as home vector length (Narendra 2007; Freas et al. 2017).

### Cognitive Maps

A more complex navigational tool thought to be in use in many vertebrate species is the cognitive map. Here, animals maintain mental



representations of the spatial layout of objects in the animal's environment. This allows animals to navigate successfully from locations they have not previously visited. The presence of a cognitive map in insect/arthropod cognition remains hotly debated in the scientific community, with skeptics contending that both path integration and view-based matching provide alternative, simpler explanations for the observed navigational abilities in arthropods. For further analysis of this topic and the debate surrounding its presence in invertebrates, please look to the cognitive map chapter of this text.

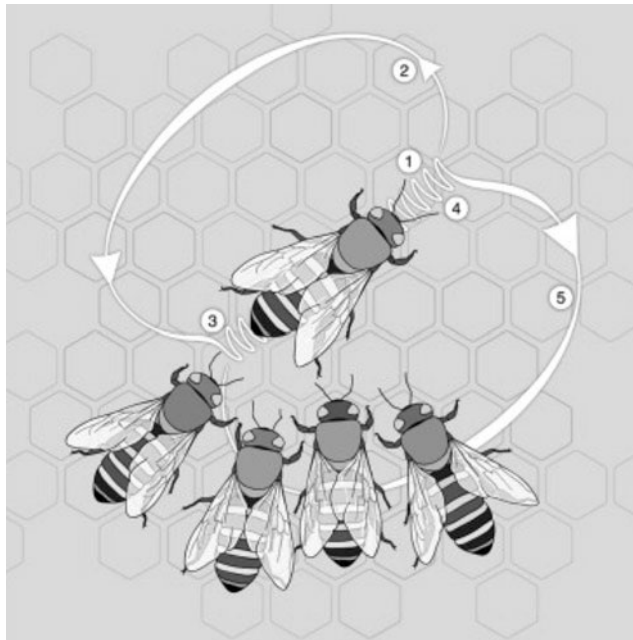
## Social Cognition

Multiple arthropod species are highly social, a characteristic commonly associated with members of the insect order Hymenoptera, which

comprises sawflies, wasps, bees, and ants. Of these, the honeybee has developed a unique behavior for communicating foraging information to hive mates in the form of dance behavior.

### Honeybee Dance

Foraging honeybees retain long-term memories of path integration cues after returning to the hive. Not only do they use this information on subsequent foraging trips, but they can also broadcast this information to other foragers. Upon returning to the hive, a successful forager will perform a dance behavior, characterized by a looping figure-8 like pattern (Fig. 3; von Frisch 1967; Grüter and Farina 2009). This dance conveys to the forager's hive mates information about both the distance and the direction of the food source they visited. The orientation of the zigzag portion communicates to observing hive mates the direction of the food relative to the sun's position, and



**Arthropod Cognition, Fig. 3** An example of the figure eight honeybee waggle dance with both the dancer (center individual) and follower bees (bottom four individuals). The dancer bee (1) performs the waggle portion of the dance, represented by the jagged line, and then turns to one side, here the left, and loops (2) back to the start of the waggle portion. At the start of the waggle portion (3), the dancer performs a second waggle run (4) and then typically

loops in the opposite direction, in this case to the right (5). This dance provides follower bees multiple pieces of information, including the direction, distance, and quality of the potential food source. (Image reprinted from *The honeybee waggle dance: can we follow the steps?*, Grüter and Farina (2009) (Fig. 1), published in *Trends in Ecology & Evolution* by Elsevier and reprinted with the publisher's permission (Elsevier Publishing, <https://www.elsevier.com/>))



the duration of the zigzag portion indicates the distance the food is from the hive.

This dance behavior also provides an example of associative learning in honeybees, albeit under natural conditions rather than under controlled experimental testing (Fig. 1). Hive mates of the dancing forager will follow behind her during the dance, and the dancer will regularly drop the scented nectar of flower patches she visited in her path (Fig. 3). This behavior allows the followers to learn the scent of the flowers the dancer successfully visited.

### Observational Learning

The dance behavior of the successful forager and the information passed on to the following foragers provides examples of two abilities seen in honeybees: functionally referential communication and social learning. Functionally referential communication denotes signals that refer to events or objects in the world, such as the successful honeybee forager signaling where a food source can be found. Social learning is the ability of an animal to learn information or behaviors from another animal, typically a conspecific (member of the same species). In this context, the observing honeybees are learning information about the spatial location of a profitable food source, yet a number of arthropods have been shown to observe and then duplicate behaviors of conspecifics in a range of contexts.

Social learning experiments commonly involve the separation of individuals into naive observers and experienced demonstrators. The observer, as the name suggests, observes, as the demonstrator, usually a trained or more experienced conspecific, performs a behavioral choice or test. When these observers are subsequently presented with the same behavioral choice or test, they are able to use information learned from the demonstrator in their own behavioral decisions. During mating, *Drosophila* females exhibit social learning by watching the mating behavior of other *Drosophila*, preferring to mate with males that have the same characteristics as demonstrator males that were observed to be successful at mating (Mery et al. 2009). This learning occurs even when the characteristics of the male flies have no influence on reproductive success.

*Drosophila* females also show social learning in their egg-laying site preferences. Females who observe other females choose between two equally profitable egg-laying sites and are more likely to choose the same site as the demonstrator for their own eggs (Battesti et al. 2012). In a foraging context, bumblebees learn which flowers are more rewarding by observing and then copying the flower preferences of other, more experienced foragers. In jumping spiders, when an observing spider watches a conspecific decline to attack a novel prey type, this spider will also show increased hesitation to attack this prey type when they experience them in the future.

Observers can even learn nonnatural behavioral tasks demonstrated by trained conspecifics. In bumblebees, in what has been described as “bumblebee football,” researchers (Loukola et al. 2017) taught individuals to drag a wooden ball to a goal area in order to receive a food reward (example of associative learning). Once the demonstrator bee was trained, it performed this task in front of an observer bee multiple times. This observer was then presented the same test where it also successfully rolled the wooden ball into the goal. This research shows that not only are these animals capable of learning complex cognitive tasks, but they can also learn behavioral patterns that are not associated with their typical behavioral routines through observing and learning from other bumblebees.

Social learning can also extend to the individual recognition of nest mates. Remembering individual characteristics of a nest mate when living in large colonies containing thousands of members appears unlikely, but some arthropod species live in small colonies where recognizing specific nest mates may be valuable. Individual recognition can also be valuable in solitary species that regularly compete with other conspecifics for resources. Individual recognition cues are commonly olfactory, with individuals remembering specific chemical cues associated with familiar conspecifics. Solitary hermit crabs learn the individual scents of previously encountered individuals and will link this scent with past experiences of that individual, specifically the quality of that conspecific's shell. In ants, unrelated queens learn the chemical cues of previously encountered queens

and regulate their behavioral response based on this familiarity (D'Ettorre and Heinze 2005). These recognition cues can also be visual; individuals learn the patterns or markings of conspecifics. Social paper wasps perform a form of individual recognition by learning the distinct black and yellow pattern on the front of conspecifics' faces, a visual cue associated with social dominance. When the facial patterns of a known conspecific are experimentally altered through painting, other individuals act more aggressively to the painted individual regardless of whether the paint created a higher- or lower-dominance signal (Sheehan and Tibbetts 2011).

### Distributed Cognition

A more recent field of cognitive study, distributed cognition, encompasses cognitive processes that reside outside of the organism's central nervous system and has been exhibited across a number of phyla, including arthropods (Cheng 2018). One variety of distributed cognition is termed embodied cognition and covers cognition that occurs in areas of the organism's body outside the brain.

### Embodied Cognition

Female crickets showcase embodied cognition in their search for mates. Male crickets attract females through the production of songs, and females are attracted to males who produce the loudest of these songs. Females find their preferred mate by receiving these auditory cues through their ears, which in crickets are located on each of the front legs. These ears are connected through a tracheal tube. This tube allows the female to detect the direction of the sound's origin. Within the structure of the female cricket's ears and tracheal tube, there are a number of interneurons, which control her turning behavior. The act of identifying the loudest male's song and its direction occurs only in the structures of the female cricket's tracheal tube and the eardrums. Once these structures have processed the incoming information, the signal goes out to the motor system for the female cricket to turn in the direction of the chosen male song. This entire process occurs wholly outside the cricket's brain.

*Drosophila* fly larvae also show evidence of embodied cognition, through the offloading of the cognitive processes associated with locomotion to nerves along their body. *Drosophila* larvae have elongated, legless bodies, yet can crawl through the environment through coordinated body movements. These larvae are constantly searching for food using these coordinated body movements, and remarkably, input from the brain is not needed for the larvae to move. When the larvae's brain is blocked from sending signals to its body, the peripheral nerves along the body of the larvae will still coordinate the necessary movements, though directed movement to goals still requires the brain (Berni et al. 2012).

### Extended Cognition

Extensions of cognitive processes beyond the central nervous system can also encompass areas beyond the organism's body, including structures or objects created by the organism, a phenomenon called extended cognition (Cheng 2018). Recent research (Japyassú and Laland 2017) has explored extended cognition in the webs of spiders, proposing that changes in web tension represent the extension of the spider's cognitive processes into its web. As a spider's hunger level increases, it will adjust the tension level of the web's threads. When the web is tightened, smaller insects will cause disturbances that draw the spider's attention. When the spider is not very hungry, having recently eaten, it will loosen the web's threads, and these same smaller disruptions no longer draw the spider's notice. Thus the spider calibrates the web as a result of its current state, and the web in turn provides different levels of feedback to the builder based on this state. This link creates a flow of information in both directions between spider and web.

### Conclusions

This chapter highlights the cognitive abilities exhibited by different arthropods. That members of this group have small brains does not limit their ability to draw upon complex behavioral repertoires across an array of contexts. Arthropods display high degrees of behavioral flexibility, with the ability to learn and retain a multitude of

cues for use over both the short and long term. These attributes make this group highly valuable to researchers interested in cognition, and unsurprisingly, arthropod species such as the honeybee and *Drosophila* fly are model species for the study of learning and memory. Though some of this research has focused on modest cognitive processes such as associative learning, this chapter has also discussed more complex cognitive processes such as extended cognition, cue integration, and social learning. The study of arthropods can provide us with an understanding of how complex cognitive processes can be achieved by organisms with limited nervous systems. Furthermore, the diversity of this phylum and the broad range of behaviors and ecology can help researchers uncover how such processes evolved.

## Cross-References

- [Arthropod Morphology](#)
- [Arthropod Navigation](#)
- [Associative Learning](#)
- [Bear Sensory Systems](#)
- [Cognitive Map](#)
- [Copying](#)
- [Insect Sensory System](#)
- [Learning](#)
- [Long-Term Memory](#)
- [Navigation](#)
- [Olfactory Discrimination](#)
- [Olfactory Perception](#)
- [Short-Term Memory](#)
- [Social Learning](#)
- [Visual Perception](#)
- [Visual Recognition in Birds](#)
- [Visual Search](#)
- [Working Memory](#)

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## Arthropod Diet

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## Synonyms

[Invertebrate food habits](#); [Invertebrate forage](#)

## Definition

An arthropod is an invertebrate animal in the phylum *Arthropoda*. The nomenclature of arthropod is a nod to the invertebrates “jointed” (arthros) “legs” (pod) (Tugel and Lewandowski 2001). Diet is simply coined as the food an individual consumes for the purposes of health and survival.

## Introduction

Arthropods do not have a backbone or internal skeleton, but instead rely on a hard outer exoskeleton made of chitin for protection. Arthropoda is a diverse phylum that includes animals such as beetles, ants, crustaceans, spiders, ticks, centipedes, millipedes, and scorpions. These animals are often soil dwellers and provide the benefit of soil aeration and mixing as they move about. Marine arthropods provide the same benefit to the ocean floor as well.

Arthropods exhibit a wide array of feeding modes such as carnivory, herbivory, detritivory (organic matter produced by the decomposition of organisms), fungal feeders, filter feeders, and parasites. These animals typically have mouthparts that are highly adapted to their feeding mode, allowing for easier capture and consumption of prey. Examples of these specialized mouthparts include: piercing mandibles for herbivorous ants, claws for crabs, lapping mouthparts for nectar intake by bumblebees, and piercing-sucking mouthparts for mosquitos (Vila 2017). Some arthropods (such as spiders and scorpions) even utilize venom when capturing prey, and this venom is usually quarantined to a specific location within the arthropod's body. For example, scorpions of the order Scorpiones use venom enclosed within the tip of their tail in capturing prey and self-defense.

The digestive system of arthropods is composed of three main parts: (1) foregut (pharynx and esophagus leading to the stomach), (2) midgut (stomach), and (3) hindgut (colon and anus) (Vannier and Chen 2007). The foregut and hindgut are composed of the same material as the

exoskeleton, and are shed along with the exoskeleton during the molt. Some components of the digestive system for arthropods are varied based on their eating mode, but the midgut generally contains the digestive enzymes that are essential for breaking down food and absorbing nutrients. The four main categories of arthropod feeding modes and relating diets are described below.

## Shredding Arthropods

Arthropods that are classified as shredders are typically larger in size and are more commonly seen on the soil surface as opposed to deep within the soil. These animals consume food by using their strong mouthparts to shred dead plant matter, while also consuming bacteria and fungi on the surface of the plant material. Decaying plant matter is the primary source of their diet. Consumption of these items is vital for nutrient cycling within the ecosystem and also aides bacteria and fungi in the soil, which act as decomposers. Common examples of arthropod shredders are: sowbugs (*Oniscus* spp.), earthworms (*Lumbricus* spp.), and millipedes (*Euryneridesmus* spp.) (Moldenke et al. 2000). In a forest setting, shredders contribute to the soil recycling pattern because when they consume dead plant material, they only absorb the most available nutrients, and the remaining materials are excreted as waste back into the soil.

Though consumption of decaying plant material by shredding arthropods has many environmental benefits, some shredder species can be problematic in an agricultural setting. Sowbugs, pillbugs, and other shredding species may cause issues for farmers if they begin to consume their growing crop. Fresh and healthy plant material is not a common dietary source for shredders, but in the absence of an abundant amount of decaying plant material, they turn to live material as a secondary food source. Termites (*Isoptera* spp.) are another common arthropod shredder that can cause substantial damage to homes and other structures. Termites feed on decaying wood

using protozoa in their gut to digest cellulosic material, such as wood (Cleveland 1923). Degradation to the wood can cause costly repairs for homeowners if undetected over time. However, termite feeding behavior is not always destructive – in a forested setting, termites break down woody debris which would otherwise be accumulated as waste in the environment.

Shredders are commonly found in the pedosphere, which means they live within the soil. This behavior is attributed to their morphological characteristics, such as their specialized mouthparts for shredding, adapted for abundant dead and decaying plant material in the soil. Ability of arthropods to navigate deep within the soil is restricted by size and other morphology. For example, sowbugs are less capable of occupying deeper soils due to their size, restricting their diet to the organic material closer to the surface of the soil. Alternatively, shredders like the desert millipede (*Orthoporus ornatus*), which can grow up to 8 in. long, can delve deeper within the soil and have greater access to a variety of food resources, such as decaying roots. The presence of these animals is an essential component of a healthy and properly functioning ecosystem, as they aerate and mix the soil through their movements, along with aiding in the nutrient recycling process.

## Predatory Arthropods

Arthropods exhibiting predatory behavior are a very diverse group, which includes but is not limited to spiders (Order Araneae), centipedes (Class Chilopoda), scorpions, crustaceans (Subphylum Crustacea), and ants (Family Formicidae). Predatory arthropods can be further broken down into two groups: generalists and specialists. Generalist predators have an expansive diet, and are not selective in making prey choices. Specialist predators are adapted to target only one or a few desired species as prey. Because of their size, most arthropod predators consume other invertebrates. However, there are some predatory arthropods that are large enough to consume vertebrate animals, such as spiders and



certain crustaceans. One well-known example of this is the Goliath birdeater tarantula (*Theraphosa blondi*), which is considered a generalist predator. This arthropod is native to South America and weighs up to six ounces. It is considered an ambush predator, hiding behind rocks or in shallow burrows waiting to ambush unsuspecting prey. As denoted by its name, this tarantula on occasion consumes bird eggs or young birds, but it will also eat beetles, earthworms, rodents, toads, bats, lizards, snakes, and other prey opportunistically (Striffler 2005). Crustaceans, such as lobsters (Family Nephropidae), are another example of a generalist predator, consuming clams, mussels, fish, crabs, and at times, other lobsters. It is common for generalist predator arthropods to consume other types of arthropods, such as shredders or herbivorous arthropods, and even on occasion other predatory arthropods. Arthropods exhibiting specialist predatory behavior are less common than their generalist counterparts. Even more rare is a true monophagous predator, which means that the predator only targets a single prey resources. A spider from South Africa, ammxenus termite feeder (*Ammoxenus amphalodes*), is one of the few examples of a true monophagous predator. It has been shown in a replicated laboratory setting that *A. amphalodes* would not accept, nor even attempt to capture any other prey source other than the termite species, African harvester termites (*Hodotermes mossambicus*) (Petráková et al. 2015). Another example of a loosley monophagous predator is the goldenrod crab spider (*Misumena vatia*). This spider does not weave an intricate web and wait for prey to become entangled; instead it hides within a flower and waits to ambush prey of a few target taxa. A common colloquial name for this spider is “the flower spider” due to the fact that it hides within the center of a flower, typically the goldenrod flower, camouflaging itself within the golden yellow center. Then when an unsuspecting bee or wasp comes to the center of the flower, the spider uses its long front legs and bite to immobilize its prey (Heiling et al. 2004). It is also widely known to change color to match the flower color it is hunting from as a form of crypsis.

## Herbivorous Arthropods

Herbivorous arthropods are numerous, and often they are considered pests in cropland areas. It is currently estimated that approximately one million phytophagous (feeding on plants) insect species rely on plants as their only food source (Jander and Howe 2008). These arthropods consume both aboveground and below ground plants and commonly consume roots. Examples of herbivorous arthropods are: cicadas (Superfamily Cicadoidea), crickets (Superfamily Grylloidea), root-maggots (Family Anthomyiidae), and rootworms (*Diabrotica* spp.). The mode of feeding employed by these arthropods is based on their mouthparts, and there are four different categories: leaf chewers, leaf miners, gall makers, and piercing/suckers (Buddle 2012). As denoted by their name, herbivorous arthropods consume plants, but they are not just limited to leafy foliage; these arthropods consume all plant parts, such as: leaves, flowers, roots, fruits, xylem, and phloem.

In recent years several herbivorous arthropod species have shifted more into a “pest” role. This is caused by the urbanization of previously natural areas, such as fields and small forested areas. Homeowners will often combine a mixture of ornamental lawn decoration and natural vegetation to adorn their houses, which may attract herbivorous arthropods that consume the ornamentals. One example of this is the increased levels of generalist herbivores like spider mites (*Tetranychid* spp.) in urban areas, which cause damage to plants by puncturing the plant cells (Raupp et al. 2009). As with most scenarios, vegetation is a vital driver for biodiversity, meaning that with an increase in vegetative diversity in the area, there is also an increase in the biodiversity of herbivorous arthropods in the area.

The diet of herbivorous arthropods is expansive and inclusive. This is often the root of the issue with crop damage in agricultural settings, as the herbivorous arthropods are difficult to control, and damage is often caused by more than one species. The garden symphylan (*Scutigera immaculata*) is a soil dwelling arthropod related to the centipede who feeds on subterranean plant



parts and seedling roots. As a result of this feeding, plants have poor vigor, growth, and survival rates. These arthropods cause prominent damage in agricultural fields, impacting crops such as: broccoli, beets, onions, carrots, corn, spinach, and squash. Due to their size and mouth part limitations, smaller seeds and seedlings are more susceptible to predation by symphylans than larger seeds/seedlings. In combination with commercial pesticides used to commonly control insect pests, tillage of the soil is also used to control garden symphylan populations in agricultural soils.

### Fungal Feeding Arthropods

The final category of arthropod feeding contains the fungal feeders. These subterranean arthropods are generally soil dwellers that consume fungi and (a small amount) of bacteria off of vegetative root surfaces. Examples of arthropod fungal feeders include the hairy fungus beetle (*Typhaea stercorea*), springtails (Subclass Collembola), certain mites, and silverfish (*Lepisma saccharina*) (Shetlar 2011). There are several factors that will impact the presence of arthropod fungal feeders within the soil such as root biomass, microfungi diversity, hyphal (filamentous structure on fungi) length, temperature, water content, pH, organic matter content, and many others (Klironomos and Kendrick 1995). Though many of the arthropods in this category are microscopic soil dwellers, there are some larger ones that move around on leaf surfaces above the soil surface and consume fungi residing on plant leaves. This is a vital ecosystem service provided by the arthropods because fungus on the plant surface is often mixed in with beneficial bacteria. In the process of feeding, the arthropods disturb, consume, digest, and excrete beneficial bacteria within soil. From there, the nutrients within the waste are further broken down and redistributed by other microorganisms in the soil. This distribution increases the soil's fertility and its ability to store nutrients.

There are hundreds of types of fungi and bacteria consumed by fungal feeding arthropods, but what they have in common are the physiological parts of the fungi that are ingested. The two main components of fungi eaten by fungal feeding arthropods are: hyphae and spores (Basset 1991). The fruiting body (mycelium) is the main bulk of the fungus, and it is made of fine filamentous network of hyphae. Fungal spores are single celled reproductive units representing functional organisms that are capable of producing new fungi without any other outside components.

As with most other species of arthropods, fungal feeders are present in urban areas and are oftentimes considered pests by homeowners, despite their environmental benefits. Silverfish will commonly infest older homes, especially those with unknown mold infestations or older amounts of decaying material (i.e., vintage books or clothing collections). These areas frequently contain fungi as well as palatable carbohydrates, providing abundant feeding grounds for silverfish (Lindsay 1940). Springtails are another common nuisance species, as they are found in high moisture areas and can appear in or around a household after times of extreme flooding or an unexpected leak.

### Conclusion

Though their presence in urban areas is often viewed as an annoyance, arthropods bring about more benevolent circumstances than harmful ones with their invaluable role in transferring nutrients within the ecosystem. Shredding arthropods are vital ecosystem recyclers, aiding bacteria in the decomposition process and continually renewing the soil, which in turn results in healthier plant material. Though many are coined as a nuisance in urban areas, predatory arthropods are an indispensable form of natural pest control within the environment. A key example of this is spider species consuming pest species such as mosquitos, which can harbor dangerous diseases. Herbivorous arthropods are often threats to agricultural

lands, and they do cause destruction and damage to crops, but they are an integral component of the food chain, not only providing food to higher orders but also to other arthropods as well. Lastly, fungal feeding arthropods perform a role similar to that of shredding arthropods. The difference being that fungal feeding arthropods consume and excrete fungal waste, aiding in the breakdown of microorganisms in a more complex way than shredding arthropods, and increasing soil nutrient content and fertility.

## Cross-References

- Arthropod Cognition
- Arthropod Life History
- Arthropod Morphology
- Arthropod Navigation
- Bacteria
- Bear Sensory Systems
- Camouflage
- Color Change
- Foraging
- Fungi
- Herbivore
- Insect Diet
- Insect Life History
- Insect Locomotion
- Insect Morphology
- Predator

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## Arthropod Life History

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### Definition

The changes undergone by an arthropod during its lifetime.

### Introduction

Arthropods account for over 80% of the species on earth. As such, the diversity of life histories of arthropods practically spans that of all life. Arthropods are born, grow to sexual maturity, reproduce, and die; discovering variation and patterns of these major life events is to study life history of arthropods (Stearns 1992).

There are four major groups of extant arthropods. Chelicerates (>100,000 species) include animals like spiders, mites, harvestmen, and the four extant species of horseshoe crab; Crustaceans (>70,000 species) include groups like crabs, shrimp, barnacles, woodlice, and brine shrimp; Myriapods (>16,000 species) include centipedes and millipedes. The most speciose group, insects (>2 million, and perhaps as many as 30 million), includes beetles, butterflies, flies, and bees, among many others. Extant arthropods range in size from the crustacean giants to maxillopod miniatures. The Japanese spider crab is the largest of all arthropods with a 2.8 m leg span and the American lobster is the heaviest, weighing over 20 kg. Coconut crabs are the world's largest terrestrial arthropods, weighing over 4 kg, and with a 1 m leg span. Tantulocarida – highly specialized parasitic crustaceans – includes the smallest arthropod species, measuring only 85  $\mu\text{m}$ . This vast richness of life presents a variety of life histories, which are discussed below.

## Reproduction

Most arthropods reproduce sexually in a bisexual population. Like all things in arthropod life history, however, there are interesting exceptions. Some species (e.g., most barnacles) are hermaphroditic, such that a single individual has both male and female sexual organs (Charnov 1987). These species often mate with other individuals, but self-fertilization can also occur (Yusa et al. 2011). Other species are parthenogenic (e.g., some bees and scorpions), where unfertilized ova develop without sperm.

Nevertheless, most arthropod species need to find a mate and transfer sperm to reproduce. Arthropods can have internal or external fertilization, depending on the species. Aquatic arthropods may release gametes into the water column, where sex occurs externally. All terrestrial arthropods, and many aquatic species, engage in internal fertilization, where sperm are inserted into the reproductive tract of the female by some mechanism. The most common mechanism for internal fertilization is the spermatophore, a packet of sperm deposited by the male and retrieved by the female (Proctor 1998). The simplest form of spermatophore deposition occurs when males leave spermatophores in the environment for females to find. Alternatively, courtship rituals can be used to direct females to the spermatophore, which may be deposited on sclerotized (hardened cuticle) stalks (Weygoldt 2000). Further, spermatophores may be deposited directly into the female via a variety of organs, including pene and gonopores (Macías-Ordóñez et al. 2010). Females of many species have mechanisms to store sperm for multiple clutches, or divert it away from eggs to avoid fertilization from an unsuitable male (Andersson 1994). Spermatophores can include nutrients to support offspring survival, or hormones to change female behavior (Gillott 2003; Vahed 1998).

Arthropods may be semelparous or iteroparous (one vs. multiple reproductive events). Some species produce a single clutch of eggs before senescence, while others produce multiple clutches in a season, year, or across multiple years. Arthropods can produce very few to thousands of offspring

per reproductive event. According to life history theory, arthropods, like all organisms, should maximize reproductive fitness by optimizing the relationship between the quality and quantity of offspring. Some arthropods, like Theraphosid spiders, produce hundreds of tiny offspring, of which only a small fraction survive to adulthood. Still other arthropods, however, produce very few young (e.g., some tsetse flies produce only a single egg; Tobe and Langley 1978). Variation in offspring number and size is also in part explained by environmental variation, with substantial variation occurring within species (Fox and Czesak 2000).

## Parental Care and Sociality

The level of parental investment varies in arthropods more than any other group. Forms of postzygotic parental care include nest and burrow building, territoriality, caring for eggs, caring for young after hatching, and provisioning young with food, even after offspring are independent (Clutton-Brock 1991; Trumbo 2012). Notable behaviors include exclusive paternal care seen in many harvestmen (Opiliones) – only the male contributes postzygotic resources (Tallamy 2000; Pinto-da-Rocha et al. 2007). Many arthropod species engage in matrophagy (>3000 species; Ostrovsky et al. 2016), where offspring consume a parent (usually the female) to increase offspring survivorship, and presumably, parent inclusive fitness (Ostrovsky et al. 2016). Most scorpions carry offspring on their dorsum for protection, and may even provide food to young (Polis 1990).

Parental care is one of the two evolutionary routes to sociality (Bourke 2011). In the most basic sense, an offspring receiving care from one or both parents is a social group. Social groups lasting longer than this initial period have evolved in many Arthropod groups. Groups made up of relatives are termed fraternal groups, while groups made up of nonrelatives are termed egalitarian groups (Bourke 2011). Fraternal groups include the social bees, wasps, and ants (of the order Hymenoptera), termites, and some species of beetle, true bugs, and thrips, all of which form large

colonies with one or a few reproductive individuals. This reduction in reproductive individuals insures genetic relatedness among colony mates. Some species of spider form large fraternal groups, but, unlike social Hymenoptera, have little skew in reproduction across individuals of a colony. Instead, colonies maintain high relatedness by inbreeding (Bilde et al. 2005; Agnarsson et al. 2006). As mentioned, egalitarian groups are social groups composed of nonrelatives. Examples include arthropods that group around a resource like spiny lobsters, harvestmen, or amblypygids that aggregate around high-quality microhabitat (Zimmer-Faust and Spanier 1987; Machado 2002; Chapin 2014).

## Birth and Growth

All arthropods are born from eggs, although ovoviviparity, in which eggs hatch inside the mother, which then gives birth to free-living young, occurs in some species (scorpions, in particular). Eggs can be deposited into the environment (water column, on vegetation), in a built structure (burrows, silk chambers), or are carried by the female.

Arthropods grow by molting a sclerotized exoskeleton (Gilbert and Frieden 1981). Many arthropods have a series of molts, the last of which results in sexual maturity, and, in the case of insects, wings. Thus, arthropods not only increase their size with successive molts, but also change morphologically as they develop into adult forms. These growth patterns are often binned into three categories, based on the level of change that occurs during development: ametaboly, hemimetaboly, and holometaboly. Ametabolous (sometimes termed direct development) arthropods maintain general morphology from hatchlings to adulthood. All myriapods, bristletails, and silverfish, for example, exhibit this form of development. Many arthropods engage in hemimetabolous development (sometimes termed simple or incomplete metamorphosis), which has three stages (egg, nymph, and adult) and more minor changes in morphology than complete metamorphosis. Examples include insects like

true bugs, crickets, and cockroaches, which have young that generally resemble adults, but without wings or reproductive organs.

The most complex form of metamorphosis is holometaboly, also called complete metamorphosis. Holometabolous arthropods exhibit four developmental stages: egg, larva, pupa, and adult. Eggs hatch and the larva (e.g., caterpillars, maggots, and grubs) undergo several molts before entering the pupa stage, during which the arthropod is usually inactive. After some time, the adult molts from the pupa, usually with notable morphological differences from the juvenile form. Holometabolous arthropods include butterflies, beetles, and flies. An estimated 45–60% of all living species are holometabolous insects (Hammond 1992). Some arthropods, like Amblypygi and female Theraphosid spiders, have postultimate (after-maturity) molts (Chapin and Hebets 2016). These species also tend to have extended lifespans, and multiple reproductive events.

## Conclusion

Arthropods make up the majority of Animalia and, thus, represent the enormous variation in life histories. Adapted life histories range from living hours to decades, producing a few to thousands of offspring, and providing little to huge offspring benefits. The diversity that Arthropoda captures is exceptional, and so is the life history of animals in the world's largest phylum.

## Cross-References

- [Arthropod Cognition](#)
- [Bear Sensory Systems](#)
- [Insect Sensory System](#)

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## Arthropod Morphology

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### Definition

Arthropods are the invertebrates that constitute the largest group of the animal kingdom. These animals can be easily recognized and differentiated into different types due to their distinct external body appearance or morphology. An arthropod's morphology features include an exoskeleton, paired jointed appendages, and a segmented body.

### Introduction

The phylum Arthropoda (in Greek, *arthros* means jointed and *podos* means foot) is the largest and presumably the most variegated group in the

animal kingdom. The most remarkable adaptive diversity of arthropods helps them survive in every habitat, such as marine, freshwater, terrestrial, and aerial. They are found to be the most successful invaders of the terrestrial habitat on the earth. More than 800,000 species have been described. Thus, Arthropoda is approximately 80% of all known animals (Ayyar and Ananthakrishnan 1994).

This group is of particular interest to mankind as many of the members are economically significant. On the one hand, many members such as prawns, lobsters, shrimps, and crabs contribute to man's food supply; others pollinate flowers, destroy pests, supply useful products (lac, silk, honey, etc.), and provide other valuable services. On the other hand, many insects destroy crops, food stores, household goods, clothing, furniture, etc.; inflict injury as parasites; and transport organisms of dreadful diseases to man and his livestock. Arthropods are thus directly or indirectly concerned with the health, wealth, and prosperity of humanity.

### General Characteristics

Arthropod's body is bilaterally symmetrical. Their body parts are arranged like a mirror image of one side to the other. The body is metamERICALLY segmented, where the segmentation is noticed right from the anterior to the posterior axis. These segments are known as metameres or somites (Hickman et al. 2003).

The body is covered with an exoskeleton made of the chitinous cuticle, which is often thick and hard, but in places on the trunk and limbs, it is flexible to provide movable joints. The exoskeleton forms armor for protection and prevents the loss of water; this has enabled Arthropoda to invade the land. The chitinous covering or exoskeleton is cast off and renewed periodically, and the growth of the animal takes place during the intervals. This process is known as ecdysis or molting (Hickman et al. 1988).

Typically, each segment of the body bears a pair of appendages that are also segmented, with the joints' soft membrane. A segment of the limb



is termed a podomere. This jointed nature of the appendages is implied in the name Arthropoda. The appendages are variously modified in the different groups of the phylum Arthropoda and the body's various parts in the same animal as legs, gills, jaws, etc. Cilia are absent from all parts of the body.

Sense organs include antennae and sensory hairs, compound eyes and ocelli, auditory organs, and statocysts. Sexes are separate and sexual dimorphism is commonly seen. Internal fertilization occurs, and the development is direct or indirect with larval stages.

## Classification

The phylum Arthropoda is divided into three significant subphyla: Trilobitomorpha, Mandibulata, and Chelicerata (Brusca and Brusca 2003; Miller 2005).

### Subphylum Trilobitomorpha (Gk., Tri = Three + Lobos = Lobe)

They were reported abundant during the Cambrian and Ordovician periods (440–550 million years) and disappeared at the end of the Permian period (around 260 million years ago). All extinct marine forms were mostly bottom dwellers with a body size ranging from 2 to 67 cm in length. The name indicates a trilobed body caused by a pair of longitudinal grooves. The body was depressed and consisted of the head (cephalon), middle thorax, and posterior pygidium. The thorax and pygidium together form the trunk. The head has a pair of antennae, a pair of compound eyes, a mouth, and four pairs of jointed appendages. Each body somite except the last possesses a pair of biramous (two-branched) appendages on the ventral surface. Although pygidium possesses segmental appendages, its segments are fused, for example, *Dalmanites* and *Triarthrus* (Fig. 1).

### Subphylum Chelicerata (Gk., Chele = Claw + Keras = Horn + Ata = Group)

Chelicerates encompass animals such as spiders, scorpions, horseshoe crabs, ticks and mites, sea



**Arthropod Morphology, Fig. 1** Triarthrus

spiders, and sea scorpions (extinct). The body is divided into an anterior cephalothorax (prosoma) and a posterior abdomen (opisthosoma). Chelicerates are the only group of arthropods without antennae and mandibles. They have (a) six pairs of appendages, including a pair of chelicerae (for grabbing and shredding food, hence the name Chelicerata); (b) a pair of pedipalps; and (c) four pairs of walking legs (except in horseshoe crabs where a pair of chelicerae and five pairs of walking legs are seen). This subphylum has been divided into three classes:

#### Class Merostomata

This includes marine forms, and only four species are currently living, for example, *Limulus* (horseshoe crab) (Fig. 2). Their body is dorso-ventrally flattened. Prosoma is protected with a carapace of horseshoe shape. It has three longitudinal ridges (one median and two lateral), paired ocelli, compound eyes, and ventrally located mouth. The appendages around the mouth are a pair of chelicerae, four pairs of chelate legs for locomotion and mastication, and one pair of the non-chelate leg for digging. Opisthosoma is movably articulated with the prosoma, and it consists of six segments with lateral spines and a telson (caudal spine). The opisthosoma also bears six pairs of appendages.



**Arthropod Morphology, Fig. 2** *Limulus*

#### Class Arachnida

This includes many familiar organisms like spiders, scorpions, mites, and ticks. Their prosoma bears six pairs of appendages, but opisthosoma is usually without appendages, for example, scorpion (Fig. 3). *Palamnaeus*, the common black scorpion, has an elongate body and grows up to 10–15 cm. The segmented body is divisible into a short anterior prosoma, middle mesosoma, and posterior metasoma. The carapace bears a pair of median eyes close to the middle line and two or three pairs of smaller lateral eyes in the anterolateral margin. Prosoma possesses six pairs of appendages, one pair of the small chelate chelicera, one pair of large chelate pedipalps, and four pairs of walking legs. Mesosoma and metasoma are apodous. The last five segments of metasoma constitute the “scorpion tail.” Behind the last segment of the metasoma lies the postanal sting with a vesicle and spine.

#### Class Pycnogonida

This includes marine chelicerates known as sea spiders. They are not spiders, but the name sea spider is based on superficial similarities such as eight long legs and a small body. Pycnogonids are commonly small animals, and their body length mostly varied from 1 to 10 mm, but deep-sea species may attain a length of more than 6 cm, for example, *Nymphon* (sea spider) (Fig. 4). The body is usually narrow and tubular with three regions – the head (cephalon), trunk, and abdomen. Cephalon bears two pairs of ocelli and at its



**Arthropod Morphology, Fig. 3** Scorpion



**Arthropod Morphology, Fig. 4** *Nymphon*

anterior end a cylindrical proboscis with a mouth at the distal end. The appendages of four-segmented cephalons are mainly one paired chelicerae, one pair of pedipalps, one pair of ovigerous legs (egg-carrying legs), and one pair of walking legs. The trunk is composed of three segments and carries three pairs of long walking legs. The rudimentary abdomen possesses no appendages but an anus.

#### Subphylum Mandibulata (L., Mandibula = Mandible + Ata = Group)

All mandibulates have mandibles on the third head segment for chewing or grinding food. The body can be divided into the head, thorax (or cephalothorax), and abdomen. Appendages of the head consist of one or two pairs of the antenna, a pair of the mandible, and one or two pairs of the maxilla. Members of this subphylum include freshwater, marine, and terrestrial forms. This subphylum has six classes:

### Class Crustacea (L., Crusta = Shell)

A chitinous exoskeleton covers the body. Head appendages are paired antennules, antennae, mandibles, and two paired maxillae. Paired biramous appendages are seen on each segment of the thorax and abdomen. Crabs, prawns, lobsters, water fleas, and barnacles are coming under this class, for example, marine prawn (*Penaeus*) (Fig. 5). The elongated and more or less spindle-shaped body can be divided into a cephalothorax (fusion of the head and thorax) and abdomen. The body consists of 19 segments, and each segment carries a pair of appendages. Appendages are also segmented, and these segments are called podomeres. Cephalic appendages are composed of five pairs: paired antennule, antenna, mandible, first maxilla, and second maxilla. Thoracic appendages are eight pairs. The first three pairs are specialized for feeding and are called maxillipeds or foot jaws. The succeeding five pairs are walking legs. Abdominal appendages, known as pleopods or swimmerets, are of six pairs and are used for swimming. The first pair of pleopods is varied in males and females. The second to fifth pairs are typical. The broad and flat sixth pair is known as uropods.

### Class Chilopoda (Gk., Cheilos = Lip + Pous = Foot)

The members of this class are commonly known as centipedes (centi = 100 + ped = foot). The number of legs varies from 15 to 191 pairs. They are

terrestrial carnivorous with a dorsoventrally flattened body. The body can be divided into a head and many-segmented trunks. The head bears antennae and three paired jaws, namely, mandibles, first maxillae, and second maxillae. The trunk is many-segmented, and each segment carries one pair of uniramous walking appendages. The legs of the first trunk segment are maxillipeds (forcipules). These are enlarged and modified as poison claws. The anal legs on the last trunk segment are not locomotory and are variously modified, for example, *Scolopendra* (Fig. 6).

### Class Diplopoda (Gk., Diploos = Double + Podos = Foot)

Diplopods are commonly known as millipedes. They vary in size (2 mm to 30 cm). Their exoskeleton is heavily calcified. The body is long and cylindrical with a head and multi-segmented trunk. The head bears one pair of short antenna, one pair of the mandible, and one pair of the maxilla. The maxillae of the two sides are fused to form a gnathochilarium that resembles insects' labium. Externally, the trunk consists of a series of the segment like cuticular rings, and most of these rings are diplosegments. Most diplosegments possess two paired legs (Diplopoda) and spiracles. Many of them possess special glands called repugnatorial glands or stink glands that produce



**Arthropod Morphology, Fig. 5** *Penaeus*



**Arthropod Morphology, Fig. 6** *Scolopendra*



**Arthropod Morphology, Fig. 7** *Spirostreptus*

an irritating fluid on disturbance, for example, *Spirostreptus* (Fig. 7).

**Class Symphyla** (Gk., Syn = Together + Phylon = Tribe)

Members of this class are commonly known as centipedes. The body is soft and small, 2–10 mm long, and made of the head and trunk. The head bears paired antenna, mandible, a first maxilla (long), and a second maxilla (fused to form labium). The eyes are absent, but the sensory organ (Tomosvary organ) is well developed at the antenna's lower end. The trunk bears 14 segments covered by 15–24 tergites. Trunk segments 1–12 bear walking legs, segment 13 bears a pair of spinnerets, and the last segment bears a pair of sensory structures called trichobothria. The trunk terminates in a tiny telson, for example, *Scutigera* (Fig. 8).

**Class Pauropoda**

Pauropods are minute animals ranging from 0.5 to 2 mm in length. The body is divisible into a head and trunk. The head bears one pair of antenna, one pair of the mandible, and one pair of the maxilla. The eyes are absent, but pseudoculi (a pair of the peculiar disc-like sensory organ) are present. The antenna is six-segmented and three branched (trifid), a feature that distinguishes pauropods from all other tracheates (insects, centipedes, millipedes, and symphylans). The trunk contains



**Arthropod Morphology, Fig. 8** *Scutigera*



**Arthropod Morphology, Fig. 9** *Pauropus*

11 segments and a telson, for example, *Pauropus* (Fig. 9).

**Class Insecta**

These are commonly terrestrial and aerial and seldom aquatic. The body is divisible into a head, thorax, and abdomen. The head consists of six segments fused together in the adult. The head is with paired compound eyes, ocelli (up to three unpaired), and antenna. Mouthparts are suitably modified for biting sucking, siphoning, chewing, piercing, etc.). They have three-segmented thoraces with a pair of legs on each segment and pair of wings on the second and





**Arthropod Morphology, Fig. 10** Butterfly

third segments. But some insects are wingless, and some others have only one pair of wings. The abdomen is usually composed of 9–11 segments and a telson. The abdomen is devoid of appendages in the adult, for example, butterfly (Fig. 10) and stick insect.

#### **Subphylum Onychophora (Gk., Onych = Claw + Phor = To Carry/Bear)**

They are soft-bodied (hence called velvet worms) wormlike terrestrial animals with numerous paired segmented appendages. The head is not well marked off from the trunk, and it bears one pair of antenna, one pair of the mandible, and one pair of the oral papilla. The trunk consists of 13–43 pairs of trunk appendages, and these appendages are uniramous, short, stumpy, unjointed, conical, and fleshy called lobopods. Each lobopod terminates in a pair of sclerotized claws (hence the name Onychophora), for example, *Peripatus* (Fig. 11).

#### **Conclusion**

The phylum Arthropoda is the largest phylum in the animal kingdom. Segmentation of the body is the characteristic of this phylum. The head consists of the antennae, eyes, and mouth parts. Some trunk segments are often fused with the head to form the cephalothorax in the Crustacea and Arachnida. The number of segments forming the thorax and abdomen varies in the different classes.



**Arthropod Morphology, Fig. 11** *Peripatus*

In all Arthropoda, except *Peripatus*, the body is covered with a thick cuticle and forms an exoskeleton, giving protection to the body and serving the muscles' attachment. Arthropoda's eyes except *Peripatus* are simple eyes (ocelli) and compound eyes (faceted eyes). Statocysts are present in many crustaceans as organs of balancing. Sexes are generally separate. Development is always accompanied by metamorphosis.

#### **Cross-References**

- [Arthropod Cognition](#)
- [Bear Sensory Systems](#)
- [Insect Morphology](#)

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## Arthropod Navigation

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### Synonyms

Crustacean exploration; Insect movement; Insect navigation

### Definition

The mechanisms by which arthropods maneuver to and from resources, such as shelter, food, and breeding grounds.

### Introduction

Animals in the order Arthropoda include crabs, bees, ants, and any insect or invertebrate with an exoskeleton. Arthropod navigation is a mechanism by which arthropods maneuver through their environment and locate resources necessary for survival and reproduction. Arthropods exhibit four primary types of navigation, including path integration, spatial memory, image matching, and map-like behavior.

### Path Integration

In path integration an animal tracks the sequence of movements, direction, and distance traveled and can use that information to orient to a place of origin. Path integration is also known as dead reckoning, which is better used when no landmarks are present. Path integration has been

shown to be an important navigational tool in cataglyphis ants like the desert ant (*Cataglyphis* spp.), which inhabit barren terrains (Wehner and Mandyam 1981; Wehner and Wehner 1990). On unfamiliar ground, path integration is the only available means of navigation in many arthropod species (Collect and Collect 2000). In familiar surroundings, however, guidance by landmarks may override guidance by path integration, with individuals using path integration as a secondary navigation strategy when landmark navigation fails (Collect and Collect 2000).

### Spatial Memory

Spatial memory is a fundamental cognitive faculty in many species. Studies of animal spatial memory often provide a proxy model for human memory due to the ability to transfer experimental paradigms among species (Birds and Burgess 2009). Insects will use spatial memories to help hold a position in air, to return to safety, and/or to forage location (Collect et al. 2013). Spatial memory allows the insect to recall spatial location which may be passed onto offspring through information sharing mechanisms.

### Image Matching

Image matching allows the arthropod to recall previous landmarks and make a comparative determination of whether the individual has experienced that landmark on a previous occasion. Egocentric navigation can be found when an individual uses image matching to rely on information continuously collected en route and then uses the process of path integration to integrate all angles and distances navigated to determine a mean home vector (Wehner et al. 1996). For example, the image of the horizon skyline surrounding the nest entrance is



retinotopically stored in some arthropod species and is recalled when the animal approaches the goal along its vector course. Specific locations are pinpointed by a form of image matching whereby the insect navigates to maximize the fit (i.e., reduce the visual discrepancy) between the retinal image and its memory of surrounding landmarks related to its goal (Collect 1992).

## Map-Like Behavior

Map-like behavior is the reliance on site-specific information rather than information that has been collected by coming and going continuously. Map-like behavior is considered geocentric, centering navigation on the earth's position. An arthropod exhibits geocentric (map-based) navigation when it has the capacity to determine its spatial position within the larger environmental framework (Wehner and Wehner 1990).

## Conclusion

Studies on arthropod navigation have aided scientists in understanding movement mechanisms that arthropods use to locate shelter, forage, and other features important to survival and reproduction. Yet comprehensive understanding of arthropod navigation is still not fully developed and will be important in a changing environment. Environmental changes resulting from climate and weather extremes may pose difficulties for arthropod navigation if the landscape is substantially altered.

## Cross-References

- [Arthropod Life History](#)
- [Bear Sensory Systems](#)
- [Dead Reckoning](#)
- [Insect Life History](#)
- [Insect Locomotion](#)
- [Landmark](#)

- [Locomotion](#)
- [Memory](#)
- [Navigation](#)

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## Articulatory Rehearsal Loop

- [Cognition](#)

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## Artificial Food Patches

- [Food Patch](#)

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## Artificial Foraging Trays

- [Food Patch](#)

## Artificial Fruit

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### Definition

An artificial fruit is an experimental apparatus which functionally mimics natural food items, where an outer shell or casing must be removed via manipulation in order to access an edible core or kernel.

### Artificial Fruits and the Two-Action Method

The term “artificial fruit” was first used by Whiten et al. (1996) to describe an apparatus provided to both human children and chimpanzees (*Pan troglodytes*). This apparatus built upon the “two-action method,” first used by Dawson and Foss (1965) in their study of observational learning in budgerigars (*Melopsittacus undulatus*). Two-action tasks expose naïve “observer” animals to “demonstrator” or “model” animals which operate on a task designed to be dealt with in either of two (or potentially more) alternative ways. The observer animals are then given access to the task, and the ways in which they interact with it are recorded. If observer animals tend to manipulate the task using the action modelled by the demonstrator more frequently than the alternative action, this indicates that social learning occurred. This method allows researchers to distinguish low-fidelity forms of social transmission, such as *stimulus enhancement* (in which animals learn to orient their behavior towards a particular object) from higher-fidelity forms of social transmission, such as *imitation*, in which an animal learns the form of a behavior through observation. Low-fidelity social transmission within a two-action artificial fruit task would lead to observers being

attracted to the apparatus more than control individuals who saw no model, but then solving the task by trial-and-error, so this would not result in animals matching the demonstrator’s solution more frequently than the alternative action.

Although two-action artificial fruit tasks identify relatively high-fidelity social learning, they do not necessarily differentiate *imitation* (copying the form of actions, like sliding versus lifting a door) from *emulation* (copying the results of actions, such as “the door slides” versus “the door rises,” which could be achieved using actions different to those observed). Alternative methods, such as *ghost controls*, can be used to distinguish between these relatively high-fidelity forms of social learning.

Artificial fruits can incorporate multiple barriers, each of which may be removed in different ways in order to access a reward, thus exemplifying the two-action method. For example, Whiten et al.’s (1996) task featured bolts which could be removed using either a poking or twisting action, a barrel latch incorporating a pin that could be removed using either a turning or spinning action and a handle that could be turned or pulled upwards. However, artificial fruits do not necessarily require high levels of manipulative complexity; some designs have incorporated barriers as simple as a door which could be either lifted up or slid to one side to access a food reward within a box (e.g., the “doorian,” Horner et al. 2006).

While retrieving the food from within all artificial fruits requires physical manipulation of the task, the first artificial fruits did not generally require the use of tools. More recently, the term has also been used to describe tasks requiring tool use. Though some of these tool-use tasks (e.g., the “Pan-pipes,” Whiten et al. 2005) require forms of behavior that are perhaps more analogous to wild primate behaviors such as termite-fishing or honey-dipping, rather than fruit processing (and so perhaps might be better termed “artificial foraging tasks”), they fulfil the same goal of providing a manipulative task that can be solved using one of at least two distinct behaviors, and so can be broadly described as “artificial fruit approaches.”

## Applications

Artificial fruits have primarily been used to examine social learning processes in both humans and nonhuman animals but have also been incorporated in experimental paradigms examining cognitive abilities such as behavioral flexibility and planning (e.g., Miyata et al. 2011). Within the field of social learning, artificial fruits have been used in dyadic settings to investigate the capacity of multiple species, including great apes (chimpanzees: Whiten et al. 1996, gorillas: Stoinski et al. 2001, orangutans: Custance et al. 2001), and other nonhuman primates (marmosets: Caldwell and Whiten 2004, capuchin monkeys: Custance et al. 1999), birds (keas: Huber et al. 2001), and human children (e.g., Whiten et al. 1996), to engage in high-fidelity social learning. They have also been used to study social learning biases (such as from which models animals are most likely to learn, and the impact of context upon such biases) and the social dynamics which affect the transmission of behaviors within groups.

## Cross-References

- [Cultural Transmission](#)
- [Culture](#)
- [Ghost Control](#)
- [Imitation](#)
- [Social Learning](#)
- [Stimulus and Local Enhancement](#)

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## Artificial Selection

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## Definition

Artificial selection is the modification of desirable phenotypes in plants and animals through its propagation in the successive generation by human intervention.

## Introduction

Artificial selection is the process by which natural variations that are advantageous from the perspective of humans are selected unnaturally

or artificially. Charles Darwin discussed the concepts of artificial selection as domestication in his classic monograph *On the Origin of Species by Means of Natural Selection* in 1859 (Darwin 1859). Later, in 1868, he published a two-volume work *The Variation of Animals and Plants Under Domestication* devoted entirely to the process of domestication that he had discussed in the *Origin of Species* (Darwin 1868). His publication presented concepts and examples about the plant and animal breeding as well as the analogy between the artificial selection and natural selection. According to Darwin, artificial selection operates in similar way as natural selection and can produce concrete results if effectively applied. Darwin conceptualized selection into three types as natural selection, methodical artificial selection, and unconscious artificial selection (Gregory 2009). Methodical artificial selection is the deliberate or intentional enhancement of the desired trait of interest, while the unconscious selection refers to the passive form of artificial selection in which humans naturally preserve the desired trait without any intention of altering it and thus may result in long term effects in phenotypes unknowingly. Natural selection, as compared to artificial selection, is an environmentally driven selection of individuals possessing more advantageous traits as compared to less advantageous traits. The reproductive success of individuals is independent of selective breeding or domestication by humans.

There are several approaches to carry out the artificial selection experiments (Fry 2003). One of the most common approaches to carry out artificial selection is the traditional breeder's approach. The method employs the measurement of phenotypic traits of interest among individuals of a population and the propagation of extreme values of phenotypic traits of interest to the next generation by breeding. The process of artificial selection depends on the method, strength, and consistency of the selection (Fuller et al. 2005). The artificial selection experiments performed in the laboratory play an important role in the study of the history of evolution, adaptation process, mechanisms of genetic variation, and several

other evolutionary processes involving trade-off, mutation rate, and frequency-dependent selection. The study of artificial selection in the laboratory is a valuable tool to study genetic parameters of traits such as covariance, correlation and regression in a natural population, and their effects on fitness. Such kind of experiments are performed in the laboratory by experimenter by selecting individuals with the specific traits and propagating it along the generation or by causing the selection indirectly by fixing the environmental factors instead of direct breeding (Hill and Caballero 1992).

## Responses to Artificial Selection

The response to artificial selection is predicted by the equation  $R = h^2S$  in evolutionary biology (Falconer and Mackay 1996). Here,  $R$  represents the response to selection,  $S$  represents the selection differential, and  $h^2$  denotes the narrow sense heritability. The selection differential  $S$  represents the difference in the mean of the subset selected for breeding and the mean of the entire population, while  $R$  denotes the change in the mean of the trait per generation. The realized narrow sense heritability is the ratio of  $R$  and  $S$ . The response to the strength of the selection is attributable to the level of heritability, i.e., higher the level of heritability, greater is the strength of selection. However, the selection response on the heritable traits may not always result in the expected phenotypic response and may be biased. This may be attributable to the presence of environmental correlation between the trait of interest and fitness or due to the presence of the environmental correlation among the relatives. The response to selection also depends upon a number of factors such as the magnitude of additive genetic variance of the trait that is expressed, the temporal and spatial variation of additive genetic variance, and reproductive capacity as well as the mean age of parents ( $L$ ) at which the progeny is born. The expected rate of response per year is determined by the ratio of response of selection ( $R$ ) and mean age of parents, i.e.,  $R/L$  (Hill 2001).

## Artificial Selection in Plants and Animals

The use of artificial selection has been extensively applied in the breeding of animals and modifications of plant varieties for domestication purposes. The conscious selection of phenotypic traits and its perpetuation by humans have resulted in the forms which differ in external characters as compared to their wild form in nature.

The domestication of most of the plant species from wild forms involves genetic modification through prolonged artificial selection methods. The agronomically important traits that meet human needs are specifically chosen for the selection process. Such traits are related to growth and flowering, higher yield, resistance to biotic and abiotic stress, and production of more valuable products. The phenotypic shift in traits brought about in the process of domestication is categorized as “domestication syndrome,” and it includes increased seed production, lower seed dispersal, increase in seedling vigor, more rapid germination, loss of seed dormancy, larger inflorescence, and altered photosensitivity (Gepts 2004).

Maize domestication represents the most striking example of strong artificial selection on specific agronomically important genes. The domestication of wild grass teosinte into modern maize demonstrates the rapid phenotypic evolution through the process of artificial selection. The genome of Mexican annual forms of teosinte and modern maize is similar to such an extent that they can be easily cross-hybridized, but they exhibit extreme differences at the level of adult morphology (Doebley 2004). The adult morphology of maize differs from the wild teosinte in terms of inflorescence, architecture, yield, habit, and biochemical composition. Such an extreme difference in morphology is the result of human selection during the process of domestication. The fact that Mexican annual teosinte is the wild progenitor of modern maize has been addressed by several cytological evidences such as presence of similar chromosomal arm length, similar centromere position, and presence of knobs in the interstitial position (Longley 1941).

Other than cytological evidence, the isozyme studies revealed the presence of indistinguishable allele frequencies between Mexican annual teosinte and maize. Other than maize, many other domesticated seed plants such as rice, wheat, and barley also show a variety of changes under the influence of artificial selection.

The long-term artificial selection experiment is also conducted in laboratories to understand the genetic changes in the population. The Illinois long-term selection experiment is one of the longest running genetics experiment which aims to elucidate the genetic control of traits in response to divergent selection. For the commencement of selection lines, open pollinated variety of maize, Burr’s White, was utilized as founder population to start the selection lines with low and high, oil and protein content. The four selection line Illinois High Oil, Illinois Low Oil, Illinois High Protein, and Illinois Low Protein represent the extremes of protein and oil concentration in maize. Dudley (2007) used classical quantitative genetics techniques along with QTL to study the impact of artificial selection on oil and protein content in Illinois selection lines and concluded that selection is a powerful tool to create divergent lines. The selection lines provides immense knowledge about the role of genes in oil and protein accumulation as well as it also acts as a unique source to understand the dynamics of evolutionary changes.

The overall process of domestication through artificial selection has given rise to different breeds. The genetic change that occurs during the transition from nature to captivity in a population of animals undergoing domestication is the consequence of chance factors and selection pressure. Artificial selection in animals for the purpose of domestication has been considered as one of the main genetic factors other than chance factors such as inbreeding and genetic drift (Mignon-Grasteau et al. 2005). Artificial selection in animals is done in captivity by humans by selecting the breeding animal and controlling the environmental conditions. One of the common examples of artificial selection in animals is the modern domesticated dog (*Canis lupus familiaris*). The domestication of

dog provides insight into the evolutionary changes that occur during the short-term evolutionary process and provides information about the genetic architecture of phenotypic variation. The work done by Akey et al. (2010) shows that most of the phenotypic variance in size, shape, and behavior in domesticated dogs originated recently through strict breeding and intense artificial selection, although the process of selection dates to over 14,000 years ago. Their work showed that over 155 genomic regions show evidence of strong selection in recent times and possess candidate genes for different phenotypes that vary among different breeds. Other valuable mammal species which have been domesticated extensively using human intervention are cattle, sheep, goat, pig, and horses (Teletchea 2019).

Numerous selection experiments have been performed in *Drosophila* to understand the dynamics of the evolutionary process in real time. *Drosophila* has been extensively utilized in quantitative genetics to study the short-term and long-term selection processes. Clayton and Robertson (1957) used the estimates of heritability and variance to study the selection response in the abdominal bristle number in *Drosophila melanogaster*. They found that the distribution of bristles number in different selection lines was nonoverlapping due to long term selection process. Similarly, Ahuja and Singh (2008) employed a secondary sexual characteristic of *D. melanogaster*, i.e., male sex comb, to study the genetic architecture of variation through an artificial selection process. The divergent artificial selection of sex comb bristle number for twenty-four generation resulted in a significant response toward low bristle number. Brown et al. (2017) performed selection experiment for odor-guided attractive and aversive behavioral response toward aromatic and ester compounds for thirty generation in *Drosophila*. They found that selection lines differed in their olfactory responses toward chemicals as compared to control. Their further investigation also showed the presence of correlated responses between life-history traits and feeding behavior due to the selection process.

## Conclusion

The artificial selection had played an important role in the domestication process in the history of human civilization. Selective breeding through human intervention has enhanced the desirable traits in both plants and animals. Long-term selection on traits, when carried through many generations, produces traits that hardly resemble the original one, i.e., they show extensive changes at the level of morphology and physiology. However, selective breeding is also known to decrease genetic diversity in plants and animals (Liu et al. 2019). Other than the domestication process, selection experiments in the laboratory give estimates of genetic parameters, which help in understanding the dynamics of the evolutionary process.

## Cross-References

- [Directional Selection](#)
- [Evolution](#)
- [Natural Selection](#)
- [Self-Domestication Hypothesis](#)

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## Artiodactyl

- [Artiodactyla Diet](#)
- [Artiodactyla Morphology](#)

## Artiodactyl Cognition

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## Synonyms

[Ungulate cognition](#)

## Introduction

The order of Artiodactyla is a large diverse group comprised of even-toed ungulates. Taxonomists debate which taxa are part of the order, but most agree that it includes Ruminantia (cattle, sheep, goats, antelope, deer, giraffes), Tylopoda (camels, llamas, alpacas), and Suliformes (hippopotamus, pigs, wart hogs, peccaries) (Etnyre et al. 2011; Rees and Cranston 2017). The estimated 210 species in this group are native to five continents (not Australia nor Antarctica) in a vast array of habitats from arctic and alpine tundra to tropical rain forest and desert. They are also diverse in size ranging from large hippopotami and tall giraffes to the diminutive mouse deer, which weighs 2 kg and is 23 cm tall. With the exception of pigs and peccaries, who are omnivorous, Artiodactyls graze or browse on vegetation. Species' social systems vary from living solitarily to large multi-male, multi-female herds. Social systems and habitat choice are partly a function of predator defense and availability of forage (Etnyre et al. 2011). Some species are migratory (e.g., caribou and wildebeest), and others are territorial (water chevrotain, duikers, dikdiks) (Leuthold 1977). Finally, among the Artiodactyls, several groups

have been domesticated starting 10,000 years ago with sheep and goats (Etnyre et al. 2011).

This diversity invites many questions about the kinds of cognition and their extent among the Artiodactyl. Unfortunately, because most species are large bodied, most of the research has been conducted on domesticated or zoo animals. The process of domestication or capture and confinement of wild species in a zoo results in populations of animals that are perhaps more docile, less sensitive to human interaction, etc. Briefer et al. (2014) asserted that two factors reduce brain size and cognitive capacities: (1) relaxed selection pressure for foraging, predator detection, and predator defense and (2) enhanced selection pressure to tolerate the human environment. Research with domestic animals can point to subjects' capabilities, but not the full extent of their counterparts' cognitive capacities. Another limitation to the scope of research on Artiodactyl cognition is that much of the research has been designed to serve agricultural practices and not to answer basic research questions about cognition.

Beliefs in the cognitive capacity of Artiodactyl are ubiquitous among livestock handlers, wildlife managers, and zookeepers. Anecdotes provide many examples of animals learning and remembering that suggests to the casual observer that these species are capable of complex thinking, reasoning, and understanding. The field of comparative cognition seeks to explain such anecdotes as species-general mechanisms and to trace the phylogenetic development of these mechanisms (Shettleworth 2013). It is difficult to design and conduct the rigorous research that will rule out general stimulus-response mechanisms, especially given the challenges of working with large-bodied individuals.

## Social Cognition

The social brain hypothesis is that social species use more advanced cognitive capacities to maintain group cohesion and remember conspecific relationships (Perez-Barberia et al. 2007). The costs of group living (easy detection by predators, foraging competition) selects for larger brains.

Perez-Barberia and colleagues (Perez-Barberia et al. 2007) have reported that among the Artiodactyl, smaller-brained taxa tend to have more fluid social organization. However, they note that moose, muntjac, brocket deer, and bushbuck are the few solitary species with large brains. These large-brained, solitary species live in closed habitats (temperate forests, tropical forests, and swamps), where it is easier to elude predators and more difficult to stay in contact with multiple conspecifics. Other large-brained species live in groups and most live in relatively open habitats.

It is difficult at this stage to know which characteristic evolved first, large brains or habitat selection. Social complexity should correspond with cognitive changes in a lineage (MacLean et al. 2012). Investigating cognitive differences between solitary and group living animals are worthy of study, e.g., solitary moose and elk (whose cows live in large herds dominated during the rut by bulls). Whiten (2018) has suggested that social species develop higher generalized intelligence than solitary species.

Funding and accessibility to species have led to most of the cognition research in Artiodactyla to domesticated species. Domestic pigs (species within the Suidae) are one commonly studied group. In a study of designed primarily to determine the value of housing pre-weaned piglets with their sows in groups vs. solitarily, van Nieuwamerongen et al. (2017) demonstrated that subordinate piglets in a pair were capable of remembering the location of the baited bucket from the previous trial and that dominate piglets were capable of using the subordinate piglet to lead them to a baited bucket. However, contrary to previous research, the housing situation had no effect on the piglets' abilities. The researchers cited studies of boar, where dominate animals used subordinate animals to lead them to food sources, then the dominate animals supplanted the subordinates. Subordinate boar were wary of using a food source in the presence of a dominate individual. This would suggest that pigs are aware of the dominance hierarchy and use that to their advantage. It would also suggest that pigs are capable of a theory of mind, acting on the knowledge of others.

A similar perspective-taking ability was also reported in the review article on cognition in pigs (*Sus domesticus*) by Marino and Colvin (2015). The authors reported that piglets show object, locomotor, and vocal play behavior. In Y-mazes, pigs show the ability to discriminate odors and auditory playback cues. Additionally, pigs are capable of discriminating familiar from unfamiliar conspecifics and adopt the emotional responses of other pigs trained to anticipate either an appetitive or aversive event (Reimert et al. 2015).

Among the Ruminata, social cognition in dairy cattle has shown that cows used vocalizations to express emotions in positive and negative contexts and that individuals recognized known conspecifics' vocalizations. However, Green et al. (2019) explored the implications of the research for animal husbandry, rather than for understanding the extent of Ruminata social cognition.

## Nonsocial Cognition

While perception of conspecifics is within the domain of social cognition; sensory and perceptual capacities are also important for animals' nonsocial cognition, such as navigating the environment, predator avoidance, and food finding. Researchers are naturally constrained by their own sensory capacities, which make understanding other species' *umwelt* – self-world, difficult (Shettleworth 2013). An artiodactyl species comparison of sensory capacities does not exist. There are focused studies on one or more aspects of a sensory system which includes one representative artiodactyl, but nothing truly comparative (Vater and Kossel 2011).

One nonsocial domain of *umwelt* is hearing. The large, flexible ears of artiodactyl suggest that their hearing is keen, but the hearing range varies among the species. More problematic for researchers to investigate is olfaction.

It would be preferable for researchers to find the common capacities within a genus or a family based on common challenges in their wild habitat, establishing the procedures with domestic species, then testing the same capacity in closely related species living in a zoo setting, followed

by investigating individuals in a free-range setting. In conjunction with establishing the related species capacities, one could suggest how this capacity might have provided an adaptation to their wild living situation and its phylogeny. If a comparative approach were used, our understanding of these taxa's cognitive capacities would be greater.

Instead, because the nonsocial cognitive research is scattered and conducted more to serve animal husbandry and livestock production purposes, the following discussion will focus on reporting the research species by species. For domestic pigs (*Sus domesticus*) the range of hearing is 42–40,000 Hz, and they have a high density of tactile receptors in their snouts (Marino and Colvin 2015). Marino and Colvin (2015) reported that olfaction is pigs' keenest sense. These authors reviewed several studies of pig cognition which showed that their memories for object discrimination can last up to 5 days. They are also capable of discriminating between sites with food caches, preferring more plentifully stocked caches. They cite Cerbulis' (1994) thesis research that two potbellied pigs were able to understand gestural and verbal symbols of objects and actions, e.g., “fetch the frisbee.” This line of research, if pursued in a comparative framework, would advance understanding of the taxa.

Another line of research that has been pursued is pigs' spatial learning using a holeboard with baited wells. Grimberg-Henrici et al. (2016) compared the effect of enrichment during development in pigs (*Sus scrofa*). Pigs living in the enriched environment were regularly given new toys, in their more spacious enclosure. All pigs were able to learn the locations of the baited wells, but pigs in the enriched environment searched faster and did not revisit wells. Measures of cortisol at the end of the study showed no differences between the two groups. How wild Suliformes search for food validates, this test of spatial discrimination, working memory, and reference memory (how to do the task from one trial to the next).

Albiach-Serrano et al. (2012) directly compared the differences between domestic pigs and wild boar (*S. s. domestica* and *Sus scrofa scrofa*)

on a two-container food finding task. They used one of four cues: slope of board hiding food container, a container that was shaken or not shaken, the sight of a baited container changing position, and a human touching, pointing at, or looking at the baited container. The animal subject's ability to find the baited container was determined by its previous exposure to the cue, not its wild or domestic status. If only more of these direct comparisons existed in the literature!

Judgment bias tasks have been used to assess differences in pigs, based on birth weight (normal vs. runt of the litter) and on rearing conditions (barren vs. enriched). This might be used productively in other artiodactyl species as well as to establish the animals' use of working and reference memory.

Roelofs et al. (2017) used the holeboard task as part of a set of tests to tease apart the independent facets of working memory and reference memory in pigs. This task is linked to an animal's propensity to avoid aversive (negative) stimuli and seek out appetitive (positive) stimuli. An acoustic cue (200 Hz or 1000 Hz, counterbalanced) was used to signal a large reward (positive), and the other acoustic cue was used to signal a small (negative) reward. Then researchers presented an ambiguous acoustic cue. A positive bias would occur if the pig selected the response for the large reward in the face of the ambiguous cue and a negative bias would occur if the pig selected the response for the small reward. The authors concluded that positive and negative biases are a valid proxy for pigs' emotional responses. Luo et al. (2020) determined that pigs reared in barren conditions were more reactive to negative contrast in maze running for rewards. As in primates and rodents, early rearing conditions do impact pigs' cognitive capacities.

Another way of assessing the impact on pigs' cognitive capacities is to investigate the effect of being the runt (low birth weight/intrauterine retardation) in a litter. This has implications for pigs' social behavior, agricultural practices, as well as human development. van Nieuwamerongen et al. (2017) noted that body size in pigs influences an animal's place in the dominance hierarchy. Roelofs et al. (2019) determined that low birth

weight pigs required more training, compared to normal birth weight pigs. Otherwise, the judgment bias test as described above produced the same positive bias for normal and low birth weight groups. In another study, Murphy et al. (2015) also used the judgment bias test and a reward discrimination test. Results showed that low birth weight pigs displayed a more negative affect and differences in emotionality compared to normal pigs.

To remedy the problem of low birth weight, Schmitt et al. (2019) provided various levels of dietary supplementation to piglets with varying degrees of low birth weight characteristics (none to severe) postnatally. At weaning, they tested piglets' cognitive abilities on a T-maze that involved spatial learning and an object recognition task that involved memory for familiar objects. The results did not suggest clear cognitive deficits in the low birth weight piglets, nor did it show a clear effect of dietary supplementation. However, half the piglets could not habituate to the testing situation, but those that did showed spatial memory and object memory.

Taken together, these studies show that domestic pigs have effective spatial memories, memories for objects in their environment and memories about amount of rewards in choice tasks of various kinds.

One experiment with domestic goats (Briefer et al. 2014) has shown that goats easily learn how to find forage and retained the information for 6 months. Because observing a conspecific performing the foraging task for themselves did not enhance learning, the researchers suggested that domestication results in animals being less reliant on conspecifics for foraging help. The authors speculated that domestic goats may have retained independent foraging abilities, in spite of domestication.

To understand the *umwelt* in cattle (*Bos taurus*), a preference test of foraging was conducted as they moved through a field (Hirata et al. 2019). Cattle discriminated between green and dry forage patches from a distance up to 3 m. The patches were constructed to minimize olfactory cues, suggesting that vision was the primary sense used during foraging. Researchers manipulated

access to visual cues in a discrimination test. Cows were either blindfolded or not during a choice test in a feed trough. Results showed that cattle who were blindfolded did not reject the dry forage, until they had tactile contact with it. When cattle were allowed to see the forage, they chose the green forage, before touching it with their muzzle or tongue. Olfaction seemed to have secondary influence under both blindfolded and non-blindfolded conditions (Hirata and Kusatake 2020).

Giraffe (*Giraffa camelopardalis*) memory processes of object permanence, short-term memory, and the use of acoustic cues to locate a food item were investigated in a zoo environment (Caicoya et al. 2019). Giraffes were given the opportunity to “participate” in the research for a food reward or feed themselves from the freely available forage. Object permanence and short-term memory were investigated by showing the animals a food item (carrot or apple) in a sealed opaque container. Then the container was closed, then the giraffes were asked to select one of the two containers (filled or empty) by touching it with their tongues or noses. In the acoustic cue tests, the containers were filled out of the animals’ sight, then the experimenter performed either a shake full (noisy) trial or a shake empty (quiet) trial. The shaken container was rewarded if the giraffe selected it. The giraffes demonstrated an understanding of object permanence but could only remember the correct container after a short 30 s delay, not the longer delays of 60 and 120 s. The full, noisy, shaken container was selected correctly by the giraffes, but the empty, quiet, shaken container was not selected correctly. These experiments demonstrated that giraffes and perhaps other artiodactyl are capable of complex cognitive processes. The techniques used in interacting with the zoo giraffes provide a good model for experiments with other species. This research begs for a comparison between the fission-fusion group living giraffes and the solitary living okapi (*Okapia johnstoni*).

A study of domestic alpacas (*Vicugna pacos*) demonstrated that they do not show the errors of persistence in a detour task. Unlike horses, donkeys, and dogs, when an opening was moved from

one end of a barrier to the other end, alpacas were able to modify their route, rather than continue to search for the previously learned opening. This suggested behavioral flexibility that is worthy of further investigation in this group (Abramson et al. 2018).

An interesting approach to linking behavior and brain organization has been conducted on laterality of behavior in wild elk (Found 2017), wild saiga antelope, (Giljov et al. 2019), captive ibex (*Capra pyrenaica*) (Sarasa et al. 2014), and domestic sheep (*Ovis aries*) (Barnard et al. 2016). While each study pursues a different approach, they all link the side that the animal prefers for particular tasks to the organization of the brain. Lateralized behavior can reveal brain structures in artiodactyl because their eyes are lateral to their heads and their vision is monocular for each eye (Sarasa et al. 2014). This might be a fruitful approach to connecting social cognitions to brain function and represents a potential for more comparative investigations.

## Conclusion

The study of cognition in artiodactyl is in its infancy. There is much unrealized potential in using the comparative approach with this order.

## Cross-References

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## Artiodactyl Life Cycle

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## Artiodactyl Life Story

### ► [Artiodactyla Life History](#)

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## Artiodactyla Diet

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## Synonyms

[Artiodactyl](#); [Cloven-hooved](#); [Even-toed ungulates](#); [Feeding behavior](#)

## Definition

Feeding strategies and dietary habits of artiodactyls.

## Introduction

The artiodactyls are even-toed ungulates. There are three main suborders found within the order Artiodactyla. Two suborders have multiple-chambered stomachs to utilize and rely on rumination to process foods, while the other has only one simple stomach that is not capable of rumination. The suborders Ruminantia and Tylopoda both are capable of and reliant on rumination and are found to be primarily herbivorous, while the members of the suborder Suiformes are not capable of rumination and are composed of animals who are mainly omnivorous. The majority of these hoofed mammals are obligate herbivores, which forage for grasses, leaves, fruits, flowers, twigs, aquatic vegetation, roots, and nuts. Species in the suborder Suliformes, such as pigs, peccaries, and warthogs, are known to eat the same herbivorous diet as previously mentioned, but they will also opportunistically eat rodents, snakes, bird eggs, and nestlings (Etnyre et al. 2011).

This reliance on a plant-based diet is complicated by the fact that artiodactyls do not possess the enzymes required for the digestion of cellulose and lignin, both of which are found in plant matter. To compensate for this lack, the members of

Artiodactyla depend upon bacterial fermentation in order to break down these compounds, through the process of rumination. In addition to the true stomach, or abomasum, these Artiodactyla species have at least one additional chamber within the foregut which facilitates bacterial fermentation (Etnyre et al. 2011). Suliformes have only a two- to three-chambered stomach that does not allow them to ruminate. While this family is considered omnivorous, their digestion of cellulose is not as efficient as that of the other artiodactyls who can ruminate. This has pushed the members of the Suliformes family to expand their diet to be omnivorous and more opportunistic feeders to insure they obtain all nutritional needs. Dietary requirements as well as the behavioral and physiological adaptations that facilitate these habits for Artiodactyla will be described in more detail throughout this entry.

### Suborder Ruminantia

The suborder Ruminantia is composed of animals that utilize and depend on rumination for the breakdown of their complex plant material diet. Examples of these animals are found within families such as Bovidae, Cervidae, Giraffidae, Tragulidae, Moschidae, and Antilocapridae. Ruminantia species are considered true ruminants. These animals begin to digest plant matter utilizing a four-chambered stomach. In addition to the true stomach, or abomasum, bovids have three additional chambers where bacterial fermentation takes place (Gomez et al. 2011). First, gastric fermentation in the rumen extracts lipids, proteins, and carbohydrates, which are then absorbed and distributed throughout the body via the intestines. The rumen, being the first chamber of the rumination process, is where large amounts of foodstuff is held after ingestion. Second, the partially digested large food particles that are left over are then formed into a bolus, a ball of food that is also referred to as cud that is regurgitated and rechewed to assist in the cellular wall digestion of the plant material that was ingested. Third, after the bolus is rechewed and then swallowed again, the food particles pass into the reticulum and then

to the omasum and finally into the abomasum. Along this pathway, cellulose digestion via bacterial fermentation results in high nitrogen microbes that are occasionally flushed into the intestine and are subsequently digested and utilized (Etnyre et al. 2011). These high-nitrogen microbes serve as an important protein source for many artiodactyls, especially ruminants. As stated above, ruminants can store large amounts of forage in their stomachs for later digestion. This is seen to be helpful for these species in an attempt to effectively defend themselves against predation by constantly moving while also productively grazing. This allows the animals to continually graze and store food gathered until they can find a safe place to then rechew and properly digest their food.

### Bovidae Diet

This group is composed of animals such as bison antelope, sheep, goats, etc. Most animals found within this family are observed in captivity, though research of their wild counterparts gives us an insight to the overall families feeding habits. Bovidae feeding strategies are often correlated with body size. Most *bovids* are classified as either grazers or browsers. Small-bodied *bovids* are more solitary animals that tend to be frugivores and browsers in dense wooded areas. Large-bodied *bovids* are seen to live in extensive herds that rely more heavily on grazing strategies in open grasslands. Gomez et al. (2011) states that large *bovids* consume high-fiber vegetation, which contains more cellulose and lignin than the diet of the smaller-bodied forest-dwelling species. The large animals retain greater amounts of food in their alimentary canal for longer periods of time and are seen to be more capable of digesting highly fibrous foods (Gagnon and Chew 2000). Because of the *bovids'* ruminating digestive system, the high amount of cellulose and lignin consumed is broken down and converted into an abundant protein energy source. Each subfamily within the suborder Bovidae has unique dietary habits. For example, Bovidae species rely on both scattered and abundant sources such as fresh grasses, whereas members of Caprinae (which is composed of deer) are more flexible with their

dietary needs and can sustain themselves in low-productivity habitats (Gomez et al. 2011). Cephalophinae are uniquely known to follow canopy-dwelling primates to collect dropped fruit. These factors in accessibility and selectivity to certain foods are seen to restrict smaller-bodied bovids to diets of easily digestible, higher-quality foods, whereas larger animals can utilize poor-quality food in large quantities (Demment and Van Soest 1985).

### Cervidae Diet

All *cervids* are obligate herbivores with their diets ranging from grasses to leafy plant material. Unlike other Ruminantia species, Cervidae are more particular about the selection of their diet and will forage for easily digestible vegetation rather than consuming all available food options within their range (Holmes and Webster 2011). They are considered concentrate selectors because of their selective browsing tendencies. For example, some species are unique and select for more rare or non-traditional species of browse than others such as the sika deer (*Cervus nippon*) who have a tolerance to tannin-rich plants and select for this type while other ruminants do not. Foraging by *cervids* has been shown to have a significant impact on plant diversity in the animals' foraging ranges. Within these ranges, *cervids* foraging habits might lead to changes from one plant type to another within a given range (e.g., hardwoods to conifers) (Holmes and Webster 2011).

### Giraffidae Diet

The family Giraffidae is composed of two species: the giraffe and okapi. Okapis are usually found to be solitary animals in dense forest-like habitats. Giraffe species are herd animals of up to 25 members occupying a large home range in open savannah-type habitats. Both members are ruminants with long prehensile tongues that reach over 12 in. These prehensile tongues allow these animals to more effectively browse and forage for food. Giraffidae species differ in that shorter species, such as okapis, have evolved to consume a diet consisting primarily of a mix between low-lying browse and grasses, while the taller species (e.g., giraffe) are nearly exclusively browsers

utilizing their long necks to reach into tree canopies to feed. Both giraffes and okapis are selective browsers and will seek out plants with high-nutrient value such as fresh leaves and buds (Bertelsen 2015). Giraffes have a consistently higher protein level intake than other grazing artiodactyl species because of their ability to forage for food nearly anywhere in tree canopies. The foraging strategy of the giraffe species allows them to maintain a healthy metabolic threshold for year-round maintenance (Pellew 1984). Okapi have been seen eating over 100 different species of plants, mainly composed of buds, leaves, and branches of plants. Okapis have even been observed eating plants that are poisonous to humans as well (Aguilar 2020).

### Tragulidae Diet

Tragulidae are ruminants which lack a well-developed omasum and hence have a three-chambered stomach compared to the four-chambered stomach of other members of Ruminantia. These animals' diets include grasses, leaves, and some fruit, making them mainly herbivorous, but they will also include invertebrates, small mammals, and even carrion into their diet when needed as well (Myers 2001). These animals do not need to gather large quantities of food at a time and can afford to be more selective for food that is easily digestible. Because of this selective foraging, their easily digestible food is able to slip past the rumen and reticulum through a special groove directly to the abomasum (Meijaard 2011). These animals still utilize some aspects of rumination, but due to the higher-quality food selected, they lack a fully functioning ruminating system.

### Moschidae Diet

Moschidae, or musk deer, are very closely related to *cervids*. However, these species differ from *cervids* by not demonstrating antlers and by exhibiting a musk gland which the *cervids* lack. Members of Moschidae are solitary animals living in dense and rocky forest-type regions. Their diets consist of grasses, browse, and forbs while occasionally selecting some mosses and lichens to include in their diet as well. These animals are

observed to be concentrate feeders and are known to select herbaceous and woody plant leaves and avoided eating grasses, mosses, and lichens for much of the year (Green 1987).

### Antilocapridae Diet

Pronghorns are the only living members of this family and have adapted a high positioned eye set that allows them to maintain looking out for predators while continually grazing (Myers 2000a). Feeding patterns for these animals change with the seasons, and during summer months, they are active in the morning and late evening hours, while in winter they are forced to increase their range and movements to find shrubs to supplement their nutritional requirements (Cain et al. 2017). The pronghorn diet in the cool arid season is composed of shrubs, and in the warm rainy seasons, their diet is mainly herbaceous broadleaf plants. These animals are able to utilize a wide range of foods, and when forage becomes limiting during undesirable periods, pronghorns will select whichever available forage that best fulfills nutritional needs (Tsukamoto 2003).

### Suborder Tylopoda

The suborder Tylopoda is composed of the camelids. These animals have a similar digestive tract to the true ruminant species in that they are both capable of rumination. The camelids have only a three-chambered stomach compared to the four-chambered stomach of Ruminantia members. They differ from the Ruminantia in gross anatomy in that there is no clear distinction between the third and fourth chambers. In tylopods, the esophagus enters directly into the rumen, while in true ruminants, it joins the stomach between the rumen and the reticulum (Wilson 1989). Also, the true ruminant reticulum has a honeycomb-like appearance, while the camelids reticulum has a glandular sac-like appearance. As Wilson (1989) states, it is conventional to refer to the different parts of the Tylopoda stomach by the same terminology as used for the true ruminants, but it is not certain that the parts which perform analogous functions are truly homologous. All

camelids are herbivorous and feed primarily but not exclusively on grasses and browse (Myers 2000b). The camelids are specialized for life in dry arid habitats. These animals can digest plants with high salt content that other artiodactyls cannot digest and therefore find intolerable (Etnyre et al. 2011).

### Camelid Diet

All camels are generally found in arid or semiarid areas, and the much-studied Old World camels have a remarkable ability to conserve water (Myers 2000b). The natural food of the Old World camels derives from browse, many of these being leguminous trees and shrubs and many being salt bush plants of the family Chenopodiaceae and similar families. An important feature of camels' browsing habits is that they are not in direct competition with other domestic stock either in terms of the type of feed eaten or in the height at which they eat above the ground. Camels usually select feeds that are high in moisture, nitrogen, electrolytes, and oxalates. Under open range conditions, camels are able to take in a wide range of plants in their diets due to them quickly moving from one feeding station to the next (Wilson 1989). Camels are ruminating grazers and browsers which allows them to survive in habitats with sparse vegetation (Etnyre et al. 2011).

### Suborder Suliformes

The suborder Suliformes is made up of animals such as pigs, warthogs, peccaries, and formerly hippopotamuses. This Artiodactyla suborder is considered omnivorous, though some animals in this suborder diverge from this classification and are considered more specialized herbivores. For example, some species in the family Suidae found within this suborder are specialized herbivores such as the family Tayassuidae. The animals within the suborder Suliformes all have large heads and snouts that are used to root for food. This suborder is composed of the sister families Suidae, Tayassuidae, and Hippopotamidae. The sister families Suidae and Tayassuidae have

one false stomach, whereas the family Hippopotamidae has two (Etnyre et al. 2011).

### **Suidae Diet**

*Suids* have a two-chambered stomach and do not ruminate. They will use their specialized muscular snout to forage for food. The common image of the tendency for pigs to overeat is not necessarily true. Being omnivorous the *suids*' diet includes fungi, grasses, browse, roots, bulbs, tubers, fruit, snails, earthworms, small vertebrates, eggs, and carrion (Fox and Myers 2000b). Some members of this family are more specialized herbivores rather than fully omnivorous. The species babirusas, giant forest hogs, and warhogs are all considered specialized herbivores. Even then with three species observed as specialized herbivores, the Suidae family is still the most omnivorous of the two extant Suiformes families. This is because members of this family will, when acting on opportunistic hunting instincts, kill and eat small animals including rodents, snakes, bird eggs, and nestlings (Etnyre et al. 2011). Because of the rooting behavior of these animals, they are known to cause environmental damage to areas they forage (Fox and Myers 2000b).

### **Tayassuidae Diet**

The Tayassuidae family is also considered omnivorous, but there is evidence to suggest that these species rely more heavily on plant material as the bulk of their diet than the *suids* (Etnyre et al. 2011). The peccary forages for a variety of plant and animal material in large herds range from a few animals to several hundred (Fox and Myers 2000c). The food intake of the peccary is dependent on the range of habitat it occupies and the season. In tropical forests, these animals are highly frugivorous eating over 128 plant species, while in desert environments they are consuming various cactus species. The peccaries feed on several species of cactus, and it is believed that they obtain all or most of their water intake needs from the ingestion of cactus plants. As stated, these animals rely on a wide variety of food resources including fruits, seeds, stems, leaves, tubers, roots, rhizomes, invertebrates, turtle and bird eggs, frogs, fishes, snakes, small mammals, and

carrion. Behavioral observations, analyses of stomach contents, and feces indicate that fruit and seeds are primary food resources, followed by leaves and roots. Earthworms are also important, providing a significant protein source (Taber et al. 2011).

### **Hippopotamidae Diet**

Hippopotamuses are considered more specialized herbivores than either sister family within the suborder Suliformes (Etnyre et al. 2011). Hippopotamidae species will primarily feed on grasses but are also known to forage for fruits and leaves as well. The members of Hippopotamidae spend the majority of their time submerged in aquatic environments and therefore tend to feed on aquatic plants found there. Hippopotamuses also rely on terrestrial forage and often tend to leave the water and forage several kilometers away (Fox and Myers 2000a). When doing this, they are usually responsible for damage to crops and rangelands due to their foraging habits and their travel to their foraging areas. Hippopotamuses also have low metabolic rates, and in captivity are often prone to obesity because of this.

## **Conclusion**

There are over 210 members of Artiodactyla, which can be found in many diverse habitats. Their exposure to diverse and extreme ecosystems have enabled artiodactyls to evolve unique foraging strategies which are affected by seasonality, conspecific and interspecific interactions, as well as climate change. There is also an exceptional variation in body size and structure of these animals which also affect the type of diet that is obtainable and the amount of food needed for each species.

## **Cross-References**

- [Artiodactyl Cognition](#)
- [Artiodactyla Life History](#)

- [Artiodactyla Locomotion](#)
- [Artiodactyla Morphology](#)
- [Artiodactyla Navigation](#)

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## Artiodactyla Life History

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## Synonyms

[Artiodactyl life cycle](#); [Artiodactyl life story](#);  
[Even-toed ungulate biology](#); [Ungulate demographics](#)

## Definitions

Artiodactyla are a taxonomic order of mammalian ungulate species that exhibit an even number of functional toes on each foot. Life history, synonymous with life cycle, is a characterization of the strategies and/or changes that an organism undertakes pertaining to survival and reproduction over the course of its life.

## Introduction

Life history reflects patterns, or strategies, typical of a species that will maximize individual fitness and population persistence over time. The physiological and behavioral evolution of animals as a response to their environment is a significant driver of a species' life history. Understanding a species' life history is key to understanding how an organism interacts with its environment, as well as developing management strategies tailored to a species' needs, and assessing drivers of change in behavior or physiology.

The Artiodactyl taxonomic order contains a vast and diverse remain breadth of species



represented either naturally or through human introduction in every continent except Antarctica. This order includes pigs (*Sus* spp.), giraffes (*Giraffa camelopardalis*), deer (family Cervidae), camels (*Camelus* spp.), pronghorn (*Antilocapra americana*), bison (*Bison* spp.), buffalo (*Bubalus* spp.), and many more. The diversity of species within this order is equally represented by the wide variety of environments in which they inhabit. The life history of the approximately 220 species classified as artiodactyls includes a suite of highly adapted physiological and behavioral characteristics that allow some artiodactyl species in this order to take advantage of “adaptive zones” that are not available to other groups (Köhler and Moyá-Solá 2009). These habitats, spanning Arctic tundra to arid deserts in Africa, offer harsh environmental conditions and require highly specialized physiology and behaviors to survive. There is intrigue in how the developmental strategies of large ungulates allow Artiodactyl species to adapt and survive in environments that have reduced energy richness. These strategies may include trade-offs among life history traits (e.g., reproduction and survival) to maximize fitness (Morano et al. 2013).

### Debate: Cetacea as Artiodactyl

Much debate centers around whether whales and dolphins of the order Cetacea should actually be included within the Artiodactyla order. Fossil records for prehistoric species of whales, dolphins, and porpoises demonstrate a transition from terrestrial life to aquatic life. Researchers have proposed that these cetacean species should be included in a newly renamed order, Cetartiodactyla, due to paleontology, morphology, and molecular evidence (Shimamura et al. 1997; Lusseau 2003).

### Physiological and Morphological Adaptations in Artiodactyls

Artiodactyl species are typically highly adapted to the range of environmental conditions found

within their preferred habitats, and these adaptations often drive life history characteristics that aid in survival and reproduction. Adaptations to maximize survival and fitness include a suite of physiological, morphological, and behavioral characteristics to facilitate greater success in these environments. For example, caribou (*Rangifer tarandus*) live in harsh tundra conditions in circumpolar distributions in North America, Northern Europe, and Siberia. This species has adapted a long distance, large herd migratory strategy to facilitate access to food resources. Caribou feed primarily on lichens during the overwintering period but will also consume birch and willow leaves, in addition to sedges and grasses. They also have several physiological adaptations to allow persistence in harsh environments, including specialized nasal characteristics to maximize extraction of water from the air and seasonally changing footpads to allow for traction in the summer tundra and winter ice and snow.

In contrast, camels (*Camelus* spp.) inhabit some of the most arid places on Earth and have highly adapted physiological mechanisms for fatty deposits, in addition to other morphological features that allow them to traverse hot, sandy terrain. Camels are a long-lived, large-bodied group of species, with life spans up to 50 years. Concentrations of fatty deposits in their humps decrease the distribution of fat in other parts of the body, reducing potential insulative effects that would otherwise increase body temperature in arid systems. When metabolized these fatty deposits provide a vital water source for this species known to survive for extended periods (up to 10 days) without access to water. Camels have other adaptations to allow them to survive in such extreme conditions, including thick mouth lining to aid in consumption of thorny desert plants, third eyelids and long eyelashes to prevent injury to eyes from sand, ability to tolerate widely fluctuating thermal conditions during the night and day, and long legs and thick pedestal tissue on the sternum to reduce body contact with hot desert surfaces.

In addition to camels, llamas (*Lama* spp.), also in the Camelidae family, have unique foot physiology that has led to an adaptive form of

locomotion. Instead of hooves, camels and llamas have specialized secondary digitigrades (i.e., walking on secondary set of toes), broad foot paths, and pacing gaits that allow the animals to be sure-footed on unstable ground (Janis et al. 2001). The large feet of camels also allow for improved mobility in desert sand while distributing body weight across a wider surface area (Gebreyohanes and Assen 2017).

The long neck of giraffes (*Giraffa camelopardalis*) has also been attributed to adaptations resulting from resource competition in African savannahs and woodlands (i.e., access to leafy vegetation of *Acacia* and other woody plant species). Fossil records indicate that the ancestors of giraffes had shorter necks and that elongation over time became a heritable trait which was passed down through generations (Williams 2016). This partitioning of resources would allow access to an unexploited niche to reduce competition with other herbivore species. It is also thought that vascularized bony ossicones on the giraffe's skull may have adapted to aid in thermoregulation in hot African climates, in addition to weaponry used in male-male competition for mates.

### Sexual Selection in Artiodactyls

In many species sexual selection is a key factor in maximizing fitness and becomes an important component of an individual's life history. It is widely speculated that the evolution of distinguishing sexual characteristics is attributed to intrasexual competition for mates (Vanpe et al. 2010). Many artiodactyls display physical and behavioral characteristics that may be important drivers of mate selection. A physical, or morphological, difference that allows individuals to distinguish males from females in a species is known as "sexual dimorphism." Phenotypic characteristics (physical traits) are essential to sexual selection in sexually dimorphic animals. Some artiodactyl species have very apparent sexually dimorphic characteristics (e.g., antlers in white-tailed deer bucks [*Odocoileus virginianus*]). In most cases males that exhibit superior secondary

sexual characteristics are favored in sexual selection, provided they can overcome the potential physical handicap and/or male-male competition that coincides with extreme forms of secondary sexual characteristics. In mountain goats (*Oreamnos americanus*), males exhibiting larger body size are not only preferentially selected for by females, but they also have a physical advantage in winning male-male contests, which allows them to access a greater number of females in estrous. Due to limited availability of mates, there are often physical competitions between males to secure successful reproduction (collectively known as agonistic behaviors). There is speculation that there is a link between female preference and body size of males, whereby over time the large body size in males becomes genetically dominant in a population (Mainguy et al. 2009). Depending on the species, this combination of female preference and male-male competition could lead to the process of runaway selection in artiodactyls, where heritable genetic aspects of female choice for more robust males are passed down among female offspring, and heritable genetic aspects of male secondary sexual characteristics (e.g., weaponry, body size, aggression) are passed down among male offspring.

In contrast, there are several other artiodactyl species such as European roe deer (*Capreolus capreolus*), where there is very low sexual dimorphism among males and females. In these cases, environmental stressors (e.g., predation risk) may have reduced selection for sexual dimorphism over time. However, in many species that lack sexually dimorphic characteristics, there are behavioral differences during mate competition that facilitate sexual selection and subsequent mate choice.

### Reproductive Strategies in Artiodactyls

Selection, resource competition and a host of other ecological and environmental factors drive reproductive strategies (e.g., mating systems, onset of reproduction, number of offspring, degree of parental care, etc.) in

artiodactyl species. Artiodactyl reproductive strategies are widely varying among species and often relate directly to social structure and availability and distribution food and space resources (Geist 1981). Body mass, gestation length, and growth rate may be an important driver of parental care and thus reproductive strategies in artiodactyls, with greater investment in a smaller number of offspring dictating the design of the species' mating system (Saether and Gordon 1994). Therefore, reproductive strategies in this group of species are directly tied to the amount of energetic investment required to successfully reproduce.

Parental care is essential for the survival of many species, but a key component in maximizing fitness of many  $k$ -selected (i.e., long-lived with limited reproductive output) ungulates. Maternal care in ewes (*Ovis* spp.) has been shown to be driven by a release of oxytocin during parturition, which cues the increase of neurotransmitters necessary to initiate maternal instinct for care (Dwyer 2013). This naturally orchestrated course of events results in the acceptance of the lamb by the mother, often expressed in the form of licking, low bleating, udder acceptance, and suckling. This maternal behavior is reserved for the singular lamb.

Most artiodactyl species breed during a single reproductive season. Thus, competition for mates can be severe and depends on distribution of females and resources in the environment. Despite variation in levels of parental care, few artiodactyl species are monogamous. More typical are forms of female defense polygyny, resource defense polygyny, or harem polygyny. In female defense polygyny, males will compete directly for females and defend them while in estrous but will move on to other females once the estrous period has ended. In resource defense polygyny, males will defend critical resources utilized by females to secure mates in an area, and in harem polygyny, males will defend multiple females (e.g., a harem) within a territory and mate with each female in estrous. Topi (*Damaliscus lunatus*), found in the savannas of Africa, are known to defend resource territories, which may reduce male-male competition for mates. However, if groups of females are

mobile and concentrated, males will shift held territories, aggregate together, and begin to exhibit lekking behavior, which includes clustering of males simultaneously competing for females in a small area (Gosling 1991). Thus topi adopt a mixed reproductive strategy that is adaptive to spatial distribution and availability of females.

## Social Order in Artiodactyls

The social order of animals is a widely studied subdiscipline of animal behavior, and the literature is ripe with research on social organization of artiodactyl species. Pigs begin to display social order when they are newborn, forming a hierarchy while suckling and commonly resulting in aggressive behaviors among litter mates. Competition to suckle in the middle teat is more intense than any other location (Skok et al. 2014). Agonistic behavior such as "head butting" and antler locking in males within social groups is common display of aggression and competition among many artiodactyl species and often relates to dominance and social order. Species such as mountain goats (*Oreamnos americanus*), musk deer (*Moschus chrysogaster*), and others have been observed exhibiting similar social hierarchy behaviors. Social hierarchy often includes dominance in artiodactyl social groups. For example, dominant members of horned Japanese black cattle (*Nihon tankaku washu*) groups have been observed laying closer to hay racks in pastures than their subordinate counterparts, excluding access to other members within their social hierarchy (Nakanishi et al. 1992). Relatedness often plays a role in social structure of many artiodactyl species. For example, collared peccaries (*Pecari tajacu*) are a highly social artiodactyl with spatial association of groups directly related to high levels of relatedness, but not necessarily degree of social interaction (Biondo et al. 2014). Similar patterns of kinship and familiarity have also been shown in hippopotamus (*Hippopotamus amphibius*), along with potential for nonlinear dominance hierarchies (Blowers et al. 2010).

## Resource Allocation/Foraging Strategy

Availability and distribution of food, water, shelter, and other resources play an important role in the life history of artiodactyl species. These factors influence the ways in which a species seeks resources and the mechanisms they use to obtain them. Distance, in combination with accessibility and distribution of resources, affects many facets of life history, including social structure, mating system, migration, and ultimately fitness. For example, white-lipped peccaries (*Tayassu pecari*), a tropical ungulate, exhibit a group-foraging strategy that facilitates location of nonuniformly distributed fruit, seed, and water resources. This involves a combination of strategies, including periods of intense foraging in one area and/or foraging forays over longer distances. The outcome of this mixed strategy is varying degrees of movement among distributed resources in different areas (Reyana-Hurtado et al. 2012).

Many artiodactyl species play a distinct role in the physical makeup of their environment while carrying out elements of their life history. Species affect growth and dispersal of vegetation in their environment by foraging, stomping, urinating, and defecating. The link between species and vegetation is undeniable making the study of foraging behavior in animals important. Scottish black face sheep (*Ovis aries*) and European red deer (*Cervus elaphus*) spend a considerable amount of time (about 50% of their day) grazing on heather and grass in their natural habitats. However, both species prefer grass over heather during the growing season, which may influence the proportional distribution of grasses compared to heather in the landscape (Hester et al. 2001). Thus artiodactyls, by nature of their herbivory, may drive as well as be driven by the distribution of forage resources in an area.

## Conclusion

Artiodactyls represent a widely varying group of mammalian species with life histories highly adapted to maximize survival and fitness in the sometimes challenging environments they

inhabit. Selection of resources, degree of movement, foraging strategy, reproductive strategy, longevity, and a host of other factors characterize life histories for each of the artiodactyl species. In general, Artiodactyla are relatively long-lived, *k*-selected (lower reproductive output) species, often with large body masses relative to other mammalian orders. They are also adapted to survive in a range of conditions, with specific measures for water conservation, heat reduction or insulation, and foraging success all key parts of their life history characteristics.

## Cross-References

- [Adaptation](#)
- [Agonistic Behavior](#)
- [Artiodactyla Diet](#)
- [Artiodactyla Locomotion](#)
- [Artiodactyla Morphology](#)
- [Artiodactyla Navigation](#)
- [Cetacean Life History](#)
- [Competition](#)
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- [Fitness](#)
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- [Migration](#)
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- [Resource Defense Polygyny](#)
- [Secondary Sex Characteristics](#)
- [Sexual Dimorphism](#)
- [Social Behavior](#)
- [Suckling/Nursing](#)
- [Ungulate](#)

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## Artiodactyla Locomotion

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## Synonyms

Cloven-hooved mammal locomotion; Even-toed ungulate locomotion

## Definition

Movement used by artiodactyls (even-toed ungulates) to traverse their environment.

The Artiodactyla, or even-toed ungulates, are an order of hooved mammals that are known to bear weight and ambulate on the third and fourth digits. The order of Artiodactyla can further be



divided into the suborders of *Tylopoda* (camels, llamas, guanacos, alpacas, and vicuñas), *Suina* (pigs and peccaries), *Ruminantia* (cattle, goats, sheep, deer, and antelope), and *Hippopotamidae* (hippopotamus) as well as several other species. Sisters to the artiodactyls are the perissodactyls, or odd-toed ungulates, consisting of horses, rhinoceros, and tapirs. Over 220 different species of artiodactyls have been found around the globe, and new subspecies are continuously being described. Artiodactyls are found throughout a variety of habitats worldwide but are not native to Australia, Antarctica, or oceanic islands, despite being successfully introduced to Australia and numerous islands (Cope 1888; Grzimek et al. 2003; Rose 1996).

Artiodactyls are mainly terrestrial herbivores and live within four different general habitats. These include open grasslands, grasslands and meadows, steep cliffs, forests, shrubland, and an intermediate habitat between forests and open lands. Each habitat provides its own unique advantages; steep cliffs provide security, grasslands allow for widespread vision to avoid predators, and forests are full of cover and vast vegetation. The Artiodactyla order is made up of animals with an abundance of different shapes, sizes, tendencies, and most importantly locomotion behaviors (Grzimek et al. 2003).

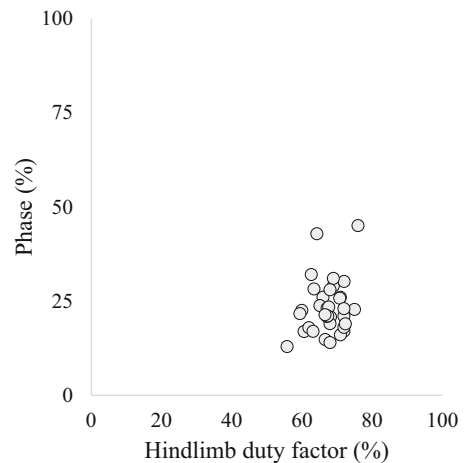
## Gait Sequences

Gait is the manner a species utilizes to traverse through terrain (Hildebrand 1977). Gait can first be divided into symmetric, in which the footfalls of the forelimb and hindlimb are separated evenly in time, and asymmetric, in which the footfalls of the forelimb and hindlimb are separated unevenly in time. Symmetric gaits are observed during walking, pacing, and trotting, while asymmetric gait are seen during galloping or bounding.

A walking gait is one with a duty factor greater than 50%. Duty factor refers to the percentage of the cycle during which a foot is contacting the terrain. The center of mass (COM) is comparable to a swinging inverted pendulum during walking gaits, as energy flows between kinetic and

potential in synchrony with the rise and fall of COM during each stride. When walking, mammals either do so in a lateral-sequence, during which each hindlimb footfall precedes an ipsilateral forelimb footfall, or a diagonal-sequence, during which each hindlimb footfall precedes a contralateral forelimb footfall. Furthermore, a couplet is that in which two limbs move together; a diagonal couplet refers to contralateral hindlimb and forelimb moving together, while a lateral couplet refers to ipsilateral hindlimb and forelimb moving together. Although these limbs may be traveling together, it is important to note that they almost always do so in slight asynchrony (Hildebrand 1989).

Walking gait patterns in the artiodactyls include the lateral-sequence lateral-couplets and lateral-sequence diagonal-couplets (Fig. 1). Lateral-sequence lateral-couplet walking occurs when ipsilateral forelimb and hindlimb move together, with the hindlimb footfall preceding forelimb footfall. Such a gait sequence is observed among long-legged artiodactyls such as the giraffe, but may be too unstable for short-legged mammals. Such instability is a result of lateral body-roll, as the trunk of the body is only stabilized by the opposite two limbs during each stride



**Artiodactyla Locomotion, Fig. 1** “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in Artiodactyla ( $n = 34$  species)



(Granatosky 2018). A lateral-sequence diagonal-couplet gait sequence occurs when each hindlimb footfall precedes that of the ipsilateral forelimb, but contralateral hindlimb and forelimb move with one another. Such a sequence provides better stability for short-legged mammals, such as the pigs and peccaries, as they spend much less time as unilateral bipods during each stride compared to lateral-sequence lateral-couplet gaits. The diagonal axis in which contact is made with the ground prevents the body-roll commonly seen with lateral-sequence lateral-couplet gait (Granatosky 2018).

A running gait is one with a duty factor less than 50%. A mammal's COM is comparable to a bouncing ball during running gait, as movements occur in phase with each other (Granatosky 2018). The artiodactyls utilize several different running gaits across their order, including the symmetrical trot and pace, and the asymmetrical gallop and pronk. As per Hildebrand (1989), the trot is the most stable of all running gaits. A trot is observed as contralateral hindlimb and forelimb stride synchronously. Hildebrand (1989) defines the pace as a running gait during which the ipsilateral hindlimb and forelimb stride synchronously. Like that of the lateral-couplet, the pace may pose some stability issues for short-limbed mammals as they spend time as unilateral bipods during such a gait. Artiodactyls such as the camels take advantage of the pace, as it prevents possible collision of ipsilateral limbs during running gait.

At higher speeds, artiodactyls transition to a gallop (Granatosky 2018). A gallop is observed when a mammal's running gait utilizes a leading foot of both the fore and rear limbs. A leading foot refers to the fore or hind limb that contacts the ground after its respective contralateral counterpart and is further ahead at time of contact. The limb that strikes the ground first and further behind is then referred to as the trailing foot (Hildebrand 1989). Artiodactyls are known to perform both forms of galloping; the first being a transverse gallop in which the leading fore and hind limbs are ipsilateral, and the second being the rotary gallop, often seen in *Suinae* (Datt and Fletcher 2012), in which the leading feet are on contralateral sides. Artiodactyls such as the pronghorn antelope also practice what is known as straddling, during which the hindlimbs are placed before and outside of the forelimbs. Doing so allows for these animals to traverse quickly without possible physical interference between the forelimbs and hindlimbs (van der Sluijs 2004).

An interesting gait sequence unique to the artiodactyls is the pronk or stott (Fig. 2). Often seen in gazelles and several species of deer, the pronk is an asymmetric running gait during which the lift and footfall of all four feet occurs together. The limbs are often held very stiff during such a movement to propel the animal up into the air. Researchers have yet to come to a consensus regarding a definitive reason for such a

#### Artiodactyla Locomotion,

**Fig. 2** Springbok (*Antidorcas marsupialis*) stotting (pronking) as it propels itself up into the air on all fours



movement, citing everything from play to predator detection in tall grasslands (FitzGibbon and Fanshawe 1988; Hildebrand 1989).

## Limb Loading

Limb loading refers to how an animal distributes weight between limbs to propel itself forward as efficiently as possible. Limb loading of artiodactyls is similar to that of most four-legged mammals. A net accelerating force is produced via the hindlimb as it trails its COM, and the forelimb is utilized for net braking forces, ahead of the COM (Granatosky et al. 2018). In terms of weight support (i.e., vertical forces) the forelimb of artiodactyls bears a greater proportion of body weight than the hindlimb. During the stance phase of slow and fast walking, goats experience a peak vertical force of about 85% of an average goat's weight. Such values could be measured via beam theory of elasticity in reference to the strain experienced by the tibia bone. When jumping, the goat will experience a peak force two to three times that of normal and fast walking. Although transverse forces play a much smaller role in the limb loading pattern of goats, these also significantly increase with jumping as opposed to slow or fast walking (Roszek et al. 1993).

## Gait Kinematics

Artiodactyls have experienced several unique evolutionary changes that impact the kinematics involved with locomotion. The lateral digits have been diminished or have become completely absent, while the medial digits have been elongated. An artiodactyl's foot is referred to as paraxonic, as an axis of symmetry exists between the third and fourth digits. Such changes to the anatomy have allowed for much lighter and longer limbs, ultimately resulting in quicker locomotion with much cheaper energy costs. In most mammals, a joint exists between the tibia and astragalus, with a pulley-shaped surface that articulates with the tibia. Artiodactyls utilize a "double-pulley" astragalus, which significantly increases

free rotation of the foot on the leg in forward-backward motion, with limited lateral rotation of the ankle (Clifford 2010; Theodor 2001).

The metacarpophalangeal (MCP) joint, along with interosseous ligaments of the foot, are significant to force production during artiodactyl locomotion. The MCP joint of artiodactyls is hinge-like and is the only location at which the interosseous ligaments cross. Each digit possesses its own interosseous muscle, which perform flexion at the MCP joints. At slow walking speeds, the MCP joint functions like a spring, and like that of an actuator at higher speed gaits. The interosseous ligaments of the foot allow for force production without the expenditure of metabolic energy. They also play a pivotal role in maintaining the unique "tip-toed posture" of the artiodactyls. Both superficial and deep flexor muscle tendons of the digits, found along the ventral surface of the foot, are important as well. The combination of elongated interosseous ligaments and flexors muscle tendons allows for increased storage of elastic energy, and ultimately more efficient locomotion (Clifford 2010).

Being both the tallest animal on the planet, as well as the heaviest ruminant, giraffes exist as a physical extreme of the artiodactyls. The giraffe's lateral-sequence walking gait is affected significantly by its long neck, limbs, and heavy body weight (Basu et al. 2019). The elbow, knee, and ankle joints all remain flexed during locomotion, although the wrist joint extends to about 10° during the support phase. The giraffe's knee increases in flexion as time passes in both the swing and support phases, which may support the idea that these animals mainly use the knees to walk as opposed to the hip joint. The head and neck, accounting for about 10% of the total body mass, play an interesting role in giraffe locomotion. Stride frequency and oscillation of the neck coincide with one another, as the neck oscillates two times throughout each stride. The neck's horizontal acceleration is opposite that of the trunk, decoupling it from the body's movement. This lessens the horizontal COM forces, which may otherwise impede on the giraffe's gait, and ultimately improves energy expenditure during walking (Basu et al. 2019; Inuzuka 1996; Loscher et al. 2016).

## Vertical Substrate-Use in Goats

In contrast to the more terrestrial lifestyle of most artiodactyls, mountain goats and bighorn sheep frequently traverse dangerous terrains (Fig. 3). Morphologically, these animals tend to have shorter and thicker bones compared to closely related non-alpine species. These osteological modifications allow mountain goats and bighorn sheep to quickly ascend and descend steep inclines without bending or breaking bones. However, the shorter, thicker legs result in higher costs of transport compared to other similar sized ungulates (Dailey and Hobbs 1989).

Beyond vertical rock faces, some goats can traverse up trees. Such movement, also known as arboreal locomotion, requires precision and stability of the limbs, which most mammals do not possess. Compared to a stereotypical rounded foot, the hoof of a mountain goat provides advantages for climbing and slip reduction. Tough keratin lines the toes of these animals allowing for effective uphill walking and a textured pad extending over the nails provides friction and shock absorption when traveling along smooth surfaces. The

interosseous ligaments between the digits also help to maintain stability when traveling on uneven terrain. The mountain goat's hoof provides an increase in lateral stability as well, preventing slippage when traveling downhill. Abad et al. (2016) applied these principles in the development a robotic foot modeled after that of the mountain goat, which required three times the work to induce slippage than a more common rounded foot. As it aids the mountain goat in climbing trees and descending from proximal terrains, it may help humans to do so as well via robotic limbs.

## Migratory Practices

While some artiodactyls, such as the goat, are much more sedentary, other members of the order including the wildebeest, mule deer, and elk may be quite migratory, traveling 50–100 km seasonally. Berg et al. (2019) defined such a concept as partial migration, as artiodactyls consist of both migratory and resident species. Conditions such as weather, seasonal change, predatory density, and access to resources play a pivotal role in determining the manner and tendency in which these species migrate. While some may follow the same migratory patterns yearly, it has been discovered that many subpopulations will migrate across several different varying routes, likely to avoid possible predators or threat of humans (Sawyer et al. 2009). The spring migration of Yellowstone elk may vary based upon how severe and long in duration the prior winter had been. After a heavy winter, the elk may delay spring migrations, but will expedite movements if early vegetation growth is observed (White et al. 2010). In regard to the autumn season, elk migration varies, as Grigg (2007) found that Madison Valley elk would migrate earlier if living within an area of hunting risk during the summer, while those that spent their summers in protected areas would migrate much later for autumn seasons. This is contrasted by the findings made by White et al. (2010), as the Yellowstone population was at no risk of hunting during the summer but migrated much sooner than its Madison Valley counterpart for the autumn season.



**Artiodactyla Locomotion, Fig. 3** Goat are capable of traversing highly variable terrain including (a) trees and (b) steep mountains. The mountain goat's unique hoof characteristics allow for stability and shock absorption while traveling up and down mountain ranges

To help conserve and build energy, the mule deer will utilize stopover sites and movement corridors during migration periods. Foraging and resting occurs at stopover sites, followed by very quick migration to the next stopover site via movement corridors. It is understood that the use of stopover sites and movement corridors allows for energetically efficient migration for artiodactyls (Sawyer et al. 2009).

## Human Interaction

Due to the vast populations of artiodactyls, it is inevitable for interaction with civilization to occur. Unfortunately, many see artiodactyls as disturbances as they may consume and destroy crops, and negatively affect quality of trade such as timber. Of note are wild boar and moose, which browse heavily during the winter, as well as roe deer, which have a significant impact on shrubs within forests. However, via browsing or foraging, these animals help to spread and tread seeds into the terrain. Their droppings help fertilize the soils and encourage growth of forestry (Reimoser and Putman 2011).

Additionally, these animals, in the process of migration, are often involved in road traffic accidents. Artiodactyls, such as the mule deer, have developed migration routes that they follow on a yearly basis. With increasing industrialization, roadways, buildings, and other man-made constructions have impeded on such routes. It is believed that these animals will avoid high-traffic areas as much as possible without heavily affecting their migratory patterns. However, avoiding these areas altogether eventually becomes impossible, and thus, deer–vehicle collisions occur. Along with possible injury and or death via collision, migrating deer that attempt to avoid highways and roads utilize much higher rates of energy expenditure, ultimately decreasing likelihood of survival between seasons. Industrial disturbances not only put the mule deer at risk, but the humans who come in contact with them as well. Due to the strong fidelity migrating artiodactyls have to their migration routes, new construction such as underpasses can play a pivotal role in

decreasing the likelihood of potential collisions and help to maintain the previously discussed movement corridors these animals utilize. Sawyer et al. (2012) found a decrease in deer–vehicle collisions of 81% in a 21 km stretch of US Highway 30 after construction of an underpass. Although other variables will likely need to be taken into account, such as available vegetation, terrain, and other human activity, these changes strongly benefit both migrating artiodactyls and humans themselves (Lendrum et al. 2012; Reimoser and Putman 2011; Sawyer et al. 2012).

## Conclusion

This entry explores the various forms of artiodactyl locomotor behaviors. Extensive research regarding the evolution of these even-toed ungulates has allowed for the understanding of how and why artiodactyls traverse terrains in several different fashions. While the tall and massive giraffe utilizes lateral-sequence lateral-couplet gait to traverse their terrain and survey their surroundings, a pig's short and close to the ground stature requires later-sequence diagonal-couplet gait to maintain stability and avoid body roll. The double-pulley astragalus, as well as the strong MCP joint and interosseous ligaments, allow for highly efficient locomotion. These animals put such traits to use in a variety of ways, as the mountain goat and bighorn sheep traverse up and down dangerous mountainsides and perform arboreal locomotion, while the gazelle leaps on all fours as it prunks to play and/or scout for predators. Spread throughout the world, artiodactyls are found in varying shapes and sizes but all share the distinctive axis of symmetry between the third and fourth digits. Ongoing research will continue to answer questions regarding the vast locomotor practices these even-toed ungulates utilize.

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)
- [Adaptedness of Behavior](#)

- Adaptive Radiation
- Artificial Selection
- Artiodactyl Cognition
- Artiodactyla Diet
- Artiodactyla Life History
- Artiodactyla Morphology
- Artiodactyla Navigation
- Basal Metabolic Rate (BMR)
- Bovine Cognition
- Bovine Diet
- Bovine Life History
- Bovine Locomotion
- Captivity
- Common Ancestor
- Dispersal Ability
- Dispersal Patterns
- Diurnality
- Domestication
- Ecology
- Evolution
- Extinction in Learning
- Gait
- Herbivore
- Home Range
- Homology
- Homoplasy
- Husbandry
- Locomotion
- Morphology
- Muscular System
- Natural Selection
- Navigation
- Paleontology
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- Safari
- Species
- Swine Cognition
- Swine Communication
- Swine Life History
- Swine Locomotion
- Swine Navigation
- Taxa
- Terrestrial
- Territoriality
- Ungulate
- Vertebrate Nervous System

- Zoo
- Zoology

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## Artiodactyla Morphology

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## Synonyms

Artiodactyl; Even-toed ungulates; Cloven-hooved

## Introduction

Some of the most well-established terrestrial mammals of the animal kingdom are the ungulates or hoofed mammals. Due to an incomplete fossil record with no readily identifiable intermediates, the precise relationship between modern and early ungulates is currently unknown. Ungulates are primarily divided into one of two orders, Artiodactyla, the even-toed ungulates, or Perissodactyla, the odd-toed ungulates. The primary distinction between these orders involves the morphology of the animals' feet as they deviate from the typical five-digit vertebrate morphology. Artiodactyla is currently considered the fifth largest order of mammals in the world, comprised of 10 families, 8 genera, and 210 species (Etnyre et al. 2011).

## Morphology of Artiodactyl Extremities

As ungulates, artiodactyls typically (with few exceptions) possess digits in which the distalmost phalanx is sheathed in a pointed hoof. They consistently exhibit a paraxonic structure of the foot, indicating that the plane of symmetry of the foot passes between or through the third and fourth digit. In these individuals, the weight of the



animal is supported by the third and fourth digit, while the first digit is always absent, and the second and fifth digits are smaller or completely absent depending on primitivity (Vaughan et al. 2015). Families which possess four functional digits include Hippopotamidae, Tragulidae, Suidae, and the forelimb of Tayassuidae members. These animals typically do not have hooves but a foot with individually spreading digits. Camelidae, Antilocapridae, Giraffidae, and some Bovidae members have only two complete toes with absent lateral digits, while some Bovidae and Cervidae possess two complete toes with reduced lateral digits (Hutchins 2003). In association with weight-bearing on the third and fourth digit, some families, such as Camelidae, Cervidae, Giraffidae, Antilocapridae, and Bovidae, have developed a fusion of the third and fourth metapodials, also known as a cannon bone (Vaughan et al. 2015). It is important to note that the term cannon bone may also be used to describe a single metapodial in Perissodactyls, as opposed to the fused bones noted in several artiodactyl species.

As one of the most expansive orders of living mammals, it is reasonable to consider the broad range of habitats for which individual species within this order are adapted. There are notable variations from this typical artiodactyl morphology noted within included families, such as Camelidae. While dromedary and Bactrian camels exhibit a splaying, partially fused third and fourth metapodial (cannon bone) similar to other artiodactyls, they have simultaneously retrogressed to a digitigrade posture, which is contrasted with the typical unguligrade stance of artiodactyls, in which only the tips of small hooved digits contact the ground during locomotion. This alteration in adaption is presumed to have resulted secondarily from their need to move over soft, sandy ground, as splayed digits prevent sinking. Other animals, such as Caribou or reindeer, maintain an unguligrade stance while developing an increased surface area of the hoof to navigate their natural environment of snow and ice (Vaughan et al. 2015). Solounias and Danowitz (2016) explain that through evaluation of morphological changes observed within a species, particularly in the distal extremities, one can

develop an accurate understanding of habitat preferences as well as phylogenetic history. Because the distal limb is most closely impacted by the environment and variation in substrates, these changes, such as slight alterations in bony anatomy or drastic variation in stance, can provide a multitude of information about that species and its natural and evolutionary history.

Due to the nature of most artiodactyls as prey animals, many possess specialized limbs adapted for speed and running. There are a variety of anatomical changes that are commonly appreciated in animals with this specialization, and many of these are present in artiodactyls of all sizes. A well-appreciated feature of artiodactyls is generalized elongation of the limbs, most particularly of distal segments (with the exception of Suidae and Hippopotamidae). When compared with other species such as canids and other carnivores, artiodactyls have a dramatic elongation of the portion of the limb extending from the carpus distally (Clifford 2010). A tendency for fusion of bones is also noted in several features of artiodactyl morphology. The distal ulna and fibula of the fore and hindlimbs are typically reduced in size or may fuse with the major weight-bearing bones of the limb, the radius, and tibia. In more derived species of artiodactyla, cuboid and navicular bones of the hind limb are also often fused within the foot, resulting in a reduced number of tarsal bones. Many suspect that the tendency for fusion of bones within the distal limbs is a morphologic attempt to lighten the weight of the limb and allow for speed. Members of this order typically also possess a reduction of musculature in the distal limb, replaced by strong tendinous attachments of more proximal musculature. Unlike most land mammals, artiodactyls also do not possess a third trochanter on the lateral femur. Instead, artiodactyls rely on insertion of the superficial gluteal muscles to the proximal tibia after merging with the biceps femoris muscle (Rose 2006). This distal attachment adds to the spring-like motion of the hindlimb experienced during running.

The astragalus, or ankle bone, is the most notable identifier of the artiodactyl hind limb and is the basis of the artiodactyl classification. The astragalus possesses deep grooves at each end to create a

“double pulley” or double trochlea (Hutchins 2003). The depth of these grooves works to maintain motion in the sagittal plane and prevent lateral motion at the site of articulation proximally with the tibia and distally with the navicular and cuboid bones of the hind limb. The astragalus, unfortunately, has also been the source of recent phylogenetic confusion for many during evaluation of the relationship between the orders of Artiodactyla and Cetacea. Molecular evidence suggests that modern ruminants are most closely related to cetaceans, which would indicate that Artiodactyla is not actually a monophyletic order as previously believed. However, cetaceans lack the tarsal structure characteristic of the artiodactyl members, creating discord about the most correct classification of cetaceans from a phylogenetic standpoint (Vrba and Schaller 2000). Thewissen and Madar (1999) suggest that the astragalus that characterizes the artiodactyl tarsus is actually a single morphologic characteristic comprised of multiple individual characters, some of which are actually not completely specific to artiodactyls. It has been shown that cetaceans possess the derived position and shape of the ectal facet (a lateral point of contact with the calcaneus) of the artiodactyl astragalus, which are the most unique characters of the artiodactyl tarsus. This supports a new belief that, despite loss of a characteristic astragalus bone, Cetacea and Artiodactyla may comprise a single order. A merging of these orders would allow reestablishment of a single monophyletic order.

### Evolution of the Gastrointestinal Tract Within Artiodactyla

As previously mentioned, artiodactyls exhibit a wide variety of adaptations among families within the order. With the exception of members of Suidae and Tayassuidae, artiodactyls are obligate herbivores by nature and possess complex gastrointestinal systems specially adapted for this lifestyle. Plant material contains a large amount of cellulose, a complex carbohydrate making up the cellular wall of plant material. A variable amount of protein or other defensive elements may also

be present, depending on the species of plant. Mammals cannot naturally produce enzymes capable of successfully utilizing these compounds as an energy source. Instead, artiodactyl herbivores rely on microbes to more completely extract nutrients from their diet. Gastrointestinal microorganisms provide a way to breakdown complex compounds and produce a more readily useable form of nutrients for the animal. The most derived species have also developed the ability to ruminate to most efficiently maximize nutritional gains. Three suborders are often recognized within Artiodactyla, each with a slightly different gastrointestinal morphology as related to gastric chambers and segmentation. Tylopoda, the camelids, have a three-chambered stomach, which is capable of and relies on rumination. Ruminantia members have a four-chambered stomach, which is also reliant on rumination. Suiformes, on the other hand, have a single stomach that is not capable of rumination. True ruminants of Ruminantia exhibit the most derived gastrointestinal system specialized for a limited herbivorous lifestyle. The rumen, or first chamber of the true ruminant, serves as a fermentation compartment that holds foodstuff after ingestion. Bacteria within the rumen offer a symbiotic relationship for the ruminant, breaking down organic material that others cannot effectively consume. Fermentation inside the rumen releases proteins, carbohydrates, and lipids from ingested material allowing for better absorption of nutrients. Remastication, or cud chewing, occurs through regurgitation of large fibers of plant material into the esophagus and oral cavity for secondary chewing and further breakdown of cellular walls. Following a second swallowing event, food passes into the reticulum, then into the omasum by negative pressure created by omasal wall relaxation, and into the abomasum by muscular contraction. The abomasum serves as the true, glandular stomach of the ruminant. Nitrogen is a natural byproduct of the digestion process of ruminants. Microorganisms within the ruminant gastrointestinal system utilize this nitrogen to make more readily available proteins, which may be then periodically digested by the ruminant as the microbes are mobilized to the intestine

(Hutchins 2003). As prey species, it is particularly beneficial to these animals to have the opportunity to consume a large amount of plant material while having an extended period of time for storage and digestion. This system may, however, become less effective than that of the perissodactyls as food becomes more abundant due to the extended time necessary for passage through the ruminant system. It has been argued that the development of foregut fermentation as exhibited by ruminants led to competitive superiority and rapid successful radiation of artiodactyls as compared to perissodactyls during later Tertiary development. However, Janis et al. (1998), suggest that the two groups are not competitively matched due to the dietary limitations experienced by ruminants. This dynamic is well-demonstrated by radiation of perissodactyls in the late Miocene period in spite of ruminant populations.

### Artiodactyla Skull Morphology

Further adaptations to a primarily herbivorous lifestyle are reflected through skull morphology of the artiodactyls. The antorbital (in front of the eye) portion of the skull is generally elongated and the skull has an overall flat profile dorsally. This silhouette may be interrupted by dorsal extension of a complete or mostly complete orbit. Almost all members of Artiodactyla possess some form of protrusion from the dorsal skull such as in the form of keratin sheathed horns of bovids, bony antlers of deer, or epidermis-covered ossicones of giraffes. Typically, these extensions have a protective function and are characteristically larger in males than females. Caudally, the artiodactyl mastoid process of the petrous temporal bone is exposed between the squamous and exoccipital bones. Most Suidae members are the exception in that their squamosal bone often conceals the mastoid process. Furthermore, suids tend to exhibit dentition separate from other artiodactyls, such as camelids and bovids. It has been recognized that suids tend to have a more diverse omnivorous diet compared to the many ruminants included in Artiodactyla. As such, suids tend to have teeth with a low crown and bunodont

(cusped) cheek teeth. Ruminants and camelids tend to exhibit classic hypsodont (high-crowned), selenodont (high-ridged) cheek teeth typical for herbivorous animals. Camelids and more derived ruminants also have no upper incisor teeth, while primitive species typically possess three incisors in each upper quadrant. Primitive species generally also possess canines that may project from the mouth or are at least well-developed. A space is almost always present between the canine and first premolar of the lower jaw (Rose 2006).

### Sexual Maturity and Reproduction

Sexual maturity of the artiodactyl is most commonly reached at approximately 18 months of age, and the females typically birth their first offspring at around 2 years of age. Delayed sexual maturity as well as increased birth weight, increased adult size, and dominance can help adult females to more effectively access resources for their young, which can lead to longer reproductive success. With this change in development, a decrease in sexual dimorphism in size and protective characteristics (such as horns) among bovids is also typically observed (Vrba and Schaller 2000). Gestation is variable between species, lasting anywhere from 5 to 11 months. Female artiodactyls possess either two or four teats with the exception of Suidae members. Suids typically possess between 6 and 12 teats as made necessary by their generally larger litters (Hutchins 2003).

### Coat and Coloration of Artiodactyls

While coloration patterns are typically species specific, artiodactyls generally possess a double fur coat. The outer coat is long, coarse, and functions to protect against various elements of the weather. A second undercoat of short, fine hairs assist in temperature control. Some domesticated species have been selectively bred to alter this natural coat and select for particular characteristics, such as sheet and their wool. Variations in coloration can be linked to basic evolutionary

pressures to effectively conceal and communicate. White or dark markings on the faces and rumps of social ungulates are particularly closely associated with their diurnal (day dwelling) nature. These markings may play a part in marking an individual as having a role or place within a social grouping, signaling of a mother to her young, or communication of aggression or other intraspecific communication (Caro 2005). Communication is also accomplished through the use of epithelial scent glands, most commonly located on the tarsi, between the hooves, or on their faces. These glands are typically paired and secrete specific chemicals that may be physically transferred by rubbing or nuzzling or aerosolized. In addition to communication of location or territory, these glands, their secretions, and urine may be used to self-mark, communicate threats, or as a physiological state identifier (Hutchins 2003).

## Conclusion

Artiodactyla is one of the broadest, most well-represented orders of animals alive today. Comprised by over 200 species of animals representing a wide variety of habitats, Artiodactyla is one of the most evolutionarily successful living orders. Despite what is known about this large order, there are several unknown factors associated with the evolution of these species and their relationship with other living orders at this time. However, the examination of artiodactyl morphology and their natural history yields a quantity of information that can be used to examine the phylogenetic development of the largest land mammals alive today and their association with several species around the world.

## Cross-References

- [Artiodactyl Cognition](#)
- [Artiodactyla Diet](#)
- [Artiodactyla Life History](#)
- [Artiodactyla Locomotion](#)
- [Artiodactyla Navigation](#)

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## Artiodactyla Navigation

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## Synonyms

[Bachelor herds](#); [Even-toed ungulates](#); [Herding](#); [Home range](#); [Migration](#); [Movement](#); [Predator swamping](#); [Space use](#)

## Definition

Characteristic movements and behaviors exhibited by members of the mammalian

taxonomic order Artiodactyla that best meet their survival and fitness needs.

## Introduction

Even-toed ungulates, classified in the diverse order Artiodactyla, traverse landscapes in their home ranges and migration routes in ways that best serve their needs to survive and reproduce. According to the IUCN Red List, there are 10 families within Artiodactyla (e.g., Bovidae, Cervidae, Giraffidae, Suidae, and others) including the recent consolidation with the 13 families of order Cetacea (i.e., Balaenopteridae, Delphinidae, Phocoenidae, etc.) to form the proposed monophyletic order Cetartiodactyla (International Union for the Conservation of Nature, [n.d.](#)). This group of marine mammals has been shown to display the closest genetic relatedness to artiodactyls compared to any other taxon through anatomical studies of paleontological and modern specimens, genetic evaluations of loci isolation, short interspersed elements (SINEs), and other molecular characteristics (Shimamura et al. [1997](#); Nikaido et al. [1999](#); Price et al. [2005](#)). Though acknowledging the current classification, this chapter will focus only on the representatives within terrestrial Artiodactyla as it pertains to generalized concepts of spatiotemporal movements.

Though their movements are influenced by numerous limiting factors, members of this order have adapted behavioral and morphological characteristics that have enabled them to mitigate the risks of navigation and be one of the most diverse and successful mammalian orders in the evolutionary arms race. Evolution of physiological and behavioral mechanisms to support artiodactyl movement have developed as results of respective climates and landscapes of species occurrence and are subject to continued changes in response to climate variability, anthropogenic influences, and other environmental factors (Post and Stenseth [1999](#)). Examples include but are not limited to dentition for morphological suitability to preferred forage strategy (Mendoza and Palmqvist [2008](#); Janis and Ehrhardt [1988](#)), hoof shape and pad traction to traverse rugged terrain (Rui et al.

[2017](#)), unguligrade foot posture, cannon bone formation (Clifford [2010](#)), various social habits (Geist [1974](#)), and specialized fat deposition and water conservation in extremely arid environments (Nelson et al. [2015](#); Cain et al. [2010](#)).

An example of behavioral adaptations includes species specialization to specific landscapes and temperature response. A study by Street et al. ([2015](#)) showed through statistical analysis of geographic movement data in association with landscape characteristic records that the strictly cold climate-adapted moose (*Alces alces*) occurring in Ontario, Canada, selected habitat based on the thermal characteristics of different stands over optimal forage capabilities. This is believed to be an effort to avoid heat exhaustion, with strong preference for well-shaded timber stands, aquatic environments, marshes, and other areas during the summer months capable of sustaining temperatures below 27 °C (Franzmann [2000](#)). Though this lends itself to optimal thermoregulation capabilities, it can be a limiting factor to overall health of individuals as these areas could potentially be sub-optimal for nutrition and reproduction. Continued observation and management for optimal cover and forage will be necessary as average global temperatures continue to increase.

## Herding Behavior

From massive herds to solitary nomads, artiodactyls exhibit various degrees of aggregation behavior dependent on factors such as species, age, sex, forage availability, spatial scales, and predator presence (Geist [1974](#)). The primary reasons for herding are thought to be based on the ability to quickly gather and communicate information for threat awareness and, to a lesser extent, resource discovery. Individuals in larger herds have lower mortality potentially due to more members present to detect danger, while members of smaller groups exhibit higher chances of being singled out by predators (Kie [1999](#); King et al. [2012](#)). Although herding is beneficial to species persistence, individuals can experience trade-offs with life in a group. The “selfish herd” theory delves into what is, perhaps, the most significant trade-

off as it pertains to predation. Though membership protection is heavily dependent on each animal, individuals may indirectly vie for the centermost position within the group using mostly random movements. This space is believed to be the area of maximum value within the herd and also serves as the area of least mortality risk; however, mortality risk is influenced greatly by group density and position. As the distance from this area increases, so do the odds of mortality. During an encounter with a predator, individuals may attempt maneuvers to gain maximum protection from the threat. Though animals on the periphery of the group are typically the ones at greatest risk of mortality, the complicated motions of individuals can confuse predators, and targeting of prey can become difficult (Breed and Moore 2016). Although there are instances in which animals, such as maternal or dominant individuals, will serve as defensive sentinels, it can be interpreted from selfish herd theory that the subordinate herd members are often the ones that are excluded from the center via competition and are the most exposed, while more dominant individuals take up the center position and make no attempt to hinder the predator's efforts (Morrell et al. 2011). However, caution should be exercised as this theory can lead to potential misinterpretation of natural selection. The oftentimes randomness of herd movement and likelihood for any herd member to face predation, regardless of social ranking, may introduce too much variance to assume that a population's genes and fitness are significantly correlated with geographic location within herd movements.

King et al. (2012) tested the selfish herd hypothesis with captive sheep (*Ovis aries*) ( $n = 46$ ) and a herding dog (*Canis lupus familiaris*) outfitted with GPS equipment to record individual locations every second to determine if the sheep were indeed making a calculated effort to position themselves in the centermost area of the fleeing herd. Their analytical models showed "classic aggregation and avoidance behavior" whereby sheep seemed to be attracted to what they cognitively approximated as the centermost location of the herd; however, the sheep did not appear to be calculating the position

of fellow herd mates relative to their position in the herd. They did note that various herd sizes, more precise individual movements relative to conspecifics, and other danger types should be subject to further selfish herd research.

Other plausible explanatory mechanisms for herding behavior include animals in herds having the opportunity to observe resource location behaviors of other herd members as well as opportunities to learn travel routes as they move across space. By using their senses, individuals can cue into movements of others around them and exploit resources discovered by other individuals to reduce energetic costs and risks of predation. Though this proves valuable for success of the herd, intraspecific competition will begin to occur within the group as discrete resources are discovered and used. This can become another trade-off of herding behavior as it is very difficult for an animal in a social unit to exclude others from resources (Breed and Moore 2016).

Sexual segregation and group size vary with season and species. During the nutritionally taxing parturition and nursing period for females, various species will exhibit moderate to high levels gregarious behavior (e.g., wildebeest, *Connochaetes* spp.), whereas others may remain relatively solitary (e.g., white-tailed deer, *Odocoileus virginianus*) during lactation and the critical stages of their young's development (Estes 1976; Bertrand et al. 1996). These behavioral differences in female representatives of species vary with taxonomic classifications, carnivore presence, and food and cover availability. Bertrand et al. (1996) stated that female white-tailed deer vigorously defended selected parturition areas from related and unrelated conspecifics leading up to and after birth of their fawns. Optimal areas, defined as areas with most available food resources and cover, seemed to be occupied by the most dominant individuals, whereas occupancy of less optimal areas seemed to descend with subordinate social levels. During the non-breeding season, however, white-tailed deer bucks are commonly known to aggregate together in what are known as "bachelor herds." These groups typically disband as the rut initiates and intraspecific competition between bucks



intensifies (Breed and Moore 2016). Though bachelor herd formation isn't exclusive to white-tailed deer or even Artiodactyla itself, it is represented well throughout the order.

Caribou (*Rangifer tarandus*) cows utilize mutual group vigilance and will rarely exclude conspecifics from parturition sites to the levels seen in white-tailed deer. However, caribou live in far northern latitudes and are considered constant migrants such that they are always on the move between summer and winter ranges and are frequently in closer proximity to conspecifics throughout the year. In contrast, white-tailed deer hinds appear to distribute themselves over more defined home ranges, with far-ranging movement behavior linked mostly to male dispersal (DeMars et al. 2013; Frame et al. 2008; Tierson et al. 1985).

Estes (1976) described wildebeest parturition as "mobile," considering the species is highly gregarious and targeted extensively by predators such as spotted hyena (*Crocuta crocuta*). Because of this, wildebeest seem to tolerate conspecifics more so than other members of Artiodactyla during parturition and take advantage of a concept known as "predator swamping." Predator swamping is defined as birth synchrony within a population that results in a "flood" of offspring which cannot be consumed by potential predators due to an influx of vulnerable prey in a very short time frame. Although this strategy is not exclusive to wildebeest, Estes mentions they seem to be a rare example in how this strategy is utilized. Offspring are fully mobile within hours after birth and accompany the mother and conspecifics immediately after they are capable of travel. This further combats predation in that there are too many mobile, young targets than what can be actually eaten. This differs from many other members of Artiodactyla in that most species isolate their offspring for various amounts of time to prevent harm coming to them by means of predation or from conspecifics themselves. Estes does make a point to mention that offspring mortality values were found to increase with decreasing herd and calf density, and found offspring in larger aggregations were not as subject to predation even when parturitions were out of synch. These

studies of artiodactyls highlight that species in this order have adapted varying parturition strategies based on movement patterns to maximize survival and fitness.

## Migration

Migration behavior is exhibited across numerous taxa and is utilized for a range of reasons, including reproduction and predation avoidance. The main driving factor, as it specifically pertains to artiodactyls, seems to be that even-toed ungulates adjust their movement patterns with the growth of new, high-quality vegetation throughout the annual cycle in order to maintain or increase fitness (Chynoweth et al. 2015; Jesmer et al. 2018; Skarin et al. 2010). The new vegetation growth is driven by weather patterns, thus affecting the scale at which animals will travel (Holdo et al. 2009). It is widely recognized that animals will travel longitudinally, from one range to another. But altitudinal migrations, between lower and higher elevations, are also prevalent especially among montane species, though these areas do not always correlate with increased foraging. Higher altitudes have been associated with predator avoidance and biting insect relief. Factors influencing altitudinal migrations include vegetation configuration, topography, landscape ruggedness, and even human activity (Skarin et al. 2010). Although not readily distinguished by observation of animal behavior alone, cues to migrate include day length, weather pattern changes, feeding changes, predator, and insect harassment. The various learned and specific physiological behaviors that react to these phenomena are what give rise to migration (Jesmer et al. 2018). Once movement has initiated, ungulates have traditionally been thought to utilize navigational methods such as following unique landscape formations, paths, and social information from experienced conspecifics. It should be noted that any movements, regardless of scale, are heavily dependent on environmental influences occurring at the time of action. This causes variation in action outcomes such as

destination, travel speed, arrival times, time spent there, or if a migration occurs at all (Winkler et al. 2014).

Jesmer et al. (2018) tracked movements of resident and translocated bighorn sheep (*Ovis canadensis*) and moose to demonstrate that ungulate migratory strategies may be rooted in learning from more experienced conspecifics. In what has been called “green-wave surfing,” a population of animals that has resided in a region for generations have been shown to follow the emergence of new vegetation by migration. These groups are called a historical population (>200 years residency), and these animals are often traveling extended longitudinal or altitudinal distances as they follow their food source. Because these movement patterns remained unbroken for an unknown amount of time, the researchers sought to answer the question if these migration routes are innate behaviors or learned from conspecifics in a process dubbed “cultural transmission.” By translocating and tracking individual bighorn sheep and moose to novel landscapes, they were able to assess if migration routes were born from inherited migratory paths (i.e., genetically heritable migratory pathways) or a product of cultural transmission in unfamiliar landscapes. After the translocations, they used data from GPS collars to measure where translocated and non-translocated animals were spending their time on a seasonal basis. They further calculated time spent in areas corresponding to the magnitude of vegetation emergence of occupied landscapes. Their findings showed a dramatic difference in translocated and historic population movements. Historic populations typically maintained their migration patterns, with 65–100% of study subjects exhibiting migratory behavior. Translocated herds remained relatively confined to the regions of their release until enough generations had passed to allow the descendants of translocated animals to gradually adapt to the movements and green-wave surfing culture of the native population over time. Only 9% of these translocated animals exhibited migration behavior. Surfing knowledge among native populations was roughly twice that of translocated animals which suggests that knowledge of local green waves

builds with experience and may be culturally handed down over generations. As this knowledge increased, the migratory propensities followed.

## Home Range Movement

An animal’s home range is the space it utilizes to carry out the majority of its life history. The spatial and temporal scale at which these spaces are utilized depends greatly on availability of resources and environmental characteristics and is often driven by seasonal weather patterns, landscape configuration, forage availability, cover, competition, population density, predator presence, habitat fragmentation, and anthropogenic land use (Gingery et al. 2017; Powell and Mitchell 2012; Wattles and DeStefano 2013). Artiodactyls often exhibit behavior conducive to the utilization of roughly defined spaces quite dynamic in scale and temporal occupation. Home ranges can span from several square meters to many square kilometers and may be utilized within a single season, across seasons, or for the duration of an entire life span dependent on species life history requirements (Börger et al. 2008). Spatiotemporal dynamics of species are influenced by the current environmental state and needs of the individual animal itself, meaning that an animal will adjust the scale of use of its home range dependent on the quantity and quality of resources, landscape configuration, and its own body condition (Bevanda et al. 2015). Home range use can further vary based on age, sex, and group size and comes with its own range of associated risks (Fennessy 2009; Marino and Baldi 2014). Duquette et al. (2015) found that female white-tailed deer in a landscape inhabited by multiple predator species adapted their movement based on areas of nutritional value and risk potential. Predators were shown to occupy areas with greater optimal forage potential value for deer, thus making these areas beneficial yet also risky, especially during seasons of neonate dependence. By monitoring telemetry data, the deer were observed interchanging their movement habits between resource-rich areas with greater direct mortality risk by gray wolves

(*Canis lupus*) and sub-optimal resource areas with reduced risk of direct mortality from predation. However, the trade-off for this movement pattern was that subsequent neonates were more exposed to predation from carnivores such as coyotes (*Canis latrans*). Movements were also shown to be plastic, or flexible, whereby if an individual's fawn was depredated, hinds would respond with a more conservative foraging strategy to reduce energy expenditure and risk of predation. Fawns from subsequent reproductive attempts were therefore more likely to have greater survival as a result of plasticity in their parent's foraging strategies.

Movement ecology, as related to an animal's resource use within its home range, is an ever-evolving field of study, and the development of new methods are necessary to continue advances in ecological research. New technological, statistical, and computational advancements are developed frequently and can advance our understanding of spatiotemporal dynamics in many species, particularly those that are difficult to observe or transient in nature (Allan et al. 2018; Hebblewhite and Haydon 2010; Millspaugh and Marzluff 2001). Common methods of spatiotemporal and movement research in artiodactyls involve telemetry monitoring by means of VHF (very high frequency) and GPS (Global Positioning System) collars. These kinds of devices and their various applications have revolutionized the study of animal movements across space (Cagnacci et al. 2010; Hebblewhite and Haydon 2010).

Rivrud et al. (2010) used GPS data to determine if red deer (*Cervus elaphus*) home range use fluctuated as a consequence of seasonal climate variables. They suggested climate changes could directly influence animal activity patterns within their home range if it impacted resources necessary for survival and fitness over time. They developed two temporal hypotheses related to season-specific variation and potential climate change effects on red deer home ranges. First they hypothesized short-scale effects of climate change as it related to daily and weekly weather events (e.g., temperature, precipitation). They further hypothesized there would be longer-term

effects at bimonthly and monthly time scales during the summer season related to vegetation growth. They collected hourly GPS collar locations from 47 red deer hinds as well as weather (i.e., temperature, precipitation, snow depth), habitat, and forage productivity covariates.

Their results correlated with their hypotheses in that animal activity seemed to be greatly influenced by different weather patterns. Home range size increased during times of abnormal winter warmth, whereas the opposite was seen during cooler summer temperatures. It is believed that the positive relationships between home range sizes and temperature are that deer respond to times of more extreme than average seasonal temperature by limiting their space use in order to conserve energy. When temperatures abnormally fluctuate in relation to normal parameters, such as higher than normal winter temperatures, deer will expand space and resource use to take advantage of thermal changes. It was noted that similar findings have been reported with cervid research, such as by Hayes and Krausman (1993). Changes in home range size as related to precipitation were different from temperature with season and scale. Positive relationships were maintained between home range size and periods of longer precipitation but contained no obvious seasonal influences. However, shorter periods of precipitation saw seasonal influence on home range size as shortened precipitation in winter maintained a positive and shortened precipitation in summer maintained a negative relationship with home range. Using the kernel method, a 10 mm increase in precipitation was projected to correlate with a 90% home range size increase. Rivrud et al. (2010) suggested that this seasonal variation in home range size resulting from shortened periods of precipitation may be related to search and utilization time for shelter by red deer, particularly in sub-optimal habitat, as precipitation can be thermally expensive to ungulates (Parker 1988). But this explanation did not correlate well with longer periods of precipitation, and further research would be needed to determine possible correlations.

Snow depth was also shown to exhibit influence on home range size – as depth increased home range size tended to decrease. Yet it was

predicted that home range size dramatically increased with a 10 cm reduction in snow depth. Home range retraction during heavy snow events could be due to reduced levels to conserve energy considering that movements in heavy snow are energetically costly (Parker et al. 1984).

Home ranges also varied in size in relation to quality of habitat in red deer, specifically in short temporal scales. In areas where forage and cover were lacking, home range sizes were larger than areas with optimal resources, but extent of home range varied with surrounding landscape characteristics (e.g., forest vs. pasture lands). This could be in response to lower densities of resources in sub-optimal areas, resulting in resident deer needing to utilize larger spatial extent to meet metabolic demands and other life history needs.

## Conclusion

Ungulate movements, particularly migrations, are recognized as one of nature's most awe-inspiring phenomena. Much scientific knowledge pertaining to mammal movements stems from migration of these charismatic fauna, such as the caribou of the arctic and the wildebeest of the Serengeti. Other findings are being published on lesser known migratory movements such as those of mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) in western North America (Sawyer et al. 2005; Lendrum et al. 2013). Anthropogenic barriers and bottlenecks (i.e., fences, extensive energy development, roads) are increasing limitations to migration paths in artiodactyls worldwide, often times completely cutting off historic routes. This poses direct survival implications for ungulates as well as human cultures dependent on these species. Depending on geographic location, ungulates must traverse rivers, rugged topography, interpret homogenous landscapes, and avoid predators. But as global climate patterns shift, vegetation growth may change spatially and temporally which could also skew migration cues and navigation. This may impact timing and magnitude of migration and may result in movements that are asynchronous with resource availability. Further research

of spatiotemporal movement is needed in the hope that these efforts to understand and preserve ungulate movements will facilitate sustainability of populations. Proper management strategies as well as new management or protection ideas for areas known to be important migration corridors, high-quality habitat, or harbor high population abundances could offer some solution to preserve these behaviors in the future (Berger 2004).

## Cross-References

- ▶ [Artiodactyla Life History](#)
- ▶ [Artiodactyla Locomotion](#)
- ▶ [Artiodactyla Morphology](#)
- ▶ [Behavioral Flexibility](#)
- ▶ [Behavioral Variation](#)
- ▶ [Competition](#)
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- ▶ [Species](#)

- Taxa
- Thermoregulation
- Translocation
- Ungulate
- Vigilance

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## Asexual Reproduction

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## Synonyms

Agamogenesis; Parthenogenesis

## Definition

Reproduction without the sexual union of male and female gametes.

## Introduction

Asexual reproduction is any form of reproduction in which a single parent organism produces offspring without combining male and female gametes. The produced offspring are either identical clones of the parent organism or are genetically similar with no additional genetic material being added. Any differences between the parent and offspring organisms that do arise are typically due to mutations or genetic recombination when undergoing meiosis. However, most forms of asexual reproduction do not make use of meiosis or the fertilization that occurs during sexual reproduction.

Asexual reproduction is primarily observed in single-celled prokaryotes, such as bacteria, as this is their primary form of reproduction. Prokaryotes are capable of transferring genes between



individuals, similar to sexual reproduction (Narra and Ochman 2006), but any new offspring are spawned asexually. Although it is rarely used as a primary form of reproduction, many species of plants, fungi, and animals are capable of reproducing asexually. By reproducing asexually, an individual can generate a high number of offspring, but each of these offspring will be genetically similar to the parent. This form of reproduction can produce short-term rapid population growth but can also limit the genetic diversity of a species.

## Binary Fission

The term asexual reproduction refers to a wide range of reproductive behaviors, including binary fission. Binary fission, also known as cellular cloning, occurs when a parent organism copies its genetic material and splits into two identical daughter organisms. This process is the primary form of reproduction used by prokaryotic organisms such as bacteria. Binary fission is similar to mitosis, which is performed by eukaryotic cells, except for the absence of a true nucleus in prokaryotes. Although eukaryotic cells divide through mitosis or meiosis, some organelles, including mitochondria and chloroplasts, divide via binary fission.

Binary fission can be classified as one of four types depending on where the division occurs. Simple binary fission can occur along any plane in the organism. Transverse binary fission occurs along an organism's transverse axis, the horizontal line that runs across the organism. Longitudinal binary fission occurs along an organism's longitudinal axis, the vertical line that runs lengthwise along an organism. During oblique binary fission, the division occurs along a slanted plane. This form of binary fission can result in daughter organisms that are unequal in size (Biology Dictionary [n.d.](#)).

Although the most common form of fission results in two organisms, multiple fission, where a parent organism splits into more than two daughter organisms, does occur in some species of protists, protozoans, and slime molds (Britannica Education Publishing 2011). During

this process, multiple copies of the parent organisms' nuclei are made before splitting into individual cells. In most forms of multiple fission, the additional nuclei are stored in the central cavity before forming daughter organisms. Some organisms, such as the marine alga *Acetabularia*, instead form compound nuclei with all of the copies stored with the parent nuclei. During this process, the nuclei separate right before gamete formation (Bonner 1998).

## Budding

Budding is another form of asexual reproduction that involves a parent organism splitting into a mother and daughter organism. During this process, a "bud" grows from the parent organism and splits after reaching full maturity, becoming a daughter organism. Some single-celled organisms, such as yeast, reproduce through budding, but this process is much more prolific in plants and some aquatic animals, including corals and sponges. Some parasites use an internal form of budding in which the daughter organism grows inside of the parent organism and is expelled upon reaching maturity (Smyth and Wakelin 1994).

During the budding process, the new cell starts to form as a bubble on the side of the parent organism and fills with cytoplasm until it is the same size as the parent organism. At this point, the nucleus divides, with one copy moving into the new cell. Following this, the daughter organism separates from the parent organism, forming a new cell. In some species, the budding process can occur at any location along the organism, but other species have specialized areas that budding is restricted to. Although daughter organisms typically separate from the parent organism once the budding process has concluded, some species do not separate and instead form colonies (Encyclopedia Britannica 1998).

## Vegetative Reproduction

Vegetative reproduction occurs when a fragment of a parent plant grows into a new plant. This process uses vegetative parts of the plant, such

as the leaves, roots or stem to produce new plants. New plants can also be formed from a specialized reproductive structure, such as a runner, rhizome, tuber, corm, or bulb. Many plants can reproduce through vegetative reproduction, with upwards of 70% of all plants being capable of this form of reproduction (Klimés et al. 1997). However, this process is rarely used exclusively as it can reduce genetic diversity.

Vegetative reproduction can be artificially induced and is used by many horticulturalists to replicate plants (Swingle 1940). When used this way, a superior plant can be reproduced endlessly and at a much faster rate than through seed propagation. Artificial vegetative reproduction can be performed by using apomictic seeds (seeds produced asexually), specialized vegetative structures, layering and cutting, grafting and budding, and tissue cultures (Perrott et al. 1998). Layering and cutting induces a plant to regenerate a lost limb; layering occurs when the lost limb is still attached, and cutting occurs when the limb is detached. Grafting and budding are the most widely used methods of propagation and involve joining multiple plant parts together using tissue regeneration. When the plant part being added is a bud, the process is called budding. Tissue cultures provide embryos and shoot tips with artificial nutrients and other inorganic elements to encourage growth.

## Sporogenesis

Sporogenesis is the production of reproductive cells, called spores, which are used by plants, fungi, and algae. Many of these spores are produced asexually but require fertilization after being dispersed to grow into a new organism. Fungi and some species of algae are capable of true asexual reproduction by producing spores that do not require fertilization before growing into a new organism (Raven et al. 2005). Fungi use a variety of methods to produce spores from mother cells that are then dispersed near the parent or ejected to be spread by wind, water, or other organisms. After landing, the spores will then wait to germinate until the environmental conditions are optimal for growth. Although fungi are

capable of reproducing asexually using a variety of methods, the creation of spores is the most commonly used.

## Fragmentation

Fragmentation occurs when an organism grows from a piece of the parent organism that was severed. This process can occur as a result of outside forces or be initiated by the parent organism. In order to reproduce using this method, organisms need to develop specialized organs or even regions of their body that can be removed without disrupting the rest of the organism. Additionally, these sections would need to be able to regenerate to form a brand new organism. Fragmentation is similar to regeneration, except that each piece has the possibility to form a new organism.

Fragmentation is used by many molds, plants, lichens, and some animals such as echinoderms and annelid worms. When performed by plants, fragmentation is a common type of vegetative reproduction. Many lichens, a symbiotic union of photosynthetic algae/bacteria and fungi, reproduce through fragmentation so that the new growths possess both of the symbionts. Some organisms reproduce through clonal fragmentation in which the parent organism splits into several fragments, each of which is capable of growing into new organisms. This form of fragmentation is used by echinoderms, such as sea stars, and is also referred to as fission. The survivability of the produced fragments is size-dependent, with the larger fragments being much more likely to grow into a new individual.

## Agamogenesis

Agamogenesis is any form of reproduction that does not involve fertilization by a male gamete. Many organisms that normally reproduce sexually are also capable of reproducing asexually through one of several processes. Parthenogenesis, also known as unisexual reproduction, occurs when an unfertilized female (rarely male) gamete grows into a new individual. Parthenogenesis

occurs in a wide variety of plants and invertebrates and is the most common form of asexual reproduction in vertebrates. Some species reproduce through parthenogenesis when there are no fertile males present or environmental conditions are not conducive to raising offspring; other species, such as the New Mexico whiptail lizard, reproduce exclusively through parthenogenesis as there are no males of the species.

The gametes that undergo parthenogenesis can be either diploid (two sets of chromosomes) or haploid (one set of chromosomes). Haploid parthenogenesis occurs in some plants and bees. During this process, a haploid gamete grows to become a haploid adult. In bumble bees (*Bombus terrestris*), haploid individuals can differ in size and reproductive success from diploid adults, with haploid males being larger and less reproductively successful than the diploid males (Duchateau and Mariën 1995). Diploid parthenogenesis is a much more common process where a haploid gamete either duplicates its chromosomes or fuses with another haploid gamete before developing into a diploid adult. Unlike other forms of asexual reproduction, these individuals are not true clones of the parent organism as the meiotic process alters the genetic material.

Although less common, apomixis is another form of agamogenesis. Apomixis occurs in sexually reproducing plants when no male gametes are available. This process involves a plant producing spores that do not require fertilization to grow into an identical offspring. Apomixis is widely used in ferns and in flowering plants but is rare in other seed plants (Wang and Tseng 2014). There are two kinds of apomixis. Gametophytic apomixis occurs when an embryo forms from an unfertilized egg that did not complete meiosis, instead undergoing a process similar to mitosis. Nuclear embryony is another form of apomixis in which an organism creates an embryo without the use of reproductive cells, instead drawing the necessary materials from other tissues. This particular reproductive method is primarily performed by citrus fruits when male gametes are not readily available. Although much rarer, male apomixis can occur with reproductive materials being derived entirely from pollen.

## Advantages

Asexual reproduction can provide many short-term benefits by allowing an organism to reproduce rapidly without having to find a viable mate. By not requiring a conspecific to reproduce, all members of a population can produce offspring, effectively doubling the rate of potential growth compared to sexually reproducing populations. This effect is known as the twofold cost of sex. By rapidly reproducing, a species can attempt to overwhelm potential competitors through sheer force of numbers. This rapid reproduction can also prevent invaders from gaining a foothold by quickly occupying a niche.

Without the need for a viable mate, asexually reproducing organisms can reproduce at any time with the requisite amount of resources and do not need to expend any extra resources or time on mating routines or to raise offspring as most asexually produced children are independent from birth. By reproducing asexually, an organism can choose when and where to reproduce and will continue to do so until conditions are no longer favorable. Without any investment from the parents, offspring are generally fully matured when born or, in multi-celled organisms, can mature faster than sexually reproduced organisms, with crops that are produced asexually reaching maturity much faster than those that are produced sexually as they do not have to grow from a seed.

This form of reproduction is especially useful for species that live in regions with low population density or few resources as many types of asexual reproduction simply split new organisms from the parent. Many species that maintain the ability to reproduce asexually do so for emergency situations when there are no viable mates or some other aspect of the environment prevents sexual reproduction from being a viable option. Asexually reproducing species can thrive in the climate that they have adapted to, including extremely hostile environments. However, these adaptations are typically very rigid, so that any changes in the environment can devastate a population that is not already equipped to deal with the new surroundings.

## Disadvantages

Conversely, asexual reproduction has a major drawback: a lack of genetic diversity. Barring potential mutations, most forms of asexual reproduction create exact replicas of the parent organism, which means that any new organisms are susceptible to the same diseases and other environmental dangers that the parent organism is vulnerable to. If a population of organisms share vulnerability to the same dangers, then a mass extinction event can occur, wiping out that population. A mass extinction event can occur even in a population that reproduces sexually, but asexual populations are much more susceptible (Wills 2003). Although a lack of genetic diversity is a concern for asexually reproducing species, many bacteria offset this cost by having a high rate of mutations, allowing for enough genetic diversity to protect a population (Suomalainen et al. 1987).

A high rate of mutations can improve species fitness over time, but it can also lead to a high number of mutations with deleterious effects. Mutations with strongly deleterious effects will quickly be removed from the gene pool through natural selection. Mutations with only mild deleterious effects can persist in a population and increase the mutation load and possibly reduce that population's fitness. Compared to sexually reproducing populations, species that primarily reproduce asexually tend to have a higher mutation load, lower fitness, and more deleterious mutations (Kondrashov 1982).

## Alternating Use

Many multi-celled species that are capable of asexual reproduction also engage in sexual reproduction to avoid the disadvantages. The ability to alternate between asexual and sexual reproduction is termed heterogamy. By switching between these two methods of reproduction, an organism can maintain a sufficient level of genetic diversity while capitalizing on the speed and efficiency of asexual reproduction. Some animal species, such as the crustacean *Daphnia*, rapidly reproduce asexually in the spring and then switch to sexual

reproductive strategies when competition starts to increase.

Bengtsson (2003) examined how often a primarily asexual population would need to engage in sexual reproduction to maintain similar levels of genetic diversity as sexually reproducing populations using genetic models. In order to maintain a comparable level of genetic diversity, an asexual population would only need to produce a few sexual individuals per generation. This method can allow for a great degree of genetic variation that can be easily compared to that in sexual populations. As the number of sexual events required to maintain a sufficient amount of genetic diversity is very low, this strategy may help explain some species that have only been observed reproducing asexually while also having a high degree of diversity (Jonsson et al. 1996).

## Conclusion

Asexual reproduction covers a wide range of behaviors that are employed by many different organisms, all of which are defined by the lack of fertilization that characterizes sexual reproduction. These behaviors can allow a species to quickly reproduce with fewer resources and investment than is required by sexual reproduction but comes at the cost of reduced genetic diversity, which can endanger a population. To counter this disadvantage, many single-celled organisms have a high mutation rate, and many multi-celled organisms use a combination of sexual and asexual reproduction depending on the environment.

## Cross-References

- ▶ [Bacteria](#)
- ▶ [Binary Fission](#)
- ▶ [Budding](#)
- ▶ [Genetic Variation](#)
- ▶ [Mutations](#)
- ▶ [Reproduction](#)
- ▶ [Reproductive Fitness](#)

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## Assemblage

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## Synonyms

Aggregation; Collection; Organization; Set; Structure

## Introduction

In nature, assemblages are everywhere: a blade of grass is an assemblage of plant cells and pores; a beehive is an assemblage of bees and beeswax; a jungle is an assemblage of animals, plants, and microorganisms. Philosophers (e.g., DeLanda 2016) define “assemblage” as a collection of heterogeneous elements located within some area of interest. An example of an assemblage might be a study area within a rainforest. Assemblages have the following features (DeLanda 2016): they have a boundary (e.g., a defined study area), they have constituent parts which occur together non-randomly (e.g., animals in the study area), the elements inside are interrelated to some extent (e.g., a rainforest ecosystem), the constituent parts might be removable (e.g., animals can depart the area; trees can be cut down) while keeping the identity of the assemblage intact (e.g., a rainforest can still be called a rainforest, if not too many elements are removed). Assemblage is a fundamental principle of “social groups” as they occur in the major transitions in evolution (Bourke 2011). However, the word “assemblage” itself has an even broader definition, applicable even to collections of highly dissimilar objects (DeLanda 2016), such as the assemblage of people, books, bricks, windows, laboratories, and buildings that make up a university campus. The way that a scientist defines an assemblage depends very much on the scientist’s goals. Assemblage is not necessarily a spatial concept (DeLanda 2016) – but in studies of animal behavior and cognition, studies of assemblages are



sometimes tied to geographic locations. Here, the focus is on two main topics: (1) comparison of different species living in the same area using a single type of test, and (2) archaeological and fossil assemblages. Examples of such studies are given below.

## Comparative Studies

In the comparative study of living animals, an assemblage is a way to organize a cross-species comparison. For example, Nevitt, Reid, and Trathan (2004) investigated the foraging cognition of an assemblage of Antarctic seabirds (petrels, albatrosses, shearwaters) focusing on the way that each species of bird uses its olfactory capabilities to detect krill (a crustacean which is a primary food source in the Antarctic Ocean). They artificially simulated the scent of krill, using vegetable oil slicks which contain the same chemical compound (3-methyl pyrazine) that give krill its distinctive scent (additionally, they had two control conditions, consisting of slicks with other/no scents). Here, the assemblage was composed of nine species of birds and how they differed in their attraction to the slicks. After the investigators put the slicks onto a patch of ocean, birds were recorded as showing interest if they showed attention to the slick (flew near it, landed on it, etc.). The investigators found that four out of nine species were particularly attracted to the krill-scented slicks, and this appeared unrelated to how much krill is typically in the species' diet. The investigators conjectured that different bird species employed different strategies to hunt krill, relying on either olfactory, visual, or social cues (or combination of each) – and that this is linked to the typical foraging strategy of the species (e.g., whether they tend to forage in large groups or how competitive/vulnerable the species is). Another example of a study using an assemblage is from Webster and Lefebvre (2004): they investigated problem solving abilities and neophobia in five wild bird species (doves and Passeriformes) who foraged in a local neighborhood in Barbados. The investigators captured the birds in traps, habituated them, and then tested the birds. They also did

a field version of the same study (using the same general method). The neophobia test measured the birds' latency to approach food that was novel (versus familiar). The problem solving test measured the birds' ability to employ novel procedures to open a transparent box containing food. The investigators found significant differences between species both in neophobia (doves had higher neophobia) and innovative problem solving ability (Passeriformes were more successful). According to the investigators, their results supported the idea that high food neophobia in a species has some inhibitory effect on problem solving capability. In the two studies mentioned above (and many others), species assemblages are used to draw conclusions about cross-species differences based on the same test. Although the term "assemblage" is not always used, it is a central methodology in the study of animal cognition.

## Fossil Assemblages

One can look at assemblages of dead animals too. Zooarcheology is the study of dead/extinct species (Crabtree 1990). By looking at animal remains (i.e., "faunal assemblages"), it is possible to draw inferences about life in the past. For example, Crabtree (1990) showed how the study of animal remains help us to learn about the relationship between humans and animals in ancient human societies: we can learn about past human diets, meat consumption, meat trade, methods of butchery, the range of animal species used for meat and pets, age of animals at death, and even social status (e.g., wealthier people would have different consumption patterns, as reflected in their refuse collections). These types of studies are location-bound: the fossils are found at a specific field site (e.g., the remains of a human dwelling) and these form the basis of conclusions about how life had been like at that location. This is congruent with the textbook definition of "assemblage" in archaeology (Joyce and Pollard 2010): referring to objects deposited at a specific location, either intentionally or accidentally, consisting either of artifacts (such as tools) or



biological matter (such as fossil bones), which are presumed to be associated with each other due to spatial proximity within the area that they were discovered. Archeological and paleontological assemblages form a complex picture of the past (Joyce and Pollard 2010), because the natural processes of deposition rarely allow findings of whole animal fossils or perfectly intact field sites; instead, objects are typically fragmented and scattered, giving the scientist a detective's job of reconstructing the findings (e.g., piecing bones together), reconstructing the past environment (e.g., what kind of ecosystem existed at that time), and reconstructing the processes of deposition (e.g., the effects of erosion or weather on the fossils since being deposited).

Fossils can also give us insights into the behavior and cognition of extinct animals. Here, the word "assemblage" is used more loosely: less about location and more about categories. For example, Naish (2014) reviewed the fossil record of birds in order to make inferences about the evolution of bird behavior. Bird fossils excavated from many field sites can be placed into an assemblage of many bird species fitted to an evolutionary timeline (cladogram). We cannot observe the behavior of extinct birds directly: with rare exceptions, we have only their bones. One method of inference is to compare the bodies of extinct birds with living birds, using the (not always true) assumption of that birds with similar morphologies will display similar behaviors (Naish 2014). For example, if a fossil bird skeleton has the claws of a raptor and a curved beak, then the bird was probably a predator. Alternately, if a fossil bird has a smaller body and a long thin beak, then it might have been a forager who probes in mud. By combining fossil evidence with evidence on the behavior of living bird species, we can make inferences about extinct birds on their methods of foraging, their diets, methods of locomotion (e.g., whether flying or not), reproductive behavior (e.g., placement of eggshells provides clues to nesting behavior), age of sexual maturity, and sociosexual display (Naish 2014). Faunal assemblages have also been studied extensively by scientists who study the evolution of the human mind (Shultz et al. 2012; Wynn 2002). The humans who went extinct – those of the *Homo*

genus, Neanderthals, and earlier – left only sparse clues to help us understand their behavior and cognition: fossils and artifacts. Looking at hominid fossils, scientists can look at the various brain sizes calculable from the inside of fossil skulls, plotted against time and compared against likely environments, in order to draw a picture of how larger brain sizes might have evolved in conjunction with certain cognitive skills such as language (Shultz et al. 2012).

## Tool Assemblages

Finally, extinct hominids also left behind an extensive assemblage of stone tools (Wynn 2002). These have been excavated from sites going as far back 2.5 million years ago (mya), and archeologists such as Thomas Wynn (2002) have compared these artifacts against psychological theories in order to study the likely cognitive abilities of our hominid ancestors. We can compare, for example, stone tools from the Oldowan industry (roughly 2.6 to 1.7 mya) to the later Acheulean industry (roughly 1.7 to 0.1 mya) and see that the later tools had far more technical sophistication. Wynn (2002) compared these industries and made inferences about the abilities of the stone tool makers (the earlier species of humans) in their ability to understand and create symmetry (which he originally did from a Piagetian perspective). Other researchers (e.g., Haslam et al. 2009) have stressed the importance of broadening the investigation of primate cognitive evolution to many more types of primate tool assemblages, from living and extinct species (including capuchin monkeys, chimpanzees, and the various extinct *Homo* species), to develop an integrated view about how cognitive tool using abilities evolved over time.

## Cross-References

- [Assortment](#)
- [Behavioral Variation](#)
- [Categorization](#)
- [Comparative Cognition](#)
- [Family Resemblance](#)

- Foraging
- Group Living
- Hominid
- Homology
- Innovation
- Neophobia
- Nomenclature
- Observational Methods
- Polymorphic
- Stone Tools

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## Assistance Dogs

- Service Dogs

## Associative Learning

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## Synonyms

Classical conditioning; Conditioning; Instrumental conditioning; Operant conditioning; Pavlovian conditioning

## Introduction

Emily has been working long hours lately, so her husband Steve sends her flowers to brighten up another stressful day. Steve has made similar gestures to help Emily throughout their relationship, so she proudly displays the bouquet on her desk. Emily's coworker Erin has a different reaction. Since Erin only receives flowers when her boyfriend has something to apologize for, she immediately assumes Steve has made a mistake. The same flowers responsible for Emily's joy make Erin skeptical and worried for her friend.

Corey travels often for work and is happy to find his favorite burrito restaurant in almost every new state he visits. Today, however, he must try for a new restaurant since his favorite one is nowhere to be found. He enjoys his usual order for lunch before returning to the hotel. Later that night, Corey becomes extremely ill and wakes many times throughout the night. He struggles through work the next day and vows to never visit this new restaurant again, no matter where he might be.

Jessica wakes up late, hungover from another night of heavy drinking. She has already lost several jobs due to her tardiness, so she rushes to work thinking which excuse to use this time. Her friends can always control themselves at happy hour, but whenever she is around alcohol, it feels impossible to stop. Even seeing the empty whiskey glasses in her cabinet at home is enough to make her reach for a drink. Despite the efforts of

her family and the threat of losing yet another job, Jessica's cycle persists.

All three of these scenarios are examples of associative learning at work in which separate events become paired together. Technically the first is Pavlovian or classical conditioning. Emily's and Erin's different histories guide their reaction to flowers. The second is a powerful example of instrumental conditioning, where one evening of sickness causes Corey to stop eating in a new restaurant. Perhaps Jessica, from the third example, should have a similar avoidance response to alcohol, given that her life is falling apart before her eyes. Her behavior is still considered to be instrumental, but it has become outcome-independent or habitual.

Each of these is a familiar example for humans, but what about other animals? Do they make the same kinds of associations? This entry summarizes some of what comparative psychologists have learned about the role of associative learning in animal behavior over the last 120 years since Thorndike's (1898) PhD dissertation and Pavlov's (1927) discovery of classical conditioning. The review that follows draws from several chapters in Papini (2008).

## Basic Concepts in Associative Learning

The importance of Thorndike's PhD dissertation can hardly be overemphasized (Boakes, 1984). Thorndike is credited with bringing the study of instrumental conditioning into the laboratory. In addition, his research had a comparative emphasis. At about the same time, Pavlov (1927) was developing a training method that allowed for an objective assessment of an animal's ability to make predictions about impending events. Both Thorndike and Pavlov opened the way for a scientific study of associative learning and also established the foundation for the two forms of conditioning, instrumental and classical, respectively, that together have shaped the field. Let's start by comparing these two forms of conditioning.

The environmental conditions in which animals live vary in the extent to which they can

control them by means of their own behavior. At one extreme are situations in which the environment changes independently of the animal's actions (e.g., daily light cycles, seasonal food availability). New events may also arise as unexpected outcomes of the animal's own behavior. A foraging animal may come across a new source of food or be the target of intense aggressive behavior after stepping into the territory of a conspecific (e.g., another male of the same species). Although an animal may have no control over the situation, it can still learn to use cues and signals that predict biologically relevant events – this is called *classical* or *Pavlovian conditioning*. As a result of such learning, a signal associated to food may induce salivation and approach responses in later encounters, whereas a clue that a conspecific is present in the vicinity may elicit freezing or avoidance responses. At the other extreme are situations in which the animal's own behavior leads to resources such as food, water, and mates. This behavior is influential in the sense that it guides the animal toward or away from significant resources – this is called *instrumental* or *operant conditioning*. In this entry, associative learning and conditioning will be considered synonyms.

Three distinctions must be kept in mind when discussing associative learning: learning versus performance, procedure versus process, and phenomenon versus mechanism. We discuss each of them next.

## Learning Versus Performance

Associative learning involves the short-term acquisition, long-term storage, and retrieval of information about events that occur in close temporal or spatial *contiguity*. Although contiguity is generally necessary for associative learning to occur, some violations are known. For example, events separated by long intervals may be associated, whereas perfectly contiguous events may fail to be associated. Conditioned taste aversion after, say, pairings between the taste of saccharin and the administration of a toxin like lithium chloride (inducing gastrointestinal discomfort),

is an example of conditioning that can occur with long temporal delays between these events (Reilly and Schachtman 2009). The blocking phenomenon, that is, a stimulus reinforced in compound with a previously trained stimulus often controls little responding by itself in subsequent testing, provides an example of an apparent failure of acquisition despite temporal contiguity (Kamin 1969). *Short-term acquisition* implies an information gain through experience. *Long-term storage* refers to the consolidation of acquired information into a stable neural record. *Retrieval* refers to the reactivation of information previously consolidated into long-term storage.

A key assumption underlying this definition of learning is that learning is not the same as performance or behavioral change. Learned information can potentially change behavior, but the effect may not be immediate. A classic demonstration of this *learning-performance dichotomy* is provided by *latent learning* (Tolman and Honzik 1930). Rats preexposed to a complex maze without receiving food reinforcement explored the environment and exhibited a moderate level of behavioral change. However, when food was introduced in a goal box, preexposed animals showed faster acquisition of the correct itinerary than animals that were reinforced from the start of training. This difference suggests that preexposed animals were acquiring and storing information about the maze despite the absence of reinforcement. That information was later retrieved when food became available in the environment. Thus, although biologically salient events (e.g., food, pain) may be needed for performance, they do not appear to be required for learning to occur. The learning-performance dichotomy makes any conclusion regarding the absence of conditioning particularly problematic. Apparent failures of acquisition must be treated with caution because they may represent failures of performance. A major alternative to acquisition failure is retrieval failure, that is, the inability of the stimulus to reactivate an acquired memory, thus failing to influence behavior. Blocking is a case in point, as under some conditions, a failure of a stimulus to provoke responding when accompanied by a previously trained stimulus may reflect a

performance deficit, more than an acquisition deficit (Miller and Matzel 2006).

## Procedure Versus Process

A second distinction to be considered is that between procedure (the arrangement of events in an experiment) and process (the learning mechanism involved). Whereas classical and instrumental conditionings are easily distinguished in terms of procedures, the underlying mechanisms are more difficult to identify. Natural behavior is likely to be usually influenced by both processes simultaneously, although in the lab they can be shown to be irreducible. What are the procedural differences between these two forms of conditioning?

In a typical experiment on classical conditioning, an animal is repeatedly exposed to a sequence of two stimuli. The first is a stimulus initially neutral that has little control over the target response. This is referred to as the conditioned stimulus (CS). Using Pavlov's famous experiment, before conditioning, the metronome (the CS) elicits little or no salivation. The second stimulus is usually (but not always) a relatively intense stimulus capable of eliciting movements or autonomic responses. This is called the unconditioned stimulus (US) and the response it elicits is called the unconditioned response (UR). In Pavlov's lab, the US was usually access to food. CS→US pairings are typically presented several times within a particular session separated by an intertrial interval. Such trials endow the CS with the new ability of eliciting a conditioned response (CR). Thus, after conditioning, the metronome can elicit anticipatory salivation. The pairing of two stimuli (e.g., CS→US, CS→CS, US→US, or any similar arrangement) provides a foundation for classical conditioning.

The CS→US procedure, called *delay conditioning*, has a unique procedural property: The occurrence of the CR (e.g., salivation to the metronome) is not required for the occurrence of the US (i.e., the food). Thus, CS→US pairings are response-independent pairings, that is, they are programmed by the experimenter, irrespective of

the animal's behavior. Pavlov's dogs did not have to salivate to the metronome to receive the food; food occurred whether the dog salivated or not. This feature makes the learning-performance dichotomy especially relevant in classical conditioning. Suppose after several  $CS \rightarrow US$  pairings, the animal shows no detectable CRs, is this due to an acquisition failure or to a failure of the CS to influence behavior? Special tests may be required to detect conditioning in cases like this, such as recording physiological responses (e.g., heart rate) that may provide a more sensitive dependent measure.

In instrumental conditioning, however, reinforcement (e.g., food presentation, shock omission) depends upon the occurrence of a response. The instrumental conditioning procedure involves, therefore, response-dependent training. The terminology used in conditioning experiments depends on whether the procedure is classical or instrumental. CS, US, CR, and UR are used in reference to Pavlovian procedures, whereas discriminative stimulus ( $S^D$ ), reinforcer ( $S^R$ ), and instrumental response ( $R_i$ ) are typically used to describe instrumental procedures. The term "reinforcer" refers to the external event (e.g., food, water, electric shock), whereas the term "reinforcement" denotes the organism's reception of a reinforcer.

Miller and Konorski (1928) first noticed these procedural distinctions between classical and instrumental conditioning experiments and also suggested that the underlying processes were different. However, this hypothesis turned out to be more difficult to demonstrate. Every time an animal responds in an instrumental situation,  $S^R$  is delivered in the presence of  $S^D$ . Therefore, there is a parallel between this  $S^D \rightarrow S^R$  pairing and the  $CS \rightarrow US$  pairing of a Pavlovian situation. Classical conditioning is always embedded in instrumental conditioning, so that disentangling the two and identifying which one is the source of behavioral change can be difficult. Consider another example. Suppose you are conducting a classical conditioning experiment in which a rat receives pairings between a light (the CS) and food (the US). Every time the light is turned on, the rat orients

toward it, approaches it, and sniffs it. As the rat is sniffing the light, food is delivered according to a response-independent procedure. Does the rat sniff at the light because the light has become a Pavlovian signal for food or because sniffing is being reinforced by food? Although from your perspective this experiment involves response-independent Light  $\rightarrow$  Food pairings, from the rat's perspective it may seem as if sniffing were required for food presentations (i.e., "accidental" Sniff  $\rightarrow$  Food pairings).

A key question is whether sniffing is sensitive to the Light  $\rightarrow$  Food Pavlovian pairing or to the Sniff  $\rightarrow$  Food instrumental pairing. One way to decide between these alternatives is to introduce *omission training* on sniffing (Sheffield 1965). If a response is instrumental, then it should be sensitive to both the presentation and the omission of the reinforcer. If the rat sniffs because of Sniff  $\rightarrow$  Food instrumental pairings, then it should stop sniffing when sniffing eliminates food. Because the rat may sniff in some trials, but not in others, omission training leads to a mixture of Light  $\rightarrow$  Food trials (no sniffing) and Light-only trials (sniffing). Therefore, the omission condition must be compared with a control condition in which the rat receives exactly the same frequency and distribution of Light  $\rightarrow$  Food and Light-only trials, but independently of sniffing. This is achieved by the *master-yoked procedure* in which the behavior of one animal (the master) determines the presentation and omission of the reinforcer in its own situation and also in the situation of the other animal (the yoked). The master-yoked procedure matches the environments, but allows for variation in  $R \rightarrow S^R$  pairings, which occur only in the master's situation.

There are two possible outcomes in an omission experiment. If the behavior of master and yoked animals does not differ, then sniffing is under the control of Pavlovian Light  $\rightarrow$  Food pairings ( $CS \rightarrow US$ ) because such pairings are equated across groups. Pavlovian responses are impervious to their outcome, but sensitive to Stimulus  $\rightarrow$  Reinforcer pairings. If, however, the behavior of master animals is lower than that of yoked animals, then sniffing is under the control of instrumental contingencies ( $R \rightarrow S^R$ ).



Instrumental responses are sensitive to their outcomes (but see below).

Omission experiments show that some responses are controlled by their outcome, but others are controlled by the strength of the preceding stimulus. For example, rats exposed to pairings between a burst of White Noise (the CS) and Food (the US) exhibit an increase in the frequency of three responses during the CS: *Startle*: a sudden body movement; *Head-jerk*: head movements oriented to the food magazine; and *Magazine*: standing motionless in front of the food magazine (Holland 1979). Omission training had no effect on the startle response, an intermediate effect on head jerk responses, and a suppressive effect on magazine behavior. Therefore, some responses within the same training situation are instrumental (magazine, head-jerks) while others are Pavlovian (startle).

Whereas omission experiments demonstrate that the distinction between classical and instrumental conditioning is more than procedural, one can still ask about the reasons for these differences. Harris et al. (2013) noted that although masters exhibit less magazine than yokes, magazine behavior still increases during training. They asked whether the omission contingency reduced magazine in master animals by increasing the frequency of incompatible responses, or whether it increased magazine in yokes because of accidental pairings with food (such pairings are eliminated in masters). They tested these hypotheses by training animals in a discrimination in which one of the stimuli was master and the other yoked, but with a twist: these stimuli had a common element. If we call the stimuli A and B, then one group received  $AB \rightarrow \text{yoked}$  and  $A \rightarrow \text{master}$ , whereas the other group received  $AB \rightarrow \text{master}$  and  $A \rightarrow \text{yoked}$ . If omission (master) increases incompatible responses, then the second discrimination would be easy because such responses are associated to the unique element, B. However, if omission elevates responding in yokes because of accidental magazine  $\rightarrow$  food pairings, then the first discrimination would be easy because the unique element, B, would receive the benefit of such pairings, which could not occur in A trials because of omission. The results indicated that the first

discrimination was unsolvable, whereas the second was easy to master. Thus, there is evidence that magazine responses in master-yoked situations are reduced in masters relative to yokes not because it is an instrumental response, but because omission contingencies increase the frequency of incompatible responses.

These results have two major implications. First, even when masters perform below yokes, the response can still be Pavlovian, the difference being related to the reinforcement of incompatible responses in master animals. Second, in relatively simple situations, most behavior, even seemingly instrumental responses such as approaching a location where food delivery is impending, are controlled by preceding stimuli, rather than by ensuing outcomes. This makes behavior impulsive. As shown below, however, some behaviors are actually under the control of their outcomes, thus showing their instrumental nature (see section on “Goal-Directed and Habitual Behavior” below).

## Phenomena Versus Mechanisms

Psychologists tend to use the term “mechanism” liberally, so it makes sense to clarify it here (Bitterman 1975; Papini 2002). *Learning phenomena* are typically induced under laboratory conditions and involve a specific difference between groups or conditions in an experiment. For example, in the omission experiments described above, a distinction between master and yoked groups. The phenomenon, in this case the “omission effect” is defined by the comparison between conditions. But learning phenomena must be the result of *learning mechanisms*, that is, a set of processes intervening between environmental conditions of training and behavior. For example, the omission effect in magazine behavior was attributed to the accidental reinforcement of incompatible responses in master animals – a psychological mechanism.

The distinction between phenomena and mechanisms is relevant to comparative research on learning and cognition. Because learning phenomena are induced under laboratory conditions



and are usually defined in terms of a comparison, they are not comparable to typical biological traits such as body size. They are not even similar to behavioral traits defined in terms of their plain presence in a given species. For example, in the statement “gorillas are a polygynous species,” polygyny (i.e., a mating system in which a male defends two or more females from other males) refers to a trait present in gorillas under natural conditions. But to say that “gorillas exhibit the omission effect” would require the experimental induction of this phenomenon in a comparison between experimental and control groups. Natural observation of gorilla behavior could suggest that some aspects of their feeding behavior are controlled by current outcome value, but these observations would not demonstrate the omission effect. Therefore, because learning phenomena are not directly observable in the natural behavior of individual animals, any reference to the evolution of learning needs to center on learning mechanisms. Learning phenomena are the arena allowing comparative psychologists to understand how brain processes produce behavioral outcomes involving learning. Learning mechanisms are those processes that intervene between the external conditions (inputs) and the behavioral responses (outputs).

A clear understanding of the concept of mechanism has far-reaching implications, from an understanding of comparative research on learning and cognition to the development of animal models of human psychological disorders. Species similarities in learning phenomena of interest to both comparative and animal-model research hinge upon the evolutionary concepts of homology (similarity due to inheritance from a common ancestor) and homoplasy (similarity due to common selective pressures, but evolving independently). Although traditionally comparative psychologists have relied heavily on behavioral similarities across species, a growing understanding of the neural processes underlying learned behavior together with advances in neuroscience methods is opening the door to a more complex view of the concept of mechanism. Species similarities in learning phenomena need to be assessed in at least four mechanistic levels before the issue

of homology vs. homoplasy of learning mechanisms can be resolved (Papini 2002): psychological, neurobiological, neurochemical, and cell-molecular levels of analysis. The next paragraphs describe these levels.

The *psychological level* is the traditional level of analysis developed by comparative psychologists and involves such concepts as  $S \rightarrow S$  associations, attentional decrement, and stimulus generalization, among others. The methodology involves the dissection of effects through experimental designs involving different conditions of training. These concepts apply specifically to an understanding of learning and provide a guide to interpret the effects of behavioral manipulations at lower levels of analysis (Bitterman and Woodard 1976). Without a psychological theory, any description of the effects of brain manipulations on learning would be restricted to presence-absence statements (e.g., “this drug affects learning”). With the guidance of a psychological theory, these descriptions can be more specific (e.g., this drug interferes with memory retrieval, but not memory consolidation).

The *neurobiological level* is the level of brain circuits. An explanation of conditioning at this level requires specifying the architecture necessary for a circuit to detect  $CS \rightarrow US$  contiguity. The methodology involves lesions and stimulation of various brain regions to determine those that are involved in a given learning phenomenon. Coincidence detectors in the amygdala, hypothesized to underlie fear conditioning, are an example of a neurobiological mechanism of learning. These are brain sites in which pathways carrying information from the CS and US converge into individual neurons. Such convergence seems to be necessary for establishing  $CS \rightarrow US$  associations.

The *neurochemical level* refers to synaptic processes. Convergent pathways involved in conditioning contain many synapses that show plasticity. Synaptic plasticity is necessary for detecting coincidences such as those involving  $CS \rightarrow US$  pairings. The main methodology for studying the neurochemical basis of learning involves the administration of drugs that affect synaptic transmission, whether systemically or in

specific brain locations. Synaptic properties can also be altered by genetic manipulations. For example, gene knock-out and transgenic manipulations are used to eliminate a specific synaptic receptor.

The *cell-molecular level* includes processes occurring inside neurons that are responsible for short- and long-term cellular changes involved in learning. A major example of such processes is a second-messenger cyclic adenosine monophosphate, or cAMP (neurotransmitters are known as the first-messenger system). Second messengers are part of a cascade of cytoplasmatic changes induced by neural activation that have the property of opening some ion channels, thus modifying synaptic conductivity. Second messengers can also influence gene transcription in the cell nucleus, initiating or terminating protein production. Because gene transcription and protein synthesis are implicated in long-term memory processes, second-messenger systems play an important role as a cellular substrate of learning.

These mechanistic levels provide a criterion for assessing the homology vs. homoplasy question. If, for example, two species exhibit a similar learning phenomenon and its analysis were to demonstrate the same underlying mechanisms at all four levels, then the hypothesis of homology would be considerably strengthened. If, by contrast, different underlying mechanisms were found in at least one level of analysis, then the hypothesis of homoplasy would gain support. Although a priori this criterion seems straightforward, in reality, this would require quite an extensive line of work. As a result, the paucity of data is no surprising. However, there are some promising examples that carry the analysis into at least one level. For example, avoidance learning seems to depend on the amygdala (or its homologous structure) in rodents (Choi et al. 2010), toads (Puddington et al. 2016), and goldfish (Portavella et al. 2004). However, because these experiments were not done within the framework discussed above, their procedures are not sufficiently analogous to be on safe ground. Still, the results are consistent with homology at the neurobiological level in avoidance learning among species from three different vertebrate classes. This problem is

further treated below, but first we acknowledge some complexities of the conditioning process.

## Complex Conditioning Phenomena

Conditioning phenomena display an impressive range of complexity. From the relatively simple delay conditioning procedure developed by Pavlov (1927), some amazing capacities have been uncovered. Three such capacities will be highlighted here. First, there is extensive evidence showing that animals respond to a CS because it activates a representation of the US and its current value. These demonstrations have been based on several procedures for the post-conditioning devaluation of the US. The rationale of this *US-devaluation effect* goes like this. During conditioning, CS→US pairings endow the CS with the ability to activate a representation of the US, which then triggers the CR. Thus, devaluation of the US representation after conditioning can change the CR. In one experiment (Holland and Rescorla 1975), rats were exposed to Tone→Food pairings, and when they were responding to the Tone, they received separate Food→Rotation pairings. Rotation activated vestibular receptors in the inner ear and produced an aversive effect. Such pairings were designed to modify the incentive value of the Food from an appetitive into a less appetitive or even aversive stimulus. Finally, rats were exposed again to the Tone, and they showed reduced responding compared to groups that had received unpaired presentations of Food and Rotation. This US-devaluation effect, which has been generalized to a variety of situations, shows that activation of the US representation when it has become less appetitive now fails to control similar levels of performance to those of control groups.

Animals apparently can also associate actual events with the reactivated representation of an absent event (Holland 1981). Rats exposed to Tone→Food pairings were later given pairings between the same Tone and a toxin that produces gastrointestinal discomfort (lithium chloride, LiCl). Thus, if the Tone reactivated a representation of the Food when the animal was made sick

by LiCl, that Food representation would be paired with sickness and, as a result, the animal should develop an aversion to the Food. Subsequent tests showed that rats consumed significantly less food than in a variety of control conditions. This phenomenon, known as *representation-mediated learning*, suggests that the representation of a stimulus has similar properties as its presentation.

Finally, a phenomenon known as *occasion setting* suggests that a stimulus (called an occasion setter, OS) may be associated not just with another stimulus (as shown by the US-devaluation effect), but with a [CS→US] association as a whole (Schmajuk and Holland 1998). The idea is that the OS bears a hierarchical relationship to a [CS→US] unit, rather than linking directly to just the CS or the US. OSs are typically diffuse stimuli lasting longer than CSs that do not acquire the capacity of eliciting responses by themselves; however, the animal responds to the CS only when this is presented in the context of the OS, so they can instigate responding. Furthermore, the simple presentation of the OS by itself, an operation analogous to extinction, does not affect its ability to influence the CS.

These complex effects highlight a major point about conditioning: with a seemingly simple mechanism (associative links), the brain can produce relatively complex outputs. Associative learning is sometimes dismissed on the assumption that it cannot possibly provide a workable explanation for complex behavior – an assumption that needs to be considered carefully in specific cases.

## Goal-Directed and Habitual Behavior

Behavioral change occurs when signals and responses are paired with outcomes. For example, Jessica (from one scenario presented in the introduction) learned to seek out for alcohol because of its taste, the social context accompanying alcohol drinking, and alcohol's ability to reduce negative emotions. These kinds of acquired behaviors, that is, those that occur as a result of seeking a favorable outcome, are referred to as *actions*. The main property of actions is that they are outcome-

dependent behaviors – behaviors controlled by current outcome value. However, Jessica's relationship with alcohol changed in time. Instead of alcohol intake always producing favorable consequences like it did in the beginning, Jessica's life is being taken over by the drug. Even in the face of losing jobs and friendships, she is unable to control her alcohol intake. Acquired behaviors that persist despite being followed by negative consequences are called *habits*. An important property of habits is that, at least in the short term, they are outcome-independent behaviors – behaviors controlled by preceding stimuli, rather than by outcomes. Under some conditions, extensively practiced actions tend to become habits, with the outcome guiding behavior early on and habitual patterns becoming “automatic” responses to stimuli or situations later on.

Understanding the transition from action to habit is relevant to the treatment of several psychological disorders. For example, substance use disorders, obesity, and compulsive behavior each have a learning component and are difficult to treat even in clinical settings. After extensive practice, typical actions such as magazine approach in rats or sharing an after-work drink in people can become automatic habits. In extreme cases, strongly ingrained habits may prevent a person to live a normal life. Once these addictive behaviors are habitual, they are insensitive to even the most aversive consequences, even when repercussions include a person's health and social life, job security, and legal status (Hogarth and Chase 2011).

In the laboratory, testing to determine whether a behavior is an action or a habit can be done using a number of reward devaluation procedures. An outcome-dependent behavior should be influenced, for example, by the organism's motivational level or by knowledge of the current value of the outcome. One way to modulate motivational levels in the laboratory is by using a satiation manipulation. If rats are instrumentally trained to work for food, food-deprived animals would show faster changes in behavior than free-fed animals. Organisms that are not hungry will not be as motivated to respond as hungry animals when working to obtain food.

Another procedure used to differentiate between actions and habits in the laboratory is to alter the value of the reinforcer by associating sickness with the outcome of a behavioral response either early or late in training. Adams (1982) used sickness to devalue the food outcome at different points in training to better understand habit formation. When food was paired with the toxin lithium chloride to make rats sick after eating, early in training they were less likely to press a lever previously associated with food. This result suggests that lever pressing during early training was dependent on their memory of the current value of the food. However, when the same toxin was administered after extensive training, animals responded to the lever as much as controls. The persistent behavioral response to work for food that had made the rats sick implies that, late in training, lever pressing was less dependent upon current reward value or, in other words, that this behavior had become habitual. It is likely that this shift from action to habit also involves a change in the underlying circuitry controlling behavior (Balleine and O'Doherty 2010; Gasbarri et al. 2014). For example, in rats, lesions of the dorsomedial striatum leave the animal less sensitive to outcome devaluation (suggesting this area is important for actions), whereas lesions of the dorsolateral striatum make behavior more vulnerable to outcome devaluation even after extended training (suggesting this area is important for habits).

Habitual behavior that seems to be independent from current outcome value is typically observed in nonmammalian vertebrates in situations involving reward devaluations. For example, toads trained to traverse the length of a runway to access a large amount of water typically acquire this behavior faster than toads reinforced with a small amount of water. This demonstrates that different reward magnitudes can affect their instrumental behavior. However, after a devaluation from a large to a small reward, toads simply adjust their instrumental behavior, instead of rejecting the smaller reward (Muzio et al. 2011). Placed under similar conditions, mammals tend to reject the devalued reward (Papini 2014). One possible interpretation of these results is that the

behavioral flexibility shown by toads in learning situations is based on habit formation, whereas that exhibited by mammals can be action or habit learning depending on the conditions of training.

## Species Similarities and Differences in Learning Phenomena

The emphasis on mechanistic levels suggested above leads to a rule that can be applied to postulate homologies and homoplasies in learning mechanisms across species (Papini 2002). Homology requires that learning phenomena observed in two different species are dependent on the same mechanisms at all levels of analysis (i.e., manipulations of training parameters, neurobiological structures, neurochemical systems, and cell-molecular processes). One would expect that homologous learning phenotypes would be more likely in closely related species. By contrast, homoplasies should be more common among distantly related species. Advances in molecular genetics since the 1980s have uncovered an unexpected degree of homology even among distantly related species (see Papini 2008). Phenotypic change is often achieved by the recruitment of old genes and molecules in the organization of new structures and functions. What are the implications of these discoveries for an understanding of learning?

Notice that mechanistic levels are hierarchically nested. Thus, a specific cell-molecular module may be activated by the operation of different neurotransmitters, in different neurobiological sites. If molecular mechanisms are generally conservative, as suggested by genetics, then one would expect a relatively stable set of cell-molecular processes involved in learning even among distantly related species. One implication is that parallel evolution of learning mechanisms should be relatively common among animal species. Constraints on the ability of molecular pathways to induce synaptic plasticity at lower mechanistic levels may result in the parallel evolution of similar learning capacities at the behavioral level. Similar learning phenomena in

different species (or in the same species, but across different conditions) may be based on different neurotransmitter systems and yet share the same cell-molecular processes for synaptic plasticity. The task for comparative psychologists is to determine whether species similarities in learning phenomena are superficial (homoplasy), based on common cell-molecular processes even if involving different processes at the neurobiological or neurochemical levels (parallel evolution), or indeed based on the same mechanisms at all four levels of analysis (homology).

When different learning phenomena are found in different species, the key question is whether the underlying mechanisms (as defined above) have diverged and the main alternative hypothesis maintains that the behavioral differences are caused by differences in contextual mechanisms. Contextual mechanisms are processes other than learning that can also affect behavior, including sensory-perceptual processes, motivation, and motor control (Bitterman 1975). Going back to our earlier scenarios, Corey may stop eating burritos in that particular restaurant because he acquired an aversion or because he is not hungry or does not know how to get to that restaurant. Such *contextual variables* can influence behavior independently of learning. Therefore, species differences in learned performance must discard alternative accounts based on the action of contextual variables before a hypothesis of a divergence in learning mechanisms can be accepted. This is the learning-performance dichotomy applied to species comparisons.

A major obstacle for comparative research on learning originates in the impossibility of equating contextual factors across species. For example, if rats and turtles are reinforced with three food pellets for traversing a runway and rats show better performance, is it because the rat's learning mechanisms are more efficient or because three pellets have a greater motivational impact for the rats than for the turtles? Perhaps turtles reinforced with six pellets would perform at the same level as rats. It is virtually meaningless to compare different species in absolute terms. The approach favored by comparative psychologists consists of comparing species in terms of how their behavior

in analogous situations responds similarly to similar manipulations of training variables. Thus, instead of asking whether the rat learns the runway task faster than the turtle, one would ask whether runway learning depends on the same set of variables in rats and turtles. For example, although rats and turtles may perform at different speeds, acquisition may improve in both species as reinforcer magnitude increases. This direct relationship between acquisition rate and reinforcer magnitude implies that depending on the training parameters, acquisition may be faster in rats or in turtles. This method is called *control by systematic variation*. Variables suggested by empirical or theoretical considerations to be important determinants of learned behavior, such as reinforcer magnitude, can be systematically manipulated across species to determine whether the behavioral adjustments are similar or dissimilar.

Discovering homologies/homoplasies in learning mechanisms requires extensive analysis of similar learning phenomena across species, at all levels of analysis. However, discovering divergence in learning mechanisms across species requires extensive analysis of the potential role of contextual factors in the target learning phenomena, in each species. It is no surprise that the comparative analysis of learning, from an evolutionary perspective, is at the beginning of the twenty-first century still in its infancy.

## Problem Solving

As shown above, associative learning involves a wide range of phenomena, from simple to complex, and it is also dependent on a diversity of mechanisms. But is conditioning, with all its complexity, sufficient to account for complex cases of behavior? This question has been pursued in the context of problem-solving behavior – the ability displayed by animals when placed in situations requiring novel and even creative behavioral strategies.

The work of Thorndike (1911) and Köhler (1925) gave rise to an influential controversy about the nature of learning. Thorndike's (1898)



experiments on the acquisition of new skills by a variety of species led him to suggest that learning progressed gradually as a result of a trial-and-error process – instrumental conditioning. For example, cats exposed to a puzzle box, in which the operation of a latching device allowed them to open the door and have access to food, showed a gradual decline across trials in the time taken to open the door. This view was contradicted by experiments that showed that animals can acquire a new skill suddenly and abruptly by *insight learning*. Köhler (1925) reported experiments with chimpanzees in which, as in Thorndike's puzzle box situation, access to a piece of food required a relatively complex sequence of responses. In a famous experiment, a male chimpanzee named Koko was shown an unreachable piece of fruit hanging from the ceiling of his cage, together with a familiar small box. Initially, Koko displayed attempts at reaching the fruit, but paid no attention to the box. After a few trials, Koko exhibited a variety of behaviors toward the box: he threw it, sat on it, and directed violent attacks to it. In a subsequent session and after a few unsuccessful attempts at reaching the fruit, Koko turned toward the box, seized it, dragged it beneath the fruit, stepped on it, and took the fruit. Koko and other chimpanzees used by Köhler exhibited insightful behavior only after extensive practice with all the elements involved in the problem-solving situation.

Consider again the insight situation, only this time with a pigeon as the subject. Epstein (1987) separately trained four different responses by reinforcing each with food according to regular procedures of instrumental shaping. The pigeon was trained to push a small cardboard box toward a green spot on the floor, to open the door of an enclosure, to step on a cardboard box fixed in a particular location, and to peck at a plastic banana. Only the object appropriate to the performance of the response being shaped was present during a given session (e.g., the cardboard box when reinforcing pushing). In a test session, the movable box was placed inside the enclosure and the banana suspended out of the animal's reach and over the test apparatus. The pigeon started by stretching toward the plastic banana, then it approached and pecked the door until it opened,

and about a hundred seconds into the session, the pigeon started to push the cardboard box that had been placed inside the enclosure in the direction of the plastic banana. When the box was about midway between its original position and the plastic banana, the pigeon stepped on it and stretched toward the plastic banana, but it could not reach it. Finally, the pigeon pushed the box a bit further, climbed on it, and pecked at the plastic banana. The entire sequence took 237 s. Although the individual components of this response sequence were trained in isolation, the test situation induced their spontaneous interconnection.

The outcome of this experiment with a pigeon is reminiscent of Koko's insightful problem-solving behavior and suggests that such a capacity is not restricted to primates. But do these animals understand that moving the box will allow them to stand on it right underneath the fruit and thus obtain a reward? If they understand the nature of the problem, then a pigeon trained as described and given a choice between two similar boxes would push the one on which it can stand (the other, nonfunctional box lacked the top surface). Cook and Fowler (2014) replicated Epstein's results, but also showed that pigeons would push either box underneath the unreachable target, thus suggesting they did not understand that stepping on the box was a means to reach the target.

A number of training paradigms have been developed that exploit the ability of animals to transfer previously acquired information into new situations. These paradigms illustrate the effects of extensive problem-solving training on the adjustment to new situations in a more systematic fashion than that characterizing the experiments reviewed above. In the *learning set* paradigm, animals are trained in a sequence of simple discriminations, each one involving a pair of stimuli. In each case, choice of one of the two stimuli is reinforced with food, whereas choice of the other is not reinforced. While the resolution of the initial discriminations is achieved gradually by a process of trial-and-error, eventually the animal's behavior can become insightful. A sophisticated animal facing a new two-choice discrimination after having successfully solved many similar problems may behave as if it were



following a *win-stay, lose-shift rule* (Harlow 1949). A reinforced choice implies that the other option is not reinforced and therefore it should keep choosing the same stimulus in future trials (i.e., win-stay). By contrast, a nonreinforced choice implies that choosing the other option will be rewarded (i.e., lose-shift).

Learning-set studies confirmed the importance of contextual variables. Rats trained to discriminate between two-dimensional visual stimuli perform poorly, even after hundreds of problems, but with tridimensional visual stimuli, spatial locations, or olfactory stimuli their performance is comparable to that of primates. Therefore, the performance of any given species in the learning set paradigm reflects not only learning skills, but also the animal's efficiency at representing the stimuli involved in the task. Such sensory-perceptual contextual factors may be responsible for the correlation between learning set performance and neocortical size reported in a large study involving primates (Rumbaugh and Pate 1984).

These experiments on discrimination learning illustrate a major point in learning theory, namely, that the development of complex problem-solving skills, including rule learning, is the ending point of a long history that starts with conditioning. Animals that have been exposed to a wide variety of situations and problems become capable of achieving new levels of processing that appear to be beyond associative learning, such as making inferences and developing rules. Rules are efficient ways of short-cutting what would otherwise be a lengthy accumulation of experience through trial-and-error. From the perspective of such cognitive processes, associative learning becomes a contextual factor. Attempts at showing such capacities must demonstrate that the behavior under study cannot be accounted for in terms of associative learning.

## Conclusions

Three scenarios were suggested at the outset to illustrate instances of associative learning. For Emily and Erin, the same object (flowers as a

present for Emily) was positive or negative depending on their prior experience. Signals for positive or negative events (e.g., food and pain) can become themselves positive and negative, and, in such capacity, they can operate as conditioned reinforcers. Corey had a negative experience in a restaurant and that shifted him to an avoidance mode for that location. Negative events can lead to escape and avoidance conditioning, a type of learning that has obvious protective effects, but can also lead to maladaptive behavior, as when a person suffers from a phobia – an extreme fear response to an object (e.g., spiders) or situation (e.g., outdoors). Jessica represents the opposite extreme. She has negative experiences related to an alcohol addiction, but the pulling from signals of alcohol is so powerful that her behavior has become automatic. In a sense, Jessica suffers from impaired avoidance learning.

These examples illustrate the widespread reach of associative learning processes that affect the behavior of organisms. Although they are represented here in terms of human behavior, many of these effects have been demonstrated in experiments with other species, including what might be considered relatively simple species based on behavior and neural organization. It is impossible to cover all relevant topics on associative learning in one encyclopedia entry, so readers are encouraged to search for other entries and additional related readings for a deeper understanding of learning phenomena and mechanisms.

## Cross-References

- [Associative Learning](#)
- [Associative Mechanisms](#)
- [Constraints on Learning](#)
- [Delay of Reinforcement](#)
- [Discrimination Learning](#)
- [Extinction in Learning](#)
- [Incentive Relativity](#)
- [Instrumental Learning](#)
- [Latent Learning](#)
- [Law of Effect](#)
- [Learning](#)
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- [Memory](#)
- [Partial Reinforcement Extinction Effect](#)
- [Passive Avoidance Learning](#)
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- [Reference Memory](#)
- [Reinforcement](#)
- [Reversal Learning](#)
- [Schedules of Reinforcement](#)
- [Stimulus Control](#)
- [Transfer of Learning](#)

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## Associative Mechanisms

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## Synonyms

[Associative learning](#)

## Definition

An association refers to a connection between concepts, ideas, events, and mental states. Associations usually develop through specific experiences or observations. Associations first became a philosophical topic with Plato and Aristotle in 350 BCE. Later, the English empiricists revived the idea and applied it to their explanations of behavior, thought, and memory. In modern psychology, associations play a role in Pavlovian and operant conditioning (aka instrumental learning). The ability to form associations between neutral stimuli and biologically relevant stimuli or events was likely a key behavioral influence in early

evolution. Associative learning has been established across a wide range of vertebrates and invertebrates. More recently, the study of associative mechanisms has been extended to include connectionist neural networks and modern cognitive and behavioral neuroscience.

## Aristotelian Associations

The idea that specific laws govern the formation of association in the mind began with Aristotle in 350 BCE. They included the laws of contiguity, similarity, and contrast. Aristotle posited that memory (and, by extension, thought) depends on the ability to form such associations. He also argued that any animal that can perceive time is capable of memory and, therefore, of forming associations.

**The law of contiguity** states that two events or thoughts that regularly occur close together in time or space will become associated, making it easier to recall one in the presence of the other. A common example is the tendency to think of thunder whenever there is lightning because both tend to occur close together in time.

**The law of similarity** states that when two events or thoughts are similar to each other, the presence of one will tend to lead us to recall the other. For example, when we are offered a cup of coffee, we may also think of tea because they are similar.

**The law of contrast** states that the presence of one event or thought may bring up the memory of its direct opposite. When we hear the word “dog,” we also think of “cat.”

Aristotle’s laws of association would become the basis of modern learning theories for over 2000 years (Henley 2019). They provided a foundation for the British empiricists of the seventeenth and eighteenth century. Later, they would become the root of early twentieth-century psychological philosophies of associationism, behaviorism, psychoanalysis, and structuralism (e.g., Pavlovian associative learning, Watson’s stimulus-responses psychology, Skinner’s instrumental conditioning, Freud’s word association exercise, and Titchener’s interaction of mental elements). Today,

these same basic laws can be found in the modern study of memory, learning, and modern behavioral neuroscience.

## Associationism and the British Empiricism Movement

Associationism is a theory that defines the association as the fundamental construct of higher mental experience. Although its bottom-up approach emphasizes associative learning, it extends beyond the simple association to place associations at the core of mental reasoning. It attempts to explain complex ideas from smaller experiential units through mental association. Throughout the Age of Enlightenment, accepting simple associative learning as a core feature of thought did not necessarily preclude acceptance of the entire theory of associationism.

British empiricism was a major philosophical movement during the seventeenth and eighteenth centuries that began with Sir Francis Bacon (b.1561–d.1626). Bacon argued that only through direct observation could the truth (aka facts) be discovered. Bacon's (1620/1902) empiricism meant that only inductive reasoning could produce overarching knowledge and that only through rigorous scientific practice would the acquired knowledge lead to a better society. His emphasis on observation and empirical evidence laid the foundation for a more inductive approach to knowledge upon which the empiricists would develop their own views on associations.

**Thomas Hobbes** (b.1588–d.1679). Following in Bacon's footsteps, Hobbes, a contemporary of Galileo and Descartes, became known as the founder of the British empiricism movement (Henley 2019). Although he favored deduction over Bacon's induction, he too emphasized experience. It was Hobbes who brought back Aristotle's laws of association, even adding several of his own, including the laws of cause and effect, and resemblance. Many subsequent empiricists accepted the notion of the association as the basis of complex thought.

**John Locke** (b. 1632–d.1704) would have the greatest influence on the empiricism movement

and on his contemporaries. In his treatise, *An Essay concerning Human Understanding* (1689/1824), he too rejected nativism, and described the mind as a blank slate, or *tabula rasa*, upon which experience and observation established the ideas and concepts of human knowledge. Although he rejected formal associationism, he later argued that simple ideas could be associated in the mind and formed into more complex ideas.

Simple ideas, the materials of all our knowledge are suggested and furnished to the mind. . .by sensation and reflection. When the understanding is once stored with these simple ideas, it has the power to repeat, compare, and unite them, even to an almost infinite variety, and so can make. . .new complex ideas. (Locke 1689/1824)

However, Locke distinguished between natural associations and accidental associations that he said explained faulty logic that opposed reason. He suggested spurious associations, formed only as a result of contiguity, produced superstitious beliefs, such as aversions to foods, activities, or even a fear of the dark.

The ideas of goblins and sprites have really no more to do with darkness than light: yet let but a foolish maid inculcate these often on the mind of a child, and [...] he shall never be able to separate them again so long as he lives, but darkness shall ever afterwards bring with it those frightful ideas [...]. (Locke 1689/1824)

These same "spurious" associations would later be recalled to form the basis of Pavlov's associative learning over a century later.

**George Berkeley** (1685–1753) was an ordained Irish deacon of the Anglican Church who opposed materialism altogether. For Berkeley, the increasing reliance on materialism threatened the position of God in the understanding of the human mind. He challenged Locke's view by arguing that experience was nothing more than a collection of perceptions. Still an empiricist, who agreed that knowledge is constructed from ideas, Berkeley used associations to explain the reconstruction of objects in the mind. He proposed that each sensory system provided distinct, perceptual information about an object. Vision, smell, touch, hearing, and taste provide only pieces of information connected to an object. Repeated experiences

provided the opportunity to associate these distinct parts into a meaningful whole in the mind. For Berkeley, the objects that we perceive are simply associated aggregates of individual perceptions.

**David Hume** (1711–1776) was a Scottish philosopher who followed in the empirical traditions of Bacon, Hobbes, and Locke. He too believed that the content of the mind derived from experiences. Like George Berkeley, he believed that experiences were nothing more than perceptions—that we have no direct physical contact with the world. Nevertheless, these perceptual experiences provide the basic building blocks of complex ideas.

Hume was a true proponent of associationism; he viewed associations as the force behind the development of highly flexible ideas. Hume emphasized three laws of association: (a) the law of resemblance, defined as the tendency to associate events or thoughts that are similar to each other; (b) the law of contiguity, defined as the tendency to associate event or ideas that occur together in space or time; and (c) the law of cause and effect, defined as associations between an outcome and the events that precede it.

Other empiricists added to the debate on the role of associations in human knowledge, thinking, and behavior. **David Hartley** (1705–1757) proposed that all behavior begins as a reflex. Involuntary behaviors gradually become associated with specific ideas or stimuli that acquire the ability to elicit the behavior in a manner that again foreshadowed the work of Ivan Pavlov a century later. **James Mill** (1773–1836) introduced the idea of the strength of an association. He argued that frequency and vividness played a role in determining the strength of an association. For **Alexander Bain** (1818–1903), the mind consisted of feelings, volition, and intellect. He suggested that the law of contiguity governed the associations that linked these three mental aspects with behavior. “Actions, sensations and states of feeling, occurring together, or in close succession, tend to grow together, or cohere, in such a way that, when any one of them is afterwards presented to the mind, the others are apt to be brought up in idea” (Bain 1855, cited in Harned 1985).

## Russian Medicine, Physiology, and Associations

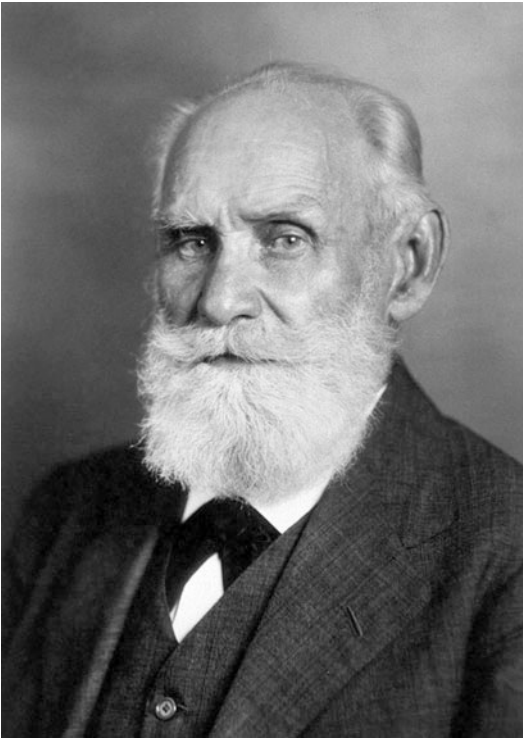
By the middle to late nineteenth century, philosophical support for “association formation by means of contiguity” had spread throughout Western Europe. But in Russia, a brewing discontent with philosophy led to its prohibition in institutions of higher learning. According to Nemeth (2001), the ideas of social reform associated with the European Age of Enlightenment led to revolts that threatened the Russian autocracy. In 1848, Czar Nicholas I censored the teaching of philosophy in all institutions of higher education in an attempt to protect Russia from “intellectual infection.” Although psychology was still allowed, the moratorium on philosophy remained intact until 1863, and did not begin to recover until 1889 (Koretzky 2013; Nemeth 2001).

**Ivan M. Sechenov** (1829–1905). Despite the censorship on the teaching of Western philosophies, progress in medicine and physiology prevailed in Russia. Sechenov (1863), promoted a purely mechanistic version of overt and mental behavior. In his account of mental life, he argued that all behavior was reflexive. The difference between humans and animals was that human reflexes could be elicited by thoughts. Initially perceived as a serious potential threat to the censorship on philosophy, the Russian courts ultimately decided that his work was presented as pure science, and as such did not technically violate the moratorium on revolutionary philosophical ideologies because of its mechanistic approach (Koretzky 2013). This opened the door for his student Ivan Pavlov to begin his investigations into the conditional nature of reflexive salivation.

## Pavlov’s Associative Learning

**Ivan Petrovich Pavlov** (1849–1936) was a Russian physiologist and student of Sechenov. His research cemented a permanent place for the “association” in modern animal learning and prompted the rise of behaviorist learning theory in American psychology (see Fig. 1). His classical conditioning method (see Fig. 2) provided a



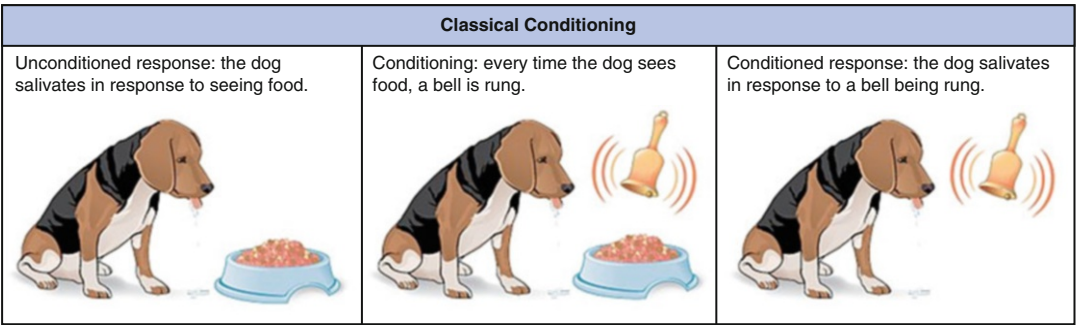


**Associative Mechanisms, Fig. 1** Ivan Petrovich Pavlov (Public Domain). (Photograph of Ivan Pavlov. Photographer unknown. This image is in the public domain. Retrieved from [https://en.wikipedia.org/wiki/Ivan\\_Pavlov#/media/File:Ivan\\_Pavlov\\_NLM3.jpg](https://en.wikipedia.org/wiki/Ivan_Pavlov#/media/File:Ivan_Pavlov_NLM3.jpg))

paradigm for the development of concrete, measurable associations between a neutral stimulus and a biologically relevant stimulus. In his seminal work on the salivary reflex in dogs, Pavlov surgically implanted a cannula next to the oral salivary gland so he could directly observe salivation during his experiments. He noticed that the dogs would begin to salivate prior to the introduction of food into the mouth. Merely the sight of the food was sufficient to produce salivation. This observation led him to experiment with other stimuli such as a metronome and tuning forks. In each case, he reported that after repeatedly presenting an otherwise neutral stimulus prior to the introduction of food, the stimulus would gradually begin to elicit “psychic secretions” (Domjan 2015).

Pavlov called these responses *conditional reflexes* because their ability to elicit salivation was conditional on the formation of a neural connection or association between the neutral stimulus and the reflex’s biological releaser. Being a physiologist, his explanation for classical conditioning hinged on a neural process in which a neutral stimulus (NS) could become a substitute for the unconditional stimulus (US, or natural elicitor of the reflex).

According to this view (see Fig. 2), the US naturally stimulates the US brain center



**Associative Mechanisms, Fig. 2** Diagram of Pavlov’s classical conditioning method. A neutral stimulus (NS: bell) is paired with a biologically relevant, unconditioned stimulus (US: food). Food naturally elicits salivation in dogs; bells do not. However, after repeated NS/US pairings, an association between the NS and the US develops, such that the bell alone (now a conditioned stimulus or CS) will elicit salivation on its own. This

image is licensed under the Creative Commons Attribution 4.0 International license. (A diagram demonstrating unconditioned, neutral, and conditioned stimuli as well as unconditioned and conditioned responses in Ivan Pavlov’s research on digestion, Salehi, S. Attribution-ShareAlike 4.0 International (CC BY-SA 4.0), Retrieved on Jan 17, 2019 from: [https://upload.wikimedia.org/wikipedia/commons/0/0a/Classical\\_Conditioning\\_Diagram.png](https://upload.wikimedia.org/wikipedia/commons/0/0a/Classical_Conditioning_Diagram.png))



responsible for producing the unconditioned reflex (UR). The introduction of a NS simply stimulates only the brain regions that process that information. However, over many contiguous pairings of the NS and US together, a neural connection or association develops that gradually allows the previously NS to directly stimulate the US brain center. The result is that the NS is no longer neutral (with respect to the reflex). It has become a conditional stimulus that could now directly produce the reflex (now called a conditional response or CR). This explanative reasoning became known as Pavlov's stimulus substitution theory. His reasoning formalized a physiological mechanism for the formation of an association. His work legitimized the study of reflexes in Russia and initiated empirical/behavioral investigations into the associative processes responsible for simple learning.

In 1903, Pavlov presented his preliminary findings in a lecture at the 14th International Medical Congress in Madrid, Spain (Bandrés and Llavona 2003) entitled *Experimental Psychology and Psychopathology in Animals*. In 1904, Pavlov earned a Nobel Prize for his work in physiology, becoming the first Russian scientist to receive a Nobel award. In his acceptance speech, he foreshadowed John B. Watson (1913), calling for a more empirical, scientific psychology (Fig. 3).

Only by observing this condition would the results of our work be regarded as fully conclusive and as having elucidated the normal course of the phenomena. (Pavlov 1904)

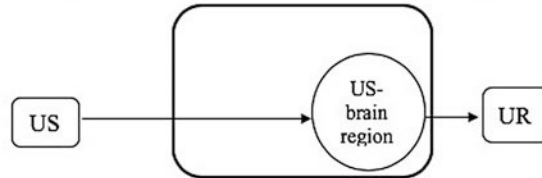
After publishing his findings in English (Pavlov 1924), Pavlov's findings spread throughout the European and American psychological community. Associative learning would go on to

# Associative Mechanisms,

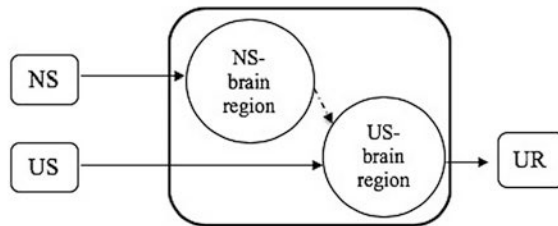
**Fig. 3** Pavlov's stimulus substitution theory explains the underlying neural mechanisms responsible for associative learning. (This is my own diagram. No permissions required)

## Stimulus Substitution Theory

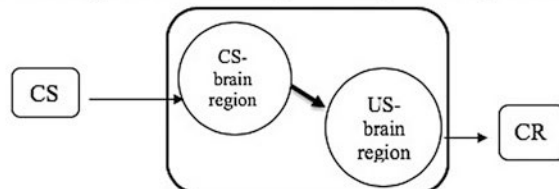
a) US activation of US brain region leads directly the UR



b) Pairing of NS and US activates both regions and allows for a neural connection to develop



c) After repeated pairings, the NS becomes a CS, capable of stimulating the US brain region and producing a CR.



spark over a century of research in the study of reflexology in Russia and, ultimately, lead to the development of a strong American tradition of classical conditioning research in psychology.

## The Association and American Behaviorism

**John Broadus Watson** (1878–1958) was an American psychologist trained at the University of Chicago where he initially studied the relationship between brain myelination and learning in rats (see Fig. 4). As part of his educational training, Watson read Pavlov's writings and found inspiration that would lead him to write his behaviorist manifesto: *Psychology as the Behaviorist Views It* (1913). As Pavlov had done before the

turn of the century in Russia, Watson (1913) posited that psychology was a purely objective science. By 1920, his stimulus-response theory of behavior, an extension of Pavlov's stimulus substitution theory, became the first real behaviorism in America. Of course, early American behaviorism was little more than a revival of the dualism of the British empiricists manifest in modern experimental methods, and again the driving force was the association.

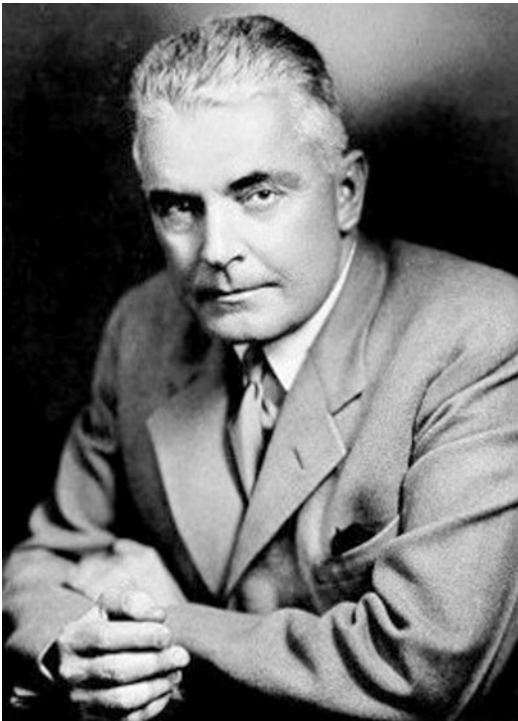
Historically, Watson's translation of Pavlov's associationism into a broad stimulus-response behaviorism would ultimately pave the way for Skinner's operant conditioning that was less reliant on the formation of unseen associations between stimuli and reflexes (see B. F. Skinner, ▶ "Instrumental Learning").

## Comparative Classical Conditioning

The majority of research on associative learning has been conducted using mammals in the laboratory, including primarily rabbits, rats, and mice. Evidence of associative learning, using Pavlovian techniques across a wide variety of species within the kingdom Animalia (both in the laboratory and in zoos and aquaria), has secured Pavlovian mechanisms as a fundamental learning process. Table 1 presents examples of laboratory-based associative learning across a variety of taxonomic categories.

Recently, Domjan and Krause (2017) have provided a convincing, functional, and evolutionary account of classical conditioning. All behavioral mechanisms evolved as valuable mechanisms for adaptation. The breadth of interspecies ability to be classically conditioned supports the notion that forming associations is key to survival in the animal world. In short, the ability to form associations between salient CS stimuli and critically important US stimuli like food, mates, toxins, illness, rivals, etc. may confer advantages that may have historically served as a selection mechanism.

Ginsburg and Jablonka (2010) argue that conditions favoring increasingly complex nervous systems during the Cambrian era would have also favored classical conditioning as a functional



**Associative Mechanisms, Fig. 4** John B. Watson (CC BY-SA 4.0). (Photograph of John B. Watson. Author: Angelin lidyea. CC BY-SA 4.0. Retrieved from [https://commons.wikimedia.org/w/index.php?search=john+b.+Watson&title=Special%3ASearch&go=Go&ns0=1&ns6=1&ns12=1&ns14=1&ns100=1&ns106=1#/media/File:John\\_b\\_watson.jpg](https://commons.wikimedia.org/w/index.php?search=john+b.+Watson&title=Special%3ASearch&go=Go&ns0=1&ns6=1&ns12=1&ns14=1&ns100=1&ns106=1#/media/File:John_b_watson.jpg))

**Associative Mechanisms, Table 1** An exemplified list of species (excluding laboratory rats, mice, and pigeons) with evidence of Pavlovian conditioning with authors and dates of publication. Note: This table is not exhaustive.

| Phyla/class                          | Common name/genus species                              | Researcher (date)                |
|--------------------------------------|--------------------------------------------------------|----------------------------------|
| <b>Invertebrates</b>                 |                                                        |                                  |
| Ciliophora                           | Paramecium <i>Paramecium caudatum</i>                  | Hennessey et al. (1979)          |
| Coelenterata                         | Sea anemone <i>Cribina xanthogrammica</i>              | Haralson et al. (1975)           |
| Planaria                             | Planaria <i>Dugesia dorotocephala</i>                  | Block and McConnell (1967)       |
| Platyhelminth and Annelida           | Flatworms and segmented worms                          | Jacobson (1963) – Review article |
| Nematoida                            | Nematode worm <i>Caenorhabditis elegans</i>            | Rankin (2004)                    |
| Arthropoda                           | Flies <i>Drosophila</i>                                | Tully and Quinn (1985)           |
|                                      | American cockroach <i>Periplaneta americana</i>        | Watanabe and Mizunami (2007)     |
|                                      | Field crickets <i>Gryllus bimaculatus</i>              | Matsumoto and Mizunami (2002)    |
|                                      | Honeybees <i>Apis mellifera</i>                        | Bitterman (1983)                 |
|                                      | Green crab <i>Carduus maenas</i>                       | Feinman et al. (1990)            |
|                                      | Spiny lobster <i>Panulirus argus</i>                   | Fine-Levy et al. (1988)          |
| Mollusca                             | Sea slug <i>Pleurobranchaea californica</i>            | Mpitsos and Cohan (1986)         |
|                                      | Octopus <i>Octopus vulgaris</i>                        | Boycott (1954)                   |
| <b>Vertebrates (Cordata)</b>         |                                                        |                                  |
| Amphibians                           | Northern leopard frogs <i>Rana pipiens</i>             | Zavala (1968)                    |
|                                      | Green toads <i>Bufo viridis</i>                        | Ghira et al. (2010)              |
|                                      | Collared lizards <i>Crotaphytus collaris</i>           | Davidson and Richardson (1970)   |
|                                      | Aldabra tortoises <i>Geochelone gigantea</i>           | Weiss and Wilson (2003)          |
| Boney fishes ( <i>Osteichthyes</i> ) | Siamese fighting fish <i>Betta splendens</i>           | Thompson and Sturm (1965)        |
|                                      | Blue gouramis <i>Trichogaster trichopterus</i>         | Hollis (1984)                    |
|                                      | Zebra fish <i>Danio rerio</i>                          | Valente et al. (2012)            |
| Birds ( <i>Aves</i> )                | Japanese quail <i>Coturnix coturnix japonica</i>       | Domjan et al. (1986)             |
|                                      |                                                        | Domjan et al. (2004)             |
|                                      | Parrots family: <i>Psittacoidea</i>                    | Wilson and Luescher (2006)       |
| Mammals                              | Starlings <i>Sturnus vulgaris</i>                      | Reboreda and Kacelnik (1993)     |
|                                      | African giant pouched rats <i>Cricetomys gambianus</i> | Poling et al. (2010)             |
|                                      | Cows <i>Bos taurus</i>                                 | Willis and Mein (1983)           |
|                                      | Dogs <i>Canis lupus familiaris</i>                     | Obrist (1965)                    |
|                                      |                                                        | Hall et al. (2015)               |
|                                      | Guinea pigs <i>Cavia porcellus</i>                     | Justesen et al. (1970)           |
|                                      | Horses <i>Equus caballus</i>                           | McCall (1990)                    |
|                                      | Macaques <i>Macaca mulatta</i>                         | Randall et al. (1975)            |
|                                      | Peccaries <i>Tayassu pecari</i>                        | Nogueira et al. (2014)           |
|                                      | Rabbit <i>Oryctolagus cuniculus</i>                    | Gormezano et al. (1962)          |
|                                      | Wombats <i>Lasiorhinus latifrons</i>                   | Swinbourne et al. (2014)         |

mechanism for selection. Comparative evidence is consistent with this perspective (see Table 2, derived from implications in Domjan & Krause). The extensive comparative evidence of associative learning extending widely across phyla suggests that a comparative assessment of the functional and evolutionary value of classical conditioning is a reasonable one and warrants further investigation.

## Modern Associative Learning Theory

Interest in associative mechanisms resurged in the latter third of the twentieth century with renewed enthusiasm for a quantitative analysis of classical conditioning, spearheaded by behavior analysts Rescorla and Wagner (1972). The development of associative strength in an otherwise neutral stimulus lies at the heart of associative learning.

**Associative Mechanisms, Table 2** Examples of naturalistic US/CS pairings that may have provided evolutionary value favoring associative learning as a functional behavior system.

| US stimulus                | UR response                                                | CS stimulus                                      | CR response                                         | Function                                        |
|----------------------------|------------------------------------------------------------|--------------------------------------------------|-----------------------------------------------------|-------------------------------------------------|
| Food, water                | Salivation, eating                                         | Visual contact with item or correlated cue       | Sign tracking, salivation                           | Increases digestion, improves foraging success  |
| Sickness                   | Regurgitation                                              | Flavor                                           | Item avoidance                                      | Reduced risk of toxic poisoning                 |
| Pain inflicted by predator | Species-specific response: freeze, run, hide, defend, etc. | Visual contact with predator                     | Escape, avoidance                                   | Reduced risk of predation                       |
| Pain inflicted by opponent | Species-specific response: pursue, fight                   | Visual contact with opponent                     | Visual threats, anticipatory attack                 | Increased probability of deflection of opponent |
| Sexually receptive partner | Sexual arousal, sexual behavior                            | Olfactory or auditory stimuli, context, location | Anticipatory response, sign tracking, goal tracking | Increase reproductive success                   |
| Mother-infant interactions | Grooming, milk letdown response                            | Olfactory cues, auditory cue, social cues        | Anticipatory milk letdown and release               | Increased infant survival                       |

The Rescorla-Wagner model of classical conditioning attempted to quantify how associative strength accumulates in the CS over trials. In short, as Pavlovian conditioning trials proceed, the US progressively imparts associative strength to the CS.

**The Rescorla-Wagner equation:**

$$\Delta V_n = \alpha\beta(\lambda - \Delta V_{n-1}),$$

where:

- $\Delta V_n$  is the change in associative strength imparted from the US to the CS on trial  $n$ .
- $\alpha$  is the salience of the CS stimulus.
- $\beta$  is the salience of the US stimulus.
- $\lambda$  is the maximum associative strength available for the US.
- $\Delta V_{n-1}$  is current associative strength already acquired by the CS on all previous trials.

To better understand the equation, we must first review the assumptions made by the model.

**Rescorla-Wagner Assumptions:**

1. Associative strength is acquired in a cumulative fashion. The association gets progressively stronger across conditioning trials.

2. Only a limited amount of associative strength can be imparted to the CS by the US. Called the asymptote of association ( $\lambda$ ), this upper limit is fixed and is determined by the salience of the US.
3. The saliences of the CS ( $\alpha$ ) and the US ( $\beta$ ) are constants in the equation. In any given (laboratory-based) conditioning scenario, it is assumed that the CS and the US will not change.
4. The associative strength gained by the CS on any trial is merely a percentage ( $ab$ ) of the total associative strength remaining after all previous trials.
5. Any change in the associative strength depends on how strongly the US is predicted by the CS. In simple terms, the more surprising the CS-US relation is, the greater the percentage of learning on each trial will be.

**Successful Predictions**

In addition to making accurate predictions regarding traditional Pavlovian conditioning, the Rescorla-Wagner model also predicts several

well-known phenomena found in classical conditioning. For example:

1. The model accurately predicts a negatively accelerating learning curve during standard classical conditioning.
2. The model accurately predicts a negatively decelerating learning curve during extinction.
3. The model accurately predicts certain classical conditioning phenomena including Pavlovian extinction, inhibitory conditioning, the blocking effect, and the overexpectation effect.

### Strengths and Shortcomings of the Model

*Strengths.* The Rescorla-Wagner model has enjoyed noteworthy success and respect within the scientific community due to several strengths. It uses language that is intuitive and appealing across various scientific disciplines, such as biopsychology and neuroscience. The model successfully predicts a number of well-known Pavlovian effects while requiring few independent variables, and it has few free parameters. It generates clear, testable ordinal predictions and has generated substantive research.

*Shortcomings.* The Rescorla-Wagner model remains silent (failing to make specific testable predictions) with respect to certain phenomena related to Pavlovian conditioning. Examples include (a) temporal relations between the CS and the US, (b) CS pre-exposure which typically slows learning, (c) spontaneous recovery following extinction, and (d) sensory preconditioning.

In nearly five decades, the Rescorla-Wagner model has undergone significant adjustments, but at its core, the quantitative, associative mechanism model remains a powerful, quantitative explanation of associative mechanisms. Alternative models have been proposed, including the Mackintosh (1975) model and the Pearce-Hall (Pearce and Hall 1980) model that addresses some of the issues neglected by the Rescorla-Wagner (1972) model. However, since its inception, the Rescorla-Wagner model has successfully

maintained the science of Pavlovian associations in the forefront of modern learning theory and research.

### Associations and Operant Conditioning

Operant conditioning is also considered dependent on the formation of associations, specifically between contexts, discriminative stimuli, responses, and consequences. The efficacy of operant conditioning in many nonhuman animals is directly affected by temporal contiguity in ways that suggest that the ability to form an association is sensitive to the timing of these associative elements. In fact, some researchers argue that operant stimulus control reflects both classical and operant elements (Weiss 2014). Although a comprehensive review the research related to the formation of operant associations is not possible here, Williams (1975, 1978, 1999) provides illustrative examples of the unique nature of operant associations.

Just as temporal contiguity alone does not ensure associative learning (Kamin 1969), Williams (1999) highlights the phenomenon of operant blocking as evidence that temporal contiguity alone is insufficient to establish an operant association. In classical conditioning, when a US is already fully predicted by CS1, the classical conditioning of a second stimulus (CS2) is ineffective (see Domjan 2015; Kamin 1969). This phenomenon is consistent with, and predicted by, the Rescorla-Wagner model. Williams (1999) notes that operant research has been consistent with this effect as well and argues that the ability to block response-reinforcer associations is consistent with the idea that temporal contiguity alone is not sufficient for the formation of response-reinforcer associations as well. However, operant blocking has been found to exhibit some unique qualities, independent of Pavlovian blocking.

When presented with a 5-s response-contingent keylight (SD1) followed by food after 10 s, pigeons responded reliably to the stimulus (Williams 1975) – evidence that an operant (response-reinforcer) association has formed. However, when a second stimulus (SD2) was presented during a 10-s delay to reinforcement,

the rate of responding to SD1 was greatly reduced. In short, the presentation of a better predictor of food (SD2) functionally reduced the association between SD1 and reinforcement. Interestingly, many assumed that the observed blocking effect was due to interference by a Pavlovian association between SD2 and food. However, in a replication of the first study, Williams (1978) showed that by simply eliminating SD2 after being established as the blocking agent, the blocking effect was eliminated; in other words, the association between SD1, the response, and the reinforcer was still intact. In 1999, Williams further demonstrated that where the SD2 signal occurs in the delay between the SD1 response and the reinforcer determines whether SD2 serves to enhance responding to SD1 or serves to block the SD1 response-reinforcer association. Increasing the delay to 30 s allowed for the presentation of SD2 either the first 5 s or the last 5 s of the delay. From a traditional operant perspective, SD2 should function as a conditioned reinforcer in both cases. But the data showed that the nature of the SD1 response-reinforcer association changed as a result of the SD2 temporal placement. Early placement led to a marked enhancement of responding – allowing SD2 to function as a conditioned reinforcer by marking responses to SD1. However, late placement of SD2 functionally blocked the ability to learn the contingency between SD1 responses and reinforcement altogether. These findings suggest that operant associations (specifically with regard to operant blocking) are qualitatively different from the associations formed in Pavlovian blocking, despite having some analogous effects on learning.

### **From Associationism to Connectionism to Cognitive Neuroscience**

Modern associationism encompasses a variety of viewpoints and theories that attempt to explain complex phenomena such as blocking, overshadowing, and latent learning. Associative models, such as the Rescorla-Wagner (1972) model, the MacKintosh (1975) model, and the Pearce-Hall (1980) model, have dominated these

efforts (for a detailed comparison of these associative models, see Wasserman and Miller 1997). With the advent of the modern cognitive revolution, a flood of connectionist and physiological theories, designed to explain how these associations are formed, have resulted in research positing theoretical, cerebral, and neural structures responsible for simple learning and more complex thinking and reasoning (for examples see Abraham et al. 1972; Acevedes-Piña and Quinn 1979; Benowitz 1972).

Wasserman and Miller (1997) provided a detailed account of the field of associative learning through the 1990s. They highlighted the importance of classical conditioning in future progress toward a coherent and complete understanding of human cognition. They invited neuroscientists and cognitive scientists to join forces with experimental psychologists in an interdisciplinary effort to understand and explain the complexities of associations and mental behavior. Although a comprehensive review of connectionism and neuroscience research related to associative learning is beyond the scope of this review, a brief summary and a few seminal examples may suffice to illustrate the approaches.

### **Associations, Connectionism, Neuroscience, and the Single Cell**

By the 1990s, the synthesis of mathematics, computer science, and associative learning came to the forefront of integrative science. Mathematical algorithms, combined with the concept of the “hardware” of the brain, led to complex computational theories designed to account for how the brain manages the associations responsible for a wide array of behaviors. Although not a new idea (Hebb 1949), the technological advances of the late twentieth century allowed for new efforts to connect associative learning to the biology of the brain.

**Connectionism** attempts to explain mental behavior using mathematical models called neural networks. The approach blended Hebb’s (1949) proposal that the connection between two neurons is strengthened whenever both are activated at the



same time with the concept of the association. The result was a division of computer programming that would focus on simulating the development of associations with an emphasis on higher mental behaviors like memory, language, and reasoning. The fundamentals of connectionism are based on interconnected networks of neural “units.” Using a series of algorithms, connections between neural units are strengthened (Waskan 2010).

According to a connectionist perspective, mental states are described as a pattern of activation values. Memories or thoughts are created and modified by changing the strength of specific neural connections. Neural units theoretically represent neurons or clusters of neurons; activations can be thought of as neural firings. Being highly mathematical in nature, these theories lack grammar and symbols, making them applicable to non-verbal learning in animal populations (Kehoe 1989). As activations occur between neural units, connections develop and associations are formed and strengthened. Commonalities between connectionist mechanisms and Pavlovian associations have been drawn and discussed (Kehoe 1989). In a simple example, Pearce (2002) contrasts his own connectionist theory with the Rescorla-Wagner model.

*Limitations.* A number of limitations to the connectionist approach have been noted. First, only as computer technologies advance does connectionism follow. The models are inextricably linked to the current state and underlying limits of computing technology at any given time. For example, as early digital serial-processing computers were replaced by the invention of parallel distributed processing systems, changes to the connectionist models necessarily followed. With the advent of the Internet, and other forms of distributive knowledge, connectionism is merging with a new “connectivism” that includes unit connections with nonhuman appliances and non-biological sources of information (for a review, see Goldie 2016).

A second criticism of the associationist/connectionist approach points to its lack of confirmatory evidence with biological systems. Connectionist models are purely mathematical and theoretical; confirmatory evidence is often produced through computer simulations rather

than through data fitting with real animal or human data. Kehoe (1989) provided some of the earliest attempts to fit preexisting classical conditioning acquisition curves using a connectionist model. However, connectionism as a field has moved more in the direction of linguistics and human language (Ellis 1998), leaving the advancement of connectionist models of classical conditioning to only a few researchers (Gingrich and Byrne 1987; Kemp and Eckerman 2001; Mignault and Marley 1997). In 1991, Commons, Grossberg, and Staddon edited a volume on the current state of network modeling, conditioning, and action. Baxter et al. (1991) reviewed connectionist networks and elements that simulate both classical and operant conditioning processes and phenomena. Specifically, they provide a detailed review of work related to single adaptive elements, small empirically derived neural networks, and tests of simulations. But, at the time, little experimental data was available.

Since the 1980s, the biological science of associationism has rapidly come to the forefront of classical conditioning research. Advancing neural technologies have opened the door to a sophisticated behavior neuroscience.

## Associations and Neuroscience

The initial emphasis on large neocortical structures led to a better understanding of the regulatory importance of the hippocampus in association-based learning and performance.

In 1975, Berger, Alger, and Thompson reported substantial increase in hippocampus activity in rabbits undergoing either paired (CS+/US+) or unpaired (CS+ only or US+ only) trials. The CS+ stimulus was a tone; the US was a puff of air. They measured anticipatory blinking of the nictitating membrane as the dependent variable. Marked increases in blinking during the CS+ test condition were noted for the CS+/US+ condition only. Hippocampal responding developed within a very few training trials. The authors suggested that, at the time, this hippocampal response was perhaps the earliest cerebellar indicator of associative learning. Berger et al. (1976) later suggested

that pyramidal neurons are the cell type that accounts for the increases in hippocampal firings. In 1984, Berger demonstrated that long-term potentiation of the hippocampus prior to training increased the rate of CR acquisition. Over the next decade, the search to identify other brain areas involved in associative learning was well underway.

By the early 2000s, a fairly clear picture of the brain structures involved in classical fear conditioning was established. Christian and Thompson (2003) provide a review of the various neural substrates implicated in rabbit eyeblink conditioning, including the hippocampus, the frontal cortex, the amygdala, the motor cortex, as well as specific pathways related to the US, CS, UR, and CR. But the desire to understand the underlying neural mechanisms responsible for the formation of associations necessarily invited a greater interplay between the fields of learning, experimental psychology, and neuroscience. As the foundation for this new neuroscience movement, associative learning was accepted as an ideal paradigm for studying the how the physical brain accomplishes sophisticated behaviors like classical conditioning, associative memory, and the generalization of associations. Throughout the late twentieth and into the early part of the twenty-first century, the focus on the underlying neural substrates of learning has continued to increase.

## Single-Cell Associative Learning

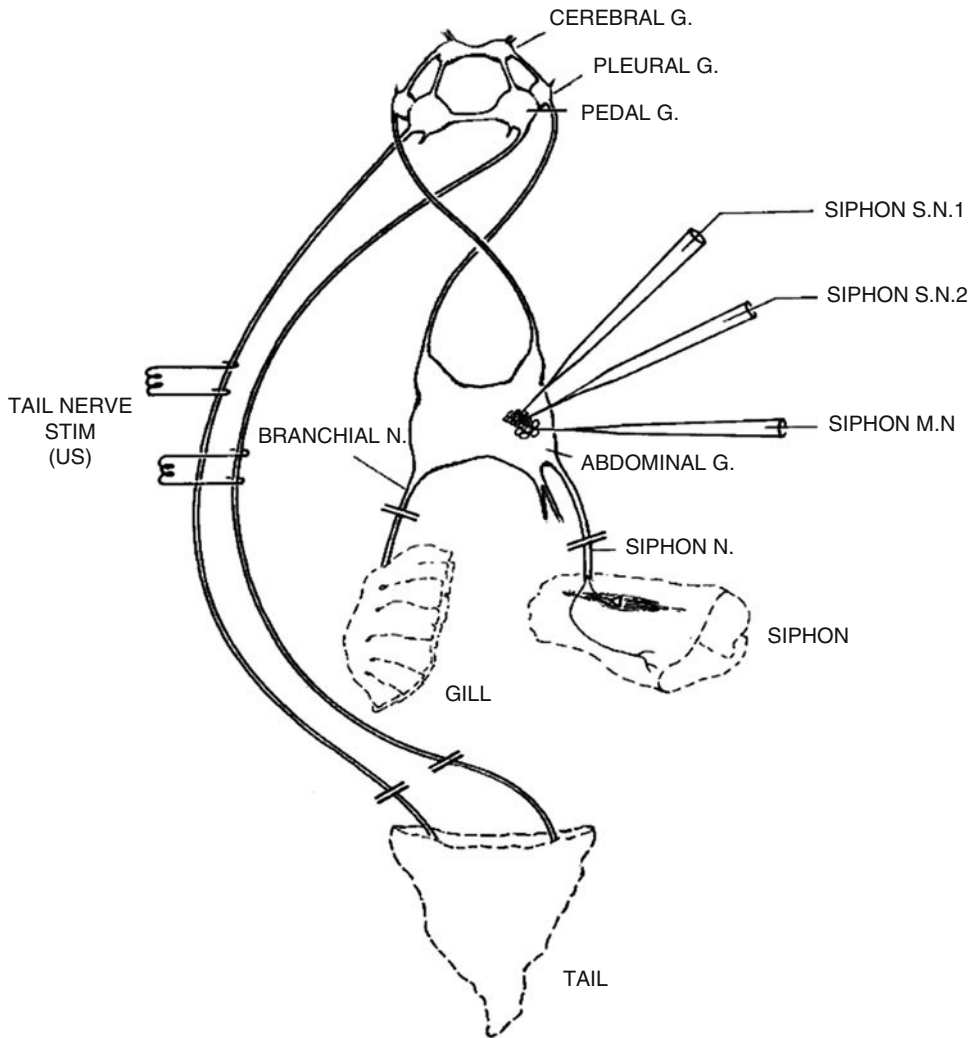
In one of the earliest behavioral demonstrations of classical conditioning in an invertebrate, Kandel and Schwartz (1982) showed that weak, tactile stimulation of the siphon or mantle of the marine snail *Aplysia* (CS) paired with electrical shocks to the animal's tail (US) results in prolonged responsiveness to additional tactile stimulation in the absence of the US: evidence of classical conditioning.

By 1983, Walters and Byrne had proposed a cellular/neural mechanism for appetitive associative learning based on the associative conditioning of individual sensory neurons involved in the same tail withdrawal reflex of the *Aplysia*. They applied a cellular analog of Hebb's (1949)

classical conditioning using a dissected split-foot preparation with two intact sensory neurons and one motor neuron from an *Aplysia* (see Fig. 5). They applied a series of nine suprathreshold depolarizing pulses to the sensory neurons as the CS+ stimulus and an electrical shock to the motor neuron as the US stimulus. In the "paired condition," CS+ pulses to one sensory neuron were paired with the US shocks to the motor neuron; in the "unpaired condition," CS+ and US stimuli were presented equally often but never together. A third control condition involved US stimulation only. Firing on the motor neuron was measured during CS-only tests. Results showed the synaptic connection between the CS+ sensory neuron and the motor neuron in the paired condition was significantly strengthened relative to the other two conditions.

Subsequent studies (for a brief review, see Glanzman 1995) suggest that this form of cellular classical conditioning is mediated, not only by a presynaptic cellular mechanism but by postsynaptic and peripheral synaptic mechanisms as well. Glanzman's continued research with classical conditioning has led to a better understanding of the mechanisms of associative learning and synaptic plasticity in invertebrates and vertebrates (Roberts and Glanzman 2003).

Following up on previous work, Watanabe and Mizunami (2007) extended previous behavioral findings to neural measurements of classically conditioned salivation in surgically altered cockroaches. They tested sensitivity to appetitive odor (CS+) conditioning using exposed salivary duct nerves that consist of two neurons with large-diameter axons (SN1 and SN2) with cell bodies in the suboesophageal ganglion (SON), as well as several smaller-diameter axons. Before conditioning, the neurons respond similarly to vanilla and peppermint. After only five classical conditioning trials with vanilla and saline (V-) and peppermint and sucrose (P+), both the SN1 and SN2 exhibited significantly greater neural responses to peppermint alone than to vanilla alone. In fact, post-training responses to vanilla alone approximated responses to peppermint before training although the animals had previously shown a natural preference for vanilla over peppermint.



**Associative Mechanisms, Fig. 5** A schematic of the typical experimental split-foot preparations in *Aplysia* (as per Carew et al. 1984). The tail nerve (posterior pedal nerve – P9) was used to deliver US stimulation and to record motor nerve firings. One sensory neuron (SN) received paired CS+/US stimulation; another SN received unpaired CS+/US stimulation. Reprinted with

permission from *The Journal of Neuroscience*. (The typical experimental split-foot preparation in *Aplysia* (as per Carew et al. 1984). Anyone may reprint original *JNeurosci* material without requesting permission. A full journal reference and link to the version of record, where appropriate, must be included. <https://www.jneurosci.org/content/rights-permissions>)

Mizumani and his colleagues have gone on to use crickets to investigate the role of octopaminergic and dopaminergic neurons in mediating reward and punishment signals in insect visual learning (Unoki et al. 2006), as well as in appetitive and aversive memory (Mizunami et al. 2009). He has also identified context-dependent discrimination learning at the neural level in cockroaches using visual context

and olfactory and gustatory cues (Sato Matsumoto et al. 2012).

Although we do see gradual progress in the mapping of brain structures and neural stimulation associated with fear conditioning in mammalian brains (Maren 2001), Mazunami has suggested that cockroach neurons may serve as a valuable model for studying the cellular mechanisms of

associative learning due to their simple nature. In mammals, even reflexive responses like salivation are much more complex in comparison. Neuroscience research with mammals remains largely at the structural level. But the current progress in understanding the underlying neural mechanisms of associative conditioning appears to be led (at least for now) by studies with insects such as fruit flies, *Drosophila* (Berry et al. 2008; Davis 2005; Heisenberg 2003; Honjo and Furukubo-Tokunaga 2009; Schroll et al. 2006; Schwaerzel et al. 2003; Thum et al. 2007), honeybees (Farooqui et al. 2003; Giurfa 2007; Hammer and Menzel 1998; Menzel 2001), and moths (Dacks et al. 2005; Daly et al. 2004).

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- Classical Conditioning
- Instrumental Learning

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## Associative Striatum

### ► Medial Striatum

## Assortative Mating

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## Synonyms

Nonrandom mating; Assortative pairing; Assortment; Homogamy; Assortative mating; Disassortative mating; Heterogamy

## Definition

Assortative mating is defined as a pattern of non-random mating, where there is a correlation (positive or negative) between male and female genotypes and/or phenotypes across mating pairs. Positive assortative mating (also called

homogamy) implies a tendency to mate with genetically or phenotypically similar individuals. Conversely, negative assortative mating (also called heterogamy or disassortative mating) implies a tendency to mate with genotypically or phenotypically dissimilar traits. In the speciation literature, assortative mating is considered as a mechanism that drives reproductive isolation within a diverging population or between distinct species.

## Introduction

An important focus in the field of sexual selection over the past decade has been to understand how and why animals choose their mates. In some cases, mate choice has been found to rely on absolute criteria: individuals share the same preferences and choose a mate who offers them the best direct benefits to increase their survival or fecundity (e.g., high-quality territory, nuptial gifts), or the best indirect genetic benefits to increase offspring's fitness (often reflected by ornament-based choice). In other cases, mate choice has been found to rely on relative criteria, where individual preferences vary according to their own genes or phenotype. Assortative mating represents a process of mate choice based on relative criteria. It is a mating pattern commonly observed in animals (Jiang et al. 2013) and has attracted interest from both empiricists and theoreticians due to its importance in population genetics and speciation.

In animals, positive assortative mating between breeding pairs has been found for numerous phenotypic traits, including morphological traits (body size, coloration, ornament), physiological traits (age, pheromone response), or behavioral traits (diet, personality), and across many taxa, including insects, crustaceans, gastropods, amphibians, fish, birds, reptiles, and mammals (see Jiang et al. 2013 for a review). The traits under assortative mating often – but not always – reflect individual phenotypic condition and/or genetic quality. For instance, in wild American goldfinches *Carduelis tristis*, the carotenoid-based yellow plumage colors of males and females reflect individual quality and are

positively correlated across breeding pairs (MacDougall and Montgomerie 2003). Assortative mating has been particularly well studied in humans. Many studies have found that men and women tend to mate with someone who is similar to themselves, on one or several phenotypic traits, including physical appearance (facial traits, eye and hair color, body height), socio-economic status, education, age, religion, or personality traits (see Štěrbová and Valentová 2012 for a review).

In contrast, negative assortative mating on phenotypic traits seems to be comparatively scarce in nature (Jiang et al. 2013; Thiessen and Gregg 1980). It has been reported, for example, in some birds where two color morphs coexist and where individuals prefer to mate with the opposite morph (Jiang et al. 2013). Inbreeding avoidance is often observed in animals and may or may not represent disassortative mating (avoidance of close kin does not specifically require choosing the opposite trait in mates, but just a different trait from self). At the genetic level, most examples of disassortative mating come from studies of the Major Histocompatibility Complex (MHC). The MHC is a highly polymorphic cluster of genes involved in immune function and pathogens recognition. As MHC alleles are expressed codominantly, choosing a dissimilar mate at MHC might increase the likelihood of obtaining a genetically diverse offspring at MHC genes, which in turn allows the offspring's immune system to recognize and fight a broader array of pathogens. Females of many species have been found to pair preferentially with MHC-dissimilar males (Piertney and Oliver 2006), including in humans (Havlicek and Roberts 2009). However, MHC-disassortative mate choice is not always observed, and in some cases mate choice for MHC-similar mates is reported within the same species.

It is important to distinguish between assortative mating *pattern* and *preference*, because the mating pattern of a population is not necessarily a direct consequence of the mating preferences of individuals (see discussion below). To test empirically for a *pattern* of associative mating in a given population, one needs to calculate the correlation between the values of homologous phenotypic or genotypic trait

(s) across breeding pairs. This correlation coefficient gives a measure of the strength and direction of assortative mating. To test for an assortative mating *preference*, animal studies investigate female or male mate choice, for example, in a two-way apparatus where the focal individual can choose between a homotypic (similar for a given trait) and heterotypic mate or observe true mating preferences in controlled experimental design (Egger et al. 2008). In human studies, raters are typically asked to assess the attractiveness of composite or real faces or bodies that are similar or different to themselves (Bovet et al. 2012) or match unknown partners' faces (Bereczkei et al. 2004).

### Which Mechanisms Can Generate Assortative Mating?

Whereas patterns of assortative mating are often observed, the underlying mechanisms that cause them are difficult to understand and disentangle (Jiang et al. 2013). A large number of different processes can lead to assortment. Assortative mating preferences (where one or both sexes show an active preference for similar or dissimilar partners) can evolve adaptively in some cases, under the action of sexual selection. In other cases, assortative mating patterns can be generated by nonadaptive processes.

#### Adaptive Hypotheses

Pairing with genetically similar or dissimilar individuals can be adaptive because it increases the fitness of a pair's offspring. Disruptive selection (individuals with extreme values of a trait have higher fitness) will favor the evolution of positive assortative mating to avoid producing less fit intermediate offspring (Dieckmann and Doebeli 1999; Kirkpatrick and Ravigné 2002; Kondrashov and Shpak 1998). Many insects and birds mate assortatively on the basis of similar color patterns to avoid producing offspring with maladaptive patterns that would, for instance, make it more easily detected by predators or less attractive as a mate (Jiang et al. 2013). In contrast, stabilizing selection (individuals with intermediate values of a trait have higher fitness) will favor

the evolution of negative assortment to reduce the production of less fit extreme offspring.

Assortative mating can evolve in response to inbreeding or outbreeding depression for similar reasons. Mating with a partner of relatively similar genetic background might be evolutionarily advantageous because it decreases outbreeding depression in offspring. Outbreeding induces a fitness cost in several species, either because of the disruption of locally co-adapted gene complexes in offspring, underdominance (selection against the heterozygotes), or epistatic interactions (Epinat and Lenormand 2009). Conversely, negative assortative mating is expected to evolve to avoid inbreeding depression, which increases the risk of expression of recessive deleterious alleles in offspring (Epinat and Lenormand 2009). For example, avoidance of close kin as mating partners (and thus inbreeding depression) is known to be enforced in several species by a biological mechanism (called the Westermarck effect), where individuals develop a strong sexual aversion toward co-residents during infancy, generally close kin members (Marcinkowska et al. 2013).

Given the severe negative consequences of inbreeding, it is surprising that positive assortative mating is more frequently observed than negative assortative mating. In fact, the "optimal outbreeding theory" posits that individuals have evolved to choose a mate with some degree of relatedness, representing the optimal balance between inbreeding and outbreeding, as an adaptive compromise between these opposing selection pressures (Bateson 1983). In short, individuals should mate with partners who are relatively genetically similar, but not close relatives. Positive assortative mating may thus be more often selected to avoid outbreeding depression, given that inbreeding is already prevented by other biological (Westermarck effect) or social mechanisms (such as incest taboos in humans, Bovet et al. 2012). Consistent with this hypothesis, a growing body of literature shows that individuals prefer an optimally – rather than maximally – dissimilar partner at MHC genes, as excessive MHC diversity may prevent an efficient immune response or disrupt locally adapted allelic combinations (Piertney and Oliver 2006).

Several other hypotheses have been proposed to explain the prevalence of positive assortative mating preferences. First, a preference for self-resembling individuals may be adaptive because, as suggested by kin selection theory, cooperation and altruism between potential mating partners are promoted when they share a high number of genes (Thiessen and Gregg 1980). Second, positive assortative mating may be adaptive because it increases the number of shared genes between parents and the probability to transfer own genes in offspring (Genetic similarity theory: Rushton 1989). These two hypotheses nonetheless require that assortative mating is based on a large number of genetically heritable traits and that phenotypic cues of assortative mating are a reliable measure of genetic proximity. Third, selection for positive assortative mating could also be based on non-genetic, but fitness-maximizing, mechanisms. For instance, behavioral similarity between partners may promote within-pair compatibility, via a better coordination or share of parental investment, and results in higher reproductive success. In zebra finches, it has been found that offspring survival during the rearing period increases with behavioral similarity between parents (Ihle et al. 2015). In humans, homogamy seems to enhance marital stability and fertility (Štěrbová and Valentová 2012).

Regardless of the type of selection involved, assortment can be the consequence of mutual mate choice from both males and females or occur through the mating behavior of one sex only. In species with bi-parental care, mutual mate choice based on quality-indicating ornament(s) is frequently observed, since the evolution of discriminating males and females for partners with equal investment is adaptive to both sexes (MacDougall and Montgomerie 2003). In contrast, only female mate preference for assortative mating on male nuptial coloration seems responsible for the rapid diversification of cichlids (Egger et al. 2008).

### Nonadaptive Hypotheses

Assortative mating may not always be adaptive, but arise as an incidental consequence of other aspects of pair formation (Crespi 1989).

The first mechanism is temporal segregation (or allochronic isolation). In phytophagous insects that use several host plants which fruit or bud at different times, mating on different host plants can lead to allochronic isolation of mating pairs (Groman and Pellmyr 2000). Age-assortment is often generated by temporal segregation between generations or by age-specific access to reproduction.

Spatial segregation among phenotypes is a second mechanism that could generate incidental positive assortment: when there is covariation between a phenotype and the habitat in which individuals mate, the probability of encountering phenotypically similar mates increases. This can occur when individuals with similar phenotypes have similar habitat preferences. For instance, in insects that mate on their host plants, consistent individual preferences for a specific host lead to spatial segregation of breeding pairs (Feder et al. 1994; Malausa et al. 2005). In several arthropods, size-assortment arises because individuals of similar sizes aggregate in the same patches (because size determines resource or substrate use) (Crespi 1989). By extension, positive assortative mating in humans may often be a consequence of the fact that individuals who are similar in socio-economic status, interests, or personality are more likely to meet and thus mate with each other (Štěrbová and Valentová 2012). Covariation between phenotype and habitat can also occur when there are phenotypic (or genotypic) clines in the spatial distribution of a population, due, for instance, to adaptation to an environmental gradient. In animals, assortative mating arising as an incidental outcome of temporal and spatial segregation may be an important process facilitating sympatric speciation (see paragraph below on the evolutionary consequences of assortative mating).

Third, mate similarity can arise as a by-product of intrasexual competition for mate and intersexual conflict (Crespi 1989). Under strong intrasexual mating competition, individuals with high-quality (or attractive) phenotypes will choose their preferred mate from the available pool first, leaving low-quality (or unattractive) individuals to pair with those who remain unpaired, causing positive assortment despite the



fact that all individuals prefer mates belonging to the same category. In many invertebrates, both female fecundity and male competitive ability are positively correlated with body size (Crespi 1989). Thus, large competitive males choose large, highly fecund females, whereas the losers have to accept smaller and less fecund females, resulting in positive size-assortative mating (Harari et al. 1999; McLain and Boromisa 1987). In the case of intersexual conflict, larger females are better able to resist mating attempts from large, aggressive males, and only the largest males are able to mate with them, again resulting in positive assortment.

Fourth, assortative mating can be generated by mechanical constraints during copulation that prevent random mating. For example, copulation can be physically difficult between males and females of different size, because of a lack of coincidence in anatomical parts, resulting in size-assortative mating (Crespi 1989).

Fifth, a higher similarity between breeding pairs compared to nonbreeding pairs can simply arise from the behavior of the partners converging over time (“postpairing convergence”). In the convict cichlid *Amatitlania siquia*, behavioral similarity between mismatched partners increases after pairing, because one partner adjusts their behavior to the other (Laubu et al. 2016).

Thus, the observed mating *pattern* of a population is not necessarily a direct consequence of the mating *preferences* of individuals. Patterns of assortative mating can be determined by both the mating preferences of individuals and many possible processes of pair formation (Jiang et al. 2013). As a result it is impossible to make definitive statements about the assortative mating preferences of individuals simply by observing the mating pattern of a population. Accordingly, it is impossible to predict the mating pattern of a population from the mating preferences of its constituent individuals. Studies thus need to address both mating preferences and pattern concomitantly.

### Variation in the Strength of Assortative Mating

The intensity of both adaptive and incidental assortative mating should not be viewed as

constant in a population or species, but rather is likely to vary across time according to the different selection pressures at play (Jiang et al. 2013). If assortative mating evolves as a response to inbreeding and outbreeding depression in a way to optimize the degree of relatedness among mating partners, inbred populations should exhibit disassortative preferences and outbred populations assortative preferences. This may explain the contradictory results of MHC-biased mating preferences across different human populations (see Havlicek and Roberts 2009 for a review).

Similarly, if assortative mating arises as an incidental outcome of competition for mates, variation in the intensity of intrasexual competition and/or intersexual conflict within or across population(s) may determine the intensity of assortment (Harari et al. 1999; McLain and Boromisa 1987). Population density, the operational sex ratio, and ecological conditions are known to influence the intensity of both intra- and intersexual competition and can thus affect assortment. For example, positive assortative mating increases with population density in milkweed longhorn beetle *Tetraopes tetraophthalmus* because large males are more likely to interfere when small males copulate with large females at high density (McLain and Boromisa 1987).

A recent meta-analysis has emphasized that the frequency and strength of assortment differ significantly among taxonomic groups, among populations, and among different traits for the same population (Jiang et al. 2013). Quantifying the direction and strength of assortative mating can shed light on the nature of the underlying mechanisms (i.e., adaptive versus incidental assortative mating) by testing whether it covaries with the intensity of competition.

### What Are the Phenotypic Cues of Assortative Mating Preferences?

Several mutually nonexclusive proximate mechanisms have been proposed to explain how individuals can detect genetic and/or phenotypic similarities in unfamiliar potential mates.



First, assortative mating preferences can be mediated by self-referent phenotype matching, where individuals compare phenotypes of unfamiliar individuals with their own phenotypes and choose those who are similar to themselves (Hauber and Sherman 2001). Animals have been shown to detect similarity between their own phenotypes and those of unfamiliar individuals through visual cues, odors, vocalizations, or environmental predictors (Hauber and Sherman 2001). The internal representation necessary to do self-referencing might be learned and/or unlearned (environmentally or genetically determined, Hauber and Sherman 2001). In the latter case, mating preferences are genetically determined and in linkage disequilibrium with loci coding for phenotypic traits used in assortment. In *Heliiconius* butterflies, for instance, hybrid color morphs inherit mating preferences from both parental morphs and mate assortatively with morphs of their own color pattern (Melo et al. 2009).

Second, assortative mating can be mediated by sexual imprinting, a nongenetic mechanism where individuals acquire mate-choice criteria during development by using their opposite-sex parent as the template (Hauber and Sherman 2001). Sexual imprinting can either be positive, when individuals shape a preference for their parents' characteristics (Bereczkei et al. 2004), or negative, when individuals develop a sexual aversion to individuals similar to their parents (Marcinkowska et al. 2013). The learning period is thought to be confined to an early sensitive period when only closely related individuals are likely to be present and will shape mating preferences until adulthood. Consistent with this hypothesis, cross-fostering experiments in birds and mammals (where offspring are transferred to a non-natal family) have shown that males prefer sexual partners who are similar to the female who has reared them (see Hauber and Sherman 2001 for a review). Sexual-imprinting-like mechanisms have been argued to influence human mate choice too, with studies reporting facial resemblance between a mate and his partners' opposite-sex parent (Bereczkei et al. 2004), but its importance remains debated.

Because offspring are expected to resemble their parents owing to genetic similarity, the resemblance between the mate and the opposite-sex parent may not be caused by sexual imprinting but rather by self-referent phenotype matching. Cross-fostering experiments in animals help to distinguish between those two mechanisms: if the cross-fostered animal shifts its sexual preference towards individuals of the foster phenotype, preferences are likely to be imprinted. The two mechanisms are nonetheless nonmutually exclusive and both seem to exist (Hauber and Sherman 2001).

Regardless of the mechanism involved, individuals can rely on many different phenotypic cues (or a combination of them) to mate assortatively. Individuals can rely on visual cues, such as plumage coloration in birds (MacDougall and Montgomerie 2003) or morph coloration in butterflies and fishes (Egger et al. 2008; Melo et al. 2009). In birds, assortative mating is often mediated by vocalizations during courtship (Clayton 1990). Assortative mating can also be mediated via pheromonal communication in insects or body odors in mammals.

## What Are the Evolutionary Consequences of Assortative Mating?

Assortative mating has several important evolutionary consequences on the genetic structure of populations and on the speciation process.

### Assortative Mating and Population Genetics

When genetically similar individuals mate, offspring are more likely to receive two copies of the same allele at the loci coding for the trait(s) used in assortment. As a result, positive assortment increases homozygosity within genomes (Crow and Felsenstein 1968; Thiessen and Gregg 1980). Assortative mating will nonetheless not lead to complete homozygosity, as would inbreeding, because it affects only the loci coding for the trait(s) used in assortment.

Positive assortative mating also alters the probability that a particular allele will be associated with other alleles, and consequently promotes

linkage disequilibrium between loci (in particular between the loci coding for mating preferences and the loci coding for the traits under assortment). This increase in homozygosity and linkage disequilibrium in genomes resulting from positive assortative mating in turn (1) inflates the genetic variance of quantitative traits by favoring extreme types and (2) increases heritability between parents and offspring (Crow and Felsenstein 1968). The variance-enhancing effect of assortative mating can be understood in a simple one-locus system. If homozygotes mate assortatively ( $AA \times AA$  and  $aa \times aa$ ), they only produce more of their own type, whereas if heterozygotes mate ( $Aa \times Aa$ ) they will leave only half as many of their type in the next generation: the extreme phenotypes are favored at the expenses of intermediate ones, causing an increase in the genetic variance. Note that positive assortative mating by itself does not affect allele frequencies of a population (individual allele frequencies do not change and no alleles are gained or lost from the population). It affects only genotype frequencies, by restructuring the allelic composition of individuals and creating deviation from Hardy-Weinberg disequilibrium within loci (Crow and Felsenstein 1968).

The increase in genetic variance due to positive assortative mating (1) increases the response to selection of populations and the rate of evolutionary change (since more genetic variation leads to quicker and larger genetic shift in the value of the trait under selection) and (2) might be an important mechanism that maintains variance in phenotypic traits, despite the variance-eroding effects of other forms of sexual selection – i.e., choice for absolute, rather than relative cues (Arnqvist 2011).

In contrast, negative assortative mating increases heterozygosity within genomes, maintains polymorphism, prevents allelic fixation, and facilitates the maintenance of sexually antagonistic variation (Crow and Felsenstein 1968; Thiessen and Gregg 1980).

### Assortative Mating and Speciation

Assortative mating plays a key role in speciation in two contexts. First, it can be a mechanism of

prezygotic isolation that reduces gene flow between phenotypically divergent populations and causes a population to split into two, resulting in sympatric speciation where two daughter species arise without geographical isolation of the mother population (Kirkpatrick and Ravigné 2002). Female and/or male preference for assortative mating is thought to be responsible for the rapid speciation of many species, as illustrated in cichlids (Egger et al. 2008). Second, assortative mating can participate to maintain the genetic isolation of two populations that come into secondary contact and prevent them from merging back into a single population (Kirkpatrick and Ravigné 2002; Kondrashov and Shpak 1998). For example, two subspecies of Indonesian zebra finches living in sympatry were found to exhibit strong assortative mating on plumage coloration and song to discriminate and mate with members of their own subspecies, leading to the maintenance of reproductive isolation (Clayton 1990).

In models of speciation, reproductive isolation via positive assortative mating evolves in response to disruptive selection, to reduce the production of less fit phenotypically intermediate offspring (Kirkpatrick and Ravigné 2002). Conversely, stabilizing selection favors the evolution of negative assortative mating, to reduce the production of less fit phenotypic extremes (Kirkpatrick and Ravigné 2002; Kondrashov and Shpak 1998). However, theoretical models have shown that positive assortative mating does not always lead to speciation even in a population under disruptive selection. In particular, if the loci coding for the phenotypic traits that are used for assortative mating act independently from the loci that are under disruptive selection, recombination will break up associations between loci affecting survival and those determining mate choice, so that there is a low probability of speciation (Kirkpatrick and Ravigné 2002). If, however, assortative mating is pleiotropically controlled by the same loci that are under disruptive selection (pleiotropy describes the fact that a single gene influences multiple phenotypic traits – here mate choice and survival), antagonism between recombination and selection is reduced so that initial assortative mating can be enhanced

by reinforcement, and speciation becomes much more likely (Dieckmann and Doebeli 1999; Kirkpatrick and Ravigné 2002). Several theoretical models have shown that speciation can happen even in the absence of pleiotropy (Dieckmann and Doebeli 1999; Kondrashov and Shpak 1998), but it remains unclear whether the assumptions of these models are met in nature. Overall, the most favorable situation for sympatric speciation is when assortative mating is based on a trait directly under disruptive selection (Kirkpatrick and Ravigné 2002). Those traits have been called “magic traits” by some researchers that questioned the generality of this mechanism in generating sympatric speciation. However, there are some clear examples of ecological divergence directly causing assortative mating, such as when habitat preferences lead to spatial segregation of mating pairs (Feder et al. 1994; Malausa et al. 2005).

Positive assortative mating is, however, likely to trigger costs that may potentially delay or prevent speciation processes (Otto et al. 2008). Potential costs of assortative mating include the energetic costs of searching for compatible mates (rare phenotypes are less likely to find mates than are common ones), the risk of rejecting all potential mates and remain unmated, and the costs of mechanisms that allow perception of similarity in potential mates. However, the costs of assortative mating may rarely hinder the evolution of reproductive isolation, unless they are sufficiently high (Otto et al. 2008).

## Conclusion

Assortative mating has attracted the attention of evolutionary biologists because it relies on relative criteria and because it can influence the genetic structure of a population and the rate of evolutionary changes and promote speciation in some circumstances. Determining the causes of assortative mating has nonetheless proven difficult and studies that clearly distinguish between alternative hypotheses of assortment are lacking. In both animals and humans, assortative mating is predominantly positive (Jiang et al. 2013). Since disruptive selection (favoring positive assortative

mating) and stabilizing selection (favoring disassortative mating) on phenotypic traits occur at similar frequency and strength in natural populations, positive and negative assortment should occur at about the same frequency. Therefore, it has been suggested that disruptive or stabilizing selection is not the primary forces driving the evolution of assortative mating (Jiang et al. 2013). The second adaptive explanation of assortative mating involving direct selection favoring trait-matched breeding pairs might explain the asymmetry between positive and negative assortative mating, although this process is not widely documented (Jiang et al. 2013). Clearly, assortative mating evolves adaptively in some cases, but nonadaptive processes generating positive assortative mating patterns appear important in explaining its prevalence. Future studies that distinguish between alternative hypotheses of mate assortment are needed to elucidate this question.

## Cross-References

- Additive Genetic Variance
- Allelic Association
- Assortment
- Heritability Estimate
- Imprinting
- Inbreeding Depression
- Phenotype Matching
- Speciation

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## Assortative Pairing

### ► Assortative Mating

## Assortment

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## Synonyms

Law of independent assortment

Definition

When alleles at a locus separate during gamete formation, their assortment is independent of the separation of alleles at other loci.

Introduction

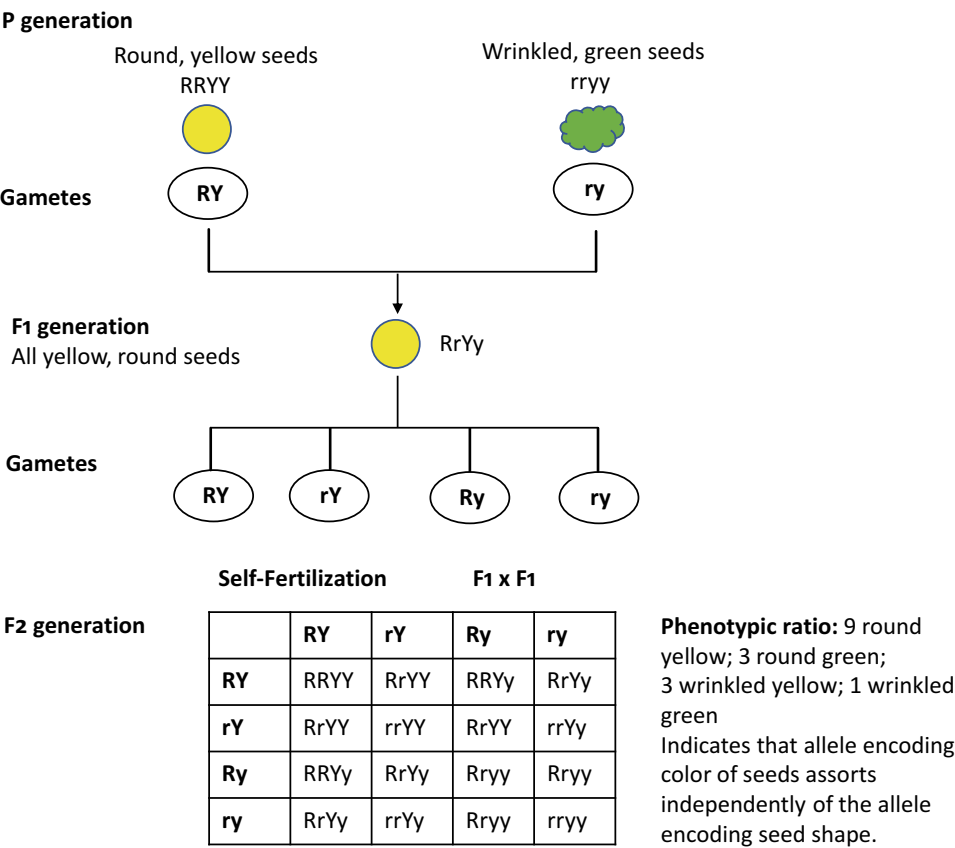
Independent assortment is widely known as the second law of Mendel which was proposed in 1865 during his study of genetics in pea plant. This principle was formulated after the law of segregation had been described. According to the law of segregation, the alleles for a trait separate during gamete formation, and one allele is passed on to each of the gamete. The law of segregation was discovered through performing monohybrid crosses (using plants differing only in a single trait) and also described the concept of

dominant and recessive traits. Four important inferences were drawn from monohybrid crosses:

- Two alleles exist for each trait.
- These alleles separate during gamete formation, and one allele goes into each gamete.
- There are dominant and recessive alleles. Dominant alleles reappear in F1 generation, whereas recessive alleles disappear or are suppressed in F1 generation.
- The two alleles separate with equal probability into gametes.

Dihybrid Cross

Mendel crossed varieties of peas that differed in only two characteristics. Such crosses are referred as dihybrid crosses, and always a ratio of 9:3:3:1 was obtained in the F2 generation (Fig. 1). This



**Assortment, Fig. 1** Mendel’s dihybrid crosses explaining law of independent assortment (Figure adapted and modified from Klug et al. (2012))

ratio can only be obtained due to the principle of independent assortment since alleles at different loci separate independently of each other. In F1 generation of a dihybrid cross, offsprings have heterozygous genotypes (RrYy in Fig. 1). When F1 is fertilized to produce F2 generation, the independent assortment of these alleles becomes evident. As shown in Fig. 1, R, r, Y, and y can assort independently to produce four gametes with genotypes (RY, Ry, rY, and ry) in equal proportions. Two new allelic combinations (Ry and rY) are also obtained as a result of independent assortment.

## Independent Assortment and Meiosis

Independent assortment of genes occurs during meiosis in eukaryotes. Each pair of homologous chromosome separates independently of all other pairs in anaphase I of meiosis. Genes located on different homologs will therefore assort independently. However, if the genes are located on the same chromosome, they may or may not assort independently. Genes that are located apart might undergo recombination during meiosis. Recombination allows scrambling of maternal and paternal genes to produce new combinations of genes in the offspring. In effect, recombination increases the chances of independent assortment of genes present on the same chromosome.

## Linked Genes: Inconsistency of Independent Assortment

When genes are located close together on the chromosome, they are said to be linked. So, the alleles are inherited together as a unit more frequently than expected, and this phenomenon is referred to as genetic linkage. The strength of linkage between two genes depends on the distance between them on the chromosome. Linked genes were first observed and reported by William Bateson, Edith Rebecca Saunders, and Reginald C Punnett in 1905. They noted that traits for flower color and pollen shape in sweet pea plants appeared to be linked together (Pierce 2012). Later, work of T.H. Morgan and his student on

*Drosophila* also reported gene pairs that did not segregate randomly according to Mendelian principle, instead tended to be inherited together.

## Conclusion

Mendelian principle of independent assortment based on dihybrid crosses explains that all possible combinations of alleles can be formed during gamete formation with equal probability. However, linked genes are an exception to this principle and are more than frequently inherited together.

## Cross-References

- ▶ [Assortative Mating](#)
- ▶ [Genotype](#)
- ▶ [Linkage Analysis](#)
- ▶ [Mendel's Laws](#)
- ▶ [Mendelian Crosses](#)
- ▶ [Phenotype](#)
- ▶ [Recessive](#)
- ▶ [Recombination](#)

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## Attachment

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## Synonyms

[Arousal regulation](#); [Bonding](#); [Mother-infant bonding](#)



## Definition

Attachment in animals can be defined primarily as the psychological bond between a mother and an infant, although there are some species in which an infant is bonded to its father. The strength of the attachment bond is measured by the degree to which the infant attempts to remain in proximity to the caregiver and the relative extremity of distress experienced by one or both of the members of the bond when access is restricted. Attachment quality is further assessed through the degree that an infant's arousal is reduced by the presence of their mother. The strength and quality of the attachment bond impacts the long-term trajectory of development, including future peer and romantic attachment relationships.

## Introduction

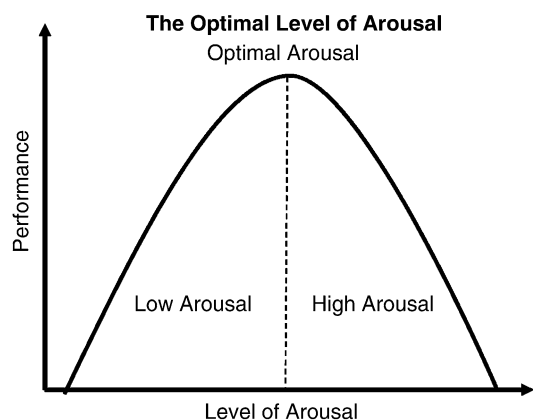
A child seeks his attachment-figure when he is tired, hungry, ill, or alarmed and also when he is uncertain of that figure's whereabouts; when the attachment-figure is found he wants to remain in proximity to him or her and may want also to be held or cuddled. By contrast, a child seeks a playmate when he is in good spirits and confident of the whereabouts of his attachment-figure; when the playmate is found, moreover, the child wants to engage in playful interaction with him or her. (John Bowlby 1969, p. 307)

In altricial species, natural selection has favored processes that keep infants close to their caregiver, most often their mothers who provide protection and assure nutrition, warmth, and, ultimately, survival. Lorenz' studies on imprinting illustrate this process, with hatchlings inherently following the most salient, moving individual they see after emerging from their egg (1937). In primates and other species with larger brains and extended periods of development, mechanisms that keep infants close to their caregiver assure that the infant has sufficient time, as well as a "teacher", to learn the behaviors necessary to survive and successfully exploit their environment. Attachment between an infant and its primary caregiver involves a component of trust, wherein the infant trusts that the caregiver will consistently respond

to its needs, providing psychological and physiological support. Rooted in maternally-induced reductions of infant arousal, the mother adjusts her mature and flexible behaviors to meet the needs of her immature infant, facilitating an attachment bond.

That a mother reduces infant arousal via parenting behaviors to promote infant attachment bonds (arousal regulation theory) is grounded in the Yerkes-Dodson Law, proposed in 1908 by Robert Yerkes and John Dodson, which law posits that an optimal level of arousal is preferred for optimal performance (see Fig. 1).

While mothers are mature enough to regulate their own arousal, altricial infants' brains are not equipped to do so due to their immature emotional neural circuitry. For species in which natural selection has favored a prolonged process of post-natal brain development, where synapses are formed and maintained if they are useful and pruned when they lack utility, the brain has a preprogrammed set of expected inputs, known as the experience-expectant brain. Through forming attachment bonds, adequate experiences occur and expected inputs are received, largely by repeatedly "turning off" the anxiety circuit in the brain as the caregiver nurtures and cradles her infant. By responding to her infant's over-arousal, the mother modifies her own behavior, with a goal



**Attachment, Fig. 1** The optimal level of stress is thought to promote optimal performance on a variety of tasks. This theory has also been applied to development, with a caregiver promoting an optimal level of arousal in its infant until the infant can regulate its arousal on their own

of maintaining her infant's arousal at the optimal level. Optimal arousal is most readily achieved when a mother sensitively responds to her infant's needs, individualizing her care. Likewise, when an infant is under-aroused, a mother will engage her infant, allowing it to explore and play, with a goal of increasing its arousal to the optimal level. By so doing, the mother sensitively engages the immature neural pathways in an experience-expectant manner until the infant matures to point that it can adequately regulate its own arousal.

## Rhesus Monkeys

Forming an attachment bond with a caregiver is a primary feature of primates, infants of which are born altricial and have a relatively long period of infancy when compared to raptors, reptiles, and rodents. Studies of rhesus macaques (*Macaca mulatta*) provide critical insights to the development of attachment theory. To date, they are the most-studied primate in terms of mother-infant relationships. Rhesus monkeys live in complex social groups, organized around matriline, with intricate rules requiring emotional regulation and social intelligence to survive. Infants are largely dependent on their mothers for the first few months of life. Indeed, during the first month of life, an infant rhesus monkey spends virtually all of its time in physical contact with its mother. Mothers provide nourishment, physical touch and warmth, protection from threats, as well as psychological comfort (Harlow 1958). As will be discussed, attachment is based on primary reinforcers, which lead to maintaining close proximity with the caregiver and seeking to eliminate negative reinforcers (Bowlby 1969). As the mother fills basic needs and provides sensitive and persistent parenting, an attachment bond forms rapidly between mother and infant. A mother facilitates an environment in which the infant can grow and develop, learning how to survive in a world much larger than itself. Once the attachment bond is formed, the infant insists on being cared for by its mother, as evidenced by its cries

for retrieval by its mother when it is carried away by another female in the troop, persisting until it is reunited with its own mother. For infant primates, only *their* mother will do. Harry Harlow's anecdote about the first surrogate mother is a prime illustration of this exclusivity (1958). When the first surrogate-reared monkey was born (see below), the surrogate body was ready, but the head was not yet designed. In its place was a faceless ball of wood. When the infant was 6-months-old, it was placed with two cloth surrogate mothers who had painted faces. To the surprise of the experimenters, the infant persistently turned the painted heads until it could only view a blank face, despite experimenter efforts to reorient the face. Later, they observed that the infant learned to remove the painted head entirely, rolling it to a corner of the cage.

That an infant rhesus monkey is attached to *their* mother is similarly illustrated in a study utilizing dogs as surrogate mothers (Mason and Kenney 1974). Infants paired with surrogate dogs were tested to determine whether they formed attachment bonds to *their* surrogate dog mother or whether they would respond similarly to any dog. To do so, the monkeys were given a choice of their familiar dog mother surrogate, an unfamiliar dog, or an unfamiliar inanimate surrogate mother. The monkeys choose their familiar dog surrogate almost exclusively, suggesting a unique attachment bond between the infant rhesus and its specific dog surrogate. When only the unfamiliar dog and the unfamiliar surrogate were available, the infant monkeys chose the unfamiliar dog almost exclusively, suggesting that infants seek out a caregiver that possesses certain expected traits, a finding best understood in the context of developmental theory.

In the wild, on the first day following birth, mother rhesus monkeys spend a great deal of time inspecting their infants' genitalia and looking at their infant's face, presumably assessing the sex of the infant and becoming familiar with their infant's characteristics. Early on, when an infant strays from its mother, it is rapidly retrieved and, should it attempt to nurse from another female, it is rejected, at times vigorously (personal

observations, J.D. Higley), perhaps facilitating rapid infant discrimination of its mother from all other females in the group.

As infant rhesus monkeys develop, it is driven by two primary urges, an inherent desire to explore and play, and a secondary desire to remain in close contact with its mother. As an infant's motor skills mature, it will begin to explore its larger environment, using its mother as a secure base (Hinde and Spencer-Booth 1967). The rhesus infant begins by exploring the area immediately around its mother, engaging in social interactions with its peers. About the time that an infant matures to the point that its motor skills allow it to move farther from mother, a fear of strangers emerges, motivating the infant to remain in close proximity. Arousal regulation is a fundamental aspect of this, as infants experiencing low levels of arousal will seek to increase their arousal via peer play. Then, when they become over-aroused by their environment or by feelings of tiredness or hunger, they will return to their mother, she will comfort them, and they will resume their exploration of their environment.

Perhaps the most defining trait of primates, and one that has made rhesus monkeys the second-most prolific primate (humans being the first-most prolific primate), is the capacity of the species to adapt to a variety of settings and environments, living in diverse ecological niches, including the foothills of the Himalayas and the desert lands of Africa. Such adaptation comes from their propensity for behavioral flexibility, but at the cost of prolonged immaturity and altricial needs. Primate infants are born seeking a familiar caregiver (most often a mother) that, evolutionarily, they expect will provide protection, nourishment, and warmth, as well as social stimulation and support in times of need (Bowlby 1982). Later, the infant must acquire the necessary social skills to become part of the larger society and the specific skills to adapt to their environmental setting. The necessary high levels of advanced cognition and cognitive complexity cannot occur without a prolonged period of learning and advanced brain potential. For primates, most brain cortical development occurs postnatally, and, while there is a clear genetic plan for brain development, synaptic and

axonal growth and pruning must have the right environmental input at the appropriate age, with normative neurodevelopment occurring only after certain expected experiences occur.

## Peer-Rearing

A major function of an attachment bond is to assure that proper input is provided to the infant so that normative development occurs. Evolution has favored mothers as the instrument to provide this input. Absent mother, age-appropriate neuronal development does not occur and developmental abnormalities persist, particularly in arousal regulation. To understand the influence of maternal presence and attachment, differential rearing-conditions are used among laboratory-living rhesus macaques. For these experiments, infant monkeys are assigned at birth to a mother-rearing, a peer-rearing, or a surrogate peer-rearing condition (see Shannon et al. 1998 for a detailed methodology). Briefly, mother-reared (MR) monkeys are raised by their biological mother in conditions approximating the natural environment. Peer-reared (PR) and surrogate-peer-reared (SPR) monkeys are separated from their biological mothers following birth and are hand-raised in a nursery for 30 days, at which time they have access to an inanimate, cloth-covered surrogate mother. At 30 days of age, PR monkeys are rehoused with 3–4 same-aged peers, to which they develop strong attachment bonds in nearly all cases. Starting at 30 days of age, SPR monkeys are giving access to 4 same-aged, similarly-reared peers for 2 h per day.

While PR monkeys receive social stimulation in the form of their peer-groups, their peers are not capable of regulating their arousal the way a mother can. SPR monkeys are also deprived of a mother's regulatory capacities, and are further deprived of normative social stimulation. Thus, via examining developmental differences between these three rearing groups, researchers attempt to disentangle the effects of maternal presence and peer presence on development in rhesus monkeys.

The absence of mother during periods of attachment formation results in SPR and PR

monkeys exhibiting infant-like clinging well into adolescence. SPR and PR monkeys appear to never learn how to be entirely independent and tend to attain lower social dominance rank positions than MR monkeys, with SPR monkeys occupying the lowest ranking positions (Bastian et al. 2002). Further, SPR and PR monkeys tend to engage in anxiety-driven, self-directed behavior (i.e., hair-pulling, self-biting, sucking on hands or feet) (Suomi 1991), whereas MR monkeys rarely engage in such behavior. PR monkeys tend to be more anxious overall, particularly in response to novelty (Higley et al. 1991b; Dettmer et al. 2012), suggesting that, with no mother to regulate their arousal, they remain chronically over-aroused. PR monkeys also tend to engage in anxiety-mediated high alcohol intake (Higley et al. 1991a), when compared to MR monkeys. Furthermore, PR monkeys tend exhibit infrequent, but more vigorous and wound-producing bouts of aggression than do MR monkeys, suggesting deficits in their abilities to self-regulate.

Brain differences are also present among PR monkeys, which exhibit enlargement in stress-sensitive areas of the brain (i.e., dorsomedial prefrontal cortex, dorsal anterior cingulate cortex) (Spinelli et al. 2010), when compared to MR monkeys. They also showed variety of central nervous system (CNS) deficits (Espinell and Higley 2013).

## Components of Attachment

For the majority of primates, the first weeks of life are spent in almost constant physical contact or at least in close proximity to their mothers, who provide for their physiological and psychological needs. Rhesus infants are unable to thermoregulate or find food adequately during the first 2 weeks of life, driving the fragile infant to cling to their mother for their every need. This is likely a crucial feature of forming an attachment bond, as the infant learns to trust their mother as the provider of their needs. Later, infants use their mother as a secure base from which they can safely explore, keeping within her in sight just in case their arousal becomes dysregulated. As a

student of the Yerkes-Dodson law, Harry Harlow noted how mother rhesus monkeys reduce their infant's arousal, becoming a source of security in a sometimes frightening, unknown world. Harlow had already challenged the prevailing learning theory of the day by showing that infant monkeys possess an inherent curiosity about the world, as they would repeatedly open a "peep-hole" to simply see what was outside when placed in an opaque box (1958). Harlow found that this drive to discover the world and to explore and play with peers is attenuated when an infant is over-aroused. The genius of his surrogate mother experiments was to show that a soft, terry-cloth surrogate mother possesses the primary features necessary for attachment to form, demonstrating the types of experiences that the brain requires for normative development. Real mothers allow infants to cuddle, leading to arousal reduction and reduced fear and anxiety. Subsequent studies showed the importance of warmth and vestibular stimulation, as lesser but additional aspects of arousal reduction and security of attachment (Harlow 1958, 1960).

When a mother is not available, infants will seek out an attachment figure that is most like a mother. In his seminal studies on mother-infant attachment in rhesus macaques, Harlow concluded that the attachment bond between an infant and a caregiver is not based purely on the physiological need for nourishment, a common viewpoint at the time (Harlow 1958). In this study, he separated infants from their mothers after birth and reared them in a nursery where they had access to a wire and a heated, cloth-covered, inanimate surrogate mother. To determine an infant's preference for the wire or the cloth-covered mother, Harlow put the bottle from which the infants fed on either the wire or the cloth-covered mother, forming two conditions under which he observed the duration of infant time spent on each mother. The availability of the food on the wire mother was clearly of negligible importance to the infants, which spent the majority of their time on the soft, warm, cloth-covered mother. The infants even went as far as to cling to the cloth mother, while leaning over to nurse off of the wire mother, maintaining



**Attachment, Fig. 2** Illustration of the infant motivation to form attachment bonds based on a specific set of needs that clearly go beyond the physiological need for nourishment early in life (Harlow 1960)

constant contact with the warm, cloth-covered mother (Fig. 2).

That the infants were observed seeking out comfort from a secure base, despite the availability of food elsewhere, suggests that it is a crucial component of the attachment bond. When an infant's arousal is dysregulated by fear or discomfort, they seek to be cuddled by a warm, soft mother on which they can count on to supply their needs.

Vestibular motion provided to the infant by the mother is also a component of the attachment bond for the first 6 months of life, as demonstrated by Harlow (1960). To investigate this, infant monkeys were given access to a constantly rocking, cloth-covered surrogate mother and to a stationary, cloth-covered surrogate mother at birth. For the first 6 months of life, the infants consistently spent more time on the rocking surrogate, suggesting that the kinesthetic motion that the mother provides is a part of the specific needs of the infant. After the infant is 6 months old, the duration of time spent on either of the surrogates is comparable, suggesting that, when the infant reaches 6 months of age, they are developed enough to provide themselves with adequate proprioceptive stimulation.

Contingent feedback, is another crucial component of the attachment bond. From this, the infant learns what is acceptable and what is not acceptable, and what they should fear and what they should accept as part of their world. Work by Mason and Kenny (1974) and Mason and Capitanio (1988) demonstrates that the availability of a secure base allows the infant to learn the basis of all future social skills, reciprocity, through contingent stimulation. They found that infants raised with dogs as surrogate-mothers (they both move and respond to the infant), were more likely to explore and showed more competent peer relationships. While dogs are not as adept as are mother rhesus monkeys to adjusting their behaviors according to their rhesus infant's needs, sensitive dog parenting was enough to meet the expected needs of the infant and adequate social skills developed. Furthermore, when Brunelli et al. (2014) gave infants access to responsive and non-responsive surrogate mothers, it was clear that the infants raised with the responsive surrogate mothers exhibited more confident behaviors, as well as improved social skills.

## Evolutionary Basis of Attachment

To Harlow, the central aspect of attachment was that a mother possessed both the qualities for survival and for normative psychological and socioemotional development. Studies suggest that sensitive parenting leads to reduced arousal (Levine et al. 1985) and, over repeated episodes, maternal reduction of anxiety and arousal induces survival and pruning of the cortical axons and synapses that project to and from the older mammalian stress and bonding centers of the brain, areas that attenuate the stress response (Zhang et al. 2005). The advanced cortical wiring of primates is based on the experience-expectant brain, with genetics providing a directional map and mothers providing the necessary input at the age-appropriate time.

John Bowlby, the founder of attachment theory, was an admirer of Charles Darwin's evolutionary theory and viewed attachment as a facet of evolution. In his book, *Attachment*, he describes



**Attachment, Table 1** Infant behaviors in separation paradigm are thought to be divided into phases, grounded in attachment theory, and based on the infant motivation to get back in close proximity with their caregiver

| Protest phase                                 |                                                                             | Despair phase                                                                                  |                                                                                                          | Detachment phase                            |                                                                                        |
|-----------------------------------------------|-----------------------------------------------------------------------------|------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------|---------------------------------------------|----------------------------------------------------------------------------------------|
| Behavior                                      | Evolutionary basis                                                          | Behavior                                                                                       | Evolutionary basis                                                                                       | Behavior                                    | Evolutionary basis                                                                     |
| Crying, screaming, increased motoric activity | Draw the attention of caregivers, to reduce the risk of injury or predation | Silencing, despondency, reduction of motoric activity, and fetal-positioning in rhesus monkeys | Reduce likelihood of injury from excessive movement and the likelihood of calling attention to predators | Resum normal activity without the caregiver | Cast off old attachment bonds in the preparation to make new bonds with new caregivers |

A

the influence of Harlow as central to the development of attachment theory (1969).

Trained as a psychologist and psychiatrist, Bowlby was struck by the response of human children to separation from their mothers for routine hospital procedures. Noticing the parallel responses of human and rhesus monkey infants to separation, Harlow’s studies of rhesus monkeys were critical in forming the theoretical model of attachment. While Bowlby noted that human infants display a specific sequence of behaviors when they are separated from their mothers, Harlow showed that rhesus infants vocalize loudly and ardently in attempts to elicit maternal retrieval. Infant motivation during separation from their attachment figure is largely based on getting back in close proximity with their caregiver, who offers them the best chance of survival (Bowlby 1969). If they are not retrieved by their caregiver, infants typically enter a despair phase, where their overall motor activity decreases and their cries cease. If the despair phase persists, some infants enter into a detachment phase, where they resume their normal activities, absent a caregiver. While these infants show maternal independence, they exhibit atypical responses to peers’ solicitations to play and to social challenge, suggesting that their development is impacted by the lack of a reliable, sensitive caregiver. When it is clear that the caregiver is no longer available, orphaned rhesus infants are sometimes adopted by other members in the troop, increasing their chance of survival to adulthood and allowing normative socioemotional development to occur.

Based on Harlow’s findings with rhesus monkeys, Bowlby believed that infant response

during separation is evolutionarily driven, and divided into phases, with responses in each phase optimally supporting the infant’s survival (see Table 1). These phases have been observed in most primate species undergoing an experimental separation paradigm, lending support to the evolutionary basis of attachment.

In the detachment phase, Bowlby saw the underlying change in behaviors shift from a focus on only mother to a post-mother attachment state. According to Bowlby, infants that find their caregiver no longer available prepare to form an attachment bond with a new caregiver. This was illustrated by Mason and Kenny (1974) while investigating attachment bonding between infant rhesus monkeys and dogs. Following separation from their familiar attachment-figure (the dog), infants entered into a protest phase and reacted in fear to unfamiliar dogs presented to them as potential new attachment-figures. This fear diminished rapidly and, thereafter, the infant monkeys spent their time in frequent contact with previously unfamiliar dogs, sleeping, playing, and remaining in close proximity, showing similar attachment-like behaviors as they did to their earlier surrogate-dog mother. When the previously unfamiliar dogs were separated from the infants for an exercise period, the infants now exhibited protest-phase-typical behaviors, suggesting that an attachment bond had been formed.

Attachment Quality

Bowlby’s student, Mary Ainsworth, was instrumental in developing methods of assessing the



quality of attachment (1979). While attachment quality has not been quantified in animals in the same manner that Ainsworth and her students did in humans, it is clear that the quality of attachment varies between mother-infant pairs. Even in rodent species, pups that receive normative maternal care (licking) show varying outcomes in response to how much they have been licked by their mother (Weaver et al. 2004). Parenting quality is a predictor of the quality of attachment-bond formation and is a feature of normative development. Monkeys reared in peer-groups without mothers show atypical development, likely because PR monkeys lack the maturity to modify their behavior sensitively according to their peers' needs. Thus, PR monkeys receive virtually no sensitive care, as their caregiver is absent and the feedback from their world is in the form of the fearful responses from their same-aged, equally maternally absent peers. Consequently, their development does not occur along a normal trajectory, and while Ainsworth's attachment styles have not been rigorously applied to other animals or primates, there is clear evidence that nonsecure attachments occur when an attachment source fails to respond sensitively to an infant's needs.

As further evidence, one study investigated attachment in PR monkeys through assessing specific attachment to most-preferred peers (i.e., "best buddies") versus familiar peers and unfamiliar peers (Higley et al. 1992). Subjects' attachment behaviors were compared to MR controls. In the home-cage, clear preferences for peers emerged. The behaviors that the subjects displayed with their most-preferred peer (i.e., ventral clinging, vocalizations, etc.) are comfort-seeking behaviors typically exhibited by infant monkeys toward their mothers to reduce arousal. To test for peer-preference, a focal animal was placed in a circular chamber with several clear plexiglass doors that could also be covered with opaque doors. Familiar animals from their PR group, including their most-preferred peer, as well as strange, same-aged animals were placed behind these doors. The doors were opened in a sequential manner, allowing access to their most-preferred peer, a familiar peer from their group, or

to an unfamiliar peer. Not surprisingly, subjects spent significantly longer time in close proximity with their most-preferred peer than with all the other animals combined, including with familiar peers from their natal group. They exhibited reductions in stereotypies (an indication of anxiety) when they were with their most-preferred peer, and decreased stereotypies when they were with any other animal. However, when compared to MR subjects, PR monkeys exhibited more vocalizations and more self-mouthing even in the presence of their "best buddy," which could be interpreted as a sign of a nonsecure attachment, as they failed to derive the same level of security from their "best buddy" as did the control MR subjects from their mothers.

Subtle differences in the mother-infant relationship can also lead to differences in attachment quality. For example, Rosenblum and colleagues (1984) have spent the past three decades studying mother-reared bonnet macaques (*Macaca radiata*). Experimenters varied the environmental demands for maternal foraging so that food was easily obtained (low foraging demand (LFD)), difficult to obtain (high foraging demand (HFD)), and in a third category of variable and unpredictable foraging requirements (variable foraging demand (VFD)). While on its face, it might seem reasonable to predict that the increased amount of time that HFD requires for the mother to obtain food would lead to maternal inaccessibility and a nonsecure attachment, the results showed that the unpredictable nature of VFD made maternal accessibility unpredictable and, consequently, led to what could be considered nonsecure infant attachment, with the infants showing less affiliation, more negative emotions, and a subordinate rank when compared to the infants from the other two conditions. Moreover the VFD group exhibited high CSF corticotropin-releasing-hormone (CRH), 5-hydroxyindoleacetic acid (5-HIAA), norepinephrine, and low growth hormone, suggesting deficits in CNS development. Many of these behaviors and the underlying CNS differences persisted into adulthood, suggesting long-term effects of early nonsecure attachment.

## Genetic Contributions to Attachment

Studies assessing genetic contributions to attachment in animals have focused on genes that have implications on stress-response and behavioral reactivity. For example, certain mu-opioid receptor polymorphisms (OPRM1) are thought to increase the activation of the endogenous opioid system (Barr et al. 2008), with infants carrying a G allele presumably experiencing enhanced feelings of reward when in contact with their mothers, as compared to infants not carrying a G allele. Indeed, Barr and colleagues (2008) show that infants with a G allele show significant increases in attachment-related behaviors at baseline and during periods of separation, when compared to infants not carrying a G allele.

Another gene commonly assessed in studies of attachment is the serotonin transporter gene (5HTT), with the short allele commonly linked to dysregulated serotonin system function and the long allele linked to normal functioning. It appears that early maternal deprivation modulates the effects of possessing a short allele, with PR monkeys with a short allele exhibiting deficits in central serotonin functioning, while MR monkeys with a short allele appear undifferentiated from MR monkeys with a long allele (Bennett et al. 2002). This suggests that early maternal presence may compensate for the effects of certain deleterious genes, while maternal absence may exacerbate the negative outcomes.

## Effects of Child Abuse on Attachment Outcomes

From the first day of life, mothers are a reliable secure base, providing protection and accessibility to resources (Kraemer 1997). With a secure base, novel experiences become learning experiences from which the infant learns critical information necessary to understand normative, social and nonsocial, cause-and-effect relationships. Infants generalize their experiences from the mother-infant relationship to their later

experiences, impacting how they relate to others in the future. If mothers cannot be relied on to provide a secure base, then, as infants become juveniles, they develop the same set of expectations about peer and other relationships (Ainsworth 1989).

Aberrant attachment relationships, relegate a primate to a life-long pattern of difficulty in social relationships, emotional deficits, and often a life of low social status and, at times, social ostracism. One of the most devastating effects on attachment is that of abuse by a mother. That an infant forms and maintains an attachment to its abusive caregiver speaks to the intense motivation for an infant to form an attachment. As the mother is the only secure base available to an abused infant, her abuse elicits increased infant attempts to cling and seek relief, which too often lead to more abuse. Periods of abuse are followed by periods of normative maternal care and solicitude (Maestripieri 1998). At an age that is critical to developing what Bowlby and Ainsworth would have characterized as “felt security,” abusive mothers reject, often aggressively, their infants’ attempts to cling to them and to use them as a secure base. This lack of sensitively responding to their infants’ psychological needs appears to have a more negative effect on infant developmental outcomes than the abuse itself, an indication of the importance of mothers adjusting their behaviors to sensitively respond to their infant’s needs. Consequently, a mother who abuses her infant creates a mother-infant attachment bond characterized by approach-avoidance. Her lack of sensitivity to her infant and coordination of her behaviors when the infant is aroused leads to an attachment quality that in many ways parallels the disorganized attachment classification seen in human infants that are abused and neglected, characterized by freezing, stereotypes, and other indices of stress and fear (McCarthy and Taylor 1999; Main and Solomon 1990; Lyons-Ruth et al. 2013).

There is an abundance of negative consequences for infants who develop in an abusive environment. For nearly two decades, researchers

at the Yerkes National Primate Center have studied a group of rhesus monkey adult females that abuse their infants. These abused infants show evidence of pathological negative emotionality: increased fear and anxiety to social stressors and high levels of aggression (Howell and Sanchez 2011). Studies suggest that abused infants develop a cognitive bias to classify facial cues as being aggressive (often even when the cues are not aggressive), and to respond to typical challenges with inappropriate levels of aggression (Howell and Sanchez 2011). Not surprisingly, they also show elevated levels of resting cortisol. Other measures of hypothalamic-pituitary-adrenal (HPA) axis functioning also show abnormal dysregulation. For example, in response to a CRH challenge, they show increased cortisol, but blunted adrenocorticotrophic hormone (ACTH), perhaps an indication of prolonged hypercortisolemia which leads to blunted ACTH (Sanchez et al. 2010). Interestingly, the effect on the HPA axis is more pronounced in abused female infants than in abused male infants. Abused infants also show high levels of epigenetic marks in genes that modulate white blood cell functioning, primarily due to early and frequent maternal rejections, possibly leading to a biological tendency for increased illness (Sanchez et al. 2007). Even as infants, abused subjects show evidence of biological damage, as evidenced by damaged, shortened telomeres. They show impaired central nervous system serotonin functioning, with low CSF 5-HIAA concentrations. They show reduced white matter in the cortex and as well as reduced white matter tract integrity (Howell et al. 2013). Risk for maternal abuse increases if the infant is born with the deleterious short allele of 5HTT (McCormack et al. 2009). Furthermore, there is evidence that females abused as infants are at risk to abuse their own infants when they become mothers. As shown by cross-fostering studies, female infants learn from their abusive mother to respond to their own future offspring as they were treated, with females who were abused infants much more likely to become abusive mothers as they reach adulthood and have their own offspring (Maestripieri 2005).

## Conclusion

The attachment bond between an infant and its caregiver is a critical feature of normative development for primates. Infants are born requiring that a specific set of needs are met by a caregiver, which must be reliable and sensitive to their changing needs, and which will provide them access to necessary resources to ensure their survival. As altricial infants do not have the capacity to self-regulate their arousal, their caregiver plays a crucial role in maintaining an optimal level of arousal in the infant through calibrating their parenting behaviors to meet the infant's needs.

Evolutionary theory suggests that attachment bonds have developed between mothers and infants to ensure infant survival to reproductive age and to ensure normative socioemotional development. Mothers or other caregivers tend to supply infants with experiences that promote this development. Individuals raised without their mothers tend to exhibit anxiety and reduced social skills, reducing their capacity to reproduce and become parents themselves. Individuals raised with abusive mothers tend to exhibit disorganized attachment bonds and neurodevelopmental deficits, and are at risk to abuse their own infants in the future.

Certain genetic and environmental factors are useful in understanding the development of the attachment bond. It is clear that both genetic and environmental factors play a role, interacting to produce the attachment bond. Understanding the impact of genetic risk and sensitive parenting on the attachment bond and the impact of attachment bond quality on later outcomes are central features of attachment research.

## Cross-References

- ▶ [Affiliative Bond](#)
- ▶ [Altricial](#)
- ▶ [Human Infancy and Childhood](#)
- ▶ [John Bowlby](#)
- ▶ [Konrad Lorenz](#)
- ▶ [Parental Investment](#)

- Parenting
- Reproductive Fitness

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## Attention

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Attention, then, is the name given to a device, whatever its nature, whereby one stimulus has its effectiveness increased over that of others whose physical energy may be greater...a device to secure reaction to the most vitally important of several stimuli acting at once upon the organism. (Margaret Floy Washburn 1908, pp. 313 & 316)

## Definition

Attention – broadly defined as “selection for processing” – has been a focus of psychological inquiry since the birth of psychology as a science. Wilhelm Wundt, William James, James McKeen Cattell, Edward Titchener, James Mark Baldwin, Herman von Ebbinghaus, Walter Bowers Pillsbury, and other early psychologists studied and wrote about attention in the late 1800s and early 1900s. As is clear from the quote from Washburn’s (1908) classic *Animal Mind: A Textbook of Comparative Psychology*, researchers interested in *animal* thinking and behavior were also curious about the process by which organisms experience, to borrow the well-known phrase from James (1890), “...the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others and is a condition which has a real opposite in the confused, dazed, scatterbrained state which in French is called *distraction*, and *Zerstreuung* in German” (pp. 403–404).

Note that the focus of M. Washburn’s definition of attention emphasizes the selection and prioritization of stimulus information that does not compel observation and response by virtue



of intensity, priority, frequency, salience, or similar physical reason. Washburn described the process by which animals may arrest responses to prepotent sources of stimulation so as to select and to react to other channels of information. This, for Washburn and a host of scholars who followed her, became the signature of attention, demonstrated not so much in the fact that organisms respond to stimuli, but rather in the fact that they respond to a selected subset of stimuli – with selection not dictated solely by stimulus potency – accompanied by diminished response any unattended stimuli.

### Attention as Observing Responses

During the half-century period of American behaviorism, research on attention declined and changed dramatically. Indeed, there was considerable controversy during this period as to whether the construct of attention was even necessary and useful to account for nonhuman animal behavior (Roitblat 1987). Of the nearly 5000 publications indexed by PsycINFO prior to 2021 with “attention” as the subject term and “animals” as the population, only 1 (Dashiell 1920) was an empirical study published during the behavioristic heyday of 1920–1960, and attention was not the central focus of that maze-learning research. This, of course, reflects the more general trend in psychology during this period of history, as less than 1% of the PsycINFO publications in which “attention” is a subject term appear in the half-century following Watson’s (1913) behaviorist manifesto.

This is not to suggest that the experimental analysis of behavior ignored stimulus selectivity altogether; to the contrary, what had previously been inferred as “attention” was operationally defined as “observing responses” or some similar measurable behavioral indicators of selection. Studies of discrimination learning, especially those relating to the phenomenon of blocking, allowed researchers to investigate conditions in which animals that almost certainly sensed multiple simultaneous stimuli or stimulus features (e.g., the color and shape of a stimulus), only learned to respond to a subset of those cues (e.g., perhaps to

color). Other cues that were available in the stimulus array failed to control behavior discriminatively. In a classic blocking experiment, Kamin (1968) exposed rats to electric shock preceded by a signal. The signal was first comprised of a single element (e.g., noise). The signal was then compounded with a second element (e.g., light). Rat subjects responded to the first conditioned stimulus (i.e., noise) with a reduction in an appetitive response, but this behavior was not extended to a light signal when presented alone. Whether this pattern of behavior was due to the subjects not noticing the second stimulus dimension or intentionally ignoring it, the subjects demonstrated selection.

Like blocking, overshadowing is a phenomenon observed in traditional behaviorist experiments where animal subjects appeared to attend selectively. With overshadowing, subjects attend to one of two or more stimulus features more acutely due to salience. In the aforementioned blocking experiment, Kamin (1968) also presented rat subjects with compound stimuli in learning trials. That is, these rats were exposed to a simultaneous light and noise signal before the onset of electric shock. When the compound stimulus was decoupled, rats demonstrated more suppression of the appetitive response with the light signal than the noise signal. This again demonstrates that nonhuman animal subjects were able to sense both dimensions of the compound stimulus but were weighting these dimensions selectively. These results led researchers (e.g., Sutherland and Mackintosh 1971) to conclude that nonhuman animals employ two processes: one for the selection of relevant stimulus dimensions and a second for the relative weighting of these stimulus dimensions. Interpretations of these and similar blocking, overshadowing, and cue-competition studies produced learning models that included a limited capacity for the acquisition of unique associations (e.g., Rescorla and Wagner 1972).

The so-called cognitive revolution of the late 1950s and early 1960s was catalyzed in large measure by a return to the experimental study of attention by psychologists. Scholars like Donald Broadbent, Colin Cherry, Anne Treisman,



George Miller, J. A. and Diana Deutsch, Ulrich Neisser, and others brought information-processing (i.e., cognitive) perspectives to the study of limits and selectivity. The metaphors (e.g., filters and bottlenecks, resources, spotlights) and methods (e.g., vigilance, visual search, Stroop, flanker, cuing) from the study of human attention were applied by comparative psychologists to the study of animal cognition. Additionally, behavioral neuroscientists made substantial headway in the understanding of the neuroscience of attention through the use of animal models (e.g., see reviews by Posner and Petersen 1990; Pribram and McGuinness 1975). Whereas in recent decades, the cognitive neuroscience of attention has benefitted greatly from neuroimaging and electrophysiological studies of humans engaged in attention-related tasks (e.g., Hopfinger and Slotnick 2020; Rueda et al. 2015), this work has consistently been complemented (an indeed preceded) by studies of attention in animal models, using cell-recording, pharmacological interventions, and other techniques (e.g., Rahi and Kumar 2021). Animal research has informed much of what is known about the bilateral dorsal frontoparietal network that is active during controlled or endogenous attention, and the right-lateralized ventral frontoparietal stream that is implicated when attention is captured exogenously, as well as the brain structures within these pathways that are differentially activated by the different types or functions of attention. Thus, the dorsal and ventral pathways map on, appropriately enough, to “top-down” (i.e., concept-driven or goal-directed) and “bottom-up” (i.e., data-driven or reflexive) cognitive processing. The present review cannot do justice to the hundreds of published studies that examine the neurobiological mechanisms of attention in animals but acknowledges that this invasive work from behavioral neuroscience has frequently outpaced the purely cognitive and behavioral investigations of animals paying attention.

Similarly, any brief review of the behavioral research on animal attention is unavoidably selective. Attention has become a fruitful topic of investigation in comparative cognition;

additionally, many scholars who study other aspects of animal cognition have also contributed to the literature on attention. More detailed reviews of animal attention have been published (e.g., Bushnell 1998; Herbranson 2017; Roitblat 1987; Washburn and Tagliatela 2012; Zentall 2012). The goal of the present review is to highlight some of the major figures and most common behavioral paradigms that have contributed to our understanding of animal attention. As an additional caveat, it should also be noted that the present discussion ignores the substantial and growing comparative literature on social attention, including studies of joint attention, attention-seeking and -getting behaviors, and attention to social stimuli such as faces and dominance cues. These are interesting applications of attention for the study of social cognition but seem less relevant to the present more foundational review of what attention is and how it manifests in animals.

The comparative study of attention was greatly influenced by three of the first behavioral researchers to discuss the topic in the years following the cognitive revolution. Nicholas J. Mackintosh conducted early research and reviews that culminated in a theory of attention in discrimination learning (Mackintosh 1975). Donald S. Blough’s research program included innovative studies of visual search by pigeons – a topic also examined extensively by Patricia M. Blough (see review by Blough 2006). Donald “Al” Riley combined the aforementioned research topics, studying selective attention in pigeons’ discrimination-learning and visual-search performance, making both direct contributions to the understanding of processing of multidimensional stimuli (Riley and Roitblat 1978) and also inspiring other comparative psychologists to study attention and similar cognitive topics, many summarized in a published volume in his honor (Zentall 2013).

## Types of Attention

The work by these seminal scholars serves to illustrate two of the three primary types or

functions of attention that have been identified from extensive research with humans: Attention Focusing (i.e., selection, filtering, resistance to distraction, concentration) and Attention Scanning (i.e., shifting, switching, orienting, dividing). The third primary subskill of attention is Attention Sustaining (i.e., vigilance, alerting, watchkeeping, signal-detection; see Posner and Petersen 1990 for discussion of these three attention systems). This multidimensional character of attention has long been acknowledged, although there has been debate about the number and nature of the attention factors or types. Whereas there may be other identifiable attention skills, there is strong agreement about these three, and each has been examined in the animal-cognition literature. To date, sustained attention has been the least studied aspect with animals by far. Tests of sustained attention require animals to monitor a source of stimulus input (e.g., a computer display) or a period of seconds or minutes while they wait for the appearance of a to-be-detected stimulus. The signature finding associated with sustained-attention research is the vigilance decrement: responses are slower and errors (missed targets) are more frequent as the watch-period increases. Most of the literature on animal vigilance-related performance is neuroscientific in focus (see summary by Sarter et al. 2001), in which sustained attention is somewhat easier to test because the animals are commonly restrained so that the psychophysiological correlates of alertness and vigilance can be recorded. However, there are a few published behavioral studies of animals' capacity to sustain or extend attention (e.g., Bettie and Rosati 2021; Frigaszy et al. 2009; Maki 1975). Some of this behavioral work measures extended attention based on social cues, but more traditional testing paradigms have also been used, like signal detection paradigms in which an organism must respond to the presentation of a target stimulus, the appearance of which might be delayed for some period of time, and might follow presentation of a sequence of nontarget stimuli.

The scanning of attention is well illustrated by the visual search paradigm, a classic test of the spatial orientation of selective attention. The goal is to locate a target stimulus that is presented in a

simultaneous array of nontarget images, and to do so as quickly and as accurately as possible. Countless studies with human participants established the signature findings for attention in this paradigm: target-detection generally increases as the size of the search array increases, unless the target is physically dissimilar from the nontargets (e.g., finding a T embedded in an array of letters like C, G, and O), in which case, the target pops out with equal rapidity and accuracy irrespective of the number of nontargets. Set-size slopes correspond to the serial, spatial scanning of attention. Since Blough's systematic demonstrations of target location by pigeons, subsequent research on attention using the visual-search paradigm was conducted with primates, dogs, rats, birds, fish, and other animals (e.g., Cook et al. 2012; Tomonaga 2008; Washburn and Tagliatela 2006; Zhou and Desimone 2011). For example, Reichenthal and collaborators (2020) provided an extensive review of the visual-search literature in humans and animals, including new data showing serial-search and pop-out effects for archerfish performing a battery of visual-search tasks requiring location of target stimuli distinguished by color, size, shape, or a conjunction of features.

Attention shifting has also been studied using variations on a cuing paradigm. For tasks in which stimuli can appear in multiple locations, response time and accuracy may be facilitated by directing the organism's attention to the spatial location in which the target will appear, just prior to the presentation of that target. This shift in attention can be exogenous: for example, a flash to the periphery will elicit an involuntary shift toward the sudden flash or perceived movement. Conversely, organisms can be trained to divert their attention to a spatial location endogenously: for example, a symbolic cue (e.g., an arrow) might be used to train an animal to shift attention either to the left or the right of a fixation point. Faster and more accurate responses on cued trials than on uncued trials – or on invalid cuing trials, in which the target stimulus appears in a position other than the one that was cued – is taken as evidence of a covert shift in attention (Eckstein et al. 2013). Cuing tests such as these are popular for the study of human attention and have also

been employed in the study of attention with nonhuman animals. For example, Li and collaborators (Li et al. 2021) found that mice were significantly faster and more accurate in the validly cued compared to the invalidly cued trials, for both the endogenous and the exogenous conditions. In the most demanding form of the cuing paradigm – the antisaccade task – a cue in one stimulus location requires the shifting of attention in the opposite spatial direction. For example, a flash to the left of fixation signals that the discriminatory stimulus will subsequently appear to the right of fixation; thus, responding can be facilitated if the organism can resist the exogenous pull of the flashing cue and shift attention endogenously instead in the opposite spatial direction. This antisaccade task, which has proven to be one of the most important measures of the capacity to control the spatial orientation of attention in humans, has been successfully employed in the study of animal attention (e.g., Johnston et al. 2009). For example, Everling and DeSouza (2005) examined the role of the prefrontal cortex in resolving the competition between reflexive attention capture and goal-directed, endogenous shifts of attention by monkeys that were trained to make prosaccade (i.e., toward the flash) and antisaccade eye movements.

The antisaccade task makes a fitting transition to tests of attention focusing or concentration: endogenous or goal-directed control over the direction of attention shifting is also related to the intensive, mental-effort aspects of attention that are included in this dimension, frequently called “executive attention.” The focusing of attention has been studied with various procedures that indicate which stimuli have been selected for processing and response and which have been ignored (e.g., DeSouza and Everling 2004). To disambiguate the degree to which the organism is actually *selecting* (i.e., choosing which stimuli to process), in contrast to having attention elicited involuntarily on the basis of stimulus intensity or salience, it is typically necessary to put stimuli (or stimulus features) in competition with one another. That is, one studies attention focusing by testing organisms under conditions in which the to-be-responded-to

stimulus is not the most intense, salient, or prepotent cue. The aforementioned discrimination-learning paradigms provide one example of this strategy: Given stimuli with multiple features to which an organism may respond, some subset of the cues get selected and others – even others that would otherwise be most salient – get ignored (e.g., Castro et al. 2020; Leith and Maki 1975). Ironically, this means that the mark of focused attention lies in the fate of the unattended or unselected stimuli – or, as MF Washburn (1908) wrote, “The most fundamental characteristic of attention, then, is perhaps that aspect of it which has been called *abstraction*, the diminished effectiveness of stimuli not attended to” (p. 293).

Focused attention then is the promotion of some stimuli, particularly those that might not be selected for processing on their own strength, and the abstraction or demotion of other stimuli, despite what might be the natural predisposition to select these latter sources of stimulation. Nowhere is this activity of attention better (or, at least, more frequently) illustrated than in the Stroop paradigm (Washburn 2016). With thousands of articles on Stroop effects in the literature, the task is one of the most familiar in psychology. Participants are required to name the color of stimuli, which may themselves be incongruous or congruous names of colors (e.g., the word BLUE written in red, or the word RED written in red – where the correct response in both cases should be “Red”). Innumerable variations of the Stroop paradigm have been developed and tested, each pitting stimulus cues in competition with one another, and with the response requirements to ignore (if possible) the strong stimulus–response habits associated with one cue (e.g., the strong tendency to read and process word meanings) and to respond instead on the basis of the less potent stimulus–response association (e.g., name the print color). Relative to control conditions, such as naming the color stimuli like “XXXXX” or of noncolor words, responses are slower and more error-prone when the word–meaning and the word–color are incongruent. Conversely, responses may be facilitated when word meaning and word color are congruent. D. Washburn (2016) reviewed this literature and reported such Stroop-

like effects for rhesus monkeys tested on a numerical variant on the paradigm. On this variant, number-experienced monkeys were slower and less accurate to select the array of stimuli with more items when the stimuli in the arrays were themselves incongruent numerals (e.g., to select five 2 s as larger than four 7 s). On a range of variations on the task, other animals have also demonstrated the capacity to focus attention on relatively weak cues, albeit with interference from response competition from the stronger, prepotent stimulus dimensions.

Flanker tasks, in which a target stimulus is surrounded by congruent or incongruent flanking stimuli, have also been used extensively to study focused attention in humans. Ineffective concentration of attention is evidenced by interference or facilitation of the flanking stimuli, relative to trials in which target stimuli are unflanked or are surrounded by neutral stimuli. For example, Bramlett-Parker and Washburn (2016) reported that rhesus monkey could use top-down control to over-ride the bottom-up interference from incongruent flanker stimuli. You and Mysore (2020) similarly reported endogenous and exogenous attention by unrestrained mice in an innovative flanker paradigm.

Focused attention can also be demonstrated in relatively enhanced processing of the attended stimulus. For example, D. Washburn studied the effects of stimulus movement on learning, memory, and other cognitive processes. In a series of studies, humans and monkeys learned and remembered better when they had to use a joystick to pursue and catch moving stimuli on a computer screen, compared to when the stimuli remained stationary as the participants brought a computer-generated cursor into contact with each. This “stimulus movement effect” was not a result of attention capture from the natural predisposition to orient attention toward motion, but rather reflected the focusing of attention elicited by the mental effort required to capture the moving stimuli (Washburn 1993). In one study, the enhancement of learning and memory for stimuli that moved on the screen was accompanied by a decline in performance on a concurrent, secondary tone-detection task. This type of

complementariness in dual-task performance has been used in hundreds of studies with human participants to measure the allocation of attention resources between tasks, such that the more attention is concentrated on one task, the fewer processing resources are available for the concurrent secondary task. Smith and collaborators (Smith et al. 2013) provide an example of this dual-task paradigm in the comparative literature, reporting that monkeys showed disruption of attention-demanding uncertainty-monitoring performance (but not basic perceptual performance on a psychophysical judgment task) as their attention was demanded for a concurrent memory task.

## The Control of Attention

To summarize, psychologists have been curious about the selectivity of stimulus processing since its birth as a science, and have investigated with particular enthusiasm the following questions over the last 60 years: What is attention? How is attention realized neurobiologically? How is attention controlled or determined? Studies with animals by comparative psychologists and behavioral neuroscientists have helped to elucidate the multidimensional nature of attention and its neural substrates, complementing the findings from human cognition that attention serves functions that are captured by the popular attention metaphors of filters, spotlights, resources, gates, glue, and so forth. In reviewing these metaphors, Fernandez-Duque and Johnson (e.g., 2002) highlighted the debate over the answer to the third of the aforementioned questions – What are the determinants of attention? – by contrasting theories in which attention is the *cause* of selection, information processing, and behavior from those that describe attention as the *effect* of selection, processing, and behavior.

As noted above, the control of attention allocation between competing tasks or stimuli may sometimes be exogenous and reactive: selection is elicited involuntarily in response to environmental constraints like movement or novelty, or selection is conditioned reactively on the basis of experiential constraints like habits and priming.

At other times, attention is allocated endogenously, via the willful and effortful control of selection. In recent years, it has become common to refer to the willful, intentional allocation of attention as “executive attention” and there have been many studies in which animals’ capacity for this type of selection has been examined (e.g., French et al. 2018; Posner and Rothbart 2018; Rossi et al. 2009). The important conclusion is that, at every moment, there are at least these three sources of bias (environmental, experiential, and executive) vying for control over attention – and, by extension, control over behavior, because the effects of attending are measured behaviorally. The dichotomy between top-down and bottom-up control of attention is a second-order oversimplification (Awh et al. 2012) as it ignores the distinction between bottom-up reflexive attention-capture by change and motion and the bottom-up stimulus control that results from conditioning and experience, and that was the primary focus of attention studies with animals during the decades in which behaviorism held sway. Contemporary understanding of the control of attention reflects, perhaps, the clearest example of the cumulative achievements of our discipline, in which cognitive neuroscience builds on and complements the insights provided by years of systematic studies within the experimental analysis of behavior – principally animal behavior (Beran et al. 2016).

## Cross-References

- [Blocking](#)
- [Bottom-up Processing](#)
- [Cognition](#)
- [David Washburn](#)
- [John David Smith](#)
- [Meta-cognition](#)
- [Michael J. Beran](#)
- [Overshadowing](#)
- [Saccadic Eye Movement](#)
- [Stroop Effect](#)
- [Tom Zentall](#)
- [Top-Down Processing](#)
- [Vigilance](#)
- [Visual Search](#)

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## Attention Bias

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### Definition

Attention bias is the tendency to drive or sustain attention to specific stimuli or types of information before others.

Attention bias is a phenomenon firstly noticed in humans during line dissection and cancellation tasks. In these neuropsychological tests, in which participants are required to search for and cross out targets, humans primarily attend to objects in the left side of space (Rogers et al. 2013). No longer viewed as a characteristic unique to humans, attention bias is widespread in the animal world, suggesting that this type of cognitive bias may be a fundamental feature of most vertebrate brains. Attention biases could manifest in any number of domains, but the most commonly studied varieties in the animal kingdom are visuospatial attention and social attention.

For example birds, like humans, primarily attend to visual items located in their left visual hemifield (Diekamp et al. 2005). The latter was

demonstrated during a food detection task (similar to the “cancellation” task used in humans) in which birds were required to sample food grains uniformly spread on a surface placed in front of them. A leftward visuospatial bias (right hemisphere activity) was observed in pecking activity over the experiment, supporting the specialization of the right hemisphere for visuospatial analysis (for review, see Rogers et al. 2013). This visuospatial attention bias may also be related to motor lateralization, as has been found in canine species (Siniscalchi et al. 2016). In this case, motor lateralization was first determined during a motor task in which dogs were selected for their preferential use of forepaws (paw preference) to hold a puzzle feeder device while eating its content (i.e., namely, the Kong test) (Siniscalchi et al. 2016).

Then, during a food detection task similar to that previously described in birds, a left-visuospatial bias in the total number of food items eaten from the testing apparatus (Fig. 1) was observed in dogs with a left forepaw preference during the Kong test, but a right-visuospatial bias was reported for dogs with a right-paw preference. No significant visuospatial attention bias was reported in ambi-pawed subjects (i.e., dogs that use both forepaws equally to hold the food device).

Biases during the allocation of social attention have been reported in nonhuman primates, birds, farm animals, and dogs. Like humans, macaques (*Macaca mulatta*) exhibit sustained attention toward potentially threatening social stimuli compared with neutral stimuli (pairs of adult male conspecific face images – one with an aggressive expression, one with a neutral expression) (Bethell et al. 2012). In a similar way, chimpanzees (*Pan troglodytes*) viewing a movie depicting naturalistic scenes involving the whole-body expressions of conspecifics looked longest at scenes depicting agonism, suggesting an attention bias toward threatening situations (Kano and Tomonaga 2010).

Eye gaze tracking methods have also been used to study attention bias during gazing behavior in different animal models. In dogs, results from eye

**Attention Bias,**

**Fig. 1** Experimental apparatus used to study visuospatial attention bias in dogs. The testing apparatus surface was divided into an array of seven identical vertical sectors to the right and to the left side of the central one “CTR.” For each dog, all food items within each sector were counted



tracking experiments show attention biases in their gaze behaviors which resemble those reported in primates studies: dogs exhibit prolonged attention on socially relevant visual stimuli like faces and eyes (eyes attention bias was irrespective of the emotional signals expressed by the face) (Somppi et al. 2016). In addition, the dogs preferred photos representing conspecifics over those depicting inanimate items or humans and exhibit specific attentional biases toward potentially threatening social stimuli (images depicting threatening dog faces) (Somppi et al. 2016).

Although emotion-related social attention biases have been repeatedly observed in animals (especially that of threat), the specific social features that are attended to preferentially are often species-specific. For example, humans look at the mouths of pleasant faces most, while dogs, chimpanzees, and rhesus monkeys show sustained attention toward threatening mouths compared to pleasant ones (Somppi et al. 2016). This difference may be due to the fact that the mouth area is a determinant cue in humans for the detection of a smile, but in both nonhuman primates and dogs it is relevant for the recognition of threatening social expressions (Somppi et al. 2016). The biological relevance of visual stimuli also plays a role in visual scanning strategies of threatening social signals since dogs look longer at threatening

conspecific faces than at other canine facial expressions, but avoided looking at heterospecific (human) threatening faces. This could be explained by the fact that conspecific faces are more biologically significant for dogs, eliciting a prevalent activation of the limbic pathways (e.g., the amygdala drives attention to arousing emotional stimuli) that led to sustained attention in the brain (Rogers et al. 2013; Somppi et al. 2016). Alternatively, avoidance behavior in dogs in response to threatening human faces could be driven by enhanced prefrontal modulation associated with submissive behavior or memory-based social evaluations (Somppi et al. 2016).

Attention biases towards threatening stimuli are enhanced when animals are in anxious states indicating a clear link between negative affective states and attention biases. For example, increased attention and vigilance toward a potential threat stimulus were observed in rhesus macaques in anxious states after a stressful procedure (Bethell et al. 2012). Similarly, in birds, increased threat perception (e.g., increased vigilance to an alarm call) was observed in starlings denied access to water bathing compared with birds that were able to water bathe, indicating that anxious birds (due to compromised flight ability) allocated more attention to the threatening stimulus (Brilot and Bateson 2012). Furthermore, pharmacological studies in farm animals demonstrated increased

attention towards the threat of a dog when both sheep and cattle were in a pharmacologically induced anxiety state compared with when they were in a calm state (Lee et al. 2017). Overall, these findings suggest that testing attention bias will open the door to new ways of measuring the affective states of animals with direct implications for animal welfare.

Behavioral studies indicate that attention bias to threatening stimuli is also affected by brain lateralization (i.e., the different specialization of the two side of the brain in both structures and functions) (for review, see Rogers et al. 2013). In dogs, a left gaze bias and an orienting head turning response to the left side were observed in response to human threatening faces (Racca et al. 2012) and alarming visual stimuli (Siniscalchi et al. 2010), respectively. Given that the lateral hemifield of each eye of most vertebrates projects mainly to the contralateral side of the brain, these results are consistent with a specialization of the right hemisphere for the analysis of threatening and arousal stimuli (Rogers et al. 2013).

Lateralization is a phenomenon distributed widely in the animal kingdom, and it manifests in many ways (from social attention to visuospatial attention); they are influenced by physiological state and brain organization and can have practical applications for animal handling and assessing their affective states.

## Cross-References

- [Cognitive Bias](#)
- [Face Processing in Different Brain Areas and Face Recognition](#)
- [Laterality Effect \(Face Perception\)](#)

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## Attention Span

- [Cognition](#)

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## Attentional Set-Shifting Test

- [Wisconsin Card-Sorting Task](#)

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## Attention-Deficit Disorder (ADD)

- [Attention-Deficit Hyperactivity Disorder](#)

## Attention-Deficit Hyperactivity Disorder

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### Synonyms

Attention-deficit disorder (ADD); Attention-deficit hyperactivity disorder

### Definition

It is a chronic mental health condition evident by persistent inattention, hyperactivity, and occasionally impulsivity.

### Introduction

Attention-deficit hyperactivity disorder (ADHD) is a neurodevelopmental disorder that can be diagnosed during childhood. Those who suffer from this mental disorder have trouble maintaining attention for a long period of time and exhibit uncontrollable impulsivity and restlessness. These patients find it difficult to coordinate and organize their thought processes. This hampers performance in academics, workplace, and social settings. Such performance deficits and the resulting behavior of others put individuals with ADHD at the risk of developing other mental disorders over time, such as oppositional defiant disorder (ODD), major depressive disorder (MDD), anxiety disorder, conduct disorder (CD), etc.

Although it is called a disorder of the childhood, diagnosis of ADHD in adults is also common (Daley 2006). It is likely that these adults must have had ADHD initially in their childhood, which was left untreated. Adults with ADHD are prone to substance abuse later in their life in order to cope with their disorganized life. This necessitates the early detection of ADHD in childhood as proper management and intervention plans can lead to a better prognosis.

In 1980, ADHD as a mental disorder first appeared in the *Diagnostic and Statistical Manual of Mental Disorders-III* (DSM-III 1980). It was known as attention-deficit disorder (ADD) as scientists categorized *inattention* as the highlighting feature of the disorder. While importance was also given to *hyperactivity*, it was mostly seen as a secondary complication. Thus, DSM-III stated it as ADD with or without hyperactivity. The following revised edition of DSM-III, known as DSM-III-R (1987), improved on the definition and treated *hyperactivity* and *impulsivity* as primary criteria along with *inattention*, thus changing its name to ADHD (Lange et al. 2010). DSM-IV (1994) further classified ADHD into three sub-types depending upon the group of symptoms that are dominant in the patient: inattentive type, hyperactive type, or a mix of both known as combined type. These sub-types are now referred to as clinical presentations in DSM-V (Association 2013).

The exact cause of ADHD is unknown, and consequently a treatment for this disorder is still a challenge for the scientific community. A myriad of novel treatment options have been sprouting each decade as the disorder is gaining more recognition. The disorder is deemed to be complex and heterogeneous in nature, and hence some physicians and researchers doubt over its existence, owing to the fact that almost every symptom can be found in other mental disorders and that it is idiopathic (Moncrieff and Timimi 2010). Currently, researchers are searching for better diagnostic markers based on objective neurobiological and genetic perspectives as detecting the disorder using the subjective criteria leads to potential misdiagnosis.

### Diagnosis and Symptoms

Detecting ADHD in early childhood is a challenging task for clinicians. Several symptoms such as difficulty in attention, impulsivity, anxiety, etc. are not unique to ADHD and share similarity with various other mental disorders. The absence of any defining etiological feature of ADHD makes differential diagnosis complex. Moreover, the inconsistencies between adult symptoms and childhood symptoms make the diagnosis even more intricate. DSM-V acknowledges the fact that ADHD symptoms are not rigid, and these clusters of symptoms can change as a person matures. A patient who displayed the inattentive subset of ADHD as a child could very well develop the hyperactive- or mixed-type subset of ADHD as an adult.

ADHD diagnosis takes place in several steps and varies from place to place as different clinicians follow different guidelines. In case of children, apart from direct observation, information about their behavior is usually collected from parents, colleagues, and teachers. It is believed that even in adults, the symptoms must have occurred somewhere in the patient’s childhood. Thus, accounts of their life history from various sources are immensely helpful to

the examiner. For diagnosis in children, the DSM-V criteria state that at least six symptoms listed in the guidelines (Table 1) should be present in either inattentive or hyperactive division and should persist for a minimum period of 6 months. In adults, at least five symptoms should be exhibited in either of the domains (Association 2013).

ADHD is often accompanied by emotional dysregulation. It is characterized by erratic behavior, aggression, frustration, and unstable emotion in patients. About 25–45% children and 30–70% adults with ADHD display this cluster of behaviors. Changes to motivation are also a highlighting feature, as it has been observed that patients with this disorder tend to prioritize immediate reward over delayed reward (Shaw et al. 2014). Thus, the presence of emotional dysregulation is helpful to diagnosis and increases the likelihood that this disorder might be present.

ADHD diagnosis is usually aided by rating scales to screen the symptoms and provide some objectivity to the listed criteria in the DSM-V. These scales constitute a set of questionnaires that assess the behavioral cues in order to measure the extent of impulsiveness and hyperactivity, which will determine the presence and severity

**Attention-Deficit Hyperactivity Disorder, Table 1** Criteria for diagnosing ADHD according to diagnostic and statistical manual of mental disorders V (DSM-V)

| Inattention                                                                                                                  | Hyperactivity and impulsivity                                |
|------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------|
| Unable to focus on details most of the times and carry out careless mistakes in schoolwork, work, or during other activities | Fidgets with or taps hands or feet or squirms in seat        |
| Has difficulty sustaining attention in tasks or play activities                                                              | Leaves seat in situations when remaining seated is expected  |
| Does not seem to listen when spoken to directly                                                                              | Runs about or climbs in situations where it is inappropriate |
| Does not follow through on instructions and fails to finish schoolwork, chores, or duties in the workplace                   | Unable to play or engage in leisure activities quietly       |
| Organizing tasks and activities is difficult for him or her                                                                  | Is “on the go,” acting as if “driven by a motor              |
| Avoids, dislikes, or is reluctant to engage in tasks that require sustained mental effort                                    | Excessive talking                                            |
| Frequently loses things necessary for tasks or activities                                                                    | Blurts out an answer before a question has been completed    |
| Is easily distracted by extraneous stimuli                                                                                   | Find it difficult to waiting his or her turn                 |
| Is forgetful in daily activities                                                                                             | Likely to interrupts or intrudes on others                   |



of this disorder. Some common scales used are Conners rating scales; Swanson, Nolan, and Pelham-IV (SNAP-IV); Vanderbilt ADHD rating scales; ADHD Rating Scale-IV; etc. (Collett et al. 2003).

## Prevalence

ADHD is one of the most frequently diagnosed psychiatric disorders. Following the DSM criteria, its prevalence ranges between 3–10% in children and 4–5% in adults. This disorder occurs worldwide, and geographic location does not seem to influence its prevalence rate (Polanczyk et al. 2007). Although considered a disorder of the childhood, 50% of the patients carry this abnormality into their adulthood (Spencer et al. 2007). Sex differences are also visibly pronounced in ADHD as males are four to five times more likely to be diagnosed than females. This discrepancy can account for the genetic and hormonal differences between males and females, as well as the fact that males are more susceptible to environmental risk factors (Biederman et al. 2002; James 2008). Among those diagnosed, the male-to-female ratio for the combined type is about 3:1, while for the inattentive type, it is 2:1.

## Pathophysiology

Biomedical imaging techniques have revealed a notable disparity between the ADHD brain and normal brain. Structural MRI studies in children with ADHD have shown a reduced volume of the basal ganglia and prefrontal cortex (PFC), as well as reduced cortical thickness and abnormal white matter microstructure in various neural circuits associated with sustained attention, motor inhibition, and motivation (Batty et al. 2010; Nagel et al. 2011; Nakao et al. 2011). However, the reduction in volume and cortical thickness abnormalities were almost undetectable in adults. These observations are backed by a consistent set of longitudinal studies which suggest these changes attenuate as the person ages, insinuating a delayed

maturation of certain brain regions (Frodl and Skokauskas 2012; Shaw et al. 2007). Studies that focused on hippocampus and amygdala have also found volumetric differences. Emotional dysregulation is a common feature in ADHD patients and might implicate a link to changes in amygdala (Frodl et al. 2010). A deficit in the activity of prefrontal, premotor, and frontal-striatal circuits has also been reported in ADHD patients when monitored using PET and fMRI scans. Thus, even after all of these correlational findings, further elucidation needs to be carried out by researchers to establish these morphological differences as a causal factor for ADHD.

Neuropsychological functions such as cognition, attention, emotions, as well as memory and learning are regulated by intricate levels of neurotransmitters, noradrenalin, and dopamine, which work in conjunction. These functions are associated with a diverse range of interconnected neural circuits found in the brain regions such as PFC, caudate, and cerebellum. Several studies have reported reduced functionality of these neurotransmitters in the aforementioned brain regions and have been hypothesized to relate with the observed symptoms in ADHD. There are ADHD medications that antagonistically bind to dopamine and noradrenalin reuptake channels on the presynaptic neurons, which result in an increased levels of neurotransmitters at the synapse (Seiden et al. 1993). They also seem to inhibit monoamine oxidase, a family of enzymes that aids in the catabolism of these neurotransmitters (Pliszka 2005). All of these findings clearly indicate that stimulating the neurotransmission via direct agonists may mitigate the symptoms. However, drugs such as piribedil and amantadine do not seem to offer relief to ADHD patients, suggesting a much more complicated biology (Pliszka 2005).

## Genetic Studies

It has been long known that ADHD can be passed down through generations. Multiple studies conducted on family lineages and twins confirm its high genetic heritability ranging from 60%



to 90%, which is on par with that of bipolar disorder and schizophrenia (Hawi et al. 2015). It has become paramount for scientists to identify those genes to gain a novel insight into its functioning. Till date, no specific causal genes have been discovered, which hints at a multi-gene interaction that results in ADHD phenotype (Thapar et al. 2013). The observed changes to the neurochemistry of ADHD brain have provided incentives to look for gene variants associated with reduced dopaminergic neurotransmission (Spencer et al. 2005). Using the candidate gene approach, susceptible genes have been identified that encode for dopamine receptor sub-types D4 (DRD4) and D5 (DRD5), as well as dopamine transporter (DAT-1). Risk factors related to serotonin receptors have also been reported (HTR1B and SLC6A4) (Gizer et al. 2009).

## Treatment

Without a firm understanding of ADHD, formulating a concrete, evidence-based treatment plan is a challenging task for researchers. A complete cure for this disorder is yet to be discovered; however, some of the known treatment methods have displayed effectiveness in tackling the symptoms so that they do not interfere with their daily life.

## Pharmacological Interventions

Pharmacological intervention techniques have paved their way into clinical practice since the understanding of the neurochemical basis of ADHD. They have proved efficacious in bringing about symptomatic relief and are recommended by various physicians to ADHD patients with mild to severe impairment (Kendall et al. 2008). The first-line of medication includes the prescription of stimulants, a class of psychoactive drugs that elevate the brain activity. These drugs increase the overall availability of the neurotransmitter dopamine and noradrenaline at the synaptic sites (Pliszka 2007). The most widely used among them are amphetamines and

methylphenidate and have been approved in the USA by the Food and Drug Administration (FDA).

However, the benefits provided by these psychostimulants are not without risks. Physicians therefore strictly adhere to the clinical guidelines and follow dosage limit set by the international standards. These drugs are known to cause mild alterations to cardiovascular physiology, such as an increase in the blood pressure and heart rate, and hence may pose threat to patients with risk of cardiovascular diseases. For that reason, medical examination of the patient is carried out before any pharmacological therapy can be recommended. Psychostimulants are highly susceptible for substance abuse. These drugs modulate the dopamine levels in certain brain regions involved with reward and euphoria, which increase the chances of developing an addiction (Lakhan and Kirchgessner 2012).

Physicians may resort to non-stimulant medication as a second line of treatment if stimulants fail to provide symptomatic relief to ADHD patients. A well-known non-stimulant for ADHD is atomoxetine, a non-epinephrine reuptake inhibitor. This drug is also known to inhibit the dopamine reuptake in certain brain regions such as the PFC (Sauer et al. 2005). It also has a lower risk for abuse as it does not act on the striatum, unlike the psychostimulants, and hence is preferred for patients with a history of substance abuse (Banaschewski et al. 2004). Atomoxetine is less efficacious than methylphenidate thus chiefly serves to function as an alternative medication (Hanwella et al. 2011).

## Non-pharmacological Interventions

Behavioral therapies are usually the first line of treatment recommended for children with ADHD (Kratochvil et al. 2009). Most of these include parental interventions, cognitive behavioral therapy, social skill improvement programs, psychoeducational programs, etc. (Association 2013). These management programs strategize by coordinating with child's parents designing sessions that involve various

physical and psychological activities ranging from puzzle solving to aerobic exercises. Early interventions in academic environment can also bring visible relief and a better prognosis for the child. Coordination by the teacher and colleagues can result in better school performance (Tresco et al. 2010).

## Conclusion

ADHD is a common neurobehavioral disorder that begins in childhood and often continues to adulthood. Estimates show two out of every three children with ADHD continue to have symptoms later on. There are three basic types of ADHD: primarily inattentive type, primarily hyperactive/impulsive type, and the combined type. All types are identified by the symptoms of hyperactivity, impulsivity, and inattention. Children with ADHD have difficulty in making and keeping friends, and if left untreated, it may interfere with daily life activities at school and work. It also hampers the social and emotional development.

## Cross-References

- Behavior Systems
- Cognition
- Dopamine Receptor
- Maternal Behavior
- Neurotransmitters
- Paternal Behavior
- Social Behavior

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## Attention-Getting Behaviors

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## Introduction

Attention-getting behaviors (AGB) are described as communicative cues that aim to gain attentional state of the audience. They will mostly cluster into

visual, auditory, or tactile signals, depending on the perceptual system used. Intentional nature of communicative cues has been highlighted as a crucial feature in animal communication systems (e.g., for a review: Townsend et al. 2017). For instance, several species (e.g., in great apes: Halina et al. 2013; Prieur et al. 2016a) have been shown to communicate with each other by gesturing. To be considered as intentional, gestures must fulfill several criteria (Bates et al. 1975; Leavens et al. 2005): (1) the gesture is goal-oriented and the signal persists or is completed with other signals until the desired outcome is reached; (2) the gesture is adjusted in accordance to the attentional state of the audience, whose attention can be regained by the use of additional attention-getting behaviors; and (3) the gesture is supported by visual orienting behaviors alternating between the recipient and the distal object of interest (gaze alternation). While gestural studies highlight potential intentional communication, similar evidence from animal vocal communication is still debated. But some studies suggest that vocal and nonvocal sounds are used intentionally. For instance, Campbell's monkeys (*Cercopithecus campbelli*) use vocalizations in a controlled manner that implies flexibility and intentionality (Lemasson et al. 2013). Moreover, multiple studies have shown vocalizations to be dependent on the surrounding social audience in a variety of species (e.g., Marler et al. 1986), suggesting that these sounds are used intentionally.

Here, we will focus on various aspects of attention-getting behaviors that are used intentionally in humans and animals. AGB are used to communicate with conspecifics in social contexts such as play, grooming, moving, or agonistic encounters (Prieur et al. 2016a). Also, these behaviors can be exhibited by domestic and/or captive species interacting with humans (interspecific context), to request distant objects or food. (e.g., Maille et al. 2012). This happens particularly when the recipient is not responding or is not attending. Thus, AGB can be observed during spontaneous social interactions or, experimentally, by observing subject reaction according to the visual attention of the experimenter with special emphasis on the state of the eyes (open

vs. closed) and how flexibly the subject tailor visual- and auditory-based behaviors to elaborate their communication as a function of whether or not the experimenter can see them (Bourjade et al. 2014; Gaunet 2010; Malavasi and Huber 2016).

AGB are characterized by using visual modality stimuli such as alternate gazing or deictic gestures (i.e., mechanically ineffective body movements made to elicit specific behaviors on a recipient, repeated until the effect is obtained or failure is clearly indicated, Bates et al. 1975), such as begging gestures, defined as gestures produced toward an item placed just in front of a recipient or held directly in the recipient's hand(s), whereas pointing gestures are produced toward an external item of the environment (e.g., Maille et al. 2012). AGB could also be characterized by auditory-based gestures such as banging (e.g., Bourjade et al. 2014) or slap hand and clap hand (Prieur et al. 2016a) or vocalizations (Hopkins et al. 2007). This entry will explore attention-getting behaviors in different modalities and their development, mechanisms, and functions in human and animal species.

## Development

The attention-grabbing quality of the human infant cry is well recognized (Dudek et al. 2016) as well as those from distress calls in different species (Newman 2007). In human, from 3 months of age, and throughout the first year, vocalization rate increases (Camp et al. 1987). It has been noted that the child's limited vocabulary between 1 and 1.3 years old seems to serve only for denoting attention to an object or an event, with true lexical functions coming in between the ages of 1.3 and 1.6 years old (Camp et al. 1987). Prelexical comment demonstrated an early capacity for conveying topic and comment together in the form of speech sounds combined with an attention-getting gesture well before the emergence of multiple-word utterances.

Infants produce some hand forms resembling pointing gestures very early in their development. Index-finger extensions are visible in infants as young as 3 months (for a review: Rohlfing et al. 2017). Some authors (e.g., Bates et al. 1975)

presume that these gesture-like hand forms serve infants' own attention regulation and are coupled with object exploration. In human infants, the most frequently used communicative type is deictic hand gesture, and these emerge between 9 and 12 months (Rohlfing et al. 2017). Within their second year of life, infants point increasingly using their index finger rather than their whole hand; this form seems to be related to other advances in communication such as pointing comprehension or later language. In addition, around 18 months of age, some authors observed that infants begin to coordinate their gesture and gaze systematically and to ascertain that the partner is looking at them before pointing (Franco and Gagliano 2001). Finally, there is a developmentally prior coupling between the vocal and motor systems. Iverson and Fagan (2004) studied arm gestures in infants as young as 6–9 months and found a temporal coordination of canonical babbling with rhythmic hand movements, an important basis for the integrated speech-gesture system.

For nonhuman species, visual signals (e.g., body postures, movements, and facial displays) have been reported at early stage of life. Facial expression has been reported in rhesus macaques (*Macaca mulatta*) on the first day of life (e.g., Ferrari et al. 2012). In other macaque species (e.g., *Macaca tonkeana*, *Macaca silenus*), playful facial expressions are typically performed by infants to initiate social play. During ontogeny, the play face (PF; mouth opened with only the lower teeth exposed) is replaced by the full play face (FPF; the mouth is opened in a relaxed mood with both upper and lower teeth exposed (Palagi 2008)). However, nonhuman primate (NHP) infants appear to display few visual and tactile signals compared with the richness of their vocal repertoire (Maestripietri and Call 1996).

Communicative gesture could present different patterns. For instance, captive bonobos infant (from 10 to 24 months) expresses different action to initiate mother carries, such as grab side/venter, spread legs, step foot, and spin body (Halina et al. 2013).

## Mechanisms

For communication in humans, most of the language functions are under the control of the left

hemisphere of the brain and involve neural networks in which Broca's and Wernicke's areas play a key role for the production and for the comprehension of language, respectively (Meguerditchian et al. 2011). The study of manual asymmetries for gestural communication in apes and monkeys constituted an indirect approach to investigate the brain and neural basis of communicative attention-getting gestures. For instance, studies at the population level in chimpanzees and gorillas showed predominantly performance of attention-getting behaviors (e.g., slap hand and clap hand) with the right hand (Prieur et al. 2016a, b). Signalers used their hand ipsilateral to recipients for tactile and visual gestures and their contralateral hand for gestures involving auditory communication and a communication tool. These recent results further support the hypothesis that laterality in gestural communication might represent a precursor of the left-hemispheric lateralization of language. Producing attention-getting behaviors also requires cells functioning for recognizing a conspecific (e.g., in the anterior superior temporal sulcus). Authors as well reported the activity of a cell responsive to attention down (i.e., head, eyes, and body posture directed down) (for a review, see Emery 2000).

Some studies proposed that particular mechanisms are involved in the production ability of AGB such as individual learning through a process slightly different than ontogenetic ritualization (i.e., the forms that behavior takes derive directly from the social interactions in which an individual participates; Tomasello 2008). In this process, a signaler learns that when he performs a certain action (such as one that produces noise), this has the effect of drawing the attention of a nearby agent. This then leads the signaler to later produce that action intentionally with the purpose of drawing attention. Such learned attention getters in apes might include gestures such as clap, slap object, and tap other (Halina et al. 2013). Other studies support the hypothesis that social learning participates in the acquisition and use of attention-getting vocalizations as well as gestural communication such as auditory gestures (e.g., in chimpanzees: Prieur et al. 2016a; Tagliatalata et al. 2011).

Attention-getting behaviors are also reflecting underlying processes such as mutual attention



(gaze of individuals A and B is directed to one another) and joint attention (individual coordination with others' attention to external targets) (Emery 2000). Joint attention could correspond to the use of a social agent to obtain an object or the use of an object to obtain attention from the social agent; thus, in both cases, attention-getting behavior could be involved until achieving a certain goal and could be seen to be examples of cognitive ability for means-ends reasoning (Leavens et al. 2005).

### Functions and Behavioral Differences According to the Studied Species

The first function of attention-getting behaviors is to communicate with another social agent. In the case of interspecific context, most of the studies on human-animal interaction report attention-getting behaviors expression to obtain food. This happens particularly when the recipient is not responding or is not attending. Thus, AGB can be characterized by observing subject reaction according to the visual attention of the experimenter. For instance, olive baboons (*Papio anubis*) will express auditory-based gestures consisting of banging a plexiglas panel when experimenter is not visually attentive or visual orienting behavior that took the form of gaze alternation bouts between the experimenter's face and the food (Bourjade et al. 2014). It has been shown that red-capped mangabeys (*Cercocebus torquatus*) showed more and faster begging gestures (for food) when both the body and the head of the experimenter were oriented toward them than when they were oriented away (Fig. 1) (Maille et al. 2012).

Bottlenose dolphins (*Tursiops truncatus*) convey the attention of a recipient to a food target by maintaining the alignment of their bodies with it while alternating gaze between the target and the recipient (Xitco et al. 2004).

In domestic species, attention-getting behavior could also reflect communication with a human observer about the location of an unreachable reward. Experiments showed that domestic dogs (*Canis familiaris*) use alternate gazing when communicating the location of a hidden target (toy or food) and even adjust their own position in space

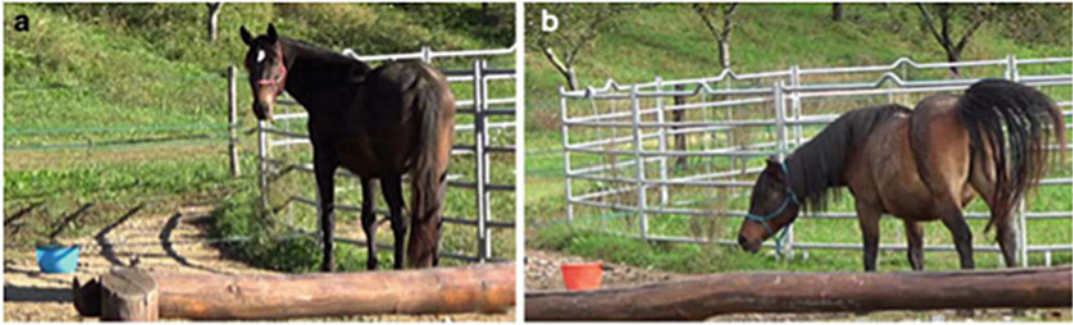


**Attention-Getting Behaviors, Fig. 1** Left-arm begging gesture performed by a juvenile male red-capped mangabey, (Maille et al. 2012)

to gaze at their owner according to the direction of the owner's gaze (e.g., Gaunet and Deputte 2011). When dogs obtained a different target to the requested one, they showed persistence in attention-getting behaviors, i.e., repeated gazes and vocalizations until they obtained the correct target, but did not elaborate their requests; e.g., no new behavioral technique emerged (Gaunet 2010). Domestic horses (*Equus caballus*) communication with a human experimenter about the location of a desired target was explored with a bucket of food out of reach. The rate of gaze alternation and indicative (pointing) (Fig. 2) and non-indicative (nods and shakes) head gestures was higher when the experimenter was frontally oriented toward the horse. Horses also elaborated their communication by switching from a visual to a tactile signal (i.e., prompting action via physical contact) when the experimenter was not attentive and demonstrated perseverance in their communication (Malavasi and Huber 2016).

AGB could also reflect an attachment signal toward human. Ohkita et al. (2016) focused on domestic dogs' attention-getting behavior such as whining and whimpering, looking at the owners' faces, pawing, and approaching in response to their owners' direct gazes. When the owners gazed at them, the durations of whining and whimpering and looking at the owners' faces were longer than when the owners averted their gazes. Attention-getting vocalizations toward





**Attention-Getting Behaviors, Fig. 2** Pictures of (a) gaze to the experimenter and (b) point at the bucket in horses, (Malavasi & Huber 2016)

humans have also been described in captive chimpanzees to request food. Three attention-getting vocalizations have been identified including the “raspberry,” the “extended grunt,” and the “kiss” (Hopkins et al. 2007). It has been shown that these attention-getting vocalizations are socially learned and voluntarily and selectively produced to capture the attention of an otherwise inattentive human (Hopkins et al. 2007).

In more spontaneous context, some studies showed the expression of ground hand slapping when a young gorilla wants to “invite” a social partner to play (Pika et al. 2003). Moreover, in play invitations, young apes produce significantly more visual signals when the social partner is attentive but more auditory or tactical gestures when the recipient is inattentive (e.g., (Pika et al. 2003).

## Conclusion

Attention-getting behaviors are communicative cues that aim to gain attentional state of the audience. They are mostly cluster into visual, auditory (vocal and nonvocal), or tactile signals. They happen particularly when the recipient is not responding or is not attending. Thus, in order to characterize AGB, methods can use observation of spontaneous social interactions or experimentation, by observing subject behaviors according to the visual attention of the conspecifics or an experimenter. If the subject is able to use this behavior in a flexible way, it suggests that he

comprehends its meaning. The signaler has previously learned that when he performs a certain action (such as one that produces noise), this has the effect of drawing the attention of a nearby agent. This then leads the signaler to later produce that action intentionally with the purpose of drawing attention.

It is nevertheless important to take into account that some behaviors that are used as attention getters can change their function with conditions. For instance, subject rate of gazes toward the request distant objects or food can be interpreted as a “waiting” reaction, whereas gazes used during alternation (with the experimenter) will give a communicative meaning (Gaunet and Deputte 2011; Malavasi and Huber 2016).

Finally, different patterns of attention-getting behavior exist, some are species specific, but more comparative research in other species is hence needed and further questioning between patterns per se in order to understand whether expressing alternative gazes, pointing (i.e., toward an external target), begging (i.e., from an experimenter), nonvocal auditory sounds, vocalization, or tactile stimulation requires differential cognitive means for attracting the partner’s attention.

## Cross-References

- [Intentionality](#)
- [Joint Attention](#)
- [Means-End Reasoning](#)

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## Attentive

- Arousal

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## Attraction

- Zigzag Display

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## Audition

- Catarrhine Communication
- Mustelidae Navigation
- Primate Sensory Systems

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## Auditory Coding

- Cognition

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## Auditory Perception

- Depth Perception

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## Auditory Processing and Perception

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Animals use a variety of complex signaling mechanisms to convey information to conspecifics and heterospecifics alike. Among those modalities, acoustic signaling is a widespread behavior across vertebrate groups. Acoustic signals can carry information over long distances, and precise changes in frequency and temporal sequencing can encode high-resolution information in a very efficient way. These signals generally contain information about traits of the individual producing them, and they can divulge everything from the individual's location in space, to its identity, physiological state, and even complex semantic content as in the case of human speech. Together, these features make acoustic signals and the associated auditory processing and perception an excellent means of communication.

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## Behavioral Value of Hearing and Acoustic Signaling

Acoustic signals move at great speeds through the environment and can be detected at long distances from their source. Therefore, auditory perception affords an excellent means of detecting and localizing other individuals in the environment. That ability can confer an advantage in noticing the movements of possible prey or detecting the approach of a nearby predator. Even beyond those unintended signals associated with movement, acoustic signals can also be produced intentionally

in the form of vocalizations such as alarm calls. Because sound radiates from its source in all directions, these calls can inform the behavioral responses of many individuals, including members of the individual's own species and eavesdropping members of other species. For example, Madagascar spiny-tailed iguanas (*Opluris cuvieri cuvieri*) eavesdrop on the alarm calls that Madagascar paradise flycatchers (*Terpsiphone mutata*) produce in response to detecting a nearby predator (Ito and Mori 2010). Those two species share a mutual threat, and iguanas become hyper-vigilant in response to flycatcher calls (Ito and Mori 2010). Thus, by eavesdropping on the acoustic signals produced by species that are similarly wary of specific nearby predators, it is thought that this helps iguanas evade predation.

Another key aspect of acoustic signaling and auditory processing is the recognition of individual identity. Identifying individuals is critical for distinguishing a mate, kin, or a threat from others within a group, and recognition of individual participants is necessary for almost all social behaviors. For example, wolves (*Canis lupus*) are capable of recognizing individuals based on the acoustic characteristics of their howls (Palacios et al. 2015). Similarly, female northern fur seals (*Callorhinus ursinus*) learn the calls produced by their pups, and a female will approach speakers that play the calls of their pups but ignore speakers playing the calls of other pups (Insley 2000). The elements of the nervous system that underlie that form of auditory processing incorporate not only sensory areas but also areas involved in memory, as a female seal's ability to use auditory processing to recognize her offspring persists even after several years of separation (Insley 2000).

Along with revealing an individual's identity, acoustic signals may also serve as an indicator of the individual's physiological state. For example, the vocalizations of rock hyraxes (*Procavia capensis*) contain cues about the physiological state and social rank of the individual (Koren and Geffen 2009). These examples are just a few of the almost innumerable cases in which acoustic signals and auditory perception play fundamental roles in the lives of many different types of organisms.

## Hearing in Birds and Mammals: Structures and Mechanics

Upon first inspection, a striking difference between mammals and birds is the presence of pinna in mammals, such as the prominent ears on rabbits and many dogs, but the absence of any such structure in birds. Those external structures in mammals are thought to confer an advantage because they help to funnel sound into the ear canal, making even very faint sources of sound easier to detect (Yost 2006). Beyond that external difference, however, the physical structures involved in detecting and processing sound are broadly similar between mammals and birds. For example, both groups have ear canals that are open to the surrounding air and that are diametrically opposed on the sides of their heads. This arrangement enables organisms to compare the timing with which a signal hits one ear first and then the other ear some brief time later. This interaural comparison is an integral component of how animals localize the source of that sound, reminiscent of how widely spaced eyes facilitate perception of visual depth. Despite the absence of pinna, some birds use the shape of their heads and specialized feathers to help funnel sounds into the ear canal in a way that is especially beneficial in detecting the location of the sound source (Wagner et al. 2013). Thus, similarities emerge even in the case of the most obvious anatomical difference between mammals and birds if we investigate the system more carefully.

When sounds are produced in the environment and detected by the auditory system, acoustic energy propagating as vibrations of molecules in the air enters the outer ear and causes movement of the structures that transduce that energy into perception of sound (Yost 2006). Through the action of pinna or specialized feathers, acoustic energy is funneled into the canal of the outer ear, where it is eventually captured and transduced into neural activity by the remaining structures of the middle and inner ear.

In the middle ear, membranes and small bones serve as a conduit for the transmission of sound from movement of air into movement of the fluid in the inner ear (Yost 2006). Through those

intricate mechanisms, the movement of air molecules that is inherent to acoustic energy is converted into motion of fluid in downstream structures where those motions are eventually transduced into activity of auditory neurons (Yost 2006). This transduction of acoustic energy and the associated physical motion into activity of neurons in the inner ear is broadly conserved across vertebrate groups (Manley 2017), but the structures and mechanisms that are employed to achieve sound transduction vary.

In both mammals and birds, acoustic energy in the canal of the outer ear impacts a thin membrane called the tympanic membrane (commonly called the “ear-drum”), and the tympanic membrane induces motion of a set of tiny bones that are collectively called the ossicles (Tucker 2017). These small ossicles within the middle ear are connected to form a chain for transmission of movement from the tympanic membrane to the opening to the inner ear known as the oval window (Yost 2006). At this level of resolution, additional differences begin to emerge between this system in mammals and the set of corresponding structures in birds, particularly in the number and relative orientation of the ossicles. For example, the ossicles consist of three bones – the malleus (hammer), incus (anvil), and stapes (stirrup) – in mammals and one bone – the columella – in birds (Tucker 2017; Yost 2006). Despite those structural differences, each of those systems achieves the same function of transferring movement and pressure from the outer ear, through the middle ear, and into the cochlea in the inner ear. For both groups, that pressure results in movement of the fluid and membranes within the inner ear. One of those membranes, the basilar membrane of the cochlea, contains sensory hair cells that are very sensitive to movement of the surrounding fluid. When those movements occur, they induce changes in the voltage of the hair cells, and those changes in voltage can be detected as electrical impulses, called action potentials, in neurons in the auditory nerve (Yost 2006). In both birds and mammals, these hair cells are the first step in routing auditory information into the central nervous system.

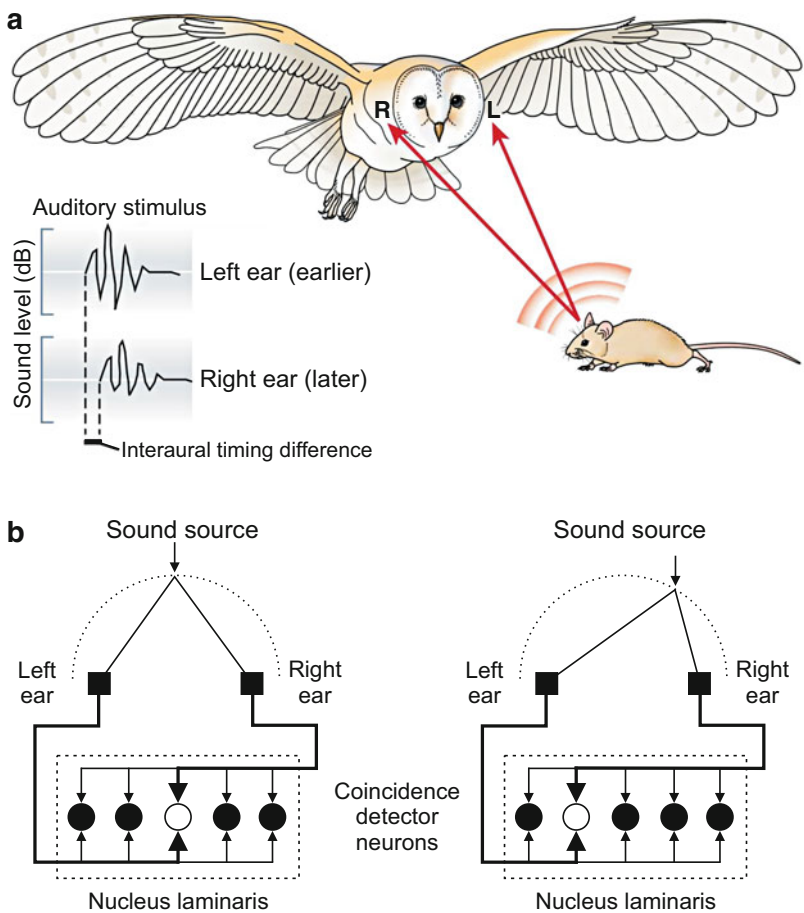
This comparison between mammals and birds makes it clear that nature has solved the challenge

of auditory processing in several different ways. Behavioral studies performed using those groups and others have revealed that auditory information serves similar purposes across many species (e.g., localizing sound sources, permitting communication and social interactions). Many of the studies that have revealed what we know about these processes have been performed in birds, and for that reason many of the examples described in the remainder of this text focus on lessons learned from studies of birds.

## Auditory Processing of Sound Location

The ability to resolve the location of a sound source is quite beneficial for detecting features of the ambient environment. This process is driven by comparing the timing of sounds arriving at each ear, with the sound produced by a specific source arriving first at the ear that is closer to the source and later at the ear that is farther from the source (Fig. 1). Mammals and birds have auditory systems that are excellent at localizing sounds by computing with millisecond accuracy the differences in time that it takes sound to reach each ear (Ashida and Carr 2011). The seminal studies that revealed this neural mapping of auditory space were performed using barn owls (*Tyto furcata pratimcola*) (Knudsen and Konishi 1978). Those owls are nocturnal predators, and they are exceptionally good at locating prey using only acoustic signals even in complete darkness. In order to locate their prey, such as a scurrying mouse, they rely on hearing and specifically on a mechanism called “coincidence detection” (Fig. 1). In this mechanism, action potentials associated with sounds arriving at the left and right ears are relayed to a specialized set of neurons in the brainstem (Wagner et al. 2013). Each of these specialized neurons receives input from each ear. Activity from either ear alone is not sufficient to activate those specialized brainstem neurons, but activity from each ear simultaneously is sufficient to activate those cells (Wagner et al. 2013). This requirement of activity from multiple inputs at the same time is the origin of the name “coincidence detectors.”





**Auditory Processing and Perception, Fig. 1** The location of a sound source in the surrounding environment gives rise to activity at a specific location within a specialized neural network. **(a)** Acoustic energy generated by the mouse's movements or vocalizations reaches the owl's left (L) and right (R) ears at different times and with different intensities depending on the mouse's location in space. In this case, the left ear receives an earlier and more intense stimulus compared to the later and less intense signal received by the right ear. The difference in time of arrival between each ear is the interaural timing difference.

(Adapted from Fig. 1 in Knudsen 2002). **(b)** Coincidence detector neurons in the auditory brainstem (nucleus laminaris) receive input from each ear with different latency. Input from either ear alone is insufficient to activate those cells (filled circles), but those neurons respond robustly (open circles) when input from both ears arrives at the same time. Thus, each coincidence detector neuron becomes an indicator of the position of a sound source in the surrounding environment. (Adapted from Fig. 1 in Salomon et al. 2012)

Through an elegant means of comparing the latency of activity from the left ear versus the latency of activity from the right ear (Fig. 1), each neuron in the brainstem population becomes an indicator of a discrete interaural time difference. Activity from each ear propagates centrally from the ear to these brainstem neurons, and in nearly all cases, the activity from one ear affects a given brainstem neuron at a different time than

activity from the other ear. But at one point in that convergence from each ear onto these brainstem neurons, activity from each ear reaches a given cell at the same time (open circles in Fig. 1b). In that case, coincident input has occurred and that cell is activated (Fig. 1). Neurons that perform this comparison of arrival times in each ear reside in the nucleus laminaris (NL) in the brainstem of birds and in the homologous medial superior



olive (MSO) in the brainstem of mammals (Ashida and Carr 2011). Thus, the activity of a given coincidence detector neuron indicates the presence of a sound source at the corresponding point in the surrounding space, enabling the organism to identify the position of the sound source in the horizontal plane. Barn owls have the additional impressive trait of asymmetric ear openings, with one ear biased toward detecting sounds that come from sources below the owl's head and the other ear biased toward detecting sounds from sources above the bird's head (Wagner et al. 2013). In this way, barn owls are able to detect the position of a sound source along both the horizontal and vertical axes, revealing the position of that source in high resolution and all as a result of auditory input even in the absence of visual input.

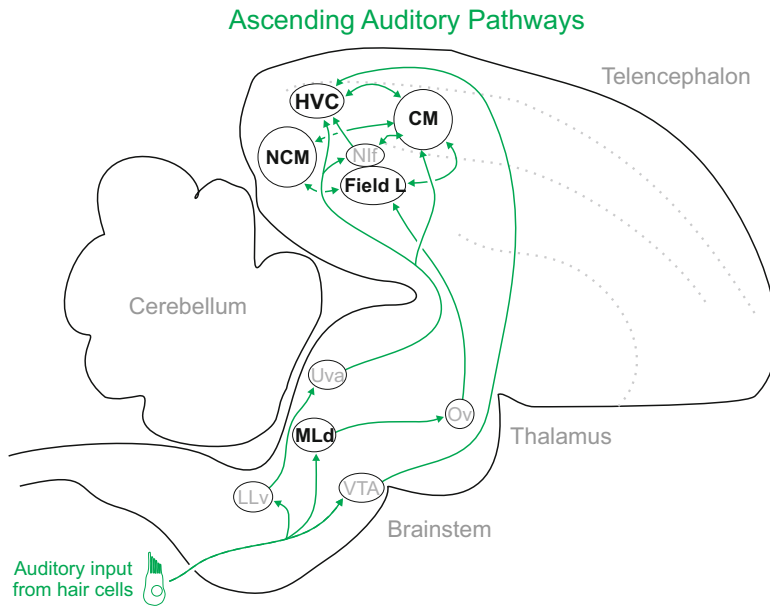
### **Auditory Processing of Social Information**

In addition to serving as a beacon of the location of a sound source, many acoustic signals such as speech and songs performed by birds also convey important social information. For example, song plays many key roles in songbird social behavior, including revealing the singer's identity, helping the singer establish and maintain a territory, and playing a central role in courtship and mate choice (Catchpole and Slater 2008). In most of the species that have been studied, especially those that reside in North America, male birds sing but females do not (Catchpole and Slater 2008). That ability of male birds to sing is associated with a network of specialized brain sites that are large and obvious in the male brain but are atrophied to much smaller sizes or are absent in the female brain (Mooney et al. 2008). Intriguingly, male songbirds learn their songs in a developmental progression that is strikingly parallel to the way that humans learn the sounds that we use in speech (Doupe and Kuhl 1999). In that process, the learner imitates the sounds that he hears performed by other members of his species and relies on auditory feedback to refine his imitations of those vocalizations, and many investigations have focused on determining how and where

those complex auditory signals are processed in the songbird brain.

Electrophysiological recordings and pathway tracing studies from many research groups have revealed that activity originating in hair cells of the inner ear is propagated through a network of auditory neurons in the brainstem and thalamus and eventually reaches a forebrain area called Field L, which is the avian analog of the mammalian primary auditory cortex (Fig. 2) (reviewed in Prather 2013). From Field L, activity is passed along to secondary cortical areas including the caudal mesopallium (CM) and the caudomedial nidopallium (NCM) (Fig. 2) (Vates et al. 1996). As we ascend through that circuit, neurons become more selectively responsive to specific characteristics of those behaviorally relevant sounds (i.e., songs and calls). For example, Field L is broadly responsive to both song and a wide variety of other sounds including pure tones and white noise (Lewicki and Arthur 1996). In contrast, neurons in CM and NCM are more selectively responsive to specific aspects of auditory stimuli such as the novel or familiar status of the stimulus (Gentner and Margoliash 2003; Mello et al. 1995) and the identity of the associated individual that produced that vocalization (Menardy et al. 2012). Furthermore, immediate early gene expression within NCM is also positively correlated with the strength of song learning (Terpstra et al. 2004), suggesting that these forebrain areas may contribute to not only auditory processing but also formation and recall of memories regarding these behaviorally relevant auditory experiences.

Additional studies have also revealed highly selective auditory sites that are interconnected with CM and NCM. One of those sites is a forebrain nucleus called HVC (abbreviation used as a proper name, Fig. 2), and the auditory responses of HVC neurons are among the most selective sensory responses ever described. For example, HVC neurons respond to not only song but also more specifically to the bird's own song as opposed to songs or calls produced by members of the bird's own species (reviewed in Mooney et al. 2008). Furthermore, HVC neurons can even represent different songs in the bird's repertoire (Prather et al. 2008),



A

**Auditory Processing and Perception, Fig. 2** Auditory input is processed through an ascending neural network. In this depiction of a parasagittal section of the songbird brain, auditory input is transduced by hair cells in the cochlea and passed through the brainstem, thalamus, and eventually to auditory processing centers in the telencephalon. Areas highlighted in this text are in black font, and additional areas are shown in gray. Not all connections are shown. Arrows indicate the directionality of each connection, and gray dotted lines indicate lamina that serve as landmarks that are helpful in identifying locations in the brain. Some structures, such as HVC, are sexually

dimorphic (large in males and smaller or absent in females). Other structures, such as MLd, Field L, CM, and NCM, are robustly present in both sexes. Abbreviations are: *CM* caudal mesopallium, *Field L* auditory thalamorecipient neurons in the forebrain, *HVC* abbreviation used as a proper name, sometimes referred to as the high vocal center, *LLv* lateral lemniscus, ventral nucleus; *MLd* dorsal lateral nucleus of the mesencephalon, *NCM* caudal medial nidopallium, *Nif* nucleus interfacialis of the nidopallium, *Ov* ovoidalis, *Uva* nucleus uvulaeformis, *VTA* ventral tegmental area. (Adapted from Fig. 2 in Prather 2013)

revealing that those neurons are not simply representing classes of vocalizations (e.g., self-generated songs vs. songs performed by others). Instead, they are representing specific sounds used in vocal communication. In support of that idea, HVC neurons that respond to individual songs in the bird's own repertoire are responsive to specific elements of those songs (e.g., one specific transition between two notes), and those cells respond to playback of that element regardless of whether it was performed by the bird where that HVC cell resides or by another member of its species (Prather et al. 2008). Beyond simply responding to acoustic parameters of the song, an integrated approach combining behavioral observation and electrophysiological recording of the activity of individual HVC neurons in awake and freely behaving birds also revealed that some HVC neurons respond to not simply the acoustic properties

of auditory stimuli, but rather the animal's perception of the identity of those stimuli (Prather et al. 2009) and the syntax in which those sounds are produced (Fujimoto et al. 2011). Thus, neural activity in the songbird brain is correlated with many specific aspects of auditory processing, affording researchers many opportunities to study the neural mechanisms that underlie auditory processing and perception.

## Summary

The studies described here highlight the value of birds as a behaviorally rich and experimentally tractable context in which to continue to investigate how the brain enables auditory processing and perception. Regions of the mammalian cortex are also specialized for auditory processing, yet

our understanding remains incomplete regarding how the structure of individual neurons and the circuits they compose results in auditory perception. Cortical areas that are specialized for perception and performance of the sounds we use in speech have been identified in the human brain, yet our understanding of the functional role of those sites also remains incomplete. For example, Wernicke's area in the human brain has been implicated in our perception of the sounds that we use to communicate using language, and another region of the human brain called Broca's area has been implicated in the production of those sounds. Recent research has blurred the distinction between those brain sites, suggesting that both areas contribute to both performance and perception of the sounds that compose one of the primary ways in which we use auditory processing in our everyday lives (Flinker et al. 2015; Tremblay and Dick 2016). The obvious behavioral significance of those human brain areas highlights them as important areas for additional study, but the function of individual neurons and the circuits they compose remains challenging to detect and interpret in humans. By incorporating a blend of behavioral and neurobiological approaches, animal studies such as those performed using songbirds afford an opportunity to understand the relation between activity in specific neurons and the emergence of an organism's perception of auditory experiences.

## Cross-References

- [Auditory Signals](#)
- [Cognition](#)
- [Nervous System, The](#)
- [Owls](#)
- [Songbird Learning](#)

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through a medium (air, water, or a substrate), and its perception by one or more perceivers. Auditory signals are omnidirectional, can be transmitted to a large number of individuals, and can reach long distances. They are produced by a wide range of animal taxa which evolved several mechanisms for producing and perceiving sound-based signals. The use of sound for communication purposes has been reported in many mammals, birds, fishes, amphibians, insects, crustaceans, and reptiles (Bradbury and Vehrencamp 1998). Across this range, auditory signals are used in a diverse set of behavioral contexts such as mating, agonistic encounters, group coordination of movement, parent-offspring interactions, and predator avoidance.

Transmission of auditory signals can be affected by several biotic (sounds produced by other animals, including humans) and abiotic factors (vegetation, water bodies, wind, etc.). These factors can interfere, degrade, or create obstacles to sound transmission. A set of different morphological structures and behavioral strategies evolved to cope with these interferences and increase the probabilities of successful signal transmission.

## Auditory Signals

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## Synonyms

Acoustic signals

## Definition

Auditory signals are animal-produced sounds that evolved via natural and sexual selection for the purpose of influencing the behavior of perceivers.

## Introduction

The auditory communication process involves signal emission by a signaler, its propagation

## Sound-Producing Mechanisms

Sound waves can be modulated at different dimensions. It can be frequency modulated (varying in pitch) or amplitude modulated (varying in loudness), and it can also vary in periodicity, the temporal pattern in which sounds are produced. This allowed for the evolution of an enormous diversity of auditory signal systems, from begging and alarm calls to birdsong and language.

Animals evolved a diverse array of specialized sound-producing structures to emit and modulate auditory signals. It is possible to classify them in two broad categories, those found in animals that breathe air actively and the ones found in animals that obtain oxygen passively (Fletcher 2007). Active air-breathing animals use the muscular control of inhaling and exhaling to force the air-flow through some kind of valve and excite a resonant flap or membrane. Animals that do not

breathe air actively need to resort to muscle-driven vibration mechanisms to produce auditory signals. A noticeable exception is the madagascar giant cockroach (*Gromphadorhina portentosa*). It emits hissing sounds that are produced by forcefully expelling air through abdominal openings called spiracles. Cicadas, some other hemipterans, and moths have a special sound-producing organ called tymbal, a drum-like ribbed membrane that can emit very loud sounds at over 100 decibels. Cicadas produce mating calls by contracting tymbal muscles which cause a series of ribs to buckle one after the other. This produces a sequence of clicks that we perceive as a buzzing sound (Young and Bennet-Clark 1995). Most insects produce sounds via stridulation, which consists of rubbing or scraping two different specialized body parts against each other, a plectrum and a file (a set of ridges). The shape and exact location of these structures can vary across different species. For example, crickets and katydids rub different parts of their wings (forewing veins and the anal wing region), while grasshoppers and locusts rub the inside of their hind legs against the forewing.

### Vocalizations: The Larynx

The mechanisms of sound production in humans are well understood and have been extended to other mammals and avian species. Notably, the source-filter theory of voice production has had a major impact on our understanding of vocal communication systems. The source-filter theory was originally proposed as a two-stage process to explain speech production in humans, but it has been generalized to approach vocal communication in nonhuman mammals and avian species (Fitch 2006). In humans and most other terrestrial mammals, auditory signals are produced by the larynx, the source, and subsequently filtered by the supralaryngeal vocal tract, the filter. The air that is expelled from the lungs and forced through the closed glottis causes oscillation of the vocal folds within the larynx, and its rate determines the fundamental frequency, also perceived as voice pitch. The sound waves produced by this oscillation travel up from the larynx and through the pharynx and oral and nasal cavities, which comprise the supralaryngeal vocal tract, to the lips and

nostrils, through which vocal sounds are radiated. In the process, the vocal tract acts as a resonator and filters the sound, attenuating certain frequencies, thus producing formant frequencies that affect our perception of voice timbre.

### Vocalizations: The Syrinx

The syrinx is the sound-producing organ of birds. It consists of a set of tympaniform membranes that vibrate as air from the lungs is forced through them. This mechanism of sound production is similar to the larynx in mammals. However, the syrinx is located further down in the trachea, close to the junction of the bronchi. The airflow coming from the lungs is modulated by the tympaniform membranes as it goes through each bronchus. The location of the tympaniform membranes varies across bird species. In most songbirds (Oscines), it is located at the medial or internal section of each bronchus, hence called medial tympaniform membranes. Songbirds employ an additional mechanism to modulate airflow. They can extend a labium opposite to the medial tympaniform membrane. These fleshy protuberances allow them to alter or even interrupt the airflow by closing each bronchial tube independently. Sound production can be controlled separately by each side of the syrinx, which allows some songbird species to produce two different sounds at the same time (Suthers and Zollinger 2004).

## Sound Detection Mechanisms

### Sound Detection in Invertebrates

Insects are the only invertebrate group in which hearing is widely used. Among different insect taxa, the skin, cartilage, and bone have been modified to serve as sound-detecting structures (Stebbins 1983). They can be categorized in antennal ears that are sensitive to the displacement of air particles and pressure-sensitive tympanal ears (Goepfert and Hennig 2016). Antennal ears are found in mosquitoes, midges, honey bees, and some flies. They are used as velocity receivers that respond to air particle movements. These movements are detected by Johnston's organ, an arrangement of densely packed mechanosensory



neurons located in the pedicel (the second segment of the antenna). In fruit flies (*Drosophila melanogaster*), different neuron subgroups in Johnston's organ respond to specific mechanical stimuli, e.g., sound vibrations, wind, and gravity.

Tympanal ears are sound-receiving eardrum-like membranes that vibrate in response to sound pressure. They have evolved independently many times in different insect orders and can be located on several parts of the body, depending on the species. For example, crickets have tympanal organs in their forelegs, while grasshoppers also have them in abdominal sections next to the thorax. Tympanal ears are composed of a tympanum, a thin cuticle that vibrates in response to pressure change; a tracheal sac, used for impedance matching between the inner side of the membrane and the external medium; and the tympanal organ, which converts mechanical vibrations into neural signals (Yager 1999).

### Sound Detection in Vertebrates

Besides some anatomical modifications such as the presence of pinnae in mammals and auditory channels joining the two ears in birds and reptiles, the general structure of the auditory system is similar across vertebrate taxa. Sound waves are guided through the ear canal to the inner ear and hit the tympanic membrane (eardrum), a small and thin membrane that separates the outer ear from the inner ear. The tympanic membrane then vibrates sympathetically with the air molecules around it. These vibrations are conveyed into the cochlea through an ossicle in the middle ear, the columella. Thus, it is possible to obtain the necessary agitation inside the cochlea, so that the hair cells of the inner ear can identify the frequencies that make up a certain sound and transmit this information to the brain in the form of electrical impulses. The cochlea has two canals, the scala vestibuli and the scala tympani, which are separated by the cochlear duct. Sound vibrations are transmitted to the cochlea through the oval window, traveling up to the scala vestibuli and returning through the scala tympani to the base and then absorbed by the round window. The scala vestibuli and the scala tympani are canals filled with fluid. This liquid fluctuates

sympathetically to variations in sound pressure received by the tympanic membrane (Bradbury and Vehrencamp 1998). The basilar membrane is a thin strip of tissue located in the cochlea. It follows the contours of the cochlea and separates the scala vestibuli from the scala tympani. It follows the coiled shell-shaped curvature of the cochlea. It becomes gradually wider as it gets further away from the base of the cochlea. The basilar membrane is covered with hair cells (hair cells at different points along the basilar membrane are sensitive to different sound frequencies) that translate sound into electrical impulses that are then transmitted to the auditory areas of the brain through the cochlear nerve.

### Sound Transmission

Sound is the result of mechanical disturbances that are transmitted to a medium as longitudinal waves. Sound waves propagate as particle compressions and rarefactions in solid, liquid, and gaseous media. The same general principles of wave propagation apply to sound waves. Because of its nature, sound cannot be polarized (as light waves), but it suffers from the action of other phenomena such as attenuation, interference, and noise. Auditory signals are structurally designed to minimize these effects and improve signal detectability.

### Sound Attenuation

Sound attenuation is the gradual decrease in the amplitude of sound waves as they propagate farther away from a sound source. This loss or dissipation of energy occurs mainly due to spherical spreading and atmospheric absorption. The magnitude of amplitude loss is proportional to the frequency of the sound wave, the higher the frequency the larger the amplitude loss. Hence, low-frequency sounds can propagate farther away than high-frequency sounds, even if they are produced at the same amplitude. Additional sound attenuation can result from other factors such as wind and temperature gradients, medium absorption, and scattering. Animals evolved different strategies to minimize the effects of sound attenuation on



auditory signals, including the use of hollow structures in the environment to amplify signals, signaling during certain times of the day when atmospheric conditions are more appropriate for long-distance sound transmission, and using redundancy in signal production to improve its detectability.

### Sound Interference and Noise

Sound interference results from the superposition of two or more sound waves. If two sound waves are produced in consonance (at the same time and at the same point), the wave amplitudes will add up, resulting in constructive interference. In contrast, if sound waves are out of phase, they cancel each other out. Small-bodied animals need to cope with a related phenomenon called acoustic short-circuiting. It happens when the sound source is smaller than the wavelength of the sound it produces. Sounds radiated from opposite edges of the body are out of phase, causing destructive interference and reducing sound pressure. Insects such as tree crickets overcome this problem by using leaves as baffles. They cut out holes in the center of leaves and calling from inside it. In this way, they effectively extend their body surface by making the sound travel to the leaf edge (Mhatre 2018).

Noise is another source of sound interference. Signal-to-noise ratio is a measurement of the amplitude of an auditory signal in a noisy environment. It compares the amplitude level of a signal with the level of background noise. The higher signal-to-noise ratio, the lower is the effect of background noise on the signal. There is some evidence that birds can shift up the frequency or increase the amplitude of songs in order to avoid interference from background noise in environments greatly affected by anthropogenic activities, such as big cities' traffic, industrial zones, airport zones, etc. (Rabin et al. 2003).

### Conclusion

The use of auditory signals is widespread across multiple taxa. Sounds can be modulated at different dimensions (frequency, amplitude, and periodicity) allowing the production of highly

complex auditory signals. A great variety of mechanisms evolved to facilitate the production, transmission, and detection of sound-based signals.

### Cross-References

- [Alarm Calls](#)
- [Auditory Processing and Perception](#)
- [Bear Communication](#)
- [Canine Communication](#)
- [Catarrhine Communication](#)
- [Cetacean Communication](#)
- [Communication](#)
- [Countersinging](#)
- [Crocodilia Communication](#)
- [Dawn Solo/Chorus](#)
- [Equine Communication](#)
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- [Pinniped Communication](#)
- [Primate Communication](#)
- [Prosimian Communication](#)
- [Salientia Communication](#)
- [Songbird Duets](#)
- [Swine Communication](#)
- [Warning](#)

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## Aunting

### ► Alloparental Care

## Australopithecus afarensis (A. afarensis)

### ► Lucy

## Autobiographical Memory and Procedural Memory

### ► Long-Term Memory

## Autoshaping

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## Synonyms

Classical conditioning; Conditioned approach; Pavlovian conditioned approach; Pavlovian conditioning; Sign-tracking

## Introduction

Autoshaping (also called sign-tracking or conditioned approach or Pavlovian conditioned approach) is a form of Pavlovian or classical conditioning. The discovery of autoshaping by Brown and Jenkins (1968) was historically significant because it showed that Pavlovian conditioned stimulus (CS)-unconditioned stimulus (US) pairings reliably induced the acquisition and maintenance of a novel type of Pavlovian conditioned response (CR). The Pavlovian autoshaping CR is a complex sequence of CS-directed, skeletal-motor responses. The autoshaping CR is reliably induced by repeated pairings of a small object (CS) with a reward (US). In the Brown and Jenkins (1968) experiment, CS-US pairings induced the pigeons to approach the keylight CS, contact the keylight CS, and peck the keylight CS. Important to the understanding of autoshaping, the food US was delivered on each trial regardless of what the pigeon did.

The discovery of autoshaping was important because complex, directed, skeletal-motor responses were widely viewed as strictly goal-directed instrumental or operant behaviors, subject to conditioning only by experience with response-reinforcer pairings (Skinner 1948). Autoshaping raised the possibility that Pavlovian skeletal-motor CRs may be induced during operant discrimination learning procedures wherein subjects experience pairings of a discrete object CS with a reward US. In this way, autoshaping CRs may be induced to then interact with operant responses in ways not previously considered.

As noted by Brown and Jenkins (1968), the induction of autoshaping CR performance is particularly likely during operant discrimination learning procedures that employ a localized reward cue. And, the use of a reward cue projected onto a small circular response key will provide the CS-US pairings conducive to the acquisition of autoshaping CR performance. Moreover, the typical operant response to obtain food reinforcement is to peck the illuminated keylight. Thus, the autoshaping CR will be pecking that is targeted at the keylight CS that also serves as the target of the operant response. Under these conditions, the

autoshaping keypecking CR is likely to develop and resemble the topography or form of the operant keypecking response.

In addition, both responses, autoshaping and operant, are directed at the same target; consequently, the autoshaping CR is likely to be “misconstrued” as an operant response. The discovery of autoshaping and the realization of the possibility of “mistaken identity” resulted in the re-evaluation of some perplexing behaviors, including positive behavioral contrast, feature-learning, misbehavior, and drug addiction.

### **The Discovery of Autoshaping: The Brown and Jenkins (1968) Experiment**

Autoshaping was first reported by Brown and Jenkins (1968). In their experiment, pigeons received 160 conditioning trials consisting of 8 s of keylight illumination (the conditioned stimulus, or CS) followed by 4 s of access to a food magazine filled with pigeon grain (the unconditioned stimulus, or US). The interval of time between each CS-US pairing trial was approximately 60 s. Presentation of the food magazine US was independent of responding and occurred on each trial regardless of what the subject did. Surprisingly, pigeons began to peck at the illuminated keylight CS even though they were not required to do so to obtain the food US. The autoshaping conditioned response (CR) resembled the unconditioned response (UR) to the presentation of the food US, which was to approach the food US, then make pecking motions directed at the food US, then perform an open-beak pecking motion to contact and consume the food US. The autoshaping CR was similar to the UR, except the action sequence of the CR was directed at the keylight CS instead of the food US. That is, after a few CS-US pairings, the pigeons began to approach the location of the keylight CS. With additional CS-US pairings, the pigeons began to make pecking motions directed at the keylight CS, and, with still further CS-US pairings, the pigeons unleashed a ballistic, keylight-directed, striking response, resulting in physical contact with the keylight CS. Their forward thrusting of the head,

in an open-beak, pecking motion made it appear as though they were attempting to “consume” the keylight CS. The topography of the autoshaping CR closely resembled the topography of the UR to the food US. This was consistent with the hypothesis that, due to CS-US pairings, the pigeons had learned to associate the keylight CS with the food US. The CS-US association hypothesis was supported by evidence that little or no keypecking was observed in control groups that received keylight illumination only (CS only), food presentation only (US only), or backward pairings (US followed by CS).

The discovery of autoshaping had an enormous impact upon investigators of basic animal learning processes, who saw, for the first time, that repeated CS-US pairings of an object CS with a reward US will reliably induce the acquisition and maintenance of Pavlovian conditioning of complex CS-directed skeletal-motor CRs. The discovery of autoshaping was totally surprising and completely unexpected. Prior to the discovery of autoshaping, responses of this sort, a complex sequence of CS-directed, skeletal-motor actions, were viewed exclusively as goal-directed instrumental or operant responses. The discovery of autoshaping complicated matters considerably, because while the autoshaping CR will have the appearance of an operant response, its behavioral characteristics will be that of an acquired Pavlovian reflex. The autoshaping CR will be cue-elicited, automatically triggered by the presentation of the CS, and involuntary, or very difficult, if not impossible, for the subject to suppress or control. These characteristics of Pavlovian CRs are in sharp contrast to the characteristics of instrumental or operant responses which are generally described as voluntary, emitted, goal-directed, intended, and skilled skeletal-motor performances.

### **Early Investigations of Autoshaping**

The discovery of autoshaping set off a flurry of research activity to establish the boundary conditions under which autoshaping CR performance was observed (for reviews, see Locurto et al.

1981; Tomie et al. 1989). The species generality of the autoshaping phenomenon was of particular interest, and with varying degrees of success, autoshaping CR performance was documented in birds (pigeons, ring doves, finches, domestic chickens, chicks, and quail), mammals (rats, mice, hamsters, guinea pigs, gerbils, horses, dogs, and cats), amphibians (frogs), reptiles (monitor lizards and turtles), fish (tilapia fish, goldfish, blue gourami, cuttlefish, sharks, halibut, and cod), nonhuman primates (cynomolgus monkeys, rhesus monkeys, and squirrel monkeys), and human beings (human children and human adults).

It should be acknowledged that the vast majority of autoshaping experiments used Pavlovian delay conditioning procedures to train pigeons or rats. Stimuli employed as the CS by investigators reporting the acquisition and maintenance of autoshaping CR performance include the brief insertion of a retractable lever, the illumination of a small cue light, a small houselight, or a small pilot light on an infusion pump, the brief insertion of a sipper tube, the presentation of a variety of small objects, including a stuffed animal, a plastic toy, a ball, a wooden coin, a live conspecific male rat, and an auditory stimulus projected from a small loudspeaker. Autoshaping has also been induced by a wide range of stimuli employed as the US. These include response-independent delivery of access to a solid food (grain pellets, mixed grains, mash), access to a sipper tube containing a liquid solution (water, saccharin, sucrose), access to a sipper tube containing a solution of an abused drug (alcohol, cocaine, chlordiazepoxide, opiates, etc.), access to warmth provided by a radiant heat source, access to brief social interaction opportunity (with a conspecific, with a sexual partner), delivery of rewarding electrical brain stimulation, and intravenous injection/infusion of drugs (cocaine, opiates, amphetamines, benzodiazepines, etc.).

### Effects of the CS-US Contingency

Early investigations of autoshaping provided compelling evidence that the acquisition and maintenance of autoshaping CR performance was reliably induced by experience with CS-US

pairings. Further experimentation revealed that more than mere CS-US pairings were required, as responding was neither acquired nor maintained, despite frequent CS-US pairings, when the food US was equally like to occur in the absence of the CS (Gamzu and Williams 1973). Thus, autoshaping is sensitive to the positive contingency between the CS and the US. That is, when the CS and the US are presented independently of one another, as in a random control procedure, then autoshaping CR performance is neither acquired nor maintained, despite the fact that, due to chance alone, the CS is sometimes followed closely in time by the US. Finally, experience with the negative CS-US contingency arrangement (i.e., presenting the US only in the absence of the CS, as for example in backward conditioning procedures or in CS-US unpaired procedures) induced the subject to withdraw from the vicinity of the CS (Wasserman et al. 1974). This response, withdrawal from the vicinity of the CS, is opposite to the CS-directed autoshaping response, to approach the vicinity of the CS, and is consistent with the view that the negative CS-US contingency induces conditioning of inhibitory CR performance (Rescorla 1968).

The initiation of the first autoshaping keypeck in the pigeon is clearly dependent upon the positive Pavlovian CS-US contingency between the illumination of the keylight CS and the presentation of the food US. But, thereafter, it is possible that the autoshaping CR may be strengthened superstitiously by the adventitious pairing of the autoshaping CR with the presentation of the food US shortly thereafter (Skinner 1948). To evaluate the possibility of superstitious conditioning, autoshaping investigators employed omission training procedures to eliminate pairings of the autoshaping CR with the food US (Williams and Williams 1969). In their experiment, pecking the keylight CS resulted in the cancellation of the food US which would have otherwise been delivered. They found that despite eliminating all keypeck-food pairings, sustained keypecking was reliably acquired in all 13 subjects, revealing that the development of autoshaping CR performance did not depend upon pairing of the keypeck CR with the food US. While the results of

omission training studies discredit an account of autoshaping based on superstition (Locurto et al. 1981), it should be noted that autoshaping is not immune to the effects of instrumental factors. For example, delay of reinforcement and the application of aversive or negative reinforcement contingencies influence the maintenance of autoshaping CR performance and do so in a manner that is consistent with an analysis based on operant reinforcement principles (Tomie et al. 1989).

### Effects of Trial Duration and Trial Spacing

The proportion of the total session time that is devoted to the presentation of the CS is highly predictive of the acquisition of autoshaping CR performance (Gibbon and Balsam 1981; Jenkins et al. 1981). When the duration of the intertrial interval (ITI) is held constant, the longer the duration of the CS, the more slowly the keypeck autoshaping CR is acquired. On the other hand, when keylight CS duration was held constant, autoshaping CR performance was initiated more quickly, requiring fewer CS-US pairing trials, with longer duration intervals separating successive CS-US pairings. According to Scalar Expectancy Theory (Gibbon and Balsam 1981), each presentation of the food US increases the associative strength of all stimuli that are present, including incidental background contextual stimuli, in direct and inverse proportion to their salience and duration, respectively. The shorter duration keylight CS accrues association with food more rapidly than does the background context. Autoshaping CR performance is elicited when the associative strength of the keylight CS, relative to the associative strength of contextual background stimuli, exceeds some threshold value. Scalar Expectancy Theory provides a formal model for deriving estimates of associative strength of a CS; moreover, it uncouples, to some extent, those factors that determine the associative strength of the CS from those that determine performance of the autoshaping CR. In addition, the model emphasizes the conditioning of contextual stimuli, which is important because the acquisition of autoshaping is profoundly retarded if the contextual stimuli have been paired with the food US (Tomie 1981). Scalar Expectancy Theory is an

example of a comparator theory of autoshaping (Miller and Schachtman 1985), which propose that autoshaping CR performance is not determined by the associative value of the keylight CS *per se* but rather by the value of the CS relative to the value of its context.

### Theoretical Implications of Autoshaping

The discovery of autoshaping showed that Pavlovian conditioning procedures, consisting of CS-US pairings, induced the acquisition and maintenance of Pavlovian CR performance of a complex sequence of directed skeletal-motor responses. This discovery contradicted the widely held view that Pavlovian conditioning procedures influenced responses that were distinct from the skilled and voluntary skeletal-motor actions of instrumental goal-directed responses. According to widely held versions of traditional twofactor theory (e.g., Rescorla and Solomon 1967), Pavlovian CRs were viewed as discrete visceral and physiological responses. Traditional Pavlovian CRs include salivary CRs, eyeblink CRs, nictitating membrane CRs, galvanic skin conductance CRs, heart rate CRs, knee-flexion CRs, etc., whose performance was mediated largely by activity of the autonomic nervous system. Furthermore, with respect to the effects of Pavlovian CRs on instrumental behaviors, Pavlovian CRs were seen primarily as emotional reactions, such as fear, which influenced the subject's motivation to perform goal-directed instrumental behaviors. For example, a tone CS for shock US elicits the conditioned fear CR, which reduces the subject's motivation to press a lever to obtain the instrumental food reinforcer. According to Two-Factor Theory, instrumental behaviors were viewed as complex sequences of peripheral motor responses that were mediated by the skeletal-motor musculature. Responses of this sort were widely regarded as subject to conditioning only by instrumental procedures. The discovery of autoshaping challenged the theoretical framework that had long served to distinguish between operant and Pavlovian responses.

Brown and Jenkins labeled this new form of Pavlovian conditioning "autoshaping," because the pigeons appeared to automatically "shape"



themselves to perform the prototypical operant key-pecking response. But the impact of autoshaping went far beyond the mere simplicity and convenience afforded by automatically shaping the performance of the operant response. The discovery of autoshaping opened the door to an expanded view of the possible ways that the Pavlovian CR may interact with instrumental responding, including the intriguing possibility of mistaken identity. That is, under some circumstances, it is entirely possible that what appears to be an instrumental response may actually be an autoshaping CR. With this in mind, it is important to note that even though autoshaping may be induced during operant reward training procedures, autoshaping CR performance is not performed to serve the instrumental purpose of acquiring the food reward US. Autoshaping that is induced during operant procedures does not increase operant goal-directed behavior. Autoshaping increases non-operant performance of operant-like responding.

### **Autoshaping and Positive Behavioral Contrast**

Positive behavioral contrast was initially reported by Reynolds (1961), who evaluated the rate at which pigeons peck the response key when the key was illuminated by a distinctive color, either red or green, that signaled the schedule of food reinforcement in effect. During non-differential training procedures, the alternating keylight colors signaled the same schedule of reinforcement, and Reynolds found that the pigeons responded at comparable rates to the red and the green keylights. When he changed the schedule in effect during the red keylight to extinction, he found that the response rate to the unchanged green keylight increased markedly, even though the rate of reinforcement during the green keylight component was unchanged.

Schwartz and Gamzu (1977) suggested that autoshaping may account for the positive behavioral contrast effect. They noted that many operant discrimination learning procedures, like those of Reynolds, provide for keypecking-contingent presentations of food reinforcement. And, in addition, food reinforcement was available for responding only in the presence of the green

keylight that was projected onto the operant response key. According to their Additivity Theory, this arrangement is conducive to the acquisition of autoshaping CR performance of green keylight CS-directed pecking, and they proposed that this autoshaping CR performance is the source of the positive behavioral contrast effect (Schwartz and Gamzu 1977). That is, the positive behavioral contrast effect, the increase in keypecking to the green keylight, is not due to the development of additional goal-directed operant keypecking, but, rather, is a case of mistaken identity. According to Additivity Theory, the effect is actually due to the acquisition of Pavlovian autoshaping keypecking CRs, which so closely resembled operant keypecks that, to the naked eye, investigators could not tell them apart. While autoshaping and additivity do not account for all instances of positive behavioral contrast (Williams 1983), it should be noted that the majority of the studies that have reported the positive behavioral contrast effect have employed conditions providing for Cue-At-Manipulandum (CAM). Tomie (1995, 1996) has noted that CAM arrangements are conducive to the development of Pavlovian autoshaping CR performance, such that the form of the autoshaping CR and the target of the autoshaping CR resemble the operant responding that induced it. According to the CAM hypothesis, the positive behavioral contrast effect is merely one example of an instance where arrangements providing for CAM may have induced autoshaping CRs that were mistaken for operant responding. A number of investigators have proposed that this type of mistaken identity may also account for characteristics of responding observed in a number of other operant procedures that provide for CAM, including studies of feature-learning (Hearst and Jenkins 1974), reports of misbehavior (Breland and Breland 1961), and symptoms of drug addiction (Flagel et al. 2009, 2017; Tomie 1995, 1996; Tomie et al. 2016; Tomie and Sharma 2013).

### **Autoshaping and Feature-Learning**

In feature-learning studies, the intrusion of autoshaping CR performance induced error-prone responding during operant discrimination



learning procedures. In a typical study, the subject responds by touching the stimulus display, which is the response manipulandum. The S+ display is a red dot on a green background. The S− display is the same, except without the red dot. This is the feature-positive discrimination, which yields excellent accuracy. The feature-negative procedure reverses the displays, so that the red dot, the distinguishing feature, is on the S−. Note that both the feature-positive and the feature-negative arrangements provide for CAM, which will induce autoshaping CR performance. Although the stimulus displays used in the two discrimination tasks are equally distinguishable from one another, subjects in the feature-negative condition make far more errors. Analysis of the location of responding supports an autoshaping interpretation of the feature-learning effect (Hearst and Jenkins 1974). Autoshaping guides feature-positive subjects to respond correctly at the red dot, but responding to the green background induces incorrect responding for feature-negative subjects. This suggests that feature-negative errors were induced by autoshaping CRs that were counted as operant responses.

### **Autoshaping and the Failure of Self-Control**

With respect to obtaining the rewarding US, the performance of the autoshaping CR is unnecessary. It serves no purpose and is a complete waste of time and energy. This is because the subject receives the rewarding US regardless of whether or not the autoshaping CR is performed. For this reason, sustained performance of the autoshaping CR is a bit odd or bizarre and may be seen as somewhat maladaptive. The performance of the autoshaping CR makes little sense because moving toward the CS typically serves to move the subject away from the location where the food US will soon be delivered. Thus, performing the autoshaping CR serves to delay the opportunity to eat the food reward US. If the subject were able to control the performance of the autoshaping CR, then the subject should simply stop doing

it. But that is not the case. Subject after subject, in experiment after experiment, perform the autoshaping CR during trial after trial, even though it gains them nothing. This indicates that the autoshaping CR is itself evidence of the failure of self-control.

As noted earlier, during omission training procedures the subject receives the food reward US only on the trials where the subject refrains from performing the autoshaping CR by not contacting the CS. This is the negative automaintenance procedure, which has generated numerous reports of the persistent maintenance of autoshaping CR performance despite the omission training contingency (for review, see Locurto et al. 1981). The negative automaintenance effect reveals that the autoshaping CR is extremely difficult for the subject to suppress and serves as the first of many demonstrations showing that the autoshaping CR is largely refractory to a wide range of its negative consequences.

For example, in long box studies (Hearst and Jenkins 1974), brief illumination of a keylight CS was paired with brief access to a tray of mixed grain (US). The pigeons began to approach and peck the keylight CS, performing the autoshaping CR, even though this removed them from the vicinity of the food US, which was available for a limited amount of time. Even though traveling from the keylight CS to the food US reduced the amount of time available to eat, subjects persisted in performing the autoshaping CR on trial after trial. Extinction of the autoshaping CR was observed only after moving the keylight CS so far away from the food trough that the pigeons could not obtain any food. When the extinguished keylight CS was illuminated, the pigeon did not run and peck it, and, as a consequence, the pigeon was able to eat the food US from the tray on that trial. This pairing of the illumination of the keylight CS with food US was sufficient to convince the pigeon to reinstate running to peck the keylight CS on subsequent trials. The long box studies reveal that the pigeons were unable to control their keypecking that was so detrimental to eating the food US, and this was the case despite their experience with eating the food US on trials where they did not engage in keypecking.

Autoshaping CR performance has been reported despite the effects of contingent shock punishment. The brief presentation of a visual cue that signals the operation of the cocaine infusion pump induces autoshaping of cue-directed approach responses. It has recently been reported that the cocaine cue is so irresistibly attractive that rats will cross an electrified grid floor to approach the location of a light cue that had previously been established as a signal for the operation of an infusion pump that delivered intravenous injections of cocaine (Saunders et al. 2013). This effect was observed even though during drug self-administration training the autoshaping response had no effect on cocaine delivery and, during the shock punishment test, the light cue was presented without infusions of cocaine. Thus, the illumination of the cue light that had previously signaled cocaine infusion “goaded” the rats into crossing the shock grid even though there was no reason for the subject to run across the electrified grid floor, other than to approach the cocaine cue light. That is, autoshaping CR performance was elicited by the light cue, despite the aversive consequence of the contingent shock punishment, and this effect was observed even though there was no drug reward for executing the response. The effect is consistent with the hypothesis that the autoshaping CR is not under the control of the subject.

The “misbehavior of organisms” was first reported by professional animal trainers who successfully applied instrumental reward training contingencies in the training of animals in a variety of tasks (Breland and Breland 1961). They did, however, experience some rather perplexing instances where things did not go according to plan. In a typical example, a raccoon was initially trained to simply pick up a wooden coin, then carry the coin to the bank, then deposit the coin into the bank, to obtain a morsel of food. While initially things went well, with further training, the raccoon began to experience problems. The raccoon seemed unable to let go of the coin. The raccoon often dipped the coin into the slot only to pull them out again. In the end, the coins were chewed, licked, scratched, clawed, rubbed, and washed, but rarely deposited.

Misbehavior is observed when formerly well-behaved subjects begin to persist in maintaining contact with the object. In the end, the raccoon was receiving a very small percentage of the available food rewards, and increasing the raccoon’s hunger drive by imposing a longer period of food deprivation prior to the training session, made matters worse. Ultimately, the trainers were forced to give up with this raccoon and start over with a new raccoon subject, only to learn that the same thing happened in raccoon after raccoon. Other abandoned projects attempted similar training with pigs, rats, squirrel monkeys, chickens, turkeys, otters, porpoises, and whales.

The misbehavior effect reveals the failure of self-control due to autoshaping CR performance that is induced by pairings of the coin CS with the food US. Autoshaping is important because it provides us with a way of understanding how behavior can become irrational and defy free will. Note that the disconnect between the raccoon’s intentions and the raccoon’s actions are not unlike those of the drug abuser, who intends to restrain drug-taking, but, instead, finds himself or herself unable to control the impulse to have yet another. In both cases, the subject is unable to control the performance of consummatory responses directed at the object that predicts reward. This suggests that the overlooked basis for the loss of control of drug-taking, the inability to terminate an ongoing drug use episode, is autoshaping of drug-taking.

## Autoshaping and Drug Addiction

Objects employed as cues that are associated with drugs of abuse elicit autoshaping responses. For example, rats will develop autoshaping CRs to small discrete object cues that are paired with cocaine, opioids, or alcohol (Carroll and Lac 1997; Tomie and Sharma 2013; Valyear et al. 2017). Incentive Sensitization Theory (IST) proposed by Robinson and Berridge (1993) suggests that autoshaping is the overt behavioral manifestation of the sensitization of incentive salience accrued to drug cues due to repeated activations of the dopamine reward pathways by abused

drugs. Consequently, drugs increasingly trigger the experience of “wanting,” which is responsible for the dramatically exaggerated motivation for drugs displayed by addicts.

There are substantial differences between individuals in their tendency to exhibit autoshaping CRs and also in their tendency to exhibit vulnerability to drug addiction. Addiction scientists have found that these tendencies covary within an individual, suggesting that autoshaping is a behavioral marker of vulnerability to drug addiction (Flagel et al. 2009; Flagel and Robinson 2017). Autoshaping procedures, consisting of repeated pairings of a discrete CS with food US, induce some rats, sign-trackers (ST), to exhibit autoshaping CR performance, while other rats, goal-trackers (GT), react to the CS by approaching the location of the food trough where the US will be delivered. When subsequently tested for self-administration of an abused drug, ST rats relative to GT rats more rapidly acquire the drug-taking response, self-administer the abused drug more frequently, and are more vulnerable to relapse to drug-taking following periods of drug abstinence. Thus, vulnerability to autoshaping confers vulnerability to drug addiction.

Those rats prone to develop autoshaping also exhibit a constellation of other addiction-like behaviors. For example, ST rats tend to be more impulsive than GT rats (Beckmann et al. 2011). ST rats also exhibit physiological traits associated with vulnerability to drug abuse (Tomie et al. 2008) as well as neurobiological markers differentially associated with drug addiction (Flagel and Robinson 2017). Therefore, addiction scientists have concluded that the tendency to perform autoshaping CRs may be the overt behavioral expression of a personality trait that confers vulnerability to drug addiction.

An alternative autoshaping account of drug addiction has also been proposed by Tomie and his associates (Tomie 1995, 1996; Tomie et al. 2008, 2016; Tomie and Sharma 2013). According to their Sign-Tracking Model of Addiction (STM), the behavioral symptoms of drug addiction, the excessive, reflexive, and involuntary drug-taking triggered by drug-associated cues, are actually autoshaping CRs that masquerade as

operant drug self-administration responses. Note that drug-taking procedures employed by humans provide for CAM, because the object employed to self-administer the drug is also a drug cue. Repeated voluntary acts of drug-taking provide pairings of the small object CS (i.e., cocktail glass, bong, tooter) with the drug’s rewarding effects. CAM arrangements induce Pavlovian autoshaping CR performance, such that the form and target of the autoshaping CR resembles the operant responding that induced it. In this way, repeated acts of drug-taking will transition voluntary drug use into the poorly controlled drug-taking of the addict. In addition, because drug-taking procedures provide for CAM, the autoshaping CR will be camouflaged to pass for operant drug self-administration, leaving the addict to complain that they were blind-sided when they try to quit and find that they can’t. STM, therefore, provides a novel theoretical account of the etiology and nosological progression from social, recreational, voluntary drug use into the realm of the excessive and poorly controlled drug-taking of the drug addict.

## Conclusion

The discovery of autoshaping in 1968 revolutionized learning theory by showing that Pavlovian CS-US pairings induced a Pavlovian CR, an acquired reflex triggered by the CS, that is described as a complex, CS-directed, skeletal-motor action sequence. Early work on autoshaping focused on establishing the robustness and generality of the phenomenon, meanwhile careful experimental analysis revealed that autoshaping was reliably induced during operant discrimination learning procedures that provided for Cue-At-Manipulandum (CAM), but were misconstrued as operant responses. More recently, addiction researchers have proposed that autoshaping provides an account of several prominent features of drug addiction. These include the user’s failure to maintain self-control of drug-taking, the user’s vulnerability to drug cues that trigger drug-taking, and the co-variation within a subject of vulnerability to autoshaping and

vulnerability to drug addiction. The emerging literature on autoshaping and drug addiction suggests that autoshaping may provide an animal learning model of the addictive personality.

## Cross-References

- B.F. Skinner
- Contingency
- Discrimination Learning
- Free Operant Response
- Goal-Directed Behavior
- Instrumental Learning
- Ivan Pavlov
- Learning
- Motivation
- Operant Conditioning
- Pigeon (*Columbidae*)
- Reflex
- Reinforcement
- Self-Administration
- Shaping
- Sign-Tracking
- Skinner Box
- Stimulus Control
- Unconditioned Response
- Unconditioned Stimulus

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## Autosome

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## Synonyms

Euchromosome; Somatic chromosome

## Definition

All chromosomes except the sex chromosomes are referred to as autosomes. They exist in pairs in the somatic cells whereas singly in the gametic cells.

## Introduction

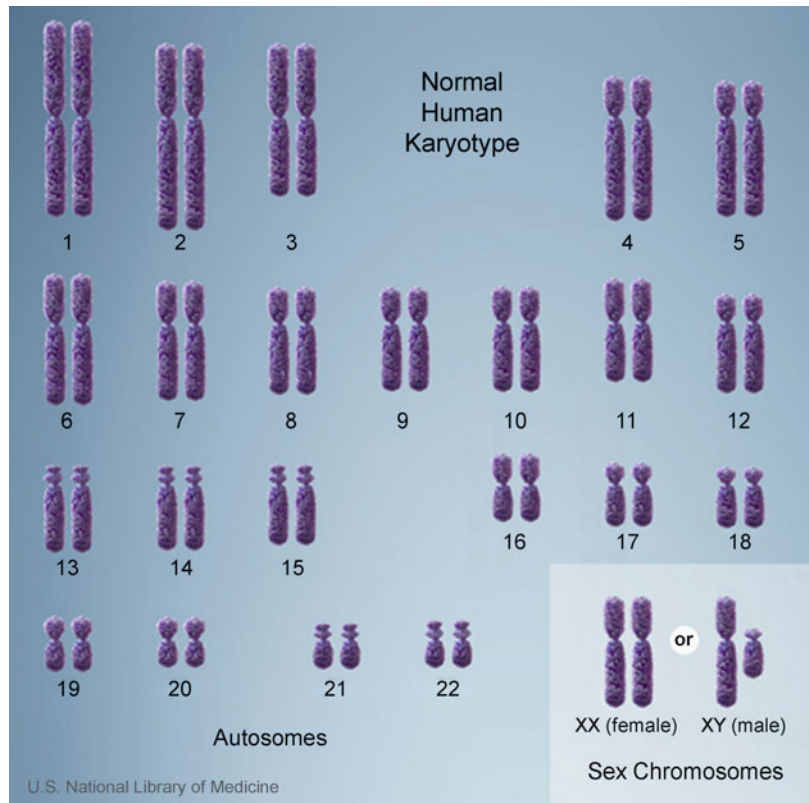
Chromosomes can be categorized in two categories – autosomes and allosomes (sex chromosomes). All the chromosomes other than the sex chromosomes are autosomes. For example, in case of human diploid genome, 44 autosomes (22 pairs) are present along with 2 allosomes (a normal female will have a pair of X chromosome whereas a normal male will have a pair of X and Y chromosome). Autosomes have been numbered on the basis of their sizes from 1–22 in the human genome in contrast to the letters (X and Y) used for the allosomes. Genes located on these autosomes affect males and females in the same way (Ohno 2013). Another striking property of autosomes is that they are homomorphic, i.e., the position of the centromere is identical unlike the case of the male sex chromosome which is heteromorphic (Fig. 1).

The evolutionary processes in case of autosomes are fueled by homologous recombination and mutation.



**Autosome,**

**Fig. 1** Figure depicting normal human karyotype. Homomorphic nature of the autosomes and heteromorphic nature of the male sex chromosome is clearly evident from this figure (Credit: U.S. National Library of Medicine (National Library of Medicine 2017))



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## Mapping of Autosomes

The mapping and identification of the human chromosomes is performed by extracting the chromosomes from a cell that has been arrested in the metaphase or prometaphase followed by their staining with the suitable dye (Alberts et al. 2002; Craig and Bickmore 1993). These stained chromosomes are further arranged in the standard format on the basis of their size and position of the centromere in chromosomes called as karyogram or ideogram.

The utility of this type of arrangement is that large-scale aberrations can be easily identified on comparison of the karyogram of a diseased person to that of a normal person (Therman and Susman 2012). Chromatic aberrations are the resultant of missing, extra, or irregular portion of the chromosomal DNA. Chromosomal aberration can occur in both autosomes and allosomes, but most abundantly they are found in autosomes in the form

of monosomies and trisomies ([http://anthro.palomar.edu/abnormal/abnormal\\_4.htm](http://anthro.palomar.edu/abnormal/abnormal_4.htm)).

### Monosomies

In case of a normal human being the total number of chromosomes should be 46 ( $44 + XY$  or  $44 + XX$ ). But a patient suffering from a monosomy of a particular autosome would have one copy less ( $43 + XY$  or  $43 + XX$ ) than the original chromosome number.

Cri du chat syndrome is an example of the monosomy in humans. It occurs due to the partial deletion of the end of the short p arm of chromosome number 5. The disease has been named as such because the person affected undergoes a malformed larynx which leads to distinctive cat-like voice (Niebuhr 1978).

### Trisomies

In trisomies of autosomes, one additional copy of an autosome is present ( $45 + XY$  or  $45 + XX$ ).



Down's syndrome is a very common autosomal trisomy disorder of chromosome number 21. The symptoms range from mild to moderate mental retardation along with some distinct physical traits (<https://www.cdc.gov/ncbddd/birthdefects/downsyndrome.html>). More examples are Edward's syndrome, which occurs due to the trisomy of chromosome number 18, and Patau syndrome, which occurs due to the trisomy of chromosome number 13. Apart from this, trisomy of chromosome numbers 9, 8, and 22 also occur.

## Autosomal Inheritance

The pattern of inheritance wherein transmission of alleles, present on autosomes, occurs is referred to as autosomal inheritance. This type of inheritance pattern is generally categorized into two types: autosomal dominant and autosomal recessive inheritance. In autosomal dominant disorders the mutated gene is dominant. In this condition only one copy of the mutated gene is required to be affected by the disorder. Huntington disease and Marfan syndrome follow this inheritance pattern. In autosomal recessive condition, both copies of the gene are mutated. These disorders occur when both parents are carriers. Two carriers have a 25% chance of having an unaffected child who is also a carrier and a 25% chance of having an affected child with two recessive genes. Cystic fibrosis and Sickle cell disease follow this kind of inheritance pattern. (<https://ghr.nlm.nih.gov/primer/inheritance/inheritancepatterns>).

## Conclusion

Autosomes are the chromosomes having genes for anything that is not related with sex determination. They carry genes that control somatic traits and are different from the chromosomes governing the sex determination in a lot of aspects. Each pair of autosomes is identical genetically and morphologically. Humans have 22 pairs of autosomes which are numbered from 1 to 22 depending upon their size. Chromosome 1 has approximately 2800 genes while chromosome

number 22 has around 750 genes. Mutations in the autosomal chromosomes lead to different kind aberrations like monosomies and trisomies of that particular chromosome. Furthermore, in case of mutations of the genes present on autosomes, the nature of the gene determines the pattern of inheritance that would be followed.

## Cross-References

► [Chromosomes](#)

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## Autozygosity

► [Homozygosity](#)

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## Auxiliary

► [Alloparental Care](#)

## Avian

### ► Entopallium

## Avian Cognition

### ► Alex the Parrot

## Avian Striatal Complex

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## Introduction

The basal ganglion in amniotes (mammals, birds, and reptiles) is a part of the forebrain telencephalon, located below or ventral to the cerebral cortex. The basal ganglia receive information about the position of the body in space and the motivational state of the animal. The basal ganglia is divided into an upper or dorsal division which underlies the control of voluntary movement and motor learning and consists of the striatum and the globus pallidus or pallidum (GP; “pale globe”), based on its appearance in brain sections. The ventral striatum (consisting of the nucleus accumbens, Ac, and olfactory tubercle, TuO) and the ventral pallidum (VP) together constitute the ventral basal ganglia, which are important for emotional and visceral functions.

A proper understanding of striatal function is only possible in context with its cellular composition and that of corticothalamic basal ganglia loops present in the amniote brain (Fig. 1). The striatum is composed mainly of inhibitory (GABAergic) medium spiny neurons (MSNs, ~7 µm in diameter),

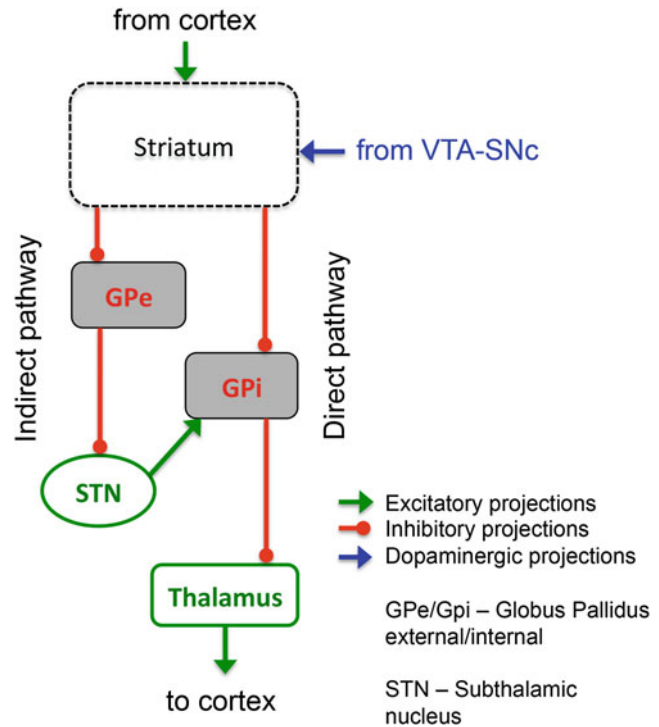
which have numerous spines on their dendrites and project to GABAergic pallidal neurons. In mammals, excitatory (glutamatergic) neurons in the cerebral cortex project to MSNs in the striatum. “Direct pathways” are formed by projections of the striatal neurons onto the internal segment of GP (GPi). GABAergic neurons within GPi project onto excitatory thalamic neurons which project to the cortex, forming loops (cerebral cortex → striatum → GPi → thalamus → cerebral cortex) important for initiating movements. The direct pathway functions through thalamic “disinhibition” as a result of two sets of GABAergic neurons (striatal and pallidal) immediately upstream to it.

Actions of the direct pathways are opposed by “indirect” pathways also involving the striatum. These circuits consists of striatal projections to the external part of the GP (GPe), which project to the strongly excitatory subthalamic nucleus. Disinhibition of the subthalamic nucleus leads to the activation of GPi (GABAergic) which inhibits the thalamus, leading to a decrease in excitation of the motor cortex (cerebral cortex → striatum → GPe → subthalamus → GPi → thalamus → cerebral cortex). The direct and indirect pathways therefore work in concert with each other to ensure that all movements are smooth. In addition to cortical input, the striatum also receives dopaminergic projections from the substantia nigra, pars compacta, which is important for movement and learning (Kuenzel et al. 2011).

## Organization and Development of the Avian Striatal Complex

The avian basal ganglia also consist of striatal and pallidal components and are separated from the overlying cortex or “pallium” by a group of axon fibers called the lamina pallio-subpallialis (LPS). Avian striatal neurons are similar to those in mammals in that they receive projections from the pallium and dopaminergic projections from the substantia nigra. Striatal regions in all birds (vocal learners and non-learners) are similar in terms of structure, connectivity, and functions. The avian dorsal striatum underlies the processing of sensory-motor information for the production

**Avian Striatal Complex,**  
**Fig. 1** Organization of the  
 direct and indirect pathways  
 of corticothalamic basal  
 ganglion loops in amniotes



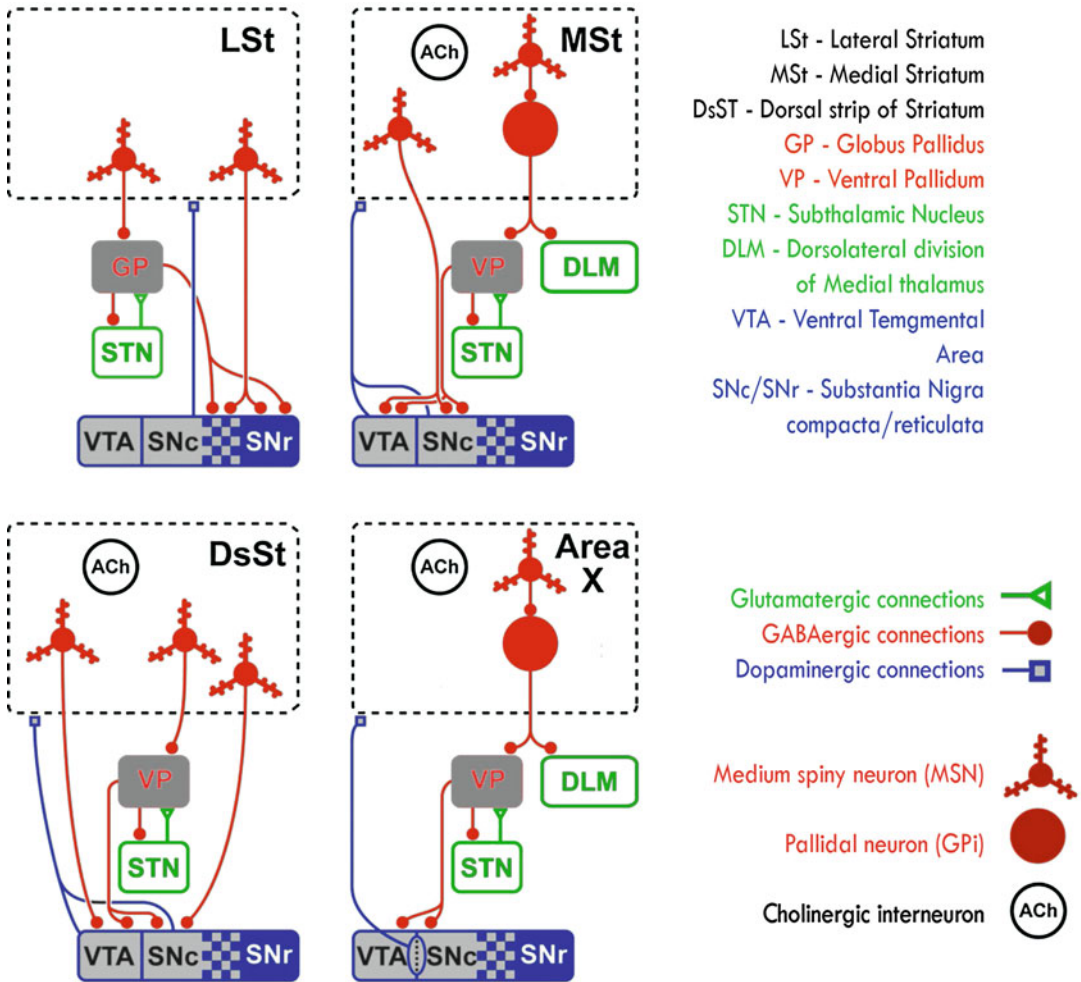
and integration of auditory, visual, and singing behaviors. This part of the striatum consists of two major subdivisions, the dorsal part of the medial striatum (MSt) and the lateral striatum (LSt). In songbirds, the song control region Area X, a specialized area dedicated to song learning as well as context-dependent singing in adulthood is located within the rostral part of MSt. A thin strip of striatum dorsal and lateral to Area X, named DsSt, is also present in rostral MSt. The dorsal striatum sends projections to the globus pallidus (GP). The ventral part of the avian striatum consists of TuO, ventral MSt, and nucleus accumbens (Ac), which are connected to the ventral pallidum (VP). The ventral basal ganglia are viscerolimbic in function, contributing mainly to food, water, sex-related reward, and motivation in appetitive behavior (Fig. 2).

During embryonic development, a structure called the basal telencephalic anlage (embryonic primordium) gives rise to the striatum and pallidum. Whereas the dorsal striatal part of the anlage gives rise to dorsal and ventral parts of striatum, its ventral part gives rise to the dorsal

and ventral parts of the pallidum. Besides these structures, the preoptic part of the anlage gives rise to the subpallial amygdala and cholinergic neurons in the basal forebrain, some of which migrate into the striatum learning (Reiner et al. 2004; Person et al. 2008; Kuenzel et al. 2011).

### Cellular Composition of the Avian Basal Ganglia

The cellular composition of both dorsal and ventral divisions of the avian striatum is almost identical to that of the mammalian striatum, in terms of morphology and histochemical and electrophysiological properties. All four main classes of striatal neurons essential for normal function are present in the medial striatum (MSt) and Area X. These include medium spiny neurons (MSNs), which are GABAergic. They also express substance P or enkephalin (neuropeptides) and DARPP32 (dopamine- and cAMP-regulated neuronal phosphoprotein). Other neuronal subtypes include fast-spiking interneurons which are



**Avian Striatal Complex, Fig. 2** Organization of neural circuits of the avian striatal complex. (Adapted and modified from Fig. 20 in Person et al. 2008)

positive for the calcium-binding protein parvalbumin, tonically active cholinergic interneurons, and low-threshold spiking interneurons which express somatostatin, neuropeptide Y, and nitric oxide synthase. Similar neurons are also present in Ac and rostral and dorsolateral TuO, which represent the ventral striatum in birds.

One of the major differences between Area X, MSt, and the mammalian dorsal striatum is the presence of pallidal neurons intermixed with MSNs throughout the medial subdivisions of the avian striatum. Components of the avian ventral striatum (Ac and TuO) are similar to their dorsal striatal counterparts in that pallidal neurons are

present throughout these regions, intermixed with MSNs and other cell types. In this regard, LSt and DsSt (also present within MSt) are similar to the mammalian striatum, since they are composed only of MSNs. Further, the mammalian dorsal striatum can be divided into “patches” or “striosomes” and the intervening “matrix.” Whereas projection neurons in the patch compartment are rich in mu-opioid receptors, they have less of acetylcholine esterase and the calcium-binding protein, calbindin, compared to the matrix. A second notable difference between the avian and mammalian striatum is the lack of the patch-and-matrix organization in the avian

striatum. Finally, cholinergic interneurons are present in MSt, Area X, and DsSt but not in LSt.

Besides the pallidal neurons which are present in Area X and MSt, the avian brain also contains a clearly demarcated globus pallidus (GP) which is reciprocally connected to the subthalamic nucleus and sends projections to the substantia nigra. As is the case for mammals, pallidal neurons are larger in size (~13  $\mu\text{m}$ ) than MSNs, are GABAergic, and contain LANT6 and parvalbumin. Pallidal neurons similar to those in mammalian GPe and GPi have been identified in the GP, ventral pallidum (VP), and deeper part of TuO in birds. The GPi neurons, which project out of the striatum, mostly express parvalbumin.

### Corticothalamic Basal Ganglia Loops in the Avian Brain and Their Functions

Neural circuits involving the avian striatum are organized in the form of corticothalamic basal ganglia pathways, as in mammals. All parts of avian striatum receive excitatory (glutamatergic) projections from the pallium and project to VTA-SNc directly or indirectly via GP and/or VP and receive dopaminergic projections from VTA-SNc complex which modulate the activity of MSNs through specialized dopaminergic receptors.

#### Medial Striatum

Among the different subdivisions of the avian striatum, the lateral part of the medial striatum (MSt) receives somatosensory, visual, auditory, and motor information from different parts of the pallium. Parts of MSt surrounding Area X in songbirds are involved in processing movement-related information (like wing-whirring and hopping) and receive multimodal input from the pallium surrounding the song control nucleus LMAN (lateral magnocellular nucleus of the anterior nidopallium), called the  $\text{LMAN}_{\text{shell}}$ . Medium spiny neurons in MSt project directly to VTA-SNc (ventral tegmental area-substantia nigra complex) and to pallidal neurons, within MSt. Collaterals of the axons of pallidal neurons in MSt project to VP and the ventromedial part of

thalamic nucleus, DLM (dorsolateral division of the medial thalamus) and to the subthalamic nucleus via VP. Further, the medial part of MSt is known to be viscerolimbic in function and receives information from the hippocampus and olfactory bulb (Feenders et al. 2008; Paterson and Bottjer 2017; Johnson et al. 1995).

#### Area X

As described above, Area X is a specialized part of the medial striatum dedicated to singing and song learning. It is a part of the anterior forebrain pathway (AFP), a neural circuit important for song learning and context-dependent singing in songbirds such as zebra finches. Medium spiny neurons (GABAergic) in Area X receive glutamatergic projections from the pallial song control regions HVC (abbreviation used as the proper name) and LMAN. The MSNs project to GABAergic GP neurons, also within Area X which project to the dorsolateral part of DLM. Since DLM projects to the central part of LMAN ( $\text{LMAN}_{\text{core}}$ ), a loop is formed within the AFP. Both HVC and LMAN also project to RA (robust nucleus of the arcopallium), a premotor nucleus which controls the movement of the syrinx through its projections to the tracheosyringeal branch of the 12th (hypoglossal) nerve. While singing, Area X receives a copy of motor command from HVC, which is modified by the AFP to generate variability and matched to innate song template learnt by juvenile birds during the sensitive period for song learning. This ability to generate variable songs is a form of learning by trial and error, which helps young songbirds produce and practice their songs, which become adult-like over time (Kubikova et al. 2007).

Area X is also linked to circuits important for the motivation to sing and context-dependent singing through its projections to VP, which in turn projects to VTA-SNc. When juvenile birds sing in the presence of their fathers or when adult males sing to females, higher levels of dopamine are released into Area X by the VTA-SNc than when birds sing alone. Interestingly, the medial part of Area X appears to be important for the production of female-directed song, whereas the lateral part of this nucleus appears to be important

for singing undirected song, in adult male zebra finches. Additionally, Area X also controls acoustic properties of songs such as its frequency, pitch, or length of song syllables via its connections to LMAN (Sasaki et al. 2006).

### Dorsal Strip of Striatum

Besides Area X, the “dorsal strip” (DsSt) appears to be present exclusively in songbirds. Medium spiny neurons in this region project directly to VTA-SNc and also indirectly, through their projections to VP. However, the functions of this region have not been identified so far.

### Lateral Striatum

Besides the movement-related and song-related functions of the medial striatum, the lateral striatum (LSt) is a part of both direct and indirect pathways. As a part of a direct pathway, MSNs in this region receive input from somatic pallial regions and project to SNr (substantia nigra, pars reticulata) and GP. Pallidal neurons further project to the avian motor thalamic nucleus (ventrointermediate area or VIA), which innervate the motor pallium in the Wulst or hyperpallium. Since striatal LSt neurons also project to the avian subthalamic nucleus via the GP, LSt forms part of an indirect pathway similar to that in mammals. In addition to its somato-motor functions, LSt receives input from the entopallium (E), which is a part of the tectofugal visual system and therefore plays a role in processing visual information. In terms of its cellular composition, a unique feature of LSt is that it is the only part of avian striatum which does not have either cholinergic interneurons or pallidal neurons.

### Olfactory Tubercles

The olfactory bulb, hippocampus, piriform cortex, and areas of the brain related to the autonomic nervous system project to the superficial (striatal) part of TuO, which further projects to pallidal neurons within the same region. Based on the fact that these neurons innervate the hypothalamus, TuO appears to be important for integrating olfactory, limbic, and visceral information.

### Nucleus Accumbens

The avian nucleus accumbens is located in rostral ventromedial MSt and is important for motivated goal-directed behavior, reward mechanisms, and emotions. It receives input from several brain regions including the hippocampus, septum, piriform cortex, caudal VP, and arcopallium. As in mammals, the avian Ac forms a “limbic loop” consisting of projections from the medial pallium (similar to the prefrontal cortex) which innervate Ac. Nucleus accumbens may be involved in learning and memory through its connections to VP which projects to the avian counterpart of the dorsomedial thalamic nucleus, which is known to be involved in these functions (Bálint and Csillag 2007).

### Cross-References

- [Auditory Processing and Perception](#)
- [Axon](#)
- [Behavior Systems](#)
- [Cognition](#)
- [Corvids](#)
- [Dendrites](#)
- [Dopamine Receptor](#)
- [Entopallium](#)
- [Medial Striatum](#)
- [Motivation](#)
- [Neocortex](#)
- [Neurotransmitters](#)
- [Nucleus Accumbens](#)
- [Passerine Sensory Systems](#)
- [Passerine Vocal Communication](#)
- [Songbird Learning](#)

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## Avoidance

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## Synonyms

Discriminated avoidance; Free-operant avoidance; Sidman avoidance; Signaled avoidance

## Definition

Behavior that prevents or postpones exposure to an anticipated aversive stimulus or threat.

## Introduction

Avoidance is an adaptive and versatile defensive behavior that helps protect many taxa from engaging with dangerous situations and harmful stimuli. In the wild, prey may seek refuge when an alarm call is heard or flee if the scent of a predator is detected, thus eluding a potentially fatal encounter or serious injury. Avoidance is distinct from escape, which refers to behavior that terminates an ongoing exposure to an aversive stimulus or threat. The roles of learning, fear, and anxiety in avoidance behavior have been the focus of laboratory research for many decades. This interest arose in part from the puzzle that avoidance behavior posed for theories of reinforcement: What is the reward for a behavior that is followed by a nonevent? It has persisted because of the insights that animal models of avoidance behavior can contribute to our understanding and treatment of human psychopathologies including generalized anxiety disorder, hoarding, obsessive-compulsive disorder, post-traumatic stress disorder, social anxiety disorder, and phobias.

## Avoidance Is Ubiquitous in Nature

Avoidance is used by wild animals to minimize predation risk while foraging, searching for mates, or procuring other resources. Whereas predator escape behaviors are predominantly innate, having evolved through the process of natural selection, predator avoidance behavior can be acquired or fine-tuned through learning. Life experiences provide a rich supply of opportunities for animals to gather temporal, spatial, and sensory information that can be used to avert hazardous encounters with predators. Decisions about when or where to forage are influenced by perceived predation risk in a diversity of prey, including termitophagous ants (*Pheidole titanus*), fathead minnows (*Pimephales promelas*), dark-eyed juncos (*Junco hyemalis*), herons (*Ardeidae*), larval tiger salamanders (*Ambystoma tigrinum*), Anolis lizards (*Anolis Sagrei*), Merriam's kangaroo rats (*Dipodomys merriami*), caribou (*Rangifer tarandus*), African buffalo (*Syncerus caffer*) and

elk (*Cervus elaphus*). With knowledge of the relative prevalence of aerial, aquatic, and terrestrial predators, mallard ducks, for example, can adjust time spent in shallow or deep water or on land. Similarly, learning to identify the referential meaning of different alarm calls enables individuals to deploy predator-appropriate defensive strategies without needing to locate the specific threat. Such use of referential specificity in alarm calls has been demonstrated in several avian and mammalian species, including chickens (*Gallus gallus*), Japanese great tits (*Parus major minor*), Siberian jays (*Perisoreus infaustus*), Gunnison's prairie dogs (*Cynomys gunnisoni*), meerkats (*Suricata suricatta*), Campbell's monkeys (*Cercopithecus campbelli*), Diana monkeys (*Cercopithecus diana*), ring-tailed lemurs (*Lemur catta*) and vervet monkeys (*Chlorocebus pygerrhus*).

Learning about the temporal and spatial patterns of predators and the meaning of alarm calls likely involves Pavlovian conditioning. This conditioning process may also play a role in learning about predator-related cues such as scents, sounds, and appearance. In such cases, the survival of captive bred animals released into the wild can be improved by predatory threat exposures prior to their release. A separate learning process, instrumental conditioning, may also influence avoidance behavior depending on the consequences of that behavior. The potential contributions of these two learning processes to avoidance behavior have long been the focus of intense theoretical and empirical analysis.

## Avoidance in the Laboratory

The study of avoidance behavior has occupied a central role in the history of learning theory. The major problem confronting researchers was to explain the emergence and persistence of a behavior for which there was no tangible reinforcement. This issue directed much of the empirical research. Theories of avoidance behavior that emerged from this tradition have typically conceded that both Pavlovian and instrumental conditioning processes are involved.

## Avoidance Procedures

The standard procedures for the experimental analysis of avoidance behavior are discrete trial signaled (discriminated) avoidance and free-operant (Sidman) avoidance with mild electric shock as the aversive stimulus. Using these two methods, successful avoidance has been demonstrated in fish, birds, and mammals, including humans.

In a typical signaled avoidance task, a trial is initiated by a warning stimulus (WS). What happens next depends on what the subject does. If the designated avoidance response occurs within a predetermined interval following onset of the WS, the WS is turned off and no shock is delivered. The subject has successfully avoided the shock. If this deadline is missed, shock is turned on. As soon as the designated response occurs, both the WS and the shock are turned off. The subject has successfully escaped the shock.

In a typical free-operant avoidance task, brief shocks are scheduled to occur at a specific rate (the shock-shock interval); the designated avoidance response extends that interval by canceling or postponing the upcoming scheduled shock (the response-shock interval). Robust avoidance is obtained when the response-shock interval is longer than the shock-shock interval. Timing is critical for this task as only temporal information can be used to predict shock delivery.

## Nature of the Avoidance Response

Some avoidance responses are readily acquired whereas others are not. In rats, for example, jumping over a hurdle to avoid shock can be established in just a few trials. Pressing a lever to avoid shock, however, can take many hundreds of trials and performance is not as robust. This variability in acquisition and consistency among avoidance responses has been attributed by some researchers to variations in interference from either innate behaviors or Pavlovian conditioned responses (CRs). For example, Bolles (1970) pointed to differences in the compatibility of the designated avoidance response with the animal's innate defensive responses to danger. He argued that evolutionary adaptation to predators had equipped animals with species-specific defense

reactions (SSDRs) to danger. Rats, he alleged, might freeze, flee or fight depending on details of the threat. Thus, if the avoidance response was part of the animal's normal repertoire of defensive behavior, acquisition was rapid; if not, acquisition was poor and unreliable. The predatory imminence hypothesis expands further on the ecological and evolutionary effects on avoidance behavior (Fanselow and Lester 1988).

### The Instrumental Contingency

There is little doubt that an animal's biology can exercise considerable influence on avoidance behavior in the laboratory. However, evidence that avoidance behavior can be affected by its consequences suggests that appeal to SSDRs or CRs alone is not sufficient to understand all aspects of avoidance behavior (Mackintosh 1983).

In one of the earliest studies to hint at the critical role of the instrumental contingency between the avoidance response and the aversive consequences, Brogden et al. (1938) trained some guinea pigs to run inside a wheel to avoid shock. After only a few days, they performed perfectly. Whenever the WS came on, these subjects turned the wheel and avoided the scheduled shock. The importance of the response consequences was demonstrated by the comparatively inferior performance of a second group of guinea pigs trained with a purely Pavlovian contingency. For these subjects, shock always occurred 2 s after the WS came on regardless of their behavior. Running in the wheel was never reliably established in these animals even after many days of training.

### The Role of Escape in Avoidance Behavior

Escape responses were once considered indispensable to avoidance behavior. According to this view, reinforcement could only occur on escape trials when the response successfully terminated or removed the aversive event. This account made two strong predictions: escape and avoidance responses had to be identical and response extinction should occur on avoidance trials. Neither of these predictions was confirmed. Studies have shown, for example, that animals can learn to make one response to escape shock and a

different response to avoid shock (Mowrer and Lamoreaux 1946). Solving the avoidance puzzle, that is how a nonevent can strengthen a response, came to dominate research on avoidance.

## Theories of Avoidance

Theoretical analyses of avoidance have considered three fundamentally distinct solutions to the avoidance puzzle: avoidance behavior is reinforced by fear reduction; avoidance behavior is self-reinforcing; avoidance behavior is determined by response expectancies.

### Fear Reduction

Two factor theory accounts for avoidance behavior through an interaction of Pavlovian and instrumental conditioning. Briefly, fear is conditioned to the WS on escape trials when it is paired with shock. This is the Pavlovian conditioning process. Now, there can be a reduction in fear on avoidance trials when the WS is turned off by the designated response. This reduction in conditioned fear serves to reinforce or strengthen the connection between the WS and the avoidance response. This is the classical stimulus-response (S-R) instrumental conditioning process. Turning off the WS on an avoidance trial has the same effect as turning off the shock on an escape trial; behavior is reinforced by a reduction in fear and thus becomes more likely to be elicited by that situation in the future (Mowrer and Lamoreaux 1946).

Assessment of two factor theory largely focused on its predictions about the relationship between fear of the WS and strength of the avoidance response and the necessity of terminating the WS after the designated response has occurred. The results of such studies have suggested a more complicated picture. Fear of the WS is not a simple function of response strength and WS termination is critical for training some responses but not others. The popularity of two factor theory, however, has not been entirely diminished by these findings or by contemporary theoretical developments regarding the goal-directed nature of instrumental behavior.

### Reinforcement Through Conditioned Inhibition

The major alternative to two factor avoidance theory employs the concept of conditioned inhibition of fear (Rescorla 1968). Building on evidence that a stimulus which predicts the omission of an expected aversive event becomes a conditioned inhibitor of fear, researchers proposed that internal stimuli correlated with performance of the avoidance response similarly acquire inhibitory properties. According to this view, the WS provides an expectation of shock through Pavlovian conditioning on escape trials; on avoidance trials, the WS in conjunction with the response is followed by the omission of the expected shock and a period of safety. This discrimination establishes the response feedback stimuli as conditioned inhibitors of fear (safety signals) which function to strengthen avoidance responding through positive reinforcement. In this way, avoidance behavior can be viewed as self-reinforcing.

Consistent with this analysis, studies have shown that arranging for the avoidance response to be accompanied by an external stimulus establishes that stimulus as a conditioned inhibitor of fear (Rescorla 1968). In addition, explicit safety signals enhance avoidance responding even if the WS is not terminated on avoidance trials. This analysis helps address the persistent nature of avoidance behavior because the reward value of safety signals derives from their status as conditioned inhibitors, which are known to be immune to the effects of simple extinction.

### Response Expectancies

Expectancy theory is classified as a cognitive account of avoidance. It asserts that two expectancies are learned: that shock will occur if the designated response is not made and that no shock will occur if the designated response is made. The decision to respond is based on a conscious appraisal of this information. Lovibond (2006) has been a forceful proponent of expectancy theory in its application to human avoidance behavior.

Observations consistent with this view include the persistent nature of avoidance responding, the

effects of response prevention, and the decoupling between response strength, and fear of the WS with extended training. However, results of recent studies manipulating outcome expectancies after initial training and failing to find appropriate changes in avoidance behavior have challenged this approach.

### Current Directions in Avoidance Research

Maladaptive avoidance is recognized as a significant component of many clinical pathologies in human behavior. Efforts to improve cognitive, behavioral, and pharmacological therapies have catalyzed a renewed interest in theories of avoidance behavior and the underlying neurobiological mechanisms (Krypotos et al. 2015; LeDoux et al. 2016). These endeavors are complemented by research using relatively new model systems. A number of escape and avoidance assays have been developed for use with larval and adult zebrafish (Colwill and Creton 2011). For example, just 1 week after fertilization, free-swimming zebrafish larvae imaged in multiwell plates show avoidance of computer-generated moving visual stimuli as well as dark or open areas. With its tractable genetics and rapid development, the zebrafish provides opportunities to study mechanisms involved in the development of fear and anxiety disorders and to screen novel pharmaceutical compounds with therapeutic potential.

### Conclusion

Avoidance behavior is likely to be determined by a confluence of factors including innate dispositions in reactions to threats, learning about cues predictive of danger and safety, and effects arising from response consequences and repetition. Maladaptive avoidance behavior in humans may represent abnormal functioning of one or more components of a complex system designed to protect an individual from harm.

## Cross-References

- [Alarm Calls](#)
- [Associative Learning](#)
- [Classical Conditioning](#)
- [Escape Response](#)
- [Fear Response](#)
- [Operant Conditioning](#)
- [Passive Avoidance Learning](#)
- [Zigzag Display](#)

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## Avoidance Test

- [Human Approach Test](#)

## Awareness

- [Catarrhine Cognition](#)
- [Self-Awareness](#)

## Axial Skeleton

- [Skeletal System](#)

## Axon

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## Synonyms

[Nerve fiber](#)

## Definition

A long specialized structure of a neuron that conducts an electrical signal from the cell body to the axon terminals.

## Introduction

Axons are a long specialized structure of the neuron that conducts an electrical signal from the cell body to the terminals. Axons play an integral role in neural communication, as they allow nerve impulses to travel to neurons, muscles, and glands around the brain and body. They are essential in the propagation of an action potential as their unique structural properties allow for the efficient conduction of electrical signals. When signals are received by the dendrites, they are collected at the axon hillock, a structure adjacent to the cell body. If the combined signal is strong enough, it will trigger an action potential. The axon has a unique

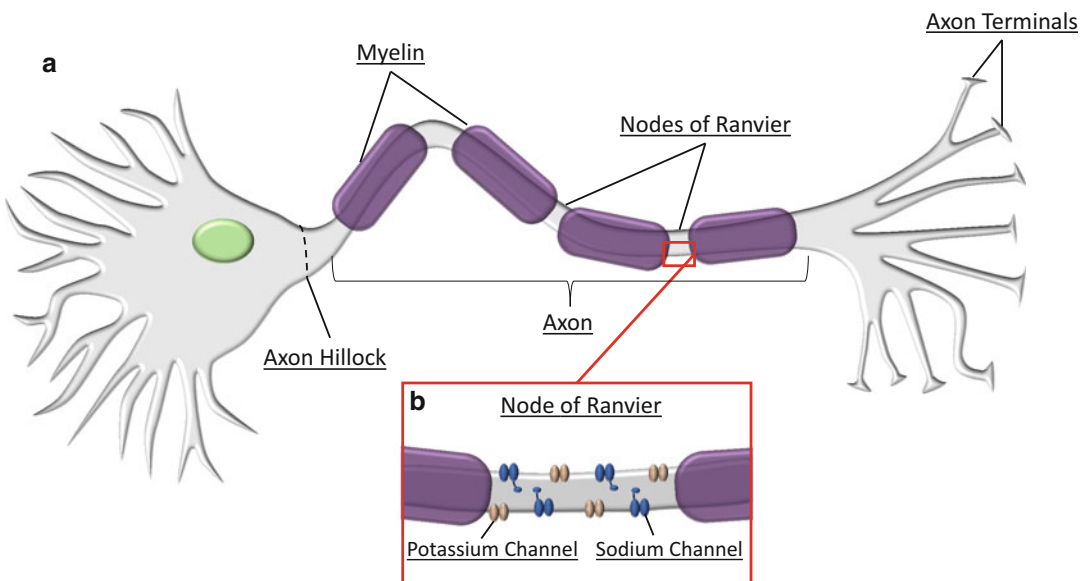
cytoskeletal structure that is essential to the life of the neuron as it is used to transport important materials back and forth the cell. A prominent characteristic of an axon is the presence of a myelin sheath, which serves to insulate the structure and hasten propagation. Faster conduction velocity afforded by myelin allows for quicker neural processing, which helps all aspects of functioning, like fine motor movements. As such, up to 90% of cerebral neurons are myelinated. Given the importance of the axon, damage caused by injury, disease, and trauma can lead to neuronal death and a number of conditions that affect the nervous system.

## Structure and Function

The axon stems from a neuron's cell body and serves to transmit signals to the terminals (Fig. 1a). Adjacent to the cell body is the initial segment of the axon, also known as the axon hillock. This area collects the signals from the cell body and is the point of action potential initiation. It features a high density of voltage-gated sodium ion channels (Fig. 1b) that make the area

more excitable and facilitate the initiation of an action potential (Wollner and Catterall 1986). Further down, the axon features a collection of voltage-gated ion channels along its membrane that open when a reversal in the neuron's charge occurs. In unmyelinated neurons, these ion channels are dispersed evenly across the cell, while ion channels in myelinated neurons are concentrated at high densities at the gaps between myelin (Fig. 1b), also called the nodes of Ranvier (Squire et al. 2008).

Axons, as a whole, get their structure from a cytoskeleton that contains microtubules and neurofilaments. In the axon, all microtubules are arranged from the soma to the terminals in a plus-end-out formation. This indicates that the positive side of the microtubule is away from the cell body. This critical formation differs from that of the dendrites, which have microtubules arranged in both directions. Another important function of the axon is to transport materials, such as nutrients, growth factors, and neurotransmitters, back and forth from the cell body. Along the axonal microtubule, dynein and kinesin are two primary proteins used for active transport of vesicles. Dynein moves to the minus end, towards the soma, while most



**Axon, Fig. 1** Structure of a neuron. (a) General structure of multipolar neuron containing the axon hillock, axon, myelin, nodes of Ranvier and axon terminals. (b) Close-up of node of Ranvier showing the accumulation of ion channels



kinesin move toward the axon terminals (Lodish et al. 2000a). While microtubules work to elongate the axon, neurofilaments are arranged radially and determine the diameter. Axons contain more neurofilaments as they increase in diameter (Lobsiger and Cleveland 2009). This is an important characteristic as larger diameter axons feature faster action potentials (Salami et al. 2003).

## Development

Much of a neuron's function comes from its polarity, which influences the development of the axon. In a developing neuron, small projections, called neurites, grow out of the cell body. In a multipolar cell, one neurite grows into an axon while others grow into dendrites. This development occurs as a result of signaling pathways triggered by extrinsic and intrinsic signals. Extrinsic signals are secreted by neurons into the extracellular environment, while intrinsic signals remain inside the cell and are modulated by the expression of a gene. UNC-6 is a protein found in the extracellular environment that guides the direction in which an axon grows. Neurotrophins, another extrinsic factor, bind to the cell and trigger a series of events that enhance the formation of the axon. Intrinsic signals, such as Ras and PI3K, trigger biochemical cascades that cause conformational changes in the arrangement of microtubules and neurofilaments. Knocking out these protein-producing genes leads to the inhibition of axonal formation, while overexpression leads to the development of multiple axons. Both intrinsic and extrinsic signals are necessary for the proper polarization of a neuron (Arimura and Kaibuchi 2007).

## Role in Action Potential

The axon plays an important role in the propagation of an action potential. In order to propagate the signal, the axon relies on several aspects of its structure. The inside of a neuron is negative relative to the outside due to the cell's permeability and availability of ions inside and outside of the cell. An action potential usually begins at the axon

hillock when the combined afferent signal becomes strong enough to cause a reversal in charge. However, a neuron can also receive signals and initiate an action potential by receiving input directly to the axon. This is known as an axo-axonic synapse. There are two main ion channels, sodium and potassium, that are present along the axon and serve to depolarize and repolarize the cell, respectively. Due to the slow activation of the potassium ion channel, these processes do not occur at the same time. As the cell depolarizes, the current travels down the axon and activates more ion channels, propagating the signal down the axon. (Lodish et al. 2000b).

## Myelination

Myelination is paramount to proper neural functioning, as it allows an electrical signal to propagate more quickly. (Salami et al. 2003). Myelin works by insulating an action potential as it is pulled by the concentration and electrostatic gradients. The signal travels down the axon by a process called saltatory conduction, where it jumps between the gaps of myelinated segments. These gaps, called nodes of Ranvier, contain a high concentration of voltage-gated ion channels that allow the action potential to quickly regenerate (Salzer 1997). Axons become myelinated with the help of glial cells within the body. These supporting cells, including oligodendrocytes and Schwann cells, myelinate axons within the central and peripheral nervous systems, respectively. When myelin is lost, the electrical charge traveling down an axon slows down. This loss of conduction velocity, and subsequent slower processing, results in various neurocognitive diseases such as multiple sclerosis (Squire et al. 2008).

## Deterioration in Injury and Disease

Due to the brain's complexity, axonal injury can result in a myriad of neurological impairments, especially in densely configured myelinated axons. Axons can be damaged in many ways, including traumatic brain injury (TBI) and disease. Common in TBI, diffuse axonal injury

(DAI) is characterized as damage to the axon or its structure, including disconnection from the cell body or microtubule breakage. Injury occurs as the rapid acceleration and deceleration of the brain puts a large strain on the axon cytoskeleton. Damage following DAI results in a cascade of events leading to the degeneration and eventual death of a neuron, including interrupted axonal transport and disorganized neurofilaments (Tang-Schomer et al. 2010). Pathology associated with TBI arises in the form of poorer cognitive processing and memory formation. Alzheimer's dementia (AD) is a common form of disease-driven axonal deterioration. In AD, axonal damage arises from the buildup of plaques and tangles that disrupt normal cellular function, usually in structures associated with learning and memory. In AD, Tau proteins dissociate from the microtubule, causing their breakdown and neuronal death. Furthermore, the loose Tau proteins bundle and form tangles that can strangle other neurons (Mattson 2004). In both injury and disease, axonal transport is interrupted and can lead to the death of the cell, highlighting the importance of an axon to the overall health of the neuron.

## Cross-References

- [Action Potentials](#)
- [Dendrites](#)
- [Myelination](#)
- [Nervous System](#)
- [Neuron](#)
- [Neurotransmitters](#)

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## B.F. Skinner

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### Introduction

Burriss Frederick Skinner (March 20, 1904–August 18, 1990), also known as B. F. Skinner, was an American research psychologist, radical behaviorist, social commentator, and writer. He is considered the father of operant conditioning and modern behavior analysis. He was the Edgar Pierce Professor of Psychology at Harvard University from 1958 until his retirement in 1974. He received the Citation for Outstanding Lifetime Contribution to Psychology from the American Psychological Association shortly before his death in 1990. He is considered the foremost eminent psychologist of the twentieth century (Haggbloom et al. 2002). He published 19 books, and nearly 200 journal articles. He received honorary degrees from over 20 universities worldwide (B. F. Skinner Foundation 2016a). During his lifetime, he would receive dozens of major awards for his work (see Table 1).

### Biography

B. F. Skinner was born in Susquehanna, Pennsylvania, in 1904. His father was a lawyer, and his mother was a housewife. As a youngster, he had a penchant for building things. But by high school, he had developed a love of literature and writing. He later attended Hamilton College in Clinton, New York, where he majored in English. He never felt that he fit in at Hamilton. He wasn't particularly good at sports. He resented the chapel attendance requirement and was a self-admitted troublemaker. Following graduation from Hamilton in May of 1926, Skinner spent 2 years as a writer (rather unsuccessfully). Then, at age 24, he enrolled at Harvard University to study psychology (Skinner 1976).

### Harvard University (1928–1936)

Early in his graduate school career, Skinner was influenced by a number of important individuals including Charles Darwin, E. L. Thorndike, and especially, John B. Watson, whose *Psychology as the Behaviorist View It* (1913) advocated for an empirical science of behavior and rejected both Wundt's introspective methods and the elaborate psycho-analytic theories of Freud and Jung. Skinner embraced Watson's behavioristic philosophy that rejected explanations based on a

**B.F. Skinner, Table 1** List of awards, degrees, and positions conferred on B. F. Skinner. (Compiled from Skinner 1979, 1988; Smith and Morris 2004; B. F. Skinner, Wikipedia Skinner 2019)

| Year      | Award, degree, or position                                                                               |
|-----------|----------------------------------------------------------------------------------------------------------|
| 1926      | A.B.. Degree, English, Hamilton College                                                                  |
| 1930      | M.A. Degree, Psychology, Harvard University                                                              |
| 1930–1931 | Thayer Fellowship                                                                                        |
| 1931      | Ph.D., Psychology, Harvard University                                                                    |
| 1931–1932 | Walker Fellowship                                                                                        |
| 1931–1933 | National Research Council Fellowship                                                                     |
| 1933–1936 | Junior Fellowship, Harvard Society of Fellows                                                            |
| 1936–1937 | Instructor, University of Minnesota                                                                      |
| 1937–1938 | Assistant Professor, University of Minnesota                                                             |
| 1939–1945 | Associate Professor, University of Minnesota                                                             |
| 1942      | John Simon Memorial Guggenheim Fellowship (postponed until 1944–1945)                                    |
| 1942      | Howard Crosby Warren Medal, Society of Experimental Psychologists                                        |
| 1945–1948 | Professor and Chair, Psychology Department, Indiana University                                           |
| 1947–1948 | William James Lecturer, Harvard University                                                               |
| 1948–1958 | Professor, Harvard University                                                                            |
| 1948      | Elected to the American Philosophical Society                                                            |
| 1949      | Elected to the National Academy of the Sciences                                                          |
| 1958      | Distinguished Scientific Contribution Award, APA                                                         |
| 1958–1974 | Edgar Pierce Professor of Psychology, Harvard University                                                 |
| 1964–1974 | Career Award, National Institute of Mental Health                                                        |
| 1966      | Edward Lee Thorndike Award, APA                                                                          |
| 1966–1967 | President of the Pavlovian Society of North America                                                      |
| 1968      | National Medal of Science, NSF                                                                           |
| 1969      | Overseas Fellow in Churchill College, Cambridge                                                          |
| 1971      | Gold Medal Award, American Psychological Foundation                                                      |
| 1971      | The Joseph P. Kennedy Jr. Foundation for Mental Retardation International Award                          |
| 1972      | Humanist of the Year, American Humanist Association                                                      |
| 1972      | Creative Leadership in Education Award, New York University                                              |
| 1972      | Career Contribution Award, Massachusetts Psychological Association                                       |
| 1974–1990 | Professor of Psychology and Social Relations Emeritus, Harvard University                                |
| 1978      | Distinguished Contributions to Educational Research Award, AERA                                          |
| 1978      | First National Association of Retarded Citizens Award                                                    |
| 1985      | Award for Excellence in Psychiatry, Albert Einstein School of Medicine                                   |
| 1985      | President's Award, New York Academy of Science                                                           |
| 1990      | Williams James Fellow Award, APS                                                                         |
| 1990      | Citation for Outstanding Lifetime Contribution to Psychology, APA                                        |
| 1991      | Outstanding Member and Distinguished Professional Achievement Award, Society for Performance Improvement |
| 1997      | Scholar Hall of Fame Award, Academy of Resource and Development                                          |
| 2011      | Induction to the Pantheon of Skeptics, Committee for Skeptical Inquiry                                   |

metaphorical science of the “mind” including mental states, beliefs, memory, or goals. Like Watson, Skinner rejected the “mind” as a useful scientific construct, and he argued that the goal of any science of behavior was to predict and control

behavior through an analysis of the interaction between the organism the current stimulus environment.

At Harvard, Skinner found a mentor in psychology department chair William Crozier,

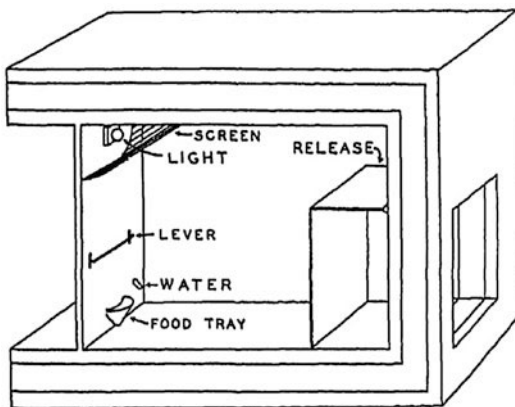
a physiologist interested in sensation and perception. Crozier was committed to laboratory experimentation using intact organisms. He believed that only through experimental control could a clear understanding of behavior emerge. He also rejected current popular beliefs that ascribed cause to internal states (B. F. Skinner Foundation 2016b). It was in Crozier's lab that Skinner was allowed to develop his own research program focused on the influence of environmental contingencies on behavior. Skinner was afforded great freedom at Harvard under the direction of Crozier. He spent much of his time alone in the laboratory "doing exactly as I pleased," studying the behavior of rats (B. F. Skinner Foundation 2016b).

**Inventions.** With his fundamental engineering skills and a healthy dose of trial and error, he fashioned the first conditioning chamber (See Fig. 1) and the cumulative recorder, a seismograph-like device for recording individual responses as a function of time (slope indicates the rate of responding). The recorder revealed the unique effects different behavioral contingencies had on response rates and response patterns (See Fig. 2).

**Operant Conditioning.** Skinner's work at Harvard rejected the current line of behavioristic thinking, based on the work of Pavlov and Watson, that all behavior is reflexive, elicited by the stimuli that precede it (S-R theory). Rather,

Skinner argued for a different type of behavior – voluntary behavior that is instrumental in changing the surrounding environment. Skinner coined the term *operant* and defined it as any non-reflexive behavior that operates on the environment. Furthermore, he showed that various arrangements of consequences in time directly influenced response strength, likelihood, and probability differently. He called this new kind of learning "*operant conditioning*," aka instrumental conditioning (See "► [Instrumental Learning](#)", "► [Operant Conditioning](#)").

Using his uniquely engineered equipment, Skinner systematically and comprehensively, investigated the effects of environmental consequences on behavior. Studying rats in experiments that strictly controlled the consequences of behavior, he painstakingly outlined the effects of positive reinforcement and extinction on the rate of lever pressing. He developed alternative laws for these operant behaviors, including the laws of reinforcement and instrumental extinction. He addressed the development of the conditional nature of discriminative stimuli as excitatory or inhibitory occasion setters. The foundations for his later famous three-term contingency (antecedent->behavior->consequence) were laid at this time. This seminal work, *The Behavior of Organisms*, was published in 1938.

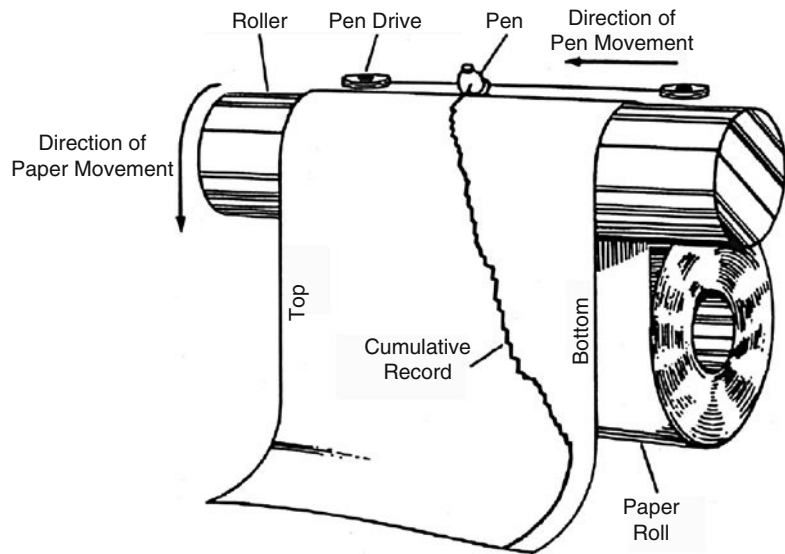


**B.F. Skinner, Fig. 1** The original conditioning, aka operant, chamber as proposed by Skinner in 1938. This graphic is reproduced from Skinner (1938). (Catania 2017)

## The Minnesota Years

After completing his doctoral degree at Harvard University in 1931, where he remained as a research associate until 1936, Skinner accepted a professorial position at the University of Minnesota in Minneapolis and remained there through 1945. While there, he conducted his top secret "Pigeons in a Pelican" study in an attempt to contribute to the war effort. With \$25,000 in funding from the National Research Defense Committee, Skinner successfully trained pigeons to peck at a target as the primary missile guidance system in simulated military warheads (Stromberg, 2011). In tests, the pigeons provided a reliable guidance system even when descending

**B.F. Skinner, Fig. 2** The main components of a cumulative recorder. Paper is driven at a constant rate (e.g., 2.4 min/in.); each response moves a pen a fixed distance (aka tic) across the paper in real time. When the pen reached the top of the page (1100 responses), it resets automatically. Response rates are measured as responses per minute. Slope indicates response rate (e.g., a slope of  $45^\circ =$  about 45 responses per min). (This graphic is reproduced from Catania 2017)



rapidly, and even when surrounded by loud warlike noises (B. F. Skinner Foundation 2016b). The project was discontinued when another federally funded, secret missile guidance system based on radar was deemed more viable. This unique project is described in detail in Skinner's book *Cumulative Record* (1959).

## The Harvard Years

In 1945, Skinner accepted the position of Chair of the Psychology Department at Indiana University in Bloomington, Indiana. He remained there only 2 years. The field of behavior analysis was growing rapidly and in 1947, he was offered the William James Lecturer position at Harvard University, where he remained for the rest of his academic career. In 1948, the Harvard Pigeon Laboratory was established and remained an active research laboratory for the next 50 years (Heyman 2002). Under Skinner's leadership (and later under both Skinner and Richard J. Herrnstein), the lab produced some of the most productive behavioral psychologists of the twentieth century (for a list of his graduate students, see Baum 2002). Many of these renown and respected psychologists provided their own insights and reminiscences about their time in the Harvard pigeon lab in 2002 in a retrospective

issue of the *Journal of the Experimental Analysis of Behavior* (Lattal 2002).

According to Skinner and Herrnstein's former students, life in the Harvard pigeon Lab was the most formative time in their lives, marked by great intellectual growth and experimental freedom (for a comprehensive overview of life in and the impact of the Harvard pigeon lab see Azrin 2002; Baum 2002; Belke 2002; Boakes 2002; Catania 2002; Dews 2002; Fantino 2002; Ferster 2002; Gollub 2002; Green 2002; Heyman 2002; Himeline 2002; Lattal 2002; Lindsley 2002; Logue 2002; MacSweeney 2002; Miller 2002; Morse and Dews 2002; Staddon 2002; Zuriff 2002).

**Schedules of Reinforcement.** In 1950, Skinner began what is considered by many to be his biggest contribution to the study of behavior. Together with research fellow Charles Ferster, they began what would be 5 years of intense laboratory work dedicated to a comprehensive analysis of the nature of different schedules of reinforcement (Ferster 2002; Morse and Dews 2002). What emerged was evidence that uniquely scheduled contingencies of reinforcement produced distinctive and observable patterns of responding. For example, when the number of responses required for reinforcement was fixed (aka fixed-ratio schedule), a stereotyped (step-function) pattern of responding emerged. Similarly, if the delay before a response would



produce reinforcement was held constant (aka fixed-interval schedule), a different response pattern (scallops) emerged. But when the response requirements varied and were unpredictable (as with variable-ratio and variable-interval schedules), response patterns became more regular and stable.

A detailed compendium outlining simple and complex schedule effects was published as *Schedules of Reinforcement* in 1957 (Ferster and Skinner 1957) (See “► [Instrumental Conditioning](#)”, “► [Operant Conditioning](#)”, “► [Schedules of Reinforcement](#)”).

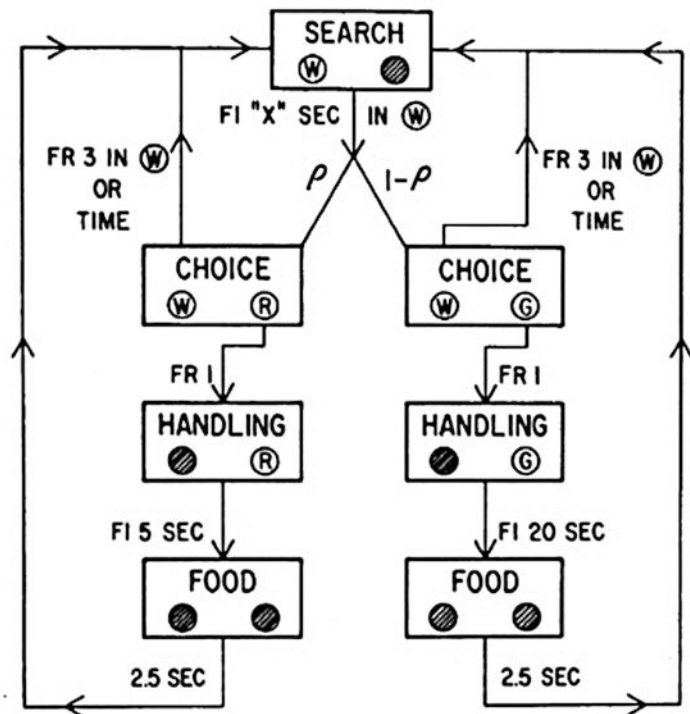
**Schedules of Reinforcement and Foraging Research.** The operant conditioning chamber and complex schedules of reinforcement (e.g., chain schedules, multiple schedules, mixed schedules, tandem schedules, and random ratio schedules) provided the groundwork for detailed laboratory analyses of the factors that influence foraging-related choice behavior. Psychologists adapted operant conditioning-chamber procedures to simulate the contingencies imposed by the various phases of the foraging process.

Searching, choice, handling, and consumption could be isolated and manipulated independently allowing for excellent experimental control.

In 1979, Lea developed an operant analogue of foraging designed to mimic foraging-related choices in an operant conditioning chamber (See Fig. 3). Pigeons searched by pecking on a white key programmed on a fixed interval schedule. Upon completion of the search phase, the second key was illuminated either Red or Green. This was the Choice Phase. A single response to the colored key turned off the white search key and committed the bird to either a FI 5-sec or FI-20 sec response requirement representing two different Handling Phases (aka 2 different prey items requiring different amounts of effort or time to obtain). Alternatively, three responses on the white Search key reinstated the next search phase; in this way, the bird could reject the Red FI 5-sec or Green FI 20-sec alternative. Completion of the handling requirement produced 2.5 sec of food. After food delivery, the next search phase began.

Lea manipulated search duration to test foraging selectivity as a function of prey density. Lea

**B.F. Skinner,**  
**Fig. 3** Flowchart of the foraging procedure developed by Lea (1979). Rectangles represent the different foraging phases. Circles represent the response keys in the operant chamber. Pigeons responded on either of 2 keys throughout the experiment. Key color changes represent shifts between the various phases. Response contingencies for each phase are noted. (Lea 1979)



found that acceptance of the FI 20-sec option increased with longer searches. With short searches, birds rejected the less-preferred option (FI 20-sec) often; with longer search times, the birds exhibited greater indifference between the two choice options.

However, he also found that preference did not track predictions based on simple optimality theory (E/T); it did not produce a sudden step-function change in preference from one schedule to the other. Instead the birds perseverated on the preferred (FI-5) alternative beyond the point where optimality theory (see “► [Optimal Foraging Theory](#)”) dictated a change to the less preferred schedule.

Lea's (1979) results prompted questions about this persistent impulsivity and the gradual nature of preference change. Moreover, similarities between Lea's procedure and the more common concurrent-chains procedure in psychology operant labs were noted. Abarca and Fantino (1982) observed that Lea's handling phases were analogous to the terminal links of concurrent chains. Impulsive biases had been previously noted using FI schedules in the concurrent chain procedure. Abarca and Fantino replicated Lea's study, replacing the FI schedules with variable interval (VI) schedules (considerably more appropriate for simulating actual handling). The probability of either alternative was set to 50%. Search time was varied from a FI 4-sec schedule to a FI 63-sec schedule. They too found that preference for the less-preferred option increased with increases in search time. Again, the preference shift was gradual and delayed, not abrupt as predicted by optimality theory.

In a second experiment, Abarca and Fantino (1982) also changed the FI in the search phase to a VI (also a more realistic simulation of searching). Again, they found the same relationship between search time and acceptance of the less-preferred alternative. The similarity between Lea's procedure and the more common, and well-studied concurrent chains procedure opened the door for psychological explanations of the persistent impulsivity observed in both sets of experiments. In particular, Herrnstein's matching law (1961), Baum's (1974) generalized matching law and

Fantino's delay reduction hypothesis provided insights into the observed asymmetry of choice in foraging situations.

Of particular interest, the delay-reduction hypothesis (now theory) introduced a new commodity, other than just energy as a function of time, that is influential in foraging-related choice: namely, conditioned reinforcement – the ability of cues that signal primary reinforcement to influence choice. More of a psychological commodity, animals' sensitivity to reductions in expected delays to reinforcement highlights the importance of schedules of reinforcement in the discovery of a deeper and more complex understanding of foraging-related choice. In particular, Fantino's delay reduction theory serves as an example of the ongoing impact of Skinner's early work with schedules of reinforcement on the modern study of animal behavior. (For additional contributions of operant conditioning to the study of foraging-related choice, see Abarca et al. 1985; Baum 1983; Fantino 1987; Fantino and Abarca 2010; Shettleworth 1988; Williams and Fantino 1994.)

**Superstition in the Pigeon.** In his famous study, Skinner (1947) explained how accidental reinforcement could lead to the development of idiosyncratic behaviors. He argued that response-reinforcer contingencies are nothing more than coincidental, albeit reliable, instances of immediate positive reinforcement. In an effort to demonstrate the power of temporal contiguity, he presented food to eight hungry pigeons every 15 sec. In six of the eight cases, the birds developed highly stereotyped behaviors. From head bobbing to turning in circles, each of the six birds developed its own “superstitious” response pattern. To further demonstrate the strength of these responses, he placed them on extinction (see ► [“Extinction in Learning”](#)). It took over 10,000 responses for the behaviors to cease. Skinner drew comparisons between the birds' behavior and the development of superstitious behavior in humans (e.g., the behavior of bowlers as the ball approaches the end of the alley). He argued that their appearance was merely the results of “accidental correlations” between behavior and presentations of the reinforcer.

In an attempt to further explore Skinner's findings, Staddon and Simmelhag (1971) replicated Skinner's study but examined the resulting behavior in greater detail. They found that although idiosyncratic behaviors emerged early in the interval, the behaviors at the end of the interval were dominated by only a few species-typical response patterns associated with foraging and feeding (e.g., looking at the food cup; pecking near the food cup). They called the early behaviors *interim responses* and suggested that they reflected other sources of reinforcement. The late behaviors (which were much more uniform across birds) were labeled *terminal behaviors*.

In 1985, Timberlake and Lucas returned to the famous superstition studies to investigate the nature of the interim behaviors more thoroughly. They conducted nine separate experiments. Their findings suggested that early, idiosyncratic behaviors simply reflect earlier phases in the foraging sequence such as searching (e.g., head bobbing and circling). They proposed that a behavior systems approach would explain the increases in certain types of behaviors. By presenting food, the feeding system is triggered, increasing a collection of organized feeding-related behaviors. These food-related behaviors become more likely in general and may stretch from the beginning to the end of a short interval in a manner that simulates more naturalistic foraging tendencies (see "► Behavior Systems").

The long history associated with Skinner's superstition study highlights the relevance, the impact, and the importance of Skinner's early work. The breadth of his experimentation and theoretical work has provided a basis for continued investigation for decades.

## Radical Behaviorism

Skinner considered himself a behaviorist, influenced by such traditional behaviorist figures as E. L. Thorndike, Ivan Pavlov, and John B. Watson. However, his approach differed from those of his predecessors. He called himself a "radical behaviorist" because of his departure from the popular Pavlovian/Watsonian S-R

theories of the time. Sometimes interpreted as a type of logical positivism, Skinner clarified his radical behaviorism by saying:

... some versions of logical positivism ruled private events out of bounds because there could be no public agreement about their validity. Introspection could not be accepted as a scientific practice, and the psychology of people like Wilhelm Wundt and Edward B. Titchener was attacked accordingly. Radical behaviorism, however, takes a different line. . . . Radical behaviorism restores some kind of balance. It does not insist upon truth by agreement and can therefore consider events taking place in the private world within the skin. It does not call these events unobservable, and it does not dismiss them as subjective. It simply questions the nature of the object observed and the reliability of the observations. (Skinner 1974)

It was Skinner's belief that the study of behavior is a natural science that firmly places environmental influence as the major determinant of complex behavior in both human and nonhuman animals. His radical behaviorism promoted the idea that the powerful influence of the environment on behavior should be the emphasis of modern psychology. According to Skinner, radical behaviorism would always be responsible for explaining all behavior, public and private, and that strong empirical evidence of environmental influence would be required to offset mentalistic accounts of behavior (Skinner 1974).

Skinner acknowledged the role of physiology and confidently expected the field of physiology to provide a complete accounting of the internal processes associated with all behavior. In 2004, Morris, Lazo, & Smith published a comprehensive review article in which they evaluated Skinner's own writings for evidence of his discussion of biological participation (aka genetics, physiology, and evolution) in operant learning. Their paper was intended to address criticisms that Skinner denied or dismissed the role of biological processes in learning and behavior. They found that Skinner addressed biological participation in 97 of his 289 primary source publications, stretching across his 61-year publishing career. In his 1988 book chapter, *Genes and Behavior*, Skinner concludes that a complete understanding of behavior would require a synthesis of genetic, behavioral, and cultural influence (see "► Behaviorism").

## From Darwin to Selection by Consequences

Perhaps the most detailed treatise of the developmental relationship stretching from the publication of Charles Darwin's *Origin of Species* to the behaviorism that launched Skinner's early work is offered by Boakes' (1984) *From Darwin to Behaviorism: Psychology and the Minds of Animals*. Boakes, a product of the Harvard pigeon lab himself, outlines the transitions of evolutionary nobility, from Darwin to Romanes to Lloyd Morgan. Throughout those early years, a growing reliance on comparative psychology, direct observation, and empirical evidence gradually led to people like James, Wundt, Helmholtz, and Thorndike. Their emphasis on laboratory research, combined with American university administrative and economic influences produced a nationwide academic growth spurt that favored animal psychology (Baum 1985; Boakes 1984). It was in this climate that J. B. Watson was empowered to write his famous manifesto (1913), arguing against introspection as a scientifically valid method, and insisting that the goals for psychology be redefined as the prediction and control of behavior. It was in this context that Skinner's radical behaviorism emerged.

In 1981, Skinner published a telling article in the journal *Science*, where he outlined his theory of selection by consequences and clearly established the origins of his overarching principles of operant conditioning as coming from the earlier concept of natural selection. In it, he argued that the ability of behavioral consequences to differentially select one behavior over another had begun in the primordial soup with the evolution of powerful laws that govern the relationships between organism and environment. Citing traditional natural selection as the first selection mechanism, Skinner suggested a second kind of selection: one that operates at the level of the individual and that evolved in parallel with natural selection (see "► [Natural Selection](#)").

Skinner (1981) outlined the selective properties of operant conditioning and their importance to the individual (as opposed to the species as a whole). Adaptation, he argued, involves both

species level and individual-level selection mechanisms. He explained that adaptation at the behavioral level often occurs before the mechanism of natural selection has the chance to exert species-level selection. According to Skinner, the individual that adapts behaviorally has less need for an innate repertoire. In that way, "operant conditioning could not only supplement the natural selection of behavior, it could replace it." He went on to explain how selection by consequences could build on an organism's susceptibilities to the reinforcing properties of food and sexual behavior, and how selection by consequences opens the door to new forms of behavior. Despite his controversial claims, it is clear from Skinner's own thesis that his connection to the foundations of animal behavior is forged. The synthesis of Darwin's evolutionary theory and B. F. Skinner's selection by consequences ensures the operant conditioning and Dr. Skinner himself will continue to have an important and relevant place in the history of the study of animal behavior.

## Cross-References

- [Behavior Systems](#)
- [Behaviorism](#)
- [Instrumental Learning](#)
- [Ivan Pavlov](#)
- [John B. Watson](#)
- [Natural Selection](#)
- [Operant Chamber](#)
- [Operant Conditioning](#)
- [Optimal Foraging Theory](#)
- [Schedules of Reinforcement](#)

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## Babbling

### ► Cognition

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## Bachelor Herds

### ► Artiodactyla Navigation

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## Back-Test

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## Synonyms

n-back task

## Procedure

The back-test, or n-back task, is commonly used to assess working memory. Subjects performing this task are presented with a continuous series of stimuli (e.g., sounds or spoken words, visual images, spatial locations, odors, etc.) and required to respond in a certain way when the currently presented stimulus is identical to the one presented  $n$  items previously in the series. For example, in a 2-back task, the response is required for any item that is the same as the one presented two items earlier. Tasks usually range from 1-back to 3-back versions with 4-back and 5-back tasks being rarer; a 0-back control version in which subjects have to respond every time a specific target appears (regardless of whether or when it had appeared earlier in the series) may also be administered, often to assess baseline performance in neuroimaging studies.

## Application

As such, the n-back task, developed by Kirchner (1958), primarily tests a subject's ability to protect working memory contents from interference from competing or external stimuli (Barch and Smith 2008) – though critical analyses have pointed out that performance on the n-back task may depend on “familiarity- and recognition-based discrimination processes” rather than active memory recall (Jaeggi et al. 2010). It has applications mainly in clinical and cognitive neuroscience research with humans but has also been claimed, alongside other paradigms such as complex span-tests, to be a useful training tool to improve working memory performance and general intelligence (Jaeggi et al. 2008; Au et al. 2015).

## Animal Versions

Despite its popularity as an assessment tool for human working memory capacity, the n-back task has not yet been picked up by researchers interested in studying animal working memory. Only recently has the search begun to develop a version of the n-back task that can be used with animals,



primarily to facilitate the development of animal models of working memory and subsequently their use in the assessment and treatment of memory impairments (Dudchenko et al. 2013). The most notable efforts have been made by Ko and Evenden (2009), who developed an operant version for rodents, although they reported some difficulties regarding training rodents to learn the task demands in the 2-back version.

Outside of the operant box, paradigms that might be considered conceptually related to conventional n-back tasks are those that focused on animals' memory of sequentially presented stimuli (such as locations, objects, odors, etc.). In most of these paradigms (though there are continuous variations as well, see Kesner et al. 2001), subjects are initially presented with a sequence of stimuli, followed by a forced-choice test between a pair of probe stimuli – allowing the experimenters to test the subject's recollection of whether a stimulus had appeared earlier or later in the sequence (e.g., Chiba et al. 1997; DeVito and Eichenbaum 2011). Though these tasks do not require the subject to actively indicate whether a stimulus had previously appeared at a specific position in the sequence relative to the currently presented stimulus, as the n-back task does, they do allow an assessment of whether the perceived stimuli are encoded in a sequential order. There is additional evidence that this discrimination ability is not simply a result of recent exposure: DeVito and Eichenbaum (2011) demonstrated that their rodents were capable of forming distinct representations of the internal order of separate sequences, as they did not discriminate between pairs of stimuli from different sequences.

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## Bacteria

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## Cross-References

► [Working Memory](#)

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## Synonyms

[Basal cognition](#); [Unicellular cognition](#)

## Definition

Cognition in this context is defined as the complex of sensory and other information-processing mechanisms an organism has for becoming

familiar, valuing, and interacting with features of its environment in order to meet existential needs, the most basic of which are survival/persistence, growth/thriving, and reproduction.

## Introduction

The idea that single-celled organisms, such as bacteria, display cognition is highly controversial, although the notion has had scientific advocates since the early twentieth century. As the tools to observe, study, and challenge the behavior of microbes have improved dramatically over the past few decades, the number of scientists ascribing cognition to phylogenetically basal organisms is slowly growing. Those who endorse the idea tend to be influenced by the surprising genomic and molecular similarities among diverse kinds of organisms. They also tend to be concerned with tracing the origin and evolution of the biological function of cognition and the molecular mechanisms that underpin cognition in animals, both with and without nervous systems, as well as in plants. On this account, the inference that biological cognition is more rather than less coextensive with cellular life is easily drawn.

## Two Approaches to Cognition

There are, broadly speaking, two approaches to the study of animal cognition (Lyon 2006). The first and most common approach is to characterize some feature of human cognition and then look for and analyze apparent correlates in other animals. Examples include the **mirror self-recognition** test, which is designed to detect self-awareness in nonhuman animals; most animal experiments for studying **theory of mind**, an animal's ability to infer what another animal might be thinking; and most animal experiments for studying **imitation**. These and other tests are based on the human experience of cognition. The second approach to animal cognition begins with the facts of biology – what it takes for an organism to make a living – and extrapolates from these the kind of function cognition might be. This

approach treats cognition as a biological function like other biological functions (e.g., respiration, digestion), albeit one of special interest, particularly in its more complex forms.

The former, which takes the human case as its starting point and has long dominated comparative psychology (see, e.g., Shettleworth 1993), has been called the *anthropogenic approach* to cognition because it arises from (has its *genesis* in) human beings (*anthropos*) (Lyon 2006). The latter, which takes biology as its starting point, is the *biogenic approach* to cognition; it arises from (has its *genesis* in) the living state (*bios*) rather than in a particular animal species. Both approaches are necessary for a complete understanding of human cognition, and, in particular, for identifying animal models of different human cognitive capacities that cannot be explored in human subjects for ethical reasons.

From an anthropogenic standpoint, however, bacterial cognition makes very little sense. As a result, bacterial *chemotaxis*, the directed movement of a cell toward or away from a chemical gradient, has long served as an example of readily anthropomorphized, non-cognitive behavior (e.g., Dennett 1987). Some microbiologists have even dismissed the idea of cognitive-seeming bacterial behavior as an anthropomorphic fantasy (Redfield 2002). By contrast, from a biogenic standpoint, which is grounded in the reality of evolution and the requirements of surviving, growing, and reproducing in an unpredictable world, the possibility of bacterial cognition is less easily dismissed. Thus, increasing numbers of neuroscientists have pointed to microbes for an evolutionary origin story for the aspects of cognition that they study (e.g., Allman 1999; Damasio 1999; Greenspan 2007; Sterling and Laughlin 2015).

This entry is written from a biogenic point of view. It does not assume that continuity necessarily exists between the behavior-generating capacities of unicellular organisms and highly complex cognitive traits such as self-awareness, metacognition, theory of mind, and the capacity to imitate. However, it does assume a degree of continuity with those basic behavior-generating capacities normally considered cognitive in multicellular animals, including humans.

## Bacterial Cognition and Scientific Opinion

Darwin's intuition that all forms of life share certain (unspecified) basic features, which organisms differ in "degree but not kind" along both physical and mental dimensions of their existence (Darwin 1874/1909), remains controversial but has deep scientific roots, not merely philosophical/religious ones. Aristotle, the founder of European life science (Lennox 2001), sets out the earliest systematic account – beginning with plants – of what the Greeks called *psuche* (psyche), an untranslatable term that combines features of vitality and mind (Nussbaum and Putnam 1992). Antonie van Leeuwenhoek, the seventeenth-century Dutch lens maker who was the first to study the microbial world, famously gave the name *animalcules* (tiny animals) to the single-celled organisms whose behavior he observed through his microscopes. In the modern era, Herbert Spencer appears to be the first psychologist to suggest that mind and life have a similar tendency, "the continuous adjustment of internal relations to external relations" (Spencer 1855; p. 374) and that this similarity has important implications for the study of mind.

Debates about the Darwinian proposition began in earnest in the early twentieth century. One pole of the empirical debate was exemplified by physiologist Jacques Loeb, who argued that animal behavior is for the most part mechanical, reflex-like, innate, purely physiological, and therefore non-cognitive (Loeb 1900). At the opposite pole of the empirical debate was zoologist H.S. Jennings, considered the founder of mathematical genetics, whose microscopic observations of bacterial and protist behavior convinced him of the basic soundness of Darwin's intuition about continuity (Jennings 1905/1962). The most influential US textbook on comparative psychology of the early twentieth century, *The Animal Mind* by Margaret Floy Washburn (Washburn 1936), includes an entire chapter on amoeba. Washburn, the first woman to be awarded a PhD in psychology, cites Jennings' work extensively but leaves open the question of whether amoebae have "mind." This largely was due to

the intimate linkage of mind with consciousness, a nexus that James B. Watson's **behaviorism**, which was heavily influenced by Loeb, was explicitly designed to sever (Watson 1913).

Although there were always discontents (e.g., Von Uexküll 1926), behaviorism of one form or another became the dominant theoretical approach in comparative psychology and animal ethology during the twentieth century (Greenspan and Baars 2005). It arguably still is, if much less so. In essence, behaviorism assumes the reflex concept covers most behavioral contingencies in animals. "Bacterial behavior" (to say nothing of plant behavior) was regarded by many as verging on an oxymoron. All that changed with the investigation of bacterial chemotaxis by three US research teams, headed by Julius Adler at the University of Wisconsin/Madison, Howard Berg at Harvard University, and Daniel Koshland Jr at the University of California, Berkeley.

Adler's laboratory made the study of bacterial chemotaxis possible, starting in the early 1960s, by developing (1) an objective assay to establish that bacteria are actually capable of movement (not simply drifting); (2) growth media that enabled bacterial movement and/or promoted the synthesis of *flagella*, whip-like molecular motors that propel the cell; and, finally, (3) an assay for bacterial chemotaxis (Adler 2011). Genetic studies led to chemotactic knockout mutants, which greatly advanced the research. By 1965, unpublished news of the lab's discoveries led to Adler being invited to speak about bacterial chemotaxis at a Cold Spring Harbor symposium on "Sensory Receptors" in animals, an invitation most would have considered at best highly improbable and most likely inconceivable. The following year "Chemotaxis in Bacteria" (Adler 1966), the seminal article in the field, was published in *Science*.

Adler's lab demonstrated that the common gut bacterium *Escherichia coli* is both positively and negatively chemotactic; it is attracted, or will move toward, some chemical stimuli, and is repelled by, or will move away from, others. This movement is enabled by changes in the methylation state of binding sites on proteins called *chemoreceptors* that sense different

chemicals, and combinations of chemicals, in the environment. Adler's lab also discovered that bacteria "make decisions" when faced with conflicting information, meaning their behavior choices are based (like many animals') on non-linear calculations, not straightforward linear summations of the available information on positive and negative states of affairs (Adler and Tso 1974).

First at Colorado, then at Harvard, Berg and colleagues invented and progressively refined a microscope to track bacterial behavior in three dimensions (Berg and Brown 1972), which enabled progress on understanding the molecular mechanics of bacterial chemotaxis. At Berkeley, Koshland's lab discovered that bacteria possess a form of memory (Macnab and Koshland 1972); correctly hypothesized the general process by which signals are transduced within the cell, from environment to flagellum (Koshland 1977), the molecular logic of which was later found to be quite general, including in animals, and demonstrated how these responses in bacteria can be fine-tuned by mechanisms also known to operate in animals, such as habituation (adaptation) and sensitization (amplification) (Koshland et al. 1982).

Meanwhile, without regard to the findings described above, Chilean neurobiologist Humberto Maturana, co-author of one of the seminal papers in early neuroscience (Lettvin et al. 1959), was working through the implications of a novel, highly abstract but internally coherent framework for conceiving the biological function of cognition (Maturana 1970; Lyon 2004), which he concluded must apply to bacteria as well as to animals with nervous systems. *The Biology of Cognition* would not be widely available for another decade. Contemporaneously, Koshland published a monograph advancing an argument that bacterial chemotaxis could provide a productive model for animal behavior generally, including neurally driven human behavior (Koshland 1980).

However, Maturana's and Koshland's theoretical work appears not to have much effect on microbiology specifically or biology generally, to say nothing of neurobiology. When scientists

rediscovered the possibility of something like cognition in bacteria, "minimal" or otherwise, they more or less reinvented the wheel based on more recent findings and different theoretical concerns. These include bacteriologists Klaas Hellingwerf (Hellingwerf et al. 1995), Joseph Lengeler (Lengeler et al. 2000), and James Shapiro (2007); computational biologist Dennis Bray (2009); and biochemist Jeffry Stock (Stock et al. 2002; Baker and Stock 2007).

## Bacteria and the Cognitive Toolkit

The idea that a "toolkit" of behavior-generating processes and capacities exists that comprises what we ordinarily call the biological function of cognition was proposed more than two decades ago by philosopher Peter Godfrey-Smith (1996). While he did not precisely specify the contents of the toolkit, the human psychological literature provides many suggestions (e.g., Rathus 2016): sensing and acting; memory and learning; anticipation and prediction; assessing value (often grouped under emotion and motivation); integrating multiple sources of information and making decisions about risk and reward under various degrees of uncertainty; and communication. Table 1 sets out one possible version of a cognitive toolkit of basic cognitive capacities defined from a biogenic standpoint (Lyon 2015). Needless to say, the toolkit was derived from the human case in the first instance and forms the basis of much comparative psychological investigation, past and present, between and among different types of animals.

*E. coli* exhibits all of these capacities. As stated above, it has been known for decades that the bacterium possesses memory, displays valenced behavior, and makes decisions in the face of conflicting information based on poorly understood nonlinear dynamics, which still cannot be predicted. Moreover, it is now known that *E. coli* possesses complex arrays of chemoreceptors, numbering in the thousands, which are individually responsive to combinations (even within one protein) of multiple different sources of chemical information (Porter et al. 2011). These protein

**Bacteria, Table 1** A basic toolkit of cognitive capacities. (Adapted from Lyon 2015)

| Basic cognitive toolkit (functions/capacities) |                                                                                                                                                                                                                                   |
|------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Sensing/perception                             | The capacity to sense and recognize (re-cognize) existentially salient features of the internal and surrounding milieu                                                                                                            |
| Memory                                         | The capacity to retain information about the immediate (and possibly distant) past and to calibrate the sensorium to take account of this information (e.g., via signal amplification)                                            |
| Valence                                        | The capacity of an organism to assign a value (positive, negative, neutral) to the summary of information about its surroundings at a given moment, relative to its own current state                                             |
| Decision-making (signal integration)           | The capacity to combine information from multiple sources, because all known organisms to date appear to be capable of sensing more than one thing                                                                                |
| Behavior                                       | The capacity of an organism to adapt via changing its spatial, structural, or functional relation to its external or internal milieu                                                                                              |
| Error detection                                | The capacity of an organism to determine whether a behavior has succeeded or failed                                                                                                                                               |
| Learning                                       | The capacity to adapt behavior to existentially salient stimuli according to past experience by altering the threshold for response                                                                                               |
| Anticipation                                   | The capacity to predict what is likely to happen next based on an early stimulus                                                                                                                                                  |
| Communication                                  | The capacity to interact productively with other organisms, notably (but not limited to) conspecifics, including initiating collective action, which may or may not include an explicit means of differentiating “us” from “them” |

arrays, dubbed “nanobrain” by some, are capable of highly complex computations (Stock et al. 2002) and appear to function as “neural networks” or “integrated circuits” in bacteria with flagella (Hellinger et al. 1995; Baker and Stock 2007; Bray 2009).

*E. coli* also has been shown to exhibit anticipatory behavior; it can predict what is likely to happen next when presented with particular information, such as a certain increase in ambient temperature (Tagkopoulos et al. 2008). This anticipatory behavior can be changed by conditioning or associative learning (Mitchell et al. 2009). It is currently assumed that this form of associative learning takes place at a population-level over generations via epigenetic mechanisms, but it is already well-demonstrated that *E. coli* possesses nonassociative types of learning shared with vertebrates, such as habituation and sensitization. For a discussion of bacterial communication, see the section on Sociality below.

Finally, despite the above, it is worth noting that *E. coli* is not particularly well-endowed in terms of the kinds of signal transduction systems associated with more complex behaviors in the bacterial world (Lyon 2017). These systems include two-component systems, chemotactic systems, and extra-cytoplasmic alternative sigma factors, the latter of which are environmentally

sensitive transcription factors believed to expand a bacterium’s response repertoire under challenging, and possibly novel, conditions (Pinto and Mascher 2016). In short, *E. coli* is not the smartest bacterium on the block, but it does not have to be; it is not developmentally complex.

**Sociality, Communication, and Development: Ratchets for Complexity**

The idea that most bacteria live not as solitary individuals but in large groups or multicellular consortia called *biofilms* is now widely accepted, although its discovery is relatively recent (Shapiro and Dworkin 1997). *Sociomicrobiology*, proposed 12 years ago as the study of microbial social behavior, including the degree to which it is determined by nature (genetics) or nurture (development, behavior), is now a mainstream concept (Whiteley et al. 2017). As is the case with social animals, the more dependent on coordinated behavior the bacterial species is, the more complex its behavior tends to be, and the richer its endowment of potentially cognitive mechanisms (Lyon 2017). The most complex behaviors of which bacteria are capable – such as coordinated predation, bioluminescence, social motility, nutrient scavenging and distribution, developmental



sequences leading to sporulation, and synthesis of virulence factors – are performed by multicellular aggregates of individual cells responding to chemical or physical signals that serve as forms of communication.

The most commonly known form of bacterial communication goes by two interchangeable labels: autoinduction and quorum sensing (Miller and Bassler 2001). *Autoinduction*, the original term of art, was introduced because the phenomenon involves a cell's own synthesis, export, and subsequent detection of particular molecules, which bring about a significant, energetically costly change in the cell's genetic expression (in some cases, the expression of hundreds of genes) and, thereby, its physiology. In short, the cell produces molecules (autoinducers) that induce a change in itself (autoinduction) that affects its subsequent survival, growth, or reproduction. *Quorum sensing* was introduced when it became apparent that autoinduction is a means by which a cell determines that it is in a sufficiently large population at which a change in physiology is energetically advantageous. A single cell acting alone – to synthesize a virulence factor, say, or bioluminescence – is not only ineffective but also highly vulnerable. If an insufficient number of conspecifics are in the vicinity, the quorum sensing molecules diffuse away from the cell, and nothing happens. If there are large numbers of cells nearby, the autoinducers aggregate and are detected by the cell. A change in the structure or function of the cell is induced when a threshold is reached.

The autocrine and paracrine activity of quorum sensing molecules has been compared favorably to the activity of hormones in multicellular animals and plants (Sperandio et al. 2003), and some have speculated that autoinducing peptides may be the prototypes, if not the precursors, of neuropeptides. At the time of writing, eight different types of bacterial quorum sensing signal had been identified (Whiteley et al. 2017). In general, Gram-negative bacteria primarily synthesize acyl homoserine lactones (AHLs) for quorum sensing, while Gram-positive bacteria often use oligopeptides. However, some bacterial species are capable of synthesizing both types, and

several species have been identified that operate two or more different quorum sensing systems (Bassler and Losick 2006).

*Myxococcus xanthus*, a rod-shaped soil-dwelling predator with a highly complex life cycle, uses three chemically distinct intercellular signals in the developmental sequence leading to the formation of spore-filled fruiting bodies under conditions of nutrient decline (Lloyd and Whitworth 2017). Fruiting body formation is a dramatic behavior involving massive aggregations that have been likened to the mass animal migrations of the central African plains (Shimkets 1999). Cooperative “wolf packs” of *M. xanthus* hunt other bacteria, archaea, and fungi. Because they are much slower-moving than their prey, *M. xanthus* secrete molecular products to attract, for example, *E. coli* (Shi and Zusman 1993). Recently *M. xanthus* also has been shown to respond to AHL-based quorum sensing molecules produced by other bacteria as indicators of potential prey. AHLs, which *M. xanthus* cannot synthesize, nevertheless appear to enhance myxobacterial motility, stimulate predation, retard sporulation, and promote germination of myxospores (Lloyd and Whitworth 2017). Please note: the autoinducers are not in themselves nutritive for *M. xanthus*; the bacteria that produce them are.

Some bacteria also use physical signals – notably electricity generated by membrane-embedded ion channels – to communicate quickly over long distances in environments where diffusion is ineffective (Prindle et al. 2015). As is well-known, ion channels are critical to the transmission of information by neurons. Bacterial ion channels long served as models for understanding how neuronal ion channels operate, even as their function in microbes remained obscure. A recent series of experiments demonstrated that *Bacillus subtilis* uses electricity generated by ion channels to send signals across a biofilm, from the center to the periphery (Prindle et al. 2015). As the colony grows, the distance between the founder population and the periphery increases, making it difficult for nutrients to diffuse across the numerous layers of cells to the center. Meanwhile, the population at the “eating edge” of the periphery is able



to feed so long as nutrients are available. When the cells at the center begin to starve, they generate electrical impulses that propagate to the peripheral cells, which stop feeding, allowing nutrients to diffuse to the core. A “resume” signal is sent when nutritional homeostasis is restored. The important point is that *B. subtilis* (at least) uses ion channels to generate electrical signals for the same reason neurons do: to transmit information rapidly over significant distances comprised of intervening cells.

It is now widely accepted that signaling-mediated aggregative behavior of individual cells in the domain of prokaryotes (bacteria and archaea) as well as in eukaryotes (amoeba, protists, fungi) was a critical step in the evolution of multicellular animal life (Kaiser 2001). There is now a growing body of evidence to suggest that bacterial signal transduction and motility, the autocrine and paracrine activities of quorum sensing molecules within cell populations, and the neuron-like electrical signaling of bacterial ion channels may have played a more direct role in the evolution of animal cognition.

## Conclusion

The idea of bacterial cognition significantly expands the possibilities for understanding the biological function and evolution of cognition more generally, by introducing to cognitive science the methods that have brought the greatest progress in other areas of biology, particularly at the level of molecules, genetics, genomes, and development. The study of bacterial behavior makes it conceivable to connect the dots – the real continuities as well as the obvious discontinuities – across not only the prokaryote-eukaryote divide but also across the transitions from unicellular to multicellular life and from nonneural behavior to the origin and evolution of nervous systems.

Some may object: Why call it “cognition”? The only reasonable response, given the almost unimaginable scientific advances of the past two decades, is: Why not? There is *no scientific consensus about what cognition is* and where it is to be

found on the tree of life. None. Arguably, this is the result of keeping one eye firmly on *Homo sapiens* whenever cognition is studied. In turn the anthropogenic tendency, which implicitly dictates an overriding emphasis on human brain structure, has only served artificially to distance cognitive science from the rest of biology, and thus stymied attempts at the kind of generalization that has facilitated rapid advances elsewhere in the life sciences. From a biogenic standpoint, the costs of this practice now clearly outweigh the benefits.

Obviously, bacteria are not at all like humans. Bacterial cells are orders of magnitude smaller than the smallest human cell, the red blood cell. Size should be irrelevant for understanding cognition as a biological function, however. What counts, at least from the standpoint of the biogenic approach to cognition, is whether the behavior-generating capacities exhibited by bacteria system fit comfortably within a toolbox of capacities typically considered cognitive in more complex organisms and whether the mechanisms that generate these capacities in bacteria can shed light on cognitive capacities in other organisms.

## Cross-References

- [Behaviorism](#)
- [Conjugation](#)
- [Cognitive Impenetrability](#)
- [Imitation](#)
- [Mirror Self-Recognition](#)
- [Theory of Mind](#)

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## Badgers

► [Mustelid Communication](#)

## Balance

► [Cetacean Sensory Systems](#)

## Balanced Polymorphism

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## Synonyms

[Balancing selection](#)

## Definition

Balanced polymorphism or balancing selection is a phenomenon by which more than one morph

exists in the population at a stable frequency at a given time.

## Introduction

Polymorphism refers to the occurrence of two or more forms of phenotypes in a population. Balanced polymorphism occurs in a population when alleles exist in a population in stable frequencies due to selection. The term balanced polymorphism was coined by an ecological geneticist F.B. Ford (1901–1988). The superiority of heterozygotes over the homozygotes allows the maintenance of balanced polymorphism in population. This **heterozygote superiority** is also referred as **overdominance** or **single locus heterosis**. Under balanced polymorphism, there is neither the fixation of alleles nor the elimination of alleles. If the heterozygote of any mutation is fitter than the mutant homozygote and confers an adaptive advantage, then the mutation is maintained at an intermediate, balanced frequency rather than being fixed (Sellis et al. 2011). According to Dobzhansky and Pavlovsky (1960), if the heterozygotes for a pair of alleles,  $A_1A_2$ , are possessing adaptive value greater than the corresponding poorly adapted homozygotes,  $A_1A_1$  and  $A_2A_2$  then in sexually reproducing and cross-fertilizing populations, natural selection will establish an equilibrium state at which the two alleles,  $A_1$  and  $A_2$ , will continue to occur in the population with certain frequencies. Other possible sources other than heterozygote advantage through which the balancing selection is maintained in the population are negative frequency-dependent selection as well as temporal or spatial heterogeneous selection (Hedrick 2012).

## Examples of Balanced Polymorphism

Most of the alleles for which balanced polymorphism is maintained in the human population are associated with certain disease or pathogen resistance. One of the classic examples of balanced polymorphism in the human population is sickle cell gene polymorphism. **Sickle cell disease** is caused by the single nucleotide mutation of the  $\beta$  globin gene, thus causing production of abnormal

hemoglobin resulting into sickle shape like red blood cells. The sickle-shaped red blood cells are fragile and clog the blood vessels thus causing damage to organs, severe anemia, as well as heart failure. Heterozygous carriers ( $\text{Hb}^A/\text{Hb}^S$ ) of sickle cell trait in a population possess mixture of both normal erythrocytes having normal hemoglobin and sickle-shaped cells, while homozygous carriers ( $\text{Hb}^S/\text{Hb}^S$ ) of sickle cell gene in the population have greater proportion of sickle cells in blood. Despite the deleterious character of homozygotes, the sickle mutation exists in human population since the heterozygotes possess selective advantage of being malaria resistant. This was firstly confirmed by the work of A.C Allison (Allison 1954), linking heterozygotes to protection from malaria in Ugandans. Hence, in area where malaria is prevalent, sickle cell heterozygotes will survive more and tend to increase the frequency of sickle cell gene over normal homozygotes ( $\text{Hb}^A/\text{Hb}^A$ ) as they are more susceptible to malaria. Therefore, sickle cell trait shows a case of balanced polymorphism where advantageous heterozygotes coexist with disadvantageous homozygotes in a population. In addition to this, there are also several other hematological diseases which are maintained in population as a result of balanced polymorphism such as **glucose-6-phosphate dehydrogenase deficiency,  $\beta$ -thalassemia, and ovalocytosis** in which the homozygote hemoglobinopathy is balanced by the heterozygote advantage of protection from malaria.

Another potential example of balanced polymorphism involves **Tay–Sachs disease** conferring advantage to heterozygotes from tuberculosis. Tay–Sachs disease is an autosomal recessive genetic disorder mostly occurring in children's due to mutation in HEXA gene, situated on chromosome 15. HEXA gene codes for enzyme hexosaminidase A, absence of which causes the progressive accumulation of GM2 gangliosides in the nerve cells of brain thus causing damage to the cells. The accumulation of gangliosides causes deterioration of mental and physical abilities ultimately leading to death by the age of four to five. Being an autosomal recessive disorder, the individual must acquire two Tay–Sachs alleles to

exhibit the disease, i.e., they must be homozygous for it. Tay–Sachs allele is known to be most prevalent in Eastern European people of Jewish descent (Ashkenazi Jews). Although being deleterious in nature, the allele is maintained in the population by its virtue of providing protection to heterozygotes from *Mycobacteria tuberculosis*, the causative agent of infectious disease tuberculosis, thus showing balanced polymorphism. Similarly **cystic fibrosis**, an autosomal recessive disorder most commonly found in Caucasian population, shows balanced polymorphism through heterozygote advantage to the fatal diarrheal disease cholera. It is caused by a mutation in the gene cystic fibrosis transmembrane conductance regulator (*CFTR*) which results in defective chloride channel. Presence of mutation in both copies of the *CFTR* gene in a person causes cystic fibrosis. Cystic fibrosis causes accumulation of mucus in the lungs and gastrointestinal organs thus causing infection and other related defects. Cholera is caused by toxin secreted by the bacterium *Vibrio cholerae* in the small intestine. The toxin acts through intracellular guanine nucleotide binding protein which consequently causes the release of cAMP which in turn induces chloride ion movement through chloride channel into the lumen of the gut. This process causes an osmotic loss of sodium ion and water into the lumen resulting into watery diarrhea (Withrock et al. 2015). In case of *CFTR* heterozygotes where chloride ion channels are less functioning as compared to the normal homozygotes, the influx of ions into the gut lumen is reduced thereby dropping the chance of diarrhea. This selective advantage of CF carriers against cholera allows the maintenance of detrimental CF gene in high frequency by balanced polymorphism. The blood group system in human population also shows balanced polymorphism. The alleles for A, B, AB, and O blood group do not show selective advantage over each other, and genotypic frequencies remain constant from generation to generation for each population.

Apart from human population, balanced polymorphism has also been known to be maintained in animals. **Warfarin resistance** in rats demonstrates one of the best illustrations of balanced

polymorphism (Smith et al. 1993). Warfarin is an anticoagulant which is commercially used as rat poison. It inhibits the production of vitamin K-dependent clotting factor and anticoagulant proteins by disruption of vitamin K synthesis pathway. Warfarin resistance in brown rats (*Rattus norvegicus*) is controlled by an autosomal dominant allele R. However, the resistant individuals also possess a low fitness due to altered vitamin K metabolism. The resistant homozygotes having two R alleles have 20-fold increased demand of vitamin K as compared to heterozygotes (with R and wild-type susceptible S allele), where demand of vitamin K is reduced to as much as two- to fourfold. The resistance allele R exists in balanced polymorphism in the population due to the higher fitness of heterozygotes (RS) over homozygotes (RR) and susceptible (SS). Homozygotes suffer loss of fitness as a result of vitamin K deficiency, whereas susceptibles are affected due to warfarin poisoning. Balanced polymorphism for several genes and inversions is also known to exist in several species of *Drosophila* such as *D. pseudoobscura*, *D. persimilis*, *D. robusta*, *D. ananassae*, etc. due to heterozygote advantage (Singh 2013).

### Evolutionary Significance of Balanced Polymorphism

Balanced polymorphism has known to be one of the important factors in maintaining polymorphism, hence genetic variability in the population. This variability allows an organism to adapt rapidly in the face of changing environmental conditions. In contrast to directional selection where only a particular allele is favored in changing environment, balancing selection maintains the favored allele in an intermediate equilibrium, thus increasing the variability in the genomic region nearby the concerned locus.

### Cross-References

- Directional Selection
- Frequency-Dependent Selection

- Heterozygote Superiority
- Natural Selection

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### Balancing Selection

- Balanced Polymorphism

### Basal Cognition

- Bacteria

Basal Metabolic Rate (BMR)

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Metabolic Rate and Various Types

The total amount of energy used by the animal at a time interval is called its metabolic rate. Basal metabolic rate (BMR) is the rate of energy expenditure by the body during complete physical, mental, and digestive rest (Anthanont et al. 2017). Resting metabolic rate (RMR) is the rate of energy expenditure to perform all vital chemical reactions of the body at rest (McClune et al. 2015).

BMR Versus RMR

BMR differs from the RMR in the fact that BMR is measured under stringent conditions. The RMR is less accurate than the BMR but is used owing to the convenience of measurement. Mitchell defined BMR as the “basal metabolism of an animal is the minimal rate of energy expenditure compatible with life” (Mitchell 1964). The word “basal” in basal metabolic rate refers to the absence of physiological and pathological conditions like exercise, stress, disease, etc.

Standard Metabolic Rate

BMR is applicable only for homeothermic animals that can maintain stable internal body temperature regardless of external influence. Standard metabolic rate (SMR) is used for poikilothermic animals like reptiles and fishes. In

the case of fishes, SMR is the energy demand of all metabolic processes except those associated with swimming, digestion, and catabolism (Benetti et al. 1995).

Conditions to Measure BMR

The BMR measurement should be done in an isolated room ensuring the removal of all psychological and physiological factors that can cause excitement. The subject must be on 12–14 h of caloric fasting and after a night of restful sleep. No strenuous activity must be allowed 1 h before the test and during the test. Thermoneutrality of the subject should be maintained by keeping the temperature of the room between 68 °F and 80 °F.

Conditions Affecting BMR

BMR is affected by both physiological and pathological factors. Lean body mass is the major determinant of BMR. Lean body mass is the weight of a person’s body that is not fat. So, muscular people have more BMR and obese people will have less BMR. Because of relatively more fat, females tend to have less BMR compared to males. Ageing is associated with fatty infiltration of muscle tissues and decreased BMR. Height and weight determine body surface area (BSA). Greater the BSA, greater the heat loss, thus BMR increases. Based on this relation, mammalian basal metabolic rate is proportional to body mass<sup>2/3</sup> (White and Seymour 2003).

BMR increases during growth, reproduction, lactation, and emotionally excited state. Hormones like thyroid hormone, androgens, growth hormone, epinephrine, cortisol also increase BMR.

| ↑ BMR              | ↓ BMR                       |
|--------------------|-----------------------------|
| Fever (pyrexia)    | Protein energy malnutrition |
| Hyperthyroidism    | Hypothyroidism              |
| Cold environment   | Addison’s disease           |
| Cushing’s syndrome | Starvation                  |
| Cachexia           | Obesity                     |
| Exercise           |                             |



## Methods to Measure BMR

Calorimetry (direct and indirect), heart-rate monitoring, and doubly labelled water are the methods used for the calculation of BMR.

Biochemical energy used in the body is released as heat so we can simply measure the heat released by the animal to measure BMR. For this purpose, calorimetry is used. Direct calorimetry involves placing the subject a thermo insulated air chamber. The air temperature within the chamber is maintained at a constant level by forcing the warm air through pipes in a cool water bath. The rate of heat gain by the water bath is measured with an accurate thermometer. This heat gain is equal to the rate at which heat is liberated by the subject's body. Direct calorimetry is practically difficult to perform. So, it is used only for research purposes.

Indirect Calorimetry is based on the concept of “energy equivalent” of oxygen. More than 95% of the energy expenditure of the body is due to reactions of oxygen with the different foods. So, the rate of oxygen utilization gives an accurate measurement of the metabolic rate. One liter of oxygen releases 5.01 calories of energy when metabolized with glucose, 5.06 calories with starch, 4.70 calories with fat, and 4.60 calories with protein. Thus, the quantities of energy liberated per liter of oxygen consumed are nearly equivalent when different types of food are metabolized. For an average diet, the quantity of energy liberated per liter of oxygen used in the body averages about 4.825 calories, which is called the “energy equivalent of oxygen.” By using this energy equivalent, the rate of heat liberation in the body is indirectly calculated.

The heart rate of an animal is directly proportional to its energy expenditure. However, due to physiological variations such as age, sex, body size, and nutritional status, the relationship between heart rate and energy expenditure must be calibrated for each subject measured.

In the doubly labelled water technique, individuals are administered two stable isotopic (nonradioactive) forms of water ( $\text{H}_2^{18}\text{O}$  and  $^2\text{H}_2\text{O}$ ). The rate at which  $^{18}\text{O}$  and  $^2\text{H}$

disappear from the body is monitored for about 7–21 days. Based on the differential rates of disappearance,  $\text{CO}_2$  production is calculated and finally, energy expenditure can be calculated.

BMR is expressed as calories per hour (or per day). The other units of energy like joules and megajoules can also be used.

## BMR in Torpor and Hibernation

Torpor is a physiological state of decreased activity and metabolism seen in many birds and small mammals. Hibernation is the prolonged torpor. In both these instances, the basal metabolic rate of the animal is significantly reduced (Ruf and Geiser 2015).

## Cross-References

► [Torpor](#)

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## Base of Skull

### ► Cranial Base

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## Base Pair

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## Synonyms

DNA; Nitrogenous base

## Definition

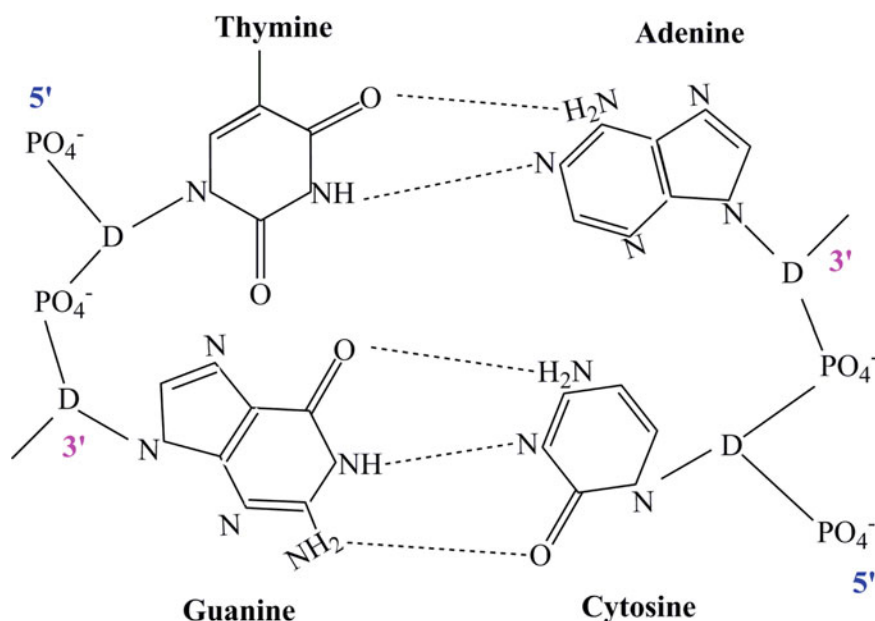
A base pair is a unit of the DNA double helix structure.

## Introduction

A very important unit of DNA is the base pair (bp) which is formed between two nucleobases. Nucleobases are nitrogenous biological compounds and form nucleoside which is component of nucleotide. Nucleotides are monomer units of the nucleic acid polymers DNA (deoxyribonucleic acid) and RNA (ribonucleic acid). Nucleotides are composed of three subunit molecules: a nitrogenous base, a five-carbon sugar (ribose or deoxyribose), and a phosphate group; while the nucleosides (such as cytidine, uridine, adenosine, guanosine, thymidine, and inosine) are nucleotides without a phosphate group (Alberts et al. 2002; Zhurkin et al. 2005). The nucleobases are bound to each other by hydrogen bonds to synthesize the building blocks of the

DNA double helix and contribute to the folded structure of both DNA and RNA.

Base pairs through specific hydrogen bonding patterns allow the DNA helix to maintain a regular helical structure that is finally dependent on its nucleotide sequence of pyrimidines and purines. Pyrimidine is an aromatic heterocyclic (six-membered heterocyclics with two nitrogen atoms in the ring) organic compound, nitrogen atoms situated at positions one and three in the ring (Joule and Mills 2012). In nucleic acids, pyrimidine derivative nucleobases are cytosine (C), thymine (T), and uracil (U). While purine (heterocyclic aromatic organic compound) consists of a pyrimidine ring and fused to an imidazole ring. They include the nucleobases adenine (A) and guanine (G). According to Watson-Crick base pairs, a model of DNA structure shows that the molecules (purine and pyrimidine) are cross-linked double-stranded helix where adenine is paired with thymine and cytosine paired with guanine, which projects inward from the deoxyribose sugars and is joined by hydrogen bonds (Zhurkin et al. 2005) (Fig. 1). The nucleotide bases at each position in the DNA double helix are complementary. Complementarity is defined as a relationship between two helices following the lock-and-key principle, and mainly it is the base principle of DNA replication and transcription which have the property to share nucleic acid (DNA/RNA) sequences, when they are aligned antiparallel to each other and termed as complementary. The complementary base pairing allows cells to copy specific information from one generation to another and repair the damage of stored information in the sequences. The structure and data of DNA double helix make DNA well suited for the storage of genetic information. Base pairing also provides the best-suited mechanism for DNA replications using DNA polymerase and transcription by RNA polymerase. These base pairing mechanisms are very specific to recognize the regulatory region of genes. While, in the case of RNA, base pairing occurs within single-stranded nucleic acids, in which guanine-cytosine and adenine-uracil (Watson-Crick base pairs) allow the formation of short double-stranded helices and non-Watson-Crick interactions



**Base Pair, Fig. 1** Chemical structure of base pairing through hydrogen bond in between adenine and thymine (double bond) and guanine base pair with cytosine (triple

bond). The phosphate backbone is situated on the outside and the base pair stands in the middle (D; five-carbon sugar, ribose or deoxyribose)

(e.g., G—U or A—A) allow RNAs to fold (Berg et al. 2002). In between transfer RNA (tRNA) and messenger RNA (mRNA), base pairing creates the foundation for the molecular recognition events that gives result in the nucleotide sequence of mRNA, which are translated into the amino acid sequence of proteins through the genetic code.

Base pairs are the unit to measure the size of an individual gene or an organism's entire genome. Hence, the number of nucleotides in one of the strands is equal to the number of total base pairs. The haploid human genome, i.e., 23 chromosomes, is observed to be about 3.2 billion bases long and to contain 20,000–25,000 different protein-coding genes.

High GC content makes DNA more stable than DNA with low GC content (Yakovchuk et al. 2006). The larger nucleobases like adenine and guanine are the member of double-ringed chemical structures called purines, while the smaller nucleobases (cytosine, thymine, and uracil) are members of single-ringed chemical structures called pyrimidines. The purines and pyrimidines are complementary to each other and effectively

make the pairing. The pairing between pyrimidine-pyrimidine shows unfavorable pairing due to the molecules that are too far to create hydrogen bonding to be established, while purine-purine is very close to pairings so they also show unfavorable pairing and causes overlap repulsion. The proper pairing is found in between purine-pyrimidine base (AT or GC or UA). Base pairing in between GC (purine-pyrimidine) content shows higher melting temperatures, therefore, the genomes of extremophile organisms such as *Thermus thermophilus* are particularly GC-rich (Lorenz et al. 2017).

## Base Analogs and Intercalators

Some chemical analogs of nucleotides can replace the place of appropriate nucleotides and begin a noncanonical base pairing, leading to mutations. One common mutagenic base is 5-bromouracil, which resembles thymine (T) but can base pair to the guanine (G) in its enol form. On the other hand, some analogs of bases are intercalators ethidium bromide and acridine which cause frameshift mutations. The bp (base pairs), kbp

(kilo base pairs), Mb (mega base pairs), and Gb (giga base pairs) are commonly used to describe the length of a DNA/RNA molecule.

## Role of Base Pair in Animal Cognition and Behavior

The four base pairs of DNA cause variations in the living world due to the variations in the sequences of DNA by their interactions with the environment. The genetic diversity of a species exists at three levels (I) heterozygosity (genetic diversity within individuals), (II) genetic diversity between individuals within a population, and (III) genetic variations between populations (Mandal 2015). Genetic diversity is the heritable variation within a population and between populations. Genes and chromosomal mutations also cause the genetic variations. Mostly genetic variation due to base pairs over a single generation occurs through shuffling of the homologous chromosome, fusion of gametes during sexual reproduction, and cross-over. All the variations depend upon environmental conditions whether such changes (structural and functional) are beneficial or harmful or neutral in the present as well as for the future.

Evolutionary responses of previous populations are allowed by genes for selection of behavior. The genetic characters are mainly resolute by genes which play role in many behaviors, a change in single protein brings distinct phenotype. Expression of genes is mainly influenced by the external environmental factors via nervous and hormonal mechanisms. Synthesis of one polypeptide is governed by the gene, which is the functional unit of the genome. In a gene, cistron is the functional unit and contains over a hundred points where the mutation can take place, which causes the detectable phenotypic effect (Lehninger 2000). Cistron is responsible for coding of the polypeptide chain of an enzyme. The genes carry specific codes for amino acid which can synthesize protein. Monomorphic loci (section on the chromosome) contain the single most common segment of code which is 95–99% similar to each individual. Evolutionary responses of previous populations are allowed by genes for selection of behavior (Davis and Shaw

2001). The genetic characters are mainly resolute by genes which play role in many behaviors, a change in single protein brings distinct phenotype. Expression of genes is mainly influenced by the external environmental factors via nervous and hormonal mechanisms (Booij et al. 2015).

## Summary

The genetic information is carried in the linear sequence of nucleotides in DNA. Each molecule of DNA is held together by hydrogen bonds between G—C and A—T base pairs and forms two complementary strands of nucleotides. The copy of the genetic information occurs by the use of one DNA strand as a template for the formation of a complementary strand. DNA stores all genetic information for all the proteins that organism will ever synthesize.

## Cross-References

- Behavior
- DNA
- Genes
- Protein
- RNA

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## Base-Rate Neglect

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## Synonyms

[Biased decision making](#)

## Introduction

Base-rate neglect is a phenomenon in which under certain conditions, humans are known to reliably overestimate the probabilities of events, even though there is sufficient information provided to arrive at the correct probability (Kahneman and Tversky 1972). In a common version of the problem, originally proposed by Tversky and Kahneman (1980), participants are told that patients presenting with a particular set of symptoms have a 10% chance of having contracted a particular disease. Furthermore, they are told that there exists a diagnostic test, the accuracy of which is 80% (in detecting the disease when it is present and in correctly indicating that the disease is absent when it is not present). Participants are then asked, “Given that the symptoms are present, and the test results are positive, what is the probability that the patient has the disease?” Most participants guess that it is very likely (between 60% and 80%) that the patient has the disease.

In making this judgment, the participants fail to consider sufficiently the fact that the disease is relatively rare (i.e., they tend to underestimate the effect of the base rate on the probability). In fact, the conditional probability of correctly identifying the presence of the disease is equal to the probability that the disease is present, times the probability that the test is correct, which is  $0.10 \times 0.80 = 0.08$ , whereas the probability of incorrectly identifying the disease when it actually was absent is equal to the probability that the disease is absent times the probability that the test is incorrect, which is  $0.90 \times 0.20 = 0.18$ . This means that the probability of being correct given a positive test is only  $0.08/(0.08 \times 0.18) = 0.31$ , or less than one chance in three. Thus, humans generally overestimate the likelihood that the disease is present because they underestimate the base rate. Similarly, the relative neglect of base-rate is responsible for the exaggerated fear that people have of air travel, of walking the streets of New York City, or of their children being shot at school.

## Base-Rate Neglect in Pigeons

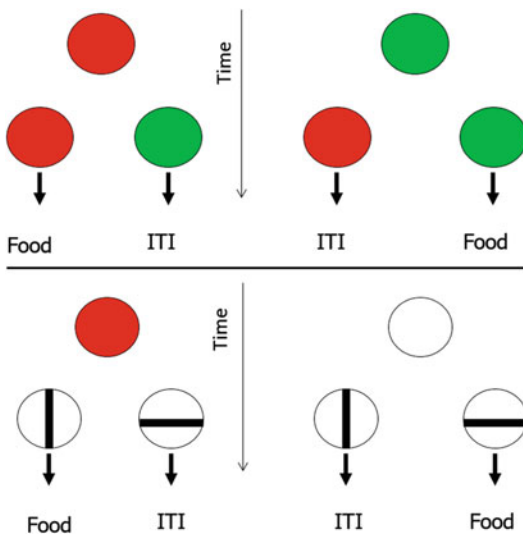
Are other animals subject to the same kind of errors? To answer this question, one needs to examine the performance of animals on a task in which base-rates may play a role. In a conditional discrimination (e.g., matching to sample), an initial or sample stimulus indicates which one of the two (or more) test or comparison stimuli is correct (Skinner 1950). According to Hartl and Fantino (1996), in such a task, comparison choice for pigeons should depend on two factors: (1) if the sample can be remembered, the conditional probability of each comparison being correct, given presentation of one of the samples and (2) if the sample cannot be remembered, the relative probabilities of reinforcement associated with the comparisons.

Typically, the two samples are presented with equal probability and the relative probabilities of reinforcement associated with the comparisons are the same. If those probabilities are not the same, however, and one introduces a delay

between the offset of the sample and the onset of the comparison stimuli, one might expect to see a bias in comparison choice (see Goodie and Fantino 1995, 1996 for evidence of such an effect with humans).

Alternatively, one could introduce a second matching task that involves two new comparison stimuli and one new sample, but the second task shares the other sample with the first matching task (see Fig. 1; Zentall and Clement 2002). Thus, there would be three rather than four samples, and the frequency of presentation of one sample would be twice that of each of the other two. Given the presentation of a pair of comparison stimuli, however, the probability that it had been preceded by one of the two possible samples would be equal.

Thus, if each of the four trial types appeared equally often, each of the comparison stimuli would be associated with reinforcement on 25% of the reinforced trials. However, the same would not be true of the samples. Two of the samples would each be presented on 25% of the trials, whereas the third would be presented on 50% of the trials.



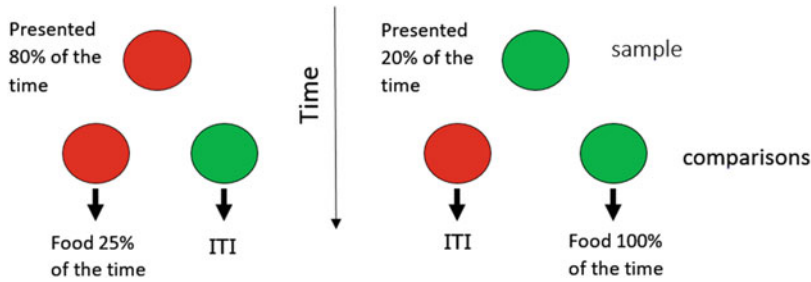
**Base-Rate Neglect, Fig. 1** Design of Zentall and Clement (2002). Pigeons were trained to choose the red comparisons when the sample was red and the green comparison when the sample was green. They were also trained to choose the vertical comparison when the sample was red and the horizontal comparison when the sample was white

The question is, if a delay is introduced between the offset of the sample and the onset of the comparison stimuli, assuming that there is forgetting of the sample, would the pigeons use the probability of reinforcement associated with the comparison stimuli (the base-rate) to determine choice or would the pigeons be influenced by the sample probabilities (neglect the base-rate). One of the samples appeared twice as often as the other but half of those occurred with the other pair of comparison stimuli. Zentall and Clement (2002) found a strong bias to choose the comparison associated with the more frequently occurring sample, even though that sample had not occurred more frequently with either comparison stimulus. These pigeons neglected the base-rate.

Another approach to base-rate neglect was used by DiGian and Zentall (2007). In that study, the bias was induced by presenting one sample on 80% of the trials, but correct choice of the associated comparison was reinforced only 25% of the time (see Fig. 2). The other sample was presented only 20% of the time, but correct choice of the associated comparison was always reinforced. With this design, in the absence of memory for the sample, choice of either comparison stimulus was reinforced 10% of the time (the base rate). Nonetheless, with increasing delay between the offset of the sample and the onset of the comparison stimuli, the pigeons showed a strong preference for the comparison associated with the more frequently presented stimulus. Once again, the pigeons were influenced by the irrelevancy of the sample frequency.

A third approach to the question of base-rate neglect was developed by Zentall et al. (2008). They also used three samples, but only two comparison stimuli (see Fig. 3). On 1/3 of the trials, the sample was green and correct choice of the green comparison was reinforced 100% of the time. On 1/3 of the trials, the sample was red and correct choice of the red comparison was reinforced only 50% of the time. On the remaining 1/3 of the trials, the sample was yellow and correct choice of the red comparison was reinforced 50% of the time. Thus, the green comparison was correct on 1/3 of the trials, whereas the red comparison stimulus was correct on 2/3 of the trials, but

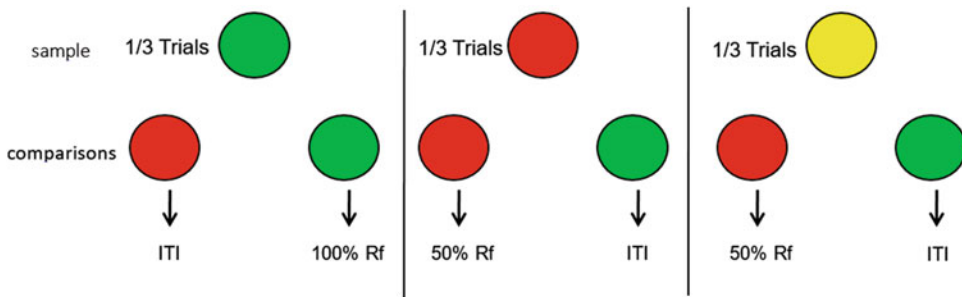




B

**Base-Rate Neglect, Fig. 2** Design of DiGian and Zentall (2007). Pigeons were trained to choose the red comparisons when the sample was red and the green comparison when the sample was green. Red sample appeared 80% of

the time but correct red comparison responses were reinforced only 25% of the time. Green samples appeared 20% of the time and correct green comparison responses were reinforced 100% of the time



**Base-Rate Neglect, Fig. 3** Design of Zentall et al. (2008). Red, green, and yellow samples were presented equally often. Correct green comparison responses were

always reinforced. Correct red comparison responses were reinforced 50% of the time, whether the sample was red or yellow

correct choice of it was reinforced only 50% of the time. With this design, in the absence of memory for the sample, choice of either comparison stimulus was reinforced 1/3 of the time (the base rate). Once again, because samples associated with red comparison occurred on 2/3 of the trials, the pigeons were biased to choose the red comparison. They did so, in spite of the fact that, in the absence of memory for the sample, the probability of reinforcement for choice of either comparison was the same (1/3).

are two sample, correct-comparison response chains. If that was all that they learn, then in the absence of memory for the sample there should be no comparison response bias.

## Cross-References

- [Delayed Match-to-Sample](#)
- [Matching-to-Sample: Comparative Overview](#)
- [Oddity](#)
- [Relational Concepts and Symbolic Logic](#)

## Conclusions

The results of these experiments demonstrate that pigeons show an effect of base-rate neglect similar to that of humans. The results are also inconsistent with Skinner's (1950) claim that when animals learn a conditional discrimination all they learn

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## Basic Rank

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## Synonyms

[Dominance rank](#); [Rank](#); [Status](#)

## Definition

The relative position of an individual within a group or within a population only affected by physiological or morphological characteristics or both.

## Introduction

In many animals, individuals compete over access to limited resources such as food, water, mating partners, space, and so on. This competition can

take the form of physical combat, mere displacements, or displays; or it may be decided by one individual retreating spontaneously without preceding interactions (interactions obvious for a human observer; Dugatkin 2014). Competition occurs between individuals of the same group, between groups of individuals, or between solitary individuals. If individuals (or groups) are able to recognize each other and interact repeatedly, the outcome of their interactions, i.e., winning or losing, can be more or less stable so that the relative position of an individual (or a group) can be predicted with high certainty. In this situation, an individual or a group can be assigned a status or dominance rank (or rank, for short) relative to another individual or another group; one individual (one group) is said to be higher or lower ranking than another (Clutton-Brock 2016).

On the most basic level, the outcome of competitive interactions is related to the morphological or physiological characteristics of an individual; a condition known as “basic rank” (Kawai 1965). Despite the fact that groups can compete against other groups and a rank can be assigned, the concept of basic rank has only been applied to individuals. Importantly, beyond the effects of morphology and physiology, additional factors can influence the outcome of a competitive interaction and, hence, the relationship between two individuals. The resulting system is coined “dependent rank” (Kawai 1965). Originally, Masao Kawai (1965) found that the presence of kin changed the rank relationship between individuals in Japanese macaques. Today, such effects are known for several primate species, spotted hyenas, and jackdaws (Clutton-Brock 2016). We also know a multitude of other influences on rank such as winner-loser effects, bystander effects, audience effects, and so on (Dugatkin 2014). Still, the basic rank of an individual relative to others is the underlying characteristic of competitive relationships within groups and populations.

## Individual Characteristics and Rank

In the simplest case, the outcome of a competitive interaction between two individuals can be

characterized based on three variables: (i) the value of the resource that is contested, (ii) the potential costs of the contest, and (iii) the probability of winning (or losing) (Maynard Smith and Parker 1976; Dunbar 1988). If we assume for simplicity that the value of a resource is similar for both contestants (which is usually not the case in reality; imagine a satiated and a starving individual vying for the same food item), we can model the way in which the costs and the probability of winning will vary (Enquist and Leimar 1983). In such a case, we can safely assume (see examples below) that those fighting abilities will determine the outcome that are related to body size, strength, or weaponry such as canine size, size of antlers, etc. An individual facing an opponent with particularly large canines has a high risk of injury. A bigger or stronger animal has a higher chance of winning. These aspects immediately explain why younger and smaller individuals often occupy lower ranks than older and larger individuals (a situation resulting in “age-graded” ranks). However, even adult individuals vary in size, strength, and weaponry, such that the ranks of two individuals or the rank order within an entire group correlates with fighting abilities (Kappeler 2006). Pinnipeds and ungulates provide good examples both for females and for males, although the connection with age, body size, and weaponry is not always consistent (Clutton-Brock 2016).

In addition to morphology, physiology can also play a crucial role. Winning a physical combat can be decided by the aggressiveness of an individual, which in turn is often a function of the hormonal status such as the level of androgens (Wingfield et al. 1990). Again, this may relate directly to the age and developmental status of males, because androgen levels increase during ontogeny. However, even among adult males, androgen levels differ. Particularly during periods of instability, dominant males may be characterized by higher levels of testosterone, higher aggressiveness, and lower stress levels (lower corticosteroid levels) than lower ranking males (Sapolsky 1993). As with fighting abilities, the relationship between physiological variables and male rank is not always consistent but varies across populations

and species (Clutton-Brock 2016). In a few species, such as in spotted hyenas, a tight relationship between androgens and rank has been described for females. Notably, here a female’s rank and hormonal status during pregnancy has consequences for the aggressiveness of her cubs. Cubs, both females and males, of high-ranking mothers are exposed to high levels of androgens during fetal development and express high levels of aggression later on (Dloniak et al. 2006). Thus, basic rank does not only relate to competitive interactions and rank of a female but can have downstream effects on her offspring.

## Conclusion

Basic rank refers to the dominance rank of an individual purely based on individual characteristics such as hormonal status, maturity, and more generally size, strength, and weaponry. It is important to note that the basic rank of an individual is often affected by additional variables such as the actual status of an individual (e.g., hunger level which affects the value of a resource) and the social environment through kinship, winner-loser effects, bystander effects, audience effects, and the like.

## Cross-References

- [Age-Graded](#)
- [Agonism and Social Status](#)
- [Agonistic Behavior](#)
- [Dominance](#)
- [Dominance Hierarchy](#)
- [Honest Signaling](#)
- [Rank](#)
- [Resource Holding Potential](#)
- [Resource Holding Power](#)

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## Bateman Gradient

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## Synonyms

[Sexual selection gradient](#)

## Definition

The slope of a (usually simple, linear) regression of the number of offspring on the number of mates.

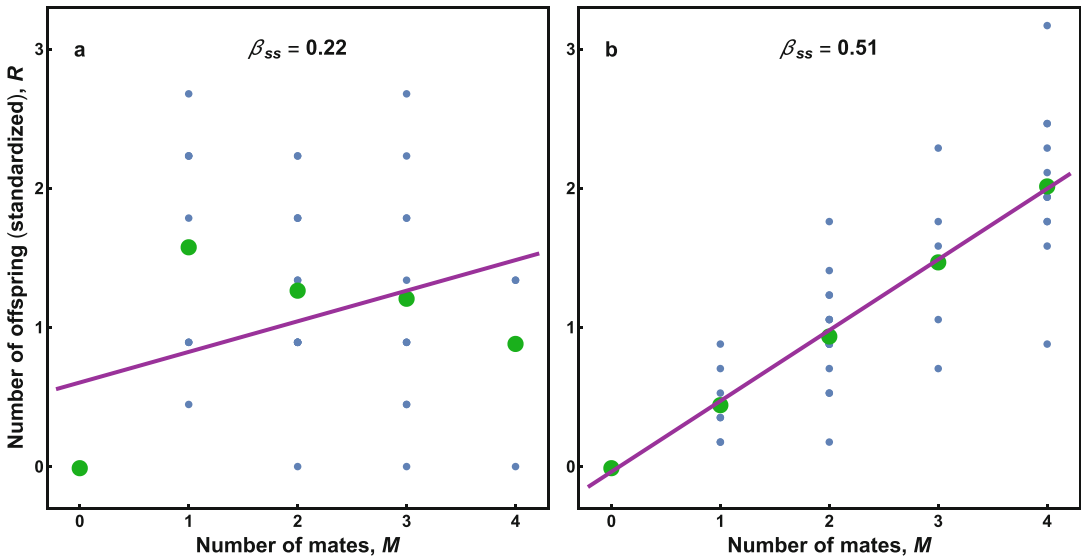
## Introduction

In 1948, the English geneticist Angus John Bateman published a pioneering study of genetic parentage in

the fruit fly *Drosophila melanogaster* (Bateman 1948). Bateman set up small breeding populations of flies and used visible mutations to determine the mother and father of the resulting offspring. He then used these data to address the question of why competition for mates is usually stronger in males than in females. Although some authors have criticized empirical details of Bateman’s study (e.g., Snyder and Gowaty 2007), his conceptual framework has profoundly influenced modern sexual selection theory.

When males and females occur in roughly equal numbers – as they do in *D. melanogaster* – the average number of offspring produced by members of each sex must also be equal, because each offspring has exactly one mother and one father. Bateman showed, however, that the variance in offspring number was higher in males than females. He attributed this result to two main causes: (1) males were more variable than females in the number of matings they achieved, and (2) the correlation between offspring number and the number of mates was stronger in males than in females. This stronger relationship, Bateman argued, arises from the fundamental sex difference in gamete size. Because sperm are smaller and more numerous than eggs, female offspring production is less strongly limited by fertilization opportunities. Males should consequently experience stronger selection to increase their number of mates, at least in species where their only contribution to the next generation is their sperm.

Bateman’s ideas lay largely dormant until the renaissance of sexual selection theory in the 1970s, where they were revived in particular by Trivers (1972). Bateman’s observations and conclusions were integrated with formal selection theory (Arnold and Duvall 1994; Jones 2009; Henshaw et al. 2018), which led to more precise quantitative definitions of Bateman’s principles. Perhaps the most important insight was that the strength of sexual selection is related to the slope of the relationship between reproductive success (number of offspring) and mating success (number of mates). Arnold and Duvall (1994) showed that this relationship could be quantified using a regression coefficient (Fig. 1), and they named this quantity the *sexual selection gradient*.



**Bateman Gradient, Fig. 1** Hypothetical relationships between an individual's number of mates  $M$  and their number of offspring  $R$ , assuming that (a) additional mates after the first are detrimental to average offspring production, or (b) average offspring production increases linearly with the number of mates. Small blue circles represent individual mate and offspring numbers; large green circles

represent the average offspring number of individuals with any given number of mates (i.e., the Bateman function); the purple line represents the simple linear regression of offspring number on mate number. The Bateman gradient  $\beta_{ss}$  is the slope of this regression line. Offspring number has been standardized to have a mean value of one

Andersson and Iwasa (1996) later suggested the name *Bateman gradient* to distinguish it from other types of selection gradients.

## Definition

The Bateman gradient  $\beta_{ss}$  quantifies the slope of the relationship between an individual's number of mates or matings (i.e., their mating success  $M$ ) and their number of offspring (i.e., their reproductive success  $R$ ). Most commonly, Bateman gradients are calculated as the slope of a simple linear regression of reproductive success on mating success (Arnold and Duvall 1994; Jones 2009; Henshaw et al. 2018; Fig. 1). Explicitly, this means that:

$$\beta_{ss} = \frac{\text{cov}(M, R)}{\text{var}(M)}$$

Bateman gradients are estimated separately for each sex, usually over a constrained time period such as a breeding season. They are best

calculated using *relative* reproductive success, which is standardized by dividing each individual's reproductive success by the mean reproductive success of all individuals of the same sex (Jones 2009). In this case, the Bateman gradient can be interpreted as a linear selection gradient on mating success (Arnold and Duvall 1994). Some authors additionally recommend mean-standardizing mating success (Jones 2009).

## Measurement and Interpretation

Three issues should be kept in mind when measuring and interpreting Bateman gradients. First, the most intuitive interpretation of a Bateman gradient is causal – how much would a typical individual's reproductive success increase if they were granted an extra mating? Despite this intuition, Bateman gradients are most often measured in freely mating populations, where mating and reproductive success covary naturally (Anthes et al. 2017). Such correlative studies are vulnerable to confounding factors that affect both

mating and reproductive success, which complicates interpretations of the Bateman gradient. If potential confounders are identified and measured, then they can be included as covariates in the regression of reproductive success on mating success. The Bateman gradient can then be defined as a partial regression coefficient (Henshaw et al. 2018). Nonetheless, the potential for unmeasured confounders means that manipulative experiments are essential to pin down the causal relationship between mating and reproductive success (Anthes et al. 2017).

Second, Bateman gradients condense the relationship between mating and reproductive success into a single number (the “slope”). However, such relationships are often not straight lines; rather, their steepness may vary with the number of matings. More generally, a *Bateman function* represents the average reproductive success of individuals with each integer number of matings (Fig. 1). For individuals with zero mating success, reproductive success is necessarily also zero, as no offspring can be conceived without mating. After the first mating, reproductive success may continue to increase, remain flat, or even decrease (e.g., if mating itself is dangerous or harmful), depending on a species’ ecology and mating system (Anthes et al. 2017). Despite these nuances, the interpretation of Bateman gradients as selection gradients on mating success always holds, regardless of whether the Bateman function is linear or nonlinear.

Third, Bateman gradients are highly sensitive to technical issues affecting estimates of mating and reproductive success. In many studies, matings are not observed directly, but rather inferred by reconstructing the parentage of offspring. Only matings that lead to offspring are counted towards an individual’s “mating success,” which can lead to a spurious strengthening of the estimated relationship between mating and reproductive success. Unsurprisingly, Bateman gradients based on genetic information alone are almost always higher than those based on observations of mating interactions (Anthes et al. 2017). Another issue is that when individuals are sampled from natural, open populations, mating and reproductive success are inevitably sampled incompletely for some individuals. This can lead to biased estimates of Bateman gradients. Statistical approaches exist to

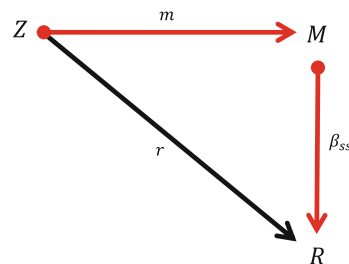
ameliorate such bias as long as certain assumptions are met (Jones 2015).

## The Strength of Sexual Selection

Sexual selection can be conceptualized as a type of natural selection that acts via causal pathways involving mating or fertilization success (Henshaw et al. 2018). Selection via mating success in particular is sometimes termed *pre-mating sexual selection* (Fig. 2). Using a path-analytic framework, the strength of pre-mating sexual selection acting on a trait can be decomposed into two components, with one component representing the association between the trait and mating success and the other representing the association between mating and reproductive success (Arnold and Duvall 1994; Jones 2009; Henshaw et al. 2018). One such decomposition is:

$$x = \beta_{ss}m$$

Here  $x$  is the strength of sexual selection,  $\beta_{ss}$  is the Bateman gradient (calculated as a simple or partial regression coefficient), and  $m$  is the covariance between the trait and mating success (known as the *mating differential*). For traits that are standardized to have a variance of one, the strength of pre-mating sexual selection  $x$  is limited in magnitude by:



**Bateman Gradient, Fig. 2** Pre-mating sexual selection is any selection acting via causal pathways involving mating success  $M$  (shown in red). Pre-mating sexual selection on an arbitrary trait  $Z$  can be decomposed into two components: the mating differential  $m$ , which represents the relationship between the trait and mating success, and the Bateman gradient  $\beta_{ss}$ , which quantifies the relationship between mating success and reproductive success  $R$ . The variable  $r$  represents any remaining selection acting on  $Z$ , other than pre-mating sexual selection



$$|x| \leq |\beta_{ss}| \sqrt{\text{var } M}$$

This upper bound, known as the *Jones index*, is informative even for traits that are not included in the analysis (Jones 2009; Henshaw et al. 2018). It is unbiased only if the estimate of  $\beta_{ss}$  controls for all factors that confound the relationship between mating and reproductive success. The Jones index was highly correlated with the strength of pre-mating sexual selection in a simulation study (Henshaw et al. 2016).

## Sex Differences in the Bateman Gradient

In most animal species, males contribute only their sperm to the next generation. In such cases, Bateman gradients are invariably larger for males than for females (Janicke et al. 2016). However, large female Bateman gradients may occur for at least two reasons. First, if mate encounters are rare, then both males and females may often be mate-limited. Second, if males contribute substantial resources towards raising offspring, or provide nuptial gifts to their partners while mating, then female reproductive success may increase steeply with the number of mating partners (Trivers 1972). In rare cases, including several species in the pipefish family, paternal investment in offspring has led to female Bateman gradients exceeding their male counterparts (Janicke et al. 2016).

## Cross-References

- Anisogamy
- Sex Differences
- Sex Ratio
- Sex Role Reversal
- Sexual Selection

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## Batesian Mimicry

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## Definition

Mimicry – or the phenomenon of one organism (the mimic) displaying characteristics of an unrelated organism (the model) – is divided into different categories, depending on the function or outcome of the imitation. In the case of **Batesian**

**mimicry**, the acquired resembling characteristics offer a protective function to the mimic, in that the chances of the organism being eaten by potential predators are reduced. Batesian mimicry therefore involves three parties: the model, the mimic (also known as the signaler), and the predator (also known as the signal receiver or the operator), all of which belong to different species found in the same geographical area (but not necessarily in strict sympatry).

## Background

Batesian mimicry is named after the nineteenth century British naturalist, Henry Walter Bates, in honor of his work with Amazonian butterflies (Bates 1862). Bates documented dozens of butterfly species belonging to the families Ithomiinae and Heliconinae, noticing that several unrelated species living in the same areas showed strikingly similar appearances. His explanation for this phenomenon was that some of these species must be unpalatable or noxious to predators such as birds, so other butterflies evolved similar colors and patterns, “deceiving” the predators and so avoided being preyed on. These observations and explanations came in a timely manner with the newly emerging theory of natural selection, providing one of the strongest arguments for predator-mediated selection. In fact, both Charles Darwin and Alfred Russel Wallace were greatly inspired by Bates’ work, Darwin mentioning it several times in his most famous publication, *The Origin of Species*.

## Conditions of Batesian Mimicry

The conditions that shape Batesian mimicry, and by which it is upheld, involve (1) the noxiousness, distastefulness, or general unpalatability of the model; (2) the accuracy of the mimic in imitating the model; and (3) a capacity for learning to avoid the noxious models (and hence the mimics too) by the predator (Rettenmeyer 1970; Mappes and Alatalo 1997). Expanding on the first point, the effectiveness of the mimicry therefore depends on

factors such as the noxiousness or unpalatability of the model. Generally, this translates as a distastefulness or toxicity for the predator brought about by certain chemical compounds known as allomones, which in insects, for example, are divided into Class I chemicals such as alkaloids and cyanides which poison, irritate, or injure predators; and Class II chemicals such as aldehydes and aromatic ketones, which deter predators through adverse smells, but are essentially harmless. On the other hand, a potential prey item can also become unpalatable if it has developed physical defense mechanisms such as spines, stings, and/or aggressive-defensive behavior.

The next point regarding the conditions for Batesian mimicry involves the mimic’s accuracy in imitating the model, which may at times be a more subjective matter. In other words, the human perception of a mimetic form may differ from the predator’s making a seemingly “imperfect” mimic in fact effective to the predator’s sensory system. Nevertheless, numerous studies have addressed the issue of the variation in mimetic forms, whereby some mimics appear to imitate their models almost perfectly, whereas others show less of a resemblance, earning the title of “poor” or “imperfect” mimics (Edmunds 2000). Explanations for the existence of these “imperfect” mimics, apart from observer subjectivity, include the possibility of the mimic imitating more than one model, thus having a general rather than one-species-specific form. Alternatively, the selection pressure to closely resemble the model may not be very strong if, for example, the model is highly toxic and an approximate resemblance suffices for protection from predation. An “imperfect” mimic may also simply be in the process of converging toward the model’s phenotype (i.e., the expressed character). Finally, while selection would favor a more model-specific phenotype, there are trade-offs involved, including the loss of polymorphism (from the Greek meaning “many forms”), an evolutionarily advantageous condition for populations (Lindström et al. 1997; Joron and Mallet 1998; Sherratt 2002; Penney et al. 2012).

The final point relates to the theory that for Batesian mimicry to be effective, the mimics should not outnumber the models, otherwise

predator learning will be compromised. This ties in with the theory of frequency-dependent selection, where the higher the proportion of models to mimics, the more likely the predator is to learn to avoid the prey (Pfennig et al. 2001). Conversely, if there is a relatively high density of mimics, the predators may only ever encounter the harmless mimic, not learning to avoid that particular phenotype. Predator learning is not essential in all cases of Batesian mimicry, as predator avoidance toward certain stimuli can also be innate. Nevertheless, many cases of Batesian mimicry exist where a “naive” predator must first suffer an adverse reaction from consuming harmful prey, before learning to avoid organisms displaying a specific characteristic related to the harmful prey. In many cases, this characteristic involves bright colors and patterns presumed to be “warning signals” advertising the potential prey’s noxiousness to predators, a phenomenon known as aposematic coloration or aposematism. An example of aposematism in insects is the yellow-and-black striped abdomens of bees and wasps, signaling the presence of their stings and venom. The hoverflies, a group of harmless insects, have acquired the yellow-and-black striped abdomen characteristic, thus turning them into Batesian mimics, not of any species in particular, but of the whole aposematically protected group of bees and wasps. So Batesian mimics can rely on the resemblance of a general characteristic, or they can mimic specific model species, at times very accurately.

## Visual Batesian Mimicry

When talking about Batesian mimicry, the predator’s sensory channel targeted by the mimic must be specified. Most recorded cases are of visual Batesian mimicry, relying on the predator’s sense of sight to exert the resemblance. Visual Batesian mimicry can be found from model-mimic systems of species belonging to the same family, through to taxonomically distant groups even from different phyla, keeping in mind that greater resemblance is more easily achieved in evolutionary terms between closely related

models and mimics. The systems which sparked W.H. Bates’ interest and brought forth his developing the theory were in fact between butterfly species mostly belonging to the same – or closely related – families, as mentioned earlier. Another example of a model-mimic system in which both parties belong to the same family is the Batesian mimicry by several tenebrionid beetle species of a particular genus, *Eleodes* (Tenebrionidae), which deter predators by producing noxious chemicals (Smith et al. 2015). In vertebrates, a thoroughly studied example of Batesian mimicry between closely related groups relying on aposematic coloration is the mimicry complex between several species of the highly venomous coral snakes (six genera of the family Elapidae) and their Batesian mimics which include the scarlet snakes (family Colubridae) *Cemophora coccinea* and *Lampropeltis elapsoides*. In other vertebrate groups, examples of Batesian mimicry include the harmless cardinalfish *Fowleria* sp. (family Apogonidae) resembling the venomous Scorpionfish *Scorpaenodes guamensis* (family Scorpaenidae) (Seigel and Adamson 1983), the red morph of the red-backed salamander *Plethodon cinereus* (family Plethodontidae) mimicking the highly toxic Eastern newt *Notophthalmus viridescens* (family Salamandridae) (Brodie and Brodie 1980), or in mammals perhaps the resemblance of the insectivorous aardwolf to the striped hyenas in their fur pattern.

Within the phylum Arthropoda, due to their extreme diversity, an immense number of cases of Batesian mimicry can be found between members of different orders and classes, especially the insects (Rettenmeyer 1970). Within the insects, the ants are an outstanding group of models for Batesian mimicry, due to one – or a combination – of the following characteristics: colonies with high numbers of individuals, aggressive nature, hard cuticles in some cases with spines, bites, stings, and the presence of formic acid in some families. It therefore comes as no surprise that ant mimicry, in particular myrmecomorphy (the morphological resemblance to ants), has evolved at least 70 times in arthropods, with more than 2000 described species, belonging to over 200 genera in

54 families from groups such as the plant bugs, staphylinid beetles, and spiders (McIver and Stonedahl 1993). Ant-mimicking spiders can be found in at least 13 families, with the jumping spiders (family Salticidae) containing the highest number of myrmechomorphic genera and species (Cushing 2012).

Some salticid genera's species are exclusively Batesian mimics of ants. An example is the genus *Myrmarachne*, which contains around 200 described, globally distributed species, which resemble ants in general body shape, coloration, and texture. The high species diversity of this genus backs up the numerous strategies within the Batesian ant mimicry, which have evolved in different *Myrmarachne* species. For example, many species display what is known as transformational mimicry, whereby a different ant species serves as a model at each of the spiders' instars (the phase between two molts during their growth), keeping the relative sizes of the model and the mimic similar (Edmunds 1978). The protective benefits of Batesian mimicry are further enhanced by species such as *Myrmarachne melanotarsa*, which – unlike most spiders which are solitary – aggregate into groups, thus resembling ants in colonies even more, in a strategy termed collective mimicry (Nelson and Jackson 2009). Many species of the genus also display sexual dimorphism, meaning that males and females are different in some way. In the case of *Myrmarachne*, the males have enlarged chelicerae (or fangs), a character thought to be sexually selected. Although this might appear to reduce the males' resemblance to ants, in fact the enlarged chelicerae are probably a case of compound Batesian mimicry, where the spider looks like an ant carrying something (usually dead ants) in their mandibles (Nelson and Jackson 2006). As mentioned before, polymorphism is widespread among natural populations. Hence, many species of ant-mimicking spiders are also polymorphic, mainly in coloration and patterns. In some cases, the polymorphism fits in with individual mimics from the same species resembling different model ant species (Ceccarelli and Crozier 2007), which in turn may favor the overall dynamics of frequency-dependent predator-mediated selection.

Finally, Batesian mimicry can even be found in model-mimic systems between distantly related species belonging to different phyla. Such is the case, for example, in the chordate-arthropod model-mimic example where the hawk moth caterpillar (*Hemeroplanes triptolemus*, family Sphingidae) extends its segments to resemble a snake and thus ward off potential predators (Hossie and Sherratt 2013).

## Behavioral Batesian Mimicry

In some cases of Batesian mimicry, the visual resemblance of the mimic to the model is enhanced by the mimic's behavior. Although this is strictly speaking visual mimicry as well, it deserves a special mention, since it is not only the morphology which has adapted, but also some behavioral traits, usually the way in which the model moves. In the examples given above, behavioral mimicry can be observed in the hawk moth, which does not only have a fake “snake's head,” but also moves the fake head from side to side, as a snake does. A special case of behavioral mimicry can also be observed in many ant-mimicking spiders. Since spiders have four pairs of legs and no antennae, while ants have three pairs of legs and a pair of antennae, to increase the resemblance to ants, several Batesian ant-mimic spiders lift their first pair of legs and wave them around as ants wave their antennae. This behavioral mimicry carried out by many spiders is known as “antennal illusion” and is in some cases further reinforced by special colorations of the spiders' first pair of legs (Ceccarelli 2008).

## Acoustic Batesian Mimicry

Visual Batesian mimicry is, as mentioned before, by far the strategy with the most cases recorded, emerging from ecological interactions where the predators hunt by using visual cues. However, many predators (especially nocturnal ones) also use their sense of hearing (and smell) to find prey, so there are also documented cases of acoustic

Batesian mimicry, where the mimic imitates a model's sound to deter potential predators. One example of such a system is the imitation by other moths of the noxious tiger moth's ultrasonic warning sounds in response to bats echolocation. The red bats (*Lasiurus borealis*), for example, learn to avoid the tiger moths (*Cynia tenera*) by associating the moth's warning sounds to the noxious prey, so when the palatable moth species produce similar ultrasonic sounds they will not be preyed on by the bats (Barber and Conner 2007). Another example of acoustic mimicry is found in the burrowing owl (*Athene cunicularia*), which produces a hissing sound like the warning of rattlesnakes (*Crotalus* spp) (Rowe et al. 1986). In this case, the potential predator may span a wide range of organisms which are deterred by the sound of a rattlesnake, thus avoiding the burrowing owl. The asp viper (*Vipera aspis*) is another venomous snake which serves as a model for Batesian mimicry by the harmless viperine snake (*Natrix maura*), visually as well as acoustically through the resemblance of the hissing sound produced by the two snakes (Aubret and Mangin 2014).

## Batesian Mimicry Evolution

It is clear that the study of acoustic Batesian mimicry lags behind the multitude of studies on visual mimetic systems. In any case, Batesian mimicry in general is a topic of great interest to biologists and continues being an ever-expanding field. In particular, with the advancement of molecular-based studies, the evolution of mimicry can be investigated at a genetic level. While a theory (Charlesworth and Charlesworth 1975), backed up by a genomic study in butterflies (Joron et al. 2011), has been put forward stating that mimicry is likely to be based on supergene complexes, much work remains to be done on an empirical basis. Similarly, more empirical studies backing up the various mathematical models of the evolution of mimicry are required (Nur 1970; Matessi and Cori 1972; Holmgren and Enquist 1999). The evolutionary dynamics of Batesian mimicry are very varied depending on the nature of the species involved, ranging from

one-sided advergence (Brower and Brower 1972) or even adaptive radiation of the mimic with no effect on the model (Ceccarelli and Crozier 2007), through to coevolution type scenarios where the presence of the mimic has an effect on the fitness of the model, thus influencing its evolution (Turner 1995).

## Cross-References

- ▶ Aggressive Mimicry
- ▶ Aposematism
- ▶ Auditory Signals
- ▶ Bear Sensory Systems
- ▶ Charles Darwin
- ▶ Coevolution
- ▶ Deception
- ▶ Evolution
- ▶ Evolutionarily Stable Strategies
- ▶ Frequency-Dependent Selection
- ▶ Heritability of Behavior
- ▶ Mimicry
- ▶ Müllerian Mimicry
- ▶ Predation Risk
- ▶ Signaller
- ▶ Stabilizing Selection

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## Bats

### ► Microchiroptera Life History

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## Bear Cognition

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## Synonyms

### Bear intelligence

## Definition

The study of the cognitive capacities and the evolutionary mechanisms driving cognitive development of species within the family *Ursidae*.

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<sup>#</sup>Both authors contributed equally to this manuscript



## Introduction

Studies related to bear (*Ursidae*) cognition emerged relatively recently in scientific history compared to other mammalian groups (e.g., rodents, primates), and have focused strongly on establishing the cognitive capabilities of this taxa and the evolutionary mechanisms responsible for driving their cognition. The relative sociality of a species has been suggested to be linked to the evolution of key cognitive capabilities such as concept formation, language, and complex problem solving (Sewall 2015). This a critical area of research, as the Ursids are relatively solitary in nature compared to other caniform carnivores (e.g., domestic dogs, wolves). However, bears exhibit delayed ontogeny, remaining with their mothers for a period of up to 3–5 years, depending on the species and habitat, which allows for vertical transmission of skills (social learning from mother to offspring). Additionally, many species continue to stay with their siblings after leaving their mothers, allowing for horizontal transmission of skills (social learning from sibling to sibling, Gilbert 1999). Some, however, argue that it is not necessarily sociality of a species, but larger relative brain size to body size that is related to greater cognitive sophistication (Benson-Amram et al. 2016). Bears are known to have one of the largest brain-to-body-size ratios of terrestrial mammalian carnivores (Benson-Amram et al. 2016). Still others look to ecological factors that may have played a role in the evolution of these capabilities. Specifically, hunting/foraging strategies and diet are of particular interest to researchers (Gilbert 1999). Evidence gained from studying bears, could help clarify the mechanisms at play in driving cognitive evolution.

Bear cognition has been studied from a basic research approach as well as from an applied, animal welfare perspective. The knowledge gained from basic research aimed at understanding what cognitive abilities bears possess and why/how these abilities may have evolved hope to inform animal welfare policies both within animal facilities that house bears, but also conservation efforts and improved human-wildlife interactions in the wild. In addition, less formal research done by caretakers in animal facilities

offer unique insight into capacities not fully understood in strictly controlled experimental settings.

## Basic Research on Bear Cognition

**Concept Formation** The ability to organize stimuli in the environment into concepts has been well documented in a wide variety of non-human species. Concepts are mental representations of information formed during the process of categorization. Increased experience corresponds to an increased cognitive complexity, enabling the comprehension of complex concepts as well as linkages between these concepts. The links within and between concepts allow for painting a broader picture of the perceptual and social world.

**Natural Concept Formation at Varying Levels of Abstraction** Little research on bear cognition occurred after Gordon Burghardt's pioneering work in the 1970s and 80s (e.g., Bacon and Burghardt 1976, 1983), but there has been a lot of recent interest in the area of bears' ability to form concepts for natural categories at what is referred to as, different levels of abstraction. Essentially, natural categories build on themselves from least to most inclusive and from least to most abstract. This ability is essential for survival in the wild – for example, for the distinction between venomous and non-venomous snake species (Rogers et al. 2014).

Using a computerized touch screen task previously used to test the same skills in great apes (gorillas, orangutans, and chimpanzees), Vonk et al. (2012) tested three captive American black bears' (*Ursus americanus*) ability to form concepts at five levels of abstraction: concrete – black bears (S+) versus humans, concrete/intermediate – polar bears (S+) versus mixed bears, intermediate – primate (S+ for two bears) versus hoofstock (S+ for one bear), intermediate/abstract – carnivore (S+) versus noncarnivore, and abstract – animal (S+) versus nonanimal. Categories at the least inclusive and most concrete level, such as black bears or humans, contained

the most perceptual similarity within categories and less perceptual similarity between categories, making it easier to discriminate categories on the basis of perceptual cues alone. Categories at the most inclusive and abstract level such as *animals* or *nonanimals*, contained significantly less perceptual similarity within the categories. The task was a two-alternative, forced-choice (2AFC) task, where two images were presented simultaneously, side by side on the touch screen monitor and the bears were rewarded for touching images representing only one of the categories (S+). The order in which the bears received the different discriminations were varied so that one, Dusty, moved from most to least abstract while the other two tested in a pseudo-counterbalanced fashion. Importantly, most previous work on levels of abstraction ordered the discriminations from least to most abstract for all subjects, intentionally stressing the perceptual similarities within categories to the subjects. Vonk et al. (2012) were the first to suggest that perhaps presenting the more abstract categories first can aide in successfully forming those categories by reducing reliance on perceptual similarity that might occur after overtraining with concrete discriminations. The bears worked on each discrimination until they reached a criterion of 80% correct in four consecutive sessions or 90% correct in two consecutive sessions. After reaching criterion, they were presented with a novel set of images from the same two categories to test for transfer learning.

All three bears were capable of forming concepts for natural categories at all five levels of abstraction, an ability once thought to be restricted to nonhuman primates and humans. The bear that started testing with the most abstract categories outperformed the other two with regards to both acquisition and transfer on that discrimination. These findings reinforce the possibility that overtraining animals to use perceptual cues via an extensive training history with concrete discriminations could contribute to their failures to demonstrate the formation of abstract concepts in previous work (Vonk et al. 2012).

Not only did this work demonstrate that black bears are capable of forming concrete level

concepts that rely strongly on perceptual similarities, it showed that they are capable of forming abstract level concepts. Although typically observed in social species, bears likely developed this ability as a result of their diet and resultant foraging strategies. Bears are omnivores; thus, they are adept at various search strategies – dependent upon the desired target (in this case, a food item). One natural category for animals is food – a category that, for some carnivores requires a relatively concrete behavioral repertoire and search strategy, as they are reliant on hunting behaviors to obtain food (e.g., big cats). However, generalists such as ursids, may rely on a wider breadth of cues with which to make a determination regarding behaviors likely to obtain a food reward. The broad range of category differentiation in order to locate and determine what constitutes food may contribute to the capacity for discriminating categories at a more abstract level (Vonk et al. 2012).

It is important to note, however, that further research has indicated that there are some limitations to bears' abstraction capabilities. While the bears showed success using a 2AFC task, one of the same bears that previously demonstrated successful formation of abstract concepts failed to do so using a match-to-sample (MTS) task (Vonk and Jett 2018). In these tasks, a single sample image was presented, then that same image was presented along with a different image after a very brief delay. The bear was reinforced for choosing the image that matched the sample image. This task requires the animal to extract a general (abstract) rule to determine what is correct (i.e., the sample is the target). The bear was not capable of discerning that general rule, thereby failing to demonstrate abstraction in this task (Vonk and Jett 2018). It should be noted that only a single bear received extensive training in this task, and apes also failed to learn MTS after extended training (Vonk, unpublished data).

Vonk and Jett (2018) also presented two black bears with a list memory task that required them to select three images that had just been presented from a group of images that included these three test images, along with images from two other unrelated categories. Each bear was randomly assigned a training set of images from one of

five categories: Shrek characters, SpongeBob characters, sports cars, Spiderman, and computer motherboards. The three images from each category appeared in random locations within a grid of six other images from untrained categories. The task for the bears was to choose only the images they had previously seen in training to get rewarded. As an example, one bear was given Shrek images first with Spiderman and sports cars as distractors. His task was to touch only Shrek images during the test phase. Upon reaching criterion on the first set, he was trained with Spiderman as the target stimuli and SpongeBob and sports cars as distractors. In order to be successful in the subsequent tests, he would need to extract (abstract) a general rule regarding the relationship between correct selections and what he previously learned about getting reinforced (e.g., touch the images from the training category to get rewarded). Both bears failed to clearly demonstrate this capacity to abstract a rule of category membership in this task, suggesting that there could be limitations to bears' abilities to form abstract concepts, some of which are based on task complexity (Vonk and Jett 2018). However, these results from a limited number of subjects stress the necessity of testing a larger number of subjects as well as a wider variety of species.

***Social Concepts at Varying Levels of Abstraction*** Vonk and Johnson-Ulrich (2014) expanded upon this work and investigated the American black bears' ability to form concepts for the social concept of mothers and offspring. Their performance was compared to that of chimpanzees – a more social species. The same 2AFC procedure was used to test these discriminations in both species. The categories varied in inclusivity with a discrimination consisting of conspecific (same species) mother/offspring images paired with images consisting of the same species representing other social relationships. The next discrimination for all subjects consisted of primate mother/offspring groups paired with other groups of primates. Lastly, all subjects were presented with animal mother/offspring groups of varying species with other social relationships of a diverse group of species (e.g., birds, snakes).

The subjects were also presented with nonsocial category discriminations to test if a general rule other than the construct of a social relationship was being utilized. Specifically, it could be argued that instead of representing the mother/offspring relationship, the subjects could be using a perceptual rule of choosing the image of the larger animal paired with smaller, visually similar animal. The nonsocial category examined produce groupings (berries, vegetables/mushrooms, and fruit) that mimicked the perceptual patterns described above with the “mother/offspring” groups depicting one piece of produce that was clearly perceptually larger than the others in the image and the paired image that did not follow that rule (Vonk and Johnson-Ulrich 2014).

All subjects were reinforced for choosing the mother/offspring pairings in both the social and nonsocial conditions. Importantly, the goal was not to teach the animals the concept, but to assess whether that concept was something they were innately capable of representing. The researchers predicted that the social species, chimpanzees, would outperform the more solitary species, black bears, in the social tasks. However, the authors noted that, if a perceptual rule was being used to discriminate the categories, then there might not be a significant difference in performance between the species. Additionally, black bears, like many others in the family Ursidae, experience delayed ontogeny. As mentioned previously, this extended period of development could be related to cognitive advancement as has been seen in more traditionally considered social species, like primates and corvids. In this sense, bears could be argued to be fully capable of distinguishing this specific social concept, whereas others, like dominance, may not be as relevant (Vonk and Johnson-Ulrich 2014).

Interestingly, neither the bears nor the chimpanzee in this study showed clear evidence of a social concept of mother/offspring. The bears were generally unsuccessful at generalizing the concept in the social tasks and it was not clear that they were abstracting the general perceptual rule of “choose the image with the larger and smaller one(s).” The chimpanzee, however,

appeared to use the perceptual rule at least initially to succeed on the tasks, but indicated some use of the social concept as he moved through the transfer and control images. Both species, however, did not excel at this measure of the concept, which is not necessarily unexpected considering the use of static, two dimensional (2D) images. It is unlikely these species do not have a concept for mother/offspring relationships at all, but it is likely that these relationships are determined in nature by a wide variety of perceptual cues, including visual, auditory, and olfactory cues. The images in the current task failed to adequately portray this complexity; therefore, both species found it difficult. The chimpanzee, however, was more successful, indicating at least some advantage of sociality in this task (Vonk and Johnson-Ulrich 2014).

**Picture Object Recognition** One criticism of the use of 2D images for testing concepts in animals is how much information they can extract from those images in comparison to experiencing the stimuli in real life. For example, 2D stimuli fail to depict behavioral and vocal cues as to mother/offspring relationships that would be present when interacting with live individuals (Vonk and Johnson-Ulrich 2014). To determine the extent to which bears might view 2D stimuli as representative of real-life objects, Johnson-Ulrich et al. (2016) investigated picture-object recognition in an adult, captive-raised American black bear. Objects were randomly paired and one was set as the S+ and the other was the S-. The bear was trained to choose the S+, but the modality of the stimuli varied from session to session. In some sessions, the bear experienced the pairs in pictures while in other sessions, the bear experienced the pairs as real objects. If the bear was trained on pictures of the items, testing for transfer was done with real items. If the bear was trained on real items, testing for transfer used pictures (Johnson-Ulrich et al. 2016).

The subject was found to be capable of recognize the correspondence between pictures and objects, both when they were first trained as real objects then tested as images and when they were trained as images first then tested as real objects.

Notably, it appeared to be easier for the bear to transfer from real objects to pictures than from pictures to real objects. This finding is important to studies using 2D images as stimuli in cognitive tasks as it lends support to bears' ability to extract visual information from photographs that represent the objects in real life (Johnson-Ulrich et al. 2016). While this study was conducted with only a single bear, it provides support for the use of 2D images to test cognitive abilities in bears and provides further insight into the cognitive capacities of bears.

**Quantity Estimation** Vonk and Beran (2012) investigated another cognitive capacity in American black bears: the ability to discriminate quantities (larger and smaller amounts). As bears are generalist foragers, it could be argued that the ability to determine if a food patch has a larger relative amount of food, would be beneficial to survival. Especially considering the fact that bears must obtain a large amount of calories in a shortened period of time in order to be able to survive hibernation, this ability to quickly and efficiently gain those calories by preferring areas with higher density of food (larger amounts) seems like a beneficial skill. The researchers in this study used the same adult, captive-raised bears as were included in the previous studies of natural and social concepts (Vonk et al. 2012; Vonk and Johnson-Ulrich 2014) on a similar 2AFC task, but instead of discriminating category membership from photographs, the bears were tested on their abilities to judge smaller (S+) from larger (S-) quantities (two bears – Bella and Dusty) or larger (S+) from smaller (S-) quantities (one bear – Brutus).

The methods used were based on testing previously done with primates (e.g., Beran 2008); therefore, the results are truly comparative in nature. The stimuli used, filled circles (henceforward called dots) varied in size (diameter) and quantity. They also could vary in color (red or black). Different subsets could be created in the stimuli where, for instance, only the color indicated the dots to be quantified by the bears. Additionally, the sets could also vary by

amount of space (area) the dots took up on the screen. Trials could either contain dots that were congruent between size and quantity, indicating that the larger quantity also represented more space on the screen (and vice versa for the smaller quantity) or the dot array could be incongruent, where the larger quantity actually took up a smaller amount of screen space than the smaller quantity. These differences were important to ensure that numerosity (indicated by the number of stimuli present), not quantity (indicated here by the area presented on the screen), was the cue most associated with the determination of which stimulus was larger or smaller (Vonk and Beran 2012).

All subjects reached above chance levels of performance, eventually, but the time it took to reach criterion on the different tasks varied significantly by both individual and task. The bear that was trained to choose the larger quantities, performed best with congruent dot arrays (where the larger quantity also took up more space) on the static and moving images. However, he relied heavily on area for the moving stimuli, indicating that judging quantity in static arrays is less taxing than in moving arrays. He was capable of judging the larger quantity in both congruent and incongruent trials in the moving subset trials, though, suggesting that the ability to judge number in dynamic sets is not completely absent. For the two bears that were trained to choose the smaller number of dots, their success was limited to the incongruent trials (meaning the smaller quantity of dots took up more space than the larger quantity). These results imply that they relied heavily on area and less on number. Taken together, the results of the experiment indicate that judging larger quantities relative to smaller quantities is easier for the bears, as indicated by the fact that the other two bears had such difficulty learning their task of choosing the smaller quantity in all conditions (Vonk and Beran 2012). These results probably reflect the adaptive value of preferring larger quantities of food, which would allow for the highest intake of calories with the lowest expenditure of energy possible. An early study of food preferences in black bears found that they preferred foods high in protein and carbohydrates across seasons (Bacon and Burghardt 1983).

**Spatial Cognition** Many of the previously discussed studies cite bears' diets as a possible ecological force in the evolution of cognitive skills. Because of their omnivorous diet, bears must exhibit a high degree of behavioral flexibility to obtain food in a variety of contexts, including foraging, hunting, and scavenging – all of which occur in a wide range of contexts depending upon environment, prey species, learned associations, and other factors. In order to effectively forage, hunt, and/or scavenge at a moment's notice, bears must rely on a wide range of cues, search strategies, and strategy in order to locate food.

There are many foraging strategies that animals utilize, including extractive foraging, in which a tool or appendage is inserted into something in order to extract the contents (e.g., a chimpanzee using a stick to get termites from a mound). Extractive foraging is contrasted with non-extractive foraging, where the animal finds food that is out in the open or not contained within something (e.g., a bear finding berries on a bush). Bears use both extractive and non-extractive foraging techniques but have not conclusively been shown to be tool-users (see next section for a possible exception). In the wild, bears are known to occupy home ranges and oscillate between productive patches seasonally, in order to maximize foraging efforts, as well as seek out mates and evade potential conflicts with other bears (Apps et al. 2004). Additionally, bears are known to cache large amounts of food – particularly following predation on a large ungulate or other prey species – to which they return later to feed (Elgmork 1982). This aspect of their foraging ecology, along with their large home range sizes, suggests that they should demonstrate good spatial memory.

One test of spatial cognition involves spatial memory, where subjects are shown baited locations, either in real life or a simulation, and then asked to recall those locations either immediately or after some time delay. Two studies, one with giant pandas and one with American black bears, investigated bears' ability to remember the spatial location of stimuli, but using different



methodologies. Perdue et al. (2009) used a 2x3 light grid to test giant pandas on their ability to recall which lighted location was associated with a reward (food). Essentially, the bears were shown a lighted grid with a light of specific brightness indicating the location of the reward. The grid was then darkened and the bears were to respond by indicating the location of the light associated with the reward in order to be reinforced and receive the food reward. Both pandas tested were capable of learning the task, indicating some evidence of spatial working memory in bears (Perdue et al. 2009).

Zamisch and Vonk (2012) employed a spatial memory task using baited locations within the enclosure of four adult, captive-raised American black bears to investigate their capacity to recall the locations of baited sites. The experimenters set out with the goal of using eight possible sites with four sites baited. This number was reduced to four with two sites baited for two of the three experiments conducted to reduce memory load and task complexity. They were interested in several factors that could impact recall, including time delay between learning and recall, the impact of competition through the influence of a knowledgeable foraging partner. It was predicted that, as the time between learning and recall increased, fewer sites would be recalled. Additionally, search strategies were investigated with the prediction that there would be some form of systematic search strategy that emerged (e.g., minimizing distance to the baited sites by bypassing closer, unbaited locations during the recall test). It was also of interest, in the knowledgeable partner condition, to see if the bear who had experience with the sites during the learning phase changed their behavior in any way when there was competition (e.g., using a more systematic search strategy to increase probability of obtaining food) (Zamisch and Vonk 2012).

Overall, it was found that the bears did not forage efficiently by first approaching baited sites. Only one of the four demonstrated that if the same sites are repeatedly baited over several sessions (rather than changing each session), she was capable of bypassing unbaited sites for baited sites that were a longer distance from the start

point. This capacity, however, was not clearly demonstrated in the other subjects (Zamisch and Vonk 2012). Vonk et al. (2015) demonstrated similar findings in grizzly bears, who demonstrated no evidence of learning as a result of either spatial or visual cues. It would, however, be problematic to draw the sweeping conclusion that bears do not possess spatial working memory based only on the results of these experiments. A major limitation of any study done in captivity is the lack of ecological pressures that could drive cognitive development. Bears in captivity have a limited range due to the constraints of their enclosures in comparison to their wild counterparts. As Zamisch and Vonk (2012) indicate, it could be that the total size of the bears' enclosure in this experiment likely represents one medium-large food patch in the wild. This is due to the fact that there is no need to search efficiently when little energy is required to search all possible sites. Additionally, there are no real pressures to forage for food in captivity as it is freely given to them, usually in a centralized location. These ontological (developmental) factors could impact the expression of spatial memory skills (Tarou 2004; Zamisch and Vonk 2012). As with most work done in captivity, replication with wild populations and in a wide variety of captive settings is vital to fully understanding this capacity in bears.

An important aspect of spatial memory is the capacity for object permanence (objects continue to exist if no longer in sight) and short-term memory (STM). It would appear that one of the shortcomings of the bears in Zamisch and Vonk's (2012) study was the inability to hold the spatial locations in their minds after a delay, an ability that is made possible via STM. To understand bears' ability to follow the locations of invisible objects, Hartmann et al. (2017a) tested Indian sloth bears (*Melursus ursinus*) and Bornean sun bears (*Helarctos malayanus euryspilus*) on three traditional spatial cognition tasks. The first task measured basic object permanence in a task, also known as the "shell game", used with both human children and a wide variety of nonhuman animals. In the simplest form of this task, two inverted cups are placed in the view of the subject. A food



reward is shown to the subject then hidden, while the subject is watching, under one of the two cups. The subject is then allowed to make a choice to indicate where they think the food was hidden. Both species made the correct choice at above chance levels, so it was determined they possessed object permanence. A similar study was conducted with sloth bears using a three choice paradigm and holes in a large log to increase ecological validity, mimicking extractive foraging. The bears performed above chance only when allowed to search immediately or when provided with acoustic cues but not after relatively short delays, leading the authors to conclude that they had object permanence but poor STM (Amici et al. 2017).

STM was measured by Hartmann et al. (2017a) in the two species previously described using a spatial transposition task called the visible displacement task. This task measures the spatial transposition skill of rotation and involves two different degrees of transposition: 180° and 360°. In the 180° transposition, task, two inverted cups are placed on a tray in front of the animal. Food is then hidden under one of the two cups while the animal watches. After the food is hidden, the experimenter then rotates the tray 180°; therefore, the baited location is on the opposite side of the tray. In order to be successful, the animal must have followed the baited cup to its new spatial location and recalled that when given the opportunity to choose during the test. On this task, the sloth bears and only one of the sun bears were successful, indicating that the ability to follow 180° rotations, while more challenging than no transposition, is possible in these groups and that they have the STM capacity to hold spatial information in their minds during these movements (Hartmann et al. 2017a). Further work is needed to reconcile their findings with those of Amici et al. (2017).

Lastly the researchers introduced a 360° rotation task, which included both a reverse and an orbital rotation. In the reverse rotation, the two cups were rotated 180° as in the previous experiment, but then rotated back to their original positions by moving them in the opposite direction by 180°. The orbital rotation rotated the baited cup

180° then continued the path in the same direction until the bait was back in its start position. Only the sloth bears were tested on this experiment, but they were successful in recalling the location of the bait after both the reverse and orbital rotations (Hartmann et al. 2017a). Taken together, these results provide support for the assertion that bears possess the base requirements for spatial memory, despite other bear species not consistently demonstrating other types of spatial memory (e.g., Vonk et al. 2015; Zamisch and Vonk 2012). Bears appear to outperform domestic dogs in the 180° transposition task as dogs, when given a three-choice task, were not consistently successful at following the 180° side rotation that resulted in the bait ending on the opposite side to its start position (Broadway et al. 2017). Perhaps domestication impacted dogs' abilities in comparison to the ecological pressures experienced by bears, despite the two groups having the largest brain to body size ratio of all other mammalian carnivores (Benson-Amram et al. 2016).

**Tool Use and Problem Solving** Tool use was long believed to be restricted to humans, then extended only to certain great apes, like chimpanzees. However, our knowledge of tool use capabilities in nonhuman animals has grown vastly over the past few decades, expanding to many species of mammals outside of the primate order (e.g., otters, elephants, and dolphins) as well as several bird species (e.g., crows and finches) and even invertebrates like octopi. One of the issues within the study of tool use is that the definition of what constitutes tool use is not always agreed upon by researchers. A relatively basic agreed upon definition of tool use includes the use of an object external to oneself to manipulate another object (e.g., an otter using rocks to pry open a bivalve) or something on one's own body (e.g., a person using a brush to comb their hair, Deecke 2012).

Bears, however, are understudied in the area of tool use. There is some evidence of tool use in captive brown bears (Waroff et al. 2017), along with a reported failure in sloth bears in a similar

paradigm where bears had to maneuver an object under a hanging food reward to retrieve it (Amici et al. 2017). One observation from a wild Alaskan brown bear (*Ursus arctos*), provides an example of what appears to be spontaneous tool use when a subadult male brown bear was documented picking up a rock with barnacles on it, grasping it with its paws and claws, then using it to rub its face. This behavior was repeated three times with different rocks during the same observation period. It was suggested that the bear was using the barnacled rock as a grooming aid after consuming oily remains of a whale (Deecke 2012). Observations such as this suggest that bears may be capable of tool use, as it is currently defined in the literature (see the Bear Management chapter for more information on wild ursid behavior).

As with tool use, the ability to flexibly solve problems has also been heralded as a sign of advanced cognitive evolution. Benson-Amram et al. (2016), argued that it is relative brain size that is related to problem solving, with those species that have larger relative brain to body sizes possessing more sophisticated cognitive skills in comparison to those with smaller relative brain to body sizes. This hypothesis, in essence, links relative brain size with intelligence. Within most taxa, there is a wide variety of relative brain to body size ratios, with some having larger and some having smaller ratios. The Carnivore order fits that description, with Ursids and Canids having the largest relative brain to body size and Viverrids (civets and genets), Hyaenids (hyenas), and Herpestids (mongooses) having the smallest brain to body size ratios of the order (Benson-Amram et al. 2016).

Given that information, it could be predicted that, given a problem-solving task, species with large relative brain sizes should outperform species with smaller relative brain sizes. If, however, sociality impacts the development of these skills instead, then species with higher degrees of sociality (e.g., hyenas) should outperform species that are less social (e.g., bears), despite their differences in relative brain size. Problem solving ability can be measured in many ways. Benson-Amram et al. (2016) used a puzzle box that had a

slide-bolt secured door that had to be pulled back to release the door and allow for retrieval of the food reward inside the box to test 140 individuals representing 39 species within the order Carnivora. They accommodated for the wide variety of sizes of differing species by creating a small and a large box. Success was defined as opening the door by any means (e.g., sliding the bolt or moving the box until the door came open). It was found that the most successful groups, overall, were Ursids, Procyonids (e.g., raccoons, coatis, and kinkajous), and Mustelids (e.g., otters, ferrets, and badgers). Herpestids were the least successful group at opening the puzzle boxes. Their analyses showed that other factors (e.g., sociality) were not related to success in opening the box; only relative brain size showed statistical significance as it related to likelihood of success, with species with larger relative brain to body sizes succeeding that the task more often than those with smaller relative brain sizes, supporting their hypothesis (Benson-Amram et al. 2016).

However, it is important to note a few things when examining these conclusions. One is that this study narrowly defined sociality as living in large, complex social groups throughout development. It neglects the concept of delayed ontogeny, which many of these species exhibit, and has been linked to providing the time for the development of larger brains as well as opportunities for social learning. Therefore, the development of a larger relative brain size is confounded with social factors, like delayed ontogeny. Additionally, the authors used a narrow definition of success by using a dichotomous measure - either opening or failing to open the box. It is possible that other outcomes, such as time it took to solve the task or persistence, might have provided more inclusive measures of problem-solving abilities. Benson-Amram et al. (2016) also failed to account for ecological factors, such as use of extractive versus non-extractive foraging and diet, in their analyses, leaving room for many other possible contributing mechanisms that impacted success or failure (Vonk 2016). While this study was the first of its kind in terms of breadth of species, more work is needed to conclusively determine the mechanisms at play.

**Self-awareness** Thus far, we have focused on aspects of physical cognition. Unfortunately, there is very little work addressing social cognition in the relatively solitary ursids. However, there is at least one study investigating mirror self-recognition (MSR), or the ability to recognize oneself in an image created by a mirror. MSR develops over time in humans, with the human infant first lacking the ability, but with time and experimentation, they learn that what they see when they look in a mirror is not a conspecific, but their own reflection. Consistent with hypotheses outlined above, species that are both highly social and have larger relative brain size have tended to demonstrate MSR when tested via the mark test. The mark test involves placing a mark of some type (e.g., paint) on the individual's face, or other area not easily seen without the assistance of a mirror, and then providing the opportunity for the individual to investigate their reflection in a mirrored surface. Researchers then record how the subjects interacts with the mirror and watch for any mark-directed behaviors, indicating that the subject recognizes that the reflection in the mirror is themselves and the mark is an anomaly to their typical appearance. In a study conducted with giant pandas (*Ailuropoda melanoleuca*) using the mark test, it was shown that the pandas fail to recognize the image in the mirror as themselves, instead responding in a manner that indicated viewing the image as a conspecific, with some acting in an aggressive manner upon first inspection of the reflection (Ma et al. 2015). This is similar to the reaction of many primate species including monkeys and prosimians (Paukner et al. 2004).

A major criticism of all MSR tests with non-humans is the ecological validity of a mirrored surface. In nature, coming across a clear pool of water is likely to be the only time an animal might encounter their own reflections, rendering the ability to recognize their reflection in a mirror unnecessary or irrelevant. It is possible that, in these cases, they simply ignore their reflections entirely as they are missing other perceptual cues (e.g., olfactory or auditory) to indicate the presence of a conspecific and have no need to be

concerned with the reflection (Ma et al. 2015). However, to date, giant pandas are the only bear species to be tested on MSR, so conclusive evidence is not present for the lack or presence of MSR in bears. However, it is also possible that visual cues relating to one's own reflection is not salient to the majority of wild animals in the context of their evolutionary history, as was suggested by Horowitz (2017) who demonstrated that dogs are able to differentiate between their own odor and that of another dog, and investigate their own scent signature for a much longer period of time if it has been altered. Thus, according to Horowitz, there is a need to determine self-awareness in a biologically relevant manner. This has not been investigated in ursids, to our knowledge. However, this approach does have interesting implications for this area of study. It is possible that the research community simply needs a new way to ask this old question, that is more biologically relevant to the target species.

**Conclusions Regarding Basic Research on Bear Cognition** The work presented in this entry represents only a summary of key findings regarding our current knowledge on bear cognition. However, the simple fact remains that more work is needed to fully elucidate the inner workings of the ursid mind. The vast majority of what we know about bear cognition has been driven by a few individuals of approximately five different species. Most of the work discussed here, has been done with animals born and raised in captivity. We are well aware of the potential positive and negative impacts captivity can have on animals. In order to truly understand the species, we must work to overcome the challenges and test wild populations.

## Cross-References

- [Bear Life History](#)
- [Bear Sensory Systems](#)
- [Bear Management](#)
- [Bear Navigation](#)
- [Carnivora](#)
- [Numerosity](#)

- Problem-Solving
- Tool Use
- Visual Self-Recognition

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## Bear Communication

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## Synonyms

Olfaction; Scent; Signals; Ursid communication; Vocalization

## Introduction

There are eight extant species of bear in the order Carnivora. Bears inhabit a wide variety of habitats on every continent except Africa, Australia, and Antarctica and are largely solitary, although they may temporarily aggregate at a concentrated food source or during breeding. Bears employ four primary modalities of communication: olfactory, visual, auditory, and gustatory signaling. Of these, olfaction seems to be the most important and the best-studied across all eight species of bear. Scent marking uniquely allows animals to communicate remotely, over time, with multiple other animals, thus allowing them to avoid potentially energetically expensive physical conflict. Solitary species like bears may benefit from advertising their location and reproductive status to expedite mate selection during the breeding season. Throughout the rest of the year, communication of this information could facilitate temporal avoidance by conspecifics, reducing competition for limited resources. The sensory systems and communication



modalities of the brown bear (*Ursus arctos*), American black bear (*Ursus americanus*), and the giant panda (*Ailuropoda melanoleuca*) are the most researched. Minimal research has been conducted on communication in the other five species.

## Olfactory Communication

Although bears are generally regarded as having an extremely acute sense of smell, it is difficult to quantify olfactory sensitivity, as the olfactory response to a stimulus is affected by numerous factors. Odorant detection may be altered by airflow to the olfactory region, which can change due to obstruction of the airway, differences in sniffing behavior, or swelling of the epithelial cells due to increased blood flow. Odorant binding to receptors may be affected by mucosal viscosity, physical and chemical properties of the odorant, and the presence of airborne particles like dust and bacteria. Experimental quantification of ursid olfactory capabilities remains a largely unexplored area of research.

### Rub Trees

One of the main ways that ursids communicate via olfaction is by marking rub trees by rubbing their bodies against them or by clawing or biting the bark of the tree, often leaving fur, frayed bark, and scars on the tree trunk (Burst and Pelton 1983; Taylor et al. 2015). Rub trees may be used for generations (Schaller 1985). Rubbing behaviors may deposit secretions from sebaceous and apocrine glands, while clawing may leave scent from pedal glands. Biting may deposit saliva, and urination and deposition of anogenital gland secretions (AGS) may also be important forms of communication (Clapham et al. 2013). All species except polar bears (*Ursus maritimus*) have been observed using rub trees (Burst and Pelton 1983; Clapham et al. 2013; García-Rangel 2012; Laurie and Seidensticker 1977; Schaller 1985). Scent-marking behaviors performed at rub trees vary with species, age, and reproductive status (Clapham et al. 2014) but typically include two or more of the following actions, often in the order listed: (1) investigating the tree; (2) rubbing the head, neck, and/or

shoulders on the mark tree; (3) rubbing their sides against the tree while in a quadrupedal stance; and (4) turning away from the tree bipedally to rub their backs and necks (Clapham et al. 2014; Taylor et al. 2015). Trees may be damaged by clawing, biting, and intense rubbing, sometimes resulting in tree breakage and death (Burst and Pelton 1983).

Scent marking is not without energetic cost. The time and energy spent marking could detract from other activities, like foraging and reproduction (Nie et al. 2012). To minimize this cost, bears must select objects that will readily attract the attention of the signal receiver. Rub tree selection varies between species. A study conducted on spectacled bear (*Tremarctos ornatus*) scent-marking behaviors showed that bears mostly marked live trees but occasionally used fallen trees, dead standing trees, or wooden poles as mark sites. Many (38.8%) of the mark trees were aromatic, and 46.9% were a food source for spectacled bears (Filipczykova et al., 2016;). Brown bears may prefer coniferous trees; exuded sap may help preserve scent marks (Nie et al. 2012). A 6-year study of 116 trees in Yellowstone found that brown bears preferred to mark trees along trails, usually on the side facing the trail. The average maximum height of rub marks was 1.7 m. Only 9% of trees bore claw or bite marks. Most marking occurred between late May and July, during peak breeding season and the molt (Green and Mattson 2003). American black bears may mark trees, telephone poles, and signposts. In a study in the Great Smoky Mountains National Park, marks were most concentrated at 1.6–1.7 m off the ground, usually on the side of the tree facing the trail. Bear hair or mud were occasionally adhered to sap or bark. Mark trees that were not associated with a man-made trail were adjacent to a game trail 74% of the time. Some rub trees were up to 15 m away from the game trail, with a clearly defined path leading to the tree (Burst and Pelton 1983). Spectacled bears marked trees on average 1.7 m from ground level, using trees adjacent to bear trails and marking the sides of the trees that face the trail (Peyton 1984). The function of scent marking in this species is not yet known. However, when spectacled bears were detected via camera trap, the probability that a different bear would appear at the same site was elevated for several days, implying some



form of chemical communication. In addition to facilitating intraspecific communication, rub trees may also function interspecifically: American black bears used rub trees less after brown bear use (Shaffer 1971).

### Pede Marking

Pede marking is the process by which bears scent mark the ground by grinding their feet into the substrate, typically before or after using a rub tree. One study of black bear rub tree use in California found that black bears pede marked exclusively after scent marking a rub tree, with pede marking occurring in a third of rub tree uses (Taylor et al. 2015). Brown bears have eccrine glands on the footpads and sebaceous and apocrine glands on metatarsal/metacarpal and interdigital skin (Sergiel et al. 2017). Brown bears also sometimes engage in pede marking near rub trees (Sato et al. 2014), grinding and stomping their paws into the ground. At times these marks are clearly visible as depressions in the ground near the tree, but sometimes substrate consistency renders these scent marks invisible to a human observer (Clapham et al. 2013).

In contrast to black and brown bears, in which pede marking is often secondary to use of a rub tree, polar bears inhabit sea ice for much of the year and lack access to similar fixed marking features. In the absence of rub trees, pede marking may be a much more important form of scent marking for polar bears. Polar bears have apocrine and sebaceous glands on interdigital skin. In tests of 26 adult polar bears, males spent more time investigating interdigital scent swabs from females than from males. Male bears investigated samples from females in estrus significantly more than samples from non-estrus females during the spring breeding season and were more likely to exhibit flehmen behavior, which transfers scent to the vomeronasal organ to assess sex and sexual receptivity of the signaler (Owen et al. 2014). During the breeding season, male polar bears find mates by following females' tracks (Molnár et al. 2008), sometimes traveling 100 km or more, often while fasting for days at a time (Stirling 2011). Given the low density of polar bear populations and the immense energetic cost of such pursuit, the ability to identify estrus females

by pedal scent may be critical to a male's reproductive success. Interdigital scent glands similar to those found in polar bears were not found in sloth bear (*Melursus ursinus*) pedal skin samples (Patil et al. 2016). Additional research is needed to determine whether other species possess specialized pedal glands for marking.

### Anogenital Secretions, Urine, and Feces

Giant pandas (Yuan et al. 2004) and brown bears possess anal glands that produce secretions that may be an important form of olfactory communication in these species. There is no consensus as to which, if any, of the other six bear species has anal sacs (Rosell et al. 2011). Researchers examine how bears glean information from AGS by comparing gas chromatography results from AGS samples from different classes of bears (e.g., male or female) and looking for differences in the relative abundance of various substances and for substances that are present in one group but absent in the other. Key components of AGS should have high molecular weights. This lack of volatility ensures that scents remain where placed for as long as possible.

Brown bears' large home ranges preclude frequent scent marking, so long-lasting AGS marks would be energetically advantageous (Rosell et al. 2011). Adult brown bear AGS is not waxy like that of the giant panda (Taylor et al. 2015). It is gray or black, foul-smelling, and claylike, with male AGS tending to be darker than female AGS. Anal sacs are paired and open at the cutaneous zone of the anal canal. Sex differences were found in the relative abundance of five substances (Rosell et al. 2011). Therefore, it is possible that brown bears can distinguish the signaler's sex from AGS deposits.

Giant pandas are solitary but their home ranges overlap with those of other pandas of both sexes. Additionally, female pandas enter estrus once a year and are receptive to mating for only 24–72 hours. Therefore, chemical communication is essential to avoiding conflict and attracting mates. Pandas do not respond to urine after it is a few weeks old, but they continue to react to AGS months after collection (Swaigood et al. 2000; White et al. 2002). Urine and AGS differ in

chemical composition and may relay different information to the receiver. A gas chromatography and mass spectrometry study of AGS from 24 adult and subadult pandas of each sex indicated that these waxy secretions consist mostly of steroids and saturated and unsaturated fatty acids. Comparisons of each age-sex class revealed that age and sex may be signaled by the relative amount of each compound rather than by the presence or absence of specific compounds. The nonvolatile components of AGS may make it ideal for leaving scent marks that last for extended time periods or that serve as a delayed message (Yuan et al. 2004). There is high individual variation in the relative quantity of AGS components, as well as in the types of compounds that are present; it is possible that each panda has its own distinctive AGS signature that makes it identifiable to other bears (Zhang et al. 2008).

Male giant pandas scent mark year-round, whereas females primarily scent mark during the breeding season (Swaigood et al. 1999; Nie et al. 2012). Additionally, males spend equal amounts of time investigating male and female scent samples, while females are more interested in male scents. Therefore male scent marking likely has a variety of functions, whereas female scent marking may be exclusively related to reproduction (Swaigood et al. 1999). Males mark significantly more when exposed to female odors than when presented with male scents, possibly to increase the likelihood that their marking will be detected by the female (Swaigood et al. 2000). Giant pandas deposit urine using four different postures: squatting, quadrupedally backing into a vertical surface, urinating with a single leg raised, and while performing a handstand (White et al. 2002). This handstand posture may be used in part to place urine at nose height. Pandas rub themselves against the marking surface vigorously while AGS marking but not while urine marking (Nie et al. 2012). Females commonly squat to urinate, while the handstand posture is almost exclusive to adult males and may serve as an indicator of body size and competitive ability to conspecifics. Pandas of all age-sex classes spent more time investigating adult male urine placed 1 m above ground level than when the same urine

was presented at ground level or when female urine was left in the same locations. Pandas, especially subadult males, also stayed farther away from the elevated male scent mark, possibly to avoid a potentially costly interaction with a large, more dominant animal (White et al. 2002). Captive adult males performed the handstand posture less frequently when in another animal's pen than when they found another animal's scent in their own enclosure. Given that pandas are quasi-territorial, this bolsters the conclusion that handstand urination is a range-marking behavior. An intruding animal would avoid provoking conflict with the resident by minimizing marking, whereas resident pandas would be motivated to reinforce their scent markings when confronted with an unfamiliar male's scent (Swaigood et al. 2000).

Giant pandas scent mark with AGS in addition to urine, typically while following ridgelines (Nie et al. 2012; Schaller 1985). A 1-year study of 6.9 km of such ridges found that 11.5% of eligible trees within 1.5 m of the trail bore panda scent marks (urine, AGS, or both). Pandas chose trees with the roughest bark for urine marking and preferred rough-barked, moss-free trees for AGS marking. It is possible that extremely rough-barked trees were selected for urine marking to prevent the urine from flowing down the tree or being quickly removed by rainfall. Of the 2186 available trees, 219 were marked with AGS, 34 were marked with urine, and 5 trees bore both marks. 38.3% of mark trees were remarked at least once. Most marks were deposited in February during the main breeding season or in November when a second breeding cycle sometimes occurs (Nie et al. 2012).

Olfactory cues can alter male sexual behavior. In a study of 11 male giant pandas, scent (AGS and urine on fir bark as well as feces) from one or multiple other male pandas was placed in each panda's home pen during the breeding season; control group males were presented with unscented fir bark and their own feces. Females in estrus were housed in alternating enclosures between males, and each male was randomly assigned to one of the three treatment groups every 2 days. Males exposed to odors from other males spent more time investigating their

environment and observing, following, and sniffing females. No differences were found in scent-marking behaviors, bleating, or footscraping. The increase in most female-oriented behaviors and the lack of change in territorial behaviors support the observation that wild male pandas pursue females and fight competing males; given the brevity of the female receptive period, mate-guarding is likely a more successful strategy than territorial behaviors (Bian et al. 2013).

Social context alters panda reproductive behavior during the breeding season. Adult female pandas typically signal most prolifically during peak estrus, but females housed in an enclosure between those of two other female bears signaled less than bears housed with at least one male neighbor or with no neighbors. Similarly, among captive female sun bears (*Helarctos malayanus*), 70% of those housed with a male bear entered estrus at least once per year, while 66.7% of females housed alone or with another female failed to cycle (Frederick et al. 2013). The presence of other females may inhibit signaling behaviors, allowing the focal female to conserve energy by not broadcasting to inappropriate receivers (Owen et al. 2016).

Bears may use olfactory cues to avoid inbreeding. Female panda cubs that had been raised with their mothers for 6 months, then reared separately for 5–6 months, spent more time investigating urine and body odor from unfamiliar adult female bears than they did examining their mother's scents. Mother bears also spent more time inspecting scents from unfamiliar age-matched cubs than they spent on odors from their kin. This suggests that pandas remember the scents of their kin and/or that they use self-referent phenotype matching (the “armpit effect” – comparing their own phenotype to a new odor) to identify unfamiliar bears. Female pandas disperse upon reaching maturity, while males remain closer to their mother's home range. It is possible that females use scent recognition to avoid female relatives in selecting their new home ranges, thus avoiding inbreeding with their father, as male home ranges overlap those of their mates (Gilad et al. 2016). One study of panda urine and AGS found that kinship odors – compounds present in urine and AGS that

correspond to genetic relatedness – were detectable only in male scent marks during the breeding season (Liu et al. 2008).

Male American black bears use olfactory cues to assess a female's receptivity to mating. Gonzales et al. (2013) found that semi-free ranging males sniffed the female's urogenital region in over 80% of interactions that led to the male mounting the female. Males also smelled urine and feces from females, often exhibiting a flehmen response that suggests vomeronasal involvement. Males mated with females most frequently when females were in peak physiological estrus. Additionally, during the Gonzales study, male bears abandoned mounting attempts in 53% of unsuccessful encounters, providing further evidence that males can detect a female's receptivity to mating. Eight of the 11 females studied displayed temporally synchronized estrus; while this is usually not observed in wild bears, it could indicate that females are able to detect conspecific reproductive status via chemosensory cues (Gonzales et al. 2013). In breeding pairs of brown bears, males often smell the female's genitalia, which may offer scent cues as to her reproductive status (Steyaert et al. 2012).

## Visual Communication

Ursids are often said to have poor visual acuity, but little research has been done to confirm this assertion. An American black bear successfully discriminated objects of differing shapes and sizes, even when the positive stimulus had been rotated and when the background color was changed (Bacon 1973). Some ursids have color vision. Giant pandas can discriminate green and red from gray. Females can also see blue; male bears have not been tested (Kelling et al. 2006). L-cones and S-cones are present in polar and brown bears, indicating that these species may have dichromatic color vision (Peichl et al. 2005). American black bears have at least some hue discrimination; their ability to tell blue and green from gray indicates that they have more than monochromatic vision (Kelling et al. 2006).

Visual signals only last as long as the sender is signaling. In bears, visual signals often take the form of body postures, which may serve as ritualized displays that allow individuals to avoid injury or behavioral displays. For example, male American black bears posture during the breeding season, sliding their front paws smoothly over the ground with stiffly held front legs in the presence of females in estrus or other males (Boone et al. 2003). Bears may charge other animals when threatened and may or may not make physical contact; sloth bears may charge or chase unfamiliar bears or other animals when they approach too closely (Joshi et al. 1999). American black bears may also lunge forward, simultaneously swatting the ground with their paws and exhaling explosively (Jonkel and Cowan 1971).

Behavioral displays are very important to the reproductive process of giant pandas. In the wild, as a female panda enters estrus, multiple males gather to court her. She avoids them until she is ready to breed, sometimes by climbing a tree. Captive male bears exhibited relatively constant courtship behaviors toward females throughout the estrus cycle, while female pandas switched from aggressive displays to increasingly proceptive and receptive behaviors as they approached peak estrus. Aggressive behaviors included paw swatting and charges in addition to threatening or defensive vocalizations; behaviors exhibited by females at peak estrus included approaching the male, walking backward, presenting the hindquarters to the male, and lordosis. Only females showed mixed aggressive and affiliative behaviors – i.e., alternating aggressive and affiliative vocalizations or making sounds containing elements of both types of vocalization. As this behavior was seen frequently in female pandas near peak estrus, it may be a signal to males that the female is nearly ready to mate (Owen et al. 2013). Non-behavioral visual cues may also contribute to the courtship process. As female American black bears enter estrus, their vulvas become engorged and inflamed. Males may visually assess the vulva of a female to determine reproductive status (Gonzales et al. 2013).

Spectacled bears have spectacle-like, often asymmetrical markings on their faces that can extend down the animal's chest. However, these

markings are not reliable indicators of age, sex (García-Rangel 2012), or kinship. In this species the nose becomes pinker as the bear ages (Van Horn et al. 2015), so nose pinkness could signal an individual's age to other bears, although this has not been confirmed experimentally. It is possible that spectacled bears learn individual patterns of markings to identify familiar bears. Pandas can discriminate between panda face-like masks, indicating that color patterns may facilitate individual recognition (Dungl et al. 2008).

## Auditory Communication

Sound can transmit complex signals long distances quickly, although signal persistence is low, and this type of signal is not necessarily easy to locate. As bears are generally solitary, non-territorial mammals, they usually use auditory signals at close range. One unusual manner of vocal communication exhibited by bears is “humming,” a sound produced mostly by cubs but sometimes by adults, generally in association with nursing, contentment (Kenny and Bickel 2005; Derocher et al. 2010), and sucking (Peters et al. 2007). Sun bear cubs hum, squawk, croak, and whine (Hall and Swaisgood 2009). Giant pandas are the only ursid that does not hum. Humming consists of a bear making short, single, usually monotonous sounds every 0.1 s punctuated every 3.5–10 s by inhalation (Peters et al. 2007). Cubs also produce screaming or crying vocalizations, which are often preceded or followed by sounds associated with discomfort (Kenny and Bickel 2005; Van Gessel 2015). Van Gessel (2015) observed that screaming seemed to stimulate captive mother polar bears to respond to their cubs; a dying cub vocalized less and less and thus received less care, which may have contributed to its death. Because disturbance may cause hibernating bears to abandon their dens, wild mother bears and cubs are usually studied only after they emerge from the den. Therefore, most studies of denning mothers and cubs are conducted on captive animals and may not be representative of wild animals.

Sloth bears may growl when threatened by another bear (Joshi et al. 1999). They roar when

fighting other bears, and a scream-like call is emitted during fights. Cubs yelped when separated from their mothers, prompting their mothers to return to them; treed females with their cubs on the ground made a grunt-whicker. Sloth bears huff, possibly as a warning sound. Sloth bears also make chuffing-like sounds, often while retreating from a disturbance. Bears foraging for termites and other invertebrates make characteristic sucking and blowing noises that may advertise the bear's location, facilitating avoidance of other animals (Laurie and Seidensticker 1977). Brown bears have also been described as huffing, growling, and roaring, as well as woofing and bawling (Egbert 1978).

Courting pairs of American black bears used several modes of auditory communication. Courting males quickly blew air through their mouths to produce sound when another male approached a female in estrus, apparently to deter the newcomer. Both males and females made clicking and popping sounds with their jaws and throats during courtship (Boone et al. 2003). Giant pandas also use vocalizations to communicate during the breeding season. Pandas may be able to distinguish males from females using the formant frequencies in the other panda's bleat or the interaction of the formant with other elements of the call; low formants correspond to large body size and therefore to male pandas (Charlton et al. 2010b). Each panda's bleat is highly acoustically distinctive and may be used in individual recognition or possibly in distinguishing kin from unrelated bears (Charlton et al. 2009b). Non-estrus female pandas primarily rely on amplitude modulation to tell bleats from different males apart (Charlton et al. 2009a). Fertile females produce harsher, longer chirps than pre-fertile females, and males approached and remained near playback speakers significantly more after hearing calls from fertile females than after hearing calls from pre-fertile females (Charlton et al. 2010a). This distinctive chirp vocalization may be unique to the giant panda (Schaller 1985). Estrus females vocalized more than non-estrus females upon encountering male scents, and, similarly, males vocalized more in response to estrus female odors than to scent marks from nonreceptive females

(Swaigood et al. 2000). However, another study of adult pandas (10 females and eight males) found that, during the breeding season, males increased marking behavior in response to a playback of bleats from a female in estrus. Females in estrus did not alter marking behavior upon hearing recorded bleats from a male during the breeding season. In this study neither sex was found to alter its vocal behaviors in response to bleat playback (Xu et al. 2012). These studies all featured captive animals that may have already been somewhat familiar with one another; further study of wild pandas is necessary to confirm these results.

## Gustatory Communication

Taste may be an important form of communication for bears during the breeding season. Male American black bears licked (and sniffed) females' urogenital areas during courtship, apparently to assess the female's reproductive status (Boone et al. 2003). Courting males also licked urine and feces deposited by females, sometimes while the female was urinating (Gonzales et al. 2013). Both male and female giant pandas lick scent deposits from conspecifics. Males licked female chemosensory stimuli more than they did male stimuli, which may indicate that they are using nonvolatile chemical components of the scent to assess female reproductive status (Swaigood et al. 2000).

## Conclusion

Ursids use visual, auditory, gustatory, and olfactory signaling to communicate with other animals. Olfaction seems to be the most important channel through which bears signal. Olfactory signals differ between species and include the use of rub trees, pede marking, urination, defecation, and AGS, which may allow bears to convey information about sex, reproductive status, and location to other animals. Ursids may also use taste to examine scent deposits. Visual signals include diverse postural displays that allow bears to communicate physical and reproductive fitness from a distance.



Bears make a variety of vocalizations which can be used as threats during agonistic encounters, to advertise sexual receptivity, or for communication between a mother bear and her cubs. The communication modalities of brown bears, American black bears, and giant pandas have been relatively well studied, but further research is needed in the remaining five species, and experimental manipulations of captive animals must be validated by studies of wild bears.

## Cross-References

- [Bear Cognition](#)
- [Bear Diet](#)
- [Bear Life History](#)
- [Bear Locomotion](#)
- [Bear Morphology](#)
- [Bear Navigation](#)
- [Bear Sensory Systems](#)
- [Canine Communication](#)
- [Carnivora](#)
- [Communication](#)
- [Feline Communication](#)
- [Mustelid Communication](#)

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## Bear Diet

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## Synonyms

### Feeding habits

## Introduction

The variety in the diet of the eight bear species reflects their wide-ranging habitats, from the desert to the Arctic and from the coast to the mountains. Although bears are omnivores, there is a dietary range from mostly herbivorous (e.g., the giant panda (*Ailuropoda melanoleuca*)) to mostly carnivorous (e.g., the polar bear (*Ursus maritimus*)) and from generalists (e.g., the brown bear (*Ursus arctos*)) to specialists (e.g., the giant panda). Nutritional content of the diet influences distribution, population density, foraging strategy, body mass, survival, and reproduction (Stirling and Derocher 1990; Stringham 1990; Welch et al. 1997; Hilderbrand et al. 1999a, b; Rode and Robbins 2000; Robbins et al. 2007; Schwartz et al. 2010; McLellan 2011; Mowat et al. 2013). Although all bear species will consume human foods (i.e., garbage, agriculture, livestock) opportunistically, this entry focuses on the natural diets of bears.

## American Black Bear (*Ursus americanus*)

The diet of the American black bear varies by sex and age class. They also vary seasonally and geographically reflecting food availability. Across the majority of their range, plant matter is the primary diet item of American black bears with the remainder of their diet being composed

of animal matter, primarily insects (e.g., beetles (Coleoptera) and ants (Formicidae)), small mammals, and salmon (*Oncorhynchus* spp.) (Graber and White 1983; Inman and Pelton 2002; Fortin et al. 2006; Baldwin and Bender 2009; McLellan 2011). Hard (e.g., acorns (*Quercus* spp.), beechnuts (*Fagus* spp.), and hickory nuts (*Carya* spp.)) and soft mast (e.g., huckleberries (*Vaccinium* spp. and *Gaylussacia* spp.), blackberries (*Rubus* spp.), cranberries (*Oxycoccus* spp.), etc.) species are the highest caloric plant matter consumed by American black bears (Graber and White 1983; Inman and Pelton 2002; Baldwin and Bender 2009). Other plant matter consumed includes grasses (Poaceae) and herbaceous leaves and stems (Graber and White 1983; Inman and Pelton 2002; Baldwin and Bender 2009). Coastal black bears consume a higher level of meat, in the form of salmon, except where they are largely excluded from salmon use by sympatric brown bears (Jacoby et al. 1999; Belant et al. 2006; Fortin et al. 2006).

## Andean Bear (*Tremarctos ornatus*)

The diet of the Andean or spectacled bear is mostly herbivorous, although the importance of different plant species varies across their range in the Peruvian Andes, from the scrub desert to the tropical forest. The succulent hearts of bromeliads (Bromeliaceae) are the primary food of Andean bears when and where fruits are unavailable (Peyton 1980; Suarez 1988; Troya et al. 2004). Fruits are the second most important dietary item, including figs (*Ficus* spp.) and fruits of motilón (*Hyeronima macrocarpa*) (Peyton 1980; Troya et al. 2004). In the driest areas of their range, cacti (Cactaceae) are a food source and serves as an important source of water (Peyton 1980). Other plants commonly consumed include palm (Arecaceae) frond petioles, orchid (Orchidaceae) bulbs, the cortex of the pasallo tree (*Bombax discolor*), and shoots of bamboo (*Guadua* and *Chusquea* spp.) (Peyton 1980; Suarez 1988). In addition, insects, rodents (Rodentia), ungulates, birds, and honey are occasionally consumed (Peyton 1980; Suarez 1988; Troya et al. 2004).

### Asiatic Black Bear (*Ursus thibetanus*) and Sun Bear (*Helarctos malayanus*)

The Asiatic black bear and the sun bear are omnivores and have similar diets despite competition between the two species because of their overlapping habitats. Both species depend heavily on fruits and insects; however, it appears that neither species is able to meet their nutritional requirements on insects alone (Wong et al. 2002). The primary dietary items of both species are fleshy (e.g., figs, berries, and drupes) and hard fruits (e.g., acorns and stone pine seeds (*Pinus* spp.)), when and where available (Huygens and Hayashi 2001; Hwang et al. 2002; Wong et al. 2002; Fredriksson et al. 2006; Koike 2010; Steinmetz et al. 2013). Insects are the second most important dietary item to both species, with the sun bear consuming more insects than the Asiatic black bear, primarily ants, beetles, and termites (Wong et al. 2002; Augeri 2005; Fredriksson et al. 2006; Koike 2010; Steinmetz et al. 2013). Sun bears and Asiatic black bears also consume other plant matter, including leaves, stems, flowers, and legume pods, and on the rare occasion meat, including birds, eggs, reptiles, fish, and small vertebrates (Hwang et al. 2002; Wong et al. 2002; Augeri 2005; Fredriksson et al. 2006; Koike 2010; Steinmetz et al. 2013). In addition, sun bears consume honey and occasionally earthworms (*Lumbricus* spp.) and mushrooms (*Fungi*) (Augeri 2005). Across the range of both species, the dietary intake of fruits and insects depends on availability, spatially and temporally.

### Brown Bear (*Ursus arctos*)

As the most widespread species of bear, the omnivorous brown bear exhibits great diet plasticity, varying between seasons and years and between and within populations from coastal Alaska to the Gobi desert (Servheen 1983; LeFranc et al. 1987; Elgmork and Kaasa 1992; Jacoby et al. 1999; Schwartz et al. 2003; Batsaikhan et al. 2004; Mowat and Heard 2006; Vulla et al. 2009; Edwards et al. 2011; Gunther et al. 2014). The variation between and within

populations depends on social dynamic, learned behavior, individual preference, and population density (LeFranc et al. 1987; Gunther et al. 2014). The importance of meat and other high-caloric foods, such as hard mast and fleshy fruits, varies across their range.

In North America, the importance of meat to brown bears varies between coastal and interior bears and within different interior populations. In the Greater Yellowstone Ecosystem, grizzly bears consume  $\geq 266$  species within 200 genera from 4 kingdoms (Gunther et al. 2014). Salmon is the primary diet item in coastal brown bear populations (Jacoby et al. 1999; Schwartz et al. 2003; Belant et al. 2006; Fortin et al. 2006; Mowat and Heard 2006). Coastal brown bears also consume other meat (e.g., moose (*Alces alces*)), grasses, forbs, and berries (Jacoby et al. 1999; Schwartz et al. 2003; Belant et al. 2006; Fortin et al. 2006). Meat, primarily caribou (*Rangifer tarandus*), moose, bison (*Bison bison*), elk (*Cervus canadensis*), and small mammals, is the primary food item for some interior population, such as the Arctic, Greater Yellowstone, and Northern Continental Divide Ecosystems (Jacoby et al. 1999; Mowat and Heard 2006; Schwartz et al. 2014; Teisberg et al. 2015). Other dietary items include insects (e.g., ants, yellow jackets (Vespidae), and army cutworm moths (*Euxoa auxiliaris*)), grasses, forbs, berries, and seeds (e.g., whitebark pine (*P. albicaulis*)) (Jacoby et al. 1999; Schwartz et al. 2003, 2014; Gunther et al. 2014; Teisberg et al. 2015; Senset et al. 2016). There are some interior grizzly bear populations, such as the Cabinet-Yaak Ecosystem and interior British Columbia, where meat is less available and diets consist of berries (e.g., huckleberries, chokecherries (*Prunus* spp.), and crowberries (*Empetrum* spp.)), grasses, forbs (e.g., dandelions (*Taraxacum* spp.), fireweed (*Chamaenerion* spp.), and cow parsnip (*Heracleum* spp.)), roots, tubers, seeds, and fungi (LeFranc et al. 1987; Jacoby et al. 1999; Schwartz et al. 2003; Mowat and Heard 2006; McLellan 2011). These populations still consume, albeit in smaller quantities, ungulates (e.g., moose and deer (*Odocoileus* spp.)), insects (ants), and small mammals (e.g., voles (*Microtus* spp.) and

pocket gophers (Geomyidae spp.)) (LeFranc et al. 1987; Jacoby et al. 1999; Schwartz et al. 2003; McLellan 2011).

In European populations, there is a latitudinal gradient of meat consumption, with meat being a primary dietary component of brown bears in northern populations (i.e., Sweden and Norway), with decreasing dietary importance toward the southern populations (i.e., Italy and Greece) (Vulla et al. 2009; Niedziałkowska et al. 2019). Meat is consumed as prey and carcasses in the form of ungulates (e.g., moose, wild boar (*Sus scrofa*), and deer), insects, and small mammals (e.g., voles and ground squirrels (Sciuridae spp.)) (Clevenger et al. 1992; Elgmork and Kaasa 1992; Batsaikhan et al. 2004; Paralikidis et al. 2010; Štofik et al. 2013; Ciucci et al. 2014; Senset et al. 2016; Niedziałkowska et al. 2019). The diets of southern populations primarily consist of fleshy fruits (e.g., berries, rose hips (*Rosa* spp.), kiwi (*Actinidia* spp.), and plums (*Prunus* spp.)), hard mast (e.g., acorns and beechnuts), grasses, forbs (e.g., dandelions, firewood, and cow parsnip), roots, tubers, seeds, and fungi, with decreasing importance toward the northern populations (Clevenger et al. 1992; Elgmork and Kaasa 1992; Batsaikhan et al. 2004; Paralikidis et al. 2010; Štofik et al. 2013; Ciucci et al. 2014; Senset et al. 2016; Niedziałkowska et al. 2019).

Asian populations of brown bears do not show the same latitudinal gradient in meat consumption and are largely herbivorous. In northern Asia, the brown bear is more likely to rely on the Siberian pine (*P. sibirica*) than meat (Niedziałkowska et al. 2019). Other vegetation includes forbs (e.g., lagwort (*Petasites japonicus*), fennel (*Foeniculum* spp.), hogweed (*Heracleum* spp.), rushes (Juncaceae), grasses, acorns, and fruit (e.g., kiwi and berries) (Ohdachi and Aoi 1987; Sato et al. 2005; Sidorovich 2006; Niedziałkowska et al. 2019). Animal matter is a small part of their diet, mostly in the form of insects (e.g., beetles and ants), ungulates (e.g., deer, wild boar), small mammals (e.g., rodents), and crowfish (*Cambaroides japonicus*) (Ohdachi and Aoi 1987; Sato et al. 2005; Sidorovich 2006; Niedziałkowska et al. 2019). Along coastal Japan, brown bears also eat

seaweed, salmon, crab (*Paralithodes brevipes*), and shellfish (*Mollusca*) (Ohdachi and Aoi 1987).

### **Giant Panda Bear (*Ailuropoda melanoleuca*)**

The giant panda differs from the rest of the bear species in that it is an obligate herbivore with a diet comprised of approximately 95–99% bamboo (*Bashania* and *Fargesia* spp.) (Schaller et al. 1985; Reid and Jinchu 1991; Long et al. 2004). In contrast to other obligate herbivores, the giant panda retains the “simple stomach and short gastrointestinal tract” of the carnivore (Dierenfeld et al. 1982). To compensate, giant pandas consume large quantities of bamboo shoots and leaves (Hu et al. 1985), shift species of bamboo, age of the plant, and the plant part they consume to optimize nutrient intake (Hansen et al. 2010; Nie et al. 2015) and contain gut microflora to digest bamboo fibers (Zhang et al. 1988; Hirayama et al. 1989; Wei et al. 2007).

### **Polar Bear (*Ursus maritimus*)**

Polar bears are the only bear species that are almost exclusively carnivorous. The main prey item of polar bears is seals, primarily ringed seals (*Pusa hispida*) and to a lesser extent bearded (*Erignathus barbatus*), harp (*Pagophilus groenlandicus*), and hooded (*Cystophora cristata*) seals (Smith 1980; Ramsay and Hobson 1991; Derocher et al. 2002; Stirling 2002; Bentzen et al. 2007; Thiemann et al. 2008; Iverson et al. 2013). On occasion, polar bears will kill walruses (*Odobenus rosmarus*), narwhal (*Monodon monoceros*), and belugas (*Delphinapterus leucas*) (Killian and Stirling 1978; Smith 1985; Calvert and Stirling 1990; Smith and Sjare 1990; Thiemann et al. 2008). During long periods without sea ice, during which some polar bears are on land, they will consume coastal marine plants (e.g. algae), marine invertebrates, birds and eggs (e.g., snow geese), terrestrial plants (e.g., grasses, forbs, mosses (*Bryophyta*), and berries), mushrooms, and terrestrial animals (e.g., caribou, small

rodents) (Russell 1975; Ramsay and Hobson 1991; Derocher et al. 1993; Gormezano and Rockwell 2013; Iverson et al. 2013). However, polar bears are unlikely to meet their energetic requirements feeding on terrestrial foods in the long term (Stirling and Derocher 1990; Ramsay and Hobson 1991; Hobson et al. 2009; Stirling and Derocher 2012; Derocher et al. 2013). Although polar bears feed on whale carcasses where they are predictable due to subsistence harvesting by Native people or in unpredictable events, such as whale strandings, these carcasses are not a substitution for their natural prey of seals (Derocher et al. 2002; Miller et al. 2006; Bentzen et al. 2007). Some polar bears fast, or feed very little, while onshore in response to low food availability and the higher cost of locomotion on land (Latour 1981; Derocher and Stirling 1990; Ramsay and Hobson 1991).

### Sloth Bear (*Melursus ursinus*)

Although all bears, except polar bears, feed on insects, the sloth bear is the only one with special adaptations for feeding on insects. The sloth bear's diet is comprised of approximately 39–83% insects, primarily termites, ants, beetles, and other insects (Schaller 1967; Laurie and Seidensticker 1977; Joshi et al. 1997). The sloth bear has adapted to myrmecophagy with an elongated, bare snout; a long, flexible tongue; reduced incisors and post-canine teeth; and a gut microbiota similar to other myrmecophagous mammals (Seidensticker 1993; Sacco and Van Valkenburgh 2004; Delsuc et al. 2014). The majority of the rest of their diet, 14 to 61 percent, is comprised of fruit, including figs, dwarf date palm (*Phoenix roebelenii*), black plum (*Syzygium cumini*), and Chinese and sherbet berry (*Lycium* spp.) (Schaller 1967; Laurie and Seidensticker 1977; Joshi et al. 1997). They also consume flowers, grass, honey, and carrion (Laurie and Seidensticker 1977; Joshi et al. 1997).

### Conclusion

In this entry we described how diet varies by species, populations within species, and

seasonally. Most bears are generalist, omnivores that consume high-caloric foods when available, such as meat (e.g., ungulates and insects), hard mast fruits (e.g., acorns), and soft mast fruits (e.g., berries). Grasses, forbs, and other lower-caloric food items are consumed when high-caloric foods are limited and often meet the dietary needs of individuals because of their predictability spatially and temporally. A few species, polar and panda bears, are specialists and are primarily carnivorous and herbivorous, respectively. Understanding the dietary needs specific to each population of the eight bear species, and the subsequent habitat selection, is important for conservation and management. The diet of some species, such as the Alaskan brown bear, has been extensively study, whereas little research has been completed on other species, such as the Andean bear.

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## Bear Gaits

### ► Bear Locomotion

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## Bear Intelligence

### ► Bear Cognition

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## Bear Life History

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## Synonyms

[Birth](#); [Death](#); [Fitness](#); [Life history strategies](#); [Life history traits](#); [Life table](#); [Natural selection](#); [Reproduction](#); [Survival](#)

## Introduction

Life history traits are age- and state-specific characteristics that affect the life table of an organism. These traits are the result and the cause of variation within life cycles. Each of these life history traits is linked to the timing of events that make up the life of an animal and are investments in growth, reproduction, and survivorship of the individual or species (Gittleman 1986, 1993; Stearns 1976). Life history characteristics help to explain how an organism's anatomy, behavior, life span, reproductive development and behavior, and post-reproductive behavior are all influenced and shaped by natural selection and thus include various survival and reproductive strategies (Gittleman 1986, 1993). Therefore, these life history tactics can be thought of as a set of coadapted traits designed via natural selection to solve specific ecological problems. For example, reproductive strategies that lead to successful propagation may include things like seasonality of breeding,

litter size and frequency, age of weaning and independence of offspring, reproductive life span, and age of sexual maturity. Survival strategies encompass such characteristics as an organism's adaptations to inclement weather or conditions, defenses against predation, escape methods from altered or deleterious habitat, methods of moving through its environment, and specific foraging tactics (Garshelis 2004).

Ursidae, the second smallest family in the order Carnivora, includes eight extant bear species that can be found in a diverse range of habitats across North America, South America, Europe, and Asia. These species include the brown bear (*Ursus arctos*) found in Canada, the United States, Russia, Scandinavia, and Central Asia; the American black bear (*Ursus americanus*) found in the United States, Canada, and Mexico; the Asiatic black bear (*Ursus thibetanus*) of China and India; the polar bear (*Ursus maritimus*) of Russia, Scandinavia, Canada, and the United States; the giant panda (*Ailuropoda melanoleuca*) found in China; the spectacled bear (*Tremarctos ornatus*) of South America; the sloth bear (*Melursus ursinus*) of China, India, and Southern Asia; and the sun bear (*Helarctos malayanus*) of China, India, and Southeast Asia. Because of the low number of extant species within this family, less variation in life history traits might be expected in comparison to other carnivoran families (Garshelis 2004). However, because bears inhabit such a wide range of habitat types spanning from the tropics to the arctic, the potential for extensive variation among species exists. Whereas the polar bear is a tundra-dwelling species that traverses across the sea ice that covers the Arctic Sea during the winter months, the spectacled bear, sloth bear, sun bear, and Asiatic black bear all live in tropical forests, mountains, or lowland habitats. The American black bear, the giant panda, and the brown bear are all considered temperate species. However, individuals within a species may range across broad geographic areas and habitat types, thus allowing for variation in life history traits within a single species and not just among species.

Variation among bear species and within individual bear species can be explained by geography, habitat, and food habits (Gittleman 1986;

Garshelis 2004). It is difficult to make species-specific generalizations about the life history characteristics of bears, and there is likely far more variation than is presently acknowledged among the different species (Garshelis 2004). Some traits may not yet have been studied in all bear species, or certain traits may have not yet manifested in certain species because the conditions necessary for that trait's expression were not studied. Although several of these bear species have been studied extensively and much is known about their ecology and life histories, there are a few species that are still lacking research, and little is known about their life histories other than what can be gleaned from captive individuals.

### Reproductive Life History Traits

For most bear species, the breeding season occurs during the late spring and summer months, mainly between May and July. However, several species have breeding seasons that span outside this typical range. Polar bears engage in courtship behaviors and mating on the ice as early as April and May (Richardson 2014). Giant pandas have the earliest breeding season of all bear species, starting in March and typically ending in May (Zhu et al. 2001). Bear species reaching into the far northern latitudes like the American black bear and Asiatic black bear may continue to breed as late as August. Bears in warmer tropical climates, such as the sun bear, can mate at any point during the year, though females will only spend a few days to a week on breeding behaviors (Garshelis 2004). All bear species for which information about mating systems is available are considered promiscuous, meaning males and females frequently mate with more than one individual. Thus, because males will mate with multiple females in a given area, males do not assist in rearing cubs. Additionally, copulation is thought to occur numerous times in order to induce ovulation in females (Garshelis 2004).

After breeding, female bears utilize a strategy known as delayed implantation, or embryonic diapause, where the embryo does not immediately implant in the uterine lining after the egg has become fertilized. Instead, the embryo is

maintained in a state of dormancy where little to no development takes place, thus elongating the gestation period. Delayed implantation is thought to be a strategy to reduce risk during unfavorable environmental conditions, so that animals can time the birth of their offspring to line up with widely available food sources and more pleasant weather conditions, and to give offspring the highest chance of survival prior to birth (Garshelis 2004). In American black bears and brown bears, this embryonic diapause may last for several months, followed by approximately 2 months of gestation after implantation of the blastocyst in the uterine lining (Garshelis 2004).

Other than sun bears, which may breed and give birth to cubs at any point throughout the year, most other bear species will produce a litter between the months of November and February (Garshelis 2004). Giant pandas, however, may give birth between August and September. Whereas bears may give birth to litters ranging from one to six cubs, a litter will most commonly consist of one to three offspring, depending on food resources and maternal body condition. Because reproductive output is linked to maternal condition and maternal body condition varies over space and time, reproductive output also varies among and within bear species (Garshelis 2004; Robbins et al. 2012). American black bears and brown bears may have as many as four to six cubs in a single litter, if resources are plentiful. Giant pandas, in contrast, almost always give birth to twins, though only one cub typically survives (Zhu et al. 2001; Garshelis 2004). Sex ratios of bear cub litters born in the wild are very close to 50M:50F, although sample sizes for these studies are frequently small and deviation may not be detected accurately (Garshelis 2004).

Bear cubs of all species are born altricial, meaning they are born in an underdeveloped state (i.e., lightly furred or naked, and eyes closed) and completely reliant on their mothers to take care of them. In most species, including brown bears and American black bears, cubs are born during the winter and thus during the hibernation period (Robbins et al. 2012; Zedrosser 2006). Although not all bear species hibernate, almost all bear cubs are born in some sort of secluded

denning area such as a rock cave, a hollow tree, or an excavation in the dirt or snow (Garshelis 2004). On average, bear cubs are approximately 300 grams when born. Giant pandas show the most deviation from other bear species as birth weight of panda cubs is usually 90 to 130 grams, only about 1/800th the size of an adult female (Garshelis 2004; Peng et al. 2001; Zhu et al. 2001). Whereas other species of bears produce cubs that are lightly furred, pandas are the only species that produce naked, pink-colored cubs that develop fur and coloration patterns several weeks after birth (Peng et al. 2001).

Once born, cub growth rate and development among bear species vary. While Asiatic black bears are typically the first to open their eyes at 7 days and start walking at 4 days, they have one of the slowest growth rates among bear species (Yudin 1993). Asiatic black bear cubs born in January only reach a mass of approximately 2.5 kilograms by May (Yudin 1993). Giant pandas, due to extreme underdevelopment at birth, are just learning to crawl after the first 2 months (Peng et al. 2001). Conversely, most of the other bear species open their eyes and begin walking after the first month or so of life. In most cases, bear cubs remain in the denning area with their mothers for approximately 2 to 4 months, until they can emerge and walk about on their own (Garshelis 2004).

Although brown bears and American black bears will nurse throughout the duration of hibernation and into the spring and summer of their birth year, many other bear species continue to nurse for 2 years or more as a supplement to the cubs' other food sources. American black bear cubs, spectacled bear cubs, and sun bear cubs leave their mothers the earliest, becoming independent at 12–18 months. All remaining bear species stay with their mothers for the first 24–36 months of their lives. For this reason, many female bears will reproduce only every 3 to 4 years, rather than in a yearly cycle (Garshelis 2004). Females without cubs will enter estrus and mate when possible.

For many bears, peak reproductive age is between 4 and 20 years. Only three bear species reach sexual maturity at 3 years of age: sun bears,

sloth bears, and Asiatic black bears. All other bears attain sexual maturity at 4 years or later, with females typically maturing earlier than males. In polar bears and brown bears especially, males will breed later than most females for the first time because males need to gain enough size and mass to compete with more experienced, older male bears for breeding rights. Thus, male polar bears do not reach sexual maturity until 6 years of age and may not breed until 8 to 10 years of age. Because of these long time spans between birth and maturation, maturation and breeding, and one successful reproduction to the next, bear species are thought to have low birth rates (Garshelis 2004). Most bears are considered to be reproductively active until their early 20s, when they may start to experience senescence (Garshelis 2004).

### Survival Life History Traits

Adult bears can vary greatly in size, depending on species, sex, location, habitat, and food availability. Sun bears are the smallest of the bear species, often between 120 and 150 centimeters long and weighing only 27 to 80 kilograms even when full grown (Wong 2002). Spectacled bears, sloth bears, and Asiatic and American black bears are considered medium-sized bear species as they are typically larger than sun bears but still significantly smaller than the largest species. Polar bears are the largest bear species with the most massive of adult males measuring up to 3 meters long, 160 centimeters tall at the shoulder, and weighing up to 700 kilograms (Richardson 2014; Tartu et al. 2016). Brown bears and giant pandas are also large-bodied bear species like the polar bear. In all bear species, sexual dimorphism results in adult males often being larger than adult females (Richardson 2014).

While having to fuel a large body can often be stressful if food resources are scarce, a large body size is still beneficial in other ways. Because of their bulk, bears are not likely to be predated upon by any other animal. In most cases, bear mortality is caused by another bear, a human, old age, or lack of food. In fact, bear survival strategies and

life history traits commonly revolve around food sources and how to reach them (Garshelis 2004). Having a large body enables bears to move through their environment with relative ease, so that they can locate and move to seasonally available food sources (Garshelis 2004). Many bear species make large seasonal movements and have vast home ranges that they move through during certain times of the year. For example, polar bears travel on the Arctic sea ice during the winter months to hunt and gain significant amounts of fat, in order to survive the summer months on land without access to typical food sources. Brown bears frequently move to higher elevations to den for hibernation but then move down the elevation gradient after emergence to have access to berry crops and salmon spawning streams. Home range size and movement through the home range are almost entirely dependent on food availability and distribution within the environment (Swihart et al. 1988). When food is more abundant and more widely available in the environment, the home range tends to shrink as less area is needed to effectively gather food.

Male bears will typically establish larger territories than female bears, as they cover greater distances in search of mates during the breeding season. In fact, male territories frequently overlap home ranges of multiple females as a way of keeping track of potential mates (Wielgus and Bunnell 1994). However, intraspecific avoidance of males by females has been documented in five of the eight bear species. Females of several bear species specifically avoid areas that males are frequent once cubs have been born to avoid potential infanticide. Males ready to breed will often attack and kill cubs in an attempt to bring a female bear back into estrus (Wielgus and Bunnell 1994; Zedrosser 2006).

Despite these rather large home ranges that expand and contract with food availability and distribution, most bear species are rarely territorial. Home ranges within a species frequently overlap, though this also seems to vary with food availability and bear density (Garshelis 2004). Even with this overlap, bears tend to be mostly solitary in nature due to their large body size and large food requirements often barely met



with dispersed and/or nonnutritive food sources (Garshelis 2004). However, there are instances of bears displaying social behaviors outside of family groups and male-female interaction during the breeding season. Brown bears in Alaska frequently gather to feed on the same salmon streams, and polar bears and brown bears in Alaska have been observed feeding on whale carcasses and at dumps together. In these circumstances, bears will compete for the best feeding positions. Social hierarchies are established usually with the largest males in the prime spots, and younger bears and females relegated to the lower-quality feeding spots.

### Special Adaptations

With abundant food sources being restricted by dominant bears and main food sources changing seasonally, it is important that bears maintain a sort of dietary flexibility. Regardless of environment type (i.e., tropical or temperate), food availability varies widely by year, season, elevation, and habitat. In response to this constantly changing availability and distribution, bears are mainly opportunistic generalist omnivores, meaning they eat a wide variety of things. Bear diets are chiefly vegetation and plant material including roots, tubers, flowers, fruits, nuts, berries, grasses, and forbs but may also contain carrion, ungulates, fish, birds, eggs, insects, and smaller mammals (Rode and Robbins 2000).

Not all bear species follow this pattern of dietary flexibility, however. For example, polar bears have evolved to be almost exclusively carnivorous, feasting mainly on ringed seals (*Phoca hispida*) and eating only vegetative material, birds, eggs, and whale carcasses when forced ashore in the summer months after the sea ice melts (Richardson 2014; Tartu et al. 2016). Giant pandas, in contrast, have evolved to be almost exclusively herbivorous, in that their diet is restricted almost completely to bamboo. The panda's thumb is a modified sesamoid bone that helps to maintain a firm grip on bamboo shoots while eating, and powerful jaw muscles support a bite force strong enough to break through bamboo

shoots (Wei et al. 2015; Zhu et al. 2001). Pandas rarely eat other grasses, tubers, birds, or rodents, but a typical diet shift is from one species of bamboo to another. Another deviation, though not quite as extreme, is the sloth bear. The sloth bear is still considered omnivorous and opportunistic, but members of this species have a specially adapted lower lip and palate used to feed on insects and highly developed sickle-shaped claws for digging in termite mounds (Joshi et al. 1997). Depending on the time of year, sloth bears can shift diets from predominantly ants and termites to predominantly fruit and honey (Joshi et al. 1997).

When food is limited or disappears from the environment entirely, as is common in northern latitudes during the winter months, it becomes difficult for bears to maintain regular metabolisms and activity patterns without intaking food. Therefore, three of the eight bear species that range throughout these northern latitudes undergo a prolonged period of fasting and inactivity known as hibernation. American black bears, brown bears, and some Asiatic black bears in the colder, more northern portions of their range will hibernate. None of these species are obligate hibernators, however, meaning that hibernation does not need to occur if food is still seasonably available. American and Asiatic black bears in the southern portions of their range do not typically hibernate. During hibernation, the metabolism drops to 25% of basal rates, the body temperature lowers by several degrees centigrade, and heart rate decreases from 50–60 beats per minute to about 8–10 beats per minute (Hellgren 1998). Bears will not eat, drink, or defecate during hibernation. Instead, the bear survives by slowing utilizing the massive fat stores it accumulated during the summer and fall preceding hibernation (Hellgren 1998). Bears can lose 20–40% of their body mass by the end of hibernation but do not lose the use or strength of their muscles or bones (Hellgren 1998). Hibernation serves as an adaptation to surviving inclement weather conditions and periods without access to food.

Most bear species have specialized in the ability to climb trees, allowing them more access to three-dimensional space and potential food sources within their environments (Garshelis



2004). American black bears can frequently be found in trees, especially cubs waiting for their mother to return from foraging. Sun bears and spectacled bears are considered the most arboreal of the bear species and are known for their climbing abilities and the propensity to build tree nests for resting (Brown and Rumiz 1989; Wong 2002). However, not all bear species spend such large proportions of their time in trees. Polar bears, a tundra species, live in habitats that are mostly treeless, and their great body size would prevent them from being effective at tree climbing. Instead, brown bears and polar bears rely mainly on their body size and aggressive behaviors to ward off dangerous advances from humans or other animals (Garshelis 2004).

In general, bears have keen hearing and olfactory senses. Many bear species are able to smell and locate food from quite a distance away. For example, polar bears are thought to be able to detect food from 1.6 kilometers away, even if it is buried under a meter of snow (Rosing 1996). Additionally, many bear species are adapted to be strong swimmers. American black bears and brown bears are formidable swimmers, but polar bears have been known to regularly swim distances of over 48 kilometers at a time in search of stable sea ice, mates, and ringed seals (Pagano et al. 2012). Polar bears are also especially adapted for the cold temperatures of their Arctic habitat. They have large feet covered in papillae (i.e., tiny projections), built for walking across ice and snow and for propelling them through the water. Their long claws are designed for digging into the ice, and their bodies are insulated with adipose tissue to keep them warm.

## Senescence and Death

Bears are typically long-lived species, though cub mortality and adult mortality due to unnatural causes are not uncommon. Brown bears, polar bears, and American black bears frequently live into their 20s or 30s in the wild, and all eight species of bears have lived to at least 30 years in captivity (Garshelis 2004). There is limited information that suggests that bears may experience

declines in reproductive rates with old age, but most bear species continue to produce cubs into their 20s (Garshelis 2004). Research suggests that reproductive senescence could potentially follow a decrease in body mass or body condition later in life for many animals (Derocher and Stirling 1994; Richardson 2014). Thus, it is thought that bears that are unable to accumulate appropriate fat stores for reproduction may be unable to ovulate, conceive, or raise surviving cubs due to the influence of maternal body condition on these processes (Derocher and Stirling 1994; Richardson 2014). However, senescence in bears and its impact on other life history traits have not yet been investigated rigorously.

## Cross-References

- [Bear Diet](#)
- [Bear Locomotion](#)
- [Bear Morphology](#)
- [Bear Sensory Systems](#)
- [Carnivora](#)
- [Hibernation](#)

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## Bear Locomotion

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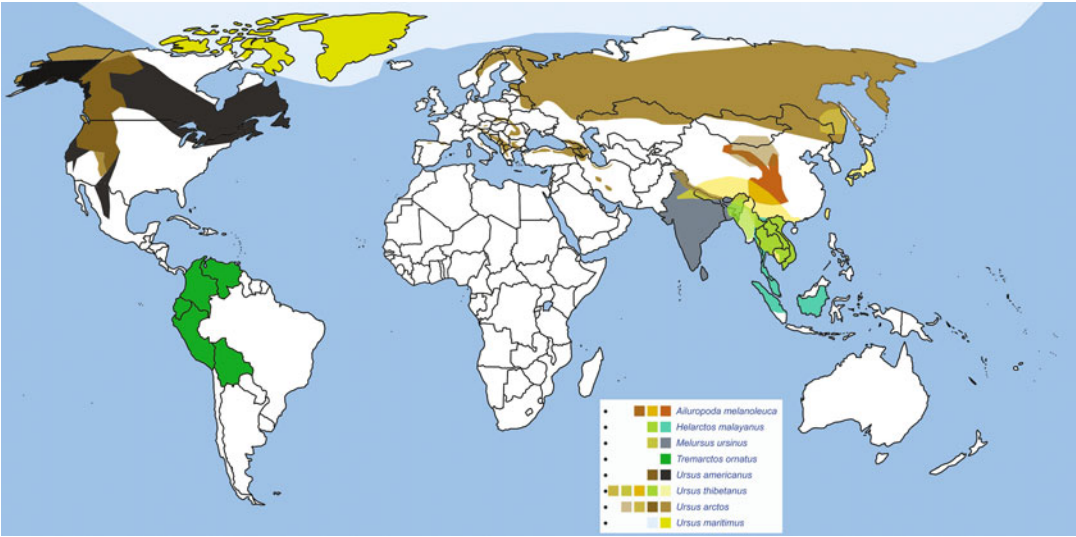
## Synonyms

Bear gaits; Ursid locomotion

## Definition

Movement used by members of the family Ursidae to traverse their environment.

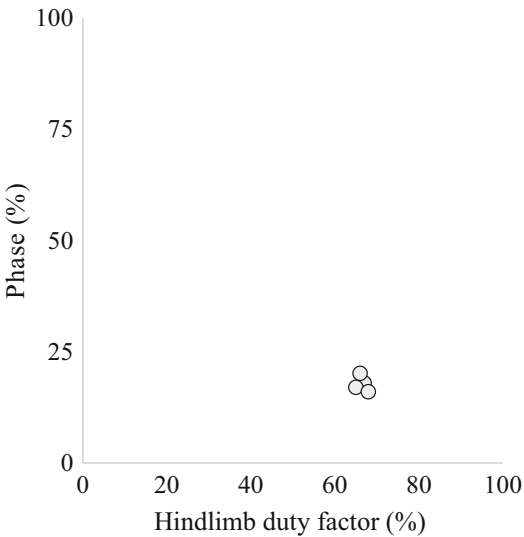
All bears belong to the family Ursidae. There are only eight recognized species of living bears, most belonging to the genus *Ursus*. Despite their limited taxonomic diversity, they have a near global range and can be found on all major land-masses except Antarctica, Africa, and Australia (Fig. 1). Members of the family come in various forms and sizes and range in body mass from the 68 kg sun bear (*Helarctos malayanus*) to the 700 kg polar bear (*Ursus maritimus*). Despite the range in body size and anatomy, all bears live fairly solitary lives with large home ranges. The need for these sizeable habitats requires bears to be highly adaptable and flexible in terms of diet and locomotor behavior. Bears range in diet from bamboo specialists to the largest land carnivores. In terms of locomotor modes, some species are highly arboreal while others utilize mixed aquatic and frozen tundra landscapes (Nowak 1999). This article discusses some of the general aspects of **bear locomotion**, while briefly touching on some of the more specialized locomotor behaviors observed in the family.



**Bear Locomotion, Fig. 1** Map demonstrating the current range of extant ursid species

**Bear Gaits and General Locomotor Behaviors**

Bears’ walking gaits consist of slow speed lateral-sequence lateral-couplet footfall patterns (Fig. 2). A lateral-sequence gait is one in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb). Commonly, during walking gaits, the forelimbs and hindlimbs are traveling together as a slightly asynchronous couplet. When the ipsilateral forelimbs and hindlimbs are traveling together, this is referred to as a lateral couplet; when the contralateral forelimbs and hindlimbs are traveling together, this is referred to as a diagonal couplet. Very rarely do the limbs move together in perfect synchrony. Lateral-sequence lateral-couplet footfall patterns tend to be present in long-legged terrestrial animals and are assumed to be the best mechanism in preventing interlimb interference. However, this footfall pattern is thought to be inherently unstable because a majority (~66%) of the stride is spent as a unilateral bipod (i.e., only two ipsilateral limbs in contact with the support), which tends to roll the body side-to-side throughout the stride. This instability is argued to be negligible for long-legged animals (Granatosky 2018; Hildebrand 1976).



**Bear Locomotion, Fig. 2** “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in ursids ( $n = 4$  species)

As locomotor speed increases, bears tend to change gait type. The gallop is the preferred means of locomotion when traveling at speeds more than  $4 \text{ m s}^{-1}$ . At intermediate speeds ( $2\text{--}3 \text{ m s}^{-1}$ ), bears deviate from the usual mammalian pace or trot, and instead utilize a running walk, which is a footfall sequence consistent with

their normal pattern of walking, but with decreased overlap between the feet. The trot and the pace require forelimbs and hindlimbs of equal length, with a straight short back; bears are characterized as having a relatively long, sloping back and this may limit their use of these gaits. One of the benefits of the running walk over a trot or a pace is the limited vertical fluctuation in the center of mass, as well as the ability to maintain contact with the ground with at least one foot throughout the stride. This suggests the apparent lack of a trot by grizzly bears may have implications for energetics as well. A lack of spring-like behavior in the bears' wrists may also be a reason why they prefer a running walk gait. A trot is more efficient for animals that store elastic energy in their tendons. Due to the shorter overlap between steps in a running walk, it is less affected by the need for elastic energy storage (Shine et al. 2015).

As with most nonprimate mammals, the forelimbs of bears tend to support the majority of their body weight (approximately 54–60%) (Granatosky et al. 2018). At walking speeds, the limb loading forces seen in the hindlimb have a characteristic M-shape pattern, which is possibly due to limb stiffness (Shine et al. 2015). This pattern is not seen in the forelimbs and is likely due to differences in impulses and weight distribution. The hindlimbs also tend to have the greatest rate of force development except at fast locomotor speeds. In terms of fore-aft forces, the forelimbs tend to be net breaking across all speeds. The propulsive impulses of both the forelimbs and hindlimbs are very similar. Bears differ from other large mammals in having substantially higher forelimb and hindlimb mediolateral forces. Such ground reaction force patterns may be attributable to the lumbering and splayed postures of the limbs (Shine et al. 2015).

### Plantigrade Locomotion

Foot postures are referred to as plantigrade when the complete length of the foot, involving the podials and metapodials, is positioned on the ground. This foot posture is observed in both bears and humans (Cunningham et al. 2010;

Pagano et al. 2018). Some hypothesize that plantigrady infers energetic benefits as the larger contact area minimizes directional change of the center of mass trajectory, which in turn lessens mechanical energy loss (Cunningham et al. 2010). Pagano et al. (2018) tested this hypothesis in bears by collecting mass-specific energetic costs of locomotion in grizzly (*Ursus arctos*) and polar (*Ursus maritimus*) bears. At routine walking speeds, they observed that polar bears and grizzly bears exhibited similar costs of locomotion and gait kinematics. Minimum cost of transport while walking in both species was comparable to predictions for similarly sized quadrupedal mammals, but these costs doubled at higher speeds. Similar to humans, bears appear to exhibit a greater economy while moving at slow speeds. Despite walking costs that were similar to those of other quadrupedal mammals, Pagano et al. (2018) found that both polar bears and grizzly bears have postural costs that are more than double predictions based on other quadrupedal mammals. The increased postural cost in both bears may in part be a result of their plantigrade posture as more erect limb postures (e.g., digitigrade and unguligrade) are known to have lower muscle mass and greater effective mechanical advantage (Biewener 1989; Reilly et al. 2007). Increased costs of running associated with plantigrade locomotion may also be attributable to the heel that absorbs energy once the stride begins. This eventually restricts storage and rehabilitation of elastic strain energy, mainly in the extensor muscles of the ankles.

### Arboreal Locomotion

Arboreal movement remains an understudied aspect of the locomotor repertoire of bears. However, not all bear species are equally proficient. The Malayan sun bear (*Helarctos malayanus*) is largely arboreal and is known as the best tree climber within the Ursidae. The sun bear is characterized by strongly curved, pointed claws and large paws with naked soles, which make them well adapted for climbing trees. Additionally, this species is capable of supinating the ankle,



allowing the hindfeet to “grip” the substrate rather than relying on claws or branches. In comparison, the larger brown bear shows little propensity for arboreal locomotion. These species are unable to “grasp” with the hindlimbs and instead keep the feet in a highly dorsiflexed position during vertical ascent (Fig. 3). Sasaki et al. (2005) demonstrated that these differences in relative climbing abilities have distinct consequences on the anatomy of the hindlimb. Specifically, they observed that the tarsal joint and foot of the sun bear and giant panda are more flexed and supinated than the polar bear and brown bear. Additionally, the tendon of the *m. tibialis cranialis*, a dorsiflexor and supinator of the foot, is shorter in the Malayan sun bear and the giant panda compared to other species. The combination of both traits allows the foot of arboreal bear species to be dynamically fixed and stable to external forces while positioned in a supinated posture.

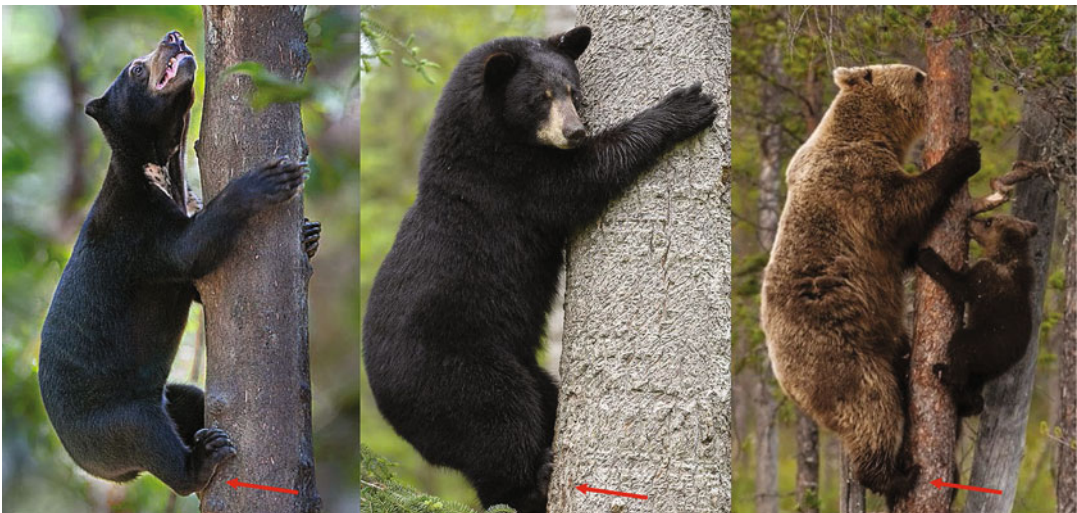
The black bear (*Ursus americanus*) is also quite adept at arboreal locomotion (Bull et al. 2000) and will quickly ascend into trees or other high places when feeling threatened. Often, bear–human interactions result in black bears refusing to leave trees. Such instances often require wildlife professionals to intervene and safely remove the bear from the tree (Wolfe

et al. 2008) and relocate it to an area away from human interference.

## Swimming

All North American bear species (i.e., black bears, brown bears, and polar bears) are all capable of swimming. Bears will take to the water for purposes of fishing or travel. In the water bears can reach swimming speeds upwards of 2.7 m/s. Swimming is most important for polar bears as they move between sea ice patches. Pagano et al. (2012) reported that the duration and distance of long-distance swimming ranged 0.7–9.7 days and 53.7–687.1 km in polar bear. They demonstrate that adult female polar bears and their cubs are capable of swimming long distances during periods when extensive areas of open water are present. However, long-distance swimming appears to have higher energetic demands than moving over sea ice.

Griffen (2018) demonstrated that mean metabolic rate for a swimming polar bear to be  $2.75 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ . When compared at the same movement rate, the cost of transport for swimming was estimated to be approximately  $5 \times$  that of walking. These findings demonstrate that increasing



**Bear Locomotion, Fig. 3** Arboreal capabilities of the Malayan sun bear (*Helarctos malayanus*; left), black bear (*Ursus americanus*; middle), and grizzly bear (*Ursus*

*arctos*; right). Note the supinated versus dorsiflexed position of the ankle in the highly arboreal Malayan sun bear versus black and grizzly bears

frequency and duration of long-distance swims in polar bears is energetically stressful. Energetic and thermodynamic costs of long swims may be further exacerbated by recent declines in body condition that have been documented due to climate warming.

### Captive Pacing Behavior

Species held captive in zoo like settings are often recognized for having particular behavioral abnormalities. Abnormal behavior in captive animals can include stereotypic behaviors – highly repetitive, invariant, functionless behavior, such as repetitive pacing, swaying, head-bobbing, bar-biting, over-grooming, or excessive licking. These behaviors can result from the frustration of natural behavior patterns, impaired brain function, or repeated attempts to deal with some problem (Swaigood and Shepherdson 2005). For bears held captive, their daily activities include exploration and foraging but the bulk of it consists of pacing (40–60%). Pacing behavior is continuous walking back and forth or in a circle, following the same path. Signs of regular pacing include definite paths worn in the ground. Observational studies have explored pacing in depth and have confirmed a stereotypic pattern of pacing present in certain bear species and not others. The black bear, for example, shows a classic and stereotypic pacing behavior in contrast to sloth bears. The black bear paces up to 8 hours/day with increased rates before and after feeding time. Cless et al. (2015) proposed a quantitative definition of pacing based on a reduction of locomotor variability compared to other “directed locomotor tasks” in polar bears. Such a finding indicates that pacing may constitute a similar invariant repetitive behavior similar to patients with autism. However, Granatosky et al. (2020) note that locomotor rhythmicity is a normal component of bird and mammal locomotion independent of pacing behaviors. The factors that predispose bears to pacing in zoos may be linked to large home range size, large daily travel distance, or large body size (Mason and Clubb 2004).

### Conclusion

As a group, the bears represent some of the largest living land carnivores. While they are limited in taxonomic diversity, they occupy a large geographic range. The quadrupedal gaits of bears are consistent, both metabolically and spatiotemporally, with other similarly sized mammals at slow speeds, but vary considerably when speed increases. Specifically, bears use running walks that are associated with increased costs of transport instead of trotting or pacing gaits. Limb loading for bears is distinct compared to other mammals due to relatively high mediolateral forces. These odd gait features may be attributable to plantigrade foot postures present across all bear species. Beyond terrestrial locomotion, some bear species are quite proficient at arboreal movement. The propensity to locomote in the trees varies considerably across the living taxa and is largely driven by body size (i.e., smaller species are more arboreal) and the ability to supinate the ankle joint. As a consequence of either large home range size, large daily travel distance, or large body size, bears are especially prone to pacing behaviors in zoos. Research to curb such behavior is active and ongoing.

### Cross-References

- [Adaptation](#)
- [Arboreality](#)
- [Canine Locomotion](#)
- [Evolution](#)
- [Zoology](#)

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## Bear Management

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## Synonyms

Ursid husbandry; Wild ursid management

## Definition

A review of the use of cognitive measures to improve the care and management of captive members of the family *Ursidae*, as well as the use of behavioral data to design mitigations for human-bear interactions in the wild.

## Introduction

Bears are large but intelligent terrestrial carnivores capable of complex spatial reasoning

tasks, such as tool use. This, combined with their size and aggressive behavior, makes them difficult to manage in both wild and captive settings – as they often interact with humans negatively. They are common culprits of depredation, property damage, and threats to human safety. In captivity, their size and complex cognitive requirements provide adequate cognitive and physical enrichment in order to prevent the development of stereotypical behavior and promote species-typical behavior. However, through understanding natural bear behavior and cognition (see the “► [Bear Cognition](#)” chapter of this encyclopedia for a review), managers are able to develop new and innovative interventions for wild and captive bears, to enhance their welfare as well as mitigate human-wildlife interactions.

## Managing Bears in the Wild

Efforts aimed at promoting wild carnivore conservation hinge on an ability to prevent and mitigate negative human-wildlife interactions. This requires a focus on aversive conditioning, the use of repellents and deterrents, controlling exposure to attractants, an understanding of species differences in threat perception, and knowledge regarding the general behavioral ecology of the target species.

Attempts to utilize classical conditioning to intervene in cases of livestock depredation by creating taste aversion to farmed animals and produce have yielded mixed results. These efforts have focused on bears, as well as wolves (*Canis lupus*) and coyotes (*Canis latrans*), and have featured the use of emetic chemical compounds (e.g., lithium chloride, cupric sulfate, or alpha-naphthylourea) combined with targeted bait items aimed at reducing the animals’ desire to consume this particular item again in the future (Smith et al. 2000). This approach has been demonstrated to be effective in reducing black bear depredation on beehives (Colvin 1975; Polson 1983), as well as in mitigating the raiding of campsites to obtain human food items by habituated wild black bears (Ternent and Garshelis 1999). Still, negative results have also been reported in similar contexts

(Smith et al. 2000); thus, further research into the cognitive processes involved in the selection and acquisition of prey items may be necessary to properly apply this mitigation technique effectively.

The principles of classical conditioning can be further applied to wild bear management through simply creating an association between a negative stimulus and humans and human settlements. This approach has also produced mixed results in nuisance grizzly bears in the Greater Yellowstone Ecosystem (GYE). Here, considerable work has been conducted to evaluate the methods of avoiding human-bear conflict in developed areas such as campsites, farms/ranches, and cities. In an attempt to create an association between pain and anthropogenic bear attractants, nuisance bears already possessing radio collars were baited with attractants. As the animals approached the attractant, they were fired upon using a Thumper Gun using bear-deterrent flash bullets as well as rubber bullet shot from a 12-gauge shotgun. This unconditioned pain stimulus was then paired with recordings from two non-native bird species (California quail and the ladder-backed woodpecker). The purpose of this approach was to create an association between the painful shot and the noise. Thus, in future encounters, researchers would simply play the sound stimuli in order to deter the bears from approaching developed areas. While this approach was effective for some nuisance bears, animals with compromised dentition, and those known to be long habituated to humans, did not alter their behavior in order to avoid humans and developed areas (Gillin et al. 1994). Radio-collared black and grizzly bears in Alaska exhibited aversive behavior in association with humans and human settlements after exposure to aversive stimuli such as plastic slugs and cracker shells. These methods cannot occur in a vacuum, however, and require human behavior change as well. Thus, public education programs including the promotion of bear-resistant food containers to control exposure to reinforcing stimuli and also temporary site closures due to increased bear activity are necessary for the effective mitigation of human-bear interactions in the wild (Schirokauer and Boyd 1998).

## Managing Bears in Captivity

In captivity, it is critical that a species' natural behavior is considered when designing enrichment and exhibits in order to reduce stereotypical behaviors (e.g., repetitive behaviors such as pacing, as well as more serious self-injurious behaviors) and promote optimal physiological and psychological welfare, exhibited by an increase in species-typical behaviors (e.g., digging, exploring the habitat, etc.). Clubb and Mason (2003, 2007) argue that bears, as wide-ranging carnivores, are particularly vulnerable to the exhibition of stereotypical behaviors, requiring both cognitive enrichment and species-specific enclosure improvements to promote optimal psychological welfare. Naturalistic enclosures that include soft substrate (such as dirt or sand) benefit bears as these materials allow for resident animals to engage in species-typical behaviors such as digging (O'Grady et al. 1990). This allows animal care staff to facilitate species-typical behaviors by introducing novel enrichment in the form of burying food and other enrichment items. When considering the design of naturalistic enclosures, it is critical to consider what constitutes *naturalistic behavior* for each species of ursid. For example, polar bears (*Ursus maritimus*) appear to benefit from flat enclosures, rather than the rocky or uneven habitats that benefit grizzly bears (*Ursus arctos*; Van Keulen-Kromhout 1978). Enclosures that provide a view extending beyond the animals' enclosure itself are associated with a reduction in stereotypical behaviors such as pacing (Shepherdson et al. 2013). Further modifications to enclosures to encourage naturalistic foraging behaviors such as pitfall feeders and log piles are useful in encouraging species-typical behaviors (Law and Reid 2010). Exposure to environmental enrichment is likewise critical in providing optimal welfare outcomes for bears living in human care. Common approaches to environmental enrichment for bears include object-based enrichment designed to encourage natural foraging behaviors such as honey logs, underground food pipes, wobble tree feeders (Veeraselvam et al. 2013), and live fish. Other enrichment such as scent trails has been demonstrated to be effective in stimulating species-typical exploratory and foraging behaviors in various bear species (Law and Reid 2010).

While it is important to keep the cognitive capabilities of bears in mind while designing both enclosures and enrichment, it is also useful in evaluating environmental enrichment protocols. For example, Keen et al. (2014) demonstrated that, through building upon existing knowledge regarding quantity discrimination in bears (e.g., Vonk and Beran 2012), cognitive bias tasks can be successfully employed in order to assess welfare in captive grizzlies. Still, this assessment found no effect of enrichment manipulation. Additional work with one black bear revealed that the bear responded optimistically in general; however, this study did not evaluate the effects of enrichment specifically (McGuire et al. 2017). Ross (2006) found that choice and control over enrichment were directly tied to positive welfare outcomes (i.e., an increase in species-typical behaviors and reduction in stereotypies). Additionally, physiological measures such as fecal glucocorticoid metabolites (FGM) have been found to be strongly linked to stereotypical behaviors in bears (Shepherdson et al. 2013).

There are many who argue that, in addition to this naturalistic approach to environmental enrichment for captive bears, artificial cognitive enrichment should also be considered as a viable approach to improving captive bear welfare. Specifically, training through operant conditioning challenges the animals cognitively in novel ways. Training captive animals to voluntarily participate in regular veterinary procedures (i.e., blood draws, examinations, etc.) as well as daily husbandry tasks (i.e., stationing in a particular place to allow caretakers the opportunity close a gate, etc.) has been shown to reduce behavioral and physiological indicators of stress in marine mammals (see Clark (2013) for a review). In bears, participation in such training – as well as training associated with their participation in cognitive testing (i.e., the use of a touchpad) – has been demonstrated to be enriching (Perdue 2016).

## Conclusion

As zoological institutions become more involved in the long-term conservation of large carnivores such as bears, it is even more critical that new and

innovative behavioral interventions be instituted to ensure the quality of the captive environment. In addition to managing captive populations, our understanding of ursid behavioral ecology, cognition, and problem-solving capabilities further enhances our ability to coexist with and conserve these apex predators in the wild.

## Cross-References

- Bear Cognition
- Bear Life History
- Bear Navigation
- Bear Sensory Systems
- Carnivora

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## Bear Morphology

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## Introduction

The family Ursidae comprises eight extant species, generally classified into three subfamilies:

Ursinae (polar bear *Ursus maritimus*, brown bear *Ursus arctos*, American black bear *Ursus americanus*, Asiatic black bear *Ursus thibetanus*, sloth bear *Melursus ursinus*, and sun bear *Helarctos malayanus*), Ailuropodinae (giant panda *Ailuropoda melanoleuca*), and Tremarctinae (Andean bear *Tremarctos ornatus*) (Wagner 2010). Bears evolved about 20–25 million years before present (McLellan and Reiner 1994). Of the extant species, the giant panda diverged 12–20 million years ago, followed by the Andean bear about 7–13 million years ago, whereas the six species in the Ursinae diverged during the last 5 million years (Kumar et al. 2017). Bears attained a wide geographical distribution, mostly in the northern hemisphere (Kumar et al. 2017).

Morphologically and taxonomically, bears possess the distinguishing traits of Carnivora but, with the exception of the polar bear, are not obligate carnivores and often have diets comprised predominantly of plant matter. The generalist omnivore strategy that most bear species evolved with allows them to successfully occupy a broad range of habitats (Robbins et al. 2004). However, feeding on plant material with the typical carnivore digestive tract means relatively inefficient digestion. Complex hydrocarbonates

cannot be dissolved if not thoroughly chewed by flat crunching teeth and fermented properly in a complex stomach and long intestines. Bears compensate for these inefficiencies by consuming large quantities of food and selecting more easily digestible plants or plant parts, such as fruits. Many partly digested seeds remain viable for germination, thus making bears excellent seed dispersers (Koike et al. 2011).

General Morphology

The Ursidae family represents the largest terrestrial carnivores, although body mass ranges substantially from the largest polar bears to the smallest sun bears (Table 1). Bears have a robust body with a short tail and short but powerful limbs. All bears are quadrupedal plantigrades with five nonretractable claws. The head is large and has an arctoid shape with small eyes and rounded, erect ears. Bears have prehensile lips and tongue; the tongue is particularly long (20–25 cm) in sun bears and aids in the consumption of honey and insects. The coat consists of long guard hair and underfur of variable density depending on species and season. Sun bears do not have underfur, whereas underfur in sloth bears

Bear Morphology, Table 1 Adult body measurements of extant bear species

| Species                       |                     | Body dimensions          |                   |                         |                          |
|-------------------------------|---------------------|--------------------------|-------------------|-------------------------|--------------------------|
| Latin                         | English             | Body mass (kg)           | Total length (cm) | Height at shoulder (cm) | Chest circumference (cm) |
| <i>Ursus arctos</i>           | Brown bear          | F: 80–250<br>M: 130–550  | 160–290           | 90–150                  | F: 110–140<br>M: 130–160 |
| <i>Ursus maritimus</i>        | Polar bear          | F: 150–250<br>M: 300–650 | 190–290           | 130–160                 | F: 175<br>M: 200         |
| <i>Ursus americanus</i>       | American black bear | F: 40–150<br>M: 60–225   | 130–200           | 70–100                  | F: 45–100<br>M: 45–125   |
| <i>Ursus thibetanus</i>       | Asiatic black bear  | F: 35–140<br>M: 60–200   | 120–200           | 70–100                  |                          |
| <i>Melursus ursinus</i>       | Sloth bear          | F: 50–95<br>M: 70–145    | 150–200           | 60–90                   | F: 85<br>M: 90–95        |
| <i>Helarctos malayanus</i>    | Sun bear            | F: 25–65<br>M: 35–80     | 105–155           | 70                      | 60–80                    |
| <i>Ailuropoda melanoleuca</i> | Giant panda         | F: 70–100<br>M: 85–125   | 135–195           | 60–90                   | 70–105                   |
| <i>Tremarctos ornatus</i>     | Andean bear         | F: 60–80<br>M: 100–175   | 130–190           | 70–80                   | 130                      |



is generally lacking or light, an adaptation to climatic conditions of their distributions. Bears are skillful in running, jumping, swimming, standing on hind legs, climbing, digging, and tearing.

## Coat

Although several bear species were named based on their coat color, substantial variations exist within each species. Brown bears have mostly light to dark brown fur, but the legs and shoulder hump can be almost black, including light-colored tips of hair that give these bears a “grizzled” look and contributed to the common name of grizzly bear used in interior portions of their range in North America. A small percentage of brown bears have fully black coats (Fig. 1). Young bears frequently have white patches, typically in the form of a chevron on the chest and neck. These patches become smaller with age and usually disappear fully, but some bears keep them their entire lives. Of all bear species, color morphs of American black bears (Fig. 2) are most geographically defined. They are uniform black in much of eastern North America, but different shades of brown are common in western regions and particularly the southwestern USA. Some populations on the Pacific coast of British Columbia, Canada, have many completely white individuals (“Kermode”

black bears), whereas a gray color morph occurs in southeastern Alaska. Because coat color is an inherited trait, different color morphs can be observed in a single litter of offspring. Polar bears are also called white bears because of the white appearance of their fur, but polar bear hair is free of pigment with a transparent, hollow core that scatters and reflects visible light. Some individuals may appear yellow or even light brown due to oils in their fur from prey they consume. The skin of polar bears is black. The unique and contrasting black and white fur of the giant panda has become one of the most recognizable symbols of wildlife conservation worldwide. They have a thick, woolly coat with black limbs, ears, and band across the shoulder and oblong-shaped, black eye patches. The remaining four species are all predominantly black, but their fur characteristics vary. Sun bears have the shortest fur of any bear species, whereas sloth bears have the longest fur, sometimes up to 20 cm, particularly around the neck, shoulders, and back, which likely facilitates cubs in climbing and riding on the back of their mother (Fig. 3). Almost all Asiatic black bears, sun bears, and sloth bears have a cream-colored crescent shape on the chest. This shape gave rise to the names “sun” bear (Fig. 4) and, for the Asiatic black bear, “moon” bear. These shapes and patterns vary and have been used to identify unique individuals in field studies (Ngoprasert et al. 2012). Andean bears have rough

### Bear Morphology,

**Fig. 1** The coat color of brown bears is quite variable and can even be almost black, like this of a young European brown bear male in Croatia. (© D. Huber)





**Bear Morphology,**

**Fig. 2** Female American black bear with cub, Custer-Gallatin National Forest, Montana, USA. (Courtesy C. Whitman – US Geological Survey)



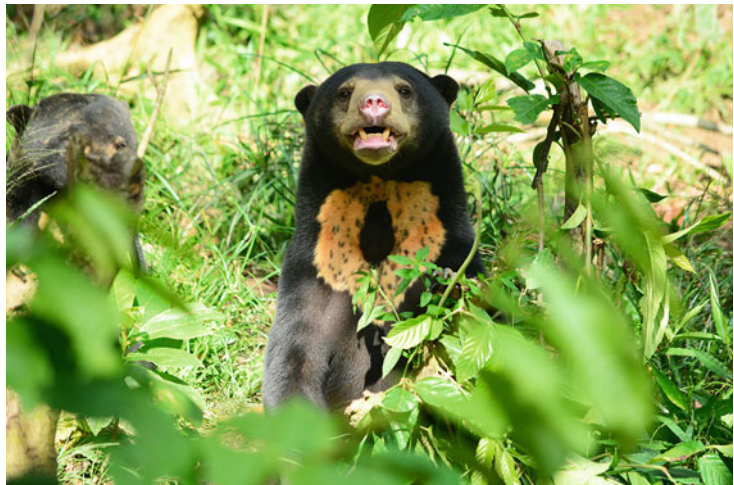
**Bear Morphology,**

**Fig. 3** Sloth bears have the longest fur of any bear species, which facilitates cubs routinely climbing and riding on the back of their mother while searching for food, particularly termites and ants. (Courtesy © J. Swenson)



**Bear Morphology,**

**Fig. 4** Several bear species, such as this sun bear, have a cream-colored crescent shape on the chest. The shape and pattern vary and have been used to identify unique individuals in field studies. (Courtesy © L. M. Chiew – Bornean Sun Bear Conservation Centre)



black fur and unique, highly variable patterns of cream-colored fur around the eyes, which led to the common name spectacled bear. These patches of light-colored fur often extend down to the throat and chest and are sufficiently unique to identify individual bears.

## Body Shape and Skeletal Structure

Body mass varies greatly among species, within species, among different sex and age classes, seasons, and geographic areas. The sun bear is the smallest species, with adult body mass ranging from 30 to 80 kg, whereas body mass of adult male polar bears and brown bears can be ten times greater (Table 1). Although polar bears have the largest overall average size of all bear species, some individual brown bears in highly productive habitats can reach a body mass comparable to the largest polar bears. Sexual dimorphism occurs in all bears and can be particularly pronounced in the larger species, with males sometimes reaching double the body mass of females. Female bears typically reach their maximum skeletal size and body mass soon after sexual maturity, when they start investing in reproduction and rearing offspring, whereas male bears continue to grow and reach maximum structural body size years later, gaining competitive advantage for breeding and reproductive success (Bartareau et al. 2011). Body mass can vary by season, which is most prominent during fall hyperphagia among bears in temperate climates, when they consume copious amounts of food in preparation for hibernation and reach peak seasonal body mass (Kojola and Laitala 2001; Swenson et al. 2007). Habitat productivity strongly influences bear diets and, in turn, affects body mass and size. For example, all morphological measurements for both sexes were different in a study of four brown bear populations in Alaska, USA, with access to salmon resources as a key determining factor (Hilderbrand et al. 2018). Additionally, morphological measures within populations exhibited twofold differences for females and three- to fourfold differences for males. These differences suggest substantial plasticity in life history strategies, allowing brown

bears to adapt to changes within and across a variety of ecosystems (Kingsley et al. 1988; Hilderbrand et al. 2018).

Bears have a robust skeletal structure, with relatively short limbs and heavy bones and large scapula and pelvis to support their body mass. The forelimbs are strong and are used in various activities, ranging from digging for foraging or den construction to killing prey and interactions with other bears. Bears are quadrupedal with large, plantigrade feet, which likely enhances support of their large body mass and provides balance when they stand on their hind feet, which they frequently do to obtain olfactory or visual cues from their surroundings (Fig. 5).

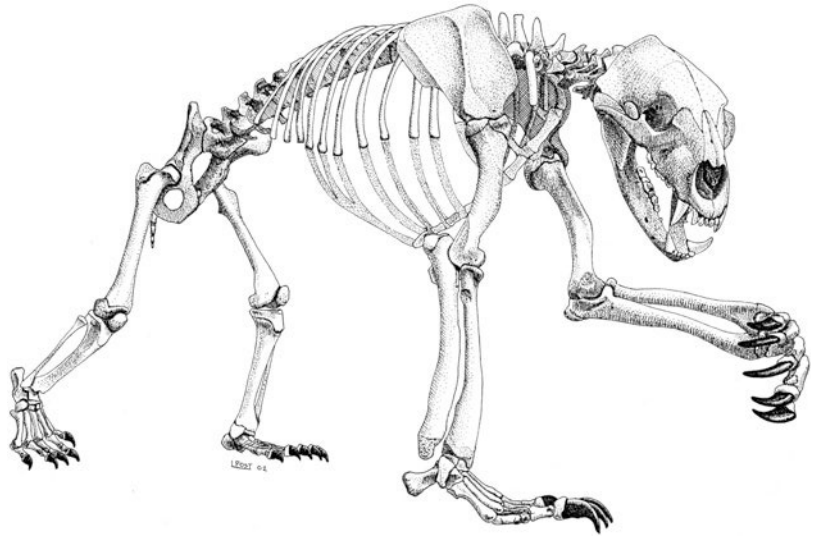
The front paws of bears are sufficiently dexterous to aid in foraging for fruits, leaves, and insects. This dexterity is enhanced in the giant panda with an enlarged radial sesamoid bone that acts as a pseudo thumb for grasping bamboo stems. The digital and plantar foot pads range from nearly naked in sloth bears and sun bears to extensive hair separation in polar bears, providing traction on snow and ice. In sloth bears, the digital pads are fused. Bears have nonretractable claws that they use for climbing, digging, and tearing. Front claws are larger than hind claws. Claw size and shape are characteristic morphological features among bears, revealing key differences in their ecology. Curved claws benefit bears that often climb trees to forage, rest, or den, including sun bears (Fig. 6), Andean bears, and American and Asiatic black bears, whereas long, elongated claws are important tools for digging roots or ripping (brown bear) (Fig. 7), or excavating termites (sloth bear). Polar bear claws combine these features and are thick, curved, and sharp to catch and hold large prey and provide traction on ice.

## Locomotor System

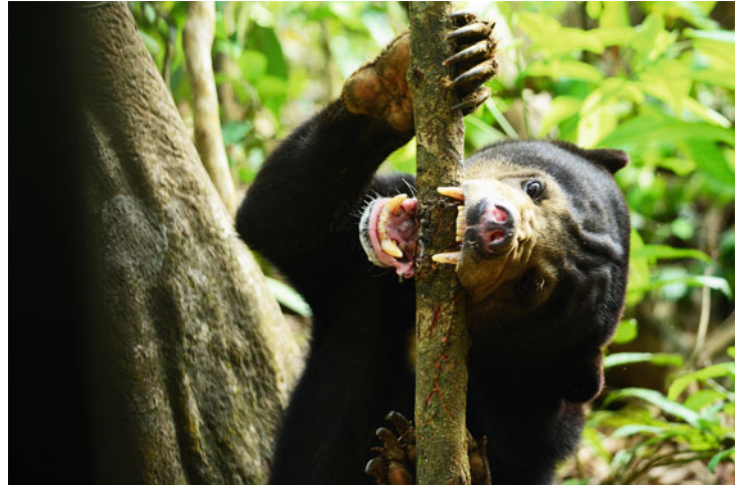
With their body mass distributed toward the hind feet, walking locomotion is in the form of a lumbering gait. Bears can reach speeds as high as 55 km/h for short periods of time, but the energetics of their plantigrade posture dictate a greater

**Bear Morphology,****Fig. 5** Bear skeleton.

Bears have plantigrade locomotion and heavy skeletal structure to support their large body mass. They have powerful forelimbs and large feet to support a wide variety of activities. Their skull is massive and accommodates large and strong chewing muscles. Illustration is of an American black bear specimen from the Pratt Museum, Homer, Alaska, USA. (Courtesy © L. Post)

**Bear Morphology,**

**Fig. 6** Sun bears have long, sharp claws and large, robust canine teeth, which aid in opening up tropical hardwood trees to access bees and other insects, larvae, and honey. (Courtesy © L. M. Chiew – Bornean Sun Bear Conservation Centre)



economy while moving at relatively slow speeds. For example, the average locomotor speed of female polar bears over 10-min intervals on sea ice averaged 3.4 km/h (Pagano et al. 2018). Muscles of the bear body have an intensive activity of enzymes of aerobic and anaerobic metabolism that may help support the wide-ranging movements typical of bears; ATP-ase points to the high contraction capacity of muscle fibers (Kozarić et al. 1989).

The sacral vertebrae are fully fused in adult bears and firmly connected to pelvic bones. The short tail has no function in locomotion. The pelvis and femur are connected with the largest

muscles of the body, some of which extend to the knee. The whole system from the caudal portion of the backbone to the tibia is compacted, which assists in strong and enduring pacing and galloping. The fibula is small and of minor importance. Tarsal, metatarsal, and phalangeal bones support a large sole and relatively short hind claws. The scapulohumeral joint is shallow and the clavicle is missing. However, shoulder muscles are large and allow a wide range of motion.

A supratrochlear foramen in the humerus of brown bears can be observed only in some young individuals, indicating common ancestry with the Felidae but also early evolutionary



### Bear Morphology,

**Fig. 7** Claws of the front (top) and hind (bottom) feet of a brown bear. Claw size and shape are characteristic morphological features among bears, revealing key differences in their ecology. (F. T. van Manen – US Geological Survey)



separation, and now occurs only as a sporadic atavistic trait (Gužvica et al. 1995). The radius and ulna are not connected where they articulate proximally with the humerus and distally with the carpal bones and are crossed so the paw faces the ground, as is typical for a quadrupedal animal. This means that the proximal ulna is medial to the radius, whereas the distal ulna is on the lateral side (Adams and Crabtree 2012). Hence, the elbow joint allows a large angle of flexion and extension but also supination and pronation. Carpal, metacarpal, and phalangeal bones are packed with joints that give strength and stability for walking while providing the dexterity described previously, which is aided by curved or elongated claws.

Four bear species are arboreal or semiarboreal (sun bear, Andean bear, Asiatic black bear, American black bear) and whereas giant pandas spend most of their time on the ground, they are excellent climbers. Common to these species, curved claws facilitate climbing and are particularly well developed in sun bears, the most arboreal bear species. Several adaptations in the hind limbs aid tree climbing. For example, studies on the sun bear and giant panda showed that their hind limbs have a well-developed fleshy portion of the musculus tibialis cranialis that reaches the distal end of the tibia and is attached to the ossa metatarsalia via a short tendon (Sasaki et al. 2005). Additionally, the

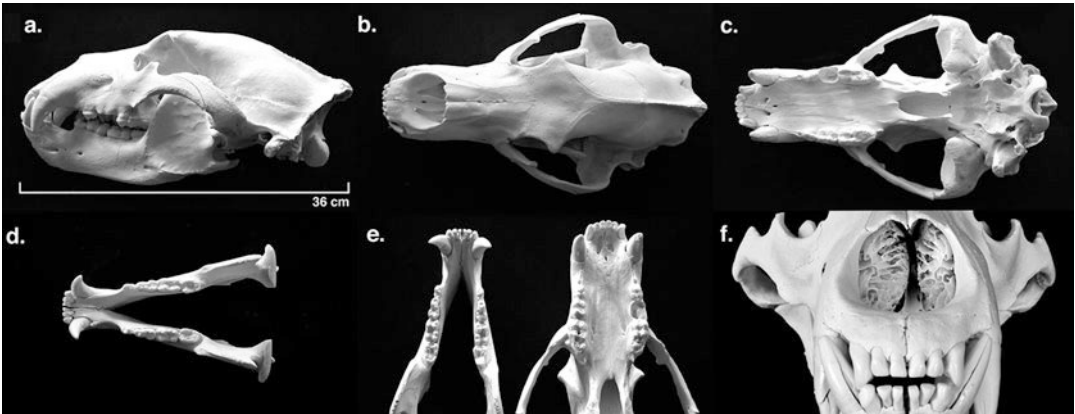
musculus popliteus inserts near the distal end of the tibia. Combined, these adaptations allow stable dorsiflexion and supination of the foot and efficient pronation of the crus by leverage (Sasaki et al. 2005).

### Skull and Dentition

The arctoid shape of the head is supported by a massive and distinctive skull. Male skulls have a pronounced external sagittal crest (crista sagittalis externa) and are larger than female skulls (Farkas et al. 2009). The skull of bear species has diagnostic morphological features (including brown bears vs. cave bears; Gužvica et al. 1996), but distinct differences can exist even among populations of the same species. For example, measurable differences in skull morphology have been reported among brown bear populations (Fig. 8) (Sladek 1991; Colangelo et al. 2012). The brain case is “squeezed” by spatial temporal fossa (fossa temporalis) to accommodate large and strong chewing muscles. The space for muscles is bridged by a markedly wide zygomatic arch. In addition to the large surface of temporal bones, the most dorsal portions of the temporalis muscles have their origin on the external sagittal crest, which is most pronounced in adult males. On the mandible, musculus temporalis attaches to an extended and

large coronoid process. Strong masseter muscles originate at the zygomatic arch with insertion on tuberosity and outer surface of the mandibular ramus, and, aided by pterygoid muscles, they together exert enormous bite force (Christiansen and Wroe 2007). The typical extended nose accommodates spatial nasal conchae covered by epithelium with millions of olfactory cells, giving the bear an extraordinary sense of smell. The eyes are located in relatively small fossa orbicularis and are pointed forward. With such positioning of eyes, bears have a relatively narrow angle of vision but better three-dimensional sight, similar to primates. The maxilla and mandible host sets of very specialized, strong teeth (Table 2). They each hold 6 (3 + 3) relatively small incisors, placed and shaped to efficiently procure smaller-sized food

items and to scratch edible surface tissue from bones. The two pairs of large canines facilitate various aspects of food consumption (e.g., kill and hold down large prey, ripping trees or logs) but also serve as a formidable weapon in intra- and interspecific interactions. In the closed mouth, they fit closely together, paired from the upper and lower jaw. Posterior to the canines are two to four small, premolar teeth. The first three premolars are vestigial remains of atavistic jaws and serve no function in chewing food. The second and third premolars are small and often do not form or erupt, or are lost, leaving a diastema between the canines and functional cheek teeth. Premolar teeth are used by researchers and managers to age bears based on cementum annuli analyses (Matson et al. 1993). Carnassials are



**Bear Morphology, Fig. 8** Brown bear skull. (a) Lateral view, (b) dorsal view, (c) ventral view, (d) dorsal view of mandible, (e) dentition, and (f) anterior view detail showing complex nasal conchae. Scale bar applies to figures

(a)–(e). Specimen is of a 9-year-old male brown bear, Yellowstone National Park, USA. (F. T. van Manen – US Geological Survey)

**Bear Morphology, Table 2** Dental formulas of extant bear species

| Species                       |                     | Dental formula                      |
|-------------------------------|---------------------|-------------------------------------|
| Latin                         | English             |                                     |
| <i>Ursus arctos</i>           | Brown bear          | I3/3, C1/1, PM2–4/2–4, M2/3 = 34–42 |
| <i>Ursus maritimus</i>        | Polar bear          | I3/3, C1/1, PM2–4/2–4, M2/3 = 34–42 |
| <i>Ursus americanus</i>       | American black bear | I3/3, C1/1, PM2–4/2–4, M2/3 = 34–42 |
| <i>Ursus thibetanus</i>       | Asiatic black bear  | I3/3, C1/1, PM2–4/2–4, M2/3 = 34–42 |
| <i>Melursus ursinus</i>       | Sloth bear          | I2/3, C1/1, PM2–4/2–4, M2/3 = 32–40 |
| <i>Helarctos malayanus</i>    | Malayan sun bear    | I3/3, C1/1, PM2–4/2–4, M2/3 = 34–42 |
| <i>Ailuropoda melanoleuca</i> | Giant panda         | I3/3, C1/1, PM2–4/2–4, M2/3 = 34–42 |
| <i>Tremarctos ornatus</i>     | Andean bear         | I3/3, C1/1, PM2–4/2–4, M2/3 = 34–42 |

the modified fourth upper premolar and the first lower molar paired to occlude in a shearing manner. Bears have a flattened and more blunt carnassial pair than felid or canid species. This trait reflects the bear's diet, as the flattened carnassials are effective both for slicing meat and grinding vegetation. The two upper and three lower molars are bunodont and are evidentiary that a large proportion of the diet of bears consists of plant matter. Although molar surfaces are quite flattened, they are distinctly different from molars found in true herbivores.

## Digestive Tract

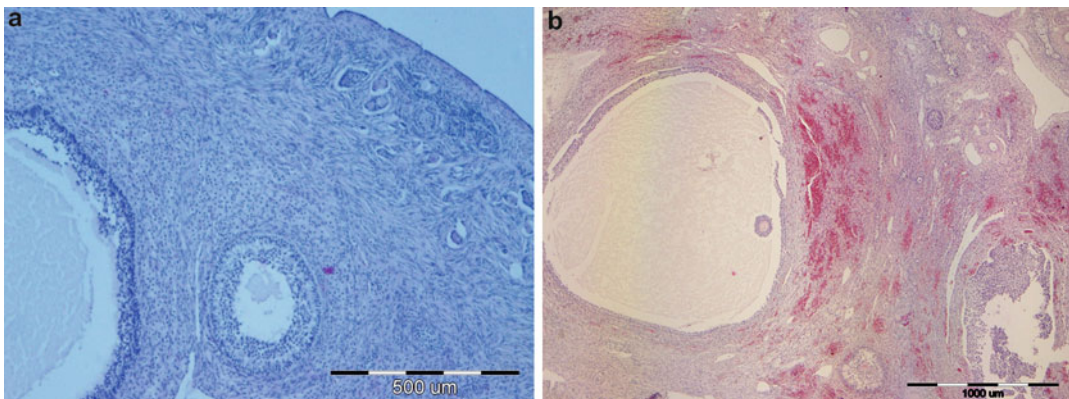
The gastrointestinal tract of bears is typical of Carnivora, with a monogastric stomach and short, undifferentiated intestines. Food can move through the digestive tract in as little as 6–8 h, sufficient for digestion of sugars, starches, fats, and proteins (Pritchard and Robbins 1990). However, because bears lack a cecum or other specialized gastrointestinal areas, cellulose digestion is poor. As a result, bears consume large quantities of food and seek out the most nutritious and abundant foods in generally omnivorous diets. The polar bear and giant panda are exceptions and represent the extremes of an extraordinary range of diets within the Ursidae. Polar bears are obligate carnivores and have evolved as apex

predators of the northern Arctic sea ice, with ringed seals as their chief prey (Durner and Atwood 2017). Because prey availability is low, polar bear stomachs can expand to hold as much as 20% of their body mass. In sharp contrast, giant pandas are specialized herbivores, with approximately 99% of their diet consisting of bamboo species. However, digestion of fibrous plant matter in bamboo is limited by the carnivorous gastrointestinal tract, and recent studies showed that giant pandas do not possess the specialized gut microbiome typical of herbivores that assist in the digestion of cellulose and hemicellulose (Guo et al. 2018). Giant pandas may compensate for these limitations through increased food intake.

## Other Organ Systems

### Reproductive

Ovaries produce eggs in Graaf follicles during the mating season, but ovulation is typically postcoital (Fig. 9). Fertilized eggs develop to the blastocyst stage when they reach the uterus, which has two fully divided horns (uterus bicornis). In the horns of the uterus, one to four (exceptionally five or six) embryos spend up to 6 months in a dormant stage called embryonic diapause or delayed implantation, a reproductive specialization that occurs in approximately 100 mammalian species of 7 different orders (Renfree and Shaw 2000).



**Bear Morphology, Fig. 9** (a) Cortex of the brown bear ovary containing multiple follicles; Bar: 500  $\mu\text{m}$  (b) tertiary follicle in the cortex of the ovary; Bar: 1000  $\mu\text{m}$ .

Ovaries produce eggs in Graaf follicles during the mating season but ovulation is typically postcoital. (Courtesy © P. Kierzkowski)



**Bear Morphology,**

**Fig. 10** Bears have a multi-lobed (reniculate) kidney with increased surface area for removing toxins from the body more efficiently compared with a non-lobed kidney. Specimen is of a brown bear. (Courtesy © S. Reljić)



B

The proposed evolutionary significance of delayed implantation is that it uncouples the timing of breeding from parturition so they both occur during environmental conditions favorable for reproductive success. A consequence of this strategy is that newborn cubs of all bear species are very small (~0.5% of maternal body mass) and altricial, with closed eyes and short hair, fully depending on nourishment in the form of lactation and care from their mother. Thus, pregnant females of all bear species, including non-hibernating bears, give birth in a protective, maternal den and remain there until the cubs are 2–3 months of age.

In the tubules of testicles (vesiculæ seminales) of adult males, active sperm can be found during all seasons. The penis is supported by a penis bone (baculum) as in all carnivores and cetaceans.

**Urinary**

The bear kidney is multi-lobed (reniculate kidney) as is also found in pinnipeds and cetaceans (Fig. 10). Bovines are the only other terrestrial mammals whose kidneys do not lose their fetal lobulation. Kidneys with this morphology have increased surface area for removing toxins from the body more efficiently compared with a non-lobed kidney. This may be particularly important for bears during hibernation, when they demonstrate a remarkable ability to recycle urea nitrogen (Stenvinkel et al. 2013).

**Respiratory and Circulatory**

Similar to other organic systems in bears, the organs for breathing and blood circulation are massively developed and satisfy a broad range of needs, from short bursts of strenuous activities such as chasing prey, to climbing trees or walking hundreds of kilometers in search of food or other resources, to extended periods of fasting and hibernation. Respiration and heart rates in hibernating bears decrease much more than non-hibernators can achieve, although not as low as typically observed in smaller hibernating mammals (Hellgren 1998).

**Cross-References**

- [Bear Cognition](#)
- [Bear Diet](#)
- [Bear Life History](#)
- [Bear Locomotion](#)

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## Bear Navigation

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## Synonyms

Homing; Movement; Olfaction; Ursid

## Introduction

Some bears occupy incredibly large home ranges, particularly in low-productivity habitat. It is thought that, for some species of bear, home range size is primarily influenced by the availability of food (Koehler and Pierce 2003). Bears are highly mobile and can travel immense distances, which is critical in species that often rely upon ephemeral food sources. Some species like the sloth bear (*Melursus ursinus*) have comparatively small home ranges, possibly due to the prevalence of concentrated, relatively ubiquitous food sources like insects and fruits in their diet. More omnivorous bears such as brown bears (*Ursus arctos*) and American black bears (*Ursus americanus*) tend to have larger home ranges in less productive habitat like arctic tundra and smaller home ranges in highly productive areas, like coastal regions with salmon streams. Polar bears (*Ursus maritimus*) inhabit some of the largest home ranges of any ursid. As the most purely carnivorous bear, they depend largely upon irregularly distributed seals for food and must move across shifting ice to locate their prey and find mates. Polar bears sometimes travel long distances to return to land to create maternity dens or to fast during sea ice breakup when open water makes terrestrial fasting more energetically efficient than continuing to hunt. Regardless of home range size, navigation is essential in locating food sources and mates. Due to the inherent difficulty of studying wide-ranging large carnivores and the special challenges relating to the study of animal navigation, little is known about how bears navigate large and sometimes featureless landscapes.

## Polar Bear Navigation

Navigation-related questions are particularly intriguing with respect to marine animals that lack immobile external landmarks to guide them. Polar bears live in a dynamic high-latitude environment of sea ice, which may consist of more stable, landfast ice or drifting pack ice characterized by continual changes in extent and configuration as ice sheets break, refreeze, and collide

(Ferguson et al. 2000). Therefore, more pelagic polar bears (i.e., bears that primarily live on sea ice and rarely spend time on land) like those inhabiting the Barents Sea lack fixed navigational landmarks. Barents Sea polar bears perform seasonal migrations but do not alter their large-scale movements to negate displacement caused by the drifting sea ice, likely because local prey availability is more important than maintaining a home range in a certain absolute location (Mauritzen et al. 2003). However, some studies have shown that polar bears on pack ice can compensate for sea ice drift (Larsen et al. 1983) and maintain site fidelity for activities that are typically terrestrial, like denning. This implies that bears are able to sense their position on moving ice and compensate accordingly. Note that most polar bear movement data is from collared females: collars do not stay in place on males because the circumference of their necks is greater than that of their heads (Pagano et al. 2012).

Unlike other bear species, polar bears regularly undertake long-distance pelagic swims. A study of 52 adult females in the southern Beaufort and Chukchi Seas showed that 38% of these bears swam long distances ranging from 53.7 to 687.1 km in length and lasting 0.7–9.7 days, often accompanied by dependent cubs. The average distance traveled was 154.2 km over a period of 3.4 days. These swims were point-to-point and often occurred near the September sea ice extent minimum as bears traveled from unstable, unconsolidated sea ice to land or to pack ice (Pagano et al. 2012). Polar bears' ability to use olfactory, visual, and auditory cues would be diminished during long swims. Additionally, their destinations may be so distant as to be beyond their sensory capabilities, suggesting the presence of other navigational mechanisms. However, navigational mechanisms like internal compasses or the use of magnetic fields have not been studied in ursids (Sahanatian 2015).

In many locations, polar bears travel to land during the summer when the sea ice extent is nearing its minimum. It is unknown how females locate their summering grounds. Female polar bears in Hudson Bay preferred to come ashore at familiar areas for the summer during ice breakup

rather than stay on the sea ice longer and return to land at an unfamiliar location. Because these bears hunt while on the ice but fast on land, by maintaining site fidelity, they cost themselves the opportunity to gain additional energy (Cherry et al. 2013). Polar bears typically display fidelity with respect to spring feeding areas and denning locations (Wiig et al. 2003). Female polar bears returning to hunting grounds with cubs-of-year followed a similar heading and remained parallel to other traveling family groups. These females did not take the shortest route to the ocean and did not follow landscape features like streams (Ramsay and Andriashek 1986). The linear travel of these family groups suggests that polar bears have exceptional navigational abilities.

Polar bears could be using olfaction to navigate. Sea ice deforms to create ridges that average 2 m in height and 12 m in length, making use of vision to locate prey challenging. Indeed, ringed seal behavior seems to indicate that bears use olfaction while hunting. Hauled-out ringed seals face downwind, which would allow them to sense bears approaching from upwind via olfaction and would allow them to see bears approaching from downwind. A 2-year study of 123 Hudson Bay polar bears fitted with GPS collars revealed that bears traveled crosswind when winds were slow ( $<36$  km/h) in the winter, which would be consistent with crosswind olfactory search for prey. Crosswind movement is optimal for detecting odors in steady winds or during large-scale searches (Togunov et al. 2017).

## Homing

Studies of homing tendencies can also illuminate navigational strategies. Many bear species have remarkable homing abilities that often stimulate attempts to translocate problem animals. Homing research conducted using translocated bears has shown that it is unlikely that ursids rely exclusively on landmarks to navigate. In a 1986 study, five American black bears (two adult females, one subadult female, and two yearling males) were radio-collared and monitored for at least a year to establish the boundaries of their

home range. Each bear was then captured, drugged, and transported up to 60 km from their home range; they were unconscious for some or all of the transportation period. Despite their novel surroundings, the two adult females traveled homeward quickly (one averaged 11.4 km/day). One female returned to her home range in 9 days; the other disappeared while on a direct course toward her home range, having traveled 43 km closer to home when she was last located. The adult bears moved at a steady pace homeward regardless of wind direction, so it is unlikely that they were solely dependent on receiving olfactory cues from their home range (Rogers 1986).

The younger bears did not home consistently. One male yearling did not return home, while the other yearling returned home in 1 week. The female subadult returned home after being translocated 25 km. She was then recaptured and transported 66 km (Rogers 1986), after which she did not return home. The mixed homing tendencies seen in these younger bears may be because bears leave their family groups and disperse as subadults. In American black bears and brown bears, male subadults are typically more likely to disperse and may travel farther away, whereas females may exhibit natal philopatry or disperse smaller distances (Larivière 2001; McLellan and Hovey 2001; Steyaert et al. 2012). This movement away from their mother's home range may be a way to avoid inbreeding (Steyaert et al. 2012).

A meta-analysis of 8 studies involving 77 translocated American black bears found that the 43 bears that did not return to their home range still exhibited a homeward orientation in their travel. This indicates that bears are not using random exploration or search patterns to return home. Moving bears very far ( $>120$  km) from their home range did not alter the proportion of bears that moved homeward, as might be expected if bears navigated using landmarks – hypothetically, bears would be less familiar with distant landmarks and would fail to navigate as well as bears released closer to their homes. However, bears translocated over 1400 km moved in random directions after release (Rogers 1987).

This suggests that American black bear navigation may depend upon local cues accessible only within shorter ranges. Some bear populations regularly, predictably make shorter-range movements: in some areas, bears travel long distances to take advantage of seasonally available ephemeral food sources like fruits and nuts (Noyce and Garshelis 2011), and select populations of bears migrate to denning areas. Studies of these seasonal shifts in bear movement could illuminate which cues are most important for successful navigation.

## Social Cues

One such study was conducted on an American black bear population in Minnesota. Eighty three female and 124 male bears were radio tracked from 1981 to 1990, with 64 bears of each sex being tracked for multiple years, in an attempt to determine how bears know when and where to migrate in the fall. These data indicated that it is unlikely that cubs learn migratory behaviors or routes from their mothers: migrations performed while cubs accompanied their mother did not influence whether the cubs later migrated as independent juveniles. Siblings behaved differently following family dissolution. Some siblings migrated, while some remained in their summer home ranges. In cases where multiple siblings migrated, in all but one instance, siblings traveled in different directions to different final destinations. Numerous males migrated to denning areas despite the fact that their mothers never migrated to den. Additionally, fall movements did not appear to be instinctive, as bears followed different routes to varying locations each year. Landscape features included wetlands and lakes. Bears traveled around lakes but directly through wetlands. It is possible that in more extreme landscapes, geographical formations could funnel bears into more distinct paths. Bears did not appear to use food gradients to navigate because highly productive foraging grounds were patchily distributed rather than present along a gradient (Noyce and Garshelis 2014). This study reinforced earlier research (Rogers 1986) showing

that bears were likely not reliant on long-distance olfactory indicators of ripening food sources, as their movements did not follow prevailing winds. Bears departed at different times and traveled in different directions, which would not be the case if wind-borne scents instigated their movements. The authors suggest that bears used social cues to determine their routes. In 1988 an anomalously large number of females (32) left their home ranges in late summer. During these migrations, 53% of these bears were located in association with a neighboring female bear that normally occupied a home range adjacent to the focal bear's range. Similarly, of 28 bears that were located while moving to a denning area near another collared bear, 24 were associated with a bear from a neighboring home range. Subadults and female bears often foraged, denned, and traveled in corridors away from adult males, while adult males used other areas. Most bears that were tracked since cubhood did not return to the areas where they had foraged with their mothers. Male bears may disproportionally influence population movement patterns, as their long-range travel as subadults may give them greater knowledge of distant food resources. Additionally, they may more directly influence the movements of other bears, as females and subadults often stay away from adult males to avoid conflict (Noyce and Garshelis 2014). Chemical communication via rub trees and other marked objects may influence subadult behavior; some bear species are capable of discerning at least age, sex, and reproductive status from scent cues alone (Rosell et al. 2011; White et al. 2002, 2004). Additional research is needed to concretely demonstrate the link between social cues, navigation, and large-scale movements.

## Working Memory

On a smaller scale, bears may rely upon working memory to locate active feeding sites or other resources. Captive adult giant pandas (*Ailuropoda melanoleuca*; eight males, nine females) were administered a spatial memory task between November 2009 and February



2010, when wild male pandas experience elevated testosterone and expand their ranges prior to the breeding season. Eight feeders were placed in a circle. Four were baited, but all feeders were scented with the food item, and feeders were structured such that there were no visual cues to indicate if the feeder was empty or full. Pandas were allowed to explore the feeders. The next day, all feeders were scented, but none contained food. All pandas were more likely to visit the previously baited feeders during the first four trials. In the remainder of the nine trials, male pandas were significantly more likely to visit previously baited feeders than were females. Males were less likely to revisit feeders that they had already checked during that session than females. The authors suggest that these results reflect the importance of working memory in male giant pandas during range expansion, which allows males to better track the locations of females and marking sites and thus potentially be more reproductively competitive (Perdue et al. 2011).

## Conclusion

Although many bear species routinely travel long distances and exhibit site fidelity, only a few species have well-characterized home ranges, dispersal tendencies, and long-range movement patterns throughout their range. Bear navigational mechanisms remain largely unknown. Ursids exhibit remarkable homing capabilities and may use social cues to determine movement patterns. Bears may follow olfactory cues to find prey, other bears, and to return to familiar sites from new locations, but because they seem to be able to navigate regardless of wind directionality, they are likely also using other navigational mechanisms like celestial or magnetic cues.

## Cross-References

- [Bear Life History](#)
- [Bear Locomotion](#)
- [Bear Sensory Systems](#)
- [Bear Cognition](#)

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## Bear Sensory Systems

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## Introduction

Bears evolved and diverged beginning in the late Oligocene and early Miocene, about 20–25 million years ago, attaining a wide geographical distribution range. The family Ursidae includes eight extant species, generally classified into three subfamilies: Ailuropodinae (giant panda *Ailuropoda melanoleuca*), Tremarctinae (Andean bear *Tremarctos ornatus*), and Ursinae (Malayan or sun bear *Helarctos malayanus*, sloth bear *Melursus ursinus*, American black bear *Ursus americanus*, brown bear *Ursus arctos*, polar bear *Ursus maritimus*, and Asiatic black bear *Ursus thibetanus*). Morphologically and taxonomically, they possess all the traits of carnivores but, with the exception of the polar bear, have diets

often comprised primarily of plant matter. Most of the current bear species evolved with a generalist omnivore strategy, which allows them to occupy a broad array of habitats (Robbins et al. 2004).

Diverse habitats and their physical characteristics create challenges that influenced the evolution of sensory structures in bears. Bears must detect meaningful cues and signals through complex and challenging environments. An extreme example of this is the semiaquatic habitat that creates a unique sensory challenges for polar bear, a terrestrial mammal living as a marine mammal, which is not aquatic in the sense of navigating or hunting underwater like pinnipeds yet must still sense and interpret stimuli in both water and on land (Togunov et al. 2017; Lone et al. 2018). Additionally, bears are solitary and non-territorial, and as such, they benefit from conveying multi-modal cues to expedite the breeding season, to recognize family and kin, and to avoid conspecifics. Available anatomical, histological, and behavioral evidence suggests that bears are somatosensory specialists, with an excellent olfaction (Togunov et al. 2017), color vision (Bacon and Burghardt 1976), good hearing (Nachtigall et al. 2007; Owen and Bowles 2011), and sense of taste accommodated by gustatory papillae of both herbivorous and carnivorous characteristics (Pastor et al. 2008; Pastor et al. 2011). Bears also possess neuroanatomical correlates for the sensations received by their extremities (e.g., Kamiya and Pirlot 1988). They have been shown to rely mostly on olfaction, audition, and vision, although the significance and relative quality of some modalities remains to be investigated. Along with these commonly recognized senses, bears may also receive and respond to one other type of sensory information: magnetic fields. Evidence suggests that at least two terrestrial carnivores may respond to magnetic fields, and the retinas of bears contain a light-sensitive pigment that may react to magnetic fields (Nießner et al. 2016). However, although some individual bears can navigate without using familiar physical landmarks, the ability of bears to detect magnetic fields has not been tested.

## Visual Perception (Vision)

Overall, the eyes of bears are broadly similar to that of most mammals. As in all mammals, the retinas of bears' eyes contain two general types of receptive cells: rods and cones. Rods are more sensitive to light than cones, which require strong light stimuli. Rods are used to perceive movement, while cones permit the perception of color. Humans and some but not all primates are trichromatic. That is, they possess three kinds of cone cells. It's been suggested that this type of color vision has evolved to help some primates find fruits. However, although several bear species forage heavily on fruits at least seasonally, no bears possess trichromatic vision: bears do not see color as we do (Peichl 2005).

New research methods have recently revealed more diversity in mammalian photoreceptors than was previously known. Genotyping the areas responsible for the five vertebrate photoreceptor opsins (proteins) has revealed two cone types in the retinas of most diurnal mammals, including bears, making them dichromatic. The relative abundance of the two cone types in bears has not been evaluated, but those two types of cones should permit discrimination of short wavelength hues (violet, blue) from long wavelength hues (green, yellow, orange, red), but not between different long wavelength hues (Peichl 2005). The visual conditions under which polar bears live are unique among bears: the polar bear's snow- and ice-covered habitat has little variation in color, but great variation in illumination depending on weather and season. In addition, polar bears are semiaquatic, and light travels through water differently than through air. Given these environmental factors, polar bears might be expected to have reduced color vision, or to lack color vision altogether, as do many marine mammals (Peichl 2005), including their most common prey (Levenson et al. 2006). However, behavioral testing of polar bears and analyses of their DNA indicate that their color vision is similar to that of other terrestrial dichromats, with peak responsiveness to both violet-blue and green (Levenson et al. 2006). There has been little other behavioral testing of bears'

ability to discriminate among colors, but giant pandas discriminate green, red, and blue from gray (Kelling et al. 2006), and American black bears discriminate blue and green from gray (Bacon and Burghardt 1976). It is believed the remaining bears have similar abilities.

The broad pattern in mammals is for vision to evolve in ways that enable the mammal's ecological niche (Peichl 2005). It's believed that bears use their visual abilities primarily in foraging and in communication with other bears. Due to the orientation of their eyes, bears have binocular vision, which narrows their field of view but enhances their depth perception. Like other carnivores and many other placental mammals, the eyes of bears contain a reflective layer, the tapetum lucidum, which improves their ability to see under low conditions. In the wild, several if not all bear species display shifts in activity patterns that reveal their ability to use either brightly lit or poorly lit conditions to optimize their foraging success or avoid other individuals of the same species or potentially hazardous individuals from another species, including humans. Bears are often active primarily during the day (diurnal) when humans are not present, and at least two species, the Andean bear and the sun bear, are quite arboreal, but unlike other some other diurnal arboreal mammals (e.g., tree squirrels), their retinas are not cone-heavy. Thus, a bear's eye functions well at low light levels but without high spatial and temporal acuity.

## Auditory Perception (Hearing)

### Sound Perception

Bears have well-developed external ears with moderately stiff pinnal flanges and are assumed to have good hearing across species. American black and brown bears appear to use auditory cues in salmon streams (Klinka and Reimchen 2002). Polar bears can hear well in air the relatively low frequencies of vocalization produced by seals, their prey (Owen et al. 2016). The behaviors used by bears to locate sound are described as erecting the ears while lifting the head, then visual scanning to follow the source

of sound, and sniffing if the sound is of other animals, especially potential prey (Nachtigall et al. 2007).

The anatomy of the auditory region provides important insights about the hearing capacity. Anatomical descriptions of the auditory region exist for some among extant ursid species (giant panda, Andean bear, sloth bear, American black bear, polar bear, and brown bear; Segall 1943), as well as for some extinct bears. Until now, the polar bear and giant panda remain the most studied bear species in terms of auditory perception, investigated using evoked potentials or behaviorally (go, no-go response protocols). The size of the mammalian hearing apparatus increases throughout the class Mammalia in modest proportions with increasing body size. The middle ear ossicles have to withstand the forces produced by the tympanic membrane vibrations. Thus a large mammal with a large tympanic membrane, such as a polar bear, needs massive middle ear ossicles, which in turn results in a decreased capability for the transmission of high-frequency sounds. Therefore, considering their size, polar bears were expected to have moderately good low-frequency hearing; Owen and Bowles (2011) showed in-air best hearing sensitivity between 8 and 14 kHz and its upper limit to be 10–20 kHz lower than that of the small terrestrial carnivores. A decline in functional hearing in polar bears was observed at 125 kHz. Earlier work by Nachtigall et al. (2007) noted good hearing sensitivity of polar bears within a range of 11.2–22.5 kHz: absolute thresholds lower than 27–30 dB. The frequency range of the polar bear's hearing is wider than in humans, and they can hear well the relatively low frequencies of vocalization produced by seals, in air. Polar bears' auditory adaptation for underwater hearing remains unknown. Giant pandas have functional hearing into the ultrasonic range, with best sensitivity at 12.5–14.0 kHz and the lower and upper limits at 0.10 and 70 kHz, respectively (Owen et al. 2016). Compared with the polar bear, the giant panda's hearing is similar, although more sensitive at and above the frequency of 16 kHz. Interestingly, the sensitivity of panda hearing is lower within the range of

cub vocalizations, making cubs potentially vulnerable to dampening and fitness-reducing effects of anthropogenic ambient noise. An awareness of the studies species' acute and relatively wide-frequency hearing, and vulnerability for acoustic signals to be masked by anthropogenic noise during sensitive life stages, should be applied in anthropogenic noise management, as noise may impact bears. In the light of the deleterious potential of noise, additional research on the high-frequency hearing of all bears is needed.

### Vocalizations in Bears

The ability of bears to produce sound is strengthened by the presence of epipharyngeal pouches, which are constant and unique features throughout the family Ursidae. The histological structure of the pouches strongly suggests its functional involvement in the respiratory system. Additionally, they can enlarge and retract in response to various states of air inflation, apparently important in ursid phonation (Weissengruber et al. 2001). Bears vocalize during agonistic interactions with conspecifics, for example, to both defend young and secure resources. The agonistic vocalizations include “huffing” (loud deep breathing), “snorting” (loud expelling air through mouth and nostrils), “gurgling” (low-pitched warbling, throaty rumble), and “loud growling.” There have also been other close range vocalizations (e.g., “chuffing”) described for some of the bear species, with suggested but untested functions of appeasement, reassurance, greeting, coaxing, and maintaining contact at close range, most frequently used by females with cubs, by males and females during courtship and mating, and by adults and juveniles during friendly close contacts. Giant pandas will also “bleat” and Andean bears will also “trill,” but other bear species appear not to use these vocalizations. “Humming” has been observed in all bears but the giant panda, sometimes by adult bears but largely restricted to cubs (Baotic et al. 2013; Peters et al. 2007). Cub vocalizations are mainly restricted to nursing and grooming contexts and consist of calls such as “chuffs,” “croaks,” “growls,” “grunts,” and “huffs,” as well as

“barks,” “cries,” “screams,” “squalls,” “squawks,” “squeals,” “whimpers,” “woofs,” and “yelps” emitted in distress situations, and “humming” to communicate well-being to the mother.

While relatively little is known about the importance of auditory cues in bear foraging or risk avoidance, compared with other modalities used, vocalizations and their role in intraspecific communication have been thoroughly researched in some bear species. The giant panda is the most studied species in those aspects, with quantitative descriptions of the acoustic structure of male and female bleats showing that they code for sex, age, and size that is important to receivers in reproductive contexts. Individuals perceive and attend to this information when assessing potential rivals and/or mates. Male and female giant pandas can then adjust their behavioral responses according to the age- and size-related information broadcasted by bleats (Charlton et al. 2012). Several previous studies have provided verbal descriptions of other bear vocalizations, but quantitative descriptions, based on the analysis of acoustic properties, are relatively rare (Pokrovskaya 2013; Baotic et al. 2013).

### Olfactory Perception (Olfaction)

Adult bears are solitary, which is associated with a greater reliance on olfaction for communication. Although behavioral data suggests that bears use olfaction in foraging, such data also suggests that the most important use of olfaction by bears is in communication with other bears. Olfaction has been most thoroughly studied in the brown bear, polar bear, and giant panda, but indirect behavioral evidence on olfaction has been collected in all bears.

Research on the morphology of olfaction assumes that the relative surface area or size of a physical structure is correlated with the importance of that structure. The nasal cavity of bears, like other mammals, includes a maze of thin bones covered by a thin layer of skin with numerous chemical receptors. These receptors convert airborne molecules into electric impulses that are transmitted to and processed by the bear's brain.

The predatory polar bear has a relatively large portion of its nasal cavity devoted to olfaction, compared to the American black bear, brown bear, and other more omnivorous carnivores. In bears, the relative size of the olfactory bulb, the brain area focused on olfaction, is larger than expected based on the trend seen in other carnivore species (Gittleman 1991), and the size of the bony plate dividing the nasal cavity from the olfactory bulb is larger than would be expected in the American black bear, the brown bear, and especially the polar bear (Bird et al. 2014). Thus, bears appear to rely more on olfaction than do most other carnivores. Airborne compounds stimulate nerve impulses not only in the nasal cavity but also in the vomeronasal organ (VNO), which humans do not possess. The VNO is located on the roof of the oral cavity, and in many mammals, it is important for the reception and processing of compounds involved in intraspecies communication. Only a little research has been done on the morphology and function of the VNO in bears, but the VNO of brown bears and Asiatic black bears is well developed and similar to that of doglike carnivores, except that some gland cells are perhaps uniquely developed in bears.

Olfaction requires the conversion of airborne molecules into nervous impulses. Little is known of this process in most bears, but various proteins which bind airborne molecules are distributed differently in the nasal cavity and in the VNO of brown bears than they are in other mammals. The other limited information available suggests that the molecular mechanisms of olfaction in bears are tuned to compounds linked to foraging and to communication among individual bears.

Bears commonly receive olfactory information from other bears through sniffing, in which airborne molecules are brought into the nasal cavity. Individual bears are known to sniff others' feces, urine, deposits on marked trees, and footprints. This behavior has been reported by male and female bears of all ages, but it is most often reported from adult males, especially during the mating season (Clapham et al. 2014). Another behavior, called flehmen, brings airborne molecules into contact with the VNO. Flehmen

involves raising the upper lip, closing the nostrils, and inhaling through the open mouth. Flehmen has been reported in all bears but sloth bears, which presumably perform it; flehmen is almost always performed by male bears, not females.

Bears use various diverse and complex behaviors to release compounds with olfactory information. These behaviors vary across species with individual age, sex, reproductive status, and perhaps dominance status and population density. Individual bears of several species are known to claw, bite, or rub their chest, neck, shoulders, head, back, or flanks on woody vegetation or surrogates that humans place in bear habitat (e.g., wooden power poles). In addition, American black bears, Andean bears, brown bears, and sloth bears are now known or strongly suspected to actively deposit molecules with their feet in a behavior called pede marking (Owen et al. 2014; Sergiel et al. 2017). Giant pandas may also deposit scents with their feet, but individual pandas more obviously communicate with others by depositing anogenital secretions as high as possible against vertical substrates by performing a handstand.

Giant pandas possess a well-developed anogenital gland which produces unique secretions, while other bears release secretions from less well-developed anogenital sacs (Rosell et al. 2010). The skin of the footpads and between the toes of brown bears and polar bears contains prominent glandular cells (Owen et al. 2014; Sergiel et al. 2017). Glandular cells on the backs of adult male brown bears produce an oily substance only just before and during the breeding season. It is unknown whether this is so in other bears.

Brown bear feet produce compounds that could differentiate males from females (Sergiel et al. 2017). Scents produced by giant pandas may vary among males and females and in various ways between the breeding and non-breeding season (Wilson et al. 2019). Variation of scents in giant panda urine and anogenital secretions may contain information about the sex, age, reproductive status, and perhaps even individual identity of the panda producing the odors (Zhou

et al. 2019). Similarly, anogenital secretions of brown bears contain enough variation to differentiate males from females (Rosell et al. 2010). The urine of female brown bears and female Andean bears releases airborne compounds that vary seasonally with levels of reproductive hormones.

Knowledge of what bears perceive through olfaction is incomplete. Giant pandas of both sexes and all ages can discriminate conspecific sex via the scent of urine (White et al. 2004). Similarly, subadult brown bears appear to differentiate between anogenital secretions of adult male and adult female brown bears (Jojola et al. 2012). Finally, male polar bears differentiate the sex and reproductive condition of other polar bears through their pedal scents (Owen et al. 2014).

Some researchers have explored the use of olfaction to repel American black bears, brown bears, and polar bears, with mixed success for ammonia and with the most consistent success for red pepper spray (Smith et al. 2008). Food-based scents have been used to attract Andean bears, American black bears, and brown bears for research and management purposes, but it's not well-known how the response to those attractants varies within and among bear populations and with the individual bear's past experiences. The compounds which bears use to learn about their environment and other bears must be readily airborne, but they must also persist over time. The life span of these compounds depends not only on molecular characteristics but also on environmental factors such as airflow and humidity. There has been a little theoretical and empirical research on how environmental factors affect olfaction by polar bears (Togunov et al. 2017), but those predictions might be dramatically different in the forested habitats in which most other bears live.

## Tactile Perception (Touch)

While the senses of vision, hearing, olfaction, and taste have their own organs, the sense of touch depends on sensory nerve endings distributed



over the entire body. There are sensory nerves connected to each hair follicle, pain and temperature receptors scattered throughout the skin, and motor nerves that innervate the erector pili muscles and glands. This rich innervation is crucial to sense the environment and react accordingly. The extent of innervation depends on the nature of the tissue, but mammalian skin and skin-related tissues are relatively highly innervated with apparent regional differences. Specialized skin cells (Merkel cells) involved in touch sensation reside in the epidermis, passing mechanical stimuli on to sensory neurons. In some mammals, including bears, they are concentrated in the paws and vibrissae (whiskers). Whiskers are specialized sensory structures relaying vibrotactile information from the environment to the central nervous system. Most mammals possess them, with location, numbers, and function varying across species. Many mammals use them for active discrimination of tactile cues (e.g., rodents, felids, and many pinnipeds), but in bears vibrissal movement is relatively passive, and the hair shafts of vibrissal follicle-sinus complexes are reduced in size, similar as in dogs and other canids (Marshall et al. 2006). Deeper in the skin there are corpuscular receptors, of which Meissner corpuscles (tactile corpuscles) respond to light touch and Pacinian corpuscles (lamellated corpuscles) respond to vibrations. These receptors tend to be concentrated in the most touch-sensitive body regions of mammals, such as fingers, palms, and paws.

Bears appear to be quite “manual” and use their paws for foraging and manipulating food, exploring, and marking. Both American black bears and brown bears were observed to use tactile (and acoustical) cues when shifting from visually oriented foraging during the day to foraging in the darkness while fishing for salmon in forest streams (Klinka and Reimchen 2002). In addition to foraging, tactile senses are relevant to various social behaviors, orientation, and navigation. In bears, relatively extensive touching and rubbing is observed during play and in maternal, sexual, and social contexts. Tactile contacts are also present during aggressive interactions.

## Gustation (Taste)

Bears’ sense of taste is thought to be primarily used in foraging. Although polar bears are primarily carnivorous, giant pandas are almost entirely herbivorous, and sloth bears are primarily insectivorous, the other four bear species are omnivorous with diets that vary among species, among populations, and even among individuals. Bears’ taste receptors are located within their mouths in small structures (papillae) with both herbivorous and carnivorous characteristics (Pastor et al. 2008, 2011). Research into the nutritional ecology of bears has improved our understanding of the complexity and function of foraging across bear species, but that research alone does not reveal the sensory cues by which bears select their diet. It’s thought that most mammals use different receptors to perceive five classes of taste: sweet, umami, bitter, salty, and sour. Selective foraging by bears can be very fine-scaled, which may reflect temporally variable chemical and nutritional characteristics of potential food items, which bears presumably detect through differences in flavor. Genetic analyses have suggested that, in general, as the diets of various mammals have changed, their sense of taste has also changed. However, it’s unclear that differences in diet among the different bear species are reflected by differences in their sense of taste. In addition, although some marine carnivores have lost the ability to taste sweet, bitter, and perhaps umami flavors, those functions have not yet been evaluated in the semi-marine bear, the polar bear. In experimental tests, Andean bears, known to eat at least 300 species of plants and 40 species of animals, have preferred foods containing sugars and some other sweeteners (Jiang et al. 2012).

Although incomplete, the most-developed research linking a bear’s sense of taste, foraging, and nutritional ecology has been conducted in the giant panda. Giant pandas only rarely eat meat, and it’s been suggested that they’ve lost the perception of umami (Zhao et al. 2010), which reflects amino acids in foods. Molecular and behavioral evidence indicates that giant pandas, similar to Andean bears, taste simple sugars and



prefer foods with them (Jiang et al. 2014). That preference may mediate the seasonal shifts in foraging preference among wild giant pandas for bamboo culm versus bamboo leaves, coinciding with seasonal shifts in the relative abundance of sugars and nondigestible fiber in those plant tissues (Knott et al. 2017). In addition to sweet flavors, bamboo also includes bitter-tasting compounds. Consistent with the potential for bitter flavors to be important cues for the giant panda, the giant panda possesses genes for bitter taste receptors that are not found in several carnivores that do not feed on bitter-tasting foods, including the polar bear (Shan et al. 2018); it is not known bears with more diverse diets perceive or respond to bitter flavors.

There have been attempts to use bears' sense of taste (e.g., reaction to capsaicin as in hot peppers) to repel them from potential sources of conflict with people and to teach them to avoid anthropogenic food sources. These attempts have not been consistently successful and have revealed complex interactions among sensory systems; although pepper spray may repel brown bears and polar bears when in an aerosol form, the non-aerosol form of that same mixture may attract bears, possibly through its flavor (Smith et al. 2008).

## Cross-References

- Bear Cognition
- Bear Communication
- Bear Diet
- Bear Life History
- Bear Locomotion
- Bear Morphology
- Bear Navigation

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## Begging

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## Synonyms

[Bleating](#); [Offspring solicitation behavior](#)

## Definition

Begging is a form of communication in which organisms solicit resources provided by other organisms. It almost always occurs when dependent young solicit resources from their parents and often involves multiple signals designed to induce parental provisioning.

## Introduction

Begging is a familiar behavior in birds and mammals. Begging in nestling birds has a striking visual component: nestlings stretch their necks upward towards the parent and widen their gapes (Jacob et al. 2011). Equally conspicuous are the acoustic signals of begging birds, which make high-frequency and repetitive sounds that subside once they are fed (Budden and Wright 2001). Placental mammals employ analogous “bleating” calls during the period of lactation, and

invertebrates such as burying beetles may wave their legs and touch parents in order to induce provisioning (Parker and Mock 1997; Smiseth and Parker 2008). Begging is present in amphibians: in several species of poison dart frogs, the larvae “beg” visually and vibrationally by approaching the mother, stiffening their tails, and moving their body from side so that their mother will deposit unfertilized eggs to feed them (Stynoski and Noble 2011).

Offspring begging occurs only in organisms in which parents provision resources for offspring and in which this provisioning is partially inducible by the offspring. A key implication of begging behavior is that offspring are not passive receptacles for parental nourishment, but that they are to some degree in control of the amount of parental investment they receive, as well as the distribution of resources among the offspring (Trivers 1974). The amount of provisioning can only be controlled by offspring in species in which provisioning is continuously supplied by parents, rather than as a fixed initial supply in the form of yolk (Furness et al. 2015). Begging is only present in species with a reliable degree of parental provisioning of offspring. In species in which young disperse far from the parents and only provision themselves, begging has not been selected for (Smiseth et al. 2003).

The definition of begging is almost always restricted to postnatal contexts. It has been proposed, however, that this definition should be expanded to include the prenatal environment. Trivers (1985) suggested that chemical messages sent from embryo to mother via the mammalian placenta could function similarly to postnatal auditory begging calls, and other researchers have classified hormonal signals sent from fetus to mother as begging signals (Kilner and Johnstone 1997). However, unlike begging calls, placental hormones do not show fluctuation in accordance with physiological changes and are instead likely to convey relatively invariant information such as “vigor” or “quality” (Haig 1996). In contrast, a prenatal begging signal could be emitted more strongly by an individual in good condition than by an individual in poor condition, but a given individual would not emit a hormonal signal at the same level of intensity regardless of

its hunger. Additionally, because the two genetically distinct individuals (mother and fetus) share the same physiological pathways, receptors in the maternal bloodstream that respond to hormonal signals cannot determine whether the hormone originated in mother or offspring. But in postnatal forms of resource solicitation, there is no ambiguity as to the source of a message: a mother bird easily differentiates between her own body's signals and those of her offspring.

The literature on begging is rich with theoretical models explaining how begging behavior might arise and be maintained under a specified set of conditions. Like most species-general behaviors and morphological traits, begging behavior warrants an evolutionary explanation. Two main perspectives on begging have developed over time in the literature: begging as a form of manipulation and begging as a form of honest signaling.

### Begging as a Form of Manipulation

Reviews of animal communication prior to the 1970s primarily assumed that animal signals were straightforward and informational, resulting in reduced ambiguity about the environment for the receiver (Cullen 1966). In the 1970s, however, verbal models of signaling began to consider the fact that signals evolve because they benefit the signaler, and so we should expect them to be manipulative and often dishonest (Krebs and Dawkins 1978). Researchers in the field of animal behavior increasingly realized that Hamilton's rule ( $rB > C$ ) specified not only the conditions under which an individual should behave selfishly towards a relative but also the evolutionary limits of selfish behavior (Hamilton 1964; Parker and Mock 1997). Thus, even within families, there would be a fitness "nonoverlapping zone," reflecting the different genetic interests of individuals. Trivers's central insight in his seminal paper "Parent offspring conflict" was that the genetic interests of parent and offspring differ; parent and offspring are expected to "disagree" over the length and amount of parental investment (Trivers 1974).

Since dependent offspring are generally incapable of *physically* overpowering their parents, Trivers reasoned, we should expect offspring to evolve ways of *psychologically* manipulating their parents into providing them with resources.

Parker and MacNair (1978) developed a series of models expanding on Trivers's insight, showing that alleles causing greater resource solicitation from offspring spread under conditions of both monogamy and promiscuity. If ignoring offspring solicitation signals incurs costs, the model expects offspring solicitation to push parental provisioning above the optimal amount for the parents, but below the optimal amount for offspring (Parker and MacNair 1979; Parker and Mock 1997). In these "pro rata" models, parents and offspring bargain over the level of investment, and offspring's bargaining power comes from the reduction in fitness caused by intense begging via metabolic, predation, or physical costs (Roulin 2000). According to some verbal models, offspring begging can conceivably "blackmail" parents into provisioning more than is optimal for them (Zahavi 1977). However, the pro rata models generally show that any "blackmailing" that evolves is generally unlikely to be evolutionarily stable, and only under very specific conditions does any party emerge as the "winner" of the conflict.

The evidence for the prediction that parent-offspring conflict results in deceptive signals on the part of offspring is scant in the literature, and only a few studies have examined interspecific variation in the honesty of begging. Trivers (1985) suggested that broods with lower relatedness between siblings would experience a higher degree of parent-offspring conflict. Lower relatedness between siblings would incentivize higher sibling competition and increase the disparity between optimal provisioning from the mother's perspective and optimal provisioning from the offspring's perspective. A comparative analysis of begging behavior across 60 bird species found that offspring begging was less honest in species where parents produce more broods and where parental divorce or death reduces between-brood relatedness (Caro et al. 2016). However, subsequent analysis demonstrated that this might be a

premature conclusion, as the two sets of half-siblings produced by divorced parents should have equal or higher inclusive fitness value to an individual offspring than a single set of full siblings. Thus, individuals in species with higher rates of parental divorce would not necessarily be incentivized to act more selfishly at the expense of their siblings. If begging signals are less honest in species with higher rates of parental divorce, it is not explained by kin selection (Bebbington and Kingma 2017).

Begging signals certainly demonstrate features that appear designed to capture the attention of parents (Kilner and Hinde 2008). In birds, solicitation behaviors consistently involve repeated calling of a single note and displaying of a red, yellow, or orange patch. Canary nestlings with artificially red-dened gapes receive preferential provisioning from parents (Kilner 1996). The brightly colored mouths of nestlings in many bird species are surrounded by an area that reflects ultraviolet light well, and nestling tree swallows have been found to make longer, louder calls across a wider frequency range when ambient noise increases (Hunt et al. 2003; Leonard and Horn 2005). Scramble competition models of begging assume that parents allocate food in proportion to the signal intensity of the offspring relative to the average of the brood as a whole (Royle et al. 2002; Dugas and Rosenthal 2010). In the scramble competition model, begging is not necessarily honest or dishonest. Rather, parents passively respond to the stimuli that are most salient to them, so that they are in a sense manipulated into allocating food in a certain way by their offspring. Selection on both parents and offspring may favor a stable begging communication system. It is unclear that easily noticeable and even flashy begging signals are necessarily manipulative.

Failing to pay attention to offspring signals may be costly to both parents and offspring, and instances of true offspring manipulation by begging are apparent in brood parasitic Horsfield's bronze-cuckoo chicks, which closely resemble the structure of Superb fairy-wren begging calls (Colombelli-Negrel et al. 2012). True offspring manipulation has also been observed in brood parasitic Horsfield's hawk-cuckoos which mimic

the yellow wing patches that simulate three begging chicks in the nest (Tanaka and Ueda 2005; Langmore et al. 2011). In the case of brood parasite manipulation, Trivers's theory of parent-offspring conflict need not be invoked. Honest signaling systems are always susceptible to invasion by deceptive mimics of other species that fool receivers' sensory systems. But manipulation has not yet been shown to be a general rule of begging communication systems, and host parents are expected to exert frequency-dependent selection against such manipulation due to the costs that they bear (Jamie and Kilner 2017).

According to Trivers, an individual offspring should maximize the amount of resources it receives relative to its siblings. On the other hand, parents are expected to maximize the number of offspring that survive. Under this asymmetry, parents should be selected to allocate resources equally to each of their offspring. And offspring should be selected to manipulate parents into giving them more than their fair share of resources. Parents should be selected, in turn, to resist offspring manipulation.

Honest begging models have called into question the idea that allocating resources to offspring equally to each of their offspring is optimal for the parents. Additionally, they call into question that begging signals by offspring are necessarily manipulative rather than informative. Rather than driving an endless tug-of-war between parent and offspring, parent-offspring conflict may instead result in an evolutionary "compromise" between both parties: an honest signaling system (Godfray 1995b; Kilner and Hinde 2008). The signal of need hypothesis and the signal of quality hypothesis are the two major functional explanations of honest begging.

## Models of Honest Begging

Early models showed that parent-offspring conflict could give rise to an evolutionarily stable equilibrium in which an offspring solicits resources in a way that reduces its fitness, and parental provisioning increases so as to prevent further expensive solicitation signaling (Stamps et al. 1978; Parker



1985). Godfray (1991) presented an alternative explanation for costly solicitation. He showed that the level of offspring solicitation can be an honest reflection of offspring need as long as solicitation is costly and the benefit of extra resources increases with need. Godfray's (1991) model helped to shift the landscape of begging models from ones that define the extent of parent-offspring conflict to those that predict its resolution (Godfray 1995b). Godfray expanded his model of an evolutionarily stable signaling system between offspring and parents by modeling the influence of within-brood relatedness, offspring condition, and the total amount of resources available for the brood (Godfray 1995a).

Godfray's model also offers a theoretical analysis of both intrabrood and interbrood competition. Intrabrood competition occurs when an individual demands resources at the expense of other brood members, and interbrood competition occurs when one brood demands resources at the expense of future broods. Godfray assumes that the parent provides a fixed amount of resources and that the young may differ in condition or state, which determines the degree to which they will benefit from an increased share of the resource. By honestly signaling their condition or state with begging calls, the young increase the efficiency with which the parent allocates resources. In theory, the higher the marginal benefit of extra resource is to an individual offspring, the more an offspring will be expected to invest into solicitation signaling. Whether signaling is a truly costly phenomenon is unclear. Two studies in birds have shown significant increases in metabolic rate resulting from increased begging, and one study in house sparrows has shown that begging behavior may compromise immunocompetence (Bachman and Chappell 1998; McCarty 1996; Moreno-Rueda 2010). However, these findings do not conclusively demonstrate that the metabolic or immunological costs of begging exceed the threshold needed to maintain honesty. There is some evidence that begging signals attract predators, but few empirically informed cost-benefit analyses of begging in relation to predation have been performed (Redondo and Castro 1992; Haskell 1994).

The assumption built into Godfray's model, that costs are associated with honesty, is not a necessity for offspring-parent signaling systems. Godfray's model also incorporated the idea that offspring begging may be influenced by the condition of siblings in the same brood. Thus, along with reflecting the state of the signaler (that signaler's condition or temporary hunger), it may also reflect the state of its surrounding siblings (Kilner and Johnstone 1997). For example, nestling barn owls may refrain from vocalization when a rival sibling is hungrier than they are, and they may escalate their own begging once that rival is fed by parents (Roulin et al. 2000). Additionally, begging intensity has been shown to decrease with brood size, as the inclusive fitness cost of gaining resources at the expense of one's siblings is higher when there are more of them (Cotton et al. 1996; Roulin et al. 2000). In the case of expressing information about their need and (in an indirect way) expressing information about the level of need of their siblings, offspring are assumed to be communicating information about their state that is otherwise cryptic to the parent (Godfray 1991). Many researchers have tried to identify correlates of hidden condition, such as body size or physical development. However, many of these cues are not cryptic and thus a begging signal would be redundant and of lower value if a parent could merely assess visible cues of condition to get the same information (Mock et al. 2011; Schwagmeyer and Mock 2008). Another problem with the "signal of need" literature is that overall condition, the "need" that Godfray's models refer to, and temporary hunger, are frequently confused. Food deprivation experiments have repeatedly demonstrated that the intensity of offspring solicitation signaling increases in response to hunger. But hunger is not clearly related to fitness, so in order to determine whether offspring solicitation intensity is truly a function of need, hunger and condition must be decoupled (Mock et al. 2011). The confusion between proximate-level wants and ultimate-level needs has likely contributed to the neglect of viable hypotheses explaining the evolution of begging other than "signal of need."



The second major honest signaling hypothesis explaining the evolution of begging is the signal of quality hypothesis. The signal of quality hypothesis makes the opposite prediction of the signal of need hypothesis: that better-condition signalers emit stronger signals because they can afford them. The model builds upon the handicap principle, the idea that a signal's honesty is maintained by the fact that it suggests something about the signaler's condition. If the signaler were in poorer condition, it would not be able to bear the costs of the signal (Zahavi 1975). Compared to the signal of need hypothesis, the signal of quality hypothesis has been largely neglected in the literature despite its theoretical and empirical plausibility (Grafen 1990; Weary and Fraser 1995; Saino et al. 2000). The adaptive value of responding to a begging signal that honestly advertises quality is obvious when it is considered from the perspective of the parent. That is, parents should be selected to put limited food resources where they will have the highest fitness returns.

Hypothetically, parents that respond to signals of need and allocate more resources towards offspring in poor condition may risk wasting their limited resources on offspring that will not have high fitness returns either way. On the other hand, if parents direct resources towards offspring in better condition, they may be able to increase their fitness returns, measured in the number of grandoffspring, to an even higher level. Though tests of the signal of quality hypothesis have been limited relative to tests of the signal of need hypothesis, SoQ may explain results in the begging literature more effectively than SoN. For instance, provisioning rate predicts fledgling size and recruitment as breeders in a house sparrow population (Schwagmeyer and Mock 2008). In house sparrows, parents are responsive to begging calls and posturing and allocate resources according to begging signal intensity. This relationship between eventual condition and provisioning rate would not arise if needier offspring invested more energy into signaling. And videotaped house sparrow parents skew allocations towards larger offspring (Mock et al. 2009). Additionally, when nestling house sparrow mouth flanges were painted to resemble nestlings in

good condition, parents shifted their feeding patterns to prefer them over nestmates (Dugas 2010). This suggests that some components of begging, particularly the brightly colored (and high UV-reflecting) mouthparts of young engaged in solicitation behavior, may be hard-to-fake cues to offspring condition rather than merely flashy signals designed to manipulate parents.

In a completely different taxon, earwigs, offspring nutritional condition is revealed by variation in a chemical signal, cuticular hydrocarbons. If cuticular hydrocarbons are extracted from deprived or well-fed offspring, mothers respond more strongly to the chemical stimuli from the well-fed offspring and allocate more food towards them (Mas et al. 2009). More recent studies in wrens have shown that experimentally food-supplemented nestlings (nestlings in better condition) begged more intensely for food than nestlings that were not supplemented. Parents responded to the more intense begging signals of the nestlings in better condition, increasing their provisioning rate to them, but not to the offspring in poorer condition (Bowers et al. 2019). And in tadpoles, begging effort and performance were higher in more developed and higher condition tadpoles and actually declined with food deprivation (Dugas et al. 2017). Mothers allocated more food to more developed tadpoles as well as those who vibrated (a component of their begging behavior) at a higher speed.

Despite the encouraging results (so far) in support of the SoQ hypothesis over the SoN hypothesis, it is unlikely that there is a single explanation for the varied forms of begging behavior that have evolved across taxa. For example, some recent work in poison frog mimics that *does* account for the distinction between proximate-level wants and ultimate-level needs has found that begging is an honest signal of need (Yoshioka et al. 2016; Kilner and Johnstone 1997). Contrary to the predictions of the SoQ hypothesis, offspring not fed a supplemental diet over a certain period of time begged more intensely than offspring fed a supplemental diet during the same time period. Clearly, the literature on the evolution of begging is not settled and is in need of more empirical tests that consider more explanations and remain

unbiased about which one is correct. But the overwhelming theoretical and empirical consensus on the honesty of begging seems like it will stand uncontested, even if parent and offspring's genetic interests do have a nonoverlapping zone.

## Conclusion

While the bulk of begging research has focused on answering ultimate-level evolutionary questions, developmental perspectives on begging and quantitative genetic perspectives of parent-offspring interactions continue to enhance our understanding of the proximate mechanisms behind begging signals (Leonard and Horn 2005, Kölliker and Richner 2001). More recently, researchers have become interested in the endocrinology of begging, finding that hormones play a large role in regulating begging behavior in birds and inspiring research in other taxa (Smiseth et al. 2011). Innovations in genetic sampling and analysis will further our understanding of how this key parent-offspring interaction functions across taxa and bolster evolutionary claims. In addition, developmental and genetic perspectives can help to expand our understanding of begging evolution by inspiring questions about selection pressures at different life stages and how genetic variation in offspring begging is maintained despite selection. Additionally, research on begging has recently been expanding in scope to include taxa other than birds, and this is increasingly providing fertile ground for empirical tests of the extensive begging models that theoreticians have already developed.

## Cross-References

- Auditory Signals
- Chemical Signals
- Cuckoo Brood Parasitism
- Honest Signaling
- Parental Investment
- Parenting
- Signaller

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## Begging Paradigm

### ► Bucket Experiment

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## Behavior

- Caudata Cognition
  - Crocodilia Diet
  - Equine Communication
  - Lagomorpha Navigation
  - Squamata Diet
- 

## Behavior Catalogue

### ► Ethogram

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## Behavior Modification

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## Synonyms

Applied behavior analysis; Behavior therapy;  
Conditioning

## Definition

A set of procedures for changing behavior (through reinforcing it or subjecting it to extinction) that are largely based in the principles of operant conditioning.

## Introduction

Behavior modification refers to the application of a set of procedures (largely based in the principles of operant conditioning and rooted in classical

conditioning) in order to bring about changes in behavior. It is more frequently referred to in contemporary parlance as *applied behavior analysis*. Typically, the goal of behavior modification is to change behavior through an initial assessment of its functional relationship with the individual's environment. An understanding of the function of the behavior is then utilized to develop and deploy a set of controlled experiences (see below) that are aimed at meeting that function by means of a more desirable behavior. Behavior modification aims to reduce the frequency of an undesirable behavior and increase the frequency of desirable behavior and to bring about such changes with a minimum of aversive experiences for the individual whose behavior is being modified. Thus, behavior modification generally involves increasing the frequency of a desired behavior through the use of reinforcement and/or decreasing the frequency of an undesired behavior (or extinguishing it) through subjecting that behavior to extinction.

The phrase “behavior modification” was perhaps first suggested by the American psychologist Edward Thorndike in his text *Animal Intelligence* (1911), in which he makes frequent reference to the concept of “modifying behavior” through manipulation of the consequences to that behavior that an organism experiences. Through his work in observing how animals changed their behavior in response to their experiences, Thorndike derived what he called the “Law of Effect”: the tendency of a behavior with “desirable” effects – that is, one that is followed by a desirable consequence – to be repeated in the future, while behaviors that were followed by undesirable consequences tended to fall out of the individual's repertoire. The principles employed in behavior modification to bring about behavioral change are seated in the work of early “behaviorists” like Thorndike, as well as in the work of the Russian physiologist Ivan Pavlov.

## Principles of Behavior Modification Derived from Pavlov's Work

Pavlov had begun his scientific career investigating the contributions of the salivary system to digestion – work for which he was later awarded

the Nobel Prize in Medicine. As part of his procedures for that work, Pavlov had made visible the salivary output of dogs, through cannulization of their salivary ducts, which allowed for all saliva produced to be output directly into a collecting tube. Through this means, Pavlov was able to measure the amount and rate of output of saliva in response to different triggers (foods varying in texture and palatability) placed in the mouth of the dogs by his research assistants. What came to fascinate Pavlov over time is the observation that, with repeated experience, his dog participants began to salivate in response to the sight of the research assistants or of being placed into his research apparatus. He hypothesized that this change in salivation behavior in response to a previously neutral stimulus (such as the sight of his research assistants) was a consequence of the experience of that key stimulus reliably preceding the placement of food in the mouth. In his subsequent work on what he called “psychogenic” salivation, Pavlov documented more formally the experiences required to bring about a change in behavior in response to a given stimulus (the sight of the research assistants, in the original instance). A collection of his lectures published in 1928 details his work on this topic. With respect to behavior modification, Pavlov’s work on what has come to be known as classical conditioning is among the early demonstrations that intentional manipulation of experience could bring about long-lasting and predictable changes in an organism’s behavior – a point of view that is the essential base in the field of behavior modification.

Classical conditioning as a model for how some behavior changes with experience has been used to explain a variety of normal and abnormal behaviors in organisms. For instance, it has been used to explain how something like the sound of a box clicker or a whistle (what animal trainers typically refer to as a “secondary reinforcer”) can come to have a value to the animal hearing that sound. If the sound reliably precedes the presentation of a desired item or event (such as food or the opportunity to play with a favorite toy), the sound itself begins to be capable of sustaining the repetition of whatever behavior caused it to be presented.

Similarly, phobias and other fears have been theorized to develop through inadvertent classical conditioning. A sudden loud sound resulting from the banging of a loose door may cause a horse that had previously had no fear of that doorway to be no longer willing to pass through it. The sight of the doorway now predicts a possible frightening event (the loud and startling sound), and thus the doorway itself is now an object that elicits fear. The text below will shortly review some applications of classical conditioning as they are routinely employed in behavior modification. The practice of systematic desensitization – the gradual reduction of a conditioned fear response through slow, systematic pairing of the feared stimulus with responses incompatible with fear (such as relaxation) – is one way in which classical conditioning principles have been used to improve the lives of both human and nonhuman animals.

### **Operant Conditioning Techniques and Behavior Modification**

Additional evidence in support of the idea that behavior could be intentionally modified through control of experience came from the work of behaviorists such as John Watson (1930) and B.F. Skinner (1953). Watson and his research assistant Rosalie Rayner, for instance, applied the techniques described by Pavlov to induce fear of a rabbit in a human child (Watson and Rayner 1920), thus documenting that the phenomena described by Pavlov were applicable to humans as well as to nonhuman animals. Skinner in his work elaborated upon Thorndike’s “Law of Effect.” Specifically, behaviors that were followed by desirable consequences were “reinforced” – more likely to be repeated in the future; while those followed by undesirable consequences were “punished,” or less likely to occur in the future. Any consequence to a behavior that increased that behavior’s likelihood of being repeated in the future was a reinforcement, while any consequence to a behavior that decreased the behavior’s likely display in the future was a punishment. These constructs are further discussed elsewhere in this encyclopedia, but a brief review of them is presented here, to



facilitate the discussion of their explicit use in behavior modification that is to come in this particular encyclopedia entry.

How behaviorists have come to describe the consequences of reinforcement and punishment and their variants has led to no end of confusion, because of the common connotation of “bad” or “wrong” associated with the English word “negative” and the common connotation of “good” associated with the word “positive.” What the behaviorists mean by “positive,” however, is the *addition* of a stimulus, and what is meant by “negative” is the *subtraction* of a stimulus.

Behavior can be reinforced by *adding* an appetitive stimulus (positive reinforcement). For example, if a dog’s placing its hindquarters on the ground in response to the spoken word “sit” is followed reliably by a food treat or play with a favorite toy, the likelihood of that behavior occurring again in response to the word “sit” increases. *Subtracting* an undesirable stimulus such as social or physical pressure (an example of negative reinforcement) can *also* increase the likelihood of a behavior occurring again. Applying physical pressure with a heel or spur to the right flank of a horse when mounted will cause the horse to move its hindquarters to the left. The rider “reinforces” that step to the left by immediately removing the pressure of his/her heel. Over time, the horse will begin to move its hindquarters to the left in response to little more than detection of a contraction of the rider’s right calf; by doing so, the horse avoids the addition of unwanted additional pressure to the right side of its body. Thus, a behavior that the rider wishes to *increase in frequency* (moving the hindquarters to the left) has increased through the *subtraction* or removal of an aversive stimulus (the physical pressure of the rider’s heel against the horse’s side).

Behavior can be decreased in frequency (or punished) by *adding* an aversive stimulus (positive punishment). Applying a verbal reprimand (“No!”) or a slap with the hand in response to a behavior that one wishes to see decrease in frequency is an example of *positive* (as in something being *added* in order to change behavior) punishment. But *subtracting* an appetitive stimulus (typically one’s attention, or the liberty of the

trainee) can also be used to decrease the likelihood of a behavior occurring again. If the undesirable behavior is a dog’s jumping up on a human, one can decrease the frequency of this behavior by simply subtracting one’s attention – ignoring the dog until all four of its feet are back on the ground. Behaviorists refer to this consequence to a behavior as *negative* (as in something being *subtracted* in order to decrease behavior) punishment. In terms of their perceived rank order of aversiveness, positive reinforcement is considered to be the least ethically controversial consequence to behavior and negative punishment to be the least aversive form of punishment. The other two consequences (negative reinforcement and positive punishment) have been associated in the literature with fear, stress, and aggression in a number of species (see, e.g., Fernandes et al. 2017; Freymond et al. 2014; Hendriksen et al. 2011; McGreevy and McLean 2009; Innes and McBride 2008; Emurian et al. 1985) and are therefore not typically considered of value as modifiers of behavior in the practice of behavior modification.

Skinner (1953) recognized the application value of the possible consequences to behavior described above, inasmuch as such application could bring about desired changes in behavior in human clients presenting with behavioral problems. The primary practice for the treatment of such individuals at the time was psychotherapy in the form of talk therapy, still largely seated then in the psychoanalytic approaches of Freud and his followers. Skinner rejected Freud’s emphasis on constructs such as unconscious motivation which could not be empirically observed and verified, preferring instead to focus on the functional value of a given problem behavior to the individual engaging in that behavior and manipulating that value to bring about changes in behavior. Indeed, the Functionalism practiced by psychologists in America in the early 1900s still permeates behavior modification in practice today, as will be shown shortly.

### Functional Behavior Analysis as a Hallmark of Behavior Modification

Contemporary behavior modification still reflects Skinner’s valuing of the individual case and the



functional value of behavior as its sustaining impetus. The hallmark of behavior modification (applied behavior analysis) in practice is the use of an initial procedure for the evaluation of behavior referred to as *functional behavior analysis* (FBA). The protocols for such an analysis may vary, but generally FBA will include the following elements:

- An initial observation of the problem behavior, with no effort to intervene (unless the behavior is life-threatening). In this observation, the focus on the part of the observer is to try to identify possible triggers for, consequences of, and/or functions of the behavior. Specifically, an effort is made to clarify the *antecedent* to the behavior, the nature of the *behavior* itself, and the *consequences* of the behavior (these elements are sometimes referred to as the “ABCs” of functional analysis).
- Systematic manipulation of suspected antecedents, followed by observations of the results of those manipulations. Does the behavior occur at all following the suspected antecedent? Does it occur at a different rate or intensity? What do the consequences appear to be, if they are different from the original situation?

The FBA procedure is employed in such a way as to vary the order of testing of different suspect antecedents and functional consequences, in order to produce quantitative and qualitative data that can be used to come to a conclusion regarding the most likely triggers for and functional values of the problem behavior. This information is then used to design a training plan that is aimed at replacing or reducing the frequency of the problem behavior through control of its antecedents and/or changing of its functional consequences. Finally, such training plans generally involve the application of different positive reinforcement opportunities (as opposed to punishments); if punishment of any kind is employed, it is generally in the form of negative punishment.

As positive punishment is a consequence that by definition reduces the likelihood of a behavior's occurring again, the reticence to use punishment on the part of behavior analysts may

seem surprising. However, a behavior may also be eliminated from an individual's repertoire if it no longer results in the consequence that had served to sustain it. In the parlance of behavior modification, removing the functional consequence of a behavior effectively extinguishes the behavior; once the consequence is no longer forthcoming, the behavior undergoes extinction and eventually ceases to be performed. It is primarily through modification of what behaviors or aspects of a behavior are reinforced by the behavior modification practitioner and what behaviors are ignored that behavior change is brought about with a minimum of aversiveness.

A common means by which a change in behavior is brought about via changes in what is reinforced involves what is referred to in the behavior modification literature as *differential reinforcement*. As the term implies, the practitioner determines what behaviors he or she will reinforce going forward, as opposed to the problem behavior that had been perhaps inadvertently reinforced in the past. In some cases, the new behavior selected to be reinforced is intentionally one that cannot be engaged in at the same time as the original problem behavior is being performed. Such a strategy is called *differential reinforcement of an incompatible behavior (DRI)*. For instance, if the problem behavior in a dog is jumping up on a human, the human may choose only to reinforce (in the form of his/her attention, a treat, play, or a combination of these) behavior that results in all four of the dog's feet being on the ground. This latter behavior is incompatible with jumping up – the dog cannot be simultaneously jumping up and have all four feet on the ground. *Differential reinforcement of an alternative behavior (DRA)* is also as it sounds. In this practice, a behavioral alternative to the problem behavior is selected, and then that alternative is what is reinforced, while the problem behavior (or any other behavior) is ignored. As an example, consider a dog that indicates its wish to go outside by scratching violently at the door. An alternative to this behavior might be to nudge a bell with its nose to tell its owner that it wishes to go out. In DRA, the behavior of nudging the bell would be shaped and reinforced to the exclusion of any other means

that the dog may endeavor to employ in order to be let out. Other strategies for differential reinforcement include *differential reinforcement of other behavior (DRO*; reinforcement of any behavior other than the problem behavior) and *differential reinforcement of lower rates of behavior (DRL*; reinforcement of lower rates of a given behavior, with a goal of reducing but not eliminating the frequency of that behavior).

#### The Application of Behavior Modification to Nonhuman Animal Behavior

For most of its history, behavior modification as it has been described here has been used to reduce problem behavior and/or to increase the frequency of desirable behavior in humans. For example, the techniques of FBA have been used with great success to reduce rates of self-injurious behavior and increase rates of pro-social behavior in children on the autism spectrum (for a recent review, see Newcomb and Hagopian 2018).

However, others have seen the utility of such systematic assessments and training protocols designed specifically to respond to these assessments as having equal value when applied to non-human animals. For instance, in the late 1970's, Hal Markowitz (then Director of Zoological Research at the Portland Zoo in Oregon) observed what he considered to be an undesirable rate of abnormal stereotypic behavior and overall lethargy in zoo animals. Much as would a behavior modification practitioner, Markowitz made careful observations of the apparent functions served by the stereotypic behaviors he saw (such as pacing or rocking) and then endeavored to put into place modifications to the animal's environments that provided more valuable reinforcement for alternative behaviors. For instance, he trained animals to use puzzles to gain access to food or to receive an opportunity to chase an automated "prey" item (see Markowitz 1982, 2011 for a review of some of this work). Markowitz's work was foundational in the field of environmental enrichment, and it was also an early demonstration of the applied value of systematic behavior analysis and modification for improving the lives of nonhuman animals.

Zoos continue to be one of the common environments in which the practice and principles of

behavior modification are applied to nonhuman animals (Forthman and Ogden 1992; Bloomsmith et al. 2007; Maple and Segura 2015). In one such example, a chimpanzee who was being housed in isolation for a variety of health reasons had taken up spitting and throwing feces at human passersby. Potential contingencies supporting these undesirable behaviors were tested, and a program of DRA was employed in conjunction with extinction that ultimately reduced the frequency of these problem behaviors by 83% (Martin et al. 2011). Similarly, functional analysis of aggressive behavior in a captive lemur revealed that human attention was the primary reinforcing contingency. Removing this contingency and reinforcing alternative behavior successfully reduced rates of aggression in this individual (Farmer-Dougan 2014).

Self-injurious behavior (SIB) – such as hair pulling, self-biting, or feather plucking – is another behavior problem sometimes observed in captive animals. Often, such behavior is inadvertently reinforced by attention on the part of an animal's caregivers. Behavior modification techniques have been used to eliminate or reduce the frequency of SIB. In one example, self-biting and hair pulling were the problem behaviors observed in a female olive baboon. Systematic functional analysis suggested that inadvertent positive reinforcement in the form of attention from caregivers was supporting the problem behavior. It also revealed several low-frequency behaviors that were identified as preferred alternatives to the SIB. A training program was instituted that reinforced these alternative behaviors with the attention that had previously been given to the problem behavior. The results were an increase in the alternative behaviors and decrease in the SIB (Dorey et al. 2009).

Similarly, feather plucking in a zoo-housed black vulture, when subject to functional analysis, was found to be reinforced by contingent attention from caregivers. Eliminating this attention and implementing a DRO reinforcement strategy eliminated feather plucking in this animal (Morris and Slocum 2019).

Behavior modification techniques have also been used with success in domestic species.

In one novel approach to functional analysis, a survey of 128 dog owners was conducted to try to identify contingencies that might maintain stereotypic behaviors in pet dogs. Owners reported a wide variety of antecedents to the onset of stereotypic behaviors such as circling or light-chasing. Follow-up studies with several additional dogs revealed that owner attention was the functional reinforcer for stereotypies in two of the dogs, and sensory stimulation reinforced the problem behaviors in two others. DRO employed to reduce the problem behavior was successful but in some cases only if the owner was not the trainer. The authors conclude that a variety of functions might be served by stereotypic behavior in pet dogs and that a “one-size-fits-all” program treatment may not be appropriate (Hall et al. 2015).

In another study of four dogs presenting with the problem behavior of jumping up on people, functional analysis revealed several possible contingent reinforcers, such as attention from the human and access to a desired item that the human might be holding. Removal of these contingencies reduced the rate of jumping up behavior in all dogs (Dorey et al. 2012). Similarly, functional analysis was used to determine reinforcing contingencies in a study of three dogs living in an animal shelter and displaying problem behaviors such as leash pulling and aggression. Subsequent training to eliminate identified contingencies reduced the problem behaviors and increased the perceived adoptability of the dogs (Winslow et al. 2018).

Classical conditioning procedures have also been used to modify behavior in dogs, particularly to reduce fear and anxiety. The process of systematic desensitization has been successfully used, for example, to treat separation anxiety in dogs (Butler et al. 2011). The procedure entails exposing the animal to low levels of the anxiety-provoking stimulus (perhaps just the owner picking up his or her keys), and then rewarding non-anxious behavior with immediate praise and interaction with the owner. The process of separation from the owner is gradually expanded until the dog is able to tolerate that separation without a return of the anxious behavior.

Counter-conditioning has been used similarly to treat separation anxiety in dogs (Rogerson 1997). In this procedure, the anxiety-provoking separation from the owner is paired with conditions conducive to relaxation (such as the presentation of a desired food). The assumption here is that fearfulness and anxiety are incompatible with relaxed eating. Repeated exposure to the pairing of the previously anxiety-provoking situation of separation from the owner and the relaxed opportunity to eat a desired food item replaces that anxiety with a more desirable emotional state.

Horses have been another domestic species to benefit from the application of behavior modification techniques. In one study, DRO was used to successfully reduce pawing of the ground in three horses (Fox and Belding 2015). In another, biting and chewing in two horses were similarly reduced through the use of DRO (Fox et al. 2012). A third study showed that differential reinforcement was effective in improving trailer loading and reducing inappropriate behaviors in this context in four horses (Slater and Dymond 2011).

Behavior modification techniques differ from many other approaches to changing behavior in the willingness to focus on the individual case. Careful and systematic assessment of the antecedents of a problem behavior, the precise nature of that behavior, and the consequences that suggest its function are used to inform well-designed training protocols tailored to the individual case, with the overall goal of reducing problem behavior through the use of a minimum of aversive experiences and increasing desirable behavior through positive reinforcement. The literature suggests that these methods are effective in bringing about desirable changes in behavior with a minimum of adverse effects. Clearly, the field of behavior modification has much to contribute to the overall behavior and well-being of non-human animals (Overall 2012).

## Cross-References

- [B.F. Skinner](#)
- [Classical Conditioning](#)
- [Functionalism](#)

- **Functionalism**
- **Ivan Pavlov**
- **John B. Watson**
- **Negative Reinforcement**
- **Operant Conditioning**
- **Positive Reinforcement**
- **Punishment**
- **Reinforcement**
- **Unconditioned Response**
- **Unconditioned Stimulus**

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## Behavior Plasticity

### ► Strategy Reversibility

## Behavior Systems

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## Beginnings in Ethology

Nikolaas Tinbergen (1942) began to speak in terms of systems of behavior in his first manifesto of ethology. As there are systems of respiration and systems of digestion, for instance, in which multiple chores are accomplished in coordination by different parts to perform a complex function, there can be said to be systems of behavior that collectively accomplish complex chores such as feeding, finding mates, avoiding pain, and perhaps less obvious functions as well, such as play, grooming, or sociality. Tinbergen (1942) stressed that behavior has an organization and that this organization is hierarchical (Fig. 1).

## Behavioral Context of Behavior

At the core of a behavior systems approach is concern for how the various behavioral propensities of an animal's repertoire interrelate. Feeding, for instance, requires the unfolding of a complex

sequence of behaviors. Focus on the interdependence of related behaviors sets behavior systems approaches apart from more analytical approaches in biology and psychology that treat behavioral variables as discrete and independent. What began as a hypothesis about behavior being hierarchically organized matured into a set of methods concerned specifically with the organization of an animal's behavioral repertoire.

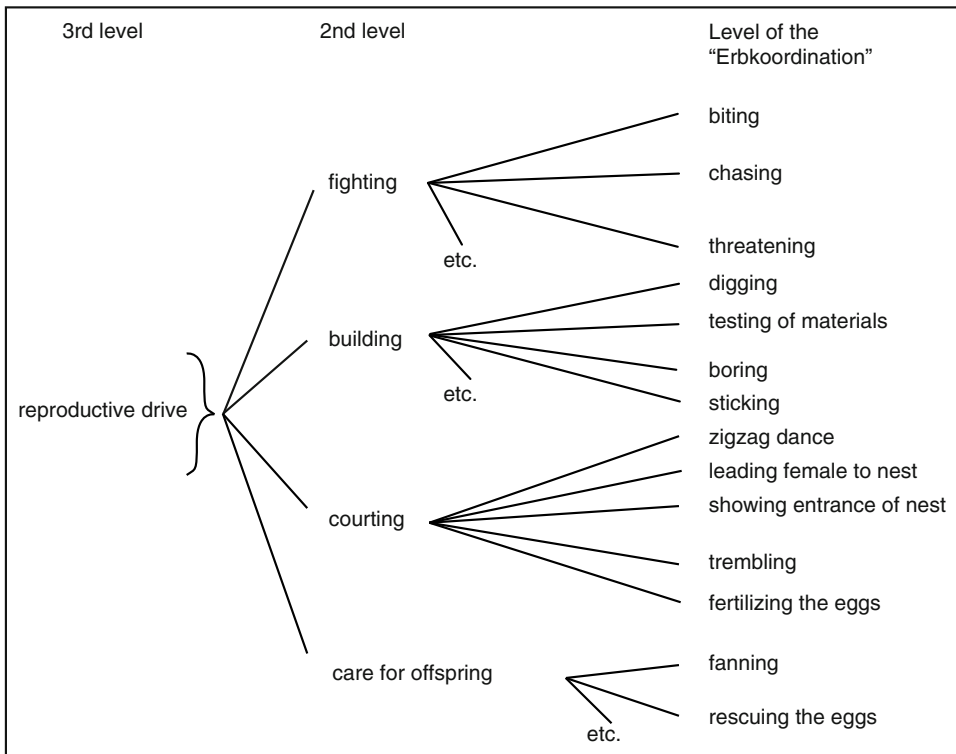
While the rest of ethology grew progressively more analytical over the twentieth century, Gerard Baerends (1941, 1976) retained focus on sequential relations among behaviors, how different behaviors interrelate temporally, and which situations lead to which responses. In Baerends' approach, one monitors behavior of animals in the wild for extended periods. Monitoring can be continuous or by sampling at regular intervals. Focus on the interrelation of behavioral forms invites use of advanced statistical or modeling techniques to identify patterns of concurrence. To clarify causation, field experiments are conducted where possible and necessary.

Although behavior systems approaches that followed differed from Baerends' in many respects, a central concern with situating behavior in a behavioral or motivational context is held in common.

## Model of the Animal

Behavior systems approaches involve multiple kinds of theory. At its most general, a behavior systems approach comprises a set of assumptions and a way of talking about them. It is not a hypothesis to be tested, but a way of approaching behavior that embraces its complexity, focusing specifically on its organization. It is an interpretive and investigative strategy or framework.

One output of this strategy is a model of how the animal's behavior is organized. Figure 2 shows one such model. This model of the animal is also a kind of theory, but still not a theory in the familiar terms of species-general or system-general capacities or processes, like learning or reasoning, but of the species and system itself. This produces an apparent problem: such models are not in a form



**Behavior Systems, Fig. 1** Tinbergen's 1942 hierarchy of moods model of the reproductive drive in stickleback fish (From Tinbergen 1942)

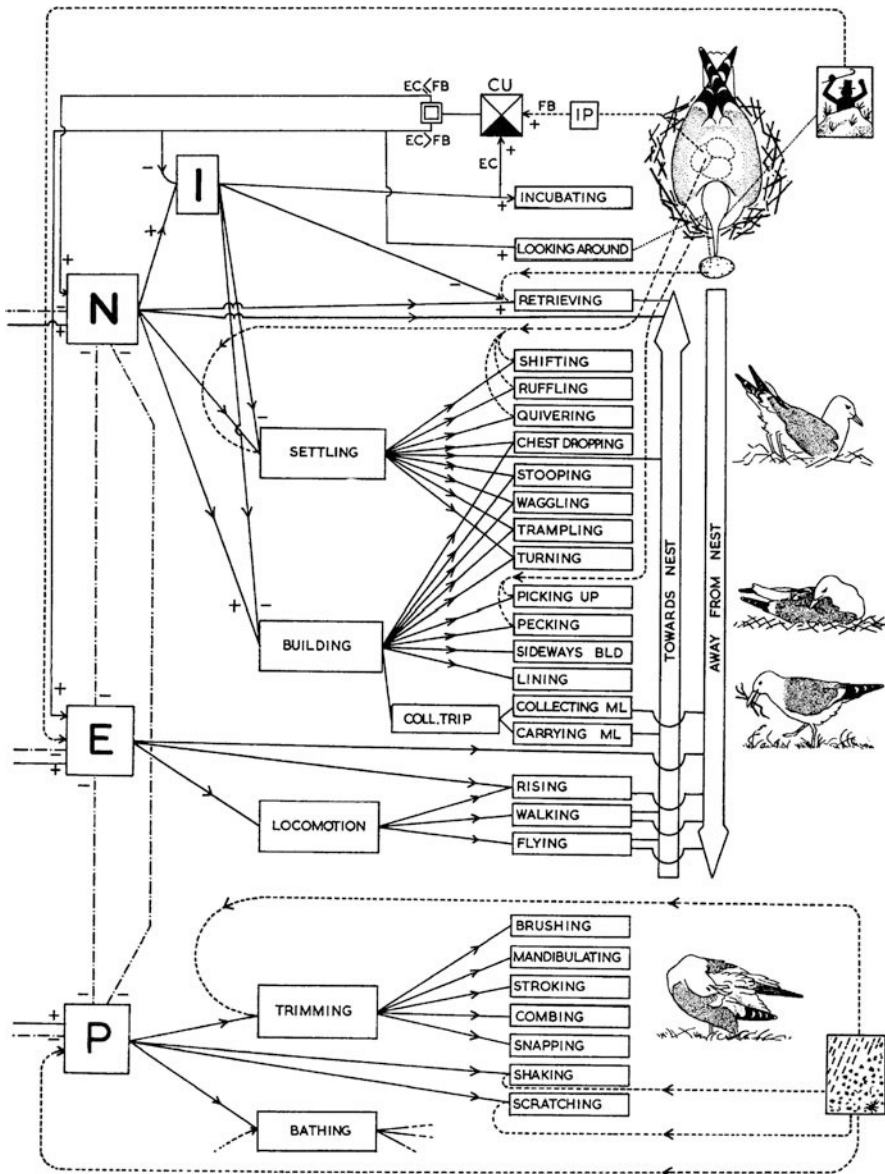
that is readily interpretable in terms of more common theories or familiar interpretive frameworks. While pondering the detailed models of herring gull nesting (Fig. 2) or digger wasp provisioning (Baerends 1941), which sometimes look like wiring diagrams, one is surely impressed, and perhaps awed by the work involved, but may then wonder what is to be done with such specific models of relatively obscure animals and systems.

The detailed models produced by such analyses are more than mere curiosities of natural history. With a theory of the animal and system in hand, one then has a basis upon which to situate further analyses and test hypotheses in more familiar terms, such as a theory about some cognitive phenomenon. Analyses of abstractly phrased capacities or processes can be embedded within an independently developed model of the specific animal's behavioral organization. This way behavior systems solves a problem for psychology that arises in any preparadigmatic science:

some description should precede assessment of theories, but the terms of description (what is measured and what it means) are determined by the theory. Thus, without an independent foundation, abstractly phrased theories of capacities specify the terms of their own assessment. For instance, checking a food trough is often taken as an indicator of expectation of food, without concern for when that animal might otherwise perform the same behavior. A behavior systems perspective solves this dilemma by providing a theoretical basis for description in terms specific to the animal, system, and circumstance.

This model of the animal approach, by which one first describes the structure of the behavior in a given system and then uses this to situate analyses of phenomena of interest, is a thermomorphic approach (Timberlake 2007). It provides a manner of foundation, but unlike chemistry, for instance, which has just one periodic table, the kind of foundation provided by a behavior systems





**Behavior Systems, Fig. 2** Baerends' model of nesting behavior of herring gulls (From Baerends 1976)

framework is specific to the animal, system, and circumstance. This can be aptly contrasted with common alternative interpretive frameworks. One common way of interpreting behavior is by anthropomorphism, wherein one uses suppositions about human cognition or behavior as a model to provide a basis for describing or understanding the behavior of other animals. The dangers of anthropomorphism have been aptly

identified (as well as solutions to some of them), although explicit and implicit anthropomorphic approaches remain prevalent in animal cognition research. Another common approach bases analyses on normative theories. A fault with normative approaches is that they permit interpretation only of behaviors that are clearly and directly instrumental. The benefits of normative approaches can be recovered, however, by

embedding such analyses in a behavior systems framework. In general, abstractly phrased approaches concerned with capacities tend to permit interpretation of only a very limited range of behavioral variables. A primary gain of alignment with a behavior systems approach is an ability to interpret a broader array of behaviors.

Behavior systems may be said to involve yet another level of theory insofar as one views a motivational system as a model the animal holds about the world. This aligns behavior systems, at least superficially, with “theory theories,” views that attribute a naïve theory to the animal, such as a “theory of mind” or “naïve physics” or *Umwelt*. A similar point can be made regarding some graphical model-based views, including those that assume that the animal forms a representational model of relevance relations. Caution is warranted when drawing analogies between naïve theories or graphical models, and motivational systems, for the terms are typically different. Still, such analyses may often be complementary.

## Evolution

Behavior systems is an evolutionary approach. Evolution is used to permit a connection with ecological pressures, similar to other evolutionary approaches in psychology. However, focus on systems and behavioral interrelations, as opposed to discrete behavioral traits, sets it apart from typical evolutionary approaches. The benefit of restricting evolutionary hypothesizing to interrelated components of systems is that it narrows focus on local selection pressures. Modeling the structure of behavior systems relies heavily on evolutionary thinking, which it uses as a source of hypotheses, and to provisionally fill the many gaps in knowledge concerning perceptual, motor, and motivational factors. Admittedly, behavior systems are highly complex, with sensory, motor, and motivational components evolving in tandem, and this produces substantial uncertainty regarding the specific selection pressures and their impact on evolution. This problem, however, is not unique to behavior systems approaches.

## Behavior Systems/Neural Systems/Motivational Systems

Although behavior systems theory was developed within ethology as its leaders were working to establish ethology as a science of observable behavior, the earliest behavior systems models referred to drives or moods or nervous centers. In the context of sciences of behavior growing progressively uneasy about internal variables, this reference to unobservables drew fire. An early response to this was to talk literally about behavior, as contemporary ethology does. One sees this approach in Baerends’ work and thinking, and it is the more typical approach to take among ethologists.

Tinbergen’s (1951) own conception of behavior systems, in contrast, was primarily concerned with nervous structures. This view is echoed in the writing of later ethologists, as well as neuroscientists (e.g., Fanselow 1994). This conception of behavior systems has been criticized as physiologizing, but it has also produced some successes. Michael Fanselow (1994), for instance, applied such an approach to produce a model of defensive behavior in rats with reference to specific neural structures.

A third way of conceiving of behavior systems is closest to the initial formulations, in motivational terms. This is the more common approach among psychologists, notably William Timberlake (1983a, 1994, 2001) and Michael Domjan (1994), and the approach that has undergone the most development. This conception has provided the basis for a theory of learning (below) and opens behavior systems analyses to investigation of cognition more generally.

One difficulty faced by views of behavior systems phrased in strictly behavioral terms, as opposed to motivational, is that the specific patterns of behavior an animal exhibits appear to depend heavily on the response supporting characteristics of the apparatus and the details of the procedure. Different circumstances may afford different manifestations of a given motivational status, and this adaptability to changing environmental demands is an important part of Timberlake’s approach, which allows a behavior

systems model to remain relevant outside of an animal's specific niche. The niche itself might vary widely. A strict behavioral phrasing appears to imply that behavior will be brittle, not adaptable to changing circumstances, whether considering the variability encountered within the niche or between the niche and evolutionarily unforeseen environments like a Skinner Box.

Baerends generally adopted an ethologists' attitude and attempted to develop his thermomorphic models as situated within the species' niche and test them there. In such environments, the distinction between motivational and behavioral systems can be blurred. Timberlake, in contrast, primarily remained in the laboratory. He stressed that behavior exhibited in laboratory settings is no less natural or relevant to understanding the animal. Timberlake recognized the importance of the specifics of the apparatus and procedure for producing specific patterns of behavior, but there is no pretense, by this view, that a more naturalistic setting would necessarily be more appropriate. Where one is interested in helping to make sense of laboratory findings, a replication attempt may often be the place to start. Specific aspects of the apparatus may limit or otherwise constrain behavior in ways that produce patterns of behavior that appear to support some theory artificially (Timberlake 1983a). Identifying such cases has historically been among the clearest critical successes of behavior systems work.

Note that by Timberlake's usage, a behavior system refers not only to its motivational component but to perceptual and motor components as well. The motivational component receives focus by this approach, depending on the specific problems addressed, but it is remembered to be embedded within the motor and perceptual realities of the animal. Behavior will depend on all of these factors, as well as the current circumstance.

### Timberlake's Theory of Learning

William Timberlake (1983a) applied a behavior systems approach to learning, and the resultant theory (confusingly) took the name, behavior

systems theory. The primary innovation was a shift in the conception of the unconditional from discrete stimuli to systems. By behavior systems theory, learning is a means of finding a match between the structure of one's environment and the structure of internal motivational systems. Tinbergen and Lorenz had talked about learning in similar terms, but left these intuitions undeveloped.

By a range of views, terminal feeding behaviors are reinforced through association with acquisition of food. By a behavior systems perspective this is only a part of a more complex system of behavior, the rest of which may be unsupported or even prohibited by the apparatus, or just not measured, for the purpose of isolating specific, quantifiable responses. Rather, when animals learn about associations in their respective worlds, they are learning how stimuli fit into a behavior system. An unconditional stimulus engages not just a single unconditional response but a whole motivational complex. An associated cue is fit into this complex.

### Three-Mode Model

Timberlake (1990, 2001) presented the three-mode model which begins by dissociating three phases of system-specific behavior: consummatory, focal search, and general search. Earlier thinkers (Craig 1918; Konorski 1967; Bindra 1961) had dissociated consummatory (or terminal) from appetitive (or preparatory) behaviors. Consummatory (derived from the Latin, *cōsummare*: to complete, accomplish) responses are behavioral end points, what happens when the goal is in hand, for example, killing the prey or copulating. These are the responses most typically in focus in conditioning studies, such as a pigeon's pecking a light that signals food. Appetitive behavior consists of the set of behaviors that lead the animal to such an end, such as hunting or courting. The three-mode model divides appetitive behavior further into focal search and general search. A predator's behavior changes strikingly when it spots prey. At that moment, the predator enters focal search mode, and they move in to kill, now focused on a particular target. However, the hunt had started long

before this moment, as the animal exhibited a very different set of behaviors: general search. For some predators, general search manifests as roaming, some lie in wait. Each step in this sequence biases the animal differently in order to produce the conditions for the next phase, bringing the hunter progressively to a specific end. The animal solves a complex problem by dealing in sequence with just one segment of the problem at a time. Similarly, feeding on berries, one shifts between exploiting the current patch, searching locally for the next berry on a bough (focal search), and exploring, leaving the current patch to find the next (general search). This example accentuates the counter-intuitive point that feeding-related general search behavior often moves the animal away from food.

In addition to the response producing characteristics of motivational systems, Timberlake's approach stresses the response supporting characteristics of apparatus and procedure. Conditional responding can manifest in very different ways that depend not only on the significance the cue acquires to a system of behavior or motivation, which is related to the motivational significance of the US, the system evoked, involving such factors as temporal or spatial distance from the US, and reliability of the CS-US relation, but also on the manner of response the environment affords. A consummatory conditional response is most likely when the CS is close, recent, and reliable in relation to the US. A general search CR is expected with long CS-US delays (e.g., Akins et al. 1994). If the CS is another rat, the behavior elicited is the social response connected with feeding; if the CS is a protrusion from the wall, manipulation and biting; if a moving sphere, chasing and grabbing and carrying (Timberlake and Grant 1975; Timberlake et al. 1982; Timberlake 1983b). Embedded in this analysis is a critique of general-process approaches insofar as they lose sight of how their procedures

and apparatus produce patterns of behavior (Timberlake 1983a). More positively, behavior systems theory permits interpretation of a broader range of response forms that occur in conditioning studies and bringing these behaviors into an analysis gives it depth.

Although the three-mode model was developed in the context of feeding in rats, models with the same essential basis have been applied with success to sexual behavior in Coturnix quail (Domjan 1994) and fear behavior in rats (Fanselow 1994).

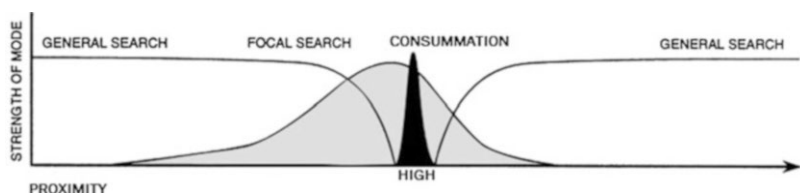
Francisco Silva and Timberlake extended the three-mode model in an important way that places focus on the specific effects of temporal and spatial factors on motivational interactions. Figure 3 illustrates change in strength (vertical axis) of the three modes in relation to each other over a dimension of CS-US proximity (horizontal axis). This proximity dimension brings conceptual unity of various factors in conditioning studies, including temporal, spatial, correlational, and evolutionary relatedness. This basic model and its predictions have proven surprisingly robust in application to conditioning phenomena (Silva et al. 1998a, b; Timberlake 2001).

## Connections with Other Sciences

Behavior systems theorists have long stressed integration of sciences and viewed behavior systems as means of accomplishing this. For Tinbergen (1951), it served as a theoretical link between ecological and physiological analyses and the basis for his first attempt to bring physiology into ethology. Timberlake's extensions of behavior systems (Timberlake 1983a; Timberlake 2001) provided a theoretical basis for principled integration of ethology with psychology. Both thinkers were also dedicated discipline bridge builders,

### Behavior Systems,

**Fig. 3** A depiction of the Three-mode model (From Silva et al. 1998a; Timberlake 2001)



investing heavily throughout their careers in providing institutional infrastructure to enable integration of sciences.

Throughout its history, depictions of behavior systems took the form of networks of interrelated drives or behaviors. These networks represented hierarchical organization, which was stressed in the initial presentations (e.g., Fig. 1), but behavior systems theorists otherwise took little inspiration from network theory. Similarly, the reference to systems was not principled application of systems theory. These potential connections remain unplumbed.

Gordon Burghardt has suggested that a behavior systems approach might be applied to emotions (Burghardt and Bowers 2017). The suggestion appears promising, but it awaits empirical support.

Robotics has contributed to the study of animal behavior methodologically by providing an independent means of testing hypotheses, and the two fields connect in the areas of synthetic biology and artificial life. Inspiration specifically from behavior systems thinking, particularly hierarchical organization and task decomposition, is apparent in the layered architectures used in some robotics communities, notably subsumption architecture (Brooks 1986). Layered architectures produced an initial boom in robotics research, permitting behavior-based robots to succeed at tasks that had stumped earlier generations of robots. However, the initial success was followed by a bust, which may have been helped by better communication between these fields.

In general, a behavior systems approach can be viewed as a strategy for addressing questions throughout psychology, a portable foundation to carry around that is based on a model of the animal and system, rather than of a general capacity (e.g. memory, causal reasoning), one that gives some guidance on how to apply abstract theories to real animals.

## Cross-References

- [Constraints on Learning](#)
- [Michael Domjan](#)

- [Nikolaas Tinbergen](#)
- [William Timberlake](#)

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## Behavior Therapy

- [Behavior Modification](#)

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## Behavioral Accommodation

- [Adaptedness of Behavior](#)

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## Behavioral Adaptations

- [Adaptation](#)

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## Behavioral Contrast

- [Contrast Effects](#)

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## Behavioral Control

- [Inhibition](#)

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## Behavioral Disorders

- [Animal Psychopathology](#)

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## Behavioral Diversification

- [Behavioral Variation](#)

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## Behavioral Evolution

- [Stone Tools](#)

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## Behavioral Flexibility

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## Synonyms

[Behavioral plasticity](#)

## Definition

Behavioral adjustments in response to external or internal stimuli.

## Introduction

The ability to respond to changing conditions in innovative ways is a key evolutionary adaptation of humans and other animals (Lefebvre 2013). This behavioral flexibility, which describes the changes in an individual's behavior in response to environmental stimuli, is often used synonymously with behavioral plasticity (e.g., Brown and Tait 2010; Holekamp et al. 2013; Wong and Candolin 2015). Behavioral flexibility is sometimes erroneously confused with behavioral



variation when comparisons of behavioral differences among individuals of the same species across space are conflated with those of the same individuals over time (Strier 2017). However, while behavioral flexibility necessarily produces behavioral variation, the converse is not always true because behavioral variation can also arise as a result of other mechanisms, including local directional selection pressures or drift. In theory, the strongest evidence for behavioral flexibility comes from behavioral changes that track environmental or social stimuli and that can reverse in the absence of the stimuli that elicited the responses initially. Comparisons across individuals, groups, or populations of conspecifics can yield evidence of intraspecific behavioral variation, but temporal comparisons are required to identify the existence of behavioral flexibility.

Behavioral flexibility can be described as an individual or a species-specific trait. Differences among individuals in their levels of behavioral flexibility are often attributed to personality, coping styles, or behavioral syndromes, which are correlated behavioral responses (Coppens et al. 2010). Intraspecific behavioral differences across groups or populations may reflect responses to local environmental conditions with either or both learned and genetic components, whereas interspecific behavioral differences have an additional effect of phylogeny, which can either facilitate or constrain plasticity (Kappeler and Kraus 2010; Kappeler et al. 2013). There is also increasing evidence that individual differences in behavioral flexibility may reflect experiential differences at earlier stages of life, which can either increase or decrease plasticity (Stamps 2016; Stamps and Biro 2016).

The ability to adjust one's behavior in response to local social and environmental conditions is generally considered to have direct fitness consequences (Coppens et al. 2010). Behavioral responses to changing conditions would be particularly advantageous when the changes occur faster than the rate at which behavioral evolution could occur. Presumably, natural selection would favor the capacity for behavioral flexibility whenever local conditions are subject to frequent but unpredictable change or fluctuations. Variation in the conditions that both elicit specific behavioral

responses and select for behavioral flexibility could account for behavioral variation across groups and populations of the same species, as well as for differences in the degree of behavioral flexibility across species. Genetics, developmental constraints, and life history characteristics also affect both individual and species-specific differences in behavioral flexibility. Correlated behavioral responses can limit the flexibility of responses to particular stimuli, even to the point of being or appearing to be nonadaptive (Sih et al. 2004).

Distinguishing between conservative, species-specific patterns of behavioral flexibility and intraspecific, population or individual variation in behavioral flexibility remains a challenging area of investigation (Coppens et al. 2010; Strier et al. 2014). Not surprisingly, high levels of behavioral flexibility have been associated with long-lived, large-brained, highly social animals, such as primates, whose slow developmental rates and overlapping generations provide extended opportunities for social learning. These life history traits also increase the likelihood that individuals will experience fluctuations in social, demographic, and ecological conditions over the course of their long life spans, making the ability to respond to new or changing stimuli highly adaptive. However, the same slow life history traits that make behavioral flexibility so adaptive for primates may also contribute to their greater extinction risks compared to other mammals with relatively faster reproductive rates and shorter generations (Lindshield 2017).

## Ecological Flexibility

Seasonal changes in ambient conditions, such as temperature, rainfall, or day length, can alter the availability and distribution of critical resources such as food, water, or mates and result in predictable behavioral changes. These include shifts in the allocation of time and energy devoted to different activities, as well as in changes in diets, patterns of ranging and habitat use, and the types and rates of social, reproductive, and thermoregulatory behaviors. Among primates, seasonality in food availability typically results in different

combinations of adjustments in diet, ranging, and grouping patterns that are at least to some extent predictable based on the degree of dietary specializations (Strier 2016). For example, species with highly specialized diets are more likely to adjust their ranging and grouping patterns than species whose more generalized diets permit them to maintain stable social groups despite scarcities in their preferred food sources. Sympatric species that occupy different feeding niches may respond differently to identical stimuli, whereas different populations of the same or closely related species typically differ more in the degree of their responses relative to local conditions than in the kind of their responses.

The repertory of flexible behavioral responses elicited under normative, seasonal fluctuations may be inadequate to meet the challenges posed by extreme or unpredictable climatic events such as prolonged droughts and major hurricanes. These kinds of extreme events are known to be responsible for high levels of mortality in wild primate populations, and they are predicted to become increasingly common as a consequence of global climate change (Meyer 2017). Although some animals are capable of shifting their geographic ranges as climate and vegetation change, habitat loss in general and fragmentation in particular represent major barriers for others, such as the majority of primates, which are largely dependent on forests. Exceptions to this, such as macaques (*Macaca* spp.) that have adapted to urban settings, have been distinguished as “weed” species specifically because of their exceptional ecological flexibility (Richard et al. 1989).

## Social and Demographic Flexibility

Many animals adjust their grouping patterns in response to ecological stimuli. These adjustments can be distinguished into aggregations, such as the antipredator tactics that result in the formation of schools of fish or flocks of birds, versus social groups, which are comprised of two or more individuals that differentially associate and interact with one another.

Nonetheless, aggregations provide opportunities for social interactions, and conversely, members of social groups may fission into different combinations for varying periods of time, thereby disrupting their associations and opportunities to interact. Such “fission-fusion” societies are observed in primates such as chimpanzees, bonobos, and spider monkeys, as well as in dolphins, elephants, and spotted hyenas, and are generally predicted by ecological variables (Aureli et al. 2008).

Some of these species (e.g., chimpanzees, dolphins, and elephants) with fission-fusion societies also possess large brains relative to their body sizes and sophisticated cognitive abilities, but there is currently no clear evidence of a generalized link between social flexibility and cognition (Aureli et al. 2008). Indeed, although fission-fusion societies may require particular skills, such as memory to keep track of the status of social relationships without continuous access to one another, there may also be equally complex but different cognitive skills required for negotiating and repairing the strains on social relationships that are more likely to arise as a result of the higher frequency of interactions in cohesive groups.

The occurrence of cohesive groups versus fluid, fission-fusion societies, along with many other features of animal social and mating systems, has been explained by ecological variables including the availability and distribution of food and other resources (e.g., Jarman 1974; Emlen and Oring 1977; Wrangham 1980). The size and composition of groups simultaneously affect individual social options and are affected by demographic variables such as population-wide sex ratios and population densities, which can change rapidly over the duration of individual lifetimes, and by life history variables such as reproductive rates and dispersal regimes, which tend to be phylogenetically conservative (Strier 2008, 2011). Demographic changes have been implicated in switches between predominantly single-male and predominantly multi-male groups and in deviations from both male-biased and female-biased dispersal regimes. In addition, among primates, the flexibility to switch between

cohesive and fission-fusion groups is also associated with both high demographic variance and female or bisexual dispersal (Strier et al. 2014). For example, a sixfold increase (from 50 to more than 300 individuals) in the size of an isolated population of northern muriqui monkeys (*Brachyteles hypoxanthus*) inhabiting a protected forest fragment in southeastern Brazil has been implicated in two successive behavioral changes (Strier and Mendes 2012). First, the doubling of one study group (from 23 to 57 individuals) over a 15-year period was accompanied by a shift from cohesive to fluid, fission-fusion associations, presumably to minimize per capita travel costs in the quest for food and direct feeding competition. Continued population growth over the next 15 years was subsequently associated with an expansion of the muriqui's vertical niche to include increasingly frequent use of the ground and terrestrial resources. Although the initial shift was probably stimulated by ecological necessity, terrestrial behaviors spread along social networks, and the diversity of terrestrial activities expanded to include resting and socializing, reflecting a further extension of their behavioral flexibility (Tabacow et al. 2009).

Another example of pronounced behavioral flexibility comes from the social transition documented in a troop of wild olive baboons (*Papio anubis*) after its most aggressive males succumbed to a respiratory disease (Sapolsky and Share 2004). The remaining troop members adopted more relaxed, peaceful relationships, with higher rates of grooming and other affiliative behaviors that persisted despite the immigrations of males from other troops with less pacific traditions.

Both the adoption and persistence of the baboon's relaxed sociality and the spread of the muriqui's terrestrial tradition bear similarities with processes commonly associated with cultural innovation and transmission (Laland and Hoppitt 2003). Other forms of behavioral flexibility, initially stimulated by ecological or demographic stimuli and enhanced through learning and sociality, are also considered to have been fundamental steps in early hominin behavioral evolution (Meindl et al. 2018).

## Flexibility to Anthropogenic Changes

Behavioral flexibility is a critical component of the adaptive capacity of animals to respond to rapid and unpredictable change. However, our understanding of these capacities is limited by an absence of detailed comparative data on the behavioral repertoires of most animal species. Even when comparative data exist, our ability to distinguish behavioral flexibility from other sources of behavioral variation is often limited by the short temporal scales over which the comparisons can be made (Strier 2017).

Tragically, contemporary field studies of the behavior of wild animals are now faced with the challenge of distinguishing behavioral adaptations that have been selected over evolutionary time, from behavioral responses to rapidly changing conditions as pressures from human activities encroach on animal habitats and populations (Hockings et al. 2015; McLennan et al. 2017). The alarming rapidity of these anthropogenic changes often precludes evolutionary adaptations. While some species may be able to adjust their behavior and even keep pace with rapid climate changes (Beever et al. 2017), the prospects for many others remain grim. The selection of sub-optimal habitats following rapid environmental change can lead to ecological traps (Hale and Swearer 2016), a subset of the broader phenomenon of evolutionary traps in which past adaptive behavioral responses to environmental stimuli are detrimental, or maladaptive under current conditions, and can lead a population or a species to extinction (Schlaepfer et al. 2002; Robertson and Chalfoun 2016). Thus, understanding both the potential for behavioral flexibility and its fitness consequences has important implications for the conservation of biodiversity.

## Conclusion

According to the IUCN's best estimates ([http://cmsdocs.s3.amazonaws.com/summarystats/2018-1\\_Summary\\_Stats\\_Page\\_Documents/2018-1\\_RL\\_Stats\\_Table\\_1.pdf](http://cmsdocs.s3.amazonaws.com/summarystats/2018-1_Summary_Stats_Page_Documents/2018-1_RL_Stats_Table_1.pdf) 30 January 2018), 41% of all amphibians, 13% of birds, and 25% of mammals

were threatened with extinction as of 2017. For major groups, such as primates, these percentages may already be as high as 60% (Estrada et al. 2017). High levels of behavioral flexibility may buffer some animals from extinction, but ultimately it will require greater behavioral flexibility by humans than we have so far expressed to reduce these impending threats.

## Cross-References

- Adaptation
- Adaptedness of Behavior
- Aggregation
- Behavior Systems
- Behavioral Variation
- Cognition
- Conservation
- Conspecifics
- Coping Style
- Cultural Transmission
- Culture
- Environmental Influences
- Evolution
- Fission-Fusion
- Group Living
- Hominid
- Human-Animal Interaction
- Learning
- Life History
- Natural Selection
- Optimal Group Size
- Personality in Animals
- Primate Cognition
- Primate Social Structure
- Social Behavior
- Temperament
- Terrestrial

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## Behavioral Genetics

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## Introduction

Genes are the basis of all life, and variations in the genetic code significantly affect a variety of physiological traits in animals, e.g., body confirmation traits, production and fertility, or the susceptibility to diseases. Behavior, in contrast, resembles rather an action or reaction than a physiological trait, so does the concept of a genetic contribution to trait variation between individuals also apply for behavior?

Probably one of the first evidence for a genetic background of animal behavior can be found in the evolution and breed history of the domestic dog (*Canis familiaris*). In the course of the domestication of dogs, the traits under selection, be it natural or artificial, were also of behavioral nature, e.g., tameness and attachment to humans and later



hunting and herding behavior. Subsequently, in the formation of the different dog breeds, the modern dog as we know it today, was shaped among others by selecting dogs with favorable personalities.

Dmitry Belyaev demonstrated this process of behavioral selection in canid domestication in a similar species, the silver fox (*Vulpes vulpes*). In his selection experiment beginning in 1959, farm foxes were selected for tameness only in a standardized environmental setting: after birth and weaning, pups were caged with litter mates and kept under minimal contact with humans. In the first months of their lives, a pups' tameness was evaluated in a series of behavior tests and only the ones with the highest scores for tameness were selected for breeding. The selection over multiple generations resulted in a shift towards tame behavior, with a growing percentage of animals within every generation that expressed docile behaviors. Based on these observations Belyaev concluded that behavior has a genetic background to some extent. After multiple decades of selection, experimenters refer to these animals as domesticated foxes, as they were eager to establish human contact, they whimper to attract attention and sniffing and licking experimenters like dogs (Trut 1999).

Now, the idea that genetic variations besides environmental factors and individual experiences contribute to the way an animal behaves in response to external stimuli and in certain situations is widely accepted. However, to which extend behavior variations are influenced by either genetic or non-genetic (environmental) factors is excessively discussed in the nature vs. nurture debate. More likely than exclusive influences of nature (genes) or nurture (environment) is an interaction between both factors: genetic variants can determine how environmental stimuli that trigger behaviors are received and processed (e.g., by modifying the sensory system) and the environment can alter the inner state of an animal (e.g., a lack of food leads to hunger) which in turn can regulate gene expression (Bendesky and Bargmann 2011).

In the era of molecular genetics, research on behavior genetics in animals can evolve from descriptive observations from selection

experiments to the detection of causal variants and molecular mechanisms involved in the genetic architecture of behavior. Comprehensive data from various molecular levels, e.g., genome, transcriptome, and metabolome information, can now be used to meet the still growing interest in the genetic contribution to behavior variation in animals: dissecting the genetic background of animal behavior has its relevance in animal welfare in domesticated species (e.g., breeding for stress-resistance in livestock), can give insights into the evolutionary importance of behavior in wild populations, and finally, can provide general information which might be related to behavioral conditions or psychological disorders in humans.

In the following, the basis of the genetic architecture of animal behavior is described and relevant candidate mechanisms with known influence on behavior variation in animals are introduced. Then, methods for behavior phenotyping and the subsequent genetic analysis are presented and examples for the genetic contribution to specific behavior traits or patterns are given. Additionally, the interactions between non-genetic (environmental) and genetic factors in relation to behavior variation are presented. In the conclusion, the challenges and perspectives of animal behavior genetics are briefly discussed.

## The Genetic Architecture of Behavior

Behavior itself is a complex trait and so is its genetic architecture. A Mendelian inheritance pattern for behavior traits, meaning that a trait variation is controlled by one locus only, is rare. Instead, the inheritance of most behavior traits is of polygenic nature, i.e., there are multiple genetic loci contributing to the observed behavioral differences of which many have a small affect and just a few have a moderate or even a large effect (York 2018).

To which proportion behavior has a genetic component is highly variable for specific behavior traits: genetic loci associated with courtship or feeding behaviors explained significantly more phenotypic variance in different species than genetic loci associated with other behaviors



(York 2018). It is assumed that behavior traits like courtship, which are positively correlated with the reproductive success and thus the genetic fitness of an individual, might be involved in evolutionary processes and subsequently are more likely to be under genetic control. In contrast to courtship or feeding behaviors, it was shown in laboratory rodents that genetic variants explained on average under 10% of the variation in behaviors related to locomotion, addiction, or emotions in different test situations (Flint 2003).

The genetic architecture of animal behavior consists of different genetic components. Genetic variation of behavior is referred to as additive when deviations from the mean behavior phenotype are caused by a specific genetic variant A (allele A) or variant B (allele B) and the combination of both alleles (heterozygote genotype AB) results in the intermediate behavior phenotype between the homozygote genotypes AA and BB. If there is a non-additive interaction between the alleles at a given loci, and thus, the heterozygote genotype effect is unequal to the mean phenotype, this is referred to as dominant variance. The third component is the epistatic variance which also described a non-additive interaction between two alleles but in contrast to the dominant variance, at different loci.

Dissecting the genetic architecture of behavior into these three components is rare; most studies report the additive genetic variance. In great tits (*Parus major*), however, additive and non-additive genetic effects on exploration and boldness have been analyzed and dominance effects were identified as major determinant of behavior differences besides additive genetic effects (van Oers et al. 2004).

Another factor that needs to be considered for the dissection of the genetic architecture of behavior is the genetic correlation. Genetic correlations are the results of either pleiotropy (when one genetic locus affects multiple traits) or less common of linkage (when genetic loci which affect multiple traits are inherited together) and can occur between behavior traits and behavior traits and non-behavior traits. A selection experiment in the Red Junglefowl, which are ancestors of the domestic chicken, demonstrated a genetic

correlation between fear of humans and other behaviors like fearfulness and exploration in other contexts (Agnvall et al. 2012). And even when behavior traits share only little common genetic loci contributing to the behavior variation, the same molecular pathways can be affected by the individual genetic variant and thus a phenotypic correlation is observable (York 2018).

Evidence for a genetic correlation between behavior traits and non-behavior traits is once again delivered by the process of domestication: both the domestication of the dog and the farm fox experiment demonstrate a link between the selection for behavior and morphological traits. In the creation of dog breeds, for example, functionality was closely linked to morphological features. Breeds excelling in hunting behavior often have different skull and body shapes compared to breeds selected for guarding or herding. In a genome-wide association study, genetic variants that were associated with fear or aggression in various contexts were also associated with morphological traits (Zapata et al. 2016). Likewise, Belyaev's farm foxes changed their appearance with progressing selection: depigmentation, brown mottling, grey hairs, shorter legs and tails, and upward curled tails as in dogs occurred in the tame foxes compared to the unselected control group (Trut 1999).

Besides direct genetic effects on behavior within animals, interacting genetic effects between individuals (indirect genetic effects) can occur. Indirect genetic effects describe the phenomenon that the phenotype of an individual is influenced by genetic variations of conspecifics, e.g., maternal effects on the offspring or an individual's adaptation on behaviors of opponents or family members. It is assumed that indirect genetic effects can contribute to the expression of behavior variances in the context of social interactions and may therefore also affect evolutionary dynamics: for example, highly aggressive Mediterranean field crickets (*Gryllus bimaculatus*) reduced aggressive behavior in opponents due to indirect genetic effects and this in turn reduced the total genetic variance of aggressiveness for the whole population (Santostefano et al. 2017). Moreover, the indirect genetic effect on the variance of aggressiveness

also affected the non-social trait “exploration” in the Mediterranean field crickets, indicating that indirect genetic effects are an important part of the multivariate genetic architecture of behavior.

## Candidate Mechanisms for Behavior Genetics

Complex physiological structures are involved in receiving, transmitting, and processing information that lead to a behavior response. Genetic variations which affect these structures are the origin of the genetic background of behavior. Variations in the genetic code (single nucleotide polymorphisms, insertions or deletions, structural variants) due to mutations can modulate the expression of genes (gene regulation) and protein structures, and thus complex circuits. Target structures underlying behavior modifications with a genetic component are primarily proteins, hormones, or neurotransmitters themselves affecting complex circuits belonging to the sensory system or neuromodulatory pathways (Bendesky and Bargmann 2011).

At the genetic level, a few strong candidate genes for behavior traits or personality have been described among species that affect the level of neurotransmitters, like the dopamine receptor D4 (*DRD4*), monoamine oxidase A (*MAOA*), and serotonin transporter (*SERT*) genes. Across species, allelic variations in *DRD4* were associated with personality traits like exploratory or novelty-seeking behaviors (Fidler et al. 2007; Garamszegi et al. 2014). Allelic variations in *MAOA* and *SERT*, for example, can alter the enzyme activity and thus affect the neurotransmitter levels, which was linked to aggressive behavior in different species (Sacco et al. 2017; Wendland et al. 2006).

It is assumed that proteins involved in modulating behaviors have general functions, like protein kinases, e.g., the cGMP-dependent protein kinase (PKG). Genetic variations that affect PKG activity are described to mediate various behaviors across multiple species, e.g., foraging in *Drosophila melanogaster*, circadian rhythmicity in rats, and addiction and anxiety in mice

(reviewed in Reaume and Sokolowski 2009). Genetic variations in G-protein-coupled neurotransmitter receptors (GPCR) and their regulators (*Rgs2*, *Avpr1a*, *tyra-3*, *npr-1*) are also associated with behavior traits in several animals of which all have in common that the animals internal state is affected by the GPCR system (Bendesky and Bargmann 2011).

Candidate hormones, especially in regard to social interactions like paternal care, are oxytocin and vasopressin. Oxytocin is a neuropeptide released by the hypothalamus that acts in the brain and it affects the reproductive system but also behaviors related to social bonding. Vasopressin, likewise, is produced in the hypothalamus and modulates stress response-related behaviors (fight or flight). Its effects are often antagonistic to oxytocin and therefore it is considered as oxytocin’s counterpart.

Considering complex circuits that play a role in the biological background of behavior, the hypothalamus itself is part of the hypothalamic-pituitary-adrenocortical (HPA) axis, a system that is involved in the physiological response to stress and thus can mediate behavior as well. For example the corticotrophin-releasing hormone is a major modulator of the HPA axis and changes in the expression of corticotrophin-releasing hormone receptor genes were shown to affect the susceptibility to stress and anxiety behavior in mice (Bale et al. 2000).

## Assessing the Genetic Background of Animal Behavior

### Determining the Behavior Phenotype

In the era of high-throughput genotyping methods, determining a suitable phenotype is key for the success of association studies. This is especially true for complex behavior traits as they are often confounded with each other and there are multiple ways of measuring them. Important features of suitable behavior phenotypes are (I) an easy recording and (II) a clear characterization under the consideration of environmental factors. An easy recording of behavior phenotypes is crucial because generally, large sample sizes are

needed for genetic studies and labor, time and space intensive methods of behavior recording would interfere with that. A clear characterization of behavior traits and appropriate methods to measure the target trait under the consideration of environmental factors are important to control for confounded traits and environmental variation. However, some behaviors are often interwoven with each other, which hinders a separate consideration, e.g., a separate dissection of fearful and aggressive reactions in challenging situations is difficult because aggression can be a consequence of fear (fight or flight response).

Generally, the above-described features can be better accounted for in experimental settings using behavior tests compared to field studies which normally include intensive observations. Common behavior tests in experimental settings for laboratory animals like rodents are the open-field test or the elevated plus maze test and their variations (e.g., the novel-object test). The open-field test comprises behavior records when animals are exposed to an (unknown) arena, and it is supposed to measure behavior traits like fear, novelty, or risk seeking and exploratory behavior. Typical measures are time spend close to the walls or in certain sections of the field, time being active or inactive, frequency of urination or when an object is placed in the open-field (novel-object test), the frequency and duration of animal-object contact. The elevated plus maze test is a plus-shaped runway with two arms enclosed and the others open and is usually used to characterize anxiety in rodents by measuring the time animals spend in the different types of arms.

Methods like the open-field test can also be applied to larger model animals or livestock species. In the case of livestock species, however, the behavior trait of interest, e.g., for genomic selection, is often temperament in response to human handling or contact. Therefore, behaviors in the presence of humans are measured, either in test situations (e.g., flight-speed or novel-human test) or in everyday handling situations (e.g. milking, weaning, regrouping or weighting). In test situations, objective measurements like the speed when leaving a chute (flight-speed test) or frequency of human-animal contact (novel-human

test) can be elaborated to characterize temperament whereas in handling situations, temperament scores are normally given by handlers, and therefore they might be subjected to a certain subjectivity.

Subjectivity is also one of the limitations when behaviors, especially personality, are assessed via owner-questionnaires which is a common method in pets. For example, the Canine Behavioral Assessment & Research Questionnaire (C-BARQ) is frequently used for the behavior phenotyping in genetic studies of dogs (Zapata et al. 2016). As advantages, questionnaires are a useful tool to acquire large sample sizes and assess every-day behaviors that are not biased by a test setting.

Sometimes however, experimental settings are not appropriate to phenotype behavior. This is the case when the target behavior cannot be replicated in the laboratory or under captivity, e.g., mating or nesting behaviors and habitat choice, or when the animals of interest are wild species (Merrick and Koprowski 2017). Observations can be automated, for example, tracking methods for social interactions, but manual observations remain important techniques for characterizing behavior variations in wild animals.

## Genetic Analyses

When the extent to which genetic variants contribute to behavior differences between individuals is of interest, heritabilities can be estimated. Heritability estimates are calculated based on observations for related individuals by partitioning the behavior differences to a genetic, an environmental, and a residual (error) component. Relationship information can be assessed from pedigrees or from genotypes, which is especially valuable in wild populations. Generally, heritability estimates for behavior or personality traits tend to be low or moderate, with only a few exceptions of traits with a high heritability (York 2018).

Besides heritability estimates for behavior traits, specific genetic variants underlying behavior differences and their effects can be identified. Before specific genes and their variants that underlie behavioral differences can be identified, a genome-wide scan is normally conducted to localize genomic regions (quantitative trait loci;

QTL) that are associated with the behavior trait (QTL study or association mapping). To achieve this, one utilizes the circumstance that a genetic variant, which is often referred to as genetic marker in these studies, is either the causative mutation itself which is associated with the behavior trait or is in close distance to the causative mutation and thus they are inherited together. Prerequisites for these genome-wide scans are genetic variants, either SNPs or microsatellites, that are distributed across the genome and for which animals can be genotyped by SNP genotype array technologies or by whole-genome sequencing (WGS). The genotyping technology affects the resolution of the genotype information available for the QTL mapping or association study: whereas SNP genotype arrays meanwhile cover hundreds of thousands of loci for most animals, WGS provides an even more complex picture.

The availability of genetic markers (type and number), the structure of the population under analysis, and the scientific objective determine which genetic method is suitable to analyze the genetic background of behavior. For linkage mapping, which can be applied in related individuals, the genetic distance between markers is utilized. Therefore, a genetic map (or linkage map) is calculated first, which describes the frequency of recombination between two markers. The following principle applies: The further away two markers are from each other, the higher is the likelihood that they are inherited independently from each other, or in other words, the higher is the recombination rate and thus the genetic distance. Information on the linkage map can be used to map QTL (QTL mapping) assuming that markers and causative mutations that are linked to the behavior variation segregate together in related individuals. Favorably intercrosses or backcrosses of strains which show a high variability of the trait of interest are used for these studies. Laboratory rodents as mice and rats are predominant animals for QTL mapping studies (Flint 2003) due to the availability of inbred strains, short generation intervals, and the high number of offspring. Another advantage of laboratory animals for QTL mapping studies is the fact that the

environment can be standardized for all individuals to minimize interactions between genes and the environment and variations due to environmental influences.

QTL mapping is a useful tool to determine genomic regions associated with the behavior trait of interest. However, the application of QTL mapping is not only limited to assess general insights into behavior genetics using experimental populations, it can also be used to identify candidate genes with strong effects on the behavior phenotype. In accordance, QTL mapping was successfully applied to tackle behavior conditions in livestock species, e.g., the porcine stress syndrome (PSS) in pigs. PSS is an inherited condition that causes pigs to have severe muscle contraction, hypermetabolism, and an elevation in body temperature when inhaled anesthetics or when exposed to environmental stress. With QTL mapping, the swine stress gene (*hal*) was identified on chromosome 6 because variants in this gene were associated with PSS (Davies et al. 1988).

Pinpointing associations to specific genetic loci is the underlying objective of genome-wide association studies (GWAS). In contrast to QTL mapping studies, GWAS use the actual physiological positions of genetic markers to identify QTL and study objects can be unrelated individuals making GWAS an ideal tool for analyzing behavior in wild populations with unknown pedigree. The underlying principle of a GWAS is the linkage disequilibrium (LD) that exists for genomic regions. If LD and the genetic marker (SNPs) distribution are sufficient, genetic markers and causative mutations are linked to each other and an association can be found between allele frequencies and behavior variations. In unrelated animals, much more crossing-over has occurred, decreasing the LD and thus requiring a higher coverage of genetic markers. GWAS have higher power to detect QTL with small effects compared to QTL mapping studies, which might be useful for the dissection of the genetic architecture of behavior in animals. Accordingly, GWAS have significantly contributed to the dissection of the genetic architecture of behavior, for example, strong candidate genes for feeding behavior and eating efficiency in pigs were identified (Do et al. 2013).

Pinpointing the causal variation, however, often requires a fine-mapping of the identified genomic region associated with the behavior trait. Therefore, instead of scanning the whole genome, single genes can be explored for associations with behavior variation: the genotyping can be limited to candidate genes for association studies or functional analyses of candidate genes can be conducted. Candidate genes can be determined either by using the genes harbored by QTL identified in other studies (positional candidates) or based on their known function in pathways that modulate behavior (functional candidates). Based on what can be learned from laboratory rodent studies, regions of DNA should be appropriately prioritized to find the molecular variants, for instance by looking at sequences that control the level of gene expression rather than variants in coding regions (Flint 2003).

The first mapped candidate gene for behavior which is conserved across species is the foraging gene *for*. The *for* gene codes for the cGMP-dependent protein kinase (PKG) and variants in the *for* gene were linked to foraging behavior in *Drosophila melanogaster* first, but over the years, a similar function in multiple other species was described in studies using *for* as functional candidate gene (Fitzpatrick et al. 2005).

Once the positional or functional candidate gene is recognized, the causal variants can be identified and verified by linking genotypes with trait variation or by generating knock-out strains and comparing the behavior of the knock-out strain with the wild type. A recent genome editing technique for the creation of knock-out models is the CRISPR-Cas9 approach. Briefly, this approach works as following: Directed by a specific RNA which binds at the target sequence in the genome and to the Cas9 enzyme, the Cas9 enzyme cuts at the target DNA sequence and the own repair mechanism of the cell can be used subsequently to modify the DNA sequence by adding, removing, or replacing specific segments. This approach of creating knock-out animal models has been demonstrated to be useful in the analysis of genetic variations with a strong effect on the behavior phenotype (Lee et al. 2018).

For future studies on the genetic background of animal behavior, the combination of high-throughput genotyping methods like WGS and the use of animal models created with precise genome editing methods like the CRISPR-Cas9 approach will largely contribute to a better understanding of the genetic architecture of behavior (York 2018).

## Genetic Background of Specific Behaviors

Behavior comprises single traits to complex patterns, and all of them can show intra- and inter-species variation: some behaviors are conserved across species, like general behaviors as aggression and fear, while other more specific behaviors are only expressed exclusively in certain species, e.g., communication patterns like a courtship song only observed in *Drosophila melanogaster* or pointing behavior in some dog breeds. This inter- and intra-specific variation of behaviors is also manifested in the genetic background.

Regardless of the type of variation (inter- or intra-species), behaviors that have a strong influence on an individual's fitness are more likely to be under genetic control. Such behaviors are normally related to reproductive success (e.g., maternal or mating behavior) and survival (e.g., adaptation or hunting behavior).

Social interactions comprise some of these evolutionary relevant traits (maternal care, mating choice, and affiliative or aggressive interactions between individuals) and are therefore often analyzed for their genetic background. Maternal behaviors, for example, include parenting skills like nest building, cleaning and feeding, or social interaction (communication and recognition) with the offspring. For the latter, genetic variants, which affect the level of hormones like oxytocin, have turned out to be a target mechanism. Assessing and evaluating the genetic background of maternal behavior is especially relevant in livestock species, because maternal behavior affects the survival of the offspring and thus the productivity. For example, in sows, behavioral reactions towards human handling and towards screams of



the piglets were genetically correlated with the survival of the offspring indicating the possibility of genomic selection for behavioral traits in livestock species (Grandinson et al. 2003).

Considering variations in social interactions between conspecifics, which can among others be characterized by aggressiveness or affiliation, an individual's adaptation ability on changing environments is one of the major modulators. Again, this is especially relevant and therefore frequently analyzed in livestock species, where regular regroupings or handling situations require substantial resilience to stress. For example, an animal's failure to cope with this stress can lead to an increased aggressiveness towards conspecifics or littermates and in the worst case, affect the fitness of the entire population or group. For stress reactivity, genetic variants that influence the activity of the HPA axis play a crucial role (Muráni et al. 2010).

Another central aspect of social interactions between animals of the same species that influence a wide variety of behaviors relevant for the individual fitness, e.g., mating behavior, can be attributed to communication abilities. Accordingly an effect of genetic variants on communication skills has been shown, e.g. variants in the *period* gene that affected courtship songs and thus mating in *Drosophila melanogaster* (Wheeler et al. 1991).

The *period* gene is also a classical and well-studied example for the genetics of circadian behaviors in animals. Interestingly, the genetic background of circadian behaviors in model species like *Drosophila melanogaster* can be transferred to behavior genetics in humans (Toh et al. 2001) and thus indicates the relevance of animal behavior genetics for human behavior. Therefore, behavior genetics in animals often serve as prerequisites for behavior genetics of conditions like addiction or psychiatric disorders in humans. To study the genetics of addiction to specific substances like drugs, alcohol, or tobacco, genetic analyses are frequently performed using mouse models: in mice, variants in *nAChR* subunit genes were linked to the behavioral effects of nicotine and nicotine addiction or *GABA* genes to alcohol and other addictions and provided

valuable insights into general mechanisms of addiction that can be used in humans (Li and Burmeister 2009). Knock-out mice exposed to stressful situations can give insights into the background of mood-related behaviors and are also valuable models for the analysis of psychiatric disorders like anxiety and depression in humans (Cryan and Holmes 2005).

A specific interest exists in the genetic background of animal personality. "Personality," "temperament" or "behavior syndrome" comprises the pattern of a wide range of behavior traits like fear, aggression, or social interaction of which variations that are relatively stable across situations are characteristics for an individual (Sih et al. 2004). For example, some animals tend to be more aggressive or bold in various circumstances in contrast to others. Personality can be assessed for a variety of species and is assumed to have a genetic background, because these individual characteristics (or reaction norms) lead to different fitness abilities across environments (Penke et al. 2007) and might therefore affect natural selection in an ecological or evolutionary context. In accordance, genetic studies have shown a heritable component of different aspects of personality (e.g., aggression, boldness, risk-taking) in different species (e.g., sticklebacks, great tits, chimpanzees, dogs, and sheep) ranging from 0.01 to 0.66 (van Oers et al. 2005). However, compared to evolutionary more important behavior traits like courtship, personality variations are less attributable to a genetic control (York 2018).

## Interactions Between Genes and Environment

As addressed in the nature vs. nurture debate, behavior has a genetic and a non-genetic (environmental) component. The effect proportion of both components on behavior variation usually depends on the behavior trait or pattern itself. Generally, it is assumed that most behaviors are to a greater extent affected by the environment and just a few behaviors, e.g., courtship, have a moderate to strong genetic background. Some of



the environmental factors that can affect behavior in animals are weather conditions, the feed availability, the presence of other animals, and individual experiences. Environmental factors can modulate individual behavior throughout the whole lifespan, whereas the genetic predisposition is fixed: The genetic predisposition defines the reaction norm (range) in which behavior variations in the sense of adaptation can occur when the environmental situation changes. The relationship between genetic and environmental components is not necessarily linear (in the sense that an individual carrying a specific variant is always superior across environments), but they can interact with each other. This interaction between genes and environment can result in different reaction norms and thus in different preferences of genotypes over environmental influences. For example, a specific genetic variant 1 in a gene can cause bold behavior in an environment A and a genetic variant 2 in the same gene can also cause boldness, but only under the conditions of environment B (van Oers et al. 2005). This interaction is especially interesting from an evolutionary point of view of behavior: Assessing the genetic predisposition for specific behavioral traits in wild populations and the genetic correlation between these traits and environmental conditions can give insights into behavioral adaptation to changing environments in the course of evolution (Atwell et al. 2012).

In the analysis of interactions between genes and environment that affect behavior variation at the population and the individual level, behavioral plasticity plays a central role. Plasticity describes the within-individual adaptive abilities to environmental changes within the reaction norms provided by the genetic predisposition. Analyzing the genetic background of behavioral plasticity can also give insights into consistency and stability of behavioral traits or patterns, e.g., personality, across situations, and over time (Dingemanse et al. 2012).

But how exactly do genetic and environmental factors interact with or influence each other and thus affect adaptation abilities in animals? On the genetic side, genetic variants can determine how environmental cues are received, transmitted, and

processed, for example, by modifying mechanisms of the sensory system, such as chemoreceptors or sensory organs like eyes and ears. In this case, even if animals receive the same environmental cues, some can be more susceptible than others due to a predisposed higher sensitivity. Then, experiences play a crucial role in the development of different behaviors in individuals and genetic variants can affect how these experiences are processed and stored through modulating the memory and learning abilities. Environmental factors themselves can influence the inner state of an individual, e.g., increased hunger through reduced feed availability, and thus, affect biological mechanisms like gene expression and hormonal levels.

## Conclusions

Dissecting the genetic architecture of behavior in animals includes some caveats that need to be addressed, but once these challenges are overcome, animal behavior genetics can provide valuable information in an evolutionary, an animal welfare and a human genetics, context.

One of the major challenges in the analysis of behavior genetics is the phenotype itself. Caveats are that many behaviors are correlated, e.g., fear and aggression considering the fight or flight response, and that the trait distribution is most of the times unsuitable for statistical models, which often require normally distributed traits. Therefore, the behavior trait or pattern needs to be defined carefully and tested for correlations and data transformation might be considered. For example, instead of measuring the frequency of urination in a fear test in rodents, where probably just a few animals show the trait at all, transforming the trait “urination” into a binary trait (urination yes or no) can avoid a skewed distribution and can be analyzed with the appropriate statistical model.

Second, sometimes only subjective scores exist, e.g., for temperament in cattle, instead of “measurable” behavior traits, which can introduce bias when the scoring was performed by different observers. To address this problem, it can be

helpful to dissect complex behaviors to measurable sequences: for example, break down “maternal behavior” to the time the mother spends feeding and grooming the offspring. And third, genetic studies require a large sample size which is difficult to achieve with a complex, i.e., time intensive, behavior observation or testing.

However, there is a growing interest in the genetic dissection of behavior in animals regarding putative applications (genomic selection for behavior) and basic research (evolution and human behavior genetics). Selecting for behavior is especially relevant in domesticated species, as livestock and companion animals. The possibility to select for favorable behavior traits like tameness and reduced aggression towards humans or stress resistance (adaptation to changing environments) can affect both the animal’s welfare and the welfare of the handler or owner. Finally, generating insights into the genetic background of animal behavior might help to tackle behavioral and psychological disorders in humans by identifying new candidate genes and thus involved physiological pathways that can be targeted by medications.

## Cross-References

- [Additive Genetic Variance](#)
- [Candidate Gene](#)
- [Genetic Variation](#)
- [Heritability of Behavior](#)
- [QTL Linkage Analysis](#)

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## Behavioral Genomics

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## Synonyms

Gene; Genetics; Omics

## Definition

The influence of gene expression on behavior.

## Introduction

The diversity of behavior across the animal kingdom, including both invertebrate and vertebrate classes, is vast, complex, and is not always predictable or easily explained by physiological makeup (Harris and Hofmann 2014). Nature versus nurture debates have been long standing; however, since the development of genomic analysis, it has become apparent that there is a relationship of environmental impact on physiological and behavioral phenotypes, inextricably linking nature and nurture together in the phenotypic expression of diverse behaviors (Hofmann 2003).

The primary constituents of deoxyribonucleic acid (DNA) are four nucleic acids: adenine (A), guanine (G), thymine (T), and cytosine (C) arranged in a double helix. Sections of DNA of a specific order, called genes, are hereditary and some encode for proteins that form and maintain cellular components and processes throughout an organism. Genes are either active or silent, and vary depending on hereditary succession. Gene regulatory expression can be modified, however, especially during developmental periods, by events such as toxin exposure, malnutrition, or hypoxia (Khurana et al. 2019; Lalonde et al. 2020;

Murray et al. 2020). These events lead to changes in offspring that can often be heritable – known as epigenetic modification. Other behavioral differences can occur through chromosomal or gene mutations and deletions that lead to permanent changes in the DNA sequence. The advance of molecular technology used to study modifications, mutations, and heritable status of the genome has expanded scientific understanding and exploration of different aspects of animal behavior, such as cognition, social interactions, and pathologies.

## Cognition

Often defined as the ability to acquire and process new knowledge, cognition involves experiential learning, perception, short- and long-term memory, evaluation, and decision making. Cognition in animals with neural complexity comprises multiple brain regions and neural pathways. Normal cognitive function is important in an animal's success, which, on a basic level, is survival and reproduction.

Epigenetic regulation of parental alleles, variants of a gene, can lead to monoallelic expression or co-expression providing a refined modulatory effect on neural networks (Ho-Shing and Dulac 2019). Use of novel high throughput molecular technology such as Next Generation Sequencing (NGS) can reveal DNA sequences including abnormalities and variations such as copy number variants, deletions, and insertions. Investigation of brain regions at various stages of development using NGS implicates stage-specific and region-specific sensitivity of gene regulation in the brain (Ho-Shing and Dulac 2019).

The functionality of synaptic transmission and plasticity – fundamental processes to multiple aspects of cognition – relies on proper cellular operation and maintenance. Deletion of maternally expressed genes can change neuronal firing patterns, vesicle turnover rates, as well as long-term depression and potentiation (Ho-Shing and Dulac 2019; Jiao and Li 2011; Sun et al. 2015; Wallace et al. 2017). Expression changes in the genes involved in these processes have been linked to memory deficits and interrupted sleep

patterns in mice and is directly associated to Birk-Barel Intellectual Disability Syndrome as evidenced by the rescue of the phenotype with paternal alleles of the gene (Cooper et al. 2020; Gotter et al. 2011; Ho-Shing and Dulac 2019).

With chromosomal microarray analysis, a process that detects deletions and additions by comparing genomic data to a normal control, behavioral phenotypes with impaired cognition show copy number variants present in a specific gene, *CHRNA7* (Gillentine et al. 2017). Duplication of *CHRNA7*, a gene that encodes for a subunit of a neuronal nicotinic acetylcholine receptor, is related to intellectual deficits, autism spectrum disorder, and attention deficit hyperactivity disorder (Gillentine et al. 2017).

Normal cognitive variation is also heavily attributed to genetic expression, which is influenced by the environment (Tucker-Drob et al. 2013). Enriched environments promote increased learning and memory function in rodents, as well as increased genetic expression in genes responsible for synaptic transmission and plasticity (Rampon et al. 2000). Environmental enrichment alters cognitive abilities sufficiently such that substantial research is focused on ameliorating disorders by using it as a treatment, such as in Alzheimer's disease, which presents with cognitive decline and memory loss (Griñán-Ferré et al. 2018; Jake Rogers et al. 2019).

Developmental plasticity through environmental exposure can lead to a variety of adaptive and maladaptive cognitive phenotypes (Lafuente and Beldade 2019). Behavioral modifications through context-dependent genetic expression, induced by the environment, may be heritable and occur through a myriad of multifaceted processes such as histone acetylation, methylation of CpG islands on gene promotor regions, and microRNA regulation. The end results are a change in differential expression and a downstream effect on cellular functioning and neural networks. The changes in cognitive abilities can vary depending on the species and the stage of development. Further to cognitive function, social behavior is an important aspect of animal behavior and is subject to genetic influence.

## Social Interactions

Social interaction is not a significant component of all animal classes, but it is pertinent for many, especially in nonhuman primates (Sueur and Mery 2017). Social interactions influence group hierarchy, learning, and mating success (Kurvers et al. 2014; Senior et al. 2016; Silk et al. 2003; Sueur and Mery 2017).

Hierarchy in some social groups leads to increased mating success and preference as well as preferred resource allocation. Inherited phenotypes can lead to offspring dominance succession; however, candidate genes for social dominance have not been replicable in other studies (van der Kooij and Sandi 2015). Relatable traits for aggression and reward behavior, however, have been associated with social rank in offspring (van der Kooij and Sandi 2015).

When presented with a novel conspecific, vervet monkey reactions to the strangers were recorded and analyzed, showing variability in aggression that was associated with genetic differences (Jeffrey Rogers 2018). Analysis of grooming behavior in chimpanzees has shown variations in the arginine vasopressin receptor gene, *AVPR1A* (Jeffrey Rogers 2018). Increasingly, multiple studies are producing similar results, providing further evidence of a genetic component to social behavior in animals.

Adaptive cognition and social interaction have implications for survival and fitness; however, genetics can also influence deleterious diseases and disorders.

## Pathology

Predominantly, animal research into behavioral pathology focuses on human-comparative animal models and are often not wild, free range expressed behaviors; however, some researchers have begun implementing tasks devised to enhance animal participation rather than forced manipulation (Spanagel 2017). Early research in the 2000s began to link genetics as a putative factor in psychiatric disorders (Inoue and Lupski 2003). Technology quickly advanced over the next two decades

and led to sincere developments in genetic predispositions and foundations for a number of disorders such as schizophrenia, bipolar disorder, major depressive disorder, and addictions (Maldonado et al. 2021; O'Donovan and Owen 2016).

Increased expression in regulatory genes in the ventral tegmental area and a decrease in DNA methylation within the prefrontal cortex of rodent animal models have been associated with food addictive behaviors (Maldonado et al. 2021). Substance abuse addictive behaviors are also explored using animal models, including transgenic mutant models, whereby researchers utilize gene editing, such as CRISPR/Cas9, to modify a gene of interest by insertion or silencing (Spanagel 2017).

Contextually-inappropriate aggression has been linked to attention deficit hyperactivity disorder, schizophrenia, and bipolar disorders and is another focus of human-comparative animal studies (Zhang-James et al. 2019). Excessive aggression and violence are maladaptive behaviors modeled in feral animal studies that have illuminated serotonin signal malfunction through receptors (de Boer 2018). A large, integrated analysis of the human genome; animal transcriptomes from mice, rats, zebrafish, and *Drosophila*; and genetic knock-out studies has linked aggression to functional gene pathways common to both humans and animals, leading to putative targets for further research in psychiatric disorders (Zhang-James et al. 2019).

Anxiety can lead to inhibition, indecisiveness, and retreat of social interactions. For some animals, inhibition and reluctance to explore can be a protective mechanism and increase chances of survival; however, it could also lead to loss of opportunity for food and potential mates. Anxiety disorders in humans are common and research on animal models is abundant (Purves et al. 2020; Schiele and Domschke 2018). Serotonergic and methyltransferase genes are among the list of putative targets for treatment of anxiety disorders (Gottschalk and Domschke 2017). Some evidence has also linked single nucleotide polymorphisms (SNP), which is a gene with a substituted nucleotide, to anxiety; however, the combined efforts of genetic research currently does not account for the heritability of anxiety disorders, leading



researchers to turn to epigenetic modifications (Schiele and Domschke 2018).

## Relevance to Understanding Human Behavior

Often, animal models aim to glean information that might ultimately be relevant to human phenotypes. The study of behavioral genomics is longstanding in human models as well, beginning with Sir Francis Galton, who studied twins who varied in reported similarity to ascertain the extent to which individual differences in some traits, such as intelligence, appear heritable. He suggested that similar twins remained similar as they aged, even if they were raised in different environments. This approach led Galton to conclude that genetics is a major determinant of human behavior (Galton 1875). Today, research has highlighted the role of genetics in accounting for upward of 20–50% of variance in human intelligence (Plomin and Von Stumm 2018). Researchers now recognize the role of gene x environment interactions in shaping psychology and behavior. For example, Caspi et al. (2002) showed that adverse effects of childhood maltreatment in terms of manifestation of conduct disorder were strongest among children who also exhibited low monoamine oxidase (MAOA) activity via a functional polymorphism in the gene encoding for MAOA. Other research has demonstrated that individuals exposed to stressful life circumstances are more likely to experience depression and suicidality if they also have a short allele in the promoter region of the serotonin transporter (5-HTT) gene relative to those who were homozygous for the long allele (Caspi et al. 2003). Today, the diminishing cost of genomic sequencing has made the field more accessible, leading some to describe behavioral genetics as a postgraduate growth area in the field of psychology (Willyard 2010).

## Conclusion

Animal behavior is complex and variable across species, sexes, and stages of development. Within

each of those categories, there is significant variability in many behavior phenotypes including but not limited to cognition, social interaction, aggression, and anxiety which appear to be best predicted by consideration of both genetic and environmental factors. Modification of gene expression can occur via different intricate processes influenced by the environment and by parental inheritance that can be linked to variability in animal psychology and behavior.

## Cross-References

- Alleles
- Candidate Gene
- Copy Number Variant (CNV)
- Genotype
- Heritability of Behavior
- Methylation
- Nature Versus Nurture

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## Behavioral Innovation

### ► Innovation

## Behavioral Lateralization

- Hemispheric Specialization
- Laterality (Handedness)

## Behavioral Levels

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The contemporary model of development, relational developmental systems (Overton and Lerner 2014), is very much grounded in Darwinian evolution, but not the modern synthesis of this position. One can understand the important role that ideas of evolution play in behavioral development without adopting a reductionist, determinist, or otherwise innate perspective (Lerner and Overton 2013; Lickliter 2016). Behavior develops and changes, a result of a myriad of influences (endogenous and exogenous) almost from the moment of conception and, based on current understanding of epigenetics (e.g., Moore 2015, 2016), perhaps before as well. Evolution, of course, is itself about change, and therein lies the crucial relationship between biology and psychology.

The fundamental law of Darwinian evolution is that change results from *natural selection*. But, as with all theories in science, Darwinian evolution has itself been subject to change and modernization. Accordingly, I follow Ho and Saunders in understanding *increasing complexity* (i.e., anagenesis) to be a second law of evolution after natural selection (Saunders and Ho 1976, 1981). Others who have adopted this line of thinking (e.g., Stebbins 1969; Smith and Szathmáry 1995) did so from the perspective of the idea that there is a hierarchy of levels of increasing complexity and organization with evolution. Indeed, this idea can be considered “a central phenomenon of life” (Vrba and Eldredge 1984, p. 146). That this principle is extremely important in scientific understanding was recognized early by Pringle (1951) who noted that “The characteristic of living systems which distinguishes them most clearly from the non-living is their property of progressing by the process which is called evolution from less to more complex states of organization” (p. 175).

This hierarchical principle applies as well to the sciences which can be divided into areas of study based on qualitative changes in complexity of organization: physics and chemistry address lower levels of complexity; biology, psychology, and sociology address higher levels of complexity. This idea appears to have originated with Auguste Comte in the late 1800s (see Boorstein 1998, p. 223) and was subsequently developed in the twentieth century by others such as Novikoff (1945) and Feibleman (1954) (Greenberg and Partridge 2010; Greenberg and Tobach 1984), conceptualized as the “concept of integrative levels.” Aronson (1984) described this idea as a crucial organizing principle in science which is “... a view of the universe as a family of hierarchies in which natural phenomena exist in levels of increasing organization and complexity. Associated with this concept is the important corollary that these successions of levels are the products of evolution. Herein lies the parallel with anagenesis” (p. 66).

In their important book, Michel and Moore (1995) noted that T. C. Schneirla, among the pre-eminent comparative psychologists of the twentieth century, applied this thinking to behavior invoking the idea of phyletic levels. Michel and Moore note that by advancing “the idea that the study of evolution could be informed by developmental analysis” (p. 120) Schneirla emphasized that both biology and psychology are developmental sciences. The historical record is clear that as evolution has continued it has resulted in increasingly more complex forms of animal life. In the context of this discussion it is evident that, with few exceptions, more recently evolved forms are more complex in their biology and their behavior than are earlier evolved forms. Schneirla pointed out that we can “begin to understand the differences between species by noting gross differences in behavioral complexity” (Michel and Moore 1995, p. 121) in a hierarchical relationship reflecting a strong correlation between both biological and psychological complexity.

Applying this idea to behavior, Tobach and Schneirla (1968) proposed an anagenetic, hierarchical ranking of behavioral levels across species,

based loosely on the fact of increasing neural complexity with evolutionary advance. The behavioral levels are separated into two groups, one at which biological factors dominate behavior and one at which psychological and social principles become important. The levels they identified are: *Taxis*, at which behavior is under immediate stimulus control, an example of which is a moth flying toward a light source; *Biotaxis*, a higher level at which behavior is influenced not only by the immediate presence of a stimulus but also by the presence of biochemical sequelae from other organisms such as pheromones; and *Biosocial*, the level at which the social interaction of groups of animals plays an important role in organizing and regulating behavior. In Schneirla’s analysis of army ant behavior, he saw their cyclic activity to be a result of reciprocal social stimulation provided by the enormous number of individuals in an ant colony. That cyclic activity is absent in single ants and is seen only when ants are together in large numbers; *Psychotaxis*: Psychology becomes important at this phyletic level in the form of mediation by past experience. Rosenblatt and Schneirla (1962) demonstrated with cats that the relationship between infant and mother begins with biotactic orientation by the kitten to its mother by means of tactile and olfactory stimuli. Subsequently, higher-order processes (e.g., learning and reinforcement) enter in at later stages of that relationship; *Psychosocial*: at this highest level behavioral organization is regulated by complex social bonds and social interactions characteristic of advanced vertebrates. Among primates, for example, lasting social bonds result from initial complex biosocial and biotactic interactions between an infant and a mother such as those involved in rocking, providing of contact comfort, and nursing.

Tobach and Schneirla (1968) ended their analysis with the description of the psychosocial level. There is, however, merit in developing the system somewhat further to differentiate among phyletic levels of primates and their corresponding communication behaviors. Whereas the behavior of all primates falls into the psychosocial level, at least with respect to communication there are less and

more complex forms. All primates communicate, but a few individuals of some species have developed complex communication skills, bordering on true language (Savage-Rumbaugh et al. 1993). Accordingly, it seems appropriate to further subdivide the psychosocial level into three separate behavioral sub-groupings (Psychosocial I, II, and III; Greenberg and Haraway 2002), distinguished by the nature of communication complexity: a communication only, nonlanguage level (e.g., vervet monkeys); a proto-language level (e.g., chimpanzees and bonobos); and a true language level (only *H. sapiens*). Each of these behavioral levels is demarcated by the evolutionary appearance of species whose behavioral repertoires are increasingly more plastic and complex (Lerner 1984) as are their nervous systems. This ordering of these levels is similar to that of traditional phylogenetic taxonomies.

The utility of the application of this behavioral taxonomy can be seen in the way Greenberg and Haraway (2002) demonstrated its use for feeding behavior and its complexity across phyla and species. As animals became more complex with evolutionary advance, their nervous systems and feeding behavior became increasingly diverse and flexible. Table 1 lists major animal groups and shows at which behavioral (phyletic) levels their feeding behavior may be organized.

**Behavioral Levels, Table 1** Levels of behavioral complexity displayed by major animal groups in feeding behavior

| Major groups           | Higher levels of complexity illustrated |
|------------------------|-----------------------------------------|
| <i>Protozoa</i>        | Taxic                                   |
| <i>Cnidaria</i>        | Taxic                                   |
| <i>Cnidaria</i>        | Biotaxic, biosocial                     |
| <i>Echinodermata</i>   | Biotaxic, biosocial                     |
| <i>Platyhelmenthes</i> | Biotaxic, psychotaxic                   |
| <i>Molusca</i>         | Biosocial, psychotaxic                  |
| <i>Arthropoda</i>      | Biosocial, psychotaxic                  |
| <i>Osteichthyes</i>    | Biosocial, psychotaxic                  |
| <i>Amphibia</i>        | Biosocial, psychotaxic                  |
| <i>Reptilia</i>        | Biosocial, psychotaxic                  |
| <i>Aves</i>            | Psychotaxic, psychosocial               |
| <i>Mammalia</i>        | Psychotaxic, psychosocial               |

This notion is directed at the classification of behavior. Note that for most groups feeding behavior is organized at more than one level and that individual species can function behaviorally at more than one level (for example, at different stages in its development). Each animal then should be classified at its highest level of behavioral complexity in respect to a behavior, with the idea that a higher classification subsumes the levels below it. In Protozoa, such as the ameba, feeding is regulated solely by the presence of appropriate chemicals at appropriate intensities; they are thus organized taxically for this behavior. Among the Cnidaria, such as Hydra, feeding is mostly a taxic process, although the ability of these animals to distinguish among living or recently living foodstuffs for prey suggests some biotaxic organization. Feeding by mollusks shows even higher organizational processes at work, allowing learning to become an influence of their feeding behavior. Among the vertebrates, feeding complexity, the influence of conspecifics, and many components of learning (e.g., the remarkable caching ability of some birds) show their feeding behaviors to be organized at the highest levels. This organizational system was applied by Greenberg and Haraway (2002) to a full range of behaviors further attesting to its utility and is shown in Table 1.

The heuristic value of Schneirla's use of the levels concept in this way can be seen in replies to criticisms that have been leveled against it (Tobach and Greenberg 1984). Against hereditarianism, the concept poses the question about how genes might function at different levels; there is no special value placed on any level, succeeding levels integrate preceding ones, and the formulation of a question determines the appropriate level of inquiry; the concept does not imply anything about the "proper" research to be done as investigations are needed at all levels; the levels concept provides for the generation of critical hypotheses, especially regarding developmental issues; and finally, "the levels concept . . . belongs to the province of the science historian" (Tobach and Greenberg 1984, p. 6) which is reflected in the statements of Pringle and Aronson cited earlier in this entry.

## Cross-References

- [Approach/Withdrawal Theory](#)
- [Comparative Psychology](#)
- [Epigenesis](#)
- [Ethel Tobach](#)
- [Evolution](#)
- [Language Research: Great Apes](#)
- [Primate Communication](#)
- [Protolanguage](#)

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## Behavioral Neuroscience

- [Matching-to-Sample: Comparative Overview](#)

## Behavioral Plasticity

- [Adaptedness of Behavior](#)
- [Behavioral Flexibility](#)

## Behavioral Profile

- [Coping Style](#)



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## Behavioral Qualities

### ► Phenotype

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## Behavioral Response

### ► Arousal

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## Behavioral Stochasticity

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“Behavioral stochasticity” is a term that is used to characterize the randomness or apparent indeterminacy of behavior. To call behavior “stochastic” implies more than an observer’s ignorance about the behavior’s provenance. Instead, it implies that the behavior is either deliberately unpredictable or else is fundamentally unstructured. Hereafter, “stochastic” and “random” will be used interchangeably. A lack of behavioral stochasticity, by contrast, is called behavioral stereotypy. Some caution is needed in interpreting these terms when they appear in the literature, particularly “random,” which has a wide range of technical meanings (Nickerson 2002).

Among scholars of animal cognition, there are at least two senses in which behavioral stochasticity is invoked. The first is as a measure of the residual variability of all behavior. The second is as a deliberate strategy or beneficial adaptation. The boundaries between these senses are ambiguous, as behavior may be unpredictable for many reasons. Additionally, behavior that may look very structured on a large scale may simultaneously look unstructured at a small scale (or vice versa), so it is important to specify one’s level of analysis (Shimp 2014).

## Measure of Behavioral Variability

Often, stochasticity refers to the intrinsic variability of the behavior of organisms, such as variations in reaction time or motor plan. As such, a single behavior may have both a predictable and an unpredictable component: A deliberate reaching motion may successfully make contact with a target, but each successful reaching motion varies slightly from previous attempts. Because all behavior varies for a multitude of reasons, many of which cannot be measured, stochasticity is ubiquitous even in consistent and patterned behavior. Even when specific sequences of behavior are selectively rewarded, the manifestation of other behavioral combinations persists at background levels (Stokes 1995). The degree of uncertainty in any measured behavior can be described, in absolute or relative terms, using the tools of information theory (Jensen et al. 2013).

Even very simple mechanical systems, such as two-armed pendulums, can display highly unpredictable behavior, a phenomenon studied by chaos theory (Robertson and Combs 1995). Braitenberg (1986) demonstrated the relevance of this to the behavior of organisms with his “vehicles” (so-called because they were too simple to be called “robots”). Despite having only rudimentary sensors and motors, connected in a non-networked fashion, these deterministic virtual agents displayed highly variable and intentional-seeming behaviors. A big reason for this emergent variability is that even with a simple mechanical agent, any realistic environment is full of variation (e.g., uneven terrain or luminosity). If behavior varies in response to the interaction between the agent’s moving frame of sensory reference and the natural variations in environment, that variability may be described as having been “induced” by the environment. If, on the other hand, the source of variation is internal to the agent (such as fluctuations in the electrochemical signaling of long-range neurons), then it may be described as “intrinsic.”

Both induced and intrinsic stochasticity in behavior are usually seen as passive, in the sense that they are treated as residual error from some measured central tendency. Nevertheless, they are



useful measures, particularly when taken longitudinally. Given that induced variability requires sensitivity to environmental cues, compromised health in many cases results in reduced behavioral variability. Similarly, insofar as intrinsic variability arises from the complex interactions of different body systems, dysregulation can result in more stereotyped patterns of activity. For example, reduction of heart rate variability (HRV) is a common symptom of myocardial difficulty (Malik and Camm 1994). When asked to generate motor movements, patients with a schizophrenia diagnosis generally produce more stereotyped motions (Hornero et al. 2006). Measuring changes in “intraindividual variability” over time can also be a revealing diagnostic indicator in age-related cognitive decline and dementia (Martin and Hofer 2004). Although there is a popular conception that pathology, and especially mental illness, results in behavior that is “more random,” it is instead typically the case that behaviors that are symptomatic of pathology are socially inappropriate (and thus unexpected), rather than being unpredictable *per se*.

A commonly reported form of induced behavioral variability is that observed during the extinction phase of a schedule of reinforcement. In general, once subjects become accustomed to a reliable contingent relationship between rewards and behavior, cessation of rewards results in a dramatic increase in the variability of behavior (Stokes 1995). According to a very long tradition in animal psychology (reviewed in Guthrie and Horton 1946), the great diversity of these “frustration” responses creates a strategic opportunity, because animals may discover that a never-before-tried behavior is able to resolve their current difficulty. This result, in particular, blurs the line between variability that is incidentally induced and that which serves a functional purpose.

### Strategic Stochasticity

Although all behavior necessarily has a random component, it is sometimes adaptive to behave very unpredictably. One example of this is

“protean behavior,” in which animals react to an alarming stimulus (such as a loud noise or the appearance of a predator) by moving in a fashion that is difficult for an observer to predict (Driver and Humphries 1988). As in all cases of strategic stochasticity, the scope of this variability is constrained. For example, a hare who is evading a fox will intermix leaps forward, to the left, and to the right in a way that is difficult for a less maneuverable fox to anticipate. However, such protean escape behavior never includes random freezing or backward motion: The hare will always move away from the fox.

Being difficult to capture confers a clear evolutionary advantage to prey animals, but the same selective pressures operate on predators. The gains in fitness from protean behaviors can thus best be understood in terms of what game theorists called a “mixed strategy” (Barracough et al. 2004). Since any prey animal using a simple strategy (such as “run straight”) would ultimately have a predator adapted to defeat that strategy, being entirely random (including stopping) is almost always counterproductive, as a species is expected to adapt a level and scope of behavioral stochasticity that balances the benefits of predator confusion with the costs of accidentally counterproductive behavior (such as leaping into a predator’s jaws).

Stochasticity is not only strategic at evolutionary scales. It is also beneficial for most animals to learn when to behave more or less randomly in response to environmental cues. In foraging problems, for example, the complexity of the environment usually exceeds the memory capacity and/or spatial reasoning ability of the animals that inhabit it. A limited and contextually sensitive degree of variability is important to discovering opportunities that might otherwise have gone undetected (Stephens and Charnov 1982). There are perhaps no organisms more limited in memory capacity than *E. coli* bacteria. When moving through a medium interspersed with nutrients, these bacteria move in straight lines as the nutrient gradient increases but are more likely to tumble randomly as the gradient decreases (described in Driver and Humphries 1988). This cognitively minimal approach (vary when bad, maintain when good)

effectively replicates a Monte Carlo algorithm for mapping the relative density of nutrients (Siettos 2014).

As noted in the preceding section, behavioral or autonomic stereotypy can be an indicator of poor health or neural dysregulation. This may explain why, in some contexts, behavioral variability is an honest signal of fitness and thus the object of sexual selection. The clearest example of this is bird song: In a variety of species, female songbirds display a preference for males who display more complex songs, as well as to modulate their level of variability on the basis of cues, such as whether a female is currently visible (Catchpole and Slater 1995). This implies that birds are able to perceive differences in levels of variability (Young and Wasserman 2001). When vocalizing for rewards, the variability of bird song has even been shown to come under stimulus control (Manabe et al. 1997).

This last study is just one example of a body of work showing that many species display considerable behavioral stochasticity when incentivized to do so. According to this view, the stochasticity of a behavior is an “operant,” that is, a dimension of behavior that can be manipulated through the delivery of feedback (reviewed in Neuringer (2002) and Neuringer and Jensen (2010)).

A major advance of this field was made by Page and Neuringer (1985). Pigeons were initially rewarded for emitting novel sequences of left and right key presses (labeled the “VAR” phase). During this time, the sequence of which trial numbers were rewarded or not was being recorded. Then, in later sessions (the “YOKE” phase), the previously recorded sequence of rewards was delivered again, trial by trial, regardless of the patterns that subjects generated. By directly measuring the information entropy of sequences of behavior during both phases, Page and Neuringer showed that subjects generated high-entropy sequences during VAR and low-entropy sequences during YOKE, despite the two phases having identical reward histories. Under the traditional Skinnerian interpretation of an “operant,” contingent reward delivery should result in increasing behavioral stereotypy. By showing that variability itself acts as an operant, the authors demonstrated that

rewards could decrease stereotypy, provided that positive feedback was contingent on highly variable behavior. Subsequent work by Neuringer and colleagues demonstrated similar reward-contingent variability in rats (Grunow and Neuringer 2002) and humans (Jensen et al. 2012).

As in the evolutionary example of predator avoidance above, studies of operant variability also demonstrate that variability only increases within the scope of what is functionally advantageous. In an especially striking study, Ross and Neuringer (2002) had human participants draw rectangles using a computer mouse. Each response could vary independently in terms of (1) the position of the rectangle’s center, (2) its total area, and (3) the ratio of its length to its width. Participants earned rewards by varying two of these dimensions while keeping the third static but were never given instructions regarding the experiment’s objective. Furthermore, over the course of the experiment, there were unsignaled changes in which of the three dimensions needed to be held constant. Participants reliably varied their responses only among the two target dimensions, adapting to the changing feedback. However, when debriefed, participants were generally unable to describe the strategy they had used, despite succeeding at the task.

## Stochasticity’s Underlying Mechanisms

The mechanical origin of stochastic behavior remains a topic of debate among theorists. According to one view, the studies above do not really demonstrate that behavioral stochasticity is sensitive to feedback as such. Instead, changes in variability are seen as the product of traditional reinforcement learning mechanisms (Machado 1997). In effect, behavioral variability is the result of feedback constantly moving the behavioral target that an organism is trying to approximate. As with Braitenberg’s “vehicles,” the source of behavior’s apparent variability is, according to this view, the organism’s interaction with a changing and unpredictable environment. Others have gone further to argue that variability cannot sensibly be described as a dimension of behavior on

which feedback can operate (e.g., de Souza Barba 2012). This view is not skeptical of the phenomenon of apparently stochastic behavior; rather, it argues that the origins of that stochasticity can be explained in mechanistic (or even deterministic) terms, using mechanisms like reinforcement learning and implicit memory.

At the opposite extreme, Neuringer (2002) argues that behavior has an intrinsically stochastic substrate that is sometimes suppressed and at other times given control. For a given behavior, an “endogenous stochastic generator” (ESG) would generate variability by default, and the ESG would need to be inhibited in order for behavior to appear stable or structured. The core of Neuringer’s argument is that a memory-based model may explain a task in which subjects generate simple sequences but that more complex sequencing (or behavior varying along a spatial continuum) yields a combinatorial explosion of possibilities that cannot be manageably encoded. Furthermore, pharmacological manipulations that impair memory, such as D-amphetamine (Ward et al. 2006), undermine memory-based performance but do not undermine feedback-driven stochasticity. Tervo and colleagues (2014) report a possible neural mechanism consistent with an ESG hypothesis: Transitions between structured and stochastic behavior appear to be governed by the locus coeruleus input into the anterior cingulate cortex (ACC). According to this interpretation, stochastic behavior is observed when the ACC is suppressed, as this results in behavior that is less dependent on memory or past experience.

As the study of variable or unpredictable behavior has transitioned to a more cognitive mode of theorizing, the basic debate remains: When variable behavior is observed, is it the result of a model the brain has constructed of the world, or is it due to the brain setting aside its model in favor of a more exploratory strategy? Given the ubiquity of reward/punishment signals in the brain and the consensus view that these signals are used to educate internal models of the world using error prediction (e.g., Nassar et al. 2010), it would be disadvantageous for learned models to become hard-wired, as this would leave

organisms of a certain age unable to adapt to changing circumstances. When the mind’s present model fails, the brain needs a way to “opt out” of its own model (Karlsson et al. 2012). Defaulting to high-variability behavior provides a way to do so.

The widespread consensus in behavioral neuroscience is that organisms rely on induced intrinsic variability as a source of behavioral variation (Gold and Shadlen 2007). This not only has the advantage of making mixed strategies cost-effective (since unpredictability can always be called upon) but also for engaging in exploratory behavior in novel environments without needing a prior history of feedback. This view is more compatible with Neuringer’s ESG hypothesis than it is with de Souza Barba’s skepticism. However, rather than freeing behavior from a Skinnerian model shaped by reinforcement, the approaches utilized in neuroscience emphasize the brain’s simultaneous reliance on cognitive models and (when past models are not effective) their occasional reliance on intrinsic variability to escape the behavioral constraints imposed by those models.

## Cross-References

- [B.F. Skinner](#)
- [Environmental Influences](#)
- [Extinction In Learning](#)
- [Game Theory](#)
- [Operant Conditioning](#)
- [Reaction Time](#)

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## Behavioral Syndrome

### ► Coping Style

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## Behavioral Syndromes

### ► Personality in Animals

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## Behavioral Variation

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## Synonyms

[Behavioral diversification](#)

## Definition

Variations in the behavior among individuals belonging to the same species in response to genetic, phenotypic, or environmental changes.

## Introduction

Study of behavioral variation concerns with the behaviors displayed by individuals and how these behaviors vary among individuals both within and among populations. Animals have evolved specific contextual behaviors, such as defense, reproduction, and exploration. Variations in these behaviors have fundamental implications on an individual's ability to acquire, process, and respond to novel information or stimuli. These differences in behaviors can result from differences in life history stage, i.e., juveniles vs adults, or physiological differences, i.e., healthy vs diseased individual. The study of behavioral variations helps in understanding the impact of altered environmental factors and population shifts in genetic/phenotypic differences.

## General Description

Consistent individual differences in behavior, frequently termed as behavioral syndromes or animal personality are set based on the degree of behaviors like aggression, foraging activity, vigilance, competitive interactions, predator-prey interactions, habitat selection, risk-taking, and singing displayed by the animal. These individual variations occur due to genetic or phenotypic variation and differences in life history stages. The personality of the animal acts as a deciding factor during courtship, mate choice, escape from predators, or survival against harsh climatic conditions (Killen et al. 2013). These variations are also reflective of an individual's response to various stressors, owing to the differential sensitivity of animals in response to the changing environment. Certain behaviors may be masked or revealed based on how the individual responds to stress. Like for example, dark-eyed junco groups

become less aggressive during the winter. Ecological changes, behavioral, and physiological responses are interlinked and have a cause-and-effect relationship wherein slight shift in the former will cause variations in the latter two. For example, fasted animals generally show increased boldness during foraging activity. Environmental stress, such as food deprivation, causes physiological changes which can result in consistent behavioral differences among individuals or in a group, eventually leading to phenotypic variation. As a result, behavioral variation precedes morphological modifications followed by ecological speciation (Phillips and Suarez 2012).

These behavioral variations also cause changes at the neuronal level. One form of behavioral variation is observed in seasonally breeding birds and migratory birds. Migratory birds display a behavior known as *Zugunruhe*, also known as night-time restlessness, which is a migratory preparedness behavior displayed when there is a shift in photoperiod from short day to long day and vice versa. The birds during this stage undergo physiological changes in the form of increased fat accumulation, hyperphagia in preparation for migration, change in testicular volume, and changes in neuropeptide levels in the migratory brain regions (Mishra et al. 2016). Similarly, in seasonally breeding bird species, the males display directed singing and nest building behaviors while courting the female and the volume of song control areas in the brain increases during this stage (Healy et al. 2010). Sudden changes in behavior cause the brain areas responsible to express immediate early genes (IEG) like *c-fos*, *ZENK*, etc (Sadananda and Bischof 2002). Increased expression of these molecules in conjunction with increased levels of corticosteroid is taken into consideration while studying behavioral response of an animal to the novel object.

## Conclusion

These adaptive changes not only influence the survival of the individual/species but also play a role in ecological speciation. Any variation in behavior can be traced back to changes in



neuropeptide, immediate early genes (IEG), and neurotransmitter levels in related brain areas.

## Cross-References

- [Gene Expression](#)
- [Genetic Variation](#)
- [Neurogenesis](#)

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- as to how the mind organizes information, the factors that affect the mind, and the structure of the mind. Sigmund Freud contributed to this mentalistic approach by focusing on internal conflicts that take place in the unconscious mind and how these unresolved conflicts could lead to psychopathology. Freud's work spread quickly and took a stronghold in Europe. Many psychologists in the United States believed in Freud's work, but there were a few who wanted psychology to return to a science, including John Watson.
- John Watson founded behaviorism with the goal to scientifically study human behavior (Watson 1913). The primary goals of behaviorism are to predict and control behavior, with the secondary goals focusing on a scientific and objective approach to measuring and explaining behavior. This movement led to the scientific advancement of psychology as theories, methodologies, and its applications began to rely on objectivity.
- As psychology was advancing, so was behaviorism. There are three stages of behaviorism: associationism (1897–1930), neobehaviorism (1930–1960), and sociobehaviorism (1960–Present). Together, these three schools of thought informed research and its application in psychology.

## Associationism

The associationism period formally began in 1870, but learning by association was discussed more than 2000 years ago by Aristotle (Schultz and Schultz 2016). Aristotle suggested that humans learn by associating an object and a response together. Aristotle's work was revisited by the British associationists, British philosophers, especially by John Locke and David Hume. They spoke about how associations could lead to reflexive responses, particularly as the strength of the association increased (Schultz and Schultz 2016). Locke referred to humans' minds as *tabula rasa*, meaning blank slate. He believed human beings are born without knowledge and that all learning occurs as a result of their experiences. Hume argued that all thoughts are a result of the individual's experience, specifically the individual's impression of a stimulus determines their

## Behaviorism

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## Introduction

Psychology initially lacked objectivity, and thus it was difficult to label it as a science. Drawing on Wilhelm Wundt and Edward Titchener's works, psychology was focused on examining one's consciousness through introspection. Psychologists at the time were not concerned with observable behavior but rather mental states such as thoughts and feelings. From this, assumptions were made



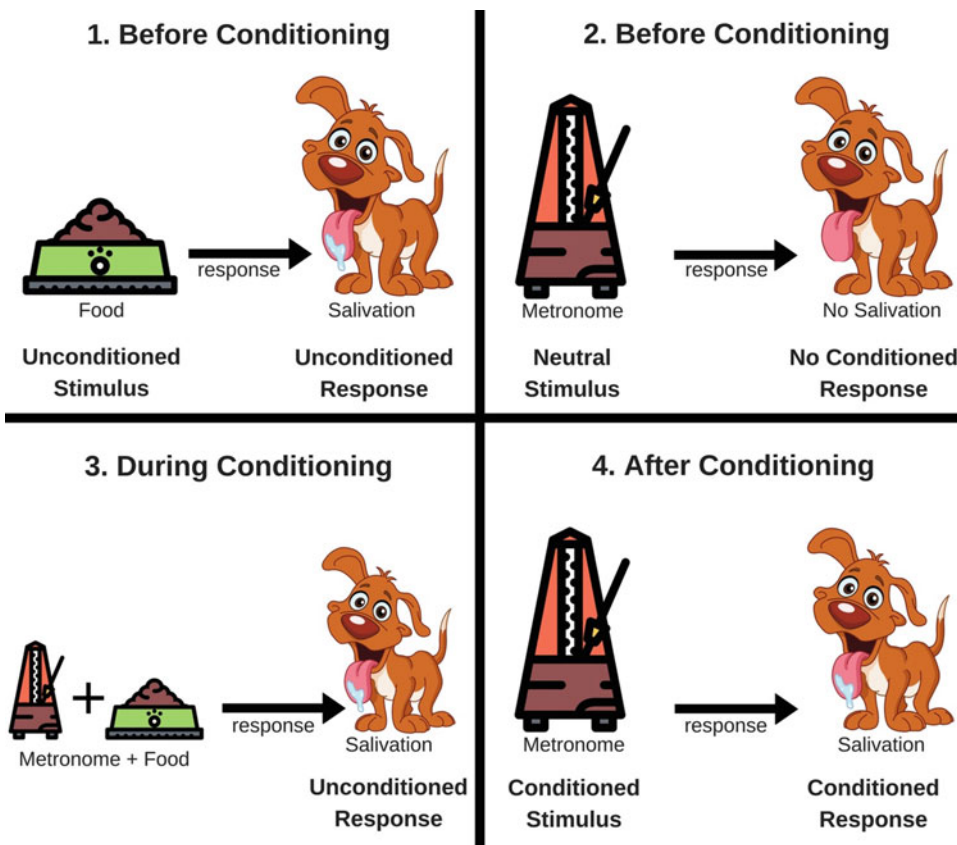
ideas. This is to say, the individual does not have unique thoughts, but rather his thoughts are dictated by linking impressions and ideas learned in his experience. These links are solidified through resemblance, contiguity, and cause and effect (Hume 1740/2012). While Hume's ideas about solidifying the relationship between impression and ideas were found to be true, there was no scientific evidence for this at the time.

Ivan Pavlov's (1849–1936) work on *classical conditioning* was the first scientific support for associations. Pavlov, a Russian physiologist, noticed that immediately before he went to feed his dogs, they were already salivating; it was almost as if they knew they were going to be fed. Being an effective scientist, Pavlov systematically examined this behavior. Pavlov's typical experiment involved a dog in a dark room. A light would turn on, and 30 s later, food was presented,

eliciting the salivation response (Pavlov 1928). This pairing occurred several times and resulted in the dog salivating once the light was presented, even if the food was not presented. Pavlov showed that the dog was conditioned to salivate when the light was turned on.

In classical conditioning terms (Pavlov 1928), the food is known as an unconditioned stimulus (US). The unconditioned response (UR) is when the dog automatically salivates as the food is presented. The light begins as a neutral stimulus (NS) and as it is repeatedly paired with the US, the light becomes known as the conditioned stimulus (CS). The repeated pairing of the US and CS conditions a dog to salivate when the room is lit, the conditioned response (CR; see Fig. 1).

Another common example of classical conditioning (aka respondent conditioning) that Pavlov studied was teaching a dog to salivate to the sound



Behaviorism, Fig. 1 Classical conditioning

of a metronome. The sound of a metronome begins as a NS, as it does not originally produce a response. Presenting food, the US, elicits a salivation response/reflex, a UR, from the dog. If the experimenter were to present the metronome and then shortly afterward present the food, the dog would salivate. After several trials, the sound of the metronome, the CS, becomes paired with food, and the dog elicits a salivation response, CR, even when just the metronome is presented. Take note that in both examples, the CS was presented *shortly before* the US. Studies have shown that conditioning a response when the CS is presented after the US is not very effective (Pavlov 1927). In fact, conditioning occurs most rapidly when the CS is presented one-half second before the US.

Throughout his work, Pavlov founded several principles of conditioning, such as extinction, stimulus generalization, stimulus discrimination, and higher-order conditioning.

### Extinction

A CS can cease to produce a CR if the CS is repeatedly presented alone. By repeatedly presenting the light without the food, the dog learns to not salivate. This process is known as *extinction* (Pavlov 1927, 1928). Pavlov found that even when the CR seems to be extinguished, it is possible for the CR to reappear after the CS has not been presented for some time. Pavlov labeled this *spontaneous recovery* (Pavlov 1927, 1928). Let's use the example above. A dog is trained to salivate when light is paired with food, but after several trials of presenting the CS alone, the dog no longer salivates. If a delay of several hours is administered before the next presentation of the CS, the dog is likely to produce the CR, even though the CS and the US were not paired together. Spontaneous recovery can be extinguished by repeatedly presenting the CS without the US. If the CS and US were occasionally paired together during this process, it would only strengthen the association.

### Stimulus Generalization and Discrimination

In most classical conditioning experiments, only two stimuli are paired together, the CS and the US; however, the CR will be elicited not just from the

CS but also from similar stimuli to the CS. The more similar a stimulus is to the CS, the more likely it will elicit the CR. This process is known as *stimulus generalization* (Pavlov 1928). Let's refer back to Pavlov's prototypical study where he paired a metronome (CS) with food (US), causing the dog to salivate. After several pairings, the dog is likely to salivate to the stimuli resembling the sound of the metronome, such as wind chimes, a doorbell, or hitting a glass with a utensil. The dog is not likely to salivate to sounds that do not sound like a metronome, such as dropping a book on the floor, making a cup of coffee, or a siren wailing. This ability to differentiate between the CS and other stimuli, and not produce the CR, is known as *stimulus discrimination* (Pavlov 1928). Pavlov could enhance the dog's ability to discriminate between the CS and other stimuli by deliberately pairing the metronome with food and then present another tone without the food. The dog will begin to discriminate between the two tones and respond just to the CS.

### Higher-Order Conditioning

Pavlov took his research one step further by demonstrating that once a dog was fully conditioned to a CS, he could then pair the CS with a new NS. The previous CS takes the place of the US and is known as a first-order CS. This process is called *higher-order conditioning* (Pavlov 1928). For example in second-order conditioning, Pavlov trained a dog to salivate to a metronome (the first-order CS) and then paired it with a black square (the new CS), to teach the dog to salivate at the sight of a black square. Pavlov found in some instances third-order conditioning could be derived; however, he could never surpass third-order conditioning.

### John Watson

Pavlov's work on classical conditioning became more influential when John Watson made it the bedrock of his theory, behaviorism. Watson was not happy with the direction of psychology, as he viewed it to be unsystematic. In 1913, Watson published the article "Psychology as the Behaviorist Views It," commonly known as the "Behaviorist Manifesto." Watson proposed that a

behaviorist views psychology as a purely objective science, concerned with only what is observable and objectifiable. This was contrary to mainstream psychology of Watson's time. Most psychologists believed in introspection and consciousness. Watson rejected these terms because they were not observable and could not be empirically validated. He treated psychology as a science and promoted operationalism through clearly defining terms and observing behaviors. This branch of behaviorism is known as *methodological behaviorism*.

Watson envisioned behaviorism as the *prediction* and *control* of behavior based on sound scientific methods. Watson and Rayner (1920) demonstrated this through classical conditioning. In his famous experiment, Watson took a 1-year-old boy named Little Albert and conditioned him to be afraid of a white rat. Watson first measured Albert's baseline by observing Albert's physical response when he was presented with a white rat, rabbit, dog, monkey, seal fur coat, Santa Claus mask, and fire. Albert had a positive response to these stimuli, according to Watson's report. Watson then presented a white rat to Albert while simultaneously hitting a steel bar with a hammer. The loud noise was an aversive stimulus to Albert. Watson repeated the pairing several times and Albert began to cry. Watson then presented the rat alone and it evoked a fear response, known as a *conditioned emotional response*. Albert's fear response of crying and crawling away from the stimulus generalized to animals and objects like a white rat (e.g., rabbit, fur coat, Santa Claus mask). An example of stimulus discrimination, Albert did not emit a fear response when presented with a monkey, as the monkey did not resemble the white rat (Watson and Rayner 1920).

Watson never cured Albert's conditioned fear response, as Albert's mother and him moved at the end of the experiment. In 1924, Mary Cover Jones worked on her dissertation under the supervision of John Watson and provided methodological behaviorism with the first glimpse of applied research and a treatment approach. She tested a variety of methods to eliminate the fears (e.g., frogs, fish, rabbits, rats) of a 3-year-old boy named Peter, most notably systematic desensitization and

modeling (discussed in detail later in the chapter). Cover Jones drew on Pavlov's and Watson's works on how conditioned emotional responses form. She recognized that Peter learned to associate rabbits as an aversive stimulus and, therefore, avoided rabbits. Cover Jones decided to recondition Peter by incrementally exposing him to a rabbit with an appetitive stimulus present. Cover Jones placed Peter in a high chair with his snack (an appetitive stimulus) and positioned a caged rabbit across the room. Initially, Peter expressed fear, but after several presentations, the fear response subsided. The following day, Cover Jones brought the caged rabbit within 12 ft. of Peter as he was snacking, which was just enough to evoke a slight arousal from Peter. She repeated this process for several days, each time bringing the rabbit closer and closer to Peter. She eventually let the rabbit out of its cage and had Peter touch the rabbit. The last two steps in this hierarchy were to have Peter fondle the rabbit affectionately and then to let the rabbit nibble his fingers (Cover Jones 1924). This study is the beginning of *systematic desensitization*, which is still commonly used to treat anxiety.

### Behavior Therapy

Cover Jones's work on systematic desensitization earned her the title "Mother of Behavior Therapy." Her work went largely unnoticed until Joseph Wolpe, a psychiatrist from South Africa, formalized the treatment approach (Wolpe 1958). In 1944, Wolpe was working as a military medical officer and found psychoanalysis to be ineffective in treating "war neurosis"; as such, when he returned from the war, he began to research an effective way to treat neuroses. Using cats as his subjects, he placed them in a cage and shocked them repeatedly until it produced an anxious response. Trying to cure this response, Wolpe attempted several unsuccessful methods, including no longer shocking the cats when they were in the cage. What he did find to be effective was to leave the cats in a *slightly* anxiety-producing situation (e.g., shocking them) to the point where they would still eat. Wolpe would repeat these exercises, gradually increasing the intensity. The cats eating while anxious is an example of *reciprocal inhibition* or counterconditioning

(Wolpe 1958). Reciprocal inhibition is the process where an organism cannot be relaxed and tensed simultaneously, and, therefore, the feeling of anxiety can be *counterconditioned* if the organism performs a relaxing behavior (e.g., eating). In Wolpe's study, the cats eating inhibited the cats' anxiety.

Wolpe created four steps for systematic desensitization in humans: diagnose the patient, construct a hierarchy, teach relaxation, and conduct therapy sessions (Wolpe 1958). The first step was to examine the presenting problem and provide a correct diagnosis. Then, the therapist and patient created a hierarchy of anxiety-producing situations ranging from least anxiety producing (0) to most anxiety producing (100). Wolpe found that instead of instructing his patient to eat when feeling anxious, teaching him (her) how to relax via progressive muscle relaxation (PMR; Jacobson 1938) inhibited their anxiety. PMR involves the patient tensing different muscle groups in their body and then relaxing via deep breathing. Lastly, Wolpe would expose the patient to low-grade anxiety-producing situations, and the patient would practice PMR until their anxiety had reduced to 20 or lower. He would continue this process, gradually climbing up the hierarchy. Wolpe found systematic desensitization to work especially well when treating phobias, an extreme or irrational fear.

Wolpe believed that the principle of reciprocal inhibition could be applied to those who feel socially anxious, as well as those who feel angry. He was a pioneer of a technique called *assertiveness training* (Wolpe 1958). Similar to when he was treating those suffering from anxiety, assertiveness training involves counterconditioning the patient's angry or passive response with a friendly and affectionate response. Wolpe would have his patients practice the assertive response in the therapy session to replace the patient's passive or aggressive response.

Wolpe's work on systematic desensitization, assertiveness training, and applying PMR earned him the title "Father of Behavior Therapy." His work led to many other great findings, including exposure therapy (Telch et al. 2014). Exposure therapy is similar to systematic desensitization,

in that the patient is exposed to fearful stimuli; however, the fundamental premise is different. Systematic desensitization is based on the principle of reciprocal inhibition (Wolpe 1958), whereas exposure therapy is based on habituation (cf. Schare and Itzkowitz 2017). Systematic desensitization attempts to gradually replace an anxious behavior with a relaxing behavior. Exposure therapy immerses the patient in a highly anxiety-producing situation, and the anxiety-provoking stimulus is repeatedly presented until the patient's arousal level begins to decrease. A key component of exposure therapy is preventing escape (leaving an anxiety-producing situation) and avoidance (not engaging in anxiety-producing situations). Escape and avoidance both work against habituation and only increase the association between the stimulus and anxiety and the patient's response. Exposure therapy is just as effective as systematic desensitization and requires considerably less time in treatment. Habituation is likely to occur at a faster rate if the stimulus is high intensity and presented frequently. Exposure therapy is used to treat anxiety disorders, obsessive-compulsive disorder (OCD), and posttraumatic stress disorder (PTSD).

Exposure therapy can be conducted one of three ways: imaginal, in vivo, or virtual reality (VR). Imaginal exposure therapy involves having the patient visualize the anxiety-provoking stimulus. The benefits of imaginal exposure are that it does not require any additional resources on the part of the therapist and the therapist controls the stimulus. In vivo exposure involves presenting the patient with the real anxiety-provoking stimulus (e.g., spider, heights, social rejection). The drawback of in vivo exposure is the therapist's lack of control over the environment. The therapist has more control over creating an imaginal stimulus as opposed to presenting an in vivo stimulus. VR exposure is relatively new and provides an alternative to imaginal and in vivo exposure (Parsons and Rizzo 2008). In VR exposure, the patient is presented with a virtual creation of the target stimuli. The therapist has control over what stimuli are presented (contrary to in vivo exposure), and it is one dimension closer to resembling a real stimulus compared to imaginal exposure. Current

research is inconclusive as to which approach is most effective, though all three approaches are validated (cf. Telch et al. 2014; Parsons and Rizzo 2008).

Pavlov's work on classical conditioning has been very influential in explaining how learning occurs through associations and has led to the abovementioned therapeutic techniques. It has helped not only explain, control, and predict behavior but also replace maladaptive behaviors with more functional behaviors. However, it cannot explain how all behaviors are learned, and as such, researchers continued to look for other explanations.

## Neobehaviorism

### Methodological Behaviorism and Radical Behaviorism

While scientific method legitimized psychological research and gave merit to the field, observable behavior alone cannot account for the entirety of an organism's experience. *Radical behaviorism* posits that there is merit to considering the private mental activity of an organism (such as thoughts and feelings), along with biological factors and genetic factors. Yet, radical behaviorists do not believe that private experiences are a cause of behavior. Radical behaviorists seek to demonstrate connections between behavior and environment and are focused less on causation due to thoughts and feelings (Baum 2011).

Early insights that contributed to the philosophy of radical behaviorism were provided by early psychologist *Edward Lee Thorndike* in the late nineteenth century. Thorndike aimed to investigate animal intelligence. He confined a cat inside a puzzle box that contained various objects, some of which would open the box and encouraged the cat to escape confinement by placing a scrap of fish outside the box. Thorndike took care to record the specifics of his experiments, from the dimensions of the boxes to the ages of the thirteen cats he used as subjects (Thorndike 1927). This showed an experimental design that diverted from the common case study approach that was popularized in psychology at the time and several years before

Watson introduced the Behaviorist Manifesto. Thorndike's experiment could be replicated by any interested reader and featured multiple subjects (a group of cats instead of one individual cat). These studies reflected the scientific integrity and objectivity that Watson later promoted as a tenet of behaviorism.

Each cat was placed in the same puzzle box several times over. Thorndike observed that the first time the cats escaped, it was by trial and error. The cats would claw or bite objects until the door opened. Every time the cat was placed back in the box, they would escape faster than the previous time. The cats learned that manipulating certain objects led to a favorable outcome that freed them. Thus, Thorndike deduced that the cats learned how to open the box through successive trials. Thorndike termed his resulting theory the "law of effect," which stated that when a behavior has a satisfying consequence, the behavior would be more likely to be repeated and when the response is unpleasant, the behavior would be less likely to be repeated. Thorndike viewed the cats as being "pleased" by escaping the box and attaining the fish, which caused them to escape the box quicker (Thorndike 1927). From Thorndike's foundations and theory of behavior came a new model of operational behavior or behavior that operates on the environment the way that the cats manipulated objects to leave the boxes.

### Skinner's Operant Conditioning

The model of operant conditioning that Thorndike conceptualized was later actualized by B.F. Skinner. Skinner was an inventive, studious man who attended college intending to study writing. Yet, he left graduate school in the pursuit of psychology because he had "nothing important to say" as a writer (Skinner 1967). His research built upon the findings of Thorndike and Pavlov, and yet, Skinner moved away from their ideologies in his own conceptualization of behavior. Skinner believed that Thorndike's references to mental states using the term "pleasure" was an inaccurate label to use when it came to studying behavior. In addition, Skinner (1938) did not completely believe that Pavlov's (1927) work on reflexive behavior accounted for all learning. For example,



a student may tremble at the sight of their teacher carrying a large stack of exam papers into the classroom. Yet, classical conditioning cannot account for why the same student studied every day for an entire week leading up to the exam. Skinner's resulting conclusion was that there must be another way to learn behavior, because not every behavior is reflexive. He referred to these other behaviors as being "emitted" by an organism and explained these emitted behaviors through operant conditioning.

*Operant conditioning*, or instrumental learning, was defined by Skinner as behavior that occurs because it was previously instrumental in producing certain consequences (Skinner 1938). It is a behavior that changes consequences in an organism's environment. For example, it is a logical assumption that the student studied every day for their exam so that he would receive an impressive grade on the exam. This student may have learned that when he operates in a certain way and carry out a certain behavior (in this case, studying), his grades improve. A grade is an outcome that makes the student study more, and by studying, the student "operates" upon their environment. Or, perhaps this same student did not study for a previous test in this same class and they received a poor grade. The student's studying behavior could also be a way to avoid an unfavorable grade. The student's studying behavior is instrumental in establishing the outcome. This led to Skinner's development of the "Law of Effect – Reinforcement," where he identified that behavior that is reinforced will repeat and is "strengthened" and that behavior that is not reinforced will extinguish or "weaken" (Skinner 1938).

To study the ways that organisms operate upon their environments, Skinner created boxes similar to Thorndike's, referred to as "Skinner boxes." An animal, such as a rat, would be free to move around the box. A lever in the box, when pressed, would deposit water or a food pellet. The rat would press the bar and receive the reward and having been reinforced for pressing the lever would be more likely to press the bar with greater frequency. The *rate* of the response increased due to the rat being positively reinforced. The *operant response*, in this case the lever press, has a

positive effect on the environment and will be more likely to be repeated (Skinner 1938).

## Contexts of Operant Conditioning

### Reinforcement

Skinner (1938) identified that there were three types of responses that could follow behavior: neutral, positive, and negative. A neutral operant is a response from the environment that does not increase or decrease the amount of times that a behavior is repeated. Reinforcement is a response that increases a behavior and can be either positive or negative. It is important to note that the terms "positive" and "negative" are used to refer to "addition" and "subtraction," respectively. They are not supposed to signify something that is "good" or "bad."

*Positive reinforcement* is when a behavior is strengthened through the addition of a rewarding stimulus (Skinner 1938). Imagine that when a child makes his bed, he receives \$10 from their parents. He is positively reinforced (\$10) for his behavior (making the bed), which will make him more likely to make his bed in the future. Or let's consider the student who studied for his test because they received a good grade when he studied in the past. The good grade is the reinforcer, and the behavior is studying. Skinner praised positive reinforcement as the most effective way to reinforce a behavior.

*Negative reinforcement* is when a behavior is strengthened through the removal of an aversive or noxious stimulus. A negatively reinforced behavior allows the animal to escape from an unpleasant stimulus/consequence (Skinner 1953). There are two specific types of negative reinforcement: escape and avoidance. *Escape* is when an animal attempts to alleviate an aversive stimulus by leaving an unpleasant condition. An example of this is when someone takes an aspirin to alleviate a headache. Taking aspirin removes the aversive headache, so the behavior is negatively reinforced. On the other hand, *avoidance* is when an animal engages in a behavior to prevent the presence of an aversive stimulus. Putting on sunscreen before a day at the beach is a behavior to avoid a future negative consequence (sunburn).



Reinforcers can also be “primary” or “secondary.” A *primary reinforcer* is a reinforcer that is satisfying on its own without being linked to another reinforcer. This can include food, water, sleep, shelter, touch, or feelings of pleasure. All of these examples have innate reinforcing qualities to organisms. A *secondary reinforcer* (also referred to as a conditioned reinforcer) has no innate reinforcing value until it is linked with a primary reinforcer – one example is money. Green pieces of paper are not innately reinforcing to humans. Yet, humans learn that money can be used to acquire primary reinforcers (e.g., food, water, shelter). This paired association is what makes money reinforcing.

### Punishment

Reinforcement is a stimulus that increases the likelihood of a behavior, while punishment is a stimulus that decreases the likelihood of a behavior. The term “punishment” does not have any connotation of “good” or “bad” in behaviorism. Instead, it simply indicates a decrease in a response. There can also be positive and negative types of punishment, like positive and negative reinforcement.

*Positive punishment* is when an unpleasant stimulus is introduced to decrease or weaken a behavior (Skinner 1953). A classic example of positive punishment is corporal punishment. Perhaps a parent hits a child after the child steals from the cookie jar before dinner. The unpleasant consequence (hitting) will decrease the undesired behavior in the future (stealing cookies). However, in behaviorism, the term “punishment” does not always indicate a penalty. Another example of a punisher is when the child leaned on the counter to get into the cookie jar, and rested their hand on the hot stove in the process. The introduction of an unpleasant consequence (a burned hand) will decrease the likelihood that the child will engage in the behavior (touching the stove to get the cookie jar) in the future. Thus, the cookie-stealing behavior is weakened.

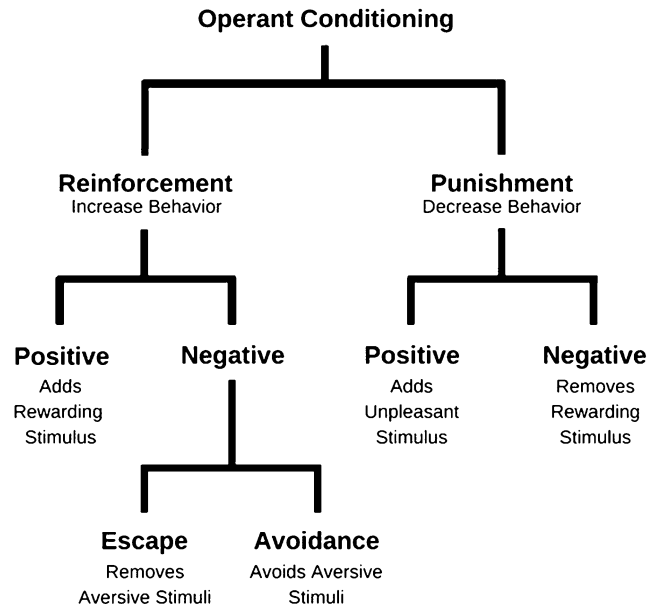
*Negative punishment* is when a favorable stimulus is removed after a behavior occurs, to decrease or weaken the behavior (Skinner 1953). One common example of negative punishment is

when a student breaks the rules and receives detention. The student is removed from a favorable environment (leaving school on time to go home) in order to decrease their rule-breaking behavior. Another example of this is placing children in time-outs or when a parent takes away cellphone/computer/TV usage. There is no noxious consequence added, but there is something positive taken away, and this removal of the positive consequence will cause a reduction of the undesired behavior (see Fig. 2).

**The Case against Punishment** Skinner spoke out against all uses of punishment and stated that they were ineffective compared to reinforcement. He expressed that while punishment is the most common type of behavioral control used in the world, that punishment would only temporarily “suppress” a behavior and that it could create other unwanted consequences (e.g., fear and aggression; Skinner 1953). There is some sound logic in Skinner’s claims. When an animal is punished, a response is decreased, but, if a desired target behavior is never increased, the animal will not have any other response to the stimulus. Punishment *does not* promote learning. It is commonly accepted that when an undesired behavior is decreased, a desirable target behavior should be increased as well. If a teacher ignores a child every time the child speaks without raising her hand, the teacher should call on the child when she raises her hand appropriately (and can even compliment the child, as well).

Instead of punishment, Skinner believed in extinguishing behaviors through nonreinforcement and spoke out widely against the use of punishment to control behavior. Research was conducted in a laboratory on the same floor as Skinner’s office by Tom Azrin who attempted to undermine Skinner’s poor view of punishment. Overall, Azrin and his colleague Holz (Azrin and Holz 1966) determined that punishment is uniquely effective compared to other forms of behavioral suppression. When performed correctly, punishment is just as effective in extinguishing behavior as extinction. Punishment operates on a different schedule of effectiveness compared to reinforcement. Continuous punishment produces the

**Behaviorism,**  
**Fig. 2** Operant  
conditioning



greatest reduction of behavior, rather than an intermittent schedule of punishment. A sudden introduction of an immediate and intense novel punishment is the most effective way to use punishment to reduce behavior.

There are times that punishment has an appropriate place in behavioral reduction. Lang and Melamed (1969) treated a 9-month-old infant who was regularly regurgitating his food. The infant was at risk of death due to starvation. The only solution that worked after multiple failed medical interventions was to provide a brief, painful shock to the infant's leg every time he began to regurgitate. This is an example of an ethical use of positive punishment. This life-saving punishment procedure reduced the undesirable behavior faster than extinction would have.

#### Schedules of Reinforcement

Behavior is rarely *continuously* reinforced; more often, animals are reinforced *intermittently*, meaning that reinforcement is not always consistently contingent upon the introduction of a stimulus. For example, a cat that prowls the streets for a good meal might not catch a mouse every time he goes out hunting. Yet, the cat does not stop hunting, as the cat has been reinforced for

it. It is important to understand the *schedule of reinforcement* or the schedule that determines how often a reinforcer is delivered after a behavior. These schedules affect the ways that an animal learns a response and then how the response is maintained over time (Ferster and Skinner 1957).

Continuous reinforcement is most effective when first beginning to teach a response. To teach a dog to sit on command, the most effective method is to reward the dog for sitting every time she hears the word "sit." Two paradigms define intermittent schedules of reinforcement: *fixed* or *variable* and *interval* or *ratio*. Fixed reinforcement refers to a set number of responses or length of time between reinforcements. Variable refers to when the number of responses or length of time varies. Intermittent reinforcement can also be delivered on an *interval* or *ratio* basis. Interval means that the schedule is based on the amount of *time* that passes between the reinforcements. Ratio means that the schedule is based on the *number of responses* between reinforcements. Thus, there are four different types of intermittent reinforcements. These are listed in order from the "weakest" to "strongest" (Ferster and Skinner 1957).

A *fixed-interval schedule* of reinforcement is when a behavior is rewarded after a set amount of

time. A washing machine that always runs on a 45-min cycle operates on a fixed interval of reinforcement. The individual doing laundry will be more likely to perform the reinforcing response (checking to see if the clothes are clean) closer to the end of the 45-min time frame, opposed to immediately after the laundry is loaded. There is a significant pause after reinforcement, where the individual will not perform the response until it comes time for reinforcement to occur again. This creates a “scallop-shaped” response (see Fig. 3).

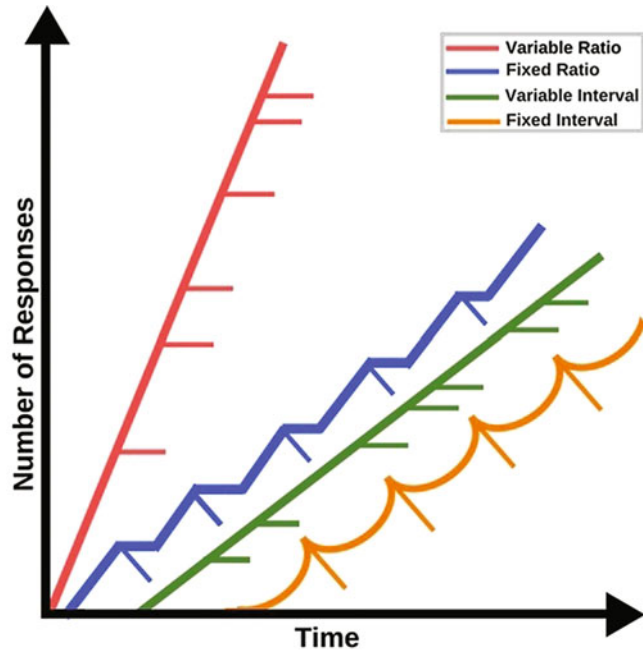
In a *variable-interval schedule*, a behavior is reinforced based on varied amounts of time. It is unpredictable, so an individual can never be sure when the reinforcement will be delivered. A professor may deliver pop quizzes on a variable-interval schedule by giving the quizzes at unpredictable times. During 1 week of class, students may take two quizzes. On other weeks, there may be no quiz at all. This reinforces students to study because they will not know when they will have a pop quiz. The rate of responding in a variable-interval schedule is moderate but constant. The students will likely not study the way they would for a large exam the next day.

There is typically very little pause after reinforcement is given.

A *fixed-ratio schedule* means that reinforcement is delivered after a certain number of responses. A student earns allowance from her parents for every five homework assignments that she completes. Fixed-ratio schedules promote quantity of response, meaning this student will be likely to do her homework every single night. However, she may not work hard and receive a failing grade on all of them, because the quality of her response is not promoted. A fixed-ratio schedule results in a high, consistent response rate until the reinforcement is delivered. After the reinforcer is administered, there will be a pause in responses before responding resumes.

In a *variable-ratio schedule*, the reinforcement is delivered after a varied number of responses. This schedule creates the highest and most consistent rate of responding of any of the reinforcement schedules. The animal cannot predict when the reinforcer will be delivered. An example of this is the way that slot machines operate. A slot machine operates on an unpredictable win schedule, but players know that eventually there will be

**Behaviorism,**  
**Fig. 3** Schedules of  
reinforcement



a payout because there is a constant probability of hitting the jackpot. Players hesitate to stop playing at the machine even after continual losses due to the possibility that the next game will be a winner.

### Extinction

Of course, an individual would not sit at a slot machine forever on the expectation of winning if there was never any reward. In Skinner's autobiography, he told the story of how he discovered extinction in the operant conditioning paradigm. Though much of Skinner's experiments were performed with intention, he found extinction through an accident in his laboratory. A rat was in a Skinner box, pressing a lever for food pellets when the pellet dispenser broke. The rat continued to press the lever for pellets, but no pellets came (thus, the rat was not reinforced for pressing the lever). Soon, the rat stopped pressing the bar in the same way that Pavlov's dogs stopped salivating to the sound of a metronome when no food was delivered (Pavlov 1927; Skinner 1979). Both responses, the lever-press and the salivation response, were extinguished through *extinction*. Extinction is when a behavior is no longer reinforced (the lever-press stopped delivering pellets), and so the response decreases until it stops (the rat stopped pressing the lever; Skinner 1938).

When a behavior no longer leads to reinforcement, there is sometimes an increase in the target behavior before there is a decrease. This is referred to as an *extinction burst*. There may be new behaviors that accompany the increase behavior. A child throwing a tantrum in the store may scream louder or drop to the floor and roll around, all behaviors in escalation of their original tantrum behavior. The extinction burst serves a behavioral purpose. A behavior that has previously produced rewarding consequences might still have a chance of producing a rewarding consequence.

### Differential Reinforcement

To increase target behaviors while decreasing other target behaviors, simple schedules of reinforcement and extinction are used together in differential reinforcement procedures. *Differential reinforcement of alternative behavior (DRA)* decreases an undesirable behavior through extinction

(or, less commonly through punishment) while reinforcing an alternative response (Miltenberger 2008). An example of DRA is when a parent ignores their screaming child and only responds when the child uses calm coherent words.

*Differential reinforcement of other behavior (DRO)* is also referred to as "omission training." This is when a positive reinforcer is only delivered (and delivered periodically) when a subject engages in something besides a target response (Miltenberger 2008). A child with a nail-biting habit can be reinforced when he does anything with his hands besides biting his nails, such as clapping or keeping his hands in their lap.

*Differential reinforcement of incompatible behavior (DRI)* decreases an undesirable behavior through introducing a competing behavior. Both behaviors cannot occur at the same time, and the competing behavior is reinforced instead of the undesirable behavior (Miltenberger 2008). Owners who are teaching their dog not to jump on guests should have the guests ignore the dog when it jumps on them. When all four of the dog's feet are on the ground near a guest, he can be provided with reinforcing pats on the head or treats. The dog cannot engage in the jumping behavior and the standing behavior at the same time.

### Shaping and Chaining

Many individuals who are handicapped rely on a service dog for assistance. The dog may perform tasks that the person is not mobile enough to complete without help, such as loading the laundry machine. But, a dog does not understand how to do laundry nor can a dog comprehend verbose instructions. Likewise, the process of loading a laundry machine is far more complicated than a simple command (such as "sit" or "stay"). The seemingly monumental task of teaching a service dog can be approached through *shaping*. Shaping is defined as differential reinforcement of "successive approximations" that will eventually lead to the full response (Skinner 1953). At first, the dog may be reinforced every time he looks at a sock. Then, he will be reinforced any time he looks at a sock and also steps toward it. The dog should no longer be reinforced for simply looking at the sock. Through the use of shaping these successive

approximations, the dog will eventually be able to pick up the sock.

Another reinforcement technique that may need to be used for this dog is *chaining* or the process of linking behaviors together so that the result of each behavior becomes the stimuli for the next behavior (Skinner 1934). The dog may be taught to pick up the sock and then bring the sock near the laundry machine. Once the dog has successfully picked up the sock and brought it to the machine (the first and second behaviors in the chain), the dog can be taught to drop the sock into the laundry machine. The desired behavior can be taught as an entire series with specific prompts for each step in the chain (e.g., the dog picks up the sock with its mouth, walks to the washer machine, stands up on his hind legs, opens his mouth, and drops the sock into the washer machine).

### Applied Behavior Analysis

Skinner boxes are an effective way to reinforce one rat at a time, yet the external world does not tend to isolate an individual for behavioral observation. The principles of Skinnerian behaviorism and radical behaviorism serve as the foundation to the field of *applied behavior analysis* (ABA). The difference between ABA and operant conditioning exists in examining the function of a behavior in the environment and developing systemic interventions to modify behavior. The first “A,” *applied*, is a focus placed on the social significance of the behavior, taking the behavior out of a “box” and placing it into the environment. The behavior must be observable for objective measurement. The last “A,” *analysis*, indicates that behavior must be measured in ways that demonstrate the impact of the environment. An effective behavior analyst should have an understanding of the environmental settings that make an organism engage in a behavior (Baer et al. 1968).

Success has been gained through the use of the principles of applied behavior analysis in reinforcing target behaviors in a larger population. Specifically, *token economies* can reinforce specific target behaviors on a large scale with many individuals in a system (such as students in a school or inmates in a prison). Tokens are

provided as a secondary reinforcer and can be exchanged for desirable items. These may be tallied as points, kept on a chart, or distributed as physical currency. The tokens are provided when a desired target behavior is performed and can be distributed by teachers or correctional officers. For example, tokens can be administered at a school when a student clears their tray at lunch. Other students will be motivated when they see the first student earn a reward. The tokens can be exchanged in a “store” for backup reinforcers, such as toys, food, or passes for leisure time (items that “back up” the tokens and give the tokens value). Token economies are effective in increasing target behaviors when the tokens are provided consistently and immediately in response to a target behavior. Though token economies are not transferable out of a closed system into the open world, they can effectively target and change behavior within the system.

### Skinner’s Philosophy of Behaviorism

It is important to note that many individuals view radical behaviorism as a means to predict all behavior of all organisms. This suggests that organisms do not have any true free will and that all sequences of behavior are inevitable. The philosophy that all behaviors are predetermined is referred to as *determinism*. Skinner openly stated that he believed free will to be an illusion, because operant conditioning suggests that consequences are predictable. An organism will engage in specific behaviors depending on the environment in which the organism exists (Skinner 1974). Skinner also stated that it would be nearly impossible to map out every behavior in which an organism would ever engage (Skinner 1938). Since it is impossible to identify all the variables determining a target behavior, the adoption of a fully deterministic approach can appear extreme. Yet, one can still support determinism while understanding that it is impossible to know all the predictor variables and their value to the organism.

Skinner believed that there was a definition of freedom that was still in line with the deterministic approach. He argued that empowering individuals was a useful tool to incite rebellion against oppressive political authorities. Yet, he pointed

out how these overcontrolling authorities were only in power due to the government that humans built. The freedom that Skinner supported was to submit to the forms of control that are the most scientifically effective, opposed to maintaining a façade of autonomy under self-imposed political oppression. Along with reshaping freedom, Skinner rejected the notion of dignity or the idea that individuals deserve credit or punishment for their behaviors. He suggested that society does not provide credit to those who behave under duress or control and that there are forces in control of all individuals (Skinner 1971). In this view, individuals do not act creatively upon their environments and should not be rewarded as if they do.

The publication of Skinner's novel *Walden Two* (Skinner 1948) brought his idealistic sociopolitical worldview into prose in a fictional utopia founded on behaviorism. He spoke of learning incentives that could contribute to human happiness while reducing systemic injustice and power imbalances. The fictional society *Walden Two* is built on a program of behavioral engineering that begun at birth for all members that makes individuals motivated and cooperative. Man is assumed to not be autonomous. There is a community-based governance that is modified with empirical evidence at the heart of *Walden Two*, with no governing body. Individuals engage in work simply because they enjoy contributing to the community. Personal expressions of gratitude toward other individuals are outlawed, as this supports the idea of dignity. Skinner described the citizens of *Walden Two* as harmonious and happy, though only provided a foggy description of how their daily lives functioned. He gave no discussion on how interpersonal conflict or differences could be resolved. Nonetheless, the theoretical society gave Skinner a platform to put his behaviorism into a context where a system of reinforcement could produce all of society's advances.

## Sociobehaviorism

Despite Skinner's beliefs, not everyone believed reinforcement and associations could account

for all learning. Albert Bandura, a professor at Stanford, is most recognized for proposing how social interactions lead people to learn new information. He believed learning could occur through *modeling* (aka *observational learning*), watching someone else perform the behavior (Bandura 1986). Bandura posited that most learning is achieved through modeling, and at times learning can only be achieved through modeling. A medical student does not learn about surgical procedures by practicing on patients but instead watches an accomplished surgeon perform the procedure. Bandura expanded his work into a theory known as *social learning theory*, which became the cornerstone of sociobehaviorism.

There are three tenets of social learning theory: (1) People learn through observations (modeling). (2) Internal mental states are an integral component of observational learning. (3) A new behavior can be learned, but it does not mean the person will perform the behavior. Bandura changed the name of social learning theory to *social cognitive theory* to stress the importance of internal mental states, deviating from typical behaviorist ideals.

## Reciprocal Determinism

Social cognitive theory proposes a *continuous, dynamic* relationship with personal factors, environmental factors, and behavior, known as *reciprocal determinism* (Bandura 1986). These three factors do not equally influence behavior, but rather the factors' influence varies based on context. Personal factors include cognition (e.g., expectations and self-judgments), self-efficacy, motivation, and personality. As stated above, Watson and Skinner did not account for these factors. Bandura believed self-efficacy greatly impacts behavior as individuals with higher self-efficacy, the degree to which an individual can master a skill, are more likely to have confidence in their abilities and thus behave differently than those with low self-efficacy. When an individual believes a behavior will be effective, their motivation to perform the behavior increases. If the behavior *is* effective, the individual may be rewarded through *intrinsic reinforcement* (e.g., pride, satisfaction, sense of accomplishment) or if the behavior is ineffective, the individual may



be punished through *intrinsic punishment* (e.g., disappointment, shame, guilt).

Environmental factors include the situation, models, relationship to the models, roles, as well as reinforcers and punishers. As discussed above, the environment may reinforce or punish a behavior, which is likely to impact the behavior re-occurring. A model demonstrates how to perform the behavior. The model and the individual's relationship to the model can alter how quickly the individual learns the behavior. Placing importance on self-efficacy, Bandura believed that the environment should improve self-efficacy to motivate the individual to perform the behavior.

The third factor is behavior, and it includes knowledge, complexity, duration, and skill of the behavior. The knowledge of the individual and the complexity of the task influence the motivation of the individual to perform the behavior. In addition, the individual's skill level influences how well the individual thinks he will perform on the task, which relate to low self-efficacy. When an individual has low self-efficacy, he is less likely to perform the behavior.

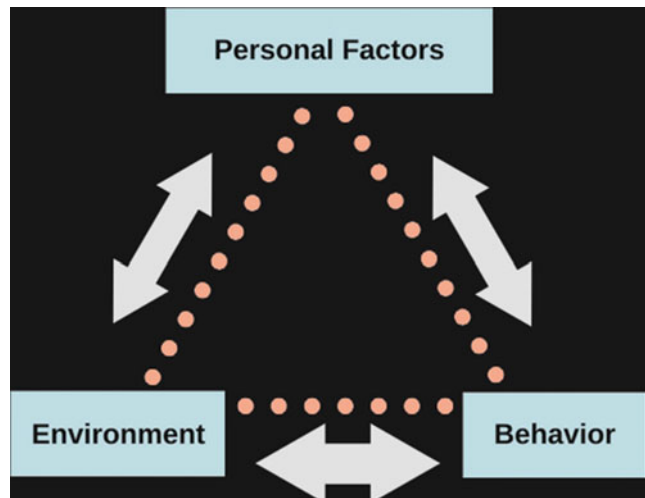
As mentioned above, Bandura believed that all three of these factors (personal, environmental, and behavior) influences behavior. An example of how all three factors influence one another is when a father teaches his son how to hit a baseball. The son first watches the father (model) swing the bat (environmental factor). The son then

thinks he is able to swing the bat the same way (personal factor) and models his father's behavior (behavior). The father then rewards his son by saying "good job" (environmental factor). This increases the son's self-efficacy (personal factor), which means the son is more motivated and thus more likely to believe he can swing the bat, increasing this behavior (behavior) (Fig. 4).

### Observational Learning

As seen in Bandura's concept of reciprocal determinism, social interactions influence behavior. Bandura emphasized how observing another perform a behavior can lead to a change in behavior. He first noticed this in his classic studies known as the *Bobo doll experiments* (Bandura 1965; Bandura et al. 1961, 1963). He had children watch adults either aggress (verbally and physically) on or ignore a clown toy called a Bobo doll. The children who saw the adults act aggressively were more likely to aggress (verbally and physically) on the Bobo doll. Bandura found that while watching the adults aggress was important, the sexes of the adults and children played a role as well. The boys watching adult males physically aggress on the Bobo doll were the most likely participants to imitate physical aggression. Interestingly, Bandura found that girls who witnessed adult females verbally aggress on the Bobo doll were most likely to imitate verbal aggression (Bandura et al. 1961). This led Bandura to

**Behaviorism,**  
**Fig. 4** Reciprocal  
determinism



conclude that humans learn through observations and that the characteristics of the model are also important.

The second Bobo doll experiment reemphasized that a model's characteristics are important (Bandura et al. 1963). Bandura stated that there are three basic models of observational learning: live, verbal instructions, and symbolic model. Live observational learning is watching the model perform the behavior in vivo. Verbal instructions are when the observer reads a description of the behavior. Symbolic models are real or fictional characters performing a behavior in other forms of media (e.g., books, movies, television programs).

Bandura (1965) built on the previous Bobo doll studies by examining how children reacted when they watched a video of a model aggress on the Bobo doll and the model was either reinforced (given candy), punished with the warning, "don't do it again," or experienced no consequences. Bandura found that children who were shown a video where the physical aggressor was punished were less likely to be aggressive. The next phase of the study asked the children to imitate the behavior they saw on the video. The children were able to accurately imitate the behavior, showing that reward and punishment do not influence retaining information, but rather, only if the behavior is demonstrated. This is a core concept of social cognitive theory, emphasizing how a behavior can be learned but not performed due to the individual's lack of motivation, not lack of knowledge.

There are four steps the observer must engage in for the model to effectively transmit the information: attention, retention, reproduction, and motivation (Bandura 1986). The observer must pay *attention* to the model to process the information. There are several factors that influence attention: accessibility, relevance and complexity of the task, functional value of the behavior, as well as the observer's characteristics – cognitive capability, values, preconceptions, emotional arousal, and self-efficacy. In addition, accessibility is influenced by how much the observer identifies with the model and the observer's expectations of the behavior. *Retention* is the observer's ability to

remember how the behavior was performed, as well as the result of the behavior (i.e., reinforced, punished, or neutral). It may involve the individual mentally reenacting the behavior. The third step is physically *reproducing* the behavior so that it leads to skill advancement and improvement. This step may also include feedback from individuals, including the model. The last step is *motivation*. The observer learns the skill by the reproduction phase but must be motivated to perform the behavior. Two factors that affect motivation are vicarious reinforcement and intrinsic reinforcement. If the observer sees the model reinforced for their behavior, the observer has increased motivation to perform the behavior. This is known as *vicarious reinforcement*. Even though the model was reinforced, vicarious reinforcement leads to a positive emotion for the observer as he is excited about the potential of receiving the reward. If vicarious reinforcement is not experienced, the observer may learn the behavior, but may not be motivated to perform it, relating back to the third concept of social cognitive theory mentioned above. Also mentioned above, motivation may increase based on intrinsic reinforcement (e.g., pride, satisfaction, sense of accomplishment), leading to the production of the behavior.

### Outcome Expectations and Self-Efficacy

After watching the model perform the behavior and seeing the result (i.e., reinforcement, punishment, or neutral), the individual begins to develop expectations of the outcome. The individual does not necessarily believe that the *same* reward or punishment may occur but recognizes that behavior is context dependent and instead a *similar* outcome will occur. *Outcome expectations* (Bandura 1986) are an individual's predictions about the functionality of a behavior and how the environment will respond to the behavior. Bandura believed that outcome expectations along with efficacy judgments are the *best predictors* of behavior. If an individual has high outcome expectations and efficacy judgments, he is more likely to engage in the behavior. *Efficacy judgments* (Bandura 1986) are the individual's appraisals of how well he can perform the specific

behavior. For example, a child learning to read may be reinforced for every sentence he reads correctly (outcome expectations). However, the child may not believe he can read even three words correctly (efficacy judgments) and, therefore, may not read. Generalized efficacy judgments directly relate to *locus of control*. Rotter (1966) explained locus of control as the extent to which one believes he has control over the situation. The spectrum of locus of control ranges from internal to external. An example of complete internal control is the individual believing that he has absolute control over the outcome. Complete external control is the individual believing that he has no control over the outcome.

These cognitions (outcome expectations, efficacy judgments, and locus of control) relate to self-efficacy (Bandura 1986). As mentioned above, self-efficacy is the individual's belief that he can master a skill. Self-efficacy affects how goals, tasks, and challenges are approached. If an individual believes he can perform the behavior well and produce a positive effect, he is more likely to behave. If the individual does not believe he can perform the behavior well and/or produce a negative effect, then he is less likely to engage in the behavior. Bandura found that individuals with high self-efficacy are more likely to model behaviors than individuals with low self-efficacy. He credited this finding to the belief that individuals with low self-efficacy believe they will not perform the task well and thus avoid the tasks.

Bandura (1986) believed that increasing an individual's self-efficacy could produce therapeutic effects, such as the individual having a more positive affect and produce more functional behaviors. Bandura presented three ways self-efficacy could be increased: mastery experience, social modeling, and improving physical and emotional states. *Mastery experience* has the individual focus on simple tasks that are easy to achieve, gradually increasing to more complex tasks. This increases the individual's efficacy judgments, which increases their motivation to perform the behavior. *Social modeling* is having the individual participate in observational learning. An individual with low self-efficacy can develop it by paying close attention to a model's behavior. Compared

to the individual with high self-efficacy, Bandura believed that the individual with low self-efficacy may need to watch the model perform the behavior more often. This is not because he does not retain the information but rather because he does not *believe* he retains the information and/or will not be effective. Bandura (1986) also emphasized *improving physical and emotional states*. An individual who is stressed is less likely to believe he can effectively perform a new behavior, compared to an individual who is rested.

Bandura's social cognitive theory is one of the first behavioral theory focusing on cognitions. He described how the environment, behavior, and the personal factors (e.g., cognitions) dynamically influence one another. He called into question Skinner's claim that reinforcement and punishment can account for all learning; instead, Bandura believed that observational learning accounted for more learning than operant conditioning did. Social cognitive theory's addition of cognitions addressed the growing disconnect of research showing thoughts can influence behavior.

## Conclusion

Behaviorism rose from rebellious beginnings as an alternative movement in a world of unobservable psychology. With the rise of behaviorism, mentalistic approaches toward patients became outdated. However, the latter half of the 1900s marked a time for psychology to change again, with a new focus on the importance of cognition. Noam Chomsky, a linguist, philosopher, and cognitive scientist, wrote a review of Skinner's work that served as a call to arms. Chomsky did not deny the points that Skinner made but argued for the importance of examining higher mental states. Specifically, Chomsky believed that language acquisition could not be explained through traditional behaviorist belief (Chomsky 1959). Thus, the cognitive revolution began, though behaviorism was not forgotten. As Bandura expressed through his social cognitive theory, the two could be blended effectively into a new paradigm. In 1986, Clark noticed that cognitive misinterpretations of physical sensations would cause patients

to catastrophize symptoms of anxiety (e.g., “I am having a heart attack”), causing panic attacks. He posited that there was merit to treating the cognition that maintained the behavior (Clark 1986). Thus, came the beginnings of cognitive behavioral therapy. Cognitive behavioral therapists hypothesize that the activating events lead to cognitions that then affect one’s behavior. These cognitions are treated as new stimuli and new responses in the stimulus and response chain. Behavior therapies placing an importance on thought and internal experiences created a well-rounded therapeutic orientation that allowed for patients to express their thoughts and feelings while also implementing behavioral change (Rachman 2009).

Modern therapeutic application of behaviorism calls for clinicians and patients to work together in addressing, and ultimately changing, behaviors that interfere with the patient’s functioning. The tenets set forth in Watson’s writings transformed psychology into a science. Behaviorism values observation over assumption in research and behavioral change over mentalistic introspection in therapeutic practice. New waves of behavior therapies are created, researched, implemented, and popularized in cycles. Yet, they all build off the foundational underpinnings that were laid out by the forerunners of behaviorism.

## Cross-References

- Aristotle
- Associative Learning
- B.F. Skinner
- Classical Conditioning
- Cognitive Imitation
- Counterconditioning
- David Hume
- Edward Thorndike
- Extinction in Learning
- Free Operant Response
- Instrumental Learning
- Law of Effect
- Learning
- Negative Reinforcement
- Operant Conditioning

- Positive Reinforcement
- Reinforcement
- Social Learning
- Spontaneous Recovery
- Unconditioned Response
- Unconditioned Stimulus

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## Benefits for Aggression in Humans

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## Synonyms

Aggressiveness; Anger; Hostility; Impulsivity; Violence

## Definition of Aggression

Within psychological literature, aggression is defined as any behavior that intends to cause harm (Stanford et al. 2003). The intentionality of aggression is a key consideration of the definition. As such, an automobile accident that results in a passenger having a broken bone or a dentist drilling a tooth to fill a cavity and causing residual pain would not be considered aggressive acts. Aggression itself can be experienced as an overt act (e.g., hitting, kicking, punching) or covert act (e.g., spreading of malicious rumors, bullying, or intentional social exclusion; Yamasaki and Nishida 2009).

## Introduction

The following is a summary of the current aggression literature. It provides a framework by which to understand the benefits of human aggression, as well as the limitations of historic models. Specifically, this entry outlines current definitions of aggression and theoretical models by which current aggression literature is conceptualized and ends with the consideration by which aggression can be seen as evolutionarily beneficial.

## Categorizations of Aggression

The extensive exploration of aggression in research literature resulted in the categorization

## Benefectance

### ► Self-Serving Bias



of aggression in three distinct ways: reactive-inexpressive, reactive-expressive, and proactive/instrumental (Yamasaki and Nishida 2009).

### Reactive-Inexpressive

Reactive-inexpressive aggression, also referred to as hostility, is aggression that is often expressed without clear reason or purpose. This typically occurs as a result of provocation or frustration and is evidenced as acts of impulsivity (e.g., an infant crying and flailing its limbs as a result of being restrained). In a study of peer relationships among school-aged children, those children displaying reactive-inexpression aggression were found to have fewer friend groups (Yamasaki and Nishida 2009). Within most cultures, reactive-inexpressive aggression is regarded as primitive and erratic and, as such, is often stigmatized (Campbell 1999).

### Reactive-Expressive

Reactive-expressive aggression encompasses overtly aggressive acts – namely verbal aggression and physical violence – in response to environmental and personal triggers. The interaction of frustration and provocation has been shown to shape these responses (Bandura and Walters 1977). Additionally, an individual's emotional state and perception of unfolding events also contribute to the likelihood of displaying reactive-expressive aggression (Dodge 1996).

### Proactive/Instrumental

Although proactive aggression may include a verbal component, the primary difference of this model is that the aggression is deliberate and is used to accomplish a specific goal (Stanford et al. 2003). By way of spreading rumors, this type of aggression occurs in order to manipulate social networks, break human relationships, and/or ostracize targets from their peers (Yamasaki and Nishida 2009). Proactive aggression can be used to obtain a goal other than injury to a target, but aggressors in this model willfully cause harm to specific targets in the pursuit of that goal (Bushman and Anderson 2001).

## Sex Differences in Types of Aggression

Early aggression research largely focused on overt physical aggression as opposed to indirect and relational aggressive measures. As such, the field largely indicates males to be more aggressive than females (Bettencourt and Miller 1996).

Currently, more comprehensive research has now found that each sex tends to favor different forms of aggressive behavior with most males resorting to direct aggression (usually reactive-expressive) and females tending to use indirect aggression (proactive/instrumental) (Campbell 1999; Björkqvist and Österman 2018). This is frequently hypothesized to stem from physical differences between the sexes (i.e., men are usually larger and stronger than women, making personal injury more likely) as well as the stigmatization of outwardly aggressive women (i.e., as “irrational” or “crazy”) (Campbell 1999). Further, there is evidence that, whereas male aggressive patterns are relatively stable throughout formative years, female children exhibit less physical aggression (replacing it with verbal aggression) as they get older (Österman et al. 1998).

## Theories of Aggression

### Instinct Theories

*Psychoanalytic theory (1927).* One of the oldest theories on aggression belongs to Freud. The psychoanalytic theory posits that humans possess an internalized death instinct (Thanatos) that propels them toward death and underlines all acts of violence. This instinct can be redirected externally through socially appropriate means (e.g., vigorous or high energy work or play) or via less desirable means (e.g., disparaging others, physical confrontations, and/or destruction of property). Aggressive urges can also manifest internally via self-harm, mutilation, or suicide (Steiner 2009). Within this model, physical aggression is seen as the release of violent forces intrinsic to the human condition.

*Ethological Theory of Aggression (1966).* Another theory, by Konrad Lorenz, also views aggression as instinctual but postulates that aggression is an intrinsic survival instinct. Lorenz



presents an ethological model of human aggression, citing resource competition among males in a variety of species. Lorenz visualizes aggression as a force that builds up and motivates the host organism (humans) to behave outwardly aggressively as a means of survival (Lorenz 2002).

While both Freud and Lorenz present aggression as an internal human force, Freud believes aggressive forces are inherently self-destructive. Conversely, Lorenz holds that aggression is an internal survival instinct. He argues that physical aggression is essential for self-protection, resource control, and continued survival within a hostile world.

### Social Learning Theories

*Bandura's Social Learning Theory (1973, 1989).* Bandura's social learning theory suggests that children learn aggressive behavior by observing models (parents, peers, any person they see in media or in the physical world). According to Bandura, children are primed to behave aggressively by witnessing aggressive acts, either in person or through media. One experiment ("Bobo the Doll") clearly illustrates these effects: 5- to 6-year-old children watched a video of an adult playing with a Bobo doll (a large, inflatable, and weighted doll) either violently or nonviolently. After watching the video, the children in the study were allowed to play with the doll unsupervised. Children were likely to repeat the actions they saw modeled by the adult in the video, suggesting that individual behavior is influenced by direct observation, reward, and punishment (Bandura and Walters 1977).

*Dodge's Social Information-Processing Theory (1994).* Crick and Dodge's social information processing model explains how aggressive behavior could develop in children. Their model recognizes reactive and proactive aggression and holds that children pass through five cognitive stages that may allow them to rationalize and further support their aggressive behavior. The stages are as follows: encoding of social cues (evaluating offender's reaction to the offense), interpretation of cues (deciding whether the offense was intentional), response access (possible reactions), response evaluation (possible outcomes and

relation to desired outcome), and response enactment (aggressive or nonaggressive action) (Dodge 1996).

### Cultural Interpretation or Display of Aggression

Societal factors affect aggressive displays and their interpretation. In the United States, a study by Condry and Ross (1985) evaluates the influence of gender on participants' views of aggressive behavior. In the experiment, participants are asked to watch a video and rate the aggressiveness of two children playing together. In the video, the sex of the two children is impossible to discern due to the thick snowsuits they are wearing. Viewers are given varying sex information about the children dyads (male-female, male-male, female-male, female-female) as they engage in "rough and tumble" play. The findings indicated that most individuals rated the play to be more aggressive when viewers believed the antagonistic child was female. Conversely, the results indicated the assignment of lower aggressiveness scores for the exact same video when participants were told the two children playing were males. This study suggests a cultural expectation and acceptance of aggressive play specifically by males, a "boys will be boys" mentality.

Further illustrations that culture influences aggression can be found in a cross-cultural study by Forbes et al. (2009). In their sample, they found that individualistic societies tended to exhibit aggression more frequently than collectivistic ones. It is worth noting that, in these studies, females used indirect aggression more frequently than males, although males were observed to be more aggressive overall than females. This relationship held constant across the three countries observed in the study.

### Physiological Differences in Aggression

#### Brain Activation and Hormones

Aggression is shown to activate neural pathways within the amygdala. This portion of the brain is

also associated with anxiety and defensive behavior (Craig and Halton 2009). Brain scans reveal heightened activation of the amygdala in very aggressive subjects compared with nonaggressive subjects (Nelson and Trainor 2007).

The hormone oxytocin plays a role in human defensive aggression: Oxytocin has long been linked to bonding and commitment, especially regarding human mothers and their offspring. However, oxytocin has also been found to increase a mother's likelihood to respond aggressively to external threats against her children (Campbell 2008).

The prefrontal cortex of the human brain helps restrain aggression; as such, damage to this region has been associated with increased aggression (Nelson and Trainor 2007). Specifically, the amygdala plays a significant role in aggression and emotional processing and is most responsive to fearful facial cues (Davidson et al. 2000).

Pheromones, found in humans and animals, are also thought to contribute to aggressive interactions. Specifically, androstenol (a human pheromone released by males via sweat glands) was shown to affect women during their monthly cycle, causing them to report feeling more submissive (Benton 1982). Other studies have shown that, during their monthly cycle, heterosexual women are more likely to desire sexual relations with more aggressive mates. This tendency is negated when women take birth control pills that suppress menstruation (Lehmiller 2017).

## Socioeconomic Status and Aggression

Just as cultural norms and social cues affect interpretation and display of aggression, an individual's socioeconomic status (SES) is also indicative of the types of aggression likely to be employed. Specifically, higher SES individuals are more likely to use proactive and reactive aggression to accomplish social goals, whereas lower SES individuals are more likely to use physical aggression (Baş and Yurdabakan 2012). Research indicates an overall inverse relationship between aggression and SES that goes beyond the display of specific aggressive styles: Low SES

individuals are likely to score higher on willingness to use aggressive measures than higher SES individuals (Letourneau et al. 2013).

## Benefits of Aggression

Consideration of the aggression literature with a focus on competition helps illustrate the benefits of aggression – especially in ritualized customs like organized sports (Bushman and Anderson 2001). Obvious benefits of aggression include the following: enabling cooperation, fostering in-group loyalty, pooling of resources, defense against attacks, deterring future aggression, status negotiation within a group hierarchy, and deterring sexual infidelity by childrearing partners (Buss and Shackelford 1997). The importance of shared social communications is important, as aggressive displays intended to intimidate and circumvent conflict will not have the desired effect if both parties do not interpret the aggressive signals in the same way. An observable case of social differences in content and context of aggressive displays failing to prevent violence is the 1991 meeting between Iraqi and US officials to resolve a conflict in Kuwait. While the US representative was verbally aggressive, the Iraqi representative did not believe the validity of the message because it was not delivered with the expected physical display of aggression (e.g., shouting, striking surfaces with a fist, and throwing an item in anger; Triandis 2000).

## Procreation

Previous literature has documented that females responding aggressively to provocation and maternal aggression is a clear benefit to otherwise vulnerable children (Campbell 1999). Interestingly, evidence suggests that, while actively breastfeeding, human mothers behave more aggressively to provocation, compared with control subjects who were provoked while bottle-feeding their children (Hahn-Holbrook et al. 2011).

While aggression has been linked to genetic markers, research has indicated that situational factors are known to activate (or suppress) the expression of particular genetic traits. Further,

both biological and environmental influences appear to equally influence a child's development of aggressive tendencies, but in adulthood, hereditary inclinations appear to be stronger (Craig and Halton 2009).

### Animal Studies of Aggression

Within animal cohorts, males are usually more physically aggressive than are females. It has been postulated that aggression is largely influenced by androgens (e.g., testosterone). Test results from these and other studies are not conclusive: Mice displayed increased aggression after being injected with testosterone. A study conducted by the same researchers the following year received the same results after injecting the rats with estrogen. Researching at the human level, four independent studies were conducted injecting androgens into human males; only one study found a resulting increase in aggressive behavior (Björkqvist 1994).

Lab experiments removing the male-determining gene from Y chromosomes in rats yielded subjects that still exhibited aggression, indicating that other genes on the Y and X chromosomes also influence aggression (Craig and Halton 2009). Research involving mutated mice lacking androgen receptors indicates that mice lacking these receptors are not aggressive (Nelson and Trainor 2007). Although it appears to have not been tested, hormone sensitivity (specifically testosterone) could be a significant factor in the level of aggression displayed by individuals. The neurotransmitter serotonin has been linked to emotional regulation and aggression – particularly when the serotonin supply is disrupted (Davidson et al. 2000).

Situational conditions also affect animal aggression, particularly stress. Mice were found to be more aggressive after periods of physical restraint (this effect was replicated in dogs by restricting their spatial views) and more likely to aggress (even against larger opponents) after winning a series of fights. However, mice were found to be less aggressive after losing multiple aggressive encounters, even when confronted with smaller and weaker opponents (Sandi and Haller 2015).

Resource competition, especially fertile mates, often require increased aggression. Among the very aggressive elephant seals, 5% of the population's males sire 85% of the offspring conceived during the mating season (Buss and Shackelford 1997).

### Conclusion

The aggression literature reveals an intricate patchwork of research findings. Indeed, environmental and genetic factors only further establish the complexity of studying aggression. Our current understanding of the field (i.e., theories, contexts, sociocultural factors, brain activation, etc.) is established as a result of the combination of extensive human and animal studies. While often associated and portrayed as a negative quality, aggressive behavior on its own may not be overwhelmingly negative. In fact, several research studies display benefits of aggressive behavior.

### Cross-References

► [Aggression](#)

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## Bennett G. Galef

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Bennett “Jeff” Galef, Jr., was born on May 23, 1941 in New York City. After receiving his BA in Psychology from Princeton University and his MA and PhD in Physiological and Comparative Psychology from the University of Pennsylvania, Jeff migrated north to McMaster University in Ontario, Canada, and began a remarkably productive career studying Animal Behavior. Like many classically trained experimental psychologists at the time, Jeff’s research interests focused on feeding behavior. His work, however, departed significantly from psychological traditions in two important ways. First, it was highly integrative. Inspired by Daniel Lehrman, the great Comparative Psychologist, and Niko Tinbergen, the equally great Classical Ethologist, Jeff merged the strengths of these disciplines into his research program, allowing him to be able to think meaningfully about the mechanisms and development of feeding behavior along with the ecology and evolution of foraging. While such an integrative approach to studying behavior has long been considered the ideal for animal behavior research, few research programs have been able to integrate all of these levels of analysis so seriously and successfully as has Jeff’s.

Jeff’s second departure from classical experimental psychology was to study how social behavior plays a role in food and foraging site selection. Jeff was one of the first to realize that social factors were critical to foraging decision processes. Up to this point, social factors were

typically considered to be noise variables that needed to be removed from study. In contrast, Jeff set out to devise a means to study social influences on behavior while maintaining exacting standards of experimental control. The consequences of this work were effectively to create a new field of scientific inquiry in biopsychology into the mechanisms and function of social learning, a field that is still of pronounced interest to this day.

Jeff sets out to answer a seemingly simple question: Why is it so difficult to get rid of rats? As any farmer with a rat infestation will explain, poisons are moderately effective at first, but become ineffectual very quickly afterward. Rats seem to learn to avoid the poisons. Jeff was determined to examine how this occurs working under the hypothesis that rats might learn from one another about what to eat and what not to eat. Jeff created an experimental procedure where a “demonstrator” rat who had eaten a food with a novel flavor would interact with an “observer” rat, who was naïve to the flavor of the food the demonstrator had previously eaten. After only a single, brief interaction with the demonstrator, the observer would reliably gain a strong and lasting preference for the food the demonstrator had eaten. Jeff had discovered that rats can indeed communicate about food preferences.

With effect (and new procedure (Galef and Wigmore 1983) in hand, Jeff conducted an extraordinary number of experiments designed to isolate the mechanism by which the social transmission of preference occurs. For example, he examined whether the observer gained a preference for the food if the demonstrator with whom she interacts was anesthetized (she did), or euthanized (she did not), or only dusted with food (she did not). Over the course of these and many more experiments, Jeff found that the mechanism that created the transmission of preference involved the observer smelling the food odors on the demonstrator paired with carbon disulfide – a volatile chemical in rat breath. Together, these odors are necessary and sufficient to provide an observer rat a preference for the novel food. In addition, Jeff discovered that there are myriad other social mechanisms that emerge throughout rats’ lifetimes (some of which start prior to birth) that

combine to give rats preferences for foods and foraging sites.

Ironically, after all of these experiments, the original question about how rats learn to avoid poison was never strictly answered. Rats do not seem to learn socially to avoid anything. The many redundant social learning systems function to give rats preferences for foods but not aversions. One of Jeff’s astute interpretations of this work is that ecology filters social information such that only information about good quality food sources ever returns to colonies. Rats with bad social information – those who have eaten poison – do not return to the colony (and do not produce carbon disulfide). Thus, all the information present in colonies on the breath of other rats is valuable information about good foods, and no social information exists about bad food sites. This leads rats to make complex, adaptive decisions about food with a relatively simple series of behavioral and cognitive mechanisms.

Even though Jeff is no longer studying the social transmission of preference system, his experimental procedure remains a highly popular model across many disciplines of science, including chemistry, neurobiology, endocrinology, social learning, and animal behavior.

While Jeff’s signature work has been on social learning in rats, he has also made important contributions to a wide variety of topics. His work with partner and collaborator Mertice Clark provided a classic demonstration of epigenetic transmission of acquired characteristics across development mediated by parental care (Clark and Galef 1994). He has studied bats, quail, wild rats, gerbils, agoutis, mice, jungle fowl, and fish and has even dabbled with humans.

The area of social learning in animals would arguably not exist today without Jeff. It certainly would not exist in its present form. He brought his highly exacting standards from his own research to the area and “encouraged” others to follow suit. He created consistent definitions, he set standards of evidence, and he provided a highly disciplined approach for interpreting results from experiments in the lab and field (Zentall and Galef 1988; Heyes and Galef 1996). The area is vibrant today, and hopefully researchers will continue to hold to these principles in the future.



In addition, Jeff has been a dedicated member of the community, serving on an extensive list of editorial boards and scientific committees. He has created conferences, has trained countless students in his lab, and is always available to assist, collaborate with, and give advice to young researchers. Speaking personally, I can attest to his tireless, rigorous, and caring support as a mentor.

Across his prolific career, Jeff sets the standard for the process of science. He has been awarded with numerous awards including the highly prestigious Fellowship of the Royal Society of Canada. Finally, Jeff is a Renaissance man. He has wide-ranging interests that include photography, chess, art, fly-fishing, and alpine skiing and is a consumer of fine sushi.

## Cross-References

### ► [Social Learning](#)

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## Bernd Heinrich

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## Introduction

Bernd Heinrich is a Professor emeritus in the Department of Biology at the University of

Vermont. He is internationally renowned for his pioneering work on insect physiology and behavior as well as on raven social behavior and cognition. He is also renowned for being an excellent field biologist, who is thoroughly testing the hypotheses derived from his observations, and a gifted artist and writer, who skillfully disseminates his findings to the scientific and lay audience alike. Bernd Heinrich’s major contributions to the fields of animal behavior, physiology, and evolution have been recognized via numerous prizes and awards, two honorary doctorates, and elected memberships in societies like the American Academy of Arts and Sciences.

## Heinrich’s (Unconventional) Life and Educational Background

Bernd Heinrich was born on April 19, 1940, in the area of today’s Poland as son of the zoologist Gerd Heinrich and Hildegarde. At the end of World War II, the family lived for several years as refugees in a cabin in the woods of Northern Germany before they emigrated to the United States of America in 1950. At their arrival, they were personally welcomed by the famous evolutionary biologist Ernst Mayr, who knew Bernd Heinrich’s parents as zoological experts and specimen collectors for museums. Bernd’s parents resumed work as collectors shortly after arriving in the USA.

Heinrich spent his high school and college years in Maine, graduating in Zoology at the University of Maine, Orono, in 1964 (BS) and 1966 (MS) respectively. He then moved to California, where he received his PhD in Zoology from University of California, LA, with distinction in 1970. Already a year later, he accepted a position at University of California, Berkeley. Between 1976 and 1977, he was a Guggenheim and Harvard fellow, and in 1978, he became Professor of Entomology in Berkeley. In 1980, he accepted a professorship at University of Vermont, where he was Professor of Biology until his retirement in 2004. In that time period, Heinrich was also in Israel, 1992 as Lady Davis fellow, and in Germany, 1988–1989 as an Alexander von Humboldt senior scientist fellow.



Heinrich has four children (Erica, Stuart, Eliot, Lena) and three grandchildren (Gabe, Liam, Mia). Upon his return to the east coast, he built himself a wooden cabin in the forests of Western Maine, which has served him as a field site and as a place of unlimited inspiration for his research ever since. Originally dividing his time between Maine and Vermont, he is now living permanently in a (newly built) cabin in the Maine woods together with his partner Lynn Jennings.

Aside biology, Heinrich's passion had been long-distance running. He holds world-records in ultramarathon distances for master runners and set American national records for any age in distances 100 km, 200 km, 100 miles, and longest distance run in 24 h. Due to these achievements, he was included in the American Ultrarunning Association's Hall of Fame. He also reflected on his favorite sport as scientist in his best-selling book "Why we run: a natural history."

## Scientific Career and Output

Bernd Heinrich can be characterized as evolutionary biologist and behavioral ecologist, who works on the interface between the field and the laboratory. Specifically, he is interested in physiological, behavioral, and cognitive adaptations to a species' environment.

Heinrich received international recognition for his innovative studies on insects, most notably for the discovery that sphinx moths maintain the same high body temperature during continuous free flight over a wide range of air temperature (Heinrich 1970). He then elucidated the physiological mechanism whereby this is accomplished, and followed with comparative studies over a wide range of other insects (e.g., Heinrich 1972, 1974). The thermal physiology studies of bumblebees were extended to their energetics and their foraging and learning behavior as a model for elucidating flower evolution (e.g., Heinrich and Raven 1972; Heinrich 1974, 1975). His studies on honeybees resulted in the discovery of how the thousands of bees in a swarm cluster regulate its temperature largely by individual initiative rather than communication (Heinrich 1981).

Heinrich is also famous for his work on ravens that got kick-started by the seemingly trivial observation of noisy crowds feeding at a moose carcass in Maine. Wondering how and why unrelated birds share information about food (Heinrich 1988), he was the first to reveal the complex pattern of cooperation and competition among nonbreeding ravens, providing experimental evidence for the active recruitment of conspecifics to overpower the food defense by dominants (Marzluff and Heinrich 1991). He then moved on to study raven "intelligence," a topic which had been present in the scientific literature for decades but almost entirely on an anecdotal level (he found >1000 anecdotes vs. 1 experiment in the mid-1990s). His pivotal studies on insight (Heinrich 1995) and knower-guesser differentiation (Bugnyar and Heinrich 2005) using the string-pulling and caching/pilfering paradigm, respectively, were highly influential for the emerging field of avian cognition.

Bernd Heinrich's scientific output contains numerous research papers (>70 on insects, >30 on ravens, many of them in top journals), semi-popular articles (>70), book chapters (>50), and award-winning books like "Bumblebee Economics" (1979), "Ravens in Winter" (1988), and "Mind of the Raven" (1999). Aside his main research topics, Heinrich has authored 20 books of natural history, almost all best-selling and award winning like the John-Burroughs-Medal for Nature Writing. Since retiring from the University of Vermont, he has published 24 nature essays as "Naturalist at Large" for Natural History Magazine, and 16 peer-reviewed scientific papers on various topics sparked by natural history observations where he lives in the Maine woods.

## Cross-References

- ▶ [Adaptedness of Behavior](#)
- ▶ [Corvids](#)
- ▶ [Energy](#)
- ▶ [Evolution](#)
- ▶ [Foraging by Honeybees](#)
- ▶ [Social Behavior](#)
- ▶ [Territoriality](#)
- ▶ [Thermoregulation](#)

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## Introduction

The formation of dominance hierarchies is a common feature in animals that live in group. In this kind of social organization, individuals are organized in ranks based in agonistic interactions to portioning resources among the group members. The dominant individual, the one that wins the fights over all other is called alpha. The second individual in the rank is the beta, the individual who loses fights with the alpha but wins over all others (Cafazzo et al. 2010). The beta animal will, most of the times, replace the alpha one when the alpha is no more considered the dominant for some reasons, as for example, when the dominant dies or when it is removed from the group (Whiteman and Côté 2004). Normally, beta is the rank position that receives more aggressive behavior from the dominant (Cafazzo et al. 2010), and defensive and submissive behaviors towards the alpha characterize the beta behavior. Towards other group members, beta is characterized by aggressive behavior.

## Best-Fit Models

### ► Model Fitting

## Beta

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## Synonyms

Subdominant

## Definition

In a dominance hierarchy, beta is the individual that occupy the second position in the rank, just after the alpha.

## Advantages of the Beta Position

There are a lot of variable consequences of being beta, depending mainly on the species and on the social organization. Although most studies did not distinguish between beta and the other subordinates, we can observe some advantages of the beta position. When putting together to interact, alpha and beta mice did not lose weight, whilst subordinates do. Moreover, in more despotic groups, when alpha males are highly aggressive, subordinates have a lower testosterone level when compared to alpha and beta males, whereas testosterone of alpha and beta were indistinguishable (Williamson et al. 2017). In the passerine Taiwan Yuhina (*Yuhina brunneiceps*), alpha and beta males can sing the territorial song together, although the alpha male always sings more than the beta. Other subordinates (also called gamma) never sing in the presence of the beta or alpha. Furthermore, for females of the same group, although alpha tend to have higher number of laid eggs than beta, other subordinates did not reproduce at all (Yuan et al. 2004).

However, the most obvious advantages of being the beta is to get the alpha position when the alpha dies (e.g., in coyotes (*Canis latrans*, Gese et al. 1996) and in the male lance-tailed manakins (*Chiroxiphia lanceolata*, DuVal 2007)).

## The Beta Position and Stress

Besides to have some advantages, the beta position is still a subordinate position, and subordinate positions are, most of the times, associated with some level of stress. How stressful it will be to be subordinate will depend on the species and on the social characteristics of the group. Levels of cortisol, a physiological marker of stress, will be higher in subordinates when they (1) were subjected to higher rates of stressors, (2) experienced decreased opportunities for social (including close kin) support (Abbott et al. 2003), (3) are minimally related to other members of their social group, and (4) are in an enclosure too small to allow subordinate individuals to evade dominant ones (Sapolsky 2005).

## Conclusion

Beta individuals can be considered as the second-in-command or the highest rank subordinate. As in an intermediate position in the dominance hierarchy, it will have advantages and disadvantages depending on the species and, mainly, on the characteristics of the alpha and the group composition.

## Cross-References

- Alpha
- Dominance
- Dominance Hierarchy

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## Betta Splendens, the Siamese Fighting Fish

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*Betta splendens*, more commonly known as the Siamese fighting fish or *Betta*, is a small (males, shown in Fig. 1, are around 6.5 cm long, females somewhat smaller) domesticated version of a fish native to small ponds and streams in what today is Thailand (Smith 1927). It is a member of the family Anabantidae. The *Betta* breathes by means of a lunglike labyrinth organ rather than gills. Through selective breeding over the last 110 years, the *Betta* has been transformed from a small-finned brown fish to one of the most visually and behaviorally striking of the so-called tropical fish. Both the domesticated male and female have bright iridescent colors, and the

**Betta Splendens, the  
Siamese Fighting Fish,**  
**Fig. 1** A male *Betta*.

(Photo credit: <http://www.animalsindetail.com/betta-fish-siamese-fighting-fish-betta-splendens/>)



male has long, flowing fins. It was first described in the scientific literature by Regan (1909) and introduced to the United States in 1927. It is a popular fish not only with amateur and professional aquarists but also with behavioral researchers. The latter's findings are the focus of this article.

The most conspicuous behavior pattern of either a male or female *Betta*, at least in the absence of a conspecific, is its periodic trip to the surface of the water, where it exchanges expired air for fresh air and then quickly swims to a lower level. The reason for this behavior is the breathing apparatus noted above; the fish must process air through lunglike structures rather than the gills that serve this function in most fish species. This breathing mechanism has been suggested to underlie the *Betta*'s reproductive behavior (Braddock and Braddock 1959). Unlike most egg-laying fish, male and female *Bettas* build their nests on the water's surface. The nests, appropriately called bubble nests, are composed of a conglomerate of mucous-covered air bubbles. To construct the nest, the *Betta* surfaces, gulps a mouthful of air, covers it with a saliva-like material, and extrudes it to the surface. The process repeats until several hundred bubbles are created and attached to one another. Both nest construction and egg production are optimal around 26.67 °C (Goodrich and Taylor 1934). Successful nests for raising fry are compact and

at least 6 cm<sup>2</sup>. Braddock and Braddock (1959) observed that almost all such successful nests were constructed by males.

Gravid females are treated quite inhospitably by male *Bettas*, at least by human standards. On entering the territory of a sexually receptive male, as indicated by the presence of a bubble nest, the male chases the female around the territory, nipping at her fins (which are far less pronounced than the male's) and sides for anywhere from a few minutes to several hours. Following this, the male wraps his body around that of the female and squeezes a few eggs from her ovum. Simultaneously he releases sperm cells into the water. He then releases the female, gathers the falling eggs into his mouth, and extrudes them into the bubble nest. This process repeats over up to several hours until all the eggs are ensconced in the bubble nest. The female plays no role in nesting, beyond providing the eggs (Braddock and Braddock 1959). The aggressive overtones of the sexual act are obvious in this description. In fact, females typically are injured and often killed as a result of a sexual bout with a male *Betta*.

*Bettas* exhibit a species-typical aggressive response pattern when they encounter a same-sexed conspecific. Although these attacks are more popularly associated with males, Braddock and Braddock (1955) observed fighting between 35 of 51 pairings of female *Bettas*. Of the two

sexes, the response of the male is the more intense, often being life threatening. Thompson and Sturm (1965, see also Simpson 1968) identified four distinct components of the *Betta*'s aggressive response: (1) frontal approach to the releasing stimulus, (2) fin erection, (3) gill cover erection/extension, and (4) undulating movements. In addition, there can be a darkening of color, and often dark vertical bands occur along the lateral side of the fish's body. The two fish then swim in parallel to one another for several minutes prior to the actual attack. Braddock and Braddock (1955) speculated that the preliminary display is critical in building to a threshold of aggressiveness, beyond which the actual attack is released. During the attack, fins and body are the most frequent targets, although damage to gill covers and eyes also occur. Attack and counter-attack can last from a few minutes to 3–4 h. There are anecdotal reports that fighting is suspended when the oxygen-deficient contestant breaks the encounter to replenish its oxygen supply. Visual stimuli are most crucial in releasing the aggressive response pattern, but other sensory modalities such as tactile and auditory stimuli also may be implicated (Evans et al. 1958). There is some variation in both the probability and intensity of aggressive behavior of male *Bettas*, but the aggressiveness of individual fish seems to be rather stable over time (Bronstein 1994). In general, the larger of the two fish usually is the winner (Braddock and Braddock 1955; Evans et al. 1958). Because of such aggressive attacks, it is usual to house *Bettas* separately from one another, although tropical fish hobbyists often house females together in community tanks without evoking serious attacks.

The aggressive display of both male and female *Bettas* also can be released by the presentation of visual images resembling another *Betta*. These visual images have included models of a *Betta*, photographs, video clips, and still photographs of a conspecific, as well as mirror images of the fish itself. Between 15 °C and 35 °C, the strength of the aggressive display depends on the water temperature and the degree of similarity between the visual image and a live *Betta* (Hess 1953). The aggressive display of *Bettas* habituates with repeated exposure to either a

conspecific or to a visual image of a conspecific (e.g., Clayton and Hinde 1968), exemplifying an elementary form of learning. As such, it has been the focus of a good bit of research. Using a Pavlovian conditioning procedure, components of the aggressive display of males can be elicited by a previously neutral stimulus that is paired with 15-s presentations of a mirror image of a *Betta*. Punishing the aggressive display with response-dependent electric shock can suppress the aggressive display relative to its occurrence in either the absence of shock or response-independent shocks occurring at the same frequency as the response-dependent ones (Adler and Hogan 1963).

The reactivity of *Bettas* to live and visual images of conspecifics has been mostly widely investigated in the psychology of learning and motivation by using them as reinforcers for some other, operant, response. This latter response produces either a conspecific, usually without physical access to the latter, or a visual image of it. Thompson (1963) conducted a paradigm-establishing experiment in which male *Bettas* learned to swim through a small "O" ring when the consequence was access to a mobile model of a male *Betta* with its fins erect and gill covers extended. In subsequent research involving visual reinforcement with male *Bettas*, the reinforcer for the operant response has included the range of visual stimuli noted above that release the aggressive display. The most frequently used visual image is a mirror image of the fish. There are few direct comparisons of the relative efficacy of these different types of visual reinforcers.

Responses of *Bettas* maintained by visual reinforcement also are a function of several parameters of the visual reinforcer. Thompson and Sturm (1965) reported an interaction between the color of the fish and that of the model as a reinforcer, with dissimilarly colored models maintaining more responding than similarly colored ones. Movement also may affect the quality of the reinforcer, although stationary models also release the aggressive display. Fifteen-second durations of visual access to the image maintained more responding than shorter ones (Wirth et al. 2003). Virtually all of the research on visual-image reinforcement with *Bettas* has been conducted with



males; however, similar operant responses of female *Bettas* also develop and maintain when those responses produce mirror images of themselves (Elcoro et al. 2008).

In most experiments involving visual reinforcement of *Betta* operant responses, each such response produces access to the visual stimulus, that is, a fixed-ratio 1, or continuous, reinforcement schedule has been used. Sustained responding under fixed-ratio schedules of up to a six-response requirement for reinforcement has been reported. Compared to behavior under similar schedules where responding is maintained by food reinforcement, however, response rates do not increase with increasing response requirements (Hogan et al. 1970). In general, intermittent reinforcement maintains relatively low response rates, perhaps in part because the response usually measured is that of swimming to either a particular location or through some barrier such as an “O” ring. Responding previously maintained by an FR 1 schedule was eliminated when the absence of that operant response (swimming to a designated location) for up to 600 s was required to produce brief visual access to a film image of a *Betta* in aggressive display (a differential-reinforcement-of-other-behavior schedule; Turnbough and Lloyd 1973). Because response rates maintained by visual reinforcement are quite low compared to those of more commonly used laboratory species for research on learning, such as rats or pigeons, fixed- or variable-interval schedules of reinforcement often end up being functionally continuous reinforcement schedules because the time between successive responses often exceeds the programmed interreinforcer interval specified by the schedule. Eliminating the visual reinforcer or delivering it independently of responding reduces response rates relative to those maintained when it is response-dependent. Extinguishing responding previously maintained by a visual reinforcer also can result in the resurgence of a previously, but not currently, reinforced response (da Silva et al. 2014).

Operant responses of *Bettas* also can be brought under stimulus control by reinforcing those responses, with either access to visual images or food, reinforcement, in the presence of

one stimulus and not reinforcing that same response in the presence of an alternative stimulus. In what is perhaps the first learning experiment conducted with *Bettas*, Benuic (1932) reported establishing a discrimination between two colors by reinforcing with food approaching one of the stimuli but not the other. The type of stimuli used as the basis for the discrimination also may be important. The present author had little success in establishing an operant discrimination between the presence and absence of mirror-image reinforcement based on either the presence or absence of a change in the color of an incandescent light, but a discrimination was established and maintained when the presence or absence of air bubbles was used as the basis for the discrimination (Wirth et al. 2003).

As a laboratory species for experimental studies of learning, *Bettas* are easy to obtain and maintain, and they typically remain healthy for the duration of an experiment. They also are relatively easy to breed, offering the potential of an inexpensive, replenishing supply of subjects. Their popularity with hobbyists and the material reviewed in this article illustrate that there is sufficient information about their maintenance and general behavior patterns to inform even the most *Betta*-naïve of investigators. To this point, *Bettas* have been a niche experimental subject, used primarily to investigate the reinforcing properties of its unique responses to visual images of itself or other *Bettas*. The *Betta* seems a poor substitute for more common experimental animals such as rats or pigeons for the study of general learning processes because of the, at least presently, not-well-understood limits of its responsiveness to intermittent reinforcement and a lack of data on the sensory systems that underlie its susceptibility to the stimulus control of its behavior. The reproductive and aggressive behavior patterns of *Bettas*, however, have engendered considerable interest and behavioral research.

## Cross-References

- [Aggression](#)
- [Classical Conditioning](#)



- ▶ [Conspecifics](#)
- ▶ [Free Operant Response](#)
- ▶ [Instrumental Learning](#)
- ▶ [Operant Conditioning](#)
- ▶ [Reinforcement](#)
- ▶ [Reproduction](#)
- ▶ [Species-specific Behavior](#)

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## Biased Decision Making

- ▶ [Base-Rate Neglect](#)

## Bigamy

- ▶ [Polyandry](#)
- ▶ [Polygynandry](#)

## Bilateral Symmetry

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## Synonyms

[Plane symmetry](#); [Reflection symmetry](#)

## Definition

Bilateral symmetry can be defined as the body plan of those animals, which can be divided into

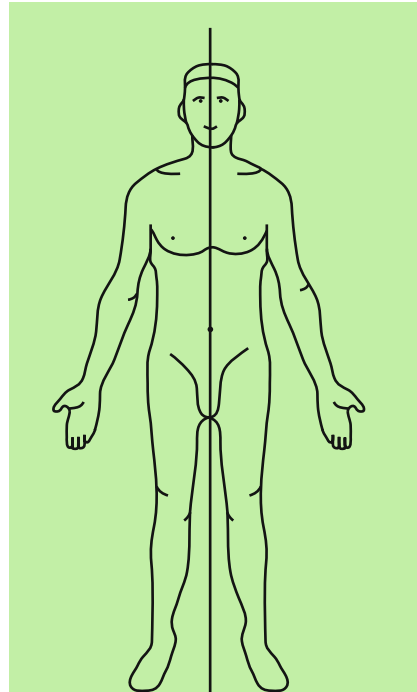
two equivalent right and left halves along the vertical plane passing through their midsagittal axis.

## Introduction

Body symmetry can be defined as the morphological resemblance of parts in distinct regions and orientations of the body. Because of symmetry, the animals can be broadly divided into bilaterally symmetrical, radially symmetrical, and asymmetrical animals. Animals that can be divided into two equal right and left halves, if they are split in the perpendicular plane passing through their midsagittal body axis, e.g., flatworms, earthworms, humans, etc., are known as bilaterally symmetrical. Organisms that can be divided into two equivalent halves if they are cut through any of the radial planes are described as radially symmetrical, e.g., jellyfish, corals, and sea anemones. Animals that cannot be divided into two identical halves through any plane are described as asymmetrical animals, e.g., sponges, adult snails, etc. (McMurrich 1896). However, precise spherical symmetry is not found in the animal body plans. Interestingly, symmetry type can be either broken or altered from one body type to another during an organism's lifespan (Moubayidin and Ostergaard 2015).

## Bilateral Symmetry

Since bilateral symmetry plane divides an individual into mirror-image halves, this symmetry is also known as plane or reflection symmetry. But, in this case, internal organs are not necessary to be symmetrical. Most of the animals are bilaterally symmetrical with respect to anterior-posterior (AP) and dorsal-ventral (DV) axes, including insects, birds, reptiles, and humans (Fig. 1). These AP and DV axes are formed during early embryogenesis and provide a 3-D coordinate system that gives vital spatial cues for growing cells, tissues, organs, and appendages. The anterior or dorsal end of these animals is characterized by a presence of sensory organs, like visual and the olfactory system (Genikhovich and Technau 2017).



**Bilateral Symmetry, Fig. 1** Bilateral symmetry in the human body along the axis of symmetry

## Advantages of Bilateral Symmetrical Body

Bilaterally symmetrical animals have greater mobility as they tend to move toward a frontal end, which finally led to the localization of their sensory organs in the anterior end or head (through a process defined as cephalization) (Finnerty 2005). This also makes the brain or central nervous system to identify various orientations and positions, thus creating visual perception easier. Moreover, these animals have a more streamlined body shape, which helps in the economical expenditure of energy during movements on land, air, and water. The presence of a similar organ or portion of the body on another side also provides a backup system for critical functions.

## Phylum in Animal Kingdom Showing Bilateral Symmetry

Phyla Platyhelminthes, Aschelminthes or Nematelminthes, Annelida, Arthropoda, Mollusca (except

adult snail), Echinodermata (except adult forms), Hemichordata, and Chordata are the different phyla in animal kingdom showing a good example of bilateral symmetry.

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## Bill McGrew

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## Introduction

William Clement McGrew, born in 1944, is a Scottish-American primatologist and anthropologist, one of the world's foremost experts on chimpanzee behavior and ecology. His scientific productivity is massive, an insatiable writer of more than 450 scientific publications, as articles, books, book chapters, reviews, and commentaries which altogether have been cited more than 13,000 times. These publications cover 15 primate species on a wide range of topics, making an enormous contribution to the development of primatology over the last 50 years.

## Academic Studies and Career

McGrew's academic career started in 1965 with a BSc in Zoology at the University of Oklahoma, USA. In 1970 he was awarded his first doctorate, DPhil in Psychology at the University of Oxford,

UK. In 1990 he obtained another PhD in Social Anthropology at the University of Stirling, UK. In 2009 he was awarded a third PhD in Biological Anthropology by incorporation, from the University of Cambridge, UK.

From 1973, and for almost 20 years, McGrew was first a lecturer, then senior lecturer, and reader in psychology at the University of Stirling, UK. From 1993 to 2005, he was on the other side of the Atlantic, as a full professor in the Departments of Anthropology and Zoology at Miami University, Ohio, USA. In 2005, he returned to the UK, as a lecturer in biological anthropology and soon after became professor of evolutionary primatology at the University of Cambridge, UK. He retired in 2011, becoming emeritus professor at Cambridge and honorary professor at the University of St. Andrews, UK, where he has been based since 2017. During his career, he held visiting appointments at the University of California-Berkeley, University of New Mexico, University of North Carolina-Charlotte, Tulane University, and Earlham College in the USA, and at other academic institutions in Hungary, France, and Germany. McGrew is a fellow of The Royal Society of Edinburgh, Scotland, of the American Association for the Advancement of Science, and of the McDonald Institute for Archaeological Research, Cambridge. He has received the Howells Prize (USA), the Prix Delwart (Belgium), and the Osman Hill Medal (UK).

## Research

The initial subjects of McGrew's first research were young children; his PhD thesis in psychology, entitled *An Ethological Study of Social Behaviour in Preschool Children*, was published as a book (McGrew 1972) and several articles. But in 1972, his research shifted from human primates to nonhuman primates, from children to chimpanzees (McGrew and Tutin 1973). His first ape mentors were captive chimpanzees at the Delta Primate Research Center, in Louisiana, USA, observed during his postdoctoral training (Stanford University, USA). Then, they were the

wild chimpanzees of Gombe Stream National Park, Tanzania, where he was a research associate, when Jane Goodall's famous project was just entering its second decade.

While at Stirling, besides teaching and supervising graduate students, he established a field site in Niokolo-Koba National Park, Senegal. Together with Pamela Baldwin and Caroline Tutin, McGrew was a pioneer in the observation of savannah chimpanzees in the hot, dry, and open habitat of Mt. Assirik. For 4 years in the late 1970s, McGrew made ecological and behavioral observations on the Assirik chimpanzees. Despite these apes being minimally habituated to humans, not allowing observation of their behavior at close range, the naturalistic eyes of McGrew and his team revealed behaviors for comparison with projects of Gombe and Mahale in Tanzania, where the apes were better habituated to human observers. In the following years, McGrew and colleagues published a stream of 42 articles on the Assirik chimpanzees, including highly cited papers that became points of reference in the literature on savannah chimpanzees (e.g., McGrew et al. 1981; Baldwin et al. 1982; Tutin et al. 1983).

Elementary technology has always been central to McGrew's research; one of his first publications on great apes was on captive chimpanzees using tools for dental care (McGrew and Tutin 1973), shortly followed by a detailed description of wild chimpanzees using tools to feed upon driver ants (McGrew 1974). His interest in chimpanzee technology and material culture and their implications for human evolution consolidated in the following years at Stirling. This was the topic of his second PhD, published as a highly-cited book in 1992: *Chimpanzee Material Culture: Implications for Human Evolution* (McGrew 1992). It explores tool use and tool making, diet and food-processing, sex differences, and social customs in the chimpanzee species. It was the first systematic review of the material culture of a nonhuman species and proved to be provocative for scholars in the human sciences. This book, plus two other edited volumes (Wrangham et al. 1994; McGrew et al. 1996), were inspirational to younger generations

of primatologists, stimulating their research and that of scholars of other disciplines.

Unlike most other great ape researchers, such as Jane Goodall, Richard Wrangham, Toshisada Nishida, McGrew was not linked to a single population at a specific field site but instead visited and worked at nine study sites, spanning five African countries. He acquired a wide perspective on the chimpanzee species and a special sensibility for noticing behavioral differences across populations. He hypothesized that a particular grooming posture, the grooming handclasp, seen in some communities of wild chimpanzees, but not in others, may exemplify a social custom in a nonhuman species (McGrew and Tutin 1978). McGrew anticipated the cross-disciplinary debate of the following years on the existence of culture in chimpanzees, in other nonhuman primates, and in non-primate species. He took an important role in the debate in numerous publications (Whiten et al. 1999; McGrew 2004) and in organizing conferences and symposia.

With a remarkable scientific curiosity, excellent communication skills, and a multidisciplinary approach that emerged early in his research, McGrew collaborated extensively with other primatologists as well as researchers of other disciplines, such as zoology, psychology, biological and social anthropology, and archaeology. In the 1990s, he investigated laterality of manual function (handedness), in a series of studies on chimpanzees and other species, which yielded many publications (e.g., McGrew and Marchant 1997). He established long-lasting collaborations with Japanese primatologists Toshisada Nishida and Tetsuro Matsuzawa, contributing significantly to the interaction of Japanese and Western primatology (Nishida et al. 1992). In 1996, he co-organized the symposium Cebus Meets Pan, convening researchers studying tool use, cognition, and other aspects in one or the other species (Visalberghi and McGrew 1997). With Andrew Whiten, he coordinated the collaborative efforts of wild chimpanzee researchers that led to the characterization of chimpanzee culture (Whiten et al. 1999) and the development of cultural primatology (McGrew 2004). Similarly, in more recent years, he had a key role in

organizing symposia and workshops on primate archaeology (Haslam et al. 2009).

Finally, McGrew is an exceptional mentor, with a rich academic lineage. During his career he supervised the research of 18 PhD students and 6 masters students. He has many academic descendants, including grandchildren and great-grandchildren, making him one of the most influential primatologists on earth. Primatology would be a very different world without McGrew's contribution.

## Cross-References

- Andrew Whiten
- Behavioral Flexibility
- Behavioral Variation
- Cultural Transmission
- Culture
- Cumulative Culture
- Elisabetta Visalberghi
- Frans de Waal
- Grooming
- Jane Goodall
- Laterality (Handedness)
- Nut-Cracking
- Primate Diet
- Primate Social Structure
- Primates
- Richard Wrangham
- Sex Differences
- Social Behavior
- Tool Use

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## Bimodal Activity Pattern

- Crepuscular

## Binary Fission

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Binary fission is a method of cell division where the cell divides into two halves by any

plane of division. The classifications of division on the basis of axis of plane are longitudinal (*Euglena* sp.), transverse (*Paramecium* sp.), oblique (*Ceratium*), or just a simple irregular plane of division (*Amoeba*). Bacteria mainly divide by this simple process and have manifold propagation. The cell doubles in its size duplicates the genetic material and finally splits into two. A number of research laboratories have comprehended the underlying molecular mechanisms for this type of asexual method of reproduction in forming clonal cells. Binary fission is also followed by eukaryotic cell organelles like mitochondria and chloroplast which are believed to share bacterial modified genome as theorized by the bacterial endosymbiotic theory.

## Mechanism

Firstly the DNA duplication occurs aided by the action of proteins and enzymes. Then the DNA is segregated to the extreme poles of the cell so that it remains undamaged during division and each cell receives a complement of genes while preserving high fidelity. The site of cleavage finds the assembly of the division apparatus which is comprised of the FtsZ, a class of novel proteins forming a ringlike structure at the center of the cell with its monomers (Angert 2005). Gradually the new cell wall materials are accumulated following the invagination of the cell envelope, and two copies of identical cells are produced.

Hale and de Boer (Hale et al. 1997) were the first to propound a model of bacterial division in *E. coli*.

In Gram-negative bacteria, binary fission is mediated by a group of periplasmic proteins and 12 essential membrane-associated proteins to form the divisome. The assembly of Fts class of proteins like FtsQ, FtsL, and FtsB, forming the FtsBLQ complex, acts as a coordinator for an array of reactions in the divisome (den Blaauwen and Luirink 2019). Evidences of FtsBLQ to have roles in septal peptidoglycan synthesis have been demonstrated for complete division (Boes et al. 2019; Tsang and Bernhardt 2015).

## Proteins and Their Roles in Binary Fission

### Fts Proteins

The Fts class has a multitude of proteins enabling easy prokaryotic fission, and FtsZ is the most vital and highly conserved group in the family. It plays a role in prokaryotic cytokinesis and has structural and functional similarities to the eukaryotic tubulin that aids in the formation of mitotic spindle in eukaryotic cell division. This class of proteins remains conserved even in cellular organelles (like mitochondria and chloroplast) as well as in members of *Archaea*. FtsZ and tubulin are homologous structures (Angert 2005) and share a common ancestor in the line of evolution. These group of proteins form filaments and rings by energy from guanosine triphosphate (GTP).

The various types of Fts proteins that assemble with the Z ring are FtsA, FtsI, FtsQ, FtsL, and FtsW (Angert 2005).

FtsK in *E. coli* were experimentally found to be important in both initial and latter stages of cytokinesis (Begg et al. 1995).

### Other Proteins

It has been reported in *Bacillus subtilis* that Noc<sup>19</sup> do not allow Z ring to assemble at the middle of a cell until the nucleoid segregates. MinCD and DivIV prevent the assembly of Z ring at the poles, EzrA helps in maintaining stability of FtsZ polymers and allow the assembly of FtsZ ring at particular location and YneA destabilize Z ring formation on detection of DNA damage (Angert 2005).

## Conclusion

Du and Lutkenhaus (2017) had reported that majority of the divisome proteins of *E. coli* have been identified although their assembly and septal formation for division is yet to be studied. FtsW is being identified as a putative PG glycosyl-transferase protein for division in coordination with FtsI (Liu et al. 2016). Various proteins encoded by genes contribute toward the



functionality of cellular division while retaining the exact behavior of the cell. This is the most striking feature of binary fission and aids in complete development of a new cell from an older mother cell. Since binary fission indicates toward the clonal propagation of cell by means of an absolutely asexual means of reproduction, hence lack of variation is witnessed by this process. The daughter cells being exact copies of the parent cells have extremely low levels of genetic variation which hinders their survival rate in adverse environments.

## Cross-References

- [Asexual Reproduction](#)
- [Budding](#)

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## Binocular Depth Cues

- [Cognition](#)

## Binocular Vision

- [Depth Perception](#)

## Binomial Nomenclature

- [Nomenclature](#)

## Biodiversity

- [Safari](#)

## Biodiversity Hotspot

- [Hotspot](#)

## Biogeography

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Biogeography is the study of the geographic distribution of flora and fauna and the factors that drive this distribution across space and time. Biogeography is an integrative biological science that uses many tools from physical geography to help analyze the composition of species located in any one area. Factors that affect the composition of plant and animal species at one site are varied and depend upon specific climatic and physical characteristics (local climate, latitude, elevation, isolation), geological factors (from plate tectonics to soil composition), and evolutionary history (colonization, extinction, and speciation). Further, the ability of any given species to adapt to the local conditions will affect both its range and its ability to disperse further on the landscape. Biogeography and landscape ecology are closely

related subjects, the former more concerned with connectivity and movement over the landscape and the latter more focused on the functional aspect of the habitat at varied spatial scales. Landscape ecology concerns itself with the processes (biotic and abiotic) and organisms that preserve proper ecosystem functioning and ecological integrity. Anthropogenic effects leading to fragmentation and loss of connectivity can decouple mobile organisms and processes from their ecosystem role and lead to an impoverished and unstable habitat structure that changes species dynamics and composition.

Much of the early genesis of modern biogeography stems from the works of notable nineteenth-century geologists, explorers, and naturalists. In particular, the works of Alexander Von Humboldt and after him, Alfred Russel Wallace stand out as most influential. Von Humboldt was an explorer and travelled extensively, recording detailed geophysical measurements as well as describing his journeys and the species he encountered with the help of a botanist, Aimé Bonpland. Von Humboldt was a prolific writer and published accounts of his travels, as well as specialized works on astronomy, botany, and zoology. Wallace also was an avid explorer and collector of specimens. His work focused on species distribution across the world by integrating evolution by natural selection (which he co-proposed with Charles Darwin) and geography. By carefully noting geographical features of the many thousands of species he studied, Wallace noticed that places on Earth that shared similar climate and terrain did not necessarily share similar species. In particular, he noticed a clear demarcation of species between the neighboring islands of Java, Sumatra, and New Guinea and how species in Java and Sumatra were more closely related to the Asian continent and that New Guinean species bore a close resemblance to Australian species. He delineated six biogeographical regions on the planet that eventually matched up with continental drift and plate tectonics.

Robert MacArthur and Edward O. Wilson wrote one of the seminal works of biogeography, *The Theory of Island Biogeography* (MacArthur and Wilson 1967). The authors developed a model

to explain species richness on oceanic islands based on a series of extinction and re-colonization experiments conducted off mangrove islands off Florida. Their theory proposed that smaller, more isolated islands contain fewer species and that these species are more prone to extinction. Research on arthropods (Simberloff and Wilson 1969) and birds (Diamond 1973, 1974; Terborgh 1974) supported this theory. Researchers found that immigration and emigration relate to the distance to the mainland source population (colonists) and extinction rates correlate inversely to island size (i.e., the larger the island, the smaller the probability of extinction due to stochastic events). Eventually, the island populations/communities stabilize at equilibrium. Biologists drew parallels between real islands and isolated ecosystems on continental mainland. However, when biologists applied the island biogeography models to empirically test virtual “islands” such as land-locked reserves and isolated mountaintops, they found that extinction (and emigration) rates surpassed colonization rates and that no equilibrium was reached (Brown 1971). Others found a correlation between extant diversity of species and the quality of the habitat, i.e., both the gross area and heterogeneity of the landscape (Newmark 1986). Early applications of island biogeography also drew criticism as researchers found that under heterogeneous habitat conditions, smaller refuges could harbor a larger total number of species (Blake and Karr 1986; Quinn and Harrison 1988; Simberloff and Abele 1976) and that subdivided populations were more likely to persist (Quinn and Hastings 1987). The key finding was that heterogeneous landscapes provided more opportunity for species diversity. With the development of phylogenetics combined with known dispersal drivers, predicting patterns of species dispersal has become more rigorous and successful and has led to developments in the field of conservation biology.

Using satellite imagery to map changes in the habitat as well as the effects of human encroachment, modern biogeography focuses on how environmental and anthropogenic factors can influence the distribution and persistence of specific species of study. Modern biogeography can

play an important role in detecting likely changes to the distribution patterns of species, help identify movement corridors, and predict long-term persistence of species in the face of climate change and other sources of landscape-wide threats.

## Cross-References

- [Assemblage](#)
- [Dispersal Patterns](#)
- [Divergent Evolution](#)
- [E.O. Wilson](#)
- [Ecology](#)
- [Evolution](#)
- [Migration](#)
- [Speciation](#)

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## Bioindicator

- [Indicator Species](#)

## Bioinformatics

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## Synonyms

[Biological databases](#); [Computational biology](#);  
[Genomic context](#); [Machine learning](#); [Next generation sequencing](#); [Sequence analysis](#)

## Definition

Bioinformatics is a field of biological data storage, retrieval, management, and analysis by applying techniques from computational sciences, mathematics, and statistics.

## Introduction

Biological sciences have been undergoing a paradigm shift due to tremendous progress in experimental methods over time. These methods are generating biological data at an unprecedented rate at genomic and organismal levels. It includes DNA and protein sequence data and their three-dimensional structures, taxonomic data-aiming to catalog every living species on the earth, metabolic reaction data which charts metabolic pathways in an organism to understand physiology, molecular interaction data which reveals how cellular components interact to drive biological processes, gene expression data which provides snapshots of RNA species present at a particular

time point in a cell, and biomedical text data which provides a rich source of biological information scattered in literature. These data are diverse in nature and analysis is generally challenging due to inherent complexity of biological systems. Data analyses require skills not only from biological sciences but also from computational sciences, statistics, and mathematics. The field of bioinformatics bridges this knowledge gap by dealing with biological data storage, retrieval, management, and analysis by using computational tools and techniques in statistics and mathematics. The field of bioinformatics is vast, evolving over time and difficult to describe in a single chapter. This chapter provides a glimpse of the bioinformatics tools that are useful for experimental biologists and covers selected important developments in the field.

## Biological Databases

Biological data is mostly available in relational databases with user-friendly interfaces accessible online. With few exceptions, biological databases are publicly available for research. Many prediction and inference web tools were developed in parallel to biological databases for in-silico biological discoveries. The available web tools and databases are thousands in numbers and ever increasing. In 1965, Margaret Dayhoff collected 65 protein sequences that were sequenced by the time and reported them in a book titled *Atlas of Protein Sequence and Structure*. It subsequently led to the foundation of bioinformatics and the first online database, the Protein Information Resource (PIR). Dayhoff was also first one to compare sequences using computer program (Eck and Dayhoff 1966). Meanwhile, efforts made to develop the GenBank, a nucleic acid database which was eventually released in 1982. Since then, GenBank, as a part of the National Center for Biotechnological Information (NCBI), has become the first stopover for research in almost all biological fields and growing at an exponential rate, containing millions of sequences including thousands of completely sequenced genomes (Wheeler et al. 2000). GenBank

provides up-to-date information about nucleic acid sequences wherein each entry is further hyperlinked to other related resources providing fine-grained information such as protein sequence, taxonomy, metabolic pathway, etc. The universal protein knowledgebase (UniProt) is a modern database which contains as of July 2017, 555,100 manually annotated and reviewed protein sequence records with information extracted from literature about molecular functional aspects, and 88 million sequences with electronic annotation, i.e., translated from nucleic acid sequences from GenBank-like databases (SIB Members 2016). Researchers are continuously analyzing sequences in these databases and others to gain biological insights and to create several specialized databases.

The list of biological databases is never ending but the most important databases are: Pfam, a database of protein families and domains related information; ProSite and InterPro are databases of protein functional sites or patterns found specific to a particular protein family which include active sites, binding sites, unique patterns, etc.; Gene Ontology (GO), a database of structured and hierarchical classification of genes into three functional categories that are biological process, cellular component, and molecular function, each further refined up to seven levels from the broader to finer functional subclasses; the Kyoto Encyclopedia of Genes and Genomes (KEGG), a database of metabolic enzymes, reactions, and pathways; DNA Binding Domain (DBD), a database of predicted transcription factors in completely sequenced genomes; JASPAR, a database of transcription factor binding sites; Online Mendelian Inheritance in Man (OMIM) database provides quality information on human genetic disease related genes; the Ensembl database provides user-friendly programmatic access to annotation and sequences of eukaryotic genomes; PubMed, a biomedical literature database containing millions of research publications; the Protein Data Bank (PDB) database contains 3D structures of macromolecules and associated information, whereas the superfamily database contains PDB structure-based protein family and domain classification system. Searching these

databases is easy and can be done by using a sequence, gene or protein names or keywords associated with them. More complex Boolean queries are also possible through advanced search options for filtering relevant information. Table 1 enlists these and few other important databases with weblinks for access. Readers are further encouraged to explore the resources available at NCBI, EBI, ExPASy, and the UCSC genome browser, which have strong user support (Table 1).

## Overview on Sequence Homology-Based Protein Function Prediction

For many centuries, the homology term has been used to describe the common ancestry between a pair of biological entities based on notable common features. In the early 1960s, Emile Zuckerkandl and Linus Pauling analyzed sequences available at that time and observed that the homologous sequences share a high degree of similarity and small number of differences. They speculated that the comparison of homologous sequences from various organisms can be used

to understand the process and rate of evolutionary changes at molecular level. This observation was key to the development of a series of computational methods to align, compare, and analyze sequences (Altschul et al. 1997). Given a query sequence, Basic Local Alignment Search Tool (BLAST) and phmmer (part of hmmer package) web/stand-alone tools search it in sequence databases like GenBank, UniProt, or PDB. Generally, if these tools identify database sequences (called hits), with more than 60% identity with the query sequence and an e-value (the measure of obtaining hits with as high identity by chance in the database) below  $1e-4$ , then it is very likely that identified the query sequence's homologues. If there are homologues with known functions, these may be putative functions for the query sequence. The BLAST and phmmer are pair-wise alignment tools and can search databases of millions of sequences within a minute. Hits with 30–60% identity to the query sequence and a significant e-value can be used to construct multiple sequence alignments using several available tools. Clustal family tools are the most used ones. Due to mutations, insertions, and deletions, sequences diverge during evolution – however,

**Bioinformatics, Table 1** List of selected databases for protein and nucleic acid sequence and structure related information

| Database    | URL                                                                                       | Usage                                           |
|-------------|-------------------------------------------------------------------------------------------|-------------------------------------------------|
| NCBI        | <a href="https://www.ncbi.nlm.nih.gov/">https://www.ncbi.nlm.nih.gov/</a>                 | Many databases and analysis tools               |
| EMBL-EBI    | <a href="http://www.ebi.ac.uk/services">http://www.ebi.ac.uk/services</a>                 | Many databases and analysis tools               |
| ExPASy      | <a href="https://www.expasy.org/">https://www.expasy.org/</a>                             | Protein databases and analysis tools            |
| GenBank     | <a href="https://www.ncbi.nlm.nih.gov/genbank/">https://www.ncbi.nlm.nih.gov/genbank/</a> | Nucleic acid sequence information               |
| UniProt     | <a href="http://www.uniprot.org/">http://www.uniprot.org/</a>                             | Protein sequence information                    |
| Pfam        | <a href="http://pfam.xfam.org/">http://pfam.xfam.org/</a>                                 | Sequence based protein domains and families     |
| Superfamily | <a href="http://supfam.org/SUPERFAMILY/">http://supfam.org/SUPERFAMILY/</a>               | Structure based protein domains and families    |
| PDB         | <a href="https://www.rcsb.org/pdb/">https://www.rcsb.org/pdb/</a>                         | Protein 3D structures and information           |
| ProSite     | <a href="http://prosite.expasy.org/">http://prosite.expasy.org/</a>                       | Protein patterns, active and binding sites      |
| InterPro    | <a href="https://www.ebi.ac.uk/interpro/">https://www.ebi.ac.uk/interpro/</a>             | Protein patterns and sites                      |
| GO          | <a href="http://www.geneontology.org/">http://www.geneontology.org/</a>                   | Functional classification                       |
| KEGG        | <a href="http://www.genome.jp/kegg/">http://www.genome.jp/kegg/</a>                       | Metabolic enzymes and pathways                  |
| DBD         | <a href="http://www.transcriptionfactor.org/">http://www.transcriptionfactor.org/</a>     | Transcription factor information                |
| JASPAR      | <a href="http://jaspar.genereg.net/">http://jaspar.genereg.net/</a>                       | Transcription factor binding information        |
| OMIM        | <a href="https://www.omim.org/">https://www.omim.org/</a>                                 | Genetic disorder related gene information       |
| Ensembl     | <a href="http://www.ensembl.org/index.html">http://www.ensembl.org/index.html</a>         | Genome sequence and annotation                  |
| UCSC        | <a href="https://genome.ucsc.edu/">https://genome.ucsc.edu/</a>                           | Interactive visualization of human genomic data |
| PubMed      | <a href="https://www.ncbi.nlm.nih.gov/pubmed/">https://www.ncbi.nlm.nih.gov/pubmed/</a>   | Literature                                      |

functionally and structurally important regions are conserved and can be revealed in multiple sequence alignment for functional inferences.

Distantly related homologues will often not be identified by above-mentioned tools, typically if they share less than 30% of their amino acid sequence with the query sequence. In order to identify them, more sensitive sequence-profile based tools such as Position-Specific-Iterative BLAST (PSI-BLAST) or Jackhmmer (hmmer package) can be used. In the first round of database search, these tools identify definite homologues of the query sequence. Using resulting pair-wise alignments of query and hits, at each position of the query sequence, the occurrence of each of the 20 amino acids will be computed. The resulting matrix is called profile and captures the information from several hits about the amino acid changes that evidently happened at each position of the query sequence. The tools then search the profile instead of the single sequence in the next rounds of database searches to find remote homologues. It has to be noted that a

large fraction of eukaryotic proteins harbors more than one domain, each with its own homologues. A domain is a region of a protein sequence which evolves independently, performs a specific function, and adopts a characteristic three-dimensional structure. PSI-BLAST or Jackhmmer often fail to detect true homologues for multi-domain protein sequences. It is recommended to use specialized tools to identify these domains. Pfam and Superfamily databases provide Hidden Markov Models (HMM) of all known sequence or structure-based domains, constructed using profiles of homologous sequences of each domain. Each HMM contains evolutionary model of a individual protein domain. A protein sequence can be submitted to these databases, to identify its domain architecture using programs from hmmer package and HMM library of all domains (Finn et al. 2015).

Essentially, if above-mentioned tools identify a single well-characterized homologue for a protein of interest, then user is already close to deduce its function at molecular level (Table 2). When all

**Bioinformatics, Table 2** List of powerful bioinformatics analysis and visualizations tools

| Web tool           | URL                                                                                                               | Usage                                   |
|--------------------|-------------------------------------------------------------------------------------------------------------------|-----------------------------------------|
| BLAST              | <a href="https://blast.ncbi.nlm.nih.gov/">https://blast.ncbi.nlm.nih.gov/</a>                                     | Sequence analysis                       |
| hmmer              | <a href="http://www.ebi.ac.uk/Tools/hmmer/">http://www.ebi.ac.uk/Tools/hmmer/</a>                                 | Protein sequence and domain analysis    |
| hhpred             | <a href="https://toolkit.tuebingen.mpg.de">https://toolkit.tuebingen.mpg.de</a>                                   | Distant homologue prediction            |
| PSORT              | <a href="http://www.psort.org/">http://www.psort.org/</a>                                                         | Subcellular localization prediction     |
| Phyre2             | <a href="http://www.sbg.bio.ic.ac.uk/phyre2/">http://www.sbg.bio.ic.ac.uk/phyre2/</a>                             | 3D structure and ligand prediction      |
| I-Tasser           | <a href="https://en.wikipedia.org/wiki/I-TASSER">https://en.wikipedia.org/wiki/I-TASSER</a>                       | 3D structure and ligand prediction      |
| Chimera            | <a href="https://www.cgl.ucsf.edu/chimera/">https://www.cgl.ucsf.edu/chimera/</a>                                 | 3D structure analysis and visualization |
| Jalview            | <a href="http://www.jalview.org/">http://www.jalview.org/</a>                                                     | MSA visualization and analysis          |
| Cipres             | <a href="http://www.phylo.org/sub_sections/portal/">http://www.phylo.org/sub_sections/portal/</a>                 | Phylogenetic analysis tools             |
| iTOL               | <a href="https://itol.embl.de/">https://itol.embl.de/</a>                                                         | Tree and associated data visualization  |
| Motifs             | <a href="http://meme-suite.org/">http://meme-suite.org/</a>                                                       | Sequence motif analysis                 |
| Galaxy             | <a href="https://usegalaxy.org/">https://usegalaxy.org/</a>                                                       | Interactive NGS data analysis           |
| VISTA <sup>a</sup> | <a href="http://pipeline.lbl.gov/">http://pipeline.lbl.gov/</a>                                                   | Tools for comparative genomics          |
| GEO                | <a href="https://www.ncbi.nlm.nih.gov/geo/">https://www.ncbi.nlm.nih.gov/geo/</a>                                 | Gene expression analysis                |
| iHOP <sup>b</sup>  | <a href="http://www.ihop-net.org/">http://www.ihop-net.org/</a>                                                   | Gene-gene centric text mining           |
| String             | <a href="https://string-db.org/">https://string-db.org/</a>                                                       | Functional protein interactions         |
| NEAT <sup>c</sup>  | <a href="http://floresta.eead.csic.es/rsat/index_neat.html">http://floresta.eead.csic.es/rsat/index_neat.html</a> | Network prediction and analysis         |
| Cytoscape          | <a href="http://www.cytoscape.org/">http://www.cytoscape.org/</a>                                                 | Network visualization and analysis      |
| iPATH              | <a href="https://pathways.embl.de/">https://pathways.embl.de/</a>                                                 | Interactive pathway visualization       |
| IGV                | <a href="http://software.broadinstitute.org/software/igv/">http://software.broadinstitute.org/software/igv/</a>   | NGS track visualization                 |

<sup>a</sup>Also provides comparative genome visualization tools

<sup>b</sup>Returns sentences mentioning query gene from literature

<sup>c</sup>Also provides several tools for regulatory sequence analysis, metabolic pathways, etc.



sequence-based tools fail to identify homologues, Phyre2 or I-Tasser-like three-dimensional structure prediction tools may be used, because structures are more conserved than sequences. These tools also include putative ligand binding sites in their structure prediction results. These approaches can only infer functions of proteins that are homologues to already well-characterized proteins. The fact that biologist determines protein functions in controlled laboratory setup where most protein coding genes do not express.

## Overview on Nonhomology-Based Protein Function Prediction

On an average, 40% proteins from sequenced genomes do not show sequence similarity with well-characterized proteins. Their functions are crucial to understand the complete biology of organisms. The post-genomic researchers developed several methods to provide broad functional roles to these proteins. Proteins involved in the same biological processes are often under the same functional constraints and tend to co-occur in genomes where that function is required. Phylogenetic profiling method detects such co-evolving protein pairs. The function can be inferred for uncharacterized protein based on the functions of characterized proteins coevolving with it. MirrorTree method also captures coevolution of protein pairs but at amino acid level changes. The idea is based on the need of physical interaction between cooperating proteins to drive function. Hence, mutations at the interface in one protein are likely to be compensated by mutations in the other. This information can be computed from multiple sequence alignments of two protein families.

Chromosomal proximity of genes often indicates coregulation and hence the requirement to express them at the same time point in the cell. The protein products of such coregulated genes often physically interact with each other and contribute to protein complexes. Coregulated proteins can be detected by the intergenic distance between the genes encoding them. Coexpression of genes is a hallmark of their coregulation, which can be computed from hundreds of gene expression

datasets for various organisms publicly available at Gene Expression Omnibus (Table 2).

Generally, these methods detect interacting partners of proteins encoded in the same genome. The function of an uncharacterized protein is often deduced from the functions of its interacting partners; hence, these methods are known to employ the guilt-by-association principle or genomic context (Snider et al. 2015). These methods do not provide functional information at molecular level but often deliver clues to the biological process or pathway in which the protein of interest may act. String web server implements several such methods and can be searched using sequence or gene name to identify interactions (Table 2).

## Machine-Learning Classifiers in Bioinformatics

Bioinformaticians have spent significant effort in classifying millions of publicly available sequences into various categories. For instance, databases like Pfam and Superfamily contain HMM for almost all known proteins or domains. Unclassified protein sequences can be classified into known families based on HMMs using hmmer-like tools. Given a positive and negative training data set, machine-learning techniques build classifiers based on certain features derived from training dataset. The classifier can be defined as a mathematical or statistical coding of the features, which distinguish instances of the positive or negative class and classify also new instances. Machine-learning classifiers have been developed for the classification of almost all biological entities. The list includes the prediction of genes in completely sequenced genomes using Genmarks, Genscan, Fgenesh, etc.; to the prediction of promoter sequences and transcription factor binding sites using Jasper; the prediction of subcellular localization of proteins using Phobius, SignalP, PSORT, TargetP, etc; to the prediction of gene expression using codon (genetic code) usage and prediction of protein–protein interactions using genomic context; secondary and tertiary structures of proteins using PSI-Pred, Phyre2, I-Tasser, and several others. This list of machine

learning classifiers developed in bioinformatics is never ending (few in Table 2) and encompasses almost all possible applications (Libbrecht and Noble 2015).

## Next-Generation Sequencing Data Analysis

Next generation sequencing (NGS) technology caused a paradigm shift in experimental biology. Sequencing the genome is no longer an expensive and time-consuming affair. NGS technology is coming up with wide applications and can be used to sequence complete genomes, RNAs (along with gene expression profiling), transcription factor binding sites, nucleosomes bound DNA regions, and several other (Lee et al. 2012). NGS generates data in the form of millions of short segments of DNA regions called reads. These reads are then further refined to prepare the data for analysis. The choice of tools depends on the length of the generated reads. Every NGS analysis starts with the assembly of the processed reads to recover the complete DNA regions of interest (Martin and Wang 2011). This step is easy when a reference genome sequence is available for the organism for which the NGS data was generated. Reads can be mapped to the genome and assembled. The assembled reads then can be analyzed further depending on the type and aims of NGS analysis. Galaxy is the best online tool for NGS data analysis from preprocessing of the reads to inferring biological meaning.

NGS data analysis is already making an impact on all fields of life science, from basic biology to translational research. The Encode project used NGS technology to decipher gene expression in several human tissues, refine gene boundaries, promoter usage, isoform usage, genome-wide mapping transcription factor binding sites, and mapped epigenetic modifications across genomes in several cell tissues and cell lines. Many metagenomics (sequencing microbial community without culturing) projects have been completed providing snapshots of microbial diversity in several sites in oceans and also in human body (Oulas et al. 2015).

## Cross-References

- [Amino Acid](#)
- [DNA](#)
- [Gene Expression](#)
- [Gene Expression Profiling](#)
- [Genes](#)
- [Homology](#)
- [Protein](#)

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## Biological Clocks

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## Synonyms

Biological cycle; Biorhythm; Body clock; Circadian rhythm; Circannual cycle

## Definition

Internal mechanism responsible for the behavioral changes that occur through yearly, seasonal, or daily cycles.

## Introduction

Biological clocks are universal in that they are found in virtually all living organisms. These clocks are constituted of molecules that play important physiological roles in activities that are integral to the existence of living organisms. Such activities include vital bodily functions such as sleep-wake cycles, daily eating habits, and the regulation of body temperature. Not only do biological clocks contribute to daily changes such as circadian rhythms, but they also influence an individual through a variety of temporal scales, such as seasonal and lifetime changes. These circannual clocks are often associated with reproduction. The animal kingdom has a variety of adaptations that are governed by these biological clocks.

## Daily Cycles: Circadian Rhythms

The circadian rhythm is a type of biological clock that operates throughout a daily cycle.

Circadian rhythms impact both mental and behavioral changes that are associated with diurnal periods. These cycles are controlled and regulated by a part of the brain within the central nervous system that triggers different activities as a result of exposure to extrinsic signals. These periods occur even when it is not exposed to constant environmental cues, thereby maintaining the bodily functions necessary to occur for survival.

Circadian rhythms within the animal kingdom occur due to exposure to a variety of external cues. A common external cue such as a light stimulus can instigate the circadian rhythm. Subsequent variations in interval and extent of light exposure can in turn impact the latency and duration of daily sleep cycles. Other than light, there is a diverse range of external cues that impact the circadian rhythms within the animal kingdom. For example, some species use tidal rhythms to determine when to forage in the sand while other species, such as marine worms, rely on the rise and fall of the moon to decide when to spawn (Martin and Swiderski 2001). Aside from tidal and lunar clocks, some animals, such as honeybees, have shifts in their respective circadian rhythm dependent on their social roles. Forager honeybees tend to have more regular circadian cycles, while nurse bees undergo shifts in their circadian rhythms to adjust to caring for their larvae (Eban-Rothschild and Bloch 2012). Furthermore, not all biological clocks within the animal kingdom span a 24 h period; in fact, some animals like the Somalian cave fish experience a much longer cycle, reflecting the slower environmental changes that occur within the darker caves (Beale et al. 2016). On the other hand, animals, such as the voles, undergo shorter cycles that last for about 2–3 h (Gerkema et al. 1993).

Biological clocks are not only important in producing these circadian rhythms but are critical in their regulation as well. Animals rely on the successful regulation of these internal cycles in order to sustain day-to-day functionality and survival. The variations in circadian rhythms, spanning differences in duration, trigger stimuli and, more, showcase the diverse ways by which animals in the animal kingdom respond and adapt to daily changes.

## Seasonal Cycles: Migration and Dormancy

Animals change their behavior and physiology in daily or annual cycles. Many aquatic species perform diel (daily) vertical migrations, where they move up in the water column to forage at night and move down during the day. Other organisms prepare to move to different locations at different times of the year. Large marine mammals, such as humpback whales, migrate to high latitudes to feed on krill and move to the tropics to breed and rear young (Baker et al. 1990). Birds experience *Zugunruhe* which is a change in behavior that includes increased activity around dusk and changes in their sleep cycles during migration periods (Rattenborg et al. 2004).

Another annual adaptation is seasonal dormancy, which is characterized by inactivity and decreased metabolism. Aestivation is seasonal dormancy in summer months and hibernation occurs in winter. Many invertebrates and ectothermic vertebrates have an aestivation cycle to conserve energy. Endotherms, such as mammals, are the most likely group to experience hibernation. Bears spend winter months in hibernation, spending long periods of time sleeping to reserve energy during the time of year when food is least plentiful. Female bears put their energy into gestation during hibernation, giving birth to their young during hibernation or shortly afterward. Hibernation can affect circadian cycles as well. In European hamsters, the circadian rhythm loses its 24 h oscillation during hibernation periods (Revel et al. 2007).

## Age/Fertility

As animals age, they experience a variety of changes in their behavior and form. Most notably, organisms experience a shift from non-reproductive to fertile life stages. Species such as butterflies and amphibians experience metamorphosis, altering their body shape to become reproductive. Other species, such as mammals, go

through a physiological process that allows them to reach sexual maturity with little or no change in form. Many species engage in sexual behaviors, such as copulation or courting. Mating begins once an animal reaches reproductive age. In female cockroaches, it has been shown that reproductive aging caused by delayed mating resulted in reduced choosiness of mates (Moore and Moore 2001). Few species have a post-reproductive life stage. One such species is the killer whale, where females that reach post-reproductive age provide leadership to their family groups (Brent et al. 2015).

## Conclusion

Biological clocks play an important role in animal behavior. Changes in behavior are often associated with reproductive success. Disruptions in these daily and temporal cycles could lead to complications impacting survival and overall health. Although biological clocks are an internal and self-sustained mechanism, they are often regulated due to exposure of external cues. From an evolutionary perspective, adapting to external stimuli that may impact biological cues could prove to be highly advantageous especially in the current climate facing constant environmental changes.

## Cross-References

- [Biological Rhythms](#)
- [Circadian Rhythms](#)
- [Day/Night Cycle](#)
- [Diurnality](#)
- [Endogenous Oscillations](#)

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## Biological Cycle

- [Biological Clocks](#)

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## Biological Databases

- [Bioinformatics](#)

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## Biological Evolution

- [Selection Study](#)

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## Biological Material Derived from Living or Recently Living Organisms

- [Biomass](#)

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## Biological Motion

- [Point Light Displays](#)

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## Biological Nomenclature

- [Nomenclature](#)

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## Biological Preparedness

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### Definition

Biological preparedness is a broad explanation for why some associations are learned more easily than others, invoking the evolutionary history of the animal.

### Introduction

Animals appear to learn about some stimuli in the world better than others, and a number of studies have shown that some sets of stimuli seem to be more easily associated than others. Some explanations exist for why this might occur, including ideas of belongingness and preparedness. Biological preparedness was first introduced as a term by Martin Seligman in his seminal paper “On the generality of the laws of learning”

(Seligman 1970). As with any trait, learning and behavior in any species are the result of evolutionary processes. Broadly speaking, learning enables an animal to use past experience to inform future behavior. Learning allows an individual to better track a changing environment, and this plasticity forms the foundation of flexible behavior. While the neurological mechanisms underlying learning are highly evolutionarily conserved and shared among animals, we see large differences in what animals can learn about, and what associations animals can make more easily than others. Seligman explained these differences as a product of the biology of the animal and of its evolutionary history: An individual of a species is born more prepared to learn about some associations than others because those associations were more useful for the ancestors of that individual. This makes intuitive sense when one considers that animals are bombarded with stimuli and potential associations from birth. If all stimuli were held equal, the extended trial and error learning required to differentiate among the potential stimuli and outcomes would likely result in incredibly high mortality in young animals. And, indeed, there are many examples of spectacularly fast learning in the natural world. For instance, butterflies can learn associations of where to lay eggs after single experiences (e.g., Snell-Rood and Steck 2015), and cues of predation or danger are very quickly learned from conspecifics (e.g., Cook and Mineka 1990; Ferrari et al. 2012).

### **History: From Behaviorism to Preparedness, Constraints, and Adaptive Specializations**

Early in his writings on learning, Thorndike (1911) speculated that the neural connections present within an animal may constrain what it can learn. Twenty years later, Thorndike (1932) wrote that the elements within learning that “belonged” together are more easily associated than elements lacking such a relationship. He referred to this as belongingness. Thus, how well something is learned is not determined by contiguity alone. In Thorndike’s view, an animal that is thirsty would

more readily learn an association that contained an effect of water because such an effect belongs to the needs of the organism. An effect that “belonged” less would not elicit as strong a reaction. In this way, animals would show better learning to more appropriate pairings of stimuli and effects than to less appropriate pairings. Thorndike’s view of belongingness emphasizes the particular states of the individual, but how should differences in species be interpreted?

The approach of behaviorism saw the testing of many animal subjects under tightly controlled and replicated conditions. It was generally hypothesized that learning was governed by a series of common laws, and detailed study of model species could then apply broadly across all animals. During the 1960’s and beyond, a larger variety of species and tasks were being used in studies of learning. This led to an increasing number of potential exceptions to the generally regarded laws of learning, including two frequently cited studies which provide good examples of selectively learned information. In a study with dogs, Dobrzecka et al. (1966) compared qualitative and directional auditory cues in differentiation learning instrumental task. In a right leg-left leg differentiation task, dogs almost exclusively learned using the directional cues with the qualitative cues not being learned even after more than 1000 trials. Complicating the conclusions further, they found that in a go-no go task, dogs acted with the quality of the cue 80% of the time, but acted with the direction of the cue 20% of the time. In this study, not only are certain stimuli and responses learned better than others, but the effect is task-specific. During the same year, Garcia and Koelling (1966) showed that rats select the cues used as stimuli dependent on the nature of the reinforcement. Rats were given water that differed in taste and in audiovisual characteristics: “bright-noisy” water and “tasty” water. Rats drinking these types of water were later made ill using X-rays and lithium chloride. Garcia and Koelling found that avoidance reactions developed based on the taste cues but not the audiovisual cues. However, when paired with shocks, rats learned the audiovisual cues better than the taste cues. Again, different cue types are being learned in



different tasks. Both papers were thought to pose challenges to the assumed generalities of the laws of learning and sparked a debate on the possibilities and potential types of biological constraints on the general process of learning (e.g., Seligman 1970; Shettleworth 1972; Logue 1979; Damianopoulos 1989).

A major idea proposed to explain the phenomena found by Dobrzecka, Garcia, and others was that of biological preparedness. Seligman (1970) argued that animals are born biologically prepared to learn certain associations, meaning that there is no equivalence of associability across all learning and all animals. Animals can also be contraprepared to learn. Contraprepared learning describes the difficulties in conditioning animals with certain tasks, such as with having a cat lick itself to escape a box. Seligman argued that animals show a continuum of preparedness, where learning about different events could be prepared, unprepared, or contraprepared. Examples from classical and instrumental conditioning, and discrimination and avoidance learning were discussed, with preparedness argued to be relevant to each of these types of learning. Whether prepared learning is qualitatively different from general learning was left an open question by Seligman due to the lack of experiments at the time. Additional questions proposed by Seligman were whether prepared learning covaried with additional cognitive or physiological mechanisms.

Shettleworth (1972) proposed a more general idea of biological constraints on learning in a detailed review of such constraints in every step of the learning process. Biological constraints on learning are essentially species-specific reactions to certain learning situations which are overlaid upon the factors operating in traditional learning theory. In other words, associative learning is the same across all species and situations with the exception of these biological constraints. She criticized Seligman's notion of preparedness as being focused on associative learning as the cause for observed differences in associative learning that also could be due to nonassociative processes. Shettleworth also discussed the importance of learning in the wild and described how

psychological ideas of learning could be applied to behaviors such as movement patterns and orientation. Shettleworth suggested that in studying learning, the behavior of animals in the lab should be related back to their behavior in the wild. Robert Bolles wrote about specific examples of this, proposing that some responses are likely constrained by Species-Specific Defense Reactions (e.g., Bolles 1970). He used example of flight reactions in rats when presented with aversive stimuli such as shocks.

In the following years, ideas of biological constraints became more specific, and were spoken of as adaptive specializations (e.g., Rozin and Kalat 1971; Shettleworth 1994). The notion of adaptive specializations specifically addresses the covarying cognitive and physiological mechanisms mentioned by Seligman. The use of the term adaptive specializations implies that such differences are the result of natural selection. Within the specific context of memory, Sherry and Schacter (1987) described the evolution of specific memory and learning systems as a result of functional incompatibilities between different tasks. Evolved modules would be well-suited to performing different tasks, such as food storing and retrieval behaviors in birds (e.g., Shettleworth 1990), and these adaptive specializations could then explain examples of preparedness described in learning. The notion of adaptive specializations is not without critics, but certainly every exception to general processes of learning does not require an explanation rooted in adaptive specializations (e.g., Krause 2015). Constraints do exist, and arguments using evolutionary adaptive logic can and should be empirically tested.

### **Prominent Examples of Preparedness: Taste Aversion, Fear, and Phobias**

The biological importance of taste aversion is straightforward to invoke as forming fast associations to enable avoiding potential toxicity in food is undoubtedly adaptive. An indeed, a taste aversion was invoked frequently as an early example of preparedness (e.g., Rozin and Kalat 1971; Logue 1979).

This logic is especially true for generalist foragers such as rats, with a well-described mechanism for social learning of food odors. The textbook example of preparedness is the work by Garcia and Koelling (1966). Among other results, they found that rats quickly formed associations between taste and nausea, but were unable to form associations between light and sound, and nausea. This work was the start of a burgeoning literature on biologically prepared taste aversion. Recent work on prepared learning and taste aversion in an ecological context is looking at how predators learn to avoid aposematically colored and toxic prey. Aposematic coloration, or warning coloration, poses an evolutionary question because the potential prey item is conspicuous to predators and every predator must first learn that association between coloration and toxin (Skelhorn et al. 2016). First, there is prepared learning for bitter tastes and toxicity, resulting from an evolved response to bitterness reliably predicting toxic effects (e.g., Skelhorn and Rowe 2010). Additionally, the conspicuousness of the prey enables an easier detection by the predator, is easier to learn, and less likely to be forgotten (e.g., Alatalo and Mappes 1996; Prudic et al. 2007; Roper and Redstone 1987). Thus, within one ecological paradigm, multiple levels of preparedness can be predicted and observed.

A second area with a deep literature on preparedness with fear and phobias, primarily in humans and other primates, is fear conditioning, which like avoiding toxic food, is easily tied logically to ecological relevance. Animals should more quickly form associations among stimuli that can result in their harm or death. The most famous of these examples is the work of Cook and Mineka (1990), who demonstrated selective associations at play in the observational conditioning of fear in rhesus monkeys. In their study, monkeys selectively associated snakes with fear and did not selectively associate more biologically neutral stimuli, such as flowers, with fear. Additional studies of fear conditioning generally confirmed these results across a range of ecologically relevant and neutral stimuli (e.g., Ohman and Mineka 2001). This type of fear conditioning has also been proposed to be evolutionarily tied to the development of phobias.

Phobias in humans seem to develop around specific objects, animals, or situations and are not equally distributed among other types of stimuli; thus, it is widely thought that phobias may represent a particular case of preparedness (e.g., Seligman 1971; Ohman and Mineka 2001).

## Mechanisms for Preparedness

A specific mechanism proposed for some examples of preparedness is that of selective associations. Selective associations require an interaction between the stimulus and reinforcement that results in faster acquisition of a CR with one CS than with another, but an opposite effect with a different reinforcement (LoLordo 1979). Additionally, the differences in learning must be due to this interaction and not to any differences in any particular properties of the stimulus used, such as its salience or intensity. This quite specific definition requires a series of controls to ensure that the observed differences are indeed due to selective associations, and LoLordo reviews possible methodologies to use for testing for a selective association. A straightforward approach is provided by Linwick et al. (1981), and they emphasized using correctly chosen controls and using a bidirectional design such that excitatory and inhibitory effects upon the dependent measure could be seen, without any floor or ceiling effects that might mask important differences. It is important to note that selective associations are not the only form of preparedness described in animals, as evidenced by the many other mechanisms that can result in prepared or contraprepared learning. Selective nonassociative processes may be adequate to produce the biologically appropriate, or prepared, response to the situation.

Given that natural selection acts upon fitness rather than mechanism, the output of the learning and not the process may be what should be considered from an evolutionary point of view. Seligman predicted that physiological and cognitive aspects would vary along with the continuum of preparedness for learning specific associations in animals. Evolutionary processes can prepare animals to learn some associations more easily

than others through acting on multiple cognitive systems, from perception to motivation to learning and decision making. In a broader biological view of learning, we know that this must be the case. Harkening back to Shettleworth's list of biological constraints, an additional 45 years of work on the neurobiology and sensory biology of cognition have finally enabled a more full conception of mechanisms through which preparedness happens. For instance, there is currently a strong emphasis on the role of sensory bias in the evolution of animal behavior (e.g., Ryan and Cummings 2013; ten Cate and Rowe 2007), and a myriad of ways that such a bias might be accomplished across perceptual systems (Stevens 2013). Once perception of a stimulus is possible, both selective attention and sampling behavior, the tendency to encounter stimuli and the experiences which lead to forming associations can affect what is learned (e.g., Knudsen 2007; Snell-Rood and Steck 2015). Within nonassociative learning, we can predict that biological prepared learning may be enhanced through greater sensitization and more difficult to habituate to. Within classic associative learning, two relevant paradigms address how biological preparedness may enable certain associations to become learned over others. The first is that when multiple stimuli are present as the animal learns, the more salient stimulus can overshadow potential learning of another stimulus. The second is that a prior exposure to a salient stimulus can then block the learning of any future presentations of a different stimulus. Both overshadowing and blocking occur frequently in studies, and are a predicted consequence of preparedness (e.g., LoLordo 1979). Prepared learning should also be resistant to extinction: being persistent in performing a learned response in the absence of the original reinforcement (like a reward or a shock). We can also predict that biologically prepared learning should be forgotten less quickly. Work in both psychology and behavioral ecology predict that more important information should be remembered for a longer period of time; forgetting will be adaptive for certain stimuli and experiences (e.g., Dunlap et al. 2009; Ferrari et al. 2012; Kraemer and Golding 1997).

## Predicting Preparedness

The majority of work to date on preparedness in learning has focused on post hoc explanations of observations or of patterns uncovered in behavioral experiments. There are exceptions to this. For instance, Domjan et al. (2004) hypothesized differences between arbitrary and ecologically relevant stimuli in sexual conditioning contexts. While predictions of preparedness in terms of fear conditioning and phobias have been made, empirical results can be mixed. A primary problem has been the lack of predictive models. The first general theoretical model on how preparedness can evolve focuses on the reliabilities of stimuli that can be learned about (Dunlap and Stephens 2014). Building upon earlier models of the evolution of learning broadly (e.g., Dunlap and Stephens 2009; Stephens 1991), reliability is set as a contingent probability of a given cue accurately predicting an outcome. Because statistical properties of change are both measureable and empirically tractable, this allows for direct tests of when prepared learning will evolve. And, indeed, using the techniques of experimental evolution, it is possible to evolve prepared learning about some modalities of stimuli over others, directly testing this theory; Dunlap and Stephens showed exactly this with fruit flies, evolving flies that learned about color better than odor, and other flies that learned about odor better than color, matching the predictions of the model. By making predictions from reliabilities of stimulus-outcome contingencies, preparedness can also be more directly tested within single lifespans, in addition to across generations.

## Conclusion

Notions of biological preparedness have a long history in the study of animal cognition. Preparedness has most often been invoked to explain quick learning in high-risk situations: predation, harm, potential poisoning. While it is easy to imagine the evolutionary implications of death, biological preparedness can equally apply toward appetitive or sexual stimuli. Although much past work has

focused primarily on the role of selective associations in preparedness, evolution selects on outcomes and not mechanisms and biological preparedness in learning can be accomplished through a number of mechanisms, both associative and nonassociative. The evolution of biological preparedness can be predicted through an analysis of patterns of reliability of relevant stimuli, thus providing a guide for empirical work rather than a reliance on post hoc explanations.

## Cross-References

- ▶ [Adaptedness of Behavior](#)
- ▶ [Associative Learning](#)
- ▶ [Avoidance](#)
- ▶ [Blocking](#)
- ▶ [Classical Conditioning](#)
- ▶ [Cognitive Bias](#)
- ▶ [Constraints on Learning](#)
- ▶ [Contrapreparedness](#)
- ▶ [Domain Specificity](#)
- ▶ [Extinction in Learning](#)
- ▶ [Fear Response](#)
- ▶ [Habituation](#)
- ▶ [Innate Behaviors](#)
- ▶ [Innate Releasing Mechanism](#)
- ▶ [Instinct](#)
- ▶ [Learning](#)
- ▶ [Motivation](#)
- ▶ [Naturalistic Stimuli](#)
- ▶ [Operant Conditioning](#)
- ▶ [Overshadowing](#)
- ▶ [Sensitization](#)
- ▶ [Taste Aversions](#)
- ▶ [Unconditioned Response](#)
- ▶ [Unconditioned Stimulus](#)

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animals to time reproductive activities such that offspring will be born during seasons of food abundance. White-tailed deer mating season takes place in autumn with the resulting fawn being born during the spring months when food supplies are becoming more abundant for these herbivorous animals. Some animals exhibit changes in predation behaviors according to lunar cycles. Nocturnal predators increase activity levels during the full moon (high nocturnal light levels) compared to new moon (low nocturnal light levels) to facilitate predation, while prey species exhibit the opposite behavioral pattern to avoid predation (Nelson 2011). The temporal variation in behaviors, such as mating and predation, presumably reflects temporal variation in the physiological processes governing the behaviors; the relationship between temporal variation in behaviors and physiological processes is the basis of biological rhythms. **Biological rhythms** are recurring events within an organism that take place at generally regular intervals (Kalmus 1935). Biological rhythms are a characteristic shared by many organisms, even single-celled life forms (Takahashi 1991). Biological rhythms work by way of biological clocks to not only govern the timing of activities such as mating, foraging, and sleeping, but they also govern internal physiological processes such as hormone secretion. Understanding how biological clocks receive, evaluate, and integrate environmental information to control physiology is of great importance, because chronic disturbances of circadian rhythmicity have been linked to pathological states.

## Biological Rhythms

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### Introduction

Organisms have evolved to time activities, such as feeding, drinking, sleeping, locomotion, and mating, to specific temporal niches. Timing specific activities may confer an evolutionary advantage to organisms. For instance, it is advantageous for

### Biological Rhythms Are Maintained by Biological Clocks

Biological rhythms are composed of several key components, including a period, frequency, amplitude, and phase. The **period** is defined as length of time for one complete cycle of the biological rhythm. The **frequency** of a biological rhythm quantifies the number of biological rhythm cycles per unit time. **Amplitude** refers to the amount of change above or below the average biological function. A **phase** of a biological



rhythm refers to some point in the rhythm to an objective time point during the cycle. For instance, diurnal animals' (active during day) phase of onset of activity corresponds to the onset of light. **Phase-shifts** occur when an animal adjusts to alternative timing of environmental cues. If environmental cues are phase-shifted (e.g., if lights are turned off 6 h later), a laboratory-kept hamster will adjust activity timing to the temporal shift of environmental cues (Nelson 2011). Humans experience a similar phase-shift incident when traveling to different time zones (jet lag). A biological rhythm may overlap with or influence other biological rhythms. For example, human body temperature oscillates around a set point established by the hypothalamus. Studies have shown that when humans enter the sleep portion of the sleep-wake cycle, they also enter a low temperature phase of a temperature rhythm (Nelson 2011).

Biological rhythms are maintained by the use of **biological clocks**. In the instance of biological rhythms running over a 24-h period of time (circadian rhythms), there are often multiple input pathways feeding into the clock that work to **entrain** the clock and keep it synchronized to stimuli from the environment (Bear et al. 2016).

#### Input Pathway → Biological Clock → Output Pathway

The inputs/cues that govern such biological rhythms are called **zeitgebers**, from the German meaning "time giver." Light, dark, and temperature are examples of common zeitgebers. Temperature serves as a primary zeitgeber for poikilothermic (body temperature varies considerably) animals and may serve as a secondary zeitgeber for mammals and birds. Light acts as a primary zeitgeber for homeothermic (constant body temperature) animals. Other zeitgebers have also been proposed. Rabbits, which live in dark burrows, may possess unique zeitgebers governing anticipatory behaviors displayed by rabbit pups. Rabbit pups exhibit anticipatory behaviors (independent of light stimuli) of the mother returning to the burrow at regular

intervals (Jilge 1993). In this case, the precise zeitgeber is not known, but it could be a nutritional, hormonal, or social zeitgeber (Nelson 2011). Some mammals utilize maternal hormones as a first zeitgeber, while other adult animals use food/water availability, social contact, or noise-quiet cycles as zeitgebers (Wollnik 1989). The process of synchronizing endogenous biological rhythms to zeitgebers is called **entrainment**. Once entrained, an animal will still exhibit the biological rhythm in the absence of the zeitgeber, but the rhythm is "approximated." For instance, the circadian rhythm utilizes light as a zeitgeber. The circadian rhythm is entrained at 24 h when environment cues (light/dark) are present. If a subject is placed in isolation (constant light or dark environment), the circadian rhythm is still present but approximated at 22–26 h (Palmer et al. 1976). Biological rhythms not synchronized to environmental cues are called **free-running rhythms** (Nelson 2011). Free-running rhythms occur if an animal is kept in constant conditions in the absence of zeitgebers. Humans have a free-running circadian period of 24.5–25.5 h, while mice have a 23-h free-running period and hamsters are close to 24 h (Bear et al. 2016). If subjects are housed together in the absence of zeitgebers, there will be variation among individuals in the precise duration of the free-running rhythm, suggesting the subjects' biological rhythms are not synchronized to other members of the isolated experimental group. Rather, the rhythm is internally generated and maintained on an individual basis. Some zeitgebers have a modulatory effect on biological rhythms, such that the degree of intensity of the zeitgeber significantly influences the biological rhythm. Minor food restriction (leading to 15% of body weight loss) of Sprague-Dawley rats minimally disrupted the female estrous cycle. The estrous cycle persisted, but the rats exhibited attenuated lordosis behaviors (Tropp and Markus 2001). Major food restriction (leading to 50% of body weight loss) of Sprague-Dawley rats significantly delayed sexual maturation of females pups (Merry and Holehan 1979) and induced anestrus in mature female rats (Knuth and Friesen 1983).



## Exogenous and Endogenous Rhythms

For hundreds of years, biological rhythms were thought to be **exogenous biological rhythms**, or those rhythms generated by the presence of geophysical cues. The works of French astronomer and chronobiologist Jean-Jacques d'Ortous de Mairan challenged the notion that biological rhythms could only be ascribed to external factors. De Mairan observed that the tension-relaxation of a mimosa plant, which leaves open during the day and close at night, continued even when the plant was kept in darkness for days (De Mairan 1729). De Mairan did not immediately ascribe his findings to an internal clock mechanism, however. More than a century later, Swiss botanist Augustin de Candolle observed similar behavior in the mimosa plant kept in constant light conditions and noted that the leaf opening and closing cycle ran over a 22 h period of time, demonstrating a free-running biological rhythm (Coleman 1986). Over the course of the next 200 years, observations similar to De Mairan's were reported; yet, it was not until the twentieth century that scientists slowly began to accept the presence of **endogenous biological rhythms**. **Endogenous biological rhythms** involve internal timekeeping of physiological processes within an animal, meaning the rhythm is generated within the organism in the absence of environmental cues. In technical terms, endogenous rhythms are similar to active systems in which oscillations are internally generated as long as an energy supply is maintained (Aschoff 1981). Endogenous rhythms are genetically controlled; several "clock" genes have been discovered in neurons and peripheral tissues, meaning that body cells can independently generate rhythms (Bear et al. 2016). Although most biological rhythms are now thought to be endogenous, many rhythms are entrained and influenced by various zeitgebers (Reinberg and Ashkenazi 2003).

## Main Types of Biological Rhythms

There are four types of biological rhythms coupled to geophysical cues. **Circadian**,

**circatidal**, **circalunar**, and **circannual** (where the prefix "circa-" comes from the Latin root meaning "about") biological rhythms are coupled to cues from an organism's environment. **Circatidal** biological rhythms are those influenced by the tides. Marine animals often possess biological clocks governed by the ebb and flow of the high and low tides every ~12.4 h. During tidal changes, there will be corresponding changes in pressure and/or salinity which may serve as zeitgebers. The fiddler crab (*Uca pugnax*) emerges from sea-side burrows at low tide to forage and mate (Palmer 1990). Green shore crabs (*Carcinus maenas*) remain hidden until high tide to forage and mate. Interestingly, when the crabs are removed from their environments and kept in constant conditions, the Fiddler crab still exhibits heightened locomotor activity at the expected time of low tide and quiescence at high tide, at nearly 12.4 h intervals (Palmer 1990). Palmer (1990) reports that there is a 2–3% deviation from the expected 12.4 h cycle. Similarly, the green shore crab has heightened activity levels at expected time of high tide and diminished activity levels at expected time of low tide, every 12.4 h (Reid and Naylor 1990).

**Circannual rhythms** are those governed by the seasons of the year, with the entrained period length being 365.25 days. In many animals, circannual clocks are synchronized with the external environment by photoperiod (length of day), light intensity, or temperature. Many migratory birds and mammals possess circannual rhythms. When kept in constant laboratory conditions, birds showed weight gain, reproductive competence, and restlessness associated with the pre-migration time period (Gwinner 1986). The dependence of a given bird species upon seasonal cues can vary. Equatorial birds, for example, have a relatively low dependence upon photoperiod, while non-equatorial birds' circannual rhythms show a close correlation with seasonal changes and photoperiod (Wikelski et al. 2008). Many mammals exhibit circannual rhythms. Ground squirrels show annual cycles of weight gain and reproductive competence; if the temperature and food supply are sufficiently low, the squirrels will also hibernate. Yet, ground squirrels vary quite a

bit in the periodicity of circannual rhythms. They commonly range between 229 and 445 days (Davis 1976). Sheep exhibit reproductive quiescence in response to a long photoperiod ( $>13$  h), but gonadal reactivation occurs during short photoperiods ( $<12$  h). Hamsters exhibit the opposite reproductive response to photoperiod changes, with reproductive quiescence taking place during short photoperiods and gonadal reactivation during long photoperiods. The reproductive quiescence in hamsters will only persist for 18 weeks regardless of photoperiod duration (Wollnik 1989). In general, species with a “breeding season” time reproductive activities according to specific circannual rhythms.

**Circalunar rhythms** are governed by the 29.5-day lunar cycle and are mainly utilized by marine invertebrates. These rhythms may be entrained by nocturnal light levels, where the full moon represents a time of increased nocturnal light. Bristle worms (*Platynereis dumerilii*) possess a circalunar rhythm to regulate reproductive activities. Bristle worms live in large populations, and they will collectively transform into heteronereis (sexual phase) in concert with the arrival of the full moon. This allows bristle worm to coordinate mating activities and improve odds of successful mating. Such a synchronization may give the animals an evolutionary advantage by improving odds of reproductive success (Zantke et al. 2013). Ant lions (*Myrmeleon obscurus*) are predatory insects which build extensive pits in order to catch prey. The ant lions build larger pits during the full moon than new moon. When ant lions are laboratory-kept in constant conditions, ant lions still build larger pits during the full moon (Youthed and Moran 1969). Youthed and Moran (1969) also noted that ant lions are most active 4 h after moonrise (solar-day rhythm) and proposed that the pit-building behavior represents the interaction of a solar-day and circadian rhythm. This evidence suggests that organisms likely possess multiple types of biological clocks.

**Circadian rhythms** are the most widely studied and best understood of all biological rhythms. Circadian, from the Latin roots *circa* (about) and *diem* (day), rhythms are those relying upon a 24-h light/dark cycle, with light serving as a zeitgeber

(Bear et al. 2016). Many animals regulate their activities (i.e., feeding, mating) and internal physiological processes (i.e., hormone secretion) over a 24-h time period. Animals are often classified according to when their highest activity levels occur relative to the day-night cycle. **Diurnal** animals (e.g., ground squirrels, many primates, chickens) are active during the day, while **nocturnal** animals (e.g., raccoons, owls, hamsters) are active at night. **Crepuscular** animals (e.g., deer, rabbits) are active at dawn and dusk, while **catheimeral** animals (some lemurs and howler monkeys) exhibit irregular activity at any time of night or day (Engqvist and Richard 1991). The majority of mammals are classified as nocturnal. A study showed that of 2,966 species of non-threatened mammals, 70% were nocturnal, 19% were diurnal, 9% were catheimeral, and 2% were crepuscular (Bennie et al. 2014).

In mammals, the circadian rhythm is thought to be entrained by input to the suprachiasmatic nucleus (SCN) of the hypothalamus, which projects to the pineal gland. In vertebrates, light enters the eyes and stimulates specialized photoreceptors within the retina. The axons of retinal ganglion cells form the retino-hypothalamic tract which projects from the retina and synapses on the dendrites of SCN neurons (Kandel 2013). Several studies point to the SCN as the predominant circadian oscillator. First, bilateral lesion of the SCN eliminated circadian-controlled behaviors and physiology (Nelson 2011). Second, destruction of the SCN and retino-hypothalamic tract in golden hamster eliminated or modified entrainment to night-day cycles. The hamsters exhibited free-running light cycles and exhibited abnormal circadian rhythms for drinking and activity (Rusak 1977). Third, transplantation of SCN tissue into a recipient caused the recipient's circadian rhythm to match that of the donor (Lehman et al. 1987). Fourth, each cell in the SCN is autonomous and generates its own specific circadian rhythm (Hastings et al. 2003). SCN neurons also exhibit light sensitivity, with broad receptive fields exhibiting high sensitivity to light intensity, as opposed to motion or orientation (Bear et al. 2016). Remarkably, the SCN neurons are able to generate circadian rhythms in the absence of

action potentials. Communication between cells in the SCN is poorly understood, but generation of the circadian rhythm is not dependent upon action potentials or chemical synaptic transmission (Bear et al. 2016; Kandel 2013). “Clock genes” are likely responsible for the circadian behavior of the SCN neurons (Bear et al. 2016). The SCN has output pathways to other nuclei within the hypothalamus, the midbrain, and the pineal gland. The SCN is not the circadian oscillator for all animals. In birds, the pineal gland serves as both a photoreceptor and circadian oscillator. Removing the pineal gland from these animals leads to disruption of circadian rhythms (Takahashi et al. 1989). Individual cells also possess a circadian clock that is active when isolated from the body and grown in culture. The cells’ circadian rhythms are not expressed *in vivo*, as the cell is then under the control of the SCN clock. The SCN exerts its influence on cells of the body largely by way of the autonomic nervous system (Bear et al. 2016). The autonomic nervous system’s central regulation network includes other hypothalamic nuclei (see “Vaso-vagal stimulation” entry) that receive innervation from the SCN.

In humans, circadian rhythms likely play a role in mood regulation. Clock genes are localized to neurons of the ventral tegmental area, amygdala, nucleus accumbens, and prefrontal cortex – structures of the brain’s reward system. Additionally, dopamine is a neurotransmitter of the brain’s reward pathways whose levels oscillate on a circadian basis within the nucleus accumbens. Many studies demonstrate that dopamine neurotransmission is diminished in major depression (Dunlop and Nemeroff 2007). If the attenuated dopamine neurotransmission is due to circadian arrhythmia, therapies targeted at re-synchronizing the clock may be effective. Some evidence suggests this may be the case. Sleep deprivation has been shown to improve depressive symptoms in 40–60% of patients. Similarly, bright light therapy and lithium are other effective treatments for depression. Each of these therapies evokes changes in circadian rhythm (Albrecht 2013).

Some biological rhythms have no known geophysical cue. **Ultradian rhythms** are those shorter than circadian rhythms (but higher frequency),

while **infradian rhythms** are those longer than circadian rhythms (but lower frequency). However, ultradian and infradian rhythms do not have specific geophysical cues, unlike circadian, circatidal, circalunar, and circannual rhythms. The rapid eye movement (REM) sleep cycle, lasting approximately 90 minutes, is an example of an ultradian rhythm. Hormone secretion patterns, such as those for corticosterone and Luteinizing Hormone, also follow ultradian rhythms (Wollnik 1989). Ultradian rhythms are repeated over the course of a day. Like ultradian rhythms, infradian rhythms do not have specific geophysical cues. The female estrous cycle, which lasts for 4 to 5 days in rats and hamsters, is an example of an infradian rhythm (Nelson 2011). All biological rhythms, whether they rely upon geophysical cues or not, are important for the appropriate timing of behaviors and physiological processes to meet the needs of an organism.

## Cross-References

- Biological Clocks
- Circadian Rhythms
- Day/Night Cycle
- Diurnality
- Endocrine System
- Endogenous Oscillations
- Estrous
- Free-Running Cycle
- Homeostasis
- Hypothalamus
- Internal Clocks
- Light/Dark Cycle
- Nervous System
- Neuron
- Neurotransmitters
- Photoperiod
- Vaso-Vagal Stimulation

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## Biological Time

### ► Lifetime Expectancy

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## Biologically Significant Stimuli

### ► Naturalistic Stimuli

## Biomass

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## Synonyms

Biological material derived from living or recently living organisms; Total mass of living matter

## Definition

Biomass is the renewable organic material obtained from agricultural product, animal, and municipal wastes and can be used as a source of fuel or energy.

Biomass is an organic matter produced directly or indirectly by living organisms and probably the largest energy source after the sun. The biomass in plant matter is produced by the process of photosynthesis in which carbon dioxide and water from the environment are converted into carbohydrates (sugars, starches, cellulose and lignin) by using energy from sunlight. Lignocellulosic biomass have been recognized as a potential sustainable source of mixed sugars for fermentation to biofuels and other biological products of industrial importance. Several technologies have been developed during the past that allow this conversion process to occur, and the clear objective now is to make this process cost-competitive in today's markets (Himmel et al. 2007). Biomass feedstocks that can be used as a potential source of energy include agricultural crop residues, forestry residues, algae, wood processing residues, municipal waste, agro-industrial wastes, sorted municipal solid waste, etc.

Due to increasing demand of energy resources and overexploitation of fossil fuels that impacts on the global warming, the use of renewable energy resources is becoming necessary for sustainable growth. Most common form of renewable energy is the biomass and widely used as alternative

energy resources in the worldwide in the recent few decades. Significant attention has been focused on identifying suitable and efficient biomass sources that can conveniently provide high and efficient energy outputs so that the conventional fossil fuel energy sources may be replaced. The type of biomass required is largely determined by the energy conversion process potentialities and the form in which the energy is required (McKendry 2002). However, energy can be produced by biomass, using various biological, physical, and chemical processes. Conversion of complex biomass to biogas has been of great interest to the scientific community in recent years. Several recent studies have been conducted to understand the anaerobic digestion process and to characterize responsible microbes for the possible biochemical conversions (Azman et al. 2015).

The complete reliance on fossil fuels is recognized as unsustainable throughout the world. Due to emission of significant quantities of greenhouse gases associated with fossil fuel exploration and combustion, rapid declining of fossil fuel reserves is observed in various countries. Algal biofuels also called third-generation biofuels appear to be promising in supplementing sustainable and complementary energy resource. Algae-based biomass can be converted into various biofuel products, such as hydrogen, biodiesel, bioethanol, as well as biogas through different processes such as biochemical and thermochemical processes. Thermochemical conversion process is considered as efficient and economical in comparison to existing problems associated with biochemical conversion such as higher reaction time, low conversion efficiency by microbes and enzymes, as well as high production costs (Raheem et al. 2015).

The dual application of microalgae for phycoremediation and biomass production for sustainable biofuel production is a feasible option. Microalgae as an environmentally friendly renewable feedstock can be processed into biofuels via various conversion technologies such as algal lipid upgrading, liquefaction, pyrolysis, gasification, and bioethanol technology. As a unique chemical reaction, pyrolysis of microalgae yields useful chemicals like light olefins, alkanes, and



syngas, as well as the bio-oils with less oxygen, more hydrocarbons, and higher gross heating values than the bio-oils derived from cellulosic biomass (Rawat et al. 2011). Designing novel catalysts and optimizing culture conditions for the growth of algae and the selective conversion of microalgae into fine chemicals may increase the effective use of microalgae and the economics of the process. Due to the advancement of scientific innovations and technology catalytic pyrolysis, technology has the potential to process microalgae into biofuels as well as some other industrially important fine chemicals (Yang et al. 2019).

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## Biomonitor

### ► Indicator Species

## Biorhythm

### ► Biological Clocks

## Biosociology

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Like its better known cousin sociobiology, introduced by entomologist E.O. Wilson in 1975 (Wilson 1975), *biosociology* refers to the modern study of biology as it relates through an evolutionary framework to social behavior. Sociobiology has many detractors who argue that it revives biological determinism, sexism, racism, and social Darwinism. Some prefer the term “biosociology” because it avoids the negative connotations of sociobiology and has importantly different slants on theory and research methodology.

When it was formulated and popularized, sociobiology presented issues uncomfortable to modern students of human behavior. It focused on *ultimate* causes of human nature, ignoring *proximate* mechanisms through which behavior directly operates. An example is the sociobiological theory of sex differences in mating strategy. Males produce offspring with an ejaculation; females invest a long period of pregnancy and nursing. So males maximize genetic fitness (i.e., the representation of their genes in succeeding generations) by spreading their genes among many females, whereas females are selective, limited their pregnancies to the finest available males, preferably those committed to child support. Emphasis is on evolution through the distant past, ignoring those recent influences of psychology and culture, the explanatory currency of the social sciences. Ultimate theory cannot explain why one culture is polygamous, another monogamous, why marriages in some societies are arranged by parents and in others by romantic attraction, and why divorce and birth rates vary over time and place.

Some of sociobiology’s claims defy common observation. Most social scientists do not maximize their genetic fitness, instead limiting their children to two or less, and some “waste” resources by adopting unrelated infants.



Entomologist Wilson likened human homosexuals to sterile ant workers that maximize fitness not with their own offspring but by nurturing the fitness of siblings.

An offshoot of sociobiology, called “evolutionary psychology,” fixed some of these issues. Its leaders, themselves students of human behavior, were interested in a reformulation that avoids implausible statements about people. Their most important innovation was to reintroduce proximate causation in the form of an “adapted” brain. Social scientists of the 1960s thought of the brain as John Locke’s blank slate, upon which a particular culture and language were written during a period of socialization. Evolutionary psychology endowed the brain with innately specialized mechanisms for parenting, emotional communication, kinship, mate choice, sex, aggression, danger avoidance, mate guarding, childcare, and so on (Barkow et al. 1992). Most notable is the Chomskyan mechanism for language, present before birth though requiring a period of learning to accommodate any particular language.

Evolutionary psychologists emphasized that our minds have evolved, not our disembodied behaviors: evolution produced the mind, and the mind produces behavior. This is a clever modification of sociobiology’s exclusive focus on ultimate causes. With a language-speaking mind as a proximate mechanism, one can incorporate learning, socialization, and cultural differences – all notions that are important to social science but excluded from sociobiology.

The adapted mind eliminates the unacceptable tenet that humans maximize inclusive fitness. Instead our actions are explained by the calculations of these minds, which balance, say, a diabetic’s primitive urge to eat sweets with her physician’s advice to abstain. Married couples, whom sociobiologists required to have as many children as possible, are allowed by evolutionary psychologists to weigh their reproductive urges against the costs of a college education or the demands of a two-career family. The male mind still desires sex with many women, but the penis may be held in check by moral strictures or caution about venereal disease or fear of discovery by

a wife. The female brain still seeks long-term commitment from a dominant male, but actual behavior may depend as well on availability of birth control pills and a desire for even temporary closeness and sexual pleasure.

Evolutionary psychology, having solved some of sociobiology’s inadequacies, went on to produce some of its own. Its adapted mind is a postulate; its various modules are conceptualizations without empirical verification.

Perhaps, too, evolutionary psychology focuses too narrowly on humans, ignoring our primate cousins, who seem to share with humans a broad primate model of behavior. Consider, for example, the theory of male and female mating strategies, which should apply to apes as well as humans. Male gorillas and orangutans seek multiple mates, while females are usually limited to a single male, consistent with the theory. But gibbons and siamangs are monogamous. Among chimpanzees, both sexes mate with multiple partners. Among bonobos, females freely seek sexual relations with males and other females. Thus the hypothesized sex difference is not apparent in most apes nor in those most closely related to humans, the chimpanzees, casting doubt on the theory’s underlying reasoning.

Despite its shortcomings, by introducing a thinking mind that is capable of being influenced, evolutionary psychology took a long stride toward reconciling natural selection with sociology, at the same time eliminating implausible claims from sociobiology. But the ideological divide between sociology and natural selection remains wide. Social Darwinism in its various incarnations has too strong a taint, trying to justify why some people are inferior to others.

Biosociology avoids speculations about ultimate causes conjectured about the unknowable past. Its focus is on proximate causes, for example, the neurohormonal mechanisms underlying human behavior. Biosociology emphasizes that human behavior follows a primate pattern and therefore values comparative studies of other primate species, whereas analogs with insects, birds, and fish are too distant to be useful (Mazur 2005, 2007). Biosociology’s research methods are diverse but usually have a tight link to theory.

Biosocial hypotheses should be falsifiable by practical empirical means.

Few sociologists have requisite training in biology, so most relevant research is conducted in neighboring disciplines including social psychology, primatology, anthropology, genetics, and behavioral economics. Primatology has had the greatest impact, leaving no doubt that human behavior in face-to-face groups fits the general pattern of higher primates – with the supremely important addition of language-based cultures. The hormones testosterone and cortisol have become important variables in biosocial studies of dominance in face-to-face groups and of antisocial behavior (e.g., Carré et al. 2013). Currently there is much interest in a “dual-hormone” hypothesis whereby testosterone and cortisol jointly regulate social dominance (Mehta et al. 2010). Brain imaging techniques are showing how different areas of the brain respond to social engagement (Lieberman 2013). Behavioral genetics demonstrates that some personality traits, long thought to be determined by early childhood socialization, are strongly inherited and highly correlated in identical twins raised apart. Population geneticists, tracing specific variants of the Y chromosome in men and mitochondrial DNA in women, infer the migratory paths of major ancestral groups of *Homo sapiens* during the past 50,000 years (Wells 2006). This sampling of findings barely suggests the potential of biology to revise our understanding of human social behavior.

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## Biosonar

- [Echolocation](#)

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## Biotype

- [Genotype](#)

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## Biparental Care

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## Definition

Biparental care is when offspring is cared for by both the male and the female parent.

## Introduction

Parental care is any form of behavior or resources provided by a parent that enhances the fitness of its offspring and that evolved (and is currently maintained) for this function. Parental care may include behavioral traits, such as incubation, food provisioning, or protection against predators, but it may also include nonbehavioral traits, such as gestation or viviparity. Many forms of parental care are costly for the parents, i.e., decreased parental survival and/or future reproduction. For example, female common eiders (*Somateria mollissima*) incubate continuously in the harsh Arctic until the eggs hatch, and she does not

even leave the nest for foraging, therefore fasting throughout the incubation period, with serious physiological and life-history consequences. Even if not that dramatic, subtler forms of parental care are also costly. For example, increasing the brood size by two nestlings in kestrels (*Falco tinnunculus*) results in an increase in metabolic activity and a reduction of parental survival. The benefits of parental care are shared between the parents (both gain fitness benefits from the increased survival of the common offspring), but these costs affect the parents individually, therefore there is an almost inevitable conflict over parental care, where each parent prefers the other to have the greater share of the work.

### Evolutionary of Sex Roles and Biparental Care

The resolution of this conflict often results in uniparental care (i.e., when only one parent cares for the offspring), and typically the female is the sex that provides more care. These conventional sex roles were corroborated by large-scale phylogenetic comparative analyses (Janicke et al. 2016). Angus John Bateman (1948) discovered that in the fruit fly (*Drosophila melanogaster*) reproductive success is more variable in males than in females and showed that reproductive success increases sharply with the number of mates in males, whereas this effect is less evident in females. He argued that the reason behind this observation is that eggs are more expensive to produce than sperms, therefore the limiting factor for the lifetime reproductive success will be different for the sexes: for females, it is resources that they can convert into eggs, while in males it is access to females. Based on these ideas Robert Trivers (1972) formulated the concept of parental investment that incorporates the costs associated with parental care and defined it as any form of behavior towards an individual offspring that increases the offspring's survival (and hence reproductive success) at the cost of the parents' ability to invest in other current or future offspring. Parental investment theory explains the evolution of sex roles and predicts that if one sex has considerably higher parental investment than the other, then member of the

former, less investing sex (typically males) will compete for the members of the other sex (typically females). Parental investment theory therefore also explains the exceptions from the conventional sex roles, e.g., in the case of phalaropes (*Phalaropus* sp.) that show so-called sex-role reversal, where females are bigger and more colorful than males, compete extensively for males who in turn provide all parental care for the offspring. Recent work, however, has shown that the direction of causality can act in the opposite way, where the sex that experiences stronger sexual selection during mating will be selected to provide less parental care (Kokko and Jennions 2008). Mating and parental care systems therefore evolve together.

Phylogenetic predisposition also has a major role in the evolution of parental care. For example, while biparental care is the norm in birds (90% of species), it is rare in mammals (5% of all species) and biparental care is generally rare in invertebrates. This discrepancy may reflect the differences in how different taxa raise their young. Invertebrates can often do little to efficiently protect their offspring, or they are selected to compensate the high rates of offspring mortality with the production of large amount of eggs. While in mammals only females lactate, in birds both males and females can efficiently provision and guard the chicks. Therefore, the sexual asymmetries in the ability of providing care are important drivers of parental care systems, but sexual conflict over parental care also promotes the evolution of sex differences in care and the ability to care.

### Evolutionary Alternatives: Remating Opportunities

Even when both parents are equally likely to provide care for the young, sexual conflict over care may arise from differing mating opportunities. When one parent has much better probabilities to find another mate than its partner, then this sex will be selected to desert the current brood and reproduce with another partner. In birds, for example, precocial species, where one parent is more likely to raise the young alone, and the sexes are often equally successful in doing so, both

males and females respond to increased mating opportunities by altering their level of care. Altricial birds, however, where the young need more provisioning, do not show these relationships (Olson et al. 2008). In cases where sexual conflict over care is intense and both sexes have good remating opportunities, the deserted parent may also decide to leave. For example, in the Penduline tit (*Remiz pendulinus*), a Eurasian passerine, during egg laying either the male or the female can desert the brood and only the other parent will incubate and raise the young. However, 30% of the eggs are deserted by both parents.

### Optimal Parental Investment in Biparental Care

In many cases, however, parents do cooperate in raising the young, but there is also conflict about how much care to provide. Several theoretical models have been proposed to predict how conflict over parental care may be resolved. These models differ in their assumptions regarding behavioral strategies available to parents and consequently the predictions they offer when a parent increases or decreases parental care. The first type of model is the “sealed-bid model” (Houston and Davies 1985) which assumes that optimal parental effort by each sex will be achieved through evolutionary time, where each parent uses a fixed level of effort given its partner’s effort. Later models extended this framework to allow for a behavioral negotiation between the parents. These “negotiation models” predict that when one parent decreases its effort, the other parent is predicted to compensate by increasing their own effort, but this compensation has to be incomplete for this model to be evolutionarily stable (McNamara et al. 2003). A third type of model, the “information model” (Johnstone and Hinde 2006) is built upon the negotiation models by assuming that when parents have only incomplete information about the brood value and need, they use their mate’s parental effort as a cue in determining the level of parental care needed to optimize reproductive success. This model may predict different outcomes (compensation or matching response, i.e., when one partner’s decrease or increase in parental care is mirrored by a similar

change from its partner) depending on the information about brood value and need available for the parents. Finally, in the “perfect family” model (Akçay and Roughgarden 2009) parents are assumed to be able to communicate directly to coordinate their parental efforts. This model predicts a matching response when one parent increases its parental effort.

### Division of Labor

Sexual conflict can be reduced and biparental care can be stable if parents use division of labor and specialize in different parental roles. For example, one of the rare examples of invertebrate biparental care also shows division of labor between the sexes. Males of *Parastizopus armaticeps*, a nocturnal desert dwelling beetle, dig, guard and extend a special breeding burrow, while the female is foraging on the surface for limited food sources which she brings back to the burrow for the developing larvae (Rasa 1998).

### Conclusion

Taken together, biparental care is affected by the combination of phylogenetic, ecological, and demographic factors. In general, biparental care is selected for in species where both parents are able to increase the offspring’s survival in an efficient way, when ecological conditions allow for and development of the offspring require both parents to care, and when the fitness benefits of parental care outweigh the fitness gained by increased survival or reproductive success by desertion. Even when biparental care is stable, sexual conflict may shape the amount of parental care provided, and when sexual conflict is intense, offspring may be better off with a single parent.

### Cross-References

- [Bateman Gradient](#)
- [Life History](#)
- [Parental Investment](#)
- [Sexual Selection](#)

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## Bipedalism

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## Definition

A type of walking and running gait in which the two hind limbs support the entire body weight.

Bipedalism involves an erect (nonsprawling) posture and a striding (sequenced between right and left) footfall pattern. Bipedalism is used by birds, fast running reptiles, primates, and, in its obligate form, humans and our fossil hominin ancestors.

## Bipedalism: An Unusual Locomotor Form

In George Orwell's *Animal Farm*, the revolutionary animals who overthrew their human masters famously wrote out a sign that said “Four legs good, two legs bad.” They had identified the singular defining character that separated them from their oppressors. They were right: bipedalism defines our species and the large group of fossil human ancestors that we call hominins.

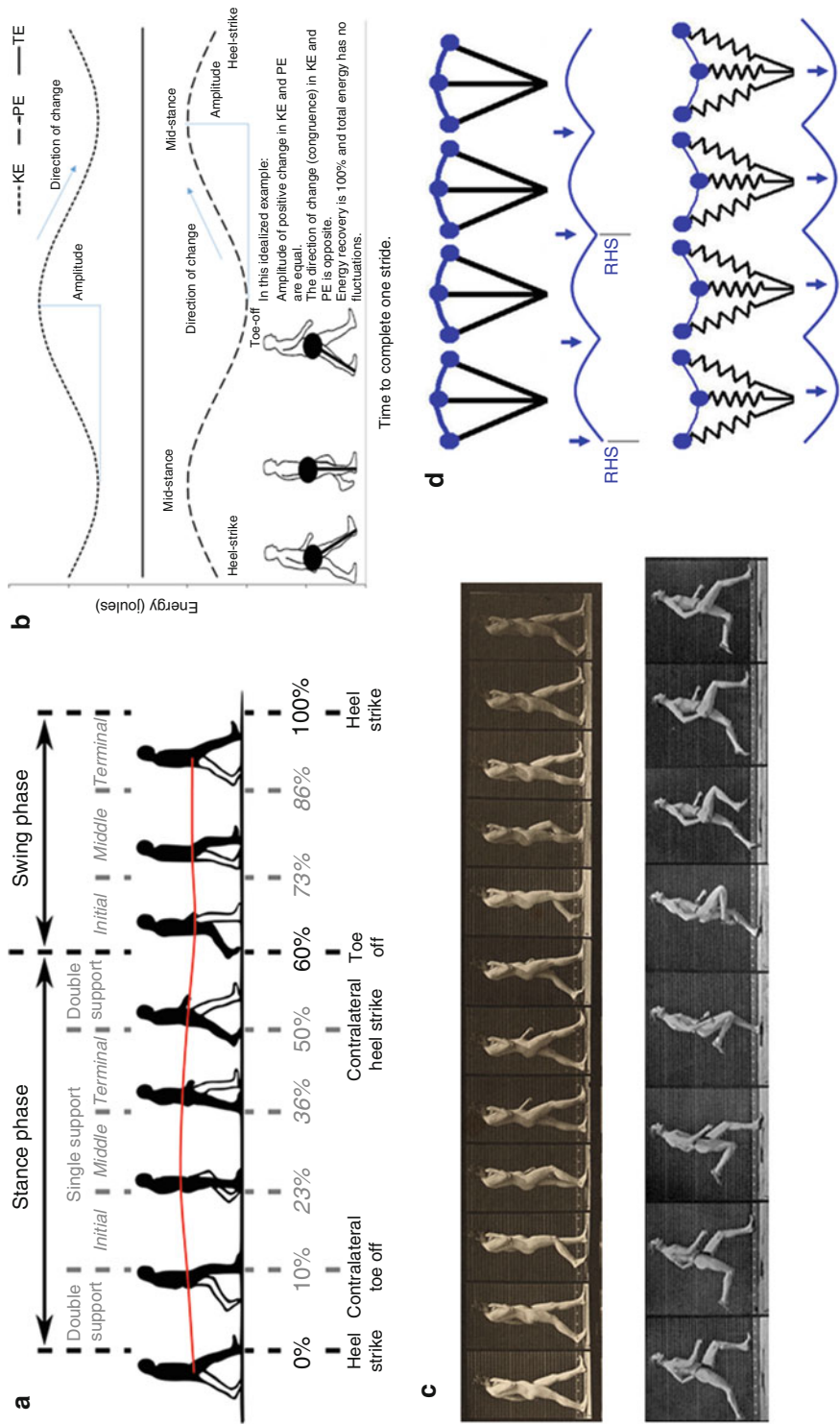
Defining bipedalism seems like an easy task at first. Humans (and birds) use two legs for walking (a gait in which there is always at least one foot on the ground and footfalls alternate between right and left sides) and running (footfalls alternate but there is an aerial phase with no feet on the ground). This unusual gait evolved in our human lineage over a period of at least 6 million years, perhaps from an ancestor that practiced a slightly different, non-obligate (facultative) form of bipedalism (see Schmitt 2003 for a review).

Bipedal walking and anatomy take time to develop in each of us as well. During childhood we develop specialized anatomy and motor control to execute this gait. Its fully adult form doesn't emerge until 9 years of age (Sutherland et al. 1980), going through many stages prior to that. So to precisely define this gait and its associated anatomical and neurological features, we need to look at its biomechanics, evolution, development, and the ways in which human bipedalism compares to that of other animals, especially other primates.

## Bipedalism in Modern Humans and Other Primates

During walking and running, humans use an upright posture in which the lower limbs are held in line beneath an erect upper body rather than sprawling to the side (Fig. 1a, b). We also use





Bipedalism, Fig. 1 (continued)



a striding gait that involves a sequenced pattern of footfalls: putting one foot in front of the other, as opposed to hopping or bounding as in kangaroos. At the beginning of stance phase (Fig. 1a, b), the hip is flexed, and the knee is extended (a pattern different from that of primate quadrupeds where the knee is relatively flexed at foot contact) with the lower limb out in front of the body. The ankle is dorsiflexed (foot at or less than  $90^\circ$  relative to the leg) when the heel makes initial contact with the ground at heel strike. It is worth noting that heel strike is a pattern not seen in all primates; it is present only in large-bodied apes (Schmitt and Larson 1995). Humans walk with relatively stiff legs, in which the hip sweeps a wide arc over a knee that flexes only slightly, and the ankle remains dorsiflexed through midstance. The ankle becomes plantarflexed (foot to leg angle that is larger than  $90^\circ$ ) at the end of stance phase so that toe-off occurs as body weight is pushed forward off the big toe (hallux) (Fig. 1a, b). Thus, the center of pressure (the anchor point of ground reaction forces) follows a proximal to distal and lateral to medial “rollover” beneath the foot from the heel to the big toe.

Modern human walking is considerably more efficient than that of any other bipedal primate and many quadrupeds (see Sockol et al. 2007; Demes and O'Neill 2013). By walking with stiff and extended legs, humans “vault” over each support leg successively, and our center of mass (COM) follows a cyclical rising and falling path from heel strike to toe-off. This “inverted

pendulum” style of movement efficiently recycles potential and kinetic energy during each stride, reducing muscular effort considerably (Fig. 1a–d) (Schmitt 2010). Although 65% of the energy needed for forward progress is recovered through this exchange process, additional muscular work is required (Cavagna et al. 1977). That additional energy needed to move forward is provided by plantarflexion of the ankle, made possible by the loading of the entire foot from heel strike to the powerful hallucial toe-off, during which the foot shifts from a role as shock absorber and energy absorber (see Griffin et al. 2015) to a stiff lever.

During running, in contrast, the knees flex deeply during the middle of the foot contact phase, causing the COM to descend in such a fashion that its movement mimics a bouncing ball (Fig. 1b, d) and, at high speeds, there is sometimes no heel strike (Hatala et al. 2013). There is no pendular energy exchange in running, though some energy is stored and returned in the ligaments of the foot (see Griffin et al. 2015). In a slightly different mechanical perspective, some have argued that the cost of locomotion is dictated by changes in direction of the COM from generally downward to generally upward, a pattern that occurs in both walking and running using a spring-loaded pendular model (Bertram 2016) (Fig. 1d). The costs of these redirections (often called collisions) is mitigated by the number of collisions, the number of feet involved in the collisions (two during a walk, one during a run),

**Bipedalism, Fig. 1** The mechanics of an adult human bipedal walking stride. (a) Stance phase begins as the limb (in black) makes initial contact with the ground at heel strike. At heel strike, the contralateral limb (in white) is still on the ground, so this portion of stance phase is called double support. At heel strike, the knee is very extended, the ankle is dorsiflexed, and the center of mass (COM, red line) is low. The knee flexes slightly to absorb impact forces as the contralateral limb toes off (10% of stride duration). At midstance (23% of stride duration), the knee is fully extended, the foot is flat on the ground, and the COM is high. Following midstance, the knee begins to flex, and the heel elevates as the ankle plantarflexes in preparation for a powerful hallucial toe-off, at which time the COM is low again. Following toe-off, the hip and knee

flex, and the ankle dorsiflexes so that the toes clear the ground as the limb swings during swing phase. Swing phase, and one complete stride, ends when the heel strikes a second time. (Image modified from Mummolo et al. 2013). (b) The rise and fall of the COM allows for efficient exchange of potential energy (large dash line) and kinetic energy (small-dash line), reducing the fluctuations of the total energy of the COM and reducing muscular work. (Images from Queen et al. 2016). (c) Walking and running differ in leg stiffness, with running showing deep knee flexion in stance phase. (Images from Muybridge 1955). (d) The COM in running behaves more like a bouncing ball compared to the inverted pendulum pattern of walking and does not facilitate exchange of potential and kinetic energy  
RHS = Right Heel Strike.

and path-matching of the COM velocity and substrate reaction forces that lead to pseudoelastic collisions.

## Bipedalism in Other Primates

Other primates can use bipedal gaits on the ground and in the trees. Almost all primates can stand easily on two legs, and many walk upright with sequenced footfalls when needed. But those primates that move bipedally do so in an occasional (facultative) way rather than in an obligate way as is the case for humans. Unlike humans, all nonhuman primates adopt deeply flexed hip postures and deeply yielding knee joints during bipedal walking and, to the extent that they can be said to do so, running (see Schmitt 2003 for a review). Thus, in walking and running in nonhuman primate bipeds, the COM is often flat or follows an arc downward between touch down and midstance and then upward again so that the COM and leg follow the path of a spring mass system or bouncing ball, as in human running. However, some chimpanzees and many macaques with long-term training in bipedalism adopt relatively stiff gaits (see O'Neill et al. 2018 for a review).

The contexts in which nonhuman primate bipedalism occurs vary across species and are sometimes the result of anatomical restrictions that preclude the use of quadrupedalism. Gibbons, with their exceptionally long arms, do not have a quadrupedal gait and must use bipedalism when moving on top of large branches or on the ground. Sifaka, highly specialized leaping lemurs from Madagascar, face the opposite problem – long lower limbs but short upper limbs with large hands – and can only rarely walk quadrupedally (Wunderlich and Schaum 2007). So when they are on the ground, they walk – or, more commonly, hop – bipedally with a sequence of footfalls that has been described as a “bipedal gallop” (Wunderlich and Schaum 2007). COM patterns of sifaka bipedal running gaits are similar to those of human gaits, but the COM during their walking gaits follows a flattened path, and they use deep knee yield during stance. South American capuchin monkeys that walk on the

ground bipedally when carrying tools also have gaits that approach, from a mechanical perspective, that of humans, though with some clear distinctions (see Demes and O'Neill 2013). During walking, capuchins show a bent-hip and bent-knee gait with a COM trajectory with its lowest point at midstance, and, as with other primates, they lack a powerful hallucial toe-off (see Demes 2011 for a review). Nor do capuchin monkeys recover energy from COM fluctuations, a pattern also seen in chimps and that is in contrast to that of humans (Demes and O'Neill 2013; Kimura 1996).

## Anatomical Features Associated with Obligate Bipedalism and Their Evolution

Nonhuman primates that use facultative bipedal gaits show limited musculoskeletal adaptations for bipedal motion, with their skeletal adaptations reflecting their primary locomotor behavior. But humans, with their commitment to bipedalism, have undergone a fundamental reorganization of the musculoskeletal system that reflects a complex compromise between varied and competing selective pressures (see Aiello and Dean 2002 for an overview). Here we concentrate on lower limb features, particularly those that were subject to interlocking and potentially conflicting demands of thermoregulation, and, in the case of the pelvis, obstetrics.

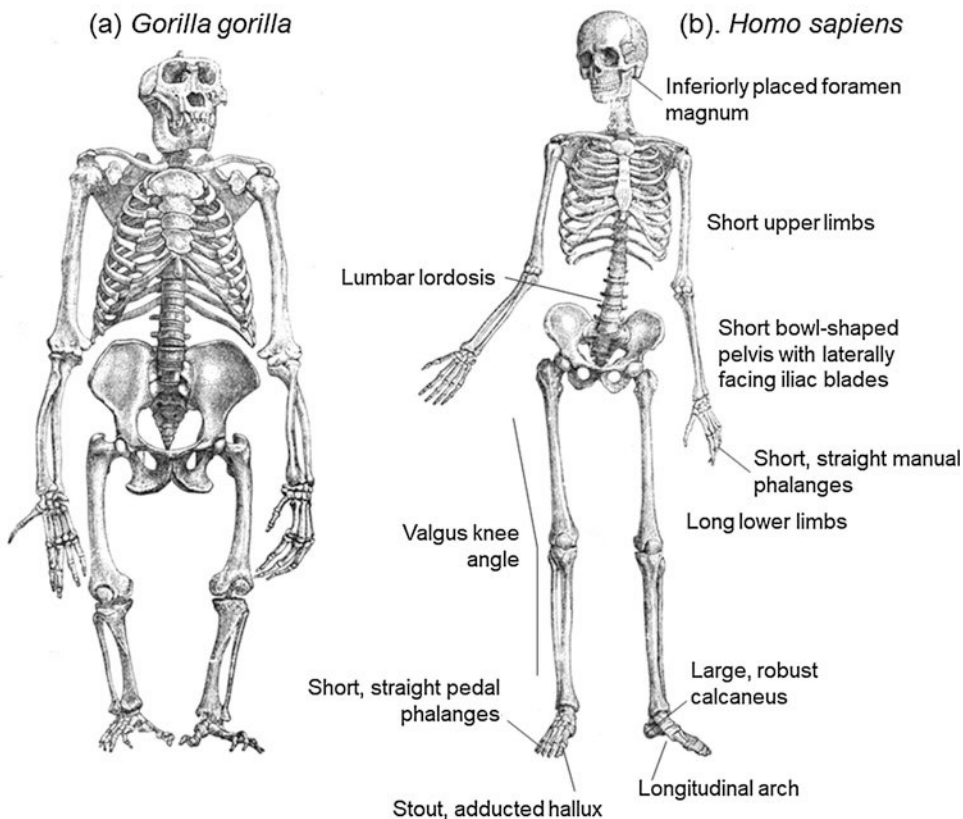
Hominin adaptations to obligate terrestrial bipedalism evolved in a mosaic fashion, evident by 4.4 million years ago (mya; Lovejoy et al. 2009a) but possibly beginning as early as 6 mya. Based on current fossil evidence, the pelvis was among the first structures to be altered for bipedalism (Lovejoy et al. 2009b). A major feature of the human pelvis that allows efficient bipedal walking is the reorientation of the iliac blades to face sideways, instead of backwards as in apes, resulting in a bowl-shaped pelvis. The human configuration allows the lesser gluteal muscles, which run from the outside of the iliac blades to the top of the femur, to efficiently balance the pelvis and upper body over a single support leg during locomotion. The orientation of the iliac

blades in humans also permits rotation of the pelvis counter to the rotation of the thorax during locomotion and thus allows the pelvis to contribute to a long stride length (Inman et al. 1981; Rak 1991; Gruss et al. 2017). Chimpanzees, in contrast, limit counterrotation of the pelvis and thorax and walk with a swaying gait and/or with their upper limbs to the side for balance (see O'Neill et al. 2018). The human pelvis has also been shortened from top to bottom compared to that of apes, which further improves our balance in upright stance (Fig. 3a–d).

Although these changes in the hominin pelvis facilitated obligate bipedal locomotion, they decreased the size of the birth canal (Gruss and Schmitt 2015). This is unlikely to have been an issue in early hominins, with their small-brained babies, but causes well-known difficulties with

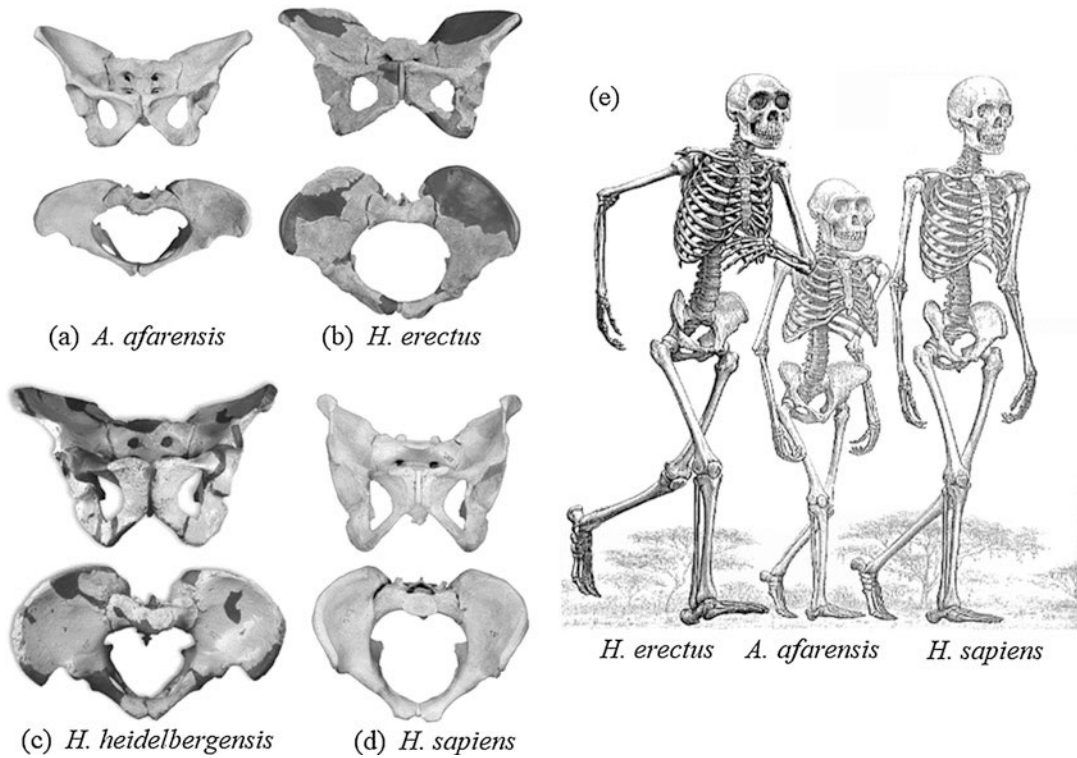
childbirth in modern and probably fossil *Homo*. Early hominins may have compensated somewhat by maintaining a relatively broad pelvis (both the birth canal and the distance between the iliac blades), a morphology seen in australopiths as well as premodern *Homo* (Fig. 3). It was long assumed in paleoanthropology that a wide pelvis would have been detrimental to locomotor efficiency, but recent experimental studies have shown that greater pelvic breadth actually provides energetic advantages in bipedal walking, particularly while carrying infants (Wall-Scheffler and Myers 2017).

Humans have long lower limbs relative to apes (Fig. 2), and this contributes greatly to the energetic efficiency of our bipedal walking and running by increasing stride length. Longer strides allow us to travel a given distance using fewer



**Bipedalism, Fig. 2** Skeletal features associated with obligate bipedalism. (a) Gorilla placed in an upright posture. (b) Modern human demonstrating anatomical features

that evolved in association with bipedalism. (Modified from public domain images on Wikimedia)



**Bipedalism, Fig. 3** Fossil hominin and modern human pelvic shape. Reconstructed pelvises of (a) *Australopithecus afarensis*, (b) *Homo erectus*, (c) *Homo heidelbergensis*, and (d) a modern human pelvis. (e) Reconstructed bipedal

locomotor posture of *Australopithecus afarensis*, *Homo erectus*, and a modern human. (Image modified from Gruss and Schmitt 2015)

steps, minimizing the number of costly collisions associated with changing the trajectory of the center of mass. Elongated lower limbs were not present in the earliest hominins. Essentially modern limb proportions evolved in *Homo erectus*, just after 2 mya, along with a number of other traits of the feet including short toes and a robust arch that may be adaptations for long-distance walking and running (Holowka and Lieberman 2018) (Fig. 3e)

The femur and tibia in humans and other hominins are also adapted for upright stance and bipedal locomotion (see Stern and Susman 1983; Lovejoy et al. 2009a, b). Compared to quadrupedal primates, hominins have larger joint surfaces in the hip and knee for bearing the weight of the entire upper body, and the femoral and tibial shafts, in addition to being longer, are more robust. The femur slants inward down from the

hip toward the knee (the *bicondylar angle* of the femur), meeting the tibia at an angle when viewed from the front. This configuration of the joint is known as the *valgus knee* (Fig. 2b). In other primates, the femur and tibia are much more parallel. The human bicondylar angle positions the knee and foot more directly under the body's center of mass, acting with the lesser gluteal muscles to improve balance during single-legged stance (Aiello and Dean 2002). In modern humans, the valgus knee develops during childhood only with habitual bipedal walking; in children who cannot walk, the typical bicondylar angle is not present (Tardieu and Trinkaus 1994). The knee is not well represented in the hominin fossil record before the Plio-Pleistocene, but a humanlike bicondylar angle of the femur is clearly evident among australopiths (Stern and Susman 1983).

The human foot has been reorganized from a mobile and grasping appendage like that of other primates to a non-grasping rigid lever (see Holowka and Lieberman 2018, for a recent review). Although humans are not the only primates to use a heel strike (chimpanzees, gorillas, and orangutans have also been observed to use a form of heel strike; Schmitt and Larson 1995), our large heel bone (calcaneus), with its associated cushioning fat pad, is thought to be adapted to withstand high impact forces associated with a bipedal heel strike. The human foot is unique in having transverse and medial longitudinal arches. The longitudinal arch is supported by ligaments (spring and other plantar ligaments) and a plantar aponeurosis running from the calcaneus to the base of the phalanges (toes). The plantar aponeurosis is stretched to store energy when the Achilles tendon pulls on the calcaneus to raise the heel following midstance, which raises the medial longitudinal arch and causes the bones of the midfoot to come in close contact with each other (essentially locking the midfoot and transforming the foot into a rigid lever). This mechanical configuration is known as the windlass mechanism (Griffin et al. 2015). Compared to other primates, humans have relatively short toes and a robust hallux that is in line with the foot and the other toes (adducted). An adducted hallux precludes grasping with the foot but allows for a powerful hallucial toe-off during human bipedal walking.

## Development of Bipedalism

The mechanics of human bipedal locomotion mature gradually (see Sutherland et al. 1980 for a review). Many infants crawl before passing through an assisted bipedalism stage in which the hands are used to help the infant balance (referred to as “cruising”). Independent walking without the aid of the hands begins around 1 year of age. At the onset of walking, there is co-activation of the calf and shin muscles (tibialis anterior, soleus, and gastrocnemius) during walking, preventing ankle dorsiflexion at the end of swing phase (Myklebust 1990). Young walkers

thus lack a true heel strike and the foot touches down with either a flat foot (plantigrade) contact or with the forefoot (toe-walking). In flat foot contact steps, the center of pressure is most often located anterior to the calcaneus at touchdown. Weight is distributed across the entire plantar surface of the foot including the medial foot pads, reducing pressure loads and shear forces acting on any one segment of the foot. Plantigrady increases the area of the base of support beneath the foot and, along with a relatively wide stance, allows for a high degree of stability. This is likely an important feature in toddlers, who lack balance control following small perturbations.

By the end of the first year of independent walking, peak pressures increase beneath the hindfoot at the beginning of stance, decrease beneath the midfoot, and increase beneath the forefoot at the end of stance. Lateral to medial rollover of the center of pressure throughout stance phase is present although a longitudinal arch is still absent until 4–6 years of age (Bertsch et al. 2004). Single limb stance phase in toddlers is very short, a phenomenon Sutherland et al. (1980) attribute to an inability to control the ankle plantar flexors (gastrocnemius and soleus) at less than 2 years of age. Around the beginning of the second year of independent walking, the ankle is dorsiflexed during swing phase and mature control of the ankle dorsiflexors (primarily tibialis anterior) and plantar flexors allows for an initial heel contact. By 2 years of age, the ankle plantar flexors are finally used in preparation for a distinct toe-off. The remaining suite of gait parameters that are indicative of mature human bipedalism (including an extended knee in the support leg at midstance, a flexed knee and dorsiflexed ankle in the swing leg during swing phase, and reciprocal arm swinging throughout the gait cycle) continues to mature until around 9 years of age.

## Why Bipedalism Evolved

The selective factors that drove the evolution of obligate human bipedalism (and for that



matter bipedalism in other lineages like birds and dinosaurs) remain an area of discussion and contention. As is often the case, natural selection forced adaptive trade-offs as bipedalism evolved. Bipedalism is in many ways less stable than quadrupedalism, but it may enhance maneuverability, frees the hands, can be practiced very efficiently, and may provide some thermoregulatory benefit. But many of these advantages accrue even when bipedalism is used occasionally by animals who are primarily adapted to quadrupedal locomotion. For example, as discussed above, bipedalism allows some primates (e.g., gibbons and sifakas) to move about effectively on the ground when their adaptations for arboreal locomotion preclude terrestrial quadrupedalism. In other cases, facultative bipedalism facilitates load carriage, vigilance, or sexual and aggressive displays (e.g., capuchins and great apes) (see Fleagle 2013 for a review).

So why give up quadrupedalism to become obligate terrestrial bipeds, instead of using bipedalism on an as-needed basis as so many living primates do? There is still no clear answer to this question (see Fleagle 2013, for a complete review), although many theories have been proposed. The most common and enduring idea is that bipedalism evolved in human ancestors to free the hands for carrying infants, food, or water, to gather food, or to use tools or weapons. Alternatively, bipedalism may have evolved to help early hominins see over tall grass or travel more efficiently between food trees, especially in an increasingly open habitat. Bipedal walking may have limited sun exposure (compared to quadrupedalism), and thus afforded early hominins a thermoregulatory advantage. But all of the above may be served by facultative bipedalism. Still others argue that, like gibbons, bipedalism was what was available to long-armed hominin ancestors when they walked on the ground, due to anatomical constraints (Stern 1975). There remains no definitive answer to this interesting question.

## Conclusions

Upright striding bipedalism is a specialized form of gait seen, among mammals, only in primates. It reaches its most specialized and obligate form in humans, who use it for efficient terrestrial walking and running. Bipedalism first appeared in the human lineage several million years ago and evolved to its modern form through a number of unique stages. Modern human bipedalism develops during the first 9 years of life, is associated with anatomical (pelvic shape, limb length, large calcaneus and hallux) and mechanical (heel strike, toe-off) specializations, and is characterized by a stiff walking mechanism that exchanges potential and kinetic energy to promote efficiency and a compliant running form. In other primates that use terrestrial bipedalism, walking and running are both compliant and inefficient, there is no hallux toe-off and often no heel strike, and skeletal adaptations like those of humans are lacking. Such gaits in nonhuman primates are used only when they must be, as in gibbons and sifaka who have no quadrupedal gait, or when carrying an object, surveying an area, or displaying.

## Cross-References

- [Adaptation](#)
- [Catarrhine Locomotion](#)
- [Catarrhine Morphology](#)
- [Gait](#)
- [Hominid](#)
- [Hominoidea Locomotion](#)
- [Hominoidea Morphology](#)
- [Homo erectus](#)
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- [Locomotion](#)
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- [Ontogeny](#)
- [Platyrrhine Locomotion](#)
- [Primate Locomotion](#)
- [Prosimian Locomotion](#)
- [Prosimian Morphology](#)



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## Bird Migrations

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### Definition

Seasonal outward and return movement of populations between regions where resources and conditions are alternately favorable and unfavorable.

### Introduction

The word *migration* recalls the images of heroic movements of large populations over vast distances. Blackpoll warblers (*Setophaga striata*) during fall migration converge on the Eastern coast of the United States and Canada before embarking on remarkable overwater flights across the Atlantic Ocean to the Caribbean or South America, a nonstop journey of up to 2,400 km or more over the course of 3 days, before reaching wintering grounds in Venezuela or Colombia. Migration here is defined as a seasonal to-and-fro movement of populations between regions where conditions are alternately favorable and unfavorable. Migrating birds can fly great distances, visiting many unique landscapes, and thus face many ecological problems which can be solved either through natural selection shaping innate behavioral programs or through cognitive processes. Although some aspects of migratory behavior are genetically predetermined such as initial departure time, direction, and distance, every migrating bird embarks on a journey that is unique, and therefore exploration, experience, and learning necessarily play a fundamental role in

overcoming the challenges of migration. Migration is a complex behavior that offers a rich study system for evolutionary biologists, as it involves countless morphological and physiological adaptations for efficient movement, behavioral adaptations for optimal use of environmental factors such as winds and sensory cues for orientation, and cognitive adaptations for map learning, long-term memory, and social interaction (Åkesson and Hedenström 2007).

### Performance (Speed and Distance)

The highly physical and energetically costly nature of movement lends itself to optimality analyses. The use of optimality perspectives in analyzing behavioral adaptations and strategies has become an essential aspect of understanding bird migration (Alerstam 2011). If migration is viewed as a conflict between (re-)fueling and movement toward a goal location, then the overall speed of migration can be determined by three variables: the rate of energy accumulation, flight speed, and rate of energy consumption during flight (Åkesson and Hedenström 2007). Fueling between migratory events is an important determinant of migration performance. The rate of fuel accumulation partially determines the overall migration speed. One might, therefore, expect adaptations which maximize both food intake and its conversion into fuel stores, such as fat, which contains the most energy per unit of mass compared to alternatives. Migratory birds are required to locate and ingest food, break it down, absorb it, and create and transport fat bodies to specialized fat deposits. These processes require special adaptations, which among others include flexible organs that grow and shrink in relation to the requirements of fueling and movement. During fueling, migratory birds have been shown to ingest and process food close to their metabolic capacity. To do so, migratory birds grow a larger intestine, gizzard, and liver to boost their food processing capacity, and grow larger flight muscles to lift and transport increasing fuel loads (McWilliams et al. 2004).

Quickly reaching a migratory goal naturally also depends upon flight speed. The sum of the

different power components (parasitic, induced, and profile power, along with the basal metabolic rate), which constrain powered flight, results in a U-shaped curve which relates power (energy consumed per unit time) and speed (Pennycuik 1975). From the power performance curve, two flight speeds of special interest can be calculated: (1) the optimal flight speed for minimizing energy costs ( $V_{mp}$  or minimum power) per unit of time (i.e., to keep flying for as much time as possible on a given energy reserve, irrespective of the distance covered); and (2) the optimal flight speed for minimizing the energy costs per unit of distance covered (i.e., the speed associated with the minimum ratio of power to velocity,  $V_{mr}$  or maximum range) found by drawing a tangent from the origin to the power curve.  $V_{mr}$  allows birds to fly the maximum distance on a given fuel reserve (Pennycuik 1975).

Temperature, air density, and oxygen concentration all decline with increasing altitude, which can have dramatic effects on a bird's flight aerodynamics, respiratory efficiency, and water economy (risk of dehydration). Ascending-descending flight behavior appears to be used for sampling the most favorable winds throughout the air column, and the horizontal wind component is thought to be the most important factor predicting cruising altitude (Bruderer et al. 1995). Migrating birds have been regularly observed flying at altitudes up to 6000 m above ground level (agl), and some migrants such as the bar-headed goose (*Anser indicus*) regularly reach altitudes of 8000 m or more when crossing the Himalayas. When confronted with barriers such as mountain ranges, birds must either make a detour around the barrier or ascend high enough to cross the mountain peaks. Birds which rely on thermal updrafts for migration have been observed at great altitudes, such as the Ruppell's griffon vulture (*Gyps rueppellii*) observed at an altitude of 11,300 m above the Ivory Coast (Braunitzer and Hiebl 1988). High-altitude migratory species are capable of such feats because they possess several types of hemoglobin which operate side by side providing a greater respiratory capacity (oxygen affinity) at high altitudes than closely related lower altitude species. For example, four different

forms of hemoglobin have been discovered in the Ruppell's griffon vulture (Braunitzer and Hiebl 1988).

## Specialization Versus Plasticity

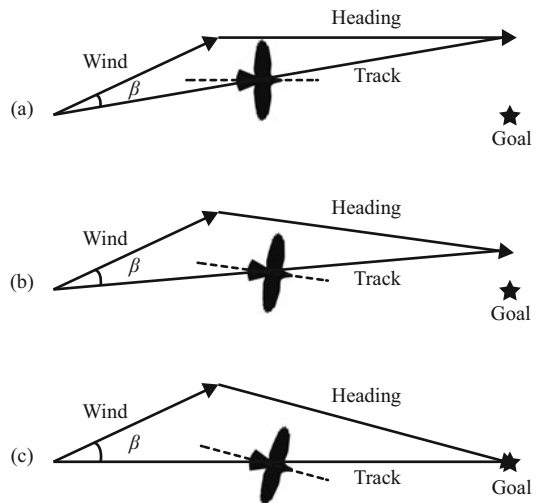
In nearly all bird species, there exists tension between ecological specialization, selecting habitats, foraging sites and food for which they are best adapted, and the ability to respond to unpredictable and novel resources. Ecological plasticity is described as the ability to adaptively respond behaviorally to variable resources in the environment. Plasticity may vary among species, individuals of the same species, and developmentally in an individual. We can assume that the transient period of migration during the annual cycle could provide the greatest challenge for a behavioral profile of dedicated ecological specialization. Stochastic events during migration may play a large role in determining the habitats that migrating birds come to occupy during stopover. Prevailing wind patterns over the Gulf of Mexico can influence the geographic position of arrival following trans-Gulf flight (Gauthreaux et al. 2006). Upon arrival decisions about stopover habitat are more influenced by physiological condition than resource cues (Buler et al. 2007). Habitats and food become more and more dissimilar the further a bird may migrate from their natal area. Stopover sites become critical during migration; the decision where to land is vital for whether sufficient resources can be found and fat reserves restored. In low-quality habitats, birds may have to leave the area completely in search of better stopover sites. Many migrating birds show consistently different habitat use and foraging preferences during the breeding and wintering periods. For example, Worm-eating warblers (*Helmitheros vermivorum*) during the breeding season forage for insects in live foliage. However, during the overwintering period throughout their Central American and Caribbean range worm-eating warblers forage on insects found in dead foliage trapped in the vegetation of the forest understory (Greenberg 1987). Greenberg's (1987) detailed observations and experiments with juveniles

have demonstrated that a complex interaction between innate habitat preference, patterns of substrate exploration, and learning play an important role in developing this seasonal foraging specialization. Similarly, foraging opportunism among *Setophaga* warblers is greatest among conifer-breeding species that winter in tropical areas. In winter, these species occupy broad-leaf habitats, and hence, necessarily employ opportunistic strategies for locating, catching, and handling a diverse array of food types. Exploring novel habitats and monitoring many diverse resources instead of a specialized few would seem likely to require unique cognitive capabilities and/or personality traits. In addition, several studies have found that migrants may use social information to gather information about the quality of habitats. For example, migrants may initially join flocks at stopover sites before foraging on their own and may use resident species as an indicator of high-quality breeding habitats. Such social interactions may support information gathering (Németh and Moore 2007).

### In Flight Decision-Making: When to Deviate from a Direct Path Toward a Migratory Goal

#### Wind and Drift

Decision-making involves determining an action given the available information about relevant environmental features integrated with past experience. One environmental feature, wind, has a very profound influence on the migratory movements of birds. Depending on the direction and strength of the wind, migrants may greatly benefit if the wind flows in the same general direction as the intended course or may be hindered during flight if the wind flows in an opposing direction (Åkesson and Hedenström 2007). In cross winds, a bird may become drifted off its intended course unless it can accurately detect and compensate for displacement. Therefore, selecting favorable winds during migration is important for optimal migration performance if “optimality” is to be achieved (Liechti and Bruderer 1998). The relationship between a migrant’s track, heading, and



**Bird Migrations, Fig. 1** The resultant velocities for three different situations (heading can also be considered air velocity and track can also be considered ground velocity): (a) full-wind drift, (b) partial drift/partial compensation, and (c) full compensation.  $\beta$  = angle between track and wind direction. Note that the body axis of the bird in the figure is aligned with the heading vector

wind direction is shown in Fig. 1. The track (movement with respect to the ground) vector is the additive sum of the heading and wind vectors. An in-flight decision of full or at least partial compensation could be achieved if a bird could perceive lateral displacement from a preferred direction. One way this could be accomplished is by monitoring fixed visual landmarks relative to a bird’s heading (Alerstam and Pettersson 1977; see also Bingman et al. 1982).

Recent studies have demonstrated that migratory birds can choose when to fly to avoid adverse wind conditions and thus improve travel speeds (McLaren et al. 2014). Successful arrival at breeding or wintering grounds depends at least in part on the ability of migrants to make time-sensitive decisions on where to orient to exploit beneficial wind patterns thus maximizing energetic efficiency. However, to expedite travel to their intended goal, migrating birds may initiate migration under nonoptimal wind conditions. During autumn migration in eastern North America, migrants in flight are often drifted laterally by crosswinds but are observed compensating for drift when near the Atlantic coast. The

tendency to compensate for wind drift along the Atlantic coast also increased through the night, while no temporal differences were observed inland. The observed behavior suggests that birds migrate in an adaptive way to conserve energy by *actively assessing* in flight the degree to which they should optimally compensate for wind drift (Horton et al. 2016). Upgrades to the United States national weather radar network to dual-polarization allows a more direct determination of migrant heading (body axis direction) and track (the resultant direction of bird movement, see Fig. 1). However, the effects of drift are difficult to quantify as differential departures of migrants with different preferred directions can occur and lead to a phenomenon known as “pseudodrift” (Evans 1966).

### Barriers

Migrating birds can store large fuel reserves and make nonstop flights of thousands of kilometers. Yet there are many cases where birds refrain from crossing barriers (like open water, deserts, or ice), which are clearly within their flight range capabilities. Why then do birds not always migrate along the most direct and shortest routes to their destinations? Many factors may influence the costs and benefits of alternative migration routes, such as drift, disorientation, predation, stopover conditions and risks of starvation, and weather, most prominently wind. Detours are found among both soaring and flapping flight birds. Large increases in the fuel stores of a bird contribute to higher total body mass, which consequently increases both parasitic and induced drag. Therefore, the relationship between fuel and flight range has a concave function, which means that birds could ultimately save energy if they migrate by short flight steps and low fuel loads rather than departing on longer flights with heavy fuel loads. This optimal fuel load configuration will promote avoidance of barriers and preference for detours if they increase the number of short flight steps travelled (Alerstam 2001). When confronted with migratory barriers or obstacles, a migrant faces a decision regarding seeking out available fuel to cross the barrier in one go, or take an alternative but longer detour around the barrier. The occurrence of directional shifts toward

a coastline during the night suggests that the disposition of migrants to cross large barriers depends in part on physical condition (Bruderer and Liechti 1998). In autumn, migrants approaching the Mediterranean Sea later in the night show a decline in motivation to cross, possibly due to lowering of fuel stores through the night and/or increasing hesitation to cross barriers of unknown extents (Fortin et al. 1999).

### Long-Term Memory

How much are decisions about suitable stopover sites influenced by prior experience? Memory of suitable stopover sites would be a great advantage for optimizing migratory routes and potentially increasing travel speeds. Banding data reveals that experienced adults typically spend a shorter period of time at a particular stopover site than inexperienced juveniles. Many migrants utilize the same stopover or wintering areas year after year (Nolan and Ketterson 1991). Such observations raise the question of whether long-distance migrants have specialized neural capabilities related to long-term memory compared to residents? In one study, migratory Garden warblers (*Sylvia borin*) and resident Sardinian warblers (*Sylvia melanocephala*) were hand-raised and subsequently allowed to explore two unfamiliar rooms during the autumn migratory period. One room contained food while the other did not. The Garden warblers remembered the room with food for at least 12 months, whereas the resident Sardinian warblers demonstrated considerably shorter long-term memory ability (Mettke-Hofmann and Gwinner 2003). Memory and experience may also influence the establishment of new migration patterns. Teitelbaum et al. (2016) demonstrated that experienced migratory whooping cranes (*Grus Americana*) could innovate new migratory routes, which once established, eventually spread to younger individuals via social learning. The presence of older individuals in a group increased the likelihood of occupying new overwintering sites, suggesting that innovative behavior often increases with age because those individuals are more experienced and thus better suited to infer adaptive solutions to novel problems.



## Navigation: Maps and Compasses

An important distinction must be made between three types navigational/homing ability as described by Griffin (1955):

1. *Type 1 or piloting.* To locate a goal by referring to familiar landmarks or landscape features, but may also entail random or systematic searches until familiar landmarks are found. For birds, landmarks are generally thought to be visual, but there is no reason why they would be limited to visual cues. Landmarks in themselves cannot provide compass or directional information, but used in conjunction with compass cues can be used to maintain directionality during oriented flight. Landmarks can also be substituted for compass orientation systems in familiar areas.
2. *Type 2 or compass orientation.* To orient in a specified compass direction without reference to landmarks when released in unfamiliar territory. This may only result in successful navigation if the compass direction leads to a goal or familiar territory. Vector navigation carried out by young birds embarking on their first migration possess inherited information about the direction and distance to population-specific wintering ranges (Berthold and Helbig 1992).
3. *Type 3 or true navigation.* True navigation allows for the determination of a specific direction toward a goal when in unfamiliar territory and in the absence of familiar landmarks or any form of sensory contact with the goal. This is often considered the most complex form of navigational ability, and it is presumed that until goal areas (e.g., breeding or wintering grounds) are established through experience no true navigation can occur.

### Compass Mechanisms

The most remarkable aspect of migration is how birds can routinely return to previous breeding and overwintering sites following migration of often thousands of kilometers. They do so using many sophisticated sensory adaptations and navigation capabilities (Alerstam et al. 2003). The

term *orient* means to determine, relative to some external cue, and keep a compass bearing, while *navigation* refers to moving from a starting location to a specific goal. To accomplish true navigation, birds are thought to use one or several compasses in conjunction with a map (Able 2001). Migratory birds have access to several compass mechanisms for orientation, using information from the sun (both the position and the pattern of skylight polarization), stars, and Earth's magnetic field.

The use of a sun compass by birds was first demonstrated by Kramer (1950). Kramer used mirrors to alter the apparent position of the sun and found that European Starlings (*Sturnus vulgaris*) altered their directional preference accordingly. The avian sun compass is based on the sun's azimuth (the angle of the sun's position projected on the horizon relative to north), with the sun's altitude being irrelevant. Because the sun appears to move across the sky during the day, the use of a sun compass requires calibration by an internal clock (circadian clock). The sun's azimuth at a particular time of day provides the directional information. By experimentally shifting the internal clock of a bird, used in the so-called clock-shift experiments, and recording directional preferences in homing pigeon or migrant orientation cage experiments, the internal clock has been shown to be important for correctly implementing the sun compass. Inexperienced birds must learn to use the sun compass; in homing pigeons, learning appears to take place after the bird is confronted with the need to home, likely spontaneously during extended exercise flights around the home loft. Moore (1987) demonstrated that the position of the setting sun functions as a source of directional information for night-migrating birds. Experimental evidence indicates that several species of migratory birds (but not all; see Wiltschko et al. 2008) are apparently able to perceive polarized light and use it as a cue for orientation. There is also evidence that information from different compass cues can be integrated. For example, researchers have provided experimental evidence that suggests that migratory Savannah Sparrows (*Passerculus sandwichensis*), Swainson's (*Catharus ustulatus*)



and Gray-checked (*C. minimus*) thrushes, and White-throated Sparrows (*Zonotrichia albicollis*) use polarized light cues at sunrise or sunset to calibrate their magnetic compass. The avian visual Wulst of the anterior forebrain and hippocampus may be involved in learning processes supported by the sun-compass in homing pigeons (Bingman and Jones 1994), though the sun compass itself is still operational after Wulst and hippocampal lesions (Bingman et al. 1984).

During the night, when the sun compass is unavailable, migrating birds may rely on information provided by other cues for orientation. In a series of classic experiments, Emlen (1967, 1969) demonstrated that indigo buntings (*Passerina cyanea*) use the stars for orientation during migration. By experimentally manipulating the location and movements of stars and constellations in a planetarium, Emlen (1967) found that buntings derived directional information from the position of constellations relative to each other and to the celestial pole, the point around which stars appear to rotate during the night. Inexperienced juvenile buntings learned the location of north by observing the rotation of constellations around the celestial pole. Star-compass orientation has been demonstrated in several species of nocturnal migrating songbirds, including Bobolinks (*Dolichonyx oryzivorus*), Savannah Sparrows (*P. sandwichensis*), European Robins (*Erithacus rubecula*), and Garden Warblers (*Sylvia borin*). Little is known about specific neural structures involved in stellar orientation other than the obvious assumption that elements of the visual system are involved. Mouritsen et al. (2016) proposed a hypothetical framework for the forebrain organization of both the sun and star celestial compasses.

The Earth's magnetic field also provides compass orientation information for migratory birds. The geomagnetic compass provides migratory birds directional information based on inclination angle and not the polarity of the field (an inclination compass; Wiltschko and Wiltschko 1995). Inclination angle or magnetic dip is the angle of Earth's geomagnetic field relative to gravity or any vertical reference. Along the magnetic equator the Earth's magnetic field runs parallel to the earth's

surface and toward the poles the angle becomes increasingly perpendicular. Observing changes in the orientation preference of European robins (*E. rubecula*) by altering the magnetic field around orientation cages by using Helmholtz coils provided the first evidence of a magnetic compass (Wiltschko 1968). To date, no studies in birds have demonstrated compass orientation derived from either total intensity or polarity of the Earth's magnetic field. Currently, the peripheral transduction mechanism used by migratory birds to gather and process information from Earth's magnetic field is under debate. Magnetic information may be detected by magnetoreceptors in the upper beak and transmitted through the ophthalmic branch of the trigeminal nerve to the brain (Mora et al. 2004). More likely, however, magnetic field direction would be sensed by special photopigments in the eyes (Ritz et al. 2000) and this geomagnetic signal would then be processed in cluster N, a specialized, night-time active forebrain region found in nocturnal migrants. European robins (*E. rubecula*) with lesions of cluster N are unable to orient to magnetic cues but can perform sun compass and star compass orientation behavior.

### Vector Navigation

Juvenile European Starlings have been shown to migrate by orienting toward a preferred direction, but not to a goal. In a classic experiment, Perdeck (1958) demonstrated that juvenile starlings displaced during fall migration from Holland to Switzerland continued southwest along their normal migratory direction ending to reach southern France. Adults, however, could compensate for their geographic displacement and reoriented northwest toward their typical wintering grounds in northern France. Migrating white-crowned sparrows (*Zonotrichia leucophrys*) were similarly displaced longitudinally across North America and only adults, but not juveniles, showed a clear goal (typical wintering area)-directed shift in orientation after displacement (Thorup et al. 2007). The presumably innate direction and distance program of first-time migrants is termed vector navigation, which is not a true navigational mechanism as no cognitive representation of a goal is defined. Only predetermined genetic

information on direction and distance is used. To gauge the distance to fly, many inexperienced migrants have been experimentally demonstrated to rely on an inherited temporal program, which specifies how long they should travel (Berthold 2003) and direction (Helbig 1991). The behavioral mechanisms, which guide inexperienced migratory birds, are a typical example of vector navigation because it is based on a simple determination of direction and distance from a starting location.

### Map-Based Navigation

Map-based navigation denotes a situation in which a bird determines its spatial position relative to a goal based solely on information available at some distant location. Based principally on homing pigeon research, fundamental differences between two theoretical representational types of map are distinguished: a mosaic map and a gradient map. The mosaic map introduced by Papi (1976) is formed from the learned spatial relationships among landscape features (for Papi, those landscape features would be odor patches) and their relative arrangement with respect to a goal. These relationships are presumed to be learned as a bird explores increasingly larger areas of its home range. Although this type of map may be useful over distances ranging perhaps a few hundred kms, for example, some large visual landmarks may be seen at great distance or remote olfactory patches can be coded as being a certain direction from a goal by winds, a mosaic map would be of little use after a displacement far removed from an animal's local experience. Mosaic maps are often considered equivalent to the so-called cognitive maps, but it is unclear whether this is correct. O'Keefe and Nadel (1978) refer to cognitive maps as a mental representation in which spatial relationships among spaces are coded with respect to not only position and direction but also distance. Thus, an animal possessing a cognitive map should be capable of inferring novel shortcuts between any two points on the map. But there is evidence suggesting that homing pigeons are capable of navigating between two such points within their range. Blaser et al. (2013) released food deprived and

satiated pigeons from an unfamiliar site, equidistant between a known food site and home loft. The pigeons knew their geographic position relative to the familiar targets and chose a flight direction reflective of their motivational state.

More discussed as a hypothetical model of map-based navigation relevant at migratory-bird spatial scales are so-called gradient maps (Wallraff 2005), which are thought to be based on at least two gradients of any physical substrate, e.g., atmospheric odors or the earth's magnetic field, which may vary systematically over large spatial scales. Utilizing a bi-coordinate gradient map, birds would learn how navigational cues change in some parameter across their familiar, experienced space. If a gradient parameter varies predictably beyond the familiar experienced space, a displaced bird could obtain an estimate of its position relative to a goal by implementing a neural algorithm comparing remembered values of stimulus at home with the measured values at the displacement site/current location.

### Kramer's Map and Compass Model

Kramer (1953) outlined what came to be called the "map and compass" model of homing pigeon navigation, which in principle would generalize to migratory birds. Kramer's conceptual framework for understanding bird navigation remains the central explanatory paradigm in the field. He described navigation as a two-step process. In the first step, a displaced individual estimates its position in space relative to a goal, such as "I am west of the goal." This step yields the direction to the goal as a bearing. In the second step, a compass mechanism is employed to identify the actual geographic direction of the goal-directed bearing, e.g., "That way is east." The map and compass model has three defining characteristics: (1) a two-component process dependent upon a position-fixing system (map) and an independent compass mechanism; (2) the positioning system computes a bearing toward a goal; and (3) a biological compass is used to identify the direction of this goal-oriented bearing. For homing pigeons, the sun compass identifies the goal direction, and countless clock-shift experiments have been performed as demonstration. Importantly, those

same clock-shift experiments also revealed that the map component remained intact, providing evidence that the position-finding component is independent of the compass component.

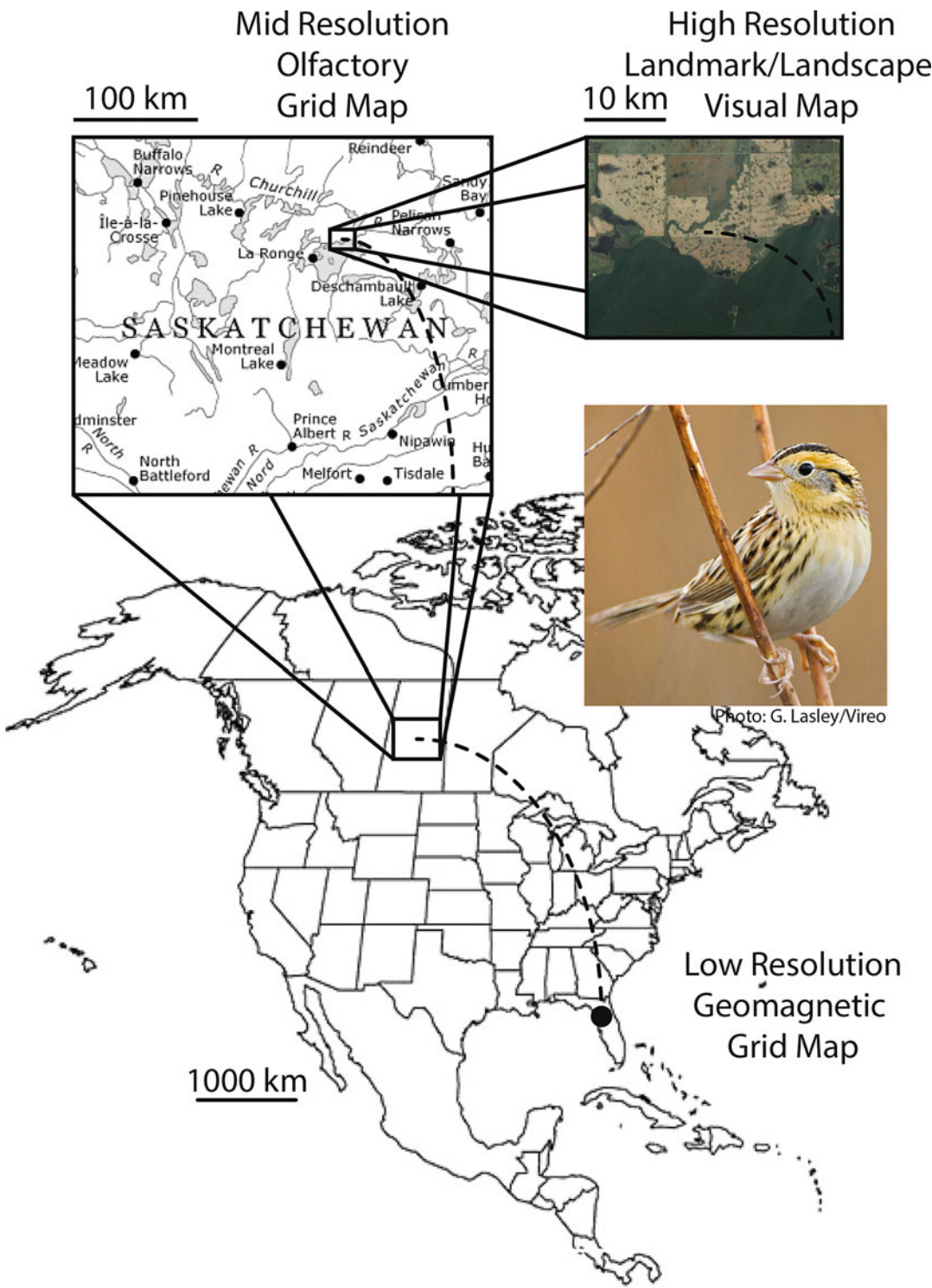
Bingman and Cheng (2005) described a hypothetical sequential model of migratory bird navigation which consisted of three phases each supported by three separate, hypothetical map mechanisms. Using a Le Conte's sparrow (*Ammodramus leconteii*) as an example of a nocturnal songbird migrant, a hypothetical spring migration from *wintering* grounds in Florida, USA, to breeding grounds in Saskatchewan, Canada, could be described (Fig. 2). At a global scale, an experienced nocturnal migrant may first use a low-resolution global gradient map, perhaps based on the Earth's magnetic field, to roughly determine its position relative to its goal location in Saskatchewan. A higher spatial resolution but shorter range olfactory gradient map of atmospheric odors could then guide the migrant in areas within a few hundred kilometers from the goal similar to the navigation of homing pigeons. Finally, an even higher spatial resolution but shorter range visual landmark or landscape map, operating within tens of kilometers from the intended goal, may help guide the final approach. The model is designed such that each "map" need only serve to provide enough spatial information to bring the migrant to within the "catchment" area of the next phase map.

## Brain Architecture

Evolution of a sedentary or migratory phenotype, and the associated evolutionary adaptations for coping with or escaping the challenges of highly seasonal environments, are known to correlate with changes in brain organization (Fuchs et al. 2014). Species which migrate longer distances typically have smaller brains than closely related sedentary species. Brain size may be energetically constrained by low food availability, developmentally constrained by short breeding seasons or restricted by bill adaptations, which can limit braincase volume. Small brain size may lead to migratory behavior which compensates for low

behavioral flexibility or vice versa. Although generally larger brain volumes are observed in sedentary compared to long-distance migratory birds, long-distance migrants are observed to possibly have relatively larger dorsal pallial regions (hyperpallium) and hippocampus (Fuchs et al. 2014). The avian pallium tends to be relatively large, comprising ~75% of the telencephalic volume. The question arises as to whether the observed differences in brain organization can be explained by differences in developmental constraints or differences in behavioral adaptations. One possible explanation for smaller brains in long-distance migrants may be a consequence of a restricted developmental window available to juveniles. Comparisons of hatching date and onset of migratory restlessness in stone-chats (*Saxicola* sp.) clearly shows shorter time available for maturation in the longer-distance migrant populations (Helm et al. 2005). These observations may account for differences in overall brain size, but cannot explain the sparing of the hyperpallium and hippocampus from volume reduction in migratory species. One functional explanation is that the hyperpallium is characterized by a visual area, which receives a strong input from the thalamus. A larger hyperpallium may correlate with high visual acuity as observed in mammalian visual cortex. Possible specialized functions such as visual control of the sun-compass and retinal-mediated, geomagnetic sensitivity hosted by the avian hyperpallium could be advantageous in migratory behavior (Bingman and Cheng 2005).

The homology between the avian hippocampal formation and the mammalian hippocampus encourages the hypothesis that the avian hippocampus plays a fundamental role in navigation by migratory birds. The hippocampal formation of migratory species tends to be relatively larger compared to closely related sedentary species (Fuchs et al. 2014). For example, a larger and more microglial dense hippocampal formation was observed in a shorebird species that migrates over a visually complex landscape compared to another shorebird species that migrates over water (Diniz et al. 2016). The growing body of evidence which correlates hippocampus morphology to migratory behavior supports the hypothesis that



**Bird Migrations, Fig. 2** Hypothetical migration map of a Le Conte's sparrow (*Ammodramus leconteii*) using a phase model of global-navigational mechanisms operating at different spatial scales and resolutions. For illustrative

purposes, an experienced nocturnal migrant begins its spring migration at *wintering* grounds in Florida, USA, and journeys to breeding grounds in Saskatchewan, Canada (See Bingman and Cheng 2005)

the hippocampal formation houses some specialized spatial representational mechanism(s), which supports navigation during migration. Notable however, there is little evidence that the hippocampus is necessary for the operation of the sun compass in both homing pigeons and migratory savannah sparrows (*P. sandwichensis*; Bingman et al. 1999). Lesions of the hippocampal formation in homing pigeons results in an impaired ability to use familiar landmarks or landscape features for navigation including the carrying out of corrective re-orientations following displacement (Gagliardo et al. 2001). Based on the homing pigeon data it is reasonable to assume that migratory birds similarly rely on the hippocampal formation when navigating a familiar, local space (See Fig. 2). The sparing (or even relatively larger) of hippocampus size reduction in migratory birds may be at least partially explained by having to hold multiple representations of local spaces (breeding, stop-over, and overwintering sites).

## Conclusions

Migratory birds are confronted with a variety of challenges, each requiring unique physiological, behavioral, and cognitive adaptations. Even mundane problems, such as selection of flight speed, are affected by several factors operating simultaneously. The seemingly routine migration of birds belies its complexity. Migratory birds successfully carry out goal-directed flight of often thousands of kilometers or more over often diverse and unique landscapes. By employing a complex multisensory navigational system, migratory birds overcome challenges encountered such as inclement weather, winds, and migratory obstacles to regularly return year after year to within a few meters of the previous year's breeding or wintering site. Migratory birds exhibit low neophobia, being less hesitant than resident species to enter novel environments, representing a personality trait that may be beneficial when encountering unfamiliar areas during migration. But migrants typically do not invest a lot of time, and consequently energy, exploring unfamiliar environments. Therefore, it is possible

that migrants, which also rely heavily on long-term memory, may be at a disadvantage responding to rapidly changing environments, either climate or human-induced, within a single generation. Social interactions may aid many migratory species, which rely on learning and experience to perhaps rapidly alter their migration patterns when confronted with environmental change. Maintaining a diverse age structure within populations, which include older and experienced migrants, may be critical in adapting to global change (Teitelbaum et al. 2016). To dampen the negative impact of environmental change on migrants, maintaining suitable habitats across the migratory journey is essential. Bird migration remains perhaps one of the most spectacular and mysterious wildlife events.

## Cross-References

- [Cognitive Map](#)
- [Compass Orientation](#)
- [Decision-Making](#)
- [Goal](#)
- [Hippocampus](#)
- [Homing](#)
- [Long-Term Memory](#)
- [Migration](#)
- [Passerine Cognition](#)
- [Passerine Navigation](#)

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## Bird Song

- [Susan D Healy](#)

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## Birds

- [Language Research: Parrots](#)

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## Birth

- [Bear Life History](#)

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## Birth Order

- [Fraternal Birth Order Effect](#)

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## Bisexual

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## Definition

Romantic or sexual attraction that is directed toward two genders, typically men and women.

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## Introduction

Bisexuality is a sexual orientation wherein an individual experiences attraction, whether romantic or sexual, that is directed toward two genders. These two genders most commonly refer to male and female, but the existence of other genders in LGBT+ communities can result in individuals expressing attraction to alternate genders. Individuals that identify as bisexual frequently do not experience equal attraction to the two genders,

instead having a preference for one over the other. Bisexuality has been observed in a wide variety of human cultures as well as some animals.

## History

Bisexual individuals have been present in many societies, with a widely varying degree of prevalence and social acceptance. In some cultures, bisexuality is virtually nonexistent, possibly due to intolerance, but in other cultures, bisexual individuals can represent a large portion of the population. In ancient Greece, having sexual intercourse with both men and women was the norm and was even used to solidify student/mentor relationships in a practice known as pederasty (Holmen 2010). Other depictions of bisexual behavior have been recorded throughout history in many cultures. However, the term “bisexual” is a recent construct that was first used in 1892 by Charles Gilbert Chaddock in a translation of Kraft-Ebing’s *Psychopathia Sexualis*, to describe individuals that had sex with both men and women.

Bisexuality was brought to the attention of the scientific community through the work of Alfred Kinsey in the 1940s. Kinsey found that human sexuality could be placed on a continuum, ranging from exclusively heterosexual to exclusively homosexual with varying degrees of bisexuality in between. These findings were used to create the Heterosexual-Homosexual Rating Scale, otherwise known as the Kinsey Scale (Kinsey et al. 1948/1998, 1953/1998). This scale rated individuals from 0, exclusively heterosexual, to 6, exclusively homosexual, with an additional group “X” for individuals that did not report any sexual attraction.

Although Kinsey continued to study sexuality, further research into bisexuality would be sparse until the 1980s when interest spiked, in part due to the AIDS epidemic and the fear that bisexual individuals would spread the disease to heterosexual women. Before the 1970s, bisexuality was believed by many to be nonexistent or even impossible; many researchers simply labeled bisexual individuals as homosexual, and

bisexuality was considered a “lesser form” of homosexuality or was described as “situational homosexuality” (Rodriguez Rust 2002). During the mid- to late-1980s, researchers slowly began to distinguish between gay and bisexual participants. By acknowledging this distinction, research focusing on bisexual individuals became more popular. Despite this increase in interest, bisexual research still lags far behind research on homosexuality.

## Theories

Although Kinsey’s original research suggested a dichotomous model of sexual orientation, this has largely been replaced by a multidimensional model of sexuality. The Klein Sexual Orientation Grid (KSOG) is a commonly used multidimensional measure with 21 scales, representing 7 dimensions of sexual orientation, which participants answer in regard to their past, present, and ideal selves. These dimensions include sexual attraction, sexual behavior, sexual fantasies, emotional preference, sexual lifestyle, and self-identification (Rodriguez Rust 2002). In this model, bisexuality, rather than being the range between heterosexuality and homosexuality, is its own distinct sexual orientation. Many similar scales have been developed in an attempt to properly define what constitutes bisexuality.

In an attempt to better understand bisexuality, researchers have defined several typologies of bisexuality using a variety of different criteria. Taywaditep and Stokes (1998) identified eight types of bisexuality among men based on different combinations of self-identity, sexual fantasies, and history of sexual involvement. Type A and B men were characterized by a high likelihood of being in a committed relationship with another man, but type A men, on average, had fewer male sexual partners than type B men. Type C and D men were characterized by identifying as heterosexual. Types E, F, G, and H all have a bisexual identity. Type E men tended to prefer female partners and reported having had the highest average number of female sexual partners.

Type F men reported having fantasies for men and women equally. Type G and H men both report a high frequency of sexual contact with other men, but few male partners, and type H men reported much higher heterosexual involvement than type G men. This is one example of the many typologies that have been developed to further define bisexuality.

## Prevalence

Early research into bisexuality has suggested that as much as 10% of the population is bisexual, but these findings were based primarily on previous sexual experience, likely inflating this percentage, especially among individuals that were more sexually active. As a number of dimensions that characterize bisexuality have been identified, more recent research has provided more accurate findings. Janus and Janus (1993) reported that 3% of women and 5% of men self-identified as bisexual. Although other estimates have been found, each of these numbers is based on a single dimension, providing estimates from 0.7% up to 14% depending on the dimension that was measured. Despite this difficulty, researchers have determined some patterns, such as bisexuality being more prevalent than exclusive homosexuality when sexual attraction, erotic responsiveness, or sexual behavior is assessed.

Studies that attempt to determine the prevalence of bisexuality have primarily drawn from American populations. As the prevalence of bisexuality widely differs between cultures, obtaining an accurate estimate of the prevalence of bisexuality in humans has been difficult. Some cultures view bisexuality as normal and thus may have a high prevalence, whereas others may condemn it as heinous and actively suppress any individuals that would otherwise identify as bisexual. Additionally, cultures change over time; in many countries, LGBT+ acceptance has been increasing with a poll in the United Kingdom showing that young adults were twice as likely as older individuals to identify as something other than heterosexual (Lawrence 2015).

## Prejudice

As members of the LGBT+ community, bisexual individuals have been the subject of prejudice and discrimination, specifically biphobia. Large portions of the general population, including many members of the LGBT+ community, continue to believe that sexual orientation is dichotomous, with heterosexuality and homosexuality being the only two possibilities. This perception has led to bisexual individuals being seen as “fence-sitters” who have yet to pick which sexual orientation they identify as. This viewpoint has also resulted in bisexual individuals being seen as a social minority in the LGBT+ community, despite being the numerical majority, resulting in biphobia from both heterosexuals and other LGBT+ members (Matsick and Rubin 2018). This misunderstanding has been difficult to disprove as for many, membership in the LGBT+ community is determined by the gender of an individual’s partner. Outside of polygamous relationships, this results in many bisexual individuals being assumed to be homosexual or heterosexual.

Research on biphobia has identified two underlying dimensions: an instability dimension and an intolerance dimension (Brewster and Moradi 2010). The instability dimension is the degree to which bisexuality is viewed as an unstable and illegitimate sexual orientation. This can manifest in beliefs by non-bisexual individuals that bisexual individuals are confused, experimenting, or simply in denial about their sexual identity. The intolerance dimension is the extent to which others are hostile toward bisexuality and bisexual individuals. Among non-bisexual individuals, this can be seen as a belief that bisexual individuals are amoral, sick, and a threat to society. These beliefs are compounded by the misunderstanding that bisexual individuals are more promiscuous than other members of the LGBT+ community.

## Animal Bisexuality

Without the concept of gender, bisexual activity in other species is much easier to define; in this

context, bisexual activity is the act of engaging in both heterosexual and homosexual intercourse. Bisexual behavior has been observed in a wide variety of animals, including primates, such as the bonobo and Japanese macaques; birds, including some gulls and penguins; and some species of fish (Owen 2004). Many of these species will engage in simultaneous bisexuality in which individuals will engage in both heterosexual and homosexual intercourse within a short time span. For the bonobo in particular, nearly all individuals engage in both hetero- and homosexual intercourse, with up to 75% of sexual encounters being non-reproductive. Other species, such as male walruses, will engage in sequential bisexuality in which periods of heterosexual behavior alternate with periods of homosexual behavior (Bagemihl 2000).

Whereas the term “bisexual” typically refers to sexual orientation when applied to humans, it can have a couple of different meanings when used with animal populations. An individual that is described as bisexual possesses characteristics of both male and female sexes. This usually refers to individuals that possess both male and female reproductive organs. This form of the term “bisexual” has been used since the late eighteenth century and is synonymous with “hermaphroditic.” A group that is described as “bisexual” is composed of both male and female members, rather than one that is “unisexual” or composed of only one sex. Both of these uses are largely restricted to biology.

## Conclusion

Bisexual activity can be seen across many cultures and even within other species. However, our understanding of human bisexuality has been complicated by having to account for gender. The inclusion of gender has resulted in a great deal of misunderstanding, both within the scientific community and the general population. These misunderstandings have resulted in biphobia, even from other members of the LGBT+ community. Further research will be required to resolve these issues and to bridge the gap between research with homosexuals and research with bisexuals.

## Cross-References

- [Hermaphrodite](#)
- [Homosexual](#)
- [Reproduction](#)
- [Sexual Identification](#)

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## Bleating

- [Begging](#)

## Blindsight

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## Synonyms

[Agnosopsia](#)

## Definition

Blindsight is the phenomenon where individuals who are completely blind in some or all of their *visual fields* (the total area where objects can be seen as one's eyes are fixed on a single point in space) are capable of detecting, localizing, or identifying a visual stimulus located in their affected visual fields despite denying that they see the stimulus (Cowey 2004).

As the oxymoronic term suggests, blindsight has two components. When presented with a visual stimulus, patients report that they see nothing at all (*blind*) but when questioned about the stimulus (e.g., where it is or what it looks like), they answer correctly more often than not (*sight*).

Blindsight does not occur in all blind patients but in some who sustain damage to the part of the brain that consciously processes and perceives visual stimuli, located in the posterior pole of the occipital lobe (the *primary visual cortex*).

## History

In humans, damage to the primary visual cortex is associated with a complete loss of vision in corresponding parts of the visual field, as demonstrated in the early twentieth century by studying soldiers injured in battle (Holmes 1918). Decades later, it was reported that four patients with

damaged primary visual cortices were not consciously aware of visual stimuli presented to them but, when prompted to respond, moved their eyes towards the location of the stimuli (Poppel et al. 1973). The term blindsight was coined shortly thereafter in a report describing a patient with a surgically removed primary visual cortex (Sanders et al. 1974). Since then, many studies have investigated patients with blindsight using a variety of methods.

## Characteristics

Blindsight exists in two forms (Weiskrantz 1997); the patient either reports being completely unaware of the stimulus (*Type I*) or is aware of the stimulus but does not acknowledge or experience that it is visual in nature (*Type II*).

Besides direct reporting of responses, assessed by presenting a visual stimulus and asking the subject to choose from a set of options characterizing the stimulus (e.g., where it was or what it looked like), several other categories of responses to visual stimuli have been reported in blind humans and nonhuman primates. These indirect measures include hormonal changes, changes in pupillary and blinking reflexes, and the effects of processing of a stimulus in the affected visual field on the processing of stimuli in unaffected parts (Cowey 2004; Stoerig and Cowey 1997).

Patients with blindsight can detect the presence of a visual stimulus and localize it well above the performance expected by chance (i.e., random guessing). However, this ability depends on several factors, including the nature of the stimulus. Generally, subjects perform less well when the shape, orientation, and color of the stimuli is investigated (Cowey 2004).

## Theories

The precise mechanism underlying blindsight is unknown, but several theories have been suggested as potential explanations (Campion et al. 1983) and have been discussed in detail elsewhere (Cowey 2010; Weiskrantz 2009).



These include that blindsight occurs when there is a generalized reduction in normal vision (as opposed to its complete absence) or when some parts of the damaged primary visual cortices or their connections remain intact. In addition, the results of studies on the phenomenon have been attributed to experimental factors such as scattered light from the visual stimulus spilling over into the normal parts of the patient's visual field or *response bias* – the tendency to systematically choose one answer over another when forced to choose between two responses (particularly when the choice is between yes or no).

## Neurobiology

Neuroanatomical changes in the connections between brain areas (within and between cerebral hemispheres) involved in visual processing have been reported in subjects with blindsight (Ajina and Bridge 2016). Intact connections projecting from the retina (through the lateral geniculate nucleus of the thalamus) to other cortical visual areas outside the primary visual cortex are also seen in patients with blindsight. The variability in the integrity of these connections may help explain why some patients with damage to the primary visual cortex exhibit blindsight while others do not (Cowey 2004). There is even evidence that blindsight may be affected by learning, with patients becoming progressively better at detecting stimuli the more they are exposed to them (Stoerig 2006).

The phenomenon has also been associated with functional activation in brain regions associated with the perception of moving visual stimuli (Barbur et al. 1993), although such responses may also arise from the anticipation of the stimulus rather than its actual perception (Cowey 2004).

## Conclusion

Blindsight is a controversial phenomenon, the basis of which is currently poorly understood. Several lines of imaging and behavioral evidence suggest that damage to the primary visual cortex is

associated with residual capacity for visual processing, occurring without conscious perception of the stimuli being processed. The investigation of this counter-intuitive and interesting phenomenon has opened up fascinating questions about the neural basis of consciousness and how stimuli are perceived, as well as about the brain's ability to reorganize and compensate for damage.

## Cross-References

► [Visual Perception](#)

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## Blocking

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## Definition

In the associative learning literature, blocking is typically defined as a deficit in responding to a conditioned stimulus (CS) that has always been paired with an unconditioned stimulus (US) in the presence of another CS previously established as a reliable predictor of the same US.

## Background

Until the late 1960s, it was generally assumed that the mere temporal and spatial contiguity between a CS and a US was a necessary and sufficient condition for conditioning to take place. The discovery of blocking by Leon Kamin (1968) was the first of a series of findings that defied this view, stimulating the development of modern learning theories. His seminal experiments on blocking relied in the experimental design summarized in Table 1. As can be seen, in this experimental design, subjects in both groups experienced the same number of pairings between a light (L) and an electric shock. However, conditioned responding (CR) to the light was significantly stronger in the control group than in the experimental group. In other words, close contiguity between a conditioned and an unconditioned stimulus (L and the shock, in this case) did not suffice to produce strong conditioning.

According to Kamin (1968), this effect reveals that pairings of a CS and a US only give rise to conditioning if the US is unexpected. In the experimental group, when L is paired with the shock, this event produces little or no surprise, because the shock is readily predicted by a previously conditioned white noise (N). This is not the case in the control group, where the shock is completely unanticipated the first time L is presented. The idea that surprise drives learning was soon implemented in formal theories of associative learning. For instance, in the influential model of classical conditioning developed by Rescorla and Wagner (1972), surprise is represented as a prediction error, i.e., as the arithmetic difference between the “expected US” and the “experienced US.” In this model, the amount of learning supported by a conditioning trial is directly proportional to this difference.

Some models developed over the following years attempted to explain blocking by postulating different mechanisms. For instance, according to Mackintosh (1975), blocking can be explained by assuming that attention is biased toward predictive stimuli. In the case of the experimental group in Table 1, when L and N are presented together for the first time, N is the most reliable predictor of the US and subjects will learn to pay more attention to it, leaving few attentional resources to process (and learn about) L. In a radically different vein, Miller and Matzel (1988) proposed that blocking is not due to a deficit in learning itself but to late processes related to the production of the conditioned response. In any case, as shown by these examples, offering a successful account of blocking soon became a touchstone for any theory of associative learning.

Although the blocking effect was initially explored in the area of animal conditioning, during the 1980s, several studies showed that it could also be detected in human predictive learning experiments (Dickinson et al. 1984). This led naturally to the conclusion that the mechanisms underlying different forms of human learning must be similar to the ones responsible for classical and operant conditioning in nonhuman animals. The following

**Blocking, Table 1** Design summary of Kamin’s (1968) blocking experiments

| Group        | Phase 1      | Phase 2      | Test | Result    |
|--------------|--------------|--------------|------|-----------|
| Experimental | 16 N – shock | 8 LN – shock | L?   | Weak CR   |
| Control      | –            | 8 LN – shock | L?   | Strong CR |

Note: N and L refer to a white noise and to the turning on of a house light, respectively; the unconditioned stimulus is a 1-milliampere electric shock; CR refers to conditioned responding

decades of research in human predictive learning were largely driven by the impetus provided by associative learning theories and animal conditioning research.

More recently, it has been suggested that blocking might not be the product of an associative learning process but rather the result of a simple deductive inference (De Houwer et al. 2002). If two conditioned stimuli predict a US, then presenting both of them together should predict and even more intense US. In a blocking design, however, the intensity of the US is exactly the same when only one CS is presented (N) and when two CSs are presented (L and N). Therefore, it can be concluded that one of the CSs (L) is not a predictor of the US. Consistent with this view, blocking seems to be sensitive to participants’ assumptions about the additivity of CSs (i.e., whether two CSs should predict a stronger US or not) or the maximality of the US (i.e., whether the intensity of the US is not changing because it is already happening at its maximal level). Manipulating these assumptions does not only affect blocking in human participants but also in nonhuman animals (Beckers et al. 2006). These findings have raised concerns about the validity of the whole associative learning framework, leading some authors to suggest that blocking and other learning effects are better understood in terms of propositional inference processes (Mitchell et al. 2009; but see Shanks 2010).

**Cross-References**

- [Classical Conditioning](#)
- [Contingency](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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**Blodgett Effect**

- [Latent Learning](#)

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## Blood

### ► Circulatory System

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## Board

### ► Touch Screen

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## Bob Cook

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Dr. Robert Cook, known to his students, colleagues, and friends as Bob, has studied comparative animal cognition and behavior for more than 30 years, exploring topics such as stimulus control, discrimination learning, and memory. His NIH- and NSF-funded Comparative Cognition Laboratory at Tufts University has been highly successful, both in terms of research productivity that has shaped the field of comparative cognition and as his monumental support and mentorship for student research and education. His lab utilizes touchscreen-equipped, computerized operant chambers to explore comparative visual and auditory cognition in both avian (pigeons and starlings) and human subjects. The Comparative Cognition Laboratory continually funds graduate students and postdoctoral researchers, as well as providing hands-on research opportunities for undergraduate volunteers and outreach programs for local high school students. He is an excellent mentor and has maintained lifelong friendships with many of his former students.

His research has investigated the mechanisms of perception and discrimination, including action categorization (Asen and Cook 2012), motion perception, change detection, the use of time to

sequentially organize behavior (Cook and Rosen 2010), visual and auditory relational concept learning (Cook et al. 2003), equivalence class formation, music perception, pattern and texture discrimination (Cook 1992), and neural substrates of these cognitive mechanisms. Dr. Cook's ultimate goal in research is to explore how birds, as the other major group of visually sophisticated terrestrial vertebrates other than mammals, can form accurate perceptions and representations of the outside world and how they conceptually form relations between real-world objects and events, using a smaller, more compact central nervous system than mammalian brains.

Dr. Cook has authored more than 150 publications, including peer-reviewed empirical articles in high-impact journals, numerous book chapters, and two online multimedia cyberbooks, *Avian Visual Cognition* (Cook 2001) and *Animal Spatial Cognition* (Brown and Cook 2006). Dr. Cook is the publisher of *Comparative Cognition & Behavior Reviews* and has served on the editorial boards of a number of top journals in comparative cognition. He has been active in a number of academic societies, most notably being a founding member and former president of the Comparative Cognition Society. With his personal and engaging style of presenting, Dr. Cook has been regarded as a rock star who does science. He has been active in broadening the visibility of comparative cognition through the Internet and hosting web-based content in comparative cognition for international academic communities and the public, promoting open-access empirical journals hosted in online formats, and offering outreach programs allowing promising high school students to get involved in university-level research. He has also championed the use of computer technology and programming in research, through his classes and research laboratory.

Dr. Cook received his B.S. in Psychology (1976) from Ohio State University and his M.A. (1980) and Ph.D. (1983) in Biopsychology from the University of California, Berkeley, with Dr. Al Riley. He was an NRSA Postdoctoral Fellow (1986) at the University of Texas Health Science Center, Houston, with Dr. Anthony Wright, before taking on a teaching and research position at Tufts

University in Boston in 1986, where he is currently a Professor of Psychology. In addition to his accomplishments in research, Dr. Cook served as Department Chair of the Department of Psychology at Tufts University and as the Dean of the Graduate School of Arts and Sciences.

In his personal life, Bob is married to Sherry, and has two wonderful children, Allison and Matt. Bob is an avid and accomplished guitarist and musician, and he regularly plays with a band of fellow academics. He enjoys swimming and formerly was an Ultimate Frisbee champion in his college days.

Lab Website: <https://www.pigeon.psy.tufts.edu/>.

## Cross-References

- [Anthony \(Tony\) A. Wright](#)
- [Auditory Processing and Perception](#)
- [Change Detection](#)
- [Comparative Cognition](#)
- [Discrimination Learning](#)
- [Memory](#)
- [Operant Chamber](#)
- [Pattern Learning](#)
- [Pigeon \(\*Columbidae\*\)](#)
- [Relational Concepts and Symbolic Logic](#)
- [Stimulus Control](#)
- [Touch Screen](#)

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## Body Clock

- [Biological Clocks](#)

## Body Decoration

- [Self-Decoration in Dolphins](#)

## Body Type

- [Morphology](#)

## Bonding

- [Attachment](#)

## *Bos taurus*

- [Bovine Cognition](#)

## Bottleneck Effect

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The term “bottleneck” refers to a point of congestion in a system, drawing an analogy to the constricted neck of a bottle that reduces the flow of a liquid. Population bottlenecks are evolutionary events attributed to the loss of genetic variability over a short period of time. These can occur due to environmental damage, hunting, limited resources, and drastic climatic changes that cause random fluctuations in the

levels of populations. The sudden reduction of population size results in a new gene pool that is not reflective of the diversity and variability of the original gene pool.

Bottleneck effects do not just occur due to a disease that kills a small group of individuals lacking a particular gene, as death due to disease is said to be aided by the process of natural selection. On the contrary, the bottleneck effect results from a sharp decline in the number of individuals in a population due to sudden occurrence of events like natural calamities or human interference, completely independent of selection. The main cause of the decline is anthropogenic activities (e.g., poaching and habitat destruction) as well as natural calamities like flood, famine, drought, earthquake, and even forest fires.

Fisher (1922), Haldane (1927), and Wright (1931) pioneered studies of the bottleneck effect by modeling experiments on evolution and justifying it with mathematical representations. The probability of extinction due to bottlenecks in resource-limited environments has been studied in detail (Wahl et al. 2002) and mathematical models have been elucidated (Levin et al. 2000) taking bacteria as a model organism as massive evolutionary changes are witnessed in them over a single controlled experiment. The concept of extinction probability of genes in the context of this chapter gains more importance than fixation probability as bottleneck effect brings radical changes in allelic frequencies in a population by the overrepresentation of a particular allelic frequency than the other or a complete loss of a particular frequency (Allendorf 1986). Hence, the dynamics of evolution are affected by this effect that renders obstruction to a beneficial

mutation from being fixed (Wahl et al. 2002). Figure 1 presents a visual representation to depict the concept of a bottleneck.

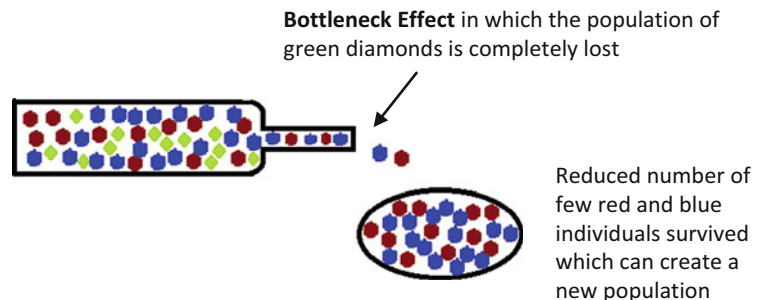
The extinction of the bearded vulture (*Gypaetus barbatus*) from the European Alps in the early 1900s due to extreme hunting is a notable example of a bottleneck effect in the early twentieth century. The drastic decline in population size was a serious cause of concern for the biologists. Pray (2008) had reported that the extirpation of this species from the wild has led the Frankfurt Zoological Society to institute a captive breeding program to revive the vulture populations by reintroduction of captive-bred vultures in the wild which is still in practice. Scientists opined that the lack of genetic variability has led to lack of adaptability among the captive as well as the released birds due to selection pressures caused by environmental dynamism.

Effective population size ( $N_e$ ) is a term denoting the genetic status of a population that reflects the level of genetic variation among populations. This is measured by pedigree data and estimated by DNA-based microsatellite analysis. The data collected from “studbooks” (a type of record of pedigree data for any captive species) as well as that obtained by microsatellite analysis of blood samples of both wild and captive vulture population were much less than that expected by conservation biologists. High  $N_e$  values are required to maintain the evolutionary potential (Gautschi et al. 2003) which if lost, may lead to the complete elimination of the species.

Another example of the bottleneck effect can be clearly seen in the African cheetah (*Acinonyx jubatus*). Population bottlenecks were experienced by the cheetah population around late

### Bottleneck Effect,

**Fig. 1** Sharp lowering of population gene pool due to wiping of a particular type of population demonstrated by the lost green diamonds in the new set of population that survived in Bottleneck Effect



Pleistocene (Raymond and O'Brien 1993) almost leading to their extinction at the end of last ice age. Raymond and O'Brien (1993) conducted genetic diversity analyses of mitochondrial DNA and hypervariable minisatellite DNA on the South African and East African subspecies of cheetah. Female cheetahs mate with multiple males and give birth to a single litter of cubs with different fathers who may be distantly related. The female cheetahs mate with unfamiliar males, and do not repeat mating with males. Thus, genetic variability is maintained via multiple fathers and a single common mother.

Northern island seals are another example of genetic bottlenecks too. This bottleneck resulted from human hunting in the 1890s that left only 20 surviving individuals at the end of nineteenth century (Trupkiewicz et al. 1997). Blood samples from northern elephant seals were collected by Bonnell and Selander (1974) and were examined for protein variations revealing underlying genetic diversity. A lack of polymorphism among the 21 examined proteins supported the lack of genetic variation among the northern island seals, compared with Southern elephant seals, which were not subjected to similar hunting pressures.

The colonial tuco-tuco (*Ctenomys sociabilis*) – threatened subterranean rodent, endemic to a 1000 km<sup>2</sup> area (approximately) in Western Limay Valley and the Patagonian tuco-tuco (*Ctenomys haigi*), the more widely distributed one in the eastern part of the valley and its neighboring areas – show marked differences in social structure, demography, and genetic variation in spite of being in close geographical proximity. These have been widely studied to record genetic variation at cytochrome b gene of mitochondrial DNA. The volcanic eruption of Puyehue-Cordón Caulle in 2011 had marked the reduction in population size and loss of genetic variations in both species, experimentally inferred by the genome level analyses from pre- and post-eruptional reduction datasets (Hsu et al. 2017). This paves the way for the study of bottleneck effects as a determinant to reduce population dynamism.

Humans have also undergone genetic bottlenecks, primarily at the end of Pliocene era, some

two million years ago. Evidence for this comes from variation in human mitochondrial DNA, beta globin, Y chromosomes, HLA alleles, and multiple loci interspersed in the genome including single-nucleotide polymorphisms, microsatellites, and human-specific Alu insertions of both current humans and the Hominid fossil record (Hawks et al. 2000).

Thus, to conclude, bottlenecks in populations create a lack of genetic information due to loss of alleles which has altered the evolutionary trajectories of the aforementioned organisms. Although conservationists try to recover declining populations, the level of deterioration in the genetic variability affects the new gene pool. However, the bottleneck effect is not the only factor in many cases. Related concepts like the founder effect or genetic drift may also play a role.

## Cross-References

- ▶ [Alleles](#)
- ▶ [Fisher](#)
- ▶ [Gene Pool](#)
- ▶ [Genetic Drift](#)
- ▶ [Genetic Variation](#)
- ▶ [Homo sapiens](#)
- ▶ [Microsatellite Marker](#)
- ▶ [Population](#)

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## Bottlenose Dolphins

### ► Self-Decoration in Dolphins

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## Bottom-Up Processing

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### Synonyms

[Data-driven processing](#); [Local bias](#); [Lower-level representation](#); [Perceptually driven processing](#)

### Definition

In bottom-up processing, an organism's perception of a stimulus relates directly to its perceptual features and does not impose a more abstract structure to the conceptualization of the object (as in top-down processing). Bottom-up processing is thus independent of prior experience

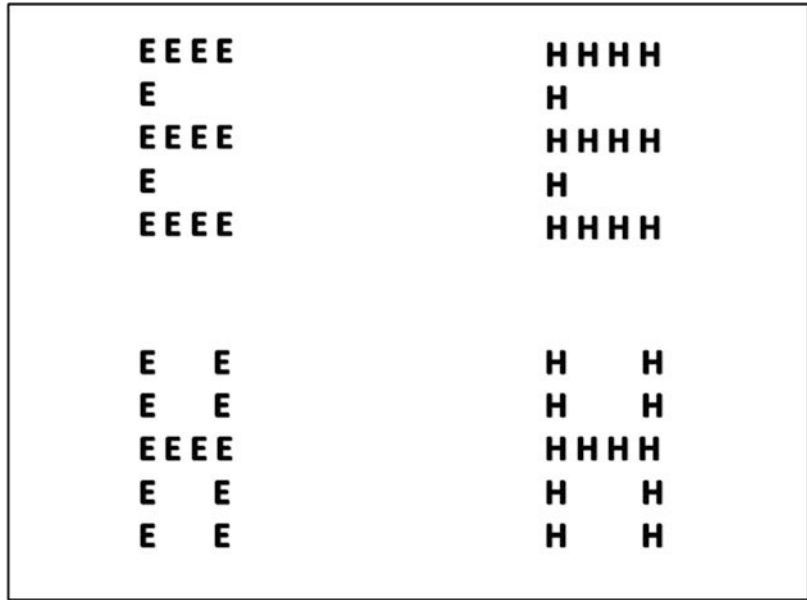
and knowledge. It is thought to represent lower levels of information processing and to focus on detailed stimulus information compared to the more integrated higher-level information that reflects top-down processing (Rauss and Pourtois 2013). For example, when viewing a rectangle, one would see four lines intersecting rather than representing the rectangle as a depiction of a doorway or a window. Although bottom-up processing is thought to be largely automatic (Theeuwes 2010), the same could be said of some forms of top-down processing; therefore, the automatic/consciously controlled distinction cannot distinguish these mechanisms. Rauss and Pourtois (2013) review other common confusions in the literature.

### Bottom-Up Perceptual Processes

More than four decades ago, Kinchla and Wolfe (1979) sought to examine whether visual processing occurred via bottom-up versus top-down mechanisms. They presented subjects with compound stimuli where a global shape (an uppercase letter) was composed of smaller elements (many smaller capital letters), deemed local elements. Bottom-up processes were implicated if subjects responded more quickly when the target letter appeared within the local, versus the global, stimulus (see Fig. 1). The results of those early studies suggested that the form of processing depended upon the size of the stimulus, suggesting that neither process had priority in that particular task. Biederman (1987) famously argued that objects could be recognized by breaking them down into their component parts, such that representations of whole objects were generalized from associations of their featural components. That is, in Biederman's account, bottom-up processing served as the foundation for all top-down processing and was the primary mechanism of object recognition even in adult humans. Although often contrasted with top-down processing, bottom-up processing often operates in concert with these more conceptually driven processes, making them difficult to disentangle (Goldstone and Barsalou 1998).

**Bottom-Up Processing,**

**Fig. 1** If the target letter is E, bottom-up processes would be implicated if choosing the bottom left stimulus the most quickly



**Categorization**

Because bottom-up perceptions are assumed to be uninfluenced by prior experience, they can most easily be studied in infants. French et al. (2004) showed that even for human infants, photographic images of natural stimuli such as cats and dogs can be categorized “solely on the basis of perceived differences in the statistical distributions of the perceptual attributes of the different categories” (p. 383). That is, the categorization of cats and dogs by infants occurs through bottom-up processes, which can be demonstrated by manipulating the relationships of inclusion of perceptual features in the two categories. The mechanism demonstrated for infants in this study is assumed to also underlie categorization judgments in many nonhuman species (Eggermont 2015). During development, human infants typically shift from reliance on bottom-up to top-down processing mechanisms (Quinn and Eimas 1997; Rakison and Oakes 2003). A question of interest for comparative psychologists is whether nonhuman animals also evidence top-down categorization (Fagot and Parron 2012).

Studies of bottom-up processing often make use of artificial categories to exclude the role of experience and learning. It is difficult to control

the role of prior experience with natural categories (Ashby and Ell 2001). However, animals are often studied for their representation of natural categories to better understand the levels of abstraction underlying their representations. If they correctly categorize stimuli as belonging to natural categories such as “animal,” they may do so by attending to observable features such as the presence of eyes and other face-like features and apparent motion rather than by abstracting a general overarching category for all living things (Vonk and Galvan 2014). If they generalize from these observable features to ascertain which stimuli (when responded to) will result in reward, they might be using bottom-up rather than top-down processes. If instead they have generalized a rule such as “choose all images of animals” and recognize that the category “animal” comprises many perceptually unique organisms, such as fish, birds, snakes, and elephants, they may be using a top-down process. Evidence for top-down processes may be determined when animals categorize stimuli, such as worms, as animals despite the lack of obvious features such as faces and limbs. Although many studies have revealed impressive evidence for generalization of seemingly abstract natural categories in species such as pigeons, squirrel monkeys (Roberts and

Mazmanian 1988), black bears, and great apes, the mechanism(s) underlying such performance is nefariously difficult to identify (Vonk and Galvan 2014).

Researchers have also returned to procedures like that originated by Kinchla and Wolfe (1979) to determine whether species like baboons exhibit local or global processing biases. Jitsumori and Matsuzawa (1991) suggested that monkeys attend to global features, whereas pigeons attend to local features when processing stimuli involving human and nonhuman faces and silhouettes. These differences may extend to other bird and primate species as starlings also show a local bias (Qadri and Cook 2015). However, Spinozzi et al. (2006) found a strong local precedence, and local interference of global processing, in capuchin monkeys, suggesting the possibility of a difference between new-world and old-world monkeys in their local/global processing biases. At the same time, Deruelle and Fagot (1998) found significant differences between humans and baboons in perceptual grouping of visual stimuli and also concluded that monkeys do not show the global precedence identified in humans. Attending to local features rather than global constructs may reflect the absence of a symbolic system for labeling exemplars from the same overarching categories that is present in humans. Fagot and Parron (2012) provide a review of several related studies suggesting differences among primates, but importantly, they conclude that top-down processes are also evident in nonhuman primates even though the exact mechanisms underlying perceptual grouping may differ.

Although the term bottom-up has most commonly been applied to processes underlying perception and categorization, more recently, the term has also been invoked to describe a general approach to the study of animal behavior, personality, or cognition. For example, Hopper et al. (2016) describe the utility of a bottom-up versus a top-down approach to studying instances of coprophagy (consuming one's own vomit) in captive primates. In this case, taking a bottom-up approach means to cast aside *a priori* assumptions about how coprophagy fits with other behaviors related to negative welfare assessments and

instead conducting analyses such as principal components to ascertain directly whether it should be included with other "abnormal" behaviors. Using bottom-up approaches allows researchers to let the data "speak for itself" in the sense that generalizations are inferred from specific observations instead of beginning with an assumption of what behavior might look like and testing observations against that model.

## Models of Personality

In research on human personality, a top-down approach would mean attempting to apply a personality structure from another species (often humans) such as the Big Five theory of personality factors onto animal personality. In contrast, a bottom-up approach would involve taking a careful inventory of behaviors specific to the study species and extracting a model of traits that accounts for the variability in such behaviors for that particular species (Vonk and Eaton 2018). Freeman et al. (2013) identified the unique challenges of each approach and developed a method that they argued incorporated both top-down and bottom-up approaches to the study of chimpanzee personality. They pointed to the benefits of a top-down approach in allowing for cross-species comparisons but acknowledged that taking such an approach might lead to poor-fitting models that fail to identify traits unique to the study species.

## Models of Cognition

In the same vein, researchers have recently advocated for a bottom-up approach to studying animal cognition where they eschew the temptation to test whether other species demonstrate evidence of abilities known to exist in humans or other closely related species and instead focus on understanding the mechanisms underlying behaviors demonstrated by the study species (de Waal and Ferrari 2010; Eaton et al. 2018). In comparative cognitive studies, this idea is particularly important as one of the major problems with the field is the anthropocentric bias in which researchers

attempt to seek evidence for human-like cognitive abilities in other species rather than pursuing a better understanding of species-specific cognition. Instead of asking questions like “Does the chimpanzee have a theory of mind?” (Premack and Woodruff 1978), researchers would instead ask: “How does the chimpanzee predict the behaviors of others?” Bottom-up approaches consider the study species to be of interest in their own right, rather than merely by virtue of their comparison to humans.

## Conclusion

Despite being commonly used within psychology, it is clear that the term “bottom-up” has multiple meanings and is sometimes poorly defined (Rauss and Pourtois 2013). In general, it can be thought of as a perceptual process that involves analysis of perceptual features without imposing a more abstract structure or concept onto the stimulus. In addition, it can be applied to strategies that focus on understanding unique cases using direct observation without reference to better known comparisons and without the need to impose a model appropriate for a different species on a lesser-known case.

## Cross-References

- [Categorization](#)
- [Object Recognition](#)
- [Perception](#)
- [Perceptual Learning](#)
- [Top-Down Processing](#)

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## Bourgeois Strategy

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### Synonyms

[Uncorrelated asymmetry](#)

### Definition

Bourgeois strategy in animal contests is a possible equilibrium solution derived from game theory: escalate when the animal is an owner and retreat when it is an intruder.

### Introduction

Conflicts between animals of the same species usually do not cause serious injury. Before the 1970s, scientists had often explained this by the idea of group selection. That is, if animals fight with full force and are often seriously injured, the survival of the species will face a crisis. However, the idea of group selection is incompatible with Darwinian natural selection, which assumes that

the primary unit of selection is the individual. Maynard Smith and Price (1973) applied game theory to analyze animal contests and succeeded in understanding contest dynamics based on individual selection, not group selection. The most important concept of game theory models is an evolutionarily stable strategy (ESS). An ESS is a strategy that is not invaded by other strategies if most individuals of the population adopt it. Since the publication by Maynard Smith and Price (1973), many contest models based on game theory have been developed. As one such model, Maynard Smith (1982) introduced the bourgeois strategy, where ownership of a resource is always respected during contests. Perhaps this idea fits human intuition. However, it has important logical problems, and researchers have tried to determine whether the bourgeois strategy is evolutionarily stable.

### History of Theoretical Research

Maynard Smith and Parker (1976) constructed a simple model of animal contests named the Hawk-Dove model. This model assumes two behavioral choices during a contest: in Hawk, escalate and continue until injured or until opponent retreats, and in Dove, display and retreat at once if an opponent escalates. In this game, the equilibrium solution is dependent on the value of the contested resource ( $V$ ) and the cost imposed on the loser ( $C$ ). When  $V > C$ , Hawk is an ESS. When  $V < C$ , neither Hawk nor Dove is an ESS. If a player can behave as Hawk with a probability of  $V/C$  and as Dove with a probability of  $1 - V/C$ , it is an ESS. This is called a mixed strategy. Then, Maynard Smith (1982) considered the so-called bourgeois strategy, where an individual plays Hawk when the individual is an owner of the resource, whereas it plays Dove when it is not an owner. It is simply assumed that each individual finds itself to be an owner or an intruder with an equal probability. Individuals can adopt any one of Hawk, Dove, or bourgeois strategies. When  $V > C$ , Hawk is an ESS, whereas when  $V < C$ , bourgeois strategy is the only ESS (Table 1). It should be noted that bourgeois strategy assumes

**Bourgeois Strategy, Table 1** A payoff matrix of the Hawk-Dove-Bourgeois game. Payoffs of individuals in the left column contesting with individuals in the first

row are indicated. Note that even if bourgeois is replaced by anti-bourgeois, the payoff matrix does not change. This table is based on Maynard Smith (1982)

|           | Hawk        | Dove   | Bourgeois    |
|-----------|-------------|--------|--------------|
| Hawk      | $(V - C)/2$ | V      | $3V/4 - C/4$ |
| Dove      | 0           | $V/2$  | $V/4$        |
| Bourgeois | $(V - C)/4$ | $3V/4$ | $V/2$        |

that ownership is not correlated to real fighting abilities (resource-holding power, RHP, Parker 1974) or to the subjective value of the resource (RV). Therefore, it is sometimes said to be an uncorrelated asymmetry hypothesis.

Since both contestants can avoid injury costs, bourgeois strategy is a cheap solution, and thus appears to evolve very easily. However, logical problems arise when one understands that the owner and the intruder are, in mathematical terms, completely arbitrary labels. The owner role and the intruder role can be replaced by any easily perceivable asymmetry so long as each individual can find itself in either of the roles with an equal probability. For example, anti-bourgeois strategy is also an ESS, where an individual plays Dove when the individual is an owner of the resource, whereas it plays Hawk when it is not an owner (Table 1). Maynard Smith (1982) stated that anti-bourgeois strategy leads to an infinite regress where displaced owners go on to displace other owners and that anti-bourgeois strategy is unlikely to evolve when resources provide real value to owners when held for a long time. Mesterton-Gibbons and Sherratt (2014) analyzed, more mathematically, the effect of infinite regress on the evolutionary stability of anti-bourgeois strategy and concluded that infinite regress can facilitate bourgeois-like conventions to some extent.

However, if resources need to be held for a long time, not only the anti-bourgeois but also the bourgeois strategy may not be evolutionarily stable. Grafen (1987) pointed out this problem. The bourgeois strategy tends to provide a positive feedback for owners and a negative feedback for intruders. If an owner wins because it is in an owner role, it tends to be an owner at the next fight and wins again because it retained the

resource in the previous fight. If an intruder loses because it is not in an owner role, it tends to be an intruder at the next fight and loses again because it did not obtain a resource in the previous fight. That is, the premise of the bourgeois strategy that an individual finds itself as an owner or an intruder with an equal probability is very hard to fulfill as long as resources are held for a long time. In this situation, intruders should be “desperados” that do not respect ownership because they lose almost nothing even if they are injured or killed in the fights. Early contest models based on game theory assumed that each contest is an independent event (e.g., Maynard Smith and Price 1973; Maynard Smith and Parker 1976). Clearly, this assumption is not fulfilled when resources are held for a long time. After the publication of the analysis by Grafen (1987), the bourgeois strategy came to be thought of as unreal in nature.

Kokko et al. (2006) breathed new life into the bourgeois strategy by constructing contest models with population-level feedbacks. Earlier contest models consider only two individuals that directly compete over the same resource of a constant value (V), accepting a constant cost of injury (C). Kokko et al. (2006) considered not only the two contestants but also the behavioral dynamics of other individuals in the population. Consequently, V and C are not constant, but dependent on the environment. This model assumes that individuals compete over breeding territories. The background mortality rate of owners and intruders, the probability of lethal injury resulting from losing fights, and the number of territories an intruder can inspect per unit time are set as fixed parameters. The number of intruders per territory, rate at which vacant territories form, etc. are set as feedback parameters (i.e., depend on population strategy). In this model, the bourgeois strategy is an ESS when the mortality



rate of owners is high and fighting is risky. The anti-bourgeois strategy is an ESS when the mortality rate of owners is high and that of intruders is low, the number of territories intruders can inspect per unit time is high, and fight costs are high. The no-respect resolution, where individuals always fight when meeting each other, is an ESS when the mortality rate of intruders is high, that of owners is low, and floaters do not encounter new territories easily. Partial respect for ownership (intruders retreat without a fight with a certain probability) is also an ESS under certain conditions.

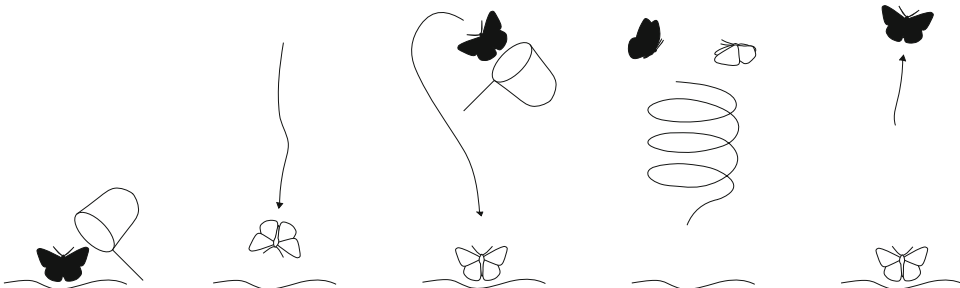
### Bourgeois Strategy in Nature

In nature, owners are likely to win contests with intruders in most animals, which is known as effects of prior residence (Kokko et al. 2006). In some animals, it is reported that contests escalated when both contestants regarded themselves as an owner (e.g., Davies 1978; Waage 1988). However, these are not necessarily an evidence of bourgeois strategy. Owners may win contests because competitively superior individuals have been accumulated as owners or because owners place higher RV than intruders and pay more costs for fighting over the resource. It is not easy to distinguish whether owners win because individuals adopt a bourgeois strategy or because of other factors.

Perhaps the most famous example of the bourgeois strategy in the real world was provided by the study of territorial contests in the speckled

wood butterfly, *Pararge aegeria* (Davies 1978). Males of this butterfly occupy a sunspot in woods as a mating station. When another male invades the territory, the owner rushes to him and the two males perform a spiral flight (ascending and descending while flying around each other). Then, one of the males retreats, and the other occupies the territory. In natural conditions, owners always defeat the intruder. To reveal the mechanism that accounts for the owners' dominance, Davies (1978) performed removal-replacement experiments. At first an owner was captured and removed from his territory. When another male came to and occupied the territory, the original owner was released back into the territory. Soon after the original owner returned to the territory, a contest between the two males occurred. In this experiment, the newcomer (the new owner of the territory) always won (Fig. 1). This result appeared to be explained by the bourgeois strategy. In addition, sunspots appear and disappear within a short time as the sun moves. This appeared to fill the requirement of the bourgeois strategy that resources are not held for a long time, and each individual is an owner or an intruder with an equal probability. Moreover, since butterflies do not have organs to attack their opponent such as horns or teeth, it seems reasonable to settle their contests by an arbitrary cue (residency). Davies (1978) had been cited as the empirical support for the bourgeois strategy for decades.

However, later studies did not support the notion that territorial contests of *P. aegeria* are settled by respect for ownership. Wickman and



**Bourgeois Strategy, Fig. 1** The results of Davies (1978): black, an original owner; white, a new owner. This figure is based on Davies (1978) with permission from Elsevier

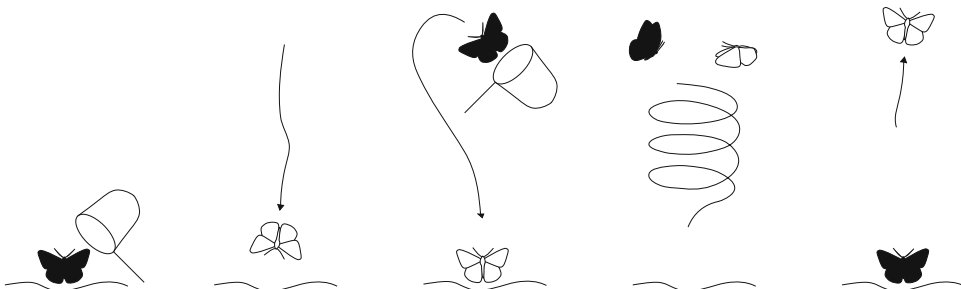
Wiklund (1983) observed a natural population of *P. aegeria* and found that original owners who had temporarily been out of their territory could defeat a male that was occupying the territory when they returned back. Thus, ownership is not respected. Kemp and Wiklund (2004) reproduced this phenomenon by refined removal-replacement experiments (Fig. 2) and suggested that intrinsically more aggressive individuals are accumulated as territory owners through contests. These results are contrary to those of Davies (1978). Takeuchi and Honda (2009) removed the difference in intrinsic RHP between contestants in removal-replacement experiments using the Japanese hairstreak, *Chrysozephyrus smaragdinus*. In their experiments, original owners always defeated the temporary owner. A possible explanation for the inconsistency between Davies (1978) and the later studies is as follows. In removal-replacement experiments, the original owner is captured and kept until a new comer occupies the territory. Therefore, there is an asymmetry between original owners and new comers: original owners are subjected to captivity stress whereas new comers are not. The level of captivity stress is dependent on the conditions imposed by the experimenter. Therefore, the inconsistencies between Davies (1978) and later studies might reflect the difference in captivity stress. In fact, Kemp and Wiklund (2004) very gently released the original owner.

These results disproved the bourgeois strategy in butterfly contests. However, the question remains of how these weaponless animals settle their contests. Takeuchi et al. (2016) provided a new point of view for understanding butterfly

contests. Interpreting past research based on Lloyd Morgan's Canon, they argued that males of territorial butterflies cannot discriminate the sex of a flying opponent (and have some uncertainty in recognizing the species of flying objects). Consequently, these male butterflies chase each other in the air because they expect their opponent to be a receptive female. The one that judges that the probability of its opponent being a receptive female is sufficiently low quits chasing. It immediately flees from its opponent because its opponent may be a natural enemy. In this framework, butterfly contests are not described as behavioral interactions between two males that try to evict their opponent from the territory. At present, this framework is sufficient to explain competition over mating opportunity in butterflies (Takeuchi 2017).

There is no empirical study providing clearer support of bourgeois strategy than that of Davies (1978). It is sometimes thought to be as an example of bourgeois strategy if an owner defeats an intruder even though the body size of the owner is smaller than that of an intruder. However, the lack of a relationship between larger body size and contest success does not indicate that ownership is used as an arbitrary cue for contest resolution. Ownership and RV are often correlated because owners would have learned the value of the resource. Owners may win because they place higher value on the resource and accept more fighting costs than intruders (Arnott and Elwood 2008). It is very difficult to separate ownership status itself and RV in the real world.

There is practically no reported example of anti-bourgeois strategy so far. In the first place,



**Bourgeois Strategy, Fig. 2** The results of Kemp and Wiklund (2004): black, an original owner; white, a new owner

there are few reports that intruders tend to evict owners. Maynard Smith (1982) cited Burgess's (1976) report on the spider *Oecibus civitas* as potentially supporting an anti-bourgeois strategy. In this species, owners surrender their webs to intruders, leading to a series of displacements. However, there have been no follow-up reports of this behavior in this or other species. In addition, although there are a few examples in which introduced intruders tended to usurp the nest occupied by the owner in the experimental arena (Fernet and Smith 1976; Peeke et al. 1998), these phenomena were not confirmed in nature.

## Conclusion

At present, there are practically no clear examples of bourgeois strategy in the real world. Today, most animal contests are interpreted by one of the following three models: the sequential assessment model (Enquist and Leimar 1983), where contest behavior is regarded as a sampling of the RHP of the opponent, and the individual that evaluates itself as weaker than the opponent retreats; the cumulative assessment model (Payne 1998), where an individual decides to retreat when the accumulated costs from the opponent's and its own behavior reach its threshold; and the energetic war of attrition model (Mesterton-Gibbons et al. 1996), where an individual decides to retreat when the accumulated cost arising from its own behavior reaches its threshold. The bourgeois strategy and its mirror the anti-bourgeois strategy appear to remain possible within purely theoretical studies. Although the bourgeois and anti-bourgeois strategies are both possible on a theoretical basis, owners enjoy considerable advantages over intruders in most fights in the real world. This may indicate that owners defeat intruders not because they use residency as an arbitrary cue for contest settlement but because owners have real advantages over intruders. However, a modern theoretical study suggested that both the bourgeois strategy and the anti-bourgeois strategy can be evolutionarily stable when being an owner increases not only an individual's fitness but also its risk of death

(Kokko et al. 2006). Finding examples of the bourgeois and the anti-bourgeois strategies in nature would itself be valuable.

## Cross-References

- Aggression
- Evolutionarily Stable Strategies
- Territory Defense

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## Bovinae

### ► Bovine Life History

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## Bovine

### ► Bovine Life History

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## Bovine Cognition

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## Synonyms

*Bos taurus*; Cattle; Cow; Intelligence

## Definition

Cognition – the mechanisms by which an individual acquires, processes, stores, and acts upon

information and includes learning, memory, and decision-making.

## Introduction

Cognition refers to the mechanisms by which an individual acquires, processes, stores, and acts upon information and includes learning, memory, and decision-making (Shettleworth 2010). Relatively few basic studies of cognition in cows have been done. Most are framed in an applied setting (e.g., training cows to access automatic feeders, determining food preferences, managing mother-calf separations). These kinds of applied studies can, however, provide a window, albeit limited, into some of the cognitive capacities of cows. But studies of cognition (and other psychological abilities) in cows (and other animals) under more natural conditions generally yield richer and more authentic results. The balance between level of methodological control and context is one that needs to constantly be evaluated when interpreting the scientific literature on cow cognition. It is also important to recognize that the literature on cow emotions, personality, and social complexity also aids in inferring cognitive capacities in these other contexts that can then be more directly tested.

Cow cognition and behavior should be understood in terms of their evolutionary history and adaptations, which include their sensory-perceptual abilities. Modern domestic cows are a genetic mixture of several lineages from as early as over 10,000 years ago, when domestication began. The cow is a diurnal herd animal who depends on all five sensory modalities and who depends heavily on the social group for protection from predators. They are highly vigilant and sensitive to sounds above the highest range of human hearing and therefore often adopt defensive postures and behaviors in the seeming absence of an observable threat.

High reactivity (also labelled nervousness or fearfulness in the comparative personality literature) is an adaptive evolutionary trait in cows. They are facultative “hidiers” in that the young often sequester themselves away from predators

and call to their mother when they are in danger or need to be fed. Mothers usually forage at least 100 m away from their offspring's hiding place and return intermittently to nurse the calf. And lasting bonds are formed between mothers and calves and among herd members.

Therefore, tests of cognitive abilities in cows must take into account the fact that their psychology has been adapted over tens of thousands of years to be exquisitely socially sensitive to conspecifics, closely bonded to offspring and other group members, and wary of strangers.

## Discriminating Objects and Humans

Most studies of cow cognition have probed discrimination abilities, that is, the ability to learn to recognize the difference between two stimuli. Cows are capable of various forms of visual and auditory discrimination learning and retention over days and, in some cases, weeks. They are able to discriminate a wide range of objects based on various dimensions, including geometric shape (Baldwin 1981), color (Gilbert and Arave 1985), size difference (Rehkämper and Görlach 1997), and stimuli differing by both brightness and size (Schaeffer and Sikes 1970).

Cows can also discriminate more complex stimuli than static geometric shapes. For example, calves, as well as adult cows, can easily distinguish between different people based on their previous experiences with them (Hotzel et al. 2005) and can discriminate among individuals who are wearing the same clothes (Taylor and Davis 1998). Some evidence suggests cows can discriminate humans on the basis of facial characteristics but only when they can see the rest of the body, implying that they attend to a number of different features in combination.

## Discriminating Conspecifics

The ability to discriminate among conspecifics forms the basis for social relationships and is an important capacity for a highly social animal

such as the cow. Individual *discrimination* is not equivalent to, but is a prerequisite for, the more complex capacity for true individual *recognition*, defined as a mental representation of an individual's identifying characteristics.

Cows are able to discriminate among conspecifics under a variety of conditions and can also discriminate members of their own species from members of other species (dogs, sheep, horses, and goats). Rigorous controls for the amount of black and white surface, size of head, and other visual aspects of the stimuli ensured that simpler features that distinguish cows from other species could not be used in these studies. These findings suggest a complex capacity for categorization as the subjects were also presented with cows of various breeds and, therefore, various phenotypes and were able to discriminate photographs of different kinds of cow faces from those of other species. That is, cows can categorize the "sameness" of other cow faces despite phenotypic variability as a separate group from the faces of other species (Coulon et al. 2007). Evidence suggests two-dimensional photographs of familiar versus unfamiliar conspecifics are perceived as mental representations of real individuals (Coulon et al. 2009, 2011). These findings suggest cows have a sophisticated visual discrimination capacity when it comes to conspecifics and are also able to mentally create hierarchical categories or, perhaps, a species concept.

## Cognitive Development

One of the broad areas sorely lacking in our understanding of cow cognition is development. Despite evidence of mental representational abilities and, perhaps, basic concept formation in terms of discriminating conspecifics from other species, there is little known about how these capacities emerge or develop over time in cows. And while there are a few studies probing the impacts of various farming practices on calf psychology, there is no robust systematic literature on bovine developmental cognition. One striking area of deficiency in our knowledge of cow cognitive development relates to object permanence.

There are no published studies of object permanence in cows despite the fact that object permanence is a vital cognitive skill that underlies a number of mental representational capacities and its study is critical for interpreting the capacity of cows for higher-order concept formation, as suggested in studies of conspecific discrimination.

One test, the Krushinskii test, which probes how well subjects can follow a moving target, has come closest to resembling a formal test of object permanence in cows. The subjects follow a slow-moving food trolley, eating as they go. When the trolley moves into a tunnel where it cannot be seen (a form of invisible displacement), the subjects move to the far end of the tunnel to await the exit of the trolley, showing they can extrapolate future movements from the past trajectory of the trolley. Cows were capable of successfully completing this task, though they were not as consistent as pigs and goats (Albright et al. 1982).

## Spatial Cognition

Spatial cognition refers to the ability to acquire knowledge of, remember, organize and utilize information about spatial aspects of one's environment, including navigation and learning to discriminate and prioritize the locations of objects and the formation of cognitive maps. Some forms of spatial learning are dependent upon mental representations in both short- and long-term memory and can form the basis of complex cognitive maps of the environment, providing the foundation for many other social and nonsocial strategic behaviors during such tasks as foraging and traveling.

Grazing animals, such as cows, have robust spatial memory abilities, allowing them to forage with optimal efficiency. Hence, they perform well in maze tests. There is a fairly decent body of evidence for this conclusion. In a Hebb-Williams closed-field test of how cows navigate through mazes using detours, they performed favorably compared with pigs, sheep, goats, and dogs (Kilgour 1981). A number of studies of radial and parallel arm maze learning show that cows learn mazes efficiently, can associate several different locations with food, and retain

this knowledge for several hours, days, or even weeks, depending on the test. In a recent study, cows retained a memory of an association between a visual cue (a plastic tub) and a food reward for at least a year (Hirata and Takeno 2014).

Although it is likely that cows use visual cues in these circumstances, other kinds of cues and sensory modalities have not been ruled out.

## Social Learning

One of the ways social species take advantage of group living is through social (observational) learning. Social learning involves observations of a conspecific's behavior and its consequences and the application of that observation to one's own behavior. Some investigators view social learning as a form of deferred imitation or emulation, serving as a mechanism for cultural transmission. But careful experimentation is needed to differentiate among the many theoretical bases for social learning in various species. Nevertheless, the general capability for social learning is one of great significance in the evolution of complex behavior, and cows appear quite capable of learning from observing other cows.

Studies of housing differences in cows provide evidence that, when reared under natural social circumstances, they engage in social learning. For instance, cows who were never afforded the chance to graze began to show normal grazing behavior more quickly when they were grouped with experienced grazers than with inexperienced grazers (Costa et al. 2016). This kind of observational learning seems to be dependent upon having a natural social group to interact with, as cows with very limited contact with conspecifics show fewer propensities to learn from others when given the opportunity.

## Communication

Communication has been defined as "The imparting of information from one organism to another in a way that evokes a detectable response from the recipient at least some of the time"



(Wittenberger 1981, p. 613). Given that communication involves the processing of information, it is an integral part of understanding cognition in any species. There has been limited research on cow communication, and most has focused upon mother-calf calls. There is evidence, however, for individually distinctive vocalizations reflecting emotional states (Hall et al. 1988; Koene 1997). Playback experiments have shown that young calves (3–5 weeks old) are able to discriminate their own mother's vocalization from those of other adult female cows. Auditory cues alone are sufficient. Up until recently it was thought that dairy cows had limited ability to recognize their own calf's vocalizations (Marchant-Forde et al. 2002). However, recent research suggests that cows can recognize and respond to their own calf's vocalizations under conditions where calves are allowed to hide (de la Torre et al. 2016). During the first few weeks of life, calves hide silently in vegetation in order to avoid predation. Hider species tend to have unidirectional communication, but when calves vocalize out of alarm, the mother must retrieve the calf and, therefore, have the ability to recognize her own offspring, thus providing a purpose for bidirectional communication.

People who work with cows report that they respond to human vocalizations. Cows learn to come when called by specific names and are, therefore, capable of learning to associate specific referential information with the distinct vocalizations of another species (i.e., humans).

In general, cow vocalizations themselves appear to carry information about identity, emotional state, and the presence of predators and serve to relate meaningful information to conspecifics. However, much more research, specifically on the use of and processing of vocalizations in cows under more natural circumstances, is necessary to obtain a full understanding of cow communication.

## Cognitive Bias

Cognitive bias, also known as negative and positive judgment bias, is an area of intense interest in

comparative psychology, and the phenomenon is evidence of the complex interaction between emotions and cognition. Likewise, it has important implications for how performance on cognitive tasks is interpreted. Negative judgment bias is sometimes referred to as pessimism and positive judgment bias, optimism. Both involve viewing ambiguous stimuli negatively or positively depending upon prior experience.

There is evidence for negative judgment bias in cows. For instance, young cows are less likely to approach an ambiguous stimulus even 22 h after disbudding (removal of horns with a hot iron) (Neave et al. 2013), and calves are more likely to see an ambiguous stimulus as one previously associated with a negative outcome after being separated from their mothers. These findings show that, much like humans and many other species, when cows are distressed, they exhibit a relatively more negative response bias toward ambiguous stimuli (Daros et al. 2014).

There are no systematic studies of positive bias in cows. Given that a large percentage of cognitive studies on cows are done in contexts that involve either unnatural or negative experiences associated with farming practices, the importance of cognitive bias on the entire cognitive literature for cows cannot be overstated.

## Conclusion

Cows have well-developed discrimination and spatial cognitive abilities and are capable of not only complex learning but feats of long-term memory. They are capable of making discriminations among complex stimuli (humans and conspecifics). They also have social learning abilities and demonstrate cognitive bias. There is evidence for specific meaning in cow vocalizations and learning of referential human sounds. Therefore, there is evidence that cows are capable of forms of learning, cognition, and communication found in many other mammals.

However, in general, the literature on cow cognition is still quite bare, and much more basic research directly probing cow learning and cognitive abilities in a wider range of domains is

needed. For instance, further studies of object permanence would be important as a comparative literature on mental representation with other animals. And other compelling areas in comparative cognition already underway in many other species, including domesticated farmed animals, such as numerosity, learning set, and time perception, beg to be addressed in cows.

## Cross-References

- ▶ [Artiodactyla Diet](#)
- ▶ [Artiodactyla Life History](#)
- ▶ [Artiodactyla Morphology](#)
- ▶ [Bovine Diet](#)
- ▶ [Bovine Life History](#)
- ▶ [Bovine Locomotion](#)
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- ▶ [Social Learning](#)
- ▶ [Spatial Orientation](#)
- ▶ [Swine Cognition](#)
- ▶ [Swine Communication](#)
- ▶ [Ungulate](#)

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## Bovine Diet

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## Synonyms

[Feeding behavior](#); [Foraging](#)

## Definition

Bovine diet refers to the feeding strategies, type, and amount of food ingested by animals that are part of the subfamily Bovinae.

## Introduction

Bovines are part of the subfamily Bovinae and include the medium- to large-sized ungulates. Bovinae members are herbivores and possess cloven hooves (i.e., split into two toes) and two or four true horns that are not branched. Bovines are also ruminants, which make them well adapted to prairie environments, but they are found across most terrestrial environments. Examples of bovines are the domestic cattle (*Bos taurus*), bison (*Bison bison*), water buffalo (*Bubalus bubalis*), yak (*Bos grunniens*), gaur (*Bos gaurus*), Cape buffalo (*Syncerus caffer*), eland (*Taurotragus*

*oryx*), some species of antelopes (e.g., *Tetracerus quadricornis*), and the nilgai (*Boselaphus tragocamelus*). Most of the knowledge on diet and feeding habits of bovines comes from domestic species, but observation of their wild counterparts has informed the similarities and distinctions. Here we will explore our understanding of what bovines eat, how they digest their food, and their feeding behavior patterns.

## What Do Bovines Eat?

Bovines are herbivores that live in almost every type of terrestrial ecosystem, from the African savannas to the tropical rainforest, to the high mountain areas of Asia. Bovines occupy many feeding niches throughout the world, but mainly they are grazers that feed on graminaceous plants (i.e., grasses, some woody plants including cereals); however some are intermediary grazer/browsers such as the nilgai (*Boselaphus tragocamelus*) and the eland (*Taurotragus oryx*) (Wallington et al. 2007) or are almost exclusively browsers such as the mountain nyala (*Tragelaphus buxtoni*) (Brown 1969).

Bovines will feed on plants of widely divergent physical and chemical compositions, such as lichens, grasses, browse (i.e., forbs/herbs, leaves, and twigs of woody plants), and wild fruits. Many bovines that are preferred grazers will still ingest some level of browse in the wild, such as the wood bison (*Bison bison athabasca*), European bison (*Bison bonasus*), red forest buffalo (*Syncerus caffer nanus*), and anoa (*Bubalus depressicornis*). Similarly, range cattle may also include significant amounts of browse in their diet (Holechek et al. 1982). Bovines will make modifications to their diet throughout the year; during the rainy season, the main diet will consist of grasses, while during dry parts of the year, the diet will contain more browse and other feed sources. This flexibility in diet is used in pasture programs aimed at maintaining botanical species diversity. Also, most bovines require salt in their diets and are known to regularly visit natural salt licks to engage in ingestion of soil, called geophagy, especially in sodium-rich areas (King et al. 2016).

Geophagy may also serve to supplement other mineral intakes, ease gastrointestinal issues, or buffer the effects of dietary toxins (Kreulen 1985).

## Feeding Behavior

### Early Life

Under natural or seminatural conditions, the calf will remain close to the dam during the first few days, but after the 2nd week of life, the calf will begin to interact with other calves in the herd and even begin to graze and ruminate beginning at around 3 weeks of age; several months later, calves will begin to graze regularly with the herd (Reinhardt and Reinhardt 1981). The social interactions of young calves are associated with the learning process of recognition and selection of a suitable diet and habitat, where selection happens through the mimicking of social companions. The progression from maternal care to independence is one of the most sensitive periods for learning among young foragers, making the dam and social peers an important influence on diet selection (Provenza and Balph 1987).

### Social Learning and Social Facilitation

Young ruminants must learn how to select and eat appropriate foods. Two phenomena are especially influential in the development of grazing behavior in young bovines. Social facilitation occurs when the stimulus of another animal eating, approaching, or manipulating feed increases attention toward the feed and subsequently encourages the consumption of feed by others (Galef 1988). A related, but mechanistically different concept, is social learning through the observation of others (Galef and Laland 2005). During both social facilitation and social learning, the mother and young companions serve as sources of information regarding predator detection and the location of food, water, and shelter and, thus, are the most effective social models (Provenza and Balph 1987). These phenomena have been demonstrated in several studies in cattle. For instance, young cattle naïve to grazing have been shown to begin grazing sooner when turned out to pasture with an

experienced social companion compared to when turned out to pasture without a social model (Costa et al. 2016). Calves that were raised in a social group from an early age were quicker to begin consuming solid feed compared to when housed alone (Costa et al. 2015).

Herbivores that feed in large mixed-generation groups, like bovines, will use social learning as a tool to pass on food-selecting information from experienced to inexperienced foragers. Social learning enables an inexperienced animal to avoid the inefficiency and risk of testing each novel feed type, since the strategy of “trial and error” can sometimes lead to the ingestion of highly toxic species (Galef and Laland 2005). Cattle are especially food neophobic, meaning they are reluctant to consume unfamiliar foods (Costa et al. 2014); it is thought to be a mechanism to avoid the consumption of non-nutritive and toxic plants (Provenza and Balph 1987). Food neophobia is known to decrease in the presence of companions and when in familiar environments (Burritt and Provenza 1997). Food neophobia is so prevailing that individuals will even consume familiar foods that previously contained toxins over novel feeds when in an unfamiliar environment (Burritt and Provenza 1997). Through this series of mechanisms and influential social factors, the young bovine learns what and how to eat in its feeding environment and establishes food preferences that last through adulthood.

### Adult Feeding Patterns

In both natural and seminatural conditions, grazing ruminants, including bovines, select their diets from a wide variety of plant species differing in nutritional composition and availability (Provenza and Balph 1987). The selection of and preference for plants to graze, or browse, will depend in part on the individual’s nutritional needs and prior experience with these food sources, as well as the ability to cope with toxins (Provenza 2003).

As gregarious species, the feeding behavior patterns of ruminants typically are performed together as a group in captivity and in the wild (Miller and Wood-Gush 1991). This behavior has

an evolutionary origin offering foraging and anti-predator benefits (Provenza 2003), but even in domesticated ruminants like cattle, this behavior persists. Cattle show crepuscular feeding patterns in which they are most active at sunrise and sunset. Throughout the day, cows will divide their feeding bouts, or visits, into meals; these meals are characterized by a cluster of feeding bouts separated by short time intervals, followed by longer time intervals separating each meal. In confined cattle, different feed bunk designs can impact aggression, feeding time, and access to the feed bunk for subordinate animals (von Keyserlingk and Weary 2010).

Most wild bovine species are also diurnal with crepuscular feeding peak activities, which has been observed in many species, from cattle (*Bos taurus*) to the nilgai (*Boselaphus tragocamelus*) (Oguya and Eltringham 1991). However, these feeding patterns can be altered by the presence of humans or predators. For example, the gaur in India is typically diurnal, but in areas of high human disturbance, they become mainly nocturnal (Duckworth et al. 2016).

### Foraging Strategies

Grazing ruminants typically only remain at a feeding site for as long as the quality and quantity of food remains and will then either search for other food sources themselves (called “producers”) or wait for others to find food and then follow them to the food source (called “scroungers”) (Giraldeau and Caraco 2000). These different foraging tactics are associated with trade-offs: producers can find higher food quality, or availability, at the front or periphery of the herd but risk predation through exposure and limited vigilance during searching and grazing. Alternatively, scrounging is a less risky foraging tactic but, consequently, may limit food quality and availability. Individuals within a herd may also adopt “leader” and “follower” roles in making decisions when to move between feeding locations (Dumont et al. 2005); however, producers of the herd may not necessarily be the leaders. Furthermore, individuals will switch between producing and scrounging depending on the quality and abundance of food sources

and depending on the frequency of individuals adopting each of these foraging tactics in the herd. This is in accordance with optimal foraging theory, which states that an animal will adopt a foraging behavior that brings the most benefits while minimizing costs and thus maximizing fitness (Kie 1999).

### Ruminant Digestive System

Bovines are part of a diverse group of animals known as ruminants, which have a specialized digestive system that allows them to digest large amounts of plant material by breaking down the cellulose fibers through fermentation prior to digestion. A significant feature of the ruminant digestive system is a specialized stomach containing four distinct chambers: the rumen, reticulum, omasum, and abomasum (Czerkawski 1986).

The rumen is the largest of the four compartments, with a capacity of over 200 L, and can be thought of as a large fermentation vat. The rumen and a second compartment, the reticulum, are typically considered one organ because they have similar functions and are separated only by a small muscular fold of tissue. Together they are referred to as the reticulorumen. The reticulorumen contains trillions of microorganisms, including protozoa, bacteria, fungi, and yeast that aid in the fermentation of ingested feed. These microbes ferment and break down plant cell walls into their carbohydrate fractions and produce volatile fatty acids (VFAs), such as acetate (used for fat synthesis), propionate (used for glucose synthesis), and butyrate from these carbohydrates (Grunberg and Constable 2009).

Because vertebrates lack the enzyme cellulase to break down cellulose in plants, ruminants rely on the anaerobic microbial flora of the rumen to digest this cellulose. These microbes function best in a slightly acidic and narrow pH range from 6 to 6.4 (Orskov 1994). Once the animal ingests and swallows forage material, the rumen microflora immediately begins to ferment and break down the plant material. Food is mixed with saliva and moves back and forth between the rumen and the reticulum. The lining of the rumen wall

contains many finger-like projections called papillae that effectively increase the surface area for absorption of volatile fatty acids into the bloodstream for energy production and biosynthesis (Czerkawski 1986).

Following ingestion of large amounts of plant material, ruminants engage in a process called “rumination.” This process involves the formation of a bolus (or clump), of partially digested food which is then regurgitated from the reticulum and re-chewed in order to further break down plant matter. The animal then swallows the bolus and repeats the process. Rumination serves to reduce particle size of plant matter (and thus increase surface area for absorption) and aids in digestion (Welch 1982). During rumination, large amounts of saliva are generated which aids in buffering the pH of the rumen to ensure an optimal environment for the microflora (Carter and Grovum 1990). Rumination occurs predominantly when the animal is resting and not eating, typically consuming about 7–12 h each day (Welch et al. 1970).

The reticulum undergoes a series of biphasic contractions occurring at regular intervals, which serves to separate particles during the passage of digesta between the rumen and reticulum. The first contraction separates the large particles and sends them back to the rumen for further digestion, and sends the finer particles through to the omasum. The second contraction serves to completely empty the reticulum in order to refill with rumen contents and initiates regurgitation of a bolus during rumination (Constable et al. 1990).

The omasum functions to receive digested plant material from the reticulum and absorbs water, minerals, and other nutrients into the bloodstream before the digesta is passed into the abomasum (Prins et al. 1972). The abomasum is the fourth compartment of the ruminant stomach, also called the true stomach, and is equivalent to that of a monogastric stomach with similar anatomy and function. The abomasum serves to further break down digesta through chemical means rather than by mechanical or fermentation methods, like the other compartments. The abomasum produces hydrochloric acid and digestive enzymes such as pepsin that hydrolyze the proteins in the food and pancreatic lipase secreted from the pancreas that

breaks down fat. These secretions help prepare proteins for absorption in the intestines. The abomasum is also equipped with the enzymes which are able to digest the bacteria and other microbes that have passed from the reticulorumen (Stewart et al. 1987). By digesting these microbiota, the ruminant is able to reclaim many of the nutrients (e.g., carbon, phosphorus, and nitrogen) consumed by the microbiota in the rumen.

The unique digestive system of bovines has allowed them to exploit fibrous plant resources, and the absorption of microorganisms in the abomasum provides essential amino acids and B vitamins, which eliminates the need to obtain these elements externally. However, this process comes at a cost: bovines must spend a large amount of time foraging to obtain adequate amounts of feed to undergo gluconeogenesis to extract appropriate nutrients for survival. In fact, the total digestion process for ruminants can take up to 60–80 h from food intake to excretion (Hartnell and Satter 1979).

## Conclusion

In summary, there is a wealth of information about wild and domesticated bovine diets, digestion, and feeding behavior. Bovines are crepuscular grazers that inhabit most terrestrial environments, with some species exhibiting characteristics of browsers. As ruminants, they have the ability to acquire most of their nutrients from forage, but this requires extended bouts of feeding and a specialized digestive system containing microflora to break down the cellulose from plant material. Bovines will learn to graze by observing social models such as the mother and young conspecifics and, as adults, will adopt foraging strategies that allow them to obtain high-quality feed while minimizing predation risk. These characteristics make bovines a unique group of herbivorous ungulates that are common across the globe.

## Cross-References

► [Bovine Life History](#)



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## Bovine Gaits

### ► Bovine Locomotion

## Bovine Life History

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## Synonyms

[Bovinae](#); [Bovine](#)

## Introduction

The Bovinae subfamily are within the Bovidae family of the order Artiodactyla and fall under the class Mammalia within the phylum

Chordata and the kingdom Animalia. In the past 20 years, the genetic divergence between species within Bovinae was largely unknown, and characterizations were made on physical differences (Janecek et al. 1996). However, since the early phylogenetic publications, molecular work has characterized differences within the Bovinae subfamily.

Bovinae are characterized as having unique BovB retroposons that identify cattle, nilgais, and spiral-horned antelope as being closely related (Nilsson et al. 2012). Bovinae members are herbivores and possess cloven hooves (i.e., split into two toes) and two or four true horns that are not branched. This subfamily includes ruminant ungulates that have diets comprised largely of grass and have sexually dimorphic characteristics. In fact, all male antelope contained within this subfamily have horns shaped to their particular fighting style for competing for mates (Lundrigan 1996) and larger skulls than females (Brakora 2012). The most common sexually dimorphic characteristic is a difference in physical size.

There are three tribes contained within the Bovinae subfamily: the Boselaphini (four-horned antelopes), Tragelaphini (spiral-horned antelopes), and Bovini (cattle and medium- to large-size herbivores) (Maceachern et al. 2009). Many species of bovines are domesticated or in close contact with humans across the globe, such as domestic cattle, water buffalo, and the yak. Some wild bovines are listed as threatened or endangered such as the banteng (*Bos javanicus*) and the lowland anoa (*Bubalus depressicornis*) or critically endangered and even could be extinct, such as the kouprey (*Bos sauveli*) and the saola (*Pseudoryx nghetinhensis*) (IUCN 2016). Here we will explore the differences between these three tribes of Bovinae, including morphology, reproduction, and some evolutionary aspects that make these animals special.

## Taxonomic Classification

### Boselaphini and Tragelaphini Tribes

The true antelope (Boselaphini tribe) includes the genus *Tetracerus*, the four-horned antelope

(*Tetracerus quadricornis*), and the genus *Boselaphus*, which includes the Asian nilgais (*Boselaphus tragocamelus*) (Nilsson et al. 2012). Tragelaphini is a much larger tribe and contains the genus *Tragelaphus*, comprised of the Bongo (*Tragelaphus eurycerus*), the Greater Kudu (*Tragelaphus strepsiceros*), the Kewel (*Tragelaphus scriptus*), Bushbuck (*Tragelaphus sylvaticus*), the lesser Kudu (*Tragelaphus imberbis*), the mountain nyala (*Tragelaphus buxtoni*), nyala (*Tragelaphus angasii*), and the Sitatunga (*Tragelaphus spekii*) (Matthee and Robinson 1999). The genus *Taurotragus* includes the elands (Matthee and Robinson 1999). These three tribes of antelopes are often used as a source of meat and hide (Maceachern et al. 2009).

**Bovini Tribe**

The Bovini tribe is largely known for its diverse array of species that are widely spread across the world and have many domesticated species that are often used as a source of food and for work. The Bovini tribe contains water buffalo (*Bubalus* sp.), cattle (*Bos taurus*), yaks (*Bos mutus*), and bison (*Bison bison*). Buffalo are divided among two genera, the *Bubalus* and the *Syncerus*, which split from the cattle and bison nearly 5–10 million years ago (Maceachern et al. 2009). The *Bubalus* genus includes the domestic water buffalo (*Bubalus bubalis*), the wild Asian water buffalo (*Bubalus arnee*), lowland anoa (*Bubalus depressicornis*), the Mountain anoa (*Bubalus quarlesi*), and the tamaraw (*Bubalus mindorensis*) (Tanaka et al. 1996). The genus *Syncerus* contains the African buffalo *Syncerus caffer* (Tanaka et al. 1996). The anoa diverged from one another over 2 million years ago, nearly at the same time as the divergence of all *Bubalus* species, and hence is represented as a unique species (Tanaka et al. 1996).

The *Bos* genus contains several species that are domesticated and typically used for farming purposes. The most well-known species include domesticated cattle (*Bos taurus*) and are comprised of two subspecies: the taurine or European cattle (*Bos taurus taurus*) and the humped zebu cattle (*Bos taurus indicus*), which diverged from their common ancestor 610,000–850,000 years ago (Machugh et al. 1997). The *Bos* genus also contains the kouprey (*Bos sauveli*), the banteng (*Bos javanicus*), the gaur (*Bos frontalis* or *Bos gaurus*), the domestic yak (*Bos grunniens*), and the wild yak (*Bos mutus*) (Hassanin and Ropiquet 2004). According to recent molecular phylogeny, the kouprey, gaur, and banteng are closely related, diverging sometime during the Pleo-Pleistocene period, while the yak are more closely related to the American bison (Hassanin and Ropiquet 2004). According to mitochondrial DNA analysis, the American bison (*Bison bison*) is a closer relative to the yak (*Bos mutus*) than it is to the European bison or wisent (*Bos bonasus*), with divergence taking place over a million and a half years ago (Zeyland et al. 2012). A taxonomic summary of the Bovinae subfamily (Table 1) is recreated below and adapted from Maceachern et al. (2009).

**Reproduction and Life History**

**Four-Horned Antelopes**

The four-horned antelope lives in Nepal, subsisting off of shrubs and grasses, and can be seen climbing to reach forage. They are geographically isolated and endangered (Amar et al. 2016). Its vigilance and tendency to hide in thick brush (Krishna Prasad 2015) make it a difficult species to study. It is the only Bovinae that has four horns, which are only present in males and used for

**Bovine Life History, Table 1** Summary of the representatives in the subfamily Bovinae

| Subfamily       | Bovinae                                                   |                                                                    |                                                |                                      |
|-----------------|-----------------------------------------------------------|--------------------------------------------------------------------|------------------------------------------------|--------------------------------------|
| Tribe           | Tragelaphini                                              | Boselaphini                                                        | Bovini                                         |                                      |
| Subtribe        | –                                                         | –                                                                  | Bubalina                                       | Bovina                               |
| Representatives | Spiral-horned antelope ( <i>Tetracerus quadricornis</i> ) | Four-horned antelope and nilgai ( <i>Boselaphus tragocamelus</i> ) | Buffalo ( <i>Bubalus</i> and <i>Syncerus</i> ) | Oxen ( <i>Bos</i> and <i>Bison</i> ) |

competition for mates during the rut. Unlike other Bovinae, they are rarely seen in more than pairs (Krishna Prasad 2015). They are seasonally polyestrous, with mating season occurring June through September, with gestation length being 7.5–8 months (Baskaran et al. 2011). One to two young are produced at birth, weighing 1 kg (Baskaran et al. 2011). They live up to 10 years in the wild (Nowak 1999). There are several species which prey on the four-horned antelope including tigers, wolves, leopards, and small cats (Norwak 1999).

### **Spiral-Horned Antelopes**

The nyala has white stripes and lives in South-eastern Africa. They prefer to graze dense vegetation near woodlands. It is best known for its spiral horns, which are only carried by males. Females reach sexual maturity at 2 years, with a gestation of 7 months (Van Rooyen 1993). Female offspring bond with the mother and stay in the herd, which is usually comprised of females (Tadesse and Kotler 2014). Females weigh 58 kg at maturity, while males weigh 100 kg (Van Rooyen 1993). They live up to 19 years and are preyed upon by lions, hyena, and leopards (Tadesse and Kotler 2014).

### **Water Buffalo**

More than 148 million buffalo are domesticated, with nearly half living in India. The river buffalo and the swamp buffalo are two types of water buffalo that are both considered domesticated, providing milk and meat, and are often used for draft purposes. Though buffalo can be breed year-round, due to temperature pressure and limited rainfall, many buffalo only cycle at certain times of the year and are often considered seasonally polyestrous (Perera 2011). The oestrus cycle is every 21 days, while the gestation period is 315 days on average (Machado et al. 2010). Buffalo bulls reach puberty at 2 years of age but are not considered sexually mature until 30–33 months of age (McCool and Entwistle 1989). Swamp buffalo cows reach puberty around 22–23 months of age (Anjum et al. 2012), while river buffalo can reach puberty earlier at

15–18 months of age (Perera 2011). The natural weaning age of water buffalo is 265 days or 8.8 months (Machado et al. 2010).

Water buffalo weigh 33 kg at birth, with no sex differences (Machado et al. 2010). River buffalo bulls weigh 1000 kg at maturity and females weigh as much as 500 kg at maturity; the swamp bulls weigh 750 kg at maturity, while females weigh as much as 550 kg at maturity. The most striking difference between river buffalo and swamp buffalo is milk production. The river buffalo produce 1000–2000 kg per lactation and are capable of digesting low-nutrient forages (Araujo et al. 2012). The river buffalo is most widely known for its use in production of mozzarella cheese (Araujo et al. 2012). The swamp buffalo, in contrast, produces 430–620 kg of milk per lactation but maintains condition better than the river buffalo (Bonfatti et al. 2012).

### **Domestic Cattle**

Cattle are the most widely distributed and highest population of Bovinae in the world. Cattle are most often used for meat, milk, and draft purposes. The Hindu religion considers cattle to be sacred in Nepal and India; therefore, only the milk is allowed to be consumed.

Cattle cycle every 21 days, are pregnant for 9 months, and are gregarious, with one to two bulls controlling the breeding within the herd, while other mature bulls live together in small groups (Salisbury et al. 1978). Due to the gregarious nature of cattle, a lead cow usually directs the grazing patterns and movement of the herd, and calves inherit the social status of the mother (Reinhardt et al. 1986). Sexual maturity depends largely on whether the cattle are taurine or zebu. Taurine cattle reach puberty around 240–470 days of age, varying largely by breed with lighter breeds such as Hereford reaching puberty sooner than heavier breeds such as Chiana (Laster et al. 1979). Brahman, a breed of zebu cattle, reach puberty much later, averaging 555 days for bulls and 715 days for heifers, though these animals are much more heat tolerant (Fortes et al. 2012). Natural weaning age is

around 8.8 months (Jensen 2009) and mature weight ranges widely by breed.

### Bison

The American bison was recently near extinction, but due to a large rehabilitation program, American bison were recently removed from the endangered list. Bison are not considered domesticated, though it is popular in Canada to raise them for a leaner meat. The American bison is seasonally polyestrous, typically being bred between mid-June and early September in comparison to cattle, who breed year-round (Rutberg 1986). The oestrus cycle is every 21 days, with the cow being receptive for 24–48 h after ovulation, while the gestation period averages 275 days (Love et al. 2017). Sexual maturity for bulls depends on age, averaging  $16.5 \pm 2.5$  months (Helbig et al. 2007). Cows typically give birth to a singleton at 3 years of age but occasionally may have twins. The natural weaning age for bison is 8 months. Forced weaning sooner has detrimental social dynamic effects, as gregarious bison inherit their mother's rank in the herd and associate with the mother for life if weaned naturally (Brookshier and Fairbanks 2003). Bison calves are around 23 kg at birth, while at maturity bulls weigh as much as 1000 kg and cows weigh as much as 500 kg. Life expectancy in the wild averages 15 years but can be as high as 20 years, depending on predation pressure (Lott 2002).

Wolves are the primary threat to bison, and their feeding behavior is modified to reflect predation pressure (Léa and Daniel 2013). For instance, Bison will spend less time foraging and leave more lush vegetation in an open meadow where wolves could be present (Léa and Daniel 2013).

### Conclusion

In summary, Bovinae is an important subfamily containing domesticated ruminants, some of which are critically important for animal agriculture, including use for food and animal labor

across the globe. Bovinae are characterized as having unique BovB retroposons, are herbivores and possess cloven hooves (i.e. split into two toes) and typically have a set of horns. Bovinae comprise three tribes, Boselaphini, Tragelaphini, and Bovini that are very distinct and heterogeneous, from 100 kg solitary forest-living animals to many thousands of herds of 1500 kg savanna-living animals. The adaptability of animals of these tribes to a variety of habitats makes them an important group of ruminants across the globe.

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## Bovine Locomotion

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## Synonyms

Bovine gaits; Cow locomotion

## Definition

Movement used by the subfamily Bovinae (e.g., buffalo, bison, domestic cattle, yak, and the four-horned and spiral-horned antelopes) to traverse their environment.

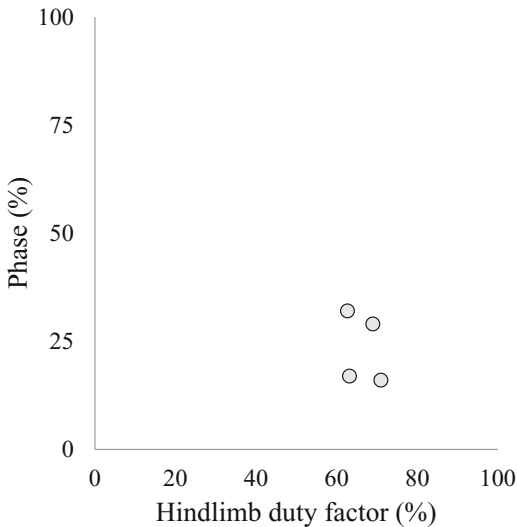
Bovinae, a subfamily of Bovidae, consist of buffalo, bison, domestic cattle, yak, and the four-horned and spiral-horned antelopes (MacEachern et al. 2009). The subfamily Bovinae consists of medium to large even-toed ungulates that can be further divided into tribes of *Tragelaphini* or *Strepsocerotini* (spiral-horned antelopes), *Boselaphini* (four-horned antelope), and finally *Bovini* (buffalo and cattle species). Bovinae have a specialized digestive system able to metabolize cellulose. This has resulted in meat, milk, and hide production with strong cultural and financial influence worldwide. The locomotor capabilities within subfamily Bovinae share many similarities although different species within the subfamily vary to a limited extent. For example, domestication of certain bovine species, especially *Bos taurus* (common cattle), has led to altered characteristics including enhanced docility and decreased size (Lenstra and Bradley 1999).

## Major Locomotor Modes

**Bovine locomotion** follows the same general patterns exhibited by most quadrupedal animals, including walking, trotting, and galloping gaits. Furthermore, bovines are also capable of jumping and swimming, but these gaits are situational and less commonly studied (Phillips 2002). Bovinae employ these gaits in the forward direction and adapt their locomotor styles depending on energy capacity and environmental necessity. These locomotor modes are generally classified as either symmetrical or asymmetrical depending on the activity in which they are engaged. During walking and trotting, the forelimbs and hindlimbs exhibit footfall with evenly spaced timing, and this is considered a symmetrical gait. The walking gait pattern most commonly observed in the bovines is the lateral-sequence lateral-couplet (Fig. 1). Meanwhile, during the bovine galloping gait, they have an uneven timing between forelimbs and hindlimbs footfall, and this is classified as an asymmetrical gait (Granatosky 2018).

Dairy cows have been investigated regarding the unusual motions that occur during swing phase (i.e., the portion of the stride where the limb is not in contact with the substrate). Gait analysis reveals that both the forelimbs and hindlimbs of dairy cows are internally rotated and adducted when the limb is first lifted off the ground, nearly contacting the contralateral limb. As the forelimbs and hindlimbs are lifted, the space between the toes, known as the interdigital cleft, becomes closed and then passively reopens at the end of swing phase (Meyer et al. 2007). Dairy cows contact the ground first with their lateral claws and add slight external rotation upon landing. Analysis of the ground reaction forces, the force exerted by the ground on a body in contact with it, during dairy cow locomotion shows that almost all the force exerted at heel strike is distributed to the lateral claw, specifically the outer surface (Meyer et al. 2007; Ossent et al. 1987; van der Tol et al. 2003).

It should be noted that walking behaviors are variable and subject to change depending on the



**Bovine Locomotion, Fig. 1** “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in bovines ( $n = \text{four species}$ )

conditions of the walking surface and overall health of the animal (Alsaad et al. 2017a, b). As such, considerable research has been devoted to understanding how substrate influences gait parameters in dairy cows and locomotor health. Poor flooring can affect animal welfare by impairing normal locomotion and thus increasing the risk of lameness (see below) and foot disorders. Pasture is the most comfortable floor for the hooves as it provides the optimal balance of the hoof horn wear and growth and a natural hoof load. Access to pasture is reported to be beneficial in reducing lameness and the risk of cows being affected by hoof disorders compared with zero-grazing herds. Alsaad et al. (2017b) confirmed that pasture results in “optimal locomotor characteristics,” such as duration of gait cycle, longer stance-phase duration, shorter swing-phase duration, higher walking speed, longer stride length, and higher peaks of foot load and toe-off. However, gait variables of cows walking on rubber mats did not show any biomechanical differences compared with asphalt floors; only stride length tended to be longer on rubber mats. Such findings highlight the importance of maintaining proper locomotor conditions for promoting animal health (Alsaad et al. 2017a, b).

Trotting is an alternative gait that is performed at a moderate speed; it is quicker than walking, but slower than a gallop. It is a symmetrical, two-beat gait characterized by diagonally opposite feet moving in phase with each other; for instance, the right hindlimb and left forelimb will be in phase with each other, and conversely the left hindlimb and right forelimb will be in phase with each other. During the trot, bovines will alternate between phases of dual support from either side of the body and phases of suspension, also known as an aerial phase. The trot provides several advantages, namely, that two legs work together in unison to propel the animal forward and provide cushioning from shock (Hildebrand 1989).

Galloping is the fastest method of locomotion utilized by bovines. Specifically, the bovines use a transverse gallop, which is also used by horses and other large, long-legged quadrupeds (Phillips 2002). In this mode, the two forelimbs contact the ground at approximately the same time; the second limb to touch the ground is referred to as the leading forelimb. The leading forelimb remains in contact with the ground for a longer time and helps provide stability. Once the leading limb is lifted off the ground, there is an aerial phase with all the legs off the ground and underneath the animal; this is referred to as the suspension phase or gathered-flight phase (Biancardi and Minetti 2012). Following the suspension phase, the hindlimbs will then contact the ground; the first foot to contact the ground is always contralateral to the leading forelimb and is quickly followed by the neighboring hindfoot. This contralateral relationship between leading forelimb and contralateral hindfoot ensures that the feet do not interfere with one another and disrupt the animal’s gallop (Hildebrand 1959). Finally, it has been determined that the hindlimbs provide a majority of the propulsive forces in the bovine gallop, unlike in other animals where the back is crucial to propulsion (Phillips 2002).

## Lameness

Lameness is an abnormal gait or stance of an animal that is the result of dysfunction of the

locomotor system. This can be caused either by neurological disfunctions or injuries. Lameness is an animal health and welfare concern, as well as a production issue. Pain due to lameness often limits growth because animals may be reluctant to eat or drink. The financial impact of lameness includes losses from decreased production, cost of treatment, prolonged calving interval, and possibly nursing labor. Lameness prevalence ranges from 14.8% in Switzerland to 54.8% in the northeastern United States (Alsaad et al. 2017a, b).

Classification systems are often used to determine the health of cows on farms. They are sometimes referred to as “locomotion scoring methods.” Locomotion scoring methods historically have used a five-level scale by which either farmers, researchers, or veterinarians score up to seven different traits of the cow. Generally, the most important gait abnormalities for detection of

lameness include asymmetric gait, arched back, head bobbing, tracking up, and reluctance to bear weight (Schlageter-Tello et al. 2014). Cows which do not meet the minimum requirements in this scale are deemed as lame (Schlageter-Tello et al. 2015; Fig. 2).

Due to the time-consuming and costly nature of this process, classification is sometimes neglected and cows progress to complete lameness. Automatic lameness detection systems have been developed which continuously detect lameness without manual scoring (Distl and Mair 1993). Another benefit is they can predict the possibility of future lameness of cows. This is done with a camera which records the gait of the cows as they pass through an alleyway. Automatic computer algorithms evaluate hoof locations during the gait. This method has shown a high level of precision and continues to be utilized and improved (Song et al. 2008; van Nuffel et al. 2015).

# **Bovine Locomotion,**

**Fig. 2** Locomotion scoring methods historically have used a five-level scale by which either farmers, researchers, or veterinarians score locomotor health and assess lameness in domestic cattle

## **Normal**

Stands and walks normally with flat back. Long confident strides

1



## **Mildly Lam**

Stands with a flat back, arches when walks. Slightly abnormal gait.

2



## **Moderately Lam**

Stands and walks with arched back. Short strides.

3



## **Lame**

Arched back standing and walking. Favors certain legs.

4



## **Severely Lam**

Constant arched back. Great difficulty moving.

5



## Conclusion

This entry introduces the locomotor behaviors observed in the Bovinae. Overall, the bovines utilize a lateral-sequence lateral-couplet method of ambulation during walking. This is the most common for quadrupeds with longer legs as stability loss is minimal. At higher speeds the bovines use trotting and transverse galloping gaits. The walking gait of cows is commonly assessed and used to identify lameness. Lameness is an abnormal gait or stance of an animal that is the result of dysfunction of the locomotor system. This can be caused either by neurological disfunctions or injuries. Lameness is an animal health and welfare concern, as well as a production issue. Free-ranging cattle on pastures have a lower incidence of lameness.

## Cross-References

- Activity Budget
- Adaptation
- Adaptedness of Behavior
- Adaptive Radiation
- Artiodactyla Locomotion
- Artiodactyla Morphology
- Artiodactyla Navigation
- Basal metabolic Rate (BMR)
- Bovine Cognition
- Bovine Diet
- Bovine Life History
- Captivity
- Common Ancestor
- Dispersal Ability
- Dispersal Patterns
- Diurnality
- Domestication
- Ecology
- Evolution
- Gait
- Herbivore
- Home Range
- Homology
- Homoplasy
- Husbandry
- Locomotion
- Morphology
- Muscular System
- Natural Selection
- Navigation
- Phylogeny
- Quadrupedal
- Safari
- Species
- Swine Locomotion
- Taxa
- Terrestrial
- Ungulate
- Vertebrate Nervous System
- Zoo
- Zoology

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## Bowerbird Aesthetics and Cognition

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## Synonyms

Bower-birds; *Ptilonorhynchidae*

## Definition

Bowerbirds are a family of passerine (perching) birds from Australia and New Guinea that are renowned for their unique and elaborately colored decorative constructions (or bowers) which are constructed by the males of the species and are used not as nests but as courtship arenas to attract females. The bowerbird family contains 20 different species in five genera (17 species of which construct bowers and the remaining 3 of which do not), and they are found in a range of different habitats such as rainforests and acacia forests.

## Introduction

As has rightly been suggested, bowerbirds became “emblematic of sexual selection ever since [Charles] Darwin’s illustrative use of their mating arenas in *Descent of Man and Selection in Relation to Sex*” (Milam 2010, p. 83). However, the initially more contentious nature of the theory of sexual selection within Darwin’s overall theory of evolution by selection mechanisms meant that the question of whether bowerbirds possessed a refined aesthetic judgment comparable to that possessed by human beings also quickly became a contentious topic. The aesthetic sensibilities of bowerbirds have indeed been periodically recognized in varying degrees in the literature for over a century, but they have also sometimes been doubted.

## History of Bowerbird Analysis

For example, in *The Descent of Man*, Darwin commented that the “playing passages of bowerbirds are tastefully ornamented with gaily-coloured objects; and this shows that they must receive some kind of pleasure from the sight of such things,” this being the “best evidence . . . of a taste for the beautiful” in birds (Darwin 1874 [1871], p. 92, 413). At the end of the nineteenth century, a “strongly marked aesthetic sense in birds” in relation to the functioning of courtship colors was deduced from the construction habits of particular Australian bowerbirds (Poulton 1890, p. 21, 320).

At the beginning of the twentieth century, George Romanes described bowerbird displays as follows: “The most consummate artists in this respect are, however, the bower-birds . . . these sundry cases [of bower construction] alone seem to prove a high degree of the aesthetic sense as occurring among birds” (Romanes 2015 [1910], p. 99–100). Elsewhere he judged that the construction of the bowers furnished “the most un-exceptionable evidence of true aesthetic, if not artistic feeling on the part of the bird which constructs them” (Romanes 1898, p. 279).

Bowerbirds actively painting or plastering the walls of their bowers with colored materials were first observed in 1920 (Marshall 1954, p. 51), further cementing the idea that these birds possessed a refined aesthetic sense. It was judged by one naturalist of the era that: “The ‘Bowers’ of the ‘Bower-builders’ are the most remarkable variants on ‘Secondary Sexual Characters’ yet brought to light” (Pycraft 1913, p. 158, Plate 29). Some early scholars even explored the link between bowerbird decoration, what was termed pre-aesthetics, and the initial origin of art itself (Soderberg 1929).

By the mid-twentieth century however, it was declared: “The fact that some bower-birds select objects that appeal to man’s sense of beauty is no proof that such articles have a similar effect on the bird,” and on a separate topic: “There is no evidence whatever that they are more intelligent than any other crow-like bird” (Marshall 1954, p. 185, 67). The idea that one central motivation for bower construction was primarily an aesthetic one was

correspondingly doubted in the literature of the period as an “anthropomorphic generalization” that was unsupported by any experimental evidence (Marshall 1954, p. 1). Instead, the bowers were conceived at this time more as a displacement nest-building activity with more conventionally avian reproductive and territorial functions (Milam 2010, p. 92), and bower painting activity was seen as straightforward courtship-related feeding behavior.

However, more recently the pendulum has swung back in the other direction, and it has been concluded that bowerbirds should be regarded as true artists with sophisticated aesthetic sensibilities and relatively high intelligence, with the bowers being both artistic and reproductive-related outputs (Attenborough 2007; Endler 2012, p. 282). This conclusion is reached partly from the techniques that are sometimes employed. For example, some bowerbirds construct forced perspective illusions for their bowers in order to manipulate the perceptions of the females. Objects are arranged on the floor leading up to the bower so that they increase in size as the spacing from the bower increases, creating a type of artificial perspective or optical illusion, this being a basic technique of human artistic composition since the Renaissance (Costandi 2012). Other bowerbirds use color constructions to influence the female’s perception of elements within the bower. The nature of bowerbird art and aesthetics and its underlying cognitive foundations will, consequently, be the main focus of the rest of this entry.

## Bowerbird Aesthetics

Art can be defined as the corpus of animal activities devoted to creating visual, aural, language-based, and/or performance-related artifacts and processes that express an individual’s (or a group’s) imaginative ideas, concepts, and/or skills and techniques; these artifacts have been designed to be consumed by an audience for their aesthetic beauty, emotional engagement, and/or intellectual stimulation (Barnett 2019). How do bowers as artifacts meet various aspects of this definition?



Bower constructions can be divided into three main types: court bowers (ground objects on a prepared open clearing), avenue bowers (objects within constructed walls made from sticks), and maypole bowers (objects within sticks around a sapling or small tree, sometimes with a roof). Variants on these also exist such as double-maypole bowers and hut-maypole bowers (Prum 2017, p. 184). The males decorate their bowers with various objects of particular selected colors: for example, satin bowerbirds prefer blue objects while spotted bowerbirds prefer green objects (Kelley 2017). These favored colorings are often tailored to species-specific female preferences. Archbold's bowerbird prefers certain ornate feathers from a particular bird of paradise for their bower decoration, these feathers being particularly difficult to find (Ridley 1993, p. 143). In addition, it has been suggested that "geographically varying bower styles may be a culturally transmitted trait, like human art styles" (Diamond 1986), although sexual selection may also play an important role in initially developing bower types (Albert et al. 2000).

The individual collected objects used for constructing and decorating the bowers include both a large variety of naturally found objects such as twigs, leaves, pieces of bark and bamboo, flowers, stones, small pieces of rock and charcoal, fungi, moss, seeds, fruits and fruit pulp, berries, shells, feathers, straw, amber, and even dead animal parts such as snakeskin, insect casings, fossils, and animal bones. Also, some man-made objects made from glass, metal, cloth, and plastic are used where they are available such as pieces of broken glass, plastic bottle tops, pieces of fabric, pins, and even clothes pegs. These found objects are carefully arranged either individually or in groups of objects, the groups being either flat or made into deliberately constructed and shaped piles, usually with appropriate color coordinations.

It has been suggested that species select their favored colors in relation to the regional light regime in which they reside. Bowerbirds in foggy ridge tops with limited visibility select black decorations whereas those in sunlit locations select bright colors (Borgia 2002, p. 1052). One observer of bowerbirds described the

operation of their evaluative judgment regarding the collected items as follows: "He found that the males are very selective about the objects they choose. They put a flower into the wall of moss they have erected, stand back, and look it over. It frequently happens that they remove it and place it elsewhere" (Eibl-Eibesfeldt 1975, p. 144). It has therefore been concluded that bowerbirds possess "an extraordinarily broad aesthetic palette" for colors, materials, and for intricate designs (Prum 2017, p. 193).

Although some bower constructions are fairly simple in composition, some others are very complex and extensive in scale and take weeks to construct, using as many as 1000 short sticks, reaching heights of up to 1.5 m and widths of up to 2.5 m; some of the outer constructions are so well-made that they are waterproof (Gould and Gould 1997, p. 204). Many of the bowers are also aesthetically pleasing even to the human eye – one bower is made in a decorated Christmas tree style – suggesting that aspects of aesthetic appreciation are common to different animal species. For example, some bowerbirds that collect blue-colored objects for their bowers collect various shades of blue objects and then arrange them in a blue-shading mosaic pattern. Other bowerbirds paint the internal walls of their bowers with various colored substances such as masticated plant matter or berry juice (Bravery et al. 2006). The bowers of many bowerbirds are continually repaired and reconstructed as is required in relation to instances of climatic, animal, or marauding competitor interference.

Finally, some of the avenues that are constructed by bowerbirds for their avenue bowers are very skillfully and carefully crafted from large groups of branches to create shaped and defined internal spaces such as ovals, triangles, or semicircles and also utilize varieties of roofing structures, indicating an understanding of the principles of architectural design, in addition to the principles of color coordination. Given this very extensive range of constructed aesthetic features and judgments, to deny that bowerbirds are indeed avian artists and architects would be highly ungenerous.

## Bowerbird Cognition

A central issue arising from bowerbirds being defined as avian artists is: what are the cognitive foundations of their various sophisticated aesthetic and architectural understandings? Various investigations into this topic have yielded some noteworthy results. For example, one recent study concluded on this issue that even accepting that “birds possess relatively large brains for their body sizes” (Gibson 1990, p. 111):

Birds building bowers have relatively larger brains than both related and unrelated species that do not build bowers. Within the bowerbird family, species that build more complex bowers possess correspondingly relatively larger brains. This is seen separately in both avenue builders and maypole builders, as well as across the family as a whole . . . although the relationship between brain size and bower complexity (a sexually selected trait) is stronger in male bowerbirds, the same trend is also seen in females. (Madden 2001, p. 836)

In other studies, a significant relationship between bower complexity and cerebellum size, rather than overall brain size, was detected, and the fact that bowerbirds had larger whole brains and telencephalon minus hippocampus regions than non-bower-building catbirds (a variety of songbird that are ancestral to bowerbirds) was also recorded (Borgia 2002, p. 1052; Day et al. 2005; Rowland 2008, p. 22). The cerebellum is usually cited as the location of implicit and procedural learning and motor skill abilities, these being key abilities used in artistic training (Molinari 2002). It has correspondingly been indicated that some bowerbirds develop and improve their bower-construction skills over time, suggesting that there is an important learnt component to bowerbird artistry (Kelley 2017).

In terms of examples of particular bowerbirds, it has been reported that the “average brain size of males of the complex bower builder *C. lauterbachii* [the yellow-breasted bowerbird or Lauterbach’s bowerbird] was 80.6% larger than that of the male catbird *A. melanotis*” (Madden 2001, pp. 835–836). The yellow-breasted bowerbird (which is around 270 mm in size and found in the grasslands of New Guinea) constructs a complex avenue-type bower with various walls made

of sticks and grass built on top of a platform made also of grass and sticks. In a departure from the standard form of avenue bower construction, the yellow-breasted bowerbird builds two parallel walls with a central avenue (as is standard), but then it also includes two additional wall constructions, one at each end of the bower, of similar size and composition to the two central walls, producing an elongated “H”-shaped enclosed space. Another unique feature of this bower is that the two central wall constructions slope outwards. The entire construction can weigh up to five kilograms (Rowland 2008, p. 121, 24; Marshall 1954, p. 4).

The bower is then decorated in the usual manner with berries, stones, fruits, clay, and so on of particular favored colors (blue, green, gray), and the walls are painted, as is the case with other bowerbird species. As has been outlined:

[This] bower architecture is of singular interest . . . The Yellow-breasted bird . . . has added an extra wall of sticks and an avenue at each end . . . In the two additional avenues it forms its own characteristic end-display and, in addition, still decorates the original central avenue and sometimes inserts ornaments among the sticks of the walls . . . [the natural history collector F.S.] Mayer believes that the older birds become “master builders” and says that their terminal avenues come to resemble “two sweeping parallel roadways.” (Marshall 1954, p. 108)

The contrast between bowers built by younger and older yellow-breasted bowerbirds is sometimes very stark, particularly with respect to the end-displays. It can plausibly be suggested that this additional bower complexity is linked to this particular bowerbird’s heightened brain capacity (which is expressed both as inherited instincts and as the capacity for learning) compared to similar non-bower-building birds such as catbirds.

As has been concluded on a related issue, “those avian species that have relatively large brains, such as corvids and parrots, also display cognitive abilities that have hitherto only been demonstrated in large-brained mammals” (Horik et al. 2012, p. 82). Although the link between brain size and intelligence is not automatic and direct across all species, whale brains are much larger than human brains, but whale neocortex is less complex than human neocortex (Fields 2008), the fact that the comparative literature on

bowerbirds compares them very appropriately to ancestral catbirds is reassuring on this issue.

## Avian Aesthetics and Cognition

While no other bird families and species construct large external artistic displays like the 17 bowerbird species, other bird species do behave and respond aesthetically in various significant ways, for example in the process of choosing mates, constructing nests, and by means of birdsong and other vocalizations. For example:

The Great crested flycatcher, *Myiarchus crinitus*, usually adds a shed snake-skin to the lining of its nest. Tree swallows, *Tachycineta bicolor*, go to apparent great lengths to gather specifically large white plume-like feathers for that purpose, and the Red-eyed vireo, *Vireo olivaceus*, adds the paper from hornet nests to the *outside* of its nest. (Henrich 2013, p. 745)

Most famously, the peacock's tail is one of the most artistically extravagant examples of body adornment in the animal world. It was initially troubling for Darwin to a significant extent as it could not possibly have evolved by natural selection, as it is functionally a "waste" of resources. He resolved the issue by developing the concept of sexual selection to explain its evolution.

The development of visually extravagant body decorations requires the parallel evolution of associated cognitive abilities in order to fully appreciate them. The fact that human beings also find the peacock's tail to be beautiful suggests again that there is a definite overlap between human and animal aesthetic understanding, it being suggested as early as the beginning of the nineteenth century that "the idea of beauty of person, is synonymous with that of health and perfect organization" (Prichard 1813, p. 41). The most well-known extravagantly decorated birds are the birds of paradise (Paradisaeidae), 42 species in 15 genera, which are known for the elaborately developed and brightly and brilliantly colored plumage of the male birds. Birds of paradise do not construct bowers but they do use display arenas for mating purposes.

In addition to bodily adornments, a key element of avian cognition has evolved in relation to the development of birdsong, which is species-specific and which is developed through a combination of instinct and learning that is very precisely tuned in different ways for each different species (Trivers 1985, p. 103). It is governed by particular interconnected regions of the avian brain designated as the song system. As Darwin outlined, birdsong functions both to attract the attention of females and as a form of competition (Darwin 1874 [1871], p. 369); vocalizations can also act as indications of territorial control and as a form of defense. For example, as well as producing birdsong, various bowerbird species are very good mimics and they can reproduce a wide range of both natural and artificial sounds when required, such vocal mimicry aiding against some predator attacks.

The complexity of some birdsong is revealed by the fact that: "Both mating partners of the African bird *Trachyphonus d'arnaudii* sing a melody in duet, in which each takes a turn and sings only certain parts. They harmonize so well that a listener has great difficulty in discerning two birds instead of one" (Eibl-Eibesfeldt 1975, p. 147). This indicates that some birds not only sing mechanically but can listen to another example of birdsong and carefully synchronize with it, indicating the presence of a form of active musical intelligence. Finally, the fact that some species of birds show "community song patterns" that can vary by region and improve aesthetically through practice suggests that something akin to birdsong culture may exist among some bird species (Thorpe 1963, p. 419, 425), and this is also indicated by some other bowerbird behaviors (Hopper and Whiten 2012, p. 463).

## Conclusion

Bowerbirds understood as avian artists who utilize an avian variant of the hypothesized "art instinct" demonstrating skill and virtuosity (Dutton 2009, p. 53) clearly illustrates that avian cognition can be highly sophisticated and is tailored to specific behavioral functions. In terms of

explaining why bowerbirds build bowers, the main theory that has been proposed in the literature is that they provide a physical protection for the females against forced copulation by the males as they display (Borgia 2002, p. 1051).

This may very well be correct as part of the solution but it cannot be a complete explanation, as the bower-adorned decorations do not serve this function, only the bower structures themselves do. Therefore to explain the sophisticated decorations, aesthetic factors may have to be included: the female may select the bower that serves as the best protection *and* is the most beautiful to behold as an expression of the particular individual that created it (Henrich 2013, p. 750), the latter choice helping to ensure that the bird's offspring will also have a highly developed aesthetic sense.

While only bowerbirds construct physical art objects, many other birds use aesthetic judgments and behaviors such as birdsong and selective mating choice. In relation to the basic concepts of evolutionary psychology, it has been suggested on the topic of brain modularity and birdsong that: "Birdsong learning shows other characteristics of modularization in that it is domain specific, is based on a localized and highly structured neural system and exhibits a level of innate specification" (Searcy and Nowicki 2019), very similar to the functional neural networks of biological modularity (Barrett 2015, p. 45). However, as is usually the case with various types of animal behavior, birdsong is a combination of innate and learnt functioning that is tailored to the individual species and specific behavioral focus under consideration.

## Cross-References

- [Bowerbirds](#)
- [Secondary Sex Characteristics](#)
- [Sexual Selection](#)
- [Songbird Learning](#)

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produce in an attempt to woo females. Of the 20 species within this family, found only in Australia and New Guinea, all are polygynous (males mate with more than one female) apart from three monogamous species of catbird. In the polygynous species, males construct some form of bower or display arena as part of their sexual display, and each species decorates these display areas using objects according to their own specific color palette (Fig. 1). Females prefer to mate with males that have well-constructed, highly decorated bowers (Borgia 1985; Madden 2003), and mating takes place either in or near the bower. It is a common misconception that bowers are nests, but they exist solely to persuade a visiting female to mate with the owner.

## Courtship

The polygynous bowerbirds provide no parental care or resources to the female. Once a female has copulated with a male, she builds a nest and raises her offspring alone. This mating system results in skewed mating success by males, where a handful of high-quality males gain the majority of copulations (Borgia 1985; Madden 2003; Kelley and Endler 2012a). Bowders are therefore of great



**Bowerbirds, Fig. 1** A spotted bowerbird (*Ptilonorhynchus maculatus*) in his bower

## Bowerbirds

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## Introduction

Bowerbirds, family Ptilonorhynchidae, are renowned for the extravagant displays that males

importance to the males, as they must help to persuade a female that the owner is the best male to father her offspring. To do this, males produce an extravagant multicomponent, multisensory courtship display. Not only can the female assess the male's bower and decorations; he also dances around the bower, produces vocalizations, and may also include other species-specific courtship components.

## Bower Types

Each species of bowerbird builds a specific type of bower, which can vary in complexity from a simple cleared area of ground covered with green leaves created by the tooth-billed bowerbird (*Scenopoeetes dentirostris*) to the large hut bower created by the Vogelkop bowerbird (*Amblyornis inornatus*). Bower styles can be classified into three main types: court, avenue, and maypole (Frith and Frith 2004). The most well-studied species of bowerbird are the satin (*Ptilonorhynchus violaceus*), spotted (*P. maculatus*) and great (*P. nuchalis*) bowerbirds that build avenue bowers, and the Vogelkop bowerbird that builds a maypole bower. Males tend to have traditional sites for bower location, where the same male will rebuild his bower each year at a location within that site. The specific location can vary due to variation in vegetation cover and therefore the lighting conditions of the display area (Miles and Madden 2002).

It can take a male up to 7 years to learn how to build a bower and to acquire a territory. Immature males may spend time at the bower of a mature male, where they will help him maintain the bower and gather decorations. However, once a female turns up, the resident mature male chases off any immature males in the area. Although the dynamics of bower inheritance are not clear, it seems that when a bower-owning male dies, his bower site is taken over by one of the immature males that have assisted at the bower. Until this time, immature males of species including spotted and great bowerbirds also build practice bowers that are poor attempts at bower construction. They often congregate at these bowers in groups to practice their courtship displays.

## Bower Decorations

Males of each species decorate their bowers with both natural and man-made objects restricted to a specific color palette. Satin bowerbirds collect blue objects, for example, spotted bowerbirds prefer green, and Vogelkop bowerbirds use red and blue. The tooth-billed bowerbird decorates his courtship arena with green leaves turned a particular way up (Frith and Frith 2004). The decorations used on each bower can also vary across populations within a species (Uy and Borgia 2000; Madden 2006; Haruyama et al. 2013). Local object availability likely plays a role, as bowers located near populated areas have higher numbers of man-made, and therefore brightly colored, objects on their bowers compared with more rural bowers.

The number and/or types of colored decorations a male displays on his bower are of interest to females, and females prefer to mate with males that have more highly decorated bowers in most species studied to date (Borgia 1985; Madden 2003). The specific decorations that best predict mating success in spotted bowerbirds (and perhaps other species) appear to vary across populations (Madden 2006). Furthermore, decorations are not always the most important aspect of female choice; in great bowerbirds, females do not appear to choose males based on decoration number or type (Kelley and Endler 2012a). Decorations are one component of the male's display, and there are other display components that a female can use to assess the quality of a male. Females may therefore vary on which aspects of display they use during mate assessment, or they may take into account several aspects of the male's display before making their choice.

In species where decorations are an indicator of male quality, the number of decorations that a male can display appears to be under social control. In spotted bowerbirds, when the number of decorations a male had on his bower was artificially increased, stealing and destruction rates from rivals increased until each male eventually returned to the number of objects similar to that originally displayed (Madden 2002). Similarly, when satin bowerbirds were all given the same



number of decorations, males that had more decorations prior to standardization had more decorations at the end of the experiment, because they were better at defending them (Wojcieszek et al. 2007). It therefore seems that in these species, males can defend a certain number of decorations against theft, which may form the basis of an honest signal of male quality that is available to females during mate choice.

What might this honest signal be? Surprisingly, the objects that males preferentially display on their bowers are not particularly costly to locate and do not degrade faster than less preferred decorations (Madden and Balmford 2004). There is likely be some small cost in acquiring decorations though, as males often reuse decorations from the previous year, moving them across to their new bower site (Doerr 2009). Males also do not preferentially display more costly decorations to the female during courtship. The physical display produced by the males may be important in holding the female's attention: in great bowerbirds, males display primarily red and green objects to the female as well as red/brown sticks. The diversity of colors and the frequency of switching to different colors affect how long females stay in the bower watching the male and assessing his display (Endler et al. 2014). The longer a female stays in the bower, the more likely she is to mate. Females may therefore not be assessing males purely on the number of types of decorations they have on their bower but also what he does with those decorations during courtship displays.

### Other Components of Courtship Displays

Alongside using colored decorations on their bowers, great bowerbirds create an extra few tricks for viewing females. Males of this species arrange white and gray stones, shells, and bones over their display courts in order of size. The smallest objects are close to the bower entrance, and they gradually increase in size as distance from the bower increases. Arranging objects in this way creates a forced perspective illusion,

which will affect the backdrop that the male displays against and may affect the female's size perception (Endler et al. 2010). Males that create higher-quality forced perspective illusions gain more mates (Kelley and Endler 2012a), suggesting that object arrangement is important (Fig. 2).

These males also manipulate the female's perception of color. They line the internal bower walls with red sticks, so that the female's eyes become adapted to red light when watching the male's display from inside the bower. This affects how she perceives the color of the decorations that the male displays (Endler et al. 2014).

Alongside the striking visual signal produced by males to attract a mate, some bowerbirds also produce a chemical signal. Male avenue building bowerbirds "paint" masticated vegetation onto the internal bower walls, and females nibble at this paint when inside the bower watching the male's display. This behavior has only been studied in satin bowerbirds, where the freshness of paint appears to be important in maintaining the signal (Bravery et al. 2006).



**Bowerbirds, Fig. 2** The bower of the great bowerbird (*Ptilonorhynchus nuchalis*), where objects on the display court are arranged by size to create a forced perspective illusion for the female inside the bower

## Mimicry

Many species of bowerbird are also proficient vocal mimics, for example, the spotted bowerbird *Ptilonorhynchus maculatus* can mimic up to 16 different species of bird, as well as human voices and other environmental sounds (Kelley and Healy 2011). Mimicry may function as a predator deterrent in some species that produce mimicry when disturbed or when sat on nests, such as the spotted bowerbird (Kelley and Healy 2012). Mimicry is a component of the courtship display in satin bowerbirds, where females prefer to mate with males that produce high-quality mimicry of a range of species (Coleman et al. 2007). Courtship mimicry has also been reported in at least six other species of bowerbird but is less well described in these species (Frith and Frith 2004).

## Bower Marauding

Bowerbirds can produce elaborate and dynamic sexual signals using their bowers as they have been removed from the constraints of having bodily ornaments such as brightly colored feathers. However, such non-bodily ornaments are more susceptible to disruption from rivals compared to more typical bodily ornaments. As females generally prefer males with lots of colored decorations on a well-constructed bower, a male can increase his attractiveness to females by stealing decorations and destroying the bowers of rival males (Borgia and Mueller 1992; Lenz 1994; Madden 2002). Such marauding behavior has a twofold benefit: it allows the marauder to increase the quality of their display while reducing the quality of his rival's display. The rival loses a decoration, and females will not enter his bower until it is repaired. However, the marauder takes a risk when he leaves his own bower unattended during marauding trips – his own bower is more susceptible to marauding from other males when it is left undefended. Males must therefore balance the risks and rewards of marauding (Pruett-Jones and Heifetz 2012).

Marauding rates vary among species, and species with bowers that are closer together seem to

maraud more. Males tend to maraud neighbors, probably because it minimizes the amount of time they leave their bower unattended. Males also don't seem to discriminate against kin or non-kin with their stealing behavior (Madden et al. 2004) and often have a reciprocal "tit for tat" stealing relationship with their closest neighbors.

## Female Choice

Bowers are an exploded lek-type mating system, where females can sample multiple males in a short amount of time. Female choice has only been studied in detail in satin bowerbirds, where females sampled lots of males early on in the mating season and then revisited a subset of males before making their final choice (Uy et al. 2001). Female bowerbirds may also be assessing different components of male displays as their interest in a particular male as a potential mate progresses. Mature females sampled a small handful of males and often revisited males that they had mated with in previous years. In contrast, younger, more inexperienced females sampled a wider subset of males before making their choice. Furthermore, females that chose very attractive males in the previous year typically chose the same male the following year, whereas females that made a poor choice the previous year spent more time searching for a more attractive mate (Uy et al. 2006).

## Bowerbird Cognition

It has been argued that the behavioral complexity exhibited by bowerbirds indicates enhanced cognitive ability and that bowerbirds can be considered to exhibit culture (Madden 2008). The polygynous bower-building species of bowerbird have relatively larger brains than the monogamous catbirds, and brain size also increases with increasing bower complexity (Madden 2001). However, more recent research suggests that the absolute number of neurons, not brain size, is important in explaining cognitive ability (Olkowicz et al. 2016).

There is conflicting evidence whether females within species base their choice of mate on his cognitive ability. Several studies on satin bowerbirds have reported a link between a male's problem-solving ability and his mating success (Keagy et al. 2009, 2011). However, there is no clear evidence of a link between general cognitive ability "g" (where males that are good at solving one type of cognitive test also perform well in others) and mating success, in this species or the closely related spotted bowerbird (Keagy et al. 2011; Isden et al. 2013). These conflicting results could be due to the complexity of identifying appropriate tasks that probe cognitive ability and different cognitive domains. It seems likely that there is some form of cognitive component to bowerbird sexual displays, as males learn how to build bowers and males vary in the quality of their bower constructions (Frith and Frith 2004). They also improve on other components of their displays as they age, suggesting that their displays are refined by experience over time (Collis and Borgia 1993; Kelley and Endler 2012b).

## Conclusion

Bowerbirds are a fascinating family of birds that exhibit some of the most elaborate courtship behavior in the animal kingdom. They offer an excellent system for examining a wide range of subjects including sexual selection, female choice, cognition, and social learning. However, there is still much that we don't know about bowerbirds given that only a handful of species have been studied.

## Cross-References

- Courtship Rituals
- Female Choice
- Mating

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## Bower-Birds

### ► Bowerbird Aesthetics and Cognition

## Brachiation

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## Which Animal Species Use This Behavior to Move?

A movement behavior of mammals, especially found in the all gibbons species (Hylobatidae) of primates, and include some other primates species, such as macaques, this primate species can jump-off the higher trees, and use their forearms to grab the branches of another trees, and stay in the canopies, some like the gibbons move behavior.

## Why Gibbons Choose This Type to Move?

Because all gibbons species live in the canopies of the higher arbors of the tropical rainforests or the subtropical evergreen broadleaf forests, they seldom go down and move on the ground. The reason is that they need to move from one tree to another tree, and if these trees are close, the gibbons would have to move a great deal longer, through a ground path. Therefore, this is typical adaptive behavior in the dense canopies of rainforests or subtropical evergreen broadleaf forests.

## How Do the Gibbons Fulfill This Behavior?

### Anatomical Structure

Gibbons use their long forearms to accomplish this behavior. For example, the species of *Nomascus leucogenys*, the whole-body length (measured from the top of the head to the anus) is between

45 and 62 cm, but their average forearm length is 76.4 cm (measured from the longest finger tip to the end of humerus, with the skeletal series of the forearm including: phalanx, ossa metacarpale, ossa carpi, ulna, radius, and humerus). Therefore, the forearm is longer than their whole body length. Meanwhile, the length of forearms is also longer than the lower limbs (average length 55.95 cm, measured from the longest toe tip to the end of femur, with the skeletal series of lower limb including: phalanx digitorum pedis, ossa metatarsi, ossa tarsi, fibula, tibia, and femur). Gibbons also have a well-developed clavícula (average length 10.6 cm) and scapula (average length 11.2 cm).

The major difference in the appendicular skeleton between gibbons and other primates species (include human beings) is basically that the ratio of head of radius to collum radius is larger. But there are many differences in the muscles of upper limbs among the primates species, including human beings. These difference reflect the adaptation in the brachiation behavior, including of the muscles on the shoulder-back, the muscles of the scapula, the muscles of the humerus, the muscles of the radius, and the muscles of the phalanx. For example: (1) cucullaris do not reach the occipital; (2) the pectoralis minor muscle has the clavicle end point; (3) the subclavius muscle starts at the second rib; (4) the musculus biceps brachii has three start points and do not start from the coracoid process; meanwhile, this muscle connect with the fibers of flexors of the forearm; (5) the musculus flexor digitorum sublimis has more ulna start points; (6) the musculus extensor carpi radialis longus always connects with the musculus extensor carpi radialis brevis, and the former has a tendon which ends at the first metacarpale; (7) the musculus extensor digitorum superficialis has the ulna start point; (8) the muscoli extensor digiti quinti proprius has the ulna start point; (9) no muscoli palmaris brevis; (10) the adductor pollicis not only ends at the phalanx but also ends at the metacarpales.

Because gibbons have these features of the forearm muscles, they could move among the canopies of the high trees. Other smaller primates, such as the macaques species, need to jump-off from higher position and then grab the branches. Gibbons, on the other hand, just use the two

forearms to grab the branches to move forward in the canopies.

## Cross-References

- [Primate Suspensory Behavior](#)

## Brain

- [Nervous System of Invertebrates](#)
- [Nervous System, The](#)
- [Vertebrate Nervous System](#)

## Brain Asymmetry

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## Definition

The brain for accurate and better functioning divides its labor by structural and functional asymmetry or lateralized by anatomical, physiological, neurochemical, psychological, and behavioral asymmetries.

## Introduction

Neuroimaging or lesion studies reveal the interesting fact that our daily activities which we perform consciously or unconsciously like preferences of ear for holding phone, foot preferences of the snowboarder, or inclination toward right hand during fine motor skills are related to brain hemisphere specialization also called lateralization.

## Evolutionary Theory of Brain Asymmetry

- (a) **Why asymmetry is required?** In general with few exceptions, the advantage of



asymmetry reflects more in motor than sensory input (Corballis 1998). Where bilateral control will decrease the conduction time between hemispheres, unilateral control will fasten the speed of performance (Ringo et al. 1994). Further advantage of unilateral over bilateral is that it avoids duplication and neural space wastage and increases the efficiency, and that's why left hemisphere is dominant for language and right hemisphere dominant for spatial attention (Mort et al. 2003). Duplication further may cause interhemispheric conflict (Corballis 1991).

- (b) **Why the variation in lateralization?** In general reverse asymmetry or lack of asymmetry is minor in a population. Direction of variation in asymmetry is either genetic or nongenetic not the matter, but it should be adaptive. Directional asymmetries may have frequency-based selection to have adaptive advantage. To escape from the predator in a group or flock, all the individuals turn in the same side, i.e., the selection (Ghirlanda and Vallortigara 2004), but the reversal may be advantageous in minority (Raymond et al. 1996). According to Annett (2013) and McManus (2002), one allele cancels rather than reverses asymmetrical influence of the other. The asymmetry and symmetry should have a proper balance because too much symmetry poses difficulty in neural programming for complex action and too much asymmetry leads to vulnerability. The balance is achieved during development. Environmental variation may attribute asymmetry, but genetic influences balance the asymmetry. In a single gene model, balance may be achieved by heterozygotic advantage (Annett 2013). In asymmetry, presence or absence is more interesting rather than opposite direction as found in a UK based study in 12,770 11 year old boys. It was reported that boys who lack clear handedness perform worse than either left- or right-handed on test of verbal and nonverbal ability, reading comprehension and mathematical ability (Crow et al. 1998). Lacking of directional allele in this case may run the risk of what is called "hemispheric indecision."

- (c) **Symmetrical oddity?** Symmetry may in some case provide cognitive adaptive advantage, but in a minority condition, oddity seems to provide creativity. Although mixed handers are weak academic achiever (Crow et al. 1998), they proved to be creative and have magical ideas (Barnett and Corballis 2002; Nicholls et al. 2005), and also they are at high risk of sensory illusion (Niebauer et al. 2002) and schizophrenia (Claridge et al. 1998; Upadhyay et al. 2004).

## Evolutionary Organization of Anatomical Asymmetry

### Expansion of Brain Size

Expansion and complexity raised in the brain over the evolutionary decades depends on the function it had to perform. In the need of functional incompatibility and simultaneous parallel processing of enhanced cognitive capacities, expansion promotes efficiency where duplication or repetition seems to be less important. Compartmentalization is the best option to avoid space competition of the different structure in the hemispheres for performing different activities rather than forming network within a single hemisphere. Consequently right hemisphere is specified for attention, memory storage as a global process, and left hemisphere for language. Further unilateral network develops in the larger brain due to corpus callosum for information transfer. Smaller callosal areas contain relatively thinner predominant tract in larger brain.

### Left Hemisphere Dominance as Volume Asymmetries

First asymmetries in left hemisphere are dominancy in language production and comprehension. Speech production and perception, the components of language are predominantly lateralized in left hemisphere. PT (planum temporale) an extension of Wernicke's area is ten times larger in left hemisphere and posits an example of left hemisphere lateralization. The only evolutionary and anatomical advantage of this lateralization is less time of language transfer



and avoidance of competition between hemispheres for controlling of speech muscle.

Second asymmetries lie in right-handedness for stereotyping behavior such as different movements and gestures associated with speech production in non-primates and early hominids as proposed by Condillac in 1746. Broca's area (area 44) which is associated with controlling muscle of the face and vocal tract is enlarged in great apes like chimpanzee and gorilla. Relation between gesture and language can be further validated by the Taiwan and Nicaragua children research on indigenous gestural language. Almost 97% of right-handers have their speech and language localized in the left hemispheres and remaining 3% left-handed are bilateral language presentation.

### Brain Asymmetry in Nonhuman Species

Brain asymmetry is not at all unique for human, a misconception carried by people for long. Rather brain asymmetry can be found in nonhuman primates, rodents, birds, and amphibia. Even left-right asymmetry is also found in invertebrates. Although distantly related, the brain lateralization associated with learning and retrieval of short-versus long-term memory in insects and birds is same. In *Drosophila* a small nucleus named Asymmetry body (AB) inside the brain found in the right hemisphere exhibits better long-term memory than *Drosophila* with bilateral AB. Similarly right antenna is showing efficiency for short-term memory and left antenna for long-term memory for odor preferences in honeybee (Rogers and Vallortigara 2008). In rat, mice, rabbits, and cats, the right hemisphere is slightly larger than the left. Mice with hippocampal asymmetry show decrease performance in spatial learning and memory. Behavioral asymmetry was also found in amphibian like toad that attacks their conspecific on the left side and prey to the right side (Vallortigara et al. 1998). Poeciliid fish shows behavioral asymmetry by turning right in presence of an opaque barrier but leftward preference confronting a predator (Bisazza et al. 2000). Passerine birds and frog utilize their left hemisphere

for song production and clasping vocalization. PT (planum temporale) asymmetry as well as longer and straighter Sylvian fissures on the left side has been found in nonhuman primates. In the epithalamus of many phyla like reptiles, frog, zebra fish and fish, a conserved neuroanatomical asymmetry has been documented (Concha and Wilson 2001).

### History and Background of Brain Asymmetry

In the middle of the nineteenth century, the pioneering work in the field of brain asymmetry was done by M Dax and P. Broca, and later Wernicke in aphasic patients showed that specific area of the brain is responsible for speech production and understanding language (Broca 1865; Wernicke 1874; Manning and Thomas-Antérion 2011). After the initial studies in aphasic patients, few decades after, lesion in different parts of the brain like lesion in the right brain is associated with decrease in emotional expression and inappropriate difference. Right brain injury reflects in left hemi-neglect affecting the left visual field unlike the left brain injury that doesn't affect right visual field. These suggest the asymmetrical nature of the brain. Further hemispheric specialization for other cognitive functions was best described by "split-brain patients" by Gazzaniga and Sperry (Gazzaniga 2005; Gazzaniga et al. 1962) where they disconnected the hemispheres by ablating the corpus callosum. Consequently lateral stimuli coming from one hemisphere are getting interrupted in free-flowing to the contralateral hemisphere. Equipped with these special features, each hemisphere activity of split-brain patients were addressed when they were given a task to perform and it was found that they couldn't recognize the object in their left visual field even by touching with their left hand. Surprisingly there was no problem with the right visual field. This confirms that the right brain perceives the information. In the coming decades, with the invention of noninvasive imaging techniques like PET (positron emission tomography), MRI (magnetic resonance imaging), and DTI

(diffusion tensor imaging), structural and functional asymmetries can be assessed in a better way by visualizing the gray matter structure, axonal tracts, and neuronal activities in the live brains.

## Few Important Facts of Brain Asymmetry

Prominent brain asymmetries can be dealt with the following important facts: petalias and related asymmetry, Sylvian fissure and related asymmetry, central sulcus and related asymmetry, ventricular asymmetry, and tissue component asymmetry.

## Types of Brain Asymmetry

### Anatomical Asymmetries

Anatomical asymmetry was first described by Geschwind and Levitsky in 1968. They reported that the left planum temporale underlying the Sylvian fissure near Wernicke's area was larger than the right in 70% of the right-handers which is left-hemispheric specialization of language. Pars opercularis (Broca's area) is larger on the left (Geschwind and Galaburda 1985).

The asymmetry in frontal and occipital lobe is quite demarcating in the two hemispheres such as the frontal region is wider and larger in the RH, whereas the occipital region is wider and larger in the LH. An asymmetry in dendritic organization was found in the left and right operculum (Scheibel et al. 1985) since left higher-order dendritic branching was greater, whereas right lower-order dendritic branches were longer. The reason behind quicker early RH development is its dendritic arborization, but after the first year of life, LH development is greater.

### Neurochemical Asymmetries

(a) Asymmetry in neurotransmitter: Neurotransmitter dopamine which is involved in motor activity and higher integrative function is lateralized to LH. Autonomic and psychological arousal controlled by noradrenergic and serotonergic neurons are lateralized in

RH. It can be said that LH is "activation regulatory" system, i.e., action-oriented controlling of the motor activity, and RH is "arousal regulatory" system, i.e., orientation to input stimuli which leads to attention control.

- (b) Asymmetry in neuroendocrine activity: During emotional situation, there is asymmetry in cortisol secretion (Wittling 1997; Davidson and Hugdahl 1995). A nice postulation can be derived regarding the gender-specific developmental asymmetry due to steroid hormone. Prenatal hemispheric asymmetry is affected by stable testosterone, whereas estrogen which is fluctuating affects the activation of neurotransmitter tracts and selectively changes callosal function.
- (c) Asymmetry in neuroimmune activity: Activation of LH seems to be immuno-enhancing, whereas RH activation leads to immunosuppression.
- (d) Asymmetry in brain receptors: Asymmetry in brain receptor like nicotinic acetylcholinergic receptors is lateralized predominantly in the right hemisphere. For example, some recreational drugs like alcohol, caffeine, and especially nicotine are uptaken predominantly in those nicotinic receptors in the right hemisphere. Some pharmacological agent like lithium bicarbonate, methylphenidate, and chlorpromazine also displays asymmetric hemispheric effect.

### Physiological Asymmetries

- (a) *Attention*: For sustained attention task activation of prefrontal and parietal segments is lateralized in the RH. Anterior cingulate cortex and left prefrontal cortex are engaged for spatial compatibility task, whereas visuospatial attention is engaged for the right parietal cortex. For divided attention task, left prefrontal cortex has been activated.
- (b) *Motor*: Left prefrontal-intraparietal areas are selectively active during unimanual choice. Dorsal premotor and superior parietal areas are responsible for spatial compatibility tasks, predominantly on the left, whereas hand movements and object manipulation activate bilateral.

- (c) *Perception*: Although perception of faces and object follows the same ventral pathway, there is more right lateralization for faces than object. For smell perception right lateralization of olfactory orbitofrontal cortex is involved. In case of visual perception, visual-form information is processed into the right occipitotemporal cortex or fusiform cortex, whereas for processing categorical information, left is important. Similarly right superior temporal cortex is responsible for processing of music, and left Broca's area/insula is for rhythm. Right prefrontal cortex is for self-selectivity recognition.
- (d) *Imagery*: Word to image generation involves the left inferior posterior temporal lobe, whereas complex imagery engages right temporal cortex. Imagery of maps involves right superior occipital cortex. Mental navigation involves the activation of left middle occipital gyrus.
- (e) *Language*:

| Features                                                          | Response in brain area                                                                                                                                                   | Comments                                                                                                           |
|-------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|
|                                                                   | (fusiform gyrus, presumably involved in sub-lexical graphemic processing) and anterior (inferior frontal gyrus, presumably involved in phonological recoding) structures | model. Both hemispheres have lexical routes ("sight reading"), but only the LH has a nonlexical ("phonetic") route |
| Listening for the moral of a fable                                | Right frontal and temporal lobe                                                                                                                                          |                                                                                                                    |
| Deaf native users of American Sign Language (language processing) | LH activation                                                                                                                                                            |                                                                                                                    |

| Features                                                  | Response in brain area                                                           | Comments                          |
|-----------------------------------------------------------|----------------------------------------------------------------------------------|-----------------------------------|
| Spoken word comprehension                                 | Bilateral medial and superior temporal gyrus                                     |                                   |
| Written word recognition with or without spoken responses | Left-lateralized<br>- Left prefrontal cortex<br>- Left posterior temporal cortex |                                   |
| Letter shape                                              | Posterior fusiform gyrus                                                         |                                   |
| Letter name                                               | Anterior and posterior fusiform gyrus bilaterally                                |                                   |
| Letter string                                             | Left posterior fusiform                                                          |                                   |
| Legal word (visual)                                       | Left anterior fusiform area with stimuli from right or left visual field         |                                   |
| Lexical access via the visual word form                   | Posterior temporal lobe bilaterally                                              |                                   |
| Phonological recoding                                     | Left-lateralized network of posterior                                            | Supports "hemispheric dual route" |

(continued)

(f) *Memory*:

| Features                                                      | Activation area in the brain                                                                   | Comments                                                                                                                               |
|---------------------------------------------------------------|------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------|
| Working memory (phonological loop)                            | Phonological store – left parietal activation<br>Rehearsal buffer – activation in Broca's area | Broca's area and left parietal areas are activated for verbal-numerical tasks; activations for nonverbal material tend to be bilateral |
| Semantic memory retrieval                                     | Left prefrontal cortex                                                                         | Tulving's hemispheric encoding-retrieval asymmetry (HERA) model                                                                        |
| Episodic memory encoding (personally experienced past events) | Left prefrontal cortex                                                                         |                                                                                                                                        |
| Episodic memory retrieval                                     | Right prefrontal cortex                                                                        |                                                                                                                                        |

(continued)

| Features                                                                | Activation area in the brain                                      | Comments                                                     |
|-------------------------------------------------------------------------|-------------------------------------------------------------------|--------------------------------------------------------------|
| Encoding and retrieval of words                                         | Left hemisphere                                                   |                                                              |
| Encoding and retrieval for patterns, faces, scenes, or nonverbal sounds | Right hemisphere                                                  |                                                              |
| Retrieval of animal information                                         | Left occipital regions                                            | Semantic domain (reflecting processing of physical features) |
| Retrieval of tool information                                           | Left prefrontal regions                                           | Reflecting processing of linguistic or motor information     |
| Generating action words                                                 | Left temporo-occipital regions                                    |                                                              |
| Recall                                                                  | Dorsal cortex – free recall<br>Ventrolateral cortex – cued recall |                                                              |
| Autobiographical retrieval                                              | Right frontotemporal network                                      |                                                              |

- (g) *Emotion*: Emotions are lateralized into left prefrontal cortex. During masked (unconscious) presentation of conditioned fearful faces, lateralized right amygdala activates (Gazzaniga 2000), but during unmasked (conscious) presentation, left amygdala activates.

### Psychophysiological Asymmetries

Anatomical asymmetries reflect into cognition, emotion, and autonomic process regulation. Neurotransmitter, neuroendocrine, immunoregulatory, cardiovascular, skin temperature, and vasomotor activity are asymmetric. Neural control of cardiovascular function is lateralized.

Sympathetic and parasympathetic pathways control the peripheral autonomic chronotopic control of cardiac activity (heart rate). Auriculoventricular conduction and cardiac contractivity are left-lateralized. Further, emotional stimuli in the

left visual field yield larger heart rate, and blood pulse volume changes than stimuli in the right visual field. Pain sensitivity is greater in the RH.

### Behavioral Asymmetries

To measure the behavioral asymmetries or effect of lateralization input, stimuli were restricted and behavioral responses or both to one sensory or motor side. Hemifield tachistoscopes with unimanual responses is used to measure the symmetries.

### Determining Factors of Brain Asymmetry

#### Environmental Factors

Although genetic factors contribute in the lateralization of the brain, prenatal and postnatal environmental stimuli further trigger it.

*Light*: The best example and well-characterized illustration of environmental impact on brain asymmetry is the chick and pigeon asymmetric development of visual pathway which is light stimulus dependent (Rogers 1982; Rogers and Sink 1988; Manns and Güntürkün 1999). During the final day of development inside the egg, the embryo turns so that light passes through the right eye and can be stimulated and left hemisphere getting activated. If the right eye is occluded, it turns in such a way that left eye becomes stimulated and right hemisphere is getting activated. If the eggs are incubated in dark for last 3 days of hatching, asymmetry will not develop during choice of grains and pebbles. In case of zebra fish, Budaev and Andrew reported that the preference of avoiding or approaching predators depends on the early exposure of embryos to light. This light could also influence the developmental asymmetry of habenular nuclei not the visual pathway where absence of light delays the habenular nuclei (Borsetti et al. 2011).

*Fetal posture and orientation*: Due to mother's visceral asymmetry, the fetus in the final trimester lies toward the left in head-down position in the mother's womb which may be the reason favoring the right-hand dominance contributing motor lateralization. Language is lateralized by stimulating the right ear since it is close to the body wall.

*Hormones:* Some independent reports found that male borns in winter are left-handed (Stoyanov et al. 2011). High level of androgen in spring season along with genetic factors may contribute to induce a left shift during fetal development showing a genetic association between handedness and androgen receptor. Gender differences in human cerebral structural asymmetries and handedness prove the influence of sex hormone in brain lateralization in animal like fish (Bisazza et al. 1998). In frog seasonal changes influences the structural asymmetry in habenular nuclei (Kemali et al. 1990).

*Genetic factors:* Genetic contribution in hemispheric asymmetry is controversial. Asymmetry in hemispheric volumes are more influential in right-handers than left-handers.

Genetics of Brain Asymmetry

Handedness and language processing asymmetry were established early in development. Before the development of true language, perception and production of language are lateralized in infants. The hemispheric dominance for handedness and language skill which is an early onset phenomenon established in fetus and degree of heritability for handedness together suggest the genetic factors in brain asymmetry.

Genetics of Asymmetry of Handedness

Handedness is either multigenic trait or controlled by single gene with two alleles of which one is dominant for right-handedness and another one is recessive for left-handedness. Linkage asymmetry and genome-wide association studies (GWAS) reveal one of the gene LRRTM1 (leucine-rich repeat transmembrane neuronal 1). The minor alleles of this gene were found associated with handedness in families of schizophrenic patients but not in healthy controls (Francks et al. 2007). GWAS further report a specific SNP of PCSK6 (preprotein convertase subtilisin/kexin 6) in dyslexic patient (Scerri et al. 2010) rather than the orientation of handedness in healthy individuals. The gene encodes an enzyme involved in the maturation of Nodal/Tgfb factors has significant

role in body asymmetries also provides a link between body and brain laterality. Another evidence is that PCSK6 knockout mice display visceral heterotaxia (Constam and Robertson 2000). The association between handedness and gender, with males tending to be more represented among left-handers (Raymond et al. 1996), was shown by Medland et al., by showing an association between handedness and the number of polymorphic polyglutamine CAG repeats in the androgen receptor (located on the X chromosome).

Genetic of Asymmetry of Language

FOXP2 is one of the genes which is involved the language asymmetry. A series of SNP of FOXP2 is involved in speech impairment. Activation of different brain areas during reading involves a specific series of SNP of FOXP2. FOXP2 expression increases in area X in bird during song learning. Silencing of FOXP2 gene by RNAi results in inaccurate vocalization.

Gender-Specific Asymmetry

Greater functional lateralization in men than women due to less sharply defined hippocampal function or larger commissural system in women.

| Area                               | Asymmetric features                                                |
|------------------------------------|--------------------------------------------------------------------|
| Hemispheric volume                 | Larger in male fetuses                                             |
| Central sulcus                     | Deeper in the left hemisphere than right only in male right-hander |
| GM asymmetry                       | Found in male compared to female                                   |
| Parasagittal asymmetry             | In the anterior callosal body                                      |
| Planum parietale and inferior lobe | Rightward asymmetry                                                |
| Right frontal petalis              | Greater asymmetries in both right- and left-handers                |
| Occipital petalis                  | Asymmetry in left-handers only                                     |

Functional Adaptation

Brain asymmetries are not always genetically determined but rather depend on early frequent exposure of sensory or motor stimuli. It is due to experience-dependent plasticity and behavior

which influence the neuronal changes in two hemispheres. For example, using of one forelimb in the postnatal period causes larger neuropil volume and lower cell packing density in motor cortex. In mice with hereditary asymmetry in whisker pads, right whisker pad is dominant with left paw preference. It shows that limb preference is associated with asymmetry in sensory input. In human, right-handed keyboard player if trained bimanual from childhood performs better in motor skill test. The absolute length of central sulcus is also associated with the age of musical training. Those who started music at early life have longest sulcus at both sides. Here motor stimuli play the role of asymmetry.

Aberrant Asymmetries and Disease

| Disease                | Asymmetrical area                                                                                                                                                                                                                                                           | Comments |
|------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------|
| Depression             | Frontal asymmetry                                                                                                                                                                                                                                                           |          |
| Schizophrenia          | Reduced hemispheric asymmetry<br>Reversal of normal petalias;<br>disproportionately reduced left hemisphere temporal lobe volumes; reduced asymmetries of the PT, the superior temporal gyrus, and the Sylvian fissure; and alterations in hemispheric gyrification indices |          |
| Stuttering             | Anomaly in cerebral dominance                                                                                                                                                                                                                                               |          |
| Bipolar disorder       |                                                                                                                                                                                                                                                                             |          |
| Developmental dyslexia |                                                                                                                                                                                                                                                                             |          |
| Semantic dementia      | Asymmetric anterolateral temporal atrophy                                                                                                                                                                                                                                   |          |

(continued)

| Disease           | Asymmetrical area                                                                                                                                                                 | Comments                                                                                                                                                                                 |
|-------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                   | (typically worse on the left side) with relative sparing of the hippocampal formation                                                                                             |                                                                                                                                                                                          |
| Dementia          | Left hemisphere more susceptible                                                                                                                                                  | CSF volume in the left Sylvian fissure rises sharply than the right                                                                                                                      |
| Alzheimer disease | A spreading wave of GM loss emerges initially in entorhinal and temporal-parietal cortices, sweeping into frontal and ultimately sensorimotor territory as the disease progresses | This sequence occurs in both hemispheres, but left hemisphere regions are affected earlier and more severely. The right hemisphere follows a similar pattern approximately 2 years later |

Conclusion

Brain asymmetry evolved for proper and fast functioning of the brain from lower-order animals to higher-order animals including human. The asymmetries can be in the form of anatomical, physiological, psychological, neurochemical, and behavioral. Two cerebral hemispheres are lateralized for performing different functions. The brain asymmetries can be gender specific. The LH is found to be specialized for motor functions and the body’s defence regulation against invading agents whereas the RH is found to be specialized for controlling of functions to support survival and cope up with stress.

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## Brain Circuit

► [Neural Network](#)

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## Brain Evolution

► [Encephalization](#)

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## Brain Imaging

► [Cognition](#)

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## Brain/Cerebral/Hemispheric Asymmetry

► [Hemispheric Specialization](#)

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## Breathing

► [Respiratory System](#)

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## Bring up

► [Nature Versus Nurture](#)

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## Brodmann Area 28

► [Entorhinal Cortex](#)

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## Broken Wing Display

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## Synonyms

[Distraction display](#); [Injury-feigning behavior](#)

## Definition

The broken wing display is a feigning behavior that some ground-nesting birds perform to lure a potential predator away from the bird's nest or chicks (Armstrong 1949a). The deception consists of pretending that the bird has a broken wing that hinders flight. If the predator is deceived and chases the bird, it will move away from the nest or chicks (Ristau 1991), thereby considerably reducing the probability of finding them. Finally, when the predator has been lured away from the nest, the bird puts an end to its distraction display and escapes.

## Description

Some ground-nesting birds employ distraction displays as part of their antipredator strategies because they nest in sites easily accessible to a wide range of predators. The aim of these behaviors is to divert predator attention away from

offspring, by drawing their attention towards false nests or an easy prey (Gochfeld 1984; Sordahl 1986; Byrkjedal 1989; Caro 2005). This deception can be articulated by displaying dishonest signals concerning their physical condition, e.g., simulating an injury that hinders their ability to escape.

The broken wing display is part of the different types of distraction behavior that birds can perform to deceive a potential predator (Armstrong 1949b). Since the deception consists of luring the predator towards a bird that is unable to fly, the behavior is displayed only against terrestrial predators, particularly mammals. There are multiple versions of distraction displays that can fit within the broken wing behavior category. However, all of them share abnormal wing movements which look like injuries to one or both wings (Gochfeld 1984), and impaired flight ability.

Although this behavior has been documented in several bird lineages, it reaches its pinnacle in

shorebirds. For this avian group, Gochfeld (1984) describes the broken wing display in different species. For instance, calidridine sandpipers perform their display running with wings half spread and with the fanned tail dragging on the ground. The plovers of the *Charadrius* genus are characterized by display with spread tail, creeping forward and beating one or both wings on the ground. But other plovers, such as the Killdeer (*Charadrius vociferous*), can extend one wing on its back and beat with the other on the ground (Gochfeld 1984).

Birds usually perform the broken wing display while moving along the ground, although they can alternate or end it with a stationary display (Ristau 1991). In both instances, some birds can use calls suggesting injury (Sordahl 1986). Some stationary displays performed by several plovers are intimately related to the broken wing display. For instance, some birds (e.g., the Kentish Plover, *Charadrius alexandrinus*) may remain motionless



**Broken Wing Display, Fig. 1** The sequence of images shows different types of behaviors performed by an adult male of Kentish plover (*Charadrius alexandrinus*) that are directly related to the broken wing display. The images

illustrate various snapshots during the performance of both mobile and stationary displays (Author: Miguel Angel Gómez-Serrano)

while keeping wings extended as if exhausted or shuffle wings rhythmically or spasmodically (Simmons 1951). The broken wing display is frequently alternated with other distraction behaviors like crouch-run, false feeding, or incubation-like displays (Simmons 1951; Gochfeld 1984) (Fig. 1). In fact, birds can modify the intensity and variety of their distraction behaviors depending on the response of the potential predator (Ristau 1991).

The distraction display usually begins at the end of egg-laying and its intensity increases with nest age (Sordahl 1986). Generally, the frequency of broken wing display intensifies as the hatching date approaches (Byrkjedal 1989), coinciding with a substantial time investment in incubation tasks by parents.

Birds performing distraction behavior incur a certain degree of risk. Nevertheless, this risk is mitigated by the fact that the performer is alert and aware of the predator. Indeed, distraction behavior is probably less dangerous than other antipredator strategies (e.g., mobbing), because it is usually performed at a greater distance from the predator (Sordahl 1990). Investment in antipredator defense increases offspring success (Caro 2005), but should be proportional to predation risk (Lima and Dill 1990). Although this trade-off must exist, there is a paucity of evidence supporting that risk assumption by parents has a positive impact on reproductive success (Byrkjedal 1987; Caro 2005; Gómez-Serrano and López-López 2017). Nevertheless, nest success has been shown to increase with the intensity of distraction displays in the Kentish plover (*Charadrius alexandrinus*), and there are differences in nest defense investment within pairs, with females performing riskier defensive behaviors than males, as is the case of the broken wing display (Gómez-Serrano and López-López 2017).

## Cross-References

- Alarm Calls
- Deception
- Displays
- Female Defense Polygyny

- Parental Investment
- Paternal Behavior
- Predation Risk
- Predator Defense
- Predator Detection

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## Brood Defense

- Territory Defense

## Brooding

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## Synonyms

Caring; Incubating

## Definition

A form of parental care behavior that occurs in egg-laying animals, during which a parent retains eggs within or near the body and provides heat, nutrients, oxygenation, and/or osmoregulation, as well as protection from predators to the developing embryos and hatched young.

## Introduction

The definition of brooding, like that of many other terms in zoology, has evolved over the years to broaden its applicability to a wider range of taxa. Strictly speaking, the word brooding means “to lie upon” and has been used since the fifteenth century to describe the behavior of hens sitting on eggs. In zoology, the term “brooding” was originally specifically used to describe a parental care behavior of birds that occurs after egg laying, in which a parent, usually the female, will sit on the developing embryos, keeping them warm until hatching. Nowadays, whilst the use of the term brooding is still limited to egg-laying animals (the equivalent in eutherian mammals being “gestation”) and parental care behaviors carried out whilst in physical contact with the offspring, its definition is no longer restricted to birds nor to heat transfer (= strict incubation). Brooding behaviors include the transfer of heat; the provision of nutrients, oxygenation, and/or osmoregulation; metabolic waste removal; maintenance of optimal humidity levels; and protection from predators to the developing offspring. These behaviors may be performed by the mother, the

father, or by both parents. At least in birds, egg laying promotes the secretion of several hormones and neurotransmitters that mediate behavioral and physiological changes that prepare the parent for brooding. These changes, together termed *broodiness*, include reductions in time spent drinking and feeding, increased tendency to incubate the eggs, and the plucking of feathers from the abdomen and chest that are used to cover the eggs. In doing so, broody birds develop a patch of featherless skin on their underside, aptly named a brood patch, that when in contact with the surface of the eggs, allows the parent to efficiently transfer body heat to the embryos. While it remains unclear whether all species that brood experience *broodiness*, brooding behavior is practised by most birds, monotremes (egg-laying mammals), several reptiles, amphibians, fishes, and invertebrates. There is also some evidence that Oviraptorosaurs, a group of dinosaur species that lived in the Cretaceous Period, used to brood their offspring. However, it is important to note that, among fish, many species provide parental care but do not brood per se despite being classified as brooders. This confusion likely arises from the fact that the mass of fertilized eggs a parent cares for is often referred to as a brood. Yet, while they may care for the brood, i.e., protect them from predators, ventilate them, and clean them, they do not care for the developing embryos or fry in or on their bodies. Examples include substrate brooding fishes. Also worth noting are the inconsistencies in the bird literature; some authors use *brooding* in reference to hatched chicks only, and *incubating* in reference to eggs only, while others refer to both phases of parental care as *brooding*.

## Evolution of Brooding

The importance of parental care to animal evolution can hardly be overstated. Investment in parental care affects the potential reproductive rate of individuals, which in combination with other factors can affect reproductive behavior, within-sex competition for mates, the mating systems displayed, and resulting intensity of sexual selection in each sex (Williams 1966; Trivers



1972). Ultimately, parental care has evolved because it improves the fitness of offspring and therefore increases the reproductive success of parents. Brooding, specifically, is assumed to have evolved in species that inhabit suboptimal, unstable, or dangerous environments for embryo development, and where the ability to protect, thermoregulate, and/or move the eggs significantly improves offspring survival. Evolution of brooding strategies has also been highlighted as a driver of speciation in some families (Jones et al. 2003). As discussed below, brooding is taxonomically widespread, mostly obligatory in the species where it occurs, diverse in expression, and incurs significant costs to the parents. Efforts to minimize some of these costs have led to the evolution of strategies, such as con- and interspecific brood parasitism, communal brooding, and brood reduction.

### Cost of Brooding and Counteracting Adaptations

Brooding incurs significant fitness costs to parents. For example, brooding has been associated with increased adult susceptibility to predation in several species (Shine 1980). However, the reduction of energy reserves, coupled with the loss of opportunities to replenish them, is likely to be the most common cost of brooding. For example, mouthbrooding cichlids cannot feed during brooding, and the resulting loss in condition delays them from breeding again. Even in species where parents can feed throughout brooding, declines in body condition have been documented. In several species of the pipefish family Syngnathidae, brooding males can absorb some of the eggs in their brood pouches, a strategy akin to filial cannibalism and a type of brood reduction, which is assumed to slow down reductions in paternal body condition. Brood reduction also occurs in many species of birds. When, for one reason or another (e.g., detrimental environmental conditions), the cost of brooding all offspring increases to the point that brooding fewer offspring is expected to result in a higher fitness payoff, then parents are expected to reduce the total number of offspring cared for (Lamey et al.

1996). Hatching asynchrony, where eggs hatch days apart, and variation in egg size, with the resulting variation in offspring size are two adaptive strategies employed by females of several bird species to optimize brooding effort and facilitate brood reduction (Clutton-Brock 1991). Maintaining offspring temperatures can be energetically costly in birds; it has been estimated to raise adult basal metabolic rates by up to 40% in some species. Yet, without some form of thermoregulation, embryos cannot survive.

Several species have evolved strategies to either minimize or entirely bypass brooding, despite brooding still being essential for their offspring survival. Conspecific brood parasitism, where females lay eggs on other female's nests, has been documented in several species and, in some cases, has been associated with a bias to parasitize nests of kin (i.e., genetically related females). Arguably more extreme, interspecific brood parasitism occurs in some bird, fish, and insect species. In these cases, individuals deceive individuals of other species into brooding their offspring, resulting in an evolutionary arms race where the "parasite" species evolve strategies to successfully deceive their hosts, and "host" species evolve adaptations to identify parasitic eggs (Rothstein 1990).

### Diversity of Brooding Behaviors

Brooding behavior can take an enormous variety of forms. Below are some examples across the animal kingdom.

*Ectothermic thermoregulation:* All python species display extended maternal brooding, with females coiling tightly around the eggs, providing protection from predators during development. In addition, brooding has been shown to have two other functions in pythons: water balance regulation and thermoregulation, although not all species accrue all the benefits. To the surprise of the scientific community in the 1830s when it was first reported, females of several species thermoregulate their eggs, keeping them within narrow temperature ranges despite experiencing variation in ambient temperatures (Vieira de Andrade et al. 2016). For example, Burmese python (*Python bivittatus*) females



increase their metabolism and body temperature by contracting their muscles in a twitching fashion. Other species, such as reticulated pythons (*P. reticulatus*) increase their body temperature through physiological means, without visible muscle contractions. Others still, such as ball pythons (*P. regius*), thermoregulate through behavioral means: females bask in the sun to raise their own body temperature and then return to brooding the eggs and transfer their body heat. Recent research has also shown that brooding allows females to regulate clutch evaporative water loss, minimizing egg desiccation and promoting egg viability.

**Gastric brooding:** Sadly both now presumed extinct, females of the Australian frog species *Rheobatrachus silus* and *R. vitellinus* displayed a most peculiar and unique form of brooding: stomach or gastric brooding. Females would swallow the fertilized eggs and brood them in their stomachs for up to 6 weeks, during which time they could not feed. At the end of the brooding period, the females would literally regurgitate fully developed offspring (Greven 2011).

**Skin incubation:** Skin brooding has evolved independently multiple times in anurans, with the genera *Pipidae* and *Gastrotheca* displaying the most remarkable adaptations. In the Suriname toad (*Pipa pipa*), females brood the embryos in temporary brood chambers that form on the skins on their backs. After attachment, the embryos bury through the skin becoming fully imbedded. The physiology of the skin changes in preparation for reproduction and throughout brooding, becoming thicker, looser, and highly vascularized to accommodate the embryos and enable nutrient and gas transfer, as well as metabolic waste removal. At birth, fully developed toads emerge from the chambers, which are then shed before the cycle is repeated. In contrast, females of *Gastrotheca* species, widely known as marsupial frogs, have permanent dorsal brood pouches. After the eggs are fertilized, the male inserts them into the female's brood pouch, and highly vascularized brood chambers within the pouch develop around the embryos, facilitating the transfer of oxygen during brooding (Greven 2011).

**Fish pregnancy:** Arguably, the most complete and complex type of brooding is provided by

males of the *Syngnathidae* family, the seahorses, pipefishes, and sea dragons. During mating, females transfer the eggs onto the males, who provide all the care until the offspring emerge as mostly developed and fully independent juveniles. Depending on the species, males may brood the developing offspring on a patch of skin on their trunk or tail, or in a brood pouch, with more complex types of brood pouches enabling males to provide greater care. During brooding, the brood pouches change morphologically and physiologically, forming highly vascularized cup-like depressions around the eggs that ensure the supply of nutrients, oxygenation, and osmoregulation to the embryos in addition to metabolic waste removal, equivalent to mammalian placentas (Stölting and Wilson 2007).

**Mouthbrooding:** Oral incubation, buccal incubation, or mouthbrooding has evolved independently multiple times and across the animal kingdom and can be performed by both sexes. Mouthbrooding occurs when a parent cares for its offspring in its mouth for extended periods of time, preventing it from feeding during that period. In some species, parents begin mouthbrooding immediately after the eggs are fertilized (ovophiles), while in others mouthbrooding occurs only at the larval stage (larvophiles).

## Cross-References

- [Basal Metabolic Rate \(BMR\)](#)
- [Clutch](#)
- [Communal Behavior](#)
- [Cuckoldry](#)
- [Deception](#)
- [Feather-Plucking](#)
- [Fraternal Birth Order Effect](#)
- [Hatching](#)
- [Incubation](#)
- [Internal Fertilization](#)
- [Interspecific Brood Parasitism](#)
- [Maternal Behavior](#)
- [Nutrients](#)
- [Ova](#)
- [Parental Investment](#)
- [Parenting](#)

- [Paternal Behavior](#)
- [Predation Risk](#)
- [Sex Role Reversal](#)
- [Spawning](#)
- [Thermoregulation](#)
- [Water Balance](#)

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## Bruce Effect

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## Synonyms

[Pregnancy block](#); [Reproductive suppression](#)

## Definition

Prevention of implantation or termination of pregnancy when offspring survival is threatened (e.g., by presence of a novel male).

## Introduction

The Bruce Effect was first described by Hilda Bruce in 1959, as a decline in pregnancy success when female laboratory mice were exposed to novel males soon after mating. This particular form of pregnancy delay can be considered in the context of reproductive suppression, a collection of adaptive strategies by which females delay pregnancy to increase their chances of reproductive success. Since 1959, the Bruce Effect has been documented in multiple species, both in the laboratory and in the wild. Biological mechanisms and the timing of the effect during gestation vary by species. The Bruce Effect can be generalized to describe reproductive suppression in response to threats to child survival.

## Bruce Effect in Mice

When exposed to unfamiliar males soon after mating, a high proportion of female mice end their pregnancy (Bruce 1959). Pregnancy block (i.e., prevention of implantation) occurs in up to 80% of female mice exposed to novel males in the laboratory, followed by a return to estrous and the ability to mate with the new male (Bruce 1961). Exposure must occur during the first 5 days after breeding; exposure to a novel male outside of this critical period will not induce the Bruce Effect, as implantation will have already occurred. The threat of the novel male is communicated via pheromones in the male's urine, and the Bruce Effect can be induced via exposure to the urine, even without the physical presence of the male (Dominic 1966).

## Adaptive Reproductive Strategy

The Bruce Effect is one mechanism of reproductive suppression. The model of reproductive

suppression describes several strategies through which females can prevent or delay pregnancy when future environmental conditions are likely to better support offspring survival, compared to current conditions (Wasser and Barash 1983). Thus, utilizing strategies of reproductive suppression may maximize the lifetime reproductive success of a female, even at the expense of short-term reproduction.

The Bruce Effect may have been conserved both as a result of competition between males and as a female strategy to avoid infanticide. New males may gain a fitness advantage by gaining the opportunity to reproduce (Schwagmeyer 1979), and females may both prevent investment in young at risk of death and make themselves available to reproduce again as quickly as possible (Labov 1981). In mice, some males engage in infanticide and kill offspring fathered by other males. Therefore, the female strategy of blocking pregnancy upon arrival of a novel male may prevent infanticide and allow the female to reproduce with the new male, thereby increasing the chance of her offspring's survival (Beehner and Lu 2013). Thus, the Bruce Effect can be considered an adaptive reproductive strategy (Labov 1981).

## Generalized Bruce Effect

Since it was first documented, the Bruce Effect has been observed in multiple species, including several species of rodents in the lab and in the wild (Schwagmeyer 1979), as well as primates (Beehner and Lu 2013). Although the Bruce Effect in mice occurs via pregnancy block, other species use different physiological mechanisms at different time points in pregnancy to achieve similar outcomes. For example, pregnancy block occurs before implantation (i.e., several days after breeding), but the Bruce Effect operates via pregnancy termination throughout gestation (i.e., up to the third trimester) in primates (Roberts et al. 2012). Taken together, these adaptive pregnancy disruptions comprise a larger set of reproductive strategies to prevent investment in offspring with low probability of survival.

The fraction of gestations terminated under the Bruce Effect varies across species and contexts

but can reach up to 80% in laboratory mice (Bruce 1961) and wild geladas (Roberts et al. 2012). The observation that some proportion of offspring survive suggests females may possess the ability to read and interpret environmental threats and to noncognitively control their response to threatening environments.

Threats beyond infanticide by novel males also lead to Bruce-like effects. These generalized Bruce Effects may be induced by social stress, subordinate rank, and high levels of female competition (Beehner and Lu 2013), as well as risk of predation and other ethologically-relevant stressors (de Catanzaro and Macniven 1992). A generalized Bruce Effect has also been identified in human populations, as increases in child mortality predict reproductive suppression via pregnancy termination (Saxton et al. 2017). Thus, the generalized Bruce Effect includes a range of noncognitive strategies to delay reproduction until environmental circumstances better support offspring survival.

## Conclusion

The Bruce Effect is one form of reproductive suppression, in which females block or terminate pregnancy to increase their lifetime reproductive success. In laboratory mice, the Bruce Effect was first identified as prevention of implantation in the presence of a novel male soon after mating. Pregnancy block under similar circumstances has since been recognized in other rodent species, while pregnancy termination at later stages occurs in a range of species. Reproductive suppression and the Bruce Effect increase maternal fitness by minimizing investments in offspring least likely to survive. A generalized Bruce Effect can describe a larger set of adaptive reproductive strategies, across multiple species, to prevent or terminate pregnancy when the environment threatens offspring survival.

## Cross-References

- [Fitness](#)
- [Life History](#)
- [Postcopulatory Selection](#)

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## Bucket Experiment

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## Synonyms

Begging paradigm; Requesting paradigm; Visual attention paradigm

## Definition

An experimental setup designed to test for the ability to distinguish between “seeing” and

“non-seeing” individuals, for instance, by begging more from an experimenter with a bucket on her shoulder than from one with a bucket over her head.

## Introduction

In 1996, Povinelli and Eddy published a landmark series of experiments designed to test chimpanzees’ understanding of “seeing.” Eight young chimpanzees were trained to “request” food from a human experimenter. This involved extending an upturned palm through a hole in a plexiglass partition, similar to a “begging” gesture also observed in wild chimpanzees. Then, during test trials, the subjects were presented with two experimenters side by side, one of whom could see them and one of whom could not.

While the chimpanzees immediately preferred to beg from experimenters who were facing them, relative to experimenters whose backs were turned, they did not discriminate between experimenters covering their ears versus their eyes with their hands, those with blindfolds over their mouths versus their eyes, or those with buckets resting on their shoulders versus placed over their heads.

Povinelli and Eddy (1996) interpreted these results as evidence that chimpanzees likely learn specific contingencies – such as “gesturing towards another’s back is always fruitless” – without abstracting such “behaviorist” rules into a more general concept of what it means to “see.” Had they possessed such a concept, the study authors argued, they would have understood the relationship between line of sight and the ability to respond to requests and always preferred the “seeing” experimenter.

This conclusion has since been the subject of much debate. Firstly, it has been argued that the performance of Povinelli and Eddy’s (1996) chimpanzees is not representative of the species and, secondly, that the setup itself is fundamentally unsuitable for studying chimpanzees’ understanding of “seeing.” Despite this, variants of Povinelli and Eddy’s (1996) basic “bucket test” have now been used with a wide variety of

species, cementing its status as an extremely influential experimental design.

## Overall Chimpanzee Performance

Over the course of 13 experiments, Povinelli and Eddy's (1996) chimpanzees were exposed to 8 different configurations of seeing versus non-seeing experimenters. In the first four trials of each condition, they were above chance only for "front facing" versus "back turned." However, the subjects did eventually learn the correct preference in a number of other conditions, including "screen next to face" versus "screen in front of face" and "looking back over shoulder" versus "looking away over shoulder."

The overall pattern of results led Povinelli and Eddy (1996) to conclude that their chimpanzees had learned a "face rule" – "gesture towards the experimenter whose face is visible" – and were perhaps in the process of learning an "eye rule," "gesture towards the experimenter whose eyes are visible." Yet, when retested several years later (Reaux et al. 1999), these chimpanzees still did not immediately and flexibly discriminate between "seeing" and "non-seeing" experimenters.

However, the chimpanzees tested by Bulloch et al. (2008) *did* immediately perform above chance in many of the same comparisons, including "mixed" ones, such as "screen next to face" versus "bucket overhead" and "blindfold over mouth" versus "eyes closed." The exceptions were "eyes open" versus "eyes closed," where the chimpanzees did not initially show a preference, and "eyes closed" versus "looking back over shoulder," where they begged significantly more from the "non-seeing" experimenter.

To Bulloch et al. (2008), these results implied that their chimpanzees were sensitive to both the visibility of the experimenter's face and the visibility of her eyes but that the chimpanzees responded more strongly to the former cue. Furthermore, the authors hypothesized that the difference with Povinelli and Eddy's (1996) chimpanzees was caused by their animals' exceptionally rich social and physical environment. This could have enhanced their cognitive

development relative to the original group of juvenile subjects, who, for example, lacked direct access to mixed-age conspecifics.

However, subsequent research suggests subtle experimental differences might have played a role. It has been argued that "choosing between two experimenters" is itself very difficult for chimpanzees (Kaminski et al. 2004), and follow-up work has involved trials with only a single experimenter at a time (Kaminski et al. 2004; Hofstetter et al. 2007; Tempelmann et al. 2011; Hattori et al. 2011). In this setup, it is compared across trials whether chimpanzees gesture more toward a "seeing" experimenter than a "non-seeing" one.

Using this modification, Hattori et al. (2011) have found that chimpanzees do not discriminate between "eyes open" and "eyes closed" experimenters when requesting food visible on a table but that they *do* gesture more toward "seeing" experimenters when requesting food held in their hands. This corresponds to the fact that Povinelli and Eddy's (1996) chimpanzees had more difficulty with the original task than Bulloch et al.'s (2008), as the former used the "table" setup and the latter the "hands" version.

Across all "bucket test" variants, it appears that chimpanzees are sensitive to the visibility of an experimenter's face and, to a lesser extent, her eyes when requesting food that she is already holding (Hofstetter et al. 2007; Bulloch et al. 2008; Hattori et al. 2011) but that they respond most strongly to the orientation of her body when requesting food that is offered nearby (Povinelli and Eddy 1996; Kaminski et al. 2004; Tempelmann et al. 2011).

This has been interpreted as evidence that the "table" version of the task is more difficult for chimpanzees, perhaps because it is less clear that the experimenter is already willing and able to provide them with food. Then the task becomes more complicated than simply attracting the attention of the correct experimenter, and the chimpanzees' ability to respond to subtle cues of 'who can see them' might be masked (Kaminski et al. 2004; Tempelmann et al. 2011).

What the chimpanzees' performance on these various versions of the "bucket test" implies for



their understanding of “seeing” as a mentalistic concept, as Povinelli and Eddy (1996) originally set out to determine, remains controversial, as discussed next.

## The Wrong Kind of Experiment

The first critique of Povinelli and Eddy’s (1996) “bucket test” came from Hare (2001), who argued that experimental setups are only “ecologically valid” if they mimic subjects’ evolutionary history or daily life experience; only in such situations are animals likely to demonstrate the full range of their cognitive abilities. The “bucket test” appears to fail this criterion, as chimpanzees rarely share food in the wild.

However, it has been argued that “low ecological validity” is in fact a desirable feature in a cognitive test (Povinelli and Vonk 2004). The “bucket test” was designed to probe chimpanzees’ understanding of “seeing” as a subjective inner experience, in order to determine whether they have a “theory of mind.” Given this objective, an “unnatural” setup might be preferable, as it decreases the likelihood that the task can be solved by either innate rules or prior learning, instead of explicit reasoning about mental states.

Going further, it has been argued that the “bucket test” is fundamentally unsuitable for assessing animals’ understanding of “seeing” as it does not dissociate between “seeing” as a mental concept and “line of sight” as an observable behavior. That is, to “pass” a “bucket test,” it is sufficient for the subject to prefer experimenters whose eyes are visible and oriented toward them; it is not necessary for the subject to additionally have any concept of what it means to “see” (Povinelli and Vonk 2004; Lurz 2009).

## Beyond Chimpanzees

Since Povinelli and Eddy’s (1996) original study on chimpanzees, many species have been exposed to the “bucket test” and its variants. Other great apes, that is, bonobos, gorillas, and orangutans, appear to act broadly similar to chimpanzees

(Tempelmann et al. 2011). Other species of primate have shown diverse responses, with, for example, tufted capuchin monkeys sensitive to the visibility of the experimenter’s eyes (Hattori et al. 2010) but red-capped mangabeys differentiating only on the basis of her body orientation (Maille et al. 2012). Other work has focused on a variety of domestic species, including dogs (Gacsi et al. 2004), horses (Proops and McComb 2010), and pigs (Nawroth et al. 2013), with all three showing some sensitivity to the visibility of the experimenter’s eyes or face.

## Conclusion

Povinelli and Eddy’s (1996) “bucket test” was designed to investigate young chimpanzees’ understanding of “seeing.” It had the animals choose which of the two experimenters to beg from, where, for instance, one was wearing a bucket on her shoulder and the other a bucket over her head. While the initial group of subjects often failed to prefer the “seeing” experimenter, subsequent work has shown that chimpanzees are at least somewhat sensitive to the visibility of the experimenter’s face and eyes when deciding whom to approach. Whether this implies that chimpanzees have any concept of “seeing” as a mental state remains controversial. Nevertheless, the “bucket test” is still a popular experimental setup for research on animal “theory of mind,” with results now available for many different species.

## Cross-References

- [Goggles Experiment](#)
- [Theory of Mind](#)

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## Bud

### ► Budding

## Budding

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## Synonyms

Asexual reproduction; Bud; Development; Growth

## Definitions

Budding may be defined as a process of development of an outgrowth in any organism. Budding leads to the formation of new living cells as the outgrowth eventually gets detached from the mother cell. Hence, it is considered as a method of asexual reproduction. It is mainly witnessed in yeast (*Saccharomyces cerevisiae*) and also in Cnidarian organisms like *Hydra* sp., sponges, corals, and echinoderm larvae. Organelles like mitochondria can also divide by budding.

## Mechanism of Cellular Budding

The cell first grows in size, and the nucleus is duplicated as an outgrowth and is visible at any end of the mother cell. Movement of the new nucleus to the bud like outgrowth and subsequent detachment of the daughter cell results in completion of budding. The new cell forms a clone of the parent and can have identical behavior and functions.

Angert (2005) has discussed the various models of budding in prosthecate  $\alpha$ -proteobacteria and *Planctomyces*, Gram-positive bacteria (with low GC content), and *Cyanobacteria* in detail, although

the molecular mechanisms are yet to be elucidated. Different bud-developing  $\alpha$ -proteobacteria like *Ancalomicrobium*, *Hyphomonas*, and *Pedomicrobium* have their own patterns of bud formation. Cellular asymmetry is essential in forming buds in bacteria; hence *Hyphomonas* is an organism of interest.

### Mechanism of Budding in *Hydra*

Asexual propagation in *Hydra* is mediated by exporting tissues into a bud, which detaches after 4 days after fully differentiating into a young polyp. A prerequisite for this detachment is the activation of fibroblast growth factor receptor (FGFR) signaling, the mechanism enabling constriction and tissue separation within the monolayered ecto- and endodermal epithelia. In *Hydra*, asymmetric cell changes are mediated by Rho, ROCK, and Myosin II via a novel pathway at its bud base to allow a basal constriction (Holz and Apel 2017). Actomyosin interactions and pathways controlled by RhoA, ROCK, and myosin (Fagotto 2014) allow tissue separation in embryonic systems.

### Budding in Yeast

In yeast, both haploid and diploid cells reproduce by budding. A small outgrowth emerges from the mother cell, the bud, enlarges up to a particular size, and finally separates from the mother cell. It has been reported by Nelson (2003) that in eukaryotic organisms like yeasts (*Saccharomyces cerevisiae*) cellular asymmetry determines the site of bud development and facilitates it by deposition of materials at that site to allow bud growth. Yeast cells undergo polarized growth during budding, their bud sites being selected differently depending on ploidy: haploid or diploid. Diploids bud in bipolar manner and haploids in an axial manner. In the axial budding pattern, proteins such as Bud3 and Bud4 may function as a transient spatial cue (Chant et al. 1995; Sanders and Herskowitz 1996). Mating is also facilitated in haploid yeasts (*Saccharomyces cerevisiae*) due to axial budding pattern. Bipolar budding is

required for formation of a branched colony under nutrient-restricted environment (Wang et al. 2017).

### Mitochondrial Budding

Dynamin-related protein (Drp1) and endoplasmic reticulum have been shown to play key roles in mitochondrial budding. Previously, electron micrographs and fluorescence images were used, but cryo-electron tomography has opened a whole new method to explore the underlying molecular mechanisms of budding in the frozen HeLa cells (intact) (Hu 2014).

### Conclusion

Budding refers to a promising new area of growth in any organism which forms a projection in cells. Researchers have thrown light so far in the different prokaryotes and eukaryotes even on eukaryotic organelle; yet many more pathways are still left to be identified and discussed. Artificial non-living model cells have been designed mimicking the living cells that gave rise to daughter vesicles with distinct interior and membrane compositions, done to study the mechanism of budding and asymmetric cell division in one-celled entities (Koback and Keating 2011). Recent research on electrochemical regulation in budding of yeast cells have been identified, which contributes to the cell polarity and bud formation (Haupt et al. 2014). Budding being an exclusively asexual reproductive means, the newly synthesized part lacks genetic variability. This has been both of a boon and a bane; boon to maintain genetic fidelity in the subsequent organelles like mitochondria but a bane abolishing genetic diversity in *Hydra* and many prokaryotes.

### Cross-References

- [Asexual Reproduction](#)
- [Binary Fission](#)
- [Reproduction](#)
- [Slime Molds](#)

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## Bush Hyrax

### ► Hyracoidea

## Bushmeat Trade

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It has been estimated that people have been hunting wildlife within tropical forests for 100,000 and

40,000 years in West and Central Africa and Asia, respectively, and the practice continues today (Milner-Gulland and Bennett 2003; Corlett 2007). In the present day, meat from wild animals that have been hunted, often illegally, for the purposes of consumption for protein (due to the lack of alternative meat sources) and/or to be sold or traded is defined as “bushmeat” (also known as “wild meat”). It is important to highlight that species are not restricted to terrestrial animals, for example, sea turtles and minke whale are also hunted (aka. “marine bushmeat”; see Clapham and Van Waerebeek 2007). Hunting for the purposes of bushmeat has been found to occur mainly in rural and developing areas of Africa, Asia, Oceania, and South America (Ripple et al. 2016). Bushmeat is commercially traded and often regarded as a luxury meat within urban areas. Consumption is driven by taste and the perception that bushmeat is healthier than commercially farmed animals (Van Vliet et al. 2017); however, there is a lack of information on the nutritional content of different forms of bushmeat. Despite this, Van Vliet et al. (2017) found that bushmeat has a positive impact on general dietary intake.

There are a wide range of taxa which are hunted for bushmeat, which will of course differ between regions, some of which include primates, ungulates, carnivores, marsupials, ratites, rodents, birds, reptiles, bats, and marine animals (Clapham and Van Waerebeek 2007; Pangau-Adam et al. 2012; Ripple et al. 2016). Specific species are likely to be more sort after within certain locations, such as primates in Central and West Africa (see Kurpiers et al. 2016), due to a range of factors such as species availability and demand, meat content, ease of capture, etc. Other factors include the availability of alternative food supplies, such as fish, as Brashares et al. (2004) found that in Ghana an increase in the frequency of bushmeat hunting and demand were found to be linked with poor regional fish supplies. Animals may be hunted for bushmeat and for a number of other reasons. For example, it has been previously estimated that approximately 13%, of 1331 bat species, are hunted for a variety of reasons such as medicinal, sport, ceremonial, with the main reason being for the purpose of consumption (Mildenstein et al. 2016).

According to Lindsey et al. (2012), the most common method used in Africa for bushmeat hunting is the use of snares. This was also found to be a commonly reported hunting method (alongside bow and arrows) as described in interviews of 147 hunters from 21 villages in Indonesia (Pangau-Adam et al. 2012). The popularity of snaring is likely to be due to the cheap cost, the fact that the equipment can be reused, and it catches live animals which is beneficial for communities which require specific slaughter methods (i.e., religious purposes (halal)) (Hennessey and Rogers 2008). However, snaring can result in a slow and painful death for the animals caught (e.g., pigs have been noted to be alive for up to a week when caught in a snare) and are indiscriminate about the animals it captures (Pangau-Adam et al. 2012). Additionally, there are a broad range of other hunting methods used, which may differ from region to region and many of which may be illegal. Other methods include traditional hunting methods (e.g., spears, bows and arrows), guns/firearms (e.g., air rifle), poison, pitfall/gin traps, felling trees, the use of dogs and fire (Pangau-Adam et al. 2012; Lindsey et al. 2012). The transport of bushmeat for the purposes of trade is likely to occur via road (facilitated by logging roads), trains, river, or by foot. However, little research has investigated methods of transportation and packaging methods, which could present potential issues for the contamination of bushmeat (Van Vliet et al. 2017).

As a result of increased bushmeat hunting due to a growing human population near forested regions and increased accessibility (e.g., logging roads), many species are currently threatened (e.g., western and Lowland Gorilla (*Gorilla gorilla*)) with extinction. To date, bushmeat has resulted in the extinction of a range of species (e.g., Miss Waldron's Red Colobus (*Piliocolobus waldronae*)) (Jost Robinson 2017). It has been previously estimated that per year five million tonnes of bushmeat are extracted for food in the Congo and Amazon basin alone (Fa et al. 2002). However, figures vary widely or are simply unavailable. Despite this, given the increase in

human population and associated demand for bushmeat within these regions, the term the "bushmeat crisis" has been coined and this type of hunting is generally regarded as an unsustainable activity.

## Human Health

Human health concerns associated with bushmeat may vary in risk and may include (i) contact via hunting, transport, (ii) butchering and meat preparation, and/or (iii) consumption of meat. Such activities have been previously linked to a range of emerging infectious diseases such as Ebola, HIV, and a range of other pathogens most likely facilitated by the increasing commercialization of bushmeat (Kurpiers et al. 2016). For example; Pourrut et al. (2011) surveyed the prevalence of gastrointestinal parasites in primates within three bushmeat markets within Yaounde City, Cameroon, and house kept pet primates within three towns in Cameroon. In total, of the 125 primates, relating to 15 different species, 78 were held for the purposes of bushmeat and 47 kept as pets. Twelve species of parasites were detected including seven nematodes, three protozoa, one cestode, and one trematode. It was found that wild primates were found to have significantly more helminths (92%) than those kept as pets (51%). Of the parasites found, route of transmission would occur either transcutaneously or via oral transmission, indicating that those individuals who consume or are involved in the butchering of bushmeat are at an increased risk of infection. Disease transmission has been noted to be of highest risk during the butchering of an animal (Van Vliet et al. 2017), although disease transmission can occur during the manual transportation of animals, if injured by an animal or during butchering. While Kamins et al. (2015) found that of the 95 hunters who came into contact with bats all of which had been scratched, came into contact with the animals blood and three individuals reported to have been bitten by bats highlighting the risk of disease transmission. More research is needed to investigate the human health risks related to

aspects of hunting methods used, the transportation of animals used for bushmeat to markets, and the preparation of meat for consumption (Wolfe et al. 2005).

Kamins et al. (2015) surveyed and interviewed 577 individuals in Ghana who were involved in the trade (hunting, selling, and/or consuming) of bats for bushmeat. The study found that no protective equipment, such as gloves, were worn by any of the hunters. Of the 132 individuals that stated to prepare bats for food, 37% stating to gut the bats prior to cooking. Furthermore, only 23% of all respondents perceived a disease risk from hunting, butchering, or eating a bat. Whereas, Friant et al. (2015) found that 55% of respondents within Nigerian communities thought that wild animals could transmit disease, yet only 26% took precautionary measures with only 3% utilizing protective clothing and less than 1% cleaning the meat. Clearly an increase in public health education is required. Friant et al. (2015) suggest that word of mouth and radio educational intervention would be the most appropriate avenues in Nigeria, and the exploration of novel, culturally acceptable protection methods requires further research.

## Tackling the Problem

Hunting wild animals for the purposes of consumption is a complex issue. Not only are there multiple factors coexisting alongside increasing hunting and commercialization, such as deforestation, loss of biodiversity, and habitat destruction, but there are also concerns from a human health aspect because of food security and emerging zoonotic and infectious diseases. Furthermore, stakeholders not only include hunters but also intermediaries, retailers, and the consumer.

As a primary source of protein, the availability of bushmeat clearly plays an important role within rural communities. A number of ways have been proposed to tackle the bushmeat crisis. For example; Wilkie and Godoy (2000) note that if cheaper meat alternatives are made available, then a decrease in hunting and improved conservation

could be seen. Gruber (2016) highlights that rodents, normally regarded as pests, could be used as a form of “mini-livestock” due to their small size and easy management. Many parts of Africa and South America currently hunt rodents, such as Cane rats (*Thryonomys swinderianus*) which can weigh up to 10 kg (Gruber 2016). The development of alternative protein sources could also be introduced through sustainable aquaculture and farming of both domestic and indigenous animals. However, farming of animals may require much more time and money in comparison to illegal hunting, which may already be well-established (Lindsey et al. 2012).

While the assessment of species is required, an emphasis on hunting of sustainable species would be beneficial from a conservation perspective. Further efforts are needed by governments with support from the international community to reduce the occurrence of illegal hunting, especially where species are under threat of extinction by imposing stricter laws and deterrents and ensuring appropriate enforcement. Kamins et al. (2015) note that alone laws and fines are unlikely to initiate sufficient changes and the potential health risk was more likely to act as a deterrent in comparison. Furthermore, the elimination and control of trade routes of illegal bushmeat and overseeing market produce is also required by local and national authorities. Human population assessment and planning near effected and protected areas may help in finding appropriate solutions. While emphasis is generally placed on individual countries, international involvement is required to support countries dealing with the bushmeat crisis. Overall, it is likely that a combined and interdisciplinary approach is required including, education, law enforcement, land/family planning, alternative food (farmed animals) and income sources (e.g., ecotourism), and improved conservation planning and protection (Lindsey et al. 2012). Other closely related areas also need to be incorporated, such as animals used for medicinal purposes and prevention of disease through public health research and initiatives (e.g., education about hygiene practices during food preparation).



## Cross-References

- [Conservation](#)
- [Hunting](#)

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# C

## C. Lloyd Morgan

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Conwy Lloyd Morgan (Fellow of the Royal Society) was a British zoologist and psychologist and one of the first exponents of comparative psychology. He participated in debates that were key in the establishment of comparative psychology as a science, contributing with relevant concepts such as *Morgan's Canon* and *Emergent Evolution*.

### About His Life

Morgan was born in London, England (February 6, 1852), but soon moved to Weybridge with his family. During his childhood, he was described as remarkably curious, as reflected in his early readings of the philosopher, George Berkeley. He started studying at Brenchley, Kent, to later enter the Royal Grammar School in Guildford.

Although Morgan was not entirely convinced of his choice – which was strongly influenced by his father – his university studies began at the

Royal School of Mines in London in 1869 to become a mining engineer. As a result of excelling in his studies, he obtained a diploma in mining and metallurgy. However, his interests went further and broke down the geo-mathematical barriers, expanding his focus to the biological sciences and the scientific method.

Because of his studies on mathematics, Morgan was offered a position as a private tutor of a wealthy family, with whom he had the chance of traveling across North and South America, with experiences that would be later reflected in his work. As a consequence of his trip to America, Morgan decided to explore science beyond the field of physics and biological sciences. Motivated by Darwin's readings, the viability of reconciling philosophy and science began to be an interesting question for him. Consequently, on his return to the UK, he had the opportunity to study for a year under Thomas H. Huxley, a British biologist recognized for his fierce defense of Darwinian theory and evolutionism, who made multiple advances in zoology and compared anatomy. The support and influence of Huxley were transcendental for Morgan's incursion in biology and animal behavior.

In the midst of Morgan's growing career, in 1878 he married Emily Charlotte Maddock, Londoner with whom he had two children, being one of the few non-academic events in Morgan's life for which there is a record.

Between 1878 and 1884, he spent his time in South Africa as professor of different areas such

as physical sciences and literature at the Diocesan College in Rondebosch, Cape Town. Five years later and back in England, he became professor of zoology and geology at the University College of Bristol and stayed there for the rest of his academic career. In 1887, he was elected for the position of principal and in 1909 vice-chancellor. Subsequently, around 1910, he continued his work as professor of psychology and ethics, retiring in 1920 as Emeritus Professor of Psychology.

## Theoretical Contributions

### In Search for a Scientific Comparative Psychology

In the first half of the 1880s, Morgan was skeptical about the viability of a science of animal minds. In that time, the basis of the knowledge about mental processes was introspection; its conclusions could be checked through verbal verification, not possible with non-human animals. This was critical to Morgan given that “verification is that which makes science science” (Morgan 1885, p. 165). Therefore, comparative psychology would not become a science, in contrast to his proposal of an objective psychology (verifiable and occupied with the nervous system and the comparison of adjustive actions between species; Böhnert and Hilbert 2018). However, his positions about the scientific status of comparative psychology began to change. Now his critiques were oriented to move the field forward. For example, Morgan (1886) asserted that inferences about animals’ mental states in light on knowledge of human psychology achieved via introspection (also known as “ejective method”) could be an erroneous path since the extent of psychical differences between species is unknown. This would imply not considering anecdotes as scientific evidence, because much of them were biased, describing facts according to the observer’s interpretations.

Considering all this, a better option was focusing research on observable behavior under different circumstances, including learned, developmental, and phylogenetic contributions to such behavior and its biological basis. This implies

letting aside the speculation on the motives of the observed action. In this way, the ejective method should be kept at minimum while the discipline becomes more professional and scientific.

Morgan’s positions were opposed to his colleague, George Romanes, who thought that a science of animals’ mental life was possible and based part of his work on anecdotes and speculation. However, the exchange between both men made Morgan soften his positions even more. For example, in 1890, Morgan accepted the viability of a science of animals’ minds and showed more sympathy toward the ejective approach to comparative psychology (Fitzpatrick and Goodrich 2017). Romanes noticed that Morgan’s critiques were no longer directed to all the inferences on animal mental activities but to particular and concrete inferences. At this time, his taxonomy of psychological faculties defined certain concepts (reflex, instinct, and intelligence) in terms of non-observable variables, much like Romanes and away from his own previous definitions in the 1880s. The main disagreement at this time was if animals could be able to reason, to which Morgan objected.

A short time later, Morgan changed his positions again, this time away from Romanes. Morgan argued that carefully designed behavioral experiments with well-controlled variables could tell us about the psychological processes underlying observable behaviors, more than “thousands of anecdotes” (Morgan 1894, p. 291). In this way, questions about the reasoning capacities of animals – and other mental processes – would be subjected to experimental verification rather than just philosophical discussion.

Morgan also argued in favor of ecological validity and criticized Edward Thorndike’s experiments for being too artificial and not allowing the display of the natural abilities of animals. Interestingly, this would be a concern later in behavioral and cognitive sciences.

His calls for the adoption of experimental methods were influenced by the spirit of the time and his correspondence with his friend, Mann Jones. The adoption of this method would be to Morgan the hallmark of a maturing science.

## Emerging Evolution

According to Doat and Sartenaer (2014), Darwin's evolution theory brought with itself, at an implicit level, a naturalist philosophy committed to the idea that evolution occurs without leaps, gradually and through quantitative, not qualitative, changes. Given this, Thomas Huxley and other evolutionists wondered about the ways in which a purely quantitative process gives rise to differences between species, a qualitative aspect. From this question, it is possible to raise the existence of what the authors understand as "new naturalism," which indicates that evolution is a creative process that produces genuine novelties, in contrast to Darwinian naturalism, committed to a reductionist form of materialism that understood that the result of biological changes was already implicit in their conditions of appearance, being impossible to think of genuine novelties.

Within this new naturalism is framed Morgan's naturalism, which he called "Emerging Evolutionism." As can be deduced from its name, this vision is based on the concept of emergence – the idea that an emergent is determined by its conditions of appearance but is not reducible to them and, therefore, is unpredictable. The concept of "emergence" associated the idea that the process by which the emergent appears is continuous and discontinuous at the same time.

Following this logic, in a continuous process, genuine novelties emerge. Thus, naturalism could be thought of as a third way between Huxley's discontinuous evolution on the one hand and Darwin's gradualist vision on the other.

The concept of "emergency," in which this line of thinking is based, cannot be fully understood without the vision of a hierarchized world, where the top of this hierarchy is more complex than the bottom. In this sense, Morgan viewed the human species at the top, in contrast with Darwin's vision on evolution.

## Animal Intelligence

Another conceptual contribution present in Morgan's theory is the reformulation of the notion of "animal intelligence" (Fitzpatrick and Goodrich 2017). It arises from the dispute with George

Romanes, who proposed that the reason could explain individual differences produced by learning. On the contrary, Morgan's skepticism about this possibility was based on the idea that reason depends on language. Thus, for him there was no theoretical reason for attributing complex cognitive abilities to non-human animals.

According to Romanes, the capacity of learning on human animals necessarily involved a conceptual understanding of the world. For Morgan, learning involved consciousness, not reason. Animal behavior is therefore explainable by a process of trial and error, a learning that is not conceptual, but associative, which Morgan called "intelligence."

## Morgan's Canon

One of the author's best-known contributions has been "Morgan's Canon." It was originally presented in 1892 at the International Congress of Experimental Psychology in England and published first in *The Limits of Animal Intelligence* (Dixon 1892), where Dixon made a synopsis of Morgan's work. It was not published by Morgan himself until 1894 in his book *An Introduction to Comparative Psychology*. The Canon states: "in no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale" (Morgan 1894, p. 53).

This statement indicated that animal behavior should not be equated with human behavior if it can be explained by "simple processes." An example of his proposal can be seen in the behavioral observations that Morgan made about his dog, Tony. One day, the animal managed to open the door to the garden, which could be interpreted as a "high-level mental process." However, Morgan had previously observed and recorded Tony's behavior in attempting to open the gate, leading him to conclude that this insightful action was a gradual trial-and-error learning process. This anecdote reflects the basis of what would become the renowned Canon, inviting us to think about whether every behavior should always be explained in the most "basic" way possible before giving it "more advanced" attributes.

Nevertheless, it has been pointed out that this interpretation is a misreading of Morgan's postulate. Indeed, the homologation of this Canon with the law of parsimony or with a version of Ockham's razor taken to psychology would be major distortions of interpretation. Some discussions argue that conclusions Morgan intended to reach were not precisely those of "simpler explanations of behavior will be the most appropriate," but rather, and as he would later explain, his proposal would relate to superiority and inferiority in terms of how new or old the process is in the evolutionary development of psychological processes (Thomas 2019). Accordingly, Morgan emphasized: "in no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (Morgan 1903, p. 59). Because Morgan's first statement is the best known, and the later erratum went largely unnoticed in the literature, there are multiple interpretations of the actual meaning of Morgan's Canon.

## Morgan's Legacy

Morgan died on March 6, 1936, in Hastings, Sussex, England, at the age of 84. Until his death, he had made multiple contributions to fields related to animal cognition and behavior.

His best-known contribution, the Morgan's Canon, serves as an anchor for research on mechanisms at the base of animal and human behavior. For example, operant conditioning – a mechanism vastly conserved in evolution – explains a wide range of people's behavior, from creativity to personality, and even maladaptive behavior, based on the simple principle of learning by consequences.

In the context of the establishment of comparative psychology, the Canon, as well as debates about the feasibility of comparative psychology as a science and its own experimental work, helped to replace the somehow weak basis of comparative psychology for more solid grounds, leading it to become a rigorous scientific discipline.

## His Published Work

His work includes *Instinct* (1884); *Psychology in America* (1891); *The Limits of Animal Intelligence* (1892); *An Introduction to Comparative Psychology* (1894); *Mental Factors in Evolution* (1909); and *Emergent Evolution* (1923); among others.

## Cross-References

- [Animal Models](#)
- [Comparative Psychology](#)
- [Consciousness](#)
- [Instinct](#)
- [Intelligence](#)
- [Learning](#)
- [Morgan's Canon](#)
- [Operant Conditioning](#)
- [Parsimony](#)

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## Cainozoic Era

### ► Cenozoic Era

## Camouflage

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## Synonyms

### Crypsis

## Definition

Strategy of an organism that decreases its detectability and recognition by prey or predators.

## Introduction

Organisms with conspicuous patterns are more easily detected by their predators and/or prey, with consequences for their success when fleeing or preying, respectively (see ► [“Predator”](#) and ► [“Prey”](#) in this book). On the other hand, a perfectly cryptic or camouflaged organism represents one of the most remarkable exhibitions of how evolution by natural selection can mold and adapt species to its environment by increasing survival and reproductive success (Brakefield 2009) (See ► [“Adaptation”](#), ► [“Evolution”](#), and ► [“Natural Selection”](#) in this book). The word camouflage comes from the French word “camoufler” or the Italian word “camuffare” with the meanings “to disguise” or “to deceive”, respectively, yet the word “crypsis” comes from the Greek word “krypsis” and means “hiding” or “concealment”. Crypsis is a camouflage strategy that prevents the detection of the organism using it

(signal emitter) by an operator (signal receiver). A cryptic organism can have morphological and/or behavioral traits that make it difficult for the operator to detect it as a discrete entity or to locate its position (Ruxton 2009) (see ► [“Morphology”](#) in this book). There is experimental evidence demonstrating that camouflage can be adaptive in organisms even though it can incur costs (e.g., internal, external, indirect, design and plasticity costs), but to assess this the factors that affect the cost-benefit trade-off need to be evaluated (Ruxton et al. 2004).

Organisms can be camouflaged by their morphological similarity with the background, which is an example of background matching. Camouflage, however, can be even more efficient when behavior is involved, such as when a camouflaged organism remains still, like the thorny devil lizard (*Moloch horridus*), which has striking morphological camouflage that works only when the lizard is immobile (Alcock 2009) (Fig. 1), or when an animal, such as a chameleon or cephalopod rapidly changes its color pattern while in movement (see ► [“Color Change”](#) in this book). Some animals flatten their bodies to avoid being detected or use stealth by taking on appearance of objects that are uninteresting to the operator. This is known as masquerade and is a kind of camouflage by which an organism resembles an object that is inanimate or inedible to the operator, such as a twig, rock, leaf or bird dropping (Skelhorn et al. 2010). Since this strategy consists of not being recognized as potential prey or predator, and includes some aspects of the abiotic background, many cases of masquerade fall somewhere between crypsis and mimicry (Ruxton et al. 2004) (see ► [“Mimicry”](#) in this book). In this sense, the difference between the camouflage strategies of crypsis and masquerade is that crypsis prevents detection by the operator while masquerade is detected but prevents recognition.

The selective pressure on camouflage also selects behavioral traits of the emitters because the benefit can be maximized when the organism adjusts itself to a background (Edmunds 2008). This is a complex task because the operator can be sensible to alterations, and so the camouflaged organism must remain similar to a background



**Camouflage, Fig. 1** The thorny devil lizard (*Moloch horridus*) shows morphological similarity with the background (dead leaves) while it remains still. (Photo courtesy of © John Alcock)



that can be dynamic (Ruxton et al. 2004). The senses of the emitter are also important for camouflage. For example, the cuttlefish (*Sepia officinalis*) can imitate texture patterns of the background but not the colors, since this species cannot distinguish some wavelengths of light (Marshall and Messenger 1996).

Another important factor is that background, is operator dependent since different operators can cause selection for different combinations of camouflage traits that are performed by the emitters in a habitat (Ruxton et al. 2004). Therefore, camouflage is a function of the physical habitat, the sensory physiology of the operator and the camouflage traits of the emitter (Ruxton et al. 2004). Since camouflage can depend on background choice, it can differ for each different phenotype in a polymorphic species (Stevens and Ruxton 2018) (see ► “Polymorphic” in this book). This can lead to apostatic selection, which is a kind of frequency-dependent selection by which predators prey mainly on more common forms (morphs) and do not prey as much on more rare forms in a population, thus maintaining polymorphisms (Bond and Kamil 1998) (see ► “Frequency-Dependent Selection” in this book).

Organisms can use several strategies that are considered cryptic to avoid being detected, such as cryptic coloration (see ► “Cryptic Coloration” in this book), disruptive coloration (see ► “Disruptive Coloration” in this book), countershading

(see ► “Countershading” in this book), or decoration (see ► “Self-Decoration in Dolphins” in this book). These strategies are likely to be affected by behavior since it has a key role in camouflage (Stevens and Ruxton 2018), and thus they differ from other strategies, such as aposematism, for example, that facilitates an organism’s detection (see ► “Aposematism” in this book).

Camouflage has been mainly studied with regard to its visual aspect since humans are principally visually oriented organisms. Humans use camouflage to hunt (interspecific interactions) and as a social or military strategy (intraspecific interactions) to avoid being detected by enemies and to avoid being attacked or to facilitate attacking. A classic example of visual camouflage is the peppered moth (*Biston betularia*), a well-studied case that is due to the alterations observed in the color patterns of their wings as a result of pollution – a phenomenon known as industrial melanism. In other words, the frequency of dark forms (melanic) of this moth increased during the Industrial Revolution because pollution darkened their background (trees with lichen-covered bark). Three main components influenced this melanism and can be applied to other species that have evolved it: (1) the environment changed as a result of pollution and the camouflage of the “typical” type was impaired; (2) moth survival improved because a mutant phenotype provided protection from predatory birds that hunt these moths when they are resting on trees in this new environment;



(3) the mutant phenotype, specified by the dominant allele at the gene for color pattern, increased in frequency under the influence of natural selection, leading to the species exhibiting industrial melanism (Brakefield 2009). Furthermore, there is evidence demonstrating that predation by birds in different backgrounds acts as a selective agent on the characteristics of these moths (Brakefield 2009).

Despite being deeply studied for its visual aspect, camouflage is a strategy that can be widely applied to other senses and vary according to the sensory universe preponderant to each organism. There are suggestions of, and evidence for acoustic, chemical, electric, motion, and tactile camouflage.

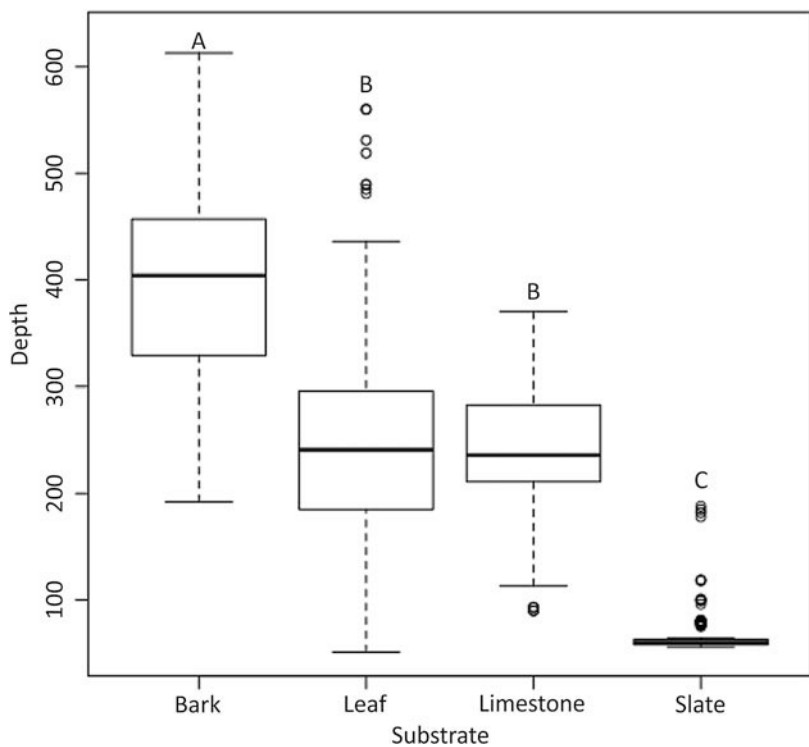
### Acoustic Camouflage

Acoustic camouflage can be expected to be a widespread phenomenon for organisms to which hearing is an important sense. In acoustic camouflage the structure of an acoustic signal is modified

in such a way that its detection by predators or prey is more difficult, with evidence suggestive of a small number of organisms in some sensory systems (Ruxton 2009). Male fowls (*Gallus gallus*) and the great tit (*Parus major*), for example, are known to use alarm calls that reduce the ability of their predators to detect the emitter, while at the same time warn companions about a predation threat (Klump et al. 1986; Bayly and Evans 2003) (see ► “Alarm Calls” in this book). Nocturnal moths are likely using acoustic camouflage when they choose to stay on rough surfaces, because on smooth surfaces they would be found with greater ease by predatory bats due to difference in the strength of echoes from the moth and its surroundings (Clare and Holderied 2015) (Fig. 2). In the visual context, when an operator detects the existence of an object it also simultaneously obtains a significant information on the position of the emitter. With sound, however, the same is not necessarily the case, since an operator can detect an emitter in its surroundings without information on its specific location (Ruxton 2009).

#### Camouflage,

**Fig. 2** Different substrates where moths rest and can be acoustically camouflaged. Bark is the most difficult surface for echolocation by bats, while slate is easier. (Photo by © Clare and Holderied (2015) licensed under Creative Commons)



## Chemical Camouflage

There are many examples of chemical camouflage, mostly of which come from eusocial insects. Because of the inconsistency with which the term ‘chemical camouflage’ has been used within chemical ecology, and the confusion that has resulted, the terminology for this kind of camouflage was recently reviewed (von Beeren et al. 2012). The accepted terminology became: ‘chemical crypsis’ when an operator does not detect an emitter as a discrete entity (background matching), and no reaction is caused in the operator; ‘chemical masquerade’ when the operator detects the mimic but misidentifies it as an uninteresting entity (causing no reaction in the operator); and ‘chemical mimicry’ when an organism is detected as an interesting entity by the operator (causing a reaction in the operator) (von Beeren et al. 2012). On the other hand, chemical masquerade can also occur when an organism lacks odor, which is known for insects, mainly obligately parasitic species, including slave-making ants. Using this strategy, parasites and queens of slave-making ants can break into a host ant species’ nest without being attacked (Lenoir et al. 2001).

The moth caterpillar (*Biston robustum*) uses visual masquerade by being visually similar to the twigs of their host plants, and thus may avoid human or bird (mainly visually oriented) detection (Akino et al. 2004) (Fig. 3). However, this species also uses chemical crypsis, with their odor resembling those of their host plants, leading them to be ignored by potential predators that are chemically oriented, such as ants (Fig. 4). Furthermore, the diet of the moth caterpillar influences its appearance and its chemical odor. Akino et al. (2004) demonstrated that when the host plant of these caterpillars is changed, the caterpillars no longer visually look like the twigs of their previous host plant and they acquired the chemical odor of the new host plant on which they were placed. The same has been documented for treehoppers (*Guayaquila xiphias*), whose chemical crypsis allows them to attract predaceous bodyguards (ants) at reduced risk of falling prey themselves since they possess high chemical similarity to their host plant (Silveira et al. 2009). The



**Camouflage, Fig. 3** The moth caterpillar (*Biston robustum*) uses visual masquerade, being visually similar to the twigs of its host plants. (Republished with permission of Springer Nature, from © Akino et al. 2004)

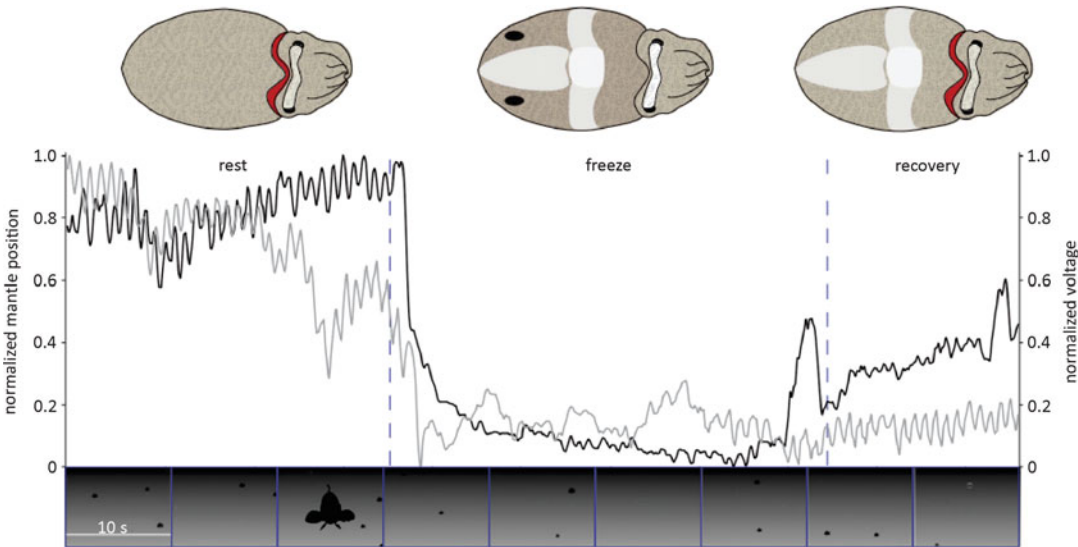
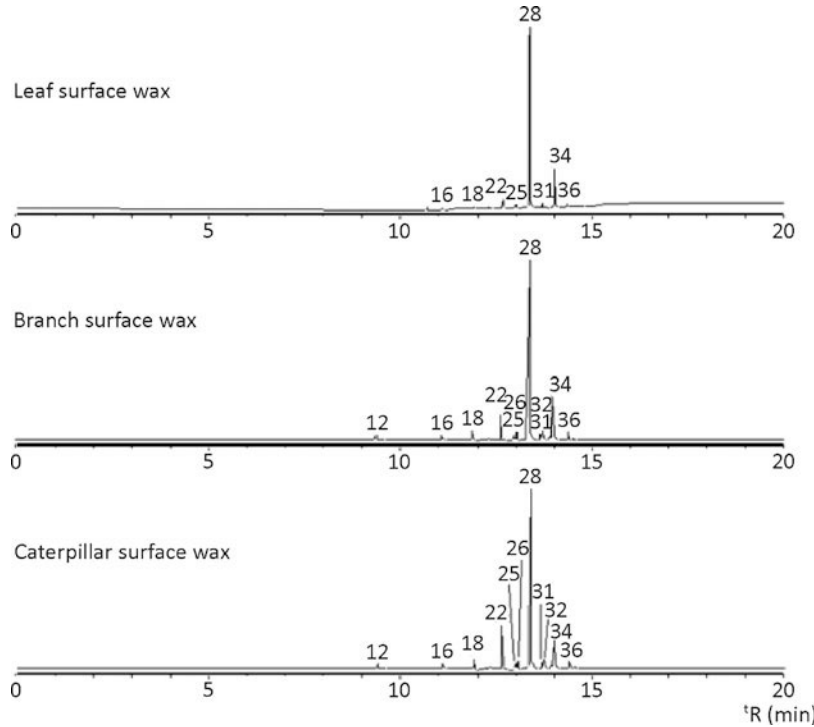
filefish (*Oxymonacanthus longirostris*) feeds on coral and also shows a diet-induced chemical crypsis that decreases its detection by predatory cod (*Cephalopholis* spp.) (Brooker et al. 2015).

## Electric Camouflage

Electric camouflage, also known as bioelectric crypsis, occurs when an electric signal is modified in a way that makes the detection of the emitter more difficult for the operator. Such electric signals are only detected in water, due to its physical properties as a medium, and are used mainly by fish, despite reports of their use by a few amphibian species. They are also only efficient over short distances but can be used to detect organisms even if they are buried, unlike vision (Ruxton 2009).

The electrical discharges that some predatory electric fish use to find their prey do no contrast with lightning noise, and thus are useful for approaching prey without being detected (Hopkins 1973). In other words, these fish likely camouflage their electrical signals to hunt. It is well-known that the cuttlefish (*Sepia officinalis*) uses visual camouflage, but these cephalopods can also use bioelectric crypsis by using a behavioral freeze response to predator stimulus by flattening themselves, diminishing their breathing rate, and closing their orifices, leading to a reduction in their bioelectric fields which predators, such as sharks, can detect (Bedore et al. 2015) (Fig. 5).

**Camouflage, Fig. 4** The moth caterpillar (*Biston robustum*) uses chemical crypsis, with its odor resembling that of their host plants. (Republished with permission of Springer Nature, from © Akino et al. 2004)



**Camouflage, Fig. 5** The cuttlefish (*Sepia officinalis*) can use bioelectric crypsis in response to a looming predator. Both the frequency and amplitude of body movements and

bioelectric cues are reduced during their freeze response. (Republished with permission of The Royal Society, from © Bedore et al. 2015)

### Motion Camouflage

Even though stillness can be essential for camouflage to work for an organism, the presence of

movement can be fundamental for another kind of crypsis: motion camouflage. Motion camouflage can be achieved if an organism's movement occurs in a way that decreases the probability of

the organism's detection (Stevens and Merilaita 2009). For example, some insects, such as males of the Australian emperor dragonfly (*Hemianax papuensis*) use motion camouflage to disguise themselves as stationary when in fact they are performing territorial aerial maneuvers (Mizutani et al. 2003) (Fig. 6).

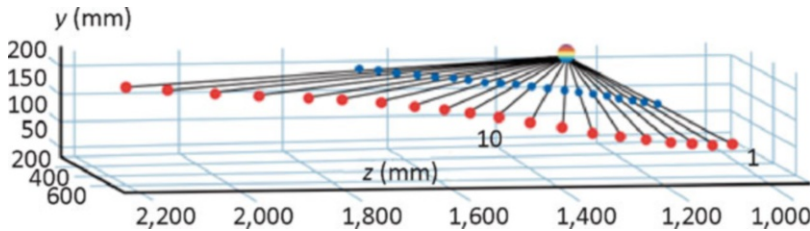
Despite looking like old leaves, the stick insect (*Extatosoma tiaratum*) pays attention to environmental cues and adjusts its behavior accordingly, such as using a swaying behavior in windy conditions to reduce the ease with which it can be distinguished visually from surrounding plants (Bian et al. 2016). Its movements are consistent in frequency with the movement of moving foliage, and thus can represent motion camouflage or masquerade, or a combination of both (Bian et al. 2016).

### Tactile Camouflage

Some organisms use touch to communicate or find prey, and thus this signal can be exploited to hamper detectability as a camouflage strategy.

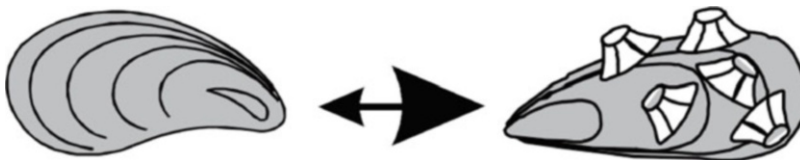
For example, due to a mutualistic association with certain sponges (*Mycale adhaerens* and *Myxilla incrustans*), scallops (*Chlamys hastata* and *C. rubida*) use tactile camouflage against starfish predators (*Evasterias troschelii*) and escape because their sponge-cover drastically reduces the adhesive ability of tube-feet by altering their surface texture, thereby significantly reducing the probability of their capture (Bloom 1975).

A chemical-tactile camouflage seems to occur when the blue mussel (*Mytilus edulis*) is fouled by its hydrozoan parasite (*Laomedea flexuosa*), because the mussel's predator, the shore crab (*Carcinus maenas*), retreats from mussels on first contact when they are thusly fouled (Enderlein et al. 2003) (Fig. 7). Theoretical models suggest that the foot morphology of some dinosaurs caused their steps to produce seismic waves that could be detected through mechanoreceptors, and thus could be camouflaged by seismic wave motion camouflage, which would reduce the probability of detection by ambush predators or by prey (Blanco et al. 2018) (see ► “[Mechanoreceptors](#)” in this book).



**Camouflage, Fig. 6** An interaction between two males of the Australian emperor dragonfly (*Hemianax papuensis*) where the emitter (smaller dots behind) uses motion camouflage to disguise itself as stationary from the operator

(bigger dots in the front), when in fact they are performing territorial aerial maneuvers. (Republished with permission of Springer Nature, from © Mizutani et al. 2003)



**Camouflage, Fig. 7** A chemical-tactile camouflage seems to occur when the blue mussel (*Mytilus edulis*) is fouled by its hydrozoan parasite (*Laomedea flexuosa*). The mussel predator, the shore crab (*Carcinus maenas*), prefers

to feed on mussels without the epibiont (arrow points at significantly preferred prey). (Republished with permission of Elsevier, from © Enderlein et al. 2003)

## Strategies Against Camouflage

Predators and prey possess their own strategies against camouflage, but these have been mainly studied in predators. Predation can maintain, or prevent the origin of, certain color patterns and polymorphisms of prey due to a variety of biological phenomena including perceptual processes, such as search images (see ► [“Search Image”](#) in this book), optimal foraging (see ► [“Optimal Foraging Theory”](#) in this book), and learning (see ► [“Learning”](#) in this book) (Endler 1988). This is because the majority of species are preyed upon by more than one species that possess different foraging strategies and perception and learning abilities, which influences the forms (morphs) that are selected (Endler 1988). Thus, some factors of the predatory species influence, as for example their cognitive and sensory abilities, food choice, timing of predation, among others, as well as some anti-predator factors such as camouflage, background choice and other conditions and defenses used against the predators after it is detected as for example running away, mechanical defenses, and distastefulness to the predators (Endler 1988).

## Conclusion

Camouflage is a strategy of an organism that decreases its detectability and recognition by prey or predators, and is dependent on behavior, background, environmental conditions, and the cognition and senses of the operator and the emitters. Although widely studied from the visual perspective, there is evidence that camouflage can also be acoustic, chemical, electric, motion, and tactile, with some organisms being able to exploit more than one kind of camouflage depending on the cognition of different operators. Nonetheless, for these other senses, there exists, in general, less evidence. This lack of evidence does not necessarily mean that these are rare cases in nature, but instead that there have been fewer studies involving senses other than vision. Furthermore, what has been learned about visual camouflage can also be studied and applied to

other senses if the characteristics of each signal are respected. There remain open questions regarding the costs performing camouflage, as well as why some organisms are selected for some kinds of camouflage and others are not, and for another strategy instead, such as mimicry or aposematism, for example. It is known that operator influences, and some characteristics of individuals can be selected due to different pressures from different operators. To elucidate the morphological and behavioral constraints to the evolution of cryptic traits, comparative phylogenetic methods seem to hold the most promise.

## Cross-References

- [Adaptation](#)
- [Alarm Calls](#)
- [Aposematism](#)
- [Color Change](#)
- [Countershading](#)
- [Cryptic Coloration](#)
- [Disruptive Coloration](#)
- [Evolution](#)
- [Frequency-Dependent Selection](#)
- [Learning](#)
- [Mechanoreceptors](#)
- [Mimicry](#)
- [Morphology](#)
- [Natural Selection](#)
- [Optimal Foraging Theory](#)
- [Polymorphic](#)
- [Predator](#)
- [Prey](#)
- [Search Image](#)
- [Self-Decoration in Dolphins](#)

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## Canalization

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## Definition

Canalization refers to reduced phenotypic variability in traits against any environmental or genetic perturbations.



## Introduction

Canalization refers to the robustness in the phenotypic traits in response to any environmental perturbations (environmental canalization) or genetic changes (genetic canalization). The concept of canalization was first introduced by Conrad Hal Waddington (1942). He described it as “wild type of an organism, the form less variable in appearance than the majority of the mutant races” (Waddington 1942, p. 563). Canalized traits show near optimal fitness value and are less phenotypically variant as opposed to traits showing phenotypic plasticity. The evolutionary role of canalization has been widely postulated by several researchers (Siegal and Bergman 2002; Flatt 2005; Debat and David 2001) and over the years the conceptual understanding of canalization has been revisited and modified repeatedly.

The idea of canalization was also suggested independently by Schmalhausen (1949). He proposed that stabilizing selection, a form of natural selection, plays a prominent role in maintaining the canalized state of a trait. A trait undergoing a stabilizing selection shows an average or intermediate value and represents the equilibrium state of a particular phenotype in a population. According to Schmalhausen, stabilizing selection tends to buffer the developmental pathways against any genetic or environmental perturbation and thus maintains the traits in a canalized state. However, it has also been now reported that the buffering mechanisms maintained by stabilizing selection can be disrupted if directional selection comes into play (Groth et al. 2018). If such a scenario occurs, there may be decanalization of traits or reduction in canalization of traits occurs.

## Canalization and Cryptic Variations

Reduction in phenotypic variation usually implies less evolutionary potentiality and reduced adaptability of traits in face of changing environmental conditions. Although canalization reduces phenotypic variation and is known to impede adaptation in the short term, it can be a “capacitor of evolutionary change” (Gibson and Reed 2008, p. 2),

when the process is followed by decanalization. The process of canalization leads to the buildup of hidden or cryptic genetic variation. The accumulated hidden genetic variation which remains invisible in the population becomes visible as a phenotypic variation when an individual encounters novel environmental conditions or if new genetic mutations occur in an individual. In the process of canalization, i.e., during the buffering of developmental pathways, if there is accumulation of new mutations that are suppressed during the process, then a new selection process can lead to potential evolutionary divergence in an organism.

As an example, in *Drosophila melanogaster* the Hsp90 heat-shock protein encoded by *Hsp83* locus acts as a capacitor for morphological evolutionary response (Rutherford and Lindquist 1998). When Hsp90 was mutated or impaired using inhibitors, varied phenotypic responses were observed in *Drosophila* flies, like developmental abnormalities in body parts, changes in wing venation and shape, and bristle duplication. Such results indicate the involvement of Hsp90 protein in promoting the canalization process by suppressing the expressivity of variations associated with the morphogenetic pathways. The uncovering of hidden genetic variants by impairment of Hsp90 allows selection to act upon the variants, thus paving the path for occurrence of morphological radiations. Similar results were obtained in *Arabidopsis thaliana*, where Hsp90 was found to buffer against genetic and environmental perturbations, and reduction in its activity resulted in enhancement of genetic variations (Queitsch et al. 2002).

## Canalization and Genetic Assimilation

Genetic assimilation refers to the process by which a phenotypic plastic character expressed in response to any environmental change gets constitutively expressed as canalized trait even in the absence of the environmental cue which evoked it (Crispo 2007). The process of genetic assimilation promotes evolutionary divergence and speciation through the establishment of a new canalized trait which tends to be more

adaptive in nature. The fixation or canalization of traits during the process of genetic assimilation occurs due to selection acting on the changes occurring in the genetic regulation of morphogenetic pathways in response to an environmental stimulus. The phenomenon of genetic assimilation was demonstrated by Waddington (1953) for cross-veinless (*cvl*) wing phenotype of *Drosophila* which possesses defects in venation patterns. When artificial stress in the form of temperature was applied in fruit flies at early developmental stages, Waddington found the occurrence of *cvl* phenotypes. When these variants were artificially selected as parents for the next generation, an increase in the frequency of the *cvl* phenotype was observed and after a number of generations he found the occurrence of the *cvl* phenotype even without heat shock treatment. Thus, Waddington was able to genetically assimilate the environmentally induced *cvl* phenotype in *Drosophila* in a canalized state.

## Conclusion

Research to date has elucidated the role of canalization in potential evolutionary consequences. In the long term, the release of accumulated cryptic genetic variants under specific decanalizing environmental or genetic conditions paves the way for phenotypic diversification in a population, thereby increasing its evolvability. However, the consensus regarding the origin and mechanisms involved behind the phenomenon of canalization still remains elusive. This is largely due to presence of gaps in the studies pertaining to measurement of canalization as well as due to ambiguity in different hypotheses provided by researchers. Waddington (1957) mostly considered canalization as an intrinsic property of a genotype that shows less variation than other genotypes. He did not take into account the role of any mechanism or process behind the phenomenon and simply considered it as the quality of an organism. The hypothesis that canalization has an adaptive role and aids in the process of evolution has now been proposed and still the molecular mechanisms involved in the process of canalization need to be elucidated (Stearns 2002). The regulatory networks involved in buffering

against environmental and genetic perturbations need to be identified. Unraveling the genetic and molecular mechanisms underlying canalization will be the focus of future research in this area.

## Cross-References

- Evolution
- Phenotype
- Stabilizing Selection

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## Candidate Gene

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## Synonyms

Genome-wide association studies; Positional candidate gene approach; Putative candidate gene

## Definition

A candidate gene is gene which is presumed to be associated with a particular disease or a phenotypic trait, whose biological function(s) is derived either directly or indirectly from other studies including animal model studies with other species (using comparative genomic studies), genome-wide association studies (GWAS), classical map-based positional cloning method, and a more recent next-generation sequencing (NGS) methods.

## Introduction

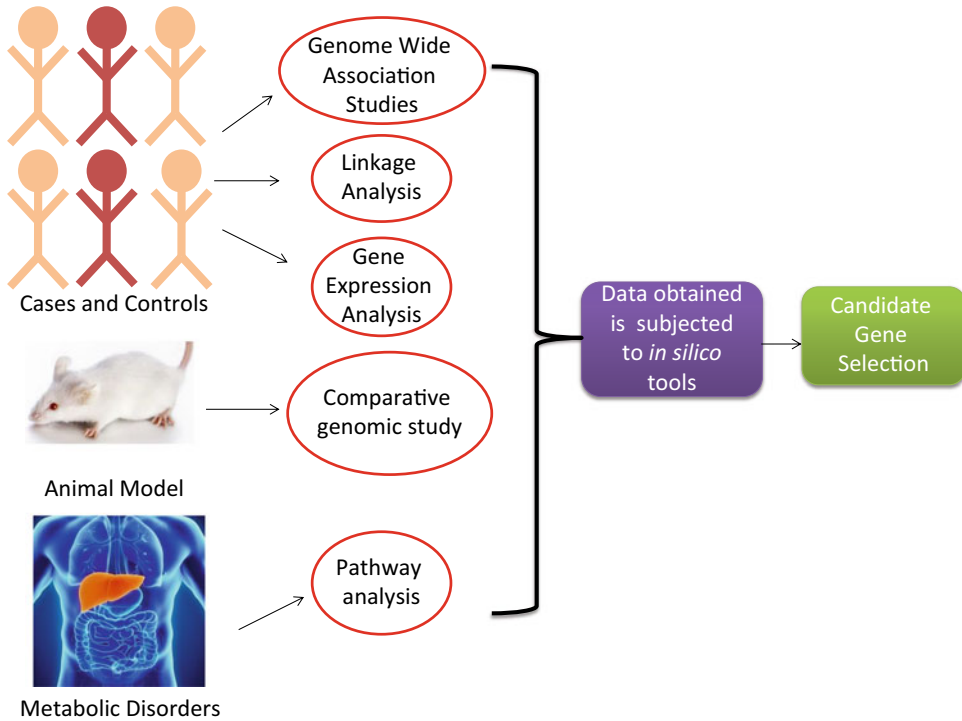
Identification of certain genes with known function causal for diseases, (e.g., *MSH2* and *MLH1* causing colon carcinoma) evolved the candidate gene approach in disease biology. Further candidate genes were discovered by either direct screening of genes in a biochemical pathway with known related functions associated with the pathogenesis of the disease (PKU, AKU), or indirectly derived from the animal model studies (e.g., *DFBN3* deafness gene identified using mouse

shaker-2 mutants) (Fig. 1). Lately, studies involving candidate genes have been used as an important aspect of genetic association studies for identification of risk associated with a particular genetic disorder. The candidate gene approach begins with the selection of a probable candidate gene, based on its role in the development of disease phenotype, which is followed by identification of polymorphisms and finally the variants are assessed for disease association. Candidate genes are generally the genes with known biological significance directly or indirectly regulating the development processes of the investigated traits, which could be confirmed by evaluating the effects of causative gene variants in an association analysis (Zhu and Zhao 2007). Candidate gene approach is population based and hypothesis driven. This is mostly based on case-control study. Due to the presence of great variability among organisms it is often difficult to distinguish SNPs from candidate genes. Currently, availability of great amount of genetic information deciphered through online databases has enabled researchers to explore the existing data and in silico tools deeply for identification of new candidate genes. A number of other methods were used to identify genes linked to disease before the candidate gene approach was fully developed. These methods are based on genetic linkage and positional cloning.

The candidate gene approach is used widely not only in animal genetics but also in plant genetics for characterization and cloning of Mendelian as well as Quantitative Trait Loci (QTLs). It constitutes a complementary strategy to map-based cloning and insertional mutagenesis. In plant genetics, the candidate gene identification is performed by looking for map co-segregation between candidate genes and loci affecting the trait. Statistical association analyses between molecular polymorphisms of the candidate gene and variation in the trait of interest have also been carried out in a few studies (Pflieger et al. 2001).

## How to Carry Out a Candidate Gene Study?

The first and the most important step in carrying out a candidate gene study is selecting a suitable



**Candidate Gene, Fig. 1** The candidate gene identification approach

gene that may plausibly play an important role in the diseased phenotype. The next step is selecting a DNA polymorphism. It is very important to decide which polymorphism would be most useful in an association study. The existing gene variants must be identified and it should be determined that which of these gene variants result in proteins with altered functions. The genetic variants can be identified through sequencing. Polymorphisms can be of much importance in studying complex disorders for which many potential candidate genes exist. The final step in carrying out a candidate gene study is to test the candidate gene in a random group of disease samples (cases) and healthy individuals (controls). But the case control study may result in fallacious association if the controls are not properly matched to the cases with respect to ethnicity and other factors which contribute to the genetic composition of an individual.

### Role of Candidate Gene Approaches in Complex Genetic Traits

The candidate gene approach is the study of genetic influences on a complex genetic trait by generating hypotheses and identifying candidate gene that may play a role in the etiology of disease and variant identification in genes that might either cause a change in the protein or its expression (Tabor et al. 2002). A candidate gene study is generally conducted in a population-based sample of affected and unaffected individuals, i.e., the case control study as discussed in previous paragraph also. A candidate gene study takes advantage of statistical efficiency of association analysis of complex diseases and the understanding of phenotype, tissues, genes, and proteins that are likely to be involved in disease. Association in candidate-gene study can be defined as a statistical dependence between two or more events which is greatly influenced by the

characteristics of the study including size of the population studied and number of variables. Candidate gene can be very useful in exploring the potential causal pathways between genetic determinants and complex diseases. There are mainly two approaches for genetic dissections of complex and quantitative traits, i.e., genome-wide scanning (GWAS) and candidate gene approach.

Digital Candidate Gene Approach (DigiCGA)

DigiCGA is also known as in silico candidate gene approach or computer-facilitated candidate gene approach. It is a web-based candidate gene identification approach that objectively extracts filter, (re)assembles or reanalyzes all possible available resources derived from public web databases mainly in accordance with the principles of biological ontology and complex statistical methods for computational identification of potential candidate gene of specific interest (Zhu and Zhao 2007). A number of online tools are available for prioritizing candidate genes such as Endeavour, Pocus, G2d, Suspects, etc. (Table 1).

Candidate Gene, Table 1 showing online tools available for DigiCGA

| Tools       | Website                                                                                                                                                                     |
|-------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| GeneSeeker  | <a href="http://www.cmbi.ru.nl/GeneSeeker/">http://www.cmbi.ru.nl/GeneSeeker/</a>                                                                                           |
| Endeavour   | <a href="https://endeavour.esat.kuleuven.be/">https://endeavour.esat.kuleuven.be/</a>                                                                                       |
| POCUS       | <a href="https://omictools.com/prioritization-of-candidate-genes-using-statistics-tool">https://omictools.com/prioritization-of-candidate-genes-using-statistics-tool</a>   |
| G2D         | <a href="http://g2d2.ogic.ca/">http://g2d2.ogic.ca/</a>                                                                                                                     |
| SUSPECTS    | <a href="http://www.cgem.ed.ac.uk/resources/suspects/">http://www.cgem.ed.ac.uk/resources/suspects/</a>                                                                     |
| BioMercator | <a href="http://moulon.inra.fr/index.php/en/traverse-team/atelier-de-bioinformatique/74">http://moulon.inra.fr/index.php/en/traverse-team/atelier-de-bioinformatique/74</a> |
| GFINDER     | <a href="http://www.medinfopoli.polimi.it/GFINDER/">http://www.medinfopoli.polimi.it/GFINDER/</a>                                                                           |
| QTL Mixer   | <a href="http://qtl.pzr.uni-rostock.de/qtlmix.php">http://qtl.pzr.uni-rostock.de/qtlmix.php</a>                                                                             |
| SNPs3D      | <a href="http://www.snps3d.org/">http://www.snps3d.org/</a>                                                                                                                 |

Limitations of Candidate Gene Approach

The findings of candidate genes are not easily reproducible in subsequent studies because of population stratification. Therefore the design of study should be very specific. Since it is a hypothesis-driven approach, the findings of candidate genes are biased as compared to anonymous approaches such as linkage analysis, genome-wide association studies (GWAS), microarrays, etc. The restricted knowledge can result in “information bottle-neck.” Hypothesis-driven genetic approaches are less likely to yield result than other approaches (linkage analysis, GWAS, etc.), which uses markers throughout the genome and do not depend on the ability to select a plausible candidate.

Conclusion

Candidate gene approach has been a pioneer in the field of genetic epidemiology, identifying risk alleles and their association with clinical traits. Candidate genes are related to a particular disease or condition and can be identified either on the basis of position or function. A positional candidate gene is located in a chromosomal region suspected of being linked to a disease and functional candidate gene is a gene encoding a product associated with the disease. Candidate gene analysis is usually the indispensable procedure for subsequent positional cloning of QTLs (Qualitative Trait Loci) controlling the major genetic variation of interested traits after initial genome scans. Candidate gene studies can utilize the data made available through comparative genomic studies from other species, genome-wide association studies, whole genome gene expression profiling, next-generation DNA and RNA sequencing, CHIP-seq to unravel a multitude of susceptible disease associations. The next-generation data and candidate gene approach can give rich dividends in terms of elucidation of complex disease mechanisms, better prognosis and diagnosis of patients in a short time, and an efficient way (Patnala et al. 2013).

## Cross-References

- ▶ [Alleles](#)
- ▶ [Genetic Variation](#)
- ▶ [Haplotype](#)
- ▶ [QTL Linkage Analysis](#)

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## Canine Cognition

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## Synonyms

[Dog behavior](#); [Dog cognition](#); [Dog intelligence](#)

## Definition

The study of the dog's mind. The process by which dogs acquire, process, and store information and conceptual skills that inform behavior, including sensing, perceiving, learning, remembering, and reasoning.

## Introduction

The species *Canis lupus* consists of two carnivores, wolves (*Canis lupus*), and a subspecies,

dogs (*Canis lupus familiaris*). Mitochondrial DNA indicates that dogs and modern-day wolves began to diverge from a common ancestor around 100,000 years ago with true domestication beginning approximately 14,000 years ago (for a review see Galibert et al. 2011). However, it is important to highlight that the place(s) of the dog's domestication event(s) and the process of how the domestication event(s) occurred remain unclear and contested.

Historically, dogs have been used as study subjects and model organisms in studies of psychological and biomedical research. Despite being the first domesticated animal, only recently have researchers recognized the unique role dogs occupy in our society (Bensky et al. 2013). In the last 30 years, the study of canine cognition has experienced a substantial boom. The number of journal articles on canine cognition and behavior has increased sixfold, from 218 papers (1993–2005) to 1307 papers (2006–2018), and increasing in trend since 2005 (Massimo et al. 2020). From these studies, scientists have discovered various cognitive abilities, many specifically related to understanding human social behavior, that make dogs a unique study species (Miklósi et al. 2003). Below, we highlight literature focusing on three main topics, presenting examples of canine: (1) perception, (2) non-social cognition, and (3) social cognition.

## Perception

Before delving into what is known about canine perception, it is important to note that dogs, arguably, represent the most morphologically diverse species on the planet. There is immense systematic variation between breeds, including size, height, facial morphology, and more. Most studies of dogs cannot possibly begin to provide a representative sample of all dog breeds, dog groups, morphological types, etc. Therefore, it is important to consider this limitation when generalizing results of perception to dogs as a whole.

Perception represents an individual's sensory experience of the world, specifically the process of identifying, organizing, and interpreting sensory stimuli through smell, sight, sound, touch,



and taste. The development of dog senses varies by modality. At birth, dog eyes and ear canals are functionally closed (for an overview of sensory development in dogs, see Lord 2013). Functional olfaction begins around 8–13 days, coinciding with the opening of the eyes. Visual forms are perceived around 25 days of age, and visually guided behavior begins at 4 weeks of age (Scott and Fuller 1965). Around this time, puppies begin to respond to sound, coordinated walking occurs, and environmental investigation begins (Lord 2013; Scott and Fuller 1965).

### Visual Perception

The majority of studies, 74%, evaluating canine cognition has presented subjects with visually based paradigms (Bensky et al. 2013). While few foundational assessments of dog vision and perception exist, many plagued by small sample sizes, research into more cognitively complex conceptions like visual discrimination, processing precedence, and face-processing has been conducted. Most commonly, the visual discrimination abilities of domestic dogs have been evaluated via object choice discrimination tasks. These studies have found that dogs can easily learn to discriminate between objects varying in color, shape, size, and quantity (for a review please see Byosiére et al. 2017). Not only can dogs discriminate between objects, but they are also adept at visually processing both humans and conspecific faces and discriminating between emotional facial expressions.

Certain similarities and differences exist when comparing dog and human visual perception. Like humans, dogs demonstrate a left gaze bias, but only when presented with upright human faces (Guo et al. 2009). Additionally, fMRI research indicates activation in brain regions responsible for face processing in humans, such as the temporal lobe and the medial and lateral frontal cortex, also appears to be associated with face processing in dogs (Cuaya et al. 2016). However, differences between human and dog visual perception have also been observed. Recently, studies of canine visual perception research have focused on evaluating how visual information is processed, interpreted, and modified, post-retinally, through studies of illusion susceptibility (Byosiére et al.

2017). These studies highlight that dogs often do not demonstrate humanlike susceptibility to certain geometric visual illusions, but rather demonstrate null or reversed illusion susceptibility. Taken together, these findings indicate that while there are parallels between dog and human visual perception, there are also differences that are important to consider.

### Olfactory Perception

Dogs are perhaps best known for their superior sense of smell. Yet, an immense gap in canine olfaction research exists (for a review of olfaction in dogs, see Gadbois and Reeve 2014). While the majority of research on canine olfaction has been conducted at either the cellular or behavioral level, few studies have evaluated olfactory perception at a cognitive level. As dogs, and their noses, are critical in applied fields, such as scent detection, understanding how olfaction and cognition interact has broad and far-reaching implications.

In comparison with a mere six million olfactory receptors in the human nose, the dog's nose is highly specialized. Dogs not only have 300 million olfactory receptors in their nose but also have a secondary olfactory organ, the vomeronasal organ. Dogs can follow scent trails, discriminate between different human individuals (including identical twins), be trained to assign novel odors to a known category, and form a representation of the objects they smell (for a brief review of olfaction and cognition in dogs, see Lea and Osthaus 2018). Preliminary evidence also suggests that dogs may demonstrate self-recognition in a modified olfactory version of the infamous mirror-self recognition test. Dogs were found to spend more time investigating odors of themselves compared to odors of themselves that were altered, indicative of the dog's recognition of their own odor (Horowitz 2017). While interesting, the question remains whether this modified olfactory test, while perhaps more ecologically valid in olfactory dominant animals like dogs, does, in fact, represent an analogous assessment of the mirror-self recognition test.

### Auditory Perception

Auditory perception, in general, is reliant on the successful transduction of sound waves into

electrical signals, the refinement and filtering of specific sounds, and the interpretation of those sounds. Dogs can hear sounds 400 m away, four times farther than humans, and are most sensitive to sounds that fall within the frequency range of 200–15,000 Hz (for a review of auditory perception in dogs compared to humans, see Barber et al. 2020). Studies of auditory perception in dogs suggest they can distinguish natural from artificial sounds and, like olfactory perception, can categorize novel sounds into known categories.

In social contexts, dogs can discriminate human spoken words based on their phonetic composition, doing so spontaneously for the same phonemes across different speakers (e.g., Root-Gutteridge et al. 2019). Additionally, there is evidence for the cocktail effect in dogs. A recent set of experiments suggests that dogs attend to their name when presented among background noise or equal or louder intensity (Mallikarjun et al. 2019). Moreover, dogs were able to recognize their name when spoken by an unfamiliar human via a loudspeaker.

While limited, due to smaller or single sample size, more complex examples of auditory cognition have been observed. Preliminary evidence suggests that certain dogs may demonstrate syntactic understanding. A single subject, Sofia, was able to generalize her behavior flexibly when presented with object-action requests. Additionally, dogs like Chaser (1022 words) and Rico (200 words) highlight that dogs can recall and recognize an exceptionally large number of proper-noun names.

## Non-Social Cognition

Non-social cognition, also referred to as physical cognition, considers how subjects perceive and respond to physical objects or stimuli within their environment. Compared to studies of social cognition, fewer studies have investigated non-social cognition (Bensky et al. 2013). Regardless, a substantial body of literature exists, specifically on topics such as canine learning, memory, object permanence, and means-end reasoning.

## Learning

Learning, which includes both classical and operant conditioning, involves the formation of an association between a stimulus and an outcome. Ivan Pavlov famously used dogs in his seminal work leading to the discovery of classical conditioning. Through surgical modification of the dogs' salivary glands, he observed that dogs were salivating when food was present (unconditioned response) but, at times, also when food was not present. Through a series of controlled experiments, Pavlov paired food (unconditioned stimulus) with a nonfood stimulus (conditioned stimulus), such as lights, sounds, and objects. After repeated pairings of the unconditioned and the conditioned stimuli, the dogs began to salivate in the presence of the conditioned stimulus alone (conditioned response). Since Pavlov's noteworthy work with dogs, these classical conditioning principles have been observed across canid species.

Through operant conditioning, also known as instrumental conditioning, behaviors are modified via their associations with positive or negative consequences. These principles are widely used in both canine cognition paradigms, for example, discrimination tasks, and applied fields, such as in the training of scent detection dogs. Frank (1980) claimed that there were differences in associative learning between dogs and wolves, with dogs being more capable of completing operant learning tasks than wolves. However, this generalization has not stood the test of time, and replication and the differences observed may well have been due to differences in rearing conditions. Thus, it is unlikely that operant learning capacities in dogs are in any way unusual when compared to other canids.

Once a dog has learned an association between a stimulus and an outcome, they may have difficulty suppressing the learned response. This has been demonstrated through the use of reversal learning tasks, in which dogs first make an association between an object and a reward in a two-choice operant learning task. When the conditions are reversed, and the unrewarded object becomes the rewarded object, dogs consistently take longer to make this new association. This outcome holds

true even when dogs are visually cued about the new location of the reward (Ashton and De Lillo 2011).

## Memory

The majority of canine memory research to date has focused on working memory. Working memory is adaptive and essential for animals, allowing them to solve problems and adjust to changes in the environment. In dogs, as in other species, performance on working memory tasks decreases as time between the initial presentation and recall increases. For example, when dogs observed an object hidden in one of four locations, they were able to successfully identify the location with 80% accuracy after 10 s and with 50% accuracy after 240 s (Fiset et al. 2003). Recently, an odor span test was used to assess canine working memory with scents, revealing that the 6 dogs studied were able to recall and discriminate between 72 odors with high accuracy (79% or higher) over a short period of time (Krichbaum et al. 2020). Furthermore, they were able to correctly identify a novel odor when up to eight intervening odors were presented, indicating that eight might be the working memory capacity for memory in dogs (for comparison, the working memory capacity in humans is seven).

Some, but few, studies have evaluated episodic memory in dogs. Episodic memory involves conscious recollection of personally lived past events, specifically the “what,” “where,” and “when” of one’s past experiences. To evaluate this in dogs, Kaminski et al. (2008) gave two dogs, Betsy and Rico, a chance to view two separate rooms with various objects located within them. The dogs were then asked to retrieve one of the objects. Rico seemed to vary his search pattern based on previous knowledge of the object’s location, indicating that dogs might possess the capacity to remember the “what” of past events. However, Betsy’s performance was less convincing as she carried out the same search pattern during each trial, regardless of the objects’ location. Overall, more research into canine episodic memory is needed before broad generalizations can be made.

Like many species, dogs demonstrate cognitive impairments associated with both aging and

dementia. As such, dogs have become a model species in the study of cognitive deficiencies in humans. Specifically, studies on canine cognitive dysfunction in dogs have supplemented our understanding of Alzheimer’s disease (Bensky et al. 2013). Memory and learning studies have been employed to both diagnose and further our understanding of canine cognitive dysfunction. For example, Adams (2000) used a delayed non-matching to position (DNMP) paradigm to both compare the cognitive abilities of young (1–3 years old) and aged dogs (8–12 years old). The authors found that aged dogs demonstrated impaired spatial learning and spatial working memory capacities when compared to young dogs. Furthermore, severely cognitively impaired dogs often failed to reach the criterion during the training phase, whereas slightly impaired and unimpaired aged dogs did not. Consequently, the DNMP paradigm can be used as a tool to diagnose canine cognitive dysfunction.

## Object Permanence

Initially set forth by Piaget, studies of object permanence offer the opportunity to evaluate an individual’s ability to understand that objects will continue to exist when they cannot be sensed. Typically in these tasks, an object is hidden in an opaque container (the displacement device) and then placed into or behind an occluder. Without the subject’s knowledge, the object of interest is then taken out of the displacement device and left in or behind the occluder. The subject, who is watching this procedure unfold, is then shown the displacement device, which is now empty. The theoretical mental process of understanding this task suggests that subjects must not only store and update information but also utilize a mental model to construct an internal map of where the object may be located.

Original assessments of object permanence in dogs were consistent with the conclusion that dogs could perform at the highest level of Piaget’s sensorimotor phase of development (Stage 6), solving both visible and invisible displacement tasks (Gagnon and Doré 1994). However, as more refined controls were added to the experimental paradigm, the results have become less

convincing. In follow-up studies, these authors suggest that within the task there is a theoretical distinction between the animal's representational ability to recognize and recall information. Recalling the object, rather than recognizing a cue association, suggests an animal possesses Stage 6 problem-solving abilities. More recent results conducted in dogs suggest that recall does not guide problem-solving in invisible placement tasks, and thus dogs likely demonstrate Stage 5 capacities at most.

More recently, Fiset and LeBlanc (2007) assessed how dogs use visual cues during invisible displacement tests. The authors found additional evidence for the conclusion that dogs demonstrate an understanding of visible displacement but not invisible displacement. In line with other studies of object permanence in dogs, the authors observed that dogs typically searched in patterns consistent with an adjacency rule, relying on locations nearest to the displacement device. Additionally, dogs used the experimenter as a local landmark when the displacement device was moved to a location close to the experimenter. Overall, the evidence suggests that dogs do not make inferences about an object's location during invisible displacement tasks and thus do not demonstrate the capacity for Stage 6 representational abilities. However, considering the mixed results, it does seem as though dogs can easily adapt and spontaneously employ a variety of strategies to complete the task.

### Means-End Reasoning

The lives of both humans and animals are riddled with everyday problems that need to be solved. Many of these are in fact novel problems that an individual may have not yet experienced. Means-end reasoning has been suggested to represent the way by which individuals get from a problem state to a desired goal state. Frequently, means-end understanding has been tested using a string-pulling task paradigm, in which a subject is presented with two string options. One string option has the desired object attached to it, and the other has no object attached. A barrier blocks direct access to the ends of both strings (i.e., where the reward is attached). If a subject identifies the

desired object can only be obtained by pulling the string, then they should be able to succeed on the novel task spontaneously. However, if the means to an end is obtained via repeated exposure and associative learning, then the individual does not demonstrate this ability.

To date, most studies of means-end reasoning in dogs indicate that dogs cannot successfully perform the task. While dogs can learn how to obtain out-of-reach desired rewards by pulling the string, they fail to do so spontaneously in a variety of experimental conditions, where ropes are crossed, straight on, or parallel. Much of this seems to be due to proximity errors (Osthaus et al. 2005; Range et al. 2011a) and may relate to confounds associated with inhibitory control. However, Range et al. (2011a) observed that dogs were able to solve means-end tasks when a board adaptation of the paradigm was used, called the "on-off problem." When two identical rewards were presented out of reach behind a fence, one lying on a board and the other lying next to a second board, dogs spontaneously demonstrated an ability to pull the correct board (the one with the food lying on top). Thus, depending on the paradigm, dogs can solve the means-end task successfully and spontaneously.

## Social Cognition

Considering their unique relationship with humans, dogs provide an interesting and exclusive model for understanding domestication and evolutionary processes. Dogs are particularly sensitive to human-given social cues and social learning (Hare and Tomasello 1999; Miklósi et al. 2003). Therefore, it is perhaps not surprising that more than half (54.7%) of the studies of canine cognition have specifically focused on social cognition (Bensky et al. 2013).

### Following Human Social Cues

Perhaps contributing to the surge in recent studies of canine cognition, numerous studies have found that dogs are uniquely attentive to human-given communicative cues. Compared to other non-human species, including our closest living

ancestors, the great apes, dogs are extremely adept at locating hidden food/toy when indicated via a human-given gesture (for a review pointing comprehension in dogs, see Kaminski and Nitzschner 2013)

Most of the studies investigating the canine response to human social cues have implemented an object-choice discrimination task. In this paradigm, a container is baited out of the subject's view. The experimenter then presents the dog with multiple containers (only one of which has food/toy inside) and provides a social cue, such as pointing, towards the target container. The dog is then allowed to select one of the containers. While many variations of cueing exist, there is overwhelming evidence that dogs perform significantly above chance when presented with a pointing cue, regardless of whether the point is proximal (less than 20 cm away from the cup) or momentary (cue is removed before the dog is released to make a choice). Dogs are also able to follow more subtle human-given cues, such as gazing in the direction of the target container (Kaminski and Nitzschner 2013). However, their performance is generally less proficient than following pointing cues, as some studies note at chance or below chance performance (for a review see Reid 2009).

Much contention exists about how this unique attentiveness to human-given social cues developed. It has been hypothesized that dogs' ability to make use of human social signals may have resulted from selection pressures during domestication. This conclusion is further supported by the fact that dogs outperform wolves (their closest relative) and chimpanzees (humans' closest relative) on gesture-assisted object choice discrimination tasks (Kaminski and Nitzschner 2013). Some researchers have found that puppies as young as 6 weeks old can follow human pointing cues in these tasks, thereby suggesting a possible genetic predisposition (for a review see Wynne 2016). However, other studies have found opposing conclusions, where puppies do not perform as well as their adult counterparts, suggesting that the comprehension of human communicative pointing cues improves with age (Dorey et al. 2010). Regardless of how this ability develops, at both

the proximate and ultimate level, there is substantial evidence to suggest that dogs are highly adept at following human-given social cues.

### Attention to Attention

Attention represents the cognitive process by which individuals process and respond to specifically relevant details within their environment while simultaneously ignoring other perceivable information. As dogs have coevolved with humans, they excel in paying attention to human communicative cues, behaviors, and vocalizations. Studies of attention in dogs have largely focused on perception or social attention to human-given communicative cues (discussed above). However, some additional studies have investigated dog's attention to both conspecific and human attentional states, both of which warrant discussion.

Inferential evidence of perspective-taking abilities in dogs can be taken from studies employing different theoretical designs. For example, Virányi et al. (2004) observed that dogs were more likely to take forbidden food when experimenters were not looking at them. Dogs also preferentially beg for food from individuals who can see them suggesting that dogs can differentiate between human attentional states. Observational research suggests that dogs are also able to take the perspective of their conspecifics. During dyadic social play, dogs have been found to display visual play signals almost exclusively towards individuals within visual view (Byosiére et al. 2015). Moreover, attention-getting behaviors, such as barks, were nearly always used when a play partner was not visually attentive to the signaler, and stronger attention-getters were used depending on the degree of inattentiveness of the play partner. These findings suggest that dogs are not only able to attend to others, but seemingly behave flexibly, matching their behaviors to the inattentiveness to their conspecific play partners.

While dogs appear to demonstrate an ability to understand the perspective of others, little is known about whether or not this means they recognize another individual's mental state, also known as theory of mind. Recently, in a replication study, Catala et al. (2017) helped address



whether perspective-taking can be attributed to theory of mind in dogs. Utilizing a guesser-knower paradigm, dogs preferred to follow a human-given pointing cue from a human who observed a food hiding event compared to a human who did not observe a food hiding event. This result provides further evidence that dogs attend and respond to others, in this case, humans, based on the information the humans have access to.

### Imitation

Historically, imitation has been difficult to define. While Thorndike's original definition suggested that imitation could occur without thinking, more recent definitions posit that cognitive complexity is integral for imitation to occur. Imitation is now frequently defined as the ability to learn and demonstrate a previously unknown action after observing another individual perform said action.

Considering that dogs tend to perform quite well compared to other animals on social cognition tasks, much interest has been generated over the possibility of imitation and over-imitation. One of the first studies to evaluate imitation in dogs found little evidence for imitative abilities. Kubinyi et al. (2003) had dogs observe a variety of human presented demonstrations. In one condition, the dog's owner pushed a handle to the left or right to release a ball from a box while their dog watched. Immediately after, the owner began to play with their dog and the ball. Alternatively, the dog could watch their owner touch the handle of the box (not releasing the ball), watch their owner touch the top of the box, or watch their owner not touching the box at all. Once the owner completed the demonstration, the dogs were allowed to operate the handle or the box. In the demonstration where the owner released the ball, dogs manipulated the handle more than the other conditions, but generally, the dogs moved the handle in the direction opposite than demonstrated. The authors concluded that the dogs did not perform according to imitative learning, but instead via stimulus enhancement, which led to the increased contact with the handle.

Since, Range et al. (2011b) trained dogs to open a sliding door in one of two ways, either

using their head or their paw. After watching a human demonstrator open the door, dogs were tested in two conditions. In one condition, dogs were rewarded for using the same body part as the demonstrator used. In the other, they were rewarded for using the alternative body part and not the one utilized by the demonstrator. Dogs were significantly more likely to learn the task in the first group, where the behavior rewarded matched the behavior of the demonstrator. Thus, the authors suggest that their results provide the first evidence of automatic imitation in dogs.

Additional studies have set out to discover whether dogs would imitate a human demonstrator via training methods. Topál et al. (2006) conducted a *Do-As-I-Do* task with Philip, a service dog. Philip could reproduce multiple behaviors, even novel ones, with high accuracy, performed by his trainer when given a "do it" command. Philip was also able to generalize the command when given by other demonstrators and could duplicate entire sequences of behaviors. While there are certainly limitations to the study, the first and foremost being sample size, the results suggest that because Philip was able to imitate the behaviors on observation alone he may have understood the link between his own behavior and the behavior being modeled by another. It is important to highlight that since this study, the *Do-As-I-Do* task has been conducted in larger samples to address broader questions regarding memory, social learning, imitation, training efficacy, and more.

### Impossible Task

The impossible task (also commonly called the unsolvable task) paradigm is commonly utilized to investigate social behavior. While there has been a great deal of variation across impossible task studies, including the type of apparatus used, the majority of studies present dogs with several solvable trials followed by an unsolvable trial (Mendes et al. 2021). In solvable trials, dogs are presented with obtainable reward (usually a piece of food or toy) within an apparatus. The purpose of these trials is to familiarize dogs with the possibility of obtaining the reward from the



apparatus, which may increase the reward-seeking response. Once successful in the solvable trials, the unsolvable trials are conducted. In these trials, the reward, which was previously obtainable, becomes impossible to access. In many cases, the apparatus is now “locked” shut. Depending on their question and behaviors of interest, researchers look at a variety of outcome variables, including duration of gazing, frequency of looking back, frequency of gaze alteration, latency to gaze, and persistence with the apparatus (Marshall-Pescini et al. 2009; Mendes et al. 2021; Miklósi et al. 2003).

Miklósi and colleagues were among the first to conduct the impossible task in dogs (2003). Their study used both bin-opening and rope-pulling tasks to investigate attraction to their caretaker's face during problem-solving, a precursor to communication with humans, in both dogs and wolves that were equally socialized with humans. The first six trials were easily solvable; the animal could lift the lid of a bin or pull a rope from within a cage to obtain a small piece of meat. During the unsolvable trial, the bin was mechanically secured, and the rope was tied to the cage, rendering the food inaccessible in both cases. The authors found that both dogs and wolves were equally able and motivated to complete the task in the solvable trials but that dogs looked back at their caregivers earlier and spent more time gazing at them than wolves during the unsolvable trials. The authors suggest that the difference between dog and wolf communicative behavior cannot be explained by socialization alone and is likely influenced by evolutionary and ontogenetic processes.

Marshall-Pescini et al. (2009) used a different apparatus to study whether dogs' training histories affected their performance on the impossible task. A clear plastic container was used to cover a piece of food on a wooden board (this method has since become the most commonly used apparatus in impossible task studies). The authors studied three different groups of dogs with various training experiences: agility, search and rescue, and untrained pet dogs. There were three solvable trials, during which the container could easily be overturned or moved off the platform to expose food. The container was then screwed onto the

platform during the unsolvable trial and could not be overturned or otherwise moved to expose the food. The researchers recorded the frequency of gaze alteration, gaze duration, and latency to gaze. Overall, the researchers found that these human-directed communicative behaviors were significantly affected by training experience, with search and rescue dogs exhibiting more gaze alterations between the people and the apparatus than untrained pet dogs, while agility dogs' behavior fell between these two groups.

A recent review has found many inconsistencies in methodology across unsolvable tasks (Mendes et al. 2021). To date, studies have shown that the human-directed communication behaviors of canine species are influenced by many factors, including genetics, domestication, age, training experience, and living conditions. However, as mentioned above, studies vary in the type of apparatus they used, the number of solvable trials, the length of unsolvable trials, the recorded behaviors, the human present (experimenter, caregiver, both), etc. These differences render it difficult to make meaningful comparisons across studies.

## Conclusion

In the last 30 years, researchers from fields such as animal behavior, ethology, evolutionary anthropology, psychology, sociology, economics, and more have developed a keen interest in the study of canine cognition. The reasons for this interest are multifaceted, including dogs' unique ability to understand human-given social cues and dogs' suitability as a model for human health, as well as their abundant distribution worldwide. As dog ownership increases and a general interest of dog behavior and cognition continues to develop, it can be expected that research interest within this field will do so as well. While canine cognition is currently booming, there remains much to learn about human's furry friends. The future of dog cognition is an exciting area of study as the field begins to evaluate areas such as (1) replicability and multi-lab assessments, (2) linking community science and in-lab experimentation, and

(3) assessing the suitability of ecologically relevant paradigms in connecting dog cognition to applied aspects of dog behavior.

## Cross-References

- Adam Miklosi
- Animal Welfare
- Animal-Assisted Intervention
- A-Not-B Problem
- Artificial Selection
- Attachment
- Behavior Modification
- Behaviorism
- Canine Communication
- Canine Diet
- Canine Life History
- Canine Locomotion
- Canine Morphology
- Canine Navigation
- Classical Conditioning
- Clive Wynne
- Cognition
- Comparative Cognition
- Domestication Syndrome
- Episodic Memory
- Go/No-Go Procedure
- Guesser-Knower Paradigm
- Human-Animal Interaction
- Imitation
- Impossible Task Paradigm
- Inhibition
- Ivan Pavlov
- Laterality Effect (Face Perception)
- Means-end reasoning
- Object Permanence
- Object-Choice Test
- Olfactory Perception
- Pets
- Pointing
- Pro-social Behavior
- Self-Domestication Hypothesis
- Service Dogs
- Shaping
- Socialization
- String Pulling
- Working Memory

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## Canine Communication

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## Synonyms

Dog communication

## Definition

Dogs may communicate with conspecifics, humans, and other domestic animals they live with. When they communicate, they use visual, auditory, olfactory, and tactile signals. Domestication has greatly changed dogs' physical appearance, and therefore, visual communication may not be equally important for dogs as for their wild relatives. Whereas some messages may be important for recognition and signaling in close proximity, others are broadcasted for long-distance communication.

## Introduction

Between the carnivores, dogs and their ancestor, wolves, can be considered as the most social. Therefore, they develop an effective communication system with an abundant number of signals to maintain cohesion of the group, no matter if that is wolf pack, human family, or a group of feral dogs (e.g., Bradshaw and Nott 1995; Feddersen-Petersen 2007). For communication and recognition in close proximity, they can use body language, body odor, touch, and certain vocal sounds. On the other hand, for distant signaling, they may leave long-term scent marks and use specific vocal sounds.

In dogs, information can be conveyed as visual, vocal, olfactory, or tactile signals, where different signaling modalities are present in different environmental conditions. Therefore, in the process of domestication, dogs have adopted new modalities of communication, those that are more suitable for life with humans in a human-made milieu (Feddersen-Petersen 2007). Indeed, in human-made environments, they need to communicate with conspecifics, humans, and other domesticated animals.

In addition, dogs are very sensitive to human social and communicative behavior (e.g., pointing gestures), as well as attention focus (e.g., they respond differently to human signals if humans have closed or opened eyes). They efficiently use information given by human companions to search for food or toys but also when they choose

to obey or to disobey (e.g., Miklósi 2007). Kaminski and Nitzschner (2013) suggest that dogs' understanding of human communication is highly specialized because of the adaptation of dogs to the specific activities they have been bred for. On the contrary, sensitivity of pet dogs to human actions and intentions may be the expression of the basic processes of conditioning as well as social and biological traits that domesticated and wild canids share rather than a special adaptation or a case of coevolution (Udell et al. 2014).

Unfortunately, because of the huge changes in dog appearance that we can see in different dog breeds, visual communication between dogs becomes challenging (Stafford 2006). Consequently, it is argued that olfactory and vocal communication become more important for dogs. Furthermore, in human-made environments, communication may occur between animals that do not live in the same household, so they can communicate only by leaving long-term olfactory messages or by vocalization, again enhancing vocal and olfactory communication over visual.

## Vocal Communication

Domestic dogs are more vocal than all other canids, and their barking can be considered as hypertrophied in comparison with wild relatives (Feddersen-Petersen 2007; Fox 1971). Because vocal communication is more important for primates, including humans, life with humans might be a reason why dogs became more vocal and developed different barking sounds (Feddersen-Petersen 2007; Miklósi 2007). Excessive barking is considered as juvenile behavior, and, in dogs, it is thought that it is associated with paedomorphosis due to domestication (Beaver 2009; Bradshaw and Nott 1995). This led to the assumption that barking is the way in which dogs communicate specifically with humans (Miklósi 2007).

From the evolutionary point of view, it seems that by differentiating their barks, dogs become more adjusted to the human environment and vocalization has become a tremendously important component of social interactions. Dogs

develop many different sounds, distinguishing them from wolves (Feddersen-Petersen 2007). For the purpose of communication, dogs may produce sounds such as barking, groaning, growling, grunting, hissing, howling, mewling, panting, puffing, screaming, tooth snapping and chattering, whining, and yelping (Beaver 2009; Bradshaw and Nott 1995). Some of those sounds are more typical of puppies: grunting, mewling, and partly screaming (Beaver 2009). Whining is considered a distress call; it may express dogs' emotional state, such as fear or pain, or it may be a way of attracting attention (Case 2010; Yeon 2007).

As suggested by Miklósi (2007), dogs can vary in at least three parameters of their bark (frequency, tonality=noise/harmony, rate), in relation to their inner state. In addition, humans are able to place the barks into the appropriate categories more often than expected by chance and therefore to associate the correct emotion with the situation. By measuring frequency and amplitude of barking, individual dogs can be distinguished, as well as their mood. Yin and McCowan (2004) recorded dog vocalizations in certain situations (e.g., disturbance, isolation, play) and found it possible to divide dogs' barks into different subtypes. In addition, humans were able to identify dogs by their bark spectrograms independent of the context of barking.

Dog breeds differ according to their frequency of barking, possibly because their tendency to bark, that is, the threshold or level of arousal required for animals to begin to bark, has been subjected to selective breeding (Fox 1971; Yeon 2007). Barking is more present in dogs living with humans, while it is comparatively rare in stray and feral dogs (Boitani and Ciucci 1995). Scientists assume that for dog-dog communication, vocalization may be less significant than other forms of signaling (Beaver 2009). Nevertheless, it seems that dogs can distinguish different barks (Maros et al. 2008). Furthermore, Simonet et al. (2005) have shown that certain vocalizations have meaning for dogs: playing dog laughter in shelters reduces unwanted distress behaviors. Finally, Adams and Johnson (1994) showed that the main reason for dogs to wake up and bark during

the night was barking of other dogs. Therefore, vocal communication may become as important as other forms of communication for dogs separated from conspecifics in nearby households, as other forms of communication demand some kind of physical contact.

In the research of Faragó et al. (2010a), three types of growling were recorded, from three different contexts: during play, guarding a bone from another dog, and reacting to a threatening stranger. Afterward, they showed a seemingly unattended bone to experimental dogs and simultaneously reproduced the recorded growling as a playback. As a result, food-guarding growls discouraged the dogs from taking away the bone more efficiently than growls recorded in the threatening stranger or the play situation. Further research (Faragó et al. 2010b) showed that dogs can extract information about the growling dog's size, meaning they were able to link the acoustic signal with the visual information provided by the dogs' pictures. Moreover, when domestic dogs perceive size-related information in growls, they adapt their behavioral response as a function of the perceived other dog's size in comparison to their own (Taylor et al. 2010).

Howling is a loud form of vocalization, and it is employed to affect companions over greater distance. In wolves, howling serves to bring individuals together, to inform rivals of pack presence, and may indicate an animal's size and aggressiveness and, thus, has a function in defending a territory (Fox 1971). Adult dogs howl in some situations, such as when some environmental sound is present (sirens, some types of music, airplanes flying overhead). Some dogs may howl when they are left alone, what resembles the social function of howling in wolves (Bradshaw and Nott 1995; Case 2010).

## Olfactory Communication

Dogs' olfactory system is tremendously more sensitive in comparison with humans. Therefore, olfactory communication has a variety of forms. Indeed, dogs have a remarkable sense of smell, i.e., they are able to detect small concentrations of



odors, and they can distinguish between them (Fox 1971). Olfactory signals may include urine and fecal droppings, ground scratching, anal sac secretions, general body odor, rubbing certain body areas against a specific object, and rolling in noxious-smelling substances (Beaver 2009; Bradshaw and Nott 1995).

Olfactory cues are used for territory marking, individual recognition, and as a method for leaving long-term messages (Fox 1971). Marks can be made on novel or familiar objects, territory, or scent marks of other individuals, or the animal may mark itself (Beaver 2009; Bekoff 2001). Unfamiliar urine, feces, or objects may be marked simply to reduce novelty (Fox 1971). In free-ranging dogs, feeding places can also be marked, probably increasing the efficiency of food source utilization (Pal 2003).

In dogs, urination and defecation have evolved into a complex behavior of territorial marking, through which one individual leaves a message about itself and acquires information about others in a given region. Dogs have preferential places for urination and defecation in their living area (Fox 1971).

In feral dogs observed by Pal (2003), females marked more frequently near the nest site after litter production and when they were in estrus. One of the messages that urine contains is about female reproductive status, and estrus females may urinate more, leaving long-distance messages for males (Case 2010). The urine of females contains a pheromone during proestrus and estrus that is attractive to males (Fox 1971). Namely, pheromones are chemical mixtures that play an important role in sexual behavior of animals. For example, a pheromone (methyl-p-hydroxybenzoate) is produced in the vagina of the female dog. The pheromones are detected by the olfactory system and the vomeronasal organ (Bubna-Littitz 2007).

Male urination can mostly be considered as scent marking (Bradshaw and Nott 1995; Pal 2003), and it is frequently accompanied by the leg-raised pattern (Fox 1971). The reason for this behavior may be that the raised-leg posture elevates the scent mark to nose height, allowing better dispersal of odor by wind, increased

evaporating surface, and minimizing the chances that the urine mark is going to be covered by snow or washed away by rain (Beaver 2009). Dogs that display raised-leg urination (RLU) may leave small quantities of urine on numerous places (Bradshaw and Nott 1995) or may deposit no urine (Pal 2003). In domestic dogs, the frequent leg-raising pattern in males is thought to be an example of behavioral hypertrophy in the domestic environment (Fox 1971). Similarly, leg-raised behavior can be observed in altered females (Bubna-Littitz 2007) but also in intact females of all smaller, more athletic breeds, where some females may even raise both back legs when urinating.

Dogs can also use defecation as marking behavior. All canids possess a pair of small glands on each side of the anal sphincter. These glands, perianal or circumanal, release some of their contents when defecation occurs (Bradshaw and Nott 1995; Fox 1971). The secretion of anal sacs is highly individual specific (Bradshaw and Nott 1995). To accentuate exposition of their communicative signal, sometimes they try to defecate on some high place, as, for example, on fences or trunks (Bubna-Littitz 2007).

Dogs show interest in their own urine and feces and that of other members of the same species. They may investigate urine or feces by sniffing and may urinate or defecate over the existing samples (Fox 1971). It is believed that dogs can extract information about the animal marked from the urine smell (Beaver 2009). Males are equally interested in urine of other males and females but over-mark more frequently on other males' urine (Bekoff 2001). In feral dogs, the leading male may urinate frequently and immediately over the urine marks of estrus females, which is termed by Pal (2003) as "possessive urine marking." Finally, dogs can distinguish between the olfactory "image" of themselves, what may be similar to mirror self-recognition in some other species (Horowitz 2017).

After urination or defecation, some canids may scratch the ground (Beaver 2009; Case 2010). In dogs, scraping with both front and hind legs may occur after urination or defecation. These behaviors may be a visual display that



attracts attention of conspecifics or a way to add odor from the paw glands after urination or defecation or may be used to mark the ground where the animal has eliminated, thus providing an additional territorial signal (Bekoff 1979; Case 2010). The probability of the occurrence of this behavior increases when the individual is aggressively aroused (Fox 1971), and it is more extensive in the presence of another dog (Bubna-Littitz 2007).

Shortly after whelping, lactating females produce the dog-appeasing pheromone (DAP) from intermammary sebaceous glands, the function of which is to calm and appease her puppies. Certain studies have shown that DAP reduces stress and anxiety in adult dogs as well, so DAP may be successfully used in veterinary clinics for the relaxation of dogs (Mills et al. 2006).

General body odor is a product of glands on the dog's feet, head, and anal region, the upper surface of the base of the tail, and between the hind legs (Bradshaw and Nott 1995). Social investigatory behavior in dogs is directed in those body areas. It starts when one dog approaches another and sniffs its head and inguinal and anal regions (Bradshaw and Nott 1995; Fox 1971).

Dogs are prone to rolling in smelly materials that they found, no matter if humans found this odor attractive or disgusting (such as carcasses of dead animals). The function of that behavior may be in collecting a desired smell or leaving their own smell (Case 2010). One possible explanation is given for wild canids, where an individual with a new smell will receive more social investigation by conspecifics after joining the pack, and that may reduce the possibility of agonistic interactions (Fox 1971).

## Visual Communication

Visual communication may include eye contact, facial expressions, ear position, tail position and movements, fur position (flat or raised), whole body postures, and movements (Bradshaw and Nott 1995; Bubna-Littitz 2007).

In dogs, eye contact can be used as a friendly greeting, but a direct stare with eyelids wide open is a threat. Although this is a subtle threat, dogs

tend to avoid eye contact when they meet the direct look of a threatening individual, to prevent further confrontation and possible injuries (Beaver 2009; Fox 1971).

In a calm dog, the mouth is relaxed and covers the teeth. In an aggressive dog, the corners of the mouth are pulled forward, and the lips are retracted vertically in snarling. As part of avoidance display, dogs may pull their lips back in a grin. Furthermore, the dog may repeatedly extrude its tongue (tongue flick) signaling intention to lick (Beaver 2009; Fox 1971), but frequent lips and nose licking can be seen in anxious dogs as appeasement signal (Mills et al. 2006). An aggressive dog may grasp the muzzle or neck of another in an inhibited bite (Beaver 2009; Landsberg et al. 2003).

In dogs, the enlarged external ears, the pinnae, have been incorporated into facial expression and may convey different motivational states. In the alert dog, the pinnae are shifted up and forward; in fear or apprehension, the ears may be flattened backward, or in greeting, ears may be flattened sideways (Fox 1971).

In dogs, the tail is used as an important visual signal, where its position and movements transfer a specific message. A tail is erected or arched when the animal is aroused, while it is lowered in unsure or anxious animals and even tucked between the legs in frightened dogs (Case 2010; Fox 1971). It may be loosely wagged for greeting or stiffly wagged in aggression. Therefore, it may be better to consider the tail wag as a context-specific behavior that may be used in different situations. Indeed, the tail may be wagged more on the right side if the dog perceives pleasing stimuli and on the left side if the dog displays withdrawal tendencies (Quaranta et al. 2007).

Whereas in wild Canidae, the coloration of the coat is adjusted to enhance visual communication, such as coloration of the face, cheeks, and tail (Fox 1971); coloration in domestic dogs depends exclusively from arbitrary breed standards set by humans. Consequently, dog breeds lost some ability for visual communication (Feddersen-Petersen 2007; Stafford 2006).

In dogs, communicative body postures play a significant role. Confident animals display a

body carriage that makes them look bigger, including rigid posture with head and tail up, or even piloerection on the hackles (Case 2010; Landsberg et al. 2003). When a dog approaches one of its own species or a human being in friendly greeting, it advances with the hind end lowered and the back arched in a “C” posture (Fox 1971). An animal may approach another and lick the corner of its mouth in greeting (Beaver 2009). Finally, a frightened dog may lie down and roll over, exposing the belly, and, if in great fear, it may urinate (Beaver 2009; Bradshaw and Nott 1995).

One communicative body posture that is used to express play intention is the “play bow.” This play-soliciting posture consists of lowering the front end of the body and raising the rear (Bekoff 1977). The whole display includes the play bow and then a quick return to a standing posture, followed by some jumping around the intended playmate. During this display, dogs may have so-called play face (Beaver 2009). When the play bow is displayed, accompanied vocalization is a call to play, but even a growl has no aggressive meaning.

Dogs’ communicative displays are complex and may include different body postures and other signals, integrated with movements. These patterns of compound signals may be seen in different contexts of dogs’ communications. For example, a dog that is showing appeasing behaviors may approach another dog with a lowered body posture, a lowered and wagging tail, squinty eyes, and a greeting grin (Case 2010). On the other hand, a more confident dog may display a ritualized attack that may be oriented in the shoulder region, the hackles, whereas the hair in that region may be erected during aggressive display (Fox 1971). Raised leg urination and ground scratching could be considered as visual signals for urine marking triggering olfactory inspection (Bekoff 1979). Finally, dogs can be in emotional conflict and show mixed signals (Beaver 2009).

As in other canids, domesticated dogs use body postures and facial expressions to communicate changes in their motivational state, their state of mind or mood (Fox 1971). Regrettably, many dog

breeds are not able to use normal visual signals due to the breeding selection of hair cover and hair type, ear carriage, and tail shape (Stafford 2006). Indeed, these breeds are obstructed from normal social interactions because they are unable to signal their intentions due to flat faces (brachycephalic), stiffed legs, very short and curled or immobile tails, drooping or erect ears, and long hair that prevents the display of piloerection on the hackles (Bradshaw and Nott 1995; Rooney 2016). Therefore, they have lost the possibility to communicate precisely due to pedomorphosis, i.e., retention of certain juvenile body features and behaviors into adulthood (Bradshaw and Nott 1995; Case 2010) and other extreme changes in morphological features (Feddersen-Petersen 2007).

There are many detrimental effects of breeding for appearance on dog behavior. For example, although horizontal and vertical lip movements can be seen, in many breeds the effectiveness of such signals is reduced because the cheeks are of the same color as the rest of the face, or covered in long hair, so the lips cannot be clearly seen (Fox 1971). Some breeds have large pendulous lips (e.g., boxers, St. Bernards) and may not be able to retract them efficiently (Beaver 2009). Furthermore, long-haired breeds cannot stare if their eyes are covered with hair (Bradshaw and Nott 1995), and this obstructed vision enhances the risk that a dog will be frightened and react fearfully. Unfortunately, the small size of some breeds may cause them to frequently suffer from fear, and thus, they may show fear-induced aggression (Beaver 2009; Rooney 2016).

In dogs, tails may be altered in comparison with wild canids. Dogs can be born with stump tails or their tails may be docked, or some may have permanently erect tails. That modification of signal structures, especially when the tail is docked and the animal is wagging the whole hind end, can have a detrimental influence on social communication (Fox 1971). Furthermore, tail docking is still performed in many countries, and, from a welfare point of view, it should be considered as a detrimental and unnecessary procedure, because it removes one of the major means of communication (Stafford 2006).

## Tactile Communication

Tactile communication is important for dogs from birth. Indeed, the sense of touch is developed before other sensory modalities are present. During the neonatal period, pups respond to tactile stimuli and probably the smell of their mother and littermates. Additionally, stimulation of the perineal region from the mother is necessary for eliminative behavior (Case 2010).

Signaling by touch may be equally important for play behavior. In research conducted by Horowitz (2008), dogs were using certain tactile play signals and attention-getting motor action patterns during play, such as putting front paws around other dogs' head, knocking other dogs with a certain part of the body, putting the nose and closed mouth to another dog, and biting or pawing at another dog's face or body.

Finally, dogs use tactile signals to get attention from their owners. For example, they may touch the owner with a nose or a paw, put the head in the owner's lap, or even try to jump in the lap regardless of their own size. Furthermore, dogs like to sleep in physical contact with the members of their family, including humans, dogs, and other pet animals.

## Canine Behavioral and Welfare Problems due to Incomplete Understanding of Communication

Most of the behavioral problems that are considered as a nuisance for owners are normal canine behaviors. For example, owners are disturbed by the quantity of dogs barking, especially in the urban environment. Whereas barking is not equally present in all dog breeds, it is a part of standard behavioral repertoire and, as such, cannot be completely stopped. Alternatively, a dog debarking, i.e., surgical reduction of tissue in the vocal chords, is a welfare issue. Debarked dogs are still trying to bark but cannot produce a sound, so they might be frustrated. On the other hand, many dogs if not debarked may end up in a shelter or euthanized (Beaver 2009). Barking noise is a special problem in shelters as well (Coppola et al. 2006).

In addition, many fundamental social communication behaviors of dogs are considered unacceptable by owners, for example, smelling the perineal region or licking the lips of humans (Stafford 2006). An example of misunderstanding between humans and dogs is when dogs are jumping on people while trying to greet them. Also, dogs' attempts to lick human faces could be considered unpleasant, so dogs might be disciplined (Beaver 2009; Case 2010). Punishing a dog for expressing happiness and love to its owner may harm the dog emotionally.

Although having a specific body odor may be a matter of self-identity for dogs (Horowitz 2017), hygienic owners wash their dogs too frequently. Furthermore, some anthropomorphic owners prevent their dogs from olfactory communication that includes smelling of another dog's back or urine and feces on the street. By preventing dogs from normal communication patterns, they seriously reduce the dog's quality of life.

Finally, dogs' visual communication is extremely changed due to the creation of different breeds. We can only scratch the surface of the problem because most purebred dogs live in human-made environments where humans control most of dogs' social interactions and, thus, prevent problems caused by misinterpretation of communicative signals.

## Conclusion

Dogs are amazing in their communication flexibility, i.e., they communicate successfully with conspecifics, humans, and other domestic species. Whereas their life has been changing from being wolves to human companions, from hunters to pets, they have succeeded to adapt their communication repertoire. Their social abilities continue to be discovered, along with the ways they use human signaling systems to harmonize their behavior with human companions.

However, many communicative behaviors are prevented by owners as well due to dogs' physical appearance. Therefore, the normal behavior of the dog might best be understood in research of feral or wild dogs like the dingo (Stafford 2006).

More knowledge of dogs' social cognition and communication modalities should create better lives for dogs and enhance their welfare.

## Cross-References

- [Animal Welfare](#)
- [Canine Cognition](#)
- [Canine Diet](#)
- [Canine Locomotion](#)
- [Canine Morphology](#)
- [Canine Navigation](#)
- [Pets](#)
- [Pheromone](#)
- [Scent-Marking](#)
- [Service Dogs](#)
- [Socialization](#)
- [Territory Defense](#)

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## Canine Diet

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## Synonyms

[Canine feeding](#); [Canine food intake](#); [Food preference](#); [Nourishment](#)

## Definition

Canine diet refers to the food intake by members of the Canidae family. Dietary intake and choices of canids are closely aligned to their behavioral, dental, anatomical, and physiological characteristics associated with ingestion, digestion, absorption, and elimination. In addition, the spatial and temporal availability of feedstuffs will impact on dietary intake and preferences. The diversity of members of the Canidae family results in a variety of potential diets, most notably observed in the domestic dog, *Canis lupus familiaris*, where human intervention and management typically regulates dietary choices and intake, occasionally in conflict with the nutritional needs of the species. For wild and free-living canids, diet is more closely impacted by typical ecological pressures such as seasonality, prey density, predator population density, intra- and interspecies relationships, and, increasingly, anthropogenic effects.

## Introduction

The mammalian family Canidae, belongs to the order Carnivora and includes three subfamilies, two of which are extinct (the Borophaginae and Hesperocyoninae) and the extant Caninae (Miklosi 2015). Members of the Caninae are known as canines and include wolves, foxes, jackals, the domestic dog, and several other species, typically described as “dog-like.” The domestic dog is notable within the Caninae subfamily, as a species that typically occupies similar ecological niches to humans and has a diet typically representative of that shared niche. This is in addition to demonstrating some evolutionary changes suggestive of adaptation to dietary provision within that niche (Axelsson et al. 2013), alongside other genetic and behavioral signatures of convergent evolution (Udell and Wynne 2008). Indeed, the domestic dog is acknowledged to be one of the earliest domesticated species and remains one of the most commonly kept domestic animals globally. This has significant consequences for their diet.

Canids demonstrate wide geographical distribution and are found naturally on every continent, with the exception of Antarctica. Their distribution across a range of diverse habitats results in a wide diversity of dietary intake, with dietary preferences ranging from general carnivore, to omnivore, to opportunist scavenger. Some species demonstrate a more specialist dietary intake represented by insectivores such as the bat-eared fox (*Otocyon megalotis*), although even such apparently specialist feeders will also demonstrate a more general, opportunistic intake based on seasonal availability (Klare et al. 2011). Canine food acquisition strategies range from scavenging and opportunistic foraging intake of animal and plant matter to either group/pack or solitary hunting. Feral dogs have also been observed to hunt medium-sized prey such as deer in packs, with reports also recording humans being hunted (Avis 1999). Consequently, there is a wide diversity within the Caninae in terms of both geographical distribution and dietary intake. For the purposes of this entry, general consideration will be given to the canine diet and notable species-specific



characteristics related to dietary choice, processing, intake, and nutritional requirements.

## Canine Dietary Ecology

Canids demonstrate a diverse range in body size and, as a result, are observed to have a wide diversity in food intake, with both physiology and ecology impacting on dietary availability and choices. Canid body weight typically ranges from about 2 kg to about 80 kg, with some species being much larger. Ingested prey species can range from small insects to large herbivore prey that can be hunted and subdued, either on a group or solitary hunting basis. Indeed, some canids such as the gray wolf (*Canis lupus*) are capable of cooperative hunting as an integral part of their dietary strategy and intake (Mech and Boitani 2003). This permits the acquisition of prey much larger than could be successfully hunted by an individual and is typically via sustained pursuit predation as opposed to the grappling and subduing of prey (Andersson 2005).

While canids are often viewed as carnivores and typically demonstrate the fundamental dentition and a digestive anatomy consistent with a carnivorous diet, many extant canids are not hypercarnivorous, with approximately 70% of their dietary intake coming from animal-derived protein sources and the other 30% coming from plants, seeds, fruits, and other materials. This move toward a more hypocarnivorous and omnivorous dietary strategy is consistent with the typical small to medium body size of many canids. Such dietary flexibility is also a survival advantage in changing environmental circumstances and in part likely accounts for the wide geographical distribution of canids. Many smaller species will undertake solitary hunting/scavenging behaviors and ingest to gut capacity, whereas larger species will have reduced frequency of predation, mitigated by both digestive system capacity and prey size (De Cuyper et al. 2019).

Feeding ecology is also critical in considering the evolutionary success of canids. The ability to survive on a mixed diet permits adaption to altered circumstances and food availability.

Consequently, dietary flexibility is, in part, one reason for the general biological success of the Caninae. Indeed, canid evolution suggests that the larger, hypercarnivorous species such as the dire wolf (*Canis dirus*) that depended predominantly on large, herbivorous species for their dietary intake were negatively affected when prey density started to decrease, with the dire wolf population commencing a decline approximately 20,000 years ago and full extinction occurring about 10,000 years ago (Dundas 1999). The dire wolf is a clear example of a species with a dietary specialization that was incompatible with altered environmental circumstances, and they were effectively outcompeted by the slightly smaller but more dietarily adaptable species such as the gray wolf (Leonard et al. 2007).

## The Canine Digestive System

The typical digestive system of canids resembles that observed in members of Carnivora and demonstrates specific adaptations to support food acquisition (via predation and scavenging), ingestion, and digestive processing. The canine gastrointestinal system is viewed as simple, monogastric, and capable of digesting an omnivorous diet, although often with a high proportion of animal-derived tissue. Consequently, similarities are observed across the Caninae subfamily, with occasional species-specific adaptations, based on specific ecological or dietary niches. The domestic dog has been extensively studied from a digestive anatomy and physiology perspective, and while there are subtle species-specific differences across the Caninae, the canine digestive system is fundamentally similar in structure and function.

### Dentition

In common with their membership of the Carnivora, canids demonstrate the presence of enlarged canines and a carnassial apparatus. These are dental adaptations for acquiring, cutting, shearing, and processing meat that are observed in both extant and extinct carnivorous species (De Muizon and Lange-Badre 2007). The



dental formula of canids is 3142/3143 and includes molars that are unmodified, in contrast to other members of the Carnivora (such as felids) that typically have a reduced dental formula and highly modified molars, congruent with a hypercarnivorous dietary strategy. Notably, the domestic dog has 42 teeth in comparison to the domestic cat, which only has 30 teeth. This dental formula is a useful classification tool and is consistent across canids, apart from the bat-eared fox (*O. megalotis*), dhole (*Cuon alpinus*), and bush dog (*Speothos venaticus*; Wallis 2019).

The carnassial apparatus comprises the fourth upper premolar and the first lower molar and is retained throughout the Caninae. However, in contrast with species that demonstrate an obligate or hypercarnivorous dietary strategy, canid post-carnassial teeth often demonstrate increased palatine surfaces suggestive of a more omnivorous dietary intake and the need for an enhanced grinding surface area, to cope with dietary components of variable shape, size, and density.

Notably, the canid jaw structure only permits vertical movements, supporting the dentition in a strong cutting and shearing action, but severely limits the ability for lateral chewing (Kim et al. 2018). Consequently, prolonged chewing and mechanical processing of ingested foodstuff prior to swallowing are limited, and typical mealtimes are short and characterized by rapid ingestion of available foodstuffs. Bite force is generated by both dentition and jaw structure, with the carnassial apparatus demonstrating a clear secodont or scissor-like action. Bite force generated is closely related to skull size, shape, and overall bodyweight (Kim et al. 2018).

### Digestive Anatomy and Physiology

Beyond dentition, the structure of the typical canid digestive system is short and simple, from point of ingestion to elimination. As a result, gastric transit times are short and there is no prolonged digesta retention time. Indeed, specific anatomical and physiological adaptations for the digestion of plant material, such as extensive microbial fermentation and an extended retention time, are not observed in canids, in contrast to the herbivorous ruminants and hindgut fermenters,

and are suggestive of a diet with high digestibility. However, canid digestion does incorporate various aspects of mechanical, chemical, and some limited microbial digestion processes (Maskell and Johnson 1993), a consequence of a variable and omnivorous intake.

Digestion begins in the mouth with the ingestion of acquired food and some limited mechanical processing due to the limited chewing ability of canids. Saliva is secreted by the salivary glands and aids lubrication and mixing of ingesta. It is widely reported that dogs lack salivary alpha-amylase, thus limiting the initiation of carbohydrate digestion in the oral cavity. However, salivary alpha-amylase has been identified in the saliva of dogs exposed to sympathetic activation, suggesting its presence could be a possible stress biomarker (Contreras-Aguilar et al. 2017) and that there may be a dietary role for this enzyme.

Taste perception occurs within the mouth from the stimulation of taste buds on the tongue, and sensitivity is identified to amino acids, nucleotides, and various organic acids, substances all abundant in animal-derived tissues and consistent with an observed canid preference for such dietary components (Kumazawa et al. 1991). Notably, dogs demonstrate a preference for sweet foodstuffs (Houpt et al. 1979; Ferrell 1984) and will often demonstrate a feeding preference for sweet-tasting materials over bitter flavors. This is likely representative of the adaptation of many canids to an omnivorous dietary strategy as scavenging and opportunistic food intake replaced hunting and prey acquisition. This is also likely to account for the occurrence of “dietary indiscretions” observed in the domestic dog, where otherwise toxic compounds, such as theobromine in chocolate intended for human consumption, can be preferentially ingested over other foodstuffs.

The canine esophagus has striated muscle only, permitting rapid peristalsis and swallowing (Stevens and Hume 1995). Mucus is secreted to permit lubrication of ingesta as it moves down the gastrointestinal tract, and movement of food from the mouth to the stomach only takes seconds (Maskell and Johnson 1993). The canid stomach is small and simple but with enormous expansion

capability to permit the ingestion of large prey items (Hume 2002) and to support opportunistic gorge feeding on large volumes of food. The stomach is where protein digestion begins, although most chemical digestion of dietary fat, carbohydrate, and protein, followed by nutrient absorption, occurs in the small intestine. The small intestine is short in length (Stevens and Hume 1995), with a significant microflora population that is increasingly linked with both gut and systemic health and can be influenced by dietary components such as prebiotic fibers (Sparkes et al. 1998).

The small intestine empties into a relatively short colon which has a key digestive role in the resorption of water and electrolytes. The microbial population within the colon is also of significance in both intestinal and systemic health and depending on dietary composition, can impact on fecal form and output. The canid cecum is typically smaller (relative to body size) than that observed in highly omnivorous species such as swine, although it is larger than observed in obligate carnivores such as felids, suggesting a proportion of cecal fermentation of digesta.

## Feeding Behavior

Feeding behavior is diverse within the Caninae subfamily and represents an evolutionary move toward a mixed dietary intake, in contrast to hypercarnivorous dietary strategies observed in other members of the Carnivora. Wild and free-living canids are often restricted in diet acquisition through availability and the fact that hunting and scavenging have an inherent energy expenditure requirement. This combined with the spatial and temporal availability of foodstuffs can impact on overall diet composition in wild and feral populations. Conversely, domesticated and managed species will often have a nutritionally consistent diet, in both content and supply. However, ancestral feeding behaviors will still be observed in such species (Bradshaw 2006).

For species that typically acquire food by cooperative hunting, gorge and intermittent

feeding is often observed, with large amounts of food ingested in a relatively short period of time and then digested over a prolonged period. This can appear as a gorge-fast cycle and is sometimes mimicked in the captive management of such species. Cooperative hunting also explains the typically rapid ingestion of food observed in canids, where competition between pack members for key resources, such as food, can be intense, and explains the social facilitation of food intake and dietary preferences often observed in canids (Lupfer-Johnson and Ross 2007).

Scavenging and opportunistic food intake are identified across canid species, including occasional hoarding behavior. This can manifest through the intake of a range of material that, for domestic and managed species, can be less than acceptable to human caregivers. In the case of the domestic dog, feeding behavior linked to the ingestion of fecal material and other waste products is often described as undesirable from both a health and human perception perspective, although such behaviors are suggestive of the evolutionary origin of these species. The domestic dog is often identified to indulge in coprophagy of their own feces, conspecific fecal matter (Hart et al. 2018), or feces from other species. While distasteful to caregivers, and often attributed to nutritional or behavioral issues, it appears that coprophagy is likely to represent an evolutionary remnant of a denning species, intended to keep the den and immediate environs clean and potentially parasite free, rather than linked to breed, gender, nutritional status, or other attributes (Hart et al. 2018).

Grass and plant eating are also widely reported in domestic dogs (Sueda et al. 2008), and while the consumption of plant material is well identified within the Caninae, plant eating in domestic dogs is often attributed to illness, digestive discomfort, or nutritional inadequacy. However, it appears that grass (and other plant material consumption) is more likely linked to natural exploratory and ingestive behaviors (Bjone et al. 2007), in addition to a preference for sweet tastes (Ferrell 1984), rather than illness or dietary deficiencies.

## Canine Nutritional Requirements

In contrast to obligate carnivores such as felids, canids are often described as facultative carnivores with metabolic and biochemical pathways and processes that have evolved to permit the biosynthesis of key biological compounds, meaning that dietary provision of animal-derived material is not always necessary. Indeed, linked with the increased humanization of domestic companion animal species, there is an increase in domestic dogs being successfully fed either a vegan or vegetarian diet (Knight and Leitsberger 2016), indicating the nutritional promiscuity of this taxonomic group.

Obligate carnivores typically demonstrate metabolic adaptation for high levels of protein consumption, limited biosynthesis of specific biomolecules, and minimal ability to metabolize dietary carbohydrate (Zoran 2002). Gluconeogenesis is critical to support the maintenance and supply of glucose levels in these species, and a diet consisting predominantly of animal material is essential for survival, also supplying key nutrients such as arachidonic acid, taurine, and pre-formed vitamin A (MacDonald et al. 1984).

Notably, taurine is often considered dispensable in canine diets where there is ingestion of adequate levels of sulfur-containing amino acids that support taurine synthesis (Kramer et al. 1995; Delaney et al. 2001) or ingestion of taurine-rich animal-derived tissue. Taurine is essential for normal somatic functions, notably ocular and cardiac. However, evidence suggests that taurine is essential in fox diets, and dog diets that are formulated to be low in protein or necessary precursor molecules (Backus et al. 2003) can produce clinical symptoms of deficiency. This has been further complicated with specific commercial diet formulations being putatively linked to apparent taurine deficiency symptoms in the domestic dog (Freeman et al. 2018), suggesting a possible nutritional value in ensuring a dietary taurine supply. Indeed, taurine supplementation is indicated for captive maned wolf (*Chrysocyon brachyurus*), a predominantly frugivorous South American canid, following

concerns about plasma taurine concentrations in animal-fed diets formulated to manage cystinuria (Childs-Sanford and Angel 2006).

In common with obligate carnivores, canids are also capable of high levels of gluconeogenesis from protein precursors, and it is well identified that the domestic dog has no specific dietary need for dietary provision of carbohydrate as a result. However, both wild and domestic canid species consume carbohydrate containing material, by both choice and opportunity. Additionally, the domestic dog has a clear genetic signature relating to the ability to digest starch, contrary to popular belief (Axelsson et al. 2013), with this ability demonstrating some breed and type differentiation. It is also recognized that a dietary intake of carbohydrate can support canine reproductive functioning (Romsos et al. 1981) and in the athletic domestic dog, for some activities, dietary carbohydrate provided in the correct form and at the correct time can support performance output and enhance recovery (Wakshlag et al. 2004).

Dietary fat and protein will be significant contributors to nutrient intake in canids consuming large amounts of animal-derived tissue, which will also provide a ready supply of other nutrients, including key vitamins and minerals. Fat appears to be a key nutrient to support canine energy expenditure and is key in the diet of domesticated, working canines (Downey et al. 1980). For domestic and managed species, nutritional provision can be easily managed and adapted to suit life stage and activity level. Indeed, key resources to support the design and formulation of diets for domestic and captive canids are based on extensive scientific research, much of it being funded by commercial pet food manufacturing companies. These guidelines are continually updated based on academic findings and are intended to ensure nutritional suitability and sufficiency is covered (NRC 2003; FEDIAF 2019). For wild and feral canids however, diet is more restricted and limited to the temporal, seasonal, and spatial availability of foodstuffs, meaning that periods of nutritional adequacy can be interspersed by periods of nutritional inadequacy.

## Conclusion

The canine diet is typically a diverse one, encompassing scavenging, omnivory, and carnivory to different extents, with a trend toward hypo- and facultative carnivory in contrast to hyper- and obligate carnivory as observed in felids. The dietary flexibility observed within canids is likely to be in part responsible for their evolutionary success and wide geographical distribution, in addition to the successful dyad developed between the domestic dog and *Homo sapiens*.

The digestive anatomy and physiology of a typical canid are simple, demonstrating few specific adaptations (such as extensive microbial fermentation and prolonged digesta retention times) required to support the digestion of plant-based material, as observed in herbivorous species. The dentition and much of the digestive anatomy are akin to a typical carnivore, although subtle alterations and adaptations are identified, notably the genetic adaption to starch digestion as observed in the domestic dog. This is in addition to the ability to synthesize some key nutrients, such as taurine, negating the absolute need for animal-derived tissues in their diet in contrast to obligate carnivores, although evidence suggests that there might be species-specific requirements.

Feeding behavior is diverse in canids, with scavenging, omnivory, kleptoparasitism, and hunting (cooperative and solitary) being observed. The flexibility to obtain nourishment via different behavioral strategies from hunting to scavenging limits reliance on the temporal and spatial availability of specific feedstuff.

The diversity observed in the dietary intake of canids is, in part, responsible for their continued success and ability to rapidly adapt to changing environmental conditions. For free-living canids, diet remains restricted by ecological factors such as season, prey/predator density, and other temporal and spatial factors such as climate and anthropogenic impacts. For species such as the domestic dog, human choices, perceptions, and control limit dietary intake in a similar way, but the nature of the human-dog dyad is recognized to have a significant impact on dietary choices made available to the dog. The risk of obesity

and associated conditions with negative links to health and welfare is significant in the domestic dog population, ironically while correlated with increasing knowledge about canine biology generally. As such, canine diet remains a critical factor in the survival and success of canids generally but also a significant topic for discussion and debate in the domesticated members of the family.

## Cross-References

- [Canine Life History](#)
- [Canine Morphology](#)
- [Carnivora](#)
- [Carnivore \(Diet\)](#)
- [Herbivore](#)
- [Omnivore](#)
- [Predator](#)

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## Canine Feeding

### ► Canine Diet

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## Canine Food Intake

### ► Canine Diet

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## Canine Gaits

### ► Canine Locomotion

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## Canine Life History

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### Definition

Canine life history describes the reproduction, growth, and survival patterns for species in the mammalian Canidae, a family within the Carnivora order with multiple species, including dogs, wolves, foxes, jackals, coyotes, and other dog-like mammals.

### Introduction

The family Canidae belongs to the suborder Caniformia, and its name comes from the Latin *canis* meaning “dog.” The dog-like caniforms emerged within the Carnivoramorphia 43 million years before present (Flynn and Wesley-Hunt 2005). Three subfamilies existed, but two became extinct, Hesperocyoninae (about 39.74–15 Mya) and Borophaginae (about 34–2 Mya), and the third, Caninae (about 34–0 Mya), is the only

surviving subfamily. Using DNA analysis the surviving members of the Canidae family have been divided into a basal Caninae group (containing the gray fox and island fox) and two tribes, the Canini (true dogs) and Vulpini (true foxes) (Lindblad-Toh et al. 2005). Canidae are the most geographically widespread family of Carnivora and are found on every continent except Antarctica. For example, the red fox and the gray wolf have the most extensive range of all land mammals. Canids live in a wide range of habitats including deserts, mountains, forests, and grasslands. Canidae today include a diverse group of around 36 species ranging in size from the fennec fox (*Vulpes zerda*) measuring only 18 cm at the shoulder and the maned wolf (*Chrysocyon brachyurus*) at over 90 cm (Sillero-Zubiri et al. 2004). One particular canid, the domestic dog (*Canis familiaris*), was the earliest known domesticated animal and remains today one of the most widely kept domestic animals around the world.

### Characteristics

The body shape of all canids (in particular jackals, coyotes and wolves) is relatively similar with long muzzles, upright ears, long legs and lithe bodies adapted for chasing prey, with the exception of the bush dog (*Speothos venaticus*), raccoon dog (*Nyctereutes procyonoides*) and some domestic breeds of dog (*Canis familiaris*) (Castelló and Sillero-Zubiri 2018; Miklósi 2014). The length of the muzzle, ears, and tail can also vary significantly between species; however, the gray wolf shows the typical basal form of the family. All canids walk on their toes showing typical digitigrade qualities enabling them to move quickly and quietly. The cushioned pads on the soles of the feet and the tip of the nose are naked. The soles consist of a three-lobed central pad and a single pad behind the tip of each toe. There are five toes on the fore feet, but the pollex (thumb) does not reach the ground. The African hunting dog is the exception to this rule, as it has only four toes. The hind feet of all canids have four toes (but some



domestic dogs have a fifth vestigial toe called a dewclaw) (Mivart 1890).

Male canids possess a bone called the baculum, which supports the penis, and a structure called the bulbus glandis at the base of the penis helps to create a copulatory tie during mating. The copulatory tie is a characteristic of mating in most Canids; during mating the bulbus glandis becomes engorged with blood and locked in the contracted vagina of the female. The two animals can remain attached by their genitals for 15 min or more, during which time ejaculation takes place (Castelló and Sillero-Zubiri 2018). All young are born blind, and their eyes open a few weeks after birth.

Most canids have 42 teeth, which are adapted for cutting, crushing, grinding, and slicing and reflect their dietary habits including hypercarnivory and a more omnivorous diet. All except the bush dog (*Speothos venaticus*), dhole (*Cuon alpinus*), and bat-eared fox (*Otocyon megalotis*) have the same dental formula of three incisors, one canine, four upper premolars, and two molars in the upper jaw, and the same in the lower jaw, apart from the presence of an additional molar (Mivart 1890).

## Lifespan

The lifespan of canid species ranges from 3 to 15 years in the wild, but most species can live substantially longer in captivity (please refer to “Lifespan” section of Table 1). Mortality rates in the wild can be high due to natural sources of mortality, interspecies competition, persecution by humans (hunting and trapping for fur, meat, sport, or to be captured and kept as tourist attractions), road kills, and pathogens and parasites. Many canids come into conflict with man due to their tendency to prey on domestic livestock and wild game (Sillero-Zubiri et al. 2004).

## Foraging Behavior

Canids employ several types of foraging strategies, which are dependent on the habitat and prey

species available. Most species are generalist hunters and foragers and consume a wide range of food items including mammals, birds, fish, amphibians, reptiles, insects, plants, fruit, and seeds (please refer to the “Food” section of Table 1). Part of the Canidae’s success is due to their ability to adapt to local ecological factors. Some more specialist hunters and foragers have also evolved to exploit particular niche environments. The majority of canid species are carnivores or omnivores, with the exception of the bat-eared fox (*Otocyon megalotis*, insectivorous), Blandford’s fox (*Vulpes cana*, insectivorous and frugivorous), and pale fox (*Vulpes pallida*, herbivorous) (Sillero-Zubiri et al. 2004). Many species are solitary hunters/foragers, due to the small size of their prey; however, the larger more carnivorous species are dependent on bigger prey for sustenance and are therefore reliant on cooperative hunting efforts (please refer to the “Foraging behavior” section of Table 1). The activity patterns of each species are dependent on their prey species and, in more urban areas, human disturbance. Most species are nocturnal, crepuscular, or diurnal (Sillero-Zubiri et al. 2004).

## Social Behavior

Nearly all canid species are social animals and live together in small family groups, which consist of the breeding male and female and their current offspring. In addition, most are territorial, or have a home range, and either sleep in the open, using a den only to raise young, or are more dependent on dens on a daily basis. Territories and home ranges are maintained through driving out conspecific intruders, scent marking, and vocalizations. Some canids are solitary species and come together only to breed; others live in larger social groups called “packs,” which have the advantage of enabling them to tackle larger prey when hunting with more individuals (Sillero-Zubiri et al. 2004). Typically, the older, more experienced individuals lead the pack, and in most cases, a hierarchy is formed, and the dominant male and female are usually the only pack members to

**Canine Life History, Table 1** Information on the 36 extant species of canids listed alphabetically by scientific name. Here we include the African golden wolf (*Canis anthus*), the red wolf (*Canis rufus*), the domestic free-ranging dog (*Canis familiaris*), and the Dingo (*Canis dingo*) as distinct species, rather than subspecies. The data provides descriptions of general aspects of life history including the species scientific name, English common name, shoulder height (in mm) and weight (in kilograms (where possible divided by sex (M = male, F = female))), the current distribution of the species, the habitat types they are found in, what food they typically eat, the foraging behavior used to obtain their food, information about their social behavior, lifespan, breeding strategy, gestation length (in days), litter size (mean and range), IUCN status and population trend (taken from <https://newredlist.iucnredlist.org/>), and finally a list of sources (please see abbreviation key at the end of the table)

| Scientific name<br>Common name<br>N of subspecies             | Shoulder height/<br>weight                           | Distribution                                                                     | Habitat                                                                                                                                  | Food                                                                                                                                                                                                                    | Foraging<br>behavior                                                                                                                                                 | Social behavior                                                                                                                                                                                                                | Lifespan                                                                                  | Breeding<br>strategy                                                                                                                                                                         | Gestation<br>length | Litter size          | IUCN<br>status/pop.<br>trend     | Source<br>abbrev |
|---------------------------------------------------------------|------------------------------------------------------|----------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------|----------------------|----------------------------------|------------------|
| <i>Atelocynus<br/>microtis</i><br>Short-eared dog             | 356 mm<br>9–10 kg                                    | Amazon<br>rainforest<br>region of<br>S. America                                  | Rainforest –<br>Amazonian<br>lowlands.<br>Often found<br>near water                                                                      | Carnivore:<br>fish, insects,<br>small rodents,<br>fruits, and<br>frogs                                                                                                                                                  | Generalist. Hunts<br>alone or in pairs.<br>Diurnal and<br>nocturnal                                                                                                  | Mainly solitary,<br>males tend not to<br>have overlapping<br>territories                                                                                                                                                       | 1–11 years<br>captive<br>(wild no<br>data)                                                | Unknown                                                                                                                                                                                      | Unknown             | 2 (1–3)              | Near<br>threatened<br>Decreasing | 1                |
| <i>Canis anthus</i><br>African golden<br>wolf<br>6 subspecies | 400 mm<br>7–15 kg                                    | North and<br>northeastern<br>Africa                                              | Desert-adapted<br>canid, but is<br>common in<br>plains and<br>steppe areas,<br>including ones<br>lacking<br>abundant water               | Omnivorous:<br>wild fruit,<br>mammals,<br>reptiles, birds,<br>invertebrates,<br>carrion, and<br>sometimes<br>lambs, sheep,<br>goats, cattle,<br>and human<br>refuge.<br>Thought to be<br>more predatory<br>than jackals | More active in the<br>daytime than<br>jackals. Pairs<br>often successfully<br>hunt gazelle<br>fawns. Observed<br>to hunt ungulates<br>4–5 times their<br>body weight | Social<br>organization is<br>peaceful and<br>flexible and<br>centers around a<br>home burrow.<br>Frequently<br>groom each<br>other, have a<br>high vocal<br>repertoire, and<br>have greater<br>facial movement<br>than jackals | 8 years on<br>average in<br>the wild, but<br>one<br>individual<br>14 years<br>(Serengeti) | Monogamous<br>and territorial,<br>yearlings may<br>remain and<br>assist in raising<br>pups. The<br>breeding pair<br>suppresses<br>sexual and<br>territorial<br>behavior of the<br>grown pups | (1–9)               | Not yet<br>evaluated | 1, 2                             |                  |
| <i>Canis adustus</i><br>Side-striped<br>jackal                | M – 448 mm<br>F – 437 mm<br>M – 9.4 kg<br>F – 8.3 kg | East and<br>Southern Africa                                                      | Game areas,<br>farmland,<br>towns, wooded<br>habitats, bush,<br>grassland,<br>marshes, and<br>montane<br>( $<2,700$ m)                   | Omnivorous:<br>wild fruit,<br>small<br>mammals,<br>birds,<br>invertebrates,<br>cattle cake,<br>grass, and<br>carrion                                                                                                    | Forages singly<br>and<br>opportunisticly.<br>Mostly nocturnal                                                                                                        | Solitary, pairs, or<br>family groups of<br>up to seven<br>individuals                                                                                                                                                          | 10–12 years<br>captive<br>(much<br>shorter in<br>wild)                                    | Monogamous.<br>Cooperative<br>rearing of<br>young,<br>alloparental<br>care likely                                                                                                            | 60                  | 5 (4–6)              | Least<br>concern<br>Stable       | 1                |
| <i>Canis aureus</i><br>Golden jackal<br>7 subspecies          | 450–500 mm<br>M – 8.8 kg<br>F – 7.3 kg               | Southeast<br>Europe,<br>Southwest,<br>South, and<br>regions of<br>Southeast Asia | Semidesert,<br>short to<br>medium<br>grasslands and<br>savannahs,<br>forested,<br>mangrove,<br>agricultural,<br>rural, and<br>semi-urban | Omnivorous:<br>wild fruit,<br>mammals,<br>reptiles, birds,<br>invertebrates,<br>carrion, and<br>human garbage                                                                                                           | Hunts singly, in<br>pairs, and rarely<br>packs. Mostly<br>nocturnal but can<br>be diurnal                                                                            | Breeding pair<br>and sometimes<br>offspring from<br>previous years<br>(4–5<br>individuals).<br>Home range<br>sizes can vary<br>between 1 and<br>20 km <sup>2</sup> . Social<br>interactions are<br>common                      | 8 years on<br>average in<br>the wild                                                      | Monogamous.<br>Cooperative<br>rearing.<br>Territorial                                                                                                                                        | 63                  | (1–8)                | Least<br>concern<br>Increasing   | 1                |

|                                                                            |                                                                                     |                                                                                                          |                                                                                                                               |                                                                                                                                                                                                    |                                                                                                                                                                              |                                                                                                                                                                                                                     |                                                                                  |                                                                                                                                                                            |            |          |                             |         |
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| <i>Canis latrans</i><br>Coyote<br>19 subspecies                            | 530–610 mm<br>M – 8–20 kg<br>F – 7–18 kg                                            | United States and Alaska, Canada (except the far northeastern regions), Mexico, and into Central America | Habitat generalist: all available habitats including prairie, forest, desert, mountain, and tropical ecosystems               | Generalist carnivore: large ungulates and livestock, fruit and insects, birds, reptiles, amphibians, crustaceans. Scavenge human-made food resources and carrion                                   | Hunts alone, but when hunting large prey, in pairs or small groups. Age, wind, habitat, and snow conditions influence their ability to hunt small mammals. Often crepuscular | Lives in family packs containing a reproductive female. Pair bonds may persist for years. In populations where elk/deer are available, large packs (<10 individuals) may form. Dominance hierarchy within each pack | Maximum age reported in wild is 15.5 years and 21 years in captivity             | Mainly monogamous. Cooperative breeders. Females that fail to mate sometimes assist their sisters or mothers with their pups. Only defends territory during denning season | 63         | 6 (1–9)  | Least concern<br>Increasing | 1, 3, 4 |
| <i>Canis lupus</i><br>Gray wolf<br>38 listed subspecies (some now extinct) | 800–850 mm<br>European 38.5 kg<br>North American 36 kg, F weight 2–4 kg less than M | Canada, Alaska, and Northern United States, Europe, and Asia from about 75°N to 12°N                     | Habitat generalist: all northern habitats where there is suitable food, densities being highest where prey biomass is highest | Carnivore: majority of food is large ungulates (moose, caribou, deer, elk, wild boar, etc.). Will also eat small mammals, eggs, insects, reptiles, amphibians, livestock, and carrion, and garbage | Generalist hunter: Winter: hunt in packs. Summer: hunt singly, in pairs, or in small groups                                                                                  | Packs consisting of mated pair and offspring. Family of 5–11 wolves (2 adults, 3–6 juveniles, and 1–3 yearlings). Packs of up to 42 individuals recorded. Distinct male and female age-graded hierarchies           | On average 6 years. Maximum up to 13 years in the wild and 20 years in captivity | Monogamous cooperative breeders and hunters with alloparental care. Territorial. Alpha female suppresses reproduction of subordinates                                      | 63         | 6 (1–11) | Least concern<br>Stable     | 1, 5    |
| <i>Canis dingo</i><br>Dingo                                                | M – 590 mm<br>F – 560 mm<br>M – 15.8 kg<br>F – 14.1 kg                              | Australia                                                                                                | Habitat generalist: tropical alpine moorlands, forested peaks, arid hot deserts, tropical wetlands, and forests               | Generalist carnivore: mammals (71 species), birds (53 species), vegetation (seeds), reptiles (23 species), insects, fish, crabs, and frogs                                                         | Changes group size and hunting strategy in order to maximize hunting success. Mostly nocturnal                                                                               | Small socially integrated groups or stable packs of 3–12 dingos, usually related. Older breeding pair. Distinct male and female hierarchies. Defend territories during breeding                                     | 7–8 years in wild (up to 13 years in captivity)                                  | Cooperative hunting and rearing of young (males and yearlings). Alpha female suppresses reproduction of subordinates                                                       | 61–69 days | 5 (1–10) | Vulnerable<br>Decreasing    | 1       |

(continued)

**Canine Life History, Table 1** (continued)

| <i>Scientific name</i><br>Common name<br>N of subspecies                      | Shoulder height/<br>weight                                                                                           | Distribution                                                                                 | Habitat                                                                                                                                                                             | Food                                                                                                                                                                                                                                                                                                              | Foraging<br>behavior                                                                                                                                                                                               | Social behavior                                                                                                                                                                                                                                                                                                                                                                     | Lifespan                                                          | Breeding<br>strategy                                                                                                                                                                                                                                                          | Gestation<br>length         | Litter size                                                                           | IUCN<br>status/pop.<br>trend | Source<br>abbrev |
|-------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------|---------------------------------------------------------------------------------------|------------------------------|------------------|
| <i>Canis familiaris</i><br>Domestic dog<br>>339<br>recognized<br>breeds (FCI) | 63–1067 mm<br>0.113 kg–155.6 kg<br>Some breeds<br>exhibit sexual<br>dimorphism, with<br>males larger than<br>females | Worldwide.<br>Free-ranging<br>dogs make up<br>75–80% of the<br>global dog<br>population      | Feral, stray,<br>free-ranging<br>village/<br>community<br>dogs (rural or<br>urban),<br>working, pet,<br>and companion<br>dogs living in<br>human homes<br>and properties            | Generalist<br>carnivore: can<br>adapt to a<br>wide-ranging<br>diet including<br>vegetables, and<br>berries, and<br>grains.<br>Primarily<br>scavengers of<br>human waste<br>and animal<br>carcasses. Also<br>consumes<br>birds, reptiles,<br>small- to<br>medium-sized<br>mammals,<br>amphibians,<br>and livestock | Free-ranging<br>dogs forage<br>singly and<br>opportunistically<br>predominantly on<br>human refuse.<br>But hunting by<br>dogs can have<br>severe impacts on<br>endemic wildlife<br>species in some<br>environments | Free-ranging<br>dogs can live in<br>stable packs<br>formed by<br>multiple<br>breeding<br>individuals of<br>both sexes, with<br>an age-graded<br>dominance<br>hierarchy<br>(agonistic and<br>affiliative).<br>Males tend to<br>dominate<br>females of a<br>similar age. An<br>age-graded<br>hierarchy is also<br>found in pet dogs<br>living in packs<br>and multi-dog<br>households | Median –<br>10–13 years,<br>oldest<br>recorded<br>26 years        | Most free-<br>ranging dogs<br>exhibit a<br>promiscuous<br>mating system.<br>Monogamy,<br>polygyny, and<br>polyandry also<br>occur. High-<br>ranking<br>individuals<br>have greater<br>reproductive<br>success.<br>Females<br>disperse from<br>the pack to<br>give birth alone | 63 days<br>Mean<br>6 (1–24) | NA                                                                                    | 1, 6, 7,<br>8                |                  |
| <i>Canis<br/>mesomelas</i><br>Black-backed<br>jackal<br>2 subspecies          | 380–480 mm<br>M – 8.1 (5.9–12)<br>F – 7.4 (6.2–9.9)                                                                  | Two separate<br>populations,<br>one in East<br>Africa and the<br>other in<br>Southern Africa | Habitat<br>generalist: arid<br>coastal desert,<br>montane<br>grassland, arid<br>savannah and<br>scrubland,<br>open<br>savannah,<br>woodland<br>savannah<br>mosaics, and<br>farmland | Generalist<br>carnivore: fish,<br>insects, small-<br>to medium-<br>sized<br>mammals,<br>reptiles, birds,<br>plants, fruits,<br>frogs, carrion,<br>and human<br>refuge                                                                                                                                             | Pairs and small<br>foraging groups,<br>packs are formed<br>in order to hunt<br>larger prey.<br>Cooperative<br>hunting increases<br>success rate                                                                    | Territories are<br>spatially and<br>temporally<br>relatively stable.<br>Intruders are<br>aggressively<br>expelled by<br>territory holders.<br>Very vocal<br>species. Home<br>range size varies<br>between 1 and<br>25 km <sup>2</sup>                                                                                                                                               | Up to 7 to<br>10 years in<br>the wild                             | Monogamous<br>cooperative<br>breeders and<br>hunters,<br>territorial.<br>Dominants<br>prevent<br>subordinates<br>from mating<br>through<br>harassment                                                                                                                         | 60<br>(1–6)                 | Least<br>concern<br>Stable                                                            | 1                            |                  |
| <i>Canis rufus</i><br>Red wolf                                                | M – 699 mm<br>F – 662 mm<br>M – 28.5 kg<br>F – 24.3 kg                                                               | Exist only in a<br>reintroduced<br>population in<br>eastern North<br>Carolina, USA           | Habitat<br>generalists:<br>coastal prairie<br>marshes,<br>historically<br>river forests,<br>and swamps                                                                              | Carnivore:<br>mammals<br>including<br>nutria, rabbits,<br>rodents, white-<br>tailed deer, and<br>raccoon                                                                                                                                                                                                          | Forage<br>individually and<br>hunt in groups.<br>Mostly nocturnal<br>with crepuscular<br>peaks of activity                                                                                                         | Extended family<br>units or packs.<br>Dominant<br>breeding pair and<br>offspring up to<br>12 individuals.<br>Territorial: home<br>range size varies<br>from 46 to<br>226 km <sup>2</sup>                                                                                                                                                                                            | In absence of<br>human-<br>induced<br>mortality up<br>to 13 years | Monogamous<br>with both<br>parents<br>providing care<br>to pups. Den<br>attendance by<br>yearlings and<br>adult pack<br>members is<br>common                                                                                                                                  | 61–63<br>(1–10)             | Critically<br>endangered<br>Decreasing<br>(wild pop.<br>nonviable<br>without<br>help) | 1                            |                  |

|                                                           |                                                     |                                                                                      |                                                                                                                                                                   |                                                                                                                                                             |                                                                                                                                           |                                                                                                                                               |                                                                              |                                                                                                                                                      |       |           |                            |           |
|-----------------------------------------------------------|-----------------------------------------------------|--------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------|-------|-----------|----------------------------|-----------|
| <i>Canis simensis</i><br>Ethiopian wolf<br>2 subspecies   | 530–620 mm<br>M – 14.2–19.3 kg<br>F – 11.2–14.15 kg | Six isolated mountain ranges of the Ethiopian highlands (altitudes of 3,000–4,500 m) | Habitat specialist: Afroalpine grasslands and heathlands, prefer open areas with short herbaceous and grassland communities where rodents are most abundant       | Specialist carnivore: feed almost exclusively upon diurnal rodents and occasionally on antelopes, hares, goslings, eggs, carrion, and sedge leaves          | Preeminently a solitary rodent hunter but also a facultative cooperative hunter. Synchronize their activity with diurnal rodents          | Lives in family groups containing up to 20 individuals older than 1 year (average pack size is 6). Each pack has a well-established hierarchy | In the wild 8–10 years; one known male in Bale lived 12 years                | Monogamous cooperative breeders, dominant females suppress breeding of subordinates. Territorial: interact aggressively and vocally with other packs | 60–62 | (2–7)     | Endangered<br>Decreasing   | 1, 9      |
| <i>Cerdocyon thous</i><br>Crab-eating fox<br>5 subspecies | 368 mm<br>5.7 kg (4.5–8.5 kg)                       | Central part of South America                                                        | Marshland, savannah, cerrado, caatinga, chaco-cerrado-caatinga transitions, scrubland, woodlands, semi-deciduous gallery, Atlantic, Araucaria, and montane forest | Omnivorous: fruit, vertebrates, insects, amphibians, crustaceans, birds, carrion, cultivated fruits, domestic fowl, and refuse                              | Opportunistic predator: nocturnal and crepuscular. Hunt individually but most commonly as pairs                                           | Social groups comprise a breeding pair and 1–5 offspring (older than 1 year). Territorial during dry season                                   | Oldest recorded individual 9.2 years in the wild                             | Monogamous. Both parents rear the young                                                                                                              | 56    | 2.6 (1–3) | Least concern<br>Stable    | 1         |
| <i>Chrysocyon brachyurus</i><br>Maned wolf                | 900 mm<br>25 kg                                     | Central South America: Argentina, Bolivia, Brazil, Paraguay, Peru, and Uruguay       | Lowland grasslands and scrublands, woodland with an open canopy (cerrado), wet fields, agricultural and pasture land                                              | Omnivorous: fruits and small- to medium-sized vertebrates, birds, reptiles, and arthropods. 50% of the diet comprising plant material and 50% animal matter | Solitary hunters/foragers, but pairs have been observed to hunt together. Nocturnal and crepuscular, forage for up to 8 consecutive hours | Pairs may defend a shared territory of approximately 30 km <sup>2</sup> , although outside of mating, the individuals may meet seldom         | In captivity, maned wolves may live up to 16 years. Lifespan in wild unknown | Facultatively monogamous. Both parents have been observed to regurgitate food for the young                                                          | 60–65 | 3 (1–7)   | Near threatened<br>Unknown | 1, 10, 11 |

(continued)

**Canine Life History, Table 1** (continued)

| <i>Scientific name</i><br>Common name<br>N of subspecies  | Shoulder height/<br>weight                     | Distribution                                                                         | Habitat                                                                                                                                                                                                   | Food                                                                                                                                                                       | Foraging<br>behavior                                                                                                                                                 | Social behavior                                                                                                                                                                                                                                | Lifespan                                                   | Breeding<br>strategy                                                                                                                                                                                                        | Gestation<br>length | Litter size | IUCN<br>status/pop.<br>trend | Source<br>abbrv |
|-----------------------------------------------------------|------------------------------------------------|--------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------|-------------|------------------------------|-----------------|
| <i>Canis alpinus</i><br>Dhole<br>3 possible<br>subspecies | 430–560 mm<br>M – 15–21 kg<br>F – 10–17 kg     | Central and<br>eastern Asia                                                          | Tropical dry<br>and moist<br>deciduous<br>forest,<br>evergreen and<br>semievergreen<br>forests, dry<br>thorn forests,<br>grassland-<br>scrub-forest<br>mosaics, and<br>alpine steppe                      | Generalist<br>carnivore.<br>Hunt mainly<br>vertebrate prey,<br>preference for<br>medium to<br>large<br>ungulates,<br>insects, birds,<br>reptiles, fruit,<br>and vegetation | Communal<br>hunters.<br>Depending on<br>prey, will also<br>hunt alone or in<br>pairs. Primarily<br>crepuscular but<br>can hunt at any<br>time of the day or<br>night | More social than<br>gray wolves.<br>Usually live in<br>clans of 5–10<br>individuals but<br>groups of as<br>many as 18.<br>Strong<br>hierarchical<br>structure<br>established by<br>pushing and<br>holding.<br>aggression is<br>rarely observed | 7–8 years in<br>the wild;<br>16 years in<br>captive        | Cooperative<br>breeders.<br>Dominant male<br>and female are<br>usually the sole<br>breeders. Hold<br>territories – but<br>pups from one<br>clan often join<br>another<br>without trouble<br>once they<br>mature<br>sexually | 60–63               | 5 (4–12)    | Endangered<br>Decreasing     | 1               |
| <i>Lycalopex<br/>culpaeus</i><br>Culpeo<br>6 subspecies   | 380–400 mm<br>M – 3.4–13.8 kg<br>F – 3.9–10 kg | South America:<br>Argentina,<br>Bolivia, Chile,<br>Colombia,<br>Ecuador, and<br>Peru | Rugged and<br>mountain<br>terrain up to<br>the tree line,<br>deep valleys,<br>open deserts,<br>scrubby<br>pampas,<br>sclerophyllous<br>matorral,<br>broad-leaved<br>temperate<br>southern beech<br>forest | Generalist<br>carnivore: wild<br>ungulates,<br>rodents and<br>lagomorphs,<br>domestic<br>sheep, small<br>mammals,<br>insects, lizards,<br>birds, fruits,<br>and berries    | Opportunistic<br>predator. Solitary<br>foragers.<br>Influenced by the<br>nocturnal and<br>diurnal activity of<br>main prey                                           | Solitary. Inter-<br>and intra-<br>sexually<br>non-overlapping<br>home ranges.<br>High variability<br>in home range<br>sizes depending<br>on availability                                                                                       | Oldest<br>caught wild<br>individual<br>was 11 years<br>old | Males and<br>females come<br>together only<br>to breed                                                                                                                                                                      | 58                  | 5.2 (3–8)   | Least<br>concern<br>Stable   | 1               |
| <i>Lycalopex<br/>fulvipes</i><br>Darwin's fox             | >300 mm<br>M – 3.26 kg<br>F – 2.91 kg          | Two<br>populations:<br>Chiloé Island<br>and mainland<br>Chile                        | Forest obligate<br>species:<br>southern<br>temperate<br>rainforests.<br>Coastal sand<br>dunes,<br>evergreen/<br>broadleaf<br>forest, and<br>dairy cow<br>pastures                                         | Omnivorous:<br>insects, small<br>mammals,<br>reptiles, birds,<br>amphibians,<br>shell fish,<br>seeds, and<br>berries,<br>sometimes<br>carrion                              | Opportunistic<br>scavenger,<br>solitary hunters                                                                                                                      | Solitary<br>carnivores when<br>not breeding.<br>Will congregate<br>at a food source<br>such as<br>carcasses. Not<br>territorial, since<br>home ranges<br>overlap                                                                               | >7 years<br>possible                                       | Males spend<br>more time with<br>pups than<br>females during<br>weaning. Pairs<br>may share their<br>home range<br>with offspring<br>from previous<br>years                                                                 | Unknown             | (2–3)       | Endangered<br>Decreasing     | 1               |



|                                                            |                                                          |                                                                                                    |                                                                                                                                                      |                                                                                                                                                                                  |                                                                                                                            |                                                                                                                                                                                |                                                                                                  |                                                                                                                                 |         |           |                               |   |
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| <i>Lycalopex griseus</i><br>Chilla<br>4 subspecies         | Unknown<br>M – 4 kg<br>F – 3.3 kg                        | Southern part of<br>South America<br>(Argentina and<br>Chile)                                      | Steppes,<br>“pampas”<br>(grasslands),<br>“matorral”<br>(scrublands),<br>and forests                                                                  | Omnivorous<br>generalists:<br>mammals<br>(especially<br>rodents),<br>arthropods,<br>birds, reptiles,<br>fruit, lizards,<br>and carrion                                           | Selective or<br>opportunistic<br>solitary hunters.<br>However, hunting<br>groups of up to<br>5 individuals are<br>reported | Male and female<br>of the pair<br>maintain an<br>exclusive home<br>range year-<br>round, which<br>does not overlap<br>with home<br>ranges of<br>neighboring<br>pairs           | Unknown in<br>wild. Up to<br>5 years in<br>captive                                               | Breeding<br>monogamous<br>pair,<br>occasional<br>polygyny,<br>sometimes<br>with additional<br>female helpers.<br>Males disperse | 53–58   | (4–6)     | Least<br>concern<br>Stable    | 1 |
| <i>Lycalopex gymnocercus</i><br>Pampas fox<br>5 subspecies | 380 mm<br>M – 4.6–5.9 kg<br>F – 4.2–4.7 kg               | Southern Cone<br>of South<br>America                                                               | Open habitats,<br>tall grass<br>plains, ridges,<br>scrub lands,<br>coastal sand<br>dunes, open<br>woodlands,<br>grazed<br>pastures, and<br>croplands | Omnivorous:<br>wild and<br>domestic<br>vertebrates<br>(particularly<br>rodents and<br>birds), fruit,<br>insects,<br>carrion, and<br>garbage                                      | Generalist,<br>solitary, and<br>opportunistic<br>carnivore<br>foraging both<br>during the day<br>and during night          | Mostly solitary,<br>comes together<br>to mate and raise<br>young                                                                                                               | Few<br>individuals<br>live more<br>than a few<br>years in the<br>wild.<br>14 years in<br>captive | Forms<br>monogamous<br>pairs; both<br>guard the den,<br>and males<br>provide food to<br>pups and<br>females                     | 55–60   | 3.4 (1–8) | Least<br>concern<br>Stable    | 1 |
| <i>Lycalopex sechurae</i><br>Sechuran fox                  | Unknown<br>3.6 kg (2.6–4.2)                              | Limited range<br>in the coastal<br>zones of<br>northwestern<br>Peru and<br>southwestern<br>Ecuador | Sandy deserts<br>with low plant<br>density to<br>agricultural<br>lands and dry<br>forests                                                            | Omnivorous:<br>vertebrate prey<br>or carrion,<br>seeds, seed<br>pods, insects,<br>fruits, and<br>rodents. Can be<br>vegetarian and<br>survive with<br>limited access<br>to water | Generalist,<br>solitary, and<br>opportunistic<br>omnivore<br>foraging<br>primarily<br>nocturnally                          | Groups larger<br>than three<br>individuals are<br>rare, and usually<br>only observed in<br>cases where food<br>sources are<br>concentrated.<br>Spends daylight<br>hours in den | Unknown;<br>generation<br>length,<br>3 years                                                     | Most likely<br>comes together<br>only to breed                                                                                  | Unknown | Unknown   | Near<br>threatened<br>Unknown | 1 |
| <i>Lycalopex vetulus</i><br>Hoary fox                      | Unknown<br>M – 3.3 kg (2.5–4)<br>F – 3.4 kg<br>(3.0–3.6) | Brazil                                                                                             | Open cerrado<br>habitats,<br>livestock<br>pastures, and<br>areas of<br>agriculture                                                                   | Omnivorous:<br>insects<br>(ground-<br>dwelling<br>harvester<br>termites), small<br>mammals,<br>grasshoppers,<br>birds, and<br>reptiles                                           | Forage as<br>individuals or in<br>loosely knit pairs.<br>Mainly nocturnal                                                  | Families share<br>largely<br>overlapping<br>home ranges of<br>around 4.6 km <sup>2</sup> .<br>They spend up to<br>35% of their<br>activity period in<br>close proximity        | Unknown in<br>wild. Up to<br>8 years in<br>captive                                               | Monogamous.<br>Both parents<br>care for the<br>offspring; there<br>is currently no<br>evidence of<br>helpers                    | 53–60   | (4–5)     | Least<br>concern<br>Unknown   | 1 |

(continued)

**Canine Life History, Table 1** (continued)

| <i>Scientific name</i><br>Common name<br>N of subspecies           | Shoulder height/<br>weight                                      | Distribution                                                                                                                            | Habitat                                                                                                                                                                                               | Food                                                                                                                                                                                     | Foraging<br>behavior                                                                                                                                                            | Social behavior                                                                                                                                                                                                                                                      | Lifespan                                                                          | Breeding<br>strategy                                                                                                                                                                                                                                           | Gestation<br>length | Litter size | IUCN<br>status/pop.<br>trend | Source<br>abbrv |
|--------------------------------------------------------------------|-----------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------|-------------|------------------------------|-----------------|
| <i>Lycan pictus</i><br>African wild dog<br>5 subspecies            | 600–750 mm<br>M – 28 kg<br>F – 24 kg                            | Southern<br>Africa,<br>southern part of<br>East Africa,<br>Central Africa,<br>and North-east<br>Africa                                  | Short-grass<br>plains,<br>semidesert,<br>bushy<br>savannahs, and<br>upland forest.<br>Current<br>distribution is<br>limited<br>primarily by<br>human<br>activities and<br>the availability<br>of prey | Carnivores:<br>medium-sized<br>antelopes<br>(Impala, Kudu,<br>gazelle,<br>wildebeest,<br>dik-dik,<br>steenbok,<br>duiker),<br>warthog, hares,<br>rodents, birds,<br>lizards, and<br>eggs | Pack hunter of<br>medium-sized<br>antelopes.<br>Hunting success<br>varies with prey<br>type, vegetation<br>cover, and pack<br>size but tends to<br>be very successful<br>(>60%) | Lives in<br>permanent packs<br>of 2–27 adults<br>and yearling<br>pups. Intensely<br>social spending<br>most of their<br>time in close<br>contact. Packs<br>may fluctuate<br>rapidly in<br>numbers. Males<br>and females have<br>separate<br>dominance<br>hierarchies | 6–10 years in<br>the wild.<br>15 years in<br>captive                              | Obligate<br>cooperative<br>breeders. Large<br>home ranges<br>are defended<br>aggressively<br>against<br>neighboring<br>packs.<br>Dominants<br>suppress<br>reproduction in<br>subordinates.<br>All pack<br>members are<br>involved in<br>caring for the<br>pups | 71–73               | 8 (2–21)    | Endangered<br>Decreasing     | 1               |
| <i>Nyctereutes<br/>procyonoides</i><br>Raccoon dog<br>6 subspecies | 380 mm<br>4–6 kg<br>Weight fluctuates<br>according to<br>season | Indigenous to<br>East Asia.<br>Introduced and<br>now<br>widespread in<br>northern and<br>eastern Europe                                 | Deciduous/<br>evergreen/<br>mixed forests,<br>heaths,<br>farmlands, and<br>urban areas.<br>Introduced<br>habitat: moist<br>forests and<br>shores of<br>rivers/lakes                                   | Omnivorous:<br>small rodents,<br>frogs,<br>invertebrates,<br>birds, eggs,<br>plants, grains,<br>berries and<br>fruit, carrion,<br>fish, and<br>crustaceans                               | Opportunistic<br>generalist<br>foragers. Mainly<br>nocturnal, forage<br>in pairs. Decrease<br>food intake before<br>entering<br>hibernation                                     | Form permanent<br>pair bonds. Both<br>male and female<br>defend the home<br>range against<br>individuals of the<br>same sex. The<br>home range size<br>varies according<br>to the abundance<br>of food                                                               | Maximum<br>lifespan in<br>wild<br>7–8 years.<br>Record in<br>captive,<br>13 years | Monogamous;<br>both parents<br>care for the<br>young                                                                                                                                                                                                           | 61–70               | 4–9 (2–16)  | Least<br>concern<br>Stable   | 1               |
| <i>Otocyon<br/>megalotis</i><br>Bat-eared fox<br>2 subspecies      | 300–370 mm<br>4 kg                                              | <i>O. m. virgatus</i> ,<br>Ethiopia and<br>Southern Sudan<br>to Tanzania;<br><i>O. m.<br/>megalotis</i> ,<br>southern part of<br>Africa | Short-grass<br>plains, open<br>scrub<br>vegetation,<br>shrub lands,<br>open arid<br>savannah,<br>open<br>grassland, and<br>woodland<br>boundaries                                                     | Predominantly<br>insectivorous:<br>termites and<br>beetles,<br>seasonal fruit,<br>small<br>mammals,<br>birds, eggs,<br>and reptiles                                                      | Foraging<br>techniques<br>depend on prey<br>type. Uses its<br>large ears to<br>locate prey.<br>Foraging peaks at<br>the height of<br>insect activity                            | In Southern<br>Africa, live in<br>monogamous<br>pairs with cubs.<br>In Eastern<br>Africa, live in<br>stable family<br>groups<br>consisting of a<br>male and up to<br>three closely<br>related females<br>with cubs                                                   | Recorded up<br>to 9 years in<br>the wild and<br>13 years in<br>captive            | Predominantly<br>monogamous<br>but also<br>observed in<br>polygynous<br>groups. The<br>male spends<br>more time<br>close to the<br>cubs than<br>females, as<br>maternal<br>investment<br>during<br>lactation is<br>high                                        | 60–75               | (1–6)       | Least<br>concern<br>Stable   | 1,<br>12, 13    |

|                                                              |                                                                  |                                                                                                                     |                                                                                                                                                                                       |                                                                                                         |                                                                                                                                                                                            |                                                                                                                                                                                                                                                     |                                                                                  |                                                                                                                                                                                                                        |       |            |                               |   |
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| <i>Speothos venaticus</i><br>Bush dog                        | 200–300 mm<br>5–8 kg                                             | Eastern Central America and northern South America, south to Paraguay, and north-eastern Argentina                  | Habitat<br>generalists. Occur near water sources. Lowland forested habitats including primary and gallery forest and seasonally flooded forest                                        | Primarily carnivorous: large rodents, small mammals, lizards, snakes, and possibly ground-nesting birds | Hunting parties consist of at least 2 individuals. Mostly diurnal                                                                                                                          | Considered the most social of the small canids living in family groups consisting of a breeding pair and their offspring, ranging from 2 to 12 individuals. Home range of 3.8 to 10 km <sup>2</sup>                                                 | Around 10 years in the wild, 13 years in captivity                               | Monogamous. Males exhibit a high degree of parental care. Dominant females suppress the estrus of daughters                                                                                                            | 67    | 3.8 (1–6)  | Near threatened<br>Decreasing | 1 |
| <i>Urocyon cinereoargenteus</i><br>Gray fox<br>16 subspecies | 300–380 mm<br>M – 4.0 kg<br>(3.4–5.5)<br>F – 3.3 kg<br>(2.0–3.9) | Central and eastern Canada, Oregon, Nevada, Utah, and Colorado in the United States south to Venezuela and Colombia | Deciduous/ pine forests, old fields, scrubby woodlands, mixed agricultural/ woodland/ chaparral/ riparian landscapes, shrub and thick brush habitats, semiarid areas, and urban areas | Omnivorous: rabbits, rodents, insects, birds, fruits and nuts, and carrion                              | Solitary hunters. More active at night than during the day. Increase their home ranges during late autumn and winter in response to changes in food resource availability and distribution | Basic social unit is the mated pair and their offspring of the year. Dens are used any time of the year but mostly during breeding season. Tree dens may be located 30 f. above the ground. Home range size ranges from 0.8 to 27.6 km <sup>2</sup> | 4–5 years in wild. However, individuals of 14–15 years are occasionally reported | Monogamous, occasionally polygynous. Pups accompany adults on foraging expeditions at 3 months. Family group remains together until the autumn, when young males disperse and females stay within proximity of the den | 53–60 | 3.8 (1–10) | Least concern<br>Stable       | 1 |
| <i>Urocyon littoralis</i><br>Island fox<br>6 subspecies      | 120–150 mm<br>M – 2.0 kg<br>(1.4–2.5)<br>F – 1.8 kg<br>(1.5–2.3) | Restricted to six of the California Channel Islands off the coast of southern California, USA                       | Habitat<br>generalist: dunes, bluffs, grasslands, sage scrub, cactus scrub, chaparral, oak/riparian woodlands, pine forests, marshes, and developed areas                             | Omnivorous: rodents, birds, lizards, insects, snails, molluscs, carrion, and fruits                     | Solitary foraging generalist. Adult foxes may also forage together on occasion. Nocturnal and diurnal activity. Skilled climbers                                                           | Breeding pairs that occupy discrete territories mean home range sizes of 0.16–3.39 km <sup>2</sup> . Not uncommon for offspring to remain in natal range                                                                                            | Up to 10 years of age in the wild                                                | Usually monogamous but extra-pair fertilization has been recorded. Dependent young accompany adults on forays                                                                                                          | 50–63 | 2.5 (1–5)  | Near threatened<br>Increasing | 1 |

(continued)

**Canine Life History, Table 1** (continued)

| <i>Scientific name</i><br>Common name<br>N of subspecies | Shoulder height/<br>weight                       | Distribution                                                            | Habitat                                                                                                                                | Food                                                                                                                                    | Foraging<br>behavior                                                                                             | Social behavior                                                                                                                                                                                                   | Lifespan                                              | Breeding<br>strategy                                                                                                                                                                                 | Gestation<br>length | Litter size | IUCN<br>status/pop.<br>trend | Source<br>abbrv |
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| <i>Vulpes bengalensis</i><br>Indian fox                  | Unknown<br>M ~2.7–4.1 kg<br>F >1.8 kg            | Indian subcontinent (Nepal to the southern tip of the Indian peninsula) | Semi-arid, flat to undulating terrain, scrub and grassland habitats, thorn or dry deciduous forests, plains, and open scrub forest     | Omnivorous: arthropods, rodents, reptiles, fruits, and birds                                                                            | Solitary opportunistic foragers. Crepuscular and nocturnal                                                       | Basic social unit of a breeding pair formed through pair bonds that may last for several years. Hide in dens during day. Larger aggregations may exist when grown pups remain in natal group                      | In captivity, the lifespan is about 6 to 8 years      | Monogamous, but extra-pair copulations are known to occur. Both parents bring food to the pups and guard the den                                                                                     | 50–60               | 2.7 (2–4)   | Least concern<br>Decreasing  | 1, 14           |
| <i>Vulpes cana</i><br>Blanford's fox                     | 200–250 mm<br>0.8–1.5                            | Middle East and Central Asia                                            | Mountainous regions, slopes, stony plains and patches of cultivation, dry creek beds                                                   | Insectivorous and frugivorous: invertebrates, fruits and plant material, vertebrates                                                    | Almost always solitary foragers only occasionally foraging in pairs. Strictly nocturnal                          | Pairs live in territories of c. 1.6 km <sup>2</sup> that overlap minimally. Size of nightly home range average 1.1 ± 0.7 km <sup>2</sup>                                                                          | Estimated 4–5 years in the wild. In captivity 6 years | Strictly monogamous, but no real evidence of paternal care                                                                                                                                           | 50–60               | 2 (1–4)     | Least concern<br>Stable      | 1               |
| <i>Vulpes chama</i><br>Cape fox                          | 280–330 mm<br>M 2.8 kg (2–4.2)<br>F 2.5 kg (2–4) | Central and western regions of Southern Africa                          | Open country, grassland, agricultural land, lightly wooded areas, dry Karoo regions, the Kalahari, and the fringes of the Namib Desert | Omnivorous: small rodents (murids), hares, reptiles, birds, invertebrates and some wild fruits, occasionally scavenge young lambs/goats | Foraging is a solitary nocturnal activity and may gather in loose groupings to forage at an abundant food source | Breeding pair with home range of 1.0–4.6 km <sup>2</sup> . Overlapping home ranges, especially in areas where food is abundant. Shelters in burrows during the day. Comes together mainly for the breeding season | 6 years in the wild but can live for up to 10 years   | Monogamous breeding pair, mate for life. Both parents feed the pups, but the vixen is the main provider; no helpers are found at dens. Both parents will defend the pups against potential predators | 51–53               | 2.9 (1–6)   | Least concern<br>Stable      | 1               |

| <i>Vulpes corsac</i><br>Corsac<br>3 subspecies    | 300 mm<br>M – 2.75 kg<br>(2.5–3.2)<br>F – 2.1 kg<br>(1.9–2.4) | Central and<br>northeast Asia                                                      | Steppes,<br>semideserts<br>and deserts,<br>avoiding<br>mountains,<br>forested areas,<br>and dense<br>bush. Depend<br>on distribution<br>of ground<br>squirrels/<br>marmots for<br>food/shelter<br>(burrows are<br>enlarged and<br>used for<br>refuge) | Predominantly<br>carnivorous:<br>small- and<br>medium-sized<br>rodents and<br>lagomorphs,<br>birds, reptiles<br>(lizards,<br>snakes, and<br>young<br>tortoises),<br>insects,<br>vegetation,<br>fruit, carrion,<br>and human<br>garbage | Opportunistic<br>solitary forager.<br>Nocturnal and<br>crepuscular. Hunt<br>by stalking prey<br>and employing<br>sudden short-<br>distance attacks | Basic social unit<br>is the breeding<br>pair. During<br>winters, several<br>cousacs often can<br>be found in one<br>den, indicating a<br>relatively high<br>degree of<br>sociality. Home<br>range sizes vary<br>widely<br>depending on<br>region and<br>density of foxes<br>(from 1 to<br>40 km <sup>2</sup> ) | Up to 9 years<br>in the wild                                      | Monogamous<br>pairs may<br>persist for life.<br>Polygynic<br>families are<br>probable under<br>favorable<br>feeding<br>conditions.<br>The male<br>assists in<br>feeding the<br>young. Helpers<br>may also<br>provide care to<br>offspring | 52–56 | 5.5 (2–10)                                    | Least<br>concern<br>Unknown    | 1                   |
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| <i>Vulpes ferrilata</i><br>Tibetan fox            | 311 mm<br>M – 4.1 (3.8–4.6)<br>F – 3.5 (3.0–4.1)              | India, east<br>across China<br>and the Tibet<br>Autonomous<br>Region, and<br>Nepal | Upland plains<br>and hills from<br>about 2,500 to<br>5,200 m,<br>sparse<br>grasslands,<br>alpine<br>meadow,<br>alpine steppe,<br>and desert<br>steppe                                                                                                 | Possible<br>obligate<br>carnivore:<br>pikas and<br>rodents,<br>insects,<br>vegetation,<br>berries, lizards,<br>and carrion                                                                                                             | Mostly solitary,<br>daytime hunters<br>as their main prey,<br>pikas. are diurnal                                                                   | Mated pairs<br>remain together<br>and may also<br>hunt together.<br>Spend<br>considerable<br>time resting in<br>small burrows,<br>hollows, and<br>rock crevasses                                                                                                                                               | 3–4 years in<br>the wild                                          | Monogamous.<br>Young stay<br>with the<br>parents until<br>they are 8 to<br>10 months old                                                                                                                                                  | 50–60 | (2–5)                                         | Least<br>concern<br>Unknown    | 1,<br>15, 16,<br>17 |
| <i>Vulpes lagopus</i><br>Arctic fox               | 250–300 mm<br>M – 3.5–4.2 kg<br>F – 3.1–3.7 kg                | Circumpolar<br>distribution:<br>North America,<br>Eurasia, and<br>Fennoscandia     | Arctic and<br>alpine tundra                                                                                                                                                                                                                           | Omnivorous:<br>rodents, birds,<br>reindeer, eggs,<br>carrion, fish,<br>berries, and<br>seaweed                                                                                                                                         | Opportunistic<br>predator and<br>scavenger.<br>Forages singly.<br>Mostly nocturnal                                                                 | Breeding pair,<br>sometimes<br>previous years<br>offspring,<br>strongly<br>territorial when<br>breeding                                                                                                                                                                                                        | 3 years in<br>wild; oldest<br>recorded<br>individual,<br>11 years | Monogamous.<br>Both parents<br>rear cubs                                                                                                                                                                                                  | 51–54 | Varies with<br>food<br>availability<br>(2–25) | Least<br>concern<br>Stable     | 1                   |
| <i>Vulpes macrotis</i><br>Kit fox<br>8 subspecies | 300 mm<br>M – 2.29 kg<br>(1.7–2.7)<br>F – 1.9 kg<br>(1.6–2.2) | Western North<br>America                                                           | Arid and<br>semiarid<br>regions<br>encompassing<br>desert scrub,<br>chaparral,<br>halophytic,<br>and grassland<br>communities                                                                                                                         | Omnivorous:<br>rodents,<br>leporids, and<br>insects, birds,<br>reptiles, fruit,<br>and carrion                                                                                                                                         | Mostly forage<br>solitarily. They<br>are mainly active<br>by night and<br>occasionally<br>exhibit<br>crepuscular<br>activity                       | Not strongly<br>territorial and<br>home ranges<br>may overlap,<br>although core<br>areas generally<br>are used<br>exclusively by<br>one family<br>group. Home<br>range size<br>2.5–11.6 km <sup>2</sup>                                                                                                        | >7 years of<br>age in the<br>wild                                 | Primarily<br>monogamous<br>with<br>occasional<br>polygyny.<br>Young from<br>previous litters<br>(females), may<br>delay dispersal<br>and assist with<br>raising the<br>current litter                                                     | 49–55 | 4 (1–9)                                       | Least<br>concern<br>Decreasing | 1                   |

(continued)

Canine Life History, Table 1 (continued)

| <i>Scientific name</i><br>Common name<br>N of subspecies  | Shoulder height/<br>weight                       | Distribution                                                                                                      | Habitat                                                                                                                                | Food                                                                                                                                                                                             | Foraging<br>behavior                                                                                                              | Social behavior                                                                                                                                                                                                                                                                     | Lifespan                                              | Breeding<br>strategy                                                                                                                          | Gestation<br>length | Litter size | IUCN<br>status/pop.<br>trend | Source<br>abbrv |
|-----------------------------------------------------------|--------------------------------------------------|-------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------|---------------------|-------------|------------------------------|-----------------|
| <i>Vulpes pallida</i><br>Pale fox<br>5 subspecies         | <350 mm<br>2.0–3.6 kg                            | Sahel of Africa,<br>bordering the<br>Sahara to the<br>north                                                       | Very dry sandy<br>and stony<br>marginal sub-<br>Saharan desert<br>and semidesert<br>areas, and<br>moister<br>Guinean<br>savannah areas | Herbivorous:<br>berries, wild<br>fruit such as<br>melons, and<br>vegetable<br>matter. They<br>also feed on<br>small rodents,<br>ground-nesting<br>birds, small<br>reptiles, and<br>invertebrates | Forages solitarily.<br>Has the ability to<br>retain water from<br>its food and can<br>go almost<br>completely<br>without drinking | Lives in small<br>family groups<br>consisting of<br>breeding pair and<br>their young.<br>They dig<br>extensive dens<br>and rest there<br>during the day                                                                                                                             | Thought to<br>be 6 years in<br>the wild               | Thought to be<br>monogamous                                                                                                                   | 51–53               | (3–4)       | Least<br>concern<br>Unknown  | 1, 18           |
| <i>Vulpes rueppellii</i><br>Rüppell's fox<br>6 subspecies | 300 mm<br>1.62 kg (1.1–2.3)<br>1.48 kg (1.1–1.8) | North Africa<br>(Morocco to<br>Egypt and<br>Somalia)                                                              | Sand and stone<br>deserts, sparse<br>to very sparse<br>vegetation<br>cover,<br>dominated by<br>small brushes                           | Omnivores:<br>high<br>invertebrate<br>content, as well<br>as rodents,<br>lizards, snakes,<br>birds, and wild<br>fruits, plants,<br>and human<br>garbage.<br>Sometimes<br>prey on<br>livestock    | Opportunistic<br>solitary foragers.<br>Either crepuscular<br>or nocturnal,<br>sheltering during<br>the day in dens                | Extended<br>families are<br>possible, as<br>sightings of<br>family groups<br>(3–15) are<br>common.<br>Cohabitation of<br>the same den<br>occurs only<br>during the<br>breeding season.<br>Territories of<br>mated pairs<br>overlap but are<br>separate from<br>neighboring<br>pairs | 7 years in<br>wild, up to<br>12 years in<br>captivity | Form<br>monogamous<br>pairs in the<br>mating season                                                                                           | 52–53               | 3 (1–6)     | Least<br>concern<br>Stable   | 1, 19           |
| <i>Vulpes velox</i><br>Swift fox                          | 300 mm<br>2.24 kg (2–2.5)<br>1.97 kg (1.6–2.3)   | Western<br>grasslands of<br>North America.<br>Reintroduced to<br>Canada<br>(Alberta,<br>Saskatchewan,<br>Montana) | Short-grass<br>and mixed-<br>grass prairies<br>and croplands                                                                           | Omnivore:<br>mammals<br>(rabbits/<br>rodents), also<br>birds, eggs,<br>insects, plants,<br>fruits, seeds,<br>and carrion                                                                         | Solitary<br>opportunistic<br>foragers.<br>Nocturnal and<br>crepuscular.<br>Known to run up<br>to 60 km/h<br>(40 mph)              | Females<br>maintain<br>territories, but<br>males emigrate if<br>the resident<br>female is killed/<br>removed.<br>Heavily<br>dependent on the<br>den as shelter<br>from predators                                                                                                    | Up to 8 years<br>in the wild                          | Monogamous,<br>but multiple<br>breeding<br>strategies have<br>been observed.<br>Additional<br>females<br>sometimes<br>help in raising<br>pups | 51                  | 2.4–5.7     | Least<br>concern<br>Stable   | 1,<br>20, 21    |



|                                                  |                                                                                                    |                                                               |                                                                                                                                                                                                                                                               |                                                                                                                                                                                             |                                                                                                                                                                                                  |                                                                                                                                                                                                                                                                                                                                                           |                                                                                                      |                                                                                                                                                                                                                         |       |                                                 |                            |              |
|--------------------------------------------------|----------------------------------------------------------------------------------------------------|---------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------|-------------------------------------------------|----------------------------|--------------|
| <i>Vulpes vulpes</i><br>Red fox<br>45 subspecies | Large<br>geographical<br>variation in size<br>350–500 mm<br>M – 6.3 (4.4–7.6)<br>F – 5.3 (3.6–6.5) | Only canid<br>present on five<br>continents<br>(83 countries) | Urban, rural,<br>city centers,<br>scrub,<br>woodland,<br>agricultural<br>land,<br>moorland,<br>mountainous,<br>grassland/<br>semidesert,<br>boreal forests,<br>and Arctic<br>tundra. Appear<br>to be closely<br>associated with<br>people in many<br>habitats | Opportunistic<br>omnivores:<br>invertebrates,<br>small<br>mammals,<br>birds, fruit, and<br>plant material.<br>Also, scavenge<br>carcasses (deer<br>and sheep),<br>bird food, and<br>garbage | Mainly nocturnal<br>and crepuscular.<br>Can be diurnal<br>where they are<br>undisturbed.<br>Solitary foragers/<br>hunters: may<br>forage in close<br>proximity where<br>resources are<br>clumped | Transient<br>individuals and<br>family groups<br>(usually a mated<br>pair with/without<br>offspring but<br>occasionally one<br>male with 2–5<br>related vixens<br>sharing a<br>territory). Social<br>group density is<br>one family per<br>km <sup>2</sup> in farmland<br>but may vary<br>between 0.2 and<br>5 families/km <sup>2</sup> in<br>the suburbs | In wild,<br>typically do<br>not live<br>beyond<br>5 years, in<br>captivity as<br>long as<br>15 years | Largely<br>monogamous,<br>polygyny also<br>reported. Both<br>parents and<br>sometimes<br>other females<br>care for the<br>young. Only<br>dominant<br>female breeds<br>and suppresses<br>reproduction in<br>subordinates | 49–58 | 5 (3–12)<br>varies with<br>food<br>availability | Least<br>concern<br>Stable | 1,<br>22, 23 |
| <i>Vulpes zerda</i><br>Fennec fox                | 180–220 mm<br>1.5 kg (1.3–1.7)<br>1.4 kg (1–1.9)                                                   | Northern Africa<br>to northern<br>Sinai                       | Arid desert<br>environments                                                                                                                                                                                                                                   | Omnivore:<br>insects, small<br>rodents,<br>lizards, eggs,<br>small birds,<br>various fruits,<br>and some<br>tubers                                                                          | Hunt alone as<br>solitary hunting<br>of small prey is<br>more efficient.<br>Lives completely<br>away from water<br>sources                                                                       | Moderately<br>social, family<br>group of mated<br>pair and their<br>offspring (up to<br>10). Young of the<br>previous year<br>may remain in<br>the family. Play<br>and affiliative<br>behavior are<br>common                                                                                                                                              | Unknown in<br>the wild, up<br>to 14 years in<br>captivity                                            | Monogamous,<br>mate for life.<br>Males are<br>aggressive/<br>protective of<br>the female after<br>mating and<br>provision her<br>during<br>pregnancy/<br>lactation                                                      | 50–52 | (1–5)                                           | Least<br>concern<br>Stable | 1            |

Source: 1, Sillero-Zubiri et al. (2004); 2, Koepfli et al. (2015); 3, Bekoff (1977); 4, Hennessy et al. (2012); 5, Mech and Boitani (2003); 6, Bonanni et al. (2017); 7, Cafazzo et al. (2014); 8, Kubinyi et al. (2018); 9, IUCN (2011); 10, De Melo et al. (2009); 11, Dietz (1984); 12, Lamprecht (1979); 13, Wright et al. (2010); 14, Vanak and Gompper (2007); 15, Harris et al. (2008); 16, Liu et al. (2007); 17, Wang et al. (2008); 18, Stuart and Stuart (1997); 19, Lindsay and Macdonald (1986); 20, Kamler et al. (2004); 21, Kitchen et al. (2006); 22, Harris and Yalden (2008); 23, Hunter (2011)

breed (Bonanni et al. 2017; Cafazzo et al. 2014; Kubinyi and Wallis 2018; Sillero-Zubiri et al. 2004). Surprisingly, for some species, detailed information about their social behavior is lacking (e.g., the short-eared dog (*Atelocynus microtis*), Sechuran fox (*Lycalopex sechurae*), and pale fox (*Vulpes pallida*); please refer to the “Social behavior” section of Table 1). For other species, captive animals have provided some insight into their social systems (Sillero-Zubiri et al. 2004).

## Breeding Strategies

The majority of canid species are monogamous, having only one mate at a time, but polygyny has also been observed in some species (the chilla (*Lycalopex griseus*), bat-eared fox (*Otocyon megalotis*), gray fox (*Urocyon cinereoargenteus*), island fox (*Urocyon littoralis*), kit fox (*Vulpes macrotis*), and red fox (*Vulpes vulpes*); please refer to the “Breeding strategy” section of Table 1) (Sillero-Zubiri et al. 2004). Many are also said to mate for life, but actual data regarding this phenomenon is lacking in most species. Polygyny is likely to occur when ecological conditions are favorable, in years with high food abundance.

## Reproduction

Canids are unusual among mammals as a whole as they exhibit several reproductive traits that are uncommon. As stated previously they are typically monogamous, in almost all cases, both the male and female have been observed to provide care to the offspring, and they have reproductive cycles with lengthy proestral and dioestral phases and have a copulatory tie during mating (Castelló and Sillero-Zubiri 2018). Some species even retain adult offspring within the social group, which provide alloparental care to raise the next generation of offspring. The breeding pair typically suppresses mating in their adult offspring through behavioral means. In females that ovulate

but fail to conceive, pseudopregnancy frequently occurs, which helps to ensure maternal behavior of subordinate females. Canids are rare among mammals in that they have monoestrus cycles: a single ovulatory period followed by pregnancy (if fertilization occurs) or by prolonged diestrous phase and then anestrus (Asa et al. 2003). Most canids breed seasonally, with species in temperate latitudes responding to changes in photoperiod, and those in equatorial regions, to seasonal changes in rainfall and/or food availability. Therefore, most have only one seasonal cycle per year; however, African wild dogs (*Lycaon pictus*), fennec foxes (*Vulpes zerda*), crab-eating foxes (*Cerdocyon thous*), bat-eared foxes (*Otocyon megalotis*), and bush dogs (*Speothos venaticus*) have been observed to sometimes have a second cycle per year in the wild and/or captivity (Sillero-Zubiri et al. 2004). The inter-estrus intervals range from 8 to 10 months, which is similar to the mean interval of most breeds of domestic dog. These nonseasonal monoestrus cycles may be due to changes in photoperiod caused by living in captivity or because the first litter was lost (Valdespino et al. 2002). In terms of gestation period, small-sized canids typically require 50 days on average and larger canids around 60 days (please refer to the column titled “Gestation length” in Table 1). Litter size appears to be highly variable within and between canid species. Arctic foxes and African wild dogs have the greatest range in litter size, and Asa et al. (2003) suggested variability in litter size might be related to ecological variability (food availability and climate). Prolactin hormone levels peak in male and female canids during the spring; usually the time pups are born, which may facilitate paternal behavior (however, prolactin levels have so far only been measured in wolves, dogs, red foxes, and arctic foxes). More research is necessary on life history and reproductive traits of small canids in particular, as data is still lacking (Asa et al. 2003).

The young are usually born in a den dug by the female in order to provide warmth and protection. They are small, blind, and helpless and thus

require an extended period of care (Mivart 1890). When the young eventually begin to eat solid food, both parents, and often other pack members, may bring food back to the den and/or regurgitate food for them. They may also accompany them on short foraging trips around the den. Young canids may require 5 months to over a year before they are ready to leave their natal group, and in some species, they will remain in the pack as non-breeding helpers. Typically, small canids tend to reach puberty earlier than larger canid species (Asa et al. 2003).

## Cross-References

- Canine Cognition
- Canine Communication
- Canine Diet
- Canine Locomotion
- Canine Morphology
- Canine Navigation
- Carnivore (Diet)
- Domestication
- Domestication Hypothesis
- Human-Animal Interaction
- Life History
- Pets
- Service Dogs

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## Canine Locomotion

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## Synonyms

Canine gaits; Dog gaits; Dog locomotion

## Definition

Movement used by members of the family Canidae (e.g., foxes, wolves, jackals and domestic dogs) to traverse their environment.

The canines are species belonging to the family Canidae in the order of Carnivora. This includes foxes, wolves, jackals, and domestic dogs (Padilla and Hilton 2015; Pessutti et al. 2008). Canines are recognized for their long slender legs and digitigrade locomotion (Carr and Dycus 2016). Modifications to the axial musculature has allowed the group to move with an emphasis on speed and agility (Granatosky 2019). The greyhound dog, for example, has deep back musculature that produces a great deal of power and force, allowing the animal to partake in a rotary galloping gait (Webster et al. 2014). The canines are widely known for their diverse ecological habitats, which include, but are not limited to, coastal regions, deserts, grasslands, and the arctic. Some species, such as the red fox (*Vulpes vulpus*) and coyote (*Canis latrans*), do exceptionally well in human-modified habitats,

such as reservoirs, forest edges, and roads (Grubbs and Krausman 2009; Trehella et al. 1988). Much of the success of the canines to adapt to such a broad range of habitats comes from their generalized cranial and postcranial anatomy (Padilla and Hilton 2015; Pessutti et al. 2008). As both omnivores and carnivores, their feeding habits are no less diverse, which include, but are not limited to insects, birds, frogs, arthropods, grasses, and fruits (Pessutti et al. 2008).

## Gait Patterns in Domestic Dogs

As a result of our close interactions with domestic dogs, we have considerable knowledge about locomotion in the canines. The large morphological disparity observed within the domestic dogs reveal considerable variation in gait patterns and locomotor capabilities. Hildebrand (1968) explored symmetrical gait patterns for 37 different breeds and observed a wide variety of gaits dependent on limb length and speed. Quadrupedal gaits in canines are usually categorized as symmetrical or asymmetrical based on kinematics and then further subdivided into walking and running on the basis of either kinematics or kinetics (Alexander 2003). Symmetrical gaits occur when footfalls of the forelimb and hindlimb are evenly spaced in time (e.g., walk, pace, or trot). Asymmetrical gaits (e.g., gallop and bound) occur when the actions of the forelimb or hindlimb are unevenly spaced in time. All walking gaits in the canines are symmetrical and are defined by the sequence and coupling patterns by which animals move their limbs (Alexander 2003; Granatosky 2018). A lateral-sequence gait is one in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb). A diagonal-sequence gait is one in which each hindlimb footfall is followed by a contralateral forelimb footfall (i.e., right hindlimb, left forelimb, left hindlimb, right forelimb). Commonly during walking gaits, the forelimbs and hindlimbs are traveling together as a slightly asynchronous couplet. When the ipsilateral forelimbs and hindlimbs are traveling together, this is referred to as a lateral couplet;

when the contralateral forelimbs and hindlimbs are traveling together, this is referred to as a diagonal couplet. Very rarely do the limbs move together in perfect synchrony (Granatosky 2018).

Lateral-sequence lateral-couplet footfall patterns tend to be present in long-legged canids (e.g., greyhounds) and are assumed to be the best mechanism to prevent interlimb interference (Hildebrand 1968). However, this footfall pattern is thought to be inherently unstable, as a majority (~66%) of the stride is spent as a unilateral bipod (i.e., only two ipsilateral limbs in contact with the substrate), which tends to roll the body side-to-side throughout the stride (Cartmill et al. 2002). This instability is argued to be negligible for long-legged animals, but can be devastating for short-limbed broad-chested canines (e.g., Pembroke Welsh Corgi) (Hildebrand 1968). For these species, lateral-sequence diagonal-couplet footfall patterns tend to be more common. This footfall sequence is inherently more stable than lateral-sequence lateral-couplet gaits due to the generally low proportion of the stride spent as a unilateral bipod (~22%), and the relatively high proportion of the stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support). In general, foot positions arranged as diagonal bipods and large tripods are thought to be highly stable (Cartmill et al. 2002; Granatosky 2018).

At higher speeds, canines adopt running gaits. The trot, amble, and pace are symmetrical running gaits observed in canines and the use of these specific movement patterns is largely driven by limb length (see Hildebrand 1968). All running gaits include some period of the cycle in which no feet are touching the ground (i.e., an aerial phase). In trotting, diagonally opposite feet move in phase with each other; in pacing, the two feet on the same side of the body move in phase with each other; and in ambling, the four feet move at roughly equal intervals, in the same order as in walking. Most canines trot when travelling at moderate speeds, but pacing is common in longer limbed species (Hildebrand 1968). Some canines (e.g., the greyhounds) are known to reach speeds of over 64 km per hour. This remarkable speed can



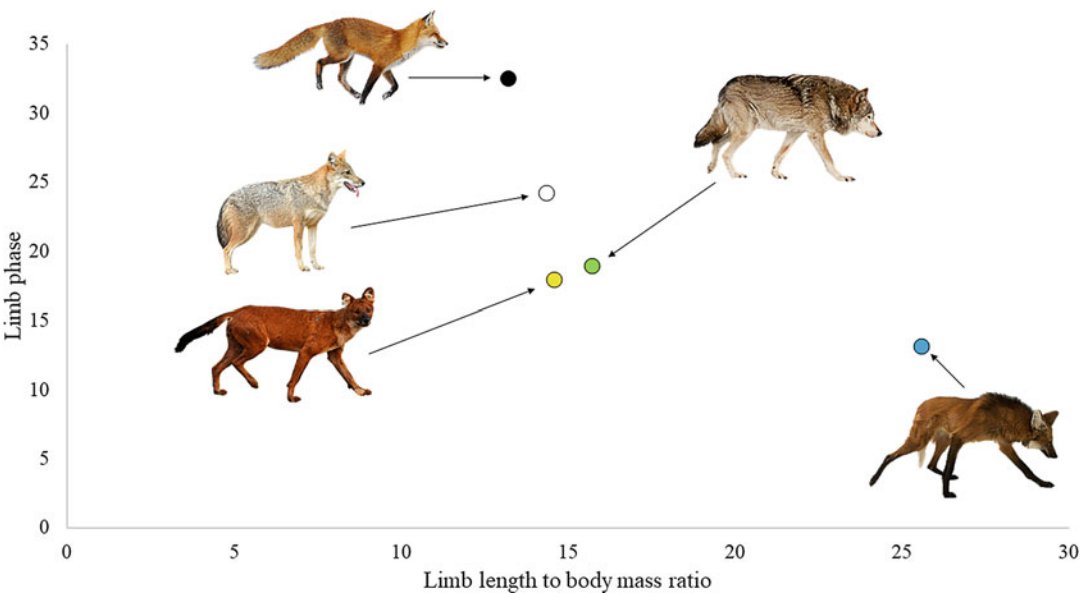
be attributed to its use of the rotary gallop, also referred to as a double suspension gallop (Bertram and Gutmann 2009; Granatosky 2019; Usherwood and Wilson 2005). The double suspension gait is a four-time, asymmetrical gait where the feet fall in a circular sequence around the body, and gets its name from the two aerial phases: a gathered aerial phase where the back is flexed and the hindfeet pass in front of the forefeet, and an extended aerial phase where the feet are stretched away from the body and the back is extended (Bertram and Gutmann 2009; Hudson et al. 2012). When running competitively, the greyhound is in the air 75% of the time (Granatosky 2019).

Gait patterns in domestic dogs are often used to determine health and check for any orthopedic (e.g., cruciate ligament tear, hip dysplasia, patellar luxation) or neuromuscular pathologies (e.g., degenerative myelopathy; Carr and Dycus 2016; DeCamp 1997). Lameness that occurs within the forelimbs or hindlimbs in dogs can be witnessed upon gait evaluation. Abnormalities of the gait can be identified as limping, skipping and staggering, favoring one side over the other, showing

weaknesses or avoidance in walking. When evaluating gait in dogs, several points must be kept in mind. Among them are selecting a platform that is flat and smooth, examining both the walk and trot, observing the dog from various viewpoints, and looking at the dog's specific characteristics if it is a performance or a working dog (Carr and Dycus 2016).

## Comparisons with Wild Canids

Overall, the quadrupedal gait patterns of wolves, coyotes, fox, and other canids are largely consistent with the patterns discussed above, and much of the variation in gait sequence is attributable to limb length (Fig. 1). Therefore, this chapter will not discuss limb phase of these other species individually. However, data on energetic expenditure does reveal interesting patterns in the wild canids compared to their closely related domestic cousins and other similarly sized animals. The wolf, coyote, fox, and dog exhibit an aerobic performance capacity that is approximately three



**Canine Locomotion, Fig. 1** The relationship between limb length to body mass ratio [i.e. limb length (mm) divided by cube root of body mass (g)] and limb phase (i.e., percentage of stride interval that forelimb footfall follows hindlimb footfall on the same side) for five

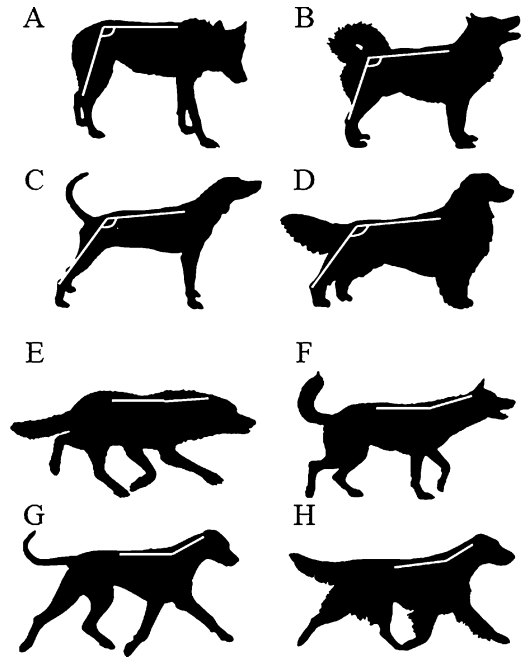
species of canine [yellow = dhole (*Cuon alpinus*); white = golden jackal (*Canis aureus*); green = gray wolf (*Canis lupus*); blue = blue-maned wolf (*Chrysocyon brachyurus*); black = red fox (*Vulpes vulpes*)]



times greater than animals of equivalent size (Bryce and Williams 2017). Arguably such energetic capabilities are adaptations for dealing with active long-distance hunting and large home range size (e.g., 259–1676 km<sup>2</sup> in wolf populations, Mattisson et al. 2013). Wolves have narrow chests and powerful backs and legs that allow for incredible stamina and speed. Wolves can cover several miles trotting at a speed of 10 km per hour and have been known to reach speeds approaching 64 km per hour during a chase. Wolf hunts can either last minutes or hours depending on whether attacks are successful or not (Muro et al. 2011).

This remarkable energetic capacity in wolves has been attributed to differences in body posture observed among the wild canids. Bryce and Williams (2017) noted that wolves tend to have a stance of a flat topline and hindlimbs positioned closer to their center of mass resulting in a small obtuse hip angle (Fig. 2). Northern breeds of canines, such as the Alaskan malamute, exhibit a near identical hip angle to the wolf even though these canines have a more upright stance. When looking at other canines, such as the hound and retriever, there is considerable divergence in locomotor posture with respect to their genetic descent. Hounds and retrievers tend to have an even more pronounced upright stance and significantly wider hip angles compared to wolves and northern breeds. This difference in stance may lead to a difference in mechanical advantage. A more upright stance may allow for a more efficient way of placing load on hindlimbs and muscles. The northern breeds tend to have a lower cost of transport when trotting and galloping compared to the hound and retriever (Bryce and Williams 2017).

As a consequence of the wide-ranging behavior of the wild canines, locomotor cost represents a large proportion of overall daily energy expenditure. Covell et al. (1996) reported daily energetic expenditure of free-living swift foxes (*Vulpes velox*) on shortgrass prairie in Colorado in relation to air temperature, daily activity period, and movement rate. They observed that the energy expended in locomotion is a substantial portion of the swift fox's field energy expenditure



**Canine Locomotion, Fig. 2** Comparative hip and topline angles of (a, e) gray wolves, (b, f) northern breeds, (c, g) hounds, and (d, h) retriever dogs. Bryce and Williams (2017) noted that (a–d) hip angles tend to be more acute and (e–h) topline angles more obtuse in wolves and northern breeds compared to hounds or retrievers. These differences in body posture have been posited to result in lower locomotor cost of transport in wolves and northern breeds. Figure modified from Bryce and Williams (2017)

(~21% of total daily energy expenditure), especially in winter. Arguably, the large daily travel distances covered by this species during the winter months (~18.5 km) when food is scarce account for such high energetic demands.

### Anthropogenic Influence on Canine Locomotion

As a result of the long history between humans and domestic dogs, canine locomotor capabilities have been exploited in terms of both work and sport. Perhaps most notable is greyhound racing, which is a competitive, organized sport in which bets are placed as greyhounds run around a track. Greyhounds are thought to be one of the oldest breeds of dogs and were bred to hunt by outrunning their prey (Thompson 2003). Through

artificial selection, greyhounds have acquired many anatomical features that allow them to reach great speeds (Williams et al. 2008a, b). Greyhounds have long, powerful legs, a deep chest, a highly flexible spine, and a slim build. The greyhounds' heart is larger than similarly sized breeds and pumps blood with higher levels of red blood cells than other breeds. As red blood cells carry oxygen, this higher level allows the hound to move large quantities of oxygen faster from the lungs to the muscles (Herrmann 1926). These attributes separate greyhounds from other dogs, specifically dogs that do not regularly participate in intense physical activity.

The ability to perform at this capacity is an extraordinary feat, but it also puts considerable strain on the body. There are many health risks and dangers that are associated with maintaining dogs in racing condition, and many former racing dogs develop complications years later post-retirement. Greyhounds are notorious for physiologic systolic murmurs associated with high aortic velocity, and large cardiac dimensions (Lord et al. 2007; Marin et al. 2007). The high aortic velocity of the blood being passed through the heart to supply the extremities with oxygenated blood causes valve failures. A popular practice among breeders and caretakers for the greyhounds that participate in these races is feeding them raw meat. A raw meat diet has been shown to provide more energy and stamina for canines. For such reasons, it is a staple diet for greyhound race dogs to create an optimal competitor. A negative outcome of this practice is the spreading of *Salmonella enterica* to not only the dogs but to humans as well (LeJeune and Hancock 2001).

Dog sledding has been a popular mode of transportation for northern region individuals in the wintertime (Cary 2009). This means of travel has further progressed into becoming a competitive sport. "Sled dogs" is a general term referring to a group of dogs primarily chosen as the "engines" for dog sledding. These breeds are, but are not limited to, Malamutes, Siberian Huskies, Inuit/Eskimo dogs, and Alaskan Huskies (Cary 2009; Huson et al. 2012). Sled dogs are bred for strength, speed, endurance, intelligence, and willingness to follow orders. Each specific breed of dog in the

group when dog sledding has a specific role. There are freight dogs and race dogs, which have different attributes that contribute to their success and efficiency (Cary 2009). Dogs are bred solely on potential athletic ability, which encompasses numerous factors, such as quickness, efficient gait, pulling strength, and endurance (Huson et al. 2012). Though the sled dogs have become accustomed to this activity and climate, there are many health risks that coincide with such vigorous activities in these harsh climates. It has been demonstrated that such intense exercise can lead to oxidative stress that may in turn lead to other more life threatening illnesses such as cancer, Alzheimer's disease, and heart disease (Van Citters and Franklin 1969). Oxidative damage is a never ending complication for sled dogs that are constantly exercising and training for long arduous sled dogs (Hinchcliff et al. 2000).

## Conclusion

As a result of adaptations to diverse ecological habitats in wild canines and selective breeding in wild dogs, canine locomotion is exceptionally diverse and well-studied. Canines deal with higher than usual energetic demands during locomotion, which may stem from dealing with active long-distance hunting and large home range size. Canines have also adopted a number of gait patterns that prevent limb interference and maximize stability, ultimately reflecting upon their body frame and limb length (Hildebrand 1968). Lateral-sequence lateral-couplet footfall patterns are observed in long-legged forms like the greyhound, while short-legged breeds like the Pembroke Welsh Corgi show use of lateral-sequence diagonal couplet footfall patterns. Observing canine gaits provides information about their orthopedic and neuromuscular health. As a result of the long history between humans and domestic dogs, canine locomotor capabilities have been exploited in terms of both work and sport. Most notable are greyhound racing and dog sledding. These sports put considerable physiologic demands on the dogs and there are a myriad of health problems observed even after the animals are retired.

## Cross-References

- [Adaptation](#)
- [Bear Locomotion](#)
- [Evolution](#)
- [Feline Locomotion](#)
- [Greyhound Racing](#)
- [Locomotion](#)
- [Quadrupedal](#)
- [Zoology](#)

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## Canine Morphology

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### Synonyms

Architecture; Canine shape; Canine structure; Form

### Definition

Canine morphology refers to the size, shape, and structure of members of the Canidae family. Morphology also relates to the form and function of constituent parts of an animal and will consider the general anatomy and physiology of the organism in question. General canine morphology is representative of evolutionary ancestry and functionality, with species-specific variations associated with adaptation to specific ecological niches and selection pressures.

## Introduction

Canine morphology considers the shape, size, structure, form, and function of members of the Caninae subfamily. The mammalian order Carnivora includes the Canidae family which consists of three subfamilies, two extinct (the Borophaginae and Hesperocyoninae), and the extant Caninae (Miklosi 2015). Canines belong to the Caninae and have a typical body plan described as “dog-like,” quadruped with athletic, slender bodies, elongated muzzles, upright ears, and locomotory ability suited to hunting and prey acquisition, although there are some exceptions that demonstrate more distinctive species-specific morphology. The domestic dog (*Canis lupus familiaris*), in particular, demonstrates a vast morphological diversity.

## The Caninae

The Caninae subfamily includes more than 36 species including foxes, coyotes, dingoes, wolves, jackals, and the domestic dog (Wang and Tedford 2007). The general morphology of these species is largely similar and is indicative of their shared taxonomic ancestry, although the gray wolf (*Canis lupus*) and the domestic dog are acknowledged to be particularly close on both a taxonomic and genetic basis, despite morphological differences in overall body shape, size, and other physical and behavioral attributes. Wild and free-living canids are terrestrial, denning species, often crepuscular or nocturnal in their habits, and can be either highly social, pack-hunting species such as the wolf or more solitary like the fox.

Canids exhibit a wide geographical distribution and occupy several specific ecological niches on every continent, except Antarctica and some islands (Clutton-Brock 1995). Some species such as the red fox (*Vulpes vulpes*) and the gray wolf (*Canis lupus*) have an extensive global range, suggestive of biological and evolutionary success, in addition to the fox (and the domestic dog) being introduced to new environments by humans. This distribution pattern

means that canine body size and bodyweight are diverse, but the typical body plan is largely consistent across different species and fulfils the classification characteristics of their membership of the class Mammalia and the order Carnivora. Notably, all canids possess the characteristic carnivore carnassial apparatus and other dentition typical of a carnivore, and dog skulls are widely accepted as representative of a “typical mammalian carnivore” for educational purposes. In addition, the basic skeletal system of canids, their sensory capabilities, and fundamental locomotory ability remain largely consistent across species. Senses relate specifically to enhancing prey locating skills, with forward facing eyes, adapted to detect movement, even in reduced light, highly sensitive hearing for prey detection, and a highly developed and sensitive olfactory capacity.

The Canidae family has been further subdivided based on genetic analysis into two “tribes” (the Canini or true dogs and the Vulpini or true foxes) and a basal Caninae group (containing the island fox and the gray fox; Lindblad-Toh et al. 2005). Members of the Canidae are thus numerous and range in size from the small fennec fox (*Vulpes zerda*) to the relatively large maned wolf (*Chrysocyon brachyurus*), with the domestic dog being an especially phenotypically diverse member of the Canidae.

Indeed, canine morphology is particularly interesting when considering the domestic dog, which is considered to be one of the most phenotypically and morphological diverse mammalian species (Boyko et al. 2010). This diversity is a consequence of intense anthropogenic artificial selection pressures based on physical appearance, behavior, and/or morphological functionality. Consequently, the domestic dog demonstrates a wide diversity in breed types and forms, with the physical structure and overall appearance of specific breeds being phenotypically constant and characteristic, in order to meet national and international “breed standards.” These breed standards are published criteria by which dogs can be identified as specific breeds and identify both desirable and undesirable characteristics for the form and function of individual breeds. Adherence to some specific standards,

combined with intense artificial selection for characteristics attractive to humans, has had some unfortunate consequences for health and well-being and is in distinct contrast to the consistency in morphology that is characteristic for wild, free-living, and feral canids.

## Canine Morphological Characteristics

The morphology of wild and free-living canid species is remarkably consistent. The body is typically slender, athletic, and of a moderate size, with canids often being categorized as mesocarnivores, based on morphology rather than the proportion of animal-derived tissue in their diet. Indeed, canids that tend toward a hypocarnivorous dietary strategy tend to be smaller in physical size, than forms commonly described as hypercarnivorous, a possible consequence of the energetic demands of predation and hunting (Carbone et al. 2007) and consistent with the evolutionary move toward larger body size in more predatory species (Van Valkenburgh et al. 2004).

The canid ears are often pricked and erect, the legs are long, and they have a tail that can be used for inter- and intra-species communication (Leaver and Reimchen 2008), through movement, carriage, and overall position. Tail morphology is diverse in the domestic dog, and carriage of the tail can vary as a result. Selective breeding has resulted in tails that can be curled, corkscrew, straight, or even absent. Surgical removal of either the full or partial tail length (docking) is occasionally conducted for prophylactic purposes in working domestic dogs, to prevent tail injuries (Lefebvre et al. 2007). Tail docking is occasionally conducted for cosmetic or visual preference purposes, as is ear “cropping,” although these are increasingly viewed as unacceptable morphological mutilations. It is often considered that the wolf demonstrates the typical canine physical form, although, clearly, individual species will show divergences in terms of physical height, muzzle length, ear shape, and tail length (Castello and Sillero-Zubiri 2018).



## Skull Morphology

A distinct cranial morphological characteristic of canids that is useful for classification and taxonomic purposes, including consideration of the fossil record, is the anatomy of the middle ear, located in the basicranial region (Wang and Tedford 2007). The bulla chamber of the middle ear is a bony area that protects the inner ear, and it ossifies in different ways. Canids have a characteristic inflated endotympanic bulla, divided by a partial septum, and there are characteristic locations of the internal carotid artery. These cranial characteristics have been retained through canid evolutionary history (Wang and Tedford 1994).

The domestic dog has a diverse variation in skull morphology, with diversity across different breeds and types, greater than that observed between different canid species (Wayne 1986a). The diversity observed in skull morphology in the domestic dog contrasts dramatically with the fact that the size and shape of the skull for wild canids are typically consistent for individual species and are in accordance with their dietary and ecological niche. Skull shapes are generally classified as mesaticephalic (medium length muzzle), dolichocephalic (extended muzzle length and narrow skull base), or brachycephalic (shortened muzzle length and broad skull base). Mesaticephalic is often regarded as closest to the basal, ancestral skull shape, and is the shape often identified as the typical mammalian carnivore. Brachycephaly and the popularity of dog breeds exhibiting this morphological characteristic have been linked to a human preference for neotenized canine facial forms that may resemble the human face (Archer and Monton 2011). Indeed, a shortening and widening of the dog skull have been more generally linked to the domestication process, concurrent with crowding, displacement, and reduction in the size of teeth (Clutton-Brock 1995).

Artificial selection in the domestic dog, for specific traits viewed as desirable, particularly relating to morphology, has resulted in a consistent, sustained, and significant alternation in skull shape (Drake and Klingenberg 2008). The alteration in skull shape has functional, aesthetic, and also welfare consequences for the domestic dog (Sandøe et al. 2017).

## Dentition

Canine dentition represents the general pattern observed in most carnivores, with elongated canines, small incisors, and a carnassial apparatus (De Muizon and Lange-Badre 2007). There are typically 42 permanent teeth and a dental formula of 3142/3143, a useful classification tool which includes unmodified molars and a greater number of teeth than observed in many obligate hypercarnivorous members of the Carnivora, such as felids. The carnassial apparatus is a dental signature of carnivory, although molars located caudally in canids often show an increased palatine surface for enhanced ingesta grinding and processing. Consistent with individual dietary niches, some canids will demonstrate dental adaptations toward hypercarnivory, with such species demonstrating large, strong premolars that are capable of breaking bones to acquire extra nourishment (Werdelin 1989).

## Jaw Morphology

The jaw of canids is characteristic in being limited in lateral movements. This supports the dentition and dietary ecology, toward cutting and shearing through ingested material, but also limits any prolonged grinding and chewing capacity (Kim et al. 2018). Bite force is important to support dietary intake and is generated by interactions between the muscles of the jaw, the temporomandibular joints, and the teeth. The skull size, shape, and the overall bodyweight impact on the bite force measured in the canine jaw, and bite force increases as skulls change from a dolichocephalic to a more brachycephalic shape (Ellis et al. 2009). This is a clear indication of the link between morphological form and functionality.

## Limb Morphology

As terrestrial species, canids demonstrate a morphology consistent with extensive locomotory ability. This is essential for food/prey acquisition, maintenance of territory, mate finding, and accessing other biological resources. Locomotion is cursorial, efficient, and athletic, supported by an athletic morphology. Limb morphology is extremely similar across canid species, and there is typically little variation between domestic dogs



and wolf-like species of a similar size (Wayne 1986b). There are however subtle differences in the fundamental skeletal morphology of limbs between dogs and wild fox-like species (Wayne 1986b), likely linked to developmental aspects. Canid limbs are characteristically elongated in the distal segments (metapodials, tibia-fibula, and radius-ulna) leading to an overall limb elongation (Wang and Tedford 2007).

Canids are digitigrade, meaning they effectively walk on their toes, and non-retractable claws permit adaptation to different terrestrial surfaces. The metapodials are lifted, in contrast to the more primitive plantigrade stance of ancestral canid forms such as the miacids, and permit an increase in stride length and shock absorption during locomotion. Digitigrade species have long carpals and tarsals, plus large, cushioned metacarpal pads (Miao et al. 2017). The metacarpal pads constitute cushioned soles, with a central pad and a pad behind each toe, of which there are five on the forelimbs (although the fifth toe is located higher up the limb and rarely touches the ground in normal locomotion) and four on the hindlimbs, although the domestic dog occasionally has a fifth, vestigial toe on the hindlimbs. Metacarpal paw pads aid in the management of ground reaction forces (GRFs) during locomotion, to protect the musculoskeletal system from impact (Whittle 1999) and reveal specific anatomical multilayer features to attenuate GRFs (Miao et al. 2017).

### **The Domestic Dog: Breed-Specific Morphology**

In considering canine morphology, the vast diversity of phenotypic morphology observed in the population of the domestic dog must also be acknowledged. The origins of the domestic dog remain subject to much scientific investigation and debate, but the process of their development, evolution, and domestication is estimated to have commenced some 20,000 to 40,000 years ago (Botigue et al. 2017), from a common wolf-like ancestor. The process of domestication is likely to have been a combination of human-directed

selection of specific individual animals and “self-domestication” by the animals themselves. The domesticated dog now maintains some characteristic canid features and traits but also displays altered behavioral and morphological characteristics, consistent with requirements of the human-dog dyad and associated selection pressures.

The diversity of cranial morphology in domestic dogs exceeds that observed in the Canidae family (Wayne 1986a), and there is similar diversity in terms of overall body size, shape, limb length, and fundamental form. This morphological diversity is a consequence of evolution and anthropogenic artificial selection pressures based on physical appearance, behavior, or morphological functionality. Many morphological variants observed in the domestic dog population are congruent with human desires for neoteny and human-like features in the species they share time and space with.

The diversity observed in specific breeds of the domestic dog are in part a consequence of adherence to breed standards, and changes in specific breeds have been directly attributed to desirable features detailed in these descriptive standards (Drake and Klingenberg 2008). Concurrent with the desire to artificially select animals for their “fit” to specific descriptive requirements is the potential for genetic issues arising from population bottlenecks, founder effects, genetic drift, inbreeding events, increased homozygosity, and restricted gene pools. All of these factors can give rise to specific genetic conditions that can produce morphological variations and are identified in other restricted breeding populations (Millien 2006).

The increase in the occurrence of specific genetic conditions linked to morphological variations can lead to an increase in the occurrence of specific inherited disorders capable of impacting on health, well-being, and longevity. For example, chondrodystrophy and chondrodysplasia are desirable morphological characteristics in several breeds of dogs, presenting as a shortened limb phenotype, but are also linked with intervertebral disk disease, a painful and potentially life-limiting condition (IVDD; Batcher et al. 2019). Genetic analysis and screening can be successfully

utilized in the selection of individual animals for inclusion in breeding programs, to limit the continuation of genotypes associated with deleterious consequences linked to otherwise desirable morphological traits.

Similarly, the increased popularity of dog breeds with a brachycephalic morphology (The Kennel Club 2020) such as the French bulldog, has raised concerns about welfare. Brachycephaly is associated with a range of disorders, notably ocular, dental, and respiratory (Packer et al. 2015), that impact on canine health and well-being. These extreme and exaggerated morphological features are attributed both to desirable breed standard characteristics (Asher et al. 2009) and human preferences (Packer et al. 2017), despite potential negative consequences for the individual animal.

Notably, morphological diversity is often observed to be greatest in breeds typically considered to be “companion breeds,” less in breeds selectively bred for working capacity, where functionality rather than appearance is critical and is most stringent for wild, free-living, and feral species (Drake and Klingenberg 2010). This observation is of critical importance in linking morphology with functionality. Certain breeds of the domestic dog are interesting to consider in terms of their intrinsic biological functionality as opposed to their functional and aesthetic purpose as companions for humans, especially where significant morphological deviations from the basal canid morphological form have been associated with significant health and well-being concerns.

## Conclusion

Canine morphology considers the body form of members of the Caninae subfamily, which includes a number of wild species and the domestic dog. While overall body size is divergent across canids, the typical basal morphological form is relatively consistent and is congruent with the typical canine life history, locomotion, dietary ecology, and terrestrial habitats. Particular morphological characteristics such as dentition and the structure of the middle ear are maintained

across different species and represent key classification tools. However, morphology can be diverse, especially in the domestic dog, where exaggerated and extreme phenotypes appear to be linked with intense anthropogenic selection for physical characteristics linked with aesthetic preferences. This selection has resulted in a hugely diverse range of morphological features, some of which are linked with negative consequences for individual animals. The effect of artificial selection pressures on driving morphological diversity in canids, compared to natural selection pressures that are likely to drive morphology toward biological functionality and success, is of significant interest in considering overall canine morphology.

## Cross-References

- [Canine Cognition](#)
- [Canine Communication](#)
- [Canine Diet](#)
- [Canine Life History](#)
- [Canine Locomotion](#)
- [Canine Navigation](#)
- [Carnivora](#)
- [Carnivore \(Diet\)](#)

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## Canine Navigation

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## Synonyms

Migration; Movement; Travel; Wayfinding

## Definition

Canine navigation refers to the process or activity of how members (either individuals or populations) of the family Canidae identify their position both temporally and spatially, and

then move to follow a given route, typically to access key biological resources such as water, food, or reproductive opportunities.

## Introduction

Navigation is the process by which an organism identifies its location in time and space and then uses that information to permit specific movement. The ability to move in a specific direction is essential to access key biological resources such as water, food, and reproductive opportunities. Consequently, movement and navigation within a given environment are essential for survival. Navigation is also critical for species that migrate, defined as a regular, long-distance movement toward a different location, and is observed across the animal kingdom, in both terrestrial and aquatic species.

The ability of species to successfully, precisely, and consistently navigate both over long distances, around or to objects, or the ability to orient to moving objects has long been poorly understood. However, the biological processes and environmental cues that individual species employ for navigation purposes are gradually being elucidated, and similar mechanisms are being identified in a wide array of species, from arthropods to mammals, including members of the family Canidae, such as the domestic dog, *Canis lupus familiaris*.

In order to navigate, environmental information and behavioral cues are integrated by an organism and then support directed movement to access biological resources. Animals move for several reasons, and movement is an essential process for both individual and overall population survival. Movement, whether over short distances or as more prolonged and defined migrations, permits and enhances access to key resources that can fluctuate seasonally or otherwise in time and space, such as food and reproductive opportunities (Dingle and Drake 2007).

Migration, and thus the ability to successfully and accurately navigate during migratory processes, facilitates evolutionary processes through the movement of individual animals and whole

populations, with the transfer of genetic material, acquisition of nutrients, and even movement of pathogens. Indeed, annual animal migrations have been identified to be of significance in ecosystem stability and biodiversity (Bauer and Hoyer 2014), although migration can also be a biologically demanding process, with the ability to navigate in time and space and having enough energy provision to support that movement, being critical for biological and evolutionary success.

**Canine navigation** specifically refers to how members of the Canidae family orient themselves spatially and temporally, integrating environmental stimuli and other behavioral cues. The family Canidae (from the Latin “*Canis*,” meaning dog) includes a wide lineage of species, including the domestic dog, wolves, foxes, coyotes, dingoes, jackals, and other extant doglike mammals. While canids do not specifically migrate in a seasonal fashion, they are typically social animals that have defined home ranges and territories of sizes representative of prey density. On this basis, movement within a territory will be observed to both follow prey species and access other important resources. Indeed, wolves have been acknowledged to migrate when their prey species are highly migratory, unless there is the presence of alternative prey (Mech and Boitani 2003).

## The Biology of Navigation

Navigation refers to the ability of animals to move successfully and is underpinned by a range of sensory abilities linked with the ability to identify and respond to specific cues, including light, position of the sun and stars (Wiltschko and Wiltschko 2015), circadian rhythms, specific geographical and visual landmarks, magnetic fields, echolocation, and scent. In some cases, movement and migration appear to be instinctive, and for others, it is learned or socially facilitated, leading to the term “collective navigation” (Berdahl et al. 2018). Navigational abilities are required in search of essential biological resources, and successful navigation skills are critical to support short-term and long-term locomotion toward resources and in the case of many canid species,

for awareness of and movement around and within specific territories. This is of relevance in highly territorial pack species such as the gray wolf (Mech and Boitani 2003).

Within the natural environment, individuals that can also effectively navigate to specific targets (e.g., prey), around obstacles, take detours, and reduce journey lengths are likely to have enhanced evolutionary value via ease of food and mate finding and/or a reduced predation risk or pack challenge. However, the ability to detour remains undetermined if it is a consequence of a mental awareness and mental representation of the environment or a “cognitive map” (Nesterova and Hansen 2009). A cognitive map provides a representation of the environment that an animal can access, in order to spatially navigate and orient successfully. It is likely that in such situations, an integration of different navigational tools is essential. The integration of multiple sources of information, including associative learning, permits navigation overall.

Indeed, several different sources of information are utilized by animals to support navigation for migration, prey finding, homing abilities, or simply moving within and around territories and habitats. The process by which animals navigate has been extensively investigated in a range of species, with different specializations identified. There also appears to be a combination of innate and learned abilities in terms of avian navigation skills (Wiltschko and Wiltschko 2015), and this is likely to be consistent in other species also. Indeed, species demonstrating significant navigational ability combine several different specific sensory mechanisms to ensure successful wayfinding. Considering the potential for both innate abilities and learned skills, the ability of the domestic dog to learn from other species, notably via human behavioral cues (Hare and Tomasello 2005), makes for an interesting consideration of joint navigational skills.

## Canine Navigation

Canids are widely distributed geographically and are found on all continents except for Antarctica.

The diverse habitats and environments in which canid species are found necessitate a range of adaptive abilities for both individuals and groups to orient in time and space. This is further complicated by the diversity of canid species, from wild examples such as the gray wolf (*Canis lupus*) to the domestic dog, and the respective selective pressures applied to species, based either on natural selection from environmental pressures or artificial, anthropogenic selection in the case of the domestic dog. The domestic dog is typically tightly managed in its locomotory freedom by human caregivers, with their territory and home range defined by anthropogenic factors. Feral and abandoned domestic dogs demonstrate distinct spatial and temporal resource use, likely because of prior behavioral consequences of human contact (Daniels and Bekoff 1989). Consequently, canine navigational abilities are likely based on an awareness and mental representation of the physical environment from specific environmental cues, in combination with genetic predisposition and developmental and prior behavioral experiences.

## Path Integration

Path integration (also known as “dead reckoning”) is one method of navigation whereby an animal identifies current direction and location based on a specific reference point. Path integration is one of the most primitive navigational systems and underpins other, more complex strategies, although it appears to be significant for short distances only, due to cumulative errors in direction (Seguinot et al. 1998). Path integration as a navigational tool has been identified in a range of species and typically involves the integration of different sensory systems, even in the absence of visual or other external landmarks, although visual landmark recognition may be involved in the development of cognitive “maps” (Collett and Graham 2004). Indeed, visual recognition of landmarks for navigation is, at least in part, employed by a range of species including birds, insects, and mammals, including humans, for navigation. Path integration to a target has been demonstrated in domestic dogs (Seguinot



et al. 1998), even in the absence of visual stimuli (Cattet and Etienne 2004). This suggests the possible functional importance of path integration as a navigational tool for canids to reach specific targets (e.g., prey) even via detours, by incorporating somatic signals about direction and movement, for example, from the vestibular system, rather than a reliance on visual, olfactory, or auditory cues.

## Navigation by the Sky

The position of the sun and other celestial bodies including stars and polarized light is also exploited for navigation and is dependent upon the presence of an internal “body clock” in the regulation of circadian rhythms. Indeed, the African dung beetle (*Scarabaeus zambesianus*) navigates using polarized patterns from moonlight (Dacke et al. 2003), combined with the location of stars for navigation, in common with birds, seals, and humans (Dacke et al. 2013). It is likely that canids will also integrate circadian signals, specifically light-dark cycles and internal body clocks as part of their navigational arsenal. Evidence suggests that feral dogs are most active during crepuscular and nocturnal periods of time and are similar to wild canids with a bimodal activity pattern (Boitani et al. 2007), although specific navigational abilities during those times are yet to be fully elucidated.

## Olfaction and Navigation

The olfactory ability of canid species is significantly greater than that of humans with the olfactory epithelium in dogs reaching up to 150 cm<sup>2</sup> in contrast to the typical human olfactory epithelial surface area of approximately 5 cm<sup>2</sup>. Consequently, olfaction is a major sense in canids and is an important form of intraspecific communication, which might also have an impact upon navigational ability.

For example, territorial marking via urination is common in dogs, coyotes, and wolves as well as signaling information about individuals and

their sexual status. Scent marking provides a long-lasting indication of the presence of individuals and populations (Bekoff 2001; Mech and Boitani 2003) and thus provides an opportunity for individuals to successfully navigate around or within a specific territorial area, in addition to determining the potential age of the deposition, through recognition of odoriferous deposits.

Interestingly, pigeons appear to utilize olfaction as an additional navigation cue (Ioalè et al. 1990). This finding is also of significance in considering canine navigation, given the olfactory sensitivity of canid species, although evidence suggests that in specific tasks, dogs do not rely on olfactory cues alone (Szetei et al. 2003), again supporting the integration of different strategies for successful navigation.

## Magnetic Fields and Navigation

The magnetic field of the earth is a particularly consistent environmental feature (Skiles 1985), unchanging based on season and light level, and is almost universally present, providing a source of positional information (Lohmann et al. 2007). Consequently, the earth’s magnetic field is exploited by a range of species for navigation, from bacteria to vertebrates (Wiltschko and Wiltschko 2015). Homing pigeons (*Columba livia*) demonstrate sensitivity to the earth’s magnetic field and use it, in combination with other cues such as olfaction for navigation (Ioalè et al. 1990; Walcott 1996).

Two types of positional information are supplied by the magnetic field, the simplest being compass or direction information that permits consistent movement in a specific direction. The ability to utilize compass or direction information supplied by the earth’s magnetic field has been identified in invertebrate, avian, and other vertebrate species (Wiltschko and Wiltschko 2015; Johnsen and Lohmann 2005; Lohmann et al. 2007). The second type of information that is supplied is in effect a “magnetic map” to permit navigation via the determination of geographical location, in the same way that humans might utilize GPS technology.



It is likely that species undertaking significant migrations such as the loggerhead sea turtle (*Caretta caretta*) use a combination of both compass and magnetic map information for consistent and successful migration (Arens and Lohmann 2004). There is also the intriguing evidence supporting the notion that species have both innate, inherited navigational abilities via instinctive responses to magnetic fields, as well as learned and experiential knowledge as a result of associations with visual and other landmarks (Giurfa and Capaldi 1999; Lohmann et al. 2001). This may also apply to canines in their navigational abilities and associated learning capacity.

Magnetoreception is essential to detect magnetic fields and it appears that two mechanisms exist in animals. Some fish and bird species that migrate have been shown to have magnetite particles located within their heads, suggesting the importance of detecting the earth's magnetic field for navigation (Begall et al. 2013). The second mechanism appears to be linked to cryptochromes, a group of blue-light absorbing flavoproteins that can be found in the retina and are involved in the circadian clock (Nießner et al. 2016). Indeed, cryptochrome 1, which appears to be like the version of the retinal receptor of the light-dependent magnetic sensing compass found in birds, has been identified in the cone receptors of members of the Mustelidae, Ursidae, and Canidae families and some primate species. Cryptochrome 1 has been postulated to be involved in the detection of magnetic fields and thus contributing to an ability to navigate (Nießner et al. 2016). This potential, linked with evidence that other canid species including the red fox (*Vulpes vulpes*) and the domestic dog appear to demonstrate degrees of magnetic alignment (Hart et al. 2013; Begall et al. 2013), supports the notion that geomagnetic fields may also be useful for canine navigation.

## Spatial Navigation in Canids

Spatial navigation is the ability to move specifically within an environment to locate biological

resources. The domestic dog is credited with many high-profile news stories of lost dogs apparently successfully making their way “home,” sometimes over vast distances and after prolonged periods of times (Boyd 2016). This apparent skillful spatial navigation, however, does not appear to be universal, especially when considered alongside the number of dogs who become lost and fail to successfully return “home.”

The ability to navigate in space is underpinned by two main strategies: egocentric strategies and allocentric strategies. Dogs appear to utilize a combination of both strategies in navigating, combined with visual, auditory, and olfactory stimuli from the environment. Egocentric strategies involve the awareness of where the body is in relation to environmental information and is useful when environmental cues are absent. Dogs also appear to be able to identify location by path integration which is achieved without environmental cues. Instead, there is the integration of information including distance traveled, directional changes, and speed, as identified in studies that removed visual and auditory stimuli from dogs (Cattet and Etienne 2004).

Allocentric navigational strategies consider the location of specific objects in time and space and appear to be predominantly based on visual awareness of specific spatial landmarks and beacons that provide positional information. Indeed, visual landmarks also appear critical for the development of human navigational and wayfaring skills (Lingwood et al. 2015). Domestic dogs appear able to acquire both allocentric and egocentric navigational skills, although they appear sensitive to an age-related decline in new task acquisition (Christie et al. 2005).

## Navigation to Objects by the Domestic Dog

Several activities and disciplines that the domestic dog partakes in are dependent upon an ability to navigate to specific objects. Retrieving specific objects is a typical task expected of many dogs, either for functional, working purposes (such as working gun dogs retrieving shot game) or for

exercise, pleasure, and competitive disciplines involving interactions between the dog and handler, such as “flyball” and competitive obedience. Activities and competitive disciplines that the domestic dog takes part in also include successful direction to and navigation around (and over) specific objects and visual targets, such as jumps in dog agility and send-away targets in obedience.

Catching airborne objects is a common activity that promotes the human-dog dyad in a playful fashion and has also developed into a competitive discipline that involves specific athletic moves by both dog and handler, culminating in the dog catching and retrieving a frisbee. Dogs appear to be highly successful in their ability to catch moving objects from the air, even when the objects are traveling at speed and with changing directions. Indeed, dogs seem to demonstrate “object permanence” in their ability to form and hold a mental representation of an object that has temporarily disappeared from vision. Dogs have been shown to demonstrate object permanence in studies that hid objects, and dogs were able to recover them after a period of time. There appears to be an ability to link specific environmental cues with the object, allowing a memory to be formed. This ability to navigate to an object is also critical for many working breeds of domestic dogs that undertake tasks related to object locating and retrieval in some cases. More generally, object permanence will likely support wild canids in their ability to detect, locate, and successfully hunt prey species during a chase.

Linked to the cognitive memory skill of object permanence is the ability to “object follow” in the case of moving objects. The ability of dogs to object follow and then navigate to that object is observed in their ability to successfully catch an airborne object. In this case, it appears that dogs utilize similar viewer-based navigational strategies to human baseball players and aircraft pilots, suggesting a common interception mechanism for moving targets in three dimensions (Shaffer et al. 2004). By examining how dogs caught an airborne frisbee, dogs appeared to maintain a linear optical trajectory (LOT) with an optical speed constancy until the object either changed direction or was intercepted. Where the object changed direction, study dogs simply established

a new LOT and optical speed (Shaffer et al. 2004). This is also in accordance with findings of predator species as diverse as bats and dragonflies for prey interception, where a consistent optical angle is maintained between predator and prey until a successful hunt conclusion (Simmons et al. 1979; Olberg et al. 2000).

## Conclusion

The ability of an animal to successfully navigate in time and space is critical for survival. Navigation permits directional movement in the pursuit of essential biological resources such as water, food, habitat, territory, and reproductive opportunities. While a wide array of techniques and biological adaptations are identified across the animal kingdom to support navigational abilities, in common with many other species, canine navigation appears to comprise a range of different strategies, with an opportunistic adoption of the most suitable strategy (or combination of strategies) in a given time and space. On this basis, identifying a single mechanism responsible for canine navigation is unlikely, and rather an acknowledgment of an integrated navigation system is pragmatic in the understanding of how canid species successfully negotiate location orientation and subsequent directional movement. A combination of innate, learned, and experiential behaviors with specific sensory skills based on visual, auditory, olfactory, geomagnetic, circadian, and other location identification abilities, in addition to local environmental conditions, helps to assist canine wayfinding and navigation, whether to a specific location, resource, or other object.

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Bear Navigation](#)
- ▶ [Canine Cognition](#)
- ▶ [Canine Communication](#)
- ▶ [Canine Locomotion](#)
- ▶ [Feline Navigation](#)
- ▶ [Migration](#)

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## Canine Shape

### ► Canine Morphology

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## Canine Structure

### ► Canine Morphology

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## Cannibalism

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## Synonyms

[Anthropophagy \(in humans\)](#)

## Definition

The practice of consuming the body – such as organs or flesh – of one’s own species.

## Introduction

Cannibalism is a widespread phenomenon in the animal kingdom. While eating the members of one’s fellow species may seem evolutionarily counterintuitive, cannibalism provides many survival advantages to a wide range of animal species – including personal nourishment and increased reproductive benefits. This entry

discusses some theories regarding why cannibalism exists in nature, the evolutionary advantages that cannibalism provides, and the various animal species that engage in cannibalism.

## Cannibalizing Mates

Multiple theories regarding precopulatory cannibalism (consuming one’s sexual partner during courtship) have been posited. One theory – the *adaptive foraging hypothesis* – states that females of some species may assess and compare the reproductive and nutritional value of potential male mates (Barry et al. 2008). Malnourished females are more likely to cannibalize their potential mate and forego the reproductive opportunity out of their need for nutrition (Andrade 1998). Support for this theory has been discovered in various insects and arachnids, including praying mantises (Prokop and Vaclav 2008), and many different types of spiders (Andrade 1998; Johnson et al. 2011; Persons and Uetz 2005). Some evidence suggests this may also affect male sexual behavior. For example, male black widow spiders are more likely to pursue female mates that are satiated (Johnson et al. 2011). While cannibalizing a potential male mate eliminates a reproductive opportunity, the nutritional benefits may outweigh the costs. For example, cannibalism in female praying mantises is associated with increases in female fecundity (Barry et al. 2008).

Some researchers have proposed a controversial theory regarding precopulatory cannibalism known as the *aggressive spillover hypothesis*. Proponents of this theory state that cannibalizing one’s mate is a by-product of aggressive female foraging behavior; however, this theory has received significant criticism (Kralj-Fisher et al. 2013).

## Cannibalizing Offspring

Cannibalizing one’s own offspring may also provide survival advantages to the mother and other offspring in the litter. Consuming unhealthy and/or weaker offspring (i.e., offspring that have a low probability of survival) decreases competition for food among the surviving offspring.

Similarly, cannibalism in some snake species provides multiple benefits for the mother. Colombian rainbow boas will consume their non-viable eggs and offspring, which provides them with significant nourishment for post-reproductive physical recovery, rapidly increasing their constricting ability, which allows for more effective post-copulatory predation (Lourdais et al. 2005).

Some researchers have also proposed that consuming some of one's own offspring may help prevent the spread of disease, effectively maximizing reproductive output by sacrificing a small sum. Cannibalizing an infected offspring directly kills the parasites and reduces the number of possible hosts for the parasites (Van Allen et al. 2017). Thus, consuming the unhealthy offspring can protect the rest of the litter from infection, thus increasing their likelihood of survival. This is a rather controversial theory because many scholars believe cannibalism enhances the spread of disease within a species. However, mathematical models illustrate that disease transmission by cannibalism is very unlikely (Rudolf and Antonovics 2007; Van Allen et al. 2017). This is due to the fact that shared consumption of victims among members of one's species is necessary for significant disease transmission to occur, but shared cannibalism is rare (Rudolf and Antonovics 2007).

## Conclusion

Cannibalism is a common occurrence among many different species. While this entry focused largely on insects, arachnids, and reptiles, it is important to note that cannibalism has been well-documented in numerous mammals – including primates – as well. For example, chimpanzees have been known to cannibalize chimpanzees from other communities (Watts and Mitani 2000). This form of cannibalism occurs after the chimpanzees have killed their conspecific for territorial or intrasexually competitive reasons. Once the attacker's territory and/or mate is secure, the victim's carcass then provides nourishment. Cannibalism often provides a wide range of evolutionary advantages to members of one's species including nourishment, decreased competition for resources, and disease prevention.

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## Canopy

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## Definition

Canopy is the crown of any type of vegetation including leaves, branches, twigs, and the flora and fauna residing in it along with their microclimate (environment).



## Introduction

The term canopy was first developed during the study of tropical rain forest. However, several other vegetation such as kelp forests, sea grasses, gardens, crop fields, etc. also support canopy. Canopy is an important part of the vegetation especially in forest. It consists of uppermost part of any vegetation along with plants, animals, microbes, and their surrounding environment (Russell 2017).

The forest canopy is most diverse and influencing among the above canopies. Canopy biology is an emerging branch of forest science, which incorporates the study of tree crown and their inhabitants and the interactions among them. The forest canopy is a structurally complex subsystem of forest and which plays a major role in forest ecosystem. The growth of individual tree crown is dependent on the surrounding tree species and their environment. The plants in a natural ecosystem are of varied ages, shapes, and sizes. There is fierce competition among the plants for getting the space and sunlight. This can lead to changes in the individual plants in the canopy without much changing in the functioning of canopy. The functioning of canopy can be accessed in terms of their cumulative response toward the environmental factors. The canopies in natural forest ecosystem are multilayered; the upper layers have greater influence on lower layers of canopy. The upper canopy layers receive maximum sunlight compared to lower canopy layers (Russell 2017).

The fauna inhabiting the canopy are the integral part of the canopy and help in maintaining its structure and function. Other vegetation such as epiphytes, woody and non-woody climbers, parasitic plants, etc. are also important components of canopy. Thus, the canopy is the whole sum of associated flora, fauna, and the surrounding environment.

the main tree trunk. However, the tree crown of different tree species varied greatly in shape and sizes depending on the type of tree. Similarly, the canopy structure of different forest type depends on the type of trees present in the forest. It varies from temperate deciduous spruce forest to temperate evergreen pine forest, from tropical dry deciduous to tropical rain forest. The canopy structure also depends upon distribution of tree species in the forest. The canopy may be stratified into one to three regular canopy strata, with individual emergent plants and understory continuous layer of smaller trees.

The fauna inhabiting the canopy use it for browsing, feeding, nesting, mating, and resting. The animals live in the canopy are varied according to the canopy type, e.g., the fauna inhabiting the temperate forests are different from tropical forests. The species richness is highest in tropical forest canopies as they provide a wide array of niche due to their climatic conditions.

The main function of canopy is exchange of gases from the atmosphere mainly in the form of carbon dioxide, oxygen, and water vapor through photosynthesis and transpiration. The forest canopies generate microclimates by mitigating and equilibrating the disparity in climatic conditions, generating the gradient of mean PAR (photosynthetically active radiation) and changes in temperature and relative humidity. The forest canopies also affect the course of precipitation by trapping the rainfall and snow fall. The architecture and physiology of associated tree species and epiphytes in a forest canopy plays a crucial role in creating the microclimate which is further determined by the type of species, growth behaviors, and age distribution. Thus, the forest canopies play a crucial role in various biogeochemical cycles especially in water and carbon cycle. The microclimate generated by the forest canopies helps in sustaining a major part of earth biome.

## Architecture and Function of Canopy

A single tree crown is composed of the leaves, small twigs, and lateral branches emerging from

## Forest Canopies and Biodiversity

Forest canopies are biodiversity hotspots as they have one of the most species rich habitats on the



planet earth. Forest canopies especially rain forest canopies support a wide range plant, animal, and microbial species. Besides the associated tree species, the variety of epiphytic and climber plant species are the integral part of canopy (Nadkarni et al. 2013). However, plant species composition among the canopies varies according to the type of forests.

Invertebrates are the dominant fauna of the canopy; it comprises more than 90% of the species browsing the canopy. Vertebrates including temporary and permanent inhabitant (mammals, birds, reptiles, and amphibians) of canopy are merely 1% of total species inhabiting the canopy (Erwin et al. 2004; Robinson 1986). Arthropods are the dominant invertebrate fauna of forest canopies; Erwin (1995) found  $3.4 \times 10^{10}$  terrestrial arthropods per hectare in western part of central Amazonian rain forest. Insects, spiders, centipedes, millipedes, and mites are dominant among arthropods. Insects are the largest group of arthropods dwelling the canopies, several species of insects such as ants, beetles, butterflies, moths, and wasps. These insects including other arthropods are part of a complex food wave of canopies. They nearly present at all trophic levels of a food wave, from herbivorous beetles to predatory praying mantis. They occupy nearly about all possible niches in the canopy and perform crucial ecological functions such as pollination and seed dispersion, which are necessary to sustain a canopy.

Birds, lizards, and mammals are the dominant vertebrate fauna of the forest canopy. Food availability is the major governing factor for vertebrate fauna. Only tropical evergreen forests produce the food all over the year for herbivorous and insectivorous vertebrates. In deciduous and seasonal forests, the species which browse the canopy either browse on ground or hibernate during the scarce period (winter or dry). Nearly, all canopy dwelling mammals are found in evergreen tropical forests and are mostly scansorial. The timing and spatial distribution of flowering and fruiting plays a crucial role in controlling the behavior of these mammals. Anurans, lizards, and, up to some extent, snakes are the true canopy dwellers as they perform most of the

activities including foraging and mating in the canopy. Birds and bats are also one the most important elements of the canopy. The birds in the canopy are mostly insectivores, e.g., in the tropics nearly 50% birds are strictly insectivores, about 8% feed on both insect and nectar (Erwin and Zamorano 2017). These animals develop various special morphological adaptations in their limbs to browse the canopy, which provides firm grip on twigs, leaves, and scaly bark of the canopy trees. The ability to leap within canopy is the most common adaptation among neotropical mammals along with frogs and lizards as it conserves the energy and time to browse the canopy trees to find resources (Erwin 2013). However, the flying birds and bats are among the dominant vertebrate fauna of the tree canopy. Several other morphological adaptations help these organisms to camouflage in their environment which further enables them to avoid the predator and to capture the prey.

## Conclusion

The canopy is a broader term and it includes all the flora and fauna along with the associated microclimate. The interactions between canopy organisms and their surrounding environment have greater impact on the earth's climate. Canopies are the engines of the earth that drive the major biogeochemical cycles of carbon and water through photosynthesis and transpiration. The canopy harbors a great amount of species diversity of various plants and animals. The complex interaction among these organisms leads to the development of complex food waves. Various types of invertebrates and vertebrate fauna including spiders, insects, birds, frogs, reptiles, and mammals browse the canopy. The canopy animals develop several types of morphological and biochemical adaptations which enable them to efficiently utilize the resources present in the canopy. Thus, canopy is the one of the most influential and species-rich environment which governs the major biological and climatic aspects of the earth biome.

## Cross-References

- [Feeding](#)
- [Herbivore](#)
- [Hotspot](#)
- [Mating](#)
- [Predator](#)
- [Prey](#)

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and scientific research and education, for companionship, for their labor, and for their own benefit (in particular sheltering and treating lost and sick animals). Many of these animals have been domesticated, and this domestication process raises ethical questions of its own, but here we will focus on wild animals in zoos and the question of under what circumstances it is morally justified to keep them in captivity.

Animal ethicists have put the interests of individual animals on the map and have argued that the interests of sentient animals and humans should receive equal consideration in like circumstances (Singer 1975) or that we should respect the rights of animals not to be unnecessarily harmed by us (Regan 1983). This translates into a rejection of the use of animals for purposes such as recreation, entertainment, education, or generating a profit. For this reason, animal ethicists are generally not supportive of keeping animals in zoos. As they focus on individual animals, the argument that zoos might be instrumental in the conservation of endangered species does not convince them. After all, animal ethicists generally hold that individual animals are the sole locus of moral concern, as they alone have experiential well-being, while collectives such as species or ecosystems are human-constructed categories that have no independent moral standing (Palmer 2009). Regan (1995), for example, argues that animals can only be kept in zoos if this aids the protection of the particular animals in question. An example could be the sheltering of former circus bears that can no longer be returned to the wild. For utilitarians, conservation in zoos in theory could contribute to the interest of a group of animals, but in practice they tend to bring about too many welfare problems to be justified. In other words, the future survival of a species does in their eyes not trump the interests of currently existing individual animals; we cannot make a trade-off between the interests of individuals and their group. Others, on the other hand, have argued that both the interests of individual animals *and* the interests of their population or species should matter to us and that we should embrace a

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## Captivity

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## Introduction

Animals are kept in captivity for many different purposes, such as recreation or entertainment, for their products, for medical experimentation

bifocal view on animal welfare and species conservation (Keulartz 2015), or what Ramp and Bekoff (2015) have termed “compassionate conservation.”

In this contribution, we first discuss inherent objections to keeping wild animals in captivity. We will in particular discuss the question of whether animals have an intrinsic interest in freedom. Next, we will address moral justifications for and objections to keeping animals in captivity. In the second part of the chapter, we discuss the questions of under what circumstances harm to the interests of individual animals is acceptable for species conservation and what it would imply for the organization of zoos were they to take their conservation role seriously.

## Is Animal Captivity Inherently Wrong?

From the animal rights spectrum of animal ethics, it has been argued that keeping animals in captivity is inherently morally wrong, because it commodifies them and turns them into property (Francione 2010) or fails to respect their inherent value, as it treats them solely a means to our ends (Regan 1995). Even though animals might in practice be treated as though they were property or lacking in inherent value, it is not entirely clear why this would be a consequence of captivity by definition. After all, animals kept in wildlife refuges or as pets are not entirely free either, but this does not mean they are used as solely a means to our ends. Moreover, regarding animals as property from a legal perspective – as is common in many countries – does not mean they are commodified in a moral sense. Even though companion animals are deprived of certain freedoms, they are not commonly regarded as property, with which we can do whatever we want, but rather as friends or even family members.

Nevertheless, it has been argued that animals have an interest in freedom as such (p.e. Pluhar 1995; Rollin 1992). Cochrane (2009) disputes this; he makes a distinction between an instrumental and an intrinsic interest in freedom. Freedom is an instrumental interest for animals in so far as it facilitates “other goods, such as the avoidance of

suffering” (Cochrane 2009, 661). However, it is – at least theoretically – possible to deprive an animal of freedom without depriving it of these other goods. Most human beings, on the other hand, do have an intrinsic interest in freedom, or liberty, because they have a stake in being free from control and being the author of their own lives. According to Cochrane, they have this interest due to the fact that they are autonomous agents who have the “capacity to frame, revise and pursue their own conception of the good” (idem, 665). He argues that most animals (save perhaps primates and cetaceans) do not possess the relevant type of autonomy characteristic of human beings, which is dependent on the capacity to have “second order” desires, or in other words being able to reflect on one’s desires. (Indeed, lawyers and scholars from the Nonhuman Rights Project have argued that chimpanzees Leo and Hercules, due to their sophisticated mental capacities, should be accorded the status of legal persons. This would imply that they cannot be deprived of freedom. See <https://www.nonhumanrights.org/?s=hercules>.) The interest humans have in freedom stretches beyond a purely instrumental interest in wellbeing. Even if they would be perfectly happy under conditions of captivity (for example in slavery), taking away the possibility of being the author of their own lives would render captivity in itself wrong for them. But do animals not possess the required type of autonomy to give them an interest in being the author of their own lives? It could be argued that we should understand autonomy as a gradual notion, as is common, for example, in medical ethics. After all, a person in the first stages of dementia can still decide what she wants to have for dinner or what television program she wants to watch, but this person can no longer make important financial decisions. Could something similar count for animals? And would this mean that they have an intrinsic interest in liberty, albeit in a more limited sense?

It seems likely that animals have an interest in making certain decisions for themselves, such as what conspecifics to mate with, even though they may not be able to foresee the implications of larger decisions, for example, about their far

future. This would suggest that perhaps the distinction between instrumental and intrinsic interest is not as strict as Cochrane suggests. According to Gruen (2011), many animals are able to frame their own conception of the good life. She cites evidence that shows that many animals at least have concepts and she argues that many animals can devise their own plans in life. She argues that many animals pursue certain ends, shape their own lives, adapt to changing circumstances, make choices, and try to improve their environment, not only on their own but also by means of collective action (Gruen 2011, 150). The jury is still out on the question of whether this toned-down version of autonomy means that animals have an intrinsic interest in being free from captivity. Even though many examples exist of animals trying to escape captive situations (Hribal 2011), the question remains whether this should be interpreted as a simple fear- and flight response, or as an objection to captivity as such. We are inclined to think that many animals do have an intrinsic interest in liberty, but that this interest is not absolute. This entails that the interest in liberty could be trumped in certain cases, provided that the animal is treated well, for example, when the animal in question is a member of an endangered species that can only be saved when bred in captivity or when its own native habitat is no longer suitable for survival.

### Justifications Versus Objections

Even if animals can be said to have an intrinsic interest in or right to liberty, this does not have to lead to an absolute obligation on the part of humans to liberate all animals. The interest would still have to be weighed against other interests (or the right could be trumped by other rights). Therefore, we also have to take a look at possible justifications that could be given for animal captivity and weigh these against animals' instrumental and intrinsic interests in liberty. Both humans and animals themselves could have an interest in captivity in zoos. Of course, humans benefit from the entertainment zoo animals provide, but zoos can also play a role in education and

scientific research. Animals in captivity – provided they are well cared for – enjoy shelter from the elements, protection from predators, medical care, and a steady food supply. It is at least not self-evident that a life in the wild is better for animals than a life in the zoo. For example, in the wild many animals die at a young age; this in fact is part of evolution.

On the other hand, many objections have been levelled at zoos. Of course, when wild animals are not able to live in their natural habitat and carry out their species-specific behavior, when they have less space to roam around and have their social structures disrupted (by not being able to select their own mates, for example), this will lead to animal welfare problems (Jamieson 1985). How these problems weigh up against the benefits experienced from zoos is dependent on the assessment of the gravity of the harm done to the animals vis-à-vis the seriousness of the human or animal interests involved. The outcome will differ from practice to practice.

It should be noted here that while this assessment definitely has an empirical component, its outcome also very much depends on the particular concept of animal welfare that is used. Animal welfare is not just a biological term; rather it is an evaluative term that combines biological knowledge and moral norms (Bovenkerk and Meijboom 2013). In general, three views on animal welfare can be distinguished: (1) the view that animal welfare is guaranteed when animals can cope with the conditions they find themselves in; (2) the view that it is guaranteed if the animals experience subjective well-being; and (3) the view that the extent to which an animal can carry out its natural or species-specific behavior is constitutive of its (Fraser 2003). In particular the last view on animal welfare has proven difficult to meet in zoos, due to limitations of space and budget, but also due to moral considerations. After all, feeding a predator live prey, while conducive to predator welfare, will lead to pain and distress on the part of the prey (and human zoo visitors). Also, if we consider that animals have a right to reproduce, what do we do with the resulting surplus animals (Kasperbauer 2016)? These animals may have to be killed and it is this practice of

“zoathanasia” that elicits a lot of criticism. (For example by Marc Bekoff. <https://www.psychologytoday.com/blog/animal-emotions/201208/zoathanasia-is-not-euthanasia-words-matter>) Being exposed to human visitors, especially when animals do not have a place to which they can withdraw, can lead to stress. In zoos stereotypical behavior, such as pacing, self-biting, and excessive self-grooming, are found, and these point to welfare problems according to all three views on animal welfare. Stress, boredom, and social isolation are the most common causes of these behaviors. (A study has shown, for example, that gorillas in zoos that are confronted with many visitors are more likely to show stereotypic behaviour – consisting of autogrooming, abnormal behaviour (such as teeth clenching, body rocking, and more banging on the separation barrier) taking less rest, and aggression towards other gorillas – than those who are confronted with low visitor density. This indicates that visitor density leads to stress in the animals. See Wells 2005, who also cites other studies with similar conclusions.) Loss of freedom and lack of control over an animal’s life can lead to what animal welfare scientists refer to as this animal’s “learned helplessness.” (The theory of learned helplessness was first put forward by psychologist Martin Seligman 1972, who showed that dogs that have been given electric shocks become so passive that they fail to avoid further adverse stimuli, even if there is an easy possibility of escape. They are in effect conditioned to believe that harm is inescapable.)

In sum, whether human and animal interests in zoos outweigh disadvantages in a particular practice of captivity is not a straightforward assessment, but will be open to discussion about how we weigh animal interests and what we mean by animal welfare in the first place, and will of course depend on the efforts made by a particular zoo to counter welfare problems. However, objections that go beyond welfare issues can also be levelled against zoos.

First of all, it could be argued that wild animals in zoos become less wild. One could even wonder to what extent we are still dealing with wild animals, in particular when animals were born in the zoo. This judgment, of course, would depend on

one’s definition of wildness (see Palmer 2016 for a discussion of different types of wildness). If we were to regard wildness as a gradual notion and animals less wild the more they are dependent on humans and the better they are adapted to humans, it would appear that many zoo animals score high on the factor of dependence and low on the factor of adaptation (Swart and Keulartz 2011). We can discern a tension here: on the one hand the animals will experience better welfare if they score high on both factors, but on the other hand, if they are in a breeding program and they will eventually be returned to the wild, it would be best if they scored low on both factors.

But why is wildness of zoo animals important? Similar to the interest in liberty that we discussed above, it could be argued that wildness can be either an intrinsic or an instrumental value. As an instrumental value, wildness can be important to animals because it implies freedom to roam about and carry out self-willed action (Palmer 2016). As an intrinsic value it refers more to a quality about the animals that human beings attach value to and that is quite hard to grasp: It refers to having come about independent from human action, inspiring awe for evolutionary processes, and being somehow in harmony with nature. Regardless of how one interprets wildness, it is a fact that many people visit the zoo to encounter wild animals, not domesticated ones, and the objection is that zoos are presenting visitors with an illusion.

A second criticism of zoos is that they do not live up to their claim that they perform a role in educating the public. First of all, research on the educative effect of zoos is inconclusive (Marino et al. 2010). Secondly, it could be questioned what watching wild animals in enclosures teaches people about the human-animal relation and what attitude towards animals it engenders. Does it adequately convey to children that animals such as bears when encountered in the wild, are actually dangerous? Does it inspire respect for animals or show that humans are superior to the animals on the other side of the glass that have been captured and tamed by us? In particular when wild animals are made to perform in zoos, doesn’t this interfere with their wild dignity (Gruen 2011;

Brando 2016)? Finally, can the supposed educational benefits of zoos not be acquired in a different way, such as watching nature documentaries or attending lectures (Jamieson 1985)?

All of the aforementioned considerations play a role when we have to weigh the arguments in favor and against keeping animals in zoos. So far, we have mainly looked at pros and cons regarding individual animals. Next, we will look more closely at the argument that zoos play an important role in species conservation.

### Captivity for Conservation?

Today, the animal world is under growing pressure, with the result that animals suffer massive losses of freedom of movement and of control over their own lives. In fact, we are in the midst of the so-called “sixth mass extinction.” Paleontologists speak of a mass extinction when the Earth loses more than three-quarters of its species. This has happened only five times in the past 540 million years, the last time 65 million years ago when dinosaurs disappeared from this planet. Experts estimate the current extinction rate at 100–1,000 times the normal rate between mass extinctions, the so-called “background extinction rate.”

However, to fully assess the current situation, one should not only consider the extinction of species but also the decline in numbers and sizes of populations. The 11th edition of the WWF *Living Planet Report* from 2016 shows that the population sizes of vertebrate species (mammals, birds, fishes, reptiles, and amphibians) have dropped by almost 60% in little more than 40 years and are likely to reach 67% by the end of the decade. Mainly due to habitat fragmentation and habitat loss, an increasing number of wildlife populations are declining and teetering on the brink of extinction. When we consider that population extinctions are a prelude to species extinctions, it becomes clear that “the window for effective action is very short, probably two or three decades at most” (Ceballos et al. 2017, 7).

As a response to this critical situation, and in order to find a new justification for keeping

animals, zoos began to turn their attention to the conservation of endangered species and wildlife in the 1970s and 1980s. *Captivity for Conservation* became a crucial slogan for the modern zoo. A major milestone in this development was the Convention on Biodiversity which was signed at the Earth Summit in Rio de Janeiro in 1992. In the wake of the Earth Summit, the first *World Zoo Conservation Strategy* was launched in 1993. Its conclusion explicitly stated that at a time when species, habitats, and ecosystems worldwide are threatened with extinction, modern zoos must commit to the conservation of species and wildlife.

Another important milestone concerns the so-called One Plan Approach that was officially proposed to the IUCN World Conservation Congress in 2012. This approach is intended to address the problem that both captive and wild populations are often not viable on their own. Like zoo populations, wild populations increasingly suffer from the lack of sufficient space to maintain self-sustaining populations due to the ongoing reduction and fragmentation of their habitats. To tackle this problem, the One Plan Approach promotes the interactive exchange of animals between wild and captive populations. With animals moving in both directions, the stability and sustainability of wild and captive populations can be greatly enhanced. Captive populations can be used for restocking in areas with declining populations or for reintroduction in areas where populations have gone extinct. And genetic founders from wild populations can boost the demographic and genetic viability of captive populations (Byers et al. 2013).

### Towards a Bifocal View on Zoo Animals

With the One Plan Approach, the distinction between in situ (on site) and ex situ (off-site) conservation is becoming increasingly blurred. The collapse of the fences between the “wild” and the “walled” and the integration of zoo-based tools and techniques in species conservation has led to manifold conflicts between animal protectionists and wildlife conservationists



(Minteer and Collins 2013). Whereas animal protectionists reject the whole idea of “captivity for conservation,” conservationists generally perceive animal welfare and animal rights concerns as obstacles to species conservation. Both parties adhere to opposing ethical frameworks: the individualistic framework of mainstream animal ethics in which species are of little or no moral relevance, and the holistic framework of environmental ethics that tends to make the rights and welfare of individual animals subordinate to the interests of the greater whole of which they are part, such as species or ecosystems.

Animal ethicists and environmental ethicists usually not only differ with regard to the locus of moral concern – individual organisms or greater wholes – they also tend to use different species concepts (Sandler 2012, 4). Animal ethicists have generally adopted a *conventionalist* species concept; they see a species merely as a category or class with arbitrarily drawn boundary lines that may serve as a convenient mapping device for theoretical purposes only (Jamieson 1995, 61). Environmental ethicists, on the other hand, generally hold a *realistic* species concept. Holmes Rolston, for instance, argues that a species is a real historical entity, a “dynamic historical lineage” that can persist as a discrete, vital pattern over time (Rolston 1988, 151).

In order to put an end to the seemingly intractable controversies between animal protectionists and wildlife managers and to integrate their conflicting ethical frameworks, one will have to develop a bifocal view in which zoo animals are simultaneously perceived as individuals in need of specific care and as members of a species in need of protection. It can be argued that animal welfare and wildlife conservation are two sides of the same coin, “by showing that the integrity of habitats and the populations they contain are inextricably linked to the welfare of the individual animals that constitute those populations and occupy those habitats” (Paquet and Darimont 2010, 179). If animal welfare concerns are ignored, wildlife conservation policies are likely to fail, and vice versa (Fraser 2010, 123).

From a bifocal view on zoo animals as individuals and species members, zoos can pursue an

ethically defensible policy only if they succeed in achieving a fair balance between animal welfare concerns and species conservation commitments. The prospects for the zoo to achieve such a balance are promising. Since early twenty-first century, zoos have made serious and sustained efforts to ensure and enhance animal welfare. At the same time, the zoo’s contribution to species conservation has also improved considerably.

### Overcoming Welfare Problems Caused by Space Shortage

Many of the welfare problems of zoo animals are produced by spatial limitations. Due to the lack of sufficient space, an animal’s freedom of movement and its options for the expression and development of species-specific behaviors are severely restricted – the enclosures are simply too small. Furthermore, to the extent that conservation breeding programs are successful, the animal populations will almost certainly exceed the zoo’s carrying capacity. This situation creates the so-called “surplus animal problem.” Traditional methods to solve this problem include culling the surplus animals or selling them to dealers, where they often end up in substandard facilities (Carter and Kagan 2010).

To address the welfare problems caused by space limits, zoos have a number of options. They can reduce the number of species they maintain that are not threatened and specialize in species that are. “Specialization is key to every successful threatened species propagation program” (Conway 2011, 5). In addition to specialization, zoos can increase and improve regional and global cooperation. In order to be demographically and genetically viable, the size of captive populations managed in isolation generally needs to be very large. The problem of low zoo animal numbers can be addressed by collaborative management and the exchange of animals among zoos.

Another strategy to combat the problem of limited space is the shift away from large charismatic mammals – such as elephants and giraffes – towards smaller species, particularly amphibians,

invertebrates, and some species of fish, which occupy less space, are relatively inexpensive to keep, generally experience less welfare problems in captivity, have a high birth rate, and are easy to reintroduce, while maintaining their social structures. Several initiatives have already been launched on this front, not least the Amphibian Conservation Action Plan, a partnership involving the World Association of Zoos and Aquariums (WAZA) (Gewin 2008).

Yet another, recent and very promising, strategy to overcome the problem of space shortage concerns the improvement of enclosure design by creating walkways between enclosures that allow animals greater freedom of movement. Building a network of trails, in particular top tree trails, gives animals the opportunity to rotate between various interconnected display and off-display areas, such as dens, basking sites, and foraging areas. Animals may spend mornings in one area and afternoons in another (Coe 2004). An additional benefit might be the reduction of stress induced by high visitor densities.

### **Improving Animal Welfare by Environmental Enrichment**

In recent years, zoo management has undergone a real transformation to the benefit of animal welfare due to the introduction of “environmental enrichment” programs (Kleiman 2010, xi). The main goals of enrichment are to reduce stress, to enable animals to show species-specific behavior, and to increase their capacities to survive and reproduce if released into the wild.

A growing number of options for providing environmental enrichment have been developed recently: physical enrichment involves the introduction of “toys and treats” that induces play behavior and exploratory activities; occupational enrichment encourages exercise and training; feeding enrichment takes many forms, such as increasing the number of daily feeding sessions, making the feeding schedule less predictable, and making the food less easy to obtain; and sensory enrichment makes use of visual, auditory, and olfactory stimuli.

The perhaps most powerful and successful type of environmental enrichment is social enrichment, which provides animals the opportunity to interact with other animals, either conspecifics (same species) or contra-specifics (other species). Mixed-species exhibits are a good example of the latter. They provide an interactive and dynamic experience for the animals, visitors, and zoo staff. In mixed-species enclosures, activity levels are typically higher, with more play behaviors, and this generally has a positive effect on both the physical and the mental health of the animals. Moreover, interspecific interactions can contribute to successful reintroductions. Animals from mixed-species exhibits are more likely to cope with the complexity of their natural habitat after introduction. Even “negative” interspecific interactions, e.g., controlled nonlethal exposure to predators, may be beneficial in survival post-release (Veasey and Hammer 2010). In order to increase the success of breeding in captivity and reintroduction into wild habitats, pre-release training needs to be given. This will also (at least partially) help to overcome the problem, mentioned above, that zoo animals become less wild. Pre-release training is aimed at maintaining or developing the skills that may have been lost in captivity such as orientation and navigation, finding or building suitable nest sites, hunting and foraging behavior, and predator avoidance (McPhee and Carlstead 2010).

### **Broadening the Zoo’s Conservation Role**

Since the early years of this century, zoos have not only succeeded in substantially improving animal welfare, they have also made real progress regarding their contribution to species conservation. The new *World Zoo and Aquarium Conservation Strategy* of 2005 outlines a much broader conservationist role for zoos than the first *World Zoo Conservation Strategy* of 1993, including research, training, education, awareness campaigns, and direct support for in situ projects. In the latest strategy, the primary mission of zoos is to integrate all these elements with their efforts to protect endangered species and conserve healthy

ecosystems (Mace et al., 2007; Bowkett, 2008; Lees and Wilcken 2009). Insofar as captive-breeding for reintroduction is considered necessary and appropriate, it should be accomplished as part of such a larger, integrated, holistic program (Hutchins 2003, 18).

The simplest way for zoos to assist in situ conservation is through financing and fundraising. The amount spent on conservation by zoos is significant. Members of the WAZA are the third largest financial supporter of species conservation in their natural habitats (providing US\$350 million/year), after the Nature Conservancy and the World Wildlife Fund (Conde et al. 2011).

Another important way for zoos to contribute to in situ conservation is through research and training. Exporting expertise is at least as important as repatriating animals (Stanley Price and Fa 2007, 169). As natural habitats continue to be damaged and destroyed at the current pace, the tools and technologies developed by zoos are becoming increasingly relevant for in situ conservation. Research within zoos, such as behavior studies, genetics, reproduction, and nutrition, are increasingly relevant for research in the wild. Moreover, zoos can support in situ conservation by providing technical skills and by training conservation scientists (Zimmerman 2010, 282).

But the perhaps most important contribution of zoos to in situ conservation comes from education, awareness, and advocacy. It is realized by now that the 700 million people that annually visit zoos are significant conservation assets, at least as valuable as the zoos' animals. Only recently have zoo professionals begun to objectively assess their educational impact on visitor conservation knowledge, awareness, and behavior, in order to learn and improve their competence as agents of change. There still remains much to be done in order to achieve this educational impact.

To enhance the effectiveness of zoo visits to inspire conservation awareness and action, zoo professionals have shifted the focus from cognitive learning to affective learning. In addition, they have recognized that behavioral change on a measurable scale is only feasible if zoos succeed in encouraging accessible actions that people can

take to support wildlife. A good case in point is Monterey Bay Aquarium that hands out the Seafood Watch Pocket Guide to its visitors. As it turned out, this guide significantly changes the seafood-buying habits of 80% of visitors who take one home (Routman et al. 2010).

## Conclusion

In this chapter, we have argued that the distinction between intrinsic and instrumental interest in freedom for animals is not as strict as Alistair Cochrane suggests. If we conceive of autonomy as a gradual notion, it appears that animals have an intrinsic interest in liberty, albeit a more limited one than is the case for most human beings. This entails that the interest in liberty could be trumped in certain cases – provided that the animal is treated well – for example, when the animal in question is a member of an endangered species that can only be saved when bred in captivity or when its own native habitat is no longer suitable for survival.

In order to make a sound moral judgment about animal captivity, we have to take a look at possible justifications that could be given for animal captivity and weigh these against animals' instrumental and intrinsic interests in liberty. We have discussed the objection that zoos lead to animal welfare problems due to limitations of space, budget, and the inability to carry out species specific behavior. Objections beyond welfare also have to be taken into consideration: zoo animals become less wild and the educative potential of zoos can be questioned. In the end, a judgment will have to be made taking into account the specific context. Some zoos are better able to meet the stated objections than others, and there are certain criteria that zoos will have to meet to be morally acceptable: they should specialize in threatened species, focus on smaller animals, innovate their design to overcome space problems, provide enrichment, practice pre-release training, and broaden their conservation and education role.

On the basis of present trends – the development of animal enrichment programs on the one hand and the improvement of the contribution to

in situ conservation on the other – one can conclude with some confidence that the prospects for zoos to achieve an ethically acceptable balance between animal welfare concerns and species conservation commitments are indeed promising. However, the zoo community still needs to deliver on this promise. Today there are between 7,000 and 10,000 zoos worldwide, many of which will not meet the high standards of the 1,600 zoos which are members of WAZA or of its affiliated associations at national and regional levels. And even among the members of these accredited zoo associations, the implementation of high standards and good practices leaves much to be desired. The direction is clear, but there is still a long way to go.

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## Caracara Locomotion

### ► Falconiformes Locomotion

## Cardinality

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## Synonyms

[Exact number](#)

## Definition

“The number of elements in a set or group.”

## Introduction

Cardinality can be defined in multiple ways, depending on the theoretical stance that is being taken (e.g., for some theoreticians, it can involve the number of points that make up a geometric line). For the purposes of research on the development of number concepts in young children and nonhuman animals, it is generally defined as the symbolic representation of the exact number of items in a set. Thus, for English speakers, given the set “apple, apple, apple, apple, apple” and the query “How many?”, the cardinality of the set is represented by “five.” “Apple” can be replaced with anything, from a subatomic particle to a planet, to sounds or actions, and the response to “How many?” will be the same, because

cardinality is not based on mass, contour, density, or any other irrelevant attribute but only specific numerical quantity (e.g., Mix et al. 2002).

### Cardinality in Relation to Other Numerical Concepts

A simpler, implicit understanding of cardinality also can exist, as when young children respond to the equivalence of very small sets (1–3 items), but such behavior is not the same as understanding explicit cardinality (see discussion in Carey 2009). Here children are creating working-memory models of the sets and relating the sets on the basis of various associations (e.g., 1:1 matches), but do not need to use symbolic representation of number.

Use of numerical labels for cardinality is also very different from use of such labels in an analog system. The analog number system, or ANS, allows *approximations* to cardinality, proportional to the number of objects in the set – that is, based on Weber’s Law (see Dehaene 2009). Thus, if subjects lacking symbolic representation of number are asked in some manner to distinguish sets of more than about three items, their responses form a curve around the correct cardinality, with the broadness of the curve becoming proportionally fatter as the number to be determined increases (e.g., Platt and Johnston 1971). The ANS is evolutionarily ancient, and just about every animal studied is capable of its use, from bees and salamanders to fish, many species of birds and various nonhuman primates (review in Carey 2009).

### Cardinality and Counting

Cardinality is inherent in understanding “counting principles” and the “successor function.” For children to acquire counting principles (CP), they must have a symbolic ordinal numerical list, in which each symbol represents the exact cardinal value for every numeral in the list. CP, according to Gallistel and Gelman (1992), state: numerals must be applied in order to items in a set to be

enumerated, must be applied in 1–1 correspondence, and the last numeral in a count represents a set’s cardinal value. To understand cardinality, children must also understand the successor function, which means that they recognize that each number in the list represents exactly one more item than the number before it (see also Fuson 1988). No evidence exists for mental representations of exact cardinal values of sets greater than four by adult humans in cultures lacking verbal numerals or a tally system (Frank et al. 2008; Gordon 2004; Pica and Lecompte 2008), deaf adults lacking natural language input (Spaepen et al. 2011), preverbal infants (e.g., Feigenson et al. 2004), or most nonhumans (except those taught explicit symbolic representations, see below; see Pepperberg and Carey 2012).

CP acquisition is difficult and children take several years to acquire the requisite numerical skills, which allow for cardinal understanding of all numbers (see Carey 2009; Fuson 1988; reviewed in Pepperberg and Carey 2012). Two-year old English learners can produce a count list, but some use idiosyncratic orders of numerical symbols (e.g., “one, two, six. . .”; see Gelman and Gallistel 1978). They assign exact cardinal meaning only to “one”; other numerals mean “some” or “plural”. Some nine months later, they learn “two”; other numerals are “more than two”. A few months later they master “three”, and a bit later “four”; by about this point in their development (and for many children even earlier) they also produce a standard count list. Only at this stage (generally close to four years of age), however, are children able to induce the CP: They make the connection between the count list and the quantities, infer that each successive numeral in the count list is exactly one more than its predecessor, and can thus induce the cardinality of larger numbers from their ordinal position on the count list.

### Cardinality and Nonhuman Subjects

Only three nonhumans have acquired symbolic representation of number – and thus likely cardinality. Two were chimpanzees (*Pan troglodytes*),



Matsuzawa's Ai and Boysen's Sheba; the third was a Grey parrot (*Psittacus erithacus*), Pepperberg's Alex. Notably, Ai could respond correctly only up to and including the number nine; Sheba and Alex were successful only up to and including eight. All three subjects could both comprehend and produce numerical symbols within this range with equivalent facility. Production, which came first for all subjects, involved seeing a collection of items and using a verbal label (either an Arabic numeral or a numerical vocalization) to identify the quantity. Comprehension involved seeing an Arabic numeral or hearing a vocal numerical label and picking out the corresponding collection of objects. Such comprehension-production equivalence is critical for claiming that the symbols comprise a true representational system (Savage-Rumbaugh 1986) and, thus, that these subjects understood cardinality. Sheba and Ai, however, did not immediately transfer their numerical knowledge to comprehension tasks and had to be trained after succeeding on production (Boysen 1993; Biro and Matsuzawa 2001); in contrast, comprehension emerged without training for Alex (Pepperberg and Gordon 2005). Interestingly, each of these subjects took many years beyond those needed for children to reach the same stage of numerical competence (Biro and Matsuzawa 2001; Boysen 1993; Boysen and Berntson 1989; Boysen et al. 1993; Matsuzawa 1985, 2009; Matsuzawa et al. 1991; Pepperberg 1987, 1994, 2006; Pepperberg and Carey 2012; Pepperberg and Gordon 2005; Tomonaga et al. 1993).

Of note, too is that neither ape engaged in the bootstrapping process that underlies children's mastery of the counting principles and, at some level, understanding of cardinality; that is, being able to infer the cardinality of novel numbers from their ordinal position on the number line without training (e.g., Carey 2009). Only Alex succeeded at that task (for a discussion of possible reasons for his success, see Pepperberg and Carey 2012). Alex's exact representation of number was also tested in ways not tested with other nonhumans (Pepperberg and Carey 2012): Given trials including differently colored sets of nine or ten items at the same time as sets of seven and eight (e.g., a

tray consisting of many pieces of wood – seven blue, eight green, and nine orange, all randomly arranged) and asked "What color seven?" or "What color eight?", Alex never once gave the color of the 9- or 10-item set, despite the fact that these sets are approximately eight. Such responses also show that he did not simply look for the largest set to label with his largest actual cardinal numeral, or use an ANS. If given trials with differently colored sets in which the targeted set was absent (e.g., "What color six?" when no set of six existed), he did not respond with the label indicating a set close in number but responded with the label "none", demonstrating that he knew that the exact set was missing.

Cardinality is also required for performing mathematical manipulations. Both Sheba and Alex could perform addition for small sets; that is, they could combine the cardinality of two or more sets each represented by an Arabic numeral and then represent this total by the appropriate Arabic numeral (Boysen and Berntson 1989; Pepperberg 2012). In both studies, the nonhumans were asked about the sums when the addends were no longer visible; that is, they had to remember the separate addends, perform the summation, and then either touch (Sheba) or produce vocally (Alex) the symbol that represented the exact total quantity. Number symbols were thus abstract representations of real-world sets. Importantly, neither Sheba nor Alex had had specific training prior to their testing, and neither was making judgments based on relative quantity between or among sets, but rather they were exactly mapping their answers to the cardinal value of the total number represented by the Arabic numerals. Their results were not subject to issues such as Weber's Law (i.e., they did not use an ANS). Sheba could sum two sets representing combinations of the Arabic 0, 1, 2, 3, 4 to a total of four at a statistically significant level. Alex could sum two sets representing various combinations of the Arabic 1, 2, 3, 4, 5 and sometimes an empty cup (zero) to a total of eight, and three sets of various combinations of the Arabic 1, 2, 3 and sometimes one or two empty cups to a total of six at a statistically significant level. He died before all possible combinations could be presented.

Thus, acquiring some level of understanding of cardinality does not seem to be a uniquely human trait. It does, however, appear to be one that requires considerable processing power and instruction, more so for nonhumans than for humans.

## Cross-References

- [Absolute Number Discrimination](#)
- [Addition](#)
- [Approximate Number System \(ANS\)](#)
- [Arabic Numerals](#)
- [Counting](#)
- [Irene M. Pepperberg, PhD](#)
- [Numerosity](#)
- [Ordinality](#)

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## Cardiovascular System

### ► [Circulatory System](#)

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## Care Staff

### ► [Caretaker Effect](#)

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## Caregiver

### ► [Caretaker Effect](#)

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## Caretaker Effect

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## Synonyms

[Caregiver](#); [Care staff](#)

Caretaker effect refers to any direct (e.g., feeding) and/or indirect (e.g., noise levels that result from husbandry activities) influence that staff exert upon the animals under their care. Caretakers are involved in most aspects of the lives of the animals for which they are responsible and therefore play a significant role in determining their quality of lives and psychological welfare levels. Wild animals that live in their natural habitats constantly engage in decision-making and employ various responses to the many challenges that they meet daily. This ability ensures their survival and is an inherent part of their adaptableness. However, the ability of animals that are housed in captive settings such as biomedical facilities, agricultural farms, and zoos to demonstrate such flexibility is often restrained. Thus, for example,

the ability to react to the motivation to flee in a response to a threatening stimulus, or to emigrate from the natal group upon reaching puberty in order to search for unfamiliar mates in other groups is greatly curtailed due to decisions made by humans (In this case, confine the animals in cages). Decreased ability to control the environment and to successfully cope with its challenges by producing appropriate reactions has been suggested to be detrimental to the welfare of the animals (Dawkins 1990; Hill and Broom 2009). Furthermore, humans, particularly caretakers, are in charge of many decisions that animals would otherwise make on their own. For instance, caretakers are responsible for feeding the animals with certain foodstuffs at particular times and in a specific fashion (e.g., chopped vs. whole), and are intimately involved in the determination of the animals' social environment (e.g., which animals will be housed in the same room). Additional factors such as the temperature and humidity, veterinary care, and in some cases even the end of life are all in the hands of the humans who interact with the animals every day, namely the animals' care takers. Clearly, the caretaker effect on the lives of the animals is quite dramatic. While many of the caretaker activities are required for the proper functioning of the facility and are mandated by regulatory guidelines, the manner in which they are executed is to a large extent in their hands. Caretaker-animal relationships are developed during continuous close-up interactions, and many studies have demonstrated that different approaches for care yield different types of relationships and ultimately different results. Among farm animals, for instance, negative interactions which involve rough handling induce high levels of fear (Brajon et al. 2015). Similarly, laboratory-housed nonhuman primates are more fearful and aggressive toward caretakers with whom they have had prior negative experiences. Conversely, while some routine husbandry procedures may be perceived as threatening, laboratory-housed animals who maintained positive relationships with their caretakers are less likely to be disturbed by these activities (Waitt et al. 2002). In some cases, caretakers may even

play a surrogate social role and thus enable animals to express species typical behaviors, which otherwise would be prohibited and/or expressed inappropriately. A more structured form of positive interactions is the use of positive reinforcement training, in which the trainer (who is often the caretaker) gradually shapes a desired behavior of the animal with the use of rewards. The use of this technique not only creates a platform for the expression of positive behaviors towards the animals, but also offers the animals with means to predict events in their environment and better control it (Claxton 2011). Generally, positive interactions with caretakers have been shown to contribute to the wellbeing of captive animals as evident in both behavioral (e.g., more affiliative and less stress-related behaviors) and physiological measures (e.g., higher levels of oxytocin, weight gain, and lower blood pressure). Caretakers are likely to benefit from establishing such positive relationship as well. Indeed, routinely engaging in positive interactions with animals facilitates their management, by, for example, gaining the animals' cooperation when shifting them between enclosures, and having the ability to provide some medical care without the necessity of restraint (Laule et al. 2003). Positive caretaker effects are additionally linked to increased productivity among farm animals. The recognition of the significant constructive effects that positive caretaker-animal interactions are likely to yield on the animals is additionally reflected in formal regulatory documents such as the United States Department of Agriculture Animal Welfare Act and Animal Welfare Regulations.

## Cross-References

- [Adaptedness of Behavior](#)
- [Affiliative Behaviors](#)
- [Aggression](#)
- [Animal Welfare](#)
- [Avoidance](#)
- [Captivity](#)
- [Coping Style](#)
- [Dominance](#)
- [Escape Response](#)

- [Ethics](#)
- [Evolution](#)
- [Fear Response](#)
- [Human-Animal Interaction](#)
- [Husbandry](#)
- [Motivation](#)
- [Observational Methods](#)
- [Operant Conditioning](#)
- [Oxytocin](#)
- [Positive Reinforcement](#)
- [Primate Research Centers](#)
- [Species-Specific Behavior](#)
- [Zoo](#)

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## Caring

- [Brooding](#)

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## Carl Woese

- [Woese's Three Domains of Cellular Life](#)

## Carnivora

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## Synonyms

[The mammalian carnivore order](#)

## Definition

Carnivora is a mammalian order that includes bears, cats, dogs, seals, skunks, and weasels, among other species.

## Introduction

The mammalian order Carnivora encompasses 15 families and 286 species (Fig. 1) including humankind's longest domesticated companions, cats and dogs. It includes both terrestrial carnivores (fissipeds) and aquatic carnivores (pinnipeds). Although there is ongoing debate regarding its taxonomy, molecular and morphological evidence supports organizing Carnivora into two suborders: (1) Feliformia that includes the families Eupleridae (Malagasy carnivores), Felidae (cats), Herpestidae (mongooses), Hyaenidae (aardwolf and hyenas), Nandiniidae (African palm civet), and Viverridae (civets, genets, linsangs, and relatives) and (2) Caniformia that includes the families Ailuridae (red panda), Canidae (dogs, foxes, wolves, and relatives), Mephitidae (skunks and stink badgers), Mustelidae (badgers, otters, weasels, and relatives), Odobenidae (walruses), Otariidae (eared seals and sea lions), Phocidae (earless seals), Procyonidae (raccoons and relatives), and Ursidae (bears) (Wilson and Reeder 2005). Within Caniformia, the superfamily Musteloidea consists of Ailuridae, Mephitidae, Mustelidae, and Procyonidae. Terrestrial species of Carnivora occur naturally across the world except in Antarctica,

Australia, New Guinea, New Zealand, and many oceanic islands. The dingo (*Canis lupus*) was likely introduced by humans to Australia during prehistoric times and has since established wild populations. The aquatic pinnipeds (families Odobenidae, Otariidae, and Phocidae) tend to be restricted to colder waters in the northern and southern hemispheres, although some species inhabit warmer waters. The wide variation in body size, life history traits, and behavior across Carnivora make this order particularly suitable for comparative studies.

## Morphology

A distinctive characteristic in most species of Carnivora (hereafter referred to as carnivores) are teeth adapted to cutting and shearing meat. All species except sea otters (*Enhydra lutris*; 3/2), sloth bears (*Melursus ursinus*; 2/3), and pinnipeds have small incisors numbered 3/3. The canines are large, recurved, and pointed. Often a specialized pair of shearing teeth known as the carnassials are present, which consist of the last upper premolar and first lower molar (Fig. 2). Carnassials are less developed or greatly modified in ursids, procyonids, and pinnipeds. The other teeth behind the carnassials vary in number among carnivore families. The jaw joint has a transverse hinge which allows for up and down movement associated with biting and cutting meat but prohibits side to side grinding movement. Other adaptations to carnivory include forward pointing eyes, a large brain, acute sense of smell, flexible vertebral column, and in some species a long tail. Anal and forehead scent glands are present and used in social communication. Anal glands are modified in mephitids and other species to excrete noxious chemicals when threatened. The digestive system is adapted for carnivory and consists of a simple stomach with a short or absent caecum.

Usually five, but occasionally four, clawed digits are present on each foot. Claws are blunt in species such as ursids and canids but sharp and retractable in certain groups including the felids and African palm civet (*Nandinia binotata*).





**Carnivora, Fig. 1** Representative members of the order Carnivora: **(a)** least weasel (*Mustela nivalis*). (Photo by Keven Law, used by permission under Wikimedia Commons, License: Cc-by-sa-2.0). **(b)** Pallas's cat (*Felis manul*). (Photo by Sander van der Wel, used by permission under Wikimedia Commons, License: Cc-by-sa-2.0). **(c)** Giant panda (*Ailuropoda melanoleuca*). (Photo by J. Patrick Fischer, used by permission under Wikimedia Commons, License: Cc-by-sa-3.0). **(d)** Northern elephant

seal (*Mirounga angustirostris*) male, female, and pup. (Photo by Michael L. Baird, used by permission under Wikimedia Commons, License: Cc-by-2.0). **(e)** African wild dog (*Lycaon pictus*). (Photo by Charles J. Sharp, used by permission under Wikimedia Commons, License: Cc-by-sa-4.0). **(f)** Banded palm civet (*Hemigalus derbyanus*). (Photo by Charles J. Sharp, used by permission under Wikimedia Commons, License: Cc-by-sa-4.0)





**Carnivora, Fig. 2** Carnassials of a dog. (Photo by Kreuzschnabel, used by permission under Wikimedia Commons, License: Cc-by-sa-3.0)

Species such as canids and felids are digitigrade and walk on their toes, while others including ursids and procyonids are plantigrade and walk on the soles of their feet. Carnivores are typically fast runners even among the stockier ursids. In particular, some species are highly adapted for cursorial locomotion, such as the cheetah (*Acinonyx jubatus*) which can obtain speeds of  $29 \text{ ms}^{-1}$  (Sharp 1997). Most carnivores are terrestrial, ranging from semi-fossorial to arboreal. The binturong (*Arctictis binturong*) and kinkajou (*Potos flavus*) have prehensile tails that aid in climbing. Several fissiped species are semiaquatic such as river otters and the polar bear (*Ursus maritimus*) or fully aquatic like the sea otter. Pinnipeds are highly adapted for aquatic life with streamlined bodies, insulative blubber, small or absent external ears, and limbs modified as flippers. The families Odobenidae and Phocidae primarily use their front limbs for propulsion through the water, whereas members of the family Otariidae mostly use their hind limbs for propulsion. Carnivores range across several orders of magnitude in body size from the least weasel (*Mustela nivalis*; 35–70 g) to the male southern elephant seal (*Mirounga leonina*; 5,000 kg). Many species exhibit sexual dimorphism with males tending to be larger than females (Lindenfors et al. 2007). Males of most species also have a baculum except notably those of the family Hyaenidae (Nowak 1999).

## Ecology

While the name Carnivora implies this order is strictly meat eating, many species are omnivores and consume substantial amounts of plant material such as the black bear (*Ursus americanus*). Species often specialize or are opportunistic in obtaining prey from a variety of sources or methods including hunting of terrestrial or aquatic prey and scavenging carcasses. A small number are primarily herbivores or frugivores such as the giant panda (*Ailuropoda melanoleuca*) and kinkajou. Carnivores occupy almost all terrestrial and aquatic habitats across their worldwide distribution including forests, grasslands, deserts, tundra, open ice, freshwater lakes and streams, coastal waters, and the open ocean. Space use ranges from nomadic to territorial either by solitary individuals or by a group such as in lions (*Panthera leo*). Population density is highly variable among carnivores, but large-bodied species usually occur at lower density than small-bodied species (Carbone and Gittleman 2002). Juvenile dispersal is typically male-biased, and females exhibit natal philopatry in many species (Clutton-Brock and Lukas 2012). Home range size increases with metabolic needs as determined by body mass and social group size. In addition, carnivores with a greater proportion of meat in their diet have larger home ranges (Gittleman and Harvey 1982). Longevity in the wild ranges from 1 year in smaller mustelids to over 40 years in some pinnipeds.

Carnivores serve a variety of important ecological roles through predation, disease transmission, and plant dispersal (Ripple et al. 2014; Roemer et al. 2009). Apex predators impact ecosystems through trophic cascades, directly reducing prey abundance or altering their behavior, which in turn alters plant communities and their associated species. Large-bodied carnivores can be keystone species in ecosystems, increasing the overall species diversity through trophic cascades. For example, wolves (*Canis lupus*) change the abundance and behavior of large herbivores, leading to increases in woody riparian plants and associated animal species such as beaver (*Castor canadensis*) and migratory songbirds (Ripple

and Beschta 2012). Smaller carnivores can serve as important seed dispersers as a greater proportion of their diet often derives from plant material than larger carnivores. In Spain, foxes and mustelids feed on the fleshy fruit of *Prunus mahaleb* and typically disperse seeds greater distances than birds (Jordano et al. 2007). Diseases such as parvovirus, canine distemper, and rabies are reported in almost all terrestrial carnivore families. Smaller carnivores that occur at greater densities often serve as disease reservoirs that facilitate transmission to humans or domestic animals (Deem et al. 2000; Krebs et al. 2003; Steinell et al. 2001).

## Behavior

Studies of domestic and wild carnivores have revealed sophisticated levels of cognition such as forming natural categories, discriminating quantities, recognizing cues of human emotion, and discriminating kin (Vonk and Leete 2017). Badgers and sea otters are known to use rudimentary tools. Many behaviors are driven by their carnivorous life history. Brain size relative to body size is largest in species that hunt vertebrates, intermediate in herbivores, and smallest in insectivores. The relative cerebrum size tends to be larger in more socially complex species (Holekamp et al. 2015).

Most carnivore species are solitary or form pairings for mating, but a few species are gregarious. Social carnivores (hyenas, wolves, etc.) form extensive social hierarchies where position is influenced by factors such as sex, age, and kinship. Social position can determine access to resources and breeding opportunities (Creel 2005). Mating systems range from serial monogamy to extreme polygyny such as in the southern elephant seal where males defend and breed with large harems of females (Fabiani et al. 2004). Once reaching sexual maturity, females typically give birth once a year, but a small number of species may give birth to multiple litters per year such as weasels or go several years between births such as walrus (*Odobenus rosmarus*, 5–6 years between births). Gestation ranges from 49

to 113 days; however, delayed implantation in ursids, pinnipeds, and some mustelids greatly lengthens time between mating and birth. Litter size ranges from 1 to 13 young. At birth, carnivore young range from altricial as in bears where cubs are born blind and completely dependent on the mother to precocial as in some seal species where pups can swim within a few minutes of birth. The mother nurses and cares for the young, but the father also provides parental care in some species. Some canid and mongoose species practice cooperative breeding which can take the form of allo-nursing, feeding of prey, and other parental care duties (Lukas et al. 2012). Young may remain with the parents for extended periods after weaning to learn how to hunt prey.

Species range from nocturnal to diurnal in activity. Hunting behavior varies depending on habitat and targeted prey but often involves stealth and sprinting to subdue prey. Some species such as the cougar (*Puma concolor*) lie in wait and ambush passing prey, whereas wolves and lions actively pursue prey over longer distances. Social species may employ group hunting tactics allowing them to restrain and kill larger prey (Bailey et al. 2013). Some ursids and the European badger (*Meles meles*) engage in shallow torpor during winter by reducing their body temperature  $\sim 5^\circ\text{C}$ , whereas striped skunks (*Mephitis mephitis*) engage in daily torpor during cold periods (Geiser 2010). Pinnipeds are adapted to foraging at depth underwater for extended periods without supplemental air. The most extreme diving behavior is observed in Weddell seals (*Leptonychotes weddellii*) which can remain under water over an hour and reach depths of 600 m (Schusterman 1981).

Carnivores use visual, acoustic, and odor signals to communicate. In particular, their well-developed olfactory system allows for a variety of signals (reproductive condition, identity, and territory) to be communicated via gland secretions, urine, and feces (Gorman and Trowbridge 1989). Acoustic signals primarily from vocalizations are used in many species to immediately communicate at close (e.g., alarm calling or growling) or long distances between groups or individuals (e.g., howling in wolves) (Peters and Wozencraft

1989). Pinnipeds rely heavily on vocalizations produced above and below the water to communicate information and identity among individuals (Schusterman and Van Parijs 2003).

## Conservation

According to the International Union of Conservation of Nature (IUCN) of the 285 Carnivora species assessed, 5 were extinct, 8 were critically endangered, 24 were endangered, 39 were vulnerable, 27 were near threatened, 163 were of least concern, and 19 were data deficient. Overall 26.7% of Carnivora species were threatened or extinct (IUCN et al. 2008). Major threats include habitat loss and degradation, human persecution, overexploitation, and depletion of prey (Cardillo et al. 2004; Crooks et al. 2011).

## Carnivora Families

A brief overview of each Carnivora family is provided below based on reviews in Hunter (2011), Nowak (1999), and Vaughan et al. (2015). Taxonomy is based on Wilson and Reeder (2005).

### Suborder Feliformia

Eupleridae: This Malagasy carnivore family includes eight species in seven genera that are only found in Madagascar. Three of the species are civet-like and the other five mongoose-like in appearance. They feed on invertebrates and small vertebrates. They range from 500 g to 12 kg in body mass. The nocturnal fossa (*Cryptoprocta ferox*) is the largest member of the family and is cat-like with retractable claws. It is arboreal and eats vertebrates including small lemurs.

Felidae: The cat family consists of 40 species in 14 genera that are distributed worldwide except the Arctic, Australia, Antarctica, Madagascar, and most oceanic islands. Cats are highly specialized for predation with well-developed carnassials, retractable claws (except in cheetahs), strong forelimbs, and concealing color patterns. They are typically good swimmers and agile climbers

with well-developed sensory systems. They have a tapetum lucidum within the eye that creates superior night vision. They eat a variety of prey including fish, mollusks, and small and large vertebrates. Body mass varies among species from 1 to 325 kg. Many species are solitary, but some form pairs or groups.

Herpestidae: The mongoose family includes 14 genera and 33 species. They occur in southern Asia, southeastern Europe, and Africa and are typically the most common carnivores across their range. They are long-tailed and long-bodied ranging from 270 g to 5 kg. They have small, elongated heads with pointed snouts and short ears. Herpestids are primarily insectivorous and found in forests to open deserts. Most species are terrestrial, but a few are semiaquatic. Some species such as meerkats (*Suricata suricatta*) live in groups with complex social systems.

Hyaenidae: Members of this family include the aardwolf (*Proteles cristata*) and three hyena species in three genera. They are restricted to grassland, bush country, and open forests in Africa, Turkey, the Middle East, and India. They are the most specialized carnivore family for carrion feeding. The hyena species (25–86 kg) are heavily built with strong jaws, well-developed carnassials for crushing bones, and forelimbs longer than hind limbs. While the other 2 hyena species live solitary or in small groups, spotted hyenas (*Crocuta crocuta*) live in groups of up to 80 individuals and have complex social behaviors. Aardwolves (9–14 kg) are more delicately built and secrete a noxious fluid from anal glands when threatened. They primarily feed on termites and other invertebrates.

Nandiniidae: The only species in this family, the African palm civet, occurs across sub-Saharan Africa as far south as Angola and Zimbabwe. African palm civets are arboreal and omnivorous, feeding primarily on fruit. They weigh from 2 to 5 kg. They are nocturnal and live solitarily.

Viverridae: The viverrid family includes 35 species of civets, genets, linsangs, and relatives in 15 genera. They occur in southern Europe, southern Asia, and Africa. They have long tails and short legs and range in body mass from 600 g to 20 kg. Viverrids are agile climbers, and some

species have retractable claws. The binturong is the only member of this family that has a prehensile tail. Viverrids are primarily carnivorous and feed on small vertebrates and invertebrates. Several species are semiaquatic and feed on fish and amphibians. Most viverrids are nocturnal and live solitarily.

### Suborder Caniformia

**Ailuridae:** The sole member of this family is the red panda (*Ailurus fulgens*). This arboreal species (3–6 kg) is found in isolated forests of northern Burma and South Central China. They have an enlarged radial sesamoid bone (false thumb) that assists in grabbing branches and handling food. They are primarily herbivores that feed on leaves and other plant material. Red pandas are not closely related to the giant panda but eat bamboo leaves in a similar manner.

**Canidae:** The canid family consists of 13 genera and 35 species of dogs, foxes, jackals, wolves, and relatives. They occupy a diverse range of habitats from arctic to tropical on all continents except Australia, Antarctica, Madagascar, and most oceanic islands. Most are omnivorous, but a minority are mainly carnivorous and a few insectivorous. Body size ranges from 2 to 80 kg. Canids typically have a long rostrum that is associated with an exceptional sense of smell. They usually have well-developed carnassials and postcarnassial teeth that have crushing surfaces reflecting an omnivorous diet. Several species live in social groups, but only wolves hunt cooperatively.

**Mephitidae:** The mephitid family includes ten skunk and two stink badger species in four genera. Skunks are native to North and South America, whereas the stink badgers are endemic to Indonesia, Malaysia, and the Philippines. Mephitids feed on a variety of animal material including small vertebrates, invertebrates, and carrion. They are small bodied (0.5–4 kg), nocturnal, and have conspicuous white and black markings that warn predators. When threatened they spray a noxious fluid from anal glands that causes irritation. They are solitary in nature.

**Mustelidae:** The mustelid family consists of 59 species of badgers, otters, weasels, and

relatives in 22 genera. They inhabit all land masses except Australia, Antarctica, Madagascar, and most oceanic islands. Mustelids are small to medium sized (25 g to 45 kg) with a long body and short limbs. The skull has a long braincase with a short rostrum. They are primarily carnivorous and occupy a variety of habitats including forests, grasslands, deserts, and tundra. Many mustelids are agile hunters that aggressively chase prey above and below ground. River otters are semiaquatic, and the sea otter is almost fully aquatic.

**Odobenidae:** The walrus family has only one living species, *Odobenus rosmarus*. They inhabit arctic waters of the Atlantic and Pacific Oceans. Walruses have a thick, nearly hairless body (400–1,700 kg) and rounded head with thick skin and an insulative blubber layer. The upper canines are modified into elongated tusks that grow throughout life and are used for fighting. They have a highly sensitive mustache of thick bristles that is used to search for mollusks on the seafloor. Walruses are polygynous and can congregate in large groups of more than 1,000 individuals.

**Otariidae:** The otariid family contains 7 genera and 16 species of eared seals and sea lions. They are found along the coasts of the Pacific Ocean and areas of the South Atlantic and Indian Oceans. The otariids are less modified for aquatic life than phocids and can use their hind flippers for terrestrial locomotion. Body mass ranges from 60 to 1,000 kg with significant sexual dimorphism in some species. They have small external ears and oar-like flippers with small claws. They are strictly carnivorous feeding on fish and squid. Otariids are typically gregarious, forming large breeding colonies of thousands of individuals.

**Phocidae:** The phocid family consists of 19 earless seal species in 13 genera. They occur in polar and temperate oceans along coastlines and ice fronts. Some species live in tropical waters or inland bodies of water. They are highly specialized for aquatic life with streamlined bodies (65–5,000 kg), insulative blubber, and no external ears. Most phocids feed on fish, cephalopods, and mollusks. Two species including the crabeater seal (*Lobodon carcinophagus*) filter feed on crustaceans and plankton through specialized cheek

teeth. Some species are monogamous, whereas others are polygynous such as elephant seals that form large breeding harems and exhibit extreme sexual dimorphism.

**Procyonidae:** The procyonid family includes 14 species of raccoon, ringtails, and relatives in 6 genera. They occur in North and South America primarily in forested temperate and tropical environments. Body mass ranges from 1 to 20 kg. They have reduced carnassials with poor shearing abilities. Procyonids are predominately omnivores that feed on seeds, fruit, invertebrates, and small vertebrates. In the tropics, they are primarily arboreal, such as the kinkajou that has a prehensile tail. Many species are nocturnal; however, coatis which live in groups are often diurnal.

**Ursidae:** The bear family consists of five genera and eight species. They are historically found throughout North America and Eurasia and the Malay Peninsula, the Atlas Mountains of North Africa, and the Andes of South America. Ursids occupy many habitats from arctic ice floes to tropical forests feeding on plants, invertebrates, vertebrates, and carrion. They are primarily omnivores except for the carnivorous polar bear and the giant panda that feeds mostly on bamboo. The ursids are powerfully built (27–780 kg) with muscular limbs, recurved claws, and a large skull with poorly developed carnassials. In colder areas, some bear species gain substantial amounts of fat and enter shallow torpor during the winter.

## Cross-References

- ▶ [Bear Cognition](#)
- ▶ [Bear Communication](#)
- ▶ [Bear Diet](#)
- ▶ [Bear Life History](#)
- ▶ [Bear Locomotion](#)
- ▶ [Bear Morphology](#)
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- ▶ [Canine Navigation](#)
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- ▶ [Pinniped Cognition](#)
- ▶ [Pinniped Communication](#)
- ▶ [Pinniped Life History](#)
- ▶ [Pinniped Morphology and Locomotion](#)

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## Carnivore (Diet)

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## Synonyms

[Flesh-eater](#); [Meat-eater](#); [Predator](#)

## Definition

Carnivore (diet) refers to any species that ingests animal tissues, either wholly or in part.

## Introduction

A **carnivore** is defined as an organism that consumes animal tissue. With specific reference to the carnivore diet, the term relates to foodstuffs ingested, digested, absorbed, and utilized by an organism and identifies that ingested foodstuff consists wholly, or in part, as tissues derived from other animal species.

The dietary niche inhabited by a given species is an important aspect of ecological classification.



What nutrients an animal requires and how an animal acquires those nutrients constitute the dietary niche of a given species. Carnivory is viewed as one of the three major dietary classifications, the other two being omnivory and herbivory. The term carnivore is derived from the Latin *carn*, meaning “flesh,” and *vor*, “to devour,” and essentially means “flesh eating.” Consequently, carnivorous organisms obtain their dietary nutrient and energy requirements from animal tissues, either exclusively or in part. Those animal tissues can be insect (insectivore), invertebrate (invertivore), avian, lizard, amphibian, fish (piscivore), or mammalian in origin. Hematophagy (the consumption of blood) can also be viewed as a form of carnivory. Carnivory is viewed as forming the third trophic level, and carnivores are typically regarded as secondary consumers, although carnivores that prey and feed on other carnivorous species are typically classed as tertiary consumers and apex predators.

### Evolution of the Carnivore Dietary Strategy

For one species to consume the tissues of another, specific adaptations are required to acquire, consume, and effectively digest the tissues of the ingested species. The consumption of animal tissues represents an effective form of both energy and nutrient acquisition. Indeed, carnivory has appeared across different taxonomic orders, in several mammalian clades (Van Valkenburgh 1999), and at multiple times during evolutionary history. The repeated appearance of carnivory as a dietary strategy demonstrates its success as a nutritional niche, with the consumption of animal tissues representing a nutrient-rich food source in terms of protein, fat, vitamins, minerals, and other key nutrients. Carnivory can also be viewed as an effective dietary strategy that did not necessitate the evolution of the highly specialized additional physical, physiological, and microbial adaptations typically needed to digest vegetation, as observed in the ruminants and hindgut fermenters (Stevens and Hume 1995).

However, the carnivore dietary strategy has been dependent upon the development of key evolutionary adaptations for successful predation, scavenging, ingestion, and processing of food-stuffs. Consequently, a range of physical, physiological, metabolic, and behavioral characteristics are observed across those species with a carnivorous diet. Indeed, the characteristic dentition of members of the mammalian order Carnivora, that includes enlarged canines and a carnassial apparatus, is also evident in the fossil record of the family Miacidae, the earliest members of this order that appeared over 40 Ma (Wang and Telford 1994). Indeed, evidence suggests that there is striking similarity in dental adaptations for carnivory in different groups of flesh-eating species, both extinct and extant (De Muizon and Lange-Badre 2007). There is now a wide variety of adaptations supportive of carnivory that can be identified in extant species, and the consumption of animal tissues remains widespread in nature.

### Classification of Carnivores

Carnivorous organisms can be broadly classified based on the approximate percentage of animal-derived tissue in their diet. Contrary to popular belief, not all carnivores have a diet that exclusively consists of tissue derived from other animal species. Carnivorous species with greater than 70% of their diet consisting of animal tissue are defined as hypercarnivores; those with between 30% and 70%, mesocarnivores; and species with a dietary composition of less than 30% animal tissue, hypocarnivores (Van Valkenburgh 2007). It is also worthy to note that the term mesocarnivore is sometimes used to refer to carnivorous species that are of a medium morphological size, such as foxes and other canid species, for classification purposes.

### Carnivorous Organisms

The term carnivore is often used to refer to the mammalian order Carnivora, which includes the terrestrial flesh-eating mammals (suborder

Fissipedia), such as canids and felids, and the aquatic mammals that feed on fish (suborder Pinnipedia), such as seals and walruses. However, a carnivore diet is not exclusive to this order, and equally, not all members of Carnivora are obligate hypercarnivores (i.e., they absolutely require animal tissues in their diet), and some demonstrate substantial adaptations for other dietary niches. The giant panda (*Ailuropoda melanoleuca*) is one such species, a specialist bamboo feeder that retains the innate characteristics of a carnivore digestion system but has evolved other characteristics associated with the digestion of cellulose, including a symbiotic microbiome population, capable of cellulose metabolism (Zhu et al. 2011).

There are also many species with a carnivorous dietary strategy that are not members of the order Carnivora, including birds, insects, lizards, amphibians, fungi, fish, and even some plants. Carnivorous plant species trap and digest insects and small animals as a source of nutrients and energy. These plant species demonstrate high levels of physiological and morphological similarity as adaptations in support of carnivory (Ellison and Gotelli 2009). Genomic analysis also reveals molecular similarities in carnivorous plant species, suggesting convergent evolution and limited evolutionary pathways toward plant carnivory (Fukushima et al. 2017).

Similarly, the class Insecta contains approximately 14,000 species known to feed on blood (Adams 1999). These organisms are highly adapted for blood feeding and are responsible for significant levels of morbidity and mortality in human and animal populations because of disease transmission, annoyance, and reduced productivity (Lehane 2005). Consequently, while carnivory is often associated with mammalian members of the order Carnivora, it is a dietary strategy not exclusive to that order, and the consumption of animal tissues can be observed in a much wider taxonomic range of species.

Indeed, evidence suggests that “opportunistic carnivory” is sometimes observed in species otherwise considered to be entirely herbivorous in their dietary strategy, without deleterious consequences. Domestic rabbits have been observed to consume animal carcasses suggesting both

opportunity and behavioral adaptations (Clauss et al. 2015). Similarly, snowshoe hare (*Lepus americanus*) have been observed to scavenge from carcasses of lynx and other hare, possibly as a strategy to deal with dietary inadequacy, especially in winter months (Peers et al. 2018). Deer have also been noted to consume tissues and indulge in osteophagia (consumption/chewing of bone) from carcasses in an opportunistic manner (Meckel et al. 2017). Evidence of species not traditionally viewed as carnivorous, consuming animal tissues in this way, demonstrates the diversity of species in which a carnivore diet (either whole or in part) can be observed.

### Obligate Carnivores and Facultative Carnivores

Clearly, the proportion of animal tissue in the diet of carnivores varies. Obligate carnivores are those species that depend entirely upon animal tissue for the supply of their nutrient requirements, whereas facultative carnivores will also consume and obtain nourishment from non-animal-derived material. The definition of facultative carnivore or omnivore remains obscure, with the amount of animal-derived dietary material versus plant-derived material not being fully defined. However, facultative carnivores typically demonstrate physical adaptations in support of carnivory, such as a relatively short, simple gastrointestinal tract, elongated canine teeth, and a carnassial apparatus that might not be observed in a more omnivorous species such as swine (*Sus scrofa*). Obligate carnivores (e.g., felids and mustelids) typically demonstrate specific metabolic and biochemical specializations that further limit their ability to survive without animal-derived material in their diet (Legrand-Defretin 1994). This has ramifications in considering ecological niche survival and in the formulation of diets for captive and companion animals, where obligate carnivores have very specific nutritional requirements that need to be fulfilled in prepared dietary provision.

Conversely, while facultative carnivore species typically retain physical and physiological characteristics of carnivory (dentition, simple digestive

system, scavenging/hunting behavior), some species also demonstrate genetic signatures that are indicative of an evolutionary adaption to other sources of nutrition. This supports a nutritional ecological niche that includes the consumption of a range of foodstuffs and an ability to derive appropriate nourishment from them. The domestic dog (*Canis lupus familiaris*), for example, has a molecular signature supporting adaption to the presence of carbohydrate, specifically starch, in their diet (Axelsson et al. 2013). These findings support the development of specific dietary adaptations in otherwise carnivorous species, based on their ecological niche and parallel evolution with other species, including humans (Perry et al. 2007).

## Nutritional Requirements of the Carnivore

The obligate carnivore absolutely requires animal tissue as a source of key nutrients in their diet. Correspondingly, these species (felids are particularly well documented and studied) demonstrate a biochemistry and metabolism with limited intrinsic biosynthesis of specific compounds. These species are metabolically adapted for higher levels of protein metabolism and a limited ability to metabolize dietary carbohydrates (Zoran 2002). Their requirement for maintenance of glucose levels in the body is predominantly met via gluconeogenesis from protein precursors, rather than via the provision of dietary carbohydrates. This contrasts with many facultative carnivores that appear to have evolved metabolic strategies and pathways that permit the biosynthesis of many key compounds from alternative precursors, meaning that a dietary source of animal-derived nutrients is not always essential for survival.

For example, felids are well described as lacking the ability to synthesize adequate levels of both arachidonic acid and vitamin A (MacDonald et al. 1984). Consequently, an adequate dietary supply of these substances must be provided. A diet based on animal-derived tissues typically fulfils these nutritional requirements. Similarly, the amino acid taurine is also essential in feline diets and fox diets. Taurine is critical for several normal bodily

functions, and deficiency symptoms typically manifest as feline central retinal degeneration (FRCD), reproductive issues, impaired fetal development, and heart issues, notably dilated cardiomyopathy (DCM). Taurine biosynthesis is extremely limited in obligate carnivores, in contrast to most herbivores and omnivores (Chesney 1985), supporting their dietary need for taurine. This is a consequence of the feline liver having a limited enzymatic ability to convert the precursor amino acids methionine and cysteine to taurine, combined with an obligate loss of taurine via the feces and intestinal microbe degradation (Morris and Rogers 1992). Mammalian tissue is rich in taurine, especially the brain, heart, and skeletal muscle, meaning that obligate carnivores will typically obtain enough dietary levels, providing there is adequate consumption of animal-derived tissue.

However, taurine appears to be dispensable in the diets of facultative carnivores such as the domestic dog that ingest adequate amounts of sulfur-containing amino acids to support taurine biosynthesis (Kramer et al. 1995; Delaney et al. 2001). Conversely, diets low in protein (Sanderson et al. 2001) or low in bioavailable precursor amino acids (Backus et al. 2003) can result in taurine deficiency and the appearance of clinical signs such as DCM.

Similarly, the maned wolf (*Chrysocyon brachyurus*) is a largely frugivorous canid of South America and in captivity is typically fed a higher proportion of animal tissue than would naturally be encountered. However, problems with cystinuria in captive individuals and the feeding of formulated diets to reduce this risk resulted in severe reductions in plasma taurine concentrations (Childs-Sanford and Angel 2006). Taurine supplementation to such diets for the captive maned wolf is now indicated. More recent reports of cases of DCM in domestic dogs with a correlative link to taurine metabolism, apparently linked to the formulation of specific commercial diets (Freeman et al. 2018), have raised further discussion about the dietary need for taurine in facultative carnivores, although it is likely that a range of biological variables including physiological, metabolic, genetic, and dietary factors are involved, and further investigation is required.

## Characteristics of the Carnivore for Diet Acquisition and Processing

Organisms with a carnivore dietary strategy demonstrate specific adaptations to enhance their ability to obtain dietary animal tissue and nourishment from it. These adaptations are characteristic of many carnivorous species and are useful classification tools. However, the range of species in which carnivory is observed does make generalizations difficult.

Animal tissue included in the diet of carnivores can be obtained either via hunting and predation or by scavenging. Specific physical, physiological, behavioral, and metabolic adaptations are observed in carnivorous species as a result and are functionally important for the acquisition of dietary material (e.g., by hunting) as well as the processing of animal tissue in the digestive tract. The dentition of vertebrate carnivores is a prime example of such adaption, with highly specialized teeth specialized for killing, ripping, tearing, bone crushing, and varied degrees of grinding ability. Notably, animals with a more omnivore-like dietary strategy, such as the domestic dog (*Canis lupus familiaris*), have more teeth (42 compared to 30) than obligate carnivores such as felids. This is attributed to an increased number of molars and premolars, permitting increased mechanical processing of ingested material. Genomic signatures of carnivores also indicate a clear adaptation for the consumption and digestion of animal tissue, alongside adaptations for successful predation and other associated attributes (Kim et al. 2016).

Carnivorous mammalian species demonstrate flexibility in the diversity of prey consumed and thus in the adaptations required. Species that are hypercarnivorous (such as the polar bear, *Ursus maritimus*) tend to be large, show specific predatory adaptations and higher hunting energetic costs (Carbone et al. 2007), and demonstrate dentition capable of dealing with the processing of bones and other difficult tissues, as seen with early hyaenid carnivores (Werdelin 1989). Species that tend toward a hypocarnivorous strategy are typically small to medium-sized and often undertake frequent, solitary hunting behavior. Small carnivores appear to eat to gut capacity regularly, in contrast to larger species who

typically demonstrate reduced predation frequency because of both gut capacity and increased prey size (De Cuyper et al. 2019), revealing that both ecological (including temporal and spatial) and physiological factors impact on dietary choices.

For carnivores that are dependent in hunting for prey acquisition, physiological characteristics permitting strength, sensory awareness, and speed are critical, in addition to behavioral adaptations likely to enhance hunting success. Behavioral adaptations may take the form of cooperative hunting strategies or solitary strategies. Scavenging behaviors can also be observed in species that do not hunt or in an opportunistic way by those that would otherwise hunt for prey.

The typical mammalian carnivore digestive system is short and simple in contrast to the highly sacculated and specialized digestive systems observed in many herbivorous species. This corresponds to the high digestibility of the carnivore's diet compared to herbivores and the lack of requirement for prolonged retention of ingesta or significant levels of microbial fermentation. The stomach is considered simple but is often capable of expansion to permit the ingestion of larger prey items (Hume 2002). The small intestine is typically short, although it is notably longer in marine carnivores compared to terrestrial carnivores (Stevens and Hume 1995). If present, the caecum tends to be small, and the colon is also characteristically short.

In other species, such as carnivorous birds, amphibians, reptiles, and fish, the digestive systems are also simple and short, reflective of the high digestibility of ingesta. Carnivorous birds (especially raptors) have specialized beaks and talons to aid the separation of indigestible portions of prey or scavenged material prior to ingestion. Where indigestible material is consumed by carnivorous birds such as owls, it is separated in the gizzard and then egested as a formed "pellet" (Klasing 1998).

## Conclusion

The carnivore diet is one that consists of tissues from other animals, either wholly or in part. Those

tissues can be obtained via predation or scavenging. The carnivore dietary strategy is observed in a wide range of taxonomic orders and appears to have arisen multiple times during evolutionary history. As a dietary strategy, carnivory represents a dietary niche that exploits and utilizes highly digestible foodstuffs and requires few specific system adaptations to support prolonged retention, microbial fermentation, and other mechanisms to permit the digestion of otherwise indigestible material, as seen in many herbivorous species.

Predation is associated with the development of specific behavioral and physiological adaptations to enhance hunting success, although for many predators, prey availability is affected by temporal, spatial, and other ecological factors. Many predators are obligate carnivores and require animal tissues to supply key nutrients that cannot be synthesized within the body. Consequently, many of these species would be classed as hypercarnivores, with animal-derived tissues forming most of their dietary intake. Scavenging behavior is also observed in many species that actively ingest other animal tissues and can be either on an opportunistic or intentional basis, occasionally in species that would otherwise be unexpected to actively consume animal tissues.

Carnivory is a successful dietary strategy. It is observed across a wide diversity of species, which demonstrate a wide range of specific adaptations to support this life and diet strategy. Similarities are evident however, even across orders, at the physical, molecular, and nutrient requirement levels.

## Cross-References

- ▶ [Bear Diet](#)
- ▶ [Canine Diet](#)
- ▶ [Cannibalism](#)
- ▶ [Carnivora](#)
- ▶ [Feeding](#)
- ▶ [Feline Diet](#)
- ▶ [Herbivore](#)
- ▶ [Insectivore Diet](#)
- ▶ [Mustelidae Diet](#)
- ▶ [Omnivore](#)
- ▶ [Predator](#)
- ▶ [Prey](#)

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## Carrier

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## Synonyms

Genetic carrier; Hereditary carrier

## Introduction

In genetics, a carrier or a hereditary carrier is referred to an organism that has inherited or has been passed on with a recessive allele for a genetic trait or gets that recessive allele due to mutation but does not display that trait in its phylogeny. However, carriers can pass on that recessive allele to their offspring and their offspring can either show the recessive trait or not in their phylogeny



|   |                           |                            |
|---|---------------------------|----------------------------|
|   | A                         | a                          |
| A | AA<br>Homozygous dominant | Aa<br>Carrier              |
| a | aA<br>Carrier             | aa<br>Homozygous recessive |

**Carrier, Fig. 1** Punnett square depicting a cross between two genetic carriers and showing a 25% probability of an offspring being homozygous recessive

depending upon the allele that it received from the other parent. If the allele received from the other parent is a dominant allele then the offspring would again be a carrier but if the allele received from the other parent is a recessive allele then the offspring will show the recessive trait in its phylogeny (Krasnewich 2017). Henceforth, it can be complied that the probability of two carriers (of a disease) having an offspring with a disease is 25%. This can be understood by the Punnett square diagram shown in Fig. 1.

In the study of genetic diseases, it is important to determine the frequency of the carriers prevalent in the diseased population. For this Hardy-Weinberg formula was devised which applies to a gene with exactly two alleles and the frequency of those alleles are related to the frequency of their three genotypes in a large population.

For instance, if “p” is the frequency of the dominant allele “A” and “q” is the frequency of recessive allele “a,” then according to Hardy-Weinberg principle the terms  $p^2$ ,  $2pq$ , and  $q^2$  are the frequencies of the genotypes AA (homozygous dominant), Aa (heterozygous or carrier), and aa (homozygous recessive) respectively (Andrews 2010).

Carriers or organisms with heterozygous genotype have an important role to play in case of the genetic diseases that are caused by the recessive allele.

1. **X-Linked Hemophilia** (Bolton-Maggs and Pasi 2003; National Library of Medicine 2012a): X-linked hemophilia occurs due to the presence of an abnormal allele of a gene present on the X chromosome that is required for the blood clotting. Since males have only one X chromosome therefore, if a male encounters this altered allele then he will suffer from hemophilia whereas in case of females two possibilities can occur:

- If the female gets both the altered alleles for the said gene then she will suffer from hemophilia.
- If the female has one altered and the other “normal” allele, then the female would be an asymptomatic carrier. This female would continue to pass on this altered allele to half of her offsprings.

2. **Cystic Fibrosis** (National Library of Medicine 2012b): Mutations in the cystic fibrosis transmembrane conductance regulator genes (CFTR gene) lead to cystic fibrosis. It is an autosomal recessive disorder. The impact of this disease in the Caucasian people can be understood by the fact that 1 in every 25 individual was a carrier of this disease which means that they possess one mutated CFTR allele and one “normal” CFTR allele. Carriers remain unaffected in this disease as the “normal” CFTR allele codes for a normal protein which compensates for the mutated CFTR allele. Cystic fibrosis is only seen in people who have both mutated alleles for the CFTR gene (O’Sullivan and Freedman 2009).

3. **Sickle Cell Anemia (SCA)**: Sickle cell anemia is also an autosomal recessive disorder. It is a very common disease in the African Americans. SCA comprises of the red blood cells and their ability to carry oxygen. Unlike the normal red blood cells which are smooth, round and are easily motile through the vessels, red blood cells of the patients in this case become stiff and sticky. Moreover, their shape transforms to that of a sickle and hence causes clustering leading to a blockage of the flow of blood. Carriers in this case also have a normal allele along with an altered allele. The normal allele compensates for the function of the

altered allele and henceforth carriers are typically asymptomatic (Luzzatto 2012).

### **Heterozygote/Heterozygous Advantage:**

There are certain conditions in which the heterozygous genotype is more advantageous than either homozygous dominant or homozygous recessive genotype. These conditions are described by the heterozygote advantage. Overdominance is a particular case of heterozygote advantage in which the phenotype of the heterozygous individual is far more different than the range of the homozygous dominant and homozygous recessive individuals, thus providing more fitness to the heterozygous individual.

Heterozygote advantage is the fundamental mechanism for the heterosis or hybrid vigor which describes the increased affectivity of any biological quality in case of a hybrid offspring. Some examples of the heterozygote advantage are:

1. In case of malarial outbreaks in the SCA population, the heterozygous individuals have a distinct advantage over the homozygous recessive and the homozygous dominant individuals. The malarial parasite resides in the red blood cells of the infected patients and triggers an abnormal drop in the oxygen level in the cells. In case of carriers, this sudden drop in the oxygen level catalyzes a reaction through which the infected cells experience a sickle cell condition and are removed from the circulation resulting in the inhibition of the progress of infection. In case of patients having both the altered alleles for SCA might survive the malarial outburst but will eventually die of SCA unless they get medical attention. In case of individuals having both the alleles of “wild type” or homozygous dominant for SCA will not be affected by the SCA but are more susceptible to death by malarial before they successfully pass on their genes to their offsprings. Henceforth, it can be concluded that in case of SCA heterozygous individuals are more resistant and have a better chances of survival during malarial outbursts (Ringelmann et al. 1976).
2. In case of cystic fibrosis, researchers have shown that the heterozygous individual has

an advantage over both the homozygous individuals with respect to resistance against tuberculosis, respiratory advantage and also in case of cholera which remains debatable (MacKenzie 2006; Högenauer et al. 2000).

Other examples of heterozygote advantage include triosephosphate isomerase deficiency (Ralser et al. 2006), resistance to Hepatitis C virus infection (Hraber et al. 2007) etc.

## **Conclusion**

A carrier in genetics is referred to an organism that is genotypically heterozygous for a particular trait. It comprises of a recessive allele which has been either passed on to it or undergone some mutation. Carriers have a humongous role in case of genetic diseases. They can pass on their altered alleles to their offsprings without themselves being symptomatic of the disease. Therefore, their analysis and determination in a particular population becomes increasingly important and is done through the Hardy-Weinberg law. Additionally, a heterozygous individual might be open to some advantages or increased fitness which makes them more resistant to either the homozygous dominant or homozygous recessive individuals termed as heterozygous advantage.

## **Cross-References**

- [Heterozygote Superiority](#)
- [Recessive](#)

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## Cartesian Dualism

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## Definition

A philosophic doctrine originating from Descartes stating that there are two categories of things in existence, the physical and the mental.

## Introduction

Cartesian dualism was created by Descartes, a seventeenth-century Frenchman who made significant contributions to philosophy, mathematics, and science. He is primarily known as the father of modern philosophy and a key figure in the scientific revolution due to his mathematical legacy, weakening of the church’s influence on philosophy, and inspiring future scientists like Newton. One of his greatest contributions to philosophy was his revival of several key philosophy debates from the Greeks, including that of monism versus dualism. The doctrine of monism asserts that everything in existence can fit within one category, or type, of “thing.” Monism has two primary facets: materialism and idealism. Materialism is the theory that all things are physical in nature. Idealism is the less popular belief that all things are primarily from a mental plane. Sometimes this is characterized as coming from an ideal plane. Dualism is the opposing view that there are two distinct kinds, or types, of things that are needed to characterize all of existence. While there are many proposed pairs of types, the distinction remains between physical and non-physical things.

## The Context of Cartesian Dualism

Descartes was both a philosopher and scientist during a critical point in the renaissance. While religion and theology had dominated philosophy, society, and acceptable knowledge, science was now rapidly expanding both its tools and its acclaim. Descartes began to explore the relationship between the mind and the body. He held both theology and religion, as well as mathematics and the scientific study of the laws and nature, in high regard but struggled to bring such disparate methods together. For him, this presented the need for dualism to explain the validity of both the aforementioned as they do not focus on the same type of thing.

## The Creation of Cartesian Dualism

In his book *Discourse on the Method*, Descartes famously introduces his doubt argument, with the

well-known conclusion “Cogito ergo sum” or “I think therefore I am” (Descartes 1637/2007, p. 16). This lays the groundwork for dualism and the necessity of dualism. In the doubt argument, Descartes sets out a thought problem he utilized to search his own beliefs and purge any that he was not confident were true. Through this process of doubt, Descartes introduces many challenges to the truth of our own experience and thought, such as the idea that our current existence is just a dream and a malevolent demon giving us our sensations and perceptions and tricking us into believing that they are our own. This made Descartes doubt the vast majority of his beliefs. He could doubt all of physical reality, all of his sensations, but believed he could not doubt that he himself is mentally doubting all of these things. From this, he is assured that he exists because he is committing this act of doubting. If he can doubt all that is physical, but he cannot doubt this act his mind is committing, then there are different properties, and thus two different types of things are needed (Descartes 1637/2007). This argument was a convincing defense of the necessity of dualism, allowing Descartes to move the Greek notion of dualism away from matter and intellect and move it toward matter and consciousness. This is sometimes referred to as Descartes first argument for the separation of the mind and body.

In the Sixth Meditation of Descartes’ *Meditations on First Philosophy*, he offers additional arguments to reinforce that the mind and body are separate. Descartes asserts that if two things are perceived to be separate, and to have different properties, they are not the same type of thing (Descartes 1641/2007, p. 30). This is followed by Descartes stating that he perceives with certainty that he exists as a thinking thing. He also perceives with near certainty that his physical body is not a thinking thing (Descartes 1641/2007, p. 30). From this he derives that the mind and body must be different because they have different properties, and he perceives them as different. Secondly, Descartes asserts that while the physical body is divisible into parts that then make up the whole, the mind is not indivisible, once again showing different properties that require them to be separate types of things (Descartes 1641/2007, p. 33). With these arguments,

Descartes set the stage for the modern mind-body problem, where the relationship and distinction between what is part of the mind and what is part of the body, or if they are even truly separate, are still contended.

Once the mind is considered separate from the body though, many questions are still left unanswered. In a later book *Treatise on Man*, Descartes more directly outlines his new form of dualism. He explains that the human body was created by God and works like an “earthen machine” (Descartes 1998, p. 1). Since the body is made of matter, it can be explained in purely mechanical terms and is subject to the laws of nature, such as those outlined by physics, like a machine is made up of various systems to perform specific operations such as breathing, eating, and walking (Descartes 1998). This mechanistic view of how the body functions seems very in line with our modern scientific perspective of our biological systems, as well as neurological systems and reflexes. Descartes himself was the first to propose a mechanism for which human behavior could be produced from and proposed the simple reflex was the building block for the behavior of the body and for animals that did not possess a mind explained their behavior completely (Skinner 1931). Similar to his contemporary, William Harvey, who first proposed the circulation of blood in *Exercitatio Anatomica de Motu Cordis et Sanguinis in Animalibus*, Descartes proposed a system within the body that circulated animal spirits where reflex actions resulted from a stimulus and the flow of animal spirits to nerves it caused (Descartes 1998, p. xxiv). This gave him a rough system that explained physical beings in terms of machines, for both humans and animals, and explained their actions including that of the brain. The only exception then was the mind. The mind being nonmaterial did not need to obey the laws of nature and escaped the rules of science and instead resided in the realm of theology. This made dualism an issue of theology versus physics and science for Descartes. These two fields were both very influential on Descartes’ life, and his time period, but were at odds. This provided a solution to this as each focused on one facet of Cartesian dualism and thus has two completely separate content areas. Theology was what

characterized and studied the mind, the existing immaterial souls and spirits, as well as moral and ethical concerns. Physics was then relegated to modeling the physical phenomenon of the material things and there it stayed.

## Interactionism

With Cartesian dualism outlining two completely different types of substances, the problem of how they can coexist and could interact arises as a problem. Humans have both a constant experience of the physical world that has an easier time being objectively characterized and communicated, but we also have a constant experience of our mind as humans doubt and think. The difficulty in accounting for the ability for these two different substances to interact is a vulnerability that drove many thinkers to reject dualism and favor forms of monism instead. Descartes attempts to clarify this ambiguity in the Sixth Meditation of his *Meditations on First Philosophy*. The majority of dualist theories preceding Descartes were unidirectional, stating that the mind, or equivalent immaterial side, was superior to the physical able to overrule its laws and was the origin of our highest abilities. Descartes continued this, privileging the mind as the superior of the two, but thought of them as being able to reciprocally affect each other (Descartes 1641/2007). For example, basic needs not being met for the body, like severe hunger, could start to influence the mind as we lose focus on anything but food. Cartesian dualism clarifies the difference between the brain and the mind with the brain being material and the mind immaterial; functions of the brain could potentially affect the mind. Strong emotions are a function of the brain that could lead the body to overwhelm the rational mind as the emotions affects our behavior and thoughts.

Even with the relationship between the two clarified, the matter of how, and where, these separate substances can interact still had to be addressed. In the *Treatise of Man*, Descartes asserts that the location for this interaction was the pineal gland, a small endocrine gland with the shape of a pine cone that is located near the center

of the human brain (Descartes 1998). What drew Descartes' attention to the pineal gland were mainly false assumptions of the anatomy of the brain, some of which were already disproven in his time. Descartes believed that the pineal gland was held between the ventricles and surrounded by small arteries that brought it the animal spirits aforementioned (Descartes 1998, Figs. 54 and 55). He also thought that the pineal gland is not lateralized at the time it was thought to be one of the few parts of the brain that did not have symmetry across both sides of the brain, and it seemed central. Among his contemporaries, the pineal gland was not thought to have special qualities to give it such an exalted status.

## Implications for Nonhuman Animals

With the cognition of animals already being heavily discredited as anything complex, there was little interest in further research, and Descartes considered them to have no amount of mind. The religious values of the day viewed animals as soulless, lesser beings, and Descartes considered them to be purely constituted by material, physical things. This for Descartes meant animals were not complex enough to think, or doubt, and he even doubted their true ability to feel pain as he thought of them as purely driven by reflexes. His involvement in this topic was a strong push for human chauvinism in regard to comparative cognition and set the stage for centuries of scientific inquiry to work under the presumption that animals were fundamentally lesser. With this, animals were treated like they were inanimate objects, and all rules regarding ethical treatment were thus an unnecessary measure.

## Modern Context

Within the modern world, dualism has fallen into a minority view within academia, with physical monism now being the accepted view for the body of science. Dualism though is still in many ways an intuitive view that holds a lot of attraction to a general audience. Many religious beliefs require a degree of dualism as things that fundamentally



differ from the physical world are purported, such as a soul or any other aspect of a being that is unchanging and carries on beyond a body. There are also many nonreligious discussions that are prone to dualism. For example, complex issues involving the mind such as consciousness tend to have elements that intuitively feel different than something categorically physical, such as what makes humans conscious and how could anything physical create a sensation of experience that we have as conscious being. So while dualism is not normally accepted within the scientific tradition, it is still a prevalent position in modern day. Cartesian dualism is itself rarely believed in an unmodified form and instead is referenced for its historic influence on setting the context for the mind-body problem and modern solutions to it, whether with dualism or monism.

Since Cartesian dualism was first proposed, there have also been many breakthroughs in both the philosophy of mind and science in general that now affect how we view Cartesian dualism and the mind-body problem. Darwin's theory of evolution proposed in *On the Origin of Species* was a huge step in science and profoundly affected Cartesian dualism and the mind-body problem. Evolution links our development as a species to the rest of the living organism that inhabit the planet, undermining the idea that humans are innately superior in terms of mind and intelligence as we are closely related to other animals. This makes the existence of the mind more nuanced than Descartes' conservative stance that nothing but humans existed outside of the physical and reflexes. Advances in neuroscience also stand against much of Descartes' assertions around our neuroanatomy. Our understanding of our nervous system, including the brain, has greatly increased, disproving the idea of a system of nerves full of animal spirits and finding no evidence of the pineal gland being this special point where the mind and body are linked. We have also seen the mind-body problem be addressed in many different ways and recontextualized by philosophers such as Immanuel Kant, Thomas Huxley, and John Searle. Lastly, as the scientific study of consciousness has risen as a field with the works of researchers like David Chalmers who created the

"hard problem" and put the mind-body problem into a new context (Chalmers 1995).

Due to the rapid growth of technology in the modern age, we further have an obscuration of the line between what is mind and what is body. New interfaces are constantly being made that push the limits of our definitions as we develop integration between the organic and the artificial. This is shown with technology like synthesized and mechanical organs, as well as prosthetics that are controlled by our thoughts and neural activity. Examples like the aforementioned have called into question what should be considered part of a person or the environment or part of their mind. With this as well as advancement in the technology, we have to measure the activity of the brain; the mind-body problem naturally had to shift in the modern era in reaction to development in society and science.

## Conclusion

Cartesian dualism revived the Greek debate of monism vs. dualism and brought the focus of dualism away from intellect and toward consciousness setting the stage for the modern mind-body problem. The rise of Cartesian dualism additionally helped give a conceptual structure to the rapid growth of science in Descartes' era as it managed to embrace the laws of physical science and the mechanistic view of humans as constituted by systems with specific purposes. And it still maintained a place for the religious view of the immaterial soul, and superiority of humans over other animals, which characterized his time period. Currently though, Cartesian dualism, and dualism in general in academia, has fallen out of acclaim. The questions brought up by Cartesian dualism concerning what constitutes humans, and what is part of the body and what is part of the mind, continue to be extremely relevant in the modern age.

## Cross-References

- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)
- ▶ [Consciousness](#)
- ▶ [Meta-cognition](#)



- [Self-Awareness](#)
- [Theory of Mind](#)

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## Cartilaginous Fishes

- [Chondrichthyes Morphology](#)

## Cas9

- [Targeted Mutation](#)

## Caste

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## Introduction

In group-living organisms, tasks are often partitioned among individuals specializing in

particular roles. Such a division of labor improves the efficiency of task execution and is likely a major benefit of social living. The term “caste” describes the inter-individual differences in behavior (behavioral castes) and, in cases where behavioral roles are associated with different morphology, distinguishes between these physical forms (morphological castes). Morphological castes are typically associated with, and indeed are extensions of, differences in behavior, though differences in behavior need not be associated with differences in morphology.

## Behavioral Castes

Behavioral castes are fundamental to the division of labor in social organisms. This term is typically employed in place of “morphological castes” to describe social groups in which individuals specialize in different roles, such as reproduction or helping, but are otherwise undifferentiated. These individuals are not physiologically constrained to any particular role (i.e., are “totipotent”) and are capable of role switching. Behavioral castes may thus change during an individual’s lifetime, and in many cases roles are age dependent (i.e., temporal polyethism). Behavioral castes (as distinct from morphological castes) are found in many animal societies, including cooperatively breeding vertebrates (both birds and mammals) and social insects which lack morphological castes.

## Morphological Castes

Morphological castes are extensions of behavioral castes, in which specialization of group members on particular tasks is associated with specialized morphology. This phenomenon is distinct from sexual dimorphism resulting from inter- and intra-sexual selection. Morphological castes allow a higher degree of specialization than possible in behavioral castes, as development of unique characteristics and/or modification of existing characteristics allows new tasks to be performed and/or tasks to be performed more efficiently (Oster and Wilson 1978). This specialization comes at a cost to individual

flexibility and totipotency, which can lead to obligate mutual interdependence among castes. For example, queens and workers in many social insects cannot exist independently of one another, as the former are specialized for reproduction and are not capable of many labor tasks, while the latter are modified specifically for labor and may be incapable of reproduction.

Morphological castes are most frequently found in the social insects and have evolved at least 18 times in bees, wasps, and ants (Brady et al. 2006). Morphological castes have also been documented in at least one vertebrate, the naked mole rat, which is unique among vertebrates in having societies which share many characteristics with those of social insects (O’Riain et al. 2000).

In addition to characters directly associated with their particular role, such as enlarged heads and mandibles in soldiers and larger reproductive organs in queens, differences in morphology among group members may also be associated with variation in a suite of physiological and life-history traits, such as disease resistance and longevity. For example, whereas the lifespan of some ant queens can be measured in decades, that of workers of the same species may be measured in weeks (Hölldobler and Wilson 1990).

## Diversity of Morphological Castes

Morphological castes exist in their most fundamental form as part of the reproductive division of labor in societies in which one caste (queens) specializes in reproduction while the other (workers) undertakes nonreproductive tasks. In most social insects, the reproductive caste is larger than the worker caste, and species with larger colonies tend to exhibit a higher degree of caste dimorphism. This differentiation can exceed two orders of magnitude, though the degree of caste differentiation varies considerably between species and depends on a number of life-history traits (Hölldobler and Wilson 2009). Dimorphism is also greater in the ants than in bees or wasps, almost certainly because the loss of flight in the former has removed limitations on the evolution

of more diverse characteristics (Peeters and Ito 2015).

Reproductive castes are, unsurprisingly, specialized for reproduction. In extreme cases in social insects, this can include morphological specializations such as physogastry (distension of the abdomen to accommodate larger reproductive organs at the cost of mobility). Such females are effectively “egg-laying machines” and the rate of egg production in some species can reach tens of thousands per day (Gotwald 1995). These females are otherwise largely helpless, however, and must be tended by workers. Reproductive castes may also exhibit specialized traits for dispersal. New colonies are initiated by newly emerged and mated queens, and in many ant species it is only the queens (and males) that are winged. These ant queens accordingly possess enlarged thoraces to house large flight muscles, and have larger eyes than those found in workers.

Worker castes instead have traits suitable for labor tasks and typically have reduced reproductive capacity or may lack reproductive organs altogether (and be completely sterile). Workers perform the bulk of the labor tasks and thus undertake the greatest diversity of roles in the colony. In some groups, labor tasks are performed by morphologically distinct worker forms. For example, the leaf-cutter ant species *Atta sexdens* has four morphologically distinct castes: gardener-nurses, within-nest specialists, forager-excavators, and soldiers (Wilson 1980). Defense of the colony is critical for social insects, and specialized fighting castes (soldiers) exist in a range of ants, thrips, and termites. Soldiers may have enlarged and/or specially shaped mandibles and enlarged heads to house the associated musculature. Alternatively, morphological adaptations may be entirely defensive: in turtle ants, specialized soldier castes use their plate-like heads to block the entrance to the nest, effectively making them “living doors.” In other ant species, more unusual worker castes with highly specialized functions have evolved in response to strong environmental pressures. In several arid-zone species, for example, workers called “repletes” function as specialized living storage organs and have expanded abdomens in which they retain liquid food for the colony.

## Basis of Morphological Caste Formation

Morphological castes are formed via differential growth of different parts of the body during development into adults (i.e., allometry; Hölldobler and Wilson 1990; Oster and Wilson 1978). Different castes can arise in this manner from the same genotype though variation in environmental factors such as nutrition or social context. For example, the feeding of “royal jelly” helps push developing larvae into the path leading to the queen caste in honey bees. On the other hand, queen development in various social insect species is suppressed by the presence of a fertile queen in the nest via pheromonally mediated feedback loops. Recent evidence suggests that these environmentally induced effects on caste development are likely to function via their influence on the process of DNA methylation (Weiner and Toth 2012). In other cases, caste formation is partially or entirely determined by genetic differences between castes, and current evidence suggests that the degree to which environmental and genetic factors contribute to the development of different castes varies considerably between species (Schwander et al. 2010).

## Cross-References

- [Altruism](#)
- [Division of Labor](#)
- [Superorganism](#)

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## Cat Behavior

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## Cat Locomotion

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## Cat Senses

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## Cat Sensory Systems

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## Catarrhine

### ► [Haplorhini](#) ► [Primate Sensory Systems](#)

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## Catarrhine Cognition

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## Synonyms

[Apes](#); [Awareness](#); [Monkeys](#); [Reasoning](#); [Thought](#);  
[Understanding](#)

## Definition

A comparison of cognitive abilities within the primate parvorder Catarrhini (Old World monkeys, gibbons, and great apes).

## Introduction

The catarrhine primates include Old World monkeys (family Cercopithecidae), gibbons (family Hylobatidae), and great apes (family Hominidae, including humans, chimpanzees, bonobos, gorillas, and orangutans; Perelman et al. 2011). Old World monkeys account for an estimated 40% of extant primate genera; however, the phylogenetic relationships of some species are highly debated. The family is broken up into two subfamilies, Cercopithecinae (12 genera) and Colobinae (10 genera; Perelman et al. 2011). Gibbons (small apes) diverged between Old World monkeys and great apes. The family divides into four genera with 12 extant species, although the phylogenetic relationship between species is also controversial (Takacs et al. 2005).

The comparison of Old World monkeys, gibbons, and great apes provides the opportunity for a unique comparison of cognitive abilities between three evolutionarily diverged species. Here we will review cognitive processes of species within these families, with an emphasis on concepts and categorization, tool use, memory, self-awareness, and social cognition. Due to the large volume of species included in Catarrhini, we will focus specifically on key similarities or notable differences within each topic. A thorough review of primate cognition and its subcategories is well documented in published literature (for full reviews on primate cognition, see Deaner et al. 2006; Tomasello and Call 1997; and Washburn 2007). A discussion of communication within Catarrhini is found in a separate entry in this volume, and will not be covered here. Additionally, cognition in humans (*Homo sapiens*) will not be included in this entry.

## Primate Cognition

Cognition is multifaceted, integrating perception, learning, memory, and decision-making. Essentially, it is the process of sensing and processing information about the world, remembering that information, and deciding to act on it (Shettleworth 2001). Comparisons between primate species on this and other cognitive traits are problematic due to the highly variable research methodologies across studies. Even when researchers employ identical or similar methodologies, interspecific differences in motivation and perception may influence performance. Additionally, the majority of published studies in primate cognition have small sample sizes, making it difficult to ascertain true statistically significant differences between species.

Meta-analyses indicate that certain species perform at higher levels on specific cognitive tasks, although in other tasks there are no significant differences observed between species (Deaner et al. 2006). Current research suggests that great apes are superior to gibbons and Old World monkeys in formal cognitive tasks and in measures of intelligence extracted through principal components analysis (Reader et al. 2011). Phylogenetically, it is reasonable to expect that gibbons would outperform Old World monkeys in these tests; however, in many cases they perform inferiorly to monkeys in formal testing situations. However, note that cognitive tests of gibbons are less common than other catarrhines, and additional research is essential for a full understanding of their cognitive abilities. Recent genetic analysis suggests that multiple evolutionary events influenced the development of intelligence across primate lineages; in catarrhines, pronounced differences in independent responses to selection were evident in baboons, macaques, and the apes (Reader et al. 2011).

## Concepts and Categorization

Two fundamental aspects of cognitive abilities include the formation of concepts and the capacity

to discriminate and/or generalize environmental stimuli into meaningful categories. There is no standard operational definition for identifying concept formation in nonhuman animals, although most researchers agree that the creation of a concept involves the perception and classification of objects or events into physical or relational classes using explicit response rules. Current research suggests that Old World monkeys are distinguishably inferior to apes in their capacity to conceptualize. In this section, we will specifically look at species comparisons for object permanence, conservation, and discrimination.

Object permanence is the understanding that an object continues to exist, even when out of sight. Apes and macaques are able to perform this Piagetian developmental task and have shown evidence of creating perceptual categories during test administration. Gorillas, chimpanzees, and orangutans all reach Stage 6 of the object permanence task, although only gorillas have demonstrated an ability to understand non-adjacent displacements. Macaques do well on visible displacement tests, but do not perform above chance levels on invisible displacement tests. Research on object permanence in gibbons is limited, but suggests that they have abilities similar to those of the great apes (see Fedor et al. 2008, for a review).

Piagetian conservation involves the ability to understand that the physical properties of an object remain the same despite changes in the perception of the object. Great apes appear to possess this ability for discrete quantities and continuous quantities, but with species differences. Bonobos succeed significantly more with discrete quantity tasks; chimpanzees perform better with continuous tasks; orangutans are equally successful with both types. Additional research also indicates that gorillas are capable of relative quantity discrimination of whole sets of stimuli, performing at equal levels to the other three non-human great ape species (Hanus and Call 2007). Limited research on Old World monkeys and gibbons exists; rhesus macaques are successful in the task, though they are not as proficient as the great apes (Beran 2007).

Discrimination studies in nonhuman animals may take several forms, including same/different discrimination tasks, match-to-sample tasks, and stimulus response measures. Stimuli presentations may be visual, auditory, tactile, or olfactory. Interspecific and even interstudy comparisons are problematic due to the vast number of potentially confounding variables. For example, previous experience as well as the type of trials, rewards, and methodologies used affect animal performance (Deaner et al. 2006). Comparative discrimination studies involving all three subfamilies of catarrhine are extremely limited. However, recent meta-analysis found that macaques, gorillas, and chimpanzees performed equally well on object discriminatory tasks, superior to the performance of both gibbons and orangutans (Deaner et al. 2006). Macaques and baboons perform significantly above chance in quantity discrimination learning and do not show significant variation from chimpanzees and orangutans (Schmitt et al. 2012). Additionally, object discrimination reversal learning research suggests that chimpanzees and gorillas exceed the abilities of orangutans, which score higher than macaques. Cercopithecines outperformed gibbons in this particular meta-analysis. Delayed response tasks also demonstrate interspecific differences, ranking from highest to lowest as follows: orangutans, baboons, mandrills, gibbons and macaques, and cercopithecines (see Deaner et al. 2006, for a full review).

## Tool Use

The use of tools in both wild and captive settings involves several aspects of cognition, including causality and representation. Tool use requires the individual to understand how the manipulation of the object will affect another object. Great apes and macaques are the only catarrhines with known widespread tool use in the wild; this may be a reflection of manual dexterity as well as imitation skills and gregariousness, suggesting that social cognition and intelligence play a large role in the development of this skill (Gumert et al. 2011). Studies of tool use in gibbons are lacking, although reviews can be found in Cunningham

et al. (2016). In general, gibbons demonstrate less innovative tool use than macaques, which is surprising given their phylogenetic position in the parvorder.

Chimpanzees use tools for extractive foraging and often begin early in development. They tend to have higher rates of object manipulation and more diversity in those manipulations in comparison to bonobos, gorillas, and orangutans, with gorillas demonstrating the least amount of tool use in both wild and captive settings (Meulman and van Schaik 2013). Chimpanzees also demonstrate observational learning and cultural transmission of tool use, and may even save tools for future use (Mulcahy and Call 2006). Use of tools in primates may be related to enculturation; for example, orangutans and bonobos rarely use tools in wild populations, but are frequently observed using tools in captive or rehabilitative contexts (Furuichi et al. 2015; Meulman and van Schaik 2013). Additionally, social structure may play a large role in tool use, with more gregarious species such as chimpanzees showing higher levels of social learning compared to less social species such as the orangutans (Meulman and van Schaik 2013). However, as mentioned by Furuichi et al. (2015), these observed species differences might not be related to cognitive abilities; rather, they may be indicative of divergent behavioral predispositions. In captive groups, bonobos engage more frequently in playful behaviors with tools compared to chimpanzees, and this may reflect an inherent preference for this type of behavior. See Gruber and Clay (2016) for a full review of chimpanzees and bonobos.

## Memory

The cognitive process of memory provides an individual animal the opportunity to adjust their behavior based on past experience (Shettleworth 2001). Memory divides into several subtypes, including episodic memory (memory of personally experienced life events), spatial memory (environmental orientation), and prospective memory (forming intentions). Within the catarrhines, the majority of memory research has been conducted with the great apes.



Chimpanzees, bonobos, and gorillas demonstrate evidence of episodic-like memory, which is hypothesized to relate to social relationship formation (Schwartz and Evans 2001). Both chimpanzees and orangutans have shown aptitude for remembering episodic components of a task after a delay of 3 years (Martin-Ordas et al. 2013), and chimpanzees show spontaneous memory retrieval without prompt (Schwartz and Evans 2001). Spatial memory is important for primate foraging behavior. The development of spatial memory may be a reflection of ecological pressures; that is, chimpanzees, which have a more distributed food availability, prefer to incorporate spatial strategies when solving a memory foraging task. Bonobos, in contrast, have more continuous food access and therefore lack the more sophisticated spatial memory seen in chimpanzees (Rosati and Hare 2012). In terms of prospective memory, chimpanzees demonstrate the ability to encode information, retain that information for an extended period, and then implement the recalled information for a reward (Beran et al. 2016).

Limited research is available on the study of memory in gibbons and Old World monkeys, with the exception of rhesus macaques. Awareness of memory has been a topic of particular interest within this species, and individuals have exhibited episodic-like aspects of memory in foraging tasks (Hampton et al. 2005). Experimental evidence suggests that macaques are capable of reporting whether or not they remember an answer and are adept at memory maintenance (Basile and Hampton 2013). Note that memory studies in any nonhuman animal may have several alternative explanations, and additional research and debate is needed for a more complete understanding and interspecific comparison.

## Self-Awareness and Social Cognition

The study of animal cognition is often criticized by the sometimes-anthropomorphic nature of its methodology. However, some authors believe that anthropomorphism may be useful in creating testable hypotheses. The majority of these relate to emotional attributes rather than cognitive states. Human terms of cognitive states cannot be

attributed to mental processes in animals in which subjective feelings are projected onto another individual, such as the belief that a predator is dangerous. However, it is possible to interpret an animal as *wanting* another individual to believe something, as in the case of deception. Perhaps monkeys and apes are able to engage in deceptive and manipulative behaviors by monitoring conspecifics and identifying their intentions (Whiten 2013).

The question of whether nonhuman primates possess a human-like theory of mind, in which they can attribute separate mental states to others, is highly debated. In general, monkey and apes demonstrate the fundamental components of theory of mind, including gaze-following and understanding intentions (Platt et al. 2016). Chimpanzees, for example, can follow gaze, but it is unknown whether they can infer the experimenter's mental state related to the gaze. Macaques and sooty mangabeys are also adept at gaze-following, although succeed better at the task when the gaze is provided by a conspecific (Meunier 2016). In terms of understanding the intents and goals of another individual, chimpanzees appear to be able to distinguish between purposeful and accidental behavior (Seed and Tomasello 2010), and it is reasonable to assume that the other great apes share this ability. Rhesus macaques also demonstrate the ability to infer goals, although additional replication studies are needed to confirm this finding (Meunier 2016). Cognitive ability plays a large role in the ability to form adaptive social bonds and understand the intentions of other members in the social group; therefore, it is not surprising that catarrhines show evidence of these traits.

Social living may come at a great cost to individuals. For example, large groups are more conspicuous to predators, and diseases and parasites spread quickly. There is greater competition for food, and subordinate males expend more energy in dealing with dominant group members. Alternatively, large groups have a greater defense against predators and assistance is readily available from others for dealing with pathogens. Foraging improves due to information sharing, and subordinates are provided the safety of the group (Alcock 2009). In Old World monkeys,

females form long-term, stable relationships and engage in affiliative behaviors such as grooming. These close social bonds provide more protection while sleeping or feeding and prevent the loss of offspring. Furthermore, females with strong social bonds cope with stress more efficiently, as measured by levels of stress hormones; this also benefits offspring, as high stress levels are harmful to their health and behavior. Therefore, cooperative social bonds likely have a strong influence on individual fitness, even in the absence of competitive advantages such as ally support and dominance rank (Platt et al. 2016).

One of the most significant inquiries in the field of comparative psychology is the question of self-awareness in nonhuman animals. The cognitive ability most related to this feature of consciousness is that of self-recognition. Mirror Self-Recognition (MSR) tasks have been investigated with several species of catarrhines across all three families. Chimpanzees, bonobos, and orangutans all demonstrate MSR abilities, although social exposure is an important component for development. MSR in gorillas is less obvious, with a few individuals testing positive for the ability while others fail. No gibbons or Old World monkeys have been successful in an MSR task to date. Monkeys may respond socially to a mirror, but do not show self-directed behaviors. For a full review of MSR in primates, see Anderson and Gallup (2015).

## Conclusion

Although the study of cognition in primates dates back several decades, only recently have interspecific comparisons become an area of high interest. The catarrhines provide a unique opportunity for a phylogenetic comparison of cognitive abilities due to the divergent branching of their evolutionary history. The great apes (particularly chimpanzees) and macaques have a disproportionate amount of research compared to gibbons and other Old World monkeys. The future of the field holds many exciting possibilities for the understanding of primate cognition.

## Cross-References

- ▶ [Catarrhine Communication](#)
- ▶ [Catarrhine Life History](#)
- ▶ [Cognition](#)
- ▶ [Comparative Cognition](#)
- ▶ [Decision-Making](#)
- ▶ [Declarative Memory](#)
- ▶ [Episodic Memory](#)
- ▶ [Memory](#)
- ▶ [Mirror Self-Recognition](#)
- ▶ [Nonhuman Primates](#)
- ▶ [Primate Cognition](#)
- ▶ [Primates](#)
- ▶ [Self-Awareness](#)
- ▶ [Theory of Mind](#)
- ▶ [Tool Use](#)

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## Catarrhine Communication

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## Synonyms

Apes; Audition; Facial expression; Gesture; Modality; Multimodal; Old world monkeys; Olfaction; Sensory channel; Signal; Touch; Vocalization; Vision

## Definition

Old world monkeys and apes exhibit a large array of visual, acoustic, tactile, and olfactory signals.

## Introduction

Communication presents the foundation for all social behavior of primates, and the need to navigate their complex social environments has contributed to the evolution of sophisticated communication systems (Semple and Higham 2013). This entry provides an overview of communication patterns identified in catarrhines, a primate clade constituting two superfamilies: Cercopithecoidea (old world monkeys) and Hominoidea (apes). Catarrhines are distinguished from other primates by downward-facing nostrils, opposable thumbs, and a reduced vomeronasal organ, among numerous other traits. Species of this taxon are generally diurnal, live mostly in social groups, and exhibit extended

periods of maternal care; characteristics that are thought to have important implications for the evolution of their communicative systems. Catarrhines communicate with conspecifics to solve problems of survival (e.g., predation and defense of food sources), reproduction (e.g., sexual behavior and mother-offspring coordination), and group living (e.g., alliance formation and conflict resolution) (Liebal et al. 2013).

Given the immense variety regarding definitions of communication in the literature, it should be first clarified what this entry considers as a “signal”. Following the “influence” concept of communication, signals represent traits that exert influence on other individuals through sensory stimulation, and have been under selection specifically for their communicative function (Higham and Hebets 2013). In recent years, the communication of catarrhines tended to be mainly divided into three behavioral modalities – gesture, facial expression, and vocalization – encompassing the sensory channels of vision, touch, and audition (Liebal et al. 2013). The comparative research on ape and monkey communicative behavior has been widely used to trace the evolutionary roots of language, often focusing on underlying cognitive abilities such as intentionality and reference (Arbib et al. 2008). Owing to this comparative bias, most reviews of primate communication focused on behavioral signals only, with communication defined based on assumptions about potential underlying cognitive mechanisms rather than evolutionary function. Defining communication as involving behavior on the signaler’s behalf results in the neglect of other important signal types in definitions, such as genital swellings and the bright facial colors of the mandrill *Mandrillus sphinx*. Moreover, the conceptual focus on signal production and form rather than signal perception and function (Semple and Higham 2013) meant that the visual sensory channel has often been treated as two modalities of “gesture” and “facial expression” (Fröhlich 2017). However, to understand the function of animal signals, it is vital to consider the role of receiver perception and thus the receiver’s sensory systems that are stimulated (Higham and Hebets 2013). This

entry will follow the suggestion of Semple and Higham (2013) and present communication in terms of sensory modalities through which signals are perceived by the recipient, but also with regard to production and the different forms in which they are produced by the signaler.

Catarrhine primates produce and perceive signals in multiple sensory modalities, including the visual, acoustic, tactile, and olfactory channel, which differ in precision with regard to intended receivers (“locatability”), range, and persistence over time (“fade-out time”). Thus, the usage of different sensory modalities is constrained by features of the physical and social environment. In arboreal and densely vegetated settings, visual signals like facial expressions and gestures are transmitted less effectively and are thought to play a less important role than acoustic signals, especially if opportunities for close-range interactions among conspecifics are limited. While we would not expect a large repertoire of visual signals, these environments may favor the evolution of a complex vocal repertoire (Marler 1965). Since catarrhine primates are commonly diurnal, most close-range communication is visual, whereas long-range communication is predominantly audible. Moreover, the social structure and mating system profoundly influences communicative interactions within a species. Primates vary enormously in the complexity of their vocal, visual, and olfactory signaling repertoires, and the hypothesis that social complexity is linked to communicative complexity (Freeberg et al. 2012) has gained popularity among primatologists in recent years. While there is some evidence that group size in primates is positively correlated with both facial and vocal repertoire (Liebal et al. 2013), these findings should be viewed with caution given that signals are often highly graded, and researchers seldom agree on how to classify repertoires (Semple and Higham 2013). Nonetheless, sociality is supposed to favor the communication via multiple channels, as the interacting animals are spatially close enough to see, hear, smell, and/or touch each other. Multimodal signals may thus be especially suitable for short-distance communication, which is prevalent in many group-living

species of the primate order (Marler 1965). Although this entry introduces communication in the sensory modalities of vision, audition, touch, and olfaction separately, it is important to recognize that primates produce and perceive signals rarely in a unimodal format. As outlined below (section “Multimodal Use of Signals”), the simultaneous and sequential organization of signal elements must be considered to decipher complex signal function.

## Visual Communication

Catarrhines rely heavily on visual information, and the role of vision in primates’ neural and sociocognitive specialization has been emphasized by several comparative studies. In particular, primates’ elaborated visual system has evolved towards high visual acuity compared to most other mammals (Liebal et al. 2013). Catarrhines have evolved a comparably high level of orbital convergence (i.e., eyes facing in the same direction, namely forward), which resulted in binocular visual fields enabling stereotypic vision. Accordingly, the variety of visual signal types is very large, spanning from sexually selected signals like morphological swellings to behavioral signals such as gestures and facial expressions. The main benefits of the visual channel are fast transmission rates, short fade-out times, and the rapid locatability of the sender. Visual signals like facial expressions and piloerection tend to be effectively perceived only at close proximity to the signaler, but their precision makes them exceptionally suitable for dyadic, close-distance communication.

### Skin Coloration and Swellings

The evolution of uniform trichromatic vision in catarrhines seems to have led to a variety of red skin signals. An extraordinary example of visual communication is presented by the case of mandrill face coloration: males were shown to use the rank-dependent brightness of another male’s red coloration to assess individual differences in fighting ability (Setchell and Jean Wickings 2005).

Further research on the perception of the facial blue-red contrast suggested that the multicolored face of mandrills represents a multicomponent signal perceived within the same sensory channel (Renoult et al. 2011).

During specific phases of the ovarian cycle, females of numerous catarrhine species exhibit conspicuous swellings of the perineal skin. These hormone-dependent sexual signals are among the largest and the most colorful signals exhibited by any mammal. The exaggerated size of swellings has caused many evolutionary biologists to speculate that sexual selection has strongly influenced their evolution. With respect to signal function, the best-supported theory is probably Nunn’s (1999) “graded-signal hypothesis”, stating that sexual swelling size contains information about the intra-individual likelihood of ovulation. In this probabilistic model, swellings are larger when the likelihood of ovulation is greater within a cycle. However, the study of swellings has rarely been expanded beyond the element of swelling size. Since mate choice theory poses that males are likely to use multiple signal components of sexual signals, recent studies have emphasized that other visual elements, such as color, shape, and symmetry might also play a role in mate choice. For instance, size of female sexual swellings in female olive baboons *Papio anubis* may facilitate to assess fertility and parity of the signaler, whereas color was shown to be related to parity only (Higham et al. 2008).

### Facial Expression

Catarrhines have a remarkable facial mobility, and most species employ specific facial expressions through movements of the jaws, lips, ears, eyelids, and other facial features. Facial expressions have been commonly assumed to be expressions of emotional states that are largely innate and involuntarily produced (Tomasello 2008). While frequently studied as emotional displays, research has also considered them as true signals, evolved to allow receivers to predict the behavior of senders and to allow senders to manipulate receivers (Waller and Micheletta 2013). Some expressions, like the bared-teeth display, are



shared universally among the primate order. The precise meaning and context of the bared-teeth expression can vary between species, but it has long been argued that these similar expressions, including the human smile, comprise homologous traits (van Hooff 1972). Likewise, relaxed open mouth displays are frequently found in the repertoires of different primate species, usually associated with play, and thought to be homologous with human laughter (van Hooff 1972) and playful open mouth expressions seen in other mammals, such as dogs, bears, and even rats (Waller and Micheletta 2013). Facial expressions have been suggested to serve as “meta-communicative” devices to clarify the meaning of ambiguous, potentially agonistic behavior. For example, great apes frequently produce a “play face” when approaching others for play solicitation, presumably to assure that a hitting gesture or wrestling is perceived as intention to play and not as an aggressive approach (Rijksen 1978).

Some facial expressions are less ubiquitous and are only found in specific species or taxa. The “lip-smack” expression, for example, is a dynamic display that involves the fast-paced rapid closing and opening of the mouth and lips (Ghazanfar et al. 2012). Mainly associated with affiliative behaviors (e.g., social grooming) and suggested to facilitate tolerance, it is observed in many old world monkeys, particularly macaques and baboons (Van Hooff 1967). These species often produce lip-smacks during friendly approaches or face-to-face greetings, as well as during mother-infant interactions. While lip-smacking is a multimodal signal with both an audible and a visual element, the visual component has been shown to be sufficient in rhesus macaques to elicit reciprocation of this signal. Recent studies have highlighted the role “lip-smacking” facial expressions might play for understanding of language precursors, proposing that rhythmic facial movements required for speech production evolved from facial movement patterns in a primate ancestor (Ghazanfar et al. 2012). This theory is based on evidence that the temporal pattern and developmental trajectory of “lip-smacking” (starting with a variable “babbling” phase) in rhesus macaques resembles the timing and ontogeny of speech.

## Visual Gestures

Gestures have been defined as socially directed, mechanically ineffective movements of the extremities, head or body, as well as body postures that exert influence on another individual without coercion (Call and Tomasello 2007). Unlike research on human gesture, which usually focuses on the visual channel, research on primate gestures involves three sensory channels, since gestures can be perceived visually, tactilely, and/or acoustically. Gestural studies, mainly conducted in captive settings, have firmly established that old world monkeys and great apes frequently use visual gestures in their natural intraspecific communication. Visual manual and bodily signals are used in a wide range of social contexts (Call and Tomasello 2007) and are often accompanied by context-dependent facial expressions and postures: For instance, begging gestures solicit food transfers, beckoning gestures initiate sex and submissive gestures (e.g., presenting hindquarters) signal subordination towards a threatening dominant male. Male hamadryas baboons, *Papio hamadryas*, use various visual gestures to coordinate group movement and negotiate travel direction: the so-called notifying behavior involves an “approach – turn body – present hindquarters – look back” sequence, and group travel is initiated often by a male setting off in his preferred direction with a purposeful gait (Fischer and Zinner 2011).

Primates’ employment of visual gestures has often been used to infer whether a particular signal is used in a goal-directed (“intentional”) way. Communicating more/only via visual gestures only when the audience is visually attending and thus receptive to the signal suggests that the sender has an intention to manipulate the receiver’s behavior (Liebal et al. 2013). Recent studies on the gestural development in wild chimpanzee infants suggested that visual gestures increase at the expense of tactile signals with decreasing mother-infant proximity and increasing interaction rates with nonmaternal conspecifics (Fröhlich et al. 2016b). Numerous lines of comparative research suggested that nonhuman primates have considerably more intentional control, flexibility, and interactional awareness of



their productive gestural communication than of their vocalizations or facial expressions (Arbib et al. 2008; Tomasello 2008). With accumulating evidence for flexible and goal-directed use of vocalizations and facial expressions, this view has however been alleviated in recent years.

## Acoustic Communication

Sound plays a crucial role for maintaining group cohesion, allowing for long-distance communication with spatially disparate group members in dark and/or densely vegetated environments where opportunities for visual communication are limited. Compared to visual and tactile communication, acoustic signals are seldom targeted precisely at specific receivers, and broadcasted rather indiscriminately. While vocalizations are the most common form of acoustic communication, communication through sound does not always involve the vocal folds: auditory gestures and unvoiced calls are other acoustic communicative means employed by several catarrhine species.

## Vocalizations

Vocalizations are defined as utterances resulting from vibrations of the vocal folds within the larynx, which can exhibit a large variation in acoustic structure. The production of a vocalization involves air expulsion from the lungs, resulting in rhythmic opening and closing of the vocal folds that can be perceived as sound waves. Frequency, amplitude, and temporal pattern can differ according to recipient and physical environment. With the benefit of traveling large distances, vocalizations function to defend territories and food resources, and to locate conspecifics. Within a social group, vocalizations are produced in contexts like foraging, travel, copulation, and aggression. Research on contact call function in foraging primate troops has revealed that call rate increases with the distance to the nearest neighbor and habitat density (Bradbury and Vehrencamp 1998). With increasing separation distance, Japanese macaques, *Macaca fuscata*, may increase call duration, amplitude, and frequency modulation to enable the reunion with group mates (Koda

2004). Several catarrhine species rely on vocalizations as consensus-building departure signals to coordinate group travel: in mountain gorillas *Gorilla beringei beringei* and chacma baboons *Papio ursinus* several individuals increase the production of grunts before the initiation of travel (Fischer and Zinner 2011), whereas in chimpanzees (*Pan troglodytes*) only particular individuals produce “travel hoos” that seem to be directed at closely bonded individuals (Gruber and Zuberbühler 2013). Social intragroup calls are often not broadcast indiscriminately, but affected by identity and dominance rank of the receivers. Rhesus macaques, *Macaca mulatta*, were shown to give five acoustically different “screams” when interacting with opponents varying in rank, relatedness etc., which elicited different responses from group mates depending on opponent type and agonistic situation (Gouzoules et al. 1984).

While primates’ intragroup calls generally exhibit a lower amplitude and higher acoustic variation, intergroup calls often travel long distances through the environment. Territorial “loud calls”, as produced by gibbons, are thought to function to announce the location of the caller within the territory and to repel other individual and groups. Predator-specific alarm calls are another class of “loud calls”, which can address the predator and close-by group members (Zuberbühler 2001). It has been argued that alarm calls of several catarrhine species qualify as “functionally referential”, that is, they are correlated with the occurrence of objects or events in the external world of the signaler, and induce the receiver to respond adaptively in the absence of direct cues from the eliciting stimulus. This context-sensitive semanticity has been demonstrated for several species of old world monkeys, with individuals responding to acoustically distinct calls with particular types of antipredator responses even in the absence of the predator. For instance, vervet monkeys *Chlorocebus pygerythrus*, Diana monkeys *Cercopithecus diana*, and Campbell’s monkeys *Cercopithecus campbelli* all use distinct alarm calls for different predators, eliciting appropriate escape responses in other group members (Zuberbühler 2001).

Vocal turn-taking, defined as coordination of vocal contributions by two individuals, has been evidenced in Campbell's monkeys (Lemasson et al. 2011), and from the lesser apes, siamangs *Hylobates syndactylus* (Geissmann and Orgeldinger 2000). In siamangs, pair-bonded males and females produce loud and ritualized "duetting" vocalizations for territorial defense, but also to strengthen existing pair bonds or to attract new mates (Geissmann and Orgeldinger 2000). Reports of vocal turn-taking in the great apes are limited to reports of male chimpanzees chorusing with pant-hoots, an acoustically distinct long-distance call. Chorusing in male chimpanzees seems to reliably reflect short-term affiliation, facilitating feeding tolerance and predicting support in agonistic interactions (Fedurek et al. 2013).

### Unvoiced Calls

Sounds produced with the mouth but not involving the vocal tract have been termed unvoiced or voiceless calls and include "kiss squeaks", "raspberries", "whistles", and "lip-smacks" (see section "[Facial Expression](#)"). The kiss squeak is produced by a sharp intake of air through pursed lips and has been demonstrated to serve as alarm call in wild Bornean, *Pongo pygmaeus*, and Sumatran orangutans, *Pongo abelii*, in response to encounters with potential predators or conspecifics (Rijksen 1978). In some populations, the "kiss squeak" is performed by positioning a hand or a hand with leaves in front of or against the lips during production (van Schaik et al. 2003). "Raspberries" are spluttering sounds that are produced by orangutans of some wild populations during nest building (van Schaik et al. 2003) and by captive chimpanzees as attention-getting sounds towards their human caretakers (Liebal et al. 2013). Orangutans have been shown to copy "whistling" sounds from humans, demonstrating the ability to acquire a novel voiceless call belonging to a repertoire of a different species. However, although human-ape experimental setups have the potential to reveal apes' cognitive abilities, they cannot provide insight into strategies that are employed in their natural communication with conspecifics (Liebal et al. 2013).

### Auditory Gestures

The most popular example of a gesture producing sound is probably the gorillas' "chest-beat", which is used as part of their display behavior or to invite others to play. Many of the reported auditory gestures in great apes (e.g., "clip leaf" and "slap object") have been suggested to serve as "attention-getting" signals that do not convey specific information about the context. The signaler's message might be rather conveyed in the context-typical facial expressions (e.g., "play-face") or body postures (Tomasello et al. 1994; however, see Liebal et al. (2013) for different view). Most gestures producing a sound element are actually considered audio-visual gestures, as they normally also have salient visual components. Hence, the visual orientation ("attentional state") of the recipient must always be assessed to infer which components of a signal were salient for perception (Fröhlich 2017). Adult chimpanzees and bonobos are commonly observed to drum on the trunks of trees, by beating their hands and feet against on the hard surface. Drumming by chimpanzees, often accompanied by "pant-hoot" vocalizations, is performed in multiple contexts including traveling, display, inter-group encounter, and when arriving at large food sources (Crockford and Boesch 2005).

### Tactile Communication

Tactile signals, similar to visual signals, enable rapid and precise communication particularly suitable for dyadic, close-distance communication. Out of the four communicative modalities presented, tactile signaling is arguably the most intimate and risky, since it is the only one that requires the renunciation of individual space and, in many cases, the exposition of vulnerable body parts. Surprisingly, touch is often neglected as a communicative channel in reviews of primate communication. Primates rely on tactile signals to resolve conflicts, mediate courtship, reaffirm affiliative and dominance relationships, and coordinate group movements. Tactile appeasement tactics and signals are of particular importance for maintaining peace in groups, involving post-conflict

reconciliation, third-party consolation, allogrooming, and greeting displays (Bradbury and Vehrencamp 1998). Reconciliation acts following conflicts frequently involve close contact, particularly the winner approaching and embracing, kissing, or grooming the loser. Chimpanzees are thought to reconcile particularly often after conflicts, but this behavior is also reported for old world monkeys like macaques and baboons. Consolation behavior after conflicts, usually by a closely bonded individual not involved in the conflict, involves embracing, grooming, and other types of touch such as licking and genito-genital rubbing. Third-party consolation is observed in chimpanzees and bonobos but less frequently in old world monkeys (Bradbury and Vehrencamp 1998). Both reconciliation and consolation serve to decrease the occurrence of anxiety behaviors in the victim through comforting or reassuring. Allogrooming, the grooming of another individual, is a universal behavior and probably the most widespread interaction involving touch in catarrhine primates. While one obvious function of this behavior is the removal of parasites and debris from the body surface of the groomed animal, it also serves to reaffirm affiliative bonds or the relative dominance status between groomer and groomee. As a major tension-reducing strategy in primates, allogrooming can be exchanged for other “goods” such as mating opportunities, tolerance, or agonistic support in future conflicts. Allogrooming has a crucial communicative function, as the act of grooming carries the message that the recipient is considered a valuable social partner, which can be used to infer the partner’s willingness to support each other in high-risk collaborations. It is most commonly observed between related group members, within female matrilineal groups among old world monkeys and among males in chimpanzees, but also beyond kin relationships. In several catarrhine species, individuals greet the arrival of a known conspecific with physical contact, such as when baboon males touch each other’s genitalia, chimpanzees clasp the partner with one arm in a loose embrace, or bonobos engage in mutual genital rubbing.

Tactile gestures can be distinguished from mere physical actions in that they are not

mechanically effective (i.e., they do not function through coercion) and communicate a specific intent. For example, gently touching an individual’s back during a grooming session to indicate a desire for that individual to lie down would be a tactile gesture, as opposed to the direct physical action of forcefully pushing the other to the ground. Tactile gestures are particularly common in affiliative contexts like grooming and reassurance. A recent study on play-soliciting signals in immature chimpanzees found that infants used tactile gestures predominantly in interactions with their mothers, with whom predictable outcomes and high familiarity have been established in many previous interactions (Fröhlich et al.).

## Olfactory Communication

Chemical signals, perceived using olfaction, provide the advantage of persisting over time but lack precision with regard to receivers. Old world monkeys, apes, and humans have traditionally been considered as “microsmatic”, with decreased reliance on olfactory senses in comparison to other sensory modalities such as vision. The olfactory system of catarrhines is thought to be considerably less complex than in prosimians and new world monkeys, as accessory olfactory bulbs (AOBs) are lacking and the vomeronasal organ is markedly reduced (Barton 2006). The majority of evidence for olfactory communication in primates, such as scent and urine marking, stems from prosimians and callitrichids. These taxa possess numerous scent glands producing secretions containing so-called pheromones, substances secreted by an animal with specific effects on the behavior or physiology of conspecific.

However, the importance of olfactory communication in catarrhines has been increasingly recognized in recent years (Vaglio et al. 2016). Odor and the main olfactory system are thought to be involved in sexual and social behaviors, and specifically the attraction of males to estrous females (Barton 2006). Observational studies suggested that pheromones play a critical role in the sexual context, as olfactory inspection (“sniffing”) by male catarrhine primates is commonly observed.

Sternal-gland secretions in mandrills have been shown to signal sex, age, male dominance, and possibly individual identity and group membership, suggesting that scent-marking serves territorial functions but also sociosexual functions of communication in this species (Vaglio et al. 2016). Chimpanzee males show an intensified interest in copulation around the period of female ovulation, which has been related to their ability to detect olfactory signals produced by the female at the time of ovulation. A few studies suggest that vaginal secretions during estrus of female chimpanzees contain pheromones that signal reproductive capacity and physiological status. While chimpanzee females produce a mix of volatile fatty acids in vaginal secretions, only isobutyric acid increases during the ovulation period, which might affect male sexual responsiveness (Matsumoto-Oda et al. 2003). However, as the females of many primate species develop sexual swellings varying in shape, size, and color (see section “[Skin Coloration and Swellings](#)”), and thereby multicomponent signal of two sensory modalities, it is important to disentangle how these different signal components contribute to male responses.

### Multimodal Use of Signals

Communications systems of primates are intrinsically multimodal, often involving a simultaneous and sequential production of different signal components in multiple sensory channels. In fact, research on catarrhine communication at both the behavioral and neuronal level has demonstrated a widespread capacity to flexibly combine signals from different modalities (Liebal et al. 2013). A vivid example for a complex communicative scenario was described by Higham and Hebets (2013) for the context of sexual behavior: “[...] male baboons are highly aroused by the visual signal of female sexual swellings (which themselves vary in multiple components such as size, shape, symmetry, and colour), which they then touch (possibly to assess how inflated the swelling is), before sniffing the vagina and its secretions, which they then taste. If the male

chooses to mate with the female, she is likely to give a copulation call during coitus, which may indicate further aspects of her status to this and other males”.

Fixed multimodal signals are those whose components are obligatorily coupled due to the mechanics of signal production (e.g., a “scream face” necessarily accompanies a “scream” vocalization in chimpanzees) (Smith 1977). By contrast, free multimodal signal combinations are those whose component signals may be produced separately or combined flexibly with other signals (Tomasello 2008). From the perspective of perception, cross-modal integration of vocal and visual signal elements has been shown in both monkeys and great apes, which were able to recognize the correspondence between species-specific facial and vocal expressions, termed “audio-visual matching” or “face/voice integration” (Partan and Marler 2005). From the production side, several studies in both wild and captive environments indicated that great apes use signal combinations conveying context-specific information that would not be available from a single sensory input (Liebal et al. 2013). For instance, male bonobos have been shown to use the same vocalization (“contest-hoot”) for play and aggression, but add gestures to distinguish between the two contexts (Genty et al. 2014). This way ambiguous messages sent in one channel can be clarified by adding a more specific component in another channel (Partan and Marler 2005).

### Conclusion

Catarrhine primates, like most other animals, produce and perceive signals of various sensory modalities. The modalities employed are thought to underlie the heavy influence of social and ecological factors. Primates are generally thought of as “visual” mammals, as they exhibit an elaborated visual system with forward-directed large eyes enabling stereoscopic vision. Accordingly, the largest variety of signals is found in this domain, including colorful sexual swellings, facial expressions, and gestures. Sound also plays a major role in catarrhine life, with

vocalizations used to defend territories and food resources, negotiate social interactions, and to locate conspecifics. Touch is an often-neglected sense of communication in primates, but signals involving body contact have been shown to play an essential role in affiliation and mother-infant coordination. Although primates are traditionally considered microsmatic, olfactory signals (i.e., pheromones) are used by catarrhines in the recognition of the reproductive status of females. Catarrhines frequently combine signals from different sensory modalities simultaneously and sequentially, thus research on single modalities in isolation results in missing much of the complexity inherent to communicative acts. Moreover, future studies of primate communication should adopt a multimodal, inclusive approach focusing on modalities in terms of both production and perception (Liebal et al. 2013; Fröhlich 2017). If primate communication is examined from the perspective of the signaler and signal form alone, researchers might fail to distinguish the proximate from the ultimate explanations for signals.

## Cross-References

- [Catarrhine Cognition](#)
- [Prosimian Communication](#)

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long periods of gestation and nursing and have high encephalization quotients (brain to body ratio), thus requiring large amounts of energy to function properly. The energetic demands of primates' large brains alone require daily consumption of large amounts of energy-rich foods (Aiello and Wheeler 1995).

Within the diverse parvorder *Catarrhini* (which encompasses old-world monkeys, apes, and humans), there is a great deal of dietary variability, ranging in degree of folivory (leaf eating), frugivory (fruit eating), granivory (seed eating), and graminivory (grass eating). Lambert and Rothman (2015) state that most primate species are in fact what they call “flexible omnivores,” meaning that not only do primate species switch between different food sources, but that the foods themselves (both food type and nutrient composition) vary based on location, seasonality, and time of day. Even among many of the catarrhine species who are classified under the dietary categories of “folivore” or “frugivore,” there is still a great deal of dietary variability. It should be noted that even with this dietary flexibility, there are still a few primates that will preferentially select, and are specialized for, certain types of foods (i.e., leaf-eating colobines, grass-eating gelada baboons, etc.). Additionally, within all primate species, the use of fallback foods, or foods that are eaten when preferred foods are unavailable, is regularly observed. Moreover, large-bodied primates, such as catarrhine species, serve a vital role as seed dispersers which aid in the development and maintenance of the ecosystems and habitats (primarily forested areas) in which they live.

## Catarrhine Diet

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## Introduction

Most primates are morphologically and physiologically adapted as frugivores and seek out energy and nutrient-dense foods. Primates have

## Old-World Monkeys

The largest group, with the most species within *Catarrhini*, is the old-world monkeys. Old-world monkeys range throughout the continents of Asia and Africa (and one species in South Europe), are typically larger bodied than their New World counterparts, and are generally flexible feeders. Within the old-world monkeys are the two subfamilies Colobinae (African and Asian colobines) and Cercopithecinae (cheek-pouched monkeys).



## Colobines

Colobines are also known as the “leaf-eating” monkeys, though their diet is much more complex and varied (Fashing 2011; Kirkpatrick 2011). All colobines have specialized multi-chambered or sacculated stomachs that allow for fermentation of high-fiber foods (Kay and Davies 1994). This fermentation process also helps to detoxify plants and is achieved by the symbiotic relationship with species-specific microbiota that live in their intestines. This ability to ferment low-quality foods, such as mature leaves, allows for colobines to survive on a diet many other animals could not. Moreover, all colobine species have adaptations in addition to sacculated stomachs that allow them to process leaves including enlarged salivary glands and molars capable of processing tough plant foods. Colobines tend to prefer young leaves and fruit to mature leaves but will forage and feed on mature leaves when necessary.

*Asian colobines:* Asian colobines have, according to Kirkpatrick (2011), diets that vary by season and include leaves, fruits, and seeds. While most Asian colobines’ diet is primarily leaves, Kirkpatrick (2011) states that about a quarter of their diet consists of fruits and seeds, and while invertebrate consumption is rare, it does occur (Newton 1992).

*African colobines:* Like their Asian counterparts, African colobines are leaf-eating monkeys. However, similar to the Asian colobines, their diet does alter seasonally, and fruit, seed, and flower consumption is regularly observed. While some of the larger-bodied African colobines don’t have a problem relying on mature leaves when other food sources aren’t available, some of the smaller-bodied species might not be able to ingest such low-quality foods.

## Cercopithecines

The cercopithecines span both the continents of Asia and Africa (and one macaque species in Gibraltar). These primates, which share morphological characteristics of cheek pouches and ischial callosities (thick-callused pads on the buttocks), include African papionins (baboons, gelada baboons, mangabeys, mandrills, drills),

macaques (the most successful primate species, second only to humans), guenons, and vervets. Save the gelada baboon, cercopithecines are largely flexible omnivores, though like all other primates, foods are chosen based on nutrient content.

***Baboons and Baboon-Like Primates*** Baboons (*Papio* sp.) eat a wide variety of foods and are considered opportunistic omnivores. As they are the most widely disbursed primate in Africa, troop diets may vary depending on location. For example, baboons who live near the ocean have been observed eating and foraging for shellfish and mermaid’s purses (shark eggs), while some baboons who live near soda lakes hunt for flamingo. Many of these foraging strategies are culturally passed from generation to generation. Additionally, they use their short, dexterous fingers to dig for underground storage organs and feed on flowers, fruits, gums, seeds, leaves, grasses, and various animal prey. Baboons tend to choose diets that are low in fiber, high in protein, and high in fat. As baboons are capable of a great deal of dietary flexibility and as human and baboon populations continue to collide, baboons have begun foraging in trash heaps, crops, and settlements.

One interesting and specialized cercopithecine that is commonly referred to as a baboon, though not a member of the genus *Papio*, is the gelada baboon (*Theropithecus gelada*). Gelada baboons are grass specialists (graminivores) who spend their days foraging on the grasses in the highlands of Ethiopia, the only place in the world where they are found. Because they spend their days foraging on grasses and sitting down, some interesting behavioral and morphological adaptations have emerged. Behaviorally, gelada “chatter” or verbally groom one another throughout the day, as they don’t have the time to physically groom one another. Morphologically, gelada have bald, red patches on their chests which indicate health and reproductive status.

***Macaques*** Macaques are the most widely disbursed and successful primate, other than humans, in the world. They range throughout Asia and are

also found in North Africa and in Gibraltar. Macaques successfully live and thrive in varied habitats and climates ranging from Southern India to mountainous regions in Japan, with heavy snowfall. Macaques are generally thought of as frugivores; however, depending upon seasonality and habitat, their diet can include a great deal of other foods including seeds, animal protein (invertebrates), bark, leaves, flowers, herbaceous growth, and roots. Many macaques are also heavily reliant on humans as a food source either through crop raiding or at temples or tourist spots, where they are provisioned.

## Apes

Apes show varying reliance on fruits, but all are considered somewhere on the spectrum of a frugivore-folivore or folivore-frugivore. Apes are the largest bodied and have the highest encephalization quotient (brain to body ratio) of all of the primates. While some apes (i.e., mountain gorillas) are more folivorous than frugivorous, the majority shows a preference for fruits, which are higher quality and have higher calorie content, supporting the energetic demands of a larger brain and body. Among the great apes, which includes chimpanzees (*Pan troglodytes* sp.), bonobos (*Pan paniscus*), orangutans (*Pongo abelii* and *Pongo pygmaeus*), gorillas (*Gorilla gorilla* sp. and *Gorilla beringei* sp.), and ancient and modern humans and their ancestors (*Australopithecus* sp. and *Homo* sp.), diets include, but are certainly not limited to, fruits, leaves, piths, and invertebrates. It has been shown that when given the opportunity, all great apes will preferentially eat fruits (Remis 2003).

### Asian Apes

**Gibbons and Siamangs** Gibbons and siamangs are the smallest bodied of the apes, which allow them to utilize more of the forest canopy than some of their conspecifics and are found only in Southeast Asia. Gibbons are highly frugivorous, relying most heavily on ripe fruits, though some

species are more folivorous than others. Diet also consists of flowers, insects, and young leaves.

**Orangutans** Orangutans are a highly frugivorous species which impacts their overall social structure. Some of the preferred foods of orangutans are durian fruit and figs. Additionally, tool usage has been observed in orangutans to obtain insects and saps from trees as well as hunting of other animals (i.e., slow loris) (van Schaik et al. 2003). As they are the largest-bodied arboreal animal, and trees fruit in patches, it's difficult for orangutans to live in social grouping. Females and their offspring will live together for up to 8 years, while dominant, or flanged, males will overlap in range with multiple females and their offspring.

Every few years, an ecological phenomena known as a masting or mast fruiting will occur, which produces an abundance of fruits on multiple trees of the same species simultaneously, allowing for large numbers of orangutans to congregate. Orangutans in the wild have been known to become obese during a mast fruiting. When mast fruiting occurs, orangutans will switch from their typical diet of leaves, bark, and some fruits to gorge themselves solely on high calorie fruits and fatty seeds until they are no longer available. It is not uncommon for orangutans, at the end of these periods of fruit abundance, to have enlarged fat deposits, which they rely on during the fruit scarcity that follows a mast fruiting.

### African Apes

**Gorillas** Habitat, elevation, and ecological niche greatly influences the diet of gorillas, the largest-bodied living (or extant) primate. Much of our knowledge of gorilla diet, ecology, and behavior come from the groundbreaking work on mountain gorillas (Fossey and Harcourt 1977; Schaller 1963). Because of these studies, all gorillas were long thought to be ground-dwelling leaf eaters. However, while mountain gorillas are specialized to higher altitudes and do forage mainly on the ground for leaves and herbaceous growth (Fossey and Harcourt 1977; Schaller 1963), western lowland gorillas are typically found in lower-altitude

forests with a diet that varies seasonally (Yamagiwa and Basabose 2006). Moreover, western lowland gorillas are known to spend time in the trees, with females being able to move among the higher and smaller branches as they are smaller bodied and more agile than males. This increased access to multiple levels of the forest allows for more food availability for females and juveniles.

Western lowland gorillas are now commonly classified as folivore-frugivores, as they prefer ripe fruit but will utilize leaves and herbs as staple foods and fallback foods (Remis 1997, 2003; Yamagiwa and Basabose 2006). Additionally, they will eat invertebrate animal prey (Tutin and Fernandez 1985) (typically by breaking open termite mounds), though it is not a significant source of their daily protein intake. High fruit consumption occurs during seasons when fruit availability is higher (Goldsmith 1999; Remis 1997), but they will switch to lower energy, fibrous herbs, leaves, and bark, when fruit availability is scarce (Dierenfeld 1997; Goldsmith 1999; Masi et al. 2009; Remis 1997; Rothman et al. 2008; Wobber et al. 2008).

Gorillas have an enlarged cecum and colon (portions of the large intestine) that is rich in species-specific gut microbiota, which facilitate the digestion of a high-fiber diet (up to 200 g/day). Wild gorilla diets are high in many vitamins and minerals, though sodium is often sought out in various ways depending on the species. Where mountain gorillas will eat decaying wood as a source of sodium, western lowland gorillas will travel to clearings in the forest called salines (along with other species, including forest elephants), to ingest mineral-rich soils.

**Chimpanzees and Bonobos** Chimpanzees in the wild eat a variety of foods including fruits, leaves, herbs, bark, and invertebrate and vertebrate animal protein (including eggs) (Wrangham 1977; Goodall 1986). Both chimpanzees and bonobos are highly frugivorous, and most of the protein content of their diets are plant based in the form of herbaceous leaves. In addition, chimpanzees are successful hunters and often cooperate together to

obtain prey. A favorite food of chimpanzees, where available, are red colobus monkeys. Bonobos, on the other hand, rarely eat animal protein (though they will eat duiker sporadically) and eat a more frugivorous-folivorous diet. Chimpanzees and bonobos both regularly utilize tools to extract foods, most famously for termite fishing.

**Hominins: Humans and Their Ancestors** The similarities between the diets and dietary preferences among extant African apes and modern humans, prior to domestication, suggest that our last common ancestor likely shared a similar diet. For instance, gorillas, chimpanzees, and humans share similar gut morphology (Chivers and Hladik 1980), save the elongated large intestine of the gorilla. Moreover, apes and humans exhibit taste perception and food preferences that overlap (Dierenfeld 1997; Masi et al. 2009; Remis 1997; Rothman et al. 2008; Wobber et al. 2008). These similarities suggest that diets of very early hominins were likely more similar to those of extant (living) African apes than to contemporary human populations.

As hominins diverged from the common ancestor shared with gorillas and chimpanzees, there were shifts in diet, including the emergence of food preparation (Conklin-Brittain et al. 2002; Marshall and Wrangham 2007; Wobber et al. 2008; Wrangham 2009), food acquisition (and thus a greater variety in foods eaten), and eventually domestication. Changes in diet and the coinciding physical adaptations, including changes in cranial and dental morphology, are considered hallmarks in hominin evolution. As soft tissue cannot fossilize, it has been hard to understand the full morphological consequences of these dietary shifts to early hominin digestive anatomy and physiology over the course of evolution. However, while generalized gut morphology can be reconstructed from changes in torso shape in fossil species (Aiello and Wheeler 1995), gut morphology is plastic and is able to change in minor ways over short periods of time, depending on diet (Milton 1999).

The use of fire and subsequent heating and cooking of hominin foods alter the chemical structure and nutritional composition of consumed foods

(Wrangham 2009). Moreover, a study has shown that even captive great apes, who have never eaten cooked food, when given the option, prefer it (Wobber et al. 2008). In addition, as hominins moved out of the forest and into the savanna, fallback foods likely shifted to underground storage organs (i.e., roots and tubers), which are lower in fiber content and more calorically dense than typical forest fallback foods such as mature leaves, herbaceous leaves, bark, and pith (Conklin-Brittain et al. 2002). Moreover, fossil evidence suggests that during this time, hominins increasingly relied on wild game (Milton 1999).

While the advent of agriculture and crop domestication is relatively recent from an evolutionary perspective, humans have been domesticating and eating grains and other soft foods for thousands of years. Even with this prolonged exposure, humans physically appear to have been unable to keep pace with the myriad of dietary changes that have occurred with the advent of agriculture and the Industrial Revolution (Milton 1999).

## Cross-References

- [Cattarrhine Morphology](#)
- [Insectivore Diet](#)
- [Primate Diet](#)

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## Catarrhine Life History

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### Synonyms

Apes; Old world monkeys; Lifestyle;  
Reproduction

### Definition

A general life history of the primate parvorder Catarrhini (Old World monkeys, gibbons, and great apes).

### Introduction

Catarrhine primates include species from three families: Cercopithecidae (Old World monkeys; 159 extant species), Hylobatidae (gibbons and siamangs; 19 extant species), and Hominidae (great apes and humans; 7 extant species; Mittermeier et al. 2013). Most nonhuman

Catarrhini are found in tropical and subtropical forest habitats throughout parts of Europe, Asia, and Africa (Redmond 2008). Many species within this parvorder are listed by the International Union for Conservation of Nature (IUCN) as vulnerable, endangered, or critically endangered, primarily due to hunting and habitat loss from logging, urbanization, and human agricultural activity (Mittermeier et al. 2013). Catarrhine primates are generally long-lived and highly social, with complex social organization. This paper addresses key life history traits for this parvorder, focusing primarily on reproduction, growth, lifespan, and social structure. Information on diet, communication, and cognition within the parvorder Catarrhini is covered elsewhere within this encyclopedia and will not be addressed here. Human (*Homo sapiens*) life history parameters will not be included in this entry.

### Life History Parameters

Key life history parameters discussed below are reviewed for all extant catarrhine species in Mittermeier et al. (2013).

### Reproductive Cycles

The ovulation cycle of catarrhine primates ranges from 22 to 52 days, though 30–35 is typical. Unlike other mammalian species, catarrhine reproductive cycles include a period of menstruation, generally lasting 1–8 days (Hrdy and Whitten 1987). Female signaling of sexual receptivity often involves both physical and behavioral cues. In many catarrhine species, females exhibit only moderate swelling or color change of the skin surrounding the genitals; however, in some species, the physical changes are much more conspicuous and include large perineal swellings and/or reddening of the face or perineum (Hrdy and Whitten 1987). In Gelada baboons, cutaneous vesicles (blisters) also swell on the bare skin of the chest/ventral area and change color over the course of the reproductive cycle (Alvarez 1973). Olfactory cues, such as vaginal secretions, are also used in many primates as an indicator of a female's reproductive state (Hrdy and Whitten



1987). Behavioral signals of female sexual receptivity include a variety of solicitation postures and gestures, such as the presentation of hind-quarters, head-shaking, and crouching (Hrdy and Whitten 1987).

### Reproductive Maturity

Across parvorder Catarrhini, it is typical for females to become reproductively mature well before males. However, it should be noted that it is often difficult to determine when males become reproductively mature in a number of species as males often do not show obvious signs of maturity and may not reach their full reproductive potential until they are able to physically compete for females, which may be several years after the testes begin to produce viable sperm (Alberts and Altmann 1995). Age of sexual maturity seems to be related to adult brain size (Harvey and Clutton-Brock 1985), with larger bodied individuals (e.g., great apes) experiencing a longer period of development. Environmental factors (e.g., access to food resources) and social factors (e.g., stress, harassment) also play a role in age of sexual maturity. For instance, in some species, such as rhesus macaques, higher-ranking females become sexually mature before lower-ranking females as these individuals have more access to food and experience lower levels of social stress due to their rank (Melnick and Pearl 1987).

### Reproductive Seasonality

Reproductive seasonality is variable among catarrhine primates, though it tends to be more common in species that live in temperate regions or high elevations (Zinner et al. 2013). Seasonality is predominantly driven by the availability of primary food sources, though whether this food availability is timed for copulation (to initiate breeding cycle) or birth (ensuring sufficient energy for lactation) depends on the predictability of the environment (Brockman and van Shaik 2005). Harsh environmental conditions can also contribute to reproductive seasonality. For instance, in black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) living in the eastern Himalayan highlands where winter temperatures

are often below freezing, birthing is timed to take place when temperatures are increasing (Huang et al. 2012).

### Gestation, Birth, and Weaning

Gestation periods within Catarrhini range from 4 months to 9 months, with longer gestation periods being associated with larger adult body size (Harvey and Clutton-Brock 1985). Females typically give birth to a single offspring per birth; twin births can occur but are rare (Williamson et al. 2013; Zinner et al. 2013). Weaning in Old World monkeys typically occurs between 1 and 2 years of age (Zinner et al. 2013), while in the great apes, offspring are not weaned until 3–8 years (Williamson et al. 2013). Females typically do not give birth to another offspring until their current offspring is weaned, thus, in species in which infanticide is common (e.g., baboons, some colobus), females may wean their infants early in order to reduce interbirth intervals (Zinner et al. 2013).

### Dispersal

In most catarrhine species, dispersal is male-biased, with males typically leaving their natal groups upon reaching sexual maturity (Pusey and Packer 1987). Female dispersal is not common but occurs among the great apes and a few species of Old World monkey, whereas both sexes disperse in several species of langur and red colobus (Williamson et al. 2013; Zinner et al. 2013). If males do not immediately transfer to a new group upon leaving their natal group, they may live as solitary individuals or form an all-male group with other males. Species living in open habitats (e.g., Gelada baboons, *Theropithecus gelada*, and patas monkeys, *Erythrocebus patas*) are more likely to create all-male groups, likely to reduce predation risk (Pusey and Packer 1987).

### Body Size

Body size among catarrhine primates is highly variable. The smallest species (Southern talapoin monkey, *Miopithecus talapoin*) weighs in at approximately 1 kg, while the largest (Eastern gorilla, *Gorilla berengei*) can weigh up to



209 kg (Mittermeier et al. 2013). There is sexual dimorphism among most catarrhines, with female weights typically being 50% that of males; however, extreme sexual dimorphism is prevalent only among a few species of Old World monkey (mandrills/drills, *Mandrillus* spp.; baboons, *Papio* spp. and *Theropithecus gelada*) and the great apes. Arboreal species tend to be smaller than terrestrial species as large body size is a disadvantage when moving through dense vegetation and accessing fruits or young leaves located on thin terminal twigs (Harvey and Clutton-Brock 1985).

### Lifespan

Little information is known about the longevity of catarrhine primates as the sustained observations of many decades that would be required to determine lifespans are generally not feasible in most areas. Therefore, much of what is known about lifespan in primates comes from data collected from captive primates (Hakeem et al. 1996), though long-term studies have been carried out for some species (Williamson et al. 2013). Lifespan in Old World monkeys ranges from 18–45 years, while gibbons and great apes generally have longer lifespans (30–58 years). There appears to be a moderate correlation between lifespan and adult brain size (Harvey and Clutton-Brock 1985).

### Social Organization

For species-specific social organization parameters, see Mittermeier et al. (2013).

### Group Composition

Catarrhine primates are highly social, spending much of their time traveling, interacting, and foraging in groups. Group composition is highly intertwined with mating strategy, though foraging strategy, habitat size, and predation pressure also contribute to group living dynamics. The most common grouping patterns in catarrhine primates include multiple male, multiple female groups and single-male, multiple female groups; however, the number of females in these groups is highly variable, even within a single genus

(Wrangham 1987). For instance, the Angolan colobus (*Colobus angolensis*) lives in small groups of 3–4 individuals with a single male, while the Gureza (*Colobus guereza*) is commonly found in groups of 6–10 with a single male (Zinner et al. 2013). Generally, groups are more likely to consist of multiple males when there is a large number of females in the group (Mitani et al. 1996) or if there is overlap in female breeding receptivity (Nunn 1999). Increased predation risk might also lead to a greater number of males within a group, as is the case for several species of *Colobus* in Africa in which adult monkeys are susceptible to predation by eagles (Van Shaik and Höstermann 1994). Monogamous pair-living, which consists of monogamous parents and two or three offspring (Redmond 2008) is comparatively rare among catarrhines and seems to be primarily limited to the Family Hylobatidae (Wrangham 1987). Only one catarrhine, the orangutan (*Pongo* spp.), is considered semi-solitary, which is due to a greater spacing between individuals than is observed in other primate species. However, the social organization of this species might better be described as loose communities, centered around a single, dominant long-calling male (Delgado and van Shaik 2000).

### Group Size

Group size within Catarrhini is highly variable, ranging from small family groups of 2–6 individuals to extremely large groups consisting of several hundred individuals. Group size is driven by both ecological (e.g., predation pressure, food distribution, and habitat structure) and social factors (e.g., mating strategy, intergroup interactions, and infanticide; Wrangham 1987). In some catarrhine species (e.g., *Macaca fascicularis*, *M. fuscata*, *M. sinica*, *Pan troglodytes*), individuals generally live in large groups, but divide regularly into smaller groups during foraging. It is more common among Catarrhini for small groups to fuse with others to form “supergroups.” A notable example of this is found in hamadryas (*Papio hamadryas*) and gelada baboons (*Theropithecus gelada*), where the basic social unit is a single male with multiple females and their dependent offspring. However, these social units join

together with several others to form “clans” and several clans often join together to form “bands” of up to 1000 individuals (Zinner et al. 2013). Similar multi-level societies are found in snub-nosed monkeys (*Rhinopithecus* spp.), doucs (*Pygathrix* spp.), and proboscis monkeys (*Nasalis larvatus*; Zinner et al. 2013).

### Parenting

Compared to other mammals, primate infants are born altricial and undergo a lengthy period of dependency on their parents (Nicolson 1987). During this time of dependency, young primates learn how to forage, recognize and escape predators, and the social rules of the group (Preston-Mafham and Preston-Mafham 1999). Parental investment may differ between male and female infants in some species, with male infants requiring more parental care than females (Arlet et al. 2014). The care of young primarily falls to the mother, though there are some exceptions, the most notable of which is the Siamang (*Sympalangus syndactylus*). Male siamangs take over as the primary caregiver in the second year of life, which may serve to reduce the period of infertility following cessation of lactation in females, leading to a shorter interbirth interval (Lappan 2008). Infants are carried on the bodies of their parents, either ventrally or dorsally. Female olive colobus (*Procolobus verus*) are known to carry infants in their mouth for the first few weeks of life, likely due to short hair that is difficult for the infant to cling to (Zinner et al. 2013). Alloparenting, in which individuals other than the parents care for the offspring, is observed in a number of catarrhine species but is particularly common among Asian colobines. Typically, alloparents are related females, though in some species males may engage in alloparenting behavior (e.g., Barbary macaque, *Macaca sylvanus*; Olive baboons, *Papio anubis*; mountain gorillas, *Gorilla beringei*; Whitten 1987). Alloparenting may serve a variety of functions, including: mothering practice, enhanced status of alloparent, increased foraging efficiency of mother, increased survival of orphaned infants, and infant protection from conspecifics (Nicolson 1987; Whitten 1987).

### Grooming

Social grooming (also called allogrooming) consists of the manipulation of skin and hair of another individual (Cooper and Bernstein 2000) and is observed across a number of catarrhine species. Such behavior can take on many forms and involve a variety of individuals. For example, bonobos engage in grooming cliques, in which one individual receives grooming from three others, while in grooming clusters a larger number of individuals (range: 2–11 individuals) groom one another (Sakamaki 2013). Mutual grooming in bonobos occurs between one adult male and one adult female, whereas triadic grooming clusters involve two adults and one juvenile or infant (Sakamaki 2013). In gorilla troops, the dominant male may groom adult females, but he will also allow young juveniles to groom him (Preston-Mafham and Preston-Mafham 1999). While allogrooming may serve the purpose of removing ectoparasites and dirt from areas individuals cannot reach themselves (Hutchins and Barash 1976), the behavior primarily serves a social function. Allogrooming is generally used to build and maintain relationships between group members (Dunbar 1991), but it may also be used to obtain access to or maintain proximity with sexual partners (D’Amato et al. 1982; Gumert 2007), to obtain aid or defense in future agonistic encounters (Seyfarth and Cheney 1984), or as a mechanism for reducing tension or reconciling after agonistic encounters (Shino et al. 1988).

### Conclusion

Parvorder Catarrhini includes Old World monkeys, gibbons, and great apes. While all catarrhines are long-lived and highly social, the diversity of species within this parvorder makes it difficult to make generalizations about their life history patterns or behavior, even within the same family or genus. Variability in ecological and social conditions contribute greatly to this diversity. Members of the family Homonidae are the most different among the catarrhines, with longer gestation and weaning periods, later reproductive maturity, and longer lifespans.

## Cross-References

- [Catarrhine Cognition](#)
- [Catarrhine Communication](#)
- [Catarrhine Diet](#)
- [Catarrhine Locomotion](#)
- [Catarrhine Morphology](#)
- [Catarrhine Navigation](#)
- [Catarrhine Sensory Systems](#)

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Catarrhine Locomotion

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Synonyms

Cercopithecine; Cercopithecoid; Colobine;  
Hominoid

Definitions

- Bipedal      Locomoting using only hind limbs for support and propulsion.
- Brachiation      Below branch, hand-over-hand suspensory locomotion, where body weight is supported by the forelimbs. This is also sometimes known as “arm-swinging.”

- Bridging      Crossing a gap in the canopy where contact with one support is maintained while contact is made with another.
- Climbing      Progression up a vertical or near-vertical support
- Digitigrade      A locomotor posture where the mass of the forelimb is supported by the digits and metacarpal heads of the hand. The palm does not contract the substrate.
- Knuckle-walking      A form of quadrupedal locomotion where the mass of the forelimb is supported by the second to fifth middle phalanges of the hand.
- Leaping      Propulsion, primarily by the hind limbs, as a means of crossing gaps in the canopy.
- Palmigrade      A locomotor posture where the palm and fingers of the hand contact the substrate, which is either ground or branch.
- Quadrupedal      Locomoting using all four limbs for support and propulsion. Above-branch quadrupedalism is progressing by walking or running on top of tree branches, with terrestrial quadrupedalism on the ground.
- Scrambling      An above or below branch progression in which each limb grasps a different support.

Introduction

Catarrhines are a monophyletic group of primates divided into two taxonomic superfamilies: Cercopithecoidea and Hominoidea. Cercopithecoids are Old World monkeys (those found in Africa and Asia), and hominoids are apes, including humans. Cercopithecoids currently have greater species numbers, wider geographic distribution, and more diverse ecological niches, whereas modern apes are less species rich but are more diverse in terms of postcranial morphology and locomotor behavior. This can largely be explained by comparing the evolutionary

history of each group. Hominoids were more diverse both taxonomically and behaviorally and also had a wider geographic range during the Miocene (23–5 million years ago) (Ward 2015). Since then, apes have become geographically more restricted such that modern apes are now limited to the tropical forests of Africa and Asia. The cercopithecoid radiation, by contrast, is much more recent. Modern Old World monkeys are currently species rich but have diverged less in locomotor behavior (Fleagle 2013).

Locomotor behavior is strongly tied to postcranial morphology, especially the proportions and features of the limbs. Differences in locomotor behavior are reflected in the postcranial morphology among hominoids and cercopithecoids. Overall, catarrhines have a relatively primitive mammalian body plan, as do primates in general. Unlike other mammals, primates lack specializations like hooves or wings but retain four limbs with grasping digits and opposable thumbs and big toes (with some exceptions). Catarrhines differ from one another mainly in terms of degrees, such as lengths of the limbs, digits, or tail. One common measure of these differences is the intermembral index (IMI), which gives the relative lengths of the forelimb to the hind limb. It is measured as a ratio of humerus plus radius length over femur plus tibia length (usually multiplied by 100 for ease of interpretation). Therefore, any animal with an IMI of 100 has equally long forelimbs and hind limbs. A value of less than 100 indicates longer hind limbs than forelimbs, whereas a value greater than 100 indicates longer forelimbs. Intermembral indices reported here are from Napier and Napier (1967).

## Cercopithecoids

Cercopithecoids are divided into two subfamilies, cercopithecines (including baboons, macaques, and guenons) and colobines (including leaf-monkeys, langurs, and African colobus). A typical cercopithecoid monkey is an arboreal quadruped, walking above branches on all four limbs in a palmigrade posture. Many cercopithecines spend much of their time on the ground, whereas most

colobines are entirely arboreal. Traveling between trees is often done by leaping, although colobines generally leap with greater frequency and over farther distances than cercopithecines. Forelimb suspension (progressing below branches using only the forelimbs) has been recently reported among certain larger-bodied colobines but is not seen among cercopithecines.

The Old World monkey body plan reflects adaptations for running and leaping, either on the ground or in the trees. They have a long, flexible back with seven lumbar vertebrae, a mediolaterally narrow but dorsoventrally deep thorax with laterally placed scapulae, and retain a tail. Like all primates, they have grasping digits, with opposable thumbs and big toes (with the exception of *Colobus*, see below). Grasping hands and feet are crucial for arboreal travel. The shape of the thorax places the feet near the midline for efficient running, the flexible back provides a greater range of flexion and extension for propulsion during running and/or leaping, and the tail acts as a balancing organ.

## Cercopithecines

Cercopithecines are largely found in Africa and are quadrupeds that mainly differ in the extent to which they are terrestrial. While cercopithecines range from almost entirely terrestrial to almost entirely arboreal, most are primarily arboreal with some terrestrial behavior. Nonetheless, the variation in degree of terrestriality has relatively little effect on the overall cercopithecine body plan. More terrestrial forms tend to have more equal limb lengths and shorter digits and walk in a digitigrade posture, whereas arboreal forms have longer hind limbs, a longer tail, and longer digits and walk in a palmigrade posture. Since even the more terrestrial forms still forage and/or sleep in trees, these similarities are likely related to the necessity of safely utilizing the arboreal environment (Rollinson and Martin 1981).

Macaques (genus *Macaca*) are the most geographically widespread nonhuman primates, ranging from Morocco to Japan to Bali, in a broad range of environments. Macaques differ in size and tail length between species, but overall, their relatively generalized body plan allows them to exploit



environments as different as the deserts of Morocco to the temperate, snowy forests of Japan. Macaques are quadrupeds that engage in infrequent leaping. Their behavioral adaptability allows more than one macaque species to live in the same geographic range. For example, in Borneo, the larger pig-tailed macaque (*M. nemestrina*) is largely terrestrial (but still feeds in trees), whereas the smaller, sympatric long-tailed macaque (*M. fascicularis*) is almost entirely arboreal (Rodman 1991).

Mangabeys (*Cercocebus*, *Lophocebus*, *Rungwecebus*) are forest dwellers in Africa. Species of the genus *Lophocebus* are arboreal quadrupeds, whereas *Cercocebus* is largely terrestrial (Gebo and Chapman 1995; McGraw 1998a). While these taxa have largely similar body plans, *Cercocebus* limb bones show features related to terrestriality not seen in *Lophocebus* (Nakatsukasa 1996). The kipunji (*Rungwecebus*) has only been described recently, and their locomotor behavior is currently not well known.

Baboons are the largest monkeys. Savannah baboons (*Papio*) are found in Africa and the Arabian Peninsula in a wide variety of habitats, from semidesert and savannah to woodland and tropical forest environments. They are the most terrestrial monkeys, which are reflected in their postcranial morphology. Baboons have fore- and hind limbs of roughly equal length (IMI of 95); a long, narrow scapula; and short digits on their hands, which they utilize in a digitigrade posture when walking. Despite these terrestrial adaptations, baboons sleep either in trees or on rocky outcroppings, and as such, they still retain grasping thumbs and big toes to engage in arboreal locomotion.

The gelada baboon (*Theropithecus*) is found in the highlands of Ethiopia. They live in grasslands but sleep in rock formations at night. Like savannah baboons, they have limbs roughly equal in length (IMI of 94), with short digits and are digitigrade.

Mandrill (*Mandrillus*) behavior has not been extensively studied, but mandrills live in dense tropical forests of Africa, where they are known to forage along the forest floor (Swedell 2011). Morphologically, mandrills are similar to baboons in that they are large-bodied, have relatively equal limb lengths (IMI of 94), and have short digits with large thumbs.

Guenons (*Cercopithecus*), and their close relatives, the swamp monkeys (*Allenopithecus*) and the Talapoin monkey (*Miopithecus*), are found primarily in the tropical forests of Africa. They are quadrupedal, primarily arboreal, leap less frequently than colobines (see below), and vary between species as to the amount of terrestrial and arboreal locomotion. For example, the blue monkey (*C. mitis*), Diana monkey (*C. diana*), and Talapoin monkey (*Miopithecus*) are almost entirely arboreal. De Brazza's monkey (*C. neglectus*), L'Hoest's monkey (*C. lhoesti*), and Campbell's monkey (*C. campbelli*) are partly terrestrial, while the sun-tailed monkey (*C. solatus*) is largely terrestrial (McGraw 2002). Guenon species are often sympatric, but will occupy different levels of the canopy. Despite the differences in the amount of terrestriality, guenons are largely similar in terms of postcranial anatomy, such as possessing relatively long hind limbs (IMI of around 80), typical of most cercopithecines.

Vervet monkeys (*Chlorocebus*) are closely related to guenons and are found in African woodland habitats. They are described as "semiterrestrial," although one study found only 20% of activity was terrestrial (which is less than some of the guenons above) (Rose 1979). Perhaps due to this close relationship and retained reliance on arboreal settings, vervets have similar limb proportions to guenons (IMI of ~80).

Patas monkeys (*Erythrocebus*) live in wooded steppe and woodland habitats. They are largely terrestrial quadrupeds and are the fastest primates, having been clocked running 55 km/h (~34 mph) (Hall 1966). They have long limbs that are roughly to equal in length (IMI of 92), which provide them with a long stride. They have short fingers and are digitigrade when walking on the ground. Like other monkeys, they climb into trees to feed or rest. Because most trees in their habitat are widely spaced, they usually walk between trees but will leap across narrower gaps.

### Colobines

Colobines are found in both Africa and Asia, with separate radiations on each continent. Compared to cercopithecines, colobines are more arboreal and leap both farther and with greater frequency



(Gebo and Chapman 1995). Colobines, like other leapers, tend to have longer hind limbs compared to forelimbs. Colobines also tend to have long digits but reduced thumbs. There are a few exceptions among the larger-bodied Asian colobines, with some semiterrestrial forms and some that display suspensory locomotor behaviors.

The three genera of African colobus monkeys are named by their coat color: black and white colobus (*Colobus*), olive colobus (*Procolobus*), and red colobus (*Piliocolobus*). All are forest-dwelling leapers and arboreal quadrupeds. In one study, all three African colobine genera were found to leap with more frequency than two guenon and a mangabey species living in the same forest (McGraw 1998a). The black and white colobus and olive colobus are typical of colobines, in that they have relatively long hind limbs (IMI of ~80) and long tails. They have short thumbs, and one species of black and white colobus in particular, *Colobus guereza*, lacks an external thumb altogether.

The red colobus, like other African colobines, is an arboreal quadruped and leaper. However, they will also commonly engage in climbing and scrambling behaviors (McGraw 1998b). The red colobus will occasionally hang by their forelimbs. Other African colobines will land from leaps on top of branches on all four limbs, while the red colobus will swing below the branch by its forelimbs. The red colobus has longer forelimbs than the black and white colobus.

Asian colobines are divided into two groups, the langurs or leaf monkeys and the odd-nosed monkeys. The langurs are largely typical colobine arboreal quadrupeds and leapers, with the exception of the Hanuman langur, which is partially terrestrial. Odd-nosed monkeys are larger in body size and more diverse in their locomotor behaviors.

Langurs of the genera *Presbytis* and *Trachypithecus* are found in South and Southeast Asia. Both taxa are arboreal quadrupeds and engage in leaping. All have longer hind limbs than forelimbs, typical of leapers (IMI of ~80). A comparison of *Trachypithecus obscurus* and *Presbytis melalophos* in Malaysia found that both were quadrupedal and leapers, with

*T. obscurus* primarily quadrupedal and *P. melalophos* relying more on leaping and also engaged in occasional arm-swinging (Fleagle 1978). Delacour's langur (*T. delacouri*) is quadrupedal but spends much of its time on cliff faces in Northern Vietnam (Workman and Schmitt 2012).

The gray or Hanuman langur (*Semnopithecus*) has a range from Sri Lanka to the Himalayas. They are roughly equally terrestrial and arboreal. They are perhaps the most terrestrial colobine and among the most adaptable (Ripley 1967). They have long limbs but with limb proportions similar to arboreal, leaping leaf monkeys.

Odd-nosed monkeys are among the least studied, but what is known shows that they are the most variable colobines in their locomotor behavior. The snub-nosed monkey (*Rhinopithecus*) ranges from tropical Vietnam to temperate China, where snow is typical in winter. *Rhinopithecus roxellana* and *R. bieti* are partially terrestrial (Kirkpatrick et al. 1998; Zhu et al. 2015). Arm-swinging is seen in juvenile *R. bieti* individuals, but not in adults (Wu 1993). The douc langur (*Pygathrix*) lives in Vietnam. They are largely quadrupedal but have been observed to brachiate with relatively high frequency (Byron and Covert 2004). The proboscis monkey (*Nasalis*) lives in Indonesia in riverine environments and sleeps along marginal river environments. They are entirely arboreal, with leaping as a large component of their locomotor repertoire, but also have been observed arm-swinging (Su and Jablonski 2009) and will occasionally swim across rivers. The Simakobu monkey (*Simias*) is found only on islands off of Sumatra. Little is known about their locomotor behavior; other than that, it is arboreal and leaps less than other colobines (Su and Jablonski 2009).

## Hominoids

Modern apes are largely restricted to the tropical forests of Africa and Asia. Each living ape group has their own unique suite of locomotor behaviors but shows a number of similarities (with modern humans being the exception). No modern ape is strictly an above branch palmigrade quadruped.

The Asian apes (orangutans and gibbons) are strictly arboreal and utilize suspensory (below-branch) forms of locomotion. African apes (chimpanzees and gorillas) are partly arboreal and terrestrial, utilizing varying locomotor behaviors in the trees, but are knuckle-walkers when terrestrial. Despite their different locomotor behaviors, modern apes have largely similar postcranial features. They have, to varying degrees, long forelimbs and digits, a broad thorax with dorsally positioned scapulae, shorter and less flexible lower backs (great apes have three to four lumbar vertebrae, compared to seven for cercopithecoids), mobile wrist and shoulder joints and lack an external tail. Although these similarities might suggest homology among these features, there is increasing evidence that these are merely convergent features as adaptations to being large-bodied arboreal primates, although this is still controversial (e.g., Begun 2007; MacLatchy 2004; Ward 2007).

Gibbons (*Hoolock*, *Hylobates*, *Nomascus*) and siamangs (*Symphalangus*) are the smallest living apes and are found only in the tropical forests of Southeast Asia. Gibbons are brachiators *par excellence*. Unlike other primates that will cautiously arm-swing below branches, brachiation by gibbons includes an aerial phase, where neither hand is grasping a support (often called “richochetal brachiation” (Hunt 1991)). Thus, gibbons progress in an acrobatic, pendular below branch fashion. As adaptations for this, gibbons are highly derived from the typical monkey body plan. Gibbons have extremely long arms (IMI of ~130) and fingers and have highly flexible wrists and shoulders. Gibbons arms are so long that they walk bipedally when they are on the ground or on large branches. Unusually for hominoids, they cross between gaps in the canopy by leaping.

Orangutans (*Pongo*) are the largest strictly arboreal mammals and are found only on the islands of Borneo and Sumatra in Southeast Asia. Similar to gibbons, orangutans locomote in a below-branch manner but, because of their large size, do so in a slow, deliberate mode often called quadrumanus (literally, “four handed”) climbing. Orangutans will progress in the trees in an upright posture supported from above by their forelimbs and often below by their hind limbs. Their

extremely mobile fore- and hind limbs allow them to grasp multiple supports, such that an orangutan may be grasping four different branches simultaneously. Orangutans cross gaps in the canopy by bridging or “tree swaying,” where the animal (more commonly, males) will use their weight to sway a tree back and forth, until it is close enough to the neighboring tree for them to cross (Sugardjito 1982). Male orangutans often must descend a tree and terrestrially walk to the next, as small terminal branches cannot support their large size. Orangutans have long forelimbs and short hind limbs and have an IMI of ~140. Orangutans also have extremely long fingers, mobile fore- and hind limbs, and a short lower back.

Gorillas (*Gorilla*) are the largest primate; male eastern lowland gorillas have an average mass of 175 kg (Smith and Jungers 1997). Gorillas are restricted to the forests of central Africa. Lowland gorillas live in the tropical rainforests of central Africa, and mountain gorillas are found in the montane forests of Uganda and Democratic Republic of Congo. The locomotor repertoire of gorillas therefore depends on their habitat, although they are the most terrestrial of nonhuman apes. Mountain gorillas are almost entirely terrestrial, as large trees are sparse in montane forests. Lowland gorillas are more arboreal; however, the larger size of male gorillas mainly restricts them to the larger branches near the trunk, whereas female gorillas, which are roughly the size of male orangutans, utilize more of the forest canopy (Remis 1995). When terrestrial, gorillas are knuckle-walkers. Like other apes, gorillas have a short lumbar spine, broad thorax with dorsally positioned scapulae, and longer forelimbs than hind limbs (IMI of 117) but have shorter digits.

Humans’ closest living relatives are the common chimpanzee (*Pan troglodytes*) and the bonobo or pygmy chimpanzee (*Pan paniscus*). Chimpanzees’ habitats range from the dense rainforests of Central Africa to the more open woodlands in the east to Tanzania. Chimpanzees are partly arboreal and terrestrial. Terrestrial travel is largely done by knuckle-walking, like gorillas (Tuttle 1969). When arboreal, chimpanzees are less suspensory than Asian apes, but more so than gorillas (Doran 1996). Chimpanzees are

diverse in their arboreal locomotor behaviors. They knuckle-walk on large supports and vertically climb up tree trunks. They engage in some suspensory locomotion and will often “scramble” or “clamber,” progressing in an uneven fashion, where the limbs are grasping multiple supports while the trunk is upright or orthograde (Hunt 1992). Bonobos are restricted to tropical forests south of the Congo River in Central Africa. Bonobos are both more arboreal and suspensory than chimpanzees (Doran 1993) but are otherwise similar in their locomotor behavior. Both species will occasionally walk bipedally, usually while carrying objects. Chimpanzees have longer digits and limbs overall but a lower IMI (107) than gorillas. Like other great apes, chimpanzees also have a broad thorax, mobile shoulders, and short lower back.

Modern humans (*Homo sapiens*) are unique among primates, and indeed among mammals, for our form of upright terrestrial bipedality. Humans walk with the trunk balanced over the hips, knees, and feet. Humans are the only primate to travel entirely on their hind limbs, and our postcranial skeleton reflects this. Humans have an S-shaped spine with an inward curving (lordotic) lower back, placing the center of mass above the feet while standing upright. Humans have a wide pelvis, with the gluteal muscles positioned laterally instead of posteriorly, allowing them to stabilize the pelvis during walking. Humans have valgus (inwardly angled) knees, placing them below the center of mass. Humans are also the only primate without a grasping big toe and have feet with arches, which act as shock absorbers. This lack of an opposable big toe makes human arboreal activity awkward. While the selective pressures that lead to this shift in our locomotor behavior remain controversial, bipedality (along with our large brains and tool use, both which appear much later in the fossil record) has allowed humans to permanently inhabit every continent except Antarctica.

## Conclusion

With the notable exception of modern humans, the locomotor specializations of modern apes have

largely restricted them to increasingly narrow geographic niches in the tropical forests of Africa and Asia. In contrast, cercopithecoids are relatively generalized, which has allowed them to not only exploit tropical forests but also niches as varied as the deserts of Morocco, the mountainous grasslands of Ethiopia, and the temperate forests of Japan and the Himalayas. While this is certainly related to numerous behavioral and demographic factors, the more generalized locomotor behaviors and postcranial morphology of cercopithecoids have allowed them to better exploit more varied environments better than modern apes.

## Cross-References

- [Catarrhine Life History](#)
- [Catarrhine Morphology](#)

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## Catarrhine Morphology

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## Definition

All the Old World higher primates, including monkeys, apes, and humans

## Introduction

Catarrhine primates are the haplorhine [i.e., non-strepsirrhine (=lemuroids and lorisooids)]

anthropoids (i.e., non-tarsiers) of the Old World, and they represent the most diversified group of primates living today. They have obtained their name from the Greek words that describe the placement of the nostrils, which face downward (κάτω (kato) = down + ρίνα (rhina) = nose), as opposed to their sister group, the New World monkeys, or platyrrhines, which bear a broad nose with nostrils facing outward (πλατύς (platy) = broad + ρίνα (rhina) = nose). They are currently represented by almost 183 different species, consisting of the well-known and highly diversified African baboons, drills, guenons, and mangabeys; the Asian macaques, langurs, and odd-nosed leaf monkeys; the Asian gibbons, siamangs, and orangutans; the African gorillas, chimpanzees, bonobos, and cosmopolitan humans. Their body mass ranges from the 1.1 kg of the female Angolan talapoin monkey to the 175 kg of a male African eastern lowland gorilla. Extant catarrhines mainly range in the tropical, the subtropical, and, in many cases, the temperate areas of both Africa and Asia. Nevertheless, they are the sole living primates that are not confined to the tropics. Some species are actually found in higher temperate latitudes, as in northern Africa, central China, and central Japan. In all these areas, they inhabit a very wide variety of habitats: lowland and montane tropical forests, gallery forests, woodland and savanna interface, savannas, semi-arid environments, lowland and montane temperate forests, rocky habitats, as well as high montane snow-covered deciduous and coniferous mixed forests. Their diet varies considerably. Most of the species are herbivorous (i.e., feed on plant items), and they may rely mainly on fruit, or they may feed principally on leaves. On the other hand, many species are omnivorous (i.e., they feed on both plant and animal food items), supplementing their diet with small invertebrates (larvae, insects, arthropods, worms, etc.) or more rarely, small vertebrates (amphibians, lizards, birds, or small mammals). Finally, a few species, such as the chimpanzees and humans, include a considerable, but variable, carnivorous component to their alimentary preferences, by hunting larger mammalian prey. In terms of habitat use, catarrhines may be exclusively arboreal,

exploiting the highest levels of tree canopies; semiterrestrial, being at home in both trees and the ground; or primarily terrestrial, using the trees only during resting and, occasionally, feeding, or even at all! This large primate clade also displays some remarkable ways of traveling around their habitat. Up in the trees, many species engage in frequent arboreal and quadrupedal walk and run and habitual leaping in between tree peripheries, and some of them employ cautious arm swinging along arboreal pathways or a very fast more acrobatic arm swinging mode, known as brachiation. On the ground, most species travel through terrestrial quadrupedal walk and run, whereas the great apes may prefer knuckle walking, fist walking, as well as obligate bipedal walking (e.g., humans)! Compared to the other primate groups, catarrhines are exclusively diurnal, i.e., they limit their activities during the light hours and sleep when it is dark; there might be some exceptions to the rule, but this is an occasional and not usual habit. On the other hand, catarrhine diversity is also expressed in their social organization and life. Among catarrhines, almost all different modes of social life are encountered, from solitary species, where both males and females range individually, with the former possessing extensive home ranges that overlap with many of the latter, to different levels of gregariousness, where a variable number of individuals travel and feed together in groups. Very few species (especially among the Asian lesser apes) form stable pair bonds, with variable roles between males and females (e.g., mate guarding or infant carrying), or polyandrous groups, composed of a single reproducing male and several sexually active females, which form a sort of communal breeding system. On the other hand, many species live in polygynous groups, consisting of one adult reproductive male and several females with their offspring. Satellite males form all-male bands and may interact with the group in variable ways. However, most species actually live in multi-male multi-female groups, which include several reproductively active adult males, females, and the offspring, characterized by a complex network of social relationships. In some species (e.g., chimpanzees), these social groups are more fluid,



modifying the size and composition of the group depending on source availability and individual relationships. In this case, females and the offspring tend to travel and forage together in smaller groups, whereas groups of males roam separately. These subgroups may join in at particularly rich food sources or form more long-lasting groups during the period of abundant resource availability. Finally, other species (e.g., baboons, snub-nosed monkeys) form multilevel societies, composed of multiple one-male units, each made up of an adult male, several adult females, and their offspring which congregate into large groups of many individuals. This great variety of ecobehavioral adaptations is accompanied by an analogous diversity in cranial, dental, postcranial, and soft tissue morphology, which is important for differentiating the diverse radiations of the group. However, they all share some common morphological characters that distinguish them from other primate groups, such as the strepsirrhines, the tarsiers, and the New World monkeys. These common traits actually characterize the group, and the present chapter aims to briefly describe them.

## Catarrhine Origins

In order to trace down the morphological traits of catarrhines, it is important to understand their origins and closest relatives within the fossil record. The current fossil evidence demonstrates that the earliest representatives of the catarrhines first appeared in the Afro-Arabian geographical zone during the early Oligocene, some 29–32 million years ago (Ma). However, molecular evidence suggests that catarrhines may have a much earlier history, which may extend back into the middle Eocene, some 40–44 Ma (Chatterjee et al. 2009). Despite this incongruence, the early catarrhines, geographically restricted to Afro-Arabia, diversified into many different groups until the early Miocene, some 17–18 Ma, when they first migrated to Eurasia (Harrison 2013). These fossil groups include the propliopithecids from the early Oligocene (29–32 Ma) Fayum deposits in Egypt, the saadanioids from the late Oligocene (28–29 Ma) Harrat Al Ujayfa in western Saudi

Arabia, the dendropithecoids from several early Miocene (15–20 Ma) East African sites, and the pliopithecids from several early to late Miocene (18–7 Ma) Eurasian sites from Spain to China. Moreover, they include two other groups, the hominoids (apes and humans) and the cercopithecoids (Old World monkeys), which comprise all the currently living catarrhines. Despite their great diversity, all these groups share some cranial, dental, and postcranial features that are essential for their definition. The major ones are the absence of a lateral orbital fissure, a highly reduced postglenoid foramen, a tubular ectotympanic, a dental formula of 2.1.2.3 (with the reduction of the number of premolars to two in each half of the upper and lower jaws), an anteriormost premolar shaped as a simple tooth with a broad buccal surface, a posteriormost premolar always shaped as a semi-molariform tooth, relatively square upper molars, relatively broad lower molars that increase in size from m1 to m3, lack of a dorsal epitrochlear fossa on the distal humerus, and possession of a saddlelike carpometacarpal joint of the thumb (Harrison 2013). Through the millions of years of evolutionary radiations within the catarrhines, some of these features have been retained, while others have been modified and are diagnostic of the different groups.

## Major Cranial Characters

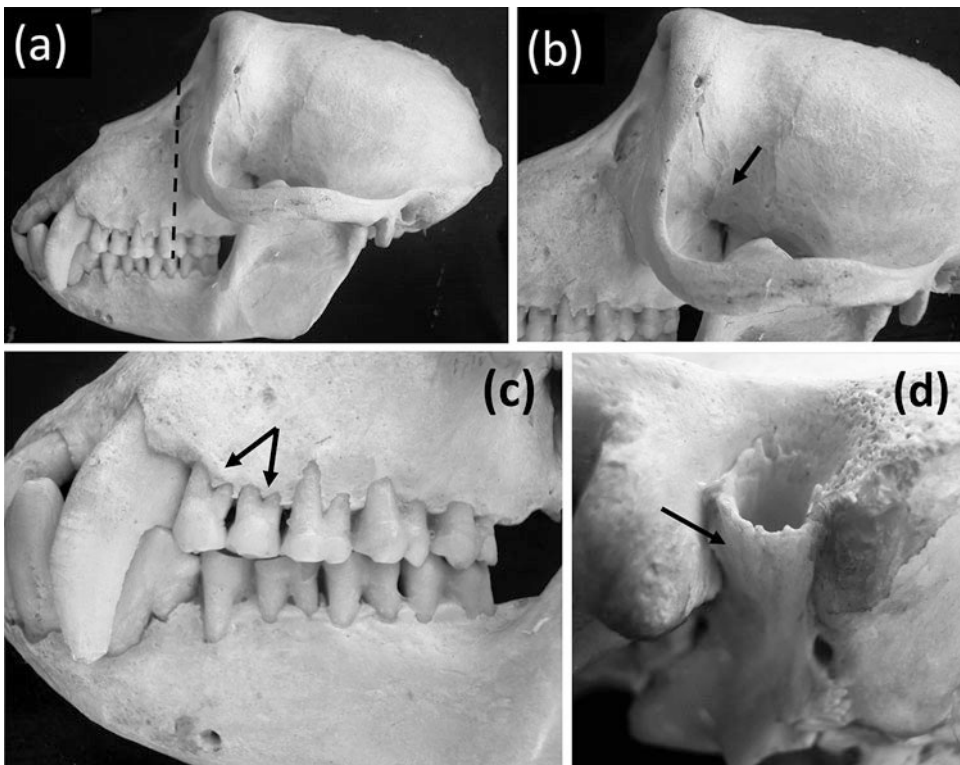
Catarrhines have inherited from their anthropoid ancestors a skull with a generally enlarged neurocranium and a relatively short snout (Fig. 1a). These morphological modifications are also associated with a relatively reduced internal nasal region, which is followed by a reduced number of nasal conchae, the narrow, curled, spongy bones that protrude from the nasal cavity walls and are responsible for regulating the air-flow through the nasal cavities. Moreover, the reduced function of the nasal passages and the associated decrease of the role of olfaction in more derived primates are further depicted by the shortening of the nasolacrimal duct, already in the haplorhines. In strepsirrhine primates the



nasolacrimal duct empties its contents into the anterior end of the nasal vestibule and contributes to the moistness of the wet rhinarium (nose) and open lips, which are an integral part of the role of the vomeronasal organ in functional olfaction. In contrast, haplorhine primates developed a dry rhinarium coupled with closed hairy lips. In platyrrhines, this nose is relatively broad and the nostrils are wide and directed laterally (outward), whereas catarrhines possess quite narrow nostrils that tend to face ventrally (downward), a significant external character that is responsible for their name. The new arrangement of the dry rhinarium and closed lip forced the nasolacrimal duct to shorten, to be redirected more vertically, and to open more caudally than in the nasal vestibule. This rearrangement is very likely associated with the reduced emphasis on vomeronasal-based olfaction and is further suggested by the relatively small accessory olfactory bulb in anthropoids

(i.e., tarsiers and platyrrhines), and its subsequent loss, as well as that of the vomeronasal organ in catarrhines (Rossie and Smith 2007). The short snout and the relatively reduced nasal bones appear to have compelled the positioning of the lacrimal bone within the orbit, rather than external to it on the snout, a character that catarrhines have further inherited from their anthropoid ancestors.

In catarrhines, as in all anthropoids, the orbits, the bony sockets where the eyes lie, tend to face forward in conjunction with their well-developed stereoscopic vision (Fig. 1a). However, in catarrhines the anterior margins of the orbits have slightly migrated posteriorly and are located at the level of the molars (Fig. 1a), instead of the level of canine-postcanine junction, the condition of ancestral anthropoids. The important role of vision in higher primates is further suggested by the bony rearrangements that surround the eyes. Whereas in strepsirrhines, the eyes are laterally



**Catarrhine Morphology, Fig. 1** Skull of macaque showing the most important cranial characters of catarrhines: **a** short snout, placement of the orbits (*dashed*

*line*); **b** frontal bone-sphenoid bone junction; **c** enlarged canines, two upper and lower premolars; **d** tubular tympanic bone

encircled by a postorbital bar, a strut composed of the frontal and zygomatic bones, the eyes of anthropoids, and therefore catarrhines demonstrate a completely different condition. Thus, the frontal, zygomatic, and sphenoid bones expand to form a bony plane that surrounds the eye latero-caudally and separates it from the temporal fossa behind, a condition known as postorbital closure (Fig. 1a, b). In this way, the eye lies protected within a bony cup, which presumably isolates the orbital content from the stresses imposed by the chewing muscles, acting at the level of the temporal fossa (Heesy et al. 2005). The walls and floor of the orbits are separated by several fissures that contribute to the transmission of specific nerves and allow the passage of vessels and veins. Most primates are characterized by three fissures, the superior, the inferior, and the lateral one. Anthropoid primates have retained distinctive superior and inferior fissures, but have significantly reduced the lateral one. Catarrhines are unique in having completely lost the lateral orbital fissure (Harrison 2013).

The increased role of vision is also implied by the anatomy of the eyes in higher primates. In contrast to prosimians, which possess an extra reflecting inner layer, known as tapetum lucidum, that enhances night vision but reduces visual acuity, anthropoids lack this reflecting layer. Instead, they bear a specialized area called the retinal fovea on the posterior surface of their eyeball. In this area, the light-sensitive cells are packed extremely close together, allowing very good visual acuity. This acuity is further correlated with the relative size of the optic foramen that allows the connection between the eye and the brain via the optic nerve (Kay and Kirk 2000). All catarrhines are characterized by full color vision similar to that found in most humans, with three types of color-sensitive cells (cones), each one sensitive to a different part of the visual spectrum (Jacobs 2009).

On the external surface of the lateral side of the skull, just behind (caudally) the closed eye socket, merge the frontal, parietal, zygomatic, and sphenoid bones. Catarrhines are distinctive from all other primates, in that the frontal bone contacts the sphenoid bone and separates the zygomatic

bone anteriorly from the parietal bone posteriorly (Fig. 1b; Fleagle 2013). In the other anthropoid group (the New World platyrrhines), the zygomatic contacts the parietal and separates the frontal bone dorsally from the sphenoid bone ventrally.

The middle ear of primates is characterized by the presence of the auditory bulla, a thin cup of bony tissue that derives from the petrous part of the temporal bone and covers the inferior surface of the middle ear. Moreover, the spatial relationship between auditory bulla and the tympanic ring is considerably variable and is important for distinguishing in between different primate groups. Among higher primates (anthropoids), the tympanic ring is attached (fused) to the lateral wall of the auditory bulla. But in catarrhines, the tympanic ring not only is attached to the wall of the bulla but further extends laterally to form a bony tube, the external auditory meatus (Fig. 1d; Harrison 2013).

Another important diagnostic catarrhine cranial character lies on the ventrolateral surface of the skull, just posterior to the glenoid facet where the mandible articulates with the skull. There lies the postglenoid foramen, a passage to where leads the sulcus of the petrosquamosal sinus and accommodates the joint anterior and middle venous plexuses from the middle cranial fossa, as well as the veins from the posterior cranial fossa. Lower primates and tarsiers are characterized by a large foramen, whereas catarrhines, as a group, possess a reduced postglenoid foramen, forcing the principal drainage of the brain to obtain a more posterior exit (Kay et al. 2008).

In the foremost part of the skull, the two premaxillary bones are completely fused together early in life, and therefore there is complete closure of the interpremaxillary suture, a cranial character which is defining for catarrhines. In an analogous manner, the two halves of the mandible are also fused together in their foremost part. This feature has been inherited from the anthropoid ancestors of catarrhines and seems to be functionally associated with the development of vertical lower incisors in anthropoids, in contrast to the more procumbent ones found in prosimians (Fleagle 2013). However, detailed ontogenetic

analyses have provided evidence that in ancestral catarrhines, this mandibular fusion is actually based either exclusively or majorly on the superior transverse torus over the inferior transverse torus of the mandible. Functionally, this condition probably minimizes stresses associated with lateral transverse bending and dorsoventral shear of the mandibular symphysis during mastication (Panagiotopoulou and Cobb 2011).

## Major Dental Characters

The dental characters in primates, as in other mammals as well, are usually the features that are very characteristic for each major primate radiation. All catarrhines possess two incisors in each quadrant. They are never procumbent, as in prosimian primates, and this is a trait that characterizes all anthropoids. The canine teeth are usually large with a large root and are always larger and usually taller in height than the incisors (Fig. 1c). These teeth have been further differentiated in being strongly bilaterally compressed with a single mesial groove and sexually dimorphic in Old World monkeys. A major feature that distinguishes catarrhine primates from their platyrrhine relatives is the number of premolars on each quadrant. Catarrhines only possess two premolars, in contrast to the three premolars of New World monkeys. This leads to a dental formula of 2.1.2.3 (Fig. 1c). The morphology of the anteriormost premolar is quite distinctive, as it is often a simple tooth with a broad and high buccal surface that sharpens the upper canine. On the other hand, the posteriormost premolar is always a semi-molariform tooth. Catarrhines have retained three upper and lower molars. The upper molars are usually relatively square shaped with low and conical cusps. Usually, the lower molars are relatively broad, with moderately high and conical cusps and low and rounded crests, and increase in size from the first toward the third.

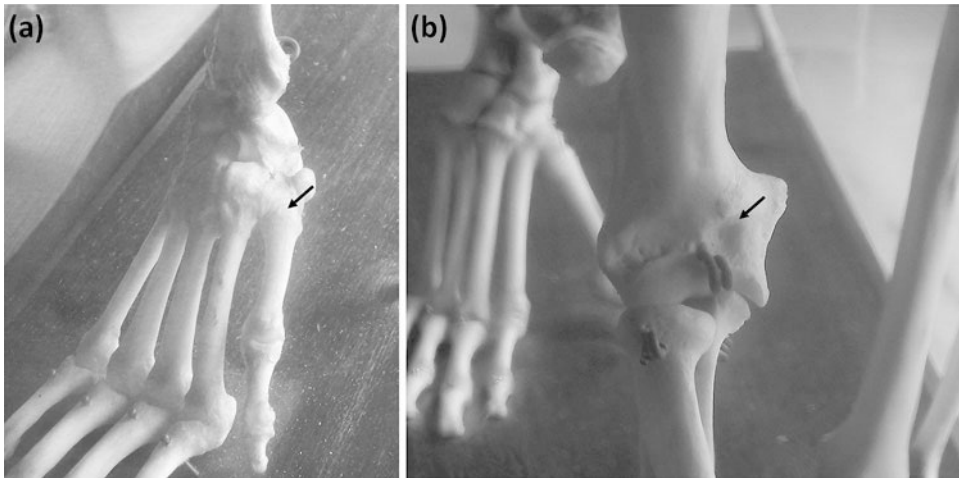
## Major Postcranial Characters

As in all anthropoids, the forelimbs and the hind limbs are more similar in length. This is the case

for platyrrhines, but in catarrhines there is a great variability which is related to the very divergent locomotor modes that this very diverse group has adopted. Thus, cercopithecoids (Old World monkeys) in general possess more or less equally long forelimbs and hind limbs. There are however some exceptions to the rule, such as some Asian odd-nosed colobines, which apparently engage frequently in forelimb suspensory locomotion. The pattern is a somewhat different in hominoids, and especially the living ones, where the forelimbs are longer than the hind limbs. This is not very evident in chimpanzees and bonobos, or even gorillas, but orangutans and gibbons and siamangs, which frequently use cautious and fast forelimb suspensory locomotion, respectively, possess quite long forelimbs compared to their hind limbs. Humans are the only hominoid primates with particularly long hind limbs in relation to their obligate bipedalism.

All catarrhines lack grooming claws and possess flat nails on all digits. Catarrhines are characterized by a saddle-shaped carpometacarpal joint of the thumb (Fig. 2a; Harrison 2013). This arrangement, between the trapezium bone of the carpus and the first metacarpal, allows a wide range of rotatory mobility, as well as abduction and adduction of the thumb contributing to thumb opposition and enabling powerful grasping capacity (Lewis 1989).

On the distal side of the anterior surface of the humerus, most primates are characterized by the presence of a variably wide foramen, called the humeral entepicondylar foramen, which accommodates the median nerve and the brachial artery. Although its presence is not that consistent in some primate groups, catarrhines are characterized among primates, by the complete lack of this foramen (Fig. 2b). The deep fascia and the tight skin at the distal humerus already protect the median nerve so the entepicondylar foramen may not be necessary. Moreover, this absence in catarrhine primates has been associated with increased forearm abduction in association with brachiating locomotion, has been considered as a by-product of the narrowing of the humeral distal articular facet and the reduction and posterior placement of the medial epicondyle, or even related to



**Catarrhine Morphology, Fig. 2** Skeletal features of catarrhines (macaque): **a** saddle-shaped joint between the trapezoid wrist bone and the first metacarpal bone of the thumb; **b** absence of entepicondylar foramen

stochastic events, and was subsequently related to some functional purposes (Garbino and de Aquino 2016).

At the ischial area of the body, all Old World monkeys, the gibbons, and the siamangs have thickened layers of tissue overlaying expansions of the hip bones (ischial tuberosities). These ischial prominences on each side beneath the anal area are provided with horny epidermal thickenings creating a pair of well-developed sitting pads. These pads are commonly known as ischial callosities (Pocock 1925). Only, the Asian and African great apes and humans lack these callosities. In the females these pads are separated in the middle line, and the opening of the vulva is typically situated inferiorly between them. In males, where there is no such obstacle, the pair of callosities sometimes tends to fuse completely across the middle line below the anus, although in the majority of the cases they retain their distinctness. Their functional importance is still debated, but they are probably related to the frequent use of seated postures on slender branches during both resting and sleeping, as well as during feeding, as they provide a wide area that contributes to comfortable and stable sitting (McGraw 2017).

Living catarrhines represent a highly diversified group of primates. However, in general the living catarrhines are among the largest of living

primates. Their body mass ranges from the 1.1 kg of female talapoin to the 175 kg of male gorillas. Definitely, they are on average much larger than the representatives of their sister group, the platyrrhines. These latter usually range between 100 g of pygmy marmosets and 13 kg of the largest atelid monkeys. Moreover, living catarrhines are much more terrestrial than other groups of prosimians and monkeys, as many species, such as some baboons, some mangabeys, many guenons, some langurs, gorillas, and humans, make extensive to exclusive use of the ground (Fleagle 2013). Another distinguishing feature indicating the great diversity of catarrhines is the large proportion of specialized folivorous (leaf eating) species. Supplementing the dietary regime with leaves is a relatively widespread habit among primates, especially during periods of fruit scarcity. However, catarrhines evolved whole radiations that morphologically and behaviorally adapted to regular folivory, such as the colobus monkeys of Africa and the langurs (leaf monkeys) of Asia, all belonging to the subfamily Colobinae of the cercopithecoidea.

## Conclusion

All these cranial, dental, and postcranial characters render catarrhines one of the most diverse

groups of primates. This diversity is also demonstrated in the variety of characters that further differentiate between the different adaptive radiations, such as the cercopithecines and colobines within the cercopithecoids and the lesser and great apes within the hominoids. All these morphological characters are beyond the scope of this chapter. Despite this variety, the characters presented here are those that unite all catarrhines as a unique group of single origin that has conquered and shaped the world.

## Cross-References

- [Catarrhine Diet](#)
- [Catarrhine Sensory Systems](#)
- [Primate Diet](#)
- [Prosimian Morphology](#)

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## Catarrhine Navigation

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## Introduction

Primates are different from other animals in several ways: they possess hands with at least one flat nail instead of paws and claws, their big toes are opposable (except humans), and they have relatively large brains. Such broad anatomical differences also exist within the primates, and this has been the reason why taxonomists have set catarrhines apart from all other primates. Most prominently, catarrhines are the only primates that have dry noses with the nostrils pointing forward or downward, just like our human noses. Catarrhine species share additional anatomical features, but it is not easy to see how these should affect their navigational abilities and set them apart from other primate clades.

A factor that may be important, however, is the fact that catarrhines are generally larger than other primates and therefore have higher energy requirements. Unlike other animals with very large bodies such as elephants and horses, they cannot obtain more energy by extending feeding times into the night. So, what are their options?



Leaf-eating monkeys (Colobinae) have solved this problem by evolving a specially adapted stomach supporting bacterial colonies that allow them to digest the cellulose in their diet of leaves, unripe fruits, and seeds. Feeding on such abundant foods has the advantage that food is generally available and nearby (Byrne 2015).

However, other large-bodied catarrhines rely on particularly energy-rich ripe fruits. Unfortunately, fruit is unreliable, because it is often available only at specific places in space during short time periods per year. Some trees fruit at irregular time intervals and do not necessarily synchronize their fruiting state with conspecifics. To make things worse, some catarrhines complement their fruit diet with a wide variety of additional foods located at other places their home ranges. Some live in large groups, comprising up to 100 members, and some inhabit areas with pronounced seasonal changes in food occurrence. To find enough and adequate food for all these mouths, these groups require large home ranges that cannot be overlooked from one location, nor walked in a single day. To deal with the unreliability of their food, these catarrhine primates need to be experts in remembering spatial locations, food types, fruiting periods, and experienced navigators to travel among them efficiently. According to the “cognitive map hypothesis” (sometimes called the “ecological intelligence hypothesis”), some primates have evolved large brains to overcome this specific set of problems, permitting advanced cognitive operations (Milton 1981, 1988). This puts a broad group of catarrhines into the spotlight: the cheek-pouch monkeys (baboons and macaques), guenons, gibbons, orangutans, gorillas, chimpanzees, and humans, who are all relatively large-bodied, live in large groups in large home ranges, and rely on ripe fruit, at least to some degree.

However, how do catarrhine primates navigate large-scale space? Do they really find their food by means of more sophisticated cognitive operations than do other animals? How do they memorize feeding events? How do they represent spatial relations among different places? And – most importantly – how can we find out?

## The Concept of Cognitive Maps

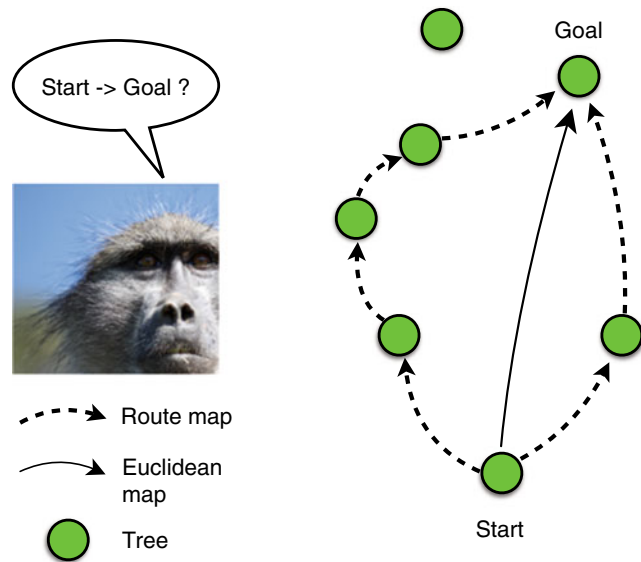
During their observations of rats running complex mazes, Tolman and Honzik (1930) noted that animals learn about space just by exploration, even if they do not experience any positive or negative events therein. To investigate how quickly rats learn to recover a food reward at a specific out-of-sight maze location, they formed three rat groups. Each group obtained a different treatment: individuals of group A found the reward from the first trial onward, while the rats in group B were given the opportunity to explore the maze without reward for a couple of trials, before being rewarded during the next couple of trials. Group C was a control group. They found that group B rats – the ones who had been allowed to explore the maze – learned to recover the reward much quicker than group A. Obviously, they had formed a memory of the layout of the maze during exploration in the absence of food and were able to apply it to revisit the goal location quickly when needed. Tolman (1948) claimed that the brain, rather than forming infinite numbers of associations between stimuli and responses, filtered important spatial stimuli and put them into context with others, forming an integrated “inner image” or “mental representation” of space that encoded several events and some spatial properties between them. He called this mental construct a “cognitive map” and stated that such maps could be relatively simple and strip-like or broad and comprehensive, containing large numbers of locations where important events had taken place and the spatial relations between them. He pointed out that the degree of comprehensiveness of this map decided how flexible an animal could navigate space.

Psychologists found Tolman’s concept useful and refined his ideas. They distinguished route maps (sometimes also called network maps) from Euclidean maps (synonymous of survey maps or vector maps) to describe the mental representations that animals have of spatial locations and events (Fig. 1). Route maps are thought to represent the paths through an environment and nodes of intersection. They contain sequences of memorized landmarks and knowledge about what



**Catarrhine Navigation,**

**Fig. 1** Behavioral consequences of using a cognitive route map and a Euclidean map. Euclidean maps allow animals to take novel shortcuts to out-of-sight goals



to do at each landmark, perhaps in the form “big rock with dead log, go left; field of thorn bushes, go straight ahead; etc.” (Byrne 2000). Theoretically, such a route map ties individuals to relatively narrow standard paths, beyond which they get lost. A route map can represent a single familiar route or constitute in a network of many routes and intersections that extend over an animal’s entire home range, connecting a large number of important locations with each other.

Euclidean maps, in contrast, are thought to resemble a mental image similar to what a bird can see when flying over an area, a “view from above,” from which all important locations and their spatial relations are visible at once. Euclidean maps are encoding distance and direction information among all important resources and consequently allow animals to flexibly take least-effort routes between any two resource places. The behavioral manifestation used to distinguish whether cognitive maps are based on route or Euclidean information is shortcutting: only a Euclidean map allows an animal to take a novel shortcut to reach a destination.

Neuroscientists use the concepts of egocentric (or self-referenced) versus allocentric (or map-based) representation to describe the neuronal processes involved in mammal navigation. This concept is closely related to the mental map

concept, but it is important to understand their fundamental differences. According to this view, animals using an egocentric navigational mechanism are thought to locate objects in space with reference to themselves by means of “path integration.” Path integration requires active body movement which allows to constantly integrate distances traveled and turns taken. It enables an animal to return to the starting point, for example, the nest, in a straight route at any time. During allocentric navigation, an animal is thought to use the spatial relationships among landmarks to determine its own position in the environment. Thereby, distances between landmarks are thought to be estimated by means of path integration. According to this concept, the egocentric and allocentric systems always work hand in hand in many mammal species, with the availability of landmarks determining which one currently dominates. In humans, it has been suggested that mechanisms of formation of episodic and semantic memory have evolved from egocentric and allocentric navigation in the physical world, as the brain networks that support these navigation mechanisms and memory formation extensively overlap (Buzsaki and Moser 2013).

The remainder of this entry will refer to the concepts of route maps and Euclidean maps, as they formed the basis for many studies on the

cognitive aspects of nonhuman catarrhine primate navigation in large-scale space.

## Integrated Memories of Location and Food Type

Many catarrhine primates have a long-term memory for several food locations. For example, mangabeys living in the African rain forests approach distant, non-visible trees where they have previously fed on ripe fruit more frequently and faster than they approach trees without fruits (Janmaat et al. 2006). Before encountering spatially predictable economical food or water sources, baboons inhabiting the sub-Saharan savannas and semideserts usually travel rapidly and in a linear manner over large distances. Sometimes, they start speeding up their travel shortly before reaching important places where they spend some time feeding or drinking, but with the fruit trees or water holes still out of sight. In contrast, more indirect and slower travel precedes encounters with less predictable and less economical foods. This has been interpreted as evidence that they aim at specifically important places (Sigg and Stolba 1981; Kummer 1997).

Thus, if catarrhine primates approach memorized places in a goal-directed manner, do they expect specific rewards at these locations? Menzel (1991) investigated this question in free-ranging Japanese macaques (*Macaca fuscata*). He walked with these animals and from time to time placed either a piece naturally occurring but currently out-of-season akebi fruit or a piece of equally preferred chocolate on the ground. As soon as an individual ate the food, he recorded start location and subsequent behavior. What the macaques did after finding akebi fruit was different from what they did after discovering chocolate. Akebi finders stared upward, walked to and inspected distant trees containing akebi vines. In contrast, chocolate finders returned to the precise location of their finds hours later, sometimes on the following day, to visually and manually inspect the location. Control animals who found nothing did neither enter akebi vines nor go back to the start location. Thus, macaques who found a known

food – akebi – relied on the specific spatial long-term memories generated by multiple previous encounters with that food type. By doing so, they would have found many more items of the same food – had akebi only been available. Macaques who found a novel food type – chocolate – lacked any spatial memories of additional “chocolate trees” and were forced to base their search on a memory generated by that single recent find.

## Anticipation of Food Type

At what point along a foraging trip do these memories become available? Do baboons recall a food source ahead of them when they start speeding up their travel? Does a chimpanzee recall a fig tree containing sweet fruit when waking up in the morning? Do catarrhines think of future visits to distant locations before they fall asleep?

Noser and Byrne (2007a) noted that departure times from the sleeping site of a baboon group living in a South African woodland savanna depended on the fruit type that was first consumed in the mornings. Generally, these baboons took up foraging sooner on hot days compared to colder ones, obviously to forage during the cooler mornings and to have enough time to rest in the cool shade during noon. However, departure times were particularly early when they breakfasted on out-of-sight mountain fig fruit (*Ficus glumosa*). In contrast, when they breakfasted on out-of-sight marula fruit (*Sclerocarya birrea*), they left the sleeping cliff significantly later. What caused these varying departure times? Figs were confined to a couple of small trees, and many baboon groups fiercely competed for access to them, as only a single group could occupy and deplete a tree at a time. In contrast, ripe marula fruit occurred in quantities that supported the entire baboon population in the area for weeks, in addition to a wide variety of additional mammalian and bird foragers. Thus, Noser and Byrne (2007a) proposed the ability of anticipating breakfast type soon after waking up to be a cognitive tool to buffer competition: only those baboons who

arrive early at the fig trees are able to obtain fig fruit that had freshly ripened overnight.

This idea was confirmed in chimpanzees (*Pan troglodytes*) living in the Tai rain forest in Ivory Coast (Janmaat et al. 2014). Similar to the baboons, these chimpanzees departed earlier from their nest when breakfasting on figs and later when breakfasting on other fruit. Moreover, while baboons usually reuse a small number of safe trees or cliffs to sleep in at night, chimpanzees build a new nest on a different tree every evening. As a consequence, distances and directions to the breakfast fig trees alter from morning to morning, making the task of arriving early at the fig trees more difficult. Nevertheless, the chimpanzees managed to arrive early at the fig trees: when the nests were located further away from the fig trees, the chimps left their nests earlier, while they left later when the fig trees were situated at shorter distances. In line with Noser and Byrne (2007a), Janmaat et al. (2014) argued that the chimps did so to outcompete other chimpanzees, birds, or squirrels, who also like to feed on newly ripened figs.

Thus, catarrhine cognitive maps encode several integrated memories for locations in large-scale space where different food types had been consumed. These memories can be formed through a single foraging episode and allow for flexible decisions about travel onset that affect the likelihood to successful encounters with anticipated food. It is not known to date whether non-human catarrhine primates anticipate more than a single future event.

## Travel Among Several Locations

If the cognitive maps of catarrhines contain several locations in space, how efficiently do they travel among them? Or in terms of the “traveling salesman (or salesperson) problem”: given the positions of several places on a scaled map, which is the routing that will take a monkey or ape to all of these locations covering the shortest possible overall distance? The answer to this general problem is not simple, because overall travel distance is to a large extent affected by the order in which goals are visited. Places may differ in

reward or other intrinsic features, so that many past experiences must be compared. How do catarrhine primates behave in the context of this sort of problems?

In his seminal study, Menzel (1973) investigated how captive chimpanzees navigate among several food sources. For this purpose, an experimenter carried around one of six young chimpanzees and allowed him or her to watch a second experimenter hide some fruit in each of 18 places in a large outdoor enclosure. All six chimpanzees were then simultaneously released and allowed to forage in the outdoor enclosure. Time when each piece of fruit was found (or the corresponding place was rechecked) and the identity of the animal involved were subsequently recorded for 1 h. The informed animals found a total of 12.5 fruit pieces per trial; the ignorant ones found only 0.21 pieces. Importantly, the informed chimpanzees did not follow the routes the experimenter had taken when hiding the fruit, but they ran from one place to the next, no matter how distant this place was situated from the previous one. They did not minimize overall travel distance, but kept it fairly short. Thus, captive chimpanzees who forage under the eyes of hungry conspecifics are not particularly good at any attempt to solve the traveling salesman problem.

## Route Maps Versus Euclidean Maps

Altmann and Altmann (1973) were the first to notice that baboons (*Papio cynocephalus*) that forage in their natural habitats forage on the basis of an extensive spatial knowledge about food and water sources and use a cognitive map.

Sigg and Stolba (1981) studied the cognitive maps of a group of baboons (*Papio hamadryas*) in detail. This group lived in a semidesert in Ethiopia and traveled extraordinarily large distances each day (up to 20 km). They carefully mapped travel routes and feeding and drinking locations. When superimposing these maps, it became evident that the baboons neither used narrow standard routes predicted by a simple, strip-like route map nor did they flexibly take least-distance routes between any two resources as predicted by a Euclidean

map. Instead, they often traveled along standard “street segments,” by definition 150 m wide and at least 500 m long, which they flexibly combined each day so that their location could never be predicted. The relative large width of the street segments suggests that the baboons recognized distal landmarks or scenes and used them as reference points along remembered routes.

While these results still suggested an impressively detailed route map, this study also highlighted a major problem that researchers generally face when studying animals in the wild. How can we know whether a given travel route is novel? A route that we record only once in a 2-year field study can nevertheless be a well-known route that the animals regularly used before we watched. On the other hand, the fact that we do not find any evidence for Euclidean mental maps in routine foraging in the wild is per se not evidence against them. Perhaps, the baboons do use Euclidean knowledge, but it becomes evident only in particular situations.

In an attempt to overcome these problems, Noser and Byrne (2007b) studied how the presence of competitors altered space use of a small baboon group (*Papio ursinus*, Fig. 2). These baboons normally approached important locations in a goal-directed way and from different angles, confirming that they possess a detailed route map. Because their daily routine was rather constant over the months, it was possible to predict their goals with high confidence. However, group encounters altered the baboons’ routine. Noser and Byrne’s idea was that Euclidean knowledge – if present at all – should allow this small group to flexibly alter space use and take detours around others.

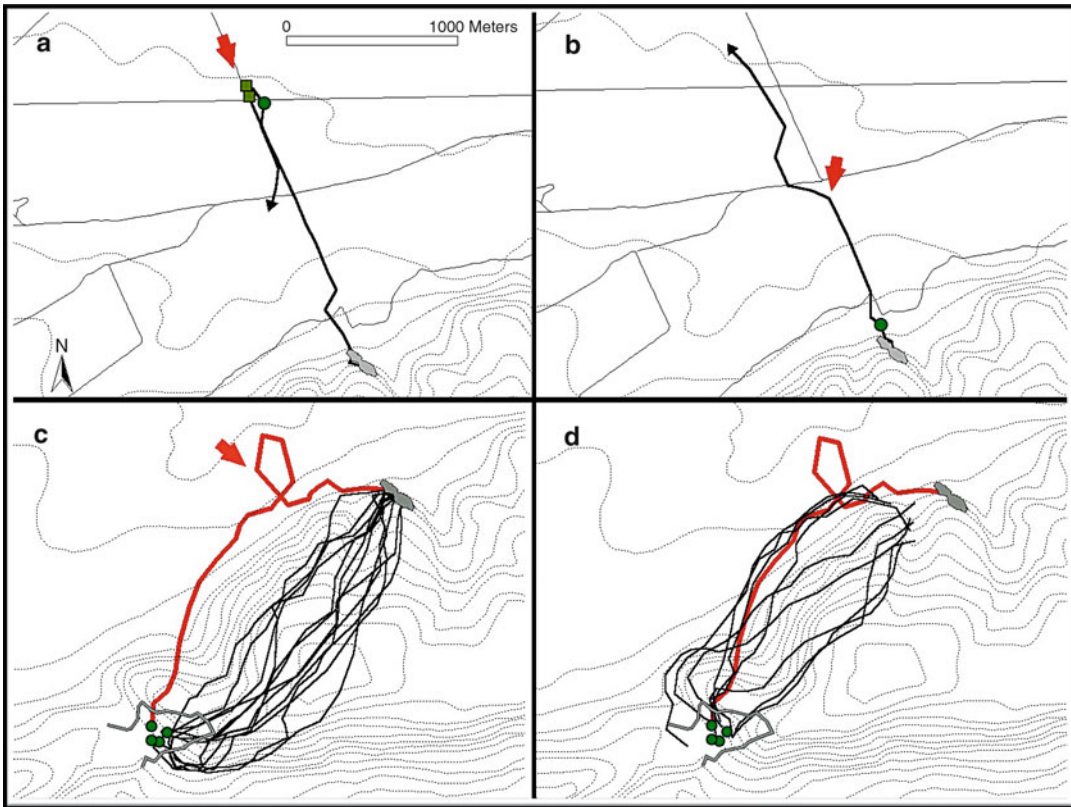
They found that this was indeed the case when the baboons could use topological structures as reference points: on and in an area of around 1,000 m of a hill, the small group reoriented to alternative fruiting areas or water holes situated at large distances, and they took large detours of several hundred meters that were out of sight of the initial routes. However, in a poorly structured plain area of their home range, space use after group encounters was very inflexible: when becoming aware of a nearby baboon group, the

focal group often remained on their initial routes, movement came to a halt, and the animals spent up to 60 min waiting on the spot until the others disappeared, before travel was resumed. Detours did occur in this area, but they were so small that visual contact with the initial routes could always be retained. Impressively, a whole day journey was abandoned on one occasion, causing the group to return to the sleeping site in the morning to feed on low-quality food until dusk. Thus, baboons expertly use landmarks present at distances up to a km in relation to which they organize travel. However, they do not use Euclidean knowledge about space to avoid group encounters, but rely on route knowledge. Evidence from other catarrhine species does not contradict this notion.

## Large-Scale Navigation in Humans

But how about humans? Navigating the sea has been of particular importance for humans for many centuries. In some cultures, this gave rise to the invention and spread of a variety of navigational instruments such as the sextant, the compass, the chronometer, and the GPS, allowing measurement of angles, directions, distances, locations, and trajectories. In other cultures, however, navigation remained instrument-free until very recently. Navigation techniques of the Pacific islanders, who traditionally made long canoe voyages with a high degree of accuracy, are a particularly interesting case.

In Polynesia, instrument-free navigation between distant islands is challenging because the islands are too far apart to be seen from each other. The sea lacks any stable landmarks to guide the trips from one island to the next. Experienced navigators were highly esteemed in their societies for their ability to memorize and combine large numbers of cues and their complex interrelations that guided their trips. They used sequences of stars that disappeared below the horizon in the desired direction, the sun’s path on the water, current wind directions, but also minute observations of long wavelength swells produced by distant winds and those of smaller waves interacting



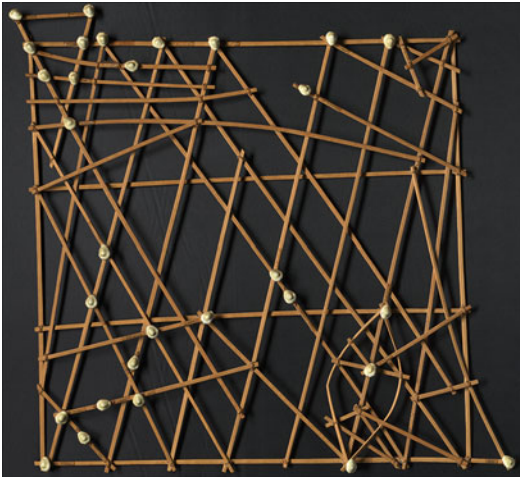
**Catarrhine Navigation, Fig. 2** Baboons abort their journey (a) or take small detours (b) as a response to encountering larger baboon groups (large arrow) in areas of their home range where rich topological structures are lacking. Reorientation (c, d) and large detours (not shown) take place only in the vicinity of rich topological structures (a hill). (c) After leaving the sleeping site, the baboons slowly headed SW, while another group was repeatedly calling from that direction. After a period of silence, they took up rapid travel into a SSW direction, where their main

water hole and important berry bushes were situated. They encountered the other group (large arrow) and turned back in a large circle. They then reoriented NW, where another large feeding area was situated. (d) To reach this area, they traveled a route that they usually used counterclockwise, from the NW feeding area back to the sleeping site. Dotted lines: contour lines. Circles and squares: locations where movement came to a halt for feeding (dots) or resting (squares). Foraging journeys (black lines) start at the sleeping site (small gray area)

with the swells and with land, of the location and form of clouds in the sky, and of the occurrence and behavior of sea animals. Because these cues were available only during a fraction of the journeys and sometimes entirely absent, integrating multiple cues created a “toolkit for navigation” for which redundancy was a critical feature (Huth 2016). Thus, rather than a Euclidean map that represented distances and directions among the islands, navigators used an extensive knowledge of sequences of external cues and landmarks that confirmed their actual positions along their journeys.

Indeed, the traditional “rebbelibs” or stick charts (Fig. 3) crafted by Micronesian navigators constitute a beautiful example of the kind of cognitive maps that humans can build. These charts are composed of wooden sticks that represent swell and wave patterns of the sea. Small shells attached to the support sticks represented the locations of the islands. Because they are constructed on the basis of personal experiences at specific locations, rather than on a “bird’s perspective,” each navigator constructed its own, unique rebbelib that looked different from those of his fellow navigators. However, rebbelibs represent





**Catarrhine Navigation, Fig. 3** “Rebbelib” stick chart used by the Marshallese to navigate the Pacific Ocean by canoe, indicating sailing directions for atolls and islands. Seashells depict the atoll and island locations. Each *straight stick* represents regular currents or waves around the low-lying atolls, while the *curved sticks* depict ocean swells (Source: National Library of Australia, MAP RM 4388)

integrated information about the relative spatial locations of the islands that are, in fact, spread out across several hundred miles, with body movement information that navigators had collected when lying on the canoe floor and sensing the rhythmic seas (Huth 2016). Thus, although these stick charts may not encode exact distances and directions, they constitute an allocentric representation of the spatial relations between important locations.

While only few individuals excelled in navigation among the Pacific islands, Maguire et al. (2000, 2006) confirmed that the neuronal basis of navigation is remarkably flexible in humans. London taxi drivers, who flexibly use their extensive knowledge of thousands of streets, places of interest, and their interconnectivity on a daily basis, show larger amounts of gray matter in the posterior hippocampi – one of the areas in the brain involved in navigation – than both a control group who do not professionally drive and London bus drivers who follow predetermined routes. The increase in neurological tissue occurs during the time when taxi drivers undergo extensive training to obtain their license, and this is also

the time – of course – when spatial knowledge dramatically increases. In contrast, trainees who fail exam and a control group who does not go through training at all do not show these structural and knowledge changes (Woollett and Maguire 2011).

Another important feature of human navigational ability is its large variation, spanning from the impressive abilities of Polynesian navigators and London taxi drivers to a significant number of healthy humans with severely impaired navigational abilities (Iaria and Barton 2010). Whether such differences exist in nonhuman catarrhine species remains open to future research.

## Conclusions

Catarrhine primates use space in a way suggesting that they possess a cognitive map that encodes information about several routes to important locations and content at these locations. Because they anticipate the content of their next goal, nonhuman catarrhines can act to positively alter future outcomes. However, there is no solid evidence that they anticipate more than a single goal at a time, and they do not minimize travel among multiple locations, but keep the overall distance short. To date, there is broad evidence for the usage of route-based representations of space. Only humans additionally routinely construct symbolic maps that encode information about the relations of objects and events as if viewed from a bird’s perspective. In contrast, evidence that nonhuman catarrhines are able to take novel shortcuts, a characteristic property of a Euclidean mental map, has remained feeble.

## Cross-References

- [Anticipation of Future Events](#)
- [Cognitive Map](#)
- [Edward C. Tolman](#)
- [Egocentric Frame](#)
- [Foraging](#)
- [Goal-Directed Behavior](#)
- [Intelligence](#)



- ▶ [Landmark](#)
- ▶ [Richard Byrne](#)
- ▶ [Traveling Salesman](#)

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## Catarrhine Sensory Systems

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## Definition

The Catarrhini are an Infraorder of the Order Primates that includes the Old World monkeys, apes, and humans. Sensory systems are the ways in which animals perceive and experience the world around them.

## Introduction

All living things have evolved sensory modalities to take in information about their environment, allowing them to react in appropriate ways to best enhance their survival and reproduction. In mammals, these modalities are often discussed as the five senses (i.e., sight, hearing, smell, taste, and touch). However, the mammalian sensory system also includes rarely considered senses, such as proprioception and other senses internal

to the body. Below, we discuss each of these modalities and how catarrhines use them.

## The Five Senses

### Vision

Primates rely primarily on visual information for many important daily activities, including evaluating predation threats, navigating interactions with conspecifics, and during foraging bouts. Among the primates, some have developed a specialized ability for color vision (trichromacy) which is unique in comparison to other eutherian mammals, who are thought to be either dichromatic or monochromatic. However, not all primates are consistently trichromatic; routine color vision evolved only in the catarrhines and in one other taxa (New World howler monkeys). All catarrhine species are considered routine trichromats, where both males and females are capable of color vision (Lucas et al. 2003). More specifically, this means that all catarrhines have the ability to distinguish between lights of different spectral composition regardless of brightness, and further, between red and green coloration (Surridge et al. 2003). This is in contrast to most platyrrhines (New World monkeys excluding howlers) and all strepsirrhines (lemurs and lorises), where trichromacy is generally a polymorphic trait and only females are capable of trichromacy.

Physiologically, trichromacy in primates is achieved through the actions of photoreceptor cells, called cone cells, in the retina of the eye. These cone cells generate responses that are then compared with each other by neural mechanisms to generate color signals. Some of this processing of color cues is thought to occur in the primary visual cortex (V1), but it is not yet clear to what extent. Cone cells house photopigments; in primates, the primary photopigment is opsin. Importantly, these cone cells differ in their spectral sensitivity, or more simply, the wavelengths of light they are sensitive to. Most mammals possess only two kinds of cone receptors, one of which responds to short-wavelength light of about 430 nm and is conventionally known as the

S cone and another that responds to long-wavelength light of about 560 nm and is conventionally known as the L cone. The combination of only two cones renders most nonprimate mammals dichromatic. However, in catarrhines, trichromacy is possible due to an additional cone receptor in the eyes that is maximally sensitive to middle-wavelength light of about 530 nm, which is conventionally known as the M cone. This additional cone arose early in the catarrhine lineage through a duplication in the gene for the long-wavelength cone that caused it to diversify into two kinds of cones with differences in peak sensitivities. More specifically, routinely dichromat primates possess a single gene coding for L cone pigments and M cone pigments, which is located on the X chromosome. However, in catarrhines, this gene was duplicated resulting in separate L and M cone pigments with differing spectral sensitivities. The signals produced by this additional M cone are then compared by a second neural subsystem: the relatively more modern “red-green” mechanism compares L with M cone signals, while an evolutionarily older “blue-yellow” mechanism compares S cone signals with both L and M cone signals combined. Because most platyrrhine primates do not have this duplicated M/L gene, males are thus genetically restricted to receiving only either an M or L opsin pigment on their X chromosome in addition to an S opsin (which is encoded by an autosomal gene). This limits them to dichromacy. Thus, among platyrrhine primates other than howlers, only heterozygous females can express trichromacy, but both male and female catarrhine primates are trichromatic.

In catarrhines, trichromacy is thought to have evolved to aid in foraging, either in the selection of ripe fruits or young leaves. This is because younger and more preferred leaves tend to be redder in color than more mature (and thus less preferred) leaves, which become green at mature stages of growth. The additional M cone enables all catarrhines to see young leaves among mature foliage, as the phylogenetically newer L/M subsystem allows for the detection of brighter, more colorful targets amidst a contrasting green

background. In addition, ripe fruits shift to a variety of colors during maturation, causing them to stand out as well among unripe fruits and leaves. Therefore, for catarrhines foraging for either young leaves or ripe fruits, consistent color signals are thought to be a more reliable strategy in finding food than other cues such as lighting or form. This is simply because lighting and form cues can be much more variable and thus less reliable than color cues. Further, the evolution of full trichromatic vision appears to coincide with a deterioration of the sense of smell, suggesting an increased reliance on such visual coloration cues. It has also been proposed that trichromacy can be useful in detecting intraspecific signals (Allen 1879). For example, ovulating females of some species display distinctive red sexual swells, males may signal high testosterone with red skin ornaments, and many colobine infants have bright neonatal coats in orange hues.

Another primate visual adaptation is the evolution of orbital convergence. Forward-facing eyes allow for binocular vision leading to excellent depth perception. This is important because early primates spent much of their time in trees. Binocular vision could therefore have allowed tree-dwelling primates to accurately judge distances when jumping between trees and branches. Additionally, the presence of a fovea centralis amplifies the effect of increased depth perception in haplorrhines as well as that of trichromacy in the catarrhines. The fovea centralis is a tiny pit located in the central retina that enables these primates to see sharp details and color and to have excellent central vision. In the fovea, light is able to fall directly onto the cones to produce maximum visual acuity. The fovea is thought to have evolved in stem haplorrhines and is a visual feature characteristic of both catarrhine and platyrrhine primates (Williams et al. 2010).

### Audition

In general, primate vocalizations serve to convey information about internal motivational states and the surrounding environment, including conspecifics and inanimate objects (Hauser 1993). These vocalizations are produced through movements of

the lungs, larynx, and the supralaryngeal vocal tract (Ghazanfar 2010). Hearing is known to be a multimodal sensory ability in primates, in that the auditory cortex integrates information from multiple sensory avenues. This includes the integration of visual information, such as when one links visual and auditory communication signals (e.g., matching facial expressions to congruent vocal expressions). The speed and accuracy of the visual orienting reflex is also an example of the integration of auditory and visual areas in the brain. Interestingly, auditory areas also appear to integrate tactile information, for example integrating the kinesthetic feedback from one's own speech movements with heard speech. In early primates, increased visual field overlap may have been associated with selection for increased sound localization abilities (Dominy et al. 2004). This is because in other animals, increased visual acuity positively correlates with a well-developed ability to localize a sound in space. More specifically, in other mammals sound localization abilities correlate with the width of the field of best vision, in that species with narrow fields of best vision (i.e., a fovea) have better abilities to localize sound than mammals with broad fields of best vision (Heffner 2004). Importantly, this trend holds for primates; the two species for which visual acuity and field of best vision are both known are relatively good sound localizers. As others have proposed, it may be that good sound localization acuity was evolutionary selected for its usefulness in directing vision (Heffner 2004). Primates are also similar to other mammals in that smaller species are capable of hearing relatively higher frequencies than larger species, but all primates appear to have relatively good low-frequency hearing; humans in particular have highly restricted high-frequency hearing.

Regarding the auditory sense, there are distinctive anatomical features that separate the catarrhine auditory sense from that of other primates. For example, all catarrhines have evolved a complete bony canal that leads from the ear drum to the external auditory meatus (outer ear hole) and is visible on the outside of the skull. This bony canal is called the ectotympanic tube. The

ectotympanic tube is formed by the ectotympanic bone, which consists of both a bony part and an external cartilaginous part. Put simply, this tube connects the tympanic membrane to the external ear. Tarsiers have also evolved a bony ectotympanic tube, but New World monkeys and prosimians have not (though in many species, a tube made up of cartilage is present). In regards to function, the ectotympanic tube has been proposed to be an adaption to reduce the amount of noise produced during mastication (Fricano and DeLeon 2016).

The ability to produce and comprehend speech is perhaps the most unique catarrhine capability but is restricted to only one extant species: humans. Physiologically, nonhuman primates are constrained in their ability to produce language by their anatomy and neural mechanisms. However, the neural mechanisms available in nonhuman primate brains are likely to have contributed to the evolution of human speech, in that human language appears to have built on mechanisms and structures available in nonhuman primate brains. Language processing is multimodal and is carried out in part by several different regions of the brain, including the well-identified Broca's and Wernicke's areas. These areas are well known to be crucial in the production of language (Broca's area) and in the comprehension of language (Wernicke's area). The only nonhuman primates thought to have a well-developed frontal lobe containing a functional homologue to one of these areas are catarrhines. In catarrhine primates, the anatomical and functional homologue to Broca's area is thought to be located in a section of the monkey premotor cortex (Fogassi and Ferrari 2007). Interestingly, this area houses audiovisual mirror neurons that discharge when a monkey performs an action and hears the corresponding sound (e.g., tearing paper and hearing a rip). This area and related structures may have evolved to exercise control over orofacial actions related to communication, but in humans may have come to control actions related to speech as well. Thus, the production and comprehension of language is a complex ability limited to humans but has clear roots in the anatomy and neural structures that currently exist in nonhuman primates.

## Olfaction

Relative to other mammals and other primates, the catarrhine sense of smell is reduced. Mammals usually have two systems to take in scent information from airborne molecules, the main olfactory system, which detects volatile odorants, and the accessory olfactory system, primarily made up by the vomeronasal organ (VNO), which detects nonvolatile odorants of heavier molecular weights (e.g., pheromones) (Dominy et al. 2004). However, catarrhines have lost the use of the VNO and the olfactory bulb that processes scent information is small relative to other primates. It has been hypothesized that the importance of trichromatic color vision in catarrhines may have relaxed the need for sensitive smell. Old World monkeys, apes, and especially humans have all lost the functioning of many of their olfactory receptor genes, which have been replaced by pseudogenes. Trichromatic New World howler monkeys show a similar pattern but this high rate of loss in functional olfactory receptor genes is not seen in dichromatic species or those polymorphic for color vision (Gilad et al. 2004). The timing of loss of the VNO in the catarrhine lineage also corresponds roughly with the evolution of trichromacy 25–40 million years ago. Catarrhines are notable for the degree to which color is used as signals of dominance and fertility, so it is possible that visual information that was available with routine trichromacy made information on pheromones gathered from the VNO redundant (Liman 2006). Even without a VNO, catarrhines are still known to detect some phenomenal cues but appear to do this with the main olfactory system.

## Gustation

It is appropriate to discuss taste immediately after smell, since the two are intricately linked when animals are selecting and experiencing resources. Gustation actually occurs when the stereochemical structure of a substance being tasted is recognized by taste bud sensory cells on the tongue, causing gustatory nerve fibers to fire, transmitting impulses to the brain of different taste sensations. However, what people normally think of as the "taste" of something is actually the interaction of a suite of sensory perceptions, including most

strongly the odor and reaction of taste receptors, but also the feeling of it touching the tongue, any irritation to the mouth caused by compounds within it, and perception of the temperature (Hladik and Simmen 1996). Prior to more intensive research, it was thought that primates could recognize four basic tastes, including salt, sweet, bitter, and sour. The taste of umami, which includes glutamic acid and its derivatives was added to this list later (Kawamura and Kare 1987). The notion of basic tastes is still often used but research on taste physiology has shown that most of the taste bud sensory cells located on the tongue will react to several substances though they may have higher affinities for certain ones (Faurion 1987). This suggests that taste sensations are more of a continuum rather than a set of basic tastes. Research on several primate species has shown that tasting abilities cluster in closely related taxa and differ when species are less related. In accordance with this, human and chimpanzee tasting abilities are very similar but some minor differences have been found between apes and Old World monkeys (Hellekant et al. 1997).

Taste perceptions, preferences and aversions have clear evolutionary importance. For instance, bitter, sour, and astringent substances elicit a strong taste aversion in primates and many of these (e.g., alkaloids, tannins, saponins, terpenes) are toxic. The three other “basic tastes,” sweet, salty, and umami often indicate nutritive content (Liman 2006). Primates show a correlation between body size and the threshold in the ability to detect sucrose and fructose, important sugars found in fruit. Larger primates have lower thresholds and thus a greater ability to detect minute concentrations of sugars. This may be due to larger animals having a greater area of lingual mucosa on the tongue leading to better taste acuity. This ability likely allows these larger primates to find a wide array of food stuffs palatable, helping them maintain their body size (Hladik and Simmen 1996).

### Somatosensation

The sense of touch can be defined as somatosensory perception that allows an organism to take in information on pressure, vibrations, itches, pain,

and temperature. Sometimes included in somatosensation are also the muscular and visceral sensations that can be perceived from inside the body (interoception). Primates appear to have a strong awareness of their internal homeostatic afferent activity and if the physiological condition of any part of the body is not normal this will be perceived by autonomic motor control and communicated to the brain with sensations such as thirst, hunger, discomfort, or pain (Craig 2003).

Different types of cutaneous receptors take in various forms of tactile information. Touch is perceived with rapidly adapting cutaneous mechanoreceptors like Meissner corpuscles, hair follicle receptors, and free nerve endings. Pressure is more likely to be detected with slow adapting cutaneous mechanoreceptors like Merkel corpuscles. Temperature is perceived with thermoreceptors and pain and itch are perceived by nociceptors (Mada 2000). The anthropoid primates, a classification that includes all catarrhines, are particularly notable for the density of cutaneous mechanoreceptors on the hand (Dominy et al. 2004). The hand is the most important sensory organ for tactile stimulus in catarrhines and almost all species have fine motor control, long fingers, an opposable or semiopposable thumb, and nails instead of claws, allowing the sensitive finger tips to be exposed. Mechanoreceptors for touch are especially located on the glabrous skin of the palm and palmar aspect of the fingers, where different types of sensory endings are found in the thick epidermal layer that forms patterns of ridges and grooves (Vallbo and Johansson 1984). Parts of the brain in the thalamus and cortex are primarily responsible for taking in somatosensory information.

Touch plays an extremely important role in communication in catarrhines, allowing information transfer through tactile means. Different types of touch are ascribed meaning but this may be changed or tempered depending on the situation and the duration or intensity of the touch (Hertenstein et al. 2006). For instance, a kick may be aggressive but if it is done lightly in a playful situation the meaning can be changed completely. The most developed sensory modality for infant catarrhines at birth is touch and it has



been shown to regulate infant psychological states and aid in normal biological and social development. In humans, physical contact between mothers and infants is key in bond formation, with more frequent and nurturing contact from the mother leading to more secure children later. As the other senses become keener into adulthood, touch does not have the over-riding importance that it has for infants; however, it is still vital for people in many interactions, in particular compliance, power relations, intimacy, and hedonic perception (Hertenstein et al. 2006).

One of the main tactile behaviors seen in catarrhines (in both nonhumans and humans) is grooming. While grooming does have a hygienic function, it is also very important in bonding and status maintenance. In Old World monkeys and apes, individuals generally spend more time grooming those that are kin or closer to them in dominance rank and grooming tends to go up the hierarchy with more dominant individuals receiving more than subordinates (Schino 2001). Grooming has also been shown to relieve stress, aid in reconciliation following aggression, and build bonds that may later lead two individuals to support one another in aggressive encounters (Dunbar 2010).

## The Neglected Sense

### Proprioception

In order for animals to control their movements, they must be aware of where their body is in space. Three systems are primarily used to do this, the felt position of the body (proprioception or the kinesthetic sense), visual cues regarding where the body (and each limb) is located, and tactile cues of body parts touching substrates. All of this information is processed in the premotor cortex in catarrhines. In particular, proprioception has been discussed in four broad sets of sensory perceptions: the sense of position and movement, the sense of tension, the sense of effort or heaviness, and the sense of balance (equilibrioception). Different but related mechanisms appear to be used for these four sets of perceptions (Gandevia 1996). Tendon organs allow a sense of tension and

the central nervous system is responsible for the sense of effort. Sensing of position and movement is done through muscle spindles and receptors in skin and joints but also through the vestibular system, which additionally provides the sense of balance. The vestibular system in the inner ear contains three semicircular canals that sense rotational movement and two otolith organs, called the utricle and saccule, that sense acceleration. Research has shown that the vestibular system has extensive convergence with many other sensory systems, acquiring constant signals from the eyes, muscles, joints, and skin, making it extremely important in everyday function for animals (Angelaki and Cullen 2008).

## Conclusion

Compared to primates that retain more primitive ancestral characteristics, catarrhine sensory systems are most notable for routine trichromatic color vision, a reduction in the olfactory sense, and the importance of the hand as a sensory organ.

## Cross-References

- [Platyrrhine Sensory Systems](#)
- [Primate Sensory Systems](#)
- [Prosimian Sensory Systems](#)
- [Sensory Receptors](#)

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## Categorization

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## Definition

A category is a knowledge/memory structure that summarizes an animal's understanding of perceptually variable but environmentally equivalent objects – especially relevant ecological natural kinds (e.g., blossoms for hummingbirds). Through category learning, animals come to behave consistently/adaptively toward these kinds. Animals have possessed a categorization capacity for hundreds of millions of years. Vervet monkeys (*Chlorocebus pygerythrus*) even employ eagle calls to alert conspecifics to dangerous category members. These calls “name” a member of Category Eagle, functioning like lexical items or words. Because categorization is an essential cognitive capacity, it has been a sharp focus of comparative research. Theory in animal categorization tries to explain the representational content of animals' categories and the process by which objects are perceived and categorized. Extensive research furthers this mission of psychological explanation. However, categorization raises difficult issues for comparative psychologists relating to learning, memory, generalization, abstraction, and symbolism.

## Introduction

Sections “[Theories in Animal Categorization](#),” “[Tasks in Animal Categorization Research](#),” and “[Stimuli in Animal Categorization Research](#)” in this entry survey the influential theories in animal categorization, the structure of categorization tasks, and the diverse stimuli employed. Section “[Prototypes and Exemplars in Animal Categorization Research](#)” explains why one theory – prototype theory – carries especially heavy weight when explaining animals’ categorization. Section “[What Kinds Are Natural?](#)” provides an evolutionary context for section “[Prototypes and Exemplars in Animal Categorization Research](#)” conclusion, paying attention to natural kinds in the environment. Section “[The Search for Rules and Hypotheses in Animal Categorization Research](#)” asks whether animals may learn categories through active hypothesis testing, and whether they then categorize by following the dimensional rules that are those crystallized hypotheses. Section “[The Search for Relational Concepts in Animal Categorization](#)” considers animals’ higher-level categories – the conceptual-relational categories like same or different. This section considers whether animals can transcend category groupings based on perceptual similarity, and the nature of the psychological processes that let them do so. Animals’ use of abstract concepts raises intriguing questions about the roots of human cognition and about the affordance that language offers to abstraction and symbolism. Finally, section “[A Broader Synthesis](#)” integrates across the entry to show why animal categorization research suggests a transformative theoretical synthesis.

## Theories in Animal Categorization

The literature is usefully organized around three dominant theoretical perspectives.

*Prototype theory.* Influential research by Rosch and others (e.g., Rosch and Mervis 1975) formed the basis for prototype theory. This idea is that minds average their experiences with categories, like predator eagles, to construct the central tendency or category prototype. This prototype could

be the mental content of the animal’s category. Then, as a processing matter, the animal could compare new items – new possible threats – to the prototype and include them in the category if similar enough. It will become clear that this theory has merit in explaining important aspects of animal categorization.

However, it presents problems, too. First, having a platonic ideal of eagle in mind does not tell you the category’s useful generalization radius. Where does eagleness stop, and vultureness begin? Baby vervet monkeys illustrate this problem by sometimes making tiny eagle calls for airplanes! Second, prototype averaging requires the brain algorithms by which the essence of many experienced exemplars can be extracted. These averaging algorithms are not trivial. Third, though some categories can be based in prototypes, others are logical (e.g., exclusive-or categories), ad hoc (e.g., items to try to save in a flood), or random (e.g., who is in my foraging group today). So, even if prototype theory has merit, categorization theory should leave room for the possibility that animals and humans might have different categorization processes for managing different categories.

*Exemplar theory.* Exemplar theory is diametrically opposed to prototype theory. This idea is that animals store specific exemplars as separate and individual memories, refer new items to these multiple stored category members, and include the new items as members if they are – in summed total – similar enough to the stored exemplars. Thus, exemplar theory envisions the vervet monkey’s Eagle category as a slide carousel of many eagle memories.

Exemplar theory presents problems, too. First, memory-capacity limits may fail the animal given thousands of experiences with common categories. Second, the resolving power of mind may not let the animal hold separate the thousands of experienced eagles. The exemplars may melt together in memory like chocolate drops in an excellent cookie, creating de facto a Rosch prototype representation. Third, the animal may be taken by the eagle while it is still working through its Eagle Rolodex to decide if it should flee!

However, exemplar theory has one remarkable aspect that explains its long dominance in the

literature. It potentially makes the psychology of categorization parsimonious and unitary, with only one exemplar storage/comparison process to understand. In essence, all categories could be deemed equivalent, solvable by just memorizing the exemplars to refer back to. Thus, one might not need to suppose species differences in categorization, or task differences in categorization strategies, or different brain circuits for managing different category tasks. It is an important question whether this parsimonious account is also the psychologically true account. Comparative science must pursue the latter.

*Classical or rule theory.* Classical Concept Theory predated both prototype and exemplar theory. This idea was that categories might be defined by criterial (100%-diagnostic) attributes for category membership (e.g., triangle-3 sides; dog-barks). This idea figured prominently in Bruner's work on concept formation (Bruner et al. 1956). Child psycholinguists favored this theory because they thought that young children might progressively carve up their conceptual worlds appropriately by adding criterial features to make finer conceptual distinctions, for example, animal (living), then bird (living-flying), and then parrot (living-flying-squawking). Classical Theory faced problems, too. First, many natural-kind categories may not have criterial features (e.g., voiceless dogs and hairless cats are still categorizable). Second, Classical Theory expects that all category members should be equally good category members because they all have the defining attributes. But this is patently false. Everyone agrees that golden retrievers are prototypical dogs, while dachshunds – on the fringes of the category – barely cling to dogness by their stubby paws. Third, there is no guarantee that animal species have the cognitive capacities that lie behind hypothesis testing for criterial features or systematic rule application in category tasks.

A range of research exploring these theoretical perspectives will be covered in sections “[Prototypes and Exemplars in Animal Categorization Research](#),” “[What Kinds Are Natural?](#),” and “[The Search for Rules and Hypotheses in Animal Categorization Research](#).”

## Tasks in Animal Categorization Research

The tasks of animal categorization have the familiar character of discrimination-learning tasks. A stimulus is presented, then the animal identifies it by choosing among several responses (e.g., left or right operant levers, abstract icons A or B). During learning, of course, the assigned identification response may vary as the animal proceeds unevenly toward concept mastery. Feedback is delivered following the animal's response on each trial – perhaps a food reward for a correct category-identification response, perhaps a tri-allell time-out period for an incorrect response.

However, discrimination and category tasks are crucially different in one way. Discrimination tasks commonly present two contrasting stimuli (two tonal pitches, two shades of red) – so that one stimulus maps to each response. This is the nature of psychophysical procedures, threshold assessments, sensory-sensitivity titrations, and generalization/habituation paradigms. In contrast, category tasks commonly have a many-to-one structure. There may be many members of Category A and B in these tasks, and the members will be perceptibly different, to varying degrees of dissimilarity. The animal must find some way to generalize inclusively among stimuli within categories while still discriminating exclusively across categories. This is what it means to say that a category is a psychological or behavioral equivalence class. The animal's psychological understanding of Category A must be broad enough to encompass the range and extent of its stimuli. Then, the animal can behave equivalently toward those stimuli, making the same identification response to all. Category tasks give the comparative researcher an extraordinary window on the kinds of generalizing and synthesizing processes that animals are able to apply, and about the kinds of generalization glues that a species may not be able to supply.

Given this general task logic, the researcher can make many different decisions to suit the particular question being asked.

*Category size.* The researcher can create categories that contain few or many category members (e.g., Smith et al. 2004; compared to Smith

et al. 2008). This choice has consequences. Large exemplar sets may challenge exemplar memory and push processing toward prototype averaging. Small exemplar sets may push processing toward exemplar memorization. After all, John, Paul, George, and Ringo are easily individually remembered – this category needs no prototype.

*Within-category similarity.* The researcher can decide how similar the members of a category will be to one another. A tightly coherent cloud of exemplars in psychological space may defeat individuated exemplar memories and encourage prototype averaging. A far-flung set of disparate exemplars may affect strategy in the opposite way. Readers are warned by this discussion that the category structure chosen for research is an important aspect of design that affects performance and theoretical interpretation. Caution: The fix may be in.

*Between-category dissimilarity.* Likewise, the researcher can decide how separate and dissimilar the two sets of instances, for Category A and Category B, will be from each other. Here, too, it is useful to imagine the A and B instances as two clouds of points in a Cartesian space. The two exemplar clouds can be close together, far apart, or even overlapping/colliding. The latter case will create confusable categories that are difficult to learn. It is also possible that this difficulty may distort the learning situation, so that the organism's normal processes of category learning become impossible and helplessness strategies ensue instead. This visualization of exemplar clouds is not just figurative. In many formal categorization models, this assumption is explicitly made mathematically, and the ideas of proximity, distance, and so forth are taken deeply seriously. Homa and colleagues (e.g., Homa et al. 1979) showed that, as category learning progresses, the category clouds condense and self-tighten within each cloud (because the organism's developing understanding of the categories draws the instances closer together), while the clouds of instances move apart from each other in similarity space (because the organism more clearly understands the distinguishing contrasts among them).

*Structural ratio.* The previous two aspects of category structure can be combined and frequently are. For example, one can take the degree of

within-category similarity displayed by Category A and Category B and divide this by the degree of between-category similarity, which can be measured as the degree of similarity between Category A and B items. In the generic situation, the numerator of this ratio would be large, the denominator small, producing a high structural ratio indicative of well-structured, learnable categories. In contrast, a category structure presenting a structural ratio near 1.0 would be extremely difficult, because items would be as much like opposing category members as they are like their own category members. This kind of category task was common in early cognitive research on categorization, and this presented serious interpretative issues.

*Linear separability.* This last aspect of category structure is technical but still supports an important intuition. For linearly separable categories, the following is true: There is an additive weighting of the stimulus dimensions in the task, such that, using that weighting, all the members of Category A would be called A and all the members of Category B would be called B. Geometrically, with two stimulus dimensions, there would be a straight line through perceptual space that successfully partitions all the As from all the Bs. In a three-dimensional space, this partitioning boundary would be a plane.

The intuition is simple. If the members of your family generally have the same eyes, the same hair, the same nose, and the same hair color, your family could be linearly separable from other sets of siblings – even if not everybody has everything exactly the same. But if there is a goose in the duck family, this family would be nonlinearly separable relative to another duck-duck-duck family. There would be no way to cleanly (geometrically, mathematically) partition the family groups. Important theoretical conclusions have emerged from tasks involving nonlinearly separable categories containing exceptions of just this kind.

## Stimuli in Animal Categorization Research

Important considerations also attend the stimuli chosen for animal categorization research.

*The ecological dimension.* One important choice dimension is the naturalness of the stimulus materials. For example, in one of the most venerable animal categorization experiments – Herrnstein et al. (1976) – researchers presented pigeons with slides of real-world scenes that contained tree elements (trunks, branches, and leaves) or did not. Pigeons showed clear mastery of some kind of “Tree” category. Their category knowledge clearly generalized when new tree/not tree slide sets were swapped in.

Wasserman et al. (1988), in another influential example, presented pigeons with realistic images of chairs, cats, cars, or flowers, giving the pigeons four response keys for identifying the category of the presented image. Pigeons became robustly accurate in performance and generalized successfully to new instances. Moreover, the pigeons’ success with chairs and cars makes plain that birds are capable of learning human artifact categories, not only ecologically relevant (even genetically ingrained) categories like Tree.

Using ecological materials has the strength that it may tap into animals’ truest, most natural categorization capacities, that is, the processes they would use and the representations they would develop when learning the natural-kind categories of their own world. This makes the use of these stimulus materials highly ecologically valid.

Using ecological materials has the weakness, though, that there is no control over the dimensions of stimulus variation, the relative salience of perceptual dimensions, and the within-and-between-category metrics defining the category structures. For example, it is not known what is varying in the hundreds of tree slides, or even what pigeons may be perceiving therein. And one does not know how perceptually coherent or tightly knit the categories are. So, ecological materials are rich, valid, and intriguing but present important unknowables.

At the other pole, away from naturalness, researchers have also used stimulus materials that are clearly highly artificial. For example, Cook and Smith (2006) used beach-ball stimuli with many colored pie-slice sectors, not like any natural kind animals experience. Likewise,

Smith et al. (2008) used nine-dimensional random-polygon shapes, equally artificial and nonecological. The weakness is that these materials may not elicit from animals their most natural and ecological category-learning strategies. But the compensating strength is that one can know, as Cook and Smith knew, exactly the dimensions of variation in their stimuli, the ranges of variation, the balanced salience among the dimensions, the similarity separation between opposing categories, and even potentially the allocation of attention that a pigeon chooses across the stimulus dimensions. Likewise, in Smith et al. (2008), a fully developed psychophysics of perception and similarity lay behind the use of those random-polygon categories. Here, ecological validity was traded off for experimental control and psychophysical precision. Clearly, the researcher must choose the strength they pursue, the trade-off they choose, and the sacrifice they make.

*Generating category-member variability.* Researchers also make different choices about the ways in which stimuli will vary within a category. One very common approach is to have categories defined along many dichotomous features. So, for example, in Cook and Smith (2006), different color sectors of the stimulus disks could be red-green, yellow-brown, blue-gray, and so forth. This means that each feature can only take on two values, an artificial, nonecological feature of the stimuli. It also means that many stimuli will have features shared identically with members of the opposing category, for example, the disk in Category A with the gray sector may have an important feature shared with B category members. The possible effects of this must be clearly understood by researchers. Others have used richer and more graded dimensional variation, so that Category A stimuli might have dimensional values 1, 2, 3, and the Category B stimuli 4, 5, 6. Jitsumori (e.g., 1996) has used a richer stimulus-generation methodology like this to elegant effect. Finally, as shown below, others have used more complex statistical-distortion methods to create stimuli that are carefully controlled variations of a central prototype and graded in psychophysical similarity to it.

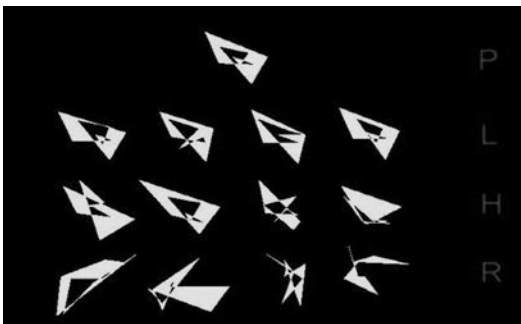


## Prototypes and Exemplars in Animal Categorization Research

Extensive research has tempered the early dominance of exemplar theory toward the present consensus that prototype abstraction plays the dominant role in animals' categorization. In meaningful synergy, this consensus has reached across to refashion the human literature. In this way, animal participants have been extraordinary behavioral ambassadors to cognitive science.

**Prototype abstraction.** For example, Smith et al. (2008) used a method of category construction in which category members were created at different distortion levels from an originating, central prototype. Grounded in stimulus-distortion techniques with a 50-year history in experimental psychology, prototypical, highly typical, untypical, and unrelated polygon shapes were generated. The first three of these item types composed a prototype-centered, family-resemblance category. The last item type should be rejected from category membership. These stimuli are illustrated in Fig. 1.

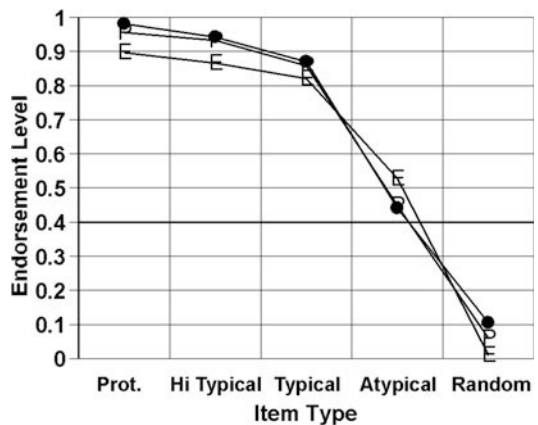
Smith et al. (2008) let macaques (*Macaca mulatta*) learn these categories. The open circles in Fig. 2 show how often a monkey endorsed different item types into the category. He maximally endorsed the prototype into the category,



**Categorization, Fig. 1** A dot-distortion category. *Note.* The originating prototype (P), low-level distortions (L), high-level distortions (H), and unrelated shapes (R) from top to bottom. This is a family-resemblance category with category typicality decreasing from the prototype outward. (Adapted from "Prototype Abstraction by Monkeys (*Macaca mulatta*)," by J. D. Smith, J. S. Redford, and S. M. Haas, 2008, *Journal of Experimental Psychology: General*, 137, p. 391. Copyright 2008 by the American Psychological Association. Reprinted with permission)

and category endorsements declined from there. Smith et al. used standard modeling approaches to emulate prototype-based and exemplar-based minds learning these categories. The exemplar model assumed that monkeys refer to-be-categorized items to multiple, memorized separate instances. The prototype model assumed that monkeys refer items to the prototype average derived from their exemplar experience. The models were controlled and matched but for this representational assumption.

The exemplar model (Es) failed to capture monkeys' performance. It sharply underpredicted monkeys' performance on the most typical items. These modeling errors are essentially disqualifying given the formal sophistication in this literature. That macaques exceeded those predictions shows that their minds are not referring items to collections of individuated exemplars. In contrast, the prototype model (Ps) fit monkeys' performance so perfectly that these symbols are barely discernible. Something like a prototype was the macaque's cognitive



**Categorization, Fig. 2** The proportion of times a macaque endorsed items as a category member. *Note.* As shown in Fig. 1, decreasing typicality was a function of increasing shape distortion from the prototype. Exemplar (E) and prototype (P) models fit the macaque's performance. These models differed in assuming many memorized exemplars as cognitive reference points in categorization or a single, central, prototype reference point. (Adapted from "Prototype Abstraction by Monkeys (*Macaca mulatta*)," by J. D. Smith, J. S. Redford, and S. M. Haas, 2008, *Journal of Experimental Psychology: General*, 137, p. 395. Copyright 2008 by the American Psychological Association. Reprinted with permission)



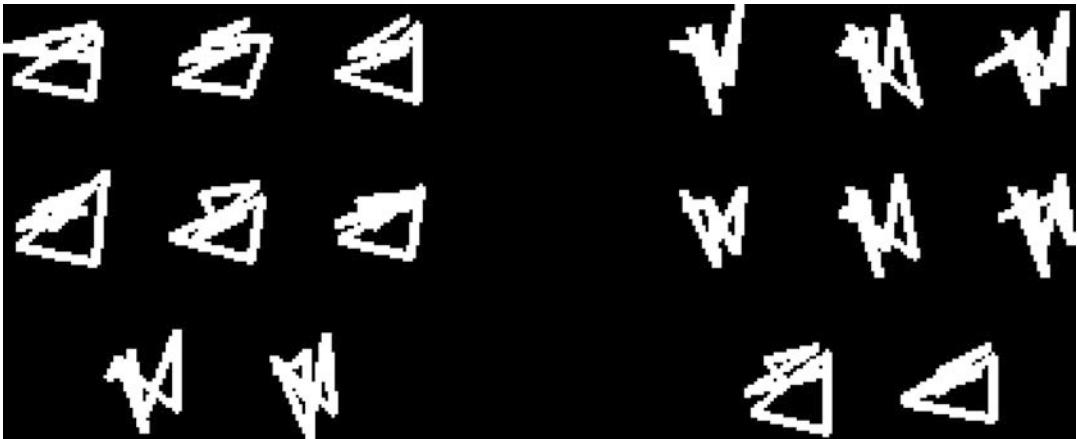
reference point, a conclusion reinforced by other studies (e.g., Jitsumori 1996). Monkeys were blending their exemplar experience into something like a prototype reference standard by which they categorized. This experiment shows conclusively that exemplar processing is insufficient to explain all of what categorizing animals do, though still it may account for some of what they do.

*Exemplar theory's failure.* This experiment also lets one explain why exemplar theory's fundamental representational/processing assumption can be falsified. Exemplar theory's idea is that categorizers store exemplars as separate memory traces spread out like droplets in a cloud in the mind's psychological space. Then test items are compared to these multiple traces. It is simply impossible for a test item to be highly similar to all the comparative standards for categorization – it will always be near to some but far from others. Therefore, the overall category-belongingness signal will inevitably be weakened, reducing performance predictions for typical items, which the exemplar model showed but the macaques did not. The remarkable thing is that the exemplar model's failure here is inherent, inexorable, and incurable. In contrast, if the animal averages experience into a prototype, then a test item can be indefinitely close to the prototype in

psychological space, and the performance expectation can be indefinitely high. This the prototype model predicted, and the monkeys confirmed.

*Prototype-exception categories.* Prototype-exception tasks also allow researchers to contrast prototype and exemplar processing (Fig. 3). The eight shapes on the left (right) are all reinforced as Category As (Bs), though the second-row stimuli seem to belong to the opposing category. If monkeys assume prototype-based categories based in perceptual family resemblance, they will have difficulty mastering exception items, because they will continue to group those exceptions with the prototype of the OPPOSING category. But if monkeys simply memorize the exemplars and associate correct responses to them, they should be able to master the exceptions as well (just as you could learn the membership of rock group Beatles, even if they were John, Paul, George, and Cardi B).

Figure 4 shows macaques' performance (Smith et al. 2010). The macaques persistently erred on the exception items, even performing then below chance. They showed minimal capacity to memorize and respond appropriately to exceptions. If their natural threat categories had exceptions as here (e.g., eagles in sheep clothing), it would be a fitness disaster (for the monkeys, not the eagles).



**Categorization, Fig. 3** A prototype-exception category task. *Note.* The left and right stimulus groupings represent two categories. Six stimuli in each case are variations of that category's central prototype. Two exception stimuli are variations on the theme of the opposing prototype. (From "Stages of Category Learning in Monkeys

(*Macaca mulatta*) and Humans (*Homo sapiens*)," by J. D. Smith, W. P. Chapman, and J. S. Redford, 2010, *Journal of Experimental Psychology: Animal Behavior Processes*, 36, p. 43. Copyright 2010 by the American Psychological Association. Reprinted with permission)

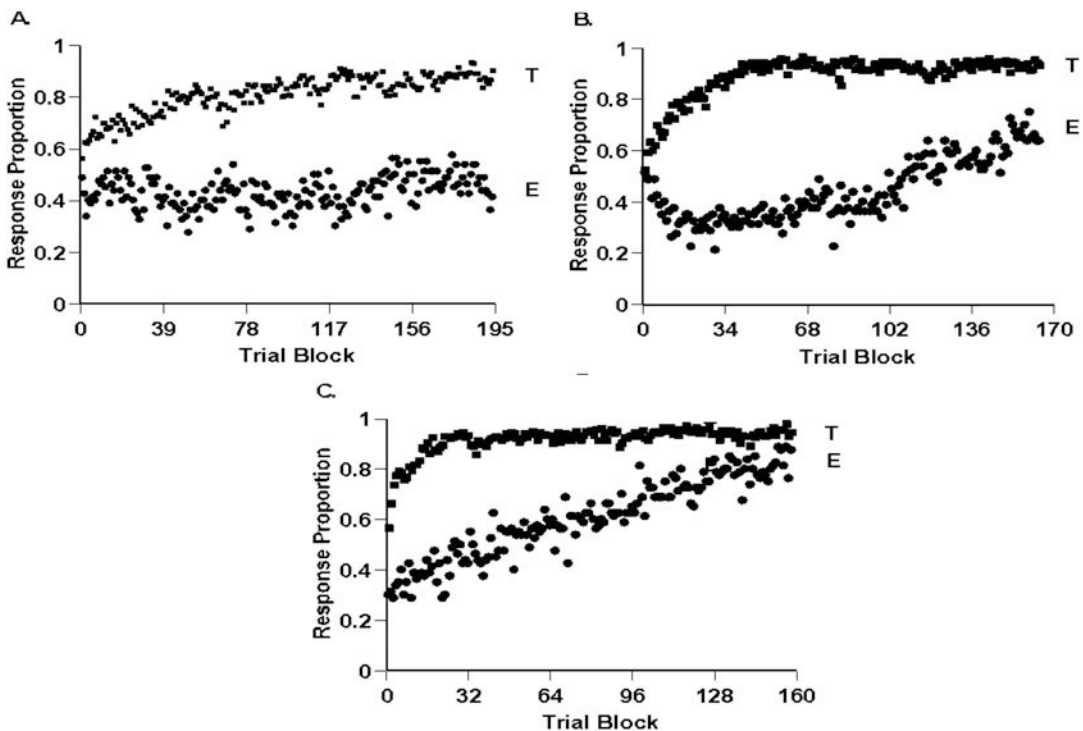
Rather, the monkeys (sensibly) assumed that they were confronting two perceptually coherent, well behaved, family-resemblance categories. By this strategy, of course, cross-categorizing the exceptions is perfectly correct. Humans show similar phenomena (Smith and Minda 1998). Section “What Kinds Are Natural?” considers whether possibly the natural world is sensible in the same way.

Figure 4 shows that monkeys somewhat mastered the exceptions by experiment’s end. This is why the literature does not exclude exemplar theory from consideration, but rather emphasizes that animals may have different processes available for managing different kinds of category problems. This mixed perspective presently seems best for understanding animal and human categorization.

*The phylogenetic depth of prototypes.* Cook and Smith (2006) took a broader evolutionary

perspective toward these phenomena. They tested prototype-exception tasks with an avian species (pigeons – *Columba livia*). The birds classified prototypical, typical, and exceptional disk-sector stimuli as belonging to Category A or B. Pigeons made the same family-resemblance assumption that macaques and humans do. They cross-categorized the exceptions, producing high error rates on those items. And pigeons’ performance was not fit by an exemplar-based model, because pigeons performed too well on the prototype items and too poorly on the exceptions. These prediction errors are as expected given the discussion above. But pigeons showed the same late transition to exemplar memorization as monkeys. Again, there was a late-breaking exemplar capacity, after hundreds of trials, to finally somewhat learn/memorize exceptions.

*Isolating the exemplar process.* A third productive approach in this area has been to eliminate

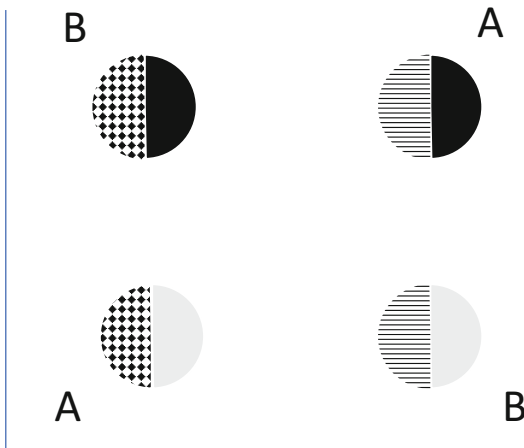


**Categorization, Fig. 4** Performance by three macaques in the category task of Smith et al. (2010). Note. Curves T and E show the proportion of correct responses made to the typical and exception items that were illustrated in Fig. 3. (From “Stages of Category Learning in Monkeys

(*Macaca mulatta*) and Humans (*Homo sapiens*),” by J. D. Smith, W. P. Chapman, and J. S. Redford, 2010, *Journal of Experimental Psychology: Animal Behavior Processes*, 36, p. 48. Copyright 2010 by the American Psychological Association. Reprinted with permission)

from the tested categories any sense of family-resemblance cohesiveness or prototypy, so that this form of processing is ruled out and the need for exemplar processing stands alone. An exclusive-or (XOR) category task can achieve this process isolation (Fig. 5). Here, the Category A instances would “average” into the central point of perceptual space – but so would the two Category B instances. Moreover, in this case, one must place perfectly opposite stimuli with zero shared features into same category. Prototype averaging is doubly pointless. But exemplar processing would be fostered, because there are only two distinctive and memorable instances of each category to learn.

Smith et al. (2011) gave macaques two-, three-, and four-dimensional XOR tasks. Figure 5 illustrates the two-dimensional task – the others are more elaborate. Monkeys found these tasks stripped of prototypy very difficult. They made thousands of errors on the way to low levels of terminal performance. Thus, even facing the sharp and exclusive need to memorize exemplars, macaques showed a minimal capacity to do so.



**Categorization, Fig. 5** Illustrating an XOR category task. *Note.* Stimuli vary in the patterning of the leftward semicircle and the shading of the rightward semicircle. Stimuli with no shared features must be categorized together. Stimuli with shared features must not be categorized together. Prototype-averaging processes cannot work in this task. Exemplar memorization is recommended instead

In this respect, comparative and human research have a strong resonance. Early on, exemplar theory was dominant partly because researchers relied on poorly structured categories as already defined, including XOR categories. Thus, they defeated prototype processing, while fostering the memorization of exemplars within small categories. And yet, about half of humans in these early experiments were never able to reach the established learning criterion. Humans display an exemplar-processing deficit in category learning just like animals do. Exemplar processing’s role in the learning and processing of category information thus must be delimited carefully and narrowly. It is likely that it plays only a supporting role relative to prototype processing.

This area of the literature can be summarized. Animals make a strong family-resemblance assumption in category learning, assuming they will encounter perceptually coherent classes of mutually similar objects (i.e., linearly separable as defined above), and usefully organized around a category prototype. Their exemplar-processing capacity in category learning is far weaker and empirically shy – recruited weakly toward poor performance, recruited only late in testing after dogged training, and recruited poorly even given the ideal circumstances focusing on exemplar processing and only allowing exemplar processing. Far from the dominant theoretical status that exemplar theory once enjoyed, a mixed-process theoretical perspective toward category learning appears to be mandatory based on current research, with something like prototype processing playing the dominant role.

### What Kinds Are Natural?

Why, though, do animals have a frail exemplar capacity in categorization? Why do they commit strongly to prototypes in categorization? These questions raise the larger question of how animal minds *should* be organized – optimally and toward fitness – toward category learning.

This issue has received theoretical attention. Briscoe and Feldman (2011) noted that storing individual exemplars might store information too

specifically and at the wrong grain for generalizing to new items. After all, for a bat to store in detail every eaten mosquito is useless – those mosquitos will never need categorizing again. Here, a generalized representation might be better. However, they also noted that in certain situations high-specificity exemplar storage might be valuable.

Brooks (1978) explained why organisms might have occasional need for prototype-averaging and exemplar-memorizing processes. There are times – as in coping with an alpha conspecific – when exemplars must be understood individualistically. There are thinly populated categories (e.g., patriotic songs) wherein individual exemplars stay individuated. But there are densely packed categories, too, for which a generic representation may be cognitively economical. In fact, the research just presented shows how different category structures can press category processing toward prototypes or exemplars. Thus, it would not be surprising if animals and humans potentially brought multiple and alternative strategies to the table during category learning.

Ashby and Alfonso-Reese (1995) discussed the problem that organisms often encounter exemplars one at a time spread out in time. But then how is the organism to estimate the underlying statistical distribution of these exemplars? Their idea was that if prototype-based categories were encountered very frequently in nature, the organism could safely come to expect that structure, producing a distinctive processing advantage as that structure organized the next exemplar pool. These authors speculated that animals may actually be tuned this way cognitively, because the world may be tuned this way. Conversely, though, if nature continually presented chaotic exemplar distributions, the organism would have to drop all prior assumptions, and then an exemplar-memorization approach would become uniquely powerful.

Smith (2014) situated the results in section “[Prototypes and Exemplars in Animal Categorization Research](#)” ecologically. If monkeys constantly faced chaotic category structures requiring exemplar memorization (e.g., XOR

tasks), then they would not have survived, or else they would have developed a robust exemplar capacity. That they have not developed that capacity suggests that the world is not exemplar demanding in that way. But if the world were mostly averageable into prototypes and family-resemblance clusters, then prototype processes might have proved advantageous – as suggested by Briscoe and Feldman (2011) and Ashby and Alfonso-Reese (1995) – and selected for during cognitive evolution. Then, monkeys would resonate strongly to prototypes as shown here. They would make a default family-resemblance assumption as they do. They could safely be lousy at exemplar memorization, as they are. In short, monkeys’ categorization could be a good illustration of Shepard’s (2001) idea that cognitive systems are sometimes shaped by the structure of the natural world.

In fact, it does appear that nature rarely presents chaotic categories demanding exemplar processing. Rather, monkeys experience things such as snakes, leopards, eagles, insects, nuts, seeds, and so forth – all coherent family-resemblance categories, all prototype averageable. Malt (1995), in a seminal review, drew on cognitive and cross-cultural studies to describe the generic category structure that characterizes natural kinds and is accorded psychological preeminence in all human cultures worldwide.

All in all, there is a consensus that there are probably multiple processes potentially underlying category learning, with organisms potentially tuning toward different processes for different niches, tasks, and situations. However, the animal research suggests an imbalance among these processes given an evolutionary tuning between prototypes in mind and family-resemblance categories in nature. In essence, animals have sent the message through their results that they have not relied on exemplar processes in category learning for a hundred million years. In this, they have made an extraordinary contribution to categorization science, even refocusing the human literature. This area shows the constructive synergies that are possible across human and animal research.

## The Search for Rules and Hypotheses in Animal Categorization Research

The search for animals' rules/hypotheses during category learning has deep roots in comparative psychology. Noncontinuity theory proposed that animals spontaneously tune their receptors toward one focal dimension in discrimination learning (an attentional "hypothesis"). Classical Theory tried to define categories by criterial features best learned as rules (bachelor: unmarried). Krechevsky (1932) reported on uncertain evidence that even rats were trying out dimensional hypotheses during discrimination learning. Harlow's (1949) work on animals' learning-set rules (that allowed instantaneous behavioral reversals) is well known. His lingering doubt is less well known: He wondered whether the labels "rule" and "hypothesis" should be given to learning sets that are wordless/languageless. Still today, language and verbalization are important theoretical considerations in this area. This area has been strengthened by its integration with cognitive neuroscience. In fact, neuroscience provides a good introduction to this area, through its careful differentiation between explicit and implicit systems for category learning.

*Dissociable category-learning systems.* One candidate learning system – the explicit system – is allied to the cognitive utilities of executive attention and working-memory that could support hypothesis testing and rule learning. This system would generally map onto brain circuits involving prefrontal cortex, the anterior cingulate gyrus, the hippocampus, and so forth. This system displays typical features. It learns low-dimensional category rules through active hypothesis testing, possibly discovering rules suddenly through conscious insight. These rules are accessible to declarative cognition (verbalizable by humans).

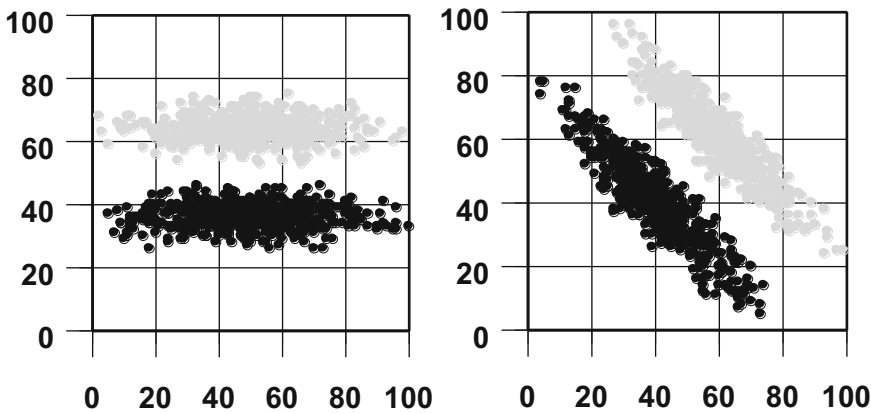
Another system – an implicit system – is allied to operant learning and the brain's reinforcement mechanisms. It is likely grounded in the basal ganglia – the caudate nucleus is well situated to associate percepts through to responses. Learning in this system (e.g., discrimination learning)

occurs associatively through processes akin to conditioning – slowly and gradually, with category "knowledge" not present in working memory, not conscious, and not verbalizable or otherwise declarable.

Readers will see immediately how this dissociation from neuroscience is relevant to comparative research. Were the attentional foci of noncontinuity theory protorules? Were Krechevsky's rat "hypotheses" akin to human hypotheses? Did Harlow's learning sets amount to explicit performance rules? One can fairly ask whether other species than humans share something like this dissociative structure of implicit/explicit category learning, and especially whether they share something like an explicit learning system more toward the conscious/declarative pole of cognition. But to do so, one must come armed with appropriate dissociative paradigms.

Figure 6 shows a useful paradigm. Its categories (the stimulus ellipses) are defined within a two-dimensional perceptual space. For example, stimuli might be boxes defined over 100 sizes and 100 densities of internal lit screen pixels. In the figure, each black (Category A) or gray (Category B) symbol would specify the bidimensional dimensional specification and perceptual appearance of a particular exemplar. Participants of course would never be shown this map of the category structure but would have to learn to differentiate the categories based only on trial-by-trial cycles of stimulus-response-reinforcement. In such a task, one could insightfully realize conscious dimensional rules, or slowly develop conditioned, unconscious response habits. This paradigm lets one diagnose these different learning strategies.

The rule-based (RB) task (left panel) favors explicit rules. Dimension Y – only – contains valid category information. A dimension Y rule is optimal. It is known (e.g., Smith et al. 2014) that humans' rules in these tasks are explicit – held in working memory – conscious, narrowly dimensional, and declarative in language. The information-integration (II) task (right panel) defeats rule use, because both dimensions offer only partial category information. Instead, one must integrate information across dimensions



**Categorization, Fig. 6** Rule-based and information-integration category structures. *Note.* Left: A rule-based category structure depicted within an abstract  $100 \times 100$  stimulus space. The black and gray symbols, respectively,

indicate Category A and Category B stimuli. Right: an information-integration category structure, depicted in the same way

(hence the II descriptor). The cognitive system accomplishes this integration implicitly – essentially learning a low-level response habit that responds accurately without awareness.

The RB and II tasks are only a slight rotation apart in perceptual space. They are equal in category size, within-category exemplar similarity, between-category exemplar dissimilarity, structural ratio, and linear separability – those aspects of category structure discussed above. They are a minimal pair of category tasks that contrast only in the learning process they elicit from human minds. And so, they have utility for comparative researchers because they may allow researchers to assay implicit and explicit categorization in animal minds, too.

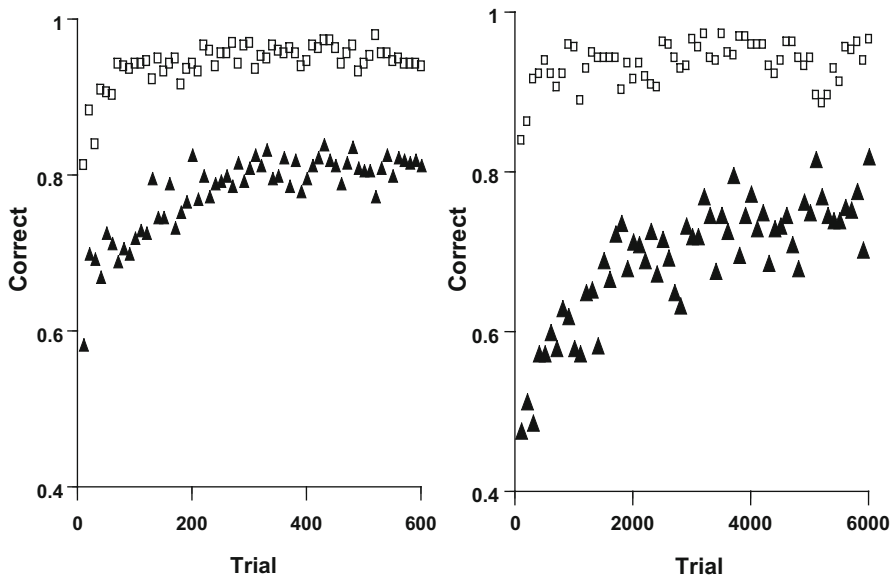
Accordingly, researchers gave humans and macaques RB and II tasks (reviewed in Smith et al. 2012). Humans (Fig. 7, left panel) strongly preferred rule tasks, learning these much faster to higher terminal-performance levels. (They also verbalized their unidimensional category rules.) Macaques (right panel) produced the identical RB advantage, though they learned more slowly (and said nothing!). The researchers suggested that macaques share with humans some – not all – aspects of the hypothesis/rule system that humans access through consciousness and language. There is generous room for further

research to specify both these unshared and shared aspects.

Zakrzewski et al. (2018) demonstrated an important unshared aspect. Following on research by Ashby and his colleagues, she showed that humans' rule knowledge is fully abstract and freely transferable to new stimulus domains that are different in perceptual appearance. She made this demonstration by training humans on RB and II tasks in one region of perceptual space, and then transferring them to a new region (Fig. 8). Humans transferred perfectly in the RB task (left panel), signifying that their category learning was abstract enough to be applied to novel stimuli. However, transfer faltered in the II task (right panel), signifying that their implicit category knowledge was welded to the original stimulus contexts of training (as would be expected for associative, stimulus-response learning).

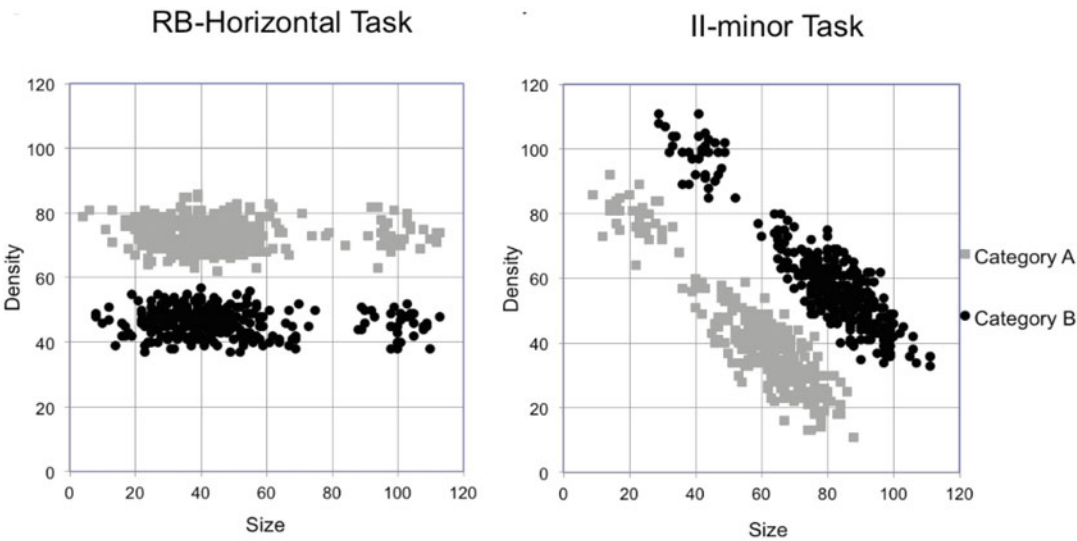
However, Zakrzewski et al. (2018) found a different result with macaques. Even their performance-advantaged, supposed rule knowledge in the RB task faltered badly at transfer. That knowledge was poorly transferable, not abstract and general as human's rule knowledge is. It is an interesting riddle to explain why macaques show such strong performance advantages on RB tasks over II tasks, while still





**Categorization, Fig. 7** Humans’ and macaques’ performance in rule-based and information-integration Tasks. *Note.* Left: Proportion of correct responses in each 10-trial block for 30 humans who performed 600 trials of a rule-based (RB) category task (open symbols) and an information-integration (II) category task (filled symbols). Right: proportion of correct responses in each 100-trial block for three macaques who performed 6,000 trials of

an RB and II category task, depicted in the same way. (From “Implicit and Explicit Categorization: A Tale of Four Species” by J. D. Smith, M. E. Berg, R. G. Cook, J. Boomer, M. J. Crossley, M. S. Murphy, B. Spiering, M. J. Beran, B. A. Church, F. G. Ashby, & R. C. Grace, 2012, *Neuroscience and Biobehavioral Reviews*, 36, p. 2359–2360. Copyright 2012 by Elsevier. Reprinted with permission)



**Categorization, Fig. 8** Category structures to test the transferability of category knowledge. *Note.* Training trials were drawn from the long stimulus ellipses that extended across 80 stimulus levels. In transfer, 25% of trials presented stimuli from the short ellipses that extended across 40 stimulus levels. (From “The Transfer of Category

Knowledge by Macaques (*Macaca mulatta*) and Humans (*Homo sapiens*)” by A. C. Zakrzewski, B. A. Church, & J. D. Smith, *Journal of Comparative Psychology*, 132, p. 62. Copyright 2018 by the American Psychological Association. Reprinted with permission)

demonstrating – even in RB tasks – some stimulus-bound aspects typical of associative-learning processes.

*Alternative reinforcement environments.* Smith et al. (2018, 2020) demonstrated an aspect of explicit category learning shared between animals and humans. The brain's primary reinforcement mechanisms are time constrained. Thus, associative learning depends on the temporal contiguity among stimulus, response, and reward. This dependence has been appreciated since Pavlov. Yagishita et al. (2014) used an elegant technique to gain temporal control over stimulus and reward brain pathways. He showed that even a 2 s temporal separation made associative learning falter.

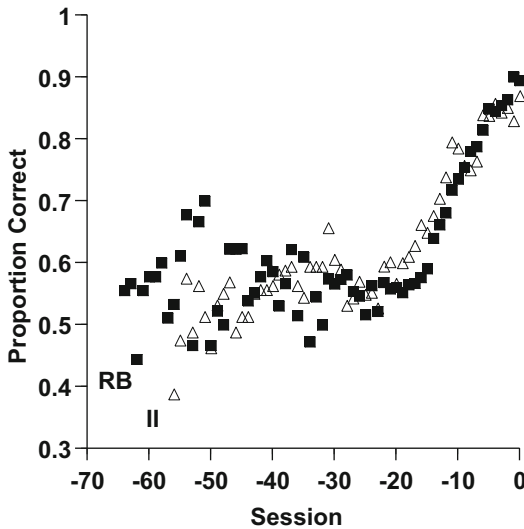
The method of temporally displacing reinforcement is thus a powerful tool by which comparative researchers may disable important forms of associative learning, so to study the alternative forms of learning that humans and animals turn to instead. For example, Smith et al. (2018) used trial-lagged reinforcement – after each trial, participants received feedback not on that trial but on the previous trial. In this way, the reinforcement signal was displaced away from the SR pairing, perhaps untrackably to an associative-learning system. But an explicit-declarative hypothesis-testing system could hold in working memory the hypothesis it was actively considering and judge how well that potential category rule was generally faring over trials. Predictably, then, Smith et al. (2018) found that displaced reinforcement impaired II learning, suggesting that necessary associative processes were disabled by that reinforcement regimen. But displaced reinforcement left RB learning intact, suggesting that RB tasks tap explicit-declarative cognitive processes that proceed independently of trial-by-trial reinforcement.

Smith et al. (2020) made an initial demonstration in this area with macaques. Macaques learned discrimination tasks well even given only trial-lagged feedback. This reinforcement regime does more than just delay the animal's receiving reinforcement – associative learning processes might bridge this delay interval in some way. It also reinforces a previous trial after a second stimulus has masked the first stimulus, and a second response has masked the first response. This

could make assigning reinforcement credit associatively very difficult. Macaques should fail to learn in this situation if they have no alternative system of learning on which to draw. They do not fail.

A strong contender for the alternative system of learning they are turning to is a kind of hypothesis-testing strategy, shown by humans in the identical paradigm, proposed for animals by Krechevsky (1932) nearly a century ago. Therefore, the method of displaced reinforcement may hold great promise. It is a transformative idea that one can dissociate away the important processes of associative learning by disabling them, leaving the animal to use – if it can – other learning processes that may lie on a more explicit-declarative level.

*A broader comparative perspective.* The theoretical import of this issue is sharpened by taking a wider species view. Researchers studied pigeons' RB-II performance (reviewed in Smith et al. 2012) but found qualitatively different results than with humans and macaques (Fig. 9). Now there was no RB performance advantage – pigeons learned RB and II tasks equally fast and to the same level. It seemed the pigeons were learning two tasks of the same difficulty and psychological character (to them!), without preferring or possibly even realizing the unidimensional rule embedded in one of them. This equivalence would be predicted if pigeons were processing the task stimuli holistically or integrally (not dimensionally and analytically). This equivalence could even suggest that pigeons lack the selective-attention capacity to bring the RB task's dimensional rule into sharp focus. Rats also appear to show “the pigeon result,” extending that pattern to another vertebrate lineage (Broschard et al. 2019). Thus, two species pillars of comparative cognition – rats and pigeons – show nonanalytic categorization without the dimensional analysis or rule preference shown by primates. The differences across vertebrates, primate species, and humans encourage the theoretical idea that animals' categorization capacities are potentially multifaceted and layered, rather than explainable as just a unitary associative-learning capacity or just a unitary exemplar-memorizing capacity.



**Categorization, Fig. 9** Pigeons learning information-integration (II) and rule-based (RB) tasks. *Note.* The proportion of correct responses by session is shown from the criterial block backward for 8 II-learning pigeons and 8 RB-learning pigeons. (From “Implicit and Explicit Categorization: A Tale of Four Species” by J. D. Smith, M. E. Berg, R. G. Cook, J. Boomer, M. J. Crossley, M. S. Murphy, B. Spiering, M. J. Beran, B. A. Church, F. G. Ashby, & R. C. Grace, 2012, *Neuroscience and Biobehavioral Reviews*, 36, p. 2364. Copyright 2012 by Elsevier. Reprinted with permission)

## The Search for Relational Concepts in Animal Categorization

Researchers have also studied animals' capacity to learn conceptual categories that are grounded in relations like sameness. Here, too, humans present the gold standard of relational cognition, for it grounds humans' higher-level cognition (e.g., analogical reasoning). Indeed, many have suggested relational cognition as the locus of a fundamental discontinuity between animal and human cognition.

A very early relational task shows that the theoretical stakes are high in this area. In a transposition task, a positive S+ stimulus (e.g., a Size 4 disk) is rewarded in training, in contrast to a nonrewarded S- (e.g., a larger Size 5 disk). Then, subjects are tested for their choice preference between Size 3 (a novel stimulus) and Size 4 (the rewarded S+ stimulus). Animals from

chimpanzees to chickens choose the smaller Size 3 disk, apparently acting against their associative learning. Behaviorists reacted strongly against results like this because they might show animals transcending their stimulus reactions in favor of relational cognition. Spence's (1937) Peak Shift model took direct aim at such results, though it could not explain all relevant findings (Gonzalez et al. 1954). (As a matter of history, the Gestalt psychologists loved the transposition results because they showed animals processing whole perceptual Gestalt configurations.) The study of relational cognition has always placed the behaviorist and cognitivist theoretical approaches in opposition.

*Pigeons: A fragile same-different capacity.* Recently, the same-different task has been dominant, with animals needing to identify a relation of sameness or difference. The matching-to-sample task could be one such task. A stimulus is presented (the sample), and later the animal must select the sample again when it is presented along with the foil. However, this successive task (with the sample presented at two points in time) is problematic, because animals might respond successfully by just gravitating behaviorally toward a “hot” or fluent trace in immediate memory, rather than responding toward the abstract relation of same.

Nonetheless, the matching task has played a valuable role. Zentall and his colleagues (e.g., Zentall and Hogan 1974) trained pigeons on matching tasks in one stimulus domain and then transferred them to another. They could confirm that they have learned an abstract relational rule – respond same – by transferring that rule to the new stimulus domain, but they did not do so. This suggests that pigeons are using some low-level stimulus cue that is domain specific, not the true relational strategy.

Most researchers now accept that the simultaneous same-different paradigm is the more robust way to test animals' capacity for relational cognition. Here, the animal sees two stimuli simultaneously and chooses between its same and different abstract response icons (e.g., the letters S and D). This task cannot be solved by memory fluency, because no sample is presented twice, and

because the response icons bear no resemblance to the trial's stimuli. Still, pigeons have great difficulty identifying pairs of stimuli that are same or different.

Seeking to create stronger relational displays for pigeons, researchers have used 16-item simultaneous same and different displays (e.g., Young et al. 1997). Now pigeons can reliably discriminate same arrays from different arrays. However, this task presents an interpretative difficulty, because it contains a low-level perceptual (visual-entropy) cue. The 16-item same displays appear visually calm and regular; the 16-item different displays appear visually noisy. This first-order visual cue is directly perceivable and requires no abstract relational judgment. Thus, once again, pigeons are not showing a robust relational capacity in this task. In fact, as the visual arrays shrink from 16 items to 8 items to 4 to 2, pigeons' performance collapses, demonstrating that the entropy cue is dominant. Humans' performance does not collapse.

Of the well-tested species, pigeons have the most limited same-different competence. Premack (1978) concluded that it would be difficult to "talk to a pigeon" because they respond so strongly to absolute stimulus cues and so weakly to relational cues. If you tried to shop with a pigeon, you would constantly think "this will go great with my couch" – a relational thought. The pigeon would think "it's teal; it's definitely teal" – an absolute-stimulus perception). The pigeon same-different research is a major achievement of modern research in animal categorization, because it characterizes so clearly the capacity of an important research species in an important comparative area.

*The transitional same-different capacity of primates.* The difficulty of simultaneous same-different tasks is that the animal must transcend the first-order perceptual appearance of the test stimuli. Two identical stimuli may be same whether they are grapes or Cheerios. This is why relational responding is deemed cognitively sophisticated and why it may be phylogenetically restricted as we have just seen.

Even the nonhuman primates find relational tasks difficult and taxing, so that they default

instead to first-order, stimulus-based strategies. Illustrating this default tendency, Shields et al. (1997) tested macaques with pairs of stimulus boxes filled with lit pixels. The box pairs could be (1) sparse and same density, (2) sparse but different density, (3) dense and same density, or (4) dense but different density. Animals were to make the response same for box-pair type 1 and type 3, and the response different for box-pair type 2 and type 4. But instead, macaques strongly gravitated toward contrasting box-pair types 1 and 2 from box-pair types 3 and 4 – a first-order sparse-dense perceptual strategy instead.

Premack (1978) provided a thought-provoking rule of thumb to this area. He suggested that probably many vertebrate species process both absolute stimuli and abstract relations as they perceive and conceive their worlds. But the question is the balance between these processing channels. One could say that for pigeons the absolute stimulus channel is loud but the abstract-relational channel soft, creating their performance tendencies in same-different tasks. One could say that for monkeys the two channels are almost at parity, so that macaques default to absolute stimuli but can transition to abstract relations. Several lines of research show that macaques and monkeys have more robust same-different capacities than do pigeons. Premack's further thought on the basis of this rule was that apes should join humans in thriving in relational-cognition task, and this is probably true as well.

*Higher-order relational performances by primates.* In fact, there are higher-level relational tasks for testing (possibly) higher-level species. The preferred task for this purpose is the relational matching to sample task (RMTS). In this task – illustrating here with a same trial – the animal would see as a sample two identical photos of pizza slices. Later, another pair of identical photos (say, two identical keys) would be given as one (the correct!) matching choice, and a pair of different stimuli (say, a banana and a yo-yo) would be given as the other (incorrect!) matching choice. Now, to make the relational choice, one really must let go the concrete perceptual appearance of things, reflecting on abstract relationships only.

In research by Thompson and his colleagues, several chimpanzees (*Pan troglodytes*) succeeded in an RMTS task, as did chimpanzee Sarah in David Premack's research. Based on results like these, Thompson and Oden (2000) famously made a theoretical distinction between the paleological monkey (concretely perceiving, not succeeding on RMTS trials) and the analogical ape (abstractly conceiving, succeeding on RMTS trials and perhaps on other analogical-reasoning tasks). These results did extend Premack's intuitive rule of thumb farther through the primate species. Perhaps the relational channel is gaining additional psychological volume.

However, these ape studies did have an unavoidable confound. The participant chimpanzees had extensive laboratory-training histories, in which they were all given forms of abstract symbol training, and in one case even abstract tokens denoting the relations same and different. This relational symbol training alone could have fostered relational cognition, besides the cognitive sophistication of inherent chimpanzeeness.

Nor do humans escape this confound. Declarative language provides a vast symbolic resource to us. Formal schooling teaches relational cognition relentlessly. It is good to remember that just as chimpanzees reflect their training history in their cognitive successes, so do we, and not all those successes purely reflect our inherent humanness.

Monkey species perform differently in RMTS tasks from ape species. For example, Smith et al. (2013) used a perceptual fostering paradigm to facilitate macaques' RMTS performance. A training RMTS task gave macaques a first-order perceptual cue and a second-order conceptual cue on each trial. Just as was discussed above, macaques defaulted to using this perceptual cue. But then the first-order perceptual cue was gradually weakened, using the random-polygon method described in section "[Prototypes and Exemplars in Animal Categorization Research](#)" here. The hope was to wean macaques from their perceptual default, leaving them to match relationally. That hope was dashed. As the perceptual cue was weakened, macaques' performance disintegrated at a quantifiable faintness of the perceptual cue. There was an intriguing perceptual-conceptual

barrier that the macaques could not cross psychologically. Their relational capacities are restricted.

Fagot and Parron (2010) used a spatial fostering paradigm with baboons (*Papio papio*). Their RMTS task began with conjoined color patches as sample and choice stimuli, so baboons were essentially matching long color bars to one another. Later, the bars were divided to be separated spatially, so that baboons had the chance to match conceptually pairs of same or different color bars. This progressive training also failed. Baboons' performance faltered given even a small spatial gap. Fagot and Parron (2010) concluded the baboons did not group the spatially separated elements into a higher order relational structure.

Flemming et al. (2011) tried to contrast their same and different RMTS trial by giving these two trial-kinds different outcomes (e.g., correct same and different responses might earn double or single food pellets, respectively; incorrect same and different responses might earn long or short time-outs). This hedonic fostering approach also failed. Macaques seemed to show some relational matching during differential outcome training but dropped to chance when differential outcomes were removed.

Monkey species do not universally fail RMTS tasks. Fagot and Thompson (2011) trained baboons doggedly in RMTS tasks. Of 29 baboons tested, 6 achieved 80% correct given 15,000–30,000 trials on an RMTS task constructed using ten repeating geometric shapes. Five baboons showed some retention of their successful RMTS performance over a year. Thus baboons (and very possibly their close phylogenetic kin macaques) have some cognitive capacity for conceiving and matching relational sameness and difference.

All in all, the nonape findings document the empirical shyness of RMTS performance absent supplementary supports (spatially contiguous stimuli, differential outcomes, and perceptual similarity). However, they do not document the absence of that capacity, given the findings of Fagot and Thompson. In fact, these results reinforce Premack's intuition that the nonape primates represent transitional species, strongly attracted toward low-level perceptual cues, but still having some potential for responding relationally,

enough to show glimmers of RMTS success. To us, these results suggest that the monkey species are ideal for studying the roots of humans' sophisticated relational matching and analogical reasoning capacities. Here, too, as with the literature on category rules already discussed, it seems best to consider that a two-level or two-layer conceptualization of categorization may be best for organizing the empirical findings theoretically. A unitary-process description emphasizing animals' associative learning does not seem to do so as effectively. And modern neuroscience perspectives may usefully formalize Premack's intriguing rule of thumb, with multiple systems of learning standing in for multiple volume controls in mind.

## A Broader Synthesis

This multiple-systems perspective appears to offer new ways to understand a broad range of findings in comparative psychology. Two important areas of animal categorization research – those discussed in sections “[The Search for Rules and Hypotheses in Animal Categorization Research](#)” and “[The Search for Relational Concepts in Animal Categorization](#)” – draw a similar phylogenetic map of different cognitive capacities. Section “[The Search for Rules and Hypotheses in Animal Categorization Research](#)” showed that humans and other primate species show strong performance advantages on rule-based tasks and share the ability to still learn rule-based category tasks when trial-by-trial reinforcement is absent. These results show human-primate continuities in aspects of the explicit-declarative category-learning system that rule tasks emphatically elicit in humans. In contrast, several converging studies show that pigeons appear not to favor rule-based category tasks at all. These findings are distinctive because one might suppose that single-dimensional category differentiations would obviously be psychologically simpler and preferred. They are not. Rats have also failed to process rule tasks with psychological privilege. Thus, not all species have made the preliminary steps toward rule-based categorization that primates have made and that humans have robustly

made. Given all of these findings, a possible hypothesis is that rats and pigeons illuminate a stem, ancestral vertebrate category system that clearly functions beautifully in managing the perceptual, family-resemblance category tasks discussed in sections “[Prototypes and Exemplars in Animal Categorization Research](#)” and “[What Kinds Are Natural?](#)” here. There is broad species continuity in this domain. However, it seems that some species supplement these basic categorization processes with others that emphasize stimulus analysis, dimensional attention, and possibly primitive forms of hypothesis testing. This shared dimensional-attentional cognitive ground will be important to study in future comparative research.

Section “[The Search for Relational Concepts in Animal Categorization](#)” drew the same species map – but now regarding the relational-judgment tasks. Smith et al. (2013) showed that humans discover their relational rules in sudden, conscious insights, just as they do category rules. Smith et al. (2019) showed that working-memory interference impairs humans' relational learning and RMTS performance. These results suggest that humans' relational performance – just as their rule-based category learning – falls more toward the explicit-declarative pole of cognition.

Monkeys learn same-different tasks robustly, and some data even suggest some explicit cognitive processes attending this learning. For one thing, monkeys can make metacognitive uncertainty judgments regarding their same-different performance (Shields et al. 1997). For another thing, baboons' RMTS performance is impaired – just as it is in humans – when a concurrent cognitive load is present (Maugard et al. 2013). However, in this domain, too, monkeys were shown to have clear constraints in performance facing higher-level relational tasks. And here, too, pigeons in multiple studies have shown a minimal capacity for performing relational tasks, unless provided directly perceivable cues like the visual calm or busyness of multiple-item same and different displays. Again, a natural hypothesis is that some species are supplementing the basic perceptual-level processes of many vertebrate species, with this supplementation more clearly displayed by the primates.



This pattern even transcends the domain of categorization. In the large literature on animal metacognition (entry ► “Meta-Cognition” in this volume), consensus holds that animals’ metacognitive performances cannot be explained through a unitary system of associative responding but requires assuming more executive cognitive processes monitoring associative processes. For example, research shows that a working-memory load suppresses macaques’ metacognitive reports while leaving intact their primary perceptual responses within a task. Humans show this effect, too. The same concurrent-load phenomenon is observed in baboons and humans’ RMTS performance, and in humans’ rule-based category learning.

However, pigeons have consistently not demonstrated clear forms of uncertainty responding or metacognition, just as they have not shown robust relational learning or advantaged rule-based category learning.

Thus, a major contribution of animal categorization research is to point out this broad convergence. Many findings – on rule-based categories, relational cognition, and even metacognition in rats, pigeons, monkeys, baboons, apes, and humans – recommend a new theoretical perspective, one that envisions a basal vertebrate system of associative learning and perceptual categorization that in some species is supplemented with some kind of more decisional and working-memory-intensive processes. Really, one must give Premack full credit for his important working analogy in this area, with absolute-stimulus control softening through cognitive evolution, but relational appreciation strengthening. We would just add to that view that the basic stimulus-associative system is being layered over with a system more similar to humans’ explicit-declarative system of cognition and categorization. This addition will not be surprising to students of human cognition. They will know that the same overlaying of implicit processes by explicit processes is the hallmark of contemporary cognitive science that has revolutionized cognitive theory. Thus, animal categorization research foreshadows the potential transformative influences that a similar systems approach could have within comparative psychology.

## Cross-References

- Analogical Reasoning
- Associative Learning
- Attention
- Cognition
- Comparative Cognition
- Comparative Psychology
- Declarative Memory
- Divided Attention
- Episodic Memory
- Exemplar Theory
- Family Resemblance
- Meta-cognition
- Operant Conditioning
- Primate Cognition
- Same/Different Learning

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## Cathemeral

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## Synonyms

Day-night activity; Diel activity; Polyphasic activity pattern

## Definition

Translated as “through the day” in Greek, this behavioral trait is a non-adherence to a strict

diurnal (i.e., active during the day) or nocturnal (i.e., active during the night) activity, often showing several peaks over the diel (i.e., 24 h cycle) day (Tattersall 1987).

## Introduction

Cathemerality is a term applied to the pattern of an organism's activity that occurs during both the light and dark portions of the 24 h cycle. Thus, a cathemeral organism does not strictly adhere to a diurnal (i.e., active during the day), nocturnal (i.e., active during the night), or crepuscular (i.e., active during twilights) phase, but rather shifts its activity throughout the 24 h. Put more simply, “the activity of an organism can be regarded as cathemeral when it is distributed approximately evenly throughout the 24-h of the daily cycle, or when significant amounts of activity, particularly feeding and/or travelling, occur within both the light and dark portions of that cycle” (Tattersall 1987). The word “significant” assumes a particular importance in Tattersall's definition. In fact, it is important to note that bouts of activity that include only a few behaviors (e.g., vigilance or body movements within a sleeping tree) or that account only for a small proportion of the overall activity during the 24-h cycle (the threshold is usually set at 10%) should not be enough evidence to consider a species cathemeral. Several activity patterns (i.e., monophasic, biphasic, or polyphasic) or activity rhythms (i.e., circadian or ultradian) may result in cathemeral activity (Halle and Stenseth 2000).

Sometimes it is difficult to classify a species' activity as cathemeral as this is an intrinsic flexibility that may not be evident when ecological conditions do not make this behavior advantageous. The description is especially problematic when species activity is described in captivity or over one season or in a limited number of localities as the animals react to local conditions that may make them fully diurnal or fully nocturnal, thus masking this behavior (Fox and Bellwood 2011; Donati et al. 2013).

Light and dark phases of the diel (i.e., 24-h cycle) day represent contrasting sensorial environments (Halle and Stenseth 2000; Donati

and Borgognini-Tarli 2006). As opposed to a year-round diurnal or nocturnal activity, or even crepuscular activity, taxa exhibiting cathemerality are presented with the challenge of compromising between adaptations for light and dark phases of the 24-h cycle (Prugh and Golden 2014). Even if the visual characteristics of cathemeral animals are often mixed between diurnal and nocturnal traits, they appear to exhibit an intermediate visual morphology allowing them to cope with these contrasting demands (Donati and Borgognini-Tarli 2006).

Cathemerality is inherently flexible and is exhibited across a wide array of organisms, including temperate and tropical fish (Fox and Bellwood 2011), reptiles (Vermunt et al. 2014), and many mammalian Orders within Metatheria, Prototheria, and Eutheria (Curtis and Rasmussen 2006). As cathemeral taxa inhabit a diverse range of ecoregions (e.g., arctic, temperate, and tropical), the environmental pressures within each are highly variable. Thus, cathemeral activity may confer different adaptive advantages within each habitat (Curtis and Rasmussen 2006; Fox and Bellwood 2011). While cathemeral activity appears common among mammals, it is very rare in primates and thus has become the focus of intense research (Donati et al. 2013). Some primates in the Cebidae family (i.e., *Aotus* spp.) and the Lemuridae family (i.e., *Eulemur* spp., *Haplemur* spp., and *Lemur catta*) regularly display cathemeral activity patterns in a variety of habitats (Donati and Borgognini-Tarli 2006; Donati et al. 2013; Eppley et al. 2015).

## Environmental Cues

For cathemeral taxa, activity cycles are modulated by external factors (e.g., lunar luminosity, temperature) that either stimulate or inhibit activity at certain times of the 24-h day (Donati et al. 2013; Eppley et al. 2015; Halle and Stenseth 2000). Variations in day-length due to the seasonal shift of sunrise and sunset times can act as a zeitgeber, that is, an environmental cue that works as a synchronizing or an entrainment agent to control the onset and cessation of activity. Because of this

tight link with photoperiodic variations, temporal activity shifts are often associated with seasonal changes in light-dark ratios that provide a somewhat reliable cue when describing cathemerality (Donati et al. 2013). This also implies that at higher latitudes, the duration and distribution of activity change dramatically due to significant seasonal changes in daylength (Halle and Stenseth 2000). Among many mammals, moonlight suppressed nocturnal activity (Prugh and Golden 2014), though for most cathemeral primates, lunar luminosity increases nocturnal activity (Donati et al. 2013; Eppley et al. 2015). Regulated by photoperiodic changes and nocturnal luminosity levels, these daily activity variations are undoubtedly linked with the degree of habitat seasonality of the taxa studied.

## Adaptive Value of a Flexible Activity Pattern

Across various taxa, cathemeral activity has been linked to a multitude of non-mutually exclusive explanations, including thermoregulatory strategies to avoid cold/heat stress, anti-predator strategies, metabolic dietary-related needs, and the avoidance of interspecific competition (Curtis and Rasmussen 2006; Donati and Borgognini-Tarli 2006).

Thermoregulatory strategies, i.e., the avoidance of extreme temperatures, appear to be a common driver for cathemeral activity across many taxa. For example, some large herbivores such as eastern grey kangaroos (*Macropus giganteus*) reduce heat stress during the hot daylight hours by resting in the shade, and as a result, they increase nocturnal activity (Clarke et al. 1995). Some small- and medium-sized mammals have been recorded to constrain their nocturnal activity during days of low ambient temperature (Halle and Stenseth 2000), a thermoregulatory strategy also employed by tuatara (*Sphenodon punctatus*) (Vermunt et al. 2014).

Foraging success is determined by the need to minimize predation risk, thus activity patterns influence the probability of interactions among predators and prey. For example, in several brown lemur species (*Eulemur* sp.), a shift towards

nocturnal activity can reduce the perceived risk from diurnal predators, representing a predator avoidance strategy (Curtis and Rasmussen 2006). Predation masking effects have been observed in a tropical reef fish, the golden lined rabbitfish (*Siganus lineatus*), which completely shifts its activity pattern based on potential predation pressures in specific habitats (Fox and Bellwood 2011).

In many small mammals, cathemerality is a behavioral strategy to cope with seasonal dietary shifts and increase foraging efficiency. Basically, activity is extended across the full 24-h period in order to maximize energy and nutrient intake. This is a consequence of small body size causing an extremely high relative metabolic rate and a limited capacity for fiber digestion, as observed in shrews and voles (Halle and Stenseth 2000). In primates with simple digestive systems (e.g., *Eulemur* spp.), cathemerality may explain shifts in activity during periods of increased fiber intake (Donati et al. 2013).

Lastly, cathemerality has been suggested as a strategy to minimize interspecific competition. Among species that are morphologically and ecologically similar, a variation in activity cycle may assist in maintaining sympatry, i.e., existing in the same geographic area, when the expected potential for competition is strong. Several studies on mammals offer evidence of temporal niche partitioning by shifting their 24-h activity. For example, the short-tailed vole (*Microtus agrestis*) maintains activity during its preferred time window, while the sympatric bank vole (*Myodes glareolus*) shifts its activity peaks (Halle and Stenseth 2000). In the seasonal dry forests of north-western Madagascar, mongoose lemurs (*Eulemur mongoz*) and common brown lemurs (*Eulemur fulvus*) show different patterns of cathemerality to minimize the overlap in core home ranges, sleeping sites, and diet (Curtis and Rasmussen 2006).

## Conclusion

In conclusion, cathemeral activity provides varying adaptive values in different ecological contexts. This activity is clearly not the result of a single ultimate reason but rather the ability

to adjust behaviorally to different biotic and abiotic pressures. In all cases, the advantages of cathemerality must be significant since the lack of specialization toward one of the phases of the 24-h cycle comes with high costs for an animal, e.g., being exposed to diurnal and nocturnal predators or temperature extremes.

## Cross-References

- [Activity Budget](#)
- [Circadian Rhythm](#)
- [Crepuscular](#)

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## Cat-Human Bond

► [Feline Cognition](#)

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## Cattarine Morphology

► [Precision Grip](#)

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## Cattle

► [Bovine Cognition](#)

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## Caudata

► [Caudata Sensory Systems](#)

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## Caudata Cognition

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## Synonyms

[Amphibia](#); [Behavior](#); [Migration](#); [Newt](#);  
[Salamander](#); [Sensory systems](#); [Territoriality](#)

## Definition

Mental processing of environmental and social information and sensory input in salamanders.

## Introduction

There are approximately 8,000 species of known amphibians, about 500 of which are salamanders (Frost 2019). Amphibians arose about 360 million years ago with the oldest salamander fossil dating to the Miocene (Petranka 1998). Members of the class Amphibia are ectothermic tetrapods, lack scales, and have heavily glandular skin. Salamanders are unique from frogs and caecilians, most obviously, by always having a tail and forelimbs; a few salamander species lack hind limbs. Many species have biphasic life cycles where they spend the first portion of their lives in water and their adult life on land; however, there are some species that are solely terrestrial and solely aquatic (Petranka 1998). Modes of respiration include gills, lungs, and gas exchange through the skin (i.e., cutaneous gas exchange). Some groups and species (e.g., Proteidae, *Eurycea* spp.) are permanently aquatic, remaining in a somewhat larval form through life, and have conspicuous external gills. *Ambystoma tigrinum* heavily rely on gas exchange through lungs even as fully aquatic neonates. Adult *A. tigrinum* breathe through their nares or mouth using a two-stroke buccal pump (a method of ventilation where the animal moves the floor of its mouth in a rhythmic manner that forces air into the lungs). However, Plethodontidae lack lungs entirely and rely on cutaneous gas exchange.

Larval and adult-form (i.e., post-metamorphic) salamanders are carnivorous, with a diet consisting mostly of insects and other invertebrates. The largest species sometimes eat fish or small animals such as frogs and mice (Petranka 1998). Salamanders of the family Sirenidae (*Siren*, *Pseudobranchius*) also eat plant and algal material (Hill et al. 2015). Salamanders are prey to a variety of animals including fish, snakes, small mammals, birds, and invertebrates (Petranka 1998).

Cognitive research on all amphibians has been limited, especially compared to mammals and birds (Agrillo 2014; Kundey et al. 2016). Cognition is inarguably a broad field, so here we will mainly focus on how information from an



organism's environment may be used to modulate the organism's behavior. For example, quantitative discrimination is often used as a measure of cognitive ability, in contrast to nonnumerical discrimination (Agrillo 2014). Nonnumerical mechanisms that organisms may be using to discriminate quantities include the surface area of an object, density, amount of movement, element configuration, and/or overall brightness. For example, salamanders are able to discriminate between groups of live prey by choosing the larger group, but performance dropped to the chance level when the movement of prey was controlled for (Krusche et al. 2010). Concepts of cognition also extend to include mating behavior, recognition of individuals, territoriality, and foraging success, among others. By experimentally testing these behaviors in the lab and in the field, researchers are better equipped to infer which behaviors are instilled in organisms by instinct and what may be the result of learning from their environment.

## The Brain

Herrick (1948) provided a detailed description of the tiger salamander brain (*Ambystoma tigrinum*), which is an appropriate model for general brain structure of salamanders. The brain is divided into three main parts: the striato-amygdaloid complex, the hippocampus, and a large olfactory bulb. While brain function is not well studied in salamanders, the large olfactory bulb clearly is associated with the strong influence of pheromonal and other olfactory information on virtually all aspects of salamander natural histories. Apparently in anticipation of spring season foraging and mating, chemosensory cells and cells in the telencephalon portion of the brain, which contains the olfactory bulb, proliferate in number during this season (Dawley et al. 2000).

Roth (1987), with special attention to the visual system, also provided morphological descriptions of the brain. He also found that the visual perception and recognition of prey could be a useful tool for studying cognition, as he found that the

behavioral preferences of the salamanders for specific prey depended upon previous experience with those prey. He further generalized that movement by prey items is crucial to prey recognition in salamanders and coalesced these findings to posit a functional model of a neural "recognition module" concept.

## Cognitive Ecology

Cognitive ecology encompasses the interface of cognitive phenomena with the natural and social environments and experiences of an animal. Cognitive ecology is not itself a cognitive phenomenon, like memory may be. Rather, cognitive ecology is a framework to interpret the basic natural history and behavioral functions of an animal, from which we may infer some essential cognitive abilities. By considering the effects of information processing on animal fitness, the specifics of a species' cognitive ecology may be assessed. An example from feeding, which certainly is a direct influence upon fitness, prior to experience with prey appears to influence feeding behaviors. For example, naive *Plethodon cinereus* offered either dead or live fruit flies consumed more flies per minute on their second trial compared to their first, which is indicative of learning (David and Jaeger 1981). Additionally, adult *Plethodon cinereus* capture novel prey more quickly than do neonate or yearlings (Gibbons et al. 2003). Expanding beyond foraging behaviors, and more related to shelter and perhaps homing, salamanders (*Ambystoma tigrinum*) trained to either go left or right in a maze toward a reward of a moist microhabitat continued to go the direction in which they were trained even after the maze was rotated 180° (Kundey et al. 2016). This suggests that the salamanders preferentially used a learned turning response over visual cues.

## Courtship and Reproduction

Courtship is highly variable among salamanders, with few commonalities. In many species,

especially of ambystomatids, plethodontids, and salamandrids, courtship involves complex series of ritualized visual, physical, and pheromonal phenomena (Petranka 1998). For example, in some cases, the male deposits a spermatophore on the substrate and guides the female into the appropriate position so that she can take it up into the cloaca. In the best studied plethodontid salamanders, complex, coordinated, and species-specific courtship rituals include tail-straddle walks, physical contact, and body-stroking as part of the sequence to guide the female into position over the spermatophore. With no evidence to indicate learning, these displays and responses are assumed to be innate. Both males and females process spatial information, such as body size, for themselves and for potential mates during courtship displays. Such processing allows the salamanders to align the male's spermatophore with the female's cloaca. Roth (1987) reviewed experimental studies that demonstrated the importance of coloration in mate recognition and choice in aquatic newts (*Triturus* spp.) that have highly visual mating rituals.

### Quantitative and Numerical Discrimination

Organisms should evolve foraging strategies that maximize caloric gain while reducing caloric output. Functionally, such strategies would act as caloric intake/output calculators using information from numerosity and/or mass discrimination. This suggests that they should be able to distinguish a number of prey items and not just a larger overall quantity (i.e., mass) of prey. *Plethodon shermani* and *P. metcalfi* were given a choice of 8 versus 16 and 8 versus 12 prey items (crickets: *Gryllus bimaculatus*). They significantly chose 16 over 8, but there was no significant difference in the 8 versus 12 trials (Krusche et al. 2010). *Plethodon cinereus* chose the larger numerical quantity of prey (*Drosophila virilis*) when choosing between one versus two flies and between two versus three flies (Uller et al. 2003); but there were no differences when the animals were offered 4 versus 6 and 3 versus 4.

### Chemical Communication

All salamanders may rely heavily on olfactory cues in all aspects of their behaviors. Plethodontid salamanders have unique grooves in the skin of the snout that lead from the margin of the upper lip to the nostrils; the grooves encourage uptake of chemical cues from the substrate, or the body surface of other salamanders, directly into the nostrils and their sensory cells. Physical damage to these grooves, from external parasites or aggressive interactions with conspecifics, can reduce subsequent foraging abilities (Jaeger 1981). The importance of chemical sensation in salamanders is underscored by multiple examples of cave-dwelling species that are blind and swamp-dwelling species with very reduced eyes. Nevertheless, the eyes of salamanders are similar to those of all amphibians in having a unique visual sensory cell type known as green rods; these cells contribute to remarkable visual abilities in very low-light situations.

Salamanders may communicate sex and species identity information through pheromones. Jaeger and Gergits (1979) found that males and females of *P. cinereus* and *P. shenandoah* can discriminate between their own substrate versus a substrate upon which a conspecific had been housed. In addition, both males and females of *P. cinereus* avoided the substrates of conspecifics. However, female *P. cinereus* did not avoid substrates of heterospecific, male *P. shenandoah*. This suggests that salamanders exhibit pheromonal (conspecific) and allomonal (heterospecific) communication, and these chemicals may confer information about the species and sex of individuals.

### Visual Communication

While olfactory cues appear to be a primary source of perception in salamanders, Roth (1987) presented experimental and theoretical evidence supporting the importance of visual stimuli in salamanders, both in the context of feeding and mate selection. *Plethodon cinereus*, presented with dead prey items, used chemical

cues but not visual cues were used to successfully locate, recognize, and ingest prey (David and Jaeger 1981). In the wild, immobile prey may comprise 5% of the diet of these salamanders, indicating foraging is mediated both chemically and visually (Roth 1987). Immobile preys typically are not dead individuals, but rather items such as chrysalises or nonmoving snails, etc.

Fecal inspection is commonly observed in *P. cinereus*. Females that had been fed low-quality diets showed similar rates of squashing and inspection of fecal pellets of females and males that were fed a high-quality diet (Karuzas et al. 2004). The authors concluded that this behavior is used to select foraging areas. Males may take advantage of this behavior by defecating around their territory to attract females.

Larval and fully aquatic adult salamanders (e.g., *Amphiuma* spp.) have pressure-sensitive lateral line organs, as seen in fish and larval or fully aquatic frogs. The role of this sensory system in salamander perception has not been well studied.

## Homing, Migration, and Orientation

Sensory systems involved in orientation appear to include olfaction, magnetoreception, and extra-ocular (i.e., pineal) photoreception. Many species of salamanders spend much of their adult life in terrestrial habitats, migrating to appropriate bodies of water to reproduce. Semlitsch (2008, p. 260) defined amphibian migration as movements toward and away from aquatic breeding sites. This definition distinguishes the behavior from various forms of simple dispersal. Although migrating salamanders tend to remain in or return to the area of hatching, dispersal by populations into areas does occur (Semlitsch 2008), even if the associated exploratory excursions rarely are observed.

Long-distance homing behaviors, which differ from strict migrations, have been well studied in the newt *Taricha rivularis* (Twitty et al. 1964) and less so in a few other salamanders. When *T. rivularis* were displaced, their movements

were strongly oriented toward their home even when it was several kilometers distant from the release site. Such a displacement distance is far greater than would be typical of a breeding migration or individual dispersal.

## Territoriality and Nesting

Jaeger and Forester (1983) reviewed various forms of territoriality and agonism in plethodontid salamanders – the best studied group by far – but other groups also have been surveyed (e.g., ambystomatids; Ducey 1989). Four characteristics of territoriality in salamanders are as follows: (1) the individual must have a “space” to be defended; (2) the individual must have the ability to defend this space through agonistic behavior; (3) individuals demarcate the space through pheromonal or visual displays; and (4) individuals are able to resist intrusion from invading salamanders.

Familiarity with a territory affects a resident salamander’s aggressiveness with intruders (Nunes and Jaeger 1989). Other factors that influence territoriality include body size of the resident, body size of the intruder, reproductive condition (i.e., courting season), number of intruders, condition of the tail of either salamander (e.g., complete vs. incomplete, amount of fat reserves), and food quantity/quality in the territory. Residents of a territory are more likely to initiate aggression than the unfamiliar salamander introduced to the territory (Jaeger 1981). In addition, there was more aggression observed when a resident was in contact with an unfamiliar salamander compared to a familiar salamander. When aggressive, the salamander’s bite is directed toward the tail or snout. Salamanders keep important fat reserves in their tail, and scar tissue on the snout negatively affects a salamander’s chemoreceptive abilities, leading to decreases in individual fitness.

Anthony et al. (1997) compared aggressive behavior in intra- and interspecific contexts in two species of sympatric salamanders: *Plethodon ouachitae* and *P. albagula*. These species have similar ecological requirements, but *P. ouachitae*

is slightly smaller than *P. albagula*. *Plethodon ouachitae* were extremely territorial in both intra- and interspecific experiments, delivering bites 14 times more than in any previously studied *Plethodon* sp. Similar levels of aggression by *P. ouachitae* were observed when the salamander was an intruder into conspecific or heterospecific territories, indicating that elevated levels of aggression in this species also occur outside of the context of territorial defense.

The energy that male salamanders will expend defending their territory is proportional to the value of the territory. Adult male red-backed salamanders that have preferable prey (termites) are more likely to bite intruders than resident males that had less preferable prey (ants; Gabor and Jaeger 1995). Aggressively defending a territory sends honest signals to intruders that a territory is valuable. However, residents weigh these costs against the benefits of deterring the intruders. Female *P. cinereus* stay with their eggs while only occasionally leaving to forage, and her neonates stay with her for 2 weeks. Nest guarding behavior is known in many plethodontid species, as well as in Amphiumidae, Cryptobranchidae, and other examples. Kin recognition is consistent with the phenomena of territoriality and nest guarding and appears to occur in *P. cinereus*. Hungry females preferentially consume unrelated neonates compared to related neonates (Gibbons et al. 2003). Putative kin recognition and mother–offspring interactions have not been well studied beyond *P. cinereus*.

### Sexual Differences in Territoriality

Salamanders show sex differences in choice of cover, searching unoccupied territories, and in mate guarding behaviors. Mathis (1990) showed that choices of cover objects, for both males and females, are positively correlated with body size. After removing salamanders from a section of the forest floor, females invaded unoccupied territories more often than did the males. Females may be more competitive because not only does she have to brood her eggs there, but she also must

have sufficient prey (energy) in order to adequately provision eggs with yolk.

Males in a mated pair spend significantly more time threatening male intruders than do the females in the same mated pair (Lang and Jaeger 2000). However, when the intruding salamander is female, the female in the mated pair acts more aggressive than their male counterpart. Pairs co-defend territories, but not cooperatively because they show disproportional aggression toward same-sex intruders. In addition, both males and females aggressively attack their partners if the partner is anointed with pheromones from other opposite-sex individuals, which would indicate that they have been involved in social polyamory (Prosen et al. 2004).

There also are sexual differences in cost-benefit considerations of energy. For females, the cost-benefit ratio of territory defense depends on the number and sex of intruders, as Kohn et al. (2005) found that female salamanders defended their territory when one male was present, but not when there were two males present. In this case, it appears that the energy cost of defense was acceptable in the context of one male but unacceptable in the context of two.

Evidence suggests that females prefer substrates of partner males over those of unfamiliar males (Gillette et al. 2000). Social monogamy is preferential to both males and females because the female can take advantage of the male's resources and the male can insure that she will mate with him. However, males showed no preference between their partner's pheromones and an unpaired female. This suggests that adults display social polygamy when there is an unpaired female available. Additionally, interactions that display social monogamy are exclusively seen during the courtship season (Gillette 2003).

### Dear Enemy Recognition and Mating Systems

Dear enemy recognition (Jaeger 1981) is a phenomenon in which salamanders have territories in

close proximity to one another, where there will likely be an aggressive interaction between the residents. Regardless of the outcome, a second aggressive encounter between residents is less likely – evidently because the salamanders recognize their former enemies. *Plethodon cinereus* is able to distinguish between familiar and unfamiliar conspecifics. McGavin (1978) found that if a resident salamander was presented with either an unfamiliar salamander or familiar salamander, the resident bites the unfamiliar individual significantly more frequently. Similar results were found despite the sex of the resident.

Jaeger et al. (1995) found that juvenile *P. cinereus* are attracted to territorial pheromones of male and female adult *P. cinereus*. Adults were more tolerant of sharing their territory with a juvenile than an adult and more tolerant of a familiar juvenile compared to an unfamiliar juvenile.

## Conclusion

Much remains unknown about Caudata, but recent research suggests that salamanders are more cognitively complex than previously thought. There is evidence of intricate inter- and intraspecific dynamics both in the field and the lab. Clearly, cognitive abilities are manifest in many areas of an organism's life including searching for a territory, choosing a mate, and foraging, among others. Being the most basal group in the phylogeny of tetrapods, amphibians form the comparative basis for all other cognitive studies with tetrapods, as well as with fishes.

## Cross-References

- Caudata
- Caudata Locomotion
- Caudata Sensory Systems
- Chemoreception
- Homing
- Intersexual Selection
- Life History

- Mate Guarding
- Mate Provisioning
- Maternal Behavior
- Migration
- Scent-Marking
- Territory Defense

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## Caudata Locomotion

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## Synonyms

[Salamander or newt locomotion](#)

## Definition

Movement used by salamanders to traverse their environment.

The Caudata are amphibians that generally show the basal tetrapod body plan. They are lizard-like in appearance with slender bodies and short limbs (Girling 2013). They tend to have four toes on the forelimb and five on the hindlimb. Some fully aquatic species, like sirens and amphiumas, have reduced or absent hindlimbs. Like all amphibians, the Caudata have a distinct larval and adult stage. They have permeable skin that usually makes them reliant on habitats in or near water or other cool, damp places. Some salamander species are fully aquatic throughout their lives, while others take to the water intermittently, and others are entirely



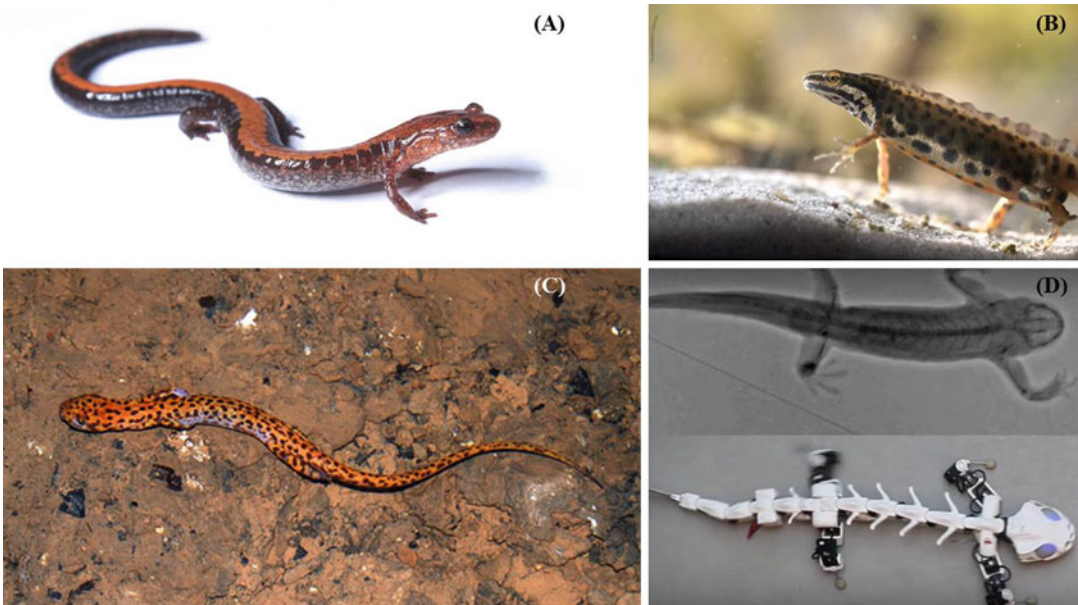
terrestrial as adults (Duellman and Trueb 1994; Stebbins and Cohen 1997).

## Major Locomotor Modes

**Caudata locomotion** can be broken down broadly into terrestrial and aquatic movement (Duellman and Trueb 1994; Karakasiliotis et al. 2016; Stebbins and Cohen 1997) (Fig. 1). Terrestrial gaits in the Caudata are highly variable and characterized by considerable variation in both limb-loading (Granatosky et al. 2020) and timing (Ross et al. 2013). All terrestrial **Caudata locomotion** involve symmetrical lateral-sequence walking gaits in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb) (Fig. 2). Commonly, during walking gaits the forelimbs and hindlimbs are traveling together as a slightly asynchronous couplet. When the contralateral forelimbs and hindlimbs are traveling together, this is referred to as a diagonal couplet. Very rarely do the limbs move together in perfect synchrony (Cartmill et al. 2002;

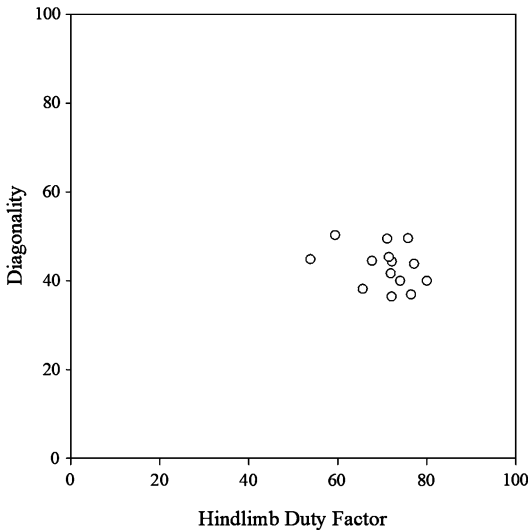
Granatosky 2018). All the Caudata use a lateral-sequence diagonal-couplet footfall patterns (Karakasiliotis et al. 2016; Nyakatura et al. 2019; Reilly et al. 2006). This footfall sequence is inherently quite stable due to the generally low proportion of the stride spent as a unilateral bipod (~22%), and the relatively high proportion spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support).

Literature on gait transitions (a speed related switch from walking to running) in Caudata is scant and it does not appear that the Caudata can adopt asymmetrical running gaits (e.g., gallop or bound). Experiments on tiger salamanders reveal that gait transitions are not visually detectable based on limb phase definitions (Reilly et al. 2006). It is the case though that if one bases the definition of a gait transition off of center of mass movements rather than limb phase definitions then both walking and running center of mass movements are present (Reilly et al. 2006). However, the use of these walking and running center of mass movements are not speed dependent (Reilly et al. 2006) and therefore are not



**Caudata Locomotion, Fig. 1** The Caudata are primarily restricted to (a) terrestrial and (b) aquatic quadrupedal gaits and (c) undulatory swimming. Biologically accurate (d)

bio-inspired robotics have been developed to replicate and further understand Caudata locomotor patterns



**Caudata Locomotion, Fig. 2** “Hildebrand” plot displaying diagonality against hindlimb duty factor collected during quadrupedal walking in Caudata ( $n = 14$  species)

synonymous with the gait transitions observed in birds and mammals (Granatosky et al. 2018).

Unlike mammals and birds, *Caudata locomotion* is characterized by a sprawling posture (Ashley-Ross 1994; Ashley-Ross et al. 2009; Karakasiliotis et al. 2013; Nyakatura et al. 2019). Sprawling postures are those in which the humerus and femur cannot attain an orientation with their long axes vertically directed. Limb movements during sprawling gaits are complex and limb posture changes considerably during a stride cycle. Rather than moving in a fore-aft arc underneath the body, the humerus and femur move backwards, outwards and downwards during stance phase. For sprawling Caudata, the highly abducted limb and lateral rotation of the zeugopod relative to the autopod results in a kinematic arrangement in which the ankle and wrist flexor musculature are not in line with the travel path at the end of stance phase (Ashley-Ross 1994; Karakasiliotis et al. 2016; Nyakatura et al. 2019).

Lateral body undulation plays an important part in *Caudata locomotion* and is integrated with limb movement (Karakasiliotis 2013). Standing wave patterns, where points of no lateral bending nodes alternate with areas of maximal

bending internodes, are clearly present during terrestrial walking (Karakasiliotis et al. 2016; Nyakatura et al. 2019). At the start of a stride, the trunk between the forelimb and hindlimb is maximally displaced to one side, although lateral trunk displacement is substantially less than during aquatic swimming (see below), while the neck, head, tail are maximally displaced in the opposite direction. About halfway into the cycle, the trunk bends maximally in the opposite direction, forming a mirror image of the start of the cycle. Hence, during terrestrial walking, the body axis forms a single standing arc that undergoes one full oscillation during a locomotor cycle (Frolich and Biewener 1992).

The Caudata larval stage is entirely aquatic. Like the adults, these larvae have relatively elongate slender bodies making them closer in appearance to certain fishes rather than the short globular anuran tadpoles (Frolich and Biewener 1992; Hoff et al. 1989). Also, they are ambush predators like many fishes rather than herbivores like tadpoles (Hoff et al. 1989; Stebbins and Cohen 1997). However, Caudata larvae have exposed gills and well-developed limbs throughout most of their larval stage that distinguish them from fishes, and these limbs interfere with their swimming performance. In general, salamander larvae do not swim in a straight path at a constant velocity nearly as effectively as either tadpoles or fishes. They have far greater maximum amplitude at high swimming speeds, and far less anterior stability. The drag induced by exposed gills and limbs may account in part for the inferior performance of the salamanders (Hoff et al. 1989). The Caudata larvae are designed for movement among the rocks and vegetation of the substrate, and for high acceleration over short distances, such as those used during a lunge at prey (Duellman and Trueb 1994; Stebbins and Cohen 1997).

For adults, aquatic locomotion involves both walking and swimming gaits (Ashley-Ross et al. 2009; Frolich and Biewener 1992; Stebbins and Cohen 1997). Kinematics of aquatic walking appear to be largely similar to what is observed on land (Ashley-Ross et al. 2009). Therefore, this chapter will not discuss these gait kinematics in further detail. However, swimming represents a

substantially differing motor pattern (Ashley-Ross et al. 2009; Frolich and Biewener 1992; Ijspeert and Cabelguen 2006; Karakasiliotis et al. 2016; Karakasiliotis et al. 2013). During swimming, individuals tuck arms and legs close to the body and use a traveling wave of lateral undulation (Ashley-Ross et al. 2009; Frolich and Biewener 1992; Ijspeert and Cabelguen 2006; Karakasiliotis et al. 2016). The propagation of this traveling wave can be clearly seen by the timing of maximal lateral displacements along the length of the trunk during a locomotor cycle. Maximal lateral displacements of the trunk tend to be dramatically higher during swimming compared to either terrestrial or aquatic walking. As the locomotor cycle begins, a wave of maximal lateral displacement is initiated on the right side near the shoulder girdle. This wave then travels with a constant velocity down the right side of the animal. As the locomotor cycle progresses, this right-side wave reaches a position posterior to the forelimbs and a new wave is initiated on the left side. As the next locomotor cycle begins, the first right-side wave is at the base of the tail, the left-side wave has reached the anterior region of the trunk, and a new wave is initiated on the right side. This pattern is repeated with waves passing alternately down the right and left sides of the animal (Frolich and Biewener 1992). As a result, the body axis is always thrown into an S-shaped curve that travels down the animal. Some Caudata species, such as sirens and amphiumas, have reduced or absent hindlimbs and become fully aquatic. As such, this undulatory locomotor mode is their primary means of movement (Gillis 1997).

### Influence of Caudata Locomotion on Neuromechanics and Bio-inspired Robotics

*Caudata locomotion* has served as a model system for understanding the function of central pattern generators (CPGs), which are networks of neural circuitry that receive a single input signal and output a cyclical or rhythmic motor command in response. Locomotor CPGs generate from

within the spinal cord as opposed to the brain (Andersson et al. 1981; Golubitsky et al. 1999; Kiehn and Butt 2003) and are found in nearly all vertebrate species (Golubitsky et al. 1999; Grillner and Zangger 1975; Grillner 1975; Guertin 2009). These neural networks result in rhythmic activities such as walking, running, swimming, and even chewing. Activation of salamander CPGs display rhythmic movements in both walking, trotting, and swimming as muscle activation travels from head to tail and between the left and right sides of the body (Ijspeert 2008; Ijspeert and Cabelguen 2006; Karakasiliotis et al. 2013; Knüsel et al. 2013). Sensory feedback in salamanders are instrumental for gait transition dynamics, where proprioceptive sensory inputs were essential for walking gait sequences, as opposed to trotting gait sequences which rely more on central CPG influence (Harischandra et al. 2011). Gait transition between the two may be induced by increasing activity of the descending drive originating from the mesencephalic locomotor region and can be aided by sensory inputs at the forelimb and hindlimb regions of the spinal cord. Progressively increasing the drive signal from a frequency of about 5 Hz to 20 Hz in mechanical models of salamanders with artificial mesencephalic locomotor regions has been shown to result in a transition from walking to swimming (Ijspeert et al. 2007).

The information derived from salamander CPGs has served as the foundation to develop bio-inspired salamander robots (Fig. 1). Most notable is Pleruobot developed by Karakasiliotis et al. (2016) to model the terrestrial and aquatic locomotor mechanics of the Iberian ribbed newt (*Pleurodeles waltl*). Pleruobot's kinematics and anatomical scaling were inspired from biplanar cineradiography and high resolution micro computed tomography. Through these data, the degrees of freedom of the live animal's musculoskeletal system were reduced in complexity to only the most essential and influential connections and joints. As a result, Pleruobot can achieve biological accurate terrestrial and aquatic locomotor mechanics with only 27° of freedom distributed throughout the spine, limbs, and two free

unactuated joints (Ijspeert et al. 2007; Karakasiliotis et al. 2016).

Beyond just accurately recreating the locomotor movement and timing of Iberian ribbed newts, Pleurobot has been designed in a manner to replicate a functioning CPG (Harischandra et al. 2011; Ijspeert 2008; Ijspeert et al. 2007; Knüsel et al. 2013). From live-animal experiments, limb and spine kinematics were coded into the CPG and sent to the servomotors powering Pleurobot (Karakasiliotis et al. 2016). Pleurobot's CPG has served a vital role in coordinating timing, efficiency, and accuracy of servomotor movements using incremental continuous rather than discrete input stimuli (Ijspeert 2008). Such a system allows Pleurobot to make gait transitions between terrestrial and aquatic mediums (Ijspeert and Cabelguen 2006), while maintaining biologically relevant internal and external limb forces, joint kinematics, and spatiotemporal gait characteristics (Karakasiliotis et al. 2016). Bio-inspired robotics allows researchers to alter aspects of the anatomy and motor control and directly assess how these changes alter overall system performance. Such manipulation is not possible with living animals.

## Cross-References

- [Adaptation](#)
- [Evolution](#)
- [Squamate Locomotion](#)
- [Zoology](#)

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## Caudata Sensory Systems

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## Synonyms

Caudata; Caudate; Urodela

## Introduction

Amphibians in the Order Caudata (or Urodela, salamanders, and newts) have the basic vertebrate senses that utilize the same receptor cells that are organized in the same basic patterns as all other vertebrates. This chapter is organized by receptor cell types: (1) Mechanosensory hair cells, which populate the inner ear or are located in structures embedded in the skin; (2) Olfactory/vomeronal chemoreceptor cells located in the nasal cavity; (3) Taste chemoreceptor cells located in the oropharynx; (4) Photoreceptor cells in eyes and parietal organ; and (5) Cutaneous receptors. Life cycles differ among caudates. Some species are aquatic both as larvae and adults; some are aquatic as larvae and terrestrial as adults; and some have the larval stage completed within the egg and hatch in terrestrial form (they are direct developers). Such distinctions affect the morphology and function of the different sensory systems. The large cell sizes of caudates also affect sensory system structure. Cell size affects number of receptor cells and subsequent organization of sensory organs and their targets in the central nervous system (Roth et al. 1992).

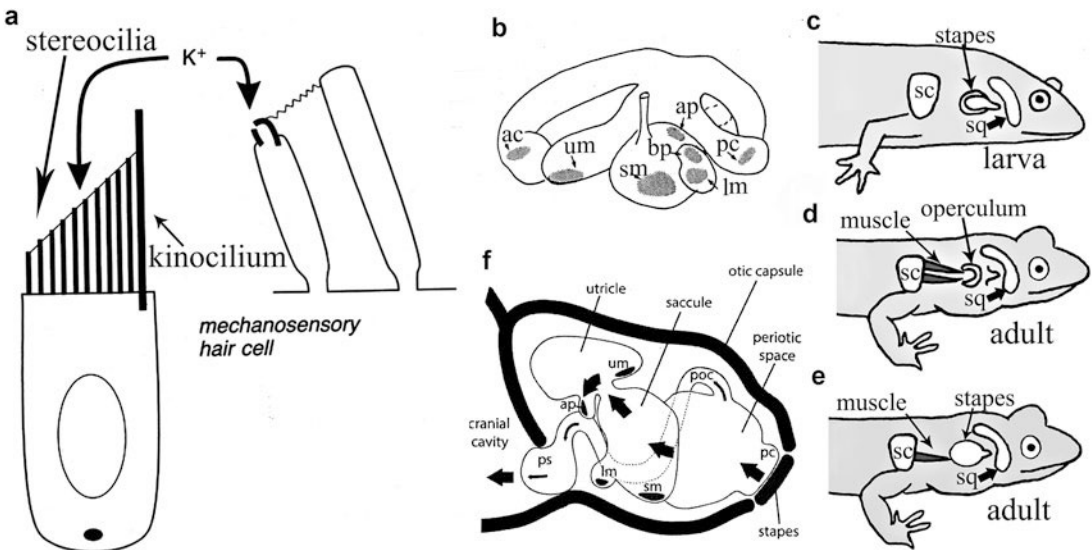
## Mechanosensory System: Body Position and Movement, Hearing, Lateral Line, Ampullary Organs

Mechanosensory hair cells are the sensory cells in all inner ear regions, lateral line neuromast organs, and ampullary organs of salamanders. The apical

surface (surface at the top) of hair cells has a cluster of stereocilia (stereovilli) arranged in a graded series by height, with the tallest adjacent to a single kinocilium (a true cilium), and the tip of each stereocilium is connected to the next higher stereocilium, and the tallest to the kinocilium, by structures called tip links (Fig. 1a). Tip links at the shorter of each stereocilia insert into a mechanically gated cation channel. If the kinocilium is deflected away from the stereocilia, tips links on adjacent stereocilia are tightened and cation channels on the stereocilia open, allowing cations, particularly potassium and calcium, to flow into the hair cell. This depolarizes the hair cell, ultimately causing excitation of the neuron that synapses with it. If the kinocilium is deflected in the opposite direction (toward the stereocilia), all tip links relax, closing the channels, which hyperpolarizes the cell, causing neuronal inhibition.

### Sense Organs of the Inner Ear

Mechanosensory hair cells are distributed in sensory patches within the inner ear, which is a membranous labyrinth of sacs and ducts, filled with endolymph (Fig. 1b). The membranous labyrinth is completely or partially encased within the cartilage or bone of the otic capsule of the skull, although there is a periotic labyrinth between it and the otic capsule (described further in section “Additional Structures Involved in Hearing: The Periotic Labyrinth”). The dorsal (superior) part of the membranous labyrinth is an elongated sac (utricle) from which the three semicircular canals emerge. The sensory patch of the utricle (macula) is overlain by a gel matrix with calcite crystals (otoliths). Movements of the endolymph cause the gel-otolith cap into which the stereocilia project to move, which then cause the stereocilia to bend. The utricular macula, which is set in a horizontal plane, measures position in space with respect to



**Caudata Sensory Systems, Fig. 1** Components of the caudate ear: (a) Mechanosensory hair cell with insert showing tip links that connect one stereocilium to adjacent stereocilia or to the kinocilium. The basal surface of the hair cell (opposite the apical surface) is where synapses are located. (Adapted from Fritzsche and Neary 1998); (b) Membranous labyrinth of inner ear showing positions of hair cell patches (labeled). (Adapted from McCormick 1992); (c) Middle ear structures of a typical larva; (d) Middle ear structures of a metamorphosed adult of some species with terrestrial stages; (e) Middle ear

structures of an adult of direct developing species; (f) Periotic labyrinth associated with membranous labyrinth surrounded by otic capsule. *ac* anterior semicircular canal crista, *ap* amphibian papilla, *bp* basilar papilla, *lm* lagena macula, *pc* posterior semicircular canal crista, *poc* periotic cistern, *ps* periotic sac, *sm* sacculus macula, *sq* squamosal, one of the bones of the skull near the inner ear, *um* utricular macula. Small and large arrows in (f) show direction of sound pressure displacement, which ultimately exits otic capsule to the cranial cavity. (Adapted from Capshaw and Soares 2016)



gravity and linear acceleration (it is gravistatic, responding to gravity). Each of the semicircular canals has an ampullary enlargement that contains a sensory patch covered by a gelatinous cupula (ampullary cristae). Each detects angular acceleration in a different plane through movements of the endolymph against the crista.

Ventral (inferior) and connected to the utricle is the largest chamber of the entire labyrinth, the saccule, which contains another gravistatic macula and three recesses. Each recess has its own hair cell sensory patch. In salamanders, these recesses are: (1) the lagena with its gravistatic macula, (2) a recess located near the opening of the lagena that houses the basilar papilla, and (3) a recess that houses the amphibian papilla. Note that in total there are three gravistatic maculae: the utricular macula, the saccular macula, and the lagenar macula. The basilar and amphibian papillae are small hair cell patches each overlain by a gelatinous tectorial membrane (which is more sensitive than the gel-otolith cap of gravistatic maculae) into which the stereocilia project. Both papillae respond to sound waves. In comparison to amniotes (Reptiles, including Birds, and Mammals), which have only a basilar papilla, amphibians have two sensory organs for sounds, although the basilar papilla can be reduced or absent in some salamanders. Thus, the amphibian papilla is considered the primary auditory organ. Neurons from the 8th cranial nerve carry all sensory information from the inner ear to the medulla.

### Additional Structures Involved in Hearing: The Middle Ear

Most terrestrial Vertebrates have middle ear structures that transfer sound pressure waves from the air with low resistance to movement to the incompressible fluid of the inner ear. These terrestrial innovations include a large diameter tympanic membrane connected to one or more middle ear ossicles within a middle ear cavity, which insert into a small diameter oval window (the opening of the otic capsule to the periotic labyrinth surrounding the membranous labyrinth).

Among Amphibians, although most anurans (frogs) have large tympanic membranes and

a middle ear cavity, salamanders lack both. This means that sound passes through tissue to cause the less responsive middle ear ossicle (embedded in tissue rather than within a middle ear cavity) to move. There are two amphibian middle ear ossicles, a stapes (columella), which is homologous to the stapes of other terrestrial Vertebrates, and an operculum, which is present only in some species of postmetamorphic (juvenile and adult stages after metamorphosis) amphibians. Both ossicles, if present, insert into the oval window. The operculum is connected to the scapula by muscles, and proposed functions for this system include detection of airborne sounds or substrate vibrations, enhancement of vibrational sensitivity, protection against intense sounds, or modulation of frequency sensitivity. During caudate development, a stapes is the first middle ear element to form and is movable and functioning during the aquatic larval period (Fig. 1c). In species with aquatic adults that never metamorphose into terrestrial forms, only the stapes is present. In some caudate species with adults that spend some of their time on land, the stapes becomes fused to the otic capsule during metamorphosis and the operculum is the only movable element (Fig. 1d). In many terrestrial, direct developing species, only a stapes is present, which is connected to the scapula via muscles and functions like an operculum (Fig. 1e). These observations support the idea that a middle ear ossicle attached to the scapula via muscles is important for sound reception on land.

### Additional Structures Involved in Hearing: The Periotic Labyrinth

Another component necessary for perception of airborne sounds is a periotic labyrinth of ducts and sacs filled with perilymph, which occupies the spaces between the membranous labyrinth of the inner ear and the otic capsule. Thus, sound pressure waves drive the ossicle that inserts in the oval window, which then drives the perilymph in the cistern internal to the oval window through a pathway (periotic canal) that passes by the sensory patches of the amphibian and basilar papillae (Fig. 1f). This then sets into motion the tectorial membrane against the stereocilia. Among salamanders, the periotic labyrinth varies in pathways and

diameters of the periotic ducts, which likely corresponds to differences in how sound is directed toward sensory patches. In addition, the periotic ducts pass adjacent to the saccular and the lagenar maculae, suggesting that they may function in audition as well. Thorough reviews of caudate ear structure and evolution can be found in Hetherington (1988), Fritzsche and Neary (1998), Mason (2007), and Capshaw and Soares (2016).

### Auditory Abilities

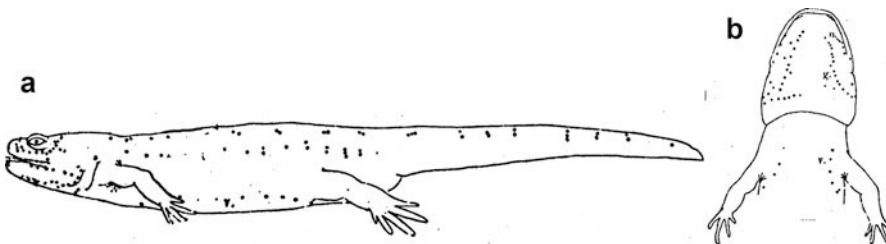
Aquatic larvae and terrestrial adults appear to have similar abilities to hear underwater sound, substrate vibrations, and air-borne sounds. For both, sound underwater is detected through water borne vibrations transferred through the head and then middle ear ossicle to inner ear but may be enhanced in adults of some species via air induced pressure detection using air in the lungs. Substrate vibrations may be detected through the pectoral girdle linked to the operculum/stapes (adult) via muscles, and air borne sound waves may be detected using the middle ear ossicle, if air borne sound can cause the ossicle to move relative to the head. Nevertheless, hearing in air for caudates shows improved sensitivity and frequency range when compared to the abilities of fishes. This is likely due to structures not present in fishes: an oval window, a movable ossicle, and an amphibian papilla that uses a more sensitive tectorial membrane (Christensen et al. 2015).

### Lateral Line Organs and Electrosensory Ampullary Organs

Caudates also possess mechanosensory lateral line organs (neuromasts) that use hair cells as

receptors (Fritzsche and Neary 1998). Neuromasts are in the epidermis and consist of hair cell patches surrounded by support cells, capped with a gelatinous cupula into which the stereocilia project. The gelatinous cupulae extend into surrounding water. The neuromasts are arranged in three to four discrete lines along the body and along lower jaw, above and below the eye, and in the occipital region of head (Fig. 2). Neuromasts are stimulated by low frequency water movements parallel to the major axes of the lines (a kind of distant touch). Distinct lateral line nerves project to a dorsal nucleus within the medulla oblongata. Lateral lines are present in aquatic larvae and adults and may be retained during metamorphosis, although the neuromasts are often covered by skin when terrestrial and only some reappear when adults return to water. Lateral lines are lost in terrestrial, direct developing species. Lateral lines are used in foraging by aquatic forms and cave forms, and in avoiding predators. There is evidence in one caudate Family (Hynobiidae) that males respond to the tail undulations of other males, and sexually receptive females orient toward male tail undulations, through their lateral lines.

Ampullary organs are invaginations of the skin with a cluster of hair cells plus support and mantle cells around the base of the ampulla, and no cupula. They are sensitive to small changes in electric fields, like those emitted by small prey. They are found alongside the lateral lines of the head, except in terrestrial, direct developing species. Aquatic larvae and adults, particularly cave forms, rely on ampullary organs, in addition to lateral line organs and chemoreception.



**Caudata Sensory Systems, Fig. 2** Lateral line system in *Ambystoma*. (a) Lateral view, (b) ventral view. (Adapted from Kingsbury 1896)

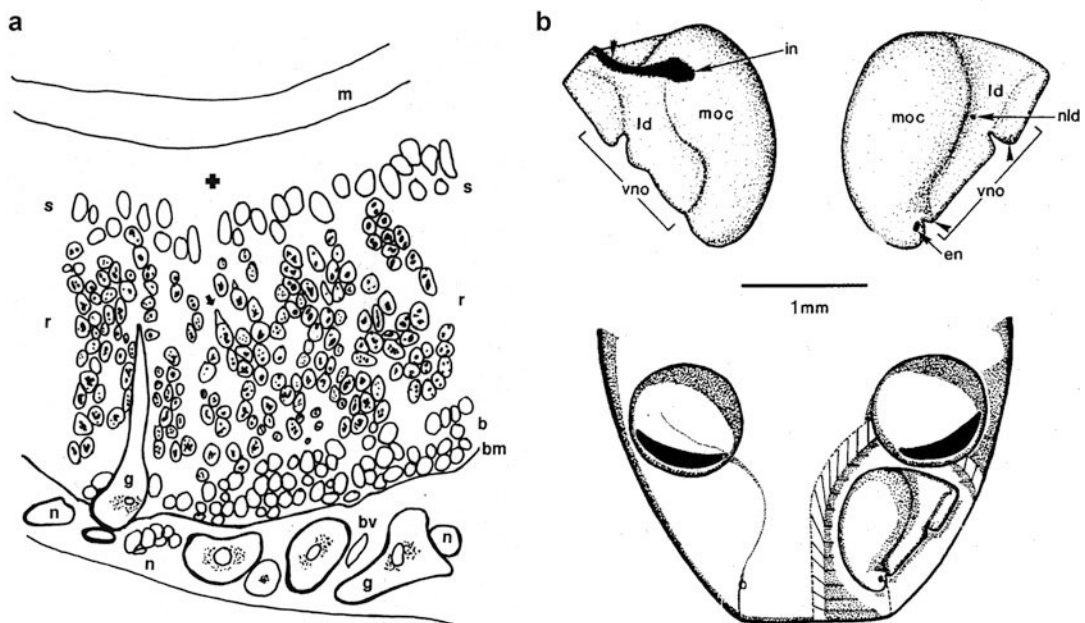
## Olfactory/Vomeronasal Chemoreception

The caudate olfactory and vomeronasal sensory systems consist of epithelia (a thin layer of tissue) located in the nasal cavity that is composed of three cell types: olfactory receptor neurons, supporting cells, and basal cells, as is the situation in all Vertebrates (Fig. 3a). Underlying the epithelial layer is a region (lamina propria) often richly populated by various glands, particularly in terrestrial species. One of these gland types, Bowman's glands, supplies the surface of the olfactory epithelium of terrestrial vertebrates with a watery mucous solution containing odorant-binding proteins.

Olfactory/vomeronasal receptor neurons are bipolar, with a dendritic process that projects to the epithelial surface, which is studded with cilia or microvilli containing the receptor sites for odorant detection. Each receptor neuron expresses only one or few odorant receptor genes (ORG)

from a large family of ORGs (*Xenopus* frogs with 410 genes; mice with >1000 genes) or vomeronasal receptor genes (VRG), and individual genes are expressed in subpopulations of cells (Niimura and Nei 2006). ORGs/VRGs code for G-protein coupled receptors (GPCR) in the cell membrane, to which odorants bind, triggering a signaling cascade that subsequently leads to an action potential propagated through the axon. The axonal processes of receptor cells project to the main or accessory olfactory bulbs of the telencephalon (olfactory and vomeronasal, respectively). Supporting cells also possess microvilli; these cells have several glial-like functions and contribute to the overlying mucous layer. Basal cells are stem cells that produce new receptor neurons.

The paired nasal cavities (Fig. 3b) are dorso-ventrally compressed sacs (if terrestrial) or more tube-like (if aquatic), each with an external naris that opens into the main olfactory chamber, which



**Caudata Sensory Systems, Fig. 3** Caudate olfactory/vomeronasal systems: (a) Olfactory epithelium; (b) Olfactory and vomeronasal organs in place in *Plethodon cinereus*. b basal cells, bm basement membrane, bv blood vessel, en external nares, g Bowman's gland, in internal nares, ld lateral diverticulum housing the

vomeronasal organ, m mucus layer, moc main olfactory chamber, n nerve, nld nasolabial duct, r receptor, s sustentacular cell, vno vomeronasal organ; arrow head points to slit-like extension of internal nares. (Adapted from Dawley 1998)

is partly lined with olfactory epithelium (Reiss and Eisthen 2008). An internal naris exits into the buccal cavity. In aquatic larvae and adults, a nonsensory vestibule connects the external naris to the main chamber. Each main olfactory chamber has a lateral diverticulum (ventromedial in few species) that houses the vomeronasal organ, which is partly lined with a flat vomeronasal epithelium. In aquatic salamanders, whether larval or adult, the main chamber epithelium is ridged, with the olfactory epithelium confined to grooves between ridges. In terrestrial salamanders, the olfactory epithelium of the main chamber is a flat sheet of variable thickness, being thickest mid-dorsally and mid-ventrally, which positions the greatest number of olfactory receptor neurons in the pathway of greatest air flow during inhalation (Kauer 2002). In species that metamorphose from aquatic larvae to terrestrial adult, there are four major changes in the olfactory system: (1) the olfactory epithelium changes from ridged to flat, (2) which is accompanied by a changes in sensitivity of the epithelium from mainly water-borne odorants to include volatile odorants, (3) the shape of the main chamber changes from tube-like to a dorsoventrally flattened sac, and (4) the vestibule is lost. Both olfactory and vomeronasal receptors can be classified as to whether they detect air-borne or water-borne odorants, thus there is no support for the simple dichotomy that main olfactory receptors are specialized for air-borne odors and vomeronasal receptors for water-borne odors. However, there are different classes of ORGs/VRGs for either air-borne or water-borne odorants, but not both, and those that detect air-borne odors increased in the evolutionary transition from water to land (Niimura 2009; Niimura and Nei 2006). The vomeronasal organ is considered a tetrapod adaptation, which is lost in some aquatic species (Proteidae) but retained in most other species. Access to the vomeronasal organ has usually been shown to involve physical contact with an odor source, such as nose-tapping by salamanders in the Family Plethodontidae (the caudate Family that includes the majority of living species). Nose-tapping involves touching the upper lip with its nasolabial grooves (structure unique to plethodontids that convey

liquids preferentially to the vomeronasal organs) to an odor source. In plethodontid salamanders, the vomeronasal organ is more anteriorly situated, which directly connects the vomeronasal organ with the nasolabial grooves.

Several lines of research, particularly rich for species in the Families Salamandridae (Treer et al. 2013) and Plethodontidae (Houck 2009), have shown the importance of chemoreception in salamander social behavior. Studies of Red-backed Salamanders (*Plethodon cinereus*) have demonstrated that individuals can discern sex and species information, as well as familiar versus unfamiliar conspecifics through chemoreception. Territorial scent marking is accomplished using fecal pellets and secretions from unspecialized and specialized skin glands (post-cloacal glands pressed to the substrate), and nose-tapping is involved in odor sampling. Skin glands secretions can also function as sexual attractants, serving to locate potential mates. Modified glands of the cheek, chin, or cloaca produce pheromones that are wafted to or rubbed on female nares (Salamandrids) or inoculated in the skin or delivered to her nares (Plethodontids). Pheromones delivered to female nares were shown to specifically activate vomeronasal receptor neurons. These pheromones increase female receptivity to mating and then induce typical mating behaviors in females (Treer et al. 2013). These sorts of studies have fueled the notion that the vomeronasal system is more important than the main olfactory system in social interactions, particularly those involving pheromones, but other studies have shown that the olfactory system is involved as well. Based upon molecular analyses of salamander pheromones (Sodefrin Precursor-like Factor (SPF) system), it is thought that these pheromones likely date back to the earliest salamanders (Janssenswillen et al. 2014). Those living species that do not use these pheromones during courtship probably represent a loss of the pheromone character.

Olfactory/vomeronasal chemoreception is used in foraging, particularly for nocturnal or cave dwelling species with small eyes, including aquatic forms. Otherwise, vision predominates for adults of most salamander species. In addition,

salamanders, particularly larvae, avoid becoming prey by reacting to the chemical stimuli from predators by decreasing movement and spending more time in refuges.

## Taste Chemoreception

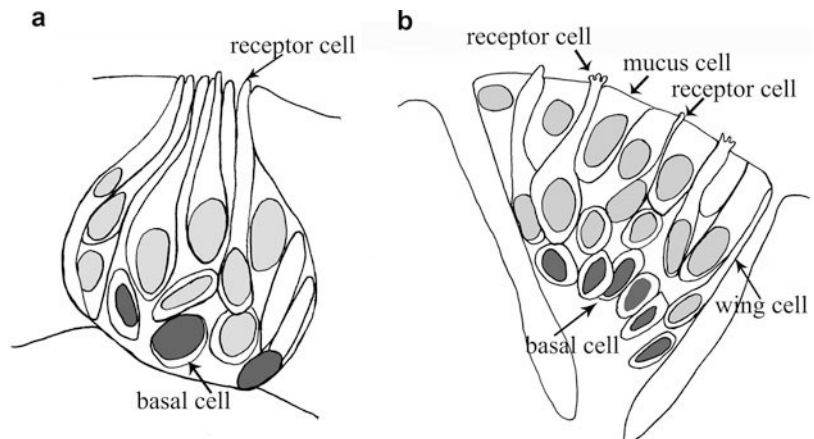
Taste receptor cells respond to only one of five basic tastes: sweet, savory (umami), bitter, sour, and salty, a model well supported by mammalian studies. The apical ends of the taste receptor cells, which end in microvilli, comprise the taste receptor area that interacts with taste molecules. Microvilli protrude above the surface of the epithelium in Amphibians (Fig. 4a, b). Taste molecules bind with receptor sites to trigger the transduction cascade (the conversion of the taste stimulus at the apical end of the cell to release of neurotransmitter at the taste cell-sensory neuron synapse), leading to taste recognition. Taste cells are innervated by branches of cranial nerves 7, 9, and 10 (facial, glossopharyngeal, and vagus), which project to the nucleus of the solitary tract located in the hindbrain. Sweet and umami receptors are part of a small family of G-protein-coupled receptors, and both trigger behavioral attraction. Bitter receptors belong to a different group of G-protein-coupled receptors and act to prevent ingestion. Sour and salty are both mediated by membrane channels. Although there have been molecular studies in fish to identify types of taste receptors, similar studies have not been done with caudates.

Information about taste reception in caudates has come from electrophysiological studies of transduction of taste stimuli, which provided evidence of the same five basic tastes in amphibians, although the ability to taste sweet may be lacking in caudates (Barlow 1998). Aquatic salamanders, specifically mudpuppies (*Necturus maculosus*) and larval tiger salamanders (*Ambystoma tigrinum*), have been the subjects of these studies of transduction mechanisms, but nothing is known about other species, particularly, those with terrestrial adult stages.

Amphibian taste receptor cells are grouped into units called taste buds (Fig. 4a) or taste disks (Fig. 4b), which are scattered throughout the oropharynx. Because caudate taste systems were first described in species that are aquatic even as adults, it was thought that caudates at all stages possess taste buds. In contrast, while aquatic larval anurans have taste buds, they metamorphose into adults with taste disks. More recent studies have shown that caudate species with terrestrial adult stages also have their taste receptor cells organized into structures that look more like taste disks. Taste buds are aggregates of cells arranged in a rosette, which may reside upon papillae (raised epithelium surrounded by a trench) or bulges or directly embedded in the epithelium within the oropharyngeal cavity. Taste disks are larger aggregates of cells with a broader receptive surface and with some different cell types than taste buds. They are also located in tongue papillae or directly embedded in epithelium.

### Caudata Sensory Systems,

**Fig. 4** Amphibian taste bud (a) and taste disk (b), based upon these structures in larval and adult *Salamandra salamandra* (Zuwala and Jakubowski 2001)





Taste receptor cells in both taste buds and taste disks are fusiform cells that extend the length of the bud or disk. Within taste buds there are also basal cells, which are disk-like cells that lie at the base of the bud. Some basal cells may have a neuromodulatory role with the receptor cells, and others likely are stem cells. Within taste disks, in addition to basal cells and receptor cells (and there are sometimes reported a glia-like cell), there are large mucus cells and uniquely shaped wing cells. Wing cell bodies lie beneath the mucus cells and their flattened apical processes separate the mucus cells. The mucus cells contribute to making the receptive surface broader than that of taste buds, and likely are adaptations to terrestriality (Zuwala and Jakubowski 2001).

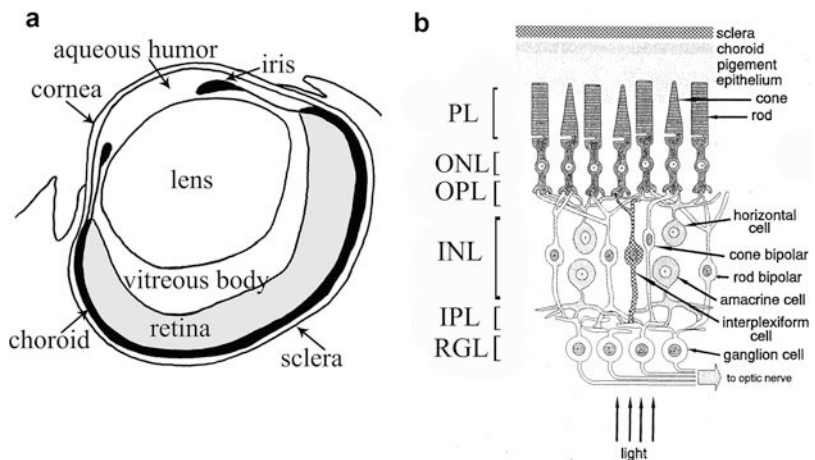
A transition from taste buds to taste disks on the tongue and on the lining of the oropharynx occurs with metamorphosis. In the permanently aquatic, neotenic axolotl (*Ambystoma mexicanum*), taste buds in larvae are scattered over the surface (floor and roof) of oropharynx and they begin to erupt at hatching. They increase rapidly in number, reaching adult number by 10 weeks, and are highly concentrated on the lingual surfaces of lower and upper jaws, including the primary tongue, and less so on the visceral arches. In caudate species that have been examined that undergo metamorphosis (*Salamandra salamandra*, *Hynobius retardatus*, *H. dunni*, and *H. leechi*), the primary tongue with taste buds is replaced by a secondary tongue with taste disks,

and taste buds in the lining of the oropharynx are replaced by taste disks. In direct developing caudate species, taste buds never develop, and newly hatched young possess the adult secondary tongue with taste disks, as well as taste disks on the lining of the oropharynx (Budzik et al. 2016). In adults of these species, the tongue is densely covered with taste disks, as well as the palate and lingual surface of upper and lower jaws. The positions of taste buds or discs suggest that taste is used to sample potential food items as they are pulled into the mouth by suction or use of jaws and prehensile tongue. Hence it is likely that taste is used in rejecting food, and other senses (vision and olfaction) are important for finding food.

## Photoreception

Caudate eyes are composed of the same elements as are all vertebrate eyes. Here the deepest structures are described first followed by progressively more superficial structures (Fig. 5a). The sclera and choroid layers (both dense connective tissue) are external-most. The retina (Fig. 5b) is composed of five layers, with the photoreceptor layer located in the deepest layer (ONL, the outer nuclear layer), and followed a very thin outer plexiform layer (OPL) composed of synaptic contacts. A thick layer of interneurons, the inner nuclear layer (INL) composed of horizontal, bipolar, and amacrine cells, is found next, followed by

**Caudata Sensory Systems, Fig. 5** Caudate eye (a) and details of retina (b). (a, Adapted from a photograph of *Bolitoglossa subpalmata* Roth et al. 1998). (b, Adapted from Butler and Hodos 1996). *INL* inner nuclear layer, *IPL* inner plexiform layer, *ONL* outer nuclear layer, *OPL* outer plexiform layer, *PL* photoreceptor layer, *RGL* retinal ganglion cell layer





a thick inner plexiform layer (IPL) of synaptic contacts. The retina is capped with a retinal ganglion cell layer (RGL), whose axons coalesce to form the optic nerve that exits the eye to synapse with brain targets. The bipolar cells connect the photoreceptor cells to the ganglion cells, while horizontal and amacrine cells modulate activity in this pathway by coupling or uncoupling photoreceptors. Superficial to the retina is a relatively thin vitreous body, then a large lens, followed by a watery aqueous humor filling the spaces in front of the lens, and, finally, a large cornea occupying nearly 1/3 of the eye surface (Fig. 5a). The cornea, aqueous humor, lens, and vitreous body function to refract incoming light, focusing it on the retina. In terrestrial salamanders, the large, curved cornea is the main refractive apparatus, while aquatic salamanders have a flatter cornea, and the nearly spherical lens is the main refractive apparatus.

The two layered ONL contains both types of vertebrate photoreceptors, rods and cones (Sherry et al. 1998). Both rods and cones have two compartments, an outer segment that is composed of stacked discs that contain the visual pigment molecules and an inner segment with nuclei and terminal branches of the cell. The cells are oriented with the inner segment adjacent to the OPL, where the synapses between photoreceptor cells and bipolar cells are located. Visual pigment molecules consist of an opsin protein bound to a carotenoid chromophore (retinal) to form a G protein-coupled photopigment within the membranes of the stacked discs. Most rods contain the photopigment rhodopsin (opsin + retinal1, a derivative of vitamin A1) in terrestrial caudates, or porphyropsin (opsin + retinal2, a derivative of vitamin A2) in some aquatic species, with maximum absorbance in the green spectrum. In addition, certain caudate genera (*Hynobius* and *Ambystoma*) and anurans possess a second rod type, a blue sensitive rod (confusingly named green rod) in addition to the green sensitive (normal) rod. In some anurans, the blue sensitive rod allows them to distinguish blue and gray under dark conditions, but it is unclear whether the same is true for caudates because only the blue-sensitive cone pigment is expressed in both rods and cones, suggesting it could not function

under dim light. There are three types of cone opsins in caudates, with names reflecting their maximum spectral sensitivities: very short (VS or violet/ultraviolet), short (S, or blue), and long (L, or red), with the latter being the most common type. A medium (M, or green) cone opsin is missing. UV sensitivity may be widespread across caudates despite the assumption that UV vision should not be favored in animals that live under forest canopies, or under water, or are nocturnal (all describe caudates). In nocturnal caudates, rods are the most numerous photoreceptor.

Light absorbed by the photopigments of the rods and cones creates an electrical neural signal carried to the brain by the axons of the retinal ganglion cells (RGC). Since visual acuity is partly determined by the diameter and packing of rod/cone outer segments, a large number of small diameter rods and cones increases acuity. Caudates, especially plethodontids, because of their relatively small eyes but large cell sizes, have “astonishingly low” numbers of RGC axons (a count of number of RGCs within the optic nerve). Yet they have “excellent visual abilities” (Roth et al. 1998). Most optic nerve fibers cross at the optic chiasm to the opposite side of the brain, traveling as the optic tract. The superficial layer of the optic tectum (a mesencephalic structure) is the major target of retinal cell axons, where this sensory information is mapped in topographic order. The caudate optic tectum is organized into two zones (superficial and deep), compared to the nine layers of alternating fibers and cellular layers of anurans, which, itself, has fewer layers than the tecta of teleosts and reptiles. Amphibian visual systems are considered secondarily simplified, with cell size negatively correlated with complexity of the optic tectum (Roth et al. 1992).

And yet, for most caudates, vision is the major sense used in prey detection and capture. Prey size, speed, movement patterns, and shape are the major cues used by salamanders, who are able to fixate binocularly on prey; orient toward prey with eye, head, or body movements; walk toward prey or ambush them; snap and seize with mouth or, in some species, seize with a protrusible

tongue. While at night prey movement is the most important visual cue, stationary prey are recognized by size, shape, and orientation cues, and salamanders can even discriminate quantity via prey movement (Krusche et al. 2010). Many species have a large visual field, some covering 360°, because eyes are frontally oriented; species with more laterally placed eyes have a binocular field of 65°. The most spectacular visual feats are accomplished by bolitoglossine plethodontids (a large group of Neotropical species), which all have free, projectile tongues with a reach of up to 2/3 snout-vent length, which are faster and more precise than that of any other amphibian, despite the most simplified optic tectum. They have highly developed stereoscopic vision and several unique adaptations that compensate for reduced number of neurons in the visual system, including a 1:1 ratio of photoreceptors to RGCs, which converts the entire eye to a functional fovea (a depression in the retina with a high concentration of photoreceptors).

Vision is also important in interacting with other organisms, along with chemoreception. A wealth of research on *Plethodon cinereus* (e.g., Kohn and Jaeger 2009; Duhaime-Ross et al. 2013) has shown that individuals signal aggression or submission toward conspecifics via postures; mates may assort with each other based upon visual cues (red and lead phases); and they can use visual cues to escape from predators. Because many temperate zone amphibians are active at dusk, it has been suggested that color skin patches reflecting UV light may be used in sexual communication, which would explain why functional genes for very short opsins are widespread among caudates (Mege et al. 2016).

Caudates, like many nonmammalian vertebrates, possess an extraocular photosensory organ, the pineal organ, which is an extension of the dorsal diencephalon. It is an intracranial, sac-like structure composed of rod-like photoreceptor cells, support cells, and neurons (like RGCs) that send axons to targets in the brain (in this case, dorsal diencephalon). The photoreceptor cells possess a basal axon, and inner and outer segments, the latter segment with photopigments sensitive to short (likely UV) and medium

wavelengths. These photoreceptors are sensitive to the plane of polarized light, and thus mediate celestial compass orientation, but also are sensitive to earth-strength magnetic fields and thus serve as a magnetic compass (Phillips et al. 2010). Migrating newts (Eastern red spotted, alpine newts, palmate newts) have been shown to use magnetic cues during nocturnal homing. In addition, the pineal organ is part of the mechanism regulating the body lightening reaction in larval amphibians.

## Cutaneous Receptors

Cutaneous receptors are free or encapsulated nerve endings in the epidermis or dermis that respond to light and strong touch, injuries (pain), vibration, and temperature (Heatwole 1998). Their cell bodies reside in the spinal cord dorsal root ganglia, thus they are spinal nerves, or in the hindbrain and travel through the trigeminal cranial nerve to the head. The receptor potential is generated by mechanical deformation of the nerve plasma membrane. The few studies specifically about caudate cutaneous receptors have concentrated on the Rohan Beard cells of embryos and early larvae and the Merkel cell-neurite complex of larvae and adults. The cell bodies of Rohan Beard cells form quite early in development to populate the length of the dorsal spinal cord, sending processes to the skin. They detect transient touch stimuli, initiating swimming or struggling. Merkel cells are located in the epidermis and are distinguished by small, finger-like surface processes, cytoplasmic Merkel granules (membrane bound granules), and are associated with tactile sensory nerve fibers of spinal nerves. Merkel cell-neurite complexes function as low threshold, rapidly adapting mechanoreceptors, and perhaps are the only mechanoreceptors in caudate skin.

## Cross-References

- [Caudata Cognition](#)
- [Chemoreception](#)

- [Electroreceptors](#)
- [Evolution of Animal Color Vision](#)
- [Mechanoreceptors](#)
- [Pheromone](#)
- [Salientia Sensory Systems](#)
- [Sensory Receptors](#)
- [Stereoscopic Vision](#)
- [Vertebrate Nervous System](#)
- [Visual Recognition of Prey and Predators](#)

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## Caudate

### ► Caudata Sensory Systems

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## Caudate Nucleus

### ► Medial Striatum

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## Causal Understanding

### ► Tool Use

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## Cecilia Heyes

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Cecilia Heyes, known as “Celia,” was born and brought up in Ashford, a small town in the southeast of England where her grandparents had worked on the railways and, in the surrounding countryside, as gamekeepers and domestic servants. The first member of her family to go to university, she chose to study psychology because she wanted to work in mental health, but her head was turned to the evolution of cognition by the inspirational lectures of Henry

Plotkin. After studying for a PhD at University College London (1981–1984), under Plotkin’s supervision, she was awarded a Harkness Fellowship to work for 2 years in the United States with the distinguished social psychologist Donald Campbell at Lehigh University and with two philosophers: William Wimsatt at the University of Chicago and Daniel Dennett at Tufts University in Boston. During a second period of postdoctoral study, as a Research Fellow at Trinity Hall, University of Cambridge (1986–1989), she was adopted by the laboratory of Anthony Dickinson and Nicholas Mackintosh, experts on associative learning. Their research tradition, animal learning theory, was diametrically opposed to the evolutionary approaches in which she had marinated before going to Cambridge. After 5 years of theory and nature, she learned the importance of experiments and the power of nurture. By the time she returned to University College London, now as a member of faculty, Heyes had been educated into a state of deep, rich confusion. She wanted to know more about how nature and nurture work together to build minds but had no idea how to find out. In retrospect, Heyes’s research over the next 30 years – at University College London (1988–2008) and then at All Souls College, University of Oxford (2008–present) – makes sense in the light of that ambition, but there was no grand plan. At any given time, she felt as if she was following her nose, being pragmatic enough to get research funding, taking opportunities provided by gifted students and postdocs, and hoping she would not be ejected from the wonderful but demanding world of academic research.

Heyes has focused on social cognition, principally social learning, imitation, mirror neurons, and theory of mind. She has done experimental work with nonhuman animals (rodents and birds), with adult humans (neurotypical and people with autism), and, in collaboration, with human infants and children. She has also published synthetic theoretical work on nonhuman primates and on broader themes relating to the evolution of human cognition. Although firmly rooted in experimental psychology, Heyes’s research also draws on behavioral economics, evolutionary biology,

neuroscience, philosophy of mind, and philosophy of science.

When Heyes began her research in the 1980s, it was widely believed that social learning – learning assisted by other agents – depends on psychological processes distinct from those enabling asocial learning and that the mechanisms of social learning had evolved specifically to enable transfer of information between agents. Heyes contested this view initially for non-imitative forms of social learning; cases in which one agent learns through interaction with another (e.g., about the location of food, or what to eat), but the learner does not copy movement topography – the way in which parts of the actor’s body move relative to one another (e.g., the model’s gait or foraging technique). She did this in two ways. First, in a wide-ranging conceptual analysis and empirical review of the literature on social learning, reaching back to the beginning of the twentieth century, she showed that each known type of social learning (e.g., stimulus enhancement, observational conditioning, imitation) corresponds with a known type of asocial learning (Heyes 1994). Second, developing new empirical methods (the “two-action test” and “ghost control”; Fawcett et al. 2002; Heyes et al. 1994; Heyes and Saggerson 2002), Heyes’s group completed a program of experimental work with rodents and birds showing that animal learning theory could provide mechanistic explanations for a broad range of social learning effects. At the beginning there was a good deal of resistance to Heyes domain-general analysis of social learning, but it is now widely accepted that most, if not all, social learning in animals is mediated by the same core mechanisms as asocial learning. The “social” part of social learning is attentional; the psychological processes that encode information for long-term storage are the same whether the input is from the social or inanimate world (Heyes 2012a).

Initially, Heyes accepted the view, established by Edward Thorndike in the late nineteenth century, that imitation is special. An early and influential article (Heyes 1993) queried the assumption that imitation is especially important for the cultural inheritance of information but acknowledged that no mechanistic solution had been found, in learning theory or elsewhere, for

imitation’s “correspondence problem.” This problem, explicated by Jean Piaget, is roughly: When imitators cannot see their own movements, how does the cognitive system convert visual input from a model into motor output that is topographically similar to the model’s behavior from a third-party perspective? More pithily: How does the cognitive system convert the seen but unfelt into the felt but unseen (Meltzoff and Moore 1997).

Starting in 2000, Heyes took up this explanatory challenge (Heyes and Ray 2000; Heyes 2001; Catmur et al. 2009). Her associative sequence learning (ASL) model of imitation proposes that the correspondence problem is solved by bidirectional excitatory links between visual and motor representations of the same actions and, crucially, that these links, or “matching vertical associations,” are forged through social interaction in the course of childhood. Synchronous drills and games, exposure to optical mirrors, and imitation of infants by adults provide correlated experience of seeing and doing the same action and thereby build the repertoire of matching vertical associations that gear motor sequence learning to perceptual sequence learning processes to make imitation possible.

Shortly after the ASL model was first published, Heyes applied it to mirror neurons – individual neurons that discharge when an action, e.g., grasping, is performed and when the same action is observed (Gallese et al. 1996). She opposed the consensus view that the visuomotor properties of mirror neurons are an adaptation produced by natural selection operating on genetic variants. In contrast, her analysis suggests that mirror neurons start out as ordinary motor neurons and become connected to corresponding visual neurons through associative learning in the context of self-observation and specified types of social interaction.

Some of Heyes’s most outstanding empirical work has tested her ASL model of imitation and mirror neurons. In studies of nonhuman animals, her group showed that budgerigars are capable of imitating body movements as well as vocalizations (Mottley and Heyes 2003; Richards et al. 2009) and that like humans, birds



(Mui et al. 2008), and dogs (Range et al. 2011) engage in automatic as well as goal-directed imitation. Using behavioral (“automatic imitation”) and neurophysiological methods (electromyography, functional magnetic resonance imaging, transcranial magnetic stimulation) with adult humans, her group showed that imitation and mirror neurons are highly plastic. As the ASL model predicts, imitative tendencies and mirror effects can be induced, enhanced, abolished, and reversed by novel visuomotor experience (Cook et al. 2014; Heyes 2010). For example, motor-evoked potentials recorded from the hand indicate selective activation of muscles controlling the little finger during observation of little finger abduction and of muscles controlling the index finger during observation of index finger abduction. However, this mirror effect can be reversed by training in which subjects respond to little finger movements with index finger movements and vice versa (Catmur et al. 2007), and this counter-mirror effect depends on the same areas of premotor cortex as those responsible for the original mirror effect (Catmur et al. 2011).

Alongside her work on social learning, imitation, and mirror neurons, Heyes has taken a lively interest in another aspect of social cognition – theory of mind (also known as “mindreading” and “mentalizing”). A target article in the *Behavioral and Brain Sciences* (Heyes 1998) offered a conceptual framework for research on theory of mind in nonhuman primates, argued that research to date provided no compelling evidence that nonhuman primates can ascribe mental states, and laid out a new experimental strategy with the power to provide evidence that nonlinguistic subjects can ascribe “seeing” to another agent. This strategy, the “goggles procedure,” has now been used many times with human children, where it has confirmed mental state ascription, and with nonhuman primates, where it has not. In later work on theory of mind, Heyes provided a detailed critique of research purporting to show that young infants can ascribe false beliefs (Heyes 2014a) and argued that much of the implicit or automatic mentalizing reported in adults is due to domain-general “submentalizing” (Heyes 2014b).

Because Heyes offers lean, mechanistic explanations for behavior, she has a reputation as a critic among some primatologists and

developmental psychologists. This complaint was never wholly convincing because her critical work was always accompanied by specific alternative hypotheses, proposals for how those hypotheses could be tested against the received view and, in many cases, new data reporting the outcomes of such tests (Heyes 2012b). However, the constructive breadth and originality of her thinking did not become fully apparent until the 2010s when she began publishing a series of articles (e.g., Heyes 2012c, 2016a; Heyes and Frith 2014), and ultimately a book (Heyes 2018a, 2019a), on the cultural evolution of human cognition. This work integrates cognitive science with cultural evolutionary theory for the first time. Previously, cultural evolutionists – mostly biologists, anthropologists, and mathematicians – had blackboxed cognition (Heyes 2016b). They concerned themselves with observable behavior and everyday characterizations of the mind. By bringing computational cognitive science to cultural evolutionary theory, and vice versa (Heyes 2018b), Heyes offered a radical, empirically grounded alternative to traditional evolutionary psychology. Her “cultural evolutionary psychology” focuses on distinctively human cognitive mechanisms; domain-specific processes – such as mentalizing, imitation, moral cognition (Heyes 2019b), and explicit metacognition (Heyes et al. 2020) – which are absent in other animals or present there only in some nascent form. It marshals evidence that, although their development is supported by a genetic “starter kit” (Frith 2001), these mechanisms are inherited socially rather than genetically, and they have been made fit for purpose primarily by natural selection acting on cultural rather than genetic variants. They are, in her terms, not “cognitive instincts” (Pinker 1994) but “cognitive gadgets.”

Heyes is a Fellow of the British Academy – the UK’s national academy for the humanities and social sciences – and a Past President of the UK’s Experimental Psychology Society.

## Cross-References

- [Cultural Transmission](#)
- [Ghost Control](#)



- Goggles Experiment
- Imitation
- Meta-Cognition
- Parsimony
- Social Learning
- Theory of Mind

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## Cell Division

- Mitosis

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## Cell Membrane

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The cell membrane is also referred to as the plasma or cytoplasmic membrane. It is a membrane that encloses every cell in order to differentiate between the inner cell contents and the outer cellular environment. This is the outermost layer in animal cells. However, bacteria, fungi, and plants contain a layer beyond the plasma membrane (known as the cell wall) which in addition to cell support also prevents large molecules from diffusing in (Yawata 2003).

### Structure and Function

The cell membrane is approximately 7.5–10 nm (Nano is  $10^{-9}$  m) thick and is composed of a phospholipid bilayer (Yawata 2003). Hence, the membrane contains two layers of multiple phospholipids aligned across from each other. Each phospholipid contains a phosphate head and two lipid (fatty acid or oil) tails. The tails are all oriented inside and the phosphate heads stick out in forming the lipid bilayer (Fig. 1).

The lipids are rod-shaped and hydrophobic (water repelling). The phosphate head groups are hydrophilic (attracting water). This results in the membrane's selective permeability which allows specific molecules to diffuse through at different rates (Lombard 2014).

The movement of molecules can either be active or passive, which either requires an input of energy or does not, respectively.

### Proteins and Gases in the Membrane

A number of proteins can be found embedded within the membrane and interacting with the respective hydrophobic and hydrophilic positions (Lombard 2014). Likewise, the lipid

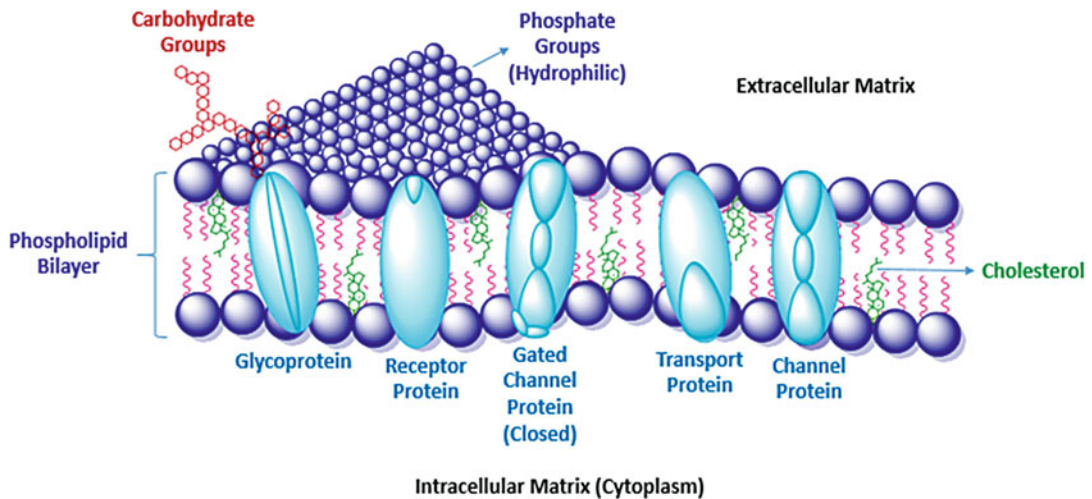
bilayer acts as a fluid mosaic at physiological temperature, which allows for the phospholipids and proteins to move about the bilayer which is each composed of differing phospholipids. Furthermore, cholesterol are biological molecules that aid in the membrane rigidity of the cell (Lehninger et al. 2008). Overall there are four major components to the fluid mosaic phospholipid bilayer, cholesterol, proteins, and carbohydrates.

Gases are allowed free exchange across the membrane because they are lipid soluble, such as oxygen ( $O_2$ ) and carbon dioxide ( $CO_2$ ) (Lehninger et al. 2008).

### Protein Channels in the Membrane

Protein channels are also allowed free movement about the membrane. There are varying types of protein channels which are specific to the content they allow to diffuse in and out of the membrane. This type of diffusion is known as active diffusion because it provides the energy needed to diffuse the otherwise nonpermeable molecule. In other words, these protein channels are essentially pumps that allow material to be exchanged from inside and outside of the cell, thereby providing the essential nutrients to the cell and expelling the wastes (Lehninger et al. 2008).

A receptor protein is activated by a specific molecule, known as an antigen. This antigen binds to the receptor protein outside of the membrane bilayer and causes a signal to be trickled down into the cell. Each antigen is specific to one receptor and carries only one message such as letting the cell know to prepare for cell division, metabolize glucose (sugar) into energy if it is low in the body, gene expression, etc. A channel protein is always open and allows a specific molecule to enter and leave the cell freely based upon concentration gradients. A gated channel protein works as a pump, to pump ions across their concentration gradients ( $Na^+$ ,  $K^+$ ,  $Ca^{+2}$ , and  $Cl^-$ ) in response to a chemical messenger such as a ligand which binds to it on the extracellular or intracellular matrix. Transport proteins (integral



**Cell Membrane, Fig. 1** Cell membrane components: phospholipid bilayer, cholesterol, proteins, and carbohydrate groups (Created using ChemDraw)

membrane proteins) are proteins that span across the entire membrane and allow molecules to pass through via facilitated diffusion (active diffusion). Lastly, glycoproteins are proteins with a carbohydrate chain attached to them (via glycosylation) that function to stabilize the membrane via hydrogen bonds with the extracellular environment (Miller and Levine 2008).

## Cenozoic Era

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## Cross-References

- ▶ Electrophoresis
- ▶ Mosaics
- ▶ Nondisjunction
- ▶ Protein

## Synonyms

Age of Mammals; Cainozoic Era; Kainozoic Era

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## Definition

The most recent era of the earth's history, which began 65.5 million years ago (mya), is known as the "Cenozoic Era." This is that time frame in which the geological changes gave rise to the world map's current face, and the biological changes enriched it with today's flora and fauna. Despite representing only 1.4% of the earth's history, comprehensive knowledge is available pertaining to this era.

## Introduction

Cenozoic, spelled initially as Kaniozoic, means “recent life” as newer forms of life, similar to the present-day biota appeared during this era. Cenozoic derives its name from two Greek words *kainós*, meaning “new,” and *zoic*, meaning “animal life” (Harland et al. 1990). British geologist John Phillips coined the term in the year 1840.

Anthropologically, Cenozoic is significant because the entire primate evolution and the subsequent human evolution occurred during this era. Besides primates, other mammals, birds, most flowering plants, and grasses experienced substantial evolutionary radiation during this phase of the earth’s history.

## The Beginning of the Cenozoic Era

This most recent subdivision of the Phanerozoic Eon is supposed to have begun about 65.5 mya, at the Cretaceous-Paleogene (K-Pg) boundary, marked by a catastrophic extinction event. This devastation led to the extermination of 75% of the life on earth, including the non-avian dinosaurs.

The reason for this extinction event has been a subject of debate for a very long time (Brusatte et al. 2015). The most widely accepted theory is the catastrophic impact from an asteroid (10 km diameter), which created the Chicxulub crater in Yucatan, Mexico. The effect is proposed to have thrown enormous dust into the atmosphere, blocking sunlight (for about a year), setting in a prolonged winter, killing the flora, suppressing the potential global dinosaur habitats, and subsequently leading the dinosaurs to extinction (Chiarenza et al. 2020). The presence of iridium, a rare earth metal but more common in meteors and asteroids in the K-Pg boundary, further supports the theory.

Some researchers propose Deccan volcanism as the main abiotic driver of the K-Pg mass extinction (Keller et al. 2011). Rapid and massive volcanic CO<sub>2</sub> and SO<sub>2</sub> emissions appear to have caused acid rains, high continental weathering, global warming, ocean acidification, and a carbon

crisis in the marine environment, ultimately leading to the dinosaurs’ extinction.

Post dinosaur extinction, vacant ecological niches were occupied and exploited by other life forms, especially mammals, which flourished and diversified across the globe. For this reason, the Cenozoic Era is also known as the “Age of Mammals.”

## The Cenozoic Timescale

In 2009, the International Union of Geological Sciences (IUGS) formally adopted the division of the Cenozoic Era into three periods, namely, the Paleogene (65.5–23 mya), the Neogene (23–2.6 mya), and the Quaternary (2.6 mya to the present). The Paleogene (*palaiós* = old + *genes* = born) is subdivided into three epochs – the Paleocene (65.5–55.8 mya), the Eocene (55.8–33.9 mya), and the Oligocene (33.9–23.03 mya). The Neogene (*neo* = new + *genes* = born) period comprises two epochs – the Miocene (23.03–5.332 mya) and the Pliocene (5.332–2.588 mya). The Quaternary includes two epochs – the Pleistocene (2.588–11,700 years ago) and the Holocene (11,700 years ago to the present).

## Cenozoic Events in a Chronological Order

### Paleocene (65.5–55.8 mya)

The Paleocene derives its name from the Greek words *palaiós* = old and *kainós* = new, referring to the organisms that survived the K-Pg extinction and subsequently evolved into the primitive forms of the modern lineages.

Forming the base of the Cenozoic, the Paleocene saw the surviving mammals grow in size and number and diversify into rodent-like mammals, scavenging medium-sized mammals, and large herbivorous and carnivorous mammals. These mammals evolved bigger, became more ferocious, and spread throughout the world as the dominant predators.

The Paleocene is subdivided into three stages, the Danian (65.5–61.7 mya), the Selandian (61.7–59.2 mya), and the Thanetian (59.2–55.8 mya).

#### Paleocene Fauna

**Mammals:** Due to the paucity of fossil evidence, relatively little is known about the Paleocene mammals. The few lineages that survived the K-Pg extinction, primarily consisting of small nocturnal herbivores and insectivores occupying a limited number of ecological niches, were suddenly free to fill the void. Most of these Paleocene mammals belonged to the primitive (or archaic) groups and included the following:

- Monotremes – egg-laying mammals such as *Monotrematum*, a relative of the platypus.
- Marsupials – pouched mammals such as opossum.
- Multituberculates – an extinct group of herbivorous animals with rodent-like teeth, which were the most successful Mesozoic mammals.
- Placentals – mammals with a reproductive system that allows the fetus to develop entirely within the female before birth. They became the most diverse and successful group of mammals consisting of the following:
  - Condylarths – hoofed animals that evolved toward herbivory while still retaining insectivorous-carnivorous traits.
  - Primates – mammals that displayed characteristics intermediary of insectivores and lemurs. They became abundant in the middle Paleocene.
  - Creodonts – catlike and doglike primitive carnivores.

The fossil records document explosive adaptive radiation of mammals characterized by a dramatic increase in therian mammals' diversity (including the marsupials and placentals).

**Birds:** The global destruction of forests associated with the K-Pg event served as a strict filter against the tree-dwelling stem birds. The ground-dwelling crown birds that survived

the holocaust rapidly diversified and gave rise to the modern tree-dwelling birds (Daniel et al. 2018).

**Reptiles:** While the non-avian dinosaurs and large marine reptiles became extinct at the end of the Cretaceous, ancestors of modern reptiles not only survived through the K-Pg boundary but also underwent great adaptive radiations into turtles, lizards, crocodiles, and snakes.

**Amphibians:** These, which originated during the Jurassic, were not much affected by the holocaust. Giant salamanders, hellbenders, aquatic salamanders, New World frog, and real toads appeared during the Paleocene.

#### Paleocene Oceans

It took millions of years for life to recover in the early Paleocene oceans following the mass extinction event. The primary producers, diatoms, dinoflagellates, and coccolithophores, which experienced a significant setback, underwent adaptive radiations during Paleocene and regained their pre-K-Pg diversity. The reef systems that collapsed in the extinction event recovered very slowly and diversified after eight million years. By the late Paleocene, multiple groups of marine invertebrates diversified from the Mesozoic survivors. Marine fauna more or less resembled modern fauna, with sharks becoming the top predators.

#### Paleocene Flora

The plant fossil records and asteroid impact models provide strong evidence for the devastation of forests at the K-Pg boundary. In the initial phase of disruption, the energy dissipated by the impact could have released intense heat, igniting wildfires at a global scale and destroying vegetation in a diameter of 1,500 km. The next phase of disruption possibly included the release of sulfate-rich vapors that resulted in acid rain, destroying vegetation. Ejection of enormous soot potentially blocked photosynthesis for several years and induced global cooling. Suppression of sunlight delayed the recovery of forests and perhaps led to the proliferation of saprotrophs (Daniel et al. 2018).



Postimpact recovery of flora occurred in two phases. The first phase saw a fern spike, with ferns, the pioneer species of devastated landscapes, becoming dominant over the surviving angiosperms and conifers. This “fern spike” is seen in the terrestrial Paleocene strata, immediately overlying the K-T boundary (Stanley 2001).

The second phase was marked by the re-establishment of canopy vegetation dominated by new angiosperms and conifers characterized by low taxonomic diversity. The Paleocene saw the evolution of modern plant species, including the cacti and palm trees. The warm global temperatures favored tropical, subtropical, and deciduous forests worldwide. Interestingly, the ice-free polar regions were covered with dense coniferous and deciduous trees.

#### Paleogeography

During the Paleocene, the shape of continents was similar to that of the present day, but they were in different positions. Laurasia and Gondwanaland, the supercontinents in the northern and southern hemispheres, respectively, began drifting to their present-day positions. The Gondwanaland components moved apart from each other forming Africa, South America, Antarctica, and Australia. In comparison, the components of Laurasia drifted apart to form North America, Europe, and Asia.

North America and Asia were still interconnected by the land bridge, while Greenland began to separate from North America. Equatorial seas separated South America and North America. Africa and India started drifting northward, slowly closing in the Tethys Ocean. In western America, the Laramide orogeny that began in the late Cretaceous uplifted the Rocky Mountains.

#### Paleoclimate

During the Paleocene, the earth gradually became warmer and more humid, showing a global warming trend. The climate was completely different then, with no polar ice caps and a cold temperate climate. Equatorial areas had tropical climates; the lower latitudes were hot and arid, while the continents in higher latitudes were warm with temperate climate.

#### Eocene (55.8–33.9 mya)

The Eocene derives its name from the Greek words *eos* = dawn and *kainós* = new, meaning the appearance of modern fauna. It is generally divided into the Early (56–47 mya), Middle (47.8–38 mya), and Late (38–33.9 mya) Eocene. The Eocene is formally subdivided into the Ypresian (56–47.8 mya), Lutetian (47.8–41.3 mya), Bartonian (41.3–38 mya), and Priabonian (38–33.9 mya) based on the characteristic rocks.

Around 56 mya, when the earth was entering the Eocene Epoch, the gradual warming trend reached a tilt point, and the global temperatures surged by about 5 °C within just 20,000 years. This event, known as the Paleocene-Eocene Thermal Maximum (PETM), brought about dramatic change in the existing flora and fauna (Keller et al. 2018).

It is proposed that the massive release of greenhouse gases trapped in the deep ocean led to this drastic global warming, but the exact reason is still a topic of debate.

Methane released from the decay of dead microbes falling to the deep ocean floor gets trapped in a cage-like structure of water molecules in the cold, dark, high-pressure conditions and forms clathrates. These clathrates serve as the most massive methane sink, but they can melt if the sea bed temperature rises beyond a certain point and release methane gas. By the end of the Paleocene, deep-sea temperatures had grown enough to cause the melting of clathrates, releasing billions of tons of methane into the atmosphere leading to PETM.

Other researchers strongly propose the volcanism-associated release of CO<sub>2</sub> from the North Atlantic Igneous Province as the primary driver of PETM (Gutjahr et al. 2017).

The thermal maximum resulted in extinctions on both land and water. Except for the extinction of deep-sea calcareous benthic foraminifera, the PETM is considered a migration and origination event that kick-started various short- and long-term evolutions (Speijer et al. 2012).

#### Eocene Fauna

The Early Eocene saw a dramatic increase in mammals' abundance and diversity with the gradual decline of older primitive forms. Warming up



of the northern hemisphere facilitated the migration of these new mammalian orders toward higher latitudes. They were only about 60% of their Paleocene counterparts' size, suggesting that smaller body size would have helped them better manage the Eocene heat. The earliest forms of the modern mammalian orders that appeared during the Early Eocene weighed less than 10 Kg. These included the bats, artiodactyls (even toed ungulates), perissodactyls (odd toed ungulates), proboscideans (elephant-like animals), primates, rodents, and marsupials. *Eohippus*, a fossil perissodactyl from the Early Eocene, was widespread in both North America and Europe, indicating the existence of land connections between the continents.

By the Middle Eocene, all the modern groups of horses, rhinos, and tapirs were present. They had low crowned teeth, well suited to feed on the tropical and subtropical vegetation's soft leaves and fruits. Artiodactyls also became abundant. Land connection between North America and Europe was lost by the Middle Eocene, and the isolated species followed different evolutionary paths.

Global temperatures started to fall by the Late Eocene, and seasonality became more pronounced. Many archaic groups of mammals became extinct, and only those who adapted to the changing climate survived. Forests gave way to the first open grasslands, which favored an increase in body size and led to the evolution of enormously huge perissodactyls, like *Embolotherium* and *Indricotherium*. Cursorial adaptation, like lengthening of legs, the fusion of limb and ankle bones, and reduced toe number, improved their survival rates in these grasslands.

Reptiles were represented by the enormous crocodile *Deinosuchus*, pythons, and turtles in North America.

Modern birds made their first appearance during the Eocene. Global climatic conditions of the Early Eocene favored avian diversification, and after that, the evolution rate slowed down until the Oligocene (Lindow and Dyke 2006).

#### Eocene Flora

The hot and moist Early Eocene climate favored the spread of forests throughout the earth. Warm temperate to subtropical rainforests fringed

Antarctica, and tropical rainforests stretched as far as Europe.

By the Middle Eocene, earth began to cool, which led to the drying of continental interiors and the thinning of forests. Grasses started to evolve but were confined to river banks and lake edges. This global cooling set the platform for different seasons. Consequently, deciduous trees, better adapted to the changing climate, started replacing the tropical plants.

By the Late Eocene, deciduous forests covered large parts of North America, Eurasia, and the Arctic. Simultaneously, rainforests became confined to the equatorial regions of South America, Africa, India, and Australia. Open savanna-like vegetation started to become more common, with a corresponding reduction in forests. Antarctica became much colder and was covered by vast stretches of tundra by the beginning of the Oligocene.

#### Eocene Oceans

Deoxygenation due to the warming of the oceans during PETM resulted in the massive extinction of deep-sea organisms, whereas many planktons living in the shallower seas flourished and diversified. High levels of CO<sub>2</sub> in the atmosphere led to ocean acidification, affecting organisms with calcium carbonate skeletons, and, in particular, led to the significant extinction of calcareous benthic foraminifera (Speijer et al. 2012). Cetaceans and sirenians transformed from being terrestrial to fully aquatic during the Eocene.

#### Eocene Geography

North America and Europe, which were connected through Greenland, began to drift apart, and by the Middle Eocene, the continents had lost connections. This led to the opening of the North Atlantic Ocean. During this time, the tectonic activity gave rise to mountains in the west of North America, forming lakes in their flat basins. In Europe, the Tethys shrank, and the Alps uplifted. India continued to move away from Africa and began to collide with Asia. By the Middle Eocene, the Tasmanian gateway began to form as Australia started to separate from Antarctica. South America was still connected to Antarctica.

### Eocene Climate

The PETM began at the end of the Paleocene and lasted for about 100,000 years. The global mean annual surface temperature was about 13 °C warmer than the current temperature. This phase saw high precipitation, lack of any permanent ice, and CO<sub>2</sub> concentration of approx. 1,400 parts per million volume (ppmv) (Burke et al. 2018). Global climate was homogenous with little variation from the equator to poles.

The Middle Eocene marked the end of the Cenozoic warming trend, and the earth started to cool gradually. Around 45 mya, the shallow Tasmanian gateway gave rise to the earliest Antarctic circumpolar current (ACC), causing Antarctica's thermal isolation and subsequent cooling (Bijl et al. 2013).

By the Late Eocene, the Antarctic region cooled down, transient continental ice sheets formed, and the surrounding ocean began to freeze.

The Early Eocene, referred to as the Eocene greenhouse, has been a subject of interest in recent years as a warm analog of the current earth. The anthropogenic greenhouse gas emissions can lead to an Eocene-like climate, which would mean reversing a 50 million year cooling trend in less than 200 years (Burke et al. 2018). This ultrafast rewinding of the climate clock can lead to a worst-case scenario of sixth mass extinction (Keller et al. 2018). Thus, a better understanding of the Eocene climate can help us cope with the current global warming.

### Oligocene (33.9–23.03 mya)

The third and the final epoch of the Paleogene period derives its name from two Greek words *oligos* = few and *kainos* = new, referring to the few numbers of modern animals that appeared during this epoch. This epoch serves as a transition phase between the archaic tropical Eocene and the relatively modern Miocene ecosystems. The Oligocene is formally subdivided into the Rupelian (39.9–28.1 mya) and the Chattian (28.1–23.03 mya). The Eocene-Oligocene transition (EOT) is marked by the onset of a significant cooling event that transformed a largely ice-free

“greenhouse” world into a glaciated “icehouse” world. A decline of about 1.6× of atmospheric CO<sub>2</sub> across the EOT (e.g., from 910 to 560 ppmv), accompanied with the new ocean circulation, resulted in unipolar Antarctic glaciation, which drastically lowered the mean annual temperature and set in more significant seasonality worldwide (Hutchinson et al. 2020). This seasonal fluctuation led to the extinction of many animals that depended on the warm and stable Eocene climate. As a result, the cold-blooded animals that survived did not flourish the way warm-blooded animals did. This new climate favored the rise of mammals like rodents and all modern-hoofed animals.

With continued Antarctic glaciation, more and more ocean water got locked up, causing sea levels to drop, eventually connecting Europe and Asia by the Early Oligocene. This was followed by a significant, sudden, terrestrial faunal turnover called Grande Coupure. It features the extinction of many European Eocene endemic mammals and their replacement by new Asian immigrants, primarily the artiodactyls and perissodactyls (Costa et al. 2011).

The sources for the significant oil reserves of Iraq and western Iran date back to the Oligocene.

### Oligocene Fauna

The extinction of archaic vertebrates of the Eocene Epoch gave a modern aspect to Oligocene vertebrates of the northern continents. The overall mammalian diversity was low during the Oligocene due to continued global cooling and reduced endemism. Relatively free interchange of vertebrates between the northern continents during the Early Oligocene resulted in similarities between the various vertebrate faunas. Pigs and peccaries that appeared in Europe during the Early Oligocene spread to North America by the end of this epoch. Bats also became widespread in this epoch. Many perissodactyls became extinct during the Oligocene, and the ones that survived included the rhinos, horses, tapirs, and chalicotheres, which were better adapted to a colder, drier world dominated by grasses. During this epoch, artiodactyls, which included the creodonts, camels, and early ancestors of deer

and cattle, became more common than perissodactyls. Open grasslands favored a general increase in the size of these herbivores. *Indricotherium*, the hornless rhino, from the Oligocene, was the largest land mammal ever.

Availability of plenty of food and a tropical climate near the equator allowed the evolution and diversification of early primates. Fossils of the earliest apelike *Parapeticus* and the Old World monkeys from the Oligocene are known from Egypt.

Being completely isolated during the Oligocene, South America developed a unique mammalian fauna exhibiting extreme parallelism to forms found elsewhere in the world. One such parallelism was the appearance of New World monkeys in South America. It was also home to unique toothless mammals or edentates, including the anteaters, sloths, and armadillos.

Australia stood isolated from all continents with few ancestral marsupials. In the absence of competitors and predators, they exploded in forms and numbers from herbivores and carnivores to scavengers and insectivores, occupying every possible evolutionary niche.

By the Late Oligocene, horses had undergone extensive anatomical modifications and evolved better adapted cursorial limbs.

Caprimulgiformes, the insectivorous, nocturnal, soft-plumaged birds, and the diurnal raptors such as falcons, eagles, and hawks appeared for the first time.

#### Oligocene Flora

Grasses started to expand from their water-bank habitat to open tracts. On a global scale, tropical forests became confined between 15° latitudes; subtropical forests with broad-leaved evergreen trees were restricted to the lower latitudes (35°); and temperate, broad-leaved trees became common over large regions of the northern hemisphere. Extensive lowland temperate vegetation became more common in the Arctic region.

By the mid-Oligocene, broad-leaved deciduous forests started extending toward the southern regions, previously occupied by the broad-leaved evergreen species.

The Late Oligocene was marked by the global expansion of grasslands and prairies. The northward movement of South America favored forests in the southern parts.

#### Oligocene Oceans

The cooling trend resulted in reduced diversity of marine planktons, with the foraminiferans and protists becoming very prominent. It also led to province fragmentation of the marine fauna, with the migration of organisms better suited for the cold climate toward the higher latitudes. In Western Europe, the transgression of the sea brought in new mollusks characteristic of this epoch. Baleen and toothed cetaceans appeared during this epoch, as did the charcharinid sharks. The mid-Oligocene was marked by regression in the number of marine species worldwide. By the Late Oligocene, marine mammals like seals, walruses, and sea lions appear to have evolved from bear-like or otter-like ancestors.

#### Oligocene Geography

Continents continued to drift to their current positions. As Australia moved toward the lower latitudes and Antarctica moved toward the South Pole, permanent glacial ice caps began to form. Complete separation of South America from Antarctica opened up the Drake Passage allowing the ACC to flow around Antarctica, rapidly cooling the continent.

Continuous northward pushing of the African plate into the Eurasian plate further uplifted the Alps in Europe. North America and Europe, which were connected by land during the Early Oligocene, eventually got separated.

#### Oligocene Climate

The establishment of ACC resulted in rapid global cooling at EOT, and long-term glaciation began in Antarctica. In the northern hemisphere, warm temperatures prevailed, and glaciation started only in the following epoch. This disparity in glaciation is attributed to the fact that the CO<sub>2</sub> threshold for the inception of ice sheet in the northern hemisphere was lower, implying that climate should have been much colder than in Antarctica to initiate glaciation (Hutchinson et al. 2020).

## Miocene

The Miocene, the first epoch of the Neogene period, spans from 23.03 to 5.332 mya and was named by Sir Charles Lyell. The name is derived from the Greek words *meios* = less and *kainos* = new, referring to the reduction in the appearance of modern sea vertebrates by 18% compared to that in the Pliocene. It is generally divided into the Early (23–16 mya), Middle (16–11.6 mya), and Late (11.6–5.3 mya) Miocene. It is formally subdivided into six ages, corresponding to their rock stages: the Aquitanian (23–20.4 mya), Burdigalian (20.4–16 mya), Langhian (16–13.8 mya), Serravallian (13.8–11.6 mya), Tortonian (11.6–7.2 mya), and Messinian (7.2–5.3 mya).

It was a time of warm global climates compared to the preceding Oligocene and succeeding Pliocene, but the Antarctic ice cap remained intact. This temperature rise favored an increase in the total number of mammalian species. The land-dwelling mammals of this era were essentially modern, representing half of the currently existing mammalian families.

### Miocene Fauna

The formation of polar ice caps, shifting of continents, and changing climate patterns caused sea levels to drop and inland seas to shrink, thus opening land routes between continents encouraging animal migration.

Ancestors of modern elephants and apes ventured out of Africa and settled in parts of Eurasia, eventually making their way to North America along the Bering land bridge, whereas rabbits, pigs, saber-toothed cats, and modern rhinos moved from Eurasia to Africa. In North America, horses grew considerably larger and displayed a single toe on each limb. They quickly spread to Europe and Asia, subsequently reaching Africa, where some species evolved into zebras. Surprisingly, these “invading” species did not force a large number of native species to extinction. Animals that became extinct most probably failed to adapt to the changing climate and vegetation.

The geographically isolated South America was enriched with unique animals represented by carnivorous marsupials, edentates (including

anteaters, armadillos, and sloths), litopterns (hoofed mammals like horse and camel), and toxodon (mammals with long, curved incisors). South American monkeys evolved continuously during the Miocene.

Miocene primates, particularly the apes, underwent significant evolution. Around 16 mya, Orangutans or Asian apes separated from the African ape or hominid line, and around 9 mya, chimpanzees separated from the hominid line. Primates spread to southern parts of Europe, where gibbon-like *Pliopithecus* remains were found in the Miocene rocks. Similarly, *Dryopithecus's* remains, an advanced humanlike ape, were found in Miocene rocks of Europe and Africa.

As the Miocene progressed, the earth began to cool, and the arid climate brought about the spread of coarse grasslands. This brought about the Miocene extinction around 9 mya, which wiped off many herbivores feeding on fruits, juicy ferns, and shrubby plants. Animals such as the giant camels, which could not adapt to the colder climate and coarse grassy vegetation, became extinct, whereas mammalian herbivores like equids, rhinos, and many artiodactyls adapted to more open, arid habitats, and coarser vegetation survived. Primitive deer, antelope, and giraffe appeared in Eurasia. The first dogs, bears, hyenas, and saber-toothed cats appeared during the Early Miocene in North America and spread to Asia by the Late Miocene.

Birds like ducks, herons, eagles, rails, crows, pheasants, partridges, plovers, owls, and cockatoos appeared in the Miocene. By the Late Miocene, almost all modern bird families were present, and marine birds reached their highest diversity of this epoch.

### Miocene Flora

Gradual warming accompanied by aridity during the Early Miocene led to the evolution of tough scrub plants and extensive development of grasslands like the steppe in Europe. In Australia, rainforests started to shrink and were replaced by dry forests, grasslands, and deserts. C4 grasses that could assimilate CO<sub>2</sub> and water more efficiently than the C3 grasses became ecologically

more significant (Pagani et al. 2005) and well established by the Late Miocene (6–7 mya). The expansion of these silica-rich C4 grasses brought about the extinction of those herbivorous species which lacked high-crowned teeth.

Cyclical warming and cooling resulted in the appearance of kelp forests, consisting of large brown algae, called kelp (*Macrocystis pyrifera*). These kelp forests soon became one of the most productive ecosystems and played an essential role in the evolution and sustenance of marine life, such as sea otters, fishes, and invertebrates.

By the Late Miocene, drastic cooling resulted in the further shrinking of tropical and coniferous forests. Ninety-five percent of the modern plants had made their appearance by the end of this epoch.

#### Miocene Oceans

Due to global cooling, the changing ocean current circulation patterns brought about a change in nutrient distribution patterns, affecting the productivity of different regions. Miocene oceans saw accelerated evolution among marine plankton and mollusks and biological diversity in others. Marine mammals like seals and whales flourished, and cetaceans, with over 20 genera, attained their greatest diversity during this time. Gigantic predators like the megatooth sharks and raptorial sperm whales emerged during the Miocene. By the Late Miocene, almost all the modern whales, primitive seals, and walrus appeared.

#### Miocene Geography

Except for the land connection between South and North America, most of the modern geological features were formed by Miocene's end. Continents continued moving to their current position.

The Indian plate's collision with the Asian plate caused a massive upthrust of the Asian continent, creating the Tibetan Plateau and the Himalayas. During the Middle Miocene, the African-Arabian plate union with the Eurasian plate interrupted and contracted the Tethys Sea leading to the Mediterranean Sea formation. Southern Europe became arider between 19 and 12 mya, and the Tethys Sea disappeared. By the Late Miocene (5.96–5.33 mya), repeated

isolation from the Atlantic Ocean driven by tectonic activity led to nearly complete desiccation of the Mediterranean Sea, known as the Messinian salinity crisis (Krijgsman et al. 1999).

In North America, the Sierra Nevada and Cascade mountain ranges were formed, whereas in South America, the Andes were uplifted. During the Late Miocene, the upliftment of East Africa created a rain shadow in the East, making it dry, and the tropical rain forests also shrank. Australia moved to lower latitudes and became drier.

Growth of the polar ice caps and the associated drop in sea levels during Miocene exposed Florida for the first time in Miocene.

#### Miocene Climate

The Early Miocene saw an increase in global temperature. As Miocene progressed, the earth began to cool again, and the climate became arid. As a result, mammalian diversity started falling again. The upliftment of mountains in the Americas and Asia altered the air circulation and weather patterns adding to the overall dryness.

About 14 mya, global temperatures dropped drastically and is commonly known as Middle Miocene Climate Transition (MMCT). A similar temperature drop occurred once again around 8 mya, wherein the Antarctic ice sheet attained its present-day size and thickness. Variation in the carbon cycle involving the terrestrial and deep ocean carbon reservoirs played an essential role in driving Late Miocene cooling. This global cooling culminated in ephemeral northern hemisphere glaciations between 6 and 5.5 mya (Holbourn et al. 2018).

#### Pliocene

The Pliocene, the upper epoch of the Neogene period, spans from 5.33 to 2.588 mya. Sir Charles Lyell named the Pliocene from the Greek words *pleios* = more and *kainos* = new. It means “newer” or “continuation of the recent” as this era has more fossils of still-existing species, particularly modern marine mollusks. The Pliocene was relatively cooler than the preceding Miocene. The Pliocene is subdivided into the Zanclean (5.3–3.6 mya) and the Piacenzian (3.6–2.6 mya).

### Pliocene Fauna

In North America, mastodons, gomphotheres, opossums, weasels, dogs, and fast-running hunting bears flourished. Hoofed animals like camel, deer, and horse declined. Rhinos, tapirs, and chalicotheres went extinct. Mastodons, the elephant-like animals, evolved and diversified significantly during the Pliocene.

In Eurasia, rodents, elephants, gomphotheres, stegodons, cows, and antelopes flourished. Tapirs and rhinos did reasonably well, whereas the primate distribution and horse diversity declined. Some camel species and some predators like bears, dogs, and weasels migrated to Asia from North America, while hyenas and hyraxes migrated northward from Africa.

Hoofed animals dominated Africa, where early giraffes appeared and cows and antelopes diversified. Elephant, horse, and modern rhino populations increased. Camels, dogs, bears, and weasels migrated from North America through Asia. These carnivorous immigrants joined cats and civets as African predators forcing the hyenas to adapt as scavengers. Primates continued to evolve around 5.2 mya; the first humanlike primates (hominins), the australopithecines, evolved in East Africa. They descended from apes and probably lived at the edges of forests. They were adapted to walk upright and could make tools.

Around 3.5 mya, the North and South American tectonic plates joined, which resulted in the Isthmus of Panama formation. The newly formed land connection brought about the Great American Interchange, wherein the previously isolated species migrated and intermixed. Weasels, dogs, cats, bears, and horses migrated from North America to South America. In contrast, glyptodonts (giant armadillo-like animals), giant ground sloths, smaller armadillos, opossums, and porcupines migrated to North America by the Late Pliocene. *Titanis*, a South American large phorusrhacid (flightless terror birds), which migrated to North America, flourished as the top predator.

In Australia, marsupials, the dominant mammals, included both the herbivore and carnivorous forms. First, rodents reached the island continent

only by the Pliocene, and the modern duck-billed platypus (a monotreme) appeared.

As the climate cooled, crocodiles and alligators perished in the higher latitudes. Venomous snakes diversified in parallel to the evolution of rodents and birds.

### Pliocene Flora

Colder, drier, and seasonal climate reduced tropical species worldwide. Tropical forests became restricted to a tight band around the equator. Deciduous forests proliferated, evergreen coniferous forests became established in the higher latitudes, tundra covered the frozen arctic, and grasslands spread to all continents (except Antarctica). Hardy plants such as sedges, mosses, and lichens that can tolerate a short growing season inhabited the permanent tundra encircling the North Pole. Lower latitudes were covered with grasslands, and deserts began to appear in Asia and Africa. These habitats supported less animal diversity due to limited food sources.

### Pliocene Oceans

As the Arctic ice cap formed, the climate became dry, and the cold, shallow currents increased in the North Atlantic Ocean. Sea lions, sea cows, and seals flourished in the Pliocene seas.

Formation of the Isthmus of Panama divided the surrounding waters into the Atlantic and Pacific, setting the segregated marine life on different evolutionary paths. It also severed the final remnant of the circum-equatorial current, contributing to further cooling the oceans worldwide.

The end of the Pliocene was marked by large climatic fluctuations and sea-level oscillations, which led to a major extinction among the marine megafauna (seabirds, mammals, sharks, and turtles). This extinction was three times more devastating than the rest of the Cenozoic, with the extinction of 36% of the Pliocene genera (Pimiento et al. 2017).

### Pliocene Geography

Continents continued drifting to their current position. They covered a distance of 180 km during the Pliocene and reached positions only 70 km



away from their present locations. The Indian plate's further collision deep into the Asian plate raised the Tibetan Plateau and formed the Himalayas. This geological activity continued in the succeeding epochs and is still in the process. The Mediterranean Sea, which was dried up by the Late Miocene, was reclaimed by the Atlantic Ocean during the Zanclean flood in the Early Pliocene. The Alaskan land bridge reappeared between Eurasia and North America.

By the mid-Pliocene, around 3.5 mya, an eastward shift of the Caribbean tectonic plate led to the joining of the North American and South American tectonic plates. This unison of plates formed the Isthmus of Panama that connected the two continents by land.

#### Pliocene Climate

The cooling trend that set in during the Eocene continued through the Pliocene. Based on the then prevailing climatic condition, the Pliocene can be divided into a warm Early Pliocene, the mid-Pliocene with a short-lived “warm blip,” and the Late Pliocene – a period of high-magnitude climatic fluctuations associated with the glacial/interglacial cycles (Haywood et al. 2008). During the mid-Pliocene (3.3–3 mya), the average global temperature was 2–3 °C higher, the CO<sub>2</sub> level was the same, and the global sea level was 25 m higher than that of today.

Following the emergence of the Isthmus of Panama, the formation of the Atlantic and Pacific oceans impacted the global temperatures by cutting the warm equatorial ocean current and initiating the Atlantic cooling cycle. Climates became cooler, drier, and seasonal.

By the mid-Pliocene, ephemeral Arctic ice caps were formed, and by the Late Pliocene, extensive glaciation set in over Greenland. About 2 mya, both the poles were covered with permanent ice sheets.

#### Pleistocene

The Pleistocene, the first epoch of the Quaternary period, spans from 2.588 mya to 11,700 years ago (ya). The Pleistocene derives its name from the Greek words *pleistos* = most and *kainos* = new, meaning “newest.” Sir Charles Lyell introduced

this term in 1839 to describe strata in Sicily, whose 70% molluscan fauna is still living today.

The Pleistocene can be subdivided into four ages corresponding to their rock units as the Gelasian (2.6–1.8 mya), the Calabrian (1.8 mya to 780,000 ya), the Ionian (780,000–126,000 ya), and the Tarantian (126,000–11,700 ya). The Ionian and Tarantian ages await approval by the ICS.

Pleistocene is also popularly known as the “Great Ice Age” because of the repeated glacial cycles, where cold periods of glacial were interspersed with warmer phases of interglacial.

#### Pleistocene Fauna

Changing geography due to the upliftment of mountains and plateaus, the emergence of new migration routes, and the large climatic fluctuations profoundly impacted the Pleistocene fauna and flora. Every time the glacial ice advanced, plants and animals would retreat southward in response to the tremendous stress resulting from the temperature changes, reduced rainfall, food shortage, and reduced living space. Nevertheless, the Pleistocene megafauna diversity was much greater than it is today.

Large mammals like the woolly mammoth, woolly rhinoceros, moose, reindeer, and musk ox adapted to the Arctic conditions and inhabited the periglacial areas, whereas mastodon, elephant, hippopotamus, giant beaver, bison, horse, ground sloth, and deer inhabited the temperate regions.

Pleistocene is of particular interest to humans as *Homo sapiens* evolved from early hominids during this epoch and spread to all continents. The oldest species of the genus *Homo*, *H. habilis*, probably evolved from *Australopithecus* during the Late Pliocene. *Homo habilis* appeared about 2 mya and roamed in Africa till 1.5 mya. Around 1.6 mya, *H. erectus* possibly evolved from *H. habilis* in Africa and thrived as the dominant human species in parts of the Old World for over one million years. *Homo sapiens* evolved 315,000 ya in Africa. About 250,000 ya, during the last interglaciation, *H. neanderthalensis* (Neanderthals) appeared in Europe and western Asia. Around 60,000 years ago, *H. sapiens* migrated out of Africa and

arrived in Europe 45,000–43,000 years ago. Both *H. sapiens* and *H. neanderthalensis* coexisted in Europe for about 10,000 years, after which the Neanderthals disappeared 35,000–30,000 ya. By the end of the Pleistocene, *H. sapiens* had spread to most parts of the world.

The Pleistocene ended with a major extinction of many large mammals, particularly in North America. Thirty-two genera of large mammals, including the mastodons, mammoths, giant beavers, horses, and ground sloths, vanished within roughly 2,000 years. As small mammals, reptiles, and amphibians were not much affected, it is hypothesized that the extinctions were the result of overpredation by humans or due to the abrupt changes in climate.

#### Pleistocene Flora

The Pleistocene climate was primarily dry, and the vegetation belts shifted toward lower latitudes. By the end of the Pleistocene, North America's temperate zones and central Europe were occupied by the tundra vegetation, consisting of grasses, herbs, and a few trees. South of the tundra belt was a mostly sparse pine forest, and deciduous forests could only be found along Mexico's gulf. Due to the lower sea temperatures, the weak trade winds gave rise to a continuous EL Nino like condition that resulted in open grasslands where Amazon forests stand today. Whereas, heavy precipitation in central America and coastal Colombia gave rise to tropical rainforests and great lakes in the present south-western desert states. While in other cold and dry places, deserts emerged and expanded like the Sahara desert.

#### Pleistocene Oceans

The direct influence of the ice sheets brought about drastic changes in the North Atlantic Ocean. Polar marine fauna that generally occurred north of 70°N during interglacial intervals extended south to about 45°N during glaciation.

#### Pleistocene Climate and Geography Defined by Glaciation

Continents had drifted to their present position by the Pleistocene. The natural cooling of the earth that set in at the start of the Cenozoic Era

culminated in the Ice Age consisting of a series of glacials interrupted by interglacials or warm periods. During the glacial phase, ice sheets expanded from Antarctica, Greenland, and even around high mountains along the equator. It is estimated that, at the last glacial maximum, continental glaciers reached about 40°N in North America and 50°N in Eurasia. The permafrost stretched southward to a few hundred kilometers in North America and several hundred kilometers in Eurasia.

During the last glacial maximum, roughly 30% of the land area was covered with ice, locking a large amount of water in thick continental ice sheets, dropping global sea level by 100–120 m. The exposed wide coastal areas and land bridges enabled the migration of fauna, flora, and humanity across the earth. The rapid melting of the last massive glaciers raised the sea level, displaying the present level by the Middle Holocene.

Analyses of  $^{16}\text{O}/^{18}\text{O}$  in the shells of marine microorganisms from deep-sea sediments provide a better chronological record of the Pleistocene climatic events. The shells secreted in cold waters contain more oxygen-18 isotope than those secreted in the warm waters. The marine oxygen isotope record, unlike most terrestrial records, is a continuous record that serves as a standard and can be correlated to climatic events on land (like glaciation). Based on this correlative study, the Pleistocene is known to have more than ten glacial-interglacial cycles. During the early Pleistocene, glacial cycles were shallow and frequent; in the later phases, the cycles became more intense and widely spaced with the pronounced temperature difference between the glacial and interglacial. The higher latitudes experienced far more dramatic temperature differences than near the equator.

Many theories have been proposed to explain the Quaternary glaciations, but the theory of astronomical cycles is considered the best explanation so far. Astronomical cycles, also known as the Milankovitch cycles, are determined by three parameters, namely, eccentricity (departure of the earth from its circular orbit), obliquity (tilt in the earth's axis), and precession (wobble of earth's axis). These parameters collectively determine the amount of solar radiation incident on any latitude.

These latitudinal radiation variations caused by orbital parameters and the other feedback mechanisms seem to account for the Pleistocene climate change.

The air bubbles found in the drill cores from Greenland and Antarctica show a reduction of greenhouse gasses, CO<sub>2</sub>, and methane in the mid-Pleistocene, which correlates with the reduced global temperature. Lower levels of atmospheric CO<sub>2</sub>, increased amount of dust, and increased reflection from the snow-covered earth's surface would have contributed to the feedback mechanism and together caused increased cooling (Willeit et al. 2019).

### Holocene

The Holocene, the next epoch of the Quaternary period, is an interglacial phase which began about 11,700 years ago at the end of the Weichsel glaciation (the last glacial maximum of the Pleistocene) and continues till today. It is the shortest and the most intensively studied epoch in the entire geological timescale as it contains diverse and remarkably well-preserved evidence. Sir Charles Lyell named the Holocene from the Greek words *holos* = whole/entire and *kainos* = new or modern, meaning “entirely recent.”

The Holocene has been recently subdivided into three stages: the Greenlandian or Early Holocene (11,700–8,236 year b2k, i.e., before the 2000 calendar year), the Northgrippian or Middle Holocene (8,236–4,250 year b2k), and the Meghalayan or Late Holocene (4,250 year b2k till today) (Walker et al. 2019).

As humans have greatly influenced the Holocene environment, especially the latter stage, it is sometimes referred to as the Anthropocene or the “Age of Man.” The development of complex human cultures, the origin of agriculture, and the expansion of neolithic settlers transformed the landscape and altered the environmental dynamics.

### Holocene Fauna

At the beginning of the Holocene, large animals like mastodons, mammoths, saber-toothed cats, and giant sloths became extinct. Over time, man domesticated dogs, cats, and ungulates like

cattle, horses, pigs, sheep, and camels. During the Holocene, animals did not evolve much, but their distribution pattern changed.

In the last two thousand years, many species such as moa, quagga, dodo, and great auk have become extinct due to human activities like habitat destruction, overhunting, increased interspecific competition, the introduction of exotic species, and infectious diseases. This widespread extinction of species during the modern Holocene is termed as the Holocene extinction event.

### Holocene Flora

Pollens and spores well preserved in lakes, swamps, and sea sediments provide a basis for reconstructing the paleoenvironment and estimating the local vegetation. These reconstructions show a warming and drying trend, favoring cold-tolerant water-loving plants like birch and spruce in high latitudes and altitudes. These studies also provide insights into the migration of plants in response to warming. Integrating such studies with climate model predictions will help evaluate if major tree populations can migrate rapidly enough to a suitable habitat during global climate change.

During the Early Holocene, tundra gave way to birch forests in the high latitude and midlatitude. By the Middle Holocene, they were replaced by pine, followed by the oak, beach, or mixed forest. In the midlatitudes, continental interiors, facing hot summers and cold, dry winters, saw expanding prairie or steppe. More significant moisture in the polar regions led to the disappearance of the steppe tundra.

### Holocene Geography

As a result of plate tectonics, continents have drifted to their current position by about 1 km over the entire Holocene. Through the Holocene interglacial, Greenland and Antarctica, situated at higher latitudes, have retained their glaciers. In comparison, the midlatitudinal ice sheets disappeared at a tremendous rate and increased the sea level by 35 m. With the rise of sea level and removal of the glacial load, the earth's crust responded buoyantly, resulting in progressive postglacial upliftment or crustal rebound. Places at about 40°N, previously loaded with thick

glacial ice, rose to about 180 m and are still rising. In cases where the rate of rising water level was more significant than the rate of land rise, temporary marine transgression occurred. The post-glacial rebound has resulted in the Hudson Bay formation in North America and the Baltic Sea in Scandinavia.

### Holocene Climate

Holocene climate has been relatively stable, comprising changes that were primarily regional compared to Pleistocene's global climate changes. The general climate showed a warming trend from the beginning of the Holocene to 7,000 years ago. This was followed by the Holocene climatic optimum, which ended about 5,000 years ago, with temperatures 0.5–2 °C warmer than today. This was the time when the earliest human civilization began to flourish in Africa and Asia. At this time, the Nile River in Africa was three times its present volume, and the Sahara desert was a fertile land. Then, the Holocene earth entered a period of minor glaciation that lasted until 4,000 years ago. The earth went through short cooling and warming trends over the years. From AD 1100 to 1300, the climate was slightly warmer and is known as the Little Climatic Optimum or Medieval Optimum. This was followed by the Little Ice Age, the coldest period of the Holocene, which lasted till AD 1850. During this time, a large part of the population died due to crop failure and famine in Europe.

Many researchers believe that the Holocene is an interglacial period, and the earth will return to a new phase of glaciation in another 3,000 years.

### Conclusion

The Cenozoic Era, the 66.6 million years of earth's history, holds the evolutionary secrets of all life on earth today. Stacked below the earth's crust, each layer unfolds stories about the formation of continents, mountains, climatic zones, unimaginable glaciation cycles, the evolution of the mighty *Indricotherium*, majestic woolly mammoth, and the unbeatable human race from the small nocturnal mammals.

The step-by-step evolution that has taken place over millions of years is at stake as humans are taking command of their immediate environment, affecting the greater environment culminating in irreparable and irreversible losses. Though climate changes and extinctions have been a part of the earth's story, the current changes occur in a span of a few hundred years, giving meager opportunities for life to adapt.

A better understanding of the earth's past holds the key to a better future.

### Cross-References

- [Adaptation](#)
- [Hominid](#)
- [Homo sapiens](#)
- [Migration](#)
- [Primates](#)
- [Ungulate](#)
- [Woolly Mammoth](#)

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## Center of Mass

### ► Gait

## CentiMorgan (cM)

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## Synonyms

### Map unit

## Definiton

CentiMorgan is defined as the distance between genes on the chromosome and is used to measure the recombination frequency.

## Introduction

It is a map unit used to measure the genetic linkage, which is defined as the distance between two positions along the chromosome that results in 1% recombinant individual out of 100 progenies. The distance corresponding to this 1% recombination frequency is called centiMorgan (cM) (Lodish et al. 2004).

The term centiMorgan is given to genetic unit in honor of the great scientist Thomas Hunt Morgan.

$$100 \text{ centiMorgan} = 1 \text{ Morgan}$$

If two loci are 1 cM apart, then a crossover occurs between them at an average of 1 in 100 meiosis. Therefore, cM is a measure of the genetic or linkage distance between two loci. One map unit is equal to 1 cM and 1 cM is equal to 1% recombination. Thus, two genes that recombine with a frequency of 3.5% are said to be located 3.5 map units apart. This is not the same as physical distance, which is measured in base pairs. However, in humans, 1 cM is roughly equivalent to  $1 \times 10^6$  base pairs (bp) (Fig. 1).

## Relation to Recombination Frequency

The centiMorgan (cM) values for DNA segments are measurements of how likely the segment is to

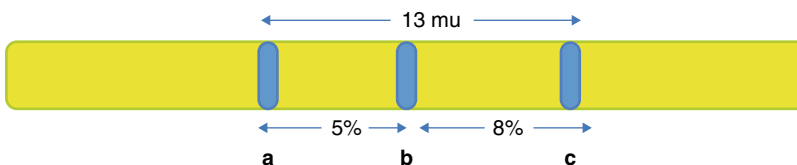
recombine as it passes from parent to offspring. Segments with higher cM values have a greater probability of recombining in any one generation. Therefore, when you share DNA segments with larger cM values with a match, your common ancestors are likely to come from generations that are more recent (Benzamine 2005).

The frequency of crossover events expressed in centiMorgan cannot be correlated with the physical distance between the markers employed. This has been demonstrated, for example, in cereals (Heslop-harison 1991), in the tomato chromosomes, and more extensively in the chromosome 4 of *Arabidopsis* (Tangkley et al. 1992). Among the progeny of parents that are heterozygous for a number of linked genes, a genetic map that places the genes in a linear array can be constructed. The distance between loci represents the frequency of occurrence of recombination and is not equivalent to a precise physical distance. However, approximations for the value of percentage recombination and the number of base pairs of DNA have been deduced by correlating physical chromosome maps with genetic maps.

So,

$$\text{map distance} = \frac{\text{Number of recombinant offspring}}{\text{Total number of offspring}} \times 100$$

CentiMorgan length represents the percent of recombination between the genes on the chromosome. The recombination rates vary among the individuals and chromosomes. The genome wide recombination rate was studied in ten *Eucalyptus globulus* and was found as between 2.71 and 3.51 cM/Mb. Not only genome wide, the recombination rate varies across the chromosome also. The 11 chromosomes of *Eucalyptus globulus* were found to have different recombination rate ranged from 1.98 to 3.81 cM/Mb (Gion et al. 2016).



**CentiMorgan (cM), Fig. 1** Recombination frequency between genes *a* and *b* is 5% and between *b* and *c* is 8%. Genetic distance between these genes is 13 m.u. or centiMorgan (cM)



CentiMorgan length also varies across the position on the same chromosome. As it was seen in *Anopheles gambiae*, the recombination rate varies from  $>7$  cM/Mb at the telomeric end of the X chromosome to  $\sim 0.2$  cM/Mb at the centromeric end (Pombi et al. 2006). The average rate of recombination varies among the individuals also like in *Drosophila* the average rate of recombination is 1.5 cM/Mb (Nachman 2002) and in human beings, it is 1.1 cM/Mb (Kong et al. 2002).

## Conclusion

CentiMorgan (cM) is a unit to measure the distance between genes on the chromosome. It is denoted by map unit. One centiMorgan is equal to one map unit and same will be the recombination frequency. The recombination rate varies not only among the individuals but also the chromosomes.

## Cross-References

- [Centromere](#)
- [Crossover](#)
- [Gene Frequency](#)
- [Gene Map](#)
- [Genetic Variation](#)

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## Central Dogma of Life

- [Gene Expression](#)

## Central Executive

- [Cognition](#)
- [Rehearsal](#)

## Central Nervous System

- [Nervous System, The](#)
- [Vertebrate Nervous System](#)

## Central Place Foraging

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## Definition

A foraging strategy in which prey or resources are transported to a nest or other habitual base rather than being consumed in situ.

## Introduction

Many animals use one or more habitual locations as nests, shelters, or storage caches during all or part of their lives and transport resources to this central place. Examples include birds bringing food to their nests to feed their chicks, bees storing honey at their nest to feed brood and provide food during periods when no flowers are available, male terns bringing food to females during courtship, chipmunks stockpiling seed for the winter, or eastern woodrats collecting nesting materials. A central place can also function as a store of information, as in ant colonies where pheromone trails radiating from the nest encode the sum of the colony's knowledge about available food sources or honeybees which dance inside the nest to communicate the position of flowers. Humans, too, are central place foragers, transporting everything from food to fuel, building materials and even status symbols or the spoils of war to their homes, often over great distances.

## Modeling Optimal Strategies

Central place foraging theory is an offshoot of optimal foraging theory, making quantitative predictions about foraging behavior by assuming that animals attempt to optimize their net gain per unit of time or energy invested. The requirement to return to a central location imposes time and energy costs in addition to those incurred by searching for, capturing, and handling prey items. These additional costs can alter the optimal strategy, which also depends on whether animals are single-prey loaders, which catch and transport a single item at a time, or multiple-prey loaders, which can acquire many items on a single trip (Orians and Pearson 1979).

To optimize foraging performance, multiple-prey loaders ought to spend longer searching for (and collecting) food, and carry larger loads, when foraging at distant locations than at those closer to the nest. Single-prey loaders, unable to increase their load by collecting more items, are predicted to prefer larger prey items further from the nest and to accept a smaller range of prey sizes. The logic

underlying these predictions is illuminated by an analogy to human shopping: it can be worthwhile to visit a local shop to pick up a few items only. Conversely, if a shop is time-consuming to reach, it is only worthwhile if the produce is particularly good and if you stock up on everything you are likely to need for some time to come.

Choice of prey gives animals an opportunity to adjust the profitability of a trip. Foragers should be choosier and more likely to specialize on the most profitable food sources when foraging further from their central place, although the optimal prey choice strategy varies in complex ways depending on the relative profitability and abundance of different items and on the time taken to handle different types of prey (Houston 1985). Smaller or less profitable items are more likely to be harvested when the best items are rarely encountered or require time-consuming handling, as well as when the round-trip time is lower. In some species, foragers will consume small prey in the field but transport larger items to the nest.

Foragers should become less selective as costs associated with foraging increase. Within a foraging trip, animals should become progressively less choosy as time spent foraging increases. Thus, single-prey loaders may return from a long foraging trip with items less profitable than they rejected at the start of the trip (Houston and McNamara 1985).

Many animals process their food before eating it. Processing prey at the point of capture will result in lighter loads to carry back to the nest, resulting in time and energy savings. Beyond a certain distance, these savings result in a lower round-trip time, and a forager should switch from processing at the central place to the point of capture. If processing can be done in stages, progressively greater levels of processing are expected at increasing distances from the central place (Rands et al. 2000).

A further prediction is that animals should choose nesting sites at the centers of profitable foraging areas, particularly when food supplies are unpredictable. Nest-searching bumblebee queens, for example, will spend weeks searching for suitable sites and in the process may first sample foraging resources before deciding where to settle.

## Empirical Tests

Empirical tests show broad qualitative support for the major predictions of the theory. For example, animals from birds to honeybees have been found to take larger loads when foraging further from their central place. Quantitatively, however, animals' behavior often departs significantly from models' predictions. Chipmunks collecting sunflower seeds spend longer filling their cheek pouches and carry heavier loads when foraging at patches further from their nests, as predicted, but neither the actual sizes of the loads nor the function describing the relationship between travel distance and load size is accurately explained by theory (Giraldeau and Kramer 1982). Although merlins switch from processing their prey at the nest to the point of capture as the distance to the nest increases, they do so at around 1/50 of the distance predicted by a model (Rands et al. 2000), suggesting that either the model used unrealistic inputs or that other factors influence the birds' decision, such as ectoparasite removal or strategies to avoid kleptoparasitism.

## Criticisms of Central Place Foraging Models

Models of central place foraging are vulnerable to the same criticisms that have been directed at optimal foraging models in general (Pyke 1984), namely, that they do not account for constraints on the ability of natural selection to optimize any particular function; that they require unrealistic simplifications of natural situations; that they ignore environmental stochasticity; that their proponents cannot determine what "currency" foraging animals ought to optimize; and that, because very different predictions can be arrived at by varying the model parameters, they can be used to explain any empirical result and so, by explaining too much, they fail to explain anything at all.

The real world is more complex and variable than that of simplified mathematical models, and it is unlikely that natural selection could equip any organism with the optimal response to every

possible scenario. Instead, evolution is likely to favor general behavioral rules that perform well on average, in the natural environment typically faced by a given species (McNamara and Houston 2009). Two conclusions follow: perfectly optimized behavior may not occur under any specific set of conditions; and the optimal behavioral rules for a given species will depend on its biology and ecology. Understanding the needs of animals within their environment and the mechanisms by which they fulfill these needs is the key to a fuller understanding of how foraging strategies evolve.

## What to Optimize

The optimal behavior in a given situation depends on what you hope to optimize. Most models use the currency of net rate of energetic gain and zebra finches, for example, forage in ways consistent with such currency; but honeybees aim to maximize energy efficiency, the ratio of energy gained to energy spent. The choice of currency may depend on the biology of the species in question. For example, social species like ants share information on the location and quality of food sources. It can be beneficial for foragers discovering a high-quality source to cut short their foraging trip to disseminate information, raising the long-term rate of energetic return of the colony at the expense of their individual short-term profitability (Dornhaus et al. 2006). Constraints, such as the need for small birds to acquire enough energy to survive the night, may mean that under certain conditions optimizing foraging efficiency is less important than simply getting enough to eat.

## Spatial Cognition and Foraging

Many models assume an animal has perfect knowledge of the distribution of resources and how to reach them. In fact, organisms start their foraging career with no specific knowledge of their environment. This is significant because the mechanisms by which they acquire and use spatial information, along with constraints and limitations on those mechanisms, determine where and

how they forage. The need to balance learning about the environment with the exploitation of known resources is an important factor in explaining why predictions of optimal foraging behavior seldom provide a perfect fit to empirical data.

Central place foragers must learn to navigate their environment and return successfully to their starting point. They must explore in search of food and develop efficient routes to get to and from foraging patches. A variety of navigational strategies are employed by central place foragers (Collett et al. 2013). Path integration involves keeping a constantly updated memory of one's position relative to a central location and can operate independently of the features of the environment. Other strategies involve learning and recognizing environmental features and include matching a visual scene to a memorized snapshot or following an olfactory or chemical gradient. In rats, grid cells and place cells provide a neural architecture for the animal to keep track of its position in space (Moser et al. 2008).

Species from insects to primates visit multiple destinations on a single foraging trip. Multi-destination routes reveal several ways in which foraging behavior is richer than previous models have accounted for. One is that foraging decisions involve more than just determining when to leave a patch: visiting many patches in turn is efficient if no single patch is rich enough to gather a full load in a reasonable time frame and can also reduce the costs of competition. Another is that the length and geometry of an entire route are likely to be more important than simple distance from the nest in determining the optimal strategy. Bumblebees visit locations in repeatable sequences that often converge on the most efficient route (Lihoreau et al. 2012), although experiments in which they do not find an optimal route have revealed that they use heuristic strategies that lead to good results over a range of situations. In addition to multiple destinations, primates like spider monkeys also use multiple sleeping sites, allowing reduced travel distances in large home ranges while retaining the benefits of a central place.

## Conclusion

The features of the environment an animal attends to, and the navigational strategies it employs, are tailored to its habitat and lifestyle. These mechanisms determine what information is available for foraging, which will influence the optimal strategy. The animal's ability to remember and follow routes will affect which patches are best to exploit, while the mechanisms by which it finds and captures prey will influence the optimal choice of food. Such information must be integrated with central place foraging models to improve success in predicting real behavior.

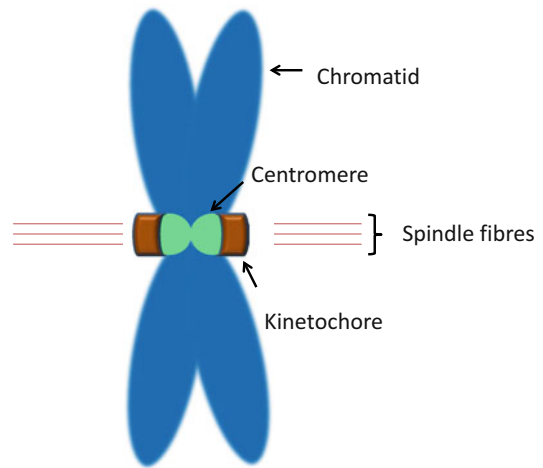
## Cross-References

- [Cognitive Map](#)
- [Food Patch](#)
- [Foraging](#)
- [Home Range](#)
- [Navigation](#)
- [Optimal Foraging Theory](#)
- [View-Based Homing](#)

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**Centromere, Fig. 1** Simplified illustration of a typical centromere and arrangement of complexes around it

(microtubules) associate with centromere through kinetochore to pull apart the two sister chromatids toward the opposite sides of the cell (Fig. 2). The presence of centromere ensures that each of the daughter nuclei receives one copy of each chromosome.

## Centromere

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### Definition

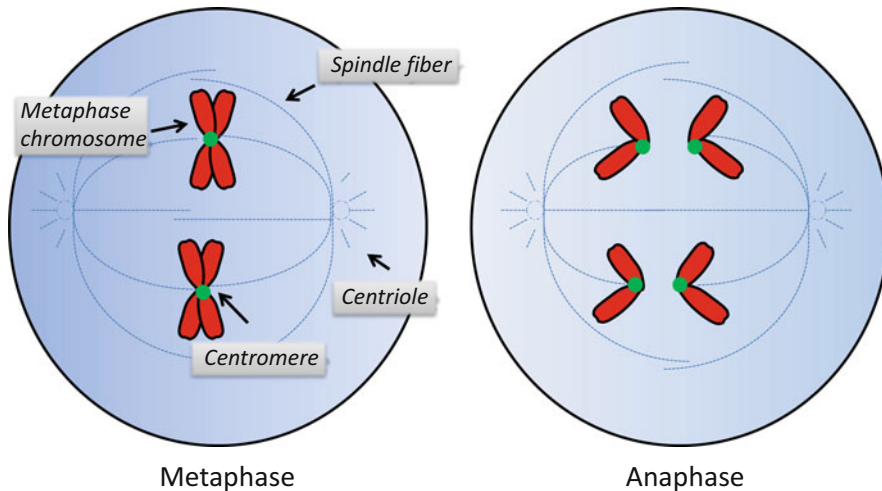
Centromere is a primary constriction site in all eukaryotic chromosomes where sister chromatids are held together (Fig. 1), and it plays an essential role in proper segregation of chromosomes during cell division (O'Connor 2008).

### Introduction

Centromere serves as a site specialized for attachment of spindle fibers. The site is characterized by the presence of specific DNA repeat sequences and associated complex of kinetochore proteins. In metaphase stage of cell division, spindle fibers

### Molecular Structure of Centromere

Centromere is a functional structure not just a sequence. Therefore, at molecular level, centromeres have two counterparts: first **centromeric DNA** sequence and second assembly of special proteins around it. The DNA sequence may or may not be sufficient or even essential to form a functional centromere. **Centromeric chromatin** sequences are specialized by the presence of special variant of histone protein **H3** called **centromeric protein A (CENP-A)** or **CenH3**. The presence of **CENP-A** at the centromere is common among most of the eukaryotes and assumed to be epigenetic characteristic for facilitation of kinetochore assembly at centromere. Further, **CENP-A** mediates recruitment of other centromeric proteins. For example, humans have a complex of 17 centromeric proteins associated with centromeric chromatin throughout the cell cycle, termed as **constitutive centromere-associated**



**Centromere, Fig. 2** Representation of microtubule attachment at centromere and chromosomal segregation during cell division

**network (CCAN)** (Westhorpe and Straight 2013). The complex is essential for recruitment of kinetochore proteins during cell division. Abnormal expression of many of these proteins including CENP-A has been reported to cause centromere dysfunction. Centromere dysfunction consequently results in chromosomal instability especially formation of aneuploidy and micronuclei due to improper chromosomal segregation. These phenomena are known to be linked directly with spontaneous abortions and many cancer types.

### Diversity Among Centromeres

Based on size and distribution of centromere, chromosomes have been broadly classified in to two categories; viz., (1) **monocentrics** refer to the presence of single site for centromere and represent most of the eukaryotes (Fig. 3a), and (2) **holocentrics** denote distribution of centromere along whole length of the chromosomes (Fig. 3b). Holocentrics have been reported in multiple plants and invertebrates.

Further, there are two classes of centromeres among **monocentrics**: **point** and **regional** (Fig. 4). A **point centromere** is represented by single stretch of ~125 bp specific DNA sequence

with a single nucleosome having **CenH3**. In this case, sequence is reported to be self-sufficient and necessary for the assembly of kinetochore proteins. In contrast, regional centromere DNA sequences are broad and consist of array of short tandem repeats called **alpha satellite** or **alphoid DNA** sequence ranging from 250 to 5,000 kb. Sequence similarity among alpha satellites is in a range of ~50–70%. In rare instances, formation of centromere has been reported at sequences dissimilar to alpha satellites, viz., **neocentromeres**. Moreover, inactivation of centromere in intact **alpha satellite** sequences has also been observed (Aldrup-Macdonald and Sullivan 2014). Due to these two reasons, regional centromeres are specified on the basis of epigenetic modifications particularly the presence of array of **CENP-A** histones in place of **H3** histones, and DNA sequence is assumed to be nonessential.

**Holocentrics** are now considered to be polycentrics having large array of multiple point centromeres (Steiner and Henikoff 2014). These have also been categorized into two classes by the presence or absence of CenH3 proteins. In earlier description, **CENPA/CenH3** is shown to be essential for most of the eukaryotes; exceptionally some lineages of insects, for example, lepidopterons, have been evolved having centromeres with no **CenH3**.



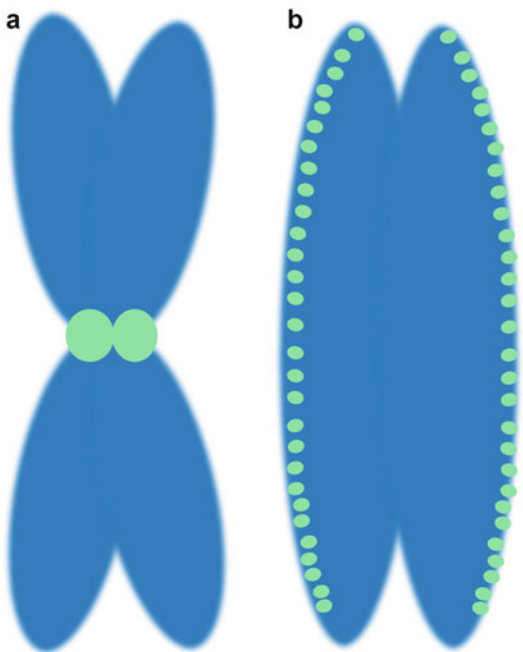
**Chromosomes with Unusual Centromere: Dicentrics, Acentromerics, and Neocentromere**

**Dicentrics** have two centromeres resulted from joining of two broken chromosomes both having centromeres. In such cases, often one of the

centromere gets inactivated by unknown mechanism and resists chromosomal segregation. A dicentric forms nucleoplasmic bridge after nuclear division often leads to cell death (Fig. 5).

Acentromeric bodies also result from chromosomal damage. Since acentrics cannot be segregated properly, they get excluded during formation of nucleus consequently form micronuclei in cytoplasm (Fig. 5) and get lost in further cell divisions.

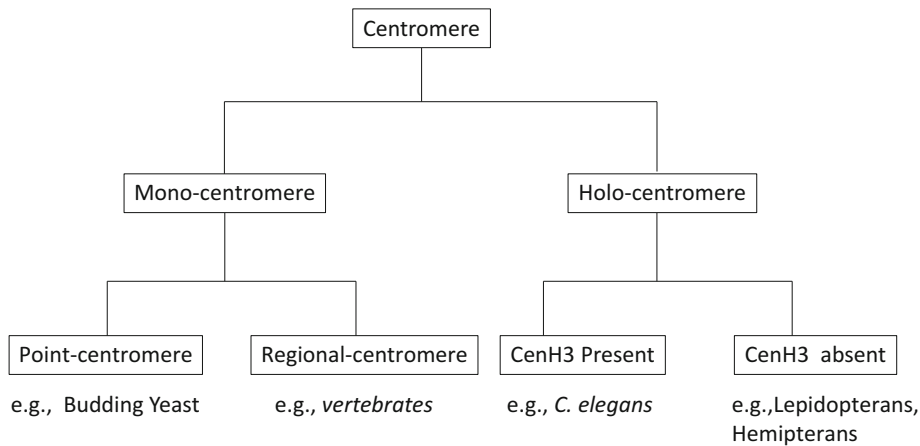
**Neocentromere** is a recent observation which refers to formation of centromere at unconventional sites at chromosomes different from alpha satellite sequence. Formation of neocentromere is observed in cells with chromosomal damage mostly on acentric fragments for their mitotic rescue. They have also been observed in cancer patients having chromosomal instability. However, this phenomenon is not well understood yet and is in recent trends of centromere research.



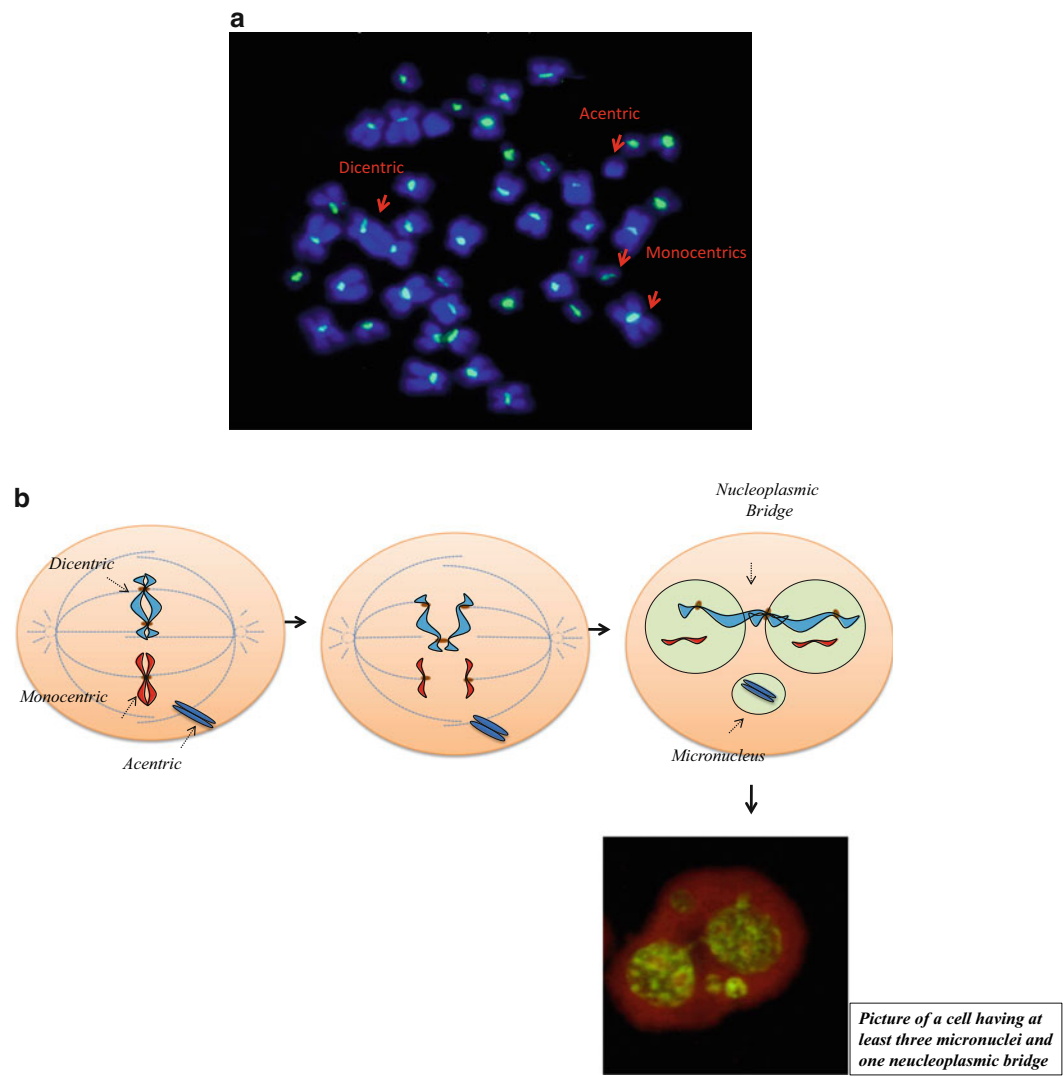
**Centromere, Fig. 3** Distribution of centromere in a monocentric (a) and holocentric chromosome (b)

**Shape and Morphology of Chromosomes Defined on the Basis of Location of Centromere**

Position of centromere is one of the important criteria for identification and nomenclature of a chromosome. The presence of centromere divides a chromosome into half shorter and termed as **p arm** (p stands for petit in French which means



**Centromere, Fig. 4** Categorization of centromeres

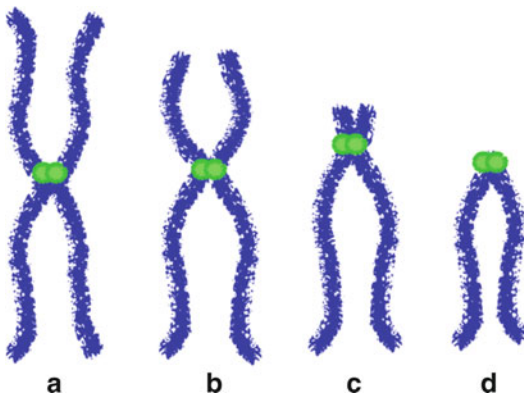


**Centromere, Fig. 5** (a) Chromosomal spread from human metaphase with monocentric, dicentric, and acentric bodies. Centromeres are hybridized with sequence-specific fluorescent probes. (b) Pictorial demonstration of a dicentric, monocentric, and acentric chromosome segregation; a monocentric chromosome segregates equally

between daughter nuclei, whereas a dicentric often is not separable due to inactivation of one centromere and results in formation of nucleoplasmic bridge. On the other hand in the absence of centromere, a chromosome gets excluded from main nucleus and forms micronucleus in cytoplasm

small), and longer part is denoted as **q arm**. Any locus/gene is identified on the basis of the arm it resides in and its distance from the centromere. There are four classes of chromosomes on the basis of centromere position (Fig. 6) (Levan et al. 2009).

1. **Metacentric chromosomes:** centromere is in the middle of the chromosome and both p and q arms look equal.
2. **Submetacentric chromosomes:** centromere is little above the center of the chromosome making p arm shorter than the q arm.



**Centromere, Fig. 6** Classification of chromosomes on the basis of centromere position metacentric  $p = q$  (a) submetacentric chromosome  $p < q$  (b) acrocentric  $p \ll q$  (c) and telocentric with no p arm visible only q arm (d)

3. **Acrocentric chromosomes:** centromere is located well above the center, and p arm is considerably smaller than the q arm.
4. **Telocentric chromosomes:** centromere is located at the tip of the chromosomes; apparently no p arm is there.

## Conclusion

Centromeres are essential for proper segregation of chromosomes. They serve as a site for kinetochore formation and microtubule attachment and hold sister chromatids together until the cell is ready for chromosomal segregation. Abnormalities in centromeric function may lead to aneuploidy, aberrated cell division, and cell death.

## Cross-References

- [Chromatid](#)
- [Chromosomes](#)
- [Nondisjunction](#)

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## Cephalization

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Cephalization is an evolutionary trend to concentrate sensory and neural organs anteriorly in a head. In the field of the neurosciences, it may be defined as the progressive growth of the (cephalic) nervous system during the evolution of animal life. Each species develops characteristic aspects of brain anatomy and organization that better suit a specific evolutionary trend and environmental niche. Up to a certain point, the growth and maturation of the embryonic brain summarizes the progressive phylogenesis of the species.

Cephalization is very evident in vertebrates, and the avian and mammalian brains are especially complex architectonically. The vertebrate brain is organized differently in the diverse clades, and neural cells may form efficient aggregates with a common chemical language, either in the form of nuclei or layers, the latter possibly functionally organized in columns. In vertebrates, amphibians and reptiles have brains that fall in the range of teleost fishes. Elongated animals (e.g., snakes, salamanders, eels) have proportionally smaller brains since they have heavier bodies

in comparison to animals with a robust body structure. Birds have brains 6–10 times larger and mammals around 10 times larger than reptiles of similar body weight (Van Dongen 1998).

## From Cephalization to Encephalization

Animal psychology and comparative cognitive neuroscience require trustable methodologies for a comparative analysis of the nervous system in different taxa. Many recent works have drawn attention on the relationship between evolutionary changes in brain size and behavioral complexity. However, the easiest way to compare the brain of two species within the same clade is to consider the mass of the brain in relation to body mass. The relationship of brain size to body size was the basis of Dubois' (1897) "index of cephalization." Dubois' proposal for an equation was further developed by Jerison (1973), to obtain what was then referred to as encephalization measured as encephalization quotient (i.e., EQ). Specifically, EQ is defined as the ratio between observed and expected brain mass, that is,  $EQ = E_i/E_e$ , a parameter widely applied in comparative mammalian neuroanatomy (Boddy et al. 2012). In this equation,  $E_e = E_i/0.12P^{0.67}$ , where  $E_i$  and  $P$  are the mean weight of the brain and body, respectively. The EQ value indicates, thus, whether a species possesses a brain larger ( $EQ > 1$ ), equal ( $EQ = 1$ ), or smaller ( $EQ < 1$ ) than expected for its body mass. Alternatives to the value of the exponent or to the equation originally indicated by Jerison (1973) have been proposed by several authors (Grabowski et al. 2016).

Encephalization occurs when the actual brain size (positively) diverges from the expected brain size for a species of a given mass. The difference from the expected value is used as predictor of an animal's adaptive capabilities.

The comparison of brains in different vertebrate clades such as anurans and birds are further limited by the fact that each group had its own and very long evolutionary history formed by unique adaptations. A comparison is the more complicated if animals do not have the same brain bauplan, i.e., if brains are constructed by different

structural principles, such as, e.g., the insect brain and the cephalopod brain.

Focusing on mammals, a great attention has been dedicated to inter- and intra-order comparisons among different species, using almost constantly wild specimens as a paradigm. It has been hypothesized that brain expansion in mammals is evolutionary associated, among other parameters, to sociality (Shultz and Dunbar 2010).

## Brain Size and EQ in Mammals

Evolutionary pressure can alter the brain/body size ratio in at least two ways. It could directly affect brain size or alternatively be a consequence of increase or decrease of the body size. The role of a greater or lesser magnitude of the brain is still a topic widely debated. The brain is one of the organs requiring the most energy (preceded only by the heart) and the cost of its operation is about 8–10 times higher per mass unit than that of skeletal muscles. Evolution is an "economical process" and does not enlarge an organ from which the body cannot derive a real benefit. In mammals, the increase in size is due predominantly to the enlargement of the forebrain and neocortex, leading to an increase of the primary areas (receiving thalamic afferents: motor area, visual, auditory, somatosensory) as well as secondary ones (higher mental functions). Progressive specialization and diversification in the mammalian brain arises precisely from the differential development of these areas.

Studies on brain size generally group species of different orders and apply indexes to assess the evolutionary position of each group. If we accept that brain and body size grow allometrically in vertebrates (Shultz and Dunbar 2010), we should also consider that mammals show specific evolutionary trends. In general, mammals at the top of the food network (high trophic levels) may have an absolutely large brain (e.g., the large whales) or a high EQ (e.g., primates and dolphins; Steinhausen et al. 2016). Within some (but not all) mammalian taxa, there seems to be a strong evidence for specific macroevolutionary increase in brain size, possibly explained by the social

brain hypothesis that links changes in sociality and relative brain size (Dunbar and Shultz 2007).

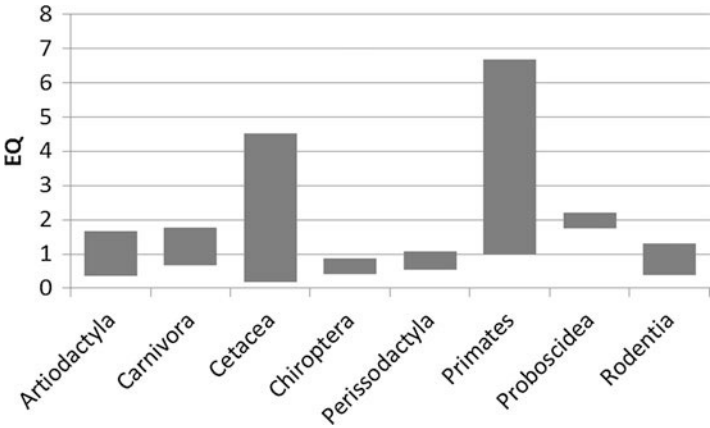
The mammalian species that have EQ >1 include apes and some cetacean species, mostly small-sized dolphins (Fig. 1). Elephants, killer whales, and female sperm whales are the only large mammals (weighing far more than 1 ton) with an EQ >1. It is common knowledge that sperm whales (SW; *Physeter macrocephalus*) and killer whales (KW; *Orcinus orca*) possess the heaviest brains on the planet (SW: 9.20 kg, KW: 9.30 kg) but the enormous body mass of SW prompts a relatively low EQ value (EQ <1) (for details see Cozzi et al. 2016). Other large bodied mammals like Perissodactyla (e.g., horses and rhinos) and terrestrial Cetartiodactyla (e.g., hippos, giraffes, and several even-toed mammals) fall in the group of the below-the-expected EQ (EQ <1).

Evidence shows that larger EQs or relative brain size endow species with improved cognitive abilities and behavioral flexibility, such as the ability to respond successfully to novel environments or to alternate between feeding strategies (Shultz and Dunbar 2010). These findings seem to agree with the fact that humans, dolphins, and chimpanzees have the largest known EQs. The EQ is not per se a sign of intelligence; however, a EQ <1 possibly suggests certain limitations to cognitive capabilities (e.g., self-recognition, use of tools) or to the ability to build complex social interactions with fellows of the same and other species.

It is also possible that larger animals have the tendency to minimize expensive neural tissue unless a specific function played by a certain nucleus or area is fundamental for survival and thriving. The overall value of the EQ and cortex analyses as predictors of cognitive capacities is doubtful, at least in primates, for which absolute brain size results a better prognostic factor. Furthermore, the relationship between EQ and body mass in unfavorable for the largest species within each group. The importance of interspecies variations should also be emphasized: a discrete number of horses have an EQ in the range of the cat, elephant, and close to the inferior limits of primates (Cozzi et al. 2014). Furthermore, analysis of “individual” carnivores (i.e., musteloids, bears, small felidae), whose life habits are quite solitary, but endowed with a relatively large EQ, contradicts the social hypothesis of brain development.

Within a complex and largely unexplained tendency to augment brain mass, the intense gyrification of some mammalian species (i.e., large herbivores, *Delphinidae*) suggests the presence of evolutionary factors promoting selective development of the telencephalon and adaptive shaping of the cortical columns. Based on the general concept that an increase in size of a given brain region must (or should) provide some amelioration in function, and given the limits of the behavioral complexity explanation, one must wonder why Perissodactyla and Cetartiodactyla (including marine species) developed such a cortex. Current hypothesis for the

**Cephalization,**  
**Fig. 1** Ranges of EQs in selected mammalian orders. Data from Steinhausen et al. (2016)



intensive gyrencephaly include analogies between hoofed animals and cetaceans, based on gyrification, cortical thickness, and reduction (or absence) of cortical layer-4. However not all the factors evoked to explain cortical growth may apply to all species, predominantly those that consider sociality. Apparently, the cortex of large herbivores is structurally oriented to process sensory inputs and respond with immediate motor strategies. Is it thus possible that the control of complex quadrupedal locomotion requires a larger cortical mantle but not a larger brain? However, attempts to correlate complex behaviors with brain structure or size are problematic. So, the differences in the EQ between, i.e., small-toothed cetaceans and *Bos taurus* (and like terrestrial Cetartiodactyla) are possibly related to evolutionary adaptation to different environments, feeding strategies, and consequent sensorial specialization.

## Conclusion

It is widely believed that the nervous system underwent a progressive increase in size over the course of evolution with the consequence, more or less explicit, that at each increase of magnitude corresponds to an increase in function. Learning skills, foraging strategies, or habitat management capabilities have been variously linked with this aspect, and sometimes considered the primary cause. To date, the most likely hypothesis for mammals remains the social brain (SBH, social brain hypothesis) developed in primates (Dunbar and Shultz 2007), but applicable also to various degrees to carnivores and terrestrial Cetartiodactyla. It is based on the principle that complex social groups, such as those of primates, or gregarious animals as can be ungulates, develop relational dynamics that often require the ability to manage individual conflicts and the need to remain in the group, thus the need to cope with huge computational demand, contributing to the progressive increase of brain size within a given systematic group (Shultz and Dunbar 2010).

## Cross-References

- [Intelligence](#)
- [Ontogeny](#)
- [Phylogeny](#)
- [Social Darwinism](#)
- [Socialization](#)
- [Sociobiology](#)
- [Vertebrate Nervous System](#)

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## Cephalopod Adaptations

### ► Cephalopod Cognition

## Cephalopod Behavior

### ► Cephalopod Cognition

## Cephalopod Cognition

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### Synonyms

[Cephalopod adaptations](#); [Cephalopod behavior](#); [Invertebrate cognition](#); [Mollusk cognition](#)

### Definition

Cephalopods are a class of marine mollusks that are soft-bodied and contain a decentralized nervous system. Through these and other unique physiological adaptations, cephalopods have acquired a complex behavioral set unseen in other invertebrates (Mather and Kuba 2013).

### Introduction

When discussing complex nonhuman cognition, the species examined are typically mammals, corvids, or even sometimes fish. It is unusual to think of invertebrates as having intelligence comparable to these animals, but there are a few that might – coleoid cephalopods. Since ancient Greek and Roman times, philosophers have marveled at the apparent intelligence of cephalopods, and that fascination has continued well into today and for good reason. Coleoid cephalopods are often

regarded as the most intelligent and cognitively complex group of invertebrates (Schnell et al. 2021). Coleoid cephalopods (henceforth cephalopods) are part of the class Cephalopoda in the phylum Mollusca that includes species of octopus, squid, and cuttlefish. These animals have shown evidence of being able to solve intricate puzzles, change their appearance and behavior to blend in with their environment, and use tools, and they are also capable of performing similarly to humans on several cognitive tasks (Mather and Kuba 2013). The unique physiology of cephalopods provides evidence for the theory that intelligence has evolved separately, but in a similar capacity, multiple times in very different species (Schnell et al. 2021). Cephalopods have a unique ability to edit their own RNA to change their neural gene expression. This allows cephalopods to change their neural proteins, which may explain their unique nervous systems and behavioral diversity; however, it may have also stunted genome evolution that is typical in other animals (Liscovitch-Brauer et al. 2017). Each cephalopod species has its own particular adaptations that allow them to perceive and react to their environment in a way that best suits their environment. Cephalopods inhabit almost every marine environment on the planet from shallow reefs to the depths of underwater trenches. This variety of environments has required each species of cephalopod to develop highly specialized physical and behavioral adaptations. The adaptations of cephalopods have allowed them to exhibit a diverse behavioral repertoire and to perform abilities not seen in other invertebrates.

### Chromatophores and Camouflage

Cephalopods also have specialized small organs in their skin called chromatophores. Cephalopod chromatophores can be contracted and relaxed by the neuromuscular system of the cephalopod. This allows cephalopods to expose or hide pigmentation in their skin, effectively changing the individual's coloration. Cephalopods also have the capability to change their skin texture and appearance at will, giving them extreme camouflage

capabilities (Messenger 2001). They may replicate the appearance of a rock, coral, or some seaweed to avoid predation or being detected by potential prey, and they can change their entire physical appearance in a matter of seconds (Hanlon and McManus 2020). Along with changes in coloration and skin texture, some cephalopods are able to replicate the behaviors of other animals in order to hide from others. A prime example of this can be seen in the mimic octopus's (*Thaumoctopus mimicus*) ability to replicate the appearance and behaviors of other animals that share their environment. The mimic octopus can assume the general shape and movements of multiple animals including a banded sea snake (Gómez-Moreno 2019), a lionfish, and a flounder (Norman et al. 2001). They imitate these animals only in specific scenarios; for example, the form of a sea snake is only taken up when encountering the very territorial and aggressive damselfish. This ability to alter their physical appearance is not solely used to avoid predators. For example, male mourning cuttlefish (*Sepia plangon*) change their appearance to deceive sexual competitors. Large males typically guard multiple females during mating events to give themselves as many mating opportunities as possible. Rather than trying to challenge the larger males to gain access to females, smaller males will replicate female patterns to get past competitors and mate with females undetected. The small males may even retain the half of its body that is facing the large male in female patterns while presenting as male on the half facing the female so that she will mate with him (Brown et al. 2012). Cephalopods' ability to change their physical appearance is an impressive feat for hiding in plain sight, but it can also help them stand out as well. Most cephalopods will change their appearance to blend in with its environment. Sometimes when flamboyant cuttlefish (*Metasepia pfefferi*) are attacked by a predator, utilizing its typical tactic of blending in with its surroundings, they flash a bright display of colors across their body. While it is still not known for sure why this happens, it appears to startle the predator long enough for the cuttlefish to get away (Hanlon and McManus 2020). Cephalopods' ability to

change their appearance effectively and rapidly has helped them survive without any exterior protection for millennia.

## Extraordinary Eyes

Cephalopods also have a complex visual system that allows them to see polarized light and find contrasts easily, which aids in hunting prey as well as identifying how best to camouflage (Hanlon et al. 2009). Cephalopods also have unique eye morphology that can improve their sight. For example, have a "w" shaped pupil that helps aids in horizontal vision (Mäthger et al. 2013). This high level of visual acuity is useful for identifying threats, as well as conspecifics in their environment. Their vision is so advanced; octopuses can even perceive and remember individual human faces (Anderson et al. 2010). Giant Pacific octopuses (*Enteroctopus dofleini*) were tested to see if they could discriminate two unfamiliar novel humans. One human would feed the octopus during each interaction over a 2-week learning period; the other human would touch the octopus with a bristled stick. Then the octopuses' physical reactions to these humans were recorded. They found that octopuses tended to point their funnels and water jets away from the human that fed them, which provided evidence of familiarity with that person. Alternatively, the octopuses would point their funnels and jets directly at the person who touched them with the bristle stick, showing that they recognized the individual and remembered how they were not comfortable with them based on their previous encounters (Anderson et al. 2010). Another anecdotal piece of evidence can be seen from the popular documentary *My Octopus Teacher*, in which the subject of the film, Craig Foster, develops what he considers a mutual learning relationship with a singular wild common octopus (Ehrlich and Reed 2020).

## Investigative Arms and Minds

Cephalopods have a nervous system unlike that of most other cognitively complex animals. Well

studied in octopuses, these animals typically have a decentralized nervous system that extends into each of their arms and allows their appendages to react to stimuli seemingly independent of the animal's conscious awareness. Cephalopods also have armlike appendages that are lined with hundreds of individual suckers. These suckers do more than just help the cephalopods grip on to objects or prey; they are actually lined with multiple chemoreceptors that allow them to essentially taste and smell through the suckers. The suckers can also move and grip independently of one another for improved flexibility and multitasking (Mather and Kuba 2013). Cephalopods will often use their independent arms and hundreds of suckers to help them investigate and manipulate objects in their environment for their own benefit (Mather and Kuba 2013). Exploration of their environment or novel objects can lead to play behaviors in cephalopods. Play or manipulation of an object without a clear goal is often viewed as an adaptive behavior in juvenile mammals because it allows them to learn how to do necessary and potentially hazardous tasks without any real danger (Kuba et al. 2006). For example, after an exploration period, giant Pacific octopuses shoot a water jet at a novel object to move it around with seemingly no real function (Mather and Anderson 1999). Outside influences such as predation and food availability are often believed to inhibit play behaviors in animals, which are viewed as superfluous, because they redirect the animal's attention to behaviors essential to survival. However, further research found that, regardless of how much food an octopus was presented with, several individuals still engaged in play behaviors, suggesting that play is somehow adaptive to cephalopods (Kuba et al. 2006). Perhaps one of the ways play is adaptive is transitioning from exploring and playing with objects to using them as tools.

One of the most documented cases of tool use in octopuses can be seen in the veined octopus (*Amphioctopus marginatus*), often referred to as "the coconut octopus." The veined octopus earned this nickname because of its tool-use behavior of carrying hard objects to defend itself from potential predators. The octopus will find some form of

discarded object and carry it around with them and hide inside of it when a predator approaches them. The octopuses will continue to carry these objects with them, most likely to prevent attacks at another time (Finn et al. 2009). Another example of tool use in octopus was observed by documentary filmmakers of the special *Blue Planet II*. They caught a common octopus (*Octopus vulgaris*) gripping multiple shells in its suckers and surrounding their mantle with the shells in an attempt to either camouflage with the substrate or act as an outer defense layer to prevent predation from sharks (Jeffs and Brownlow 2017). It has also been shown that other octopus species, including juvenile common octopuses, will use objects in their environment to create or modify a defensive den to live in and to protect themselves from predators (Mather 1994). Squids and cuttlefish have not shown evidence of being able to utilize outside objects for protection or hunting. However, some species including bobtail squids (*Sepietta* sp.) and the common cuttlefish (*Sepia officinalis*) have been shown to use their water jets to shoot pressurized water at substrate to help them dig burrows. The cephalopod will then sit in that hole and cover themselves in sand to avoid predation (Mann and Patterson 2013).

## Higher-Level Functioning

The octopus does have a central nervous system housed in their mantle that contains both the common mollusca ganglia as well as lobes that execute higher-order functioning. This system can aid in cognitive tasks such as learning and memory in cephalopods (Carls-Diamante 2019). Most cephalopods have shown evidence of having long-term memory. Both octopuses and cuttlefish have demonstrated evidence for short-term memory as well (Schnell et al. 2021). One species of squid (*Euprymna scolopes*) has shown that an individual can learn that a prey item is inaccessible after one failed attempt at accessing it and then retain that knowledge for up to 12 days after the training period (Zepeda et al. 2017). Cuttlefish have shown evidence that on top of possessing both short- and long-term memory, they may also

have episodic memory. Researchers argue that cuttlefish foraging behavior shows evidence of episodic memory. Cuttlefish appear to keep track of what they have eaten, where, and how long ago, all aspects that are required of an episodic memory. Cuttlefish will remember the location where they hunted, what the food source was, and approximately how long it has been since they hunted there before the food source would replenish (Jozet-Alvez et al. 2013). Cuttlefish will change their foraging strategy and where they choose to hunt based on the availability of preferred food items (Billard et al. 2020). Cuttlefish exhibit high levels of self-control. Cuttlefish were trained on a delay-maintenance task, meaning that if they were presented with a small reward, but did not take it right away, they would be offered a larger reward. After their training trials, cuttlefish were capable of waiting for up to 2 min for a larger reward (Schnell et al. 2021). The common octopus has shown evidence of social learning. One study found that untrained common octopuses learned to correctly select a target object much faster when they were able to observe a trained conspecific complete the task first versus those who had to be trained via traditional conditioning techniques (Fiorito and Scotto 1992). This is an interesting finding because the common octopus, like most octopus species, is typically a solitary creature meaning that natural occurrences of observational learning would be unlikely and, therefore, not a very adaptive skill to have. However, cuttlefish that often live within closer proximity to others of its kind, unlike octopuses, do not seem to show any evidence of being able to socially learn (Huang and Chiao 2013). Octopuses seem to be able to take previous knowledge and apply it in novel scenarios. Common octopuses were trained to manipulate a container to retrieve a food reward. Then in later trials, the situation was changed, from how the container was placed, how they could gain access to it, and barriers placed between them and the container. Despite each of these situations being different in some way, the octopuses were still able to take their previous knowledge on how to manipulate the container and successfully retrieve their reward (Richter et al., Richter et al. 2016).

## Conclusions

The unparalleled physiology of cephalopods has given them behavioral adaptations unseen in most of the animal kingdom. The lack of hard parts in their bodies, accompanied by specialized pigmentation organs, allows them to fit in or stand out in any environment (Messenger 2001). Their extraordinary visual and nervous systems perceive, explore, and manipulate aspects of their environment to their greatest advantage, even without full conscious awareness (Mather and Kuba 2013). They learn and remember how to solve tasks quickly and efficiently (Richter et al. 2016). Cephalopod cognition is very advanced, and there is still so much to uncover in the minds of these creatures.

## Cross-References

- Camouflage
- Cephalopod Communication
- Cephalopod Diet
- Cephalopod Life History
- Cephalopod Sensory Systems
- Deception
- Episodic Memory
- Long-Term Memory
- Mimicry
- Mollusk
- Play Behavior
- Short-Term Memory
- Social Learning
- Tool Use

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## Cephalopod Communication

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## Introduction

All living organisms need information, but they send, receive, and deal with it in many different ways. Not all information received by animals is the result of communication, as some is accessed directly from the environment, and communication consists of signals initiated from and received



by organisms. Bradbury and Vehrencamp (2011) define such signals as “produced by a sender and monitored by a receiver, to the average net benefit of both parties” (page 4). The benefit must be average, as it is not always obvious what the receiver gains, and that communication actually has taken place may also be difficult to prove. It should result in a change in the behavior of the receiver, but this will not be seen if the communication is designed to deceive, as in camouflage. Deception is communication – passage of information – though with a different goal. Communication can also be directed to several classes of receivers: conspecifics, potential predators, and possible prey. Bradbury and Vehrencamp (2011) point out that communication must also be dependent on the delivery capacity of the communicator, the sensory abilities of the receiver, and the environmental context in which the information passes. The cephalopods’ environment and physiology are different from mammals’, and their behavior is little known. Thus, this account is based only on the species and situations that have been accessed.

There are approximately 800 species of coleoid cephalopods, an offshoot of the ancient and now extinct belemnoids. They have lost the protective molluscan shell and developed high-performance physiology, a centralized brain and acute senses, probably as a result of competition with the bony fishes. A few shelled nautiloid species have completely different physiology and sensory capacities and will not be considered here (see Darmaillacq et al. 2014). Since fishes dominate the oceans, much of the cephalopods’ communication must have been shaped by pressure from this group, and thus matched to their receiver characteristics. As a medium for communication, water is excellent for transmission of mechanical deformation signals due to its high density. It is also a good medium for passage of chemical signals. As water filters out light, visual information is only available in the surface waters, but for many species bioluminescent signaling is common in the depths. Unfortunately, the depths are inhospitable to air breathers such as humans, and the modern laboratory to its inhabitants, and so little research has been carried out on the

communication of deep sea cephalopods. However, observations from the deep-diving ROVs showed surprising display of repertoires, especially of squid (see Darmaillacq et al. 2014).

## Visual Communication

Communication must depend on the sensory structures, and coleoid cephalopods have a lens-type eye (Gleadall and Shashar 2004) that is an excellent example of convergent evolution with that of the mammals and birds. However, they have only a single photopigment with a peak at 492 nm and are thus functionally color blind, although they can discriminate the plane of polarization of light, an ability which may be used in intraspecific communication. There is only a 10 degree frontal overlap of the field of view of the two eyes, so cephalopods are functionally monocular, with information passing initially contralaterally to the brain. Octopuses can discriminate visual shapes based on several characteristics, including vertical and horizontal extent, size, edge/area ratio, and shape, and can learn to attend to salient cues (Wells 1978). The skin display system (Messenger 2001), particularly of cuttlefish and squid, is the most important output system for intra- and interspecific communication, though the bases of its control and feedback about its operation are complex and not well known. Chemicals may also be very important for communication, especially in octopuses and cuttlefish, but they are poorly studied. Although cephalopods have sophisticated mechanoreceptive capacity, its use in communication has never been studied.

The skin display system of the coleoids is their primary means of visual communication. A surface layer of chromatophores consisting of elastic sacs containing yellow, red, and black pigment and muscles with direct neural control to expand them (Packard 1995) is the main unit for signaling. When these sacs are contracted, a deeper layer of leucophores that reflect ambient wavelengths of light and iridophores that reflect in the blue range is visible and changes the animals’ appearance. Formation of skin displays is assisted



by the muscles in the skin that modify its texture and by actions and postures that change appearance. One nerve projects to several chromatophores, and several nerves may project to each chromatophore, producing graded output in terms of both intensity and area (Messenger 2001), which allows extensive signal modulation (Mather 2016). Polyphenism, or ability to change appearance, can allow cephalopods to match general background (Darmaillacq et al. 2014) or specific items (masquerade) including seaweed and animals such as flounders and hermit crabs. As predators learn the general appearance of prey, changes in skin pattern over seconds will mean the animal's appearance fails to match the predator's "search image," so it avoids detection. Skin appearance is apparently controlled at three levels (Mather and Alupay 2016). One is a reflexive adjustment of chromatophore diameter due to illumination level, which is not a communication. A second is programmed adjustment to background-matching appearance (Darmaillacq et al. 2014) by several techniques (see Fig. 1 for a catalogue of repertoires), so as not to be noticed. A third level is specific signals to prey, predators, or conspecifics, modified by learning of receiver characteristic and situations.

A first step to understanding the communicative function of cephalopod visual displays would be to make a catalogue of species-typical repertoires. Skin displays are hierarchically organized; many units make up a component, and many components combine to a whole-body pattern (Messenger 2001), of which there may be around 12–15; see also Mather and Alupay (2016). Just over 20 fairly complete catalogues appear in the literature (see Fig. 1), and many squid pattern repertoires are known mainly by sexual displays occurring only at the end of the lifespan. Combinations of components have only been assessed for *Octopus insularis* and variation and context in specific displays quantified for *Sepioteuthis sepioidea* (Mather 2016). Some details of pattern development are mentioned for *Octopus vulgaris* (Packard and Sanders 1971) and *Sepia officinalis* cuttlefish (Hanlon and Messenger 1988). Thorough investigation of the communicative function of these displays has only been conducted for the

camouflage patterns of *S. officinalis* and the male sexual displays of the loliginid squid.

## Skin Displays for Camouflage

Skin displays can produce camouflage in several different ways, including but not limited to disruptive coloration, background matching, and distraction (Darmaillacq et al. 2014), so that the animal is either not detected or not recognized as an animal. Researchers began the investigation of simple background matching and found that cuttlefish produced three display patterns – uniform, mottle, and disruptive – when placed on background with different visual pattern characteristics. An animal has to perceive a visual image in order to produce a match to it. The researchers assumed that, like humans, cuttlefish processed a visual scene by spatial frequency assessment, breaking down illumination changes by Fourier analysis of spatial phase and frequency, i.e., measuring unit size and contrast. They used Marr's (1982) proposal that bottom-up analysis of an image begins with local feature detection and then elaboration of these features into a "2 ½ dimensional" representation of the scene (see Darmaillacq et al. 2014). Such an analysis fits well with the hierarchical component combination theory of skin displays (Hanlon and Messenger 1988) and allowed them to see how local background features could stimulate the production of one or another of these three background matches. Chiao et al. (2015) have a good review of the work.

First with manual analysis and then using Fourier transformations, they discovered that component size of checkerboard stimuli was a major driver of camouflage pattern choice, as animals placed on backgrounds with small components produced uniform, larger ones mottle and largest the large-unit disruptive pattern. Mean background intensity was secondarily important, as darker substrates tended to evoke a larger disruptive response. Pattern production was also strongly evoked by abrupt changes in intensity (edges), although a natural environment rarely has complete edges. Cuttlefish were as likely to

| Group:             | Species                       | Authors and Date          | Special note                     |
|--------------------|-------------------------------|---------------------------|----------------------------------|
| <b>Octopuses:</b>  | <i>Octopus vulgaris</i>       | Cowdry, 2011              | Bermuda: may be <i>insularis</i> |
|                    | <i>Octopus vulgaris</i>       | Packard & Sanders 1971    | Also maturation, actions         |
|                    | <i>Octopus cyanea</i>         | Roper & Hochberg 1978     | GBR species                      |
|                    | <i>Octopus burryi</i>         | Hanlon & Hixon 1980       | -----                            |
|                    | <i>Eledone cirrhosa</i>       | Boyle 1981                | -----                            |
|                    | <i>Octopus bimaculoides</i>   | Forsythe & Hanlon 1988    | -----                            |
|                    | <i>Octopus briareus</i>       | Hanlon & Wolterding 1989  | -----                            |
|                    | <i>Octopus vulgaris</i>       | Mather & Mather 1994      | Bermuda: may be <i>insularis</i> |
|                    | <i>Abdopus aculeatus</i>      | Huffard 2007              | 'social' octopus                 |
|                    | <i>Octopus insularis</i>      | Leite & Mather 2008       | Combinations                     |
| <b>Cuttlefish:</b> | <i>Sepia officinalis</i>      | Hanlon & Messenger 1988   | Also maturation                  |
|                    | <i>Metasepia pfefferi</i>     | Thomas & MacDonald 2016   | -----                            |
|                    | <i>Sepia pharaonis</i>        | Nakajima & Ikeda 2017     | Also actions                     |
| <b>Squid:</b>      | <i>Loligo vulgaris</i>        | Hanlon et al. 1999        | -----                            |
|                    | <i>Sepioteuthis sepioidea</i> | Moynihan & Rodaniche 1982 | Subjective                       |
|                    | <i>Sepioteuthis australis</i> | Jantzen & Havenhand 2003  | Sexual displays                  |
|                    | <i>Alloteuthis subulata</i>   | Cornwell et al. 2009      | -----                            |
|                    | <i>Loligo forbesi</i>         | Portiero et al. 2009      | -----                            |
|                    | <i>Octopoteuthis deletron</i> | Bush et al. 2009          | Deep water                       |
|                    | <i>Doryteuthis plei</i>       | Postuma & Gasalla 2015    | -----                            |
|                    | <i>Dosidicus gigas</i>        | Trueblood et al. 2015     | Deep water                       |
|                    | <i>Sepioteuthis sepioidea</i> | Mather 2016               | Sexual, quantified               |

**Cephalopod Communication, Fig. 1** Catalogues of the display repertoire of cephalopods

respond with disruptive patterns to fragments of edges, even as little as a quarter of a circle, as they were to complete figures, and appeared able to complete edges fragmented by gaps, an operation also present in humans and used in the Gestalt approach to visual pattern analysis. Researchers checked aspects of background matching, including that cuttlefish used simple luminance contrasts, reinforcing that they could not perceive

color. Camouflage was assisted by position of the arms, as cuttlefish lined up with vertical orientation of arms to match vertical stripes on a wall behind them.

Both background and skin patterns are more complex than the assessment of simple low-level features and the production of three simple skin patterns. Principal components analyses (PCA) of the 42 chromatic, textural, and postural

components separated these smaller units into combinations (Darmaillacq et al. 2014) and gave a more sophisticated test of matching. Additionally, cuttlefish were tested with local versus global luminance changes, where patches of “objects” with high internal contrast were placed on a uniform background, resulting in more disruptive components of displays, suggesting perceptual grouping. Even a few white elements on a dark background evoked a disruptive pattern, and only high-frequency information was necessary to stimulate the production of disruptive with white discs, whereas both high and low frequency were needed for black ones. The perceptual processing system was clearly much more sophisticated than the original three-pattern model suggested, though based on low-level component analyses. We know little about how feature integration and pattern production are carried on, though. Stimulation of the optic lobes of the brain produced whole skin patterns, not specific to particular regions of these lobes (Liu and Chiao 2017), suggesting that this is the location of such integration.

Ironically, few experiments have given cuttlefish choices of substrates on which to camouflage. *S. apama* giant cuttlefish actively chose substrates with a high variance in intensity when producing camouflage, while males producing agonistic display stripes chose simpler ones, presumably to more clearly convey a message rather than blend into the background. With several actual substrates, *S. officinalis* cuttlefish chose not by visual characteristics but by “looseness,” so that they could bury into the surface. Given substrates of different unit sizes, juvenile cuttlefish chose small ones (Mather 1986); they would camouflage on larger stones but bury into smaller-grained sand. If the first choice of response to substrate is burial, it is astonishing that the sensitivity and repertoire size of the response of visual cue matching are so sophisticated. No ethological observations of *S. officinalis* in its natural environment have been conducted, so the ecological reasons for these abilities and choices have not been traced.

Sophisticated analysis of visual information was also used in a different predator threat situation, when a predator had detected a cuttlefish.

Escalated threat brought a sequence of cephalopod responses (see Darmaillacq et al. 2014). Cuttlefish (Langridge 2009) responded with a dorsal surface eyespot deimatic display to a fish approach, and these spots could be expressed unilaterally. Cuttlefish deimatic responses consist of four components – light background, eye spots, black rings around the eyes, and black lines along the fins. These displays presumably startled a potential predator and inferred a large animal by the placement of the dark “eyes.” When approached by sea bass, cuttlefish commonly showed eye ring and spots, which appeared to disrupt the fish’s attack sequence (Staudinger et al. 2013), and then the cuttlefish fled. Cuttlefish learned the appropriate species to which to employ deimatic, as they did not show the display to crab or dogfish predators who use chemical rather than visual cues to locate prey. Similarly, they did not address large sea bass with a deimatic display, only juvenile ones (Langridge 2009). Large predators elicited a camouflage flamboyant display or flight and smaller ones the eyespot display, so assessment of the predator risk preceded choice of actions. This evaluation was partly due to visual assessment of stimulus characteristics (Cartron et al. 2013). A looming stimulus was projected onto one side of a container in four shapes: circle star, rectangle, lozenge, and fish. More and more intense deimatic responses were made to the star and the approaching-fish shapes than to the other three stimuli. In the natural environment, squid used different approach characteristics (size, speed, distance) to choose appropriate avoidance behavior from different fish species (Mather 2010).

Thus, the sophisticated analysis of visual stimuli is both domain general and flexible.

## Male Sexual Displays and Game Theory

In a totally different area of research, male squid displays have been evaluated in the context of game theory (Smith 1974) and sexual selection. In sexual encounters, male individuals “ought to” display their resource-holding potential in contests between one another, either tournaments

with physical contact or displays without it. Generally the resource-holding potential will be accurately displayed but not always, and winners of such contests gain access to resources, in this case a female – but again not always. Males can adopt alternate access strategies to females, either ontogenetically changing with maturity or quickly changing dependent on the particular rival. Researchers in this area have a tendency to use value-laden words, such as sneaker, owner, deception, and cheat for these strategies, as if there was a correct or more appropriate set of actions. Semelparous cuttlefish of the genus *Sepia* (see Hall and Hanlon 2002) and squid of the family Loliginidae (*Loligo*, *Doryteuthis*, and *Sepioteuthis*) tended to aggregate for reproduction during the end of their lifespan at specific sites where females laid eggs. Males were attracted to these “mops” of eggs and were stimulated by both chemical and visual cues from them. *S. sepioidea* did not aggregate but maintained long-duration groupings (Mather 2016), which may account for its more nuanced displays and interactions. Within these aggregations, animals carried on scramble competition, with considerable female choice and a variety of display and contest behaviors, and escalation that Schnell et al. (2015a)

described as mutual assessment strategies, while unfortunately disclosing little of the behaviors involved.

To gain a complete picture of the displays and other behaviors involved in sexual encounters, three components – ethogram of the display repertoire, male behaviors during contest escalation and within alternative strategies, and display repertoire of females – are necessary, and only Mather (2016) reports for all these areas. Monitoring of signals in other sensory modalities and knowledge of identity of individuals are also needed (see the next section), and a component might either not be present or just have been overlooked. Visual displays by males were a component of their agonistic interactions (Fig. 2), but every species observed except *S. sepioidea* escalated from displays to physical contact. Perhaps because they only used display contests, males of this species had spatial and intensity variation in the aggressive zebra, from minimal area of stripes on a pale brown background, aimed unilaterally to a rival (Mather 2016), to the escalating intense pale background, spread arms, and over-under position of the “formal” zebra contest. Adamo and Hanlon (1996) found that intensity of *S. officinalis* zebra displays varied spatially by

| Species                                   | Location    | Male-Male Display | Physical Fight | Consortship | Alternate Strategies | Female Choice |
|-------------------------------------------|-------------|-------------------|----------------|-------------|----------------------|---------------|
| <i>Sepia apama</i>                        | Field & Lab | Yes               | Yes            | Yes         | Yes                  | Yes           |
| <i>Sepia plangon</i>                      | Field       | Yes               | ---            | Yes         | Yes                  | ----          |
| <i>Sepia officinalis</i>                  | Field & lab | Yes               | Yes            | Yes         | ----                 | ----          |
| <i>Sepioteuthis australis</i>             | Field       | Yes               | Yes            | Yes         | Yes                  | Yes           |
| <i>Sepioteuthis sepioidea</i>             | Field       | Yes               | No             | Yes         | Minimal              | Yes           |
| <i>Loligo plei</i> ( <i>Doryteuthis</i> ) | Field & Lab | Yes               | Yes            | Yes         | Yes                  | ----          |
| <i>Loligo vulgaris</i>                    | Field       | Yes               | Yes            | Yes         | Yes                  | Yes           |
| <i>Loligo pealei</i>                      | Field       | Yes               | Yes            | Yes         | Yes                  | Yes           |

Cephalopod Communication, Fig. 2 Sexual strategies of some cuttlefish and squid

extension of the first lateral arm and also in intensity by the addition of a dark “face” component. They pointed out that the dark face is a signal of agonistic intensity and that, contrary to game theory, it appeared at the beginning of the contests. However, males attempted mating with any individual that did not display the zebra, so dark face might be a token of maleness that prevented mating attempts. The male fin base stripe of *S. sepioidea* was displayed both to females as a component of sexual displays and to males alone and might also be a sexual identifier (Mather 2016). All the known repertoires of sexual displays consist of many components, and the “meaning” of most of them has not yet been studied.

Despite this, the system has many similarities within the squid and also across to the cuttlefish (Fig. 2). Males competed and escalated these contests, and the winner was generally the larger individual (see Smith 1974). Males guarded females against rivals, though the consortship was as short as a few minutes and both males and females had multiple partnerships. In some cases, utilizing the polyphenism of the skin system, males used alternative strategies to gain matings. In several species, small males dashed in close to a female and mated with her even though a guarding male was present. In *Sepioteuthis sepioidea*, a smaller peripheral male sometimes gained a mating opportunity when a pair of large males was involved in a formal display contest, or repeatedly challenged a larger male so that he never gained the opportunity to pass a spermatophore to the consort female. Given the polyphenism of the skin system, smaller males sometimes adopted a display that was normally found in a female and gain access to a guarded female (Hall and Hanlon 2002). Sometimes the sexual pattern was expressed directionally. A male *S. sepioidea* sometimes displayed a sexual stripe pattern to the side of his consort female at the same time as showing an agonistic zebra to a rival male on the other side. Escalation of zebra pattern intensity might be the result of increase of motivation and hormonal modulation, as cuttlefish contest losers that were given an opportunity to mate with a female increased their subsequent

display intensity (Adamo and Hanlon 1996). But this choice of two different displays with contrasting motivational contexts to two receivers on either side must have cognitive capacity underpinnings.

Not as much attention has been paid to the communication of females within this system, but observers all noted that female choice controlled whether a spermatophore was accepted, and the female rejection rate could be as high as 70% of attempted matings (Hall and Hanlon 2002). Sperm deposition only occurred in *S. sepioidea* if females performed a parallel swim with males (Mather 2016). Female *S. apama* rejected males with a unilateral longitudinal white stripe display (Schnell et al. 2015b) and encouraged them with extended white arms (Hall and Hanlon 2002). Other components in the long list of display catalogues probably acted as modifiers in sexual interactions. Components of the diverse *S. sepioidea* display repertoire were suggested to be the equivalent of components of a human language. Despite the complexity of the displays of this species, the messages all appeared to be communication about the sender alone, and thus not an equivalent of language (Mather 2016). Still, there are many display components whose “meaning” has not been evaluated, and their role in communication needs to be worked out.

## Chemical Communication

As for many marine animals, cephalopods have acute chemical sensing from sensory receptor cells in several different areas – the suckers, the “lips” surrounding the mouth, and the “olfactory organ.” The olfactory organ of octopuses contains more than one receptor cell type (Polese et al. 2015), and it has been considered the location for distance chemoreception, and see Morse et al. (2017) for *Haplochlachena*, although result of testing for its function can be ambiguous. Nevertheless, cells in each olfactory organ are sensitive to several chemicals. However, not all chemical reception can be considered communication, as chemical cues are picked up about predators, prey, items in the environment such as

conspecifics' eggs, as well as conspecifics. A dictionary definition of a pheromone is a chemical that is released and subsequently causes a change in the behavior and/or physiology of conspecifics. Thus, sensory cues from eggs are not strictly pheromones, despite their designation as such, although they had a strong effect on agonistic behavior of males nearby. Testing for the effect of a water-borne chemical cue is difficult, and ideally both change in receiver behavior and physiological effect of specific chemicals on the olfactory epithelium would be carried out – but such a thorough assessment is rare for cephalopods. One general behavioral response, simplistic but probably important because of that, was arousal as judged by the ventilation rate of a stationary animal, first used systematically for different sources by Boal and Golden (1999) in cuttlefish. Ventilation rate must be used as a behavioral measure with caution because ventilation rate is a general response to stimuli as varied as food cues, a potential predator, a conspecific, and a cephalopod ink, even to water from a new source. In addition, any stimulation such as the movement to a test tank and/or introduction of a new water flow caused a change in the ventilation rate. Yet approach behavior such as a choice of arms in a Y maze might not have been an appropriate action after recognition of a chemical cue from a conspecific and was not always observed. Such an approach to the source of stimulation might be more appropriate to chemical cues from a potential food source, and chemical cues from conspecifics' ink discharge triggered escape behavior. With these caveats and a lack of general information about identity of chemicals and appropriate behaviors, there are two different areas where chemical communication has been shown to be important for cephalopods (Fig. 3).

Earlier accounts of the reproductive behavior of cuttlefish emphasized vision. Boal (2006) felt that while visual displays were important for male-female competition and courtship, female choice might be also linked to chemical signals. Females given a choice of two males to approach did not choose the larger, and they preferred males who had given fewer visual zebra displays, even after observing these agonistic interactions. They

did prefer males who had more recently mated, which made her wonder if chemical cues were involved in attraction. Ventilation rate of juvenile males increased significantly to water that had housed conspecifics, though also to many other stimuli. However, testing in a Y maze did not result in choice of the arm which had water from the tank of a conspecific. Perhaps this cautious behavior was necessary because cephalopods are cannibalistic (Ibanez and Keyl 2010), and approaching for mating could place a male in danger from his partner. Nevertheless, some octopuses were attracted to water-borne cues about conspecifics and chose an arm of the Y maze with chemical cues from them. Such approach behavior also varied across the sexes, given that male *S. officinalis* attempted to mate with any mature conspecific that did not return their zebra display. A well-controlled study of *Hapalochlaena* octopuses found that females increased ventilation rate to water with male odor, but males showed no difference in response to any chemical (Morse et al. 2017). Many more studies with closely controlled conditions are needed to sort out the stimuli and responses.

Responses to ink from a conspecific have been more consistent, even though ink is not normally thought of as a communicative stimulus. Many cephalopods released ink at predator approach, either diffusely to shield the animals from the predator's view or with mucus to make a distracting "pseudomorph" imitation of the self. Inking was accompanied by clear body appearance and escape jetting (York and Bartol 2016), another use of polyphenism. The chemicals in the ink also affected the behavior of the receiver. Derby et al. (2007) tested the aversive characteristics of the ink of nine mollusk species, three *Aplysia* sea hares and six cephalopods. All contained high levels of free amino acids which might have caused sensory disruption, and ammonium, matching the receiver sensitivity of fish and crustaceans. Ink was both a visual and a chemical defense, delaying predation but also affecting ingestion by the fish and essentially communicating unpalatability. At the same time it caused a ventilation increase and an escape response. Thus, a substance which was likely



| Species               | Sense    | Source of stimuli  | Test type                      | Result                        | Authors           |
|-----------------------|----------|--------------------|--------------------------------|-------------------------------|-------------------|
| <b>Cuttlefish:</b>    |          |                    |                                |                               |                   |
| <i>S. officinalis</i> | Chemical | Females-> males    | Approach                       | mated males                   | Boal              |
| <i>S. officinalis</i> | Chemical | Females-> males    | Y-maze                         | No orientation                | Boal & Marsh      |
| <i>S. officinalis</i> | Chemical | Many               | Ventilation                    | Increase all                  | Boal & Golden     |
| <i>S. officinalis</i> | Chemical | Eggs not behavior  | Identified                     | Yes                           | Enault            |
| <b>Octopuses:</b>     |          |                    |                                |                               |                   |
| <i>O. bimac</i>       | Chemical | Prey consp eggs    | Ventilation<br>Y maze          | Increase all<br>No food       | Walderon          |
| <i>O. maya</i>        | Chemical | Prey               | Y-maze                         | Approach                      | Lee               |
| <i>O. bocki</i>       | Chemical | Ink & turtle       | Attack                         | Ceased                        | Caldwell          |
| <i>Eledone</i>        | Chemical | Prey               | Ventilation                    | Increase                      | Boyle             |
| <i>Hapalochlaena</i>  | Chemical | Conspecifics       | Ventilation                    | F more to M                   | Morse             |
| <b>Squid:</b>         |          |                    |                                |                               |                   |
| <i>Loligo</i>         | Chemical | Eggs               | Aggression                     | Male increase                 | Buresch           |
| <i>Loligo</i>         | Chemical | Chemicals          | Na blocker<br>K blocker<br>Ink | No effect<br>Effect<br>Effect | Gilly<br>& Lucero |
| <i>Sepioteuthis</i>   | Chemical | Ink -> conspecific | Alarm cue                      | Escape                        | Wood              |
| <i>Doryteuthis</i>    | Chemical | Ink -> fish        | Deterrent                      | Pred stops                    | Derby             |

**Cephalopod Communication, Fig. 3** Distance chemical sensitivity of cephalopods

primarily aversive to predators secondarily became an interspecific alarm cue.

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## Cephalopod Diet

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## Introduction

Throughout their lives, cephalopods are ravenous predators (Budelmann 1996). Within just a few days of hatching, cephalopods begin actively seeking food and are able to successfully capture prey (Villanueva et al. 2017). Most cephalopods are generalist feeders, with the majority of cephalopod diet made up of crustaceans, fish, and molluscs (Budelmann 1996). The predatory lifestyle of cephalopods has led to the development of advanced sensory systems used in the detection of prey (Budelmann 1996; Villanueva et al. 2017), as well as a repertoire of hunting (Hanlon and Messenger 1996) and feeding behaviors (Hanlon and Messenger 1996; Mather and Scheel 2014; Villanueva et al. 2017) that have been recorded in both natural and laboratory settings. The following text will review the nutritional requirements and prey preferences of cephalopods, the sensory systems used for detecting prey, modes of hunting, and feeding behaviors utilized by

cephalopods. Gaps of knowledge will be addressed with suggestions for directions of future research.

## Nutritional Requirements and Prey Preferences

Yolk reserves are crucial for the survival of cephalopods during the first few days after hatching, fueling metabolism while hatchlings' prey-capture skills develop (Vidal et al. 2002). However, the energy contained in the yolk is rapidly depleted and hatchlings must quickly capture enough food to meet their metabolic requirements (Vidal et al. 2002). Large protein and amino acid contents are necessary for maintaining growth and fulfilling energy demands, especially in fast growing, shallow water cephalopod species (Navarro et al. 2014; Villanueva et al. 2017). Lipids and long-chain polyunsaturated fatty acids (PUFA) also play an important role in the cephalopod diet due to their inability to synthesize these nutrients (Monroig et al. 2013; Navarro et al. 2014). The elemental composition of cephalopods' natural diet suggests that copper, a key element in the respiratory function of haemocyanin (a protein which transports oxygen in the bodies of some invertebrates), is essential to many cephalopod species (Navarro et al. 2014). Sulfur is essential for the common octopus (*Octopus vulgaris*) and cuttlefish (*Sepia officinalis*) to sustain formation of muscular proteins, vestigial shell, and chitinized structures such as beaks (Navarro et al. 2014). Additionally, strontium is crucial for statolith development and, subsequently, for normal swimming and survival of newly hatched cephalopods (Navarro et al. 2014).

All cephalopods are carnivorous, and many species of cephalopod exhibit a preference for live prey, with an exception being the deep-sea species vampire squid (*Vampyroteuthis infernalis*), which feeds mainly on detritus (Villanueva et al. 2017). Crustaceans are present in nearly all cephalopod diets, allowing for the nutritional requirements outlined above (i.e., lipids and copper) to be met (Mather and Scheel 2014; Villanueva et al. 2017). In addition to crustaceans, cephalopods prey on

shrimp, fish, mollusks (including bivalves and gastropods), polychaetes, echinoderms, and hydroids (Mather and Scheel 2014; Olmos-Pérez et al. 2017). Larger cephalopod species, such as the giant Pacific octopus (*Enteroctopus dofleini*) and the Brazilian reef octopus (*Octopus insularis*) will also occasionally feed on marine birds (Anderson and Shimek 2014) and the jumbo squid (*Dosidicus gigas*) has been found to prey on skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*; Olson et al. 2006). Cannibalism is common in most cephalopod species and is influenced by a number of factors including stress, population density, food availability, environmental variations, body size, and sexual dimorphism (Ibáñez and Keyl 2010).

Studies conducted on feeding behavior in cephalopods have suggested prey recognition and preferences may be both innate and/or learned depending on the species. For example, Portela et al. (2014) found that, despite being exposed to visual and chemical stimuli from shrimp 48 h before and after hatching, or being fed only shrimp 16 days after hatching, early Mexican four-eyed octopus (*Octopus maya*) still preferred crabs when given the option between crab and shrimp. However, Darmaillacq et al. (2006, 2008) found that the common cuttlefish's (*Sepia officinalis*) innate preference for shrimplike prey could be changed to a preference for crabs by visually exposing new common cuttlefish hatchlings or embryos during late stage embryonic development to crabs. This preference change was dependent on the length of time and number of crabs that were exposed (Darmaillacq et al. 2006). Both innate and learned preferences have their benefits. Innate prey preferences may aid in reducing the time spent searching for and testing alternative prey and in decreasing the risk of mistaking a deadly predator as prey (Robin et al. 2014). Being able to learn the visual characteristics of prey during late stage embryonic development and immediately after hatching allows for preferences of prey abundant in the immediate area (Robin et al. 2014). This may aid in the transition from yolk utilization to active predation, a period in which hatchlings are at risk of starvation (Robin et al. 2014).

## Detecting Prey

Cephalopods have complex sensory systems, considered the most sophisticated out of all invertebrates and comparable to the equivalent vertebrate systems (Budelman 1996). These sensory systems are used in a wide range of behaviors, including predation. Arguably, the most important sensory system for predation in cephalopods is the visual system. With the exception of *Nautilus*, cephalopods have highly developed eyes and are extremely visual animals (Cosmo and Polese 2017). Cephalopods are sensitive to polarized light, which enhances their ability to detect and recognize prey (Villanueva et al. 2017). For instance, Shashar et al. (1998) found that squid hatchlings attacked planktonic prey at a 70% greater distance under polarized illumination as opposed to depolarized illumination. Polarization vision has also been shown to aid cuttlefish in prey detection in murky waters (Carton et al. 2013).

Chemoreception also plays an important role in prey detection in cephalopods. Most coleoids (i.e., octopus, squid, and cuttlefish) are nocturnal, or live at depths where little light is present, making the ability to detect prey through chemoreception vital to their success as predators (Budelman 1996). Cephalopods use either contact (taste) or distant (smell) chemoreception to detect chemical cues (Cosmo and Polese 2017). The organs used in distant chemoreception are the rhinophores of *Nautilus*, which are located right below the eyes, and the olfactory organs of coleoids, located below and posterior to the eyes (Budelman 1996). Behavioral evidence for distant chemoreception shows that a blinded octopus will move in the direction of a scent that it perceives as a food source (Chase and Wells 1986). Additionally, cuttlefish with previous exposure to crab odor exhibit more sophisticated predation techniques on their first attacks on crab than cuttlefish that had not been previously exposed (Boal et al. 2000). The receptors used in contact chemoreception are located on the distal region of the long digital tentacles of *Nautilus* and in the lips and suckers of coleoids (Budelman 1996). In octopuses, there is an estimated 10,000 chemoreceptors per sucker, totaling 16 million cells per animal

(Budelman 1996). In cuttlefish, only 100 chemoreceptors are present in each sucker (Budelman 1996). This difference may be due to the fact that octopuses often search for food in areas they cannot see, using their arms and suckers, whereas cuttlefish and squid do not (Budelman 1996). Behavioral evidence for contact chemoreception has shown that nautiloids are still able to detect odor when one or both rhinophores are blocked but are unable to orient towards the odor source (Basil et al. 2000) and the response of blinded *octopus vulgaris* to sardine blood is unaltered by the removal of their olfactory organs (Wells and Wells 1956).

Along with vision and chemoreception, cephalopods are equipped with a lateral line system. The lateral line system consists of epidermal hair cells arranged in lines located on the head and arms and is sensitive to water movement (Budelman 1996). This sensitivity allows cephalopods to detect prey in darkness or in murky waters. Behavioral physiological studies lend support to this. For example, Budelman et al. (1991) found that after surgical destruction of 75% of the epidermal lines, the hunting success of cuttlefish in complete darkness diminished to 30% of that of intact cuttlefish. Budelman (1996) has also reported that a cuttlefish that is partially buried is able to detect a moving fish 1 m in size from about 30 m away using the lateral line system.

## Predatory Strategies

Various modes of hunting are used by cephalopods dependent on the species, though hunting strategies can be flexible and there may be an overlap of techniques employed (Hanlon and Messenger 1996). One common hunting strategy is ambushing. Many species of octopus will lie and wait for prey to pass by before attacking. For example, the Atlantic pygmy octopus (*Octopus joubini*) has been seen hiding in empty bivalve shells waiting for prey to pass before reaching out and grabbing them (Hanlon 1983) and the common octopus (*Octopus vulgaris*) has been shown to hide behind stones before attacking passing crabs (Hanlon and Messenger 1996). Squid also

ambush predators. Species of bobtail squid, such as *Sepiola affinis* and *Euprymna scolopes*, hide in the substrate, striking at passing prey (Hanlon and Messenger 1996) and the longfin inshore squid (*Doryteuthis pealeii*) will lie in the sand, camouflaged, and strike at fish passing by (Hanlon and Messenger 1996).

Along with ambushing prey, cephalopods may use a lure, enticing prey close enough to capture. Though there is no conclusive example of cephalopods luring prey, it is speculated that cuttlefish (*Sepia*) and reef squid (*Sepioteuthis*) do so (Hanlon and Messenger 1996). Prior to attacking shrimp, the common cuttlefish and the broadclub cuttlefish (*Sepia latimanus*) often darken and raise their first, and sometimes second, pair of arms, waving them from side to side (Hanlon and Messenger 1996). Reef squid exhibit similar behavior but may also lighten the tips of their tentacles and hold them in a curved position (Hanlon and Messenger 1996). Though it is thought that these behaviors are used to lure prey, it is also possible that these behaviors serve to direct the prey's attention away from the tentacles that will be used in the capture of the prey (Hanlon and Messenger 1996).

Cephalopods have also been known to stalk and pursue prey while hunting. Stalking involves a slow approach to prey before a final, sudden, attack (Hanlon and Messenger 1996). Cephalopods reserve stalking for large, fast prey and utilize different modes of hunting for smaller, slower prey (Hanlon and Messenger 1996). Caribbean reef squid (*Sepioteuthis sepioidea*) stalk fish and shrimp and the northern shortfin squid (*Illex illecebrosus*) often stalk trout (Hanlon and Messenger 1996). Stalking behavior has not been reported in octopuses (Hanlon and Messenger 1996). Pursuit occurs when prey has recognized a predator and flees (Hanlon and Messenger 1996). Two kinds of pursuit are recognized in cephalopods: guided pursuit and ballistic attack (Hanlon and Messenger 1996). During guided pursuit, the predator uses visual feedback to change its pursuit path according to the position of the prey, such as when shortfin squid (*Illex*) pursue trout (Hanlon and Messenger 1996). During ballistic attack, predators establish the

position of prey and propels itself at it on the assumption that the prey will not move (Hanlon and Messenger 1996). Ballistic attack is used by octopuses to catch crabs (Maldonado 1964) and by cuttlefish to catch prawns (Messenger 1968). Pursuit may also involve interception of a prey's flight path (Hanlon and Messenger 1996). Though this behavior has not been demonstrated reliably by cephalopods, it is possible that cuttlefish anticipate the flight path of fish by attacking from the front (Messenger 1968). Cuttlefish will also continue to pursue prey that has moved out of sight, a behavior that has not been reported in any other cephalopods (Hanlon and Messenger 1996).

Although octopuses have an acute sense of vision and are able to make visual attacks on prey, they often engage in speculative hunting (Hanlon and Messenger 1996). During speculative hunting, octopuses will pounce with their web expanded and then feel around under their web for food (Yarnall 1969). This behavior has been observed in many species of octopus, including the Caribbean reef octopus (*Octopus briareus*; Hochberg and Couch 1971), the big blue octopus (*Octopus cyanea*; Yarnall 1969), the common octopus (*Octopus vulgaris*; Mather 1991), and the giant Pacific octopus (*Enteroctopus dofleini*; Hartwick 1983). Octopuses, such as the common octopus, the white-spotted octopus (*Octopus macropus*), and the big blue octopus, may also extend their arms into crevices likely to contain prey in search of food (Hanlon and Messenger 1996). A form of speculative hunting, where sand is pushed around with the arms to uncover buried shrimp, has also been observed in Caribbean reef squid (*Sepioteuthis sepioidea*; Hanlon and messenger 1996).

Lastly, cephalopods may disguise themselves while hunting by making locomotor, postural, textural, and chromatic adjustments (Hanlon and Messenger 1996). For instance, the caribbean reef squid may disguise itself as sargassum weed while it hunts, hiding in the clumps of sargassum before striking at prey (Hanlon and Messenger 1996). The Caribbean reef squid has also been observed swimming backwards while displaying two false eye spots so that it looks like a herbivorous parrotfish (Hanlon and Messenger 1996). In



doing so, the Caribbean reef squid is able to swim amidst and prey upon small reef fish (Hanlon and Messenger 1996). It is speculated that the elaborate body patterns shown by blue-ringed octopuses (*Hapalochlaena*) in association with algae could also be a form of hunting in disguise (Hanlon and Messenger 1996).

## Feeding Behavior

Once prey has been captured, cephalopods must ingest it. Some cephalopods secrete toxins from their posterior salivary glands (Hanlon and Messenger 1996). These toxins are used to immobilize prey while cephalopods prepare them for ingestion (Hanlon and Messenger 1996; Villanueva et al. 2017). Cuttlefish and squid often deliver these toxins via a bite, whereas delivery of toxins by octopuses, which feed mostly on crustaceans and bivalves, is associated with drilling through the shells of bivalves, and the carapace or eyes of crustaceans (Hanlon and Messenger 1996; Villanueva et al. 2017). The use of these toxins has been documented in coleiods, however not all coleiods produce toxins and the extent to which this occurs throughout cephalopods remains unclear (Hanlon and Messenger 1996).

Hard shells protecting bivalves, crustaceans, and other prey present a challenge to those cephalopods, looking to consume the soft tissue inside (Mather and Scheel 2014). Several methods are used by cephalopods to overcome this challenge. Octopuses may use their strength to pull open bivalve shells or, as mentioned earlier, may drill into shells or carapaces using their radula and salivary enzymes (Mather and Scheel 2014; Villanueva et al. 2017). Cephalopods may also chip prey with their beaks (Mather and Scheel 2014) and shell crushing has been reported in the deep-sea octopus *Graneledone* (Villanueva et al. 2017). Cephalopods likely use the most cost-effective behavior based on previous experience, however which behavior is used may also be influenced by a number of factors including cephalopod size and weight, prey size and weight, and beak size (Villanueva et al. 2017).

Due to having small mouths and a narrow esophagus, cephalopods are unable to swallow their prey whole (Hanlon & Messenger). Instead, cephalopods use a combination of their beak, radula (a toothed, tongue like structure), and salivary enzymes to break up their prey (Hanlon and Messenger 1996). Cephalopods show differences in digestion rates that are related to their habitat and lifestyle (Hanlon and Messenger 1996). Bottom dwelling cephalopods, such as *Sepia* and *Octopus* can take from 16–20 h to digest a meal, whereas cephalopods such as *Loligo* and *Ommastrephes*, which actively swim throughout the day and night, may take only 3–6 h to digest (Hanlon and Messenger 1996). There is evidence that some octopuses, such as *Eledone* and *Octopus*, begin digestion of crabs externally, secreting digestive enzymes into the carapace to destroy musculoskeletal attachments (Hanlon and Messenger 1996). No evidence has been found for external digestion in cuttlefish and there is very little evidence for external digestion in squids (Hanlon and Messenger 1996).

## Conclusion

Cephalopod species are diverse and exhibit a wide range of feeding behavior. All cephalopods are carnivores and many species require diets high in lipids and copper (Villanueva, et al. 2017). Most cephalopod species are generalist feeders, preying on a wide variety of animals, from shrimp, mollusks, and crustaceans, to birds and tuna (Anderson and Shimek 2014; Budelmann 1996; Olson et al. 2006). Cannibalism is also common among cephalopods (Ibáñez and Keyl 2010). In general, octopuses have a propensity for feeding on crabs and bivalves, cuttlefish tend to feed mainly on shrimp-like crustaceans and fish, and squid feed on fish, crustaceans, and other cephalopods (Hanlon and Messenger 1996). However, what an individual cephalopod eats at any given time is often a compromise between preference and availability (Hanlon and Messenger 1996).

Cephalopods are equipped with an arsenal of adaptations for detecting, pursuing, and capturing



prey. Cephalopods have advanced nervous systems and use a combination of photo-, chemo-, and mechanoreceptors to acquire information about potential prey (Villanueva et al. 2017). The hunting strategies used by cephalopods varies within and between species and include ambushing, luring, stalking, pursuit, speculative hunting, and hunting in disguise (Hanlon and Messenger 1996). Once prey is captured, some cephalopods inject toxins into their prey to immobilize it (Hanlon and Messenger 1996; Villanueva et al. 2017). How widespread this behavior is throughout cephalopods is unknown and further research, especially in squids, is needed (Hanlon and Messenger 1996).

Cephalopods that prey upon bivalves and crustaceans must first get through hard outer shells in order to feed on the soft tissue inside (Mather and Scheel 2014). Several methods are employed by cephalopods to overcome this obstacle including pulling shells apart (Mather and Scheel 2014), drilling into shells and carapaces (Mather and Scheel 2014; Villanueva et al. 2017), chipping shells with their beaks (Mather and Scheel 2014), and crushing shells (Villanueva et al. 2017). Research on feeding behaviors, and on cephalopod diet in general, has focused on coastal cephalopod species due to their accessibility in the field and their ability to be housed and maintained in laboratory conditions (Villanueva et al. 2017). Conversely, further research on deep sea cephalopods is necessary, as little is known about their feeding strategies and behaviors (Villanueva et al. 2017).

## Cross-References

### ► Cephalopod Morphology

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## Cephalopod Life History

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### Introduction

The life span of cephalopods varies depending on the species. Most cephalopods live only 1–2 years (Mather and Scheel 2014). The smallest

cephalopods live only a few months (e.g., 3 months for the pygmy squid, *Idiosepius notoides*) while the largest cephalopods can live up to 5 years (e.g., the giant Pacific octopus, *Enteroctopus dofleini*; Mather and Scheel 2014). Cephalopod life span is correlated with size and water temperature, with those species that mature at larger sizes and residing in colder water having longer life spans (Anderson et al. 2002; Mather and Scheel 2014). However, there is a stronger relationship with water temperature than with size (Mather and Scheel 2014). Regardless, all cephalopods “live fast and die young” (Anderson et al. 2002). They hatch from eggs, may go through a paralarval phase, grow quickly, mature, and mate (Anderson et al. 2002). Females of some species brood eggs, and many species experience a senescent state before dying (Anderson et al. 2002). The following text will review the physiological, morphological, and behavioral changes that occur during each phase of the cephalopod life cycle.

### Egg to Paralarvae

The transition from egg to paralarvae is a critical phase within the early life history of cephalopods (Robin et al. 2014). This phase begins at hatching (Robin et al. 2014). The oceanographic environment surrounding eggs affects embryonic development and hatching success (Robin et al. 2014). Cephalopod embryos are vulnerable to thermal fluctuations (Robin et al. 2014). Embryos that experience temperatures outside the optimal thermal range may result in abnormal embryonic development, premature hatching, and mortality (Oosthuizen et al. 2002). Salinity, more so than temperature, has also been shown to affect hatching rate, egg size, and hatching time in cephalopods, with low salinity levels having severe effects on embryonic development and survival (Chung 2003). Hatching conditions in cephalopods are flexible in order to optimize survival posthatching (Boletzky 2003). Hatching periods vary greatly depending on species, ranging from 2 days in *Octopus laqueus* to 78 days in the giant Pacific octopus (*Enteroctopus dofleini*; Robin et al. 2014). Mechanical stimulation of eggs, such as agitation by brooding females, has been

suggested to promote hatching in benthic (i.e., living on the seafloor) octopods under both wild and laboratory conditions (Villanueva and Norman 2008). Environmental factors can also trigger hatching (Robin et al. 2014). For instance, light has been proposed to regulate the hatching process, with most hatching events occurring at night (Villanueva and Norman 2008). Tidal and lunar rhythms are also associated with the onset of hatching (Villanueva and Norman 2008).

Upon hatching, many species of octopus, and some species of cuttlefish and squid, have yet to develop into their adult form and lifestyle (Mather and Scheel 2014). These hatchlings are referred to as paralarvae (Young and Harman 1988). Paralarvae are planktonic (i.e., free-floating among the plankton in open waters; Mather 2006) and exhibit morphological differences from adults (Robin et al. 2014). In many cephalopods, the shape and features of the beak of paralarvae differ from those of adults (Robin et al. 2014). Along with the size of the beak being smaller in paralarvae, many species of octopods, such as the common octopus (*Octopus vulgaris*), the Atlantic pygmy octopus (*Octopus joubini*), the curled octopus (*Eledone cirrhosa*), the paper nautilus (*Argonauta argo*), and the common blanket octopus (*Tremoctopus violaceus*) have a row of teeth on the upper and lower portions of the beak (Robin et al. 2014). The common European squid (*Loligo vulgaris*) and the longfin inshore squid (*Doryteuthis pealeii*) also have toothed beaks, however teeth are only on the lower portion of the beak (Boletzky 1971). Arm and tentacle morphologies may also differ between paralarvae and adults. The paralarvae of the family of squid ommastrephidae have a proboscis that separates into two tentacles as individuals grow and reach adulthood (Robin et al. 2014). Additionally, in cephalopod families such as Onychoteuthidae, Enoploteuthidae, Pyroteuthidae, Ancistrocheiridae, Octopoteuthidae, Gonatidae, and Cranchiidae, some suction rings develop into chitinous hooks which aid in the capture of prey (Engeser and Clarke 1988).

Along with morphological differences, paralarvae exhibit behavioral differences from adults. Paralarvae of all cephalopod species are solitary and social behaviors do not present until later

stages in life (Robin et al. 2014). Most of the behavioral differences are related to feeding, such as prey size and preferences, and predatory behaviors (Robin et al. 2014). For example, newly hatched opalescent inshore squid (*Doryteuthis opalescens*) exhibit a singular basic attack, in which the arms and tentacles are spread apart and thrust forward (Chen et al. 1996). Forty days post-hatching, this basic attack is replaced with arm net and tentacular strike behaviors (Chen et al. 1996). The paralarval stage ends when individuals begin capturing prey and settle into their adult lifestyle (Robin et al. 2014). Many species of cuttlefish, along with deep sea octopus species and some squid species, do not have a paralarval phase (Boletzky and Villanueva 2014; Robin et al. 2014). Upon hatching, these species immediately adopt a benthic lifestyle and begin capturing size-appropriate prey (Mather and Scheel 2014).

## Nonreproductive Adulthood

Depending on whether or not a paralarval phase exists, the juvenile phase of the cephalopod life cycle starts at either the end of the paralarval phase or at hatching (Boletzky and Villanueva 2014). Cephalopod juveniles are often referred to as subadults. A subadult is an individual who appears to be functionally and morphologically similar to an adult but is not yet reproductively mature (Young and Harman 1988). During this time, most cephalopod species are solitary and asocial (Hanlon and Messenger 1996). With that, behavior during this phase is less concerned with members of the same species and more concerned with predatory pressures and finding and consuming prey (Mather 2006). For instance, visual displays during this stage of life are primarily used for camouflage and predator evasion (Hanlon and Messenger 1996). For the few social species of cephalopods, schooling behavior presents in this stage of life. For instance, schooling behavior in the European squid (*Loligo vulgaris*), opalescent inshore squid, longfin inshore squid, and Argentine shortfin squid (*Illex argentinus*) presents between 20 and 60 days after hatching (Vidal et al. 2010).

Minor morphological changes take place during this stage of life. In benthic octopuses with a

paralarval stage, the change from paralarvae to subadult occurs at settlement (Robin et al. 2014). The changes associated with the adoption of a benthic lifestyle include positive allometric arm growth; chromatophore, iridophore, and leucophore growth; the loss of K  lliker organs that cover the surface of the body; and the loss of the lateral line system (Villanueva and Norman 2008). Those cephalopods with toothed beaks during their paralarval stage lose their teeth upon entering the subadult phase (Boletzky and Villanueva 2014). This phase is also marked by sexual differentiation, during which male and female organs grow (Boletzky and Villanueva 2014). Males of most coleoid cephalopods develop a specialization of one or more arm tips, known as a hectocotylus, which is used to transfer spermatozoa to females (Robin et al. 2014). However, not all cephalopods develop a hectocotylus. *Nautilus* spp. develop a large erectile mass known as a spadix (Arnold 1987), and cirrate octopods have no specialization for spermatophore transfer (Mangold 1987). Males of some cephalopod species, such as the big blue octopus (*Octopus cyanea*) and the southern dumpling squid (*Euprymna tasmanica*), develop secondary sexual characteristics, such as extra-large suckers on the second and third arms (Robin et al. 2014). These suckers may be used for displaying to members of the same species (Packard 1961), and/or in chemoreception (Voight 1991). Females of some cephalopod species, such as *Argonauta*, develop specialized dorsal arms which secrete a calcareous (i.e., containing calcium) chamber used for brooding eggs (Robin et al. 2014). Additionally, females of the species *Leachia pacifica* develop brachial photophores that are used to attract mates (Young 1975). Cephalopods transition from subadults to adults with the attainment of sexual maturity (Robin et al. 2014). In coastal cephalopods, sexual maturation is reached in about a year (Mather and Scheel 2014).

## Reproductive Adulthood

Upon reaching sexual maturity, cephalopod behaviors shift from growth related to those

related to reproduction (Mather 2006). Many cephalopods, including octopus and cuttlefish, migrate to specific areas, where they mate and lay eggs (Mather 2006; Robin et al. 2014). The nature and magnitude of migration varies among cephalopod species (Robin et al. 2014). Cephalopods may migrate between inshore and offshore habitats, as is the case with the Patagonian squid (*Loligo gahi*; Arkhipkin et al. 2004); move in and out of current systems, such as the northern shortfin squid (*Illex illecebrosus*; Dawe et al. 2000) and the Japanese flying squid (*Todarodes pacificus*; Sugimoto and Tameishi 1992); or have significant inshore movements, for example the southern calamari (*Sepioteuthis australis*; Pecl et al. 2006). Some open-water cephalopod species, such as *L. pacifica*, *Eledonella pygmaea*, and the clawed armhook squid (*Gonatus onyx*), undergo vertical migrations from near-surface waters to waters at depths of 1,000 m or more (Robin et al. 2014). Regardless of the type or extent of migration, it appears this behavior is associated with increased chances of finding a mate, along with finding a suitable place for egg attachment or release (Robin et al. 2014).

The first indication of sexual behavior in cephalopods is a shift from using visual displays for concealment and predator evasion to courtship and reproductive behavior (Mather 2006). Males of species such as the southern calamari (Jantzen and Havenhand 2003) and the Cape Hope squid (*Loligo reynaudii*; Hanlon et al. 1994) exhibit multiple, complex, chromatic, postural, and locomotor patterns while courting females. Common cuttlefish (*Sepia officinalis*; Boal 1997) and Caribbean reef squid (*Sepioteuthis sepioidea*; Mather 2006) males present an agonistic, striped body pattern, known as the intense zebra display, to other males while courting females. Caribbean reef squid also produce the sexual Saddle (pale mantle with brown ring) and a pre-mating on-off flicker to mature females (Mather 2006). Subadults are also capable of producing these displays, but often produce the displays out of normal sequence or to individuals of the wrong sex (Mather 2006). Aside from visual displays, other complex courting behaviors can be seen in cephalopods.

Some cuttlefish species, including the giant cuttlefish (*Sepia apama*), use a mating strategy known as female mimicry, in which smaller males switch between the appearance of a female and that of a male in order to foil mate-guarding attempts of larger, dominant males (Robin et al. 2014). Additionally, male mourning cuttlefish (*Sepia plangon*) will deceive rival males by displaying male courtship patterns to potential mates on one side of their mantle, while simultaneously displaying female patterns to the rival male on the other, thus preventing the rival from disrupting courtship (Brown et al. 2012). However, not all cephalopods exhibit such elaborate courtship behaviors. Most octopods display little or no courtship behaviors before mating.

Direct female mate choice occurs in cuttlefish (Robin et al. 2014). However, the traits and ornamentations selected for by females are not well defined (Robin et al. 2014). Boal (1997) found that female common cuttlefish show consistent preferences for the most recently mated males and those showing fewer zebra displays, as opposed to males whose characteristics correlated to male dominance (e.g., body patterning and size). Boal (1997) suggested that olfactory cues, as opposed to visual cues, are used by female cuttlefish for assessing males to mate with. Female giant cuttlefish have also been observed actively rejecting mating attempts (Robin et al. 2014). No clear female mate choice has been observed in octopuses (Robin et al. 2014). Females of many cephalopod species, including loliginid squid and cuttlefish, may mate with and store spermatophores from multiple males (Robin et al. 2014; Mather and Scheel 2014). Once sperm is stored, females may actively influence which sperm is used to fertilize their eggs, leading to multiple paternity within egg strings (Mather and Scheel 2014).

Once a mate has been chosen, copulation occurs, during which the male inserts his hectocotylus into the female's mantle cavity and deposits his sperm, where it is stored until the female is ready to fertilize her eggs (Mather and Scheel 2014). Females release eggs from their oviduct, fertilize each one using stored sperm, and encases them in a protective layer (Robin et al. 2014). Cuttlefish often deposit their eggs

on supports, such as in crevices among corals (Mather and Scheel 2014). Squid deposit large egg masses on or under bottom substrate, such as in sand or under rocks (Mather and Scheel 2014). The majority of cuttlefish and squid species do not provide parental care to their offspring, though brooding behavior has been seen in the Gonatidae and Bathyteuthida squid families (Mather and Scheel 2014; Robin et al. 2014). Most species of octopus deposit their eggs by cementing them inside the roof of their dens (Mather and Scheel 2014). Those species of octopus that do not reside in dens or shelters, such as the brown striped octopus (*Octopus burryi*) and the wonderpus octopus (*Wunderpus photo-genicus*), carry their developing eggs in the web of their arms (Robin et al. 2014). Octopuses then exhibit egg-brooding behaviors, such as manipulating each egg strand and blowing jets of water across them to clean and oxygenate them (Mather and Scheel 2014). Female octopuses will continue to brood their eggs until hatching or until they die (Mather and Scheel 2014).

## Senescence

Senescence is a stage in the cephalopod's life cycle that often occurs shortly after mating and before death (Anderson et al. 2002). Upon reaching sexual maturity, cephalopods' digestive glands cease to function properly, and they slow their feeding or stop eating entirely (Anderson et al. 2002; Mather 2006). It has been postulated that starvation is what ultimately leads to the cephalopod's death during this stage (Anderson et al. 2002). As cephalopods begin to lose weight, their bodies shrink, causing the skin around their eyes to retract (Anderson et al. 2002). White lesions may appear on the skin of senescent cephalopods (Anderson et al. 2002; Mather 2006). These skin lesions can easily become infected due to healing processes being shut down during senescence (Anderson et al. 2002). The brain tissue in senescent cephalopods deteriorates, resulting in undirected and uncoordinated activity (Anderson et al. 2002) and the attenuation of behavioral sequences (Mather 2006). Chichery and Chichery (1992) found that cuttlefish first



underestimated the distance of prey, resulting in undershooting with their tentacles, then detected but failed to pursue prey, and finally stopped orienting towards prey completely during a 2 week period of decline during senescence. Additionally, 2 year old cuttlefish were slower to learn an avoidance task, had less retention of the task, and were more variable in their learning than 1 year old cuttlefish. An examination of the nervous system showed axon degeneration in the senescent cuttlefishes' brains, especially in the motor centers of the peduncle area and basal lobes (Chichery and Chichery 1992). There was also degenerating fibers in the tracts leading to and from the vertical lobe (Chichery and Chichery 1992). The degeneration of these motor output areas correlates well with the decline in response to prey found in cuttlefish (Mather 2006). In an experiment to evaluate hormonal control over senescence, Wodinsky (1977) removed the optic gland in brooding, female Caribbean two spotted octopus (*Octopus filusus*). He found that those females with their optic gland removed stopped brooding, began to eat again, and lived longer than females that still had their optic gland. This experiment has yet to be performed with male octopuses.

## Cross-References

- [Cephalopod Diet](#)
- [Cephalopod Morphology](#)

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## Introduction

With approximately 700 species, cephalopods exhibit a wide range of forms (Budelmann 1994). However, all these forms have a similar, molluscan body plan, with a head, a foot, and a visceral mass covered by a mantle (Hanlon and Messenger 1996). The cephalopod head is markedly developed, with the largest brain of any invertebrate and sophisticated sense organs (Hanlon and Messenger 1996). The cephalopod foot has developed into a funnel, as well as eight arms found in all coleoids (i.e., octopus, squid, and cuttlefish) and tentacles found in decapods (i.e., cuttlefish and squid) and *Nautilus* (Hanlon and Messenger 1996). The mantle forms a sheltered space around the viscera (which includes circulatory, digestive, excretory, and reproductive systems), known as the mantle cavity (Hanlon and Messenger 1996). The mantle cavity contains the gills (2 in coleoids and 4 in *Nautilus*) and is where the gut, kidneys, and gonads open into (Hanlon and Messenger 1996). In most mollusks, the mantle also secretes a protective shell (Hanlon and Messenger 1996). However, among living cephalopods the shell has been internalized (such as in decapods) or lost completely (such as in octopods; Hanlon and Messenger 1996). Only *Nautilus* has retained an external, chambered shell which is used for protection and buoyancy (Hanlon and Messenger 1996). The following text will review the morphology of cephalopods and address gaps of knowledge.

## Cephalopod Morphology

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### Definition

**Morphology** The branch of biology that deals with the form of living organisms, and relationships between their structures.

## The Nervous System

The cephalopod nervous system is the most complex of any invertebrate (Budelmann 1995) and can be divided into three parts (Hochner 2004). The first part is the central brain (Hochner 2004). In coleoids, the central brain contains 40–45 million nerve cells and surrounds the esophagus (Hanlon and Messenger 1996; Hochner 2004). The central part of the brain can be divided into sub-, peri-, and supraesophageal areas, which can be broken down further into 25 major lobes (Budelmann 1995). A few of these lobes are

further subdivided, giving a total number of 37 lobes in octopods (i.e., octopus) and 38 lobes in decapods (i.e., cuttlefish and squid; Young 1971). These lobes vary in size from species to species and most do not have an individual, exact function (Budelmann 1994). In general, the subesophageal lobes are lower motor centers and the peri- and supraesophageal lobes are intermediate and higher motor centers, as well as associative centers for learning and memory (Budelmann 1994). The *Nautilus* brain is simpler than coleoid brains (Budelmann 1995). It is made up of a system of three ganglionated nerve cords: a supraesophageal cerebral cord, and an anterior and posterior subesophageal cord, which are subdivided into 12 lobes (Budelmann 1995). The *Nautilus* brain lacks the structures for intricate motor control of the arms (Budelmann 1995). Additionally, the centers dedicated to learning and memory in the coleoid brain, and the giant fiber system in decapod brains, are absent in *Nautilus* (Budelmann 1995; Hanlon and Messenger 1996).

The other two parts of the nervous system, the optic lobes and the peripheral nervous system, are located outside the brain and are autonomous systems (Hochner 2004). The optic lobes are lateral to the central brain (Hanlon and Messenger 1996) and contain between 120 and 180 million nerve cells (Hochner 2004). The size of the optic lobes varies from species to species and is correlated to the size and complexity of the eyes (Budelmann 1996). Generally, the optic lobes are smaller in octopods than in decapods (Budelmann 1996). The optic lobes analyze visual input and regulate visual behavior (Budelmann 1995). They also store visual memory (Hanlon and Messenger 1996) and are the centers for visual discrimination learning (Budelmann 1995). The peripheral nervous system is distributed along the arms and contains 350 million nerve cells (Budelmann 1995). It is made up of five brachial nerve cords, with each nerve cord having one large axial cord, four smaller, peripheral, intramuscular cords, and as many brachial ganglia as suckers (Budelmann 1995). Each sucker also has its own sucker ganglion (Budelmann 1995). Many of the neurons in

the peripheral nervous system are lower motor neurons that control the muscles of the suckers (Budelmann 1995). The peripheral nervous system also processes sensory information gathered by several million sensory cells in the skin and suckers of each arm (Hochner 2004).

## Sense Organs

### Mechanoreceptors

Cephalopods are sensitive to tactile stimuli over the entirety of their body (Hanlon and Messenger 1996). Several types of mechanoreceptors have been described in the rim of the suckers in octopods and decapods (Graziadei 1971). The tactile information gathered by the suckers travels to the highest centers of the brain for learning (Hanlon and Messenger 1996). It has been shown that *Octopus* can readily learn to discriminate objects with different textures (Wells 1961). However, *Octopus* cannot be trained to discriminate between objects with equally irregular surfaces, differing only in the allocation of irregularities, or between objects with the same texture but different shape using only tactile information (Wells 1961). This is because *Octopus* lack awareness of the position of their suckers in space (i.e., proprioceptive information), which is likely due to the arms lacking joints and being extremely flexible (Wells and Wells 1957). Along with the mechanoreceptors in the suckers, decapods and octopod hatchlings have rows of epidermal hair cells on their head and arms that can detect local water movement (Budelmann et al. 1991). These rows of hairs are known as the lateral line system (Budelmann et al. 1991). Behavioral data indicate that the lateral line system is used in prey detection (Budelmann et al. 1991), allowing decapods to detect a fish 1 m in length from a distance of 30 m (Budelmann 1994, 1996). It is likely that the lateral line system is also used in predator detection and avoidance and schooling behavior, but this remains to be seen (Budelmann 1994).

Cephalopods also have a specialized set of mechanoreceptors known as statocysts (Budelmann 1994). Statocysts are a set of organs located in the cartilage below the brain, that gather

information used in equilibrium control, similar to the vestibular system in vertebrates (Budelmann 1994). *Nautilus* statocysts are simple, oval-shaped cavities, lined with hair cells and are used as a gravity receptor system (Budelmann 1994). Statocysts in octopods and decapods contain two receptor systems (Hanlon and Messenger 1996). The macula–statolith–statoconia system gathers information about the direction of gravity and linear acceleration (Hanlon and Messenger 1996) and regulates countershading reflexes (Hanlon and Messenger 1996). The crista-cupula system gathers information about angular acceleration (Budelmann 1994). The information gathered by both receptor systems is used to govern the orientation of the head, eyes, funnel, and body (Hanlon and Messenger 1996). Surgical destruction of both statocysts causes cephalopods to spiral and zigzag in all three planes as they swim (Boycott 1960). The statocysts also provide the brain with information on infrasound (i.e., low-frequency vibration; Hanlon and Messenger 1996). Whether or not cephalopods can actually “hear” has been of much debate. Attempts made by Hubbard (1960) to train octopuses to respond to frequencies of 100 Hz, 900 Hz, and 2,000 Hz were unsuccessful. However, Packard et al. (1990) trained *Sepia*, *Loligo*, and *Octopus* to associate sound stimuli between 1 Hz and 100 Hz with a small electrical shock, with the most sensitive part of the frequency range being below 10 Hz. Packard et al. (1990) suggest that cephalopods can sense low-frequency sound using particle motion detection via the statocysts rather than sound pressure. Whether this can be considered hearing is a problem of definition (Hanlon and Messenger 1996). If using a narrow definition, cephalopods cannot hear, as they lack air-filled cavities and the associated sensory structures that can be compressed by the pressure wave of underwater sound (Budelmann 1994).

### Chemoreceptors

Cephalopods can detect chemical signals using two chemoreceptor systems: a chemotactile sense and distant chemoreception (Budelmann 1996). The receptors involved in contact chemoreception are in the distal region of the long digital

tentacles of *Nautilus* (Budelmann 1996) and in the buccal lips, mouth, and suckers of octopods and decapods (Graziadei 1964). There are about 10,000 chemoreceptors in each sucker in octopods, totaling 16 million receptors per animal (Graziadei 1964). In contrast, cuttlefish have only 100 chemoreceptors per sucker (Graziadei 1964). This difference may be because octopods, but not decapods, use their arms and suckers to look for food in out-of-sight habitats (Budelmann 1994, 1996). The ability of the common octopus (*Octopus vulgaris*) to “taste by touch” was investigated by Wells (1963), who found that octopus can distinguish between porous objects soaked in plain seawater and seawater with hydrochloric acid, sucrose, or quinine sulfate added by touch. Further, they were able to detect these substances in concentrations 10–1,000 times lower than the human tongue can (Wells 1963). Additionally, Wells and Wells (1956) found that the responses of blind octopuses to sardine blood were unaltered by the removal of the olfactory organs.

The organs involved in distant chemoreception are the rhinophores in *Nautilus* and the olfactory organs in octopods and decapods (Budelmann 1996). Rhinophores are elongated, sac-like structures lined with two types of ciliated cells and are located below the eye (Budelmann 1996). The rhinophores allow *Nautilus* to detect and follow odor trails to their source in three dimensions (Basil et al. 2000). If the rhinophores are blocked, either uni- or bilaterally, *Nautilus* is still able to detect odor using its tentacles but is not able to guide orientation behavior toward the odor source (Basil et al. 2000). Like rhinophores, the olfactory organs in octopods and decapods are located below and behind the eye, and contain five types of ciliated cells (Budelmann 1996). Behavioral studies have demonstrated the importance of distant chemoreception in varying aspect of cephalopod ecology. For instance, distant chemoreception is an important aspect in prey detection (Hanlon and Shashar 2003) and conspecific odor perception (Hanlon and Shashar 2003; Walderson et al. 2011). Distant chemoreception also plays a role in the reproductive behavior of some cephalopods. Female chambered nautilus (*Nautilus*

*pompilius*) are attracted to the odor of males and extend their tentacles fully when tracking male odors (Basil et al. 2002), while sexually mature males are attracted to females by excretions of the rectum (Westermann and Beurlein 2005). It has been suggested that chemical signals intercepted by the olfactory organs and integrated in the olfactory lobes could initiate the shift from growth-related behaviors to those related to reproduction in the common octopus (Polese et al. 2015), but this has yet to be tested.

### Photoreceptors

Cephalopods are known for their well-developed eyes and complex visual behavior (Budelman 1994, 1996). In *Nautilus*, the eyes lack a lens and function similarly to pinhole cameras (Budelman 1994). However, the eyes of most cephalopods resemble those of vertebrates (Hanlon and Messenger 1996). However, the retina is much simpler in cephalopod eyes, with only two neural components and no separation into rods and cones (Budelman 1994; Hanlon and Messenger 1996). The eyes of cephalopods contain only one visual pigment, suggesting that cephalopods lack color vision (Hanlon and Messenger 1996). The single exception being the firefly squid (*Watasenia scintillans*), whose eyes contain at least three visual pigments (Matsui et al. 1988) indicating the firefly squid may have color vision (Hanlon and Messenger 1996; Matsui et al. 1988). Though unable to see color, cephalopods can see the plane of polarized light (Budelman 1994).

Cephalopods also have photoreceptors other than the eyes (Hanlon and Messenger 1996). Photoreceptor organs have been described on the head of hatchling squid and cuttlefish and photosensitive vesicles (PSV) are present in coleoids (Hanlon and Messenger 1996). The PSV are especially well developed in mid- and deep-water cephalopods (Young 1977). Though their function is not well understood, Young (1977) posited that the PSV may monitor the downwelling light to regulate the light mid- and deep-sea cephalopods emit from their own photophores. It has also been suggested that the PSV could be involved in diel vertical migration of some cephalopods (Hanlon and Messenger 1996).

## Effectors

### Muscles

Effectors are organs of the body that carry out the response an animal makes to a stimulus (Hanlon and Messenger 1996). The most common effectors are muscles (Hanlon and Messenger 1996). When looking at behavior, cephalopods have seven main muscle groups that form six major structures: the fins, mantle, funnel, head and eyes, arms and tentacles (see next section), and the skin (see section “Skin”; Hanlon and Messenger 1996). Fins are present in all decapods, in *Vampyroteuthis*, and in cirrate octopods and are used to help the animal swim (Hanlon and Messenger 1996). The shape and size of cephalopod fins differ depending on the way the animal moves (Hanlon and Messenger 1996). Benthic cephalopods may also use their fins to help bury and conceal themselves in the sand (Hanlon and Messenger 1996). The muscles of the mantle play an important role in jet propulsion and respiration (Hanlon and Messenger 1996). The main function of the funnel is to steer cephalopods (Hanlon and Messenger 1996). However, the funnel also aids in burying benthic cephalopods, can be used to jet water at prey or predators, and is used by female octopuses to aerate and clean their eggs (Hanlon and Messenger 1996). Head movement is also important in steering, whereas eye movements are important for localizing predators and prey (Hanlon and Messenger 1996).

### Arms and Tentacles

All coleoids have eight arms that extend from the head (Hanlon and Messenger 1996). Coleoids use their arms for handling prey, manipulation of objects, locomotion, and reproduction (Kier 2016). Octopods also use their arms for grooming, burying, defense, chemosensing, and tactile sensing (Kier 2016). Decapods have two additional appendages, termed tentacles, which are specialized for prey capture (Hanlon and Messenger 1996; Kier 2016). Octopod arms undergo significant, active elongation and shortening, are capable of intricate and diverse bending and curling movements, and can control stiffness (Kier 2016). Unlike octopod arms, decapod arms do not

undergo significant length change (Kier 2016). However, decapod tentacles are capable of rapid elongation (Kier 2016). The arms and tentacles are lined with complex organs known as suckers (Hanlon and Messenger 1996). Sucker morphology and innervation differs between octopods and decapods (Hanlon and Messenger 1996). The musculature of the suckers allows for strong adhesion and the small ganglion below each sucker coordinates motor and sensory information (Graziadei 1971).

*Nautilus* spp. have 90 thin tentacles, which are considerably different from those of coleoids (Hanlon and Messenger 1996). The tentacles are organized into three groups: a pair of postocular and preocular tentacles, a variable number of labial tentacles surrounding the buccal mass, and 19 pairs of digital tentacles that surround and extend beyond the labial tentacles (Kier 1987). The tentacles are composed of an extendable cirrus enclosed in a protective sheath (Kier 1987). The cirri of the ocular tentacles are thought to be sensory, with the preocular tentacles being chemosensory and the cirri of the postocular tentacles likely containing mechanoreceptors, though their actual function is unknown (Hanlon and Messenger 1996; Kier 1987). The digital tentacles are used to capture and manipulate prey and to attach to surfaces (Kier 1987). The cirrus of both the ocular and digital tentacles have fine, circular grooves and secrete a glycoprotein that make the tentacles adhesive (Hanlon and Messenger 1996). The labial tentacles are mainly used in reproductive behavior (Hanlon and Messenger 1996; Kier 1987). Some of the labial tentacles are modified to form sexual organs, such as the male spadix which is used to transfer spermatophores during copulation (Hanlon and Messenger 1996).

### Skin

The skin of cephalopods contains multiple effectors that enable cephalopods to have remarkable camouflage abilities. Among these effectors are two musculature systems: the skin papillae and chromatophores (Hanlon and Messenger 1996). Skin papillae, which are found in octopods and some decapod species, allow for changes

in skin texture (Hanlon and Messenger 1996). Chromatophores are complex organs consisting of a sacculus containing pigment granules, surrounded by 15–25 radial muscles (Hanlon and Messenger 1996). The pigments contained in the sacculus include red, orange, yellow, brown, and black (Hanlon and Messenger 1996). Chromatophores can be expanded or contracted, creating patterns on the skin (Hanlon and Messenger 1996). The number and density of chromatophores vary between species; however, cephalopods with more intricate patterning repertoires have higher densities of chromatophores, and *Nautilus* spp. have no chromatophores (Hanlon and Messenger 1996).

The skin also contains reflecting cells and photophores (Hanlon and Messenger 1996). There are at least three different reflecting cells found in the dermis, around the eyes and ink sac, and in the photophores (Cloney and Brocco 1983). Iridophores are responsible for the blue and green coloration in cephalopods, though they may also reflect pinks, yellows, and silvers (Cloney and Brocco 1983). Reflector cells, which are known only in octopods, also reflect blues and greens (Cloney and Brocco 1983). Leucophores are broad-band reflectors that provide the “white spots” found in some cephalopod species (Cloney and Brocco 1983). Though they look white under white light, leucophores will appear blue in blue light and yellow in yellow light (Hanlon and Messenger 1996). The ability of the leucophores to reflect the predominant wavelength in the environment is important for achieving color resemblance to the background when camouflaged (Hanlon and Messenger 1996). Photophores are light organs that can produce a steady glow or occasional flashes of light (Hanlon and Messenger 1996). Photophores are used in ventral counter-illumination and signaling, though little is known about how they are controlled (Hanlon and Messenger 1996).

### Buccal Mass

The buccal mass is in the center of the arms and is comprised of the beak, the radula, and the salivary papilla and glands (Hanlon and Messenger 1996). Cephalopod beaks are chitinous and contain



strong musculature (Hanlon and Messenger 1996). Beaks vary significantly among cephalopods and features of the lower beak are different enough to allow taxonomic identification at the generic and/or species level (Clarke 1986). The radula is a toothed ribbon that carries food toward the esophagus and is used by some octopods to drill through mollusk shells and the exoskeletons of crustaceans (Hanlon and Messenger 1996). The salivary papilla, which lies just below the radula, is also used for drilling. It is muscular, and its anterior face is covered with small teeth (Nixon 2009). It also carries the duct from the posterior salivary gland, whose secretions, when delivered to the drilling site, aid in breaking down mollusk shells and the exoskeletons of crustaceans (Hanlon and Messenger 1996). What exactly these substances are is not yet known (Hanlon and Messenger 1996).

### Ink Sac

The ink sac contains the ink gland and a reservoir with sphincters (Hanlon and Messenger 1996). Cephalopods can produce thick clouds of ink that are used as smoke-screens or as pseudomorphs (small mucus-bound blobs that act as decoys) against predators (Hanlon and Messenger 1996). The ink may also act as an alarm substance for other nearby cephalopods (Hanlon and Messenger 1996). Cephalopods that live at great depths, such as *Vampyroteuthis*, cirrate octopods, and some deep-water genera of the family Octopodidae, as well as *Nautilus*, do not have ink sacs (Hanlon and Messenger 1996).

### Cross-References

- Cephalopod Diet
- Cephalopod Life History

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## Cephalopod Sensory Systems

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### Introduction

Cephalopods, the group of invertebrates that contain the octopus, squid, cuttlefish, and *Nautilus*, exhibit wide diversity in form and habitat. The smallest cephalopod is a mere 1.5 cm (*Idiosepius*), with the largest reaching up to 18 m (*Architeuthis*). They inhabit nearly every part of the ocean, from shallow waters to the deep sea

(Hanlon and Messenger 1996). As such, cephalopods require a variety of means for sensing predators, detecting prey, and finding mates. One of the greatest advantages that the cephalopods have in navigating their environment is the ability to utilize multiple sensory modalities to access their surroundings. The most prevalent sensory systems in cephalopods include (1) photoreception with well-developed camera eyes; (2) mechanoreceptors that respond to water movements, pressure, and touch; and (3) chemoreception through olfaction and chemotactile sense (Budelman 1996). Through the acquisition of a variety of sensory information, cephalopods have thrived and proliferated for millions of years, making them one of the most successful animals in the ocean.

### Photoreception

With few exceptions, the eyes are the most prominent sensory features of cephalopods (Budelman 1996), with the optic lobes being the most dominant region of the brain (Young 1962). Resembling the vertebrate eye, the cephalopod eye incorporates a large posterior chamber, lens, iris, retina, choroid, sclera, and argenta (Budelman 1994). However, there are several key differences between the cephalopod and vertebrate eye anatomy. Cephalopods have a rhabdomeric structure of the retina in which there are no rods or cones, as found in other mollusks and arthropods (Mäthger et al. 2009). The visual image also falls directly on the photoreceptor cells without interneurons, as found in the retina of vertebrates (Budelman 1994). The photoreceptors contain only one visual pigment peaking in spectral sensitivity around 480–500 nm. One exception is the firefly squid, *Watasenia scintillans*, which has been found to have no fewer than three pigments (Budelman 1996; Hanlon and Messenger 1996). By having only one visual pigment, cephalopods are technically rendered color-blind, which has been supported through behavioral studies (Mäthger and Hanlon 2006). Recent studies, however, have used computer modeling to suggest that

even with a single photoreceptor, cephalopods can achieve color discrimination through the principle of chromatic aberration, whereby different wavelengths come to focus at different distances behind the lens (Stubbs and Stubbs 2016). Unlike the eyes of most teleost fish, cephalopods have motile pupils that respond to changes in illumination, and the time required for pupil closure is far less than in most other animals. The common cuttlefish (*Sepia officinalis*) and brief squid (*Lolliguncula brevis*) require only 0.32 s and 0.49 s, respectively, to attain half maximal constriction, while the fastest teleost fish response is 0.75 s (Douglas et al. 2005). Cephalopods have laterally placed eyes and consequently see their environment monocularly. As the eyes are utilized individually, the pupils of squid, cuttlefish, and octopus respond independently to light (Douglas et al. 2005). The highly evolved visual system of cephalopods likely plays a large role in predator detection and successful escape (York and Bartol 2016).

## Mechanoreception

In addition to their complex visual system, cephalopods can detect disturbances from small water movements using mechanoreceptors on their head and arms (Bleckmann et al. 1991). Octopods, cuttlefishes, and squids have a receptor system equivalent to the lateral line system of fishes (Budelman and Bleckmann 1988). In the squid *Loligo vulgaris*, five epidermal lines are present on each side of the head running in an anterior-posterior direction (Budelman and Bleckmann 1988).

The cephalopod lateral line system is not as well described as the fish lateral line, but consists of polarized epidermal hair cells that have several kinocilia and an axon extending from their base (Budelman and Bleckmann 1988). Polarization occurs in a precise pattern (anteriorly, posteriorly, left, and right), allowing the animals to respond to water movements as low as 18.8  $\mu\text{m/s}$ , which is equivalent to the sensitivity of fish lateral lines (Douglas et al. 2005). It has been shown that the lateral line plays a role in predator detection and

successful escape responses at the paralarval (hatchling) stages, as well as aiding visual cues in juvenile and adult squid (York and Bartol 2014; York et al. 2016).

In addition to the lateral line system, cephalopods are highly sensitive to touch. In the octopus, suckers on their arms pass on tactile information to the brain. Behavioral experiments have shown octopus discriminate between surface textures and shapes (Wells and Wells 1956). It has been suggested that the cephalopod brain differentiates textures through the proportion of mechanoreceptors stimulated through the suckers (Wells and Wells 1956). The capability of the octopus to learn tactile information appears to be associated with two lobes in their brain, the inferior frontal and subfrontal lobes. Interestingly, these lobes are not present in the cuttlefish or the squid (Hanlon and Messenger 1996).

As in vertebrate systems, the cephalopods have paired organs in the cartilage of the brain, called statocysts, that provide the necessary information about gravity and acceleration required for maintaining proper body orientation while swimming (Budelman 1994). Additionally, the statocysts are responsible for camouflaging the animal through behavior that incorporates the contraction of chromatophores on the ventral side of the animal, breaking up the outline of their body and making visual detection from below more difficult (Budelman 1996). When the statocysts are surgically removed, animals perform erratic swimming behaviors and cannot maintain proper swimming orientation (Budelman 1994). The decapods (squid and cuttlefish) and octopods have major differences within their statocyst systems. Both cephalopod groups have statocysts with a *macula-statolith-statoconia* system and a *crista-cupula* system, each relying on polarized hair cells to detect mechanical disturbance (Budelman 1994).

The macula system uses information of gravity and acceleration to regulate the orientation of the head, eyes, and body, as well as the countershading response. In the decapods, there are three maculae in each statocyst, while in octopus, only one is present, which is likely a reflection of the different ecologies of these groups (Hanlon and

Messenger 1996). The crista system provides information about rotational acceleration, which enables the animal to regulate the position of the head, funnel, and eyes (Budelmann et al. 1987). In decapods, four cristae sit at right angles to each other, allowing the cristae to be stimulated differentially when the animal rotates in the pitch, yaw, or roll axis. Octopods, alternatively, have nine cristae.

Additionally, there are differences in the organization of statocysts of different cephalopod species, which are seemingly correlated to locomotive lifestyle (Young 1984). For example, in the fast-swimming squid groups, the loliginids and ommastrephids, the statocysts form canals which slow down the movement of fluid over the hair cells, making them less sensitive and therefore better suited to measure the effects of rapid body movements. Alternatively, deep-sea neutrally buoyant squid, which move slowly and steadily, have statocysts in which the canals are not present (Hanlon and Messenger 1996).

The statocysts are also the most probable organ for sound detection in cephalopods (Budelmann 1990). While it has long been shown that cephalopods are sensitive to low-frequency vibrations (below 10 Hz) (Packard et al. 1990), newer studies suggest that squid and octopods might detect sound up to 1600 Hz (Hu et al. 2009). Mooney et al. (2010) used auditory evoked potentials with electrodes placed near the statocysts to measure physiological responses to both low- and high-frequency sound waves. Their results suggest that squid detect sound within the same range as most fish, with the statocyst acting as an accelerometer to allow squid to detect the particle motion component of a sound field (Mooney et al. 2010).

## Chemoreception

Cephalopod chemoreception also provides an important source of sensory information (Nilsson et al. 2012). Cephalopods are able to detect chemical cues in two ways: (1) through either contact, using receptors on their arms (Graziadei 1965), or (2) distant chemoreception

(Boyle 1983). In cephalopods, the known chemical sensory epithelia are buccal lips and mouth, isolated sensory neurons all over the body surface, arm suckers, and olfactory organs (Di Cosmo and Polese 2017). These sensory neurons appear to act as a sophisticated system that plays a vital role in navigating their environment (Boyle 1983; Gilly and Lucero 1992).

In the octopus, there are approximately 10,000 primary receptors on each sucker on the animal's arm. Given that an octopus has approximately 200 suckers on each arm, there are 16 million sensory cells per animal (Graziadei 1964). Research suggests that with these receptors, the octopus is capable of discriminating between substances at concentrations 10 to 1000 times lower than humans (Wells 1963; Wells et al. 1965). Behavioral studies indicate the use of distant chemoreception, where the addition of fish scent to water causes predatory movements in octopus (Wells 1963) and in cuttlefish (Messenger 1977). It is also possible that chemosensory cues are used in predator avoidance (Hanlon and Messenger 1996). Gilly and Lucero (1992) found that in restrained squid, L-DOPA and dopamine, which are chemicals found in squid ink, stimulated an escape response. These findings suggest that ink might be used as a conspecific warning in predator avoidance.

## Conclusions

Cephalopods are extremely mobile and fast moving predators, as well as highly sought after prey source, requiring an advanced and effective range of sensory modalities. Compared to their phylogenetic relatives, it is not surprising that cephalopods have the most sophisticated nervous and sense organs of all invertebrates (Packard 1972). While the sensory abilities differ by taxa and ecological niche, cephalopods have extremely versatile means of navigating their environment through combinations of mechanoreception, photoreception, and chemoreception, which have contributed to their success since the Cambrian era (Hanlon and Messenger 1996).

## Cross-References

- [Camouflage](#)
- [Cephalopod Communication](#)
- [Chemoreception](#)
- [Countershading](#)
- [Evolution of Animal Color Vision](#)
- [Mechanoreceptors](#)
- [Predator Detection](#)
- [Sensory Receptors](#)
- [Visual Perception](#)

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## Ceprano (A “Transitional” *Homo calvarium*)

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Ceprano is a human calvarium (calvarium, or *calvaria*, means a cranium without facial bones) that was occasionally found in several fragments in March 1994 near the homonymous town in southern Latium, Italy (Fig. 1). When discovered, a geo-stratigraphic approach was performed at the regional level and suggested an age of the layer of deposition close to 800–900 ka (Ascenzi et al. 1996, 2000). According to this date, in the mid-1990s, Ceprano contributed to the denial of the so-called short chronology for the earliest inhabitants of Europe (Manzi et al. 2001). In addition, the archaic features of the specimen were related to Mode 1 techno-complexes scattered in various sites across the Ceprano basin, albeit there are also

Acheulean assemblages in the same area (Ascenzi et al. 1996; Biddittu et al. 2020).

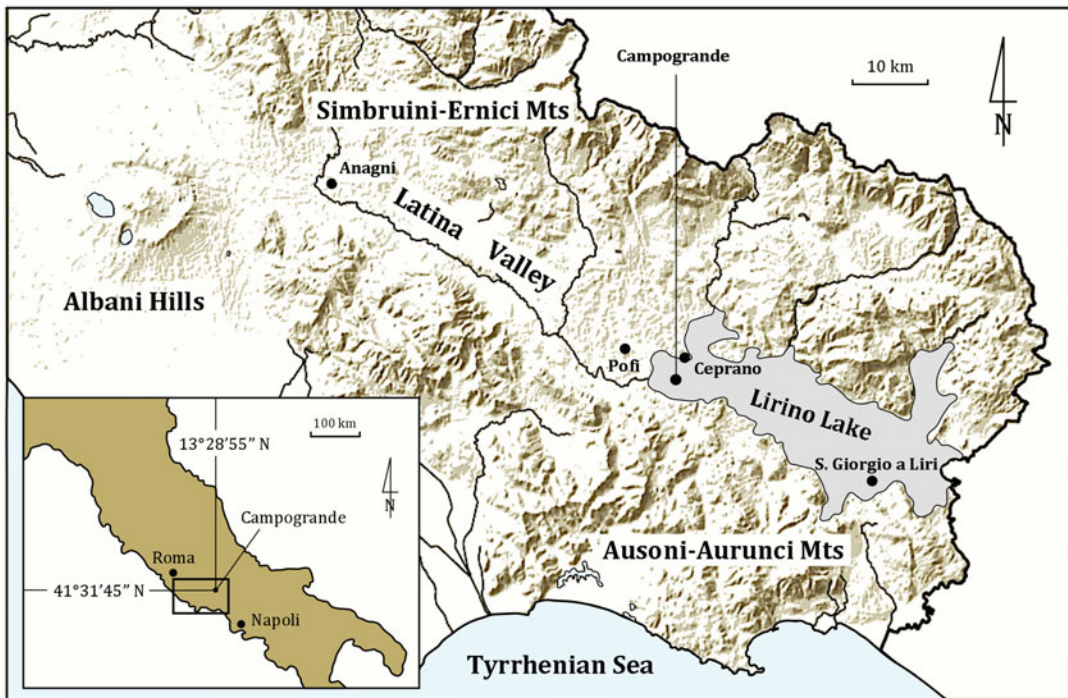
Starting from 2001, a project of field studies was developed for almost a decade, with the aim to validate the previous geo-chronological model and improve the available paleontological and archaeological records. In contrast to the expectations, the results of this multidisciplinary work consistently showed that Ceprano is more recent than previously believed, pointing to a time range close to the beginning of MIS 11, that is, between 430 and 385 ka (Manzi et al. 2010). It was also pointed out that the Ceprano hominin died in a floodplain environment with a low topographic gradient, where a fluvial meandering channel occurred after the retreat in extension of the ancient Lirino Lake (Manzi et al. 2010; Di Vincenzo et al. 2017; Biddittu et al. 2020).

The reconstruction of the human calvarium from dozens of fragments (Fig. 2) required the combined efforts of various experts and, overall, about 5 years (Ascenzi et al. 2000). After a first attempt described in 1996, a revised one was obtained in 1999, which has been then accurately re-evaluated, documented (including a microCT-scan recording), and published in various international journals (e.g., Manzi et al. 2001).

From a taxonomic point of view, Ceprano was originally considered to be a European representative of *Homo erectus* sensu lato (Ascenzi et al. 1996; Clarke 2000), whereas in more recent papers its affinities were reconsidered (Ascenzi et al. 2000; Manzi et al. 2001; Mounier et al. 2011), arguing that only less than two-thirds of its character states are consistent with those that are commonly observed in *Homo erectus* and/or in *Homo ergaster* – to such an extent that the variability of these taxa considerably increases when Ceprano is added – while other traits appear more derived.

For a proper phylogenetic interpretation of Ceprano, it is necessary to take into account that different sources of data consistently point out to the time window between 1.0 and 0.5 Ma for the emerging of a derived kind of *Homo* (i.e., distinct from *Homo ergaster/erectus*). This discontinuity most probably originated in Africa (Profico et al. 2016), from where these new humans started to spread across Eurasia, together with the





**Ceprano (A “Transitional” *Homo calvarium*), Fig. 1** Location of the site where the Ceprano calvarium was discovered in 1994, along the Latina Valley near the town of Ceprano, approximately 100 km southeast of

Rome; the gray area corresponds to the inferred maximum extension of the Lirino Lake during the Early/Middle Pleistocene (Biddittu et al. 2020)

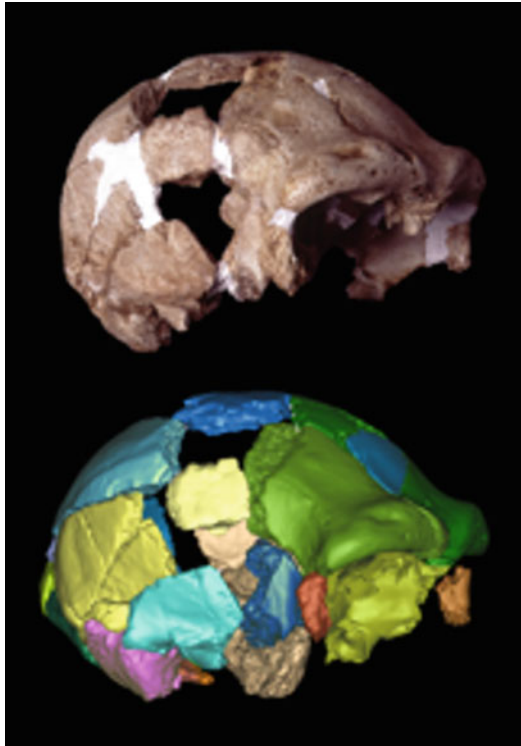
Acheulean techno-complexes they made (Biddittu et al. 2020). This humanity is referred by many authors to a polymorphic and widespread single species; priority rules confer to this *taxon* the name of *Homo heidelbergensis*. In addition, in view of the occurrence of different lineages that are recognized during the Middle Pleistocene as belonging to such a putative species, it has been suggested the identification of chrono-geographic varieties or subspecies (i.e., potential incipient species) of *Homo heidelbergensis* (Manzi 2016).

Given this scenario, although the broad architecture of the Ceprano calvarium is close to the general shape that is shared by fossils referred to *Homo erectus* (*sensu lato*), a number of discrete features may be viewed as derived, suggesting a connection with other humans of the Middle Pleistocene. Moreover, Ceprano does not display any Neanderthal trait, differently from a great part of the European samples of the Middle Pleistocene, whereas it shows affinities with penecontemporaneous African specimens (Manzi et al. 2001;

Bruner and Manzi 2007; Mounier et al. 2011). Therefore, its peculiar morphology exhibits a unique combination of archaic and derived features that suggests a puzzling scenario of human evolution in Europe, which involves the occurrence of a considerable phenetic diversity beforehand the evolution of *Homo neanderthalensis*, but concurrently with samples clearly belonging to the Neanderthal lineage (Manzi et al. 2001; Manzi 2016).

In this light, Ceprano documents the occurrence of an archaic variety of *Homo heidelbergensis*, whose cranial morphology was partially lost along the subsequent trajectory of human evolution in Europe. By contrast, this morphology was preserved elsewhere: namely, in Africa and in mainland Asia. Given this scenario, the hypothesis is that the Italian specimen was confined in an eco-geographical *refugium* and retained features of the ancestral stock of *Homo heidelbergensis*. This original morph, in turn, gave rise to the hominin variability observed during the Middle Pleistocene and was ancestral to modern humans





**Ceprano (A “Transitional” *Homo* calvarium), Fig. 2** The Ceprano calvarium (above) and its digital reconstruction (Di Vincenzo et al. 2017)

(*Homo sapiens*), in Africa, as well as to the Neanderthals (*Homo neanderthalensis*), in Europe, and the so-called Denisovans, in Northeastern Asia.

In conclusion, in view of the shape and morphological features displayed by Ceprano, it may be assumed that this specimen represents the best candidate available at present to describe the ancestral cranial morphology of the still largely unknown original variety of *Homo heidelbergensis* (Bruner and Manzi 2007; Mounier et al. 2011), which may be referred to as the stem chrono-subspecies of this taxon to be named *Homo heidelbergensis heidelbergensis* (Manzi 2016).

## Cross-References

- Evolution
- *Homo erectus*
- *Homo ergaster*
- *Homo heidelbergensis*
- *Homo sapiens*
- Paleontology

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## Cercopithecine

- Catarrhine Locomotion

## Cercopithecoid

### ► Catarrhine Locomotion

## Cerebellum

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## Synonyms

Little brain; Rhombencephalon (hindbrain) with-  
out brain stem

## Definition

The term cerebellum (Latin for a “small brain”) can be described as the miniature of the cerebrum. It is differentiated from the metencephalon during the fifth week of the fetal brain development (Ghosh et al. 2017; Kandel et al. 2000). It is the major subdivision of the hindbrain.

## Introduction

The cerebellum is a dorsally projecting region of the brain located at the base of the skull (Fig. 1). In an adult human being, the cerebellum weighs about 150 g and makes up to one-tenth of the total volume of the brain (Snell 2010).

It plays a major role as a unit of motor control for the body and contributes to its fine movement, precision, and time accuracy. The cerebellum is involved in some non-motor functions such as cognitive activities (language and attention) and in regulating pleasure and fear responses (Wolf et al. 2009). It is also associated with long-term synaptic depression (Purves et al. 2014) concerned with motor learning. It maintains the balance and posture of the body and coordinates movements (voluntary). Coordination of timing and forces of different muscle groups for body movement is one of the main cerebellar functions. It also aids in motor program adaptation and its fine-tuning for making accurate movements (Knierim 1997).

## Evolution

The cerebellar evolution is basically associated with the change in volume and surface folding (foliation) expansion across species. The initial role of the cerebellum was in motor control and is variously involved in a range of cognitive purposes including learning, memory, and language in humans (Hall et al. 2013). The presence of cerebellum-like structures in the non-vertebrates and cerebellum development in vertebrates suggests the existence of a common ancestor passed on as a homologous feature (a feature that is inherited from a common ancestor that also had the similar feature) (Bell et al. 2008).

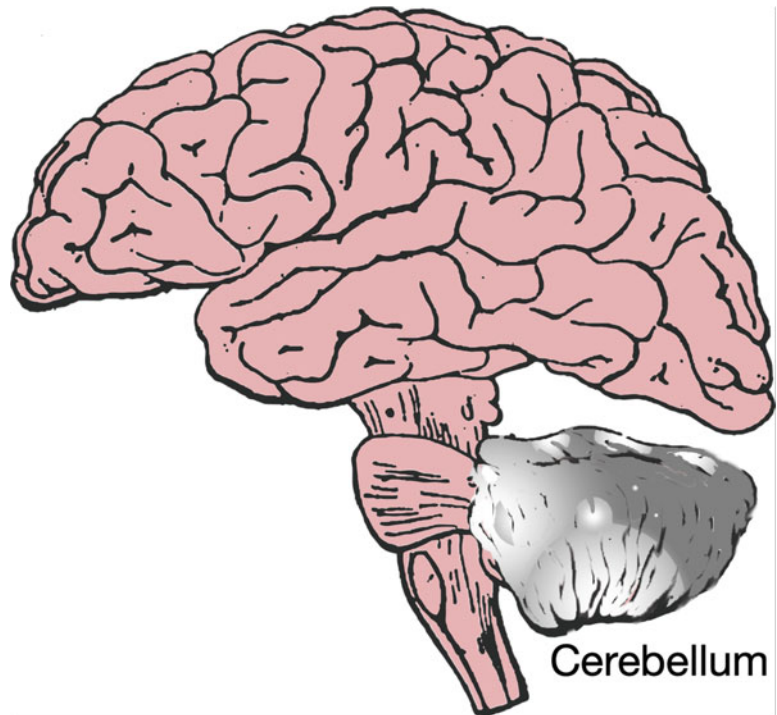
## Evolution in Invertebrates

The cerebellum-like structures are responsible for the sensory inputs in invertebrates. These structures are thought to have been evolved into cerebellum. These structures are sensory in nature and receive inputs from peripheral deep layer and molecular layer parallel fibers.

In primitive chordates such as Myxinoidea and lampreys, there is no cerebellum. Parts of cerebellum-like structures called medial octavolateral nucleus (MON), dorsal octavolateral nucleus (DON), and Purkinje cells are responsible for information processing. DON and Purkinje cells are not present in Myxinoidea (Bell et al. 2008).

**Cerebellum,**

**Fig. 1** Lateral view of the human brain showing location of cerebellum (in gray)

**Evolution in Vertebrates**

Evolution from invertebrates to vertebrates has shown an increase in the cerebellar surface folding which in turn shows an increase in its neural processing or circuit and allows greater processing qualities and motor functions. A set of spinocerebellar tracts are involved to bring input to the cerebellum on body position and movements in all vertebrates. Termination of spinal tract is seen in the vermis and immediate adjacent cortex.

In most lower vertebrates (anamnia, cyclostomata), all classes of fishes, and most amphibians in place of a cerebellum, there exists an individual sensory system known as the lateral line, which is responsible for all seismosensory and mechanical movements (Kasumyan 2003). In birds, a small trace of cerebellar hemisphere is observed. The remaining part of the cerebellum is covered with vermis (Sultan and Glickstein 2007).

**Evolution in Mammals**

Anatomically, in humans and the higher primates, there are large cerebellar hemispheres with

upward and medial extension and complex folding of the cortex. Due to the extension of the hemisphere, there is almost complete covering of the vermis.

Input to the cerebellum in most humans and other mammals comes from the cerebral cortex through a relay in the pontine nuclei. Presence of flocculus (an essential lobe of cerebellum involved in the vestibulo-ocular reflex) is seen, which is responsible for motor control in all mammals and also in receiving input from the vestibular system and senses that signal the body's position in space (Sultan and Glickstein 2007). Different parts of brain involved during evolution in different organism is shown in Table 1 (Bell et al. 2008).

**Comparison Between Cerebellum-Like Structure and Cerebellum**

Granule cells, Golgi cells, unipolar brush cells, parallel fibers, stellate cells, and spine-covered molecular layer dendrites of principal cells are common in both of these structures. The two

**Cerebellum, Table 1** Different parts of the brain involved during evolution in different organisms. (\*) denotes presence of the structure; (–) denotes absence

|               |                    | Cerebellum | Medial octavolateral nucleus | Dorsal octavolateral nucleus | Dorsal cochlear nucleus |
|---------------|--------------------|------------|------------------------------|------------------------------|-------------------------|
| Invertebrates | Myxinoidea         | –          | *                            | –                            | –                       |
| Vertebrates   | Lampreta           | –          | *                            | *                            | –                       |
|               | Chondrichthyes     | *          | *                            | *                            | –                       |
|               | Amphibia (Urodela) | *          | *                            | *                            | –                       |
|               | Reptilia           | *          | –                            | –                            | –                       |
|               | Aves               | *          | –                            | –                            | –                       |
|               | Mammalia           | *          | –                            | –                            | *                       |

inputs to cerebellum-like structures and the two inputs to cerebellar Purkinje cells present highlight the crucial similarity between them. Parallel fiber and peripheral input is received by the cerebellum-like structure while the parallel fiber input and climbing fiber input is received by the cerebellum through the Purkinje cells. One common characteristic between them is that the parallel fiber input conveys a variety of information to an entire principal cell set or to the Purkinje cells as the first input. Also as a second input, the peripheral input in cerebellum-like structure and the climbing fiber in the cerebellum relay specific information that subdivided the set of Purkinje cells that share the same parallel fiber input (Bell et al. 2008).

**Morphology**

The cerebellum consists of a massive white matter core covered by a cortical layer. The cerebellar nuclei buried in the white matter of the cerebellum receive their major input from the cerebellar cortex. Cerebellar output is then connected to structures in the thalamus and brain stem through the cells of the cerebellar nuclei. There are three lobes, an anterior lobe, a posterior lobe, and flocculonodular lobe, divided by two transverse fissures and small subdivisions in each lobe of the cortex called folia. Corpus cerebella, the main mass of the cerebellum, is formed by the anterior and posterior lobe together (Sultan and Glickstein 2007).

**Anatomy**

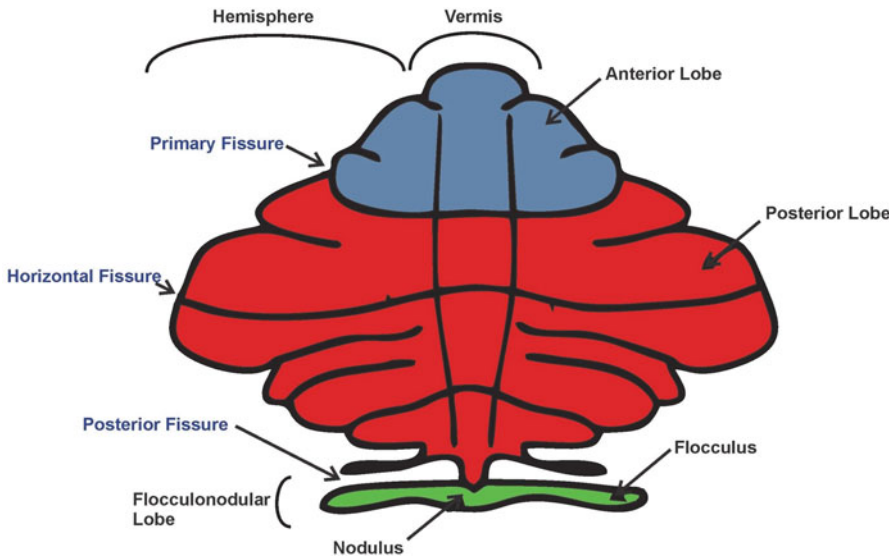
The cerebellum is located in the posterior cranial fossa behind pons and medulla. Tentorium cerebella (a layer of dura mater) separates the cerebellum

from pons and medulla. The fourth ventricle lies in between the cerebellum and the pons and medulla (Fig. 2). The cerebellum has an outer superficial layer in the gray matter known as the cerebellar cortex. This cortical region comprises a large number of parallel spaced grooves, which are predominantly composed of granule cells.

Beneath the cortical surface lies the white matter within which lie four deep cerebellar nuclei forming a tree-like structure called arbor vitae. Longitudinally, the cerebellum is divided into three parts, a vermis near the midline and two hemispheres surrounding the vermis from both sides. There are three peduncles in the cerebellum, which connects the cerebellum with the rest of the nervous system through several afferent and efferent fibers. The superior peduncle (brachium conjunctivum) connects to the cerebral cortex by carrying the efferent fibers to the upper motor neurons (UMNs). The middle peduncle (brachium pontis) receives inputs from pons relayed by the cerebral cortex. Inferior peduncle (restiform body) receives input from the spinal cord, vestibular nuclei, and the tegmentum. It also sends efferent fibers to the reticular formation and the vestibular nuclei.

**Division of Lobes in the Cerebellum**

The cerebellum is divided into three lobes by the two transverse fissures. The anterior lobe lies above the primary fissure and the posterior lobe just below it. The anterior and posterior lobe together forms the main mass of the cerebellum, also known as corpus cerebella. On the ventral surface, the flocculonodular lobe is separated by the rest of the cerebellum by the posterolateral fissure.



**Cerebellum, Fig. 2** Schematic representation of the subdivision of the cerebellum

#### Functional Classification of the Cerebellum

The cerebellum has three major divisions that have distinctive functions and connections: vestibulocerebellum, spinocerebellum, and cerebrocerebellum. The vestibulocerebellum is the oldest part of the cerebellum. It comprises the flocculonodular lobe and the lingual (most primitive part of the vermis). These receive visual and vestibular inputs and send them to the vestibular nuclei, participating in regulating body equilibrium and eye movements.

The spinocerebellum is also called as the paleocerebellum. It consists of the entire anterior lobe except the lingual. It receives proprioceptive and somatosensory inputs from the spinal cord and projects them to the cerebral cortex and brain stem. This region is concerned with maintaining the fine tune of the body and limb movements.

The most recently developed part of the cerebellum is the cerebrocerebellum. It consists of the lateral part of the hemisphere. Its input and output are connected to the cerebral cortex through pontine nuclei, which primarily participates in executing and planning voluntary movements. It has been reported that the cerebellum may also have a role in cognitive functions like working memory (Kandel et al. 2000).

#### Microcircuit of the Cerebellum

The entire gray matter of the cerebellum is arranged uniformly into three layers: granular layer, Purkinje layer, and molecular layer. These layers possess distinctive neurons, one efferent, and two afferent fibers and perform different functions.

##### Granular Layer

It is the innermost layer that rests on the white matter. It has about 100 million granule cells that make the layer looks densely packed. The layer also contains few Golgi interneurons, brush cells, and synaptic glomeruli. Granule cells are very small and numerous in number. The mossy fiber (one of the afferent fibers) terminates in the granular layer and synapses with short dendrites of granule cells in the synaptic complexes called cerebellar glomeruli. The axons of granule cells move to molecular layer and divide into parallel fibers (forming a T junction from each parent axon).

##### Purkinje Cell Layer

It is the middle layer consisting of the cell bodies of Purkinje cells. The dendrites of the Purkinje cells move vertically upward entering into the molecular layer. These dendrites receive input



from the afferent fibers and interneurons present in the molecular layer, while the axons of Purkinje cells extend downward into the white matter and synapses with the deep nuclei. Purkinje cells use GABA as a neurotransmitter and they are inhibitory to the deep nuclei.

### **Molecular Layer**

It is the outermost layer of the cerebellar cortex. They have two inhibitory interneurons: stellate cells and basket cells. They make connections with the parallel fibers of the granule cells and the extensively branched dendrites of Purkinje cells. Both are GABAergic and form inhibitory connections with Purkinje cells.

### **Afferent Fibers of the Cerebellum**

Mossy fibers arise from the cell bodies of the brain stem and spinal cord and terminate in the granular layer. They carry sensory information and form excitatory synapses with the dendrites of granule cells. Further, the axons of granule cells project the information to a large number of Purkinje cells.

Climbing fibers originated in the inferior olivary nucleus in the medulla. They carry sensory information and terminate in the molecular layer by passing the granular and Purkinje cells layers. Each climbing fiber climbs up to many Purkinje cells and synapses on them.

### **Efferent Fibers of the Cerebellum**

Efferent fibers are the axons of the Purkinje cells that project the information to the deep nuclei of the white matter. They are inhibitory to their targets. The flocculonodular lobe projects some efferent to the brain stem.

### **Deep Nuclei**

The core of the white matter has four cerebellar nuclei of gray matter: dentate, emboliform, globose, and fastigial. All the outputs of the cerebellar are from these cerebellar nuclei. These receive inhibitory inputs from the Purkinje cells and collateral inputs from the afferent fibers (mossy fibers and climbing fibers).

### **Connections of the Cerebellum**

The cerebellum has direct and indirect connections with the cerebral cortex and the spinal cord. Spinocerebellar pathways convey proprioceptive information to the cerebellum, which is responsible for maintaining body posture and controlling muscle tone. The cerebral cortex conveys information to cerebellum through centers present in the brain stem, such as the corticopontocerebellar pathway, cortico-olivocerebellar pathway, and corticoreticular cerebellar pathway. The cerebrocerebellar connections are concerned with the planning and execution of voluntary movements of the body. The cerebellum projects information to the thalamus, which then relays it to the cerebral cortex. The vestibular connection of the cerebellum through the semi-circular canals and the otolith organs helps in regulating balance and eye movements. The input from vestibular receptors and proprioceptors help make postural adjustments through the modulation of commands to motor neuron, which then compensates the shift in body movements or changing load of the muscles (Knierim 1997).

### **Cerebellar Dysfunctions**

Cerebellar dysfunctions are associated with ataxia (hereditary or acquired). Hereditary ataxia can be autosomal recessive (Friedreich ataxia, ataxia-telangiectasia, abetalipoproteinemia, ataxia with isolated vitamin E deficiency, and cerebrotendinous xanthomatosis) or autosomal dominant (spinocerebellar ataxia). Acquired ataxias involve neurodegenerative disorders, systemic disorders, multiple sclerosis, cerebellar strokes, repeated traumatic brain injury or toxin exposure or idiopathic reasons.

### **Disorders of the Cerebellum**

Cerebellar disorders can be diagnosed through clinical evaluation, MRI studies, and genetic testing and neuroimaging. The disorders are clinically diagnosed and a systemic disorder involves a



proper family history search. Treatment is usually supportive and sometimes involves surgery and treatment of the causal issues. The two major disorders are:

### 1. Cerebellar Motor Syndrome

The basic deficit common to the motor incapacity is impairment of rate, rhythm, and force of contraction. In the early stages of cerebellar degenerative disorders, balance is poor, and there is inability to stand on one leg or perform tandem gait. The patients show ataxia (impairment of gait), dysarthria (motor speech disorder), dysgraphia (difficulty in swallowing), hypotonia (low muscle tone), dysmetria (lack of coordinated movements), and dysdiadochokinesia (inability to perform rapid movements) (Schmahmann 2004).

### 2. Cerebellar Cognitive Affective Syndrome

This syndrome is characterized by difficulty in executive function (deficient planning, set-shifting, abstract reasoning, working memory, and decreased verbal fluency), impaired spatial cognition (including visual spatial disorganization and impaired visual-spatial memory), personality change (flattening or blunting of affect and disinhibited or inappropriate behavior), and linguistic difficulties (including dysprosodia, agrammatism, and mild anomia) (Schmahmann 2004).

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## Cross-References

- [Fetus](#)
- [Homunculus](#)
- [Medulla Oblongata](#)
- [Species-Specific Behavior](#)

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## Cerebral Asymmetry

- [Laterality \(Handedness\)](#)

## Cerebrotypes

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The vertebrate brain consists of distinct regions and subregions that differ in structural composition and functionality. Brain regions vary in size between species and population both in terms of absolute size and proportional size within the brain. These size differences are believed to reflect

differences in functionality with increased size providing more processing power, the hippocampus, for example, a brain region that is important for the formation of spatial memory tends to be larger in foodstoring birds than in nonfoodstoring birds (Clayton and Lee 1998). Cerebrotypes (*plural* cerebrotypes) refers to a specific type of brain composition that is shared between groups of animals. Most often, cerebrotypes are determined by dividing the volume of all major brain regions by the volume of the entire brain to create a series of volume fractions, which combine to make up an animal's cerebrotypes (Clark et al. 2001). This method allows a comparison of relative brain composition to be performed independent of total brain size and also takes into account that some brain regions are more anatomically and functionally linked than others resulting in correlated size evolution.

Cerebrotypes have been identified across a range of species, from mammals (Clark et al. 2001) and birds (Iwaniuk and Hurd 2005) to fish (Yopak 2012) and amphibians (Doré et al. 2002), with closely related species often sharing more similar cerebrotypes than more distant species. Multivariable analysis has revealed that some cerebrotypes cut across clades and can be related to a particular ecological or developmental niche shared by distant species. The extent to which cerebrotypes relate to phylogeny or ecology varies among species and lineages and therefore provides a useful tool for examining the evolution of brain composition in light of phylogeny, behavior, and ecology (Iwaniuk and Hurd 2005).

Cerebrotypes characteristics are not limited to the size of the major brain regions, but can affect many levels of brain anatomy. The patterns of gyrification (folding) of the cerebral cortex for example varies considerably between and within mammalian orders (Ventura-Antunes et al. 2013) and the number of neuronal and nonneuronal cells that make up the different brain regions have different neuronal scaling rules between orders. When comparing species, neuron number tends to increase with brain size, but often at a lower rate, resulting in a decrease in neuronal density with increasing brain size. Yet some orders, like

primates and parrots, are characterized by very high neuronal density, despite having relatively large brains. In parrots, for example, this is due to an exceptionally neuron-dense pallium, the brain region that is involved in higher cognitive processing in birds (Olkowicz et al. 2016). Similar to brain region size, these differences in brain region folding and neural density are believed to reflect both differences in processing power as well as phylogenetic constraints.

While cerebrotypes-based measures have mainly been used to look for interspecific variation, the method can also be used to compare brain compositions between populations of the same species. Intraspecific differences in brain composition between recently diverged populations have been identified in several species, but are especially well documented in domesticated species, where the domestication process has led to substantial changes in brain size and composition, resulting in domesticated animals having a different cerebrotypes than their wild progenitors (Kruska 2005; Henriksen et al. 2016). The advantage of interpopulation studies is that any difference in brain composition is more readily related to the environments in which the populations live and less confounded by changes in brain composition acquired at some point in the past and thus of little relation to the present environment, as can often be the case for interspecies studies. Therefore, although differences in cerebrotypes found within species may not be as extreme as those found between species, population comparisons within a single species can be used to associate brain composition with environmental or behavioral variation. Interpopulation differences have most notably been used to disentangle the genetic architecture underlying brain composition, mainly testing the independent (mosaic brain evolution) versus constraint (concerted brain evolution) hypothesis about brain composition evolution using quantitative genetics (Hager et al. 2012; Henriksen et al. 2016). The former hypothesis postulates that individual brain regions can develop and grow independently in size while the latter argues that different brain regions have been limited by developmental constraints and that the brain alters predominantly as a whole.

In summary, the term cerebrotypes has a broad definition and application. It can be used to characterize and distinguish brain composition at different anatomical levels, from neuronal density to brain regions size and it can be used to compare animals of the same species or from distinct species to answer ultimate questions about the evolution and functionality of brain composition as well as disentangle the underlying mechanism that underlies variation in brain composition between animals.

## Cross-References

- [Domestication](#)
- [Hippocampus](#)
- [Phylogeny](#)

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## Cetacean Behavior Toward the Dead and Dying

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## Evolutionary Origin of Grieving Among Mammals

Behavioral patterns and psychological dispositions toward the dead – including grieving, mourning, and bereavement – have been studied thoroughly among humans, but similar behaviors are poorly understood when performed by non-human mammals. The shared roots of grieving among humans and other animals were recognized early by Charles Darwin (1872) and the evolutionary meaning and significance of grieving were later elaborated in the work of authors such as John Archer, John Bowlby, and Colin M. Parkes. Their insightful writings explain that grief is ultimately a reaction to a deficit, arising as a by-product of the broadly similar reaction to separation. In other words, grieving is the cost of commitment (Parkes 1972), the downside of attachment and love (Archer 1999), and its emotional responses have evolved from the basic need of maintaining proximity with a partner or offspring. The maladaptive aspects of grieving have been seen as a trade-off with other adaptive

features, needed to maintain a stable relationship. Grieving results from the breaking of attachment bonds and its intensity generally parallels the strength of attachment: as Archer states, “if there is no attachment, there will be no grief.” When a dear one dies, the longing remains largely intact and the experience of loss often produces responses including distress, depression, and compulsive behaviors that may ultimately threaten the survivor, as documented by studies of humans and by a limited number of studies on other mammals (particularly primates).

While understanding death is generally regarded as a human attribute, such understanding *per se* does not necessarily help us overcome behavioral patterns and emotional responses that are deeply rooted in our evolutionary history. Observations of cetaceans (the taxonomic group that includes whales, dolphins and porpoises) suggest that at least in some cases – most notably upon the death of an offspring – behavioral patterns and emotional responses can parallel those found among humans and other terrestrial mammals. Whether or not they are explicitly referred to as grieving, cetacean reactions to a loss can be behaviorally extreme, strikingly maladaptive, and long-lasting. Such reactions possibly reflect aspects of bereavement, generated by terminal breaking of the strong social bonds known to exist among some cetacean species.

## Epimeletic Behavior

The term “epimeletic” (but also “caregiving,” “supporting,” “nurturant,” and “succourant”) has been employed with reference to cetacean behavior toward the dead or dying. The term is a catch-all to characterize a range of behavioral patterns encompassing rescue and resuscitation attempts, postmortem bereavement, the use of surrogates, and compulsive stereotypic behavior (Bearzi and Reggente 2017). Epimeletic behavior (Fig. 1) typically refers to one or more individuals who consistently stay near an injured or dead one, maintaining physical contact, lifting or keeping it afloat, and moving or carrying it along. If the dead individual is taken away by observers, or



**Cetacean Behavior Toward the Dead and Dying, Fig. 1** An adult striped dolphin *Stenella coeruleoalba* of unknown sex performing “epimeletic behavior” toward a dead conspecific (a subadult female) in the Gulf of Corinth, Greece (Photo by Silvia Bonizzoni/Dolphin Biology and Conservation)

approached by predators, the caregivers may behave aggressively or defensively. If a cetacean naturally strands, caregivers may remain in the area for some time and potentially risk stranding themselves. Epimeletic behavior involves other maladaptive aspects such as prolonged contact with a decomposed and potentially diseased carcass. While epimeletic behavior typically refers to a healthy adult caring for an impaired or dead individual (often a calf), the term is sometimes used with reference to behaviors that may not have truly epimeletic (i.e., altruistic) components.

## Cases of Epimeletic Behavior

Possibly more than one hundred cases related to epimeletic behavior have been documented in captive or free-ranging cetaceans (Norris and Prescott 1961; Caldwell and Caldwell 1966; Reggente et al. 2016), but reports tend to be opportunistic with an anecdotal, descriptive, and nonexperimental character. Early reports tend to be particularly blurry and most pre-1970 cases refer to either animals killed by whalers, observations resulting from the deliberate harming and killing of animals “for science,” or cetaceans held in captivity, not ideal settings for unbiased observations of natural behavior. The discussion

in this entry refers to post-1970 published literature of cetacean behavior in the wild.

Cetaceans include 89 extant species, but the published reports of epimeletic behavior are restricted to a much smaller subset of relatively well-studied species. Of 45 published reports of cetacean behavior toward dead or dying conspecifics, 24 (53%) refer to only two genera: *Tursiops* (17 cases) and *Globicephala* (7). The remaining reports are scattered across 12 other genera, all within the family Delphinidae except for two cases involving the beluga *Delphinapterus leucas*, one involving the sperm whale *Physeter macrocephalus* and one involving the humpback whale *Megaptera novaeangliae*. The number of reports per species depends in part on opportunities of observing a relatively rare behavior, which vary depending on species abundance, distribution (e.g., increased accessibility due to proximity to shore), and other factors. Even considering these factors, cases of caregiving behavior appear rare among mysticetes (most cases are dated whaling episodes where individuals reacted to harpooned calves or group members; Caldwell and Caldwell 1966). Cases also appear to be uncommon among some intensively studied odontocetes. For instance, only one published record of epimeletic behavior exists for the highly social and cognitively advanced killer whale *Orcinus orca* (the observation of a female carrying a dead neonate in her mouth; Reggente et al. 2016).

Apart from the differences among species (cetaceans differ greatly in body size, cephalization, ecology, behavior, and social organization), differences are likely to exist within species. Attitudes towards the dead are known to have remarkable individual and cultural variability among human and nonhuman animals alike (Archer 1999; King 2013). Variability within the same cetacean species, or even within populations or groups of conspecifics may occur, due to differences related to age, sex, relationship with the deceased, ecological context, predation risk, and a number of other nontaxonomic factors. Because of the small sample size and other sampling constraints, the known cases of cetacean behavior toward the dead or dying may not represent the “typical” repertory of a particular species.

## Caregivers and Receivers

Among humans, grief parallels the strength of attachment between caregiver and receiver, and the loss of a child is regarded as the most difficult to bear. Mothers generally show higher levels of attachment than fathers, because females make the greatest parental investment and paternity among males is uncertain (Archer 1999). Consistent with studies of wild terrestrial mammals, the caregiver among cetaceans is invariably an adult and the receiver is mostly a dead calf or juvenile (89% of 45 events directed toward conspecifics). When cases involve dead calves and the sex of the caregiver is known ( $n=12$ ), it is typically a female (92%). Published observations of known male caregivers are limited to the single case of an adult short-finned pilot whale *G. macrorhynchus* carrying a dead calf in his mouth while swimming among other group members (Baird 2016). While this behavior was interpreted as grieving by the author, it may have alternative explanations. For instance, cases of infanticide and violent aggression directed toward conspecifics (and nonconspecifics) are not uncommon among common bottlenose dolphins *T. truncatus* and have been reported to occur in several other cetacean species. Considering these cases, it cannot be ruled out that a male may be carrying a dead calf – that he might have killed himself – to ensure the calf’s mother stays with him (possibly resulting in reproductive benefits when the time comes), as a “trophy,” or for other unknown reasons (Shane 1994).

Female caregivers are often inferred to be the mothers of the dead or dying calf, but parenthood is rarely confirmed. In one well-documented case, an unrelated female was observed providing most of the care to another female’s dead calf (Quintana-Rizzo and Wells 2016). A related observation involved a bottlenose dolphin mother who spent considerably more time with her grandson following the death of her own calf (Mann and Barnett 1999), possibly as a form of “compensation.”

In approximately 10% of the published observations from the wild, the main caregiver is assisted by other individuals, sometimes called



“escorts,” which actively help support a dead or dying calf at the surface by pushing or nudging the carcass. Compared to these observations involving dead calves, records of multiple individuals targeting a dead adult or subadult conspecific (five observations, 11% of the total) appear to belong to a different category of behavior. All of the five observations include instances of arousal such as belly-to-belly contact, erected penises, and mating attempts targeting the deceased. Conversely, no cases of arousal have ever been observed among escorting group members when the receiver is a dead calf. Cases of necrophilia with dead conspecifics, and non-conspecifics alike, have been observed among wild marine mammal males (Harris et al. 2010), but these behaviors are rare in most mammalian species. Among cetaceans, cases of arousal in the presence of a dead adult or subadult conspecific seem to be common when several group members are present. In one of the five observations, the dead target was a subadult male bottlenose dolphin (Dudzinski et al. 2003); in another, an adult male humpback whale that was killed during a competitive interaction with conspecifics (Pack et al. 1998). Sexual arousal may be triggered by physiological responses related to stress or be expressions of dominance, devoid of a reproductive purpose.

### Learning to Mother

The hypothesis known as “learning to mother” has been proposed to explain the carrying of dead offspring by nonhuman primates (e.g., Warren and Williamson 2004). This hypothesis contends that benefits can be gained by carrying a corpse, for instance, to learn useful motor skills while traveling and foraging. Because even brief exposure to infants can improve maternal skills among primates, it has been conjectured that carrying a dead infant may make a mother more capable of dealing with subsequent offspring that need to be carried. Practicing of parental skills also has been proposed to explain epimeletic behavior and carrying of dead calves by cetaceans, though none of the extant cetacean species

would “carry” their living calves, and the benefits of practicing such behavior are dubious.

### Resuscitation Attempts

Grieving can reduce the survival of the caregiver due to energy expenditure, stress, increased exposure to predation risk, lower foraging opportunities, and other factors. The reactions of caregivers, however, can potentially have an adaptive component. While no inference can be made as to whether the caregiver knows that the receiver is alive or dead, observations of terrestrial mammals suggest that an inanimate receiver can return to life following forceful manipulation, hits, and strokes by a caregiver. Protracted manipulation of an inanimate body may be the animal equivalent of cardiopulmonary resuscitation. The typically energy-expensive initial phases of grieving, involving a “denial of reality” (Archer 1999), and active or even aggressive behavior may therefore have the occasional benefit of rescuing an apparently dead individual.

Cetacean mothers are known to respond to nonbreathing newborns by lifting them to the surface and stimulating the first breath, arguably an evolutionarily important behavior which general pattern might be related to similar attempts following perinatal death (Krasnova et al. 2014). Whether or not persistent manipulation actually results in occasional resuscitation among inanimate cetaceans is not known, but this possibility cannot be ruled out. Among cetaceans, however, such behavior is not limited to the time immediately following death, as one would expect if handling was exclusively related to resuscitation attempts having any chance of success. For instance, forceful handling involving tossing and vigorous strikes has included calves and juvenile cetaceans in moderate decomposition.

### Length of Carry and Phases of Grief

Whether or not the caregivers can discriminate between life and death, or have an understanding



thereof, proximity with the deceased facilitates acceptance of death, or at least can contribute to the necessary behavioral and emotional transitions. Among humans, there is a consensus that it is helpful for parents to see or hold their baby following a stillbirth. Human mothers need a period of time to come to terms with the loss, and maintaining proximity with a dead baby may help mitigate the trauma of separation. In such a context, grieving may have therapeutic benefits (Archer 1999). A cetacean corollary is that the well-intentioned decision of taking dead calves away from caregiving dolphins – often reported in the published literature (29% of the sample) – may not be in the best interest of the surviving animal(s), particularly in the early phases of grieving and following perinatal death.

In later phases, attachment and social bonds represent powerful psychological mechanisms delaying abandonment and the caregiver may become incapable of letting go. Unwillingness to leave the dead may prompt behaviors to become compulsive and stereotypic, with an increase in apparently maladaptive and aberrant components. Several odontocete species have been observed carrying calves in advanced decomposition, sometimes flaccid remains beyond recognition or even body parts (e.g., a truncated head). Only a few mammal species, all of which are primates, are known to carry the dead as long as cetaceans. Primate mothers of several species can carry their dead infants for days or weeks before abandoning them, sometimes until they are mummified – a behavior that has been related to extreme climatic conditions slowing down decomposition and extending the periods over which dead infants can be carried (Fashing et al. 2011).

Cetaceans can carry a dead calf over long distances while swimming and diving. Facilitated by reduced gravity, these aquatic mammals can afford carrying dead bodies for long periods of time, and some foraging obviously must occur when the carrying is protracted for weeks. Odontocete species with a dorsal fin may find it easier to carry a dead calf on their dorsum, draped over the anterior edge of their fin, while continuing to move and forage. Carrying may be

comparatively more costly for deep-diving cetaceans or fast-moving gregarious species. For most terrestrial mammals, transporting a dead body can be challenging, or even virtually impossible. For example, giraffe mothers *Giraffa* sp. can remain vigilant in proximity to their dead calf for periods up to several days (Bercovitch 2013), but would not be able to actually carry it. Ring-tailed lemurs *Lemur catta* can hardly carry infants that do not hold themselves to their fur, and have been documented moving between a dead infant and their troop (Nakamichi et al. 1996). A comparatively lower energetic cost of carrying, for at least some cetacean species, may contribute to delayed abandonment as compared to other taxa. An additional factor that might delay abandonment of a decomposing carcass is the apparent lack of olfaction and taste in most cetaceans (Cozzi et al. 2017), which could potentially result in weak avoidance mechanisms. In terrestrial mammals with a pronounced olfaction, decomposition processes and the smell of death likely deter proximity to decaying bodies, implying a risk of disease transmission that triggers avoidance as decomposition progresses.

What causes a female to eventually stop carrying a dead calf? Among primates, physiological changes in the mother associated with infant death have been suggested to play a role in the abandonment. For instance, postpartum amenorrhea is shortened after an infant's death, and the hormonal changes preparing the mother for the arrival of a new infant may contribute to a gradual release of the attachment to the dead infant and its remains (Biro et al. 2010). Among human mothers, the absence or cessation of breastfeeding may increase the desire to hold their baby, but such a desire will tend to fade over time. Similar physiological and psychological changes mediated by hormonal shifts are likely to occur among cetaceans as well, creating the conditions for abandonment. Other factors that may contribute to promoting detachment from the dead include the risk of losing contact with other group members when the rest of the group moves away, fear or uneasiness resulting from isolation and increased predation risk, and hunger.

## Surrogates and Other Species

While caring for a living conspecific is clearly adaptive (Clutton-Brock 2009), the evolutionary meaning of caring becomes blurred when targets are living individuals or carcasses of other species, or even objects. In some of these cases, non-conspecifics and objects may become surrogates that help mitigate separation distress and address an overwhelming need to maintain attachment, if merely an illusion thereof. Even in these cases, the caregiver may respond in a protective manner when observers attempt to approach or remove their burden – whether unrelated animals or objects.

A vivid example – though not necessarily representative of natural behavior – is given by a captive beluga whose dead calf was removed from the pool postpartum. The female first started carrying her own placenta, and after the placenta was removed she resorted to a buoy, which she continued carrying for several months (Kilborn 1994). Possibly related observations (for a total of seven occurrences) were made in the wild, where belugas of undetermined sex were reported carrying a newborn, a placenta and amniotic sac, a piece of seine net, planks up to 2–2.5 m long (four cases), and the entire skeleton of a dead caribou *Rangifer tarandus* (Smith and Sleno 1986). These short-lasting and nonsystematic observations could document a need for surrogates following the death of previous calves, similar to the case observed in captivity, though some cases may have different meanings, such as playful behavior.

A particularly puzzling series of observations involved several short-finned pilot whales persistently carrying dead California sea lions *Zalophus californianus* in various stages of decomposition (“from freshly dead to furless blubbery corpses with bones extruding”; Shane 1994). This behavior was performed consistently by several pilot whales in 19 separate events observed over 12 days, with only two cases attributed to adult males. Considering the lack of social bonds between pilot whales and sea lions and several other aspects inconsistent with the hypothesis of epimeletic behavior or grieving, these events were tentatively explained as a way of conferring a particular status to the carrier (Shane 1994).

However, the interpretation of these and other cases involving the carrying of dead non-conspecifics remains largely conjectural.

Cases of nonoffspring “adoption” and care toward living nonconspecifics are not uncommon among cetaceans and other mammals and may represent practice to deal skillfully with one’s own offspring. Caregiving behaviors directed toward living and dead nonconspecifics may also express (and potentially reinforce) “compassionate” behaviors that – beyond being apparently misdirected byproducts of generally adaptive models – can yield long-term net benefits. Such behaviors may include unexpected targets, adding striking aspects to the vast cetacean repertory. For instance, “interspecific altruism” was postulated to explain the repeatedly observed mobbing of mammal-eating killer whales by humpback whales, apparently intended to protect other cetacean species, but also pinnipeds and even a fish (the ocean sunfish *Mola mola*; Pitman et al. 2017).

## Neural Basis of Grieving

What is the neural basis behind the complex behavior shown by some cetacean species towards the dead and dying, and is such a neural basis shared by all mammals displaying similar behaviors? “Higher” emotional behavior in humans and other primates has been at least partially localized in the orbitofrontal cortex, and instinctive behavior may be organized and activated by sensory areas, by the cingulate cortex and the amygdala (Rolls 2011). These parts, and their connections, may be identified and compared in different species by certain anatomical boundaries, but especially by their structure (i.e., the way the neurons that constitute them are placed, connected, and communicate chemically).

The functional anatomy of the cetacean brain has been particularly well studied in the common bottlenose dolphin (Cozzi et al. 2017). The structure and functional organization of the neocortex of this species disclose a thinner cortex and a different, apparently less complex, circuitry. The human neocortex (but also that of rodents and terrestrial carnivores), including the orbitofrontal,

is a six-layered structure in which the fourth layer from the top plays a pivotal role and appears prominent in the brain's sensory and associative areas. Among cetaceans, the fourth layer is absent or extremely reduced (Hof et al. 1999), and the projections of the cortex from and to the rest of the brain must follow a different pathway, with a circuitry similar to that of hoofed mammals (Cozzi et al. 2017).

An analysis of cetaceans' limbic lobe leads to similar conclusions: a large part of the components of the limbic lobe in terrestrial mammals are phylogenetically and physiologically linked to the olfactory lobes and the perception of smell. Odontocetes have no olfactory nerve and lack all of the connected structures (Cozzi et al. 2017). Mysticetes have remnants of the olfactory structures, but their functionality remains to be validated. All that is left of the limbic lobe in cetaceans is an extremely reduced hippocampus (Morgane et al. 1982), so small that it may be difficult to identify even in very large brains (as a comparison, the same structure may amount to 1/5 or 1/6 of the entire telencephalon in some hoofed mammals).

The neuroanatomical aspects summarized above suggest that the structures of the dolphin brain potentially (by comparison) involved in emotional and instinctive behavior follow a strikingly different organization compared to humans and other terrestrial mammals: they have fewer neural layers, alternative neurochemical communication, and relatively simpler circuitry. Therefore, the grieving behavior of dolphins and that of humans and other well-studied terrestrial mammals cannot be based on comparable neuroanatomical and neurophysiological patterns. Observations of caregiving dolphins reviewed in this entry may lead to psychological analogies that remain unexplained by our current understanding of the structures physiologically involved in the neural basis of such behavior.

## Conclusion

Beyond the remarkable differences in neuroanatomy, we concur with Darwin that if related species

show similar responses under similar circumstances, the underlying proximate processes are probably homologous (i.e., derived from a common ancestor) rather than analogous (i.e., independently evolved) – a view consistent with recent research on mammalian empathy (de Waal and Preston 2017). A wide variety of vertebrates showing social attachment and parental care have a motivation to help distressed and vulnerable targets (de Waal and Preston 2017), and reactions equivalent to human grief can be expected among social animals separated by a companion with whom they have an evolutionarily important prolonged relationship (Archer 1999). Field observations of odontocetes suggest neural perception-action mechanisms similar to those observed among social terrestrial mammals such as primates – particularly when an adult female and a dead calf are involved. Nevertheless, several other aspects of cetacean behavior toward the dead and dying remain obscure, particularly when the target is a dead adult conspecific, or a dead nonconspecific. Clearly, much remains to be done to achieve a satisfactory understanding of the cognitive and behavioral aspects surrounding death among cetaceans.

Occurrence of caregiving behavior among different cetacean species deserves to be better investigated and framed in the larger context of research on behavioral patterns that may be expressions of empathy in nonhuman vertebrates.

## Cross-References

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- Kin Selection
- Maternal Behavior
- Parental Investment
- Rescue Behavior
- Stress

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## Cetacean Cognition

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## Synonyms

Dolphin; Thinking; Whale

## Definition

Cetacean cognition concerns thinking mechanisms like perception, memory, and forms of communication in dolphins and whales. Cetaceans are divided into two suborders: odontocetes (toothed dolphins and whales) and mysticetes (baleen whales).

## Introduction

Cetaceans' ancestors were land mammals, but the first “whales” appeared a very long time ago – more than 50 million years in the past – and adaptation to aquatic life occurred slowly over the millennia. Not only did those adaptations include shifts like the movement of the “nostrils” from the front to the top of the head (today’s “blowhole”), but they also led to changes in systems critical to cognition like sensory and perceptual processes and the structure of the brain, which

in turn coevolved with effective behaviors for life in the water. Here we discuss some of those processes and behaviors with specific focus on perception, communication, social learning, learning and memory, and other approaches to the study of cognition. (For recent reviews, see Herzing and Johnson 2015.) Because the study of cognitive mechanisms typically requires controlled studies, most of this entry is based on data with small odontocetes, particularly the robust bottlenose dolphin (*Tursiops truncatus* or *Tursiops aduncus*). (For reviews from many marine mammal laboratories, see two issues of the *International Journal of Comparative Psychology*, 2010, edited by Kuczaj.) However, on occasion other odontocetes are also included as well as a section on the complex and cognitively interesting songs of the humpback whale, a mysticete.

Most experimental research on dolphin cognition and sensory studies in captive settings are based on studies of only a few subjects, frequently only one. Replication studies by different researchers at other laboratories are rare. It is assumed that cognitive attributes, usually to questions concerning “can a dolphin do X?”, displayed by any single dolphin are shared by others. Observational protocols in captive or, more often, in natural settings usually involve larger sample sizes but lack the controls to definitively determine cognitive processes.

## Echolocation and the dolphin's Perceptual World

Sound travels very efficiently in water – more than four times faster than in air – and cetaceans take advantage of that fact. Their perceptual world is strongly influenced by sound; however, perception of other kinds of energy is also important to dolphins. Their visual systems are well developed for underwater and aerial viewing. Underwater visual acuity is about 8 arc minutes and in air 12.5 arc minutes, good vision for non-primates but in the vicinity of “legal blindness” for humans. Dolphins are monochromats, suggesting that they would not have color vision. Nevertheless, there is some experimental evidence that they might be



able to discriminate color through rod/cone interactions. Much less is known about tactile perception, although morphological and evoked potential studies indicate somatic sensitivity, especially rostrally, which might be useful in monitoring water flow. Olfactory bulbs are absent in odontocetes which suggests an absent or weak sense of smell. Investigations of the anatomy of the dolphin tongue indicate reduced receptor development, although a limited number of psychophysical studies suggest good sensitivity for some tastes. Anatomical and correlational evidence based on locations of live stranding sites and migration routes in odontocetes and mysticetes suggests that they might navigate using magnetic detection. (See reviews of perceptual systems in Supin et al. 2001; Thewissen and Nummela 2008; Wartzok and Ketten 1999.)

A great deal about what a dolphin knows about its environment comes from sound. For example, odontocetes investigate their world through their ability to echolocate. To echolocate, the dolphin produces click sounds within the nasal passages underneath its blowhole, the opening at the top of the head through which the dolphin breathes. The very short (40–70  $\mu$ sec), very loud (180–225 dB re 1  $\mu$ Pa at 1 m) click is directed through the viscous “acoustic fat” in the dolphin’s melon (the bulbous front of its head) in a narrow beam of sound that bounces off objects in the environment and returns to the dolphin in the form of an echo, which is received primarily through the lower jaw. (See Au 1993, and Surlykke et al. 2014 for reviews.) Dolphins usually send out a click and wait for its returning echo before sending out another click, likely in order to process the echo in terms of the attributes of the click, although they may produce packets of clicks when targets are distant. Because echoic object investigation can happen in seconds or less, the dolphin’s click train usually sounds like a buzz to the human ear but would be perceived differently by a dolphin because dolphins process sound so quickly. Sounds that occur more than 264  $\mu$ sec apart are heard as separate sounds by a dolphin.

Dolphins can control their click trains to get more information about the objects in their environment. They hear across a very broad frequency

range, beyond 120 kHz (compared to humans’ 20 kHz upper limit), and so have effective options for creating a good signal within noisy conditions. For example, dolphins can produce high-frequency clicks to avoid low-frequency noise, more clicks, and louder clicks in order to get echoes that are easier to decode. The dolphin’s brain is built for processing sound. For example, the inferior colliculus, important for hearing, is 40 times larger in dolphins than in humans even though these two species’ brains are similar in size. Dolphins likely represent acoustic information in great detail.

Although we do not know exactly how dolphins recognize objects using echoes, we do know some of the echoes’ attributes that might help. (See Harley and DeLong 2008, for a review.) For objects that vary only in size, like different-sized disks, dolphins can use differences in amplitude to discriminate among the disks. For objects that vary only in material, like an aluminum versus a stainless steel cylinder, dolphins may use different pitches to tell the objects apart. Once objects get more complex and vary across many features simultaneously, it is more difficult to know how the dolphins manage recognition tasks because echoes from different attributes interact. For example, echoes returning from different angles of the same object can sometimes vary more than echoes from different objects vary. At present, no man-made sonar system is nearly as effective as a dolphin’s biosonar system in terms of object recognition.

Echoic object recognition is more than a sound-matching task (Harley and DeLong 2008). Dolphins can recognize an equivalence between the features of an object that they see and the features of an object that they detect through echolocation alone as evidenced by their ability to match unfamiliar objects across modalities: They can see an object in air where they cannot echolocate (the density differences between air and water are too great for dolphins to echolocate in air) and then recognize that same object again when it is presented behind a visually opaque but echoically transparent screen underwater. They can also integrate visual and echoic information: Visual information can disambiguate objects that are similar echoically and vice versa; in such



situations, dolphins are better at object recognition when they can simultaneously get visual and echoic information at the same time. These findings indicate that dolphins organize their information about objects around objects because they use information about how an object looks and how it sounds within a single representation of that object.

A non-echolocating dolphin can also get enough information to recognize some objects when it is simply listening to the returning echoes of a very close neighbor who is echolocating. Hence, dolphins swimming closely together can likely determine with some specificity to which aspects of the environment a close neighbor is attending. This ability to attend jointly to an object suggests that dolphins likely use echolocation as a method for cooperation and communication.

## Communication

Although echolocation is usually considered a method of investigating the world, its accessibility to other listening dolphins makes it likely that it is also part of the dolphin's communication system. Other vocalizations on which we know dolphins rely for communication are whistles and burst-pulse sounds. (See Harley 2008, and Janik 2009, for reviews on communication.) Burst-pulse sounds are broadband sounds (include many frequencies at once) that are essentially echolocation clicks produced at a very high rate. These sounds are often associated with socially intense encounters like group feeding or conflict situations. Although most of the energy in these sounds often occurs above the human hearing range (above 20 kHz), humans do hear the lower-frequency components of these vocalizations and describe them as squawks, blats, mewings, raspberries, brays, and more. Our ignorance of the dolphin's perception and use of burst-pulse sounds invites more study.

Whistles appear to be central to communication for many odontocetes. Whistles can occur at many frequencies, but they often have a fundamental frequency between 5 and 15 kHz, accessible to human hearing, with high-frequency

harmonics. The most well studied of dolphins' whistles is the signature whistle, a typically long and repeated whistle that appears to serve as an individual identifier in order to maintain group cohesion. Each dolphin's signature whistle has a unique frequency contour such that the pitch changes in a specific way over time, e.g., it may move from 5 kHz to 8 kHz to 5 kHz and then slowly rise to 6 kHz across a second of time. Dolphins can tell these whistles apart and associate them with specific producers. Dolphins also can and do imitate each other's whistles. Although signature whistles tend to be stable after their initial development in the first year of a dolphin calf's life, the whistles of older animals that spend a great deal of time together sometimes reflect influences of the signature whistles of their close associates.

Dolphins can produce both the narrowband whistles and the broadband pulses simultaneously, although the functions of these dual emissions are unknown. Vocal productions can be very rich and complex in that there is a ratio of repetition and variability sometimes associated with information transfer. At present, however, most of the dolphin's sounds remain indecipherable to us.

We do know that dolphins can glean information from sequences. Dolphins in human care have learned to respond differentially to sounds and human gestures presented in different orders. For example, when the dolphin Akeakamai at Louis Herman's lab in Hawaii saw gestures associated with specific items and actions, she responded differently depending upon the orders of the gestures: *Frisbee Ball Fetch* (IndirectObject DirectObject Verb) led her to bring the ball to the Frisbee, whereas *Ball Frisbee Fetch* led her to bring the Frisbee to the ball. Her sensitivity to sequence was so powerful that she could respond appropriately to new commands she had never experienced based on her understanding of the placement of items in a sequence, e.g., she could treat an item as an indirect object because of its position in the string of gestures. Further work with the same animal indicated that she could respond flexibly within this human-directed communication system on many counts: She could respond appropriately to queries about the presence and

absence of objects, identify objects based on location, respond to commands conveyed via video screen, interpret anomalous commands systematically, learn to respond with specific body parts in novel ways, and more. Another dolphin in the same lab confirmed good sequence processing when she learned to categorize melodies as going up or down even when they had been shifted to new tones. Related to sequence, dolphins can recognize relative number magnitudes in an ordered series when the size of the objects and background area is controlled. For example, when all pairwise comparisons between 1 and 8 differentially sized circles are tested, the subjects correctly select the lesser number. (See Pack 2015, for a recent review of laboratory work with dolphins.)

Dolphins can also be trained to respond appropriately to pointing gestures presented by humans (including direct and cross-body pointing), and they can point themselves to communicate with humans. In one study, dolphins swam in a pool in which there were fish within jars, and they began to spontaneously indicate the presence of a jar when they found one. In these cases, the dolphin would point his rostrum (bottlenose) toward the jar, often turn his head toward a trainer swimming toward him as though monitoring the human, and then turn his head back to the jar. The presence of the person was important to the behavior; the dolphins never pointed when a human was not in the water and rarely pointed when a trainer was in the water but behind a barrier.

### Social Learning in the Laboratory

As their communicative behaviors suggest, dolphins are socially capable and are good at learning from others. Not only do dolphins imitate each other's signature whistles, but dolphins in human care have also spontaneously imitated trainers' whistles, computer-generated tones, both fundamentals and harmonics, and a pulsed sound. (See Harley 2008, for a review.) To demonstrate a concept of sound mimicry, imitation was brought under stimulus control when a single dolphin was presented with a model sound followed by a signal "to mimic" and rewarded when she matched the model.

Vocal behaviors are not the only behaviors learned socially. Initially, the ability of cetaceans to imitate, a cognitively sophisticated form of social learning, was suggested by frequent observations of synchronous behavior in the wild, usually swimming, respiration, or leaping behavior seen as dolphins traveled at the surface. (See Herman 2002, and Whitehead and Rendell 2015, for reviews of social learning.) Synchrony is one of the earliest behaviors seen during ontogeny by bottlenose dolphins, beginning shortly after birth, and may be the basis for their powerful social learning abilities (Fellner et al. 2012).

Anecdotal evidence of observational learning was also provided in examples from commercial cetacean shows. A false killer whale learned without training the show behaviors of a pilot whale, and two rough-toothed dolphins produced each other's routines, for which they had not been trained. A bottlenose dolphin copied within minutes the unique jumping behavior of a spinner dolphin, *Stenella longirostris*, newly introduced to its tank even though bottlenose dolphins do not normally exhibit this type of spinning jump. Dolphins even mimicked non-cetaceans including fur seals and humans, e.g., cleaning the algae for port windows in their tank with a seagull feather and other objects while making noises and releasing bubbles of air like the scuba divers who cleaned the underwater windows and, in another example, a nursing calf releasing a cloud of milk toward an underwater window in response to a visitor smoking a cigarette and blowing a cloud of smoke.

Controlled experimental studies have supported these informal observations. Young dolphins trained to do the same behavior as a human model successfully mimicked a wide variety of species typical and novel behaviors like blowing bubbles and putting an object in a basket. Similarly, dolphins learned to respond to a specific hand sign that indicated an imitator should perform the behavior of a model dolphin, live or via television screen, even after a delay. Blindfolded dolphins can imitate behaviors based on acoustic or possibly tactile cues. Dolphins can also perform behaviors synchronously when only one of the pair knows the behavior to be produced:

A companion dolphin was able to perform simultaneous behaviors with another dolphin that alone had seen a hand sign indicating the required behavior. Video analysis indicated there were trials with no apparent leader but with a short delay, suggesting some type of preparation. Although most studies revealed powerful imitative abilities, imitation does not always occur readily; differences in training history, age, dominant-subordinate relationships, or other factors may affect imitation.

Altogether, this laboratory evidence indicates that dolphin's observational learning behavior is a clear cognitive strength. Dolphins can imitate the behavior of other species including humans. They are facile at imitating in both the vocal and motor domains, a characteristic apparently rare among mammals, although reported in birds. Mimetic behavior is displayed spontaneously and under experimental stimulus control, both synchronously and after delays, which indicates at least some short-term stability of behavioral representation. The ability to mimic on command suggests that dolphins have a concept of mimicry a concept even robust enough to be displayed in response to dolphin and human actions presented on a television screen.

Studies in the laboratory allow demonstration of dolphin's mimetic capabilities, but they do not show how mimesis might be used in the wild. Alternatively, research in natural settings can show how mimicry can be used in the wild, but they usually do not allow for the controls necessary to exclude other explanations for similarity of behavior, such as ecological pressure and genetic causation. Nevertheless, careful analysis reveals that a variety of behaviors observed in the wild likely emerged through social learning.

## Social Learning in the Wild

The baleen whales (mysticetes) engage in a variety of behaviors that suggest complex cognition (vocalizations, cooperative feeding, memory for migratory destinations) but the lack of controlled studies makes it difficult in most cases to separate tightly genetically controlled systems from

learned behaviors. Humpback whale song, however, is an exception where evidence indicates that learning processes are important in the production of structured and changing vocal displays. (For reviews of humpback whale song, see Payne 1983, and Whitehead and Rendell 2015.)

Humpback whales migrate between polar regions, where they feed during summers, and tropical waters, where they calve and mate during winter months. In tropical waters, males sing an elaborate song at frequencies between about 30 Hz and 4 kHz. The songs are hierarchically structured with themes comprised of phrases and phrases comprised of units. Songs generally have fewer than ten themes, but for any one song, the number and order of themes are fixed. The major area of flexibility in a song is the number of phrases in a theme, but the themes are always presented in the same order. When the sequence of themes is finished, the song is repeated, usually without pause. Repetitions may last for hours. The length of a song may vary, generally between 10 and 30 min, depending on the number of phrases in a song and the length of units within phrases. The units of a song may last from 0.15 s to 8 s and include tonal whistles and broadband sounds of varying complexity.

Humpback whales are found in discrete populations where exchange of individuals is unusual. All the humpback whales in a population sing the same song. The song changes over the course of a season and between seasons for the group by changing, adding, or dropping themes, a characteristic that is consistent with vocal learning. More evidence that the songs are learned is provided by the pattern of transmission. South Pacific songs move from east to west, while at the same time there is very little actual east-west movement by individual whales. Therefore, the changes in song in a population do not represent a movement of individuals singing the same song; it represents movement of information.

To learn, remember, and produce complex, changing songs would appear to place substantial cognitive demands on male humpbacks. It is therefore intriguing that Guinee and Payne (1988) report that they found rhyme-like structures called multi-themed sub-phrases in songs.

These structures form similar beginnings and endings of adjacent phrases. The presence of these rhyme-like structures is strongly, positively correlated with the number of themes (i.e., the amount of material to be remembered) in a song, but not their duration, which suggests a possible mnemonic function, such as rhyme serves in human communication.

Foraging is another category of behaviors observed in the wild that suggests observational learning. Dolphins use a wide variety of foraging techniques unique to specific groups. For example, some dolphins in Shark Bay in Western Australia display a behavior called sponge feeding in which they carry a sponge over their rostrums while foraging. The hypothesis is that they use the sponge to avoid getting painful spikes from fish on the murky bottom. Although a genetic contribution is suggested by the fact that in one group studied 14 of 15 dolphins all belonged to the same genetic female line, the one exception indicates that if the trait is genetically controlled, it is not by a single gene. Supporting evidence is provided by another genetically unrelated, separate group, although they, too, share a common, female genetic lineage. However, there are members of these lines that are not sponge users, which weakens the case for a simple genetic transmission and strengthens it for social learning.

Another example of foraging involving dolphins is symbiotic fishing between humans and dolphins which has been reported since Pliny the Elder (~70 AD) described these interactions around the Mediterranean. More recent examples of cooperative fishing between humans and dolphins have been reported in multiple sites including Australia, Brazil, Myanmar, India, and Mauritania (Whitehead and Rendell 2015). The fishery off Laguna Brazil is well-described, although the origin of the cooperative arrangement is unknown. In response to fishermen wading in the mud flats, dolphins herd fish toward these shallows (a typical dolphin cooperative feeding behavior) where the fishermen are. Dolphins then engage in behaviors that alert the fishermen to throw in their nets. Not all dolphins participate, so it is important that the fishermen

recognize specific dolphins that engage in the cooperative enterprise. The dolphins do not herd the fish toward mammals other than humans. The benefit to humans is more fish, and we assume that this is also the case for the dolphins.

From a cognitive perspective, the flexibility and cooperation in which killer whales (*Orcinus orca*) engage as they forage are especially intriguing and indicate an ability to learn specialized skills. Killer whales are apex predators, and their prey vary extensively and include beaked whales, salmon, herring, seals, cephalopods, gentoo and chinstrap penguins, humpback whales, gray whales, gray seals, blue whales, sea turtles, minke whales, emperor penguins, elephant seals, sharks, deer and moose, and more! And while killer whales can hunt successfully alone, they usually hunt together. Sample capture methods include corralling, whales create a barrier in deeper water while an affiliate rushes the prey animal; and beaching, whales surf onto the beach and grab a pinniped while it is transitioning from swimming to getting onto the land. Young killer whales are often not as successful as adults in the same hunting waters, and sometimes adults accompany younger animals and float nearby while they hunt (Lopez and Lopez 1985). In these cases, the adults sometimes participate in the events without capturing prey. For example, in one area, an adult and juvenile would beach simultaneously about 4 m apart, and the adult would catch a sea lion and toss it toward the juvenile that either kept the sea lion it had already caught itself or, when it had no animal, would push the tossed sea lion or grab it with its mouth. Although the evidence for teaching is ambiguous, the younger whales' capacity to learn was very clear. Laboratory studies should investigate how similar skills can be transmitted among these animals.

One of the most interesting (if terrifying) examples of killer whales' collaborative hunting is the capture of seals on ice floes off the Antarctic Peninsula (e.g., Visser et al. 2008). Typically, small groups of whales (five to seven individuals) are involved, and they appear to choose prey that are on the frailest first-year sea ice. In one vivid and detailed description of a capture, a group of five

killer whale hunters began by spy-hopping around the floes to see possible prey. Upon spotting an adult crabeater seal, two whales submerged 15 m from the floe and swam together at and under it, which tipped the ice through “wave-washing” and broke it into pieces. Six wave-washes later, the piece of ice on which the panting seal was lying was quite small and had been pushed into deeper water via the whales’ rostrums and vortices at the floe’s edge created when the attackers submerged nearby. Bubbles blown near the ice’s edges cleared the surrounding debris. The encounter ended when one whale kept its rostrum on the ice while the other four lined up in pairs some distance from it, turned on their sides, and swam fast just under the surface as they blew bubbles and went under the ice on either side of the stationary whale. This action created a wave that tilted the ice in multiple directions and poured over it, washing the seal into the water where it ended up in a whale’s mouth. The sophistication of the skill set employed by these whales suggests cognitive capacities about which we should learn more.

Claims have been made – and disputed – for killer whale’s “culture,” and social learning is critical to that claim. (See Whitehead and Rendell 2015, for a review.) Transmission of skills suggests that killer whales may engage in imitation, and some data lend support. A few laboratory studies suggest behavioral and vocal imitation. For example, killer whales’ vocalizations are affected by their pool mates: Animals raised with bottlenose dolphins emit more click trains and whistles versus whales raised without dolphins that produce more stereotypic killer whale calls. Vocalizations in natural settings also suggest vocal flexibility. Like other odontocetes, killer whales emit a complex repertoire of whistles, echolocation clicks, and pulsed calls. In killer whales’ communication, pulsed calls are salient and the best studied of their vocal productions. These calls are generally stereotypic and sequentially patterned; the same call is often repeated. From the earliest scientific reports on killer whales’ vocalizations, the variability of call types between killer whale social groups was striking enough to garner the nomenclature

“acoustic clans” for groups that shared specific calls maintained at least in part through what could be termed cultural transmission.

## Learning and Memory

Dolphins remember well and display an ability to learn a variety of concepts. Dolphin’s working memory has been studied with delayed match-to-sample (DMTS) procedures. In most matching tasks, an animal experiences a sample item which is then removed, and the animal must find a replica of that item among a group of alternatives presented in a display. These DMTS tasks with dolphins have varied in many ways including offering two, three, or more alternatives; testing an associative conditional match in which the sample item is paired with a second different item (A to B) as well as the standard identity (A to A) match; and probe procedures in which small test trials are embedded within a larger session of familiar trial types (e.g., A’ to A embedded within A to A trials). For example, to determine that dolphins remember sounds, DMTS tests with open sets (e.g., multiple sample and test objects) of computer-generated sounds in an identity match showed that dolphins performed near 100% accuracy for delays of up to 1 min and over 80% at 2 min. When sets were closed, containing only two acoustic stimuli differing in frequency and amplitude modulation, performance started to drop off at 50 sec., probably due to memory interference among the few stimuli. Memory performance with conditional stimuli, in which different sounds previously mapped onto the sample stimuli were used as test stimuli, was similar to that of the identity match. Reducing the duration of the sample from the 2.5–4 sec used in previous tests to 3 msec did not substantively alter DMTS performance. Dolphins can also remember relative spatial positions after short delays. In addition, they exhibit the “recency effect” when presented with a list of sounds, i.e., they recall the later items better than earlier sounds in the list.

Dolphins also show memory for action events as indicated by asking a dolphin to do the same



behavior it has just done after a short delay. Dolphins demonstrate facility at this task and can repeat familiar behaviors and novel combinations of familiar behaviors. They also repeat behaviors that involve actions on an object when multiple objects are available. (See Mercado and Delong 2010, for a review.)

Studies of long-term memory are rarer, however, dolphins may remember signature whistles for long periods. Captive dolphins across sex and age (calf, juvenile, adult) classes showed memory for these whistles after periods of over 15 years in a habituation-dishabituation design (Bruck 2013). Although it is hard to know much about exposure levels to specific whistles over such long intervals, long-term recognition of signature whistles would probably be adaptive for long-lived animals in fission-fusion (groups that separate and come back together across time) societies, such as dolphins.

Many odontocete species, e.g., *Tursiops truncatus*, *Delphinus delphis*, *Phocoena phocoena*, *Inia geoffrensis*, and *Lagenorhynchus obliquidens*, are apt at instrumental conditioning tasks like discrimination learning across different modalities, especially vision and audition/echolocation. Often these learning studies focus on determining the boundaries of the species' perceptual systems, e.g., whether the dolphin can recognize a reference target when it is paired against a variety of other targets that differ from the reference target in fine-tuned ways (just barely thicker, just barely louder, etc.). (See Nachtigall 1980, for a review of echolocation discrimination learning.) Dolphins are good at negotiating such tasks.

At one time, development of learning sets (learning to learn), a rule-governed procedure, was considered a candidate for a comparative measure of intelligence. Although it may not have such general utility, it is still a notable cognitive ability, and the dolphin, Kea, provided sound evidence of its presence in cetaceans. She was presented with hundreds of pairs of sounds, one correct and one incorrect. The key evidence for understanding the concept was second trial performance: If the first trial was correct (e.g., sound A), then the same choice (A) was correct on the second trial; if the first trial was incorrect (e.g., sound B), then the

correct choice was the other alternative (A). Therefore, a win-stay/lose-shift strategy was required. Ultimately, her performance ranged from 75 to 90%+. Dolphins can also apply this concept (with specific sounds or their locations) to a reversal learning task in which the same stimuli reverse roles, i.e., the negative stimulus (B) becomes positive (the correct choice) and the positive stimulus (A) becomes negative. (See Herman 1980, 1986, and Herman et al. 1993, for reviews.)

Dolphins are good at learning abstract rules like the matching rule discussed earlier. They have also demonstrated generalized same/different discrimination which works as it sounds: The dolphin indicates whether two stimuli are the same or different by going to specific paddles (one for *same*, another for *different*) or staying at a paddle, for example, *same* versus moving to another paddle for *different*. Stimuli in these experiments have included auditory and 3-D and 2-D (planar) visual stimuli. Dolphins were able to classify pairs of unfamiliar three-dimensional objects in air on the first trial and then transferred this learning to presentation of unfamiliar planar objects underwater. They were also able to generalize the same/different concept to trials in which three objects were presented. They identified trials with three identical objects as same and trials with two same and one different object as different (Mercado et al. 2000).

Dolphins also appear to be able to learn an "innovate" rule: Do something you have not done within a set of behaviors or perhaps ever done before. The earliest example of this was a study of two rough-toothed dolphins (*Steno bredanensis*) that were required to produce a behavior not previously used in the innovation training sessions. One new behavior per session was reinforced. Familiar behaviors were common at first, but "new" behaviors began to appear regularly after some experience with the routine. Eventually, after 32 sessions and 16 reinforced (i.e., "innovated") behaviors, it became difficult for the experimenters to discriminate among behaviors (Pryor et al. 1969). Other similar studies with bottlenose dolphins have shown an ability to select familiar behaviors not recently used or novel behaviors. (For reviews, see Mercado and



DeLong 2010; Kuczaj and Yeater 2006.) “Newness” or “novelty” of behaviors is difficult to establish, so novel behaviors may in fact be rare behaviors not previously observed by the experimenters. Under any circumstances, unlike the previous win-stay/lose-shift strategies described earlier, this task required a win-shift/lose-stay strategy.

Most dolphin studies have dealt with the past or present, but a few studies have addressed planning. (For a review, see Kuczaj and Walker 2006.) Most of the evidence for planning in cetaceans comes from anecdotes such as the killer whale foraging incidents described above. Two experimental studies indicate that dolphins can engage in planning behavior. These dolphins were given a task in which four weights placed in an experimental feeding device within a specific timespan led to the release of a fish. The dolphins learned the task by observing a human putting the weights in the device only one at a time. When the weights were close to the device, the dolphins put them in as they had observed, one at a time. When the weights were later placed further away, the dolphins eventually carried multiple weights, taking the more efficient option; they avoided multiple trips and provided evidence of planning over time. In another study, the dolphins were presented with three feeding devices and a single weight. Each device contained a fish that would be released if the weight was placed in the device. Two of the devices had a hole in the bottom, which allowed the weight to fall through making it available to drop into another device. Since the lone device without a hole did not allow recovery of the weight, it limited the number of fish a dolphin could get to only one or two if it was used first or second. The strategic action was to select it last. That is exactly what the dolphins learned to do.

### Other Approaches to Cognition: Brain, Behavior, and Consciousness

This article’s title, *Cetacean Cognition*, evokes not only the perceptual, communication, and learning and memory studies described here but also their material basis, the brain, as well as the

general milieu of thinking that we often reference as “mind.” For humans, knowledge of mind can feel quite personal: One knows “mind” through one’s own mind, an experience typically known as phenomenal consciousness. As Descartes put it, “I think, therefore I am.” This section presents some information relevant to the brain and the search for aspects of consciousness in cetaceans.

Many species of cetaceans, most notably among the odontocetes, have large brains and high encephalization quotients (EQs), an index of brain size adjusted for body mass. For example, the brain size of a bottlenose dolphin (*Tursiops truncatus*) is about 1600 g, and its EQ is 4.14. (See Marino 2004, for a review of cetacean brain sizes.) For comparison, humans have a brain size of about 1300 g and an EQ of 7.0. The comparatively large brain size of cetaceans has led several researchers to postulate high levels of intelligence among cetaceans. Unfortunately, without detailed knowledge of neural connectivity, neuron density, and specific brain/behavior relationships, it is difficult to make definitive statements about the intelligence of cetaceans based on neurobiology alone. (See Oelshlager 2008, for more about the dolphin brain.) Behavioral measures provide the gold standard for understanding cetacean cognition.

Some studies have tried to access aspects of consciousness in dolphins through behavior, but the lack of a clear characterization of consciousness and the behaviors that require it precludes conclusions on this score. Approaches include mirror/video self-recognition and metacognition studies. (See Harley 2013, for a review.) Most of the self-recognition studies used the mirror-mark test in which an animal is marked with a visible (colored/opaque) or invisible (clear) fluid which creates, respectively, mark versus no-mark/sham-mark conditions. The fluid is placed on a part of the animal’s body that it cannot see without a tool, e.g., a mirror or video camera. Most animals engaged in studies like these have appendages (e.g., chimp hands or elephant trunks) that allow them to touch the marked area, and researchers record touches and code other behavioral responses to the marks/absence of marks as social or self-referential. The dolphin’s streamlined body

and non-differential or ambiguous responses to the marks/absence of marks have made this method unprofitable thus far for studying dolphin self-recognition. Other similar lines of evidence used to address consciousness (e.g., self-imitation, identification of body parts) also run into challenges of interpretation.

Metacognition, knowing what one knows, was studied by having a dolphin listen to tones and report, via paddle presses, whether they were “high” or “low”; some tones were close to the edges of these high- and low-frequency categories. After training with two paddles, the dolphin was also allowed to choose a third “uncertainty” paddle that led to a delay and an easy (clearly high or low) trial. The dolphin learned to use this paddle when the tones were perceptually difficult to categorize. It may have known that it did not know how to categorize the tones, or it may have chosen the third paddle after delaying its own response or for some of the middle tones. Knowing that we do not know suggests this area for future work.

## Conclusion

The study of cetacean cognition is relatively new. These animals’ perceptual worlds are fascinating; their use of sound is unparalleled. Cetaceans’ communication systems are complex, difficult to interpret, and understudied; we have much to learn in this arena. Many cetacean species engage in social learning across contexts via a variety of mechanisms, which may support development of culture. They are flexible learners with good memories. The order Cetacea offers rich opportunities for future discovery.

## Cross-References

- Cetacean Communication
- Cetacean Life History
- Chemoreception
- Cultural Transmission
- Delayed Match-to-Sample
- Echolocation

- Encephalization
- Fission-Fusion
- Imitation
- Language Research: Dolphins
- List Memory Effects (Primacy and Recency)
- Long-Term Memory
- Louis M. Herman
- Matching-to-Sample
- Memory
- Meta-cognition
- Mimicry
- Mirror Self-Recognition
- Photoreceptors
- Reference Memory
- Ronald Schusterman
- Short-Term Memory
- Social Learning
- Stanley Kuczaj
- Stimulus Control
- Vision
- Working Memory

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## Cetacean Communication

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## Introduction

When animals are grouped in time and space, social behavior can evolve. If individuals only encountered each other once, they would not have the potential to establish a knowledge base about the other individual. When associations persist over time, individuals repeatedly come into contact with each other and establish a knowledge base of interactions. Repeated interactions lead to the development of relationships (e.g., dominance, cooperative foraging, and mating coalitions). A description of the various relationships in a group can lead to a description of the social structure of the group (e.g., polygamous,

female-bonded). Thus, the social structure of the group is based on an abstraction of the nature, quality, and patterning of relationships, and relationships are built upon a series of interactions between individuals. These interactions are mediated by signal exchange, communication.

Communication is ubiquitous among animals requiring a sender to produce a signal that might alter a receiver's subsequent action(s) or response. The exchange of information from one individual to another via a signal that typically elicits a response is communication (Perrin et al. 2009). The function of communication is diverse and covers topics ranging from mate attraction, maternal care, mediation of social relationships, group coordination, and more. For all animals, including cetaceans, signals are exchanged through a variety of modes (i.e., chemical, visual, tactile, acoustic) that are produced in air and water via both anatomical and physiological mechanisms (e.g., coloration patterns, behavioral displays, vocalizations, etc.). These mechanisms can generate communicative signals via a single mode or via multiple modes in order to augment the message. Communication allows individuals to establish and maintain relationships, convey information about internal states or reproductive status, and coordinate activities.

Cetaceans are fully aquatic and include two taxonomic groups: (1) odontocetes, or toothed whales; and (2) mysticetes, or baleen whales. The odontocetes include sperm whales (*Physeter microcephalus*), beaked whales, river dolphins, oceanic dolphins, porpoises, and the monodontidae [Belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*)], while the mysticetes are comprised of skim feeders (right and bowhead whales, *Eubalaena* sp. and *Balaena mysticetus*), rorquals [e.g., humpback (*Megaptera novaengliae*) and fin whales *Balaenoptera physalus*], and the bottom feeder or gray whale (*Eschrichtius robustus*). Cetaceans adapted their signaling to an aquatic lifestyle, for example, relying more on acoustic signals and less on chemical signals as compared to terrestrial species. Odontocetes and some mysticetes live in complex social groups that require consistent, coordinated mediation of relationships;

communication is key to a successful social life. To understand communication in a given species, it is important to know the mode of the signal (i.e., visual, acoustic, tactile, gustatory, or olfactory), medium in which the signal is transmitted (air and/or water), mechanisms of signal production (anatomical and/or physiological), function(s) of the signal (e.g., aggression/submission, mate attraction, parental care, territorial defense), and whether signals are single or multimodal.

## Components of Communication

For any two individuals to share information, to communicate, there are several required components. The *signal* is the vehicle by which two individuals share information. At least two individuals are involved in any communicative event—the *sender* and *receiver*. The *sender* selects the signal to convey a *message* to an identified recipient. The message is the content that the sender wants to provide to the recipient but what the recipient understands from the signal is its *meaning*. That is, the message can be modified by the context or setting in which both actors (*sender*, *receiver*) are placed as well as the recipient's history (i.e., predictive scenarios based upon memories of previous experiences) to yield the *meaning* of the signal by the receiver. Because the sender and receiver are different individuals and have different histories, the message and meaning of a signal are never identical. Drastic differences (e.g., in social experience, age, etc.) between the sender and recipient can result in miscommunication.

Acoustic signals can be conveyed to recipients that are not in view, which can result in miscommunication more readily than close-range signal use (e.g., visual or tactile modes). Production of a very low-frequency sound (e.g., 20 or 40 Hz) can broadcast a message over kilometers (Richardson et al. 1995), although the sender would have little control over whether the message is received or how the signal might be distorted during travel through ocean topography. The sender also has little-to-no control over who might hear the message (i.e., eavesdrop) on these sounds: predators, prey, competitors, or mates. For example, the fish-

eating ecotype of killer whale (*Orcinus orca*) in the Pacific Northwest uses echolocation to hunt and communicate with conspecifics while foraging whereas the mammal-eating killer whale ecotype hunts silently (Barrett-Lennard et al. 1996), likely because prey of the latter would hear the hunter's vocal signals. In contrast, high-frequency (e.g., 2–15 kHz) sounds travel over shorter distances and are likely to be received by a specific audience. For cetaceans, baleen whales typically produce very low-frequency sounds also called infrasound while toothed whales produce both sonic and high-frequency sounds called ultrasound.

### Modes of Communication Signals

Signals are the means by which individuals share information and they can be used independently or synergistically depending on the content and function of the message. In general, signals are transmitted through chemical, visual, tactile, and acoustic modes. Dudzinski et al. (in Perrin et al. 2009) reviewed examples of communication signals from within all modes available to marine mammals. For cetaceans, the olfactory lobes are much atrophied as is the external nasal anatomy; that is, the relaxed position of the blowhole in all cetaceans is closed. Thus, while dolphins and whales may have a rudimentary sense of taste, they likely do not possess a sense of smell. That said, recent research suggests that dolphins might actually sample chemical signatures in the urine or feces of conspecifics as a form of individual recognition (Kremers et al. 2016). Visual signals include body postures and color patterns that offer information about social activity or travel patterns, etc. Visual acuity is excellent in those species for which it has been studied; however, visual signals are limited by underwater particulate matter and visibility. Similarly, most cetaceans are quite tactile and share information through body rubs, touches, and other tactile signals. These signals are functional at close range. Because sound travels faster in water and over a relatively large area as compared to in air, underwater acoustic signals likely evolved to be the principal mode of information transmission for cetaceans (Perrin et al. 2009).

Acoustic communication includes both vocal (e.g., humpback song, dolphin whistles) and non-vocal signals (e.g., breaches, tail slaps).

### Acoustic Communication

Acoustic studies of whales and dolphins began in the mid-1950s (Au 1993; Richardson et al. 1995). Over the last 50+ years, recording and analyzing cetacean sounds have become relatively inexpensive and straightforward, but determining the context and function of sounds is much more difficult, especially since the advent of passive acoustic data collection that does not contain any associated behavior or vocalizer identification of acoustic signals. In addition to meticulous documentation of the context for call production, playback research is required to determine the function of sounds. For example, Deecke (2006) summarized several studies using playback techniques to examine the sound function. Still, the application of playback studies is often confounded for cetaceans because a one-one correlation between an acoustic signal and a behavioral function is not often available.

Sounds can be used for intrasexual selection to compete against other members of the same sex or to establish dominance to gain access to mates. Sounds are also used for intersexual selection to advertise fitness and strength among males to nearby females. Acoustic signals may help to maintain group cohesion or coordinate movements, defenses, or the activities of a social group of aquatic mammals. Killer whales are an excellent example of a marine mammal that regulates group movements and cohesion via acoustic communication; killer whale family pods use dialects for one mode (acoustic) of identification (Filatova et al. 2012) – even humans can readily recognize the vocal dialects of different family pods. There are also acoustic differences in call types between the different killer whale ecotypes (Barrett-Lennard et al. 1996), and evidence for cultural transmission of their dialects (Filatova et al. 2013).

Generally, the information animals send tends to be context-sensitive, especially to behavioral



state. In turn, receivers make inferences based on what they hear and react accordingly by integrating previous experience with emotional states and (likely) genetically influenced perceptions. Variation in sound(s) (e.g., frequency, amplitude, etc.) can be caused by different factors, such as levels of excitement, stress, background noise, or motivation. So, to understand the function of a sound, a researcher must know the role amplitude plays, as well as the context in which calls might be produced. High amplitude signals may emphasize a message or low amplitude signals may aid in selective communication between mother and offspring.

Even when a vocal signal has been well studied, context may factor into potential meanings; for example, male humpback whales produce complex songs comprised of units that form patterns grouped into phrases and finally into themes (see Mann et al. 2000; Au and Hastings 2008). These songs have long been considered important to the humpback mating system. Still, their exact function has been difficult to pinpoint with respect to function. Multiple hypotheses have been proposed regarding the function of these songs: intersexual interactions, mate attraction, male spacing, and social ordering (Mann et al. 2000). The explanation with the strongest evidence currently is that songs are used for mate attraction, namely males will begin singing after joining groups with mother-calf pairs and stop singing if lone males join the social group. Once the lone male moves on, singing restarts. Males that sing while with mother-calf pairs typically have greater reproductive success, suggesting that the songs may have evolved for mate attraction but have a cost since other males can hear the songs and may join for prospecting purposes, not social ordering.

One noted exception of a vocal signal with an agreed-upon, though historically much debated, function is that of bottlenose dolphin (*Tursiops truncatus*) signature whistles. In 1965, Melba and David Caldwell identified and investigated individually distinct whistles that they termed “signature” from recordings of identified captive bottlenose dolphins. The whistle contours (as represented on frequency versus time plots called spectrograms) were individually distinctive

and stereotyped in certain acoustic features. Since the late 1960s, signature whistles have been suggested for several species, including but not limited to Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), Atlantic spotted dolphins (*Stenella attenuata* and *S. frontalis*), and spinner dolphins (*S. longirostris*). Much debate ensued over the years related to determining the function of signature whistles; Rachel Smolker and colleagues confirmed that mothers and their offspring use signature whistles during separations and reunions for bottlenose dolphins in Monkey Mia. The signature whistle is a contact call to maintain group cohesion and identify the location of the sound-producing dolphin (Smolker et al. 1993; King et al. 2014). Sayigh et al. (1990) determined that a unique signature whistle develops early in a dolphin’s life, and it may be created in relation to the signature whistle of a dolphin’s mother. Through playback studies, bottlenose dolphins were confirmed likely to produce the signature whistles of peers as a method of labeling or contacting those individuals (King et al. 2014). Whistle copying (aka matching) is produced by close associates (at least in bottlenose dolphins), which suggests an affiliative function in the maintenance of social bonds in a fission-fusion society (King et al. 2014). Signature whistles in bottlenose dolphins help maintain individual animal identities within a group. Bruck (2013) demonstrated that individual dolphins are able to recognize signature whistles of dolphins they were once housed with, apparently up to two decades previously. Other vocalizations have been linked to various behaviors in dolphins, including foraging and feeding behavior, excitement or anxiety, courtship, aggressive behavior, and sexual play (Herzing 1996).

### **Mysticetes – Acoustic Communication**

The Mysticetes or baleen whales are the largest cetaceans with females typically larger than males (Mann et al. 2000). Baleen whales have no teeth; they have keratinized material called plates that hang from the roof of the mouth that are used for filtering prey from the water. Most baleen whales make long seasonal migrations between feeding and breeding grounds, annually. There are



14 mysticete species comprising four families: (1) Eschrichtiidae (single species of gray whale), (2) Balaenopteridae (eight species of rorquals), (3) Balaenidae (four species of right and bowhead whales), and (4) Neobalaenidae (one species of pygmy right whale).

Baleen whales produce low frequency sounds that travel long distances in water. Sounds can range in duration from 0.5 s to several minutes, if not longer. Blue (*Balaenoptera musculus*) and fin whales produce very low-frequency calls, as low as 20–40 Hz (Richardson et al. 1995; Au and Hastings 2008), whereas humpbacks produce songs that can last tens of minutes and range from a few hundred hertz to 1.5 or 2 kHz (Mann et al. 2000). Male humpbacks also produce social sounds on the winter breeding grounds. Broadly, baleen whale calls have been categorized into simple calls (low frequency <1 kHz, narrow band, frequency- and amplitude-modulated), complex calls (broadband, 500 Hz–5 kHz, frequency- and amplitude-modulated), and grunts and knocks (<2 ms, 3 kHz–30 kHz) (Perrin et al. 2009). Mysticete chirps and whistles tend to be >1 kHz, but change frequency rapidly and are less than 0.10 s in duration. These pure tones involve harmonics and seem to be produced by most baleen whales.

Several social functions have been proposed for mysticete sounds that include long-range contact, assembly calls, sexual advertisement, greeting, spacing, threat, and individual identification; however, only rarely has a specific sound been associated with a given behavioral event. It is probable that sounds produced by mysticetes serve to synchronize biological or behavioral activities in listeners that promote subsequent feeding or breeding. Known and examined baleen whale sounds seem to fall into three basic categories: low-frequency moans, short thumps or knocks, and chirps and whistles. Low-frequency sounds (20 Hz) of blue whales are recorded across ocean basins at distances of several 100 km. Blue whales are the largest creatures to inhabit the earth; they traverse large expanses in a relatively short time. It is no wonder then that the social structure of these animals reflects a scale that we are only beginning to comprehend. However,

tracking the distinctive vocal behavior of this species may provide important clues. “Old blue,” a single blue whale, was tracked for nearly 80 days using its distinctive, repeated, 20 Hz signal received by bottom-mounted SOSUS (Navy hydrophone) arrays off the coast of the eastern U.S. (Perrin et al. 2009).

Additional calls produced by several species include moans, sweeps, pulse-like sounds, upsweeps, downsweeps, grunts, groans, songs, and more. For example, Clark (1990) documented southern right whale (*E. australis*) sounds in relation to behavior and found that their sounds were not random, but were related to social context and activity. Resting whales were least soniferous, whereas mildly social groups produced the most varied suite of sounds, including high, hybrid, and pulsive calls, body and flipper slaps, and forceful blows. Clark’s work showed that “up calls” functioned as a request for contact between whales. Minke whale (*Balaenoptera acutorostrata*) “boing” sounds went unidentified for 50 years; the calls were first identified in the 1950s but only confirmed recently as part of the minke whale repertoire (Rankin and Barlow 2005).

### Odontocetes: Acoustic Communication

Toothed whales produce many types of sounds broadly classified into two types: clicks and pulses (amplitude-modulated) and pure tones (frequency-modulated). The former are clicks, click trains, and echolocation while the latter are exemplified as whistles, chirps, screams, etc. that are used in communication. Not all odontocetes have been shown to produce whistles; however, all species are believed to produce pulsed or click sounds.

Burst pulses occur when dolphins release clicks so rapidly (e.g., 200–1700 clicks per second) that it is not believed that they are able to gain any sonar information from the returning click echoes. Burst-pulse sounds are a series of broadband pulses with substantial ultrasonic energy that have been associated with agonistic behavior, have an aural component (to the human ear) that sounds singular (though these calls are often composed of 100 s or 1000 s of individual clicks), and have been identified as expressing

emotional content or communicating excitement, agitation, and other emotions (reviewed by Herzing 1996). Dolphins of many species release bursts pulses when they are excited or angry, and burst pulses are thought to convey information about a dolphin's emotional state.

Blomqvist et al. (2005) found a very specific burst signal produced by bottlenose dolphins that appears to be a "play" signal – indicating to other dolphins that "it's time for games, so I'm not really being aggressive." Burst pulses can be extremely loud, and dolphins may use them during aggressive encounters – possibly to hurt the "ears" of other dolphins. Burst pulse sounds are often seen in a social situation where males are herding female dolphins, where burst pulses are directed at the genital region of the fleeing females (Mann et al. 2000; Herzing 1996). They have also been observed when a mother emits a loud burst pulse directed at a misbehaving calf (McCowan and Reiss 1995). Different types of burst pulse sounds used during aggressive encounters have been called "squawks" and "barks" – these click trains are often produced so rapidly that to the human ear they sound like a continuous sound, however, they are a series of tightly spaced clicks. It is not always easy to tell the difference between a burst pulse and an echolocation click train; only in the last few years are scientists understanding more on how dolphins use burst pulses in social situations.

Echolocation (also known as sonar or biosonar) comprises broadband, amplitude-modulated, short-duration clicks, with a peak frequency represented in the ultrasonic range (Au 1993). Burst-pulse sounds more often have a lower source level and shorter interclick interval than echolocation click trains, although both have a highly directional beam-pattern (Au 1993). Sperm whales produce codas or sets of clicks up to 30 kHz and from 1 to 90 clicks per second that may be used in echolocation. Some researchers propose that each coda or set of clicks is an identifier for the individual sperm whales when feeding in very deep water allowing their sounds to be detected at 10–15 km away (Antunes et al. 2011). Madsen et al. (2013) used DTags to study sound generation in sperm whales, suggesting that this species' head to be

the largest sonic generator on the planet. Air is recycled within the head for continued production of clicks while diving deep during foraging activity. Pilot whales (*Globicephala melaena*) also produce a variety of calls – both tonal and pulsed.

Whistles have fundamental frequencies between ~4 kHz and 30 kHz that likely contain higher harmonics (whole number multiples of the fundamental frequency), are omnidirectional, and are categorized according to their plotted spectrographic shape of the fundamental frequency with time. Examples of categorization contour shapes include constant frequency, upsweep, downsweep, concave (hill), convex (valley), or sinusoidal waves. Harmonics likely play a role in group coordination and movement, at least among Hawaiian spinner dolphins (Au and Hastings 2008); hearing the number of harmonics in a whistle likely plays a role with respect to which direction group members will move when commencing night foraging activity.

While all delphinids produce pulsed and click vocalizations, not all species whistle (Madsen et al. 2012). Generally, whistling odontocetes are highly social. Whistles can be pure tones, frequency-modulated, increasing or decreasing in pitch, or fluctuating in tone. Whistles are produced singly or in series and can possess harmonics or not. There are at least four groups of nonwhistling odontocetes, including the porpoise family (Phocoenidae, including Dall's porpoise *Phocoena dalli* and harbor porpoise *Phocoena phocoena*), Commerson's dolphins (*Cephalorhynchus* sp.), pygmy sperm whales (*Kogia* sp.), and sperm whales. For example, dusky dolphins (*Lagenorhynchus obscurus*) are one of the few nonwhistling delphinids; Vaughn-Hirshorn and colleagues compared dusky dolphin audio data from Argentina and New Zealand and showed that these dolphins likely use single, short duration sounds with a constant interclick interval, as well as closely spaced clicks for communication (see Würsig and Würsig 2010). Interestingly, these species do not have the single, thin, midline vocal fold found in most other species of odontocetes. For species that do whistle, there is experimental evidence from dolphins that indicates whistles can be generated by the left

phonic lip while click sounds can be simultaneously generated by the right phonic lip (Cranford et al. 2011; Madsen et al. 2012).

### Stereotypy

Stereotypical calls produced by members of a social group that vary among populations have been termed dialects and have been described in at least two species of odontocetes. In British Columbia, matrilineal groups of killer whales have repertoires of call types that are unique to each pod. Cultural transmission (a cognitive process based on social learning that results in the modification of current behaviors; Henrich 2001) has been implicated in the development of killer whale dialects (Filatova et al. 2013). In sperm whales, codas are stereotyped sequences of 3–40 broadband clicks usually lasting less than 3 s in total. Luke Rendell and Hal Whitehead categorized these codas into six acoustic “clans” for populations in the South Pacific and the Caribbean (see Au and Hastings 2008; Antunes et al. 2011). These vocal clans have ranges that span thousands of kilometers, are sympatric, and contain many thousands of whales. Like killer whale dialects, the codas produced by these clans may result from cultural transmission.

### Mimicry

Scientists have learned that dolphins are amazing vocal mimics – able to reproduce manmade whistle structures with precise accuracy (Caldwell and Caldwell 1972; Reiss and McCowan 1993). Dolphins produce whistles during social situations, when separated from peers, when excited, when happy, and when panicked (reviewed in Herzing 1996). Different whistles are produced in different situations, and scientists have been attempting to catalog and categorize whistles from different study populations for years. This is an extremely complicated process, and much has been written about how various species develop and use whistle communication. The whistles and other vocal calls of killer whales have received considerable attention (e.g., Barrett-Lennard et al. 1996), and scientists have discovered that family groups (clans) appear to reliably produce distinct categories of whistles and other calls that are stable across

time, and that appear to be taught to new members of the group.

### Nonvocal Communication

All cetaceans engage in nonvocal acoustic communication. Breaches, tail slaps, pectoral fin slaps, jaw claps, etc. are examples of actions or behaviors that have a percussive quality or function. These actions do not appear to be produced indiscriminately or reflexively, but rather are under the intentional control of the animal exhibiting the behavior. Baleen whales have been observed to produce a group of behaviors termed surface-active that can be viewed from the surface and involve one or more whale bodies or an extremity being shoved above the water and slapping or crashing back down onto the surface. These percussive behaviors are audible under water for several kilometers around a whale. Most toothed whales produce a slapping noise at the water surface using powerful strokes of their fluke that are called lob-tails or tail (fluke) slaps and of their pectoral fins, as well as “head” or “chin” slaps. Fluke slaps are often considered a sign of frustration or irritation though these actions have been documented during play among dolphins (Mann et al. 2000; Greene et al. 2011). These behaviors yield a percussive sound that can travel several hundred meters. While underwater, dolphins also have been observed to fluke slap at fish, other dolphins or nothing; the result is a loud clap-like sound with numerous tiny bubbles that cavitate from the water off the fluke tips. Several toothed whale species produce a jaw pop or jaw clap during aggressive contexts that include males herding females during socio-sexual activity (Mann et al. 2000).

Dusky dolphins are perhaps the most acrobatic delphinid producing three types of leaps confirmed to be functionally related to foraging and socializing activity; the three types include head-first re-entry leaps, noisy leaps, and social, acrobatic leaps. Resulting sounds from their breach-like leaps have been described to travel up to 1 km (Würsig and Würsig 2010): the noisy leaps likely function to draw peers to a fish ball while also disorienting prey keeping them tightly schooled. Upon water re-entry after a spin, a

breach, a back slap, or a head or tail slap, Hawaiian spinner dolphins generate omnidirectional noise that propagates over short to intermediate distances. Some bottlenose dolphins (*Tursiops* sp.) use tail slaps to create a percussive bubble production in shallow waters over sea grass beds to scare fish from vegetative cover, termed *kerplunking* (Mann et al. 2000). Many odontocetes produce loud tail slaps at the water surface, which seem to indicate distress or aggression.

Both baleen and toothed cetaceans of all sizes breach (i.e., leap either partially or fully out of the water). Though potential functions for breaching remain unclear, it is likely that the resulting percussive sound when a cetacean's body re-enters the water carries information to conspecifics in the near vicinity. Breaches likely function as a display during aggressive or agonistic activity or during play.

## Visual Communication

Although humans generally tend to think of communication occurring with sound (thanks in part to our reliance on language), much communication also happens within the visual modality. Visual displays can be simple (e.g., sexually dimorphic features) or complex (e.g., behavioral sequences) and can be detected both above and below the water surface depending on visibility (Reynolds and Rommel 1999). Movements and postures often are highlighted in species with conspicuous color patterns (e.g., killer whales, humpbacks). In clear water, visual signals provide cetaceans a close-range alternative to acoustic signaling; however, a display could inadvertently alert predators or prey. Visual cues include everything from gestures to movements to coloration. Disruptive coloration (spots, stripes, bold colors) likely evolved for social signaling, or to deceive prey and predators. Pelagic species tend to live in large, mixed-species schools with the most complex color patterns among small cetaceans.

Overt actions and gestures such as open-jaw threat displays, aerial leaps, tail lobes, flared pectoral fins, and S-shaped postures form the majority of behavioral visual displays expressed by cetaceans.

Color pattern complexity may be important for species and individual recognition, as well as social signaling (Thomas and Kastelein 1990). For example, Atlantic spotted dolphins slowly develop spots as they age, with adult dolphins covered in mottled spot patterns – this quickly conveys information about a dolphin's age (Herzing 1996). Many color patterns – like counter-shading and the distinctive black and white markings of killer whales – are likely used for camouflage or to help when hunting prey species. However, some of the markings also help species to quickly tell the difference between animals belonging to the same or different species.

Sexual dimorphism is rare in cetaceans. In general, males tend to be larger and bulkier – males are larger because they need to fend off competition from other males. Male Amazon river dolphins accumulate scars all over their body that turns their skin bright pink, making it easier to pick out males from females (Martin and Da Silva 2006). Male narwhals usually have a single long tusk – unlike females who rarely develop a tusk. This may be a signal to other males about the size and power of the individual sporting the biggest tusk (Perrin et al. 2009). For the harbor porpoise and many baleen whales, the female is actually larger than the male, but for the sperm whale, males are as much as three times larger than the females. These differences between the sexes signal vital information that individuals can use to determine how to approach social situations.

## Postures

Overt actions and gestures such as open-jaw threat displays, aerial leaps, tail lobes, flared pectoral fins, and S-shaped postures form the majority of behavioral visual displays expressed by cetaceans. Changes in posture can be used to communicate to conspecifics, predators, and prey. Posture and behavioral signaling can be used to synchronize actions among individuals or groups as a signal for group coordination or for social interaction (e.g., synchrony between male coalitions of bottlenose dolphins when herding a female, Connor and Krützen 2015). During aggressive encounters, dolphins may flare out their pectoral fins in an attempt to appear larger, and open their

jaws – a threat signal. Male belugas, dolphins, and gray whales hold S-shaped postures during courtship encounters with females, presumably a visual signal to females indicating the male's interest (reviewed in Hill et al. 2015).

### Bubbles

Cetaceans (Odontocetes) often release bubbles from their blowhole when making whistle sounds, although the release of bubbles does not always coincide with the production of whistles. Bubbles appear to be an extra communicative signal and can take a variety of forms: bubble streams, bubble clouds, and bubble rings. A large bubble cloud is a conspicuous signal and often is produced as a threat. Dolphins, belugas, and other toothed whales often blow bubble streams and bubble clouds in a variety of social situations, and while these are primarily visual signals, the production of a large bubble cloud also produces a distinctive noise that can likely be heard over short distances.

### Object Carrying

Some dolphins in Australia have been observed using sponges as foraging tools – not a communicative signal at all, but in the Amazon, the Boto (or Amazon river dolphin) has been seen carrying sticks and rocks in its mouth apparently as a visual display meant to impress potential mates (Martin and Da Silva 2006). Males will collect objects and often swim out of the water holding the rocks or sticks in the air before slowly sinking back into the water. These object carrying displays may signal to the females the male's worth and attractiveness to the females, although this hypothesis has not been evaluated fully. Moreover, it is unclear as to how these behaviors are acquired. Perhaps they are learned from other dolphins, or they may be innate tendencies. Additional research is needed to better understand the mechanisms operating behind these behaviors.

### Tactile Communication

Visual displays are useful for close-range communication and, because of close proximity, visual displays may readily become tactile signals. Extensive touching and rubbing occurs in

cetaceans in both managed care and free-ranging settings during play, sexual, maternal, and social (affiliative and agonistic) contexts using the rostrum, mouth, flippers, fins, flukes, abdomen, and the entire body (e.g., Dudzinski et al. 2010; Dudzinski and Ribic 2017). Perhaps one of the most important modes of signaling in a dolphin's world is the use of touch. Dolphins have skin that is quite sensitive to even the lightest touch. Dolphins are known to rub their bodies against each other and also to engage in intricate rubbing behaviors using the pectoral fins (e.g., Dudzinski et al. 2010; Dudzinski and Ribic 2017). Dolphins will rub their fins into the fins of other dolphins, engaging in a behavior that looks a lot like holding hands. Sometimes dolphins will seek out rubs by positioning their bodies under the fin of another dolphin. Most all of this type of tactile behavior is thought to be a sign of affiliative contact that is performed intentionally as indicated by preferences for partners and positions. Much less is known about touch in other cetaceans. Contact between free-ranging belugas occurs during large social congregations in shallow areas for belugas, but it is unknown if the contact is intentional, as implicated in the dolphins, or a byproduct of proximity. Research with belugas in managed care suggests that contact occurs primarily between young belugas, mothers and their offspring, and between males (Hill et al. 2016). Observations of free-ranging mysticetes like humpbacks and grey whales suggest that contact primarily occurs between mothers and their offspring. These limited observations suggest that there may be species differences in the frequency of touch and the participants involved.

Not all contact behavior, however, is friendly. Tactile contacts often are observed during aggressive behavior but are characterized by more overt actions, such as biting, raking, ramming, wrestling, and butting. During aggressive encounters, dolphins can body slam each other, butt heads (melons), and ram each other with their rostrums. They also smack each other with their powerful flukes, and have even been observed leaping out of the water at each other and slamming into each other while airborne. With sensitive skin, these kinds of aggressive contacts surely must hurt, and these are clearly aggressive signals.



An inclination for tactile responsiveness has been noted in the studies of wild cetaceans as well as of those individuals in managed care. Among mysticetes, the gray whales of San Ignacio Lagoon, Mexico, are noted for approaching and rubbing under small boats, and for their tolerance of petting by tourists. In the wild, both Atlantic spotted and bottlenose dolphins rub body parts against conspecifics as well as into the sand or along rocky edges. Affiliative contact behavior (petting, stroking, nuzzling) has been documented in many cetacean species (e.g., humpback and North Atlantic right whales, *Eubalaena glacialis*) and is especially common among mothers and their calves (Hill et al. 2016). Contact swimming bouts, where one dolphin lays its pectoral fin on the flank of a conspecific, have been recorded in bottlenose dolphins in Shark Bay, Australia (Mann et al. 2000). Dudzinski et al. (2010) confirmed that pectoral fin contact is conserved across dolphin species and habitats, as well as contacts sharing similar function across body parts contacted. All observed odontocetes in managed care seek and are receptive to gentle body contact. Mild tactile stimulation (e.g., rubbing of gums, flippers, or dorsal fin) serves as an effective re-enforcer in training of most delphinids.

## Cetacean Communication Cognition

As described previously, communication signals may be as simple as body coloration or posture presented or as complex as a series of behaviors or sounds produced. Signals may be expressed with or without intention, which is obviously difficult to assess. Signalers can actively emit a signal, whether acoustic, visual, or tactile, with an objective that it will be received by the receiver and responded to with an appropriate response. Similarly, a signal may be emitted reflexively stimulated by a particular stimulus. Unfortunately, we cannot ask the animals about the intention of said emitted signal. Rather, researchers must rely on behavioral patterns and context to determine questions of intentionality or cognition. For example, bubble streams are often produced at the same time as whistles by immature cetaceans. However,

air released through the blowhole is not necessary to produce a whistle. Thus, these bubble streams may indicate a lack of control over blowhole air release during sound production and are unintentional. By comparison, older animals may be able to “choose” when to emit bubble streams as they will produce the bubble streams with or without corresponding vocalizations. Moreover, these older cetaceans can manipulate the amount of air released and the bubble shape produced with apparent intention (e.g., bubble rings, bubble bursts, Perrin et al. 2009). In contrast, the disruptive coloration pattern or mottling of certain species or dimorphic characteristics, such as the narwhal tusk or the killer whale dorsal fin, are honest visual signals that are outside of cognitive control. Similarly, tactile and acoustic signals likely have both reflexive and cognitively mediated components. Cetaceans may choose to direct certain types of contact or sounds toward specific individuals or during certain contexts, or they may simply respond to a specific stimulus with a stereotypical response. There is increasing evidence that cetaceans are modifying their acoustic signals to combat the increase in anthropogenic noise within their ocean habitat, which is indicative of cognitive control (e.g., right whales get louder, Parks et al. 2011). Finally, as expressed before, the least understood signal is chemical communication. Observations have suggested that individuals will swim through the excrement of a conspecific, sometimes with a mouth open and sometimes not. Additionally, experimental discrimination studies and anatomical/physiological research have begun to provide corroborating evidence for possible chemical signals. However, it is highly unlikely that these signals are cognitively controlled, as the chemicals are produced by the body in response to internal processes (i.e., estrus, illness, metabolic processes).

## Summary

Cetaceans have an entire suite of communication signals at their disposal. Clearly, life history and environment play a role in dictating the type and context in which signals are emitted. Mysticetes



tend to travel in small groups and are spaced over large distances. Their primary communication mode inherently is acoustic-based. However, many species do socialize with each other during breeding seasons and at various feeding grounds. These close-proximity interactions are likely facilitated by the other communication systems. Odontocetes tend to travel in larger groups and inhabit many different types of environments, making a diverse but comprehensive suite of communication signals necessary. Turbid, murky waters make eyesight virtually useless underwater as in the case of botoes, which make the reliance upon acoustic signals, tactile signals, and possibly chemical signals much more critical (Hanke and Erdsack 2015). Much remains to be discovered about the various communication systems of cetaceans despite over 50 years of research effort.

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## Cetacean Diet

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## Definition

Cetacean diet refers to the types and amount of food taken by whales, dolphins, and porpoises, all of which belong to the mammalian order Cetacea.

## Introduction

Cetaceans are typically top predators in marine (and in a few cases riverine) ecosystems, i.e., they are situated at the top of the marine food chain, and they may play an important role regulating the populations of their prey and contributing to the stability of the ecosystem. Cetaceans have few natural predators aside from sharks, although killer whales (*Orcinus orca*) take adults and juveniles of other cetacean species and the bottlenose dolphin (*Tursiops truncatus*) is known to attack and kill (but not eat) smaller cetacean species such as the harbor porpoise (*Phocoena phocoena*). Recent evidence indicates that gray seals also prey on harbor porpoises (e.g., Leopold et al. 2015).

Present-day cetaceans have evolved from an original common design to be able to exploit different kinds of prey. Their morphological adaptations to different diets form the primary basis for the division of the order Cetacea into two suborders: the Mysticeti (baleen or *mustached* whales), which feed on small organisms such as zooplankton and small fish, and the Odontoceti (toothed whales, odontocetes), which feed mainly on fish and cephalopods. The mysticete whales are characterized by the presence of baleen plates, made out of keratin, a protein that is also found in other mammals' hair and nails/claws. The baleen plates hang from the upper jaw of the whale and form a filtering mechanism by which it is able to trap shoals of the zooplankton and other small organisms (e.g., krill, copepods, amphipods, and even small fish) that constitute its food. The small size of these prey does not limit the size of the whale, and, in fact, the blue whale (*Balaenoptera musculus*), which belongs to this group of cetaceans, is the largest living animal. In addition to the baleen plates, Mysticeti have enlarged mouths, adapted for the filtering of huge amounts of food. Because of the nature of the filter-feeding process, baleen whales might not be expected to display cooperative hunting. However, some species (notably humpback whales) may cooperate in groups of up to 20 individuals, using *bubble netting* to concentrate prey. One whale in the group dives to locate prey and herds them to the surface,

releasing air bubbles while spiraling toward the surface. The bubbles form a tubular *net* that *traps* the prey which the whales then take (see, e.g., Wiley et al. 2011).

As their name implies, most odontocetes have teeth, although the number and size vary greatly among species. Their prey ranges from small fish and crustaceans to the giant squid (*Architeuthis* spp.), remains of which have been found in the stomachs of sperm whales (*Physeter macrocephalus*). Those cetaceans feeding on squid (teuthophagous) tend to have fewer teeth or less visible teeth, while those feeding on fish (piscivorous) tend to have long jaws and numerous small teeth. Some odontocetes have developed echolocation, using the echoes returned when their emitted sound hits the target, to aid in the locating of food, and some also display cooperative hunting of prey.

In this brief overview, we draw examples largely from the Northeast Atlantic, but the general principles apply globally.

## What Do Cetaceans Eat?

As already mentioned, cetaceans eat a wide range of prey, in terms of both the type and size of animal consumed. Baleen whales typically feed on small crustaceans, but the type depends on the species of whale and also on the area. For example, in the Antarctic, the main prey of rorquals (family Balaenopteridae) (and of many other species) is euphausiids (krill), of which only one species, *Euphausia superba*, makes up the bulk of the diet of all these predators. In other parts of the world, other euphausiid species are consumed by whales (e.g., *Meganyctiphanes norvegica* in the North Atlantic) together with other crustaceans, such as copepods. Small fish are also known to be eaten, notably by minke whales. Rorquals search for shoals of small prey, and, when they find them, the whales are able to expand their furrowed throats letting big volumes of water and prey into their mouths. Once maximum capacity is reached, the whale uses the muscles in the throat to force water out through the baleen plates – which are shorter and broader than

those of the other families of baleen whales. The prey are retained by the baleen, and the whale then swallows the millions of small organisms that constitute its diet. Because of the way they feed and where their prey are found, rorquals are moderate to shallow divers and swimmers and show a coastal but also deep-ocean distribution.

Because the copepods and the other organisms on which they feed are relatively immobile, whales of the family Balaenidae are slow swimmers and shallow divers and tend to have a coastal distribution. They have long baleen plates but no furrows in the throat, and they feed by swimming with their mouths open, getting water in but making it pass through the baleen on its way out trapping the prey. Feeding can take place at the surface and in the water column, and when feeding at the surface, this type of feeding is called *skimming* or *skim feeding*. This family includes the right whales (*Eubalaena* spp.), so called because they were the *right whale* to hunt due to the ease with which they could be captured and the fact that they would float after being killed.

Gray whales (*Eschrichtius robustus*) (Eschrichtiidae) have specialized in taking benthic crustaceans such as amphipods and isopods at the seafloor.

Odontocetes have teeth developed to feed on fish and squid. Unlike most terrestrial mammals, these teeth are usually all the same shape (homodont), typically conical or spade-like, although male narwhals (*Monodon monoceros*) normally develop a single tusk (very rarely two tusks) that grows from one of the two teeth the species has retained. There are many species of odontocetes, which range widely in size from less than 2 m in length in the smaller porpoises to over 18 m in the sperm whale. Species feeding mainly on squid tend as a general rule to have fewer or less visible teeth, while those feeding on fish tend to have long jaws and numerous small teeth. It has been hypothesized (MacLeod et al. 2006) that the mode by which an odontocete captures its prey conditions the size of prey it can take, with those species that possess long jaws and many teeth able to capture a wide variety of relatively large prey (for the size of the predator) using their jaws as pincers and employing suction feeding.

Representatives of this group would include many small cetaceans such as the common (*Delphinus delphis*), striped (*Stenella coeruleoalba*), and bottlenose (*Tursiops truncatus*) dolphins and porpoises (e.g., *Phocoena* spp.). Bigger toothed whales such as the killer whale would also belong to this group. The diet of all the smaller species mentioned above has been recorded as being mainly based on fish but with some cephalopods also being consumed (e.g., Santos et al. 2013). Crustacean remains have also been found in some stomachs but usually as a minor component of the diet.

In odontocete species with fewer teeth (e.g., the beaked whales, family Ziphiidae), the food consists mainly of cephalopods which are ingested using suction feeding. This method of feeding, however, restricts the size of the prey that can be consumed, and therefore a relatively narrow range of prey sizes is usually eaten (MacLeod et al. 2006). This group includes species that are able to perform dives that are among the deepest and longest known in cetaceans, presumably in search of their prey. Oceanic squid of several families (Histiotteuthidae, Cranchiidae, Ommastrephidae, Gonatidae, etc.) has been reported as the main prey of most of these species (Cuvier's beaked whales, *Ziphius cavirostris*; northern bottlenose whales, *Hyperoodon ampullatus*; sperm whales, e.g., Santos et al. 1999). However, some beaked whales of the genus *Mesoplodon* have been found with only remains of fish in the stomachs.

The sperm whale could be considered an exception to the general rule, as a largely teuthophagous species in which the number of teeth has not been reduced (although teeth are only present in the lower jaw). It has been suggested (Clarke 1980) that teeth are only used to grasp prey, since fresh prey has been found generally intact in stomachs and because food has been found in the stomachs of young sperm whales in which the teeth had not yet erupted and in the stomachs of whales with deformed jaws (Rice 1989). Sperm whales have been found to feed on a wide range of cephalopod and fish species with a wide range of body sizes (see reviews by, e.g., Rice 1989; Whitehead 2003).

The sperm whale is known to dive to more than 1,000 m, as revealed by animals found dead entangled in undersea cables and damage to cables that was attributed to sperm whales even when the carcass was not found.

Finally, earlier we mentioned the killer whale or orca. While some populations (ecotypes) do feed on marine mammals including cetaceans, seals, and sea otters, others specialize on fish. They may also eat penguins, squid, turtles, seabirds, and even moose.

## Feeding Strategies

We have already touched on feeding mechanisms and feeding preferences in the previous sections without saying much about the behavioral processes involved. As noted, many cetaceans have apparently specialized in feeding on fish (piscivorous), while others specialize on cephalopods (teuthophagous). Some cetaceans take both kinds of prey.

It has been often asserted or assumed that, once a basic preference for (or adaptation to) feeding on fish or squid is taken into account, most cetaceans are opportunistic feeders, selecting their prey, in terms of species and sizes eaten, according to availability – the alternative being specialization, whereby a predator selects a *preferred* prey species and will only consume other prey types when the preferred prey is not available. These ideas about feeding strategies can be traced back through various paradigms, including optimal foraging theory (e.g., Hughes 1980) and functional responses (Holling 1959), but, as Dunnet (1996) pointed out, opportunism, selection, and availability are “in fact shorthand for very complex biological interactions about which we know only a little in quantitative terms,” and the existence of these strategies in cetaceans is difficult to prove (Santos et al. 2013).

In predators that can be readily observed in captivity or indeed in the field, and in which the behavior of individuals can be followed, it is relatively straightforward to gain insights into prey selection behavior. However, with the current methods to study cetacean diet, regardless of

whether dead or live animals are sampled, we normally have only a snapshot or average of diet choices. However, an approximation which has been explored is to analyze the relationship between prey abundance and their importance in stomach content samples. The rationale behind such analyses is that there would be a positive relationship between prey abundance and their importance in a cetacean stomach if the prey is a preferred prey. Because other prey would only be eaten only if preferred prey are not available, there would be a less clear relationship between abundance and importance in the stomach contents (and their importance in the diet would decrease as the abundance of preferred prey increases). However, direct comparisons between abundance of prey species and consumption by cetaceans are not always possible because of the different scales on which data on predator diet and prey abundance are usually available, and the spatial variability in occurrence of prey patches, such that environmental variables may be better predictors of prey occurrence than sampling the prey directly (Torres et al. 2008).

The selection pressures affecting diet selection may go beyond considerations of energetics and nutrients. Feeding on some prey can have lethal consequences, as evidenced by findings of dead cetaceans, which had apparently died from asphyxiation due to fish lodged in their throats. Interestingly, a recent study shows that bottlenose dolphins have learned to decapitate catfish, apparently to avoid ingesting spines which can cause fatal injury (Ronje et al. 2017).

## Methods to Study Diet

There are several methods available to infer the diet of cetaceans, and we will mention some of their advantages and disadvantages. Knowledge of cetacean diet can provide a valuable insight into their biology and their role in the marine ecosystem in addition to helping answer questions about the potential effect of predation on prey populations and on threats to cetaceans, for example, arising from interactions with fisheries (Pierce and Boyle 1991).

Knowledge of cetacean diets has improved over the years with the establishment of systematic data collection (latterly from strandings and bycatches) that has allowed access to larger sample sizes, development of new prey identification methods, and new techniques to infer the diet of individuals over longer time scales and various numerical and statistical tools (e.g., quantitative fatty acid signature analysis, mixing models applied to stable isotope data). Several reviews of methodology have been published, including Pierce and Boyle (1991) and Tollit et al. (2010), so we will not attempt to cover all available methods here.

### Stomach Content Analysis

When cetacean were hunted, information on diet was gathered by the examination of the stomach contents of recently killed individuals or observations of the food remains regurgitated by the whales after being harpooned. In some cases, the material observed led to mistaken assumptions, as can be seen from the following quote referring to baleen whales caught off Bermuda:

“Their feeding on grass, growing at the bottom of the sea, appeared by cutting up the great bag of maw, in which was found two or three hogsheads of a greenish grassy matter.” (Anon 1665)

Investigations on diet through the systematic identification and quantification of the prey remains found in the stomachs provided the first evidence about the prey species (and the sizes and amounts) consumed and allowed scientists to make inferences on the ecology of the whale and dolphins based on their diet. The late Malcolm Clarke pioneered the use of cephalopod mandibles (beaks) in whale stomachs to make inferences about diet, and, in some cases, cephalopod species new to science were first identified from remains found in the stomachs of deep-diving cetaceans such as the sperm whale and beaked whales (Clarke 1980).

Stomach content (and fecal and regurgitation) analysis is relatively straightforward in that it does not require specialized equipment. However, it is time-consuming, since it involves the identification, counting, and measurement of the hard prey remains (e.g., fish bones and otoliths, cephalopod mandibles, and crustacean exoskeletal remains)

present to characterize and quantify diet and to back-calculate original prey size. Prey identification can be aided by the existence of reference material and the availability of reference guides (i.e., Clarke 1986; Härkönen 1986), but experience in identification is also important. The process may be simplified by using only otoliths to quantify fish in the diet, but this can result in incomplete and biased results. A major issue, especially in relation to (calcareous) fish otoliths, is the effect of acid digestion which can reduce size, remove key identification features, and ultimately entirely dissolve otoliths, to varying degrees depending on the species and size of fish. Some authors have *corrected* for effects of digestion, while others recommend using only undigested prey remains.

The advantages of, and possible biases in, dietary information derived from the analysis of stomach contents of stranded and/or bycaught animals have been discussed in detail in the literature (e.g., in the reviews by Pierce and Boyle (1991) and Tollit et al. (2010)). Biases can arise both from the source of samples, e.g., stranded animals may not be representative of the population because sick/injured animals or animals feeding near the coast are overrepresented. Concerns have also been raised when the origin of the samples is fishery interactions, because bycaught animals could have been feeding near the nets and species present in the nets could be overrepresented compared to the typical diet. Biases also arise from the samples themselves, for example, due to digestion or to secondary ingestion, whereby the remains found include prey remains from the stomachs of larger prey. Even with these potential biases, stomach content analysis remains the most widely used method to determine the diet of cetaceans, because it can provide fully quantitative information. Such data are needed for trophic models that can help determine the role of cetaceans in the ecosystem. Many other approaches either lack resolution (e.g., bulk stable isotope analysis), are not fully quantitative (e.g., DNA-based prey identification), or rely on availability of stomach content results to facilitate interpretation (e.g., fatty acid and stable isotope analyses).



## Fatty Acid Analysis

Cetacean blubber (the vascularized layer of fat beneath the skin) can represent up to 50% of body weight and is used for energy storage, as an insulator, to aid in thermoregulation, and buoyancy, and gives a dolphin or whale its hydrodynamic shape. Blubber is mainly constituted by triacylglycerols consisting of three fatty acids each attached to one of the three carbons of a glycerol molecule with an ester bond through the oxygen atom. Although animals can synthesize fatty acids, these compounds are mainly incorporated through the diet (especially in the case of polyunsaturated fatty acids which are biosynthesized only by phytoplankton and macroalgae). Fatty acids from the prey are not degraded, but they accumulate in the blubber during the lifetime of the animal; thus, blubber fatty acid composition can reflect the diet over a period of days or months (Iverson et al. 1995).

Fatty acids have been used to infer the diet of predators following this principle, with the possibility to quantitatively determine the proportion of each prey type consumed by a predator using quantitative fatty acid signature analysis (QFASA) (Iverson et al. 2004), a numerical modeling approach that uses fatty acid signatures of putative prey species to estimate the most likely contribution of each prey species to the diet, based on the observed predator tissue composition.

Although, in comparison with stomach content analysis, analysis of fatty acids requires specialized equipment (e.g., a gas chromatograph), it has the potential advantage over the former that information on diet can be obtained from animals with empty stomachs, samples can be taken from live animals (using biopsies), and the technique provides dietary information integrated over a longer time period.

However, several issues need to be taken into account when interpreting fatty acid values: first, cetacean blubber is stratified, with differences between the fatty acid profiles of the inner blubber (which has a more recent dietary origin) and outer blubber (that has a more structural role); secondly, lipids break down during the decomposition of a dead animal, and fresh carcasses may be needed to obtain reliable fatty acid profiles. Thirdly,

although most fatty acids are incorporated from the diet, others can be biosynthesized (mainly short-chain fatty acids), and it appears that amounts deposited may not be exactly proportional to amounts ingested. Therefore, *calibration coefficients* are needed that take into account predator lipid metabolism and deposition when estimating diet using the QFASA approach. For seals, these calibration coefficients were calculated using captive feeding experiments (Iverson et al. 2004), but to date there are still no calibration coefficients for cetaceans, although recent work on polar bears proposes that diet and calibration coefficients can be estimated simultaneously from the same data set (of predator plus prey fatty acid profiles) (Bromaghin et al. 2017). Finally, QFASA assumes that the fatty acid compositions of *all* potential prey are known and it is also clear that prey fatty acid profiles vary with age, season, sex, area, etc., of the prey – and of course also with the diet of the prey.

Although quantitative fatty acid analysis has been more successful when applied to invertebrate predators (e.g., squid, for which calibration coefficients are apparently unnecessary), useful semiquantitative results have been obtained in cetaceans, e.g., seasonal changes in fatty acid profiles of porpoises broadly matched expected changes based on stomach contents (Learmonth 2006).

## Stable Isotope Analysis

Similar to fatty acid analysis, stable isotope analysis (SIA) follows the assumption that the isotopic composition in the tissues of a predator reflects the isotopic composition of its prey. Isotopes are different forms of atoms characterized by the same number of protons (the same atomic number) but different number of neutrons (hence different masses). The most commonly used isotopes are those of carbon ( $^{12}\text{C}$  and  $^{13}\text{C}$ ) and nitrogen ( $^{14}\text{N}$  and  $^{15}\text{N}$ ), although isotopes of sulfur and oxygen and strontium, among others, have also been used. These isotopes are all stable (non-decaying, hence nonradioactive) as opposed to, say,  $^{14}\text{C}$ . Lighter isotopes are preferentially exhaled or excreted when food is metabolized producing an enrichment of the heavier isotopes in the tissues of the

predator relative to its prey. This *fractionation* process takes place at each trophic level which means that the higher in the food web a predator is situated, the higher the enrichment of the heavier isotopes in its tissues and, in principle at least, this enrichment takes place in a predictable way. For carbon it has been estimated there is an enrichment in the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  of approximately one part per thousand for each trophic level while for N, the increase is around 3% (Kelly 2000).

Having information on two isotope ratios in the predator provides very low-resolution evidence on diet composition, but stable isotope analysis is widely used to obtain data on the trophic position of individuals and populations and also to determine where the animal has been living, with C isotopes, for example, acting as chemical tracers of different sources of primary productivity (e.g., inshore versus offshore) and also varying with latitude. For these reasons, SIA has also been used to infer, or confirm, migration and population substructure of cetaceans (e.g., Fernández et al. 2011).

As is the case for fatty acids, SIA can provide information for animals with empty stomachs, and different tissues (with different turnover rates) can be used to provide information on diet integrated over different time periods (soft tissues, teeth, and bones can also be sampled). Another advantage of stable isotopes is that information can be obtained from specimens in museum collections, allowing us to reconstruct the past environment and trophic positions of individuals.

Again there are issues that need to be taken into consideration when interpreting the results from SIA. One of the most important is that the isotope fractionation, between the diet and the predator's tissues, can differ in different tissues (Tieszen et al. 1983). Captive feeding experiments in cetaceans suggest that the fractionation seen in C and N isotopes can be a long way from the *typical* values of 1 and 3% (e.g., Caut et al. 2011). In addition, isotopic fractionation can vary depending on food quality and the nutritional stress of the individual (Schmidt et al. 2004). Finally, it is important to note that sample extraction methods and sample storage can affect the

results obtained. In particular, the isotopic signatures of lipids differ from those of other body components.

Despite these issues, the advent of compound-specific SIA, in which isotope ratios are calculated separately for different amino acids, can greatly enhance the information obtained. The increased amount of data generated potentially provides much higher resolution of dietary composition (e.g., Matthews and Ferguson 2014; McMahon et al. 2016). Another relatively recent development is the calculation of isotope ratios in individual growth rings of *recording structures* such as teeth, such that dietary information can be obtained for each year of an animal's life (e.g., Borrell et al. 2013).

## Other Methods

Several other methods have been used to obtain information on the diet of cetaceans. These include direct observations of animals feeding at the surface or using underwater cameras attached to the animals or to nets or other structures; the collection of feces and discarded prey remains from the water after detecting feeding behavior, for example, in the case of whales filter feeding baleen whales; and the identification of the soft tissues of prey in stomach contents. The latter approach has evolved from the use of electrophoresis to identify prey proteins, through raising antisera to detect proteins of specific prey, to identification of prey DNA. Molecular prey identification, for example, based on mitochondrial DNA, is increasingly the method of choice for a wide range of marine predators (e.g., Parsons et al. 2005) and has become relatively much less expensive than when first developed. Fully quantitative DNA-based diet analysis remains to be developed: the amount of DNA of a particular prey species amplified may bear little relation to the amount of the species in the stomach contents.

## Conclusion

There are many reasons why knowledge of the diet and the feeding ecology of a cetacean species

may be useful. Firstly, it provides insights into its biology and ecology, including habitat preferences, prey selection, competition and resource partitioning with other predators, energy transfer, population substructure, etc. In addition, understanding the effects of predators on the populations of their prey, and how predators cope with changes in prey abundance, is essential to predict responses of marine ecosystems to perturbation. Finally, diet analysis can provide important insights into threats including prey depletion and fishery bycatch. The diet is the main route by which various pollutants enter cetaceans, including toxic elements, persistent organic pollutants, and plastics. By understanding diet, we can gain a better understanding of these various threats and therefore contribute the conservation of these species.

## Cross-References

- ▶ [Amino Acid](#)
- ▶ [Cetacean Morphology](#)
- ▶ [Cooperative Hunting](#)
- ▶ [DNA](#)
- ▶ [DNA Marker](#)
- ▶ [Optimal Foraging Theory](#)
- ▶ [Predator](#)
- ▶ [Prey](#)

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## Cetacean Life History

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## Definition

Cetacean life history describes the reproduction, growth, and survival patterns for species in the mammalian order Cetacea, which includes whales, dolphins, and porpoises.

## Introduction

Cetaceans are a diverse order of water-dwelling mammals that inhabit all of the world's oceans and many freshwater ecosystems. Cetaceans are split into toothed whales (Odontoceti), which include dolphins and porpoises, and the typically larger baleen whales (Mysticeti). Cetacean species range from just a few feet long to 100 ft in length, can be very long lived, and have diverse patterns of behavior. Though the reproductive strategies of each species vary, most cetacean mothers invest considerable time gestating and caring for a single offspring at a time. Research on life history parameters has been collected via historic whaling records, stranded and bycaught animals, and current research which includes using photo-identification to track individuals across years, tissue sampling, radio-satellite tagging, use of aerial surveys, and information obtained from cetaceans in human care. The general parameters of both mysticetes and odontocetes are discussed in each section; however, research for many species remains ongoing, as most statistics are based on a limited number of species within each suborder. Learning about each species' life history is necessary for a better understanding of how each survives in a variable, aquatic environment and how conservation efforts can be better focused to increase rates of survival amidst many anthropogenic threats.

## Reproduction

### Mating

Traditionally, researchers agree that cetaceans do not conform to a monogamous mating system but instead have suggested several alternatives including one male mating with several females, one female mating with several males, and both sexes having multiple mates (Brownell and Ralls 1986; Clapham 2000; Connor et al. 2000). In some species, females may be selective in choosing male partners, while in other species males form alliances with other males in order to guard and mate with a female who is ovulating.

In a mating system where females have multiple sexual partners, males have evolved mating strategies that utilize sperm competition. Sperm competition can be inferred from the presence of large testes size combined with absence of secondary sexual characteristics, the occurrence of solitary individuals and small group sizes, as well as from the infrequently recorded agonistic behavior between males. Such features are present in right whales (*Eubalaena australis*), bowhead whales (*Balaena mysticetus*), gray whales (*Eschrichtius robustus*), pilot whales (*Globicephala* spp.), and harbor porpoises (*Phocoena phocoena*) (Brownell and Ralls 1986; Frasier et al. 2007; Learmonth et al. 2014). In other species such as humpback whales (*Megaptera novaeangliae*) and sperm whales (*Physeter macrocephalus*), increased agonism within male-male interactions, smaller testicular and penis size, and some degree of biased reproductive success appear to be the alternative to sperm competition (Brownell and Ralls 1986).

### Age at First Birth

Females consistently mature faster than males because their sexual maturity depends exclusively on physical maturity (Perrin and Reilly 1984). Males tend to take longer to mate, as physical maturity often precedes the social competence necessary for mating (Clapham 2000). Sexually mature females are identified by the presence of the corpus luteum and corpus albicans, temporary

endocrine structures in the ovaries. Given paternity uncertainty, observations with a dependent calf are another indicator of sexual maturity in females, but not for males. Rather, the presence of spermatozoa in testes and epididymis and the change in diameter of seminiferous tubules would be the main indicators for males. The age at which sexual maturity is attained greatly varies in cetaceans. Sexual maturity in toothed whales ranges between 3 and 20 years old, with most species converging on a modal age of 10–12 years (Perrin and Reilly 1984). For baleen whales, females tend to become sexually mature between 5 and 8 years of age, while most males will not sire a calf until they are at least 15 years old (Pomeroy 2011).

### Birthing Interval

The number of years between when calves are born varies widely for both mysticetes and odontocetes. For baleen whales, estimates range from 1 to 5 years, with a modal interval of 2–3 years (Clapham 2000; Lockyer 1984). Toothed whales show an even greater variation with birthing intervals of 1–14 years (Perrin and Reilly 1984). However, most species have a modal interval of 3 years (Gaskin et al. 1984). Some species, including humpback whales, harbor porpoises, vaquita porpoises (*Phocoena sinus*), and bottlenose (*Tursiops* spp.) and common dolphins (*Delphinus* spp.), may have consecutive pregnancies and may nurse while also becoming pregnant again (Perrin and Reilly 1984). The interbirth interval is often dependent on the duration of the pregnancy and the duration of calf dependency, which can range extensively between species.

### Parental Care

All cetaceans give birth to a single, very precocious calf. While multiple fetuses have been documented in several species, its occurrence is extremely unusual (Lockyer 1984). Because of paternity uncertainty, parental care is exclusively provided by females. While toothed whales rely on a relatively lower energy investment during pregnancy compensated by a long period of calf dependency, baleen whales require a much higher energy investment during pregnancy,

compensated by a significantly shorter calf dependency period (Oftedal 1997). Most cetacean gestation periods last between 10 and 12 months (Pomeroy 2011). Species with extreme gestation periods include pilot whales (15–16 months), sperm whales (16–17 months), beluga whales (*Delphinapterus leucas*, 15–16 months), and killer whales (*Orcinus orca*, 12–17 months) (Perrin and Reilly 1984).

Lactation is likely the most energetically expensive aspect of cetacean reproduction. Females produce milk high in fat and protein content, which allows for rapid growth and development of calves (Lockyer 1984). Baleen whales typically nurse their calves for 4–10 months (Clapham 2000). Weaning in most migratory baleen whales falls on a continuum; some calves separate from their mothers during or after the summer feeding season, while others return to breeding grounds before separation occurs. Toothed whales show greater variability regarding the duration of lactation periods with estimates ranging from 8 up to 60 months. Most species appear to converge on estimations of 18–20 months (Gaskin et al. 1984; Perrin and Reilly 1984).

### Senescence

In certain cetacean species, including killer and pilot whales, females can live over 20 years after the birth of their last calf (Marsh and Kasuya 1986). This post-reproductive period of the life span is called senescence. Two main hypotheses have been proposed to explain the occurrence and maintenance of this phenomenon. Kinship theory states that post-reproductive females maximize their inclusive fitness by assisting their offspring, ultimately improving offspring survival and reproductive success (Foster et al. 2012). Alternatively, Nichols et al. (2016) proposed that senescence was originally the result of asynchrony between reproductive system aging and aging of the rest of body and that female senescence may be adaptive in species where adult males remain in the same group or home habitat, therefore reducing the chance that a female will mate with her adult male offspring.

## Growth

### Neonate Size

When compared to other mammalian species, cetacean calves are large in proportion to adult size. At birth, odontocete calf length can range from 40% to 48% of the mother's total body length. Two of the smallest cetacean species, harbor porpoises and vaquita porpoises, have a high calf length to mother length proportion with calves born 70–75 cm and 60–76.4 cm long, respectively. Birthing larger calves likely increases chances of calf survival for these smaller cetacean species. Atlantic bottlenose dolphins are born approximately 116 cm for male calves and 114 cm for female calves. Beluga whales are born on average 130 cm, whereas false killer whales (*Pseudorca crassidens*) are born 160 cm. Calves of larger odontocete species, such as pilot whales and killer whales, are even born as long as 180 cm and 257 cm, respectively (Perrin and Reilly 1984). From birth, mysticete species tend to be larger overall than odontocete species with comparatively smaller proportion of calf length to mother length (29%). The fin whale (*Balaenoptera physalus*), a large baleen species, is born on average 6.5 m in length and can weigh 1.75 tons, while the humpback whale calf is approximately 4.5 m, and the blue whale (*Balaenoptera musculus*) calf is born 6.5 m (Whitehead and Mann 2000).

### Patterns of Growth

Although cetacean species span a large range of body size, most species follow a similar trend in physical growth. Rapid neonatal growth occurs immediately after birth and throughout weaning. Vaquita porpoises, a smaller odontocete species, can reach 62% of adult length by the second year of life (Hohn et al. 1996). For both odontocete and mysticete species, rates of growth tend to slow once weaned. In general, mysticetes tend to wean earlier than odontocete species likely as a result of differing foraging strategies. Mysticetes have evolved disproportionately large mouths with thin keratinous plates rather than teeth which allow them to strain schools of small fish



and invertebrates from the water, ensuring foraging efficiency (Wursig 1989). In contrast, odontocetes use more specialized foraging styles that typically require rapid and precise movements. Foraging for odontocetes may be more difficult for calves, so calf survival may largely be dependent on a longer nursing and weaning period that provides opportunities for learning and becoming efficient at these more specialized foraging techniques.

Harbor porpoises exhibit rapid growth until approximately 6 years old, likely to maximize size and effectively increase calf and juvenile survival. Atlantic bottlenose dolphins and Amazon river dolphins (*Inia geoffrensis*) exhibit similar patterns of development, growing approximately 4.8 kg per year for the first 4 years. Likewise, killer whales grow rapidly for the first 3 years of life. Bowhead whales, a large mysticete species, typically grow in length and weight rapidly until they complete weaning at around 1 year old; body growth rates then begin to decrease, while the head and baleen continue a steady growth rate until around 5 years old (George et al. 1999). Growth rates usually slow until sexual maturity, when some species such as killer whales and Atlantic bottlenose dolphins exhibit a short increase in male growth rate in preparation for mating. Killer whales at sexual maturity also exhibit a spike in dorsal fin growth, where male dorsal fins reach heights of 1.8 m, while female dorsal fins only reach heights of 0.9 m (Kastelein 1998).

Most cetaceans overall show some degree of sexual dimorphism, where one gender grows larger or faster than the other. Females tend to reach lengths 5% longer than males in baleen whales, porpoises, and river dolphins. In harbor porpoises, for instance, females (95 mm/year) even grow faster than males (55 m/year). Larger females can advantageously birth larger calves with higher chances of survival. However, in other odontocetes, such as beluga whales and Risso's dolphins, males attain lengths 2–10% larger than females. Sperm whale males, the largest odontocete species, can even reach lengths 60% larger than females. In certain

species such as the pilot whale where males mature 6–7 years after females, the larger sex likely physically matures years after the smaller sex, simply because growing larger may take a longer time. For large species with longer life spans, such as bowhead whales, growth rate likely remains steady until mid-life, approximately 40–50 years old, when growth rates decrease and stabilize (George et al. 1999).

### Maximum Size

While more data remains to be collected for some larger cetacean species with longer life spans, the literature contains extensive data on smaller cetacean species, particularly odontocetes, which have a comparatively shorter life span. Harbor porpoises only reach 155 cm for males and 165 cm for females (Lockyer 1984). Finless porpoises (*Neophocaena phocaenoides*) can reach up to 192 cm for males and 175 cm for females (Gaskin et al. 1984). Another small odontocete, Risso's dolphins (*Grampus griseus*), exhibits a large range of adult lengths, 193–308 cm for females and 186–323 cm for males. The Atlantic bottlenose dolphin and the Amazon river dolphin can reach similar maximum lengths of 250–270 cm for the Atlantic bottlenose dolphin and 196–255 cm for the Amazon river dolphin (Reidenberg and Laitman 2009). Larger odontocete species such as killer whales can display striking sexual dimorphism at maturity, where individuals grow up to 770 cm for females and 900 cm for males (Reidenberg and Laitman 2009). Likewise, pilot whale adult males can grow as long as 570 cm and weigh up to 2,000 kg, while adult females only grow as long as 380–450 cm and weigh on average 600–1,000 kg (Reidenberg and Laitman 2009). Unencumbered by physical boundaries characteristic of terrestrial environments or gravity, some mysticete species can reach extraordinary lengths. For instance, fin whales during their 80-year life span can reach lengths of 22.5 m for females and 21.5 m for males and can attain weights as large as 80 tons (Reidenberg and Laitman 2009).

## Survival

### Longevity

Assessing aspects of cetacean survival can be a challenging endeavor, given the difficulty in following these animals over extended periods of time and considerably large habitats. The use of satellite tagging (Fig. 1) and photo-identification can help; however, research in this area will only continue to grow over time.

The average and maximum life spans of many cetacean species are still not established, though the existing research indicates that these figures vary greatly between species and even vary between different populations of the same species. In general, larger species have a longer life span, and smaller species have a shorter life span (Whitehead and Mann 2000). The bowhead whale has been found to exceed 100 years old, whereas other mysticete species can live 45–95 years (George et al. 1999; Whitehead and Mann 2000). On the other end of the spectrum, some small odontocete species may have a

maximum life span of just over 20 years (Whitehead and Mann 2000). Many harbor porpoises may not exceed 20 years of age (Whitehead and Mann 2000). Larger odontocete species such as the pilot whale and the sperm whale may live as long as 60 years and 85 years, respectively (Whitehead and Mann 2000). Killer whales are reported to have a typical maximum life span of 80 years for females and 60–70 years for males, though some individuals are known to live to older ages; however, these ages may vary in different populations of killer whales (Olesiuk et al. 2005). Bottlenose dolphins are reported to have an average maximum age of about 45–50 years, which may also vary according to population (Whitehead and Mann 2000). Bottlenose dolphins in both the wild and human care have even been reported to reach 60 years of age.

The above numbers indicate the maximum age these species may reach, but these may differ from the average life expectancy. For example, some populations of killer whales comprised of individuals 80 or 90 years old may only have an average



**Cetacean Life History, Fig. 1** Satellite tag deployed on a humpback whale (Photo by Fernando Félix Grijalva)

life expectancy of 30–45 years (Olesiuk et al. 2005). Similarly, bottlenose dolphins may have an average life expectancy of 15–25 years, depending on the population (Stolen and Barlow 2003). These estimates attempt to include individuals that die from injury or illness prior to maturity and calves that do not survive, though it can be difficult to estimate this figure. In Shark Bay, Australia, 56% of known calves survived to age 3; however, calf mortality may vary for other populations (Mann et al. 2000).

### Predation

Cetaceans do not face many other ocean-dwelling predators. Sharks are known to attack both young and adult odontocetes, with most reports being in well-studied populations of bottlenose dolphins. In particular the dolphins in Shark Bay, Australia, face a higher rate of predation than other populations, with almost 75% of the study population having shark bite scars (Heithaus 2001).

The other predators of cetaceans are the transient ecotype of the killer whale, which sometimes prey on small odontocetes, such as Dall's porpoises (*Phocoenoides dalli*), and the calves of larger mysticete species, such as the humpback whale (Baird 2000).

### Movement Patterns

Predation by killer whales and seasonality of prey availability are both hypothesized reasons that some species, including the humpback whale, migrate thousands of kilometers each year (Corkeron and Connor 1999). Lower latitudes and shallow, warm water environments during the winter months provide increased protection for pregnant humpback whales and calves from both killer whale predation and male conspecifics attempting to mate. Females and their calves return to colder waters during the summer season to take advantage of the abundance of prey in the nutrient-rich waters. Migratory timing for humpback whales is closely linked to reproductive success (Craig et al. 2003). The distribution of humpback whales within wintering grounds appears to vary by temperature, which suggests that warmer waters may influence reproductive success (Rasmussen et al. 2007). Other large

species, including the sperm whale, gray whale, and blue whale, migrate as well, though not all members of a species migrate every year (Wursig 1989).

Many odontocete species also display movement patterns that may include inshore/offshore seasonal movements, following prey along the coast, or diurnal movements to hunt and avoid predators (Wursig 1989). Movement patterns may also differ by sex. For instance, male belugas show more dispersal than females, although most animals seem to return to a phylogenetically distinct summering ground (O'Corry-Crowe et al. 1997). Amazon river dolphins also move seasonally with their prey, and males and females typically occupy different parts of the habitat, likely to protect mothers and calves (Martin and da Silva 2004). Finally, the different ecotypes of the killer whale have distinct movement patterns. Some killer whales remain in one area year round, while others travel more extensive distances, though it is unclear if any north-south migration occurs (Baird 2000).

### Feeding Ecology

Closely linked to migration in many species is the location of the optimal food source. The food sources of cetaceans can vary greatly, from the marine mammals consumed by some killer whales to the small krill consumed by many mysticetes. The flexibility in cetacean foraging strategies can be seen not only in their diverse food sources but also different hunting or prey-capture techniques. Killer whales are known to work as a cohesive unit to wash prey from floating patches of ice, chase pinnipeds up onto beaches, and stun fish with their flukes before capturing them (Baird 2000). Bottlenose dolphins are also known to chase fish onto beaches, use sponges over their mouths when foraging, and create clouds of muddy water to trap fish (Whitehead and Rendell 2014). Other odontocetes consume a variety of fish, squid, and other available prey.

Mysticetes are well known for their migrations to nutrient-rich feeding grounds in both Arctic and Antarctic waters. While some whales, such as the bowhead whale, do not leave Arctic waters, many other species travel to these colder waters on a

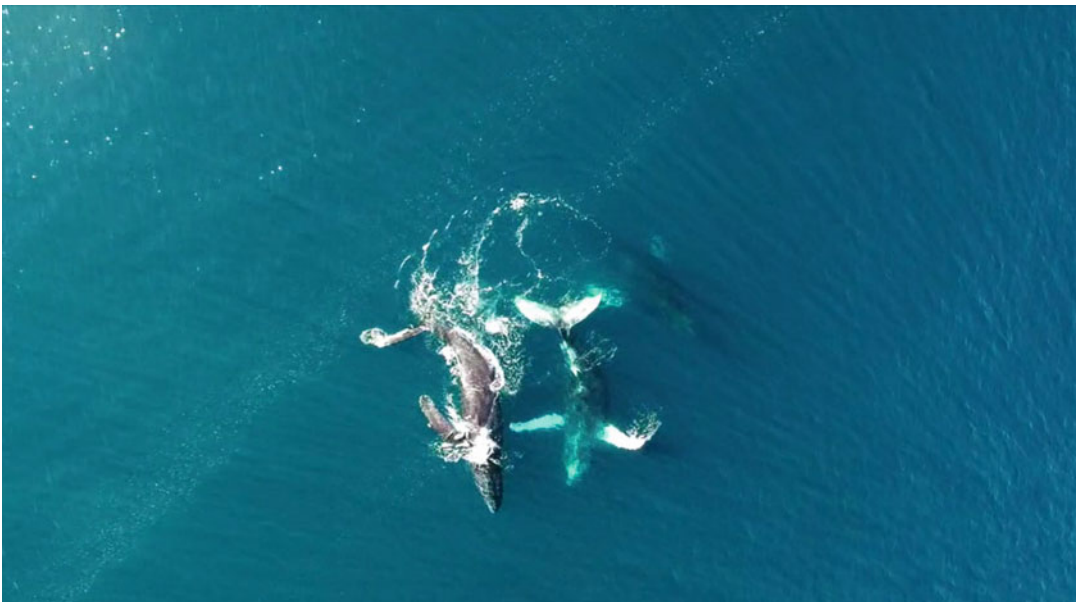
seasonal basis to take advantage of the abundance of prey (Corkeron and Connor 1999). Other variations in movement and feeding patterns also exist. Humpback whales migrating from Antarctic to tropical waters continue feeding on fish and krill throughout the migration, a behavior which may vary by prey availability along the migration route.

## Conclusion

As was discussed in each section above, extensive diversity exists among cetaceans in reproduction, growth, and survival life history parameters. There are several methods of research which have only just begun to expand comprehensive, detailed knowledge for more cetacean species. One of these methods is the use of drones which are able to obtain aerial videos and even samples of a whale's exhalation with minimal disturbance to the animal (Fig. 2). Another method includes analyzing fecal matter from whale defecation and skin samples from breaching whales collected opportunistically by nearby research vessels. Investigating paternity is also a relatively

promising field, as genetic analysis methods become more accessible for field researchers studying wild populations (Fig. 3). Paternity assessment has revealed the polygynous mating system in humpback whales, where some males sire up to three offspring, while others sire none (Cerchio et al. 2005), as well as the effectiveness of male bottlenose dolphins' alliances in successful mating.

Finally, the increase in sufficiency of satellite tagging can help answer many questions regarding cetacean life history, including migratory patterns, behavior, and habitat use. More attention should be directed toward developing tagging methods that are appropriate for younger animals, as there is a lack of information on early life history for many species. Improvements in tag design, technology, and the methods of attaching tags continue to be an area of focus for research in many species. Based on life history parameters, models for specific populations of animals can be created and used to assess that population's recovery from the impacts of whaling, the effects of current anthropogenic threats, and predictions of future population dynamics that can be used to inform conservation policies. The future of many



**Cetacean Life History, Fig. 2** Drone picture of interaction between humpback whales (Photo by Eric Angel Ramos)



**Cetacean Life History,**

**Fig. 3** Tissue sample collected from an adult male humpback whale (Photo by Natalia Botero-Acosta)



cetacean species will depend on the effectiveness of research on life history and the implementation of actions to conserve species based on that research.

**Cross-References**

- ▶ [Alloparental Care](#)
- ▶ [Cetacean Diet](#)
- ▶ [Cetacean Locomotion](#)
- ▶ [Cetacean Morphology](#)
- ▶ [Cetacean Navigation](#)
- ▶ [Fission-Fusion](#)
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- ▶ [K-Reproductive Strategy](#)
- ▶ [Maternal Behavior](#)
- ▶ [Parental Investment](#)
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- ▶ [Sociosexual Behavior](#)

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## Cetacean Locomotion

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## Synonyms

## Movement

## Definition

The morphology, physiology, and behavioral aspects of cetacean movement through water.

## Introduction

Cetaceans have evolved to thrive in their own unique environment. They carry out all aspects of their lives in water, unlike other marine mammals, such as seals and sea lions (pinnipeds),



otters (mustelids), and polar bears (*Ursus maritimus*), who exit their aquatic environment periodically to mate, raise young, rest, or thermoregulate. Transportation via water is economical for cetaceans because less energy is spent supporting the weight of their body (Fish 1993). Cetaceans are neutrally buoyant in water because their body tissues have similar densities to the water they live in. Movement underwater is also advantageous because it is easier to generate propulsion (Fish 1993). The challenge of living full-time in water, however, is these animals are subject to a greater amount of drag forces that act upon them as they move through their environment because water is denser and more viscous than air. It is for this reason cetaceans adapted to have specialized morphology, physiology, and behavior to facilitate exceptional underwater locomotion.

## Morphology

Many aspects of cetacean morphology ultimately aid them in reducing drag, the resistance to movement in water, while also providing better means of maneuverability, and lift and thrust production (Reidenberg 2007). Most noticeably, their characteristic body shape combats drag by having a rounded front edge of their beak-like rostrum, a wider middle body, and tapering end from the mid-body to their tail flukes, resembling a tear-drop or torpedo shape. This fusiform shape streamlines and allows water to flow more efficiently around the body, creating less wake (Fish et al. 2008). The flukes are also fusiform shaped, much like wings of an airplane or a boat propeller. The leading edge is thick and rounded around the tail stock and gradually decreases in thickness to the trailing edge to streamline and help produce greater thrust for locomotion (Fish et al. 2007). The cross-section of flukes are very similar in all species, but there is some variation between species in the planar geometry which dictates their locomotion efficacy (Fish et al. 2007). Some differences in planar shape include the area, distance between the two tips, and the interaction of these two measurements to form the aspect ratio (Fish 1998) (see [Physiology](#) section).

Cetacean appendicular skeleton aids in a streamlined body design, with the loss of exterior hind limbs, and forelimbs that are scaled down and sculpted for optimal hydrodynamic performance (Williams 2009). Today, cetaceans only have traces of hind limb skeleton that can be found in the body wall. Its presence is variable in some species, occurring less often in odontocetes (the suborder containing toothed whales; Adam 2009). The forelimbs, pectoral fins (often referred to as flippers), are mainly used to stabilize the body and maneuver through their environment by generating lift and controlling flow of water around the surface of the fin (Weber et al. 2014). Unlike flukes and the dorsal fin, pectoral fins contain forelimb and digit bones. For this reason, they have greater variation in the shape and characteristics of their hydrodynamic properties depending on the skeletal structure of each species. Differences in shape can be linked to the movements necessary for species ecology and their individual foraging techniques. For example, killer whales (*Orcinus orca*) have round paddle-like pectoral fins designed for excellent maneuverability to help them pursue agile prey, whereas fin whales (*Balaenoptera physalus*) have pectoral fins that are more pointed and tapering, which provide low drag to support their lunge feeding techniques (Weber et al. 2014).

Another characteristic external feature that increases cetacean locomotor efficiency is the absence of fur. The properties of fur which allow it to hold heat well are greatly reduced when submerged in water. Fur also has the disadvantage of creating unwanted drag (Reidenberg 2007). Cetaceans possess a thick integument with a waterproof sheet of skin and underlying layer made of fat, and elastic and collagenous fibers called blubber. The outermost layer of skin (epidermis) is elastic and smooth which cuts down drag because there is less friction being created when water slides past the body. Another important aspect of cetacean skin is the rate at which epidermal cells are produced. Compared to humans, bottlenose dolphin (*Tursiops truncatus*) epidermal cells are produced 250–290 times faster (Fish and Hui 1991). The high turnover rate of skin cells helps minimize drag by decreasing the likelihood that smaller organisms like barnacles or natural slime will attach to the

body and create unwanted resistance (Fish and Hui 1991). There are some hypotheses of hydrodynamic capabilities regarding the unique internal structure of cetacean skin, such as a dampening function from its elastic properties, and flow control by dermal ridges. However, neither of these hydrodynamic functions have been fully demonstrated (Fish 2006; Cozzi et al. 2017). Underneath the skin, a thick layer of blubber helps to insulate, store energy, control buoyancy, and reduce the effects of drag. As mentioned previously, cetaceans have a fusiform shape. Blubber helps to mold the body into its shape by being unevenly layered in a way that tapers the body more gradually over the muscles, especially between the mid-body and flukes (Iverson 2009). Along with its ability to help form a streamlined body, blubber also aids locomotion with regard to buoyancy. However, this depends on how it is stored on the individual's body and used when expending energy (Iverson 2009).

## Physiology

Locomotion is energetically more expensive when you compare cetaceans to fish. Because cetaceans are mammals, a large portion of their energy goes toward producing body heat. For an animal to thrive, there needs to be a positive balance between the costs of maintaining body functions and energy gained from food. The amount of energy cetaceans acquire depends on the type of food they ingest, which can vary between species and the environment they live in. Cetacean energetics can be elaborate, as there are many different factors to consider, such as energy needed for prey acquisition, thermoregulation, metabolism, activity, growth, repair, reproduction, and energy storage. Their bodies have specialized internal structures and mechanisms to utilize and conserve energy while in motion.

Cetaceans have a unique way of swimming by using lift-derived propulsion. Lift is the force that acts perpendicular to the flow of fluid against an object (Hall 2015). The flukes act as a flexible hydrofoil to facilitate lift, and their shape affects how much thrust power can be gained from a

stroke and how much energy it will cost the animal (Fish 1998). An aspect ratio can be calculated to show how hydrodynamically effective flukes are (Fish 1998). As mentioned earlier in this chapter, the shape of flukes varies between species. The flukes of species with a high aspect ratio are long and narrow which enable the animal to propel themselves more effectively through the water. This is because they are able to generate a larger amount of lift while expending a small amount of energy with less drag acting against the movement. Therefore, slower swimming cetaceans such as the Amazon River dolphin (*Inia geoffrensis*) are found to have shorter, wide flukes with a low aspect ratio (Fish 1998). To swim forward, tail flukes oscillate up and down; both upward and downward strokes produce a great amount of thrust (Fish 1993). This undulating movement takes place mostly in the last third of their body, however, minimal movement can be seen at the front of the body with the rostrum moving upward simultaneously with the flukes. The amplitude of the undulatory wave of motion increases as it travels down the body (Skrovan et al. 1999). The type of swimming in which undulations occur mainly in the tail end of the body is called thunniform swimming (also carangiform swimming with a crescent shaped tail) (Fish and Rohr 1999). At the base of the flukes, a joint allows them to be pitched around an axis to change the angle of the directed force of each stroke (Fish and Rohr 1999). Longitudinal hypaxial and epaxial muscles connecting to the dorsal and ventral side of the spine are the main muscles used for propulsion. Vertebrae in the tail and trunk portions of the vertebral column have particularly long spinous and transverse processes to help with muscle attachment. They enhance muscle power output by acting as a lever to amplify swimming mechanics (Fish and Rohr 1999). Frequency of propulsive strokes depends on the size of the species and how fast they are swimming. Larger species of cetaceans have a lower stroke frequency compared to smaller species (Williams 2009).

During the majority of their daily activities, cetaceans spend time down in the water column

and often dive deep to forage. They have evolved to facilitate seemingly effortless dives while combating body drag and hydrostatic pressure. When humans dive underwater, we quickly feel changes in the small pockets of air in our sinuses and ears from the weight of the water above us. Since air is compressed with increasing depth, buoyancy of a marine mammal at depth is greatly affected. Cetaceans are able to dive so efficiently because their buoyancy decreases as they swim deeper due to the compression of their lungs (Skrovan et al. 1999). This influences their energetics and mode of swimming. During a deep dive, they modify their swimming behavior (gait) at different depths to accelerate in the most adept way (Skrovan et al. 1999). At the start of their descent, they use repeated strokes until they meet a certain depth, then switch to gliding. This change in gait is due to the reduction in buoyancy when their lungs begin to collapse. Therefore, the deeper they travel, the longer they glide (Skrovan et al. 1999). During a dive, oxygen stores in the lungs, blood, and muscles are consumed. A remarkable adaptation for diving is the high amount of myoglobin, an oxygen binding protein, cetaceans have in their muscles. Species that have a larger body mass with higher numbers of myoglobin are able to stay down for longer periods of time (Noren and Williams 2000). Another physiological occurrence observed in cetaceans is a decrease in heart rate (bradycardia) during dives, even when compared to their resting heart rate. However, it could be possible that their heart rates can be modified during a dive to manage oxygen consumption (Noren et al. 2012). When deep divers are ready to ascend, they use a considerable amount of locomotor effort with strokes that have a large amplitude. As they rise, hydrostatic pressure lessens, their lungs begin to re-inflate, and they switch to a stroke-and-glide locomotor pattern as their buoyancy increases.

## Behavior

For many years, people have taken notice of cetaceans “effortless” swimming abilities. Their drag reduction properties and propulsive mechanisms

allow them to reach surprisingly high speeds underwater. Sprinting speeds for odontocete species can range between roughly 6.1 and 12.5 m/sec, with killer whales (*Orcinus orca*) at the top end of this range. For mysticete whales (suborder containing baleen whales), their sprinting speeds range from 4.1 to 13.3 m/sec (Williams 2009). Though swimming at top speed can be useful at times, such as when feeding, it can also be energetically exhausting. Cetaceans usually swim at a routine pace that is slower and considered more casual swimming, which varies remarkably less between species compared to their top speeds. Routine speeds for odontocetes range from about 1.8 to 3.6 m/sec, with beluga whales (*Delphinapterus leucas*) on the slower end. Mysticetes routine speeds range from 2.1 to 2.6 m/sec (Williams 2009).

Cetaceans need to come to the surface often to breathe air. This can be costly when traveling because energy is lost and higher speed is limited when resistance is encountered from another drag force created by surface waves. Therefore, cetaceans often swim more than half a body length below the surface to avoid wave drag (Fish 1993). They have also developed noticeable behavioral strategies for reducing the effects of drag and its energetic costs. When traveling at high speed, porpoising is one behavior that can help facilitate gas exchange in the most energy-conserving way (Weihs 2002). Porpoising is a behavior that is characterized by a series of fast ballistic jumps that occur in between hasty bouts of swimming not far below the surface (Fish and Hui 1991). It allows an opportunity for the blowhole to be exposed to air quickly enough for respiration, and, while above a certain speed, it is more energetically advantageous to move through air as opposed to water (Au and Weihs 1980).

Another behavior cetaceans perform to conserve their energy while swimming is drafting or swimming in formation. They travel next to and slightly behind one another without touching and receive swimming assistance from pressure waves created by other individuals (Weihs 2004). This type of behavior is especially significant for neonates and calves. When cetaceans are born, they must immediately begin swimming and thus need

to stay close to their mother for feeding and protection. To swim next to a highly experienced adult would be a considerably difficult task for a young dolphin with a small body and without fully developed muscles (Noren et al. 2008). To keep up with their mother's speed, calves align themselves in different positions around her that help make swimming easier for them. As the adult swims, the water in front of her is pushed forward by her motion, then water behind her moves forward to replace her body mass that was previously occupying the space. This is called the displacement effect. The calf profits by positioning itself in the forward moving water where it is able to "ride" next to mom in her pressure wave (Weihs 2004), which is also referred to as a slip stream. Another force that is acting to aid the calf when it is in a position beside its mother is the Bernoulli suction. When the two are swimming close to each other, water is accelerating as it moves through the small space between their bodies, which creates a drop in pressure and attracts them towards one another (Weihs 2004). There are three common positions in which calves swim with their mother. The first, neonate position, occurs shortly after the calf is born. It stays a few centimeters from its mother around her upper flank (Weihs 2004). As it gets a few months older, the calf swims in echelon position, located more to the side of its mother's flank near her mid-body (Weihs 2004). In this position, calves benefit greatly by having higher average swim speed, and less effort is needed for each swimming stroke. Also, they are often observed gliding in this position, which rarely happen when young calves are swimming independently (Noren et al. 2008). When the calf gets larger its mother will need to expend more energy to support it in echelon position. Around a year of age, the calf has become a more experienced swimmer and its mother will encourage it to swim below her tail section with their head near mom's abdomen in infant position (Noren et al. 2008). Though this position has fewer hydrodynamic benefits compared to neonate and echelon position, the calf continues to prosper from close proximity to its mother's milk supply and an easy place to hide from predators

(Noren and Edwards 2011). All calf positions aid in their survival, as it gives them the ability to stick close to their mom while she is constantly on the move while foraging, socializing, traveling, and avoiding predators.

Similar to formation swimming and drafting, cetaceans are also known to ride in pressure waves created by other vessels. Bow-riding is one common behavior that has been observed in many odontocete species (but not all). Dolphins will ride the waves that are produced from the forward motion of a boat at high speeds which stretch outward from the bow and stern (Williams et al. 1992). Relative to the boat, they can hitch a ride at many distances, depths, and in different body positions and postures (Fish and Hui 1991). Individuals will benefit from utilizing this behavior to conserve energy when they are traveling at a fast pace. Compared to free swimming, bow-riding individuals will experience lowered heart-rate, respiratory rate, and blood lactate because the demands of swimming with aid are far less than without it (Williams et al. 1992). Cetaceans are also able to use naturally created waves from wind or surf to catch a ride. Instead of pressure waves, they use the energy produced by the wave at a particular slope and distribute their weight accordingly, the same way we would if we were trying to surf (Fish 1993). Although these riding behaviors are energetically advantageous for traveling, it has also been suggested that they occur as a form of play (Wursig 2009).

## Conclusion

Cetacean ancestors were once land mammals who eventually returned to the water, unlike fish whose ancestors have always lived in water. Considering this "shorter" amount of evolutionary time, cetaceans are capable of extraordinary locomotor abilities. They are some of the most efficient swimmers on the planet, aided by their morphology, a major adaptation to aquatic life. A fusiform shape and streamlined features greatly reduce resistance they encounter while moving in water. Along with their streamlined body, a hallmark of

cetacean locomotion is their physiology. Their body is designed to use lift-based thrust to propel themselves continuously through the whole stroke cycle with great power. During deep dives, they are able to adjust their swimming patterns to control for changes in hydrostatic pressure, and their internal organs are adapted to maximize dive duration by conserving oxygen in various ways throughout the dive. Finally, cetaceans have several behavioral tactics to reduce the work needed for swimming, by catching a free ride from pressure waves created by others and sea-faring vessels. All of these unique components of their body plan and clever behavior manifested from evolutionary adaptations to living in water and ultimately reduce their cost of locomotion.

## Cross-References

### ► Cetacean Morphology

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## Cetacean Morphology

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Cetacea (whales, dolphins, and porpoises) are mammals fully adapted to life in water so that some typical mammalian traits are not visible from their exterior appearance. The body of cetaceans is streamlined in shape. The head is connected to the body without a distinct neck so that it is merged to a single unit. The large boneless caudal fin (fluke) as the actual organ of locomotion is an evolutionary innovation. It is horizontally orientated and not vertical as in fishes or ichthyosaurs. Accordingly, spine and trunk muscles of cetaceans are designed primarily for dorsoventral movements. Moreover, a boneless connective tissue formation represents the unpaired dorsal fin. Flippers (forelimbs) and dorsal fin only control and stabilize the body's position while swimming.

### The Origin of Modern Cetaceans

At the end of the last century, the knowledge about cetacean fossils was so sparse that one could not be sure what the ancestors of the cetaceans looked like. During the last 25 years, however, the topic has played a decisive role in the field of evolutionary biology. Today, it is certain that cetaceans belong to the same order (Cetartiodactyla) of even-toed hoofed animals (formerly classified alone as Artiodactyla) (Perrin et al. 2009). The ancestors of cetaceans were land mammals that lived about 60 million years ago. Their close relationship with the artiodactyls is clear from molecular studies that indicate that the cetaceans are closely related to the hippos (Hippopotamidae) (Price et al. 2005). The monophyly of the Cetacea is well established by morphological and molecular biological

characteristics. The traditional systematic classification in toothed whales (Odontoceti) and baleen whales (Mysticeti) is well secured.

On the morphological level, fossil findings of nearly complete skeletons revealed that the ankle joint (hock) of middle-Eozän Archaeoceti were clearly like that of even-toed ungulates since they had a talus bone (Astragalus) of the typical double-pulley form, an autapomorphy of Artiodactyla. Further characteristics (apomorphies) of cetartiodactyls are the par-axis extremities and the fibroelastic type of penis with a proximal sigmoid flexure. In comparison with the hippos, cetaceans share a multilocular (multichamber) stomach system, the nearly hairless skin, and the structure of the larynx entrance (Frey et al. 2015).

The Cetacea derived from the Mesonychidae, a group from the main line of ungulates († condylarths) in the Paleocene. From them the archaeocetes emerged in the lower Eocene, about 50 million years ago, as the earliest group adapted to the aquatic lifestyle. Probably due to their endothermy it was possible for the archaeocetes to populate all sea habitats and large river systems regardless of the ambient temperature. Because of the higher oxygen content of air in comparison to water, oxygen uptake via lungs is more effective than respiration by gills. This was another advantage for the evolution of these agile giant forms in the water.

### Outer Appearance and the Head

The sizes of cetaceans range from approximately 1.25 m of length and 25 kg weight for the La Plata dolphin (*Pontoporia blainvillei*) up to a length of 33.5 m and 190 t for the blue whale (*Balaenoptera musculus*). Despite this size range, solid compact bones are no longer necessary in cetacean due to the buoyancy of water. The main skeletal elements are cancellous bone, which are lighter, more flexible, and also more intense circulated by blood. Cartilage tissues have similar hydrostatic properties that would explain why cetaceans tend to have more cartilaginous skeletal elements in comparison to terrestrial mammals. Even fat is, in addition to its function for energy storage, found within the



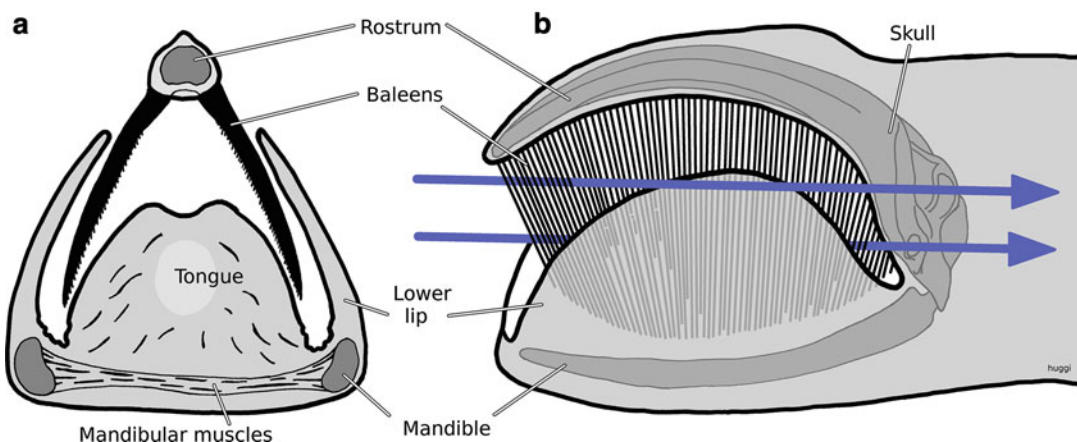
cetacean skeleton to replace solid bone tissue. Due to their densities, the combination of these three tissues – bone, cartilage, and fat – may thus contribute to a balanced buoyancy of the cetacean body in water.

In comparison to terrestrial mammals, the skull of cetaceans shows three fundamental changes: (1) a far forwardly projecting bony rostrum, (2) shifts in the nostrils to vertex of the skull, and (3) deformation and rostrocaudal shortening of the skull. The rostrum and mandible are responsible for the typical form of the cetacean head. Many dolphins have long and narrow beaks, although some species show a more globose shape of the head. The mouth of baleen whales is huge in relation to body size.

In the cranium, the individual skull roof bones slide over each other (telescoping). The most shortened skull elements are the nasal and the frontal bones, while the parietal bone is deformed. The occipital bones become the largest elements of the neurocranium. They are very high, nearly perpendicular, and constitute the caudal part of the skull. Due to these modifications, the nasal passages are nearly vertical so that the blowhole is situated at the highest point of the head. Accordingly, it appears first at the water surface when dolphins surface. When breathing, cetaceans do not need to interrupt their natural swimming movements, which is highly energy saving.

The long mouth of baleen whales houses the filter apparatus of baleens in the upper jaw. This probably brought the recent baleen whales a decisive advantage in the food network of the oceans. Baleens are keratin plates arranged in parallel to form a weir system in the whale's mouth. In this way, they "filter" large quantities of plankton (mainly crustaceans) and smaller fishes from the water (Fig. 1). Thus, baleen whales are, although they feed on small animals, "grazer" rather than carnivores. This concept of diet and the baleen weir system was so successful in evolution that the representatives of the baleen whales became the largest animals living on our planet. The blue whale is the largest animal that ever lived. The fact that the ancestors of the recent baleen whales had teeth can be recapitulated by the discovery that the teeth are developed as anlage in the baleen whale fetus but are not visible in the newborn.

The sister group of the baleen whales, the toothed whales, developed a different strategy during the course of evolution to hunt for their prey. By the use of an echolocation system (an active bio-sound navigation and ranging system, bio-sonar), they hunt for larger prey items (in relation to their body size) than the baleen whales. Toothed whales actively emit click sounds, and the echoes are perceived by the animal and converted into an "acoustic image" of the environment. Thus, toothed whales can navigate



**Cetacean Morphology, Fig. 1** Schematic cross section (a) and lateral view (b) of the head of a bowhead whale (*Balaena mysticetus*). When swimming, water (blue

arrows) flows into the mouth frontally and out through the baleens. Prey items are filtered by means of the baleen system and can then be swallowed regularly

and locate fish and squid in total darkness with the echolocation system. In order to catch their fast prey, the agile carnivores are usually much smaller than the great baleen whales and, in case of many dolphin species, capable of acrobatic performances. The largest representative of the toothed whale, the sperm whale (*Physeter macrocephalus*), however, has found its ecological niche in the deep sea. It hunts in the Mesopelagial zone, often far more than 200 m (and often much deeper than 1000 m) below sea level. The same is true for another group of large toothed whales, the beaked whales. Sperm and beaked whales stay on the surface or close to only for the time required to supply with the vital oxygen and to recover from their hunt excursions into the depth. In order to locate the prey in these extreme depths, the echosounder of the sperm whales reaches over several hundred meters. In comparison, however, in the dolphins it only works successfully in the near area (up to approximately 115 m). No other species hunts in the oceans or other aquatic environments with the help of echolocation.

To catch their prey, toothed whales use their jaws mostly equipped with many polyodont and homodont teeth (meaning that they have many teeth, all of the same dimension and shape). The teeth in the maxilla and mandible, up to 260, are usually cone shaped. There is only a single dentition. Some toothed whale species such as the beaked whales do not have teeth or only a single pair. All toothed whales suck in the prey by the help of their strong gular and hyoid musculature and swallow it whole. Due to the short neck region, which contributes to the streamlined body contour, the hyoid bone is very close to the sternum.

The base of the cetacean skull is characterized by bony structures responsible for hearing. The ancestors of all recent whales already showed adaptations for hearing underwater. The archaeocetes showed ear bones almost completely detached from the skull. The achievement of advanced hearing underwater requires a reduced mastoid process that allows disconnection of the ear bones from the skull and was found in both baleen and toothed whales since the Oligocene (around 30 M years ago). As a result, the middle ear and inner ear structures could vibrate freely from the rest of the

skull and thus improved directional hearing underwater. Toothed whales have, additionally, specialized fat bodies in the mandibles that couples acoustically the surrounding water to the ear bones.

The tiny middle ear ossicles of the hammer, anvil, and stirrup are enclosed in a bony capsule at the base of the skull. The three middle ear ossicles, a unique mammalian trait, represent an effective filtering and amplifying system unknown in other aquatic vertebrates. The audible range of dolphins includes an extensive spectrum from sonic low frequencies below 20 Hz to the ultrasonic range up to 280,000 Hz. Mainly the ultrasonic frequencies are used for their echolocation system. Baleen whales communicate with infrasonic and sonic frequencies because these long sound waves may travel over very long distances (hundreds of kilometers) underwater.

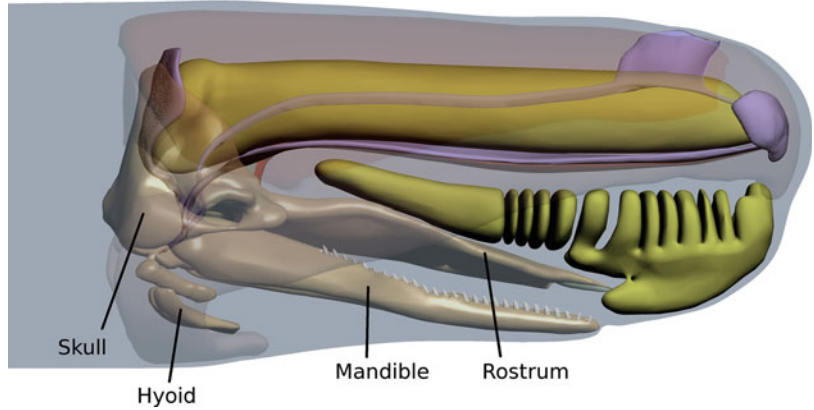
A prerequisite for echolocation of toothed whales is, next to a fine-tuned hearing system, a loud "voice." For the echolocation click sounds, a hypertrophic complex in the nose of these animals evolved to generate, emit, and focus sound underwater without any significant loss of energy. Thus, dolphins and other toothed whales generate the sound in the nose and not, as usual in other mammals, with the larynx. In the sperm whale, the nose is particularly impressive: the nasal complex degrades the skull to an insignificantly small structure. The skull of 18 m large sperm whale bull is almost 6 m long. It forms a long "armchair" in which the nasal complex is located (Fig. 2). This nasal complex is formed primarily by two huge fat bodies so that more than a quarter of the total weight of the sperm whales is due to the weight of the nose. Sperm whales generate the loudest sound in the animal kingdom with their nose, up to 236 dB re. 1  $\mu$ Pa which, in theory, would yield 205 dB in air.

### The Brain

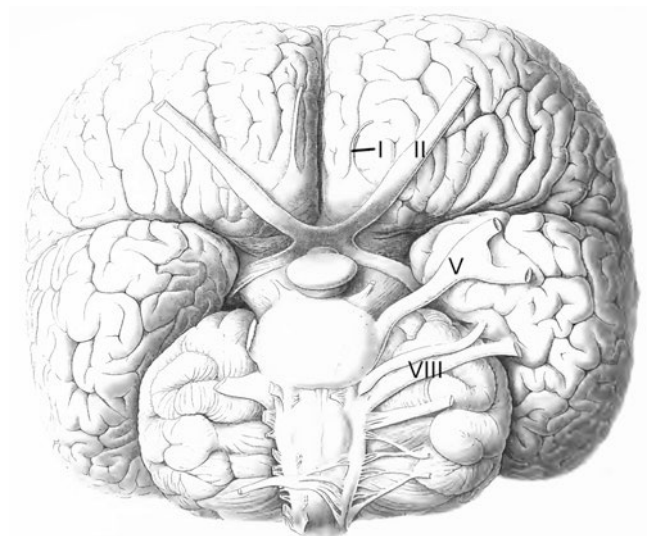
Dolphins (and to a certain extent whales) have relatively large brains for their body mass, similarly to apes. The cetacean brain is wider and shorter than the brain of a terrestrial mammalian brain of the corresponding mass, due to the modifications of the cranial cavity. The transition from a terrestrial to the aquatic lifestyle changed the proportional relationships of various parts of the

**Cetacean Morphology,**

**Fig. 2** Right lateral view of the head of the sperm whale. The structures of the nose, i.e., the nasal fat bodies (yellow), are extremely prominent. The air connecting system (nasal passages and adjacent air sacs) is depicted in purple

**Cetacean Morphology,**

**Fig. 3** The brain of the beaked whale (*Hyperoodon ampullatus*) from below (ventral view). Note that the neocortex is massively folded showing a complex pattern of gyri and sulci. I, olfactory nerve; II, optic nerve; VIII, vestibulocochlear nerve (Adapted from Kükenthal 1893)



brain. With the acquisition of echo-orientation, the acoustic pathways became the absolute dominant part of the brain. In parallel, cetaceans have a hypertrophied cerebral cortex with a strongly developed groove pattern (gyrification) (Fig. 3). However, the gray matter of the neocortex is thinner than in humans with only about half number of neurons in case of the bottlenose dolphin (*Tursiops truncatus*).

The structure of the cetacean neocortex follows the bauplan of terrestrial Cetartiodactyla, i.e., the functional units (cortical columns) of most areas exhibit five cortical layers (primates and rodents generally show six layers) composed of different neuron populations with characteristic features as to size and shape of perikaryon as well as the arrangement and local distribution of their

processes. In general, the dolphin neocortex is dominated by large- and medium-sized pyramidal neurons. Whereas there is a layer IV in every primary sensory area in the human, the situation in dolphins is reverse. Adult dolphins show only more or less discontinuous residues of layer IV in a restricted area of the primary visual cortex. In all primates, layer IV is the main termination of thalamo-recipient fibers. Furthermore, layer IV is particularly conspicuous in the primate association areas of the frontal cortex. However, a distinct layer IV does not exist in cetaceans, as in Perissodactyla and terrestrial Cetartiodactyla. Several hypotheses have been forwarded to explain the functional circuitry and projections of a five-layered cortical column. Most of them, however, are based on the model of the agranular human

motor cortex (in which layer IV is limited or absent), and so their applicability to whales and dolphins remains to be verified.

The two cerebral hemispheres are connected by a relatively thin corpus callosum. Interestingly, during sleep periods, only one brain hemisphere is awake and controls the body, while the other hemisphere rests. Sleeping is probably rare in cetaceans, and there are only about 3–5 min continuous sleep interrupted by pauses of breathing.

In toothed whales, the various cortical and subcortical components of the limbic system show different degrees of development. The hippocampus and the mammillary body are extremely reduced and interconnected by a relatively thin fornix. The anterior thalamic nuclei and the habenulae, however, are further developed than in other mammals. In contrast to the nucleus of the olfactory tract, the amygdala complex is well developed in microsmatic species (baleen whales) and in anosmatic species (toothed whales). This indicates that, apart from olfactory stimuli (see below), input to the amygdala arises from other sources, among them the auditory system. Furthermore, the remarkable development of the cortical limbic lobe (periarchicortex), and the specific paralimbic lobe, also points to the largely nonolfactory character of this system in the dolphin (Cozzi et al. 2017).

## The Sense Organs and Cranial Nerves

As seen for the hearing system and the toothed whale nose, aquatic life placed very different demands on the mammal-specific sense organs of cetaceans. Here, because of the nasal sound generation, toothed whales have reorganized their whole nasal system so that they do not develop an **olfactory** epithelium. In general, toothed whale embryos display the anlage of an olfactory bulb which, however, completely disappears in the subsequent fetal stages. Thus, adult toothed whales do not have an olfactory mucosa or an olfactory nerve and bulb. A vomeronasal organ is also absent in cetaceans.

Adult baleen whales still have a small but functional nose equipped with an olfactory

nerve, an olfactory bulb, slender olfactory peduncle, and an olfactory tubercle, a situation resembling that of many terrestrial microsmatic mammals. Interestingly, the functional significance of the detection of airborne odors for an animal living in the oceanic environment is not clear.

Dolphins are clearly sensitive to chemical stimuli but most cetacean species have no taste buds. Since the olfactory part of the nose was completely reduced, dolphins may relay probably on the trigeminal innervation of the oral cavity for chemoperception (Oelschläger and Oelschläger 2009). The trigeminal nerve is the thickest cranial nerve in baleen whales but the diameters of the axons tend to be thin. In the smaller toothed whales so far investigated, the trigeminal nerve contains 82,000–156,000 axons (human: 140,000). The trigeminal nerves in the large whales have 400,000–500,000 axons. This high number of axons may be explained by the extreme size of the forehead region innervated in these animals. However, the sense of touch was reported to be insignificant in cetaceans although the skin is richly innervated around the mouth, the blowhole, and the genitals.

Cetaceans have laterally placed **eyes**, and a binocular visual field is present only in small species (including most dolphins) and limited to a reduced rostral and ventral area. Other possible reduced fields are placed dorsally and slightly caudally. However, the sense of sight may play only a minor role underwater; the eyes of cetaceans, except some river dolphins, are reported to be fairly well developed and equipped with a spherical lens. With this spherical lens, a sharp image on the retina may be produced in low-light conditions underwater as well as in air in bright-light condition. Both eyes can be moved individually. In the bottlenose dolphin 147,000–390,000 axons were found in the optic nerve compared to 1,200,000 in the human. In baleen whales, the optic nerve may contain approximately the same number of axons as in the bottlenose dolphin, whereas in the sperm whale only 172,000 axons were counted.

Dolphins have a thick retina comprised of rods and cones. The fovea centralis (area of best visual

resolution) is band shaped, and the neurons in the ganglionic layer are very large (up to 150  $\mu\text{m}$  in diameter). The optic fibers show a complete or almost complete decussation.

Electrophysiological mapping studies in dolphins have located the visual cortex not in the dorsocaudal or occipital part of the hemisphere as in most mammals but in a more central position near the midline.

The **auditory system** in the brain of whales and dolphins corresponds to that in terrestrial mammals but shows a significant increase in size. According to the impressive diameter of the vestibulocochlear nerve, i.e., the number of fibers of its cochlear part, the all auditory nuclei are very large in cetaceans. And, thus, the secondary auditory fiber tracts (trapezoid body, acoustic striae) are well developed.

A comparison between relative volumes of other auditory nuclei in the common dolphin and the human is impressive. There are multiples for the dolphin cochlear nucleus ( $16\times$ ), lateral superior olive ( $150\times$ ), nuclei of the lateral lemniscus (up to  $200\times$ ), inferior colliculus ( $12\times$ ), and medial geniculate nucleus ( $7\times$ ) (Oelschläger and Oelschläger 2009).

In general, auditory structures are smaller in baleen whales than in toothed whales. The components of the midbrain tectum differ in size in baleen whales and toothed whales. In most baleen whales, the inferior colliculi (audition) are smaller or as large as the superior colliculi (vision). Toothed whales have very large inferior colliculi. This fact demonstrates the dominance of the sense of hearing in toothed whales and the importance of their echolocation system. The auditory system shapes the morphology, size, and connectivity of the whole toothed whale brain due to the necessity of processing vast amounts of acoustic information and the high propagation velocity of sound in water. Toothed whales scan their surroundings with their echolocation system constantly and additionally communicate by the help of the various vocalizations. Accordingly, they have extended neocortical auditory projection fields in comparison to other neocortical areas.

The diameter of the vestibular nerve is only one-tenth that of the cochlear nerve, a fact that

correlates well with the very small semicircular canals and the low number of vestibular ganglion cells in toothed whales.

## Skin

The structure of the skin and blubber of cetaceans is highly organized and complex. It was described to have a smooth rubbery texture without glands. The epidermis of cetaceans is characterized by the lack of keratin and by a prominent interdigitation of epidermal rete pegs and long dermal papillae. The thickness of the epidermis varies depending on species, age, and location sampled between 1 and 10 mm in mean. The ventral body wall tends to have the thickest epidermal layer.

The dermis and subcutis join to the thick blubber layer which is multifunctional. It is the primary site for metabolic energy storage, provides thermal insulation, and contributes to positive buoyancy. The blubber also functions to streamline the cetacean body and to form specialized locomotor structures such as the dorsal fin, propulsive fluke blades, and caudal keels. Construction of the blubber structures relies not only on lipid but also on the fiber equipment of collagen and elastin.

There is a plexus of parallel running arteries and veins in the fluke, dorsal fin, and flippers. Here, thick and muscular walled central arteries are surrounded by a plexus of veins running alongside and function like a heat exchanger to regulate body temperature.

Toothed whales possess shallow, regular cutaneous ridges of the surface of the skin over much of their bodies. They are usually faint and can be seen by close inspection of the skin of a living animal at an oblique angle. These ridges are generally quite shallow at the surface (less than 10 to slightly over 100  $\mu\text{m}$  high) and range in width from 0.4 to 1.7 mm in dolphins.

## Respiration, Circulation, and Diving

The oxygen uptake of cetaceans is very effective. They can exchange about 75–90% of the air



volume in the lungs with each breath (land mammals about 10–15%). To dive, oxygen is mainly in body tissues, in particular in the muscle, which is rich in myoglobin. Although the stored blood oxygen content is relatively low, the blood represents an important oxygen storage because dolphins have two to three times greater relative blood content per kg body weight (120–180 ml kg<sup>-1</sup>) as terrestrial mammals. When diving, the oxygen consumption is reduced. Cardiac activity and blood circulation slow down, and some organs can be temporarily separated from the oxygen supply.

For respiration air is rapidly exhaled first when surfacing, which happens with a loud blow because air is blown under strong pressure through the narrow nostrils. The cooled and depressurized air may condense into a cloud of fog called “the blow” in large whales. After exhaling, the inhalation follows immediately. The entire respiratory exchange lasts less than a second in dolphins and can be repeated after a longer dive several times. The diving duration varies depending on the species and situation. Many dolphins usually dive only for a few minutes, while sperm whales and beaked whales can stay submerged well over 1 h without surfacing to breathe.

How the dolphin’s body rules the pressure at great depths remains a mystery in many ways today. Since oxygen is mainly bound to body tissues, cetaceans need little air in their lungs while diving. The cetacean lungs are relatively small; their wall is stabilized up to the level of the entrance to alveoli with cartilage rings. During deep dives, the lungs must collapse almost completely similarly to the bellows of an accordion and pressed to the thoracic spine and ribs. Other organs (except the air-filled middle ear) are generally rich in water and fatty liquids and thus are nearly incompressible. Therefore, they can withstand the intense pressure. Arteries with increased muscular walls form widely branched meandering systems, called *retia mirabilia*, fill out many cavities of the body like thick cushions. These *retia* may control blood pressure when the water pressure is changing. Probably they also prevent the formation of gas bubbles in the

blood during rapid emergence and thus reduce the risk of decompression sickness.

## Inner Organs

The main distinctive feature of the digestive system of cetaceans is the presence of a multi-chambered stomach. In dolphins, the stomach has three sections that continue with a pyloric chamber. The first section is the fundus, which is responsible for the storage and mechanical processing of food. It is followed by the main body of the stomach and the pyloric stomach, both draining their digestive glands. Most beaked whales have five stomachs; other cetacean species possess even more chambers. Small intestine and colon can be distinguished from each other only histologically. The relatively large liver has no gall bladder.

The kidneys show a grape-like structure with up to 10,000 lobules (renculi) in the large whales. Interestingly, similar features can be found in the human fetus and in bovine.

From the skeleton of the hind limbs, only small **pelvic** rudiments inside the body are present in dolphins where the strong penis musculature or the vaginal muscles originate. The testes are intraabdominal and moved far dorsally just behind the kidneys. The fibroelastic penis is to a large extent within the abdominal cavity between the pelvic bones. It runs in an S-shaped curve into a longitudinal belly fold, which opens with a narrowly elongated slit caudally of the umbilicus. The apical portion which is located in the penis fold is only superficially comparable to a glans penis, since there is no independent corpus spongiosum. For erection, the penis straightened because of the blood filling the unpaired corpus cavernosum and also because the two parallel retractor muscles (that keep the S shape of the organ at rest) relax.

The female reproductive organs are shifted dorsally. The uterus has two horns and the embryo usually develops only in the left uterine horn although the placenta partially extends into the contralateral horn. The vagina opens into an elongated fold, which lies directly in front of the anus.



There are only fragmentary information and estimates about the reproductive biology of most cetaceans. In many whales, both sexes show a seasonal reproductive cycle, and the seasonal increase in activity of the testes in the males is linked to the estrous cycle of the females. Most cetaceans are promiscuous.

The gestation periods are generally long in cetaceans. In dolphins, it varies depending on the species between 9 and 17 months, although it is not necessarily correlated with the body size of the animals. Twin pregnancies are very rare. The birth takes place tail first, as breech birth, but the head position is also possible. In any case, the newborn must be quickly brought to the surface so that it can take its first breath.

The newborns are fully developed and reach about one-fifth of the length of the mother. Thus, they are comparable with advanced precocial birds or running hoofed mammals. A correspondingly high birth weight is made possible because the birth canal can greatly expand due to the rudimentary pelvic bones. In some species, infants are tended not only by the mother but also sometimes by several “aunts.” Since cetaceans do not have absorbent lips during lactation, the teat is taken into the mouth, and the milk is ejected by the mammary gland by muscle actions. The two mammary glands are on either side of a line between the umbilicus and the vaginal slit. Lactating *mammas* may be swollen, so that the otherwise hidden teats slightly protrude outward. The milk is extremely nutritious (fat content 16–36%, only about 5% for most land mammals) and facilitates fast growing. Nevertheless, the young dolphins are breastfed unusually long, from several months up to 8 years (bottlenose dolphin). Calving intervals range from 1 year in the smaller dolphin species to 8 years in killer whales. Sexual maturity is reached in the small species (i.e., the common dolphin) within 6 years and up to 16 years in killer whales.

## Cross-References

- [Artiodactyla Morphology](#)
- [Cephalization](#)

- [Echolocation](#)
- [Encephalization](#)

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## Cetacean Navigation

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## Synonyms

[Directed movement](#); [Orientation](#); [Travel](#)

## Definition

The process that mysticetes and odontocetes employ to move from one place to another, often by determining one's position over time and space.

## Introduction

Animals that dive to great depths or migrate long distances in the open ocean must employ a wide variety of methods to navigate their environment. Navigation techniques sometimes differ by species, and likely include a combination of sensory systems depending on the situation and perception cues available. There is still much to uncover about the mechanism of each sensory modality used for navigation by cetaceans. Because of the difficulty of experimenting on large cetaceans, many inferences about the mechanisms of cetacean navigation have been made from studies conducted on sea turtles, birds, and small odontocetes. Experiments on captive odontocetes have informed discoveries on sensory modalities used with echolocation and magnetoreception. Bio-logging techniques on wild populations have revealed information on the use of geomagnetic, visual, and passive acoustic cues for long-distance migration. Although there are other sensory modalities used by cetaceans (e. g., chemoreception, somatosensation, electroreception, balance) (Torres 2017), we have reviewed the literature for each sensory modality as it relates to cetacean navigation and describe the most commonly documented methods below, including acoustic, visual, geomagnetic cues, and cultural transmission.

## Acoustic Cues

In the marine environment, sound plays an important role in navigation. Sunlight is rapidly attenuated with depth and in turbid water. Even where light is available, it can be difficult to see to equivalent distances compared to in-air environments. Sound, however, travels roughly five times faster in water than in the air, and low frequency sounds can propagate many miles (Payne and Webb 1971). As a result, sound is the primary sensory cue for cetaceans interacting with their environment.

Toothed whales, dolphins, and porpoises (odontocetes) have developed highly sophisticated echolocation systems to sense their

surroundings. Similar to man-made sonar, an echolocating odontocete sends out packets of short-pulsed high-frequency sounds ranging from 40 to 150 kHz. When the directional sounds hit an obstacle, they bounce back to the animal's lower jaw, allowing the odontocete to discriminate among items, localize in three-dimensional space, and estimate distances to other animals, objects, the seafloor, and the surface (Au 1993). While echolocation has been extensively studied for its use in sensing and capturing prey, it also assists cetaceans in navigation. Wild finless porpoises (*Neophocaena phocaenoides*) inspect upcoming areas up to 77 m away with regular echolocation clicks before they swim silently at ranges closer than 20 m (Akamatsu et al. 2005). Large inspection distances have been documented for wild and captive bottlenose dolphins (*Tursiops truncatus*) that use echolocation up to 140 m and 113 m, respectively (Au 1993). These and other odontocetes use echolocation to first establish an understanding of their environment at greater distances before engaging in short-distance foraging-related echolocation.

Baleen whales, or mysticetes, do not possess the anatomical structures that odontocetes have for active echolocation. However, they can listen to the returning echoes from their own vocalizations to gain information about the environment (Payne and Webb 1971). One example of a mysticete that uses passive listening to navigate its environment is the bowhead whale (*Balaena mysticetus*). Bowheads migrate annually between their summer feeding areas in the Beaufort Sea and winter breeding areas in the Bering Sea, spending most of their time beneath sheets of ice. They create breathing holes by breaking through areas of thin ice with their large heads. This requires a mechanism for assessing ice condition to determine if ice is thin enough to break through. To do this, bowhead whales use the relative level of echoes from their frequency-modulated calls bouncing off the ice (Ellison et al. 1987). They typically target ice less than 20 cm thick, but can break through ice up to 60 cm, while actively avoiding multiyear ice floes 10–20 m thick. By using this passive

listening mechanism, bowheads are able to navigate safely beneath Arctic ice sheets.

Passively listening to external sounds may provide additional details about environmental surroundings. The source of these external acoustic cues may be biotic (biological) or abiotic (nonbiological). There are many sources of biotic sound in the ocean, including social sounds made by members of the same species. For example, humpback whales (*Megaptera novaeangliae*) form and maintain acoustic herds similar to terrestrial herds that are maintained by visual contact (Payne and Webb 1971). This species-wide acoustic behavior may have evolved in response to the extensive 12,000-mile migration between winter breeding grounds and summer feeding grounds. Acoustic herds have been detected outside breeding grounds along migration routes, and therefore can be used by humpback whales to find, join, and remain within migration corridors (Norris et al. 1999). Propagation models have also suggested that the 20-Hz sounds produced by fin whales (*Balaenoptera physalus*) should be audible to ranges of 525 miles if propagating within the deep sound channel. This allows fin whales, who lack fixed breeding regions, to come together at will by maintaining an acoustic herd over their entire distribution range (Payne and Webb 1971).

Other biotic noise generated by snapping shrimp, fish, invertebrates, and abiotic sounds like relative levels of surface and benthic noise, may serve as landmarks for migrating whales. These soundscapes can indicate proximity to land, relative depth, and even substrate type. Shore noise, which generates sounds within 100–1000 Hz, falls within the ideal inferred hearing range of baleen whales. Western gray whales (*Eschrichtius robustus*) have some of the longest known migrations of any cetacean, and are able to maintain their coastline routes by keeping the sound of the surf to one side, especially in more bathymetrically complex portions of the coast (Mate and Urban-Ramirez 2003). Because grey whales remain close to the shoreline while migrating, they likely combine these acoustic cues of the breaking waves with in-air visual cues of the coastline itself.

## Visual Cues

Given the highly specialized hearing and echolocation abilities of cetaceans, vision would seem to be of less importance when it comes to navigation. However, many cetaceans spend a substantial proportion of their lives in well-lit shallow waters, where underwater vision remains evolutionarily adaptive. The disproportionately large pupils of humpback whales collect large amounts of light, enabling them to see even in the deep ocean. Direct observation and experimental studies of dolphins in managed care have shown that dolphins have excellent in-air and underwater vision. Their visual acuity is better in-water than in-air, but the range for many species of cetaceans is comparable to terrestrial mammals. Cetaceans also have lateral vision, which can provide a 120–130° visual field (Kremers et al. 2016). As a result, both in-air and in-water vision are likely used by cetaceans to inspect their surroundings.

In shallower waters, where there is greater visibility from incoming sunlight, whales may use bathymetric features as visual landmarks to navigate. Humpback whales departing from New Caledonia display widely dispersed migratory paths with multiple routes. However, their migrations include multi-day stops at La Torche and Antigonina, two shallow seamounts off Australia (Garrigue et al. 2015). Seamounts, which are widespread throughout all ocean basins and irregular in size and shape, create distinct cues in the open ocean where there are few visual cues. Additionally, the complex three-dimensional habitats on seamounts host high densities of invertebrate and vertebrate species (Morato et al. 2010). This creates further visual distinction, which may also be assessed with other sensory systems using acoustic, chemical, thermal, or hydrodynamic cues. Seamounts also have distinct geomagnetic signatures, so whales may be using the magnetic field of seamounts to navigate as well (see *Geomagnetic Cues*).

All cetaceans must surface to breathe at regular intervals. A special surface behavior, called spyhopping, has been documented in both odontocetes and baleen whales. Rather than the

typical horizontal surfacing associated with normal respiration, spyhopping involves the animal lifting its head straight up and out of the water. Combined with their lateral vision, spyhopping allows cetaceans to inspect objects above the water, which may provide further orientation information (Kremers et al. 2016). Gray and humpback whales regularly display this behavior on their migration route. Mysticetes may spyhop to combine visual cues with acoustic cues of the surf break to remain oriented to the coastline (Pike 1962). Although dolphins do not usually engage in long-distance migration, they may use this and other surfacing behaviors such as porpoising to visually assess their surroundings (Madsen and Herman 1980).

The use of celestial bodies for navigational purposes is better understood in other species, including birds and bees. However, some hypothesize that cetaceans can visually orient with the sun, moon, or stars (Horton et al. 2011). Tagged humpback whales in the South Atlantic and South Pacific Oceans were found to travel along a straight path migration route (within 1° of precision) (Horton et al. 2011). The magnetism of the Earth varies too widely to attribute this ability by geomagnetic cues alone. However, the additional visual information gleaned from the position of the stars and the moon would allow these humpback whales to maintain straight-line trajectories. Therefore humpback whales may combine visual cues with geomagnetic compass mechanisms to navigate their long journeys (Horton et al. 2011).

## Geomagnetic Cues

Migrating animals like sea turtles and birds can sense and use the Earth's constant dipole magnetic field (Wiltshko and Wiltshko 2005). The geomagnetic intensity is highest (>60,000 nT) near the Arctic and Antarctic, and is lowest (<30,000 nT) in the tropics (Kremers et al. 2016). Magnetic disturbances caused by electromagnetic radiation from the sun (daily fluctuations), sun spot activity (irregular variations), or even local geology, such as iron-dense rocks, can alter the local magnetic field and create anomalies, disrupting

the otherwise reliable geomagnetic topography of the Earth (Wiltshko and Wiltshko 2005; Klinowska 1985). Therefore, a geological valley (area between hills or mountains) does not necessarily equate to a geomagnetic valley (area of low magnetic intensity) and vice-versa. A number of studies investigating the potential use of magnetoreception in navigation have found correlations among geomagnetic topography and some cetacean strandings (Kirschvink et al. 1986; Klinowska 1985). However, not all strandings result from errors in magnetoreception (Balcomb and Claridge 2001).

All documented live strandings of cetaceans in the United Kingdom over a 70-year period occurred in areas where the geomagnetic anomalies were very low and geomagnetic contours were perpendicular to the coast (Klinowska 1985). Another research group observed a similar relationship between beached cetaceans and areas with relatively low magnetic intensity on the east coast of the United States (Kirschvink et al. 1986). Yet another study found a link between mass sperm whale (*Physeter macrocephalus*) strandings in the North Sea and solar storms, which temporarily affected the Earth's magnetic field (Vanselow et al. 2017). Because cetaceans appeared to strand due to misguided orientation caused by geomagnetic topography or anomalies, researchers inferred that they must also use geomagnetic cues in normal circumstances (Klinowska 1985). This would be particularly successful in the open ocean where there are few landmasses and magnetoreception would be most adaptive. Reports of fin whales (*Balaenoptera physalus*) that were observed actively migrating in geomagnetic valleys support this hypothesis (Walker et al. 1992). In addition, offshore species of cetaceans such as false killer whales (*Pseudorca crassidens*) live-stranded more frequently than inshore species such as the harbor porpoise (*Phocoena phocoena*), indicating that geomagnetic cues may be more utilized and relevant to offshore cetaceans that may target areas of low magnetic intensity while traveling long distances in the open ocean (Klinowska 1985).

While growing evidence supports the use of magnetoreception by migrating mysticetes and

open-ocean cetaceans for navigation, causal relationships can only be established with experimental testing, controlled conditions, or (in the case of large and elusive species) longitudinal repeat tracking (Allen 2013; Walker et al. 1992). There are also many unknowns regarding the method(s) of geomagnetic navigation, its precise mechanism, and if inshore dolphins utilize it at all (Kremers et al. 2016). The simplest method of geomagnetic navigation, vector navigation, relies exclusively on directional information such as heading south in winter (Wiltschko and Wiltschko 2005). In true navigation, an animal possesses the compass from vector navigation and can sense the intensity and inclination of an area, which may be used to extrapolate relative position as on a map (Allen 2013; Wiltschko and Wiltschko 2005). To find out which method humpback whales used, one study compared the tracks of tagged whales migrating from Alaska to Hawaii to modeled tracks of bicoordinate geomagnetic navigation (Allen 2013). Most of the whales' routes matched the modeled tracks, suggesting that humpback whales use true navigation. However, this study's small sample sizes call for further investigation.

There are two main hypotheses regarding the precise mechanism behind cetacean magnetoreception. Perception based on induction suggests that because cetaceans live in such a conductive medium (i.e., salt water), they can detect magnetic fields through specialized electroreceptors (Wiltschko and Wiltschko 2005). Perception based on magnetite particles (i.e., iron oxide) in the skull suggests that the particles can align with the Earth's magnetic field and transmit this information through the central nervous system. Although the neurological pathways mitigating this connection are unknown, crystals of magnetic iron oxide have been found in the brains of humpback whales and in the membrane surrounding the brain and spinal cord of short-beaked common dolphins (*Delphinus delphis*) and bottlenose dolphins (*Tursiops truncatus*) (Bauer et al. 1985). If cetaceans can use magnetoreception, then it is possible that they have specialized mechanisms for both detecting magnetic intensity and mediating directional information (Wiltschko and Wiltschko 2005). It is also possible that they use

both induction and magnetite particles (Kremers et al. 2016).

It is still uncertain whether most odontocetes can use magnetoreception. An observational research project was not successful at identifying geomagnetic cue use in wild short-beaked common dolphins (Hui 1994). However, experimental studies on captive dolphins have found that respiration, electrocardio, and galvanic skin responses, as well as response time, alter in response to changes in a magnetic field or a magnetized object, respectively (Kremers et al. 2016). These results suggest that at least some species of odontocetes can discriminate stimuli based on their magnetic composition, a prerequisite for magnetoreception-based navigation.

## Cultural Transmission

While not sensory modalities, memory and learning through cultural transmission may be crucial aspects of cetacean navigation. Whitehead and Rendell (2015) define culture as information transfer among conspecifics. There is evidence that cetaceans have the ability to gain information about their surroundings over time and transfer this knowledge to one another (Brent et al. 2015; Whitehead and Rendell 2015). Information can be transferred many ways. Southern right whales (*Eubalaena australis*) migrate annually from Antarctica to New Zealand because they display a site fidelity preference encoded in their genes and/or learned about mating opportunities in warmer waters from other individuals (Whitehead and Rendell 2015). In the event of either (or both) of these scenarios, cetaceans shape the migration routes, memories, and navigation abilities of their decedents (Torres 2017). While many cetacean species are capable of cultural transmission, the most researched are bottlenose dolphins, killer whales (*Orca orcinus*), sperm whales, and humpback whales (Whitehead and Rendell 2015).

Cultural transmission has been observed through mother-calf, group-specific, and rapid-spread social learning. These three categories may be utilized together or alone based on the distance, age, gender, and/or social dynamic of



both the sender and receiver of information (Whitehead and Rendell 2015). Cetaceans have a fission-fusion society, where relationships between individuals are fluid. However mother-calf pairs have a very strong and stable bond, especially in the first several years of a calf's life. Humpback whale calves remain with their mothers far beyond the required 6 months of nursing, and will stay by her side at least until their first migration. As mothers lead their calves between warm-water breeding grounds and the cold-water feeding grounds, calves may begin to learn the route for themselves (Whitehead and Rendell 2015). This transmission of information from mother to calf may be reinforced with the addition of other sensory modalities, such as vision and magnetoreception. Using a combination of senses, calves may memorize the geomagnetic patterns, geographical shapes, and coastal landmarks year after year (Torres 2017). Similarly, beluga whale (*Delphinapterus leucas*) calves that complete initial migrations with their mothers continue to navigate the same route as adults (O'Corry-Crowe et al. 1997).

Even after young whales separate from their mothers, entire populations of migrating cetaceans will travel to equatorial breeding grounds at relatively the same time. Humpback whales were found traveling in small groups more often than not. Therefore, even if juveniles are not prepared for a solitary migration, they have the opportunity to learn how to navigate the open ocean from a group. Group-specific social learning can also be found in sperm whales that consistently displayed different traveling behaviors (i.e., heading, interanimal distance, and straight-line distance) between groups, but kept behaviors similar within groups (Whitehead 1999). The *many wrongs hypothesis* assumes that a larger group will produce fewer inaccuracies on their route, and that the older more experienced individuals will be making the bulk of the navigational decisions (Rozhok 2008). Post-reproductive killer whale matriarchs transferred ecological knowledge to group members by leading the group's collective movement through feeding grounds, especially in years of low prey abundance (Brent et al. 2015).

While mother-calf and group-specific social learning is usually passed down vertically from one generation to another, rapid-spread transmission occurs horizontally within generations (Whitehead and Rendell 2015). Examples include the transmission of novel methods of foraging (e.g., humpback lobtail feeding) and playing (e.g., southern right whale tail-sailing). Rapid-spread transmission also facilitates the homogenous whale song alterations from year to year, and therefore may help maintain humpback whale acoustic herds that aid in navigation (see *Acoustic Cues*).

## Conclusion

Similar to their use of multimodal sensory systems while feeding (Torres 2017), cetaceans likely integrate many sensory modalities to navigate through their environment. Acoustic, visual, and geomagnetic cues and cultural transmission are not the only methods cetaceans use to navigate, but are currently the most documented. There is evidence that humpback whales use the distinct change in temperature along coastal fronts to navigate (Reinke et al. 2016), and it is possible that unknown tactile methods and sensory modalities are being used as well. Inexperienced cetaceans may not have full control of their abilities, and must learn to use sensory cues to avoid getting lost or stranding during travel. They must also learn to adapt to naturally occurring environmental changes, such as the effect of solar flares on magnetoreception (Vanselow et al. 2017). Anthropogenic activities can further disrupt the mechanisms of navigation. For example, increased noise from ship traffic can mask acoustic cues (Erbe 2011), and climate change may force whales to change their navigation routes in search of food (Meyer-Gutbrod and Greene 2017). More research is needed to understand the four navigation techniques described herein, as well as other potential methods used for navigation. This will be especially important for conservation as managers seek to mitigate threats to endangered and threatened cetacean species.



## Cross-References

- Cetacean Cognition
- Cetacean Communication
- Cetacean Life History
- Cetacean Locomotion
- Cetacean Sensory Systems
- Communal Behavior
- Compass Orientation
- Culture
- Landmark
- Social Facilitation
- View-Based Homing

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humpback whale, *Megaptera novaeangliae*) and the odontocetes (the toothed whales, such as the bottlenose dolphin, *Tursiops truncatus*). These two groups have very different ecological niches, spatial and temporal distribution patterns and social structures, and this is reflected in their very different sensory capabilities. In addition, as several species of odontocetes can successfully be kept in captivity, it is for these species that we have the greatest understanding of sensory systems and abilities. The most information is available about vision and hearing; the other senses (chemoreception, balance, somatosensation, electroreception, and magnetoreception) have received comparatively little attention.

## Vision

Cetaceans appear to use vision in a variety of contexts (e.g., communication, prey capture), and cetacean vision relies on the same structures and principles as vision in terrestrial mammals. Light enters the eye and is refracted by a lens and cornea onto the retina, which contains the sensory cells of the eye (the rod and cone cells) (Kröger and Katzir 2008). Underwater vision is constrained by several factors however. In general, light levels in the aquatic environment are reduced due to scattering by particulate matter and high levels of absorption. Light absorption is wavelength specific; red light (~650 nm) is absorbed very quickly, while blue light (~475 nm) has the least absorption and therefore has the deepest depth of penetration (Kröger 2008). The refractive index of water is very different from air, requiring adaptations to the terrestrial eye for proper light refraction; however, many cetaceans use vision above and below the surface, requiring eyes that work well in both environments. Finally, the diving behavior of cetaceans introduces rapidly changing light levels and additional physical stresses such as high ambient pressure (Kröger and Katzir 2008).

Cetacean eyes are positioned laterally but directed slightly anterior-ventrally. Visual fields are as wide as 130°. The eyes are mobile, although less so than in humans, and movements are

## Cetacean Sensory Systems

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## Synonyms

Balance; Electroreception; Hearing; Magnetoreception; Smell; Taste; Touch; Vision

## Introduction

Cetaceans diverged from terrestrial mammals approximately 55 million years ago, and therefore, cetacean sensory systems have evolved from terrestrial mammalian systems, and many structures and functions are similar. However, the aquatic environment is radically different from the terrestrial environment in terms of signal production, transmission, and reception. Consequently, considerable adaptation and modification of the sensory systems has been observed in the cetaceans.

The two major taxonomic groups of cetaceans are the mysticetes (the baleen whales, such as the

relatively slow. All cetaceans (except the Ganges and Indus River dolphins, *Platanista gangetica gangetica*, *P. g. minor*, see below) have the standard mammalian oculomotor muscles but have an additional retractor muscle allowing axial movements (in-out) of the eye. The eyes and eyelids can move independently of each other, a feature that is easily observable when cetaceans sleep. The eyes of dolphins can move anteriorly by up to 15 mm, so that visual fields overlap by 20–30°. However, uncrossed optic fibers have not been found in dolphins, therefore true binocular vision based on the interaction of crossed and uncrossed optic fibers may not be present. Eyes in cetaceans are anteriorly flattened (as opposed to nearly spherical in terrestrial mammals) (Supin et al. 2001; Mass and Supin 2007).

In terrestrial mammal eyes, most light refraction (for focusing on the retina) is accomplished by the cornea, which separates air from the fluid-filled eye, although small adjustments of the lens also contribute. This mechanism depends on the large difference in refractive indices between air (refractive index  $\sim 1$ ) and the corneal tissue ( $>1.35$ ). However, seawater has a refractive index similar to the eye, severely reducing the refractive power of cornea. Cetaceans have adapted to this problem by developing large, nearly spherical lenses to focus light on the retina (similar eye morphologies are observed in other aquatic species, e.g., fish). The large curvature of a near-spherical lens increases refractive power and provides well-focused images on the retina (Mass and Supin 2007). This provides cetaceans with high levels of underwater visual acuity. For example, underwater visual acuity of the bottlenose dolphin, *Tursiops truncatus*, was measured at 8.2 arc minutes at 1 m (Madsen and Herman 1980).

Adaptations for underwater vision have obvious importance for cetaceans, however many cetaceans also use vision above the surface of the water and therefore must retain visual acuity in the aerial environment. Refraction at the cornea should result in cetaceans being severely myopic (nearsighted) in the aerial environment but this is prevented by several mechanisms. The cornea is characterized by flattened regions with little refractive power, centered in the nasal and

temporal regions of eye (approximately anteriorly and ventrally from the optical axis). Aerial myopia is also prevented by muscular movement of the eye to reduce intraocular pressure and by displacing the lens further into the eye. Finally, aerial myopia is prevented by drastic pupil restriction. In this way, the eye behaves like a pinhole camera, allowing dimmer images but with good focus over a wide depth of field (Supin et al. 2001; Mass and Supin 2007). Although the mechanisms for the reduction of aerial myopia are not fully understood, these features appear to provide high levels of aerial visual acuity (e.g., bottlenose dolphin aerial visual acuity 12.5 arc minutes at 2.5 m and longer, Madsen and Herman 1980).

The pupil must be able to accommodate a wide range of illumination levels due to diving (which in many species extends to hundreds or even thousands of meters). In most species, the upper part of the iris has an operculum that can occlude the pupil. In low light levels, the operculum is raised to produce a round pupil that maximizes light entry. With increasing illumination, the operculum extends downward, eventually reducing the pupil to a U-shaped slit. At high illumination levels, the operculum advances fully leaving only two small holes in the iris for light to pass through (Kröger and Katzir 2008). Like the flattened areas of the retina, these holes are centered in the nasal and temporal regions of eye. Some baleen whales have small opercula not capable of occluding the pupil to this extent, and the Amazon River dolphin (*Inia geoffrensis*) does not have opercula but instead has round pupils even when constricted (Mass and Supin 2007, 2009). Like eye and eyelid movements, pupil movements are independent between eyes (Mass and Supin 2009).

Cetaceans, like terrestrial mammals, have densely packed photoreceptors in the retina (e.g., 400,000 cells/mm<sup>2</sup> in bottlenose dolphins; Dral 1977). The cetacean retina has a large number of rod cells, achromatic photoreceptors sensitive to low light levels. However, there are few cone cells, photoreceptors sensitive to higher light levels that can give rise to color vision (about 1–2% of photoreceptors; Peichl et al. 2001). Most terrestrial mammals have two types of cone receptors (S-opsin and L-opsin) allowing

for dichromatic color vision, however only L-opsin cone receptors have been found in cetaceans. This arrangement is also observed in nocturnal, terrestrial mammals. Therefore, cetaceans lack dichromatic color vision, and color discrimination is relatively poor (Reuter and Peichl 2008; Fasick and Robinson 2016). Some color sensitivity is based on the comparative signals from rod cells and cone cells (best sensitivity 488 and 525 nm, respectively; Jacobs 1993). The maximum sensitivity of cetacean rod cells is shifted toward blue wavelengths, which maximizes visual sensory input while at depth. This blue-shifting of maximum sensitivity is more pronounced in deep diving species (Fasick and Robinson 2016).

Like terrestrial mammals, retinal ganglion cells are not homogeneously distributed. While terrestrial mammals have single areas within the retina of high ganglion density, most odontocetes and all mysticetes studied have two high density areas connected by a region of higher cell densities. Ganglion cell densities have been found to be as high as 800 cells/mm<sup>2</sup>. The spatial pattern of these areas overlaps that of the flattened areas of the cornea and the pupil openings: in the nasal and temporal regions of the eye. Therefore, images with minimal distortion are projected onto these high resolution areas of the retina. It is thought that in aerial vision, the temporal high-resolution area of the retina is primarily used, while for underwater vision, both high-resolution areas are important (Supin et al. 2001). Unlike other cetaceans investigated, the Amazon River dolphin has only one high-sensitivity area in the retina (Mass and Supin 1989). In comparison to the terrestrial mammals, cetaceans have unusually large ganglion cells and low ganglion cell density; however, there is no clear explanation for this arrangement (Mass and Supin 2007).

Cetaceans also have a blue reflective tapetum lucidum behind the retinal pigment epithelium. This reflective protein layer reflects blue light back into the eye, increasing sensitivity in low-light conditions. The tapetum lucidum in cetaceans covers a large proportion of the eye's

interior in comparison to terrestrial mammals (Mass and Supin 2007).

Retinal ganglion cells transmit impulses from the photoreceptors through the optic nerve (cranial nerve II). Consistent with the large size but low density of the cetacean retinal ganglion cells, the optic nerve has a large diameter but a low density of nerve fibers (e.g., about 25% that of primates). The total number of optic fibers is highly variable across the cetaceans but roughly scales with body size. The visual system is well represented in the superior colliculus (midbrain), the lateral geniculate body (thalamus), and the visual cortex in the occipital lobe (Mass and Supin 2009).

Bottlenose dolphins have demonstrated inter-modal transfer between visual and auditory sensory systems. Objects that are known visually can be recognized acoustically through echolocation and vice versa (Harley et al. 1996). While most cetaceans have retained vision as an important sensory modality, the Ganges and Indus River dolphins are functionally blind. These odontocetes lack a crystalline eye lens and have no oculomotor muscles. In the now-extinct Yangtze River dolphin (*Lipotes vexillifer*), the eyes were functional but reduced. This regression of visual ability was potentially due to their low-visibility habitats; however, other cetaceans that live in low-visibility habitats (e.g., the Amazon River dolphin) do not have decreased visual systems (Mass and Supin 2009).

## Hearing

While light does not propagate well in aquatic environments in comparison to terrestrial environments, sound propagates unusually well. Sound attenuation is very low, especially for lower frequency sounds. Sound also travels much faster than in air (approximately 1500 m/s for sea water, approximately 345 m/s for air). Finally, while the acoustic impedance (a measure of how the acoustic medium dynamically responds to sound pressure) of air is very different than

biological tissues, the acoustic impedance of water is quite similar. These features of sound in water have led to a high dependence on sound for various activities and to a highly modified auditory anatomy. This dependence on acoustics and anatomical modification is especially pronounced in the odontocetes, who use echolocation for foraging and navigation (Au and Hastings 2008). Unlike vision, hearing is highly specialized for underwater hearing, and adaptations for terrestrial hearing have largely been lost.

As a group, cetaceans are able to hear an extraordinary range of frequencies; however, there is considerable specialization between the odontocetes and the mysticetes. Odontocetes specialize in high-frequency hearing, and this group has demonstrated the ability to hear frequencies from 200 Hz to above 200 kHz (for comparison, good human hearing is 20 Hz–20 kHz). High-frequency hearing in this group supports the use of high-frequency echolocation (e.g., peak frequencies >120 kHz), which provides better spatial resolution than low frequencies. High-frequency hearing has also been found for Microchiropteran bats, the other group which has demonstrated highly developed, high-frequency echolocation abilities (Au and Hastings 2008). Comparatively, little is known about the hearing thresholds of mysticetes; however, as a group they are specialized for low-frequency hearing. Mysticetes generally produce very low frequency communication sounds (mainly below 5 kHz, down to 10 Hz) which have very low acoustic attenuation, and these animals likely communicate over hundreds or even thousands of kilometers. Largely based on their sound production, mysticetes are thought to be able to hear frequencies below 10 Hz up to 30 kHz. This is supported by studies on ear anatomy and behavioral responses to sounds (Au and Hastings 2008; Ketten 2000).

The acoustic impedance of mammalian tissue is very similar to that of water; therefore, the typical terrestrial mechanisms of sound channeling and impedance-matching of the outer ear (e.g., elaborate pinnae, patent horn-shaped external

auditory meatus) are not effective nor necessary. Consequently, external pinnae are absent in cetaceans, and vestigial auditory meatus are thin and occluded, and appear to have no role in sound transmission (Hemilä et al. 2010). The challenge for cetaceans is that the similar impedances cause sound waves to travel directly from the medium into the body, causing vibrations in bony structures such as the skull (bone conduction). Because of this, and the increased speed of sound in water, the directional cues used by terrestrial mammals are challenging (interaural time-of-arrival and intensity differences). Cetaceans avoid bone conduction by isolating their ears from the rest of the skull (see below). In addition, the large size of many cetaceans and the sensitivity to high-frequency (and therefore short wavelength) sounds results in good directional hearing in cetaceans (Au and Hastings 2008).

The route in which sounds reach the ears has been well studied in odontocetes, especially bottlenose dolphins. Odontocetes appear to have two frequency-dependent sound paths. Lower frequency sounds (e.g., whistles, used in many species for communication) appear to be transmitted through lateral pathways on the head (i.e., near the vestigial external auditory meatus) (Ketten 2000). In bottlenose dolphins, this pathway is most sensitive to frequencies between 16 and 22.5 kHz (Popov et al. 2008). Dolphins have also developed a novel method for the reception and transmission of high-frequency sounds to the ear. The lower mandible is very thin and filled with a fatty tissue which conducts acoustic vibrations very efficiently. This mandibular fat pad extends posteriorly to the middle ear, acting as a sound channel. The mandibular sound channel is most sensitive to high-frequency sound from the anterior direction, and therefore appears to have evolved for the reception of the return signals from echolocation (Au and Hastings 2008). In bottlenose dolphins, this sound channel is most sensitive to sounds between 32 and 128 kHz (Popov et al. 2008). In both cases, sounds are transmitted directly to the middle ear; the tympanum in odontocetes has little or no function in hearing but instead has a role in



pressure regulation (Numella 2009). The exact sound route in mysticetes is unclear. Fin whales appear to use bone conduction for low-frequency hearing, likely applicable to other mysticetes due to similarities in ear anatomy (Cranford and Krysl 2015).

Like all mammals, the middle and inner ears are surrounded in bony cavities (the auditory bullae), but cetacean auditory bullae are unusually dense. The tympanic and periotic bones of the auditory bullae have separated from the rest of the skull, and are known as the tympanic bullae or the tympano-periotic complex, and house the inner and middle ears. In odontocetes, the tympanic bullae are completely isolated from the rest of the skull by ligaments, mucosa, and air sacs. This isolation is thought to facilitate directional hearing and may prevent the transmission of self-produced sounds directly to the ears. In mysticetes, the isolation of the tympanic bullae is not complete, and large body size may be more important for directional hearing (Au and Hastings 2008; Ketten 2000).

In terrestrial mammals, the middle ear ossicles (the malleus, incus and stapes) connect the tympanic membrane to the oval window of the inner ear. Vibrations are transmitted along the ossicular chain in order to set the inner ear fluid in motion. In odontocete cetaceans, the ossicular chain does not connect to the tympanic membrane but instead connects to the tympanic plate (the thin lateral wall of the tympanic bone). The mandibular fat pat extends to the tympanic plate, and sounds from this route vibrate the tympanic plate and consequently the ossicular chain (Hemilä et al. 2010). The ossicular chain also contacts the thin lateral wall of the temporal wall of mysticetes; however, the term tympanic plate is a specific, functional term for the odontocete thinning of the tympanic bone, as it has a function in hearing. It is not known if the thinned part of the tympanic bone has a similar function in mysticetes (Numella 2008). Cetacean ossicles are enlarged and heavy in comparison to terrestrial mammals; however, this does not decrease frequency response as it would in terrestrial organisms as heavy ossicles are able to

transmit high frequencies in water (Numella 2009).

As in all mammals, the cetacean inner ear is known as the cochlea. The cochlea is a coiled structure filled with endolymph and perilymph. Vibrations at the oval window are transferred to the fluid within the cochlea, which cause displacement of the auditory sensory hair cells in a structure known as the organ of Corti. The organ of Corti is supported by the basilar membrane, both of which run the entire length of the coiled cochlea. As sound waves entering the cochlea cause the basilar membrane to vibrate and deform, the physical properties of the basilar membrane determine the frequencies to which the ear is sensitive. In odontocetes, the basilar membrane is very stiff, allowing them to perceive and process very high frequencies, while in mysticetes, the basilar membrane is relatively flexible and more suitable for detecting low frequencies. While odontocetes have about the same number of cochlear hair cells as many other mammals, they have  $2\text{--}3\times$  as many associated ganglion cells, which is certainly a key component in their exceptional hearing abilities (Au and Hastings 2008; Ketten 2000).

Bending of the hair cells in the organ of Corti leads to nerve impulses in the cochlear nerve (part of the vestibulocochlear nerve, cranial nerve VIII). Acoustic nerve impulses travel to the inferior colliculus (midbrain), lateral geniculate body (thalamus), and to the auditory cortex. In odontocetes, the auditory cortex has been found in the suprasylvian gyrus, located along the vertex of the hemispheres, and in the temporal lobe (Ridgway 2000; Hof et al. 2005). As in all mammals, tonotopic organization is observed from the inner ear to the auditory cortex (e.g., in the basilar membrane, the base is most sensitive to high frequencies and the apex to low frequencies, and this frequency organization is conserved throughout the acoustic nervous system) (Au and Hastings 2008).

The importance of the auditory system can be observed in the degree of neural investment. For example, the ratio of nerve fibers in auditory nerve in comparison with optic nerve is up to three times



greater in cetaceans than in terrestrial mammals. In odontocetes, which make more use of acoustic information due to their dependence on echolocation, the inferior colliculus and medial geniculate body are far larger than their visual counterparts (the superior colliculus and the lateral geniculate body). Odontocetes in particular have developed very rapid auditory temporal processing, high sensitivity, and frequency discrimination (Au and Hastings 2008).

## Chemoreception

In cetaceans, chemoreception can occur through taste and smell; however, chemoreception abilities are reduced in the cetaceans in comparison to terrestrial mammals. The vomeronasal organ (organ of Jacobson) is absent in modern cetaceans, although evidence for a vomeronasal organ has been found in a neonate gray whale (*Eschrichtius robustus*; Kienle et al. 2015). It has been suggested that chemoreception, at least in odontocetes, is a combined sense involving aspects of both taste and smell (Kuznetsov 1990).

Taste (or gustation) is the ability to detect waterborne compounds. Cetaceans generally have simple tongues with few or no taste buds (the sense organs of taste), although some studies have found taste bud like organs contained in pits found in dolphin tongues. Despite this, bottlenose dolphins have been shown to detect a variety of tastes, including the four tastes that humans perceive (sour, bitter, salty, and sweet) at level similar to humans. Nervous pathways are not well understood but may involve cranial nerves V, VII, IX, and/or X. Taste is thought to be perceived in the parietal lobe of the brain (Kremers et al. 2016).

Smell (or olfaction) is often defined as the ability to detect airborne volatile compounds, although waterborne olfaction is present in fish (Hemilä and Reuter 2008). In olfaction, molecules dissolve in the mucous of the olfactory epithelium. This activates olfactory receptors on the cilia of sensory neurons, transmitting impulses through cranial nerve I, which leads to the olfactory bulb in the frontal lobe for processing

(Kremers et al. 2016). As cetaceans close their nasal apertures underwater, any olfactory senses are likely limited to the aerial environment.

Odontocetes lack olfactory bulbs and cranial nerve I and are generally thought to have no olfactory capabilities (Pihlström 2008). However, innervated chemoreceptor cells have been found in the nasal cavities of harbor porpoises (*Phocoena phocoena*), therefore some level of olfaction may be present (Berhmann 1989). Olfactory bulbs have been reported in several mysticetes and have been well documented in bowhead whales (*Balaena mysticetus*). Olfactory epithelium has also been found in bowhead whales, and this species appears to react to airborne smells. It is thought that any sense of olfaction may be useful in locating the presence of planktonic prey by airborne smell (Thewissen et al. 2011).

## Somatosensation

Somatosensory systems include the sense of touch, pain, temperature and body position, and involves several receptors including mechanoreceptors (for touch) and nociceptors (for pain). While other sensory systems have receptors concentrated in the head, this is not the case for somatosensation. For example, mechanoreceptors are spread over much of the surface of the body. Cetacean skin is well innervated and is very sensitive to touch. Dolphins are most sensitive in their anterior region (the rostrum, eyes, melon, and near the blowhole), corresponding to high numbers of cutaneous mechanoreceptors. High sensitivity near the blowhole is likely important for determining when the blowhole is above the surface before breathing (Kremers et al. 2016; Thewissen 2009). Tactile contact also appears to be an important form of communication in several species (e.g., *Atlantic spotted dolphins*, *Stenella frontalis*; Dudzinski 1998). Because of the high density of water, cetaceans can detect mechanical disturbances in the environment at comparatively large distances. Some species have facial vibrissae (e.g., the Amazon River dolphin, mysticete cetaceans), and it is thought that deflection of these

hairs provides additional tactile information (Dehnhardt and Mauck 2008). Somatosensory information is processed in the posterocruciate gyrus of the cerebral cortex (Supin et al. 2001).

## Balance

Like all mammals, cetacean's sense of balance, or the perception of movement and spatial orientation, is achieved through the vestibular system located in the inner ear. The vestibular system consists of two independent motion sensors. First, two well-developed otolith organs are located in the utricle and saccule. These are responsive to linear acceleration (e.g., changes in gravitational direction). Changes in inertia displace the position of the otoliths, which are detected by sensory hair cells. Although this system is well developed in cetaceans, relatively little is known about the cetacean otolith organs (Spoor and Thewissen 2008). The second type of motion sensor is the semicircular canal system, which perceives angular movements. The three semicircular canals (anterior, posterior, and lateral) are embedded within a bony matrix. Each canal contains a semicircular duct which is connected with the utricle, forming an endolymph filled circuit. At one end of each semicircular duct, a dilation (the ampulla) containing a gelatinous structure (the cupula) seals the canal. Acceleration and deceleration cause the endolymph to lag behind due to inertia, and such lags are detected by hair cells in the cupula. As the three semicircular ducts of each ear are approximately orthogonal, any rotation can be sensed by at least one canal (Spoor and Thewissen 2008; Spoor 2009).

In general, more agile and maneuverable mammals have larger-arc'd semicircular canals. Although many cetaceans are highly agile and maneuverable (e.g., spinner dolphins, *Stenella longirostris*), cetaceans have relatively small semicircular canals (arc and lumen size) in relation to body size. For example, the semicircular canals of blue whales are slightly smaller than those of humans. This is thought to be because

cetaceans are generally quite buoyant and therefore, do not experience significant gravitational forces, nor are they normally in contact with the substrate. In addition, cetaceans have reduced mobility of the head in relation to the body (e.g., some species have fused cervical vertebrae). This could potentially lead to stronger rotary input (from the entire body) and overstimulation of the vestibular system. Therefore, reduced semicircular canals may be an adaptation to avoid overstimulation of the vestibular system, especially during acrobatic movements. Another notable difference between cetacean semicircular canals is that the lateral canal is the largest while the posterior canal is the smallest, while in other mammals the lateral canal is the smallest (Spoor and Thewissen 2008; Spoor 2009).

Nervous impulses from the vestibular system likely reach the central nervous system through the vestibulocochlear nerve (cranial nerve VIII). Information is processed in the vestibular brain stem nuclei and motor nuclei to facilitate movements to stabilize the body (Sipla and Spoor 2008).

## Electroreception

Electroreception is common in aquatic vertebrates but is rare in mammals. The Guiana dolphin (*Sotalia guianensis*) has well innervated, enlarged hair follicles on the lower jaw which have been shown to be sensitive to weak electrical fields. It is thought that this sense may be used to find fish buried in the sediment. Although electrosense has not been found in other cetacean species, mandibular hair follicles are found in other cetaceans. The benthic foraging behavior of other cetacean species suggests that electrosense may be more widespread in the cetaceans (Wilkins and Hofmann 2008; Czech-Damal et al. 2012).

## Magnetoreception

Magnetoreception, the ability to perceive magnetic fields, has been suggested for cetaceans,

but virtually nothing is known about if they possess this sense or how it is used. Magnetoreception was first suggested for cetaceans based on field observations of strandings, as the locations of strandings were found to be correlated to geomagnetic minima. It has also been suggested that baleen whales could use geomagnetic sense for long-distance migration, as fin whale migration routes in the western Atlantic were correlated with low geomagnetic intensity. Magnetite has been found in the brains of humpback whales, bottlenose dolphins, and short-beaked common dolphins (*Delphinus delphis*). Associated nerve fibers were also found in the short-beaked common dolphin. Few controlled studies have been carried out on cetacean's ability to detect magnetic fields, and results have been contradictory; far more research in this area is required before this sensory system is confirmed in cetaceans, let alone understood (Hofmann and Wilkens 2008).

## Conclusion

Cetacean sensory systems and abilities have undergone tremendous adaptation from their terrestrial ancestry in a relatively short time. All cetaceans appear to have a great dependence on acoustics, especially the odontocetes who use echolocation for foraging and navigation. Vision has been retained as an important sensory modality despite the limitations of vision underwater and the challenges of having eyes that function in both the aquatic and aerial environments. Somatosensation also appears to be an important and well-developed sense for cetaceans, while chemoreception and balance reception have been reduced. Cetaceans also appear to have some ability to detect electrical and magnetic fields. Several areas need more research, especially the sensory systems of mysticetes and nondelphinid odontocetes (e.g., beaked whales), as well as research into the less well-studied senses (e.g., electroreception).

## Cross-References

- ▶ [Auditory signals](#)
- ▶ [Cetacean cognition](#)
- ▶ [Cetacean communication](#)
- ▶ [Communication](#)
- ▶ [Echolocation](#)

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## Chaining

### ► [Shaping](#)

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## Change

### ► [Mutations](#)

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## Change Blindness

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### Definition

Change blindness is a phenomenon of visual attention in which changes to a visual scene may go unnoticed under certain circumstances, despite being clearly visible and possibly even in an attended location. For example, the appearance of an object might not be noticed if it coincides with a disruption of visual continuity such as a flicker or an eye movement. Change blindness is an example of a striking limitation to visual attention and indicates that visual representations are more sparsely detailed than would sometimes be assumed. The phenomenon can occur under a wide array of circumstances, as well as in multiple sensory modalities, and has been demonstrated in some nonhuman animals.

### Introduction

The first experimental investigations of change blindness were of saccade-contingent changes: changes that occur at the same time as eye movements. McConkie and Currie (1996), for example, had human participants view photographic displays on a computer screen while monitoring their eye movements with eye trackers. During

viewing, sudden changes were made to the display and participants were asked to search for them. For example, an object in the scene might change color, change location, or disappear entirely. Changes that happened during an eye saccade were more difficult to detect than those occurring during a fixation. Even prominent changes encompassing a large portion of the screen frequently went unnoticed if they happened while the viewer's eyes were in motion.

Subsequent research using different methods showed that this kind of failure to detect changes is not limited to eye movements; change blindness can occur under a wide variety of conditions and at any time. For example, in the flicker task, one of the most commonly used methods of investigating change blindness, participants search for a difference between two sequentially alternating visual scenes that are identical save for a single feature (Rensink et al. 1997). If the scenes alternate instantaneously, with one image or the other always visible, the change is usually seen quickly and effortlessly. Participants often report that the change “pops out” at them. On the other hand, if a short inter-stimulus interval (ISI) is inserted between each image, during which the screen is blank, the change is much more difficult to identify and requires an active, location-to-location search. Consequently, accuracy is worse, and latency to identify the change is longer. The flicker task is particularly appealing to experimental psychologists because it allows them to easily isolate and manipulate specific aspects of a change, such as its size, location, or salience. The method also establishes the practical importance of change blindness, by showing that change blindness can occur at virtually any time, regardless of what the participant is doing or where she is looking. The earlier demonstrations of saccade-contingent change blindness constrained it to the short moments of time when the eyes are in motion.

While the flicker task has been the most widely used procedure for studying change blindness, other methods have emerged that show the same pattern of results and illustrate that change blindness can occur under widely varying conditions. For example, one method is similar to the flicker

task, in that participants attempt to identify changes in alternating images. However, instead of including an ISI to induce a global visual disruption, a set of small local disturbances (“mudsplashes”) are superimposed onto the image at the moment of change (O’Regan et al. 1999). These mudsplashes are located so as not to obscure the change, but their presence nevertheless makes it more difficult for participants to identify the difference between images. Thus, the procedure illustrates that a global visual disruption (as in the flicker task) is not necessary for change blindness to occur. Yet another method uses gradual changes to produce change blindness. In this method, two images are prepared that are identical save for one feature (such as the presence, location, or color of an object). One image is presented initially, but gradually dissolves into the other over the course of several seconds, and participants are asked to search for and identify the change (Simons et al. 2000). In this case, there is no visual disruption at all, and yet participants often fail to notice the change, especially if the rate of change is slow.

Not only can change blindness be produced by a widely varying collection of laboratory procedures, there appear to be parallels in other sensory modalities. Using parallel methods, researchers have shown that people can be made to fail to detect changes in auditory (Gregg and Samuel 2008), tactile (Gallace et al. 2007), and olfactory (Sela and Sobel 2010) stimuli. While less research has been done on these nonvisual equivalents of change blindness, their existence would seem to suggest that change blindness could be due to a general nonmodality specific feature of attention.

Research programs on change blindness carry some important implications for cognitive science and our understanding of how we experience the world around us. While our momentary experiences during visual fixation may be quite detailed, very little of that detail is maintained from one view to the next. Instead, the visual memory that persists from moment to moment is quite sparse, consisting of little more than the meaning or gist of a scene (Simons and Levin 1997). Thus, we fail to notice many feature-level changes because the representations of those initial features are

transitory and do not persist across the change. Nevertheless, the details that are preserved appear to be sufficient to allow people to interact with a complex world quite successfully, at least under most everyday circumstances.

## Change Blindness in Nonhuman Animals

If change blindness is in fact a wide-ranging general consequence of sparsely detailed representations of visual scenes, we might expect to see the same phenomenon in some nonhuman animals that have similar visual systems. Indeed recent research has shown predictable change detection failures in nonhuman animals using methods patterned after those originally developed to investigate change blindness in humans.

Primates, of course, are closely related to humans and have visual abilities that are comparable in many ways. Thus, they make a logical population for initial comparative research into change blindness. Tomonaga and Imura (2015) used a variant of the flicker paradigm to study change blindness in chimpanzees and humans. They presented alternating displays consisting of several line drawings on a CRT monitor in a task inspired by the flicker paradigm. On each trial, one of those line drawings changed between alternating displays by either shifting position, changing shape, or appearing/disappearing, and chimpanzees were trained to touch the location of the line drawing that changed. As in other implementations of the flicker task, some trials included a blank field that appeared at the time of a change, producing a global disruption of visual continuity. Inclusion of those blank fields led chimpanzees (like humans) to make more errors and to respond more slowly to all three kinds of changes, indicating that change detection was more difficult.

Cavanaugh and Wurtz (2002) used a similar approach to study change blindness for motion change in macaques. Their monkeys viewed several fields of moving dots on a display, one of which could change its direction of movement. Monkeys were then rewarded for making an eye movement in the direction of the field that had



changed its direction of movement (or for not making an eye movement if no change had occurred). As with other change blindness tasks, they included a global visual disruption on some trials by presenting a brief blank field at the onset of the change. Change detection accuracy was impaired on those trials that featured a blank field, a standard change blindness effect. Accuracy on blank field trials improved if the location of the change was cued ahead of time, indicating that monkeys were still capable of detecting those changes, and indeed could strategically use information to attenuate the effects of change blindness.

Pigeons are more distantly related to humans, but have excellent visual acuity and have long been used to study visual attention in comparative psychology. Herbranson et al. (2014) used a version of the flicker paradigm to study pigeons' ability to detect changes in a visual display. Birds viewed alternating collections of features (up to eight lines of varying orientations) projected onto three response keys in an operant chamber. One of the line features present on one response key appeared and vanished across presentations, and after observing a required number of iterations, pecks to the location of the change were reinforced. Some trials contained an ISI between successive displays (causing a global visual disruption) and other trials did not. Pigeons were less likely to peck the location of the change if an ISI was present, the same change blindness pattern seen in the flicker task with human participants. Accuracy remained better than chance however, showing that pigeons were still capable of correctly identifying changes on some ISI trials. Subsequent research in the same lab (Herbranson and Jeffers 2017) used the same methodology to demonstrate change blindness for color changes, a potentially more subtle variety of change. Again, pigeons were less likely to detect a change if an ISI was present. Furthermore, change blindness in pigeons appears to be affected by some of the same factors that affect change blindness in humans and in the same way. Specifically, the magnitude of impairment caused by visual disruption depends on both the duration of an ISI and the salience of the change (Herbranson 2015; Herbranson and Davis 2016).

Whereas the flicker task produces change blindness via a global visual disruption, recall that such a disruption is not necessary in humans, who also show change blindness for gradual changes that involve no visual disruption at all. Hagmann and Cook (2013) showed that this is also the case for pigeons. They trained birds to detect continuous, gradual changes in brightness on a computer display using a go/no-go procedure. Pigeons viewed a colored rectangle that was either constant or continuously changing in brightness. Pecks on constant-brightness trials were reinforced on a VI schedule, and pecks on changing-brightness trials resulted in a timeout. Birds suppressed pecking on changing trials, but took longer to do so when the rate of change was slower. Thus, more gradual changes were more difficult to detect, as they are for humans. Again this shows that changes may go unnoticed, even when there is no disruption of visual continuity to obscure the change. In the context of the previously described comparative research, it also shows that change blindness in pigeons is not tied to one specific laboratory procedure such as the flicker task.

## Conclusion

Change blindness has been a topic of considerable interest in cognitive psychology in recent decades. Research on humans indicates that it can occur in a wide variety of situations, and consequently can be studied using many different procedures. The resulting collection of research tools includes several tasks such as the flicker paradigm that can be readily adapted to study change blindness in non-human animals. While only a small number of species have been tested and only a subset of the developed change blindness tasks have been adapted, the available results show striking parallels with the results produced by humans.

Change blindness research has thrived in part because it presents results that do not match most people's subjective perceptions. Our momentary visual experience appears detailed, even though that detail is transitory and does not persist across views, and most people overestimate their ability to detect changes ("change blindness blindness";

Levin et al. 2000). The existence of change blindness in nonhuman animals might initially seem just as puzzling, given that vigilance and the ability to quickly and accurately detect changes would intuitively seem to have survival value for many animals. Simons and Levin (1997) propose that the sparsely detailed visual representations that give rise to change blindness may serve to provide stability and continuity from moment to moment. Thus, one can have a detailed perceptual experience at any instant, but by preserving only those components that are likely to be important, the relevant features in the next glance can be quickly matched up without the overwhelming task of tracking and linking each and every minute detail. Presumably this logic would apply as well to nonhuman animals, who often have to solve the same perceptual problems as humans, with even more limited neural resources.

## Cross-References

- [Attention](#)
- [Change Detection](#)
- [Cognition](#)
- [Same/Different Learning](#)
- [Search Image](#)
- [Short-Term Memory](#)
- [Visual Perception](#)
- [Visual Search](#)
- [Working Memory](#)

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## Change Detection

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Understanding memory is one of the great scientific challenges of the twenty-first century. An essential component of all memory is the ability to store and process information in working

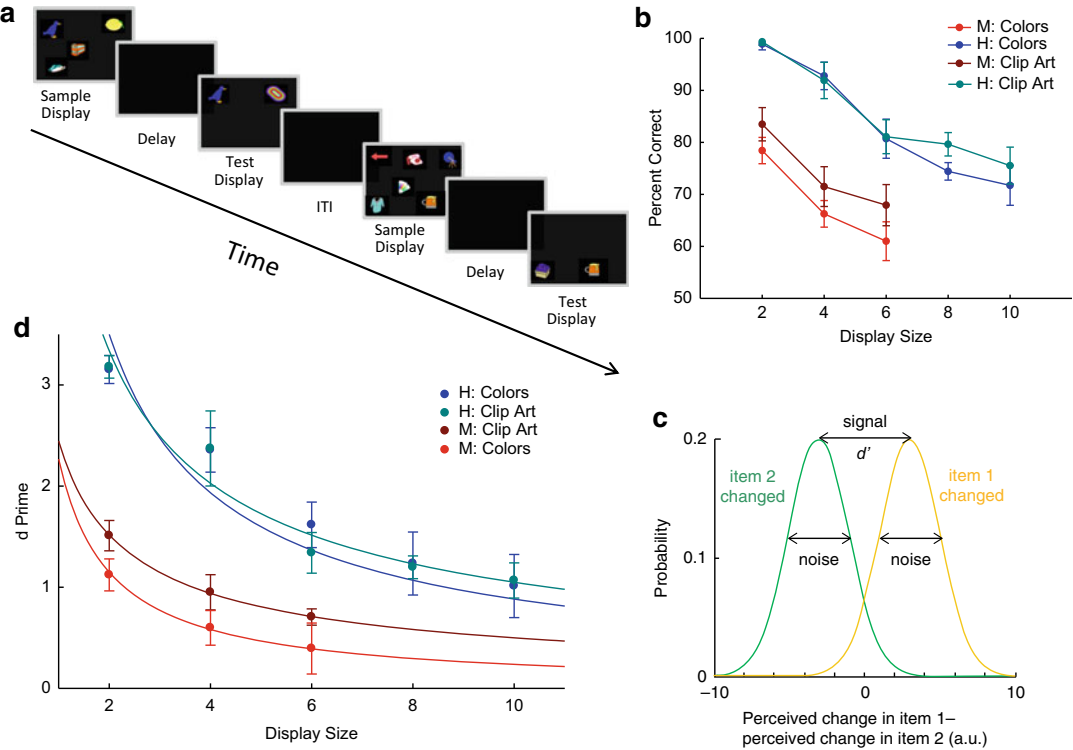
memory (WM, sometimes called short-term memory, See also chapters “► [Working Memory](#)” and “► [Short-term Memory](#)”). Over the past 29 years, the working-memory task of choice has been *change detection* where (mostly) humans have been presented with an array of visual stimuli and following a short delay they report which stimulus changed, or whether there was a change (e.g., Alvarez and Cavanagh 2004; Cowan 2001, 2005; Eng et al. 2005; Luck and Vogel 1997; Pashler 1988; Rensink 2002). Conclusions from human change-detection memory research has suggested that human visual working memory (VWM) is limited in capacity to about  $4 \pm 1$  items (e.g., Cowan 2001, 2005). In one version of change detection, several objects (e.g., colored squares or clip art) are presented as a sample array, to be remembered. Following a retention delay, a test array is presented with one object changed; the test array can include all unchanged sample-array objects or a smaller number, for example one changed object and one unchanged object in a 2-alternative forced-choice test. Subjects typically identify the changed object, for example by touching the changed object. Change detection is well suited to investigating working memory because many memory objects can be presented simultaneously within the encoding time period of VWM. Furthermore, change detection has been shown to utilize visual memory, independent of verbal rehearsal, making it a suitable task for testing VWM of nonhuman animals with well-developed visual systems (Alvarez and Cavanagh 2004; Luck and Vogel 1997). It is important to understand how VWM works in nonhuman species to understand VWM generally, including evolutionary continuity of this important early memory processing stage. But difficulties in obtaining the necessary high performance (see also chapter “► [Evolution](#)”) accuracies have stymied attempts to obtain viable animal VWM results from change-detection tasks until recently (Buschman et al. 2011; Devkar et al. 2015; Elmore et al. 2011, 2012; Elmore and Wright 2015; Gibson et al. 2011; Heyselaar et al. 2011; Lara and Wallis 2012; Lazareva and Wasserman 2016; Wright et al. 2010; Wright and Elmore 2016).

## Comparing Monkey and Human Change Detection

Rhesus monkeys are an ideal species to compare to humans because they perform well in other visual memory tasks (e.g., list memory) and because they are the standard medical model for humans. Much of what we learn about VWM in rhesus monkeys should be applicable to understanding human VWM. A memory model with rhesus monkeys can provide the foundation for types of memory studies that are difficult or impossible to conduct with humans, such as lesions, electro physiological recordings, pharmacological and gene expression manipulations.

One such recent investigation compared two rhesus monkeys and six human subjects tested in nearly identical change-detection tasks (Elmore and Wright 2015). The basic task is illustrated in Fig. 1a. Two important parameters were manipulated in order to investigate the functional relationships of VWM: display size and stimulus type. Display size refers to the number of items presented in the sample array. Monkeys were tested with display sizes of 2, 4, and 6 and humans were tested with display sizes of 2, 4, 6, 8, and 10. Both species were tested with two types of stimuli, clip-art and colors (Fig. 1a). Monkey and human performance was high and above chance (50%) at all display sizes and decreased as display size increased (Fig. 1b).

Comparing monkeys and humans in terms of VWM capacities, the monkeys showed capacities equal to (clip art) or less than one item (colored squares), a result that makes little or no sense for a species' survival. Therefore, a continuous-resource, detection-theory account of VWM was used to compare these species VWM (Fig. 1c). Unlike fixed-capacity accounts (e.g.,  $4 \pm 1$  items), the continuous-resource account predicts that working memory limitations stem from noise in the internal representation of each item. As display size increases, an item will receive less resource on average and consequently has a noisier internal representation (e.g., Wilken and Ma 2004; Bays and Husain 2008). Determining which stimulus has changed in a change detection task becomes



**Change Detection, Fig. 1** (a) Progression of events for two clip-art trials in the change-detection task. (b) Percent correct for humans and monkeys tested with clip art and with *colored squares*. (c) Calculations of  $d'$  values for each stimulus type and display size, where a *hit* ( $H$ ) was a correct response to the lower numbered location in the test display. A *false alarm* ( $FA$ ) was defined as a response to the lower

numbered location when that location did not contain the changed item. And  $d'$  varied according to  $d' = \frac{[z(H) - z(FA)]}{\sqrt{2}}$ . (d)  $d'$  values were fit by power-law functions because memory sensitivity ( $d'$ ) should be proportional to  $1/N$ , where  $N$  is the number of items in the display,  $Y$  is a constant, and  $x$  is the exponent:  $d' = Y \cdot N^{-x}$

more difficult as display size increases, not because the capacity has been exceeded, but rather because it becomes a problem of extracting a signal (memory for the stimuli) from a noisy representation. Differences between humans and monkeys can be explained by differences in level of overall attention to the task, as attention has the effect of increasing the signal-to-noise ratio. In the continuous-resource model, attention can vary over a wide range of attention levels, unlike the fixed-capacity account. Further, as attentional variability contributes to noise levels, it is already accounted for by the continuous-resource account. The continuous-resource account employs  $d'$  values from signal detection theory as a measure of memory sensitivity (Wilken and Ma 2004; Green and Swets 1966; Macmillan and Creelman

2005; Elmore et al. 2011). Moreover,  $d'$  decreases as display size increases and are well fit, as they should be, by a power law function in Fig. 1d.

As with capacity estimates,  $d'$  was found to be greater for human subjects than for monkeys. Monkey  $d'$  values were well fit by power law functions; the  $R^2$  values were 0.98 for color stimuli and 0.99 for clip art. Human  $d'$  values from both the color and clip art condition were also well fit by power law functions;  $R^2$  was 0.75 for colors and 0.70 for clip art. The continuous-resource account of monkey and human VWM memory fits into 50 years of development of signal detection theory. Signal detection theory is the dominant framework to account for how humans and animals perceive stimuli in noise (Green and Swets 1966; Macmillan and Creelman 2005).

Functional relationships showing how performance ( $d'$ ) changes with memory load (sample display size) according to the continuous-resource model go beyond functional relationships of percent correct changes with sample display size (e.g., Fig. 1b). The latter is a descriptive account without accounting for *how* memory varies with display size or *how* the brain might produce these memory results. The continuous-resource account postulates that  $d'$  changes should vary inversely as a power function of display size. The fixed-capacity model, on the other hand, predicts that capacity will be the same at all display sizes, except for display sizes less than the capacity limit where performance should be perfect (100% correct). Perhaps most discriminating for these VWM accounts and models is how memory might operate at the neural level. The fixed-capacity model says that each item is stored and remembered perfectly – or not at all. When all the memory slots are filled, then nothing is remembered about any additional item for that VWM bout. This is problematic from a neurobiological point of view. The storage, maintenance, and retrieval of information (i.e., memory) are all likely probabilistic. In a broader sense, the nervous system is inherently noisy and its computations are probabilistic (e.g., Bays and Husain 2008; Ma and Jazayeri 2014). The continuous-resource model captures the noisy nature of the nervous system – and hence provides a plausible account of how the VWM system might work, in general.

## Comparing Pigeon, Monkey and Human Change Detection

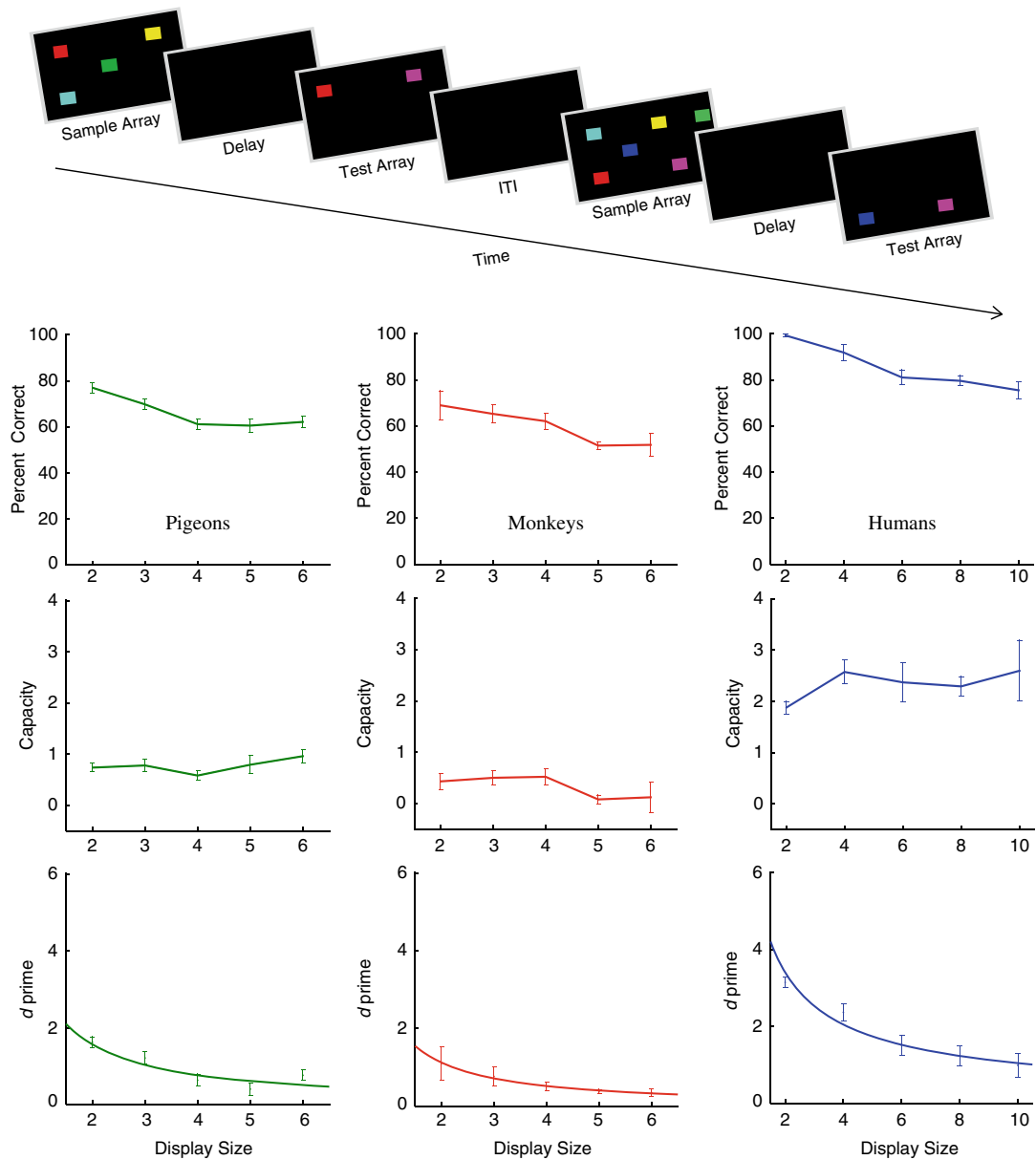
Another recent comparative change-detection study was conducted with pigeons using the same basic change-detection procedure (2-stimulus test) for direct comparisons to the results from monkeys and humans that were shown in Fig. 1 with colored-square stimuli (Wright and Elmore 2016). The top of Fig. 2 shows the task progression with colored-square stimuli and below are graphs of percentage correct, computed capacities, and  $d'$  power-law functions for pigeons, monkeys, and humans. Percent correct performance

declined as a function of display size with humans outperforming pigeons and monkeys by 15.4% and 27.3%, respectively. VWM capacity was calculated from:  $A = \left[\frac{N-C}{N}\right]^2 \times 50\% + \left\{1 - \left[\frac{N-C}{N}\right]^2\right\} \times 100\%$ , with  $A$  being the empirical accuracy,  $N$  the display size, and  $C$  the VWM capacity (Eng et al. 2005). The mean capacities with colored squares were 0.77, 0.71, and 2.46 for pigeons, monkeys, and humans, respectively. While human capacity estimates are greater than two items, the animals had capacity limits less than a single item according to the fixed capacity account. Such capacity limits make little or no sense; how could pigeons and monkeys survive (predators, food sources, mates, etc.) with working memory capacity limits substantially less than one item?

By contrast to fixed-capacity limits, pigeon, monkey, and human performances were well characterized by the continuous-resource model with  $d'$  power-law exponents that characterize the rapidity of change in  $d'$  over the range of set sizes tested. Comparing exponents across species revealed small but orderly differences:  $-1.03$ ,  $-0.94$ , and  $-0.86$  for pigeons, monkeys, and humans, respectively. Multiplicative coefficients of the power law characterize “level” of the function, the Y-axis intercept, extrapolated memory for a single item, and overall memory sensitivity ( $d'$ ). Not surprisingly, humans far surpassed the animals in this measure. But interestingly, pigeons showed a marginally superior coefficient compared to monkeys (3.18, 2.27, and 6.34) for pigeons, monkeys, and humans, respectively with a significant difference in coefficient among species.

## Mechanisms of Working Memory by Manipulating Change

Studies aimed at understanding the neural correlates of VWM content limitations have so far been guided by fixed-capacity models (Buschman et al. 2011; Vogel and Machizawa 2004). According to these accounts, only a fixed number of items (referred to as the capacity) are held in memory with high quality and no information is retained



**Change Detection, Fig. 2** *Top*: progression of events for two trials with colored squares in the change-detection task. *Bottom left*: pigeon percent correct performance, capacity, and power-law fits for  $d'$  values. *Bottom middle*: monkey percent correct performance, capacity, and power-law fits for  $d'$  values. *Bottom right*: human percent correct performance, capacity, and power-law fits for  $d'$  values

about any other items (e.g., Pashler 1988; Cowan 2001, 2005; Luck and Vogel 1997). More recently, alternative proposals have gained scientific following where “memory resource” is distributed across all items seen and memory precision is inversely related to the number of

objects in the visual scene (Wilken and Ma 2004; Bays and Husain 2008; Van den Berg et al. 2012; Keshvari et al. 2013). To test among fixed-capacity and multiple types of distributed resource models, monkeys and humans were tested with the same change-detection procedures

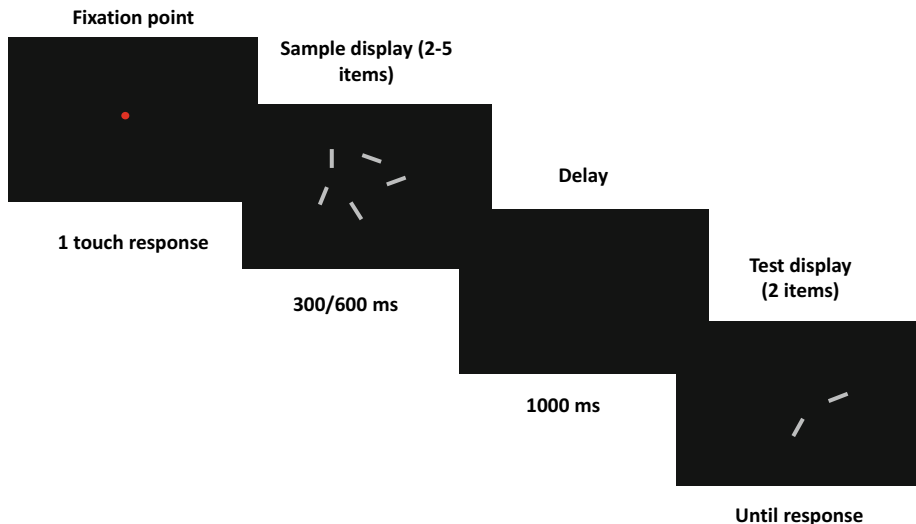


where multiple items (line tilts) were presented with different magnitudes of change at test (Devkar et al. 2015; also see Keshvari et al. 2013). Three monkeys and 10 humans viewed sample arrays of 2, 3, 4, or 5 randomly oriented lines/bars (in 6 possible locations); following a delay subjects were presented with two (randomly chosen) items from the sample array with one item changed ( $10\text{--}90^\circ$  in  $10^\circ$  steps) in orientation (Fig. 3). Correct responses of touches to the changed item were reinforced with Tang orange drink or banana pellet (monkeys) and green light and tone (humans). Trials were separated by 3 s. Monkeys and humans each were tested on 11,520 total trials and 1152 trials, respectively and their mean results are shown in Fig. 4.

Results from monkeys and humans were evaluated according to four of the leading models of VWM: Fixed Capacity, Equal Precision, Fixed Capacity plus Equal Precision (identified as, Fixed Cap + Resource), and Variable Precision (Fig. 5). According to the Fixed Capacity account, a fixed number of items (the capacity) are kept in memory with infinite precision, while remaining items are absent from memory (e.g., Pashler 1988; Cowan 2001; Luck and Vogel 1997). According to Equal Precision, all items are remembered with

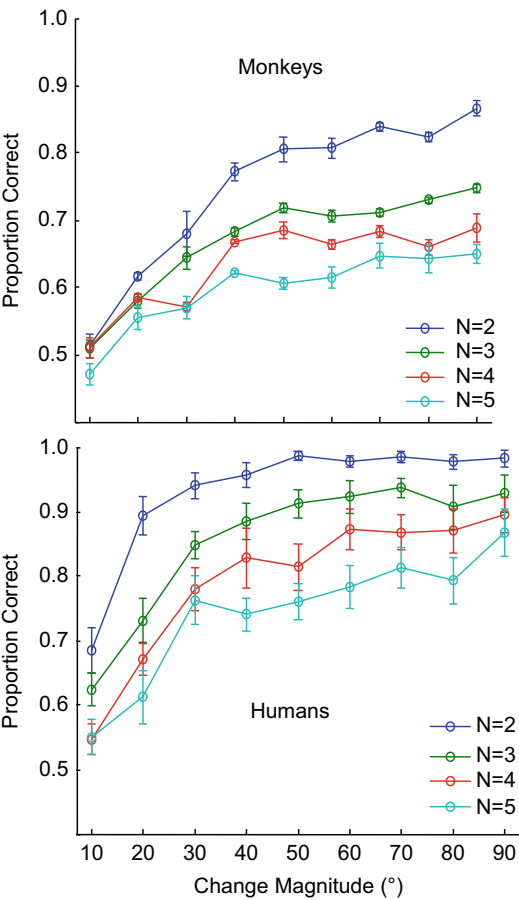
equal memory precision which decreases with increasing set size. Fixed Capacity plus Equal Precision (Fixed Cap + Resource) combines elements of Fixed Capacity and Equal Precision where only a fixed number of items share limited memory resource (e.g., Zhang and Luck 2008). Variable Precision is where memory resource is distribution across all items but in variable amounts and can vary from item to item and trial to trial (e.g., Van den Berg et al. 2012; Keshvari et al. 2013).

Evaluations were determined by maximizing (i.e., bootstrapping) the likelihood estimation of parameters from each model, and the model fits are shown in Fig. 6 (see Devkar et al. 2015). The data from both species were well accounted for by a noise-based model in which memory precision is variable across items and trials (Variable Precision) as shown by 94% and 80% of variance ( $R^2$ ) accounted for, compared to 83% and 59% for Equal Precision and 32% and 23% for Fixed Capacity for monkeys and humans, respectively. These findings are consistent with previous findings with humans (e.g., Keshvari et al. 2013; Van den Berg et al. 2012). Moreover, combining Equal Precision with Fixed Capacity helped (86% and 71%, respectively) but did not fully salvage



**Change Detection, Fig. 3** Progression of events for a trial that begins with a touch to a centered *red dot*, followed by a sample array containing five line-tilt stimuli presented

for either 300 ms (humans) or 600 ms (monkeys), a delay of 1 s, and a test of two sample-array stimuli with one changed in orientation



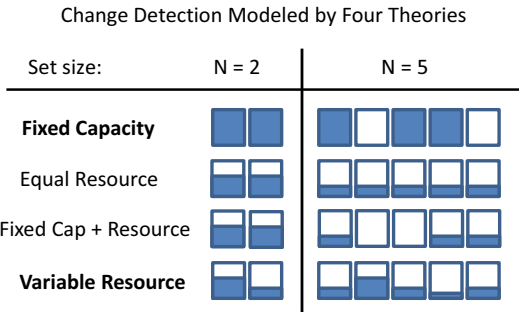
**Change Detection, Fig. 4** Mean psychometric functions of for monkeys and humans with set sizes of 2, 3, 4, or 5 line-tilt items

the Fixed Capacity account as hoped (e.g., Anderson et al. 2011; Zhang and Luck 2008). Indeed, Bayesian Likelihood Factor analyses showed that the Variable Precision account was 178 million times more likely than the next best account, Fixed Capacity plus Equal Precision (see also chapter “► Model Fitting”).

Such clear conclusions about Variable Precision being the fundamental underlying process of monkey VWM as well as humans, establishes rhesus monkeys as model system of human VWM for exploring how VWM works in these species, including the neural networks that support VWM.

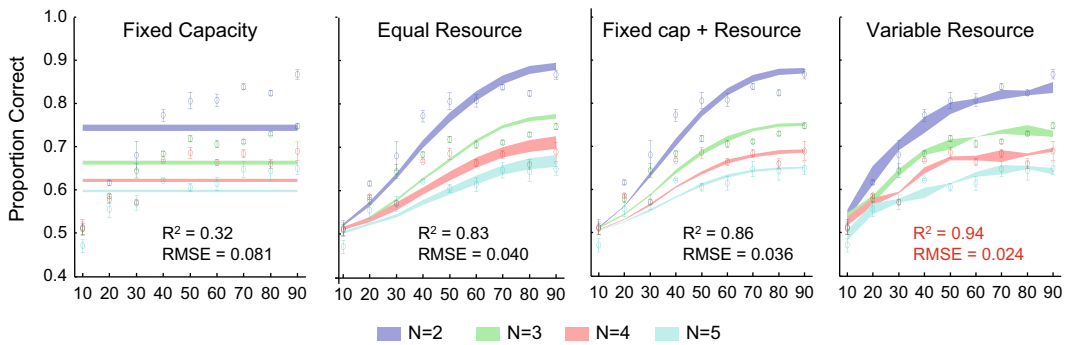
**Decision Mechanisms in Change Detection**

The previous section on VWM mechanisms discussed how variations in encoding precision of sample display items influences VWM. Precision also influences decisions in the observer’s decision-making stage that are separate from item encoding precision (see also chapter “► Decision-Making”). The change-detection task taps into both of these stages of VWM processing: The observer encodes and maintains information about the sample stimuli, compares its memory of the sample stimuli with the test stimuli at the corresponding locations, and then makes a decision about which test stimulus has changed leading to a response (Fig. 7b). In change-detection tasks, the inherent precision of one or more task-relevant stimuli can be manipulated by changing the reliability of the stimulus. In the example presented in this section, two different ellipse stimuli (different length/width ratios) were used to change precision in detecting orientation changes (Devkar et al. in press). The low-reliability ellipse was shorter and wider (fatter) making the orientation change more difficult to discriminate than the alternative high-reliability ellipse that was longer and narrower (see Fig. 7a). These combinations of reliable and unreliable stimuli were used to influence how monkeys and humans made decisions about which stimulus changed in orientation. Humans have been shown to make optimal decisions in VWM-based

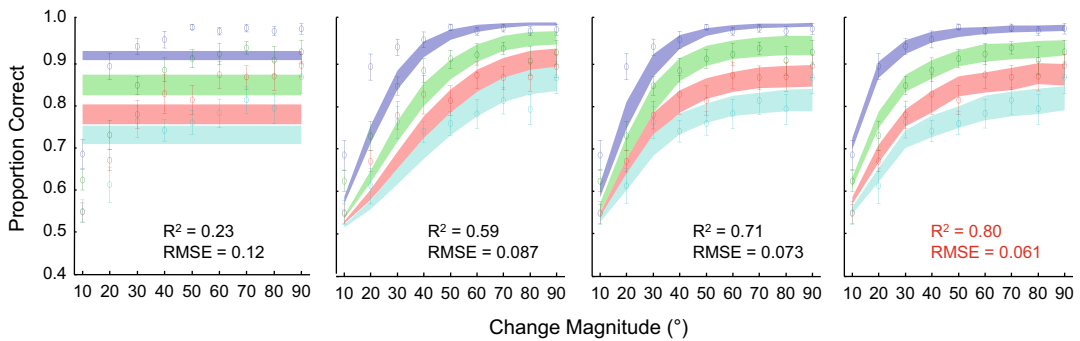


**Change Detection, Fig. 5** Schematics of four VWM theories for presentations of two or five items to be remembered in accordance with how “memory slots” are filled with memory resource

## Monkeys



## Humans



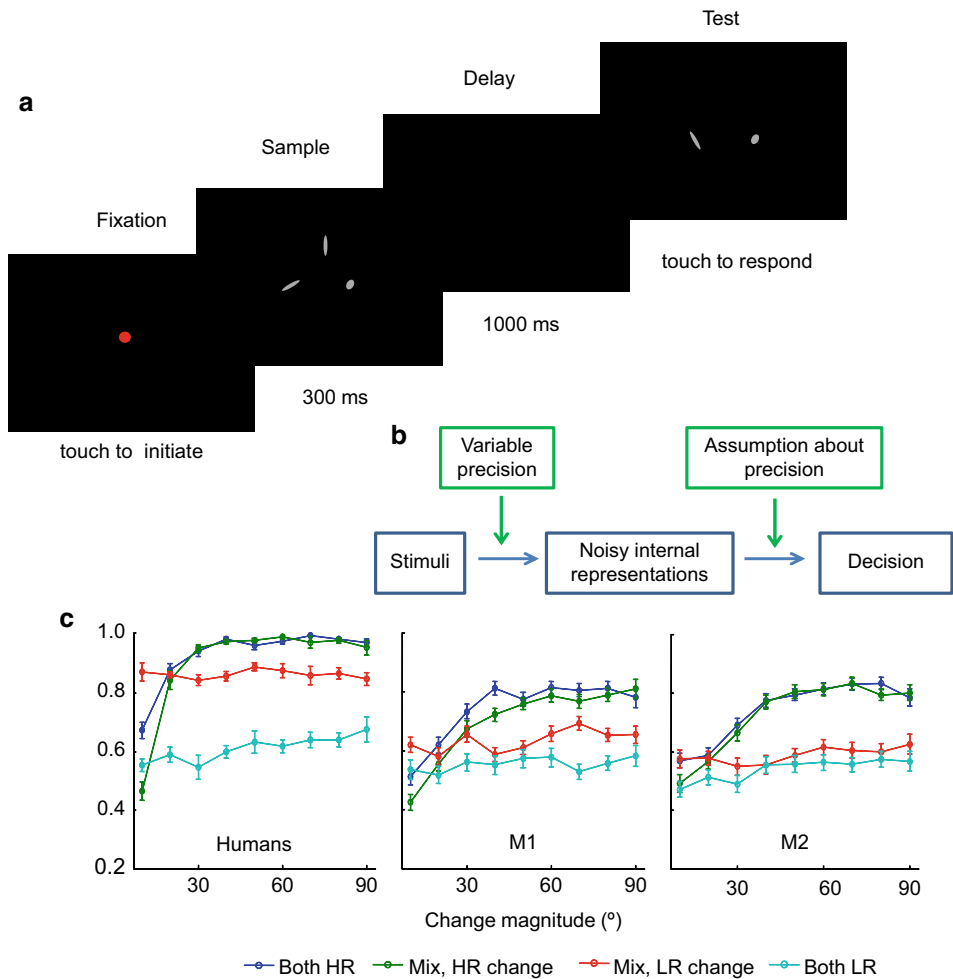
**Change Detection, Fig. 6** Model fits for human and monkey performance shown in Fig. 4 according to the four VWM theories shown in Fig. 5

comparison tasks (Devkar et al. 2015; Keshvari et al. 2013; Van den Berg et al. 2012) and therefore might give more weight to the more reliable stimulus (longer and thinner ellipses) than the less reliable stimulus (shorter, wider ellipses). Based on the computed relative weight of evidence, the observer tends to choose the location with the higher probability of change (Ma 2012). Although monkeys and humans were shown in the previous section to have similar VWM encoding mechanisms (Variable Precision), the issue here is whether monkeys would employ similar (or different) decision processes in such a change detection task as do humans.

Two rhesus monkeys and ten humans were tested to determine similarities or differences in decision processes in nearly identical change detection tasks (Devkar et al. *in press*). Subjects were briefly presented with sample arrays containing three randomly oriented ellipses with reliability types (high and low reliability) also being

randomly selected, and were randomly located in 3 out of 6 positions on an imaginary circle (Fig. 7a). Following a delay, a test array was presented containing two randomly selected ellipses from the sample array, with one of the chosen ellipses undergoing a random orientation change (10–90° in 10° steps). As in the previous section, the correct response was to touch to the item with a changed orientation followed by reinforcement (monkeys) or feedback (humans).

Tests consisted of four possible conditions. Two conditions contained the same reliability stimuli, either both of high reliability or both of low reliability. The other two conditions were mixtures of both reliability stimuli, but in one condition, the change occurred in the high reliability stimulus and in the other condition, the change occurred in the low reliability stimulus. Of particular interest is how these subjects dealt with these stimuli in making their decision about which test stimulus changed.



**Change Detection, Fig. 7** (a) Trial example used to test monkeys and humans beginning with a *red* fixation dot, followed by a sample array containing three elliptical stimuli (two types) in any one of nine angular orientations. After a 1 s delay, two of the sample-array stimuli were tested with one changed in orientation. The correct response was a touch to the stimulus that changed in orientation. (b) Processing scheme leading to the decision

about which stimulus changed. (c) Psychometric functions for a mean of ten humans and two individual monkeys presented with either two high-resolution (HR) ellipses (*blue*), two low-resolution (LR) ellipses (*aqua*), or mixtures of HR and LR ellipses with orientation changes in the LR ellipse (*red*) or orientation changes in the HR ellipse (*green*)

The psychometric function results are shown in Fig. 1c. Humans and monkeys both showed the highest proportion correct in the condition where both test ellipses were of high reliability. They also showed the lowest proportion correct in the condition where both test ellipses were of low reliability. In the mixture condition, when the change was in the high-reliability stimulus, not surprisingly accuracy was higher than when the change was in the low-reliability stimulus, reflecting training to spot changes in orientation. Nevertheless,

when the change was to the low-reliability stimulus in the mixture condition, performance was better than when both test stimuli were of low reliability. Such results have important implications for decision-making strategies by monkeys as well as humans.

These findings converge on the conclusion that when confronted with choosing between a changed low-reliability stimulus and an unchanged high-reliability stimulus, monkeys and humans more often choose the low-reliability stimulus.

Moreover, they did so independent of being able to detect an orientation change in the low-reliability stimulus. How they must have accomplished this inductive conclusion was by detecting no change in the high-reliability stimulus, they weighted their decision based on information from the high-reliability stimulus and selected the low-reliability stimulus despite their inability to see any orientation change. This is an example of *inferential reasoning and decision making by exclusion* (see also chapters “► Reasoning by Exclusion”, and “► Meta-Cognition”). It is also an example of metacognition: “you know what you can detect and you know what you cannot detect.” These are complex, sophisticated cognitive processes, particularly so for nonhuman species like rhesus monkeys.

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## Change of Primary Caregiver

### ► Primate Orphans

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## Character

### ► Nature Versus Nurture

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## Charles Darwin

### ► Jean Baptiste Lamarck

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Charles R. Menzel was a primatologist and scientist in the making from as early an age as he can remember. He recounts that even as a child he had the opportunity to explore freely in the woods and rivers of Florida and Louisiana and that this led to early exposure to animals and his early interest in their behavior and cognition. He watched and kept wild and domestic animals and learned how to care for them and observe them as they developed into adults. His grandfather, Emil W. Menzel, Sr., was an amateur naturalist who had kept a vast

number of animals in his house (deer, pythons, pangolins, to name just a few) while raising his sons in India. His father, Emil W. Menzel, Jr., was a man of high creativity who could make just about anything interesting. He studied nonhuman primates as a research psychologist and took Charles to visit the lab buildings and apes of the Yerkes Laboratories of Primate Biology in Orange Park, Florida, many times before the age of seven. Charles lived in Japan in 1963 and 1964, and during that time his father took him to watch Japanese monkeys in the hills outside of Osaka. That was a highly impactful experience for Charles. The experience of living in another culture and being treated kindly as a foreigner made a lasting impression on him, as evidenced by his continued desire to work in different parts of the world.

As a teenager, Menzel spent time observing apes and monkeys at the Delta Regional Primate Research Center in Covington, Louisiana, and watched wild primates for brief periods in field settings (Kenya, Tanzania, and Saint Kitts). In Louisiana, he frequently observed a group of young chimpanzees inventing ladders and observed the experiments that his father was conducting on leadership and communication in the same apes. He recalls the excitement of meeting and engaging scientists who were colleagues of his father when they visited.

Menzel completed his B.S. in Zoology from Duke University in 1977. During his undergraduate study, he conducted several behavioral tests with tamarin social groups. The results of those studies indicated that tamarins had an acute ability to detect novelty and changes in objects within their structurally complex greenhouse environment. Menzel also conducted a senior thesis on head cocking behavior in tamarins at Stony Brook University and in gentle lemurs at Duke University, under the guidance of Kenneth Glander and Peter Klopfer. The data he collected indicated that head cocking behavior in primates is elicited primarily by novel visual stimuli, is most frequently seen in young animals, and serves primarily a visual function (Menzel 1980; Menzel and Menzel 1980). These efforts led to an opportunity to spend a summer doing comparative behavior



studies at the Brookfield Zoo in 1977. This was the first of two opportunities to work with the ethologist, Benjamin Beck. They later worked on studies of spatial orientation in golden lion tamarins during 1989–1991 at the National Zoo (Menzel and Beck 2000).

Beginning in the 1960s, William Mason, Hans Kummer, and Emil Menzel, Jr., had developed and articulated a broad comparative approach to primate behavior. They shared what Mason called a “naturalistic bias,” taking as a primary source of data and research problems what animals do under everyday conditions. Charles Menzel absorbed all of their writings, along with those of Niko Tinbergen and the ecologist Peter Rodman, and decided to go to UC Davis for graduate school and conduct Ph.D. research under Rodman and Mason, who both exemplified the ideals of scholarship and careful analysis. They encouraged Menzel to develop a perspective – a logical or heuristic scheme – that could guide his research across future settings and years. Menzel grew interested in the ways that primates learned and discriminated categories of environmental structures and assigned value to them. This included the issue of how animals learned associations between types of food items and classes of environmental features, locations, time periods, and situational variables. It also included the problem of how well animals recalled events – food discoveries – that had occurred in areas out of view from the current location, and the stimulus factors that could facilitate remembering and appropriate search patterns. His discussions with Michael Andrews, Gustl Anzenberger, Leo Berenstain, Jane Gagne, Theodore Grand, Robert Lickliter, and Sally Mendoza were particularly important in helping him formulate these ideas during graduate school and beyond.

After completing his Ph.D. in 1986, Menzel was awarded an NRSA postdoctoral grant to study the complex interactions between primates and their environments in a field setting. Kummer served as his postdoctoral advisor. Naosuke Itoigawa invited Menzel to work at the Minoo and Katsuyama prefectural parks, where Osaka University maintained field research sites. Itoigawa had been a pioneer in studies of Japanese monkey social behavior. Menzel’s research

focused on this question: where does a free-ranging monkey go after it finds a single piece of experimentally introduced food, and what does this imply about its memory and the inferences that it forms? He found that the macaques responded very differently according to the type of food item discovered. If the food item was of a type that occurred naturally in the home range, this discovery appeared to reactivate a memory of something specific and an appropriate search “routine,” as if the animals knew that the type of food could be found in particular classes of environmental structure. For example, when finding akebi fruits that typically occurred in vines above the ground, monkeys stared upwards and entered trees that contained akebi vines. In contrast, if the macaques found a non-native food, such as chocolate, that had no history of association with the environment they instead searched near the location of the current find (Menzel 1991).

Kummer encouraged Menzel to pursue this mode of investigation with a captive colony of long-tailed macaques at the University of Zurich. This provided Menzel with an important opportunity to bring a behavioral phenomenon from the field into the lab for detailed study. Over a period of 6 years, he worked with Kummer and his colleagues, exploring social and ecological aspects of macaque learning and their ability to extrapolate their search beyond one or a few initial food items. They found that macaques used the close spatial proximity of a food item to a visible environmental structure as a cue to organize a wider search targeting similar structures. This was a form of innovative behavior, and it might be an optimal strategy for opening up a new food source under natural conditions. The macaques altered their foraging patterns in response to an unexpectedly wide range of stimulus factors and showed excellent memories for single events (Hemmi and Menzel 1995; Menzel 1996a, b).

This focus on single events, and memories of those events, played heavily in the next phase of Menzel’s career. He moved to Atlanta, GA, to work with Duane Rumbaugh and Sue Savage-Rumbaugh at the Language Research Center at Georgia State University, where he continues to conduct research and teach in the Department of

Psychology. He has collaborated on experimental studies of perception, cognition, and tool use in apes (chimpanzees and bonobos) and monkeys (rhesus macaques and capuchin monkeys) at the Language Research Center. He took a leadership role in establishing the research colony of capuchin monkeys at the Language Research Center which is now one of the largest colonies in the world. He developed a laser pointing device that apes can use to request objects and to pinpoint the locations of hidden objects. With Ted Evans, he developed training methods that successfully trained capuchin monkeys to use the laser pointing device flexibly and adaptively to request objects that lie beyond arm's reach.

At the Language Research Center, he also developed a novel and highly influential paradigm for using artificial language as a tool for studying recall and episodic memory in apes (Menzel 1999). The procedures are adapted as much as possible to the individual preferences of the ape. The work considerably extends the approach he used to study memory in New World monkeys and macaques, and it makes contact with current debates regarding the nature and extent of recall, episodic memory, and planning capabilities in nonhuman animals (Menzel 2005, 2010; Sayers and Menzel 2012). Menzel also has strongly contributed to empirical and theoretical discussions of the biological value and operation of primate cognitive capabilities in the natural habitat. His research includes efforts to assess prospective memory (Beran et al. 2012) and intentional communication (Menzel et al. 2002; Roberts et al. 2014). More recently, he has worked on problems of foraging and tool use (LaCour et al. 2014), navigation in simulated environments (Dolins et al. 2014), cognitive control (Beran et al. 2016), and risk sensitivity from a comparative and evolutionary perspective (Sayers and Menzel 2017).

Throughout his career, Menzel has received support for his research from a variety of sources, including the L. S. B. Leakey Foundation, the National Institute of Child Health and Human Development, the Wenner-Gren Foundation, the National Institute of Mental Health, the National Science Foundation (USA), and the Swiss National Science Foundation.

## Cross-References

- ▶ [Duane Rumbaugh](#)
- ▶ [Episodic Memory](#)
- ▶ [Panbanisha and Panzee](#)
- ▶ [Planning](#)
- ▶ [Sue Savage-Rumbaugh](#)

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## Charles Robert Darwin

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The chronology and information contained in this entry can primarily be referenced from two biographies of Charles Darwin. The information regarding Darwin's pre-voyage life and mid-voyage experiences can be found in *A Modest Genius: The Story of Darwin's Life and How His Ideas Changed Everything* by Hanne Strager (2016), and the post-voyage information can be found in *The Reluctant Mr. Darwin: An Intimate Portrait of Charles Darwin and the Making of His Theory of Evolution* by David Quammen (2006).

### Charles Darwin: Overview

Charles Robert Darwin was born February 12, 1809 – the fifth of six children born to Robert Darwin and Susannah Wedgwood in Shrewsbury, Shropshire, England. He attended the Anglican Shrewsbury School until the age of 16, when he would go on to study at Edinburgh University to

pursue a career in medicine. At 19, he began his education at Christ's College, Cambridge, at the order of his father. Here, he would engage in small game hunting and insect collecting. In 1831, Darwin set sail aboard the HMS Beagle as the gentleman companion to captain Robert Fitzroy. The Beagle was set to sail around the southern tip of South America, and on this journey, Darwin served as naturalist, collecting specimens from the rainforests and from a net towed behind the ship. After circumnavigating South America, the Beagle went west where it would famously stop at the Galapagos Islands before returning to England in 1837. During his years aboard the Beagle, Darwin kept detailed notes and journals that would later see publication and inform his theories.

After returning to England, Darwin went about his scientific business cataloguing his specimens and corresponding with various experts while writing his findings for publication. During this phase of his research, he and his colleagues noted the patterns of species variation as a function of their biogeographical circumstances. He would then spend the next 22 years developing his theory in various notebooks. *On the Origin of Species* was published in 1859.

Darwin married Emma Wedgwood in 1839. The couple would go on to have ten children, three of whom would die in childhood. The Darwin family lived in the small village of Down beginning in 1842, moving there to escape the political volatility of London. Darwin died on April 19, 1882.

### Early Life and Education (1809–1831)

Charles Robert Darwin was born February 12, 1809 in Shrewsbury, Shropshire, England. Charles was the fifth of six children born to Robert Darwin and Susannah Wedgwood. Darwin's father was a self-described freethinker and a physician with a passion for scientific undertakings such as chemistry and psychology. His paternal grandfather, Erasmus Darwin, was also a physician and authored *Zoonomia: or the Laws of Organic Life*. Charles began his studies at the Anglican Shrewsbury School, where he was

afforded a traditional education into his teenage years. However, in the early nineteenth century, science was not valued by the English educational system. This resulted in tension between Charles and his headmaster and classmates. At the age of 16, Charles was sent to Edinburgh University to study medicine at the order of his father. It was there that he would learn the fundamental scientific principles that would later inform his most influential and iconic theories. Even still, Charles' relationship with his father was complicated by his father's expectations.

Robert Darwin's fervor for science and propriety was at odds with Charles' passion for small game hunting and insect collecting. Robert was disappointed with his son's interests, going so far as to scold Charles explicitly, saying that he would be a "disgrace" to himself and the Darwin family. Robert served as an authority, emphasizing discipline in his otherwise aimless son. Susannah passed in 1817 from an unidentified gastrointestinal illness, so Charles was mostly cared for by his older sisters and maids. Robert's opinion of Charles would not change until he had established his career as a naturalist, travelling the world and conducting scientific observation. The initial seeds for this endeavor were planted during Charles' time at Edinburgh University where he was exposed to sciences that were not presented in more traditional schools.

In the beginning of the nineteenth century, traditional Anglican schools such as Oxford and Cambridge would not allow certain theories to be discussed. In fact, so-called radical students who doubted the divinity of humanity over nature were denied degrees and their lectures censored. This is why Edinburgh attracted many dissenting scientific minds – minds to which Charles was exposed during his time as a student there. One such scholar to whom Charles had attached himself was Robert Edmond Grant, a student of Jean-Baptiste Lamarck. Grant was among the first to echo Charles' sentiment regarding the origins of complex species. Both Grant and Darwin believed that biologically primitive creatures such as the sea slugs they had collected could inform upon the processes by which complex creatures had developed. This was where Charles began his study of

marine invertebrate zoology, a readily welcomed change of course for one who was so repulsed by the bloody business of human anatomy and surgery. However, his father was not satisfied with this education or direction. Naturalists, Robert thought, were more suited to be educated by the church.

At the age of 19, Charles began his education at Christ's College, Cambridge. This represented a drastic change in his educational environment. Whereas Edinburgh University was characteristically populated by academic dissenters and radicals, Cambridge was an institution that banned such dissenters. Moreover, Cambridge did not challenge Charles. While he learned botany and anatomy, he was free to indulge in his aimlessness. Here, he would drink, hunt small game, and collect beetles with his friends, just as he would at home in Shrewsbury. Charles did not forget the passions that were instilled in him at Edinburgh, though, and he eagerly accepted his botany teacher's suggestion of traveling to the southernmost point of South America aboard the HMS Beagle.

### **The Beagle (1831–1836)**

At the suggestion of his botany teacher, John Stevens Henslow, Darwin embarked as the gentleman companion of captain Robert Fitzroy on the HMS Beagle. The initial purpose of the journey was to survey the land and establish trade relations in Patagonia, as well as to return Christianized natives to Tierra del Fuego. With Charles Lyell's *Principles of Geology* and some blank notebooks in hand, Darwin set sail aboard the Beagle on December 27, 1831. He was to accompany the captain as a gentleman companion. This was a welcome change in title for Darwin, as he would not be expected to engage in any medical practice during the voyage. Rather, he was free to embark on his own excursions to observe the local wildlife and take specimens for study. Despite the grueling seasickness, this voyage represented a uniquely inspiring transition in the young naturalist's life.

In January of 1832, the Beagle arrived at the Cape Verde Islands, and Darwin was torn between

his endless fascination with his scientific pursuits and his unrelenting seasickness. He towed a net behind the ship during the days at sea collecting plankton to be studied. In the following months, he explored the rainforests of Salvador and Rio de Janeiro, collecting specimens of invertebrates and birds. The wildlife in these areas inspired both awe and fear in Darwin, as he saw not only the beauty of their anatomies and behaviors but also the horrific results of the arms race between predator and prey. The very same aversion to witnessing pain that prevented his pursuit of a career in medicine was also present in seeing the natural mechanisms of tropical wasps hatching their larvae in live hosts. Nonetheless, Darwin continued to take extensive fieldnotes during his excursions, examining the geology and wildlife of the many lands visited by the *Beagle*. He would spend his evenings translating his fieldnotes into more detailed records in his notebooks. He also diligently kept a journal of his experiences, which would eventually become the *Journal of Researches* (1839; retitled *Voyage of the Beagle* in 1905).

In July of 1832, the *Beagle* continued southbound along the eastern coast of South America. Through the summer and into the winter of 1832, Darwin was witness to rebellions and genocides of native peoples in Uruguay and Argentina. Continuing south to Tierra del Fuego in December, Darwin encountered more natives in the southern jungles. These experiences inspired in Darwin a fascination with culture among humans. Specifically, he was intrigued by the development of such vastly differing cultures within one singular species. This was exacerbated by his familiarity with the Christianized natives that were among the ship's population. These individuals represented the possibility for change between such widely differing cultures. Cultural differences among humans was one of many questions Darwin ached to answer. He continued his observations between bouts of seasickness, filling his notebooks with hypotheses, questions, and musings throughout the voyage.

During Darwin's time along the southeastern coast of South America, he would unearth fossils of extinct megafauna that he would then transport

back to the *Beagle*. This became a favorite pastime for him as it represented a tangible window into the past. In those 2 years, he expanded the fossil records quite substantially. He also made note of the geological changes that resulted in the formation of the Andes Mountains. In January of 1835, he would personally witness the mechanisms at work as Mount Osorno on the southwestern coast of the continent erupted and raised the land with it. As he had read in Lyell's book, these geological changes were constant and persistent, and they explained how fossils of seaside plant and animal species could be found at such altitudes in the mountain range. At the rates of geological change about which Lyell wrote and which Darwin witnessed, it would take thousands of years for such specimens to reach such heights. By thinking of natural processes as occurring over thousands of years, Darwin was able to expand his view on the natural processes of the development of species. However, he would not fully conceptualize this theory until after the *Beagle* landed back in England. Meanwhile, the ship was set to leave South America and explore the islands to the west.

In September of 1835, the *Beagle* departed from Peru and began its journey west. This is when the ship landed at perhaps its most famous destination: the Galapagos Islands, a chain of volcanic islands populated by prisoners. Here, Darwin collected specimens of what he believed to be several species of songbirds including orioles, wrens, and grosbeaks, many of which he neglected to label. He also made notes of the local tortoise species, some of which joined the crew of the *Beagle* as pets. Though he made note of physiological differences in the species by island, he would not realize the significance of such differences until his theory started to take shape back in England.

As the *Beagle* continued its journey west into the Indian Ocean, Darwin made note of the presence of coral reefs on mountains, speculating that their presence was the result of geological shifts similar to those he witnessed in Chile in the previous winter. Meanwhile, Darwin continued to deal with the hardships of life on the *Beagle* – those of seasickness, unsteady ground, and

cramped quarters. Moreover, he was preoccupied by the questions left unanswered during his years abroad. He wondered about the comparative physiologies of the birds on the neighboring islands in the Galapagos chain, about the extinction of megafauna in Argentina and Uruguay, and about the presence of marine fossils high in the mountains. This preoccupation inspired feverish note-taking during his final weeks aboard the *Beagle* and still would not result in a finalized theory until much later. Despite his lingering questions, he was nonetheless gladdened by the prospect of returning to the solid, dry, familiar grounds of England.

### **Life After the Beagle Voyage (1836–1837)**

Darwin's scientific reputation had preceded him in England before the *Beagle* landed in Falmouth, Cornwall on October 2, 1836. His letters had been distributed to scholars by his former teacher, John Stevens Henslow. He was kept busy by the work still left to do compiling his notes and specimens. The young man who left on the voyage was quite different from the man who returned. This difference was one of the first observations made by his father upon his return home. Robert welcomed his son home excited to see that the formerly aimless small game hunter had adopted and fortified a scientific fervor akin to his own. Following visits home to Shrewsbury and Cambridge, Darwin eventually settled in London, a short walk from the British Museum and the Zoological Society where he had sent crates of his specimens over the course of the *Beagle*'s voyage. His new priority was to collect these specimens and get them identified by the experts in the field. Luckily, because of Henslow's bolstering, Darwin already had some standing in scientific crowds despite his spending the last 5 years travelling around the globe aboard the *Beagle*. This standing made his correspondence with the ornithologists and geologists charged with identifying his specimens much easier than it would have been as an amateur naturalist. While his specimens were sent to their respective experts, Darwin was charged with

publishing a record of the *Beagle*'s voyage by Captain Fitzroy.

While Darwin began excitedly drafting his book using the diary that he had kept aboard the *Beagle*, he settled into the quiet life of a London scientist. He attended meetings of the Zoological Society and the Geological Society, joined social circles of political writers and historians, and even met with Charles Lyell whose book kept him company in his confined cabin during his voyage. Reading, writing, and discussing scientific theory was a refreshing change of pace for Darwin. Just 4 months later, these social connections would reveal to Darwin that he was on to something more scientifically significant than he had realized during his adventures in South America.

In January of 1837, Darwin heard the report from John Gould, the ornithologist charged with identifying the poorly labeled specimens collected from the Galapagos. What Darwin assumed were wrens, orioles, and grosbeaks were, in fact, all finches. During a follow-up meeting with Darwin in March, Gould further informed him that he had collected specimens from 13 new species of finch. They noted discrete morphological distinctions. Namely, the species could be distinguished by the shape of the beak. Unfortunately, Darwin neglected to properly note on which islands he had found each specimen. However, Gould also noted three new species of mockingbirds that were labeled by island. A pattern was now evident, as each species was distinct to a separate neighboring island. This pattern brought into question the stability of species, as it appeared that these animals were morphologically distinct based on the circumstances available to them in their separate environments. Meanwhile, the results of other specimens raised similar questions. The fossils of extinct megafauna that Darwin had collected in Argentina and Uruguay were identified as giant armadillos, capybaras, and ground sloths – all of which were found in regions inhabited by the non-giant versions of the species. Moreover, the reptilian specimens including iguanas and tortoises were also shown to have island-specific differences. As more and more identifications were made in the analyses of Darwin's collected specimens, the evidence



seemed to point toward species instability as a function of environmental necessity.

Darwin was cautiously coming to the conclusion that species change over time, and this was not the first idea of this ilk. He had heard of progressive change in species during his time at Edinburgh University from Robert Grant, a former student of the French zoologist Jean-Baptiste Lamarck. However, the idea that a species can change over time opposed the traditionally taught creation myth of Christianity, the official religion of England at the time, which had not yet been divorced from the scientific culture. After his meetings on finches, giants, and iguanas, he was beginning to believe that species could change, though he lacked a mechanism or process by which this would occur. Despite Darwin's personal development that occurred during his arduous trip around the world, he was not so emboldened as to come forward with this sacrilegious theory before developing it more fully.

### Development of the Theory (1837–1859)

Prioritizing clarity, Darwin began scribbling thoughts into a new notebook, labeled simply, "B." He started by reviewing his grandfather's medical book, *Zoonomia*, and found that Erasmus had also speculated on the origin of species. Erasmus had suggested that all warm-blooded species shared a common ancestor, though this claim was not reinforced with sufficient evidence. He also found that Erasmus was intrigued by the importance of sexual reproduction and the mechanism by which individuals of the same immediate family were able to differ from one another. Darwin went on to question what the eventual effects of such individual differences would be, arguing that species necessarily change. Notebook "B" contained Darwin's personal development toward these ideas, as well as principles from geology, zoology, botany, and biogeography, all of which were used to come to his conclusions. At the time, he referred to this change as "transmutation."

While Darwin quietly developed his theory and finished his Beagle manuscript, he shrank away from his social circles and began the sizable

endeavor of editing a new multi-volume collection of writings from assorted experts that would be titled *The Zoology of the Voyage of the H.M.S. Beagle*. In taking on this project, he continued to contribute to the very scientific culture that he was afraid would blacklist him as a radical for his private thoughts. These thoughts he carefully kept hidden in Notebook "B" and then later in Notebooks "C," "D," and "E." Meanwhile, he continued to take in information from the fields of agriculture, natural history, and animal and plant breeding. He talked with his father, with farmers, and with explorers. Remembering the principles about which Charles Lyell wrote in *Principles of Geology* and which he witnessed during the eruption of Mount Osorno, Darwin knew that the changes he was predicting would likely be exceedingly gradual. If a species were to change fully into a new, distinct species, thousands and thousands of years would be necessary. As Darwin's confidence in the evidence he had compiled grew, his health deteriorated steadily. His notebooks, however, illustrate the determination Darwin had to develop his theory in pursuit of scientific understanding.

Darwin's health became a significant issue that seemed to coincide with the development of his theory. In September of 1837, he began to note heart palpitations, vomiting, headaches, and anxiety. At a doctor's order, he began to reduce his time spent in his scientific pursuits in favor of a more restful life. In letters, he specified the stimuli that triggered episodes of palpitations and anxiety. This list included social events, conversation, and conflict. He spent some time at home in Shrewsbury to help alleviate the symptoms that seemed to come with the stress of his scientific pursuits. It was at this point in his life that he began to consider starting a family of his own, despite his responsibilities including the compiling of the massive volumes of zoology from the Beagle and continuing to document the crates of specimens sent back from his voyage.

The prospect of starting a family introduced two new sources of anxiety for Darwin: marriage and money. To this point, he had been living fortunately from the allowance sent to him by his wealthy father, who did so in order to allow

his son to pursue his scientific exploits. This was a boon that Charles himself specifically noted as a fortunate circumstance that allowed him to write the manuscript of the Beagle's voyage. Although this allowance was enough to continue the life he was living, it would not be enough to sustain a wife and children as well. Darwin thought out his decision as scientifically as he could, by writing out the pros and cons of marrying or not marrying. This and his theories would demand his thoughtful attention for months. In June of 1838, he sought to escape his responsibilities by travelling to Scotland to carry out geological fieldwork. On his way back to London, he visited his family in Shrewsbury where his father assured him that he need not worry about money or marriage. Continuing back toward London, he also visited his cousins, the Wedgwoods, one of whom he would later marry. With the issue of marriage weighing on him, Darwin continued to ruminate over his theories.

In Notebook "D," Darwin extensively considered the work of Thomas Malthus, an English scholar who published the *Essay on Population*. In this essay, Malthus described species' tendency to reproduce beyond the limitations of their available resources. His logic was laid out arithmetically, illustrating that populations grow by multiplication, not by addition. Because of this property, populations can quickly outgrow their means, resulting in competition and eventual starvation. Darwin, still seeking the mechanism or process by which species can change over time, ruminated over Malthus's arguments as they applied to nonhuman populations. Darwin began to think of competitive advantages between individuals for the various challenges faced in nature. If a population outgrew the available resources, which of them would be able to take advantage of the available resources? Which individuals would be more likely than others to be caught by predators? The answers, Darwin knew, could be found in those individual differences that result in differential survivability. He would later describe this process as "natural selection." This framework represented a promising development in his theory and served as a springboard to Notebook "E." Around the same time, he began writing of tangential questions in Notebook "N."

Additionally, around this time, he travelled home to ask Emma Wedgwood to be his wife. The two were married on January 29, 1839, and left immediately for London so he could continue his work.

Between 1839 and 1842, Darwin had developed his theory, his career, and his family. He published his *Journal of Researches* in 1839, and that was met with notable success. Additionally, Emma had given birth to their first son, William, in December of 1839 and their first daughter, Anne, in March of 1841. In 1842, the climate in London had become so politically volatile that Charles and Emma decided that it was time to move to the countryside – a small village called Down. That summer, Emma gave birth to a second daughter, Mary, who would only live 3 weeks. After moving to Down House, Darwin indulged in the seclusion, only travelling to London occasionally and instead relying on letters to correspond with his colleagues. In 1843, he would begin correspondence with botanist Joseph Hooker.

After Hooker's own nautical voyage as a naturalist, he had agreed to study the plant specimens that Darwin had collected while aboard the Beagle. In studying Darwin's plants, Hooker also noted the variation between plants found on separate neighboring islands. Seeming to grow impatient with his withholding of the conclusions he had drawn, in January of 1844, Darwin wrote his theory in a letter to Hooker. In doing so, Darwin also noted that his conclusions were distinct from Lamarck's unsupported theories of progression. In response, Hooker began studying Darwin's Galapagos plant specimens with a new framework in mind, and Charles began his work addressing the process by which a species might change.

With the logic of his theory finally articulated, Darwin set forth with a new sense of motivation to investigate the plausibility of his proposed mechanism. As he began putting his theory on paper and, with nearly 200 pages already written, he instructed Emma to ensure that his work would be finished and published if he were to pass before finishing. His vomiting and headaches would still return sporadically, after all, making his health a noteworthy concern. The shortlist of scholars who could be selected to finish his work included close friends such as Charles Lyell, Joseph Hooker, and Robert Grant. As Darwin himself became bolder,

vocalizing his conclusions in writing to other scholars, other theoreticians were at work. In October of 1844, an anonymous author published *Vestiges of the Natural History of Creation*, a volume of scientific writings addressing many of the same issues about which Darwin had been ruminating for nearly a decade. The volume proved to be very successful, read by scholars and laypeople alike. However, unlike Darwin's theory, *Vestiges* argued that the transmutation of species was a function of a divine hand and that humans were preordained by that hand as the superior species. Darwin was vocally unhappy about this new publication, though he knew that it could pave the way for a more developed and scientifically rigorous theory like his own. In any case, his growing confidence was shaken, and he turned his attention back to the *Beagle* geology and zoology volumes.

At this point in his life, Darwin became much quieter than he had been in previous years. The confidence he had garnered from his developing theory had waned drastically. His publications since disembarking from the *Beagle* had seen mild to moderate success, and he had made a name for himself among the scientific community. He set about revising new editions of his publications and otherwise kept to himself. In these publications, it was clear that Darwin had edged fairly close to his broader question of species' change over time and the function of environmental conditions in the process. On October 1, 1846, just shy of a decade after the *Beagle* landed in Falmouth, Darwin finalized his writings on the geology of South America and began working on his last sample of barnacles collected in the Galapagos. Barnacle taxonomy would then demand his complete attention until 1854. In his 8 years agonizing over barnacle anatomy and physiology, dissecting and investigating specimens collected from all over the globe by his contacts, Darwin had fostered a sizable network of scholars. During this period, he experienced the stresses of the project, of academic poaching, and of the death of his father in 1848, all of which exacerbated his stress-related health problems. During his travel back to Shrewsbury for his father's funeral, he wrote an apology for his chronic unwellness in a letter to his wife.

Darwin's barnacle work slowed as he focused on his health problems. He engaged in a combination of homeopathic treatments and a water-based method meant to draw blood away from his stomach at the order of Dr. James Gully. The treatments worked, and Darwin began to cut his working hours in order to reduce his stress. Slowly but surely, his barnacle work progressed until his daughter, Annie, had become ill. After a bout of scarlet fever in 1849, Annie had yet to fully recover, and several months later, she had begun presenting with similar symptoms to those chronically experienced by her father. Annie was then sent with her younger sister, Henrietta, to Malvern to receive treatment from Dr. Gully. When her condition worsened, Charles went to her side. Annie passed in April of 1851, and 2 days later, Charles was back in Down to mourn with his then-pregnant wife. It was during this time that another naturalist was independently coming to conclusions very similar to those that Darwin had drawn in his lettered notebooks.

Alfred Wallace, a young, uneducated, middle-class naturalist embarked on his own voyage exploring the Amazon. Wallace was well-read, having studied *Vestiges of the Natural History of Creation* and Darwin's *Journal of Researches*, among many other works that inspired his exploration and his theories. Wallace's journey began in 1848. Unfortunately, a fire aboard the ship bound for England destroyed the specimens in 1852. He was able to save some of his notes and sketches, but he lost everything he had spent the last 4 years collecting. After the life-threatening journey, Wallace arrived back in England in the summer of 1852. Despite his newly developed aversion to sailing, he began to plan another expedition in order to resolve the unanswered questions regarding the progression of species. After his journeys, Wallace began publicly discussing his theory on progressive development, unaware that Darwin had developed similar theories in secret.

Wallace's presence in the scientific community sparked in Darwin a pressure to vocalize his theories more clearly and with more support than he had in the past. He began testing the mobility of plant seeds to see if it was possible for them to survive a journey to a new island in the digestive system of a bird. He began to ask his contacts for

specimens of bird and mammal bodies that he could then dissect and compare. He began breeding his own flock of pigeons to examine the effects of selective breeding. He set out to figure out what caused variation as a naturally occurring phenomenon in reproduction of both wild and domestic species. His theory, after all, rested upon the notion that differing environments would naturally possess distinct selective pressures resulting in change in a species over time. Wallace's theory was published in 1855 with no substantial uproar in the scientific community. It was enough, however, for Darwin's colleagues to encourage him to publish his more developed theory.

In the summer of 1858, Wallace had written to Darwin about his new breakthrough. He told Darwin about his idea whereby species change due to the inherent struggle to survive as a species grows beyond its resources. Essentially, Wallace had come to the same conclusion as Darwin whose book was still incomplete. Darwin was significantly unhappy with this development, knowing that if he had not taken so much time to develop his theory, he could have been the first to publish. Suffering through the death of another child and his persisting illness, he continued to correspond with his colleagues who encouraged him to continue working on his book. When it came to the presentation of these ideas, Wallace was given partial credit. He was content with this arrangement as a younger and relatively less educated naturalist, as this meant he was welcomed into the scientific community paired next to Charles Darwin himself. In May of 1859, Darwin's writing was finished, and in November, *On the Origin of Species by Means of Natural Selection*, would be in high demand days before its official publication.

### **After *Origin* (1860–1882)**

For the most part, Darwin's assertion that species have descended from common ancestors through change over time was widely accepted. The argument that many biologists took issue with was that of natural selection being proposed as the primary driving force behind such changes. This was due to the prevalent natural theology whereby evolution occurred by a divine hand. Darwin's

arguments suggested no intentionality of the variations that naturally occurred; variations were simply the result of selective pressures in the environment. Among theological scientists – including those who formerly taught Darwin the foundations of his scientific education – the book was panned as overly materialistic. In the commentaries and critiques published in response to *Origin*, the concept of natural selection was brought into question frequently. Even Alfred Wallace would argue a limit on the scope of natural selection as a process by asserting that it could not have resulted in the human brain. Meanwhile, zoologists, biologists, and geneticists were exploring the mechanisms of inheritance, further informing Darwin's arguments regarding variation. Regardless of these theoretical developments, Darwin felt a substantial relief now that his theory was essentially out of his hands, published, and no longer a secret in need of such meticulous development.

Darwin's health began to improve without the stress of his book weighing on him. He produced several more editions of his publications but otherwise kept to himself. With each edition, he addressed some criticisms and adjusted his language accordingly. Over the years following the publication of *Origin*, he had resolved to avoid being as provocative as he had cautiously been in the past. In 1875, he published *Insectivorous Plants* with the help of his sons, Francis and George. This volume was far less provocative by design, and thus did not perform as well as *Origin* did. Emma took to caring for her elderly husband in the late 1870s. In 1876, hearing the news that Francis' wife was pregnant, Charles began to write his memoirs. He was very close with his new grandson, Bernard, through the rest of his life.

In 1881, Darwin began to experience more heart problems. On April 19, 1882, he passed fitfully of degenerative heart failure. Because of his contributions to science, he was buried in Westminster Abbey along with his close friend and colleague Charles Lyell who had been interred there in 1875. In his final days, Darwin finished more work on the beetles that he loved to collect and how they dispersed across territories. "On the Dispersal of Freshwater Bivalves" was his last publication, appearing as a note to *Nature* just 13 days before

his passing. In this, Darwin discussed the likelihood with which a larval mollusk might adhere to water beetles who would then fly them to new bodies of water. In this last publication, Darwin added more support for his theory on the process of evolution by natural selection.

## Publications by Charles Darwin

- 1839 – *Journal of Researches into the Geology and Natural History of the Various Countries Visited by H.M.S. Beagle, Under the Command of Captain FitzRoy, R.N. from 1832 to 1836*. London: Henry Colburn.
- 1839 – “Observations on the Parallel Roads of Glen Roy,” *Philosophical Transactions of the Royal Society of London*, 39–81.
- 1842 – *The Structure and Distribution of Coral Reefs. Being the first part of the geology of the voyage of the Beagle, under the command of Capt. FitzRoy, R.N. during the years 1832 to 1836*. London: Smith, Elder.
- 1851–1854 – *A Monograph of the Sub-Class Cirripedia*. Vol. I: *The Lepadidae, or Pedunculated Cirripedes*, 1851. Vol. II: *The Balanidae, (or Sessile Cirripedes); the Verrucidae, etc.*, 1854. London: The Ray Society.
- 1851–1854 – *A Monograph of the Fossil Lepadidae, or Pedunculated Cirripedes of Great Britain*, 1851. *A Monograph of the Fossil Balanidae and Verrucidae of Great Britain*, 1854. London: Palaeontographical Society.
- 1859 – *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- 1862 – *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects, and on the Good Effects of Intercrossing*. London: John Murray.
- 1868 – *The Variation of Animals and Plants Under Domestication*. London: John Murray.
- 1872 – *The Expression of Emotions in Man and Animals*. London: John Murray.
- 1875 – *Insectivorous Plants*. London: John Murray.
- 1875 – *The Movements and Habits of Climbing Plants*. London: John Murray.

- 1877 – *The Different Forms of Flowers on Plants of the Same Species*. London: John Murray.
- 1881 – *The Formation of Vegetable Mould, through the Action of Worms, with Observations on Their Habits*. London: John Murray.
- 1882 – “On the Dispersal of Freshwater Bivalves,” *Nature*, vol. 25, April 6, 1882.

## Cross-References

- ▶ [Erasmus Darwin](#)
- ▶ [Evolution](#)
- ▶ [Heritability of Behavior](#)
- ▶ [Jean Baptiste Lamarck](#)
- ▶ [Natural Selection](#)
- ▶ [Sexual Selection](#)
- ▶ [Social Darwinism](#)

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## Chasm

- ▶ [Contagious Yawning](#)

## Cheating

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## Synonyms

[Deceit](#); [Deception](#); [Dishonesty](#); [Fraud](#)

## Definition

Cheating is a behavior by which a person intentionally tries to reach a goal by breaking the rules or through immoral procedures. The cheater is characterized by trying to obtain undeserved advantages and acting from their own interests.

## Introduction

In the framework of social, cognitive, and evolutionary psychology, cheating is a complex form of social interaction according to which one person intentionally introduces one set of false beliefs into the other, for personal gain (Rivière 1991). Cheating always includes a deliberate manipulation of the behavior of others. This manipulation occurs through the introduction of a false belief in others by adulterating information for personal benefit (Perner 1991).

Cheating behavior is based on a human cognitive system through which the person recognizes that he/she has a mind and also attributes it to others; this act of “mentalization” is complemented by consciousness, corresponding to the attribution that their actions are intentional (Rivière et al. 1994). The conceptual system that serves as the basis of cheating and manipulation has received the name of “Theory of Mind” (ToM). ToM is all that cognitive framework that permits to the human beings distinguish their view of the world from the view of others. By means of ToM, the humans can define and distinguish mental status in themselves and in others, and also predict or influence in its behaviors (Premack and Woodruff 1978).

## Phylogeny

From the phylogenetic point of view, one of the pioneers in the study of the cognitive mechanism of the ToM is Humphrey (1976, 1983) who formulated the hypothesis of “social function of intellect”; according to this hypothesis, the social intelligence has an important role in the development of the human mind. The research of this author was based on observation of no-human

primates. Humphrey (1983) reach the conclusion that primates are smarter than other animals because in its evolutionary process, they have had to face social problems as fights for power or for mating and the solutions to this problems requires alliances or cooperative strategies. Other strategies may include manipulate others, for example, a chimpanzee that, to be able to mate, cheats to a competitor offering him food to distract his attention; in this moment it can be said that the behavior of cheating was born, phylogenetically speaking.

In a more recent research, Fehr and Fischbacher (2004) support the idea that humans have evolved by the branch of psychosocial development rather than by the physical control of the environment; this characteristic has separated them from the other primates, because the psychosocial development has allowed human to control deception and increase cooperation. This particular type of development has been consequence of a combination between self-consciousness and ToM.

From this perspective, deceive behaviors are related with the intentionality of human beings; the person not only have to be conscious of his own mind but also to know that others have mind. Humans, unlike others primates, has the capacity of form and use consciously the ToM which for some authors (McCabe et al. 2000) is at the basis of human phylogeny.

Rivière and Nuñez (1994) have shown that although in nonhuman primates and in young children (under 4 years) there are situations of deception, they are not generated from the intentional introduction of false beliefs in others to obtain personal benefits (which are characteristic of the human development of the ToM). As a result of this research, the authors conclude that cheating in the early ages and in primates occur as a consequence of the detection of intentions in the others and the manipulation of this intentions.

## Ontogeny

From an ontogenetic point of view, the capacity of mentalization is progressively developed in the



period between 1 and 5 years of age, approximately (Wellman et al. 2001). At this age, the child acquires the complete cognitive system that allows him to differentiate his mind from that of others; those system includes the important notion of “false belief” (Wimmer and Perner 1983). Although with some controversy (Bloom and German 2000), the false belief is one of the widely used criteria to determine if a person has the capacity of deliberately transmitting to another person a mistaken belief in order to obtain a benefit. This ability to deceive is an indicator of the develop the ToM and, joint with a conscience of its own actions, a child will be able to detect or produce a deception, a trap, or a lie.

The ability of cheating constitute an indicator of the mentalization because at this point the child understands the mind as a belief system that can be used for manipulate others for his own benefit, but simultaneously, the child also understands that others also have a system of mental representations and therefore can manipulate and deceive (Rivière 1991).

Other indicator used to detect the ToM in children is the tactical deception. This concept may be defined as the capacity to modify part of the repertory of behaviors to adapt it to a cheating role (Riviere and Nuñez 1998). Again, some controversy between authors was found. On the one hand, some researchers as Perner (1991) consider that cheating is atypical among preschoolers, and other (La Frenière 1988; Hoogenraad and McKenzie 1995) considers that cheating is a common and spontaneous behavior in children’s behavior and that it is a valid criterion for measuring the ToM.

Hoogenraad and McKenzie (1995) developed a measure to evaluate the ToM in small children by examining its deceive capacity. The model propose three steps in the development of cheating, the first is related to the manipulation of behavior through learned strategies, for example, to cheat to avoid a punishment. The second stage is characterized by a comprehension of mental states. In this phase appears the concept of false beliefs and the understanding of the intentions of others. The children has access to this information that allows it to deceive. The third stage,

developed in elder children, its related to the use of cheating with altruistic purposes. According to Rivière and Nuñez (1994), between age of 4 and 5 a child may recognize that a behavior comes from a belief and this, in turn, comes from an information source, coinciding with the second stage proposed by Hoogenraad and McKenzie.

Some authors (Astington and Gopnik 1991; Bruner 1990) agree on the relevance of the social and cultural context in the mentalization process. According to this view, the child’s understanding and awareness of the representations of his/her own mind and those of others is a social process transmitted through cultural ways, the same occurs with the ability to deceive.

## Major Advances and Applications

### Mirror Neuron System

One of the major advances on the last years that has allowed to deepen in the origin and the nature of the deception is the discovery of the mirror neurons in the premotor cortex and in the parietal lobe of the primates (Gallese et al. 1996). During the last two decades, two neural systems involved in personal interactions have been discovered. On the one Hand, the Mirror Neuron System (MNS) that allows to understand the imitative actions and behaviors and, on the other hand, the “mentalization system,” which has allowed the anatomical definition of the ToM, locating it in the precuneus, the temporoparietal junction and the medial prefrontal cortex (Van Overwalle and Baetens 2009).

The relationship between both systems is now under discussion because there is still no complete explanatory paradigm that confirms the activation of mirror neurons in complex situations of cheating (Agnew et al. 2007; Schippers et al. 2010).

What has been found so far in that the MNS is activated when a subject executes an action, and when observing others executing an action (imitation), this activation occurs in both primates and humans, which share very similar mirror neurons. In spite of these similarities, the reaction to the deception is different as found in some experiments with simple deception situations. For

example, in an experiment in which the task was to collect a caramel, the mirror neurons are activated in both primates and humans when candy is indeed present, but in situations where there is no candy (cheating), only the mirror neurons of humans are activated. Through this experiment, it is shown that in the evolutionary process human primates, being immersed in situations of very complex social interaction, developed the capacity to deceive and that this capacity has a neurological correlate in the MNS.

### Variables Associated with Cheating

There is an increasing interest in knowing and deepening the origins of cheating interactions and the mechanisms that help to mitigate them. There is also a broad interest in deepening the characteristics of the cheater. For example, it has been investigated whether personal characteristics such as gender, socio-economic status, or age influence the tendency to deceive.

Regarding the influence of gender, some studies have shown that men report a more favorable attitude to deception and also a greater propensity to engage in deceptive behavior, although the differences vary according to the scope, method of data collection, and country. A meta-analysis by Whitley et al. (1999) based on 48 studies related to attitudes and misleading academic behavior has shown that there are differences in attitude between men and women although the size of the effect has been moderate ( $r = 0.21$ ), with respect to cheating behavior the effect size is even lower ( $r = 0.08$ ).

Houster et al. (2015) have focused on the study of acts of dishonesty including parents and children. In this study, they have found that there are higher levels of deceit when parents are not with their children and when deceit benefits children more than their own parents; in the presence of children, parents act more honestly but there are differences in gender: parents act deceitfully in front of their sons more often than in front of daughters.

Regarding socioeconomic status, research converges to find that people with higher status have

more favorable beliefs towards the deceive and are more likely to commit acts of dishonesty, such as cheating to win a prize (Piff et al. 2012).

With respect to age, some studies have focused on analyzing cheating behaviors in young children, in an experimental study by Kotaman (2017), conducted with children between 4 and 6 years; it is concluded that children who are offered a reward for solving a task (puzzle) tend to perform more traps than children who are not offered reward. The authors have also found that cheating behavior was not related to parenting styles. On the other hand, Pan Ding et al. (2014) studied the cheating behavior in children of elementary school, between 8 and 12 years of age, they found that cheating behavior decreases with age and that executive function has a double influence on deception; on the one hand, its development inhibits this type of behavior and, on the other, it makes the cheating mechanisms more sophisticated.

### Cheaters Detection in Social Interaction

An topic widely studied by evolutionary psychologists (Sperber et al. 1995; Liberman and Klar 1996; Carlisle and Shafir 2005) is the detection of cheaters in social interaction; this authors frame the research in the context of the social contract theory. This theory postulates that humans have a cognitive architecture that enables them to detect cheaters in contexts of social relationships. The postulates of the theory have been tested by the Wason's task of selection, in which it has been proven that people have developed module of "detection of cheaters" that causes them to detect them automatically in scenarios of social exchange.

Recently a study by Van Lier et al. (2013) revised this automatic character of the "detection of cheaters" using the selection task, the authors established that the performance in the versions of the social contract did not depend on the cognitive capacity nor the age and that the experimental burden of cognitive resources with a secondary task had no impact on detection in the social contract. However, in all experiments,

performance in a nonsocial contract version depended on the available cognitive ability. In general, the findings validate the automatic and effortless nature of social exchange reasoning.

On the other hand, numerous experiments have been carried out on memory and facial recognition of cheaters; however, no conclusive results have been found. Buchner et al. (2009) have found that source memory is increased but not recognition memory. In contrast, Yamagishia et al. (2003) find that if there is greater facial recognition of individuals recognized as cheaters compared to those known as cooperators. Dellanrosa (1999) has found that people of high rank are more likely to detect deception in their subordinates than vice versa.

## Assessment of Cheating

One of the most interesting applications among scientists and professionals, especially in the area of legal psychology, is the development of measures of deception. There are three main strands in the study of these measures: on the one hand, psychophysiological techniques that are based on the measurement of vegetative-physiological activity (heart rate, blood pressure, respiration, skin conductance, dilation of the pupils, eye tracking, neuroimaging...); on the other hand, the study of verbal behavior (voice fluctuation, rapidity of responses, discourse analysis...); and finally, the analysis of nonverbal behaviors (behavioral observation, analysis of nonverbal behavior...).

The origins of the deception detection go back to the beginning of the SXX with the first measures of the blood pressures carried out by Martson (1917) who is considered the father of polygraphy. The next step was the development of the Relevant/Irrelevant Technique (RIT; Larson 1932) which compares answers to relevant questions with answers to irrelevant questions, RIT techniques have been criticized because the relevant question can produce physiological changes by the mere fact of having a greater emotional content. Due to this lack of validity of the RIT method, another technique called Control Question Technique (CQT; Reid 1947) was proposed.

CQT was based in generating irrelevant questions with greater emotional content. The CQT is a polygraph variant that has been used until now in different countries but in a more sophisticated way, with quantitative scores originally proposed by Backster (1962) and computerized scoring systems originally proposed by Raskin (1982).

In the 1960s, Likken proposes an alternative technique for the psychophysiological detection of deception, called GKT (Guilty Knowledge Test; Lykken 1960). This approach differs from the CQT because it does not use direct questions, instead it uses indirect questions about details of the event of interest (for example, a crime) that would only be known to someone who has been involved in it. Format of responses are multiple-choice and are based on the comparison of the options that provide pertinent information with options that contain irrelevant information.

A third approach to the study of the cheating detection is the Differentiation of Deception (DoD; Furedy et al. 1988). The study of the deception through the DoD consist in to ask the examinee a series of questions (they may be of an autobiographical nature) and instruct him to respond honestly to half of them and deceptively to the other half. Currently, this mechanism is used with some variants such as asking the examinee to answer the same question in a sincere and deceptive way; the last test format has been called SLT (Sheffield Lie Test; Spence et al. 2001).

Measurement techniques of the dependent variables (psychophysiological) also has changed through the time, from initial measurements based almost exclusively on blood pressure, respiration, and heart rate (basic measurements of the polygraph) to the use of modern neuroimaging techniques such as PET (Positron Emission Tomography) or fMRI (functional Magnetic Resonance Imaging). Last techniques were incorporated into scientific research on the 1990s (Farwell and Donchin 1991; Rosenfeld et al. 1991) and have been increasingly used by researchers interested in detecting deception (Gamer 2014; Ganis 2015; Meijer and Verschuere 2015).

Other measures recently used to detect deceive have been response times (Seymour et al. 2000), eye movements (ET, Eye Tracking, Schuetzler

2012), and detection by “expert judges” who are people with special abilities for the detection of cheaters (Vrij et al. 2006); last technique has been object of controversy (Bond et al. 2007; O’Sullivan 2007).

Despite the recent interest in measuring deception through more objective and sophisticated techniques such as ET, PET, and fMRI systems, there are still many doubts about the reliability and validity of the deception measurement process. In a recent review of existing literature, Meijer et al. (2016) concluded that most of the scientific literature that uses neuroimaging for the detection of deception has important conceptual and methodological problems. The most important of which is that there is no differentiation between the dependent variable and the approach for the evaluation (DoD, GKT, or RIT).

To conclude this section on the measurement of deception, it is important to mention the importance of other types of measurement, for example, the analysis of the verbal content of discourse, among which two approaches stand out: content analysis based on criteria (Masip et al. 2005) and the technique of reality monitoring (Alonso-Quecuty 1992; Vrij 2000). Nonverbal approaches that attempt to measure deception through behavioral indicators and observation of the behavior of the examinee are also important, emphasizing nonverbal cues as a basis for detecting deception (Zuckerman et al. 1981). Finally, it is worth mentioning the development of instruments to measure the attitudes towards cheating as proposed by Gardner and Melvin (ATC, 1988), who present in their article evidence of reliability and validity through a negative correlation between ATC scores and cheating behavior measured by a study guide.

## Academic Cheating Behavior

With regard to academic fraud, numerous investigations have been carried out in different areas of knowledge and also at various levels of education, especially in university students, specially in the last decades in which fraudulent behavior as copying on exams or plagiarism have been increasing

(Vandehey et al. 2007). Among the investigations found, it is worth mentioning the studies Perceptions and Attitudes toward Cheating among Engineering Students (PACES-1; Carpenter et al. 2002), in which it has been found that the behaviors of deception depend on the attitudes towards cheating, that is to say, those students with more permissive attitudes tend exhibit more cheating behavior.

Another common result in some investigations is the influence of the context (Diekhoff et al. 1996): several situational variables such as the level of studies, make fraud in secondary school, or the rationalization of the fraud by neutralization (e.g., to blame the teacher) have wide influence in the cheating behavior. Despite the wide influence of the context, there are psychological factors that condition the cheating behavior independently of the context, for example, certain types of personality facilitate or, on the contrary, deterrent the fraud. Some studies have found that students with greater morale and more shameful exhibit less fraudulent behavior despite the context (Finelli et al. 2003). On the other hand, some studies (Perry et al. 1990) have found that competitive students with high achievement motivation (Type A personality) tend to exhibit greater tendencies to fraud; however, other studies (Huss et al. 1993) refute this hypothesis not being clear yet the association between these variables of personality and cheating behavior. Finally, another area with interest are the development statistical indices for the detection of answers copied in exams (Wollack 2003).

## Conclusions

Although deception is a topic of great social and academic interest, much research is still needed to be done, especially, to implement the important contributions offered by the field of neuroscience. This chapter has addressed the phylogenetic and ontogenetic origins of deception, some major advances and applications, but not other applications that have been extensively studied in scientific research such as cheating in sports, in games, and in pair relationships. Several authors have

critiqued the literature about cheating behavior, because different studies have measured dishonesty in many different ways; therefore, it is a challenge for the future to design measures of deception more adjusted to the proposed theoretical models.

## Cross-References

- Behavior Systems
- Behavioral Levels
- Cognition
- Cognitivism
- Cooperation
- Deception
- Evolutionary Psychology
- Imitation
- Meta-cognition
- Primate Cognition
- Social Behavior
- Social Learning
- Theory of Mind

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## Chelonia Navigation

### ► Testudines Navigation

## Chemical Communication

### ► Pheromone

## Chemical Cues

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## Synonyms

### Chemosensory cues

## Definition

Compounds used by organisms as a source of information to interpret environmental stimuli even though they did not evolve in the emitter for this function.

## Introduction

Organisms obtain information available in the environment through cues, which can be acoustic, chemical, electric, magnetic, tactile, and visual. Chemical cues are compounds used by organisms as a source of information to interpret environmental stimuli even though they did not evolve for this function in the emitter (see ► “[Evolution](#)” in this book). Numerous compounds of several chemical classes can act as chemical cues, including cuticular hydrocarbons (CHCs) and other molecules such as peptides and proteins (see ► “[Protein](#)” in this book). Like other cues, chemical cues can influence the behavior of a receiver and are sensed by all organisms that use them for varied aspects of life, such as orientation, location of food, nest sites or partners, threat detection, recognition of conspecifics, parental care, and

territorial defense (Stevens 2013; Nielsen 2017) (see ► “[Conspecifics](#),” ► “[Orientation](#),” and ► “[Territory Defense](#)” in this book). Chemical cues can indicate a suitable mating partner; provide information about the immune system, health or diseases, and food quality; and be used to recognize kin (Wyatt 2014; Nielsen 2017).

It is possible that chemical cues are the oldest form of obtaining information from the environment since even the earliest organisms had receptors for receiving and interpreting chemical cues and because of the enormous variety of compounds available in a potentially unlimited number of possible combinations (Wyatt 2014). Organisms detect chemical cues in the atmosphere and water and from the surface of other organisms or animate or inanimate substrates through olfaction (olfactory cues) and taste (gustatory cues) (Nielsen 2017; Elgar 2019).

Different from other cues, chemical cues require a physical interaction between molecules and receptors located in the sensory organs of the receiver and can transport information over considerable distances, although not as precisely targeted or as fast as acoustic or visual cues, for example (Wyatt 2014; Elgar 2019). Molecules acting as chemical cues can be volatile or involatile, soluble or insoluble, and large or small, depending on whether they are carried to the receiver in air or water; they can also, for example, be deposited on the sensory organ of the receiver, and be short or long range, or act on contact (Wyatt 2014).

Animals share similarities in the ways they use chemical cues, with several parallels in uses and sensory processes, which can be the result of evolutionary convergence or common ancestry (Wyatt 2010). Organisms can respond to chemical cues from individuals of the same species or from different species. A chemical involved in a chemical interaction between organisms is called a semiochemical. Semiochemicals that act between members of different species are called allelochemicals, of which there are various kinds, including allomones, kairomones, and synomones, which benefit the emitter, the receiver, or both the emitter and the receiver of different species, respectively (Wyatt 2014). Some

semiochemicals that act between members of the same species evolved for communication as chemical signals, such as pheromones, for example; other semiochemicals that act between members of the same species, or among different species, that did not evolve as signals can be exploited as cues (Wyatt 2014) (see ► “[Chemical Signals](#)” and ► “[Pheromone](#)” in this book).

## Chemical Cues and Signals

Distinguishing between chemical cues and signals is not always an easy task because it is context dependent and because a chemical may act simultaneously as a signal and as cue. For example, a pheromone (chemical signal) emitted by an animal to communicate with another member of the same species may act as a chemical cue for a predator that can identify it as belonging to its prey. A signal is any act or structure that influences the behavior of other organisms (receivers) and which evolved specifically because of that effect and functions because the receiver’s response also evolved (Stevens 2013; Wyatt 2014). However, unlike chemical signals, chemical cues did not evolve exclusively for that purpose in the emitter (Wyatt 2014). For example, humans eliminate carbon dioxide (CO<sub>2</sub>) through breathing, which mosquitos sense and use to locate human hosts to acquire blood. Thus, CO<sub>2</sub> works as a chemical cue since its elimination by humans did not evolve exclusively to modify mosquito behavior so as to find humans. Cues usually benefit the receiver but can also benefit the emitter, and since they did not evolve specifically to influence a receiver, they are not distinctive from the environment, and thus organisms must to be able to distinguish them from environmental noise (Stevens 2013).

Chemical signals, such as pheromones, may evolve from chemical cues that have been in the environment for other reasons long before any suitable receptors existed (Steiger et al. 2010; Wyatt 2014). Many molecules act as pheromones, which suggests that almost any molecule can evolve into a pheromone if it gives a selective advantage (Wyatt 2014). There are two main routes

by which chemical cues can evolve into signals: emitter preadaptations and receiver preadaptations. These involve, respectively, signals that start as chemical cues released by the emitter that can be sensed by the receiver and molecules that are selected by the receiver because they match its already existing sensitivity (Wyatt 2014).

## Signature Mixtures

Signature mixtures are chemical cues (a subset of molecules in an animal's chemical profile) that animals learn and use to recognize another as an individual (e.g., lobsters, mammals) or as a member of a social group (e.g., ants, bees, mongoose) and can also be used to recognize castes, conspecifics, and sex (Wyatt 2010, 2014). All signature mixtures are detected by olfaction, with the component molecules being produced by the organism itself, acquired from a shared local environment, or produced by other organisms (Wyatt 2010). In contrast to chemical signals, signature mixtures of animals, be they social insects or mammals, are constantly changing and need to be learned (Wyatt 2010, 2014) (see ► [“Learning”](#) in this book). Organisms can learn signature mixtures through imprinting during a particularly sensitive period of early life (Wyatt 2010) (see ► [“Imprinting”](#) in this book). This learning can allow organisms to recognize their social groups and, consequently, choose a sexual partner that is not related to them and avoid inbreeding or to selectively care for their own offspring, for example (Wyatt 2014).

Signature mixtures of social insects comprise mainly CHCs that, depending on the species, are partly genetically determined and partly influenced by the environment (Wyatt 2010). Distinguishing between signature mixtures (chemical cues) and pheromones (chemical signals) can also be difficult because some hydrocarbons act as pheromones.

Since animals learn and rely on signatures mixtures for their recognition, other animals can likewise exploit them. For example, some animals are able to acquire CHCs similar to those of social insects through diet, contact, or biosynthesis and employ a strategy of chemical mimicry or

chemical camouflage to enter the societies of social insects to exploit them (Akino 2008) (see ► [“Mimicry”](#) and ► [“Camouflage”](#) in this book).

## Conclusion

Chemical cues are present in the environment and used by organisms as sources of information for all aspects of life, thus influencing the behavior of a receiver. Unlike chemical signals, chemical cues did not evolve in the emitter for this function but are used by the organisms that can benefit from them. Chemical signals evolve from chemical cues when they evolve for this function in both the receiver and the emitter. Distinguishing between chemical cues and signals is not always easy because a given chemical may act simultaneously as a signal and as a cue in different organisms.

Many animals can learn their own signature mixtures and recognize members of the same species or colony, as well as sexual partners, and direct their parental care, communication, and other behaviors. Since animals depend on recognition, other animals can acquire their signature mixtures to exploit them.

## Cross-References

- [Camouflage](#)
- [Chemical Signals](#)
- [Conspecifics](#)
- [Evolution](#)
- [Imprinting](#)
- [Learning](#)
- [Mimicry](#)
- [Orientation](#)
- [Pheromone](#)
- [Protein](#)
- [Territory Defense](#)

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## Chemical Signals

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### Synonyms

Gustatory signals; Olfactory signals

### Related

Pheromones, Chemical cues, Olfactory cues, Gustatory cues, Kin-recognition, MHC, Arm-pit effect, Self-referent phenotype matching.

### Definition

*Chemical signals* can be defined as messages transmitted through chemosensory modalities (smell and taste) and include things like pheromones, which are secreted chemical signals used to trigger a response in another individual.

This section includes chemical communication with little effort to distinguish between cues and signals. For some, the difference between a cue and a signal relates to intentionality or whether the communication is incidental (Maynard-Smith and Harper 2003). For others, costs and benefits to the sender and the receiver help make the determination between signals and cues, and this is tied closely to evolutionary analysis (Laidre and Johnstone 2013). Therefore, I will review the diversity of messages possible and the unique aspects of gustation and olfaction as communicative modalities. Chemical signals are special in that an animal often gives a small piece of itself in its message. Therefore, this is a communication channel unique for its ability to convey identity.

## Taste and Smell

Chemical signals use the modalities of taste and smell. Often it is difficult to find clear distinctions between the two when it comes to chemical communication as these signals are often combined into an amorphous chemosensory modality. The distinction, however, is important as some animals possess gustation, but not olfaction. The toothed whales, for example, lack olfactory bulbs, yet possess the ability to taste surprisingly well (Cozzi et al. 2016; Nachtigall 1986) despite a reduction in taste receptor genes related to sweet, sour, umami, and bitter sensations in bottlenose dolphins (Feng et al. 2014). As such, we fail to explore one chemosensory modality upon the lack of the other. Furthermore, the tight association between olfaction and gustation causes a lack of clarity as to the role of each in chemical communication. This is seen most strikingly in the flehmen response where animals like giraffes, sheep, cats, and horses will sample urine on their tongues and inhale to provide the vomeronasal organ with stimuli (Mueller-Schwarze 1979). These cues are very important in reproductive assessment (Bland and Jubilan 1987; Swaisgood et al. 2002), but the relative role of gustation versus vomeronasal stimulation remains unknown. Study into the relative

influence of gustation and olfaction might elucidate some of the conflicting results surrounding the taste capacities of anosmic humans (Crosland et al. 1926; Hyman et al. 1979).

## Chemical Signals and Social Recognition

Social recognition is a very important aspect of the natural world. Recognition at the species level (Todrank and Heth 1996) allows for much more successful mating outcomes, as reproductive behavior directed to individuals outside of one's conspecifics rarely results in increased fitness. Repeated, long-term social relationships in animals may facilitate more refined social discriminations either at the kin (Mateo 2003; Todrank et al. 1998) or individual level (Sayigh et al. 1998; Zenuto and Fanjul 2002). Kin recognition without individual specificity exists in many animals as a tool for helping organisms direct kin-selected helping behaviors, avoid inbreeding (Hamilton 1964; Linsenmair 1987) and is often mediated by self-referent phenotype matching (Mateo and Johnston 2000). Colloquially referred to as the "armpit effect," here an organism uses its own odors and the similarities in scent molecules between itself and conspecifics to assess relatedness (Mateo and Johnston 2003). The benefit with such a system is that decisions about who to help and who not to can be made quickly as it does not require previous experience with individuals, a long association or long-term social memory to gauge relatedness (Mateo 2010; Sherman 1977). Conceptually, individual recognition is the most precise social recognition system (Vetter and Caldwell 2015) and the one that is often most difficult to definitively provide evidence for, as one must always be mindful to separate evidence for familiarity from evidence for individual-level knowledge (Tibbetts and Dale 2007). In most mammals, it is the olfactory system that provides the majority of social information (Thom and Hurst 2004) as odor is tied closely to reproductive status, stress (Mackay Sim and Laing 1980), and also relatedness through mediation by the major histocompatibility complex (MHC) (Lawson et al. 2001; Schaefer et al. 2002; Todrank et al. 1998).

No vertebrate has yet been shown to possess pure gustatory social recognition, but the biological blueprint for this capability is present in the mantis shrimp (*Gonodactylidae*). Here highly aggressive individuals use urine to make individual-level distinctions between conspecifics. Species that frequently contact a limited number of individuals over a longer time period are most likely to develop individual-level recognition sometimes as a consequence of aggressive mate-guarding and/or monogamy (Caldwell 1985; Vetter and Caldwell 2015). Shrimp process "taste" using aesthetascs which are unimodal chemosensory sensilla found on their antennules (Mead and Caldwell 2011), but even in this invertebrate species, the socially distinguishing molecules remain unknown (Mead and Caldwell 2011; Vetter and Caldwell 2015). Multichannel variations in individual recognition are present as well, as some closely related species of shrimp, for example, are able to utilize vision, acoustics, and chemical perception together to identify conspecifics down to the individual level (Vetter and Caldwell 2015). Because competitive interactions between these shrimps are usually lethal, it is important to assess whether conspecifics pose an actual threat or possibly present a mating opportunity.

## Chemoreception and Sexual Signals

There is a great deal of variation in chemosensory structures leading to a range of uses for chemicals in sexual signaling. In humans, the olfactory membranes are about the size of two postage stamps, whereas in fair-sized dogs, the same organs would be the size of a pocket handkerchief (Burton 1976). As a result, smell is used in sexual signaling very differently between these two species. Dogs can use smell to determine the presence of prostate cancer in human urine (Cornu et al. 2011), a skill harnessed from an adaptation related to social-sexual identification in their own species (Dunbar 1977). Legendary are the chemoreceptive abilities of moths, capable of detecting a female's sex pheromone 11 km away (see Symonds et al. 2012 for comprehensive



review). Perhaps understudied, however, is the role of eavesdropping by predators and parasites upon these conspicuous chemical signals (Zuk and Kolluru 1998). Parasitic wasps are notorious for their assaults on sexually signaling aphids (Hardie et al. 1991). This eavesdropping phenomena is being explored as a way to mitigate pests in agriculture, by simulating sexual signals (both to catch eavesdroppers and intended targets) and offers a profitable application to the study of chemical signals (Zuk and Kolluru 1998).

## Cross-References

- ▶ Bear Sensory Systems
- ▶ Chemical Cues
- ▶ Chemoreception
- ▶ Communication
- ▶ Individual Recognition
- ▶ Insect Communication
- ▶ Insect Sensory System
- ▶ Major Histocompatibility Complex
- ▶ Olfactory Discrimination
- ▶ Olfactory Perception
- ▶ Pheromone
- ▶ Rodentia Communication
- ▶ Scent-Marking
- ▶ Swine Communication

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## Chemoreception

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## Synonyms

Gustatory; Olfactory; Sensory Drive

## Introduction

Chemoreception refers to the process in which an organism responds to external chemical stimuli within their environment. In particular, it influences olfaction and gustation, or the sense of smell and taste, respectively. The base mechanism that facilitates chemoreception is the interaction between a chemical stimulus and the outer membrane of a cell. The outer membrane contains protein receptors, and when a particular chemical, which is designed to bind to a specific receptor, is engaged, it initiates a cellular response; a signal travels to the brain or a peripheral neuron (Wyatt 2014). This base mechanism is universal across single and multicellular organisms, though as a result of varying adaptations there is diversity in multicellular organisms' chemoreceptive organs.

## Chemoreceptor Variation

Invertebrate chemoreceptors are contained within hair-like structures and are in variable places, ranging from their antennae to their feet. In vertebrates, the olfactory, vomerolfactory, and gustatory senses are connected to the brain via cranial nerves and interpreted by different regions of the brain. Taste receptors are bundled together to form taste buds that cover the surface of the tongue. The type and number of taste buds vary across taxa and among individuals (Butler and Hodos 2005).

In most tetrapods, the olfactory system is partitioned into the main olfactory system and an accessory system including the vomeronasal organ (VNO). Although there is some overlap between the two systems, it is understood that the VNO is specialized for detection of heavier chemicals, while the main olfactory system is specialized for detection of airborne chemicals (Fortes-Marco et al. 2013). Though the VNO was initially hypothesized to function solely in detecting pheromones, current research does not support this, as the VNO can also detect non-pheromone chemicals.

The VNO in amphibians and reptiles is connected to their mouth. Snakes and some lizards collect cues by tongue-flicking. Some ungulates and felids collect urine-borne pheromones on their tongues through licking and lip-curling. Though there is an on-going debate as to whether humans have a functional vomeronasal system (Hohenbrink et al. 2012), olfaction plays a significant role in how animals including humans, engage with conspecifics, other organisms, and the environment. There are many contexts where the sense of smell is used including foraging, mate selection, risk identification, and long-distance travel.

## External Cues

Among volatile odorants derived from various animals, insects, plants, and microorganisms in the external world, the odorants that are beneficial only to perceivers and not to the emitter are called kairomones. Conversely, odorants that are advantageous only to issuers, such as antifeedant volatiles from plants, are called allomones. Odorants that benefit both the perceiver and emitter are called synomones. Together, all three classes of odorants kairomones, allomones, and synomones are called allelochemicals (Wyatt 2003).

The sensory drive hypothesis proposes that evolution influences signal production and signal detection in a dynamic world and predicts that selection favors mechanisms that facilitate communication depending on the environmental

background (Endler 1992). Chemical signals and cues must reach the recipient; then the recipient must be able to detect the intended cue to respond appropriately. Chemical signals must travel through varying abiotic conditions such as wind and humidity. Chemoreception plays a vital role in how organisms engage with the world around them.

## Cross-References

► [Olfactory Discrimination](#)

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## Chemosensory

► [Platyrhine Sensory Systems](#)

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## Chemosensory Cues

► [Chemical Cues](#)

## Chemotaxis

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### Definition

The term “chemotaxis” has been derived from two words – “chemo” meaning chemical and “taxis” meaning movement. Thus, it can be defined as the directed movement of a cell or an organism in response to chemical stimulus (Willard and Devreotes 2006).

### Introduction

Chemotaxis is one of the most important phenomena occurring commonly in the living beings. It is exhibited by a variety of organisms ranging from unicellular to multicellular. In unicellular organisms like amoebae and bacteria, chemotaxis is primarily adopted as foraging machinery (Willard and Devreotes 2006). However, in multicellular organisms, it plays an essential role in wound healing and inflammatory responses as well as in cell migration during development (de Oliveira et al. 2016). In addition to this, it is major contributing factor in the metastasis of cancer cells. Chemotaxis can either be positive or negative depending on the direction of motion of the cell in response to the chemical signals. If the cell moves towards the direction of the signal, it is termed as positive chemotaxis and the chemical signal is then considered as chemoattractant. But if the cell moves against the direction of the signal, it is known as negative chemotaxis and the chemical signal in such case is regarded as chemorepellent.

## Chemotaxis in Prokaryotes

In general, flagellated bacteria use the process of chemotaxis for locomotion purpose. It involves a series of dispersed run and tumble movement guided by chemical stimulus which ultimately helps the bacteria in reaching favorable environment (such as food) and avoiding unfavorable conditions (such as toxins). Berg and Brown (1972) have extensively studied the basic mechanism underlying this behavior in *Escherichia coli* which is as follows:

- (i) Specific chemoreceptors located on the surface of bacterial membrane sense and bind chemical cues (ligands).
- (ii) Binding of ligand to chemoreceptor activates the two-component signaling pathway (when repellents are present or attractants are absent) across the cell membrane leading to the autophosphorylation of CheA, a protein histidine kinase. This in turn, results in the increased phosphorylation of CheY (a response regulator).
- (iii) Phosphorylated CheY diffuses freely through the cell and binds to FliM (a flagellar protein) when it comes into contact with the flagellar motor.
- (iv) Then phosphorylated CheY-FliM complex shifts the orientation of flagellar rotation from counterclockwise to clockwise direction, thereby inducing tumbling movement. Thus it can be inferred that clockwise rotation promotes tumble whereas counterclockwise rotation promotes run.

## Chemotaxis in Eukaryotes

The process of chemotaxis in eukaryotes is quite different from that of prokaryotes. Prokaryotes being smaller in size cannot directly sense concentration gradient. They detect their surrounding temporally and swim continuously by redirecting themselves every time they perceive alteration in the gradient. In contrast to this, eukaryotic chemotaxis comprises of spatially detecting

concentration gradient through asymmetric activation of receptors known as G protein-coupled receptors (GPCRs). GPCRs are present uniformly throughout the cell surface which binds specific chemoattractants and generate signal that controls movement (Levine and Rappel 2013). GPCRs signaling are involved in the deployment of immune cells such as neutrophils, monocytes, macrophages, etc. at the site of infection and tissue injury in mammals. In addition to the immune cells, a large group of cells namely, mast cell, fibroblast, endothelial cells under certain physiological conditions are considered to show motility because of GPCRs signaling (Kedrin et al. 2007).

Furthermore, GPCRs signaling assists social amoeba *Dictyostelium discoideum* in their foraging mechanism by mediating chemotactic responses. Besides this, GPCRs are also associated with the starvation response in *Dictyostelium discoideum*. During starvation, distinct amoeba form aggregates. This process of aggregation is governed by gradients of cAMP and is followed by a series of morphogenetic transformation and cell fate selection which leads to the formation of multicellular structures enclosing spores that can withstand starvation (Willard and Devreotes 2006). Several studies conducted on G proteins have not only proved its role as “molecular switches” but also demonstrated how GPCRs signaling functions in relation to chemotactic signaling and regulate directional movement by deciphering the direction of external concentration gradients (Franca-koh et al. 2010).

## Conclusion

Chemotaxis can be regarded as a fundamental sensory process. Its role in prokaryotes is quite similar to the decision-making capabilities of higher living organisms having brains for processing sensory information. However, in eukaryotes, G proteins have an indispensable role in regulating signaling pathways in response to chemotactic ligands under controlled space and time. In addition to this, there are different chemotactic receptors which exhibit diverse type of specialized mechanisms to bind the ligands

and subsequent activation of downstream proteins via transmembrane signaling. Recent advancements have been made in understanding the molecular mechanism that regulates transmembrane signaling. Although, a deep understanding of how these signaling pathways interact with each other is still required to develop new models.

## Cross-References

- Chemical Cues
- Chemical Signals
- Decision-Making
- Eukaryota
- Foraging
- Migration
- Protein
- Taxis

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## Chicken-Like Bird Locomotion

- Galliformes Locomotion

## Chimpanzee

### ► [Hominoidea Navigation](#)

## Chimpanzee Between-Group Lethal Competition

### ► [Chimpanzee Raiding](#)

## Chimpanzee Raiding

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## Synonyms

[Chimpanzee between-group lethal competition](#); [Chimpanzee sociality](#); [Coalitional raiding in chimpanzees](#); [Intercommunity aggression](#); [Patroling behavior in chimpanzees](#)

## Definition

The coordinated incursion of a coalition of adult chimpanzees into the territory of an adversary chimpanzee community that often leads to either the displacement or elimination of the rival group's members.

## Introduction

Phylogenetic comparative studies have identified that conspecific killings are widespread across nonhuman taxa. Gómez et al. (2016) estimated the level of lethal aggression in 137 families involving 1024 mammalian species. In contrast

to within-group attacks, intergroup killings were found in substantially fewer taxa. To date, reports of lethal between-group interactions (Gómez et al. 2016; Wrangham 1999) can be found in grey wolves (*Canis lupus lupus*), lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), and cheetahs (*Acinonyx jubatus*). Additionally, some non-human primates, including spider monkeys (*Ateles belzebuth*) and mountain gorillas (*Gorilla beringei beringei*), have exhibited related behaviors. Moreover, lethal intergroup conflict has been studied in great detail in chimpanzee (*Pan troglodytes*) communities. Observations and analyses of violent interactions between chimpanzee groups have been scientifically received with varying levels of acceptance due to the potential implications of such findings. The current entry covers fundamental hypotheses and related empirical studies that have attempted to characterize this behavioral phenomenon.

## Evidence of Chimpanzee Intercommunity Killings

Jane Goodall's primatological observations challenged the notion that only state-level human societies engage in lethal intergroup conflict. Early in her study of chimpanzees in Tanzania, Goodall established a feeding location near her research station to normalize her presence within their ecology through habituation. Subsequently, she identified two chimpanzee subgroups, northern and southern, based on the routes that individuals took after feeding at the camp. Initially, Goodall considered these parties to be entirely independent of each other; however, closer inspection revealed that both northern and southern chimpanzees were once part of the same community. By 1973, she had officially named both groups based on their physical proximity to geographical landmarks. The northern community, named Kasekela, occupied the area between the Katombe and Kasekela valleys. The southern group occupied the Kahama valley and was named accordingly. Despite their common origin, interactions between Kahama and Kasekela chimpanzees ranged from avoidance to open hostility (Goodall 1986). Five years after its detection,

intense intercommunity clashes reduced the southern Kahama's range from 10 km<sup>2</sup> to less than 2 km<sup>2</sup>. Any remaining females went on to join rival groups, evidencing the end of the Kahama community. Their elimination allowed Kasekela to expand its range to 17 km<sup>2</sup>. Although during this period, Kasekela experienced a considerable expansion in its community range area, their growth eventually halted. Since Kahama's territory previously acted as a barrier between Kasekela and other southern factions (such as Kalande; Goodall 1986), the northern community experienced a series of raids leading to its territorial reduction. Intercommunity aggression at Gombe also had substantial demographic effects. Williams et al. (2008) estimated that half of the 12 male Kahama and Kasekela deaths between 20 and 30 years of age were the product of intercommunity conflict (taking both suspected and observed cases).

Even though some researchers initially received Goodall's reports from Gombe with skepticism, independent evidence would support her observations of lethal agonistic interactions between chimpanzee groups. Nishida et al. (1985), for instance, reported similar findings from the Mahale Mountains in Tanzania. Initially, two communities, named K-group and M-group, occupied neighboring territories. In less than 20 years, K-group experienced a demographic collapse. This process began with the systematic disappearance of most of its adult males. By 1983, only one adolescent male and three females remained. Nishida and colleagues, however, did not observe M-group coalitions killing K-group males. Later, based on circumstantial evidence, the authors estimated that approximately 4% of the K-group's deaths could have been the outcome of intercommunity aggression (Nishida et al. 2003). The authors noticed that as the number of adult males' decreased, female dispersal increased, concluding that demographic changes encouraged cycling females to affiliate with M-group males (Nishida et al. 1985).

Recently, Nakamura and Itoh (2020) revisited the demographic patterns reported from K-group and M-group to determine whether it was unusual for communities to lose six males in 20 years or

less. The authors found that a higher number of M-group males died or disappeared relative to those of K-group, dispelling Nishida's original claim that the loss of K-group males evidenced an abnormal demographic change. The main difference between the communities instead rested on the number of adolescent males reaching adulthood. Even though Nakamura and Itoh included other potential causes underlying the loss of K-group males, such as old age, disease, and injury, according to the authors, these factors could only have weakened the community and facilitated M-group raids, not been a sole cause of demographic shifts.

In addition to Mahale, observations conducted at Kibale National Park, Uganda, counter the claim that intercommunity killings are exclusively the product of anthropogenic factors, such as food provisioning, and instead of adaptive behavior (Watts et al. 2006). Mitani et al. (2010) analyzed patrol data collected from the Ngogo chimpanzee community at Kibale. In ten years, Ngogo coalitions eliminated 18 (21 if adding inferred cases) foreign rivals. Over 90% of the killings occurred during Ngogo patrols, whereby coalitions of individuals, mostly comprised of males, traveled beyond the community's border, generally in a single file formation, in search of rival groups (feeding and socializing decreases during such patrols). Over 60% of the killings transpired near Ngogo's northeastern border.

Because the authors lacked the exact number of individuals inhabiting the targeted community, Mitani et al. (2010) employed a series of heuristics to calculate the killing rate in that northeastern region. Imputing an average of 47 individuals from 8 different chimpanzee communities, the researchers calculated a rate of 2790 chimpanzees killed per 100,000 per year. Alternatively, if instead assuming that the Ngogo and northeastern communities had an equivalent group size of 150 individuals, the rate decreases to 867 killed per 100,000 per year. Mitani et al. predicted that the estimates from Kibale were considerably higher, relative to those computed for nine other chimpanzee communities spread throughout Africa, partially because patrolling occurs more



frequently at Ngogo (Mitani and Watts 2005a; Watts and Mitani 2001; Watts et al. 2006).

The elimination of foreign rivals led to Ngogo's territorial expansion. Mitani et al. (2010) observed an increase in the amount of time Ngogo chimpanzees socialized, traveled, and foraged in annexed regions. Additionally, in a previous publication, Mitani and Watts (2005a) considered the ecological and evolutionary correlates of chimpanzee patrolling events at Ngogo. The study considered the size of male patrol groups, the availability of fruit, the presence of estrus females, hunting episodes, and the presence of intruders. A logistic regression model determined that only male party size and fruit availability significantly predicted patrolling events. Consistent with previous studies (e.g., Mitani and Watts 2005b), these two variables were correlated. Additionally, a model limited to those latter two predictors determined that only male party size had a significant contribution to the model.

Similarly, Wilson et al. (2012) analyzed behavioral and ecological data from the Kanyawara chimpanzees inhabiting Kibale National Park. The study considered associations between the number of adult males, the number of estrous females, the number of infants, the distance between an encounter's location and the center of the territory, as well as the percentage of fruit consumption (disaggregated into different fruit species) on 120 intercommunity encounters. The analysis revealed that in over 80% of the cases, individuals limited their agonistic interactions to vocal displays. Additionally, over 60% of these interactions transpired close to Kanyawara's southeastern boundaries (Wilson et al. 2012). The authors found that fruit consumption, particularly that of *Uvariopsis congensis*, as well as the average number of adult males in a patrol party, positively and significantly predicted the distance traveled from the center of the territory to the location of an encounter.

The literature reports noticeable differences in the frequency and intensity of between-group conflicts among chimpanzee field sites. Boesch and collaborators (2008), found that, in contrast to Budongo (Reynolds 2005), Gombe (Goodall

1986), Ngogo (Watts et al. 2006), Kanyawara (Wrangham et al. 2006), Mahale (Nishida et al. 1985), and Loango (Boesch et al. 2007), Taï chimpanzee communities exhibited lower death rates due to intergroup aggression (Northern Group = 0.00; Middle Group = 0.00; and Southern Group = 0.27). Boesch and colleagues attributed this difference to the nearby presence of in-group members ready to aid potential victims of intercommunity aggression. For instance, the authors described that in over 25% of all visual contacts, individuals provided support to in-group targets. Moreover, in all observed instances of adult female sequestration (foreign males corraling the victim, hindering her from returning to her community), supporters assisted the target and facilitated her escape (Boesch et al. 2008). In contrast to this pattern, at the time of the latter publication, only four cases of support in other chimpanzee communities had been observed, three at Ngogo, and one at Kanyawara.

### Empirical Examinations of Anthropogenic and Adaptive Hypotheses

Despite the evidence gathered over the years, some academics remained unconvinced with evolutionary and adaptive explanations of this phenomenon. Instead, those authors claim that anthropogenic pressures better fit the data. In a thorough examination, Wilson and collaborators (2014) summarized the various points raised by critical authors over the years. For Wilson, the human impact hypothesis predicts the following behavioral patterns: (a) chimpanzees and bonobos should exhibit similar killing rates; (b) the killing rate should display a positive trend over time; (c) males and females are equally expected to be the perpetrators and victims of these attacks; (d) the age of individuals should not influence the probability of becoming a victim; (e) genetic relatedness between attackers and victims should not predict killings; and (f) there should not be any numerical asymmetries between perpetrators and victims during attacks. Contrarily, the adaptive strategies hypothesis predicts the following:

(a) chimpanzees should exhibit higher killing rates than bonobos; (b) killing rates should not increase over time; (c) males should be the main perpetrators and victims of lethal competition; (d) infants close to their mothers should be especially vulnerable to these attacks; (e) attackers should target genetically unrelated individuals in rival communities; and (f) killings should occur more often when prospective attackers outnumber their victims.

Wilson et al. (2014) compiled data from four bonobo communities and 18 chimpanzee communities (Eastern = 12; Western = 6), studied for over 50 years. The database contained information on 152 instances of lethal aggression, including 58 observed, 53 suspected, and 41 inferred killings. The authors also gathered information on: (a) whether or not researchers used provisioning as part of the habituation process; (b) the size of the protected area (in km<sup>2</sup>); (c) the intensity of human disturbance; (d) the geographical location of the chimpanzee community (eastern or western); (e) the mean number of adult males per community; and (f) the mean population density per community. The first three indicators are directly related to the human impact hypothesis, whereas the remaining three are associated with the adaptive strategies hypothesis. The authors employed a series of Poisson regressions, controlling for observation time. Wilson et al. (2014) also calculated fit indicators (QAICc), along with their respective  $\Delta$ QAICc and weights, to adequately compare the competing models. Their analyses revealed that chimpanzees had higher killing rates relative to bonobos. The model containing the dimension of the protected area, the severity of human disturbance, and the occurrence of food provisioning received little support ( $\Delta$ QAICc = 3.8; weight = 0.06). All three predictors had negative associations with killings. The best model included the mean number of adult males per community and the population density per community ( $\Delta$ QAICc = 0.00; weight = 0.40). Overall, the ratio between QAICc weights suggests the adaptive strategies hypothesis is 6.8 times more supported than the human impact hypothesis.

When looking at the identity of the attackers and their targets, males were found to participate

in over 90% of the killings. Moreover, the study detected significant sex differences after controlling for observation time, wherein, relative to females, males were more likely to kill a conspecific. Females would attack only adult rivals and participate only when part of a male-led coalition (Wilson et al. 2014). In the case of the victims, infants and adult males were usually targeted. In the majority of cases, the attackers and their targets inhabited different communities and were therefore genetically distant (Wilson et al. 2014). Targets could however include mothers with offspring or solitary victims. The authors estimated that a median of nine males per party was required to outnumber the victims. Wilson and colleagues also estimated the proportion of attackers relative to targets. Raiders outnumbered targets 8:1 (analysis restricted to 30 cases featuring data on party size).

### Power Imbalances and Numerical Assessment

The imbalance-of-power hypothesis provides an adaptive framework through which one can explain coalitional, between-group, killings in chimpanzees (Wrangham 1999). It was formally introduced by Richard Wrangham and colleagues but is traceable to Jane Goodall. The hypothesis claims that lethal violence intrinsic to raiding can provide a selective advantage to aggressing societies in nonlethal contexts, such as the accumulation of resources. This process occurs through a balancing of the costs and benefits of individual raids. Since the associated behaviors involve guaranteed costs, such as time and energy spent patrolling, and potential costs, such as injury or death, attacks are carried out strategically to be most worthwhile to the broader society (Manson et al. 1991; Wilson 2013; Wrangham 1999). The key variables relevant to action are the size and constitution of parties when they detect one another. The larger an opposing party, the less likely another party is to attack, and by extension, the more likely they are to be attacked. Thus, if a patrolling group of males finds a single member of a neighboring society without nearby defenses,

the likelihood of severe injury or death to group members during an attack is quite low. Meanwhile, the neighboring society, which may compete for resources or mates, experiences a slight competitive disadvantage from the loss.

Wilson et al. (2001) played a previously recorded “pant-hoot” from an unknown male to parties composed of anywhere from zero to nine adult males. Pant-hoots are a common form of chimpanzee communication, audible up to two kilometers away and utilized to signal anything from newly discovered food to violent conflict. Multiple variables were measured to investigate underlying influences on response patterns and possible differences based on group composition. Included were the location and proximity to society borders (both those of the loudspeaker and the party), number of individuals by approximate age and sex, and individual agonistic rank (Wilson et al. 2001). The only variable that significantly predicted both a vocalization response and a physical approach was the number of defending members in a group. This provided strong preliminary support for the claim that chimpanzees possess the ability to determine their likelihood of success in performing a raid through knowledge of their group’s strength and an auditory understanding of that of their opponents.

Another study, this one ethological, at Kanywara, contributed further to answering these questions (Wilson et al. 2002). Over 15 years, Wilson and colleagues collected data on multiple parties, from their composition, which included counts of infants, adult males, and females in estrus, to their proximity from societal borders, and even the value of food resources based on category and proximity to the center of the range. Food resource valuations were based on the amount of time individuals spent foraging in the proximity of a resource disputed by members of multiple societies. Although most interactions between members of opposing groups occurred from a distance greater than one hundred meters apart and remained nonphysical, the number of males in each party was once again the only variable to significantly predict the approach. Those with a sufficient numerical asymmetry, previously determined to be any group with 1.5, or more,

times as many adult males as the opposition, were likely to approach (Wilson et al. 2002).

In summary, chimpanzee societies must respond to ecological pressures, such as continuous scramble competition for ripe fruit, by leveraging their opportunities to disadvantage nearby rivals physically. The relative fitness of neighboring societies appears to depend heavily on their dominance over one another in capturing and maintaining an adequate supply of food and mating-based resources. These crucial and ever-fluctuating markers of between-group dominance encourage the selective killing of valuable members of competing societies when the costs render such behaviors to be actionable and reasonably safe, within the thresholds discussed above. Though many factors impact vulnerability to attack, the likelihood of action still appears to be based solely on the numerical asymmetry between parties. The imbalance-of-power hypothesis nests these individual asymmetries of conflict within broader societal continua, relevant to the overall fitness, and demographic well-being, of competing societies in a given population.

### Intercommunity Conflict and Fitness Outcomes

According to Wilson (2013), as well as Wilson and Wrangham (2003), scientific explanations often consider one or more of the following potential benefits obtainable through violent intergroup conflict: (a) gaining access to feeding grounds; (b) recruiting foreign females; (c) decreasing the risk of becoming a target of intergroup aggression; (d) reducing the probability of foreign males copulating with native females; and (e) eliminating sexual rivals.

Empirical evidence supports some of these predictions. For example, Williams and collaborators (2004) analyzed behavioral and ecological data collected on Gombe chimpanzees over 18 years. The study explored the direct and indirect associations of community range size with both chimpanzee social interactions and life history indicators. Even though the authors did not find a significant association between a broader range

and the total number of females, additional models detected that range size positively predicted the amount of time that individuals allocated to foraging in larger feeding parties, as well as a frequency of contact between males and sexually receptive females. A larger community range size also negatively predicted female interbirth intervals, suggesting that access to resources, in this case as a product of area expansion, has a direct effect on reproductive output. Researchers have also found that a larger range and a lower population density are associated with heavier body mass (Pusey et al. 2005).

Other perspectives have also considered the influence of contextual factors. According to the *group augmentation hypothesis* (Langergraber et al. 2017), individuals are willing to accrue a personal cost and not obtain an immediate benefit by participating in patrol parties, as long as that contribution facilitates the group in increasing its size and leads to greater reproductive success. Langergraber et al. (2017) analyzed behavioral, kinship, and genetic data collected from male chimpanzees inhabiting the Ngogo community at Kibale, Uganda. A generalized linear mixed model identified that male paternity success, along with male rank in the dominance hierarchy, positively predicted patrol participation. Other indicators, such as the number of maternal kin in the group or male age, did not reach statistical significance. Langergraber et al. analyzed the paternities of 11 adult males. The authors calculated that males, based on over 110 births, sired on average 3.3 offspring. The data revealed that all males participated in patrols, even if they did not have offspring at the time. Only 36% of all adult males did not reproduce. These results indicate that, although adult males do not obtain a direct fitness benefit from patrolling, indirectly, their probability of successfully reproducing increases as an outcome of the group's expansion. Contrary to other publications, the analyses also identified a negative association between the number of males in the group and males' participation in border patrols, suggesting a rise in social defection as the number of participants increased.

Past research at Kibale has also found male dominance rank to be independent of patrol frequency (Watts and Mitani 2001). In contrast,

patrolling behavior was shown to have a positive and significant association with the mean percentage of copulations (this association became non-significant after controlling for the individual's dominance rank; Watts and Mitani 2001). Additional analyses concluded that even though the proportions of patrolling behavior (the number of times a male participated in a patrol, given the number of opportunities the individual had to join a patrol party) did not predict male mating success, controlling for the individual's rank had a positive relation with the criterion variable (Watts and Mitani 2001).

In addition to the group augmentation hypothesis, other views have also considered the role of the group characteristics on conflict. According to the intergroup dominance hypothesis, all individuals in the community benefit from expanding the territory, for instance in obtaining access to feeding grounds, and in the case of males, the ability to recruit more females (Crofoot and Wrangham 2010). Some evidence supports this perspective. Lemoine and colleagues (2020b) examined demographic and behavioral data from four chimpanzee groups over 54 years of observation in Taï National Park, Ivory Coast. The authors developed a neighbor pressure index, comprised of the frequency of intergroup interactions, the value of the location according to its yearly usage, and the relative physical distance between the location where the interaction occurred and the center of the territory's center. Lemoine et al. (2020b) also considered the number of adult males per group as a potential proxy for intergroup competition. Additionally, the study considered the number of weaned individuals as an indicator of intragroup competition. The analyses revealed that exposure to intense neighbor pressure during pregnancy had a negative association with prenatal offspring survival. This pattern, however, did not generalize to postnatal infant survival. In a subsequent analysis, the authors computed a Linear Mixed Model estimating the association between the mean number of adult males, the neighbor index, and the mean number of wean individuals, with female interbirth intervals (IBI's). As predicted, both the neighbor index and the number of wean individuals increased female IBI's, whereas the number

of adult males had a significantly negative relation on IBI's.

Lemoine et al. (2020a) explored, in a later publication, the link between group dominance, territory size, and neighbor pressure. Their study found that group size had a positive and significant relation with the size of the territory. Likewise, larger groups scored lower on the neighbor pressure index. Model comparison determined that the total number of individuals, rather than the number of adult males, better predicted the criterion variables. The results from these studies suggest that neighbor pressure and territorial expansion could mediate the association between group size and reproductive outcomes.

### Intergroup Killings in Chimpanzee and Human Societies

Due to their phylogenetic proximity, studies exploring the ecological and evolutionary correlates of chimpanzee intercommunity conflict could provide researchers with a deeper understanding of human between-group aggression (Glowacki et al. 2020; Wrangham and Glowacki 2012; Wilson and Glowacki 2017). Wrangham et al. (2006) gathered data on human and chimpanzee lethal aggression. The database included information on nine chimpanzee communities, observed over the course of 158 data-years. During this period, the authors counted at least 49 observed and 27 suspected instances of intercommunity killings. Aggregating these instances across all communities generated a mortality rate of approximately 125–306 deaths per 100,000 individuals per year (Wrangham et al. 2006). The authors also gathered information on intergroup mortality rates in small-scale human societies. The median mortality rate from intergroup aggression in these human societies varied depending on the type of subsistence economy (Hunters:  $n = 12$ , median = 164, per 100,000 per year; Farmers:  $n = 20$ , median = 595, per 100,000 per year). Significance tests identified that farmers had higher mortality rates relative to hunters (Wrangham et al. 2006). The killing rates of chimpanzees and hunter-gatherer societies thus exhibited a considerable overlap. The authors,

however, noticed a slight difference between the groups. Whereas in chimpanzee communities, infants, adolescents, and adult males were generally the victims, in human groups, adult males were usually the only targets of these attacks.

### Discussion

Although lethal aggression is a widespread phenomenon across human and nonhuman taxa, intergroup killings occur in a small subset of species. Although primatologists have described between-group attacks in nonhuman primates (Crofoot and Wrangham 2010), most of the literature on this subject concerns intercommunity killings in chimpanzees. Initially, reports of intergroup attacks in Gombe and Mahale were met with considerable skepticism. Critics claimed that anthropogenic factors, including the use of food provisioning as part of the habituation process, artificially increased the frequency and intensity of conflict between communities. Observations of intergroup lethal attacks in non-provisioned field sites countered these claims. Skeptics also contended that habitat destruction and human encroachment better explained chimpanzee territoriality and lethal coalitional aggression. Recently, however, cross-community comparisons exploring the influence of food provisioning, degree of human disturbance, territory size, population density, the mean number of males, and location, concluded that the anthropogenic variables do not adequately predict intercommunity killings. Thus, adaptive hypotheses currently provide the most explanatory depth for these behaviors and therefore find themselves best supported within the relevant literature.

### Cross-References

- [Aggression](#)
- [Nonhuman Primates](#)
- [Primate Social Structure](#)
- [Primates](#)
- [Raiding](#)
- [Tai Chimpanzees](#)

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## Chimpanzee Sociality

### ► Chimpanzee Raiding

## Chondrichthyes Communication

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## Definition

Chondrichthyes' communication is the exchange of information and social behavior, both intraspecific and interspecific, between a sender and a receiver, and at least one of these is a chondrichthyan.

## Introduction

Chondrichthyes belong to one of the oldest and most diverse vertebrate groups (entry ► [“Vertebrates \(Chordata\)”](#)). Featured by two synapomorphic characteristics, a cartilaginous skeleton superficially mineralized by prismatic calcifications and the presence of claspers (evolutionary distinct than any similar structure in other clades, derived from pelvic-fin modifications) in male representatives for internal reproduction, the group is recognized for its evolutionary success involving historical persistence, having survived several events of mass extinctions over the past 400 million years (Carrier et al. 2012). The extant diversity of the group, with 1282 valid species (Fricke et al. 2021), can be divided into 2 branches: the Elasmobranchii (sharks and rays) and the Holocephali (chimeras and their relatives).

Representatives of this group can navigate thousands of kilometers to mate, prey, lay eggs, and other reasons. Some mechanisms by which chondrichthyan species can perceive their environment and navigate by it include mechanoreception (mainly auditory and lateral line systems), electroreception, chemoreception, and vision (entries ► [“Chondrichthyes Locomotion”](#), ► [“Chondrichthyes Navigation”](#), and ► [“Chondrichthyes Sensory Systems”](#)). In addition, the senses listed previously also aid in the communication present in the group, as presented below.

The definition of animal communication is somewhat troublesome since there is no consensus in the literature (for a review, see ► [“Communication”](#)). However, some elements that usually define it are the existence of a **sender** and a **receiver**; the presence of an emitted **signal**; and the **communication** between parties, enabled by such signals. In general, animals communicate using visual, acoustic, chemical (including olfactory), tactile, and electrical signals, and all these modes are present in Chondrichthyes.

In Chondrichthyes, communication is essential for several of their behavioral patterns. For example, some species have their survival enhanced by presenting certain luminescence patterns,

functioning as backlighting to avoid predators and attract prey. Behaviors involving communication, mainly sensory-induced behaviors, function as mediators of rheotaxis (orientation to water currents), detection of prey, prevention of predators, and hydrodynamic imaging to locate objects (Carrier et al. 2012). Furthermore, social communication and schooling are also major behaviors of the group.

Most of the published data on Chondrichthyes communication is reported for elasmobranchs. However, we will also present chimeroid communication, whenever information is available in the literature. This entry will focus on chondrichthyans' communication modes, being divided according to subsequent classifications and their specification: (1) **visual** (eyesight, agonistic and reproductive postures, type of swim, patterns, colors, and light emission), (2) **acoustic and mechanoreception** (hearing and other mechanosensory receptors), (3) **chemical** (flair and pheromone), (4) **tactile** (recognition bite, feeding frenzy, and mating), and (5) **electrical** (electroreception). Finally, behavioral studies are reasonably scarce for chondrichthyans, so that morphological (entry ► "[Chondrichthyes Morphology](#)") and physiological studies are the main sources of information about their ecological aspects that are difficult to observe in the wild.

## Visual Communication

Chondrichthyes' visual communication is not highly discussed in the literature. Despite a somewhat large body of evidence that chondrichthyans have well-developed visual systems (see Hart et al. 2006 for a revision), there is little information on the role of vision in their everyday life and which visual targets provoke behavioral responses. Here, we will focus on aspects of visual communication, signal, and meaning that can be found in the literature.

Several anatomical features indicate aspects of visual behavior and communication patterns. For example, chimeras, usually deep-sea fishes, frequently have prominent eyes, and, as the size of an animal's eyes influences its visual capabilities,

several works suggest vision may be particularly important for those fishes (Lisney 2010). Most chimeras have a pure rod retina, which allows them to notice the presence of predators and prey once the individual enters their visual field, even in zones with low sunlight levels (Bozzano and Collin 2000). Furthermore, the *tapetum lucidum*, a structure present in chondrichthyans (as well as in several other vertebrates), reflects the light that has passed through the photoreceptors back to them, improving visual accuracy in darker environments and being a primary mechanism to enhance visual sensitivity. Comparing two species of chimeras from different depth intervals, interspecific differences in the aspects of the *tapetum* indicate the species that occupy deeper waters might have higher light sensitivity than the species closer to the surface (Maddock and Nicol 1978).

In contrast, elasmobranchs present a variety of retinal configurations, from pure rod to rods and cones. Cones are most abundant in the retinal configurations of predominantly shallow-dwelling, diurnally active species, and multiple cone types suggest some elasmobranchs have the potential for color vision (Hart et al. 2006). Even though several freshwater lineages exist, most elasmobranchs occupy marine environments, whose tridimensional structuration is variable, and the role of vision for environment perception and communication might correlate to the species lifestyle (occupying coastal or open ocean areas, depth at the water column, and so on). Furthermore, the quality of vision in these animals depends not only on anatomical factors but also on ecological factors that affect their visual sensitivity and communication, acting as a receiver or a sender. Nevertheless, visual signals dictate visual behaviors within the group, mainly involving reproduction, aggression, and predation (Lisney et al. 2012).

## Agonistic Postures

A very common class of behavior among animals is agonism, which occurs in different competitive contexts and is important for the social dynamics and evolutionary aptitude of many animals. For example, individuals that are defeated or displaced during agonistic behaviors (interspecific or

intraspecific competitions) most often disperse to suboptimal environments, causing a reduction in their food and reproductive capacity (Reese 1978).

The agonistic display is best known in the gray reef shark (*Carcharhinus amblyrhynchos*) that features a “hunch display” in which the snout is lifted, and the back is arched. This stance occurs in response to persecution or possible agglomeration caused by divers or other animals (Johnson and Nelson 1973). There are four postural elements of this display: (1) snout raised, (2) pectoral fins depressed bilaterally and to the same angle, (3) arched back, and (4) lateral flexion of the body. Besides, these postures are combined with two locomotive elements: (1) side swimming and (2) rolling and/or looping, spiral swimming (Johnson and Nelson 1973). All these postures can occur when the animal feels threatened (Hart et al. 2006) and increase in intensity according to the signal emitted by the sender, as well as to the degree of restriction of the escape route (Johnson and Nelson 1973). Also, if the signal persists, the hunch display may turn into a withdrawal strike or a quick, open-mouthed slashing attack (Johnson and Nelson 1973). This “hunch display” may occur both as an interspecific behavior likewise against conspecifics (Myrberg and Gruber 1974).

Another agonistic behavior presented by the white sharks (*Carcharodon carcharias*) is the great “tail slap” on the water surface, a representation with visual and acoustic components used to keep competitors away, whether they are from the same species or not (Klimley et al. 1996). The intensity and frequency of such signals can transmit information about the relative strength of the sender, indicating its fighting quality to the receiver.

### Reproductive Postures

Characterized by internal fertilization, the patterns of reproduction and development in Chondrichthyes are diverse, but very little is known about their reproductive behavior. Mating observations are generally made in captivity, with few observations in the natural environment. Some copulatory behaviors were observed involving partner recognition and

courtship in elasmobranchs, with the female usually initiating the court (Hart et al. 2006).

Copulatory cues mainly use pheromones combined with visual displays, such as the arching of the female’s back, an inclination as a form of “submission,” and dilation of the cloaca, signaling receptivity to the male (Pratt and Carrier 2001). However, male gray nurse sharks (*Carcharias taurus*) usually initiate the mating behavior, expressing increasing aggression and displaying clasper flexion (Gordon 1993).

### Patterns and Colors

Despite elasmobranchs generally having neutral colors to the human eye (when compared to the bright colors seen in many other fishes), non-subjective spectroradiometric color measurements indicate most elasmobranchs present some degree of countershading that tends to be more apparent in active pelagic sharks, besides benthic and deepwater sharks (Hart et al. 2006). The markings’ shape and color notably contrast against the background and may work as camouflage, crypsis, or disruptive coloring. There is evidence that female nurse sharks (*Ginglymostoma cirratum*) appear to select larger and darker males, suggesting that coloration could be also used in intraspecific communication for partner selection (Pratt and Carrier 2001).

### Light Emission

Literature shows us that, more than anything else, the ability to see probably shaped the evolution of vision in fishes as a way of avoiding obstacles and finding shelter, besides recognizing prey and predators (Paitio et al. 2016). However, for all these behaviors to effectively occur, the presence of light in the environment is a central component, and light is scant in deep environments. Even though sunlight does not naturally reach deep waters, these are not devoid of light (from the perspective of nonhuman animals) due to two distinct phenomena of light emission by several organisms: bioluminescence and biofluorescence.

Bioluminescence is the ability of a living organism to produce, through chemical reactions, and emit visible light, being reported for 46 fish families so far (Paitio et al. 2016). Among

elasmobranchs, bioluminescence is present in, at least, three Squaliformes families (Etmopteridae, Dalatiidae, and Somniosidae) (Duchatelet et al. 2021), and it seems to be nonexistent or has not been yet confirmed in rays, skates, and Holocephali (Paitio et al. 2016).

The light organs can perform several functions, and their locations are somewhat associated with the functions of the emitted light (Paitio et al. 2016). This light can be used by the sender for intraspecific communication, recognition, schooling, and mating. In the case of interspecific relationships, luminescence also plays a role in prey and predator detection. To avoid predators, back-lighting is particularly used, a method called counter-illumination: the species emits light in the ventral body region, matching the light from above, confusing the predator, and camouflaging itself. In bioluminescent sharks, numerous small light organs are predominantly present in the ventral region of the body, but lower densities can even reach the dorsal areas in dalatiid species (Paitio et al. 2016).

Different from bioluminescence, biofluorescence is the phenomenon where the organism absorbs low wavelength (deep blue) from the environment and emits high wavelength (green) light. To date, there are only five known elasmobranchs with this feature: one stingray (family Urotrygonidae), one wobbegong (Orectolobidae), and three catsharks (Scyliorhinidae). Given that these families are not evolutionary closely related, biofluorescence seems to have evolved at least three independent times within Chondrichthyes. Thus far, no specimen of Holocephali has been shown to be biofluorescent (Gruber et al. 2016).

In a Scyliorhinidae species, *Cephaloscyllium ventriosum*, light emission is possibly a sexually dimorphic feature, with females presenting more body regions able to emit light, and males with claspers greatly fluorescent. These elasmobranchs are not only able to emit but also to perceive the high wavelength light emitted by conspecific others, in clear visual communication. However, because predators might not be adapted to see this light, these animals become invisible to those who lack a similar visual capability in a dark environment (Gruber et al. 2016).

## Mechanoreception and Communication

The propagation of sound occurs in different ways depending on the medium: in water, due to its higher density, mechanical waves propagate about 4.8 times faster than in the air. Therefore, the ability to detect vibrational stimuli in the water provides animals a great source of information about the environment. Chondrichthyes perceive low-frequency stimuli through their inner ears and the lateral line system, but it is difficult to discriminate the vibration perception between these two systems. Both systems are part of mechanoreception, playing an important role in chondrichthyan orientation on the environment, participating in currents and hydrodynamic imaging to locate objects (Coombs and Montgomery 1999), besides prey and predator detection.

### Acoustic Signals

The inner ear of chondrichthyans presents three sac-like structures at the base of the labyrinth (the lagena, sacculus, and utricle), and two of them are involved in hearing. Inside those structures, hair cells, the *macula neglecta*, and otoconial masses are responsible for transducing external vibrations into electric nerve impulses, participating in the understanding of acoustic signals. Otoconia are also sensitive to accelerations produced by a sound field, helping chondrichthyans to localize sound sources; besides, hair cells move against otoconia of different shapes and sizes, allowing the perception of sound information differing in direction and frequency. The *macula neglecta*, otherwise, is present in the posterior canal ducts of the semicircular canals, and this structure's variation appears to be linked to foraging behavior (Corwin 1978).

Surface piscivorous elasmobranchs tend to have better hearing than deep-sea elasmobranchs due to the presence of a larger sound detection structure (Myrberg 2001). A laboratory experiment showed, through detected behaviors and audiograms, that the tested piscivorous elasmobranchs can detect and be attracted to low-frequency sounds (Myrberg 2001). Furthermore, blacktip sharks' (*Carcharhinus tilstoni*) vestibular hair cells can detect hydrostatic pressure

variations from storms (Heupel et al. 2003). Despite having specializations for sound detection, communication using acoustic signals is not known in chimeras so far (Lisney 2010).

### Laterosensory System Perception

Located around the snout and along the lateral midline, Chondrichthyes present a lateral line canal bearing neuromast organs. These organs are bundles of hair and support cells covered by a gelatinous cupula that are stimulated by water movement or pressure, working as a “distant touch” that enables the detection of water waves compression. Because canals’ neuromasts detect movements generated by other organisms disturbing the water, small-scale flows and pressure changes allow chondrichthyans to navigate, locate prey and predators, and interact with conspecifics during social behaviors (Hueter et al. 2004). There is also some evidence that the lateral line canal system could participate in acoustic detection of low-frequency vibrations (Montgomery et al. 2009). Neuromasts of non-pored canals, contrarily, may function in the tactile perception of contact with the substrate, prey, or conspecifics during social interaction (Gardiner et al. 2012; Maruska 2001).

## Chemical Communication

Chemoreception plays an important role in the behavior of sharks, rays, and chimeras. Odor detection is essential for prey location, navigation, and sexual behavior, linked to the detection of pheromones during reproduction (entry ► “Pheromone”).

### Olfactory Signals

Chondrichthyan olfactory organs are located in chambers at the side, or a sac at the ventral surface of the head, where olfactory hair cells and microvilli are responsible for receiving and transducing chemical signals from the external environment.

When comparing chondrichthyans’ species, olfactory lamellae occur in a smaller number in chimeras, resulting in lower olfactory sensitivity (Boisvert et al. 2019). However, larger olfactory

bulbs configure greater olfactory sensitivity and are present mainly in pelagic, oceanic, and coastal sharks, all of which have a high dependence on smell for migration over long distances (Boisvert et al. 2019). Furthermore, the internostril distance plays a role in directional olfactory detection, in such a way that, when a smell is stronger in one nostril than the other, the animal can orient itself better in the direction of the signal.

### Gustatory Signals

Gustation is related to the chemoreception in body parts that are related to food intake and handling (orobranchial region), being perceived through the oral papillae (which present taste buds and oral denticles). The abundance and distribution of oral papillae might correlate to feeding habits, capturing strategies, and prey processing. The taste buds can be used to find out if a target is a potential prey or not, meeting the criterion for a recognition bite.

Rays with more general diets (entry ► “Chondrichthyes Diet”) have fewer taste buds and comparatively more oral denticles, which is related to a less-specific prey selection (Boisvert et al. 2019). Dissimilarly, some sharks present larger quantities of oral papillae throughout the mouth and in the pharyngeal region, related to a more restricted diet and more specific prey recognition (Boisvert et al. 2019). In chimeras, recent studies show the presence of a palatal organ with low density of taste buds, probably involved in food selection (Ferrando et al. 2016).

## Tactile Communication

For many animals, the act of touching something becomes essential for recognition, communication, and action. In Chondrichthyes, the way to perform this action is directly related to their mouth, that is, the bite.

Altogether with gustation perception, chondrichthyans may use bites for target recognition. In addition, some sharks bite during feeding frenzy: intraspecific biting may work as an agonistic communication during feeding and is common due to the dietary overlap of the competitors (Carrier et al. 2012).

Another biting communication is present during copulation. Among male elasmobranchs, the act of biting to hold a female appears to be universal (Pratt and Carrier 2001). In most observed species, the male elasmobranch bites the female to hold her in a pre-copulatory act, maintaining adequate position and proximity for clasper insertion (Springer 1967). Usually, those bites occur on the fins and flanks. The biting of female sharks on males can also occur during copulation, probably to synchronize the mating sequence and indicate a sexual hierarchy (Gilmore et al. 1983).

## Electrical Communication

Electroreception in Chondrichthyes is due to modified neuromast organs that form a modified ampullary organ, frequently referred to as the ampullae of Lorenzini, that is exquisitely sensitive to low-frequency electric stimuli and detects electric fields of abiotic or biotic origin (Hueter et al. 2004). The electroreception system in chondrichthyans can be divided into two types: passive electroreception, which consists of the detection of low-frequency and continuous current fields, and active electroreception, in which the animal itself presents structures that generate electrical discharges for the perception of the environment (Crampton 2019). Passive electroreception is used for prey detection, recognition of intraspecific communication signals, and environmental orientation, including ocean orientation based on Earth's electromagnetic fields, allowing elasmobranchs to capture information about buoyancy and direction of movements in general (Kramer 1996). Active electroreception, otherwise, can be used to perceive the environment (detecting changes in the electric field generated by the individual itself) but may also play a role in interspecific recognition (Kramer 1996). Nevertheless, the role of electroreception in chondrichthyan communication and navigation appears to be of importance, since the region of electroreception information integration at the telencephalon is usually enlarged (Lisney 2010).

## Conclusion

Chondrichthyes have a wide spectrum of communication behaviors, defined as the interaction between a sender and a receiver (that can be conspecifics or from different species) through a signal. Despite being still poorly understood, within the group there are five communication modes: visual, acoustic and mechanoreception, chemical, tactile, and electrical. Among these modes, there are behaviors related to chondrichthyans' postures, skin color and camouflage, light emission, acoustic and water movement perception, olfactory and gustatory awareness, touch recognition, and electrical perception. However, most of the published behavior studies target just a few species, so that morphological and physiological studies are the main sources of information about Chondrichthyes' communication. Besides, among Chondrichthyes, sharks receive more attention than rays and chimeras in behavioral studies, implying these last groups should be the focus of future studies for new insights on the topic. Therefore, communication in Chondrichthyes presents itself as a broad and valuable field for the consolidation of new research.

## Cross-References

- [Chondrichthyes Diet](#)
- [Chondrichthyes Locomotion](#)
- [Chondrichthyes Morphology](#)
- [Chondrichthyes Navigation](#)
- [Chondrichthyes Sensory Systems](#)
- [Communication](#)
- [Pheromone](#)
- [Vertebrates \(Chordata\)](#)

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## Chondrichthyes Diet

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### Synonyms

Consumption; Feeding; Food; Prey

### Introduction

The class chondrichthyes comprises the sharks, skates, rays, and chimera. Characteristically these fishes lack bone, instead possessing a partly calcified cartilaginous skeleton (Berkovitz and Shellis 2017), giving rise to the name cartilaginous fishes. There are currently in excess of 1200 extant chondrichthyan species globally (Marra et al. 2017). Their evolutionary history dates back to between 400 and 450 million years (Wilga et al. 2007), and they can be classified into Holocephali (chimeras) and Elasmobranchii (sharks and rays), with further subdivisions into Selachii (sharks) and Batoidea (skates and rays) (Compagno et al. 2005). This class of fishes shows a diverse array of morphological, behavioral, and ecological adaptations. They are found globally in both marine and freshwater systems, and the range of their feeding strategies that have shown to be as diverse as the species themselves is of note.

Historically, members of this class of fishes were deemed to be opportunistic feeders (Huber et al. 2019). However, this interpretation has been shown to be incorrect for many species and many have specialised feeding mechanisms that allow them to consume specific prey items. There are a number of feeding mechanisms employed by chondrichthyan species including the use of suction feeding, ram feeding, biting and filter feeding (Moss 1977; Frazzetta 1994), and these are largely influenced by the ecology and behavior of specific species (Huber et al. 2019). Studies on diet within the class chondrichthyes have led to a better

understanding of patterns of migration and movement and have provided insight into the sexual segregation of many species within this class. In addition, the understanding of the dietary requirements for chondrichthyan species can help to inform a better understanding of the trophic interactions of many systems.

It is well documented that species within the chondrichthyes feed at all trophic levels, from plankton through to large marine mammals (Motta and Wilga 2001). Some species have very specific prey preferences. The lemon shark (*Negaprion brevirostris*) was found to prey mainly on teleost fish, while other species, such as the blue shark (*Prionace glauca*), exhibit a more generalist feeding strategy (Harvey 1989; Cortés 1997). Understanding the diet preferences of chondrichthyan species is complex and changes in diet can occur not just specifically between species, but also ontogenetically, seasonally or geographically within a species (Cortés 1997; Heithaus 2004). The tiger shark (*Galeocerdo cuvieri*) is one such example and is generally considered an opportunistic feeder. This species has been shown to demonstrate an ontogenetic dietary shift. As juveniles the diet consists largely of teleosts and cephalopods with the diet encompassing a wider range of prey items including elasmobranchs, turtles, and crustaceans as individuals mature (Motta and Wilga 2001). The school shark (*Galeorhinus galeus*) was found to exhibit both an ontogenetically and seasonally varied diet with both juveniles and adults showing diverse consumption. Juveniles were shown to prey largely on benthic invertebrates, while adults consumed mainly squid (Lucifora et al. 2006). Prey selection within this species also found to change throughout the year with benthic teleosts being the main prey item for adults from December to February, with increased consumption of squid again from March to April (Lucifora et al. 2006).

It has been documented that feeding in some chondrichthyan species does not take place consistently, but occurs in short bursts. These are often followed by a period of reduced feeding while the consumed prey are digested (Weatherbee and Cortes 2004). This is certainly

true for many of the larger sharks and early reports suggested that sharks generally consume between 3 and 14% of their body weight per week (Budker 1971). The dietary intakes of many more chondrichthyan species have been studied since this report and estimates have been given for weekly intake values for a number of species. For elasmobranch species these values range between 0.2% and 4.34%  $\text{bw}^{-1}$  (Weatherbee and Cortes 2004). Many of these figures are derived from captive species, where observations of feeding can be made. Pups of captive broadnose sevengill sharks (*Notorynchus maculatus*) consumed approximately 2% body weight in food daily, whereas juveniles and adults had a much lower rate of consumption at 0.6% and 0.2% body weight per day respectively (Van Dykhuizen and Mollet 1992). Few estimates of food intake for holocephalans have been proposed due to limited specimens in captivity. However, daily consumption rate of the cockfish (*Callorhynchus callorhynchus*) estimated that an adult would consume approximately 1.4% of its body weight per week, similar to those figures calculated for a cold-water elasmobranch species (Di Giacomio et al. 1994).

## Filter Feeders

It is widely recognized that some of the largest species of fish on the planet consume planktonic organisms. There are currently noted to be 13 filter feeding species within the class chondrichthyes. The whale shark (*Rhincodon typus*), basking shark (*Cetorhinus maximus*), megamouth shark (*Megachasma pelagios*), manta ray (*Manta birostris*), and all nine species of devil ray (genus *Mobula*). Despite demonstrating a characteristic method for consuming prey the mechanisms by which these species feed has been shown to vary as has the target prey. For such large organisms it is clear that individuals require high density patches of prey to make feeding viable energetically (Rohner et al. 2013). Increasingly the diets of these species are being studied in order to better understand the evolution and ecology of the study organisms. Specific

feeding behaviors exhibited by a number of large chondrichthyan species have helped to explain some of the patterns of movement demonstrated in certain populations.

Multiple studies have been carried out for the largest fish in the ocean, *R. typus*. One such study observed ram filter feeding in *R. typus* in the Yucatan Peninsula, Mexico, which is considered the largest site of whale shark aggregations globally (Motta et al. 2010). The sharks were observed to seemingly seek out aggregations of plankton containing the largest organisms and would repeatedly turn to remain in contact with densely populated aggregations of plankton. Plankton samples collected around the feeding sharks indicated that the sharks were targeting aggregations that were dominated by a range of planktonic organisms that included sergestid shrimp, calanoid copepods, chaetognaths, and fish larvae (Motta et al. 2010). Plankton samples taken from up to 10 km away from where the sharks were observed to feed were found to contain aggregations dominated by calanoid copepods, fish larvae sergestid shrimp and chaetognaths (arrow worms), suggesting that sergestid shrimp are a crucial element of the diet for this species.

Similar observations were made for *R. typus* captured off the coast in Tanzania. Analyses of the stomach contents determined that mysid and sergestid shrimp along with copepods were the main prey item found in the stomachs of these individuals (Rohner et al. 2013). An interesting observation made during this study is that *R. typus* was found to shift their diet diurnally, presumably to fully utilize the varying nutritional availability, feeding at the surface in coastal waters while remaining close to shore and feeding in deeper waters on deep-water zooplankton and fishes when undertaking long distance migrations (Rohner et al. 2013). Further to these findings Borrell et al. (2011) suggested that not only do *R. typus* show diversity of feeding with proximity to the shore, but observations based on a small number of specimens suggest that this species could possibly show differences in diet based on sex.

It would appear from the literature that *R. typus* also shows specific and targeted feeding at certain

times of year to maximally utilize the prey that are available. *R. typus* observed in the Gulf of Mexico were noted to feed in areas rich with mid-embryonic phase fish eggs, with  $5 \times$  higher levels of fish eggs recorded in the water where feeding took place than at control sites (Hoffmayer et al. 2007). Similar findings were reported by (de la Parra et al. 2011) who studied the Afuera aggregation of whale sharks, north of Cabo Catoche, off Isla Holbox on the Yucatán Peninsula of Mexico. The research also discovered that *R. typus* was feeding on aggregations of fish eggs. Genetic analyses of the fish eggs in both studies revealed that the eggs were little tunny (*Euthynnus alletteratus*) and it was surmised by Hoffmayer et al. (2007) that the feeding by *R. typus* was timed to coincide with the spawning of *E. alletteratus* given the developmental stage of the embryos. Aggregations of *R. typus* in Belize were also observed to feed on newly spawned fish eggs, including those of cubera snappers (*Lutjanus cyanopterus*) and dog snappers (*Lutjanus jocu*) (Heyman et al. 2001).

The same feeding patterns have been observed for other megaplanktivores. The second largest fish in the sea, *C. maximus*, were observed to forage in relation to thermal fronts, actively feeding in areas where dense aggregations of zooplankton were observed, remaining for up to 27 h within large aggregations of zooplankton that exceeded  $1 \text{ g m}^{-3}$  (Sims and Quayle 1998). Basking sharks were also observed to surface-feed on aggregations of calanoid copepod that are 2.5 times as dense ( $\sim 1500$  organisms per  $\text{m}^3$ ) and 50% longer ( $\sim 2 \text{ mm}$ ) compared to areas where feeding doesn't take place. It seems that *C. maximus* will selectively forage for specific aggregations of their preferred zooplankton species (Sims and Quayle 1998) and appear to be highly specialized feeders (Sims and Merrett 1997). Such is the specific nature of the feeding that *C. maximus* were also found to demonstrate diel vertical migration (DVM) reportedly in response to prey densities. It appears that *C. maximus* feed on copepods (*Calanus* spp.) and euphausiids (krill) and follow the diurnal movements to actively feed on these species (Sims et al. 2005). Other studies suggest that

*C. maximus* favor *Calanus* as a preferred prey item. Plankton samples collected close to feeding individuals in the English Channel off Plymouth were shown to be dominated by calanoid copepods, specifically *Calanus helgolandicus* (Sims and Merrett 1997).

The diet of several ray species have also been examined and in some species similar feeding patterns to *C. maximus* were observed, whereby one prey item dominated the diet. Almost 62% of the diet of the reef manta ray (*Manta alfredi*) was found to consist of calanoid copepods, whereby it appears to actively seek out large aggregations of these species (Bennett et al. 2016). The bentfin devil ray (*Mobula thurstoni*) and spinetail devil ray (*Mobula japonica*) in the Southwest coast of the Gulf of California were found to feed mainly on *Nyctiphanes simplex*, the most abundant euphausiid in the seas of that area (Sampson et al. 2010). The stomach contents of the giant manta ray (*Manta birostris*), Chilean devil ray (*Mobula tarapacana*), spinetail devil ray (*Mobula japonica*), and smoothtail devil ray (*Mobula thurstoni*) from the Bohol Sea, Philippines were examined, and no trophic separation between the species was found with 91% of examined stomachs containing the krill, *Euphausia diomedea* (Rohner et al. 2017). This suggests that planktivorous rays also follow a pattern of discriminate feeding, seeking out dense aggregations of larger individuals of their favored prey.

## Pelagic Feeders

Despite all megaplanktivores within the class chondrichthyes feeding pelagically the mechanisms by which they harvest prey differ significantly from those that actively hunt highly motile organisms. Many chondrichthyan species inhabit the pelagic zones of the world's oceans and hunt larger prey items. Determination of the diet of chondrichthyans that forage in open water and consume larger prey has proven to be more complex than it first appeared. Much of the information is determined from analyses of the stomach contents of captured sharks with few visual

observations of feeding activity. The information on diets for open-water chondrichthyan species is relatively scarce, but what is apparent is that most of those studied were found to have consumed a variety of prey items, but in most cases teleost fishes dominated the diet. Notable among the research is that alongside a mainly piscivorous diet many species were also found to consume cephalopod species, mainly pelagic squid. Dietary overlap was discovered for several species of pelagic shark (bronze whalers (*Carcharhinus brachyurus*), dusky sharks (*Carcharhinus obscurus*), and smooth hammerheads (*Sphyrna zygaena*)) (Rogers et al. 2012). However, in some species which are highly migratory, including the common thresher (*Alopias vulpinus*) and the shortfin mako (*Isurus oxyrinchus*), the diet appears more specialized.

Some species, such as the white shark (*Carcharodon carcharias*) and the tiger shark (*Galeocerdo cuvier*) were found to be versatile in their feeding, consuming a wide range of prey items. A recent report into the diet of *G. cuvier* noted the presence of up to 10 species of terrestrial passerine bird in 39% of the sharks examined (Drymon et al. 2019) an unexpected finding considering the aquatic prey available. It is also of note that in some species, such as *C. carcharias*, there is an ontogenetic shift with smaller sharks consuming a different diet from that of adults. It has been observed that individuals up to 3 m in length tended to prey predominantly on fish, whereas beyond this size diet was dominated by pinnipeds and cetaceans (Tricas and McCosker 1984). Other research has concurred with these findings but note that in some cases *C. carcharias* above 5 m in length have been shown to contain only teleost fish and chondrichthyan species in their stomachs, often as a result of limited availability of marine mammal prey (Malcolm et al. 2001). The same ontogenetic shift in diet has been noted for *G. cuvier*. As the length of the sharks increased, the incidence of teleost and cephalopod prey items was found to decrease, with larger sharks preying on elasmobranchs, turtles, land mammals and crustaceans (Lowe et al. 1996). What is clear from the literature is that most chondrichthyan species that feed in open water

will diversify their diet depending on the availability of food. This diversity of feeding has been noted in a number of pelagic species belonging to the class chondrichthyes. The studies comprise investigations mainly into the diets of shark species as this group of fishes has many species that form part of pelagic communities. These species are able to chase and hunt down prey and have adapted to feed on faster-moving individuals.

Research carried out on thresher sharks has shown that the diet is largely dominated by teleost fish (Smith et al. 2008). *A. vulpinus* is noted to feed on small- to medium-sized fish, including anchovy, hake, mackerel and sardine and will supplement its diet with pelagic invertebrates, such as squid (Smith et al. 2008). Investigations into the stomach contents of 165 *A. vulpinus*, captured off the Californian coast, concur with this. Northern anchovy (*Engraulis mordax*) constituted the main prey, followed by Pacific hake (*Merluccius productus*), Pacific mackerel (*Scowbey japonicus*), and Pacific sardine (*Sardinops sagax*) (Preti et al. 2001). Market squid (*Loligo opalexens*) and pelagic red crab (*Pleuroncodes planipes*) were also found to have been consumed (Preti et al. 2001) but in much less quantity and fewer individuals. Further investigation into the stomach contents of 225 *A. vulpinus*, captured in the Californian current, recorded *E. mordax* to be the most highly consumed prey item, followed by Chilean pilchard (*Sardinops sagax*) (Preti et al. 2012). Similar to earlier findings by Preti et al. (2001) the research also revealed the presence of other teleost species including *M. productus* and *S. japonicus* plus two cephalopod species, *Loligo opalexens* and the jumbo squid (*Dosidicus gigas*) (Preti et al. 2012).

Similarly, the big eye thresher (*Alopias superciliosus*) is noted to feed on hake, squid, scombrids (mackerels and tunas), alepisaurids (lancetfish), clupeids (herrings and sardines), istiophorids (marlin), and elasmobranchs (Smith et al. 2008). Research into the stomach contents of 28 individuals captured off the coast of California noted that teleosts of the family barracudinas (Paralepididae) were the most consumed prey and considered the most important (Preti et al.



2008). This was followed by *M. productus*, Pacific saury (*Cololabis saira*), *S. japonicus*, and *E. mordax*. In contrast to the stomach contents of *A. vulpinus*, eight taxa of cephalopods were identified, with *D. gigas* being the dominant cephalopod prey (Preti et al. 2008). In contrast to this research carried out on specimens of *Alopias* spp. from Peru found that the stomach contents of 128 thresher sharks showed a diet consisting of prey from 10 taxa, but suggested that the diet was generally dominated by *D. gigas* (González-Pestana et al. 2019).

Studies on the stomach contents of another pelagic species, the shortfin mako, have determined that there is geographical separation in terms of diet for this species. According to the research, specimens of *I. oxyrinchus* from the Northwest Atlantic and Australia followed a similar pattern to that of the thresher sharks, consisting mainly of teleost fishes and cephalopods (Stillwell and Kohler 1982; Stevens 1984; Maia et al. 2006). For some specimens sampled off the Australian coast it was noted that large pelagic teleost and cephalopod prey dominated, although a variety of other species were noted including scombrids and short beaked common dolphin (*Delphinus delphis*) (Rogers et al. 2012). Specimens of *I. oxyrinchus* sampled off the coast of California were found to differ in their consumption, with *D. gigas* being of higher importance, followed by *C. saira* (Preti et al. 2012). Other prey were also detected in these specimens with sardines, mackerel, and mullet being present. In addition, several individuals had been observed to consume elasmobranchs, including blue sharks (*Prionace glauca*) and marine mammals including *D. delphis* (Preti et al. 2012). In contrast, shortfin makos captured off the coast of South Africa were found to consume prey dominated by small elasmobranchs, which constituted almost 80% of the stomach contents of those specimens examined (Cliff et al. 1990).

The diet of the white shark has been well studied and it is known to be a versatile predator. As the third largest extant fish species, adult *C. carcharias* require high energy inputs to maintain growth and functionality. Much research has been undertaken into the feeding habits of

*C. carcharias* which have led to a much greater understanding of the ecology and behavior of this species. As previously noted smaller individuals consume prey consisting mainly of fish (Tricas and McCosker 1984) including both demersal and pelagic teleost species (Casey and Pratt 1985). Specimens of *C. carcharias* recovered from beach protection shark nets in South Africa were shown to consume a diverse range of prey from a number of functional groups, including elasmobranch, mammals, teleosts, and cephalopods (Hussey et al. 2012). Juvenile and adult *C. carcharias* have also been shown to scavenge on carcasses of whales (Carey et al. 1982; McCosker 1985; Long and Jones 1996; Dudley et al. 2000; Dicken 2008; Fallows et al. 2013) further demonstrating their opportunistic nature.

There are a large number of pelagic shark species that have been investigated in terms of diet preferences and many of these have similar feeding strategies, whereby the preferred food items consist of teleost fish, followed by cephalopods. The porbeagle (*Lamna lamna*) (Francis et al. 2008) and blue shark (Nakano and Stevens 2008) are two of note that have been widely studied. Other less well studied pelagic species appear to have a more defined piscivorous diet, such as the silky shark (*Carcharhinus falciformis*) (Compagno 1984), which has been noted to consume a wide range of species fish species including yellowfin tuna (*Thunnus albacares*), albacore (*Thunnus alalunga*), and scomber species (Bonfil 2008). The oceanic white tip (*Carcharhinus longimanus*) has also been shown to consume a wide variety of fish species, but more diverse taxa have been observed in the stomach of this species, including stingrays, seabirds, turtles, and marine gastropods and crustaceans (Compagno 1984). It would appear that for most pelagic feeding chondrichthyes teleost fishes alongside cephalopods are the mainstay of their diets, supplemented by a number of other taxa as opportunity presents itself.

## Benthic and Demersal Feeders

A large number of sharks, skates, rays, and chimaera are benthic and feed on or above the seabed.



These feeding strategies often result in a diversity of feeding. Some small benthic shark species are known to scavenge and the lesser-spotted catshark (*Scyliorhinus canicula*) has been shown to feed widely on the discards from fishing vessels (Olaso et al. 1998). The diverse range of feeding strategies allow members of the class chondrichthyes to adapt to a range of habitats globally and means that many benthic species are highly adapted to a number of environments.

Food consumption in the chimera has been little studied, mainly due to the fact that many species occur at depths below 500 m, although several reports do exist. It appears that many species within the Holocephali feed on the epibenthos, indicating a benthic lifestyle. The stomach contents of the cockfish (*Callorhynchus callorynchus*) captured in the northern San Matías Gulf, Argentine Patagonia were examined, with 50% of prey consumed consisting of scallops with a wide variety of other taxa making up the rest of the diet (Di Giácomo et al. 1994). The diet of the rabbitfish (*Chimaera monstrosa*) has been studied from specimens from the Mediterranean and New Zealand. Individuals from New Zealand were found to prey upon a wide range of organisms which comprised echinoderms, decapods, crustaceans, and polychaetes with evidence of consumption of infaunal species (Macpherson 1980). Didier (1998) examined the stomach contents of the *C. monstrosa* from the Mediterranean and noted that marine worms and mussels dominated the diet of this population. The stomach contents of the ratfish (*Hydrolagus collieri*) suggest that like many benthic species they consume a wide spectrum of food items. It was noted that smaller individuals had a more specialized diet, feeding largely on polychaetes, with a wider range of taxa found in the stomach of adults (Quinn et al. 1980). Decapods, bivalves, crustaceans, mollusks, annelids, echinoderms and algae were identified (Quinn et al. 1980). The cape elephantfish (*Callorhynchus capensis*) also demonstrated a wide dietary preference, preying mostly on benthic invertebrates. Remains of many taxonomic groups were found in stomach contents, including bivalves, crustaceans, gastropods, sea urchins, polychaetes and teleost fishes (Freer and Griffiths

1993). It appears that from every report of the dietary intake of chimera that these are diverse feeders and will adapt their feeding strategies to suit the availability of prey.

A review of the published literature revealed that most skate species show a dietary preference predominantly of decapods and fishes, followed by amphipods and polychaetes (Ebert and Bizzarro 2007). Two skate species from the Western Mediterranean followed this pattern but differed in their choice of prey. Stomach contents of the blonde ray (*Raja brachyuran*) and the brown ray (*Raja miraletus*) revealed that juvenile *R. brachyuran* fed mostly on crustaceans, but as they matured the diet shifted to become dominated by bony fishes. For the brown ray the diet appeared to remain consistent, with crustaceans being the main prey of all size classes (Follesa et al. 2010). A similar pattern of feeding was also noted in the Antarctic starry skate (*Amblyraja georgiana*). The stomach contents of 206 individuals were examined and the dominant prey, particularly of larger individuals was found to be fish, followed by Antarctic krill (*Euphausia superba*). In addition this species was also shown to have a varied feeding regime with amphipods, polychaetes, and other benthic fauna being identified as having been consumed (Main and Collins 2011). An analysis of the stomach contents of broadnose skate (*Bathyraja brachyurops*) from the coast of Argentina revealed teleost fish as the main part of their diet, followed by isopods (Belleggia et al. 2008). There are a numerous studies on the feeding ecology and behavior of members of the skate family and the feeding preferences show a similar pattern, whereby fish and crustacean species appear to dominate. Once again, a common theme of these fishes is the diversity of feeding habits shown across a number of species.

A large number of benthic shark and ray species found globally have been investigated to determine diet preferences in order to get a better understanding of the ecology of the species studied and to better understand their role in marine ecosystems. Many of these examine depth stratification, size-related feeding, or feeding related to specific habitats. In a study from the Balearic Sea

in the Mediterranean, the stomach contents of eight demersal elasmobranch species, consisting of three shark and 5 batoid species, were examined (Valls et al. 2011). The sharks (velvet belly lanternshark (*Etmopterus spinax*), lesser-spotted catshark (*Scyliorhinus canicula*), and the blackmouth catshark (*Galeus melastomus*)) and rays (common eagle ray (*Myliobatis Aquila*), cuckoo ray (*Leucoraja naevus*), speckled skate (*Raja polystigma*), brown ray (*Raja miraletus*), and thornback (*Raja clavata*)) were found to differ slightly in their feeding habits. This was found to relate to the position of the species in relation to the continental shelf and slope. The research regarding habitat position showed differences in feeding strategies, with those species inhabiting the continental shelf consuming prey mostly comprising crustacean and teleost species, while those inhabiting the slopes were found to consume higher densities of euphausiids and cephalopods (Valls et al. 2011). The same trend appears to be apparent in other ray species. The marbled electric ray (*Torpedo marmorata*) from the Northern Mediterranean was found to have a predominantly teleost-based diet, with the presence of some cephalopods observed in the stomachs of some species (Capapé et al. 2007). The thornback ray (*Raja clavata*) also feeds mainly on teleosts although a large part of the diet is made up of crustaceans and cephalopods (Kadri et al. 2014). The research found that *R. clavata* also consumed a number of gastropod and polychaete species, although these were found in much smaller numbers and were found to be consumed only occasionally (Kadri et al. 2014). Ontogenetic shifts in diet have been observed in ray species. The diet of *R. clavata* showed significant changes, with crustaceans constituting the greatest proportion of the diet of smaller rays (Kadri et al. 2014). In the undulate ray (*Raja undulata*) a dietary ontogenetic shift was found to occur based on the length of individuals, classed in to three distinct length groups (200–550 mm; 550–750 mm and 750–1000 mm). The diet was seen to shift as the rays increased in length, with smaller individuals consuming large numbers of small, semi-pelagic fish and larger individuals switching to large benthic prey as they increased in size.

As with the skates, rays, and chimera, a number of shark species are also benthic and feed on demersal or benthic prey. The blackspotted smoothhound (*Mustelus punctulatus*) shows an overlap with a number of ray species where its diet is concerned, consuming mainly crustaceans teleost and mollusk species. Again, the prey consumption is diverse, and a number of taxa are consumed, with polychaete, sipunculid, echinoderm, and tunicate remains discovered in the stomachs of this species. As with many species discussed here there is also an ontogenetic shift in diet as individuals grow with a shift from crustaceans to teleosts and then to mollusks (Saidi et al. 2009). In the epaulette shark (*Hemiscyllium ocellatum*), a stomach content analysis revealed the consumption of five groups of prey item. Worms and crabs were found to be the most consumed groups, constituting over 91% of the diet, with lesser species consumed being shrimps, small fishes and amphipods (Heupel and Bennett 1998). Examination of the stomach contents of the port Jackson shark (*Heterodontus portusjacksoni*) showed that this species is a highly opportunistic feeder and that the dietary intake of this species was high. The research revealed that this species consumed prey from 32 taxa although the diet was dominated by mollusks, teleosts, and cephalopods. As with many other species documented here investigation into ontogenetic shift revealed that diet differed significantly by ontogenetic stage. Juveniles and subadults were shown to have diets made up largely of benthic infauna and epifauna. Adult diets were found to be dominated by demersal/pelagic prey (Powter et al. 2010).

## Conclusion

The examples provided here offer a glimpse into the diets of a number of chondrichthyan species, and many more examples exist within the literature. What is apparent is that far from being opportunistic and mindless predators many species with the class chondrichthyes are rather more sophisticated and selective in their feeding preferences. Many are opportunistic in as far as they will

change their prey depending on environmental, migratory, or geographical factors, but will seek out the most appropriate items to consume given the prey available. In addition, it is clear that for many species there is a clear ontogenetic shift in diets as individuals grow and mature, possibly due to the higher energy requirements of larger individuals. From the literature, it is also evident that there is a clear dietary overlap for a large number of chondrichthyan species and similarities with species that inhabit similar habitats. There also appears to be some diversity in feeding between species that inhabit geographically differing habitats. Many of the studies examined the differences between sexes and depth segregation and the answers here are not as clear-cut. In most cases, the diets did not differ between the sexes, but there were more differences in depth segregation and this relates to the availability of prey within specific environments. What is apparent from the large body of literature available is that members of the class chondrichthyes are extremely efficient and highly adapted predators which has enabled them to survive in a range of diverse habitats.

## Cross-References

- [Arthropod Navigation](#)
- [Bear Diet](#)
- [Canine Diet](#)
- [Carnivore \(Diet\)](#)
- [Cephalopod Diet](#)
- [Cetacean Diet](#)
- [Crocodilia Diet](#)
- [Platyrrhine Diet](#)
- [Squamata Diet](#)

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## Chondrichthyes Locomotion

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## Synonyms

Ray locomotion; Shark locomotion; Skate locomotion

## Definition

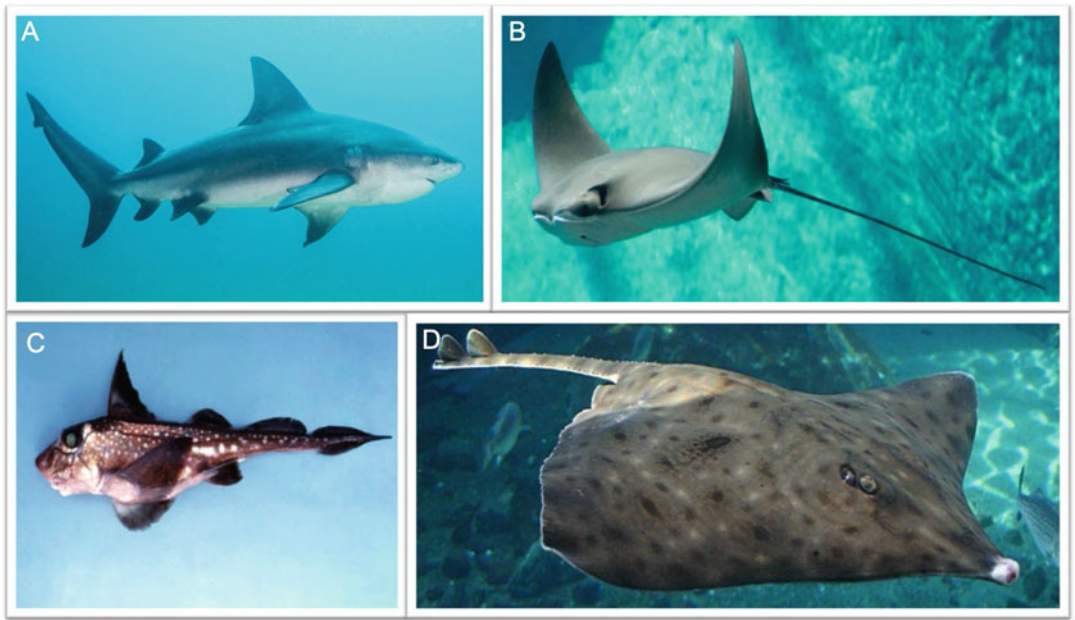
Movement used by sharks, rays, skates, and chimaeras to traverse their environment.

The class Chondrichthyes is comprised of sharks, rays, skates, and chimaeras. They are among the oldest jawed vertebrate fish (de Bellard 2016). Chondrichthyans are classified as cartilaginous fish because they lack boney structures and instead contain a partially calcified cartilaginous skeletal structure. Historically over 1,200 species have been identified globally, dating as far back as 400–450 million years. The Chondrichthyes class is further divided into two subclasses: *Elasmobranchii* (sharks, rays, skates, and sawfish) and *Holocephali* (chimaeras, or ghost sharks). The *Elasmobranchii* are further subdivided into *Selachii*, or sharks, and *Batoidea*, including skates and rays (Crooks 2019) (Fig. 1). Chondrichthyes have adapted to a variety of water systems globally, including marine and freshwater, and their feeding behavior reflects that diversity. Species within Chondrichthyes are well known to feed at all trophic levels, ranging from plankton to marine mammals (Crooks 2019). As a result of the diversity in geographical location, feeding behavior, and body forms, chondrichthyans have developed a wide variety of locomotive behaviors. This entry will discuss general and alternative modes of locomotion, as well as how the study of these animals has progressed human innovation.

## Major Locomotor Modes

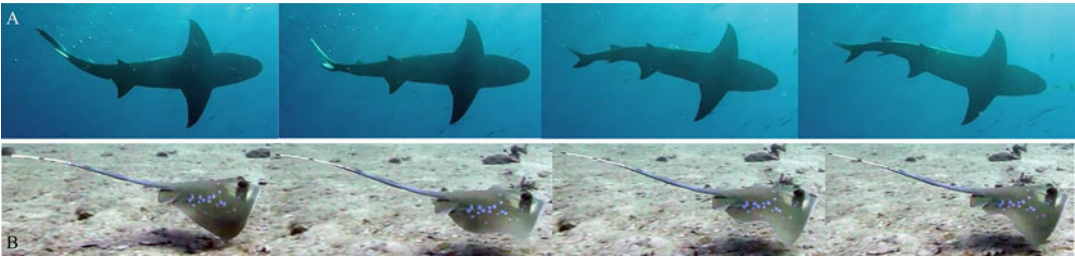
Sharks are highly adapted for high-speed locomotion and precision maneuvering through the water. While there are a great range in body forms, all sharks use generally similar swimming biomechanics. Rotation around the body's longitudinal axis allows all sharks to create wave-like undulations of the caudal fin (Lauder and Wilga 2000) (Fig. 2). The movement of the caudal fin generates force that propels the animal forward. Current literature suggests that the caudal fin, or heterocercal tail, is the most important component of movement for allowing horizontal thrust. This structure is unique because the upward bend of the axis of the notochord creates an asymmetrical shape to the caudal fin (Thomson 1976). The asymmetry of the heterocercal tail, along with the positioning of





**Chondrichthyes Locomotion, Fig. 1** Representative species of the class Chondrichthyes. (a) *Carcharhinus leucas*, the Bull Shark. (b) *Rhinoptera bonasus*, the

Cownose Stingray. (c) *Hydrolagus colliei*, the Spotted Ratfish. (d), *Dipturus laevis*, the Barndoor Skate



**Chondrichthyes Locomotion, Fig. 2** (a) Shark swimming is characterized by longitudinal rotation of the body that creates undulations of the caudal fin in most sharks. This movement generates forward thrust of the animals. (b)

The bluespotted ribbontail ray (*Taeniura lymma*), showing undulations of the pectoral fins that can be seen in a variety of batoid species

the lateral pectoral fins, produces a net upward or “lifting” force. The weight of the fish counteracts this upward force to allow uniform horizontal locomotion (Thomson and Simanek 1977).

The paired pectoral fins, located between the head and caudal fin, likely play a role in ascending, descending, and rolling maneuvers. Through the observation of leopard sharks, *Triakis semifasciatus*, it has been determined that the positioning of the pectoral fins can create positive or negative lift, causing the body angle of the shark

to change and thus resulting in an increase or decrease in depth, respectively (Lauder and Wilga 2000, 2002). Minor changes in the relative positioning of the pectoral fins allow for sharks to make quick and agile maneuvers in the water. The reliance on the caudal fin as a driver of locomotion in sharks may explain the highly adapted shape of this structure. In contrast, the more simplified shape of the pectoral fins may be explained by their use for less drastic changes in relative position of the animal.

Batoidea are a group of cartilaginous fish that are closely related to sharks and are comprised of rays and skates. Anatomically, these organisms differ from sharks in that their bodies are dorso-ventrally compressed with enlarged pectoral fins that span the length of the body and fuse to the head (Hall et al. 2018). As a direct result of this unique body structure, these organisms use their pectoral fins as the main driver of locomotion. Two major locomotive behaviors have been described in these animals. The first, termed “rajiform,” is an undulatory motion of the pectoral fins, and is defined by having multiple waves present on the pectoral fin at a given time (Rosenberger 2001; Breder 1926) (Fig. 2). This behavior is used by skates and rays and appears to be important during feeding and other activities that occur close to the floor of the ocean, as it is not ideal for long-distance swimming (Hall et al. 2018). The second behavior, termed “mobuliform” is an oscillatory “flapping” of the pectoral wings used by manta rays and other pelagic batoids, and is described as having no more than one-half of a wave present on the pectoral fin at a given time (Rosenberger 2001; Webb 1994). With each stroke, the pectoral fin is angled precisely with respect to the water such that it is able to create lift, which in turn translates to propulsion of the animal (Rosenberger and Westneat 1999). This form of movement is specifically advantageous for animals that feed in open waters, as it lends the ability to swim faster and more steadily (Fontanella et al. 2013). While these two swimming patterns have been classified separately, it is likely that organisms utilize a combination of undulation and oscillation on a continuum dependent upon the behavior and locomotive goal of the animal (Rosenberger 2001).

Chimaeras, comprising the group Holocephali, rely solely on their pectoral fins to produce movement (Combes and Daniel 2001). Unlike sharks, the caudal fin remains rigid during swimming and it is not thought to contribute to forward movement (Higham et al. 2018). Moreover, the locomotion of Chimaeras is unique in the fact that both oscillatory and undulatory motions are observed in the pectoral fin movement of these animals (Combes and Daniel 2001). As the pectoral fin is

flapped in an oscillatory manner, an undulatory wave travels down the pectoral fin from anterior to posterior (Combes and Daniel 2001; Wilga and Lauder 2000). A study of the spotted ratfish (Foster and Higham 2010), *Hydrolagus colliei*, suggests that these animals have adapted larger abductor and adductor muscles that are responsible for movement of the pectoral fin, as compared to the spiny dogfish, *Squalus acanthias*. Dogfish, which are more closely related to sharks, rely on undulations of the caudal fin to produce thrust (Foster and Higham 2010; Wilga and Lauder 2002). It is possible that the enhancement of these muscles is necessary to facilitate precision maneuvers while navigating their environment and supports the observations of their reliance on pectoral fins for movement.

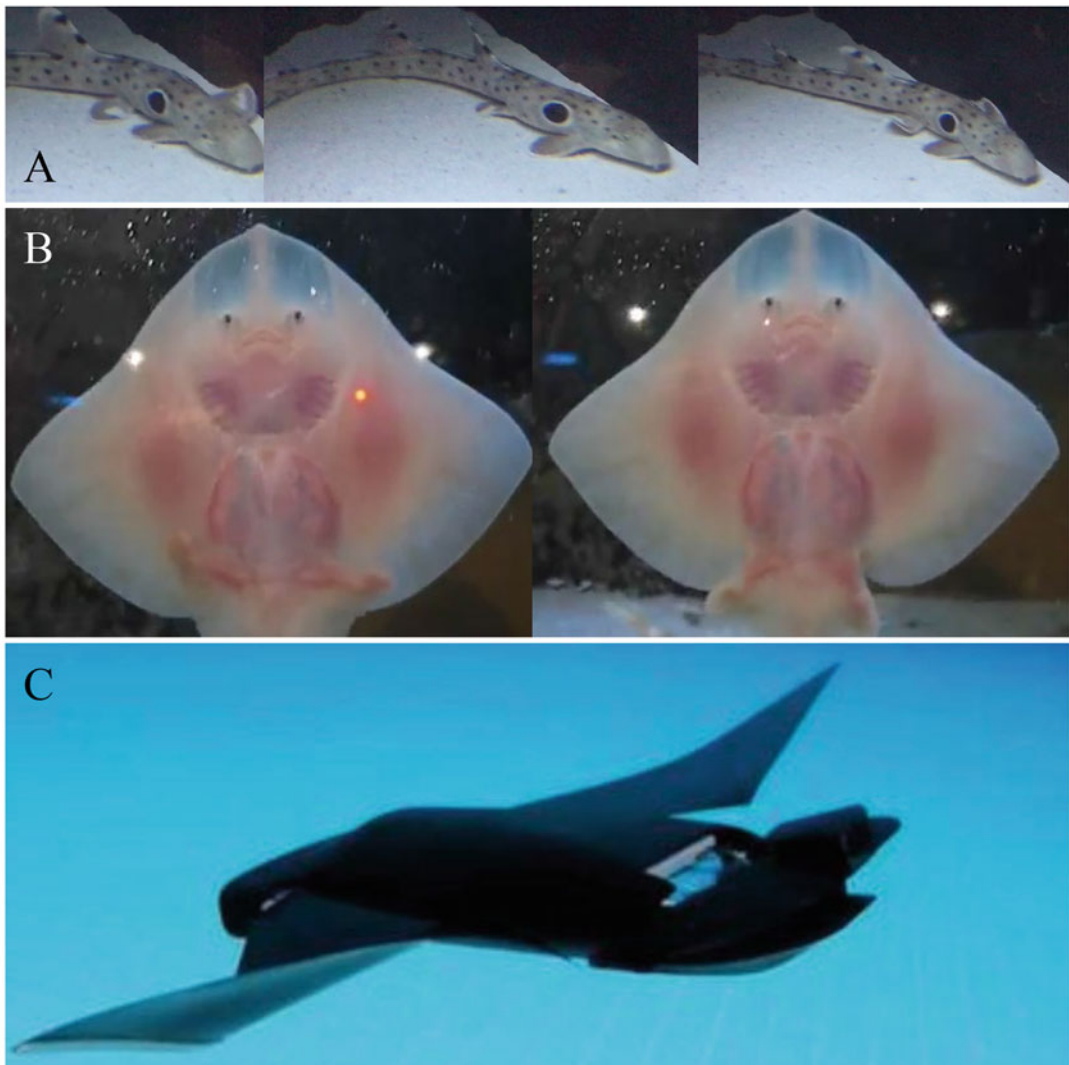
Chondrichthyans are widely distributed through the oceans of the world; however, as ocean depth increases, they become scarcer, and are thought to be absent at ocean depths greater than 4,000 m (Priede et al. 2006). One possible explanation (Treberg and Speers-Roesch 2016) for this observation is the reliance on high-speed locomotion for hunting. This requires vast amounts of energy, which may not be available at depths greater than their current zone of habitation. Treberg and Speers-Roesch (2016) also noted that chondrichthyans maintain high levels of lipids in their liver, possibly to control buoyancy and aid in locomotion. The group reported a correlation of increased accumulation of buoyancy-specific lipids, such as squalene, in species that are more suited for deeper water, and higher concentration of energy-specific lipids in shallow water species, that rely on continuous movement to maintain buoyancy. The data presented represents an excellent example of an evolutionary trade-off, and may help explain why a majority of these animals occupy shallower waters where food sources are more abundant.

## Alternative Locomotive Strategies

While sharks are commonly renowned for the speed and agility of their swimming, they also possess some impressive alternative forms of locomotion. Some species of sharks have

specialized their fins such that they can “walk” on the bottom of the ocean. *Hemiscyllium ocellatum*, also known as the epaulette shark, is one such species which uses both its pectoral and pelvic fins for locomotion (Fig. 3). Initial studies into this behavior show that epaulette sharks walk only in short bursts when submerged before they change their direction of movement or speed. Analysis of their gait pattern demonstrates two

important principles. First, the epaulette shark’s locomotion shows alternating function of the pelvic and pectoral fin pairs consistent with a lateral sequence diagonal couplet symmetrical gait pattern (Hildebrand 1989). Second, there is a strong relationship between the movement of the pectoral fin and movement of the head. When the left pelvic fin’s musculature is activated, the right pectoral fin advances, stimulating the head to



**Chondrichthyes Locomotion, Fig. 3** (a) *Hemiscyllium ocellatum*, the epaulette shark, walking on the bottom of the ocean. The animal engages both its pectoral fins and pelvic fins to traverse across the ocean floor. (b) Punting behavior of stingrays. The animal utilizes its pelvic fins,

along with undulation of the pectoral fins, to traverse across the ocean floor. (c) Picture of an AUV, termed MantaDroid, that was inspired by the anatomy of batoids, designed by a team of researchers at the National University of Singapore

move both laterally right toward the pectoral fin and vertically down toward the ocean floor. This triggers subsequent activation of the right pelvic fin, progressing the left pectoral fin forward and leading the head to move back upward to midline, before repeating the downward curvilinear motion to the left. During this process, the head never contacts the ground. In contrast, the tail also exhibits lateral motion with forward pectoral movement, but remains in contact with the ground throughout the cycle. The range of the tail's lateral motion increases with speed of movement, traveling further laterally with faster speeds to prepare for transition into swimming (Pridmore 1994).

Batoids also display an alternate form of locomotion to swimming, which has been described as punting. A punt is a specialized form of locomotion similar to a jump. While batoids propel themselves with their large pectoral fins during swimming, punting is characterized by involvement of their smaller pelvic fins. During the punt, batoids will sweep their pelvic fins anteriorly and plant them into the ground. This maneuver propels the body anteriorly, by pushing off of the bilateral pelvic fins (Macesic et al. 2013). There are two different forms of punting found in batoids distinguished by the extent of involvement of these pelvic fins. "True punting" is done using only the pelvic fins, while "augmented punting" uses both pelvic and pectoral fins for propulsion. True punters rely only on their pelvic fins for propulsion because the musculature surrounding their pelvic fins has undergone greater specialization than that of augmented punters, particularly the propterygium depressors and elevators (Macesic and Kajiura 2010). This enables them to travel further with each punt. Because augmented punters lack specialization of the propterygium muscles, they have developed the compensatory method of supplementing propulsion with the pectoral fin movement. In this technique, the pelvic and pectoral fins activate at the same time, with the pelvic fin pressing into the surface and the pectoral fins undulating in a manner resembling the undulatory swim pattern seen in some species. The pectoral fin reaches maximal height just before the pelvic fins are fully

extended, ending the thrust phase and entering the recovery phase (Macesic et al. 2013) (Fig. 3).

Studies regarding the walking and punting of aquatic species have received significant attention in recent years, as it is believed that the first terrestrial species evolved from underwater walking locomotion before transitioning to land. The alternating left/right movement of the limbs indicate that sharks and rays are likely utilizing ancient neuromuscular patterns that are shared with quadrupedal tetrapods (Jung et al. 2018).

## Locomotor Migrations

The waters of Southeast Florida see an enormous seasonal influx each year as massive aggregations of migrating blacktip sharks (*Carcharhinus limbatus*) enter the nearshore waters in the winter. Over a 4-year period from 2011–2014, shark abundance peaked in the winter (January–March), but by late spring (April–May), it had sharply declined to 1.1% of its peak, where it stagnated until spiking again in January of the following year. Shark abundance was observed to be inversely correlated with water temperature (large numbers found only when water temperatures were below 25 °C) and with the day of the year. Shark migration along the eastern seacoast of the United States has been shown to correspond with the spawning of baitfish species (Kajiura and Tellman 2016).

In the western Atlantic, five Rajidae species show a range of migratory patterns from very little movement in smooth skate and thorny skate to long distance migration in winter skate. Of the five Rajidae species examined in the study, clearnose skate, little skate, and winter skate seem to make longer seasonal migrations compared to species without clear seasonal trends in reproduction. Little skate and winter skate seem to make partial migrations, but further studies are needed to identify if partial migration explains the observed distribution patterns, or if these result from stock-specific migratory behavior. The deep-watered thorny skate and smooth skate do not seem to exhibit strong seasonal migration patterns, and reproduction does not seem



especially related to season. Even though the study professes sparse data usage, its evidence suggests that not only are live-bearing batoids highly migratory, but that also many egg-laying species have complex, moderately long-distance migratory behavior (Frisk 2010). The differences in the migratory patterns of different species of all chondrichthyans in relation to their preferred method of locomotion would be of particular interest for future studies.

## Bioinnovation

The extensive evolutionary history of sharks and rays has allowed them to go through immense evolutionary adaptations to optimize their shape and biomechanics. One way that we can improve the efficiency of our technology is through simulation of these evolutionary adaptations. For example, biomimicry can be used to design and construct structures that are inspired from the natural world. One such example of biomimicry has come from observing shark skin. Sharks display a particular pattern of scale's (denticles) that are designed to affect the lift to drag ratio as they swim. Lift is the aerodynamic force on a body traveling through any fluid, causing the said body to rise. Drag is a force on the object that resists motion, causing friction and reducing the velocity of travel. Lift to drag ratio is important for any structure traveling through a fluid, including helicopters, planes, turbines, and submarines. Low lift to drag ratios negatively affect the ability to travel, increasing energy demands. Shark denticles are plate-like scales with a trident appearance, sporting three ridges, with the central ridge being taller and longer than the lateral ridges. Experiments have shown that airfoils (structures with curved surfaces to give a favorable lift to drag ratio) covered with denticle-like structures could improve the lift to drag ratio by both decreasing drag, and increasing lift, creating vastly heightened ratios (Domel et al. 2018). The lift to drag ratio increase is caused by reduction in contact of the shark to micro turbulent vortices that occur while swimming, which decreases transfer of momentum and shear stress, reducing

drag. This also has another important characteristic; it keeps them naturally clean because it makes it difficult for microorganisms to attach to the skin. This is best seen when comparing older sharks and whales, as the shark's skin still appears smooth and clean whereas barnacles and other growths are often found on aged whales. The unique nature of the denticles is being considered in many fields, including for the manufacturing of medical equipment (Bixler and Bhushan 2013).

Batoids have also provided humans with inspiration for improvement on technology. New autonomous underwater vehicles (AUVs) are inspired by their fast, high efficiency swimming (Fig. 3). These agile movements result from specializations of their pectoral fins, specifically the stiffness of the fin tip, which resist hydrodynamic bending forces while creating large forward propulsion forces (Liu et al. 2015). The pectoral fins are composed of cartilage segments that act as a support system, connecting at joints to form radial elements that originate at the root and extend out toward the edge. Near the tip of the fin, the cartilage segments are organized closer together, lending a greater structural integrity than at the base of the fin and creating their relative rigidity. This is a necessary evolutionary adaptation since the tips of the fins experience the greatest displacement, and therefore the greatest strain levels of the fin. The exact structure of the fin varies between species, but all fins demonstrate a distinctive interradi joint pattern (IRJP) that helps to determine the way the fins move in the water, whether through oscillation or undulation. Current research is still examining the exact mechanism by which IRJP creates these efficient swimming patterns, however, this assessment of the fins' internal structural characteristics has already and will continue to play an important role in understanding underwater kinematics and developing practical mechanical versions of Batoidea fins (Russo et al. 2015).

## Conclusion

The chondrichthyans are a group of organisms that display a wide range of diversity in body morphology and locomotive strategies. Use of

the caudal fin as the main driver of locomotion, as seen in sharks, has been vastly studied, as has pectoral fin locomotion that is seen in the batoids. Within the batoids, the use of undulation versus oscillation of the pectoral fins varies between species and has been linked to be adapted to the animal's aquatic environment. Chimaeras utilize solely pectoral fin locomotion, but have uniquely adapted use of both undulatory and oscillatory motions. In addition to major locomotive motions, various additional locomotive strategies have been studied. The epaulette shark's ability to utilize its pectoral and pelvic fins to traverse the floor of the ocean gives insight into the evolutionary transition of organisms from aquatic to terrestrial environments. The ease at which these organisms traverse their environment has been an inspiration for human innovation to improve our own technology, with various underwater vehicles being adapted directly from their anatomical designs. Continued study of this group of animals will further our knowledge of the vastly unstudied biology of our oceans and the way that organisms have adapted to live there.

## Cross-References

- [Adaptation](#)
- [Basal Metabolic Rate \(BMR\)](#)
- [Chondrichthyes Communication](#)
- [Chondrichthyes Diet](#)
- [Chondrichthyes Morphology](#)
- [Chondrichthyes Navigation](#)
- [Chondrichthyes Sensory Systems](#)
- [Common Ancestor](#)
- [Ecology](#)
- [Evolution](#)
- [Gait](#)
- [Home Range](#)
- [Locomotion](#)
- [Morphology](#)
- [Muscular System](#)
- [Natural Selection](#)
- [Navigation](#)
- [Predator](#)
- [Zoo](#)
- [Zoology](#)

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## Chondrichthyes Morphology

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## Synonyms

Cartilaginous fishes

## Definition

It is a class of fishes whose skeleton is made up of cartilage instead of bone.

## Introduction

Members of the class Chondrichthyes are popularly known as cartilaginous fishes as their skeleton is made up of flexible and soft cartilage which is covered by hard tissue instead of mineralized bones and these include sharks as large as 50 ft long to the most common dogfish of 1–2 ft. The class Chondrichthyes includes batoids (rays, skates, sawfish, and guitarfish) and chimaeras or ratfishes.

Cartilaginous fishes are true fishes having paired fins, and they breathe with gills, each placed in a separate cleft, without operculum over the gills except in Holocephali subclass. The features that distinguish cartilaginous fishes from bony fishes, the Osteichthyes is the presence of paired nostrils on the side of the head that never

open in the mouth cavity and minute tooth like placoid scales present on a tough skin. Almost all the fishes in this group are carnivorous or scavengers: the skates and rays are bottom-living relatives, feeding mostly on invertebrates. Many unique structural, physiological, and behavioral characters make these fishes of particular interest to scientists. These fishes are living fossils, for many of the living sharks and rays are placed in the same genera as species that swam the Cretaceous seas over 100 million years ago.

Classification

| Scientific classification |                |
|---------------------------|----------------|
| Kingdom                   | Animalia       |
| Phylum                    | Chordata       |
| Subphylum                 | Vertebrata     |
| Infra phylum              | Vertebrata     |
| Class                     | Chondrichthyes |

Within the Infra-phylum Gnathostomata, cartilaginous fishes are diverse from all other jawed vertebrates. The class Chondrichthyes includes two significant subclasses – the Holocephali and the Elasmobranchii. Elasmobranchs categorized into the sharks and rays. Sharks are called Selachians and Batoids. The Chondrichthyes are known to have existed from the Devonian period, the so-called Age of Fishes, from 350 to 400 million years ago (evidence present in fossil records).

Selachians

Sharks

There are approximately 350 species of sharks. Sharks possess a graceful streamlined body called fusiform as they swim long distances in open water. They swim haphazardly from back and forth while moving its head laterally. The main characteristics of sharks are a heterocercal tail (in which the upper half is longer than the lower half) which is a modified caudal fin, five to seven-gill slits located behind the mouth for respiration, and a rounded body tapered at both ends. Teeth pointed and sharp fixed in the gums in several

rows not embedded in the jaws; therefore, it easily broke off and replaced smoothly and continuously. The jaws of Selachians not affixed to the cranium. At its anterior end, the pointed snout is called the rostrum that helps in overcoming the resistance of water while swimming. The eyes are similar to that of human although very prominent. Presence of large spiracle, which is the first-gill cleft, posterior to the eyes permitting water passage into the mouth for respiration. Also, there are several pores called ampullae of Lorenzini present around the eyes, nostrils, and snout that sense change in salinity, temperature. and water pressure. Shark feeding habits widely varies. Some sharks like the bull shark or the tiger shark primarily feed on other small sharks. A few sharks like hammerhead sharks are skilled in eating stingrays (Maricapo.edu).

Batoids (Rays, Skates, Guitarfish, and Sawfish)

This group comprises of 470 kinds of species having differences, yet many similar characteristics in common; like its body is flat (also called depressiform) that swims like a flying bird and, mostly, its head is attached to the elongated pectoral fins. These elongated fins look like wings. The geographical distributions of Batoids include almost all the oceans and even freshwater bodies of the tropical region.

Sawfish (*Pristidiformes*) can exceed 7 m (23 ft) in length; they have a long snout lined with saw-like teeth. Guitarfish or shovelnose rays (*Rhinobatiformes*) characterized by a long, thick body and slender like pectoral fins; they mainly feed near to sandy bottom on small invertebrates. Skates are located mostly in deep water; they feed on insects and distinguished by a set of thorns on the tail.

The order Myliobatidiformes contains a different kind of ray. The eagle rays are giant, which needs muscular pectoral fins so that it can swim very fast. Manta rays are known as the largest rays, with the widths of approximately 7 m; like the largest sharks, they bear specialized mouth-parts for feeding on plankton. Stingrays (*Dasyatididae*) have a tail ending with a flexible, whip-like section that equipped with one or more poisonous spines. Torpedo, also known as numb

fishes or generally as electric rays, evolved itself to have muscles which act as an electric organ. This organ so modified in some rays that it is capable of producing 200 volts of electrical current in one single shot, most of these unique creatures found in freshwater bodies only.

### Holocephalans (Chimaeras or Ratfish)

The approximate 25 species of ratfishes are mostly bottom dwellers in some of the deeper marine habitats. They feed primarily on mollusks and different available invertebrates, by crushing their hard shells by the help of its flat teeth. Ratfishes have a voluminous head and eyes. It also characterized by a long, thin tail. They possess an operculum which is a tough bony layer of tissue that keeps the gills covered, which is absent in all other cartilaginous fishes but a significant feature of bony fishes (Heinicke et al. 2009).

## General Features

### Distribution and Abundance

Most of the sharks and rays are marine living fishes, but many of them also found in estuaries; some also travel up to the freshwater bodies like rivers, but a few of the members are permanent residents of freshwater. Most species are found in the moderately shallow waters of the continental shelf or near offshore islands; a few species wander far in the vast spaces of the oceans. Some lives very deep, some in mid-waters or at the bottom; most of them are surface swimmers.

Cartilaginous fishes have adapted themselves in living in all kinds of depths and all aquatic ecosystems, but not yet in the extreme conditions. However, a wide variety of cartilaginous fishes restricted to a particular zone of the ocean. On an average, 50% of species live in the continental slopes, which are up to 200 m, and 35% dwell in the depths between 200 and 2000 m. Only 5% of these fishes inhabit the open ocean. For example, the manta rays go for yearly migrations, while the great white shark (*Carcharodon carcharias*) has known to travel between South Africa and Australia.

The elasmobranchs occupy the broadest range of habitats – even the icy cold waters of the Antarctic and the Arctic Ocean. They cannot tolerate the extreme conditions such as high salinity or the oxygen-deficient depths. Therefore, sharks do not live very deep water.

### Food Habits

#### Sharks

The sharks are carnivorous having plentiful food choices, but there are also some exceptions because of the difference in the size and availability of fish. The most preferred food of the sharks, skates, and stingrays involve sea turtles, squid, sea lions, crustaceans, and dead dogs, and sadly, it can also be garbage that is thrown away from ships.

Individuals usually live alone but sometimes come together as a group to explore food resources or to reproduce. During these mating, some fishes may show particular supremacy structures, generally based on size. When the correct prey discovered, first of all, sharks start circling it, and then appears out of nowhere and approaches from the downside. Eating habit is activated by growing numbers and fast swimming when more than three sharks appear in search of food. All of a sudden, sharks progress encircling the prey by rapid crisscross to make the victim give up.

Sharks have varying biting methods with teeth evolved for sawing and shearing to assist in adequately grabbing along with body motions; this includes rotation of the whole body including turning and twisting movements of the head and tail and furious head vibrations. When the shark comes into position, they protrude their jaws out and locking the teeth into the correct place.

Sharks locate its food by smell. They also possess some other important senses that help them to discover food. Sharks sense their prey by detecting vibrations in the water; for this, they have a series of sensory pores in the sideline of the body. The network of ampullae permits shark to sense even faded electrical signals caused by prey; their eyes so acutely developed that they can easily discriminate the shape, size, and shade of their prey. Altogether, these sensory organs contribute to a well-integrated system for searching for prey.

## Rays

The batoid fish are major bottom dwellers, which prefer prey near to the seafloor. They mainly feed on invertebrates, crustaceans, and mollusks. Whip-tailed rays by the help of their full pectoral fins unearth shellfish from the muddy or sandy surface. Skates capture their food by hovering over it, and then it lay upon them, a habit adapted to hunt appropriately at night.

Electric rays also recognized for their sluggish habit characterizes Torpedinidae as they are bottom-living fish. They eat invertebrates and tiny fish, which are paralyzed by the electric shock produced from their specialized electric organ. They are even capable of eating very active fishes such as eel, dogfish, and salmon because of their ability to generate electricity and wide extensible jaws. Upper-water rays are observed to capture fish by surprisingly raising the front disk of their body while keeping the margins low, in a way forming a hollow cavity and fishes are drawn by powerful inrushing of the water.

Chimaeras and ghost sharks swim near the coastal lines and deep in the waters, to at least 2500 m of depths (about 8000 ft). They are more functional at night, feeding mostly on small fishes.

## Form and Function

The elasmobranchs are fish kind of vertebrates. The fins which are present on its back are known as **dorsal fins**. Many of these fishes possess only a single dorsal fin; others may have two dorsal fins. These fins along with fin spines sturdy and rigid, but not erectile. The dorsal fin acts as a stiff spine in some fishes, and in other, there may not be any spine. A few species are characterized by possessing a poisonous barb on its dorsal fins. These fins provide stability to sharks and help sharks from turning over while swimming. The **caudal fin** that is the strongest and largest fin on the sharks' body helps fish steer without the use of much energy.

The fins that are on the side of the shark are the **pectoral fins**. Pectoral fins used for steering and give the shark lift in the water. They are known as sharks' brakes that act like wings of an aeroplane, and with its help, sharks move backwards and up and down in the water. The **pelvic fin** is found on

the shark's stomach and is used to stabilize the shark in the water. In the male sharks, there may be an organ present called clasper that is used during mating.

The **anal fin** is found between the caudal and pelvic fins on the underside (base of the tail) of the shark. It is usually not found on all sharks. The anal fin is also used for stabilization.

The tail, also known as caudal fin, has an upper and lower part. These two parts look almost the same but differ in size or shape. This tail fin helpful in propelling the shark in the water ([cbfieldstation.org](http://cbfieldstation.org)).

Sharks have an internal cartilaginous skeleton which is robust, flexible, and durable but lightweight. It helps sharks from sinking, and it allows sharks turn in a much tighter radius in the areas in the body where it requires more strength than the other parts, like in jaws and backbones; their cartilage is calcified means calcium salts are present in them.

Some other parts, such as the teeth edging the mouth (beak) of saw sharks and sawfishes, the spines of stingrays are structurally well-advanced scales. They are called rover predators as they can swim more or less continuously when searching for its prey and the body is so structurally developed as it has pointed head, terminal mouth, narrowed caudal peduncles, and forked tails. In the mouth, teeth are arranged in the form of rows just attached through a delicate fibrous membrane over the jaws. As the teeth are not firmly attached so when a tooth broken or accidentally lost, it soon replaced by another tooth, present behind in the next row. Rudimentary teeth are present at the base of the innermost row, and tooth buds developed, and it moves forward when in need.

The body of cartilaginous fishes possesses a lateral line that allows them to sense changes in the pressure of the surrounding water and alert them to move so that they never run into each other. Their tail is a heterocercal tail which is an ancient form of a lunate or crescent shape. These fishes have no swim bladder and are heavy in front that makes its body deliberately downward driving design which supplemented with horizontal, plane like pectoral fins that transformed that downward force into a horizontal, forward driving force.

The rays vary externally from sharks possessing gill openings which are confined only to the lower surface. The eyes of the rays are present on the dorsal surface, and the lateral lines of the pectoral fins are fixed to the head from the sideways just in front of the gill openings. In some rays, scales are absent, and some others variously marked with thorns, prickles, or tubercles, all of these are an advanced form of scales.

The tails of these fishes vary from species to species; some have long tail equipped with toothed spines, a few may have a tail with poison glands. The sawfishes have prolonged snout, but flat and blade-armed on any of the side of the snout with teeth.

The chimaeras possess single gill opening externally. The skin of the adult fishes is smooth on each side of the head, and scales are generally not present; the teeth comprises of six pairs of crushing plates. The dorsal fin and spine are erectile. Male chimaeras too have claspers that act as an organ to transfer sperm in the female cloaca during mating, but they also have a clamping device which is erectile called as the tentaculum, present in front of pelvic fin.

### Equilibrium of Fishes in Water

The typical shark is a long-bodied fish in which the air-filled bladder is absent, which is commonly found in the bony fish, and that is the reason cartilaginous fishes are required to swim continuously to remain afloat. Light oils assist buoyancy in the liver, which can comprise up to 25% of a shark's total body weight and has to, therefore, swim by the passage of waves of contraction along with the metamerically arranged muscles. The sharks are excellent swimmers, where the upturned tail and the fins ensure stability and control of directions. The dorsal lobe of the tail is more significant than its ventral portion and is called as heterocercal and helps the head in keeping in the downward direction. It is corrected by the flattened shape of the head itself and by the pectoral fins, which acts as aerofoils, allowing steering in the horizontal plane. The fins keep them stable as it moves through the water or will enable it to become temporarily unstable and

hence change the direction. To ensure static stability of the body, the fins modified in such a shape that it delivers forces which let the fish move again into its last kind of movement even if it gets deviated in the waters.

### The Skin of Elasmobranchs

These predatory animals are attackers and do not possess a very heavy external armament. The skin is tough covered by layers of the epidermis that feels like sandpaper. Under which lies a thick layer of connective tissue having fibers which are attached to it perpendicularly giving a muscle of high strength and flexibility.

The skin is characterized by a cover of denticles or small rough placoid scales. Each of these consists of a pulp cavity around the edge of which lies a layer of odontoblast secreting the calcareous matter of the scale, known as dentine. The dentine form outside wrapped by the lining of enamel, which is secreted by ectoderm. The scales are similar to teeth, which considered as specialized denticles developed on the skin of the jaws.

The skin of fish provides it protection by the color, secreted by a layer of cells called as chromatophores present below the epidermis. Different types of skin pattern are also observed; some sharks have a wavy or spotted texture that makes them almost invisible when they swim in the water.

### Senses

The sense of smell is very much developed and is the primary means for locating food and helps the predator in moving in the direction of the prey. When a favorable movement of water current is given, sharks are incredibly talented in detecting even minute concentrations or say a fragment of a part per million of particles present in the water bodies, for example, blood.

Their eyes are although functionally and structurally adapted for seeing object or prey, it is noticed that their visual ability to differentiate the color and form of any substance varies among species. It has a tapetum lucidum meaning a reflecting layer Behind retina. This structure is made up of layer of parallel, flat cells filled with crystals of silver guanine that reflects light passed from retina boosting visual signals when there is

low amount of light. Some sharks also develop a nictitating membrane that protects the eye by closing off whenever sharks are feeding or get closer to some object, connected to the eating habits of any species. Predatory sharks which are fast have more accurate and sharp vision, and among some deep-living species, the eyes are accordingly developed to increase detection of encompassing light.

The hearing organ, situated in the cranium to its auditory capsule, is combined with a system of canals that are accountable for equilibrium maintenance. Sharks are remarkably alert to sounds which are even of precise frequency, and to acquire this extraordinary faculty they have the ability for directional hearing. It has not yet confirmed whether the hearing sense is compassionate than the sense of smell.

Sensory organ discovered acts like taste buds are present on the sides, floor, and roof of the mouth or on the tongue, as well as in the throat. Large sharks are capable of discriminating food types – they mostly prefer tuna. However, in some situations, these sharks get out of control, where they attack anything in a frenzy way, even so, attacking its own kind.

Sensory organs are present in the sharks, chimaeras, and rays which receive a high range of vivid information – low frequencies vibrations, salinity, pressure, temperature, and small electrical signals, which are generated by another fish even at a great distance. These sensory organs are situated in the lateral line system, in groups of pores, called ampullary organs, which are capable of detecting electric stimulus found on the head, mouth region, and sometimes near the jaws ([Fisheries and Oceans, DFO](#)).

### Reproductive Behavior

Some of the species of sharks get segregated by sex when they become mature individuals. They come together during the mating period; the larger-sized males become more aggressive and usually stop eating. The sharks get segregated to protect female as a part of their behavioral adaptation. During mating, the principal act used by male fish to start copulation is biting and then gripping the female with teeth. The male holds

female in this particular way so that it can easily insert a clasper, which is a kind of modified fin, into the female genital part called cloaca. When mating is over, both the gender gets separated again. The pregnant female lives in solitude to protect itself from other females of similar size. At the time of parturition, the expecting female moves away to a place which is environmentally suitable for nursery care of the young ones. During the childbirth, the sharks stop feeding and get departed as soon as the parturition completed.

Nursery grounds differ from species to species. The bull shark uses shallow water of the ocean and bays. The spiny dogfish of Atlantic Ocean carries its baby, almost after a couple of years of mating, generally during the winter season, far away on the continental coastal lines of northeastern America.

A few skates which have been noticed mating may also be one of the properties of other rays too. The male ray species holds the female by biting its pectoral fin and then presses its ventral surface against the female while interjecting the clasper, and in some species both the claspers, into her cloaca. Skates possess several claw-shaped spines on both sides of its pectoral fin, which are used for holding female at the time of mating; claw-like spines are of prime importance because they are retractile in the channels of skin.

The eggs of skates have been noticed to be extruded in series, generally of two eggs at a time but sometimes one. Rest periods of at least 5 days occur between extrusions ([Heinicke et al. 2009](#)).

### Respiration

Sharks breathe by opening the mouth while expanding the mouth-throat (buccopharyngeal) cavity and contracting the gill pouches to close the gill slits. With the mouth closed, they contract the buccopharyngeal cavity along with dilating gill pouches. Hence, by drawing the water above the gills, this is the site where the exchange of gases takes place. The mouth remains closed, the fishes contract the gill pouches, and mainly the buccopharyngeal cavity. However, the gill slits are opened to remove the water.

The rays take in water through the spiracles, which gets closed by the contractile movement



generated by anterior margin, which has a similar valve and gill filaments. The water is prevented from entering the throat by the presence of a folded membrane on the floor and roof of the mouth and is directed towards the gill opening. Skates sometimes inhale water through the mouth because it keeps its head a little above from the bottom. Many fishes like stingrays, angel sharks, skates, and guitarfishes reverse the flow of water through the spiracles, for clearing the passage if in case any undesirable foreign particle enters the cavity.

Chimaeras take up the water from the nostrils mainly, during which the mouth remains closed. There is a groove extended from the nostrils, which lead to the mouth, and this groove helps the water enter into the mouth (Cowen 1996).

## Conclusion

Class – Chondrichthyes are those marine animals which possess streamlined structure and have endoskeleton made up of cartilage. The mouth is centrally located. The notochord is present throughout life. Gill slits are disconnected and have no operculum (which is also known as gill-cover). The skin is hard, containing tiny placoid scales. Teeth are qualified placoid scales which are present backwardly. The jaws are mighty. The air bladder is absent, so they are required to swim continuously to avoid sinking. The heart is two-chambered (one ventricle and one auricle).

A few species possess electric organs (e.g., Torpedo) and many of them own poison sting (e.g., Trygon). They are poikilothermous or cold-blooded animals, i.e., they cannot maintain their body temperature. They are monoecious, meaning sexes are different. The fertilization occurs internally, but many of them may be viviparous, e.g., Scoliodon (Dogfish), Carcharodon (Great white shark), and Trygon (Stingray).

## Cross-References

- [Adaptation](#)
- [Chondrichthyes Sensory Systems](#)

- [Evolution](#)
- [External Fertilization](#)
- [Phylum](#)

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## Chondrichthyes Navigation

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## Synonyms

[Migration](#); [Movement](#); [Orientation](#)

## Introduction

The ability of animals to navigate has long been of interest to science and has been widely studied. As far back as 1757, Linnaeus investigated the migratory routes of birds in order to discover how they were able to navigate accurately over long distances. Despite this research lineage, the mechanisms employed by animals to navigate are still relatively poorly understood. There is a large amount of conflicting evidence based on several fundamental issues which means that science cannot satisfactorily explain the mechanisms of long-distance migration (Alerstam 2006). Many

species, including birds, fish, insects, sea turtles, bats, and sea mammals have been shown to accurately navigate over varying distances. Navigation may be considered as short, mid, or long distance and the reasons for making these movements are varied. Food location, mating, egg laying, or live birthing are among those reasons.

The ability to navigate to seemingly specific destinations is still the cause of some speculation. For some terrestrial species, the use of geographical features or landmarks is proffered as a plausible explanation for this to be achieved. The homing pigeon (*Columba livia*) has provided crucial insights into the ability of animals to navigate. Over familiar landscapes *C. livia* has been shown to utilize linear landmarks, such as railway lines, roads, and rivers and they are able to follow these back to their home ranges (Guilford and Biro 2014). True navigation, however, is demonstrated when an animal is able to reach a relatively precise target which is located over a considerable distance without the need for familiar landmarks (Gould and Gould 2012). For longer distance navigational feats, it has been suggested that other mechanisms are at play, including magnetic and celestial cues. In addition it is believed that animals use other senses, such as auditory, visual, gustatory, and olfactory cues. Auditory cues have been attributed to navigation and it is believed that disruption to the auditory navigational map was responsible for the loss of 60,000 homing pigeons lost in 1997 over the English Channel. It appears that the lack of navigational success occurred when the flight path of *C. livia* crossed that of Concorde as it reached supersonic flight. The associated sonic boom is believed to have caused disruption to the pigeon's navigational map causing them to be displaced.

Navigation, in the marine environment is commonplace and occurs within all marine zones, being performed by a large number of species from a range of taxonomic classes. What has really interested scientists is the ability of marine organisms to navigate over long distances, especially those which inhabit a seemingly featureless pelagic environment and can therefore not rely on the associated visual markers available to shallower water species.

In comparison to other species, navigation in organisms belonging to the class chondrichthyes (cartilaginous species comprising the sharks, rays, skates, and chimera) has been relatively little studied and is poorly understood. What is apparent is that there are a variety of mechanisms utilized in the orientation and navigation of chondrichthyan species that allow them to locate themselves over both short and long distances. The chondrichthyes include over 1050 extant species and shows a diverse range of life histories and occur in almost all marine habitats. Many species are benthic and movement occurs over a relatively small area. Other species have been shown to make oceanic migrations over several thousand kilometers. The mechanisms by which chondrichthyan species are able to navigate have been suggested to include the octavolateralis senses (auditory and lateral line system), vision, and electroreception. It would appear that a different sensory array is utilized for different navigational purposes.

### Short-Range Navigation

Short range navigation in chondrichthyan species has been suggested to involve the use of auditory and lateral line senses, as well as vision and olfaction (Montgomery and Walker 2001). It has been suggested that these short range movements are associated with prey and mate location and small-scale movements around territory. Many small shark species, such as the small-spotted catshark, *Scyliorhinus canicula*, are resident across most of their range (Rodríguez-Cabello et al. 2008) showing little movement away from an area. In this case, the visual, olfactory, and octavolateralis senses would be utilized more heavily due to the senses being applied to reactions to environmental stimuli, prey capture, and mate location. Contrary to popular belief many chondrichthyan species have very well-developed visual systems, and it is believed that vision is utilized in navigation (Hart et al. 2006). For some species, or indeed populations, depending on geographic location, vision may not necessarily facilitate accurate migration. For species that inhabit deeper waters

or those that experience high turbidity levels it may be necessary to utilize a different suite of senses and these are thought to dominate. These include olfactory and electrosensory senses that can be an important mechanism to allow for short-range navigation in chondrichthyan species.

## Vision

Very little research that examines vision in chondrichthyan species has focused on the use of vision for navigational purposes. Historically, and until relatively recently, it was believed that vision was poorly developed in chondrichthyan species and evolved specifically for use in dim light. This notion was perceived due to early descriptions of the structure of the retina showing the presence of only rod cells. Rod cells are located on the periphery of the retina and are associated with vision in low light environments. Cone cells, which are clustered in the center of the retina and are responsible for the perception of fine detail and color, were not described in early reports of the eye morphology of cartilaginous fishes. Hart et al. (2006) provide a comprehensive discussion on the morphology of elasmobranch visual apparatus and indicate that far from the early beliefs that chondrichthyan species having poor eyesight that many have well-developed vision. With the exception of several skate species (Ripps and Dowling 1990) and a number of deep dwelling chimera, it has since been discovered that a vast majority of chondrichthyan species possess a both rod and cone cells and many species do in fact have excellent visual capabilities (Lisney et al. 2012). Indeed the white shark (*Carcharodon carcharias*) is thought to have eye sight that is comparable with humans, with many chondrichthyan species far exceeding this. Ablation studies have revealed that many chondrichthyan species rely heavily on their visual sense. This has been noted in smaller species where vision has been found to be important in the location and detection of prey items, conspecifics, and refugia (Hart et al. 2006).

Many chondrichthyan species navigate widely throughout home ranges and experience changes

in light intensity. Several species of shark do carry out diel vertical migrations (DVM) and migrate across a range of light regimes. These migrations can range from tens to many hundreds of meters, occurring at a range of depths from surface waters (Sims et al. 2006) down to the bathypelagic zone (Kyne and Simpfendorfer 2010). One such example is the blue shark (*Prionace glauca*) that has been shown to migrate vertically to depths of below 600 m in under 10 min. This would indicate that species showing DVMs would have to have well-developed eyes in order to adapt rapidly to the changes in light availability at varying depth.

Early studies by Parker (1909) on the dusky smooth-hound (*Mustelus canis*) determined the response of the shark upon severance of the optic nerve. It was discovered that once the optic nerves had been severed that the shark demonstrated a decreased swimming speed and could not orientate itself in the aquarium environment, constantly colliding with solid objects within the enclosure. It was also noted that the individuals that had their optic nerves severed did not recover their ability to navigate within the environment, fundamentally rendering the individual blind. It was also observed that when only one optic nerve was severed the individuals navigated as an unaffected individual would, with only occasional contact with solid objects. Therefore, Parker (1909) concluded that retinal function is important for the orientation and navigation in this species.

Subsequently, research has been carried out on another species of shark to determine the importance of vision as a navigational aid. Lemon sharks (*Negaprion brevirostris*) were the subject of two studies that rendered them temporarily blind in order to determine patterns of movement and behavior. The first carried out by Gilbert (1963) examined the effects of vision on predation while the second observed the homing behavior of visually impaired juvenile *N. brevirostris* (Sundström et al. 2001). In neither case was the navigational ability of *N. brevirostris* seemingly affected when vision had been impaired. It could therefore be considered that the importance of vision as a navigational aid is more crucial in some species than others, and this would depend largely on habitat preferences.

## Olfaction

It is widely recognized that cartilaginous fishes have a highly developed sense of smell and it has long been thought that elasmobranch fishes possess greater olfactory sensitivities than teleost fishes (Meredith and Kajiura 2010). Olfaction in many shark species has been linked to a number of activities including the location of mates (Johnson and Nelson 1978), prey (Schwab and McComb 2007; Gardiner et al. 2014; Yopak et al. 2014), and the avoidance of predators (Rasmussen and Schmidt 1992). Several authors have also suggested that olfaction is used for navigation and homing in many species (Edrén and Gruber 2005; Heupel and Simpfendorfer 2005). However, in relation to the number of studies on the olfactory ability of many cartilaginous species relatively little have considered the role that olfaction plays in navigation. Considering the understanding of the olfactory cues in the navigation of many other species, including avian and teleost species, it is surprising that so little research exists on the role of olfaction on chondrichthyan navigation. This is especially true considering the environmental changes that occur in many marine environments and the disruption to olfactory cues that may occur. It has been noted that not only can aquatic contaminants potentially damage a fishes olfactory organs, but the change in chemical composition of the water may also affect the ability of many species to detect chemical cues within the water body. According to a study by Dixon et al. (2015), ocean acidification can dramatically impact olfaction in shark species, which can lead to an impairment of homing ability. It seems that for some species, olfactory cues play an important role in the navigational process.

In one study, *N. brevirostris* were displaced between 4 km and 16 km from their home ranges, both during the daytime and at night. Although no attempt at causing anosmia was made, the ability of *N. brevirostris* to navigate back to the home range was clear with all specimens, bar one, navigating back to their home range. Although not focused primarily, olfaction observations were made that the water currents were potentially carrying

olfactory cues to the fish, allowing them to orientate back towards the capture sites. This was based on the fact that the animals orientated themselves in a home-oriented direction shortly after release, and it is believed that using the currents as orientation indicated detection of the presence of chemical cues in the water (Edrén and Gruber 2005).

In another study, temporary anosmia was induced in blacktip sharks (*Carcharhinus limbatus*) through the insertion of cotton wool and petroleum jelly into the nares of the study animals (Gardiner et al. 2015). The individuals were then translocated 8 km away from their home range and released. Those individuals where olfaction had been blocked took a significantly longer time to return to the home range than those sharks where no intervention had been made. A similar study to that of Gardiner et al. (2015) was undertaken on the leopard shark (*Triakis semifasciata*). The same method of anosmia was performed and the results demonstrate a clear trend in navigation whereby the sharks released after anosmia had taken place showed a nondirectional pattern of swimming. This is in contrast to the control group whereby the swimming pattern was clearly directional and orientated towards the shore (Nosal et al. 2016).

It has been suggested that the cause of these anosmic behaviors could be due to the size of the olfactory bulb. It would appear that there is a large variation in the size of the olfactory bulb of many shark species (Yopak et al. 2014). It seems evident that the species that possess the largest olfactory bulbs are those that inhabit pelagic waters, such as the great white shark (*Carcharodon carcharias*) which undertake long-distance migrations and possess large olfactory bulbs relative to brain size. This species, amongst others, are proffered to use olfaction as one means of navigation in a seemingly featureless environment.

## Long-Distance Navigation

Although evidence is starting to emerge that cartilaginous fishes use a range of sensory apparatus

to orientate themselves and to navigate over short distances, the instances of long-distance orientation and navigation are still puzzling. As recently as 2001, it was suggested that true navigation was not demonstrated in cartilaginous species. It was also noted that a great deal of speculation surrounded the ability of (elasmobranch) species to utilize sensory mechanisms that allowed large-scale movement (Montgomery and Walker 2001). Many theories have been proffered that suggest a range of environmental cues to enable navigation over longer distances. Celestial cues, tidal patterns, and temperature and pressure gradients are all suggested to play a part, but none has been studied in detail for chondrichthyan species. However, the internal mechanisms used by individuals of this class of fishes are clearly not understood. In 2003, a female white shark was tagged off the coast of South Africa and over a period of 99 days travelled to the coast of Western Australia. The authors clearly state that the mechanisms by which the shark navigated over 11,000 km to Australia and back remain a mystery, especially given the lack of topographical features along the migratory route (Bonfil et al. 2005). However, they do proffer the use of celestial cues as a possible explanation. Despite this lack of understanding of the mechanisms used for long-distance navigation in this species, it appears that members of the chondrichthyes can indeed navigate over long distances and perhaps do demonstrate true navigation.

Much of the literature that reports on long-distance navigation of chondrichthyan species focuses on the concept of geomagnetic orientation. It has been proffered that chondrichthyans could utilize the earth's magnetic field either directly by utilizing biosynthesized magnetite or indirectly by using the highly developed electrosensory system (Montgomery and Walker 2001). The presence of magnetite has been little explored and has so been reported in a handful of chondrichthyan species and has been little studied. The use of the electrosensory system for navigation in chondrichthyes has been more widely studied and seems a plausible explanation for large-scale navigation of this class of fishes.

## Electroreception

Despite being a common attribute amongst many species, electric sense is one of the last of the chondrichthyes senses to be fully understood (von der Emde 1998). As far back as 1687, Lorenzini described the presence and the gross anatomical features of pores on the skin of chondrichthyan species. However, their true function was misunderstood. Lorenzini suggested that they were secretory glands used to cover the body in a gelatinous substance. This misconception was due to the presence of a conductive mucopolysaccharide gel found within the canals of the ampullae. The structure of the ampullae of Lorenzini (AoL) in marine species, which is made up of an ampulla and a subdermal canal that terminates in a single pore on the surface (Sisneros and Tricas 2002), have been well studied and are now better understood. The AoL is now known to have a much more complex function than mere secretion, forming part of the sensory array of chondrichthyan species. It appears that the structure of the AoL is common to most chondrichthyan species, and is located around the head region of sharks and the disc margins in rays, and is visible as small pores.

It was not until the 1930s that the true function of the AoL was first discovered. Observation made by Dijkgraaf in the 1930s noted that specimens of the lesser-spotted catshark (*Scyliorhinus canicula*) were seen to react to a rusty wire in the water (Dijkgraaf and Kalmijn 1962). Since then, it has been discovered that the use of electroreception is varied, being utilized for prey detection (Lim et al. 2010) as well as the location of conspecifics for courtship and reproduction (Crooks and Waring 2013). The electric sense of chondrichthyan species is noted as a short range sense. In *S. canicula*, it is thought to be effective at a range of 15 cm or less (Kalmijn 1971). However, it has been noted that the chondrichthyes have the ability to detect extremely small currents as weak as less than 1 nanovolt per centimeter (Kajiura 2003). It is well known that all living organisms produce minute electrical currents and these are easily detected by the ampullae of Lorenzini once the cartilaginous fish is within range of its prey. It



is this interaction with living organisms that has been the focus of most of the research on electroreception of chondrichthyan species.

However, most chondrichthyan species are also thought to utilize electroreception in navigation. It is noted that members of the class chondrichthyes possess electrosensory capabilities that allow them to detect even the weak electric fields given off by their own bodies as they swim through the earth's magnetic fields (Paulin 1995). It appears that the earth's magnetic field can provide information that can be used to determine position for chondrichthyan species that will allow them to both orientate and navigate (Courtney et al. 2014). Evidence exists that a number of animal species can determine their position based on magnetic fields and as a result many scientists believe that members of the chondrichthyes also navigate using the magnetic fields that encompass the earth (Anderson et al. 2017).

More recently, as an understanding of the ability of cartilaginous fishes to detect the earth's geomagnetic field and electrical currents in the environment is more fully understood, more attention has been given to the detection of weak electrical fields found throughout aquatic environments in relation to chondrichthyan navigation. Many scientists are now hypothesizing that despite being a short-range sense in terms of prey and/or conspecific detection that chondrichthyan species make use of this electroreceptive capability not only to orientate themselves in the water but also to navigate over long distances. Indeed, many behavioral experiments demonstrate the ability of members of the chondrichthyes to detect changes in the geomagnetic field which vary depending on location. It is suggested that many chondrichthyan species can detect the earth's magnetic field (Akoev et al. 1976; Klimley 1993; Kalmijn 1982, 2000; Anderson et al. 2017) and this has led to increasing evidence that for many species the use of a geomagnetic field is the most feasible explanation for long-distance migration (Molteno and Kennedy 2009). This seems especially feasible where topographical landmarks are limited or missing and may help to answer the question of how chondrichthyan species manage to maintain a

direct heading with no other visible cues. It has been hypothesized that scalloped hammerheads (*Sphyrna lewini*) demonstrate a positive topotaxis (Klimley 1993). They have been observed to locate seamounts by traversing ridges and valleys, potentially mapping in relief a geographical area where there are no visual clues. This is believed to aid in swimming direction and orientation of individuals. This is certainly true of the transoceanic journey made by the female white shark from South Africa to Western Australia. Bonfil et al. (2005) note that it is possible that over such long distances in deep waters that the use of the earth's geomagnetic field could offer an explanation as to how an individual is able to navigate, seemingly accurately, over such large, featureless distances.

It appears that the use of the earth's magnetic fields in a highly likely explanation for navigation within the aquatic environment (Paulin 1995). According to Kalmijn (1981, 1984), elasmobranch species may use both an active and passive mode of electroreception when navigating. It is prophesized that as the fish swims voltage gradients are produced within the organism and these are used to orientate in a particular environment. The increase or decrease in voltage away from a magnetic field helps the individual to orientate itself in the desired direction. As it turns away from the magnetic field, there is an increase in voltage and reorientation can take place to maintain a particular heading. Passive mode is theorized to work slightly differently in that the voltage gradient is detected through the body from electrical fields that occur within the environment and which take place through water induction. Kalmijn (2000) summarizes that using both active and passive modes means that it is possible for the organism to simultaneously sense drift within ocean currents with their magnetic compass headings.

However, Paulin (1995) notes that although it appears evident that cartilaginous fishes do use electroreception to navigate, the theories suggested by Kalmijn (1981, 1984) may not be able to account for the biological function of the electrosense in chondrichthyes. It appears that DC voltages cannot be detected by the electroreceptors found within chondrichthyan species.



In addition, Kalmijn (1981) states that the electric sense is used to determine the direction of swimming using fixed reference points by using motion to calibrate movement. Paulin (1995) suggests a theory whereby electroreception provides a compass bearing and neural activity of the shark is utilized in a far greater way than merely detecting changes in voltage by comparing vestibular and electrosensory signals.

Despite this range of evidence, it is clear that there is a great deal of uncertainty as to the exact sensory mechanisms and pathways involved in detecting the earth's magnetic fields (Anderson et al. 2017). In addition, the exact stimuli that are detected remain unclear and the way in which chondrichthyan species are able to fully utilize the magnetic fields across the oceans needs further research to gain a fuller understanding of the mechanisms at play.

## Conclusion

It is clear from the literature that relatively little is known about the mechanisms of navigational capability of members of the class chondrichthyes. What is evidenced is that members of this class of fishes undertake accurate and often long-distance movement and migrations and some species have the ability to navigate over long distances in a seemingly featureless environment. Although there is evidence to suggest that longer distance navigation may involve a complex use of the electrosensory system, the use of other senses should not be ruled out when considering long-distance navigation. Clearly chondrichthyans have very well-developed senses and it would appear that the use of these for navigational purposes is only starting to be understood. The utilization of all senses in combination for orientation and navigation should not be overlooked as there is an evident lack of understanding of the process involved. It would seem that geomagnetic cues are used to guide long-range navigation, while visual or olfactory cues allow animals to pinpoint precise locations within an environment. Very little literature currently exists on the ability of chondrichthyan species to utilize other environmental cues, such as celestial patterns,

temperature, pressure gradients, and gustation to navigate. It would appear that the mechanisms surrounding the navigational processes still need to be better understood, especially in an environment that is being increasingly utilized and changed through anthropogenic activity. According to Montgomery and Walker (2001), more in-depth and structured studies of orientation and navigation in chondrichthyan species is needed in order to lead to a better understanding of navigation in this class of fishes.

## Cross-References

- ▶ [Lagomorpha Navigation](#)
- ▶ [Swine Navigation](#)
- ▶ [Testudines Navigation](#)

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## Chondrichthyes Sensory Systems

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### Definition

Chondrichthyes' sensory systems are part of the nervous system responsible for receiving external and internal stimuli and translating them into nerve impulses that are transmitted to the central nervous system where they are processed.

### Introduction

The Chondrichthyes are the basalmost extant branch of Gnathostomata and comprehend a monophyletic group of fishes with fossils and

extant representatives distributed in 65 families with 1282 valid species. Despite several recent findings regarding the relationships of early chondrichthyans (see Maisey et al. 2017 for more information), the extant chondrichthyans are divided into two groups, the Elasmobranchii (sharks, rays, and their kin) and the Holocephali (chimaeras and their kin), and can be recognized by the presence of some apomorphic characteristics, such as prismatic calcification of the cartilaginous endoskeleton, the presence of placoid scales, and pelvic fin modified in claspers in males.

All Chondrichthyes live in aquatic environments (mostly marine ecosystems), and they perceive external (and internal) stimuli through the sensory system, which is the part of the nervous system responsible for receiving the stimuli and translating them into nerve impulses that are transmitted to the central nervous system (entry ► [“Vertebrate Nervous System”](#)) where they are processed.

The life in aquatic environments brings particular conditions to stimuli perception when compared to the terrestrial environment; in such a way, chondrichthyans (as also other aquatic vertebrates (entry ► [“Vertebrates \(Chordata\)”](#))) have some sensory organs more prominent than others, used to navigate their environment (entry ► [“Chondrichthyes Navigation”](#)). For example, chemoreception is largely important in chondrichthyans' perception of the environment, since chemical particles propagate more rapidly in water than in air. Yet, the refractive index of water is close to that of the cornea, so that in aquatic vertebrates the lens is the primary refractive structure in the eye, being almost spherical when compared to terrestrial vertebrates' lens (which tend to be more oval, and the cornea is the primary refractive structure).

The evolutionary success of Chondrichthyes' lineage is in part related to not only their sophisticated battery of sensory organs, but also to Chondrichthyes' morphology (entry ► [“Chondrichthyes Morphology”](#)) and to ecomorphological features (Compagno 1990). However, advances in the understanding of chondrichthyans' sensory biology mostly rely on

information regarding elasmobranchs (see Lisney 2010 for a compilation).

This entry will focus on chondrichthyans' special sensory organs, which are usually localized and respond to specific stimuli. These special sensory organs will be primarily divided by the kind of stimuli, and then by corresponding organ or local: (1) **Chemoreception** (olfaction and gustation); (2) **Photoreception** (vision and parietal organ) (entry ► “[Photoreceptors](#)”); (3) **Mechanoreception** (lateral line system, auditory system, and membranous labyrinth); and (4) **Electroreception** (ampullary organs) (entry ► “[Electroreceptors](#)”).

### Chemoreception

The chemoreceptors are sensory receptors specialized in receiving and translating chemical stimuli. Chemoreception is essential for aquatic animals to identify prey, mates, and habitats, and even avoid predators. The senses commonly associated to chemoreception in vertebrates are olfaction and gustation. Despite olfactory and gustatory receptors perceiving the environment in a similar way, olfactory receptors are distributed in the nasal passage and vomeronasal area, and the gustative are in the oropharyngeal cavity.

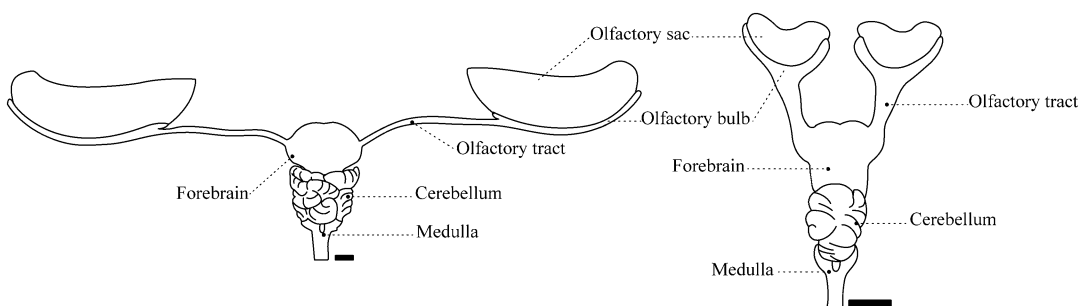
### Olfactory System

Olfactory receptors (entry ► “[Olfactory Perception](#)”) are neurons specialized in odorants' detection. The olfactory system of chondrichthyans is essential to locate prey. They develop from paired neurogenic placodes, which invaginate and form

nasal sacs. The walls of the nasal sac form the **olfactory epithelium** which, besides the olfactory receptors, presents basal and sustentacular cells that secrete mucus and support the receptors. **Olfactory sensory cells** bear microvilli at its apical end, while ciliated sensory cells, which are common in other vertebrates, are lacking in this class. The sensory cells send an axon into the **olfactory bulb**, forming the **olfactory nerve**. The olfactory bulb is connected to the olfactory lobes via the **olfactory tract** (Fig. 1).

The olfactory organs of elasmobranchs have rosettes located in the lateral cavities on either side of the snout. These cavities have folds of tissue called lamellae, which are separated by a central raphe and covered by olfactory epithelium. The number of lamellae in this organ can vary between species (see Meredith and Kajiura 2010).

Living chondrichthyans in general are known to excel in their olfaction, this being one of the most prominent (or the most prominent) sensory systems. Some taxa, such as the hammerhead sharks, have an even more significant increase in the area and volume of olfactory organs and, likewise, of their integration region at the brain telencephalon, the olfactory lobes (Fig. 1, left) (Compagno 1990). Differences in olfactory capabilities in elasmobranchs are more related to functional aspects than phylogenetic relationships (Schluessel et al. 2008). Elasmobranchii of benthopelagic habitat has a high number of olfactory lamellae and a larger olfactory epithelial surface than benthic and demersal species. However, no correlation was found between the mass of the



**Chondrichthyes Sensory Systems, Fig. 1** Brain and olfactory organ of a hammerhead shark *Sphyrna lewini* (left) and an Atlantic stingray *Dasyatis sabina* (right).

*Sphyrna lewini* drawing based on Yopak et al. (2015). *Dasyatis sabina* drawing based on Meredith et al. (2013). Scale bars 1 cm

olfactory bulb and the occupied habitat (Schluessel et al. 2008).

Furthermore, some studies indicate that the lateral line system also plays a role (odor-stimulated rheotaxis), together with the olfactory system, in the location of odor source of elasmobranchs.

#### Gustation

Gustatory receptors are chemoreceptors located in the epithelium of body parts involved with food intake and handling, such as the lips, oral cavity, tongue, and pharynx of Chondrichthyes, and are organized in **oral papillae**.

The oral papillae consist of modified epithelial cells and associated receptors, with multicellular peripheral chemoreceptors forming **taste buds**, besides solitary **chemosensory cells**. These structures are usually interspersed with **oral denticles** (reduced placoid scales). Both the oral papillae and denticles feature a phyletic variation regarding morphology and distribution.

Despite the gustation being relatively less studied than other senses (Lisney 2010), the number and distribution of taste buds appear to vary widely among chondrichthyans (Gardiner et al. 2012). A **palatal organ** was described for chimaeras and might have a role in gustation, despite its low taste buds' density. Abundance and distribution of oral papillae and denticles might correlate feeding habits, capture strategies, and prey processing.

#### Photoreception

The photoreceptors are sensory receptors specialized in receiving and translating radiation stimuli. Luminous energy used in Vertebrates' photoreception usually lies between 380 nm (violet) and 760 nm (red) of wavelength. Shorter wavelengths (ultraviolet radiation) are rapidly absorbed by water and not used in aquatic vertebrates' photoreception.

To perceive luminous information, the photoreceptive cells contain a **visual pigment** that absorbs light energy, which initiates a chemical reaction that generates nerve impulses. Differences in light intensity are translated as contrasts, and differences in wavelength are translated as different colors.

The senses commonly associated with photoreception in vertebrates are vision, photoreception regarding the pineal complex, and infrared radiation. Regarding Chondrichthyes, we will deal with **vision** and **pineal complex**.

#### Vision

Chondrichthyes occupy environments with different structures, such as water columns, coastal and ocean areas. Some eye adaptations are correlated to the different light inputs experienced in each environment. Likewise, chondrichthyans that have a vision as a prominent sense also have the processing centers at the brain (such as the optic tectum at the midbrain) notably enlarged.

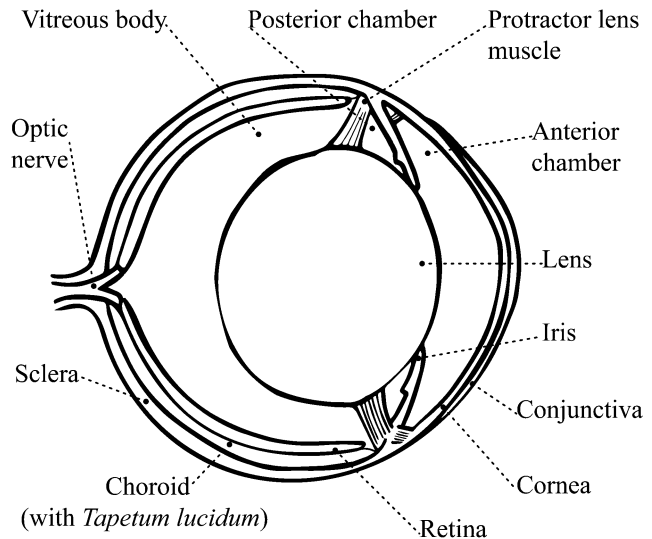
Chondrichthyes' eyes have no eyelids but might have a **nictitating membrane**, and are arranged laterally or dorsolaterally in its chondrocranium. Since the hammerhead shark has a wing-shaped snout, the eyes are also more elongated, which possibly improves its visual field. Also, some batoid species have eyes situated on the anterior margin of the chondrocranium and oriented parallelly, which provide a frontal view with a binocular overlap.

Remarkably similar to other vertebrates, elasmobranchs' eyes have the following main structures: **anterior chamber, choroid, conjunctiva, cornea, iris, lens, optic nerve, posterior chamber, protractor lens muscle, retina, sclera, and vitreous body** (Fig. 2). In the eyes of Chondrichthyes, as well as other vertebrates adapted to see in low-light conditions, there is a structure called **Tapetum lucidum**. This structure reflects the light that has passed through the photoreceptors back to them and improves visual accuracy in dark environments.

Both **rod** and **cone photoreceptors** are present in most elasmobranchs (except for the skates and some deep-sea or strongly nocturnal sharks, which only have rod photoreceptors), the first being more sensitive than the second, and responsible for vision in dim light (scotopic vision). Sharks are cone monochromats; which means they have only one type of photoreception pigments and are likely color blind. Yet, rays are cone dichromats, having two types of photoreception pigments, with different spectral sensitivities that

### Chondrichthyes Sensory Systems,

**Fig. 2** Generalized chondrichthyan eye. (Redrawn and modified from Kardong (2016))



allow color discrimination (entry ► [“Evolution of Animal Color Vision”](#)) (see Hart 2020).

Chondrichthyes’ visual accommodation (the ability to focus sharply on objects) occurs through the movement of the lens related to the retina. The eye is supported in the orbit by a rod-shaped optic pedicel, and eye movements occur via six extraocular eye muscles. A lateral position of the eyes on the head, combined with moderate eye movements, indicates that for most elasmobranchs each eye has an almost panoramic monocular visual field, with just a small binocular overlap (e.g., Hart 2020).

Considering the body mass, sharks from oceanic areas tend to have relatively larger eyes than sharks from coastal areas (Lisney and Collin 2007). The size of the eye can vary from 60 mm (as in the thresher shark *Alopias superciliosus*, which possesses very large eyes) to 7 mm (Lisney and Collin 2007). Also, meanwhile, some elasmobranch species have continuous eye growth, and others present ontogenetic variation in eye-to-head proportions (Litherland et al. 2009).

In chimaeras, the eyes are the best studied sense organ (Lisney 2010). They are positioned laterally on the head, and due to their relatively larger size in several species, vision might be an important sense to them (Lisney 2010). Chimaeras living in the mesopelagic zone may have

adaptations that either increase sensitivity, as the levels of sunlight diminish with depth, or enhance resolution, allowing localization of small sources of bioluminescence against an otherwise featureless background. Most chimaeras are reported to have a pure rod retina, with a visual pigment that maximally absorbs the wavelengths of light available in deep water. However, species that live in brighter waters are reported to present cones and potentially color vision.

### Pineal Complex

The pineal complex, or median eyes, develops as embryonic outgrowths from diencephalic region of the brain and participates in the detection of light and the physiological adjustments to changes in light levels (as the ones related to day and night cycle). The pineal complex is formed by the pineal and parietal organs, with sensory neurons that extend from them to the brain.

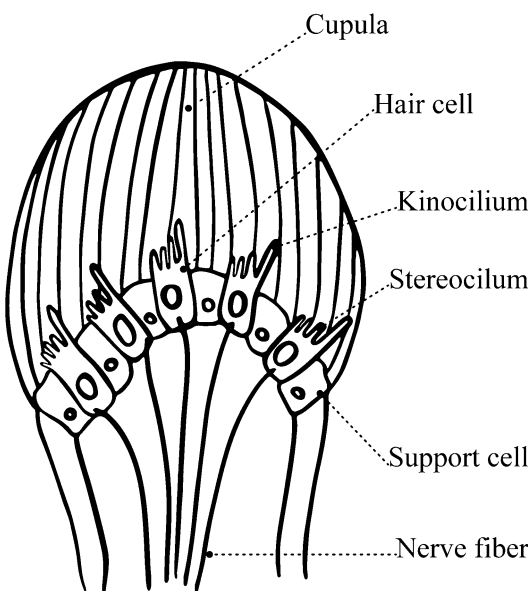
Most extant species of Chondrichthyes have a **reduced pineal organ** (absent in some electric rays, following Studnicka 1905), consisting mainly of a **neuroepithelium with photoreceptors, ganglion cells, supporting cells, glycogen-storing cells, and cytosome-rich cells** (Vigh-Teichmann et al. 1983). Despite not being completely explored for chondrichthyans, some species indicate that the pineal organ might have different responses to light and darkness, besides



correlation to the Gonadotropin-release hormone system (Mandado et al. 2001).

### Mechanoreception

Inner ear regions, membranous labyrinth, and lateral line organs detect different kinds of mechanical stimuli, but they all share the same type of sensory cell: the **mechanosensory hair cells**. Stereocilia (stereovilli) are arranged in a graded series by their height, at the apical surface of hair cells, and are also accompanied by a single kinocilium (a true cilium). The asymmetry provided by different lengths of stereocilia enables the hair cells to respond selectively to mechanical stimuli. Hair cells act like transducers that transform mechanical stimuli into electrical signals which are sent to the central nervous system (Hueter et al. 2004; Kardong 2016). The functional unit of all mechanosensory systems is the **mechanosensory neuromast** (or a modification of this), which is composed of a group of sensory hair cells surrounded by support cells and covered by a gelatinous cupula into which the stereocilia project (Fig. 3).



**Chondrichthyes Sensory Systems, Fig. 3** Neuromast organ, showing the sensory hair cells, supportive cells, gelatinous cupula, and nervous fibers. (Redrawn and modified from Kardong (2016))

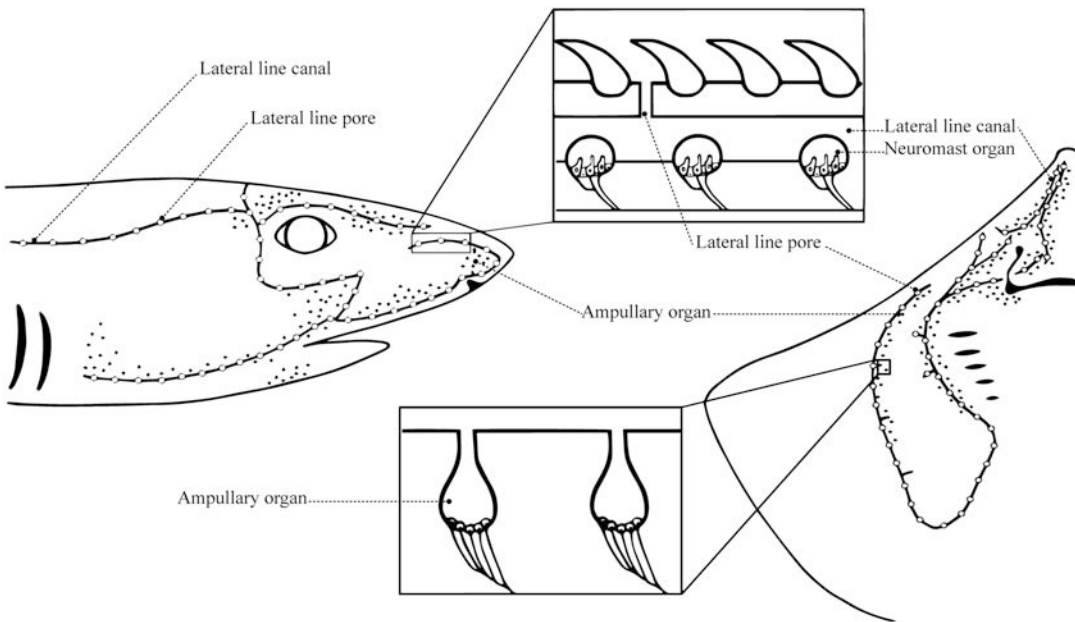
### Lateral Line System

The orientation and navigation in water (entry ► “**Chondrichthyes Navigation**”), as well as the ability to detect water movements at multiple scales, are fundamental for fishes, including chondrichthyans. Small-scale flows and pressure changes allow sharks, batoids, and chimaeras to navigate, locate preys and predators, and interact with conspecifics during social behaviors (Hueter et al. 2004). These stimuli are detected by sensory receptors located on the skin, the so-called **mechanosensory lateral line system** (Fig. 4).

The lateral line system is composed of two lateral line canals that extend posteriorly from the endolymphatic pores on the dorsal surface of the head to the tail. Anteriorly, these lateral line canals branch off over the head of chondrichthyans, showing varied degrees of complexity (Maruska 2001; Hueter et al. 2004; Gardiner et al. 2012). The hair cells are oriented parallel to and surrounding the lateral line canal, providing information about the direction in which the animal moves and on water disturbances (Kardong 2016).

Several types of mechanosensory end organs are found in chondrichthyans, differing from each other by morphology and location: **superficial neuromasts** (pit organs or free neuromasts), **pored** and **nonpored canals**, **spiracular organs**, and **vesicles of Savi** (Maruska 2001; Maruska and Tricas 2004; Gardiner et al. 2012). Superficial neuromasts are situated on the skin surface either in grooves on raised papillae, or between modified placoid scales, with their cupula directly exposed to the environment (Gardiner et al. 2012). Sharks and bony fishes differ in the position of superficial neuromast epithelium, and the configuration observed in the former may enhance water flow parallel to the cupula to provide greater directional sensitivity (Hueter et al. 2004; Gardiner et al. 2012).

Pored canals are in contact with the surrounding water via pores on the skin surface and help to detect water movements generated by prey, predators, and conspecifics, and to localize objects while swimming (distortions in the animal’s flow field) (Fig. 4). The pattern of cranial lateral line canals is similar for all chimaeroids, but its overall



**Chondrichthyes Sensory Systems, Fig. 4** Lateral view of a small-spotted catshark *Scyliorhinus canicula* (left) and ventral view of an eyespot skate *Atlantoraja cyclophora* (right), showing the pattern of lateral line canals and pores

and ampullary organs. The upper detail highlights neuromasts' positions inside lateral line canals, and the bottom detail shows ampullary organs at skin surface

unique pattern is poorly understood and difficult to homologize (entry ► [“Homology”](#)) with other vertebrates (Didier 1995).

Nonpored canals are isolated from the environment and do not respond to pressure differences. Instead, these canals may function as tactile receptors that receive information on contact with prey, the substrate, or conspecifics during social interactions (Maruska 2001; Gardiner et al. 2012). Nonpored canals are found on the ventral surface of skates and rays, and also on the head of many shark species.

Spiracular organs and vesicles of Savi are specialized mechanoreceptors isolated from the surrounding water, mainly found in rays and with some function in proprioception and tactile stimulation, respectively. However, little is known about their biological function (Maruska 2001).

The lateral line system detects differential movement between the body surface and the surrounding water. Even in low-visibility waters or during nocturnal activities, chondrichthyans can navigate around obstacles (a kind of distant touch) in their environment by detecting compression

waves in the water through lateral line system (Kardong 2016). Changes in the shape of cupula are coupled to stereocilia and kinocilia motions, causing depolarization or hyperpolarization of the hair cell. Then, the information is sent to the mechanosensory-processing centers in the hind-brain through the primary afferent neurons (Gardiner et al. 2012). There is some evidence that the mechanosensory lateral line system could play a secondary role in hearing since low-frequency vibrations result from sounds propagating through the water, in a similar way that stimuli is detected by neuromasts (Montgomery et al. 2009; Kardong 2016).

#### Membranous Labyrinth

The membranous labyrinth originates from the lateral line system and contains **three semicircular canals** filled with **endolymph** and surrounded by **perilymph**, both liquids presenting a similar consistency to the lymph (Kardong 2016). In chondrichthyans, the membranous labyrinth is connected with the environment through the **endolymphatic duct**. Three sensory areas

connected and involved in balance and sound perception are present along the semicircular canals: the **saccul**, **lagna**, and **utricle** (Fig. 5). Besides these compartments, expanded neuromasts known as **cristae** are arranged in ampullae at the base of each semicircular canal. All these components are encapsulated within the optical region (situated at the posterior end of the chondrocranium) (Hueter et al. 2004; Kardong 2016).

The sensory receptor inside the saccul and utricle is the **macula**, which is a modified neuromast with hair cells and a gelatinous cupula overlain by an otoconial mass (Gardiner et al. 2012). Head movements or changes in body position modify the orientation of maculae, and the otoconia (calcium carbonate granules) interact with the maculae, accentuating the response to angular acceleration or changes in head orientation. Semicircular canals respond to rotation and angular acceleration by differences in responsiveness of the canals and liquids within these regarding the head movements (Kardong 2016).

#### Auditory System

The hearing has different aspects when comparing aquatic and terrestrial vertebrates. The air and inner ear liquids differ regarding their responsiveness to sound waves. The evolution of medium ear and associated structures in terrestrial vertebrates

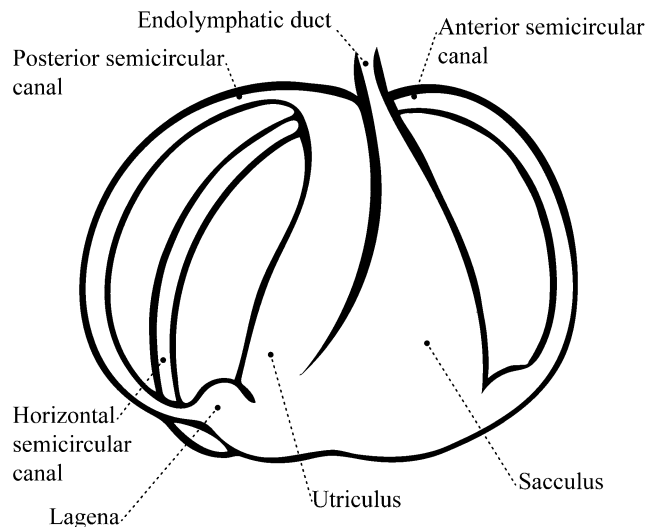
collects, amplifies, and transmits sounds from the air to the inner ear at a level sufficient to stimulate the sensory hair cells. On the other hand, in aquatic environments, both the vertebrates and their environment are composed mainly by water; in a way, both present similar frequency ranges. Thus, the sound propagates easily from the aquatic environment to the liquid inner ear environment (Gardiner et al. 2012).

The **saccul** and **lagna** (developed as an extension of the saccul) are both involved in the hearing. Hair cells located within the saccul and lagna are stimulated by sound vibrations and move against otoconia of different shapes and sizes. Otoconia are sensible to accelerations produced by a sound field and play a similar role to the otolith organs of bony fishes helping to localize a sound source. Sound information differing in direction and frequency are detected by the hair cells and transmitted to the hind brain via the VIII (octaval) cranial nerve (Gardiner et al. 2012).

A tympanic connection to the posterior semicircular canal called **fenestra ovalis** is located at the base of the parietal fossa (posterior end of the skull), which consists of a unique condition of chondrichthyans. The posterior canal ducts of the semicircular canals contain a sensory macula, the **macula neglecta**, which is not overlain by otoconia. The macula neglecta consists of one or

#### Chondrichthyes Sensory Systems,

**Fig. 5** Generalized chondrichthyan inner ear, based on Hueter et al. (2004) and Kardong (2016)



two patches of sensory hair cells that show a variety of orientations. The variation in the structure of the macula neglecta has been hypothesized to be linked to the foraging behavior (Corwin 1978), and several studies have shown the importance of the macula in detecting sound and/or vibration (Lowenstein and Roberts 1951).

Despite the auditory system being better described in elasmobranchs, some differences have been reported for chimaeras' auditory system. In the last, there are differences in position, elaboration, and enlargement of the macula neglecta, presence of a connection (*crus commune*) between the anterior and posterior semicircular canals, and absence of separation between saccule and utricle (Maisey 2001). However, the functional significance of these variations is not yet understood.

### Electroreception

Electroreception is the detection of external electric fields by specialized receptor cells that convert electric currents into action potentials (Crampton 2019). It evolved several times in Vertebrates' history but is usually found in fishes, some amphibians tadpoles, and living monotremates, albeit elasmobranchs being one of the better-known groups to use this sense.

The electroreception can be discriminated in two types: passive electroreception, the capacity of detecting weak, direct current fields or low-frequency sinusoidal fields (usually <30 Hz); and active electroreception, the capacity of the organism to generate an electric field by their electric organ discharges, and to perceive the environment by the distortions of this field caused by objects and organisms (Caputi et al. 2008; Crampton 2019).

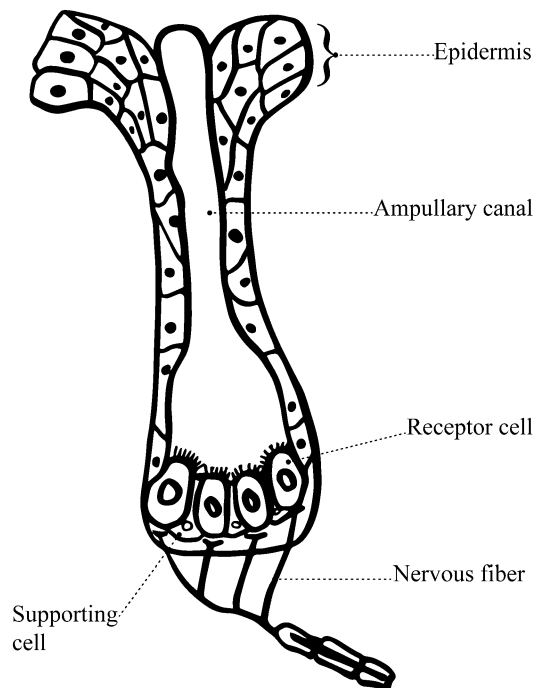
Electroreceptors (entry ► [“Electroreceptors”](#)) are **modified neuromast organs** located in pits within the skin, predominant at the anterior region of the body, and can be divided into two types: ampullary organs and tuberous organs. They usually develop from placodal tissue adjacent to the tissue that forms the lateral line mechanoreceptors; meanwhile, ampullary organs are specialized in detecting weak electric currents, and tuberous organs are specialized in responding to

high-frequency electric fields. Only passive electroreception is present in chondrichthyans, which present **modified ampullary organs**.

### Ampullary Organs

All chondrichthyans possess an elaborate ampullary electroreceptor system that is exquisitely sensitive to low-frequency electric stimuli (Hueter et al. 2004). Besides many living gnathostomes having ampullary organs, in elasmobranchs such organs are clustered on the head, adjacent to the lateral line canals, and are frequently referred to as **ampullae of Lorenzini** (Fig. 6). Chimaeroids are known to have electroreceptive ampullae that are homologous to the ampullae of Lorenzini of elasmobranchs, despite the ampullae pores of the first being usually smaller and in lesser amounts than those of the second (Lisney 2010).

The ampullary system of chondrichthyans is known to mediate orientation regarding local



**Chondrichthyes Sensory Systems, Fig. 6** Chondrichthyan ampullary organ (also known as ampullae of Lorenzini), showing the sensory receptor cells, supporting cells, and mucopolysaccharide-filled ampullary canal. The major extension of the ampullary organ lies beneath the epidermis, in the dermis

inanimate electric fields, in the detection of bioelectric fields produced by preys and predators, and also might participate in geomagnetic navigation and intraspecific social interactions (see Hueter et al. 2004 and Lisney 2010 for a compilation). Besides electroreception, the ampullary organs can participate in temperature sensitivity, which is translated into electrical information (Brown 2003).

A single ampulla consists of a small chamber and a subdermal canal that projects to the surface of the skin (Fig. 6). The ampulla chamber is formed by several small pouches, the alveoli, which present the sensory receptors and support cells aligned at its wall. The support cells also produce a glycoproteic gel that acts as an electric conductor from the ampulla pore to its sensory receptors (Hueter et al. 2004).

The ampullary organs form clusters, especially at the head of sharks and chimeras, with additional pores along the body of rays (Fig. 4). The highest density of ampullary organs is found near the mouth, being related to prey detection (Kajiura et al. 2010; Newton et al. 2019). The extended snouts of some chimaerids and elasmobranchs offer an opportunity to increase the spatial distribution of ampullary electroreceptors, with ampullary pore density relatively higher at the ventral surface of the head (Lisney 2010).

There is substantial interspecific variation in the number and distribution of ampullary organs, which might have a relation to phylogenetic relatedness, morphological similarity, species distribution within and across habitats, and diet preferences (Kempster et al. 2012). Because individuals do not grow new pores or redistribute them during development, the electrosensory resolution decreases as the inter-pore distance increases throughout ontogeny (Kajiura 2001). Therefore, as chondrichthyans age, they will experience a net loss of electroreceptive resolution, a gain in receptor sensitivity, and a larger sensory field that samples a greater water volume (Newton et al. 2019). Nevertheless, for chondrichthyans as a whole, the region of electroreception information integration (anterior and posterior lateral line lobes at the telencephalon) is usually enlarged, suggesting that electroreception (besides vision and lateral line

information) may be of importance for Chondrichthyes' sensory system (Lisney 2010).

## Cross-References

- [Chondrichthyes Morphology](#)
- [Chondrichthyes Navigation](#)
- [Electroreceptors](#)
- [Evolution of Animal Color Vision](#)
- [Homology](#)
- [Olfactory Perception](#)
- [Photoreceptors](#)
- [Vertebrate Nervous System](#)
- [Vertebrates \(Chordata\)](#)

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## Chorion

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Chorion is the thin extraembryonic membrane that covers the embryos and other extraembryonic membranes of reptiles, birds, and mammals. The extraembryonic membrane is made up of certain specialized embryonic tissue or structures that



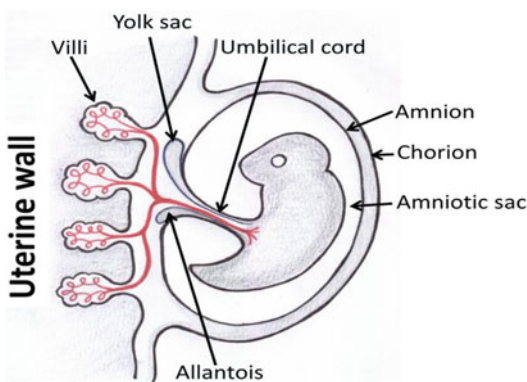
temporarily or permanently do not enter into the formation of the embryo themselves but plays an important role to fulfil the care and maintenance of the developing embryo. In the embryos of all terrestrial vertebrates, four sets of extraembryonic membranes are common, these are: amnion, chorion, yolk sac, and allantois. Out of these, chorion is the outermost one.

## Development

In developing reptiles, birds, and mammals, the lateral plate mesoderm splits into an outer somatic layer of mesoderm and an inner splanchnic layer of mesoderm. The somatic layer lies at the inner side of the ectoderm and the splanchnic layer lies at the outer side of the endodermal layer. There is also a coelomic space which is present between these two mesodermal layers. The somatic layer of mesoderm and ectoderm are collectively known as somatopleure, while the splanchnic layer of mesoderm along with endoderm forms the splanchnopleure. This extraembryonic somatopleure contributes to the formation of chorion and amnion while the splanchnopleure forms the yolk sac and allantois (Gilbert et al. 2003) (Fig. 1).

## Structure

Chorion is made up of two layers: trophoblast as the outer layer and mesoderm as the inner layer.



**Chorion, Fig. 1** Diagrammatic representation of extra-embryonic membranes

The trophoblast is made up of cytotrophoblast and syncytiotrophoblast. The cytotrophoblast is the inner one and considered to be the trophoblastic stem cells. The syncytiotrophoblast is the outer layer and made up of multinucleated type of cells (Cruz et al. 1991; Bianchi et al. 1993). In mammals, both the cytotrophoblast and syncytiotrophoblast initially helps the embryo to adhere and move into the uterine wall by digesting uterine tissue. At the same time, the uterus send blood vessels into this area and the extraembryonic mesoderm from gastrulating embryo extend outwards. This extraembryonic mesoderm then joins the trophoblastic extension and gives rise to the vessels of the umbilical cord. This fully developed extraembryonic chorion in mammals fuses with the endometrium of the female uterus to create the placenta (Renfree et al. 1982).

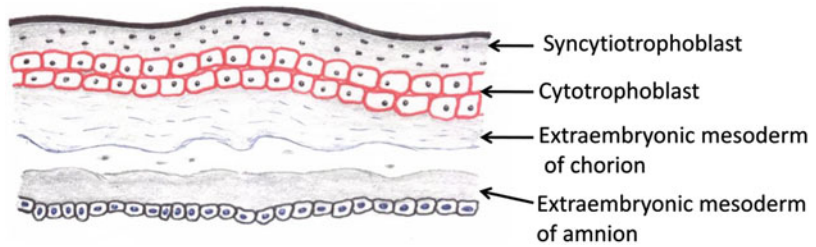
In reptiles and birds, the mesodermal layer of chorion fuses with the adjacent mesodermal layer of the allantois and formed chorioallantois or chorioallantoic membrane. This vascular membrane composes of three different layers: chorionic epithelium, the mesenchyme, and the allantoic epithelium (Fig. 2).

## Function

Development of extraembryonic membrane in reptile, bird, and mammal's embryos has taken a new evolutionary direction. Egg developing in water provides the egg with various favorable environmental conditions; however, none of the favorable features are provided on dry land. Reptiles and birds lay their eggs on dry land. Thus the eggs are subjected to desiccation and sudden change in temperature. To accomplish this, the embryo produces extraembryonic membranes to mediate with the environment. Although in mammals instead of shell placenta is present, but the basic pattern of extraembryonic membrane remain same.

Thus chorion, as the outermost extraembryonic membrane serves the following functions.

- (i) In the embryo of birds and reptiles, the blood capillaries are found between chorionic epithelial cells which closely adhere to the shell.

**Chorion,****Fig. 2** Diagrammatic representation of chorionic layers

This allows maintaining a close contact with the air present in the pores of the shell membrane. As a result, exchange of oxygen and carbon dioxide gases happen in the developing embryos.

- (ii) In birds during embryonic development, chorioallantoic membrane helps in transporting calcium into the embryos from the eggshell, thus it plays an essential role in bone formation.
- (iii) In mammals, the chorion forms the fetal portion of the placenta. Through this placenta mother provides the fetus with nutrients and oxygen, and the fetus sends its waste products (mainly carbon dioxide and urea) into the maternal circulation (Schjenken et al. 2012).
- (iv) The chorionic villi do not allow the mixing of maternal and fetal blood cells, thus it provides barriers to both the mother's and fetal immune system (Gilbert et al. 2003).
- (v) Placenta also provides hormones for the maintenance of pregnancy.
- (vi) Recent studies also suggest some placental mechanisms that block the mother's immune system from attacking foreign substances produced by the embryo (Schjenken et al. 2012).

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## Chorus

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## Synonyms

[Communal song](#); [Group singing](#)

## Cross-References

- [Embryo](#)
- [Fetus](#)

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## Definition

The non-random distribution of acoustic signals where multiple individuals signal in close temporal and spatial proximity.

## Introduction

Choruses are a phenomenon produced by diverse taxa, including birds, mammals, and

fish. Moreover, chorusing behavior is particularly prevalent in anurans and insects. During chorusing behavior, there is a substantial peak in acoustic signal production including increases in signal rate, signal diversity, and signal complexity. Chorusing, in many species, may be the by-product of male-male interactions (Rehberg-Besler et al. 2016). The acoustic signals produced during chorusing exhibit species-specific features, which may be temporal (e.g., call or song rates) or spectral (e.g., patterns of frequency modulation within a signal). Many species exhibit distinct diel patterns in the production of choruses. For example, dawn chorus behavior has been described in diverse taxa, including birds, mammals, and fish, where signal production peaks during the period immediately before sunrise (Burt and Vehrencamp 2005). The signals that make up an animal chorus are produced to serve multiple biological functions, including social bonding, territory defense, and mate attraction (Ryan et al. 1981; Burt and Vehrencamp 2005). Further, the many biological functions of chorusing are not mutually-exclusive. Despite the benefits of chorusing, however, there are risks associated with broadcasting signals through the environment, including energy expenditure and risks of predation.

## Biological Functions

Chorusing, and the associated increase in signal production, may serve multiple biological functions, including social bonding, territory defense, and mate attraction. Acoustic communication is an efficient method of signaling commitment and affiliation (Hall 2009). In many taxa, chorusing may serve an important role in social bonding between mates or between social groups (Hall 2009). The males of many species use acoustic signals to establish and defend territories and resources. In insects, the acoustic signals of males can attract and repel rival males, which facilitates the establishment of evenly distributed territories among conspecific animals (Robinson and Hall 2002). Many birds will alter their dawn chorus behavior in response to a male competitor

intruding its territory (Foote et al. 2011). In response to an intrusion by a male competitor during chorusing, the male may attack, alter signal production to challenge the intruder, or abandon the territory. In addition to territory and resource defense, the acoustic signals of choruses are produced to attract potential mates. Males of many species will advertise acoustically from locations throughout established territories that are optimal for signal transmission. In many insects and anurans, males will aggregate near resources (e.g., vernal ponds) and engage in chorusing to attract mates. In many chorusing species, females can be exposed to acoustic signals produced by multiple neighboring males. As a result, females of many chorusing species are capable of discerning and comparing the advertisement signals of potential mates and will often select higher-quality mates (Richardson et al. 2008).

## Benefits and Costs

Individuals may gain multiple benefits from participating in choruses. In aggregating species of anurans and insects, males participating in aggregations can have advantages over lone calling males (Ryan et al. 1981). Choruses with more signalers are louder in amplitude and can attract females from wider geographic areas (Ryan et al. 1981). In many taxa, such as songbirds, chorusing and the associated maximum acoustic output is associated with the time of day when atmospheric conditions are most optimal for acoustic communication in order to increase signal transmission. Despite chorusing during optimal times of day, there are energetic costs associated with the production and maintenance of complex acoustic signals. Further, while animals are occupied with increased signal production and complexity, they are not dedicating time to foraging. The acoustic signals broadcast during chorusing can be used to advertise the signaler's location to potential mates; however, many predators are also able to acoustically detect an individual's location through eavesdropping on these signals (Lang et al. 2005).

## Conclusion

Chorusing, the non-random production of acoustic signals by multiple individuals, is a widespread phenomenon exhibited by diverse taxa, including birds, mammals, fish, insects, and anurans. There are numerous non-mutually exclusive biological functions that chorusing may serve including social bonding, territory defense, and mate attraction. Although there are multiple benefits gained from chorusing, the broadcasting of acoustic signals carries risks, including increased predation.

## Cross-References

► [Dawn Solo/Chorus](#)

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## Chris Evans

Linda Evans

Macquarie University, Sydney, NSW, Australia

Christopher Stuart Evans was born in Cambridge, England, on May 25, 1959. In 1968, his family emigrated to the United States but within 2 years moved again, this time to The Netherlands. Upon returning to the United States in 1973, Chris chose to attend a prep school in the United Kingdom and so completed his secondary education at Malvern College in Worcestershire. Returning to England helped Chris to fulfil an ambition that he had nurtured since a child, which was to attend Cambridge University, as this was also his father's alma mater. After qualifying in 1977, it was at Cambridge that he subsequently discovered his vocation. Pivotal during his studies in natural sciences was his first biological experiment on the display behavior of Siamese fighting fish (Evans 1985), which not only cemented his growing interest in ethology but in animal communication, in particular.

Upon completing his bachelor's degree in 1980 and returning to his family's home in the United States, a chance visit to Washington University in St. Louis seeking summer employment instead led to the offer of a place in their PhD program in experimental psychology, which Chris commenced later that year. Under the supervision of Stephen Gaioni, he embarked on a study of mallard duckling vocalizations, devising a series of behavioral experiments that used a computerized system, the latter triggering a love of innovative technology that was to be a significant feature of his later research.

The opportunity to work with animal behaviorist Peter Marler, then in the department of behavioral sciences at Rockefeller University, saw Chris with wife (and later research assistant) Linda relocate to the Center for Field Research in Ethology and Ecology in Millbrook, New York, just prior to his graduation in late 1986. Upon the award of a three-year NIMH postdoctoral fellowship, his new line of comparative research focused on categorical

perception and referential communication, specifically the production and perception of complex acoustic signals in domestic fowl. This experience deepened Chris' knowledge of digital signal processing techniques to analyze and manipulate biological sounds and also led to his first experiments using computerized visual stimuli to elicit alarm calling in birds. Progress was interrupted, however, when in mid-1989 the Marler Lab moved to the University of California at Davis, where they joined the department of zoology (later physiology and behavior). Chris played an instrumental role in the translocation and re-establishment of the lab's 20 tons of equipment, including the successful shipment of his beloved chicken colony, an experience that both highlighted and honed his exceptional organizational skills. Work carried out at the UC Davis Animal Communication Lab included his pioneering experiments using video to elicit behavioral responses (e.g., Evans and Marler 1991) and the first demonstration of referential signaling in a non-primate species (Evans et al. 1993).

In 1993, Chris accepted a lectureship in the department of psychology at Macquarie University in Sydney, Australia. Building his lab with limited resources was challenging, but he applied himself to the task with energy and determination. Initially based in a 1940s era cottage on the Macquarie grounds, he gradually expanded the operation to include extensive aviaries for his new chicken colony and adjacent transportable buildings to house indoor birds and extra office and lab space. Soon after arriving at Macquarie, he was awarded his first major federal funding from the Australian Research Council, and this, along with many subsequent grants, allowed regular investment thereafter in new digital imaging technology to support his ever-evolving, innovative exploration of animal cognition (e.g., later use of 3D animations and animatronics). He struggled initially with the distance that now separated him from his former US colleagues (whom he affectionately referred to as his "tribe"), and so, he made it a priority to attend the annual conference of the Animal Behavior Society, where his quick wit and eloquence became legendary. He also

found new research partners in the local Australasian Society for the Study of Animal Behaviour, for which he was later elected president (2000–2001).

Chris's lab grew steadily with the addition of graduate students and postdocs (e.g., Dan Blumstein, Ann Göth, and Ximena Nelson) and so did the range of topics and species studied, which was to eventually include courtship behavior by swordtail fish (Rosenthal and Evans 1998), signaling behavior by Australian lizards (Ord et al. 2001), social learning in brush turkeys (Göth and Evans 2004), and the antipredator behavior of wallabies (Griffin et al. 2001) – although Chris' primary research interest continued to be referential signaling using domestic fowl as a model system (e.g., Macedonia and Evans 1993; Evans 1997). Indeed, his work in extending understanding of functionally referential signals is acknowledged by researchers today as a major contribution to the fields of animal vocal communication and language evolution.

The arrival of behavioral biologists Ken Cheng in 1995 and Phil Taylor in 2002, in whom he found like-minded visionary colleagues, provided a catalyst for Chris's expansion of animal studies at Macquarie, first with the establishment of the *Center for the Integrative Study of Animal Behavior* (CISAB) in 2005 and in 2007, when animal behavior was identified by the university as a *Centre of Research Excellence* (CORE). The latter led to increased financial investment and support by Macquarie, enabling Chris as director of the CORE to not only headhunt new scientists (behavioral ecologists Simon Griffith and Martin Whiting and neuroethologist Andrew Barron) but also enlarge the facilities for animal behavior research, resulting in the construction of a purpose-built laboratory building on the campus to house the new teams. By 2009, CISAB had attracted 25 PhD students and 11 postdocs and that year alone received over one million dollars in grant funding, with national and international collaborative projects that included links with industry.

Chris's vision for the future was cut short, however, when in mid-2008, after experiencing occasional weakness in his legs, he was diagnosed



with motor neuron disease (also known as ALS or Lou Gehrig's disease). Despite the bleak prognosis, he continued to apply his energies to further consolidating research in animal behavior and cognition at Macquarie and in 2009 was instrumental in founding a new department of brain, behavior, and evolution. Although soon confined to a wheelchair, he continued to plan future work and also publish extensively in partnership with his former PhD student, now postdoc, K-lynn Smith (e.g., Smith and Evans 2011), with whom he was awarded a prestigious Australian Museum Eureka Prize in 2010 for "Scientific Research that Contributes to Animal Protection." However, the awards of which he was most proud were those bestowed by his "tribe": first, his election as a fellow of the Animal Behavior Society in 2004 and then distinguished animal behaviorist in 2010. Chris Evans died on November 17, 2011, but is remembered as a leader and technological innovator in the study of animal communication.

## Cross-References

### ► Referential Communication

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## Christine Ladd-Franklin

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Christine Ladd (1865) Student at Vassar College. (Photo Courtesy of Rare Book and Manuscript Library, Columbia University)

## Introduction

Christine Ladd (1847–1930) was born in Windsor, Connecticut. Her mother died when Ladd was 12, but she received encouragement and support from her father and grandmother to receive education through high school.

Desiring to attend college, Ladd sought her grandmother's support in recruiting her father's assistance. Her grandmother objected that, after 4 years of college she would be too old to get married. Ladd replied that, although it would give her "great pleasure to entangle a husband," it was unlikely because of the females in New



England greatly outnumbered males (this was one year after the end of the American Civil War) and that she “was decidedly *not* handsome.” Therefore, she argued that if she needed to support herself, she needed a college education. Her grandmother acquiesced and, in the Fall of 1866, she enrolled at Vassar College (Furumoto 1992, p. 178).

At Vassar, Ladd reported that she devoted most of her time to astronomy under the influence of Maria Mitchell, whom Rossiter (1982, p. 12) described as “the most important woman scientist in America in the nineteenth century.” Rossiter’s opinion was supported by the following:

In 1847 Maria Mitchell not only calculated the position of a new comet but also observed it across the sky and thereby won (after some controversy) the gold medal that the king of Denmark had promised to the discoverer. This made the twenty-eight-year old a celebrity. She was soon elected the first woman member of the American Academy of Arts and Sciences ... the American Association for the advancement of Science ... and eventually (1869) one of the first American women in the American Philosophical Society of Philadelphia.

After graduation from Vassar, Ladd taught for several years at secondary schools for women, an occupation she did not enjoy.

Eventually (1882), Ladd would attend and complete the requirements for a Ph.D. in mathematics and logic at Johns Hopkins University. However, as Johns Hopkins did not officially enroll female students, she was only able to attend with the support of Mathematics Professor, James J. Sylvester, who had been impressed by Ladd’s published papers in mathematics. Ladd studied mathematics with Sylvester and logic with Charles S. Pierce which made her the first American woman to study mathematics and logic at the graduate level (Aglar and Durmus 2013). While at Johns Hopkins, Ladd married Fabian Franklin who earned his Ph.D. degree in mathematics there in 1880. Ladd-Franklin completed her Ph.D. requirements in 1882, but she did not receive the degree until 1926, occasioned somewhat by Johns Hopkins’ 50th Anniversary. At age 79, and 44 years after earning her degree, she attended the ceremony to receive it (Rossiter 1982).

Some of the most recognized historians who have written about aspects of Ladd-Franklin’s life (e.g., Furumoto 1992; Rossiter 1982; Scarborough and Furumoto 1987) have tended to emphasize Ladd-Franklin’s hard-fought career and efforts to gain recognition for women scientists and, at length, her conflict with Edward Bradford Titchener (more below), and they tended to write less about Ladd’s contributions to mathematics, logic, and psychology. This entry will include some information about Ladd-Franklin’s hard-fought career, but it will also include information about some of her contributions as a psychologist and logician.

## **Trials and Tribulations**

Among her trials and tribulations, Ladd-Franklin never had the equivalent of a tenured or tenure-track academic position, although she taught (often without pay) at Johns Hopkins and other universities, perhaps, most notably Columbia University. Fabian Franklin, by then professor of mathematics at Johns Hopkins, resigned in 1895 to become editor of the *Baltimore News*. In 1908, he became associate editor of the *New York Evening News* (Furumoto 1992) which is why Ladd-Franklin affiliated with Columbia. Most of Ladd-Franklin’s university-level positions were in psychology departments, because after she developed the Ladd-Franklin theory of color vision, she mostly self-identified as a psychologist. She also continued to teach and publish in logic throughout her career.

## **The Society of Experimentalists: Ladd-Franklin Versus Titchener**

Edward B. Titchener (1857–1927) was a founding member (1892) of the American Psychological Association (APA). By 1904, he became dissatisfied by too few presentations at APA of “pure” experimental psychology as he defined it, so Titchener resigned from APA and organized what eventually became the Society of Experimentalists. Titchener insisted on excluding

women from its membership and from attendance at its meetings. His primary reasons were that the presence of women would inhibit frank discussions and would interfere with the men's enjoyment of smoking. Ladd-Franklin's conflict with Titchener is discussed extensively in Rossiter (1982), Scarborough and Furumoto (1987), and Proctor and Evans (2014).

### Who Was Titchener?

Titchener, a native of England, earned an A.B. degree (1890) from Oxford University specializing in evolutionary biology, and he stayed an extra year to study with the eminent physiologist, John Burden-Sanderson. He then earned a Ph.D. (1892) in Psychology with Wilhelm Wundt, the widely recognized founder of experimental psychology. Titchener came to Cornell University in 1892 where he remained until his death in 1927 (Boring 1950).

### Women and the Society of Experimentalists

Many women psychologists confronted Titchener about his barring women from the Society of Experimentalists. Perhaps, Ladd-Franklin's most dramatic encounter with Titchener occurred in 1914 when the Society was to meet at Columbia University, where Ladd-Franklin was teaching, and a topic to be discussed was color vision about which she was a world authority. Seeking permission to attend, she wrote a fiery letter that included the following:

Is this good time for you to hold the mediaeval attitude of not admitting me to your coming psychological conference ... at my very door? So unconscientious, so immoral – worse than that – so unscientific!

...Both the Psychological and Philosophical Associations have long admitted women to their smokers and everything (I smoke – I should be very unfashionable if I didn't ...). It is only this acute-thinking and discussing little organization of yours (which seems to be so sadly dominated by you!) which still holds out. So mediaeval! – such an indignity! – well meant, I know – you have told me so – but such a mistaken kindness! Do quickly repent! And you need me! (Rossiter 1982, p. 280)

Titchener did not repent, and Ladd-Franklin asked James McKeen Cattell, the meeting's Columbia host, to take her as his guest, which he did. The

members, apparently begrudgingly, allowed her to attend the discussions on color vision.

After Titchener's death, Margaret Washburn and other women were admitted, but Ladd-Franklin was never invited to join.

Proctor and Evans (2014) defended Titchener against charges of misogyny. Among their points, Titchener supervised the Ph.D. degrees of 21 women, including Margaret Washburn, America's first woman to earn a Ph.D. in Psychology (1894). Titchener also supervised the Ph.B. (Bachelor of Philosophy, 1896) of Celestia S., Parrish who may be best remembered for establishing the first psychological laboratory in the southern United States, which she did at Randolph-Macon Woman's College in Lynchburg, VA (Thomas 2006). Washburn in 1927 expressed her long-term dislike for Titchener (see Scarborough and Furumoto 1987, p. 128), but in 1925 Parrish wrote that he gave her "... the most generous assistance then [referring to his role in her earning her degree] and afterwards became my very kind friend" (see Thomas 2006, p. 28).

### Ladd-Franklin's Accomplishments in Logic

Ladd-Franklin's dissertation supervisor was Charles S. Pierce. Historically, Pierce was, perhaps, America's most important logician (Putnam 1982). Ladd-Franklin's dissertation, *On the logic of algebra*, was published in *Studies in logic by members of the Johns Hopkins University* that was edited by Pierce (Agler and Durmus 2013). Agler and Durmus (2013, p. 306) wrote:

...Ladd-Franklin was not simply a pupil of Pierce, she was also his friend, managing editor, and as Shea Zellweger (1997, p. 336) writes "as much Pierce's mentor as she was his student."

*Time Magazine* in 1926 recognized that Johns Hopkins had that year awarded Ladd-Franklin's Ph.D. degree, 44 years late. About Ladd-Franklin it was written:

She completed her studies with distinction, demonstrating a form of rebuttal in argument called anti-logism, which has been recognized as "the

crowning achievement in a field [logic] worked over since the days of Aristotle” (*Time*, Vol.7 Issue 9, p. 30).

At age 81, Ladd-Franklin (1928, p. 532) reported:

I take it very ill of Mr. W. E. Johnson that he has robbed me without acknowledgement, of my beautiful word, “antilogism”. He says “Correlative to the syllogism we may here introduce the antilogism” (p. 75, Vol. II. Of his *Logic*), without any reference to the fact that the antilogism is the basic feature of my theory of deductive reasoning. (see Eugene Shen in *MIND*, pp. 54–60, 1927)

She continued by, once again, defining and illustrating the use of the antilogism. The antilogism is not easily explained, but perhaps a few quotations from Ladd-Franklin (1928, p. 532) will help.

This is, in fact, the natural form of reasoning ... invented before the more abstract and remote syllogism. I give at once an example of it – a real occurrence. A little girl of four years ... was making ... the experiment of eating her soup with a fork. Her nurse said to her, “Nobody eats soup with a fork, Emily,” and Emily immediately replied “But I do, and I am somebody.” (The connecting logic-word in the case of the antilogism is *but* instead of *therefore, so, or consequently*.) This instance (which may be taken as typical) is enough to show that the antilogism is quite as easy and as natural (in the proper circumstances) as any other form of deductive reasoning.

The interested reader is encouraged to read this entire two-page account of the antilogism as well as seek her many other contributions to logic.

## Ladd-Franklin's Accomplishments in Vision and Color Vision

On this topic, Ladd-Franklin is best known for 24 of her publications ranging from 1892 to 1926 that she compiled at age 82 for her book, *Colour and Colour Theories* (1929); the 24 publications are listed on page 281.

Before Ladd-Franklin, the two dominant theories of color vision were the Young-Helmholtz trichromatic theory and Hering's opponent process theory. Helmholtz updated Young's (1802) theory by using the latest information from physics and physiology. Hering drew from physiology but also from psychological

experiments using humans. Accompanying her husband, Fabian, on his sabbatical to Germany in 1891, Ladd-Franklin visited Helmholtz and Hering and worked in the laboratories of Helmholtz's protégé, Arthur König, and Hering's protégé, G. E. Müller. According to Kargon (2014), Ladd-Franklin added two new disciplines to her approach to color vision: evolutionary biology and symbolic logic.

Ladd-Franklin sought to reconcile the differences and deficiencies of the trichromatic and opponent process theories. The quoted summary below of her theory was based on her in-depth knowledge evident in Part I of her book of the evolution of color vision, the anatomy and physiology of the retina, the physics of light, and psychological research. Her knowledge of the various forms of color blindness also contributed to her theory of the evolution of color vision.

...there is a light sensitive substance in the rods which gives off, under the influence of light, a reaction-product which is the basis of the primitive sensation of whiteness. In the cones the next higher stage of development of the colour-sense (the yellow and blue vision of bees, that of partially chroma-blind individuals and of our own mid-periphery), the same light-sensitive substance has become, by a simpler molecular rearrangement, more specific in its response to light ... such ... that the two ends of the spectrum act separately to produce nerve excitant substances which ... when ... produced both at once, unite chemically to form the “white” nerve-excitant out of which they were developed. In the third and final stage the “yellow” nerve-excitant has again undergone a development in the direction of greater specificity, and red and green vision are acquired. (Ladd-Franklin 1929, p. 161).

## Closing Remarks

Ladd-Franklin's first publication on color vision was in the *Proceedings of the International Congress of Experimental Psychology, London* (1892) and was based on her oral presentation at the 1892 meeting. She critiqued deficiencies in Helmholtz's trichromatic theory and Hering's opponent process theory. Helmholtz was present. Overhead later that evening criticizing one of the

presentations (not Ladd-Franklin's), Helmholtz was asked what he thought of Ladd-Franklin's presentation. Helmholtz replied (English translation), *Oh, Mrs. Franklin, she understands the matter* (Ladd-Franklin 1929, p. 148). "She understands the matter" would have been an appropriate epitaph for Ladd-Franklin.

## Cross-References

- [Color Change](#)
- [Edward B. Titchener](#)
- [Electromagnetic Spectrum](#)
- [Evolution of Animal Color Vision](#)
- [Hermann von Helmholtz](#)
- [Margaret Floy Washburn](#)
- [Sensory Receptors](#)

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## Chromatid

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## Synonyms

[Daughter chromosomes](#)

## Definition

The two individual chromosomes attached together at centromere in a newly replicated chromosome are known as chromatids. They are clearly visible as two diagonal arms of a typical X-shaped chromosome in metaphase.

## Introduction

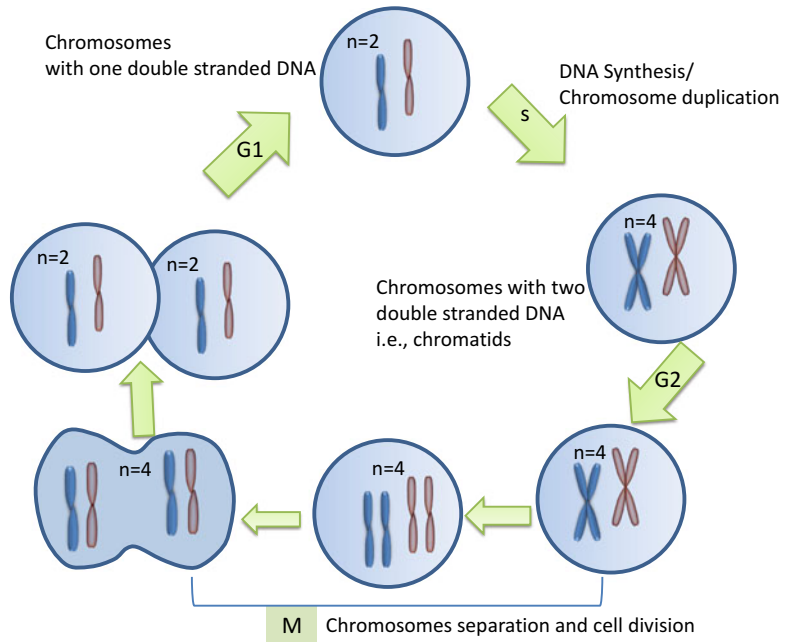
The cell, during DNA replication or synthetic (S) phase of the cell cycle, duplicates each chromosome, giving rise to chromatids containing equally divided genetic material. These duplicated chromosomes or chromatids are then separated equally with the help of microtubules to the two newly formed daughter cells (Fig. 1). The two chromatids of the same chromosome are referred as sister chromatids, while the chromatids of homologous chromosomes are termed as non-sister chromatids (Fig. 2).

## Homologous Chromosomes vs. Sister Chromatids

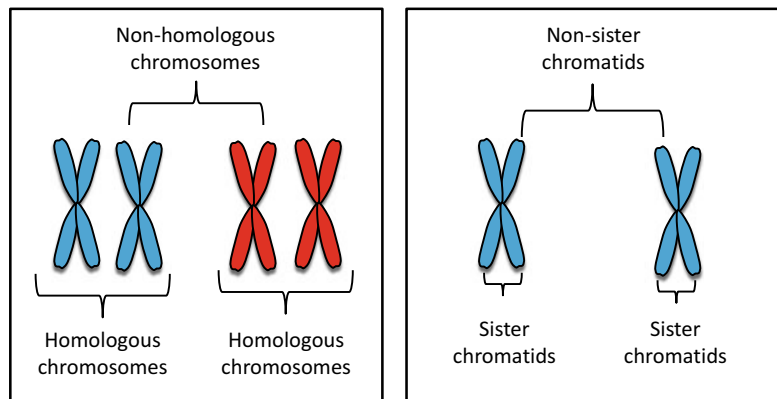
Diploid organisms like humans have two sets of individual chromosome, each of which is inherited from the maternal and the paternal gamete. These sets of chromosomes are known as homologous chromosomes (homologs) (Fig. 2). Although homologs are copies of the same chromosome inherited from two different parents, they are not identical as they might have different alleles for same genes, while the sister chromatids

# Chromatid,

**Fig. 1** Simplified dynamics of chromatids during cell division



**Chromatid, Fig. 2** The picture describes differences among homologous and nonhomologous chromosomes (a) and sister vs. non-sister chromatids (b)



are the replicated form of an individual chromosome, and hence they are identical to each other. Chromatids of two homologous chromosomes are called non-sister chromatids, and like homologous chromosomes, they carry the same genes but are not identical to each other.

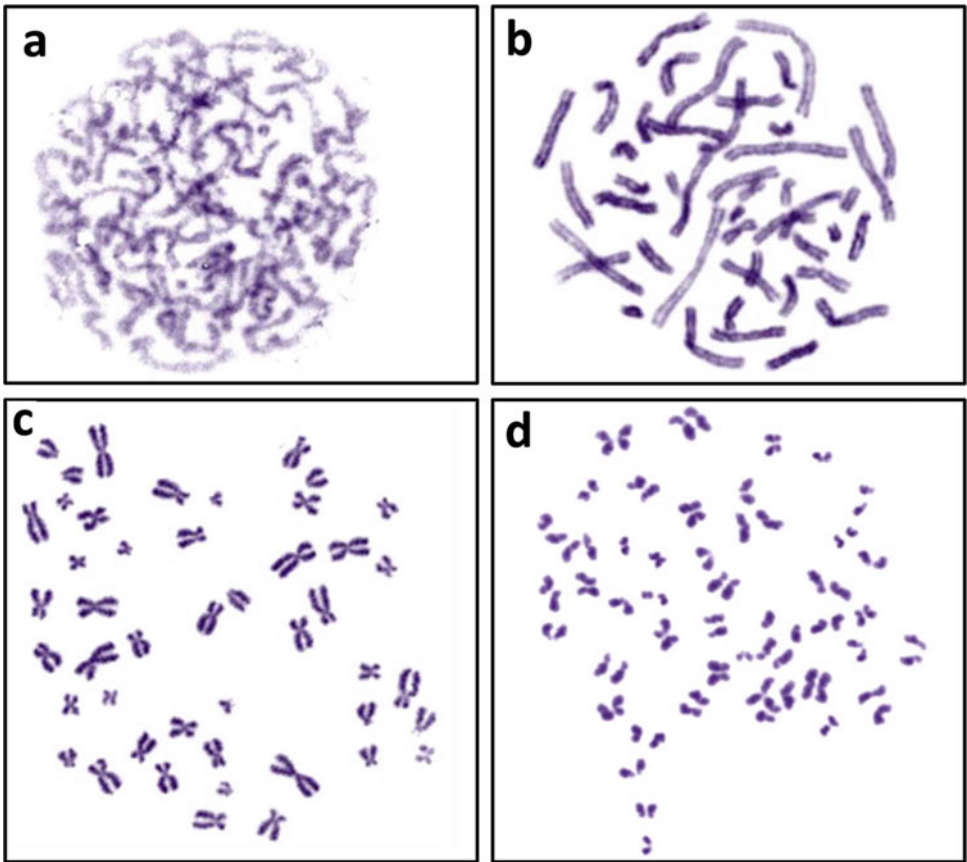
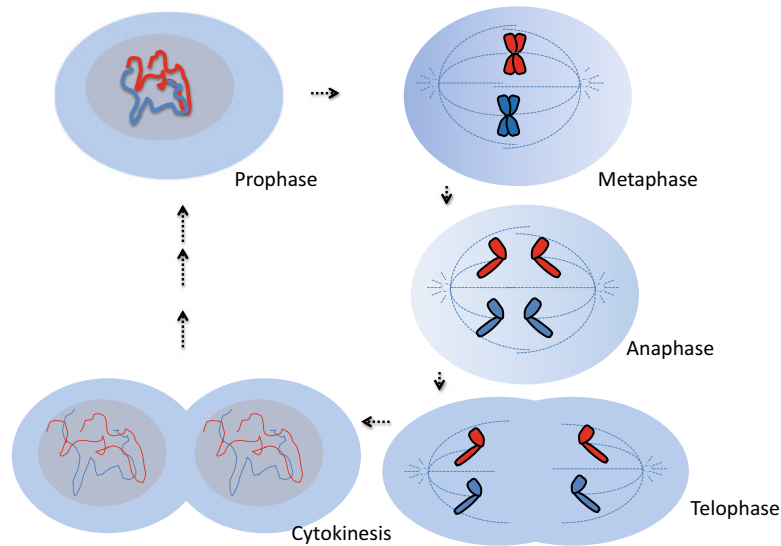
## Chromatids Are Visible in Mitotic Phases

Though chromatids are synthesized in synthetic phase (S-phase) of the cell cycle, they are not

visible until metaphase. During prophase, the chromatids are still attached together throughout their length making it impossible to visualize them separately (Figs. 3 and 4a, b). During this stage, ring-shaped protein complexes, *cohesin I and II*, encircle the two chromatids holding them together like in a “handcuff.” Cohesin complex consists of multiple proteins including *SMC I and III* (structural maintenance of chromosome), *RAD21*, *RAD21L*, *REC8*, and *STAG* proteins (Brooker and Berkowitz 2014). Cohesins at the arms are degraded as soon as cells enter into mitotic phase (M-phase), and chromatids are

**Chromatid,**

**Fig. 3** Pictorial demonstration of chromatids arrangement into mitotic phases; during metaphase all the chromosomes come at one axis, and the two chromatids are then pulled away toward opposite pole in anaphase



**Chromatid, Fig. 4** Chromosomal spreads from human peripheral blood lymphocytes representing morphology of chromosomes/chromatids at different mitotic phases of cell division. Prophase with indistinct chromatids and entangled chromosomes (**a**), late prophase/early

metaphase with partly resolved chromatids (**b**), late metaphase having chromatid arms totally separate; however they still have centromeric connection (**c**), and completely separated chromatids at anaphase (**d**)



visible separately in metaphase but are still attached together at the centromere. The appearance of chromosomes with two chromatids in metaphase is now visualized as classical X-shaped form (Figs. 3 and 4c). At anaphase protein complex called as *APC* (anaphase-promoting complex) releases *cohesin complexes* at the centromere through an enzyme *separase* (Peters 2006). Hence, with the start of anaphase, the chromatids are free to be pulled away from the centromere toward opposite poles and become separate chromosomes (Figs. 3 and 4d).

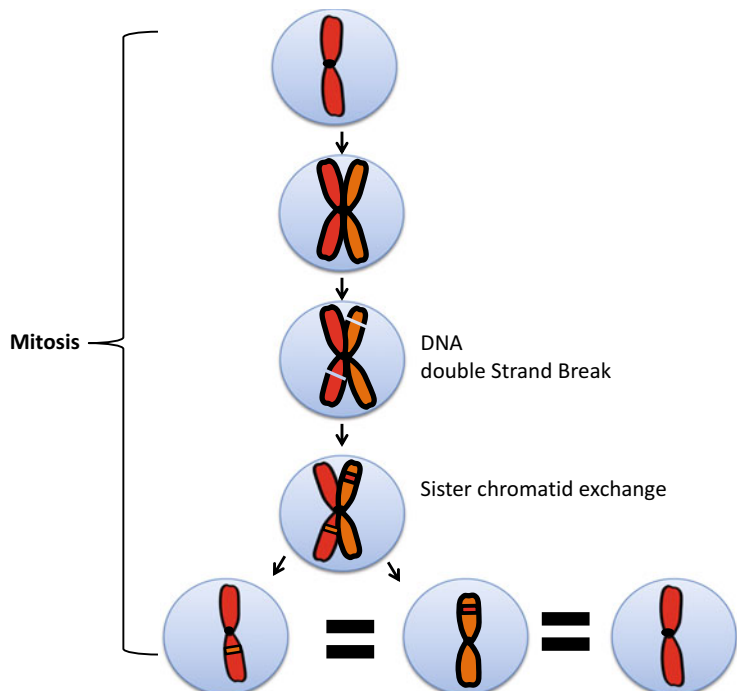
### Chromatids Play Essential Roles in DNA Repair

As described earlier, sister chromatids have identical sequence and hence provide opportunity for an essential cellular activity, i.e., DNA repair. DNA double-strand breaks (DSBs) are the most lethal type of DNA damage for a cell. They may lead to cell death or transformations through multiple kinds of chromosomal aberrations such as deletions, translocations, fragmentations,

etc. Therefore, to protect from these damages, cells are provided with extensive DNA repair mechanisms. Homologous recombination is the most accurate mechanism for DSB repair. In this repair mechanism, the genetic information lost due to DSB is restored using identical information from the sister chromatid as a template (**sister chromatid exchange**, Fig. 5) (Renkawitz et al. 2014; Goldfarb and Lichten 2010). Although sister chromatid-based HR is the predominant repair mechanism (Kadyk and Hartwel 1992), in rare instances when sister chromatids are not available, HR pathway may also use non-sister chromatids as template to recover lost information (Lafave and Sekelsky 2009).

In cases of nonavailability of sister chromatids, i.e., in pre-S-phase, sister chromatid exchange-based HR cannot take place. In such scenario, DNA repair does not necessarily involve homology and joins nearby broken ends of strands together. There are probabilities that wrong ends get joined leading to chromosome or chromatid-type aberrations. This mechanism is known as **nonhomologous end joining (NHEJ)** which is highly error prone.

**Chromatid, Fig. 5** DNA repair through homologous recombination pathway using sister chromatid exchange. Damaged part of one chromatid is resynthesized using undamaged sister chromatid as template. Sister chromatid exchange does not create recombinants as both the chromatids are identical



## Role of Chromatids in Genetic Diversity

Homology between non-sister chromatids is responsible for an important phenomenon in biological system, i.e., genetic diversity (Hunter 2015). Crossing over is a process of exchange of sequences between maternal and paternal chromosomes during meiosis and hence creating crossover/hybrid chromosomes in the gametes (Fig. 6). The process includes pairing of the two chromatids at homologous regions followed by breaking and rejoining of segments. Recombination of non-sister chromatids creates new combination of genetic material and hence diversity among genomes. Genetic diversity created during crossing over is the key reason why siblings are not identical as they receive different combination of genes. In contrast, identical twins which result from splitting of same fertilized eggs during gestation carry identical genome.

## Chromatid Aberrations Indicate DNA Damage

Chromatid aberrations are formed due to damage in one or both the chromatids independently. These aberrations are result of misrepair (joining

of wrong ends) or unrepaired DNA double-strand breaks. Major types of chromatid aberrations are briefly described below and represented in Fig. 7a, b

**Chromatid gaps:** discontinuous staining in small region of one chromatid and no positional changes in chromatids orientation.

**Chromatid breaks:** breaks in on one of the chromatid, and broken end can be observed flipping out of the chromosome.

**Isochromatid gaps and isochromatid breaks:** breaks or gaps in both the chromatid at same position not differentiable from chromosomal gap or break.

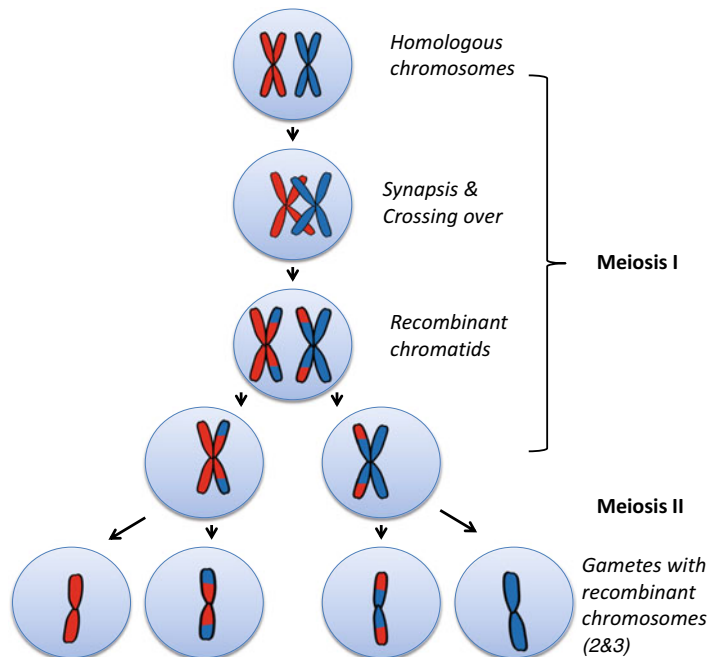
**Duplication/deletion** of sequence in one of the chromatid results in bulging of one chromatid at nonhomologous region.

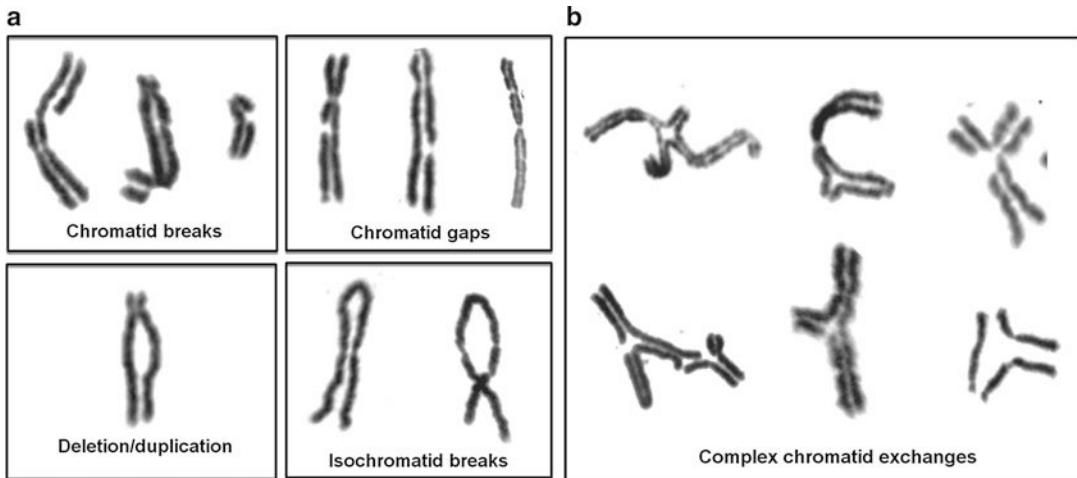
**Chromatid exchange:** just like translocation in chromosomes, chromatids also undergo exchanges resulting into biradial, tetraradial, or complex chromosomal structures.

Chromatid aberrations have significance in clinical diagnosis. The presence of high frequency of chromatid aberrations reflects extensive DNA damage as well as genomic instability. For example, smokers and cancer patients are observed to have higher frequency of chromatid aberrations (Haverić et al. 2016; Pascalis et al. 2014).

### Chromatid,

**Fig. 6** Crossing over; crossing over needs non-sister chromatid pairs, exchange happen through breaking and rejoining





**Chromatid, Fig. 7** Representative images of various types of chromatid aberrations: breaks, gaps, deletion, duplication (a), and chromatid exchanges (b)

## Conclusion

Chromatids are newly formed chromosomes in a cell about to divide into two. They offer a template for restoring damaged part for sister chromatid as well as help in creating variation among gametes by involving in crossing over. Increased levels of damaged chromatids strongly indicate genetic instability and DNA damage which could be associated with cancer and many other clinical conditions.

## Cross-References

- [Alleles](#)
- [Chromosomes](#)
- [Crossover](#)
- [DNA Repair Hypothesis](#)
- [Genetic Variation](#)
- [Nondisjunction](#)

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## Chromatin

- [Chromosomes](#)

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## Chromosomal Aberration

► [Trisomy](#)

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## Chromosomal Abnormality

► [Trisomy](#)

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## Chromosomal Anomaly

► [Trisomy](#)

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## Chromosomal Recombination

► [Crossover](#)

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## Chromosomal Translocation

► [Translocation](#)

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## Chromosomes

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### Synonyms

[Chromatin](#); [Genetic material](#)

### Definition

Chromosomes are highly compacted form of DNA molecules containing the genetic material

of any organism. Each DNA molecule inside the nucleus is wrapped around histone proteins in a highly ordered manner to form a chromosome.

### Introduction

The degree of compactness of chromosomes is highly flexible and depends on the stage of cell cycle. They are distinctly visible in the mitotic phase (particularly in metaphase), whereas in interphase they are present as indistinct entangled chromosomes fibers called chromatin. Most of the present understanding of packaging of chromatin into chromosome has come from a detailed study of exceptionally giant interphase chromosomes, viz., polytene chromosome in secretory glands of insects and lampbrush chromosome of some vertebrate oocytes.

Chromosomes facilitate the accommodation of huge DNA molecules within a tiny space inside a nucleus or a cell in case of prokaryotes. Total human genome is  $\sim 2(3 \times 10^9)$  bp, which corresponds to a total length of  $\sim 2$  m, and is condensed to approximately 10,000 times to fit in a nucleus with a diameter of few micron.

Prokaryotes have genome compiled in a single circular chromosome, which reside in a cytoplasmic territory called **nucleoid**. In addition to nucleoid, prokaryotes also have extrachromosomal DNA in a form of plasmids having independent replication ability. On the other hand, eukaryotes have larger and complex genome arranged inside a nucleus, and whole genetic material is distributed among several linear chromosomes in single or multiple copies. **Ploidy** describes multiplicity of chromosomes in a cell or organism. Organisms may be **monoploid**, **diploid**, or **polyploid** having only one, two, or more sets of same chromosomes, respectively. Polyploidy is less common among animals but frequently exists in plants. Organisms with asexual reproduction are usually monoploid, while sexually reproducing organisms are diploid. In case of diploid organisms, all somatic cells are diploid but the germ cells are monoploid which is generally referred as haploid, which after fertilization results in the formation of a diploid zygote. Thus, diploid organisms receive half set of

chromosomes from sperm while another half from ovum. The two sets of same chromosome are called **homologous chromosomes**. It should be noted that homologous chromosomes carry the same genes, but they are not identical since they are from two different parents. Eukaryotes also have mitochondrial DNA similar to prokaryotic circular chromosomes which works independently. Each species has a constant characteristic number of chromosomes. Here, it should also be noted that the number of chromosome or size of a genome barely reflects the complexity of an organism. A less evolved species may have larger number of chromosomes (Table 1), for example, *Agrodiaetus shahrami*, a species of butterfly that have 268 chromosomes, the highest number of chromosomes among metazoans (Lukhtanov et al. 2005).

**Essential Features of a Chromosome in Eukaryotic System Includes Origin of Replication, Centromere, and Telomere**

Since the chromosomes contain genetic material of an organism, therefore each chromosome must

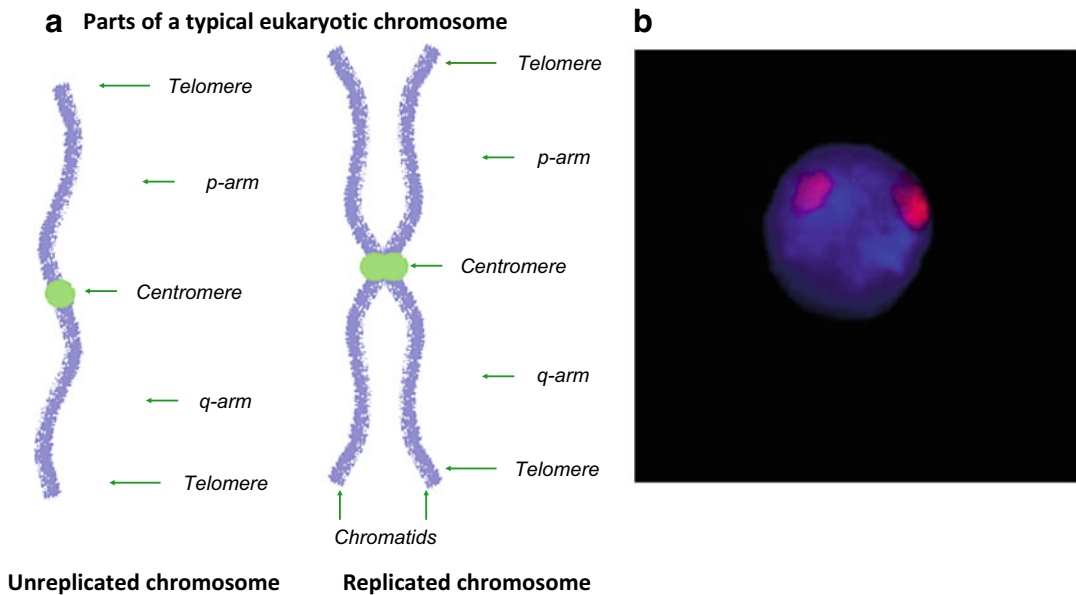
be capable of maintaining its integrity, undergoing complete replication and segregated equally between two daughter nuclei during the process of cell division. For these functions, each eukaryotic chromosome is provided with three essential parts: two telomeres, a centromere, and origin of replication (Fig. 1a.). Telomeres are heavily condensed tips of linear chromosomes, which protect the genetic material from degradation. Centromere is a point in the chromosome at which two sister chromatids of a replicated chromosome are held together before cell division attached to the centromere and segregate the duplicated chromosome between two daughter nuclei.

**Organization of DNA into Chromosome Is Achieved in Multiple Levels of Condensations**

Chromosomes have variable degrees of compaction at different stages of cell cycle. Most of the interphase chromosomes are elastic contractile 30 nm fibers known as chromatin. It is difficult to visualize them distinctly under light microscope. However upon chromosome-specific

**Chromosomes, Table 1** Characteristic number of chromosomes among various animals

|     | Animal          | Scientific name                | Chromosome number diploid (2n)                                                            |
|-----|-----------------|--------------------------------|-------------------------------------------------------------------------------------------|
| 1.  | Humans          | <i>Homo sapiens</i>            | 46                                                                                        |
| 2.  | Great apes      | <i>Gorilla</i>                 | 48                                                                                        |
|     |                 | <i>Pan (chimpanzee)</i>        |                                                                                           |
|     |                 | <i>Pongo (orangutan)</i>       |                                                                                           |
| 3.  | Rhesus monkey   | <i>Macaca mulatta</i>          | 42                                                                                        |
| 4.  | Dog             | <i>Canis lupus familiaris</i>  | 78                                                                                        |
| 5.  | Domestic cat    | <i>Felis domesticus</i>        | 38                                                                                        |
| 6.  | Mouse           | <i>Mus musculus</i>            | 40                                                                                        |
| 7.  | Rabbit          | <i>Oryctolagus cuniculus</i>   | 44                                                                                        |
| 8.  | Rat             | <i>Rattus rattus rattus</i>    | 38                                                                                        |
| 9.  | Chinese hamster | <i>Cricetulus griseus</i>      | 22                                                                                        |
| 10. | Dolphin         | <i>Tursiops truncatus</i>      | 44                                                                                        |
| 11. | Pigeons         | <i>Columba livia</i>           | 78                                                                                        |
| 12. | Mosquito        | <i>Culex pipiens</i>           | 6                                                                                         |
| 13. | Fruit fly       | <i>Drosophila melanogaster</i> | 8                                                                                         |
| 14. | Butterfly       | <i>Agrodiaetus shahrami</i>    | 268 (highest diploid number among animals)                                                |
| 15. | Jack jumper ant | <i>Myrmecia pilosula</i>       | 2 (lowest diploid number among animals, males are haploid hence have only one chromosome) |



**Chromosomes, Fig. 1** (a) Basic features of chromosomes. (b) Representation of chromosomal territory inside the nucleus: human chromosome 3 painted in sequence

specific red fluorescent probe shows its localized distribution in interphase nucleus

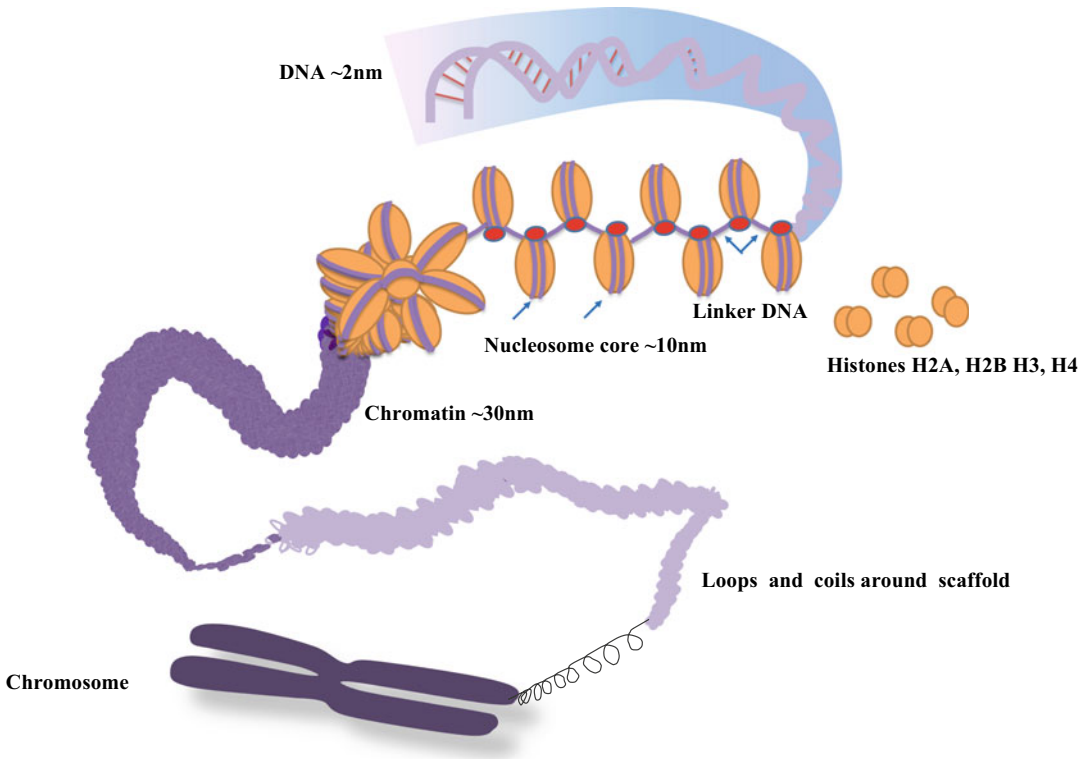
staining, it is observed that different chromatins do not mess with each other and harbor distinct territory inside the nucleus (Fig. 1b) (Misteli 2008). Thread of DNA-double helix is wrapped around octamer of **histone** proteins named **H2A**, **H2B**, **H3**, and **H4**, two units each. Each set of **histone** proteins with the DNA is known as **nucleosome** making the arrangement popularly known as **beads on a string**. Nucleosomes have ~1.65 round of DNA equivalent to ~145 bp and are connected by non-nucleosomal **linker DNA** of 10–90 bp. Nucleosomes come closer and further condense to 30 nm diameters called chromatin fiber (Fig. 2). Major proportion of chromosomes under normal physiological conditions stays in chromatin form which is a less condensed state that provides accessibility to various proteins and enzymes for gene expression and regulation. However chromosomal condensation is not uniform throughout the length, as telomeric and centromeric regions are highly condensed even in interphase and are termed as permanent **heterochromatin**, whereas the rest of the less condensed part of chromosomes are known as **euchromatin** (Fig. 3). It is notable that

heterochromatin regions are not expressible, gene poor, rich in short tandem repeats, and have higher AT content. Moreover, when expressible genes, by some means, are translocated to a heterochromatin region, they would not express the phenomenon known as **position effect** (Elgin and Reuter 2013). In contrast euchromatins possess expressible single-copy genes and have higher GC content.

### At Higher Condensation Levels, Chromosomes Can Be Distinctly Visualized Under Basic Light Microscopes

During mitosis, interphase chromatins are coiled and further compacted with the help of structural maintenance of chromosome (SMC) complexes comprising **cohesin**, **condensin**, and the **Smc5/6** proteins to make it the most condensed form of chromosomes (Jeppsson et al. 2014). The chromatin fibers form loops around scaffold proteins. At this stage, chromosomes are duplicated and two daughter chromosomes called sister





**Chromosomes, Fig. 2** Illustration of various condensation levels in a chromosome

chromatids glued together with the help of proteins named **cohesins**. Unlike interphase, all the chromosomes in mitotic phase are distinctly visible and countable under light microscope. Hence, mitotic metaphase is the best stage of the cell cycle for the study of overall shape, morphology, and anomalies of chromosomes (Fig. 4).

### Karyotype and Ideogram

A karyotype is an arrangement of chromosomes on the basis of their size and centromere position. As each species has a characteristic number and set of chromosomes, therefore karyotype also is unique for every biological species. Diagrammatic representation of karyotype is termed as karyogram or ideogram (Fig. 5c). Karyotype is prepared on metaphase chromosomes. Each chromosome is identified on the basis of its relative size and centromere position. Moreover, every

chromosome has a characteristic banding pattern upon differential staining based on their GC/AT content. Chromosomes are arranged in a descending order of their size. Karyotype is used to analyze various cytogenetic anomalies for clinical and research purposes.

A karyotype represents the following features of a species/individual:

1. Total number and sets of chromosome
2. Relative size of each chromosome
3. Types of chromosomes based on centromere position
4. Banding pattern
5. Sex chromosomes
6. Cytogenetic anomalies

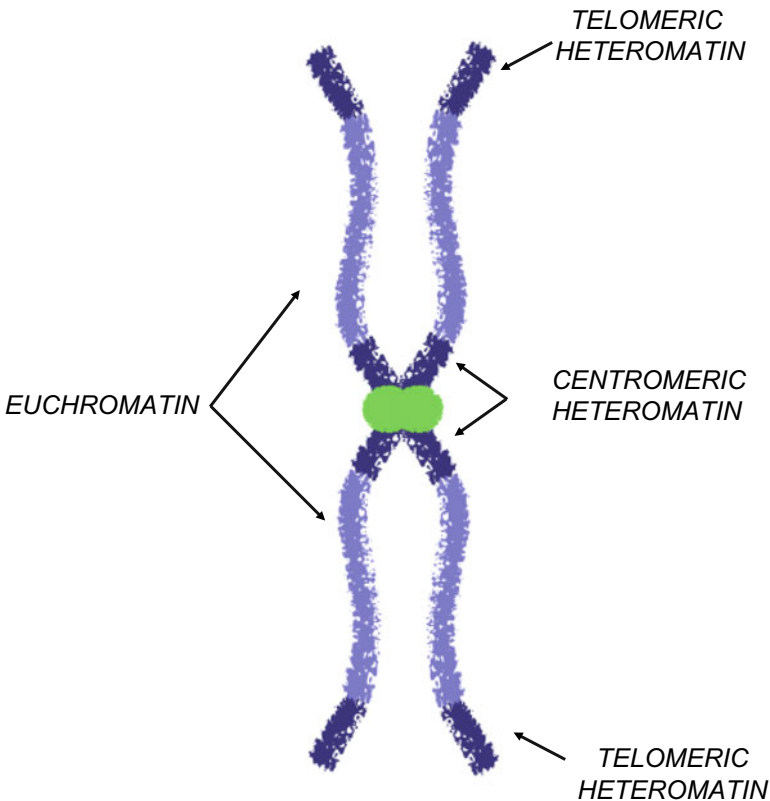
Karyotype of any normal human will show 46 chromosomes. Out of 46 we have 22 pairs of **autosomes** (chromosomes other than sex chromosome) and 2 sex chromosomes, XX for females

**Euchromatin**

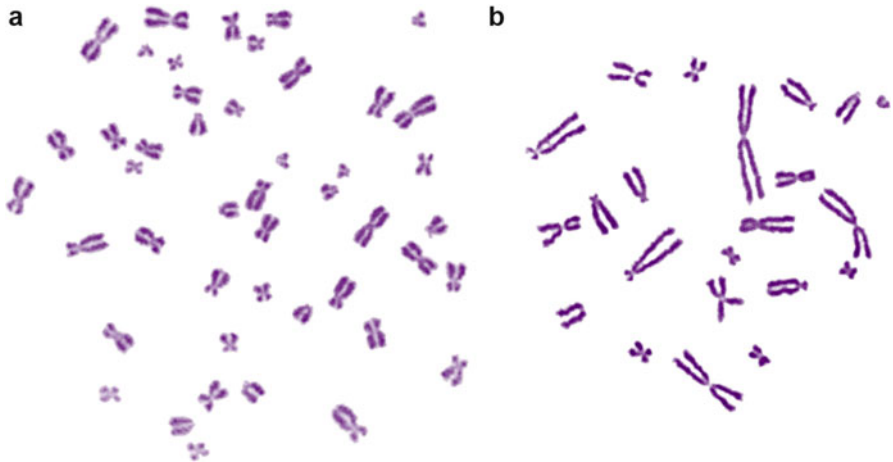
- Lightly stained regions
- Single copy genes
- GC Rich
- Expressible

**Heterochromatin**

- Darkly stained region
- Gene Poor
- Repeat Sequences
- AT Rich
- Inexpressible

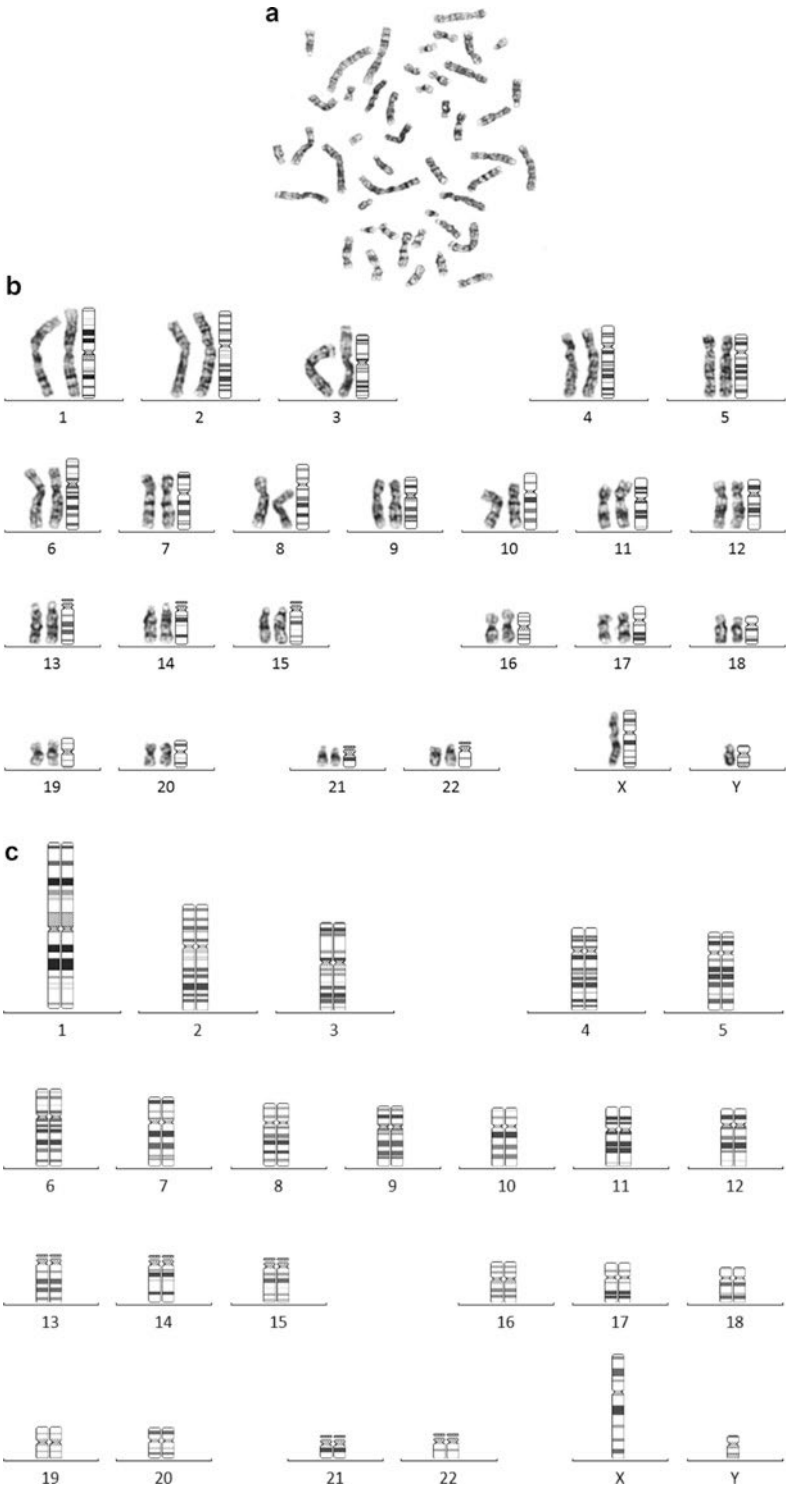


**Chromosomes, Fig. 3** Representation of major localizations of permanent heterochromatin with brief description



**Chromosomes, Fig. 4** Metaphase chromosomal spread from peripheral blood lymphocyte of a human female (a) and Chinese hamster ovary cells (b)

**Chromosomes, Fig. 5** G-banded metaphase spread from peripheral blood lymphocyte of a human male (a). Karyotype combined with a karyogram (b), along with complete karyogram of a human male (c)



and XY for males. The chromosomes are divided into seven groups as described in Table 2.

Aberrations in Chromosomes and Their Clinical Significance

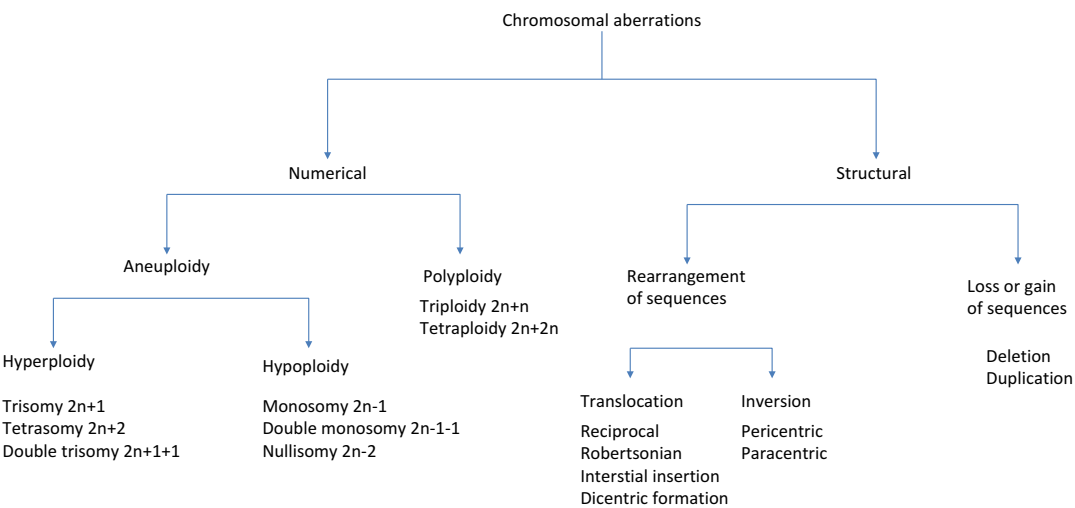
Chromosomal aberrations can be formed as a result of exposure to toxic agents such as alkylating agents, ionizing radiation, etc. These are broadly classified into two categories – **numerical aberrations** referring to changes in counts of the chromosomes which result from **meiotic or mitotic nondisjunction** of chromosomes that is unequal distribution of chromosome between daughter cells during cell division and

second one is **structural aberration** referring to morphological alterations in chromosomes. These are further subcategorized into different classes as depicted in Fig. 6. Structural aberrations include translocation of chromosomal segment to non-homologous chromosomes, joining of two chromosomes (Robertsonian translocation), and dicentric chromosome formation, inversion, and deletion of sequences. Various types of structural aberrations are described through diagrammatic and pictorial illustrations in Figs. 7 and 8.

These aberrations can be acquired from exposure to toxic agents or it can be inherited from parents. Most of the chromosomal aberrations observed are from embryonic stage receiving from one of the gametes and therefore present in

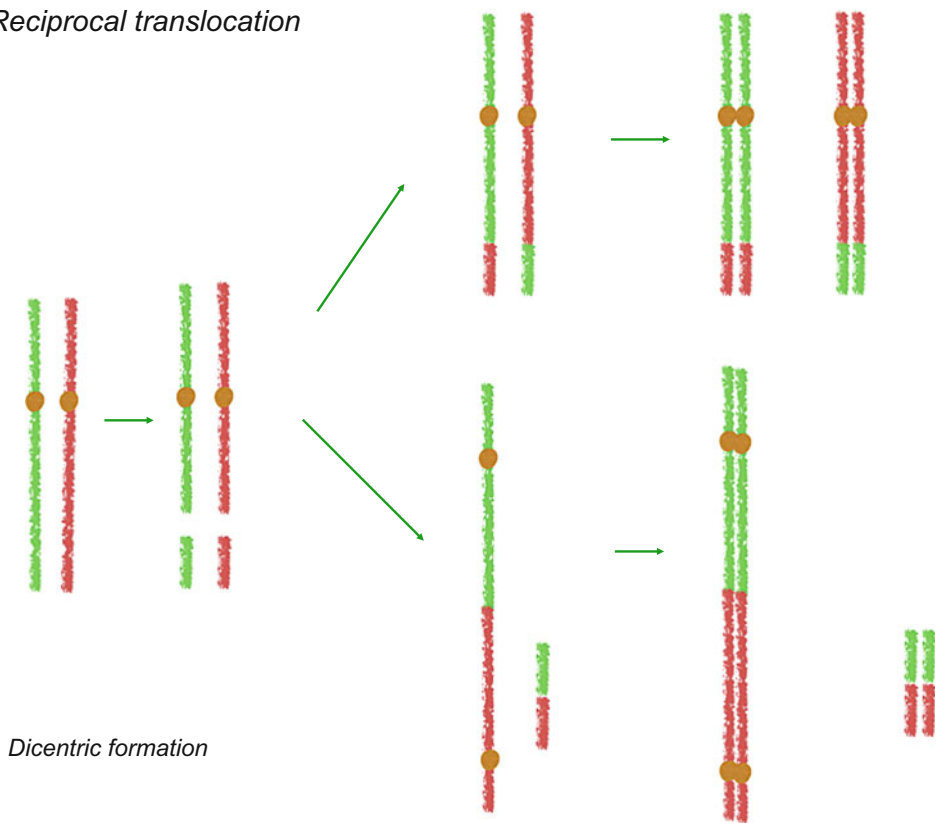
Chromosomes, Table 2 Categorization of human chromosomes based on size and centromere position

| Group           | Chromosome number | Description of chromosomes                              |
|-----------------|-------------------|---------------------------------------------------------|
| A               | 1–3               | Largest, metacentric (1st, 3rd) submetacentric (2nd)    |
| B               | 4–5               | Large, submetacentric                                   |
| C               | 6–12              | Medium, submetacentric                                  |
| D               | 13–15             | Medium submetacentric                                   |
| E               | 16–18             | Small, metacentric(16th) and submetacentric (17th–18th) |
| F               | 19–20             | Small metacentrics                                      |
| G               | 21–22             | Small acrocentrics                                      |
| Sex chromosomes | X                 | Median submetacentric, fits in “C” group                |
|                 | Y                 | Small acrocentric, fits in “G” group                    |

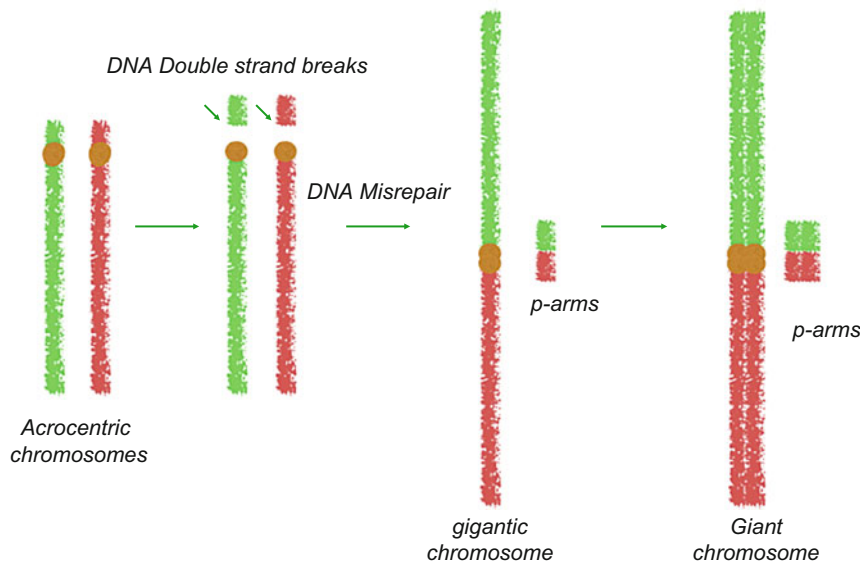


Chromosomes, Fig. 6 Categorizations of chromosomal aberrations

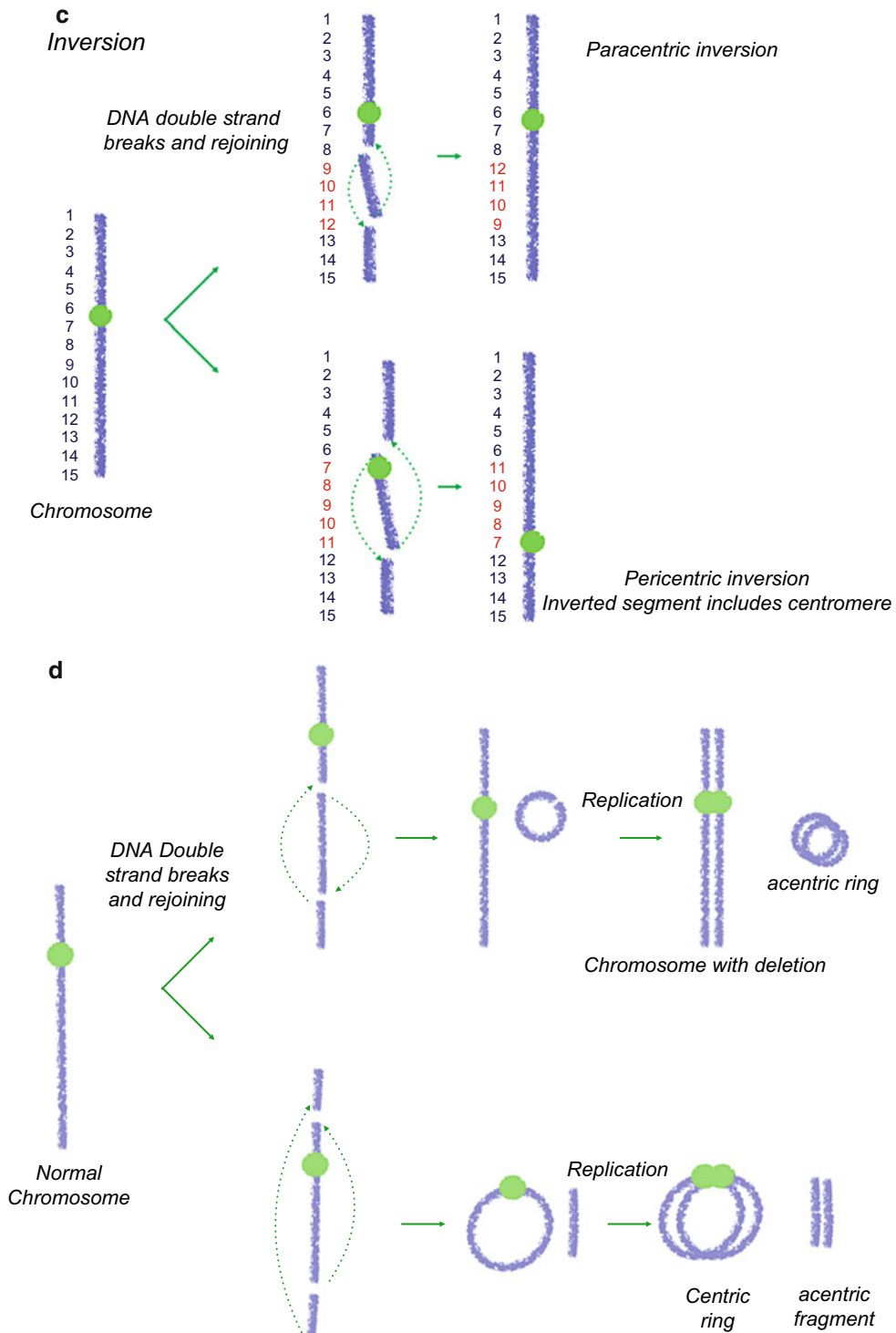
**a** *Reciprocal translocation*



**b** *ROBERTSONIAN TRANSLOCATION*



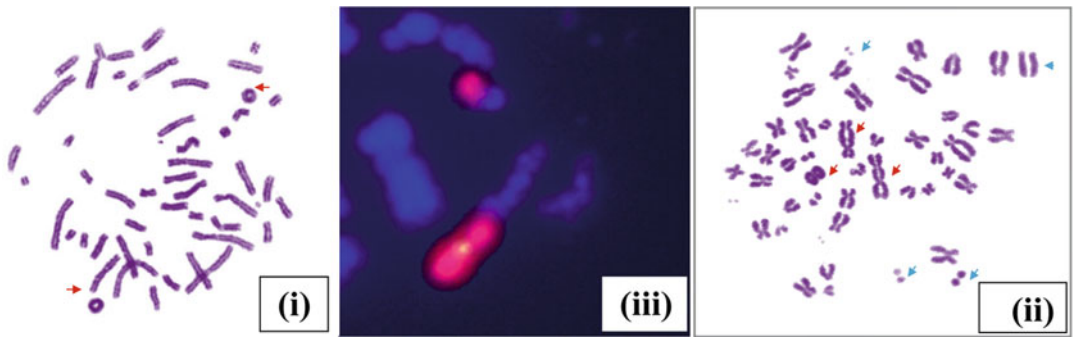
**Chromosomes, Fig. 7** (continued)



**Chromosomes, Fig. 7** The figure illustrates simplified mechanism for creation of different chromosomal aberrations. All of the aberrations are formed due to misrepair after double-strand breaks in DNA. Reciprocal translocation exchange of segments between nonhomologous

chromosomes and dicentric formation (i), Robertsonian translocation which occurs only between two acrocentric chromosomes (ii), inversion with or without involving centromere pericentric and paracentric inversion, respectively (iii), acentric and centric ring formation (iv)





**Chromosomes, Fig. 8** Chromosomal aberrations in human blood lymphocytes showing ring chromosomes with red arrow (i), dicentric chromosomes with red arrow (ii), acentric chromosomal fragments blue arrow (ii), reciprocal translocation between differently stained chromosomes (iii)

**Chromosomes, Table 3** Common genetic disorders associated with chromosomal anomalies

| Anomaly                                                       | Syndrome             | Chromosome count | Complications                                                                                                                                                     |
|---------------------------------------------------------------|----------------------|------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Monosomy X                                                    | Turner syndrome      | 44 + X           | Abnormal females, partly developed secondary sexual characters short stature, webbed neck, etc.                                                                   |
| Trisomy 21 most common trisomy (1:1000 to 1:1100 live births) | Down syndrome        | 47               | Intellectual deficiency mild to moderate, hearing problem problems, thick protruded tongue, single crease in palms, flat nose septum, etc. Survive beyond 50 year |
| Trisomy 13                                                    | Patau syndrome       | 47               | Severe neurological and muscular abnormalities<br>Mostly die within a year after birth, only ~20% may survive more than 10 years                                  |
| Trisomy 18 2nd most common trisomy (1:5,000 live birth)       | Edward syndrome      | 47               | Severe neurological problems, prenatal deaths common, survival less than a year                                                                                   |
| Trisomy X                                                     | —                    | 44 + XXX         | Almost normal phenotype                                                                                                                                           |
| Two or more Y                                                 | —                    | 44 + XYY male    | Almost normal phenotype                                                                                                                                           |
| Two or more X with Y                                          | Klinefelter syndrome | 44 + XXY male    | Fertility issues, puberty with less prominent male features, enlarged breasts, less body hair, weak muscles, etc.                                                 |

all the cells of affected individual. Although most of the embryos with chromosomal aberrations undergo spontaneous abortions silently during preimplantation stage or within the first trimester, still there are certain chromosomal anomalies which are competent for live births followed by shorter or longer survival age (Table 3). Individuals with such aberrations suffer from multiple health problems and most of them include mental retardations (MacIntyre et al. 2003).

Conclusion

Compact, flexible, and contractile arrangement of DNA into chromosomes allows a cell to properly accommodate the large genetic material, replicate, segregate, and more importantly selectively express the genome. Aberrations leading to alteration in the number of structure of chromosomes may have a range of clinical consequences.

## Cross-References

- ▶ [Autosome](#)
- ▶ [Centromere](#)
- ▶ [Chromatid](#)
- ▶ [DNA](#)
- ▶ [Nondisjunction](#)
- ▶ [Nucleus](#)

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## Chunking

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## Synonyms

[Grouping](#); [Parsing](#); [Recoding](#); [Sorting](#)

## Definition

Cognitive processes that recode multiple separate stimulus events into groups in memory.

## Introduction

**Chunking** has traditionally referred to cognitive processes that recode multiple separate stimulus events into groups in memory. Chunking has also been referred to as cognitive “recoding,” “grouping,” “sorting,” or “parsing” (e.g., Bower and Springston 1970; Bower and Winenz 1969; Capaldi et al. 1986; Fountain and Annau 1984; Pribram and Tubbs 1967).

Chunking is considered a fundamental process in cognition because it increases memory capacity and efficiency. The idea of chunking was first proposed by Miller (1956) to explain characteristics of human learning, memory, and speech phenomena from a cognitive perspective. Chunking has since been studied widely in a variety of other species by research in the field of comparative cognition (Capaldi et al. 1986; Fountain and Annau 1984; Hulse 1978; Hulse et al. 1992; Suge and Okanoya 2010; Terrace 1987, 1991; Terrace and Chen 1991a, b). Other recent evidence indicates that chunking may also occur as a perceptual process (Gilbert et al. 2014, 2015). Recent developmental research has demonstrated chunking abilities in human infants (Lewkowicz et al. 2018).

## Chunking Manipulations and Cognitive Advantages

Chunking can be manipulated. Research has shown that inserting breaks or pauses (phrasing cues) between chunks facilitates the chunking process (Bruce 1994; Lashley 1951; Spierings et al. 2015; Stempowski et al. 1999). There is also evidence that chunks can be grouped into “superchunks” of information (Capaldi et al. 1990). When elements, chunks, and “superchunks” are organized in hierarchical “structural trees” (Restle 1970) in this manner, both humans

and rats are sensitive to the hierarchical level of individual events (Fountain and Rowan 1995; Restle 1970). Aggregating related information into chunks in this manner decreases working memory load because encoding abstract structure facilitates recalling whole sets of related chunks of information. Thus, not only does chunking facilitate encoding; chunking can greatly reduce the demands on memory capacity.

## Chunking Demonstrations Across Species

Although chunking as a cognitive process was first studied in humans, results from work with animals often parallel those obtained in human studies (Ericsson et al. 1980; Miller 1956; Simon 1974). Chunking has been shown to facilitate learning in multiple modalities and tasks across a variety of species, such as rats, mice, pigeons, songbirds, and primates. The following discussion gives an overview of results observed in sequence, spatial, perceptual, and motor chunking procedures.

### Sequence Chunking

Sequence chunking occurs when animals parse sequences of events or responses into smaller chunks. Using a task where stimuli were presented on a touchscreen, Terrace and colleagues (Terrace 1991; Terrace and Chen 1991a, b) demonstrated that pigeons were capable of chunking information based on colors and shapes. A similar approach using a touchscreen showed that monkeys were also capable of chunking colors and shapes (Swartz et al. 1991). Animals in both studies were presented with series of shapes and colors, and learning the order of stimuli was quicker when similar items were presented together than when stimuli were interleaved. Chunking has also been examined in rats. In a runway task, Capaldi et al. (1990) demonstrated that rats were able to predict serial orders of food quantities and presented evidence that rats could combine chunks into superchunks that contained multiple lists. Rats are capable of chunking items together even when the items are not adjacent in a

sequence (Capaldi and Miller 1988). Other rat research showed that chunking is further facilitated by imposing breaks, therefore creating chunks even when randomly inserted in a complex serial multiple choice task (Fountain et al. 2000; Stempowski et al. 1999). Fountain et al. (2000) found that even unpredictable phrasing cues facilitate better performance on responses following phrasing cues than when no phrasing cues were provided. In addition to using phrasing cues to facilitate chunking, Muller and Fountain (2016) demonstrated that rats are sensitive to the length of chunks using the same serial multiple choice task. Rats were trained on a serial pattern with 3-response chunks and then presented with chunks of differing lengths. When presented with chunks that had more than three responses, rats attempted to make a rule-consistent chunk response after that third element, even in the absence of a phrasing cue. Garlick et al. (2017) observed that pigeons in a touchscreen version of the same task also abstract sequence structure.

### Spatial Chunking

Chunking of spatial locations based on distance from the subject and preference of reward has also been studied in a variety of animals and tasks. Menzel (1973) used a modified traveling salesman task to demonstrate that chimpanzees could chunk locations of food reward in terms of physical location and food preference. Chimps in this study retrieved preferred food items (fruit) before nonpreferred food items which indicated that they chunked preferred food types by location. Using a radial arm maze, Dallal and Meck (1990) and Macuda and Roberts (1995) both reported evidence that rats could also chunk food types by location. De Lillo et al. (1997, 1998) found that monkeys became more efficient at emptying food tray puzzles organized in arrangements that would facilitate chunking strategies relative to tray arrangements that would not facilitate chunking. Evidence for spatial chunking has also been found in bees and fox squirrels. Zhang et al. (1999) found that bees could learn and accurately recall two sets of stimuli to lead to two different locations. Bees were trained on a maze task where the goal was to reach food. When presented with a

landmark on one of two paths, bees accurately chose the correct maze that contained the location, which indicated that they chunked the landmarks with the start boxes of each maze. Delgado and Jacobs (2017) gave wild fox squirrels a variety of nuts and studied how the squirrels cached them. They found that squirrels spatially chunked their caches by nut species.

### **Auditory Chunking**

Auditory chunking, which is chunking of information presented as sounds, has mostly been studied in birds. Williams and Staples (1992) recorded songs of birds and the songs of the birds they had learned from and analyzed song chunks. They found that chunks in the song melodies were consistent with those of the tutor. They concluded that chunking in bird songs is a cognitive learning strategy because syllables were learned in sections with modal lengths of 3. Additionally, the birds delivered the songs with breaks at the chunk boundaries not unlike when humans pause to take a breath between phrases. Similarly, Nicolai et al. (2014) trained bullfinches on human melodies and then analyzed whether the melody was recalled in chunks of notes with pauses between chunks or in a single continuous chain. The finding was that bullfinches recalled songs as chunks of note groups and not chains. Phrasing cues have also been shown to impact auditory chunking (Spierings et al. 2015; Suge and Okanoya 2010). Suge and Okanoya (2010) assessed how inserting phrasing cues into the melody affected song perception and recognition. They trained a bird to respond to a tone (go tone) and then recorded the birds' songs. They then selected a fragment that included a chunk and inserted a sound (phrasing cue) either within the chunk or between chunks. Birds responded slower when the tone was inserted within the chunk relative to when the sound was located between chunks. Using a similar go/no go task, Spierings et al. (2015) assessed how phrasing cues affected chunk recognition in zebra finches by training one group on a melody with pauses and one group on a melody without pauses. Once finches were able to make the discriminations, they were put through reversal learning. The group that had previously been trained with pauses was able to discriminate

between melody chunks in a continuous string of notes while the no-pause group was unable to make distinctions.

### **Motor Chunking**

A final type of chunking found in the literature is motor chunking. Motor chunking occurs when smaller motor movements are chunked into movement sequences. Typically, motor chunking is considered an unconscious or habit-based type of chunking while the other types are considered more conscious strategies. Graybiel (1998) found that sensorimotor responses can be chunked due to activity of the basal ganglia. Ramkumar et al. (2016) used monkeys to assess kinetic movement of center-reach motor movement and found that chunking is a cognitively cost-effective way of moving efficiently.

### **Conclusion**

Whereas Miller (1956) first described chunking through the lens of human cognition, research since then has demonstrated the importance of chunking in both natural and arbitrary tasks in a variety of species. In some of the aforementioned studies, nonhuman animals appeared to chunk information, such as different food types and their locations, without requiring specific experimental manipulations designed to facilitate chunking. Other studies have shown that experimental manipulations such as phrasing cues can encourage animals to use specific chunking strategies. Current research continues to explore the behavioral, cognitive, and neural processes underlying chunking and the limits of this capacity across species.

### **Cross-References**

- ▶ [Comparative Cognition](#)
- ▶ [Encoding](#)
- ▶ [Intervening Variables](#)
- ▶ [Pattern Learning](#)
- ▶ [Rationality](#)
- ▶ [Ronald Weisman](#)
- ▶ [Serial List Learning](#)

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## Cilia

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## Synonyms

[Fibril](#); [Filament](#); [Footlet](#); [String](#); [Tendril](#); [Thread](#)

## Definition

Cilia are membrane-bounded, centriole-derived, microtubule-containing, hair-like extensions of the apical plasma membrane.

## Introduction

Cilia are common surface modifications present on nearly all cell types in mammals. The term cilium (Latin word, meaning “eyelash”) was first used by Otto Friedrich Muller in 1786. Cilia were first observed by Antoni van Leeuwenhoek in 1674–1675; he called them animalcules which mean motile thin little feet or little legs (Sengupta 2017).

Initially, the cilia would not be able to gain the importance that it deserved and was relegated to a very minor role in moving out the mucous from respiratory tract. Over the years of research, they found that the cilia were present virtually in every tissue including fallopian tubes, neurons, chondrocytes, limb bud ectoderm and mesenchymal cells, ependymal cells of brain ventricles, kidney tubule epithelial cells, pancreatic duct and islet cells, liver cells, and even many tissue culture cells. In majority of these organs, these cilia were nonmotile so they were considered as nonfunctional (Marshall and Nonaka 2006).

But recently, cilia have important role in migration of cells during development of embryo, sensory signaling pathways, and its association with number of disease syndromes; these organelles become center of attraction for biologists (Bloodgood 2009).

## Classification

Cilia are classified into three categories based on their functional characteristics:

1. Motile cilia
2. Primary cilia
3. Nodal cilia

### Motile cilia

Motile cilia are most extensively studied of all the types and are usually found on the apical domains of epithelial cells of the trachea, ependymal cells of brain ventricles, and on cells lining the fallopian tube and epididymis (Davenport and Yoder 2005). Cilia work in more precise and organized fashion and are responsible for fluid and cell movement in



the body at various sites such as clearance of mucus in respiratory tract, cerebrospinal fluid movement in the ventricles of brain, and the transport of ovum and sperm in their corresponding reproductive tracts. Motile cilia have typical  $9 + 2$  axonemal organization where nine microtubule doublets surround a central pair of microtubules. This central pair has motor protein which is important for the generation of forces inducing motility (Porter and Sale 2000).

#### Function of Motile Cilia

Cilia are motile structure which aids in transport of cells, proteins, foreign particles, and secretions from the epithelial surfaces. They are responsible for the forward movement of the sperm.

#### Primary Cilia (Monocilia)

Most of the vertebrate cells possess a single non-motile cilium per cell called the primary cilium. This microtubule-filled organelle project several microns from the cell surface (Pan and Snell 2007). They are also found in some epithelial cells such as the epithelial cells of the rete testis in the male reproductive tract, epithelial cells in the biliary tract, epithelial cells of kidney tubules, ependymal cells lining the ventricles of the central nervous system, the connecting stalk of photoreceptor cells in the retina, and the vestibular hair cells of the ear. They contain  $9 + 0$  pattern of microtubule instead of  $9 + 2$  arrangement. These are nonmotile because they lack central pair of microtubule and the microtubule-associated motor proteins (Pawlina 2016).

#### Function of Primary Cilia

Primary cilia act as antennae that receive signals from the surroundings. The receptors present on primary cilium mediate light sensations, odorant, and sound perception in multiple organs in the body. The primary cilia also contain various cilia-specific receptors, ion channels, and signaling molecules which act as chemosensors, mechanosensors, and osmosensors. This remote information is converted into signaling cascades that are initiated within the ciliary compartment and then send to the cell cytoplasm.

They also play an important role in the cell cycle and cell differentiation and for normal tissue

morphogenesis in developing tissues (Satir and Christensen 2007).

#### Nodal Cilia

Nodal cilia are found on the bilaminar embryonic disc at the time of gastrulation around the primitive node in the developing embryo. The axonemal internal architecture ( $9+0$  axonemes) of nodal cilium is similar to that of the primary cilium; the only difference is the ability of nodal cilium to perform rotational movement due to presence of motor proteins dyneins or kinesins. (Supp et al. 1997). They generate a leftward flow across the node which is detected by sensory receptors on the left side of the body. After that they initiate signaling mechanisms that differ from those on the right side of the embryo. Any defect in this mechanism causes the left–right asymmetry of internal organs (Nonaka et al. 2002).

#### Function of Nodal Cilia

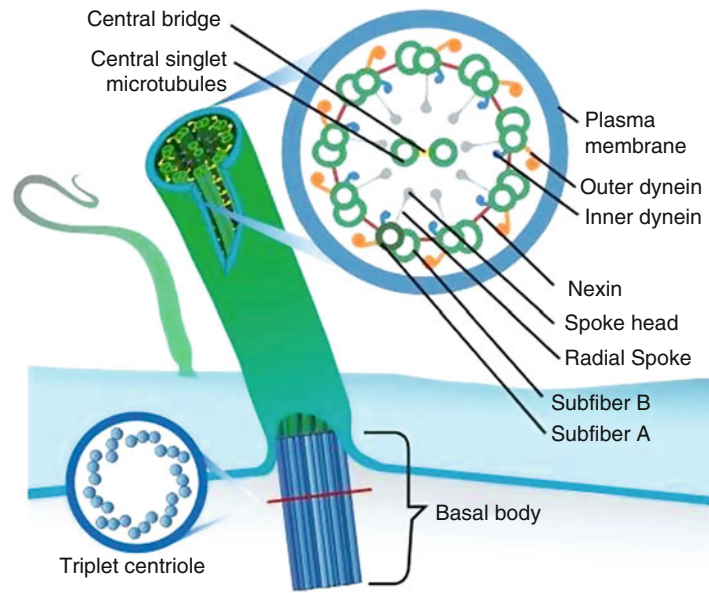
They are essential in developing left-right asymmetry of internal organs in the developing embryo.

#### Structure of Cilia

Ultrastructurally, Cilium is composed of internal core of microtubules, called axoneme on longitudinal section. But on cross-sectional view, it contains either nine pairs of microtubules or doublets of nine microtubules surrounding two central microtubules. The microtubules composing each doublet are composed of two types of microtubule – A microtubule and B microtubule. The A microtubule is composed of 13 tubulin protofilaments whereas the B microtubule is composed of 10 tubulin protofilaments (Fig. 1).

Each microtubule A exhibits a pair of “arms” that contain a motor protein “dynein.” The protein “nexin” permanently links the microtubule A with the microtubule B of adjacent doublets. Each of the nine doublets give rise to radial spokes, toward the two central microtubules. The  $9 + 2$  microtubule arrangement is continuous from the tip of the cilium to its base, whereas the outer paired microtubules join the basal body. Basal body with the

**Cilia, Fig. 1** Structure of motile cilia. (Source: <https://commons.wikimedia.org/w/index.php?curid=3145956>)



help of basal body-associated structures anchors cilia in the apical cell cytoplasm.

## Ciliary Diseases

1. Primary ciliary dyskinesia or immotile cilia syndrome: Immotile cilia affect various system of the body.
  - (a) Respiratory system: chronic respiratory distress with persistent cough, bronchitis, asthma, and sinusitis
  - (b) Ear: Otitis media
  - (c) CNS: Hydrocephalus internus or transient dilatation of inner brain ventricles
  - (d) Reproductive system: sterility
2. Polycystic kidney disease: In this disease, there is mutation in genes which are required for polycystin1, polycystin 2, and fibrocystin protein synthesis. Polycystin-1, located within the cilium (9+0 arrangement), acts as a mechano or chemo sensor and help in transmission of the signal from the extracellular fluid compartment to the interacting  $\text{Ca}^{2+}$ -channel polycystin-2. Polycystin-2 then mediates sufficient  $\text{Ca}^{2+}$  influx to activate intracellular ryanodine receptors resulting in intracellular  $\text{Ca}^{2+}$  release. Mutations in Polycystin-1 or Polycystin-2 might disable cilia-mediated mechanosensation, which is normally required

for tissue morphogenesis. Thus, these mutations in Polycystin-1 or Polycystin-2 can cause polycystic kidney disease (Sun et al. 2004).

3. Kartagener's syndrome: There is absence of dynein arms which result in failure of mucociliary transport system.
4. Situs inversus: due to defect in nodal cilia.
5. Other emerging ciliary diseases due to ciliary involvement:
  - (A) Retinitis pigmentosa
  - (B) Bardet-Biedl syndrome (Beales 2005)

## Conclusion

Cilia are emerging as omnipresent organelles which act as antennae sensing the external environment. Their defects in structure are responsible for an increasing number of disease syndromes. Almost all mammalian cells have a cilium; the functions of cilia in many organs are now known but in many other organs have not been known at all. We are only just beginning to understand, so a lot of researches are also needed to know other facts about cilia.

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## Circadian Rhythm

### ► Biological Clocks

## Circadian Rhythms

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### Introduction

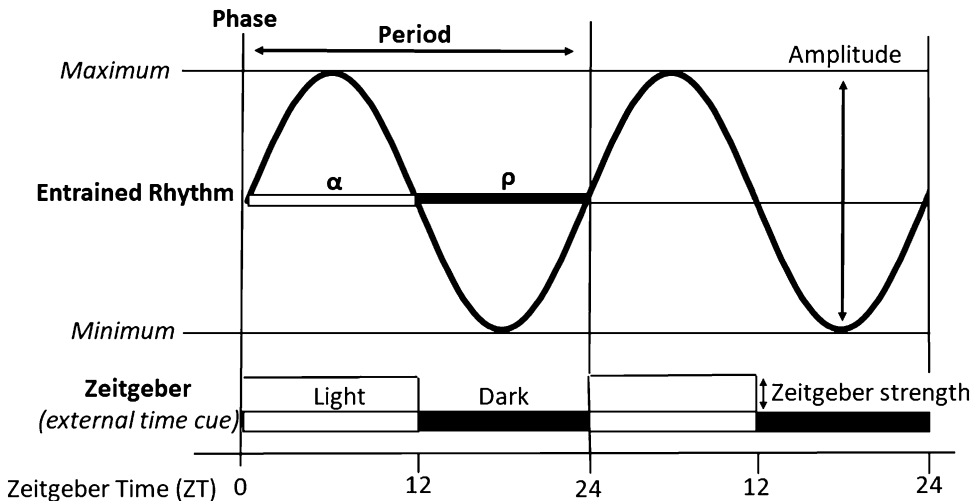
The rotation of the earth about its axis once every 24 h creates daily rhythms in light, temperature, humidity, and other factors that present both

challenges and opportunities for life on earth. It is therefore no surprise that daily rhythms in behavior and physiology are found in almost all living organisms, from single cell bacteria to humans. Most daily rhythms reflect the output of internal biological clocks that cycle with a periodicity close to 24 h. Rhythms generated in this way are classified as “circadian” (from the Latin *circa*, about and *dies*, day). Circadian clocks are believed to have evolved early in the history of life, possibly to restrict cellular processes, such as DNA replication, to the night, to avoid the damaging effects of ionizing radiation from sunlight. The adaptive value of synchronizing cellular and behavioral activities with the outside world led to the incorporation of circadian clocks into the biochemistry and physiology of nearly every organism on the planet. By internalizing the mechanism for rhythmicity, organisms gain the ability to prepare in advance for predictable daily environmental changes, rather than merely react to them.

The biologists and physicians who initiated formal analysis of circadian rhythms in the 1950s adopted the terminology employed by physicists and mathematicians to describe oscillatory processes (see Fig. 1). A rhythm is defined as any process that repeats itself at regular intervals. A device that produces a rhythm is an “oscillator.” A rhythm can be described by two parameters. One parameter is the rhythm “period” (often denoted by the Greek letter  $\tau$ ), which is the duration of a complete cycle. The other is rhythm “amplitude,” which refers to the range of values that a rhythm exhibits across the cycle. Amplitude may be expressed as the difference between the maximum value and the mean, or the maximum and minimum. “Phase” (often denoted by the Greek letter  $\phi$ ) refers to any discrete point or range of points within a cycle. If a circadian rhythm is modeled as a sine wave, then the peak value is the acrophase, and the amount of time between successive acrophases is the period.

### Entrainment

A defining feature of circadian rhythms is that they are endogenously generated. The most compelling



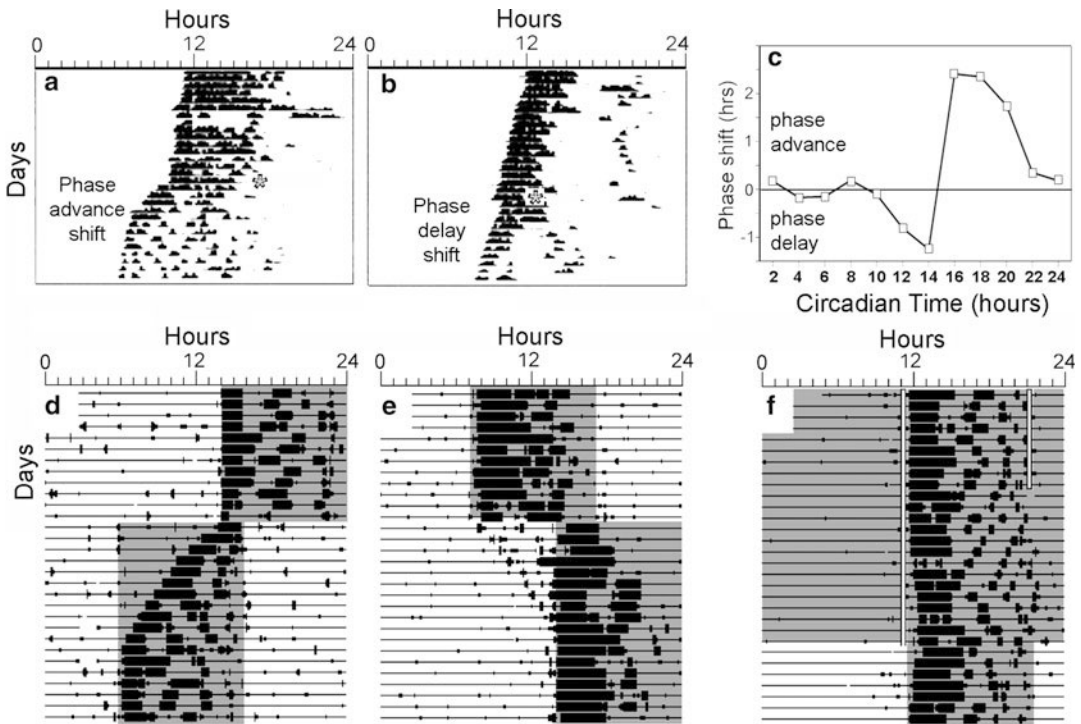
**Circadian Rhythms, Fig. 1** Sine wave representing the output of a rhythmic process, labeled according to conventional terminology in the field of circadian biology. Rhythm period is the duration of the complete cycle (often denoted by the Greek letter  $\tau$ ). Amplitude is the difference between the maximum and minimum values or

the maximum and the mean value. Phase is any point or range of points within a cycle (often denoted by the Greek letter  $\phi$ ). A Zeitgeber is any periodic stimulus that can entrain the rhythm. Zeitgeber time (ZT) is plotted in hours, where ZT0 corresponds to lights-on, by convention

evidence for this is that they persist, or “free run,” in “constant conditions” (environments lacking external time cues). In constant conditions (e.g., a cave or a laboratory vivarium in constant dark), the periodicity of the persisting rhythm is generally close to, but rarely exactly 24 h, hence the designation “circadian.” Consequently, circadian rhythms gradually drift out of normal alignment (“out of phase”) with the outside world (Fig. 2A, B). This property rules out the possibility that circadian rhythms are driven by uncontrolled external stimuli.

Given that circadian rhythms free-run with periodicities close to, but not exactly, 24 h, a mechanism must have evolved by which they can be synchronized to the external environment. Indeed, without a way of establishing a stable phase relationship to the solar day, circadian rhythms would likely be maladaptive. Synchronization of circadian rhythms to 24-h light-dark (LD) cycles is achieved by “entrainment,” defined as phase and period control of an oscillator by a periodic stimulus. It is through this active process that the mechanism driving circadian rhythms is transformed from an oscillator to a bona fide clock that matches and is therefore predictive of environmental time.

In the process of entrainment, the circadian clock is reset, or “phase shifted,” by external time cues (“zeitgebers”; from the German, “time-givers”). The magnitude and direction of phase shifts depends on both the timing and physical magnitude (e.g., intensity or duration) of the zeitgeber. The mechanism by which circadian rhythms are entrained to the 24-h LD cycle has been investigated by exposing animals to brief pulses of light during prolonged recordings in constant darkness. Light exposure late in the biological night (that portion of the circadian cycle during which the animal behaves as though it were night) and early in the biological day pushes the clock ahead to a later phase (a “phase advance”; Fig. 2A), while light late in the “biological day” and early in the “biological night” resets the clock to an earlier phase (a “phase delay”; Fig. 2B). Therefore, the response of circadian clocks to light exposure depends on the circadian phase at which the light exposure occurs. This can be represented by a “phase-response curve,” which plots the size and direction of phase shifts induced by light exposure at different points within the circadian cycle (Fig. 2C). Under a natural photoperiod, phase shifts induced by light exposure at dawn or dusk



**Circadian Rhythms, Fig. 2** How light entrains circadian rhythms. Panels A and B represent the circadian wheel running rhythms of Syrian hamsters maintained in constant dark. Each line represents 24 h of recording, and consecutive days are aligned vertically. The black bars indicate wheel running, and the blank sections indicate rest. These graphs show that wheel running is concentrated into one major bout each day, and that this bout begins at few minutes earlier each day (the periodicity is “circadian”). The single star on each chart represents a 30 min light exposure. In Panel A, the light pulse occurred at the end of the daily active phase and caused the onset of activity to occur earlier than usual the next day, defining a phase advance shift. In Panel B, the light pulse occurred earlier in the active phase, and activity onset occurred later than usual the next day, defining a phase delay shift. Panel

C illustrates the results of many such light exposures, summarized in a phase response curve in which the size and direction of the phase shift is plotted according to the circadian time of the light exposure. Circadian hours 0–12 represent the biological day, and hours 12–24 the biological night. Light early in the biological night induces phase delays, while light later in the biological night induces phase advances. Panels D and E illustrate the effects of phase shifting the LD cycle by 8 h either forward (D, an advance) or backward (E, a delay). The circadian rhythm gradually advances or delays taking about 8–10 days to reentrain. Panel F shows that circadian rhythms can be entrained by two daily light pulses (the thin opaque vertical bars), simulating dawn and dusk. With one daily light pulse, the rhythm gradually begins to delay a small amount

precisely compensate for the difference between the free-running period of the circadian rhythm and the period of the LD cycle. A rhythm with a period less than 24 h will naturally advance each day relative to the solar day, but is prevented from doing so because exposure to evening light causes a daily delay shift. A rhythm with a period greater than 24 h will naturally delay relative to the solar day, but this is prevented by morning light which induces a daily advance shift. The bidirectionality of the phase shift response ensures that the

rhythm is locked into a stable phase relationship with the solar day, regardless of whether the underlying circadian clocks naturally run fast or slow relative to 24 h. This mechanism can produce stable entrainment even if there is only one or two daily light pulses, simulating dawn and/or dusk (Fig. 2F).

Phase shifts in response to light typically exhibit a maximum size, on the order of a few hours, depending on light intensity and duration. As a result, entrainment can occur only if the period of



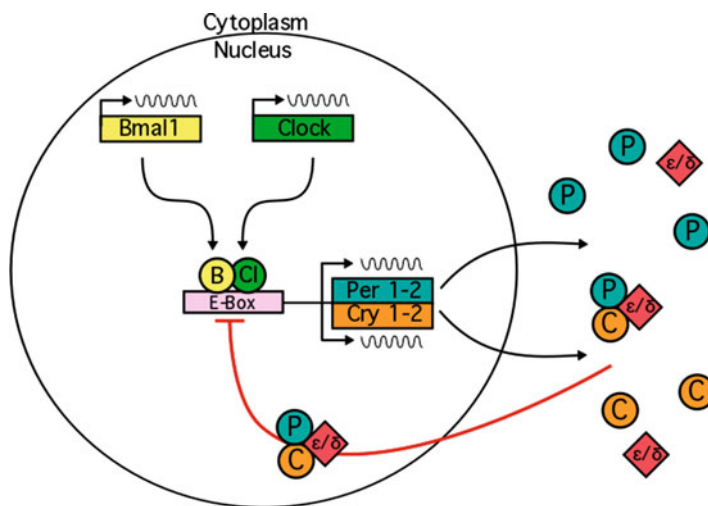
the LD cycle is within an hour or two of 24 h. LD cycles longer or shorter than this exceed the phase shifting capacity of circadian clocks, resulting in a circadian “limits to” or “range of” entrainment. Circadian rhythms under non-24 h LD cycles will either free run through the LD cycle or show “relative coordination,” as light exposure produces delays or advances that are not sufficient to offset the difference between the period of the LD cycle and the period of the circadian cycle. These limits in the magnitude of phase shifts explains the gradual resynchronization of circadian rhythms following a rapid shift in the LD cycle, such as is encountered following transmeridian jet travel (Fig. 2D, E). The temporary mismatch between environmental time and circadian (biological) time results in symptoms of jetlag (most commonly experienced as disruptions of sleep, alertness, appetite, and digestion).

### The Molecular Basis of the Circadian Clock

Given that single cell organisms exhibit true circadian rhythms, the clock mechanism in these species

must be intracellular, but the same is true of all multicellular organisms. Research on fruit flies first revealed that circadian rhythms are based on cycles of gene transcription involving so-called “circadian clock genes” encoding proteins that regulate their own expression by negative feedback (Fig. 3). Similar autoregulatory transcriptional oscillators drive circadian rhythms in other life forms. Archaea, bacteria, plants, and fungi utilize entirely distinct sets of clock genes, while fruit flies and vertebrates share some clock gene homologues. Regardless of the specific genes, all of these transcriptional oscillators are based on the principle of negative feedback, representing a remarkable example of convergent evolution.

In mammals, the transcriptional oscillator works as follows. Transcription of two clock genes, *Clock* and *Bmal1*, yields messenger RNAs that are translated into corresponding clock proteins, CLOCK and BMAL1, that partner to form heterodimers. The CLOCK:BMAL1 protein complex binds to the promoter regions and activates transcription of three *Period* genes (*Per1*, *Per2*, *Per3*) and two *Cryptochrome* genes (*Cry1* and *Cry2*). The PER and CRY proteins



**Circadian Rhythms, Fig. 3** Schematic representation of the cellular clock gene loop. Briefly, the clock genes *Clock* and *Bmal1* encode the proteins CLOCK and BMAL1, which dimerize and activate transcription of the genes *Per* and *Cry*. PER and CRY proteins dimerize, translocate from the cytoplasm to the nucleus, and suppress activation

of the *Per* and *Cry* genes by blocking CLOCK and BMAL1. As PER and CRY proteins are degraded, suppression is eventually relieved, and transcription of *Per* and *Cry* is renewed, initiating the next cycle. Accessory loops and posttranslational modifications of clock proteins stabilize and set the period of the cycle to approximately 24 h



encoded by these genes form partners, translocate from the cytoplasm to the nucleus, and block CLOCK:BMAL1 binding to the *Per* and *Cry* gene promoters. This turns off transcription of the *Per* and *Cry* genes. PER and CRY proteins are gradually degraded and removed, freeing CLOCK and BMAL1 to activate the *Per* and *Cry* genes again, initiating the next cycle. The rate of transcription and the abundance of PER and CRY proteins are further regulated by accessory loops and several posttranslational modifications that help set the period of the oscillation to the circadian range, and enhance precision and amplitude (Ko and Takahashi 2006). Some of these core clock genes regulate expression of other genes (“clock-controlled genes”), which in turn modulate expression of more genes such that a significant portion of the genome comes under clock control, thereby conferring circadian rhythmicity to a broad range of cellular functions. Despite the number of cycling genes, it is possible to break the circadian clock and eliminate circadian rhythms by removing just one clock gene (*Bmal1*). Mutations of other clock genes can alter the period of the circadian cycle (in some cases explaining why some people are extreme early birds or night owls), or in some combinations, either weaken or eliminate circadian rhythmicity. These represent remarkable examples of how striking behavioral phenotypes can be explained by changes in expression of just one or two genes.

The discovery of a mechanism for circadian clocks, based on self-sustaining oscillations of gene transcription, that generalizes across phylogeny is one of the great accomplishments in molecular biology. However, the story is not yet complete, as circadian rhythms in at least some cell functions have recently been discovered in cells that lack DNA (e.g., human red blood cells). The mechanism underpinning these rhythms remains an open question (Hoyle and O’Neill 2015).

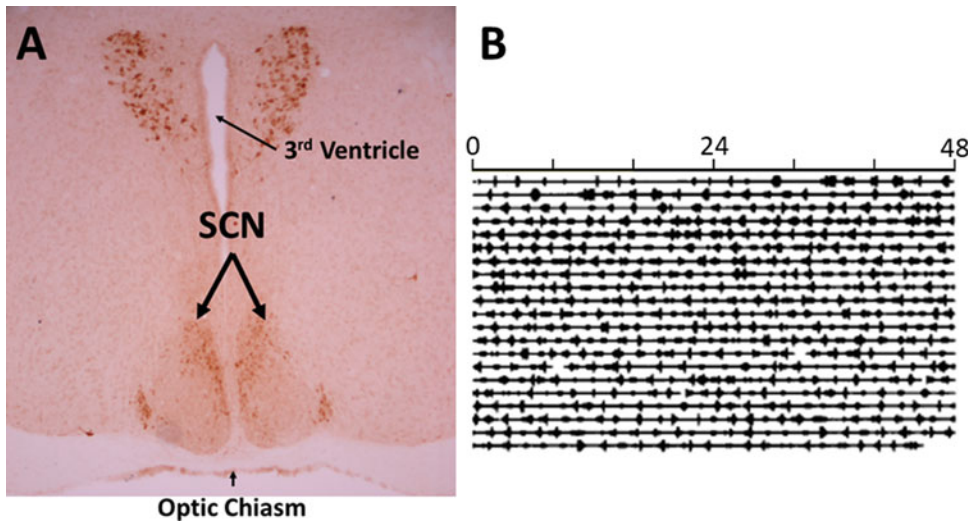
## The Structure of Circadian Systems

If the circadian clock is intracellular, where in multicellular organisms are circadian clock cells

located? Another seminal discovery in circadian biology was the recognition that circadian clock cells are found in most, if not all, tissues and organs. This raises interesting questions concerning how the circadian oscillations of clock cells are synchronized within and between tissues. Without a mechanism for intercellular synchrony, circadian oscillations at the cellular level would not translate into circadian oscillations at the tissue and organ level, and organ functions would be arrhythmic, rather than circadian. This problem was solved in part by the evolution of hierarchically structured circadian systems, in which one or more master circadian clocks (pacemakers) preside over many local circadian oscillators, analogous to the role of a conductor in an orchestra.

The first circadian clock to be identified in mammals was the suprachiasmatic nucleus (SCN), a relatively tiny collection of neurons and glial cells (only ~20,000 neurons among the billions that comprise the brain) residing at the base of the brain, on top of the optic chiasm (Fig. 4a). A majority of neurons in the SCN express circadian oscillations. While cells in many other brain regions and most body tissues are capable of oscillating, the SCN is unique in its ability to maintain synchrony within its population of clock cells in the absence of external synchronizing inputs. SCN neurons are coupled primarily via synaptic connections that enable it to produce a unified coherent output that is then communicated to the rest of the brain and body. Clock cells in most other tissues lack sufficient intercellular coupling to retain a population rhythm without direct or indirect synchronizing signals from the SCN pacemaker.

The status of the SCN as a “master pacemaker” is supported by several lines of evidence. First, destruction of the SCN eliminates circadian rhythmicity of behavior and physiology (Fig. 4b). Second, electrical or chemical stimulation of SCN neurons shifts the phase of behavioral and physiological rhythms. Third, SCN neurons, both in vivo (in the brain) and in vitro (in cell culture outside of the brain), show circadian oscillations in neural firing rate, glucose uptake, neuropeptide secretion, and gene expression. Finally, following



**Circadian Rhythms, Fig. 4** (a) Photomicrograph of a mouse brain stained for the neuropeptide VIP, which is abundantly expressed within the SCN. The SCN is located bilaterally above the optic chiasm and below the 3rd

ventricle. (b) Double plotted activity record (actogram) depicting wheel running activity in a mouse with a complete lesion of the SCN. All circadian rhythmicity in wheel running activity has been abolished

complete ablation of the SCN, circadian rhythms of behavior can be restored by transplants of fetal SCN tissue. The periodicity of the restored rhythm is determined by the genotype of the donor tissue and not that of the host, proving that the donor SCN is indeed the source of the rescued rhythmicity.

The efferent pathways responsible for communicating circadian rhythmicity from the SCN to the rest of the brain and body appear to involve both neural and humoral mechanisms. The SCN sends axonal projections to a relatively small number of other brain areas, mostly located within the hypothalamus. These brain regions control sleep and wake, feeding and drinking, body temperature, and endocrine secretions that distribute circadian timing information to additional brain regions. Circadian oscillators located outside of the brain are controlled by autonomic efferent nerves, pituitary endocrine secretions, the daily body temperature rhythm, and various stimuli associated with the daily feeding and drinking rhythms. These signals determine the timing of local circadian oscillators in a tissue specific manner, to ensure appropriate coordination of biochemical and physiological processes within and between different organs and organ systems. As

discussed below, under certain conditions, peripheral tissues are capable of either altering their phase relationship to the SCN or ignoring the SCN altogether, indicating flexibility inherent in the system.

### Clock Inputs: Light and Food

In the mammalian brain, SCN neurons are the first to receive information from the retina, via a retinohypothalamic tract (RHT) dedicated to entraining the SCN circadian clock to daily LD cycles. The RHT is composed of axonal projections arising from a specialized subset (~5%) of retinal ganglion cells that contain the photopigment melanopsin and are able to respond directly to light. These intrinsically photoreceptive retinal ganglion cells (ipRGCs) receive input from rod and cone photoreceptors, but are fully competent to mediate LD entrainment without rods and cones. Rods and cones are required for conscious vision (i.e., to see objects and movement); therefore, it is possible to be completely blind, and yet still entrain to LD cycles, as long as the ipRGCs are intact (Guler et al. 2008). Absorption of light by melanopsin activates ipRGCs,

which then release the neurotransmitter glutamate from their axon terminals in the SCN. Glutamate activates SCN neurons by opening ion channels for sodium and calcium. This initiates a series of biochemical reactions in SCN neurons that increase expression of the *Per* genes and enhance production of PER protein levels. If exposure to light occurs when *per* gene expression is normally falling (i.e., early in the biological night), increased *Per* transcription raises PER protein levels to where they were earlier in the cycle, thus delaying progression of the clock gene cycle and resulting in a phase delay. Conversely, light exposure late in the biological night, when *Per* gene expression is rising, accelerates protein production, advancing progression of the cycle and resulting in a phase advance. Thus, the same action (increased *Per* expression) can have opposite phase shifting effects depending on the phase at which it occurs (Dibner et al. 2010).

Light is not the only stimulus that can act as a zeitgeber for circadian rhythms. “Nonphotic” stimuli that can entrain circadian clocks include temperature, food intake, social cues, and behavioral arousal (Mrosovsky 1996; Mistlberger and Skene 2004). The importance of these varies by species and body tissue. In some mammalian species, the SCN pacemaker, and therefore the entire circadian system, can be shifted or entrained by stimuli that evoke behavioral arousal. This may be the means by which circadian rhythms in some of these species are entrained by social interactions. Arousing stimuli act on the SCN via inputs from several different brain structures, including the pontine Raphe nuclei, thalamic intergeniculate leaflet, and basal forebrain. Whereas photic zeitgebers are most effective at times of day when light is normally absent (i.e., the biological night), in general, nonphotic cues exert their strongest effects at times when the animal would normally be asleep (i.e., the biological day for nocturnal rodents) (Webb et al. 2014).

Daily feeding schedules can entrain the entire circadian system in some species, while entraining many but not all circadian clocks in other species. In Syrian hamsters and some mouse strains, a daily feeding schedule, imposed in the absence of a LD cycle, can entrain the

entire circadian system such that the daily active phase is synchronized with and anticipates mealtime. Food entrainment in these cases includes the SCN pacemaker and likely all local oscillators throughout the body. In many other species, including rats and some other mouse strains, temporally restricted food intake often does not entrain the SCN pacemaker, but does control the phase of circadian clocks in most other brain regions and body tissues. As a result, metabolic and physiological rhythms shift to align to the daily mealtime, so that the animals are prepared to ingest, digest, and distribute nutrients critical for survival. Importantly, one or more of these food-entrainable oscillators (FEOs) generates a behavioral rest-activity cycle, resulting in a daily rhythm of food anticipatory activity (FAA). This enables animals to adjust their daily foraging rhythms to exploit temporal regularities in food availability and focus food-seeking activity at the most productive times of day. In these species, the SCN pacemaker remains entrained to the LD cycle, while foraging behavior is controlled by a food-entrainable clock (Mistlberger 1994).

The evidence that FAA is controlled by a true circadian clock separate from the SCN is as follows. First, once FAA has developed, it persists for multiple days when feedings are withheld. Second, when mealtime is abruptly shifted, FAA does not immediately reset, but rather, shifts gradually. Third, FAA exhibits circadian limits to entrainment and does not emerge if meals are scheduled at noncircadian intervals (outside of the ~22–30 h range). Finally, while SCN ablation eliminates circadian rhythms when food is freely available, if food is restricted to a fixed daily mealtime, circadian rhythms of FAA emerge, and circadian organization of metabolism and physiology are restored. Entrainment of circadian clocks by food is also preserved in mice with clock gene mutations that eliminate or disrupt circadian rhythms entrained to LD cycles. When light-driven and food-driven rhythms diverge, most tissues, both centrally and peripherally, entrain to the feeding rhythm, with the SCN being the primary exception (Mistlberger 2011; Schibler et al. 2003).

The location of FEOs that control FAA remains to be determined. The available evidence suggests that FAA is controlled by a broadly distributed system of FEOs in the brain and possibly also the body. Some species are able to anticipate at least two daily meals, and possibly more, without the SCN. Whether this involves one FEO being used like a wristwatch to recognize and remember multiple mealtimes, or multiple FEOs entraining independently to different mealtimes, is unknown.

## Circadian Flexibility

Just as organisms are specialized for particular spatial niches, so too are they specialized for particular temporal niches. Raptors have evolved remarkable visual acuity enabling them to hunt small terrestrial prey while flying high above the ground, but this visual adaptation works only in daylight. The temporal niche of a species is typically defined as the time of day when they are most active (engage with the environment). Temporal niches include nocturnal (night-active), diurnal (day-active), and crepuscular (dawn and dusk active). Some species conform to none of these patterns and are classified as cathemeral (active during both day and night).

Despite these well-known categories, many animals are not rigidly nocturnal or diurnal. Temporal niche preference can instead be thought of as a continuum from the nearly entirely diurnal grass rat (with ~90% of its daily activity occurring during the light phase) to the nearly entirely nocturnal Syrian hamster (with well over 90% of its activity occurring during the dark phase) (Refinetti 2006).

Further complicating classification, marked differences in temporal niche preference can exist between individuals within a species. An extreme example of this is provided by the degus (*Octodon degus*). Under standard laboratory conditions, most degus exhibit a clear diurnal activity profile, while in a subset of individuals, activity is concentrated at night. More common are less dramatic individual differences in circadian timing that are likely the result of differences in free-

running period or responsiveness to zeitgebers, giving rise to the distinction between “morning lark” and “night owl” types within species.

Individual animals are also capable of changing temporal niche. These changes can occur as a result of natural changes across the lifespan, such as a hormonal-based pubertal shift that occurs in humans, degus, and possibly other species (Hagenauer and Lee 2012). As discussed above, many species can entrain to daily feeding schedules, and forage for food at times of day when they normally would sleep, if that is when food is most likely to be found. Temporal niche switching can also be triggered by metabolic challenge. For example, nocturnal mice that are forced to work for food show a gradual shift to diurnality that coincides with a gradual shift toward a negative energy balance. The shift to daytime activity allows the animals to sleep and lower their body temperatures at night, when it is normally cooler (at least, throughout evolutionary history in natural habitats). This reduces energy expenditure associated with thermoregulation. Niche switching can also be induced by competition within and between species (Hut et al. 2012).

The biological basis for phase differences in circadian timing is still unclear. Although nocturnal and diurnal animals differ dramatically in the phase relationship between the sleep-wake cycle and the LD cycle, the phase relationship between the SCN and the LD cycle is identical in both types of animals. Firing rates and *Per* gene expression in the SCN peak at approximately the same phase in both diurnal and nocturnal species, suggesting that their differences in temporal niche preference are a result of activity downstream from the master pacemaker (Smale et al. 2003). Temporal niche switching also appears to be due to factors downstream from the SCN. Mice displaying a diurnal activity profile when forced to work for food immediately revert to a nocturnal profile when food is provided freely, indicating that the phase of the SCN remained unaltered.

This flexibility in the phase relationships between the LD cycle and activity highlights an adaptive feature of the circadian timekeeping

system. It is clear that this system did not evolve to rigidly synchronize organisms to the day-night cycle, but rather to enable behavior and physiology to take full advantage of other predictable daily events or adapt to metabolic challenges. While the LD cycle is a ubiquitous environmental time cue for most terrestrial life forms, the circadian system is capable of altering its phase relationship to the solar day (as in the case of temporal niche switching) or ignoring LD cycles altogether when other stimuli (such as food availability) have more immediate consequences for survival.

## Circadian Rhythms and Cognition

Circadian clock genes oscillate in numerous brain regions, and it is therefore not surprising that cognitive processes exhibit circadian variation (for a thorough review see Smarr et al. 2014). Circadian variation is at least partly secondary to circadian regulation of behavioral state, which determines how alert animals are at different times of day. Circadian clock genes may also directly modulate cellular functions that mediate neuronal processes critical for attention, learning, and memory. Whether direct or indirect, the net result of circadian regulation are daily rhythms in attention and performance on various forms of associative and nonassociative learning and memory tasks, with peak performance typically in the organisms active phase, but sometimes in the rest phase.

If circadian clocks in the brain modulate cognitive processes, then disruption of circadian rhythms may impair cognitive performance. Disruption can be induced by exposing animals to constant lighting or LD cycle shifts, by SCN ablation or by clock gene mutations. LD shifts scheduled just before or during training impairs memory for places associated with rewards, punishments, or escape locations. Performance on these tasks is dependent on the hippocampus, a brain region critical for various forms of learning and memory. Circadian rhythms in the hippocampus are disrupted by SCN lesions, which may explain the deficits in memory for objects and rewarding places in hamsters with

SCN damage. The hippocampus shows circadian oscillations in various cellular functions, including synaptic plasticity and circadian clock gene expression. Disrupting circadian oscillations in the hippocampus itself can interfere with long-term memory formation (Eckel-Mahan et al. 2008).

Another way in which circadian clocks contribute to animal cognition is by providing a continuous readout of time of day that can be incorporated into event memories. Some species, among bees, fish, birds, and rodents, can remember the time of day that food is available at specific places in their foraging range. These species can discriminate time of day, even if no external circadian time cues are available. They must therefore be attaching an internal representation of circadian phase to the feeding event memory. This circadian time-place learning is a powerful adaptation for those animals that must forage widely for food that may vary both in time and place (Mulder et al. 2013).

The neurobiological basis of circadian time-place learning remains to be determined. A candidate circadian clock for time-place learning is the SCN. However, if the SCN does participate in time-place learning, it is apparently not required, at least when food acquisition is the event, because rats with complete SCN lesions exhibit normal time-place learning in the lab (Mistlberger et al. 1996). This suggests that FEOs that generate food anticipatory rhythms may also provide circadian time cues that associate with place information in event memories.

Circadian time cues are also used by animals, such as bees, butterflies, and birds, that can use the sun and stars as a compass for navigating and long distance migration. The sun moves across the sky at 15°/h. It can be used as a directional cue, as long as the heading relative to the sun is adjusted by the same amount each hour. This can only be done if there is an internal chronometer that can measure the passage of time, with at least hourly resolution. Experiments dating back to the mid-twentieth century have established that a circadian clock in birds, insects, and other animals can be used in this way, to permit time-compensated, sun-compass orientation (Schmidt-Koenig 1990).



## Conclusion

Circadian rhythms evolved early in the history of life on this planet. These rhythms enable optimal coordination with the environment by providing the organism with the ability to prepare for regularly recurring events, such as the daily light-dark cycle or daily variations in food availability. Circadian clocks modulate almost all aspects of physiology, behavior, and cognition and can also be utilized directly in memory formation, providing organisms with the ability to link a representation of time of day to event memories. The remarkable flexibility of the circadian system provides organisms with the ability to optimize the timing of their behavior to best take advantage of their environment.

## Cross-References

### ► Day/Night Cycle

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## Circannual Cycle

### ► Biological Clocks

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## Circulation

### ► Circulatory System



## Circulatory System

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### Synonyms

[Blood](#); [Cardiovascular system](#); [Circulation](#); [Heart](#)

### Introduction

The circulatory system is a complex system of organs and vessels that has the main function of transporting substances throughout the body. It transports blood, nutrients, hormones, and oxygen to different body organs, which are needed by tissues for survival. Along with transporting substances to tissues, it also functions to carry carbon dioxide and other wastes away from the cells (Riedesel and Engen 2015).

Another function of the circulatory system is to assist with thermoregulation (regulating body temperature). While blood circulates throughout the body, it assists with temperature stabilization by absorbing the heat released by cells during daily activity. When an increase in body temperature is noted, blood vessels in the skin begin to dilate and blood flow to the skin increases, which allows heat to be released away from the body. Conversely, when a body temperature drop occurs, blood vessels in the skin constrict and blood flow to the skin decreases, which enables heat retention by the body.

In animals, circulatory systems vary from simple to complex. All vertebrates and some invertebrates utilize a closed circulatory system where blood is strictly transported in vessels. Other invertebrates utilize an open circulatory system, where blood is found both inside vessels and in body cavities. This chapter primarily covers the vertebrate, and specifically the mammalian, circulatory system, which is a closed system.

## Circulatory Structures and Functions

The main components of a closed circulatory system include blood, the heart, and the vessels. The vessels are divided into arterial vessels, capillaries, and venous vessels. Some sources also include the lymphatic system as a component of the circulatory system.

**Blood** is a solution primarily consisting of plasma, red blood cells, white blood cells, and platelets (World Book inc 2015). Plasma is the main component of blood. It is a liquid medium that contains multiple substances including water, proteins, and minerals. Red blood cells, also known as erythrocytes, function to transport oxygen and carbon dioxide throughout the body. White blood cells, also known as leukocytes, function in immune defenses, protecting the body from disease by attacking and eliminating cells they perceive as foreign. Platelets, also known as thrombocytes, are essential cells that function in the clotting cascade to assist with the prevention of blood loss following injury to vessels (World Book inc 2015).

Blood is essential for the transportation of toxic substances such as carbon dioxide, salts, and ammonia, from cells to the liver. In the liver, the hazardous materials are converted into substances that can be eliminated from the body through the kidneys (World Book inc 2015).

Once the small intestines digest food that is ingested by the body, the nutrients from these digested foods pass into the blood via capillaries. Blood then transports these substances to the liver. The liver will then either store or release the nutrients to cells for daily activities such as energy production.

Blood volume varies between species, depending on body size and activity level. As activity level increases, blood volume has been noted to increase. Some animals, such as marine mammals, have larger blood volumes due to their need for increased blood oxygen stores. Some of the animals with the largest blood volumes are the species that are the most active and tend to have longer dive times, such as elephant seals, Weddell seals, and sperm whales. Their bodies may contain a blood volume of 200–260 ml/kg of body

weight, compared to approximately 70 ml/kg of body weight in adult humans (Ponganis 2009).

**The Heart** is a major muscular organ that functions to pump blood throughout the body. The anatomy of the heart differs between species.

In mammals and birds, the heart is divided into four chambers, with two separate pumps for systemic and pulmonary circulations (Stephenson et al. 2017). The chambers include right and left atriums divided by an interatrial septum and right and left ventricles divided by an interventricular septum. The flow of blood from each atrium to their respective ventricle is regulated by a series of valves. The anatomical variation of two separate pumps allows for the separation of unoxygenated blood, which is being delivered to the lungs by the right side of the heart, from the oxygenated blood, which is being pumped to the systemic circulation by the left side of the heart (Burggren et al. 2014). This separation enables the right side of the heart to function as a low pressure pump to the lungs, while the left side of the heart functions as a high pressure pump to systemic circulation (Burggren et al. 2014). As blood flows from areas of high pressure to areas of low pressure, the interatrial septum and interventricular septum play essential roles in ensuring that oxygenated blood makes it to the systemic organs that require oxygen to function.

**Arterial vessels** function to pump blood from the heart to the different body systems and body organs. These vessels are primarily controlled by neuronal impulses and local metabolic control. The arterial vessels consist of a high-resistance system and include the aorta, arteries, and arterioles.

The aorta is the major arterial vessel that extends from the heart to the abdominal cavity. It functions to carry oxygenated blood into the abdominal cavity for disbursement to body tissues.

Arteries function to carry blood away from the heart. Most arteries carry oxygenated blood from the left side of the heart to the remainder of the body, with the exception of the pulmonary artery. The pulmonary artery functions to take unoxygenated blood from the heart to the lungs.

Arterioles are smaller vessels which provide the main source of blood flow resistance in the

cardiovascular system (Martinez-Lemus and Laughlin 2015). They provide this resistance by vasodilating (enlarging) in areas that are in need of blood flow and vasoconstricting (shrinking) in areas that are not in need of a larger flow of blood. These are the structures that are the primary determinant of systemic blood pressure, and the pressure the heart is required to produce to ensure blood is pumped to the body systems. Systemic blood pressure is controlled by the heart rate (how many times the heart beats per minute) and the stroke volume (how much blood is pumped by each heartbeat). The size of the arterioles determines how much pressure the heart needs to overcome in order to pump blood to the body systems. How easily the heart is able to overcome this pressure gradient will determine how much stroke volume is produced.

Normally, arterioles remain in a partially constricted state (basal tone). Different tissues display different levels of basal tone depending on the tissue's resistance need. This basal tone helps prevent a sudden and dangerous decrease in systemic blood pressure if a tissue suddenly needs a large amount of blood flow, which causes the vessels to reach their maximal dilated potential (Riedesel and Engen 2015).

**Capillaries** are small vessels that function to provide gas and nutrient exchange between blood and body tissues and between arteries and veins. Being constructed with a wall thickness of only one endothelial cell enables capillaries to filter the fluid that is being transferred between the vessels and the body. Differentiated based on the number and size of pores in their endothelial walls, capillaries are found in three types: continuous, sinusoidal (discontinuous), and fenestrated. Continuous capillaries, with whole endothelial walls and basement membranes, allow water-soluble ions and molecules to cross between cells through pores or intercellular clefts. Discontinuous capillaries are required for larger whole cells, macromolecules, and particles to cross between cells as they consist of gaps between the endothelial cells and an incomplete or absent basement membrane. Fenestrated capillaries contain small pores covered by a thin diaphragm which allow water and solutes to permeate

through the capillary wall (Martinez-Lemus and Laughlin 2015).

**Venous vessels** act to collect blood and transport it back to the heart. These vessels, which consist of both elastic tissue and smooth muscle cells, are primarily controlled by neuronal impulses (Yin 2010). This system is a low-pressure system. The main types of venous vessels include veins, venules, the cranial vena cava, and the caudal vena cava.

The primary functions of veins are storage of unoxygenated blood and carrying the unoxygenated blood back to the heart from the systemic circulation. The exception to this is the pulmonary veins, which carry oxygenated blood back to the left atrium of the heart from the lungs. Veins are responsible for storing 60–80% of the circulating blood volume (Yin 2010).

Venules are small vessels that carry unoxygenated blood from the capillaries and converge to form veins.

The cranial vena cava is a large vein that extends to the cranial aspect of the body, from the heart towards the head. The caudal vena cava is a large vein that extends to the lower aspect of the body.

## The Lymphatic System

The lymphatic system is essential for maintaining appropriate plasma volume. This system is unique to vertebrates and includes lymphatic vessels, lymph nodes, and lymphoid organs. Lymphatic vessels can be found throughout the body in almost all vascular tissues except in the bone marrow and neural tissue. The largest concentrations of lymphatic vessels can be found in the skin, respiratory system, and gastrointestinal system (Aspelund et al. 2016). The lymphatic system plays important functions in the immune system, including the absorption of gastrointestinal lipids, and in filtering fluid and larger molecules between the vascular space (blood vessels) and the extracellular space. Filtering of fluid and molecules between the vascular and extracellular spaces is known as tissue fluid homeostasis (Burggren et al. 2014).

**Lymphatic vessels** function to transport fluid, macromolecules, antigen-presenting cells, and leukocytes into the lymph nodes and then into the circulatory vessels. By filtering fluid, immune cells, and plasma proteins as they are transported from the extracellular space into the bloodstream, lymphatics help to prevent edema (abnormal fluid accumulation in the body) from developing (Martinez-Lemus and Laughlin 2015). These vessels also help to protect the body against foreign antigens and molecules by transporting immune cells. Due to their size, lymphatic vessels are necessary to assist with the absorption of dietary fat and fat-soluble vitamins that are needed by the body (Aspelund et al. 2016).

## Circulation

Due to the closure of shunts shortly after birth, the circulation of blood differs greatly between fetal and adult mammals. As an adult, unoxygenated blood from the body flows through the cranial and caudal vena cava to the right atrium of the heart. From the right atrium, it is pumped to the right ventricle and then to the lungs through the pulmonary artery. In the lungs, the blood is oxygenated and then pumped through the pulmonary veins to the cardiac left atrium followed by the left ventricle. From the left ventricle, blood is pumped through the aorta to the remainder of the systemic circulation. A small portion of blood from the left ventricle is also pumped through the coronary arteries to provide blood to the heart itself (Yin 2010).

During the mammalian fetal stage, the lungs are not fully formed and have a thick smooth muscle layer in the pulmonary arterioles. This results in an increased pulmonary arteriolar vascular resistance, which necessitates the presence of shunts to maintain proper blood flow. Initially, oxygenated blood from the placenta flows through the umbilical vein to the fetal portal vein and then to the fetal liver or through the ductus venosus. The ductus venosus is a shunt which allows blood to bypass the liver and travel directly to the caudal vena cava. From the liver, blood passes through hepatic sinusoids to the caudal

vena cava, which transports the blood to the cardiac right atrium. Once in the right atrium, a large portion of the blood is then shunted through the foramen ovale to the cardiac left atrium and then to the cardiac left ventricle. The foramen ovale is a hole in the interatrial septum that allows shunting of the blood from the right atrium to the left atrium. This blood is then pumped through the ascending aorta to the coronary arteries and brachiocephalic vessels. The remaining blood from the caudal vena cava and the blood from the cranial vena cava flows through the right ventricle to the main pulmonary artery. From here, 10% of the blood is pumped to the lungs, while the remainder of the blood is shunted through the ductus arteriosus to the descending aorta. The ductus arteriosus is a shunt that connects the main pulmonary artery and the descending aorta, by-passing the lungs (Yin 2010).

Following the fetal stage, the circulatory system undergoes a transitional phase. Immediately after birth, once respiration is initiated, the lungs receive a large amount of oxygen, which causes pulmonary arterioles to vasodilate, resulting in a decrease in pulmonary arteriolar vascular resistance. This enables blood from the right ventricle to flow into the lungs. Over time, the thick muscular layer in the pulmonary arteries will atrophy, causing a decrease in the resistance and pressure in the pulmonary artery until they reach adult levels. Also during this time, the ductus venosus and umbilical arteries will begin to close and the foramen ovale will functionally close due to changes in atrial pressures; this is then followed by anatomic closure, preventing further blood shunting. Increased arterial oxygen supply also causes the ductus arteriosus to functionally close. Finally, thrombosis and fibrosis of the ductus arteriosus results in anatomic closure (Yin 2010).

## Unique Traits

Some species have developed unique traits specific to their evolutionary requirements. For example, birds have an elevated heart rate, likely due to an elevated metabolic demand from their normal behaviors.

In fish, the heart consists of only two chambers (one atrium and one ventricle) and one pump, with blood first being pumped to the gills and then to the remainder of the systemic circulation (Stephenson et al. 2017).

Amphibians and most reptiles have a three-chambered heart with two atria and one ventricle. The ventricle in these species has an incomplete ventricular septum, or ridge, which assists in minimizing the mixing of oxygenated and deoxygenated blood. Due to this incomplete ridge, most reptiles are able to shunt their blood, if needed. The exception to this is crocodilians, which have a complete ventricular septum and therefore have developed a four-chambered heart (Kik and Mitchell 2005).

As ectotherms, reptiles have also developed an adaptation which provides them with the ability to adjust their heart rate based on environmental temperature. They are able to increase their heart rate when basking in the warm sun to increase the amount of heat their bodies absorb. When cooling, they can decrease their heart rate to minimize the amount of body heat lost (Kik and Mitchell 2005).

Marine mammals have developed unique adaptations involved in their diving response, thermoregulation, and have larger blood volumes due to their large body masses and demands on their bodies. Examples of cardiovascular adaptations needed for extended and deep diving behavior are massive heart rate reduction during diving and blood flow limitation specifically to muscles that are not as active during these behaviors. In addition, adaptive traits have arisen that allow aquatic mammals to thrive in the cooler temperatures of deep waters. For example, a counter-current heat exchange system is noted in the flukes and flippers of cetaceans (whales, dolphins, porpoises) and provides conservation of body heat (Ponganis 2009).

## Conclusion

The circulatory system is a complex system of organs and vessels that functions to transport

blood, oxygen, and other substances throughout the body and assist with thermoregulation. There are two main types of circulatory systems, closed and open, which have many differences between species. In an open circulatory system, blood is located both inside vessels and in body cavities. Blood is transported solely within vessels in a closed circulatory system. The main components of a closed circulatory system include blood, the heart, arterial vessels, capillaries, venous vessels, and the lymphatic system. Blood circulation throughout the body is a highly regulated system which differs between the fetal stage and the adult life stage. Some species also have developed unique traits specific to their evolutionary requirements.

## Cross-References

- Immunology
- Respiratory system
- Thermoregulation

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## Cistron

- Polygeny

## Cladistic Analysis

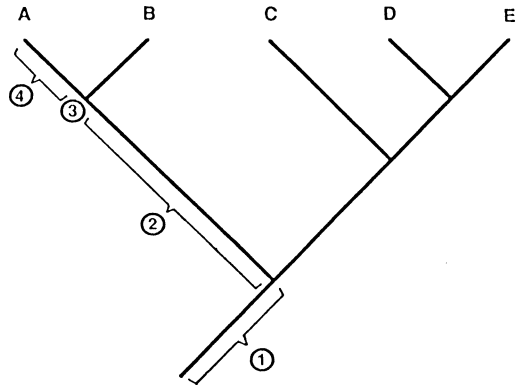
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In systematics and evolutionary literature, cladistic analysis applies to a method of character analysis first called “phylogenetic systematics” by its inventor, the German entomologist Willi Hennig (1913–1976) in several works, from 1947 up to 1981. The words and expressions “cladistics,” “cladistic analysis,” “cladist,” and “cladogram” appeared in the year 1965 in the American literature and became popular in the 1970s. From the same origin (the Greek *clados*, branch) is the word “clade” (a branch of the tree of life). Although used by the German biologist Ernst Haeckel (1834–1919) as soon as 1866 (*kladus*), clade was not much used before the late 1950s. In other words, cladistics is the study of the branching pattern of taxa. This pattern is devoted to express the phylogenetic relationships of taxa, so that Darwin’s (1859) anticipation can be fulfilled: “Our classifications will come to be, as far as they can be so made, genealogies.”

How to hypothesize interrelationships of taxa through the study of their degree of resemblance and difference?

The answer of the cladistic analysis is to study individual characters. The method is firstly based on the conceptual dichotomy made of homology/homoplasy, that is, resemblance due to kinship/fortuitous resemblance. Secondly homology is divided into the concept of character states. Resemblance due to kinship can be the result of shared plesiomorphous (that is, primitive) states of remote common ancestry, or shared apomorphous (that is, derived, transformed) states of close ancestry. Taxa grouped by apomorphy, such as A and B of Fig. 1, are called monophyletic groups (i.e., clades). Only clades have a phylogenetic dimension: they are made of the descendants of one ancestral species. This ancestral species is a hypothesis, often called “ancestral hypothetical morphotype.” This hypothetical ancestor is made of the apomorphies reconstructed by the analysis. The phylogenetic pattern is represented by a schema called “cladogram” (Fig. 1). The cladogram displays sister group relationships, that is, closely related clades (sharing the same ancestral species). The hierarchy is this system of subordinated sister groups, and the meaning of “closely related” can be summarized in the following way: a species (or taxon) A is more closely related to another species (or taxon) B than it is to a third species (or taxon) C if, and only if, it has one ancestral species in common with B that is not also an ancestral species of C. In Fig. 1 the ancestry of A, B, and C is the branch 1, and the ancestry of A and B is branch 2 (ancestral branch) as well as node 3 (ancestral node).

As a consequence, as a node of the cladogram is one ancestral species represented by one or more apomorphies shared by the sister groups, resemblance displayed by taxa is broken into three classes: apomorphy, plesiomorphy, and homoplasy. Homoplasy may be due to the presence in several taxa of the “same” derived character state by convergent evolution (not present in the ancestry), or the apparent presence of a primitive character state may be due to a reversal (and as, a reversal, not homologous with the true primitive state). These phenomena appear in all types of characters, morphological, ethological, and



**Cladistic Analysis, Fig. 1** The structure of the cladogram. This cladogram depicts the relationships of five taxa (A, B, C, D, and E), also called terminal taxa. The taxa A and B are sister groups and form clade (A, B). The clade (A, B) and the clade (C(D, E)) are sister groups. 1 = root; 2 = internal branch; 3 = internal node; 4 = external branch. The information conveyed by 2 and 3 (apomorphies of the clade (A, B)) is the same, that is, 2 and 3 are the same. According to graph theory, branch and node such as 2 and 3 are different symbols of the same connection. According to cladistics, the list of apomorphies of either branch 2 or node 3 represents the traits of the hypothetical ancestor of (A, B) – also labeled hypothetical ancestral morphotype – as well as the diagnosis of (A, B).

molecular. The important conclusion is that global resemblance between taxa is different from relationships between these same taxa.

The notions of plesiomorphy and apomorphy are relative. The same character state is plesiomorphous at one level and apomorphous at another one. The basis of the discrimination is the concept of congruence. The superimposition of the phylogenetic pattern of each individual character displays the phylogenetic hypothesis of the taxa. Congruence identifies the different levels of the transformations: (1) the five digits of both the hand and foot seen in chimp and man are a tetrapod character, deep in the tree of vertebrates (it is an apomorphy for vertebrates but a plesiomorphy for primates) and (2) the fusion of caudal vertebrae (coccyx) is an apomorphy of hominoids (man and apes) among the primates. The levels of generality of characters have been called either “mosaic evolution” or “heterobathmy.” The first means that any given organism is made of both apomorphous and plesiomorphous characters



(mosaic). The second means that these characters indicate different levels in the branching sequence displayed by the phylogenetic tree, relatively deep (such as the five fingers, 360 million years) or relatively high (the coccyx, 16 million years). As a consequence, the species *Homo sapiens* exhibit both traits of different chronologies, a foot with five toes (a tetrapod character) and a coccyx (hominoid character).

In the history of phylogenetics, the concept of congruence appeared later to be identical to the construction of the minimal length tree in terms of evolutionary steps, that is, steps from primitive to derived transformations of each analyzed character. Both maximize the hypotheses of homology (synapomorphies), that is, minimize the number transformations and, a fortiori that of transformations not related to shared ancestry (homoplasies). The algorithms of minimal length trees developed in the late 1960s and early 1970s, especially by the American phylogeneticist Steve Farris, are based on a measured distance called Manhattan distance. This distance calculates the difference (in terms of individual character states) between taxa in relation to a common ancestry and not directly (contrary to so-called Euclidean distances). These algorithms are described as parsimony algorithms.

In the 1980s, the irresistible access to personal computers made them functional for routine work.

The peculiar behavior of molecular characters (substitutions of bases in the different genes of the genome) with intense homoplasy and identical “morphology,” that is, a stereotyped information (an adenine is an adenine), leads molecular biologists to support a weighting approach (weighted parsimony), that is, weighting the different kinds of substitutions. For instance, the information given by transversions thought to be less frequent than transitions is considered more reliable. As a consequence, transversions are given more weight. In most molecular phylogenies, as the frequency of events is considered and not only the simple presence of same nucleotides, weighting turned into model methods. When models of evolution of substitutions replace weighting, parsimony algorithms are replaced by different algorithms based on probabilities (maximum likelihood and Bayesian approaches).

## Cross-References

- [Charles Darwin](#)
- [Evolution](#)
- [Homology](#)
- [Homoplasy](#)
- [Phylogeny](#)

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## Cladogenesis

- [Speciation](#)

## Clambering

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## Definition

To climb with difficulty or in a clumsy manner by using both hands and feet.

## Introduction

The word clamber is derived from the Middle English words *clamberen* and *clameren*, which are akin to the German word *klammern* denoting

the action of hooking oneself on or clinging firmly (Webster 1962). In relation to movement, it extends to a relatively awkward way of climbing, hooking, and clinging by using both hands and feet. Therefore, clambering appears to represent a mode of locomotion which incorporates the unstable, rather *maladroit*, way of negotiating rough and irregular vertical surfaces (e.g., cliffs) or navigating through unstable flexible branches in trees. Efficient clambering apparently requires cautious movements and strong holds.

### Locomotion in Treetops

In the literature related to animal, and mainly mammalian locomotion, clambering describes body displacement in multiple directions (upward, horizontal, downward) using irregular quadrupedal (i.e., four-limbed) movements across multiple, diversely oriented arboreal substrates. During these multi-directed movements, the forelimbs and hind limbs usually adopt a wide range of flexed and extended postures and may be often abducted in order to reach the diversely located available branches. Furthermore, the hooking and clinging action of clambering is assured by the grasping forefeet and hind feet that establish firm grips on the branches.

During clambering, the posture of the body may be also variable and is important for determining the ways that both forelimbs and hind limbs are used. Thus, pronograde clamber (or scramble) defines a nonsuspensory quadrupedal progression lacking a regular gait and keeping the body pronograde (i.e., horizontal) (Hunt et al. 1996). In this case, the arboreal substrates are usually small in diameter, rather flexible, bending under the animal's weight, irregularly placed, and variously angled. It usually occurs among the terminal branches of tree crowns and body progression is horizontal to slightly angled, and speed may be slow to medium-fast. This locomotor mode is often used by arboreal mammals, but behavioral percentages of use can be variable, depending on their anatomy and size. Smaller arboreal mammals tend to use clambering less frequently than larger ones, and more arboreally

committed mammals (e.g., primates) use it more often than more terrestrially adapted species.

On the other hand, orthograde clambering is an essentially horizontal or slightly angled progression keeping the body orthograde (i.e., vertical) in a forelimb-suspensory manner, but with the hind limbs assisting (Hunt et al. 1996). In this case, all four limbs move the body forward, with most body weight borne by the abducted forelimbs. However, the role of the hind limbs is to provide support from virtually any limb posture, including completely abducted. This locomotor mode can be also slow to moderately fast and usually occurs on intertwined small and flexible branches. In contrast to pronograde clambering, orthograde clambering is not very common and is usually adopted by some suspensory primates. For instance, the prehensile-tailed howler, spider, and woolly monkeys of South America moderately use this mode among small and medium branches of tree crowns (Cant et al. 2001; Youlatos 2008). In contrast, this way of locomotion appears to be more common in orangutans among apes, especially when traveling on small unstable branches within and across tree peripheries in the canopy (Cant 1987; Thorpe and Crompton 2006).

### Clambering and Cognition

Behavioral observations of free-ranging monkeys and apes have well established that pronograde and basically orthograde clambering are strongly related to locomotion upon small, fragile, flexible intertwined branches in tree crown peripheries. This fragile and unstable habitat, as a consequence of large body size, apparently represents an ever-changing and unpredictable environment that requires good knowledge and planning for competent and efficient navigation. In effect, mistakes may lead to falls from the canopy, which can be ultimately lethal. Therefore, apart from morphological adaptations that enable safe anchoring of the hands and feet, this endeavor also represents a mental challenge as it requires the failure of stereotyped behavioral responses (which suit better in more stable environments) and stimulation of

continuous experimentation (trial and error, in a relatively safer way). In this way, clambering has been supposedly reinforced by cognizance of one's actions, the ability to engage in a type of mental experimentation or simulation in which one is able to plan actions and predict their likely consequences before acting that subsequently led to the emergence of a limited self-concept (Povinelli and Cant 1995). However, data on the locomotion and postures of other great apes (gorillas, chimpanzees, bonobos) in relation to their cognitive capacities and self-concept fail to support such a strong causal interrelation: many apes depict increased intelligence and self-concept but do not seem to use high rates of clambering locomotion (Hunt 2004). Beyond that, the link between foraging for arboreal sources and development of great ape intelligence, which can be linked to clambering locomotion, as the major means for negotiating their access and acquisition, also appears not to be a strong one (Russon 1998). Large body size, complexity of social interactions, food source distribution in space and time, and food chemistry, examined within a phylogenetic context, may surely come into play, when considering the evolution of intelligence among great apes and humans (Hunt 2004).

## Cross-References

- [Ape Cognition and Conservation Initiative \(ACCI\)](#)
- [Catarrhine Locomotion](#)
- [Intelligence](#)
- [Platyrrhine Locomotion](#)
- [Primate Suspensory Behavior](#)
- [Self-Recognition](#)
- [Visual Self-Recognition](#)

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## Clark L. Hull

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Due to his rigorous and ingenious method, diligent studies, and the impact of his work, Clark Hull (1884–1952) is considered one of the most prominent researchers in psychology. He was born in a log house near Akron, New York, USA, and 3 years later, he and his family moved to Michigan to set a farm. Initially interested in engineering, Hull's decision of pursuing a career in experimental psychology occurred around 1908, during his recovery from a polio attack. At that time, he was influenced by Williams James's *Principles of Psychology* and his own search for an

intellectually growing field, one in which he could use his aptitudes in technology and his interest in building automatic apparatus (Hull 1952a) among them, one that could simulate the main characteristics of the conditioned reflex described by Pavlov. Hull obtained his B.A. at the University of Michigan, in 1913, and his Ph.D. at the University of Wisconsin in Madison, in 1918. There, he was motivated and influenced by Pavlov's book, *Conditioned Reflexes*. His dissertation, entitled *Quantitative aspects of the evolution of concepts*, was later published in *Psychological Monograph* (Hull 1920). His teaching career started early as a school teacher, before he obtained his B.A., after which he was offered a position as Instructor at the University of Wisconsin 2 years before he graduated. In 1929, he was invited to work as a Research Scientist at Yale University, due to his interest in applications and his abilities in statistics and quantitative modeling.

As experimental psychologist, Hull was attracted to a broad range of topics. Although his interest in learning was evident since his doctoral research, he also dedicated time to study aptitude testing and hypnosis, fields in which he published influential manuscripts and books. Nevertheless, a few years after he arrived at Yale, he dropped other areas of research and focused mainly on learning and motivation. Hull became one of the most cited psychologist in the 1940s in the learning and motivation literature. The formulation of his ideas into systems of principles that rule behavior included definitions, postulates, theorems, quantitative formalization of ideas, and the empirical evidence to support it. He developed his ideas in several papers (e.g., Hull 1930, 1937) and three books: *Principles of Behavior* (Hull 1943), *Essentials of Behavior* (Hull 1951), and *A Behavior System* (Hull 1952b).

Essentially, Hull's theory of learning assumes that a reinforcer works through the reduction of a drive (Postulate 3, Hull 1952b), and that the memory trace that links a stimulus and a response (i.e., habit strength) is directly related to the number of reinforced trials (Postulate 4, Hull 1952b). Then, the potential to produce a response (i.e., excitatory potential) results from the product of habit

strength and drive. These three variables (drive, habit strength, and excitatory potential) are considered intervening variables. These variables explain the observed relationship between inputs, or independent variables (e.g., number of reinforcement and hours of deprivation) and outputs, or dependent measure (e.g., latency to response). Hull proposed a definition and formalization of these variables and relationships. As more variables and interactions between variables needed to be accounted for, the system grew in assumptions to allow their codetermination. In its final version, Hull's proposed system had 17 postulates that contained a total of 178 propositions. Hull collected evidence for 121 of them and concluded that 106 were valid, 14 probably invalid, and 1 definitively invalid.

He considered the abstract reasoning processes of the organism as a mechanical process which could be explained from the laws of matter and movement. That is why in his learning theory, he tried to connect two empirical aspects of behavior (independent and dependent variable) through different theoretical concepts (intervention variables) that should have a physiological substratum.

Hull received great recognition and influence among psychologist. He was recognized with the Warren Medal of the Society of Experimental Psychology in 1945 and served as the President of the American Psychological Association in 1936. His students were strongly influential in several colleges and universities, and they continued to disseminate and complement Hull's work even after his death. Psychologist, such as Kenneth Spence, Neal Miller, and O.H. Mowrer, were among Hull's students, helping him to develop his theory, spread the use of the hypothetical-deductive model, and were very influential on their own, in the fields of learning, motivation, cognition, and behavior in humans and animals.

## Cross-References

- [Associative Learning](#)
- [B.F. Skinner](#)

- ▶ [Classical Conditioning](#)
- ▶ [Drive State](#)
- ▶ [Edward C. Tolman](#)
- ▶ [Intervening Variables](#)
- ▶ [Ivan Pavlov](#)
- ▶ [Kenneth Spence](#)
- ▶ [Learning](#)
- ▶ [Operant Conditioning](#)
- ▶ [Reinforcement](#)

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## Classical Conditioning

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## Introduction

Classical or Pavlovian conditioning is a type of learning where two or more events of the environment are associated. This type of learning helps

organisms to organize their behavior and represent their world. In a classic experiment, Pavlov (1927) discovered that a dog would salivate to the presence of a sound if this sound was previously presented contiguously with food powder. Pavlov called the food powder an unconditioned stimuli (US) that evoked a response by its own, which he called an unconditioned response (UR). The sound was originally a neutral stimulus that did not produce any relevant response, but after being presented with the food, the sound became a conditioned stimulus (CS), which elicited a conditioned response (CR). To Pavlov, this response was “conditional” to the unconditioned stimulus, thereby the name. The study of classical conditioning has changed since Pavlov’s years; we now know that classical conditioning is involved in much more than only simple reflexes and that it is a complex process involving complex responses. However, the basic concepts presented by Pavlov have remained in the vocabulary of researchers and the psychologists interested on associative learning.

A CS is a stimulus that, after training, predicts that the US will occur, usually causing an anticipatory CR. The US, by contrast, is a stimulus that does not need training to elicit a response and is usually relevant to the organism (Pavlov 1927). CSs and USs are often called by other names which allude to the same concepts. The CS is also referred sometimes as a cue or a predictor. The US is often referred as the outcome or the consequence. All these names are used somewhat indistinctively from another.

Classical conditioning is crucial for animals to be prepared for or anticipate events of the environment, and to predict what will happen around them. Consequently, it plays an important role for animals to adapt to their environment (Domjan 2005). The next sections will review how the view of classical conditioning has changed from its discovery, the basic preparation and phenomena of classical conditioning studied in the laboratory, and some of the most influential theoretical developments in the area. We will also cover how classical conditioning helps individuals to adapt to their environments, some of its main applications in therapeutic contexts, and its current state as theory and tool in Psychology.



## Historical Background

Pavlovian or classical conditioning was discovered independently in Russia and in the USA, at the end of the nineteenth century. Edward Twitmyer, at the University of Pennsylvania, investigated whether the patellar tendon or “knee-jerk” reflex worked under facilitating conditions. The sound of a bell signaled with 500 ms of anticipation the knee tapping. Shortly afterwards, Twitmyer observed that participants extended their knees immediately after the sound of the bell but in absence of any tap to the knee. Once it was demonstrated that participants were not doing it intentionally, Twitmyer concluded that some stimulus other than the usual one had elicited the reflex.

Twitmyer presented his findings at the Annual Meeting of the American Psychological Association with little impact, and he did not extend his work on conditioning. Thus, its discovery is credited to Ivan Pavlov, the Russian physiologist who worked approximately at the same time on conditioning in his laboratory, and upon realizing what he had found, dedicated the following decades of his life to the study of classical conditioning.

Pavlov’s work with conditioned responses became widely known during the first decades of the twentieth century, particularly in the USA. For instance, as early as 1914 John B. Watson and his student Karl Lashley were conducting studies in classical conditioning at Watson’s laboratory. Watson advocated in favor of the conditioned reflex as an explicative mechanism for many psychological processes and was heavily influential in its adoption by American psychologists. The publication of *Conditioned Reflexes* in 1927 (translated by G. V. Anrep, former student of Pavlov) further helped increase the interest in classical conditioning.

During the first half of the twentieth century, classical conditioning was widely studied as one of the fundamental learning processes (the other one being instrumental or operant conditioning). Basic experimental paradigms were extended from the original Pavlovian design and included preparations still in use today, such as fear

conditioning (for a detailed depiction of experimental preparations, see the corresponding section), also extended to different species including rabbits, rats, and humans. Early learning models also were developed during this time, for instance, Clark Hull’s *Principles of Behavior* (1943) and Edward Tolman’s influential *Purposive Behavior in Animals and Men* (1951). Theoretical models during this period followed closely the original Pavlovian view of classical conditioning. Primarily, the predominant conception was that conditioning was an automatic, low-level process which involved mostly smooth muscle tissue and glandular responses such as those studied by Pavlov, and that the key factor that determined how two stimuli are associated was temporal contiguity. This view shifted dramatically during the second half of the twentieth century as the result of new evidence (e.g., blocking effect; Kamin 1969), which suggested to learning theorists that classical conditioning was a more complex and rich learning process. For example, Rescorla (1988) summarized classical conditioning as “the learning that results from exposure to relations among events in the environment. . . a primary means by which the organism represents the structure of its world” (p. 152).

In parallel with this theoretical and empirical developments, there was also an important development of clinical applications based on associative principles. For example, the work of John B. Watson, Rosalie Rayner, and Mary Cover Jones showed how classical conditioning was able to explain the acquisition of fear as well as evaluate techniques to treat it. Later the South-African psychiatrist Joseph Wolpe developed the systematic desensitization procedure to treat anxiety, applying what was learned in the experimental laboratory to real life situations. These instances laid the ground for an empirical approach to psychotherapy in general and particularly for behavior therapy. The translation from basic experimental research to clinical application still continues today, with a growing corpus of empirical results in many areas.

As a result of the empirical and theoretical shift mentioned above, research in classical conditioning has growth beyond its origins and has



included novel experimental paradigms which came to be seen as associative in nature (e.g., contingency judgment and causal learning; Dickinson and Shanks 1985). An important development also occurred in models of associative learning (e.g., Mackintosh 1975; Rescorla and Wagner 1972). The mathematical formalization of learning models provided testable predictions which further helped bolster research in classical conditioning, in a trend that continues today. This expansion in the study of classical conditioning was also notorious in what is called the “functional analysis” in contemporary research (e.g., Domjan 2005; Hollis 1997), an approach that focused on investigating the role and properties of classical conditioning as an evolutionary adaptive process.

Currently, classical conditioning is an active research field, with relevant and growing links with the contemporary neuroscience and cognitive psychology, and particularly relevant as a model of information processing (for more details, see the final section of this entry).

## Major Concepts

This section will review some relevant basic aspects of Classical conditioning, such as Pavlovian acquisition, excitation, extinction and inhibition, and relevant factors such as contiguity and contingency.

The process by which the CR comes under control of the CS is called acquisition. This control is usually acquired by the CS after being paired with the US. The CS is generally a stimulus that by itself and prior to any training does not elicit the target response. Such target response is typically similar to that elicited by the US. Because of this, the CS is usually viewed as more neutral than the US, and this relative difference is used to define what the CS and the US are in any given experiment. For example, a weak electric shock can be used as US in an experiment, and as CS in a second one, provided that the corresponding CS and US are weaker and more intense, respectively. After one or more pairings (the specific number will vary depending on the

experimental preparation), subjects will respond to the CS in a similar way to how they respond to the US, or, depending on the task, with a response related to the specific features of the CS.

Several parameters affect the acquisition of a CR and thus will vary across experimental preparations. First, more intense or salient stimuli are generally associated with faster and stronger acquisition (Pavlov 1927). Acquisition also proceeds faster when the stimuli are novel, as shown by the “pre-exposure” or “latent inhibition” effect (Lubow and Moore 1959). Finally, acquisition is also affected by the temporal relationship between the CS and the US (inter-stimuli interval) and between each trial (inter-trial interval; e.g., Gallistel and Gibbon 2000).

Contiguity and contingency are two key concepts in Classical conditioning. Contiguity refers to the spatial and/or temporal relationship between the CS and the US. Contingency is the relationship of probability between the CS and the US, that is, how likely it is that both stimuli are presented together compared to the likelihood of them presented alone.

Variations in contiguity have an impact on the effectiveness of conditioning, and thus have been extensively investigated. The most used procedure is the so-called delay conditioning, in which the US begins after the onset of the CS but overlaps with it. This delay between the onsets of both stimuli can be short or long. In “trace” conditioning, there is a time gap between the offset of the CS and the onset of the US. The association in this case is supposed to occur between a trace of the already absent CS and the US, hence the name. Both stimuli can also be presented simultaneously. Finally, in backward conditioning, the usual temporal relationship is inverted, and the US is presented before the CS.

Contiguity has had theoretical value as an explanation of Classical conditioning. For instance, for Pavlov (1927), contiguity was the most important element for an association to occur. Past and current views about the role of contiguity in conditioning are discussed in detail in the corresponding section.

Contingency, on the other hand, is classified in three variations depending on the relative

probability of the CS and the US. Contingency can take positive, negative, and zero values. In positive contingency, the US is more likely to occur when the CS is presented than when it is not; in negative contingency, the US is less likely to occur when the CS is presented than when it is not; and in zero contingency, the probability of the US is the equivalent in the presence of the CS and in its absence.

The idea of contingency has been relevant for modern conceptualizations of Classical conditioning. Following the work of Rescorla (1969), contingency is thought to reflect the informational value of the CS, that is, whether the CS gives any meaningful information about the occurrence of the US. Thus, in positive contingency, the CS is a reliable predictor of the US, while in negative contingency, the CS is a predictor of the absence of the US, and in zero contingency, the CS does not give any information about the occurrence of the US. Different models give alternative interpretations for each case, and thus the role of contingency for models of Classical conditioning is further developed in the corresponding section.

The variations in the informational value of the CS regarding the US are closely related to the concepts of excitation and inhibition. Excitatory conditioning refers to when the CS is a good predictor of the US as in positive contingency. Conditioned inhibition, on the other hand, refers to when the CS is a predictor of the absence of the US, as in negative contingency.

A key feature of conditioned inhibition is that it occurs when there is a previous expectancy of the US. In other words, the organism must somehow expect the occurrence of the US so that the inhibitory CS can predict its absence, that is, there must be at least a previous excitatory context. The procedures designed to train conditioned inhibition all include a previous expectancy of the occurrence of the US. In the Pavlovian or standard conditioned inhibition procedure (Pavlov 1927), in an initial phase subjects receive CS1-US trials for the CS1 to provide an excitatory context. In a second phase, CS1 is presented together with a CS2 without the US. With this procedure, CS2 should become inhibitory, since it signals the absence of the US. In the negative contingency

procedure (Rescorla 1969), the CS is negatively correlated with the US. In this case, the excitatory expectancy is supposed to be given by the experimental context. Because the US is presented consistently in the presence of signals provided by the experimental context, it should become excitatory while the CS becomes inhibitory.

Conditioned inhibition is supposed to be contrary to excitation in that while the latter increases CRs, inhibition does not, which makes measuring it more difficult. Several techniques have been developed to overcome this problem:

- (a) Bidirectional responses: Some responses can increase or decrease compared to a baseline. Typical examples are the approach/avoidance system, or physiological responses such as the heart rate. A bidirectional response may, for example, decrease in presence of an inhibitor and increase in the presence of an exciter. Nevertheless, some responses have a very low baseline, making this type of measurement not ideal.
- (b) Summation/Retardation tests (Rescorla 1969): The summation test consists of the presentation in compound of an excitatory CS+ and an inhibitory CS-. If the CS- is effectively a conditioned inhibitor, it should decrease the response elicited by the CS+, compared to presentations of the CS+ alone. In the retardation test, the CS- is paired with the US. If the CS- did acquire conditioned inhibition, this reacquisition training should proceed slower compared to a novel CS.

After acquisition, repeated presentations of the CS alone cause a gradual decrement in the conditioned responding, which can eventually lead to its complete suppression. Both the procedure and its result are called extinction. Pavlovian extinction has been widely researched in the last decades for the study of its mechanisms and clinical applications (mainly for exposure therapy, details, see the “[Applications Outside of the Laboratory](#)” section).

One relevant feature of extinction is that its effect on behavior is usually not permanent, and the response to the CS recovers under several circumstances. Renewal is the recovery after the

subject is moved to a different context to the one in which extinction was conducted (e.g., Bouton and Bolles 1979). There are three types of renewal, depending on the procedure. ABA Renewal occurs when acquisition is conducted in a Context A, extinction in a Context B, and the subject is then tested in the acquisition context. ABC Renewal is similar, although test is conducted in a different Context C. Finally, in AAB Renewal both acquisition and extinction are conducted in Context A while testing is conducted in a different context. Spontaneous recovery is the response recovery that happens when a time interval is introduced between extinction and testing (Pavlov 1927). In reinstatement (Rescorla and Heth 1975), the response recovers when the US is presented again after extinction. Finally, when subjects receive again CS-US pairings after extinction, response recovers faster compared to the acquisition of a newly trained association (rapid reacquisition; Pavlov 1927).

## Experimental Preparations

This section will focus on experimental preparations used in Pavlovian research such as fear conditioning, taste aversion, and others. One important issue about Classical conditioning is the question regarding the generality of Pavlovian phenomena. Pavlov himself (e.g., Pavlov 1927) studied conditioning using stimuli of different modalities (i.e., visual cues, tones, tactile stimuli) to examine whether conditioning occurred or was similarly effective in all cases. The following years saw the development of many different experimental preparations, using CSs and USs of different modalities, and different ways to measure the conditioned response.

**Fear conditioning:** Fear conditioning is one of the most studied experimental preparations in Classical conditioning. It consists of the pairing of a given CS with an aversive or fear-eliciting US. After training, the CS comes to elicit responses (i.e., anxiety and/or avoidance) originally elicited by the aversive US, which can be used to measure the amount of learning about the now aversive CS.

In most of the studies, both with human participants and non-human subjects, fear conditioning is examined with the pairing of a CS or context and a mild electric shock. The shock is regulated in its intensity by the participants themselves in the case of humans, to be aversive without being physically harming. Fear is indirectly measured by several physiological and behavioral responses. In the case of human participants, these measures include skin conductance or galvanic skin response, pupillary dilation, and, particularly in the case of exposure therapy, approach/avoidance responses. In rats, freezing is usually reported as a measure of fear. Freezing can be measured as the time the rat stays without moving, which can be recorded and then examined by independent judges or by how much it disrupts the rat's normal behavior. Similar is the procedure of conditioned emotional response or "conditioned suppression." In this procedure, the rat is initially trained to press a lever for food. In a second phase, the subject receives CS-shock pairings. During testing the rat has access again to the lever, and lever press is measured in presence of the CS and in its absence. Fear is indicated by the decrement in lever pressing in the presence of the fear-eliciting CS compared to the baseline responding without the CS. There are several variations in which the effect of fear is measured against different behaviors such as licking water tubes or magazine entries for pellets, although the basic principle is the same.

A suppression ratio can be calculated as an index for the suppression of behavior. The suppression ratio considers how much responses occurred during the CS relative to the sum of those responses and the baseline responses registered before the onset of the CS. The suppression ratio ranges between 0 and 0.5, where 0 indicates no response and thus complete disruption of behavior (i.e., fear) and 0.5 indicates no fear.

**Conditioned taste aversion:** Classical conditioning plays a relevant role in the acquisition of taste preferences and aversions (Garcia and Koelling 1966). In a conditioned taste aversion experiment, subjects (typically rats) receive a flavor-CS (i.e., food or liquid) followed by sickness provoked by administering lithium chloride

or other emetic procedure. Conditioned taste aversion can be acquired after a single CS-US pairing, which is typical in aversive conditioning, but not observed in appetitive paradigms. Also, subjects may present taste aversion even if hours have passed between the presentation of the flavor-CS and the internal sickness. These features have been of theoretical relevance for discussing the role of preparedness or pertinence of the stimuli in Pavlovian learning.

**Eye-blink conditioning:** The eye blink is a reflex common to a wide variety of species. Any object approaching the eye, such as an airpuff, will elicit the reflex response. Eye-blink conditioning thus works by pairing a visual or auditory cue with a reflex-eliciting stimulus, usually an air puff or a mild electric shock (Gormezano 1966). Eye-blink conditioning has been extensively researched because of its simplicity in humans and other animals. It has also been relevant for understanding basic neural mechanisms of learning and memory.

**Sign and goal tracking:** Sign- and goal-tracking are terms that refer to similar tasks and include related preparations as autoshaping (Brown and Jenkins 1968). In sign-tracking, a visual CS is paired with an appetitive US, such that after repeated pairings, the animal responds by approaching and contacting the CS. In a typical experiment, a pigeon is trained to associate a keylight (i.e., an illuminated disc) with the delivery of grain. After some trials, the pigeon will approach the keylight instead of the food magazine and peck it as if it was a pellet of grain. In goal-tracking, the basic procedure is similar although the measured response is the approach to the place of appearance of the US.

Since both tasks are similar, some research has examined the factors that may explain whether organisms will respond with either sign- or goal-tracking. For instance, it has been shown that rats tend to show more goal- than sign-tracking, that is, rats approach the food magazine instead of the CS, while pigeons show the opposite pattern. It has also been suggested that the observed behavior depends on the contiguity between the CS and the US: goal-tracking would be more likely when the CS and the US are separated temporally and

spatially, while sign-tracking would be more probable when both stimuli are close.

Sign-tracking, and particularly autoshaping, has been historically a relevant phenomenon for classical conditioning. From the early conceptualizations of Pavlov, it was considered that classical conditioning affected reflexes and glandular responses, while responses involving skeletal muscles were the domain of operant conditioning. Sign-tracking, as primary classical conditioning procedure that involves complex skeletal responses, showed that this distinction was not empirically valid (Hollis 1997).

**Drug tolerance:** Drug tolerance is the decrement in the effect of a drug after its repeated administration or, conversely, the need of higher doses to obtain the same original effect. Drug tolerance has a learning component in what is called “associative tolerance.” Research has shown that each episode of drug administration is a conditioning trial, in which the effect of the drug is associated with, and thus predicted by, a wide arrange of stimuli (Siegel et al. 2000). For instance, the presence of friends or bottles can act as a signal for the consumption of alcohol. Within this framework, tolerance is the product of anticipatory conditioned responses to these signals that predict the drug and thus allow the organism to adapt to its effect. For example, a well-known effect of alcohol is the decrement in body temperature. The compensatory reaction by the organism is to rise the temperature to counteract the effect of alcohol intake. This response is specific to the cues or contexts associated with the drug, that is, associative tolerance will be evidenced only in the specific circumstances linked to usual drug consumption where the drug-predictive cues are present.

**Causal learning:** Causal learning is a broad term that encompasses different methods by which people learn about the causal structure of a given task. One of them is the so-called human contingency learning, although the terms “predictive learning” and “causal judgment” are also used in the literature. Participants, in a contingency learning task, are presented with sets of stimuli and then asked to assess the causal relationship between them. For example, in what is perhaps the most used causal learning task, participants assess

the causal relationship between meals or chemicals and sickness in a hypothetical patient. In such tasks there are many ways of assessing this relationship, from simply giving a prediction in an arbitrary scale to more behavioral or physiological measures like response latency and eye tracking. Contingency learning shows many of the phenomena found in classical conditioning, which is why it is usually explained in terms of associative learning models (Dickinson and Shanks 1985). For instance, acquisition and extinction of a causal relationship proceed in a similar manner to other Pavlovian preparations, as do cue competition effects.

**Conditioned Analgesia:** Stressful situations can produce an unconditioned reduction in the severity of pain. Consequently, an initially neutral stimulus, through pairings with a stressor, also comes to produce a reduction in the response to painful stimulation. Such reduction is often called conditioned analgesia (i.e., conditioned stress-induced analgesia). This preparation has been used both with human and non-human animals, who typically report or show behavior indicative of lower pain when the associated CSs are presented (see Miguez et al. 2014, for a review).

## Key Phenomena

Several learning phenomena have been historically relevant for the study of Classical conditioning and for the development of theoretical models. This section describes some of them, such as cue competition and interference phenomena.

**Cue Competition:** Cue or stimulus competition refers to a set of Pavlovian phenomena, in which multiple CSs are trained simultaneously with an outcome or US. In these cases, all CSs involved appear to “compete” with each other for the conditioned response, thus the name. When both stimuli are tested individually, one will elicit less-conditioned response than the other one.

**Overshadowing** is a cue competition effect first identified by Pavlov (1927). In overshadowing, two CSs are presented simultaneously followed by the US. The critical feature is that one of the CSs is defined as more salient than the other (i.e.,

more intense or relevant). When both stimuli are tested, subjects show more conditioned response in the presence of the more salient CS compared to the less salient one.

**Potentiation** (Rusiniak et al. 1979) is a variation of the overshadowing procedure frequently observed in taste aversion experiments. The procedure is similar to overshadowing training, but the result is the opposite, that is, the less salient CS elicits more conditioned response than the more salient CS during testing. Some factors have been suggested to facilitate potentiation over overshadowing: the trace between CS and US, the specific experimental preparation (most of the observations of potentiation have been conducted in taste aversion), and the relative salience of the trained CSs.

**Blocking** is perhaps the most investigated cue competition effect. In blocking (Kamin 1969), subjects receive an initial phase of CS1-US until the conditioned response to CS1 is reliably established. In a subsequent phase, subjects are trained with CS1-CS2-US pairings, where CS2 is a second, different CS. When both CSs are tested individually, subjects respond more to CS1 than to CS2, that is, CS2 is “blocked” by the CS1.

**Interference:** In Classical conditioning, it is frequently observed that two different independent trainings that share a common element can affect how subjects respond to the stimuli involved in each training. This general phenomenon is called “interference” (Bouton 1993).

Pavlovian interference can be examined in two different ways. In proactive interference, a first-learned association can affect responding to a second-learned association; in retroactive interference, a first-learned association can be affected by a second-learned association.

Furthermore, interference also varies depending on the common element shared by the different associations; cue-interference refers to the training in which the first- and the second-learned association share a common US but different CSs. For example, subjects trained with tone CS-shock pairings in a first phase, and light CS-sock pairings in a second phase will show less fear to the light compared to subjects that received only one of either phase of training.

Outcome-interference refers to different associations sharing the same CS but different USs or the absence of a US as in extinction. For example, in the case of counterconditioning, a tone CS can be initially paired with a shock, and in a second phase with food pellet. Another example is latent inhibition, in which subjects are presented to a CS alone (without a US or consequence) during a first phase, and then to CS-US pairings during a second phase. Such subjects acquired excitatory conditioning slower relative to subjects that did not experienced the first phase.

## Theoretical Developments

Researchers and theorists of learning have created several accounts to explain how stimuli are associated and what happens when we observe blocking, inhibition, or any other conditioning phenomena. These accounts are usually referred as theories or models of conditioning or learning.

The first theory of conditioning is as old as conditioning itself. Pavlov (1927) thought that during the presentation of the US, a node in the brain was activated, which was linked to a response node for the unconditioned response. When the CS started to be paired with the US, the CS-node began to supplant the US-node, thereby producing the same response that the US produced before. This early theory is not able to explain all the phenomena and contemporary evidence on conditioning but serves as a first explanation of how animals learn new conditioned reflexes linked to innate responses.

Most of the current models of learning are influenced by proposals from Clark C. Hull, his disciple Kenneth Spence, and Bush and Mosteller. In different ways, they all suggested that learning is a function of a maximum amount of possible learning, and what or how much the subject has learned at that moment. This rule assumes that learning is a gradual process based on error correction, that is, that the amount of learning gained each time that the stimuli are paired (the rate of change on learning) would be progressively smaller as learning progresses.

These ideas were taken by Robert Rescorla and Allan Wagner to create one of the most influential models of learning (Rescorla and Wagner 1972). This model states that learning is the difference between the maximum possible amount of learning about an outcome and the amount of information supplied by all the cues present in the past pairings with the US.

Under this conception, learning could also be considered a function of the difference between what happens and what the subject predicts that will happen. Rescorla and Wagner also proposed that learning depended on the product of how salient or intense the cues and the consequences are, which, according to them, would not change during the course of learning. The result of the equation is a quantitative measure of learning that they called associative value (V).

The Rescorla and Wagner (1972) model was the first to compute the prediction from multiple CSs simultaneously; consequently, it explains several of the competition phenomena observed in Classical conditioning, like blocking. For the model, in the first phase of training, when the first cue is paired with US, the cue becomes a good predictor of the US, but when the second stimulus is added in the second phase, this second cue does not provide much more information about the US: the subject is already good in predicting what is going to happen. In terms of the model, at the end of the pairings of the first cue with the US there is little to no difference between what happens and what the subject predicts that will happen, and when the second CS is introduced, there is little or no more to learn.

The principles of the Rescorla-Wagner model have been taken by several other learning theorists, helping to create many of the current models of conditioning and generating research until today to test the assumptions and predictions of the model.

Mackintosh (1975) and Pearce and Hall (1980) took the basic principle of the Rescorla-Wagner model but added, in two different ways, a new assumption. They assumed that the salience or intensity of the CS, what they called “associability,” would not remain constant across learning trials and it would vary proportionally to



how good of a predictor the CS becomes. These models are commonly referred to as “attentional” models, because of the shared characteristic that the subject will attribute more importance or salience to cues based on their history with the consequences.

Mackintosh (1975) proposed that cues that are better predictors will have a higher associability or attention. If a stimulus predicts a consequence, it should be considered more relevant and thereby should be paid more attention. Due to this, subjects will learn faster associations involving cues that are better predictors of consequences.

Pearce and Hall (1980) model has a seemingly opposed approach to Mackintosh’s to the problem of associability. They proposed that subjects do not need to pay attention to cues that are already known, and are good predictors. Instead, subjects should pay attention to new cues or cues that are inconsistent predictors of consequences. For Pearce and Hall, stimuli that are not good predictors of the CS, for example, before the beginning of training, will have a higher associability or attention, and as the pairings with the consequence continue, the associability will become smaller and smaller. According to the model, learning about new cues when they are paired with the US should be faster than cues that are already good predictors of the US.

The evidence shows that both Mackintosh (1975) and Pearce and Hall (1980) models correctly predict how subjects behave in various circumstances. Both models are able to explain conditioning phenomena such as blocking or latent inhibition. For example, the Mackintosh model states that in latent inhibition, when the CS is presented in absence of any consequence, the subject pays less attention to it because the cue is not a good predictor of the consequence; in the following phase, during the presentations of the cue with the outcome, subjects will take more time to learn the relation between them compared to a cue that was not pre-exposed. Pearce and Hall’s model, on the other hand, assumes that when the CS is pre-exposed, the cue becomes a good predictor of a specific consequence, being that consequence nothing. Here the absence of a stimulus can also serve as consequence after the CS. This

also causes the attention to the cue to decrease but by a different mechanism than for Mackintosh’s model. The result in both cases is the same, the subject will take more trials to learn the CS-US association due to the low associability caused by pre-exposure, but produced by different mechanisms.

Recent developments have tried to reconcile this two, seemingly opposed, proposals creating models that assume that the associability of stimuli can increase in both cases, by being a good predictor of the US and by being an inconsistent predictor of the consequence. These theories are known as “hybrid” models and have been highly discussed in the last years (e.g., Pearce and Mackintosh 2010).

A somewhat different approach was taken by Wagner (1981) who was interested in how representations are formed in memory with his theory of standard operating procedures (SOP). For this theory, stimuli consist of nodes of a number of elements. These elements and by in three different states: an inactive state, and two active states (A1 and A2). Stimuli are normally inactive, but would activate in A1 when they are directly presented. Stimuli can then be activated in A2 either by normal decay from A1 after some time or after learning when an associated cue is presented. After a stimulus is in A2, it can only move to the inactive state. Excitatory conditioning occurs when the two stimuli are in A1, and as learning progresses, the first stimulus starts to activate more and more elements of the second in A2. This theory has been fundamental to explain phenomena like context specificity of latent inhibition, and to make predictions about learning in a real-time base instead of trials as the Rescorla & Wagner model.

Other theories of learning have put focus on how the US is processed by the subject during learning. These theories assume that, in any interaction with the environment, the target US is not a simple stimulus defined by just one dimension or attribute. Consequences are always complex and involve many possible characteristics from which to learn. For example, if the presence of a dog is followed by its bite (possibly causing fear to it), this bite is not just composed by the pain itself, but

it can be divided in different parts like the vision of the bite, the motivational state that it causes (probably non-rewarding), the time of the bite (when the bite occurs both in a general timeline and since the dog was perceived), the response that it causes, and the emotional reaction, among others. Some theories have proposed that we can learn from all these attributes separately and that the rules to learn the relationship between the cue and the consequence may be different for each of its parts (e.g., Delamater and Oakeshott 2007).

Another family of theories views animals as able to learn about the complex environment when several stimuli are in place, and not only about its elements. Each stimulus can be seen as a part of a more complex structure in the subject's environment. Pearce (1987) proposed a model that elaborates on these assumptions. The model states that subjects do not learn about each stimulus separately, but at the moment of learning, they process the environment as a unique complex stimulus composed of every single present cue. Thus, individuals do not learn about relationships between a single cue and the US but about this complex cue (called "configurational stimulus" or simply "configuration") and how that stimulus is related to the consequence.

The Pearce (1987) model states that, during testing, the more similar the configurational stimulus presented is to the one encountered during training, the more the subject will respond to it; conversely, the less similar the test configuration to the original, the less response will be observed (effect known as "generalization decrement"). This model is able to explain several learning phenomena, including cue competition and others.

The theories presented above all assume that subjects respond as much as they learn. In other words, they assume that the response by the subjects is proportional to the acquired learning stated in the equation, which changed during training or acquisition. However, under many circumstances, organisms change their response without further training. The opposite also occurs and is possible to learn without any change in responding; theories of learning have considered how response changes independently of acquisition training,

and how learning can occur without an apparent change in response. Miller and Matzel (1988) provided an approximation to this in the "comparator hypothesis."

Miller and Matzel (1988) suggested that when the subject learns, it does not take in consideration how good of a predictor a cue is (as the Rescorla-Wagner model); instead, the organism learns about all the stimuli that are presented together. In other words, contiguity alone is sufficient to produce learning. Since the subject learns about all present stimuli, responding must be controlled by a different process than the contingency or the associability of each cue. Because the subject is learning via contiguity about every present stimulus, the model suggests that the organism compares which one of all the present stimuli has the strongest connection with the US. When a cue is present, subjects will compare the CS with other cues that were present during training; if the cue is the more strongly associated with the consequence, the subject will respond. Conversely, if other cues have a stronger relation with the US than the CS being presented, subjects will not respond to that CS.

The comparator hypothesis (Miller and Matzel 1988), more specifically, states that in every learning situation (when a cue is followed by a consequence or US), the cue is associated with the consequence, but this cue is also associated with any other stimulus presented during this learning procedure, which causes that when the cue is presented, the subject activates a memory not only of the consequence but also of all other stimuli that were present during training. This memory in turn also indirectly activates a memory of the consequence. When a cue is presented, the subject compares which memory of the consequence is stronger, the directly activated by the cue presented or the one activated indirectly via the memory of the other stimulus presented during testing. Due to this mechanism, the model predicts that once individuals learn, they can change responses without further training being necessary; for instance, if a good competitor that was blocking the response to another stimulus stops being a good competitor, the subject may start now responding to the previously blocked

stimulus. In this situation, acquisition relative to the blocked stimulus has not changed, just the relationship of the competitor stimulus with the CS.

Other family of models have set their focus on the temporal relation between CSs and USs as a central mechanism to learning. Models as the one proposed by Gallistel and Gibbon (2000) share with the comparator hypothesis the notion that responding to a stimulus depends on the comparison between the target stimulus and the background stimuli. However, this model differs from the comparator hypothesis in that it assumes that subjects encode temporal intervals between events and rates of reinforcement instead of a CS-US association. For this model, subjects will respond to a stimulus when the rate of reinforcement of this stimulus is considerably higher than the rate of reinforcement of the context. This and other time-focused models have been proved very useful in many circumstances and have generated a large cluster of research.

All these models and theories here presented have led to an immense increase in the understanding of how organisms learn and what is learned in classical conditioning. Moreover, the different proposals have helped to conceive a great amount of new research to test the models and account for their failures. Nevertheless, the current state of the art is likely far from having a single model that would be able to explain all the phenomena in classical conditioning. More than one hundred years of research have shown that classical conditioning is an extremely complicated cognitive process, which mechanisms can go from considerably simplistic to immensely complex in different situations and under different perspectives.

## A Functional Point of View

Classical conditioning, as presented before, allows organisms to represent themselves their world. It allows subjects to act appropriately and predict many situations in their natural environment, improve their efficiency, and increase their chances to survive. This suggests that classical conditioning is not only a cognitive tool but that

also has a great evolutionary role in the species that learn through it.

The different phenomena of classical conditioning and the mechanisms discussed in previous sections are general across all species where conditioning is observed, and apply to diverse response systems, such as fear, displeasure, pain, taste, sex, etc. This suggests that conditioning has a generalized role in how animals represent their world and is not limited to certain kinds of learning. One classical feature that shows the relevance of classical conditioning in natural environments is that learning between cues that have a “natural” relation to each other proceeds considerably faster than learning between neutral or previously unrelated stimuli. This natural relation between the stimuli can come from a CS that is part of a chain of actions that lead to the US, or of the CS being a feature of the US that initially does not elicit a response; this last case is known as “object” or “part-whole” learning (Domjan 2005). For example, learning to predict that a certain food will cause sickness is considerably easier if the predictor is the flavor of the food than if it is the sound or vision of the food. The use of naturally related stimulus in learning produces not only a faster learning but is also more robust and resistant (Garcia and Koelling 1966). This evidence implies an evolutionary predisposition to learn certain association faster than others, probably due to their importance and relative complementarity between the stimuli. Even more, animals learn to predict events that can be threatening to their lives (e.g., to predict predators, a painful stimulus, or poisoning) faster than less threatening events (e.g., to find a place, tolerance to a drug, or when food would come). From an evolutionary perspective, not learning about the former means a higher chance of dying than not learning about the latter, which would create an evolutionary predisposition to learn about dangerous stimuli faster than to other kind of stimuli.

One example of conditioning with naturalistic stimuli with nonthreatening consequences is sexual conditioning. In sexual conditioning, the sight of a female-like figure or an actual female is paired with access to copulation. Males that are subject to the pairings with the vision of an actual female as

CS are much faster in approaching the female and ejaculating. As in previous examples, when the naturalistic CS is used, learning is less susceptible to extinction and cue competition.

Conventional descriptions of classical conditioning emphasize the development of CRs to the CS. However, numerous studies have shown that conditioning also alters how organisms react to, and interact with, the US. This expands the definition of classical conditioning to not only the way organisms represent their world but also a functional process through which animals increase their chances of survival and procreation (Hollis 1997).

## Applications Outside of the Laboratory

The study of classical conditioning has been, and still is, relevant for the development and improvement of applications outside of the laboratory. This section lists and describes some of these applications in the area of Psychopathology and Psychotherapy.

Experimental neuroses in dogs and humans: Applications of classical conditioning began to be developed shortly after Pavlov's initial demonstrations of conditioning (Pavlov 1927). One of Pavlov's collaborators, Shenger-Krestinikova, is cited as the first one who examined the so-called *experimental neurosis* in dogs. Shenger-Krestinikova implemented a task in which a dog had to discriminate between two different visual cues (i.e., a circle and an ellipse), one of which was followed by food. Once the discrimination was established, indicated by the animal salivating to the circle but not to the ellipse, both stimuli were gradually made more similar. The dog discriminated successfully between both visual cues until they were practically indistinguishable, at which point the animal showed responses not displayed previously which were, according to the researchers, indicative of emotional distress or akin to neurotic behavior.

Nikolai Krasnogorski, another of Pavlov's collaborators, extended this research to human subjects with a task based on that of Shenger-Krestinikova. In his study, a 6-year-old child had

to learn discrimination between two different auditory stimuli, which were then progressively made more similar to make the discrimination more difficult. Both experiments are considered as the first ones establishing that classical conditioning could be behind the acquisition of both adaptive and nonadaptive emotional responses to novel stimuli. These results were solidified and extended by the following research.

Acquisition and elimination of fear: The next step was performed by John B. Watson, an American psychologist and founder of behaviorism. Watson conducted research aimed to demonstrate how principles of classical conditioning could explain the acquisition and elimination of fear to different objects. In what is perhaps the most known and infamous experiment in the history of Psychology, he and his assistant Rosalie Rayner (Watson and Rayner 1920) conditioned an 11-month-old child called "little Albert" by pairing a white rat, to which Albert showed previously no fear, with the sound produced by clanging iron rods behind Albert's head. After several pairings, Watson and Rayner presented the rat by itself, to which the boy showed fear. Afterwards they examined whether fear could generalize to other objects by showing Albert a rabbit, a dog, and a fur coat, to which Albert also reacted with fear. Unfortunately, Watson and Rayner never had the opportunity to treat Albert's newly acquired fear, but an attempt in this direction was made in a subsequent experiment with a child called Peter. This child showed fear to white rats and rabbits, probably by means of conditioning during his life. Mary Cover Jones (Jones 1924), developed a procedure to reduce Peter's fear by exposing the child to the fear-eliciting objects in what they called "direct conditioning." Peter was put in a chair and given a snack while in parallel a white rabbit in a cage was put on the table in a distance that did not disturb the child. The procedure was repeated the next days with the rabbit slightly closer each time, until Peter could eat with the rabbit next to him, and even while playing with it. This method is similar to the procedure of counterconditioning described previously and constitutes the bases for the development of systematic desensitization.

Systematic desensitization: Pavlov's and Watson's research showed that problematic behaviors such as fear could be explained by classical conditioning. Jones' experiment with Peter also showed that fear could be eliminated by gradual exposure to the fear-eliciting stimuli. This last result was further developed and systematized by the work of Joseph Wolpe. Wolpe, a South African psychiatrist, developed a model for the acquisition and treatment of fear and anxiety that was based on his previous work with cats as subjects. In his experimental work, cats received pairings of an auditory cue with a foot shock in an experimental chamber. After a few pairings, cats acquired fear to the auditory stimulus, which also generalized to the experimental cage. According to Wolpe's report, mere exposure (i.e., extinction) to the experimental cage failed in reducing fear responses, and thus he evaluated whether a response contrary to fear was more effective in decreasing it than exposure alone. Cats were gradually exposed and fed in situations more and more similar to the fear-inducing cage until the animals managed to eat in the experimental cage. A similar approach was used to eliminate fear to the auditory cue.

Based on these findings, Wolpe suggested the same manipulation could be used to reduce fear and anxiety in human patients. Although the procedure was first developed by Watson y Jones, it was Wolpe who systematized and published the steps of what he termed "systematic desensitization" (henceforth SD; Wolpe 1961). Wolpe based the treatment on what he called "reciprocal inhibition," the idea that anxiety could be "inhibited" by inducing an incompatible emotional state. As designed by Wolpe, a typical SD procedure has three steps:

(a) Establish a hierarchy of anxiety-related stimuli: The therapist and the patient identify the objects or stimuli that are associated with anxiety. Each item is given a rating based on the level of anxiety it provokes; (b) Train an incompatible response: The most used incompatible response is relaxation training such as meditation or breathing exercises. Patient are taught these strategies as a way to counteract the anxiety; (c) Exposure to the anxiety-related stimuli: While in the relaxed state,

the patient is gradually exposed to the anxiety-eliciting items beginning with the object with the lowest level in the scale developed in Step 1 until the patient reports no fear. Afterwards, the patient is exposed progressively to the next items in the anxiety scale. Wolpe's initial reports were followed by numerous publications showing the effectiveness of SD on a variety of disorders.

Exposure therapy: Although Wolpe's work is commonly described as one of the beginnings of exposure therapy, the basic principles are different as systematic desensitization is based on the counterconditioning procedure while exposure therapy is based on extinction, and as such does not necessarily involve the previous induction of an incompatible state. Exposure therapy is a type of cognitive-behavioral therapy in which the patient is confronted with the stimulus or event that is associated with the problematic behavior (hence the name). For example, an exposure-based approach for a phobia to spiders will involve exposing the patient, gradually or otherwise, to pictures of or real spiders until the phobic symptoms recede.

Exposure treatments have several variations depending on the procedure. On the one hand, exposure can be graded as in systematic desensitization or can begin with the stimulus with the highest anxiety level, in a procedure known as *flooding*. Exposure itself can be conducted in vivo, that is, in direct presence of the problematic object. For example, a patient with social anxiety might be instructed to give a speech to an audience. *Imaginal exposure*, on the other hand, involves instructing the patient to imagine vividly the object or situation. This is particularly useful when the anxiety-eliciting events are not available as, for example, with patients with post-traumatic stress disorder. In the last years, *virtual reality* exposure has become more common with the development of technology.

Research has shown that cognitive-behavioral therapy, and especially exposure therapy, is effective in alleviating the symptomatology of many disorders, including but not limited to phobias, PTSD, OCD, and reactivity to drug and food-related cues.

Relapse and prevention of relapse: As mentioned before, the effect of experimental extinction



is frequently temporary, and the extinguished response can recover. In the same manner, exposure therapy does not destroy the potential of the phobic object to cause the problematic response. Thus, the circumstances under which the extinguished response recovers have served as a model for the study of relapse in exposure therapy and its prevention. Relapse occurs frequently when the patient has experience with the aversive event outside of the treatment context (renewal), and when some time has passed since the last exposure session (spontaneous recovery).

Basic research has showed that some manipulations have potential to prevent relapse. One of them is massive extinction. In animal studies, it refers to the amount of extinction trials received by the subjects, which can go up to ten times the number of trials received by a control group. The results have showed that massive exposure is successful in attenuating and even completely preventing relapse, although so far it has only been examined in specific experimental preparations. A second treatment is conducting exposure in many contexts as opposed to in one. Several studies have reported in different experimental preparations that exposure in multiple contexts attenuates relapse, although its effectiveness might be qualified by several factors, such as the number of contexts in which fear was acquired, or the similarity between the exposure and/or acquisition contexts. Another technique is the use of extinction cues or retrieval cues for extinction. An extinction cue is a stimulus that is presented during exposure and then is used after it is over. Extinction cues have been shown to attenuate relapse in both animal and human studies, and with different experimental preparations. Finally, a less investigated treatment is what in the animal studies is called “deepened extinction.” In this manipulation, the patient is exposed simultaneously to multiple anxiety-eliciting cues. This is supposed to produce a better extinction (i.e., reduction in reactivity to cues) than exposure to a single cue. Some studies have shown in both animals and humans that deepened extinction successfully prevents relapse caused by the passage of time (spontaneous recovery) and by the presentation of an aversive stimulus (reinstatement).

## Current Status of the Study of Classical Conditioning

The principles of classical conditioning are related to many areas of Psychology, but their study by neuroscientist has been prolific in continuously showing the potential neural correlates to different phenomena of classical conditioning.

Several research suggested relationships between phenomena previously described here like blocking, conditioned inhibition, and extinction and the activity of the brain. Furthermore, neuroscience also has shown some evidence that relates the activity of the brain with specific theories of conditioning. One example of this evidence is the relationship between dopaminergic and norepinephrinergic activity and error correction. Structures like the basal ganglia, the cerebellum, and striatum among others appear to be involved in predicting rewards and subsequent behavior (Schultz and Dickinson 2000).

Many neuroscientists that work on areas related to the neural bases of learning choose to work on classical conditioning because it has been extensively researched and it provides with simple yet useful learning situations to analyze.

Likewise, classical conditioning is closely related to cognitive Psychology. As suggested above, many theorists of learning have stated that perception, attention, and other basic processes affect how we learn about the environment. Furthermore, a particular approach to cognitive processes called “connectionism” often uses a principle called “delta rule” that closely resembles Rescorla-Wagner’s rule for error correction. These models understand various cognitive phenomena through multiple parallel associations between inputs (stimulus) and outputs (response), which bear many similarities with the principles of classical conditioning.

All these links between classical conditioning and other areas of research, together with the continuously growing clinical application that have come from the study of classical conditioning, show that this is still a very active area. Moreover, the theories of the mechanism behind classical conditioning are still being updated and becoming more and more complex in a continuous rate.



## Cross-References

- [Associative Learning](#)
- [Autoshaping](#)
- [Avoidance](#)
- [B.F. Skinner](#)
- [Blocking](#)
- [Conditioned Inhibition](#)
- [Conditioned Place Preference](#)
- [Contingency](#)
- [Counterconditioning](#)
- [David Hume](#)
- [Disgust](#)
- [Extinction in Learning](#)
- [Inhibition of Delay](#)
- [Ivan Pavlov](#)
- [J Bruce Overmier](#)
- [John B. Watson](#)
- [Karen Hollis](#)
- [Latent Inhibition](#)
- [Learning](#)
- [Michael Domjan](#)
- [Operant Conditioning](#)
- [Overshadowing](#)
- [Plantae](#)
- [Ralph Miller](#)
- [Reflex](#)
- [Skinner Box](#)
- [SOP Model](#)
- [Spontaneous Recovery](#)
- [Taste Aversions](#)
- [Tolerance](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Definition

Curved bone of the shoulder (pectoral) girdle that typically serves to link the shoulder blade (scapula) and breastbone (sternum) in vertebrates.

## Introduction

The term “clavicle” originates from the Latin word *clavicular*, meaning little key. This describes the function of this bone in that it rotates along its axis similar to a key when the shoulder is abducted (rotated away from the body). When present, this bone serves as a strut to support the shoulder. It is in fact the only long bone, meaning a bone longer than it is wide, of the body that is oriented in a horizontal fashion (Nagashima et al. 2016). Clavicles are present in most mammals with prehensile forelimbs, but they are absent in sea mammals and animals that have evolved to be more adapted for running. The furcular bone, more commonly known as the wishbone in birds, is composed of two clavicles fused together (Larson 2009). Aside from species variations, there are several other characteristics of clavicles that make them unique.

## Classification of Organisms

### ► Taxa

## Clavicle

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## Synonyms

Collarbone

## Anatomy

The shoulder joint is comprised of both the clavicle and the shoulder blade. Humans have two clavicles that reside on either side of the bottom of their neck. Clavicles are essentially s-shaped rods that articulate laterally with the outer end of the shoulder blade that form the shoulder joint. They articulate on the midline with the breastbone or sternum. The degree of muscling of an individual can dictate the robustness of the clavicle. The clavicles serve as attachment points for numerous muscles (Nagashima et al. 2016).

## Function

The clavicle allows rigid support of the shoulder blade, leading to the ability for the limb to be

freely suspended. This gives the arm maximum range of motion and flexibility. Protected by the clavicles, there are also nerves and vessels going to the limb that run along and underneath the clavicles. Physical impacts can be transmitted from the upper limb to the core skeleton by way of the clavicles. The clavicle also serves as an attachment for several important muscles including deltoid, trapezius, pectorals, sternohyoid, and the subclavius that are crucial in movement and stabilization of the arm (Voisin 2006).

### Species or Sex Variation

In some mammals requiring greater freedom of motion, clavicles have become reduced or absent, allowing these animals the ability to run faster. Birds use their fused clavicles, termed wishbones, to strengthen their chest to withstand the harsh forces of flight. In most cartilaginous and bony fish of today, clavicles are absent, but in primitive bony fish, the clavicles were associated with the pectoral fin and were located just behind and below the gills on each side. On the fish's underside, there was a solid connection of the two, termed a symphysis (Larson 2009). In human females, clavicles are characteristically shorter, lighter, thinner, smoother, and less curved when compared to males. These classic distinct differences can be utilized in the sex determination of a human skeleton. (Larson 2009)

### Development of the Clavicle

During the development of a human embryo, the clavicle is interestingly the first bone to begin the process of ossification, essentially meaning the laying down of minerals onto a matrix that was preformed, yet it is one of the last bones to finish ossification. This process starts at approximately 5–6 weeks of gestation and is complete by 21–25 years of age. (Larson 2009) Unlike other long bones, the clavicle is thought to not have a medullary cavity, the site where the bone marrow is housed. Another unique characteristic of the clavicle is that it forms from two separate

ossification centers. The outside or lateral end of the clavicle undergoes intramembranous ossification, while the end near the midline undergoes endochondral ossification (Voisin 2006). This means that there is development of the bone via replacement of connective tissue and replacement of a cartilage matrix, respectively.

A unique congenital condition in which the clavicles are absent or imperfectly developed in humans is termed Cleidocranial dysostosis. This occurs in approximately 1 out of 1,000,000 people globally, resulting in drooping of the shoulders and the ability of the shoulder blades to meet at midline. It is thought to be associated with the RUNX2 gene that codes for transcription factor protein that is in charge of the regulation of the bone forming cells, osteoblasts (Larson 2009). There are an array of other abnormalities associated with the condition, in particular delayed ossification of the skull leading to the sinuses being underdeveloped and an open fontanelle.

### Traumatic Injury to the Clavicle

Many are familiar with broken collarbones as the result of injury or trauma. The S-shape of the bone allows for fractures to occur at the angle of greatest change in its direction. A fractured clavicle results in the sternocleidomastoid muscle lifting from the medial aspect, ultimately causing puncture of the overlying skin (Voisin 2006). Causes of clavicular fractures occur when a person falls either horizontally onto the shoulder or with an outstretched hand attempting to catch themselves. There is a transmission of forces from the core or axial skeleton onto the bone with a greater force than the strength of the clavicle. When a fracture of the clavicle occurs, it results in the trapezius muscle not being able to support the weight of the arm. This leads to the characteristic broken collarbone image of a man supporting his arm with the opposite hand. Because the clavicle is directly under the skin and is not covered with muscle, fractures can easily be felt and even seen. Interestingly, the clavicle is the most commonly injured bone of childhood, accounting for 10% of all fractures (Voisin 2006). Fractures to the shaft of the clavicle can be

managed without surgery by giving the arm a short (approximately 2 weeks) rest in a sling. Uncommonly, dislocation of the clavicles occur but are often related to contact sport injuries.

## Conclusion

The clavicle, or collarbone as more commonly known, is a bone not present in all species. It has become vestigial in some animals or completely absent in others. It is one of the most commonly broken human bones and is home to several important muscle attachments responsible for muscular structure and support of the arm. Though it is one of the first bones to begin ossification, it is one of the last to become completely ossified.

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## Clever Hans

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## Definition

Hans was a famous German Orlov Trotter horse trained by his owner, Wilhelm von Osten, who claimed that the horse was able to perform a variety of cognitive tasks, including solving

complex arithmetic operations, giving the time, showing knowledge about calendar dates, understanding German language, and so on. His ability aroused worldwide interest at the beginning of the twentieth century, gaining the appellation of Clever Hans (der Kluge Hans in German). Experimental research conducted by the psychologist Oskar Pfungst found that the horse had no particularly complex cognitive abilities, although he was extremely skilled at gathering and using information from the most subtle movements of the questioners to give the expected response. This effect, later known as the observer-expectancy effect, shows the importance of keeping a tight control in experimental research using whenever possible an automated presentation of stimulation and recording of responses and, whenever that is not possible, using what is called the double-blind experimental design in which neither the experimenter nor the subject knows what behavior is expected from the subject.

## Introduction

Wilhelm von Osten taught mathematics at a German gymnasium during the early twentieth century, and he was the proud owner of a Russian trotting horse. He tutored the horse for 4 years, teaching him how to solve complex arithmetic problems by means of tapping with his feet. Exhibition of the ability of the horse, named Hans, was given daily in a courtyard in the northern area of Berlin. No fee was ever charged for attending to the exhibition as the owner, W. von Osten, was convinced that he had developed a training method that would allow showing that the difference between animal and human minds was a question of degree rather than quality. The horse Hans was able to answer a variety of questions by tapping with his front legs, like the number of people in the audience wearing hats or the result of adding two fractions such as  $2/5 + 1/2$  by tapping first the numerator and then the denominator (9/10). He was claimed to master cardinal numbers up to 100 and ordinals at least up to 10. He was also claimed to be able to read in German, bring a piece of a particular color from a row of colored cloths, tell the time to the minute,

recognize notes and music intervals, and select which tones should be eliminated in a sequence of notes to reach a pleasant sound. Hans seem to be the living proof of Darwin (1871, p. 85) assertion: “Nevertheless the difference in mind between man and the higher animals, great as it is, certainly is one of the degree and not of kind.”

The ability of Hans, the horse, was uncanny, and he was classified by experienced educators as having the cognitive development of a 13–14-year-old teenager. Goes without saying that the interest about this particular horse spread rapidly throughout the world leading to a flood of articles in newspapers and magazines, being one of the most cited the one published on October 2, 1904, in the *New York Times*, in which it was lightly concluded that an special commission of experts decided that the horse actually used the reason. The image of the horse appeared in postcards, liquor labels, and other commercial products. Men of the greatest knowledge and reputation, of unimpeachable honor, would approach skeptical to the horse abilities, leaving convinced that they were truthful. The respected zoologist and African traveler, C. G. Schillings, was convinced by the fact that the horse was able to respond to strangers in the master’s absence, assuring that they have not made the slightest sign to guide Hans response. Spectators were counted by the thousand, and they included from trick trainers to horse fanciers, but none of them was able to discover any kind of signals that the owner could be given to the horse to solve the problems. The issue was taken so seriously that Professor Carl Stumpf, the director of the Psychological Institute of the University of Berlin, after a cursory inspection during the month of February, 1904, requested from Mr. von Osten in July to detail the method he used to instruct the horse, before finally recommending the appointment of an investigating commission on September 3, 1904.

### Von Osten’s Training Method

The method used by Mr. von Osten to train the horse was indeed quite simple and resembles the behavioral shaping method described by Skinner (1951) years later as a method of training by which

successive approximations toward a target behavior are reinforced. W. von Osten conducted arithmetic training by using different sets of wooden pins, a counting machine (abacus), a chart upon which were pasted the numbers from 1 to 100, and digits cut in brass and suspended from a string. Pieces of bread and carrots were used as rewards.

The work started by placing a single wooden pin in front to the horse and commanding him: “Raise the foot, one!” while holding the animal foot to ensure that the horse was giving only one tap. Once “one” was learned, he used two pins and the same method to train “two” and the rest of numbers. Gradually, it was not necessary to hold the foot, or to point to the pins, using directly the question “how many pins are there?” and associating the numbers with the responses. Once Hans allegedly learned the numbers, the next step was to teach the animal de concept “and,” that is, to teach the animal how to add. To teach the horse the concept of “and,” von Osten would have somebody holding a large cloth before the horse, where the wooden pins usually were placed. The cloth would be then taken up while pronouncing emphatically the word “and.” After this he would hide two of the pins behind the cloth. As a result of its previous instruction Hans would give two taps at the sight of the pins. The same procedure was repeated with three pins. The next step was to set five pins up, three of which were covered by the cloth. The horse would tap two times and von Osten would say “two.” The cloth then will be raised, Hans will give three taps more, and the trainer will say with emphasis: “and three.” The idea underlying this method was that the image of the five pins would be associated by the horse with the combined groups of two and three. The next step was to ask the question without aids, so that it could be shown that the horse had learned to add. The problems become gradually more complicated until Hans began to give solutions to new problems by himself, leading the master to believe that “he had succeed in inculcating the inner meaning of the number concepts and not merely an external association of memory images with certain movement responses” (Pfungst 1907/1911, p. 249).

Multiplication was taught to Hans by using the abacus. Von Osten would place two identical sets of balls (i.e., three balls), one in each extreme of the abacus, and would ask the horse for how many

times three balls were there, expecting two taps, then asking “how many, therefore are two times three?” Six taps. The horse was supposed to learn the meaning of the word “times” by means of the spatial separation of the groups, counting the number of groups and the number of balls in each group. Subtraction was taught by setting a given number of pins up (i.e., five), removing some of them (i.e., two) while saying emphatically “I take away, two minus. How many are still standing?” A similar procedure was used for division and for other arithmetic operations.

### The Hans-Commission

Following the recommendation of Professor Stumpf, a commission of 13 people was established with the goal of evaluating whether there was “involved in the feats of the horse of Mr. von Osten anything of the nature of tricks, that is, intentional influence or aid on the part of the questioner” (Pfungst 1907/1911, p. 117). The commission involved a variety of relevant people, including a circus manager, members of schoolboards, directors of Berlin Zoological Garden, physiologists, and the director of the Psychological Institute of Berlin and member of the Academy of Sciences, Professor Carl Stumpf.

The commission conducted a large number of tests in the two sessions that took place on the 11th and the 12th of September, 1904, trying to search for the trick that could explain the behavior of the horse. In many of those tests, von Osten was not present but on September 12, 1904 two sets of experiments were conducted in which von Osten was present in the set. In the first set of experiments, a different man questioned the horse, while von Osten was present, but outside Hans’s view. The first set of questions was solved by Hans with little errors. In the second set of questions there was another man, the Zoologist and African traveler, C. G. Schillings, whom asked the horse to tap a certain number in the absence of von Osten, left the set, and then the owner entered the room and asked the horse to perform some arithmetical operation with a number that he was not aware of which one it was. In those tests, the horse did

not perform near as well as in the other. In most tests, the horse repeated the original number, rather than the operation he was asked to perform. However, there was a misunderstanding that lead Schillings to say to the horse “you are to repeat this number for Mr. von Osten” in the first few trials so that the errors might appear to be the result of this request or at least left the possibility open for an inconclusive test.

After its careful investigation, on their report of September 12, 1904, taking in account the individual experiences of the members of the commission with the horse, the report provided by Professor Stumpf on the method of instruction, and the two sessions of exploration, the commission concluded that no tricks or aids of the traditional sort were being employed by Hans’s owner. In their report it is said “In spite of the most attentive observation, nothing in the way of movements or other forms of expression which might have served as a sign, could be discovered. (. . .) They are unanimously agreed that this much is certain: This is a case which appears in principle to differ from any hitherto discovered, and has nothing in common with training, in the usual sense of that word, and therefore is worthy of a serious and incisive investigation” (Pfungst 1907/1911, pp. 253–254). Not quite the conclusion that the press at the time actually published, but one that opened the door a further and more controlled research that was finally conducted by the psychologists O. Pfungst.

### Oskar Pfungst’s Study on Hans Accomplishments

Given that no usual trick was discovered by the commission, and following the recommendation of conducting a more incisive research about the abilities of clever Hans, Oskar Pfungst conducted a careful set of experiments with the goal of discovering the actual abilities of the horse. The experiments were conducted in the courtyard of the owner, and most of them were conducted by Pfungst himself, using carrot, bread, and occasionally a square of sugar as rewards.



O. Pfungst approached the research by using what he called two different procedures. The so-called procedure without knowledge was a procedure in which neither the questioner, not anybody in the audience knew the answer to the question the animal was asked, for opposition to the procedure with knowledge, in which the questioner knew the answer to the problem. Applying these procedures to problems that could be solved by tapping involving numbers in cards, words in placards, computation, counting using the abacus, memory tests, calendar dates, and musical abilities, Pfungst (1907/1911) found that the mean percentage of correct responses in the procedure without knowledge was about 10%, while in the procedure with knowledge was about 90%. Auditory stimuli seem not to play a role, as the animal could not follow instructions given by a questioner that was hidden from the horse's sight by blinders. Similar results were obtained in those problems that Hans solved with movements of the head and in those that were solved by approaching objects.

As the horse failed to find the solution when that solution was unknown by the people present, and the horse needed to see the questioner to give a solution, it was concluded that the horse was using some aid that was unintentionally given by the questioner. Focusing the exploration in the questioner, Pfungst (1907/1911) found that the horse behavior was controlled by minimal movements of the head and trunk of the questioner. A slight bent of the head while leaning the trunk slightly forward made the horse begin to tap with his right foot. As soon as the horse reached the right number of taps, the questioner would make a slight upward jerk of the head and the horse will stop tapping. Once these movements were isolated, Oskar Pfungst reports that he was able to control horse's behavior voluntarily, so that the horse will start tapping and stop tapping whenever the proper movements were given by the Pfungst, regardless of the question asked. In fact, he was able to control the rate of tapping by varying the angle of the inclination of the body so that greater the inclination, the faster the tapping.

The conclusion was clear "All wonderful feats of counting and computation which were

accomplished while thus experimenting with the horse are to be accredited, not to the horse, but to the questioner (...) Hans, however, was also a faithful mirror of all the errors of the questioner" (Pfungst 1907/1911, p. 142). The results of this study were reported by Carl Stumpf on December 9, 1904, in which he says "The horse must have learned, in the course of the long period of problem-solving, to attend ever more closely, while tapping, to the slight changes in bodily posture with which the master unconsciously accompanied the steps of his own thought-processes, and to use these as closing signals. The motive for this direction and straining of attention was the regular reward in the form of carrots and bread, which attended it." This last statement seems a clear description of the role of discriminative stimuli in instrumental or operant conditioning, indeed.

## Conclusion

There are some essential lessons that any person interested in animal cognition and in science in general may learn from the story of Clever Hans. The first and perhaps the most obvious one is the need of applying the principle of parsimony or Morgan's Canon in any study of animal behavior: "In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (Morgan 1895/1903, p. 59). In many occasions we tend to anthropomorphize the animal, providing it with feelings and abilities that are essentially human. It is true that we humans might tend to do the contrary at the same time, rejecting the idea that animals may have abilities that traditionally have been thought human exclusive. In that sense, it is convenient to remember that Lloyd Morgan himself completed his principle with a sentence that is often ignored by saying that "To this, however, it should be added, lest the range of the principle be misunderstood, that the canon by no means excludes the interpretation of a particular activity in terms of the higher processes, if we already have independent evidence of the occurrence of these

higher processes in the animal under observation” (Morgan 1895/1903, p. 59). This was not the case of Clever Hans, whom followed one of the perhaps more interesting features of evolution, the ability to find simple solutions for complex problems. Using the available stimuli unconsciously provided by the caretaker as discriminative stimuli for when an operant behavior would be followed by a reward was the simplest and most efficient and straightforward solution for a set of complex problems.

The second lesson that may be learned from the story of Clever Hans perhaps is not so obvious. An interesting question that is not usually raised is what led people of the beginning of the twentieth century to take so much trouble to study Hans’s behavior. Even when the so-called Hans commission concluded that there were no obvious tricks of any sort in von Osten’s behavior, the research was taken a step forward, and a systematic study was pursued. Of course, that is the way it should be done. But the question is would such a in-deep study have been conducted if there were not being a preconception about the (lack of) ability of the horse? In other words, would the same question had been applied when considering an ability that would fit the preconceptions about the species, regardless of whether they are true or not? These questions have no other goal than highlighting the need of applying Morgan’s cannon to any situation, regardless of the species involved, keeping in mind that solving a problem by simple means does not necessarily imply that the species is not able of more complex cognition but simply that the animal is not applying it to solve that specific problem.

Third, as stated above, the story of Clever Hans makes it evident the importance of using proper controls when studying cognition regardless of the species to avoid the observer-expectancy effect, an effect in which the experimenter unconsciously influences behavior of the participant in a given experiment. This effect is usually controlled by using automatic recordings of behavior and by the use of the double-blind experimental design in which neither the experimenter nor the participant know the condition in which the participant are, not the behavior it is expected from him or her. This was essentially the method used O. Pfungst to explore Hans cognitive allegedly abilities.

Finally, the way the story of Clever Hans one may tend to question whether the horse actually deserved his nickname. When the research conducted by O. Pfungst showed that Hans did not have the abilities his master ascribed to him, Von Osten was both puzzled and deceived, showing a reaction that was described by O. Stumpf as “genuine surprise, such a tragicomic rage directed against the horse” (Pfungst 1907/1911, p. 13), and explicitly forbid to conduct further experiments with him. It is easy to understand and even to share von Osten’s disappointment. However, the story may be seen from a different point of view. In the story of Clever Hans, it is implicitly assumed that the problems the horse had to face were complex cognitive problems. But let’s put ourselves in the horse’s shoes. The only problem Hans had to solve was how to get the piece of carrot that his master provided when he tapped the right number of times. The key of the solution was the rule that determined which number was right. Von Osten established a complex set of rules for determining the correct number of tapings consciously and just one unconsciously. This latter one was the one used by Clever Hans. It was so subtle that a commission formed by 13 intelligent, motivated, and highly trained people was not able to discover the rule after two days searching for it. No wonder that Hans has kept the appellation of “clever” over a century.

## Cross-References

- [Associative Learning](#)
- [Instrumental Learning](#)
- [Morgan’s Canon](#)

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## Clive Wynne

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Clive D. L. Wynne was born and grew up on the Isle of Wight, an island, 25 by 15 miles, off the south coast of England. After completing high school there, in 1980, he went to University College London to study *Human Sciences*. Human Sciences is a degree program, founded by anatomist J. Z. Young, that introduces students to all the sciences that contribute to understanding the human condition. It was at University College that Wynne was first exposed to the ideas that have influenced his thinking ever since. In classes with pioneer evolutionary psychologist, Henry Plotkin, Wynne learned that the evolutionary process of natural selection can be construed as a learning process. As organisms adapt to the world around them, they are in effect gaining knowledge of the world. Plotkin and Odling-Smee (1979; Odling-Smee and Plotkin 1984) argued that there were multiple levels at which the biological world learns about the physical world, ranging from the adaptation of organisms through natural selection as usually construed, to the individual learning of animals interacting with their environment, and even the interaction of societies. Concurrently Wynne was taking classes in epistemology from Nicholas Maxwell (e.g., Maxwell 1984). In these classes, Wynne learned about Popperian epistemology: the idea that people learn by repeatedly testing hypotheses about the nature of the world (Popper 1974). Maxwell and Plotkin explicitly drew parallels between the way that individuals learn by testing hypotheses and the way that nature “learns” by “testing” individual variations which are selected by nature. Together with classes on what was known about how animals learn, this intellectually stimulating education set the basis for much of Wynne’s subsequent research career.

From University College London, in 1984, Wynne went to Edinburgh University for his PhD. Initially he was mentored by Brendan

McGonigle, and later by Peter Caryl. McGonigle exposed Wynne for the first time to cutting edge research in animal cognition, and Caryl started Wynne’s education in classical ethology.

From Edinburgh, in 1986 Wynne applied to join John Staddon’s lab at Duke University, North Carolina, as a postdoc. Staddon, however, was on sabbatical at the University of the Ruhr, in Bochum, Germany, with Juan Delius that year, so Wynne joined Staddon there. The juxtaposition of Staddon and Delius was a very advantageous one for Wynne’s continuing education. From Staddon, Wynne learned about operant conditioning; and from Delius he learned more about ethology. Both Staddon and Delius were committed to reconciling the operant and ethological approaches within a biological, evolutionary framework – and Wynne absorbed this perspective readily.

Over the next several years, Wynne was a postdoctoral associate with Staddon at Duke University and with Delius in Bochum and later at Konstanz University in southern Germany. During this time, Wynne deepened his knowledge of operant conditioning, ethological approaches to animal behavior, animal cognition, and, thanks to Peter Holland at Duke and John Pearce from Cardiff University, on sabbatical at Duke while Wynne was there, Pavlovian conditioning.

By the time Wynne found his first faculty position, in 1993, at the University of Western Australia, in Perth, Australia, he had established two lines of research. The first concerned how pigeons adapt to changes in temporal regularities in their environment (e.g., Wynne et al. 1996), and the second an investigation of the basic behavioral mechanisms that make it possible for pigeons to achieve the apparently highly complex form of deductive reasoning known as “transitive inference” (e.g., Wynne et al. 1992; Wynne 1997)

In Australia Wynne was also able to develop simple tests of behavioral adaptation in two species of marsupials. From the little research that had been carried out, marsupials had a reputation for low intelligence. Wynne was able to show that one marsupial, the Fat-tailed Dunnart (*Sminthopsis crassicaudata*) which occupied a niche somewhat similar to a field mouse, was

in fact one of the fastest learners ever tested (Bonney and Wynne 2002a). A second marsupial species, the quokka (*Setonix brachyurus*) was a slower learner (Bonney and Wynne 2002b). Comparison of these two species showed that animals have the learning capacities that their lifestyles require of them.

From the University of Western Australia, Wynne moved to the University of Florida, in Gainesville, Florida in 2002. Here he continued research on the ability to time short intervals in pigeons (e.g., McClure et al. 2005), but found he was also very interested in the relationship between people and animals. In 2004 he published a review on the research that had been published, starting in the late 1990s, on the behavior of dogs in interaction with humans (Wynne 2004). This led to the realization that dogs would be an ideal species of study in which to combine his established expertise in animal behavior and cognition with a growing interest in human-animal interaction. It also connected with Wynne's childhood love of dogs.

At first, Wynne's dog research focused on the nature and limits of dogs' understanding of human actions and intentions, particularly in comparison to dogs' wild progenitor, the wolf (*Canis lupus lupus*; e.g., Udell et al. 2008, 2010, 2011). More recently, his research has broadened to include studies of the welfare of dogs living in shelters (e.g., Protopopova et al. 2012; Protopopova and Wynne 2015), behavior-analytic approaches to dog behavioral problems (e.g., Protopopova et al. 2014), novel methods of training Improvised Explosive Device detection dogs (e.g., Hall et al. 2015a, b), alongside basic questions of behavior and cognition in dogs (e.g., Feuerbacher and Wynne 2012; Udell et al. 2012). He also maintains an interest in the archeological and genetic studies contributing to our understanding of the origins of dogs. In 2013, Wynne moved to Arizona State University where he continues to study diverse aspects of dog behavior. Wynne's future research is likely to continue to focus on dogs and their wild relatives in interaction with human beings. He seeks to find the "pointy end" of dogs' lives with humans – those areas where most is at stake

for people and their pets. At the same time, he still strives to understand how evolution has been able to make animals like dogs which have adapted to a radically changed, anthropogenic, niche in what is evolutionarily speaking, a very brief interval of time.

## Cross-References

- [Canine Cognition](#)
- [Comparative Cognition](#)
- [Evolutionary Psychology](#)
- [Marsupial Cognition](#)

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## Cloning

- [Reproduction](#)

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## Closest Living Relative

- [Last Common Ancestor](#)

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## Cloven-Hooved

- [Artiodactyla Diet](#)
- [Artiodactyla Morphology](#)

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## Cloven-Hooved Mammal Locomotion

- [Artiodactyla Locomotion](#)

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## Clumping

- [Huddling](#)

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## Clustering

- [Huddling](#)

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## Clutch

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## Definition

A clutch refers to the number of eggs in a nest laid in a single brood produced by oviparous (i.e., egg-laying) animals such as birds, amphibians, fish, or reptiles.



## Description

Clutch size varies greatly between species, and often within species due to variations in habitat, health, resource availability, predation pressures, and time of year (Klomp 1970). However, some species are determinant layers, laying a species-specific number of eggs. Long-lived species tend to have smaller clutch sizes, as do shorebirds and monogamous birds (Klomp 1970). Ornithologist and evolutionary biologist David Lack was a pioneer in the study of clutch size. His work in the 1940s (Lack 1947, 1948) explored intraspecific variation in clutch size (including latitude – increasing latitude results in increasing clutch size – island living, seasonal variation, annual variation, and age of bird), interspecific variation in clutch size (i.e., average clutch sizes in different habitats), and factors involved in clutch size (including physiological control, species mortality, and day length variation). Lack's work led him to hypothesize that natural selection has resulted in clutch sizes evolving toward a number that produces the most surviving offspring (Lack 1947, 1948), and that the mechanism determining the upper limit to clutch size is the parents' ability to provide food for nestlings (Lack 1954, 1966). However, more recent work has found that the evidence does not support Lack's clutch size hypothesis (Vander Werf 1992).

An alternate hypothesis to explain optimal clutch size is Skutch's hypothesis, which states that higher nest predation decreases the rate at which parents can deliver food to their nestlings, and thus limits clutch size (Skutch 1949), though few studies support this hypothesis. More support exists for Ashmole's hypothesis (Ashmole 1963), which explains the latitudinal difference in clutch sizes by differences in the seasonality of resources, which result in different levels of winter mortality (see Greibeler and Böhning-Gaese 2004; Ricklefs 1980), although other factors such as cost of reproduction (Greibeler and Böhning-Gaese 2004) must be considered as well.

Clutch size can be altered within a breeding season, both naturally and artificially. "Double-clutching," defined as an oviparous animal laying two sets of eggs in a viable season, can occur after

destruction of a first clutch by predators or by removal by humans (e.g., in the California condor breeding program). In the latter case, double-clutching is used to double the production of a species' eggs specifically to increase population size.

## Cross-References

- [Actinopterygii \(Bony Fish\)](#)
- [Reproduction](#)

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## Clutching

- [Grasping Reflex](#)

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## CNVs

- [Copy Number Variant \(CNV\)](#)



## Coalition Enforcement

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### Synonyms

Cooperation; Mutualism; Proto-social behavior;  
Social behavior

### Definition

Coalition enforcement relates to the affirmation of moral or proto-moral behavior and to the related perpetration of violent punishment, to the aim of preserving cooperation.

### Introduction

The aim of this entry is to clarify the idea of “coalition enforcement.” This idea illustrates a whole theoretical background for interpreting the role of morality and violence in human and in nonhuman animal groups. In this last case, it is useful to speak of the role played in coalitions of what we humans can call – anthropomorphically – “proto-moral conflicts.”

### Coalition Enforcement Hypothesis: Morality and Violence

The coalition enforcement hypothesis, put forward by Bingham (1999, 2000), aims at providing an explanation of the “human uniqueness” that is at the origin of human communication and language, in a strict relationship with the spectacular ecological dominance achieved by *H. sapiens*, and of the role of cultural heritage. From this perspective, and due to the related constant moral and policing dimension of *Homo*’s coalition enforcement history (which has an approximately

two-million-year evolutionary history), human beings can be fundamentally seen as *self-domesticated animals*. The main value of this hypothesis consists in stressing the role of the more or less stable stages of cooperation *through morality* (and through the related unavoidable violence generated by punishment).

The hypothesis implicitly shows how both *morality* and *violence* are strictly intertwined in their social and institutional aspects, which are implicit in the activity of cognitive niche construction. In an evolutionary dimension, coalition enforcement is enacted through the construction of social artefactual niches (recently called *cognitive niches* (Laland et al. 2000)) as a new way of diverse human adaptation. Basically the hypothesis refers to cooperation between related and unrelated animals to produce significant mutual benefits that exceed costs and are potentially adaptive for the cooperators. Coalition enforcement is active at both the human and nonhuman animal level:

1. Tomasello (2009) has usefully studied various types of human and animal altruism but also human cooperation through social institutions.
2. Wilson et al. (2004) hypothesized the role of groups in engaging in coordinated and cooperative cognitive processes, thus exceeding by far the possibilities of individual thinking, and emphasized the formation of the so-called group mind whose role would be fundamental in social cognition and group adaptation. The formation of appropriate groups which behave according to explicit and implicit more or less flexible rules of various types (also moral rules, of course) can be reinterpreted – beyond Wilson’s strict and puzzling “direct” Darwinian version – as the “social” constitution of a “cognitive niche,” that is, a cognitive modification of the environment which confronts the coevolutionary problem of varying selective pressures in an adaptive or maladaptive way. It is Pinker (2010) that deeply studied the coevolution of intelligence, sociality, and language in the perspective of cognitive niches (see also Magnani (2011)).

In hominids, cooperation in groups (which, contrary to the case of nonhuman animals, is largely independent from kinship) is fundamentally derived from the need to detect, control, and punish social parasites, who, for example, did not share the meat they hunted or partook of the food without joining the hunting party (Boehm 1999) (also variously referred to as free riders, defectors, and cheaters). These social parasites were variously dealt with by killing or injuring them (and also by killing cooperators who refused to punish them) *from a distance* using projectile and clubbing weapons. In this case injuring and killing are cooperative and remote (and at the same time they have to be seen as “cognitive” activities). According to the coalition enforcement hypothesis, the avoidance of proximal conflict reduces risks for the individuals (hence the importance of *remote killing*). Of course, cooperative morality that generates “violence” against unusually “violent” and aggressive free riders and parasites can be performed in other weaker ways, such as denying a future access to the resource, injuring a juvenile relative, gossiping to persecute dishonest communication and manipulative in-group behaviors or waging war against less cooperative groups, etc.

The development of the cooperative morality is related to the so-called Machiavellian intelligence hypothesis. Posed in the late 1980s (Whiten and Byrne 1988), the “social brain hypothesis” (also called “Machiavellian intelligence hypothesis”) holds that the relatively large brains of human beings and other primates reflect the computational demands of complex social systems and not only the need of processing information of ecological relevance: the ability to manipulate information and not simply to remember it, to recognize visual signals to identify other individuals, sufficient memory for face recognition and to remember who has a relationship with whom, use of tactical deception and coalition, ability to understand intentions, to hold false beliefs, “mind-reading,” known as “theory of mind,” etc. Language itself would have evolved from physical grooming as a way of creating social cohesion as the size and complexity of the social group increased (cf. also Dunbar (1998)).

In summary, group cooperation (e.g., for efficient collective hunting and meat sharing through control of free riders) has been able to evolve adaptively and to render parasitic strategies no longer systematically adaptive. Through cooperation and remote killing, individual costs of punishing are greatly reduced and so are individual aggressiveness and violence, perhaps because violence is morally “distributed” in a more sustainable way: “Consistent with this view, contemporary humans are unique among top predators in being relatively placid in dealing with unrelated conspecific nonmates under a wide variety of circumstances” (Bingham 1999, p. 140). Hence, it has to be said that humans, contrarily to nonhuman animals, exchange a fundamental and considerable amount of relatively reliable information with unrelated conspecifics (p. 144). Here the role of docility is worth citing (which relates to the distressing human tendency to conform, displace responsibility, comply, and submit to the authority of dominant individuals, also emphasized by social psychology).

### Docility and Moral Viscosity

According to Herbert Simon (1993, p. 156), humans are docile in the sense that their fitness is enhanced by “[...] the tendency to depend on suggestions, recommendations, persuasion, and information obtained through social channels as a major basis for choice.” In other words, humans support their limited decision-making capabilities, relying on external data obtained through their senses from their social environment. The social context gives them the main data filter, available to increase individual fitness. Therefore, docility is a kind of attitude or disposition underlying those activities of cognitive niche construction, which are related to the delegation and exploitation of ecological resources. That is, docility is an adaptive response to (or a consequence of) the increasing cognitive demand (or selective pressure) on those information-gaining ontogenetic processes, resulting from an intensive activity of niche construction. In other words, docility permits the inheritance of a large

amount of useful knowledge while lessening the costs related to (individual) learning.

In Simon's work, docility is related to the idea of *socializability* and to altruism in the sense that one cannot be altruistic if he or she is not docile. In this perspective, however, the most important concept is docility and not altruism, because docility is the cognitive condition of the possibility of the emergence of altruism. Moral altruism, at least in the light of the coalition enforcement hypothesis, can be correctly seen as a sub-product of – or at least intertwined with – the violent behavior needed to “morally” defend and enforce coalitions. Given the fact groups need to detect, control, and punish social parasites, which, for example, do not share meat (food as nutrient as hard to acquire), by killing or injuring them (and any cooperators who refuse to carry out punishment), to this aim they have to gain the cooperation of other potential punishers: docility plays a positive role.

Research on chimps' behavior shows that punishment can be seen as altruistic for the benefit of the other members of the group (and to the aim of changing the future actions of the individual being punished), often together with “the function of keeping the top ranking male, or coalition of males, at top, or preserving the troop-level macro-coalition that disproportionately serves the interests of those on top” (Rohwer 2007, p. 805). The last observation also explains how altruistic punishment can serve individual purposes (and so it can be captured by individual selection models): in chimps it reflects the desire to maintain status that is a new high position in the hierarchy. Rohwer's conclusion is that “certain behaviors that can be covered by the definition of altruistic punishment need not have arisen from group selection pressures [...] as the Sober and Wilson model assumes. Seen through the lens of the linear dominance hierarchy, it is reasonable to suspect that altruistic punishment may have originated primarily through individual selection pressures” (p. 803 and p. 810). The reader that is interested to further study the puzzling problem of the distinction between individual and group selection for altruism in the framework of multilevel selection has to refer to Rosas (2008): multilevel selection

theory claims that selection operates simultaneously on genes, organisms, and groups of organisms.

Moreover, Lahti and Weinstein (2005) further emphasize the evolutionary adaptive role of morality (and so of cooperation) as “group stability insurance”: the exigence of morality as group stability would explain the “viscosity” of basic aspects of the morality of a group and why morality is perceived as having an air of absolutism. Viscosity represents the tendency of moral beliefs to *stick* to their holder in spite of the changing contexts. Indeed, the concept of viscosity provides an explanation of the gap between the absolutism of morality and the empirical evidence that moral regulations are often infringed with no major consequences neither for the whole moral system nor for the very individual who performs the infractions.

## Coalition Enforcement and Language

Furthermore, the problem of docility is twofold. First, people delegate tasks of data acquisition to their experience, to external cultural resources, and to other individuals. Second, people generally put their trust in one another in order to learn. A big cerebral cortex, speech, rudimentary social settings, and primitive material culture furnished the conditions for the birth of the mind as a “universal machine” – to use Turing's expression. It is plausible to think that a big cortex can provide an evolutionary advantage only in the presence of a massive storage of meaningful information and knowledge on external supports that only a developed (even if small) community of human beings can possess. If high-level consciousness is considered as related to a high-level organization of the human cortex, its origins can be referred to the active role of environmental, social, linguistic, and cultural aspects. It is in this sense that docile interaction lies at the root of our social (and neurological) development. It is obvious that docility is related to the development of cultures, morality, and actual cultural availability and to the quality of cross-cultural relationships. Of course, the type of cultural dissemination and possible cultural

enhancements affect the chances that human collectives have to take advantage of docility and thus to potentially increase or decrease their fitness.

### **Cultural Heritage: Extragenetic Information, Morality, and Sense of Guilt**

The direct consequence of coalition enforcement in humans is the development and the central role of cultural heritage (morality and sense of guilt included). From this perspective, the long-lived and yet abstract human sense of guilt represents a psychological adaptation, anticipating an appraisal of a moral situation to avoid becoming a target of violent coalitional enforcement. It is necessary to stress that Darwinian processes are involved not only in the genetic domain but also (with a looser and lesser precision) in the additional cultural domain, through the selective pressure activated by modifications in the environment brought about by cognitive niche construction. According to the theory of cognitive niches, coercive human coalition as a fundamental cognitive niche constructed by humans becomes itself a major element of the selective environment and thus imposes new constraints (designed by *extragenetic information* on its members) (cf. Magnani (2009) and Magnani (2011)).

Some empirical evidence (presented by Bingham (2000)) seems to support the coalition enforcement hypothesis: fossils of *Homo* (but not of Australopithecines) show, on observation of skeletal adaptations, how selection developed an astonishing competence in humans relating to the controlled and violent use of projectile and clubbing weapons (bipedal locomotion, the development of *gluteus maximus* muscle and its capacity to produce rotational acceleration, etc.). The observed parallel increase in cranial volume can be related to the increased social cooperation based on the reception, use, and transmission of “extragenetic information.” Moreover, physiological, evolutionary, and obstetric constraints on brain size and structure indicate that humans can individually acquire a limited amount of extragenetical information, that consequently has to

be massively stored and kept available in the external environment.

Hence, a fundamental role in the evolution of “non”genetic information has to be hypothesized. Appropriately, coalition enforcement implies the emergence of novel extragenetic information, such as large-scale mutual information exchange as forms of communication between unrelated kin, including both linguistic and nonlinguistic aspects (visual representations, thought experiment, analogical reasoning, but also the kinds of cognition also nonhuman animals can get through emotions and other feelings). It is noteworthy that extragenetic information plays a fundamental role in terms of transmitted ideas (cultural/moral aspects), behavior, and other resources embedded in artifacts (ecological inheritance). It is easy to acknowledge that this information can be stored in human memory – in various ways, both at the level of long-lived neural structures that influence behavior, and at the level of external devices (cognitive niches), which are transmitted indefinitely and are thus potentially immortal – but also independently of small kinship groups. Moreover, transmission and selection of extragenetic information are at least partially independent of an organism’s biological reproduction.

### **Conclusion**

In summary, to illustrate coalition enforcement, it is important to show how moral norms, cooperation, and social dominance hierarchies can be accounted for from an evolutionary point of view. Recent research acknowledges the role of social dominance hierarchies in cooperative activities of human and nonhuman animals (like social mammals), also stressing the deontic importance of moral behavior and intertwined violent components.

Evidence from comparative, developmental, and cognitive psychological research also show how they shaped the evolution of the human mind and so of human social institutions. Pressures that derive from living in hierarchical groups shaped basic concept and cognitive devices (which are not interpreted as innate modules but instead as

favored by a kind of “biological preparedness,” a propensity to develop them in a combination of genetical and environmental circumstances). These concepts and cognitive devices are in turn related to the various stages of development of cognitive niches, crucial factors to survive in those hierarchic settings. They are:

1. Recognizing and reasoning transitively about dominance relations (making rank and kinship discriminations)
2. Fast-track learning of social norms (permissions, prohibitions, and obligations)
3. Detecting violations of social norms and codes – also called *deontic effect* (cheating and deceptions to flout social norms and to have better access to reproductive opportunities through monitoring reciprocal obligations based on resource sharing)
4. Reading intentions of others and so predicting their behavior, especially – again – to favor detection of violations (but also to allow compassion and social codes based on something other than social norms).

Furthermore, perceived violations were already studied as the most common cause of aggression in primate groups (Hall 1964): without a capacity for violation detection, high-ranking individuals cannot monopolize resources and maintain fruitful alliances and preserve the peace. However, especially in human collectives, violation detection is the most precious tool for ensuring that social norms (implicit and explicit) are honored thus facilitating social regulation and promoting the emergence of altruism as a stable strategy.

Finally, it is worth noting the richness of recent research on the role of coalition enforcement in social mammals, usefully illustrated by Smith (2014). Also relying on empirical research favored by new methodologies, such as the possibility to track through less and less invasive GPS technologies an ever-growing number of species, the evolutionary puzzle of cooperation is illustrated in the framework of *kin selection theory*: Smith analyzes and discusses costs, benefits, and the direct and indirect lifetime fitness of

cooperative breeding (also active in social insects), nepotism, social tolerance, and withheld aggression in coalition formation (and so in “social evolution”). The concerned species range from primates to ungulates, from cetaceans to carnivores, from marsupials to rodents and bats. The author also shows the available evidence confirming the existence of actual fitness consequences of sociality in mammalian species including baboons (*Papio cynocephalus*), house mice (*Mus domesticus*), laboratory rats (*Rattus norvegicus*), horses (*Equus caballus*), dolphins (*Tursiops aduncus*), rock hyraxes (*Procavia capensis*), yellow-bellied marmots (*Marmota flaviventris*), and, obviously, humans. The special case of the highly cooperative behavior of dolphins and cetaceans is described in the recent Whitehead and Rendell (2014).

## Cross-References

- [Aggression](#)
- [Altruism](#)
- [Coevolution](#)
- [Ethics](#)
- [Heredity](#)
- [Machiavellian Intelligence](#)
- [Punishment](#)
- [Reciprocity](#)
- [Reputation](#)
- [Technical Intelligence Hypothesis](#)

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et al. 2008; Bygott et al. 1979; Connor et al. 1992). These members cooperate to obtain access to reproductive partners. Frequently, it has the effect of increasing the reproductive success of at least one member of the coalition. However, not every member of the coalition may participate in reproduction.

## Examples

Coalitional mating behaviors have been observed in numerous species. For instance, groups of male chimpanzees (*Pan troglodytes*) in wild populations have been observed working together to capture females from opposing groups for reproductive purposes (e.g., Boesch et al. 2008; Manson and Wrangham 1991). These males will cooperate as a group to search for mating partners of another group to be taken either temporarily or permanently from their original groups. Interestingly, males cooperating in these groups may not have direct reproductive access to taken females (Boesch et al. 2008).

Similar to chimpanzees, male bottlenose dolphins (*Tursiops* sp.) are known to form coalitions of two to three males and to then confine the movements of females (Connor et al. 1992). These coalitions of males can remain constant for years. Females are typically observed being chased by the male coalition for capture attempts. Once confined, the period of control by the male coalition has been perceived to range from several minutes to 13 days. The males will cooperate to prevent the female's escape through herding and aggressive behaviors.

In another mammal species, male lions (*Panthera leo*) have been observed forming coalitions of two, three, or more lions (Bygott et al. 1979). Larger coalitions benefit through an increased capability to seize control of the female prides. In lions, it is crucial for male coalitions to maintain control of female prides for a prolonged period due to the prevalence of infanticide by newly dominating males. Strengthening this ability, males in larger coalitions have been observed acting as nonreproductive “helpers” (Packer et al. 1991).

## Coalitional Mating

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## Synonyms

Cooperative mating

## Introduction

Coalitional mating involves individuals forming coalitions that then attempt to reproduce with other members of their species (e.g., Boesch



## Conclusion

The practice where members of the same species form coalitions with a purpose of reproducing, coalitional mating, may occur in any number of species. Some species that exhibit this behavior have been described above, including chimpanzees, bottlenose dolphins, and lions. While generally increasing the reproductive success of at least one member, interestingly some members may assist without the benefit of reproduction, suggesting some other motivation.

## Cross-References

- [Coalition Enforcement](#)
- [Cooperation](#)
- [Cooperative Breeding](#)
- [Daughter Guarding](#)
- [Group Living](#)
- [Mate Guarding](#)
- [Mating](#)
- [Reproduction](#)

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## Coalitional Raiding in Chimpanzees

- [Chimpanzee Raiding](#)

## Cocaktiel Locomotion

- [Psittaciformes Locomotion](#)

## Cockatoo Locomotion

- [Psittaciformes Locomotion](#)

## Code

- [Coding](#)

## Coding

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## Synonyms

[Code](#); [Encode](#); [Process](#); [Represent](#)

## Definition

The neural, behavioral, and cognitive processes that convert experiences into neural and cognitive

representations of experiences in sensation, perception, conditioning, memory, anticipation, problem solving, language, and related cognitive systems.

## Introduction

**Coding** is the process of creating neural and cognitive representations of information gained from experiences. Coding is the basis for neural or cognitive representations of sensory, perceptual, or cognitive experiences. Coding may be described at different levels of analysis: molecular, synaptic, cellular, neural systems, behavioral, cognitive, functional, and so forth. Information received from sensory receptor systems, such as visual, auditory, and other receptor systems, is translated into neural activity that can be stored veridically or after additional cognitive processing. Lower-level codes may represent sensory/perceptual “features” whereas higher-level cognitive codes derived from processing lower-level neural codes can represent “objects” or “concepts.” The characteristics of the resulting neural activity are specific to the stimuli or objects and thus can represent those stimuli or objects. For example, when an animal encounters a food item, the animal might experience several characteristics of the item, including odor, taste, and appearance. The neural code or codes related to the experience may represent individual or multiple characteristics of the food item, including information from sensory, perceptual, and memory systems which may store codes related to past experiences with the food item.

## Coding in Sensation and Perception

Coding of sense-specific information involves several steps: experience of the actual stimulus characteristics, creation of neuronal codes or activation of previously stored neuronal codes representing that or similar previous experiences, and processing of coded information in decision-making. Examples of sensory coding have been identified in many species, from visual system coding in invertebrates such as the fruit fly

*Drosophila melanogaster* (Harris et al. 1976) to vertebrates.

## Coding in Pavlovian and Instrumental Conditioning

The very idea of “coding” has varied in theoretical acceptability over the history of the study of animal learning and cognition. Pavlov (1927) recognized the complexity and interconnectedness of the nervous system and his understanding of classical conditioning emphasized the role of associative connections made between brain centers responsible for detecting stimuli and eliciting responses. Skinner (1934, 1950), by contrast, famously questioned whether theories of learning are even necessary. Hebb (1949) proposed that learning occurred by strengthening and weakening of large numbers of synaptic connections in patterns that coded experiences, which was followed by the discovery of long-term potentiation – strengthening of synapses – as the neurobiological basis of learning (Lomo 2003). This idea led to modern distributed memory models of animal learning, memory, and cognition as well as developments that led to modern learning and memory neural network modelling and artificial intelligence (AI). These approaches describe and explain coding at a synaptic level in Pavlovian and instrumental conditioning. Comparative cognition described complex learning, memory, and behavior in nonhuman animals via more complex forms of coding by specialized cognitive processes for coding of timing, counting, sequential learning, and spatial memory, among others (Hulse 1978; Meck et al. 1984; Olton 1978; Sands and Wright 1980b; Church 1980; Kesner and Novak 1982; Wasserman and Zentall 2012).

## Coding in Short-Term and Long-Term Memory

Short-term memory refers to an active, temporary, and limited storage for mnemonic codes representing recent events. Miller’s (1956) “magical number seven, plus or minus two” refers to

the approximate number of items of information that can be held in short-term memory storage concurrently in humans, which typically lasts for a few seconds or until rehearsal ends. Long-term memory has a much greater capacity and allows for codes to be stored indefinitely.

### **Coding in Retrospective and Prospective Memory**

Retrospective memory can be described as “looking back” memory, for example, remembering the cue that recently occurred. In contrast, prospective memory involves “looking ahead” memory, such as “remembering” what response should be produced when required (Kesner and Despain 1988; Roitblat 1980; Zentall 2010). That is, retrospective memory strategies rely on remembering what was experienced in the past as cues for what will happen in the future. This type of coding contributes most of an animal’s long-term codes as it is the memory of past stimuli. Prospective coding predicts future events based on past experiences with the same or similar cues that signaled a subsequent event. Honig and Thompson (1982) showed that rats in a radial maze employed the use of these two strategies when navigating the baited arms: remembering where they have already been (retrospective) and remembering where they still need to go (prospective). Such a flexible dual-coding system provides animals with the ability to shift from retrospective to prospective memory strategies as needed.

### **Coding in Memory for Space, Time, and Number**

Spatial coding refers to learning about the location of objects in space. Research with the radial arm maze and water maze in rats demonstrated that rats’ impressive spatial navigation and memory abilities depend on the capacity to use multiple surrounding “extra-maze” cues to code spatial locations (Olton and Samuelson 1976; Morris 1982) in addition to using local cues that can guide responses directly. Other studies

demonstrated that navigating an efficient path consisting of multiple locations depends on coding via separate reference and working memory systems (Diez-Chamizo et al. 1985).

Temporal coding refers to learning about the duration or relative timing of events, which in turn depends on sensing and encoding the temporal intervals between stimuli or responses. Two prominent theories to account for animal timing behavior include scalar timing theory (Meck et al. 1985; Church 1980; Meck and Church 1982; Gibbon et al. 1984), the behavioral theory of timing (Killeen and Fetterman 1988), and concurrent interval and circadian representations of time in rats (Pizzo and Crystal 2002). Evidence for counting in animals has come from studies that sought to rule out simpler mechanisms, such as discrimination learning, as explanations (e.g., Capaldi and Miller 1988; Davis and Memmott 1982). More recently attention has turned to distinguishing the role of numerosity and numerosness in animal counting.

### **Coding in Sequential Learning and Serial Pattern Learning**

Sequential learning refers to learning to anticipate a series of events or perform a series of responses. Poorly organized sequences, such as a list of unrelated letters or digits, are difficult to encode and remember. Highly organized sequences, such as the notes of a song, are typically much easier to learn and remember.

The serial position effect is a well-known phenomenon in human and animal memory. When a list of unrelated items is presented followed immediately by a test, items at the beginning and end of the list are remembered better than items in the middle of the list (Ebbinghaus 1885/1913). With longer delays between list presentation and the test, items at the beginning of the list are still remembered better than items in the middle of the list (i.e., “primacy” is still observed), but items at the end of the list are not remembered due to the delay (i.e., “recency” is not observed). Traditionally, better performance at the beginning of the list has been attributed to coding list items in long-term memory via rehearsal whereas better

performance at the end of the list has been attributed to temporary storage of items in short-term memory so that these items are still available at the time of test. Similar results have been obtained with monkeys remembering a list of images (Sands and Wright 1980a) and rats remembering lists of eight spatial locations presented in an radial maze (Kesner and Novak 1982). In the latter study, dorsal hippocampal lesions caused impaired primacy (i.e., long-term memory was impaired) but had no effect on recency (i.e., short-term memory was spared). Thus, primacy and recency appear to rely on independent coding processes and brain systems.

Serial pattern learning is a form of learning to anticipate or perform highly structured sequential patterns. Serial pattern learning recruits multiple concurrent cognitive processes to develop a cognitive representation of the sequence of events encountered in the task (Fountain et al. 2002; Muller and Fountain 2010, 2016). In the Serial Multiple-Choice (SMC) task, rats learn a sequence of responses in a circular array. The array can be eight levers or nosepoke receptacles, one each on the walls of an octagonal chamber with hypothalamic brain-stimulation or water reward for rats (Fountain and Rowan 1995a, b; Pickens et al. 2013) or a circular array of eight discs presented on a touchscreen for pigeons with grain reward (Garlick et al. 2017). One commonly studied pattern is 123–234–345–456–567–678–781–818–repeat. This pattern consists of three element types. The first element of each chunk is termed the chunk-boundary element. Rats use phrasing cues, located as indicated by dashes in the pattern above, as discriminative cues for chunk-boundary elements (Stempowski et al. 1999; Wallace et al. 2008; Muller and Fountain 2010; Fountain et al. 2013; Kunder and Fountain 2014). Rats use counting/timing processes to anticipate chunk-boundary elements (Muller and Fountain 2010; Muller and Fountain 2016). Chunk-boundary elements are followed in the pattern by within-chunk elements. These are encoded by abstract rule learning (Fountain and Rowan 1995a, b; Fountain et al. 2007; Muller and Fountain 2010; Kunder and Fountain 2011). The pattern may also contain a violation element, that is, an element that is inconsistent with pattern

structure. In this case, the terminal element of the last “818” chunk violates the rule structure of the rest of the pattern. The violation element is typically the most difficult element to learn because no single pattern item or rule predicts the location of the violation element in the pattern. To master the violation element, rats use “multiple-item memory” (cf. Capaldi et al. 1982) consisting of up to seven pattern elements leading up to the violation element as well as other spatial or temporal cues (Kunder and Fountain 2010; Muller and Fountain 2010, 2016). Thus, rats use multiple cognitive processes concurrently to learn such patterns as shown by previous work indicating that the different element types described above are also differentially sensitive to the effects of adolescent drug exposure (Pickens et al. 2013; Rowan et al. 2015), to acute N-methyl-D-aspartate blockade (Fountain and Rowan 2000), and to muscarinic cholinergic blockade (Fountain et al. 2013; Chenoweth and Fountain 2015, 2016). Other studies with infants have shown that sensitivity to recursive hierarchical serial pattern rules emerges in infancy. Infants 8–10 months old showed evidence of sensitivity to hierarchical rule structures whereas infants 4–6 months old did not (Lewkowicz et al. 2018).

## Coding in Animal Episodic Memory

Episodic memory refers to memory for specific events that were “unique, personal past experiences” (Babb and Crystal 2006; Zhou and Crystal 2011; Crystal 2018). Developing animal models of episodic memory required successfully developing techniques for assessing “what-where-when memory, source memory, item-in-context memory, and unexpected questions” (Crystal 2018) in nonhuman animals.

## Conclusion

It can be argued that characterizing the mechanisms of coding is the *raison d’être* for the field of *comparative cognition*. Understanding coding is one of the defining problems in comparative cognition research.

## Cross-References

- ▶ [Anthony \(Tony\) A. Wright](#)
- ▶ [Associative Learning](#)
- ▶ [B.F. Skinner](#)
- ▶ [Classical Conditioning](#)
- ▶ [Donald O. Hebb](#)
- ▶ [Duane Rumbaugh](#)
- ▶ [Encoding](#)
- ▶ [Herbert Terrace](#)
- ▶ [Instrumental Learning](#)
- ▶ [Interval Timing](#)
- ▶ [Irene M. Pepperberg, PhD](#)
- ▶ [Ivan Pavlov](#)
- ▶ [Long-Term Memory](#)
- ▶ [Long-Term Potentiation](#)
- ▶ [Numerosity](#)
- ▶ [Pattern Learning](#)
- ▶ [Place Versus Response Learning](#)
- ▶ [Prospective Memory](#)
- ▶ [Radial Arm Maze](#)
- ▶ [Reference Memory](#)
- ▶ [Relative Numerosity](#)
- ▶ [Spatial Orientation](#)
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- ▶ [Working Memory](#)

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## Coding DNA

► Exon



## Codon

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### Definition

A codon is a sequence of three nucleotides that forms the basic unit of the genetic code.

### Gene Sequences are Composed of Codons

Each protein is made of a specific sequence of amino acids that is specified by the corresponding protein coding gene. The sequence information of protein is stored at the level of DNA (Deoxyribonucleic acid). DNA is composed of a sequence of nucleotides which stores information about the amino acid sequence of the resultant proteins. DNA is first converted to RNA (Ribonucleic acid) that in turn is used to guide the synthesis of corresponding proteins.

Question arises – How is the DNA sequence deciphered into the amino acid sequence of proteins?

The answer is that nucleic acid sequences can be read as “codons.”

### What Is a Codon?

Codons are three-letter “words” that direct the protein synthetic machinery to either add a particular amino acid to the growing polypeptide chain or to initiate or terminate the synthesis of a protein. Each nucleotide acts as a letter and three consecutive nucleotides form a codon. Each codon specifies either an amino acid or acts as a start or stop signal.

Codons are usually considered in terms of RNA as RNA is the actual moiety that interacts

with the protein synthetic machinery to direct protein synthesis. The corresponding DNA sequences form the DNA codons, which is essentially the same with the exception of U (uridine) being replaced by T (thymidine).

### Advantages of a Three-Letter Codon Configuration

Codons, the underlying basis of the genetic code, are formed by three consecutive nucleotides. Triplet nature genetic code provides optimal balance in terms of requirement and complexity.

Nucleotide sequence has four possible letters: adenine (A), guanine (G), cytosine (C), and uridine (U)/thymine (T).

A single-letter word could specify only four amino acids while a two-letter word would be able to specify a maximum of  $4 \times 4 = 16$  amino acids. But there are 20 standard amino acids. So, the requirement could not be met with a two-letter code.

A three-letter code can specify up to  $4 \times 4 \times 4 = 64$  amino acids. This is enough to specify all amino acids as well as start and stop signals. Hence, triplet code satisfies the requirement. Obviously the same can be achieved by using four- or five-letter codes but the system would always prefer to avoid unnecessary complexity. This is possibly the reason why triplet code was chosen by nature.

### Experimental Identification of Codons

Experimental identification of the specificity of each triplet involved use of synthetically produced known nucleotide sequences and monitoring the incorporation of amino acids against them in cell-free systems. Initially, Nirenberg and Matthaei used homopolymers to find out the amino acid specificity of AAA, CCC, GGG, and UUU. UUU, coding for phenylalanine, was the first codon to be deciphered. Later on, Nirenberg and Leder used ribosome binding assay to decipher the rest of the genetic code. Har Gobind

Khorana used synthetic RNA with repeating units to unravel the genetic code. For example, he showed that UCUCUCUCUC, which contains codons UCU and CUC, causes incorporation of serine and leucine. RNAs with four repeating units including UAG, UAA, or UGA produced only dipeptides and tripeptides thus revealing that UAG, UAA, and UGA are stop codons.

The Nobel Prize in Physiology or Medicine 1968 was awarded jointly to Robert W. Holley, Har Gobind Khorana, and Marshall W. Nirenberg “for their interpretation of the genetic code and its function in protein synthesis.”

## The Triplet Code

The triplet code has 64 unique codons. The specificities of the codons are given in the Table 1 below:

**Start codon:** AUG codes for methionine and acts as the start or initiator codon. This is the point at which translation starts and the first amino acid is incorporated into the polypeptide chain. Usually, the first AUG after the Shine-Dalgarno (SD) sequence (prokaryotic RNA’s ribosome binding site) AGGAGG acts as the start codon, and is generally located around eight bases downstream of the SD sequence. In eukaryotes, the initiator codon is usually found inside a conserved sequence of nucleotides called Kozak consensus sequence ((GCC)RCCAUGG; R is a purine). Rarely, GUG and UUG are also used as an initiator codon. While acting as an initiator codon, they cause incorporation of methionine, although their inherent specificities are different. In prokaryotes, *E. coli* is found to use AUG 83%, GUG 14%, and UUG 3% as START codons.

**Stop codon:** Stop or terminator codons specify the site at which the translation has to end. This is where the synthesis of polypeptide chain comes to a halt and it is released from the ribosome after addition of a water molecule to the end of the chain. UAG (amber), UAA (ochre), UGA (opal) are the three stop codons. Stop codons signal the termination of this

process by binding release factors, which cause the ribosomal subunits to disassociate, releasing the completed polypeptide.

As 3 out of 64 codons are stop codons, a ribosome is expected to meet a stop codon on average after every 20 codons. Hence, the presence of multiple stop codons may be an adaptation to ensure that a polypeptide does not keep elongating if a stop codon is mutated or missed.

**Amino acid codons:** 61 out of 64 codons code for different amino acids. The specificities are listed in Table 1 below. Methionine and tryptophan are coded by single codons while leucine, serine, and arginine are coded by as many as six different codons each.

## Properties of Triplet Code

1. Code is in form of triplet codons.
2. Code is nonoverlapping, i.e., the codons are read sequentially.
3. Code is nonambiguous, i.e., a particular codon always specifies the same thing. There are minor exceptions to this.
4. Code is degenerate, i.e., multiple codons may specify the same amino acid.
5. Code is commaless, i.e., one codon starts just after the earlier one. There are no nucleotides reserved to serve as punctuation marks.
6. Code is directional. Codons are always read in 5' to 3' direction. For example, GUC is valine while the reverse CUG codes for leucine.
7. Code is universal, i.e., same genetic code is followed for all organisms, barring a few minor exceptions.
8. Some codons act to initiate translation – the start codons.
9. Some codons are reserved to terminate translation – the stop codons.

## Exceptions to the Code and Implications

There are a few rare exceptions to the otherwise universal genetic code. Use of alternate start codons GUG and UUG has already been discussed.

**Codon, Table 1** Codons and the amino acids they encode

| 1st base | 2nd base |                    |     |           |     |                       |     |                      | 3rd base |
|----------|----------|--------------------|-----|-----------|-----|-----------------------|-----|----------------------|----------|
|          | U        |                    | C   |           | A   |                       | G   |                      |          |
| <b>U</b> | UUU      | (Phe/F)            | UCU | (Ser/S)   | UAU | (Tyr/Y)               | UGU | (Cys/C)              | <b>U</b> |
|          | UUC      | Phenylalanine      | UCC | Serine    | UAC | Tyrosine              | UGC | Cysteine             | <b>C</b> |
|          | UUA      | (Leu/L)            | UCA |           | UAA | Stop ( <i>Ochre</i> ) | UGA | Stop ( <i>Opal</i> ) | <b>A</b> |
|          | UUG      | Leucine            | UCG |           | UAG | Stop ( <i>Amber</i> ) | UGG | (Trp/W) Tryptophan   | <b>G</b> |
| <b>C</b> | CUU      |                    | CCU | (Pro/P)   | CAU | (His/H)               | CGU | (Arg/R)              | <b>U</b> |
|          | CUC      |                    | CCC | Proline   | CAC | Histidine             | CGC | Arginine             | <b>C</b> |
|          | CUA      |                    | CCA |           | CAA | (Gln/Q)               | CGA |                      | <b>A</b> |
|          | CUG      |                    | CCG |           | CAG | Glutamine             | CGG |                      | <b>G</b> |
| <b>A</b> | AUU      | (Ile/I)            | ACU | (Thr/T)   | AAU | (Asn/N)               | AGU | (Ser/S)              | <b>U</b> |
|          | AUC      | Isoleucine         | ACC | Threonine | AAC | Asparagine            | AGC | Serine               | <b>C</b> |
|          | AUA      |                    | ACA |           | AAA | (Lys/K)               | AGA | (Arg/R)              | <b>A</b> |
|          | AUG      | (Met/M) Methionine | ACG |           | AAG | Lysine                | AGG | Arginine             | <b>G</b> |
| <b>G</b> | GUU      | (Val/V) Valine     | GCU | (Ala/A)   | GAU | (Asp/D)               | GGU | (Gly/G)              | <b>U</b> |
|          | GUC      |                    | GCC | Alanine   | GAC | Aspartic acid         | GGC | Glycine              | <b>C</b> |
|          | GUA      |                    | GCA |           | GAA | (Glu/E)               | GGA |                      | <b>A</b> |
|          | GUG      |                    | GCG |           | GAG | Glutamic acid         | GGG |                      | <b>G</b> |

## Mitochondrial Genes

Mitochondrial genetic code shows subtle variations from the universal code. Table 2 lists some of the important deviations from the standard universal code.

## Nuclear Genes

In some ciliates, the universal termination codons UAA and UAG code for glutamine. In euplotids, UGA codes for cysteine. CAG may be used in *Candida albicans* as an initiator codon. In some yeasts, CUG codes for serine rather than leucine.

## Nonstandard Amino Acids

Selenocysteine, a selenium containing analogue of cysteine, is coded by the stop codon UGA. Selenoprotein mRNAs possess a characteristic secondary RNA motif called the SECIS element (SECIS: selenocysteine insertion sequence), which allows the nearby UGA codons to be recognized as coding for selenocysteine.

Pyrrolysine is encoded by the stop codon UAG. It is found in some methanogenicarchaea and bacteria. Pyrrolysine is made up of 4-methylpyrroline-5-carboxylate in amide linkage with the <sup>ε</sup>N of lysine. A special transfer RNA encoded by pylT gene and a special class II aminoacyl-tRNA synthetase that charges the pylT-derived tRNA with pyrrolysine is needed for UAG to be recognized as coding for pyrrolysine.

## Codon Bias and Implications

Codon usage bias refers to the preferential use of a certain codon to code for a particular amino acid over synonymous codons. For example, GCC and GCG both code for alanine and are thus synonymous codons. Interestingly, in the human genome, alanine is encoded by GCC four times as often as by GCG. This is an example of codon usage bias.

It is possible that the composition of the tRNA pool drives the codon bias. Those codons are selected for which corresponding tRNAs are more abundant. This may especially be true for

**Codon, Table 2** Variations from the standard genetic code as seen in different mitochondrial genomes. N refers to any nucleotide

| Codon | Standard code | Vertebrate mitochondrial | Yeast mitochondrial | Invertebrate mitochondrial |
|-------|---------------|--------------------------|---------------------|----------------------------|
| AGA   | Arg           | Ter                      | Arg                 | Ser                        |
| AGG   | Arg           | Ter                      | Arg                 | Ser                        |
| AUA   | Ile           | Met                      | Met                 | Met                        |
| UGA   | Ter           | Trp                      | Trp                 | Trp                        |
| CUN   | Leu           | Leu                      | Thr                 | Leu                        |

fast growing organisms. For slow growing organisms, codon preferences are determined by the characteristic mutational biases of that particular genome. The contributing factors of codon bias are still unclear and fiercely debated.

Codon usage bias affects the synthesis of transgenic proteins in protein synthesizing host. The host may have different codon preferences compared to the organism from which the protein coding sequence is derived. Hence, a researcher needs to take into account the codon usage bias of the host organism and accordingly change the protein coding sequence to use the host-preferred codons.

**How Codons Actually Work: Meet the Anticodon**

Codons are recognized by complimentary binding with their tRNA counterpart, the anticodon. Anticodons, just like codons, are sequence of three nucleotides located in the anticodon arm of a tRNA. Each tRNA is specific for a particular amino acid and its codon(s). tRNAs form the bridge between genetic code and protein sequence by physically bringing a particular amino acid to lodge at its correct site in the protein sequence. Anticodon forms the codon recognition arm of the tRNA by virtue of its ability to base pair to its corresponding codon. Each tRNA has an anticodon that can bind to one or more codons of that particular amino acid.

For example, methionine is encoded by AUG (5'–3') and its corresponding anticodon is the sequence UAC (3'–5'). The following table shows the base pairing specificities of nucleotides in a codon-anticodon interaction.

| 1st (i.e., 5' end) and 2nd place mRNA codon | 1st (i.e., 3' end) and 2nd place tRNA anticodon |
|---------------------------------------------|-------------------------------------------------|
| A                                           | U                                               |
| U                                           | A                                               |
| C                                           | G                                               |
| G                                           | C                                               |
| 3rd place (i.e., 3' end) mRNA codon         | 3rd place (i.e., 5' end) tRNA anticodon         |
| A or G                                      | U                                               |
| U                                           | A                                               |
| U or C                                      | G                                               |
| G                                           | C                                               |
| U, C or A                                   | I                                               |

The base pairing rules are strict for the 1st and 2nd positions. These are the standard Watson-Crick base pairs. But in the third position, the base pairing stringency is relaxed and non-Watson-Crick base pairs are possible, allowing a single tRNA to recognize multiple codons of the same amino acid. This is known as the Wobble hypothesis. The third base pair is often called the wobble base pair.

As a result of wobble base pairing, tRNAs with anticodons like CCI (3'–5') can recognize multiple codons GGU (5'–3'), GGC (5'–3'), GGA (5'–3'), all being codons of glycine, the amino acid this tRNA is specific for.

This allows lesser number of tRNAs to carry out the translation process. A minimum of 31 tRNAs are required to translate, unambiguously, all 61 sense codons of the standard genetic code.

Anticodons, tRNAs, and ribosomes together make a well-synchronized, specific, and efficient pipeline to render the genetic information hidden in the codons into the functional form of proteins.

## Cross-References

- [Base Pair](#)
- [DNA](#)
- [Exon](#)
- [Genetic Code](#)
- [Messenger RNA](#)
- [Mitochondrial DNA](#)
- [Ribosome](#)
- [RNA](#)

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## Coefficient of Relatedness

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## Synonyms

[Degree of relatedness](#); [Kinship](#); [Pedigree relatedness](#)

## Definition

The coefficient of relatedness ( $r$ ) is defined as the probability that a gene in one individual is identical-by-descent (IBD) to a gene in another individual. In other words, it is the probability that

two individuals inherited a certain proportion of genes from a common ancestor. The term was introduced by Sewall Wright (1922) and is calculated as  $r = \sum (0.5)^L$ . The calculation considers that at each generation link there is meiosis, i.e., a 0.5 probability that a copy of a particular gene will be passed on to an offspring. For  $L$  numbers of generation links between two individuals the probability is  $(0.5)^L$ . Finally, the coefficient of relatedness between two individuals is the sum of coefficients calculated for each pathway by which they share a common ancestor.

To provide an example (see Fig. 1): For full-siblings (sharing both parents) we consider  $r = 2 (0.5)^2$ , as we have two generation links from one sibling to the other (one from sibling to parent, the second from that parent to the other sibling) as well as two common ancestors (mother and father), hence two pathways to sum up the degree of relatedness.

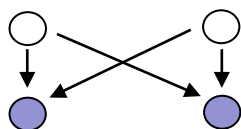
## Kin Class Versus Degree of Relatedness

The degree of relatedness can be identical for pairs of individuals who belong to different kin classes. For example, parent-offspring dyads share, on average, 50% of their genes, but so do full-siblings (Table 1).

One class which remains difficult to establish, especially in wild populations, is the class of unrelated individuals ( $r \sim 0$ ). Today, pedigree studies of free-ranging animals may include several generations of complete pedigrees (e.g., Widdig et al. 2017), hence a complete pedigree of four generations can exclude pedigree relatedness up to this generation level. Although this creates only a minor imprecision (van Horn et al. 2008), it might be relevant to have a precise measure of relatedness even among distant relatives, depending upon the study question.

## Predicted Versus Actual Degree of Relatedness

The degree of relatedness is a theoretical expectation and hence provides mean values of expected



**Coefficient of Relatedness, Fig. 1** A simple family tree including parent-offspring dyads. In blue are the individuals for which we like to determine the degree of relatedness, in white are their two direct ancestors. The degree of relatedness of the respective dyad in blue is  $r = 0.5$ , they are full-siblings

**Coefficient of Relatedness, Table 1** Degree of relatedness in relation to kin classes. Note, it is always important to consider whether ancestors are shared by one or both kin lines

| Kin class                                     | Calculation     | Degree of relatedness |
|-----------------------------------------------|-----------------|-----------------------|
| Parent-offspring                              | $r = 1 (0.5)^1$ | 0.5                   |
| Full-siblings (both parents shared)           | $r = 2 (0.5)^2$ | 0.5                   |
| Half-siblings (one parent shared)             | $r = 1 (0.5)^2$ | 0.25                  |
| Grandparent and grandchild                    | $r = 1 (0.5)^2$ | 0.25                  |
| Aunt/uncle-niece/nephew (both parents shared) | $r = 2 (0.5)^3$ | 0.25                  |
| Aunt/uncle-niece/nephew (one parents shared)  | $r = 1 (0.5)^3$ | 0.125                 |
| Cousins (if parents are full-sibs)            | $r = 2 (0.5)^4$ | 0.125                 |
| Cousins (if parents are half-sibs)            | $r = 1 (0.5)^4$ | 0.0625                |

genetic relatedness. For full-siblings, we expect that they share 50% of their genes on average; however, the actual genetic relatedness varies around its expectation due to the random nature of recombination during meiosis (Speed and Balding 2015). Genome-wide data on humans have shown differences in realized IBD among dyads with the same predicted relatedness based on pedigrees: For human full-siblings, the mean proportion of the genome-shared IBD was 49%, as expected, but the actual degree of IBD ranged from 37% to 62% (Visscher et al. 2006). Hence, it is not surprising that the coefficient of relatedness estimated from pedigrees and the actual relatedness from genetic data often differ in empirical

studies, although they are generally strongly correlated (Städele and Vigilant 2016).

### Measuring the Degree of Relatedness

Traditionally, the degree of relatedness was established via pedigrees (Pemberton 2008). However, in natural populations, pedigrees tend to be incomplete and founder individuals (often unknown) are assumed (but usually cannot be proven) to be unrelated, which is critical when assessing the degree of inbreeding (or consanguinity) (Keller and Waller 2002). In a wide range of taxa, the degree of relatedness has alternatively been estimated from genetic markers mainly through short tandem repeats (STR or microsatellites). Studies comparing relatedness derived from genetic markers and pedigrees reported a risk of misclassifying pairs of related individuals as unrelated and vice versa in the absence of pedigree data (van Horn et al. 2008). One problem arises due to overlapping distributions of relatedness among different kin classes (Blouin et al. 1996). Recent studies stressed the power increase by applying a more complex approach such as the combination of parentage analysis, sibship reconstruction, demographic information, and likelihood analysis to classify kinship (Städele and Vigilant 2016). Future studies using Single Nucleotide Polymorphism (SNP) or whole-genome sequencing data will open several new avenues, including the possibility to correctly classify distantly related individuals.

### Application of the Degree of Relatedness

Knowledge on the degree of relatedness between individuals plays an essential role in a wide range of research areas including behavioral ecology, evolutionary biology, quantitative genetics, and conservation. For example, calculating the degree of relatedness between two individuals has been widely applied in studies on social species. In particular, it has been used to explain the evolution of social behavior via kin selection from insects to humans. Kin selection theory predicts that altruistic behavior is favored by selection if the costs of the initiator are lower than the benefits of the recipient considering the degree of relatedness between the two



(Hamilton 1964). Hence, altruistic behavior is predicted to be limited to kin, with costly altruism restricted to close kin.

## Cross-References

- [Allele Sharing](#)
- [DNA Marker](#)
- [Genes](#)
- [Heredity](#)
- [Matrilines and Patriline](#)

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## Coevolution

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## Definitions

- Evolution** Evolution is a continuous process of alternation in characteristics which are inherited in biological population over generations.
- Coevolution** In biology, some naturally occurring phenomena in which two or more species evolve by reciprocally affecting each other are called coevolution.

## History

The term coevolution was coined by Paul R. Ehrlich and Peter H. Reven in 1964. But these types of evolutionary interactions have been studied many years ago in 1959. Darwin has mentioned the interaction between flowering plant and insects in his book *On the Origin of Species*.

One of the reasons for coevolution is reciprocal selective pressure on two or more species which might culminate into evolutionary arms race between the interacting species. Ultimately, coevolution results in adaptation and counter-adaptation in reproduction and survival of species interacting with each other.

## Proposed Theories

### • Red-Queen Hypothesis

According to this theory, organisms have to adapt and evolve constantly with changing environment as well as proliferate constantly to obtain reproductive advantages and to survive against continuously evolving opposing other organisms. It is also known as *Red Queen's*, *Red Queen's race*, or *the Red Queen*

effect. The Red Queen effect may result when competing species find themselves in danger, e.g., higher frequency of sexual individuals in mixed population (asexual and sexual) of fresh water snail (*Potamopyrgus antipodarum*) in the presence of trematode parasites (Jokela et al. 2003).

- **Geographic Mosaic Theory of Coevolution**

According to this theory, geographic location and community ecology play important role in coevolution of strongly interacting species in multiple populations. *Natural selection in the form of geographic mosaic, hot spot (area of strong reciprocal selection between interacting species) surrounded by cold spot (area where there is very low or no reciprocal selection), and trait remixing by means of genetic drift and gene flow* are three major parameters of geographic system that drives the coevolution in population (Gomulkiewicz et al. 2002).

Geographic mosaic may lead to either mutualism (e.g., plant and pollinator) or arms race between two species such as predator-prey, host-parasites, etc. One of the examples for coevolutionary arms race is predator whelk (*Sinistrofulgur* sp.) and the hard-shelled bivalve (*Mercenaria* sp.) prey. Whelk uses shell lips to break the shell of prey. In response to that prey has developed larger and harder shells. To beat this strategy of bivalve, whelk intensified the attack and increases their size (Dietl 2003).

Depending upon the interaction between species, coevolution is broadly divided into two categories:

- *Pairwise or Specific Coevolution*

As name indicates, this type of coevolution involves one to one interaction (i.e., coevolution of two species affecting each other), e.g., development of foot long tongue in moth in response to development of foot long flower in comet orchid plants.

- *Diffuse or Guild Coevolution*

Diffuse or guild type of coevolution involves more than two species, e.g.,

evolutionary adaptation by large number of insect species feeding on same group of plant in response to development of defensive (chemical/physical) mechanism by plant against insects.

Further, **pairwise/specific coevolution** can be divided into different categories according to type of relationship between species affecting each other's evolution.

### **Predation**

When organisms from one species survive by eating other, this kind of relationship is called predation. Prey is the organism which is being eaten by predator organism. Simply, predator dies if it does not get food and prey dies if it is eaten by predator. So, prey develops the defense mechanism to escape from the predator and predators develop ability to catch prey even more effectively. Both processes impose selective pressure on both prey and predator species. Some of the strategies and mechanisms of prey and predator which may lead to coevolution are tabulated below:

| Strategies by prey                   | Adaptation by predator            |
|--------------------------------------|-----------------------------------|
| Camouflage                           | Visual acuity                     |
| Prey escape speed                    | Speed of pursuit                  |
| Flocking and herding                 | Strategies to isolate individuals |
| Prey toxicity, aposematic coloration | Resistance                        |
| Hard seed coats                      | Large beaks                       |

Examples of predation type of coevolution are as follows:

#### **1. African Honey Badger (*Mellivora capensis*) and African Bees (*Apis mellifera scutellata*)**

African honey badger (*Mellivora capensis*) and African bees (*Apis mellifera scutellata*) are example of predation coevolution. African honey badger possesses thick and loose skin to protect itself from sting of African bees, and this property makes it relatively resistant to sting and requires full-out attack by hive. In response to this adaption of honey badger, African bees have developed the ability to

secrete pheromones as it dies to call other bees to continue attack.

## 2. Galapagos Tortoises and Cactus

Galapagos tortoises and cactus also coevolved due to dependency of tortoises on cactus for its hunger. On one of the island, tortoises are with long neck in response to higher off the ground branches of cactus. While short necked tortoises dwell on the island harboring cactus with short branches. So, in this case, cactus evolved to protect itself from being eaten by tortoises, and tortoises have developed long neck to get food from branches of cactus grow at higher level and so on.

## Parasitism

In parasitism, one species of organism (parasite) is dependent on another species organism (host) for activities such as reproduction, feeding, etc. As opposed to predation, in this type of relationship the beneficiary species does not kill the host species. In parasitism, host is under selection pressure to avoid parasitism and parasite is under selection pressure to evade host defense. In such selection pressure, host carrying advantageous allele shows selective advantages and is not affected by parasites as much and that genotype becomes common in that population. Further, to become prevalent in that population, parasite is also selected to get benefits of host population with resistant allele. This way, host parasite coevolution leads to changes in allele frequencies within population.

Examples of coevolution involving host and parasites interaction are discussed below:

### 1. *Plasmodium* (Malaria Parasite) and Human Host

*Plasmodium falciparum*, *P. vivax*, *P. ovale*, and *P. malariae* are four species of *Plasmodium* which causes malaria in human. Out of these, *P. falciparum* is predominant infectious species which leads to death. As malarial parasites infect the red blood cells, infection in humans by parasites depends on polymorphism and distribution of genes associated with hemoglobin, blood group antigens,

thalassemias, red cell membrane molecules, human lymphocyte antigen (HLA) classes, cytokines, etc. Individuals with resistant genotype can escape from being infected by malarial parasites. To evade this resistant mechanism, parasites have the tendency to make change in genotype, especially in gene of virulence. This way, human genetic polymorphism and immune response influence the structure and polymorphism in *Plasmodium* population (antigenic drift). Again new population have different targets in human population which leads to selection pressure in human population and ultimately change in gene pool of particular regional population. This way, host and parasite both influence each other to develop resistance and mechanism to invade that resistance mechanism, respectively (Evans and Wellems 2002).

### 2. Cuckoos (*Cuculus canorus*) and Different Host Bird Species

Cuckoos do not make their own nest. They lay their eggs in nest of crow. Moreover, cuckoos extrude the eggs of the host from the nest and kill the young ones in the nest. In response to this strategy of cuckoo, host develops more efficiency to distinguish own eggs and invaders. To overcome the response of host, cuckoos counter-adapt to survive. The characters adapted by cuckoos are thickened eggshells, minimization of incubation period and morphological changes to extrude out the host eggs from the nest (Rothstein 1990). Similarly, cowbird is another parasite which parasitizes the different bird (host) species in a same way as cuckoo (Rothstein 1990).

## Mutualism

When two or more species evolve together by helping each other, the interaction is called mutualism, and their process of coevolution is called mutualistic coevolution. Mutualism is divided into two categories:

### 1. Service-Service Relationship

Two species that involve in service-service mutualistic relationship get benefits from each other by providing services to each other such

as protection from their respective predators, providing shelters, etc.

## 2. Service-Resource Relationship

In this type of mutualism, one of the species provides benefits to other by providing services by some way. On the other hand, service provider species get benefits in the form of resources such as food. It is a common type of mutualistic relationship.

Some of the examples explaining coevolution in species related with each other in mutualistic manner are discussed below:

### 1. *Acacia* Ant and *Acacia*

*Acacia* ants protect the tree from prey and other plants which compete with *Acacia* tree for nourishment and other resources. In turn, *Acacia* have coevolved itself to create pores to make dwelling space for *Acacia* ants, provide them with nourishment, and protect ants' larvae (Janzen 1966).

### 2. Birds and Bird Pollinating Flowers

The pollination of flowering plants by birds is called *Ornithophily*. As plants are dependent on birds for its pollination, plants develop some characters which attract birds. In turn, birds also get some benefits from flowering plants like food, shelter, etc. Hummingbirds and ornithophilous plants are one of the examples of such type of coevolution. In this case, ornithophilous plants have evolved their flowers in such a way that they attract the hummingbirds by producing nectar, synthesizing coloring pigments of flowers which are compatible with birds' vision as well as morphological changes of the flower to make comfortable room for birds' rostrum. Moreover, ornithophilous plants flourish most during the breeding period of hummingbirds. In return, hummingbirds also adapt with the flowering plants to make maximum use of adaptations by plants, e.g., change in the morphology of beak to accommodate its beak in long corolla of flowers to get high sugary nectar and this coevolution also helps the flowering plant to place its pollen on some body part of bird (Stiles 1981; Kay et al. 2005).

### 3. Sapotaceous Tree and Dodo (*Raphus cucullatus*)

Sapotaceous tree, also known as Dodo tree, and Dodo birds both are native of islands of Mauritius. Dodo bird is exclusive pollinator for dodo trees. Hence, the extinction of dodo birds made the dodo trees to be nearly extinct on islands (Temple 1977).

### 4. Entomophilous Flowers and Insects

Flowers dependent on insects for its pollination is called entomophilous flowers. Andrenid bee (*Andrena loniceræ*) and *Lonicera gracilipes* are examples of such kind of coevolution. Andrenid bees visit the plant for nectar, and while taking nectar, some of the pollens stick to different part of bee's body. In response to that, plant has increased the nectar production. On another side, bees have also changed in morphology of proboscis to get nectar from long corolla. This way, morphological change in bees and increased nectar production in *Lonicera gracilipes* indicate the one-to-one mutualistic coevolution between them (Shimizu et al. 2014).

## Competition

When individuals of same species or different species share same niche and have common resources, they compete with each other for their existence. In this type of interspecific interaction, competitive species impose selection pressure to each other and winning species survive. In this way, they affect each other's evolution at species level and it is called competitive coevolution. Intraspecific competitions like sexual selection, sexual conflicts (Parker 2006), etc. drive the coevolution. Mostly, a consequence of within species competition is slowed growth rate and does not contribute much toward coevolution, while dependability of different species on same resources like habitat, food, etc. leads to competitive coevolution between the species (Connell 1980). The consequences of interspecific competition are competitive exclusion, local extinction, niche divergence, change in composition and structure of community, etc.

Some of the examples explaining coevolution in species compete with each other are discussed below:

### 1. Darwin's Finches

Darwin's finches are considered to be group of around 15 different species of perching birds. Due to their geographical location, they are also known as Galápagos finches and belong to Passeriformes order and Thraupidae family. Galápagos Islands are group of 21 islands. Finches on these islands have developed different food specialization such as difference in beak size and shape to decrease the competition for utilization of same limited food resources. In addition to that they have also changed their habitat for the same and occupied different islands of Galápagos Islands. Recently, some researchers have figured out the role of 240 kb *ALXI* gene (encodes a transcription factor involved in the development of craniofacial structure) in the diversification of beak size and shape of finches to optimize the utilization of limited food resources (Lamichhaney et al. 2015).

### 2. *Trifolium repens* and Neighboring Grasses (*Agrostis capillaris*, *Holcus lanatus*, and *Lolium perenne*)

*Trifolium repens* is an herbaceous perennial plant of bean family. *Agrostis capillaris*, *Holcus lanatus*, and *Lolium perenne* are perennial grass family plants. Normally, *T. repens* plants share habitat with *A. capillaris*, *H. lanatus*, and *L. perenne*. Removal of these dominant grasses from the habitat of *T. repens* led to diversification of *T. repens* into different subpopulations. This observation by researchers supports the inter-specific competition coevolution of *T. repens* and surrounding grasses (Turkington 1989).

## Cross-References

- ▶ [Asexual Reproduction](#)
- ▶ [Birds](#)
- ▶ [Charles Darwin](#)
- ▶ [Competition](#)

- ▶ [Competitive Exclusion](#)
- ▶ [Cuckoo Brood Parasitism](#)
- ▶ [Incubation](#)
- ▶ [Niche Divergence](#)
- ▶ [Origin of Species](#)
- ▶ [Predator](#)
- ▶ [Prey](#)
- ▶ [Red Queen Effect, The](#)

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## Cognition

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## Synonyms

Animal language; Arbitrariness; Articulatory rehearsal loop; Attention; Attention span; Auditory coding; Babbling; Binocular depth cues; Brain imaging; Central executive; Change blindness; Cognition; Cognitive models; Cognitive processes; Cognitive revolution; Cognitive theories; Color perception; Covert attention; Decaying; Depth perception; Digit spans; Discreteness; Displacement; Distributive coding; Divided attention; Duality; Episodic memory; Explicit memories; Fixation; Implicit memories; Inattention blindness; Interactionist theory; Language; Language acquisition device; Learning theory; Long-term memory; Memory; Memory interference; Mind; Monocular depth cues; Monocular vision; Morphemes; Morphology; Motion perception; Nativist theory of language development; Object perception; Object recognition; Overt attention; Perception; Phonemes; Phonological loop; Phonology; Photoreceptors; Pragmatics; Procedural memories; Productivity; Properties of human language; Psychophysiological responses; Saccades; Selective attention; Semantic coding; Semantic memory; Semanticity;

Semantics; Sensations; Senses; Sensory receptors; Short-term memory; Smooth pursuit movements; Spatial recognition; Specificity coding; Stereoscopic vision; Syntax; Vergence eye movements; Vestibule-ocular movements; Visual coding; Visual pathways; Visual perception; Visual sensation; Visuospatial sketchpad; Working memory

## Introduction

### What Is Cognition?

The **mind** is a complex system that creates and controls the fundamental functions integral to survival. It can vary in form and function across animals as well as among those belonging to the same species. **Cognition** is the study of the mind – what the mind does, how the mind accomplishes these functions, and which psychophysiological mechanisms are involved in these processes.

Although the philosophical underpinnings of the mind have been discussed as early as Ancient Greece, the scientific inquiry of cognition has only gained prominence in the last 70 years. The **cognitive revolution** ignited a renewed curiosity for the mind that was previously doused by the rise of behaviorism – the study of behavior measured solely by observable actions (Miller, 2003). Until the 1950s, the field of psychology was dominated by the belief that mental processes could not be methodologically quantified or observed. Instead, behaviorist psychologists, such as John B. Watson and B.F. Skinner, focused on behavioral responses to environmental stimuli. Advancements in computer technology catalyzed the rise of the cognitive revolution – particularly the discovery that machines were capable of performing logical operations. Scientists began to wonder if computers worked in the same way the human brain does. When they realized there was little research on the mind, researchers shifted their focus from behavioral psychology to cognition. The pioneers of cognition include Ulric Neisser (referred to as the “father of cognitive psychology”), Norman Chomsky (linguistics), and George Miller (memory).

Today, cognition is one of the main subfields of psychology. It is often studied alongside other



disciplines such as philosophy, neuroscience, linguistics, computer science, and anthropology. Key areas of cognition include perception, attention, memory, and language.

The study of cognition is not restricted to the human mind. Many cognitive scientists are interested in the mental processes of other species such as mammals, birds, and even sea creatures. Researchers may study nonhuman minds in order to gain a better understanding of those species' cognition. They may also study other species' brains in order to learn more about the human brain. For example, the human brain may be difficult to study because it involves many potential risks and costs to the participants. This may be especially true for drug treatments or lesions to the brain that are potentially harmful to human subjects. In contrast, mice brains, which are similar to human brains in structure and function, are easier to study and are more accessible. Therefore, it is common for cognitive scientists to study mice before or in place of human subjects.

### Methodologies

Cognitive scientists employ a range of research methods to evaluate the mind. They may use these approaches to study cognition within or between different species. Similar to other sciences, cognition can be studied and explained distinctly or across three domains: mental, behavioral, or psychophysiological. When cognition is evaluated at the mental level, it is often explained using theories and/or models such as computational, box-and-arrow, or statistical. **Cognitive theories** explain how a mental phenomenon occurs, what components are involved, and which outcomes are expected as a result of this process. These underlying cognitive mechanisms can be observed through the behavioral level. Behaviors can be measured by means of a performance on an activity such as a task or questionnaire. Finally, the psychophysiological level measures the physiological responses that arise as a result of the behavioral and cognitive levels. Examples of physiological responses include brain activation by means of an imaging machine (e.g., EEG, fMRI, or PET), electrodermal activity (e.g., skin responses), cardiovascular measures, or eye movements.

Consider the following example regarding the study of attention. There are different theories that explain how individuals process the environment and attend to particular stimuli in that environment (e.g., Broadbent's filter model of attention). Attention may be observed by means of a behavioral task in which participants have to watch a video and count the number of cars that appear on the screen. Lastly, participants can be connected to an eye-tracking device where their pupil dilations and eye movements are observed as they attend to the cars in the videos.

### Perception

How do species perceive the world? How do dogs smell? How do humans hear a friend's voice in a crowd? How do mice taste cheese? Species have sensory systems dedicated to each of the five **senses** – taste, touch, sight, vision, and smell. In these systems, sensory information is captured by means of **sensory receptors**, or specialized nerve cells designed to respond to specific sensory stimuli. These sensory stimuli are then converted into electrical impulses, which are then interpreted by the brain. This process results in a **sensation**, or a detected stimulation from the internal or external world. Different species experience the world through sensations, and their interpretations of those sensations determine their perception.

**Perception** is the process by which species identify, organize, and interpret those sensations (Levine and Shefner, 2000). For example, humans identify vibrations in the air, organize them into sound waves, and interpret them as music. Perceptual processing is complex – involving the interplay of body organs, neural networks, and environmental information. Although it is difficult to confirm how nonhumans perceive the world, scientists believe that they have similar sensory receptors and brain activation as humans. Differences in these physiological systems could result in changes in perception. In order to understand the complexity of perception, consider how species see the world. Seeing requires visual sensation and visual perception.

**Visual sensation** is the process by which electromagnetic rays – in the form of visible light – are processed from the eyes to the brain (Levine and Shefner, 2000). When a living or nonliving thing occupies space, light bounces off that object and into the visual sensory organ, or the **eyes**. The **cornea** and **lens** focus the light while the **pupil** – with the help of the **iris**, which opens and closes – regulates the amount of light that passes through the eyes. The cornea, pupil, iris, and lens work together to direct the light towards the back of the eye to the retina. The **retina** contains photoreceptors with specialized sensitivities that work together to provide vision. **Photoreceptors** respond to light in the environment and convert them into electric signals, which are later processed and decoded in the brain.

There are two types of photoreceptors: rods and cones. Although the **rods** and the **cones** both respond to light, they respond to it in different ways. **Rods** are responsible for vision in low-light environments. They detect movement, shape, as well as light and dark changes. **Cones** are responsible for color vision. Rods and cones also differ in sensitivity and acuity. Rods are extremely sensitive to light – meaning they are able to detect and respond to as little as a photon of light. However, rods have low acuity, which means they cannot detect fine details in the environment. In contrast, cones are less sensitive but have greater acuity. Cones require more light for detection. This increase in bright light allows cones to detect small details in the environment.

The photoreceptors transform visible light into electric signals. Then, these neural impulses travel through the optic nerve, optic chiasm, and optic tract – ultimately leading towards the visual cortex for processing. **Visual perception** is the process by which these electric signals are identified, organized, and interpreted in the brain to create the visual world. There are two visual streams: The What and Where Pathways (Ungerleider and Mishkin, 1982). The ventral stream (**What Pathway**) is involved in **object recognition**, or the ability to discriminate between objects. On the other hand, the dorsal stream (**Where Pathway**) is involved in **spatial recognition**, or the ability to determine how an

object occupies space. Visual perception could be divided into four categories: color, object, depth, and motion perception.

**Color perception** involves three stages: (Goldstein, 2011). In **detection**, cones respond to light wavelengths in the environment. In **discrimination**, these wavelengths are differentiated as different perceived colors. In the electromagnetic spectrum, distinct wavelengths lead to the perception of particular colors. For example, long wavelengths are perceived as the color red while short wavelengths are observed as blue. Medium wavelengths are perceived as green. Finally, **appearance** is the process by which these perceived colors are assigned color names.

Do animals see color like humans? Although it is difficult to confirm what animals actually see, scientists have made inferences based on the number of cones in their eyes. For example, dogs and mice have fairly few cones in their eyes. Scientists believe they primarily see the world in greys, blues, and yellows. In contrast, monkeys and birds are believed to have relatively good color perception.

**Object perception** is the process by which species recognize objects in the environment. Early scientists believed that each neuron coded specific stimuli in the environment. Through **specificity coding**, they believed that species had a neuron for each object in the environment (e.g., banana neuron or grandmother neuron) (Gross, 2002). However, scientists now believe that object perception is achieved through **distributed coding** in which objects are processed through a network of neurons. Species' ability to perceive objects depends greatly on where their eyes are placed. For example, many predators (e.g., primates) have eyes in the front of their heads, which allow them to detect prey. On the other hand, many prey (e.g., bunnies) have eyes on the sides of their heads, which allow them to see predators in order to avoid being eaten.

**Depth perception** is the ability to perceive the world in three dimensions. Species can detect depth based on **depth cues** – or information determining distance between and among objects – in the environment. **Monocular depth cues** are depth information that is available even when

the world is perceived with one eye alone, or **monocular vision**. They include:

1. **Occlusion**: understanding that closer objects obstruct view of other objects
2. **Relative size**: comparison of size between two objects without knowing absolute size of either one
3. **Texture gradient**: understanding that closer objects will have more visible fine details compared to objects further away
4. **Relative height**: understanding that objects at different distances from the viewer will form different heights on the ground plane
5. **Familiar size**: depth information based on knowledge of typical size of objects
6. **Aerial perspective (atmospheric perspective)**: depth understanding that objects that are farther away appear blurrier, bluer, and more scattered
7. **Linear perspective**: understanding that parallel lines in the 3D world will look like they converge in 2D images
8. **Vanishing point**: the apparent point where parallel lines recede in depth convergence

**Binocular depth cues** are depth information that is available when the world is perceived with two eyes, or **stereoscopic vision**. With two eyes, species can perceive the same object at two slightly different angles. This information is then combined in the brain to form depth information about three-dimensional images in the environment.

Finally, **motion perception** is the ability to perceive movement in the environment. Evolutionarily, some species developed motion perception in order to identify dangers in their surroundings. Motion perception is possible through **delay circuits**, which detect and combine information regarding the same object. As an object appears to move in the receptive field, that object is perceived to be moving. **Akinetopsia** is the inability to perceive motion.

Like with vision, perception of other sensory information is complex and specialized. These different processes include sound perception, taste perception, touch perception, and odor perception.

## Attention

The world is overwhelmingly full of response-seeking sensory information. Consider a monkey inhabiting a forest. In any given moment, its environment may consist of different sounds (e.g., its mate's voice calling it towards them or the bustle of other animals in the distance), sight (e.g., the appearance of its predator coming towards it or the sight of fruit on a nearby tree), and touch (e.g., the feel of the tree branches on its hands or the dirt on its feet from walking on the ground). Researchers believe that most species are unable to perceive and respond to all of the sensory information in its environment. Instead, most species can only attend to a limited capacity of environmental information. **Attention** is the ability to focus on a particular stimulus at any given time. The two main regions in the brain associated with attention are the prefrontal cortex and the parietal cortex.

Therefore, among these competing sensory information, how do species navigate their environment in order to survive? For example, if the monkey is too focused on the other stimuli, it may not see the hungry eagle approaching. It may also perceive the other sensory information in a way that leads them to overlook the fruit on the tree or their mate for reproduction. **Selective attention** is the ability to direct attention towards task-relevant information while disregarding other irrelevant information (James, 1890). In other words, if the monkey is hungry, then it is able to attend to the fruit on the nearby tree. If the monkey wants to reproduce, it may be especially focused on listening to its mate. Attention helps species filter relevant information from their environment in order to perform adaptive behaviors.

In order to selectively attend to their visual surroundings, species need to shift their focus from one stimuli to another – thereby shifting their fixations. **Fixation** is the maintenance of visual gaze on a particular location. **Overt attention** is the ability to shift attention using eye movements (Goldstein, 2011). There are four types of eye movements: saccades, smooth pursuit movements, vergence movements, and vestibulo-ocular movements. **Saccade eye**

**movements** are rapid, ballistic movements of the eyes between fixation points. Saccades cannot be controlled. Contrastingly, **smooth pursuit movements** are much slower and involve steady movement. Smooth pursuit movements are controlled. **Vergence eye movements** focus the fovea of both eyes on nearby stimuli. Lastly, **vestibulo-ocular movements** help compensate for head movements and help stabilize the eyes in order to attend to environmental stimuli. Most animals rely on overt attention to attend to particular stimuli in their environment.

Additionally, species can focus on environmental stimuli through **covert attention**, or the ability to shift attention without eye movements (Goldstein, 2011). Researchers have created different attention models for humans, with varying degrees of **selection** – the process of focusing on relevant information from the environment – from early (Broadbent, 1958), intermediate (Treisman, 1964), to late (Deutsch and Deutsch, 1963). Regardless of these distinctions in selection, covert attention models involve perceiving the environment, filtering out irrelevant information, and isolating goal-appropriate stimuli. These covert attention models are based on human functioning, but they have been speculated to apply to other species (e.g., rats and monkeys).

**Attention span** determines how long a species can focus on a particular stimulus at once. Some species have relatively short attention spans (e.g., fruit flies with 3 seconds) while others can attend to stimuli longer (e.g., sparrows). On average, humans can focus on a particular stimulus for 8 seconds and can sustain attention on tasks from 5 to 20 minutes.

Sometimes, species need to attend to multiple stimuli in the environment in order to perform a task. For example, driving requires attention to the road ahead, to the signs and landmarks in the distance, and to other motor vehicles on both the left and right sides. **Divided attention** is the ability to focus on multiple stimuli at one time. Divided attention abilities differ depending on task difficulty and automaticity. It is easier to attend to stimuli that are relatively simple. For example, it is easier to attend to both a red circle and a blue square on a computer than it is to keep

track of three pots of food cooking simultaneously. Furthermore, it is easier to perform tasks that have frequently been performed in the past. However, humans have difficulty sustaining divided attention in order to complete multiple tasks at once, or multitask. For example, research shows that most driving accidents result from unsuccessful multitasking (e.g., driving and talking on the phone or driving and texting) (Dingus et al., 2006; Strayer and Johnston, 2001).

In addition to difficulty multitasking, humans have a tendency for **inattention blindness**, or perceptual blindness. **Inattention blindness** is categorized by a failure to attend to an unexpected stimulus in plain sight – often because one is focusing on something else in the environment (Mack and Rock, 1998). For example, in an attempt to count the number of ball passes during basketball team practice, one may fail to see a person in a gorilla suit walking across the basketball court (Simons and Chabris, 1999).

Another example of the limitations of attention is **change blindness** – or the failure to notice changes in a visual stimulus (Rensink, 2002). For example, when humans are shown a scene (e.g., a street) and are then shown a second image with minor changes (e.g., different street signs, different fire hydrant colors, different store fronts), they have difficulty identifying these modifications. Change blindness has also been observed in other animals including chimpanzees and pigeons.

## Memory

Most adaptive behaviors require information from previous stimuli or environments. Consider a bird searching its environment for food. The bird must be able to remember the type of food it eats (e.g., fruit), what they look like, where they are typically located, and how to procure them. Without this ability to remember information about its food, birds would have difficulty satisfying their hunger. **Memory** is the process by which information is encoded, stored, and retrieved. Evolutionarily, species use memory in order to navigate their environment, avoid dangers, and complete

tasks. Memory has been categorized in three forms: short-term, working, and long-term memory.

**Short-term memory** is a limited-capacity system responsible for storing small amounts of information over short periods of time, or up to 30 seconds. In short-term memory, information can be represented, or **coded**, in three different ways: auditory, visual, and semantic. **Auditory coding** is based on sounds (e.g., the sound of a partner's voice) (Conrad, 1964). **Visual coding** is based on an ocular representation (e.g., the image of a cat) (Kroll, 1970). Finally, information can be represented **semantically** (e.g., traffic report on a radio station) (Wickens et al., 1976).

How much information can be stored in short-term memory? In humans, researchers have tried to measure short-term capacity using **digit spans**, or the number of digits a person can remember for a short period of time. When presented with a string of numbers, humans can typically remember five to nine items (Miller, 1956). However, humans can maximize the amount of items in their short-term memory by **chunking**, or grouping individual units into larger ones (Miller, 1956). Consider the following digits, "123403221974." Instead of attempting to remember 12 individual digits, humans are better able to remember four groups: "1234," "03," "22," and "1974."

Unlike humans, many animals have smaller short-term memory capacities. Though they store useful information necessary for survival, they often forget everything else. For example, some studies suggest that dogs forget an event happened at all after 2 minutes. However, there are some animals with even better short-term memory than humans. For example, elephants can keep track of as many as 30 family members at once. Human short-term memory lasts as long as 30 seconds, whereas cats can last at least 10 minutes.

Similar to short-term memory, **working memory** also provides limited and temporary storage of information (Baddeley and Hitch, 1974). However, working memory manipulates that information in order to complete tasks such as reasoning and judgment (Baddeley, 2000). For this reason, working memory is considered a "mental workspace" because it also serves processing

functions. Consider the addition of two digits, 21 and 37. In working memory, not only are these two digits temporarily stored, but they are also used to complete the task at hand. Human working memory involves three components: the phonological loop, visuospatial sketchpad, and central executive.

In the **phonological loop**, the **phonological store** holds verbal and auditory information for a few seconds while the **articulatory rehearsal loop** is responsible for rehearsing this information (Baddeley et al., 1984; Baddeley, 2000). Rehearsal prevents decay, or forgetting, of that information. For example, the phonological loop is useful for remembering a person's name or phone number. The **visuospatial sketchpad** holds visual and spatial information (Shepard and Metzler, 1971). It is useful for maneuvering around an environment or solving a puzzle. Finally, the **central executive** is responsible for coordinating the phonological loop and visuospatial sketchpad as well as pulling information from long-term memory in order to accomplish the task at hand (Baddeley, 1996).

Finally, **long-term memory** is a system that stores relatively more information – compared to short-term and working memory – over long periods of time. It is difficult to determine the extent to which other animals have long-term memory. Consequentially, most long-term memory knowledge is based on human processing. The duration of time can entail a few minutes or as long as an entire lifetime. Long-term memory can be divided into two categories: explicit memories and implicit memories (Goldstein, 2011). **Explicit memory**, or declarative memories, is the storage of conscious information. It consists of semantic memory and episodic memory. **Semantic memory** is the recollection for facts and general knowledge. An example of this type of memory may include knowledge that the telephone was invented in 1876. On the other hand, **episodic memory** is the recollection of personal experiences. An example of this type of memory may include the first time one used a cellular telephone.

In addition to explicit memories, long-term memories can also consist of implicit memories.



**Implicit memory**, or non-declarative memory, is the storage of unconscious information. It is comprised of **procedural memories** – recollections for performing actions and tasks. Examples of procedural memories include chewing and biting, walking, as well as riding a bicycle or flying. Both humans and nonhumans have been shown to produce some form of procedural memories.

Information can be forgotten both in short-term memory and long-term memory. Because short-term memory storage has limited capacity, information can be lost through **displacement** – the process of pushing out current information in order to accommodate the new information. Forgetting long-term memory information can occur due to a lack of consolidation, or due to interferences or decaying. It is possible that the information was not adequately consolidated into long-term memory in the first place. For example, research shows that students who cram material for a test have more difficulty recalling that information during later tests (e.g., midterm or final) – assuming they did not try to study it again after initial testing. In addition, information in long-term memory may also be forgotten due to **interference** – when past memories interact with new memories.

Lastly, information can be forgotten in long-term memory through **decaying** – the fading of memory over time. This suggests that the more time that passes since the memory is recalled, the harder it is to recall in the future. Consider a word learned in a college Japanese class: *Hiru*. A student may easily recall the word for the quiz and even the final. He or she may even bring it up in conversation a couple years after college. However, the student may have difficulty recalling the word *Hiru* after 50 years.

## Language

**Language** is a system of communication involving meaningful symbols (e.g., sounds or gestures) (Goldstein, 2011). The ability to communicate with other members of one's own species serves a multitude of adaptive functions. For example, one may learn about potential dangers in an

environment or gain information about food and shelter. Additionally, language is useful when signaling a mate for reproduction. Language has been studied in humans as well as nonhumans.

Human language is comprised of five components: phonology, morphology, syntax, semantics, and pragmatics. **Phonology** is the study of sound. In language, **phonemes** are the smallest distinctive unit of sound. On the other hand, **morphemes** are the smallest meaningful units of language. **Morphology** refers to the study of morphemes – how they're formed and organized, as well as their relationship to one another. Morphemes can be prefixes, suffixes, roots, or individual words. Consider the following word, *car*. The three phonemes – “c,” “a,” and “r” – each produce distinct sounds. The whole word is considered one morpheme. However, consider the word, *carwash*. In this example, there are six phonemes: “c,” “a,” “r,” “w,” “a,” “sh.” Furthermore, *carwash* contains two morphemes: “car” and “wash.”

Additionally, human language involves **syntax** – a set of rules governing how words are sequenced. More specifically, syntax is the grammatical structure that dictates the order in which morphemes are combined. For example, syntax determines the arrangement of subject, verb, and object. **Semantics** refers to the meaning of the string of words. For example, *Jessica reads the book* and *The book is read by Jessica* have different syntax, but they are semantically the same. Lastly, **pragmatics** is the study of how context affects meaning. Referred to as the social language, pragmatics comprises of how species use language to interact with others. It entails what is said, how it is said, and the appropriate context in which to say it.

Humans develop language within the first years of their life (Gleason and Ratner, 1998). They can discern between sounds at 3 months old, and they begin producing sounds at 6 months old – also known as **babbling**. From ages one to three, they learn morphemes and syntax. By the time they finish grade school, children have rudimentary command of their language. Throughout their lifespan, humans continue to build on that language: longer morphemes, more complex syntax, and more advanced pragmatics.



Researchers have hypothesized the reason for language development. The three main theories of language development are the nativist theory, social interactionist theory, and learning theory. The **nativist theory** suggests that each human being is born with the capacity to acquire language. Noam Chomsky, a renowned psychologist and linguist, postulates that humans have a **language acquisition device** – an innate mechanism used for language acquisition (Chomsky, 1986).

However, some researchers do not believe language is developed innately. The **social interactionist theory** hypothesizes that language is developed as a result of social interactions. Interactionist theorists, such as Lev Vygotsky, believe children learn language by imitating and adopting words and rules used by adults (Gallaway and Richards, 1999). Consider the grammar mistakes toddlers make in their first years of language. They argue that children say “goed” instead of “went” because they are incorrectly imitating grammar rules of other words.

Finally, **learning theory** postulates that children acquire language through reinforcement. Learning theorists believe that infants are rewarded for communicating through language, which lead to repetitions of that behavior. For example, when infants communicate any variation of the word “mom” (e.g., *mah* or *mama*), they are rewarded with positive facial expressions (e.g., a smile) and gestures (e.g., a hug or kiss).

Is language unique to human beings? Remarkably, animals also engage in communication with members of its own species. **Animal language**, or animal communication, is the way in which nonhuman species use sounds and gestures to communicate with one another. However, researchers believe that animal language is different than human language. There are six properties that differentiate human language from animal communication: arbitrariness, discreteness, displacement, duality, productivity, and semanticity. Researchers have observed certain animals share some, but not all, of these language properties. However, it is difficult to confirm the capacity at which animals can and do use language. These are the following properties of human language:

1. **Arbitrariness:** In human language, there is an absence of any natural connection between the way a word sounds or formed and the word’s meaning. For example, the word *cup* does not give any indication of what a cup looks like or what it is. Overall, human language is arbitrary. Animal communication also possesses some arbitrariness. For example, chimpanzees are able to signal danger by vocalizing a sound, which has no resemblance to the meaning of danger.
2. **Discreteness:** Human language is comprised of a combination of small, distinct units. Furthermore, changes – no matter how minor – among these units create completely different meanings. For example, simply changing the “r” in the word *rose* to an “n” changes the meaning of the word from a type of flower to a body part responsible for smell. Similarly, bats are able to communicate with one another through different amalgamations of distinct sounds. Elephants have also been observed to have a variety of different distinct units of communication.
3. **Displacement:** Human language can be used to communicate about objects, place, people, events, or ideas that are not in the immediate time or space. For example, a friend can talk about their sibling who is studying abroad, a breaking news segment on the television the morning prior, or the concept of immortality and death. Animal communication can possess displacement. For example, bees engage in an intricate and special dance in order to communicate the location of food – its direction and distance from the hive.
4. **Duality:** Human language is comprised of meaningful words and sounds that can be broken down into meaningless units (e.g., morphemes into phonemes). For example, the word, *phone*, denotes significance, whereas “p,” “h,” “o,” “n,” and “e” do not have intrinsic meaning. Because human researchers have difficulty identifying which sounds constitute as language for animals, they are uncertain if animal communication also involves duality.
5. **Productivity:** Human language has the potential to produce infinite different meanings and messages by combining the elements

differently. For example, there are at least 200,000 words in the English language – alluding to the creation of a multitude of different sentences and phrases. Similar to duality, researchers do not know the number of elements involved in animal communication. Therefore, it is hard to determine whether or not animal language can produce infinite different meanings from these symbols.

6. **Semanticity:** Human language has a stable and specific relationship between signal and meaning. For example, the word *water* will always have the same connotation, regardless of whether it is said or spoken in Japanese, Spanish, or Swahili. Animals also have different signals that signify meaning. For example, certain species have distinct gestures to communicate with mates and signal reproduction. This may involve a vocalization (e.g., penguins engaging in a mating call) or performance of a behavior (e.g., peacocks showing feathers).

## Cross-References

- [Attention](#)
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- [Chunking](#)
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- [Equine Cognition](#)
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- [List Memory Effects \(Primacy and Recency\)](#)
- [Pinniped Cognition](#)
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## Cognitive Bias

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### Definition

Cognitive bias refers to a systematic (that is, non-random and, thus, predictable) deviation from rationality in judgment or decision-making.

### Introduction

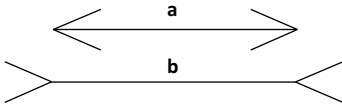
Most traditional views on human cognition propose that people tend to optimality when making choices and judgments. According to this view, which has been pervasive in many cognitive sciences (particularly Psychology and Economics), people behave like rational, close-to-optimal agents, capable of solving simple as well as complex cognitive problems, and to maximize the rewards they can obtain from their interactions with the environment. Generally, a rational agent would weight potential costs and benefits of their actions, eventually choosing the option that is overall more favorable. This involves taking into consideration all the information that is relevant for solving the problem, while leaving out any

irrelevant information that could contaminate the decision (Stanovich 1999). Whole research areas in social sciences have been built upon this assumption of rationality (see, e.g., the *Homo Economicus* theory in Economics).

However, this traditional view has been challenged in the last decades, in light of evidence coming from Experimental Psychology and related areas. Thus, a growing body of experimental knowledge suggests that people's judgments and decisions are often far from rational: they are affected by seemingly irrelevant factors or fail to take into account important information. Moreover, these departures from the rational norm are usually systematic: people fail consistently in the same type of problem, making the same mistake. That is, people seem to be irrational in a predictable way (Ariely 2008). Therefore, a theory that aims to model human judgment and decision-making must, in principle, be able to explain these instances of consistent irrationality or cognitive biases.

We can begin to examine the concept of cognitive bias by describing a similar, easier to depict, type of phenomenon: Visual illusions. Figure 1 represents a famous object configuration, the “Muller-Lyer illusion” (Howe and Purves 2005). The reader must observe the picture and decide which of the two horizontal segments, a or b, is longer.

In Western societies, most people would agree in that segment b looks slightly longer than segment a. In fact, despite this common impression, both segments a and b have exactly the same length. These segments only differ in the orientation of the adornments that round off the edges (i.e., “arrows” pointing inward or outward), which are responsible of creating the illusion that they have different lengths (Howe and Purves 2005). This example of a very simple visual illusion illustrates how people's inferences can be tricked by irrelevant information (the adornments), leading to systematic errors in perception. A similar situation can occur across a variety of domains and tasks, revealing the presence of cognitive biases not only in perception but also in judgment, decision-making, memory, etc.



**Cognitive Bias, Fig. 1** The Muller-Lyer illusion (Adapted from Howe and Purves (2005) by the author)

Typically, the consequence of cognitive bias is a form of irrational behavior that is predictable (because it is systematic). Cognitive biases have been proposed to underlie many beliefs and behaviors that are dangerous or problematic to individuals: superstitions, pseudoscience, prejudice, poor consumer choices, etc. In addition, they become specially dangerous at the group-level, since these mistakes are systematic rather than random (i.e., one individual's mistake is not cancelled out by another one's), leading to disastrous collective decisions such as those observed during the last economical crisis (Ariely 2009).

## Potential Causes

Traditionally, research on cognitive biases has tended to elaborate taxonomies, or lists of experimentally documented biases, rather than focusing on providing explicative frameworks (Hilbert 2012). Consequently, this is the way in which many textbooks and introductory manuals approach the topic: e.g., Baron (2008) lists a total of 53 biases in his introductory book to *Thinking and Deciding*.

Nonetheless, some authors attempted to offer coherent conceptual frameworks to understand what all these biases share in common and how they originate. Here, we list some of the approaches that have tried to account for cognitive biases: limited cognitive resources, influence of motivation and emotion, social influence, and heuristics. They will be examined in turn.

## Limited Cognitive Resources

First, an obvious explanation for many reported cognitive biases is the limited processing capacity of the human mind. For example, since people's

memory does not possess infinite capacity, we cannot consider any arbitrarily big amount of information when we make an inference or decision, even if all this information is relevant to the problem. Rather, we are forced to focus on a subset of the available information, which we cannot process in detail either. Therefore, in most complex problems, the optimal, truly rational solution is out of reach and we can only aim at "bounded rationality" (Kahneman 2003), that is, making the best decision after taking into consideration a limited amount of information. This explanation works well to explain certain instances of cognitive bias, such as the problems associated to thinking with probabilities. In particular, research has documented that people tend to neglect base rate information when making Bayesian inferences (i.e., a cognitive bias). However, the same problem is solved much more easily when it is formulated in terms of frequencies, rather than in probabilities (Gigerenzer and Hoffrage 1995). The calculations become simpler in the latter case just because of the more natural presentation format, and the bias seems sensitive to this manipulation.

## Emotion and Motivation

Another potential cause for at least some cognitive biases is emotion or affect. Traditionally, research on decision-making understands rationality as "formal consistency," conforming to the laws of probability and utility theory. Then, emotions are left out the rational decision-making process, as they can only contaminate the results. However, subsequent research shows that emotions play a substantial role in decision-making (Bechara and Damasio 2005) and suggests that without emotional evaluations, decisions would never reach optimality. After all, emotions are biologically relevant because they affect behavior: e.g., we fear what can harm us, and consequently decide to avoid it. Several cognitive biases could be explained by the influence of emotions. For instance, the loss-aversion bias (Kahneman and Tversky 1984) consists of the preference for avoiding losses over acquiring

gains of equivalent value, and it could be driven by the asymmetry in the affective value of the two types of outcomes. Other examples concern moral judgment. Many typical studies on moral judgment consist of presenting participants with fictitious situations such as the famous “trolley dilemmas” (Bleske-Rechek et al. 2010). In one simple variant of the problem, participants would be told that a trolley is out of control, barreling down the railways. Close ahead, there are five people tied up to the track. The participant could pull a lever to divert the trolley to a side track, in which there is one person tied up and unable to escape. Would the participant pull the lever? From a rational viewpoint, the utility calculus seems straightforward: it is preferable to save 5 people (and kill one) than the opposite outcome. Most people behave according to this utilitarian, rational rule. However, we know that the participants’ decisions in these dilemmas are sensitive to affective manipulations: for example, if the person who lies on the side track is a close relative of the participant (or their romantic partner), this would affect the decision (Bleske-Rechek et al. 2010). Therefore, emotions can drive some systematic deviations from the rational norm.

A related potential source of bias is motivation. Research has shown that people’s inferences can be biased by their prior beliefs and attitudes. That is, they can engage in motivated reasoning (Kunda 1990): when solving a task, they choose the beliefs and strategies that are more likely to arrive at conclusions that they want to arrive at. For example, participants who had to judge the effectiveness of gun-control measures to prevent crime exhibited biased processing of contingency information to eventually align with their initial attitudes toward gun control (i.e., “motivated numeracy”) (Kahan et al. 2012). This could explain many other instances of bias in reasoning and behavior.

## Social Influence

Certain cognitive biases could be produced, or at least modulated, by social cues. For instance,

Yechiam et al. (2008) examined the risk-aversion bias in a gambling task: typically, the bias consists of people preferring a sure outcome over a gamble of equivalent or higher value. Crucially, the researchers found that the bias was reduced when participants were observed by their peers. Other cognitive biases possess a more fundamental link to social cues. It is the case of the bandwagon bias, which describes the tendency of people to conform to the opinions expressed earlier by others, and which has strong influence in collective behaviors, such as voting in elections (Obermaier et al. 2015). So far, we do not know whether the contribution of social cues to this and related biases are due to people’s preference to conform to their peers or because people use others’ opinions as a source of information to form their judgments.

## Heuristics and Mental Shortcuts

Perhaps the most successful attempt to provide a coherent framework to understand cognitive biases is Kahneman and Tversky’s research program on heuristics (Kahneman et al. 1982). The rationale of this approach is as follows. First, making rational choices is not always feasible, or even desirable, for several reasons: (a) it takes time to effortfully collect and weight all the evidence to solve a problem; (b) it also needs the investment of lots of cognitive resources that could be used for other purposes; and (c) quite often a rough approximation to the best solution of a problem is “good enough,” whereas keeping on working to get the optimal solution is so expensive that it does not pay off. Therefore, the mind uses heuristics, or mental shortcuts, to arrive at a conclusion in a fast-and-frugal way. A heuristic is a simple rule that does not aim to capture the problem in all its complexity or to arrive at the optimal solution, but that produces a “good enough” solution quickly, and minimizing the effort. At this point, we can recover the example of the Muller-Lyer illusion that we described above, to realize that it can be explained as a heuristic-based inference. In real life, people’s visual system must handle three-dimensional



information to make inferences about distances and depth. This is highly demanding in terms of resources. However, the task can be simplified by looking for simple rules. Our cognitive system seems to interpret the visual input by making use of certain invariant features of the environment. In a three-dimensional world, two segments that converge at one point (as in Fig. 1) usually indicate a vertex (e.g., the edges formed by adjacent walls and ceilings typically display this configuration). The orientation of the edges can be used to predict whether the vertex is incoming (panel a) or outgoing (panel b) (first invariant). Furthermore, an edge far away from the observer will look smaller than one that is near (second invariant). In the real world that we navigate most of time, applying these two simple rules serves to correctly infer depth and distance, without implementing a costly information processing procedure. However, Fig. 1 is not a three-dimensional picture, and this is why applying the simple rules (heuristics) leads to an error or an illusion: incorrectly perceiving depth in a flat, bi-dimensional arrangement of lines and, thus, incorrectly judging the sizes of the segments. Nonetheless, Fig. 1 can be thought of as an exception, whereas most of visual configurations we see everyday actually confirm the simple rules, which explains why the heuristic is useful. In conclusion, as illustrated by the visual illusion example, judgment can be biased by the operation of heuristics that exploit regularities or invariants in the world. These heuristics are simple rules that can be expressed in an intuitive manner (such as “distant objects are seen smaller”) and need little time and effort to reach a conclusion (i.e., they are economic). While they lead to conclusions that approximate a good enough solution most of the times, they can also lead to systematic mistakes.

A great deal of experimental research has documented several heuristics that could underlie many cognitive biases. Perhaps the most famous ones are the representativeness heuristic, the availability heuristic, and the anchoring-and-adjustment heuristic (Gilovich et al. 2002).

**Representativeness** This heuristic is based on similarity or belonging and can be intuitively

formulated as “if A is similar to B (or belongs to group B), then A will work in the same way as B does.” That is, when an exemplar is perceived as representative of the group, all the features that are typical of the group are attributed to the exemplar. An example could be that of deducing that a given person is smart, just because he studies at the university or because he wears glasses. This heuristic can explain why people commit certain errors when solving Bayesian reasoning problems, such as the base-rate neglect (Bar-Hillel 1980).

**Availability** The availability heuristic is based on the ease with which a representation comes to mind. If a certain idea is easy to evoke or imagine, then it is incorrectly judged as likely to happen. A classical example is the reported overestimation of the likelihood of an airplane crash after watching a movie about airplane accidents. This heuristic can account for many common biases, such as recency bias: the piece of information that is the last in being presented is also the most easily remembered, and therefore it is usually weighted more heavily than other pieces of information, which can lead to serious errors in many domains (e.g., judicial). Another instance of the operation of the availability heuristic is the evaluation of near-win events: the fourth runner in crossing the finish line in a race often feels worse than the tenth one. This happens because this person can vividly imagine him/herself as being the third.

**Anchoring and Adjustment** This is sometimes considered as a special case of the availability heuristic. Knowing a tentative answer to a question is known to bias further attempts to answer (these answers become closer to the anchor). For instance, imagine that you are asked the question: “in which year did Albert Einstein visit the USA for the first time?”. Let us assume that you do not know the answer, so you must guess. Most people would pick up a number like “1950.” Now, imagine that you are given a tentative range of years to answer. Research shows that people who are given a range of 1200 to 2000 actually answer with lower numbers than those who are given a range of 1900 to 2000. Respondents seem to use



the range as a tentative response (anchor) and adjust their judgment away from it. The anchoring effect has been extensively studied in consumer behavior. For example, arbitrary numbers (i.e., the last digits of the participants' social security numbers) can act as anchors to affect the amount of money that participants are willing to pay in exchange for a series of items (Ariely et al. 2003).

A further elaboration of the heuristics approach is the dual-system theory of human cognition (Kahneman 2013). According to this theory, the mind has two working modes: System I is fast, intuitive, heuristics-based, automatic, and frugal, whereas System II is slow, rational, optimality oriented, and resource-greedy. People perform many everyday tasks under System I: when the task is easy, when we need a quick solution, or when an approximate solution (not optimal) is good enough. However, certain task demands can activate System II. For instance, manipulations that reduce cognitive fluency, such as presenting the problem in a nonnative language, can lead to more thoughtful, rational, and bias-free solutions (Costa et al. 2014).

## An Evolutionary Perspective

A complementary line of research focused on understanding why cognitive biases appeared in first place in the evolution course, by analyzing their associated benefits. Thus, the error-management-theory (Haselton and Nettle 2006) proposes that cognitive biases (produced by heuristics or by any other mechanism) were selected by evolution because they actually offer advantage for survival.

In ancestral environments, there is a pressure to make important, life-or-death decisions quickly (e.g., it is better to run away upon sighting a potential predator than to wait until it is clearly visible, but perhaps too close to escape). These conditions foster the development of decision mechanisms that (a) work fast and (b) produce the so-called "least costly mistake." In this example, it is better to mistakenly conclude that a predator is in the surroundings than the alternative, i.e., mistakenly conclude that there is no predator. We know this because the two errors

have very different consequences (it could be unnecessary waste of time in the former case and death in the latter) (Blanco 2016). Sometimes the least costly mistake is the less likely mistake, as it happens with the Muller-Lyer illusion above: most of times that we interpret colliding lines as three-dimensional vertexes, and as a cue to depth perception, we are right. In general, many cognitive biases seem to systematically favor the conclusion that aligns with the least-costly mistake, formulated in any of these ways.

Additionally, exhibiting certain cognitive biases can even produce other type of benefits, particularly in emotional terms. For example, one well-known cognitive bias is the illusion of control (Langer 1975), which consists of the mistaken belief that one can exert control over outcomes that are actually uncontrollable. The emotional consequences of this bias are noteworthy: a person who thinks that there is nothing that one can do to affect a relevant outcome might feel despair, or even depressed, for it is a sad realization that one has no control over his/her life. In contrast, those who develop the illusion of control (incorrectly) attribute to themselves any positive outcome that may happen, so they feel confident and safe. Furthermore, they will even feel motivated to keep trying and producing actions to affect the environment (i.e., the illusion of control produces behavioral persistence). In fact, evidence suggests that mildly depressed people are less likely to show the illusion of control (i.e., the depressive realism effect, Alloy and Abramson 1979), which highlights the connection between cognitive biases and positive emotions.

In sum, at least some cognitive biases (like the illusion of control) seem to be associated to positive outcomes, or to the long-run minimization of costly mistakes, that could have represented an evolutionary advantage for our ancestors. Therefore, the traits that underlie the bias would have been selected through our evolutionary history.

Nonetheless, the error management theory has been received with some skepticism. Admittedly, typical cognitive biases not always align with the least-costly mistake. For instance, the same bias that facilitates the quick detection of a hidden

predator (e.g., clustering illusion), thus protecting us from a serious threat, could also produce dangerous decisions in a different context, such as believing that a bogus health treatment, such as quackery, works (Blanco 2016).

## Conclusions

Cognitive biases have been defined as a general feature of cognition. As such, they are pervasive and can be observed in a vast variety of domains and tasks. Much has been studied about the impact of these biases on several key aspects of life. For example, cognitive biases could underlie highly societal issues, such as prejudice and racial hate (Hamilton and Gifford 1976), paranormal belief, or pseudomedicine usage (Blanco 2016), and more generally, the prevalence of poor decisions in many contexts, like consumer behavior (Ariely 2008).

Thus, it is not strange that researchers have tried to find out ways to overcome cognitive biases, a practice commonly known as “debiasing” (Larrick 2004; Lewandowsky et al. 2012). Different strategies have been used to develop debiasing techniques. Some are based on increasing the motivation to perform well (under the assumption that people can use normative strategies when solving tasks). Others focus on providing normative strategies to participants, so that they can replace their intuitive (and imperfect) approaches to a problem. Finally, other debiasing interventions take the form of workshops to improve critical thinking and reasoning skills.

One common obstacle that debiasing efforts have encountered is called the “blind spot bias” (Pronin et al. 2002): While people can readily identify biases in others’ arguments, they find it difficult to detect similar biases in their own judgment. This is why transmitting the scientific knowledge about how cognitive biases work (and which factors affect them) can be a useful tool to complement debiasing strategies. In sum, advancing in our understanding of cognitive biases is in the interest of all society (Lilienfeld et al. 2009).

## Cross-References

- Base-Rate Neglect
- Decision-Making
- Perception
- Problem-Solving
- Rationality

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## Cognitive Capacities

### ► Platyrrhine Cognition

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## Cognitive Control

### ► Rehearsal

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## Cognitive Ecology

### ► Equine Cognition

### ► Perissodactyla Cognition

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## Cognitive Empathy

### ► Discrimination of Emotion

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## Cognitive Flow

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## Synonyms

Optimal experience

## Definitions of Flow

Flow is a predominantly cognitive state of deep concentration and task absorption that makes a person feel one with the activity. Mihaly Csikszentmihalyi (1975/2000) identified flow in the early 1970s by interviewing surgeons, rock climbers, composers, dancers, chess players, and athletes and asking them to report their experience

when they engaged in the most challenging phases of their preferred endeavors. The interviews produced rich textual descriptions that shared six main themes: (1) focused *concentration* on the present activity, with centering of attention on a narrow stimulus field (e.g., “When I start, I really do shut out the world”), (2) *merging of action and awareness* (e.g., “I am so involved in what I am doing. . . I don’t see myself as separate from what I am doing”), (3) *loss of self-consciousness* (e.g., “I am less aware of myself and my problems”), (4) *sense of control* over one’s own actions (e.g., “I feel immensely strong”), (5) *unambiguous feedback* from the activity (e.g., “You don’t feel you have all sorts of different kinds of demands, often conflicting, upon you”), and (6) *autotelic experience*, that is, the sense that the activity is an end in itself, and hence runs independently of external rewards (e.g., “The act of writing justifies poetry”). Csikszentmihalyi named “flow” the simultaneous presence of these six components. Subsequently, Jackson and Csikszentmihalyi (1999) added three components to the definition of flow: *dynamic balance between challenge and skill* (e.g., “I feel just the right amount of challenge”), *clear proximal goals* (e.g., “I know what I have to do each step of the way”), and *loss of time-awareness or time acceleration* (e.g., “I don’t notice time passing”).

Dietrich (2004) has advanced the *hypo-frontality theory* to explain the effortless information processing that characterizes flow. The theory postulates the existence of two neural systems. The *explicit system* exerts the higher cognitive functions grounded in the frontal and medial temporal lobes, whereas the *implicit system* exerts the skill-based functions grounded in the basal ganglia. The former fosters cognitive flexibility, whereas the latter fosters efficiency. Based on the distinct functions of the two systems, flow would be a period during which a skill that has been acquired, practiced, and consolidated in the implicit system is deployed by the explicit system with no interference from the implicit system. The temporary suppression of communication between the frontal lobe and other regions of the brain can explain a number of components of flow,

such as the loss of self-consciousness and time-awareness.

There is an ongoing debate (see review by Swann et al. 2012) on two interlinked issues: (a) the set of components of flow, and (b) the separation between components of flow and other variables that may be functionally related to flow but are not indicators of flow. Regarding the first issue, positions range from assuming only one component of flow to assuming all above-listed nine components. Regarding the second issue, there are more than thirty definitional models of flow, each proposing a somewhat different partition of the nine components into antecedents of flow (i.e., factors that make flow more likely to occur or more intense), expressions of flow (i.e., components of flow), and effects of flow (i.e., consequences of having experienced flow).

## Models of Flow

The original flow model (Csikszentmihalyi 1975/2000) assumes that at any point in time of a challenging endeavor (e.g., an expert doctor performing a surgery or a chess master playing a tournament game), people assess the perceived challenges from the activity and the perceived skills in carrying out the activity, and update their perceptions depending on how well the activity is going. The model partitions the experience in the endeavor in three possible states – flow, anxiety, and boredom – that are represented as nonoverlapping areas of a challenge by skill Cartesian space. Flow occurs when there is an equivalent ratio of perceived challenges from the activity to perceived skills in carrying out the activity. Anxiety occurs when the perceived challenges from the activity exceed the perceived skills in carrying out the activity, whereas boredom occurs when the perceived skills in carrying out the activity exceed the perceived challenges from the activity. The model posits that the flow state is more likely to occur and is more intense when there is an equivalent ratio of perceived challenges from the activity to perceived skills in carrying out the activity, and both variables are high.

In the past two decades, researchers have modeled daily variations of subjective experience (e.g., concentration and absorption) over perceived challenges and skills as a linear process, and found robust support for the hypothesis that the balance of challenges and skills is key to flow, particularly in achievement contexts (e.g., Moneta and Csikszentmihalyi 1996). More recently, Ceja and Navarro (2012) argued that the variations of subjective experience at work – and hence the occurrence of flow – conform to *nonlinear dynamic models* and provided empirical evidence in support of their claim. Linear models assume that the change of outcome variables (e.g., concentration and absorption) as a function of the change of predictor variables (i.e., challenges, skills, and their relative balance) is smooth and continuous. In contrast, nonlinear models assume that as the system (i.e., the worker) departs from an equilibrium point its behavior will become increasingly unstable and turbulent to the extent that change in the outcome variable as a function of the predictor variables becomes abrupt and discontinuous. The simplest instance of such abrupt changes is provided by Ceja and Navarro's (2012) *cusp catastrophe model of flow*. The model states that the progress from a high-challenge/low-skill state to the high-challenge/high-skill state (i.e., the “flow zone”) is so turbulent that a minimal fluctuation of the levels of challenges and skills may result in either a sharp enhancement of subjective experience or a sharp deterioration of subjective experience, and the probability of either outcome is about 50%. This means that the path to the flow state is an inherently unstable process that could fail abruptly. Therefore, achieving flow at work comes at the cost of great variability of outcomes.

## Universality of Flow

The Flow Questionnaire (FQ; Csikszentmihalyi and Csikszentmihalyi 1988) was the first attempt to measure flow (for other measurement methods see Engeser 2012, and Fullagar and Delle Fave 2017). The FQ presents some of the most insightful descriptions of flow that emerged through

interviews and asks respondents whether they have ever had similar experiences. Research using the FQ in diverse samples – including blind nuns, former drug addicts, members of alpine communities, and professional surfers – from a wide range of cultures has shown that flow is a universal experience, although the specific activities that foster flow are shaped by culture and hence differ somewhat across cultures. Moreover, in all cultures flow is more likely to occur in work or structured leisure activities.

Flow was originally identified and operationalized as a state. Researchers have then conceptualized and operationalized flow also as a broad disposition, meant as the tendency to experience flow frequently and intensely across a wide range of situations, and as a domain-specific disposition meant as the tendency to experience flow frequently and intensely in a specific context such as work, study, or sports (Jackson and Eklund 2002). When measured as a state, a small percentage of respondents report never having experienced flow. When measured as a domain-specific disposition in twin studies, the heritability estimate of flow proneness is moderate in the domains of work, maintenance, and leisure and is explained by the same genetic factors across the three domains (Mosing et al. 2012). This implies that not all individuals will experience flow, and if the environmental opportunities and personal competencies/skills for flow exist, the more genetically predisposed individuals will be more likely to experience flow.

## Antecedents and Consequences of Flow

Individuals who are predisposed for experiencing flow also tend to have personality traits such as low *neuroticism* (i.e., a tendency to experience anxiety, moodiness, depression, vulnerability, and self-consciousness), high *conscientiousness* (i.e., a tendency to be self-disciplined, self-organized, hardworking, and “down to earth”), high *openness to experience* (i.e., a tendency toward unconventionality, intellectual curiosity, imaginativeness, aesthetic sensitivity, cognitive/emotional differentiation, and engagement of



experience), and *internal locus of control* (i.e., a tendency to believe that rewards and punishments are contingent on one's behavior) (Mosing et al. 2012). However, flow proneness is not associated with *intelligence* (Mosing et al. 2012).

Frequent and intense flow experiences are associated with better adaptation, coping, and subjective well-being across the life span (see reviews in Engeser 2012). Flow at work has been investigated across a wide range of occupations and organizational contexts, including scientists, medical doctors, software engineers, and school teachers (see reviews in Fullagar and Delle Fave 2017). The tendency to experience flow at work results in enhanced employee's psychological well-being and enhanced job performance, in general, and creative contributions to work, in particular. However, the link between flow and work performance is present only for individuals with high *achievement motivation* (i.e., a tendency to seek success in competition with a standard of excellence). In particular, only highly motivated employees utilize the flow zone (the combination of high challenge and high skill) to enter flow, and utilize flow to enhance performance.

## Directions for Future Research

Even though numerous traits have been linked with the occurrence of flow, a key question is still insufficiently addressed: Can one make flow happen at will? From the beginning, Csikszentmihalyi (1975/2000) postulated the existence of an "autotelic personality," one that pursues an activity purely because it is intrinsically rewarding. This personality was theorized to possess "metaskills," such as curiosity and persistence, which would enable the self-regulation (e.g., starting, sustaining, and modulating) of flow. Swann et al. (2012) conducted a systematic literature review of flow in elite athletes and estimated that 66–72% of athletes perceived flow to be controllable and useful for coping with the challenges of the competition. Recently, Wilson and Moneta (2016) developed and validated a questionnaire measuring *flow metacognitions* (i.e., people's awareness of and beliefs about the

flow state and its consequences, and about strategies for achieving and maintaining flow) and found that these allow employees to self-regulate flow at work. Because metacognitions have been shown to be modifiable through metacognitive interventions, this research development opens the possibility to coach individuals to use flow as a way of coping with demanding situations.

Even though flow was originally discovered as a solitary experience (Csikszentmihalyi 1975/2000), researchers have more recently found instances of "social flow," in which two or more interacting individuals experience interlinked forms of flow. For example, a crossover of flow between music teachers and their students was observed, which mimics the pattern of *emotional contagion* (e.g., an automatic tendency to converge emotionally). Moreover, the observation of jazz ensembles, improv theater groups, sport teams, and creative business teams has revealed that teams can develop and maintain "team flow" for the duration of a collective endeavor, and by capitalizing on continued team flow tend to produce more creative team output. These observations indicate that collective flow is highly enjoyable and builds up psychological resources at least as much as individual flow does. However, research has to date operationalized team flow simply as the sum of the individual flow states experienced by the members of the team and has hence ignored team-system dynamics. Future research should, therefore, examine the case of "autotelic teams," wherein team members feed each other to build the experience of flow interactively.

Finally, the construct of flow has been utilized to explain disruption of natural behavior in animals. In particular, it has been suggested that captivity may prevent the flow of behaviors that animals are motivated to perform, and eventually lead animals to disengage from their environment, experience a chronic state of boredom, and lose versatility of behavior and adaptability to the environment. Whether flow can be achieved in absence of metacognitions that can be verbalized is an open question that could be answered only by comparing flow-like neurophysiologic patterns in humans and animals. As neurophysiologic measures of flow keep being developed and



validated, future research will be able to evaluate the similarity of flow in humans and animals and possibly extend flow theory and its applications to animals.

## Cross-References

- [Consciousness](#)
- [Coping Style](#)
- [Domain Specificity](#)
- [Dynamic Systems Theory](#)
- [Emotional Contagion](#)
- [Heritability Estimate](#)
- [Heritability of Behavior](#)
- [Intelligence](#)
- [Stress](#)
- [Teaching](#)
- [Temporal Lobe](#)

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## Cognitive Functions

- [Platyrrhine Cognition](#)

## Cognitive Imitation

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## Synonyms

[Imitation](#); [Non-motor imitation](#); [Observational learning](#); [Social learning](#)

## Definition

**Cognitive imitation** is a type of social learning; specifically, a subtype of imitation that involves copying abstract – inferred – rules rather than observed – concrete – motor or oral responses.

## Introduction

Cognitive imitation is typically contrasted with other subtypes of imitation including, motor and

vocal or oral imitation. Like all forms of imitation, cognitive imitation involves vicariously learning and replicating specific abstract rules inferred from observation. The main difference between cognitive motor imitation, for example, is that whereas in the typical imitation learning experiment, subjects must copy representations of novel responses or sequences of specific actions (novel motor imitation), and in a novel cognitive imitation paradigm, subjects have to learn and copy abstract representations or rules. In such a paradigm, while the actions themselves may be familiar (e.g., pressing a button), the rule organizing those actions is new.

The following example illustrates the difference between cognitive and motor imitation: Imagine someone overlooking someone's shoulder and stealing their automated teller machine (ATM) password. As with all forms of imitation, in this example, the thief learns and successfully reproduces the observed sequence. The thief in our example, like most of us, presumably knows how to operate an ATM. As such, the actions associated with operating an ATM isn't what the thief is learning (or copying). Instead, the thief is likely to learn and copy one of two abstract rules: spatial or cognitive. For example, the thief may learn and subsequently copy the following spatial rule: touch the button in the bottom left, followed by button on the bottom right, then the button in the top right, and finally the one in the middle. This would be an example of motor-spatial imitation, because the thief's response is guided by an observed spatial rule. Alternatively, the thief may ignore the spatial patterning of the observed responses and instead focus on the particular markings on buttons (i.e., numbers) that were touched, generating the following abstract numerical (cognitive) rule: 7-9-3-5. Vicariously learning and reproducing this unobserved (inferred) rule to guide their response would be an example of cognitive imitation. Of course, this is not an ideal example because, in fact, unless you ask the thief, you would not know if they used a spatial or cognitive rule given that the numbers are in the same location with every attempt. However, if the numbers appeared in a new position every time you tried to enter the password – the thief using a cognitive rule would, nonetheless, reproduce the target password.

## Cognitive Imitation in Rhesus Monkeys

The term “cognitive imitation” was first introduced by Subiaul and his colleagues (Subiaul et al. 2004). In their original paper, they defined cognitive imitation as “a type of observational learning in which a naïve student copies an expert's use of a rule.” To isolate cognitive from motor imitation, Subiaul and colleagues trained two rhesus macaques to respond, in a prescribed order, to different sets of photographs (serial lists) that were displayed simultaneously on a touch-sensitive monitor. The position of the photographs varied randomly from trial to trial, preventing subjects from learning a series of motor-spatial responses (Terrace 2005). Both monkeys learned new sequences more rapidly after observing an expert monkey execute those sequences than when they had to learn new sequences entirely by trial and error. A microanalysis of each monkeys' performance showed that each monkey learned the order of two of the four photographs faster than baseline levels. A second experiment ruled out social facilitation as an explanation for these results. A third experiment demonstrated that monkeys did not learn when the computer highlighted each picture in the correct sequence in the absence of a monkey (“ghost control”), which suggests that monkeys, in contrast to human children (Hopper 2010; Subiaul et al. 2007, 2011), require an agent to motivate social learning.

## Cognitive Versus Motor-Spatial Imitation

Subiaul et al. (2012), using two computerized tasks that measure the learning of two abstract rules: cognitive rules (e.g., apple-boy-cat) and motor-spatial-based rules (e.g., up-down-right), have shown that there are important dissociations between the imitation of these two types of rules. Specifically, results have shown that while 3-year-olds successfully imitate cognitive rules, these same 3-year-olds fail to imitate motor-spatial rules (Subiaul et al. 2012). This dissociation is not because there is something inherently harder about learning spatial versus cognitive rules. A series of follow-up studies showed that

3-year-olds correctly recall spatial rules learned by trial and error following a 30s delay (Exp. 2). This result demonstrates that 3-year-olds' motor-spatial imitation problems are not due to difficulty learning new spatial rules in general. But perhaps, 3-year-olds have a problem learning vicariously from a model. To test this hypothesis, a follow-up study had 3-year-olds observe a model correctly touch the first item (e.g., Top Right) in the sequence, but then skip the middle item (e.g., top left picture) and, instead, touch the last item in the sequence (e.g., bottom left picture), resulting in an error. Upon making this error, the model said, "Whoops! That's not right!" This highlighted that the error was unintentional. This is a goal emulation learning condition, as the child has to copy the model's intended goal (top-right, bottom-left, top-left), rather than the observed (incorrect) response (top-right, top-left). In this study, 3-year-olds generated the intended (rather than the observed) sequence (Exp. 3). Three-year-old's success in the goal emulation condition excludes the possibility that 3-year-olds' motor-spatial imitation problem is due to difficulty vicariously learning (i.e., because of a lack of interest, failure to attend, problems inferring goals, etc.) a novel spatial rule from a model. Children's success in the goal emulation condition suggests that social learning may be achieved by social reasoning (inferring goals) and causal inferences (error detection), independently of any domain-specific imitation learning mechanism.

### Domain-Specificity in Imitation Learning

To further explore this dissociation between cognitive- and motor-spatial imitations, Subiaul et al. (2015) tested preschoolers (2–6 years) on a variety of learning conditions using the cognitive and motor-spatial tasks. Results demonstrated that there was no significant relationship between imitation in the cognitive and the motor-spatial task. Analyses showed that only age predicted improved imitation performance in each task. Moreover, children's ability to individually learn in each task by trial and error did not predict their ability to imitate those same rules in either task.

However, goal emulation in the motor-spatial task did predict imitation learning in the same task. This result is surprising because, children can infer the spatial rules from a model's error before they can imitate spatial rules (Subiaul et al. 2012: Exp. 3). The association between goal emulation and imitation in the motor-spatial tasks suggests that goal emulation scaffolds the development of imitation in the motor-spatial domain, but critically, it does not seem to do so in the cognitive domain. These patterns of results support the hypothesis that distinct cognitive processes underlie cognitive versus motor-spatial imitation.

### Cross-References

- ▶ Emulation
- ▶ Ghost Control
- ▶ Imitation
- ▶ Rational Imitation
- ▶ Recall
- ▶ Social Facilitation
- ▶ Social Learning

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## Cognitive Impenetrability

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### Definition

Cognitive impenetrability is a property of the basic information processes of cognition. If a process is cognitively impenetrable, then the operation of this process cannot be altered by changing the contents of mental representations (i.e., an agent's beliefs, desires, or goals). This is because the process is “wired in” and its operation must be explained by appealing to neuroscience.

### Introduction

Six decades after experimental psychology's cognitive revolution, it is now commonplace to find studies of animal cognition. In general, the term “cognition” is synonymous to “information processing.” Thus, theories of animal cognition are theories about how animals process information. However, cognitive theories also carry more technical and specific requirements. In particular, a cognitive theory distinguishes between the contents of mental representations and the information processing mechanisms that manipulate these contents. The core information processing mechanisms of cognition are called the cognitive *architecture* (Pylyshyn 1984). Pylyshyn (p. 30) defines the cognitive architecture as “the basic operations for storing and retrieving symbols, comparing them, treating them differently as a function of how they are stored (hence, as a function of whether they represent beliefs or goals), and so

on, as well as such basic resources and constraints of the system, as a limited memory.”

## Wired Cognition and Cognitive Impenetrability

One of the key characteristics of the cognitive architecture is that it is presumed to be largely innate, relatively permanent, and directly implemented by neural processes. That is, the architecture defines the properties of what has been called “wired cognition” (Magnani 2009). This is a fundamentally important property, because explaining the functioning of a component of the cognitive architecture requires an account of how the brain implements this component. Thus, by ultimately grounding a cognitive theory in an architecture, one converts a cognitive description into a cognitive explanation (Dawson 2013). The architecture is the bridge between cognition and the brain. As a result, for their cognitive theories to be explanations, researchers must identify the cognitive architecture.

## The Cognitive Penetrability Criterion

How does one defend the claim that some cognitive function is part of the architecture? One methodology, the *cognitive penetrability criterion*, is inspired by the architecture's “wired-in” nature (Pylyshyn 1984, 1999). If a function is part of the architecture, then it will not be affected by changes in cognitive content – changing beliefs should not result in a changing architecture. This means that the architecture is *cognitively impenetrable*. In contrast, if changes in cognitive content produce changes in the operation of the function, then the function is *cognitively penetrable*. “If a system is cognitively penetrable then the function it computes is sensitive, in a semantically coherent way, to the organism's goals and beliefs, that is, it can be altered in a way that bears some logical relation to what the person knows” (Pylyshyn 1999, p. 343). The architecture is *not* cognitively penetrable. Finding that a function is cognitively penetrable indicates that it is *not* part of the architecture.

In studies of human cognition, the cognitive penetrability criterion is used to validate claims that particular functions belong to the architecture. In general, this involves observing the operation of the function, then changing a belief that is semantically related to the function, and finally determining whether the operation of the function changes. If it changes in a fashion that is semantically linked to the changed belief, then the function is cognitively penetrable and is not part of the architecture. This paradigm has been used to challenge the claim that certain operations on mental images, like scanning, are not part of the architecture (Pylyshyn 1984). The cognitive penetrability criterion has also been used in the study of apparent motion to show that the processes that track the identities of objects in apparent motion are likely part of the architecture because they are not affected by changes in beliefs about whether objects are moving in depth or not (Wright and Dawson 1994). However, Wright and Dawson also show the processes that create the appearance of an object in illusory motion can be penetrated by beliefs about depth of movement and therefore are not part of the architecture.

Of course, the cognitive penetrability criterion is much easier to apply in the study of human cognition than it is in the study of animal cognition. This is because it is much harder to verify than one has manipulated the beliefs of animal subjects. However, animal investigations that parallel human experiments are possible. For instance, studies that support the claim that a particular animal behavior is controlled by instinct (and not by higher-order processing) help establish that the behavior is controlled by the architecture, given the view that instincts are examples of wired cognition (Magnani 2009).

Consider one notable example from the study of nest building by wasps. Ethologist W.H. Thorpe reviewed studies of nest building in a variety of animals, including wasps, and proposed that nest construction behaviors were controlled by an *ideal releaser* (Thorpe 1963). An ideal releaser serves the role of a cognitive representation. “The bird must have some ‘conception’ of what the completed nest should look like, and some sort of ‘conception’ that the

addition of a piece of moss or lichen here and here will be a step towards the ‘ideal’ pattern, and that other pieces there and there would detract from it” (Thorpe 1963, p. 22). With this type of theory, one would hypothesize that small damage to a physical nest, making it slightly different from the mentally represented ideal releaser, would produce behaviors that simply repair the damage to make the actual agree with the desired mental content.

However, this hypothesis is not confirmed by the behavior of the mud wasp *Paralastor* (Smith 1978). This wasp builds its nest by digging a hole in the ground, lining the hole with mud, and then building an elaborate funnel on top of the hole to keep parasites out. The funnel is a long straight tube, to which is added a marked curve; a large bell-shaped opening is attached to the end of the curve. Smith created a hole in the curve that the wasp added to the straight tube. Instead of causing the wasp to simply patch the hole as might be expected from the ideal releaser theory, this instead led the wasp to create a brand-new tube out from the hole in the curve, producing a second funnel structure built on top of the first. The irrationality of this behavior can be taken as evidence that this wasp’s nest building is cognitively impenetrable, part of the animal’s architecture, and best explained by appealing to sequences of instincts governed by stigmergy (Karsai 1999).

Researchers in animal cognition have access to other methodologies for supporting claims that particular processes are part of the architecture. These too rely on the assumption that if a process is cognitively impenetrable, then it is directly implemented by the brain; it is wired cognition. Thus, any techniques that can elucidate the neural mechanisms that instantiate specific information processing can be used to argue that this processing is cognitively impenetrable and is part of the architecture.

For instance, it has long been argued that a great deal of early human visual processing is cognitively impenetrable (Pylyshyn 1999), and this hypothesis is typically supported by grounding computational or cognitive models of visual perception in the neural circuitry of early vision (Marr 1982). This evidence is largely the product

of single-cell recording studies of animal brains. A variety of methods exist for studying how the brain implements many other cognitive processes, including learning, memory, and navigation (Kandel et al. 2013). It is reasonable to predict that this kind of evidence will more likely be used in the future to map the architecture of animal cognition than will be evidence collected using animal analogs of the cognitive penetrability criterion.

## Cross-References

- ▶ [Cognition](#)
- ▶ [Information Processing](#)
- ▶ [Instinct](#)
- ▶ [Nest Construction](#)
- ▶ [Neural Control of Behavior](#)
- ▶ [Representation](#)

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## Cognitive Map

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The notion of *cognitive map* has a more general meaning as a metaphor for relations in the experiences of life and a more specific meaning in terms of cognition of relations among spatial attributes. The general term was made famous by the American learning theorist Edward Tolman (1886–1959), who formulated the term *cognitive map* to mean cognition of relational aspects of experience (Tolman 1948). This term has seen a revival in the last decade, as a region of the brain intimately connected with spatial cognition, the hippocampus, was found to code another fundamental dimension of experience, that of time. The spatial meaning of the term cognitive map received a boost with the discovery of neurons in the hippocampus of rats that fire the most when the rat was at a particular place in its environment, an arena in a lab. This discovery of what are called *place cells* is attributed to behavioral neuroscientist John O’Keefe. The spatial notion, discussed most in rats, humans, and honeybees, continues to attract debate and controversy.

## Tolman’s Cognitive Map

While the examples that Tolman (1948) discussed in his famous paper on the cognitive map concerned movements of rats in space, his writing also made it clear that the notion was more general. Tolman (1948) wrote of the brain that “the central office is far more like a map control room than it is like an old-fashioned telephone exchange” (p. 192). Tolman reported that rats learn about what is where in space from exploring space without any motive to obtain anything. In one case, sated and un-thirsty rats wandered a Y-shaped maze and learned that water was in one arm while food was in a second arm. Later,



when the rats were made thirsty, they went to the water-containing arm on the very first trial, while hungry rats headed to the food-provisioning arm from the first trial. Work in Tolman's lab also showed that rats could learn the layout of a complex maze from wandering the maze for ten sessions without any rewards. Once these hungry rats found food at the exit of the maze on day 11, they made haste to wind their way to the exit the very next trial – they were if anything faster than rats that had been rewarded with food every time they found the exit of the maze – showing that they had learned the layout of the maze without reward, a phenomenon called *latent learning*.

Tolman thought that hesitant behavior in rats deciding which direction to take at a junction reflected the learning of spatial relations, the building of their cognitive map. Such hesitant looking behaviors are called vicarious trial and error. Systematic patterns of travel through a maze were thought to reflect a nonverbal form of hypothesis testing. If all the data on rats had not made the notion of cognitive map wide ranging enough, Tolman then wrote about various clinical and social phenomena in human behavior, such as fixations or displacement of aggression onto outgroups (Tolman 1948). It is clear that the cognitive map encompassed many aspects of life's experiences.

The nature of Tolman's cognitive map was left unclear. Even in its spatial sense, it was unclear what kinds of spatial relations were encoded. Only something of the connections between places was supposed. Perhaps one shortcut experiment suggested encoding of directions, although the study has been much criticized. In the starburst maze experiment, rats were trained to run a dog-legged path with three turns in it along a well-defined track to arrive at a goal. On a test, the usual path was blocked, with the rest of the maze transformed into an array of radiating tracks spreading from the central start platform. Most rats chose the track whose direction pointed most directly to the goal location. It is unclear from the experiment, however, what the rats had learned about the spatial properties of the set up. Instead of some map-like representation of the set up, they might have learned to aim at a

particular landmark located at the goal. Such a strategy of beaconing would not be considered as equivalent to using a cognitive map. Tolman wrote, again metaphorically, of narrow strip maps and comprehensive maps. The metric and Euclidean nature of the cognitive map only bloomed in the 1970s.

## Metric Cognitive Map

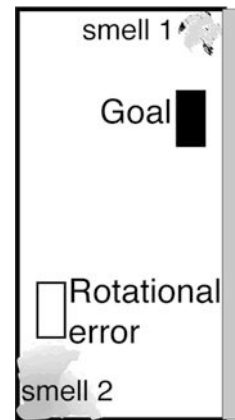
The term *metric* hails from formal geometry, meaning distances, angles, and directions, the properties that pop to mind most readily in intuitions of geometry. Metric properties make the stuff of Euclidean geometry, the typical geometry high school students would learn, perhaps in its algebraic form as Cartesian  $x$ - $y$  coordinates as well as the geometry of lines and points. A metric cognitive map was explicitly proposed in a classic and much cited book in 1978, *The Hippocampus as a Cognitive Map* (O'Keefe and Nadel 1978). Freely mixing philosophy of mind, neuroscience, and psychology, O'Keefe and Nadel (1978) likened the spatial representation of rats to having a topographic map of the environment.

A topographic map allows the traveler to plan a route of travel, to deal with unexpected obstacles, or to reorient after displacement. O'Keefe and Nadel (1978) called navigation using a cognitive map the *locale* system. The rat was said to possess as well a more route-like system of navigation called the *taxon* system. Using the taxon system is akin to following instructions cooed by the voice of the navigation aid in some cars, such as in 500 m, turn left onto X street. Or it could be like following the kind of route instructions scribbled on paper, such as go down X street; at the gas station, make a left turn; go to the next traffic light, then turn right. ... More formally, the taxon system consists of a to-do list for encountered stimulus situations. Gas stations and traffic lights define stimulus conditions; left and right turns define what to do. A rat might learn, more example, to turn left at the first junction of a maze from the start point, or to turn right when it encounters a white card on the wall.

The role of the hippocampus, as might be expected from O'Keefe and Nadel's (1978) title, is to subserve the locale system. O'Keefe is most famous for discovering neurons in the rat's hippocampus that fire the most when the rat is at a particular place in space, irrespective of how it got there or which way it is facing, the aforementioned *place cells*. O'Keefe won a share of the Nobel Prize in Physiology or Medicine for his work in 2014.

While place cells suggest suitable neurophysiology for encoding a map-like representation of space, it was unclear what characteristics the rat learns about space. In particular, it was unclear whether any metric properties were encoded. Gallistel (1990), in two substantial chapters in his influential book, suggested that many animals in fact encode metric properties. Spatial achievements that Gallistel wrote about included hoverflies that return repeatedly after excursions to just about the same point in midair, a location quite aptly described as the middle of nowhere. Gobies in tide pools sometimes find themselves in an isolated pool when the water level sinks low enough to create separated pools of water. The gobies can use some information of the topography to jump from one isolated pool in the direction of another pool. Gallistel devoted most pages, however, to the encoding of metric properties in the rat.

The study in question was one of this author's (Cheng 1986). The key clue to the use of metric properties was a curious mistake that rats often make in a rectangular-shaped arena (Fig. 1). In searching for buried sweet treats, the rodents would confuse diagonally opposite locations, a confusion called the rotational error. They did this even when many cues other than the shape of the arena, such as smells in the corner and different colored walls, disambiguated this mistaken rotational error from the correct goal. To make the rotational error, the distances and directions from surfaces had to be correct, although the relation to what can be called non-geometric cues, such as the nature of smells or the color of the surface, was incorrect. It was as if they had encoded distances and directions from walls and used only that information to locate the booty. In



**Cognitive Map, Fig. 1** Schematic depiction of the rotational error found in rats (Cheng 1986). Rats were searching for buried food in a rectangular dish, for example, at the location labeled “goal.” The goal location, to which they had been previously exposed, changed from trial to trial. Rats would often commit the error called the rotational error, at 180° rotation from the goal through the center of the space. Many disambiguating cues were arrayed around the walls, including different brightness levels (*white* vs. *black*), distinct panels in the corners (not shown), and distinct smells emanating from two corners. In making the rotational error, the rats were correct with respect to the overall shape (metric properties) of the space, but incorrect with respect to all the features (e.g., long gray wall) arrayed on the shape, colors, textures, and smells

later years, different interpretations of such studies on geometry emerged. For instance, the rat might be matching a panoramic view based on where major vertical and horizontal edges in space are. The hypothesis that the rat encodes distances and directions, metric properties, however, is commonly held.

Gallistel's (1990) conception of a cognitive map was encompassing. Any encoding of spatial relations amounted to a cognitive map. In a rectangular arena, the rat hardly travels anywhere: it is enclosed in an arena less than two meters long, whereas in real life in the wild, this rodent would travel hundreds of meters or kilometers. In Cheng's (1986) study – which stayed away from using the controversial term *cognitive map* – the rats learned to use surrounding cues to pinpoint a place. What was missing was using a map-like representation to plan new paths of travel. The next wrinkle in the concept of a cognitive map

was that an animal should be able to deduce a new, never-before-traveled path if it possessed a cognitive map.

## Cognitive Map, Detours, and Displacements

The test for such a deductive capability based on inferences from using a cognitive map is to displace an animal and see if it finds its way back. Let us say that the goal is at G; the animal has traveled to A, perhaps a feeder where food is usually found; and experimenters swoop up our test subject, disorient it, and plunk it at a distant site B. If the animal finds its way from B to G, and we could rule out other kinds of explanations, then it is warranted to attribute a cognitive map to our test animal. Such a test is not hard to do, but these other potential explanations make complications and brew controversy about the cognitive map.

The arguments have played out the most in a much-studied insect, the honeybee (*Apis mellifera*). Foraging bees routinely find their way back home from their foraging excursions. In their natural trips – as opposed to visiting an experimentally provided feeder with a bonanza of artificial nectar in the form of sugar water – they visit multiple flowers, typically in one vicinity often called a patch in the foraging literature. After filling up, they then fly directly home. Before a worker bee heads out foraging, she – all worker bees are females – flies a number of *orientation flights* to learn about her local landscape. On many of these orientation flights, she typically zooms out in one direction and then returns directly from that direction. Across different orientation flights, the budding forager would criss-cross many different directions from her hive. Displacement experiments have been conducted on free-flying honeybees over natural terrain, but the import of the results is disputed.

Chief among the alternative explanations are *path integration* and route following based on views of the scenery. Path integration means keeping track of the straight-line distance and direction of one's total travel. The continuing output of the path integrator is a vector pointing to the starting

point (typically home), that is, a distance and direction home. When the time to fly home comes, for example, when the crop is filled with nectar, the bee could fly off the calculated vector. Bees and ants have been much studied on this capability and demonstrate it ubiquitously. If a forager has flown 100 m East to a feeder, its path integrator should indicate a vector of approximately – the path integrating process, like all biological processes, gathers errors – 100 m West. If a worker relying on path integration were displaced, it would fly 100 m West. The path integration process does not account for passive displacement, whereas a cognitive mapping process should. The traveler would recognize where it is according to the scenery at the release point and plan according to where that location is on its cognitive map. The cognitive mapping bee should fly in the release-point-to-home direction.

Most of the early observations of the initial flights of such displaced bees support the path-integration hypothesis. The displaced bee trained in the hypothetical conditions of the previous paragraph would fly west initially. A different twist to the story turned up when the animals were tracked with harmonic radar over an open field. In this technology, a tiny antenna is attached to the back of the forager, and the radar tracks her *x-y* coordinates, delivering entire paths. After displacements from a feeder, yes, their initial flights were again in the vector direction indicated by path integration, which seemed to be a strong driver of initial orientation. Interesting results then transpired: after the vector had been flown, many bees would make their way either home or to the feeder again (Menzel et al. 2005).

Not everyone accepts the results of Menzel's team as demonstrating cognitive mapping in honeybees; in fact, currently most scientists studying insect navigation are in the nay-sayer camp. Their argument is based on the other main alternative hypothesis: view-based route following. View-based navigation is well established in insects, especially in ants. Ants without any vector from path integration – and experimenters create such a state in the ant by capturing it near home, making its vector effectively zero – routinely followed well-traveled routes home. The terrestrial view is

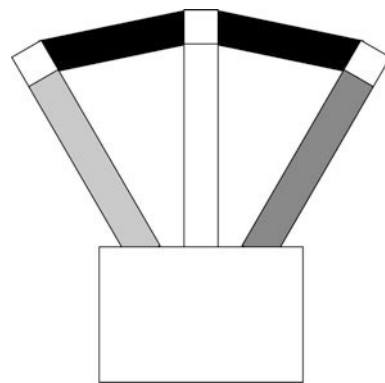
needed for such route following: when it is blocked, orientation is typically random. Such views have a certain *catchment area*, a term indicating an area wider than the typical route in which the view-matching strategy would work to steer the navigator home. Returning to the homing of displaced honeybees, these nay-sayers argue that the bees might have learned to associate a view found at a displaced site with a direction home. Even if they had not been to a displaced location before, the location is likely within the catchment area of some views they had learned. Recall that the forager would have flown in a number of directions around her hive before heading out to forage. If view-based route behavior is already well established in ants and bees, why invoke a new map mechanism? So argue the nay-sayers in calling for parsimony.

In the current state of the science, we are left with a logical and conceptual difficulty in interpreting such displacement results. In the test field of Menzel's team, the distant skyline might well be too low to be resolved by the eyes of the honeybees. But plenty of visual patterns are found on the ground of the agricultural site, such as ditches and different textures made by different plants. Something in the visual scene – or information in some other modality, but the visual scene is the most likely source – has to be recognized by the displaced bees or else navigation is impossible. This recognition process could feed either a route-like process or a map-like process, and at present, experimental techniques have not been used to try to untangle this conundrum.

The same conundrum applies to the idea of a map on a global scale – the term *map* typically coming without the cognitive accoutrement. The best case to illustrate the route versus map contrast is with sea turtles because the best data are available. Sea turtles have been shown to use magnetic cues of the Earth for navigation on a global scale. Thus, loggerhead turtles swim around the Sargasso Sea, a safe region for them in the North Atlantic. Experiments have been done displacing turtles virtually – young ones because full-grown ones are way too heavy to handle – to a place with different magnetic conditions. That is, scientists fabricated artificial magnetic conditions around the tank in which the turtles were swimming to

simulate another location on Earth. The turtles then navigated as if they had been displaced to the actual location on Earth that was simulated. The studies provide strong evidence that magnetic cues are used for navigation by the sea turtles (Putman et al. 2011). The scientists then point out that it is unclear whether a map-like mechanism is at play or something akin to route instructions. Do the magnetic conditions allow the turtles to deduce that they are now at longitude  $x$  and latitude  $y$ , on the basis of which the best direction to swim in would be  $\theta$ , or do they note that they are now under magnetic conditions  $\alpha$  and they have learned that when under conditions  $\alpha$ , swim in direction  $\theta$ ? This conundrum also remains unresolved.

Returning to rats, experimenters have more control over the travel experiences of lab rats, albeit in small arenas and mazes. Rats have been shown to cope with displacements in a map-like fashion with simple displacements effected by enforcing a new path of travel (Fig. 2). Singer et al. (2006) trained rats to travel down the right and left arms of their simple three-arm maze. Two of those arms, including the center one, contained



**Cognitive Map, Fig. 2** Schematic sketch of the setup used by Singer et al. (2006) to demonstrate a simple cognitive map in rats (not to scale). From the start platform (*big white rectangle*) during training, the rats could travel down the three long arms, each of which had different textural cues on its surface. Food was located at the ends of the center arm and one other arm (the left arm or the right arm). The connecting arms between the goal boxes at the ends of the arms (shown in *black*) were blocked. On a test after training, the connecting arms between goal boxes were open, and the rat was forced down the center arm. The question was whether the rats would take the correct connecting arm to the goal box that usually had food during training

food; the other arm was empty. In training, the connecting arms between the central arm and the side arms were blocked. Each arm had a distinct covering to make it identifiable as a place/route. After training, a test was given on which the entrances to the side arms from the start point were blocked. The untraveled connecting arms between the central platform and the side arms were opened. The rats had to travel down the center arm to get food, and the question was then whether they would know how to turn in the direction of the side arm that had been the second arm proffering food. The rats were 75% correct on the first test trial.

The astute reader would note that a path-integrating mechanism could in principle solve this task. Say the right and center arms contained food during the training. The rat would learn a vector, say, roughly  $30^\circ$  to the right from the center of the back wall. When on a test the rat was forced to go down the center arm, it was just a matter of path integrating to the right arm after an enforced detour. Desert ants handle this kind of enforced detour on their way home routinely. That path integration alone was insufficient was shown in a separate experiment in which the arms were not distinguished by distinct textures; they all looked and felt the same. For path integration, the texture and look of the arms, the routes of travel, should not make any difference. However, under conditions of identical looking and feeling arms, the rats were at chance on the test when they were forced to travel down the center arm first. The authors concluded that the rats learned a simple cognitive map.

While path integration alone seemed insufficient for Singer et al.'s rats, this process probably plays a role in building any kind of cognitive map. Path integration could supply  $x$ - $y$  coordinates, at least approximate ones, for distinct locations relative to a starting point such as one's home. Mapping might be a process of collating such coordinates onto a common frame.

On the other hand, failures at constructing a cognitive map based on separate views of the environment have also been shown in rats (Benhamou 1996). The study had rats swimming in a round pool to find a platform hidden just under surface level. Rats can swim well, but are

averse to paddling in the water, preferring to clamber onto a platform. The key question asked of the rodents was whether they could piece together different chunks of views around the pool into some integrated whole. The views were of parts of a normal lab room, decked with posters on walls, and outfitted with an array of desks, chairs, and cupboards. During training, a marquee was placed in the pool allowing only about one quarter of the view of the room from inside it. The desired platform was inside the marquee, always in the same place in the pool and in the room. Over different phases of training, the rats got to see different parts of the room from inside the marquee. On a test, they faced yet a new view inside the marquee with the contraption now offering bits of two previous separately viewed segments. Could the rats piece all the views together to figure out how to swim directly to the platform? Over several experiments, the rats failed miserably. Benhamou (1996) called his paper *No evidence for cognitive mapping in rats*.

Despite such limits, neuroscientists generally endorse a cognitive map for rats, based largely on a huge body of work probing the coding of spatial characteristics in the hippocampal formation, the network linked intimately with the hippocampus proper. The network contains, besides the already mentioned place cells, head-direction cells, which fire the most when the rat's head is facing a particular direction, and grid cells, which fire the most over a regular triangular grid of locations, among others (Cheng and Jeffery 2017). One recent variant of the cognitive map returns to Tolman's inclusive notion of the metaphoric cognitive map (Schiller et al. 2015). It now turns out that other cells in the hippocampus are sensitive to time rather than space, cells from the same hippocampal population. These cells fire the most at particular points in a sequence of events. The hippocampus then is thought to support a Tolmanian map that incorporates spatial, temporal, and likely other fundamental dimensions of experience.

In the studies addressing the rat's cognitive map, or spatial cognition in general, the spaces are tiny relative to the natural travel of rats. When released on a small rat-free island, male rats would wander all over the terrain, covering hundreds and



hundreds of meters. (Only males were released to ensure that no rat population would be established should the test animals evade trapping.) No studies have investigated their navigational mechanisms over such natural scales. In a classic study of wild rats in a suburban enclosure (Calhoun 1963), the rats established many routes around the enclosure and traveled much on routes. Far more studies of rats traveling on natural scales are needed to understand their navigation.

This piece on the controversy of the cognitive map will end with humans. Surely, big-brained *Homo sapiens* would possess cognitive maps, right? Even with humans, however, the case is less than clear-cut. Our metric estimates of space are often distorted and error-prone. One recent study using virtual realities shows that gross violations of the fundamental tenets of metric properties go mostly undetected by adult humans (Warren et al. 2017). The space was virtual: subjects donned immersive goggles that created their visual world. Virtual technology allowed tricks such as sudden displacements of subjects to be enacted without touching subjects at all, something impossible to do in physical space. In the crucial manipulation, the virtual worlds contained *wormholes*: when a traveler arrived at the middle of one wall in the square space, for example, she suddenly found herself at the middle of another wall, a 90° turn away. Subjects learned the object locations in the un-Euclidean wormhole-infested space just fine, as well as in a perfectly Euclidean wormholeless space. They used wormholes readily for routes and shortcuts, and only one participant mentioned anything strange about the wormhole-infested space.

The upshot was that Warren and coauthors suggested that humans encode a cognitive graph rather than a metric cognitive map. A graph contains knowledge of route connections between nodes on the map. It also contains rough local metric knowledge such as angles of junctions or distance to the next node. It allows some shortcutting and route planning, but falls far short of a globally consistent frame on which locations are plotted in *x-y* coordinates, an ideal of a metric cognitive map, the kind of topographic maps O’Keef and Nadel (1978) envisaged.

All in all, the notion of a cognitive map remains controversial for all navigating species, from insects to humans. Evidence for a metric cognitive map is disputed in all species discussed in this entry. Whether more clarity will emerge in the coming years remains to be seen.

## Cross-References

- ▶ [Arthropod Cognition](#)
- ▶ [Foraging](#)
- ▶ [Mustelidae Navigation](#)

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## Cognitivism

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Cognitivism in the study of nonhuman animal minds is the research area that presupposes that the behavior of nonhuman animals is sometimes best explained with reference to their internal cognitive states. Such states are often thought to be structured representations that are semantically evaluable (i.e., true or false, satisfied or unsatisfied). Cognitive explanations accordingly

involve computational processes that operate on these structured representations. These explanations are offered of phenomena that involve information processing, such as learning, memory, communication, problem solving, and tool use (Greenwood 1999). Cognitive explanations are *mental* explanations inasmuch as the dominant paradigm since the so-called cognitive revolution holds that the mind is a manipulator of representations. This description may remind the reader of the contemporary digital computer. As we shall see, this metaphor is not accidental but is instead central to the cognitivist paradigm.

One cannot properly understand cognitivism in the study of nonhuman animal minds (hereafter: “animal”) without understanding the cognitive revolution in psychology, and one cannot understand the cognitive revolution in psychology without understanding behaviorism, the received view against which cognitivism rebelled. It is thus with behaviorism that our story begins. Then we will turn to the cognitive revolution as a response to behaviorism, and only then will we be able to properly understand cognitivism in the study of animal minds. The tour finishes with two prominent challenges to cognitivism in the study of animal minds, the first being the historical challenge known as Morgan’s Canon and the second a contemporary update known as “the logical problem.” We will also look at some responses to these challenges.

## Behaviorism

In the early part of the twentieth century, the experimental methods of Wilhelm Wundt dominated psychology. For Wundt, experimental psychology meant the study of internal, conscious phenomena. These phenomena were available by a method of rigorously scientific self-observation or introspection. For the early behaviorists, the idea that an experimental science of psychology might be based on introspection was anathema. The behaviorists objected both to the introspective method and to the idea that psychology was the study of internal, conscious phenomena. Of course, these objections were connected. In

their attempt to make psychology a more scientific study, eliminating its reliance on introspective reports, behaviorists proposed to focus on the observable, namely, behavior. The goal of psychology, John Watson wrote in his 1913 Behaviorist Manifesto, is the “prediction and control of behavior,” and, as such, “introspection forms no essential part of its methods, nor is the scientific value of its data dependent upon the readiness with which they lend themselves to interpretation in terms of consciousness.” Watson went on to draw explicit connections between explanations of human behavior and explanations of animal behavior; he called for a science of psychology that treated human beings no differently than explanations of animal behavior treated animals. Just as we are unable to rely on an animal’s introspective testimony when we look for explanations of its behavior, so too should we not rely on a human being’s introspective testimony when we look for explanations of his or her behavior.

In fact, as we shall see, Watson’s move to think of animal behavior as similar to human behavior has multiple echoes in scientific attempts to understand and explain behavior. Watson was neither the first nor the last to argue that any differences between the explanations of human and animal behavior are differences in degree rather than in kind. Both Charles Darwin in the nineteenth century and Donald Griffin in the latter part of the twentieth century shared this perspective. Although, interestingly, as we shall also see, Watson’s challenge – that to treat animal and human behavior as having distinct causal origins is to fail to engage in rigorous scientific thought – has more in common with Darwin’s and Griffin’s detractors than with their supporters.

The idea that a psychological science can take as its subject matter intersubjectively unobservable data was rejected by the behaviorists. Instead, they advocated that psychology is best viewed as a science of behavior. Thus, behaviorism started with a rejection of introspection as an appropriate method for experimental psychology and with a rejection of internal conscious states as the appropriate subject matter of experimental psychology. The latter was replaced with behavior, external and intersubjectively

observable, and the former with the principle that any explanations of that behavior must themselves rely on intersubjectively observable events. Any useful or explanatory reference to mental or cognitive events can be translated into reference grounded in behavioral events. Any such reference that cannot be so translated is meaningless (Graham 2017; Greenwood 1999).

Instead of the sorts of internal states apparently found through introspection, behaviorists suggested that behavior be explained through histories of reinforcement and extinction patterns and by reference to environmental stimuli. To understand an individual’s history of reinforcement patterns related to a particular behavior is to understand why that individual persists with that behavior. Behaviorism is thus a kind of associationism. According to associationism – a theory of the mind historically attributed to David Hume (1738/1978) but often adopted in one guise or another by radical empiricists – ideas give rise to other ideas as a consequence of being associated with them, for example, because they co-occur. The same goes for behaviors. Associationism holds that when two events occur in proximity to one another, one tends to come to trigger the other. For the behaviorist an event becomes associated with a behavior, and thus the occurrence of that event comes to be the explanation for that behavior. For example, if a dog is given a treat each time it barks at a stranger, but not when it barks at an acquaintance, the pattern of rewards comes to explain why the dog barks at strangers, but not acquaintances. According to behaviorists, this sort of associationist explanation is not merely another tool in the box of possible explanations of human behavior; it is the primary, if not the only, tool in the box.

## The Cognitive Revolution

Even though behaviorism was a dominant research program in psychology (at least in the United States) from the second through the fifth decade of the twentieth century, two related factors spelled doom for this theoretical approach. The first was an alternative means of characterizing and explaining

human behavior: the emerging cognitivist approach. While both cognitivism and behaviorism postulated intervening variables in the explanation of behavior, behaviorism took these variables to be directly related to the exigencies of reinforcement, while cognitivism took these variables to be structured representations on which computations could be performed, which then yielded behavior. This proved to be a more powerful explanatory and research strategy. The other factor was a series of challenges to the orthodoxy of behaviorism. The most powerful and famous of these was Noam Chomsky's 1959 (reprinted in Chomsky 1967) review of B.F. Skinner's (1957) masterwork, *Verbal Behavior*.

By 1957, B. F. Skinner was the standard bearer for psychological behaviorism. *Verbal Behavior* was the culmination of 20 years of work (Palmer 2006). In it, he attempts to show how behaviorists can explain language use and comprehension. However, in a scathing review, Chomsky argued that the tools of behaviorism were inadequate to the task. Suppose a companion alerts Jones to the presence of a fox, by uttering the sound "fox." We might explain Jones's behavior (she looks for the fox, runs from the fox, or aims a rifle at the fox) by citing her past experiences of reinforcement related to the behavior she engaged in upon hearing the sound "fox." This explanation relies on there being previous instances of "fox" correlated with similar behaviors and with positive reinforcement. However, as Chomsky points out, the same behavior might occur without that history of hearing utterances of "fox" or of reinforcement. Chomsky's conclusion is that some other mechanism explains the behavior. There are similar problems with the behaviorist attempt to explain the production of language. Smith sees a companion step out into the street when a car is coming and yells, "watch out!" His companion jumps out of the way of the oncoming traffic. Are we to suppose that the explanation for Smith's yell is that the companion had previously reinforced that verbal behavior by jumping out of the way of oncoming traffic when Smith so yelled (and by failing to do so when he didn't yell)? Again, Chomsky concludes that the behaviorist explanation cannot be the complete explanation.

Chomsky's arguments were aimed specifically at the account of language put forward by Skinner in *Verbal Behavior*. One might take these objections to be limited to the domain of language, but as Chomsky noted several years later (1967), his unstated goal was to critique behaviorism more generally. It was in this spirit that his review was taken. His examples generalize nicely to other nonverbal behaviors. Consider Jones's response to utterances of "fox." Chomsky pointed out that Jones's behavior is predictable even without a history of reinforcement. More generally, if it is true that behavior is either random or explained by reinforcement, then novel behavior – behavior that, by definition (because it is novel), could not have been either reinforced or extinguished – should be random. In fact, much novel behavior is predictable. We would be surprised (to put it mildly) if Jones responded to "fox" by shaving her head, singing the national anthem of Greece, or begging for spare change. That is because we think that even though this may be Jones's first encounter with utterances of "fox," her behavior is caused by computations on structured internal representations that include a symbol related to "fox." Thus she might think, "In the presence of non-dangerous wild animals, look at the animal," and "A fox is a non-dangerous wild animal," and, consequently, she will look in the indicated direction.

This story – that with this one review Chomsky slew the Goliath that was behaviorism, what might be called the "origin myth" of cognitivism – is, of course, overly simplified. Even while behaviorism was the dominant research program in psychology, it was not the only research program; some psychologists continued to pursue studies of the human mind. In Europe, psychology never fell under the sway of the behaviorist hegemony. And some of the paradigm work of cognitivism predated Chomsky's review of *Verbal Behavior*. In his personal history of the cognitive revolution, Miller (1979) identifies a particular date as the birth date of cognitive science. This date, September 11, 1956, was prior to Chomsky's publication of his review of *Verbal Behavior*. (September 11, 1956, was the second day of an interdisciplinary conference at MIT.) Many of the

presenters at this conference are now recognized as the founding parents of cognitive science. One of these was indeed Noam Chomsky. Another was Miller himself, presenting his now famous research on “the magic number seven” on the limits and workings of memory (1956). Miller’s research was of foundational importance for cognitivism precisely because it showed that there was a structure governing internal processing. Similarly, the other work presented at the conference centered on the idea that the mind is an information processor (Bechtel et al. 1998). Moreover, while it is true that in the United States, behaviorism did wax and wane as the myth suggests, it has nevertheless remained a thriving discipline within psychology, even today, several decades after the cognitive revolution. Behaviorists today still reject Chomsky’s analysis of Skinner’s project (Palmer 2006).

In addition, the background against which this myth plays out, that behaviorism and cognitivism are competing and mutually exclusive paradigms and that the shift from one to the other is best described as a revolution are also misleading. Even those for whom cognitivist explanations in terms of operations on representations are the preferred mode of explanation of human behavior recognize that associationist explanations in terms of patterns of reinforcement are sometimes the correct explanations of human behavior. There is no inconsistency in holding that cognitive explanations are appropriate for some behavior and behaviorist explanations are appropriate for other behavior (Greenwood 1999).

Nonetheless, it is true that as a consequence of these developments, psychology took a turn toward cognitive explanations of human behavior. Rather than focusing on, say, patterns of reinforcement and extinction, these explanations focused on internal states including structured representations and the operations on these structured representations. It is worth emphasizing that the nature of the cognitive turn was not simply a rejection of the behaviorist doctrine that all behavior could be explained by patterns of reinforcement and extinction. Behaviorists were also willing to cite intervening, often internal,

variables. What made cognitivism stand out was the willingness to look to representations and other states as states that occurred between stimulus and response and the doctrine that those internal states were of explanatory import (Greenwood 1999). It is also worth noting in this context another factor that surely played a role in the move toward cognitivism: the rise of the computer age. A first approximation of the birth of the computer age could be taken to be the influential papers written by Alan Turing in the late 1940s, perhaps culminating in his (1950) *Computing Machinery and Intelligence* in which he proposes a general test for intelligence. The test is a behavioral test (if a human judge cannot discern a computer program from a human being, then the computer program is intelligent) and as such is firmly rooted in a behaviorist tradition that would describe intelligence as behaving in a particular manner. However, it wasn’t long before the computational metaphor, complete with its basis in operations performed on structured representations, began to influence the thinking of the new cognitivists. As Ulric Neisser (1988) observed, reflecting on those early days: “the computer had made a crucial contribution to psychology: It had given us a new definition of our subject matter, a new set of metaphors, and a new assurance.”

However, the cognitive turn was directed at explanations of human behavior alone. Watson’s (1913) call for treating human behavior as not explanatorily distinct from animal behavior was left behind in the move from behaviorist explanations to cognitive explanations of behavior. The implication was clear, if often unstated: we know that humans have internal representations (perhaps because introspection tells us this); however, we have no such evidence of the presence of internal representations in animals. (Chomsky was nearly explicit about this. He quotes Skinner’s claim that experimental work on animal behavior “can be extended to human behavior without serious modification” and spends much of his review arguing that such confidence is unsupported by both evidence and theory. As Palmer (2006) puts it, “Chomsky was betting that human verbal behavior is qualitatively different from the behavior of nonverbal

organisms; Skinner was betting that it isn't.") The division between animal and human behavior that Watson decried was once again alive and well in psychology.

## Cognitivism in the Study of Animal Minds

Watson wasn't alone in worrying about unscientifically supported attributions of psychological states. He was preceded in this by Conwy Lloyd Morgan. Morgan was not responding to the introspectionism of Wilhelm Wundt, as Watson did. Instead Morgan was motivated by what he saw as the weak anecdotal psychology of Charles Darwin and, more specifically, George Romanes. Darwin famously relied on anecdotes in his *Descent of Man* (1871) to conclude that there was a continuum of mental abilities between animals and humans. This is especially vivid in his discussion of emotions, where he writes of the anecdotes supporting the conclusion that animals engage in "long-delayed and artful revenge," of the happiness exhibited by "puppies, kittens, lambs, &c., when playing together." Even ants do not escape this anecdotalism: Romanes (1882) attributes no end of emotional fellow feeling to ants who act to remove impediments on other ants. They are, Romanes writes, "agitated," "perseverant," "fully informed," "sympathetic," and "excited" about the "rescue of" "their imprisoned comrade." Interestingly, in other moments, Romanes suggests that he'll adopt a much more cautious criterion for attributing mentality to nonhuman organisms: only consider those organisms able to make new adjustments in accordance with their individual experience, but instead of relying on this careful principle, he explicitly states that he is happy to rely on anecdotes, so long as they come either with the authority of "some name" or at least free from the possibility of "malobservation." It is not clear what he means by either of these criteria or why they should prevent the misattribution of mental states. Instead of following these criteria, Romanes seems to more closely adhere to a principle he cites, that if an inference from a particular behavior to particular mental

states is justified for one species, the same inference is justified for other species.

Morgan disagreed with both the anecdotalism and also, apparently, with Romanes's guiding principle. Rather than simply relying on comparative observations of behavior and deciding that if a piece of behavior is caused by mental states in the organisms of one species, then similar behavior is caused by mental states in the organisms of another species, Morgan offered his own canon in which he proposed that we be more careful in attributing psychological explanations.

In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale. (Morgan 1894, p. 53)

Perhaps the best example of an application of Morgan's Canon is also one of the most famous, namely, the case of "Clever Hans." Clever Hans was a horse who would apparently successfully add small numbers, counting out the solution with his front hoof and stopping when he reached the correct answer. However, it was discovered that Hans could only "add" correctly when accompanied by his trainer. The trainer would relax when Hans arrived at the solution. Apparently, Hans would detect the trainer's change in attitude and stop "counting." Thus we are presented with two competing hypotheses. According to the first, Hans was computing the answer to a simple problem in arithmetic. According to the second, Hans was merely responding to cues supplied by his trainer. Morgan's Canon dictates that we prefer the hypothesis that is the lowest "in the psychological scale." This is the second hypothesis, as it does not require us to believe that Hans was able to count, only to believe that Hans was sensitive to his trainer's cues. This is the conclusion that scientists at the time reached about Hans. (Notice that this may be different than the conclusion supported by Romanes's principle. According to that principle, if we would infer that a human being exhibiting similar behavior is genuinely counting, then we should infer that Hans is genuinely counting as well.)

Exactly the role that Morgan's Canon should play in evaluating phenomena such as exhibited in

the Clever Hans case is not clear. On the one hand, if Hans can only add when his trainer is present, then that suggests that he is not adding at all, but is responding to his trainer in some way. We can reach this conclusion without appealing to Morgan's Canon. On the other hand, maybe Hans is only interested in adding when his trainer is present. In such a case, Hans is able to add when his trainer is not present, but he simply does not want to. The presence of (and ease of devising) this alternative hypothesis suggests that some principle such as Morgan's Canon is needed to reach the conclusion that Hans is not adding, but is instead responding to cues from his trainer. We should continue to prefer the hypothesis that Hans is not computing sums because this hypothesis does not attribute to Hans the "higher psychical faculty" that is attributed to him by the other hypotheses. (There are other significant issues with Morgan's Canon. These are discussed below.)

It is worth noting that while Morgan's Canon seems to dictate that we explain Hans's behavior in some way other than by alluding to his ability to count, Morgan did not intend that the Canon rule out cognitive explanations of animal behavior. To the contrary, he firmly believed that some animal behavior was correctly explained in what we would now call cognitive terms. His goal was to ensure that such explanations were well founded, rather than based on vivid anecdote-based imagination. Despite this fact – that Morgan did not intend for his Canon to be used as an anti-cognitive cudgel – the combination of Morgan's Canon, behaviorism, and, more generally, the attitudes about animals expressed by Watson (1913) spelled doom for cognitive explanations of animal behavior (Greenwood 1999). Behaviorism teaches us that reference to cognitive states is unnecessary when it comes to explanations of human behavior. Morgan's Canon cautions us that we should always prefer lower explanations when such explanations are available. Since, according to behaviorism, there are always non-cognitive explanations available for human behavior, then it certainly seems to follow that there are always non-cognitive explanations available for animal behavior. Thus we should avoid cognitive explanations of animal behavior.

While Watson's attitudes about what counts as a reasonable explanation of animal behavior were explicitly directed at explanations of human behavior, they expressed a rejection of the idea that we would even consider explaining animal behavior in terms of mental states. Such explanations would, Watson implied, have to rely on introspective access to animal minds. Such access, unreliable in human beings, is completely absent in our investigations of and explanations of animal behavior. In tacitly endorsing this attitude toward animal minds, Watson was only the latest to rely on an argument that dated back at least to Descartes. Descartes (1637/1988) argued that language is the true, singular, mark of being minded. As animals are brutes (i.e., creatures incapable of language), they lack language, and thus they lack the ability to think. This argument, that language is required for thought, and thus that only creatures with language are capable of thought, is an appealing argument, as testified to by the fact that one can see it debated throughout the literature, even up to the present day (Allen 1992). Hume (1738/1978) supported the opposing hypothesis that the same explanations must be offered of the same phenomena whether found in humans or animals. As we have already seen, this hypothesis has a descendent in Romanes's thought, and it has echoes in contemporary scientific thinking about animal minds as well (Clatterbuck 2016).

Even when the yoke of behaviorism was lifted (as the myth goes), these prejudices about the proper explanations of animal behavior remained. So, even as founding ethologists such as Nikolaas Tinbergen and Konrad Lorenz carefully studied and reported on interesting behavior in various animals, they did not offer cognitive explanations of that behavior. It wasn't until Donald Griffin, already a well-established and respected scientist of animal behavior (elected to the American Academy of Arts and Sciences in 1952, founding Director of the Rockefeller Institute for Research in Animal Behavior in 1965), turned his attention to the study of animal awareness and consciousness in the middle 1970s (see, e.g., his 1976 publication) that the study of animal cognition became acceptable and cognitive ethology was born.



Griffin was well known as a hard scientist studying animal behavior (he was one of the scientists responsible for discovering that some bats use echolocation to navigate) when he published his book, *The Question of Animal Awareness*, in 1976. In this and in other works published at the time and in the following years, he argued that animals are conscious and that their minds should be the study of scientific investigation. This was truly the beginning of the cognitive revolution in the study of animal minds. It was only with Griffin's work that explanations of human behavior and explanations of animal behavior returned to the same realm: in both cases, cognitive explanations were now acceptable.

Of course, the history is not as straightforward as this suggests. For one thing, Griffin wasn't the first to discuss in print that animals were conscious. For example, Gordon Gallup (1970) suggested that the ability some chimpanzees apparently have to recognize themselves in mirrors suggest that they are agents with self-concepts, some of whose behavior may be best explained psychologically. Griffin may have been the most prominent researcher to endorse a positive attitude toward the possibility of animal consciousness and to encourage research in that direction. However, Griffin's suggestion that animals are conscious was met with significant hostility, even ridicule. Some scientists implied or even postulated outright that Griffin's suggestion was the consequence of an aging mind that was showing signs of dementia. Others took the suggestion seriously but argued that the evidence does not support cognitive explanations of animal behavior (see Bekoff and Allen 1997, for a catalog of different responses to the idea that animal behavior can be explained cognitively). Still, in some ways the debate about cognitive explanations of animal behavior was over before it gained any serious headway. Cognitive ethology quickly became a thriving area of scientific work. Fieldwork includes studies of communication (including alarm calls, warnings, informational calls, and differential responses to calls from different animals), learning, navigation, tool use, and cultural practices. By 1991, Carolyn Ristau, an expert in the behavior of piping plovers, reflecting

on the perspective afforded by the then well-established field of cognitive ethology, wrote that this shift in perspective led her to design experiments that she "had not otherwise thought to do, that no one else had done, and that revealed complexities in the behavior of the piping plover's distraction display not heretofore appreciated."

In addition to the growth in cognitively oriented fieldwork, there is a thriving practice of laboratory work, aimed at understanding how different animals understand the world. In addition to the areas just mentioned, this work includes studies focused on metacognition, language, and false belief tasks (Wimmer and Perner 1983). The literature on all of these is rich. A look at false belief tasks nicely reveals some of the debate in the field.

The false belief task is an experiment designed to show whether the subject recognizes that other individuals may have beliefs different from one's own. Anne may know that the cupcake is hidden in box 2, but Sally, who was out of the room when the cupcake was moved from box 1 to box 2, is unaware of this fact. Can Anne attribute to Sally the false belief that the cupcake is in box 1? If so, then Anne is able to draw a distinction between the belief she has (that the cupcake is in box 2) and the belief that Sally has (that the cupcake is in box 1). Doing so requires that Anne attribute to Sally beliefs different than her own. That is, if Anne is successful, she apparently thinks of other people as having minds. Anne is, in the parlance of the field, a mind-reader.

Versions of the Sally-Anne task, of false belief tasks, have been attempted with various animals (e.g., Hare et al. 2001). For example, in an ingenious series of experiments (one which has sparked many variations in animal experiment facilities around the world), Brian Hare et al. (2001) devised an experimental setup in which a subdominant chimpanzee is competing with a dominant chimpanzee for food. Generally, the subdominant will cede to the dominant in direct competition, but in this task, the more desirable food is hidden behind an occluding screen so that the subdominant can see it, but his dominant competitor cannot. If the subdominant attempts to retrieve the desirable food, then his behavior is an indication that he believes the dominant

chimpanzee is unaware that the desirable food is present. Like Anne in the false belief task, the subdominant chimpanzee seems to be attributing to the dominant chimpanzee, a belief that is different than his own. While the results of these and other related experiments are open to debate, the fact of the application of the task to nonhuman animals is a clear indication that Griffin's arguments have held sway: scientists are actively investigating the nature and extent of animal minds.

## Challenges to Cognitivism in the Study of Animal Minds

### Morgan's Canon

Or maybe the dominance of the cognitivist approach is not so clear. There is another way of looking at these issues. One way is, as suggested above, to notice that whatever the theoretical debate might be, Griffin's (1976) book has had a dramatic effect on the scientific study of animal behavior. But it has been 40 years and the debate has shown no signs of abating. From this other perspective, the criticisms of Griffin's book and of the cognitivist approach to understanding animal behavior are a reminder of the importance of adhering to Morgan's Canon. Those scientists who rejected Griffin's arguments were, once again, stressing the lessons learned from Morgan nearly a century earlier. Remember that, colloquially speaking, Morgan urged that we never attribute a higher-order psychological property when the behavior in question could be explained with a lower-order property. A natural way to interpret Morgan's Canon is as a proscription against loosely attributing psychological states to animals simply on the basis of anthropomorphism (as did Romanes and Darwin). Instead we ought to do so only on when the evidence demands such attributions. On this reading, Griffin's critics are objecting that when Griffin argues that animals are conscious, he is violating Morgan's Canon by opting for explanations that attribute to animals more advanced psychological states than the evidence actually demands. According to this picture, the field is divided between those who

would loosely attribute cognitive states to animals and those who are more careful to attribute those cognitive states only when no other explanation of their behavior is available.

The situation is not as straightforward as this description suggests, however. Start with the fact that any behavior taken on its own can be explained non-psychologically. For example, as discussed above, verbal behavior is taken to be the paradigm of an expression of internal psychological states. But some behavior that looks a lot like verbal behavior – the behavior of parrots, both human and avian – does not warrant a psychological explanation. This suggests that it is never the case that the only available explanations of a piece of behavior are psychological. But, on the other hand, even Morgan himself thought that some animal behavior warrants a psychological explanation. This presents a conundrum: if no behavior demands a psychological explanation, but Morgan thought that some behavior is best explained in psychological terms, then Morgan's understanding of his own Canon must have been different than the contemporary understanding (according to which Griffin is going too far by loosely attributing cognitive states to animals when the evidence did not force him to do so).

If we are to rely on Morgan's Canon as a principle guiding scientific inference, we ought to take a closer look at exactly what it asks of us and why. Which psychological properties are higher and which are lower? What is the basis for this implicit scale of psychological properties? And, perhaps most important, why should we avoid attributing higher-order properties when we could explain behavior by appealing to lower-order psychological properties? The most common interpretations of Morgan's Canon are that it is an appeal to parsimony or to simplicity. Perhaps Morgan is urging us to avoid attributing psychological states to animals when we don't need to. Or perhaps he is urging us to avoid overly complex explanations. Both of these seem like good goals.

Most endorsements of Morgan's Canon cite it as an application of parsimony (e.g., Vauclair 1996). We should prefer those explanations that avoid needlessly postulating entities that are

not required to account for the evidence. But one needs to be careful when wielding the shears of parsimony. Postulating that Hans is able to count only adds entities to our ontological ledger sheet when in doing so we are attributing to Hans abilities that we don't think he already has and when the alternative explanation does not involve attributing to Hans abilities that we don't think he already has. That an explanation cites cognitive states does not on its own make the explanation non-parsimonious. Consider an explanation of your friend's smile when she sees you. Perhaps she's happy to see you. Or, perhaps her smile is a conditioned response to your smile, and she has no emotions whatsoever. We don't reject the first explanation on the basis of parsimony; even though it relies on cognitive states absent from the second explanation, it does not rely on cognitive states that we do not already think to be present in your friend. Sometimes the parsimonious explanation is the one that cites cognitive states. If we know that Hans wants to please his trainer, then we might prefer to explain his behavior by talking about that desire to please (a desire which attributes to Hans the second-order state of thinking about his trainer's state of mind) rather than by talking about his ability to count. Because Morgan's Canon suggests that we prefer the non-cognitive explanation, but parsimony sometimes favors the cognitive explanation, Morgan's Canon is not an application of parsimony.

Another common interpretation of Morgan's Canon is that it is an appeal to the desideratum that explanations be simple (e.g., Shettleworth 2012). Unlike appeals to parsimony, which are grounded in the idea that the explanation that accounts for the data while postulating the fewest additional elements to our ontology is the explanation most likely to be correct, appeals to simplicity are grounded in the idea that the explanation most likely to be correct is the simplest. But when it comes to explanations of animal behavior, why should we think that explanations that appeal to psychological properties are simpler than explanations that do not appeal to psychological properties? Certainly some psychological explanations are more simple than some nonpsychological explanations. For example, suppose we were to be deciding

between the following explanations of Hans's behavior: the cognitive explanation that attributes to Hans the ability to count and the non-cognitive explanation that relies on a science fiction fantasy in which a nefarious neurosurgeon is controlling Hans's behavior by means of a remotely activated receiver placed in Hans's brain. In this case, the cognitive explanation seems simpler. Simplicity on its own does not recommend non-cognitive explanations over cognitive explanations. At the very least, we need grounds to think that non-cognitive explanations are somehow simpler than cognitive explanations.

The defender of Morgan's Canon might respond that Morgan himself has provided such grounds. Morgan justified his Canon with appeals to evolution by natural selection. Thus the idea is that we can categorize explanations as higher or lower with the support of evolution. We can think of this as an intuitive appeal to the idea that as evolution proceeds, organisms grow more complex and able to pursue more complex goals by more complex means. Human beings have complex representations, some of our closest relatives may have simpler representations, and animals distantly related to us have even simpler representations or no representations at all. But, as detailed in many recent attacks on Morgan's Canon in the philosophical literature (e.g., Fitzpatrick 2008), this picture is not supported at all by the current thinking about evolution. First, this way of thinking about evolution places human beings at the pinnacle of evolutionary progress, but neither is evolution a progression nor is there any pinnacle toward which evolution might progress. Nor are human beings any more advanced than any other species; each species is evolutionarily fit for its own niche. It follows from this that there is no support from evolution for a naturalistic idea of a psychological scale on which "higher" and "lower" might be placed. Second, the idea that evolution moves from simplicity to complexity is undermined by the evidence. Evolution within a species can be described as fitting a general trend according to which members of the species move from being less fit for a particular niche to more fit for that niche. This evolutionary change sometimes involves moving from a less complex

trait to a more complex trait and sometimes involves moving from a more complex trait to a less complex trait. Finally, there is no reason to think that more complexity is less simple, that organisms with complex representational abilities developed those abilities out of simpler representational abilities.

On the whole, due to arguments such as these, Morgan's Canon is out of philosophical fashion at the moment. If a challenge to the application of the cognitivist perspective to the study of animal minds relies on Morgan's Canon, then that challenge seems unlikely to succeed. However, there is another similar argument that has proved to be important in contemporary debates about animal minds: The Logical Problem.

### The Logical Problem

Unlike Morgan's Canon, which relies on an unstated principle about the nature of scientific reasoning and which seems to depend on a misunderstanding of the nature of evolution by natural selection, the logical problem makes an explicit appeal to simplicity/parsimony and makes no assumptions about the nature of evolution. The argument, originally made by Povinelli and Vonk (2003), targets the mind-reading literature, but, as we will see, it can be easily extended to experimental results in other domains.

Remember that mind-readers are individuals some of whose behavior is predicated on an inference about what another individual is thinking. Povinelli and Vonk point out that mind-reading is a two-stage process. The mind-reader must first observe the behavior of the individual whose mind is being read and then infer that the behavior signifies a particular mental state. That is, every individual who is a mind-reader is also a behavior-reader. But it follows from this that to attribute to an individual the ability to mind-read is to attribute to that individual the ability to do two things: read minds and read behavior. Thus, the logical problem is: if we can explain an individual's behavior by postulating that she is a behavior-reader, why postulate that there is also something else that she can do? Because there is no need to postulate that she is a mind-reader, any theory that makes that claim is going beyond what the evidence demands.

Notice that while Povinelli and Vonk's argument is directed at postulations of mind-reading ability, it can be easily generalized to bear on any similarly cognitive explanation of animal behavior. The cognitivist claims that between stimulus and response there is an additional step involving the manipulation of representations. In the mind-reading case, the cognitivist claims that the subject animal forms a representation of another animal's mental state, but Povinelli and Vonk object that there's no reason to suppose that the subject's behavior is mediated by a representation of the other's mind when it might be caused simply by a representation of the other's behavior. But why stop there? In a case involving learned or habitual behavior, we might ask a similar question: why suppose that the behavior is caused by a representation of the state of affairs the animal is responding to when the state of affairs might simply trigger the behavior via an associationist mechanism? (This was the behaviorist insight.) But why stop even there? When an animal does something apparently truly novel – e.g., a crow bends a stick to use as a tool to fetch food – isn't that novel behavior composed of behaviors that were rewarded individually? If we have to postulate the existence of those prior rewarded behaviors in order to explain the current novel behavior, then Povinelli and Vonk's argument supports the objection that we are postulating two intervening steps – the prior rewarded behaviors and a structured representation – when only one such step is needed. Once we have made this observation, we can see that Povinelli and Vonk, while they are avoiding the kinds of claims that bedevil Morgan – claims about higher and lower and about evolution of mental traits – are in fact providing an update of Morgan's Canon. As their argument seems to generalize to all cognitive explanations, and it favors explanations that are non-cognitive, purely on the basis that the cognitive explanations are, from a logical standpoint, needlessly complex, they are providing a sound basis for rejecting cognitivism in favor of explanations that do not cite cognitive states. And, like Morgan, they may not view themselves as giving an argument against cognitive explanations of animal behavior. Instead, they are providing a criterion for those

explanations: when we appeal to cognitive states in our explanations of animal behavior, we must not do so when our explanations include non-cognitive states which could explain the behavior just as well. The logical problem is that the cognitive explanations cite both cognitive and non-cognitive states in the explanation of some behavior when only one (the non-cognitive) is required for explaining the behavior in question.

The logical problem arises whenever we attempt to explain an instance of animal behavior; for every cognitive explanation of an instance of animal behavior, there is always a simpler non-cognitive explanation that cites fewer states. The central response to this challenge has been to accept that the logical problem arises whenever we attempt to explain an instance of animal behavior but to point out that the logical basis of the challenge shifts when we shift our attention from one instance of animal behavior to many instances. For example, Call and Tomasello (2008) argue that while it may be simpler to think that an animal is reading behavior when it acts as if a conspecific is threatening (rather than reading the behavior and inferring that the conspecific is occupying a particular mental state), but when it comes to all of the different behaviors an animal may have to read – threats, food-sharing behaviors, food-hoarding behaviors, mating behaviors, mating-avoidance behaviors, etc. – it can turn out to be simpler to postulate that the animal is engaged in mind-reading. That is, one mind-reading faculty can be useful in responding to a great variety of behaviors, while the animal without the mind-reading faculty would need a behavior-reading faculty for each of the different behaviors. Similarly, Saidel (2018) argues that Povinelli and Vonk make a mistake similar to one that Morgan makes: treating an animal's behavior in isolation from its other behaviors and from what else we know about the animal may enable us to explain the behavior more simply than we otherwise would, but it also forces us to miss the full picture. It is the full picture that ought to move us to accept or reject a cognitive explanation of the animal's behavior. These are by no means the only responses to the logical problem. These responses make it clear that Povinelli

and Vonk have stirred a healthy debate and that their objections have done nothing to slow the study of animal cognition nor the appeal to cognitive states in order to explain animal behavior.

There are other challenges to cognitivism, both in the study of animal minds and in human psychology. Some researchers who have grown out of the cognitivist tradition (and who consequently reject behaviorism) object to the idea that behavior is best explained by appealing to structured representations. According to many of these thinkers, the traditional computer metaphor for the mind has led our theories astray. Others think that the cognitivist approach is too focused on the mind that even while it pursues the scientific study of the mind, it does so from a perspective that owes too great a debt to dualistic intuitions about the relationship between the mind and the body. Instead, they propose that if we think about the mind as essential part of the body, we will come to a different and better understanding of the mind. In spirit, though, these challenges are products of the successes that cognitivism has brought, in the studies of both human and animal minds, and as such, they are testimony to the power and success of the cognitive revolution.

## Cross-References

- ▶ [B.F. Skinner](#)
- ▶ [Behaviorism](#)
- ▶ [C. Lloyd Morgan](#)
- ▶ [Clever Hans](#)
- ▶ [Donald Griffin](#)
- ▶ [Morgan's Canon](#)
- ▶ [Ockham's Razor](#)
- ▶ [Parsimony](#)
- ▶ [Theory of Mind](#)
- ▶ [Turing Test](#)

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## Coitus

### ► Intromission

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## Collaborative Hunting

### ► Cooperative Hunting

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## Collarbone

### ► Clavicle

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## Collateral Behavior

### ► Schedule-Induced Behavior



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## Collection

► [Assemblage](#)

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## Colobine

► [Catarrhine Locomotion](#)

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## Colonial Nesting

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Many animals breed at spatially restricted sites in relatively close proximity to others of the same or a different species. Colonial nesting is especially widespread in birds, insects, and spiders and can often involve unrelated individuals breeding in high density. Some bird colonies consist of up to 200,000 nests, while spider colonies can reach >50,000 individuals (Brown 2016). Colonial nesting confers three major benefits to individuals (Alexander 1974): (1) predators may be better avoided by increased vigilance, active defense, or a statistical reduction in the per capita likelihood of being a victim; (2) food-finding can be enhanced by observing where other colony members forage, cooperatively hunting, or (in rarer instances) active signaling as to the whereabouts of food; and (3) nesting sites that are safe from predators or provide otherwise appropriate nesting substrate are limited within the landscape. Colonial nesting in most species is thought to have evolved in response to one or more of these benefits, although there is still debate as to the relative importance of each (Danchin and Wagner 1997; Brown and Brown 2001).

Individuals nesting in colonies also experience costs associated with high-density breeding. Two universal ones are an increased likelihood of

contracting parasites or disease from other group members and increased competition for resources such as food, nesting sites, or mates (Alexander 1974). Other costs that apply in some species include a colony's increased conspicuousness to predators and a greater likelihood of misdirecting parental care to unrelated offspring (via extra-pair fertilizations or parasitic egg laying in nearby nests) (Brown and Brown 2001). These costs are thought to be severe enough to prevent colonial nesting in many species and are presumably overcome to various degrees by the advantages of grouping in species that are colonial.

Habitat selection appears to drive colonial nesting in some animals (Danchin and Wagner 1997; Safran et al. 2007). When settlers are naïve about the quality of breeding habitat, they may be attracted simply by the presence of other animals at a site, and in these cases colonies form as different individuals respond in the same way to the same social cues. In other cases, animals assess the reproductive success of residents at a given site and, when success is predictable between years, may use that information to select that same site the next season.

Most species that live in colonies exhibit substantial variation in colony size, with size often varying by several orders of magnitude within the same population (Brown 2016). Colony size variation may be genetically based at least in part, with individuals preferring colonies similar in size to where they were born (Brown and Brown 2000) and reflecting individuals' sorting among colonies (based on life-history traits, morphology, or behavioral propensities) to find the social environment to which they are best suited. Colony size variation is maintained in some species by fluctuating directional or stabilizing selection that alternately favors individuals in different group sizes and causes a range in colony sizes to persist over the long term (Brown et al. 2016). In other species, the costs of dispersal, reliance on imperfect information about site suitability, and collective nonrandom movement by individuals can also lead to colony size variation (Brown 2016).

Colonies often consist of collections of individuals with different behavioral tendencies or "personalities." For example, individuals

sometimes forage most successfully if their colony contains both aggressive and nonaggressive phenotypes (Keiser and Pruitt 2014). The relative proportion of different personality types may affect group dynamics and ultimately individual fitness (Bergmüller and Taborsky 2010; Pruitt et al. 2013) and thus may be important in the evolution of colonial nesting more generally.

## Cross-References

- ▶ [Central Place Foraging](#)
- ▶ [Costs of Group Living](#)
- ▶ [Extra-Pair Copulation](#)
- ▶ [Fitness](#)
- ▶ [Group Living](#)
- ▶ [Life History](#)
- ▶ [Natural Selection](#)
- ▶ [Optimal Group Size](#)
- ▶ [Social Facilitation](#)

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## Color Change

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Color change in animals is a taxonomically widespread type of phenotypic plasticity, in which the body coloration of an individual is altered over the course of seconds, minutes, days, seasons, or a lifetime. This within-individual change can be induced by external (e.g., social interactions) or intrinsic factors (e.g., circadian rhythms), may or may not be adaptive, and may or may not be reversible. Color change can refer to a change in the spectral reflectance of the entirety of an individual's body, only a small portion of the body surface, or anything in between, including changes in patterns or mottling of all or part of the body surface. Adaptive color change can serve a variety of functions, such as thermoregulation, communication, and camouflage. Mechanisms of color change are nearly as diverse as the types of color change themselves, illustrating a diversity of evolutionary strategies converging to achieve similar goals. Color change can influence the persistence of animal populations in an increasingly anthropogenically altered world by differentially affecting key life functions, including predator avoidance, thermoregulation, and mate attraction, in human-altered habitats.

## Types of Color Change

Animal color change can be broadly grouped into two categories: morphological and physiological. Both morphological and physiological color

change rely on a diversity of pigment cells (chromatophores), particularly in ectotherms. Chromatophores include melanophores (brown or black pigment), xanthophores (yellow), erythrophores (red/orange), and iridophores (iridescent), among others. Blue and some green colors in animals are typically produced structurally (e.g., via diffraction gratings or crystal fibers). Some animal colors are produced by a combination of pigments and structural colors.

Morphological (chromogenic) color changes are driven by the creation or degradation of pigments and the number or type of chromatophores, which effectively alter pigment concentration in the skin. Morphological color change can be reversible or irreversible. Long-term cyclic changes, such as seasonal increases in melanin that permit improved solar heat absorption in snakes during colder months, are common examples of morphological color change. Most ontogenetic color changes, which occur as individuals age, are also examples of morphological color change, though these tend to be irreversible changes associated with accruing sexual coloration or altering coloration to maximize camouflage from juvenile to adult habitats.

Physiological (chromomotor) color changes occur much more rapidly, in seconds to minutes, and are typically driven by the dispersal and reaggregation of pigments in chromatophores or by rapid changes in the orientation and consequently the light reflectance of crystalline plates. Mechanisms of physiological color changes have been well studied in lizards. The rapid dispersal of melanin following stressful social encounters in many *Anolis* lizards produces a color change from green to brown within seconds (Greenberg 2002). The structural colors of *Urosaurus* lizards likewise change rapidly: reducing the spacing between adjacent iridosomes decreases long-wavelength radiation scattering, which increases “blueness” of abdominal tissue with temperature (Morrison et al. 1996).

A third class of animal color change could be considered behavioral, as it relies on the choice of an individual to utilize substances to alter its coloration. Greater flamingos, for instance, produce carotenoid-rich oily secretions that are actively

spread over their plumage as “makeup” during mating seasons (Amat et al. 2011), and bearded vultures stain their plumage with iron oxide from soil, likely to advertise dominance (Negro et al. 1999). Though mechanistically distinct, these behaviorally driven color changes appear to serve similar roles in species’ ecologies as do morphological and physiological color changes.

## Functions of Color Change

Color change can provide a wide variety of adaptive functions. Though not all color change is adaptive (e.g., color change induced by pathogen or parasite infection), color change can serve innumerable beneficial roles related to survival and reproduction across animal taxa. Change in color, brightness, and pattern of an animal’s body surface is widely used for predator avoidance. The circadian rhythm-driven color change of horned ghost crabs evolved to optimize background matching in both day and night lighting conditions. Many cephalopods rapidly alter their coloration and pattern to provide maximum concealment via either background matching or disruptive coloration to mask their body outline, depending on the substrate. Predation pressure is not the only force selecting for camouflage-related color change; crab spiders utilize color change to conceal themselves within inflorescences of variable colors to deceive their prey (Anderson and Dodson 2015). In lieu of camouflage, some species use color change to deceive predators or prey via mimicry: for example, the dusky dottyback (*Pseudochromis fuscus*) can alter its coloration to mimic that of surrounding schooling fish and thereby increase prey capture success while simultaneously reducing detection by its own predators (Cortesi et al. 2015).

A variety of species exhibit body coloration changes over maturation. Juveniles of some lizard species bear bright tails to direct predator attacks to a more expendable body region, whereas adults lose bright tail coloration as their activity patterns and habitat use (and concomitant selective pressures) change with maturity. Ontogenetic color change can also be used as a strategy to avoid

mating harassment. Some female damselflies (*Ischnura senegalensis*) use immature-specific coloration to deter costly male attention, wearing “mature” colors only at sexual maturation (Takahashi et al. 2012).

Short-term alterations in social state are often conveyed by reversible changes in color. Chameleons, a lizard group popularly recognized for their color-changing abilities, rapidly darken their skin to communicate subordination in male-male contests or heighten conspicuous coloration during courtship and male combat (Stuart-Fox and Moussalli 2008). Male cichlids (*Astatotilapia burtoni*) alternate among blue, yellow, and cryptic color morphs depending on hormone concentrations associated with success in agonistic encounters (Korzan et al. 2008). Other social functions of color change include, but are not limited to, seasonal mate advertisement, mating or parental status, and honest indicators of quality or parental ability. Due to the speed and reversibility of physiological color change, many of these messages are conveyed to conspecifics in real time.

Color change is also widely used to protect individuals from abiotic pressures. One important abiotic selective pressure driving color change is solar irradiation. Many species evolved color change as a protective mechanism against excessive heat absorption (in which colors tend to lighten to maximize reflectance) and to permit more rapid warming in cooler temperatures (in which colors tend to darken). For example, some *Uca* fiddler crabs adjust carapace brightness depending on temperature as a thermoregulatory mechanism. Photoprotection is another abiotic driver of color change. Some species, such as the Kerry spotted slug (*Geomalacus maculosus*), increase melanization in response to ultraviolet light exposure to reduce the risks associated with ultraviolet radiation (O’Hanlon et al. 2017).

Color-changing species may experience conflicting color optima, particularly in species in which coloration is used both for crypsis and communication. In the western rainbow fish (*Melanotaenia australis*), subordinate males that darken their body coloration for substrate matching subsequently experience greater attacks from dominant male conspecifics, as increased

melanization is also used to communicate dominance in this species (Kelley et al. 2016).

Despite its advantages, the ability to change color can also be physiologically costly. Pigments are either derived from the environment (e.g., carotenoid pigments obtained from food) or synthesized directly (e.g., melanin), either method involving energy expenditure. For example, guppies induced to change color require greater food intake compared to those not induced to change color (Rodgers et al. 2013). In addition, some pigments required for color change are also used for other vital functions, namely immunity, exacting a potentially costly trade-off.

## Animal Coloration and Global Change

How global change interacts with animal color change will increasingly become a focus for investigation. Though color change can provide individuals with the ability to respond to natural abiotic and social changes in their habitats, if and the extent to which color change enables species to cope with anthropogenic stressors is unclear. New evidence suggests that some color-changing species may fare particularly poorly due to mismatch with current climate patterns. The white-brown springtime fur transition of snowshoe hares (Zimova et al. 2016) is now asynchronous with the current timing of the seasonal melting of snowpacks and has demonstrable fitness costs; these observations are likely repeatable in species that similarly evolved seasonal snow-related camouflage. With increasing average global temperatures, species that use color change for thermoregulation may likewise experience costs. Body color lightening in lizards for thermoregulatory purposes can conflict with body color darkening for camouflage, leading to a sub-optimal balance between thermoregulation and predator avoidance as habitats warm globally. When body color lightening is a sexually selected trait used primarily during courtship, as it is in *Uca* male fiddler crabs that temporarily lighten their carapaces during mating displays, natural selection for lighter carapaces for thermoregulatory benefits in a warming world could reduce the

strength of sexual selection for lighter carapaces, with unknown population-level consequences. Anthropogenic stress can also strongly affect color-changing sexual signals, as illustrated by the duller sexual colors of European tree frogs following exposure to traffic noise (Troianowski et al. 2017).

## Cross-References

- [Camouflage](#)
- [Communication](#)
- [Cryptic Coloration](#)
- [Disruptive Coloration](#)
- [Intersexual Selection](#)
- [Thermoregulation](#)

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## Color Perception

- [Cognition](#)

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## *Columba livia*

- [Pigeon \(Columbidae\)](#)

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## Combination

- [Recombination](#)

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## Combining Ability

- [Diallel Design](#)

## Common Ancestor

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### Definition

“Common ancestor” is defined as an ancestor shared by two or more descendant lineages, or we can describe in other way as an ancestor that they have in common.

### Introduction

“**Evolution by natural selection,**” which is one of the best theories of Darwin, is supported by evidences from a wide variety of scientific disciplines, including paleontology, geology, genetics, and developmental biology (Darwin 1859). This theory says that all the species are related to one another like sisters, cousins, and distant kin in a vast family tree of life. Another strong idea given as Darwin’s postulates was under development: the “cell theory.” According to this new theory, the cells were the most basic units of life. From these two powerful theories of Darwin, there emerged the idea of a single organism that should represent the universal ancestor of all living beings. We can say that all life on Earth has arrived from one common ancestor whose descendants underwent divergent selection; thus we would find common ancestors between ourselves and every other living organism (Pontzer 2012). But exact origin of modern human being is still a topic of debate. Thus the existence of a common ancestor to all living organisms in Earth is an outcome of Darwin’s idea of common ancestry.

### Miocene Epoch

Who is our “real ancestor”? This question would always be a topic of debate. To understand this

we need to understand the process of evolution and from what sort of animal we have evolved from!

**Miocene Epoch**, which is the major division of the Neogene Period (23 million years to 2.6 million years ago) that extended from 23 million to 5.3 million years ago. It is often divided into the Early Miocene Epoch (23 million to 16 million years ago), the Middle Miocene Epoch (16 million to 11.6 million years ago), and the Late Miocene Epoch (11.6 million to 5.3 million years ago) (The Editors of Encyclopaedia Britannica 2018).

In the Early Miocene Epoch, fossil apes were associated mainly with forest environments, and they were pronograde arboreal slow climbers and with some indications of terrestrial behavior, particularly the larger species. Thumbs in their hands were long and opposable, and the phalanges were curved. In the early Middle Miocene Epoch, the apes were still monkey-like in their body posture and were associated almost entirely with non-forest, deciduous woodland habitats, with increasing evidence of terrestrial adaptations. Hand proportions remained the same. Toward the end of the Middle Miocene (12 mya), some fossil ape species had broadened chests, long clavicles, medial torsion of the humerus, and repositioning of the scapula to the back (Andrews 2019). These adaptations may have been linked with more upright posture, as in the living apes, but unlike them, the hand phalanges were short, robust, and less curved, and the thumb remained long. Associated environments were deciduous woodland rather than forest. This body plan was retained in part in some later Miocene apes (10 Ma); some of which also had more elongated limbs and hands (thumb length not known) and hind limbs modified for greater flexibility. Other Late Miocene European apes had adaptations for living on the ground, and some of these also shared characters of the skull with orangutans. They were associated with more open deciduous woodland habitats. This body plan and environment were retained in the early hominin, *Ardipithecus ramidus*, but with a more robust postcranial skeleton and incipient bipedalism.



## Early Hominins

**Hominin**, any member of the zoological “tribe” Hominini (family Hominidae, order Primates), of which only one species exists today – *Homo sapiens* or human beings. The term is used most often to refer to extinct members of the human lineage, some of which are now quite well-known from fossil remains: *Homo neanderthalensis* (the Neanderthals), *Homo erectus*, *Homo habilis*, and various species of *Australopithecus*. Our immediate evolutionary family is comprised of the **hominoids**, the group of **primates** that includes the “lesser apes” (siamangs and gibbons) as well as the “great apes” (chimpanzees, bonobos, gorillas, and orangutans). Among the great apes, our closest relatives are the chimpanzees and bonobos. The fossil record, along with studies of human and ape DNA, indicates that humans shared a common ancestor with chimpanzees and bonobos sometime around six million years ago (mya).

The human-chimpanzee last common ancestor (HC-LCA) is the species from which the **hominin** lineage and the chimpanzee and bonobo lineage diverged. Hominins are species on our branch of the hominoid tree after the split with the chimpanzee and bonobo line, including all of the extinct species and evolutionary side branches.

Although the evolution of hominid features is sometimes put in the framework of “apes vs. humans,” the fact is that humans are apes, just as they are primates and mammals. The other apes – chimpanzee, bonobo, gorilla, orangutan, and gibbon – would not form a natural, monophyletic group (i.e., a group that includes all the descendants of a common ancestor), if humans were excluded. Humans share many traits with other apes, and those other “apes” (i.e., non-human apes) don’t have unique features that set them apart from humans. Humans have some features that are uniquely our own, but so do gorillas, chimpanzee, and the rest. Hominid evolution should not be read as a march to humanness (even if it often appears that way from narratives of human evolution). Students should be aware that there is not a dichotomy between humans and apes. Humans are a kind of ape.

Much discussion in human paleontology surrounds the evolution of a bipedal, upright stance. When and why did this occur? One thing to keep in mind is that “bipedal” and “upright” are not equivalent terms. An animal can be bipedal without having a vertical backbone. It seems clear from the fossil record of hominids that habitual bipedality preceded the evolution of a recurved spine and upright stance. Other changes in the gait, such as how the relatively “splayed” gait of chimps evolved into the gait of humans, who put one foot directly in front of the other, involve studying the hip joint, the femur, and the foot.

### Australopithecus Afarensis

This species is one of the best known of our ancestors due to a number of major discoveries including a set of fossil footprints and a fairly complete fossil skeleton of a female nicknamed “Lucy” (Johanson and McHenry 2018). These are the earliest members of the genus *Australopithecus*, hominins which were adept terrestrial bipeds but continued to use the trees for food and protection. *Australopithecus afarensis* is usually considered to be a direct ancestor of humans. This species lived between 3.9 and 2.8 million years ago. *Australopithecus* means “southern ape” and was originally developed for a species found in South Africa 1924 (Dart 1925). This is the genus or group name, and several closely related species now share this name. The word afarensis is based on the location where some of the first fossils for this species were discovered. We now know that *Australopithecus* was a highly successful genus that persisted for nearly three million years.

### The Genus *Homo*

The earliest fossils of our own genus, *Homo*, are found in East Africa and dated to 2.3 mya (Kimbel et al. 1997). These early specimens were similar in brain and body size to *Australopithecus* but show differences in their molar teeth, suggesting a change in diet. In general, *Homo* differs from *Australopithecus* in its trend

toward ecological behavior, encephalization, and flexibility in nature. Another distinction between the two – where *Homo* is defined on the basis of enlarged absolute brain size ( $>600\text{ cm}^3$ ) and “complex” behavior, including tool use and language – long formed the bedrock of investigation into the origins of *Homo*. Wood and Collard (1999) defined *Homo* as a “monophylum [the common ancestor and all the descendants] whose members occupy a single adaptive zone.”

***H. habilis*** (2.3–1.4 mya), the oldest member of the genus *Homo*, was found in East Africa and was associated with simple stone tools and butchered animal bones (Blumenshine et al. 2003). ***H. erectus*** was found throughout Africa and Eurasia and persisted from 1.9 mya to 100 kya, and perhaps even later (Anton 2003). Like modern humans, *H. erectus* lacked the forelimb adaptations for climbing seen in *Australopithecus*. Its global expansion suggests *H. erectus* was ecologically flexible, with the cognitive capacity to adapt and thrive in vastly different environments. Not surprisingly, it is with *H. erectus* that we begin to see a major increase in brain size, up to 1,250 cc for later Asian specimens.

*H. erectus*, around 700 kya, earlier in Africa gave rise to ***H. heidelbergensis***, a species very much like us in terms of body proportions, dental adaptations, and cognitive ability (Rightmire 2009). *H. heidelbergensis*, often referred to as an “archaic” *Homo sapiens*, was an active big-game hunter, produced sophisticated Levallois style tools, and, by at least 400 kya, had learned to control fire (Roebroeks and Villa 2011).

According to one theory, Neanderthals, Denisovans, and modern humans are all descended from the ancient human *Homo heidelbergensis*. Between 300,000 to 400,000 years ago, an ancestral group of *H. heidelbergensis* left Africa and then split shortly after (Rightmire 2008; Hublin 2009). One branch ventured northwestward into West Asia and Europe and became the Neanderthals. The other branch moved east, becoming Denisovans. By comparing the genomes of apes, Denisovans, Neanderthals, and modern humans, scientists hope to identify DNA segments

unique to the different groups. Early results already suggest modern humans underwent genetic changes involved with brain function and nervous system development, including ones involved in language development, after splitting from Neanderthals and Denisovans. Identifying and understanding these genetic tweaks could help explain why our species survived and thrived while our close relatives died out.

### **Homo Neanderthalensis (*Homo sapiens* Neanderthalensis)**

The name Neanderthal (or Neandertal) derives from the Neander Valley (German Neander Thal or Neander Tal) in Germany, where the fossils were first found. They are member of a group of archaic humans who emerged at least 200,000 years ago during the Pleistocene Epoch (about 2.6 million to 11,700 years ago) and were replaced by early modern human populations (*Homo sapiens*) between 35,000 and perhaps 24,000 years ago. They inhabited Eurasia from the Atlantic regions of Europe eastward to Central Asia. Until the late twentieth century, Neanderthals were regarded as genetically, morphologically, and behaviorally distinct from living humans. However, more recent discoveries about this well-preserved fossil Eurasian population have revealed an overlap between living and archaic humans (Tuttle et al. 2020).

### **Denisovans**

The Denisovans are a much more recent addition to the human family tree. In 2008, paleo-anthropologists digging in a cave in Southern Siberia unearthed a 40,000-year-old adult tooth and an exquisitely preserved fossilized pinkie bone that had belonged to a young girl who was between 5 and 7 years old when she died. Recently, scientists successfully extracted nuclear DNA from the pinkie bone and conducted comparison studies with the genomes of modern humans and Neanderthals. Studies show the girl was closely related to Neanderthals yet distinct enough to merit

classification as a new species of archaic humans, which scientists named “Denisovan” after the cave where the pinkie bone was found. Genetic studies revealed that the Neanderthals and the “Denisovans” are more closely related to each other than either group is to modern humans (Tuttle et al. 2020).

## “Ghost” Hominids

Genetic study of *Homo sapiens* DNA pool has helped many researchers to shed light on where our ancestors made contact with other human subspecies. But in a new analysis of populations from West Africa, they have started to kick up something unexpected: hidden inside genomes are signs of as-yet-unidentified genetically distinct human ancestors that we never knew existed. Geneticists call them “ghosts” population (Brahic 2018). There are no physical record of these ancient hominins, no archaeological remains, no bones, and no tools. No one has discovered remains or artifacts from this mysterious group of hominids. Yet the genetic code that they left within fossils of other hominins, and in living humans too, is offering profound insights into how our species came to be and what the world was like at the time.

Researchers believe that the ghost hominids most likely separated from the common ancestor of modern humans and Neanderthals between 360,000 and one million years ago. Durvasula and Sankararaman (2020) estimated that the ancestors of modern Africans interbred with the mystery humans at some point in the past 124,000 years. The researchers also note that it is possible that humans interbred with several waves of different hominids over thousands of years.

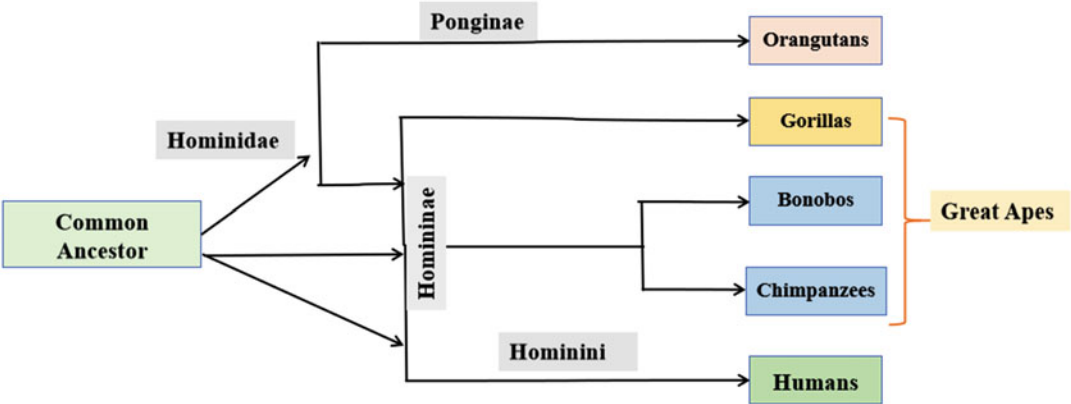
## Interbreeding

Genes from fossils have shown that the ancestors of many living people mated with Neanderthals and with Denisovans. The new

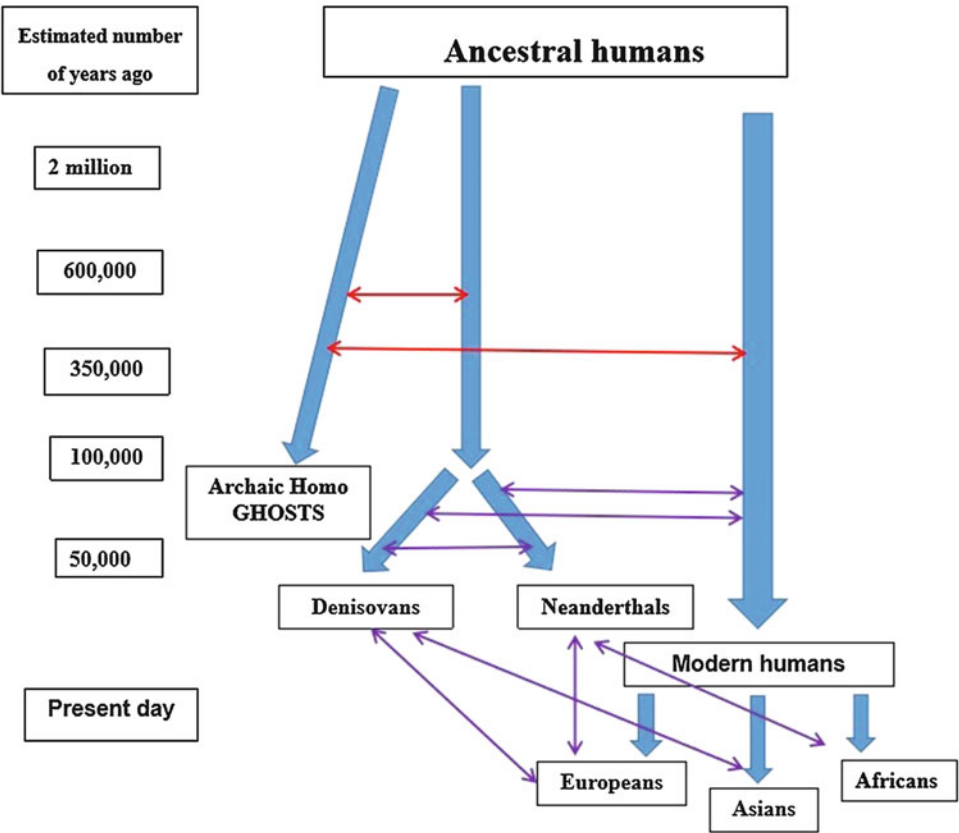
genomic studies rely on complex models of inheritance and population mixing. But, taken together, they build a strong case that even before modern humans left Africa, it was not uncommon for different human ancestors to meet and mate. The gold standard for detecting interbreeding with archaic humans is to sequence ancient DNA from fossils of the archaic group and then look for traces of it in modern genomes. Researchers have done just that with Neanderthal and Denisovan genomes up to 200,000 years old from Eurasia. But no one has been able to extract full genomes from more ancient human ancestors. So population geneticists have developed statistical tools to find unusually ancient DNA in genomes of living people. After almost a decade of tantalizing but unproven sightings, several teams now seem to be converging on at least two distinct episodes of very ancient interbreeding (Gibbons 2020).

## Summary

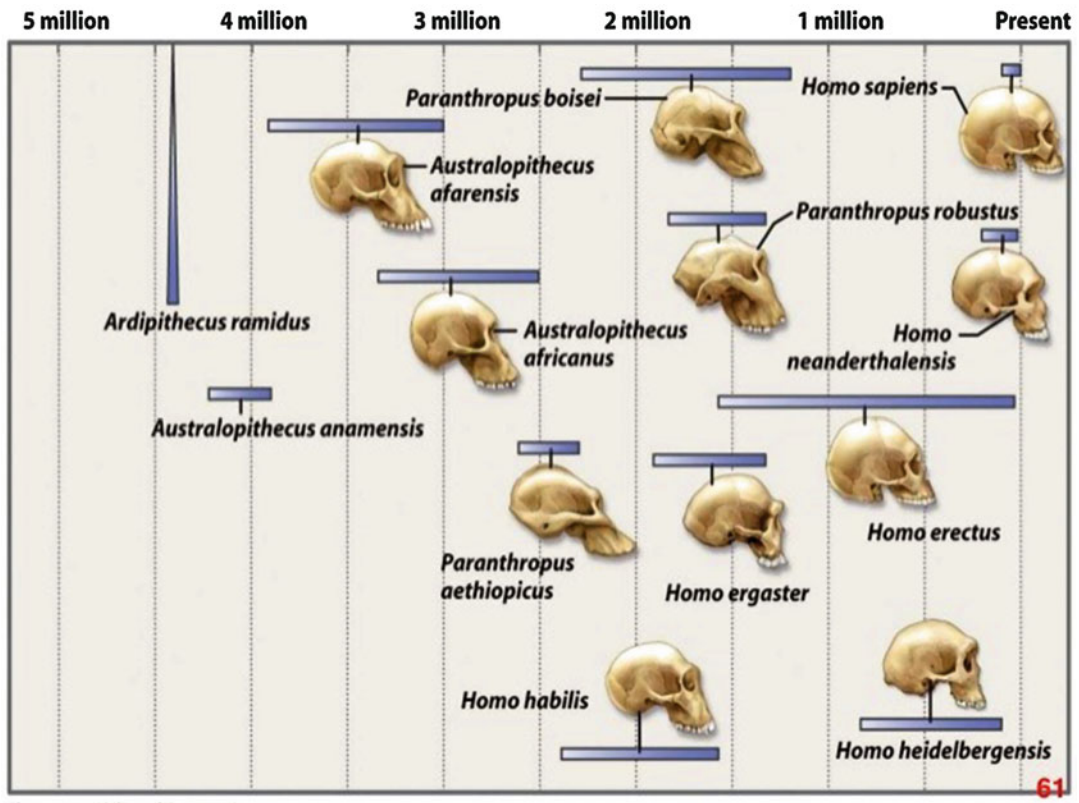
Humans, among the other living primates, are most closely related to the apes, which include the lesser apes (gibbons) and the great apes (chimpanzees, gorillas, and orangutans). These so-called hominoids – which are the gibbons, great apes, and humans, emerged and diversified during the Miocene Epoch, approximately 23 million to five million years ago. Neanderthals and Denisovans were human populations that separated from the modern lineage early in the Middle Pleistocene. Many modern humans carry DNA derived from these archaic populations by interbreeding during the Late Pleistocene. The evolution of our species from an ape-like Miocene ancestor was a complex process. No one has discovered remains or artifacts from this mysterious group (“ghosts”) of hominids, but researchers believe that they existed. Researchers around the world are expecting to learn more about these ancient humans (Figs. 1, 2, and 3).



**Common Ancestor, Fig. 1** The divergence of humans and great apes from a common ancestor



**Common Ancestor, Fig. 2** Showing “ghost” hominins interbred with the ancestors of Neanderthals, Denisovans, and modern humans



**Common Ancestor, Fig. 3** Showing possible pathways in the evolution of human lineage. (Source: Wikipedia)

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## Common Descent

### ► Last Common Ancestor

## Communal Behavior

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## Definition

Behavior exhibited by two or more individuals at the same place and time.

## Introduction

In nature, it is common to observe animals conducting joint behaviors. For example, different animals drinking from the same water source at the same time, roosting together or migrating in flocks are all examples of communal behavior. Communal behavior in its broadest sense does not necessarily imply a benefit for the individuals exhibiting such behavior. In the joint drinking example above, animals may not necessarily benefit from drinking together (drinking alone may be as beneficial). However, in order to evolve, a communal behavior (just as any behavior) is expected to provide benefits that outweigh its costs. Therefore, when individuals preferentially or exclusively exhibit a given behavior communally, this suggests a benefit of sharing this behavior. The benefit may be directly linked to the communal behavior exhibited (for example, communal roosting in birds has thermal benefits that allow individuals to save energy) or it may create the conditions for cooperation among individuals (for example, communal drinking may allow for higher rate of overall vigilance behavior and hence more efficient predator detection).

## Adaptive Value of Communal Behaviors

### Predation Risk Reduction

A classic advantage provided by communal behaviors, such as communal movements, communal feeding, or communal breeding, is that it reduces predation probabilities. This can be by a passive dilution effect as a given individual becomes less likely to be predated since more individuals are available or by increasing the probability to detect a potential predator if more than one individual is vigilant.

### Buffer Against Environmental Variation

In extreme or highly variable environmental conditions, several individuals form clusters. For example, by “huddling” individuals increase their body temperature, which allows them to keep warm while saving energy in thermoregulation (Gilbert et al. 2010). This behavior may therefore effectively reduce the negative effects



caused by the variation in ambient temperature in wild animals.

### Increased Offspring Survival

Biparental care, when both male and female parent care for their offspring, is a form of communal behavior that directly increases the number of offspring reaching independence. Several females, males, or pairs can also share the same nest and often parental duties. Such behavior can be broadly referred as communal breeding or joint nesting and can sometimes increase per female reproductive output (Barbara 1994).

### Communal Behavior and Kin Selection

Communal behaviors are often exhibited among individuals of a same species and, when so, more particularly among genetically related individuals, typically members of a same family. That is because the indirect benefits of communal behaviors, and therefore their probability to evolve, increase as the relatedness between the individuals increase (Gilbert et al. 2010). For example, in cooperatively breeding species, the “helpers” (nonbreeding individuals that assist a breeding pair in caring for their offspring) are often related to that breeding pair (Koenig and Dickinson 2016).

### Communal and Cooperative Behaviors

Cooperative behavior is a form of communal behavior which requires coordination among the individuals to their mutual benefit (McFarland 2014). Cooperation requires active help, whereas a communal behavior, while expected to be beneficial, does not require that one individual actively helps another (i.e., incurring a cost and benefitting another individual). For example, in the communal drinking example, individuals do not help each other in their drinking, but by being together at the water source they are better able to avoid predators. The behavior of watching for predators is cooperative because while an individual is watching it is not drinking. The communal behavior (going down to drink together at the river) is not, but may nonetheless decrease

predation probability by increasing predator confusion or decreasing an individual's chances of being taken by a predator.

### Communal Behavior in Entomology

In the encyclopedia of entomology (Capinera 2008), communal behavior has a slightly more precise definition and is described as “a level of sociality less than eusocial behavior. A type of pre-social behavior. It involves members of the same generation sharing a nest, but without brood care.”

### Communal Behavior in the Social Sciences

In the social sciences, communal relationships describe a behavior providing a benefit to the receiver in response to a need or to demonstrate a general concern for another (Clark and Mils 1993). Therefore, this definition does not require a shared behavior among the focal individuals. For example, a parent caring for an infant is described as a classical communal relationship (Clark and Mils 1993) while such behavior is not a communal behavior in biological sciences since the parent and the offspring do not exhibit the same behavior.

### Cross-References

- ▶ [Affiliative Behaviors](#)
- ▶ [Affiliative Bond](#)
- ▶ [Aggregation](#)
- ▶ [Altruism](#)
- ▶ [Coefficient of Relatedness](#)
- ▶ [Colonial Nesting](#)
- ▶ [Cooperation](#)
- ▶ [Cooperative Breeding](#)
- ▶ [Cooperative Hunting](#)
- ▶ [Costs of Group Living](#)
- ▶ [Exchange Behavior](#)
- ▶ [Group Living](#)
- ▶ [Helping Behavior](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Kin Selection](#)
- ▶ [Parenting](#)

- [Polyspecific Associations](#)
- [Predator Defense](#)
- [Reciprocity](#)
- [Social Behavior](#)
- [Social Grooming](#)
- [Vigilance](#)

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## Communal Song

- [Chorus](#)

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## Communication

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## Synonyms

[Language](#); [Messages](#); [Signals](#)

## Definition

In humans, communication is one of those terms that everyone knows but may be a little more difficult for some of us to define. In animal communication, biologists have been arguing over the definition for decades (see Table 1 for some, but by no means exhaustive list, of animal communication definitions). There are three things that most biologists agree upon: (1) there has to be a sender and a receiver, (2) there has to be a signal, and (3) this signal has been shaped by natural selection for the purpose of communication (this last piece becomes important when we start to define cues versus signals below).

Where biologists disagree is the relationship between sender and receiver and what is being transmitted in the signal. The relationship between sender and receiver becomes important when we think about fitness and how natural selection acts on individuals. Dawkins and Krebs (1978) proposed that communication involves a sender manipulating the receiver but failed to take into account that the receiver is also under natural selection and is not a by-stander in the communication relationship. Later, they (Krebs and Dawkins 1984) clarified that, in general, a sender is manipulating the receiver and the receiver is trying to mind-read the sender. Viewed this way, both sender and receiver are under natural selection and both are essentially trying to trick the other into doing something that benefits them. This adaptationist definition was stated best by Maynard Smith and Harper (2003, p. 3) where they defined communication as: “a sender producing a signal, which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved.” This takes the sender and receiver into account, clearly defines a signal, and allows for natural selection to act on the sender and receiver. The next thing most biologists disagree on is what, if anything, is being transferred between sender and receiver in a signal.

The Role of Information in Communication

The idea that information is transferred between the sender and receiver is incorporated either explicitly or implicitly into many definitions of animal communication (Table 1). Information, like communication, is a word everyone knows but is difficult to define. For this reason, some biologists have raised issue with the use of the word information in the formal definition of animal communication (Owren et al. 2010; Scott-Phillips 2008). Formally, information is assumed to have been transferred when a signaler influences the behavior of a receiver. As Searcy and Nowicki (2005, p. 207) note, “The sole value of a signal to a receiver is as a source of information, information that it uses in choosing the behavioral, physiological, or developmental responses that will maximize its fitness.”

The amount of information transferred can be quantified, in bits, as a reduction in uncertainty to the receiver following a communication exchange

(Shannon and Weaver 1949). For instance, if a female bird is trying to select a potential mate, she has to determine whether a bird singing near her is the correct species, the correct sex, and potentially of the highest quality. Thus, signals produced by the signaler contain potential information about species, sex, and quality and this helps the female reduce her uncertainty when making a mate-choice decision. This definition is useful insofar as it permits an objective description of the value of information. Yet, few studies ever quantify the information content of animal signals; rather, the information content is assumed to exist and thus have value. By contrast, Scott-Phillips (2008) argues that Maynard Smith and Harper’s (2003) definition of communication does not use the word information and thus, information is unnecessary in a definition of communication. But is assuming that such information exists useful?

Owren et al. (2010) had some additional arguments against the use of information, in particular “encoded information,” in the formal definition of

Communication, Table 1 Some key definitions of animal communication

| Definition                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | References                      |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------|
| Communication occurs when the sender does something that appears to be the result of selection to influence the sensory organs of the receiver so that the receiver’s behavior changes to the advantage of the sender                                                                                                                                                                                                                                                                                                                                                         | Dawkins and Krebs (1978)        |
| Building off of their definition in 1978: Communication is based upon manipulation and mindreading. They coevolve and signals are the result of this coevolution                                                                                                                                                                                                                                                                                                                                                                                                              | Krebs and Dawkins (1984)        |
| Communication involves a sender producing a signal, which is “any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved” (p. 3)                                                                                                                                                                                                                                                                                                                        | Maynard-Smith and Harper (2003) |
| Signals are characteristics fashioned or maintained by selection because they convey information to a receiver                                                                                                                                                                                                                                                                                                                                                                                                                                                                | Searcy and Nowicki (2005)       |
| Signals are stimuli produced by a sender and monitored by a receiver to the net benefit of both parties and have evolved for the purpose of relaying information                                                                                                                                                                                                                                                                                                                                                                                                              | Bradbury and Vehrencamp (2011)  |
| Communication is “the use of specialized, species-typical morphology or behavior to influence the current or future behavior of another individual” (p. 771)                                                                                                                                                                                                                                                                                                                                                                                                                  | Owren et al. (2010)             |
| A signal is “any act or structure that (i) affects the behavior of other organisms; (ii) evolved (or is maintained) because of those effects; (iii) is effective because it transfers functional information to receivers” (p. 663)                                                                                                                                                                                                                                                                                                                                           | Carazo and Font (2010)          |
| “Communication occurs if trait values of one organism (the informer) stimulate the sensory systems of another organism (the perceiver) in such a way as to cause a change in the behavior of the perceiver (compared to a situation where the trait values of the informer were different). We use ‘communication’ in the narrow sense of applying only to traits that were selected for their communicative function (that is, to signals). Thus, communication in this sense is sometimes called signaling and sometimes true communication (c.f. inadvertent information)” | Ruxton and Schaefer (2011)      |

animal communication. First, they argued that because biologists cannot agree on a definition of information in an animal communication context, using the word information creates nothing but ambiguity and a lack of testable hypotheses grounded in evolutionary biology. They continue to argue that Shannon and Weaver's definition of information (the correlation between the occurrence of one event with the occurrence of another event (Shannon and Weaver 1949)) cannot be applied to an animal communication definition that contains the idea of encoded information because it implies a "meaning or a significance of that event" (Owren et al. 2010, p. 761). Second, they argued that the use of encoded information implies a cooperative co-evolution between sender and receiver because if a sender encodes information in its signal there must be a benefit to the sender for sharing that information. Third, they argued that using the idea of encoded information puts the proverbial carriage before the horse in our understanding of the evolution of language. Instead, they suggest a definition where the sender influences the receiver and the concept of information is explicitly excluded (Table 1).

In response to these concerns about the inclusion of information in the formal definition of animal communication came a flurry of responses arguing for the inclusion of information in the definition (Carazo and Font 2010; Ruxton and Schaefer 2011; Seyfarth et al. 2010). Among other things, the respondents noted that, by focusing solely on the sender's influence on the receiver, the important role of the receiver is downplayed, which is a problem given that the receiver is an entity that is also subjected to selection. Thus, researchers seem to have circled around to the original issue: what is the role of the receiver in a communication exchange? To date, there has not been a consensus but the conceptual idea of information has value, even if it is rarely quantified, and even if many definitions of communication do not require it to be explicitly defined.

And for the purpose of this entry, we adopt a recent definition by Carazo and Font (2010, p. 663): a signal is "any act or structure that

(i) affects the behavior of other organisms; (ii) evolved (or is maintained) because of those effects; (iii) is effective because it transfers functional information to receivers." The Carazo and Font definition includes the manipulative or influential aspect of the sender on the receiver (i), it defines a signal (ii), and it acknowledges the receiver's role in the communication scheme and that, even if not intentional by the sender, information from the receiver's perspective may be obtained (iii).

## Signals Versus Cues

There is a formal but important distinction between signals and cues. Cues, like signals, modify the behavior of a receiver, but cues have not evolved specifically for the purpose of communication (Bradbury and Vehrencamp 2011; Scott-Phillips 2008). Rather, cues are attributes of or associated with other organisms that provide information to the receiver and, hence, influence the receiver's behavior. For example, when an owl uses the movement of the grass caused by a mouse foraging, the owl is using a cue not a signal because the movement of the grass has not evolved specifically for communication with the owl; rather, it is a by-product of the mouse's foraging behavior. Yet cues, like signals, may provide sources of information.

## Signal Modalities and Types

With this definition of animal communication (and the distinction between a signal and cue), the amazing diversity illustrated by animal communication systems can be explored. Animals communicate using visual, acoustic, olfactory/chemical, tactile/seismic, and electrical signals (Bradbury and Vehrencamp 2011). Furthermore, signals vary on a continuum of conspicuousness from subtle, close-range, direct signals to obvious, long-distance, broad audience signals (Laidre and Johnstone 2013). Each of these has a different active space – the effective range through which a signal can work, each is differentially

localizable, and each has constraints on the rapidity with which they vary, which has implications on the maximum amount of information transmitted. Thus, the specific modality employed may depend on the habitat in which it must be used as well as constraints on signal propagation.

Visual signals, perhaps one of the more conspicuous modalities to humans, can include colors, patterns, and/or movements. An example of color, pattern, and movement all being used together comes from the mating dance of the bird-of-paradise Wahnes's parotia (*Parotia wahnesi*) from Papua New Guinea. Males flash their multicolored, patterned iridescent chest at females, while hopping around and moving the ornaments attached to their head (see <https://macaulaylibrary.org/video/469253> for a video). The active space of a visual signal will be reduced in areas with physical obstructions, but because they can be dynamically varied, they can potentially transmit a lot of information.

Acoustic signals, another conspicuous modality to humans, include different frequency, temporal, and amplitude patterns and are thus an excellent example of signals that vary in their conspicuousness. Unlike visual signals, some of which, like color, can sometimes be “always on,” acoustic signals are by default off until they are produced. Two examples of acoustic signals on the opposite ends of the conspicuous spectrum come from birds. Many bird species have a “whisper song” or a “soft song” that is quiet and meant for close range communication between a male and female breeding pair. By contrast, mobbing calls are predator-elicited acoustic signals designed to be heard by both the predator and conspecifics. Mobbing calls are generally broadband and harsh in their acoustic structure making them very conspicuous and able to travel long distances to many receivers. Acoustic signals can travel around visual obstructions and may have large active spaces (the low frequency elephant and whale vocalizations can travel many kilometers). Because they may be rapidly modified, they can contain a substantial amount of dynamically varying information. Human language, after all, is not communicated using olfactory signals for a reason.

Chemical signaling may be the oldest method of communication (Bradbury and Vehrencamp 2011). Humans detect chemical signals both by taste and smell. Chemical signals tend to be long-duration signals because they have a slower diffusion rate (although this can be environmentally dependent and different components of chemical signals vary in their volatility (Parsons et al. 2017). An example of chemical signaling is the track that ant species lay down to allow nest mates to follow their tracks to locate food. These chemicals are species and ant colony specific. A recent realization is that the odorants used in chemical signaling may be produced by symbiotic bacteria living on or in animals.

Tactile or seismic signaling can be more difficult to define. For example, if in a male-male contest one male pushes the other, is this considered a signal? In other systems, it is easier to define. For example, in spider courtship, the males will pluck the strings of their web to communicate to the female and the foot drums of kangaroo rats contain information about individual identity that are transmitted to others within seismic range.

Some fishes (knifefish, elephant fish) are able to create electrical signals with specialized electric organs. These signals are used in territory and aggressive interactions, courtship, dominance, social coordination, and identification (reviewed in Bradbury and Vehrencamp 2011). More species seemingly are sensitive to other species' passive electric discharges. For example, short-beaked echidnas (*Tachyglossus aculeatus*) have electroreceptors on the tip of their snout that they forage with to detect prey, but it is unknown if echidnas use this sensory ability for communicative purposes (Bradbury and Vehrencamp 2011).

## What Influences Signal Transmission?

Given these possible modalities, what determines the conditions under which a specific modality is used and how it transmits? Animals are constrained on the signals they can send based on the environments they live in and based on their own abilities to produce and receive

potential signals. Endler (1992) coined the term “sensory drive” to recognize the inevitable relationship between environmental conditions, the sensory systems, and signals that work together to drive the evolution of signaling systems.

The medium in which the signal is produced can dictate choice of signal modality. For example, electric signals are used only in aquatic environments because water increases the active space of potential signals. Within a modality, the medium can have drastic effects on signal transmission and diffusion. For example, acoustic signals travel farther in water than in air.

Signals may be blocked or otherwise masked by environmental noise. For example, broad-spectrum water noise masks acoustic signals. Torrent frogs (*Odorrana tormota*) living near rapidly flowing, noisy streams in China have escaped this constraint by producing what we perceive as ultrasonic (very high frequency) signals that are able to communicate above the lower-frequency water noise. Birds vocalizing in a cicadia-filled forest or in an urban environment with road noise may shift the frequency of their songs or calls to avoid environmental masking.

Within a medium, signals both attenuate (lose amplitude and become more difficult to detect) and degrade (lose fidelity) when transmitted over space. For acoustic signals, Morton (1975) formalized this into the acoustic adaptation hypothesis where he predicted terrestrial acoustic signals will be structured to maximize transmission within the habitat they are produced. For long-distance acoustic signals, there is a small effect of the acoustic environment on signal structure. The best support for the hypothesis comes from large-scale comparative analyses of birds or studies that look at a single species across a range of environments. The effects of the environment effect signal design in other modalities as well. For example, in a paper discussing visual signals and environment, Karen Marchetti found that *Phylloscopus* warblers vary in their color patterns depending on the light intensity of their habitat with brighter species living in darker habitats (Marchetti 1993).

Finally, the sensory systems of both the sender and receiver will influence the signal modality and

signal structure. Senders physiologically need to be able to produce a signal that receivers can perceive and process and thereby evolutionary influence the signal structure through their response (Endler 1992).

## Multimodal Communication

The examples of signals so far focus on a single modality. However, in reality, multimodal communication, where a sender uses signals from two or more different sensory modalities, may be relatively common. This section will discuss the evolution, use, and prevalence of multimodal signals in animal communication.

Why use a multimodal signal over a unimodal signal? After all, producing more than a single signal is assumed to be more costly than producing one. The two main hypotheses to explain the evolution of multimodal signaling are to increase content/reliability (i.e., content-driven selection; Hebets and Papaj 2004 or the multiple messages hypothesis; Johnstone 1996) and/or to increase robustness (i.e., efficacy-driven selection; Hebets and Papaj 2004 or the back-up signals hypothesis; Johnstone 1996). These ideas were formalized into a framework by Sarah Partan and Peter Marler in 2005 to describe redundant versus non-redundant multimodal signals (Fig. 1).

Redundant signals contain the same information in the signal components where non-redundant multimodal signals contain different information in their components. Apply this to the mechanisms suggested above and redundant signals may be used to increase robustness because if one modality is blocked, the information will still reach the receiver (back-up signals hypothesis). Whereas nonredundant signals may be used to increase information content because the signals contain different information (multiple messages hypothesis).

Furthermore, within redundant and non-redundant multimodal signals, Partan and Marler (2005) considered the inter-signal relationship or how the components within a signal may interact from the perspective of the receiver. For example, in the model organism of the fruit fly (*Drosophila*



**Communication,**  
**Fig. 1** Classification of multimodal signals after Partan and Marler (2005)

|               | Stimulus | Response                                                                          | Stimulus | Response                                                                                                                                                                 | Category     |
|---------------|----------|-----------------------------------------------------------------------------------|----------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------|
| Redundancy    | A        |  | A + B    |                                                                                         | Equivalence  |
|               | B        |  | A + B    |                                                                                         | Enhancement  |
|               |          |                                                                                   | A + B    |                                                                                         | Antagonism   |
| Nonredundancy | A        |  | A + B    |  and  | Independence |
|               |          |                                                                                   | A + B    |                                                                                         | Dominance    |
|               | B        |  | A + B    |  or  | Modulation   |
|               |          |                                                                                   | A + B    |                                                                                         | Emergence    |

*melanogaster*), Fanny Rybak and colleagues found that males that use both an acoustic and a chemical component in their female courtship display have more successful matings than males that use only acoustic or chemical components (Rybak et al. 2002). This illustrates redundant enhancement (Partan and Marler 2005; Fig. 1), where both components provide information to assess male suitability (redundant), but when combined males have significantly more matings than from either component presented alone (enhancement).

Multimodal signaling, just like unimodal signaling, is subject to sensory drive and also is subject to selection for reliability. For example, Anne Leonard and colleagues focused on plant-pollinator signaling systems where most plants use both visual (color) and chemical (olfactory) signals to communicate nectar rewards to their pollinators (Leonard and Masek 2014). Selection for increased information and reliability about the nutritional reward (content-driven selection and robustness against a noisy background with multiple olfactory and visual signals bombarding pollinators (efficacy-driven selection) may increase the benefits from multimodal signals over unimodal signals.

Much of the research on multimodal communication has focused on intraspecific signaling systems, mainly antagonist and mate-choice signals.

Yet, signaling systems can also exist across species. Many aspects of multimodal signaling systems are expected to be similar within and across species, and signal reliability underlies all signaling. Interspecific communication systems have an additional component that must be considered: the need for overlapping sensory systems, sensory thresholds, and cognitive abilities. As discussed above, the sensory systems and the threshold limits within those sensory systems are important for intraspecific signaling as well. However, in general, individuals of the same species share the same sensory system, thresholds, and cognitive abilities. Therefore, when examining interspecific signaling systems, researchers need to be especially aware of the sensory systems of each species involved to understand the signaling system as a whole. As research expands into multimodal signaling systems, researchers are beginning to discover that not only are most signaling systems multimodal, but that they often consist of three and potentially even four different modalities.

**Signal Reliability and the Evolution of Signals**

To be useful to a receiver, signals must be reliable. Because selection acts on both the sender and the

receiver, reliability must be considered from both the sender's and receiver's perspectives. By ignoring unreliable signals, receivers select for signals that contain reliable information. However, no signaling system is honest or reliable 100% of the time. Signals can be unreliable in two ways: they can unintentionally not be linked to a stimulus (false signals) or intentionally presented in the absence of the stimulus (deception) (Searcy and Nowicki 2005). For example, white-winged shrikes (*Lanio versicolor*) emit alarm calls to the rest of the mixed-species flock when they detect predators. This causes the rest of the flock to cease foraging and dive for cover. This species also emits deceptive alarm calls to manipulate the rest of the flock to dive for cover permitting them to forage without competition (Bradbury and Vehrencamp 2011). Whereas these alarm calls are sometimes deceptive and not completely reliable, the signaling system persists. Therefore, the mantra of signal evolution is that signals are honest or reliable *on average* (Searcy and Nowicki 2005).

Signals are often kept honest or reliable through production costs. The magnitude of the cost needed to keep a signal reliable is often dependent on the relationship between the sender and receiver. If the sender and receiver have aligned interests, the signal needs to be less costly because the aligned interest alone can maintain honesty because the fitness benefits are linked between sender and receiver. For example, although often temporary, mobbing signals directed at conspecifics are considered to have few costs because the interest between the sender and the receiver at the time are aligned: work together to drive a predator out of the area. However, as interests start to diverge, senders will be more tempted to provide unreliable information; therefore, the costs should be greater to ensure signal reliability. For example, when males compete, each male's interests are opposed; both want to win the encounter. Signals used in these situations are expected to be costly to ensure reliability, such as seen with the costly antlers of elk and fiddler crab's giant claws. More generally, because sender's and receiver's interests rarely completely overlap, most signals impose a cost

to maintain reliability and honesty (Bradbury and Vehrencamp 2011).

An early explanation for variable costs is from Amotz Zahavi's handicap principle, where signals impose a handicap on the sender to ensure honesty, and not all senders can bear the cost (reviewed in Searcy and Nowicki 2005). They can indicate the quality or condition of the sender. All senders can produce the signal, but only certain individuals can bear the costs of the signal. The costs can be enforced in signal production, development, or maintenance. Production costs can be in the form of energy used in production, time spent signaling and away from other activities or increased conspicuousness to predators. Handicap signals can also have developmental costs. Development costs are born prior to signaling and often direct limited resources to signal development. Carotenoid expression in birds and fish is developmentally costly. Carotenoids must be acquired by foraging and are used in immunological defense systems. Therefore, any animals that can show evidence that they have acquired carotenoids (through carotenoid-dependent coloration) have demonstrated that they forage well and are of both high nutritional and immunological quality. Handicap signals can also impose maintenance costs (Bradbury and Vehrencamp 2011). Maintenance costs refer to the costs of maintaining a signal and can be energetic or act through increasing predation risk.

Index signals are signals that are constrained by the anatomy, physiology, or experience of the sender. Unlike handicap signals, not all individuals can produce the signal and honesty is enforced not by direct costs but by constraints. They most often indicate condition and quality. For example, song repertoire size in birds with open-ended learning can be considered an index signal because it cannot be faked: repertoire size is contingent on age.

Signals may also have third party costs. Third party costs can come in two forms: reciprocity or as an honesty check. Reciprocity exists in systems where individual recognition is present and previous actions are remembered. For example, allogrooming (the act of one individual grooming and removing ectoparasites from another) in primates

and ungulates is often kept honest through reciprocity: if you do not scratch my back, I will not scratch your back next time. The other form of a third-party cost is when the signal is kept honest by the responses of other individuals. For example, the songs that male brown-headed cowbirds use to attract females are maintained by other male cowbirds. Males are attacked more when they sing the female-preferred interphrase unit, which means only strong males can endure being attacked, and the signal is kept honest through these checks (reviewed in Searcy and Nowicki 2005).

### Signal Design and the Evolution of Signals

Now that we understand how a signaling system evolves and is maintained, how do the signals themselves evolve? Darwin thought deeply about the evolution of communication in his book *The Expression of Emotions of Man and Animals* and many of his ideas persist (Darwin and Prodger 1998). For example, his principle of antithesis is that aggressive and submissive displays will be structured so that they will be opposite each other. The examples illustrated here may be extensions of behaviors used when approaching or retreating.

The early Ethologists viewed signals as evolving through a process called “ritualization.” Ritualization is the process by which a nonsignal (such as a cue), used in a particular context, becomes predictive of what follows and then becomes exaggerated or stereotyped so that what follows becomes clear. Ritualization involves formalizing parts of a movement pattern. Ethologists would refer to these parts as “intention movements” not because the animals intend to do something, but rather because those movements predict (to us at least) what will follow.

Some of the displays that Darwin thought about when coming up with his principle of antithesis can be explained as having evolved through the process of ritualization. Ruffling feathers before flying away might be an intentional movement that the sparrow ritualized into a submissive display. Putting the ruff up to increase apparent size and protect

its neck might be an intentional movement that dogs used that later became ritualized into an aggressive display. Other sorts of examples include: breathing (a nonsignal) becomes ritualized into courtship song; a defensive posture (imagine a dog crouching down) becomes ritualized into a submissive signal (imagine that same dog crouching down after it has gotten caught eating your shoe); autonomic nervous system processes such as piloerection or feather ruffling often provide the source of the ritualized display. At that level, many ritualized signals may be honest indicators of how the animal perceives the world at that time. Ritualization should be straightforward to evolve because the signaler is already producing something that the receivers respond to in its own best interest.

This ritualized view of communication underlies the idea that communication functions to provide unambiguous information. However, because ritualization removes information by removing variability, once ritualized, additional signals are needed to emerge to provide more information. Thus, you could envision elaborate courtship rituals evolving by the process of ritualization of signal after signal. Cumulative selection like this is how we generally view the evolution of all sorts of complex traits.

But how do signals and signal receptors actually evolve: probably by a series of incremental fitness gains? Most are likely to be “exaptations” evolved from traits that already have some function but become specialized for another. Each step of a complex signal probably involved an incremental benefit and the potentially lengthy process of cumulative selection was driven by the fitness benefits of having a particular trait at each step of the way. Through these incremental fitness benefits, we can envision scenarios by which rather complex signals evolve.

There may be preexisting biases that make certain modalities or types of signals more likely than others. For instance, females of different taxa (some birds, some fish) find males with long tails particularly attractive, and studies of sword-tailed fish find that even in the absence of swords in a clade, sword-bearing fish are still found more attractive.

Structure is likely to reflect function. Thus, avian mobbing calls should be easily localizable if animals are to recruit others to help mob. Similarly, they should be broadband to ensure predator-directed mobbing calls are actually perceived by the predator. The mobbing call is much wider bandwidth than the avian aerial alarm “seet” calls. But even alarm calls will vary in their localizability. Bird alarm calls to terrestrial predators tend to be wider bandwidth and more localizable than those given to aerial predators. One possible explanation of this has to do with risk. Aerial predators move faster and generally are associated with a more compelling risk than terrestrial predators. Remember, not all animals call, nor do most animals call when they are really exposed to imminent predation (unless it is given to scare the predator into dropping them).

Thus, we see some convergence in the structure of aerial alarm calls in birds. Many songbirds produce similar calls when they detect raptors. This convergence in structure reflects convergent problems – warning others while not getting preyed upon themselves. The convergence works because of how the calls are structured. They fade in and fade out and are relatively high frequency as Peter Marler first pointed out in the late 1950s. The combination of fading in and fading out both in volume and also in their structure makes them relatively hard to localize. Rapid and sharp onsets are easier to localize than narrow-band, smoothly fading in sounds. Additionally, because they are high frequency, they transmit less than a lower frequency call of the same structure. Thus, birds can better target their recipients – and not advertise the fact that they have seen a raptor to all – including to the raptor. Additionally, call frequencies used are outside the best hearing range of some of their predators. Taken together, these similar selective pressures might lead to convergent call structure.

### Functionally Referential Signals

In addition to containing information that helps animals make decisions, calls may be said to have referential meaning. The referential meaning of

signals has been most studied in alarm communication and in food calls.

Alarm calls are signals emitted when an animal detects a predator. For species that emit situationally variable alarm calls, two hypotheses have been invoked to explain the meaning of variable calls. Alarm calls may vary according to the “response urgency,” or imminence of predation, the caller faces. Thus, short calls may be produced when predation is imminent while longer calls may be produced when there is more time to assess and manage the risk of predation. By doing so, calls may communicate the degree of risk the caller experiences and may be a function of the caller’s arousal. Alternatively, different alarm calls may denote different types of predators (e.g., aerial vs. terrestrial predators), or even the exact species of predator. These alarm calls are known as “functionally referential” in that the calls refer to specific external stimuli. Labeling a specific external object or event is known as “referential communication.” Such referential communication is a required component of human language and therefore is of some interest. Philosophers debate what referential communication really entails. Does it mean that animals form “images” of objects? Does it require labeling (eagle!) or could it communicate the desired action (run up a tree now!)? Does it require complex cognitive abilities? Honeybee waggle dances, after all, communicate very specific information about the quality of food, the distance to the food, and the direction to the food. Is there any biological basis for saying that referential communication in monkeys is more complex than in bees? Some researchers care about this because they would like to use human language abilities as a metric by which to contrast humans with other species. If bees and monkeys share the same abilities, then perhaps humans are not that cognitively complex. Rather than engaging in this debate, Peter Marler, Chris Evans, and Marc Hauser shifted the discussion by defining the term “functionally referential” (reviewed in Evans 1997). Functionally referential makes no reference to higher-level cognitive processes but rather focuses on production and response specificity. Thus, to quantify referential communication, it is

essential to have a high degree of production specificity – specific calls are elicited by specific predators, and it is essential that receivers respond uniquely to these calls; thus, the calls are contextually independent from the receivers perspective.

Vervet monkeys studied in East Africa (Uganda and Kenya) are a well-studied system of referential signaling. Classic work by Peter Marler, Dorothy Cheney, and Robert Seyfarth showed that monkeys produce acoustically different calls in response to different types of predators: they “chutter” to snakes, “bark” to leopards, and “cough” to eagles. Monkeys hearing chutters immediately stand bipedally and look for snakes, those hearing barks climb trees and retreat to the distal part of limbs where they will be safe from leopards, and those hearing coughs retreat to the center of trees where they are safe from eagles (Seyfarth et al. 1980). But do these signals really communicate predator type? The calls could signal information about predator behavior or act to instruct receivers about the appropriate response. These would not be referential in the same sense. For reasons like this, some have questioned the utility of using the term referential. Furthermore, recent work by Nicholas Ducheiminsky, Peter Henzi and Louise Barrett with a different subspecies of vervets in South Africa has even questioned the inferences from earlier vervet studies (Ducheiminsky et al. 2014). South African monkeys living in larger groups and under different predation risks did not have the contextual independence seen in East African vervets. If we accept that cognition is a trait subject to selection, we should expect both intra- and inter-specific differences in cognitive abilities based on their value. It is likely that the different conditions that the South African vervets lived under selected for different cognitive abilities.

Food calls are vocalizations emitted around food. Are they referential? Can they label specific types of food in ways that animals may label types of predators? The short answer is that food calls are rather complex and multipurpose. Food calls are given in both feeding and nonfeeding situations. Most species do not produce unique calls for different foods. The most common mechanism associated with food variation is changing the

calling rate, suggesting that call structure reflects the caller’s internal state rather than the food type. Additionally, there is no unifying function of calls either. Some food calls are used in situations where individuals recruit others to reduce predation risk. Some food calls seem to be used to build a reputation or to attract mates. Some food calls signal ownership of a resource and function to reduce competition. Thus, whereas alarm calls may be referential (or not), most food calls are not referential.

## Intraspecific Communication

Individuals may communicate with conspecifics for a variety of reasons. We will explore a few of the contexts that involve intraspecific communication, including the sexually selected signals used in antagonistic and mate attraction contexts, signals under kin selection, and finally social calls. It is important to reiterate that just because the sender and receiver are from the same species, interests need not be aligned because selection acts on the individual, not the group or the species.

As mentioned, antagonistic and mate attraction signals are under sexual selection, which is the evolutionary process that arises from the competition of one sex for the other. In most mating systems, males are competing for females (although there are some interesting polyandrous examples such as jacanas and a more contemporary view of mate choice recognizes that both individuals are making decisions about whom to mate with). In antagonistic contexts, including contests over mates, territories, or rank, the interests of a sender and receiver are opposed. Therefore, we expect high signaling costs to ensure honesty. Male weapons which are (often exaggerated) structures used to defend territories or females are an excellent example of high costs. Most weapons (such as antlers) are expensive to carry, produce, and/or maintain and not all males have the required nutritional history, genetic quality, or a large enough body size to support growing a weapon (Emlen 2008). These weapons are used as both assessment signals of male fighting condition or quality as well as in combat. In

general, the male with the biggest weapon usually wins.

Mate attraction also has diverging interests between males and females because of unequal investment in reproduction (females often, but not always, invest more). There is often a tradeoff between the signal and another function to ensure reliability. Many signals used in mate attraction are often correlated with some sort of information about the male: condition, foraging ability, parental care. Similar to antagonistic signals, these signals may become exaggerated by sexual selection. For example, the satin bowerbird (*Ptilonorhynchus violaceus*) builds an elaborate structure (called a bower) (<https://macaulaylibrary.org/video/456303>). Research by St  phanie Doucet and Robert Montgomerie suggests that both a male's bower quality and his ultraviolet coloration are correlated with his condition suggesting that these signals are reliable signals of male quality (Doucet and Montgomerie 2003).

Communication between kin is another common communication context. In general, when kin communicate with other kin or their parents, interests mostly overlap because of genetic relatedness. There are two types of signals that have received the most attention: begging calls by offspring and alarm calls. In birds, begging calls appear to be honest signals of need and parents respond appropriately (Searcy and Nowicki 2005). Due to the genetic relatedness and aligned interests between parents and offspring, there may not need to be heavy costs to ensure signal honesty. In fact, researchers have found only weak support for energetic or predation costs that could maintain honesty. Alarm calls are another area of research where interests, especially between kin, may be aligned. Alarm calling behavior is common in birds and mammals and usually conveys information about the predator to conspecifics (and, as we will discuss later, to heterospecifics). In species that live in family groups, this apparently altruistic behavior is often explained by kin selection: an individual gains a fitness benefit by helping a genetic relative. For example, research by Michael Griesser with Siberian jays (*Perisoreus infaustus*) has shown them to be

more vigilant and more likely to give alarm calls in the presence of kin than nonkin (Griesser 2003).

Many species live in groups. Social calls among conspecific group members may facilitate group cohesion, group predator avoidance (alarm calls), and/or group foraging (food calls). Because most individuals will benefit from being in a group when groups form to reduce predation risk, interests are more aligned than opposed and, therefore, costs on signals to retain reliability should be relatively low. Food calls, where an individual attracts others to a food source, are thought to be advantageous to the sender and receiver because the group will have reduced predation and/or the additional individuals will help form a coalition to defend the food source from others. This is thought to be the case in ravens (*Corvus corax*). Raven pairs hold territories and when a nonresident raven discovers a food source on the pair's territory, it will give food calls to attract other nonresident ravens to the food source to help defend it from the resident pair (reviewed in Searcy and Nowicki 2005).

## Interspecific Communication

Individuals from different species (even from different taxa) also communicate. Just like with intraspecific communication, the fitness benefits to both sender and receiver need to be considered as well as the signal reliability. Much interspecific communication involves eavesdropping – the use of a signal intended for another receiver. Eavesdropping by unintended receivers can be an important selective force on signal modality and structure. We might initially assume that the eavesdropping receiver always benefits (otherwise why would they eavesdrop?). However, as with all inter-species interactions, eavesdropping can be positive (+), neutral (0), or negative (–) to the sender. In alarm call signaling systems, the sender generally benefits from having eavesdroppers on their alarm signals because these unintended receivers often assist in mobbing the predator from the area (sender +, receiver +; i.e., social eavesdropping; Peake 2005). When



making habitat selection decisions, many species eavesdrop on conspecifics' breeding success to make decisions about territory and nest site location the following breeding season with little to no effect on the sender (sender 0, receiver +; i.e., social eavesdropping; Peake 2005). Some species also eavesdrop on heterospecifics. Finally, eavesdropping receivers can have a negative impact on the sender (sender –, receiver +; i.e., interceptive eavesdropping; Peake 2005), which would select for less conspicuous and more direct signals. For example, formative work by Michael Ryan and colleagues with Túngara frogs has also found that fringed-lipped bats (*Trachops cirrhosus*) use the “whine-chuck” call of male Túngara frogs to localize them. Like conspecific females, the addition of the “chuck” makes it easier for the bats to locate the calling individual. Therefore, there is a cost to producing the female-preferred “chuck” and not all males produce it. It is thought that this predatory cost may in part keep this signaling system reliable (Halfwerk et al. 2014). It is important to note that eavesdropping also takes place within intraspecific communication systems.

As demonstrated in some of the examples we present in this chapter, communication is rarely a private conversation, but rather exists in a communication network with multiple senders and receivers. A communication network is a group of animals (conspecifics, heterospecifics, or both) that are within signaling and receiving distance from one another (McGregor 2005). As with eavesdropping, the costs and benefits of multiple senders and receivers within a communication network will influence the signal. Furthermore, communication networks are not filled with symmetrical contributions across individuals or species. For example, Randler and Vollmer (2013) identified asymmetrical responses across species in a European avian mobbing communication network. Species responded most to conspecific mobbing, but responses to heterospecifics varied across species with chaffinches (*Fringilla coelebs*) having the lowest responses and blue tits (*Cyanistes caeruleus*) having the greatest. Again, the costs and benefits to the sender and receiver must be considered to understand the

complex responses that exist within communication networks. Additionally, as with eavesdropping above, communication networks also exist in intraspecific networks as well.

We initially discussed the idea that both sender and receiver should benefit in order for a signaling system to persist, but that these benefits can occur independently of each other (e.g., sender manipulates receiver, receiver gains inadvertent information). However, sometimes the benefits of the sender and receiver are linked, such as in mutualisms where one benefits if the other benefits. For example, in Kenya, Anne Rasa found that dwarf mongooses and various hornbill species have a communicative mutualism. Dwarf mongooses (*Helogale parvula*) rely on two species of hornbills (*Tockus* spp.) to be vigilant of predators and give alarm calls while they forage, and hornbills rely on foraging mongooses to displace insects during their foraging for the hornbill's consumption (Rasa 1983).

Remarkably, predators and their prey often communicate with each other. Aposematic coloration is the bright coloration and patterning that (when not a Müllerian mimic) is associated with unpalatability. Bright coloration (and often accompanying odors) is easier to learn by predators avoiding prey. This is still a sender + receiver + interaction because the prey does not get eaten (+) and the predator does not get harmed trying to eat an unpalatable prey (+).

## Applied Communication

People have been applying knowledge of communication to manipulate animals' behavior for a long time. Waterfowl hunters mimic their prey's calls, carnivore hunters mimic the sounds that carnivore's prey emit, and now, even fishers can use electronic baitfish (<https://www.livingstonlures.com/>) to attract their prey. But wildlife managers are also using the sounds that animals produce to attract and to potentially repel individuals.

Playbacks of conspecific vocalizations induce preferential settlement in several species of birds (pied flycatchers – *Ficedula hypoleuca*, Laysan

albatrosses – *Phoebastria immutabilis*) and a grasshopper (*Ligurotettix coquilletti*). These studies, and others, suggest that conspecifics may have an important impact on where animals settle and, more generally, that knowledge of conspecific attraction can help inform conservation and wildlife management.

On the Fort Hood Army base in Texas, the endangered black-capped vireo (*Vireo atricapilla*) was having limited success rearing offspring because their nests were parasitized by brown-headed cowbirds (*Molothrus ater*). Cowbirds lay their eggs in other species' nests and this parasitism has caused the decline of many species that cannot evolve the ability to reject cowbird eggs. Wildlife managers Michael Ward and Scott Schlossberg wanted to see if they could call in birds to settle on areas that were "safe" because the researchers were controlling cowbirds in specific areas. To study this, they conducted a playback experiment. In 2000, they had no call playbacks. In 2001 and 2002, they broadcast the vocalizations of black-capped vireos. They found that vireos were attracted and settled in areas with vireo playbacks and were less likely to do so in years and at locations without vireo playbacks. Thus, for black-capped vireos, it seems conspecifics may be important cues for habitat quality (Ward and Schlossberg 2004).

Knowledge that a species uses conspecifics as cues for settlement decisions can inform conservation programs. For instance, animals could be "seeded" into suitable habitat to attract others, or artificial cues could be broadcast or placed in appropriate habitat as a way to attract others. Ultimately, it may be possible to attract enough individuals to form a sustainable population.

Acoustic repellents have been less successful. Repellents can simply be painful sounds or biologically meaningful sounds used by managers to keep animals away from an area. For instance, to reduce bird strikes on airplanes, managers often shoot blanks to scare away birds from runways. Although painful sounds may work, the meaningful ones – including the sounds of predators – have been less successful. However, a series of studies led by Michael Clinchy and Liana Zanette, in a variety of habitats and locations around the world, have

shown that broadcasting the sounds of predators can have remarkable effects on the reproductive success of residents (it goes down), on the foraging behavior of prey (they are more cautious), and on the overall structure of ecological communities (they are changed) through the indirect effect of manipulating perceived predation risk (Zanette et al. 2011). Such manipulations may be an essential tool in reinstalling fear into communities where key predators have been extirpated.

## Conclusions

Animal communication involves some of the most conspicuous behaviors in the animal kingdom. There are numerous ways to communicate as well as numerous contexts for communication. We have provided a brief overview of some of the ways and contexts that animals communicate. We have discussed the importance of signal reliability in maintaining signaling systems. Signals need to be reliable on average in order to be useful and this reliability is often maintained through costs that vary in severity depending on the alignment of interests between sender and receiver. We have discussed how signals evolved and some of the selective pressures that may lead to more complex signaling systems (e.g., multimodal signaling). Animal communication is an active area of research, and there remain many unanswered questions regarding both the evolution and ecology of signaling systems.

## Cross-References

- [Auditory Signals](#)
- [Chemical Signals](#)
- [Graded Signals](#)
- [Honest Signaling](#)
- [Language Research: Parrots](#)
- [Mustelid Communication](#)
- [Plantae](#)
- [Primate Sensory Systems](#)
- [Receiver](#)
- [Referential Communication](#)
- [Species-specific Behavior](#)

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## Communication Networks, Eavesdropping, and Audience Effects

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### An Introduction to Communication Networks

Animal communication involves a signaler sending a signal that is perceived by one or more receivers (Bradbury and Vehrencamp 1998). Individuals can be both signalers and receivers and may be both simultaneously. Many studies of animal communication approach the topic from the perspective of signaler-receiver pairs; however, communication in the wild is rarely confined to a single interacting pair. There is a growing acknowledgement that communication most often takes place within communication networks in which multiple individuals are within signaling and receiving range of one another, and these networks can include both conspecifics and heterospecifics (McGregor 2005). The dynamics of communication networks can have profound effects on the evolution of signal form, signaling strategies, and social behavior.

### Eavesdropping

Eavesdropping is a phenomenon that occurs within communication networks. It involves an individual gaining information about a signaler, or two or more communicating individuals, by observing signaling behavior intended for other receivers (Peake 2005). Eavesdropping may yield

costs, benefits, or neither for the signaler, receiver, or the interacting pair being eavesdropped upon. Eavesdropping can be broadly broken down into two categories: *interceptive eavesdropping* and *social eavesdropping*.

#### Interceptive Eavesdropping

When a signaler sends a signal to their intended receiver, but this signal is also received by an unintended receiver, this is an example of interceptive eavesdropping (Peake 2005). Conspecifics may engage in interceptive eavesdropping; however, interceptive eavesdropping has most often been demonstrated as performed by heterospecifics in the contexts of (i) predators and parasites eavesdropping on the courtship signals of prey species to consume signalers or infest them with their progeny (reviewed in Zuk and Kolluru 1998) and (ii) one species eavesdropping on another species' alarm calls (reviewed in Magrath et al. 2015). Thus, interceptive eavesdropping is most commonly a feature of interspecific communication networks (Peake 2005), and the costs or benefits of such interceptive eavesdropping can vary greatly for signalers depending on the identity and motives of the eavesdroppers.

#### Eavesdropping by Predators and Parasites

Signals can be sent in multiple sensory modalities, and examples of interceptive eavesdropping have also been demonstrated in multiple modalities. The most common information that is gained by eavesdropping predators and parasites is simply prey location (Zuk and Kolluru 1998), though predators may also be able to glean information about the profitability of prey animals and the prey animal's local social environment. Below are some examples of interceptive eavesdropping across different modalities:

- (i) **Acoustic signals:** Many of the most famous examples of interceptive eavesdropping are examples in which intercepted signals are acoustic, such as predatory bats targeting calling male túngara frogs (Tuttle and Ryan 1981) and parasitic tachinid and sarcophagid flies targeting various singing insects

(reviewed in Hedwig and Robert 2014). Long-range acoustic signals may be particularly susceptible to interceptive eavesdropping due to their high amplitude, omnidirectional nature, and their ability to be detected day and night (Zuk and Kolluru 1998).

- (ii) **Olfactory signals:** Olfactory communication via airborne pheromones is an important channel for mate attraction and location in many insect species. Males of the southern green stinkbug release pheromones which are attractive to females. These pheromones are also used by female parasitic tachinid flies to home in on male hosts, resulting in high parasitism rates in males (Mitchell and Mau 1971). Such “kairomones” (eavesdropped-upon pheromonal signals) are also intercepted and used to locate host eggs by some egg-parasitoid species (Fatouros et al. 2008).
- (iii) **Visual signals:** In addition to luring hetero-specific males as prey by mimicking females of prey species, predatory female fireflies are also attracted to the bioluminescent signals produced by males of their prey species (Lewis and Cratsley 2008).
- (iv) **Seismic signals:** Seismic signals were long thought to be a communication channel relatively safe from eavesdropping. However, the ability to sense seismic vibrations is taxonomically widespread in arthropods (Cocroft and Rodríguez 2005), and examples of predators and parasites intercepting such signals have been demonstrated. Predatory spiders use the seismic signals of male leafhoppers to locate signalers as prey (Virant-Doberlet et al. 2011), and the egg parasitoid wasp *Telenomus podisi* orients toward the vibratory signals produced by female neotropical brown stink bugs but, interestingly, ignores those produced by males (Laumann et al. 2007).
- (v) **Multimodal signals:** Multimodal signals are thought to evolve because they can transmit information to receivers more reliably or effectively and/or send different kinds of messages simultaneously (Partan and Marler

1999). However, this means that signals may also be more effectively transmitted to eavesdroppers. Predatory jumping spiders were more responsive to the mating displays of their wolf spider prey when these displays were multimodal, containing both visual and seismic signals (Roberts et al. 2007).

#### The Influence of Interceptive Eavesdropping by Natural Enemies on Signaling Systems

When eavesdropping is beneficial, there may be strong selection on eavesdroppers to be better able to perceive the signals of another species. A classic example of this is the convergent evolution of ears in tachinid and sarcophagid flies to allow them to eavesdrop on the acoustic signals generated by their insect hosts (reviewed in Hedwig and Robert 2014). However, some of the most striking examples of the effects of eavesdropping on the evolution of communication are adaptations that allow species to avoid being eavesdropped upon. In many species whose signals have the potential to be conspicuous to their natural enemies, signalers employ a range of strategies to limit the ability of unwanted receivers to intercept their signals. The evolution of these strategies will be shaped by pressures to maximize attractiveness and localizability to desired conspecific receivers, while minimizing attractiveness and localizability to heterospecific interceptive eavesdroppers. Below are some illustrative examples of a few such strategies.

#### Signaling in a Modality Not Perceived by Potential Eavesdroppers

Prey species may be able to reduce the risk of interceptive eavesdropping by heterospecifics by signaling in modalities in which potential eavesdroppers show reduced, or a lack of, perceptual sensitivity. Mantid shrimp produce intraspecific signals that utilize circularly polarized light (Gagnon et al. 2015); this type of light is exceedingly rare underwater, as are the sensory capabilities capable of detecting it. This suggests it may be a covert signal unavailable to would-be eavesdroppers. In a similar fashion, males of several neotropical katydid species, in which males signal in the understory to attract females, have shifted from signaling



primarily in the acoustic domain to signaling primarily through seismic tremulations, to avoid eavesdropping by acoustically orienting bats (Morris et al. 1994). Unlike acoustic signals, seismic signals are short range and receivers of seismic signals must be in contact with the same signaling substrate to receive signals (Cocroft and Rodríguez 2005), meaning these signals are unavailable to their bat predators.

**Limiting Detectability of Signals by Eavesdroppers** Another means of decreasing the possibility of signals being intercepted by eavesdropping predators, while not necessarily shifting to an undetectable modality, is to employ signaling strategies that increase the difficulty for predators to detect or localize signals. Reducing the active space signals occupy is one means of accomplishing this. In many species of moths, males produce low amplitude ultrasonic signals that are important in female courtship; such “quiet” signals may limit the scope for interception by bats (Nakano et al. 2008). Similarly, neotropical katydids that occupy habitats containing insectivorous bats produce calls with higher ultrasonic carrier frequencies, causing greater environmental attenuation of calls and reducing the range at which eavesdropping bats can hear them (Morris et al. 1994). These same katydids nicely demonstrate another means of reducing the likelihood of eavesdropping, reducing the time spent signaling. Neotropical katydids at risk from bat predation have acoustic calls with lower duty cycles (i.e., there is a greater proportion of silent time per signal period), and males supplement this reduced calling with seismic tremulation signals (Belwood and Morris 1987). Interestingly, increasing duty cycle may also be a means to reduce the risks of eavesdropping as certain auditory systems find localizing near-constant acoustic signals more difficult than intermittent ones (Michelsen 1998).

**Detection of Eavesdroppers and Cessation of Calling** Many signaling species can flexibly respond to the presence of a predator to reduce their risks of capture. The primary response in many species is cessation of signaling when a

potential eavesdropper is detected. Calling toadfish cease calling when they hear echolocation pops made by foraging dolphins (Remage-Healey et al. 2006), and male field crickets cease calling when disturbed (Lewkiewicz and Zuk 2004). The latency for these crickets to resume calling after disturbance is positively correlated with the prevalence of acoustically orienting parasitoid flies in their population (Lewkiewicz and Zuk 2004). Animals may also be attuned to telltale signs of enemy detection by conspecifics. In túngara frogs, males cease calling in response to the abrupt cessation of calling by their neighbors (Dapper et al. 2011), and, in oak treehoppers, maternal signals induce cessation of offspring signaling during attacks by eavesdropping predators (Hamel and Cocroft 2019).

**Signaling at Safer Times or from Safer Places** Prey species can reduce the risks of interception by signaling strategically at certain times or places. The neotropical katydid *Docidocercus gigliotosi* produces a much greater proportion of seismic tremulatory signals (vs. acoustic signals) when the moon is full, and remaining inconspicuous will be more important for reducing the risks from visually hunting predators (Römer et al. 2010). Conversely, the tree frog *Smilisca sila*, which detects bat predators visually, more frequently produces calls that are attractive to bats when there is greater ambient illumination that allows for better predator detection (Tuttle and Ryan 1982). *S. sila* also chooses calling spots with high levels of ambient noise that overlaps the frequency range of their calls, as this makes their calls less attractive to bats (Tuttle and Ryan 1982).

**Shifting Receiver Preferences and Signal Characteristics** Some prey species and eavesdropping predators may be in a co-evolutionary arms race in which prey species continually shift their signals and preferences within a modality to differ from those of predators, while predators try to track these changes. In field cricket populations that have ceased producing ancestral calls due to the recent introduction of



parasitoid flies attracted to these calls, males signal to females with a novel “purr” courtship signal which attracts female crickets but not parasitoids (Tinghitella et al. 2021). Similarly, pine beetles show spatial and temporal variation in their communicative pheromone blends and show enhanced preference for the blend associated with their specific time and locality whereas this is not true for sympatric eavesdropping predators (Raffa et al. 2007). In fact, when comparing communities from Wisconsin and California, predators from each location were more attracted to pine beetle pheromones from the opposite location than to their local population, while pine beetles preferred their local conspecific pheromones (Raffa and Dahlen 1995). This suggests that populations are continually shifting these blends to evade eavesdropping (Raffa et al. 2007). However, a specialist parasitoid showed identical preferences as local conspecific receivers, suggesting this tactic may be effective only at limiting eavesdropping by generalist predators.

**Employing Social Behavior to Mitigate Risks of Eavesdropping** Species may also be able to utilize social strategies to reduce the risks of interceptive eavesdropping. Signaling aggregations occur in many species, and simple dilution effects in which signalers suffer lower per capita risk from predators and parasites could be one benefit. Acoustically signaling male túngara frogs and moths (*Achroia grisella*) experience lower per capita predation risk when calling in leks of increasing size (Alem et al. 2011; Ryan et al. 1981). Additionally, benefits of communal signaling may be enhanced by coordinated signal-timing among chorus-mates. Males of the frog *Smilisca sila* call in near-perfect synchrony, exploiting an auditory illusion in predators and parasites to reduce their attractiveness to these enemies (Leggett et al. 2020). Further, when males call in synchrony, this preserves silent gaps between synchronized calls, which may allow cues of approaching predators to be more effectively detected, allowing appropriate responses to approaching predators (Greenfield 2015).

### Interceptive Eavesdropping on Predator-Alarm Calls

Another form of interceptive eavesdropping that commonly takes place is one species gaining information about the presence of a predator by eavesdropping on the alarm calls of a hetero-specific (the ideas presented in this section are reviewed in Magrath et al. 2015). This can allow individuals of the eavesdropping species to cast the net of predator detection more widely, by increasing the number of individuals that can alert them to a predator's presence. A species may also gain better information about the presence of predators if, for instance, the eavesdropped-upon species has better predator-detection abilities or typically occupies vantage points beneficial for predator detection, e.g., a higher stratum in the canopy. The benefits of eavesdropping will be dependent on the degree to which the complements of predators that pose risks to the signaling and eavesdropping species overlap, with higher overlap allowing greater benefits to eavesdroppers. In principle, this form of eavesdropping could occur via different sensory modalities but has currently been demonstrated primarily in the acoustic modality. This is likely partly due to ease with which acoustic signals can be perceived and studied by researchers, but the rapid, loud, and omnidirectional transmission of acoustic alarm calls may make them broadly suitable for alarm signals, while also making eavesdropping relatively simple for any nearby animal.

This form of eavesdropping poses less obvious costs to signalers than eavesdropping by predators does, if any. Indeed, it may be in a signaler's benefit for heterospecifics to eavesdrop. An increased number of individuals moving to cover upon receiving an alarm call may cause greater commotion, which could confuse a predator to a greater degree (Sherman 1985). Additionally, eavesdropping heterospecifics may be motivated to form mixed-flock species allowing reciprocal eavesdropping to benefit both species. In such a case, mutualistic communication may eventually evolve, causing this to cease to be eavesdropping as individuals from the cooperating species become intended receivers. Eavesdropping by

heterospecifics may also allow opportunities for occasional dishonesty which, if kept under a certain threshold frequency, could allow exploitation of heterospecific resources, as in the case of fork-tailed drongos deceiving meerkats (Flower 2011).

#### Interceptive Eavesdropping to Locate Resources

Eavesdropping by conspecifics has focused on social eavesdropping (see next section), with less of an emphasis on interceptive eavesdropping. However, scenarios exist in which conspecifics may benefit from intercepting signals that offer information on the location of the signaler or the location of a resource that has been discovered by the signaler. Duets occur in many singing insects, in which females call in response to calling males, allowing the calling male to locate that female. Some males adopt a parasitic strategy in which they do not call but will home in on female responses to male callers to mate with them (Otte 1972). For this to be considered eavesdropping, we must assume that the female is directing the signal specifically as a reply to the calling male, rather than this being a generalized signal to all conspecific males within earshot. Interestingly, males of *Caedicia* katydids append a chirp to the ends of their calls, which seems to obscure the female response from rivals, thwarting potential eavesdroppers (Hammond and Bailey 2003). Similarly, signals may cue eavesdroppers into the location of rare ecological resources. Many animals give food calls to attract certain conspecifics to forage, and it is likely that conspecifics (and possibly heterospecifics) could eavesdrop on such calls to pilfer resources from signalers.

#### Social Eavesdropping

As discussed with regard to interceptive eavesdropping, eavesdropping on signals themselves can be informative. However, signals are selected to influence receiver behavior, and receivers are selected to respond in the way that best serves their interest, so additional information not contained within the signals themselves can be gleaned by observing the behavior of interactants within a communicative exchange. This is referred to as social eavesdropping (Peake 2005).

Information stemming from social interactions among conspecifics tends to be more salient to other conspecifics rather than heterospecifics; thus, social eavesdropping tends to be a phenomenon that occurs within species (Peake 2005).

Communicative events such as aggressive contests often involve multiple signals being sent back and forth between interactants, and multiple responses from each interactant to the signals of the other, before a favorable outcome is reached (Hardy and Briffa 2013). Individuals in social species are attentive to interactions among conspecifics (Abril-de-Abreu et al. 2015), and, by observing interactions, social eavesdroppers can glean information about the relationships between communicating individuals and/or make relative comparisons of salient traits of individuals. For example, female crayfish that observed a fight between two males preferentially approached and contacted fight winners, while females who did not witness the fight showed no preference (Aquiloni and Gherardi 2010). This suggests females use information gleaned from the outcome of male combat when choosing mates, rather than simply basing choice on characteristics of the individual males themselves.

The costs or benefits of social eavesdropping are often asymmetrical among interactants. When considering the aforementioned crayfish example, combat winners benefit from an increase in attractiveness to nearby females due to eavesdropping, while the opposite is true for the loser of the exchange (Aquiloni and Gherardi 2010). Such asymmetrical payoffs could lead to different strategies employed by individuals occupying different roles in an interaction. Victory displays are widespread in communication networks and may be a means for a winner of an aggressive exchange to capitalize on the benefits of social eavesdropping by conspecifics (Bower 2005). Conversely, losers may be expected to behave in a way that reduces the likelihood that this information spreads, such as signaling at low amplitude (Dabelsteen et al. 1998). In certain situations, eavesdropping could have similar payoffs for both individuals involved in an interaction. For example, coalition partners could both benefit from conspecifics observing them engage in affiliative

signals, as this will advertise their combined strength to potential challengers.

The benefits of eavesdropping to the eavesdroppers will likely be influenced by the risks or costs that might have to be incurred to gain information about individuals or pairs via direct sampling. For instance, if escalated combat can be highly injurious, observing that an aggressive signal from A elicits a submissive signal from B allows an eavesdropper to avoid risking combat with A if it has already been established that they are a less formidable fighter than B (and are, therefore, much less formidable than A). Additionally, the duration of combat or level of escalation of the exchange might provide information regarding how closely matched these individuals are ( $A > B$  vs.  $A \gg B$ ) (Hardy and Briffa 2013). Similarly, observing affiliative signals between coalition partners C and D may offer information regarding the likely combined reaction that an aggressive behavior directed at either C or D is likely to elicit, without having to directly elicit such a reaction. Social eavesdropping likely provides less accurate information than would direct sampling of individuals or relationships (Earley and Dugatkin 2002) but, due to lower risks and less time spent sampling individuals, it could be beneficial in a variety of situations.

#### Social Eavesdropping and Signaling Modalities

As with interceptive eavesdropping, social eavesdropping has been demonstrated across numerous signaling modalities, though it has most often been demonstrated in the visual and acoustic modalities. Below are some examples of interceptive eavesdropping in different modalities:

- (i) **Acoustic signals:** Female great tits eavesdrop on acoustic exchanges between their mate and other males and were more likely to venture into neighboring territories if their mate lost a vocal exchange (Otter et al. 1999) (see below).
- (ii) **Olfactory signals:** Male golden hamsters make judgments about the relative social salience of other males based on the configuration of overmarking of scent marks (Johnston 2005) (see below).

- (iii) **Visual signals:** Paper wasp queens who observed two other queens fighting were less aggressive toward the queen they had observed to initiate more aggression, and receive less aggression, during the fight (Tibbetts et al. 2020).
- (iv) **Seismic signals:** Social eavesdropping has not been thoroughly studied in species that primarily use seismic signals; however, it has been demonstrated in some treehopper and leafhopper species. In these species, males produce jamming signals which disrupt courtship duets between a female and a rival male, suggesting these male-female duets are recognized via social eavesdropping (Mazzoni et al. 2009).
- (v) **Multimodal signals:** Female crayfish that observed a fight between two males preferentially approached and made contact with fight winners, but only if they had been granted both visual and olfactory access while observing the fight (Aquiloni and Gherardi 2010). Many displays contain multimodal elements (Hebets and Papaj 2005); however, testing multimodal communication and eavesdropping is challenging. Many eavesdropping studies have allowed potential eavesdroppers access to only a single modality or have investigated only a single modality among several that might have been available to eavesdroppers. It is likely that many examples of social eavesdroppers utilizing multimodal communication pathways exist that are yet to be identified.

In interceptive eavesdropping, regardless of the modality of the signal, the information contained in the signal is used in essentially the same way; since the goal is usually to locate the signaler, interceptive eavesdroppers must simply orient themselves to move in the direction of highest signal intensity. In social eavesdropping, however, the interactions that must be parsed may look quite different depending on the signaling modalities used. This means that which signal features are salient to eavesdroppers, and which relationships between features of interactants' signals are important, may differ in different

modalities. To demonstrate how signal modality can influence the form that eavesdropping takes, I will elaborate on two examples of eavesdropping in different modalities: acoustic and olfactory.

A classic example of social eavesdropping is eavesdropping on acoustic exchanges in great tits. Females whose mate had “lost” a vocal exchange with an interactive playback speaker, by singing at a lower rate than the playback stimuli, were subsequently more likely to intrude into neighboring territories, potentially indicating female attempts to initiate extra-pair mating (Otter et al. 1999). The same was not true for mates of males who had “won” against this same intruder. The authors interpret this as evidence that the factor motivating female intrusions to neighboring territories is the perceived lower competitive abilities of their mates *relative* to the playback intruder. Thus, females acted on information that it was only possible to gain via listening to the acoustic interaction between their mate and the playback intruder in real time, their mate’s singing rate relative to that of a perceived challenger.

Male golden hamsters communicate in the olfactory channel via scent marks (Johnston 2005). Olfactory signals such as scent marks remain on surfaces for an extended period after the signal has been sent (or left), meaning signalers are often not present in the vicinity when receivers receive the signal. Upon encountering a scent mark, golden hamsters often scent mark on top of this other male’s scent mark, and this represents a temporally staggered social interaction among these males. In much the same way that interactants are not simultaneously present during communicative exchanges, social eavesdroppers are not present to observe this exchange in real time. However, in golden hamsters, eavesdroppers can extract social information from investigating patterns of scent mark overlap (the following research is all reviewed in Johnston 2005). In a series of experiments, males that had encountered two scent marks that overlapped were subsequently introduced to the isolated scent marks of these males, as well as that of a novel male whose scent they had not encountered previously. Subjects spent the same amount of time investigating the novel male’s scent and the

scent of the male whose scent mark had been on the bottom of the scent mark exchange, while investigating the top-marked male’s scent least. The authors interpreted this as demonstrating that the top male was perceived as more familiar; i.e., his scent had been perceived as more salient and so was remembered more strongly as a more socially salient individual. A similar phenomenon was found when males inspected female marking interactions, and this was true even when more of the bottom-marked individual’s scent was present overall. Thus, it appears to be the spatial arrangement of overlapping scents, rather than scent amount, that causes these differences in signaler salience.

The two examples above highlight how social eavesdropping can look different depending on the characteristics of the modality being employed. In the case of the acoustically signaling great tits, females could listen in real time as the communicative exchange unfolded, and simultaneously compare temporal features of songs, the relative song rates. In contrast, due to the temporal decoupling of signal transmission and reception in scent marking, golden hamsters use spatial cues pertaining to scent mark overlap to extract social information. Thus, signal modality determines which features of interacting signals will be informative to eavesdroppers.

### Social Eavesdropping, Social Structure, and Ecology

The feasibility of social eavesdropping in different modalities will likely be constrained by aspects of a species’ ecology and social structure (Otter and Ratcliffe 2005). An acoustic signaling exchange occurring among co-resident females in a cohesive group of social primates is more likely to be perceived and eavesdropped upon by conspecifics than is a web-borne tremulatory interaction between a male and female of a solitary spider species. A species’ habitat will influence the active space of signals, and this effect will differ across modalities. Species in visually cluttered environments will have fewer opportunities to eavesdrop on short-range visual signals than species occupying more open habitats, possibly leading to eavesdropping on acoustic signals to be

more common than visual. Additionally, characteristics of the habitat can influence aspects of social organization, which can have a knock-on effect on the potential for eavesdropping. Resource abundance in an environment may affect territory size and density which could make it more or less likely that an individual territory-holder, or a prospecting female, is within earshot of multiple conspecifics involved in an acoustic exchange (Otter and Ratcliffe 2005).

## Audience Effects

Audience effects represent another phenomenon that can emerge within communication networks. Many animals alter their signaling behavior depending on whether a receiver, or a specific category of receiver, is within range to receive their signal. For example, many species produce alarm calls more frequently when kin are nearby (Sherman 1977). These situations have often been referred to as audience effects in the literature. However, these examples can also simply be subsumed under the broader notion of flexibility in signaling behavior, and the term “audience” as used in some of these examples is used as a synonym for the term “receiver” (Zuberbühler 2008). This can lead to the concept of audience effects being ill-defined. As such, other researchers have defined audience effects in a more specific way, as changes in a signaler’s signaling behavior toward a receiver due to the presence of additional observers who are not themselves engaged in the interaction (Matos and Schlupp 2005). Similarly to the definition of eavesdropping used in this piece, this definition of audience effects requires that communication happens within a communication network, and it requires conspecific individuals to pay attention to, and gain salient information from, interactions between other conspecifics. Thus, the evolution of audience effects relies on an established tendency for eavesdropping in a population.

## Examples of Audience Effects

Many examples of audience effects are documented in the literature, spanning diverse

taxa. Chimpanzee females produce copulation calls when mating but exhibited an audience effect in which they produce calls less frequently when higher-ranked females are nearby, possibly to avoid receiving competitive aggression from these females (Townsend et al. 2008). In field crickets, males engaged in aggressive behavior directed more aggressive displays toward their rival when a female was present to observe the fight (Tachon et al. 1999). Interestingly, the presence or character of audience effects need not be static and may be influenced by characteristics of the signaling individual or their recent experiences. In Siamese fighting fish, males that had won a previous encounter did not show audience effects when participating in subsequent aggressive exchanges. Conversely, losers of previous encounters reduced their use of gill cover displays while maintaining similar levels of more escalated aggressive behaviors when an audience was present (Matos 2002). This differential effect of an audience may suggest differential payoffs of being observed by audiences for winners and losers and an attempt by losers to mitigate these costs.

## Conclusions

In reality, almost all communication occurs within the context of a communication network. This can exert significant influence on the evolution of the signal production and receiver evaluation, such as facilitating eavesdropping and audience effects. Though not discussed in this piece, communicating within networks can also foster interesting means by which signalers can compete with one another, such as signalers exploiting precedence effects in receiver sensory systems to be perceived at the expense of rivals (Greenfield 2015), and signalers sending jamming signals to disrupt communicative exchanges among conspecifics (Mazzoni et al. 2009). Thus, the connectivity among signalers and receivers within communication networks can have profound effects upon the evolution of communication systems and the behavior of signalers and receivers.



## Cross-References

- [Auditory Processing and Perception](#)
- [Auditory Signals](#)
- [Chemical Signals](#)
- [Social Network Analysis](#)

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## Community

### ► Population

## Comorbidity

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## Synonyms

Multimorbidity; Polymorbidity

## Definition

Comorbidity has several definitions, but all are based on a single core concept: the co-occurrence of multiple health problems in an individual. This co-occurring condition includes disease, disorders, and illness (Valderas et al. 2009).

Feinstein define comorbidity as “Any distinct additional entity that has existed or may occur during the clinical course of a patient who has the index disease under study.” (Feinstein 1970).

## Cause of Comorbidity

Comorbidity can occur for a variety of reasons. It may be a chance occurrence or may develop because two disorders have shared or overlapping risk factors (e.g., migraine and epilepsy co-occurred, often as a result of head trauma) (Klein et al. 2004). The possible risk factors are genetic susceptibility, family history, environmental factors (e.g., air pollution), different socio-demographic variables (e.g., age, sex), etc.

## Methods for Measurement of Comorbidity

Some of the valid and reliable methods to measure comorbidity are discussed below:

**Charlson index:** The Charlson index is the most extensively studied comorbidity index. This includes 19 diseases and assigns a weight of 1–6 on the basis of the strength of their association with mortality. So, the Charlson index is the sum of the weight for each comorbid condition and can range from 0 to 33 (Ronald et al. 2001).

**Index of Coexistent Disease (ICED):** This index is particularly useful in those studies where mortality and disability are the outcome of interest. ICED has a two-dimensional structure, measuring both pathophysiologic disease severity and disability (de groot et al. 2003). One dimension discusses about the severity level of 14 diseases and the other one discusses about the severity level of 11 physical and mental disability or impairment. In this index, the patient placed on

a four-point scale for each disease and on a three-point scale for each impairment. Then the peak scores of these two dimensions are summarized into a four-point scale, from 0 to 3.

**Cumulative illness rating scale (CIRS):** CIRS gives the good validity and reliability due to its close resemblance to common clinical practice. It rates 13 conceptually valid body systems (e.g., cardiac, vascular, respiratory) on a five-point severity scale, ranging from “none” to “extremely severe.” (Linn et al. 1968).

**Kaplan index:** This index was specifically constructed to investigate the complication of diabetes. It uses two forms of classification: they are type of comorbidity and the pathophysiologic severity of the present comorbid conditions.

## Consequences of Comorbidity

The comorbidity condition covered a broad spectrum of diseases so, it has multiple consequences. This mainly affects the mortality, quality of life, functional status, treatment strategy, and health care of the patients (Ronald et al. 2001).

## Treatment

Comorbidity is more difficult to treat than an alone disorder. It is mainly treated by medication and behavioral therapy (Weel et al. 2006). Sometimes a single medication benefits multiple problems. There are several ways to treat comorbidity: Integrated (treatment of all disease at the same time), sequential (treatment of diseases one by one), and single diagnosis (treatment of only one disease).

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## Companion Animals

► [Pets](#)

## Comparative Cognition

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## Background

Our world is full of organisms with remarkable cognitive abilities. For example, the Clark's nutcracker, a bird, is capable of remembering the location of thousands of seeds that it stores for the months of winter and spring (Lanner 1996). Some abilities have long been thought to be uniquely human yet more recently have been discovered in nonhuman species as well. A prominent example is tool use which has by now been observed in a variety of species – from insects to primates (see Shumaker et al. 2011). Plentiful other exciting examples can be found in other chapters of this encyclopedia.

So how do those species achieve such proficiencies and how, why, and when did such abilities evolve? Comparisons of different species, discussed in the light of evolution and ecology, may help us finding answers.

Comparative cognition is the study of similarities and differences in how organisms acquire, store, and act on information (Shettleworth 2010). Cognitive processes vary in complexity but the rankings and definitions of the levels of complexity are constantly evolving.

Studying cognition in animals is challenging as it can be notoriously hard to understand the processes within another species' mind without spoken language. Moreover, drawing conclusions about cognition purely from behavior can be deceptive. However, sophisticated tools to tackle those problems have been developed. In order to understand present procedures in comparative cognition it is important to look at its history and development.

In the nineteenth century, cognitive abilities of animals were mainly discussed on the basis of anecdotal reports. While some were carefully considered and interpreted, there are other examples that seem quite problematic to a critical mind, for example, from George Romanes (1884), who described the following incident: A monkey, who was wounded by a hunter, holds out his blood-covered hand. Romanes' interpretation proposed that it clearly did so to evoke guilt in the hunter.

When the century turned, however, critics grew increasingly skeptical about this method and pointed at its vulnerability to anthropomorphism and over-interpretation. Many called for more objective, quantifiable, and replicable methods (e.g., Morgan 1894) leading to decades of focusing such research purely on behavior while evading cognitive studies.

At that time, two traditional schools of science worked on similar questions without much exchange between each other: Experimental psychology, specifically the field of behaviorism, concentrated on answering questions on human behavior by comparing human learning mechanisms to other animals using strictly controlled laboratory experimentation, while avoiding

cognitive explanations (e.g., B.F. Skinner, Edward Thorndike, John Watson). The center of attention was set on an anthropocentric viewpoint: Can other animals do what humans do? And if so: how?

At roughly the same time, biologists, mainly in the fields of ethology and behavioral ecology, focused on detailed observation of wild animals and very naturalistic experiments (e.g., Konrad Lorenz, Nikolaas Tinbergen, and Karl von Frisch). Their interest was largely to place behavior in an ecological and evolutionary framework rather than to focus on animal-human comparisons, which can be called an ecological approach to behavior.

It took decades for both sciences to appreciate each other's values and to recognize that both approaches can complement each other, more than they contradict. Nevertheless, the tools that both schools developed during this time to investigate *behavior* still set the foundation for modern comparative research in *cognition*.

It is however important to mention that while cognitive research on animals was largely put on halt in the first half of the twentieth century, the study on cognition was not forgotten altogether during that time. Some scientists did indeed investigate cognitive processes – prominent examples include Robert Yerkes, Edward Tolman, and Wolfgang Köhler – although early on with less recognition and great controversy. The impetus for the so-called to “cognitive revolution” however was set by the disciplines of computer sciences (e.g., Turing 1950) and linguistics (e.g., Chomsky 1968). Together with the tools provided by biology and psychology it now seemed possible to draw testable inferences from behavior to cognitive processes. Today cognitive science is a thriving interdisciplinary field including cognitive neuroscience, developmental psychology, ethology, psychology, evolutionary biology, anthropology, neuroanatomy, and others.

So why do we need a comparative approach to cognition? The title of an essay written by the evolutionary biologist Theodosius Dobzhansky (1973) is a now well-known phrase: “Nothing in biology makes sense except in the light of

evolution.” But evolution itself is hard to observe. Luckily however we have a seemingly endless supply of “products” of evolution – a vast number of organisms, we can observe. Researchers of the field of comparative cognition study the similarities and differences of those organisms, compare them in respect to their socio-ecological environments and phylogeny to tackle questions on how, when, why, and under what circumstances cognitive abilities emerged.

## Areas of Cognition

As mentioned earlier, levels of complexity of cognitive processes are under constant debate. It is however helpful to define key areas of cognitive research such as fundamental mechanisms and the domains of physical and social cognition (see Shettleworth 2010).

### Fundamental Mechanisms

Those include processes such as perception, learning, and memory. Fundamental mechanisms can be seen as the backbone or building blocks of many complex cognitive abilities. It is for example crucial to perceive, that is, see/hear/smell, a conspecific, learn something about it (e.g., distinguish it as an individual), and memorize the learned, for processes that might be termed “higher” cognitive abilities such as inferring relationships between others. Nevertheless, it is crucial to distinguish whether a positive result in a task might be due to such “higher” cognitive abilities or whether they can be solved merely through “simpler” processes such as associative learning.

### Physical Cognition

How do organisms find their way around? What do they understand about casual relationships? Why do some species use tools? Do they truly understand how tools work? What understanding do they have about basic physical principles of their world? Do they plan ahead? Such and more questions are investigated in research on physical cognition.

## Social Cognition

Research in the social domain on the other hand focuses on cognitive processes that are applied in a social context. Such as: can animals learn from each other? Can they infer a relationship between others by observation? Do animals have prosocial tendencies or can they cooperate with each other? Can they infer a state of mind to others?

## Hypotheses on Cognitive Evolution

Researchers have developed a great variety of hypotheses to explain the evolution of complex cognition. However, detailed discussions are out of the scope of this entry (but see e.g., Burkart et al. 2016). To provide a basic overview however the following part presents some selected influential hypotheses. While some aim to explain the evolution of cognition in general terms, others concentrate on more specific drivers of cognition.

### Physical Characteristics as Drivers for Cognitive Evolution

Some hypotheses propose that the physical characteristics of some organisms primarily lead to larger brains and therefore evolution of complex cognitive abilities (see Dunbar 1998 for a discussion).

One of those is the epiphenomenal hypothesis, which postulates that a large brain is an unavoidable consequence of a large body, which therefore leads to higher cognitive abilities. Another is the developmental hypothesis, which names maternal metabolic input as the driving factor on brain evolution and advanced cognitive abilities as consequence of such. It suggests that the nutritive value of a mother's food intake determines whether brains evolve to larger sizes and complex cognition. Such hypotheses, however, are considered rather outdated by the majority of the modern researchers. As both, developing and maintaining brains, is very costly and evolutionary theory bases on the balance of costs and benefits, it is "intrinsically unlikely that large brains will evolve merely because they can" (Dunbar 1998). This does not imply that influences such as nutrition are not crucial fundamentals but rather that those

factors act as energetic constraints but not as primary *drivers* of the evolution of cognitive abilities.

### Adaptive Intelligence Hypotheses

Adaptive intelligence hypotheses, on the other hand, state that complex cognitive skills and increased brain size are the *result* of an iterated process of a species adaptation to its socio-ecological environment.

Ecological hypotheses propose that brain size is influenced by ecological conditions and different hypotheses have concentrated on different possible drivers. Some postulate that overall ecological complexity, hence how difficult it is to access appropriate food, to find territories and such, influences the evolution of cognitive skills or that advanced cognitive abilities work as a buffer to be able to readily apply flexibly to environmental changes (cognitive buffer hypothesis; Deaner et al. 2003). Others focus on more specific possible drivers such as increased efficiency through technical elements in foraging behavior (technical intelligence hypothesis; Byrne 1997) or advanced physical problem solving skills in tool-using species (physical cognitive adaptive specialization hypothesis; Teschke et al. 2013).

Alternative or complementary are hypotheses, which attribute advanced cognition to social challenges of a species such as learning from others, recognizing others, interacting with others, manipulating others and so forth, in addition to their ecological environments. Social life is highly complex as other individuals are difficult to predict. Therefore, cognitive abilities presumably have emerged to deal with such sets of challenges (social intelligence hypothesis; Humphrey 1976). Again, the investigation of specific social drivers of evolution yielded a variety of different hypotheses. Most prominent are probably hypotheses that attribute this evolution to factors such as the group complexity of a species, for example, how big and variable the group size of a species is (social complexity hypothesis; Bond et al. 2003), the degrees of complexity of long-term pair bonding (social relationship hypothesis; Emery et al. 2007) or cultural aspects (cultural intelligence hypothesis; Whiten and van Schaik 2007).



The examples given are not mutually exclusive and do not provide a complete picture of the great variety of hypotheses that are postulated. Rather it should provide an idea on how those hypotheses are developed and what they might be.

### Domain-General Versus Domain-Specific Intelligence

Whether there is domain-general or domain-specific intelligence in nonhuman animals is an ongoing and controversial debate in cognitive sciences. In theory domain-specific adaptations may be beneficial if the environment is rather predictable while domain-general intelligence might increase an individual's fitness when confronted with fast-changing environments. However, rather recently it has been proposed that both may be coexisting with some species relying more on one kind while another species might profit to a higher degree from the other (see e.g., Burkart et al. 2016 for a detailed discussion).

### Physical Proxies for Advanced Cognition

Note that, for simplicity, brain size was mentioned to be influential on the occurrence of complex cognitive processes. However, how exactly large brains are linked to increased cognitive abilities is a challenging question to answer. Although there seems to be a correlation between relative brain size (brain/body ratio rather than absolute brain size) and complex cognition, there is ongoing controversy on how fitting it is as a proxy. This

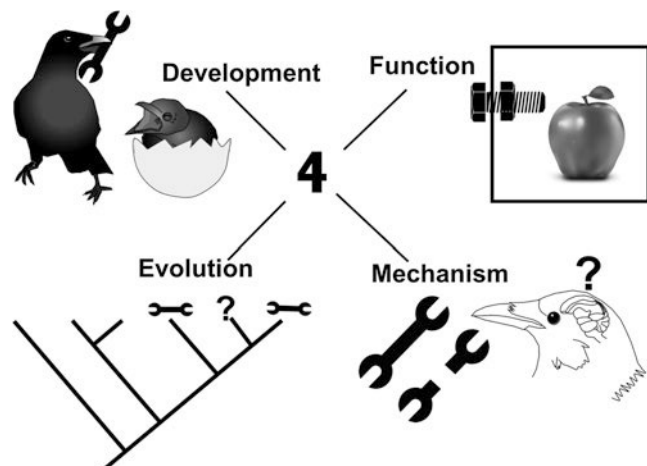
becomes particularly important when different taxa are compared as their morphological attributes (not only the size but also, e.g., the structure of the brain) can be substantially different. Most recent findings propose that absolute neuron count, which can be substantially different in brains of the same size, might be the best morphological proxy for complex cognition we have currently available (Olkowicz et al. 2016).

### Tools of Comparative Research

Although an essential aspect, evolutionary theories constitute only one part of research on comparative cognition. The ethologist Nikolaas Tinbergen (1963) famously proposed that a behavior can only be fully understood by addressing questions on four levels: ontogeny, evolution, causation, and function (see Fig. 1). This also holds true for cognition. For research on tool use for example, this means investigating how this ability (1) develops during the course of an individual's lifetime (ontogeny) (e.g., Does it need social input to occur? Does it only develop in a certain ecological environment?), (2) when it emerged in the phylogeny of this species (evolution) (e.g., Did the ability emerge in two species due to convergent or parallel evolution? In other words: Did it develop one or multiple times and when?), (3) what mechanisms are needed (causation) (e.g., What does one need to understand to use

### Comparative Cognition,

**Fig. 1** Symbolic presentation of Tinbergen's four questions on tool use. Wrenches represent tool use





tools? Which process underlay the ability? What areas of the brain are active during the process?), and (4) what function it might serve to increase fitness (e.g., Does it insure stable food supply? Is the food gained more nutritious?) (Fig. 1).

To address those questions researchers often rely on a combination of experimental and observational approaches. Experimental research focuses on investigating something – here a cognitive ability – by changing one variable of interest while keeping other variables as constant as possible. Typically, this is done by testing species, which are closely related but differ in a specific characteristic (e.g., ecology, social structures, morphology, and physiology) and distantly related species, which are similar in the trait that is investigated.

Such an approach has been integrated, for example, in the studies by Teschke et al. (2011, 2013). To investigate whether tool use was either a driver or product of advanced physical cognition woodpecker finches were compared to small tree finches, both belonging to the Darwin's finches living on the Galapagos Islands. The first has shown to be a habitual tool user while the second is not. Therefore, if tool use is either driving or resulting in higher physical competence, woodpecker finches should outperform small tree finches in physical problem solving tasks. On the other hand, this would imply that distantly related species, which also use tools, should have developed advanced physical cognition as well. To test this, Teschke et al. (2013) conducted the same experiments with tool-using New Caledonian crows (distantly related to the Darwin's finches) and nonhabitual tool using corvids, the carrion crows, who are, again, closely

related to New Caledonian crows and distantly related to Darwin's finches (see Fig. 2).

In the same manner one can test for varying social structures, differences in other aspects of feeding ecology and so forth and should, in the end, be provided with a better picture of the drivers of specific cognitive abilities.

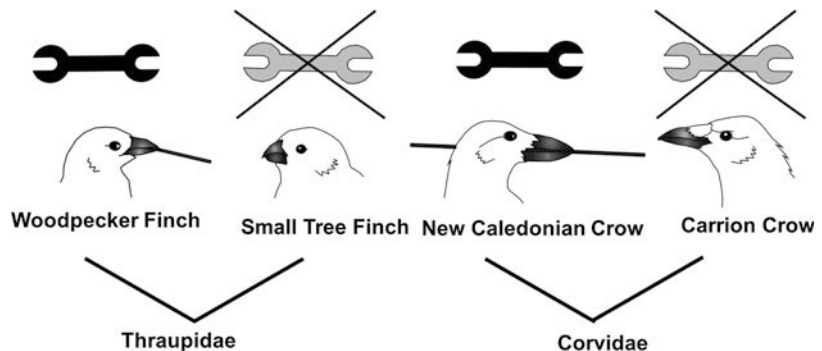
It is however important to note that comparative research is not restricted to the comparison between different species. The influences of, for example, pre-experience, rearing, sex, age, dominance, and personality can also be examined comparatively within a species. Also, some species have great intraspecies variation in socio-ecological environments (e.g., climate or group size), which can have an influence on the occurrence and proficiency of specific cognitive abilities.

Observational research is another important analytical tool for comparative cognition. Not only does it provide insight to experimental research (e.g., why might a certain cognitive ability be of advantage for an individual?) but also allows for more naturalistic investigation. It provides a source for information, inspiration, and ecological validity. For profound research, it is crucial to have a well-founded knowledge of the species at hand, preferably from observations in the wild as well as from laboratory populations.

While both approaches, experimental and observational, have their challenges and merits, both are needed for a rounded understanding of a cognitive ability and complement each other. However, in contemporary research there is no definite line between them, as experiments are often conducted in the field or observational data is collected in laboratory settings.

#### Comparative Cognition,

**Fig. 2** Comparison of physical problems solving abilities in Thraupidae (taxonomic family of Darwin's finches) and Corvidae (Teschke et al. 2011, 2013). Wrenches represent habitual tool use



## Progression and Challenges

### The Stepwise Comparison

As each research facility has a limited amount of species available, comparative research progresses largely in a “stepwise” manner. New methods to investigate certain cognitive abilities are usually proposed alongside a dataset from one or a few species. Those methods are then adopted by other researchers and used to test different species. Over time, the amount of species tested and with it the comparative data grows larger. Through iterated discussions, methodology can be developed into further detail and investigations can thus be improved. Moreover, it is often necessary to alter procedures to fit a particular species’ demands. While a primate might use a hand to grab a tool, it may be physically impossible for a bird to use the same limb. Or while novel objects might trigger an approach in one species due to a pre-existing predisposition, it might cause fear in another or indifference in yet another. While some species might rely heavily on visual information others might be more attentive to smell or show certain reactions only in a specific context. Thus, it is crucial to consider those predispositions – might they be of physical, behavioral or physiological nature – when testing different species. The advantage of this stepwise comparison is that those species-specific demands can be met and taken into account. However, modifying methods must be considered carefully as the comparative value might be lowered.

Some test paradigms are used to test for different cognitive abilities. While this is often a productive development it can also be source of confusion and misguided comparisons especially with changing or ill-defined terminology. Possibly one of the most commonly used benchmark paradigms in physical problem solving is the string-pulling test. More than 163 mammalian, avian, and insect species have been tested in over 208 studies (see Jacobs and Osvath 2015 for a detailed review). The basic idea is to attach a reward, which is out of reach to a string that is accessible to the subject. To get to the reward the string has to be pulled, which brings the reward into reach. This straightforward setup has been

frequently used partly because it is quite easy to conduct, with very little prior training and habituation. Also, it allows for a great variety of modifications and control groups. The strings can be vertical or horizontal, there can be one or multiple, strings can be made nonfunctional (e.g., through a cut), multiple strings can vary in orientation, overlap each other, be of different perceptual characteristics (e.g., color), and so forth. Also, string pulling tests have been used to investigate different mechanisms including means-end understanding, goal directedness, associative learning, functional generalization, insight, and more. This resulted in many different explanations and interpretations for similar findings, while on the other hand similar conclusions have been drawn on different outcomes. While it is desirable to go into more detail and therefore make adjustments, this has resulted in a large dataset that is challenging to compare. The paradigm has been used in at least 50 different variations, each of which brings additional factors that can influence the results and therefore researches have to include those factors in their comparisons.

Another challenge of stepwise comparisons is unpublished data. For different reasons (e.g., difficulty in publishing in respectable journal) results that are “negative” or inconclusive are rarely being published and therefore hard to access for the international research community. This can lead to limited exchange between research facilities who are sometimes facing similar sets of problems. Moreover, the value of “negative” results has often been underestimated. However, there seems to be a change in progress and designated journals are determined to close this knowledge gap.

### Large-Scale Comparisons

Because of challenges discussed above some recent studies used strictly the same methodology while testing a variety of influential factors and species. A recent example is a study by MacLean and collaborators (2014), in which 567 individuals of 36 species have been tested on self-control using two types of tasks. Their performance was then correlated to neurological measures such as absolute and relative brain size and

socio-ecological factors such as group size and feeding ecology. Testing procedures were highly conservative and strictly the same for all species. Although this remarkable effort yielded some informative results there have been justifiable questions raised on comparability. For example, one of the two aforementioned tasks required the test subjects to track the hands of the experimenter to successfully choose the correct location of a reward. Jelbert et al. (2016) found, however, that performance in this task varied with hand tracking training in New Caledonian crows. They therefore argue that the poor accuracy of birds as opposed to mammals in the original study might be due to them having greater difficulties to track human hand movements than, for example, primates. Once they received training they seemed to show as high performances as great apes in this task. In the second task, MacLean and colleagues replaced an opaque, baited cylinder with a transparent one. Whether the subjects took a detour to reach the reward inside or try to access it through the transparent wall of the cylinder was then used as a measure for inhibitory control. Vernouillet et al. (2016) tested Clark's nutcrackers in the same task and found that a learning phase was needed for them to consistently choose the detour. The authors argued that one of the explanations to this result might be that less experience with transparent objects gave some species a disadvantage to solve the task and therefore basic habituation to transparency, hence a baseline criterion, should precede the actual tasks. Those examples highlight the importance of not only taking each species predisposition but also pre-experiences into account.

Additionally, it is crucial to keep a critical mind on which species are used for the comparisons. This is especially true for broad evolutionary hypotheses and discussions. For example, in the large-scale study discussed above one of the comparisons made was that of mammals and birds. However, mammals were represented in a larger total number in general and species of each taxa, which are attributed most complex cognitive skills – such as primates in the mammalian taxa and corvids as well as parrots in the avian taxa – were not represented equally. However, once

more corvids were tested in a succeeding study (Kabadayi et al. 2016) the comparison yielded different results.

Clearly, it is never possible to test a complete set of all species and this naturally remains an issue for interpretations on broader evolutionary theories. However, as long as those limitations are kept in mind data can be discussed accordingly.

In general, one might say the biggest challenge in comparative research is the dilemma between comparable methods and compatibility to all study species as well as conclusions drawn from model species to others.

## Possible Directions

To tackle the abovementioned challenges different approaches have been proposed. The following part aims to give an overview of some selected ideas.

### Emphasis on Baseline Criteria

As discussed above, some problems concerning pre-experience and species predispositions can be limited by applying thoroughly designed baseline criteria such as hand-tracking training or habituation to transparent objects in the abovementioned study. Those provide the possibility – at least to some extent – to determine whether test subjects are equally prepared and acquainted with crucial aspects of a certain task that are not directly related to the ability in focus yet are essential to solve the task correctly.

### Multi-task Batteries

One possible approach to minimize the effects of species predispositions is using large test batteries, which aim to test cognitive domains, hence a broader spectrum of cognitive abilities of a certain category, through a variety of tasks. Therefore, the performance of multiple tasks adds up to the total performance in a cognitive domain, which – if chosen considerably – limits the possible influence of species predisposition or other influential factors in one specific task to the overall outcome.

A prominent example of a large cognitive survey, that includes a variety of primate species, is the

primate cognition test battery (PCTB), which was conducted by Hermann and colleagues in 2007. In 16 different tasks, subjects were tested in both, the physical (space, quantities, and causality) and the social domain (social learning, communication, and theory of mind). Although a test battery is not immune to biases that are more appropriate for some species than others, they are a least more robust to those influences than single tasks.

Likewise, multi-task batteries can also be established for more specific cognitive processes. Test subjects can be presented with a variety of tasks which are all designed to tackle the same question. One example of such a study was conducted by Griffin et al. (2014) to measure influential factors of innovative problem solving when confronted with an extractive foraging task. The apparatus, which was offered to the subjects, was baited with four rewards. Each reward could be retrieved through a different motoric movement. Therefore, influences of task characteristics could be recorded. This again gives a more robust picture of a species repertoire and limitations and species predispositions can be found and interpreted accordingly.

### The Multi-access Approach

Similar to a multi-task battery, a multi-access approach provides a framework, in which species predispositions can be uncovered. The crucial difference however is that only one reward is accessible to retrieve. To obtain it different kinds of strategies can be used. Auersperg et al. (2011) used a Plexiglas box, whose four sides offered

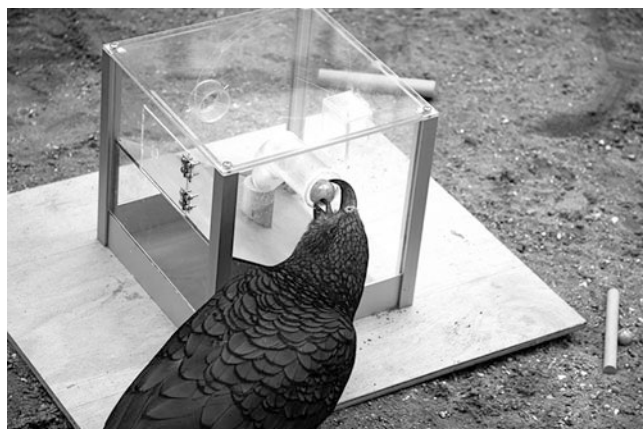
four different ways to access the reward (see Fig. 3). Test subjects were therefore free to choose how to approach this task, for example, which solutions to use, whether to stay with previously rewarding solutions or to use multiple solutions over multiple trials. Additionally, the authors were able to block solutions which were heavily used and observe how willingly different species switched between different strategies. This kind of experimental setup provides a fair chance to approach a problem differently and to explore species-specific strategies. Recently it has been used to compare birds, namely, parrots and corvids (Auersperg et al. 2011), as well as great apes (Auersperg et al. unpublished data). Despite very different demands of those distantly related species – most prominently apparent in their morphology – a comparison that has the same basic methodology but still provides opportunity for different innovative strategies has been made possible.

### Holistic Approaches

Quite commonly, experiments are designed for binary outcome: Does an individual or species solve a task correctly or not? Hence, does it have a specific cognitive ability or not? While this works in a straight forward manner it limits the possibly gained information that can be accessed by experiments. Follow-up questions usually include: Why did they fail? Why did they succeed? Which are the mechanisms used? Some experiments were specifically designed to implement ways to tackle those questions within a task itself. One such example is a study by O'Hara

### Comparative Cognition,

**Fig. 3** Kea, a parrot endemic to New Zealand, manipulating a multi-access box (Auersperg et al. 2011)



and colleagues (2015). Although the main focus of the study was to investigate inference by exclusion, which means whether test subjects could infer logical contingencies to certain stimuli – here pictures on a touch screen computer – by excluding familiar but incorrect choices, the study design made it possible to show alternative strategies used. After establishing the contingencies of two baseline pictures, those stimuli were separately paired with novel pictures in a succeeding manner. Through this procedure strategies such as preferring or avoiding novel pictures can be discovered. Therefore, species predisposition can be unveiled and discussed in the context of ecological relevance. Moreover, underlying mechanisms can be discovered in addition to answering questions on the focus ability.

### Specific Error Patterns

Similarly, specific patterns that occur when errors are made in a specific task can be used as means to detect whether similar binary outcomes are due to similar mechanisms. A variety of species have, for example, been tested on “reversal learning” through a procedure as follows: After successfully discriminating between two stimuli, the reward contingencies of those stimuli are reversed. Now the previously rewarded is unrewarded and vice versa. There are two basic ways to approach such a problem. Either one stays with the correct choice until it is incorrect for the first time (win-stay/loose-shift strategy) or one tries to anticipate when the reversal will happen (e.g., through estimating time that passes or through counting trials). Win-stay/loose-shift results in an incorrect first trial after the reversal while anticipation errors can occur also shortly before (see e.g., Laude et al. 2016). If two species are prone to the same type of error it is more likely that the same mechanisms are used to approach this task. Therefore, the position of error can give us more insight into underlying processes than just the information whether a species can learn something or not.

### Lowering Task Demands

Some authors have argued that some tasks set unnecessarily high demands on test subjects to investigate a particular ability. A classic

benchmark paradigm to investigate causal reasoning is the trap tube task. A reward is placed inside a tube and can be brought into reach by using a tool such as a stick. Through the structure of the tube two ways to access the food are possible. However, there is a trap included on one side of the tube floor. If a test subject uses the stick to push the reward towards the trap the reward is lost. The task is used to test to what degree animals understand surface continuity. Seed et al. (2009) have argued that the use of tools adds unnecessary levels of complexity. Therefore, they conducted an experiment with chimpanzees in which the fingers can be used to guide rewards toward one direction. The question of the task is still the same: Does the test subject avoid the side with the trap? However, through the exclusion of tool use as a requirement they lowered the task demands and therefore the testing paradigm can be transferred to other species – including those without tool using abilities.

### Behavioral Coding Alongside Task Performance

Another approach to gain more detailed information is to pay attention to details of the behavior elicited while solving a task. For example, while the above-mentioned study of Griffin et al. (2014) is largely focused on performance and strategies in four small problem solving tasks, they additionally recorded the latency to approach the tasks, the perseverance, through the amount on beak-to-task contacts, and the motor diversity that was used, through the number of different techniques. Although this approach is quite common, it is an important tool to be explicitly mentioned. Influential factors such as described can serve as bases to compare species with different predispositions on the same tasks.

### Outlook

As discussed, a variety of different approaches and ideas have been proposed to tackle the dilemma between comparability and compatibility. Research on comparative cognition has developed from anecdotal reports to a striving field with ever refining methodology. Hypotheses on the



emergence and drivers of cognition are being tested systematically with a growing amount of research adding to the comparative picture. While it originated mainly from two separated schools, it is now becoming common ground for interdisciplinary research which ranges from neurobiology to philosophy, from artificial intelligence to genetics. Combining theories and methods from a variety of different fields as well as new technical possibilities to examine striking cognitive abilities of others set the stage for exciting times to come!

## Cross-References

- ▶ Alex the Parrot
- ▶ B.F. Skinner
- ▶ C. Lloyd Morgan
- ▶ Detour Task
- ▶ Edward C. Tolman
- ▶ Edward Thorndike
- ▶ Evolution
- ▶ George Romanes
- ▶ Intelligence
- ▶ John B. Watson
- ▶ Konrad Lorenz
- ▶ Machiavellian Intelligence
- ▶ Matching-to-Sample: Comparative Overview
- ▶ Means-End Reasoning
- ▶ Morgan's Canon
- ▶ Nikolaas Tinbergen
- ▶ Observational Methods
- ▶ Reasoning by Exclusion
- ▶ Robert Mearns Yerkes
- ▶ String Pulling
- ▶ Technical Intelligence Hypothesis
- ▶ Trap-Table
- ▶ Wolfgang Köhler (1887–1967)

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## Comparative Psychology

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## Definitions

Comparative psychology (CP) studies the minds and behavior of different animal species describing and explaining similarities and differences across species from an evolutionary perspective. It is closely related to other disciplines, such as ethology, behavioral ecology, physiological psychology, or evolutionary psychology, with scientists frequently working across the boundaries of any restrictive definition. Ethologists and behavioral ecologists typically focus on the study of natural behavior in natural environments trying to explain how behavioral adaptations relate to environmental challenges and conditions, whereas comparative psychologists typically follow a more experimental approach to investigate behavior and psychological processes in controlled laboratory conditions. This distinction is, however, only relative, as ethologists may also conduct experiments in nature or captivity (e.g., imprinting experiments), and psychologists may rely on naturalistic observation or conduct experiments in the wild. Methodological and theoretical boundaries are fluid and flexible among CP and its allied disciplines.

In Europe comparative psychology is frequently identified with evolutionary psychology. However, in other areas, like USA, the label “evolutionary psychology” refers to a closely related but different discipline that aims to elucidate the functions and adaptations of behavioral and

cognitive traits of modern humans from an evolutionary perspective.

Historically, in Germany a more encompassing conception of comparative psychology was proposed in the early twentieth century, integrating the study of animal mind and behavior (*Tierpsychologie*) with developmental and cross-cultural psychology, as exemplified by Heinz Werner's influential "Comparative psychology of mental development," or K. Kaffka's Handbook of *Vergleichende* [Comparative] Psychology, where animal, child, and cross-cultural studies were included under that umbrella term. The idea behind this approach was to understand the origins of human mental processes from the triple "genetic" perspective of their evolution, their development in individuals, and their cultural development. Comparing similarities and differences alongside this triple axis could provide unique insights into mental phenomena. This amalgamation of disciplines was for some time mirrored by the notion of "Genetic Psychology" in America during the early twentieth century (James M. Baldwin). Although these labels are no longer used in that sense, close and fertile relationships continue to exist today between comparative and developmental psychologists, frequently studying similar topics, using similar tasks and methods in experiments, and with individuals and teams some times conducting both types of research simultaneously or closely interacting (e.g., Mike Tomasello).

### **Roles of Comparative Psychology Within Psychology**

Apart from the direct aim of describing and explaining the behavior and psychological processes of animals in comparison with those of humans, CP is seen as providing some potentially key services to other areas of psychology. For example, it has been presented as potentially allowing the study of simpler versions of complex phenomena (e.g., less complex versions of intelligence and thinking, and psychological processes that are independent of language).

Leaving aside the potentially misleading *scala naturae* assumption that may come with this view, one could argue that CP provides the opportunity of studying potentially different versions of similar phenomena, independently of their relative complexity. For example, in comparative anatomy one can analyze the different structures of hands and forelimbs across species, noting their similarities and differences, to better understand their design and functions, without considering if, for example, the design of an arm compared to a wing is more advanced or complex.

Methodologically, CP can contribute to general psychology nonverbal methods of studying phenomena such as intelligence, memory, or perception, potentially applicable to humans. For examples, in the 1920s, Köhler's tests of practical intelligence for chimpanzees (e.g., tool using tests) were very influential in developmental psychology as a way of testing nonverbal practical intelligence in children. CP, in turn, benefits from advances in other areas of psychology, for example, the looking time methods used with human infants by developmental psychology (see later).

CP in addition offers the possibility of testing hypotheses in animals with experiments that for ethical reasons cannot be conducted with humans. For example, Harry Harlow's studies on the dramatic effects of early maternal deprivation on the social development of rhesus monkeys provided essential empirical evidence to support John Bowlby's theory of attachment and decisively contributed to the development of attachment theory in psychology. This success story had, however, a controversial side, concerning the ethical dimension of research in which experimental manipulations cause deleterious consequences on animals, especially nonhuman primates. The ethics of animal behavioral experimentation, or even observation in captive or wild conditions, are an important, evolving aspect of comparative psychology.

CP can also contribute to theoretical debates about psychological processes, especially nonverbal cognitive processes and so-called implicit cognition in humans (see later).

## Historical Origins and Background

CP started in a systematic way when Darwin and his followers included psychological traits, such as intelligence, consciousness, or emotions as part of the evolutionary process. However, the method of accumulation of systematic naturalistic observation, which Darwin used so fruitfully to inspire and support his evolutionary view of nature, failed to provide acceptable scientific standards in the realm of the evolution of psychological traits. Although Darwin himself provided an excellent example of solid comparative research on the expression of emotions (Darwin 1872), his followers faced serious problems of anthropomorphic interpretation and lack of systematic empirical methodology in the study of the animal mind (e.g., George Romanes). A problem with those early attempts at charting the evolution of mental capacities was the anecdotal nature of the evidence. For example, as pointed out by Morgan, seemingly intelligent actions, in the rare occasions when their history could be traced back, frequently appeared to have emerged slowly by blind trial and error. Using rigorous experimental methods Oskar Pfungst debunked some of the more extraordinary anecdotal claims about animal mental capacities, such as “clever” horses possessing sophisticated arithmetic abilities. Seemingly complex performances (e.g., complex arithmetic calculations) could be the product of very simple associative learning mechanisms. Thus, Pfungst demonstrated that the horse “Clever Hans” had learned to stop hitting the ground with his hoof (his nonverbal way of responding to arithmetic questions) when the human questioners unwittingly braced themselves upon reaching the number corresponding to the correct response, thereby giving the horse a cue to stop. If the questioner did not know the answer, then the horse was wrong (Boakes 1984).

In the first third of the twentieth century, in response to the crisis of introspectionism (i.e., using self-observation as a source of data) in human psychology and its mirror image in animal psychology – introspectionism by analogy, i.e., an assumption that similar behaviors should

correspond to similar mental phenomena as experienced by humans –, behaviorist methods and concepts started to dominate the scene, not only of comparative psychology, but of experimental psychology in general.

Thorndike (1911) published his landmark “Animal Intelligence,” a series of carefully executed and recorded experiments showing that adaptive responses to puzzle boxes were slowly acquired by cats and other animals by trial and error, with no evidence of intelligence or understanding. Shortly afterwards J. Watson argued and exemplified how the notions of classical conditioning developed by Ivan Pavlov with dogs could be extended to humans to explain psychological phenomena like phobias. In his behaviorist manifesto, Watson proposed that psychology should focus exclusively on behavior and use only objective observational and experimental methods. The behaviorists vowed to explain both animal and human behavior through the same associationist learning principles, and indeed behaviorist psychology was dominated by animal studies (rats, pigeons), the assumption being that the laws of learning were the same for animals and humans, and laboratory studies with animals would provide the foundations for understanding human behavior (Boakes 1984).

We could term this “deep comparative psychology,” in that the whole of psychology would appear to have become comparative psychology. Because the basic processes of animal and human behavior were assumed to be the same, experiments with animals would reveal the laws of behavior, including human behavior. However, the apparent ascent of CP with behaviorism was accompanied by the important limitation of just focusing research on associative learning processes and with just a few species: mostly rats and pigeons. A second fundamental limitation was that the assumption of identity between the laws of learning across species somehow emptied the term “comparative” of its primary meaning and intended scientific value. There was little to be learned by *comparing* one species to another, since no essential differences were expected. Laboratory animals were simply an efficient and

useful tool for conducting experiments to uncover universal models of the laws of behavior.

The assumption of absolute psychological continuity across animal species was taken to the extreme by radical behaviorists, epitomized by Skinner's (1957) book *Verbal behaviour*, where he argued that the laws of learning discovered in rats and pigeons were enough to explain even the apparently most distinctive feature of humans – language, a type of behavior that just happens to be verbal. Paradoxically, through Chomsky's influential criticisms (Chomsky 1959), this book came in fact to symbolize the downfall of behaviorism in general psychology and the triumph of the so-called “cognitive revolution” and the more general, interdisciplinary enterprise of cognitive science.

This paradigm change also affected CP, which from the 1960s widened again its horizons to address the study of psychological processes other than learning. This was facilitated by the fact that a number of alternative, more cognitively oriented views had survived during the behaviorist years, and from within behaviorism itself some authors had proposed and provided evidence that undermined the strict behaviorist views.

### **Nonbehaviorist Comparative Psychology Before the 1960s**

In parallel to the behaviorist approach, there were two alternative streams of work relevant for comparative psychology during the first half of the twentieth century. One was of biological origin – ethology, the study of natural animal behavior in the wild from an evolutionary perspective (Lorenz, Tinbergen). Although more focused on the diversity of natural behavior patterns across species and how they could be explained as ecological adaptations, ethology had potential implications for understanding the evolution of psychological processes. For example, Konrad Lorenz proposed that Kant's a priori forms of knowledge should be understood as adaptations generated in the process of evolution, and ethologists provided models of motivational processes.

A second nonbehaviorist stream came from within psychology itself. In response to the crisis of introspectionism in general psychology, a new

school known as *Gestalt* psychology developed in Germany from the 1910s. Gestalt psychologists proposed an alternative scientific approach to perception and thought, one dominated by the notion that perceptual and behavioral configurations (*Gestalten*) were primary psychological structures not reducible to elementary associative analysis – perceptions and actions were more than the sum of their constituent parts. One of the earliest empirical contributions of Gestalt psychology consisted of the study of “insightful” problem solving in chimpanzees.

W. Köhler (1917/1921) questioned Thorndike's conclusion that animals do not show intelligent behavior through a series of experiments and observations with captive chimpanzees in a purpose-built facility of the Prussian Academy of Sciences in the island of Tenerife. He reported that when confronted with practical problems, chimpanzees showed evidence of intelligent, or as it became known, “insightful” behavior, i.e., adaptive actions that did not emerge out of the progressive accumulation of behavioral changes by blind trial and error. For example, when confronted with out of reach pieces of food beyond a bar fence, chimpanzees would spontaneously make use of sticks to retrieve the food; or they would move and try to pile boxes under a piece of food hanging from the ceiling to use them as towers to reach their goal.

Köhler's detailed descriptions of their behavior indicated that chimpanzees produced their solutions in a preadapted way, i.e., their actions were suited to the requirements of the problems without having to go through a slow and gradual process of trial and error. Sometimes, these good solutions appeared suddenly, after unsuccessful attempts of a different nature. Interestingly, Köhler based his argument in favor of animal intelligence not only on the successful problem solving actions of the apes, but also on their systematic mistakes. For example, some chimpanzees would try to climb upon a box, that in itself was too short to reach a target, while pressing it tightly up against a wall, as if they expected that the box would stick to the wall. On the one hand, this mistake reveals a lack of understanding of the laws of balance and support, but on the other it reveals an understanding

of the problem – the need to shorten the distance between the support box and the goal. Crucially, a mistake like this could not be explained by trial and error learning, as it cannot possibly have previously worked. It appears to reflect a partially insightful strategy generated by an incomplete “understanding” of the situation.

Köhler’s proposal of insight in chimpanzees came to co-exist with behaviorist approaches in an uneasy relationship over subsequent years. Insight was seen as a challenge to the principles of behaviorism, with good reason as it was grounded on a different, “cognitive” *avant la lettre*, view of psychology in general and comparative psychology in particular.

Behaviorist psychologists tried to explain away insight as the product of associative learning (e.g., maybe Köhler’s chimpanzees, being wild caught, had already acquired their tool using responses in the wild, and in captivity they merely generalized them to similar situations; or maybe these were based on instinctive behaviors) (Boakes 1984). The notion of insight, however, survived these criticisms and controversies, and it is still used and debated in contemporary comparative psychology (Shettleworth 2012).

One reason for its continued appeal is that the notion of insight captures a fundamental challenge for any comparative psychology – the notion of intelligence and understanding without language or explicit reasoning. One of the key potential contributions of comparative psychology to general psychology is indeed to understand forms of intelligence and cognition that are independent of language and explicit conscious experience (Gómez et al. 2017).

From within behaviorism itself, there were discordant voices calling for a CP that was more open to the role of internal processes and variables in explaining behavior. For example, E. Tolman proposed notions of mental map and latent learning based on solid empirical findings demonstrating that rats could learn to navigate mazes in the absence of differential reinforcement. In addition, in the 1960s findings on the quick learning of aversion responses to food demonstrated the role of biological preparedness for certain types of learning of special adaptive significance,

questioning the assumption of absolute equivalence across species: the laws of learning were constrained by ecological conditions and adaptations (Boakes 1984).

The existence of these alternative approaches in the shadow of behaviorism facilitated the transition of CP into the new cognitive approach of psychology and allied disciplines in the 1960–1970s. Comparative psychology turned again to studying, not only behavior, but also the mental processes and mechanisms underlying it. Intelligence, consciousness, memory, intentions, imitation, social learning, problem solving, etc., became targets of comparative research, with the benefit of the rigorous methodological and experimental approaches instilled into psychology during the behaviorist era. Behavioral and cognitive differences across species became again a central target of inquiry, and crucially the evolutionary framework took again central stage to make sense of such differences in CP. Some of the old methodological and conceptual debates (e.g., the tension between observable behavior and inferred cognitive processes, the contraposition of simple learning mechanisms and complex cognition and reasoning) re-emerged within the new framework and are part of contemporary CP.

## Practical Intelligence: Objects and Tool Use

An example of the new directions taken by CP in the 1960s–1970s was the application of Piagetian theory, originally developed to describe and explain human child development, to animal cognition – an example of interaction between developmental and comparative psychology. Piagetian theory proposed a constructivist solution to the traditional nature/nurture and associationist/cognitive debates in psychology, holding that behavioral and cognitive capacities were “constructed” during ontogeny in a dynamic epigenetic interaction between the organisms’ preexisting cognitive capacities and environmental challenges.

Piaget (1936) described cognitive development in human children as a succession of stages leading from innate reflexes to symbolic and

logical (operational) intelligence. Interestingly for comparative psychologists, the very first stage of development – sensorimotor; 0–2 years of age – corresponds to a nonverbal, perception/action dominated type of intelligence that Piaget thought could integrate into a single model behaviorist notions of associative learning and *Gestalt* notions of insight, with each mechanism corresponding to a different developmental substage. Piaget viewed sensorimotor development as a postnatal continuation of embryological development, and intelligence as an adaptation that was in continuity with, and a prolongation of, biological adaptations. This made his theory particularly attractive to comparative psychologists, even if he himself conducted no comparative studies, and only a few of his followers and disciples ever did so (Parker and Gibson 1990).

### Object Permanence

An example of Piagetian influence on CP is the capacity known as object permanence – the ability to track and find objects when they move from one location to another. Piaget described in detail the emergence of this ability in human infants and suggested that it reflected the progressive development of a fundamental cognitive adaptation – conceiving objects as independent entities that continue to exist in the world when one is not perceiving them.

When the Piagetian tasks defining each stage of object permanence were applied to nonhumans, they worked very well, especially, but not exclusively, for primates (a genus with prehensile hands adapted to the manipulation of the environment). Even such particular developmental phenomena as the transitory A-not-B error (the mistake of trying to find an object in the place where it was first hidden, despite seeing that in successive trials it is hidden elsewhere) have been reported for all primate species tested, suggesting that object understanding follows a systematic sequence of development in primates. However, comparative research shows that this overall similarity is accompanied by differences: for example, monkey species tend to pass through stages of object permanence at an accelerated rate (four times faster) than humans and maybe fail to reach the

final stage (invisible displacements). Apes, in contrast, develop only slightly faster than humans and do reach the final stage of invisible displacement (Gómez 2004).

Moreover, when object permanence skills are compared with other sensorimotor abilities, such as locomotion and tool use, a pattern of *heterochrony* emerges. Whereas monkeys and apes display independent locomotion months earlier than humans, they are slower to develop tool using skills, if at all. Different primate species offer different versions of how sensorimotor systems dominated by manipulative skills can be organized. Still other nonprimate species may offer very different versions of sensorimotor systems of action. This is a fine example of comparative research where both similarities and differences are highlighted in an evolutionary framework.

Inevitably, whenever a stage-based theory of development is used, there is a temptation to take a *scala naturae* approach, where the higher levels of intelligence are expected to appear in the closest evolutionary relatives of humans. For example, it was initially reported that the most complex level of object permanence – the ability to track the invisible displacement of objects – was only found in great apes and humans, with potentially positive results in monkey species subject to alternative interpretations. This could mean that invisible displacement understanding might require some sophisticated level of symbolic representation only found in humans and their closest relatives. However, subsequent research has found evidence of invisible displacement understanding in some avian species. Although the exact equivalence of performances and underlying cognitive and neural mechanisms is still under scrutiny and discussion, comparative psychologists have become aware of the power of convergent evolution in shaping the cognitive skills of different species.

### Object Individuation

In the 1990s, developmental psychology moved beyond Piagetian theory. New nonverbal paradigms to study infant cognition emerged requiring minimal amounts of manipulative skill and



suggesting that infant cognition could be more complex than previously thought. For example, by using looking time methods, building on the fact that infants pay longer visual attention to unexpected events, human infants revealed some understanding of object permanence before being able to correctly respond in Piagetian object search tasks (Gómez 2004). These new methods allowed the investigation of other aspects of cognition in infants, and soon they were imported into CP.

An example is the study of *object individuation*, i.e., the ability to identify and keep track of objects or infer their whereabouts on the basis of their individual identity. For example, I may have two identical apples, but know that one is in my pocket and the other on the table. They look the same, but I know and track them as different objects on the basis of their different spatiotemporal relations. Conversely, I may see that you put an apple and a banana in your bag. Although they share the approximate same location at the same time, I know they are two different objects because I individuate them on the basis of their appearance.

This problem was first studied in human babies using looking time methods with the unexpected result that at 10 months of age babies could individuate objects only using spatiotemporal information, but not featural information. For example, if babies saw a toy duck coming from behind a screen, and then, after the duck returned behind the screen, they saw a ball coming from behind the same screen and then returning, when the screen was lowered, they were not “surprised” (did not look longer) if, due to an experimental trick, only one of the objects was there, as if they had been assuming, in their representational record of what lies behind the screen, that the duck and the ball were one and the same object.

This led some developmentalists to suggest the hypothesis that so-called “featural object individuation” might be linked to language acquisition and appear only as human infants start to acquire their first naming abilities in their second year of life, as if using labels to identify objects prompted and supported their ability to individuate objects by their features (Xu 1999).

This called for comparative research: if this hypothesis was correct, then nonhuman primates should not be capable of featural/property individuation. However, several species of apes and monkeys have demonstrated that they do possess this ability. For example, in one test primates see one piece of banana dropped into a box. This is a trick box, since unbeknownst to them, the piece of banana remains in a trap never reaching the bottom, which is the only part of the box they have access to. When they try to retrieve the banana, if instead they find a piece of, say, apple (surreptitiously placed there by the experimenters), they tend to continue searching in the box more frequently than if they do find a piece of banana. This suggests that they have the ability to individuate objects by their appearance, and not just their spatiotemporal parameters, and therefore featural object individuation is not exclusively human and dependent upon language, but an evolutionarily older trait of primate cognition (Cacchione et al. 2016).

Attempts have been made to trace back the origins of this ability to nonprimate species, with mixed and still controversial results (see Fontanari et al. 2011, for a study with newly hatched chickens).

## Convergent Evolution and the Challenge of Operationalization

Historically, CP has tended to be biased by a tacit *scala naturae* attitude, that is, an assumption that the species evolutionarily closer to humans, such as primates, and among primates great apes, would show higher levels of intelligence and more complex behaviors. For example, tool use was hailed as an indication of complex intelligence in apes, whereas reports of tool use in distant species such as birds tended to be dismissed as instances of inflexible, “instinctive” like behaviors. In the last years, this attitude has changed. Evidence has mounted that nonprimate species display complex behaviors that may reflect flexible cognitive processes emerged by convergent evolution and in differently designed brains. The importance of relative brain size as a potential index of cognitive

sophistication has been questioned with proposals that other factors like neural connectivity and number of neurons may be more relevant and help understand why small brains could generate cognitive and behavioral complexity (Emery 2004; Gunturkun and Bugnyard 2016).

One of the most surprising sources of potential complex cognition in very small brains comes from insects. For example, bumblebees have demonstrated an ability to learn to solve simple “string problems” (pulling an artificial flower stem to slide it from underneath a glass and thereby gain access to pollen) and to display flexible observational learning of a basic manipulative skill (Loukola et al. 2017). One interpretation is that such findings of complex behavior in species so distant to humans and primates should be interpreted as evidence of the power of convergent evolution in producing and implementing complex cognition in very different brains. Some authors, however, propose that complex behaviors may not always require complex cognitive mechanisms, and such examples reveal that even in humans and primates in general we may overestimate the role of cognition in producing complex adaptive behavior (Shettleworth 2010).

### The Challenge of Operationalization

When probing the cognitive and motivational processes of nonverbal organisms, comparative psychologists are faced with the problem of establishing objective behavioral criteria that are proof of their existence. For example, to determine if an animal is capable of intentional, goal-directed action, we need criteria that distinguish this from other types of action (e.g., associative learning). This problem is largely shared with developmental psychologists, especially those studying early infancy. This is frequently known as the problem of “operationalization.” For the problem of intentional action, criteria typically include persistence until a goal is reached, variation in means deployed, cessation when the goal is attained, etc. For the problem of intentional communication, to the above additional criteria are added, for example, directedness to an agent, eye contact, pause to allow for a response (Townsend et al. 2016).

A problem with operationalizations is that they might appear to fail to do the job of distinguishing between different cognitive processes when their application leads to attributing complex cognitive, human-like processes to species that are very distant from humans and are traditionally not perceived as cognitively sophisticated. For example, Vail et al. (2013) applied the criteria of communicative intentionality to fish signaling behavior in collaborative hunting finding that they might qualify as instances of intentional communication. Some insect behaviors frequently appear to fulfill criteria of complex cognition at least in some limited, specialized areas. For example, one species of ants displays helping behavior to conspecifics when these are stuck in a way that could fulfill at least some of the criteria for empathic targeted help (Taylor et al. 2013).

When this happens, comparative psychologists are faced with a dilemma. They can either attribute to the species concerned the complex processes supposedly captured by the operationalized criteria, or decide to revise the criteria as being incomplete and imprecise. One problem is that this may lead to a “moving the goal post” effect, i.e., changing criteria to make them fit preconceived conclusions about which species possess certain cognitive processes. On the other hand, empirically informed and theoretically motivated refinements are necessary to advance our understanding of the structure and function of mental processes. An important part of this may consist of finding the correct positioning of operational “goal posts,” through evidence-based and conceptually justified recalibration of behavioral criteria.

### Domestication, Captivity, and Development

One species evolutionarily distant to humans that has provided a wealth of unexpected comparative findings in the last years is the dog. Dogs pass social cognitive tests that primates, including apes, find difficult. For example, in the object choice test (where subjects are prompted to choose a container with food by a human who

gestures or looks at the correct location), dogs have demonstrated a high degree of sensitivity to human referential signals, such as pointing gestures and deictic gaze, whereas apes find it difficult to make use of these communicative signals to find the hidden food, even if they can correctly interpret noncommunicative signals such as reaching (Hare and Tomasello 2004). One interpretation is that during the process of dog domestication humans artificially selected animals who were better able to respond to typical human communicative cues, whereas apes have to rely upon their own communicative abilities, or an exaptation thereof, which might be insufficient to pass such tests. One open question is to what extent the underlying cognitive and motivational processes selected in dogs are similar to those operating in human infants, or completely different mechanisms mimicking typical human responses.

Closely related to the effects of evolutionary domestication on cognition is the issue of how “domestic” rearing by humans may affect the cognitive and behavioral phenotype of wild animals reared in captivity, especially apes and monkeys, whose attachment patterns make them especially suitable for human rearing.

### **Ape in the House Studies**

From very early, comparative psychologists were tempted by cross fostering experiments where infant apes were reared by humans to test how human-like ape behavior and cognition can become when reared in human conditions. Classic studies include Kellogg and Kellogg and Ladygina-Kohts, where it was found that despite profound similarities in some aspects of development (e.g., emotional expression, tool use) and ape malleability and responsiveness to human rearing, apes decisively diverged from older child development, most crucially with the acquisition of language, which remained completely absent in domestic apes. Hayes and Hayes’ systematic and deliberate attempt at teaching speech to a chimpanzee definitively showed the futility of the attempt (Boakes 1984).

A controversial variety of this ape in the house experiment became particularly popular during the 1960s and 1970s in the so-called “linguistic

apes” experiments. In these, infant apes were systematically and intensively trained to acquire non-speech linguistic skills with a variety of procedures, ranging from computer based, artificially designed “lexigram” languages, to the use of a version of deaf signed languages to take advantage of the apes manual dexterity. Although initial reports suggested an unprecedented degree of success (with some apes acquiring several hundred “words” and combining them into rudimentary “sentences”), the results of the studies were questioned and remain controversial, both in terms of what was demonstrated about the apes’ ability to acquire linguistic skills and in terms of the ethical implications of such intrusive, largely irreversible manipulation of the lives of the participant apes (Gómez 2004).

In the best known critical study, Terrace and collaborators concluded that their chimpanzee’s acquisitions in signed language did not show evidence of grammatical organization and probably not even symbolic value and could be best described as a combination of acquired conditioned responses and copycat signing based on the signs and cues provided by his keepers. They suggested that this negative conclusion should be made extensive to all the linguistic ape studies. However, other research teams disputed this interpretation and the comparability of the conditions under which Terrace’s chimpanzee was reared and trained to their own, according to them, better conceived and executed attempts. Thus, Savage-Rumbaugh presented results that, according to her and her collaborators, suggested linguistic skills in bonobos (Savage-Rumbaugh et al. 1993).

Ape in the house studies, including language teaching experiments, have left an uncertain legacy, fraught with ethical misgivings and equivocal data and interpretations.

### **Captivity, Behavior, and Cognition**

Beyond the controversial human rearing studies, a substantial part of the findings of comparative psychology come from captive animals, in zoos, research stations, or laboratories. A potential objection to studies with captive animals is that results may lack ecological validity, i.e., that they may not reflect the “true” abilities the animals

were evolutionarily selected for, but some artifactual or atypical versions of them. However, on the other hand, it can be argued that captivity, when conditions are not impoverished and basic ecological needs of the species are taken care of, may offer especially informative insights into the plasticity and adaptability of animals in response to environmental change – a basic evolutionary process. Few studies have attempted to address explicitly the issue of how captive conditions may affect behavior and cognition from this evolutionary/developmental point of view.

An example is the study of spontaneous gestural communication in apes. Captive apes are capable of developing flexible, intentional (i.e., fulfilling operationalized criteria of communicative intentionality; see above) pointing gestures that they use to interact with humans (but rarely among themselves). These gestures are rarely observed in the wild, but typically become a standard component of the captive ape repertoire to interact with humans. Pointing gestures are a universal form of human communication, although it remains disputed to what extent they are a biological adaptation or a highly constrained behavior pattern subject to some morphological variation across cultures. The fact that they rarely appear in wild apes, or are rarely used among captive apes for intraspecific communication, opens up a number of interesting questions about the interaction between phylogenetic and ontogenetic factors in the emergence of adaptive behavior patterns (Gómez 2007).

### Enculturated Apes

It has also been suggested that apes reared in close interaction with humans might develop more complex cognition, by becoming “enculturated.” This idea is related to the Russian psychologist Lev Vygotsky’s theory about the mechanisms of human cognitive development. According to him, the natural cognitive abilities of humans are amplified through the process of sociocultural interaction and education that mediates human ontogeny, including learning to use linguistic and other symbols as cognitive tools. Tomasello and Call proposed that “enculturated” apes might be more proficient in certain tasks such as

imitation or understanding intentions, although they later qualified their claims in view of evidence demonstrating that some of these abilities could also be found in nonenculturated apes, and maybe the performance differences could point more to quantitative than qualitative differences in capacity, or be due to the superior familiarity of apes experienced with humans in solving human inspired tasks. The issue of the role of human influence on the behavioral and cognitive phenotypes of other animal species remains open (Gómez 2004).

### Experiments in the Wild: The Meanings of Animal Signals

One of the topics addressed by CP in a new way after the cognitive revolution was the nature of animal communication. Previously, animals’ signals had been assumed to be essentially different to human language – inflexible emotional responses without semantic meaning or intentionality. The linguistic ape experiments discussed above tried to uncover latent capacities for more sophisticated communication through direct training. A second approach tried to reassess the natural communicative behavior of animals through the innovative use of playback experiments in the wild and in captivity.

The logic of the playback paradigm is as follows. To know what a signal “means” to an animal, a prerecorded vocalization is played when the referent (or triggering event) of the vocalization is not present, and the reaction of the animals is observed. If they react as they would in the presence of the referent, the conclusion is that the signal “means” that referent for them. For example, Cheney and Seyfarth played recordings of alarm calls given by vervet monkeys to different predators. They found that the monkeys reacted with appropriate escape responses and even seemed to engage in visual search of the predator in the appropriate direction (e.g., the sky for an eagle alarm, or the ground for a snake alarm). This led them to claim that alarm vocalizations in monkeys might work as some sort of primitive “words” with specific meanings.

Subsequent research using variants of the playback paradigm found this phenomenon in many other primate and nonprimate species. Variants of the playback technique have been used to investigate more complex aspects of vocal communication, for example, the possibility of rudimentary syntactic combinations whereby signal combinations might change the meanings of calls (Zuberbuehler 2010).

At a theoretical level, there continues to be disagreement about what is the correct interpretation of these findings. Do the different vocalizations simply work as emotional signals without referents in a more sophisticated way than previously thought? Are they reflex or learned reactions without complex semantic representations? Or do they constitute evolutionary precursors of some basic aspects of language? (Fischer 2011).

### Intentional Gestures in Communication

An alternative cognitive approach to animal communication (and the enduring problem of language evolution) studies if other animals can engage in intentional gestural communication. Humans not only mean things with words, but also with gestures, for example, pointing gestures. While some authors were busy trying to teach language to apes, others studied their spontaneous communication with humans in captivity, reporting that they developed a repertoire of gestures both similar and different to those used by prelinguistic human children. For example, they use a whole hand version of index finger pointing (although under physical constraints like having to point through a narrow whole, they choose index finger pointing). Importantly, these gestures seem to be accompanied by joint attention behaviors (gaze following and eye contact), which in human infants is considered to be an index of communicative intent. Systematic studies of intraspecific gestural communication in the wild report complex gestural repertoires with a variety of meanings (Byrne et al. 2017). There is debate about the extent to which the underlying joint attention processes and meaning in apes and other animals' gestural communication are similar to humans, or humans display a special type of joint attention adapted to cooperative interaction

and the exchange of information. For example, apes tend to use their gestures to make requests and regulate others behavior, whereas human infants in addition make extensive use of so called protodeclarative gestures (to show things to others) (Gómez 2004).

In sum, studies of intraspecific gestural communication in apes in captivity and the wild have explored the flexibility and intentionality of their gestural repertoire. However, there remains controversy as to how the underlying cognitive and motivational processes in the communication of nonhumans compare to those of humans, including prelinguistic human infants.

### Comparative Psychology and Cognitive Science: Theory of Mind

Theory of mind (ToM), defined as the ability to adaptively react to and represent the mental states (intentions, desires, beliefs) of other organisms, has been an extremely productive area of interdisciplinary research over the last decades, involving general psychology, neuroscience, psychopathology, and philosophy, among other disciplines. The whole area was kickstarted by comparative psychology and has remained one of its most active, interdisciplinary, and influential areas of research.

Premack and Woodruff conducted an ingenious study with an original take on the classical tool-using tasks of Köhler (1921) – instead of humans observing if chimpanzees can solve problems, a chimpanzee watched a human confronted with a problem (e.g., trying to reach a bunch of bananas hanging from the ceiling). The chimpanzee – a “linguistically” trained ape, used to this type of experimental procedure – then chose one of two photographs – one depicting the correct solution (e.g., a human climbing on a box to be able to reach the bananas), the other showing an irrelevant action. The chimpanzee was able to select the correct option, thereby demonstrating “problem solving comprehension,” i.e., some understanding of what it is for others to confront and solve a problem.

Premack and Woodruff (1978) suggested that this problem solving understanding must involve



an ability to attribute mental states to other agents: understanding their intentions, desires and beliefs, or, as they termed it, having a “Theory of mind.” The chimpanzee – they suggested – had to perceive the keeper’s observable behavior – stretching the arm in the direction of the bananas – as caused by an unobservable *intention* to get them. Because to predict and explain behavior, mental states must be inferred as unobservable causes, the authors coined the term “Theory of mind” to refer to this ability. This theoretical paper was commented upon by other psychologists, ethologists, philosophers, and cognitive scientists. They came to the conclusion that the evidence presented by Premack and Woodruff for chimpanzee ToM was weak, but the question was an excellent one, and not only for chimpanzees, but for humans as well, but in need of detailed empirical exploration.

It was agreed that the best way to test if an organism has a theory of mind (ToM) was to create a situation where one has to predict the behavior of another organism that has an erroneous representation (a false belief) of reality. For example, predicting that an organism that believes that there is food in box A, when in fact the food is in box B, will nonetheless look for it in the empty box A. Unfortunately, comparative psychologists were initially unable to develop a test like this for chimpanzees or other animals. It was developmental psychologists that first reaped the benefits of the ToM debate, establishing that the landmark of false belief understanding emerges in children only at around 4 years of age, but this is preceded by the ability to understand other mental states: perceptual states like seeing at around 1 year, desires at around 2 years, and knowledge and ignorance at around 3 years (Baillargeon and Bian 2016).

The findings of developmental psychologists inspired back comparative psychologists who reported spontaneous behaviors in animals, especially primates, that might reveal some of those ToM abilities. For example, Whiten and Byrne (1988) compiled observations of tactical deception among nonhuman primates suggesting an ability to conceal things from others’ sight or even some potential examples of trying to create

false beliefs in others,. These might be evidence of ToM skills in nonhumans. This gave rise to the “Machiavellian Intelligence” hypothesis – the idea that the challenges of navigating the complexities of the social world (predicting and manipulating conspecifics’ behavior) might have been a key determinant in the evolution of intelligence, with theory of mind abilities (also known as “mindreading” or “natural theories of mind”) as a key adaptive component.

However, initial attempts to apply experimental methodology to test this suggestive evidence produced mostly negative results. A comprehensive series of experiments with chimpanzees found that they could not understand even the simplest of mental states: visual perception (Povinelli and Eddy 1996), as they did not discriminate between humans who could and could not possibly see their begging gestures (e.g., human oriented to the front with her eyes open versus human looking sideways). By the end of the 1990s, it looked as if the answer to the question posed by Premack and Woodruff was negative – chimpanzees and non-human primates in general do not have a ToM ability, which might be an exclusively human cognitive skill.

This changed shortly afterwards when Hare et al. (2000, 2001) introduced a new experimental paradigm inspired by the idea that we should not be testing chimpanzees’ theories of the human mind (as in the cooperative requesting tasks used before), but chimpanzees theories of chimpanzee minds. They devised a competitive task, based on the fact that in their natural behavior chimpanzees rarely share food, but rather compete for it, with dominant chimpanzees typically gaining access to disputed food.

They found that subordinate chimpanzees, when given a slight head start in a competitive situation, preferentially targeted food that was visible only to them over food that was also visible to a dominant individual. They were even able to take into account if a piece of food currently invisible to a dominant had been previously seen by him being placed in that location. The conclusion was that, when properly tested with a paradigm that takes into account the motives and typical behaviors of the species in natural



conditions, chimpanzees did show evidence of understanding at least some mental states like seeing and knowledge.

However, as so frequently happens in comparative psychology, critics argued that even these ingenious new experiments could not completely rule out the possibility of finding more parsimonious explanations of the animals' behavior, such as using simple behavioral associations or behavioral rules. This is an example of the traditional debate between rich and lean interpretations of animal behavior, in which critics provide reductionist re-interpretations of new pieces of experimental evidence (see problem of operationalization).

Indeed some critics (Penn et al. 2008) even proposed that it might in principle be impossible to prove beyond reasonable doubt that a nonverbal organism has a theory of mind, as it might be logically impossible to disentangle the problem of whether animals are responding to behavioral cues or to representations of the mental states reflected in the cues. The rationale is that to infer a mental state you need to detect some behavioral evidence (e.g., to infer that agent A knows that an apple was placed in location X, you need to see if the agent is present and oriented to the scene.) An observer could learn an association between being present and physically oriented and subsequently being able to find the object without representing that the reason why this happens is that by being present the agent has acquired a representation (knowledge) of the whereabouts of the object. Mentalistic understanding would be "implicit" in that behavioral procedure, but not really in the mind of the organism.

This has generated a complex debate on the nature of mentalistic explanation, the methodological limitations of research with nonverbal organisms, and the nature of implicit knowledge. This debate has recently been exported into developmental psychology to question findings suggesting an early competence to understand false belief in 1- to 2-year-old human infants – traditionally considered to emerge only at around 4 years of age – when tested with looking time methods (Baillargeon and Bian 2016).

Perner (2010) suggested that the behavior reading objection of Povinelli and collaborators is fully

applicable to the infant looking time studies. Only responses where organisms can give explicit evidence of their representations (e.g., by providing a verbal explanation) could be considered as convincing evidence of ToM. This could be seen as an overdue redress of what sometimes is perceived as double standards of scientists studying humans and animals, with rich interpretations being always more easily accepted for humans than animals. However, it also raises a problem of a philosophical nature – whether knowledge should be required to be explicit for it to count as genuine knowledge (see section on Nonverbal Thought and Implicit Knowledge).

In a further instantiation of cross-fertilization, comparative psychologists have recently imported the nonverbal false belief testing methods used with human infants to animals (Krupenye et al. 2016), with positive results for apes, suggesting that "implicit FB understanding" (whether genuinely mentalistic or not) might be shared by all great apes.

In sum, the area of Theory of mind is an excellent example of the potential of CP to interact with other disciplines and provide the sort of scientific value inherent to the comparative method. Comparative psychology has played and continues to play a fundamental role in the debate about the differences between implicit and explicit systems of knowledge, of which the area of theory of mind is but an example.

## Nonverbal Thought and Implicit Knowledge

One of the key contributions of CP to general psychology and cognitive science is to contribute to the understanding of nonverbal intelligence and thought and so-called implicit cognition. In CP there has always been a tension between researchers that try to resolve the problem of thought processes in animals by concentrating on behavior and trying to reduce mental mechanisms to associative processes, and researchers that try to find in animal behavior evidence of nonverbal or implicit cognitive processes that might help understand the origins of human cognition (Gómez et al. 2017).

The challenge of implicit, nonverbal thought is conceptual and methodological. Conceptually, it requires defining forms of thought and intelligence that work without explicit, verbally mediated or verbally expressed reasoning. Methodologically, it requires finding methods for probing and demonstrating such intelligent mechanisms in animals who cannot report about the way in which they see and approach problems. The close relation between comparative and developmental psychology examined in other sections of this entry is due to sharing both challenges (in the case of the latter only to a certain extent, since children eventually develop linguistic skills).

The challenge of nonverbal or implicit thought is not exclusive to CP. There is ample evidence that human adults engage in mental processes that are not verbally reportable: so-called “implicit cognition” is pervasive in humans, and it is uncovered through indirect, nonverbal methods and experiments. However, in general psychology and cognitive science nobody has been able to provide so far an accepted definition or characterization of implicit thought. Indeed the most important, unresolved challenge of implicit knowledge is the conceptual one – understanding its very nature. Despite the pervasive use of this notion, not only in psychology, but across many other disciplines, there is no accepted definition or model of what this intuitive notion is. Comparative psychologists are in an ideal position to contribute to solve this conceptual puzzle as they are studying animal minds, which are quintessentially nonverbal (Gómez et al. 2017).

## Conclusion

Over its long history CP has become a discipline with intense and dynamic cross-disciplinary connections (biology, philosophy, cognitive science, neuroscience) at the forefront of research on behavioral and mental processes in an evolutionary framework. Its most unique contribution is the insights provided by comparing different evolutionary and developmental versions of adaptive

systems of behavior and cognition in close interaction with other disciplines.

## Cross-References

- ▶ [A-Not-B Problem](#)
- ▶ [Attachment](#)
- ▶ [B.F. Skinner](#)
- ▶ [Biological Preparedness](#)
- ▶ [C. Lloyd Morgan](#)
- ▶ [Canine Cognition](#)
- ▶ [Captivity](#)
- ▶ [Charles Darwin](#)
- ▶ [Clever Hans](#)
- ▶ [Communication](#)
- ▶ [Comparative Cognition](#)
- ▶ [Corvids](#)
- ▶ [David Premack](#)
- ▶ [Domestication](#)
- ▶ [Edward C. Tolman](#)
- ▶ [Edward Thorndike](#)
- ▶ [Ethics](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [George Romanes](#)
- ▶ [Harry Harlow](#)
- ▶ [Herbert Terrace](#)
- ▶ [Insight](#)
- ▶ [Intelligence](#)
- ▶ [John B. Watson](#)
- ▶ [Josep Call](#)
- ▶ [Konrad Lorenz](#)
- ▶ [Language](#)
- ▶ [Latent Learning](#)
- ▶ [Law of Effect](#)
- ▶ [Michael Tomasello](#)
- ▶ [Nikolaas Tinbergen](#)
- ▶ [Object-Choice Test](#)
- ▶ [Problem-Solving](#)
- ▶ [Theory of Mind](#)
- ▶ [Wolfgang Köhler \(1887–1967\)](#)

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## Comparator, The

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### Definition

The theoretical concept of a “comparator” has been proposed in order to explain how the brain distinguishes sensory information that is expected based on our own voluntary behaviors versus that generated by events in the external world. Specifically, the comparator is thought to subtract the motor-based estimate of sensory inflow from actual sensory signal to suppress the representation of expected stimuli. This self-monitoring mechanism ensures accurate motor control and stable perception.

### Overview

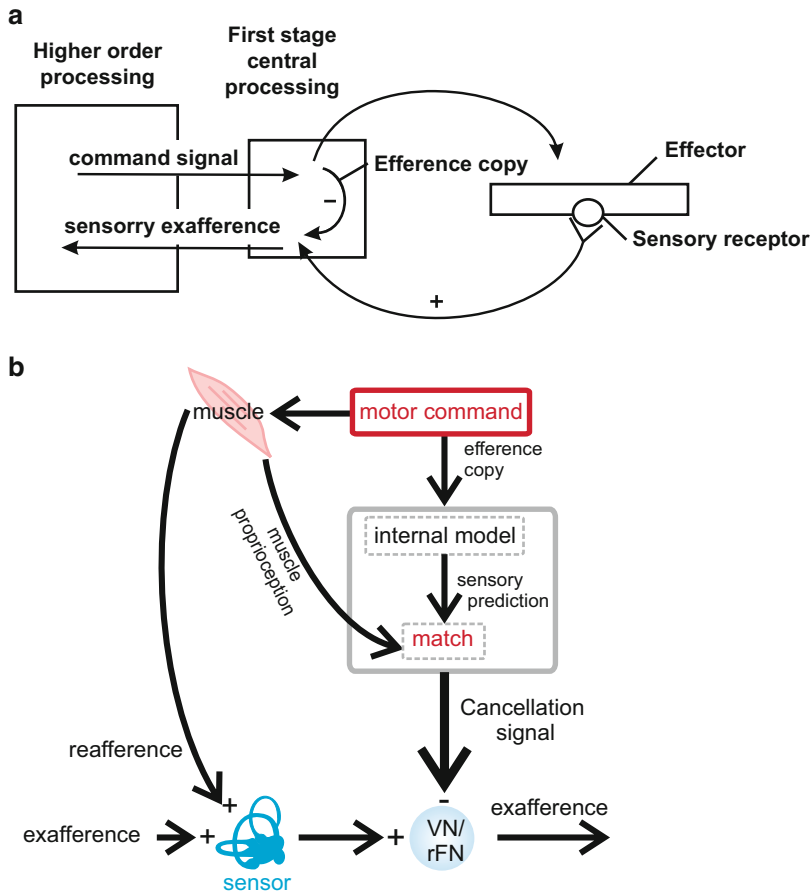
It is important to correctly detect our own actions in order to effectively interact with and build an accurate representation of our environment. However, our sensory systems are activated by both external events (sensory exafference) and our own actions (sensory reafference). The prevailing view is that the brain largely achieves control of posture and accurate perceptual representation of the environment during voluntary actions by suppressing self-generated sensory stimulation. Notably, the reafference principle proposed by von Holst and Mittelstaedt (1950; see also the reafference principle section in this publication) posited that the motor command signal splits into two processing streams: one projecting directly to the effector (motoneuron generating the action) and the second to a comparator, which then subtracts the motor-related signal from the sensory input (see Fig. 1a). This second motor-related signal is termed an efference copy (or alternatively corollary discharge) signal (for reviews see Sommer

and Wurtz 2008; Cullen 2011). Effectively, by sending a copy of the motor command to sensory areas, the comparator computes the difference between the sensory input and motor-based efference copy signal. This difference represents the component of the sensory input that was not generated by the voluntary action. In this way the brain is able to distinguish sensory information due to external factors (exafference) from sensory information arising from our actions (reafference).

### Comparator Examples

Over the past many decades, models of comparators have refined the reafference principle to more fully explain sensory processing. At the behavioral level, studies investigating the perception of self-generated versus externally applied tactile stimulation have provided insight into why one cannot tickle one’s self (Blakemore et al. 1998). Further combined behavioral and imaging experiments suggested that the cerebellum is involved in predicting the specific sensory consequences of movements and that this signal is compared to the incoming tactile information to cancel the sensory response to self-generated stimulation.

Another important example of a comparator-based model of the reafference principle comes from neurophysiological studies of the cerebellum-like structures of the electrosensory systems of mormyrid and gymnotid fish and the Elasmobranchii (reviewed in Bell et al. 2008). Notably, the afferents in these electrosensory systems are strongly driven by both exafferent and reafferent changes in electric field strength. In contrast, central neurons (i.e., the Purkinje-like principal cells of the mormyrid and gymnotid fish electrosensory lateral line (ELL) lobe and dorsal octavolateral nucleus (DON) neurons of the Elasmobranchii) are insensitive to reafferent changes in electric field strength produced by (i) electric organ discharge in mormyrid fish, (ii) tail bending in gymnotid fish, and (iii) ventilation in Elasmobranchii. Over the last decade, a series of elegant studies



**Comparator, The, Fig. 1** Comparator models. **(a)** Simplified scheme of the reafference principle of von Holst and Mittelstaedt. The motor command is sent to the effector muscle, and in turn sensory activation, resulting from the activation of sensory receptors by an effector, is returned. This reafference is then compared to an efference copy of the original motor command. Here, reafference is arbitrarily marked “+,” and the efference copy is marked “−.” When the reafference and efference copy signals are of equal magnitude, they cancel, and no sensory information is transmitted to the next levels of processing. By contrast, a difference between the reafference and the

efference copy indicates an externally generated event (i.e., exafference) that is considered behaviorally relevant and thus is processed further. **(b)** Comparator-based model to explain the mechanisms underlying vestibular reafference suppression. In this model, the brain generates an expectation of sensory feedback based on an efference copy of the motor command to move the head and compares this expectation to the actual sensory feedback; if these two signals match, an inhibitory signal is sent to vestibular-only (VO) neurons in the vestibular nuclei and to the rostral fastigial nucleus of the cerebellum to cancel the incoming reafferent vestibular signals

in mormyrid fish have provided considerable insight into the mechanism underlying the suppression of reafferent electrosensory information. Specifically, individual ELL neurons integrate incoming electrosensory information with actively generated (i.e., predictive) proprioceptive cues and corollary discharge signals. When electrosensory information is temporally paired with these predictive inputs, this induces synaptic

changes such that over time the neurons stop responding to the paired electrosensory information. When the electrosensory information is removed, this results in the production of a negative image of the response to the electrosensory stimulus when it had been presented before the synaptic changes had occurred. In this way, the predictable electrosensory stimuli are filtered out thus enhancing unexpected sensory stimuli.

Neurophysiological studies of the vestibular system have further provided evidence for comparator-based mechanism underlying the suppression of self-generated vestibular stimulation in rodents and monkeys. Specifically, a comparator-based mechanism was found in which the vestibular system selectively encodes unexpected versus expected self-motion even when they occur simultaneously (Brooks and Cullen 2014). Notably, vestibulospinal pathways selectively respond to unexpected self-motion, thereby ensuring adjustments to postural tone in response to any head movements that the brain does not expect during voluntary movements such as locomotion. This selectivity is vital, for recovering from tripping over an obstacle while walking or running, which requires a robust postural response. In addition, the vestibular thalamocortical pathway also preferentially encodes unexpected motion, to ensure perceptual stability during active versus externally generated motion (reviewed in Cullen *in press*). Recent experiments suggest that the brain contains an internal forward model that expressly represents the relationship between voluntary action (efference copy) and the sensory consequences (Brooks et al. 2015) consistent with previously proposed theoretical models (e.g., Wolpert and Miall 1996, Fig. 1b). In such models, the comparator explicitly determines the difference between the brain's prediction of the sensory consequences of the action and the actual sensory inflow. This difference is known as the sensory prediction error. In contrast, in the original comparator-based model of von Holst and Mittelstaedt (1950), an efference copy of the motor command is used to directly suppress the sensory consequences of voluntary motor actions.

Finally, comparator models have also been used to explain the origin of our sense of agency (reviewed in Haggard 2017). Our sense of agency is defined as the subjective awareness of initiating, executing, and controlling our own volitional actions in the world. If a sensory event is the result of our own action (and if the brain's internal predictive model is correct), the actual sensory feedback will exactly match the forward model's prediction, and the result of the comparison is zero. However, if a sensory event is not due to

our action, there will be a non-zero prediction error indicating that we are not the causal agent of this event. Thus it has been proposed that the sense of agency is caused by the lack of any prediction error, implying absence of any signal at the output of the neural comparator for a specific act. In fact both humans and monkeys have demonstrated that they are able to distinguish self-generated from externally generated cursor movements on a screen, demonstrating a sense of agency that relies on perceptual (visual) cues (Couchman 2015) suggesting that a comparator-like mechanism may be contributing to their sense of agency.

## Cross-References

- ▶ [Artiodactyla Locomotion](#)
- ▶ [Bear Locomotion](#)
- ▶ [Bovine Locomotion](#)
- ▶ [Canine Locomotion](#)
- ▶ [Catarrhine Locomotion](#)
- ▶ [Caudata Locomotion](#)
- ▶ [Cetacean Locomotion](#)
- ▶ [Chondrichthyes Locomotion](#)
- ▶ [Crocodilia Locomotion](#)
- ▶ [Equine Locomotion](#)
- ▶ [Falconiformes Locomotion](#)
- ▶ [Feline Locomotion](#)
- ▶ [Galliformes Locomotion](#)
- ▶ [Hominoidea Locomotion](#)
- ▶ [Insect Locomotion](#)
- ▶ [Insectivore Locomotion](#)
- ▶ [Lagomorpha Locomotion](#)
- ▶ [Locomotion](#)
- ▶ [Marsupial Locomotion](#)
- ▶ [Megachiroptera Locomotion](#)
- ▶ [Microchiroptera Locomotion](#)
- ▶ [Mustelidae Locomotion](#)
- ▶ [Neural Control of Behavior](#)
- ▶ [Neuron](#)
- ▶ [Passerine Locomotion](#)
- ▶ [Perissodactyla Locomotion](#)
- ▶ [Pinniped Morphology and Locomotion](#)
- ▶ [Placodermi Locomotion](#)
- ▶ [Platyrrhine Locomotion](#)
- ▶ [Primate Locomotion](#)
- ▶ [Proboscidea Locomotion](#)



- ▶ Prosimian Locomotion
- ▶ Reafference Principle, The
- ▶ Rodentia Locomotion
- ▶ Saccadic Eye Movement
- ▶ Salientia Locomotion
- ▶ Sirenia Locomotion
- ▶ Squamate Locomotion
- ▶ Swine Locomotion
- ▶ Visual Perception

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## Compass Orientation

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Compass orientation, in zoology, is the ability of animals to choose and maintain a particular direction using natural cues. Compass orientation

should be contrasted with *navigation*. The latter is a behavior of higher complexity when an animal first needs to detect its own position relative to a destination and then chooses a goal-ward (compass orientation) direction using any available directional references. Thus, compass orientation alone is not enough for goal-finding (*navigation*) in unfamiliar territories where a “map sense” is required to compare the animal’s current position to its destination. *Alignment* is similar in definition to compass orientation but is differentiated by the ability of an animal to maintain a specific angle of its body axis relative to a directional cue and not necessarily during the animal’s movement (e.g., alignment of a resting animal parallel to the Earth’s magnetic field). Compass orientation is usually studied in the context of animal migration but the ability to find directions is useful for any kind of animal movements, over short or long-distances, in migrating and sedentary animals.

Compass orientation deploys *compass mechanisms* that are cognitive and behavioral processes used by animals to choose and maintain directions. For instance, animals can use the apparent position of the Sun or sun-related cues (a sun compass), the stars (a star compass), the directional parameters of the Earth’s magnetic field (a magnetic compass), landmarks, and other directional cues for compass orientation.

The *sun compass* uses apparent position of the Sun as a directional reference (Schmidt-Koenig et al. 1991 for review). To keep a constant compass direction, the animal has to correct an initially chosen direction relative to the Sun’s position, while taking local daytime into account. Several studies suggested that birds (e.g., homing pigeons, *Columba livia* forma *domestica*) first have to learn how the Sun’s position is changing during the daytime and associate particular positions with local daytime hours. Once learnt, the sun compass can be used throughout the bird’s lifetime. Key evidence for the use of an internal clock with sun compass orientation includes time-shift experiments where pigeons with artificially manipulated internal biological time make directional mistakes during homing flights in sunny weather approximately corresponding to the degree of induced time-shift (15° for every 1 h shift). Additionally, there is experimental

evidence that birds can derive the Sun's position when the Sun cannot be directly seen (e.g., a partly cloudy sky and/or at sunrise/sunset) using sun position related light polarization patterns (Muheim et al. 2006).

The *star compass* is the ability to use stars for compass orientation and has been demonstrated in a range of animals (e.g., birds, fish, and insects). Most of these studies suggest that the star compass is a time-independent compass relying on visual recognition of particular stars (e.g., the North Star in the Northern Hemisphere) and/or their combinations. Stephen Emlen's studies in the 1960s and 1970s (e.g., Emlen 1967a, b) suggested that the star compass is not innate but rather requires learning. In his experiments, juvenile indigo buntings (*Passerina cyanea*, a North American nocturnal songbird migrant) were exposed to various artificial starry skies in a planetarium before the first autumn migration, and the bird's star orientation was tested in round arenas during the following autumn migration. Hand-reared experimental birds before their first autumn migration observed a starry sky at the night-time in a planetarium and learnt to recognize a particular star at (or near) the center of a starry sky's rotation, no matter whether it corresponded to the situation in the wild (i.e. whether it was the North Star or another star) or was unnatural stars and constellations. These birds used the learnt center of rotation as a directional reference in experiments during their first autumn migration. Time-shift manipulations do not appear to affect the star compass in birds species tested so far (e.g., Pakhomov et al. 2017). Therefore, the star compass is considered a time-independent compass.

The *magnetic compass* uses the direction of Earth's magnetic field as a directional cue and has been demonstrated in a wide range of animal species (Wiltschko and Wiltschko 1995; Kishkinev and Chernetsov 2015 for reviews). Some studies have argued that the magnetic compass is innate and does not require learning whereas others have suggested that the learning process is required to calibrate (i.e., compare) directions derived from the Earth's magnetic field against direction derived from astronomical cues (stars and the Sun). The magnetic compass can be either

polar or magnetic inclination based. The former can distinguish a direction toward the magnetic North Pole from that toward the magnetic South Pole, whereas the latter can only distinguish a direction toward a magnetic pole from a direction toward the magnetic equator. In most parts of the Northern Hemisphere, a poleward direction is approximately toward the geographic North and an equatorward direction is approximately toward the geographic South whereas in the Southern Hemisphere the poleward and equatorward directions are reversed. Most of avian studies have suggested that birds possess an inclination compass whereas mammals seem to have a polar one.

The sun and star compasses are thought to be vision based, however the sensory substrate of the magnetic compass is not fully understood. One line of research hypothesizes that the avian magnetic compass, so far the most studied one among the animals, is perceived visually, and cryptochromes (CRY) – a family of light-sensitive proteins found in avian retinal photoreceptors – are assumed to play a crucial role in the use of the magnetic compass. The Radical Pair Hypothesis (RPH) states that a CRY molecule gets excited through light absorption and an electron transfer reaction occurs inside the molecule forming a radical pair (RP) in which a CRY molecule and its partner have an unpaired electron each. The quantum properties of this RP and its dependent cascade of chemical reactions in the photoreceptor are both affected by the direction of the ambient magnetic field. If a photoreceptor were imagined as a "pixel" composing part of the visually perceived world, then this pixel's brightness would be dependent on the direction of ambient magnetic field line relative to the photoreceptor cell's orientation. Such signal modulation may ultimately enable birds to literally "see" the Earth's magnetic field, perhaps as visual patterns superimposed on the normal visual field. Proposed in the early 2000s, the RPH was initially hard to conceive. However, there is a growing body of experimental, though so far indirect, evidence supporting the RPH. One line of evidence comes from studies reporting that the avian magnetic compass is light-dependent because birds' ability to use magnetic compass

depends on a wavelength of the light to which a captive bird performing magnetic orientation is exposed. Caged birds appear to be unable to magnetically orient under red light but do it under the light of longer wavelengths (e.g., green and blue). The RPH explains this effect by energy transfer of photons: red light photons with relatively low energy cannot bring CRY molecules into a (magnetosensitive) excited state whereas photons of higher energies (e.g., green or blue) can. The second line of evidence comes from a bird brain study which suggests that lesions of Cluster N, a part of the avian forebrain active in dim light conditions, in European robins (*Erithacus rubecula*) leads to inability to use the magnetic compass. At the same time, Cluster N lesioned European robins were able to use the sun or star compasses and did not show any obvious vision deficiencies (Zapka et al. 2009). This suggests that the avian visual system is somehow involved in magnetic orientation. The third line of evidence for the RPH comes from the studies reporting a disturbing effect of broadband electromagnetic (EM) noise (0–10 MHz) in magnetic orientation of captive songbirds. Surprisingly, even EM noise of very low amplitudes can disturb captive birds' magnetic compass orientation in round arenas (a standard method to record orientation of migrating birds). Such an effect would be hard to explain if a magnetoreceptor were based, as alternatively assumed, on magnetized particles because such weak EM noise would have very little, if at all, effect on them. The RPH explains this EM disturbance as a resonance effect on unpaired electrons caused by the EM field, which theoretically can occur even at low amplitudes. One should mention that the RPH still lacks direct experimental evidence for the existence of CRY-based magnetoreceptors. Further, some predictions of the RPH have become recently criticized by a few biophysical modelling studies failing to explain the disturbing effect of extremely low-amplitude EM fields on the magnetic compass (Kavokin 2017).

The alternative hypothesis explaining the magnetic sense (whether it is directional sense or only the sense of magnetic field's strength) suggests the existence of magnetoreceptive cells based on

magnetized particles assumingly associated with the trigeminal nerves (the fifth pair of cranial nerves in vertebrates). Effects of brief, strong magnetic pulse on birds' orientation have been repeatedly reported since the 1990s, and they could be indirect evidence for this hypothesis. Such magnetic pulse treatments may affect (e.g., remagnetize) magnetic particles, if such existed in the bird's body. Indeed, changes in birds' orientation after magnetic pulsing have been documented, both in captive and freely migrating birds, though the mechanism of it remains unknown. Overall, one should mention that no magnetoreceptive cells have been demonstrated in the animals so far with certainty despite a few (not independently confirmed) reports in the last 20 years. Therefore, it appears to be premature to conclude how the animal magnetic compass sense exactly works.

Besides the aforementioned and most studied compass cues, there are data suggesting that animals can use the Moon, sounds, landmarks, and odour plumes (or gradient of various chemicals) for choosing and maintaining directions. Most of the animals can use a set of compasses together comprising a *compass system*. Often, multiple directional cues providing conflicting results are available to the animal at the same time. Therefore, different animals use different rules of compass hierarchy and compass calibration, i.e., how directional information is transferred from one directional cue to others. A few recent studies have suggested that in migratory songbird species a hierarchy between astronomical (the sun and stars) and magnetic compasses can greatly vary between species (Chernetsov 2017 for review).

## Cross-References

- Bird Migrations
- Cognitive Map
- Navigation

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## Competing Cues

- ▶ [Proactive Interference](#)
- ▶ [Retroactive Interference](#)

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## Competition

- ▶ [Horseback Riding](#)
- ▶ [Plantae](#)

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## Competitive Behavior

- ▶ [Aggression](#)

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## Competitive Exclusion

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## Definition

A test method for determining individual dominance ranks and the linearity (i.e., transitivity) of dominance hierarchies – especially of laboratory mice (also known as the tube-test). It was first designed by Lindzey et al. (1961) to determine differences in dominance abilities between mice of different inbred strains. The task allows for clear scores of dominance: “win,” “loss,” or “tie,” which are otherwise difficult to quantify by home-cage observations (Benton et al. 1980; Brain 1980, 1981). Some groups have expanded “win/loss/tie” outcomes, by recording the subtle behaviors mice show while interacting in the tube, including stillness, push-initiation, push-back, resistance, and retreat (Zhou et al. 2017).

## Method

To perform the task, mice are simultaneously placed on opposite ends of a long narrow tube to assess which mice consistently retreat in a face-to-face conflict. The tube is too narrow for the mice to pass by one another or turn around, thus at least one of them must retreat and exit the tube. The first mouse to retreat is given a score of “loss” and the partner subsequently is scored with a “win.” If both mice simultaneously retreat, they are given the score of “tie” – the occurrence of a tie is rare. Partners are usually tested consecutively for several trials (at least four), alternating the side of the tube. The mouse that consistently “wins” is considered dominant, and the mouse that consistently “loses” is considered subordinate – for the respective pair.

The CE task is typically administered using a round-robin tournament for mice housed together to determine the rank order of the group (Benton

et al. 1980). The tournaments can be divided into pair-tests and trials. Each pair-test consists of four consecutive trials between a pair of cage-mates, and members of the pair cannot be tested in an immediately consecutive pair-test. For instance, the first pair-test may include mouse A and B, and the second pair-test may include mouse C and D, but the second pair-test cannot include mouse A or B. Once all possible pairs are tested on a single-day, the tournament is complete. Consecutive tournaments are then administered across consecutive test days to determine whether the recorded rankings are stable (Wang et al. 2014).

## Task Validity

The task has been validated by determining whether rankings measured in the CE task converge with rankings measured in home-cage behavior, urine marking assay, food competition, and courtship vocalization (Greenberg et al. 2014; Howerton et al. 2008; Wang et al. 2011, 2014), although not all measures of dominance necessarily converge (Benton et al. 1980).

Further validation of the task is critically lacking. First, it is unclear whether the task is more likely to accurately measure stable ranks than unstable ranks. Since its inception, researchers often only consider stable dominance ranks in the CE test as true reflections of their dominance rank in the home-cage. This is problematic because mice are known to have unstable dominance ranks (Uhrich 1937), especially in despotic hierarchies, which are composed of a stable alpha and subordinates with unclear or unstable rankings. This methodological bias toward stable ranks is usually justified through reasoning that the measures must be reliable. However, it is possible to detect instability in a reliable manner if enough trials are given (albeit this has its own caveats; see second point). Reflecting this bias, mice with unstable ranks in the CE task have been systematically excluded from some studies measuring the relationship between dominance and brain function (e.g., Wang et al. 2011).

Second, the practice of consecutive testing may result in trained “dominants” and “subordinates” (Bernstein 1981; Wilson 1968). Social learning – or, training – is fundamental to the existence of dominance; however, learning in the CE task may be unique to the task itself and not representative of learned dominance in the home-cage (Miczek and Barry 1975). However, because the experience of dominance in one domain (e.g., home-cage) is not independent of that measured in other domains (e.g., CE task), programmatic experiments delineating this relationship remain to be performed. The evidence suggests, however, that this task is a measure of a novel dominance relationship. Specifically, mice need consecutive days of testing to gain enough experience with the test to reflect their dominance hierarchies as after a certain number of trials the probability of trained “dominants” and “subordinates” has been shown to increase (Varholick et al. 2018).

Third, it is likely that this task is largely affected by experimenter handling. For each trial the experimenter must simultaneously transfer mice to opposite ends of a tube, and then transfer the mice to a holding chamber before starting the next trial. If mice are not extensively familiarized to the handling procedure or are averse to their handler, their behavior in the tube might be more related to their response to the handler, rather than their response to the partner mouse. For instance, mice that are averse to their handler and subordinate may not readily retreat in the tube when “pushed” by the dominant partner. They could recognize the tube as a shelter, where the handler cannot handle them. Thus, individual mice may behave differently in the test depending on the handler. Again, this could be programmatically investigated but might be impossible to fully eliminate or control. Additionally, because this task requires an experimenter who observes the outcome of each trial, it is impossible to discount experimenter bias effects in the collection of data from each trial. These include subtle differences in the way the experimenter may handle, place, or otherwise conduct a trial having observed the outcome of the previous trial(s).

Fourth, it is worthwhile to consider whether the task appropriately acknowledges the biology



of the mouse. Specifically, mice have some ability to recognize familiar and unfamiliar individuals through odors and major urinary proteins (MUPs) (Hurst et al. 2001). Whether the mice can effectively perceive this odor, or any other odor for individual identification, before responding appropriately within the task – by retreating or pushing – remains unstudied.

Although the highlighted issues may perturb some investigators from using the task, the task can be useful for some experiments. If a research question is limited to stable dominance ranks, then it is likely that the stable ranks measured in the CE task are representative of the true dominance rank – provided the trials are not leading to trained “dominants” and “subordinates.” Also, the task may be useful for determining mice ranked alpha, because they are more likely to remain stable. In sum, one must weigh the costs and benefits of administering the task for their particular research question.

## Use Beyond Laboratory Mice

The task has also been used for other species beyond the common laboratory mouse. Several groups have used a similar test in rats (Carlini et al. 1974; Hsiao and Schreiber 1968; Miczek and Grossman 1972; Spigel et al. 1972; Wilson 1968), prairie voles (Anacker et al. 2014), and piglets (Székely et al. 1983). Some groups have also utilized the test to provide a measure of aggressivity for individuals in a controlled situation (Klomberg et al. 2002) – albeit the test was initially devised to study dominance, which is a representation of a relationship, not a trait of an individual.

## Cross-References

- Alpha
- Beta
- Dominance
- Dominance Hierarchy
- Subdominant

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## Complementary Genes Hypothesis

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## Synonyms

Complementation; Genetic Inheritance; Intergenic Complementation; Intragenic Complementation; Multiple Gene Inheritance

## Definition

Genes may produce different phenotypic effects when they are present together in an organism than either of the genes would have produced if they were present separately in an organism.

Complementary genes combine to produce unique phenotypic effects that would not be expressed if either of the genes were isolated in a separate organism. Complementary genes often exist at distinct genetic loci, either on different genes or on different sites within the same gene.

Simple examples of the effects of complementary genes include innocuous phenotypic effects such as the purple grain coloration in wheat observed by Dobrovolskaya et al. (2006). Additionally, White et al. (1996) showed the complementary effects of genes for eye color in *Drosophila melanogaster*. Further, Cornel et al. (1997) observed that the gene for red eye pigmentation in *Drosophila melanogaster* has a complementary effect in white eye strains of *Aedes aegypti*, resulting in red eye pigmentation. In this sense, complementary genes may only appear to be a chance occurrence, resulting when an offspring happens to inherit a particular combination of genes from each of its parents, and which usually generates no significant fitness benefits. However, some research has focused on fitness benefits that may be a result of complementary genes and the ways in which individuals of some species might select mates based on their potentially complementary genes.

## Mate Selection

Research has focused on the potential for complementary genes to result in offspring who bear an immune resistance to a unique array of pathogens from either of that offspring's parents. In a meta-analysis observing the effects of constrained mate choice in several species (e.g., cockroaches, fruit flies, mallards), Gowaty et al. (2007) found that offspring viability was higher when parents were allowed to mate with their preferred partners than when mate choice was experimentally

constrained. The researchers explained that, in addition to selecting mates based on physical indicators of good genes, individuals may also select mates based on the possible complementary gene effects of immune resistance, thus resulting in offspring that are less likely to die of infection.

### Complementary Genes and Mate Selection in Humans

Roberts and Little (2008) reviewed studies that investigated the ways in which humans select mating partners, and specifically, aspects of human mate selection that may have evolved as a way of selecting immune resistant partners. In particular, Thornhill et al. (2003) observed that men preferred the scent of women who had dissimilar (relative to similar) major histocompatibility complexes. Although the researchers did not observe a similar preference for women, they did observe a preference for the scent of men with high facial symmetry in ovulating women. The results suggest the possibility that men may use olfactory cues to select as mating partners women with a distinct immune resistance from themselves. Selecting mates with a dissimilar major histocompatibility complex may increase the likelihood of producing offspring with an increased resistance to infectious diseases.

At a glance, complementary genes might simply refer to the resulting phenotypic expression produced by two or more genes that, separately, would produce different phenotypes than when they occur in the same body. However, research investigating the selection of mating partners that is potentially based on complementary genes suggests greater complexity. Namely, individuals of some species may use cues to complementary genes in potential mates to produce offspring with an advantage in the form of increased pathogen resistance.

### Cross-References

- [Additive Genetic Variance](#)
- [Polygenic Inheritance](#)

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### Complementation

- [Complementary Genes Hypothesis](#)

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### Complex Arrangement

- [Neural Network](#)

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### Complex Group

- [Animal Society](#)

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## Complex System

- ▶ [Neural Network](#)
- 

## Compliance

- ▶ [Concordance](#)
- 

## Compulsive Behavior

- ▶ [Sign Tracking](#)
- 

## Compunction

- ▶ [Shame and Guilt](#)
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## Computational Biology

- ▶ [Bioinformatics](#)
- 

## Computer Interface

- ▶ [Virtual Reality Experiments](#)
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## Computer-Generated Environment

- ▶ [Virtual Reality Experiments](#)
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## Computerized Testing Paradigm in Primates

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### Synonyms

[Language Research Center Computerized Test System \(LRC-CTS\)](#); [Psychomotor Test System \(PTS\)](#); [Rumbaughx](#); [Video-task paradigm](#)

The computerized testing paradigm is a general methodology for comparative research and environmental enrichment. Computer-graphic stimuli are presented to the test subjects, and responses are made using a touchscreen, joystick, or other manipulandum in accordance with the rules of game-like tasks. The paradigm has become one of the most popular methods for conducting psychological tests with humans and many species of non-human primates, as well as various other animals.

### Personal Computers for Nonhuman Animals

The computerized testing paradigm emerged as a result of three parallel and interconnected developments in the last quarter of the twentieth century. The first and perhaps most obvious catalyst was the introduction of commercially available personal computers (PCs). These early home computers provided opportunities for word processing, calculating, record keeping, and game-playing from the desktop. The 1970s and early 1980s saw tremendous growth in the video-game industry, led by arcade-based games but with a rapidly rising sector of dedicated game systems (e.g., Atari) and PC-game software (Wolf 2008). Psychological scientists quickly recognized the potential of this technology, using computers both to control traditional research apparatus and also directly *as* research apparatus, by

programming simple tests for cognitive and learning studies for adults and children. Shortly thereafter, the technology was also applied to understand the nature and limits of animal learning. Stimulated in part by the observation that chimpanzees seemed to enjoy playing joystick-based commercial games (Savage-Rumbaugh 1986), game-like variations on common test procedures such as matching-to-sample and two-choice discrimination learning were programmed in increasingly sophisticated tests of chimpanzee cognition.

### Psychological Well-Being

In addition to these technological innovations, a legal development also catalyzed the growth of the computerized testing paradigm with non-human primates. For researchers working in the United States with these animals, 1985 witnessed an important amendment to the Animal Welfare Act: The Improved Standards of Laboratory Animals Act mandated that research facilities uphold new standards for the psychological well-being, as well as the physical welfare, of their subjects. Primate researchers everywhere scrambled to understand how to provide “an adequate physical environment to promote the psychological well-being of nonhuman primates” (Public Law 99-198, Food Security Act of 1985, Subtitle F – Animal Welfare). In effort to comply with this amended law, researchers at the National Aeronautics and Space Administration (NASA), which had long employed rhesus monkeys (*Macaca mulatta*) as an animal model of the physiological effects of space travel, contacted Professor Duane Rumbaugh of Georgia State University’s Language Research Center (LRC) for consultation. Rumbaugh described his use of the computerized testing paradigm with joystick-using chimpanzees. There were empirically sound reasons from research with the Wisconsin General Test Apparatus to doubt that macaques could learn the remote cause-effect relations required to respond to stimuli on a computer display by manipulating

a spatially discontinuous joystick (see review by Rumbaugh et al. 1989); however, Rumbaugh reasoned that the benefits would be great if he and his colleagues could succeed in training monkeys on the computerized testing paradigm. In 1986, Rumbaugh’s team of investigators developed a configuration of apparatus and a suite of training software to teach rhesus monkeys to use the computerized testing paradigm. Whereas chimpanzees could learn by observation alone to control a computer-graphic cursor by manipulating a joystick, macaques required a carefully designed, systematic training curriculum to learn – but they *could* learn, and quickly demonstrated skillful performance on the paradigm. In this way, Rumbaugh and collaborators developed a test system that would “contribute to better treatment – as well as better understanding – of several subject populations” (Richardson et al. 1990, p. 130). The resulting apparatus, henceforth referred to as the Rumbaughx (pronounced “rum-box,” to parallel the naming convention of other influential apparatus innovations in comparative psychology, such as the Thorndike problem box or the Skinner box), provided environmental enrichment that allowed for flexible, affordable testing under conditions that promoted the psychological well-being of those animals (Washburn 2015).

The original design criteria for the Rumbaughx (see Table 1 of Richardson et al. 1990), including that the apparatus be user-friendly, customizable, and easily integrated with new and existing technologies, remain today and are largely responsible for the continued utility of the testing paradigm. For hardware, the Rumbaughx test station featured equipment that was (and still is) accessible for most researchers. A computer equipped with a color monitor and speakers was housed in a secondary enclosure so that only the handle of a joystick was accessible from an animal’s home cage. Working computers that are several years old (e.g., refurbished systems or those that might otherwise be surplussed) are typically more than adequate as computerized test systems. Commercially available pellet or juice dispensers are used to reward the animals automatically. The

curriculum of training software rewards the animals initially for any joystick movements, and subsequently for increasingly precise manipulations to bring the computer-graphic cursor into contact with a target stimulus on the screen. Task difficulty is automatically titrated on the basis of performance, such that the task gets harder when an animal is doing well, and gets easier if the animal begins to struggle. Across training steps, the monkey transitions from lever-pressing with the joystick, to directing the cursor into contact with stationary targets, to using the cursor to catch moving targets, to learning to discriminate the “correct” (rewarded) target from among several on screen, and so forth, building a repertoire of task-related skills that the animal can switch between flexibly and appropriately. (Animals trained with a touchscreen rather than a joystick progress through similar stages, but with more of a key-peck than a bar-press as the initial step.) Experimenter-specified parameters and menu options allow the tasks to be tailored further to the needs of a specific animal or a particular study. Stimuli include simple shapes and characters, computer-generated patterns, clip-art images, photographs, sounds, or any other computer-compatible media that are formatted properly (Richardson et al. 1990). The software records all accuracy, latency, and topography data for subsequent analysis. Whereas these might seem like standard features to today’s researchers, they were nothing short of revolutionary for research with nonhuman primates 30 years ago.

The advantages of the Rumbaughx included that the monkeys learned and performed the tasks with little human interaction and no deprivation from food or fluids (e.g., Rumbaugh et al. 1989; Washburn et al. 1989). Monkeys did not have to be reduced in body weight for purposes of testing, but rather could have the computerized testing system available continuously, working or resting whenever they wanted. Transfer of joystick-manipulation skills to novel tasks proved to be relatively straightforward, even in instances when the manipulation of the joystick yielded different outcomes, as in the LASER task, in

which joystick movement resulted in the aiming and shooting of a beam at the target (Washburn et al. 1989). Tasks such as these are much easier to implement with computers than with manual apparatus, and it seems likely animals show competencies with computer-task testing that would not be demonstrated with manual apparatus. It seems unlikely, for example, that chimpanzees could have revealed the same impressive memory for numeral sequences without the computer-task paradigm (e.g., Inoue and Matsuzawa 2009). It seems possible, but remains to demonstrate empirically, whether new competencies may be observed with the Rumbaughx because of factors like the large number of computerized stimuli, the consistency of computer-based presentations, the speed of responding on the computer, or even changes in the cognitive competencies of animals that have been trained to master the remote stimulus-response relations required for computer-based testing.

The computerized testing paradigm also delivered on its original promise to promote the psychological well-being of its test animals (see Washburn 2015, for a more comprehensive discussion). The monkeys willingly engaged the game-like tasks and, unlike the pattern that is seen with many manipulanda or puzzles used as environmental enrichment (e.g., Bennett et al. 2016), continued to show interest in the computer tasks across months and even years. They engage in computer-task activity even when there are other favorite toys or activities available; more important, task-directed activity replaced relatively maladaptive behaviors in the animals’ repertoires. That is, access to the Rumbaughx resulted in fewer stereotypies, bouts of overgrooming or self-injurious behavior, aggression, distress vocalizations, and related signs of compromised psychological well-being (Washburn 2015). Given the opportunity, the animals direct attention to the tasks for many hours each day, leaving fewer hours for behaviors indicative of boredom or distress. Although the food rewards provided by the computerized testing paradigm clearly contribute to this sustained

interest – from one perspective, the joystick paradigm is a repeating problem box or foraging manipulandum that automatically replenishes itself – monkeys have been shown to work even when the food pellets were made freely available, and to prefer working for the food than receiving the food freely (Washburn and Rumbaugh 1992b). These game-like tasks provide individually calibrated levels of challenge and stimulation to the test animals. Given the option, the monkeys will elect to perform a variety of different tasks, and not only the easiest and most rewarding options (Washburn and Rumbaugh 1992b). The system also affords unprecedented options for the animals to control when and on what they work. Perdue and collaborators (2014) reported that the monkeys “choose to choose”; that is, they prefer to have such choices. These factors, combined with the compatibility of the system with primates’ health and social needs, make it an enrichment device that taps all four components of primate psychological well-being (comfort, companionship, challenge, and control; see Washburn 2015).

## The Rise of Comparative Cognition

Given its usefulness for enrichment and the rich corpus of data that it produces, the computerized testing paradigm quickly attracted the interest of researchers at other laboratories, and these scholars were freely provided copies of the training software and instructions for assembling the Rumbaughx. The apparatus has since been successfully implemented with many species, including lemurs, squirrel monkeys, capuchin monkeys, baboons, orangutans, bonobos, dogs, bears, elephants, pigs, rats, and many other species (e.g., Andrews 1993; Croney 1999, as cited in Marino and Colvin 2015; Hyatt 1998, 2013; Merritt et al. 2007; Vonk et al. 2012; Washburn et al. 2004), and for the purposes of studying such diverse topics as visual illusions, perception and action, attention skills, concept formation, episodic memory, mental rotation, learning, numerical

cognition, metacognition, self-regulation, symbol learning, prospective memory, social cognition, brain-behavior relations, and many other constructs (for a review, see Beran et al. 2016; see also Beran et al. 1998; Evans and Beran 2012; Leighty and Frigaszy 2003; Parr and de Waal 1999; Parr et al. 1998; Templer and Hampton 2013; Smith et al. 2012; Vauclair et al. 1993; Washburn 1993).

This breadth of topics studied with the Rumbaughx highlights the third catalyst to the development and popularity of the computerized testing paradigm: the rise of comparative cognition. A shift in theoretical focus was already underway in the 1980s when the new technology was applied to the study of animal behavior. The so-called cognitive revolution within experimental psychology was increasingly evident in comparative psychology (e.g., Wasserman 1993), and the field was ready for a general and flexible testing paradigm that could be used to explore a range of cognitive topics with a range of animals. The operant chamber or Skinner box has served the field with distinction, allowing researchers to strip away variables that complicate our understanding of learning and to focus on the stimulus, response, and reinforcement contingencies themselves; however, comparative cognition recognizes the need to embrace these complexities in order to understand the processes that may mediate and moderate the stimulus-response associations. With the computerized testing paradigm, virtually every test procedure from cognitive psychology, developmental psychology, comparative psychology, and clinical neuropsychology could be translated into game-like tasks for use with primates and other animals.

As scientists worldwide began to examine animal behavior through use of the computerized testing paradigm, innovative refinements to the apparatus and procedures were introduced. Rumbaugh and his colleagues had initially hedged their bet by training two rhesus monkeys on a joystick-based system, and a third monkey with a touchscreen-response system. The monkeys’ impressive performance with the joystick



paradigm led the research team to abandon the prohibitively expensive touchscreen technology (Washburn et al. 2017). As touchscreens have become more affordable in recent years, an increasing number of researchers have adopted touchscreen paradigms derivative of the Rumbaughx for use with nonhuman populations, including monkeys, pigeons, and rats (e.g., Drayton and Santos 2014; Fagot and Bonté 2010; Hampton and Hampstead 2006; Kangas and Bergman 2017; Mandell and Sackett 2008; Markham et al. 1996; Spetch et al. 1992). Innovations that permit computer-based testing on socially housed nonhuman primates (e.g., Fagot and Paleressompoulle 2009; Gazes et al. 2013) represent another critical methodological advance in the way that cognition is studied comparatively.

## Summary

Washburn et al. (1994) reported that for many years, comparative psychology trailed far behind other sciences in terms of its use of computer technology: In the 1970s, over 80% of the apparatus used in popular comparative journals of the time were variants of operant and maze devices, and of the small percentage that reported computer use, most was limited to the storage and maintenance of data. By 1989, the Rumbaughx was installed in dozens of facilities and in use with hundreds of nonhuman primates (Washburn and Rumbaugh 1992a). Today, computer technology has so saturated the comparative research environment in the USA and abroad that it is difficult to calculate how many facilities use variations on the computerized testing paradigm – and where indeed to draw the line between the traditional Skinner box and the Rumbaughx-like variation in which rats touch or pigeons peck computer-graphic stimuli on a touchscreen (e.g., Bussey et al. 2008; Cook et al. 2004; Sawa et al. 2005; Wasserman et al. 1995; Wolf et al. 2014). Further advancements in comparative psychology are undoubtedly pending as even newer technologies

surface (e.g., Dolins et al. 2017). With each opportunity, there must also be discussion of how each apparatus or paradigm might slant results or produce artifactual findings. That is, each new way to ask research questions also provides new constraints on the kinds of answers are obtained. The operant chamber, for instance, revolutionized the study of learning by simplifying the stimulus-response contingencies; however, the simplification that made the apparatus ideal for identifying the effects of reinforcement on behavior also limited the kind of learning that could be studied to relatively simple stimulus-response types. Related consideration of species differences in the suitability of an apparatus for different species is also important: Whereas the joystick paradigm has been used with species other than nonhuman primates, many of the nonprimate species (or even some species across the primate order) have disadvantages with respect to perceptual, motor, or other factors. For example, although rats were able to learn basic joystick-control skills (Washburn et al. 2004), the time this required combined with the animals' relatively short lifespans severely limited the range of cognitive tasks that could be introduced after this training. Discussion of these concerns, coupled with a healthy reluctance to rely too heavily on a particular method or apparatus, will promote development of a comprehensive catalog of tools that researchers can use to characterize animal behavior – a catalog in which the Rumbaughx, and the computerized testing paradigm more broadly, enjoys a position of prominence.

## Cross-References

- [Animal Welfare](#)
- [Attention](#)
- [Brain Asymmetry](#)
- [Cognitive Control](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Counting](#)
- [David Washburn](#)

- [Discrimination Learning](#)
- [Duane Rumbaugh](#)
- [Episodic Memory](#)
- [Georgia State University's Language Research Center](#)
- [Meta-cognition](#)
- [Michael J. Beran](#)
- [Prospective Memory](#)
- [Skinner Box](#)
- [Sue Savage-Rumbaugh](#)
- [Touch Screen](#)
- [Wisconsin General Test Apparatus](#)

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## Concealing Coloration

### ► Cryptic Coloration

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## Conceptual Set-Shifting Task (CCST)

### ► Wisconsin Card-Sorting Task

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## Conceptual-Driven

### ► Top-Down Processing

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## Concordance

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### Synonyms

Compliance; Congruence

### Definition

The term concordance defines as a manifestation of the same characteristic in both members of a twin pair (Smith 1972; Lewontin 1982). When the both the members of the twins have or lack a same trait then they are concordant. Identical twins are the ideal example of concordance.

**Concordance rate** is a measurement using statistical index that analyzes the relative effect of nature (which signifies the traits which are being inherited) and nurture (signifying the qualities and traits which are acquired in a lifetime) assessed altogether. Concordance rate is a

statistical index employed by the geneticists to describe the probability rate that two individual with shared genes will develop the same organic disease.

Alternatively, Hrubec proposed that the extent to which the twins tend to be concordant, that is, the extent to which the disease tends to occur in both members of twin pairs, is generally measured by concordance rates (Hrubec 1973).

### Essentiality of Concordance Study

Geneticist compares the concordance rate of identical twins to that of fraternal twins in order to decipher whether a disease or a certain trait has a genetic cause or not (Smith 1972). In identical twins analysis, the genetic makeup carried by one would very likely also be carried by the other which makes them genetically virtually identical. There is a high probability that a particular trait caused by a certain gene identified in one twin may also be present in the other twin (Smith 1972).

The twin method study is often not given the privileges or significant attentions as they deserve. Very little documentation is available since its applicability in twin study. This is partly because of the variety of statistical methods used for concordance analysis and the different genetic interpretations made on this basis in many cases erupts out as ambiguous. The probable reason for this ambiguity generally lies on the lack of expertise in statistical analysis by the users (Smith 1974).

Many of the clinical geneticists have reported about the particular characteristics of the twin concordance (Allen et al. 1967; Bulmer 1970 and Smith 1972). For example, Irving I. Gottesman and James Shields, psychiatric geneticists, conducted the behavioral genetic study among the twins to depict the concordant rate in schizophrenia, which they have published in 1972 (Gottesman and Shields 1972, 1976).

### Models for Studying Concordance

Several authors have manifested many of the suitable statistical analysis for determining

concordance. Zdenek Hrubec (1973) uses different analytical methods of concordant for assessing the involvement of genetic factors in disease etiology with the perspective of diagnosis of twins. He also describes the concordance of disease probability between the twins to identify the extent of the disease occurrence in both members of the twin pairs based on random and conditional ascertainment model. Very similarly, C. Smith has documented the use of pro-band concordance rate analysis to depict the frequency of liability between the twins (Smith 1974).

Diagnosis of twins is generally assumed to be done independently among the members who have visited the clinics. The disease diagnosis process in a twin pair may be evolved in two different ways, either (i) when the patients directly report for presence of a particular disease to a clinician or (ii) a disease symptom may accidentally come into clinician’s notice during thorough clinical investigations.

On this perspective two different models have been proposed to observe the disease alternatives (Hrubec 1973). Henceforth, the evaluation of incomplete diagnostic strategy is being determined on two basic models like:

- **Random Ascertainment Model**
- **Conditional Ascertainment Model**

A Simple Example of Concordance Study

The concordance rates can be calculated and used for data analysis as follows:

Fifty pairs of similar twins and 50 pairs of fraternal twins are chosen for concordance analysis. The collection of the twins will be in such a way that one twin in each pair will exhibit the disease morbidity. Now, for instance, if only one twin in a pair shows morbidity then the twins will be designated as **discordant** for morbidity. On the other hand, **concordant** for morbidity is said to exist when both of the twins in a pair exhibit the disease.

Next, two concordance rates can be calculated: one for identical twins and the other for fraternal twins (Table 1). The pairwise concordance rate analysis can be applied for this study.

**Concordance, Table 1** shows the number of concordant and discordant pairs assumed among the selected identical and fraternal twins

|                 | Number of concordant pairs | Number of discordant pairs | Total number of pairs |
|-----------------|----------------------------|----------------------------|-----------------------|
| Identical twins | 20                         | 30                         | 50                    |
| Fraternal twins | 12                         | 38                         | 50                    |

C<sub>I</sub> = The rate for identical twins

$$C = \frac{\text{Number of concordant Pair}}{\text{Number of concordant Pairs} + \text{Number of Discordant Pairs}}$$

First the pairwise concordance rate for identical twins has been calculated where the number of concordant identical twin pairs is 50 and the number of discordant identical twin pairs is 50.

$$C_I = \frac{20}{20 + 30} \times 100$$

$$C_I = \frac{20}{50} \times 100 = 40\%$$

Very similarly, calculate the pairwise concordance rate for fraternal twins.

The number of concordant fraternal twin pairs = 17

The number of discordant fraternal twin pairs = 83

C<sub>F</sub> = Rate for fraternal twins

$$C_F = \frac{12}{12 + 38} \times 100$$

$$C_F = \frac{12}{50} \times 100 = 24\%$$

Analysis of the Calculation

Thus, from this analysis it is found that concordant rate between the identical twin is 40% whereas the rate between the fraternal twins is



24%. These values justify the rate of pairwise similarity index for sharing a particular disease taken for consideration.

## Applications

- The concordance analysis generally confines on the pattern of heritability of a particular disease trait to offspring and to how far extent that genetic disease is being expressed between the twins.
- The study helps us to determine the linkage analyses for both MZ and DZ twin pairs taken for concordant evaluation.
- Quantitative genetic analyses and heritability assessment, encompassing correlations among concordance, can be used to investigate the relative importance of genetic and environmental influences on a particular trait (Lichtenstein et al. 2002).
- Analysis/comparison of concordance through quantitative genetic method can be applied to elucidate the importance of genetic and environmental impacts on physical traits.
- The concordance study is used to investigate the correlative index of different diseases from cardiovascular to any kind of neurological or behavioral disease among the twins.

## Drawbacks

- The genetic interpretation of many of the different measures of concordance is difficult and their value is questionable in many respects (Smith 1972).
- In a given genetic pattern there may be different phenotypic consequences in genetically identical individuals since it is not possible to have 100% penetrance.
- Developmental and environmental factors may not be identical for genetically alike individuals. If these factors contribute to the development of disease or other characteristic, there may be a chance for the evolution of distinct and nonsimilar traits; hence applicability of concordance will not be possible in this regard.

## Concluding Remarks

Concordance rate analysis in twin study estimates the correlation among twins in order to characterize the relation between a trait and the genetic factor. The correlation is genetically interpreted following the elimination of nongenetic ancestral effects on twins and calculation of the coefficient of genetic determination for the trait.

## Cross-References

### ► Quantitative Genetics

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## Condition of Birth

### ► Nature Versus Nurture



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## Conditioned Approach

### ► Autoshaping

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## Conditioned Defensive Burying Paradigm

### ► Defensive Burying

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## Conditioned Inhibition

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## Synonyms

Conditioned inhibitor; Pavlovian inhibition

## Definition

Conditioned inhibition (CI) refers to a phenomenon of associative learning in which a stimulus (a conditioned inhibitor) signals the absence of an unconditioned stimulus (US). More technically, a conditioned inhibitor is defined as a stimulus that passes both a summation and a retardation of acquisition test (see below).

## Introduction

Animals are constantly learning where to get food, safety, and comfort, through Pavlovian associations. They spend energy moving toward cues that signal appetitive outcomes and moving away from situations that predict danger. Interestingly,

as useful as it is to learn to look for food and to escape, it is to learn where and when not to, allowing the animal to save energy and effort. Environment cues can give us this type of information by signaling that an outcome will not occur right now. CI is the mechanism by which we can learn not to respond to those situations.

Within the frame of associative learning, CI has at least two meanings, it can refer to an experimental procedure that results in a conditioned inhibitor, and it can refer to the reduced responding associated with the presence of a conditioned inhibitor. Responses are usually elicited in the presence of a conditioned or unconditioned stimulus, but if a conditioned inhibitor is present, responses are reduced or might not even happen at all (i.e., they are inhibited by the conditioned inhibitor).

## Pavlov's Procedure for CI

Ivan P. Pavlov (1927) first proposed that a reduction of conditioned responding could occur in two ways: responding could be reduced by the presence of a novel stimulus (a phenomenon he denominated *external inhibition*), and it can be reduced by a previously trained stimulus, a phenomenon he called *internal inhibition*. The latter with time was renamed as *conditioned inhibition*.

In Pavlov's CI, trials of excitatory conditioning (in which a stimulus is followed by an unconditioned stimulus (US)) are interspersed with a second type of trial (inhibitory trials), in which the first stimulus is now presented in compound with a different stimulus, a second cue, in the absence of the US. Through this procedure Pavlov noted that the second stimulus became a conditioned inhibitor and that it could reduce responding to the first stimulus trained and also to another excitatory conditioned stimulus (CS), different from the one used to train the conditioned inhibitor (i.e., a transfer excitor).

As research on conditioned inhibition progressed, different experimental procedures for CI training were developed. For example, different to Pavlov's procedure, the to-be conditioned inhibitor can be presented alone during the

inhibitory trials (Lyons 1969) and the US and the conditioned inhibitor can be just present interspersed but never together (i.e., negative contingency; Rescorla 1969). These procedures may appear quite different, but they have in common that the conditioned inhibitor is always presented in the absence of the US. Thus, any stimulus signaling the absence of US may become a conditioned inhibitor, and the presence in training of a punctate excitatory CS might be irrelevant.

### Necessary Conditions for CI

At least two critical conditions must be met for CI learning to happen. The first one is that there must be an expectation of the US. A conditioned inhibitor cannot signal the absence of the US if the US is not expected by the animal in the first place. An excitatory CS typically establishes this expectancy of the US. In Pavlov's inhibition procedure, an excitatory CS creates the expectancy during the inhibitory trials, but the US is absent. This is a significant event for the animal, and the stimuli signaling it become important to learn about. In procedures where there is no excitatory CS, it is harder to identify the source of the expectancy of the US, but it is usually assumed that in those cases, the context or other non-discrete stimuli generate this expectancy.

The second condition is that the conditioned inhibitor must have a higher chance of happening without the US than with it. Outside the laboratory, CS rarely signals an event with perfect accuracy. This means that the conditioned inhibitor may occur in the presence of the US once in a while, but only if the chances of that are lower than the chances of the US occurring by itself. Both conditions are met by all the procedures previously described.

### Effects in Behavior of a Conditioned Inhibitor

The inhibitory status of a conditioned inhibitor is not always readily apparent. In some occasions, the strength of a conditioned inhibitor can be

measured directly by observing whether it reduces conditioned or unconditioned responses or not. This works well for responses that are bidirectional in nature. A response is bidirectional if it can increase or decrease from its baseline. For example, a well-documented bidirectional behavior is that of approach and withdrawal from CSs. Just like with food itself, an animal may approach a food-signaling CS. The elicited behavior in this case is appetitive. Notably, a conditioned inhibitor for food may become aversive because it is associated with the absence of food, eliciting withdrawal behavior. Measuring CI in these cases is straightforward, but not every behavior is bidirectional. For example, freezing is a common result of fear conditioning, and fear to a CS is indirectly measured by how much it reduces another behavior from baseline. As in this case, a conditioned inhibitor will not elicit behavior above baseline levels; different strategies have to be adopted to measure inhibition.

Pavlov demonstrated that two CS can summate their response levels if presented together. Similarly, a conditioned inhibitor can be tested in compound with another excitatory CS, a procedure denominated *summation test* (aka compound stimulus test or associative summation test). If the conditioned inhibitor is indeed inhibitory, responses to the compound would be lower than responses to the excitatory (transfer) CS alone. However, this test alone is not enough to be certain a stimulus is a conditioned inhibitor. A summation test can also be passed by a stimulus that commands higher attention than the excitatory CS. So, a summation test can be passed by a stimulus that is a conditioned inhibitor or another type of stimulus that somehow hoards attention from the animal. Because of this, a second test is usually used in conjunction with the summation test, a *retarded acquisition test* (aka retardation test). In this test, a supposed conditioned inhibitor is paired with the US, just like in Pavlovian excitatory conditioning. The inhibitory properties of the conditioned inhibitor are assumed to retard the rate of Pavlovian conditioning acquisition (or expression). Thus, if the conditioned inhibitor acquires excitatory strength slower than a neutral stimulus, then it passes the

test. A retarded acquisition test can also be passed by a stimulus that catches little attention. For example, a stimulus presented by itself before Pavlovian acquisition (i.e., before being paired with a US) also provokes slower acquisition of excitatory strength. This is called, somewhat confusingly, latent inhibition (Míguez et al. 2015; Reiss and Wagner 1972). This is different from conditioned inhibition in that a preexposed cue does not predict the absence of a US or any relevant consequence. It regards little attention, passing a retardation test. This circles back to the summation test, as a low attention stimulus would fail it. Both tests are used under the assumption that a stimulus cannot have high and low attention at the same time. This allows us to conclude that a stimulus is inhibitory, discarding alternative explanations for the effect of a conditioned inhibitor on behavior (Cole et al. 1997; Polack et al. 2012).

## Theories of Conditioned Inhibition

There are mainly three ways to understand how CI works (Savastano et al. 1999). The first one assumes that conditioned inhibition and excitation are opposite poles of a continuum. The second one proposes that inhibition is a separate and parallel process to excitation. The third one assumes that inhibition is a result of behavior, that is, it occurs at the level of performance instead of the associative level.

The continuum theories come from total-error-correction theories of Pavlovian conditioning such as the Rescorla-Wagner model (Rescorla and Wagner 1972), in which stimuli have a predictive value to a US, and animals learn by the correction of this value during conditioning trials. A stimulus paired with a US gains positive associative value toward it, whereas a stimulus paired with the absence of a US gains negative associative value and becomes a conditioned inhibitor. This kind of theory readily explains both summation and retardation tests. When paired with a US, a conditioned inhibitor needs to correct its negative value to neutral and then to positive values, and so it acquires positive associative value

slower than a neutral stimulus, which moves directly from a neutral to a positive value. Also, when presented with an excitatory CS, the negative value of the conditioned inhibitor counteracts the positive value of the excitatory CS, provoking less responding than to the excitatory CS alone. If the stimulus is not a conditioned inhibitor, it would have neutral or positive value, so the net sum would be equal or higher than the excitatory CS alone.

A second family of models accounts for CI in a different way. In this family, CI is a parallel process relative to conditioned excitation; although the predictive learning rules between them are similar, it assumes an inhibitory association, separate from the excitatory one, as result of that process. For example, Konorski (1967) posed that behavior is influenced by both positive associations between the CS and the US representations and positive associations between the CS and no-US representation. In the retarded acquisition test, a conditioned inhibitor must acquire a stronger US association than its no-US association, showing a weaker CR acquisition. In the summation test, both US and no-US associations compete simultaneously, resulting in low CR.

The third family accounts for behavior indicative of CI without assuming the existence of inhibitory associations. An example of them is the comparator hypothesis (Miller and Matzel 1988). For this model, conditioned responding is the result of a process involving a comparison made in the moment of performance. There are no inhibitory processes, and the strength of stimulus associations is always positive. The associative strength of a stimulus is compared to that of a comparator stimulus. In Pavlov's inhibition procedure, the comparator is the excitatory CS. When a conditioned inhibitor is presented, it is compared to its comparator stimulus, and because the strength of this comparator stimulus is much higher than that of the conditioned inhibitor, it produces little conditioned response. In other types of CI procedures where there is only a US present, the background cues (i.e., context) become the comparator. This can explain the retardation test, because the conditioned inhibitor must overcome the associative strength of its

comparator before it can produce a robust conditioned response. The summation test is also explained if it is assumed that two comparisons can summate the response potential that they each produce.

## Summary

In short, a conditioned inhibitor signals the absence of a US. This can be accomplished by pairing a stimulus with the absence of a US through different procedures, and it can be assessed with summation and retarded acquisition tests. Regarding the theoretical explanation for conditioned inhibition, it can be viewed as another pole of an excitation continuum or as the result of a different process.

## Cross-References

- Appetitive Response
- Inhibition
- Latent Inhibition
- Ralph Miller
- Unconditioned Response

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## Conditioned Inhibitor

- Conditioned Inhibition

## Conditioned Place Preference

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## General Introduction

The conditioned place preference (CPP) procedure has been widely used in pharmacology, learning, and behavioral neuroscience. Its most common, but not exclusive, application has been in studying the rewarding and/or aversive properties of drugs and as a screening tool for drug abuse potential (e.g., Bardo and Bevins 2000; Tzschentke 1998). Although there are many

methodological differences, the general CPP procedure consists of presenting a rewarding or aversive stimulus in the presence of one distinct chamber on one day and a neutral stimulus (e.g., vehicle) in another distinct chamber on alternating days. After several conditioning days, subjects receive a choice test that involves access to the entire apparatus without the presence of the stimuli. A CPP is established if subjects spend significantly more time in the compartment paired with the rewarding or aversive stimulus. If subjects spend less time in a compartment paired with a stimulus, they may be eliciting a conditioned place aversion (CPA). Whether or not a place preference or aversion occurs and to what degree depends upon numerous features of a CPP study including the apparatus used, the design of the study, and the methods. The current entry will briefly survey methodological considerations, applications of CPP for natural rewards and drug studies, and the brain mechanisms involved in CPP.

## Apparatus, Design, and Methodological Considerations

### Apparatus

**Two- Versus Three-Compartment Chambers** An important consideration of the choice of apparatus used in CPP studies is the number of compartments (Bardo and Bevins 2000; Tzschentke 1998). In a typical three-compartment CPP study, the outermost two compartments consist of distinct contextual features (e.g., grid versus cross-grid flooring), and a middle compartment has no special features. A rewarding stimulus is presented in one of the outermost compartments and a neutral stimulus in the other outermost compartment. The middle compartment is therefore not paired with either a rewarding or neutral stimulus. However, in a two-compartment CPP box, a subject has to choose between a compartment associated with a rewarding stimulus and one associated with a neutral stimulus, thereby requiring a “forced choice.” A forced procedure has the potential to bias a

subject toward or away from the compartment they were placed in during the test session.

One important difference between the two- and three-compartment procedures is that the middle compartment of the three-compartment apparatus is relatively novel on the test day, whereas neither compartment of the two-compartment apparatus is novel on the test day. Therefore, the novel compartment might appear to enhance CPP showing a reduction of time spent in the neutral compartment relative to the reward-paired compartment. This may result in a false positive since it assumes that the preference for novelty would reduce the time spent in the compartment paired with a neutral stimulus more so than time spent in the compartment paired with a rewarding stimulus.

### Design

**Biased Versus Unbiased Designs** Another important consideration in CPP studies is whether the design is a biased or an unbiased one (see Prus et al. 2009 for review). In a biased design, the initial preference of a subject for a particular compartment is assessed by measuring the amount of time spent in each compartment. The least-preferred compartment is then assigned to be paired with a rewarding stimulus. In an unbiased design, the assignment of a particular compartment for pairing with a rewarding stimulus is determined by the researcher regardless of the initial preference of each subject for either compartment.

**Pre-existing Preferences** Concerns about CPP procedures often involve the potential for pre-existing preferences for one environment over another that may alter conditioning processes (Bardo and Bevins 2000). An environmental context may be preferred before conditioning, and this may or may not alter the acquisition of a CPP. Many studies utilize a biased procedure in which the non-preferred compartment is used as the conditioning compartment to avoid misinterpretation of an initially non-preferred context. For example, a non-preferred context, prior to conditioning, could be interpreted as neutral compared to the preferred context or aversive. If the context is aversive, an increase in preference for

that context could be interpreted as less of an aversion rather than an increase in reward-related value of the compartment.

### Other Methodological Considerations

**Sensory Modalities** Sensory modalities are also an important issue in establishing a CPP because they take into account species-specific sensory capabilities. For example, in CPP studies with birds, visual stimuli such as colored walls of the chamber have been used (Levens and Akins 2001). This contrasts with the multimodal contextual cues (visual, tactile, olfactory) typically used with rats, a species that has a relatively poor visual capacity. Visually-based CPP in an avian species may offer some unique advantage in modeling conditioned drug effects that occur in the real world. For example, proximal or distal environmental cues associated with drug taking may attract abstinent drug users and cause them to seek out the drug and ultimately relapse. These environmental cues may be visual in nature.

**Drug Studies** There are additional methodological considerations of CPP that are specific to drug studies. One major consideration is in the identification and interpretation of what is learned in the CPP procedure. A common interpretation of an established CPP is that of Pavlovian conditioning, such that a distinct environment (conditioned stimulus or CS+) is paired with a rewarding or aversive stimulus (e.g., drug; unconditioned stimulus or US), resulting in increased time spent in that environment (conditioned response). Another distinct environment (CS–) is presented in the absence of the US. Bardo and Bevins (2000) describe processes other than reward or associative learning that might account for a place preference such as novelty/familiarity of contexts, state dependence, and anxiety. For example, an animal may receive equal exposure to both distinct contexts such that environmental familiarity appears to be equated in CPP experiments. However, if the drug of interest interferes with familiarization, then place preferences may reflect the tendency of rats to spend more time in a novel environment rather than a conditioned association

between the context and the rewarding effect of the drug.

Another consideration in drug CPP studies may be the number of conditioning trials. Depending on how potent the rewarding properties are of a reward-related stimulus, fewer and more conditioning trials may be needed to develop a CPP. For example, drugs that have potent rewarding properties such as amphetamine and cocaine may require fewer conditioning trials than drugs that have weaker rewarding properties, such as nicotine and ethanol (Tzschentke 1998).

### Application of CPP to Study Natural Rewards

The CPP procedure has been used to test the rewarding properties of a wide array of stimuli including food, wheel running, social interaction, and copulation. What follows is a brief overview of the application of CPP for each of these natural rewards.

**Food** Although food has been commonly used as an appetitive stimulus (one that is sought out) in behavioral studies, relatively few studies have specifically assessed the rewarding properties of food using CPP. Mace et al. (1997) tested Japanese quail chicks with a distinctly colored chamber paired with normal food and a different distinctly colored chamber paired with food tainted with methyl anthranilate (bird aversion chemical). When tested in the absence of both foods, quail chicks spent more time in the distinctly colored chamber that had previously been paired with normal food over the chamber previously paired with tainted food. In addition, the place preference for normal food over tainted food developed in as few as 2 days of conditioning. Similar findings have been reported in studies with rodents (e.g., Spyraiki et al. 1982) but without the colored walls.

An important consideration in studies examining food-induced CPP is the palatability of the food. Although the consumption of highly palatable foods such as a sucrose solution typically induces a CPP, more recent research has directly



compared food-induced CPP for highly palatable food versus standard laboratory diet. Using an unbiased CPP procedure in monkeys, Duarte and colleagues (2015) repeatedly paired one of two distinct contexts with chocolate chips (i.e., a high palatability food) and the other with standard diet (i.e., a food with comparatively less palatability) on alternating days. Compared to the preconditioning baseline, monkeys spent significantly more time in the context that was paired with the highly palatable food (i.e., chocolate chips) than in the context paired with a less palatable food (i.e., standard diet) during the test trial.

Although the majority of research on CPP has been conducted in nonhuman animal subjects, technological advances have created new opportunities for research on CPP in humans. In a recent study (Astur et al. 2014), participants were given chocolate candy (i.e., M&Ms) while they explored a distinct computerized virtual environment. On alternating sessions, another distinct virtual environment was presented in the absence of candy. The next day, participants completed a test session during which they had free access to both virtual environments through a neutral hallway. During the test session, participants spent significantly more time in the virtual environment that was paired with chocolate candy compared to the virtual environment that was not paired with candy.

**Physical Activity** Several studies have examined physical activity as a reward using CPP procedures. Lett and colleagues (2000) placed adult male rats that had been food restricted to 80% of their free-feeding body weight into enclosed running wheels for 2 hr. In a backward conditioning procedure (US before CS), rats were then removed from the running wheel (the US) and immediately placed into the appropriate conditioning chamber for 30 min (CS). On alternate sessions, rats were confined to a small chamber for 2 hr and then placed into the opposite conditioning chamber. Results showed that rats spent more time in the chamber that was paired with the residual effects of wheel running compared to the context that was not paired with the effects wheel

running. In contrast to these findings, a study using forward conditioning showed that rats developed a conditioned place aversion (CPA) to wheel running if they were placed into the conditioning chamber (CS) prior to a 60-min period of wheel running (US; Masaki and Nakajima 2008). These findings suggest that the rewarding properties of wheel running may differ depending on whether forward or backward conditioning procedures are used.

**Social Interaction** The CPP procedure has also been used to evaluate the rewarding properties of social interaction. In one of the earliest studies, Calcagnetti and Schechter (1992) employed a biased CPP procedure and showed that a play-induced CPP developed in socially dominant, individually housed (i.e., socially deprived) juvenile rats. Importantly, this CPP was induced following repeated pairings of the initially non-preferred context with a submissive, socially active conspecific that engaged in play behavior compared to the initially preferred context that was paired with a socially inactive partner that did not engage in play behavior because of treatment with scopolamine. More recent research on social interaction has focused on determining the effect of housing on CPP. In general, animals that are socially housed show a place preference for a chamber that contains other socially housed conspecifics.

**Sexual Behavior** Various aspects of copulation have been examined using CPP. In these studies, copulation with a conspecific is paired with a distinct chamber or given in the home cage just prior to exposure to a chamber. On alternating days, animals are taken directly from the home cage and are placed in the opposite chamber with no copulation. Both sexually naïve and sexually experienced male rats develop a CPP for a chamber where they have ejaculated with a female rat, but only sexually naïve males show a CPP for a chamber associated with intromissions (Tenk et al. 2009). These findings suggest that there may be hierarchy of rewarding components of sexual behavior with ejaculation being the most rewarding component.

Studies that have attempted to establish sex-induced CPP in female rats are more limited and have been less successful. Paced-mating behavior appears to be particularly important for the induction of CPP in female rats. For example, female rats that were permitted to pace the rate of a copulatory opportunity by a male rat showed a shift in preference toward a sex-associated context, but those that were not permitted to pace did not (Paredes 2009).

## Application of CPP to Study Drug Effects

CPP has been adopted to test the rewarding effect of a wide range of drugs, including legal, prescription, and illicit drugs in a wide range of species including humans, other mammals, amphibians, fish, birds, and invertebrates. Many drugs that consist of a rewarding component often have abuse potential. Therefore, it is important to identify drugs that have a rewarding component and to examine the magnitude of that reward. The current section will review CPP studies involving various drugs.

## Psychostimulants

**Cocaine** Cocaine is likely the most commonly studied drug in CPP studies. The rewarding properties of cocaine have been extensively examined (see Tzschentke 1998 for review). Early studies involved investigating parametric aspects of cocaine CPP and applying agonists/antagonists, while current studies are focused more on the cellular and neurobiological mechanisms such as with the role of various receptors and involvement of genes.

Females appear to be more sensitive to the rewarding effects of cocaine than males. Female rats develop a cocaine CPP at lower doses than males and in fewer sessions (Russo et al. 2003). This sensitivity to the rewarding effects of cocaine appears to be mediated by estradiol (E2) since cocaine CPP is attenuated in ovariectomized (OVX) females compared to gonadectomized males and females (Russo et al. 2003).

**Methamphetamine** Methamphetamine (METH) is a highly potent stimulant that produces prolonged euphoric effects. Based on this, one might assume that it has potent rewarding properties and that these would elicit a robust CPP. However, METH has been shown to induce both CPP and aversion, depending on the dose (Cunningham and Noble 1992). Also, the acquisition of METH CPP has been shown to require more pairings than needed for cocaine CPP (Zakharova et al. 2009).

While studies on sex differences and the rewarding effects of METH are sparse, reports have failed to find sex differences in METH CPP (e.g., Schindler et al. 2002). This is somewhat surprising given the differences between males and females in their response to cocaine.

**Amphetamine** Amphetamine (AMPH) is a strong stimulant that has been used medically for certain conditions; however, it does have some abuse potential. AMPH CPP has been demonstrated with both low and high doses and pretreatment with a dopamine antagonist blocked AMPH CPP (Spyraki et al. 1982). AMPH CPP has also been identified in humans. Childs and de Wit (2013) have shown that human participants rate AMPH-paired environments as more preferred and liked even if they rated it as the least preferred prior to AMPH administration (Childs and de Wit 2013). Therefore, AMPH CPP appears to be a fairly robust phenomenon.

## Opiates

The pain-relieving effects of morphine, a mu-opioid receptor agonist, are known to vary drastically between males and females. Both male and female rats develop a CPP to morphine (e.g., Karami and Zarrindast 2008). However, female rats develop a CPP with lower doses of morphine and have a more pronounced CPP at higher doses compared to males. Typically, as the dose of morphine is increased, males show reduced CPP but females continued to demonstrate morphine CPP at high doses. E2 appears to play a role in this increased sensitivity to the rewarding effects of

morphine since ovariectomizing female rats attenuates morphine CPP and E2 injections reverse this effect (Mirbaha et al. 2009).

Naloxone, a mu-opioid receptor inverse agonist, has become a primary treatment for individuals suffering from an opioid-induced overdose. In rodents, the effect naloxone has on morphine CPP is related to the time at which naloxone is administered. When naloxone is administered during conditioning, it blocks the acquisition of a CPP, whereas when it is administered on test day, it appears to enhance the expression of morphine CPP (Neisewander et al. 1990). Additionally, although naloxone pretreatment during conditioning attenuates the rewarding effect of morphine in both males and females, at a high dose males demonstrate an aversion (Karami and Zarrindast 2008).

## Ethanol

It is commonly accepted that the effects of ethanol are dose dependent with higher doses resulting in less inhibition and more sedative-like effects. With regard to CPP, low doses typically fail to demonstrate CPP, moderate doses elicit a CPP, and higher doses typically elicit an aversion (e.g., Torres et al. 2014). While ethanol-induced preferences and aversions have been well established in rats, results have been inconsistent due to strain differences and route of administration (see Fidler et al. 2004 for review).

In general, rodent studies suggest that females may experience greater rewarding effects of ethanol compared to males. Torres et al. (2014) found that an intermediate dose of ethanol induced a CPP in female rats but not in males or ovariectomized females, the latter suggesting the role of ovarian hormones. Additionally, a high dose of ethanol resulted in a CPA similarly in male and female rats (Torres et al. 2014).

## Nicotine

Nicotine (NIC) CPP studies in rodents have yielded mixed results. Some studies have found

dose-dependent CPP, while others have found no effect or CPA. It is evident that NIC CPP studies are readily influenced by methodology, strain, route of administration, and other issues (see Tzschentke 1998 for review). For example, several studies that have compared biased and unbiased CPP procedures have found that NIC has to be paired with the animal's initially non-preferred chamber to produce significant CPP (see Le Foll and Goldberg 2005 for review). In addition, NIC administration can produce either anxiolytic or anxiogenic effects that might alter the expression and/or interpretation of CPP.

NIC is one of the few drugs studied that may be more rewarding in males compared to females. Both age and sex appear to play an important role in the induction of NIC CPP, such that adolescents are more sensitive than adults to the rewarding effect of NIC and males are more sensitive to the rewarding effects than females (e.g., Vastola et al. 2002).

## Cannabinoids

**THC**  $\Delta$  (delta) 9-Tetrahydrocannabinol (THC) is the psychoactive ingredient in smoked cannabis. Research regarding the rewarding effects of THC in animals has yielded inconsistent results, with some research indicating no rewarding or aversive effects, some indicating a CPP, and some a CPA. While these discrepancies may be due to a number of factors including dose and timing of administration, another factor may have to do with the aversive qualities of THC. However, Hempel et al. (2016) have shown that reduction of residual aversive effects of THC does not mask or attenuate its rewarding effects. Therefore, it is possible that THC may have weak rewarding effects that do not support CPP.

## MDMA

3,4-Methylenedioxymethamphetamine (MDMA), also known as ecstasy, has recently been under investigation for use in the treatment of post-

traumatic stress disorder and other anxiety disorders. It is also commonly abused alone or in combination with other drugs in “rave” settings. It is therefore important to understand its reward value and abuse potential. Male mice and rats demonstrate a CPP for an MDMA-paired chamber (e.g., Daza-Losada et al. 2007), and it can be reversed by naloxone, rimonabant, and tropisetron (Braida et al. 2005).

### **Application of CPP as a Drug Screening Tool**

A relatively recent consideration for the use of CPP has been with regard to evaluating medications (Napier et al. 2013). Many FDA-approved pharmacotherapies for drug dependence tend to target direct effects of drugs of abuse rather than learned associations that cause craving and relapse. Because CPP involves the formation of learned associations between a drug and contextual cues, it may serve as a promising tool to identify treatments for drug addiction that reduce the expression of CPP (Napier et al. 2013).

### **Neurobiological Mechanisms of CPP**

Although a comprehensive discussion and review of research on the underlying neurobiological mechanisms of CPP is beyond the scope of this entry, the literature collectively suggests that they are complex and varied. This is further complicated by the fact that the specific neural and molecular substrates involved in CPP are likely to be specific for that particular stimulus. One of the few relatively unifying themes that emerges from the CPP literature is that central dopamine systems are thought to play a critical role in the development and expression of CPP, especially in the case of drug-induced CPPs (see Tzschentke 1998 and Prus et al. 2009 for reviews). In many cases, natural stimuli and drugs that stimulate dopamine activity (e.g., sex and cocaine) in the mesocorticolimbic pathway also induce CPP. The mesocorticolimbic pathway is widely accepted as critical for reward and reinforcement learning and

is composed of neural projections from the ventral tegmental area into the prefrontal cortex and limbic structures like the nucleus accumbens, hippocampus, and amygdala. In many, but not all cases, the development and/or expression of CPP may be blocked by the administration of compounds that antagonize dopamine receptors (e.g., haloperidol) or can be attenuated or abolished by lesions of these neural structures. However, the view that dopamine in the mesocorticolimbic pathway is primarily responsible for CPP is drastically oversimplified. Previous research has also implicated other neural structures (e.g., the hypothalamus, ventral pallidum, and pedunculopontine tegmental nucleus) and a wide range of neurotransmitters including serotonin, norepinephrine, acetylcholine, glutamate, GABA, orexin, ghrelin, leptin, oxytocin, and steroid hormones in CPP for drugs and natural rewards (e.g., Tzschentke 1998). Therefore, one of the major challenges for understanding the neurobiology of reward is that more comprehensive frameworks are needed that better organize and integrate our current understanding of the factors and processes that mediate reward processing.

### **Conclusions**

In conclusion, the CPP procedure is a fairly ubiquitous procedure mainly used to investigate rewarding and aversive properties of naturally rewarding stimuli and drugs. It is primarily used in rodent studies but has been modified to use in a variety of species ranging from flatworms to humans. The procedure has many advantages including allowing for testing both rewarding and aversive stimuli, testing the preference when the animal is in a drug-free state, and modeling some aspects of human drug use. Unfortunately, the procedure is hindered by methodological challenges and can result in inaccurate data due to habituation/novelty effects and/or anxiolytic effects of drugs. Furthermore, it is difficult to generate dose-effect information. In spite of these challenges, CPP studies continue to be on the rise and the applications for CPP are increasing.

## Cross-References

- Acquisition
- Appetitive Response
- Approach/Withdrawal Theory
- Associative Learning
- Classical Conditioning
- Discrimination Learning
- Learning
- Nucleus Accumbens
- Play Behavior
- Unconditioned Response

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## Conditioned Responding

- [Sign Tracking](#)

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## Conditioning

- [Acclimatization](#)
- [Associative Learning](#)
- [Behavior Modification](#)

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## Configurational Processes

- [Gestalt](#)

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## Conflicts

- [Referential Communication](#)

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## Confusion Effect

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## Definition

The reduced attack-to-kill ratio of a predator resulting from its inability to single out and catch an individual surrounded by other individuals. In other words, it is more difficult for predators to capture prey that is surrounded by other conspecifics than to capture an isolated individual.

## What Is the “Confusion” in the Confusion Effect?

The term “confusion effect” implies that the predator experiences difficulties in concentrating on one out of several moving individuals because the predator is confused by the movements of many similar-looking individuals. This implies cognitive problems to attend to multiple targets. Neural network models give support for the confusion effect (Krakauer 1995). In psychology it has long been known that humans have problems in concentrating on two tasks at once. Attention is thought to be a function with limited capacity. The more similar two tasks are, the more difficult it is to concentrate on them simultaneously. Several prey individuals moving around present multiple tasks that a predator could concentrate on and may thus overtax the predator’s ability to divide its attention. On the other hand, dealing with this task might be costly, as then less attention is available for other tasks. For example, hungry sticklebacks that preyed on daphnia swarms of high density detected a predator dangerous to themselves less often than sticklebacks preying upon a swarm of low density (Milinski 1984). This was interpreted as an inability of the nervous



system to give attention to several tasks at once (prey and own predator) and thus a cost of overcoming the confusion effect by paying less attention toward the potential presence of a predator. Neural network models demonstrated that the decrease in attack success by sticklebacks corresponded to an increase in spatial targeting error with larger group size, which depended mainly on the number of individuals in the group, not density (Ioannou et al. 2008).

### The Confusion Effect Contributes to “Safety in Numbers”

Safety in numbers refers to the benefit of being part of a group in the case of a predation event. The confusion effect represents one benefit of group living, reducing the chance of successful predation. The confusion effect contributes to “safety in numbers” together with increased vigilance (a group will discover a predator sooner than a single animal), the dilution effect (when a predator kills only one group member, the probability for a specific individual to be the victim is the smaller the larger the group is), the encounter effect (decreased probability of predator encounter per individual as detection of larger groups does not increase proportionally with group size), and the group defense (a group can defend itself better against a predator than a single individual). All individuals of the group benefit simultaneously from the confusion effect, with minimal costs. Thus, grouping due to the confusion effect can be considered as a form of mutualism, i.e., a form of non-altruistic cooperation.

### Examples of the Confusion Effect

Because the confusion effect is one out of several advantages leading to safety in numbers, it is difficult to be studied separately. Even though in both aquatic and terrestrial group-living species, the confusion effect has often been claimed to be one important benefit of group living, this has been hard to demonstrate, as confounding effects of vigilance, encounter effect, and group defense

were seldom controlled (Krause and Ruxton 2002). Nevertheless, several studies found support for the confusion effect. These studies demonstrated either that the predator’s success decreased with increasing group size or that predators preferably attacked small over large groups. Three-spined sticklebacks (*Gasterosteus aculeatus*) preferably attacked a tube containing only 2 daphnia (*Daphnia magna*) compared to a tube containing 40 daphnia (Milinski 1977). Largemouth bass (*Micropterus salmoides*) rapidly captured single silvery minnows (*Hybognathus nuchalis*), but their success decreased as the school size of minnows increased (Landeau and Terborgh 1986). Similarly, jacks (*Caranx ignobilis*) easily captured single Hawaiian anchovy (*Stolephorus purpureus*) but were less successful in capturing individuals in schools (Major 1978). And finally, the attack success per encounter with a prey (different species of fish) decreased for squids (*Loligo vulgaris*), cuttlefish (*Sepia officinalis*), pike (*Esox lucius*), and perch (*Perca fluviatilis*) as the prey’s school size increased (Neill and Cullen 1974).

One experimental study performed in captivity with a reptilian and a primate predator was able to control possible confounding variables, finding clear support for the confusion effect (Schradin 2000). The prey (mealworms and black beetles, *Tenebrio molitor*) was harmless and had no chance of predator avoidance. Thus, confounding effects of group defense and enhanced vigilance were controlled. Both leopard geckos (*Eublepharis macularius*) and common marmosets (*Callithrix jacchus*) took longer to catch one out of several prey compared to one single prey. Leopard geckos also showed more fixations (changing of head position) when confronted with 20 mealworms than when confronted with only 1 mealworm, showing indications of being “confused.” This was not the case in common marmosets, which probably moved their eyes instead of their head, which was not measured. In sum both leopard geckos and common marmosets took longer to capture one prey out of a group of harmless prey that could not avoid predation and thus could not benefit from increased vigilance or the encounter effect (Schradin 2000).

## Dazzle Camouflage Enhancing the Confusion Effect

Dazzle camouflage refers to a form of camouflage where dazzles do not conceal the individual but make it more difficult to estimate the individuals speed and heading. This is thought to be the case in many animals having stripes, such as striped mice (*Rhabdomys pumilio*), chipmunks (*Tamias* spp.), and zebras (*Equus* spp.). While this hypothesis remains largely untested in wild living mammals, computer games where humans had to track striped targets moving in groups showed that dazzle camouflage enhances the confusion effect: it was harder for humans to track striped than non-striped targets (Hogan et al. 2016). Whether high-contrast patterns may benefit animals in groups by enhancing the confusion effect remains to be tested.

## Dissimilarity Is Weakening the Confusion Effect

The confusion effect describes that it is more difficult for a predator to capture prey that is surrounded by other conspecifics than to capture an isolated individual, because it cannot focus on a single individual as it is confused by the many individuals moving around. Thus, the confusion effect is expected to be especially strong when all individuals look the same. In contrast, if one individual sticks out because it looks different, the predator might be able to focus at this single individual and thus overcome the confusion effect. This has been called the oddity effect. It has often been assumed that odd individuals, for example, white (albinos) or oddly moving (old or injured) individuals, are especially targeted by predators, maybe because focusing on them overcomes the confusion effect (Krause and Ruxton 2002). Experimental studies coloring prey, such as daphnia or fish, found empirical evidence that the confusion effect is weaker when individuals are visually distinguishable from others (Krause and Ruxton 2002). Importantly, even odd individuals benefit from grouping, as their risk to be predated is still lower than that of a single individual (Landeau and Terborgh 1986).

## Conclusion

The confusion effect is one benefit of group living with respect to predator avoidance: it is more difficult for predators to capture prey that is surrounded by other conspecifics than to capture an isolated individual. Predators of different taxa suffer from the confusion effect: cephalopod, fish, reptilian, and mammalian predators all suffer from the difficulty of capturing a single prey out of a group simply because it is surrounded by other moving conspecifics. As the confusion effect is an ultimate cause in the evolution of group living, advantages for prey not yet living in groups and disadvantages for predators not used to group-living prey must exist as soon as the prey starts grouping (Schradin 2000). The confusion effect can thus yield immediate advantages when solitary-living prey starts to form groups, thus confronting the predator with a new problem.

## Cross-References

- ▶ [Group Living](#)
- ▶ [Predation Risk](#)
- ▶ [Predator Defense](#)
- ▶ [Predator Detection](#)
- ▶ [Prey](#)
- ▶ [Vigilance](#)

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## Congruence

### ► Concordance

## Conjugation

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## Synonyms

Bacteria; DNA transfer; Horizontal gene transfer; Mating; Ti plasmid; Transformation

## Definition

Bacterial conjugation is the transfer of genetic information between bacterial cells by a bridge-like connection between two cells.

## Introduction

Conjugation is a process that promotes DNA transfer from a donor to a recipient cell mediated by physical contact (Cavalli et al. 1953; Hayes 1953). Bacterial conjugation is the mechanisms of horizontal gene transfer between two bacterial cells. Conjugation represents a key constituent in the spreading of antibiotic and virulence genes to human pathogenic bacteria.

Usually, genes encoding a factor for conjugation are present in an extrachromosomal replicon termed a self-transmissible or conjugative plasmid. The conjugation is a phenomenon of fundamental evolutionary and ecological consequence. T-DNA of Ti plasmid-mediated transfer from *Agrobacterium* species to plants appears to represent a novel form of bacterial conjugation (Lessl and Lanka 1994). DNA transfer is conciliated by membrane-associated macromolecular machinery called Type IV secretion system (T4SS). T4SSs are also involved in the transport of virulence factors by pathogenic bacteria.

The mechanism of conjugation can be divided into three functional components: the coupling protein, relaxosome, and a type IV protein secretion system. Bacterial conjugation is a course of sexual reproduction but not identical to sexual reproduction because it does not involve the fusing of gametes and the creation of a zygote. At the wide and narrow range, some of the plasmids could be transferred (R751 and F, respectively) from *Escherichia coli* to *Saccharomyces cerevisiae* (Heinemann 1991; Dürrenberger et al. 1991).

## Evidence of Bacterial Conjugation

The evidence of bacterial conjugation was performed by a well-designed experiment of Joshua Lederberg and Edward Tatum in 1946. They used two mixed auxotrophic bacterial strains and incubated the culture for several hours in the nutrient medium and then plated it on minimal medium. They used double and triple auxotrophs. One strain needed biotin (Bio-), phenylalanine (Phe-), and cysteine (Cys-) for growth,

and another required leucine (Leu-), threonine (Thr-), and thiamine (Thi-). After incubation, prototrophic colonies appeared on the minimal medium. As an outcome, the chromosomes of the two auxotrophs were able to join and go through recombination.

Lederberg and Tatum did not directly confirm that contact between the cells was necessary for gene transfer. The evidence of physical contact between cells was proved by Bernard Davis (1950). In their testing, they constructed a U-tube consisting of two pieces of curved glass tube fused at the base to form a U-shape with a fixed glass filter between the halves. The filter permitted the passage of only media but not bacteria. The U-tube was filled with nutrient medium and each side inoculated with a different *E. coli* auxotrophic strain. Through incubation, the medium was pumped back and forth through the filter to ensure medium exchange between the halves. After 4 h incubation, the bacteria were placed on minimal medium. Davis revealed that when the two auxotrophic strains were divided from each other by the fine filter, gene transfer could not take place. Therefore, Lederberg and Tatum had observed that direct contact was required for the recombination.

F- recipient cells is believed to be investigated by an interaction between the tip of an F pilus and the recipient cell surface (Novotny et al. 1968; Ou and Anderson 1972). There is evidence for the occurrence of DNA transfer between cells that were not in surface contact, but there is also both indirect and direct confirmation that conjugating cells are typically aggregated in close wall-wall association (Ou and Anderson 1972; Harrington and Rogerson 1990). After DNA transfer is finished, mating cells actively disaggregate (Achtman et al. 1978) to produce two cells that capable of donor activity (Fig. 1).

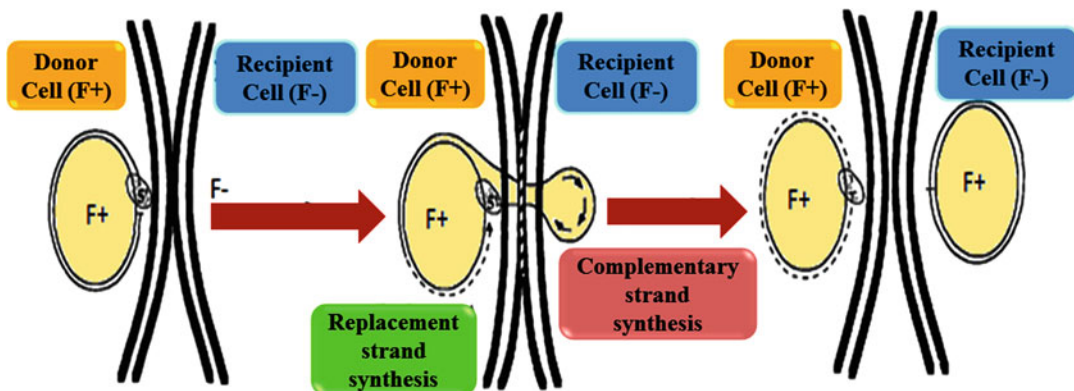
The first surface association of donors and recipients in aggregates is thought to reflect pilus retraction, mediated by depolymerization of the pilus subunit, into the donor and/or recipient cell envelope (Panicker and Minkley 1985). These donor and recipient contacts then become stabilized in a way to renders the aggregate more resistant to shear forces (Achtman et al. 1978). Recipient cells carrying mutations altering the structure of the lipopolysaccharide (Anthony et al. 1994) or the outer membrane protein OmpA (Skurray et al. 1974) also affect F- donor cell interactions, but it is unclear.

## F-Conjugation Process

The functioning of F factor mediated gene transfer was studied in liquid matings through the F- conjugation system. Contact between F<sup>+</sup> donor and

## Pull In and Push Out: Mechanisms of Horizontal Gene Transfer in Bacteria

In eukaryotes, transfer of genetic information from parent to their offspring via a core pathway



**Conjugation, Fig. 1** Showing the 5' nick is produced in plasmid DNA at oriT site which helps in transport from Donor cell F<sup>+</sup> to Recipient F<sup>-</sup> cell

of vertical gene transfer. In the case of bacteria and other prokaryotes, genetic information can also be transmitted between organisms via horizontal gene transfer and it is also known as lateral gene transfer (Keeling and Palmer 2008). Various genome-wide studies have shown that HGT occurs at a high frequency among prokaryotic species, mainly if they are closely related and present in the same environment or community (Beiko et al. 2005). HGT permits fast acquisition of a new function important for species adaptation and survival.

The advancement of the eukaryotic organism was marked by endosymbiotic events leading to permanent achievement of major cell organelles, e.g., mitochondria that originated from proteobacteria and plastids that originated from cyanobacteria, followed by organelle to nucleus gene transfer, generally referred to as endosymbiotic gene transfer (EGT) (Archibald 2015). Horizontal gene transfer (HGT) drives the transfer of antibiotic resistance genes (ARGs) serving an important role in the development of multidrug resistance (MDR) in bacteria (Forsberg et al. 2012). By means of HGT, the accumulation of genes involved in different resistance mechanisms from the exogenous DNA, bacteria are able to obtain MDR rapidly (Burton and Dubnau 2010; Syvanen 2012). For example, *Acinetobacter* and *Enterobacter* strains carrying the NDM-1 plasmid or *mcr-1* plasmid, which contain a group of resistance genes, can stand even last-resort antibiotics (Liu et al. 2016; Shen et al. 2016; Zheng et al. 2017).

There are three “traditional” methods of DNA transfer in natural history: bacterial conjugation, natural transformation, and transduction (von Wintersdorff et al. 2016).

### **Pull DNA in During Natural Transformation**

The first natural transformation was revealed in *Streptococcus pneumoniae* in 1928 (Griffith 1928). The DNA transfer during natural transformation is well conserved among Gram-positive bacteria, e.g., *Bacillus subtilis* and *S. pneumonia* (Berka et al. 2002) and Gram-negative bacteria

species (e.g., *Neisseria gonorrhoeae*, *Haemophilus influenzae*, and *Vibrio cholerae*), as well as archaea (Burton and Dubnau 2010; Johnston et al. 2014; Cabezón et al. 2015; Ilangovan et al. 2015, 2017; Veening and Blokesch 2017).

During natural transformation, Gram negative bacteria need to pull DNA across both the outer membrane (OM) and the inner membrane (IM), whereas Gram positive bacteria require overcoming the barrier of the peptidoglycan layer, which is much thicker and denser, and need to be weakened before translocation of DNA across the inner membrane (IM). In this process, dsDNA is pulled across the outer membrane (OM) in Gram negative bacteria and ssDNA is pulled across the IM in both Gram positive and Gram negative bacteria.

Exogenous DNA is pulled into the cytoplasm by the extension and pulling out of pseudopili, as a result of the assembly and disassembly of pseudopilin multimers (PilA). This is followed by the transfer of dsDNA transversely the OM protein PilQ/HofQ (for Gram negative bacteria only). The DNA receptor (ComEA) mediates the transfer of ssDNA across the inner membrane channel produced by ComEC with the help of the ATPase ComFA, accompanied by degradation of the other strand of DNA. The incoming ssDNA is protected by DprA which conveys it to RecA for homologous recombination in the cytoplasm (Fig. 2).

### **Push Out Mechanism for Transfer of DNA During Bacterial Conjugation**

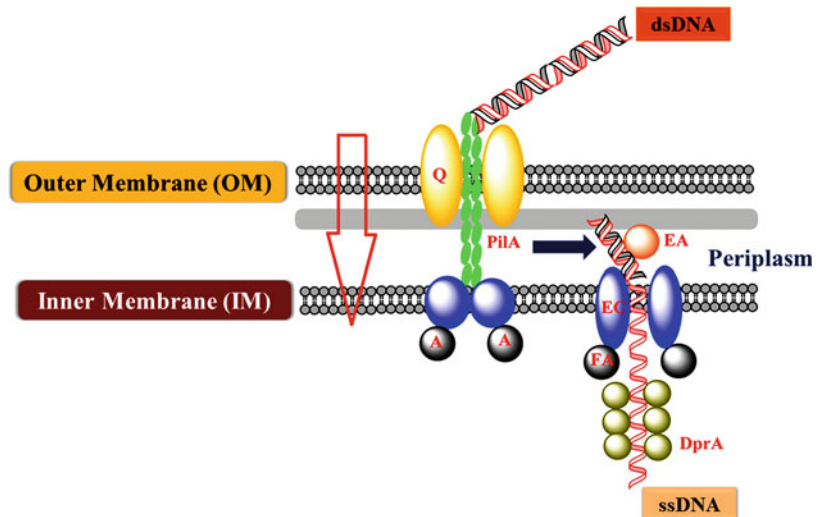
During bacterial conjugation, DNA can be pushed out from one donor cell and transported into a recipient cell. A group of mobile genetic elements, known as integrative and conjugative elements (ICEs) or conjugative transposons (Franke and Clewell 1981), has been found in many bacterial genomes (Cury et al. 2017). The transfer of conjugative DNA across the membrane of the donor bacterium depends on a large membrane-associated protein complex that belongs to the type IV secretion system (T4SS) (Cabezón et al. 2015; Ilangovan et al. 2015).

Protein-coated conjugative ssDNA is transported across the IM, periplasm, and OM through



### Conjugation,

**Fig. 2** Showing the general mechanism underlying DNA transfer during natural transformation



a membrane channel formed by a group of proteins encoded by the conjugative DNA molecule (Ilangovan et al. 2015). Inside the channel, the conjugative pilus (formed by pilins) is responsible for pushing ssDNA out of the membrane. The process of DNA transfer through conjugation has been best exemplified by the Vir system. To export DNA out of the donor cell, a complicated membrane protein complex encoded by the conjugative plasmid. During conjugation, a plasmid or ICE encoded relaxase creates a nick in one strand of the conjugative DNA at the *oriT* site, followed by ssDNA translocation across the channel formed by components of the T4SS and replication of the remaining strand, either independently from or in concert with conjugation (Ilangovan et al. 2017). During translocation across cell membranes, three ATPases (VirD4, VirB4, and VirB11) provide the energy for DNA transport (Cabezón et al. 2015; Ilangovan et al. 2015).

Further, the transport of ssDNA, a group of membrane, and periplasmic proteins are assembled simultaneously to form a large complex, which can be subdivided into four different ways: (1) the pilus is formed by the assembly of pilins (VirB2) with adhesins (VirB5) at the distal end; (2) the OM component, which consists of VirB7, VirB9, and the C-terminus of VirB10; (3) the periplasmic component which consists of VirB8, VirB10, and VirB6; and (4) the IM component, formed of VirB3, VirB6, VirB8, and VirB10. Additionally,

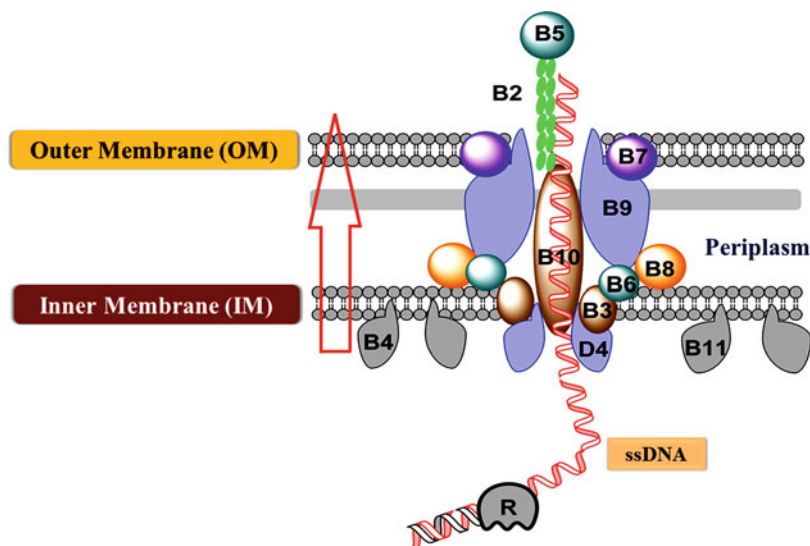
three hexameric ATPases (VirB4, VirB11, and VirD4) are attached to the IM to provide energy during DNA transfer (Fig. 3).

### Potential Applications

The gene transfer from bacterium to eukaryote has a unique and highly significant application and potential in the evolution of modern eukaryotes, which divide mainly in two main areas: research and biotechnology (Lim et al. 2008; Lacroix and Citovsky 2016). Research applications principally aim at inventing new protein properties and cellular pathways by expressing specific genes of interest which delivering gene-targeting systems, such as CRISPR/Cas9 (Nekrasov et al. 2013) and insertional mutagenesis. Genomes of interest insertional mutagenesis, for example, generating T-DNA insertion mutant libraries of the model plant *Arabidopsis thaliana* (Alonso et al. 2003; Llosa and de la Cruz 2005; Sun 2018).

Several biotechnological applications of conjugation aim at expressing the specific genes/traits of interest, such as pathogen and abiotic stress resistance genes, antibiotic resistance gene, biofuels and pharmaceuticals production through genetically engineered pathways, or expression of desired phenotypes, e.g., color and fragrance of flowers and fruits in agriculture or restoration of normal cellular functions in gene therapy. To



**Conjugation,****Fig. 3** DNA transfer during bacterial conjugation using T4SS

achieve these wide-ranging goals to adapt and optimize diverse bacterial DNA transfer systems or even discover new species of bacteria that are capable of DNA transfer to eukaryotes or use as a vector for genetic transformation of specific eukaryotic cells or microorganisms, thus allowing development of highly efficient “customtailored” DNA transport tools for each specific application.

## Conclusion

Studies of gene transfer systems are significant for their latent ecological and evolutionary importance as well as for their process for the development of novel biological tools for fundamental and practical purposes. Hence, at the global level horizontal gene transfer may have been more important for the evolution of eukaryotes.

## Cross-References

► [Bacteria](#)

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## Connectionist Network

### ► Neural Network

## Consciousness

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This chapter will address the extent to which nonhuman animals are conscious. Most important perhaps is what criteria should be used in making such a determination. We have certainly come a long way from the Cartesian view that animals are mere “automata” and do not even have conscious experience. In addition to the obvious and significant behavioral similarities between humans and many animals, much more is known today about our neurophysiological and genetic similarities. Still, there are some grey areas and genuine difficulties in interpreting some experimental results pertaining to animal cognition and in analyzing the comparative neuroanatomy.

The more general “problem of other minds,” including the so-called argument by analogy, is introduced in the section “[Animals and the Problem of Other Minds](#)”. In the section “[Lloyd Morgan’s Canon and Parsimony](#),” “Morgan’s Canon” and the related principle of simplicity is addressed especially as they pertain to attributions of animal consciousness. The section “[More on Some Hard Cases and Brain Structure](#)” focuses on some of the

harder cases, such as fish and insects, where it is necessary to delve more deeply into some comparative neurophysiology. Finally, in the section “[Animal Consciousness and Higher-Order Thought Theory](#),” the charge that one prominent philosophical theory of consciousness (the higher-order thought theory) is inconsistent with animal consciousness is explored. Here the focus is on the possibility of self-awareness and meta-cognition in animals.

Philosophical and scientific work on animal minds and consciousness has surged in recent years with the publication of several major studies and reviews, such as Tye (2016), Andrews and Beck (2018), Allen-Hermanson (2018), as well as the recently launched on-line journal *Animal Sentience* (see, e.g., Harnad 2016, Klein and Barron 2016; see also Allen and Trestman 2016, Andrews 2016). Much of this work takes on the challenge of the most difficult borderline cases, such as reptiles, crabs, insects, and fish, as well as further examination of the evolution of consciousness.

Perhaps the most commonly used notion of “conscious” is captured by Thomas Nagel’s “what it is like” sense (Nagel 1974). When I am in a conscious mental state, there is “something it is like” for me to be in *that state* from the first-person point of view. When I smell a rose or have a conscious visual experience, there is something it “seems like” from my perspective. This is primarily the sense of “conscious state” that I use throughout this chapter. Ideally, we would like to know which, and to what extent, animals are capable of having conscious subjective experiences such as pains, perceptions, and emotions. As Nagel famously asked, “What is it like to be a bat?”

## Animals and the Problem of Other Minds

It is clear that we have come a long way from the Cartesian view that animals are mere “automata” and that animals do not even have conscious experience. Other major figures in the early modern period, such as Leibniz, also struggled with the question of animal (or “brute” or “beast”) consciousness (Gennaro 1999). There has indeed

been a long history of philosophical opinion and argument about animal consciousness (see, e.g., Allen and Trestman 2016; Allen-Hermanson 2018). In addition to some clear behavioral similarities between humans and many animals, much more is known today about other physiological similarities such as brain and DNA structures. To be sure, there are also important differences and some genuinely difficult grey areas where one might have legitimate doubts about a given animal and consciousness. Nonetheless, it seems fair to say that most philosophers today agree that a significant portion of the animal kingdom is capable of having conscious mental states. Of course, this is not to say that animals can have *all* of the same kinds of sophisticated conscious states enjoyed by human beings, such as reflecting on philosophical and mathematical problems, enjoying artworks, or thinking about the vast universe or the distant past. However, it still seems reasonable to believe that animals can have at least some conscious states ranging from rudimentary pains and emotions to various perceptual states (visual, olfactory, tactile, etc.) and episodic memory.

One traditional way to approach this topic is via the “problem of other minds,” that is, how we can know that others have conscious mental states especially given the more indirect access we have to them as compared to our own minds. Although there is no generally accepted solution to this problem, most people in practice simply take it for granted that other *human beings* have mental states similar to theirs. However, knowledge of animal minds does present some particular difficulties. Nonhuman animals cannot describe their mental states using language even though they can most certainly communicate with each other (and even to us) in various other ways. Although there have been attempts to teach human-like languages to members of other species, none can do so in a way that would easily solve this problem. Instead, it would seem that despite the similarities between our behavior and those of other animals, any such knowledge of their minds would have to be less certain than what seems to be much more immediate knowledge of our own minds. Nonetheless, a strong inductive rationale for animal

consciousness seems sufficient to establish a reasonable belief that most animals have conscious mental states. Sometimes this takes the form of an “argument by analogy” such that, for example, we know how we feel when we exhibit the behavior of someone in fear or in pain and so it seems reasonable to think that the same conscious states are present when a dog or chicken displays the same behavior. This is presumably because we think of such behaviour as *caused by* the relevant conscious state. It is unlikely that we always make such conscious inferences when we observe animal behavior; rather, we probably often simply take it for granted. But this analogical strategy can be found in well-known philosophers throughout history (e.g., Locke, Hume, Mill, and Russell.) One worry about this type of argument is that it seems to generalize from my own single case, which would indeed be a rather weak instance of induction. However, we might instead suppose that it is an argument from *my species* to most individuals of another species (see Perrett 1997). Of course, the details can vary greatly from species to species.

A related line of argument is the so-called inference to the best explanation (IBE) which does not necessarily depend on self-observation. This is because it relies more on the fact that a successful empirical theory sometimes posits the existence of things that are not directly observed (such as electrons) but rather known indirectly by way of their observable effects. In a similar fashion, positing conscious states can be the best explanation of what causes an animal’s observable behavior (Pargetter 1984). IBE (sometimes called “abduction”) is a version of “hypothesis testing” which might be formulated via a “likelihood” principle according to which one hypothesis is favored over another if it alone predicts an observation that would otherwise be unexpected (Sober 2001; see also Allen-Hermanson 2018; Melnyk 1994.)

In any case, what evidence might be used to infer the presence of consciousness in animals? Although many different criteria have been proposed (e.g., Baars 2005; Seth et al. 2005; Edelman et al. 2005), most fall under one or more of the following general headings:

1. Nonverbal or non-vocal behavioral evidence.
2. Ability to use language and/or to communicate.
3. Ability to learn, solve problems, and be creative.
4. Similarity of brain structure to humans.

So, for example, rocks and tables display none of the above criteria and thus we do not think they are conscious. Trees and plants are alive but also do not meet any of the above criteria, for example, they do not jump away or scream when approached with a chainsaw or lawnmower. At the other extreme, humans normally seem to meet all four criteria. However, when we look at the animal kingdom we find that the evidence is often mixed, at least to some extent. Some animals may only meet two or three criteria whereas others might only meet one. What should we make of these cases? At the least, we might suppose that the more criteria met the more likely an animal is conscious even if none of the above criteria is conclusively necessary or sufficient for having conscious states. Of course, it may also depend upon the *degree* to which a given animal can meet a particular criterion.

Generally speaking, with regard to criterion (1), we can point to an animal's behavioral reaction to stimuli or a given bodily movement. If a dog moves in a way similar to me when someone steps on my leg, this seems to be some evidence that the dog is conscious. If mental states cause bodily movements, then it seems reasonable to infer that the mental state (pain, suffering) is present when the typical bodily effect is observed.

With regard to criterion (2), the ability to use language and/or to communicate, we obviously communicate with each other via a common language and thus we take for granted that there is conscious thought behind linguistic utterances. Unlike most philosophers, however, Dennett (1991, 1995) seems supportive of the idea that consciousness requires language in the sense of "story telling" and thus perhaps only humans are conscious. The conscious "self" is really only a kind of narrative that we tell ourselves. But even though many animals cannot linguistically communicate *with us*, it is clear that they communicate

*with each other*, such as in fairly sophisticated whale, chimp, and bird vocalizations. Treating the use of human-like language as a necessary condition for consciousness seems to be an unnecessarily high bar to clear.

With regard to criterion (3), the ability to learn, solve problems, and be creative, the fact that a human student or an animal can learn from a teacher or trainer provides some evidence that they have conscious minds. Conscious working memory and thought seem necessary for at least some kinds of learning. Further, if an animal is able to solve a somewhat novel practical problem, then it seems that at least some primitive conscious thinking is required. Many animals are able to "figure out" what to do when confronted with a challenging or unexpected situation, such as having to make a tool to acquire some food. In some cases, there can even be what appears to be a creative solution to a problem. Humans are clearly also able to be creative in a number of ways. Rocks and trees, on the other extreme, do not learn or solve problems.

Along the same lines, some use "behavioral versatility" or "stimulus independence" as good overall evidence in support of animal consciousness (Griffin and Speck 2004; Newen and Bartels 2007). If, for example, an animal adjusts its behavior appropriately in response to unpredictable challenges, it seems more likely that it is consciously thinking about its situation than when it responds uniformly. Fixed and rigid responses to stimuli seem to indicate a lack of conceptual representation whereas behavioral versatility indicates an ability to think about a given stimulus and act in a much more context-dependent fashion. This sort of capacity seems also to indicate an ability to *learn* from prior experience and to solve problems.

With regard to criterion (4), similarity of brain structure, we might use comparative neurophysiological evidence to help us to determine animal consciousness. A variety of theoretical and empirical arguments have been put forward for the conclusion that consciousness is shared across all mammals. For example, Seth et al. (2005) argue that widespread reentrant activity in the thalamo-cortical complex involve anatomical



systems that are at minimum shared among all mammals and some non-mammals. In addition, many animals share with us some rather primitive areas of the brain, such as the amygdala in the limbic system, responsible for emotions such as fear. This is how discovering specific neural correlates of consciousness in humans might in turn shed light on animal consciousness, especially given our common evolutionary history. To the extent that animals lack some of the brain structures responsible for more sophisticated mental capacities in us (such as the prefrontal cortex), it seems reasonable to suppose that they are not capable of having these kinds of mental states. However, it may also be that some mental capacities are realized in different brain areas in other species (I will return to this line of argument in the section “[More on Some Hard Cases and Brain Structure](#).”).

Of course, for *each* of our four criteria, there always appear to be counterexamples which suggest that the criterion is not *by itself sufficient* for consciousness. Present day robots and machines, just to make this point, are capable of some communication and language use (as well as some appropriate behavioral responses to stimuli). But it is unclear that either suffices for robot consciousness, perhaps partly because there is no common biological history or similarity. Bees, for example, are well-known to communicate to other bees about where honey can be found through a series of rather complicated “dances.” Perhaps bees are conscious but it is at least not as obvious as some other animals. The case is perhaps even weaker for various insects, such as ants, which nonetheless display “avoidance behavior” and some intra-species communication that allow them to survive. Weaker still would be the behavior of bacteria and single-celled organisms where the behavior in question tends to be rigidly fixed. There is also nothing remotely like a “brain” in bacteria and not much of one in some tiny insects. What about creativity? Defining creativity is difficult but someone might suppose that spiders creatively make their rather sophisticated webs even though spider consciousness is at least not that clear. Also, we can program computers to solve chess and mathematical problems but

again this hardly seems to be enough for consciousness.

It may also be that each of the four criteria is not *necessary* for consciousness, depending on unusual circumstances or one’s metaphysical views. For example, someone who is paralyzed and cannot behave or communicate may of course still be conscious. And perhaps some primitive organisms can be conscious without being able to solve problems or be creative at all.

Nonetheless, it seems that one can reach a reasonable inductive inference in favor of consciousness the more criteria that are met (e.g., in higher mammals) and a reasonable inductive inference against consciousness when, say, less than two criteria are met. It is also very important to emphasize that satisfying each criterion can come in very different degrees, for example, compare the behavior of an ape with the behavior of a lizard. Further, the matter can become very complex even within a single type of organism, such as fish (Allen 2013).

In some instances, of course, it may even be difficult to know whether *another human* is conscious, such as in coma cases and in persistent vegetative states (PVS), both of which also raise significant ethical questions (Farah 2008; Braddock 2017). However, the existence of some truly borderline cases does not rule out many other clearer cases of the presence or absence of consciousness.

## Lloyd Morgan’s Canon and Parsimony

Before delving further into some details and specific species, let us pause first to consider an important methodological issue. Much has been made recently over how considerations of “parsimony” or “simplicity” in mental state attributions to animals should be understood. We should of course be careful not to anthropomorphize, on the one hand, but also not to underestimate animal minds, on the other hand. The often quoted Morgan’s Canon says that “in no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands



lower in the psychological scale” (Morgan 1894, p. 53). On the surface, the canon seems to favor less-sophisticated mental state attributions or even explanations which only reference the body and behavior of animals under various conditions.

However, many authors have noted serious problems with this notion as well as significant ambiguity in the canon itself (Browne 2004; Allen-Hermanson 2005; Fitzpatrick 2008; Sober 2009, 2012). It is unclear how to interpret Morgan’s Canon and how it relates to the associated notions of “parsimony” or “simplicity.” For example, Browne (2004) explains that Morgan’s Canon is thus not quite the same as following a law of parsimony. He recognizes that “it is parsimonious to explain similar, complex, stimulus-response patterns by similar psychological mechanisms” (Browne 2004, p. 648). So when various animals perform in ways similar to humans on a given task, “it is unparsimonious to adopt one kind of lower-level explanation for the animal’s response on one task and a different kind of lower-level explanation for the animal’s response on [another] task” (Browne 2004, pp. 643–644). Browne thus also seems to have in mind what was discussed in the section “[Animals and the Problem of Other Minds](#),” that is, some kind of reasonable analogical or explanatory notion of simplicity. We ought to attribute mental states to animals (and thus explain their behavior) when they behave similarly to humans under similar conditions.

Michael Tye echoes much of the above sentiment and relies on a kind of argument by analogy as well as the principle of simplicity (Tye 2016, Chapter 5). Citing Newton and Reid, he approvingly borrows the slogan that “similar effects proceed from the same or similar causes.” Indeed, to assign other causes would be to introduce “superfluous causes” and run afoul of something like a principle of simplicity. With respect to animal pain, for example, Tye comments that he is “entitled to infer that the feeling of pain causes [a] behaviour in [animals] too unless I have a *defeater* to that inference, that is, a reason to believe that a causal story is operative in those animals that cannot be reconciled with the causal story that adverts to pain” (2016, p. 75). As we shall see, one potential defeater might be a difference in

neuroanatomy, but Tye ultimately rejects the notion that the lack of neocortex by itself defeats the inference to pain attribution to many animals.

## More on Some Hard Cases and Brain Structure

Aside from the obvious academic interest, there is also the very practical matter of the morality of animal experimentation and eating animals (Singer 1990; Jamieson 2018). At the very least, whether or not an animal can suffer and feel pain should be taken into account with regard to how they ought to be treated. Billions of animals are killed every year for food and used in research. Many of them are subjected to rather cruel conditions. Of course, some think that even if animals are conscious in some basic sense, they still do not deserve moral consideration especially as compared to humans. Few, if any, researchers and meat-eaters doubt that virtually all of these animals can experience pain. Pain, it would seem, is also a fairly primitive conscious state by comparison to most other kinds of mental states (Allen 2004; Shriver 2006, 2018). Still, the function of pain is not merely to avoid bodily damage; it can also have an emotional or motivational element. Thus, there has been significant focus on basic animal sentience in recent years, especially with respect to some of the harder cases, such as fish, crabs, birds, reptiles, cephalopods, and various insects (Tye 2016). Significant discussion of animal neuroanatomy seems particularly relevant to some of the literature, although behavioral responses to stimuli are inevitably also relied upon.

Neurological studies of animal pain often start with the distinction between “nociception” and pain. Nociception is the capacity to sense potentially damaging noxious stimuli and is one of the most primitive sensory capacities. Nocioceptors are linked to nerve endings in the skin, some of which are associated with initially brief and localized sharp pain and others of which result in longer-lasting pain. Neurons functionally specialized for nociception can even be found in invertebrates such as the medical leech and snails.

Since nociceptors are found in such a wide range of species and are even functionally effective in spinally transected animals, their presence in a species provides little justification in inferring conscious pain experiences. Tye explains that in humans “the painfulness of pain in humans is based on activity in two different neural regions: the somatosensory cortex and the ACC [anterior cingulate cortex]” (Tye 2016, p. 79). The ACC is more closely related to the “felt badness” or “unpleasantness” of pain. It seems that when the somatosensory cortex is damaged, what results is still an unpleasant sensation but it is not really described as “pain” as such. We should keep in mind, however, there are abnormal human cases of developmental neuroplasticity (e.g., in hydrocephaly where there is no neocortex) such that conscious states seem to be realized in different than normal neural structures from a very young age. These are indeed abnormal cases of neural plasticity in humans, but they do show that there may be reasons to think that in some animals “the absence of a neocortex does not in and of itself entail that cells homologous to those found in the neocortex are missing too” (Tye 2016, p. 84). Although a lack of neocortex must be taken into account when examining a given creature’s ability to have pains and other conscious states, Tye does not think that it defeats the inference to the presence of felt pain depending upon the extent of behavioral similarity. Interpretation of various experimental results is a matter of ongoing debate with part of the problem having to do with knowing the extent of “neural plasticity” or “multiple realizability” of a given cortical function.

Let us look more closely at some of the harder cases:

Evidence from lesions and brain imaging seems to indicate a key role in human pain for certain cortical structures, especially the anterior cingulate, somatosensory, and insular cortices (Craig 2009). Neuroanatomical factors as well as physiological changes strongly indicate conscious pain in mammals (Shriver 2006) and birds (Calabrese and Woolley 2015). Lesion studies of mammals and birds strongly suggest serious deficits in pain experience (Allen et al. 2005). Even

though there is no neocortex in birds, there are still certain sorts of constituent and ancient neuron cell types found in birds that are found in our neocortex (Tye 2016, pp. 122–125). In addition, behavioral indicators of pain as seen, for example, in farm animals include vocalizations, abnormal postures and limping, and reductions in activity (Prunier et al. 2013). Chicken most certainly actively seek pain relief when forced to live in overcrowded pens and cages. For example, under certain crippling conditions, they choose feed laced with a pain reliever far more often than a feed without it. Under these circumstances, it would seem that avoiding pain suggests that a creature can *feel* pain and thus is capable of at least some conscious states.

There is a very lively debate over fish consciousness and especially about whether fish can experience pain, stress, and suffering (see Rose 2002 and Sneddon et al. 2003 for opposing views). This is particularly relevant in the very practical context of welfare regulation in commercial and sport-fishing. The term “fish” is itself rather ambiguous and does not really correspond to any clear taxonomic group of creatures. There is an incredible diversity and number of fish groups or species, and so it is particularly difficult to make generalizations about fish consciousness (see Braithwaite 2010; Allen 2013; Brown 2015; Tye 2016, Chapter 6, for reviews and extensive treatment). Tuna fish are, for example, closer to us in many ways than they are to sharks, and not all fish are “cold-blooded.”

Nonetheless, a key issue for fish (and reptiles and other animals, for that matter) is the absence of a neocortex (Rose 2002; cf. Rose et al. 2014). Rose (2002) argues that because fish lack the anterior cingulate cortex (ACC), they may not be bothered by pain or merely have (unconscious) nociception. Sneddon et al. (2003) disagree and argue that there is adequate behavioral and physiological evidence for pain in fish (see also Chandroo et al. 2004; Sneddon 2011; Balcombe 2016). Trout, for example, have nociceptors but also respond favorably to painkillers when treated with noxious stimuli and fish react to morphine much as we do. There are numerous articles on fish consciousness in the on-line journal *Animal*

*Sentience*, including Key (2015, 2016) who argues that fish lack the necessary neurocytoarchitecture, microcircuitry, and structural connectivity for the neural processing required for feeling pain. Numerous commentators, such as Broom (2016), Seth (2016), Shriver (2016), and Striedter (2016), reply to Key. Woodruff (2017) reviews neuroanatomical, neurophysiological, and behavioral studies which leads him to the conclusion that fish do have neurobiological correlates and behavioral flexibility of sufficient complexity to support the hypothesis that they are capable of phenomenal consciousness.

Tye (2016, Chapter 6) also argues that fish can feel pain and have other conscious states. He argues at great length that a lack of neocortex is not by itself a defeater for consciousness in various animals. The overall behavior of fish, such as struggling to get away when caught on a hook, is very similar to the way we would behave in such circumstances. And since nociceptors transmit signals that generate pain in humans and other mammals, it seems plausible to suppose that fish feel pain too. Behavioral indications of fear and anxiety in many fish also seem to abound and much the same seems true of basic perceptual consciousness including smell, vision, hearing, and visual discrimination (Tye 2016, pp. 107–113). Once again, the best and simplest explanation of the extensive behavioral similarities between humans and fish, according to Tye, is that fish undergo the same experiences that we do.

A neocortex is also not present in lizards and reptiles, but Cabanac et al. (2009) present some evidence that there is felt pleasure and pain in iguanas. They argue that consciousness is shared by all *amniotes* which include all descendants of the common ancestor of living birds and mammals, such as lizards, snakes, and turtles. Some interesting behavioral indicators of consciousness are also discussed, such as “trade-off” behavior (where, e.g., fish decrease feeding attempts as electric shocks are increased until food deprivation increases), navigational detouring (which requires an animal to pursue a series of non-rewarding intermediate goals in order to obtain an ultimate reward), expression of emotion, expression of sensory pleasure, and emotional

fever (an increase in body temperature in response to a stressful situation). It does indeed often seem rather difficult to explain these behaviors entirely without also attributing consciousness. Reptiles also show spatial cognitive abilities similar to those of rats and exhibit learning or behavioral flexibility in their pursuit of food. Even though reptiles lack a hippocampus as well as a neocortex, there is some reason to suppose that the medial cortex in reptiles operates in a similar way to the hippocampus in mammals (Tye 2016, pp. 131–133).

One intriguing group of invertebrate animals that has received significant attention with respect to consciousness is cephalopods, e.g., octopuses, squids, and cuttlefish. These are clever and large-brained animals who are well-known for incredible abilities to camouflage themselves and for flexible hunting strategies. Mather (2008) argues that cephalopods exhibit many behavioral indicators of consciousness, including complex learning and spatial memory. The octopus is especially interesting. They are highly intelligent, very adept at learning, and display a variety of complex cognitive abilities (Godfrey-Smith 2013). The octopus can even escape from a jar by unscrewing it from the inside. Once again, we must be careful however. Cephalopod neuroanatomy is so very different from mammalian architecture that it may be difficult to be entirely confident in attributions of consciousness. For one thing, over two-thirds of their neurons are located in their tentacles.

Another group of animals garnering significant attention is arthropods, which includes insects, crustaceans, spiders, and many other less familiar animals (Tye 2016, Chapter 8). This is an ancient and diverse group of creatures and so, again, any generalizations should be made with caution. It is interesting, however, to note that arthropods were among the earliest animals to evolve complex active bodies and brains capable of controlling them (Trestman 2013). So, if one function of consciousness is to solve problems which arise due to controlling complex bodies (Merker 2005), consciousness may have evolved very early on among arthropods. The case for insect sentience is sometimes also made on the basis of

neuroanatomical similarity to the mammalian midbrain (Klein and Barron 2016). Klein and Barron argue that basic subjective experience is supported by the integrated midbrain and basal ganglia structures which are among the oldest and most highly conserved brain systems in vertebrates. They argue that the insect brain supports functions analogous to those of the vertebrate midbrain and hence that insects may also have a capacity for subjective experience. (Replies to Klein and Barron can be found in the same 2016 issue of *Animal Sentience*.)

The fact that honeybees recognize faces even from unfamiliar perspectives might be suggestive of mental rotation and visual imagery (Dyer et al. 2005). Jackson and Wilcox (1993) document a variety of impressive behaviors in jumping spiders, including detouring and other forms of apparent planning, as well as flexible, context-sensitive adjustment of predatory behavior to prey behavior. There are numerous studies on bees and, for example, pattern recognition, navigation, communication, visual working memory (Srinivasan 2010), and mood and emotions (Mendl et al. 2011).

Nocioceptors are missing in virtually all insects, but they still do respond to and learn to avoid a range of noxious stimuli, including honeybees. Still, it does seem that a stronger behavioral case can be made against insect consciousness since, for example, they do not move to protect injured body parts in the way that mammals do. Perhaps, however, some of these behaviors can be explained away as attempts to survive in spite of the pain. In the case of bees, there are at least some important physiological similarities and further evidence of intelligence and working memory (Tye 2016, pp. 148–156). As was briefly mentioned in the section “[Animals and the Problem of Other Minds](#),” bees are also well-known for their very sophisticated navigational abilities and intra-species communication via “waggle dances” with respect to the location of food.

Crabs are crustaceans with a highly developed sense of smell but poor vision. Elwood and Appel (2009) seem to show that hermit crabs can remember an aversive event (an electric shock) and can use that memory in later context-sensitive

decision-making (see also Elwood et al. 2009). This seems to be evidence of remembering a painful experience. Crabs also react to analgesics in the same way that honeybees do. If crabs feel pain, then surely bees also do since bees have ten times more neurons than crabs have. Indeed, bee brain *density* is ten times greater than a mammalian cerebral cortex (Tye 2016, pp. 156–158).

In some of the above cases, there are clearly some potential “defeaters” (as Tye calls them) to the conclusion that there really are conscious states in some species. It may indeed even be impossible to infer with any sense of confidence, especially with respect to some insects and crustaceans. Still, as we have seen, there may also be cases where a potential defeater might itself be defeated, such as in some instances where a creature lacks a neocortex. In addition, many kinds of creatures, such as fish and insects, come with an incredible variety of species and so there may be some exceptions which make generalizations difficult to justify.

Feinberg and Mallatt (2016) take a more explicitly evolutionary approach to animal consciousness although some of the same issues raised above are front and center (see also Godfrey-Smith 2018). When did consciousness first appear on Earth and how did it evolve? What constitutes consciousness and which animals are sentient? Using their own list of the neurobiological features that seem responsible for consciousness, Feinberg and Mallatt argue that consciousness appeared much earlier in evolutionary history than is commonly assumed. About 520–560 million years ago, they explain, the great “Cambrian explosion” of animal diversity produced the first complex brains, which were accompanied by the first appearance of consciousness. Simple reflexive behaviors evolved into a unified inner world of subjective experiences. From this they deduce that all vertebrates are and have always been conscious, including fish, reptiles, amphibians, and birds. Considering invertebrates, they find that arthropods (including insects and probably crustaceans) and cephalopods (including the octopus) also meet many of the criteria for consciousness. Part of this still controversial issue is whether or not consciousness

evolved as an adaptive function and then remained as a benefit for organisms (Maley and Piccinini 2018). For example, consciousness may allow organisms to construct an internal model of the world, learn in certain ways, or perform voluntary actions. If this is so, then consciousness confers an adaptive advantage to organisms that have it.

## Animal Consciousness and Higher-Order Thought Theory

It is sometimes alleged that one prominent philosophical theory of consciousness, the higher-order thought (HOT) theory, is inconsistent with animal consciousness (Seager 2004). Indeed, one higher-order theorist has even embraced the normally unwelcome conclusion that most animals do not have conscious states (Carruthers 2000, 2005). Others have responded by defending HOT theory as consistent with most animal consciousness (Gennaro 2009, 2012, Chapter 8).

Let us back up: HOT theory is an example of a so-called representational theory of consciousness which attempt to reduce consciousness to “mental representations” rather than directly to neural states. The notion of “reduction” at work is to explain conscious states by means of non-conscious mental states and thus without reference to consciousness (thereby also avoiding the charge of circularity). Other representational theories include first-order representationalism (FOR) which aim to explain conscious experience primarily in terms of world-directed (or first-order) intentional states (Tye 2000). Higher-order representationalism (HOR) holds that what makes a mental state *M* conscious is that it is the object of some kind of higher-order mental state directed at *M* (Lycan 2001; Rosenthal 2005; Gennaro 2012). There are various kinds of HOR theory with the most common division between higher-order thought (HOT) theories and higher-order perception (HOP) theories. HOT theorists, such as Rosenthal (1997, 2004, 2005) and Gennaro (1996, 2012), think it is better to understand the HOR as a thought containing concepts. HOTs are treated as cognitive states involving

some kind of conceptual component. A HOT is a “meta-psychological” or “metacognitive” state, that is, a mental state directed at another mental state (“I am in mental state *M*”). HOP theorists urge that the HOR is a perceptual state which does not require the conceptual content invoked by HOT theorists (Lycan 1996, 2004).

So HOR theories attempt to reduce consciousness in *mentalistic* terms, such as “thoughts” and “awareness,” rather than directly in neurophysiological terms. Thus, the idea is to reduce consciousness to mental representations. The notion of a “representation” is of course very general and can be applied to pictures and various natural objects, such as the rings inside a tree. Much of what goes on in the brain might also be understood in a representational way. For example, mental events represent outer objects partly because they are caused by such objects in cases of veridical visual perception. Philosophers often call such mental states “intentional states” which have representational content, that is, mental states are “directed at” something such as a thought about a horse or a perception of a tree.

Any theory of consciousness should seek to answer the question: What makes a mental state a *conscious* mental state? The HOT theorist will point out that conscious states, as opposed to unconscious ones, are intuitively mental states that I am “aware of” being in. This overall idea is sometimes referred to as the Transitivity Principle (TP): A conscious state is a state whose subject is, in some way, aware of being in it.

Conversely, the idea that I could be having a conscious state while totally *unaware* of being in that state seems like a contradiction. A mental state of which the subject is completely unaware is clearly an *unconscious* state. For example, I would not be aware of having a subliminal perception and so it is unconscious.

It might seem that HOT theory results in circularity by defining consciousness in terms of HOTs (since HOTs can be thought of as a kind of higher-order “awareness” of mental states, as in TP). It also might seem that an infinite regress results because a conscious mental state must be accompanied by a HOT, which, in turn, must be



accompanied by another HOT *ad infinitum*. However, the widely accepted reply is that when a conscious mental state is a first-order world-directed conscious state, the higher-order thought (HOT) is *not* itself conscious. But when the HOT is itself conscious, there is a yet higher-order (or third-order) thought directed at the second-order state. In this case, we have *introspection* which involves a conscious HOT directed at an inner mental state. When one introspects, one's attention is directed back into one's mind. For example, what makes my desire to write a good chapter a conscious first-order desire is that there is an *unconscious* HOT directed at the desire. In this case, my conscious focus is directed outward at my chapter or computer screen and so I am not consciously aware of having the HOT from the first-person point of view. When I *introspect* that desire, however, I then have a *conscious* HOT (accompanied by a yet higher, third-order, HOT) directed at the desire itself. It is thus crucial to distinguish first-order conscious states (with unconscious HOTs) from introspective states (with conscious HOTs).

In any case, it may seem unlikely that animals (and even infants) have the conceptual sophistication required for HOTs, which would then render animal (and infant) consciousness very unlikely (Seager 2004). Are cats and pigs capable of having complex higher-order thoughts such as "I am in mental state M"?

In reply, however, it may be that HOTs need not be as sophisticated as it might initially appear and, in recent years, some experiments have also strongly suggested that many animals can have metacognitive states. A number of key areas are under continuing investigation including animal memory and uncertainty monitoring. The term "I-thoughts" is also often used in the literature to mean "thoughts about one's own mental states or oneself." Thus, they are very similar to HOTs and closely linked to what psychologists call "metacognition," that is, mental states about mental states, or "cognitions" about other mental representations (Koriat 2007; Beran et al. 2012). Although some still reject the notion that most nonhuman animals have I-thoughts, the evidence seems to be growing that many animals do in fact

have them and may even be able to understand the mental states of others (Terrace and Metcalfe 2005; Hurley and Nudds 2006; DeGrazia 2009).

One area of inquiry has to do with episodic memory (EM) which is an explicitly conscious kind of remembering involving "mental time travel" (Tulving 1983, 2005). It is often contrasted with *semantic* memory, which need only involve knowing that a given fact is true or what a particular object is, and *procedural* memory, whereby memory of various learned skills is retained. Some notion of "I" or self-concept seems necessary to have a genuine EM. I recognize an EM *as mine* and as representing an event in *my* past. To give an example from animal cognition research, Clayton and Dickinson and their colleagues report convincing demonstrations of memory for time in scrub jays (Clayton et al. 2003). Scrub jays are food-caching birds, and when they have food they cannot eat, they hide it and recover it later. Because some of the food is preferred but perishable (such as crickets), it must be eaten within a few days, while other food (such as nuts) is less preferred but does not perish as quickly. In cleverly designed experiments using these facts, scrub jays are shown, even days after caching, to know not only *what* kind of food was *where* but also *when* they had cached it (see also Clayton et al. 2006). Although still somewhat controversial, these experimental results at least seem to show that scrub jays have some episodic memory which involves a sense of self over time. This strongly suggests that the birds have some degree of metacognition with a self-concept (or "I-concept") which can figure into HOTs. Further, many crows and scrub jays return alone to caches they had hidden in the presence of others and recache them in new places (Emery and Clayton 2001). This suggests that they know that *others* know (or at least "see") where the food is cached, and thus, to avoid having their food stolen, they recache the food. This strongly suggests that these birds can even have some mental concepts directed at other minds, which is sometimes called "mindreading." Of course, there are many different experiments aimed at determining the metacognitive abilities of various animals so it can sometimes be difficult to generalize across species.



There is also the much-discussed work on uncertainty monitoring with animals such as monkeys and dolphins (Smith et al. 2003; Smith 2005). For example, a dolphin is trained in a perceptual discrimination task, first learning to identify a particular sound at a fixed frequency (the “sample” sound). The dolphin later learns to match other sounds to the sample sound. When presented with a sound that is either the same or different in pitch as the sample sound, the dolphin has to respond in one way if it is the same pitch (such as by pressing one paddle) and another way if it is a different pitch (pressing another paddle). Eventually the dolphin is introduced into a test environment and forced to make extremely difficult discriminations. To test for the capacity to take advantage of his own uncertainty, the dolphin is presented with a third “uncertain” response, the Escape paddle, which yields a greater reward than an incorrect response but a lesser reward than a correct response. The dolphin chooses the Escape paddle with a similar response pattern to humans and rhesus monkeys which suggest that the dolphin is aware of his state of uncertainty, that is, he has some knowledge of his own mental state. This is clearly a metacognitive state: the dolphin is aware that he does not know something, namely, whether or not a sound matches (or is very close to) the sample sound. Nonetheless, some authors (Carruthers 2008, 2009) argue that these and other experiments do not *force us* to infer the presence of metacognition, but one might respond in a manner similar to the section “Lloyd Morgan’s Canon and Parsimony” above. That is, it is arguably more parsimonious in some circumstances to attribute metacognitive states to animals rather than mere first-order states or no conscious mental states at all accompanied by a far more elaborate explanation of the animal’s behavior (see also Gennaro 2012, Chapter 8, for some discussion).

Some authors (e.g., Carruthers 2000, 2005, 2009) cite experimental work suggesting that, say, even chimps lack the ability to attribute mental states to others (Povinelli 2000). These experiments are designed to determine if chimps take notice of when an experimenter is looking at something (say, food) or is unable to see something (for example, due to blindfolding). Chimps

were just as likely to ask for food from an experimenter with a bucket over her head as from one who could see which seems to indicate a lack of the mental concept “seeing” or “visual perception.” Carruthers further argues that animals with HOTs should also be able to have thoughts about the mental states of *other creatures*. However, it is not at all clear that having I-thoughts *requires* being able to read *other* minds and, in any case, the evidence seems to be growing that many animals can mindread. For example, Laurie Santos and colleagues show that rhesus monkeys attribute visual and auditory perceptions to others in competitive paradigms (Flombaum and Santos 2005; Santos et al. 2006). Rhesus monkeys preferentially attempt to obtain food silently only in those conditions where silence was relevant to obtaining the food undetected. While a human competitor was looking away, monkeys would take grapes from a silent container, thus apparently understanding that their human competitors would hear the noise otherwise. Subjects reliably picked the container that did not alert the experimenter that a grape was being removed. This suggests that monkeys take into account how auditory information can change the cognitive state of the experimenter. As we saw in the section “Lloyd Morgan’s Canon and Parsimony,” parsimony would seem, at least at times, to be on the side of such mental state attributions.

I lack the space here to delve further into this massive literature but for much more on the issue of mindreading and metacognition in animals and infants, see Carruthers (2009), Nichols and Stich (2003), Goldman (2006), Lurz (2011), and Gennaro (2012, Chapters 7 and 8). Goldman (2006) defends the view that self-attribution of mental states (metacognition) is prior to our capacity to attribute mental states to others (mindreading). A more modest view, offered by Nichols and Stich (2003), is that the two capacities are independent and dissociable. Carruthers (2009) argues that mindreading is actually *prior* to metacognition. The two main much discussed views are simulation theory (ST) and theory-theory (TT). ST holds that mindreading involves the ability to imaginatively take the perspective of another. TT holds that metacognition results from

one's "theory of mind" being directed at oneself. Still, many existing theories are in fact hybrids of ST and TT.

Of course, it may be that HOT theory rules out *more* animal consciousness than some other theories, but it arguably does not rule out most animal consciousness. Perhaps insects and crustaceans are *less likely* to be conscious according to HOT theory, but it may depend on some specifics. Not all birds behave in the same sophisticated way that scrub jays do but it seems reasonable to suppose that many other birds are also capable of having at least some HOTs. Other animals mentioned above, such as monkeys and dolphins, are no doubt far more sophisticated than insects. Much the same holds for dogs, lions, pigs, and other mammals. Some of the behavior of, say, bees and fish might arguably even justify the attribution of self-awareness in addition to basic conscious states.

## Cross-References

- [Analogical Reasoning](#)
- [Cognition](#)
- [Communication](#)
- [Corvids](#)
- [Episodic Memory](#)
- [Ethics](#)
- [Inductive Reasoning](#)
- [Intelligence](#)
- [Learning](#)
- [Meta-cognition](#)
- [Metamemory](#)
- [Neocortex](#)
- [Problem-Solving](#)
- [Self-Awareness](#)
- [Theory of Mind](#)

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## Conservation

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## Synonyms

Constancy; Piagetian conservation; Quantity judgments

## Definition

Conservation, first defined and assessed by Piaget as a critical developmental stage, is the

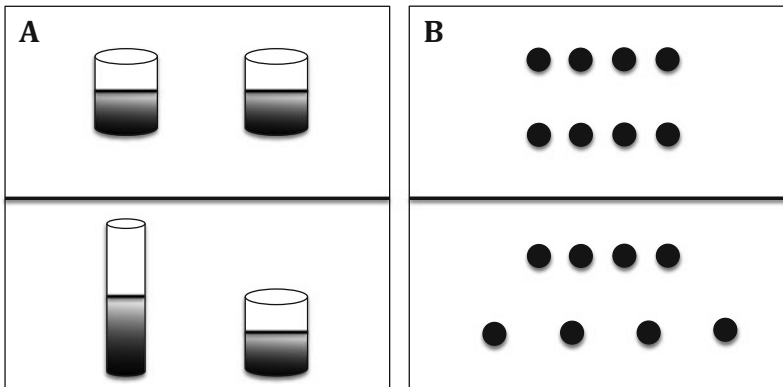
understanding that the physical qualities of a substance or object (e.g., volume, size, weight, number, quantity) do not change despite a transformation of their physical appearance. Conservation tasks are used to assess logical thinking and inferential abilities in children and nonhuman animals as a contrast to problem solving based on cognitively simpler perceptual strategies.

## Introduction

A hallmark event in cognitive development is the emerging ability to perceive, discriminate, and track quantitative information during childhood, and this capacity has been demonstrated in non-human animals. Conservation tests, first devised by Piaget (Piaget 1941/1997; Piaget and Inhelder 1966/1969), assess a subject's understanding of the constant nature of a substance's quantitative features following a transformation of its physical appearance. This ability requires representation of quantities, such that an individual is able to compare, track, and manipulate stimuli even when those stimuli are visually absent or perceptually transformed. Specifically, a substance's (e.g., liquid or solid) or object set's (e.g., a row of coins) weight, volume, number, size, or quantity is

manipulated in such a way that the transformed stimulus appears to be larger/greater than or smaller/less than it did originally. The objective is for the participant to identify whether the manipulated quantity has remained the same or has changed. In Fig. 1, a liquid (Panel A) and a number (Panel B) conservation task is illustrated. In the top portion of each panel, the quantities are depicted pre-transformation in which participants first identify the quantities as the same or equal. In the bottom portion of each panel, the quantities are depicted post-transformation in which the equal quantities now appear to be different due to the physical transformation (pouring of the first liquid into a new container or separating the bottom row of circles). Successful performance on this task is reflected in the ability to "conserve" a set's true quantity, identifying the quantities as equal despite these misleading physical transformations. Conservation is considered a test of logical or inferential reasoning emerging in the concrete operational stage of development, and children in this stage would understand the constancy of a stimulus despite its physical change in appearance (Piaget 1955).

In the classic liquid conservation paradigm, children are presented with two containers of liquid equal in volume. Once a child acknowledges



**Conservation, Fig. 1** A liquid (Panel A) and a number (Panel B) conservation task is illustrated. In the top portion of each panel, the quantities are depicted pre-transformation in which participants first identify the quantities as being equal. In the bottom portion of each panel, the quantities are depicted post-transformation in which

the quantities now appear to be unequal due to the physical transformation (Panel A - pouring of the first liquid into a thinner, taller container leads this quantity to appear greater in volume or Panel B - separation of the circles in the bottom row leads this quantity to appear greater in number or quantity)



that the liquids are the same or equal, one or both containers are poured into differently-shaped containers (continuous transformation), which cause the liquid(s) to appear greater in volume (if transferred to a thinner, taller container, effectively raising the height of the liquid) or lesser in volume (if transferred to a wider, shorter container, effectively reducing the height of the liquid). Alternatively, one container may be poured into several different containers (discontinuous transformation), which subdivides the liquid into multiple smaller vessels. Children between the ages of 7–8 years old typically understand the constancy of quantities (despite the change in perceptual cues such as liquid volume height), which is indicative of necessary or “true” conservation in line with logical reasoning (Piaget and Inhelder 1941). Younger children demonstrate varying degrees of success in tests of conservation, including a complete absence of conservation (i.e., the belief that the original quantity has changed post-transformation) or intermediary reactions (i.e., conserve following the first transformation, yet reverse choices following subsequent transformations; Piaget and Inhelder 1941).

A growing number of animal species have shown varying degrees of success in tests of conservation using both logical reasoning (indicative of a higher-order cognitive strategy) and perceptual-based strategies (e.g., using the height of liquid volume or pouring rate), which are considered cognitively simpler. In some cases, species’ performances, including those of children, are directly compared using identical stimuli and methodologies for a true comparison of ability. In this chapter, I review the comparative data on conservation and outline how the data fit in line with the original Piagetian framework in developmental psychology.

## Comparative Data

In one of the most widely cited comparative investigations of conservation in an animal species, Woodruff et al. (1978) assessed a female chimpanzee’s (*Pan troglodytes*) understanding of conservation using a same/different paradigm. Previously, the chimpanzee, Sarah, had been

trained to associate two different tokens with the concepts of same and different. For the conservation test, she was presented with two quantities of liquid (water), matter (clay), and discrete items (buttons). At the beginning of a trial, Sarah first attended to two quantities presented on a tray, after which the experimenter manually transformed one of the two substances as she watched. Sarah then responded to the stimuli using the “same” or “different” token. She demonstrated successful conservation of the liquid and matter substances following physical transformations of their quantities. For example, Sarah successfully designated whether the transformed water containers contained a same or different amount of liquid despite the alteration of water height. The matter condition included a change in the shape of the clay so it appeared larger or smaller than the alternative clay, but Sarah successfully designated equal quantities as “same” despite the change in the clay’s appearance. Importantly, Sarah was unsuccessful (i.e., designated the equal quantities as “different”) when she was not shown the quantities before or during the transformation process. This condition was crucial in that Sarah could not have relied upon perceptual cues alone (e.g., liquid volume height) when accurately responding to the conservation trials but rather appeared to use inferential reasoning and an understanding of the invariant nature of quantities to guide responding.

In addition to same/different paradigms, over-conservation tasks are used as a means to study these abilities in children and animals. In this task, subjects are presented with differing quantities (rather than equal quantities) and are trained or instructed to choose the larger of two amounts (Piaget 1968). For example, two juvenile chimpanzees indicated their choice of the larger of two quantities of a high-preference liquid (syrup) by pointing to their desired container (Muncer 1983). This discrimination procedure in which animals simply reach towards their preferred option offers a more spontaneous, prepotent, and arguably more reliable measure of quantity judgment as opposed to one that relies upon symbolic training of same/different concepts. Following the initial choice, quantities were transformed by pouring one of the two liquids into a larger container,



altering the height of the liquid. Muncer (1983) reported that one of the two chimpanzees showed evidence for liquid conservation, continuing to choose the container with the greater volume of liquid, despite being transformed such that it now had a lower height, which could have been misinterpreted as a lesser volume. The same chimpanzee, Jane, also passed a number conservation test in which two rows of candies were manipulated for length (by increasing the distance between each candy); see Fig. 1 as an example. Jane reliably chose the larger number of individual candies post-transformation, despite the larger quantity now appearing as the shorter row. Similar to the results of Woodruff et al. (1978), this chimpanzee failed the test of conservation by choosing the smaller/lesser quantity option if not allowed to examine the containers before and during the transformation procedure, indicating perceptual strategies alone could not account for performance in the critical test trials.

Following the Muncer (1983) study, several primate studies utilized the overconservation paradigm. Call and Rochat (1996) directly compared orangutans (*Pongo pygmaeus*) to 6–8-year-old children on a series of nearly identical conservation tasks. Orangutans were first trained to choose the larger quantity of preferred liquid (juice) presented in identical transparent containers via pointing which led to its immediate delivery for consumption. Children were not allowed to drink the chosen liquids but were instead instructed to choose the container under the assumption that they were “very, very thirsty” to promote maximization. In conservation test trials, Call and Rochat varied task difficulty by manipulating container shape and the type of transformation (continuous or discontinuous). They also ruled out the use of perceptual cues such as pouring duration, the sound of liquids being poured, and the flow or speed with which liquids were transferred to negate the use of these simpler strategies in solving the task. Most orangutans (three of four) performed well in the continuous conservation test, in which one of two containers of liquid was poured into a single differently shaped cup. When quantities were occluded during the transformation procedure, performance fell to chance

indicating that orangutans did not rely upon non-visual information such as pouring duration or auditory pouring cues. However, orangutans did not pass a discontinuous transformation experiment in which a container was subdivided into multiple smaller containers. In this experiment, some orangutans preferred a single cup with a higher liquid height whereas others preferred the greater number of individual cups or a combination of strategies. Thus, the Call and Rochat argued for “pseudo-conservation,” with the orangutans maximizing juice intake following relatively simple transformations of physical appearance. Interestingly, only two of 10 children succeeded in all experiments demonstrating evidence of true conservation according to Piaget and Inhelder (1941). All remaining children showed varying degrees of success across experiments, with evidence for intermediary reactions to conservation. These developmental results highlight the importance of also reporting individual differences among human subjects to shed light on the ubiquity (or not) of certain cognitive processes. We also must consider whether only one, a majority, or all individuals of a given species must “pass” a test for the results to be considered as significant, and whether those standards should be different for humans and nonhuman animals.

In a series of experiments, Suda and Call investigated conservation performance in chimpanzees, orangutans, and bonobos (*Pan paniscus*) with a specific focus on the strategy used to resolve a variety of transformations and to expand the number of individuals and species represented in this work. In the first study assessing liquid conservation, Suda and Call (2004) reported varying degrees of success within the great apes in their ability to conserve quantities of liquid across a number of transformations using differing container shapes and types. The apes appeared to most heavily rely upon visual information regarding liquid volume which depended on container shape, leading to incorrect selections of the smaller quantity because of its altered appearance. Further, the apes’ performances were disrupted to some degree when liquids were transferred to opaque cups, confirming the apes’ use of perceptual strategies (i.e., visually estimating the final

height of the liquid) to guide choice behavior. These results are consistent with previous studies of orangutan conservation performance (Call and Rochat 1997) and more recent data examining chimpanzees' responses to quantitative illusions, in which choice behavior in a series of quantity discrimination tasks was disrupted by contextual cues. Chimpanzees preferred equal and even smaller quantities of foods (both liquid quantities and quantities of discrete food items such as cereal) when presented in a container that caused the food to appear fuller or larger in size than its equivalent or perhaps truly larger counterpart (Parrish and Beran 2014a, b). Suda and Call reported that the apes were more successful when they were allowed to view the transformation process (e.g., visibly see the liquids being poured into different containers), although responding was partially guided by the use of perceptual estimation as well. These same authors discussed the role of cognitive conflict for apes that performed to intermediate levels of success (neither highly successful or unsuccessful; Suda and Call 2006). The mid-level performing apes displayed the highest degree of hesitancy in their choices (measured in terms of selection changes and simultaneous points to both quantities), which is perhaps indicative of greater cognitive conflict in reconciling how a liquid appears post-transformation versus what a liquid quantity truly is despite its appearance.

In a subsequent study, Suda and Call (2005) investigated the role of continuous (liquid) and discrete (itemized) quantities on conservation performance. Discrete quantities (for example, cereal pieces) presumably are easier to conserve than continuous quantities because although the spatial layout of the individual items is altered, the individual stimuli themselves remain constant (Peisach and Hardeman 1975). Developmental work supports this hypothesis that discrete stimuli are easier to conserve, including evidence for earlier success in number conservation tests (using items such as buttons) in younger children in comparison to liquid or solid conservation that appear later in development (e.g., Brainerd and Brainerd 1972; Gruen and Vore 1972; Samuel and Bryant 1984). Suda and Call (2005) directly pitted

continuous versus discrete conservation abilities of bonobos, chimpanzees, and orangutans to test whether this same pattern of performance held true nonhuman primates. Bonobos (but not chimpanzees and orangutans) performed better in tests of number conservation (using discrete edible stimuli – raisins) versus liquid conservation tests (juice). The authors reasoned that this performance pattern possibly was due to a more astute ability to estimate numerical versus liquid quantities and an overall greater level of experience with discrete foods versus continuous liquids on a daily basis. More convincing though, was the apparent difference in motivational state to obtain the discrete food items between species. The raisins used as the discrete stimuli were seemingly less preferred than the continuous stimulus (juice) by the chimpanzees than bonobos, which may have led to an overall lower motivational state to obtain the largest number of discrete items for chimpanzees. Future studies assessing the role of motivation in conservation performance is therefore needed. The orangutans in Suda and Call (2005) again outperformed the *Pan* species with near ceiling levels of performance in both liquid and number conservation tests, although these studies involved relatively low numbers of subjects.

In another study of chimpanzee quantity discrimination and conservation, Beran (2010) presented chimpanzees with a two-choice discrimination procedure comparing sets of liquid juice. Conservation of liquid quantities was tested by transferring one or both liquid sets into transparent or opaque containers via syringe. Consistent with their ability to discriminate discrete quantities according to the ratio between sets (e.g., Beran 2001, 2004; Hanus and Call 2007; Rumbaugh et al. 1987), chimpanzees excelled in their discrimination of continuous quantities regardless of whether both sets were visible (transparent containers) or whether one or both sets were non-visible (opaque containers). Relevant to conservation abilities, their performance was not reliant upon auditory or visual cues of liquid transfer as success rates remained high despite variations to the pouring height/rate during the transformation process. Beran reports that the success in conservation performance was

accounted for via tracking of liquid quantities as well as a perceptual strategy of estimating visual information of liquid height when sets were visible.

Other studies have extended conservation tasks to non-ape species including capuchin monkeys (*Sapajus apella*), a particularly interesting species in that they share a number of cognitive processes in common with Old World monkeys and great apes including self-control, numerical cognition, concept formation, spatial representations, and analogical reasoning (e.g., D'Amato and Colombo 1988; Flemming 2011; Kennedy and Frigaszy 2008; Wright and Katz 2006). With regard to number conservation tests, Beran (2008) demonstrated that capuchin monkeys could respond to transformations of discrete item sets presented on a computer screen. Monkeys first were trained to select the larger of two digital arrays of squares onscreen by contacting the more numerous set via joystick-controlled cursor. In test trials, after their first selection, the spatial layout of one array was manipulated to comprise a larger or smaller area by spreading out or compressing the array, a manipulation that did not actually change either quantity. Or, additional squares were added to one array, which did change the relative quantity judgment. Importantly, non-quantitative cues, such as the overall surface area of the array as well as whether the smaller or larger array was manipulated, were controlled so that the monkeys had to rely on true quantitative information to guide responding. Capuchin monkeys succeeded in this task, reliably selecting the larger of the two arrays following spatial transformations and additions to one of the two sets. These results closely aligned with data from a separate experiment assessing number conservation in rhesus macaques (*Macaca mulatta*) by Beran (2007), and both studies were key to expanding the comparative data set beyond the great apes to incorporate more phylogenetically distant primates.

In a more recent study, Pepperberg and colleagues extended conservation testing to four African grey parrots to include a non-primate in this area of research (*Psittacus erithacus*; Pepperberg et al. 2017). The researchers first

demonstrated the ability of parrots to choose between two different amounts of liquid presented in identical containers, an important precursor to testing conservation abilities. Three of the four birds reliably chose the larger quantity of liquid. The one chick that initially failed (approximately 6 months old) subsequently passed this initial testing at approximately 9 months old. This age-related change in performance demonstrates a development in quantity discrimination abilities and/or improved attention to the task. In the conservation tests, liquid quantities were either visibly (in full view) or invisibly (out of view) transferred to new containers. In invisible transformations, parrots used a perceptual strategy, selecting the container that would normally appear fuller despite being equal in amount to the alternative container. These results stand in contrast to visible transformations, in which the parrots responded on the basis of inference, seemingly understanding the invariance of liquid quantities. In these trials, they showed no preference for the equal quantities despite their change in physical appearance due to container shape. These results are consistent with earlier studies of great ape performance in conservation tasks utilizing both visible and non-visible transformation processes (e.g., Muncer 1983; Woodruff et al. 1978).

## Summary

The ability to conserve quantitative information following physical transformations (and changes in perceptual cues of quantity such as liquid volume height) is a hallmark of cognitive development within young children. Comparative research of quantity conservation suggests that an increasing number of species understand the invariance of liquid and solid quantities to some degree. Researchers have systematically assessed a variety of perceptual and decisional strategies that could account for animals' performances and demonstrate a form of pseudo-conservation that allows for the conservation of quantities through relatively simple transformations. Often, these studies have shown that animals will rely on

perceptual estimation abilities (e.g., visually inspecting the height of the transformed liquids) or may only conserve quantities through one transformation (continuous conservation) but fail tests presenting multiple transformations (discontinuous conservation). A reliance on these simpler strategies or intermediary performance suggests that an animal, or a species, has not achieved the level of “true” or necessary conservation as originally defined by Piaget and Inhelder (1941) and as demonstrated in the concrete operational stage of development (7–8 years of age). However, these perceptual strategies cannot account for all data as a number of studies have demonstrated successful conservation only when animals are allowed to inspect quantities prior to and during the transformation process (ruling out simpler strategies) as well as various experimental manipulations that rule out the use of perceptual or non-quantitative cues.

Comparative studies have assessed a number of primate species, including children, great apes, Old World and New World primate species, and most recently an avian species. A broader assessment of conservation abilities across species is needed to build a more complete phylogenetic map than we currently have. Direct comparisons using identical stimuli and methodologies are key to this development, while also balancing species-specific variables including variance in motivational and attentional states as well as quantity discrimination and perceptual abilities. Furthermore, comparisons of performance on conservation tasks to other tests of logical reasoning (e.g., other Piagetian tests) should be undertaken to help us understand better whether these cognitive abilities translate to problem solving and logical thinking outside of the quantitative domain within these same individuals and species.

## Cross-References

- ▶ [Absolute Number Discrimination](#)
- ▶ [Addition](#)
- ▶ [Approximate Number System \(ANS\)](#)
- ▶ [Numerosity](#)
- ▶ [Relative Numerousness](#)

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## Consistent Behavioral Variation

### ► Coping Style

## Consolation

### ► Post-conflict Affiliation

## Consort

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## Synonyms

Marriage; Pair bond

## Definition

To consort is to engage in a heterosexual pairing for the purpose of sexually reproducing offspring. This behavior requires the maintenance of spatial associations and some level of cooperation and coordinated behavior between paired individuals, along with spatial tolerance and the occurrence of social exchanges. Consortships are initiated by signals or displays that advertise availability and quality of potential mates. Consort pairings are observed across a variety of vertebrate and invertebrate taxa and the methods by which individuals choose and compete for potential partners varies.

## The Function, Forms and Frailties of Consort Behavior

Several factors, such as interindividual distances, population density, female sexual synchrony, and the length of female estrus, dictate when and with whom heterosexual consortships may occur. Comparatively large geographic distances due to solitary foraging behavior can serve as a challenge for potential partners to locate each other. Often, this is mediated using auditory or chemical signals to allow for heterosexual pairs



of conspecifics to come together prior to ovulation in order to mate and reproduce. To minimize the loss of reproductive opportunity, consortships in solitary living *Mustela putorius* include repeated copulations to induce female ovulation (Lodé 2011). On the other hand, potential consort partners in *Poecilia reticulata* come together in groups and engage in ritualized courtship to choose among or compete for consort partners (Kodrie-Brown 1993).

As the timing of consortships is centered around reproductions, secondary sexual characteristics in group living animals have evolved in some species to signal sexual receptivity and allow males to loosely identify the timing of ovulation. For example, in some Old World primates and apes, morphological changes in the sexual skin of females loosely reflect underlying endocrinological fluctuations, which, tied with behavioral signals, allow males to loosely determine the timing of the follicular phase (Campbell et al. 2011). Although copulations may be observed prior to or post-ovulation, mating behavior peaks around the time of maximal tumescence of the sexual skin, which serves as a graded signal to males (Campbell et al. 2011).

Over a given reproductive period, consort pairings may vary in their duration and their number due to fluctuations in partner choice, coercion, or competition. In *Macaca sylvanus*, individuals mate promiscuously within short-term consortships, which may last for several minutes or hours, and males do not use overt coercion to control female mating behavior (Campbell et al. 2011). In other species, male dominance relationships (attained through competition) and various degrees of coercion of females may influence a male's sexual access to females and the likelihood of a male being the consort during a conceptive cycle (Connor and Vollmer 2009). Females may try to resist, but in sexually dimorphic species, such as chimpanzees, dolphins, and orangutans (Connor and Vollmer 2009; Knott et al. 2010), males may have the physical advantage. In other instances where male competition is high and the number of receptive females is low, males may need to form coalitions with other males to

successfully consort with females (Connor and Vollmer 2009).

Mating systems do not necessarily correspond with the success of a consortship. In species that practice long-term monogamy, such as the black vulture, cheating is rare; thus, extra-pair paternity is low, and there is a strong overlap between the social and genetic mating system (Decker et al. 1993). However, within the bounds of well-established socially monogamous pairings, extra-pair copulations may in fact be common. Of the bird species studied, Griffith et al. (2002) found that 90% engaged in extra-pair copulations, indicating a significant discontinuity between the social and genetic mating systems of many socially monogamous birds.

Long-term consortships are facilitated by complex behavioral interactions that vary in the range of behaviors displayed and the contexts in which they occur. These relationships are characterized by strong social and spatial preferences and are mediated through neuroendocrine pathways. For example, Carter et al. (1999) describe the interplay of hormones and behavior in *Microtus ochrogaster*. Following 24 h of mating during which the female comes into estrus as the result of elevated estrogen levels, the pair bond forms between the male and female as concentrations of oxytocin, vasopressin, and corticosterone shift in the two sexes. In males, corticosterone and vasopressin increase, facilitating male-male aggression and pair bonding. In females, elevated stress levels (which can be brought on by the presence of stranger males) result in decreased fertility. Therefore, by sequestering females, via mate guarding, *M. ochrogaster* males facilitate female ovulation (via elevated estrogen levels) and allow for the formation of a pair bond (via elevated oxytocin levels) in females.

Consortships serve to provide direct fitness benefit to participants through the sexually reproduction of offspring. In some species, this requires a small degree of behavioral coordination between individuals and a short-term investment of reproductive material (e.g., Lodé 2011). However, in other cases one parent may not be sufficient to successfully raise offspring, and previous consort partners may be needed to contribute to



the care of dependent offspring. For example, in savannah baboons, a male who consorted with a female during her previous conceptive cycle may care for his potential offspring and provide social protection for mothers (Seyfarth and Cheney 2012).

In addition, when consortships require dispersal outside of the group, they may also provide indirect benefits to participants through intragroup alliances. Human “marriage” serves a sociopolitical role by creating and maintaining alliances across social units while also having socioeconomic implications through the acquisition of transmission and acquisition of resources (Thornhill 1991).

## Cross-References

- [Affiliative Bond](#)
- [Competition](#)
- [Corticosterone](#)
- [Courtship Rituals](#)
- [Cuckoldry](#)
- [Dominance](#)
- [Endocrine System](#)
- [Extra-Pair Copulation](#)
- [Female Choice](#)
- [Friendships in Animals](#)
- [Graded Signals](#)
- [Hormones And Behavior](#)
- [Inclusive Fitness](#)
- [Mate Guarding](#)
- [Mate Provisioning](#)
- [Mating Effort](#)
- [Monogamy](#)
- [Nuptial Gift](#)
- [Oxytocin](#)
- [Pair Bond](#)
- [Parental Investment](#)
- [Paternal Behavior](#)
- [Reproduction](#)
- [Reproductive Fitness](#)
- [Secondary Sex Characteristics](#)
- [Sexual Selection](#)
- [Sociosexual Behavior](#)
- [Sperm Competition](#)
- [Tolerance](#)

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## Conspecifics

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## Definition

Organisms belonging to the same species.

## Introduction

Conspecifics are all organisms belonging to the same species. In most species, conspecifics will be the ones that individuals interact most. The variability of interactions between conspecifics will vary a lot among animals, depending most on the reproductive characteristics and social structure of the species. Social structure varies from nonsocial or solitary animals, that spend most of the time without interacting with other members of their species, to the different degrees of social animals, that interacts almost all the time with conspecifics (Wcislo and Danforth 1997).

## Communication

The first step in conspecific interactions is the evolution of communication mechanisms. Communication between conspecifics is observed in many aspects of animal's life. The most basic communication must be the one involved in reproductive behavior. Male and female of the same species must communicate to: (1) analyze receptivity and fertility, (2) assess quality of their partner, and (3) species recognition (Keller-Costa et al. 2015). Conspecific communication also involves alarm calls or cues that signalize a risk of predation, evoking antipredator behavior of the conspecifics around (Kaplan 2014). Avoiding serious conflict is also acquired through conspecific communication (Arakawa et al. 2011; Kaplan 2014; Keller-Costa et al. 2015), as well as informing about food availability (Kaplan 2014) and health status of individuals (Arakawa et al. 2011). All this information (and much more) is transmitted between conspecifics using olfactory, visual, and auditory cues that are sent from one conspecific to another.

## Learning from Conspecifics

As conspecifics almost ever have a closer relationship, it is expected that individuals can learn from each other. This is especially true for most social species. Learning from conspecifics can

be observed in a variety of areas and species. Just as examples, individuals can learn about predators and predation risk (e.g., in tadpoles, *Lithobates sylvaticus*; Lucon-Xiccato et al. 2016); how to vocalize (e.g., in the zebra finch, *Taeniopygia guttata*; Jesse and Riebel 2012); and how to increase their foraging skill (e.g., in wild brown capuchins, *Cebus paella*; Gunst et al. 2007). As learning is mediated by communication, it will also use olfactory, visual, and auditory cues.

## Conclusion

Conspecifics are all the organisms belonging to the same species that interact most during their life. Interactions will be mediated by communication, and a variability of cues evolved to facilitate these interactions.

## Cross-References

- Coalition Enforcement
- Predation Risk
- Predator Detection
- Predator Defense
- Species
- Vigilance

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## Constancy

- [Conservation](#)

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## Constitution

- [Karyotype](#)
- [Temperament](#)

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## Constraints on Learning

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### Definition

“Constraints on learning” refers to violations of the generality of learning. The same scope of phenomena may be referred to positively as the specificities of learning, but it is worth remembering the negative “constraints” phrasing due to its cautionary history. The phrase “biological constraints” is often used with the same scope, but this loads an interpretation regarding what is producing an effect, and this loading is furthermore ambiguous, referring to evolutionary factors to some writers, but physiological factors to others. Alternatively, the qualifier “biological” may be intended to restrict the scope to factors related to

the organism (i.e., biotic factors), but “biotic” is insufficiently restrictive, including species- and system-general constraints, such as effects related to stimulus novelty or intensity.

### Background

Early learning researchers (e.g., W.S. Small, L.W. Kline, and J.B. Watson) stressed attention to the specificities of the animal studied, and the importance of incorporating such knowledge into the study of animal learning. Moved by pressures of repeatability and isolation of measurable variables, the pioneers exploited such specificities in developing apparatus and procedures; their successes in doing so testifies to the keenness of their observations of these specificities (Timberlake 1983). This acute awareness of the specificities of their animals waned over the following decades, perhaps because later generations of scientists inherited developed apparatus and modus operandi, and the reasons these worked so well were not in the reports. The general aspects of learning proved more memorable than the peculiarities. The field progressively embraced claims of “equipotentiality,” that the cues, responses, and reinforcers involved in a given learning circumstance are arbitrary, and can be treated similarly to any other cue, response, or reinforcer, respectively (attributable to I.P. Pavlov). Optimism in the generality of learning soared, and diversity of species and processes studied plummeted (Beach 1950). These developments yielded confidence in abstract terms of description, which provided the context for a boom in learning research and theory.

John Garcia and colleagues (e.g. Garcia et al. 1955) made a splash with their work on taste aversion learning. This was a striking example of specificity of learning, in which an animal learns to avoid novel tastes that have preceded even a single instance of nausea, even when separated by very long delays. In one demonstration, rats were presented with an audiovisual stimulus whenever they drank the saccharine-tainted water provided (Garcia and Koelling 1966). Subjects made nauseous by radiation developed aversions

specifically to the taste, whereas another group of subjects presented with foot shock selectively developed aversion to the audiovisual cue. Learning was selective. This selectivity, together with their earlier demonstrations that taste aversion learning occurred after a single pairing, and with long delays, challenged the generality of the apparent laws of learning. Although violations of equipotentiality had spattered the literature throughout the history of animal learning research, discussions of such results had tended to be peripheral. Garcia put the specificities in focus. For a variety of reasons, including some valid (perhaps overzealous; Garcia 1981) methodological concerns, doubts about whether the challenged views were indeed committed to equipotentiality, and perhaps some disciplinary conservatism (Garcia 1981), Garcia's message was initially received with resistance among some learning psychologists. Meanwhile, it was touted by others, and ultimately had great impact.

Throughout the 1960s and 1970s, the apparent generalities of learning became progressively spotted with exceptions. As the evidence mounted, it became hard to deny that the abstract principles of learning require qualification. Learning is constrained (Breland and Breland 1961; Hinde 1973; Shettleworth 1972). Typical general-process theories of learning provide no means for predicting such exceptions. There were two general reactions to this.

One reaction was to rework a general-process theory to better account for the exceptions. This strategy had been taken to account for specificities in learning models for decades, encouraged by the staunchly data-driven attitudes toward theory building prevalent at that time, particularly endorsed by K.W. Spence and W.K. Estes. This approach treats specificities as theoretically mundane, reflecting variables such as sensory or motor capacities, rather than learning per se. Learning models typically include learning rate parameters to allow for differences among stimuli in their potential to support conditioning, for example, due to salience of the cue, which will vary across species with different sensory apparatus. One problem with this approach is that such models

have no way of discerning sensory specificities from learning specificities, with all of the between-species variability hidden in the same parameters. In similar fashion, selective association effects (e.g., Garcia and Koelling 1966) could be accommodated by positing a "belongingness" principle. Such attempts to assimilate exceptions into a general-process approach continued to permit models to fit much of the available data, but elegance waned as exceptions mounted. This approach was criticized as conservative, glossing over constraints atheoretically, and appearing to save general process views of learning by absorbing exceptions into empirically tweaked parameters and provisos (Domjan and Galef 1983).

## Turning to Evolution

The other major reaction to the appearance of exceptions in the principles of learning was to turn to evolution. Widespread agreement developed that adopting the methods of biology for the study of learning held promise. However, a principled biological approach to learning proved elusive. Several attempts have been made to apply biological methods to the study of learning, with varying degrees of success. Such attempts fall roughly in three categories.

### Preparedness

One such attempt was to consider animals as predisposed or "evolutionarily prepared" (Seligman 1970) to learn about certain stimuli more readily than others. Exceptions to general laws of learning were attributed to predispositions to learn certain responses, in certain ways, with certain stimuli, in certain circumstances, that accorded with functional expectations.

This approach was dissatisfying for a number of reasons. First, this was not the paradigm shift it superficially appeared to be. Constraints were not being used to question the basis of the general process learning approach as much as to save it, using evolution to explain why there were exceptions, and treating them as such. It was again conservative; general-process approaches

could proceed as they had, just footnoted to admit occasional evolutionary anomalies (Shettleworth 1972; Domjan and Galef 1983). Second, it is unproductive. Beyond just that there are predispositions in learning, the empirical point that motivates talk of preparedness, this starting point turns out to be its only prediction, leaving it theoretically vacuous. If preparedness is defined in terms of the amount of training required to acquire an association (Seligman 1970), attempts to explain the ease of acquisition as preparedness is circular. Third, it does not give positive terms for theory to build upon. Treating constraints as exceptions explicitly denies a common explanatory framework. If various specificities share common features, this perspective gives no theoretical guidance in identifying them. This includes mechanistic bases, leaving specific learning phenomena outside of the explanatory scope of a mechanistic analysis.

Alas, this was not adoption of a principled evolutionary approach. Although it admits selectivity of learning, its appeal to evolution for explanation is post hoc. Although much of the “biological constraints” research was aimed at questioning a general process view of learning, and so not wholly atheoretical, such work generally did not have a coherent positive message concerning specificity of learning. Such research did not generate real theoretical alternatives to a general-process view of learning. Exceptions to general-process views of learning continued to be treated as exceptions. Missing was a general understanding of the newly documented breadth of learning phenomena.

### Specific-Process Approaches

Much research on learning has taken a more genuinely ethological orientation, beginning with specific-process assumptions, and treating specific learning phenomena as specific adaptations, situated in specific ecological contexts, with attention to their functional significance, and specific selection pressures. Some forms of learning have consistently been studied by this approach, such as imprinting (e.g., Lorenz 1937) and mate-choice copying (e.g. Bowers et al. 2012), while others,

such as food conditioning paradigms, have typically been approached in general-process terms. Shettleworth (1972) advocated embracing the diversity of learning, in line with an earlier recommendation of Beach (1950), and approach learning as a “multiplicity of principles.” This approach is closer to the evolutionary orientation several animal learning researchers had been advocating, and is a precursor for a principled comparative study of learning (Domjan and Galef 1983).

A biological orientation is well suited for answering some kinds of questions, but not others. Adoption of functional terms of description is only a first step toward principled application of biological methods. Although comparative methods have been applied with success (e.g., Timberlake and Washburne 1989), the literatures of at least some kinds of learning show no clear relationships with ecology or phylogeny (e.g., Bowers et al. 2012), without which comparison loses force, and the perspective loses one of its strongest methods. Approaching learning phenomena as specific adaptations embraces the diversity of learning, but does not provide answers for many questions regarding what is special about a given manner of learning, and provides no basis for a general mechanistic understanding of that diversity.

### Integrative Approaches

Several thinkers have developed hybrid strategies for retaining the benefits of specific-process approaches in ways that specifically suit the study of learning. These include Ecological Learning Theory (Davey 1989), Releaser-Induced Recognition Learning theory (Suboski 1990), and behavior systems approaches. Among these, Behavior Systems Theory (Timberlake 1983) has had the greatest impact on contemporary views of learning, providing a general framework for interpreting species- and system-specific learning phenomena that had appeared awkward for older views of learning. The principal intuition is in viewing the unconditional in terms of structured motivational systems and interrelated response forms, as opposed to discrete stimuli and responses.

## Summary: Changing Perspectives on Constraints

Describing specificities of learning as “constraints” expresses the matter negatively, as a failure of general-process assumptions, implicitly endorsing a general-process default view. An early learning researcher can scarcely be blamed for stressing generalities over peculiarities. The existence of a general-process description of a phenomenon, however, is no justification for the exaggerated faith in equipotentiality claims that followed. An abstract analysis was confused for a fact about the natural world. The mistake of “constraints” research was taking a general-process approach even to the specificities, which rather warrant a specific-process approach. However, a principled specific-process approach suited to the study of learning proved harder than apprehended, and required development of integrative approaches, a lesson that the allied fields concerned with animal learning are still slowly but surely coming to terms with.

## Cross-References

- [Adaptation](#)
- [Associative Learning](#)
- [Autoshaping](#)
- [Behavior Systems](#)
- [Behaviorism](#)
- [Bennett G. Galef](#)
- [Biological Preparedness](#)
- [Contrapreparedness](#)
- [Domain Specificity](#)
- [Frank Ambrose Beach](#)
- [Imprinting](#)
- [Ivan Pavlov](#)
- [John B. Watson](#)
- [Kenneth Spence](#)
- [Michael Domjan](#)
- [Nature Versus Nurture](#)
- [Robert Hinde](#)
- [Sara Shettleworth](#)
- [Species-Specific Behavior](#)
- [Taste Aversions](#)

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## Consumer

- [Omnivore](#)

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## Consumption

- [Chondrichthyes Diet](#)



## Contact Calls

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### Definition

Contact calls are calls that are given toward conspecifics with affiliative bonds, such as mating partners or group members. Contact calls contain various social information that is used to maintain cohesion or movement coordination and for identity advertisement.

### Introduction

Contact calls are widespread in social mammals and birds and play an essential role in mediating social interactions (Rendall et al. 2000). This role includes establishing new social bonds, affirming existing connections, or maintaining cohesion and coordinating movement among group members (Marler 2004). Contact calls are often used in the absence of visual contact, for example, when distance or surroundings restrict visibility or when visual communication with specific individuals is limited due to crowded groups. Among their functions, contact calls can be used to locate and assemble group members, recruit new members to temporary aggregations, and coordinate group position and movement for shared activities such as foraging and roosting. Contact calls can range from soft sounds to screams, depending on whether socializing animals are close together or far apart (Sugiura 2007). One of the most striking characteristics of the contact calls is that they may provide information about the identity or social affiliation of the caller (Cortopassi and Bradbury 2006). It has been assumed that the amount and type of identity

information provided by contact calls might be linked to the social organization (Kondo and Watanabe 2009). For example, socially stable species often converge on shared group-specific contact calls (Cortopassi and Bradbury 2006), while in socially fluid species, contact calls tend to be individually distinctive (Tyack 2003). Such individually unique contact calls may function as individual signatures. Signature contact calls (or whistles) have been found in primates, dolphins, parrots, and corvids suggesting that they may be essential for referential communication in societies with high fission-fusion dynamics (Kondo and Watanabe 2009).

### Types of Information

Several studies in birds and mammals have revealed that contact calls possess acoustic individuality that can be used for individual recognition (Kondo and Watanabe 2009). According to the social relationships associated with individually distinctive calls, individual recognition can be classified into three categories: mates, kin, and group members.

Mate recognition has been found mainly in group-living monogamous bird species, such as passerines (Vignal et al. 2004) and parrots (Wanker et al. 1998), showing both individual differences in contact calls and selective response to mates' contact calls. In contrast, mate recognition using contact calls is rare in mammals, in which monogamy is not a prevalent mating system. Contact calls are also involved in kin recognition such as parent-offspring vocal recognition and have been found in cooperatively breeding birds and mammals (for a review see Kondo and Watanabe 2009). Finally, individual recognition beyond such fixed social relationships is also required for animals that live in complex societies with fission-fusion dynamics in which group composition and social relations change in space and time and has been documented in a variety of species living in such complex societies ranging from primate to dolphins and birds (Kondo and Watanabe 2009).

## Conclusions

Contact calls have been traditionally thought to have comparable functions among animals with different social organization. However, previous studies on various birds and mammals provide evidence for different emphases of contact-call functions depending on the species' social structure. Animals living in stable social groups might use contact calls mainly for group cohesion, whereas animals living in fluid fission-fusion societies might use contact calls to advertise identity. Future studies that take into account the diversity of complex social systems are needed to understand the evolution of contact calls and their function in birds and mammals concerning the socioecological background.

## Cross-References

- [Affiliative Bond](#)
- [Aggregation](#)
- [Conspecifics](#)
- [Cooperative Breeding](#)
- [Fission-Fusion](#)
- [Foraging](#)
- [Movement](#)
- [Referential Communication](#)

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## Contact Comfort

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## Definition

Contact comfort is defined as the physical and emotional comfort an infant receives from being in physical contact with the mother or caregiver.

## Introduction

Contact comfort was first explored by Harry Harlow in 1958, researching affectional variables (Harlow 1958). He placed neonatal and infant macaque monkeys with two surrogate “mothers”: one that was only made of wire and provided food with a baby bottle and another that was covered in terrycloth and provided warmth and comfort, but no food. The baby monkeys spent most their time with the terrycloth mother and only went to the wire mother when they were hungry. Harlow

concluded that contact comfort is a very important variable in developing an infant's affection to its mother, and lactation is a variable of insignificant importance (Suomi and Kolb 2017). This entry summarizes the current knowledge about contact comfort, the studies that have been executed to examine this phenomenon, and most recent applications to human health and well-being.

### Contact Comfort as a Safety Net

Harlow studied how fear-producing stimuli and curiosity-manipulatory stimuli affected differential responsiveness to both types of surrogate mothers. The monkey infants were presented with various fear-producing stimuli, while in the presence of both surrogate mothers, and he recorded their differential responsiveness to each mother. Infants highly preferred the cloth mother over the wire mother, and with age and experience, this differential selectivity increased.

When examining exploration, stimuli that evoked curiosity-manipulatory responses were placed in a strange environment, and infants were placed in this situation with no surrogate mother in one session, and the cloth mother in the next session. In the presence of the surrogate mother, after a few sessions the infants became comfortable to explore the stimuli, return to the mother for comfort and then return to explore the strange environment and its stimuli again. When the surrogate mother was absent, the infants exhibited emotionality and anxious behaviors, with little exploration.

These studies illustrate the importance of a mother figure who provides comfort to infants, allowing them to explore the environment and reducing their stress level during anxious and fearful situations.

### From Harlow's Contact Comfort, to Bowlby's Attachment Theory

Observing how animal species are attached to a caregiver that provides comfort led to Mary Ainsworth exploring how human infants attach and

bond with their caregivers. Based on John Bowlby's attachment theory, which states that humans and other species are primed to become attached to a mother figure, Ainsworth (1979) developed a testing scenario called the "strange situation" experiment. In this experiment, a human infant is observed while its mother is present, separates from the infant, and then reunites with the infant. Ainsworth found that there are four types of attachment classifications; secure, avoidant, anxious, and disorganized attachment. In the general population, 55% of infants have a secure attachment, 23% have an avoidant attachment, 8% have an anxious attachment, and 15% have a disorganized attachment (Benoit 2004). These attachment styles become developed with early mother-infant interactions. Healthy, secure attachments establish from mothers that were more sensitively responsive to infant signals, than mothers who ignored their babies or were more rejecting, angry, or restricting to their infants.

With evidence that contact comfort and caregivers providing sensitive and loving care leads to a secure bonding attachment style for the infant, it is important for caregivers to be taught to provide contact comfort and not neglect the signals and emotions that infants display.

### Reducing Pain and Stress in Human Newborns

Studies of contact comfort have also influenced the development of skin-to-skin contact (SSC), defined as the placing of the newborn onto the mothers' chest, which has great benefits to human newborns by reducing pain and stress. When testing whether skin-to-skin contact reduced experienced pain of infants during a heel lance versus a control condition, researchers found that crying was reduced by 82%, and grimacing by 65% (Gray et al. 2000). It was also found that newborns in the contact group had a stable heart rate throughout the study, compared to the newborns in the control group who had a quick heart rate rise during the recovery period, illustrating the induced physiological response to pain from the heel lance.

To explain why skin-to-skin contact has dramatic effects, researchers have drawn on Kolcaba's comfort theory. Ludington-Hoe (2015) suggests that the womb fosters a sense of security, with warmth, the mother's familiar heart beat and voice, her unique scent, and rocking from the mother's breath. With birth creating a very stressful situation for the infant, a mother's skin-to-skin contact brings back a sense of comfort due to the familiar scent, voice, warmth, and rocking, reducing stress (Bystrova et al. 2003). It was shown that the "first 2 to 3 hours are a sensitive period for manifestation and control of stress," meaning that if the newborn received SSC within that time, stress diminished by the third hour of birth, but if the newborn did not receive SSC by its second or third hour after birth, the newborn continued to experience high stress levels. If a newborn receives SSC at birth, they are able to better handle stress 1 year postpartum and that an hour a day of SSC after 32 weeks, reduced stress reactivity at 3 months and at 10 years. When observing cortisol levels, it was shown that after 20 min of SSC, newborn's cortisol decreased by 70% (Gitau et al. 2002).

In terms of skin-to-skin contact reducing pain, Johnston et al. (2009) concluded that SSC alone is better than adding rocking, singing, and suckling to swaddling and facilitative tucking. SSC is a great pain reducer since oxytocin, released during SSC, increases beta-endorphin levels and c-afferent nerve activation, which produces analgesic effects, explaining how the newborns experience less pain by being in skin-to-skin contact with their mothers and caretakers (Liljencrantz and Olausson 2014).

## Conclusions

Contact comfort has been seen to have a great role in developing infant-mother attachment and bonding, while also creating a safety net for infants to allow them to cope with stress and new stimuli. The studies of contact comfort led to the development of attachment theory and skin-to-skin contact with human newborns. Attachment theory granted us the knowledge about the

importance of a caregivers' response to an infants' signal, which will create life-lasting attachment styles to other people. The effects of skin-to-skin contact have many health benefits to infants and newborns, mostly in reducing stress and pain and developing an infant's affection to its mother. SSC is very important for a newborn right after birth, and the benefits can be observed hours to years after SSC. When stress is reduced by having skin-to-skin contact with its mother, a known stimulus, it allows the infant to be more confident in its new environment, promoting exploration, emotional stability, and a healthier environment for the infant to develop. SSC also reduces pain, allowing common procedures to be done with less pain and stress to the newborn.

## Cross-References

- [Coping Style](#)
- [Stress](#)

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## Contagion

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Behavioral contagion (also referred to as instinctive imitation; Morgan 1900) is a type of social influence that refers to the propensity for certain behavior exhibited by one organism to be copied by others (see sections on imitation, affordance learning, and observational conditioning). Behavioral contagion generally applies to the copying of species typical behavior. That is, it is behavior that does not have to be learned and also will occur in the absence of a social stimulus, although not with the same probability. Examples of naturally occurring contagious behavior are yawning, laughing, crying, and eating. Contagious behavior is sometimes referred to as socially facilitated behavior (see section on social facilitation), but social facilitation more specifically refers to the effect on the behavior of an animal produced by the mere presence of another animal (Zajonc 1965).

The most frequent example of contagious behavior is contagious yawning. Humans yawn when we see another human yawn. Even the sound of yawning, thinking about yawning, or reading about yawning can make a human yawn (Provine, 1986). There are many hypotheses about the function of contagious yawning but it

has generally been viewed as a shared experience that promotes social bonding. Certain kinds of contagious behavior are associated with emotional responses, like laughing and crying, which clearly have an emotional component (see section on emotional contagion) and which are thought to be the basis for the development of human empathy but contagious yawning does not appear to be connected to any particular emotion. Furthermore, contagious yawning also has been found in several nonhuman species such as chimpanzees (Anderson et al. 2004), bonobos (Demuru and Palagi 2012), baboons, (Palagi et al. 2009), wolves (Romero et al. 2014), and, to a certain extent, dogs (Romero et al. 2013) and budgerigars (Gallup et al. 2015).

Neuroscientists have proposed that mirror neurons are involved in contagious yawning (Haker et al. 2013). Mirror neurons are neurons that have been found in the inferior frontal gyrus that fire when an animal performs a particular response as well as when that response is observed to be performed by others.

One of the more interesting examples of behavioral contagion in animals has been found with regard to eating behavior (Rajecki et al. 1976). In this research, food-deprived chickens were given free access to food until eating reached a low baseline level (they were presumably sated). When a food-deprived conspecific was introduced, the sated chickens showed a significant increase in eating as compared to control chickens that ate alone. The authors found similar effects when they conducted the experiments with water-deprived chickens given free access to water and then introduced to another water-deprived chicken.

The finding of contagious eating behavior has important implications for the assessment imitation in animals. Although one would not think of eating behavior as being a low probability behavior in the presence of food (see section on imitation), it may be inferred that the effect of the conspecific on the sated chicken represents an increase in motivation, and an increase in motivation is what is presumed to be responsible for social facilitation (Zajonc 1965; see section on social facilitation).

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- brief acme, and then a short passive expiration of breath.
- ...seeing a dog and horse and man yawn, makes me feel how much all animals are built on one structure.  
Charles Darwin, 1838 notebook.

## Introduction

Yawning is a universal everyday behavior shared by all vertebrate species. It is a stereotyped and often repetitive involuntary motor act characterized by gaping of the mouth and accompanied by a long inspiration of breath, a brief acme, and then a short expiration of breath. Yawning is not merely a simple opening of the mouth but a complex, coordinated movement involving a flexion followed by an extension of the neck and a wide dilatation of the pharyngo-larynx with strong stretching of the diaphragm and antigravity muscles (Provine 1986). Contagious yawning is the urge to yawn when thinking about, listening to, reading about, hearing, or viewing yawning. Ethologists use a better word, i.e., replication, or behavioral mimicry, whereas neurologists refer to echokinesis, a term coined by Jean-Martin Charcot (1825–1893). The widespread familiarity of contagious yawning is due in part to the fact that almost everyone has experienced the phenomenon and it occurs seemingly without volition. This behavior is well documented in humans; however, its function and prevalence in the animal kingdom and the brain mechanisms underlying it are only beginning to be understood.

## Contagious Yawning

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## Synonyms

Chasm; Gap

## Definition

The yawn is a stereotyped and often repetitive motor act characterized by gaping of the mouth accompanied by a long inspiration of breath, a

## Behavioral Framework

Yawning is morphologically similar in reptiles, birds, mammals, and fish, and no environmental input changes the sequence of movements (Walusinski and Deputte 2004). This behavior may be an ancestral vestige maintained throughout evolution with little variation, bearing witness to the early phylogenetic origins of yawning. Like any phylogenetically old behavior, yawning can be observed early in ontogeny, that is, at 12 weeks of fetal life in humans (Walusinski



2012). Behavioral and neurophysiological studies provide converging evidence that yawning occurs preferentially during rest, periods of drowsiness, and awakening. Hunger and satiety also trigger yawning. The frequency of yawning has a distinctive circadian distribution and occurs most frequently before and after sleep, that is, during periods of lower levels of vigilance and alertness (Fica and Salzarulo 2002; Walusinski and Deputte 2004).

When animals transition between behaviors, they are not merely responding in a passive way to the conditions of the environment, such as day-night succession. Rather, they are following internally generated signals produced by homeostatic processes originating in the hypothalamus (suprachiasmatic nucleus and paraventricular nucleus of the hypothalamus, where yawning is triggered). The resultant internal rhythm allows for the anticipation of transitions and triggers behavioral and physiological changes in accordance with those transitions. This results in two advantages: predictability and the possibility to detect the unexpected. Similar to sleep and hunger, yawning functions in this way and appears to be associated with transitions between periods of high and low activity or arousal. This universal form of yawning is internally elicited (Gupta and Mittal 2013; Krestel et al. 2018).

But other, externally elicited forms of yawning exist. Among mammals, morphologically identical yawns occur in situations relative to stress, social interactions, and sexuality (Kubota et al. 2014). Contagious yawning is a form of social interaction without language, triggered involuntarily. Nonconscious mimicry (“chameleon effect”) refers to an individual’s tendency to imitate a social partner’s behaviors without either party’s awareness or intent.

## Yawning in the Animal Kingdom

Yawning conveys information to other conspecifics about dominance, state of arousal or tiredness, anxiety, or fear. The combinations of different types of signals (visual, acoustic, and olfactory) establish the interaction in either

conspecifics or human counterparts. Indeed, a cross-species chameleon effect or contagiousness has now been documented for yawning between dogs and humans (Buttner and Strasser 2014; Harr et al. 2009). In nonhuman primates, teeth-bearing during yawning has led to the suggestion that this behavior reinforces dominant identity rather than signaling a threat (Deputte 1994). Accordingly, yawning has been compared with intimidating displays that dominant males usually show to subordinate males to display their dominant status. Chimpanzees, like humans, differ from Old World monkeys in that yawning by adult males is not a form of ritualized display expressed in situations of male-male confrontation.

Other ethological studies propose that yawning might induce relaxation of social tension and thus be a displacement activity, considered to indicate changes in behavioral state for the yawner and simultaneously to operate as a physiological capacity signal. In Sprague-Dawley rats, yawning associated with penile erections suggests that yawning behavior arises from the ritualization of pre-existing cues involved in perception of stimulating chemo-signals in a mating context (Moyaho et al. 2015).

## Contagious Yawning

Contagious yawning has been observed in non-human primates (chimpanzees, bonobos, stump-tailed macaques, gelada baboons, and common marmosets) (Demuru and Palagi 2012; Palagi et al. 2009), in dogs (Harr et al. 2009), in wolves (Romero et al. 2014), in sheep (Yonezawa et al. 2017), in budgerigars, the only non-mammalian specie (Gallup et al. 2015), in rats (Moyaho et al. 2015), and in elephants (Rossman et al. 2017), but not in lemurs (Reddy et al. 2016) and tortoises (Huber and Wilkinson 2011). No data are available for other species. Animal studies have reported low levels of contagious yawning in dogs, significantly lower than 33%, the rate observed in chimpanzees (Harr et al. 2009). Contagious yawning seems to be more easily triggered when models are conspecifics or have a strong social bond with the observer. The

individuals that are more “reactive” when watching yawning of conspecifics are not more reactive when exposed to other behaviors (Anderson and Matsuzawa 2006).

Observational surveys and experimental analysis of contagious yawning in humans has revealed occurrence in 65%–75% of the entire population. There is still no consensus as to whether women exhibit more contagious yawning than men (Gallup and Massen 2016). At any rate, individuals who conform spontaneously to normative social influence, and who are most receptive to advertising messages, also appear most susceptible to contagious yawning. People who scored higher on measures of empathy and mental state attribution skills were more likely to show contagious yawning (Palagi et al. 2014). These observational data, among others, are produced for linking contagious yawning and empathy.

How is contagious yawning triggered? Sight is a powerful stimulant. In spectators viewing a video showing 30 successive yawns, 55% will yawn within 5 min. The latency period varies from a few seconds to 5 min. There is no need for the face of the yawner to be in a precise visual plane relative to the subject receiving the contagion. Face to face, at 90°, 180°, and 270° relative to one another, replication occurs. The existence of a susceptibility to contagion among blind subjects confirms that sight is not the only trigger. Viewing only part of the face, such as a widely opened mouth, does not trigger replication. Therefore, a multimodal perception of the whole facial configuration and of audible respiratory moments is necessary for replication to happen, along with coordinated dynamics (Provine 1989). By animals as by humans, individual yawning in response to perceiving someone else yawn varies as a function of a host of variables that have yet to be clarified.

## The Neural Basis for Contagious Yawning

Contagious yawning is a primitive expression of cognitive processes involved in self-awareness

and theory-of-mind, that is, the capacity to build knowledge of mental states and to attribute them to others. In humans, contagious yawning first appears around 5 years of age, probably linked to the acquisition of a theory-of-mind. Humans who performed better at self-recognition and theory-of-mind exhibited more contagious yawning (Senju 2010). Yawning operates as a low-level form of nonconscious mimicry, which is necessary for involuntarily decoding the mental states of others, notably their emotions. The link between empathy and contagious yawning has empirical support but remains controversial (Massen and Gallup 2017). In line with this possible association, the empathic modeling hypothesis predicts that species that do not recognize themselves in mirrors and do not show evidence of mental state attribution ought to fail to show evidence of contagious yawning (de Waal and Preston 2017; Provine 2012).

Both developmental and neurophysiological research suggests that resonance between observed and executed actions is supported by the mirror neurons system (MNS). Brain areas that constitute the MNS, namely, the premotor area in the frontal lobe, the inferior parietal lobule, and the superior temporal sulcus, participate in the imitation of motor acts and expressions. These human mirror regions are homologous with area F5 of the ventral premotor cortex in macaques (Rizzolatti 2005). These regions are also interconnected with the insula and show activation in functional MRI studies of imitation, emotional states, and thus, empathy (Anderson and Matsuzawa 2006). The ventromedial prefrontal cortex also integrates affective signals to guide emotionally adapted behaviors. Thus, motor acts and affective states can transfer from a target to an observer in a bottom-up, goal-relevant manner through shared representations for perception and action. In this way, observing an affective posture or expression drives feed-back from peripheral motor representations to activate associated emotional states. Contagious yawning recruits brain areas that have been implicated in social cognition (empathy), self-processing, theory-of-mind, and

emotional contagion mechanisms (motor mimicry-MNS). Contagious yawning is the most basic expression of motor mimicry and emotional contagion, a rudimentary form of involuntary empathy (Brown et al. 2017; de Waal and Preston 2017). Whatever underlies contagious yawning, it does not appear to be based either on conscious imitation or higher-level, “conscious” empathy. Regardless, contagious yawning presents a powerful tool to explore the root of empathy in animal evolution (Provine 2014).

## An Error to Avoid

Equating physiological and communicative functions of yawning with non-social and social contexts, respectively, is inaccurate as both forms may occur in a social context. Indeed, ethological studies of nonhuman primates or South-African ostriches, for example, show that, at certain points, an entire group yawns. In this case, there is no contagious yawning but a synchronous behavior related to circadian rest-activity rhythms.

## Conclusion

Contagious yawning is an example where, through evolution, a behavior can be recycled for different purposes according to the increasing complexity of the central nervous system, correlated with the richness of social interactions. Yawning is managed by the phylogenetically oldest part of the brain, namely, the diencephalon and brainstem. Contagious yawning occurs by neocortex activation, which is necessary for the complex interactions of social life between individuals. It remains to be seen whether contagious yawning has any effect on the activity levels of other group members. Further research, especially in wild populations, should examine the regulating effect of yawning on synchronized group behavior in order to test its communicative function. Contagious yawning offers a neglected but fruitful avenue of investigation in the

growing fields of developmental, affective, and social neuroscience.

## Cross-References

- Contagion
- Emotional Contagion
- Empathy
- Grooming
- Imitation
- Sleep

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## Further Reading

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## Context-Dependent Strategies

### ► Facultative Polyandry/Strategic Pluralism

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## Contextual-Driven

### ► Top-Down Processing

Contingency

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Definition

In the area of learning theory, the term *contingency* refers to the extent to which the presence of an event (the *predictor* event) is associated with changes in the probability of occurrence of another event (the *outcome* event).

Main Text

Like correlation, the concept of contingency refers to the degree of covariation between two events. Although contingency can be measured in different ways, an extensively used index is  $\Delta P$  (Allan 1980), which measures the one-way dependency between two binary events. Specifically, for a predictor and an outcome that can be either present or absent this index is equal to the difference between the probability of the outcome event happening when the predictor event is present,  $P(\text{Outcome}|\text{Predictor})$ , and the probability of the outcome event happening when the predictor event is absent,  $P(\text{Outcome}|\sim \text{Predictor})$ :

$$\Delta P = P(\text{Outcome}|\text{Predictor}) - P(\text{Outcome}|\sim \text{Predictor}) \tag{1}$$

We can estimate these two conditional probabilities from our repeated experience with the presence or absence of each of the events. Since the two events are binary, there are four possible combinations: (a) both the predictor and the outcome events occur together, (b) the predictor occurs and the outcome does not, (c) the predictor does not occur and the outcome occurs, and (d)

neither the predictor nor the outcome occur. The frequency with which each of these four possibilities is experienced is typically summarized by constructing a contingency table (see Table 1). Once frequencies  $a$ – $d$  are gathered, the conditional probabilities from Eq. 1 are easily calculated. The  $P(\text{Outcome}|\text{Predictor})$  is calculated by dividing the amount of occasions in which both the predictor and event occurred ( $a$ ) by the total amount of times in which the predictor occurred ( $a + b$ ). Analogously, the  $P(\text{Outcome}|\sim \text{Predictor})$  is calculated by dividing the amount of occasions in which only the outcome occurred ( $c$ ) by the total amount of times in which the predictor did not occur ( $c + d$ ). Therefore, Eq. 1 can be rewritten as:

$$\Delta P = \frac{a}{a + b} - \frac{c}{c + d} \tag{2}$$

The  $\Delta P$  index can take any value between  $-1$  and  $+1$ . Positive values imply that the probability of the outcome event is higher when the predictor is present than when it is absent and, therefore, they are indicative of a positive statistical relationship. Negative values imply that the probability of the outcome is higher when the predictor is absent and they are indicative of a negative relationship. When the index takes a value of zero, the probability of the outcome is unaffected by the presence or absence of the predictor, that is, there is no statistical dependency between the two.

Robert A. Rescorla (1967, 1968, 1969) is known for stressing the central role of contingency in animal classical conditioning. He demonstrated that simple pairings of a neutral stimulus with an unconditioned stimulus did not suffice to guarantee that an association between the two would develop (note that in this context, the

**Contingency, Table 1** A contingency table depicting the four possible combinations of presence and absence of the predictor and the outcome

|            | Outcome | ~Outcome |
|------------|---------|----------|
| Predictor  | $a$     | $b$      |
| ~Predictor | $c$     | $d$      |



neutral stimulus acts as the *predictor* event and the unconditioned stimulus as the *outcome* event). According to the contingency approach to conditioning, for a neutral stimulus to develop an association with an unconditioned stimulus, the former must be able to predict changes in the probability that the latter will occur. That is, the contingency between the two must differ from zero. The greater the contingency, the stronger the expected associative strength. Moreover, the nature of the association will depend on the sign of the contingency: excitatory associations will form between stimuli for which the contingency is positive while inhibitory associations are anticipated if the contingency between the two is negative. In a series of classical fear conditioning experiments, Rescorla confirmed these predictions, showing that rats were sensitive to the programmed contingency both respect to excitatory (Rescorla 1968) and to inhibitory (Rescorla 1969) conditioning (see also Murphy and Baker 2004 for a more recent example of contingency sensitivity in an appetitive conditioning preparation). This general framework can also explain the basic features of several associative learning effects like extinction, latent inhibition, or delayed reinforcement, as they all refer to situations where conditioned responding becomes weaker as a result of degrading the contingency between the predictor event and the outcome event. In any case, the topic is not free of controversy, and some authors have questioned the relevance of contingency in classical conditioning (Papini and Bitterman 1990; but see Baker et al. 2001).

Several studies have shown that human causal learning is also influenced by the contingency between the event that is presented as the potential cause (the predictor) and the effect (the outcome). In causal learning studies, participants are typically presented with a computerized task that asks them to find out to what extent a causal relationship exists (e.g., to what extent a pill is effective in curing a certain disease). After being exposed to several trials in which the presence and absence of the potential cause and of the effect are combined, participants are commonly asked to rate the intensity of the causal relationship existing between the two by making use of a numerical scale. In these

experiments, causal ratings tend to be sensitive to the programmed contingency levels (e.g., Wasserman et al. 1993), although some consistent deviations from  $\Delta P$  are also observed. For instance, it has been observed that, for a given level of contingency, causal judgments tend to covary with both  $P(\text{Outcome})$  and  $P(\text{Predictor})$  (see Perales and Shanks 2007, for a review). Even in noncontingent situations, a conjunction of a high  $P(\text{Outcome})$  and a high  $P(\text{Predictor})$  tends to generate a strong impression of the predictor and the outcome being connected, giving rise to what researchers have called *illusions of causality* or *causal illusions* (see Matute et al. 2015, for a review).

## Cross-References

- Classical Conditioning
- Delay of Reinforcement
- Extinction in Learning
- Unconditioned Response
- Unconditioned Stimulus

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## Continuous Perception-Action Cycle

### ► Perception-Action Theory

## Continuous Signal

### ► Graded Signals

## Contrafreeloading

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## Introduction

Contrafreeloading (CFL) is the behavior shown when an animal prefers to work for food (“earned food”) rather than take identical food that is freely available from another, nearby source (“free food”); for reviews see Osborne (1977), Inglis et al. (1997). This term was coined by Jensen (1963) to describe his finding that rats choose to press repeatedly a foot pedal in order to obtain food rather than freely eat the same food from a bowl. This behavior is important because it appears to contradict several major theoretical frameworks (e.g., optimal foraging theory) that predict animals strive to maximize the ratio of reward, or benefit, to effort, or cost.

Since Jensen’s experiment, CFL has been demonstrated in many species of wild and domesticated mammals (e.g., rat, mouse, gerbil, pig, bear, wolf, macaque, chimpanzee, human) and birds (e.g., pigeon, chicken, jungle fowl, starling, crow) with only a very few species, e.g., the domestic cat, not showing this behavior. CFL has also been found when water rather than food is used and when the rewards are not nutritional (e.g., access to brief video clips, coins).

CFL has been most commonly studied by presenting the animal with a choice between free access to a bowl of food, and an operant task that provides response-dependent access to the same food. The schedule of reinforcement has varied between continuous reinforcement, fixed-ratio schedules, and variable-ratio schedules. Rather than have continuously available free food, some experiments have presented a choice between response-independent and response-dependent food. Nonoperant paradigms have also been employed, particularly when wild species were involved. For example, animals in mazes will take a long indirect way to food rather than a shorter direct route. They will also search or solve puzzles for food rather than take the same food from a bowl.

The criterion for a preference in CFL studies has been defined in various ways. In his review, Osborne (1977) concluded that a preference for a food source exists when the proportion of the total food obtained from that source exceeds 50% of the total food obtained during the session. However, there is no reason to suppose that 50% represents a magic point of discontinuity for the animal between “preference” and “non-preference.” Indeed as already mentioned, paradigms such as optimal-foraging theory predict there should be a total preference for the free food.

## Factors Affecting the Strength of CFL

### Training

The level of pretrial training in the response required to obtain the earned food significantly affects the subsequent level of CFL. During CFL the percentage of the pellets obtained that were

earned by, for example, bar pressing has been found both to increase and to decrease, with the number of rewarded responses made during training before the experimental trial. A possible explanation for these contradictory results is discussed later. Although prior training clearly affects the level of CFL, convincing evidence that CFL cannot solely be a function of training comes from the many experiments showing that it can be acquired and maintained when there is both no training in the response required and continuous access to free food.

### Deprivation Level

Animals do not have to be hungry in order to show CFL: many studies have found high levels of such behavior under conditions of zero deprivation. In addition animals often do not eat all of the pellets they obtain by working. Rather it has been shown that increasing hunger decreases CFL. Since hunger will decline throughout the trial, as a result of the uptake of food, the within-trial changes in the proportion of food obtained by CFL also shed light on the effect of hunger level. It has generally been found that CFL is lowest at the beginning of the trial and then increases over the trial as hunger level falls.

### Effort Required

Increasing the effort required to obtain the earned food (e.g., by raising the number of lever presses required for each pellet of food delivered) reduces CFL. However, it is not just the effort required to obtain the earned food that is important. Mitchell et al. (1982) compared the level of CFL in rats when the free food was placed in either a tall dish, which necessitated the animals climbing up the sides, or a short dish, which required no climbing. The rats with the tall free-food containers showed the greater CFL. The relative effort required to eat at the two food sources is the important factor.

### Rearing Conditions

Animals reared under sensory deprivation, or maintained under it for a long period of time during adulthood, explore more when faced with

a novel object than do animals kept under sensory enriched conditions. Similarly rats reared under conditions of sensory impoverishment show more CFL than those reared under sensory enriched conditions. Clear evidence of a link between exploratory behavior and CFL comes from the study of Nau et al. (1981). Three groups of rats were reared under different sensory conditions and then tested in a novel maze as well as under the CFL paradigm. As with the earlier studies, the rats reared under sensory enriched conditions showed the least CFL, but, in addition, it was found that the animals showing the most exploration in the maze were also those that exhibited the highest level of CFL.

### Stimulus Change

CFL is strongly affected by stimulus changes correlated with the presentation of the earned food. If visual and/or acoustic stimuli normally associated with the delivery of the earned food are removed, then CFL falls to near zero, and it recovers when these stimuli are reinstated. Working for earned food in the absence of associated stimulus changes is not sufficient to maintain CFL in an operant situation. However, it has also been found that response-produced stimulus change alone is not sufficient to maintain responding in the presence of free food. Animals work for their food only when the operant responses produce both food and stimulus change.

The degree of response-contingent stimulus change influences the level of CFL. For example, following a condition in which no stimulus was contingent upon obtaining earned food, and where there was negligible CFL, Osborne and Shelby (1975) paired the presentation of the earned food with an acoustic stimulus for one group of rats and with a visual stimulus for another group. The addition of the stimuli greatly increased and maintained CFL. When both groups later received both auditory and visual stimuli, responding was enhanced above the level of CFL maintained by either stimulus alone. It has been found that most CFL occurs when the stimuli associated with the earned food are neither very familiar nor very novel.

### Environmental Uncertainty

CFL is found in nonoperant paradigms that lack a clear response-contingent stimulus as long as uncertainty is associated with the food-gathering task. For example, in the experiment of Havelka (1956), rats entered a long goalbox containing eight alcoves arranged in two groups of four. In the group of alcoves near the entrance to the goalbox, the food was always placed in the same alcove, the “constant dish.” The other group of four alcoves was at the far end of the goalbox, and here which alcove contained the food was randomly chosen on each trial, the “variable dish.” Rats passed the first set of alcoves, ran down the goalbox, and searched the second set for the variable dish. However, when the variable dish was then kept in the same alcove on each trial, the rats shifted their preference to the dish in the set of alcoves nearest the goalbox entrance. When the uncertainty over the location of the variable dish was removed, CFL ceased. Similarly in the study of Forkman (1996), gerbils were given a choice between foraging in a site with easily accessed food, or from a site requiring a lot more work. When the amount of food available at both sites could be immediately and easily accessed, the animals preferred the most profitable food source. However, when uncertainty was associated with the least profitable food source, i.e., the food there was hidden under lids or was camouflaged, then the animals choose to work at this site. Bean et al. (1999) obtained supporting results from similar experiments conducted with starlings. They concluded that CFL is reduced when there are ways to gather information about the food patches other than by working for the food.

### Explanations for CFL

In their review, Inglis et al. (1997) concluded that, in addition to training, there were three major factors that controlled the level of CFL. First, most CFL occurs when the stimuli associated with the earned food are neither very familiar nor very novel. Second, CFL declines with increasing hunger. Third, an increase in effort to

obtain the earned food relative to the free food reduces CFL. They developed a mathematical model to simulate interactions between these factors and found it was able to account for the majority of the results published in the CFL literature. This still, of course, does not answer the question why do animals show CFL, particularly in the absence of any training?

### Training Effects

The effect of training on CFL could be the result of neophobia towards the free-food container since, while the animals had received operant training before the test, they had no prior experience of the free-food container. Mitchell et al. (1973) found that CFL was indeed negatively correlated with the familiarity of the free-food container. However, neophobia towards a novel free-food container should be greatest at the beginning of a trial and then gradually decline, and yet, as already mentioned, most feeding from the free-food container takes place at the start of the trial rather than at the end. Also this hypothesis cannot account for the CFL found in experiments where there was equal exposure to both food sources.

Two explanations have been proposed to explain why response-contingent stimulus change affects CFL. The first argues that after its repeated pairing with food presentation during training, the stimulus change becomes a secondary reinforcer. Clearly this explanation cannot account for the CFL that occurs in the absence of any training. The second explanation is that the response-contingent stimulus change is reinforcing in its own right. There is an established body of literature demonstrating that satiated animals will work solely to experience simple stimulus changes (e.g., see Kish 1966) and thus during CFL the animal is not working for food alone but for food plus sensory reinforcement. The combined reinforcement is thought to be sufficient to maintain responding for earned food in the presence of free food (Osborne and Shelby 1975). This explanation can account for CFL in the absence of training since the stimulus change should be effective from the outset.

As already mentioned, CFL has been found both to increase and to decrease with increasing numbers of training trials. If CFL is the result of sensory reinforcement, then it should decline with increasing number of training trials because greater satiation to the response-contingent stimulus change will occur. On the other hand, if secondary reinforcement is the main causal factor, then increasing the pairings between stimulus change and earned food during training will increase CFL. These two explanations are not mutually exclusive. The number of training trials will determine which effect dominates during the test period. With only a few or no training trials sensory reinforcement effects will dominate since there will be too few pairings of the stimulus change with earned food to establish it as a strong secondary reinforcer. As the number of training trials increases, there will be greater satiation of the sensory reinforcement effect and strengthening of the secondary reinforcer effect.

### **The Response Used to Obtain the Earned-Food is Self-Reinforcing**

It has been suggested that CFL occurs because the performance of the task required to obtain the earned food is reinforcing in its own right. This intrinsic reinforcement is thought to arise when the task is part of innate behavior patterns connected with appetitive and/or consummatory acts. For example, the domestic pig does not show CFL when tested using an operant response in a controlled environment, but it does when a more natural foraging task is required to obtain the earned food. However, this explanation cannot explain why, in many other species, CFL does occur when the action required to obtain the earned food involves behaviors that are not natural and have to be learned. Also CFL is found where the same behavior is required to get both earned food and free food. More importantly, as already discussed, animals stop CFL as soon as the behavioral response no longer produces the earned food, suggesting that just performing the act itself is not reinforcing. Forkman (1993) explicitly investigated this question. One group of gerbils were, for 20 min

per day for 5 days, given access to a cage containing a bowl of sunflower seeds and a bowl containing sand plus 30 sunflower seeds. After 5 days, the procedure was repeated with the cage containing a bowl of sunflower seeds and a bowl of just sand. The treatments were reversed for another group of gerbils. It was found that for both groups practically all digging took place in the bowl with 30 seeds. When this bowl contained just sand digging fell dramatically and there was no compensatory digging elsewhere in the cage. Clearly the digging per se was not self-reinforcing.

### **Competence Theory**

Some authors have explained CFL in terms of White's Competence Theory. White (1959) argued that behavior is primarily directed towards manipulating and controlling the environment and that such behavior is self-reinforcing. This theoretical position has more recently been restated in the concept of animal agency, i.e., that the animal is an active agent continually seeking to deal effectively with its environment (e.g., Wemelsfelder and Birke 1997). In the CFL paradigm, obtaining the earned food usually involves greater environmental manipulation than simply taking the free food from a dish. If this hypothesis is correct then animals should prefer to work for response-dependent food rather than take response-independent food delivered at the same rate. The studies of Singh (1970) and Morgan (1974) found that this was indeed the case. However, while it has been shown that animals give priority to being able to exercise control over minimizing effort, it is not clear how Competence Theory can account for the relationship between CFL and hunger and that between CFL and uncertainty associated with the earned food. It does also not explain why CFL can occur when the same behavior is required to obtain both free and earned food.

### **Information-Primacy Hypothesis**

Inglis et al. (1997) suggested that CFL is a form of self-reinforcing exploration and as such it could be explained in terms of the information-primacy

hypothesis (Inglis 1983, 2000). This argues that in complex and stochastic environments the ability to cope with the unexpected is essential for survival and that in order to deal with uncertainty the animal constructs models of its environment that enable predictions to be made. Such models require constant update and thus the continual gathering of information about uncertain events is vital for animals living in such environments. This ongoing behavior forms a substratum upon which other, more obviously goal directed, behaviors occur. Only when need states, like hunger, become intense enough to interrupt the information-gathering behavior do animals focus exclusively upon fulfilling those needs. Thus, in CFL animals work for the earned food partly for the food itself and partly to improve and update their estimate of the profitability of an uncertain food source that may unpredictably become the optimal place to feed. This explanation can account for the facts (a) that, in the absence of training, CFL only happens if some uncertainty is associated with obtaining the earned food, (b) that CFL declines with increasing hunger, and (c) that there is a correlation between CFL and intrinsic exploration.

Bean et al. (1999, with starlings) and Lindqvist et al. (2002, with jungle fowl and domestic fowl) tested whether animals used any information they may have gained while CFL to inform future foraging decisions. When the birds were presented with food patches containing different amounts of food mixed with filler, they showed CFL by feeding at the less profitable patches. After being food deprived, the birds were again presented with the patches but with the most profitable patch removed. They reliably choose the second best patch on the first approach.

Inglis et al. (1997) suggested that if CFL occurs in order to gain information about uncertain food patches, then it should be weak in a species whose environment does not necessitate searching for unpredictable food items. Domestic animals usually live under such conditions and Lindqvist et al. (2002) have reported that domesticated strains of fowl do indeed show less CFL than does the wild jungle fowl.

## Conclusion

Working for food when the same food was freely available nearby was initially regarded as a strange behavior shown by laboratory rats and pigeons that arose as a result of procedures adopted during the training of the operant responses required to obtain the earned food. However, subsequently it was found that a large number of wild species showed CFL when tested under a wide range of naturalistic experimental situations that did not require any training. CFL is now regarded as a normal behavior that sheds light on the ways animals cope with surviving in variable and unpredictable habitats.

Situations that allow animals to show CFL are increasingly used to improve the welfare of captive animals. Many studies have demonstrated that inadequacies in the captive environment (e.g., impoverished sensory surroundings) result in poor animal welfare, as shown by abnormal behaviors and negative psychological states such as stress. Environmental enrichment can reduce, and prevent the development of, poor welfare and giving captive animals opportunities to show CFL, for example, to search for their food rather than simply have it presented to them in a trough, has become one of the main forms of such enrichment.

## Cross-References

- [Animal Welfare](#)
- [Neophobia](#)
- [Operant Chamber](#)
- [Operant Conditioning](#)
- [Optimal Foraging Theory](#)
- [Reinforcement](#)

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## Contrapreparedness

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## Introduction

What does the term contrapreparedness mean? Martin Seligman introduced the term in his 1970 *Psychological Review* article. According to Seligman, animals have an evolutionary preparedness to associate some stimuli with a biological significant event or an unconditioned stimulus, but that other associations cannot be learned. In Seligman view, the concept of **contrapreparedness** refers to the fact that some stimuli, despite repeated pairings, cannot become associated with a specific unconditioned stimulus. The likelihood that a particular neutral stimulus will become able to elicit a conditioned response after pairing with an unconditioned stimulus reflects the salience of the neutral stimulus. Seligman proposed that preparedness makes a stimulus more salient, while contrapreparedness make a stimulus less or non-salient. In other words, salient stimuli rapidly become associated with a particular unconditioned stimulus, while nonsalient stimuli do not, despite repeated pairings, become associated with that unconditioned stimulus.

William Timberlake in 2001 suggested that the variations in what an animal can learn reflect either to predispositions or constraints. A predisposition refers to instances in which an animal learns more rapidly or in a different form than expected. Timberlake suggests that predispositions occur when environmental circumstance easily modifies the instinctive behavior system that the animal brings into the situation. Variations in learning also can reflect the impact of a constraint on learning; a constraint occurs when an animal learns less rapidly or less completely than expected. According to Timberlake, constraints on learning occur when environmental circumstance is not suited to the animal's instinctive behavior system. Several examples of contrapreparedness are presented in the next several paragraphs.



## Stimulus Salience

John Garcia examined the relative salience of stimuli paired with illness and electric shock. In the classic study by Garcia and Koelling in 1966, rats received either a saccharin taste cue or a light and tone compound stimulus. Following exposure to one of these cues, the animals received either an electric shock or irradiation-induced illness. Garcia and Koelling found that rats exhibited an aversion to saccharin when it was paired with illness but not when it was paired with shock. In addition, they developed a fear of the light and tone stimulus when it was paired with shock but not when paired with illness. Based on the results of this study, rats seem contraprepared to associate a taste cue with an electric shock or a light-tone stimulus with illness.

In his 1970 article, Seligman suggested that rats have an evolutionary preparedness to associate tastes with illness. This view is consistent with the observation that adult rats acquire an intense aversion to a flavor after a single taste-illness pairing. My colleagues and I also found that young rats also acquire a strong aversion after one pairing (Klein et al. 1975). Apparently, taste cues are very salient in terms of their associability with illness.

Seligman also proposed that rats are contraprepared to become afraid of a light or tone paired with illness. My colleagues and I did observe that animals avoided a distinctive black compartment previously paired with an illness-inducing apomorphine or lithium chloride injection (Klein et al. 1985). It should be noted that environmental events (distinctive places) are not very salient when paired with illness as many trials and careful training procedures are necessary to establish an environmental aversion unlike the single-trial learning of a flavor aversion (Riccio and Haroutunian 1977). It would seem that rats are contraprepared to associate a distinctive environment with illness.

It should be noted that while rats form flavor aversions much more readily than environmental aversions, other species do not show this pattern of stimulus salience. Unlike rats, birds acquire aversions to visual events significantly more

rapidly than they do taste aversions (Wilcoxon et al. 1971). Braveman (1974, 1975) suggested that the feeding time of a particular species determines the relative salience of stimuli becoming associated with illness. Rats, which are nocturnal animals, locate their food at night and therefore rely less on visual information than on gustatory information to identify poisoned food. In contrast, birds search for their food during the day, and visual information plays an important role in controlling their food intake.

## Species-Specific Defense Reactions

How quickly can an animal avoid adversity? Robert Bolles (1970, 1978) proposed that animals have little opportunity to learn a new behavior to avoid aversive events. Animals either possess instinctive means of avoiding danger, which he calls species-specific defense reactions or they perish. A deer does not have time to learn to avoid its predator. Unless the deer possesses an instinct for avoiding predators, it will probably wind up as a predator's meal. Bolles found that animals easily learn to run, a species-specific defense response, to avoid being shocked. Similarly, pigeons easily learn to avoid shock by flying from perch to perch. In contrast, animals have great difficulty learning to avoid an aversive event using a non-species-specific defense response to avoid an aversive event. For example, D'Amato and Schiff (1964) reported that over half their rats, even after having participated in more than 7000 trials over a 4-month period, failed to learn to bar press to avoidance shock.

Contrapreparedness also has been found to influence the acquisition of defensive behaviors in humans. Barbara Fredrickson's (2003) broaden and build theory suggests that positive emotions expands a human's attention and allows an individual to acquire new behaviors to obtain reinforcement. By contrast, negative emotions restrict a human's attention and limit one behavioral repertoire to very limited survival-oriented actions. Just as was true of Robert Bolles' species-specific defense reactions, humans are contraprepared to acquire new ways of avoiding aversive events.

## Animal Misbehavior

The research of Keller and Marion Breland suggests that contrapreparedness also influences whether or not an animal is able to learn an operant behavior to obtain reinforcement. Breland and Breland (1961, 1966) were able to use food reinforcement to operant condition a number of unusual behaviors such as a racoon putting a coin in a "piggy bank" or a rabbit playing a piano. However, the Brelands observed that some operant responses, although initially performed effectively, deteriorated with continued training despite repeated food reinforcements.

The Breland's suggested that the elicitation of instinctive food-foraging and food-handling behaviors caused by the presentation of food reinforcements lead to the decline of an operant response. These instinctive feeding-and-foraging behaviors were strengthened by food reinforcement and eventually prevented the operant behavior. They called the deterioration of an operant behavior with continued reinforcement instinctive drift, and the instinctive feeding-and-foraging behaviors that prevented the operant response an example of animal misbehavior.

Animal misbehavior is an example of contrapreparedness preventing an appetitive operant appetitive response. One example of animal misbehavior is described next. Breland and Breland (1961) attempted to train pigs to pick up a large wooden coin and deposit it in a "piggy bank" several feet away. Each pig was required to deposit four or five coins to receive one reinforcement. According to Breland and Breland, "pigs condition very rapidly, they have no trouble taking ratios, they have ravenous appetites (naturally), and in many ways are the most trainable animals we have worked with" (p. 683). Each pig exhibited an interesting pattern of behavior during conditioning. At first, the pigs picked up a coin, carried it rapidly to the bank, deposited it, and readily returned for another coin. However, over a period of weeks, the pigs' operant behavior became slower and slower. Each pig still rapidly approached the coin, but rather than carry it immediately over to the bank, the pigs "would repeatedly drop it, root it, drop it again, root it along the

way, pick it up, toss it up in the air, drop it, root it some more, and so on" (p. 683).

Why did the pigs' operant behavior deteriorate during conditioning? The Brelands suggested that the presentation of food during conditioning not only reinforced the operant response, it also elicited instinctive food-related behaviors. Food reinforcement strengthened these instinctive food-gathering and food-handling behaviors, which resulted in the deterioration of the pigs' operant depositing response. The more dominant the instinctive food-related behaviors became, the longer it took for the operant response to occur. The slow deterioration of the operant response during conditioning is an example of contrapreparedness preventing the conditioning of the operant behavior (depositing the coin in the bank).

## Conclusion

The concept of contrapreparedness refers to the fact that some stimuli, despite repeated pairings, cannot become associated with a specific unconditioned stimulus. Contrapreparedness make a stimulus less or nonsalient and nonsalient stimuli do not, despite repeated pairings, become associated with that unconditioned stimulus. Contrapreparedness also prevents the learning of defensive behaviors to avoid adversity or when instinctive feeding and foraging behaviors interfere with the acquisition of appetitive operant behavior.

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## Contrast Effects

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## Synonyms

[Behavioral contrast](#); [Crespi effects](#); [Frustration effects](#)

## Definition

In associative learning, contrast effects are changes in the strength of a subject's response in one context following a change in the reinforcement of that response in another context. An increase in response strength in one context

following a decrease in reinforcement rate or power of that same response in a second context is known as positive contrast. Negative contrast is a decrease in response strength in one context following an increase in reinforcement rate or power of that response in another context.

## Introduction

The first experiment to systematically demonstrate contrast effects was conducted by Leo Crespi in 1942. Crespi measured the running speed of three groups of rats down an alley to rewards of 1, 4, or 16 pellets. He then changed the reward for the first two groups to match that of the third, namely, 16 pellets. Crespi found that rats in the original four-pellet group ran faster than rats that started with 16 pellets, and that rats in the one-pellet group ran faster than rats in the four-pellet group. This increase in speed was positive contrast resulting from a shift in the amount of reward given for the running behavior. A second experiment by Crespi demonstrated negative contrast. Rats began by running to rewards of 16, 64, or 256. The latter two groups were then switched to a 16-pellet reward. As Crespi predicted from his first experiment, he found that rats in the latter two groups ran more slowly once the reward amount shifted, with the 64-pellet group running slower than the 16-pellet group, and the 256-pellet group running slower than the 64-pellet group. Crespi concluded that these behavioral response shifts could be attributed to an “expectation” of reward coupled with an emotional response. Subjects who found the magnitude of the reward to be greater than expected experienced an elation effect, while subjects who found a lower magnitude of reward than expected experienced frustration.

## Explaining Contrast

While the exact cause of contrast effects has been debated, several studies seem to support the notion that contrast effects are mediated by emotion or psychological state. Smaller contrast

effects are seen, for example, under the effects of barbiturates (Ridgers and Gray 1973). As well, animals that have experience in situations that may produce frustration, such as reward delays (Ferrel and Shanab 1975) or shock punishment training (Rosellini and Terris 1975), exhibit lower levels of contrast. However, developing formal theories to explain contrast is difficult, since learning theory avoids explanations that involve subjective inner motivations, such as emotion.

### Demonstrating Contrast

Two ways of demonstrating behavioral contrast have been explored. In one demonstration, known as simultaneous contrast, two stimuli are presented concurrently, and a change in the reward of one stimulus results in a change in response to the second stimulus. For example, Reynolds (1961) trained pigeons to key peck at a red or green light, which both produced the same reward. He then shifted the green light to an extinction schedule, so that pecks to that light no longer produced a reward. He found a positive shift in response to the red light. In other words, when pecks to the green light no longer produced a reward, pecks to the red light increased, despite no change in reward for the red light.

The second method of demonstrating contrast is to change the reinforcement for a certain task after a period of learning. In this kind of experiment, the shift in context is just a change in time, and this type of effect is known as successive contrast. For example, Crespi's (1942) rats were first receiving four pellets, and then were shifted to 16, causing an increase in running speed. This increase was a positive contrast effect associated with the change in time, since at an earlier period subjects were receiving a lesser reward.

In both of the above examples, subjects are discriminating between two contexts: stimuli color in the first, or time in the second. Discrimination is a necessary component of contrast, and contrast can be used as a measure of a subject's ability to discriminate between stimuli or contexts.

### Ceiling Effects

In experiments that produce contrast effects, negative contrast is often more marked and easier to measure. A subject may only respond so strongly or frequently to a stimulus. Therefore, increases in response, as seen in positive contrast, may hit a ceiling. Bower (1961) first hypothesized this ceiling. In his experiment, rats ran down one of two runways distinguished by the color of their walls. Down one runway, subjects would find a reward of eight pellets, but down the other, they would find one pellet. Two control groups ran as well, with one group only ever receiving one pellet, and the other receiving eight pellets at the end of their runways. Bower found that while subjects that originally ran the eight-pellet runway slowed down when placed in the one-pellet runway, running significantly slower than the one-pellet control group, no effect was found for subjects who switched from the one-pellet to the eight-pellet runway when compared to the eight pellet control group. He proposed that subjects in both the control and experimental groups must have run at their maximum speed for such a large reward. Experimenters must, therefore, consider such response ceilings when attempting to provoke a positive contrast effect.

### Variables Affecting Contrast

Several aspects of an experiment may affect the magnitude of behavioral contrast obtained. Greater disparities between the rewards in the two different contexts can produce greater disparities in response to those contexts. As well, motivation can affect contrast; subjects that are food deprived show higher levels of behavioral contrast than less food-motivated subjects (Cleland et al. 1969; Ehrenfreund 1971; Flaherty and Kelly 1973). In successive contrast experiments, the amount of time in between the presentation of one context and the next will affect contrast effects. For example, if subjects are presented with a smaller reward first, and then shifted to a larger reward, the amount of time in between the smaller reward presentation and the larger reward

presentation will influence behavioral contrast. Longer intervals result in smaller contrast effects (Gonzalez et al. 1973).

## Conclusion

The debate over what causes behavioral contrast continues in the field of associative learning. Several explanations, including frustration and expectation, have been offered. What is clear is that, as in other areas of learning, context is key. Behavioral contrast can only be produced when a subject is able to distinguish between contexts. Contrast effects, therefore, continue to be important and oft-used measures of discrimination and reinforcement in animal learning experiments.

## Cross-References

- [Acquisition](#)
- [Discrimination Learning](#)
- [Reinforcement](#)
- [Schedules of Reinforcement](#)

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## Contrition

- [Shame and Guilt](#)

## Control

- [Restraint](#)

## Convergent Evolution

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## Definition

**Convergent Evolution:** Convergent evolution is the process by which phylogenetically unrelated species have similar adaptations as a result of similar environmental pressures.

## Introduction

*Convergent evolution* involves different lineages independently evolving similar traits. This is the result of different species experiencing similar environmental pressures. If two distinct species live in similar environments, it is reasonable to predict that they will experience similar selection pressures and thus evolve similar traits. These species will possess the same adaptive solution to a shared environmental obstacle to reproductive success, despite their ancestral lineages

having different attributes and genes (Alcock 2013). Unrelated species should behave differently, unless they have experienced similar selection pressures. The opposite of convergent evolution is *divergent evolution*, by which related species evolve dissimilar traits due to variations in their environments, thus resulting in different selection pressures and adaptive solutions.

Convergent evolution can occur at the structural and functional level. Structures that are the result of convergent evolution are called *analogous structures*. On the other hand, a *homologous structure* would have a common origin. Analogous structures refer to unrelated organisms having structures that have the same function but are anatomically different. These similar characteristics were not present in their common ancestor, and the larger the phylogenetic separation of the two species, the more likely the shared trait is due to convergence (Papini 2002). As these adaptations have evolved separately among distantly related species, any similarities can be attributed to shared environmental selection pressures and not characteristics that were present in a common ancestor (Ridley 1993). Convergence can occur in various combinations of structure and function. It can occur at the functional level but not structural and can also occur in structure as well as function.

## Functional Convergent Evolution

Convergence can occur on the level of function, but not structure, as exemplified by flight (Seed et al. 2009). Insects, birds, pterosaurs, and bats all evolved the capability of flight (i.e., the function), while their structures for flight are anatomically different. None of these species are closely related phylogenetically; nevertheless, they evolved the similar function of flight. The structures and mechanisms used to achieve the behavioral outcome of flight are also very different. The wings of an insect are very different than those of a bird or a bat. In birds, flight evolved through the extension of the forelimb bones. However, in bats and pterosaurs, the wing is supported by extended digits. The fifth digit is extended in pterosaurs,

whereas the second, third, fourth, and fifth digits are extended in bats. The convergent evolution of wings for flight are the result of the functional constraints of flight in addition to environmental selection pressures (Van Horik et al. 2012). Each species has a mechanically different method to achieve the same function of flight.

## Convergent Evolution at the Structural and Functional Level

Convergence can also occur at both the structural and functional level, meaning that two independent lineages may evolve the same structure for the same function. This can be seen in distantly related marine mammals. Seals and whales both evolved short-wavelength colorblindness, which is adaptive for sight in the marine visual environment in coastal marine mammals. The colorblindness was achieved similarly with both species losing S-opsin cones in the retina (Peichl et al. 2001). These two distantly related groups of marine mammals converged in having the same structure for the same function of short wavelength colorblindness.

Another interesting example of convergent evolution lies with lamnid sharks, the most popular being the great white and the mako, and tunas. It has been established that hydromechanical and physical selection pressures were important in the evolution of thunniform body shapes in several groups of vertebrates, including whales, ichthyosaurs, and some species of large pelagic, or open ocean, fish. However, in lamnid sharks and tunas, the convergence is furthered as they possess morphological and functional adaptations that are unlike other fishes (Donley et al. 2004). The thunniform body shape that both tunas and lamnid sharks possess exhibits the least undulatory mode of locomotion. The two species' evolutionary pathways converged on the same mechanical design principle (Donley et al. 2004). Both lamnid sharks and tunas have internalized red muscle, which is associated with a force-transmission system (Donley et al. 2004). This morphology transmits forces posteriorly allowing for their thunniform swimming mode. These shared



characteristics most likely evolved due to the selection for continuous and fast movement. Not only are the bodies of large pelagic cruisers shaped by their environments but their morphology and internal physiology is also shaped. The convergence between lamnid sharks and tunas is a good example of convergent evolution occurring at both morphological and functional levels in two distinct species.

## Behavioral Convergent Evolution

Convergent evolution can also be observed in behavior, whereby similar selection pressures in two separate species results in similar behaviors as an adaptive response to the environment. Mobbing behavior in different species of birds is a good example of behavioral convergence. Both ground-nesting gulls and bank swallows along with other colonial swallows, exhibit mobbing behavior (Sordahl 2004). Gulls and swallows are in two different taxonomic families, the Laridae and the Hirundidae. The common ancestor of gulls and swallows lived eons ago, as exemplified by the distinct taxonomic differences. Bank swallows are distinct from gulls genetically and evolutionarily; however, they exhibit similar nesting behaviors. Both bank swallows and gulls nest in colonies where blue jays and predatory snakes feed on nestlings and eggs (Hoogland and Sherman 1976). Due to the similar selection pressures experienced by bank swallows and gulls, they have developed similar mobbing behaviors. The birds swirl and dive at their predators, which distracts the snakes and blue jays from attacking and killing their offspring, thus increasing their reproductive success. Both bank swallows and gulls, although genetically and phylogenetically distinct, have evolved similar behaviors as an adaptive solution to the shared environmental problem of predators destroying their offspring.

Colonial nesting mammals have also developed mobbing behavior in response predators, another example of convergent evolution. California ground squirrels are group living and burrow into the ground. They react to a hunting rattlesnake by surrounding it and shaking their

infrared emitting tails. If the snake does not retreat, they will kick sand in its face, making it difficult for the snake to hunt and often resulting in the rattlesnake retreating (Owings and Coss 1977). Mobbing appears to have evolved as an antipredator adaptation. It appears in a variety of species through convergent evolution as an adaptive solution to predators that attack and destroy offspring.

## Cognitive Convergent Evolution

Convergence not only occurs at structural, functional, and behavioral levels but can also occur at the cognitive level. Distantly related species that experience similar socio-ecological problems will develop similar adaptive traits to handle these problems. At first glance, corvids (crows, jays, and rooks) and parrots seem to have little in common in proportion to body size as apes (Van Horik et al. 2012). Both have large encephalization quotients, which is the brain-to-body ratio, meaning their brains are large relative to their body size. Additionally, the relative size of the forebrain in corvids and parrots is much larger than other birds (Emery and Clayton 2004). Corvids and parrots also demonstrate cognitive abilities similar to large-brained mammals such as primates, cetaceans, and elephants. Whereas the structure of avian and mammalian brains differ, they share advanced cognitive abilities (Emery and Clayton 2004). For example, in the mammalian brain, the neocortex mediates cognitive processes such as, social intelligence, memory, reasoning, and concept formation. However, in the avian brain, there is no neocortex and these processes have been found to be associated with the forebrain. These areas are analogous to the prefrontal cortex in mammals (Van Horik et al. 2012). One of the important components of the evolution of intelligence is thought to be sociality (Van Horik et al. 2012). Complex social interactions have been observed in primates (De Waal 1982), cetaceans (Marino 2002), and corvids (Emery et al. 2007b). As these species are all social living and demonstrate complex social behaviors, a theory of convergence of social cognition is supported.

A term dubbed “chimpanzee politics” has been used to describe the sophisticated social interactions of primates (De Waal 1982). As social-living species, they often forage together in the same areas for the same resources, which can result in direct competition or cooperation. Cetaceans and primates are capable of complex cooperative actions. They create cooperative coalitions among males and also exhibit alloparental care. In primate species, chimpanzees will baby-sit juveniles to protect them from predation (Nicolson 1986). Bottlenose dolphins (Brown and Norris 1956; Herzing and Johnson 1997), spinner dolphins (Norris and Johnson 1994), Atlantic spotted dolphins (Weinpress and Herzing 2015), sperm whales (Whitehead 1996), and other cetaceans also exhibit alloparental behavior.

Primates and cetaceans also exhibit cooperative behavior in their feeding strategies. Chimpanzees exhibit a cooperative hunting strategy when preying on red colobus monkeys (Boesch 1994). The chimpanzees coordinate their behavior in order to successfully hunt and capture their prey. Killer whales have been observed to cooperate and coordinate their behavior while feeding on herring (Similä 1997), and Humpback whales exhibit cooperative bubble net feeding (Jurasz and Jurasz 1979), in addition to other examples in cetaceans. The sociality in these species has led to advanced social cognition, which can be observed in their alloparental behavior and cooperative feeding strategies.

In addition to sharing patterns of social behavior such as cooperation during alloparenting and feeding, cetaceans and primates provide the strongest evidence for social convergence (Marino 2002). Although birds and elephants may also possess culture, the transmission of nongenetic information across generations, the most evidence appears to be in primate and cetacean species. Primates and cetaceans transmit behavioral traditions, such as tool creation and use, across generations. In primates, chimpanzees (Boesch 1994; Whiten et al. 2005) and Japanese macaques (Huffman 1996) have been observed to transmit information about tools. Tool use by means of sponge carrying has also been observed and transmitted across generations in bottlenose dolphins

(Smolker et al. 1997). In a nonmammalian species, tool use has been observed in New Caledonian crows that use and transport tools they have created for their daily foraging expeditions. They also change the tools depending on the functional requirements (Hunt 1996). However, tool use in birds may be functionally limited, as they possess a multifunctional beak that can often act as a tool itself (Van Horik et al. 2012). In addition to tool use in cetaceans, there are cultural traditions with dialects (Whitehead 1998) and prey capture in bottlenose dolphins (Petricig 1993) among other social behaviors.

There is no doubt that sociality in these species presents certain selection pressures that led to convergence of behaviors. Many species of cetaceans and primates live in fission-fusion societies and face challenges with adjusting to dynamic social changes. Some species of birds also, such as rooks, exhibit high levels of sociality similar to chimpanzees and cetaceans (Van Horik et al. 2012). However, some species of birds that exhibit high sociality do not live in fission-fusion societies as they are monogamous maters. This suggests that the social intelligence in these birds may have evolved as a response to the maintenance of social relationships and cooperative behavior between monogamous mates (Emery et al. 2007b). Additionally, the largest relative brain size in birds are found in the long-term monogamous and cooperative breeding species (Emery et al. 2007a).

## Conclusion

Convergent evolution occurs on many levels, structural, functional, and behavioral. These levels are not mutually exclusive, nor do they always occur together. As discussed, convergent evolution occurs when distinct lineages evolve similar traits due to similar environmental pressures. The distinct lineages face similar adaptive problems and thus evolve similar adaptive solutions in order to further their reproductive success. It is worth noting that evolution is not forward thinking – these adaptations develop as the result of selection pressures, whereby the trait that

promotes survival to reproductive age is favored by selection. When species have similar environments, they experience similar adaptive problems, leading to similar adaptive solutions. As reviewed here, convergent evolution can occur at the structural and functional levels, for example, short wavelength colorblindness in seals and coastal whales (Peichl et al. 2001). These two distinct species have evolved the same structure for the same function. It can also occur at the functional level without structure, as exemplified by flight in birds, pterosaurs, and bats (Seed et al. 2009). Lastly, convergent evolution can also be observed in behavior and cognition. Differing species of birds, bank swallows and gulls, exhibit mobbing behavior as an antipredator defense (Sordahl 2004). Sociality in large-brained mammals and corvids also presents interesting selection pressures allowing for cultural transmission of dialects and tool use along with social intelligence (Marino 2002; Van Horik et al. 2012). Convergent evolution is a comparative method that can be used to examine similar traits across a variety of different lineages and can help the understanding of the different or similar selection pressures species have faced over their evolutionary history.

## Cross-References

- [Coevolution](#)
- [Divergent Evolution](#)
- [Niche Divergence](#)
- [Phylogeny](#)

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## Coolidge Effect, The

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## Synonyms

Male sexual refractory period; Parental investment theory; Sperm competition

## Definition

A phenomenon occurring in the males of some sexually reproducing species wherein post-copulatory sexual arousal may be reignited if the male is presented with new sexual partners.

The Coolidge effect is a phenomenon observed in some sexually reproducing animals in which sexual arousal is reignited by novel sexual stimuli. The term was first coined by Frank A. Beach (Beach and Jordan 1956) and refers to a story involving US President Calvin Coolidge and his wife.

After completing sexual intercourse with a female, males will often experience a refractory period, during which they are unable to engage in sexual activity. One evolutionary explanation for the refractory period is that it prevents males from displacing their own semen from the female's reproductive tract. Another proposed adaptive benefit of the Coolidge effect is that it allows males to copulate with a new female more quickly after finishing copulation with a previous female, as the male does not risk displacing his own semen from the new female.

The Coolidge effect has been observed in a number of species. The first instance of this effect was observed in rats (Beach and Jordan 1956) and has been confirmed in more recent research which showed that, in addition to a shortened refractory period, male rats presented with novel sexual stimuli showed increased dopaminergic activity in the nucleus accumbens (Fiorino et al. 1997). This effect has also been observed in non-mammalian species such as fish (Jordan and Brooks 2010), invertebrates (Steiger et al. 2008), and hermaphroditic pond snails adopting the male role during copulation (Koene and Ter Maat 2007).

The Coolidge effect may also extend to differential sperm allocation. Research has found evidence that males of some species, such as European bitterlings, will allocate sperm differentially, such that males will produce higher-quality ejaculates during copulation with novel females than with familiar females (Pizzari et al. 2003; Spence et al. 2013). Because males have lower obligate parental investment to produce offspring to reproductive maturity than females, males possess adaptations for gaining sexual access to females. The Coolidge effect and the differential allocation of sperm to novel females are examples of adaptations that facilitate male mating.

Some evidence for the Coolidge effect has also been observed in humans. For example, one study investigated sex differences in the desire for sexual variety and found that, across cultures, men reported desire for a greater number of different sexual partners than did women (Schmitt 2003). In a more recent study, men more than women expressed a greater preference for a variety of sexual partners, regardless of the target's attractiveness (Hughes et al. 2020). The same study also reported that men more than women have a stronger preference for their partner to frequently change their physical appearance, whereas women more than men reported changing their own appearance more frequently. The results of this study suggest not only that men have a preference for sexual variety but also that women may be attuned to this preference.

While females may maximize their genetic success by enforcing their ability to choose high-quality mating partners, males may often maximize their genetic success by gaining sexual access to as many partners as possible. The Coolidge effect is one way in which males of some species are adapted to copulate with a large number of females.

## Cross-References

- ▶ [Arousal](#)
- ▶ [Sex Differences](#)
- ▶ [Sperm Competition](#)

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## Cooperation

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## Related Terms

Collaboration, Coordination, Joint action, Prosocial behavior, Altruism, Coordination games

## Definition

“The voluntary acting together of two or more individuals that brings about, or could potentially bring about, an end situation that benefits one, both, or all of them in a way that could not have



been brought about individually.” (Brosnan and de Waal 2002).

## Introduction

Cooperation is prevalent in a wide array of species and contexts. In humans, cooperation spans diverse situations from childhood play to government lawmaking. Cooperation is also seen in a wide variety of organisms, from plants to micro-organisms – such as bacteria and fungi – to megafauna. Certain species engage in complex cooperation in which individuals take on different roles, such as group hunting in chimpanzees and lions. Cooperation also occurs between animals of different species.

Historically, cooperation was largely understudied, likely for two reasons. First, the focus of animal behavior was the “nature red in tooth and claw” view that derived from our understanding that evolution was driven by individual benefits (Brosnan 2011); if was the case, why would individuals ever work together and risk benefitting another individual? This view assumed that cooperation was often evolutionarily disadvantageous and led to a widespread belief that there could not be much cooperation in the animal kingdom. Second, much animal behavior research took place in relatively easy environments, in which animals often can acquire what they need on their own. Biologists studying animals in more extreme environments, such as the tundra in Siberia, made the case that there were situations in which animals could not survive without working together and that cooperation was far more widespread than had been recognized (Kropotkin 1902). More recently, research has focused on the ways in which individuals do benefit themselves by working together, providing a solution to the apparent paradox of working together in a situation that rewards individual fitness (West et al. 2007).

There are several important factors to consider when trying to understand any behavior from an evolutionary perspective. At the most basic, there are two key features, the ultimate and proximate mechanisms. Ultimate mechanisms explain *why* individuals exhibit a behavior (i.e., what function

it plays for the animals), while proximate mechanisms explain *how* individuals exhibit a behavior (how that behavior is acquired and how it manifests). Tinbergen (1963) focused on four specific questions; understanding the ultimate mechanisms of behavior requires investigating the behavior’s phylogeny, or how the trait has evolved, and the behavior’s adaptive value, or how a behavior contributes to an individual’s reproductive fitness. Understanding the proximate mechanisms requires investigating the mechanistic explanations, or the physiology involved in a behavior, and the ontology, or how a behavior develops over an individual’s lifetime.

When studying any trait, it is crucial to distinguish between ultimate and proximate processes to avoid two key errors. First, confusing the two may lead to counterproductive debates about which explanation is “right” when in fact both explanations contribute to a full understanding by answering different questions about the trait. Moreover, different traits can share a function, but not a mechanism, or the reverse, so it is critical not to assume one from the other. For example, two behaviors may share the same function, but do so as a result of entirely different mechanisms; evolution can only work with the variation at hand, so a sufficiently important trait can evolve in different ways (for instance, insect and bird wings serve the same function, but the mechanics are quite different). In this case, assuming the same mechanisms is misleading. Similarly, having the same underlying mechanism does not guarantee the same functional outcome, because species differ in their selective pressures; to continue our example, penguins have wings, but they function in swimming, not flight (a case of divergence). Therefore, failing to separate ultimate and proximate mechanisms may potentially lead to inappropriate assumptions and conclusions.

In this entry, we first outline the approaches to cooperation. We then examine the ultimate explanations for cooperation, followed by the proximate mechanisms, including psychological, cognitive, and hormonal mechanisms. We then review the methods of studying cooperation and end by addressing the limits and potential of cooperation research.



## Four Approaches to Studying Cooperation

Cooperation is a broad topic, studied in a variety of fields, and each of these fields has developed its own terminology and approach. Bshary and Bergmüller (2008) outline four fundamental approaches: the basic social evolution theory, the ecological approach, the strategic approach, and the social scientists' approach. All overlap in some aspects and differ in others. To provide background, we first outline Bshary and Bergmüller's categorizations.

First, the basic social evolution approach explains cooperation in terms of its function. While there had been quite a lot of debate over the presence and adaptive value of altruism, this approach suggests that helping behavior more generally (i.e., minus the stringent assumptions of altruism) is selected for because cooperation increases inclusive fitness, which is a combination of direct fitness, through direct descendants (i.e., offspring), and indirect fitness through benefits provided to nonlinear kin. Sociobiological research has investigated the functional significance of behaviors such as parent-offspring conflict, differences in parental investment of sons and daughters, and female mate selection. The social evolution approach addresses what behaviors are selected for to directly or indirectly improve an individual's fitness.

Second, the ecological approach asserts that cooperation occurs when it is necessitated by an individual's social and/or ecological environment. While the social evolution approach focuses on the genetic influences of behavior, the ecological approach emphasizes environmental influences of behavior. Some environments are sufficiently extreme that cooperation is nearly a necessity. Moreover, in social groups there will be conflicts, which can be costly even to the winner of a competition. Cooperation can help individuals work together to avoid some of this conflict. Researchers in the ecological approach focus on environmental constraints such as food fluctuation and social constraints such as group size, group cohesion, or sex ratio. Much like the social evolution approach, the ecological

approach focuses on the benefits of inclusive fitness. However, it differs in its assertion that cooperation stems from social and ecological factors and that, unlike more rigid genetic influence considered in sociobiology, behavior may change as an individual develops or as environmental changes occur.

The third approach concentrates on how strategic decision-making evolved, which can be examined through average costs and benefits, such as those described in game theory. In this case, the mechanisms for cooperation include punishment, rewards, switching partners, and ending exchanges (Bshary and Bergmüller 2008). Unlike the first two approaches, the strategies approach takes into consideration the fact that individuals may alter decisions on a case-by-case basis based on previous interactions. An individual with high strategic and decision-making skills will be more apt to cooperate in a manner that will benefit themselves and will stop cooperating when exchanges result in a net loss. By maximizing benefit, and minimizing cost, an individual increases their fitness. Bshary and Bergmüller (2008) clarify that these strategies or decisions do not necessarily need to be conscious but can also be genetically determined.

Fourth, the social scientists' approach is the most exclusive of the approaches, as it only considers human cooperation. It argues that humans are unique due to complex abilities that influence our decisions, such as emotion, language, and moral judgment. According to this approach, these abilities enable humans to navigate situations in which we may or may not cooperate, including interactions with unrelated individuals or with significantly delayed rewards. Furthermore, it suggests that moral judgment provides a mechanism for human cooperation, as it is psychologically rewarding to help other cooperative individuals and to punish cheaters (Bshary and Bergmüller 2008). This approach does not address cooperative abilities in non-human species and emphasizes discontinuity – presumably due to a difference in cognitive abilities – between human and other animals. As a result, it is not particularly useful for understanding how cooperation evolved across species.

Although different fields of study may show preferences among the approaches, it is important to note that these approaches are not mutually exclusive; rather, they provide a framework to understand how cooperation has been studied. We focus on the strategic approach, as the emphasis on costs and benefits provides measurable outcomes of behavior. Additionally, we think it is important to consider the flexibility in behavioral responses, including responses across an array of social and ecological conditions, as well as how an individual may change their strategy within series of interactions with a partner, such that it explicitly incorporates the ideas of the other approaches.

## Key Hypotheses for the Evolution of Cooperative Behavior

Why would animals cooperate? The scientific literature offers four hypotheses: mutualism, kin selection, group selection, and reciprocity. Below, we discuss each of these, including psychological, cognitive, and hormonal mechanisms, and discuss specific behaviors that are hypothesized to be examples of each.

### Mutualism

Mutualism has unfortunately developed two somewhat different meanings. First is a relationship in which two or more individuals work together toward a common goal, and second occurs when individuals inadvertently benefit from the activity of the other (Dugatkin 1997). In the first case, if the individuals intentionally cooperate to achieve that mutual benefit, this likely requires at least a basic understanding of how the interaction will result in a reward. However, intentionality is not necessary for mutualism to occur. The second form of mutualism, known as by-product mutualism, is the most straightforward of the hypothesized mechanisms for cooperation as it requires no special understanding on the part of any of the individuals; each is working for their own benefit and incidentally benefits another individual in the process. As this requires no real explanation for how it would have evolved, in this entry we focus on the former.

In order for mutualism to occur, there needs to be a common enemy, or an adverse environmental factor that creates a situation in which two individuals will each benefit through cooperative behavior (Dugatkin 1997). This may occur between two or more conspecifics or may involve cooperation between members of different species, called interchange, or interspecific mutualism. Lions show intraspecific mutualism; individuals hunt alone when trying to kill small prey, and lions cooperate by hunting together for large prey, as larger groups are more successful. In this case, the lions cooperate by forming hunting groups, and all benefit when the prey is caught. A common example of interspecific mutualism is avian species “cleaning” ungulate species. The bird gets easy access to food, in the form of insects on the ungulate, and the ungulate benefits by having insects removed from its body. While neither animal has set out to help the other, both benefit through this interaction.

### Kin Selection

Kin selection describes the situation in which individuals provide a benefit to kin that their kin could not have obtained on their own. The ultimate explanation for this is that, since relatives share a proportion of their genetic material, benefitting a relative indirectly benefits one's own genes, a process called inclusive fitness. This focuses on the gene as the relevant unit of selection, rather than the organism, as it is the gene that receives the benefits when kin – who share those genes – are helped. Hamilton (1964) explained this through a simple equation known as Hamilton's rule:  $rB > C$ , in which  $r$  is the degree of relatedness between an individual and their kin,  $B$  is the benefit to their kin (the increase of offspring resulting from the helpful act), and  $C$  is the cost to the individual's reproductive fitness. As long as the product of the degree of relatedness and the benefit to the kin is greater than the cost to the individual, it is beneficial (for one's genes) to that individual to help their kin. As with mutualism, the individual does not consciously calculate this benefit, but rather the benefits and consequences of actions will eventually lead to these helping behaviors to be selected for

or against. It is important to note that kin selection emphasizes benefits that are beyond what the individual could have done on their own; for instance, helping with offspring care is only relevant to kin selection if the individual's help increases the number of surviving offspring beyond what would have been true without that help. This crucial component of kin selection is frequently overlooked, potentially resulting in the over-assumption of kin selection as motivating behavior.

Kin selection requires several mechanisms. First is kin recognition: an individual must be able to recognize their relatives, so that they direct their beneficial behavior toward relatives rather than unrelated members of a social group. This can be done through a variety of mechanisms, including familiarity (i.e., from being raised in the same nest) or phenotype matching, in which subjects match the look, sound, smell, or taste of another to their own and identify them as kin (although they need not understand this, it results in changed behavior for kin vs nonkin). Some species are not only able to recognize their own kin but are also able to recognize the familial relationships among others. For instance, when experiencing aggression from conspecifics, vervets and macaques frequently redirect aggression toward an opposing individual's relatives, suggesting that they have an understanding of the familial relationships between their opponent and other members of the group (Cheney 2011). Additionally, the individual must have opportunities repeatedly interact with the same kin.

### Group Selection

Although the use of group selection to explain the evolution of cooperation has been largely criticized, it remains a potentially important factor when studying cooperative behavior. For group selection to occur, multiple groups must display differences in trait-group productivity (Dugatkin 1997). While this argument is plausible in theory (Levin and Kilmer 1974), the reality is that the conditions necessary for group selection to transpire are so rigid that it is unlikely for it to occur regularly in animal populations. The exception, however, is group selection within humans.

Richerson et al. (2010) proposed that cultural evolution has been instrumental in human evolution through gene-culture evolution. While the selective pressures associated with human cultural changes may play an important role in our evolution, these group-level changes are likely of minimal impact in other animal species. Of note for this paper, there has also been controversy surrounding whether kin selection is merely a form of group selection (Nowak et al. 2010). This assertion was met with uproarious opposition within the field. Clearly, a great deal of controversy surrounding group selection remains.

### Reciprocity

In reciprocity, individuals trade favors and both ultimately benefit from the interactions. This is the mechanism about which perhaps the most has been written, in large part due to the variety of ways in which reciprocity can occur and the challenges in finding evidence for it. Robert Trivers originally recognized that individuals could benefit over the long term through the use of short-term exchanges to benefit one another. Specifically, he proposed reciprocal altruism, in which individuals take turns paying a cost to benefit the other; despite the short-term cost, the behavior will be selected for as long as the individual benefits in the long term (Trivers 1971). The idea was met enthusiastically, and many early studies searched for examples of reciprocal altruism in animals.

It has been trickier than expected to find them, however, at least in part due to the difficulty in quantifying costs and benefits. In addition, reciprocal altruism has high cognitive demands, as subjects must remember with whom they have interacted, keep track of favors given and received, and interact sufficiently often over a long enough lifespan that there is a reasonable chance that a favor will be returned in the future. Indeed, most of the studies purporting to show reciprocal altruism have been challenged with alternative explanations for the observed behaviors. Female vampire bats showed what was thought to be long-term, high-cost reciprocal altruism through blood sharing with conspecifics in need of food (Wilkinson 1984). However,

alternative explanations posit that these interactions may actually result from lower cost forms of reciprocity and/or kin selection, rather than reciprocal altruism.

Beyond these cognitive constraints, if subjects are exchanging different goods and services, such as grooming for food or support, how does one demonstrate that they are being traded? In most cases, scientists have either focused on a specific market or set up experimental markets in the lab. Even the latter, however, suffer from the problem that we do not know if the animals see exchanges as part of a market, and of course, even if they do, that market is still embedded within their larger social framework. Additionally, individuals may place different values on goods due to variation in need, making it difficult to calculate the subjectively perceived benefit for each individual. Finally, in most studies, whether wild or captive, scientists measure costs and benefits over a set, and often very short, time frame. However, reciprocal altruism may occur over a fairly long time span, up to years for some long-lived species. As a result, a study investigating reciprocal altruism, especially for long-lived animals, may simply not record data for a long enough duration to adequately capture reciprocal exchanges. Nonetheless, evidence continues to indicate that something of a reciprocal nature occurs.

More recently, scientists have expanded the idea of reciprocal altruism to include less cognitively demanding forms of reciprocity (although this does not circumvent all of the above problems). For example, Brosnan and de Waal (2002) outlined three categories: symmetry-based reciprocity, attitudinal reciprocity, and calculated reciprocity. Symmetry-based reciprocity is the simplest, requiring no additional cognitive ability, and is noncontingent. It is important to note that symmetry-based reciprocity is *functionally* reciprocity, but the underlying mechanism is not reciprocal, per se. Instead, the reciprocal interaction is based on symmetrical aspects of the relationships between individuals (based on age, social status, etc.) that lead to the same individuals to interact repeatedly. In short, if each individual is inclined to provide benefits (i.e., groom) and is indifferent to whom those benefits go, they are more likely, by definition, to provide them to

those with whom they spend a lot of time, for instance, because they are similar in rank or in the same family. Given the symmetrical nature of relationships, the partner will do the same. Thus, the key is that reciprocity occurs due to repeated interactions with the same individual, even if those involved are not seeking opportunities to do so and do not have any intention of being reciprocal. It is likely that quite a lot of reciprocity is based on symmetry in the relationship, even in species that have the cognitive capacity to engage in intentional reciprocity and are known to do so in other contexts. Nonetheless, recent modeling efforts indicate that symmetry of relationships alone may not be sufficient to support large-scale reciprocity.

Attitudinal reciprocity is contingent but does not require keeping track of individual interactions, nor is it intentional. In attitudinal reciprocity, the reciprocity is based on the fact that when one individual benefits another, the benefitted individual will have a positive attitude toward the donor. This makes the benefitted individual more likely to provide a benefit back to the donor within a relatively short time span. This requires a minimal amount of memory, as all that is needed is for the individuals to develop a positive feeling for the donor, and is likely to be emotionally mediated (Schino and Aureli 2010). As in symmetry-based reciprocity, attitudinal reciprocity requires repeated interactions with the same individual. However, it also requires recognizing that individual, as it is contingent on associating a positive feeling with a particular conspecific. Individual recognition is widespread across the animal kingdom, so this could be a widespread mechanism for reciprocity.

One of the best examples of attitudinal reciprocity comes from a study of captive chimpanzees exploring how grooming early in the day influenced food sharing later (de Waal 1997). Most experimental studies focus on the exchange of the same commodity, provided by the experimenter, over a very short time span (typically minutes). For the food sharing, de Waal used bundles of browse, a monopolizeable but nonetheless easily shareable food (sharing studies based on foods that chimpanzees can instantly consume, such as nuts or small fruits, rarely result

in sharing, presumably at least in part because the chimpanzees eat them too quickly). De Waal found that chimpanzees who had been groomed by another individual in the morning were more likely to share their food later on in the day and that it was specific to the individual who had groomed them; sharing did not increase toward individuals who had not groomed them. This suggests that the chimpanzees recognized a specific individual, remembered information about previous interactions with that individual, formed a positive association, and reciprocated at a later time. More intriguingly, more food was shared to individuals who did not frequently groom than those that did, suggesting that the chimpanzees not only remembered the morning's interactions but also how they related to their ongoing relationships. Finally, the chimpanzees were more likely to protest food-sharing requests made by an individual that had not previously groomed them. These results suggest contingent exchange with explicit memory for both short- and long-term relationships. This study highlights the need for experiments based on commodities that are naturally exchanged by the animals being studied, over time spans relevant to those animals.

Calculated reciprocity is the most complex form of reciprocity, as it involves contingency, the most cognitive ability, and intentionality; individuals explicitly trade commodities in a one-to-one fashion. In this, it is closest to Triver's formulation of reciprocal altruism. This form of reciprocity not only requires repeated interactions with the same individual but also recognizing them, as well as a host of cognitive features, hypothesized to include numerosity, low temporal discounting (so that they can inhibit taking an immediate reward), inhibition, the memory to remember others' reputations and the current tally of services, and the detection of cheaters. Stevens and Hauser (2004) argue that, while theoretically compelling, instances in which animals meticulously calculate the costs and benefits of every interaction are likely rare, as the cognitive requirements are simply too high. While large-brained social species may have the capacity to engage in calculated reciprocity, no evidence has been found that can completely eliminate the other forms of reciprocity. One exception to this

is humans, who have the cognitive capacity to engage in calculated reciprocity. However, while humans certainly can do so, it is likely that much reciprocity is still based on attitudes or even symmetrical aspects of the relationship.

Regardless of the type of reciprocity, there are a number of factors that must be considered. First commodities may include both goods, such as food items, and services, such as grooming or protection. While experiments often look at the exchange of goods, reciprocity in the wild quite often involves services, and it seems likely that cooperation evolved in the context of services. In comparison to goods, services are cheaper, are not limited resources, and are more difficult to take through coercion. For example, meat can be stolen, but it is very difficult to force an individual to groom you. In addition, the meat likely required substantial time and effort to obtain, whereas grooming can require minimal time and effort (depending on the length of the bout). Finally, goods are often zero-sum; if I share meat with you, I cannot share it with someone else, whereas services can, within limits, be provided to nearly anyone. This difference may also explain some of the difficulty in finding evidence of reciprocity in captive studies, which rely on goods (usually food) to motivate behavior.

Finally, while theory and experiments often focus on one-on-one exchanges, which are easier to quantify and track, reciprocity may function within a wider marketplace involving many simultaneous interactions among multiple individuals. This was formalized with the concept of the biological market, in which goods and services are exchanged and the "price" varies depending on the current supply and demand (Noë and Hammerstein 1994). In principle, this can also lead to indirect reciprocity, in which individuals may provide services to one individual but receive benefits from another.

## Mechanisms and Related Behaviors

Cooperation is supported by a variety of mechanisms. Of course, not all of these are required for each type of cooperation, nor do all individuals show them in each case. However, there are

sufficient consistencies across different types of cooperation that we consider them together. The exception may be by-product mutualism; as the cooperative outcome is simply a by-product of individuals pursuing their own best interests, few, if any, distinctive mechanisms are required.

### **Prosocial Behavior**

Prosocial behavior, or behavior that provides a benefit to another, has been observed in numerous animal species. Such helping behavior is often contingent on the identity of the actors and the circumstances. For instance, rats help conspecifics and are more likely to help individuals who have previously assisted them compared to those who have not (Rutte and Taborsky 2008). Evidence in primates is far more mixed, for reasons that are not entirely clear. Certainly, context has something to do with it, and there is growing evidence that primates may not understand the purpose of the tasks that we give them or may be disinclined to provide benefit unless there is a reason to do so.

It is important to note that prosocial behavior is distinct from altruism in that it is specifically the provision of benefit, with no assumptions about the costs to the actor. In addition, as with all behaviors, it is critical to distinguish between behavior that functions prosocially – providing a benefit to another – and prosocial motivations. The examples we discussed above are all the former, but not necessarily the latter. For a more detailed discussion of prosocial behavior, see the entry in this encyclopedia (Sosnowski & Brosnan).

### **Empathy**

Empathy is the understanding of another's feelings and goals and allows individuals to metaphorically step into another's shoes. Clearly this would be beneficial for cooperation as it provides a means to determine what the other needs. Whether animals actually have a capacity for empathy is hotly debated. On the one hand, there are ample anecdotes of behavior that appears empathetic, such as helping individuals obtain a food that is out of reach, but it is difficult to draw conclusions from these anecdotes, and while such "positive" occurrences are noted and

reported, it is unknown how many instances in which an animal could have helped and did not go unnoticed and unreported. Because of this, there is an emerging focus on studies that can provide more systematic evidence. For example, based on the fact that contagious yawning is absent in humans who are on the autism spectrum, it has been argued that contagious yawning is a sign of at least a basic form of empathy, although this relationship remains controversial. Rats, primates, and humans all exhibit yawn contagion in the presence of members of their social group, but not strangers. There is also evidence that chimpanzees, but not monkeys, console the victims of aggression, although, yet again, the degree to which this is due to empathy for the victim, rather than to calm the stress of the intervening bystander, is debated.

Some of the best evidence for empathy comes from studies exploring how individuals react when their partners are in pain, for instance, from receiving a mild shock or being trapped. Evidence from rats and mice shows a strong tendency for observers to act to help the distressed rat, and mice receiving a foot shock respond with even more pain if observing a conspecific get a shock as well, suggesting contagion. Studies from the middle of the last century provide similar results in primates, although there have been no recent studies using these methods. These results, which show more consistent findings suggestive of empathy than the prosocial studies mentioned above, suggest that empathy may be more commonly evoked in high-valence situations, possibly in particular involving pain and distress, than in the relatively low valence food-sharing situations. However, a different interpretation is that the empathetic bystanders are actually acting to reduce their own distress, either at the situation or to cease the stressful fear and alarm calls of their companion. As with many of these topics, the degree to which other species show evidence of empathy is still up for debate.

### **Inequity and Cooperation**

Several species, including primates, canids, corvids, and rats, respond negatively to getting less than a social partner. Such inequity responses



may facilitate cooperation by giving individuals a way to determine whether they are benefitting from a cooperative partnership; if rewards are equal, they should continue to participate, but if their partner consistently gets better rewards, it is time to find a new cooperative partner (Brosnan and de Waal 2014). This hypothesis, first proposed in economics, draws comparative support from two main lines of evidence. First, cooperation and inequity appear to be related at the phylogenetic level, as more cooperative species are also those most likely to respond negatively to inequity. Second, at the individual level, inequity can disrupt cooperation. For example, capuchin monkeys, who both cooperate extensively and show marked responses to inequity, cease cooperating when rewards are clumped so that they are monopolizable by one of the two subjects. Indeed, they do this from the first trial, indicating that they understand the potential outcome when rewards are clumped, and this is true for both nonkin and kin pairs. However, this may be as much due to the partner's behavior as the potential outcomes. When rewards are not monopolizable, but are unequal, cooperation is successful despite the inequity as long as subjects take turns receiving the better reward. In partnerships in which one individual dominates the better reward, cooperation drops, even in trials in which unequal rewards are impossible. Together these results suggest that cooperation and a response to inequity have coevolved and that this relationship is relatively widespread, at least among vertebrates.

To what degree, however, should inequity impact cooperation? In the case of mutualism, inequity should be irrelevant because subjects are incidentally providing the benefit to their partner in order to benefit themselves; therefore, the partner's outcome is uninformative as they are not actively helping, and there is no need to judge their value as a partner. Similarly, inequity may not be terribly relevant in kin selection; as long as the individual helping their relative is gaining more in inclusive fitness than they are paying in cost, they should cooperate. There may be situations in which one helper is providing more than another, but even in this case, if it benefits the

actor to continue helping, they should do so. Inequity should be highly relevant in direct reciprocity and biological markets, in which individuals stand to lose substantially if others are benefitting more than they are and can exercise their choice and find a new partner if the current one is not providing sufficient benefit. Finally, inequity may be far less important in indirect reciprocity, as there is no direct partner to "cheat," except if there are reputation effects; if subjects' reputations are impacted by their cooperative tendency, inequity will again be highly relevant as a marker for a non-cooperative individual. Indeed, the presence of strong inequity aversion in humans may explain why reputation effects are so much stronger in humans than other species; they provide a mechanism to detect cheaters who would otherwise render indirect reciprocity too costly (Brosnan and Bshary 2016).

In all of these cases, subjects should not respond too quickly to inequalities. It is the rare interaction that is always perfectly equally beneficial to all parties, and responding to any inequality by finding a new partner risks losing a successful cooperative relationship (in which subjects take turns being the more benefitted) over what may have been either a normal part of the relationship or an accident. Data from capuchins implies that they do not respond to every inequality but can successfully cooperate through short-term inequalities as long as the long-term relationship is balanced (reviewed in Brosnan 2011). If inequality persists over a longer duration of time, however, an individual's aversion to inequity should cause them to suspend cooperation to avoid uncooperative partners (Cheney 2011; Brosnan 2011).

### Hormonal Mechanisms of Cooperation

Hormones are key drivers of behavior, including cooperation (Soares et al. 2010), and there is a reciprocal relationship such that hormones may influence behavior and behavior may influence hormones. One key hormone is oxytocin, which has been shown to play a role in forming and sustaining social relationships, such as mother-infant bonds, pair-bonds, and friendships. Studies have implicated oxytocin in everything from the

formation of memories related to social interactions to individual recognition, to more trusting and cooperative behavior in economic game experiments (Bartz et al. 2011). There is also evidence that oxytocin is linked to the neurotransmitters associated with the brain's reward systems, including serotonin and dopamine, suggesting that social interactions are literally rewarding. As a result, the benefits of social interactions may ultimately lead to long-term social relationships (Soares et al. 2010). Despite these benefits, however, other evidence suggests that the relationship is more complex. For instance, while oxytocin often promotes in-group cooperation, it also leads to less *out*-group cooperation. In addition, a growing number of studies find no effect of the hormone, especially with exogenously administered oxytocin. The effects of oxytocin are complicated, with results influenced by individual, social, and contextual factors and, it appears, whether the oxytocin was endogenous or was exogenously administered.

Testosterone also influences cooperation in complex ways. When males experience testosterone increases in preparation for breeding, they may become less cooperative and more competitive. Conversely, this spike in testosterone may also facilitate pair-bonding and play a role in cooperative tasks such as group territory defense, suggesting that the change may be dependent on the relationship between individuals (Soares et al. 2010). According to the "Dual Hormone Hypothesis," the effects of testosterone are contingent on the presence of another hormone, cortisol. For example, there is a positive correlation between testosterone and cortisol in individuals that exhibit low levels of cortisol. In the presence of high cortisol levels, however, this relationship between the hormones is absent (Mehta and Josephs 2010). Research in humans suggests that cortisol may also play a part in the relationship between testosterone and cooperation.

## Measuring Cooperation

Cooperation occurs across a variety of different contexts. It is seen in the field in naturally

occurring contexts as well as in experimental paradigms that have been used to better understand underlying mechanisms, largely in lab settings. Both are key to fully understand why animals cooperate as well as when, how, with whom, and in what contexts they do so.

## Field Studies

Most field studies are necessarily observational, with researchers documenting cooperative behaviors such as group hunting, territory defense, coalitions, and predator defense. Considering the first of these, group hunting is seen in a variety of species and contexts, ranging from individuals opportunistically chasing the same prey item at the same time to active coordination by multiple individuals with differing roles. Chimpanzees in the Tâi Forest in Côte d'Ivoire show such complex coordination, in which individuals perform different roles in the hunt, are more successful in groups than alone, and are thought to share the prey afterward based on participation more than existing coalitions and alliances. Over the course of their lifetime, the chimpanzee takes on a series of increasingly difficult roles in the hunt as they gain experience. The skills required to successfully hunt as part of the group are sufficiently complex that it often takes 20 years of practice to be consistently successful (Boesch 2002). Intriguingly, not all chimpanzees show such complex hunts; chimpanzees in Gombe National Forest primarily hunt alone and share meat based on their current alliances. One hypothesis for this difference is that the continuous tree cover at Tâi necessitates cooperation because the monkeys can escape so easily, whereas the fragmented canopy at Gombe means that monkeys can be cornered, obviating the need for cooperation (Boesch 2002). If true, this points to the importance of understanding ecology for determining when cooperation will evolve; cooperation may be unlikely, even in species that have the cognitive capacity for it, if it is not needed.

These coordinated hunts are also seen outside of the primates. Emphasizing that cooperation does not require mammalian cognition, Harris' hawks also utilize multiple group hunting tactics, including taking turns chasing a rabbit until the

rabbit becomes exhausted and, consequently, slow enough to catch (Bednarz 1988). In this case, individuals cooperate by taking turns rather than simultaneously playing different roles like those seen in chimpanzees, but similarly to the chimpanzees, the hawks are unlikely to be able to complete the hunt on their own. Coordinated cooperation may also occur between species; recently it was discovered the grouper and giant moray eels are coordinating hunting, with grouper actively signaling specific moray eel in order to begin a coordinated hunt (Bshary et al. 2006).

In some situations, cooperation and conflict coexist within the same interaction. For example, many species show coordinated defense of the group territory. However, in some birds, social groups compete with one another for territory, only to then switch to cooperation by respecting the opposing group's boundaries. This phenomenon, known as the "Dear Enemy" effect, allows the birds to coexist without needing to constantly renegotiate group boundaries through potentially costly conflict (Dugatkin 1997). Similarly, animals routinely form coalitions or alliances to acquire or maintain rank or mating opportunities. In some cases, these relationships are unambiguously cooperative, as when male dolphins form long-term alliances despite the fact that one male will likely monopolize mating opportunities. Even within relationships, however, there will be elements of cooperation and conflict. Frans de Waal, in his book *Chimpanzee Politics*, outlined a complex relationship between two male chimpanzees who formed a coalition that allowed them to maintain dominance over a younger male, but still occasionally competed (de Waal 2007). Ultimately competition broke apart their alliance and allowed the younger male to assume the alpha position.

### Experimental Paradigms

Controlled experiments allow us to consider different factors that influence cooperation and begin to unravel causal connections, potentially providing more insight into the motives involved. One commonly used experimental apparatus is a bar-pulling mechanism, in which subjects must work together to pull in a tray with food. This

can be done by counterweighting the tray so that multiple individuals are needed to pull it in, or by using a rope threaded through the tray with two exposed ends, so that if it is only pulled on one end, it comes unthreaded and it is then impossible to pull in the tray. Such tests typically involve a mutualism condition (both pull and both receive food) as well as solo controls, or conditions in which one side of the tray has a less preferred food, less food, or no food, to see how their willingness to cooperate is influenced by reward distribution. Experimenters can also use different social combinations to explore the role of kinship or relationship quality, allow subjects free access to come and go, or restrict subjects' ability to see one another (reviewed in Brosnan 2011). These studies have been widely used in primates, dogs, elephants, and birds, all of whom cooperate in at least some contexts. For instance, numerous studies in capuchins have uncovered that these monkeys do better when they can see their partner (presumably because they are visually coordinating) and are sensitive to the relative rewards, indicating that they understand the potential outcomes of the interaction for both them and their partner. Elephants will wait until their partner is released before attempting to use the barpull, indicating that they understand the need for a partner to complete the task.

This paradigm is extremely simple, intuitive, and flexible and has ecological validity (many species acquire food by pulling it toward them; think of pulling down a tree branch to reach a fruit hanging on it). This is probably one of the reasons why it has been so successful. Intriguingly, an apparently similar procedure that requires two individuals to simultaneously press a button in order to receive a joint reward has not been as successful. Capuchin monkeys who were very successful at the barpull were unable to coordinate on this task. The authors argue that it was both less ecologically relevant (monkeys do not press buttons in the field) and not intuitive for the subjects (due to the lack of obvious connection, to monkeys, between pushing the button and getting juice; Brosnan and de Waal 2002). One key advantage of the barpull is that it offers immediate kinesthetic feedback; on a

weighted barpull, if you let go, my side of the tray becomes immediately too heavy, and on the threaded string, if you pull first, my side of the string moves out of reach. This highlights, again, the importance of testing using multiple modalities in order to ensure that the animals are given a version of the task that is appropriate and comprehensible to them.

A second experimental approach to cooperation uses games derived from experimental economics. In these tasks, subjects make a choice between one of several options and are rewarded based on what both they and their partner choose. This allows for very complex decisions to be distilled down to simple, often dichotomous, choices and is flexible enough to use for multiple types of decisions (i.e., by changing payoffs). Most studies have either used a computerized version, in which subjects make choices between icons on a shared computer system, or a manual version, in which subjects return tokens or choose targets to make their choice. These designs are often modified versions of economic games used in human studies, such as the Assurance Game, the Hawk-Dove Game, and the Prisoner's Dilemma Game (Smith et al. 2018; see Smith & Brosnan entry on Coordination Games in this encyclopedia). Much like the bar-pulling task, these games can be adapted to meet the needs of several species, enabling taxonomically broad comparisons.

Such tasks have already been informative in understanding differences among species. One collaboration has compared the responses of humans, chimpanzees, rhesus monkeys, capuchin monkeys, and squirrel monkeys (Smith et al. 2018). They found, for example, that in a coordination game called the Assurance Game, members of all species could find the highest-paying coordinated outcome, but, emphasizing that outcome is not the same as mechanism, how they did so varied across species. For instance, capuchins appeared to simply match their partner, whereas chimpanzees and humans showed evidence of having an explicit strategy for the game. They also found evidence that context is important, as human subjects, not surprisingly, more often coordinated on the highest-paying

solution when they talked to one another, and chimpanzees with extensive experience in cognitive testing were more likely to find the coordinated outcome than those without such experience. Although these tasks are not terribly ecologically valid, they provide a good foundation for cross-species comparisons, and the results can be used to make predictions about how subjects will behave in more natural contexts, which allows for testing of the results of these models.

Finally, while the previous tasks are typically implemented with dyads, real-life social interactions take place within the context of the entire social group. There has been a recent push to explore the effect of the group setting on these decisions. In some cases, researchers are repeating the barpull and economic game studies in a group setting, to determine who chooses to pair together when they have free choice and to explore what strategies emerge in this more open system. Subjects also may be in situations in which their actions benefit others in their group, but not necessarily themselves (i.e., alarm calling). In the so-called group-service experiment, individuals are given the opportunity to provide food to their group without receiving any themselves. In a group-service experiment with Japanese macaques, capuchins, and common marmosets, only common marmosets consistently completed the task to provide food to their social group (Burkart and van Schaik 2013). This supports one hypothesis for the evolution of prosocial behavior, which is that it emerged in the context of cooperative breeding. Future research will be needed to determine how cooperation is linked to other behaviors, such as prosocial behavior, and is influenced by social system, ecology, relationship, etc.

Finally, we wish to reiterate the importance of experimental design. In designing an apparatus, it is crucial to cater the design to the physical and cognitive capabilities of the species being studied (Smith et al. 2018). The subject must be able to physically complete the task and understand the task in the way that the experimenter intended (i.e., not use one ability to solve the task when the researcher was measuring another). As mentioned previously, it is important to ensure that

the task design is, when possible, ecologically relevant and that it offers appropriate feedback. There is no perfect design. For example, while computer tasks may allow for more flexibility in how the task is presented, they are presumably less intuitive than manual tasks for these animals. In addition, computer tasks can offer an environment that enhances learning (i.e., shorter delay between choice and reward, fewer extraneous cues that might distract) but only, ironically, after a fairly extensive learning period for the animal being tested. It is also important to consider social issues potentially distracting the subject; pairing the lowest-ranking subject with the alpha male will likely result in a subject who does not participate at all. In any experiment, it is important to design appropriate controls to rule out alternate explanations and help better understand how the subjects are interpreting the task (i.e., solo controls or no food controls in barpull tasks tell us whether subjects are actively trying to get food or cooperate, or are simply pulling every time they see a barpull). Finally, for comparative work, it is key to utilize similar tasks; otherwise it is impossible to know whether the results were due to the animals' actual abilities or the differences in the task. This is likely exacerbated for studies comparing humans to other species; in this case, modified tasks should be "back tested" on humans to ensure that the modified task elicits the same behavior as expected based on the human-typical version of the task.

## Future Research

Studies on animal cooperation have proliferated in the last few decades, as scientists investigate how and why animals cooperate. There are a few obvious directions for work in the next decade. First, it is clear that we need a better understanding of how social dynamics influence cooperation. There has been a shift toward conducting group-oriented experiments, such as the group-service paradigm, rather than pair-based methodology, which is a good start. In group-oriented paradigms, subjects have the ability to choose a partner for cooperative tasks. This may reduce

the likelihood that they choose not to cooperate due to an objectionable partner as well as allowing us to better understand how cooperation is influenced by who is present. Do individuals make different responses when others can see them? Does it matter who they are, or what their rank is? Recent evidence indicates that personality is influencing decisions in a variety of contexts, so does the temperament of the observer matter? Do we find evidence for reputation or third party interaction in cooperative interactions? Finally, group settings allow individuals to make decisions as part of a group, providing a social context that may influence behaviors in a manner more closely resembling those in wild populations. Indeed, then, a key advance will be when we can more directly compare results in the lab with those in the field to bridge the gap between the two approaches.

Past research has predominantly focused on species that exhibit cooperative behavior in the wild, but there is also a need to study species that have not yet demonstrated such abilities. In the case of solitary species, individuals may have the capacity to cooperate but, due to their social structure, are not presented with the opportunity to do so in natural contexts. Indeed, many of these species will happily live in social settings in captive environments, such as zoos, so this allows us to test for behavior in captivity that will literally not occur in the wild. Understanding the degree to which cooperation is, or is not, limited to social species will help us not only better understand the more solitary species' social interactions but may also help disentangle features of cooperation that are explicitly social from those that are used in a wider variety of contexts including, when the opportunity presents itself, cooperative ones.

Finally, creating additional methodologies that more successfully accommodate subjects' physical and/or cognitive abilities may illuminate cooperative abilities that were previously thought to be lacking in various species. Indeed, they may also help with comparative work. At the moment, comparative paradigms are relatively artificial (i.e., economic games) because of the need for procedures that can be easily implemented and



understood across a variety of species, who may differ in cognitive ability, body plan, and sensory system. Ideally, the predictions derived from these comparisons are then back-checked using species-typical methodologies, but this can be supplemented with other data. For example, hormonal data collection has already been instrumental in this effort, as many hormones play a similar role in many species and, therefore, facilitate between- and within-species comparisons. Ultimately, better understanding how animals cooperate and what factors influence it across phylogeny and environment will help us better understand how our own cooperative behavior has evolved.

## Cross-References

- [Coalition Enforcement](#)
- [Mutualism](#)

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## Cooperative Breeding

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### Definition

Cooperative breeding is a reproductive system in which helpers – i.e., individuals other than the parents – cooperate to raise offspring and thereby increase the immatures' growth and survival. In obligate cooperative breeders, a breeding pair is incapable of rearing offspring without the support of helpers (i.e., alloparental care), whereas facultative cooperative breeders are also able to successfully raise offspring without alloparental care.

### Synonyms and Related Notions

*Allomaternal* care refers to care provided by any individual other than the mother – including the father – and thus also includes **biparental care**. *Alloparental* care refers to care provided by individuals other than the parents and includes cooperative breeding and **eusociality**. The latter is an extreme form of cooperative breeding in which some classes of individuals forgo independent reproduction (reproductive division of labor).

## General Description

Cooperative breeding has evolved in a variety of lineages including insects, fish, birds, and mammals. Helpers are often, but not always, close relatives of the immatures, such as older siblings, and can provide a broad variety of helping behaviors including fanning eggs, and predator defense, food provisioning, and infant carrying. Regardless of the type of alloparental care, this help is beneficial in that it increases infant growth and survival.

Obviously, each taxon has a distinctive set of infant care behaviors, according to its own biology. Birds incubate eggs and may provision fledglings, whereas in mammals, the most important care behavior is providing milk by mothers. Since not all caretaking behaviors are equally amenable to allomaternal care, the type of a species' infant care behavior contributes to the taxonomic distribution and evolutionary pathways that can lead to cooperative breeding. Most importantly, breastfeeding cannot be performed by males, and as a consequence, cooperative breeding is much more prevalent in birds compared to mammals (roughly 3% of mammals, and between 8% and 17% of bird species; Heinsohn and Double 2004). Isler and van Schaik (2012) provide a systematic overview of shared infant care behaviors and their distribution among mammals. The most prevalent are infant carrying (e.g., common marmoset; *Callithrix jacchus*); provisioning (e.g., wild dogs; *Lycaon pictus*), allonursing (e.g., meerkats, *Suricata suricatta*), protection (e.g., cotton-top tamarin; *Saguinus oedipus*), and thermoregulation/babysitting (e.g., banded mongoose; *Mungos mungo*), and they typically co-occur in cooperatively breeding species. In birds, shared offspring care typically includes incubating eggs (Seychelles warbler; *Acrocephalus sechellensis*), provisioning (Acorn woodpeckers; *Melanerpes formicivorus*), and protection (Siberian jays; *Perisoreus infaustus*). In extreme cases such as in social spiders – *Stegodyphus mimosarum* and *Stegodyphus dumicola* – helpers are consumed by the offspring even when they are unrelated to them (Lubin and Bilde 2007).

Due to the help that mothers receive in rearing their offspring, they can produce more, larger, or more closely spaced offspring than would be possible if they were alone responsible for raising them (Hrdy 2005). In cooperatively breeding callitrichid monkeys, for instance, females give birth to twins, which is unusual for primates, and exhibit a postpartum estrus which allows them to get pregnant again almost immediately after giving birth (Erb and Porter 2017). They can thus simultaneously be pregnant and lactating, and the next set of offspring is born when the previous one is still not fully independent. In immatures, cooperative breeding can lead to prolonged dependence, as for instance in birds where cooperative breeding is systematically related with post-fledgling nutritional dependence (Langen 2000).

Cooperatively breeding species are group-living, often with a high reproductive skew, i.e., some individuals reproduce far more offspring than others. This is the case in obligate cooperative breeders, where breeding positions are limited because of the obligate need of helpers to successfully reproduce.

Helpers can be close kin, and are very often older siblings, or non-kin, such as immigrants of either sex, or co-breeding males. When helpers are older siblings, cooperative breeding is typically associated with delayed dispersal (i.e., the act of leaving the natal group and moving to a different area in order to start a new group or immigrate into a neighboring group). Thus, helpers incur considerable costs because instead of leaving their natal group and starting their own reproductive careers, they stay with the parents and help rearing their younger siblings. However, under certain conditions, dispersal is difficult and it can be beneficial to delay it, e.g. because of habitat saturation (Schrader and Pillay 2005) or high predation risk (Heg et al. 2004). Habitat saturation refers to situations where due to high population density and/or to harsh environmental conditions, all suitable habitats are already occupied. It is often the cause for delaying dispersal in birds. Predation risk, on the other hand, can lead to delayed dispersal because of the safety in numbers effect, and has more often been linked to cooperative breeding in fish. When the cost of dispersal

is too high, due to either biological or ecological constraints, dispersal can be delayed for an indefinite period of time, and thus also own breeding attempts (Hatchwell 2009). Due to delayed dispersal, a cooperatively breeding group usually consists of a breeding pair, and several overlapping offspring generations living together (Cockburn 1998; Lukas and Clutton-Brock 2012). This organization leads to an increase in relatedness within a given group, making it easier for cooperative behaviors to become *evolutionarily stable strategies* (ESS).

## Evolutionary Pathways

Helping behavior has a cost and it will only be selected if the benefits, direct or indirect, outweigh these costs. For cooperative breeding to evolve, it is broadly accepted that kinship and thus indirect benefits play a crucial role: when helping to rear close relatives such as younger siblings, the costs for the helpers is offset by the benefits to the offspring, depending on the degree of relatedness, according to Hamilton's rule. Kinship and indirect benefits are thought to be crucial for the evolution of cooperative breeding, but their role appears not always essential to maintain helping behaviors because the link between relatedness and helping is often weaker than one would expect. Therefore, direct benefits often linked to group augmentation (i.e., that individuals survive and reproduce better in larger groups; Kokko et al. 2001) appear to play an important role too. Emlen et al. (1991) have compiled several nonexclusive hypotheses as to why animals may directly benefit from helping to rear offspring that are not their own. These hypotheses have been tested and supported in several different taxa so far, but it is becoming increasingly obvious that there is not a single general explanation but that the importance of these factors vary contingent on biological and ecological species-specific constraints (Hing et al. 2017). Their hypotheses are:

- Helping increases infant survival, and consequently, group size. The helper would benefit from group size effects.

- Helping as a condition of being allowed in the groups by the breeders (pay-to-stay). The helper would gain benefits through access to resources.
- Helping increases group size and therefore expands the natal area. The helper would use a portion of the territory to increase breeding probability in the future.
- Helping behavior facilitates social coalition formation. The helper and its coalition partners would outcompete other individuals for available breeding positions.
- Helping would increase the chances of a helper to be chosen as a mate by a breeder. This hypothesis would be applicable to species where mate availability is a limiting factor.
- Helping behavior increases parenting experience, raising the likelihood for infant survival when the helper becomes a breeder.
- Helping behavior towards an infant would make it more likely that this infant would become a future helper when there is a new breeding opportunity.

Cooperatively breeding species appeared several times throughout evolutionary time. Given the multiple possibilities that helping behavior could be naturally selected, together with varying constraints imposed by the specific types of care-taking behaviors, one can reasonably expect that the evolutionary pathways leading to cooperative breeding differ to some extent. Some major differences in these pathways appear present in birds vs. mammals (Burkart et al. 2017; Griesser et al. 2017; Lukas and Clutton-Brock 2013).

The evolutionary pathway for cooperative breeding in pair-living birds appears to follow a two steps scenario (Griesser et al. 2017). In pair-living birds, fathers typically provide offspring care, probably because incubating and provisioning can be performed as easily by the male as it can by the female. In a first step, family living evolved when offspring stayed with the parents beyond independence, most likely because the offspring benefits from staying with the parents in terms of predation avoidance and skill learning. Family living is associated with more productive and seasonal environments and is a critical

evolutionary stepping stone for cooperative breeding in birds. When delayed dispersal is long enough until the next breeding season begins, retained offspring typically start helping in rearing the next brood; in fact, having non-helping previous offspring around is very rare in birds, just as is having non-helping fathers around. This second step towards cooperative breeding in birds, i.e., that immatures delay dispersal beyond the next breeding season, is thought to be facilitated by environmental variability and the associated less predictable food supply.

In mammals, the situation is slightly different. First, pair-living is rarer and even when it is present, the males often do not contribute to infant care, most likely because breastfeeding is typically the most important infant care behavior and cannot be taken over by males. Second, the immatures often disperse late enough that they would have the opportunity to help raising their younger siblings, yet they don't. The first step towards cooperative breeding in pair-living mammals therefore was most likely that males started to provide infant care. As a consequence, females could increase their reproductive efforts, which in turn made it more profitable for older offspring to provide help in raising their younger siblings. As in birds, this final step was most likely facilitated by more variable food availability. In both cases – birds and mammals – harsh and variable environmental conditions and high average relatedness make it easier for alloparental behavior to be selected due to higher benefits from allocare, and indirect fitness, respectively (Griesser et al. 2017; Lukas and Clutton-Brock 2012).

## Cooperative Breeding and Its Consequences

At the behavioral level, competition for rare breeding positions can be fierce among cooperative breeders, but this appears not to translate to other domains. Rather, everyday life is often characterized by high social tolerance and prosociality, which are apparently necessary to facilitate smooth cooperation among group members on a daily basis. For instance, if infants are

carried by all group members, and directly handed over from one carrier to the next, constantly high levels of social tolerance among all group members are crucial to enable such close range behavioral coordination. These links between social tolerance and proactive prosociality are well established in primates (including comparative studies over a large number of species (Burkart et al. 2014; Schaffner and Caine 2000), and increasingly so in birds (Horn et al. 2016).

Even though helpers forgo independent reproduction, behavioral coercion is typically not involved in promoting helping (Finkenwirth and Burkart 2018). This is also mirrored in hormonal glucocorticoid levels, which are generally higher in breeders rather than helpers, both in mammals and birds (Creel 2001). Furthermore, among cooperatively breeding primates, oxytocin levels raise after the birth of a new infant not only in the mother but in all group members, which is linked to infant care behaviors (Finkenwirth et al. 2016), and also to proactive prosociality among adults (Finkenwirth and Burkart 2017).

These behavioral correlates of cooperative breeding can have implications for understanding human evolution (Burkart et al. 2009). Among primates, humans and callitrichid monkeys are the only cooperative breeders, whereas allomaternal care is notably absent in other great apes. Compared to great apes, humans can have more and more closely spaced offspring, despite longer periods of dependence. For instance, humans (hunter-gatherers; Marlowe 2005) compared to great apes (van Noordwijk et al. 2018) have much shorter birth intervals (3.5 vs. 5–9 years) and wean their offspring earlier (2.5 vs. 4–8 years), yet reach their age at first reproduction later (19.5 vs. 10–14 years). This unusual *life history* pattern is exactly what is expected for a cooperative breeder and contributes to understanding the demographic success of humans (Hrdy 2009).

As a result of the behavioral predispositions associated with cooperative breeding, such as social tolerance and proactive prosociality, cooperatively breeding primates tend to perform particularly well in sociocognitive domains such as

social learning, communication, or cooperative problem solving, whereas in nonsocial cognitive domains they show regular performance as expected for their brain size (Burkart and van Schaik 2016). Similar effects likely emerged in the human lineage as well, but since these consequences were added to a much more powerful cognitive system to start with, they could release cascading effects eventually resulting in a set of uniquely human psychological and cognitive traits (Burkart et al. 2009; Tomasello and Gonzalez-Cabrera 2017).

## Conclusion

Cooperative breeding is a reproductive system in which individuals other than parents help to raise offspring and has evolved in several lineages. From an evolutionary perspective, this behavior is surprising given that individuals that forgo individual reproduction and instead help others face obvious fitness costs. Nevertheless, cooperative breeding has convergently evolved in several lineages, and theories that incorporate both the costs and benefits of helping can now delineate the conditions under which such a system is likely to evolve. Importantly, in addition to indirect benefits that emanate from helping close kin, direct benefits also play an important role in explaining these theories.

Among mammals, allomaternal care is rare, with the exception of primates. In primates, allomaternal care is more widespread than in other mammals, but the only cooperatively breeding primates are callitrichid monkeys and humans. This convergence plays an important role in current theories of human evolution because of its implications for the emergence of demographic, life-history, and psychological human traits.

## Cross-References

- [Biparental Care](#)
- [Evolutionarily Stable Strategies](#)

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## Cooperative Hunting

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### Synonyms

[Collaborative hunting](#); [Coordinated hunting](#)

### Definition

Cooperative hunting results from the coordination of group behaviors in such a way that increases the probability of a successful hunt, often of prey that are larger and able to be shared amongst those participating individuals.

### Cooperative Hunting

Cooperative hunting has been observed almost exclusively in social species, such as lions, killer whales, chimpanzees, and wolves (Bednarz 1988). Much of what is known about cooperative hunting and the conditions under which it evolves

in species sources from observations of the hunting practices of Tai chimpanzees (*Pan troglodytes*). Much of the following information derives from such observations, as this model species exhibits many hallmarks of cooperative hunting.

As cooperative hunting requires the participation of one or more individuals, there is an underlying need for cooperative hunters to exhibit social complexity. Four levels of increasing complexity characterize group-hunting. The lowest level of complexity, similarity, is characterized by individuals directing their behaviors at a single target; however, these actions lack temporal and spatial coordination. When the behaviors of the group align temporally, it is known as synchrony. Coordination represents a further increase in complexity as individuals relate their actions temporally and spatially to the actions of the other group members. Finally, the highest level of complexity is collaboration. When collaborating, individuals not only coordinate their behaviors, but also perform a variety of complementary behaviors directed at the same target (Boesch and Boesch 1989), which may require understanding the others' role in completing the goal.

The higher the level of complexity demonstrated by the group members, the increased likelihood that their hunt will be successful. Cooperative hunting yields a number of benefits for the individual group as well as their environment. The environmental disturbance from hunting is drastically decreased when hunting as a group, compared to when individuals hunt on their own (Estes and Goddard 1967). Cooperatively hunting allows individuals to take down larger prey than they otherwise would be able to when hunting alone. This increased yield for decreased energy expenditure is a central tenet of cooperative hunting (Estes and Goddard 1967). Having more individuals involved in the hunt aids in discouraging potential scavenging by other species following the kill. Hunting as a pack also allows for the protection of more vulnerable members of the group, such as mothers with young and those that are sick (Estes and Goddard 1967).



Given the plurality of benefits accrued from hunting cooperatively, it begs the question of why there are not more species that exhibit this method of hunting. There are two conditions under which cooperative hunting evolves in a society: the probability of success is low for a lone individual and there is some sort of deterrent in place that limits the access of cheaters to meat secured during the hunt (Boesch 1994; Stander 1992). The distribution of meat is central to the evolutionary stability of cooperative hunting; if there is no increase in the success of the individual as a result of their participation in the hunt, the favored strategy would simply be to hunt alone. In chimpanzees, individuals appear able to track the participation of group members during the hunt, resulting in preferential access to the meat by those who actively participated in the hunt (Boesch 1994).

It is only in societies where participating in the common task yields a net benefit that exceeds that of participating in a comparable task alone that cooperation should evolve (Boesch 2002). For example, if all individuals participate in the hunt, yet only one individual reaps the rewards of that hunt, this pattern of behaviors would not be evolutionarily stable. The observance of cooperative hunting animal societies has lent to an understanding of the conditions under which a hunting strategy is uniquely viable. Animals, such as wolves, whose main source of prey are large ungulates, which are difficult to take down individually, would benefit greatly from working as a group (Muro et al. 2011). Often, these animals face the challenge of hunting in open landscapes, necessitating more creative tactics (i.e., distractions, harassment, etc.) to effectively hunt (Bednarz 1988). In addition to open habitats, hunting in three-dimensional habitats, such as forests, also benefit from group coordination (Stander 1992).

By definition, cooperative hunts require a minimum of two individuals, and there are a number of conditions that dictate the optimal sized group. There appear to be two peaks in amount of food intake as a function of group size: the first is when there is only one individual and the second is when there is a particularly large group (Boesch 2002). When the prey item is relatively easy to

catch, smaller group sizes are more favored. When the prey item is larger and more difficult to take down, greater numbers are far more common (Stander 1992). Interestingly, as the group grows larger, there is often a higher prevalence of cheating, diminishing the advantages of cooperation for those participating (Stander 1992).

Even if a larger group size lends itself to increased cheating behavior, there is the added benefit of post-hunt protection. Lions (*Panthera leo*) may lose up to 20% of their prey to scavenging hyenas, with this value increasing as the number of lions present around the carcass decreases (Boesch 1994). This is a similar pattern to that seen in African painted dogs (*Lycaon pictus*); a group of two or three individuals have a greater likelihood of losing their kill to hyenas. An increased number of dogs would allow for a more successful counterattack against the scavenging hyenas, thus maximizing the amount of meat the dogs are able to consume following a successful hunt (Estes and Goddard 1967).

Most cooperative hunts are variants of the coordinated stalking of prey (Stander 1992). Wolves (*Canis lupus*) often rely on ambush hunts, wherein one individual lays in wait as the other members of the hunting party drive the prey toward the ambusher, as well as relay running, which is characterized by hunters rotating their roles and position with the pack during a chase (Muro et al. 2011). The division of labor – wherein members perform different, but complementary roles during a hunt – is a hallmark of cooperative hunting (Gazda et al. 2005). Role specialization within the division of labor is the tendency for individuals to consistently perform certain tasks during hunts, rather than changing the roles they perform within and between hunts (Gazda et al. 2005).

Observations of Tai chimpanzees have revealed three broad categories that individuals fall into during hunts: hunter, cheater, and bystander. A hunter directly participates in the hunt, contributing in some way to the capture of the prey. While this strategy requires the highest energy input, it is the strategy that yields the best access to meat following the hunt (Boesch 1994). Cheaters, in contrast do not participate in the hunt,

but are present following the hunt to eat the meat. They exert the least amount of effort but are also punished for their nonparticipation. The cheaters who are closely related to hunters tend to be tolerated more than distantly related individuals in the same capacity (Boesch 1994). The role of bystander is often more fluid, with those individuals moving in and out of that role into either hunter or cheater roles (Boesch 1994).

Mutualism is described as individuals accruing benefits from working together that surpass those they would have received when working alone (Boesch 2002). This explains the increased access to meat enjoyed by hunters. Reciprocity, on the other hand, is how females are able to get preferential access to meat in societies where hunting is performed by the males. Under the principles of reciprocity, the benefit to each individual is experienced at different times, and it is through repeated interactions that this relationship develops (Boesch 2002). Females are able to leverage mating access in exchange for meat following a hunt (Boesch 1994).

## Chimpanzees

Tai chimpanzees are well-known for their cooperative hunting practices, collaborating in nearly 70% of their hunts (Boesch 1994, 2002). Not only do they perfectly emulate the necessary conditions for cooperative hunting to be evolutionarily stable in their society, they are also a species that exhibits role specialization (Boesch 2002). Drivers are tasked with progressing the hunt in a certain direction, moving toward the prey, but never trying to catch up. Chasers are similar to drivers; however, they intentionally attempt to catch up to the prey. Blockers strategically place themselves at points through the forest, forcing the prey to maintain their progression in a specific direction. Finally, the ambushers position themselves in a tree where they anticipate the hunt will lead to attacking the prey once it enters that tree (Boesch 2002). Ambushers and blockers require a level of forethought in anticipating where the prey will be and at what time in the hunt. This complex

ability requires extensive training and practice; it can take up to 20 years for individuals to become consistently proficient at anticipating the behaviors of (Boesch 2002). Blockers and ambushers are more valuable than drivers and chasers to the success of the hunt, allowing them increased access to meat above and beyond that of hunters in lesser positions. The particular role adopted during the hunt supersedes any dominance hierarchies (Boesch 2002).

## African Painted Dogs

African painted dogs have an incredibly high success rate when hunting as a pack. With a hunt lasting an average of 25 min and a success rate of over 85%, they are an ideal example of cooperative hunting (Estes and Goddard 1967). There is not a clear division of labor during the hunt, as they tend to rely on a relay-running strategy when hunting, and there is always a leader who leads the pack during the chase (Estes and Goddard 1967). Resource sharing among African painted dog packs is less dependent on participation in the hunt, as is the case with other species. This is not to say that cheating is permitted within the pack, but rather that resources are shared with family members who could not be present during the hunt, such as mothers with new pups and sick individuals (Estes and Goddard 1967).

## Lions

Lions demonstrate the increased efficacy of role specialization during hunting. They commonly exhibit a hunting configuration wherein some lionesses, known as “wings,” encircle their prey, while others, known as “centers,” slowly stalk toward the group, ambushing prey fleeing from the “wing” lionesses (Stander 1992). Despite moving shorter distances than their counterparts, kills made by “centers” accounted for 73% of their successful hunts. This stalking-ambush strategy was most effective when lions were in their preferred roles during the hunt (Stander 1992).

## Harris Hawks

Cooperative hunting is not limited to mammals. Harris hawks (*Parabuteo unicinctus*) have demonstrated increased success with larger hunting parties (Bednarz 1988). These hawks follow a pattern of behavior when searching for prey in which they will “leap-frog” throughout their home range, splitting into subgroups and flying from perch to perch. After locating a prey item, they will employ one of a number of common hunting tactics. The most common is known as the “surprise pounce” wherein individuals converge on the prey from different directions (Bednarz 1988). Another tactic is known as the “flush and ambush” strategy and is employed when their prey is able to find temporary cover. In this series of behaviors, a number of hawks will attempt to penetrate the cover while other individuals wait, watching for the prey to reappear (Bednarz 1988). The least common tactic is the “relay attack,” which is a long-duration chase intended to exhaust their quarry, wherein some pursuing individuals will pause at a perch, allowing other group members to fly ahead, continuing the chase (Bednarz 1988).

## Conclusion

Cooperative hunting relies on two underlying conditions to be an evolutionarily stable strategy: the probability of a successful hunt must be higher when in a group than when alone, and there must be some deterrence against cheating behaviors. There are three roles into which individuals may fall during a hunt, and those are hunter, cheater, and bystander. Some species, such as the African painted dog, are more tolerant to those who do not participate in the hunt, while other species, such as chimpanzees, are far more intolerant of cheaters. This is not a steadfast rule, however, as female chimpanzees are able to leverage future benefits to the hunters in exchange for meat. There are numerous tactics employed by different species; however, the common thread among these strategies is a division of labor. Some species may have

a more rudimentary version of labor division, whereas the hunting success of other species is more directly tied to role specialization of the individuals. Harris hawks, for example, readily switch roles to suit the present circumstances; in contrast, lions have far higher success rates when group members are serving in their preferred position. The behaviors and conditions associated with cooperative hunting lay on a spectrum of complexity.

## Cross-References

- [Carnivore \(Diet\)](#)
- [Cooperation](#)
- [Hunting](#)
- [Tai Chimpanzees](#)

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## Cooperative Mating

- [Coalitional Mating](#)

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## Coordinated Hunting

### ► Cooperative Hunting

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## Coordinated Joint Engagement

### ► Joint Attention

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## Coordinated Person-Object Orientation

### ► Joint Attention

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## Coordinated Singing

### ► Countersinging

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## Coordination Games

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The problem of social coordination is widespread across species and contexts, ranging from group cohesion and movement to courtship, aggression, and cooperation (see chapters on “► [Pro-social Behavior](#),” and cooperation for

more information on these topics). The primary similarity across these topics, uniting them under the umbrella term “coordination,” is that the outcome is due to joint action by two or more individuals at the same time that results in a desired outcome. Coordination is often used more or less interchangeably with cooperation in biology; however in economics, coordination specifically focuses on how individuals synchronize their behavior to reach (or not) a common goal (Guastello and Guastello 1998). It is often studied using coordination games, in which subjects benefit by coordinating their responses on the same outcome. These games are part of a set of tasks used in experimental economics to explore decision-making outcomes in humans. Aside from being useful to better understand human decision-making, the games are particularly amenable to comparative research (Smith et al. 2018) and thus can provide important insight into the evolution of decision-making, including coordination (Brosnan et al. 2013). We focus on two games, a coordination game called the Assurance game (or Stag Hunt game) and the closely related Hawk-Dove game (or Chicken game), an anti-coordination game.

Economic games take complex decision situations, such as coordination, and break them down to very simple choices. These choices are often dichotomous, although they can be more complex. The experimenter can also manipulate the paradigm to explore how decisions change in different contexts or within different social environments or alter the payoffs to explore how different types of decisions compare (i.e., coordination vs. anti-coordination). Due to their simplicity, these games can be easily adapted for multiple species and for use with different types of tasks, for example, either a manual task (e.g. choosing which of multiple tokens to return) or a touch screen or joystick-based computer task (e.g. choosing by selecting one of multiple icons on a screen). This is a key advantage for comparative work, since even basic morphological differences between species can strongly impact the degree to which the same task can be used with them, making these games particularly well suited for studying the evolutionary trajectory of decision-

making. Although the games themselves are artificial, they are an excellent model system that can be used to derive hypotheses that can then be tested in more species-specific paradigms (Smith et al. 2018).

A key difference, of course, is that we cannot explain to nonhumans how the games work. This is typically solved in one of two ways; either they are allowed to learn the payoffs as they learn the task, or they are trained on the payoffs and then researchers explore whether their decisions change across different contexts. The former can be particularly useful in learning how subjects figure out what “game” they are playing, what the payoffs are, and how their decisions change as they learn the parameters. This is also relevant for understanding how people interact in non-laboratory situations. Although in the laboratory we can tell people the exact parameters of a decision task, in real life, individuals must figure out both the structure of the interaction and what the payoffs will be, the latter of which are often not foreseeable at the outset. Of course, this also means that we cannot be certain that subjects understand the task as we intended. As a result, it is important to “back-test” the adapted games that we use with animals on humans, using the same procedures that the other species received. Aside from ensuring that the humans respond to the modified game as expected, which indicates that the changes did not impact the goal of the procedure, it also verifies that any differences between humans and other species are due to differences in how they perceive or engage with the game, rather than differences in the procedure, and that similarities are really due to similarities in response, and not a result of having inadvertently made the game easier for one of the species.

### Assurance Game (Stag-Hunt)

The Assurance game (also referred to as the Stag-Hunt game) is an example of a simple coordination game with two pure strategy Nash equilibria (NE; strategies whereby no player can do better by changing their strategy if their partner’s

play remains consistent). The game was originally presented as a story by Jean-Jacques Rousseau and later modeled to a social dilemma (Skyrms 2003). In the story, two hunters can work together to take down a stag (a large prize), or they can individually hunt a hare (a much smaller prize). The dilemma is that while both individuals benefit more from working together to get the stag, if their partner does not participate, those that try for the stag outcome end up with nothing. However, they are always able to hunt the hare on their own. Thus, the dilemma is that participants both benefit the most from working together, but if they do not trust their partner, or think that their partner may not understand the task, they should make the lower-paying, but safe, choice to hunt hare.

This game is little studied in humans, likely because if the game is explained as we have just done, or a payoff matrix is presented, it is obvious that there is a mutually beneficial, high-paying outcome, which is what people overwhelmingly play. Therefore, most research studying cooperative decision-making in humans has focused on the Prisoner’s Dilemma, a cooperation game in which there is a high temptation to defect (for a better payoff), unless individuals play with the same partner repeatedly, in which case the gains from long-term cooperation outweigh the (one-time) gain from defecting on a cooperating partner, that will likely be followed by mutual defection. However, even in an Assurance game, if you do not know the payoffs ahead of time, and must learn them as you play the game, coordination may be harder to find than the human results imply. As mentioned above, this is true not only in the tasks used with nonhuman species, but often in real life. Indeed, Brian Skyrms, in his influential book on the Assurance game, has argued that it is a better model of many instances of human decision-making and deserves more attention (Skyrms 2003).

A growing body of literature has explored the Assurance game in nonhuman species. An initial set of studies, derived directly from the experimental economics literature, used two different methodologies, a manual exchange task common

**Coordination Games,**

**Fig. 1** Payoff matrices associated with the Assurance game (a) and the Hawk-Dove game (b)

|          |      | Player 1 |      |
|----------|------|----------|------|
|          |      | Stag     | Hare |
| Player 2 | Stag | 4, 4     | 0, 1 |
|          | Hare | 0, 1     | 1, 1 |

|          |      | Player 1 |      |
|----------|------|----------|------|
|          |      | Hawk     | Dove |
| Player 2 | Hawk | 0, 0     | 1, 4 |
|          | Dove | 4, 1     | 2, 2 |

in nonhuman primate studies and a computerized task that is the traditional methodology in human studies. In both cases, subjects made a choice among two options (either computer icons or tokens) and rewards were distributed according to the same payoff matrix (Fig. 1a: Brosnan et al. 2011, 2012). In the computerized task, there were two conditions, a functionally simultaneous condition, in which subjects could not see their partner's choices until both had made a choice, and a sequential version, in which subjects' choices were displayed immediately as they made them, so subjects could at least in principle use their partner's choice to guide their own decision.

Researchers have ultimately tested five species representing a wide phylogenetic range within the primate order. This included humans, as well as three other primates that are highly cooperative and social and do well on a variety of cognitive tasks; chimpanzees (*Pan troglodytes*), rhesus macaques (*Macaca mulatta*), and capuchin monkeys (*Sapajus [Cebus] apella*). Chimpanzees are often used as a comparison with humans as they, with their sister species bonobos, are the extant great apes most closely related to us. Bolivian squirrel monkeys (*Saimiri boliviensis*) were also tested, which are closely related to and live in similar habitats as capuchin monkeys (both New World primate species) but do not show extensive cooperation. This allowed a determination of whether cooperation in daily life enhanced the ability to coordinate in this task.

The overall results showed clearly that some pairs of all of these species, including squirrel monkeys, coordinate on the payoff-dominant NE (*Stag-Stag*) in some contexts. However, there was substantial variation in how they did so (Brosnan et al. 2011, 2012; Vale et al. 2019). The New

World monkeys, the most distantly related to humans, did the least well on the task. Three out of the five pairs of squirrel monkeys tested settled on the payoff-dominant NE, but while these pairs' results were statistically significant, anecdotally, their frequency of choosing the *Stag-Stag* outcome was lower than that of the other species who found the NE, possibly due to the fact that squirrel monkeys do not appear to cooperate in the wild to the same extent as the other species tested (Vale et al. 2019). Capuchin monkeys also showed low levels of success in a manual task, but all subjects found the payoff-dominant outcome in the sequential computer task. Rhesus monkey and chimpanzee pairs were able to coordinate on the payoff-dominant NE in both the simultaneous and sequential versions, as were humans, although chimpanzees were highly variable.

These studies also provided insight into the mechanisms subjects used to solve the task. Capuchin monkeys were only able to solve the task when they could see their partner's choices and were presumably using a matching strategy, with a bias towards the option that payed them better. Capuchins live in small, fairly cohesive social groups, and thus coordination likely occurs primarily when subjects are in close enough proximity to one another to see each other's choices (Fragaszy et al. 2004). Capuchins therefore may have never experienced selective pressure for a mechanism for coordination other than behavioral matching or monitoring. Rhesus monkeys and chimpanzees (as well as humans) live in much larger social groups that frequently find individuals at much greater distances, or out of view. For example, chimpanzees coordinate behavior during group hunts and territorial patrols when



they are out of view of one another (Boesch and Boesch 1989; Mitani and Watts 2005). This presumably provided selective pressure for the ability to remember partners' past patterns of behavior even when they are out of sight.

Additional studies demonstrated that even the consistently successful rhesus monkeys were using a mechanism that was different than the humans'. In a control task in which subjects played a computerized simulation that was programmed to play different rates of *Stag*, humans probability matched, playing *Stag* at roughly the same levels as the simulation. Rhesus, on the other hand, played *Stag* almost no matter what the simulation played, indicating that they had simply formed a preference for this (typically) high-paying option (Parrish et al. 2014). This is particularly interesting as rhesus monkeys are known to probability match in other contexts, reinforcing that just because a species can use a particular cognitive mechanism does not mean that they will do so in every case; mechanism cannot be assumed from outcome. Finally, chimpanzees showed a high degree of variability, with chimpanzees that had extensive experience with cognitive tasks showing evidence of maximizing strategies that they could apply to novel situations. Chimpanzees who had very little experience with cognitive tasks, however, tended to match their partner, but with no bias towards mutual *Stag* play, or show no strategy at all (Hall et al. 2019). Although matching was still a relatively high-paying option, they would have done much better by coordinating on *Stag*. These chimpanzee results are hard to explain, given their behavior in the wild, and suggest the possibility that they were either failing to understand the task or were not motivated by it.

Humans showed one other curious outcome; in the manual task, many of the pairs settled on the risk-dominant *Hare-Hare* outcome. Looking at the data more deeply, however, it turns out that these pairs did not explore the parameter space and had never experienced the payoff-dominant *Stag-Stag*. It appears that after finding the *Hare-Hare* outcome, these subjects thought that they had solved the task and did not explore further. Language may be particularly

relevant for humans in this context; in neither task were subjects explicitly told not to speak, but only in the computerized task did all pairs do so. Intriguingly, pairs that spoke about the game found the coordinated *Stag* NE, whereas pairs that never talked about the game settled on the mutual *Hare* outcome and, again, did not explore beyond this. These results may indicate that humans are using language to facilitate exploration of the parameter space.

As mentioned above, while the economic games are valuable for cross species comparisons, additional information can be gleaned from using tasks that take into account more species typical behaviors. In another series of studies, chimpanzees and children were presented with a paradigm that closely mimics the original Stag-Hunt story on which the Assurance game is based (Bullinger et al. 2011; Duguid et al. 2014). Pairs could individually forage on a low-value food (*Hare*) or move to a high-value food (*Stag*) that was only obtainable if they coordinated with their partner. Once they left the *Hare* option though, they were not able to return to it if their partner did not show up for coordination on the *Stag* option and were thus unable to acquire any additional rewards.

As in the economic games, both chimpanzees and human children were able to successfully coordinate on the mutually beneficial *Stag-Stag* option at very high rates. Both species primarily relied on a "leader follower" dynamic, where one subject would make their decision based on what the other did. Interestingly, when the experimental setup was changed so that subjects were not as easily able to see their partner's decision (similar to the simultaneous version described earlier), rates of coordination decreased for the chimpanzees but remained high for the children. The researchers evaluated rates of communication between the species and found that children were able to maintain higher rates of successful coordination than chimpanzees in this more difficult scenario by increasing their verbal communication to replace their prior visual monitoring. Together with the humans' outcomes in the Assurance Game prior game task, these results emphasize the importance of communication for humans in coordinating outcomes.

## Hawk-Dove (Chicken) Game and Snowdrift Game

Sometimes individuals may be forced to confront a scenario where *anti*-coordination is required. This dynamic is captured best by the “chicken” game (made famous in the final car scene in the movie *Grease*). If two individuals are approaching one another head on, both individuals do best if one of them yields (to avoid injury), but the optimal choice for each is to maintain their course while the *other* yields (so they gain status). The optimal decision thus depends on doing the opposite of what the other individual is doing. This game has been studied extensively in behavioral ecology as the Hawk-Dove game, which models resource conflict but reflects the same payoffs as the chicken game. Whereas in a coordination game the Nash equilibria are for both players to coordinate on the same strategy, in an anti-coordination game the NE is for players to play different strategies. The Hawk-Dove game has three NE, two pure strategy, asymmetric NE where each player plays one of the options (the other plays the opposite strategy; bottom left and top right quadrants in Fig. 1b), and a mixed equilibrium where the players switch between these two pure strategies. The mixed equilibrium is the best equally paying solution because it maximizes both players’ benefits.

In a manual version of the Hawk-Dove game, using the token-exchange paradigm described above for the Assurance game, humans, but not capuchin monkeys or squirrel monkeys, were able to settle upon stable NE solutions (Brosnan et al. 2017; Vale et al. 2019). However, in a computerized version of the Hawk-Dove game (again using the same experimental methodology as described for the Assurance game), capuchin monkeys and rhesus monkeys settled on an asymmetric NE, although they were only consistently able to do so during the sequential version, in which they could see their partner’s choices (Brosnan et al. 2017). The difference in capuchins’ play between the two methodologies is likely due to the fact that aspects of the computerized task may enhance learning; because computers are faster than humans, the reward more rapidly follows the

choice, there are more trials per session, and despite all of the controls in place during the manual tasks, there are presumably fewer distractions in computerized testing. Humans performed notably better than the other primates, with nearly half the pairs finding the mixed equilibrium, in which the players alternated between the two asymmetric NE. Indeed, this result is notable because unlike the other primates, who maintain the same level of finding the NE or do so in fewer circumstances in the Hawk-Dove game, the humans do much better in this more difficult game. One hypothesis is that, unlike in the Assurance game, where the coordinated *Hare* outcome may have seemed like a good solution in the absence of full information, the variability in this task may have meant that humans did not think that they had found a solution and were therefore more likely to explore.

A closely related game is the Snowdrift game (see chapter Snowdrift Game), modeled after a scenario in which two cars are prevented from getting home by a large snowdrift. The drivers both want the snow to be shoveled and could work together to do so, but both drivers would prefer that the other driver does it on their own. If the other driver does not do the work, however, the first driver should shovel the snow because the cost is less than the benefit of getting home (but does allow the partner to free ride). To test this, chimpanzees were presented with a situation in which they could work together to pull in food rewards or wait for their partner to pull them in (they received the same amount of food whether or not they helped). If neither individual pulled, the rewards were lost to both. Chimpanzees generally coordinated, pulling together with the partner, although they did seem to strategically minimize their effort by waiting longer to pull when the effort required for pulling was greater (Sánchez-Amaro et al. 2016).

## Conclusion

Economic games are extremely useful for both determining how outcomes are similar, or not,

across species and the underlying mechanisms behind them. Future research should focus on expanding the species tested, in particular testing species that are not known to coordinate extensively in natural contexts, to determine the degree to which individuals can find coordinated outcomes even if they have not been in environments that selected for it, or whether such an evolutionary history is critical for developing coordination. In addition, as we discussed above, the economic games are an excellent model that allows for direct comparisons across species, but they lack ecological validity. It will be important to continue to test the hypotheses that emerge from these games using more species-specific designs that allow us to explore how ecological pressures may have influenced species differently.

There are also other factors that may be influencing behavior in these games, such as hormones, social partner identity, or previous experience with cognitive testing. This will be particularly important to understand how these factors influence behavior across species. For instance, while previous research has demonstrated impacts of oxytocin on behavior in economic games in humans (Dreu et al. 2010; Rilling et al. 2012), recent work in capuchin monkeys finds no such effect (Smith et al. 2019). Social partner may also play a key role, as individuals should coordinate differently depending on their relationships, and as our chimpanzee results demonstrate, previous experience with cognitive and behavioral testing may be critical. Finally, we need data from a wider range of coordination games. The Battle of the Sexes game would be particularly relevant, as it is a coordination game with conflict (as opposed to an anti-coordination game like the Hawk-Dove game), where individuals do best to coordinate together on one outcome or the other, but there is disparity between the player's individual preferences for each outcome. The addition of a wider range of species and modeled scenarios such as this would improve our understanding of the evolution of coordinated behavior and social decision-making in general.

## Cross-References

- [Cooperation](#)
- [Decision-making](#)
- [Game Theory](#)
- [Prisoner's Dilemma](#)

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## Coping Mechanism

### ► Coping Style

## Coping Style

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## Synonyms

Behavioral profile; Behavioral syndrome; Consistent behavioral variation; Coping mechanism; Stress coping; Temperament

## Definition

A specific response pattern involving behavioral, physiological, and endocrine-immune responses in an individual animal to stressful stimuli that is consistent across time and various situations.

## Introduction

Coping styles have been widely defined in humans, from responses to disease to response to emotional stressors. Much that we know in both humans and animals is derived from Henry and Stephens in 1977. In animal research, specific coping styles were not explored until 1990 (de Boer et al. 1990), when stress hormone responses in rats shocked by electrical prod were measured. This research discerned two “types” of rats, and used the same vocabulary as in human psychology: passive rats (those that froze in response to being shocked) and active rats (those that attempted to bury the prod in bedding). These terms were later altered to reactive and proactive.

Continuing research has been conducted on a variety of species; primarily lab animals, but also poultry, swine, cattle, aquatics, wild deer, etc. Coping styles have been associated with vulnerability to stress-related diseases, evolutionary fitness, and thus, population ecology, production indexes, fear-related behavior, and aggression. Animal coping style is a qualitative measure of stress response, whereas a behavioral axis is a quantitative measure, i.e., the extreme nature or

amount of the response (Koolhaas et al. 2007; Steimer and Discoll 2005; Van Reenen et al. 2005).

## History

Before Henry and Stephens' research (1977), animals were thought to have two basal responses: fight or flight. Cannon in 1915 described the fight-flight response, where the animal has a "decision" to make when presented with stressful stimuli, either stand, analyze, and "fight" the stressor or turn and flee. Territorial control and aggressive behaviors were explained by this scheme in many different animals. It was not until Engel and Scmale (1972) when the second response type was described. They characterized it as the conservation-withdrawal response, which is controlled by cortisol release; the animal may become quiet or depressed in response to a stressor it cannot mitigate or retaliate against.

Von Holst et al. (1983) described responses in male shrews. Males, when placed in a novel environment with a resident territorial male, were characterized by their response to the threatening behavior. They described two distinct groups: an avoidant group and a freeze group. Later studies in mice reversed this study design and demonstrated two categories of readiness to attack an intruder. For example, Van Van Oortmerssen and Busser (1988) used genetics to breed high-readiness and low-readiness mice. Then, when these mice were placed within the same cage, the high-readiness mice consistently spent most of their time fleeing while low-readiness mice consistently remained immobile (Benus et al. 1991).

The hypothesis arose that the individual level of aggressive behaviors would relate to the individual's responses to environmental changes in general. Experiments testing this hypothesis in feral mice and rats demonstrated this individual tendency to follow consistent patterns in behavior in response to various environmental stimuli (De Boer & Koolhaas 2003; De Boer et al. 2003).

Behavioral correlation can be explained by Tinbergen's classifications of behavior (1972). The proximal explanation could involve

pleiotropy, where similar genes have a causal connection between traits, or similar hormones act on the same target receptors (Ketterson and Nolan 1999). Developmental explanations involve environmental conditions shaping behaviors in microenvironments on the individual basis (Stamps 2003). Functionally, certain coping styles can be selected for – or, in a historical explanation, they may be inherited from an ancestor.

It is generally accepted that coping styles are a component of the animal's overall psychology and behavior, and, when combined with behavioral axes, temperaments, and aversive responses, can perhaps be called animal personality. The idea of animal personality has become increasingly popular in animal behavior and neurobiology research; however, the general unease of anthropomorphizing has caused some reluctance to the term (see Vonk et al. 2017).

## Assessment and Utilization

There are many well-tested methods for assessing coping styles in animals. Many studies utilize neuroendocrine response levels in hormones like norepinephrine and epinephrine, and stress hormones like cortisol and corticosterone. This allows researchers to determine whether the animal is physiologically reacting in a more sympathetic or parasympathetic manner. Higher sympathetic levels should correlate with higher levels of aggressiveness, higher heart rate, and lower hypothalamus-pituitary-adrenocortical (HPA) axis reactivity, i.e., lower glucocorticoid production. The correlation between stress response and coping style determination has been challenged and a more popular hypothesis suggests a multidimensionality to individual variation.

Various behavioral tests are used depending on species. These tests strive to both assess personality components like exploration, impulsivity, and docility and the physiologic components, like heart rate, breathing rate, and cortisol levels. Tests assessing coping styles often have a restraint component or a novel component, whether it is a novel object, stimulus, or environment. Neophobia, or fear of novelty, is frequently assessed.



In piglets, one of the methods coined the “back test” involves putting a piglet on its back and restraining it for a certain amount of time (Bunter and Lansdowne 2004). Vocalizations and number of attempts to escape are recorded. Arena tests are used primarily in ruminants; the animal is placed in a novel enclosure with a human stranger. This test measures docility. The animal is measured based on how many steps it takes, how fast it moves, how far it stays away from the human, and how many vocalizations it produces. Similarly, open field tests place the animal alone in a novel area, where it cannot see other members of its flock or herd (Koolhaas et al. 2007). This test is done typically in poultry or herd animals. It assesses response to isolation and unfamiliar surroundings and exploration; vocalizations and number of steps are recorded. In larger ruminants, like cattle, flight speed is a marker of fear response after being processed and handled in a squeeze chute (Koolhaas et al. 2007). In aquatic species, fear response is measured by aversion tests with avoidance learning (Martins et al. 2011; Ferrari et al. 2013). The fish is given a chance to escape aversive stimuli and latency to eat and recovery of cortisol levels are recorded.

Homeostatic control of serotonergic neurons as well as neuropeptides like vasopressin and oxytocin have also been utilized to assess coping styles (Koolhaas et al. 1999, 2007). Vasopressin is released in higher amounts in animals that are more aggressive than animals that show little aggression. Still, there is little known about the causation of different behavioral and neuroendocrine characteristics. We cannot, of course, assess one aspect of behavior without considering the rest of the animal. The neurobiology is important to consider in research going forward to develop models in understanding coping style. Once better understood, it is possible that coping style may be used to understand disease vulnerability, population ecology, and animal welfare management.

Studies in behavior ecology have developed a model that determines how natural selection favors optimal coping styles in certain environmental contexts. Coping style as a conglomeration of territoriality, nesting behavior, foraging behavior, mating, antipredator defenses, etc., in

the wild may create an advantage for some animals and a disadvantage for others, thus affecting overall fitness. For example, aggression may be favored in an environment where territory and social hierarchy are important, but may be an inappropriate expense of energy and resources in another environment. Coping styles may provide an explanation as to why some apparently maladaptive behaviors persist throughout an environment or a species, depending on the cost of the maladaptive behavior versus other benefits, demonstrated in sunfish that chose to remain in fish pools during the day to feed, even when predation was at risk (Sih et al. 2003).

## Current Classifications

A summary table is provided below (Summary Table). The classification of coping styles is bimodal in nonhuman animals. Koolhaas et al. (1999) defined them as proactive and reactive; Wilson et al. (1994) used the terms boldness and shyness in marine animals. The proactive or “bold” animals are characterized by less fearfulness in arena tests, fast exploration in open field tests, higher aggression, and higher sympathetic responses. The reactive and “shy” animals explore the open field test more cautiously, are more likely to freeze in response to aversive stimuli, and have a relatively higher parasympathetic response to stress.

| Proactive (boldness)                  | Reactive (shyness)                 |
|---------------------------------------|------------------------------------|
| “Bold and aggressive”                 | “Cautious and shy”                 |
| Fast and superficial explorers        | Slow and thorough explorers        |
| Less fearful                          | More fearful                       |
| High sympathetic, low parasympathetic | Low sympathetic, high HPA activity |
| Lower immune response                 | Higher immune response             |

Cortisol measurements have been correlated with fear responses; thus, reactive animals usually have higher cortisol response as a result of their more reactive HPA axis.

Immune response has been recorded in relation to coping styles as well. Bolhuis et al. (2003) demonstrated that passive or reactive animals



mounted a higher immune response when infected. Thus, knowledge about coping styles could prove to be beneficial in production environments. Reactive classified piglets had increased weight gain post-weaning compared to proactive piglets (Giroux et al. 2000). In an intensive production environment, there may be selection pressure towards animals that fend off illness and have improved weight gain after stressful processing procedures. Proactive animals could be identified within a herd and managed differently to maximize their welfare and production potential.

## Conclusion

Coping styles in animals has intrigued behaviorists, ecologists, neurobiologists, and physiologists for many years. As more is discovered, it is becoming apparent that individual variation in animal personality is much more complex than we had assumed before. The two current classifications, reactive coping and passive coping, are continuing to evolve as we discover more about physiological and behavioral correlations. It is important that we continue to refine our knowledge of animal behavior and personality to fully understand animal cognition. Animal welfare, conservation, production, and medicine are all areas where understanding coping style will be beneficial.

## Cross-References

### ► Personality

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## Copulation

### ► Intromission

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## Copy Number Polymorphisms

### ► Copy Number Variant (CNV)

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## Copy Number Variant (CNV)

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## Synonyms

CNVs; Copy number polymorphisms; Copy number variation analysis; Copy number variation detection; Copy number variations

## Definition

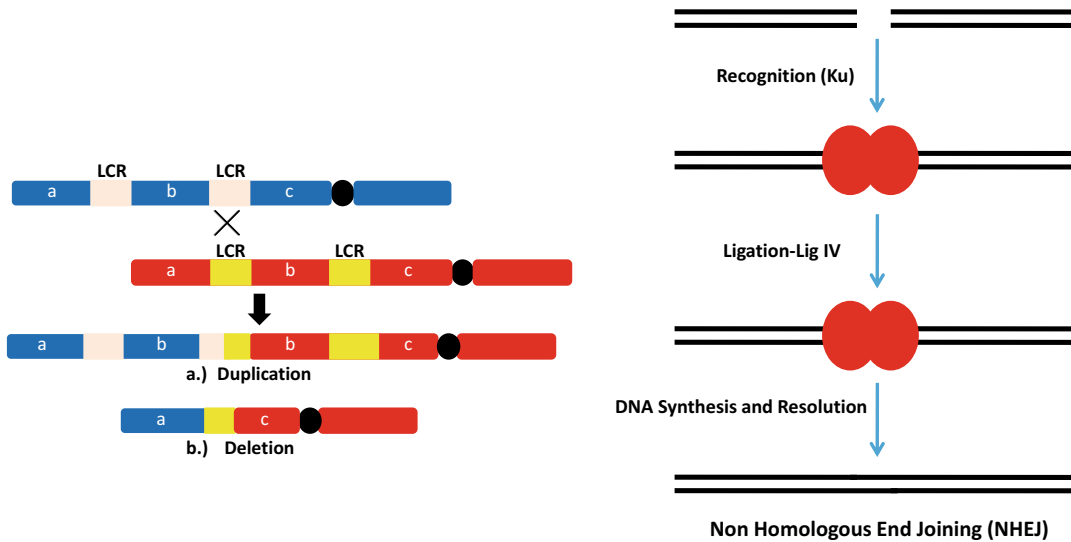
Copy number variant (CNVs) can be defined as an imbalance of genomic sequence (>50 bp) that alters the diploid status of a particular locus (Girirajan et al. 2011).

## Introduction

During the last few decades, followed by the human genome sequencing and resequencing process, it has been discovered that humans can not only differ at the level of DNA sequence but also in the number of copies of certain genes in genome. Such quantitative variation in genome, which include variation either in tandem arrays of repeats or insertions or deletions, are known as copy number variants (CNVs). Many a times CNVs lead to dosage imbalances. For instance, we carry two copies of a gene, one comes from paternal side and other one from maternal. Sometimes, only one copy may be present and on the other hand three or more than three copies may also be present. The basis for this alteration is mostly duplications and deletions, ranging in size from several hundreds to millions of base pairs.

Copy number variants play an important role in disease biology. The number of base pair differences due to CNVs between two individuals is almost more than threefold higher as compared with single nucleotide polymorphisms (SNPs). Considerable portion of human genome (approximately up to 12%; Redon et al. 2006) is considered to be CNVs. CNVs represent benign polymorphic variants present in >1% population and are well tolerated. This is also believed to play a significant role in human evolution. CNVs are a source of genetic diversity in humans often associated with genomic disorders.

CNV formation occurs by two recombination-based mechanisms, i.e., nonallelic homologous recombination (NAHR) and nonhomologous end joining (NHEJ) and retrotranspositions (Lee et al. 2007; Zhang et al. 2009). Recently a portion of CNV seems to occur as a consequence of



**Copy Number Variant (CNV), Fig. 1** Nonallelic homologous recombination (NAHR) and nonhomologous end joining (NHEJ) mechanisms for CNV formation have been shown, (1) shows NAHR which results in interchromosomal duplication and deletion, LCR is low

copy repeats, and (2) shows nonhomologous end joining in which if a double strand break is introduced, a dimeric protein Ku binds to DNA eliciting conformational changes, then sealing occurs by specialized DNA ligases (Lig IV)

fork stalling and template switching (FoSTeS) (Zhang et al. 2009; Perry et al. 2008) (Fig. 1). The mechanism of fork stalling and template switching can be summed up as under:

1. The replication fork stalls at a DNA lesion.
2. The lagging strand invades an adjacent active replication fork to a region with microhomology.
3. The lagging strand disengages once again and invades a further adjacent active replication fork where it anneals to another microhomologous region to restart synthesis.
4. Finally, the lagging strand returns to original replication fork to continue replication to the end of the chromosome.

A database named DECIPHER (Database of Chromosome Imbalance in Phenotype Using Ensembl) has been established by the Wellcome Trust Sanger Institute to enlist CNVs associated with genetic diseases. Other databases are also there, which include “Database of Genomic Variants” which was established by the Hospital for Sick Children, CNVD (Copy Number Variation in

Disease), and SCAN (SNP and CNV Annotation Database). Although majority of CNVs (~89%) are shared by diverse human races, their ancestry can be studied using CNVs, which have evolved to adapt different geographic environments.

## Mechanism of CNV Formation

The part of genome which is largely flanked by homologous repeats or segmental duplications is most likely to harbor CNVs. Tandem repetition of DNA segments lead to segmental duplications which are dispersed at different chromosomal loci through rearrangements. The CNVs which are associated with segmental duplications are mostly susceptible to chromosomal rearrangements via nonallelic homologous recombination. Some CNVs may be formed by nonhomology-based mutational mechanisms. There can be a relationship between the size of a CNV and the mutational mechanism associated with it. It has also been established that segmental duplications are generally associated with larger CNVs as compared to smaller CNVs.

## Role of Copy Number Variants in Evolution

An important aspect of CNVs which needs to be addressed is whether the pattern of CNVs is similar to other nonhuman primates or other organisms. In order to study the evolutionary significance of CNVs, chimpanzee and human CNV regions were compared. Analysis of copy number variations in human and chimpanzee genomes demonstrated greater role of CNVs as compared to SNPs. Majority of CNVs between human and chimpanzee genome is common, but one third of CNVs present in human genome is specific. Inbred strains of laboratory mice also harbor a large number of CNVs. CNVs may contribute to phenotypic variations in mouse strains. By correlating functional variations with CNVs identified in mouse it is possible to extrapolate the phenotypic consequences of orthologous CNVs in humans.

The role of CNVs in evolution can be studied by examining the persistence of different structural changes through multiple generations (Redon et al. 2006). Deletions generally experience negative pressure while presence of gene families indicates that duplications can experience positive selection.

## Analysis of Copy Number Variant

CNVs can be assayed using multiple methods, i.e., array CGH, SNP array or SNP chips with CNV markers, qPCR, next-generation sequencing platform, and high-resolution microarrays that include copy number probes and SNPs. BAC arrays were the first microarray platform used for detection of copy number variants which can detect deletions and insertions. Log ratio measurements are produced by this platform to identify deviations of patient's copy number state from normal. The log ratio values, which differ significantly from zero, represent the part of chromosome with aberrations. Copy number gains are indicated by positive log value ratios whereas loss in copy numbers is indicated by negative log value.

## CNVs and Genomic Disorders

Pathogenic role of CNVs came into picture with the elucidation of etiology of Charcot-Marie-Tooth Neuropathy type I (Lupski et al. 1991). It is well known that CNVs cover 12% of human genome and alter the gene expression; gene dosage CNVs are associated with many disorders, autism and schizophrenia being the most important in addition to sporadic and Mendelian diseases in humans. There are several neurological disorders associated with CNVs.

| Chromosomal loci | Deletion                 | Duplication       |
|------------------|--------------------------|-------------------|
| 16p11.2          | Autism                   | Schizophrenia     |
| 15q11.13         | Autism and epilepsy      | Angelman syndrome |
| 7q11.23          | Williams syndrome        |                   |
| 22q13            | Phelan-McDermid syndrome |                   |
| 22q11            | Schizophrenia            |                   |
| 17q12            | Autism and Schizophrenia |                   |

CNVs are also associated with several complex disorders, e.g., Lupus, Crohn, HIV-1. At least 20 nervous system-associated disorders which include Alzheimer's and Parkinson's disease have been reported to result from copy number variants. Gene associated with immune systems and brain development is more likely to be enriched by CNVs.

## CNV Map of Human Genome

A comprehensive atlas of CNVs in the human genome has been established. A first-generation CNV map of human genome was generated in 2006 by using SNP genotyping arrays for comparative hybridization intensities. The CNV map can be very useful in scanning for genes responsible for common diseases. CNV maps can be used to study familial genetic diseases and to target the disease-associated hot spot regions. This way a complete and accurate human genome reference sequence can be obtained.

## Conclusion

CNVs are major source of genetic diversity among humans and other organisms. CNVs also drive human genome evolution via exon shuffling and gene duplication. The pattern of CNV that each of us inherits is a reflection of our ancestry. However, frequency and occurrence of CNVs also vary in populations of different geographical locations due to selection pressure. Since CNVs often encompass gene they have an important role in diseases and drug response. CNVs, both inherited and de novo have been implicated not only in immunological and neurological disorders but also in kidney disorders, schizophrenia, autism, congenital heart disease, cardiomyopathies, etc. Genome sequencing and characterization of CNVs is required for assessing the pathogenicity of CNVs, which can be further utilized as an important tool in personalized medicine. Despite of numerous advances, many undiscovered CNVs may exist in human genome that need to be investigated for enhancing our knowledge about the formation, distribution, selection, and evolution of CNVs.

## Cross-References

- [Evolution](#)
- [Genetic Variation](#)

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## Copy Number Variation Analysis

- [Copy Number Variant \(CNV\)](#)

## Copy Number Variation Detection

- [Copy Number Variant \(CNV\)](#)

## Copy Number Variations

- [Copy Number Variant \(CNV\)](#)

## Copying

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## Synonyms

[Emulation](#); [Imitation](#); [Mimicking](#); [Object Movement Re-enactment](#)

## Introduction

Copying encompasses occurrences of social learning where observers reproduce the behavior, general behavioral organization, or actions of others. The broader term of social learning describes all instances of learning from others or their behavioral products (Heyes, 1994), so is not limited to copying; it includes simpler processes such as stimulus and local enhancement. Two main forms of copying, named imitation and emulation, are the focus of this entry.

Building upon previous classifications by Whiten and Ham (1992) and Whiten et al. (2009), we re-envision a copying taxonomy (Fig. 1), considering new developments in the field of animal social learning. Since these publications, the picture of copying has changed, and new theory and data thus warrant an update.

## Imitation

Colloquially, imitation often refers broadly to learning from others. The animal literature defines imitation more precisely, identifying subtly different forms. Whether animals imitate in ways homologous or analogous to humans is the subject of ongoing debate. Attempting to answer this question has been one of the main drivers behind dissecting copying into its many variants, as researchers traditionally attempt to rule out alternatives before concluding that behavioral similarity occurred through imitation.

## Bodily Imitation

Because imitation can enable high fidelity learning, some theorists postulate it plays an important role in the transmission of human cultures, permitting cumulative cultural evolution. In particular, “bodily imitation” is suggested to support complex cultural traits by enabling onlookers to precisely reproduce the actions they witness. For this reason, whether animals similarly match the *form* of others’ actions has received much research attention.

In one paradigm used by experimentalists, the “Do as I do” task, employed with animals ranging from primates, dogs, parrots to cetaceans, participants receive demonstrations of arbitrary and novel gestures (or sounds) before a trained request (like “Do this!”) is given. Researchers then assess whether observers faithfully reproduce the model’s bodily movements (“process copying”) without any contextual cues (end-state or location cues) that could contribute to behavioral matching. Typically, some behavioral concordance, such as in the domain of object-to-object acts, has been reported, although the proportion of actions animals reproduce is often low, and the acts that are mimicked can be imprecise (Huber et al., 2009). Such evidence suggests that some animals can, but may not readily, engage in bodily imitation. That animals enculturated by very close contact with humans seem to do better than their unenculturated counterparts in contexts such as these also has suggested that bodily imitation may not be intrinsic, but rather a learned ability facilitated by human engagement (Tennie et al., 2012).

Two-action tasks are also employed to assess copying (see Whiten et al., 2009). Groups are presented a puzzle box (sometimes called an “artificial fruit”) and demonstrations of either of two alternative means to open it. If different solutions then follow in each population, researchers conclude that individuals copied the solution demonstrated to their group. Many group level traditions have been demonstrated in diverse animal species using variants of this task, albeit the role forms of social learning other than bodily imitation may play in their formation is often not ruled out.

## Program-Level and Contextual Imitation

Two other categories of imitation, proposed by Richard Byrne, capture instances in which individuals socially learn hierarchical sequences of behaviors (“program-level imitation”) or copy the context in which to perform known behaviors (“contextual imitation”). These are distinguishable from bodily imitation as the faithful replication of behavioral form is not required. Although



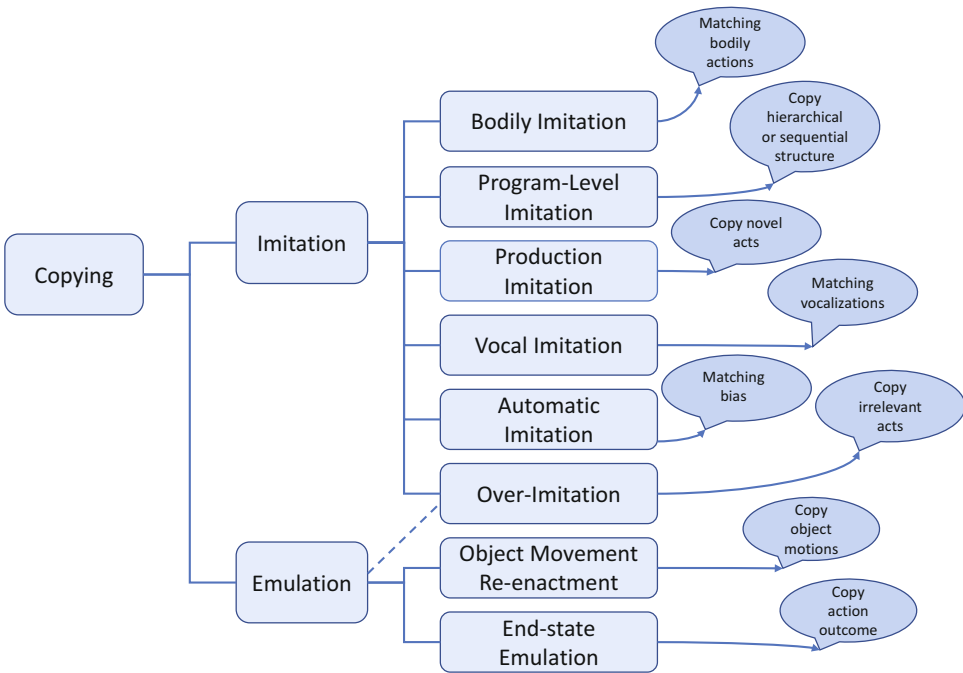
the latter is named contextual imitation, such episodes are only loosely “imitative” as users are not learning others’ behavioral actions per se but “when” or “where” to perform a known act (see Bates & Byrne, 2010).

In contrast, program-level imitation, included in our copying classification (Fig. 1), requires something of the behavioral form to be replicated or learned, even if imprecisely. When tasks are difficult, and actions are complex, it is unlikely that observers, whether human or animal, will faithfully copy them all from the outset. In this situation program-level imitation comes into play, allowing onlookers to learn something of the overall structure of behaviors (Bates & Byrne, 2010). One illustrative example is gorilla nettle processing. Captive and wild populations show similarities in the elements they use for this multistage process but differences in their overall organization (Byrne et al., 2011). This suggests gorillas learn what the authors describe as the “gist” of the behavior from conspecifics, but not necessarily the minute actions involved (Byrne et al., 2011). One can imagine that a variety of

multistep actions, placing high demands on working memory, are learned this way, requiring repeated observations and individual practice to acquire, even in humans (e.g., learning complex dances or exercise routines).

Production Imitation

On the other end of the continuum to contextual imitation is production imitation (Bates & Byrne, 2010). Behaviors to-be-copied can either be known (within one’s repertoire) or novel (new to the observer), with the latter referred to as “production imitation.” The mechanics behind learning novel and familiar actions may differ, and many researchers suggest that copying new behaviors presents a more cognitively demanding challenge than contextual imitation. The Do-as-I-do tasks described earlier offer a way to establish if animals copy unfamiliar behaviors or sounds. Similarly, novel two-action tasks are appropriate for establishing whether new solutions spread within populations.



**Copying, Fig. 1** Varieties of copying. Bubbles on the right provide brief definitions of the distinctions made and the dotted line indicates the category may be a subtype of emulation and/or imitation

## Vocal Imitation

Vocal imitation is a specialized form of social learning that enables listeners to match vocalizations with their own auditory experiences. Local “dialects,” where song structures are similar within communities but differ across communities, such as those of some whales and birds suggest vocal imitation. These local dialects can emerge by juveniles imitating sounds of older individuals. They can also evolve as new variants are introduced – an example of cultural evolution. Important to assessing vocal imitation is that *matching* occurs socially, and not because of genetic similarity. Without matching sounds or hierarchical patterns, song modified by external auditory input would be more parsimoniously described as acquired through vocal social learning.

## Automatic Imitation

Automatic copying describes the observation that witnessing other’s actions can elicit the same act in the onlooker, a response so “automatic” that it interferes with the ability to perform a different action. Evidence for this is documented in dogs, budgerigars, and children. Dogs, for example, take many more trials to learn a behavioral method different from that demonstrated by their owners (opening a door with their head when their owner uses their hand (paw) and vice versa) than dogs that were rewarded for using the same demonstrated action (matching the body part (head or paw) of their owner) (Range et al., 2011). The difference is between “Do-what-I am-doing” versus “Do-what-I-am-*not*-doing,” with longer learning periods in the latter indicating difficultly inhibiting witnessed actions. Thus, depending upon task demands and what others are doing, the automatic imitation bias can facilitate or impede one’s ability to meet these demands.

## Over-Imitation

The final form considered is over-imitation, which describes the tendency to copy all witnessed

actions, even those superfluous to the task at hand. One benefit of over-imitation is skill development without necessarily understanding why actions are performed, which can play a role in the development of cultural norms and conventions. Limited tests of animal over-imitation have been performed, but there is little indication of its occurrence beyond humans, even in our closest living primate relatives. Horner and Whiten (2005) provide an illustrative example, comparing human children and young chimpanzees. Both species, presented with either opaque or transparent puzzle boxes, witnessed demonstrations of both causally relevant and irrelevant actions to open them. Chimpanzees and children reproduced relevant and irrelevant actions when the box was opaque, but children alone reproduced the irrelevant actions in the transparent condition. This, and many more studies since, indicates that humans over-imitate even when actions seem clearly unnecessary to task success. Whether tasks designed to assess over-*imitation* in humans and animals show imitation, however, remains to be clarified. Like the two-action tasks described, other processes, such as stimulus enhancement or emulation, may lead to observed behavioral similarity. Emulative learning is the second copying category to which we now turn.

## Emulation

One take home message from the animal imitation literature is their copying is often imprecise. Many researchers suggest that animals, particularly primates, emulate rather than imitate. That is, they learn something from other’s actions but rarely copy the behaviors themselves. Following previous classifications (Whiten et al., 2009), we briefly expound three forms of emulative learning.

## End-State Emulation

End-state emulation accounts for the potentiality that organisms, including humans, recreate desirable outcomes of others’ actions but use their own means to get there. Although individual learning

occurs at the process level, the end-state is replicated, thus being considered a form of “copying” (Whiten et al., 2009). A handful of studies demonstrate such learning in humans and animals. One illustrative example from nonhuman primates, in which there is strong evidence for this form of copying, comes from the “floating peanut task.” To uncouple learning from actions as opposed from action results, Tennie et al. (2010) provided apes either full demonstrations of how to solve this task – a model spitting into a tube to raise a peanut to where it was accessible, or goal demonstrations – a model pouring water into the tube to raise and collect the nut. As apes had only the former “spit” method available to them, if copying actions (imitation) was beneficial, apes should perform best in the “full” demonstration condition. This was not what was found; apes performed similarly in both conditions, suggesting emulative learning. This and other studies paint a picture of our closest living relatives as emulators that do not regularly mimic actions but assimilate goals and end-products using their own methods.

### Object-Movement Re-enactment

In object-movement re-enactment (OMR), instead of copying bodily actions to move objects, it is the object movements that are copied. That is, even if an observer does not attend to details of body movements, they could still learn from the action consequences. One way to test OMR is using “ghost displays,” also used as a control for emulation more broadly. To remove the need for actions, therefore ruling out imitative learning, objects are “rigged” so they are automated. Ghost displays with chimpanzees and humans demonstrate emulative learning suggestive of OMR, for example, chimpanzees re-enact the side to which a sliding door moves in the absence of a demonstrator. However, observing a model’s behaviors confers added benefit when tasks are more difficult, and ghost displays also indicate affordance learning or end-state emulation could be at play (reviewed in Whiten et al., 2009).

### Affordance Learning

Emulation also comes in the form of learning object affordances from watching others interact with the objects. Through “affordance learning,” individuals learn something of the physical features of items being manipulated by others, which helps them to similarly utilize the objects in their environment. For example, the utility of a chair may be unrecognized until seeing someone sit down on one. Any subsequent act of sitting may look like imitation – there are only so many sitting movements humans make; however, similarity can arise by socially learning the chair’s properties (Whiten et al., 2009). Returning to the floating peanut task, if participants learn the properties of the tube (that it can hold water) and/or water (a peanuts float in water) from social demonstrations, we would conclude affordance learning was at play. We distinguish this form of emulation to highlight that we do not include it as constituting copying, unlike the forms described above.

### Conclusion

Copying provides animals with an extra-genetic inheritance system that enables fast and efficient transmission of potentially adaptive information and skills, avoiding some of the costs associated with personally exploring the environment. Copying also plays an important role in homogenizing group level behavior such that traditions or cultures arise. While we know that many species are capable of social learning, the degree to which the many *forms* of copying may be shared remains less well understood. Dissecting the forms is consequential for recognizing the similarities and dissimilarities between human and animal learning, with implications for identifying their phylogenetic histories.

### Cross-References

- [Andrew Whiten](#)
- [Artificial Fruit](#)
- [Bennett G. Galef](#)

- ▶ Cognitive Imitation
- ▶ Contagion
- ▶ Cultural Transmission
- ▶ Culture
- ▶ Cumulative Culture
- ▶ Deferred Imitation
- ▶ Emulation
- ▶ Ghost Control
- ▶ Imitation
- ▶ Learned Affordances
- ▶ Michael Tomasello
- ▶ Rational Imitation
- ▶ Social Learning
- ▶ Stimulus and Local Enhancement

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## Core Area

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## Definition

The core area is the more intensively used internal part of a home range. Consequently, in the case of a perfectly uniform use of space across the entire home range, there is no core area. Core areas are measured in units of area and time and are generally identified by a change in the relationship between the area used and the probability of use.

## Introduction

It is a common observation that most mobile animals repeatedly use the same area over time, instead of roaming over the entire available landscape, and this area used by an animal over a specific period of time is defined as the animal's home range (Fieberg and Börger 2012). The movements of animals within a home range are also typically not uniform (Samuel et al. 1985), with certain areas used more frequently; this area of more frequent (or intense, or concentrated) use is called the core area (Clutton-Brock et al. 1982; Powell 2000; Wilson et al. 2010; Vander Wal and Rodgers 2012), and the area of the home range external to the core area is called the home range “periphery.” Within the core area, there is hence a higher probability to encounter an individual

animal (Wilson et al. 2011), and core areas may be associated with specific habitats and ecological functions; for example, core areas in fishers (*Pekania pennanti*), small carnivorous mammals found in the boreal forest in North America, tend to be located in areas with a more heterogeneous and diverse forest structure and composition (Sauder and Rachlow 2015). The location, size, and structure of core areas hence provide information on the ecology of animal movements and can also inform wildlife management and conservation, for example, for the planning of protected areas or for assessing the impact of land use changes (e.g., planning of new roads).

### Core Areas and Home Ranges

The core area is an internal part of the home range of an animal, and thus the latter must be estimated and quantified first; consequently, all issues concerning sample size and sampling design, home range estimation methods, etc. equally apply for core area estimation (Fieberg and Börger 2012). A home range is an emergent space use pattern that results from animals restricting their movements within a certain area over a certain time period, while attempting to meet their needs for growth, survival, and reproduction (Börger et al. 2008). A home range is estimated from a regular sample of animal movements, collected over a defined time interval, typically using GPS or VHF tags attached to animals, using statistical methods such as kernel density estimation (Fieberg and Börger 2012). It is important to use such methods as they provide an estimate of the relative frequency distribution within the home range area of an animal's location over time – this is called the utilization distribution function (UD) and can be thought of as a measure of the probability to encounter an animal in a certain area. UD values range between 0% and 100% and the area enclosed by a line of constant UD value, called an isopleth line, provides measures of home range and core area size – typically, 95% or 90% isopleths are used to delineate the home range (Fieberg and Börger 2012). Thus, methods such as kernel density estimation provide

estimates of both area and probability of use, both of which are fundamentally needed to identify a core area. Unfortunately, many researchers often use a shortcut, by arbitrarily defining the core area as the 50% UD. However, home ranges, and hence also core areas, are dynamic patterns which can change by several orders of magnitude within and between individuals (Börger et al. 2006); hence using such a constant criterion for all individuals will likely lead to strongly biased results and conclusions and should be avoided (Wilson et al. 2010; Vander Wal and Rodgers 2012).

### Identifying the Core Area

The concept of a core area is fundamentally linked to the relationship between the probability of use and the size of the area used by animals within a home range. If an animal would move in a uniform way across all the home range, a linear constant relationship with a slope of 1 would be observed between the probability of use and the associated size of each home range isopleth. In other words, the increase in the size of the area covered by a 25% UD isopleth compared to a 50% UD isopleth would be equal to the increase in the associated UD value. In reality, it is a common observation that animals tend to spend a disproportionate amount of time in a relatively smaller area of the home range and move less often in the remaining areas (Clutton-Brock et al. 1982; Samuel et al. 1985; Powell 2000); hence the area of UD isopleths first increases less slowly than the associated UD isopleth value, thus with a slope smaller than 1, and increases faster, with a slope above 1, beyond a certain UD value (Vander Wal and Rodgers 2012). The inflection point of this area vs. probability of use relationship is taken as the UD value delimiting the core area. Graphical methods were firstly used to identify the core area UD value (Clutton-Brock et al. 1982; Powell 2000); Vander Wal and Rodgers (2012) presented a more rigorous and repeatable approach, based on standard linear and nonlinear statistical models applied to the UD vs. area data. A major further improvement has been achieved by Wilson et al.

(2010), using a Bayesian-based approach which allows to more robustly identify the core area boundaries and, for the first time, also associated measures of uncertainty, as well as assess if the movement data support the case of a single- or a multi-core area. Using this individual-based, robust, and repeatable approach will allow to markedly advance the study of animal core areas to understand the underlying behavioral and ecological processes.

### Beyond the Core Area vs. Periphery Dichotomy

While the core area is an important and useful concept, the internal structure of home ranges can provide more information than simple core vs. periphery dichotomies; for example, Börger et al. (2006) showed that using multiple UD isopleth measures, closely linked to clear ecological questions, can markedly increase the biological inferences obtained. If sufficiently frequently sampled movement data are available, further understanding can then be obtained by using newer methods which go beyond the UD and directly allow to identify home range areas that are intensively exploited or repeatedly visited, as well as using multi-sensor biologging methods which allow to include further metrics, such as the type of behavior displayed at specific locations or the state of individuals.

### Conclusion

The core area is the internal, more intensively used, area of animal home ranges. It is a useful metric for understanding the patterns and drivers of animal movements and space use, but it is imperative that modern, repeatable methods are used, avoiding traditionally used arbitrary approaches. Further advancement will come from using methods which go beyond the core area vs. home range periphery dichotomy, integrating space use, movement, and behavior analyses.

### Cross-References

► [Home Range](#)

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### Core Number System

► [Approximate Number System \(ANS\)](#)

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### Core/Heart of the Cell

► [Nucleus](#)



## Correlation

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## Synonyms

Dependence; Statistical association

## Definition

Correlation, in statistics, is a predictive relationship between two variables. One can find out the nature, direction, and strength of the association between two factors by using this measure of dependence.

## Introduction

The word correlation is used in everyday life to denote some form of a relation between two random variables. We might say that we have noticed a relation between unemployment and inflation. Correlation is a real number that gives us an idea of the degree of association between two variables. At a basic level, it is also known as “bivariate” statistic. Thus, correlation is a unitless value that measures the strength of the linear association between two variables and the nature of the relationship. The relation between two factors can fluctuate from absolute to not at all.

If two variables are moving in the same direction, i.e., as one increases, another also increases, or as one decreases, another also decreases, then there will be a positive correlation between those variables. For example, the gravitational force increases as the mass of the object increases. However, if the changes in the two variables are in the opposite direction, i.e., if one variable increases the other decreases or vice versa, then there will be a

negative correlation; for example, the gas volume decreases as their pressure increases or the demand for commodity increases as the price of such commodity decreases. The absence of any relationship between the two variables leads to zero or no correlation (Kothari 2004); for example, the grades obtained by students in examinations and their height.

## Correlation Estimation

There are different ways of estimating the correlation between two random variables.

### Scatter Diagram

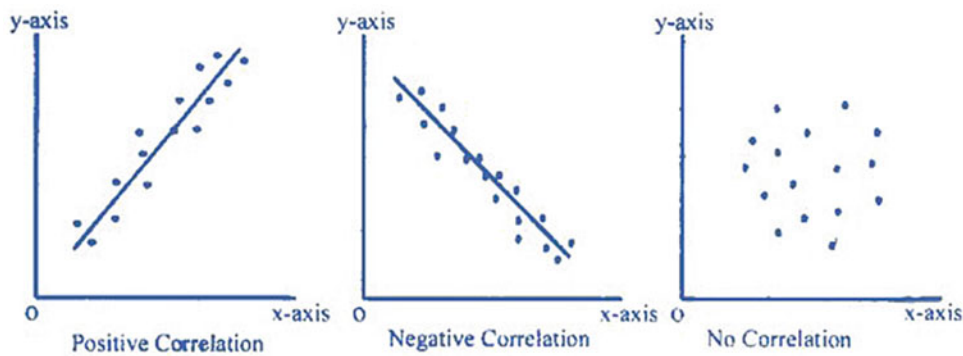
A scatter diagram is a diagrammatic method to observe correlation. Here, one variable, x-values are depicted on the horizontal axis and another variable; y-values are on the vertical axis. A pattern between the coordinates would indicate the correlation. If the trend is **downward sloping** from left to right, it means a negative correlation. If it is **upward sloping** from left to right, it means a positive correlation. If the points are scattered with no discernible linear pattern, then the variables are said to be **uncorrelated** (Fig. 1).

### Pearson's Correlation Coefficient

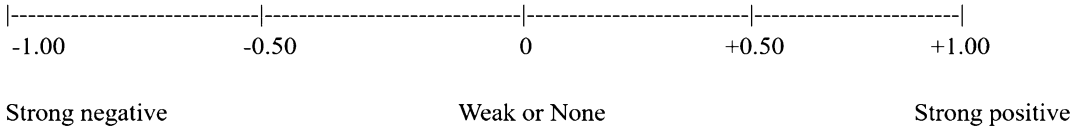
The correlation coefficient is another method of measuring the statistical relationship or strength of the association between the two variables. It is represented in an example by the value “r.” It can range from  $-1.00$  to  $+1.00$  (Fig. 2).

When the correlation coefficient approaches  $+1.00$ , it implies there is a **positive relationship (or perfect positive)** or a high level of association between both variables. It means that the greater or lower the score of a member on one variable, the greater or lower the score will be on the other variable, respectively. For instance, there is a positive correlation between height and weight of plants up to a particular age.

Though there are many measures of correlation, the **Pearson product-moment correlation coefficient**, which measures the degree of linear association between two continuous variables, is the most used measure (Gilbert 1986). Pearson's



**Correlation, Fig. 1** Scatter diagrams showing positive, negative, and no correlation between x and y variables



**Correlation, Fig. 2** The values of “ $r$ ” ranges from  $-1$  (absolute negative correlation) to  $+1$  (absolute positive correlation) including  $0$  (no correlation)

coefficient  $r$  is acquired for a sample drawn from a populace. The populace value of Pearson’s coefficient is called rho ( $\sigma$ ), and in this way,  $r$  is a gauge of  $\sigma$ . The formula for  $r$  is as follows:

$$r = \frac{N \sum xy - (\sum x)(\sum y)}{\sqrt{[N \sum x^2 - (\sum x)^2][N \sum y^2 - (\sum y)^2]}}$$

Note: In this formula,  $N$  is equal to the number of pairs of scores, and  $\sum xy$  is called the total of the cross products.

**Spearman’s Rank Correlation Coefficient**

Another measure to calculate the correlation coefficient is **Spearman’s rank correlation method**. It was formulated by an English psychologist Charles Spearman. This method uses a monotonic function to show the relation between two variables, unlike Pearson’s correlation, where it is for linear relationships only. Spearman’s correlation is a nonparametric measure and generally calculated for ordinal or ranked data (Kothari 2004).

Spearman’s correlation coefficient ( $r_s$ ) can be calculated by the following formula:

$$r_s = 6 \sum D^2 / N(N^2 - 1)$$

where

$D$  = difference between the observation of two ranked variables

$N$  = number of observations

The range of  $r_s$  is also  $+1$  to  $-1$ , similar to the Pearson’s coefficient.

**Kendall Rank Correlation Coefficient**

Kendall rank correlation method is an alternative to the Spearman’s correlation coefficient method, as the former one can be used to know the non-linear associations between the two variables. This simply means that it can measure the monotonic as well as linear correlation function. Kendall rank correlation coefficient ( $\tau$ ) is a nonparametric test and generally used for the small sample size or for

tied ranks. Kendall's correlation coefficient establishes the strength of association based on the pattern of concordance and discordance between the pairs of observations. For any given set of paired variables  $x$  and  $y$ ,  $\tau$  can be calculated as:

$$\tau = (\text{No. of concordant pairs} - \text{No. of discordant pairs}) / n(n-1)/2$$

where denominator  $n(n-1)/2$  represents the number of all possible bivariate data points.  $\tau$  also ranges from +1 to -1 for untied ranks.

### Mantel Test Coefficient

It was propagated by American biostatistician Nathan Mantel in the late 1960s. This test is used for non-normal distributions, mainly in the field of ecology and genetics, where data is presented in the form of two same dimensional matrices (Diniz-Filho et al. 2013).

Suppose there are two animal species  $i$  and  $j$ , with genetic distance ( $g_{ij}$ ) and geographical distance ( $d_{ij}$ ) between them, then Mantel test coefficient ( $Z_m$ ) can be given as:

$$Z_m = \sum_i \sum_j = 1/n \sum_i \sum_j g_{ij} \times d_{ij}$$

where  $n$  represents the total population.

Here,  $Z_m$  is just the summation of products of both distances. Therefore,  $Z_m$  will be contingent on the number of populations and the distances. In the late 1970s, the Mantel test met with several criticisms for biasedness as this test works fine only for large sample sizes. To avoid this partiality, a null distribution must be done empirically by permuting rows and columns of one of the distance matrices.  $Z_m$  ranges from +1 to -1.

### Phi Correlation Coefficient

The phi correlation method is again a nonparametric test that is used to show associations between two noncontinuous variables, for example, the number of males and females in a school. English mathematician Karl Pearson gave this method. Phi coefficient ( $\varphi$ ) can be calculated easily from the chi-square result as follows:

$$\varphi = \sqrt{(\text{chi-square} \div \text{sample size})}$$

However,  $\varphi$  is calculated only when  $p < 0.05$ ; otherwise  $\varphi^2$  (i.e., ratio of chi-square and sample size) is sufficient to measure the amount of variance in the dependent variable, which can be explained by the independent variable. For example,  $\varphi$  of 0.72 means that the independent variable accounts for 52% of the variance in the dependent variable. The  $\varphi$  ranges from 0 to +1, where +1 means there is a perfect 1 to 1 correlation between the two variables (Frey 2018).

### Significance of a Correlation Coefficient

It is essential to mention that just the value of  $r$  cannot convey any information about the good (significant) or weak (insignificant) correlation between the two variables because it also depends upon the number of observations under study. Therefore, in the absence of a sufficient number of observations, one cannot calculate the proper association between two variables.

### Conclusion

Correlation is one of the popular statistical tools to calculate the degree of relationship between two variables, and which is utilized by researchers in general. Depending upon the value of correlation coefficient ( $r$ ), one can categorize correlation as positive, negative, or no correlation. To obtain the correlation, one can proceed manually through the above formula or some readily available statistical analysis software like MS-office Excel, SPSS, etc. However, the main thing is to obtain the proper inference from the calculated  $r$  values in light of the number of samples and  $p$ -value.

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## Corridor Illusion

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## Synonyms

Ebbinghaus illusion; Ponzo illusion

## Definition

An illustration of size constancy in which two identical figures appear to be radically different in size. If the figures are placed in a picture of a corridor, the one placed in the distance appears larger than the one placed in the foreground. This is because depth cues affect expectations about true size (APA [n.d.](#))

## Introduction

In terms of visual perception, several species of animals share a common array of visual illusions. In particular, many animals are susceptible to the corridor illusion. This illusion occurs when objects of the same size appear to be different sizes due to positioning in a corridor. Humans are commonly studied for this illusion, but expansive research is currently being conducted to determine similar visual perceptions in animals. This will allow researchers to better understand the cognitive processes that animals have by comparing their visual processing to humans. Much research has focused on primates, given their high genetic similarity to humans.

Barbet and Fagot (2002) studied baboons (*papio papio*) to determine the extent these

primates experience corridor illusions. The experiment indicated chimpanzees do in fact experience corridor illusions, since the primates responded differently between stimuli (images of humans) in a corridor. More specifically, the baboons were trained to move a joystick when the images of humans appeared to be different sizes. Additional data collected by Imura, Tomonaga, and Yagi (2008) showed there are slight differences between humans and chimpanzees. Both chimpanzees and humans responded to the stimuli in a manner that signified that each perceived corridor illusions in the study, but chimpanzees were more inclined to report these illusions when the stimuli were placed closer to a ceiling; humans were more likely to notice the corridor illusion if the stimuli were closer to the floor. This was hypothesized to be caused by evolutionary differences, such as each species adapting to the environment that is inhabited.

Primates have been a major focus in research on this topic, but other studies have shown potential evidence that corridor illusions exist in species less related to humans. In one example, Hataji, Kuroshima, and Fujita (2020) tested the visual perception of pigeons, providing significant statistical support for corridor illusions being an aspect of pigeons' visual processing.

## Factors in Corridor Illusions

Contextual cues and perception are what influence visual perception causing corridor illusions, but other factors could also contribute. For example, linear perspective is a prime reason for differences in depth perception of visual stimuli, which changes the appearance of objects (Yildiz et al. 2019). Furthermore, the spatial layout of these experiments appears to enhance or reduce the corridor illusion. Spatial differences alter the perception of visual content, thus changing the perception of the observer (Richards and Miller 1971).

## Conclusion

Evidence for the perception of corridor illusions is accumulating across various species, including humans, chimpanzees, and pigeons. Importantly,

research has determined there are several factors that lead to and moderate corridor illusions. Contextual cues are often held as one of the most prominent reasons for the illusion. Other studies suggest linear perspective and evolutionary traits inhibit this visual process.

## Cross-References

- [Ebbinghaus Illusion](#)
- [Ponzo Illusion](#)
- [Visual Perception](#)

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## Cortex Man

- [Homunculus](#)

## Cortical Somatotopic Map

- [Homunculus](#)

## Corticalization

- [Encephalization](#)

## Corticosterone

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## Synonyms

11 $\beta$ ,21-Dihydroxy-4-pregnene-3,20-dione;  
11 $\beta$ ,21-Dihydroxyprogesterone; 4-Pregnene-11 $\beta$ ,21-diol-3,20-dione; Kendall's compound B; Reichstein's substance H

## Alternative Words

Corticosteroid; Steroid hormone

## Definition

Corticosterone is an adrenal steroid hormone, the major glucocorticoid released by the mammalian systems (except humans). Glucocorticoid hormones are also referred as corticosteroid hormones synthesized mainly in the adrenal cortex; however, more recently the enzymes involved in their synthesis have been found in a variety of cells and tissues, including the heart. Its main function is to regulate the metabolism of carbohydrates and proteins along with regulation of water and electrolyte balance in the body.

## Introduction

The adrenocortical layer produces corticosterone in rodents under the influence of adrenocorticotrophic hormone (ACTH). Mammals typically possess two adrenal glands; one located superior to each kidney (adrenal or supra renal) (Barrington 1963). The adrenal gland weighs on average 4–6 g and measures 4–6 cm long and

2–3 cm wide (McMINN 2003). Each limb normally measures <5 mm in width and the body should measure <10 mm in width (Sutton 2003; Prokop and Galanski 2003). Proportionately, the adrenal size is larger in neonates and infants, being almost one-third of the size of the kidney (Prokop and Galanski 2003). Each adrenal gland has two distinct structures, the outer adrenal cortex and the inner medulla, both of which produce hormones. One of the main functions of the adrenal cortex and the gonads is steroid hormone synthesis. The process in which specialized cells in specific tissues synthesize steroid hormones is generally referred to as steroidogenesis. Steroid hormones can be roughly divided into five groups according to their physiological behavior: adrenal mineralocorticoids, which regulate the salt balance and maintain blood pressure; glucocorticoids, which regulate carbohydrate metabolism and manage stress; progestogens and estrogens, which are mainly produced by the ovaries and regulate reproductive function and secondary sex characteristics in the female; and androgens, which are mainly testicular in origin and are essential for fertility and secondary sex characteristics in the male. These all share certain structural similarities and arise from a common series of pathways. Cholesterol is the precursor for all the steroid hormones, and although it can be synthesized *de novo* from acetate, most of the cholesterol needed is derived from plasma low density lipoproteins (LDL). Tropic hormones also stimulate the uptake of LDL cholesterol in addition to stimulating steroidogenesis. Most of the steroidogenic enzymes belong to the cytochrome P450 oxidation group, among which five enzymes are involved in adrenal steroidogenesis: P450scc

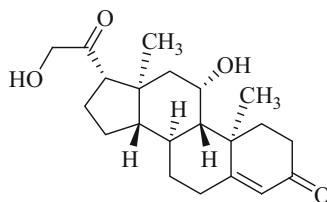
(side chain cleavage), P450c11 (11-hydroxylase), P450c17 (17- $\alpha$ -hydroxylase), P450c21 (21-hydroxylase), and P450aldo (aldosterone synthase). The first two of these are located in the mitochondria and the last two in the endoplasmic reticulum. In addition, P450aro mediates the aromatization of androgens to estrogens in the gonads. All steroid hormones are synthesized from the same precursor, cholesterol, but the end product depends on the complement of enzymes present in the tissues (Miller and Auchus 2011). Corticosterone is the precursor molecule to the mineralocorticoid aldosterone, one of the major homeostatic modulators of sodium and potassium levels in vivo (Fig. 1).

## Discovery

Corticosterone-like substance was identified by Mason et al. in the year 1937 while working with adrenalectomized dogs. In the early 1920s, Dr. Edward Kendall, a biochemist interested in endocrinological disorders, with the assistance of Drs Phillip Hench and Charles Slocum, extensively researched the adrenal gland and injected a part of adrenal extract (later known as cortisone) to 14 patients which ultimately alleviated rheumatoid arthritis leading to the receipt of the Nobel Prize in Medicine in 1950 (Kendall 1951).

## Corticosterone Biosynthesis

Adrenal glomerulosa cells mainly synthesize and secrete the mineralocorticoids, while the adrenal fasciculata cells synthesize and secrete the



(8*S*,9*S*,10*R*,11*S*,13*S*,14*S*,17*S*)-1,7,8,10,11,12,13,15,16,17-decahydro-11-hydroxy-17-(2-hydroxyacetyl)-10,13-dimethyl-2*H*-cyclopenta[*a*]phenanthren-3(6*H*,9*H*,14*H*)-one

**Corticosterone, Fig. 1** Corticosterone



glucocorticoids cortisol (in humans) and corticosterone (in rodents). The first, rate-limiting step in the synthesis of all steroid hormones is the conversion of cholesterol to pregnenolone. In mitochondria this involves three distinct reactions, which are mediated by a single enzyme, P450scc, the activity of which is not the critical factor, but rather the supply of the substrate cholesterol from the outer mitochondrial membrane to the inner mitochondrial membrane where the P450scc enzyme is located (Chapman et al. 2005).

Absence of P450scc activity results in an inability to synthesize any steroid hormone and leads to death due to mineralocorticoid deficiency. Patients with a lack of P450scc can be treated with glucocorticoid and mineralocorticoid steroid hormone replacement if diagnosed early enough. Pregnenolone may subsequently undergo one of two conversions. It may be converted by  $3\beta$ -HSD to progesterone, which is the first biologically important steroid in the pathway, or else it may undergo  $17\alpha$ -hydroxylation mediated by P450c17 to yield  $17\alpha$ -hydroxypregnenolone. Progesterone can also be hydroxylated by P450c17, resulting in  $17\alpha$ -hydroxyprogesterone. P450c17 has two activities, that of a  $17\alpha$ -hydroxylase and that of a C-17,20 lyase capable of breaking up the C-17,20 carbon bond of  $17\alpha$ -hydroxypregnenolone or  $17\alpha$ -hydroxyprogesterone, yielding dehydroepiandrosterone (DHEA) or androstenedione, respectively. P450c17 is a key branching point in steroid hormone synthesis, directing pregnenolone toward the sex steroids (both hydroxylation and cleavage activities of the enzyme), the glucocorticoids (only hydroxylation), or the mineralocorticoids, if neither of the enzyme activities is participating. After the synthesis of progesterone and  $17$ -hydroxyprogesterone, P450c21 can hydroxylate these steroids at the 21 position, resulting in deoxycorticosterone and 11-deoxycortisol, respectively. The final step in the synthesis of adrenal mineralocorticoids, and glucocorticoids is mediated by P450c11, which also mediates the final steps in the synthesis of aldosterone from deoxycorticosterone. When the P450c21 step is impaired, cortisol synthesis decreases, leading to overproduction of ACTH. Adrenal steroid synthesis is stimulated in this

condition and  $17$ -hydroxyprogesterone is converted to androstenedione and further to testosterone, leading to severe virilization of the female fetus. This disorder is known as congenital adrenal hyperplasia (CAH). Mutations in StAR cause lipid CAH, which disrupts the synthesis of all adrenal and gonadal steroids. Affected genetic males are born with normal female external genitalia (Miller and Strauss 1999; Stocco 2001).

### Hypothalamic-Pituitary-Adrenal (HPA) Axis

The HPA axis, which has traditionally been seen as the body's "stress system," and which ultimately controls levels of cortisol and other important stress related hormones, is generally underactive in people suffering from chronic fatigue syndrome (CFS) and burnout. New research is beginning to show that the HPA axis should instead be thought of as the body's energy regulator, as it is ultimately responsible for regulating many of the hormones, nervous system activity, and energy expenditure in the human body, as well as modulating the immune system and the digestive system. In CFS and burnout the HPA axis tends to be underactive, which is likely in many of the various physical and mental symptoms associated with these conditions. Under normal condition, the adrenal glucocorticoids, the end product of the HPA axis, provide a front-line of defense against threats to homeostasis (e.g., stress).

### Interrelationship between Male Gonadal and Adrenocortical System

These two axes, HPA and HPG, show significant similarity in terms of their regulation mechanisms. The hypothalamic central nervous system discharges GnRH and adrenocorticotropin releasing hormone (CRH), which is transported to the anterior pituitary, where they stimulate the gonadotrophs and corticotrophs, respectively. In response to stimulation, these cells in turn secrete the gonadotropins (FSH, LH) and ACTH. Under normal conditions, the hypothalamic-pituitary-adrenal (HPA) axis maintains frontline of defense

against stress. On the other hand, chronic HPA drive and glucocorticoid hypersecretion have been implicated in the pathogenesis of the several forms of systemic, neurodegenerative, and affective disorders. HPA axis is influenced by gonadal alteration. Functional cross-talk between the gonadal and adrenal axes is due to the interactive effects of sex steroid and glucocorticoids. This is the possible explanation why several stress-linked diseases are sex-dependent. Imbalance of one endocrine system is not without the effects on other. The adrenal axis regulates gonadal function and reproductive behaviour by modulating various components of hypothalamo-pituitary-gonadal (HPG) axis, including sex steroid release (Dallman, 1993).

In humans and rodents, stress and high doses of glucocorticoid generally disrupt all aspects of HPG function (Tilbrook and Clarke 2006). Conversely, estrogens and androgens, which form the basis for sex and individual differences in HPA function, act on several levels of the HPA axis, including adrenocorticoid synthesis, stress-induced ACTH, and glucocorticoids release. In addition to regulate the positive feedback of the HPA axis, several *in vivo* studies indicate sex differences and implicate sex steroid effects on glucocorticoids-mediated negative-feedback strength in rat (Kovács et al. 2000). This would suggest a probability for gonadal and adrenal interaction at genomic and cellular levels. Moreover, androgen and glucocorticoid receptors are capable to regulate transcription by physically interacting each other. Several brain regions, mostly hippocampus, amygdala, brain stem, several hypothalamic nuclei, show both sex and adrenal steroid receptors and functional connectivity to the HPA axis (Viau 2002).

Sex differences in both basal and stress-induced HPA activity are noticeable in a variety of species, in which males typically show lower ACTH and glucocorticoid levels under both conditions (Viau 2002). These sex differences in HPA function are credited partially to inhibitory effect of testosterone in males. ACTH and corticosterone responses to acute stress in the male rat are increased by gonadectomy, and this effect is

reversed with the replacement of testosterone or 5 $\alpha$ -dihydrotestosterone (5 $\alpha$ -DHT) (Viau 2002). This suggests that the inhibitory effect of testosterone in males on HPA function is mediated by an androgen receptor-mediated effect. So, simultaneous assessment of gonadal and adrenal activity bears great therapeutic as well as diagnostic potential in various diseases.

### Functional Defects of Corticosterone Secretion

Congenital adrenal hyperplasia due to 17- $\alpha$ -hydroxylase deficiency results from a defect in gene CYP17A1 in humans that is responsible for coding the enzyme 17 $\alpha$ -hydroxylase which results in decreased synthesis and secretion of corticosteroid with concomitant rise in mineralocorticoid production. Symptoms include hypogluccorticoid production, ambiguous genitalia in males, and failure of the ovaries to properly function during puberty in genetic females with features of hypokalemic hypertension (Yanase et al. 1992).

Secretion of corticosterone and cortisol is ACTH dependent and correlating high levels as in Cushing's disease and ACTH producing tumors; on the other hand, low concentrations may lead to ACTH deficiency and panhypopituitarism (Norris and Carr 1990). Corticosterone has also been shown to be decreased in 3 $\beta$ -hydroxysteroid dehydrogenase deficiency and 11 $\beta$ -hydroxylase deficiency; both of which are important rate-limiting enzymes in the steroidogenic pathway (Simard et al. 2005).

### Prognostic Value of Corticosterone

Corticosterone has high prognostic importance in certain diseases like in cancers (De la Roca-Chiapas et al. 2016) also in circadian and reproductive cycles of animals (Atkinson and Waddell 1997). However in some forms or the other, it is not used as medicine for clinical treatment purposes.

## Cross-References

### ► Corticosterone

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## Corvids

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## Synonyms

[The crow family](#)

## Definition

A corvid is a member of the passerine bird family Corvidae, which includes crows, magpies, ravens, jays, treepies, choughs, and nutcrackers.

## Introduction

The Corvidae family includes approximately 125 species and is part of a bigger group of more than 700 oscine passerine species, called Corvoidea, which, for example, includes birds of paradise and shrikes. Corvoidea originated in the area of Papua New Guinea and colonized the rest

of the world during the mid-tertiary, 25–40 million years ago (Jönsson et al. 2011). Today, corvid species are distributed worldwide except the southern tip of South America and the polar ice caps. They inhabit harsh environments such as mountainous regions, but also thrive in urban areas. Corvids are of broad significance for behavioral and ornithological research not only because of their ability to adapt to diverse habitats but also because of their great variability and flexibility in their social system. Corvids are renowned for their large brains and their remarkable cognitive skills in social and physical contexts. Describing similarities in cognitive abilities between birds and mammals is of special interest as the large phylogenetic separation suggests independent evolution of similar skills in certain ecological and social environments in distantly related species. The “Corvid Literature Database,” a project with the aim to record all publications on corvids, lists more than 8000 publications (<http://www.corvids.de/cld/search.php>; Droege and Töpfer 2016).

### Foraging Ecology and Physical Cognition

Physical cognition refers to cognitive skills, which facilitate processing information about the physical world, often related to complex foraging tactics, such as tool use, caching, or extractive foraging. Corvids are omnivorous generalists, feeding on many different plants and animal species, including fruits, seeds, roots, insects, worms, birds’ eggs, small vertebrates, and carrion. In response to unpredictable environments, such as seasonal availability of food, the evolution of extractive foraging is favored, defined as the act of locating and processing embedded food. Many corvid species are extractive foragers and, for example, drop nuts or mussels to remove them from their shells, use tools to extract grubs from wooden logs, or predate on eggs of burrow nesting seabirds.

Corvids evolved from a food-caching common ancestor, and most current species store and cache food for later consumption. Some species, for example, common ravens (*Corvus corax*) and

carrion crows (*Corvus corone*), scatter-hoard when competing for food with others, and recover caches rather shortly thereafter, whereas Clark’s nutcrackers (*Nucifraga columbiana*), Siberian jays (*Perisoreus infaustus*), and other long-term seed-caching species cache in order to survive long periods of food uncertainty. Food caching is generally associated with good performance in spatial memory tasks and increased hippocampal volume. Western scrub jays (*Aphelocoma californica*) do not only memorize where they cached food, but also possess a memory for the food type they cached (what), and when the cache was made, which is seen as evidence for episodic-like memory, facilitating species that cache easily perishable food, such as insects, to retrieve the food before degradation (de Kort and Clayton 2006). Further to having to protect stored food from degradation, many corvids developed strategies to protect their caches from pilfering conspecifics by, for example, caching out of view of potential competitors, caching less when being watched by others, or recovering caches to change cache sites. In the presence of conspecifics, ravens try to actively distract others and lead dominant individuals away from hidden food. Ravens have been shown to modify their cache protection in relation to whether or not a competitor has knowledge about the cache locations, and assess the competitive strategies of unfamiliar individuals by caching nonedible items. In an experiment on captive ravens, human experimenters either stole a nonedible object, which was previously cached by the focal raven, or the experimenter only looked at the cache site, but did not remove the object from the stash. The test subjects then modified their food caching behavior according to the experience made in these trials: In presence of the stealing experimenter, they cached more often out of sight of the experimenter and took longer to cache than in the presence of the other experimenter (Bugnyar 2013).

One aspect of physical cognition is reasoning about causal relationships, which cannot necessarily be perceived directly but must be inferred from the spatiotemporal relationships between objects. Whether animals possess the cognitive ability to reason about causal relationships

between objects is tested in support-relation tasks, for example, string pulling. In this task, animals are confronted with a food reward that is out of reach, but attached to an accessible horizontal string. Naïve corvids readily start to pull the string and perform a coherent sequence of actions, repeatedly pulling up and stepping on the string in order to lift and eventually reach the treat (Heinrich 2011). Another task to test whether animals understand causal relationships is the trap-tube paradigm. In this experiment, animals have to use a stick to push a food reward out of a tube, but the animal has to avoid pushing it into a trap inside the tube, because if the food falls into the trap, it is lost for the focal animal. New Caledonian crows (*Corvus moneduloides*), a species that naturally produces and uses tools in foraging contexts, can solve this physical problem by causal reasoning. Also rooks (*Corvus frugilegus*), nontool using corvids, were shown to solve the task in a modified version, in which a tool was already inserted into the tube, so that the focal animal was only required to pull or push the stick to move the food (Taylor 2014).

Several corvid species have been tested for object permanence, defined as the knowledge that an object still exists, even when out of sight or displaced. This is cognitively challenging because it requires continuous updating of representations of the unperceived object and its position while maintaining a stable representation of the stationary surroundings. Corvids, similar to primates and dogs, have been shown to master object permanence in an experiment with increasing complexity. At the start of the experiment, they had to find food hidden in one out of two containers, later on food was hidden and invisibly displaced, or in a final stage of the experiment hidden and successively displayed, all conditions in which the corvids could successfully find the food (Hoffmann et al. 2011). In relation to this, corvids have been tested for their ability to select a correct alternative by logically excluding other potential alternatives. A food reward was hidden in one of two possible locations and the subjects received different information by being shown the content of either one or both potential locations. Hence, when only the content of the unbaited

location was shown, subjects had to choose the opposite location to find the hidden food. Two caching corvid species, common ravens and carrion crows, were able to exclude the unbaited location and choose the baited one, whereas non-caching jackdaws (*Corvus monedula*) could not solve the task, indicating that within corvids, caching might be key in the evolution of exclusion performance (Mikolasch et al. 2012).

The cognitive ability to manufacture and use tools is seen as an advanced form of physical intelligence. Among nonhuman animals, chimpanzees, and New Caledonian crows are considered the most proficient tool users. New Caledonian crows manufacture different types of tools, for example, hooked twigs and stick tools, which they use to retrieve insects behind bark or from cavities in wood (Rutz and St Clair 2012). The cognitive underpinnings of tool use in New Caledonian crows have mostly been assessed in captivity. Crows are sensitive regarding the functionality of tools. When presented with ten stick tools of different lengths, crows avoided selecting unsuitable tools, which were too short to reach a food reward. New Caledonian crows can spontaneously solve a meta-tool task, in which they have to use a small stick as a tool to obtain a longer stick, which they can then use to retrieve a food reward (Taylor 2014). When crows were provided with materials to manufacture tools, they made tools appropriate in diameter to insert them into holes of differing sizes. Captive juveniles were found to manipulate objects during ontogenetic development, even before they actually use tools, and the motor patterns shown resemble components of tool use behavior in adult birds. Further, juvenile individuals, who received demonstrations of twig tool use by a human foster parent, manipulated and applied twigs more often than naïve counterparts. In a choice experiment, crows preferred to handle objects which have been manipulated by their human foster parent before, indicating that social learning might be involved in the development of tool use (Kacelnik et al. 2006). Recently, a second corvid species was discovered to use foraging tools, the Hawaiian crow (*Corvus hawaiiensis*). Within the family of corvids, New Caledonian crows and Hawaiian



crows are only distantly related but live under similar ecological conditions on remote tropical islands. This suggests that tool use in corvids is facilitated by ecological conditions, and has evolved at least twice in the family of corvids (Rutz et al. 2016).

## Social Life

Corvids express high variability in breeding systems and social organizations among species, as well as flexibility of the latter within species, depending on life history and ecological factors. Nonbreeding individuals of many corvid species form flocks, which consist of juvenile birds, adult individuals without a partner, or paired birds, which could not secure a territory. These nonbreeder flocks are characterized by fission-fusion dynamics, which means that the flocks vary in size and membership throughout the day; for example, large groups may be formed when foraging or roosting for the night, and smaller groups of variable compositions are formed when resting during the day. In order to successfully reproduce, most corvid species need to secure a territory, which is defended against conspecific competitors.

A particularly well-studied example of within-species flexibility in the breeding system depending on ecological factors is provided by the carrion crow. Carrion crows breed in male-female pairs in most European populations; however, in at least two populations in Spain, birds have been described to breed cooperatively in extended family groups of three to nine individuals, in up to three-quarter of the territories (Baglione and Canestrari 2016). Territories in these regions are of particularly good quality, for example, in terms of food availability, and are therefore defended year-round. Instead of joining nonbreeding flocks, offspring delay their dispersal from natal territories and stay with their parents for an extended period, often for a couple of years, and help their parents to raise offspring, i.e., cooperative breeding occurs. Whether the breeding system is determined by genetic or environmental factors was tested in an experiment for

which eggs were transferred from a cooperatively breeding population of carrion crows in northern Spain to a noncooperatively breeding population in Switzerland. Juveniles hatched in northern Spain delayed dispersal and became helpers, whereas the juveniles hatched in Switzerland dispersed from their foster parents' territories during their first winter. This strongly suggests that environmental conditions, rather than a genetic component, drive the expression of cooperative breeding. Indeed, in territories which were experimentally supplemented with food year-round, offspring was more likely to delay dispersal and become helpers than in control territories (Baglione and Canestrari 2016).

Cooperative breeding has been described in 27 out of 84 corvid species with known breeding system. It is correlated to geographic zone, with a higher prevalence in southern latitudes (Ekman and Ericson 2006). Other species such as Siberian jays or New Caledonian crows live in family groups but no helping occurs. Although in a majority of cases family groups consist of adult individuals and their retained offspring, 26% of groups in Siberian jays (Lillandt et al. 2003) and 61% of groups in Carrion crows contain immigrants from other territories (Baglione et al. 2003). Flexibility in social organization can also be found within one population, as exemplified by Azure-winged magpies (*Cyanopica cyanus*). While Azure-winged magpies from a population in central Spain breed in distinct territories, Azure-winged magpies in South Korea breed in colonies. Depending on weather conditions, percentage of nests assisted by helpers varies from 27 to 73 (Valencia et al. 2003). Colony living also occurs in other species of corvids, such as rooks, jackdaws and pinyon jays (*Gymnorhinus cyanocephalus*), which form large flocks year round and also, reproduce in these groups.

Within their social groups, corvids form valuable social relationships, characterized by spatial proximity, high levels of tolerance, low frequencies of aggressive interactions, and high frequencies of affiliative behaviors. These social relationships are preferably formed between kin, but also nonkin, individuals, and ultimately might result in a long-term monogamous pair



bond. Social relationships help individuals to gain access to resources such as food or territories, and individuals in social relationships are more likely to win agonistic encounter through coalitional support (Bugnyar 2013). Additionally, to these selective relationships which help individuals to cope with the challenges of living in groups, also monogamous pair bonds in corvids are characterized by complex social interactions, with high levels of cooperation, coordination, and affiliation, which could have required the evolution of advanced cognitive skills, necessary to maintain long-term pair bonds (“relationship intelligence”: Emery et al. 2007).

Especially in the context of food, corvids are highly competitive. Corvids usually form linear dominance hierarchies, in which individual A is dominant over individual B, individual B is dominant over individual C, and so on, and males generally outrank females. Some species show postconflict affiliation between former opponents after aggressive encounters, similar to so-called reconciliation behaviors described in several primates, e.g., macaques and apes. Postconflict affiliation is seen as an important mechanism to reduce the costs of aggression, for example, by reducing the stress of individuals involved in agonistic encounters or by decreasing the likelihood of redirected aggression. While in some species, e.g., rooks and Eurasian jays, no reconciliation occurs between former opponents, both the initiator and receiver of aggressive encounters engage in postconflict affiliation with uninvolved third-party individuals such as their pair-partner (Emery et al. 2007). This form of postconflict affiliation is termed consolation. In common ravens, conflicts are usually followed by consolation from uninvolved bystanders and reconciliation between former opponents (Bugnyar 2013). Generally, the relationship between individuals plays a significant role and both reconciliation and consolation occurs more often between individuals who share a valuable relationship. Common ravens in valuable relationships support each other in aggressive encounters, i.e., coalition formation. However, they were also shown to intervene in

affiliative interactions of other individuals, with aggression or by placing themselves between the affiliating individuals. This behavior is seen as an endeavor to prevent other individuals from gaining benefits from forming coalitions, which might be turned against themselves (Massen et al. 2014a).

The challenges of living in social groups are considered as a main driving force for the evolution of advanced cognitive skills (Humphrey 1976). Individuals in groups need to individually recognize group members, track relationships between individuals and others’ rank positions, as well as update that information when circumstances change. Given the complexity and flexibility of the social system in corvids, they became a prime avian model for the study of social cognition, and are well studied comparatively. In order to investigate whether living in groups in corvids accounts for enhanced cognitive skills, several corvid species with different social organization have been tested for their ability to infer and track third-party relationships. It is hypothesized that individuals living in complex groups base their knowledge about relationships of other individuals in the group on transitive inference; for example, A is dominant over B and B over dominant to C, then A is likely to be also dominant over C. The ability for transitive inference allows individuals an assessment of specific relationships, even if not all individuals have been observed interacting with each other. Pinyon jays, which live in colonies of up to several hundreds of birds, learn dyadic relationships faster and more accurately compared to pair-breeding western scrub-jays, and are better in transitive inference (Bond et al. 2003). In order to test whether common ravens possess an understanding of third-party relations, they were subjected to a playback experiment, presenting simulated social interactions of group members to a focal bird. Compared to ordinary vocal interactions between dominant and subordinate individuals, focal birds showed more self-directed behaviors, which are considered an indicator of stress, when confronted with unexpected vocal interactions, i.e., dominant calls by a subordinate individual followed by submissive calls emitted by a dominant individual. The

difference in behavioral responses by the focal individuals indicates that ravens recognize third-party rank relationships of individuals they regularly interact with (Massen et al. 2014b).

In various contexts, such as foraging and predator avoidance, corvids use information provided by conspecifics. Communal roosts of corvids can function as information centers, with naïve individuals gaining information about feeding sites from knowledgeable individuals. Departures from night roosts are highly synchronized, with most individuals departing in one direction and knowledgeable individuals leading the way (Heinrich 2011). When confronted with novel objects or food sources which they have not encountered before, corvids are generally fearful, or “neophobic”. Rooks and jackdaws consume novel food only when a demonstrator foraged on this food type before (Greggor et al. 2016), indicating social facilitation of foraging decision. Neophobia can be adaptive as it provides protection against potential risks associated with objects and foods; however, it also limits exploration, innovation, and learning. Social contexts strongly affect neophobia. Common ravens approach food sources quicker on their own, compared to when being in dyads (Bugnyar 2013), whereas in groups of cooperatively breeding carrion crows, subordinate individuals only approach food sources which have been explored by dominant individuals before (Chiarati et al. 2012). Social learning of information about dangerous humans was demonstrated in an experiment on wild American crows (*Corvus brachyrhynchos*). Humans wore a distinctive mask when capturing and banding crows, in order to associate the mask (face) with danger for the crows. Adult crows quickly learned to associate the masks with threat and responded to it with scolding, a typical antipredator response in crows. The information about the dangerous humans wearing masks quickly spread within the population of crows, and also individuals who never experienced any bad experience associated with the masks themselves started to scold at it, even up to 1.2 km from the initial capturing sites, and 5 years after the start of the experiment (Marzluff and Angell 2013). This illustrates not

only the broad and efficient spread of social information within a population, but also its long-term persistence. As social transmission occurs between individuals that observe or interact with each other, information transmission is strongly linked to characteristics of the social network. Common ravens were found to preferably observe affiliated individuals and siblings, and the observation network predicted the transmission of information in a novel foraging task (Kulahci et al. 2016).

One key question of research on cognition in corvids is whether individuals have an understanding of each other’s knowledge. Theory of Mind is the ability to attribute mental states such as intents, desires, and knowledge, to one-self and other individuals. Theory of Mind allows individuals to understand that others have mental states and perspectives that are different from their own. Whether or not nonhuman animals and prelinguistic children possess a Theory of Mind proves difficult to assess. A series of cognitive precursors have been identified; one of them is self-recognition, as it is thought to show self-awareness. Self-recognition in nonhuman animals can be assessed via studying the behavior of an animal in response to its reflection in a mirror. Usually, the focal subject is fitted with an unusual mark, such as a colorful spot on its forehead. Most animals confronted with a mirror show social behavior, usually aggressive displays, indicating that the image in the mirror is perceived as an unknown, potentially dangerous conspecific. Some primate species confronted with their mirror image show self-directed behaviors, especially trying to remove or investigate the mark, which indicates that they recognize themselves in the mirror. Similar to great apes, Eurasian magpies (*Pica pica*) show mirror-induced self-directed behavior and started to preen and scratch themselves, indicating that they are self-aware.

A second cognitive prerequisite of Theory of mind is the ability to understand that other individuals have mental states that underlie their actions. This ability is called “desire-state attribution” and has been tested in Eurasian jays (*Garrulus glandarius*), a monogamous corvid

species. During the breeding season, male Eurasian jays frequently share food with their pair-partner. In an experiment, jays have been fed with two different food types, wax worm or mealworm larvae. After eating either type of food for a certain amount of time, individuals started to show “specific satiety” against this type of food, meaning that they started to prefer the other food type. At the start of the experiment, females were given one type of food to eat and their male partners could watch their partners eating either wax worm or mealworm larvae. Later on, the male jays were given access to the two food types and they preferably fed their female partner with the food that the female had not eaten before. The males did so even when the food type the female preferred was in conflict with the male’s own desire. These results indicate that the male jays pay attention to what their female partner has previously eaten, and that they are sensitive to mental states and current food preferences of their pair-partners (Taylor 2014). The cognitive ability to take other individuals’ perspective and understand what others know and understand about the environment is tested in behavioral experiments in which focal individuals have to compete for food with individuals that have either seen where the food was placed, or did not see the location of the food. If animals are aware of what other individuals know or do not know, they should behave differently toward knowledgeable and not knowledgeable individuals. Common ravens were given the opportunity to place food caches in a testing compartment while either being observed by a conspecific or being unobserved during the caching. Afterward, the previously observing bird (knowledgeable individual) or an unknowledgeable bird was let into the test compartment, additionally to the focal individual. When a knowledgeable individual joined the focal raven, the latter retrieved more caches in order to eat the food, or recache it at a novel site, compared to when a naïve individual, which was unaware of the cached food, joined the room. This indicates that focal ravens behaved differently depending on whether or not the conspecific was knowledgeable of the location of food caches. However, it is unclear whether focal ravens

simply respond to behavioral cues given by the knowledgeable conspecifics. To test this, a further experiment was conducted in which the presence of a potential observer was simulated using a playback in a room adjacent to the testing compartment. Peepholes providing visual access to the test compartment were either open or covered, providing the opportunity to assess whether a conspecific in the adjacent compartment could potentially observe the testing compartment or not. Focal ravens protected their caches when visual access was provided via open peepholes, but not when peepholes were covered, indicating that they are aware that conspecifics could not know about the location of their caches in the latter situation (Bugnyar et al. 2016).

Various forms of cooperation can be observed in corvids; for example, common ravens reciprocate each other’s help in aggressive encounters (Bugnyar 2013), jackdaws and rooks share food (Emery et al. 2007), and Florida scrub jays (*Aphelocoma coerulescens*) coordinate their vigilance into a sentinel system, where one member of the group is standing guard in a prominent position while the rest of the group forages (McGowan and Woolfenden 1989). Cooperation often occurs between related individuals, i.e., nepotism, driven by kin selection. In Siberian jays, juvenile individuals delaying their dispersal and staying with their parents as a family group in their natal territory, benefit from vigilance and predator avoidance provided by their parents (Griesser et al. 2006). In cooperatively breeding carrion crows, adult males, who are also the most dominant individuals in a group, approach novel and potentially dangerous food sources first to explore them. Later on, they tolerate their own offspring at the food source and co-feed with them, whereas they attack group members which are unrelated immigrants (Chiarati et al. 2011). Further to kin selection, other explanations for the evolution of cooperation in nonhuman animals are reciprocal altruism, i.e., individuals help each other in order to receive help back in the future, and mutualism, i.e., individuals work together because all will profit from it. The underlying evolutionary mechanisms of cooperation in animals are investigated in laboratory experiments, using well-established

paradigms, such as the loose-string pulling or Prisoner's Dilemma paradigm, which aim at facilitating comparative studies in order to understand the evolution of cooperation in different species and taxa. Corvids have been shown to cooperate in various contexts when both cooperation partners benefit from the action. For example, rooks and ravens act together when tested in a loose-string pulling task, where two individuals have to simultaneously pull a string in order to move a board containing a food reward toward them. When given the choice to cooperate with an affiliated or not-affiliated individual, ravens preferred to cooperate with individuals they share a valuable relationship with (Asakawa-Haas et al. 2016). Notably though, rooks were not able to delay acting when they had to wait for their experimental partner, and also did not show a clear preference for an apparatus that could be operated individually, indicating that they did not seem to have understood the causalities of the task (Seed et al. 2008). In another cooperation task, New Caledonian crows successfully passed a stone to a partner in an adjacent compartment, so that the partner could then use the stone to trigger an apparatus that released food rewards into both cages. However, they also did not pass the control condition, testing for an understanding of the task, as they also dropped stones into the other compartment when tested alone (Jelbert et al. 2015). Therefore, it is not clear whether these experimental tasks provide valid tests of an understanding of cooperation in corvids, or whether individuals operate the devices simply because they learned that a certain action will provide them with a reward.

One paradigm frequently used to assess whether humans or nonhuman animals are capable of reciprocal altruism is the Iterated Prisoner's Dilemma task. In this task, two individuals are tested with each other, and each individual has a choice to either cooperate or defect. The payoff for the two individuals is based on both, the own choice and the opponent's choice. When both players chose to cooperate, both receive a medium reward, and when both players chose to defect, they both get a small reward. However, if one

player defects and one cooperates, then the defector gets a large reward, and the cooperator gets nothing. Blue jays (*Cyanocitta cristata*) tested in this paradigm failed to cooperate based on reciprocal altruism. Their poor performance in this task might be explained by blue jay's inability to cope with a delay of gratification (Stephens et al. 2002). Delay of gratification is the ability to postpone a response to an immediate reward in order to gain a more valuable reward in future, which presents a cognitive challenge for humans as well as non-human animals. The ability to successfully cope with delayed gratification is considered an essential cognitive prerequisite for reciprocal altruism, because this requires an individual to invest resources in the present in order to receive a future reward. When tested for their ability to delay gratification in a token exchange task, carrion crows and common ravens were given the opportunity to increase the quality of a reward after a given delay, by exchanging the initial token, which is a nonpreferred food item (e.g., a piece of bread), against a more preferred reward (e.g., grapes, sausage or cheese). In a similar task, subjects could increase the quantity of a reward by exchanging one piece of food against more pieces of the same food. Crows and ravens were able to cope with a delay of gratification of up to 10 min in order to increase the quality of the reward. However, they did not wait in order to increase the quantity of their reward, which is different to previously tested mammalian species such as primates and dogs (Hillemann et al. 2014).

Another cognitive prerequisite of cooperation is the ability to track efforts and payoffs of the interacting cooperation partners, and sensitivity to inequity. Being able to identify and correct unequal treatment is considered to facilitate successful long-term cooperation with unrelated individuals, through selection for collaborators and punishment for defectors. Inequity aversion was tested in carrion crows and common ravens, in a token exchange task. Birds were trained to exchange a nonedible token with the experimenter in order to receive a food reward. Subjects were then tested in pairs, experiencing inequity in work effort or reward quality. When the test subject had

to exchange the token in order to receive a reward, while its experimental partner received the reward as a gift, the test subject decreased its exchange performance. Similarly, when both, the test subject and its partner, had to exchange a token in order to receive food, but the test subject received a reward of lower quality than its partner (i.e., received less preferred food), it refused to take the reward more often compared to control conditions. These results indicate that carrion crows and common ravens are sensitive to inequity, and avoid interactions that yield uneven payoffs (Wascher and Bugnyar 2013). New Caledonian crows, however, show no sensitivity to inequity in reward distribution, indicating that while New Caledonian crows show elaborate cognitive skills in the context of physical cognition, such as the flexible tool use and causal understanding, they do not seem to have evolved elaborate cognitive skills in a social, cooperative context (Jelbert et al. 2015).

In order to successfully cooperate, individuals also need to be able to differentiate between reliable and unreliable conspecifics, and choose to interact with reliable ones. In a playback experiment, carrion crows learned to differentiate between reliable and unreliable unfamiliar individuals. Alert calls of unfamiliar carrion crows were either associated with a “dangerous” visual stimulus, i.e., a dead crow, in order to simulate a reliable alarm caller, or no visual stimulus, in order to simulate an unreliable alarm caller. Over the course of the experiment, crows started to call less frequent when listening to calls of the reliable compared to the unreliable stimulus individuals, indicating that crows are more attentive toward alarm calls of reliable birds, possibly in an attempt to gain as much information as possible in a potentially dangerous context (Wascher et al. 2015).

Vocal communication plays an important role in the social life of corvids. Corvids are open-end vocal learners, which mean they are able to acquire new calls throughout their live and not only in a specific sensitive period. Vocalizations can encode information about the calling individual, e.g., its sex, dominance status, or individual

identity, which potentially facilitates individual recognition. Large-billed crows can individually recognize group members based on their vocalizations (Kondo et al. 2012) and common ravens not only recognize conspecifics’ call, they also memorize the status of their social relationship with the caller for a number of years. In a playback experiment, common ravens were confronted with calls from unfamiliar individuals, and with calls of former group members, from which they had been separated for at least 3 years. The birds did not only differentiate familiar from unfamiliar calls, but also responded differently depending on the previous relationship with the calling individual. In response to the playback, ravens’ vocalizations were different when a former affiliated individual was played back compared to calls in response to a former foe (Bugnyar 2013).

Generally, vocal communication in corvids plays an important role in coordinating activities and providing information about the environment, e.g., presence of predators or food. Pair-bonded carrion crows and rooks use synchronized vocalizations in aggressive contexts or during territorial defense, and coordinate their behaviors and body positioning. This has been suggested to be a cooperative display increasing the effectiveness of the territory defense and strengthening the pair bond (Emery et al. 2007). Ravens use loud calls, so-called “haa-calls,” to attract conspecifics in a foraging context, and to coordinate group movements. “Haa-calls” are likely to be functionally referential signals conveying information about food quality and quantity (Heinrich 2011). Additional to distinct call types, individuals can produce numerous variations in call types, and produce complex sequences containing different call types or call variations. Siberian jays emit 14 different call types in response to predators, and encode information about how dangerous the predator is in both calling rate and call types used. Two specific call types were only emitted in response to seeing a hawk, and three call types were only used in the presence of an owl. Call types in response to a hawk also differed depending on whether the predator was perching, attaching, or searching (Suzuki 2016).

## Bird Brains?

In recent years, studies on corvids helped to shed light on a better understanding of avian brain architecture underlying complex cognitive skills. Compared to primates and other mammals, corvids have a smaller absolute brain size; however, corvid brains contain on average twice as many neurons in the pallial telencephalon (Olkowicz et al. 2016). The classical view that complex cognitive skills require a cortex, which is only present in mammals but not in other taxa, was replaced by recent neurobiological findings of homologous structure in avian forebrains. The avian Nidopallium caudolaterale is the functional equivalent to mammalian prefrontal cortex, a multimodal center processing various cognitive skills such as associative learning, quantity discrimination, audio-visual stimulus associations across time, abstraction of general principles (Nieder 2017), and tool use (Mehlhorn et al. 2010). Also, emotional stimuli are processed similarly in corvids, humans, and other vertebrates. Using neuroimaging technology, American crows' brain activity was studied in reaction to exposure of pictures of human faces, which have previously been associated either with threat (being captured) or caretaking, in order to elicit emotions. In response to viewing the pictures, amygdalar, thalamic, striatal, and brainstem regions have been activated in the crows (Marzluff and Angell 2013). This is similar to neuronal circuitry underlying emotional processing in humans and other vertebrates. Neurological data from corvids strongly points toward convergent evolution of functionally similar but anatomically very different forebrain structures across vertebrates.

## Conclusion

In recent years, corvids have become an important avian model system to study the evolution of complex cognitive skills. Similarity in cognitive performances between primates and corvids suggest a convergent evolution of certain cognitive skills in birds and mammals. Advanced cognitive

skills in corvids seem to have evolved from both, requirements in the ecological and the social environment. Corvids adapted to a wide variety of environments, are innovative problem-solvers, and possess several requirements for successfully managing multiple social relationships. Although research on a few corvid species has been flourishing in past years, there is yet much work needed to understand the evolution of sophisticated cognitive skills in corvids. From the more than 120 species of corvids, detailed studies of the behavior and cognition is only available for about 10–20 species, which all show quite remarkable behaviors or abilities, such as tool use, cooperative breeding, and advanced cache-protection strategies. In order to comprehensively understand the evolution of complex behaviors and underlying cognitive traits, comparative studies of the ecology and social behavior of different species are needed.

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## Costly Signaling

### ► Handicap Hypothesis

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## Costs of Group Living

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## Introduction

The occurrence of group formation has been recorded in many animals across diverse taxa. Such aggregation can take various forms creating a diverse array of group configurations that differ in the number of individuals, the stability of a

group's composition, the frequency of physical contact, social interactions, as well as spatial proximity and the duration of the group over time. The definitions of group living in the literature differ based on what behaviors are required from members in order to form a "group" (Krause and Ruxton 2002). That being said, every definition of group living usually require that animals need to show some degree of spatial proximity over time to be considered as a group. Wilson's (2000, p. 585) definition states that a group is "any set of organisms, belonging to the same species that remain together for a period of time while interacting with one another to a distinctly greater degree than with other conspecific organisms."

Theories on ecological pressure have proposed that the dynamic between benefits and costs for group living drove group formation to evolve independently in different taxa. Indeed, groups should occur when its benefits for the fitness of an individual outweigh its costs. The benefits and costs that arise from ecological pressure can be broadly separated into three categories: foraging and access to resources, defense from predators, and access to mates. The benefits of group living commonly include an increase in food searching efficiency, decrease in risk of predation, and increase in mating opportunities. On the other hand, the costs of group living usually include an increase in intragroup resource competition for both food and reproductive opportunities, as well as an increase in exposure to diseases and parasites. However, the presence of these costs and benefits, as well as the extent to which they can affect an individual in a group, is often influenced by the size of its group.

### Within-Group Competition

One of the main costs of living in a group is the increase in competition within the group among its members for access to resources (i.e., food, mates). Competition can be categorized into contest and scramble competition (Nicholson 1954). Contest competition occurs when the resource is distributed in a manner that allows it to be

defended or monopolized by certain individuals. Oftentimes, the winners of contest competitions are dominant individuals who can aggressively defend a resource from other group's members and subsequently obtain a larger share (van Schaik 1989). Scramble competition occurs when the resource is dispersed and shared by all members of the group. In scramble competition, the resource cannot be monopolized by the dominant individuals. Since the resource is limited in quantity, as group size increases, scramble competition will increase; thus scramble competition is often density dependent (van Schaik 1989). The type of resource greatly affects the kind and degree of competition. For example, leaves are generally more dispersed and ubiquitous than fruits, so animals with a primarily folivorous diet typically experience more scramble competition while frugivores and insectivores experience more contest competition.

The ecological-constraints model states that the upper limit of group size is constrained by costs associated with feeding and foraging. The bigger the group, the faster resources will get depleted, and the group will have to incur greater costs in order for all group members to satisfy their daily energy requirements. As group size increases, so will the group's day range and travel costs since it will need to forage greater distances to find food. In two groups of red colobus (*Procolobus badius*), a species that predominantly feed on leaves, it was found that the larger group travelled more, rested less, and had larger day and home ranges than the smaller group (Gillespie and Chapman 2001). Results from five groups of ursine colobus monkeys (*Colobus vellerosus*) concur with findings from the red colobus as day range, home range, and percentage of time spent feeding increased with group size (Teichroeb and Sicotte 2009). In frugivorous primate species, larger groups were also found to have travelled further and spent more time feeding than smaller groups (Majolo et al. 2008). These results suggest that larger groups, independent of diet composition and type of food competition, suffer greater within-group competition than smaller groups (Majolo et al. 2008). Furthermore, female fecundity was found to be lower in larger than in smaller

groups, which reflects the negative effects that bigger group sizes have on group members' physical states and ability to meet their daily energy requirements (Majolo et al. 2008).

Although the main cost of group living is food competition, there are additional costs related to feeding and foraging. Firstly, groups that devote more time to feeding and foraging trade-off on time that can be spent to strengthen social bonds, which is important for group-living animals. For example, grooming in primates is an affiliative behavior that helps strengthen social bonds, aids the formation of alliances, and functions as a form of reconciliation following agonistic encounters. If a group spends more proportion of their day feeding and foraging, then there is less time available for grooming. Similarly, there is a trade-off for time spent resting, which is important for the digestion of fibrous food, especially for folivores (Majolo et al. 2008). Secondly, individuals in larger groups have to travel greater distances to find food, which increase their risk of encountering predators in unfamiliar areas beyond their home range (Terborgh and Janson 1986). Larger groups are also more easily detected by predators due to increased noise and visibility (Terborgh and Janson 1986). Furthermore, an individual's spatial position within the group reflects the variation in predation risk. Individuals on the periphery of the group have a much higher chance of encountering predators compared to individuals adopting a more central position. In this sense, group members are in competition over preferred spatial positions to maximize safety from predators. In chacma baboons (*Papio ursinus*), dominant individuals occupied a more central position while feeding (King et al. 2011). Dominant members are able to engage in contest competition and displace subordinates from the center of the group. The predation risk associated with group living is also demonstrated by the tendency of nocturnal primates to forage individually in order to avoid being detected by predators that rely on sound to hunt (Clutton-Brock and Harvey 1977).

Another aspect of within-group competition that directly affects an individual's fitness is access to mates. In group-living animals, an

individual's social status in the group has important implications. In species with a marked dominance hierarchy, dominant individuals have fitness benefits in contest competitions over priority of access to both food resources and mating opportunities. Mandrills (*Mandrillus sphinx*) live in multi-male multi-female groups that display a dominance hierarchy, and there is intense male-male contest competition for access to fertile females. Using long-term data on a colony of mandrills, Setchell et al. (2005) found that alpha males were responsible for 94% of periovulatory mate guarding and accounted for 69% of offspring paternity. Thus, a major cost of living in groups is competition for mates which can result in disproportionate fitness costs for subordinate members due to reproductive skew favoring higher-ranking members. The alpha males also suffer group-living costs, since in mandrills, mate guarding became less effective and paternity decreased as the number of adult males in the group increased (Setchell et al. 2005).

Another cost of within-group competition is the possibility for exploitation of others' efforts, such as in the case of kleptoparasitism, which is the stealing of a resource that had been obtained by another individual. Among group-living foragers, an individual can either actively search for food (the producer strategy) or join in to feed at a food patch that has been discovered by another group member (the scrounger strategy). The presence of scroungers in a group lowers the average foraging rate of the group and is a cost to group living (Vickery et al. 1991). Kleptoparasitism is advantageous for the parasitic individual who does not need to invest as much effort into securing food. However, the costs of kleptoparasitism are borne by nonparasitic group members. As a result, a cost of sociality and group living is the presence of "cheaters" and "freeloaders" that do not contribute proportionally to the efforts of the group.

### Increase of Parasite

The other main cost of group living that has received an increased of interest over the years is

the possibility that group living could increase parasite transmission and disease. Indeed, Alexander wrote in 1974 that “the prediction is compelling that group living animals will either be plagued more heavily with parasites and diseases than their solitary living close relatives, or they will be plagued with greater expense of time and energy, and greater risk, in reducing the attacks of such organisms.” Parasitism is still widely viewed as one of the primary costs of sociality that could have a role in limiting group size. Aggregation could facilitate pathogen transmissions, and animals living in larger groups, due to their higher local density, would experience a greater exposure to parasites than those living in smaller groups or solitary animals.

The fact that aggregation could increase parasite transmission is, however, dependent on both the ease with which the pathogen is transmitted from host to host and the host group’s characteristics. Parasites can be transmitted in multiple ways going from searching parasites that can infect their host by travelling between groups either on their own (i.e., using aerosolized transmission routes) or by using a mobile vector of a different species (i.e., vector-borne) to contagious parasites that require close contact to transfer between hosts and thus are generally restricted to within-group transmissions. Parasites can also be environmentally transmitted, usually through fecal-oral transmission or from contaminated water, ground, or food. Therefore, the types of transmission have a direct influence on whether an increase in parasite transmission will be associated with group living. More mobile transmitted pathogens are density dependent, where an increase in transmission should happen with an increase in population and parasites that require intense physical contact for transmission (e.g., sexual transmission) being independent of population size.

The interactions between the types of transmission and group size could then explain the differences found among social groups, populations, and species in terms of their levels of infestation and infection by parasites. Indeed, a larger group size may increase parasitism through several mechanisms, one of them being the local density

created by group living, which could favor the establishment of infections (Anderson and May 1982). Larger groups may also seem more attractive to both conspecific migrants, which could increase the possible arrival of migrants carrying an infectious disease (Brown and Brown 2004), and vectors, which could result in an increase in the percentage of individuals being infected by vector-borne parasites (Davies et al. 1991). Moreover, members of larger groups may also have more opportunities of interaction with other group members creating a possible increase in physical contact allowing again more opportunities for parasite transmission (Dunbar 1991). Finally, as larger groups deplete their food patches faster than smaller groups, these groups usually travel farther and increase the chance of infection through environmental transmission (Freeland 1979).

When looking into the literature, multiple studies have demonstrated a relationship between certain pathogens, their types of transmission, and group size. This confirms that certain pathogens are a cost associated with group living. Cote and Poulin (1995) presented a meta-analysis demonstrating consistent positive correlations between group size and parasitism rates for parasites transmitted by close contact or by a fecal-oral route but consistent negative correlations for searching parasites and no correlation for either parasite intensity or prevalence and host mobility. Patterson and Ruckstuhl (2013) found in their own meta-analysis similar results regarding the correlation between parasite transmissions and group size but were able to demonstrate a positive association with parasite intensity and prevalence, as well as an impact of host group mobility where the intensities of parasites did not increase with group size of mobile hosts. Rifkin et al. (2012) proposed for their part another meta-analysis also supporting the association between parasite infection and group size with an effect size varying between transmission modes but found an overall positive association for environmentally transmitted parasites, vector-borne parasites, and no association for searching parasites, which differs from previous findings (Cote and Poulin 1995; Patterson and Ruckstuhl 2013).



Empirical evidence for the associations between group size and parasitism are mixed. On the one hand, studies confirming the prediction can be found. For example, the prevalence of intestinal parasites in species of African artiodactyls increased with group size (Ezenwa 2004) and higher individual infestations of lice (*Colpocephalum turbinatum*) are found in larger groups of Galapagos hawks (*Buteo galapagoensis*) (Whiteman and Parker 2004). On the other hand, studies showing the opposite result are also present in the literature. For example, the intensity of parasitism by direct transmission was significantly higher in solitary species than in gregarious species among 12 species of Indian mammals (Watve and Sukumar 1995), while the level of ectoparasite infection in an intraspecific study of alpine marmots (*Marmota marmota*) living in larger groups was not significantly higher (Arnold and Lichtenstein 1993). Faced with these contradictions, certain researchers have started to propose that previous predictions of the relationship between parasitism and aggregation might be too simple, as the reality of group living might be more complex and therefore might not always bring a cost for individuals regarding parasites transmission.

### Anti-parasite Benefits of Group Living

While the relationship between aggregation, group size, and parasite transmission is well studied, the idea that group living might confer a benefit in terms of “anti-parasite transmission” to individuals, thus reducing the pathogen costs of being social, is more recent (Ezenwa et al. 2016). This idea, and the mechanism linked to it, could ultimately explain the variation found within studies that have looked into this relationship. Indeed, benefits of group living could fully or partially offset the transmission costs through either increasing the pathogen resistance of an individual or increasing its tolerance. Resistance to pathogens is usually defined as “a property of an individual, related to genotype or level of investment in immunological and behavioral traits associated with pathogen defense” (Ezenwa et al.

2016). Resistance refers then to two types of ability, one being the capacity to avoid or prevent infections, while the other is the ability to reduce either the number or growth of parasites once infected. Therefore, resistance acts by minimizing the level of infection for an individual and can involve immunological or behavioral mechanisms. The pathogen tolerance, on the other hand, refers to “any mechanism that can reduce the health or fitness impacts of pathogen infection” (Ezenwa et al. 2016). Through this mechanism, individuals could reduce the damage inflicted by pathogens, mitigating the association between parasite transmission and group size.

Group living through sociality could then have multiple ways to influence both resistance and tolerance to pathogens, including simple byproduct of sociality such as enhanced resource acquisition or more complex ones like promoting cultural transmission of parasite defense behaviors. Such behavior can take multiple form including allogrooming, which can facilitate the direct removal of parasites between group members that increases the resistance of an individual by reducing both transmission and exposure (Akinyi et al. 2013), or thermoregulation, such as huddling behavior that could help an individual to regulate or adjust their body temperature, which could provide pathogen tolerance benefits by improving their ability to cope with fever as an example (Medzhitov et al. 2012). Thinking about these possible anti-parasite benefits of group living may be useful to challenge our understanding of the cost of parasitism, as the extent to which the risk of parasite transmission increase with sociality is still unclear.

### Conclusion

Studies on the costs of group living challenge our understanding of one of the most fascinating phenomena in animals – sociality. Indeed, aggregation creates associations between individuals that allow them to form a group, which brings advantages to its members, such as a decreased risk of predation, enhanced efficiency when searching for resources, and better access to potential



mates for reproduction. However, a trade-off exists for animals in groups, where the presence of multiple individuals brings about an increase in competition for food and mating opportunities, as well as a possible increase in parasite infection and transmission. The costs mentioned in this paper are the most commonly stated ones. However, as social behaviors are being investigated more in depth, additional costs are starting to become apparent. One of them could be the consensus costs associated with the need to reach collective decisions for certain groups. Indeed, to access the benefits of group living, individuals must stay cohesive and maintain a degree of spatial and temporal coordination in their activities (Krause and Ruxton 2002). To do so, members may use consensus to reach a collective decision regarding the time and the direction of future activities. Such synchronization brings consensus costs for group members, since different individuals have different needs. In a group, individuals will differ in their characteristics like age, sex, and internal state (e.g., level of satiety, reproductive status) (Petit and Bon 2010), which create differences in their personal needs and make them differ in their optimal timing of activities or location preferences. Thus, consensus costs emerge from the necessity to compromise with other group members, where the fitness costs will increase with the difference between the optimal timing and movement location of an individual and the actual timing and destination of their group (Conradt and Roper 2010). More research will be needed to better understand the costs of living in a group.

## Cross-References

- [Aggregation](#)
- [Competition](#)
- [Group Living](#)
- [Optimal Group Size](#)
- [Predation Risk](#)
- [Predator Detection](#)
- [Reproduction](#)
- [Scramble Competition Polygyny](#)
- [Sperm Competition](#)

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- significance (Richardson et al. 1987). This occurrence results as an alternative conditioned response to the original stimulus (Lane 2009; Pearce and Dickinson 1975; Richardson et al. 1987). Counterconditioning can involve two distinct scenarios: (a) a previously appetitive response can become aversive (i.e., appetitive-to-aversive counterconditioning) or (b) a previously aversive response can become appetitive (i.e., aversive-to-appetitive counterconditioning). Counterconditioning consists of Pavlovian conditioning in which a previously neutral stimulus (NS) is paired with an unconditioned stimulus (US) to produce a conditioned response (CR). The NS becomes a conditioned stimulus after repeated pairings with the US. Counterconditioning successfully occurs when the original conditioned or unconditioned response is modified by replacing a cue from the original CS–US relationship, with one of opposite value.
- In the appetitive-to-aversive treatment, a conditioned or unconditioned stimulus first evoking an appetitive response, be it a CR or an UR, is paired with a stimulus evoking an aversive CR or UR. In other words, the CS or previously neutral stimulus is paired with an appetitive unconditioned or biologically relevant stimulus. This pairing results in the production of an appetitive conditioned response. Subsequently, the same CS is paired with a different US (aversive) to produce an aversive CR. If the US (aversive) condition is stronger than the US (appetitive), this produces a counterconditioning effect. The other possibility for counterconditioning is the aversive-to-appetitive transfer, which is opposite in nature to the previously described paradigm. In this condition, a CS is paired with an aversive US, to produce an aversive response. After producing this response, the same conditioned stimulus is paired with an appetitive as opposed to aversive US to produce an appetitive response. If the US (appetitive) condition is stronger than the US (aversive) condition, counterconditioning successfully occurs.

## Counterconditioning

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Counterconditioning occurs when a response to a stimulus is modified by pairing that stimulus with another stimulus of an opposite emotional

This form of Pavlovian conditioning allows for either an aversive or appetitive stimulus to create an association that is opposite from the originally

learned CS–US relationship. In this behavioral technique, the organism exhibits a CR to an aversive or appetitive stimulus which is then modified through the pairing of the original CS with a new US that is opposite in nature to the initial US. For example, in an aversive-to-appetitive counterconditioning paradigm, if an animal was forcefully placed in a cage in the past, they may have a hard time entering a cage in the future due to their prior learned aversive association with that cage. However, through counterconditioning, a more positive association can be formed with the cage. While entering the cage, the animal may be provided with a favored reward in order to change the previously acquired negative association with the cage to one that is more favorable. If the new CS–US association is stronger than the one that was originally acquired, this would result in counterconditioning. This counterconditioning effect is likely to make the animal feel more comfortable and assist in changing the animal's defensive response to entering the cage (Goldstein 1969; Pearce and Dickinson 1975).

Several researchers have suggested that Pavlovian counterconditioning occurs due to a reciprocal inhibitory interaction between positive and negative motivational systems (Bouton and Peck 1992; Estes 1969; Gray 1971; Klein 1969; Pearce and Dickinson 1975; Peck and Bouton 1990). Pearce and Dickinson (1975) have found that counterconditioning assists in modifying the aversiveness of a harmful cue. In their twofold Pavlovian counterconditioning experiment, rats received a series of shocks and food presentations. The researchers assessed the ability for the shock to become a reinforcer during a conditioned emotional response (CER). However the shock actually reduced suppression of the CER for rats in the experimental group (i.e., paired shock with food), while rats that received unpaired shock and food presentations had the opposite effect. In the second experiment, they found that when keeping food presentations constant, the reduction in suppression of responding became dependent on the magnitude of the shock. Similarly, Klein (1969) found that rats that were confined in a chamber with food became less fearful of a shock after counterconditioning in comparison to those who

were either confined in the chamber without food or not confined at all.

## Spontaneous Recovery in Counterconditioning

The recovery of a previously extinguished conditioned response following a rest period is referred to as spontaneous recovery (Pavlov 1927). Researchers have observed evidence of spontaneous recovery in counterconditioning paradigms (Bouton and Peck 1989, 1992; Bromage and Scavio 1978; Krank 1985; Scavio 1974). In this experimental setup, a conditioned stimulus (CS) is paired with an unconditioned stimulus (US). For each condition, the conditioned stimulus is paired with its respective unconditioned stimulus (i.e., shock or food/water). Based on literature findings, the CS begins to elicit a conditioned response to the second US by the end of this phase. However, the appetitive-to-aversive transfer has resulted in more equivocal results. The initial appetitive conditioning has been shown to hinder, facilitate, or have no impact on aversive conditioning in the second phase in comparison to the aversive-to-appetitive transfer condition.

Bouton and Peck's (1992) findings were mostly consistent with the previous literature. In this study, researchers examined the impact of the retention interval on performance in two counterconditioning paradigms, the aversive-to-appetitive transfer and appetitive-to-aversive transfer. The aversive stimulus used in this study was a shock, while food served as the appetitive stimulus. In both the aversive-to-appetitive and appetitive-to-aversive transfer conditions, spontaneous recovery of the originally acquired response was observed when rats were tested 28 days following the end of the second phase. This observation of recovery of responding in the aversive-to-appetitive condition suggests that interference in learning is not the only cause for spontaneous recovery.

However, research by Richardson et al. (1987) challenged these findings through evidence that counterconditioning can modify the retention of previously acquired fear responses in an aversive-

to-appetitive paradigm in rats. In this study, retention testing occurred the next day after counterconditioning in comparison to Bouton and Peck's (1992) experiment, which interpolated a 28-day retention period prior to testing. Based on these findings, it can be inferred that the time between counterconditioning and testing seems to play a pivotal role in its efficacy, while results from Bouton and Peck suggest that both retroactive and proactive interference play a role in the recovery of responding based on the observation that interference did not occur during learning, but instead took place at retrieval or performance.

## Counterconditioning in Psychotherapy

Counterconditioning processes have been utilized in clinical practice through a method referred to as systematic desensitization (Davidson 1968). Systematic desensitization is a technique used in the reduction avoidance behavior and is concerned with the aversive-to-appetitive transfer condition seen in counterconditioning. In systematic desensitization, an aversive imaginal (i.e., imagined) or in vivo (i.e., actual) stimulus is paired with anxiety competing relaxation techniques. This creates a hierarchy of exposure to the feared stimulus, while aiming to gradually reduce the individual's fear.

### Systematic Desensitization

As previously mentioned, systematic desensitization gradually exposes the organism to the fear-inducing stimulus and provides an opportunity for incremental habituation. It is a technique originally developed by Joseph Wolpe (1968) to modify a range of neurotic disorders. Wolpe (1968) found that cats could be desensitized to show less fear to previously feared conditions. In his study, cats were placed in a box and given electrical shocks. In the second phase of the study, he conducted a systematic desensitization task in which the cats were first fed from a distance and then incrementally closer to the box. Through this task, he found that the cats gradually displayed levels of reduced fear toward the box.

Since then Wolpe's systematic desensitization procedure has been used to treat individuals with anxiety and phobias by gradually exposing them to the fear producing stimulus while simultaneously allowing them to practice relaxation techniques in between exposures (Milenberger 2012). This is done either through imaginal or in vivo exposure, which is a paradigm that hierarchically exposes the person to levels of fear-producing situations. Systematic desensitization has also been modified for application to animals. The animal is gradually introduced to the aversive stimulus, which allows for habituation to each step before they are fully exposed to the fear-inducing stimulus (Clay et al. 2009). Some researchers have found that systematic desensitization is more efficient than counterconditioning in reducing separation-related problem behaviors in dogs (Acton 2012). However, research by Yin (2009) found that systematic desensitization works best for low level fears, while counterconditioning is most effective for higher levels of fears.

## Conclusion

Counterconditioning refers to the replacement of an originally conditioned response with the opposite conditioned response. Through counterconditioning, an organism can come to change their behavior as a result of a changed association that they have with stimuli in their environment. Research has shown that in both aversive-to-appetitive and appetitive-to-aversive counterconditioning paradigms, organisms are able to recover the first learned associations when tested after a retention period (Bouton and Peck 1992). These findings suggest that originally learned associations are not erased in light of new associations.

Counterconditioning has also been utilized in psychotherapeutic practice through procedures such as systematic desensitization (Davidson 1968). Several researchers have found that the originally acquired association is not destroyed when an organism is presented with a new US (Bouton and Peck 1989, 1992; Bromage and

Scavio 1978; Krank 1985; Scavio 1974), whereas other researchers have found that counterconditioning can modify some aspects of the originally acquired association (Richardson et al. 1987). Based on these equivocal findings, future research would benefit from exploring the relationship between counterconditioning and the length of the retention interval prior to testing.

## Cross-References

- ▶ [Classical Conditioning](#)
- ▶ [Operant Conditioning](#)
- ▶ [Unconditioned Response](#)
- ▶ [Unconditioned Stimulus](#)

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## Countershading

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## Synonyms

[Dorsal pigmentary darkening](#); [Obliterative shading](#); [Optical flattening](#); [Thayer's law](#)

## Definition

Classically explained as an adaptation for camouflage, countershading describes the color pattern common among animals and is characterized by darker pigmentation on the side of the body that is most strongly illuminated.



## Introduction

Countershading is a color pattern that is observed in a diversity of taxa, across contrasting environments (Rowland 2009), and across ecological time (Smithwick et al. 2017). There are a number of reasons that countershading might evolve, including thermoregulation, protection against UV radiation, and defense against abrasion (Rowland 2009). The most researched hypothesis for the existence of countershading is that it enhances visual camouflage.

## The History of Countershading

The English naturalist Edward Bagnall Poulton and American artist Abbott Thayer independently proposed that the function of countershading is to enhance camouflage (Rowland 2009). Thayer went so far as to describe his hypothesis as “The law which underlies protective coloration.” Countershading was also adopted as a popular tactic in military camouflage during World War II (Behrens 1988).

## The Mechanism by Which Countershading Can Enhance Camouflage

If a uniformly colored object is illuminated from a particular direction, it reflects more light from the part of its surface facing the light than from the part facing away. Under sunlight, when light comes from above, a uniformly colored animal will appear brighter on its back and darker on its underside. This graded shading from light to dark is used by a number of animal species to perceive the shape of an object.

A countershaded pattern characterized by darker pigmentation of the regions of an animal's body that are directed toward the light cancels out the natural shading effect: a process known as self-shadow concealment. This can interfere with the perception of shape and make countershaded animals more difficult to detect

than uniformly colored animals (Cuthill et al. 2016; Penacchio et al. 2017).

## Evidence for the Concealing Effect of Countershading

Comparative analyses of the body color of primates (Kamilar 2009), ruminants (Allen et al. 2012), larval lepidoptera (Rowland 2009), and dinosaurs (Smithwick et al. 2017; Vinther et al. 2016) are consistent with countershading functioning as camouflage.

Computational models of countershading for crypsis simulate animals in realistic lighting environments and can predict optimal patterns for different weather conditions at a specific location and at specific times of the day and year (Penacchio et al. 2015). When artificial caterpillar-like prey with these putatively optimized countershaded patterns is exposed to predation, either in the field or in the lab, the rates of predation support the comparative evidence that countershading enhances camouflage by counterbalancing self-shadows (Cuthill et al. 2016; Penacchio et al. 2017).

## Countershading in Aquatic Environments

Some of the most compelling examples of countershading coloration are found in aquatic environments (Rowland 2009). The characteristics of light in air and water are different, as are the viewing angles between predators and prey (Kelley et al. 2017). This difference appears to have resulted in divergent mechanisms of concealment but similar phenotypes between the two environments: in aquatic environments, countershading appears to function by improving background matching rather than self-shadow concealment. The observed reflectance profiles of fish in different light environments do not match the optimal patterning for optimal self-shadow concealment: the body pigments of fish match the viewing background rather than concealing ventral shadows (Kelley et al. 2017).



## Conclusion

There is growing empirical and theoretical evidence to suggest that concealment of shadows is the primary explanation for the evolution of countershading. More research is required to reveal the mechanisms by which countershading affects predator perception. Whether nonhuman animals use shading as a three-dimensional cue or learn to detect a reflectance gradient remains unknown.

## Cross-References

- ▶ [Camouflage](#)
- ▶ [Depth Perception](#)
- ▶ [Predator Defense](#)
- ▶ [Visual Illusions](#)
- ▶ [Visual Perception](#)
- ▶ [Visual Recognition of Prey and Predators](#)

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## Countersinging

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## Synonyms

[Coordinated singing](#); [Matched countersinging](#); [Song alternating](#); [Song overlapping](#); [Song-type matching](#); [Vocal duels](#); [Vocal interaction](#)

## Definition

Countersinging is a form of vocal interaction that occur between males of some territorial songbird species.

## Introduction

In *The Descent of Man and Selection in Relation to Sex*, Charles Darwin (1871) introduced his theory of sexual selection to explain the evolution of traits that function in attracting mates (often, but not always, manifest in males rather than in females) and in competing with rivals for access to them. He specifically considered the songs of male songbirds as a case in point which he proposed had evolved via sexual selection. Contemporary research largely confirms Darwin's

conjectures about bird song such that male songs are now generally viewed as “dual function” signals that play a key role in mating behavior. They are used by males to attract and stimulate the reproductive behavior of females, and to mediate competition with rivals. In some songbird species, songs are used to mediate conflicts over territorial spacing. These dyadic male-male vocal interactions are called countersinging. They can be classified as: time-specific responses, in which males coordinate the tempo of their own singing output to either overlap the songs of counterparts or alternate them, avoiding simultaneous singing; or pattern-specific responses, in which interacting birds can match the structural patterns, song types, of each other (Todt and Naguib 2000). Both time-specific and pattern-specific responses are associated with aggressiveness and escalated encounters between neighboring individuals.

### Choruses and Duets

Vocal interactions in songbirds are not limited to countersinging. However, interactions involving three or more individuals are usually not viewed as countersinging but as choruses. Songbird duets are yet another type of dyadic vocal interactions, but it involves mated pairs or parents and offspring. These additional forms of coordinated singing are outside the scope of this review.

### Song Alternating and Overlapping

The alternated production of auditory signals is a widespread phenomenon that can occur among individuals that share the same acoustic space. A clear advantage of alternating signaling is to avoid acoustic interference and increase signal detectability, allowing individuals to better listen to each other (Todt and Naguib 2000). Furthermore, the timing of songs during alternate singing can be indicative of variable degrees of aggressive intent. Hultsch and Todt (1982) studied alternate singing in nightingales and identified three different interaction strategies: *inserting*, *overlapping*, and *autonomous singing*. In dyadic interactions, inserters sing during the intervals between the songs of a counterpart. Overlappers start singing

before a counterpart has finished its preceding song. Autonomous singers do not adjust the timing of their songs to fit the singing output of counterparts.

Dabelsteen and collaborators (1997) investigated the functional role of song alternating and overlapping in male robins using an interactive playback approach. Research on countersinging has greatly benefited from the use of interactive playbacks. This technique allows researchers to manipulate in real time the stimuli used to test the vocal responses of study subjects. Hence, played back stimuli can be interactively modified as a function of the changing subject's behavior. Dabelsteen et al. (1997) results led to the conclusion that song alternating and overlapping are not random and indeed have functional value. In male robins, both patterns indicate aggressive intent but song overlapping signals a higher singer arousal than song alternating. Results from research in male robins, nightingales, and great tits indicate the existence of an escalation sequence that goes from song alternating to overlapping, then close range encounter, and finally an attack (Dabelsteen et al. 1997). Research in great tits (Otter et al. 1999) indicates that the outcomes of countersinging interactions are not only relevant to the two active singing participants but also to eavesdroppers. In this species, females eavesdrop male-male countersinging and might use these interactions to assess potential extra-pair partners. Females paired to males that received de-escalated treatments (song alternating) were less prone to visit neighboring territories than females paired to males that received escalated treatments (song overlapping).

### Song-Type Matching

Songs are stereotyped sequences of vocalizations that are characterized by their structural organization and temporal patterns. They are composed of syllables, regularly grouped combinations of sound elements consistently produced together as common units. Song types are unique combinations of different syllables. Males in some territorial songbird species that possess song repertoires (two or more different song types)

can engage in song-type matching, a form of countersinging in which males can match the structural patterns of other males' songs. Although it has been reported in several species, such as song sparrows, great tits, tufted titmouses, western meadowlarks, and cardinals, song-type matching is not universal. There is a considerable number of species that do not song-type match (Catchpole and Slater 2008). Song-type matching requires that neighboring males share at least some song types. In fact, song-type matching has been mainly reported in species with small to moderate song repertoire sizes, containing less than 15 song types. In such species, there is a higher probability that neighbors will share song types. It has been suggested that small repertoires of song types containing simpler songs have a larger role in male-male interactions. While large repertoires of song types with more complex songs functions more in attracting females (Catchpole and Slater 2008).

### The Threat Hypothesis

Krebs et al. (1981) outlined what became known as the *threat hypothesis*. It proposes that song-type matching is a graded signal that communicates agonistic motivation and readiness to escalate aggressive encounters. Krebs et al. (1981) made the prediction that song-type matching should correlate with other intense agonistic behaviors. For example, males should respond faster and approach speakers closer when song-type matched in playback experiments. They also predicted that neighbors should song-type match more often early in the breeding season than later, when territorial boundaries are already established. Furthermore, Beecher et al. (2000) suggested that an additional prediction is implicit in the threat hypothesis. Namely, that males should song-type match neighbors at lower rates when compared to nonneighbors, a form of dear enemy effect.

Subsequent research has provided good support to the idea that song-type matching is a graded signal. Partial song-type matching and repertoire matching (in which males do not song-type match but sing songs that are also in the repertoire of neighbors) induce less aggressive response than whole song matches (Searcy et al. 2008). Studies

in song sparrows (Beecher et al. 2000) have shown that males song-type match neighbors more often early in the breeding season, when territories are not yet established. Playback experiments have also shown that males song-type match neighbors less often than nonneighbors. However, mixed results were found for the prediction that song-type matching should occur along with other intense aggressive behaviors.

### Conclusion

Countersinging is a male-male form of vocal interaction in which songs are used to mediate conflicts over territorial boundaries. It can occur as temporally coordinated singing, in which males can either overlap or alternate between the songs of a counterpart; or as song-type matching, in which structural patterns of songs can be matched. The study of countersinging provides insights into a sophisticated communication system in which different degrees of threat can be embodied, indicating several levels of aggressive intent.

### Cross-References

- ▶ Aggression
- ▶ Agonistic Behavior
- ▶ Auditory Signals
- ▶ Communication
- ▶ Dawn Solo/Chorus
- ▶ Dear Enemy Effect
- ▶ Passerine Cognition
- ▶ Passerine Sensory Systems
- ▶ Passerine Vocal Communication
- ▶ Secondary Sex Characteristics
- ▶ Sexual Selection
- ▶ Songbird Duets
- ▶ Territory Defense

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grasp the concept of number and how it is used during enumerative events.

Five criteria have been identified by Gelman and Gallistel (1978) as essential to counting:

1. *The stable order principle* describes the established sequence of verbal or symbolic numbers and their ordinality. To demonstrate the comprehension of this principle, it is necessary for verbal numbers or symbols to be presented in a consistent order (e.g., the second tag applied is always “2” in the Arabic numeral system and is always followed by “3”).
2. *The one-to-one correspondence principle* states that the items in the to-be-counted set and their corresponding counting tags must be paired so that each item receives a maximum of one numerical tag that is completely unique. Specifically, it would be correct to label three items “1-2-3” and incorrect to label the items as “1-1-2.”
3. *The cardinal principle* answers the question of how many things are in a set. It articulates that the final tag used when labeling objects not only represents the ordinality of said objects but also expresses the numerosity of the entire collection. For example, when four objects are labeled 1-2-3-4, the unique tag “4” not only describes the position within the sequence; it also describes the total number of objects in the counted set.
4. *The abstraction principle* illustrates one’s ability to transfer the previously described principles from one to-be-counted set to another. This includes any stimulus set from physical objects, or more abstract and non-visible sets such as sounds. This principle concludes that an individual may count anything, as long as the method of counting remains consistent.
5. *The order-irrelevance principle* recognizes that the order of enumerating items is not important as long as the stable order and one-to-one principles are followed. This means that a line of objects may be counted in any imaginable way (left to right, right to left, the middle out, etc.) and as long as each tag is unique, applied in the proper sequence, and every item receives one tag, the cardinal value will still be exact.

## Counting

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## What Is Counting?

Counting is used to specify the absolute number of items in any set, and it is an integral process that we use daily while cooking, playing games and in numerous other ways. In humans, there is evidence that enumerative processes are present even in infancy and eventually develop into formal counting abilities (around the age of 3.5–4 years; Gelman and Gallistel 1978). The ability to count is indicated by one’s capability to fully

A closely related concept is protocounting, and this term is often used to describe the performances of animals such as will be outlined here. This occurs when the most likely process underlying enumerative behavior is counting, although tests have not provided sufficient evidence for a true counting behavior. For instance, a behavior may be labeled as protocounting in circumstances where all counting alternatives have been precluded but control tests (e.g., transfer to demonstrate the abstraction principle) are lacking (Davis and Pérusse 1988).

### What Does Not Count as Counting?

Counting is one specialized mechanism for understanding and representing the absolute numerical value of an enumerated set. However, there are other related forms of numerical and quantitative processes that likely are foundational to the ability to count. These include relative quantity judgments that involve choosing between options on the basis of a “more or less” rule regarding a wide range of magnitudes (e.g., items, volumes, lengths). Sometimes, these choices must be made on the basis of numerosity of sets, and various species can make these relative numerical judgments. In other cases, absolute quantity judgments are made, where the goal is to find a specific quantity (e.g., the circle that is exactly 20 cm in diameter). And absolute numerical judgments can be made by animals, where a specific number of things is the target stimulus (e.g., a sheet of paper with exactly three dots on it). These kinds of tasks are important because they are likely far more accessible to the natural quantitative mechanisms available to other species. In fact, we know that quantity (and even number) is relevant in the judgments made by species ranging from insects (e.g., Dacke and Srinivasan 2008), to fish (Agrillo et al. 2008), to amphibians (Krusche et al. 2010), to birds (Garland et al. 2012), and to many mammals including voles (e.g., Ferkin et al. 2005), marine mammals (e.g., Abramson et al. 2011), bears (Vonk and Beran 2012), elephants (Perdue et al. 2012), coyotes (Baker et al. 2011), and horses (Uller and Lewis 2009). It is these

demonstrations that support the continued possibility that animals may even engage in formal counting, although efforts to this point have offered only tantalizing and suggestive evidence of this rather than clear and definitive cases.

### Controversial History of Counting Research with Animals

The pursuit of counting abilities in animals is one of the most controversial efforts in comparative psychology. This is important to note because that controversy first dampened the continued study of numerical abilities in animals, but after the cognitive revolution, the return to this topic was undertaken with great care. The controversy largely centered on methodological flaws involving poor control over stimulus presentation and unintentional cuing of animals (the “Clever Hans” effect; Beran 2012; Pfungst 1911). Later, it was also suggested that number was a low salience property of stimuli for other species, meaning that number would be used only as a “last resort” by animals engaging in experimental tasks (Davis and Memmott 1982). It was against this backdrop that many of the early studies of relative and absolute numerical judgments were conducted. And it was in pursuit of evidence that number was not a last resort that many of the counting studies were conducted. We now know that animals do use number as a salient property, although often in combination with other properties that tend to covary with number (such as size, density, or amount/volume). The counting studies helped outline this truth.

### Studies of Counting by Animals

With the increased recognition of concerns about cuing, and the refinement of definitions of counting offered by developmental psychologists (e.g., Gelman and Gallistel 1978), new approaches to animal research emerged. And these often produced exciting results and approximated many aspects of the counting principles. These studies have explored varying levels of “counting”



behavior and number sensitivity in diverse species, from large-brained animals to invertebrates. Not surprisingly, a sizeable portion of experiments exploring numerical competence were with great apes, specifically chimpanzees, to determine any capability of such tasks in nonhuman animals (Beran and Rumbaugh 2001; Boysen and Berntson 1989; Boysen et al. 1995; Matsuzawa 1985; Rumbaugh et al. 1989). Other species examined for numerical competence include rats (Davis and Bradford 1986), pigeons (Xia et al. 2000), parrots (Pepperberg 2006), bees (Chittka and Geiger 1995), and ants (Reznikova and Ryabko 2011).

Matsuzawa (1985) reported an impressive performance by a chimpanzee named Ai during a counting task. This chimpanzee had learned to associate symbols with various objects and colors. She also had learned to label sets of items with cardinal labels. When presented with arrays of items of various types, colors, and quantities, she would provide the relevant labels for all properties of that set and often at high levels of correctness. The range of number labeling was small relative to the counting of children over 5 years of age, but still instantiated many of the counting principles outlined above.

An equally impressive series of experiments featured another chimpanzee named Sheba. In an attempt to illustrate one-to-one correspondence, the abstract principle, and both functional and symbolic counting skills of chimpanzees, Boysen and Berntson (1989) trained Sheba to enumerate one, two, or three food pieces and random objects using Arabic numbers. Sheba demonstrated very high accuracy and then transferred her number labels to heterogeneous arrays of items. Testing eventually expanded to include the numerals 0 and 4 as well. When the number 4 was introduced, Sheba's originally high accuracy fell, and she began to use what was deemed a method of motor tagging as she touched and pointed to objects in the array. Following the initial number training procedures, Sheba completed a functional counting task and a symbolic counting task. In these tasks, researchers hid either oranges or the Arabic numbers 0–4 at three different sites around an enclosure. To complete the task, Sheba was required to travel to all three sites and ultimately

select the Arabic number that represented the sum of what she found. In both conditions, Sheba performed well above chance levels. These results suggest that Sheba's numerical skills met many of the criteria necessary to be classified as counting (Boysen and Berntson 1989), at least for small numbers of things.

In another study conducted with Sheba, researchers examined her physical indicating behaviors (i.e., her behaviors of tagging items while interacting with them; Boysen et al. 1995). Sheba correctly labeled sets of eight possible arrays well above chance levels while engaging in these indicating acts, but she tended to over-tag the objects at a near double rate, perhaps arguing against the idea of one-to-one correspondence. However, in some cases, young children also over-tag items when they are learning to count (Gelman and Gallistel 1978). It was possible that the double tags may have actually enhanced Sheba's one-to-one correspondence efforts and aided her in a more accurate count by first partitioning and then tagging each item. Additionally, it is highly probable that these tagging behaviors were a direct result of human interaction in addition to how Sheba was reared and would be highly unlikely to appear spontaneously in a more natural environment (see final section for more comments on this important issue of how to immerse nonhuman animals in environments that might engender counting behavior).

Other work with chimpanzees used computerized testing approaches. In one computerized task, a chimpanzee named Lana was trained to recognize Arabic numbers 1–3 and use a joystick to move a computer cursor to collect the corresponding number of squares on the screen and return the cursor to the Arabic number to conclude the trial (Rumbaugh et al. 1989). During the more challenging trials, where Lana needed to choose three squares, she performed at approximately 80% accuracy. Two chimpanzees (one being Lana and the other her son, Mercury) were tested using similar methods (Beran and Rumbaugh 2001). In that study, the chimpanzees expanded their above-chance performances with the numbers 1–6. However, as the requested number increased in its cardinal value, the



chimpanzees showed a decreasing performance level, reflecting what is called scalar variability. This directly challenged the idea that their performances were reflective of true counting, although it was possible that larger sets also introduced more chances for distraction. In any case, these series of computerized tasks also demonstrated some of the counting principles in the behavior of chimpanzees.

In a long-term study of the parrot Alex, clear evidence emerged of multiple counting principles (see review in Pepperberg 2006). Alex was queried about sets of items, and he had to respond vocally with the correct numeral label for that set. He could do this even when asked about subsets of things in larger arrays (e.g., being asked “How many green block?” when green blocks were mixed in with blocks of other colors and multiple colors of things that were not blocks). Most impressive was his ability to use these numeral labels for highly varied kinds of things, showing evidence of the abstraction principle. And his skills suggested that he understood the ordinal relations of his number labels as well as their cardinal values. However, it was not clear that Alex engaged in tagging of items in any way, making it difficult to demonstrate the one-to-one correspondence principle.

A study by Davis and Bradford (1986) tested rats’ abilities to “count” to the correct reward-baited tunnels while lacking spatial, olfactory, and visual cues so that their choice of the correct tunnel needed to be based exclusively on its ordinal position. To do this, the researchers used a high-walled apparatus so the rats could not rely on visual cues and they baited every tunnel, blocking off the ones that were not in the target ordinal position so as to control for any olfactory cues. Each subject quickly learned to run to its designated target tunnel number, even with varying distance placements of tunnels determined between each trial set. Davis and Bradford suggested that providing a more naturalistic test (of spatial navigation in pursuit of food) allowed the rats to achieve such good performances. Subsequent work using similar methods with rats (e.g., Suzuki and Kobayashi 2000) confirmed sophisticated, number-based responding. However, the rats’ completion of the task was not

to the level of accuracy required of true counting, and they were not able to completely demonstrate all of Gelman and Gallistel’s (1978) principles of counting.

In a task examining constructive counting (symbol converted to numerosity) over responsive counting (numerosity converted to symbol), pigeons were trained on a two-key apparatus to peck the number of times that matched a symbolically displayed number on one key and signal the end of the trial by pecking the remaining key (Xia et al. 2000). Although they performed at above chance levels, accuracy decreased as the required number of pecks increased – another case of scalar variability as seen in some of the work with chimpanzees. Pigeons were also trained to engage in a responsive counting test (Xia et al. 2001) in which a successive symbolic matching-to-sample training process was used to obtain the desired behavior. To correctly complete a trial, pigeons had to match a numerical set of stimuli to the symbol representing that number of things. Although not every pigeon was able to progress through the entire experiment, accuracy for this task was at a more stable level than the previously described study (Xia et al. 2000). This brings to light that skill in responsive counting (or what is sometimes called a “how many” task) may be more easily demonstrated than constructive counting (what is sometimes called a “give me X number” task).

Xia et al. (2001) claimed their study provided evidence of the cardinal principle (in a small range, pigeons can discriminate absolute numbers), the one-to-one correspondence principle (accurately choosing the symbol matching its numerical quantity), the order-irrelevance principle (subjects would vary the order in which they responded to stimuli), and the abstraction principle (novel stimuli were presented by switching counted elements from circles to squares, potentially providing evidence of the ability of transfer). However, despite some compelling evidence of four counting principles, there was no concrete evidence that the subjects had a fixed ordinal sequence in place as required for the stable order principle. And, as noted, evidence of scalar variability challenges the degree to which one can argue that counting is truly occurring.

Another task involved training pigeons to retain the number of flashes presented and produce the correct matching number using pecks (Tan et al. 2007). This experiment had two conditions for stimulus presentation factors that could covary with number, rate-controlled (two, four, or six flashes were presented at a constant rate) and time-controlled (two, four, or six flashes occurred within 10 s). For this task, levels of accuracy for all subjects were fairly low, and this indicated that pigeons were using temporal cues and not fully able to learn rule-based counting strategies. A second experiment attempted to control for this; however, the results proved similar to those of the first experiment of this study. Thus, counting-like performances in pigeons sometimes emerge, but are not always easily obtainable.

In one of the first studies examining counting-like behavior in bees, Chittka and Geiger (1995) trained honeybees to travel to a feeder while passing three landmarks along the way. Testing trials gradually increased and decreased the number of landmarks as well as increased the number of feeders that were to be passed on the way to the original feeder location of the training trials. It was found that during flight, if more landmarks were encountered on the way to the feeder, the bees would land at a shorter distance than in control tests. Furthermore, if fewer landmarks were placed on the way to the original feeder position, bees would end up flying farther. However, many bees did search for the food source at the correct distance, suggesting that the number of landmarks passed was not the sole factor in determining location for honeybees. In another attempt to examine potential counting behaviors in bees, researchers used tunnels with landmarks dispersed throughout (Dacke and Srinivasan 2008). During training, the position of the rewarded landmark varied although its numerical value was held constant. This restricted a bee's ability to learn a specific reward distance, thus discouraging the bees from focusing on travel distance over landmark enumeration. During test trials, the reward location was removed, and bees showed a strong preference for searching the area near the ordinaly consistent landmark to where the reward was previously found. Further experiments

manipulated the landmarks and introduced barriers so that bees were able to view only one landmark at a time. This forced them to see landmarks as sequentially experienced as opposed to simultaneously experienced like in the previous trials. The bees showed an inclination in each of these tasks to fly to their trained landmark number. One interpretation of this experiment was that bees were able to count up to four objects (Dacke and Srinivasan 2008).

In a recent study with honeybees, researchers studied potential symbolic numerical representation (Howard et al. 2019). Two groups of bees were tested. One group was required to match a displayed quantity to a sign representing the numerical value of that quantity, and the other group was to complete the task in the opposite direction. Both groups showed the ability to match appropriately. However, when the same bees were asked to transfer this knowledge by completing the opposite version of the task, both groups were unable to adapt to the new task at a level that was significantly better than chance. Although this was not presented as a test of counting behavior, the results suggest the use of absolute numerosity, and presumably an enumerative process generated the number representations of the quantity stimuli, while the symbols were perhaps organized according to their ordinal and cardinal values.

## Conclusions and Future Directions

Overall, the literature suggests that multiple species have at least some counting-like competencies when it comes to their numerical cognition, including the ability to engage in each of the five counting principles (Boysen and Berntson 1989; Dacke and Srinivasan 2008; Xia et al. 2001). However, many studies did not require individuals to label quantities (Beran and Rumbaugh 2001; Chittka and Geiger 1995; Davis and Bradford 1986; Rumbaugh et al. 1989; Tan et al. 2007). Other studies showed that bidirectional responding was not evident (e.g., Howard et al. 2019). Additionally, the scalar variability effects in relation to accuracy in labeling or constructing numbers of things weaken the

argument that species can grasp numbers higher than about 5 or 6 (e.g., Beran and Rumbaugh 2001). Thus, although there are compelling cases that demonstrate performances that could be very close to counting behavior, it remains uncertain whether other species show the full range of numerical processes and the fully developed sense of number that are required to support counting behavior.

There are three conclusions that one can draw from this literature, each of which lend itself to suggesting that future research should continue on the topic of counting behavior in animals. First, none of the performances of nonhuman species have risen to the counting performances of typically developing children over the age of 6 living in industrialized societies. However, it is important to note that not all human societies have established counting routines (e.g., Gordon 2004). And for those that do not, their performances when asked to count things sometimes look similar to the performances of animals with regard to scalar variability in responding and engagement of an approximate number system rather than a formal counting system. Second, numerous species seemingly grasp and apply some or even all of the counting principles in specific task contexts. This suggests that the foundational cognitive capacities for true counting exist, even if they do not manifest in any known natural behaviors of other species. Third, there are no studies that have provided for animals the kind of immersion in numerical thinking that many children experience (Gelman and Gallistel 1978). Children hear and see counting routines from caregivers in their very earliest experiences. In many societies, even before formal schooling begins, caregivers are modeling and expecting the routines of counting to be used in many social engagements with their children. No studies have immersed apes, dolphins, dogs, or any other species in this type of environment. The projects with Sheba, Ai, and Alex have come the closest, but even those projects did not provide the rich counting experiences that young human children have across many different daily routines. Should such immersion in a counting-rich environment happen, where production of

exact, specific counts is routinely expected (and rewarded) as part of varied daily experiences for animals, we would then better know if the counting principles emerge in a universally applied manner within individuals of a nonhuman species when the environment demands it. They may not, and the “safe money” suggests that they would not. But, it is an important experiment to try.

## Cross-References

- ▶ [Absolute Number Discrimination](#)
- ▶ [Alex the Parrot](#)
- ▶ [Approximate Number System \(ANS\)](#)
- ▶ [Irene M. Pepperberg, PhD](#)
- ▶ [Proto-counting](#)
- ▶ [Relative Numerousness](#)
- ▶ [Sarah “Sally” Boysen](#)

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## Courtship Behaviors

### ► Sociosexual Behavior

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## Courtship Rituals

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## Courtship and Mate Choice

Courtship consists of a wide variety of behaviors performed with the intention of achieving an opportunity to mate. Successful courtship results in a pair of animals copulating. Both members of the pair participate in copulation, and this often leads to situations where one individual must persuade the other to choose them as their mate. This process of persuasion occurs through courtship rituals. In some cases, courtship behaviors can be so consistent among members of a species that they are referred to as courtship rituals. These behavioral displays vary across species, but they share the central role of providing a means through which a suitor can advertise their qualities to potential mates. Through performance and evaluation of these displays, individuals engaged in courtship choose their mates; and successful courtship can lead to copulation and the formation of social pair bonds. Pair bonding behaviors and the associated social connection

can thus reinforce a mate choice that began with the performance of courtship behaviors. Individuals often incorporate a combination of bond-forming behaviors and courtship rituals to choose a mate, as social bonds may influence the effectiveness of the courtship ritual.

Courtship rituals can be performed by either males or females. Across species, most rituals involve males performing ornate behaviors to attract the attention of females and court them as potential mates (Darwin 1871). In those cases, the female serves as the evaluator of the quality of a male's displays (Zahavi 1975). Although this can make it appear that females have the sole choice in mate selection, this is not the case, as the initiation of courtship reflects a preference expressed by the male; and mating requires agreement of both participants. Suitors select a recipient of their courtship displays, and receivers evaluate those advertisements and decide whether to accept the suitor's courtship. Therefore, elaborate displays and ritualized behaviors can be important aspects of successful courtship, but they are often only one component in what is ultimately a mutual mate choice.

## Evolution and Importance of Courtship

Sexual reproduction and the variation that it can introduce are key elements in the process of evolution. Sexually reproducing organisms pass their genetic content to the next generation, propagating their species and enabling it to persist through future generations. Sexual reproduction is very common across species. As the saying goes, birds do it, bees do it, and the majority of all eukaryotic organisms engage in sexual reproduction (Goodenough and Heitman 2014). Sexual reproduction is evident in both plants and animals, but courtship rituals are behaviors that are performed across animal species. Therefore, this text will focus on animals in our consideration of courtship behaviors and how they influence reproductive success.

In order for sexual reproduction to occur, each participant must locate and mate with another

member of their species. Factors like opportunity, competition, and attraction can all influence courtship and mating success. It is advantageous for an individual to mate with a partner with high evolutionary fitness, meaning that they are well adapted to survive and produce viable offspring in their environment (Zahavi 1975). It is often said that animals express a "preference" when they choose their mate, but this term can be difficult to define. For example, in most species, individuals do not randomly mate. This has given rise to the idea that certain traits are preferred more than others. Suitors with the preferred trait will leave more offspring, and the numbers of individuals expressing that trait will increase in frequency throughout the population. As Darwin noted in his studies of sexual selection, "when we see many males pursuing the same female, we can hardly believe that the pairing is left to blind chance – that the female exerts no choice, and is not influenced by the gorgeous colors or other ornaments with which the male alone is decorated" (Darwin 1871). This reveals how tempting it can be to think that animals possess a humanlike sense of aesthetics, and the advertisement and appreciation of "beautiful" or "high quality" traits drive courtship and reproduction. The cognitive experiences of animals are the focus of ongoing research, but it remains largely unknown what mental or physiological states occur when an animal encounters a member of its species that expresses some preferred trait. Nonetheless, those traits can be strongly predictive of reproductive success; and that is what is referred to as the traits of the suitors preferred by the receivers of those courtship behaviors.

When one or both members of a pair actively choose a mate from many options, sexual selection occurs. Sexual selection arises from differences in reproductive success that are caused by differences in access to mates (Darwin 1871). Differences in access can occur because of many different factors such as males competing with one another to gain access to mates, or females only granting reproductive opportunities to males that express an abundance of certain preferred traits. Anatomical features such as size,



coloration, and other forms of ornamentation can affect this choice, but behavioral displays can also play a very significant role in affecting which individuals are chosen as mates. The strong link between mate preference and the expression of certain behavioral displays is thought to be a driving force in the emergence of courtship rituals.

Courtship rituals vary greatly depending on the preferred traits which they advertise. Traits can be advertised through many different behaviors including singing, dancing, and demonstrating physical vigor through fighting or other challenging behaviors. Complex rituals can allow for many attributes to be displayed and evaluated at once. Observers can gain insight into the sender's genetic composition, cognitive ability, health, social status, and/or access to specific resources through the quality of a display performed by a potential mate. This gives the observer a great amount of information in a compact and succinct manner. Through displays, the sender attempts to communicate both the quality of their attributes and their availability in order to influence the behavior of the observer. The observer, in turn, analyzes those displays, evaluates their quality, and uses that information as the basis of their decision about whether the sender will be selected as a mate and granted reproductive opportunity.

## Male and Female Roles in Courtship

Courtship rituals occur between two members of the same species and influence the likelihood of mating success (Darwin 1871; Zahavi 1975). Those participants are typically a male and a female, with the male acting as the primary sender of courtship behaviors and the female as the primary receiver, but both parties often make a choice in order for a courtship ritual to be successful (Johnstone et al. 1996). If a potential sender does not judge the potential receiver to be of sufficient quality to be considered as a potential mate, he will not display. If the receiver does not judge the sender and his signal to be of sufficient quality, she will not show preference or grant reproductive access. If both sender and receiver

evaluate the other as high quality, then courtship succeeds, and mating may follow. In that way, mate choice is typically a mutual decision. In the preceding example, the male was portrayed as the sender and the female as the receiver, but there was also a portion of that scenario when the female also performed behaviors to solicit copulation or otherwise indicate her preference for the male. Therefore, both participants acted as sender and receiver at different times in the process, but the male played the role of the sender more than the female.

In the preceding example, both participants made a choice, and those choices were evident in the behaviors expressed by each participant. Therefore, it would be incorrect to say that either participant was the sole sender or receiver or that either was the only one that made a choice. In light of these nuanced contributions by both participants, it can be useful to think of the roles of signaler and receiver as lying along a spectrum between the two sexes (Fig. 1). A specific example of courtship behavior can be characterized by its position along that spectrum as determined by the amount of display or choice made by the male or the female in that example (Fig. 1). Lek mating, where many of a single sex compete or display for members of the opposite sex who are observing them, can be used to illustrate the extremes of the spectrum (*lek* is adapted from the Swedish work *lekställe*, meaning “mating ground”) (Fig. 1).

Male sage grouse provide a classic example of male lekking (left end of the spectrum in Fig. 1). Male sage grouse meet in ancestral areas to lek and strut for females (Wiley 1978). They erect their tail feathers and inflate large, yellow esophageal sacs, which swell and make popping sounds when the air is released, to attract attention (Wiley 1978). They repeat this every morning for weeks, guarding their position in the lek from other males, as central locations offer better mating opportunity (Wiley 1978). At the conclusion of this competition, a small percentage of male sage grouse are selected by the vast majority of females as mates (Wiley 1978). Thus, sage grouse are a classic example of a male lekking system. Lek mating can also occur in the context where females compete to be selected by male observers



(right end of the spectrum in Fig. 1). For example, many species of dancing flies rely on female displaying leks. In these species, females gather in swarms and display, allowing males to observe their behavior and choose their mates from among the group (Funk and Tallamy 2000).

Lek mating systems illustrate the extremes of either male or female choice, but many species do not conform to these extreme examples. Mutual displays, where both sexes participate to a large degree in the courtship ritual, reflect the middle ground (middle of the spectrum in Fig. 1). In these cases, both the male and female serve as signaler and receiver, advertising their own qualities while also evaluating the qualities of their potential mates. Success of the courtship ritual depends on both participants choosing each other. For example, in the pre-copulation displays of red-crowned cranes (middle of the spectrum in Fig. 1), both the male and the female perform an elaborate combination of calls, bill movements, and wing flapping before they copulate (Masatomi and Kitagawa 1975). In this way, both the male and female display to one another, with neither serving as the primary sender or receiver, and both evaluate the quality of their potential mate (Masatomi and Kitagawa 1975). Just as there are differences at

the extremes of the spectrum, there can also be variation within the intermediate portion of that spectrum. In most species, males act as the primary senders, and females act as the primary receivers. There can be exceptions to this trend, such as gray phalaropes and dance flies, in which females act as the primary senders and males act as receivers (Funk and Tallamy 2000; Ridley 1980). These exceptions highlight the fact that courtship rituals are unique to each species. Differences among species can make it challenging to generalize about the nature of courtship rituals, and they make it clear that any study of courtship rituals must include consideration of the context in which they occur.

## Physiological Components of Courtship

Many species have developed physical adaptations that serve in signaling information. These adaptations, called ornaments, come in all sorts of shapes and colors (Darwin 1871; Zahavi 1975). The vibrant plumage of many birds, the colorful abdomen of jumping spiders, the pinnate leg scales of female dance flies, and the crimson combs of male jungle fowl are just a few examples

Greater sage grouse



Red-crowned cranes



Dance flies



Male  
Lek

Mutual  
Display

Female  
Lek

**Courtship Rituals, Fig. 1** The spectrum of displays among males and females. Male display and female choice are illustrated by male leks in greater sage grouse (left; Wiley 1978; image: Greater\_sage-grouse\_(Centrocercus\_urophasianus).jpg by the Bureau of Land Management), mutual display and choice are illustrated by red-crowned

cranes (middle; Masatomi and Kitagawa 1975; image: Red-crowned-overhead DSC9943.jpg by Casumma/CC BY-SA), and female display and male choice are illustrated by female leks in dance flies (right; Funk and Tallamy 2000; image: Dance Fly – Flickr – treegrow.jpg by Katja Schulz from Washington, DC, USA/CC BY). All images were obtained through Wikimedia Commons, licensed for reuse through <https://creativecommons.org/licenses>

of ornamentations (Dunn and Cockburn 1999; Frith and Frith 1987; Lenz 1994; Funk and Tallamy 2000; Ligon et al. 1990; Lim and Li 2004; McDonald 1989). In many cases, ornaments reflect both the genetic and nutritional quality of the signaler. High-quality ornamentation requires the associated genes to produce consistent, complex results. Similarly, extreme ornamentation reflects a healthy lifestyle that allows the signaler to expend excess energy and resources to support the development of their ornaments (Zahavi 1975). Thus, genetics define the axis along which the ornament can be developed, but it is experience that determines the degree to which that signal is actually expressed. Fairy-wrens provide a great example of this. The plumage coloration of superb fairy-wrens acts as an honest signal for both the age and nutritional quality of the males displaying those feathers (Dunn and Cockburn 1999). Male superb fairy-wrens molt and grow their new feathers months before the breeding season (Dunn and Cockburn 1999). Older males and nutritionally healthy males molt and begin expressing those colorful feathers much earlier than young or unhealthy males (Dunn and Cockburn 1999). This advantage in timing allows them to begin displaying to females earlier in the breeding season and thus display to females for a longer duration throughout the season, giving them an advantage in terms of claiming territory and attracting mates (Dunn and Cockburn 1999). Thus, the nature of the courtship that females receive is a reflection of the age and nutritional status of the males performing those courtship behaviors.

There are many examples of courtship displays that rely on the receiver's vision to detect information; however, the traits and reproductive status of a potential mate can also be advertised through signals that are detected in other ways. For example, there are nonvisual signals that have profound impact on reproductive behaviors, such as the production of pheromones. Because pheromones are invisible, the importance of these signals for other species can be easily overlooked. Pheromones are small molecules that are produced and released by one individual and are detected by another member of the same species. Like visible

ornaments, the quality of their signals can depend on both genetics and nutritional status. For example, female thynnine wasps are wingless, and they perch on the tips of plants while releasing strong pheromones that attract males (Alcock and Gwynne 1987). Winged males can detect those pheromones in very small concentrations, and they use that information to follow the gradient of increasingly greater concentration until they arrive at their source. Pheromones serve as a signal that guides males to females, and the arrival of the male is often followed by copulation (Alcock and Gwynne 1987). Thus, reproductive signaling can occur through a variety of different behaviors and sensory modalities.

## Behavioral Components of Courtship

Anatomical or physiological ornaments can require many generations to emerge and develop as indicators of an individual's status. Behavior, on the other hand, is much more plastic, allowing behavioral aspects of advertisement and courtship to emerge much more rapidly than structural aspects. Not only are behavioral aspects of courtship very flexible, they are also able to indicate additional aspects of the displayer's status. For example, aspects of cognitive ability and social standing can be displayed through behaviors in ways that may be very difficult or impossible to communicate through physical parameters of ornamentation. This is why behavior is such an important indicator of mate quality, as it reveals characteristics that are acquired within the displayer's lifetime and is thus directly related to that individual rather than an assemblage of individuals across generations. For example, zebra finches sing to attract females. Young males learn their songs from adult male tutors during early development, and the nutrition that the young bird receives during that developmental phase impacts the quality of his song performance then and throughout his life (Brumm et al. 2009). Thus, the quality of a male's song indicates not only his ability to perform that song in the present but also his life history in terms of juvenile nutrition and social environment, as well as his skill in

learning, memorizing, recalling, and rehearsing that song.

Courtship rituals often combine ornamentation and behavior to increase the amount of information signaled to potential mates. For example, intrasexual fighting is common in courtship rituals. These agonistic behaviors use direct competition to indicate the strength and health of the fighters. While the structures used to fight are often anatomically determined, animals must be healthy, reflecting good nutrition; skillful, reflecting good cognition; and strong, reflecting good genetics, in order to win the fight. While these behaviors often do not directly lead to mating, they are correlated with mating success, as victors are more likely to gain an opportunity to mate. Thus, fighting behavior can communicate information about multiple attributes, including physiological traits that an observer would not be able to detect directly. In jungle fowl, male fighting success is correlated with the amount of testosterone the male produces (Ligon et al. 1990). Other testosterone-dependent traits, like comb color and size, are evaluated by females of other species and are also important for mating success (Ligon et al. 1990). This correlation between a physiological trait and mating success is thought to emerge because males with more testosterone are able to fight competitors and court females with higher rates of success (Ligon et al. 1990).

Another form of physical courtship ritual common across the animal kingdom is dancing, in which rhythmic movements of the body are used as a signal. Dancing allows the signaler to display their physical prowess to the evaluator. Ornaments are often displayed during these courtship rituals, signaling additional attributes. Jumping spiders, for example, dance to attract females. When attempting to court, the male raises his body and flexes his vibrant abdomen while arching his legs and vibrating his palps (Lim and Li 2004). He then will skitter toward the female and tap her legs to solicit copulation (Lim and Li 2004). Male superb birds-of-paradise are famous for their elaborate, multi-step displays. The first step involves a male sleeking his plumage while crouching to attract females to his area, bowing

and displaying his unerect cape to any nearby individuals (Frith and Frith 1987). After a female lands on his perch, the male spreads his tufts and cape, creating a black oval and thrusting his brightly colored breast shield forward (Frith and Frith 1987). Iridescent pseudo-eyes above his real eyes and clicking sounds made by wing movements accompany the male as he dances near the female by hopping around her, calling, or displaying his bright yellow mouth coloration (Frith and Frith 1987). If the female finds the dance attractive, the two will copulate (Frith and Frith 1987). This dance requires strong males with healthy genetic backgrounds and nutritional experience to produce these vigorous dances and vivid ornaments.

Many animals use auditory stimuli to signal information, but none are as famous for the Passerine songbirds. Songbirds sing to communicate. Their songs, unlike anatomical ornaments, must be learned and practiced. Males learn their songs during juvenile development by copying song elements performed by adult tutors, and they rely on hearing throughout their life to practice and maintain the quality of those songs. In this way, a male's song, like that of the male zebra finch, provides insight into not only the present health of the bird but also that male's ability to learn and perhaps other aspects of his cognitive ability (Boogert et al. 2011; DuBois et al. 2018; Sewall et al. 2013). Developmental stress, poor health, and many other factors can negatively impact the male's song quality, making it an important signal for use in female evaluation of the singer as a potential mate (Brumm et al. 2009).

Courtship rituals can also incorporate features of the environment to reveal the signaler's resourcefulness and skill. For example, displayers can advertise their ability to claim and defend territory, as well as their ability to provide resources. A common form of these rituals involves nest building. Male pufferfish construct complex sand circles, ridged with sand ripples, decorated with shells, and built using small, soft sand particles (Kawase et al. 2013). These nests take days for the male to form and refine, showing the quality of the male's territory and his skill in building a shelter to provide for potential

offspring (Kawase et al. 2013). Bowerbirds, however, are possibly the most famous nest builders. Regent bowerbirds build elaborate bowers, consisting of raised walls made of sticks that come together to form a tunnel-like structure, and the males decorate those structures with objects they find (Lenz 1994). These are often very colorful objects, such as snail shells, bright leaves, and pieces of blue plastic; and the decorations are presented to females as part of the courtship ritual (Lenz 1994). Female bowerbirds visit males with quality bowers for longer periods of time, reflecting the female's preference (Lenz 1994). Other species also incorporate found objects into their courtship rituals, such as gifts of food presented by male dancing flies to females immediately prior to copulation (Funk and Tallamy 2000). These gifts are so nutritional that females in some species of dancing flies have lost the ability to hunt and are thought to depend on these nuptial gifts (Funk and Tallamy 2000).

In addition to forms of courtship in which a specific behavior serves as the primary means of display, many forms of courtship ritual consist of a combination of displays. For example, brown-headed cowbird males sing while puffing their chests and flapping their wings to attract females (Cooper and Goller 2004). This "song and dance" exertion often causes pauses in their song (Cooper and Goller 2004). Males of higher physical capability can continue with fewer pauses, and this is thought to indicate that they have the motor and respiratory capacity to handle the exertion. (Cooper and Goller 2004). Long-tailed manakins also offer a great example of complex multimodal mating rituals. These vibrant, lekking birds work in teams to attract females (McDonald 1989). One high-ranking (alpha) male and another subordinate (beta) male first attract females with a chorus of calls (McDonald 1989). Once the female has been drawn into the area and can observe their behavior, they engage in a series of backward jumps over each other while singing and fluttering in the air (McDonald 1989). If the female is receptive, the alpha may solo display then copulate (McDonald 1989). This combination of synchronized singing and dancing is especially unusual among mating rituals, as multiple males work

together to display; but only one gets an opportunity to mate (McDonald 1989). The alpha male signals his health and genetics through his bright plumage, consistent calls, and dance, while he also displays his social status in his duet and synchronized dancing (McDonald 1989). The beta, in turn learns and practices the proper method of singing and dancing and can eventually become an alpha when he is older and more skilled (McDonald 1989).

Behaviors that comprise courtship rituals can also have an impact beyond direct courtship. For example, courtship rituals can help form and maintain social bonds between two individuals. Gray phalaropes use many aspects of their courtship behaviors to bond with a male days before copulation occurs (Ridley 1980). Black swans perform the triumph dance whenever one of the pair chases out an intruder, and this behavior increases their pair bond even though it is not always followed by copulation (Kraaijeveld et al. 2004). Alpha and beta male long-tailed manakins likewise form a complex social bond through displaying together (McDonald 1989). Finally, these displays can also advertise the signaler's quality to potential competitors. In highly competitive courtship rituals, like leks, high-quality displayers dissuade competitors and take optimal positions through the use of their displays (Wiley 1978; Jukema and Piersma 2006).

## Dishonesty in Courtship Rituals

The preceding examples illustrate that courtship signals can have a number of benefits for the sender. In many cases, they are also informative and thus beneficial for the receiver. However, not all advertisements are honest signals of the sender's traits. Most courtship behaviors are reliable indicators of the quality of the associated sender. These are called "honest" signals, and they enable the receiver to form an accurate assessment of the sender's quality. Displayers of certain species, however, have developed methods of using dishonest signaling to mate with evaluators. For example, male cuttlefish can change their color and shape. Males typically

display bright patterns to females in order to court them and then guard their mates from rival males (Norman et al. 1999). Small males, however, cannot compete with larger males. Small males sometimes use deceptive signaling to copulate with females. In these cases, a small male mimics the mottled appearance of a female. He uses this deception to enter the territory of a male that would otherwise chase him off (Norman et al. 1999). The deceptive male can then attempt copulation with the guarded female when the large male is distracted (Norman et al. 1999). Male mourning cuttlefish take deception one step further. A male of this species can display male courtship markings to a female on one side of his body while simultaneously displaying female markings to a rival, territorial male on his other side (Brown et al. 2012). In this way, deceptive males can court protected females while avoiding retribution (Brown et al. 2012).

One of the most impressive examples of deceptive rituals lies with the shorebirds called ruffs. Ruffs typically protect small territories, and males engage in lekking to attract females (Jukema and Piersma 2006). What makes them so interesting is that the males come in three polymorphs, each one genetically tied to a different courtship ritual (Jukema and Piersma 2006). Independent males are large and brown, displaying their plumage to potential mates and chasing away other independent males (Jukema and Piersma 2006). Satellite males are smaller, white, and unthreatening (Jukema and Piersma 2006). Independent males tolerate satellite males in their territory, giving them the opportunity to quickly attempt copulations with the females also in the territory (Jukema and Piersma 2006). The final form of male ruffs are referred to as faeders, the smallest and most drab of the three (Jukema and Piersma 2006). Faeders mirror the plumage color and size of female ruffs and can freely move between independent males' territories (Jukema and Piersma 2006). In this way, they can attempt to sneak copulations from resident females (Jukema and Piersma 2006). In these examples, dishonest signaling is used to gain access to previously inaccessible females. While these behaviors are quite different than honest displays, their performers are

nonetheless able to use their ornamentation and behaviors to mate with females, revealing them as unusual and fascinating forms of courtship rituals.

## Summary

Reproduction is one of the most important processes for animals, providing a mechanism to populate future generations and propagate species. Sexual selection results from individuals choosing mates based on the quality of certain preferred traits that are thought to provide benefits for either them, their offspring, or both. In order to advertise their traits and assess the quality of potential mates, many species have developed ornamentation and behaviors that serve as indicators of those traits. These are used in courtship rituals to attract mates, as well as serving other uses like defending territories and strengthening social bonds. Complex courtship rituals allow for more information to be signaled, and aspects of an individual's status such as health, genetic background, life experience, and social ranking can be communicated through courtship rituals. These accurate indicators of an individual's traits are called "honest" signals. Most courtship behaviors consist of honest signaling, but the presence of "dishonest" signals in some species reveal that not all courtship rituals are meant to signal quality. These deceptive signals are the exceptions, because they can only remain successful while honest signaling is the norm. Whether it be through bright coloration, fighting, singing, dancing, gift giving, or any combination of physical attributes and behaviors, the ability to copulate with the opposite sex is vital for the survival of a species. The goal of identifying and courting a quality mate has led animals to develop the many wondrous and complex courtship rituals found in nature today.

## Cross-References

- [Affiliative Behaviors](#)
- [Affiliative Bond](#)
- [Auditory Signals](#)
- [Behavior Systems](#)



- Behavioral Variation
- Bowerbirds
- Cheating
- Chemical Signals
- Communication
- Competition
- Cooperation
- Cooperative Breeding
- Deception
- Displays
- Evolution
- Female Choice
- Fertility
- Gene Expression
- Genes
- Healthy Mate Hypothesis
- Heredity
- Heritability of Behavior
- Honest Signaling
- Intersexual Selection
- Intra-sexual Selection
- Mate Guarding
- Mating
- Mating Effort
- Memory
- Natural Selection
- Nest Construction
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- Ormentation
- Parental Investment
- Paternal Behavior
- Phenotype
- Pheromone
- Rehearsal
- Reproductive Fitness
- Ritualization
- Sensory Receptors
- Sex Differences
- Sex Role Reversal
- Sexual Dimorphism
- Sexual Selection
- Signaller
- Sneaky Copulator
- Social Behavior
- Sociosexual Behavior
- Songbird Duets
- Species-Specific Behavior
- Territoriality

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## Covert Attention

- [Cognition](#)

## Covert Copulator

- [Sneaky Copulator](#)

## Cow

- [Bovine Cognition](#)

## Cow Locomotion

- [Bovine Locomotion](#)

## Cranial Base

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## Synonyms

[Base of skull](#); [Norma basalis](#); [Norma internalis](#)

## Introduction

The skull forms a part of the axial skeleton which comprises of 28 bones, most of which are paired (11 paired and 6 unpaired bones). Out of these 21 bones are firmly connected to one another by means of sutures and synchondrosis which renders them immovable. The main functions of the skull are to protect the brain, its coverings and to help in communicating one's feelings via numerous facial expressions. These functions can be attributed to the two parts of skull (Retzlaff 1987):

1. Neuro-cranium
2. Splanchno-cranium

### Neuro-cranium

This includes eight bones, namely, frontal, ethmoid, sphenoid, occipital, temporal and parietal (the latter two are paired). These bones are

involved in enclosing the cranial cavity to house the brain and its meninges, subsequently providing protection to the structures without hindering the blood circulation. The neuro-cranial vault is called as calvaria and is composed of membranous or dermal bones, whereas the bones forming the cranial base are ossified in cartilage.

### Splanchno-cranium

This part of the skull forms the facial skeleton which has cavities (nasal, orbital), alveolar processes in upper and lower jaw to accommodate the teeth and bony palate. The splanchno-cranium provides attachments to the facial muscles which control the movements of the oral fissures, palpebral fissures, and anterior nasal apertures indirectly providing different facial expression. Structurally, 14 bones (unpaired mandible and vomer; paired nasal, maxilla, palatine, lacrimal, zygomatic, and inferior nasal concha) are involved in the formation of facial skeleton which are originating from the pharyngeal arches.

The part of skull this chapter focuses on is the cranial base which is a part of the neuro-cranium and is composed of 5 bones of the skull, namely, ethmoid, sphenoid, occipital, both frontal and both temporal. The term cranial base had

its origin from Latin term *basis cranii* and it forms the floor of the skull.

To complete the study of cranial base, it requires inspection from inside (termed as **norma internalis**) and outside (termed as **norma basalis**). Both the normas are divided into 3 subparts each as shown in Fig. 1. in order to make the topic easy to understand.

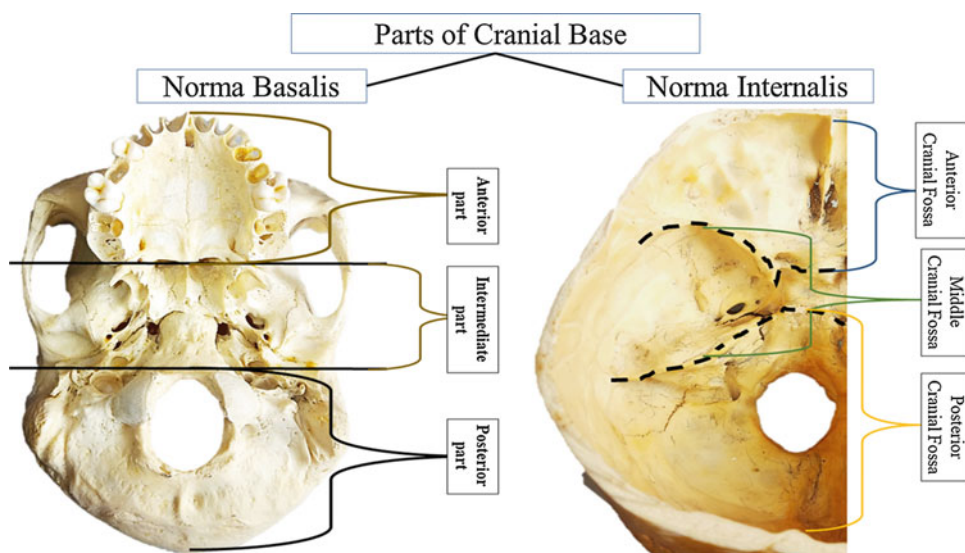
### Norma Basalis

The view of skull base from outside the cranium is referred to as norma basalis. For the ease of explanation, norma basalis is divided into 3 subparts, as shown in Fig. 1.

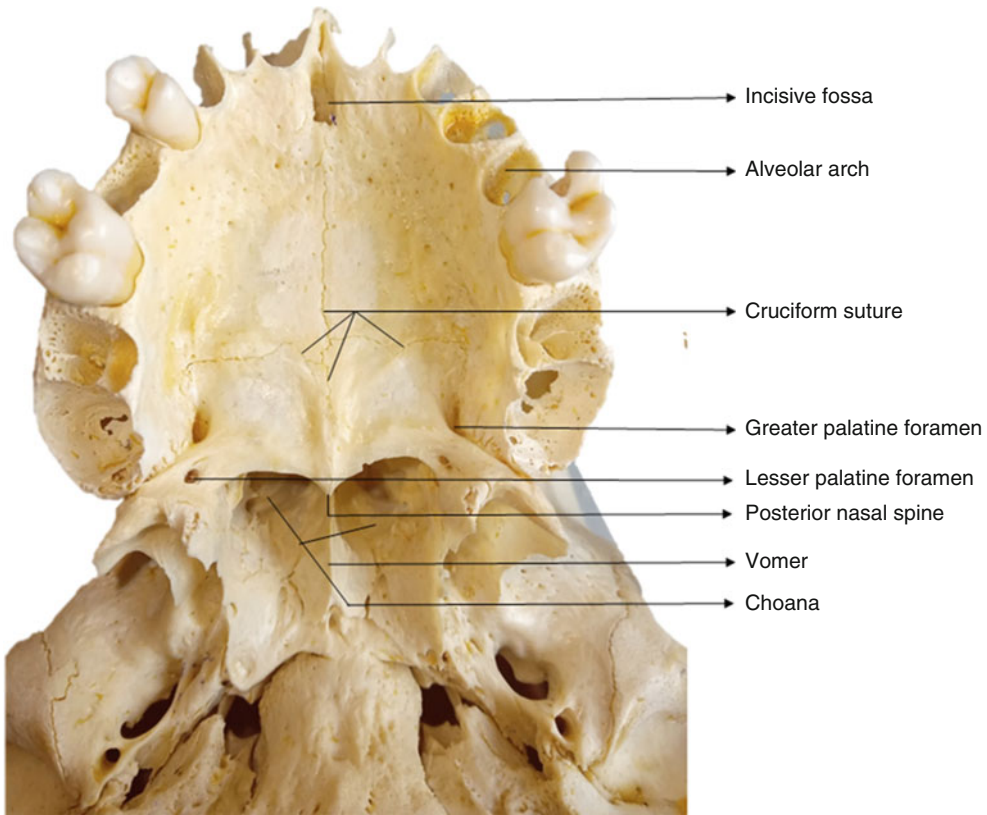
Each subpart comprises of various components, which are grouped as:

1. Bony components
2. Sutures between bony components
3. Muscular or ligamentous attachments
4. Special/characteristic features – fossa/foramen/processes/tubercle, etc.

The **anterior part of norma basalis** (Fig. 2) extends from the anterior margin of alveolar arch of maxilla to the posterior limit of the hard palate.



**Cranial Base, Fig. 1** Parts of the cranial base

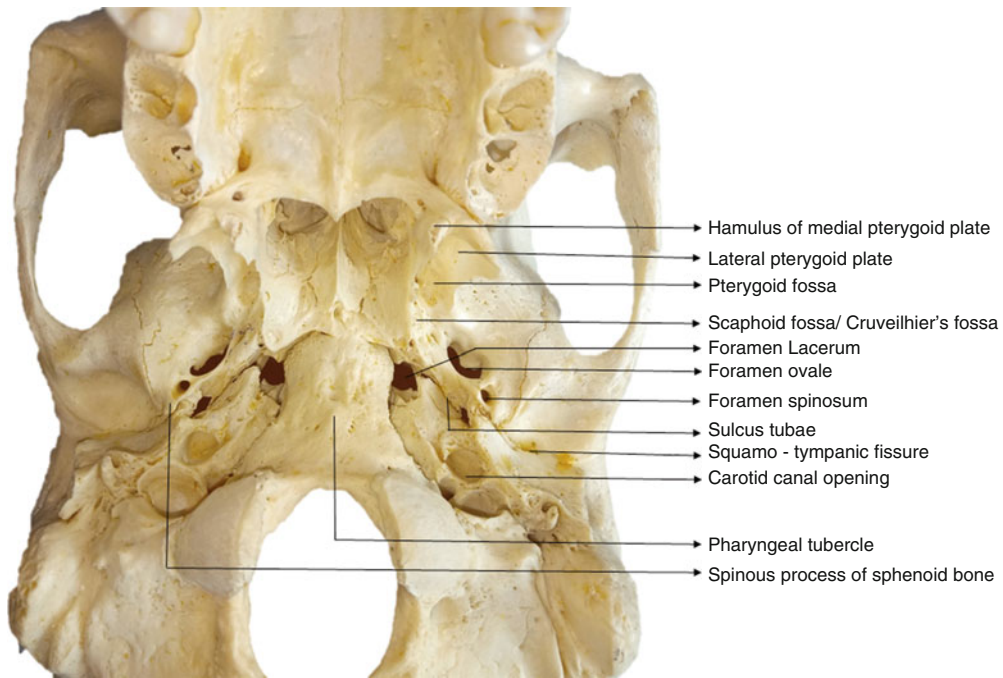


**Cranial Base, Fig. 2** Features of anterior part of norma basalis

Bony components of two subdivisions are palatine process of maxilla and horizontal parts of palatine bones for the bony palate and the second subdivision comprises of the alveolar arch of maxilla. The suture present between these bony components is called as **cruciform suture**, which is formed between palatine process of maxilla and horizontal parts of palatine bones. The special features in this part comprise of **incisive fossa**, present behind central incisor tooth affecting inter-maxillary suture, and communicates with the nasal cavity **transmitting** long naso-palatine nerve from above and branches of greater palatine vessels from below. **Greater palatine foramen** can be seen as single foramen medial to 3rd molar tooth on either side **transmitting** greater palatine vessels and nerves, and **lesser palatine foramen** are paired foramina on each side posterior to greater palatine foramen and **transmit** lesser palatine vessels and nerves. A backward projection

in the mid-sagittal plane called as posterior nasal spine gives attachment to musculus uvulae, a part of soft palate. The free margin of the palatine bone gives **insertion** to tensor veli palatini in the form of palatine aponeurosis (Datta 2009).

The **intermediate part of norma basalis** (Fig. 3) extends from the posterior limit of anterior part to transverse line across the anterior margin of foramen magnum. **Bony components** of the median part comprise of posterior border of the vomer, inferior surface of the body of sphenoid bone, and basilar part of occipital bone. Whereas the bony architecture of the para-median part has medial and lateral pterygoid plates of sphenoid bone, infratemporal surface of greater wing of sphenoid bone and temporal bone's squamous, tympanic and petrous part. On either side **squamo-tympanic fissure** is present which is divided into anterior petro-squamous fissure and posterior petro-tympanic fissure by tegmen



**Cranial Base, Fig. 3** Features of middle part of norma basalis

tympani of petrous part of temporal bone. The **muscular/ligamentous attachments** on different bony components of the intermediate part are: the **basilar part of occipital bone** gives postero-anterior attachments to pharyngo-basilar fascia, bucco-pharyngeal fascia, prevertebral fascia, and pharyngeal raphe at pharyngeal tubercle, while it also provides **insertion** to longus capitis and rectus capitis anterior muscles. The posterior border of **medial pterygoid plate** is free and has **scaphoid fossa** (or Cruveilhier's fossa) which gives origin to tensor veli palatine and also has a hook like projection called as **hamulus** which gives support for medial turning of tensor veli palatine, enabling it to enter soft palate (Standring 2016). Hamulus is connected to mandible via pterygo-mandibular raphe behind 3rd molar tooth. The **lateral pterygoid plate** gives **origin** to medial pterygoid muscle from its medial surface and lateral head of lateral pterygoid muscle from its lateral surface. The space between the lateral and medial pterygoid process is known as **pterygoid fossa**. The **infra-temporal surface of greater wing of sphenoid** forms the roof of infra-temporal fossa which is limited by the

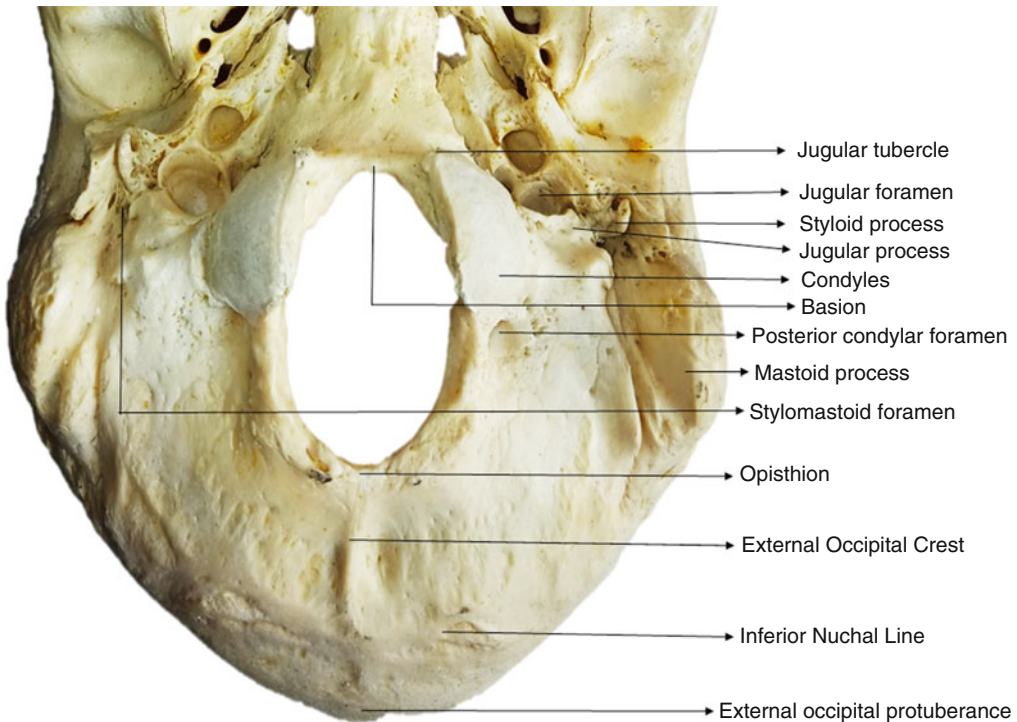
infra-temporal crest, which gives **origin** to upper head of lateral pterygoid muscle. The **spine of sphenoid bone** gives attachments to 2 muscles and 3 ligaments, namely, tensor veli palatini and tensor tympani muscles, while the ligaments are anterior ligament of malleus passing through the petro-tympanic fissure, speno-mandibular ligament, and pterygo-spinous ligament. The lateral-most bony component of intermediate part of norma basalis is the petrous part of temporal bone which gives **origin** to levator veli palatini from its apex. The **characteristic features** are **pharyngeal tubercle** on the basilar part of occipital bone which gives attachment to pharyngeal raphe on which pharyngeal constrictors are inserted, **processus tubarius** on the midpoint of posterior free border medial pterygoid plate (Thomson 1914). The **palate-vaginal canal** (or pharyngeal canal) is placed between the sphenoid bone and the palatine bone connecting the nasopharynx with the pterygopalatine fossa. An inconstant **vomero-vaginal canal** (no structure passes through it) may lie between the ala of the vomer and the vaginal process of the sphenoid bone, medial to the palatovaginal canal,



and lead into the anterior end of the palatovaginal canal. The palatovaginal canal **transmits** the pharyngeal branch of the third part of the maxillary artery and pharyngeal nerve from the pterygopalatine ganglion. The infra-temporal surface of greater wing of sphenoid is characterized by presence of **sulcus tubae**, formed between postero-medial border of greater wing of sphenoid and petrous bone for lodging cartilaginous part of auditory tube, and also by the presence of major foramina of skull such as **foramen ovale** which transmits (M. A. L. E)\* two roots of **mandibular nerve** (motor and sensory), **accessory meningeal artery**, **lesser petrosal nerve**, **emissary vein** to connect cavernous sinus with pterygoid venous plexus; **foramen spinosum** transmits nervous spinosus from mandibular nerve trunk [branch of trigeminal nerve, cranial nerve V (C. N. V)] and middle meningeal artery branch of first part of maxillary artery, posterior to the foramen spinosum lies spine of sphenoid. In between the sphenoid, apex of petrous temporal and basilar

part of occipital bone lies a triangular hole in the base of skull called as **foramen lacerum** (Latin for lacerated piercing) which is filled with cartilage after birth and so mostly nothing is transmitted through it. Internal carotid artery enters the cranial cavity through carotid canal opening present on the inferior surface of petrous part of temporal bone (Datta 2009).

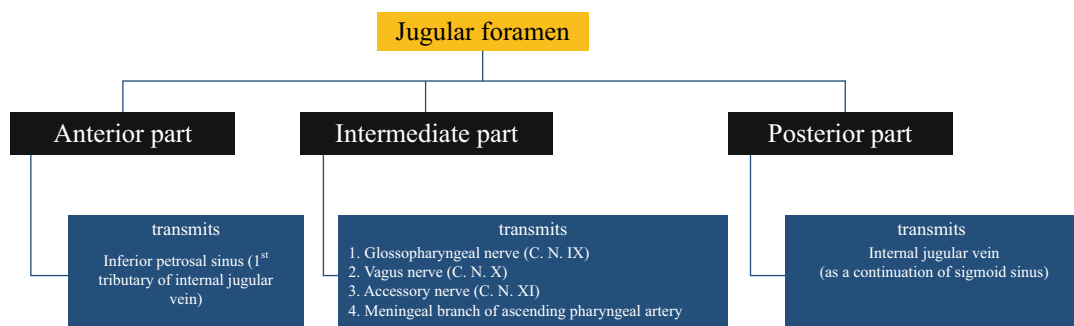
The **terminal/posterior part** (Fig. 4) of norma basalis extends from posterior limit of its intermediate part, i.e., posterior to the transverse line across the anterior margin of foramen magnum. The remaining two parts of the occipital bone, i.e., the condylar (comprising of the condyles, jugular process and jugular tubercle) and the squamous parts, constitutes the **bony components** of the median subdivision, while the para-median one is formed by remaining part of inferior surface of petrous temporal and mastoid and styloid processes of the temporal bone. The **sutural components** present in this part of norma are **occipito-mastoid suture**, which continues with



**Cranial Base, Fig. 4** Features of posterior part of norma basalis

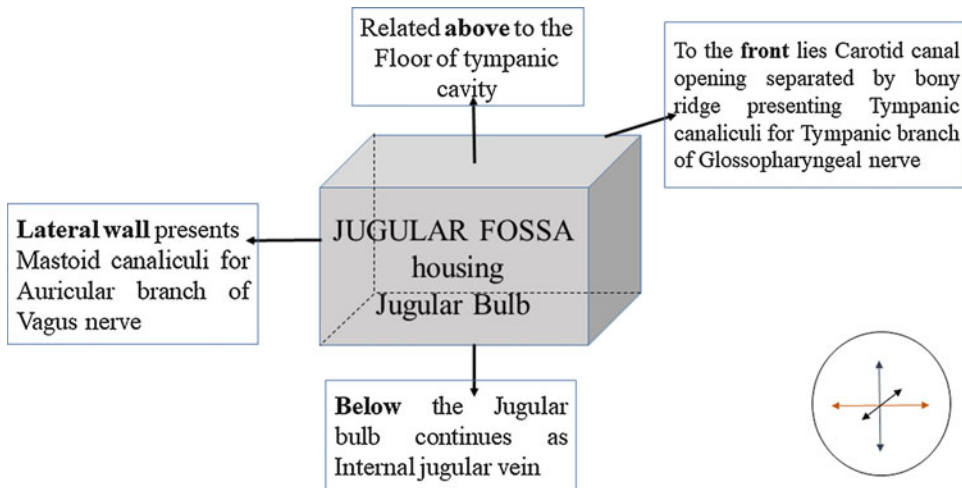
the lambdoid suture between occipital and parietal bones, and **petro-occipital suture**. The **attachments** found on the terminal part in antero-posterior direction are: **alar ligament** from dens of axis gets attached on the tubercle of occipital condyle, dividing the foramen magnum into small anterior and large posterior compartments. The styloid process gives attachment to 3 muscles (nerve supply) and 2 ligaments, thus converting into **styloid apparatus** (Datta 2009). The attachments of styloid process are styloglossus muscle (C. N. XII), stylohyoid muscle (C. N. VII), stylopharyngeus muscle (C. N. IX), and stylohyoid and stylomandibular ligaments. On the squamous part, an external occipital protuberance is seen from which appears **highest and superior nuchal lines** on both sides whereas an external occipital crest extends up till the mid-sagittal point on the posterior margin of foramen magnum called as **opisthion** (Jha et al. 2008). From the midpoint of external occipital crest, **inferior nuchal line** extends on either side of the cranial base. The external occipital crest gives attachment to **ligamentum nuchae**. The lateral one-third part of superior nuchal line gives **insertion** to sternocleidomastoid muscle, while the medial two-third part gives **origin** to trapezius muscle. Beneath the sternocleidomastoid muscle, **insertion** of splenius capitis and longus capitis can be seen on the mastoid. The area between superior and inferior nuchal line is occupied by the **insertion** of semispinalis capitis, whereas the area below the inferior nuchal line is occupied by insertion of rectus capitis posterior major, minor, and

obliquus capitis superior medio-laterally. The features that **characterize** this part of norma basalis are: in the **median part** are foramen magnum, external occipital crest, and external occipital protuberance (highest point is called as inion). **Foramen magnum** is a large oval aperture of the occipital bone for communication between posterior cranial fossa and vertebral canal. The midpoint of anterior margin of foramen is termed as basion. It is divided by alar ligament of dens into anterior small osseo-ligamentous compartment (transmitting apical ligament of dens, upper band of cruciate ligament, and membrane tectoria) and posterior large neuro-vascular compartment (transmitting medulla oblongata and meninges, fourth part of vertebral arteries, spinal root of accessory nerves, anterior and posterior spinal arteries, and part of tonsil of cerebellum). The features of **para-median part superior nuchal line, inferior nuchal line, hypoglossal canal** transmitting hypoglossal nerve (C. N. XII), **condylar fossa** with posterior condylar foramen transmitting emissary vein to connect sigmoid sinus with suboccipital venous plexus, **jugular foramen** (Fig. 5) transmitting glossopharyngeal nerve (C. N. IX), vagus nerve (C. N. X), accessory nerve (C. N. XI), and internal jugular vein, **mastoid canaliculi** in the lateral part of the jugular fossa (Fig. 6) for the entrance of the auricular branch of the vagus nerve, **styloid process** – 2.5 cm long projection developing from cartilaginous part of 2nd branchial arch, **stylo-mastoid foramen** transmitting facial nerve (C. N. VII) and provides entrance to stylomastoid branch of posterior auricular artery, in the bony



**Cranial Base, Fig. 5** Structures passing through Jugular foramen





**Cranial Base, Fig. 6** Relations of Jugular fossa

ridge dividing the carotid canal from the jugular fossa is the small inferior **tympanic canaliculus** for the passage of the tympanic branch of the glossopharyngeal nerve (Gleeson 2016).

## Norma Internalis

The view of skull base from inside the cranium is referred to as norma internalis and is divided into 3 cranial fossas, as presented in Fig. 1.

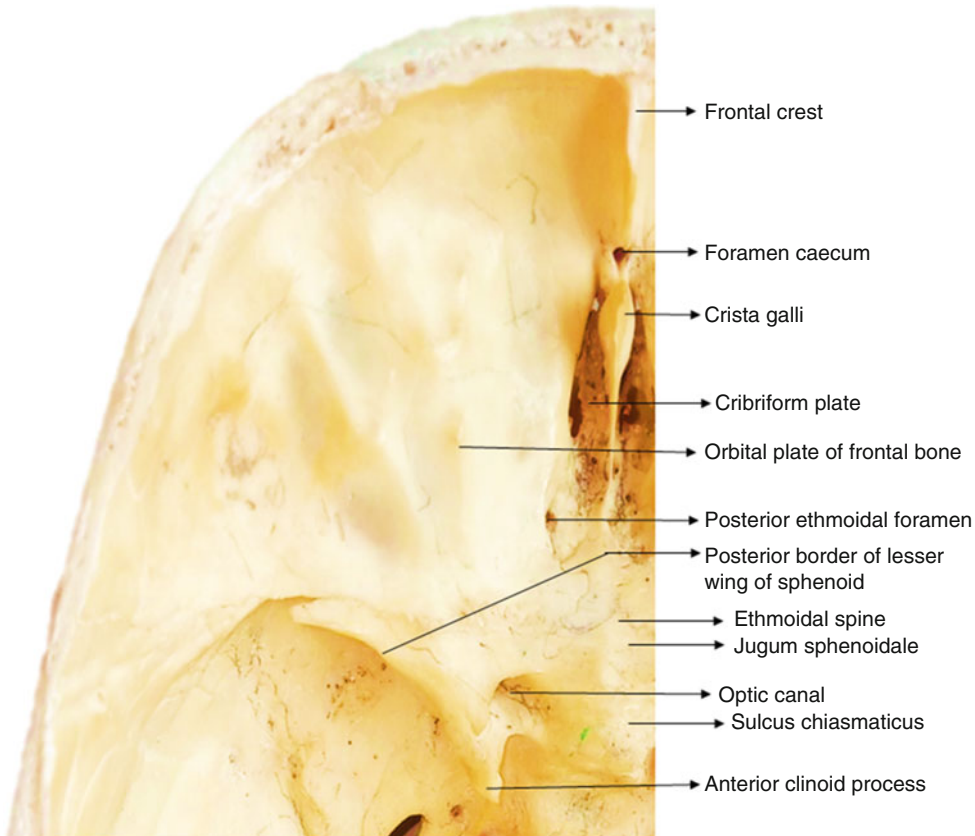
Each cranial fossa has various components to be learned of, which are grouped as:

1. Bony components
2. Special features – fossa/foramen/processes/tubercle/grooves, etc.

The **anterior cranial fossa extends** (Fig. 7) from the inner surface of frontal bone's inner table to the posterior border (also called as sphenoidal crest) of lesser wing of sphenoid on each side and anterior border of sulcus chiasmaticus in median region. Three **bones** are involved in its formation, namely, cribriform plate of ethmoid bone, orbital plates of the frontal (has impressions of sulci and gyri from the inferior surface of frontal lobe of brain), and lesser wings with jugum sphenoidale of the sphenoid bone. The anterior cranial fossa has six **special features**, (1) **cribriform plate**:

it forms the roof of nasal cavity and has numerous small apertures for passage of olfactory nerves (C. N. I) from nasal mucosa to olfactory bulb overlying the plate; (2) **ethmoidal foramina**: on both sides of cribriform plate 2 foramina can be seen, called as anterior and posterior ethmoidal foramina. The anterior ethmoidal foramen transmits anterior ethmoidal nerve, continuation of nasociliary nerve, and anterior ethmoidal artery, a branch of ophthalmic artery. The posterior ethmoidal foramen transmits posterior ethmoidal nerve, a branch of nasociliary nerve and posterior ethmoidal artery, a branch of ophthalmic artery; (3) **crista galli** (Latin for crest of the rooster), a triangular process projecting upward from cribriform plate and gives attachment to falx cerebri, a modification of dura mater; (4) **foramen caecum**, it intervenes between crista galli and frontal crest and rarely transmits vein from nasal mucosa to superior sagittal sinus; (5) **jugum sphenoidale**, a part of lesser wing of the sphenoid which articulates with ethmoid and forms the roof of sphenoidale air sinus; and (6) **anterior clinoid process**, bony projections at the medial end of posterior margin of lesser wing of sphenoid, gives attachment to anterior end of free margin of tentorium cerebelli (Koshi 2018).

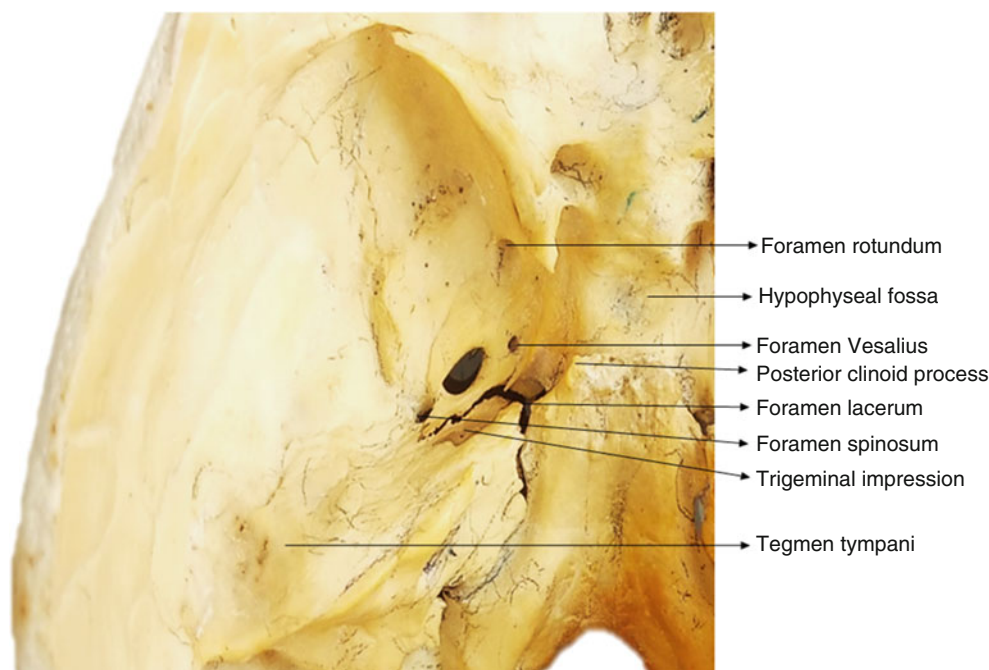
The **medial cranial fossa** (Fig. 8) is butterfly shaped and **extends** from the posterior border of



**Cranial Base, Fig. 7** Features of anterior cranial fossa

lesser wing of sphenoid to the upper border of petrous temporal on each side and dorsum sellae of sphenoid bone in median region. It is further divided into median and lateral subdivisions. The median part comprises of body of sphenoid presenting sulcus chiasmaticus in front, sella turcica behind, and carotid groove on either side, while the lateral part is formed by cranial surface of greater wing of sphenoid bone and inner surface of squamous part and anterior surface of petrous part of temporal bone (Sinnatamby 2011). The **special features** of the median subdivision of middle cranial fossa are sulcus chiasmaticus and sella turcica. **Sulcus chiasmaticus** is a transverse groove which leads to optic canal on each side which transmits optic nerve and ophthalmic artery. The sulcus is housing the optic chiasma, which lies slightly above it. **Sella turcica** (latin for Turkish seat) comprises of: (a) tuberculum sellae, the posterior limit of sulcus chiasmaticus

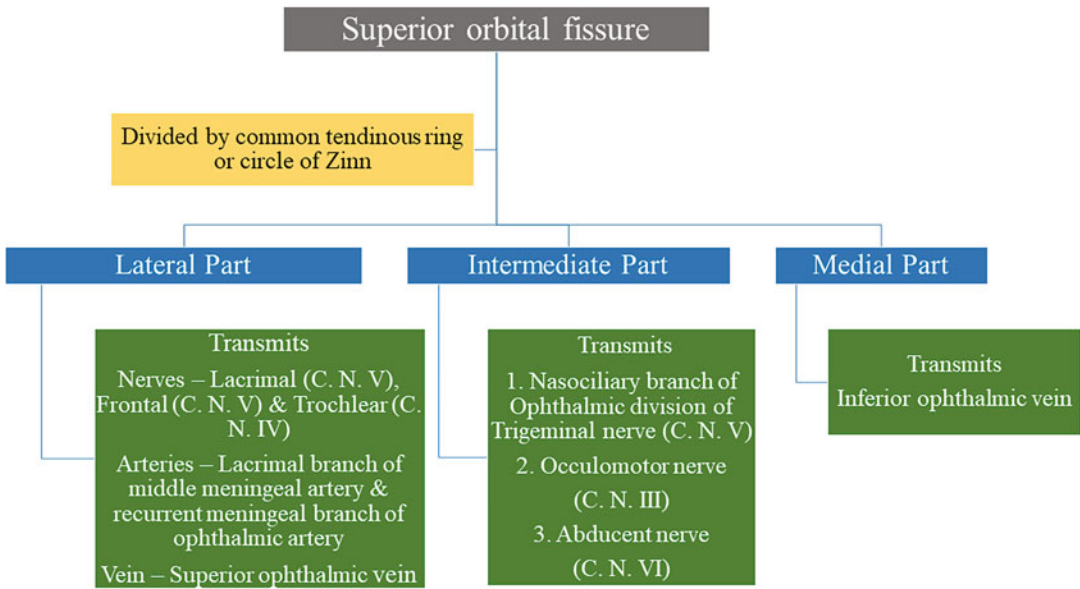
giving attachment to diaphragm sellae forming roof of hypophyseal fossa; (b) middle clinoid process, a small projection on each side of tuberculum sellae which gets connected to anterior clinoid process via carotico-clinoid ligament thus forming carotico-clinoid foramen transmitting upturned internal carotid artery. At times, ossification of the carotico-clinoid ligament occurs which can lead to compression of internal carotid artery (Özdoğan et al. 2003); (c) hypophyseal fossa, a depression containing pituitary gland, with seldom presence of cranio-pharyngeal canal (marks the original position of Rathke's pouch); (d) dorsum sellae, bony plate presenting *posterior clinoid process* on each end, which gives attachment to tentorium cerebelli. Apart from these bony features, some ligamentous features are also seen in the middle cranial fossa, these are *Oculomotor trigone*, formed by crossing margins of free and attached



**Cranial Base, Fig. 8** Features of middle cranial fossa

tentorium cerebelli on either side of the posterior clinoid process and is pierced by oculomotor (C. N. III) and trochlear nerves (C. N. IV). An osseo-ligamentous foramen called as **Dorello's canal** opening is formed by **petro-sphenoid ligament** (or **Gruber's ligament**) which connects petrosal process on the lateral margin of dorsum sellae and tip of petrous temporal, through this canal abducent nerve (C. N. VI) passes and appears in cavernous sinus (Ambekar et al. 2012). On each side of sella turcica, an italic “f” shaped **carotid groove** is seen housing internal carotid artery with plexus of sympathetic nerves around it. On the lateral subdivision of the middle cranial fossa, features can be studied with respect of parts of the bony components forming the subdivision. The cranial surface of greater wing of sphenoid presents with, (a) **superior orbital fissure** (Fig. 9), a slit enclosed between lesser wing, greater wing and body of sphenoid bone, acting as a passage between orbit and middle cranial fossa; (b) foramen rotundum, transmitting maxillary division of trigeminal nerve from trigeminal ganglion in middle cranial fossa to pterygopalatine fossa; (c) foramen ovale (see

section “**Norma Basalis**”); (d) foramen spinosum (see section “**Norma Basalis**”). The inner surface of squamous part of temporal bone presents grooves for middle meningeal vessels. The anterior surface of petrous temporal bone presents with three important features, (1) **trigeminal impression**, a fossa at the petrous apex which lodges trigeminal ganglion in dural pouch called as **cavum trigeminale**; (2) **arcuate eminence**, an elevation behind trigeminal impression overlying anterior semi-circular canal of internal ear; (3) **tegmen tympani**, a thin bony plate covering the anterior petrous surface and forming common roof of mastoid antrum, tympanic cavity, and bony part of auditory tube. It presents 2 foramina, **lateral** and **medial**. The lateral foramina transmit **lesser petrosal nerve (branch of C. N. IX)** and medial foramina transmit **greater petrosal nerve (branch of C. N. VII)**. It also divides squamotympanic fissure into 2 parts, petro-squamous anteriorly and petro-tympanic posteriorly (see section “**Norma Basalis**”). The foramen lacerum (see section “**Norma Basalis**”) can be visualized as a feature of this cranial fossa (Basmajian and Slonecker 1989).



**Cranial Base, Fig. 9** Structures passing through Superior orbital fissure

On the inferior aspect of the middle cranial fossa (externally) there are important fossas or spaces which are being mentioned in Table 1, along with the structures forming the boundaries of them and their contents (Whitefield 2016).

The **posterior cranial fossa** (Fig. 10) can be observed till up to **internal occipital protuberance** and groove for transverse sinus. It can also be divided into median and lateral or para-median subdivisions. The bony components of median subdivision are squamous and basilar part of occipital bone as well as the posterior surface of the body of sphenoid bone. The para-median subdivision comprises of posterior surface of petrous part of temporal bone and postero-inferior angles of the parietal bone. **Features** of the median part comprise of **foramen magnum** (see section “**Norma Basalis**”). Anterior to foramen magnum, a sloping surface of bone known as **clivus** is formed by fusion of basi-occiput and body of sphenoid [a primary cartilaginous joint between basi-occiput and body of sphenoid (synchondrosis) which gets replaced by bone (synostosis) at around 25 years of age] and is related to pons, medulla oblongata, separated by basilar artery and basilar venous plexus. Posterior to foramen magnum, the inner surface of occipital

bone presents **internal occipital crest**, which extends upwards to internal occipital protuberance and divides near the posterior margin of foramen magnum forming triangular fossa called as the **vermian fossa**, housing inferior vermis of cerebellum. A transverse sulcus (housing transverse sinus) extends from either side of internal occipital protuberance and continues into sigmoid sulcus (housing sigmoid sinus) involving postero-inferior angle of parietal, mastoid part of temporal, and upper surface of jugular process of occipital bone. In the para-median part, special features are seen on either side of foramen magnum. The notable features are hypoglossal canal (see section “**Norma Basalis**”) and jugular foramen (see section “**Norma Basalis**”). The three borders of petrous temporal bone are associated with venous sinuses, superior border with superior petrosal sinus, posterior border with sigmoid sinus, and antero-inferior border with inferior petrosal sinus. The posterior surface of petrous temporal bone presents with (a) **internal acoustic meatus**, 1 cm in length, it transmits facial (C. N. VII) and vestibule-cochlear (C. N. VIII) nerves and labyrinthine artery branch of anterior inferior cerebellar artery (85–100%) or basilar artery (<15%); (b) **subarcuate fossa**, a depression situated behind and lateral to internal meatus

**Cranial Base, Table 1** Anatomical spaces that lie inferior to the middle cranial fossa

| Space                                              | Principal relations (boundaries)                              | Major contents                                                  |
|----------------------------------------------------|---------------------------------------------------------------|-----------------------------------------------------------------|
| Infratemporal fossa                                | M – lateral pterygoid plate                                   | Mandibular division of trigeminal nerve                         |
|                                                    | L – ramus of mandible                                         | Otic ganglion                                                   |
|                                                    | A – posterior surface of maxilla                              | Chorda tympani nerve                                            |
|                                                    | P – styloid process                                           | Medial and lateral pterygoid muscles                            |
|                                                    | S – greater wing of sphenoid                                  | Maxillary artery and vein                                       |
|                                                    | I – opens into neck                                           | Pterygoid venous plexus                                         |
| Pterygopalatine fossa                              | M – palatine bone and nasal cavity                            | Maxillary nerve from foramen rotundum                           |
|                                                    | L – infratemporal fossa via pterygomaxillary fissure          | Nerve of pterygoid canal (Vidian nerve)                         |
|                                                    | A – maxilla                                                   | Pterygopalatine ganglion                                        |
|                                                    | P – pterygoid process of sphenoid                             | Pterygopalatine ganglion                                        |
|                                                    | S – body of sphenoid                                          |                                                                 |
|                                                    | I – pterygoid plates                                          |                                                                 |
| Parapharyngeal space (anterior to styloid process) | M – pharynx                                                   | Eustachian tube                                                 |
|                                                    | L – medial pterygoid and parotid fascia                       | Tensor and veli palatine muscles                                |
|                                                    | A – fascia covering medial pterygoid and tensor veli palatini | Ascending pharyngeal and facial arteries                        |
|                                                    | P – styloid muscles and fascia                                | Branches of the glossopharyngeal nerve (to pharynx)             |
|                                                    | S – sphenoid bone                                             |                                                                 |
|                                                    | I – hyoid bone                                                | Fat                                                             |
| Infrapetrosal space (posterior to styloid process) | M – posterior pharynx                                         | Jugular bulb                                                    |
|                                                    | L – mastoid process                                           | Internal carotid artery                                         |
|                                                    | A – styloid muscles and fascia                                | Ascending pharyngeal artery                                     |
|                                                    | P – jugular foramen                                           | Facial (VII) nerve at stylomastoid foramen                      |
|                                                    | S – petrous bone                                              | C. N. - IX, X, XI, XII                                          |
|                                                    | I – posterior belly of digastric                              | Styloid muscles – styloglossus, stylopharyngeus, and stylohyoid |
|                                                    |                                                               | Stylomandibular ligament                                        |
|                                                    |                                                               | Posterior belly of digastric muscle                             |

Key – A anterior, P posterior, M medial, L lateral, S superior, I inferior

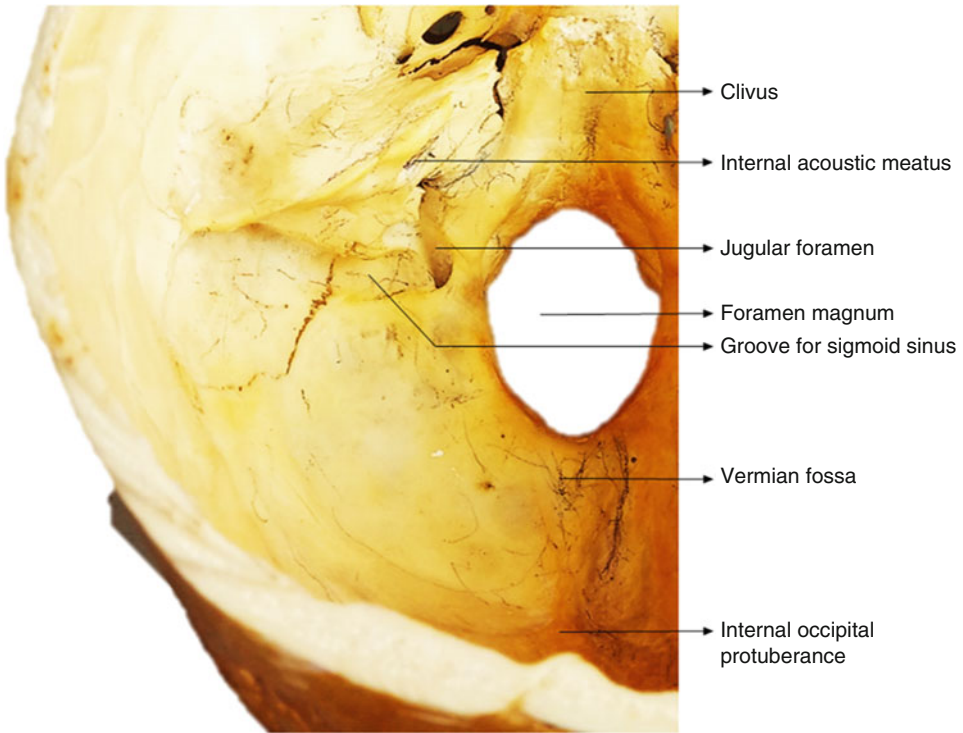
and is prominent in new born; (c) **aqueduct of vestibule**, a bony canal behind the internal meatus lodging saccus and ductus endolymphaticus; (d) **pyramidal notch**, present at the lower border of petrous temporal bone, just above the jugular foramen and lodges inferior ganglion of glossopharyngeal nerve (Basmajian and Slonecker 1989).

## Applied Anatomy

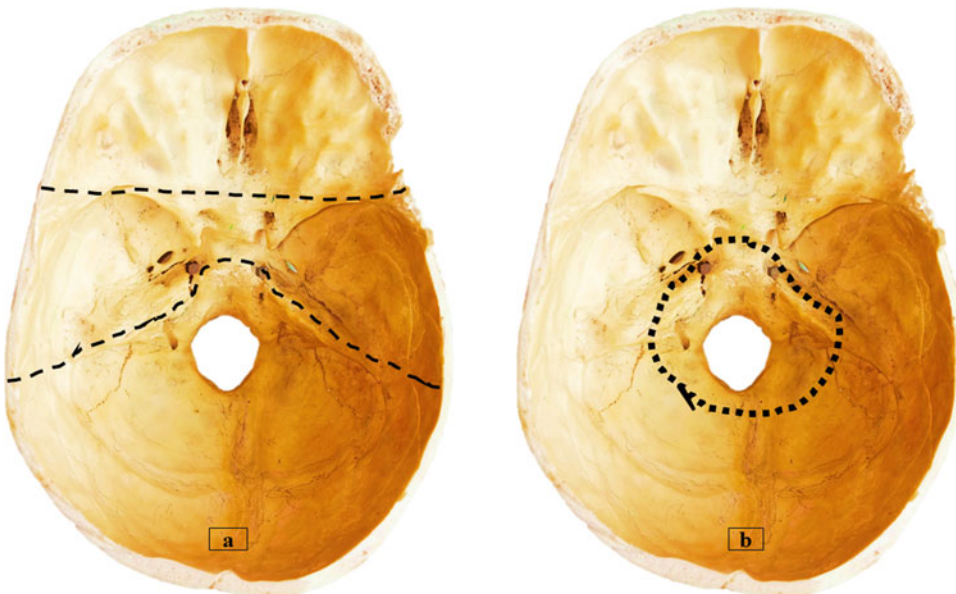
The base of skull is fractured mainly in accidents. Depending on the direction of force transmitted, the fractures of the base of the skull can be of

three types: (1) **Longitudinal fracture**, which divides the base into two halves. This can be seen in cases of run over by a vehicle where the impact can be on the face and forehead or on the back of the head or from front-to-back or back-to-front compression of the head. (2) **Transverse fracture** (Fig. 11a), where the base is divided into two parts, front and back half. This type of fracture results from an impact on either side of the head or side-to-side compression of the head as when run over by a vehicle or hit with heavy and sturdy object like baseball bat. In cases where the fracture line runs from side to side across the middle cranial cavities separating the base into two halves, anterior and





**Cranial Base, Fig. 10** Features of posterior cranial fossa



**Cranial Base, Fig. 11** (a) Dashed line depicting margins of transverse/hinge fracture. (b) Dashed line depicting margins of ring fracture



posterior, are termed as **hinge fracture**. As they are seen in majority of motorcycle accidents, they are also known as **motorcyclist's fracture** (Reddy and Murty 2014). (3) **Ring fractures** (Fig. 11b), which occurs in the posterior cranial fossa around the foramen magnum and is commonly caused by a fall from a height onto the feet. The potential energy acquired from the height of the fall if not absorbed by fractures of the legs, pelvis, or spine is then transmitted up the cervical spine. This puts pressure on the skull and causes the fracture of the occipital bone in a circular fashion around the foramen magnum and hence giving the term **foramen fracture**. In this case there occurs no injury to scalp or blood infiltration (Buris 1993).

In fracture of base of skull, cranial nerve damage is commonly seen. Fracture of anterior cranial fossa is usually due to direct impact or a heavy blow on the chin and involves escape of blood or CSF or both from nose. The middle cranial fossa fractures are seen due to direct impact behind the ear causing fracture of the petrous temporal bone and thus involving the middle ear, which allows blood and CSF to escape from the ear. The posterior cranial fossa fracture usually occurs from direct impact on the back of the head. Here, extravasation of blood is seen behind the mastoid process or the blood may escape into the nape of the neck deep to the postvertebral muscles. If the fracture disrupts foramen magnum, cerebellar contusions may result leading to hernia of cerebellar tonsils due to edema (Wineski 2019).

## Cross-References

- [Hominoidea Morphology](#)
- [Homo erectus](#)
- [Vertebrates \(Chordata\)](#)

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## Creatinine

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## Introduction

Creatinine is a nonprotein nitrogenous compound found in the blood and excreted by glomerular filtration at a constant rate (Feher 2012).

## Source

Creatinine is derived from nonenzymatic degradation of creatine phosphate which is a phosphagen for vertebrate animals. Phosphagens are high-energy phosphate compounds which supply immediate but limited energy during sudden demand for skeletal muscle and brain. Creatine phosphate is a phosphagen for vertebrate animals, whereas arginine phosphate is the phosphagen for invertebrate animals.

Adenosine triphosphate (ATP) is the energy currency of the cell required for many biochemical reactions. During the sudden demand for ATP, creatine phosphokinase enzyme catalyzes the transfer of phosphoryl group from creatine phosphate to adenosine diphosphate (ADP) to produce adenosine triphosphate (ATP). This reaction is known as Lohman's reaction.



A fraction (around 1–2%) of creatine and creatine phosphate are spontaneously

(nonenzymatically) and irreversibly converted into creatinine in skeletal muscle. Conversion of creatine to creatinine involves dehydration (removal of water). Amount of creatinine produced in an animal is constant and related to the muscle mass. A 70-kg adult male produces about 2 g of creatinine per day.

## Creatinine Clearance

Creatinine clearance is the volume of blood that is cleared of creatinine in 1 min. Creatinine is a small molecule with the relative molecular weight of 113 Da (Stevens et al. 2010). It is present in most of the body fluids and secretions. In the renal glomeruli, creatinine is freely filtered by the glomerulus because of the low molecular weight. Then, it is not reabsorbed and excreted without any alteration with the minimal secretion of creatinine by the renal tubules. Because of this property, creatinine is used as a marker of glomerular filtration rate (GFR) (Huidobro et al. 2018). Thus, creatinine clearance slightly overestimates the GFR.

Urea is another nonprotein nitrogenous compound excreted by the kidney. Urea clearance can also be used for GFR estimation. The advantage of creatinine clearance over urea clearance is given in the table.

| Urea clearance                      | Creatinine clearance             |
|-------------------------------------|----------------------------------|
| Underestimates GFR                  | Overestimates GFR                |
| Inferior to creatinine clearance    | Better than creatinine clearance |
| Depends upon flow rate              | Independent of flow rate         |
| Depends upon dietary protein intake | Independent of dietary proteins  |

The mathematical formula to calculate creatinine clearance is:

$$\text{Creatinine clearance} = \frac{\text{Urinary creatinine (mg/dl)} \times \text{Urine flow rate (ml/minute)}}{\text{Serum Creatinine (mg/ml)}}$$

The unit of creatinine clearance is ml/minute. Urinary creatinine is calculated using a urine sample collected over 24 h. As the 24-h collection of urinary samples is difficult, Cockcroft-Gault formula is widely used to find out estimated GFR (eGFR) from serum creatinine values in humans (Shoker et al. 2006).

$$\text{eGFR} = \frac{(140 - \text{age in years}) \times \text{Weight(Kg)} \times K}{72 \times \text{serum creatinine (mg/dL)}}$$

$K = 0.85$  for women and 1 for men

## Clinical Significance

In combination with serum urea level, creatinine clearance provides an important clue to the diagnosis of renal diseases especially renal failures. Different composite and surrogate markers of renal function utilize creatinine concentration, e.g., blood urea nitrogen (BUN)/creatinine ratio.

## Methods of Creatinine Estimation

Creatinine is estimated commonly by a chemical method using its reaction with picric acid (Jaffe's method). Protein, ketones, bilirubin etc. are known interfering substances in this method. In dry chemistry analyzers, enzyme (creatininase, creatinine deaminase)-based methods are used.

## Cross-References

► [Excretory System](#)

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## Crèching

► [Huddling](#)

## Cre-loxP

► [Targeted Mutation](#)

## Crepuscular

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## Synonyms

[Bimodal activity pattern](#); [Matutinal \(active at dawn\)](#); [Twilight](#); [Vespertine \(active at dusk\)](#)

## Definition

Crepuscular refers to twilight, the time shortly before sunrise and after sunset. In the context of animal ecology, it refers to those species active during these times of day. In other words, a crepuscular animal is one whose diel (24 h) activity pattern has peaks during the twilight hours (e.g., African wild dogs). Crepuscular can also be used to refer to specific behaviors of non-crepuscular species that usually occur during twilight (e.g., nocturnal smooth-tailed newts are crepuscular breeders).

## Crepuscular Behavior Patterns

Crepuscular organisms are those that are primarily active during the twilight hours: the periods just around dawn and dusk. Astronomical twilight occurs when the sun is between 0° (sunrise/sunset) and 18° below the horizon (Potts 1990). Twilight near the equator lasts approximately 70 to 85 min, though it can be much longer at higher latitudes. The light levels change dramatically during this time; within 30 min light levels can change from 100 to 0.01 lux (or vice versa; Potts 1990).

The activity patterns of crepuscular species are often referred to as being bimodal unless they are either matutinal, active only at dawn, or vespertine, active only at dusk. While species that are classified as being crepuscular exhibit their peak activity during these hours, some crepuscular species will also be active at specific times of day or night. This is because the quantity and quality of light is the ecologically relevant determining factor of crepuscular activity, not the time of day. In fact, many crepuscular species will be active in light conditions similar to twilight that occur at other times of the day as well (i.e., full moon nights, or heavily overcast days).

Species displaying crepuscular activity patterns are not the only ones who are active during these twilight periods. Many diurnal (species active during the day) and nocturnal (species active during the night) animals are also active during this time. This twilight period acts as a transition period with diurnal and nocturnal species tapering off their level of activity in preparation for a period of inactivity or ramping up in preparation for their active period. Cathemeral/metaturnal (active at regular intervals irrespective of time of day) species also frequently overlap their activity patterns with crepuscular species depending on their diet or local predation pressures.

While species whose main peak of activity occurs during twilight are considered truly crepuscular, many other diurnal or nocturnal species have crepuscular behavior patterns, i.e., behaviors they exhibit only during the dawn and/or

dusk. Smooth newts, *Triturus vulgaris*, for example, are primarily nocturnal species yet breed only during dusk (Griffiths 1985). Diurnal passerines are well known for their dawn and dusk choruses, exhibiting a peak in singing behavior most commonly at dawn, but for some species during dusk as well (Kroodsmas and Miller 1996). Many species of diurnal and nocturnal marine fish show crepuscular traveling behavior as they travel between foraging areas and the safety of burrows where they remain protected during their inactive periods (Potts 1990). Other species, such as Carangidae and Elopidae species, show crepuscular peaks in foraging activity as they take advantage of the diurnal and nocturnal species that have begun their transition too late or too early. In fact, it can often be difficult to classify a species' activity patterns as crepuscular as there can be so much overlap in the patterns of diurnal and nocturnal species making the boundary between crepuscular and nocturnal or diurnal less clear. This delineation is especially difficult when species are reacting to local conditions (such as moonlight levels or local heterospecific competitors or predators) causing shifts in their normal activity patterns making them appear more or less crepuscular than other populations.

## Prevalence of Crepuscular Activity Patterns in the Animal Kingdom

Crepuscular activity patterns are widely prevalent, with most taxa having at least a few species that exhibit this diel pattern. While crepuscular activity patterns are relatively rare in birds, reptiles, and amphibians, crepuscularity is more common in fish such as carangids, lutjanids, serranids and in some gadoids, as well as in many species of insects (Griffiths 1985; Hall and Ross 2006; Kelber et al. 2006; Potts 1990; Shine 1979). Crepuscular patterns appear more common in mammals as, while visible or somewhat active during either the day or night, mammals likely had a nocturnal ancestor, and many mammals are actually crepuscular, ramping up their activity at dawn and dusk (Halle 2006).

## Driving Forces Behind Crepuscular Diel Patterns

There are a number of theories as to why crepuscular activity patterns have evolved in such a wide range of species, but the two most common are related to either predation or competition. During twilight, as the sun sets or rises, the light changes very quickly. This rapid shift in light intensity causes many species to have trouble seeing (Caro 2005; Hayward and Slotow 2009; Potts 1990). This allows predators, even diurnal or nocturnal ones, to take advantage of the unique light conditions to catch prey that cannot detect them as easily (Hayward and Slotow 2009; Potts 1990). Although these easily caught prey should avoid this time of day, often being active during twilight is unavoidable as they are either preparing for or recovering from long periods of inactivity and can be a profitable food source for crepuscular predators (Halle 2006). Some crepuscular predators are driven more by the behavior of their prey, as opposed to the quality of light. For example, many species of marine fish follow plankton as it rises during dusk engaging in vertical migrations, while common murre, *Uria aalge*, that prey on these fish, such as capelin, *Mallotus villosus*, will peak in foraging activity as the fish migrate close to the surface (Potts 1990; Regular, Davoren, Hedd, and Montevecchi 2010). Similarly, many snake species, such as Australian elapids, will take advantage of mammals that leave their burrows at dusk (Shine 1979). For the predators that rely on these food sources, their peaks in activity tend to be related to searching for and catching these prey, thereby shaping these predators' activity patterns to follow a crepuscular or, in these cases vespertine, pattern.

Some frequently depredated species, similar to many predators, take advantage of these twilight light conditions that limit a predator's ability to visually detect them, thus lowering their chances of being depredated (Caro 2005). However, simply avoiding predators may be an even stronger drive. It is thought that the dawn, and or dusk, chorus in passerine birds occurs at twilight due to fewer predators actively hunting then, allowing these vulnerable species to sing from exposed

perches, a highly dangerous behavior (Kroodsma and Miller 1996).

While predation is a strong driving force that shapes the natural history of many species, competition, especially over food, is similarly important. Some bee species in the Andrenidae and Halictidae families, for example, take advantage of nocturnal flowers that open at dusk thereby maximizing the pollen load they can collect. By being active before the nocturnal species that visit those flowers are, these crepuscular bees gain a competitive advantage (Kelber et al. 2006). Crepuscular foraging may also help in cases where competitors also pose a risk. In the African savanna, the less dominant large carnivores, cheetah and wild dogs, are most active in a diurnal/crepuscular, or strictly crepuscular patterns, respectively (Hayward and Slotow 2009). This crepuscular activity is likely due to avoidance of competition, and possible dangerous interactions, with more dominant nocturnal carnivores, lions, leopards, and hyenas, as these activity patterns do not overlap with those of cheetah or wild dog preferred prey (Hayward and Slotow 2009).

## Adaptations for Crepuscular Behavior

As previously mentioned, twilight light quality is such that the combination of the quick change and quality of light makes it difficult for the rods and cones found in vertebrate species to operate well, resulting in decreased visual acuity and sensitivity in these light conditions (Caro 2005). Many species that follow crepuscular activity patterns have evolved features that help them adjust to these specific visual conditions. Crepuscular birds, for example, have an intermediate relationship between their visual acuity (telling objects apart) and their visual sensitivity (the ability for the eye to gather light) as opposed to diurnal birds with high visual acuity compared to sensitivity and nocturnal birds with high visual sensitivity compared to acuity (Hall and Ross 2006). This intermediate level of acuity and sensitivity allows them to cope with the specific light conditions during twilight hours (Hall and Ross 2006). Additionally, coloration or markings around the eye may also help species adjust to

these difficult light conditions. Dark eye patches are found more frequently on crepuscular species and are thought to serve an anti-glare function. This would allow crepuscular animals with eyes more well adapted to lower light conditions deal with higher intensity light, thereby allowing these species to see well across a wide range of light conditions (Caro 2005).

## General Conclusion

While truly crepuscular species are rarely described, the difficulty in determining the exact boundary between crepuscular and diurnal or nocturnal activity patterns combined with a bias toward diurnal and nocturnal activity pattern categorization suggests that more species than often reported may, in fact, be crepuscular. Additionally, while crepuscular as a descriptor is most often used for a species' peak activity patterns, many species have specific crepuscular behaviors, or simply continue past their normal active times into the twilight.

## Cross-References

- Biological Rhythms
- Circadian Rhythms
- Day/night Cycle
- Diurnality
- Feeding
- Foraging
- Life History
- Light/dark Cycle
- Megachiroptera Sensory Systems
- Owls
- Predation Risk
- Predator Detection
- Rodentia Life History
- Rodentia Sensory Systems
- Vision

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## Crespi Effects

- Contrast Effects

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## Crime

- Martin Daly and Margo Wilson

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## CRISPR

- Targeted Mutation



## Critical Period for Song Learning

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### Synonyms

Sensitive period for song learning; Sensory acquisition phase

### Definition

A species-specific developmental time window in which juvenile songbirds are especially sensitive to auditory input and are able to readily memorize the song patterns of conspecific adults.

### Introduction

Songs are an essential trait of songbirds and serve multiple communicative functions. They are used, more commonly, by males to attract and stimulate the reproductive behavior of females, to advertise territory ownership, and to mediate competition between rival males (Collins 2004). Although the process of song learning in songbirds has attracted attention and received contributions from several fields, including ethology, behavioral ecology, genetics, and neurobiology, it still stands as a major evolutionary puzzle. Song learning has drawn so much scientific interest, in part, due to its similarity to the process of language acquisition. Songbirds share with humans the very distinctive ability of vocal learning. This ability evolved in only three groups of birds (songbirds, hummingbirds, and parrots) and in few mammals (Jarvis 2004). Song learning in songbirds in many ways resembles the steps a human infant follows during the acquisition of a native language (Doupe and Kuhl 1999). As in humans, vocal learning in songbirds initiates early in life. In most species, a critical period for song learning

starts just after young birds leave their nests. However, the time span in which the learning process takes place and the detailed ways in which song patterns are learned vary widely across songbird species.

### The Study of Bird Song Learning

The scientific study of bird song learning initiated with the seminal studies of the British ethologist W. H. Thorpe. He was responsible for introducing the use of sound spectrograms to conduct research in bird song. This technique consists of the production of visual representations of sounds as plots of frequency against time, allowing the inspection and analysis of the structure of songs in fine-grain details (Thorpe 1954). For the first time, it was possible to visualize the basic components of songs. “Notes” were identified as continuous traces in sound spectrograms. “Syllables” were defined as regular groupings of notes forming units. Sequences of syllables form “phrases” and different combinations of phrases form different “song types.”

Thorpe initiated a series of studies on song learning during the 1950s using chaffinches, *Fringilla coelebs*, as his species model. His approach to the study of song learning consisted of taking wild birds from their nests at a few days of age and subsequently rearing them by hand in sound-proof rooms. He would then perform different kinds of experiments by keeping juvenile birds acoustically isolated and by carefully exposing them to tape-recorded adult songs. For example, Thorpe (1958) demonstrated that juvenile chaffinches reared in acoustic isolation (unable to listen to adult songs) develop abnormal songs. These songs had the species-specific frequency spectrum and duration but lacked many details in the structuring of notes and syllables found in normal chaffinch songs. On the contrary, hand-reared birds exposed to tape-recorded adult songs within a specific time window early in life would develop normal songs similar to those produced by wild chaffinches. These first set of experiments revealed that songbirds learn their songs early in life. In addition, they need to be exposed to adult

songs within a critical or sensitive period, a time window in which juvenile songbirds need to be exposed to adult songs in order to successfully develop normal species-specific songs.

## The Phases of Song Learning

Another important contribution made by Thorpe (1959) was the suggestion that juvenile songbirds show a bias for learning their own species-specific songs over songs from other species. This prompted him to propose the idea that songbirds are born with an endogenous “blueprint,” an innate mechanism that guides juvenile birds throughout song ontogeny by allowing them to select and focus their attention on conspecific songs; thus, filtering out songs from heterospecific males available in their environment.

### The Auditory Template Theory

Thorpe’s seminal studies provided the framework for the later theoretical development of the auditory template theory (Konishi 1964; Marler 1976), the leading and most influential model on the process of bird song learning. This model proposes that song learning goes through a two-stage sensorimotor development process. First, a sensory acquisition phase takes place. This is a period of sensitivity to auditory input in which song patterns of adult conspecifics are readily memorized. This stage is then followed by the sensorimotor phase, during which the motor development of vocal production occurs, guided by the memory of adult songs stored in the sensory acquisition phase. Although initially based on studies conducted on chaffinches and white-crowned sparrows (*Zonotrichia leucophrys*), subsequent studies have shown that the general patterns of these phases are widely shared among songbirds.

### Sensory Acquisition Phase (or Critical Period of Song Learning)

In songbirds, song learning initiates with a sensory acquisition phase. This phase is often defined

as the critical or sensitive period for song learning. During the sensory acquisition phase, juvenile songbirds are able to readily memorize the song patterns of adult conspecifics. Later on, they use the stored memory of adult songs as a model that guides the vocal motor phases of song development. The detailed aspects of the critical period show great variation across species. Songbird species can differ in factors such as the timing and length of the critical period, the level of selectivity of auditory input and the relevance of social interaction. These factors will be detailed below.

### Sensorimotor Phase

After memorizing the song patterns of adult conspecifics, juvenile songbirds go through a process of vocal motor development, called sensorimotor phase. This phase consists in the progressive development of a vocal motor program (Marler 1991) in which the singing output is guided by the stored memory of adult songs heard during the sensory acquisition phase.

### Subsongs

Songbirds produce *subsongs* at the earliest stage of vocal motor development. Subsongs have been compared to human baby babbling, because they hardly resemble fully-developed adult songs. They are quiet and show high variability of notes and syllables. It is hypothesized that singing at this stage functions as a way to develop fine sensorimotor control and to train the vocal apparatus (Hultsch and Todt 2004).

### Plastic Songs

Following the production of subsongs, juvenile songbirds go through a stage in which they start to produce louder songs that are structurally closer to those of adult males, these are called *plastic songs*. The songs produced during this stage already contain many elements found in adult songs, but these are still not stable stereotyped songs. In fact, plastic songs in some species are characterized by an overproduction of song elements, resulting from improvisation and/or error in the imitation of the adult songs memorized at

the sensory acquisition phase. However, not all of these novel elements are preserved in the fully developed adult songs.

### Crystallized Songs

The last stage of vocal sensorimotor development occurs when individuals are approaching sexual maturity. At this stage, songbirds start to produce *crystallized songs* and the structure of songs is already stable and acquires stereotyped characteristics similar to those of the adult songs memorized during the sensory acquisition phase. In some species, there is also a selection of which elements will be incorporated into the songs used later in adulthood.

### The Role of Auditory Feedback

The absence of auditory feedback during the sensorimotor phase of song learning can drastically constrain the development of normal songs. Juvenile songbirds that are unable to listen to their own singing develop songs lacking the structure of their normal species-typical songs. These abnormal songs show severe distortion in its basic component elements. Individuals deafened at earlier during the sensorimotor phase produce abnormal songs with higher levels of distortion in the structure of notes and syllables (Konishi and Nottebohm 1969). The crucial relevance of auditory feedback for the development of normal song has been supported by a set of studies conducted on experimentally deafened songbirds. For example, juvenile white-crowned sparrows deafened before the sensorimotor phase develop abnormal songs (Konishi 1965). Similar results have been reported for swamp sparrows, *Melospiza georgiana*, and song sparrows. Individuals of both species deafened between 17 and 23 days of age (prior to the onset of the sensorimotor phase) develop abnormal songs. However, some species-typical characteristics are still noticeable in these abnormal songs. For example, the high degree of element segmentation, present in the structure of normal song sparrows' songs, is still preserved in abnormal songs (Marler and Sherman 1983).

### The Timing and Length of the Critical Period

In most species, the sensory acquisition phase or critical period for song learning starts just after young birds fledge (Catchpole and Slater 2008). However, the timing and length in which this phase takes place vary dramatically between different species. For example, in white-crowned sparrows, the length of the critical period for song learning is restricted to the first months of life. Marler (1970) performing a, now classic, acoustic isolation experiment found that hand-reared juveniles develop normal songs if they are exposed to tape-recorded adult songs between 10 and 50 days of age whereas juveniles exposed to adult songs outside this 40-day period developed abnormal songs (Marler 1970). In other species, however, the critical period can last for the entire first year of life, as in chaffinches (Lachlan and Slater 2003) or it can even last for the entire lifetime in species that never cease to incorporate new elements to their songs, such as canaries, *Serinus canarius* (Nottebohm et al. 1986).

### Close-Ended and Open-Ended Learners

Traditionally, songbirds have been classified as *close-ended learners* (or age-limited) and *open-ended learners*. Close-ended learners include species in which individuals learn songs only up to a certain age, usually within the first year of life. Within this limited period, juveniles learn all song types that they will then sing for the rest of their life. The groups of open-ended learners comprise species in which individuals also start the song acquisition process early in life, but keep adding new song elements to their repertoires throughout life. The accumulated evidence about the detailed mechanism of song learning in different species has challenged this traditional classification. A large number of factors, including the level of selectivity of auditory input and the relevance of social interaction are now known to affect the timing and length of the critical period for song learning. Additionally, studies on song learning are rarely conducted beyond the first year of songbirds' lives. So, long-term research encompassing

multiple years might reveal that some species that we now think are close-ended learners are in fact open-ended learners, i.e., they continue to add new elements to songs in adulthood (Beecher and Brenowitz 2005).

### What Is Learned During the Critical Period?

The auditory template theory proposes that the brains of juvenile songbirds are not *blank slates*. According to this model, songbirds are born with a rudimentary representation of their species-typical songs, an auditory template. This template plays a fundamental role throughout the process of song acquisition. It is supposed to allow juvenile songbirds to recognize and learn songs, preferentially, from males of their own species during the sensory acquisition phase (Marler 1970; Thorpe 1958). Some studies conducted during the sensory acquisition phase, before juveniles are able to produce songs, have supported the idea that songbirds have an innate ability to discriminate their species-specific songs. For example, hand-reared swamp sparrows around 20 days of age have lower heart rates when exposed to conspecific songs than when they listen to songs of song sparrows, a closely related species (Dooling and Searcy 1980). Also, juvenile white-crowned sparrows, between 12 and 23 days of age, produce a higher number of begging calls when exposed to songs of conspecific males than when exposed to songs of heterospecific males (Nelson and Marler 1993). In addition, in many species, if juveniles are simultaneously exposed to conspecific and heterospecific songs, they will preferentially learn conspecific songs (Marler 1970).

The auditory template seems to create a preferential bias for input from conspecific songs. However, the detailed way in which song patterns are learned, might work differently even in closely related species. Some species have a rigid template and learn only song elements that closely fit to their template, whereas other species are much more flexible and can incorporate even song elements of other species. For example, juvenile

song sparrows, tape-tutored with both conspecific songs and song sparrow songs, are able to learn their own species songs and also swamp sparrow songs, whereas swamp sparrows exposed to the same song stimuli can learn only conspecific songs (Marler and Peters 1989). Cross-fostering studies offer another way to analyze the selectivity of auditory input and preferential bias. In this research approach, young songbirds are raised by adults of another species as a way to examine the degree in which different auditory input might influence song preference and development. Young zebra finches, *Taeniopygia guttata*, fostered by Bengalese finches, *Lonchura striata domestica*, later when adults, exhibit reduced discrimination of conspecific songs. They also demonstrate preference for Bengalese finch songs over conspecific songs (Campbell and Hauber 2009).

### Memory-Based Learning

Acoustic isolation experiments have shown in some species that exposition to adult songs exclusively during the sensory acquisition phase is sufficient to generate memories that will then guide the remaining process of vocal development. Juveniles from some species are able to memorize adult songs very accurately even when they have been exposed to it few times. Song sparrows, *Melospiza melodia*, for example, are able to memorize songs heard only 30 times during the sensory acquisition phase (Peters et al. 1992). In the majority of songbird species studied so far, there is a time gap between the end of the sensory acquisition phase and the onset of the sensorimotor phase. Hence, at the start of vocal motor development, juvenile songbirds need to access the stored memory of songs heard several weeks or even months before (Marler 1991). Zebra finches, though, are a noticeable exception. In this species, there is a time overlap between the sensory phase and the sensorimotor phase. Juvenile zebra finches start producing subsongs while still memorizing adult songs. Their critical period for song learning ranges from 25 to 65 days of age. However, after reaching 35 days of age, juveniles already start to vocalize subsongs (Zann 1997).

## Social Influences on Song Acquisition

### Tape Tutoring Versus Live Tutoring

Social interaction with conspecifics has been identified as a factor that can greatly influence the process of song learning. Some experiments using live tutors, instead of tape-recorded songs, have shown that social factors have a major relevancy on the process of song acquisition and can affect even the time span of the sensory phase of song learning. For example, juvenile white-crowned sparrows exposed to songs of live conspecific tutors can have their sensory phase extended beyond the typical 10–50 days found with tape-recorded song tutoring. Social interaction with live tutors can extend the sensory phase up to 200 days of age (Baptista and Petrinovich 1986). Two studies investigating song learning in song-sparrows show contradictory results from tape tutoring versus live tutoring. Tape-tutored song-sparrows learn most of their songs before 90 days of age (Marler and Peters 1989). On the other hand, song sparrows exposed at different ages (between 30 and 90 days and between 140 and 330 days) to the songs of two groups of live tutors learn most of their songs from late tutors than from early tutors (Nordby et al. 2001). In other species, tape-tutoring can be completely ineffective. In tree creeper species, *Certhia* spp., for example, social interaction is so relevant for song acquisition that juveniles are able to learn songs only from live tutors (Thielcke 1984).

### Selective Learning

Songbirds are exposed to and learn more song elements than they eventually use during adulthood. The detailed mechanism by which juveniles select their song repertoire is still unknown. Nonetheless, some studies indicate that social interactions can determine which song elements learned at the sensory acquisition phase are retained at song crystallization to be later used in adulthood. For example, in brown-headed cowbirds, *Molothrus ater*, the song acquisition process is also influenced by the social interaction with conspecific females. Juvenile birds in this species favor the crystallization of songs that better elicit mating responses, wing strokes, in

females (West and King 1988). The importance of social interaction as a determinant of song learning has pushed Nelson and Marler (1994) to propose a mechanism named “selective attrition” (or action-based learning) as an addendum to the auditory template theory. Contrary to the auditory template theory, this mechanism is not based on instruction and passive exposition to auditory content. In fact, it suggests that the selection of song elements during the song crystallization phase is an active process in which songbirds are able to retain song patterns that are better suited to their social environment. For example, Nelson and Marler (1994) showed that juvenile white-crowned sparrows, during the song crystallization phase, retain song-types that better match the regional variations on song-types (song dialects) sung by neighboring males.

## Conclusion

Around 60 years ago, researchers began to develop a scientific understanding of the developmental process through which juvenile songbirds learn their species-typical songs. Early studies indicated the existence of a critical period for song learning. Juvenile songbirds need to be exposed to conspecific adult songs within a species-specific time window in order to develop normal species-typical songs. Within this critical period, the memorization of song input is facilitated and the stored memories of adult song patterns guide the remaining stages in the process of song acquisition. Subsequent research has provided general support for the majority of these pioneering ideas and largely expanded the number of studied species. At the same time, new studies have shown that many species do not have a well-defined critical period for song learning. Additionally, the timing and length of the critical period are now known to be dramatically affected by social factors.

## Cross-References

- Auditory Signals
- Communication



- Countersinging
- Critical Periods
- Learning
- Ontogeny
- Passerine Cognition
- Passerine Sensory Systems
- Passerine Vocal Communication
- Sensitive Periods
- Signaller
- Social Learning
- Songbird Learning
- Subsong

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## Critical Periods

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## Synonyms

[Sensitive periods](#)

## Definition

The term critical period can be defined as a temporal window in an organism's life when an experience or an external stimuli has a heightened, irreversible impact on the development of its physiology, morphology, cognition, and behavior.

## Introduction

An organism's ability to interact and adapt to its changing environment is one of the decisive features for its survival. Such feat could only be accounted for a system which is not only able to efficiently process information tailored to its surroundings but would also be able to evolve over its lifespan. Thus, it is the emergence of this system in the early developmental phase of life which allows the organism to exist and even thrive in unfamiliar environments. Indeed, a particular arrangement of brain circuitry is the physical manifestation of such a system which generates an adaptive behavior. In that context, it is important to discuss "sensitive period," a brief window of time when the influence of an external stimuli on

this circuitry is strong enough to significantly modify its organization. Often, these alterations persist; however, they are prone to further changes throughout the organism's lifetime. This is known as "brain plasticity" and allows the possibility of lifelong learning. While the exact role of sensitive period is still unclear, it might play a foundational role in laying the core circuitry when the animal is in its developmental stage and any changes of learning which occurs afterwards happen within its structural constraint (Knudsen 2004). Seemingly, these modifications lead to an arrangement which is tailored to that specific environment and consequentially confers an adaptive advantage. Hence, a period of enhanced learning plays a pivotal role in guiding the organism through a new environment while it's still young and vulnerable, such as in the case of filial imprinting in ducklings (discussed further in section "[Behavioral Imprinting](#)") (Bolhuis and Honey 1998).

"Critical period" can be defined as an extreme form of sensitive period where the impact of the environment on the brain circuitry is permanent and irreversible. What's more, a lack of proper input during this window often leads to loss of function (Knudsen 2004). For example, when cats were exposed to visual input with their one eye shut during the critical period, they developed a condition known as amblyopia in which there was a loss of visual acuity in the closed eye (discussed in section "[Biological Mechanism of Critical Period: Plasticity in Visual Development](#)"). It was also noticed that depriving the input before or after the critical period did not affect normal vision development (Hubel and Wiesel 1962). Hence, critical period can be characterized by a specific opening and closing period along with a unique input signal. It is worth noting however that the input signal itself drives the onset and closure of this window rather than a timed maturational event. Hence, critical period can be delayed if there is a lack of proper input, or may not even begin in the first place (Knudsen 2004).

A time-restricted window of development acts as a double-edged sword. There is always a possibility that anomalous experiences during this phase can permanently leave its impression on the brain circuitry. Critical period, however, ensures that the acquired experience which is

imprinted on the brain is protected from being overwritten with new information. Thus, there is a trade-off between adaptability during this period and stability later on (Knudsen 2004).

## Behavioral Imprinting

Imprinting can be described as a learning process that is rapid and occurs within a particular time range, usually resulting in the formation of behavioral association to a certain stimuli. This term was first elaborated by a well-known zoologist and the father of modern ethology Konrad Lorenz based on his study on goose and duck younglings. Lorenz observed that these juveniles have a tendency to follow their mothers soon after hatching and this learning process only happens during a fixed window of time, which he termed as *critical period*. This phenomenon was consequentially known as *filial imprinting* (Bolhuis and Honey 1998).

In a series of experiments performed by Lorenz, he found that he could imprint this behavior to a substituted object if presented during the critical period. By exposing himself to newly hatched ducklings (visual stimuli) and mimicking the quacking sound of mother duck (auditory stimuli), he was able establish bonding which resulted in a similar behavior. The ducklings would even react to inanimate objects such as a red ball and begin to follow it. Filial imprinting is displayed mostly in species whose progeny are born in a relatively developed stage, so much so that they could easily wander away from their parents. This learning process ensures that the newly born stick close to their mothers as they are still dependent on them for food and shelter till the time they mature. Such species are called precocial species. This is in contrast to altricial species whose young ones are not so developed and consequentially no filial imprinting is observed as such (Mackintosh 1974).

Imprinting has been investigated in other areas as well, such as the preference for sexual partner (sexual imprinting) and the formation of social bonds (social imprinting). Sexual imprinting occurs when a species' preferred mate choice is guided by its early exposure to the characteristics

of its parents. This phenomenon has been well documented in studies concerning zebra finches, where, the young male, if reared under the female Bengalese finches (these finches have a tendency to easily accommodate members of other species), become inclined to mate as they mature with the members of the foster specie over their conspecific counterparts. This learning process seems to have a critical period and is irreversible. Sexual imprinting in birds is observed in almost half of the taxonomic order and implies a strong role in the unfolding of the evolutionary dynamics involved in maintenance of the speciation process. Speciation occurs when a population isolates and evolves to become a different species; thus, sexual selection and species recognition ensure low chance of interbreeding if the isolated populations ever comes back in contact (Immelmann 1972).

The formation of social bond within a time-sensitive period is phenomenon that is well accepted as seen by multiple incidences in nature. A classic example would be of slave-maker ants which display brood parasitism – reliance on other specie for the rearing of its younglings. These ants are known to steal the eggs and larvae during raids on ant colonies of different species. When the eggs hatch, these ants get socially imprinted and integrate in the new colony and help raise the larvae of its captors (Blatrix and Sermage 2005).

## Critical Period in Vocalization

### Songbird Learning

Songbirds belong to the suborder of *Passeri*. These perching birds have evolved an elaborate system to produce complex patterns of sounds (referred to as “song”) which could be distinguished from simple calls such as that of a pigeon. Indeed, this complexity is necessary for executing high-order behaviors which has been observed in mate call and territoriality. The mechanism underlying the development of communication in songbirds shows a strong overlap with humans and, hence, has been extensively studied by the researchers. The entire process could be distinguished into three phase, viz., sensory learning, sensorimotor integration, and song crystallization.

During the sensory phase, the hatchling is tutored by an adult male which exposes them to its species-specific song. This learning has a critical period (15–60 days in zebra finches) in which the song pattern is encoded in the brain. The sensorimotor phase is also characterized by a critical period which usually overlaps with sensory phase (30–90 days in zebra finches). The tutored youngling produces a series of vocal elements using the memorized template till it is able to match the adult song. Eventually, a surge in the testosterone levels leads to a song being permanently crystallized. It is important to note that songbirds such as canary and greenfinches could also display a seasonal cycle of learning, repeating the processes annually. However, in many species such as the zebra finches, chaffinch, and white-crowned sparrow, song learning happens only once in a lifetime (Merrill et al. 2017).

The existence of the different phases in song learning gives interesting insights in the organization of multiple critical periods. Hatchlings which were reared in solitary environment or were tutored beyond critical period did not make any stereotypical bird song. Rather, a distorted version of the song was produced, though still retaining some vocal qualities specific to the specie. Delay in early song exposure could even lead to an extension in the critical period for sensory learning, sometimes even stretching into adulthood. Moreover, the hatchling only respond to songs of their own species and even display a preference. This shows that genetic specification plays an important role in biasing the neuronal circuits towards a certain stimulus (Merrill et al. 2017).

### **Biological Mechanism of Critical Period: Plasticity in Visual Development**

A time-dependent behavioral outcome is one of the distinguishing features of the critical period. These changes often reflect a shift in the brain plasticity, usually at the level of synapses. Such chain of events unfolds to morph a system which is highly receptive towards a particular stimulus till the desired connectivity of neurons is established. Fundamentally, this signifies that the circuitry in the

brain “competes” for the desired input, and synapses which respond actively to the signal are selected and enhanced while the rest are pruned out. This process is known as activity dependent competition (Hensch 2004). Thus, critical period must have a transient “opening” and a “closing” window followed by the consolidation of such circuitry. As mentioned previously, such a mechanism would not only aid multiple systems to evolve independently but will also prove crucial when a matured circuit is needed to serve as a scaffold for the emergence of other systems (Schaefer et al. 2017).

To understand the physical basis of such event, one can look into the development of vision in animals: arguably one of the most explored sensory systems yet. The famous monocular deprivation experiment by Hubel and Wiesel in the early 1970s has described the effect of activity dependent competition during critical period. The visual cortex in adults contain a layered arrangement called ocular dominance columns which are biased towards input from one eye over the other. Indeed, an interrupted visual input from the eye during the early developmental phase of the animal is crucial for its formation. Animals who were reared with one eye shut responded only to visual input from the uncovered eye. Additionally, not only the ocular dominance region for the covered eye was absent but were taken over by the regions which responded to the uncovered eye (Schaefer et al. 2017).

Interestingly, the experience itself regulates the “opening window” of the critical period. Hence, a delay in the initial input can extend the duration of this window, though it varies from one system to another. In visual development, the maturation of GABAergic circuits, which are the principle inhibitory neuronal networks in the brain, dictates the opening and closure of the critical period. The exact mechanism is yet to be discovered; however, it is believed that this inhibition helps in the consolidation of the circuit via pruning of the nonessential synapses. Additionally, the heightened plasticity during initiation is believed to be a result of induced long-term depression (LTD) by the aforementioned inhibitory circuit. Another key component for the closure of critical period is the involvement of perineuronal net (PNN).

These extracellular structures stabilize the inhibitory synapses by enwrapping the parvalbumin-expressing GABAergic interneurons (PV cells). An inhibition of the visual input can interfere with maturation of PV cells, thereby hindering its interaction with PNN leading to a delayed closure of CP (Schaefer et al. 2017).

## Discussion

What makes critical period unique is also what makes it immensely difficult to characterize. A transient period of heightened plasticity does not always indicate that experiences cannot have a lasting effect later in life. After all, lifelong learning is what enables an organism to alter its behavior in response to a changing environment. Critical period, however, could be described as an extreme form of sensitivity where environmental input instructs the very organization of brain circuitry, and this initial foundation is what opens new avenues for future learning. This raises a possibility that even arbitrary disturbances, no matter how minuscule or sparse can steer the direction of cortical development and affect resulting behavior (Nelson and Gabard-Durnam 2020). It is difficult to establish a causal relationship between critical period and many developmental ailments given our limited understanding of it. However, compelling evidences keeps piling up, for instance, researchers are now considering that disorders such as Autism might actually be due to altered plasticity during maturation (LeBlanc and Fagiolini 2011). Additionally, few researchers have even managed to perform interventions in animals by artificially reopening the critical period via pharmacological manipulation of the inhibitory circuits. Thus, reimagining these anomalies as critical period disorders may lead to novel therapeutic strategies reorienting the altered trajectory of development (Hensch and Bilimoria 2012).

- Maternal Behavior
- Neurotransmitters
- Paternal Behavior
- Social Behavior

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## Cross-References

- Behavior Systems
- Cognition

## Crocodile

- Crocodilia Morphology

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## Crocodile Alligator Vision Hearing

### ► Crocodilian Sensory Systems

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## Crocodile Locomotion

### ► Crocodilia Locomotion

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## Crocodilia Communication

### ► Crocodilia Communication

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## Crocodilia Diet

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## Synonyms

Behavior; Foraging

## Introduction

Crocodilians (crocodiles, caimans, alligators, gavials, and their kin) superficially resemble large lizards, but they are in fact more closely related to birds, with which they share many behavioral, and presumably cognitive, characteristics. Both belong to the Archosaur clade, which included dinosaurs and pterosaurs, as well as the ancestors of the present day crocodilians. The pterosaurs and most of the dinosaurs succumbed to a catastrophe, usually attributed to a meteorite impact at the Permian-Triassic boundary. However, one group of dinosaurs, the birds, survived and still dominates the landscape in most parts of the world. The ancestors

of the crocodilians were diverse, often terrestrial predators, but all present-day members of this lineage are semiaquatic predators living at the interface between land and water.

The legacy of their terrestrial ancestors is revealed when crocodilians walk with their bodies held high off the ground with the legs propped almost vertically in contrast to the splayed-legged gait of lizards. Some crocodilians will even gallop if they need to return quickly to water, but the legs are generally used only to steer the body in shallow water. Most of a crocodilian's propulsive power comes from sweeps of its powerful tail through the water, and this restricts its foraging strategies and the vulnerability of different types of prey.

## Food and Feeding Habits

The metabolism of crocodilians is very slow, which has the advantage that they use energy very efficiently and do not have to feed frequently (Coulson and Hernandez 1983). Small- and medium-sized crocodilians can go for months without feeding, and the largest individuals can possibly survive fasts lasting several years. Many female crocodilians guard their nests during the two- to three-month incubation period, and if the nest is far from water she may not be able to feed. Female common caimans guarding nests far from water lose body condition during the incubation period in central Amazonia, but the time she can spend beside the nest may be more limited by water than energy.

The slow metabolism of crocodilians has allowed researchers to study digestive processes that would be impossible to study in typical laboratory animals, such as rats, so our knowledge of the basic physiology of digestion owes much to the study of crocodilians. The slow metabolism is not a primitive feature, and presumably the terrestrial ancestors of present-day crocodilians had much higher metabolic rates and more active life styles. Rather, it is an adaptation that allows crocodilians to obtain much higher densities and biomass per unit area than similar-sized mammals (Magnusson and Lima 1991).

Their low metabolic rates allow crocodilians to spend long periods under water, either to escape from predators or to remain concealed from their terrestrial prey. Crocodilians sometimes forage underwater, and some species are known to take terrestrial prey well away from water, but most of their prey, including aquatic organisms, such as fish, is taken in the shallows or close to the bank, so that the head is out of the water at the moment the jaws are swept toward the prey. The basic tactic for prey capture is therefore a forward lunge propelled by the tail combined with a sideways sweep of the long jaws. There are only minor variations on this theme, so most of the cognitive input in feeding relates to where and when an attack should take place for a given prey type.

Because crocodilian metabolism is tuned to low energy expenditure, they are not well adapted to prolonged activity. Strenuous exercise leads to a buildup of lactic acid in their tissues, to which they are more tolerant than most vertebrates, but they still have to rest to repay the oxygen debt. Prolonged struggling during capture can even lead to the death of large individuals, which have more difficulty flushing their muscles with oxygenated blood than do small animals.

People who are considered intelligent are often described as "quick," which implies that intelligence is associated with the ability to make quick decisions. However, a generally slow lifestyle and only small windows of time in which strenuous exercise is possible require complex planning and the ability to modify tactics during a feeding rally. Presumably, crocodilians need to keep complex maps in their heads in order to be in the right place at the right time to capture prey.

Some crocodilians, especially in the genus *Crocodylus*, undertake long annual migrations between feeding and breeding areas, some species make long marine voyages, and individuals have found their way back to their home ranges after being transported hundreds of kilometers along the coast to another river system. Young alligators have been shown to be able to use magnetic orientation to find their way home. Crocodilians therefore must have complex mental maps of the world, but it is unknown to what extent olfaction,

visual landscape features, magnetic compass orientation, and celestial navigation play in crocodilian movement planning.

Crocodilians are often described as having a generalist diet, which could give the wrong impression about how they feed. It is true that crocodilians are able to take advantage of most types of animal prey that are of the right size, so analysis of stomach contents of a large number of individuals will reveal a wide range of prey types. However, this does not mean that individuals wander around opportunistically taking any animals that come too close. At any one time, an individual is likely to be specializing on a particular type of prey and modifying its behavior to maximize the probability of contact with food that gives the highest return in terms of energy or nutrients.

Several species of crocodiles have been seen using their bodies and tails to corral fish in shallow water. The crocodile lies with its body parallel to the bank and uses its tail to block movement of fish along the bank or to sweep them toward the snout. When the fish tries to escape past the crocodile's head, it is grabbed by a sideways sweep of the jaws. The crocodile does not even need to see the fish, because it has pressure-sensitive pits along its jaws which are thought to be able to detect water movements caused by swimming prey.

Caimans have been observed waiting under frogs that call from trees, but lay eggs in the stream. Presumably, the caiman has learned that calling frogs eventually descend to the edge of the stream, often leading a female into the jaws of the caiman as well. During floods, the same caimans position themselves perpendicular to the water flow with the lower jaw just below water level and the upper jaw held just above it so that they can catch hapless animals being washed down. It is likely that both of these are learned behaviors.

One of the most spectacular sights on the East African savannas is the seasonal migration of wildebeest and other large ungulates. The herds cross the rivers at the same place each year and the crocodiles accumulate at these sites days or weeks before they arrive, indicating that crocodiles have very good long-term memories and can think ahead, as well as understanding spatial relationships.



Some caimans and crocodiles have been seen aggregated around canals where fish are funneled during migrations. Whether they find these aggregations alone, are only attracted by the concentration of other crocodilians, or are actively lead to feeding locations by other individuals is unknown. However, the latter is not unlikely. Caimans in the Brazilian Pantanal have been observed undertaking coordinated movements between pools in the dry season; one individual, usually the largest, leading the others, which follow in single file, sometimes for kilometers (Campos et al. 2003).

Because crocodilians often occur in large concentrations, social intelligence can be as important as hunting ability and not just because it is wise to follow the most experienced leader. Crocodilians have evolved into some of the most spectacular vertebrate killing machines that can bring down prey as large as themselves or, more importantly, kill another crocodilian with a single bite. Crocodilians do fight and kill each other, especially in territorial disputes. However, considering the high densities at which many species occur, fights are rare, and usually settled by one of the combatants showing submissive behavior, such as lifting its head vertically and revealing its throat.

Both crocodiles and caimans have been observed in narrow channels during fish migrations. Rather than attack haphazardly, the crocodilians form a line or a semicircle, all equally spaced, making a trap for the migrating fish. The predators do not break ranks even if the concentration of fish moves temporarily from one animal to another.

African crocodiles often have unexpected windfalls, such as a dead hippopotamus or elephant close to the water. Dozens or, in some cases, more than 100 crocodiles may gather at the carcass, but they can only feed from a small area of the soft underbelly, so the most efficient system is for them to take turns and that is exactly what they do, each individual waiting for their turn like gentlemen around a dinner table. Once an animal has pulled off a piece of meat, it moves out of the area to give the others access. There is obviously tension and all the crocodiles would probably like to be first to feed, but they apparently know their

position in a hierarchy of dozens or more individuals, even though they only encounter each other sporadically in the river.

Most aquatic habitats show strong seasonal changes in water depth, inundation of marginal vegetation, and the types of prey animal found on the banks. It is therefore likely that individuals of all species of crocodilians adjust their foraging behavior in relation to seasonal structural changes in the habitat and concentrations of different prey, and that they learn to adapt their behavior in expectation of changes before they occur, as has been shown for African crocodiles. However, because most crocodilians forage mainly at night and are secretive, especially if they have been hunted, there are no direct observations to back up these speculations.

All crocodilians must change their foraging tactics throughout their lifetime simply because their size, and hence the type of prey they take, changes drastically over time. Juveniles of all species are small, about as big as a medium-sized lizard, and they increase more than a thousand times in weight before becoming sexually mature; individuals of some species being among the largest terrestrial predators on the planet.

Crocodilians have conical teeth that vary in size, but not much in shape. They are good for holding prey but are not adapted for cutting or grinding. Therefore, crocodilians usually swallow their prey whole or tear off large chunks that are thrown backward toward the throat and are swallowed principally due to gravity. To dismember its prey, a crocodilian has to take a firm hold and then spin its body to separate the piece held in its mouth. This process depends on inertia and is more effective for large prey and large crocodilians. Dismemberment of prey is uncommon in small crocodilians.

The conical teeth are effective for holding prey but suffer severe stress during biting and when the crocodilian spins, and they are frequently broken or pulled out. Fortunately for the predator, crocodilian teeth that are lost during feeding are soon replaced by another that grows up from the same tooth socket.

Crocodilians have the strongest stomach acids of any group of vertebrates, so they can digest

most animal matter, including bones. Nevertheless, assimilation efficiency is probably greater for food types similar to that of the bodies of crocodilians, such as vertebrate muscle, than for other material, such as invertebrate chitin. Most invertebrates are also small, so that it may not be worthwhile for larger crocodilians to hunt them. The ontogenetic shift in diet is probably the most studied aspect of food habits in crocodilians and the pattern is similar in almost all species.

African crocodiles (*Crocodylus niloticus*) up to about half a meter long eat mainly insects and spiders. Individuals between 2 and 4 m eat mainly fish and snails, and animals over 4 m eat mainly mammals, but also some reptiles and fish (Cott 1961). A similar pattern is seen in all species of crocodilians, but some change the types of prey at smaller sizes, and some never make the transition to eating mainly mammals.

There are probably several reasons that small crocodilians eat mainly insects and spiders. The first is that these are probably the most common prey within the size range that they can swallow. However, capturing terrestrial vertebrates probably requires stealth and understanding of the surrounding habitat. Recently hatched crocodilians usually form crèches that are accompanied by their mother for the first few weeks or up to 2 years in some cases. Soon after, the juveniles start to disperse, probably egged on in their movements by territorial adults for the decade or more they take to get to breeding size. During that time, they may not remain in any one area long enough to develop a useful hunting map.

Large juveniles and sub adults usually eat mainly crustaceans, mollusks, and fish, the proportions depending on availability within the habitats the species occupies. Although even large crocodilians will occasionally take insects or other invertebrates, the energetic contribution of these groups tends to be negligible, and it is unlikely that large crocodilians actively seek these prey types unless they occur in unusually large concentrations.

The largest crocodilians often eat a large proportion of mammals, and these probably represent the most digestible food packets available. However, they are also often hard to catch and come

close to water infrequently. Therefore, the strategies that crocodilians use to catch them are likely to be different from those used to catch widely distributed prey, such as insects, or prey that occurs in predictable places, such as fish.

Differences among size classes in the type of prey eaten depend to a certain extent on the seasonal differences in habitats. In places with large inundated floodplains, such as flooded savannas and forests, and hence large seasonal differences in access to different habitats, diets tend to differ less between size classes, because all must move with the advancing flood waters. In habitats with less seasonal variation, such as rivers and lakes, different size classes tend to segregate in different habitats and differences are more pronounced.

The species with the greatest divergence from the usual size-related changes in diet is Schneider's dwarf caiman, *Paleosuchus trigonatus*. It lives in dense Amazonian rainforest with little primary productivity in the understory. Therefore, insects and mollusks tend to be less abundant and individuals less than a meter long eat many frogs, snakes, and other small vertebrates. Fish, which tend to be scarce in the small streams are never found in abundance in its diet and the diminutive adults, which rarely reach two meters long, eat many mammals, including pacas, porcupines, and monkeys. As porcupines and monkeys rarely descend to the edge of the stream, it is hard to imagine what strategy this species uses to capture them. They must be very successful, as they maintain higher biomass than all the mammalian carnivores together in the same type of habitat.

It is often claimed that snout-shape in crocodilians reflects their diet, fish-eating species having long, thin snouts, and species that take large prey, such as ungulates, having heavier, wider snouts. However, this is only partially true. Species that live in open-water habitats tend to have thinner snouts, but they are not any longer in relation to body length. It makes sense to have a thin snout, which causes less resistance, if you live in open water, whether you eat fish or not. Fish just happen to be the nutritionally most valuable prey in open-water habitats.

The species of crocodilians that eat the most large ungulates and other large mammals, the

estuarine crocodile, *Crocodylus porosus*, and the Nile crocodile, have snouts of intermediate width, which can be considered a generalized form for crocodilians. This form of snout appears to be adequate to withstand the stresses of capturing large prey in relation to the size of the crocodilian.

The species of crocodilians with the widest snouts, including extinct forms, do not feed on the largest prey, but all live or lived in densely vegetated habitats, such as marshes, so it seems that extreme widening of the snout is an adaptation to smashing through thick vegetation rather than protection against breakage while pulling down large prey.

## Conclusion

In summary, we know quite a bit about the morphological and physiological adaptations of crocodilians associated with feeding and digestion, but because of their nocturnal cryptic habits we know little about the cognitive and behavioral adaptations that have lead them to be the most successful and persistent nonflying Archosaurs.

## Cross-References

- [Crocodylia Cognition](#)
- [Crocodylia Communication](#)
- [Crocodylia Locomotion](#)
- [Crocodylia Morphology](#)

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## Crocodilia Locomotion

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## Synonyms

[Alligator locomotion](#); [Crocodile locomotion](#); [Crocodylia locomotion](#)

## Definition

Movement used by crocodilians (true crocodiles, alligators, caimans, gharials, and false gharials) to traverse terrestrial and aquatic environments.

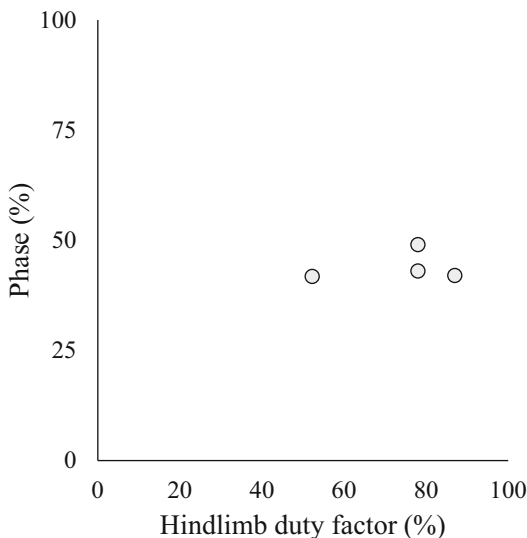
The Crocodilians are quadrupedal archosaurs closely related to living birds. Currently, the crocodilians are divided into five major groups: true crocodiles, alligators, caimans, gharials, and false gharials (Hutchinson et al. 2019). Alligators and caimans are known for their blunt heads, crocodiles for their elongated heads, and gharials and false gharials for their narrow heads (Buffetaut 1979).

Crocodilians live in warm environments inhabiting fresh and/or salt bodies of water. They range from semi-aquatic to almost fully aquatic. Although morphological differences exist between species regarding head shape, locomotor patterns appear to largely similar across the group. The crocodilians are capable of different gait patterns ranging from walking, running, galloping, and swimming. It is important to recognize that extant crocodilians are more adept at swimming compared to their locomotor efforts on land. Much of the locomotor capabilities of these species have evolved in response to improved predatory capabilities and to escape predation themselves.

## Terrestrial Locomotion

Terrestrial gaits of crocodilians include walking, running, and galloping. Walking can be further broken down into sprawling (or belly-dragging) and high-walking, and are almost always symmetrical (when footfalls of the forelimb and hindlimb are evenly spaced in time) lateral-sequence (each hindlimb footfall is followed by an ipsilateral forelimb footfall) diagonal-couplets (contralateral forelimbs and hindlimbs travel together) (Fig. 1). This footfall sequence is inherently stable due to a high proportion of the stride being spent as either diagonal bipods (two contralateral limbs in contact with substratum) and large tripods (three widely splayed limbs in contact with substratum), both of which create a line of support under the midline of the body (Granatosky 2018; Hildebrand 1976, 1989). Compared to mammals and birds, the crocodilians demonstrate low locomotor cycle rhythmicity (Granatosky et al. 2020).

Belly-dragging, characterized by a sprawled posture (limbs held lateral to body), is used for slow speed movement in muddy terrains. Some evidence suggests that crocodilians adopt belly-dragging due to its low energy expenditure



**Crocodilia Locomotion, Fig. 1** “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in crocodilians ( $n =$  four species)

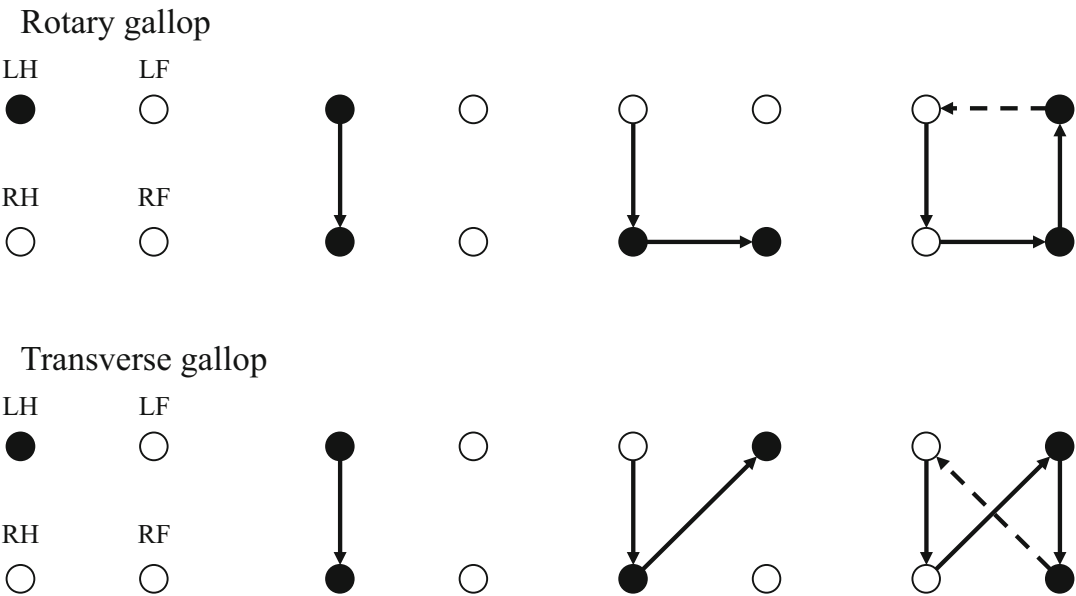
(Pashchenko 2018; Reilly and Elias 1998). High-walking is a mode of transport that uses a semi-erect posture, a posture between erect (limbs directly under body) and sprawling (limbs held lateral to body) (Reilly and Elias 1998). Alligators primarily use this high-walking posture during normal walking gaits, while crocodiles may stand more erect to navigate rough terrain (e.g., leaving water, climbing over trees, brush, and hills). During high-walking hindlimb stance phase, the hip and knee are extended, causing the body to roll over the opposite foot (Gatesy 1991; Reilly and Elias 1998; Willey et al. 2004). The medial rotation in the hip may allow for a purer sagittal plane motion (flexion/extension). As the limb retracts, the ankle plantarflexes (raising the posterior aspect of the foot off the ground). The force of plantar flexion aids the knee and hip in extension, lengthening the limb. Prior to foot-off (initiation of swing phase), the hip and knee begin to flex, allowing the propulsive force to move the limb forward. Swing phase begins with rapid dorsiflexion to lift the limb off the ground. The hip gradually extends until foot down occurs for the next stance phase. In the forelimb, forelimb excursion is mediated by the shoulder, elbow, and wrist joints and by the shoulder girdle (Gatesy 1991; Reilly and Elias 1998; Willey et al. 2004; Baier and Gatesy 2013). Lateral bending of the shoulder girdle creates greater stride length in the forelimb.

Stance phase of belly-dragging and high walking differ in hindlimb joint angles. Femoral angles of both belly-dragging and high walking remain relatively static during the stance phase; however, the femur is more protracted and abducted during sprawling, while the knee and ankle joints have more pronounced flexion (Reilly and Elias 1998; Gatesy 1991). During swing phase femoral adduction of both postures decreases slightly, but maximum adduction is achieved again immediately prior to foot down. Knee extension increases during swing phase in both postures. In belly-dragging, maximum extension is achieved well before foot down as to maintain close contact with the substrate. Knee extension continues until immediately before foot down in high-walking to maximize stride length.

High-walking alligators raise a portion of their tails off the ground but still drag a significant amount of weight (~20% of body mass), thus shifting their center of mass caudally towards the hindlimbs (Willey et al. 2004). The forelimbs provide significantly less propulsion during high-walking compared to the hindlimb, but provide a means of braking and support (Willey et al. 2004; Gatesy 1991; Baier and Gatesy 2013). Variation in limb-loading is quite high between cycles in crocodilians (Granatosky et al. 2020), which may explain increased limb bone safety factors in crocodiles compared to mammals and birds (Blob et al. 2014).

Galloping in crocodilians has been observed in several true crocodile species, such as *Crocodylus johnstoni*, *C. porosus*, and *C. niloticus*. The gallop is most often initiated from a resting position, but sometimes can be developed from the high-walk when there is a need for increasing speed. Likely, galloping behavior evolved in crocodilians as a means of rapid escape. However, such movement also allows the animals to leap or bound over obstructions such as logs and rocks (Webb and Gans 1982). Galloping in crocodilians is highly variable, and animals have been recorded using a

transverse or rotary gallop, a half-bound or a bound (Renous et al. 2002; Zug 1974). There are four different types of gallops observed in *C. johnstoni*. Type 1 corresponds to a bound with a flight, with a short lead time separating the synchronized footfalls of the forelimbs from the synchronized footfalls of the hind limbs. A Type 1 gallop is observed in about 7.5% of the crocodiles. A Type 2 gallop, seen in 31.8% of crocodiles, is a three stroke gallop, deemed, half-bound with unsynchronized forelimbs, but synchronized hindlimbs. A Type 3 gallop is a rotary gallop with leading fore- and hindlimbs on opposite sides, seen in 21% of the crocodilians. Type 4 gallop, which was most frequently observed (39.5%), is the transverse gallop with leading fore- and hindlimbs on the same side of the body (Fig. 2). All four types of asymmetrical gaits have speeds between 1 and 1.40 ms<sup>-1</sup>. However, the Type 1 bounding gait has a speed greater than 2 ms<sup>-1</sup>. Among these gaits, rotary gallop offers a higher level of maneuverability, while the transverse gallop demonstrates a higher level of stability (Renous et al. 2002). This diversity of asymmetrical gaits in *C. johnstoni* is not overly surprising considering patterns of rhythmicity in



**Crocodylia Locomotion, Fig. 2** Foot fall diagram representing the two types of gallops observed in crocodiles. LH = left hindlimb; LF = left forelimb; RH = right hindlimb; RF = right forelimb

bradymetabolic (poikilothermic) tetrapod lineages (Granatosky et al. 2020).

Crocodilian kinematic patterns change dramatically during galloping. During the gallop, the back arches vertically and the straight tail moves up and down. Such back movements are of note, as axial kinematics switch from the plesiomorphic condition of lateral undulation to a derived dorso-ventral undulatory motion (Hutchinson et al. 2019). When a crocodilian begins to gallop, the initial bound is done by raising the anterior body on the front legs while the hindlimbs quickly unfold, lifting the acetabulum, so thus the femur becomes vertical and the tibia horizontal. When the hindlimbs unfold, the forelimbs swing outward and tilt under the trunk. The end of the initial bound is marked when the forelimbs contact the substrate. The angle between the humeral and radio-ulnar portions decreases because the forelimbs begin to slightly bend and rotate. Momentum continues to move the trunk forward. Following the initial unfolding of the hindlimbs, they are folded once again and swung outward and anteriorly before being unfolded again. The hindlimbs are fully extended when they contact the substrate (Webb and Gans 1982).

## Swimming and Diving

Aquatic locomotion is essential for the crocodilians, as many species rely on their aquatic habitats for prey, reproduction, and social interactions (Seebacher et al. 2003). Accordingly, the crocodilians have evolved several anatomical features that allow for quick and maneuverable aquatic movements. Webbing between the toes provides surface area, aiding in positioning in the water and controlling speed of movement and performing turns. While swimming, the limbs are pressed against the body, reducing hydrodynamic drag thus contributing to speed. The tail is the greatest contributor to propulsion during swimming. Relative to the body, the limbs of the crocodilians are small; however, the tail is quite large and muscular. The lateral shape of the crocodilian tail increases surface area, allowing for axial propulsion in water. The tail moves in a sinusoidal or

s-shaped fashion. During steady swimming, velocity is dependent on an increase in tail beat amplitude (Seebacher et al. 2003).

The crocodilians are also capable of diving. Diving allows the crocodilians to submerge underwater for periods of time ranging from minutes to hours. The digestion of stones contributes to the dive capacity. Stone digestion has been found to increase specific gravity thus prompting the crocodilians to increase their lung volume and storage of pulmonary oxygen. This increased lung volume allows crocodilians to remain still underwater near the ground for extended periods of time without continually surfacing for air. The presence of these digested stones, or gastroliths, is positively correlated with the duration of a crocodilian dive (Uriona et al. 2019).

## The “Death Roll”

The death roll is a rapid rotation along the longitudinal axis of the crocodilian’s body. The rotational effort, or spinning, begins when the fore- and hindlimbs are pressed against the body and the head and tail are in line with the body’s axis. The crocodilian then bends into a C-shape with its limbs still pressed against its body. The ability to centralize the crocodilian mass by keeping the legs close to the body creates a powerful and fast spin by reducing drag. Upon initiating the spin, the body remains straight while the head and tail rotate around their own longitudinal axes. The end of the spin consists of the head, body, and tail straightening out and the legs abducting from the body yielding the sprawled posture. During the spin, the head, body, and tail all spin with the same direction and angular speed (Fish et al. 2007). The speed and force created by this behavior is a powerful tool to engage and dismember prey once in the animal’s jaws. The death roll is also observed during the need to escape conflict or to injure a competitor (Drumheller et al. 2019).

To better understand the forces at play in the death roll it is important to note the presence of the *roll axis*. The roll axis is parallel to the body of the crocodilian and runs from the snout to approximately near the base of the tail (Fish et al. 2007).



While the C-shape taken by the crocodilians at the beginning of the spin allows each body part to possess its own vector of angular momentum they eventually all cancel out yielding an angular momentum of zero. When the crocodilian engages the roll axis during a spin, only a tenth of the revolution around the roll axis is completed. The minor motion on the roll axis does not contribute to the angular momentum of the spin. The lack of net change in angular momentum due to the orientation of the crocodilian yields a reduced inertia and increased spin rate (Fish et al. 2007).

## Conclusion

Traditional depictions characterize crocodilian movement as slow and lumbering, but these animals are capable of a diverse range of locomotor behaviors, such as walking, running, galloping, swimming, diving, and death rolling. Walking can be broken down into belly-dragging and high-walking, each with distinct gait kinematics. Galloping provides the crocodilians a quick means to escape and traverse obstacles, and represents one of the few examples of asymmetrical locomotion in a non-mammalian tetrapod. In the water, the crocodilians are impressive swimmers that separate the functional roles of the limbs for maneuverability and the tail for propulsion. Crocodilian locomotor behavior also highlights the fact that these animals are not “mindless lizards,” but are able to utilize rocks from their environment to increase the duration of dive time. Finally, the crocodilians can use their remarkable strength to death roll that assists in prey manipulation and defense.

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Radiation](#)
- [Basal Metabolic Rate \(BMR\)](#)
- [Carnivore \(diet\)](#)
- [Common Ancestor](#)
- [Crocodylia Diet](#)
- [Crocodylian Communication](#)
- [Dispersal Ability](#)
- [Dispersal Patterns](#)
- [Ecology](#)
- [Evolution](#)
- [Extinction in Learning](#)
- [Gait](#)
- [Home Range](#)
- [Homology](#)
- [Homoplasy](#)
- [Locomotion](#)
- [Morphology](#)
- [Muscular System](#)
- [Natural Selection](#)
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- [Terrestrial](#)
- [Territoriality](#)
- [Vertebrate Nervous System](#)
- [Zoo](#)
- [Zoology](#)

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## Crocodilia Morphology

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## Synonyms

Crocodile; *Crocodylia*; *Crocodylia* morphology; *Morphology*

## Definition

Crocodylia – the clade comprised of the last common ancestor of *Gavialis gangeticus*, *Alligator mississippiensis*, and *Crocodylus niloticus* and all of its descendants (Brochu 2003)

## Introduction

Living crocodylians are some of the most remarkable reptiles on the planet, inhabiting the tropical and subtropical regions of the world where they are important faunal elements of their respective ecosystems. Currently, there are 26 accepted extant species (however, the actual number may be greater, with other potential species awaiting recognition; e.g., Grigg and Kirshner 2015) classified into three families: Alligatoridae (which includes the genus *Alligator* and the caimans of the genera *Caiman*, *Melanosuchus*, and *Paleosuchus*), Crocodylidae (which includes the genera *Crocodylus*, *Mecistops*, and *Osteolaemus*), and Gavialidae (which includes the genus *Gavialis*). The genus *Tomistoma*, today represented by a single species, has a contentious taxonomic placement, as molecular studies find it closely related to *Gavialis* (e.g., Willis et al. 2007), while most morphological studies consider it as related to crocodylids (e.g., Piras et al. 2010). Collectively, they are all part of the clade *Crocodylia*, which itself is a part of the suborder *Eusuchia* within a highly diverse group – the

Crocodylomorpha – that has had a long evolutionary history spanning from the Late Triassic or over 200 million years. This article will briefly cover the morphology of living crocodylians. For more detailed discussions on the subject, the reader is referred to the literature cited herein.

## General Appearance

The crocodylian body is characterized by a large head with a prominent rostrum (snout), a short neck, a relatively long and widened trunk, and a long, laterally compressed muscular tail that is essential for swimming (Fig. 1). To an extent, the general form of crocodylians superficially resembles that of lizards, despite the fact that they are not lizards themselves nor are they closely related to lizards. The closest living relatives of crocodylians are the birds, and together they are the only surviving representatives of the Archosauria, a clade that also includes the non-avian (non-bird) dinosaurs, pterosaurs, and other extinct forms. Upon hatching, crocodylians start their lives as very small. As adults, crocodylians are large reptiles, with the estuarine or saltwater crocodile (*Crocodylus porosus*) being known by individuals to exceed 6 m in total length and weighing over a ton; the smallest taxa (like the dwarf crocodiles of the genus *Osteolaemus*, dwarf caimans of the genus *Paleosuchus* and the Chinese alligator *Alligator sinensis*) grow around 2 m in total length (Grigg and Kirshner 2015).

The rostral shapes and proportions differ between taxa and range from the extremely elongated and thin rostra of Indian gharials (*Gavialis gangeticus*) to the short and broad rostra of the aptly named broad-snouted caiman (*Caiman*

*latirostris*). Therefore, based on rostral proportions, crocodylians can be generally categorized into three non-monophyletic groups: longirostrine or “long snouted,” mesorostrine or “middle snouted,” and brevirostrine or “short snouted” (Grigg and Kirshner 2015; Fig. 2). Importantly, this categorization by rostral shape is not necessarily indicative of close taxonomic relationships; for example, the Australian freshwater crocodile (*Crocodylus johnstoni*) is of the longirostrine morphotype, thus more similar in that regard to the distantly related Indian gharial than to the closely related brevirostrine mugger crocodile (*Crocodylus palustris*).

Crocodylians have relatively short limbs, with the hind limbs usually larger than the front. There are five toes in the forefeet and four in the hind feet (the fifth toes of the hind feet are rudimentary bones), with only the first three toes in both fore- and hind feet bearing claws (Fig. 3). The feet are webbed, with the degree of webbing being commonly more pronounced in the hind feet, while some species lack forefeet webbing.

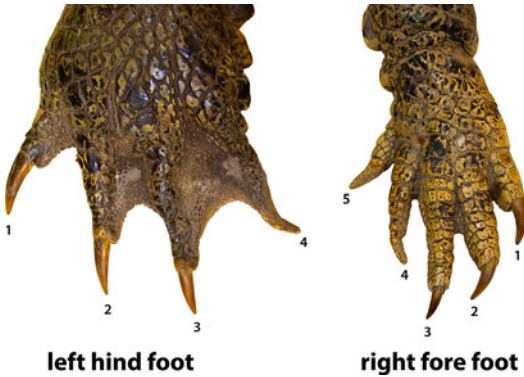
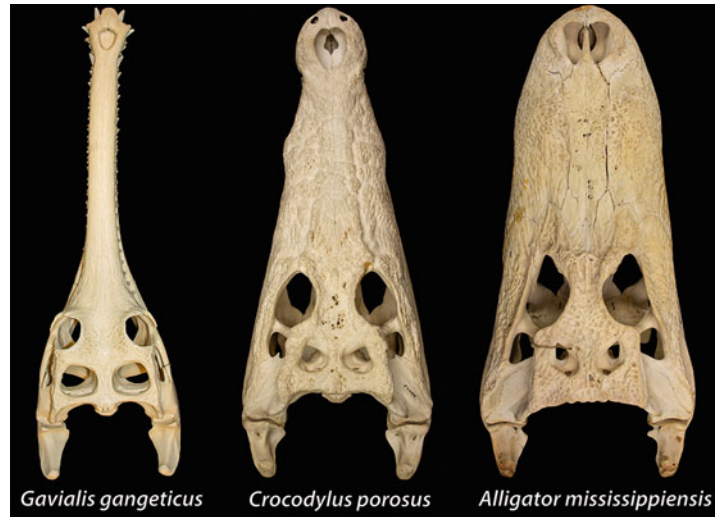
Crocodylians are sexually dimorphic (meaning there are physical differences between males and females other than their sex organs; read below), with the males typically growing larger than the females. Among all living crocodylians, Indian gharials are the most sexually dimorphic. Mature male Indian gharials possess a ghara, which is a bulbous soft tissue surrounding the nostrils that is absent in females. Apart from size, distinguishing the sex in other species is challenging, and one of the most reliable ways to do so is to inspect the sex organ inside the cloaca. The cloacal orifice is a ventral slit-like opening slightly posterior to the hind limbs, and inside it are hidden the penis (if male) or clitoris (if female).



**Crocodylia Morphology, Fig. 1** Australian freshwater crocodile (*Crocodylus johnstoni*). (Photograph by Jorgo Ristevski)

### Crocodilia Morphology,

**Fig. 2** Crocodylian skulls in dorsal view, exhibiting the three rostral morphotypes. Longirostrine morphotype as exemplified by the Indian gharial (*Gavialis gangeticus*), mesorostrine morphotype as exemplified by the estuarine crocodile (*Crocodylus porosus*), and brevirostrine morphotype as exemplified by the American alligator (*Alligator mississippiensis*). Skulls not to scale



**Crocodilia Morphology, Fig. 3** Taxidermy mount of an estuarine crocodile (*Crocodylus porosus*), fore- and hind foot. The numbers denote the digit sequence. Notice the webbing between the toes of the hind foot

### Eyes and Ears

The eyes of living crocodylians are positioned on top of their heads, such that when most of their bodies are submerged, the eyes (along with the nostrils and ears) can be subtly exposed above water, allowing the animals to observe the surrounding surface for potential prey or danger. There are two eyelids, an upper and lower, which close the eyes. Also, crocodylians have nictitating membranes, which are semitransparent tissue sheets that cover and protect the eyes when underwater, effectively acting as third eyelids. The nictitating membranes are located at the anterior corners of the eyes and stretch backward when engaged. The pupils are slit-like and

vertical, widening at night (or at low light levels) and narrowing during the day (or at high light levels). Eye color is variable among species, ranging from shades of green, brown, yellow, and black (Grigg and Kirshner 2015). Crocodylians possess a light-sensitive reflective surface at the back of the eye known as a tapetum lucidum, enhancing night vision and causing eyeshine glow when artificially illuminated at night.

The ears are located behind the eyes, with the external auditory meatus (ear opening) opened to a slit only anteriorly when the crocodylian is not submerged (Fig. 4a). The posterior portion of the meatus is almost always closed, regardless if the animal is under- or above-water. When the animal is underwater, the meatus is entirely closed. The external auditory meatus is covered dorsally by a large superior earlid/earflap and anteroventrally by a smaller inferior earlid/earflap (Shute and Bellairs 1955; Grigg and Kirshner 2015). The ear can be divided into the outer, middle, and inner ear (Richardson et al. 2002; Grigg and Kirshner 2015). The outer ear is the portion between the earflaps and the tympanic membrane (eardrum). Within the middle ear (or tympanic cavity) is a very small and thin bone called the columella, which transmits sounds from the tympanic membrane to the inner ear. The pneumatized (air-filled) middle ear cavity connects to the pharynx via complex tympanopharyngeal (often called Eustachian) tubes that may serve in pressure regulation (Young and Bierman 2019). The



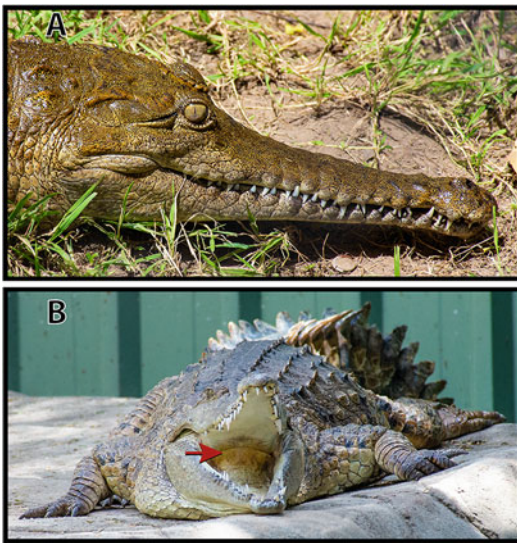
inner ear contains the semicircular canals, the otolith organs (utricle, sacculus, and lagena), and the cochlea (Grigg and Kirshner 2015).

### Skin

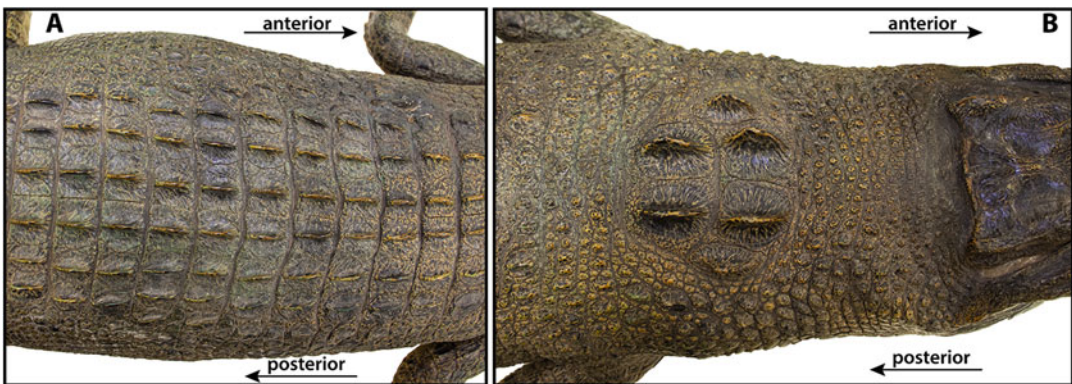
The crocodylian skin is composed of non-overlapping keratinous scales (scutes), with some body regions having osteoderms embedded underneath (read below; Fig. 5). The skin on the

face/head is tightly attached to the skull. The scales across the body are of different sizes, with the finer ones typically found around the neck and flank regions, whereas the larger are on the limbs, belly, and tail. Enlarged scales around the pectoral (chest) region are referred to as a ventral collar. The tail has large, rectangular scales present on its lateral sides, while dorsally, the tail bears two subparallel rows of upright triangular scales (double crest whorls) that converge toward the middle or slightly posterior and continue as a single row (single crest whorls) to the tip (Brazaitis 1973). Some species have smaller yet conspicuous keel-like scutes on the posterior edges of the extremities as well. Scalation patterns are usually similar within a single species (although exceptions are known, e.g., Augustine et al. 2018) but variable between different species (Brazaitis 1973).

The coloration is different across taxa (Brazaitis 1973; Grigg and Kirshner 2015) but can also differ between individuals of the same species and is dependent on the habitat the crocodylian lives in. The jaws and underside of the body are commonly lighter in color than the dorsum, flanks, and head, yet the underside tends to be darker in smaller taxa like the dwarf caimans and dwarf crocodiles (Grigg and Kirshner 2015). In some species, darker spots, blotches, and/or bands may be present on the lower jaws, backs, bellies, flanks, limbs, and tail. Skin color and patterns change ontogenetically (during growth) as well, such as in American alligators (*Alligator*



**Crocodylia Morphology, Fig. 4** Australian freshwater crocodile (*Crocodylus johnstoni*) (a) close-up of the head. The subhorizontal slit behind the eye is the ear opening. Notice the interlocking upper and lower jaw teeth (b) gaping. The gular flap in b is indicated with an arrow. (Photographs by Jorgo Ristevski)



**Crocodylia Morphology, Fig. 5** Taxidermy mount of an estuarine crocodile (*Crocodylus porosus*), dorsal scutes pattern (a) on the back and (b) neck region

*mississippiensis*) where young individuals have vibrant yellow bands over most of their bodies that disappear with maturity. Some crocodylians are able to change their skin color depending on the lighting of the environment they live in (Grigg and Kirshner 2015 and references therein; Merchant et al. 2018; Staniewicz et al. 2018). Captive *Crocodylus* individuals placed in black containment tanks were observed to change to dark shades across the dorsum and flanks, while those contained in white tanks became lighter in these corresponding regions (Grigg and Kirshner 2015; Merchant et al. 2018). Transferring individuals to alternate tanks was also associated with a corresponding color change to match the new surroundings (ventral surfaces remained unchanged across all instances). Other crocodylids (dwarf crocodiles of the genus *Osteolaemus* and slender-snouted crocodiles of the genus *Mecistops*) did not exhibit significant color change (or no change), whereas alligatorids usually did not change their skin colors at all (Merchant et al. 2018). Indian gharials and Sunda gharials (*Tomistoma schlegelii*) displayed an opposite trend to that observed in *Crocodylus*, i.e., darker conditions caused skin lightening, and lighter conditions caused skin darkening (Merchant et al. 2018); the same effect was observed in wild Sunda gharials; however, it appears that younger individuals are more capable to change color than larger adult Sunda gharials (Staniewicz et al. 2018). As indicated in the performed experiments, the change in color was triggered by visual stimulation (individuals placed in white tanks that had their eyes covered adopted dark colors; individuals placed in well-illuminated black tanks adopted light colors; Merchant et al. 2018), and temperature was not a determining factor (Merchant et al. 2018; Staniewicz et al. 2018). Aberrantly colored forms such as melanistic (meaning with darker colors) and leucistic (almost entirely white in color) are known, although melanistic forms occur more frequently than the leucistic (Richardson et al. 2002; Grigg and Kirshner 2015). Albinistic individuals are also known, which similarly to the leucistic have white skin. Albinistic individuals can be distinguished from

the leucistic by the presence of pink eyes, whereas leucistic individuals have normally colored eyes (Grigg and Kirshner 2015). Present on the skin scales are very small and black dome-like structures called integumentary sensory organs, or ISOs for short, also referred to as dome pressure receptors (DPRs) by some (e.g., Soares 2002). All living crocodylians have ISOs on their heads, jaws, and body scales, except for alligatorids which lack ISOs on their bodies. Usually, there is only one ISO per body scale; however, the ISO density is greater on the head, particularly on the snout where more than one ISO may be present on each scale. On top of the cranial table, there may be few ISOs or none (Grigg and Kirshner 2015). The functional significance of the ISOs is not fully understood yet; however, they seem to be mechanoreceptors that enable crocodylians to sense and respond to surrounding stimuli, like sensing movement underwater, during feeding, and are possibly important during courtship, among other behaviors (e.g., Soares 2002; Leitch and Catania 2012; Grigg and Kirshner 2015).

Three types of exocrine glands are present in the skin of crocodylians: mandibular (lower jaw) glands found at the posterior ventral angles of the jaws; paracloacal glands found in the lateral cloacal walls of the proctodaeum; and small glands embedded under the scales on the dorsal surface of the body (Grigg and Kirshner 2015). The mandibular and paracloacal glands secrete oily substances that may in part function as pheromones, although their full purpose is still unclear (Grigg and Kirshner 2015).

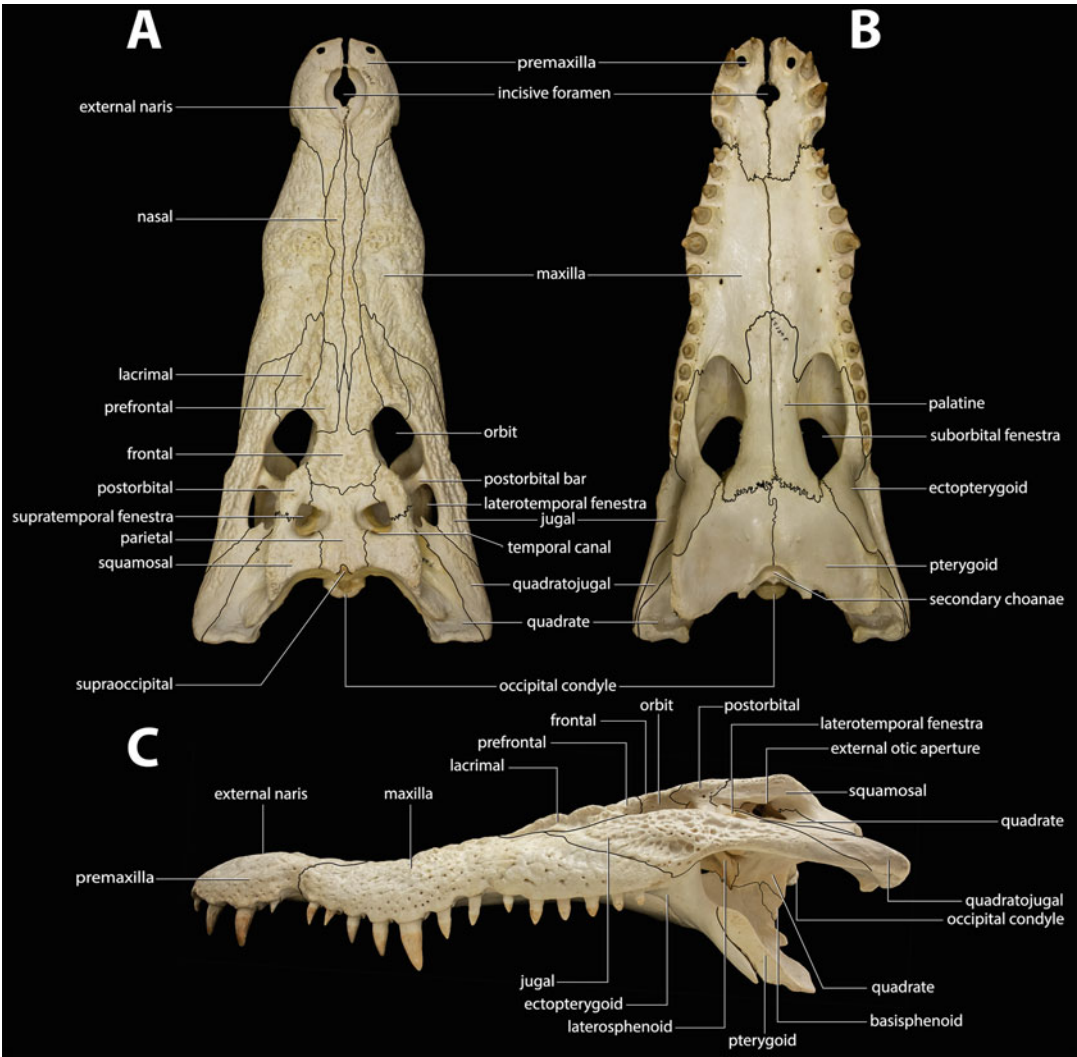
## Osteology

The following osteological description is based primarily on the estuarine crocodile, supplemented with comments on other crocodylian species.

### Skull and Mandibles

The dorsal surface of the skull (Fig. 6a) is sculptured with pits, grooves, and ridges. Sculpturing is also present on the external (in this case equivalent to the lateral and ventral) mandibular surfaces, albeit to a smaller extent than on the skull.





**Crocodylia Morphology, Fig. 6** Estuarine crocodile (*Crocodylus porosus*) skull in (a) dorsal, (b) ventral (or palatal), and (c) left lateral view

The degree of sculpturing is variable between individuals, getting more pronounced through ontogeny. The alveolar margins on the rostrum bear numerous small openings called neurovascular foramina. The anterior part of the rostrum is formed by the premaxillae. Located dorsally on the premaxillae is the large opening for the nostrils called the external naris. Another opening on the premaxillae, smaller than the external naris, is the so-called incisive foramen. The largest bones of the rostrum are the maxillae. Dorsomedially, the maxillae are separated from each other but are in

sutural contact ventrally where they contribute significantly to the secondary bony palate. The maxillae (as well as the dentaries; read below) of many species have a concavo-convex, undulating lateral profile, which is referable as festooned. Festooning is either faint or completely absent in the longirostrine taxa (Fig. 4a). The nasals are long and relatively narrow bones that are placed dorsomedially on the rostrum and reach the external naris posteriorly, where they send a short process within it. In alligators and dwarf crocodiles, the nasals are much more extensive anteriorly and

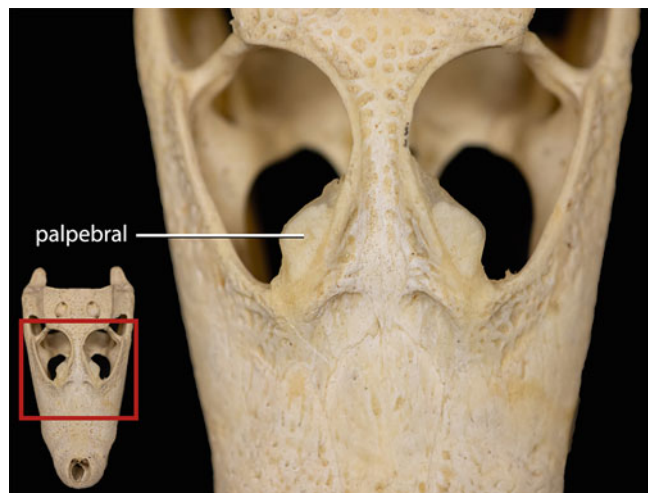
together with the premaxillae form an internarial bar (Iordansky 1973; Fig. 2). Contributing to the anterior orbital margins are the lacrimals. Some crocodile species, like the estuarine crocodile, have pronounced lacrimal ridges that stretch from the anterior margins of the orbits and forward on the rostrum. The prefrontal bones comprise the anteromedial margins of the orbits, and ventrally they send robust vertical processes called the prefrontal pillars which contact the palatines. The frontal is a large element, constituting the majority of the medial orbital margins. Anteriorly, the frontal forms an elongated pointed process that is wedged between the prefrontals and nasals. The orbits are the openings on the skull that house the eyes. Plate-like bones, called palpebrals, are situated at the medial margins of the orbits that among living species are especially prominent in the dwarf crocodiles and dwarf caimans, capping the eyes dorsally (Fig. 7).

Medially, the orbits are separated from each other by the cartilaginous interorbital septum. Dorsally between the orbits, caimans of the genera *Caiman* and *Melanosuchus* have distinctive transverse ridges. The cranial table (the portion of the skull above and posterior to the eyes) is comprised of the postorbitals, squamosals, parietal, and most of the frontal, and, in some cases, there may be a small contribution by the supraoccipital. The posteromedial part of the cranial table is formed by the parietal, which is another relatively large element.

The postorbitals form the anterolateral portions of the cranial table. Ventrally, the postorbitals send descending, pillar-like processes that form significant portions of the postorbital bars. However, in addition to the postorbitals, the postorbital bars are also formed by the ascending processes of the jugals ventrolaterally and by the ectopterygoids ventromedially. The squamosals make up the posterolateral parts of the cranial table. On their lateral surfaces, the postorbitals and squamosals bear horizontal grooves for attachment of the upper earlids. The two large openings dorsally on the cranial table are the supratemporal fenestrae. The size of the supratemporal fenestrae can range across taxa, with estuarine crocodiles having fenestrae of a smaller circumference than their orbits, but some crocodylians, such as Indian gharials, have very large supratemporal fenestrae (Fig. 2). In dwarf caimans, the supratemporal fenestrae usually close with ontogeny (Brochu 1999). The laterotemporal fenestrae are the trapezoid-like openings on the posterolateral parts of the skull, separated from the orbits by the postorbital bars. On the posterior walls of the supratemporal fossae are two small openings, called the temporal canals (or temporo-orbital foramina). The jugals are elongated bones that form the majority of the ventral margins of both the orbits and laterotemporal fenestrae. The quadratojugals are located at the posterolateral portions of the skull, contacting the jugals

#### Crocodilia Morphology,

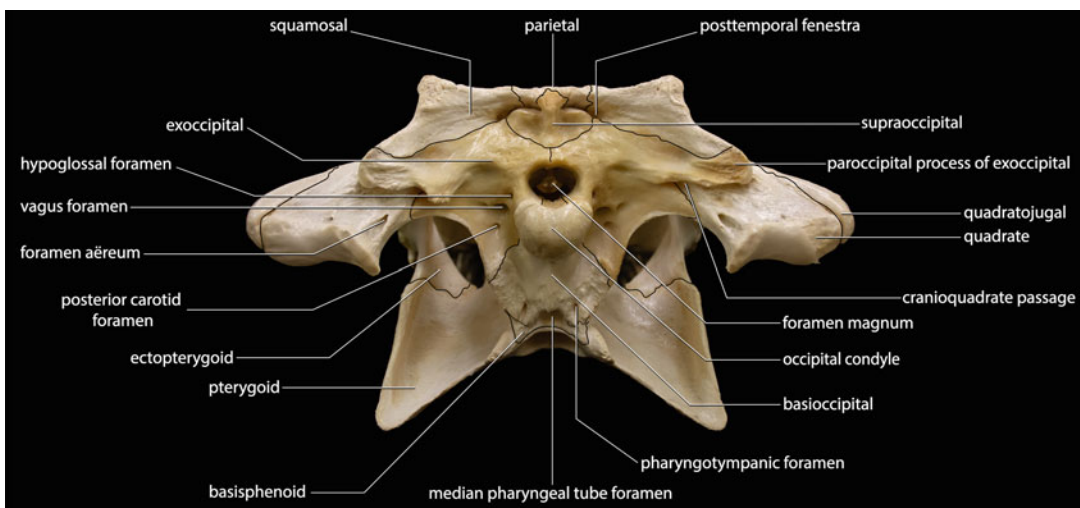
**Fig. 7** Juvenile American alligator (*Alligator mississippiensis*) skull, periorbital region (meaning around the orbits), with the right palpebral indicated



anteriorly and anterolaterally, and quadrates medially. The quadratojugals contribute to the laterotemporal fenestrae's posterior margins and within them send spine-like processes termed the quadratojugal spines. The quadrates are large, unsculptured bones found at the posterolateral parts of the skull. The distal or posterior portions of the quadrates bear the quadrate hemicondyles that articulate with the mandibles. Ventrally, the quadrates bear several crests, termed crests A, B, and D, which serve as attachments for muscle tendons; the degree of development for these crests is variable among individuals, with larger and older crocodylians commonly having more developed crests (Iordansky 1973). Additional types of quadrate crests are found in different species, but not all crests are present in a single species (Iordansky 1973). Posteromedially on each quadrate, near the medial quadrate hemicondyle is the foramen aëreum. Another opening, this time on the occipital surface (back of the skull; Fig. 8), is the cranioquadrate passage, opened between the quadrate and the paroccipital process of the exoccipital on each side.

The opening between the quadrate and squamosal is the external auditory meatus (otic aperture). Anterior to the external auditory meatus is the conspicuous subtympenic foramen; however, this foramen can vary in size in some taxa. The

external auditory meatus and subtympenic foramen are just some of the elements of the meatal chamber complex, for which an excellent review is given by Montefeltro et al. (2016). The palatines are located ventrally on the skull (Fig. 6b), and their dorsal surfaces together with those of the pterygoids form the nasopharyngeal duct. The large oval openings ventrally on the skull are the suborbital fenestrae. The pterygoids are large, wing-like elements that contact the palatines anteriorly and ectopterygoids laterally. Mature Indian gharial males have massive swollen structures dorsally on their pterygoids called pterygoid bullae (Iordansky 1973). Posteromedially on the pterygoids are the secondary choanae. One of the defining features of the Eusuchia, the clade to which all living crocodylians belong to, is secondary choanae that are fully enclosed by the pterygoids, and another feature is the presence of procoelous vertebrae (Salisbury and Frey 2001; Brochu 2003; read below). The ectopterygoids are robust bones that contact the maxillae and jugals dorsally and the pterygoids posteroventrally. Other bones of the palate are the vomers; however, in most species, these are not exposed externally at adulthood, except in the black caiman (*Melanosuchus niger*) where the vomers are situated between the premaxillae and maxillae, and

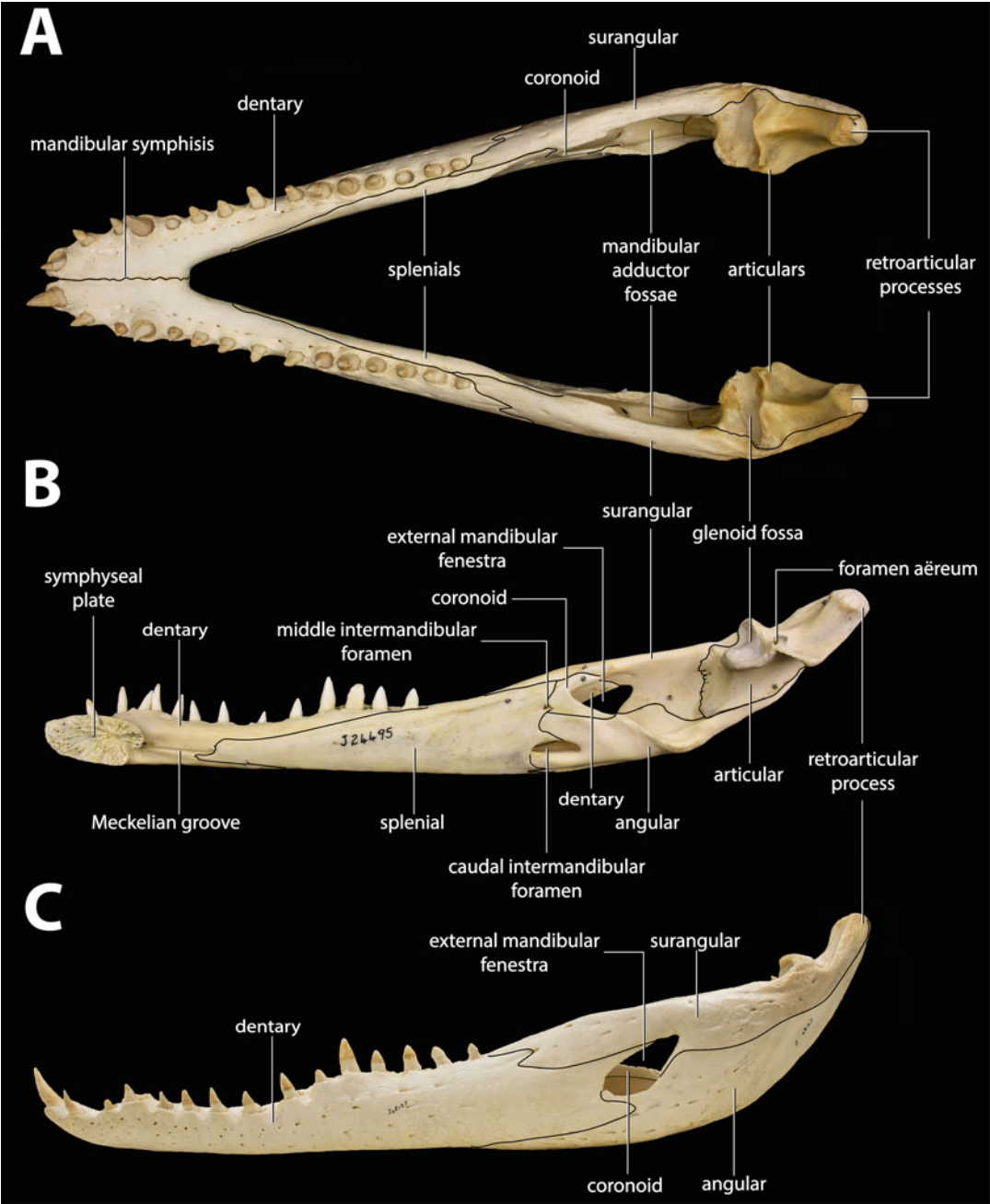


**Crocodylia Morphology, Fig. 8** Estuarine crocodile (*Crocodylus porosus*) skull in occipital view

in the Sunda gharial, where the vomers are situated between the maxillae and palatines (Iordansky 1973). The laterosphenoids compose the anterolateral parts of the braincase walls. Dorsal to the medial contact of the laterosphenoids is a large opening for the olfactory tract of the brain. Still at the medial contact of the laterosphenoids and ventral to the opening for the olfactory tract is the opening for the optic nerves, and ventrolateral to the former are the openings for the oculomotor nerves. Small foramina for the trochlear nerves also pierce the laterosphenoids. Laterally on the braincase walls are the large trigeminal foramina (openings for the trigeminal nerves, also called foramina ovals). The prootics are bones of the braincase that have small external exposure and may be difficult to observe on an articulated skull. The prootics bound the trigeminal foramina posteriorly and contact the laterosphenoids anteriorly, while the quadrates cover the prootics medially (see Holliday and Witmer 2009 for more details on laterosphenoids and surrounding structures). Dorsomedially on the occipital surface of the skull is the supraoccipital. The supraoccipital may have small exposure on the dorsal surface, wedged medially into the parietal. Set between the supraoccipital and exoccipitals ventrally and parietal and squamosals dorsally are narrow openings called the posttemporal fenestrae. The exoccipitals are one of the largest bones on the occipital surface, and laterally, they develop the paroccipital processes. Anteromedially, the exoccipitals, along with the supraoccipital and prootics, form the tympanic bullae, which house the inner ear; the tympanic bullae are visible through the foramen magnum (Iordansky 1973). The foramen magnum is the large opening at the center of the occiput. Lateral to the foramen magnum and occipital condyle, the exoccipital bears the hypoglossal foramina, the foramina vagi, and the posterior carotid foramina. The basioccipital is located medioventrally on the occiput and forms the semispherical occipital condyle. Ventral to the basioccipital on the occiput, there is a small exposure of the basisphenoid. Ventrally, posterior to the secondary choanae and between the basioccipital and basisphenoid is the foramen of

the median pharyngeal tube (following Dufeu and Witmer 2015 and Young and Bierman 2019; this opening is often referred as the median Eustachian foramen), while laterally to the aforementioned are the smaller pharyngotympanic foramina (following Young and Bierman 2019; these openings are often referred as the lateral Eustachian foramina). The basisphenoid has additional exposure posterolaterally on the braincase walls, posterodorsal to the pterygoids, and posteroventral to the quadrates (Fig. 6c); furthermore, the basisphenoid forms a mediolaterally narrow and dorsoventrally expanded sheet of the bone at the anterior portion of the braincase, called the basisphenoid rostrum, dorsomedial to the pterygoids and ventromedial to the laterosphenoids. The basisphenoid rostrum supports the abovementioned interorbital septum. The cranial cavities are pneumatized, and possess paratympanic air sinuses with their related diverticula (Dufeu and Witmer 2015).

The largest bones of the mandibles (Fig. 9) are the dentaries. The mandibular symphysis is the joint that connects the dentaries anteromedially. In disarticulated mandibles, the anteromedial portion reveals the rugose symphyseal plate (Fig. 9b). Posteromedial to the symphysis is an anterior exposure of the Meckelian groove, and within it is housed the Meckel's cartilage. Most of the Meckelian grooves are covered laterally by the splenials, which are long and smooth elements on the medial mandibular surfaces. The posterodorsal portions of the mandibles are formed by the surangular bones, while the angulars form the posteroventral. Together with the posterior portions of the dentaries, the anterior of the surangulars and angulars surround the external mandibular fenestrae, the largest openings of the mandibles. The external mandibular fenestrae can vary in size between different species. Attached medially on both the surangulars and angulars are the articulars. Anteriorly on the articulars are the concave fossae (glenoid fossae) that articulate with the hemicondyles of the quadrates. Medially on the articulars are the mandibular foramina aërea. Additionally, the articulars develop the long retroarticular processes that project posterodorsally. The smallest bones of the mandibles



**Crocodylia Morphology, Fig. 9** Estuarine crocodile (*Crocodylus porosus*) mandibles in (a) dorsal, (b) right mandible in medial, and (c) left mandible in lateral view

are the coronoids. Anteroventrally to the coronoids and posteriorly to the splenials are the small middle intermandibular foramina. Other medial openings are present in the mandibles,

these ones situated more ventrally, between the dentaries and angulars, called the caudal intermandibular foramina. Trough-like concavities on the posteromedial mandibular portions



serving as muscle attachment for the mandibular adductor muscles are the mandibular adductor fossae (Iordansky 1973).

### Dentition

The teeth of the upper jaw are set in the premaxillae and maxillae, while all teeth of the lower jaw are set in the dentaries. The number of teeth is variable among taxa, with the Indian gharial having the highest number among living crocodylians, usually between 104 and 110 in total (Iordansky 1973). The tooth count can also vary intraspecifically (among different individuals of the same species), sometimes due to ontogeny, but in some cases even individuals of the same age may differ in their tooth counts. Estuarine crocodiles bear five teeth in the premaxillae, with the fourth tooth being the largest and the second smallest. Between the first and second premaxillary teeth are two deep pits that receive the first dentary teeth during jaw occlusion (jaw closure) which may perforate the premaxillae anteriorly if they grow sufficiently large. Additional reception pits for dentary teeth are present between the third and fourth and fourth and fifth premaxillary alveoli, but these are usually not as deep as the anterior-most pits. Similarly shallow pits are present between some maxillary alveoli as well. Posterolaterally, at the sutural contact between the premaxilla and maxilla, crocodiles have a notch that fits the fourth dentary tooth when the jaws are occluded. This notch is absent in alligators. In crocodylids, the largest maxillary tooth is the fifth, while in alligatorids it is the fourth. The size of the largest maxillary tooth causes a swelling on the dorsal surface of the maxilla, more pronounced in larger individuals. Estuarine crocodiles have 14 teeth in each maxilla and 15 teeth in each dentary; thus, estuarine crocodiles have 68 teeth in total (a slightly variable number when keeping in mind individual variation). In order to more conveniently express the number of teeth in a crocodylian, dental formulae may be used. Taking the above specified tooth count, the dental formula for an estuarine crocodile would be  $5 + 14/15$  (i.e., 5 teeth in each premaxilla +14 teeth in each maxilla/15 teeth in each dentary). If the tooth count is slightly variable, the dental

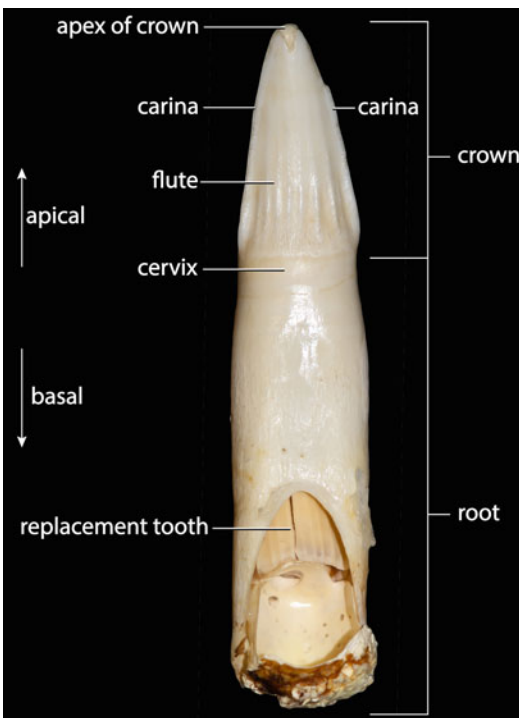
formula could instead be, for example,  $4(5) + 13-14/15$  (i.e., 4 or 5 teeth in each premaxilla +13 to 14 teeth in each maxilla/15 teeth in each dentary). Dental formulae for other species can be found in Iordansky (1973). Crocodiles and gharials have interlocking dentition, meaning when their jaws are closed, the teeth from the lower jaws are still visible and interlock with those of the upper jaws (Fig. 4a). On the other hand, alligatorids have an overbite, that is, when their jaws are closed only, the teeth from the upper jaws are visible for the most part. Crocodylian teeth are set in sockets, or alveoli, a condition referred to as thecodont. In juveniles, the teeth at the posterior of the jaws are set in grooves instead of an individual alveolus, a condition referred to as aulacodont; however, with ontogeny each tooth will eventually be enclosed in an individual alveolus, thus becoming thecodont (Bertin et al. 2018). Within its alveolus, the tooth is attached by a non-mineralized ligament, and this type of attachment is called gomphosis (Bertin et al. 2018). The teeth of living crocodylians have conical crowns and subcylindrical hollow roots (Fig. 10). In estuarine crocodiles, the external crown surfaces (covered by an enamel layer) are faintly ornamented with a fluted pattern, and the mesial (a dental term equivalent to anterior) and distal (in context of dentition, a term equivalent to posterior) sides of the teeth bear ridges called carinae.

The crown is delimited from the root by a short transitional surface called the cervix dentis (cervix in brief) or the neck of the tooth (Hendrickx et al. 2015). Crocodylians, like many other reptiles, are polyphyodont, meaning they continually shed and replace their teeth throughout life. Once fully formed, the roots start to be resorbed gradually as part of the replacement cycle. The fully grown functional tooth is accompanied by a small, bud-like replacement tooth, initially situated lingually (toward the side of the tongue, as opposed to labially, or toward the outside of the jaws) inside the alveolus that continues to grow within the (now gradually resorbing) hollow root, eventually positioning itself right underneath the functional tooth (Bertin et al. 2018). Once the old tooth is shed, the replacement tooth takes the exact same position within the alveolus.



The morphology of crocodylian teeth is generally uniform but does vary slightly. For example, alligators, caimans, and dwarf crocodiles have blunter and almost button-like posterior teeth (molariforms or pseudomolars) that are used in crushing hard-shelled prey (e.g., gastropods, turtles), while the comparatively longer and sharper anterior teeth (caniniforms or pseudocanines) are employed for seizing prey, combat, and display

(Erickson et al. 2012; Fig. 11). Due to this subtle differentiation in size and shape, crocodylian dentition can be regarded as pseudoheterodont, as opposed to truly heterodont dentition as found in mammals, where in the latter, different types of teeth exist such as incisors, canines, premolars, and molars. In longirostrine crocodylians, the teeth tend to be less differentiated in both shape and size.



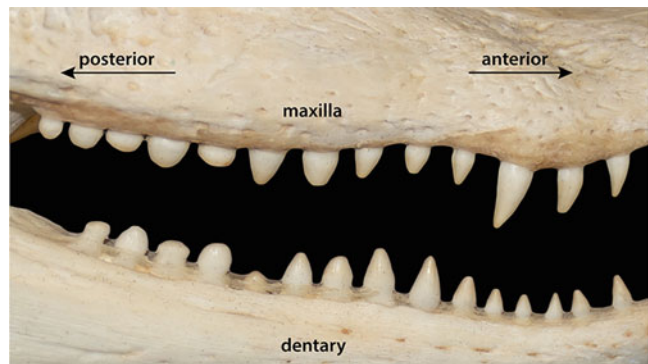
**Crocodylia Morphology, Fig. 10** Estuarine crocodile (*Crocodylus porosus*), maxillary tooth in lingual view

### Postcranial Skeleton

The postcranial skeleton (Figs. 12, 13, 14, and 15) is comprised of the vertebral column with the ribs (parts of the axial skeleton) and the limbs with the limb girdles (appendicular skeleton).

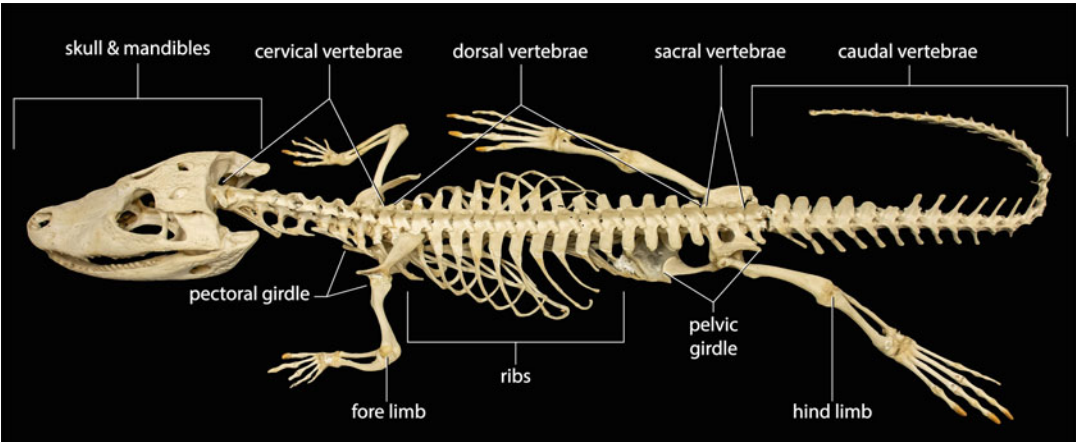
The vertebral column can be divided into cervical (neck), dorsal (subdivided into thoracic or the dorsal vertebrae that bear ribs, and lumbar, or the last three to five dorsal vertebrae that lack ribs), sacral, and caudal (tail) vertebrae (Fig. 12). The number of vertebrae is similar across all living crocodylians and usually comprises 9 cervical, 15 dorsal, 2 sacral, and depending on the species between 35 and 45 caudal (Brochu 1996; Grigg and Kirshner 2015). As mentioned above, the vertebrae of eusuchians are procoelous. In a procoelous vertebra, the centrum (vertebral body) is concave anteriorly, while posteriorly there is a semi-spheroidal convex condyle that articulates with the concave anterior (i.e., vertebral fossa) of the succeeding vertebra (Salisbury and Frey 2001; Fig. 13). All vertebrae in living crocodylians are procoelous, except for the atlas, second sacral, and first caudal vertebra. The first cervical vertebra comprises the atlas-proatlas complex which

**Crocodylia Morphology, Fig. 11** Juvenile American alligator (*Alligator mississippiensis*) skull, close-up of the jaws in right lateral view. Notice the molariform at the posterior and caniniform teeth at the anterior of the jaws

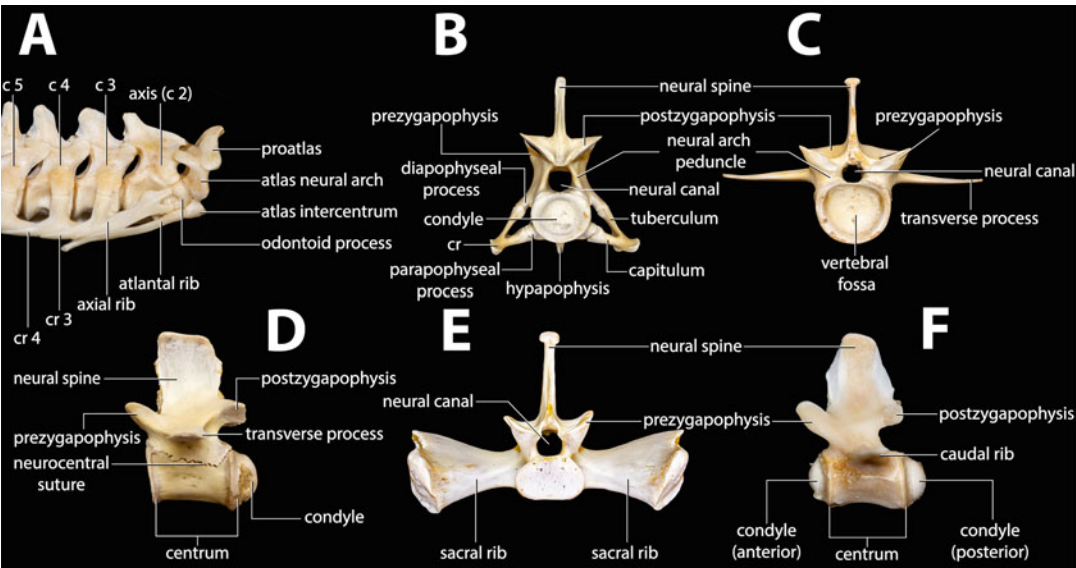


articulates with the occipital condyle of the skull and has a distinct morphology from the other vertebrae (Fig. 13a). The second sacral vertebra is biconcave, by having concave anterior and posterior ends, thus lacking the posterior semi-spheroidal condyle. The posterior articular condyle on the first sacral vertebra is weakly

developed. The first caudal vertebra is biconvex, by having semi-spheroidal convex condyles both anteriorly and posteriorly (Salisbury and Frey 2001; Fig. 13f). The second cervical vertebra is called the axis, and anteriorly it bears the odontoid process which articulates with the atlas (Fig. 13a). Attached dorsally on the centrum of a typical

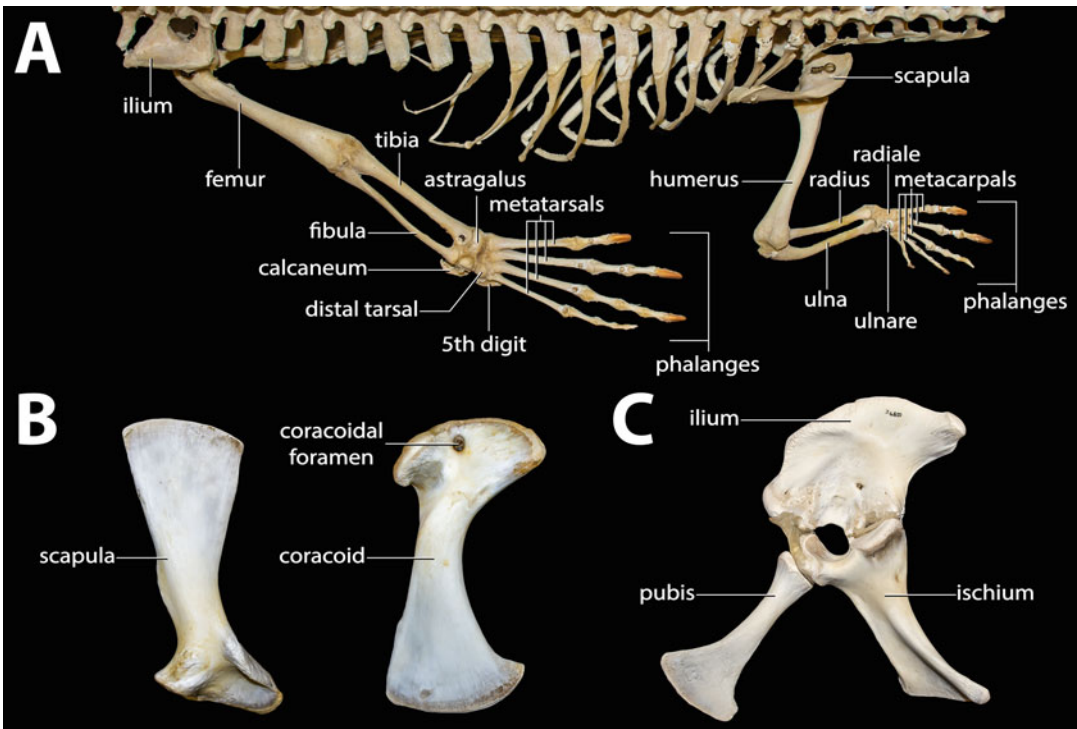


**Crocodylia Morphology, Fig. 12** Juvenile American alligator (*Alligator mississippiensis*) skeleton



**Crocodylia Morphology, Fig. 13** Crocodylian vertebrae (a) cervical vertebrae of a juvenile estuarine crocodile (*Crocodylus porosus*) in right lateral view, (b) isolated cervical vertebra of an estuarine crocodile in posterior view, (c) isolated dorsal vertebra of an estuarine crocodile in anterior view, (d) isolated dorsal vertebra of an estuarine

crocodile in left lateral view, (e) isolated second sacral vertebra of an Australian freshwater crocodile (*Crocodylus johnstoni*) in anterior view, and (f) first caudal vertebra of a juvenile Australian freshwater crocodile in left lateral view. c = cervical vertebra, cr = cervical rib



**Crocodilia Morphology, Fig. 14** Juvenile American alligator (*Alligator mississippiensis*) (a) right limbs and limb girdles in dorsal view. Estuarine crocodile

(*Crocodylus porosus*) (b) right scapula in lateral and coracoid in ventral views, and (c) left pelvic girdle in lateral view

vertebra is the neural arch, and between the centrum-neural arch contact is the neurocentral suture (Fig. 13d). The neurocentral sutures close, becoming invisible during ontogeny, with the caudal neurocentral sutures being closed upon hatching, and the cervical neurocentral sutures close last, at maturity (Brochu 1996). The neural arch is joined to the centrum via the neural arch peduncles, and the opening between the peduncles is called the neural canal (or vertebral foramen; Salisbury and Frey 2001), through which the spinal cord passes. The tall and mediolaterally thin dorsal projection on the neural arch is the neural spine. In addition to the semi-spheroidal articulation, the vertebrae also articulate by the prezygapophyses and postzygapophyses of the neural arch, where the postzygapophyses of the preceding vertebra overlay/connect to the prezygapophyses on the succeeding one. Also, anteroventrally on the centra of all cervical (except the atlas) and first three or four thoracic vertebrae are

short and thin processes called hypapophyses. Projecting laterally from the neural arches of the cervical and first two thoracic vertebrae are the diapophyseal processes, and projecting laterally from the centra of the same are the parapophyseal processes. The articular surface of the diapophyseal process (called the diapophysis) and the articular surface of the parapophyseal process (called the parapophysis) articulate with its associated rib (Fig. 13b; read below). Projecting laterally from both sides of the thoracic vertebrae neural arches are the transverse processes, which articulate with the thoracic ribs (Fig. 13c, d). Transverse processes are present in the lumbar vertebrae as well, although as stated above, these do not articulate with ribs. According to de Souza (2018), the transverse processes are a result of the merging between the diapophyseal and parapophyseal processes. The transverse processes on the sacral and caudal vertebrae are only weakly developed. The two sacral vertebrae have



**Crocodilia Morphology, Fig. 15** A selection of isolated osteoderms from an Australian freshwater crocodile (*Crocodylus johnstoni*)

sacral ribs, which are unlike the other ribs by being robust and having expanded lateral-most portions that articulate with the ilia of the pelvic girdle (Fig. 13e). The caudal vertebrae bear caudal ribs that look remarkably similar to the transverse processes of dorsal vertebrae (Fig. 13f). The ribs of the sacral and caudal vertebrae are attached to their respective neural arches and centra, specifically to the lateral articular regions called synapophyses, which are formed by the merging of the diapophyses and parapophyses (de Souza 2018). Attached posteroventrally on most caudal vertebrae are the hemal arches. In females the first hemal arch is absent, while their second is reduced

in size. Posteriorly, toward the tip of the tail region, the caudal vertebrae gradually decrease their dorsoventral heights and lose their caudal ribs and neural spines, yet their centra become more elongated, and the posterior convex condyles are also getting less prominent, until the small and elongated centra are all that remain of the last caudal vertebrae.

All cervical, thoracic, sacral, and anterior caudal vertebrae have ribs attached to them. The cervical ribs are rather short, whereas the thoracic ribs are long and slender. An exception among the cervical vertebrae are the ribs that attach to the atlas (atlantal ribs) and axis (axial ribs), which are



longer than the other cervical ribs (Fig. 13a). As described above, the ribs of the sacral and caudal vertebrae are distinct, and the following description applies to the cervical and thoracic ribs. The proximal portions of these ribs articulate with the vertebrae by two process, the capitulum and tuberculum (Fig. 13b). The tuberculum articulates with the diapophysis and the capitulum with the parapophysis. The thoracic ribs consist of three segments, which are the vertebrocostal, intercostal, and sternocostal (Richardson et al. 2002; Grigg and Kirshner 2015). Ventrally, or on their bellies, crocodylians also possess gastral (stomach) ribs or gastralia that are spread from the pectoral girdle anteriorly to the pelvic girdle posteriorly. Compared to the cervical and thoracic ribs, the gastralia are slenderer.

Located ventrally on the throat are the paired hyoid bones, which are thin, long, and curved, somewhat superficially resembling ribs.

The limb girdle associated with the forelimbs is called the pectoral girdle, whereas the limb girdle associated with the hind limbs is the pelvic girdle (Fig. 14). The pectoral girdle is represented by the scapulae, coracoids, and interclavicle. The scapula and coracoid (Fig. 14b) are in contact with each other, and at their lateral contact is the glenoid, a socket for articulation of the proximal portion (epiphysis) of the humerus. Situated ventromedially between the distal portions of the coracoids and amidst the sternal cartilage is the elongated interclavicle. From proximal to distal, the forelimb bones include the humeri, radii and ulnae, carpals (wrist bones), metacarpals, phalanges (forefoot or manual digit bones; the same term applies to the hind foot or pedal digit bones), and unguals (distal-most/terminal phalangeal bones that support the claws). The largest bone of the forelimb is the humerus, and on each humerus is a bony flange called the deltopectoral crest, which serves as a muscle attachment site. Distally, the humerus articulates with the radius and ulna. The distal ends of the ulna and radius articulate with the carpal bones ulnare and radiale, respectively; the carpal bones articulate distally with the metacarpals and the metacarpals with the manual phalanges. The ilia, pubes, and ischia form the pelvic girdle (Fig. 14c). The ilium is a relatively robust

bone that is in contact with the ischium, and together they form the acetabulum in which the proximal femoral head articulates. The ischium has two well-developed peduncles, an anterior and posterior that contact the anterior and posterior peduncles of the ilium. The pubis contacts only the ischium, which excludes the pubis from contacting the ilium. From proximal to distal, the hind limb bones include the femora, tibiae and fibulae, tarsals (ankle bones), metatarsals, phalanges, and unguals. The femur (thigh bone) is a long, sigmoid-like bone that bears a knob called the fourth trochanter which is a place for muscle attachment. The femur articulates with the tibia and fibula, and distally to the latter are the tarsal bones astragalus, calcaneum, and the distal tarsals. The tarsal bones articulate with the metatarsals. There are only four well-developed pedal phalanges.

### Osteoderms

The osteoderms are the bony plates embedded under the crocodylian's skin (Figs. 5 and 15), most prominently concentrated on the dorsal surface, with additional coverage on the flanks, limbs, and tail. The osteoderm covering serves as a shield among other functions, and the degree and pattern of osteodermal covering varies from species to species, which is useful for species identification. For example, estuarine crocodiles lack post-occipital osteoderms or the osteoderms found just posterior to the cranial table and anterior to the nuchal (neck) osteoderms (Fig. 5b). The osteodermal covering is greater in the smaller taxa, such as the dwarf crocodiles, dwarf caimans, and the Chinese alligator (Grigg and Kirshner 2015). The osteoderms can range in size and shape depending where they are located on the body (but are also variable interspecifically or between different species), and like the sculpturing on the skull, they too have pits and grooves on their dorsal surfaces, whereas ventrally they are smooth. The dorsal surface of an osteoderm has small vascular foramina, and dorsomedially there is usually a longitudinal keel. The osteoderms on the dorsal surface of the trunk are neatly arranged in six anteroposteriorly oriented and parallel rows (Richardson et al. 2002).

## Musculature

Crocodylians are strongly built animals with accordingly developed musculature. Although they lack muscles for facial expression, the masticatory muscles at the back of the cranium that insert in the mandibles are well developed. Thanks to their powerful jaw musculature, crocodylians can exert tremendous bite forces that are the strongest among living animals (Erickson et al. 2012). The jaws can be closed shut with great speed, and opening them forcefully can be very difficult. The major jaw muscles are the mandibular depressor (*M. depressor mandibulae*), external mandibular adductor (*M. adductor mandibulae externus*), posterior mandibular adductor (*M. adductor mandibulae posterior*), dorsal (anterior) pterygoid (*M. pterygoideus dorsalis*), ventral (posterior) pterygoid (*M. pterygoideus ventralis*), and pseudotemporal (*M. pseudotemporalis*) and intramandibular (*M. intramandibularis*) muscles. A comprehensive review and descriptions of the craniomandibular muscles in the broad-snouted caiman, including their origination and insertion points, can be found in Bona and Desojo (2011). Posterocranially, the axial, or trunk musculature, can be divided into two groups: epaxial, or the muscles lying dorsal to the transverse processes of the vertebrae and the ribs, and ventral to the dorsal osteoderms; and hypaxial, or the muscles ventral to the transverse processes of the vertebrae that make up the lateral and abdominal walls of the body. The epaxial musculature is comprised out of four groups, which from medial to lateral are the *spinalis* (made out of the *articulo spinalis*, *spinalis*, and *multifidus*), *tendinoarticularis*, *longissimus dorsi*, and *iliocostalis*; the hypaxial musculature includes the external oblique, internal oblique, and transverse abdominal muscles (Salisbury and Frey 2001; Grigg and Kirshner 2015). Ventrally or on the belly are the large *rectus abdominis* muscles. The chest region is ventrally covered by the large *pectoralis* muscle which inserts at the deltopectoral crest of the humerus. As the tail is used to propel the crocodylian when swimming, it has especially developed musculature. The dorsal caudal musculature includes the

*tendinoarticularis* muscle group medially and more laterally is the *longissimus caudalis*. Ventrally on the tail are the large *caudofemoralis* muscles (made of the smaller *caudofemoralis brevis* and larger *caudofemoralis longus*), and lateral to the *caudofemoralis* are the *ilioischio caudalis* muscles. Numerous muscles compose the appendicular musculature that originate and insert at the limbs and limb girdles. Detailed descriptions of crocodylian musculature can also be found in Chiasson (1962), Richardson et al. (2002), and Grigg and Kirshner (2015 and references therein), with Klinkhamer et al. (2017) focusing on the appendicular musculature of the estuarine crocodile.

## Digestive System

At its anterior, the digestive system begins with the oral cavity (mouth) that contains numerous teeth and the tongue. The tongue is affixed ventrally on the mouth and is largely (but not entirely) immobile. The tongue's surface is covered by taste buds. At the back of the throat is the gular valve, formed primarily by the gular flap ventrally, palatal flap dorsally along with smaller lateral wraps that can be engaged in order to prevent water from entering the stomach and lungs while active underwater, such as when subduing prey (Grigg and Kirshner 2015; Fig. 4b). Crocodylids possess salt glands on their tongues that aid them in excreting salt, making them adept at venturing in saline waters (Grigg and Kirshner 2015 and references therein). Salt-excreting glands are absent in alligatorids, and consequently they are more seldomly found in salt water compared to crocodylids (Brochu 2003; Grigg and Kirshner 2015). Lingual (meaning of the tongue) salt glands are also recognized in Sunda and Indian gharials; however, currently there is limited data on the salt-excreting capacity of these two species (Grigg and Kirshner 2015). Crocodylians do not masticate (chew) and instead swallow their food whole. Should the food item be larger than they can swallow, crocodylians can crush it with their posterior teeth, shake it, thrash it around, or engage in a "death roll" in order to rip it apart



into smaller chunks. Then, the crocodylian lifts and repositions its head slightly so as to plunge the food item to the mouth's posterior and into the pharynx – this technique is known as inertial feeding and is mostly implemented with the head above-water or on land (Grigg and Kirshner 2015). From the pharynx continues the long, tube-like esophagus that connects to the stomach. The stomach can be divided into four regions, with the cardia being on the left anterior portion of the stomach connecting with the esophagus, the fundus, the corpus or the largest part of the stomach, and the pylorus, which is found on the right posterior of the stomach sac and is the exit from the stomach to the small intestine, specifically the duodenum (Richardson et al. 2002; Romão et al. 2011). The small intestine is composed of the duodenum, jejunum, and ileum, with the latter segment connecting to the colon or large intestine (Romão et al. 2011). The colon connects to the cloaca. The pancreas is an organ located close to the duodenum and produces digestive enzymes as well as hormones (Richardson et al. 2002). The liver is a large, conical organ that is formed of a right and left lobe, with the right lobe being the larger of the two (Richardson et al. 2002; Romão et al. 2011).

## Respiratory and Cardiovascular Systems

Externally, the respiratory system begins anteriorly with the nostrils, which in crocodylians are located anterodorsally on the rostrum, near the tip. The nostrils are set on a slightly raised pad called a nasal disk and are controlled by the dilator muscles to open and constrictor muscles to close them (Richardson et al. 2002; Grigg and Kirshner 2015). Thus, when a crocodylian is underwater, the nostrils are fully closed, and when relaxed on land, the nostrils tend to be loosely opened (Grigg and Kirshner 2015). The relatively long nasal cavity is separated from the oral by the secondary bony palate formed by the premaxillary, maxillary, palatine, and pterygoid bones. The nasal cavity is relatively long and contains pneumatized paranasal air sinuses with related diverticula (Witmer 1997). The nasal cavity opens into the

nasopharyngeal duct which in turn opens through the secondary choanae posteriorly. Lying on the back of the throat is the glottis, a slit-like opening that connects to the larynx. The larynx then leads to the lungs via the long, tub-like trachea. Toward the posterior and near the heart, the trachea branches off into the left and right bronchi, which are short tubes that connect to the lungs. The black caiman has an unusually wide trachea anteriorly that narrows near the bronchi (Grigg and Kirshner 2015). The two lung sacs are highly vascularized and non-lobulated, each being oval in shape (Chiasson 1962; Richardson et al. 2002).

The majority of extant reptiles have three-chambered hearts, comprised of two atria and one ventricle that are only partially divided by an incomplete interventricular septum. However, crocodylians deviate from this norm by being the only living reptiles to possess a four-chambered heart – two atria (a left and right) and two ventricles (a left and right) divided by an interventricular septum – which in that regard makes crocodylians more similar to mammals and birds. Unique to the hearts of crocodylians is a small opening called the foramen of Panizza (named in honor of the Italian anatomist Bartolomeo Panizza, who published the first study describing this foramen), located within the semilunar valve between the left and right aortas. The right aorta is the main artery that supplies blood from the heart to the body. Another interesting feature of crocodylian hearts are the “cogwheel valves,” which are teethlike nodules arranged in a semicircle and located at the base of the pulmonary arch within the subpulmonary conus that lead from the right ventricle to the pulmonary aorta (Grigg and Kirshner 2015).

## Urogenital System

The two kidneys are elongated, with highly lobulated ventral surfaces, and lie ventral to the lumbar vertebrae (Chiasson 1962; Richardson et al. 2002; Grigg and Kirshner 2015). Posteriorly from each kidney stretches a short and narrow tube, the ureter, that leads to the cloaca. The cloaca is the

terminal passage for the digestive, reproductive, and urinary systems, with defecation and urination (as well as egg laying in females) going through it (Romão et al. 2011). The cloaca can be subdivided into three chambers, with the coprodaeum at the anterior (where the feces is formed), urodaeum in the middle (where urine is stored, as crocodylians do not have bladders), and proctodaeum at the posterior (Grigg and Kirshner 2015).

In males, the paired testes have an oval shape and are attached to the dorsal body cavity and located between and anterior to the kidneys (Grigg and Kirshner). The testes are smaller in immature males, with sexually mature individuals having enlarged testes during breeding seasons (Richardson et al. 2002). Posterodorsally on each testis is the epididymis, from which continues a narrow tube called the vas deferens that transports sperm to the penis. The penis sits within the proctodaeum and has no role in urination (Grigg and Kirshner 2015).

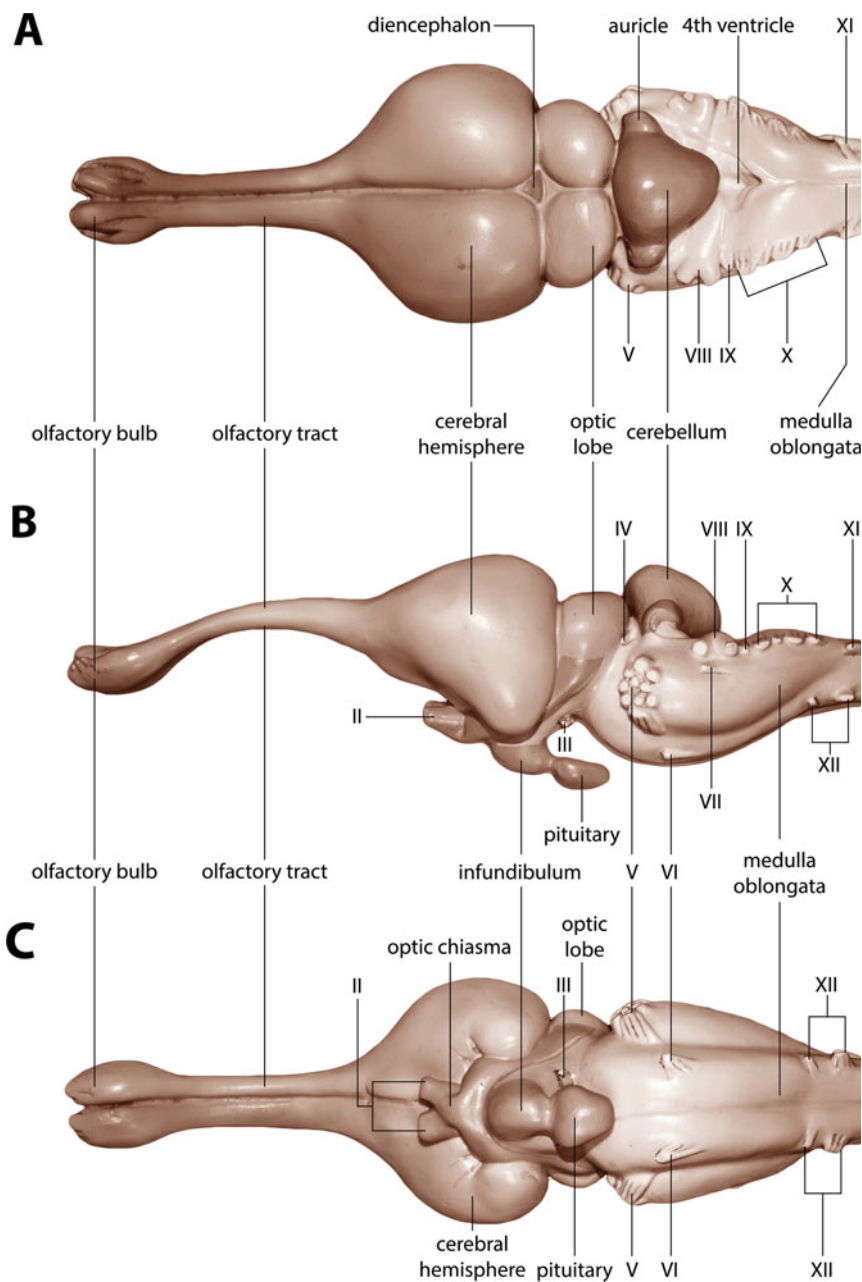
In females, the paired ovaries are located ventromedially and anterior to the kidneys. The ovaries in sexually immature females contain small ovarian follicles (spherical cellular structures) that become larger in sexually mature, breeding females. Leading from each ovary to the cloaca is an oviduct, a membranous, irregularly shaped tubelike structure through which the eggs pass. Following the summation by Grigg and Kirshner (2015), there are seven sections of the paired oviducts, which are the anterior and posterior infundibulum, the uterine tube, the uterotubular junction, the anterior and posterior uterus, and the vagina. Females also have a clitoris hidden within the proctodaeum of the cloaca, situated in a similar position as the male's penis, although the clitoris is smaller in comparison (Grigg and Kirshner 2015).

## Brain and Nervous System

The brain (Fig. 16) is housed in the braincase or endocranial cavity of the skull. The outer surface of the brain is rather smooth and covered by external membranes called meninges, while internally the brain has fluid-filled ventricles (Romer

1956). The brain can be divided into three major sections: the prosencephalon (forebrain), mesencephalon (midbrain), and rhombencephalon (hindbrain). The main subdivisions of the prosencephalon are the telencephalon and diencephalon, while the metencephalon and myelencephalon are the main subdivisions of the rhombencephalon.

Starting with the forebrain, the telencephalon includes the bulbous olfactory lobes (or olfactory bulbs) that connect to the relatively large cerebral hemispheres by the elongated olfactory tracts. The posterior portion of the prosencephalon is the diencephalon, and ventrally on it is the infundibulum, whose posterior end supports the pituitary gland (or hypophysis). The optic nerves are crossed anterior to the infundibulum, at the optic chiasma. The mesencephalon's major portion are the optic lobes (optic tectum). The metencephalon is largely consisted of the lobe-like cerebellum dorsally (with the auricles forming laterally from it) and part of the medulla oblongata. The myelencephalon is the posterior, or distal-most portion of the brain, and includes the rest of the medulla oblongata which exits through the foramen magnum and continues as the spinal cord. From the brain offshoot 12 cranial nerves, which serve important sensory and motor functions and exit through several foramina on the skull. In order, these are the olfactory (cranial nerve I), optic (cranial nerve II), oculomotor (cranial nerve III), trochlear (cranial nerve IV), trigeminal (cranial nerve V), abducens (cranial nerve VI), facial (cranial nerve VII), acoustic (cranial nerve VIII), glossopharyngeal (cranial nerve IX), vagus (cranial nerve X), accessory (cranial nerve XI), and hypoglossal (cranial nerve XII) nerves. The trigeminal nerve is the largest and branches off into the ophthalmic, maxillary, and mandibular divisions. Cranial nerves I and II originate from the prosencephalon, nerves III and IV from the mesencephalon, while nerves V–XII originate from the rhombencephalon. As mentioned above, the spinal cord extends from the medulla oblongata and runs through the neural canals of the vertebral column, almost to the tip of the tail (Richardson et al. 2002). Numerous nerves are present on the spinal cord that innervate the postcranium, with each spinal nerve branching off into



**Crocodylia Morphology, Fig. 16** Brain model of an American alligator (*Alligator mississippiensis*) in (a) dorsal, (b) left lateral, and (c) ventral view. The Roman numerals denote the cranial nerve roots. (After Romer (1956))

a dorsal and ventral ramus, innervating the epaxial and hypaxial regions, respectively. The complex network of nerves (termed a plexus) that innervate the forelimbs is the brachial plexus, and the network innervating the hind limbs and tail is the lumbosacral plexus (Romer 1956; Chiasson 1962; Richardson et al. 2002).

### Cross-References

- [Crocodylia Communication](#)
- [Crocodylia Diet](#)
- [Crocodylian Sensory Systems](#)
- [Crocodylia Cognition](#)
- [Crocodylia Locomotion](#)

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## Crocodilian Communication

### ► Crocodylia Communication

## Crocodilian Sensory Systems

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## Synonyms

### Crocodile Alligator Vision Hearing

## Definition

Sensory modalities that allow crocodilians to interact with the world.

## Introduction

Crocodilians have captured the imagination of scientists and the general public for decades. This is partially explained by their morphology and lore of being ancient hunters. Their habitat is diverse, from open waters in lakes and rivers to marshes and swamps to even beaches and the ocean. The main connecting thread among all these niches is the semiaquatic nature of their lifestyles. Aside from living and foraging in the water, crocodilians come to land to thermoregulate and rest. Typically crocodilians are endemic

to areas around the equator, with exceptions of the American and Chinese alligators, whose ranges extend as far north as the south-eastern of the United States and the Yangtze River in central China. Crocodilians also prefer the lowlands, with rare exceptions. No crocodilian permanently resides in the ocean, although in Australia some animals will swim in it. Several species tolerate brackish water of mangrove swamps and estuaries. Habitat use has been shown to be different among crocodilians (Lang 1987). The American alligator, for example, prefers habitats with open water, which have considerable floating vegetation, to dry ground and cover. Furthermore, inland alligator densities are usually lower than coastal populations, suggesting a possible preference to either open areas or brackish water. Crocodilians are diverse in their preferred habitat, with some somewhat more terrestrial, choosing edges of lakes, swamps, and ponds, where access to basking areas is easier. Others spend more time in the water and inhabit rivers and estuaries. The Asian gaviel, for example, feeds on fish and lives in the waters of swift rivers. Comparatively, the Chinese alligator prefers the slow moving waters of the Chinese floodplains. Such distribution is sensitive to seasonality and during the dry season; caimans stay in deep pools, while in the flooding season they scatter. One unique population of crocodiles in the southern edge of Africa's Sahara live in caves and burrows, and under rocks near bodies of water that dry up and disappear for months (Wilson 1987).

## Review of Crocodilians

The order Crocodylia is subdivided into three families: the Crocodylidae, in which all crocodiles are grouped; the Alligatoridae, where alligators and caiman are found; and the Gavialidae, formed by true and false garhials. There are currently 23 species of crocodilians identified. A large majority of species live in tropical regions, but the American alligator and the Chinese alligator are able to tolerate colder climates and are found in highest latitudes. The family Alligatoridae (alligators and caimans) are segregated to the



Americas, with the exception of the Chinese alligator which is endemic to eastern China. Also in the Americas are few species of crocodiles (Crocodylidae) even though most species are found in Africa, Asia, and to a certain extent in India. Indian gharials are the only species of Gavialidae and are present in that region.

## Sensory Neurobiology Intro

The physical characteristics of a habitat influence the evolution of sensory structures (Schellart 1992). A semiaquatic habitat creates a unique set of sensory challenges for crocodilians, and these animals have to detect the environment both in water and on land. The association between habitat and sensory morphology has been examined in many species of vertebrates showing a high diversity of sensory solutions (Farris 2015). Crocodilians have been shown to rely mostly on their senses of vision, audition, and mechanosensation (Fig. 1), although some modalities remain to be investigated: magnetoreception and electroreception.

## Vision

Not many studies have examined the visual system of crocodilians, but of the few, all show that the visual system of crocodilians is well adapted

to land use. This is supported by the fact that their eyes are severely defocused underwater (Fleishman et al. 1988). The spatial resolving power and spectral sensitivity of the saltwater (*C. porosus*) and freshwater (*C. johnstoni*) crocodile have been recently studied by Nagloo and colleagues (2016). In these animals, the fovea is organized in a streaked nasotemporal pattern to increase high spatial acuity. There are five photoreceptor types, with three single cones and twin cone and a rod. The single cones are violet, green, and red, suggesting trichromatic vision. The twin cones have the same maximum absorption as the red sensitive cones. The peak spatial resolving power for this fovea, for both crocodilians, is around 8 cycles/degrees.

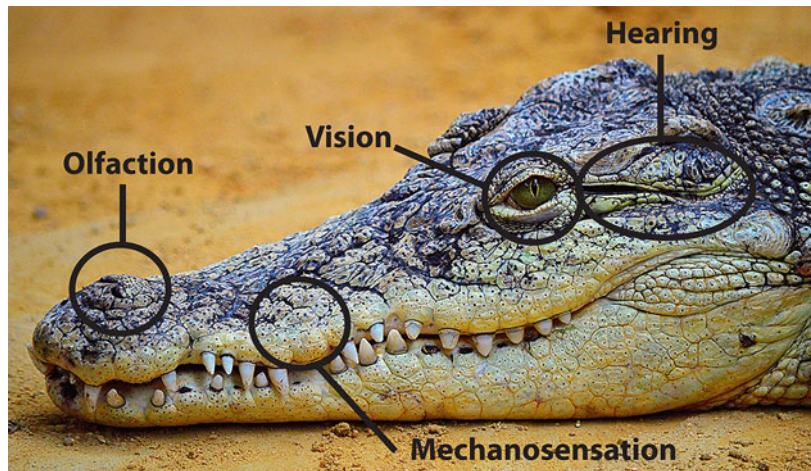
## Hearing

Crocodilians have, relatively consistent across species, excellent hearing. Their sensitivity is focused on middle tones, declines for lower tone, and quickly becomes insensitive at higher frequencies (above 3 kHz; Fig. 2a; e.g., Wever 1971; Higgs et al. 2002). Crocodilian auditory sensitivity is affected by temperature; in *Caiman*, the best sensitivity for auditory fibers moves to higher frequencies with higher temperatures (Smolders and Klinke 1984). Though hearing is most sensitive on land, a smaller but similar range

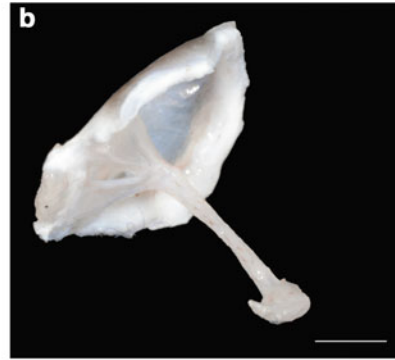
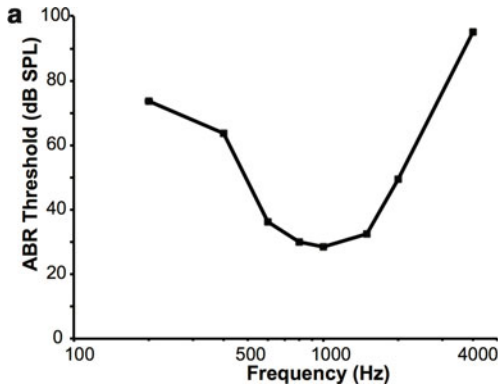
## Crocodilian Sensory Systems,

**Fig. 1** Crocodilian sensory receptor organs.

Crocodilians transduce olfactory cues via their nares, visual cues via their eyes, auditory cues via ears, and mechanosensory cues via dome pressure receptors







**Crocodilian Sensory Systems, Fig. 2** American Alligator auditory sensitivity and tympanic membrane. (a) Audiogram, generated using an auditory brainstem response recordings, shows the frequency sensitivity of

alligator hearing. (b) Tympanic membrane with attached columella dissected from juvenile specimen. Scale bar, 0.25 cm (Figures were adapted from Bierman and Carr 2015)

of sensitivity and some localization abilities have been measured in alligators with their ears submerged (Higgs et al. 2002; Dinets 2013). Vocal communication is important for maternal care and promoting group cohesiveness among the young (reviewed by Vergne et al. 2009).

Crocodilian ears are located on either side of the head caudal to the eyes. The tympanic membrane is protected by inferior and superior earlids. In air, the earlid muscle is relaxed and the earlid is slightly open (e.g., Vergne et al. 2009). Sound waves can stimulate the tympanic membrane on the external side, and also on the internal side, by traveling through canals within the animal's head. These internal pathways help the animal determine the location of sound cues (Bierman et al. 2014). Like birds, vibrations of the tympanic membrane are transmitted to the inner ear via a single ossicle, called a columella (Fig. 2b). Also like birds, the inner ear cochlear duct, which contains the hearing and vestibular organ, is short and crooked (e.g., Vergne et al. 2009). The hearing organ consists of a basilar papilla, basilar membrane, and tectoral membrane. On the basilar papilla, there are two types of sensory hair cells, tall and short, arranged in a tonotopic manner (birds also have tonotopy, but in a gradient of hair cell sizes; Gleich et al. 2004). Tall and short hair cells vary in the number of afferent fibers with which they connect the ear to higher brain structures.

## Vestibular

Along with hearing, the inner ear of vertebrates also contain vestibular organs, important for postural, reflex, and locomotor activities. Crocodilian vestibular organs, like in all gnathostomes, include two otolith organs, the utricle and saccule, and three toroidal semicircular ducts. Hair cells found in the otolith organs sense gravitational and other linear acceleration, while hair cells in the semicircular ducts sense rotational movements in three planes. The complexity of this multiorgan sensory system allows for morphological and functional variation, allowing specialization related to, “specific sensory demands imposed by an organism’s behavior, including the specifics of locomotor function” (Georgi and Sipla 2008; Sipla and Spoor 2008). Among crocodiles, differences in vestibular organ morphology are associated with the degree of aquaticity. Most crocodilians are considered semiaquatic and some vestibular organ difference are seen between these and gharial, which are highly aquatic, and a fossilized fully terrestrial basal crocodylmorph (Georgi and Sipla 2008).

## Mechanosensation

Crocodilians have various sensory organs on their skins that are responsible for the sense of touch.

Naked nerve endings, Pacinian corpuscles and Merkel cells, are present in the dermis of crocodilians. One unique specialization found across the body of crocodilians and on the heads of alligators are the dome pressure receptors (DPRs; Soares 2004). These specialized sensory organs are composed of a cluster of cells that lie in the interface of the epidermis and the keratin layer. A large nerve bundle innervates the medial part of DPRs, and in alligators, they give rise to the trigeminal nerve. This nerve is large and composed of numerous branches that travel through fenestra in the skull. DPRs are sensitive to water ripples, although it is unclear to what physical property of the water motion they are tuned. Crocodilians are stalking predators and sit on the interface of the air and water waiting for prey to appear. DPRs are able to detect disturbances that arise from prey entering or leaving the water. Another possible sensory role for DPRs is communication. Throughout the year, but particularly during the breeding season, alligators bellow to declare territory and locate suitable mates (Garrick and Herzog, 1978). Both males and females will bellow to attract mates and declare territory by sucking air into their lungs and blowing it out in intermittent, deep-toned roars (Vliet 1989). Bellowing is performed in a head-up, tail-arched posture, so the lungs are immediately underwater. Low-frequency waves from a bellowing alligator can cause the surface of the water directly over and to either side of its back to appear to “boil” in what is commonly called the “water dance” (Lang 1976; Vliet 1987). Large bellowing choruses of alligators can occur (Garrick and Lang 1977). It is unclear if DPRs are involved in communication during bellowing, but due to the nature of the stimulus, it is likely that these organs are involved.

## Osmosensation

The ability to detect different levels of salinity is advantageous for species that inhabit coastal or estuarine habitats. These animals have to cope with fluctuating osmolality by either osmoconforming or osmoregulating. Jackson

and Brooks (2007) showed that dome pressure receptors are also sensitive to osmotic pressure. Osmoreceptors sense the osmolality of a solution by expanding or shrinking in response to changes in the osmotic environment. Changes in environmental osmolality cause water to flow across cell membranes and equilibrate the osmolality of the cytoplasm. By changing cell volume and intracellular ionic strength, large changes in environmental osmolality can affect the physical state of cells and tissues. In this study, Jackson and Brooks (2007) found that when postcranial dome receptors in crocodylids are blocked, animals lose the ability to discern salinity levels. These sensory organs, which are located on the scales, also flatten when exposed to higher osmotic pressure. This is a novel and interesting role for dome sensory receptors.

## Chemosensation

Chemoreception in semiaquatic animals has to detect volatile and water-soluble compounds in both environments, but little is known about how crocodilians use their olfactory system. Neill (1971) reported that the American alligator detects blood in the water. Weldon et al. (1990) conducted behavioral and olfactometer experiments which showed that crocodilians detect both air-borne and water-soluble chemicals and use their olfactory system for hunting. When above water, crocodilians enhance their ability to detect volatile odorants by gular pumping, a rhythmic movement of the floor of the pharynx (Gans and Clark 1976; Putterill and Soley 2006). The nasal cavity of the American alligator contains two different chemosensory systems incorporated in the same sensory epithelium: the olfactory system proper and solitary chemosensory cells (Hansen 2007). Nothing is known how these two systems integrate chemosensory information.

## Electroreception and Magnetoreception

Electroreception is particularly useful for navigating, orienting, and detecting prey in low-light

conditions, such as at night or in deep, murky water. However, there is no evidence that any crocodilian has electroreceptors. Several species of vertebrates are known to orient themselves using the Earth's magnetic field, through magnetoreception (Lohmann and Johnsen 2000; Wiltshko and Wiltshko 2005). But to our knowledge, no studies to date have demonstrated that crocodilians can self-orient to magnetic fields.

## Conclusion

Although crocodilians have inhabited the imagination of scientists for numerous years, basic information about its sensory biology is still elusive. Clearly, they rely on vision, audition, and mechanosensation for interactions with the environment, but other sensory modalities still remain to be investigated.

## Cross-References

- Auditory Processing and Perception
- Crocodilia Communication
- Crocodilia Diet
- Crocodilia Locomotion
- Crocodilia Morphology
- Evolution of Animal Color Vision
- Mechanoreceptors

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## Crocodylia

### ► Crocodylia Morphology

## Crocodylia Cognition

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## Introduction

Crocodylians (crocodiles, alligators, caimans, and gharials) are arguably the most cognitively complex living nonavian reptiles. They display a rich

behavioral repertoire in a variety of contexts, such as hunting, spatial orientation, and social interactions, including communication in several modalities. Their forebrain is the largest among nonavian reptiles and they are the only order with structures resembling a cerebral cortex (Grigg and Kirshner 2015). Crocodylians are a monophyletic taxon, more closely related to birds than lepidosaurs (lizards and snakes). Studies on avian cognition have become highly prevalent in recent decades. Some birds possess complex cognitive abilities comparable to primates and other mammals, although the reptilian (including birds) and mammalian lineages split approximately 320 million years ago. Therefore, one approach to understanding the evolution of these capacities is to study the cognition of nonavian reptiles (Wilkinson and Huber 2012). Crocodylians play an important role in this endeavor due to their key phylogenetic position between birds and other amniotes. They act as a bridge between their archosaur cousins (birds) and the accumulating knowledge of cognition in lepidosaurs and chelonians (tortoises and turtles). Crocodylians also share a common ancestor with all dinosaurs, including the recent birds. Therefore, studying crocodylian cognition allows us to learn more about the lives of extinct dinosaurs, one of the evolutionarily most successful tetrapod groups.

Cognition is understudied in crocodylians. Most of our knowledge about their abilities to process information is inferred from observations and not from controlled experimental studies. In this chapter, we discuss most of the empirical literature on crocodylians in detail to showcase the many gaps which still need to be filled. We also describe various aspects of crocodylian behavior, which provide an initial level of insight into their abilities and could serve as promising starting points to develop experimental setups for future research.

## Learning

Most studies on learning capacities in crocodylians date back to the middle of the last

century. An excellent overview of this literature was provided by Burghardt (1977) and an update by Sazbo et al. (2019).

Most of the older studies are concerned with variations of the reversal learning paradigm, usually conducted in a T-maze and with the objective to avoid an aversive stimulus (heat and electric shock). For instance, small American alligator (*Alligator mississippiensis*) juveniles were placed in an arena with a heat lamp above it and two adjacent arms led to areas with cool-water pools. After establishing which arm (left or right) was preferably used by a subject to escape the heat, its preferred route was blocked with a piece of plexiglass. The alligators learned to act against their initial preference and reduced the time it took them to reach the pool over consecutive trials (Davidson Jr 1966). In a comparable experiment, spectacled caimans (*Caiman crocodilus*) learned to inhibit their initial turning preference (Northcutt and Heath 1971). The maze had a single choice point, one direction leading to a dead end and the other to a ramp to the caimans' home pen. Similar to the alligators, the caimans had to counteract their side preference, but they were not exposed to excessive heat and the results were scored as correct or incorrect choices of direction and not the time to reach the home pen. The one-year-old subjects significantly reduced the percentage of errors over five sessions. Another study used the T-maze to test which cues, spatial or visual, spectacled caimans primarily use to escape electric shock (Williams Jr 1967). The caimans had one choice point where one arm led to a trap, the other to an enclosure with a pool. Additionally, visual cues were provided with the walls of the arms having either a white or a black sheet metal panel attached to them. Seven of eight subjects learned to associate a side and a color with the goal enclosure. In the test, there was a goal enclosure at either end of the maze and for each subject, the colors on the walls were reversed. All subjects went in the same direction as in the training and did not follow the wall colors. Thus, spatial cues appear to be more salient than visual ones in spectacled caiman. In a follow-up study (Williams Jr and Robertson 1970), two groups of caiman had different training

procedures. One group learned first to associate the correct direction again by spatial and visual cues. After reaching the criterion, the correct direction was only indicated by the visual cue and could be on either side. The other group was only trained with the visual cue from the beginning. The group with visual and spatial cues reached criterion significantly quicker than the group with visual cues only. When the group with visual and spatial training had to solve the problem by the colors alone, it took them longer to reach criterion than in the previous condition. This was strong evidence that spatial cues are indeed more important. However, there probably was an effect of the training in the group with both cues, because the total number of trials in both phases (visual and spatial, and visual only) was lower than the number of trials it took the "visual cue only group" to reach criterion. While this difference was not significant, it suggests that the group with both cues did not have to learn the visual-only condition from scratch. Crocodylians are clearly sensitive to spatial cues (also see the "Spatial Cognition" section). However, in all these studies the goal was a location, an area of safety with water. It can be argued that to accurately test the importance of visual and spatial cues, the goal should have been a conceptually unrelated entity. This could have been a food reward, as crocodylians are predators and therefore unlikely to expect to find food always in the same location. Crocodylians can indeed learn to discriminate between a range of different colors as was shown in an earlier experiment using food rewards (Nickel 1960). This study ultimately had only one subject, a juvenile broad-snouted caiman (*Caiman latirostris*), but it at least serves as a proof of concept.

In a further study with the T-maze setup, spectacled caimans seemed to adopt a maximizing strategy in a probability learning task (Williams and Albinia 1972). Either side could be rewarded but with unequal probability (e.g. a side could be reinforced in 30% of the trials). Caimans reduced their proportion of choices of a side with a decreasing probability of that side being rewarded. Their performance was more similar to turtles and rats than to birds in



contemporary studies (Burghardt 1977; Williams and Albiniak 1972).

Another study employed a serial reversal learning paradigm and utilized food rewards to test learning abilities in American alligators and American crocodiles (*Crocodylus acutus*) (Gossette and Hombach 1969). The animals were trained to press against blocks on either side of an apparatus to reveal an opening through which they could receive a food reward. For each reversal, only one side was rewarded. The criterion to proceed to the next reversal was 18 passed trials out of 20 within a session. Both species showed an error reduction over consecutive reversals. Unexpectedly, the crocodiles produced significantly fewer errors than the alligators while the error curves showed a similar progression over time for either species. However, the alligators had consistently shorter latencies to manipulate the apparatus than the crocodiles. For example, in the first session of each reversal, the crocodiles took on average 43% more time to decide. Thus, the alligators were possibly more motivated to participate, which could in turn have led to a higher error number.

Crocodylians also learn to avoid chemically protected prey. Under laboratory conditions, hatchling freshwater crocodiles (*Crocodylus johnstoni*) were offered small metamorphs of the poisonous cane toad (*Rhinella marina*), which is highly invasive in Australia (Somaweera et al. 2011). The subjects were collected from an area yet uninhabited by cane toads. The test group received alternatively cane toads or crickets on feeding nights, the control group was only offered crickets. Toad-familiar crocodiles learned to avoid eating the metamorphs but still took the crickets. The toad-naïve controls were eventually offered a cane toad and they accepted them at the same rate as crickets. Hence freshwater crocodiles can rapidly learn to avoid nauseating prey that could even be lethal if consumed in large quantities or if the cane toads were much bigger. Such learning indeed appears to happen in the wild: At locations with established cane toad populations, the crocodiles were less likely to consume the invasive species than native frogs, although either prey was available at equal rates (Somaweera et al. 2011).

Chemosensory learning in crocodylians can also occur *in ovo*. When saltwater crocodile (*Crocodylus porosus*) eggs were treated with strawberry food flavoring, the hatchlings had a preference for strawberry-flavored meat pieces (Sneddon et al. 2000). Animals hatched from untreated eggs showed no such preference. This prenatally learned association was quite specific as the hatchlings from the treatment group did not discriminate between unflavored food and meat coated with orange flavoring.

## Physical Cognition

### Object Manipulation

The subduing and subsequent manipulation of prey items is probably the most common case of object manipulation in crocodylians. One challenge facing an animal is the act of picking up small objects from the ground. Due to the position of their eyes, it is often difficult to see an object or prey item if the item is not higher than their jaws. Additionally, crocodylians also lack a lot of flexibility in their neck. Thus, they twist their whole anterior body (Grigg and Kirshner 2015). This allows them to see the object or prey item and helps them grab it. When manipulating an item, crocodylians often make use of a strategy called *inertial feeding* (Grigg and Kirshner 2015). Herein, they quickly release the item and shift the grip of their jaws to a new position, relying on the item's inertia to stay put as they change the grip.

### The Potential for Tool Use

In 2013, Dinets et al. claimed to have observed a case of tool use in two crocodylian species: American alligators and mugger crocodiles (*Crocodylus palustris*) supposedly display sticks on their snouts while floating on the water surface to lure wading birds in search of nesting materials. This behavior was initially observed in captivity, at two sites where trees inside the crocodylian enclosures are used as rookeries by wild egrets and other birds. Dinets et al. (2013) reported that specimens of both species were occasionally observed balancing sticks on their snouts during



the birds' nesting season. On one occasion, an egret tried to take the stick off the snout of a mugger crocodile which led to an unsuccessful predation attempt. The authors reported anecdotal observations of American alligators catching wading birds which reached for the displayed sticks. However, none of these instances were documented and the mugger crocodile's observation is the only one described in detail. Dinets et al. (2013) further conducted a more systematic study of the behavior. They reported that American alligators also balanced sticks on their snouts in the wild and that they were more likely to display this behavior close to rookeries of nesting birds and further likelier during nesting season. The authors took these observations as evidence of tool use in crocodylians.

However, Dinets et al. (2013) did not report a single predation attempt resulting from this behavior during their systematic observations. Thus, the goal of the purported tool use was never observed. Dinets et al. (2013) also never discuss how crocodiles or alligators pick up sticks to balance them on their snouts. They only report instances where sticks were already being displayed. This raises the question of whether there was any manipulation of the supposed tool. It is plausible that the presence of rookeries, and hence birds fighting over nesting material, increases the number of sticks in the water. The sticks could have floated or dropped onto the snouts of the crocodylians by accident. However, Dinets et al. (2013) argue that this is not a likely explanation because they did not observe a higher number of sticks than normal floating in the water during these periods.

The claims of Dinets et al. received considerable attention, despite their study mainly providing a hypothesis based on anecdotes and not actual documentation of crocodylian tool use. Besides the above-mentioned issue on true tool manipulation, the stick-balancing behavior is probably not an efficient luring method. Crocodylians cannot snap for birds directly above their snout. Luring behavior usually involves releasing the tool after manipulation as was observed in wading birds. If crocodylians would let the stick float close to their head, they could launch for approaching

prey. Additionally, wading birds actively seek out areas with a high abundance of crocodylians to build their nests in the trees above them. The presence of crocodylians prevents other predators from climbing the trees and looting the nests. The birds are hence aware of the presence of crocodylians, which reduces the chances of luring to be successful.

A recent study by Rosenblatt and Johnson (2020) attempted to empirically test the hypothesis raised in Dinets et al. (2013). They investigated the stick displaying behavior at four sites with captive populations of American alligators: two with rookeries and two without. The observation periods for each site were chosen in a way to standardize the temperature and the arrival of the birds at the nesting places. Only sites with rookeries had floating sticks in the water already. Rosenblatt and Johnson added sticks to all pools to achieve equal coverage at each site and to increase the opportunity for stick balancing. They found that the alligators living at sites with no nesting birds displayed as much stick balancing as the alligators living under rookeries. In fact, at the site without rookeries and the smallest study population, alligators displayed more stick balancing than at the site with rookeries and the largest number of subjects. The latter site incidentally was also the only location where Dinets et al. reported to have observed successful predation connected to the stick displaying behavior. It was significantly colder at the smaller site without a rookery than at the other locations during the observation period; hence the alligators might have moved less and sticks had a slightly higher chance to get caught on their snout by accident. Overall, sticks were only rarely observed on alligators' snouts and usually they stayed there for less than 1 min. Instances where the "stick-balancing" behavior lasted longer than 10 min only occurred at sites with rookeries. But these observations were so rare that they are best explained with a sampling bias, as these sites had much larger alligator populations than those without rookeries.

In summary, it is plausible that few crocodylians which caught inattentive wading birds at rookery sites also happened to have

floating sticks stuck on their snouts. However, there is no empirical evidence for any crocodylian to purposefully manipulate a stick and subsequently present it on its snout with the goal to lure prey. This does not mean that crocodylians are incapable of tool use though. Empirical evaluations of anecdotal observations have a large potential to reveal more about crocodylian physical cognition in the future.

## Spatial Cognition

An important aspect of spatial cognition is the ability to return to one's familiar home range or territory, also called "homing." Several crocodylian species have been documented to home over large distances (Read et al. 2007). It is still unclear how they achieve this. Crocodylians might be able to use beacons (cues close to their goal) and landmarks (cues associated with the direction to the goal). Such cues might be sufficient in river habitats, where an animal can move up or down stream. However, crocodylians mostly travel by swimming and are hence at the lowest elevation in a landscape, which results in a suboptimal overview.

Some preliminary evidence suggests that crocodylians might be sensitive to the earth's magnetic field, which would greatly contribute to their homing abilities. In several parts of the world, it is common practice to capture nuisance crocodylians and release them in less populated areas. However, the animals will often home back to the place of capture. During relocation efforts of spectacled caimans and crocodiles in Mexico, Dominguez-Laso (2007) frequently observed such homing behavior. But he found that if magnets were taped to their cranial plates or ear flaps after capture, and removed shortly before their release, the crocodylians were unable to travel back to their place of capture. The crocodylians who had the magnets attached also moved their heads back and forth after release, as if trying to orient themselves, further indicating the presence of magnetoreception. However, to date, there has been no systematic experiment studying the presence of magnetoreception in crocodylians.

The best empirical data for long-distance navigation comes from capture–release studies on saltwater crocodiles in Northern Australia. Mature individuals can home over hundreds of kilometers. They travel along the coast, exploring several rivers, and often reach their capture site within a month. The crocodiles appear to follow external cues. The earth's magnetic field is the prime candidate, yet others are also possible, for example, stellar constellation or scents (Fukuda et al. 2019). Their homing can however be disrupted by large obstacles such as peninsulas between capture and release sites. If passing the obstacle requires extensive detouring (involving temporarily swimming in the direction toward the capture site), saltwater crocodiles appear to be unable to home. However, even substantial obstacles can be circumnavigated if the crocodile does not have to swim in the opposite direction. On one occasion, a large male saltwater crocodile was captured at the western side of the Cape York Peninsula and flown by helicopter overland (120 km) to a river on the eastern side. After spending 3 months around the release site, the animal swam along the coast up north to the cape, rounded it, and traveled south back to its capture site. It needed a month for this 411 km long journey (Read et al. 2007). The geography of Cape York (relatively straight coastlines) and its ocean currents might make it an ineffective obstacle for homing nuisance crocodiles, despite its substantial size.

Tracking data also suggests that some crocodylians might have in-depth knowledge of vast areas outside their most frequented home range. A 3.8-m long male saltwater crocodile traveled unsolicited 935 km along the coast of eastern Queensland to a different river (Grigg and Kirshner 2015). Similarly, another saltwater crocodile left its supposed home range, spent time in two different rivers, and then returned; traveling approximately 900 km in the process (Fukuda et al. 2019). Members of the same species also travel long distances to exploit temporary feeding opportunities such as fish crossing a specific river barrage during the king tide (Grigg and Kirshner 2015). Crocodylians could have learned about these feeding grounds during the decades between

leaving their hatchling pod and establishing their territory. The extent to which long-term spatial memory and other abilities play into the navigational capacities of crocodylians is a fascinating topic for future research.

## Play

In *The genesis of animal play* (Burghardt 2005), Burghardt mentions that crocodylians seem to play or are, at least, investigative. For instance, an Orinoco crocodile (*Crocodylus intermedius*) repeatedly engaged with novel objects presented to him and a young, wild American alligator swam around and snapped at trickling water from a pipe. However, all the accounts are either anecdotal or unpublished. This is also true for a more recent, extensive review by Dinets (2015). While it is very plausible that crocodylians engage in play, and many of these anecdotal accounts indicate it, the behavior needs more rigorous research.

## Spontaneous Olfactory Discrimination

In a laboratory environment, juvenile Nile crocodiles were presented with smells from petri dishes containing either meat or water (Chabrolles et al. 2017). They showed a preference for the meat stimulus if they had fasted for 2 days. In another experiment, captive, adult American alligators were presented with two paper bags containing either meat or more paper (Scott and Weldon 1990). The alligators took the meat bags more often than the controls. The alligators grabbed the control bag on several occasions but then let go without taking it; this occurred at much lower rates with the test bag. This suggests it was a challenge to go by smell alone at smaller distances and that they also used gustation to locate the food. Young American alligators also discriminate between the smells of different food items which was shown by measuring consistently different rates of gular pumping, a behavior primarily associated with sniffing in crocodylians (Weldon et al. 1992).

## Social Cognition

The different species of crocodylians vary substantially in their degree of social tolerance. All of them start in a pod with their siblings and actively seek each other's presence. For example, one study showed that hatchling American alligators preferred to group with other alligators rather than seek shelter, but they had no preference for kin over nonkin (Passek and Gillingham 1999). As adults, some species are highly territorial, while others still aggregate frequently throughout life.

All crocodylians have a rich repertoire of social signals and these are, with few exceptions, universal across the entire order. The best-studied modality is vocal communication. For instance, nest guarding female Nile crocodiles excavate their clutch when they hear their offspring call *in ovo* shortly before hatching. These "prehatching calls" are also perceived by siblings and animate them to hatch themselves (Vergne and Mathevon 2008). When swimming in the pod under parental protection, small crocodylians frequently produce "contact calls" during foraging and "distress calls" if threatened by a predator. The two calls are graded and mainly differ due to a steeper downward frequency modulation in distress calls. Hatchlings discriminate between these two calls despite their differences being subtle. In playback experiments with wild young black caimans (*Melanosuchus niger*), subjects moved into the general direction of a loudspeaker playing contact calls but froze when hearing distress calls (Vergne et al. 2011). The guarding mothers did not respond to the contact calls but approached the distress calls, which indicates that this vocalization recruits parental protection. It also carries cues to the callers' body size, which are perceived by adults. Nest guarding female Nile crocodiles preferably approach calls of smaller juveniles (Chabert et al. 2015). Contact calls in contrast appear to be strongly linked to group cohesion during foraging, which is also supported by the finding that unsated Nile crocodiles were more likely to approach an olfactory food stimulus if they simultaneously heard contact calls (Chabrolles et al. 2017).

## Cognitive Capacities Inferred by Observation

### Hunting and Feeding

Crocodylians' main hunting tactic for terrestrial animals is to lie submerged in wait for prey to drink at the water's edge and propel themselves out of the water at the opportune moment. Crocodylians must inhibit this response until the prey is in range and then respond with full force. While this is true for most predators, the instant switch from complete stasis to strike is probably most extreme in crocodylians. Detailed studies on their inhibition capacities have not been published to date.

A fishing strategy exhibited by yacare caimans (*Caiman yacare*) and saltwater crocodiles involves cruising at the water's surface and stretching out their forelimbs at right angles with raised, outward-facing hands. They then snap at fish that swim close to their heads or hands (Grigg and Kirshner 2015). A modern development within cognitive science is to not view cognition as being situated solely in the brain but to see it as embodied or even extended out into the world. This fishing strategy exemplifies the type of cognitive behaviors that this view would highlight. The crocodylian stretches its limbs out into the water to extend the area it is situated in and, thus, increases the likelihood of capturing prey.

### Nesting

Crocodylians have two modes of nesting: hole nesting and mound nesting. Approximately a third of crocodylians dig holes for their nests (Grigg and Kirshner 2015). Mound nesters include all Alligatoridae, around half of Crocodylidae, and false gharials (*Tomistoma schlegelii*) (Grigg and Kirshner 2015). The nest building can be quite involved and poses many cognitive challenges: for example, the choice of a suitable nest site. Crocodylians have temperature-dependent sex determination with only a narrow temperature range producing offspring of both sexes. Thus, the nesting site needs to have appropriate levels of warmth and moisture. Female crocodylians have been documented to abandon previous nesting grounds for sites with lower,

more stable temperatures and moisture (Grigg and Kirshner 2015). A mound is built over a period of several days or even weeks and can be comprised of a variety of materials like vegetation, soil, sand, shells, etc. The availability of materials such as these also play a role in site selection; however, crocodylians have also been shown to be flexible in this regard and make do with what is available (Grigg and Kirshner 2015). Some species are even flexible when it comes to what type of nests they build (Grigg and Kirshner 2015). Observations like these could indicate that nest building is a deliberate behavior, informed and affected by the environment.

## Conclusions

Crocodylians have striking learning and navigational abilities that are still not well understood. They also have a social repertoire which is in many ways more reminiscent of birds and mammals than other nonavian reptiles. They are a natural extension of the cognitive research conducted on birds. Due to their phylogenetic position, they may teach us much about cognitive capacities in extinct dinosaurs and the evolution of cognition in general. Cognitive research on crocodylians, particularly detailed experimental investigation, is still sparse. This is partly owed to their adult size and the accompanying handling risks. However, the cognitive capacities of most nonavian reptiles have not been studied to a comparable extent as those in other amniote taxa. The reasons for that are manifold and range from mere practical challenges to the persistence of a "*scala naturae*" inspired view of the natural world. In this chapter, we attempted to summarize the existing knowledge and highlight the potential for future research in comparative crocodylia cognition.

## Cross-References

- [Associative Learning](#)
- [Cognition](#)
- [Crocodylian Sensory Systems](#)
- [Crocodylia Communication](#)

- Crocodylia Locomotion
- Crocodylia Morphology
- Embodied Cognition
- Homing
- Reversal Learning
- Tool Use

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## Crocodylia Communication

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### Synonyms

Crocodylian Communication; Crocodilia Communication; Crocodilian Communication

### Introduction

The members of the evolutionarily ancient order Crocodylia, commonly referred to as “crocodilians” possess a wide array of communication capacities in the acoustic, visual, tactile, and olfactory domain. The behavior of crocodilians has been studied in the wild and captivity for centuries, and many visual and acoustic signals have been described in detail. Yet, the actual communicative function of these behaviors is still a topic of active research. This has several reasons. For one, crocodilians cannot easily be individually identified and followed in the wild due to their semi-aquatic lifestyle. Secondly, social interactions are usually composed of multiple signaling elements, which occur in more than one context, for example, in courtship and in territorial displays. Finally, most signals are very subtle and some of them even unperceivable to humans, such as subaudible vibrations.

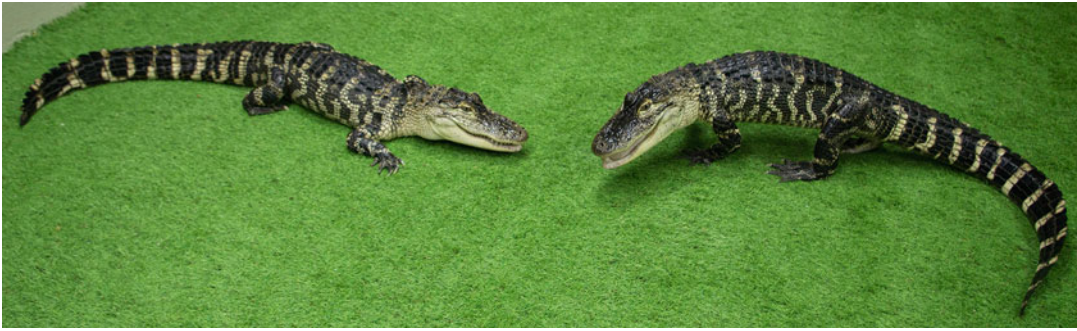
The extant Crocodylia species (at least 24, probably 27) belong to three taxonomic superfamilies: the “true” crocodiles (Crocodylidae), the alligators and caimans (Alligatoridae), and the gharials (Gavialidae). They differ vastly in adult body size and skull morphology, as well as in degree of territoriality and social tolerance. Nonetheless, crocodilians seem to share highly conserved, even partially interchangeable communication systems, which are most apparent in juveniles. All crocodilian species vocalize frequently in the first months of their lives, but

reduce their vocal activity throughout ontogeny. However, at adulthood the species differ greatly in the amount of vocal signals produced. Members of the Alligatoridae, particularly the American and Chinese alligator (*Alligator mississippiensis/sinensis*), are much more vocal than most crocodile species. The genus *Crocodylus* is especially silent and the vocalizations of some of its species have hardly ever been recorded (Grigg and Kirshner 2015). Yet, despite the dissimilar usage of acoustic signals, it is most probable that crocodilians possess one universal call repertoire (Britton 2001). All species use a multitude of visual signals for communication. Chemical signals and infrasonic vibration are still very poorly studied, but it is suspected that they play an important role in all crocodilians.

### Body Postures

Even with only parts of their body visible above the water surface, crocodilians can signal their status to conspecifics with the angle of their heads and the height of their backs. Dominant individuals raise the back of their heads disproportionately out of the water and the post-occipitals (plates caudal to the skull) are visible. In addition, a large portion of the back is above the surface (“*inflated posture*” (Garrick and Lang 1977)). Subordinate animals keep their back below the surface and hold their head low. If a dominant animal approaches a subordinate, the latter can avoid a confrontation by swimming away in this “low-profile” posture or by submerging. During a high-walk (not touching the ground with the ventral side) on land, a dominant crocodilian curves its back slightly upwards while keeping the tip of the snout low (see Fig. 1), and subordinates move out of its line of direction. Approaching a conspecific with a wide-open mouth is a clear sign of threat and aggression (Grigg and Kirshner 2015). As a sign of submission, the approached individual can raise its snout tip high up with the jaws tightly closed and displaying its vulnerable gular pouch (Garrick and Lang 1977). This signal usually has an appeasing effect and the dominant individual





**Crocodylia Communication, Fig. 1** Dominance interaction in subadult American alligators: The individual on the right displays dominance with a raised back, open mouth, and low-held nose tip. (Photo by Adrian Hiss)

gradually closes its mouth while the subordinate follows by lowering its head back to the ground.

### Tactile Communication

Crocodylians have pressure sensitive receptors in their skin, so-called integumentary sensory organs (ISO). In crocodiles, ISOs are found all over the body, while in the Alligatoridae they are limited to the jaw region (Leitch and Catania 2012). Besides their importance for hunting under water, these organs are also relevant in affiliative contexts. Particularly during courtship, mates rub their jaws slowly against each other (Vliet 2001), stimulating their own and their partner's ISOs.

### Nonvocal Acoustic Signals

A typical crocodilian threat signal is the “jaw clap,” a rapid closing of the mouth with the head lifted off the ground, which produces a loud “pop” sound (Garrick and Lang 1977). Directed at conspecifics or heterospecifics, it occurs in a variety of contexts including female nest defense and territorial intrusion. As part of a territorial display, jaw claps are often combined with “headslaps,” a behavior performed exclusively in the water wherein the head is explosively smashed onto the surface creating a splashing noise (Garrick and Lang 1977). For instance, a male American alligator will raise its head and tail out of the water, resulting in the “head oblique, tail arched”

(HOTA) position (Garrick and Lang 1977) and stay motionless for at least a few seconds. Then he will quickly open his mouth and produce a jaw clap (some individuals produce several) simultaneously hitting the water with the lower surface of the head (Vliet 1989). Following the headslap, the alligator will wag its tail ferociously from side to side thereby stirring up the water. Fainter tail wags may precede the headslap, and in some cases this display will include subaudible vibrations (SAV) and low-pitched growling. This entire behavioral series appears to mainly serve as an advertisement display announcing an individual's presence (Vliet 1989). It is performed most frequently during breeding season but may occur throughout the year. In contrast to bellowing (see below), however, it seems to be mostly directed at potential rivals and is more antagonistic. Similar forms of the headslap display have been observed across crocodilians yet with some elements differing or missing; for example infrasonic vibrations appear entirely absent in gharials (Grigg and Kirshner 2015). Before adopting the HOTA position, crocodilians frequently perform “narial geysering,” the rapid and forceful expulsion of air through the nostrils (Garrick and Lang 1977). If the snout is only slightly submerged, this results in small fountains of water droplets being thrown up (“geyser”-ing), thereby producing a loud snorting sound. Crocodilians also geyser when fully submerged, which creates a stream of air bubbles and the accompanying noises. Although narial geysering is commonly observed in territorial displays, it is also associated with courtship.

Crocodylians may swim under the head of a potential mate and blow bubbles, which then float against the gular pouch and from there past the jaw bones, caressing the ISOs (Vliet 2001).

## Vocal Communication

### “Prehatching” and “Posthatching” Calls

Crocodylians already start to vocalize while still in the egg. “Prehatching calls” can usually be heard outside the nest a few hours before hatching, but may already occur up to 5 days earlier (Somaweera and Shine 2012). These calls are acoustically distinct from calls given after hatching (“posthatching calls”) by being shorter, having less sound energy, and a lower peak frequency (Britton 2001). All these differences could be explained by the filter properties of the egg shell (Vergne et al. 2009). Calling in the egg has two probable functions. Firstly, crocodilian prehatching calls are directed at siblings and synchronize hatching. Nile crocodiles (*Crocodylus niloticus*) inside the egg respond to the prehatching calls of their siblings by calling back (Vergne and Mathevon 2008). Moreover, these calls actually stimulate the animals to hatch. Secondly, the prehatching calls are a signal to the mother to excavate the nest and aid the hatchlings to reach the water. Crocodylians build two main nest types: mounds and holes (Grigg and Kirshner 2015). Although hatchlings have been reported to escape from either without assistance, hardened substrate around the eggs can trap them, particularly in hole nests with sand (Somaweera and Shine 2012). Nile crocodile females respond to prehatching calls emerging from a substrate close to their nest by digging for the sound source (Vergne and Mathevon 2008). Immediately after hatching, young crocodylians keep calling to attract their mother. Once the female excavates the clutch, she carries hatchlings and also yet-unhatched eggs in her gular pouch to the water. There she gently cracks the eggs open and frees the hatchlings (Grigg and Kirshner 2015). However, she does not pick up any egg indiscriminately. In freshwater crocodiles (*Crocodylus johnstoni*), mothers ignore infertile

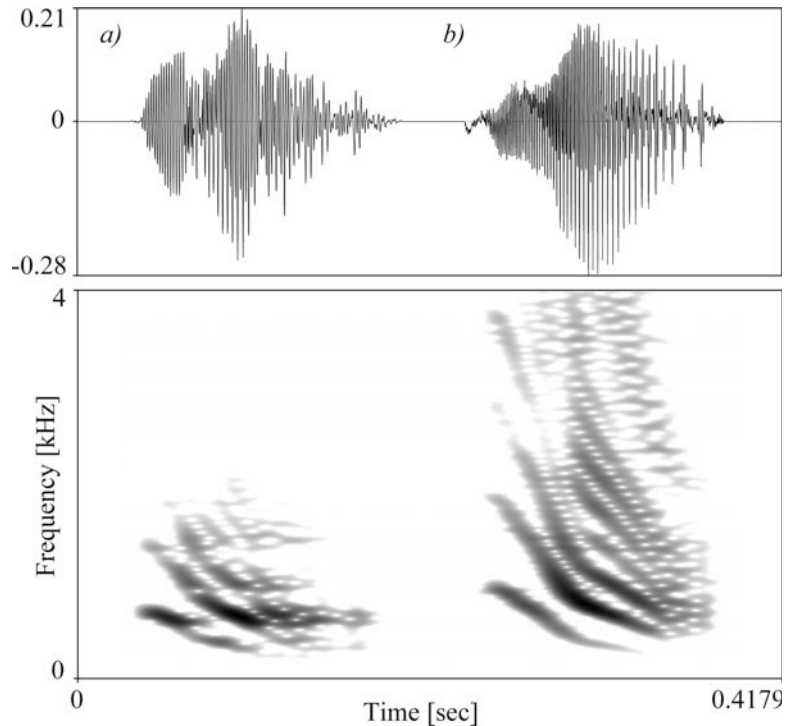
eggs (Somaweera and Shine 2012). Although it has never been investigated, it is possible that females focus their care on eggs from which they hear calls. The vocalizations of hatchlings change already in the first 4 days after leaving the egg (e.g., the fundamental frequency decreases (Vergne et al. 2007)). As will be explored in more detail below, higher frequency juvenile calls are more effective in recruiting parental attention, which could explain this finding. A hatchling might call at particularly high frequencies directly after hatching to elicit the picking up behavior from its parent, because of the high predation risk on the way from the nest to the water. There is no consensus whether these “posthatching calls” are a distinct call type. Structurally they are similar to “distress calls”; however, the context and the behavior of the hatchlings do not compare with a predator encounter.

### “Contact” Calls

Right after hatching and throughout their years as juveniles, all crocodylians frequently and spontaneously produce quiet chirps, which are commonly termed “contact calls” in the modern literature (Vergne et al. 2012). Previously they were also referred to as “grunts” or “barks” (Campbell 1973; Herzog and Burghardt 1977). Contact calls are highly stereotyped vocalizations characterized by clear harmonics and a strong frequency modulation (see Fig. 2a). A call starts with a temporally short up-sweep and ends with a longer (~75% total duration) down-sweep (Vergne et al. 2012). Contact calls are produced in a variety of nonpredator contexts, including foraging and moving in a group of juveniles (Herzog and Burghardt 1977). It was suggested that these calls serve group-cohesion because siblings forage together after hatching and prefer conspecific contact over shelter (Campbell 1973; Passek and Gillingham 1999). Young black caiman (*Melanosuchus niger*) juveniles, still guarded by their mother, responded to conspecific contact calls by gradually moving towards the sound source (Vergne et al. 2011). Contact calls are a great example for the initially mentioned potential universality of crocodilian communication. Nile crocodile juveniles do not discriminate between

**Crocodylia****Communication,**

**Fig. 2** Contact (a) and distress call (b) of American alligator juveniles of the same age, both 30 cm long (window length [s]: 0.025; dynamic range [rel dB]: 30.0)



the contact calls of conspecifics, black caimans, and spectacled caimans (*Caiman crocodilus*) (Vergne et al. 2012). Moreover, Nile crocodile and spectacled caiman juveniles show the same responses to natural contact calls and modified synthetic copies of contact calls, which only contain the first harmonic (Vergne et al. 2012). This strongly suggests that the above-mentioned frequency modulation is the key parameter defining this call type, neither amplitude modulation nor other harmonics appear to be necessary. Members of the Crocodylidae (*C. niloticus*) and Alligatoridae (*C. crocodilus*) are the most distantly related recent crocodilians. Hence, contact calls and their function are probably ancestral for the entire taxonomic order.

**“Distress” Calls**

When young crocodilians feel threatened by a predator or a hostile conspecific, they produce several “distress calls” in quick succession. These vocalizations are structurally very similar to contact calls, yet much louder, with a higher initial frequency, and a more pronounced

frequency modulation (see Fig. 2b) (Britton 2001; Vergne et al. 2011). Distress and contact calls grade into one another but are contextually distinct (Vergne et al. 2011). The main function of distress calls is to elicit maternal protection. Adult females approach the source of distress calls to fend off predators. The calls also cause responses from nearby juveniles: young black caimans react to distress calls by freezing in place and starting a chorus of distress calls themselves (Vergne et al. 2011). Mothers are much more likely to approach distress calls than contact calls. This suggests that the contagiousness of distress calling is a mechanism to increase the effectiveness of the recruitment of the mother. The responsiveness of female crocodilians to distress calls also depends on the age and size of their producers. The fundamental frequency of distress calls decreases with increasing body size of juveniles in at least five, and probably all, crocodilian species (Chabert et al. 2015). Female Nile crocodiles, either guarding their nest or hatchlings, respond with more approaches when hearing distress calls from small juveniles (total length 28–36 cm) than

from large ones (63.5–98 cm) (Chabert et al. 2015). Larger juveniles are usually no longer under maternal protection and are potential predators of smaller individuals themselves, which explains why adult females would preferably come to the aid of smaller juveniles. With increasing size, crocodilians produce fewer distress calls, probably because there are also progressively fewer predators large enough to threaten them (Britton 2001). However, subadults and even adult crocodilians utter distress calls on rare occasions, e.g., when losing a physical fight with a conspecific and trying to escape their opponent's jaws.

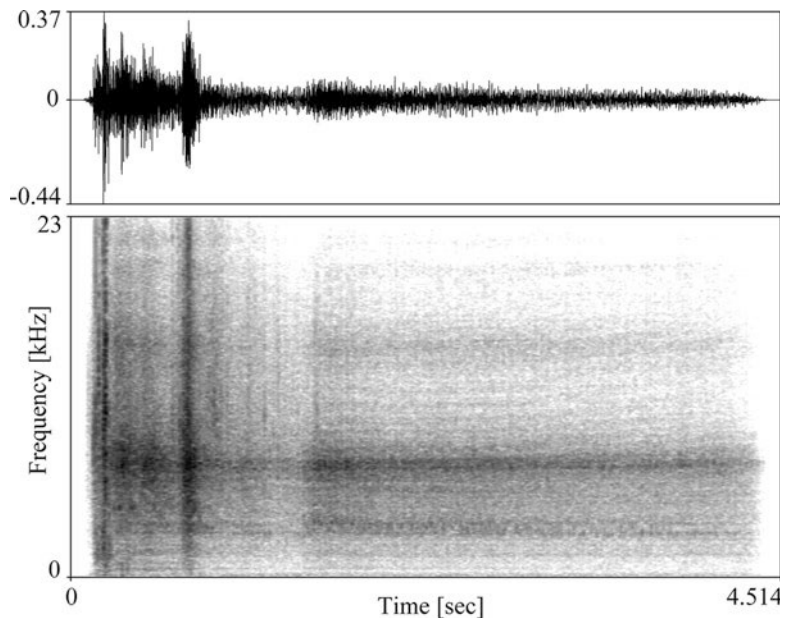
### Hissing

Most crocodilian species have been reported to hiss when threatened (Garrick et al. 1978; Vergne et al. 2009). In contrast to distress calls, hissing signals a readiness to fight and bite. Before and during a hiss, an animal would usually inflate its lungs, stand with its ventral side lifted off the ground, and the mouth slightly open. A hiss is a loud and long vocalization (>1 s) produced by a rapid expulsion of air through the glottis (Britton 2001). It is a chaotic, broadband call with no clear harmonic structure (Fig. 3).

### Bellowing and Roaring

The most conspicuous vocalizations in any non-avian reptile are the long-distance calls of crocodilians, commonly termed “bellows” in alligators and “roars” in crocodiles (Grigg and Kirshner 2015). As initially mentioned, crocodilians vary in vocal activity and bellowing/roaring are the best examples. All crocodilians seem to show a variation of this behavior, but members of the Alligatoridae bellow most frequently. It is usually performed in water, preferable in shallows, but it has been observed on land as well. The bellowing of a male American alligator is used as an example here (Fig. 4). The animal adopts the HOTA position before bellowing; if on land, the tail remains on the ground, but the head is maximally raised. The alligator lifts its body out of the water, the head is at the highest point, and the back and the neck are above the surface. During this motion, he audibly inhales maximally; a constriction of the gular pouch suggests that he additionally pushes air down into the lungs. Then the alligator lowers itself into the water until the entire back is submerged. In this position, he produces subaudible (infrasonic) vibrations (SAV), which can be felt by a human standing 20 meters away. The vibrations are so strong, they make the water seemingly

**Crocodylia  
Communication,  
Fig. 3** Hiss of an adult  
Siamese crocodile,  
*Crocodylus siamensis*  
(window length [s]: 0.05;  
dynamic range [rel dB]:  
55.0)

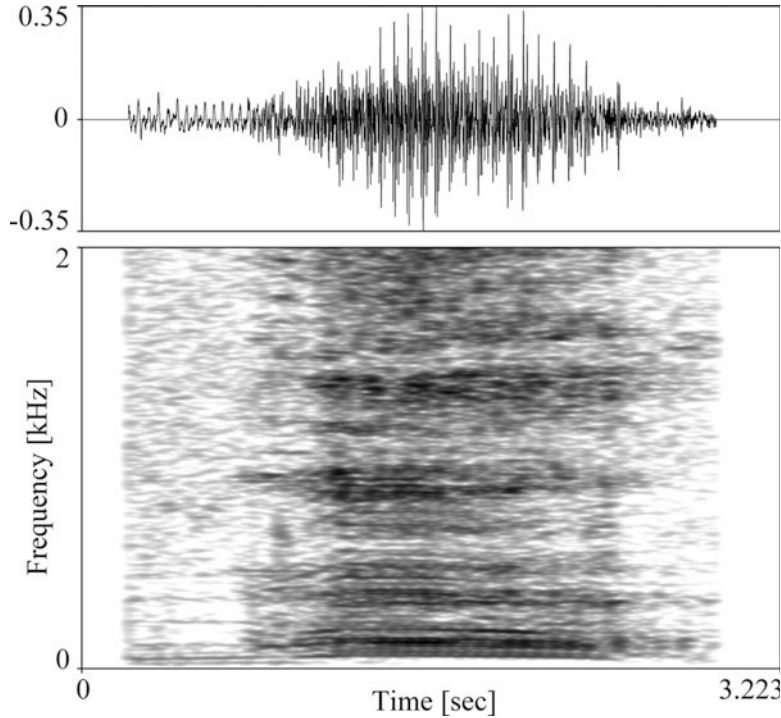






**Crocodylia Communication, Fig. 4** Bellowing sequence in a male American alligator (from left to right): Deep inhaling, producing the water dance, audible bellowing. (Photos by Stephan Reber)

**Crocodylia Communication, Fig. 5** Bellow of an adult male American alligator; notice the artifact of subaudible vibrations in the first quarter of the recording (window length [s]: 0.15; dynamic range [rel dB]: 40.0)



boil over the alligator’s back: droplets of water are sprayed upwards above the torso. This phenomenon is commonly referred to as the “water dance” (Vliet 1989). Directly following the SAV, the alligator produces the loud bellow, a rumbling, low-pitched, pulsed vocalization (Fig. 5). Usually the animal will inhale again after the first call, sink back into the water, and produce a second one. A bellowing bout commonly contains three to four calls, which grow shorter and less powerful within the series. The bellowing behavior is

sexually distinct as females do not produce SAV and hence display no water dance. However, both sexes are equally acoustically active (Garrrick et al. 1978). There are not enough empirical data on bellowing and roaring to conclude that this sexual dimorphism holds up across crocodilians. It is also uncertain whether all species even produce SAV, although it appears to be widespread (Grigg and Kirshner 2015). As crocodiles have ISOs all over their body, it is conceivable that SAV are even more important in Crocodylidae than

Alligatoridae. The actual communicative function of bellows is still not conclusively clarified. The behavior is shown year-round with the highest occurrence during the mating season. It precedes rival confrontations as well as mating. Therefore, it is commonly thought to be a territorial and a courtship display. Yet, bellowing is a contagious behavior causing animals to aggregate and to form bellowing choruses, e.g., in Chinese alligators (Wang et al. 2009). Aggression is rare in these situations, making it unlikely that it mainly serves territoriality. Bellowing and roaring are hence best described as advertisement calls (Dinets 2011). They potentially have similar function as self-aggrandizing displays in birds, which are the closest living relatives of crocodilians. It has been suggested that bellows advertise a caller's physical attributes (Garrick et al. 1978), e.g., body size. Acoustic cues to size in vocalizations of mammals are usually encoded in the distribution of the resonances ("formants") in the sound spectrum (Charlton and Reby 2016). The discovery of formants in the bellows of a female Chinese alligator was the first evidence of its kind in any nonavian reptile (Reber et al. 2015). In American alligators, the distribution of formants in bellows is strongly negatively correlated with a caller's body size (Reber et al. 2017). For instance, the distance between the first and the second formant in a smaller male (total length: 298 cm) is ~300 Hz, while in a larger male (390 cm) it is ~140 Hz. Lower formants hence indicate larger individuals. The dominant frequency is not an indicator of body size. In some other animals, e.g., red deer, callers actively extend the length of their vocal tract during vocalizations to produce lower formants (Charlton and Reby 2016). There is indirect evidence that American alligators do the same. The vocal tract during bellowing consists of the nasal and the pharyngeal cavity, and in order to extend it to its maximum length, an alligator could pull the larynx down towards the sternum. During the audible bellow, there is clear muscular tension in the pharyngeal region and a pouch is forming around the location of the larynx. This pouch probably contains the massive tongue, which is directly connected to the hyoid cradling the larynx (Riede et al. 2015). If alligators indeed pull the

larynx down, this behavior is probably easier to perform on land than in water (e.g., due to buoyancy). The bellows of American alligators have lower first formants if produced on land than in water, and the formant distribution on land indicates a more uniform tube-like ("stretched") shape of the vocal tract (Reber et al. 2017). Taken together, these findings confirm the hypothesis that bellows and roars are advertisement calls.

### Other Vocalizations

Crocodylians produce a range of other vocalizations which have received little attention to date. Adults of several species produce very low-pitched and silent grunts in close proximity, which probably serve as affiliative signals. Females guarding offspring frequently utter low rumbles, which were sometimes referred to as "burp-trill" (Hunt and Watanabe 1982) and seem to attract the hatchlings. When seized, young crocodilians may produce "annoyance calls" (Britton 2001), broadband high-frequency vocalizations, which are acoustically distinct from 'normal' distress calls; it is unclear whether they might be distress calls with altered properties due to the effect of seizing. Male Indian gharials (*Gavialis gangeticus*) have a bulbous outgrowth, a "ghara" (Hindi: "pot"), above the nostrils. It amplifies loud snorting hisses (Whitaker 2007), that might be an equivalent of bellowing/roaring in other crocodilians. Whether the "ghara" contains vibrating tissue or acts as a cavity resonator is unknown.

### Subaudible Vibrations (SAV)

The water-dance before bellowing in male alligators and similar signals in other crocodilians are clear indicators of strong vibrations below the human hearing range, hence called "subaudible vibrations" or "infrasound." Yet, these SAVs can be felt by humans, similar to the low bass from a large loudspeaker. There is substantial sound energy in the range of 16–25 Hz in male American alligator bellowing sequences (Todd 2007). Because SAVs are produced in the bellowing and roaring context, they almost certainly serve a communicative function. However, too many



variables are as of yet unknown and definite conclusions premature. It is neither clear how crocodilians produce infrasound nor whether they can actually hear it. Large mammals can produce infrasound with passive motions of their massive vocal folds alone, yet the vocal folds of crocodilians are minute in comparison and most probably cannot vibrate at such low frequencies. Crocodilians might produce infrasound with muscles in other body parts, e.g., in the flanks. The crocodilian ear, similarly to all reptiles including birds, is less sensitive to high frequencies compared with mammals. The hearing of young American alligators is very similar to birds (Higgs et al. 2002) and hence not very likely to perceive airborne infrasound, although adult individuals have never been tested. It is also possible that crocodilians do not actually hear SAVs but might perceive them via their ISOs alone. Given that only male American alligators produce a water dance before the audible bellow, this signal could consist of two distinct components: the presence or absence of the water dance advertises the caller's sex and the formants in the audible sound the caller's size (Reber et al. 2017).

## Olfactory Communication

The most visually apparent difference between an avian and a crocodilian brain is the large olfactory bulb in the latter (Vergne et al. 2009). Crocodilians have an acute sense of smell and it is probable that they also use it for social communication. There are three main types of skin glands in crocodilians: mandibular glands, paracloacal glands, and dorsal integumentary glands. They secrete a large variety of chemicals (Grigg and Kirshner 2015; Weldon et al. 1990), including some which are found nowhere else in nature, such as the aromatic ketone dieneackeron in the paracloacal glands of West African dwarf crocodiles (*Osteolaemus tetraspis*) (Whyte et al. 1999). As with other forms of crocodilian communication, olfactory signals are well described, but experimental data clarifying their function are still lacking. The mandibular glands are used during courtship, when males and females rub their

heads over each other (*C. niloticus* (Kofron 1991), *A. mississippiensis* (Vliet 2001)), suggesting that they serve a pheromonal role. The secretions from the paracloacal glands smell musky and float on the water surface. There are indications that they are used in territorial defense as they can be detected following the headslap behavior in American alligators (Vliet 1989). The dorsal integumentary glands are least well understood. They are found in several *Crocodylus* and both alligator species and seem to be most active shortly before and after hatching. After a few years posthatching, the glands seem to stop secreting fluids (Grigg and Kirshner 2015). These secretions are hence thought to play a role in early mother-offspring and/or sibling interactions (Grigg and Kirshner 2015).

## Conclusion

Crocodilians show a wide range of communication behaviors. Although many of them have been described in detail, their functions are in most cases still unclear. Further experimental evidence is required for a better understanding of Crocodylia communication. For example, it is now known that bellows are honest signals of body size; however, it has not been shown that the animals are actually sensitive to these cues. Acoustic communication in crocodilians is a particularly important field of study for comparative research: the crocodilian sound source is the larynx just like in mammals, yet they have a very avian-like brain structure. Therefore, crocodilians are an interesting intermediate model to study communication and cognition across amniotes.

## Cross-References

- [Communication](#)
- [Crocodylia Cognition](#)
- [Crocodylia Locomotion](#)
- [Crocodylia Morphology](#)
- [Crocodilian Sensory Systems](#)
- [Referential Communication](#)
- [Squamate Acoustic Communication](#)

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## Crocodylia Locomotion

► [Crocodylia Locomotion](#)

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## Crocodylia Morphology

► [Crocodylia Morphology](#)

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## Crocodylian Communication

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## Cross-cultural

► [Human Infancy and Childhood](#)

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## Cross-Fostering Studies

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### Introduction

A pulp magazine, *The All-Story*, published Edgar Rice Burroughs's *Tarzan of the Apes* in 1912. Its

fictional protagonist stands as a familiar icon of what we now call cross-fostering. As the story's plot unfolds, an ape adopts and nurtures the Earl of Greystoke's orphaned infant son, who matures to lead his troop of nonhuman rescuers. Burroughs later asserted, "I was mainly interested in playing with the idea of a contest between heredity and environment" (Taliaferro 1999). To better understand those two influences on phenotypic development, twentieth-century science embraced cross-fostering both conceptually and procedurally.

Conceptually, cross-fostering occurs when offspring are reared not by their biological mother/parents but by foster parents of the same or a different species. As a procedure, offspring are placed under the care of foster parents whose genetic relatedness to them researchers deliberately manipulate. Cross-fostering allows researchers to detect similarities and differences between the biological parents and the foster parents observed in the offspring. Further, it operationally establishes a means to assess hereditary and environmental consequences, as well as their interaction. An extensive literature exists on this topic.

The term cross-fostering underwent a dramatic uptick in the research literature during the 1960s. Few studies before that decade used the term even when investigating cross-fostering effects. Its unheralded coinage, though apt, compels those conducting literature searches to choose their keywords with diligence.

### Cross-Fostering and Animal Husbandry

During our own species' prehistory, the practice of domesticating other species likely included not only intentional breeding, but perhaps cross-fostering as well. In research literature, the term appeared with increasing frequency in mid-twentieth-century reports, especially in agricultural science. Under controlled conditions, some domesticated species rear and even nurse the offspring of alien species with behavioral outcomes supporting claims about the importance of early experience (Fox 1969).

## Ethology

It was also in the mid-twentieth century that ethology, the comparative study of behavior, emerged as a subdiscipline of zoology. It encompasses a broad diversity of methods, but its roots lie in the practices of field naturalists, observing animals where they found them. As they refined their methods, they began to examine, and eventually manipulate, parent-offspring relationships.

Cross-fostering sometimes does occur in nature. Both ancient Vedic texts and Aristotle noted that cuckoos deposit their eggs in other birds' nests to be incubated and reared by non-cuckoos. Payne (1977) described a number of such avian brood parasites. The adaptive payoff of exploiting hosts' parental investment seems obvious, but other reports document apparently accidental cross-fostering among birds. For example, two species of Australian cockatoos may nest in the same tree hollow and deposit eggs in the same clutch (Chapman and Rowley 1986). When the larger species eventually displaces the smaller in disputes over the nest, the winners then rear the hatchlings of both species. The cross-fosterlings' calls, diet, and social behavior closely resemble their foster parents and may even account for reported cases of hybrids. This outcome is interesting because, as Tinbergen (1989/1951) noted, some species kill offspring they do not recognize as their own.

Ethologists asserted that imprinting produces effects like those cases, described above, where parents wind up rearing the young of an alien species. Eckhard Hess (1959) summarized early research on imprinting, which is said to occur when innately organized responses to specific releasing stimuli promote lasting behavior patterns. Critical periods can be important insofar as the timing of stimulus onset constrains response activation. To illustrate with a common example, newly hatched ducklings soon follow the first moving object they encounter. That moving object, the releasing stimulus, is normally their mother. But it could in fact be any moving entity and loses the power to trigger proximity-seeking behavior when stimulus exposure is delayed by just a few days. The lasting effects of

imprinting include adult affiliative behavior. Douglas Spalding (1954/1873) rightly deserves the credit for first documenting the phenomenon now known as imprinting and for cross-fostering some of his subjects, probably inadvertently.

Deliberate cross-fostering between bird species by Whitman (1919) and his protégé, Craig (1908), demonstrated mating preferences manifested in adulthood. Upon reaching sexual maturity, birds tended to court members of their foster parents' species. The contributions of these two men, along with the earlier work of Spalding, laid a foundation for the emergence of modern ethology.

## Epigenetics

Since Conrad Waddington (1942) coined the term epigenetics, both biology and psychology have endorsed its explanatory value. Broadly construed, it seeks to identify bi-directional interactions between hereditary and environmental factors that influence phenotypic outcomes. Numerous studies using cross-fostering procedures have contributed to the growing field of epigenetics.

That body of cross-fostering research considers potential genetic and environmental influences on many variables, from behavior, cognition, and emotionality to socialization, stress response, and disease susceptibility (McCarty 2017). Most of the effort focused on rodents, mammals whose life cycles facilitate research of this type. A few other researchers studied non-human primates. Those studies reported both between-species and within-species crosses with subjects living in captive colonies. From an epigenetic perspective, their reported behavioral outcomes show cross-fostering's merits in efforts to identify possible interactions of heredity and rearing environment.

One between-species cross-fostering attempt placed rhesus and Japanese macaque infants with foster mothers of the opposite species. They lived in small social groups occupying separate outdoor enclosures. The attempt's success rate supported the procedure's potential for altering

environmental experience without risking adequate maternal care or infant well-being (Owren and Dieter 1989). However, subsequent analysis of long-term effects on the cross-fosterlings' vocal development produced equivocal results when their food calls were judged to fall within species-typical normal ranges (Owren et al. 1992).

A second attempt compared the development of hand preference, as measured by a simple bimanual task, among chimpanzees raised from infancy by their biological mothers with a comparison group of chimpanzees nursery-raised by humans (Hopkins 1999). Both groups were comparably large and composed of individuals identified within the captive colony from existing records (i.e., mother vs. nursery-reared). By the time of testing, all were living in colony enclosures. Hopkins (1999) concluded that chimpanzees display population-level right-handedness unaccounted for by genetic factors. A later replication with a different sample produced similar results (Hopkins et al. 2003), and a subsequent meta-analysis reached the same conclusion for both chimpanzees and bonobos (Hopkins 2006). Although the absence of cross-fostering effects in Hopkins (1999) and Hopkins et al. (2003) did support the conclusions in this series of studies, it may be wise to bear in mind methodological difficulties associated with cross-fostering (Gardner and Gardner 1998, pp. 7–8; Winney et al. 2015).

Stephen Suomi (1997) reported results based on within-species crosses of rhesus macaque infants with either aberrant or normal temperaments. Adverse consequences tend to befall youngsters who exhibit high reactivity or impulsivity. High-reactive monkeys respond to environmental disruptions with agitation and physiological arousal of greater magnitude than their normal peers. Impulsive individuals risk social encounters with conspecifics that escalate into self-injurious aggressive incidents, or they may suffer injuries if they misjudge treetop leaps. Although a minority of young monkeys display such temperamental deviations, long-term consequences can seriously disadvantage them. Worse, both traits are highly heritable. By selectively breeding infants likely to display those traits and then cross-fostering them with

unrelated, experienced mothers, the potential effects of two maternal styles could be assessed. Foster mothers were pre-selected based on their maternal behavior, and the cross-fosterlings were reared with either highly nurturant mothers or with mothers whose maternal behavior fell within the normal range. From within their first 4 days of life until 6 months of age, the infants were reared by foster mothers before moving to larger groups in the captive colony. The at-risk cross-fosterlings reared by nurturant mothers developed more secure attachments than normal infants raised by either nurturant or control mothers. Those at-risk cross-fosterlings reared by control mothers however displayed the expected behavioral deficits. Remarkably, the monkeys foster-reared by nurturant mothers became socially adept and could even achieve high social status in their groups. Those reared by control mothers achieved no such success. Further, at-risk females acquired the nurturant maternal style of their foster mothers, thereby passing on the benefits of that style to the subsequent generation. Thus, cross-fostering of this sort influences heritability of a nurturant maternal style.

Much contemporary epigenetic research focuses on our own species. Adoption studies arguably illustrate within-species cross-fostering applied to gauge the heritability of a variety of human attributes and behaviors. For human hand preference, such family studies once supported a view that heredity was the more powerful determining factor (Carter-Saltzman 1980). Recent molecular genetic research has tempered that view. Asymmetries of gene expression in the central nervous system apparently arise via interaction with environmental changes from conception through childhood to epigenetically mediate phenotypic variance in handedness (Schmitz et al. 2017).

## Apes Cross-Fostered by Humans

Burroughs's Tarzan novel capitalized on centuries-long interest on the part of scholars and laypeople alike in purported cases of "wild children." By the eighteenth century, such alleged cases of feral children, perhaps reared by



nonhumans, began to provoke serious scrutiny and debate (Benzaquén 2006; Newton 2002). At the close of that century, Victor, the Wild Boy of Aveyron, became the subject of an intensive investigation which left many questions unanswered (Lane 1976; Shattuck 1980). Believing psychological science could answer some of those questions, Winthrop Kellogg chose an empirical approach. After considering the theoretical and ethical ramifications of existing historical accounts, and a more recent report on the “wolf children of Midnapore,” he designed an experiment that cross-fostered a chimpanzee to human parents (Kellogg and Kellogg 1933). Kellogg and his spouse, Luella, assumed the roles of parents and collaborators.

A zeitgeist clearly had inspired the Kelloggs. Not long before Burroughs created his famous fictional character, Lightner Witmer (1909, p. 205) predicted that “within a few years chimpanzees will be taken early in life and subjected for purposes of scientific investigation to a course or procedure more closely resembling that which is accorded the human child.” Echoing Witmer’s emphasis on scientific procedure, Kellogg and Kellogg (1933, p. 12) insisted “. . . that the *psychological* as well as the *physical* features of the environment be entirely of a human character.” Beginning in mid-1931, they simultaneously raised, observed, and tested a female infant chimpanzee alongside their own son. The 9-month project collected a staggering amount of data, which ironically may have interfered with its cross-fostering goals. Most children do not experience such a rigorous testing regimen as routine aspects of their physical or psychological environments. Nevertheless, the Kelloggs’ cross-species comparisons present a remarkable set of similar developmental patterns. In a number of ways, the chimpanzee outperformed the child, for example, learning certain tasks more quickly. That might be attributed to her more rapid rate of maturation, but the human behaviors she acquired clearly depended on her experience in a human environment. With respect to language, her comprehension at first exceeded the boy’s. However, she never matched his ability to imitate vocalizations or ultimately to speak.

Research in Russia foreshadowed the Kelloggs’ comparison of child and chimpanzee. Although it did not follow the rigorous specifications for cross-fostering they set, the same aforementioned zeitgeist perhaps inspired it. In 1913, a young student at Moscow’s Women’s Advanced Courses Institute began observing the behavioral, cognitive, and emotional development of an infant chimpanzee (Ladygina-Kohts 2002/1935). Until his death in 1916, that chimpanzee lived with Ladygina-Kohts and her spouse, accompanying them on walks through the town, riding in carriages or on trains, and visiting wooded areas. He was however caged in a separate room at night or when his caregivers fulfilled other obligations. Ladygina-Kohts’s detailed observations preceded similar observations of her own son, born in 1925. Sequential observational periods of a chimpanzee and a Russian boy yielded important developmental comparisons. Unfortunately, a full English translation of her work did not appear until 2002, at last allowing Western scholars to compare it with that of the Kelloggs.

Neither the Kelloggs nor Ladygina-Kohts reported successful language production from their subjects. Addressing that lingering question became one of the goals of Keith and Cathy Hayes when they adopted a 3-day-old chimpanzee in 1947 (Hayes 1951). For 7 years, they raised her in their Florida home near the Yerkes Laboratories of Primate Biology where she was born. Their efforts paid off. Their subject’s vocal accomplishments and deficiencies established useful parameters for future research. By the time of her illness-induced death, young Viki could say seven “words,” four of which were crudely pronounced English words, primarily to make requests (Hayes and Nissen 1971). She also effectively communicated with gestures and pictures mounted on cards. Her behavior differed from both wild and captive chimpanzees in many noteworthy respects, and her spoken vocabulary exceeded that of any chimpanzee previously studied. Nevertheless, an inescapable conclusion emerged that speech was not the appropriate communication medium to explore with chimpanzees. The claim that human speech depends on specific vocal tract structures (Lieberman 1968), if valid,



may deprive nonhuman primates of the vocal capacity to produce it.

Allen and Trixie Gardner (1994) applied the Hayes's approach in two sequential projects cross-fostering a total of five chimpanzees. The first project began in 1966 and lasted 51 months with a single subject. The second began in 1972 and continued until 1981. All the chimpanzees lived approximately as human children do and were exposed to American Sign Language (ASL), the language of deaf culture in North America. Detailed daily records and a number of controlled tests documented the acquisition of ASL signs and their use by the five. The Gardners reported consistent year-by-year vocabulary growth, although by age 3, the chimpanzees fell behind human 3-year-olds, with incremental gaps each succeeding year.

The Gardners' success spawned several attempts at replication, which met the high cross-fostering standards set by the Kelloggs and the Hayeses to varying degrees. Some of those projects studied other ape species (Miles 1990; Patterson 1978), while another project again studied a common chimpanzee, relying heavily on an operant approach (Terrace et al. 1980). The latter generated considerable controversy with evidence the young chimpanzee produced ungrammatical strings of signs, many of which seemed prompted by human interlocutors. The authors also questioned the validity of other projects' published findings, arguably overstepping the bounds of scientific propriety.

It is unlikely other cross-fostering studies with apes will be conducted, and rightly so. Many researchers now acknowledge that the same ethical argument offered by the Kelloggs forbidding cross-fostering human infants to parents of other species applies in reverse. Should humans remove intelligent beings from their natural mothers for the purpose of scientific inquiry? I believe I am not alone in stating the answer is no.

## Cross-References

- ▶ [Affiliative Behaviors](#)
- ▶ [Attachment](#)

- ▶ [Behavioral Genetics](#)
- ▶ [Critical Periods](#)
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- ▶ [Yerkes Primate Research Center](#)

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## Cross-modal Integration

### ► Cross-Modal Transfer

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## Cross-Modal Transfer

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## Synonyms

[Cross-modal integration](#); [Multisensory integration](#)

## Definition

Cross-modal transfer is the transfer of information from one sensory modality to another sensory modality.

Cross-modal transfer is a difficult concept to measure due to its somewhat abstract nature. While its definition is rather simple, that is, the transfer of information from one sensory modality to another, examining it can prove to be rather complicated. This may be in large part due to the complications of separating sensory modalities experimentally, or in simpler terms, verifying cross-modal transfer has actually occurred. While the definition may be self-explanatory, the function of cross-modal transfer may be unclear. This concept suggests humans (and other species) take information from multiple sensory modalities and create a holistic, globally accessible version of objects/surroundings. This serves as a way for cognitive systems, in multiple species, to take information from different sensory modalities and convert them into a universal mental representation of those objects. Note the specific deviation from the term *mental image*, as cross-modal transfer goes outside of the visual domain, including auditory and haptic domains as well.

As previously mentioned, cross-modal transfer can be somewhat challenging to observe. Speaking generally, the typical formula for measuring this concept goes as follows: learn information in one modality, restrict the initial encoding modality, then test retention through a second, different modality. Dopjans, Wallraven, and Bulthoff (2009) examined this effect through the lens of visual and haptic face recognition. Facial recognition in the visual domain is a skill repeatedly practiced through most aspects of social life, while haptic facial recognition is a skill that receives little to no attention. The authors found haptic recognition performance that exceeded expectations, as well as good cross-modal transfer from both modalities. This concept of visual to haptic/tactile transfer extends outside of humans, as Solvi, Al-Khudhairy, and Chittka (2016) demonstrated a similar ability of object recognition within bumblebees. These findings suggest not only are mammals capable of producing universal representations of the world around them, but insects may also possess the same capabilities. Other mammals are capable of such transfer as well, as exemplified by multiple studies conducted on primates including chimpanzees and baboons. Martin-Malivel and Fagot (2001)

demonstrated cross-modal integration leading to conceptual categorizations with baboons. A similar ability was shown in chimpanzees by Savage-Rumbaugh, Sevcik, and Hopkins (1988), across a wider range of cross-modal transfer types. Schreurs and Kehoe (1987) assessed the degree of training required to elicit a cross-modal transfer within rabbits, finding that as few as two rounds of conditioning may be sufficient. There are limitations to this phenomenon, though, particularly involving auditory to visual transfer, as Lapid, Ulrich, and Rammsayer (2009) were unsuccessful in finding any evidence of a transfer from the auditory domain to the visual domain.

To understand the mechanisms involved in cross-modal transfer, it may be useful to examine the neural correlates proposed by this literature. Calvert (2001) conducted a review of functional neuroimaging suggesting specific roles for multiple areas, including the superior temporal sulcus, the inferior parietal sulcus, regions of the frontal cortex, the insula cortex, and the claustrum. Importantly, the specificity and networking of these regions relies upon the experimental methods used. However, there is a degree of consistency to be noted across a large body of the literature in this area. In one example, Hadjikhani and Roland (1998) examined regions involved in tactile and visual representations. Here, several of the aforementioned regions of the brain were highlighted in the transfer of tactile to visual (and vice versa), however, the right insula-claustrum was specifically highlighted for its supposed role in cross-modal matching. The claustrum's function as a sort of distribution center for multimodal cortical projections, as well as its PET activation during the study, led the researchers to believe it may play an important role in cross-modal transfer.

The implications of cross-modal transfer are somewhat broad. In regard to animal cognition, these findings seem to be very telling. Some of the aforementioned literature seems to suggest that animals, from large brain mammals to common insects, are capable of these cross-modal representations of objects in their brains. This suggests animals are capable of forming mental images and spatial representations of their surroundings. Expanding research along these lines could be very useful in providing insight into the

similarities between human and animal cognition. With regard to expanding the human cognition literature, there is still much to be found in confirming both the localization of cross-modal transfer, as well as validating the existence of cross-modal transfer across different domains.

There are limitations with some of the existing research. Specific to the findings involving neural correlates, there is often low statistical power/sample sizes, which is a problem not limited to, but noted especially in neuroimaging studies (Bossier et al. 2020). It is possible the variations in findings across these referenced studies could be due to a general lack of reproducibility. There are also slight variations in the specific regions activated during cross-modal activities. These variations may reflect the diversity of experimental paradigms used.

Future research ought to expand some of the previously mentioned literature. There is potential expansion into using neural networks and artificial intelligence to increase our understanding. For example, Albanie, Nagrani, Vedaldi, and Zisserman (2018) have used neural networks to label video data with emotional speech by facial recognition software. Overall, the literature on cross-modal transfer is expansive across both humans and animals, yet replications can provide more power to existing findings.

## Cross-References

- [Classical Conditioning](#)
- [Cognition](#)
- [Encoding](#)
- [Laboratory Research](#)
- [Navigation by Honey Bees](#)
- [Object Permanence](#)
- [PET](#)
- [Visual Perception](#)

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## Crossover

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## Synonyms

[Chromosomal recombination](#); [Nondisjunction of chromosomes](#)

## Definition

Crossing over is exchange of genetic material between homologous chromosomes during meiosis stage.

## Crossing Over

Crossing over involves exchange of genetic material between homologous chromosomes (having same genes at the same loci, but possibly different alleles). The exchange of chromosome occurs during meiosis and can be visualized as chiasma that interlocks homologous chromosomes. This is visible in form of physical overlapping between chromosomes and works opposite to the polarizing forces of the meiotic spindle (protein structures that divide the genetic material in a cell) as shown in Fig. 1. Crossing over prevents premature segregation of homologous chromosomes during first meiotic cycle (Page and Hawley 2003). Problem or interruptions in crossing over may lead to abnormalities like gene linkage, nondisjunction of chromosomes, aneuploidy, etc. (Hassold et al. 2009). Low rates of crossover and abnormal patterns of crossover are known to be associated with infertility in multiple organisms (Koehler et al. 2002).

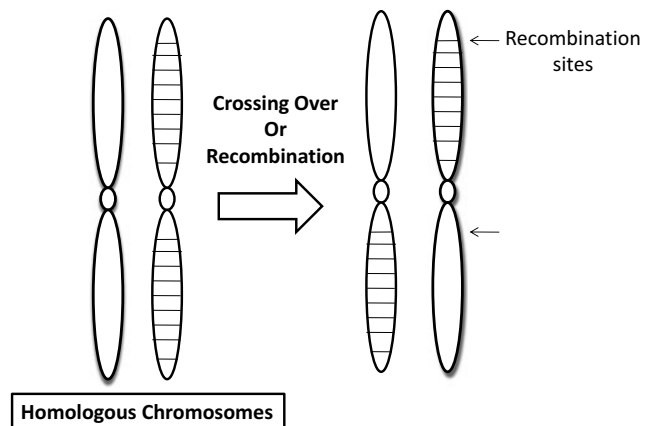
The genetic significance of crossing over is to create varying combinations of alleles and determining primary determinant of haplotype (genetic characters located on same chromosome) diversity within populations (Pritchard and Przeworski 2001). Also, crossover results in decoupling of highly fit alleles, and therefore can reduce strong association between alleles so as to facilitate natural selection (Hill and Robertson 1966).

The frequency of crossing over is quite dependent on multiple biological forces like

concentration of rate limiting enzymes involved in meiotic DNA repair, the strength of the mutagenic effect of recombination, and the rate at which recombination breaks up high fitness haplotypes. The recombination rates are also determined by essentiality of crossovers for chromosome segregation. Because of these varying factors the crossover rates are highly variable across mammals, plants, and animals. The closely related species of house mice may show differences in crossover rate by around 30% (Dumont 2017). Recombination arising due to crossover may be due to several contributing factors such as environmental exposures and involvement of individual genes (Chowdhury et al. 2009). Environmental factors include exposure to xenobiotic compounds (foreign chemical compounds) and various stress-causing agents (Vrooman et al. 2015) and various measures of stress (Singh et al. 2015). In case of diploid chromosomes, the chromosome architecture plays an important role in deciding recombination rate. A minimum of one crossover per chromosome is required for correct chromosome segregation. However, there are evidences suggesting at least one crossover per chromosome arm. The crossover analysis in voles, deer mice, shrews, and rhesus macaques reveal a high frequency of achiasmate chromosome (lacking chiasma in meiosis) arms undergoing crossing over (Dumont 2017). Besides genes and environment, the evolutionary changes in the organisms also play a crucial role in recombination rate and crossing over occurrence.

### Crossover,

**Fig. 1** Crossing over between two homologous chromosomes



## Cross-References

- [Candidate Gene](#)
- [Gene Frequency](#)
- [Geometric Encoding](#)
- [Quantitative Genetics](#)

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## Crustacean Exploration

- [Arthropod Navigation](#)

## Crustaceans

- [Arthropod Cognition](#)

## Crypsis

- [Camouflage](#)
- [Cryptic Coloration](#)

## Cryptic Coloration

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## Synonyms

[Concealing coloration](#); [Crypsis](#); [Obliterative coloration](#)

## Definition

Colors and color patterns that reduce the risk of an object being visually detected when it is potentially perceivable to an observer.

## Introduction

Avoiding detection by undesirable viewers is a key antipredator strategy, and the evolutionary solutions to this challenge are myriad. Crypsis – the use of color patterns to minimize the probability of detection – is the most prevalent form of visual camouflage and has served as an exemplar of adaptation since the inception of modern evolutionary biology (Poulton 1890). The seminal work of Abbott Thayer (1909) in *Concealing Coloration in the Animal Kingdom* and Hugh Cott (1940) in *Adaptive Coloration in Animals* lays the formal foundations for the study of crypsis, and camouflage more generally, which has since burgeoned into an active field of inquiry spanning biology, art, and technology (Behrens 2009).



## Mechanisms

The functions of cryptic color patterns have often been considered obvious, though a breadth of work continues to detail the subtle complexity of this mode of defense. Confusion surrounding the language used to describe such colors has complicated efforts, though recent calls to focus on the perceptual effects, rather than the superficial appearance, of color patterns, have proven fruitful. Stevens and Merilaita (2009) take a broad view of crypsis and summarize six principle mechanisms:

1. *Background matching* describes the use of color patterns that approximate the appearance of the broader viewing background (in color and/or brightness) and so allow an object to blend in to its surrounds.
2. *Self-shadow concealment* is achieved via countershading, wherein darker colors adorn an object's upper side and lighter colors cover its underside. This can obscure the presence of conspicuous shadows generated by directional light sources (typically the sun), which can reveal the location of otherwise inconspicuous objects.
3. *Obliterative shading* is also achieved via countershading, though here the ultimate effect is to destroy the three-dimensional form of an object by disrupting the lighting cues that underlie its perception.
4. *Disruptive coloration* relies on the use of conspicuous, contrasting markings to generate the illusion of false edges and boundaries, thereby impeding the detection and recognition of an object's "true" form.
5. *Flicker-fusion camouflage* is a dynamic form of cryptic coloration in which color patterns rely on motion-induced blurring for their background-matching, cryptic effect.
6. *Distractive markings* deflect the attention of a receiver away from identifying characteristics, such as the distinctive outlines of body regions, to prevent their detection.

These mechanisms are non-exclusive and are typically combined to achieve a more robust

cryptic effect. Self-shadow concealment and obliterative shading, for example, may draw on a similar counter-shaded appearance to simultaneously exploit the disruption of both an object's shadow and three-dimensional form (Rowland 2009). Similarly, disruptive coloration can be fruitfully combined with background matching to achieve "differential blending," wherein some components of a color pattern strongly contrast with viewing backgrounds while others are closely matched (Barry et al. 2015). This enhances the broader disruptive effect and can thus more efficiently obscure an object's true form.

## Cryptic Coloration in Art and Technology

Many of the principles that describe the efficacy of crypsis can also be found – and even trace their origins – to the visual arts. Abbott Thayer was himself an artist and regularly acknowledged the role of his artistic training in shaping his thinking on adaptive coloration (Behrens 2009). He was also quick to chide his contemporaries that lacked a similar appreciation, even suggesting that they were incapable of understanding the adaptive function of visual camouflage because it:

...can be interpreted only by painters. For it deals wholly in optical illusion, and this is the very gist of a painter's life. He is born with a sense of it; and, from his cradle to his grave, his eyes, wherever they turn, are unceasingly at work on it, – and his pictures live by it. What wonder then, if it was for him alone to discover that the very art he practices is at full – beyond the most delicate precision of human powers – on almost all animals? Thayer (1909, p. 3)

Thayer's work also directed efforts at improving the state of military camouflage during World War I, which has continued through to the present day. Cryptic patterns are now standard features of modern military uniforms, for example, and both disruptive and background-matching elements feature prominently on camouflage for vehicles and installations (Newark et al. 2002). As in the natural world, motion, shadowing, and surface texturing are enduring challenges to the effectiveness of cryptic coloration, as they can reveal the

presence of objects irrespective of their appearance. The development of radar has also rendered the use of visual camouflage largely irrelevant for larger structures, in the same way that an animal's crypsis may be broken by the use of different sensory modalities.

## Conclusion

Cryptic coloration is widespread form of visual camouflage in which color patterns are used to minimize the probability of visual detection by undesirable viewers. It has served as a key example of adaptation by natural selection, with far-reaching consequences across human domains of study.

## Cross-References

- [Adaptation](#)
- [Camouflage](#)
- [Disruptive Coloration](#)
- [Predator Defense](#)
- [Visual Recognition of Prey and Predators](#)

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## Cryptic Female Choice

- [Cryptic Mate Choice](#)
- [Postcopulatory Selection](#)

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## Cryptic Male Choice

- [Cryptic Mate Choice](#)

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## Cryptic Mate Choice

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## Synonyms

[Cryptic female choice](#); [Cryptic male choice](#); [Postcopulatory intersexual selection](#)

## Definition

Cryptic female choice (CFC) is a postcopulatory sexual selection process that, through differences in the expression of female morphological,

behavioral, or physiological traits, results in paternity biases favoring males with particular characteristics over other ones.

## Sexual Selection During and After Copulation

Since Darwin (1871) and until the 1970s, sexual selection studies were focused on intrasexual and intersexual processes occurring prior to mating. Males would compete and woo females, and females would choose among the potential sexual partners and finally determine mating occurrence. Parker's pioneering work (Parker 1970) introduced the ideas that competition among males for the fertilization of eggs can continue after female mating acceptance and sexual selection can drive the evolution of male traits to increase their success in sperm competition. In 1983, Randy Thornhill introduces the concept of cryptic female choice that implies that sexual selection through female choice can also operate during and after mating. The term "cryptic" relates to its occurrence in the female, hidden from the male, and after the decision to accept mating (Eberhard 1996). Additionally, the word "cryptic" could refer to the fact that postcopulatory sexual selection through female choice remained unknown for evolutionary biologists until the 1980s. CFC caused a revolution in sexual selection studies, revaluing and highlighting the active and essential female role in determining the fate of male paternity success.

## Mechanisms of CFC

William Eberhard, in his milestone book "Female Control: Sexual selection by Cryptic Female Choice" (Eberhard 1996), performs an exhaustive review of the mechanisms known to occur in species with internal fertilization through which females can exercise CFC by changing their responses and consequently imposing paternity biases favoring one male over other one. Some of these morphological, behavioral, or physiological mechanisms are: permitting (or not)

penetration of male genitalia to reach the site of sperm storage, finishing mating prematurely, transporting sperm to sperm storage sites, nourishing sperm, dumping sperm, ovulating, producing eggs with more or less nutrients, aiding the male in producing and depositing mating plugs that lower the possibilities of female remating, aborting, among others (see Eberhard (1996) for a complete list). Females can base their decisions on male traits sensed prior to and/or during mating. Summarizing, for CFC to occur, females must mate – at least occasionally – with more than one male prior to brood production, and there must be differences in female sexual responses to particular male traits that affect his chances of paternity (Thornhill 1983; Eberhard 1996).

In several species distributed among a variety of animal orders, males continue courting females during mating (Eberhard 1996). Male copulatory courtship would have the function of stimulating the female, inducing her to favor that sexual partner by increasing his chances of paternity. Male copulatory courtship constitutes evidence of the occurrence of sexual selection through CFC in a species. We can also expect rapid evolutionary diversification in male genitalic and nongenitalic traits involved in sexual interactions in species in which CFC is a main driving evolutionary force (Eberhard 1996).

It is important to keep in mind that in the same system, sexual selection forces such as sperm competition, sexually antagonistic coevolution, and CFC are not excluding from one another and they can be acting at the same time, challenging the determination of the main selective force driving the sexual scenario of our study model.

## Mate Choice: Looking into the Future

Arthropods, and more specifically, insects and arachnids, have shown to be promissory models for studying postcopulatory sexual selection (Peretti and Aisenberg 2015). The possibility of modifying male contact structures and restricting female abilities to sense them, checking for the effects on female responses regarding male paternity, could be crucial for confirming CFC. This

requires elegant and simple experiments with fine-scaled observations of the sexual behavior of the study species.

Advances in technology regarding possibilities, such as individualizing sperm from different males, modifying male and/or female phenotypes in traits driven by sexual selection, and estimating reproductive costs for each sex, will help disentangle the effects of female- versus male-driven mechanisms while possibly adding new cases of CFC (Firman et al. 2017). Vertebrates offer a relatively understudied scenario with many questions to answer.

This section is focused on cryptic mate choice in females. The possibility of cryptic male choice (CMC) remains almost unexplored. CMC could be linked with sperm competition, for example, varying sperm allocation strategies according to female quality. An interesting case occurs in the soldier fly where males can control copulation duration according to female size: it is longer when males mate with larger, more fecund females (Barbosa 2011). In addition, in a scorpionfly species males in poor condition exert CMC by producing larger salivary masses – that function as nuptial gifts – in matings with more fecund females (Engqvist and Sauer 2001). Systems with sex role reversal (Gwynne 1991), in which females and males show nontraditional behavioral roles, offer outstanding opportunities to study the possibility of cryptic male choice.

Finally, copulatory communication or copulatory dialogues between the sexes regarding CFC have been scarcely studied (see Rodríguez (2015) for an update) and remain as interesting areas for future research. In this scenario of intersexual communication, modulations of behavioral units (e.g., in frequency or duration) associated with sperm transfer, sperm removal, external stimulation (e.g., by tapping or rubbing each other), and internal stimulation (e.g., with male genitalia) would be expected.

- [Randy Thornhill](#)
- [Receptivity](#)
- [Sex Role Reversal](#)

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## Cuckold

- [Paternity Certainty](#)

## Cross-References

- [Arthropod Life History](#)
- [Ethogram](#)

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## Cuckolded

- [Paternity Certainty](#)

## Cuckoldry

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### Synonyms

Cuckoldry risk hypothesis; Paternity uncertainty;  
Sexual infidelity

### Definition

Female internal fertilization has posed the adaptive problem of cuckoldry, or being deceived into providing resources or investment in genetically unrelated offspring, for males across species. Cuckoldry is an adaptive problem for males because investing in a rival's offspring rather than one's own is reproductively devastating, especially for males of high-investing species. Consequently, males in species in which female internal fertilization occurs have evolved anti-cuckoldry tactics.

### Introduction

In externally fertilizing species, such as most species of fish, males can be certain of their paternity, and their paternal investment will not benefit a rival's offspring because external fertilization allows males to witness the fertilization of a female's eggs (Trivers 1985). Cuckoldry, or being deceived into providing investment into genetically unrelated offspring, is an adaptive problem that males face primarily in species in which fertilization occurs within the female, such as humans, cats, and reptiles. Although males may be cuckolded in externally fertilizing species (Jones et al. 2001), the likelihood of paternity uncertainty is lower and less consequential in terms of reproductive costs than for paternally investing males in species with internal fertilization. Internal fertilization affords females the certainty that they are the genetic parent of the offspring they produce. From an

evolutionary perspective, females benefit from internal fertilization in part because they can deceive males into providing paternal investment, such as provision of resources and physical protection, in offspring to whom they are not genetically related while producing these offspring with genes contributed by, for example, a genetically higher-quality male. In these circumstances, females may secure "good genes" from one male and investment from the cuckolded male. Cuckoldry thus can be reproductively beneficial for the female and the genetic sire of offspring, while it is extraordinarily costly and rarely beneficial for the cuckolded male.

### The Problem of Cuckoldry

Given the amount of time and resources males invest in females and their offspring, it can be reproductively devastating for a male to be deceived into allocating paternal investment to an offspring to whom he is not genetically related (Platek and Shackelford 2006). In species, such as humans, in which males provide nontrivial, and sometimes substantial, parental care, cuckoldry is especially reproductively costly. Specifically, when a female's egg is fertilized by another male, the cuckolded male will fail to have sired the resulting offspring and, moreover, will invest resources into a rival's offspring. In some instances, cuckoldry can be costly for *both* males and females. One study reported that sand goby (*Pomatoschistus minutus*) males may sneak to fertilize eggs, thereby preventing the desired male from achieving fertilization and disrupting female-driven sexual selection processes (Jones et al. 2001).

### Solutions to the Problem of Cuckoldry

To address or avoid the costs associated with cuckoldry, males of many species have evolved anti-cuckoldry tactics that may lower the risk of cuckoldry. For example, male tropical house wrens (*Troglodytes aedon*) may be able to identify paternity markers in eggs laid by females (Freed 1987). Specifically, Freed (1987) examined male destruction of eggs laid after the appearance of new males, finding that resident males appear to be able to identify paternity by behaving differently toward eggs introduced after the new males appeared – in some cases, destroying the eggs if

the new male was introduced during the female's fertile period. However, when resident males spent more time with the female during her fertile phase, they were less likely to engage in egg destruction, suggesting that greater resident male vigilance of the female lowers the risk of cuckoldry. Thus, mate guarding, or occupying the female's time and engaging in surveillance of her sexual behavior, is an anti-cuckoldry strategy that males use to lower the likelihood that the female will copulate with other males, thereby preventing cuckoldry. By entering long-term relationships or pair-bonds with females, males can guard the female more frequently or vigilantly and have more opportunities to copulate with her, increasing the likelihood that the offspring she produces are not sired by rival males (Strassmann 1981). Mate guarding is often costly in terms of time and resources, however.

Human males also use a variety of mate retention tactics, or behaviors that discourage a partner from engaging in sexual infidelity or leaving the relationship, to reduce the risk of cuckoldry (Buss 2002). These behaviors range from vigilance over a female partner's whereabouts to physical or sexual violence against the female. For example, Kaighobadi et al. (2008) reported that accusations of female infidelity predicted men's violence against their partner. Because female infidelity sometimes results in cuckoldry, men sometimes use violence against their partner to discourage them from committing infidelity.

Males may also sometimes *engage* in sperm competition, a process in which sperm from two or more males compete to achieve fertilization of the female's egg, to reduce the risk of cuckoldry. In humans, males engage in more frequent in-pair copulation and mate guarding behavior when they spend less time with their partner since the couple last copulated (Shackelford et al. 2006). Males that are unable to guard a female partner during her fertile phase risk cuckoldry. In instances of greater time spent apart since last copulation, males increase in-pair copulation frequency to engage in sperm competition, reducing the likelihood of conception by a rival male. However, in some circumstances, males engage in sexual coercion to increase in-pair copulation frequency. The

cuckoldry risk hypothesis for sexual coercion suggests that sexual coercion is a male tactic used to reduce paternity uncertainty (Camilleri and Quinsey 2009). Specifically, when a male's perceived risk of partner sexual infidelity (and consequent cuckoldry) is higher, they are more likely to sexually coerce their partner, suggesting that *engaging* in sperm competition via coerced intercourse may decrease cuckoldry risk. An additional study investigating 26 species of birds found that males copulated more frequently if the risk of sperm competition was higher, indicating that birds engage in frequent copulation to lower the risk of paternity uncertainty by engaging in sperm competition (Møller and Birkhead 1991).

## Conclusion

Female internal fertilization presents the adaptive problem of cuckoldry for paternally investing males, whereas females may reproductively benefit from internal fertilization by deceiving males into providing care for offspring sired by, for example, genetically superior males. Cuckoldry is an adaptive problem for males because cuckoldry thwarts the male from producing his own genetic offspring, thereby failing reproductively, and causes him to squander his time, resources, and investment in a rival's offspring. As such, males have evolved anti-cuckoldry tactics to lower the risk of cuckoldry, including mate guarding, mate retention tactics, and tactics that motivate participation in sperm competition.

## Cross-References

- [Extra-Pair Copulation](#)
- [Mate Guarding](#)
- [Sperm Competition](#)

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## Cuckoldry Risk Hypothesis

### ► Cuckoldry

## Cuckoo Brood Parasitism

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## Synonyms

Coevolution; Egg rejection; Host-parasite interactions; Incubation behavior; Mimicry; Nests; Parental care

## Definition

Cuckoos eliminate the energy demands of rearing offspring by laying eggs in the nest of another bird species, thereby revoking all care of hatchlings.

## Introduction

In order to fledge a clutch successfully, most birds' parental responsibilities are energy exhaustive. First, they must build a nest; then the eggs must be cared for by continual incubation. Hatchlings require continuous feeding and protection. Cuckoos (Cuculidae spp.) mitigate the energy expenditure associated with rearing hatchlings through obligate brood parasitism in which the female lays her eggs in the nest of another specific host bird species (i.e., magpies, weaver birds, bishop birds, wrens) (Langmore 2013). After laying her eggs, she removes one or more of the host bird's eggs in order to make room for her offspring to thrive and to improve incubation efficiency (Langmore 2013). After her eggs are laid, she revokes all care of her offspring, allowing the host family to adopt her eggs and offspring instead (Langmore 2013). Only about 1% of all bird species exhibit this unique behavior (Sánchez-Martínez et al. 2017).

Sixty-four of the 149 species of Cuculidae (heretofore referred to as “cuckoos”) are obligate brood parasites, laying their eggs in the nests of other species of birds (Krüger and Pauli 2017). Cuckoos lay smaller eggs relative to their host, live in open and less productive foraging habitats, are migratory, and have a large breeding range (Krüger and Davies 2002). In North America, there are three species of cuckoos: yellow-billed cuckoo (*Coccyzus americanus*), black-billed cuckoo (*Coccyzus erythrophthalmus*), and mangrove cuckoo (*Coccyzus minor*). North American cuckoos are insectivores, and their foraging is enhanced by a slender, long-tailed body of about 12 inches and a wingspan of only 17–18 inches, enabling them to graze on caterpillars in dense shrubbery (Sibley 2000). Australia, Asia, Africa, and Europe boast an impressive 54 species of cuckoos, belonging to 12 genera. Australia is

home to the most diverse group of parasitic cuckoos in the world, which all parasitize more than one host (Langmore 2013). Europe has only four species of cuckoos, all of which exhibit brood parasitic nesting, typically within the nests of magpies. These birds are somewhat larger than their North American kin, ranging in length from 12 to 15 inches, exhibiting little sexual dimorphism (Peterson et al. 1993). Finally, South America has only five species of cuckoos that are brood parasites, all dwelling within the Amazon (Sánchez-Martínez et al. 2017).

## Strategies for Brood Parasitism

Cuckoos tend to parasitize birds that are very different from their own kind. To be able to successfully compete with their hosts, they have developed some very interesting strategies: egg mimicry (thickened egg shells, color matching of the egg to the nest and to the host's eggs, smaller egg size), destroying the nests of other birds during late incubation, the eviction of host eggs by hatchling cuckoos, faster egg laying and hatching times than their hosts, and luring the host away. All these strategies reduce the likelihood that the cuckoo eggs will be rejected by the host.

### Egg Mimicry

The shining bronze cuckoo (*Chrysococcyx lucidus*) produces smaller eggs and eggs colored to the nest of its host, the Australian grey fantail (*Rhipidura albiscapa*), which camouflages the hosts' ability to see the parasitic eggs (Attenborough 1998). The African diderik cuckoo (*Chrysococcyx caprius*) employs a similar approach of egg mimicry. However, this species benefits from various hosts. Thus, each female diderik produces polymorphic egg types (i.e., each female lays a different color egg to match its host), but it is only able to lay one color morph of egg, so the female cuckoos choose the species of bird to parasitize that most closely resemble the type of egg they lay (Attenborough 1998). For instance, if the female diderik cuckoo lays blue eggs, then she will lay her egg in the southern red bishop (*Euplectes orix*) bird's nest (Attenborough 1998). If she lays a speckled

white pattern, then she will choose the southern masked weaver (*Ploceus velatus*) bird's nests (Attenborough 1998). A similar strategy can be observed in the Southern Australian brush cuckoo (*Cacomantis variolosus*), which also produces polymorphic egg types for all three of their main hosts: the grey fantail (*Rhipidura albiscapa*), the scarlet robin (*Petroica boodang*), and the leaden flycatcher (*Myiagra rubecula*) (Langmore 2013). Sometimes in egg mimicry, as seen in the brush cuckoo, the color differences can be so subtle that it is undetectable to the human eye (Langmore 2013).

### Distraction

Another strategy proven successful in the Asian koel cuckoo (*Eudynamis scolopaceus*) is where the male cuckoo will lure the host from its nest so that the female cuckoo can access the host's nest and lay her eggs without detection (Langmore 2013). This behavior is significant in that it models both coordination and planning between the male and female cuckoo, both considered to be traits of advanced cognition.

### Rapid Egg Laying and Development

Cuckoos lay their eggs within 1.5–5.3 seconds (Langmore 2013). This operates in two ways: it prevents abandonment of the cuckoo eggs and nest by reducing the chances of detection and it also reduces the chance of the host bird defending its nest with mobbing or other defensive strategies (Langmore 2013). Cuckoo eggs also grow and hatch at a rate faster than the host eggs, allowing the cuckoo chick to grow before the host chick even hatches (Stevens 2013). Being larger than its host, the cuckoo chick is able to remove its competition from the nest. Even before the cuckoo chicks opens their eyes, some cuckoo chicks evict the host eggs from the nests by balancing the eggs on their back and heaving the eggs off the side of the nest one at a time (Stevens 2013). The cuckoo chick grows so rapidly that it often outgrows its host parent before it reaches the fledgling stage (Stevens 2013). If the host chicks live to fledgling age, the cuckoo chick will again attempt to eject its competitors from the nest. The cuckoo chick performs this action to prevent rejection from the host parents due to abandonment of the

nest (Sánchez-Martínez et al. 2017). Abandonment of the nest can happen either due to recognition of differences present in the nest, such as having more than one species present or too many eggs or hatchlings present, not necessarily species differentiation (Sánchez-Martínez et al. 2017). Cuckoo chicks are also more aggressive than their competitive chicks, often biting and pecking the skulls and backs of the other chicks in the nest (Sánchez-Martínez et al. 2017).

### Destruction of Host Nests

In destroying the host's nest late in the incubation period, hosts are forced to create a new nest with very little time left in the season to successfully hatch and fledge a clutch. However, because the cuckoo has evolved rapid embryonic and hatching development relative to other species, the parasitic offspring is more likely to survive than the hosts' offspring (Langmore 2013). The shining bronze-cuckoo (*Chrysococcyx lucidus*), fan-tailed cuckoo (*Cacomantis flabelliformis*), and Horsfield's bronze-cuckoo (*Chrysococcyx basalis*) all employ this strategy (Langmore 2013).

### Offspring Mimicry

Cuckoo chicks often look completely different than their hosts' chicks, but chick mimicry has not evolved because the hosts do not typically reject the chicks in their nests even if they look different from their own (Langmore 2013). However, the cuckoo chicks have evolved to mimic the calls and cries of their hosts, which are innate cues for the adult birds to respond with care behaviors (Langmore 2013). They use these mimicked cries to acquire more food than their brood mates, if any are left in the nest with them, by crying with more exaggeration, thus obtaining more of the host parents' attention and food (Stevens 2013). The cuckoo chick must mimic the calls and cries at an exaggerated rate to compensate for its lack of a visual mouth display (i.e., opening the mouth to present an array of colors inside the mouth) (Kilner and Davies 1999), because in the chicks of the host species, the visual mouth display is brightly colored for parental signalment of food deprivation (Kilner and Davies 1998).

### Costs of Parasitism

Parasitism comes at a great cost to the host. This cost can include the death of the host's chicks, as well as the host parents. With the exaggerated mimicry cries and the larger size of the cuckoo chick, the host parents are often forced to forage for extra food (Stevens 2013).

Because of the increased burden of food and incubation activity for larger chicks, the burden of the host bird raising the cuckoo chick is about twice that of the host bird raising its own chick, especially within the first week post-hatch (Sánchez-Martínez et al. 2017). In contrast, the cuckoo needs only about half the reproductive energy of the host to achieve its reproductive success (Krüger and Davies 2002).

### Parasitized Host Mitigation

Cuckoos are elusive birds, as hosts are more likely to reject the foreign eggs if they have recently seen a cuckoo (Stevens 2013). Upon observation of a cuckoo by the host, most species will mob the cuckoo and emit alarm calls which direct other host birds to join in the cuckoo mobbing (Stevens 2013).

Masked weaver bird species of Africa, which have evolved to lay eggs of multiple different colors (i.e., white, blue, and speckled), to diminish cuckoo egg mimicry and have also designed their nests to prevent parasitism (Attenborough 1998). First, their nest is globular shaped with only one entrance and exit combined. This way, the female diderik cuckoo is unable to see what color the eggs are in the nest, so she must enter multiple nests until she finds the right color eggs present for the eggs she has evolved to lay (Attenborough 1998). Secondly, the entrance and exit to this globular-shaped nest are very small, so small, that female diderik cuckoos often get stuck trying to enter the nest and die (Attenborough 1998).

Other host species abandon their nests when more eggs than their original clutch size are observed, implying an understanding of numerocity (Langmore 2013). Others abandon their nests when one or two eggs hatch significantly

sooner than the other eggs in their nest (Langmore 2013). This strategy can be observed in the fairy wrens of Australia as a defensive strategy used to combat the brood parasitism of the Horsfield's bronze-cuckoo (Langmore et al. 2003).

Some host birds have convergently evolved a tolerance response rather than direct action. One example can be seen in the Corvidae species of the Eurasian magpie (*Pica pica*). The Eurasian magpie has evolved a larger brain size in comparison to other non-Corvids and has the cognitive ability of self-recognition and episodic memory (Prior et al. 2008). These cognitive abilities are linked to a higher development of social intelligence (Prior et al. 2008). This convergently evolved tolerance response is apparent in the Eurasian magpie's nesting behavior of co-raising the great spotted cuckoo's (*Clamator glandarius*) eggs and offspring with their own, rather than emitting the energy to eject the eggs from their nest or rebuild their destroyed nests (Soler et al. 2011). Through coevolution, the Eurasian magpies have evolved to produce a larger clutch of eggs, allowing some of their offspring to grow up with the great spotted cuckoo's (Soler et al. 2011). The evolutionary selection pressures are much less when tolerance is adapted competition with brood parasites.

## Evolution of Brood Parasitism

Brood parasitism has a direct linear correlation with habitat shift to open space, change in diet, increase of migration length, increase of breeding range, decrease in population, and decrease in egg size and an indirect correlation with a shortened breeding season (Krüger and Davies 2002). Cuckoos exhibit a wide range of these evolved brood parasitic adaptations, which have been shown to evolve with the host's defenses. Cuckoos likely evolved the ability to lay a larger clutch size after brood parasitism evolved, because they were freed from the energetic demands of incubating, caring for, and protecting hatchlings (Krüger and Davies 2002). Coevolution is a naturally occurring event where two or more species evolve as a result of adaptations and counteradaptations (Gandhi 2019). Brood

parasitism has been widely studied because it is an excellent model for coevolution in determining whether these parasites have a negative impact on their hosts (Sánchez-Martínez et al. 2017).

Most commonly seen throughout the coevolution of brood parasitism is the model in which the parasite chooses a host target, and the host suffers the cost for the parasite (Stevens 2013). The host then evolves a way to recognize the cause of their extra cost, such as recognition of foreign eggs, and then removes them from their nests. Next the parasite evolves a way to perform better mimicry of the host's eggs to avoid the host's detection, which then leads to the host evolving better detection for rejection. The cycle will continue, with the host and the parasite each getting the upper hand on each other sequentially (Stevens 2013).

There are several proposed theories as to why cuckoos evolved obligate brood parasitism, although little effort has been made to explain these strategies. First, the female cuckoos find themselves with the inability to create a nest, either due to lack of location or lack of nesting materials (Krüger and Pauli 2017). Second, the female cuckoos find themselves not able to care for their young, perhaps due to lack of food supply (Krüger and Pauli 2017). Third, their nesting sites are destroyed either due to inclement weather or predation (Krüger and Pauli 2017).

## Conclusion

Understanding cuckoo brood parasitism will require additional research, as many stages of their parasitism are still in need of classification. These examples highlight the importance of coevolution and brood parasitism and the highly unique and specialized behavior of cuckoos all over the world.

## Cross-References

- ▶ [Camouflage](#)
- ▶ [Clutch](#)
- ▶ [Coevolution](#)
- ▶ [Convergent Evolution](#)

- ▶ [Evolution](#)
- ▶ [Hatching](#)
- ▶ [Nest Construction](#)
- ▶ [Parental Investment](#)
- ▶ [Polymorphic](#)
- ▶ [Mimicry](#)
- ▶ [Mirror Self-Recognition](#)
- ▶ [Songbird Learning](#)

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## Cuckquean

- ▶ [Extra-Pair Copulation](#)

## Cues

- ▶ [Mustelidae Navigation](#)

## Culpability

- ▶ [Shame and Guilt](#)

## Cultural Transmission

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## Introduction

The term “cultural transmission” is widely and often imprecisely used in the scientific literature to refer to various forms and outcomes of social learning. This entry considers cultural transmission to refer to the specific forms of social transmission where knowledge is passed between individuals, through some form of social learning, resulting in persistent increases in behavioral homogeneity in a population or group. In this way, cultural transmission allows different populations or groups of animals to show distinct differences in behavior. As described in the social learning section (“▶ [Social Learning](#)”), social transmission occurs when the performance of a behavior by one individual (directly or indirectly) causes a lasting influence on the rate at which a second individual acquires and or performs that same behavior. While social transmission can



allow behaviors or knowledge to persist at individual level, only those behaviors or knowledge which persist long enough to become common within a group or population over time or across generations can properly be called cultural. By taking this perspective, this article is consistent with a key recent text in the field (Hoppitt and Laland 2013).

Transmission of behaviors, traits, or knowledge between individual allows for rapid adaptation to changing or novel situations (“► Copying”). This affords individuals, in most cases, lower cost alternatives to trial and error (or “asocial”) learning and allows animals to learn more rapidly, especially in group situations. In many cases, the types of things that are transmitted through a group are essential drivers of fitness at the individual level, and cultural transmission allows this information to spread relatively quickly through whole groups of animals with consequent effects on individual and, potentially, group survival, leading subsequently to potentially important evolutionary effects. Like social transmission, cultural transmission can play an important role in a wide variety of behavioral domains that are beneficial or essential to animals, including mate choice, breeding site choice, foraging decisions, predator avoidance, and migration routes (although it is important to note that it can also lead to the acquisition of maladaptive behavior). However, cultural transmission specifically can lead to distinct group level differences in behavior and behavioral repertoires in animals.

An early and archetypal empirical example of cultural transmission comes from studies of birdsong learning. For example, juvenile white-crowned sparrows, *Zonotrichia leucophrys*, acquire a specific song type or “dialect” in their first 100 days of life, and this is heavily influenced by the song that they hear sung by adults, often their father or a close relative, during that time period (Marler and Tamura 1964). After this learning period, their song type does not change with experiences of other song types, and this mechanism allows successive generations of sparrows to retain dialects that differ between regions. Later studies of cultural transmission of bird song,

in this case on Darwin’s finches (*Geospiza* sp.) from the Galapagos Island of Daphne Major, highlight the importance of the cultural transmission as an evolutionary force. Long-term studies of the finches show that song is an important factor in species recognition and mate choice, and female finches use song to choose reproductive partners, selecting males that sound different to their paternal song while avoiding hetero-specific song types (Grant and Grant 1996).

Evidence for cultural transmission has since been found in a wide variety of other species from insects (Alem et al. 2016) to whales (Allen et al. 2013). It is a highly active area of current research and new evidence continues to be produced, helping us better understand how animals make behavioral decisions in the wild, such as the tendency to conform to more frequently observed variants of a behavior (Aplin et al. 2015).

This article focuses on cultural transmission in nonhuman animals with little focus on human cultural transmission; however, it must be noted that *Homo sapiens*, as the animal with the most complex form of culture and cultural transmission, is an important reference point. Many animal studies are undertaken with the underlying comparative goal better understanding the evolution human culture and cultural transmission, even though better understanding of the subject animals themselves is a happy proximate outcome. It can of course work both ways, and studies of human cultural transmission, being the most obvious, relatable and also sophisticated form of cultural transmission, can help us understand cultural transmission in other animals. This is perhaps made more important given the increase, or at least perceived increase, in the rate of cultural evolution in human cultures, with the technically enabled abilities for global scale social connections and rapid spread of information working at speeds well ahead of other processes of biological change.

This article will discuss the pathways through which cultural transmission operates. Given that many of the underlying mechanisms and processes of cultural transmission are common to the closely related articles on social learning and culture, there will be some inevitable overlap between this and other articles. Here we will



focus on the question of why cultural transmission is an important topic of study in nonhumans. In addition there will be some discussion of the more prominent current debates concerning cultural transmission or to which further studies of cultural transmission may contribute.

## The Importance of Studying Cultural Transmission

Culture may be considered a pinnacle of social behavior and one of the key characteristics that separate humans from other animals (“► [Culture](#)”). Cultural transmission is a fundamental part of the evolution, development, and maintenance of culture, and thus a key explainer of behavioral variation in humans and nonhumans (Mesoudi and Whiten 2008). There is some disagreement as to what constitutes culture transmission, in the philosophical and psychological fields especially, as explored in Acerbi and Mesoudi (2015) and Sterelny (2017). However there is overall agreement that cultural transmission can be said to result from the combination of learning mechanisms and attentional biases through which cultural information comes to be shared between individuals such that they come to behave more like each other, in a persistent way, sometimes spanning generations (Acerbi and Mesoudi 2015; Henrich 2001; Mesoudi et al. 2006). Cultural transmission is therefore of great interest, as studying it reveals how animals in many species come to behave as they do, as well as provide clues to the evolution of human culture, enabling us to discern the differences between human and other animal cultures, and reveal how human and other animal cultures developed and continue to develop.

Cultural transmission plays a role along with ecology, geography, and genetics in shaping differences between populations and species. Behavioral modification through social and cultural transmission can allow animals to more rapidly adapt to a changing environment than genetic processes and given the challenges and stressors that animals are facing across the globe, due to climate change, habitat modification, overexploitation, and associated regional

environmental changes, understanding the role of cultural transmission in how animals adapt to changing conditions is becoming increasingly important. Understanding the propagation and persistence of learnt behaviors through animal populations, as well as why some social transmission becomes cultural or not, may help us to better manage or mitigate some of these effects.

The spread of knowledge about novel predators or novel habitats through a group may be even more important as such events become more commonly experienced by species as range shifts occur in a response to climate change or other large scale environmental perturbations. One example of cultural transmission of a new behavior comes from the transmission of a novel foraging behavior – lobtail feeding – in humpback whales, *Megaptera novaeangliae*, in the Gulf of Maine (Weinrich et al. 1992). Here the innovation and transmission of a modified version of bubble feeding, where whales slap the water with their tail prior to performing the more widespread traditional bubble feeding technique, may partially be explained by a change in the primary prey type. Lobtail feeding appears to have developed with a rise in the number of a specific prey fish, the sand lance, *Ammodytes americanus*, while more traditional feeding behaviors of these whales are associated with Atlantic herring, *Clupea harengus*. However, cultural transmission was shown to be key to its pattern of spread through the population (Allen et al. 2013).

Knowledge of and responses to novel predators may also spread through a population through cultural transmission. For example, blackbird, *Turdus merula*, mobbing behavior by experienced birds appears to promote learning in naive birds which can then learn to exhibit appropriate responses to these predators. When experienced, trained, birds mobbed an otherwise innocuous object, it induced naive conspecifics to mob those same objects when exposed to them in the absence of trained birds, and this mobbing behavior persisted over time (Curio et al. 1978). The importance of cultural transmission in an ecological setting is further illustrated by the rapid spread of information about prey cues and prey palatability through a population of predators. One such

example is the case of fringe-lipped bats, *Trachops cirrhosus*, learning to respond to a potentially dangerous novel prey. This species can use the acoustic calls of their frog prey to determine palatability, and social learning allows them to more quickly learn to differentiate between frog species. The bats learn to associate the calls of poisonous toad species, and avoid them, far more quickly when able to learn from an experienced demonstrator than when only able to learn by trial and error (Page and Ryan 2006). The study also provided some, albeit limited, evidence that the prey palatability could be spread by cultural transmission, as prey preferences were passed from bat to bat along a transmission chain suggesting that this knowledge may spread through a bat population. These examples show the important role cultural transmission can play in the spread of knowledge and development of group-wide responses to changes or potential danger in a changing environment.

However, these same processes that allow beneficial cultural information to spread through a community of animals relatively quickly can also create behavioral inertia, a resistance to change that can have potentially maladaptive consequences. An example of the consequences of the development of such inflexible transmission comes from studies of guppies, *Poecilia reticulata*, which were shown to develop sub-optimal route preferences to foraging areas. These route preferences persisted over several experimental generations, developed as individual guppies in a transmission chain followed routes based on following individuals that had been trained to develop specific and circuitous routes (Laland and Williams 1998).

Beyond enabling rapid adaptation and spreading of knowledge through a group, cultural transmission may work at a more fundamental biological level. Working in tandem with genetic transmission, cultural transmission is considered an evolutionary driver in “dual inheritance” theory, the idea that genes and culture interact and influence each other. As suggested by the bird song examples in the preceding section, this theory gives a framework for understanding how cultural transmission can, for example, help to

shape and/or maintain species and speciation. Essentially, behavioral variation caused by cultural transmission can alter selective regimes within a population, generating selection at loci whose products relate to the trait in question. Some of the best evidence for this in nonhumans (in humans it is abundant) comes from work on killer whales, *Orcinus orca*, groups of which have distinct “ecotypes” with specific learned prey preferences and hunting strategies, with some groups specializing on fish and others on sea mammals or other prey groups. Groups of killer whales from different ecotypes may be sympatric but will remain consistently different in their feeding behavior. Foote et al. (2016) showed that these groups were genetically distinct, and most separated by differences in genes related to the metabolism of different proteins more commonly associated with different prey types, suggesting that cultural differences between groups may drive genetic differences, leading to incipient speciation. Likewise, recent evidence in birds suggests that the evolution of cultural units over generations of cultural transmission can speed up the process of speciation (Mason et al. 2017).

## Key Debates About Cultural Transmission

The study of cultural transmission is central to a number of key ongoing debates in the field of cultural evolution. One concerns the differences between animal and human culture, where there is disagreement about how to define and delineate different forms of culture.

### What Social Learning Mechanisms Are Required for Cultural Transmission

Some authors place an emphasis on the types of social learning required for, or considered necessary, to lead to cultural transmission and thus culture. In these arguments only certain social learning mechanisms with high fidelity of information transfer such as ► [imitation](#) or ► [teaching](#) are thought to be capable of supporting cultural transmission and that the ability to use these social learning mechanisms may be at least part of what

makes human culture unique (Tomasello et al. 1993). Similarly, specific animal taxa may be considered capable of developing culture and while other species that use lower fidelity mechanisms of social learning cannot sustain the transmission of behaviors or knowledge through generations. This debate is made more pertinent given recent empirical support for the idea that cultural transmission can occur without the use of high-fidelity mechanisms of social learning. For example, human participants in groups where teaching and imitation were inhibited were still able to improve the performance of a design over successive generations of participants (Caldwell and Millen 2009). Certainly, there is some evidence that animals can develop what appear to be traditions using apparently low fidelity social learning mechanisms. The transmission of an alternate foraging technique, nectar robbing, by bumble bees, *Bombus terrestris*, provides one example. Bumble bees can collect nectar, by biting through the base of the flower rather than collecting nectar in the traditional manner, and this behavior was shown to be transmitted through social learning mechanisms where naive individual bumble bees were more likely to become robbers after being exposed to holes made by previous individuals, as a form of indirect copying (Leadbeater and Chittka 2008). The bumble bees did not need to observe a robbing bee to learn the technique and were therefore not using any of the social learning mechanisms regarded as sophisticated or high fidelity. It is important to point out that although the robbing technique was shown to allow transmission through a group of bees, it did not show cultural transmission as defined here, and merely that transmission of a behavior through indirect observation may be possible.

A classic example of the problems in identifying the types of mechanisms used in social and cultural transmission is the case of the transmission of milk bottle opening technique. In the early 1920s, people noticed that certain populations of blue tits, *Cyanistes caeruleus*, had begun using a new foraging behavior where they would open the tops of milk bottles and drink the cream from. This behavior spread rapidly through British and

European blue tit populations using a transmission process which was initially proposed to be based on a relatively simple social learning mechanism in conjunction with repeated inventions of similar techniques, within a similar time period in separate populations (Sherry and Galef 1984). However, the actual mechanisms at play are still indefinite and recent studies suggest that they may be more sophisticated than those originally proposed (Aplin et al. 2013).

### Are Nonhuman Animals Capable of Cumulative Culture?

The idea that humans are uniquely able to increase performance or innovate on learnt behaviors over generations, through the “ratchet effect-” like effect of cumulative cultural evolution (“► [Cumulative Culture](#)”), may be changing. Recent evidence suggests that animals can progressively increase the performance and efficiency of behaviors spread through cultural transmission (Sasaki and Biro 2017). In their study, homing pigeons developed modified and more efficient routes over successive experimental generations. However, there is no question of these animals developing through this process a solution so complex no individual could themselves invent it in their own lifetime – considered by some to be the key diagnostic of human cumulative culture.

### What Are the Other Key Factors Involved in Cultural Transmission?

While the mechanism(s) used in transmission between individuals within a group may play an important role in development of cultural transmission, it is not the only important parameter. Theoretical work has suggested that while high-fidelity information transfer is important in establishing cultural transmission of a new behavior, the stability of that behavior within a group may depend on other factors. Social learning and thus cultural transmission can depend on characteristics of naive (learner) individuals and or those of the experienced (demonstrator) individual, as well as a host of other ecological and psychological factors that have the potential to contribute to the stability and, thus, existence of animal culture (Claidière and Sperber 2009).

## What Is Transmitted During Cultural Transmission?

One key point of current debate hinges on the fact that unlike the physical transmission of genetic material between generations in biological evolution, cultural transmission does not always transmit things with obvious tangible properties (the exception being material culture), and there is ongoing debate as to how information is transmitted between individuals within a population (Sterelny 2017). The properties of what is transmitted can be ephemeral, biased, and/or modified during the process through which an individual learns, forgets, and relearns (Strimling et al. 2009). Given that transmission may be modified by both the sender and receiver, debate arises as to how cultural transmission operates. Are whole cultural units transmitted as replicated representations (or “memes”) of, for example, a specific behavior or are transmitted units instead reconstructed following sensory input of that behavior. Barkow et al. (2012) highlight the key point of the dispute by pointing out that individuals are not passive recipients of the cultural information. Individuals may consciously or unconsciously choose between sources of information and may edit that information in a dynamic process, and it can be difficult to discern between these differences. Any particular suite of behavioral traits, common among a majority of individuals within a population, may be the result of cultural editing processes operating at the individual level within that population converging on very similar behavioral traits or the result of transmission of those traits as a whole with little to no modification at the individual level. This is further complicated by the fact that different domains of information can be involved and the extent to which these domains are processed differently by the brain are subject to broad range of factors such as age, sex, and species.

Future studies into the social learning mechanisms capable of supporting and processes affecting cultural transmission may help to identify and further disentangle the differences and similarities in animal and human cultures and can help to solve these and other debates.

## Pathways for Cultural Transmission

Cultural transmission operates at the individual level using social learning mechanisms, but when aggregated can have population level consequences. The specific context and concurrent social environment can play an important part in affecting when an individual decides to learn (or copy) a specific behavior and/or who an individual learns from. Theoretical models have shown that indiscriminate social learning is not necessarily adaptive (Giraldeau et al. 2002), that in most cases naive animals should be influenced by several factors, and learning may be affected by specific changes in their environment, social or otherwise, and/or ontogenetic stage.

Cultural transmission as an inherently social process can be influenced by a number of social factors such as group size, and proportion of knowledgeable individuals can affect transmission of knowledge through a group. For example, in groups of pigeons, *Columba livia*, exposed to a new behavior, groups with a greater number of knowledgeable individuals had increased rates of transmission, while more naive individuals in a group reduced the speed of transmission (Lefebvre and Giraldeau 1994). These factors can play a role in group-wide transmission across generations, and species or individuals may develop or follow what are termed social learning strategies, which govern the decisions about “when” to learn, or “who” to learn from (Rendell et al. 2011). These strategies (such as “Who strategies” and “When strategies” described below) can in turn affect what is or is not passed through cultural transmission to other members of a group.

## Social Learning Strategies Thought to Influence Cultural Transmission

“Who” strategies can have a strong effect by biasing social learning through specific pathways. Many animals have been shown to use different social cues in learning from specific individuals, for example, individuals may favor copying from experienced individuals. Nine spine sticklebacks, *Pungitius pungitius*, have been shown to follow a “copy the larger” strategy where males prefer to copy behaviors and feeding choices of larger

males than smaller ones (Duffy et al. 2009), and domestic hens, *Gallus gallus domesticus*, use a similar strategy where hens will copy from those of higher rank in a social hierarchy (Nicol and Pope 1999). Many of these strategies can be considered proxies for learning from more successful individuals, which is suggested by theoretical models as a reliable route for long-term success (Mesoudi 2008). Although there are many examples of “who” strategies in social learning studies, there are fewer examples of these strategies working in cultural transmission pathways. This may be attributed to the relative difficulty in collecting longitudinal data of populations with cultural transmission. Explicit evidence of “who strategies” being used in cultural transmission pathways are therefore limited but some of the best evidence comes from songbird studies such as the Galapagos finches, where males tend to learn from and sing songs very similar to their fathers (Grant and Grant 1996). Similarly, “when” strategies allow individuals to make adaptive, context-dependent decisions. Choosing when to use an observed behavior or whether to copy a particular behavior at all can have important consequences for cultural transmission. One example of this type of strategy in a social learning context is the “copy-when-asocial-learning-is-costly” strategy exhibited by minnows, *Phoxinus phoxinus*, individuals of which use public information more often than asocial information when there is higher (simulated) predation risk (Webster and Laland 2008). Social learning strategies can therefore affect cultural transmission in so far as making certain behaviors or knowledge more likely to be transmitted, depending on the context within which that behavior is most commonly expressed and which individuals are doing the expressing.

### Transmission Pathways Through Populations

A key feature that crucially affects the way that cultural transmission may or may not interact with evolutionary processes is the relationship between paths of cultural transmission and demographic generations. Vertical transmission, easily understood from a human perspective, is where cultural transmission flows from parent to offspring. Cultural units are passed between

generations of individuals from one or both parents to offspring. As a classic example, in certain groups of bottlenose dolphins, *Tursiops* sp, female dolphins pass on the use of sponges as a tool for foraging on the substrate to their daughters (Krützen et al. 2005), and in many bird species, song is transmitted across generations from father to son (Mason et al. 2017). Horizontal transmission is a less focused pathway, with transmission propagating between members of a single generation, and can occur between unrelated individuals. For example male humpback whales sing very similar versions of particular song during the breeding season, and this song spreads through a population from male to male (Garland et al. 2011). Finally, oblique transmission occurs across generations from older to younger generations but where the demonstrators/models from which the younger individuals acquire their behavior are not their parents. An example here comes from roof rats, *Rattus rattus*, where pups given the opportunity to learn from un-related adults had significantly higher preferences for food eaten by those adults than those rats that had similar opportunities to learn from rats of the same age (horizontal transmission) (Chou et al. 2000).

Cultural transmission is not necessarily restricted to occur within species. Interspecies transmission is another pathway by which cultural transmission occurs and may act along any of the three pathways described above but across different species. A striking example comes from a study of cross-fostering experiments in wild birds which revealed that cultural transmission is involved in the development of behaviors long assumed to be innate. In the study, blue and great tit chicks were switched from their respective nests and thus were raised by parents of the alternate species. Blue tit chicks fostered by great tit parents learnt to use foraging sites and techniques normally specific to great tits and vice versa, and this niche-swap persisted for the life of the birds (Slagsvold and Wiebe 2011).

Limits to cultural transmission, across species and or within groups, will be revealed with further study of the parameters of transmission pathways. Exploring these pathways in different species and across different contexts will aid in the



understanding of how cultural transmission works to effect change over generations.

## Summary

When social learning results in effective and persistent transmission of a behavioral trait or knowledge through a group or population, it can become cultural transmission. This can then lead to development of, or change in, the behavior of groups, and there is some evidence to suggest that it can interact with natural selection as an evolutionary driver. Cultural transmission in combination with appropriate timescales and persistence through sufficient generations can select for specific behavioral traits within a population that may work as an additional factor in determining the evolutionary trajectory of a species or population.

The number of species, strategies, and transmission pathways through which cultural transmission works can make the generation of clear general theories difficult, but it highlights the level of ubiquity and importance of cultural transmission in the animal world. It is also an important area of current research, where many central questions remain open. Cultural transmission is an area which is currently and likely to remain a productive area of research for some time. Further evidence is needed to clarify some of the opposing theories pertaining to culture, and although cultural transmission can be much faster than genetic transmission, evidence of cultural transmission by definition requires monitoring of groups of animals over significant periods of time. Whether any, and how many animal species are capable of cultural transmission is a key step in furthering our understanding of the evolution of culture both animal culture as a whole and those of our own “special” human culture.

## Cross-References

- Cognitive Imitation
- Contagion
- Copying
- Culture

- Cumulative Culture
- Diffusion
- Emulation
- Imitation
- Social Facilitation
- Social Learning
- Social Network Analysis
- Stimulus and Local Enhancement
- Teaching

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## Culture

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## Introduction

The word “culture” may evoke many different meanings depending on the audience. Such interpretations might refer to language, national identity, table manners, a style of cooking, art, or literature, for example. Consequently, a broad definition of the term is necessary to encompass everything that a diversity of writers describe as cultural. One such definition is that culture is a package of traditions, with traditions being behavior patterns common to more than one individual in a group which are transmitted between individuals by social learning (Hoppitt and Laland 2013). Another important feature of culture is that it is at least somewhat enduring, as opposed to the transmission of transient social information like “The building is on fire!” Culture may be transmitted “vertically” (between generations) or “horizontally” (within a generation). An example of

vertical transmission would be offspring observing and adopting their parents’ hunting techniques, whereas horizontal transmission could be teaching a friend to sew. Humans are, of course, highly dependent on culture. In many societies, this is emphasized by the enormous importance placed upon formal education for children and juveniles until a mandatory age, a recognition of the difficulties one can face in those societies without this baseline of cultural capital. Of course, our absorption of social information doesn’t end at leaving school. Friends, family, colleagues, media, and now the Internet all present a constant barrage of social information that we often cannot help but incorporate into how we perceive the world and act within it. But complex cultures have of course arisen also in societies that lack formal schooling or writing, whether in present times or more universally in earlier times.

Human culture has been recognized to be uniquely complex as a result of our capacity for “cumulative culture” (Dean et al. 2014), the ability to modify learned behaviors such that they become more complex and/or efficient, then be transmitted, and further improved by others until eventually a level of complexity is attained that could not have been achieved by a single individual. However, the capacity to pass traditions through multiple generations of social learners is not uniquely human. In fact, current evidence would suggest that it is ubiquitous in vertebrates and perhaps larger swathes of the animal kingdom.

## What Do Animal Cultures Look Like?

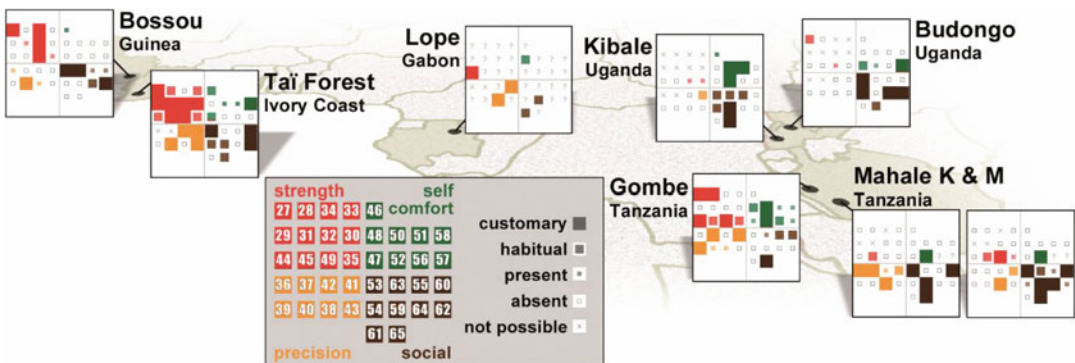
One of the earliest signs of culture in nonhuman animals (hereafter “animals”) was reported in Japanese macaques (*Macaca fuscata*). A group of monkeys on Koshima Island in Japan was regularly provisioned with sweet potatoes to supplement their natural diet, and researchers noticed that one individual, a juvenile female named Imo, had started washing her potatoes before eating them (Kawai 1965). This behavior involved dipping them in water with one hand and brushing away sand with the other, presumably to make them more palatable. In the subsequent 5 years,

this behavior spread to 15 of the 19 other individuals in her group. Consistent with social transmission, this behavior did not arise randomly in other individuals but rather followed lines of social affiliation. This crucial detail makes it likely that individuals copied others that they were close to rather than each independently discovered potato-washing behavior. A potentially problematic issue with this finding is that sweet potatoes are not a natural part of Japanese macaques' diet, and so it is not demonstrable from this study alone that they would develop cultural variants under natural conditions. However, it was enough to spark an interest in primate cultures, and several other naturally occurring traditions have now been attributed to Japanese macaques.

Later, McGrew and Tutin (1978) discovered that one community of chimpanzees (*Pan troglodytes*) was displaying a novel method of social grooming, in which the grooming partners clasp hands above their heads and groom with the other hand ("handclasp grooming"). This behavior was found to be common in one chimpanzee group in Tanzania yet absent in a second group whose territory lay only 50 km away. Given that the two groups belonged to the same subspecies and due to their geographic proximity were likely to have interbred in the recent past, the authors concluded that this behavioral difference was likely to be cultural rather than genetic in its origin. Determining the presence of culture by examining behavioral differences between communities and

whether they can be accounted for by ecological differences, such as availability of materials in the case of tool-use behaviors, is known as the "exclusion" method. This method was later applied on a much larger scale (Whiten et al. 1999) to collate observational data from seven long-term chimpanzee field sites. The researchers identified 39 behaviors which were common in some groups and absent in others (Fig. 1). These examples ranged from variation in foraging behaviors, such as nutcracking and termite fishing, to social behaviors such as handclasp grooming. The unique patterning of these traditions in each community means that one could identify the group to which an individual belongs simply by examining their behavioral repertoire, just as one might make inferences about a human's cultural identity based on their social customs. Similar approaches have since been applied to other members of the primate order, finding that orangutans (genus *Pongo*), gorillas (*Gorilla gorilla*), white-headed capuchins (*Cebus capucinus*), and spider monkeys (*Ateles geoffroyi*) all exhibit a great deal of behavioral diversity between groups that can be attributed to culture (though with fewer different traditions than chimpanzees).

However, there is some uncertainty over how conservative such counts of cultural variation are. For example, while the tools necessary for nutcracking may be available to multiple chimpanzee communities, it is not implausible that other foods are in sufficient abundance in certain



**Culture, Fig. 1** The putative cultures of wild chimpanzees reported in 1999. "Customary" acts are those typical in a community; "habitual" are less frequent but consistent

with social learning. Numbers identify behavior patterns in the catalogue attached to Whiten et al. (1999)

locations that the many years required to master nutcracking skill are not a worthwhile time investment. Genetic factors are also difficult to completely rule out. Langergraber and Vigilant (2011) identified a correlation between the cultural variation between chimpanzee communities and their genetics. However, with the geographic distances involved, one might predict this correlation regardless of whether behavioral variation is cultural or genetic in origin. Indeed, cultural variation may well drive such genetic differences. For example, in humans the cultural practice of cattle farming in certain human population appears to have led to the evolution of lactose tolerance in adults. Similarly, it has been found that cultural variation in foraging specialisms may have led communities of killer whales (*Orcinus orca*) to occupy different ecological niches for long enough that they are now demonstrating incipient speciation (Riesch et al. 2012). Indeed, if a particular cultural variant is adaptive and persists for long enough, then it will inevitably have an effect on genetic selection, which in turn may influence the development of future traditions. This feedback process is known as “gene-culture coevolution” and described by “dual inheritance theory” (Richerson and Boyd 1978).

That a significant portion of the behavioral repertoires of some nonhuman primate species is seemingly shaped by cultural inheritance presents a key point of commonality between these species and ourselves and seems likely to characterize our shared ancestry. However, this commonality extends far beyond the primate order, with compelling evidence for cultural transmission existing in a diverse range of species (Whiten 2017). For example, in meerkats (*Suricata suricatta*), researchers have found that neighboring groups differed in the time of day they would emerge from their burrows, despite frequent dispersal between groups (thus controlling for genetic differences) and a lack of any known environmental correlates (Thornton et al. 2010). Furthermore, some of the most compelling evidence for animal culture is found in the study of marine mammals. In 1980, a single humpback whale (*Megaptera novaeangliae*) was recorded as using a novel foraging method known as

“lobtail fishing.” Over three decades, researchers observed this behavior diffuse between closely associated individuals in a manner consistent with social learning (Allen et al. 2013). Further evidence of complex culture in humpback whales comes from studies of their vocal communication. Depending on where they live, humpbacks have acoustically distinct songs. However, following the migration of small numbers of individuals between two communities of whales, researchers found that their new group quickly and comprehensively changed their song to match that of the newcomers (Noad et al. 2000). This last example introduces culture in the domain of vocal behavior. As well as other marine mammals such as killer whales and sperm whales (*Physeter macrocephalus*), there is a large body of research demonstrating vocal dialects in a variety of bird and primate species. Though less often discussed than noncommunicative traditions, these are particularly interesting in that the primary function appears to lie in identifying and facilitating social relationships. This illustrates that social learning may allow individuals not only to optimize their use of their physical environment (e.g., learning to exploit a food resource) but also their social environment.

## Core Cultural Concepts

Although the typical measures by which culture in animals is quantified refer to patterns of behavior, it may be useful to think in more nuanced terms. In humans, cultural anthropologists have suggested that we should think of culture in terms of core concepts or “cultural cognitions” which may or may not elicit a range of related behaviors. A human example of this would be the emphasis placed on collectivism as opposed to individualism in Eastern cultures relative to Western ones and the ways in which these concepts manifest themselves in behaviors common to each culture. Discussing “concepts” with regard to animals is inherently problematic insofar as we cannot examine such states as we might through conversing with human participants. However, careful examination of animal behavior can allow us to

draw useful inferences. One example of how differences in “core cultural cognitions” might manifest in nonhuman animals comes from observation of stick-tool use behavior in two different Ugandan groups of chimpanzees. One of these communities (the “Kanyawara” group) frequently uses stick tools to access a variety of resources, such as termites. In another community (“Budongo”), stick-tool use is entirely absent. Knowing this, researchers (Gruber et al. 2009) introduced a novel resource, artificial honey-filled holes, to see how these two different cultures would respond. Just as with similarly located resources, the Kanyawara chimpanzees gathered stick tools to retrieve the honey, whereas the Budongo community used leaf sponges. Even when appropriate stick tools were provided next to the honey holes, a similar pattern prevailed. Kanyawara chimpanzees stripped the sticks of their leaves and used the sticks as usual, whereas Budongo chimpanzees ignored the stick and kept the leaves for sponging. This carrying over of a particular *type* of solution from pre-existing behaviors to a novel problem is perhaps suggestive that culture runs deeper than any individual behavior. Another interesting example of culture as a “mind-set” rather than a specific behavior comes from a longitudinal study of aggression in a troop of olive baboons (*Papio anubis*) (Sapolsky and Share 2004). During the 1980s, the most aggressive males of this group died of tuberculosis as a result of contact with human waste. As a result, the rate of aggressive encounters in the group was dramatically reduced, physiological measures of stress dropped in young males, and a higher than normal rate of intersex grooming and affiliation was recorded. Critically, this “pacific” culture persisted even after the remaining original males of the group had migrated elsewhere and was adopted by new males who joined the group from other communities.

### Why Is Culture Useful?

Individual or “asocial” learning is one means by which animals can adapt their behavioral repertoire to best suit their environment. It is potentially

costly, however requiring a significant amount of time or energy investment to explore different options. In more urgent scenarios, such as predator avoidance, experimenting with behaviors that have an unknown payoff may cost an individual their life. Copying the behavior of other individuals allows one to bypass this process to arrive at useful behaviors without paying these costs. Furthermore, when individuals do arrive at a novel and productive behavior, this allows for benefit not only to themselves but also for it to be passed on to kin and allies, enhancing their fitness. That cultural information may be passed through multiple generations to shape behavior in a similar manner to genetic inheritance has lead social learning to be referred to as “nature’s second inheritance system” (Whiten 2017). However, not all cultures emerge as a result of innovations to adapt to a physical environment. Innovations may also maximize the benefits of the social environment, such as facilitating social bonding (as in cultural variations in handclasp grooming behavior in chimpanzees) or identifying oneself as a member of a group (such as group-wide convergence in vocal dialects). There is much evidence that humans may give preferential treatment to those who share their language, appearance, and culture, but whether animals also demonstrate such “in-group” bias based on cultural practices is not yet known. However, in species with extended periods of parent-offspring-directed social learning or high within-group relatedness, culture may function as a useful cue for identifying kin. Some animals may even purposefully diverge from the behavior of out-group individuals in order to make the difference clear, as suggested by the fact that captive pygmy marmosets (*Cebuella pygmaea*) changed the acoustics of their vocalizations to diverge from a newly introduced neighboring group (Elowson and Snowdon 1994).

The importance of complementary experimental work, such as the honey-hole chimpanzee study described above, to check and verify field observations is illustrated by studies into the toolmaking practices of New Caledonian crows (*Corvus moneduloides*). Crows from different regions of New Caledonia are known to construct



different types of tools for foraging, despite similar apparent availability of tool materials and prey. It has therefore been suggested that this may be an example of cultural variation and even cumulative culture. However, it was later found that hand-raised crows would spontaneously manufacture and use similar tools (Kenward et al. 2005), suggesting that while social learning may well facilitate the learning of this behavior in the wild, it is not essential. This example highlights an important issue with studying culture in wild animals, which is that one is often having to make post hoc inferences about an existing distribution of behavior. One can collect data consistent with a behavior being either socially learned or developmentally fixed, but without direct observation of the propagation of a behavior (as with the cetacean examples above) or experimental intervention, it is difficult to draw firm conclusions and its cultural status. Experimental work in both captivity and the wild allows us to systematically determine a species' capacity for social learning, as well as how exactly a behavior progresses from being an idiosyncrasy to a full-fledged group-wide tradition. Questions over how culture is transmitted can be usefully split as to whether they concern social learning *processes* or social learning *biases*. Processes refer to how information is transmitted between two individuals, and biases refer to the factors that guide when and toward whom individuals choose to copy. We next summarize the literature on each of these topics. Readers are encouraged to consult the “► Cultural Transmission” and “► Social Learning” chapters within this collection for a more comprehensive treatment.

## Social Learning Processes

Social learning processes are differentiated in terms of what information is being utilized by social learners and how it is dealt with cognitively. For example, **local enhancement** is one such process, whereby individuals learn by focusing their attention on a location that others preferentially acted upon. If many conspecifics are feeding in an area, this suggests there is an abundance of

food there and it makes functional sense for the learner to focus in a similar way. **Stimulus enhancement** is very similar, except that attention is drawn to certain objects rather than locations.

Researchers have distinguished between two principal higher-level processes: **imitation** and **emulation**. Imitation refers to copying the bodily actions of an individual, for example, the technique with which they manipulate a tool to achieve a goal, such as using a saw to cut a piece of wood in half. Emulation, on the other hand, refers to learning the outcome of a behavior and finding one's own path to achieving it, for example, breaking a piece of wood over one's knee instead of using the saw that the individual observed had used. The key difference is copying the *result* rather than the *form* of an action. Depending on the task, a learner's pre-existing knowledge, and the range of options available, they may well end up using essentially the same method as the demonstrator even if learning was not imitative, making disambiguation difficult. Of the two processes, imitation is commonly considered to be the most sophisticated form of social learning, since it allows for high-fidelity transmission of complex behaviors and requires the demanding translation of visual (or vocal) patterns seen in another individual's actions into commands in one's own motor system, to bring about the correspondence between the two despite a quite different perspective.

Whether and/or which animals are capable of imitation has long been a contentious issue. Tomasello et al. (1987) found that although young chimpanzees faced with an out-of-reach reward did not precisely copy a sequence of tool-use behaviors used by a conspecific to retrieve it, they did learn something of the *function* of stick tools for reaching such objects, and this was later described as emulation. In another study (Whiten et al. 2005), a single chimpanzee in each of the two different groups was trained on alternative methods of using a stick tool to operate parts of a foraging device, which would release a food reward. These alternative techniques spread throughout the models' respective groups to become recognizably different traditions, and while some individuals did explore other



methods, they were found to eventually reconverge on the behavior most common to their group. That the groupmates of these demonstrators converged on their methods is suggestive of imitative learning. “Ghost” experiments in which the movements of the device were made without any chimpanzee responsible, so could be replicated only by emulation, failed to lead to success, reinforcing this conclusion.

Long-term care staff of captive apes frequently have a long list of anecdotes about their animals copying the behavior of their carers, such as brushing one’s teeth or scrubbing floors. These behaviors, which serve no purpose for the ape (but may have been reinforced by their carers, knowingly or not), are difficult to explain without imitative learning and were common in the diaries of researchers studying home-reared chimpanzees in particular. Indeed, the environment in which individuals are raised may be critical in shaping such tendencies. It has been found that home-reared or so-called “enculturated” chimpanzees (referring to their immersion in human culture) demonstrate a greater proclivity for imitation than chimpanzee-reared individuals (and equivalent to that of children) when tasked with copying the actions of a human demonstrator (Buttelmann et al. 2007). Some evidence for bodily imitation has also been found in species as diverse as marmosets (*Callithrix jacchus*), bottlenose dolphins (*Tursiops truncatus*), and pigeons (*Columba livia*).

A social transmission process that is thought to particularly characterize humans is **teaching**. Even preschool children have been found to engage in spontaneous teaching behavior by verbally instructing their peers on how to solve an experimental problem (Dean et al. 2012). Together with imitation, teaching has been proposed as a critical high-fidelity process of cultural transmission that allows for the unique complexity of human culture (Galef 1992). However, whether teaching can be considered uniquely human is highly dependent on how one defines the term. A popular “functional” definition of teaching in comparative studies is that it is a behavior in which an individual modifies their own behavior only in the presence of an observer, which both facilitates learning in the observer and

does not benefit the actor (Caro and Hauser 1992). Using this definition, researchers have identified a broad range of species for whom there is evidence for teaching. For example, meerkats bring home scorpions in which they first remove the sting, but later present scorpions decreasingly disabled, allowing pups to progressively discover the skills necessary to hunt this dangerous prey in a safe and structured way (Thornton and McAuliffe 2006). Evidence for teaching defined in this functional way has also been offered in bees, ants, birds, and callitrichid monkeys but seems strikingly absent in the great apes. It has been suggested that this lack of teaching in apes may be due to long periods of immaturity which allow juveniles instead to learn necessary skills through extended observational learning.

## Social Learning Biases

Culture benefits an individual only insofar as these benefits outweigh those of learning individually (asocially). If an individual copies every novel behavior it observes conspecifics performing, then they may end up copying maladaptive behaviors or replacing perfectly useful methods with less efficient ones. Consequently, in order to maximize the benefits of social learning, it has been proposed that species with an evolved propensity for social learning are likely to also have evolved a suite of biases that guide when and toward whom it should be deployed. Understanding these biases is crucial to improving our understanding of how culture emerges and propagates, as well as the contexts in which it is most useful. They can be usefully categorized into “who” and “when” biases.

“Who” or “model-based biases” direct individuals toward copying specific individuals (such as one’s mother) or categories of individuals (such as kin). Humans demonstrate a number of such biases, such as children directing their social learning toward older and more prestigious individuals. Some animals also appear to be selective in their preferential sources for social information. For example, in an experiment where the method of opening a puzzle box was introduced to

chimpanzee groups by trained models, it was found that naïve individuals preferentially directed their attention toward dominant knowledgeable demonstrators (Kendal et al. 2015). A tendency to copy dominant individuals, or “rank bias,” has been proposed as a key factor in chimpanzee social learning. It may explain why so few chimpanzee innovations are recorded as going on to become group-wide traditions, since many innovations come from subordinate individuals. Dominant individuals typically also enjoy the greatest amount of reproductive success in a group and so are perhaps likely to be good role models. If their success is a result of their behavioral preferences, then copying them might bestow those same benefits on the learner. In many cases, the characteristics that make an individual dominant, such as physical prowess or being the offspring of a dominant individual, cannot be directly copied. In this case, converging on their behavior must serve another purpose. One possibility is that behavioral similarities facilitate social bonding between individuals, in which case copying the behavior of dominant individuals may serve an additional function of improving one’s social standing. However, when researchers seeded groups with a method of opening a puzzle box by either alpha male or subordinate female chimpanzees (i.e., only one model was available, whether of high or low rank), it was found that observers were highly motivated to copy the behavior of subordinate models (Watson et al. 2017). It may be then that individuals are motivated to learn visibly productive foraging behaviors from whomsoever they observe demonstrating them since learning this can only be beneficial, whereas transmission of more “arbitrary” traditions does indeed flow primarily from dominant individual models.

A bias toward copying one’s own kin appears to be common. For example, brown capuchin monkeys (*Cebus apella*) do not copy individuals based on their relative rank but do demonstrate a bias toward copying related models (Dindo et al. 2011). The vocal production behavior of killer whales is also known to be largely transmitted within matrilineal lines (Yurk et al. 2002). The capacity for kin bias to shape cultures is neatly illustrated in

vervet monkeys (*Chlorocebus pygerythrus*). It has been found that, within the same group of monkeys, multiple distinct methods of cleaning food before consumption were present in the group and were differentiated along matrilineal lines. In some species, kin bias may only manifest during specific developmental windows. For example, observations of wild chimpanzees suggest that infants are significantly more likely to observe the nutcracking behavior of related individuals than juveniles or adults. There are many possible reasons for a kin bias in social learning. The simplest would be that if one is raised by a kin, they provide the most opportunities for social learning. Kin-specific traditions could also help related individuals identify one another, which may be useful for avoiding them when choosing a mate or banding together to form social alliances.

On the other hand, if one’s parents have had a particularly stressful life, this may indicate that they are not behaviorally well-suited to the current environment and therefore make poor role models. Experimentally elevated stress hormones in zebra finch (*Taeniopygia guttata*) nestlings caused them to switch from the developmentally typical strategy of copying their parents to exclusively copying unrelated adults (Farine et al. 2015). This finding emphasizes that social learning biases may vary greatly within a species according to an individual’s own life history. Dominant chimpanzees, for example, are less likely to use social information than subordinate individuals. Furthermore, young white-headed capuchins are more likely to be influenced by social information than older individuals, but both old and young monkeys are influenced by the relative payoffs of the behaviors they observe. These facts demonstrate that social learning biases vary not just between species, or between individuals, but also within individuals during their own lifetime. More often than not, culture is therefore likely to be the result of a tapestry of interacting biases.

Computer modeling of social learning behavior predicts that a very effective way of getting reliable social information is, instead of targeting specific individuals, to simply copy the behavior of the majority of one’s group. This tendency to be

disproportionately likely to copy the behavior of a majority (as opposed to the likelihood of copying the behavior if choosing a model at random) is known as “majority-biased transmission.” This is occasionally conflated with “conformity,” but a useful distinction is that while majority bias is something naïve individuals may do, conformist behavior requires the additional feature of relinquishing an existing behavior to converge on a majority preference. Both of these biases have been proposed as being crucial for stable, long-term culture, as without some process causing individuals to converge on a group “norm,” traditions may be eroded through copying errors and novel behaviors. Consequently, these biases have received considerable research attention.

The study of conformity behavior has its roots in social psychology. A seminal series of experiments carried out by Solomon Asch in the 1950s (Asch 1951) tasked small groups of people with judging which of three lines of varying lengths was the same length as the fourth line. Unbeknownst to the sole participant, every other individual in the group was a confederate of the experimenter tasked with unanimously giving the same incorrect answer. Even though this answer was obviously incorrect, around 30% of participants gave the same answer when it was their turn. However, they often did not do so when able to give their answer in private. This is suggestive of a powerful motivation in humans to conform to the normative behavior of those around us, an effect which has been replicated across cultures and age groups. Given that this behavior is so widespread in humans, there has naturally been an interest in whether animals behave similarly.

There is evidence for conformity in nine-spined stickleback fish (*Pungitius pungitius*), which, after learning the relative payoffs of two artificial feeders, relinquished their trained preference in favor of feeding at the same location as a group of individuals (Pike and Laland 2010). Further evidence for animal conformity comes from male vervet monkeys. After migrating to different groups, these monkeys have been found to conform to the food preferences of their new group, even though they had previously found that food to be unpalatable. Conformity has also

been identified in great tits (*Parus major*), which learned one of the two methods of operating a foraging box and then migrated to groups who used the alternative method. It was found that many of these individuals gave up their original behavior to adopt that of their new group (Aplin et al. 2015). However, a criticism of these studies, and a general difficulty with investigating conformist behavior, is that it is often challenging to differentiate the outcomes of so-called conformity from other social learning biases or even random-copying. Great methodological effort is required to disentangle these alternative explanations.

Despite the apparently wide taxonomic distribution of conformist behavior discussed above, evidence in chimpanzees is mixed. Observations of wild chimpanzees have recorded females who migrate between communities converging on the materials chosen for nutcracking used by their new group, despite no difference in availability of materials (Luncz and Boesch 2014). However, experimental studies have repeatedly failed to demonstrate such conformity. On the other hand, naïve chimpanzees preferentially copy a token-exchange behavior demonstrated once each by three individuals rather than a single individual demonstrating an alternative method three times (Haun et al. 2013), revealing a majority bias.

## Cumulative Culture

Although most researchers would now agree that culture is a widespread phenomenon across the animal kingdom, there is something strikingly unique about human culture in the way in which it continues to grow in scope and complexity over time, with each generation of learners modifying and adding to the body of knowledge that came before them. The complexity of these accumulated modifications has continued to ratchet up until most of the artifacts and processes we engage with on a daily basis could not have been invented by a single naïve person even if they spent a lifetime attempting to do so. It is this capacity to “stand on the shoulders of giants” that has allowed humans to thrive in almost every habitat on Earth, and it is known as “cumulative culture.” In this

capacity, humans are unquestionably preeminent. However, the jury is still out on whether this is a difference in quantity or kind.

Candidates for any degree of cumulative cultural evolution are rare in animals, and it may surprise some that perhaps the most compelling example to date comes from homing pigeons. Researchers found that groups of homing pigeons (*Columba livia domestica*) that had individuals replaced over time successively built on the efficiency of their homing route to the extent that the group would home more efficiently than solo individuals or groups with fixed membership (Sasaki and Biro 2017). Several candidates for cumulative culture have also been proposed in wild chimpanzees. Perhaps the most convincing of these is one community's method of termite fishing. Rather than fish horizontally at large mounds, as most chimpanzees do, this group uses a selection of stick tools to dig underground. This process involves selecting a particularly robust stick to penetrate the earth (often using a foot to provide extra force, just as one might with a spade) and several slimmer stems for insertion down the resulting tunnel, which must be stripped of leaves and pulled through their teeth to produce a "comb-like" end (Sanz et al. 2009). Though impressive, these examples still pale in comparison to the complexities of human cumulative culture, ranging from sophisticated tool kits to languages and religions.

Direct comparisons of 3–4-year-old children and chimpanzees have shed some light on this. One critical difference lies in our unique capacity for language, as children have been found to quickly engage in verbal teaching in complex tasks, allowing them to (a) inform others they have the solution, (b) impart this to them, and (c) correct any copying errors. Another potential roadblock for chimpanzees in particular appears to be behavioral inflexibility. There is some evidence that chimpanzees tend to get "stuck" on a method they have learned for solving a particular problem, thereby preventing them from "ratcheting up" the complexity of these methods in a cumulative fashion. This behavioral conservatism might also explain some absences of conformist behavior in chimpanzees described above.

However, there is some evidence that chimpanzees are motivated to relinquish an existing behavior when it becomes sufficiently inefficient and a more productive alternative is demonstrated in front of them. One thing to consider in such investigations is that although contemporary human culture changes at an unprecedented rate, our technological progress was in fact relatively static for millennia of the *Homo* genus' history. For instance, while stone-"flaking" technology dates back to between 2.6 and 3.3 million years ago, the first known cumulative development from stone flakes to more advanced "Acheulian" hand axes did not occur until around 1.8 million years ago, followed by relatively little progression for another million years or so, which corresponds to hundreds of thousands of generations. In light of these time scales, identifying instances of cumulative culture in animals is likely to be difficult – wild chimpanzees, for example, have been directly studied for only three to four generations, by comparison.

For a more in-depth review of cumulative culture, see the corresponding entry in this volume.

## Summary

Once thought to be a uniquely human trait, culture is now demonstrably widespread in the animal kingdom, incorporating a range of behavioral domains including foraging, communicative, and social behaviors. With a suite of biases to guide its adaptive use, social learning allows individuals to benefit from the hard-won knowledge of their conspecifics while paying relatively few of the costs. This capacity allows for rapid adaptation to changing environments or selective pressures that complements and has a reciprocal relationship with genetic inheritance, as the use of social learning is both shaped by genes (giving us the capacity for social learning in the first place) and may shape their further evolution. The study of culture and cultural transmission in animals is therefore critical not only in understanding this phenomenon but also for our understanding of the broader evolutionary processes that have shaped animal life. Complementary studies

of both captive and wild populations, using a combination of experimental and observational methods, are yielding an increasingly detailed understanding of cultural transmission in animals. Through comparisons with humans, this also informs us about our own evolutionary history with regard to what has made human culture unique and what common roots it developed from.

## Cross-References

- [Cultural Transmission](#)
- [Cumulative Culture](#)
- [Social Learning](#)

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increasingly more complex artifacts and systems (Boyd and Richerson 1995). By contrast, to many authors cumulative culture appears rare, if not altogether absent in nonhuman animals (henceforth “animals”).

Several animal species may show minimal or marginal grades of accumulation that we review below, but whether the products of this accumulation are truly beyond the innovative capabilities of any single individual remains a source of contention (Tennie et al. 2009). While some flexible modification of a tool, a foraging strategy, or a social behavior does indeed show cumulative like capabilities, this is arguably only a foundational step in relation to true cumulative culture. Human culture is characterized by such advanced technology that no individual could innovate the vast majority of our artifacts without using prior, socially endowed knowledge or skills. Instead, we build on the contributions of multiple innovators across generations to continually improve the productivity and efficiency of our technology, something no other animal shows such clear evidence of. Cumulative culture is also manifested in a profusion of other distinctive human domains, such as language, religion, science, and the arts.

## The Extent and Limits of Cumulative Culture in Chimpanzees

A majority of the debates on the existence of cumulative culture focus on our closest relative, the chimpanzee (*Pan troglodytes*), both because along with the less-studied bonobos, they are the species with whom we shared our most recent common ancestry and because their cultures appear to encompass the largest and most diverse arrays of traditions among nonhuman animals (Whiten et al. 1999). Chimpanzees possess some of the “raw ingredients” for cumulative culture, notably social learning (Whiten 2005), defined as learning from others, and innovative capability (Nishida et al. 2009), the latter defined as “the discovery of novel information, the creation of new behavior patterns, or the performance of established behavioral patterns in a novel

## Cumulative Culture

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## Introduction

The unique worldwide distribution and success of the human species compared to other primates are rooted in our capacity for cumulative culture, building onto and modifying socially inherited behaviors and technology to create



context” (Reader and Laland 2001, p. 788). However, long-term field studies of wild chimpanzees indicate that while innovation may be common, most innovations fail to spread through the rest of the population (Nishida et al. 2009). Although chimpanzees can potentially display relatively advanced social learning mechanisms and adaptive biases for using social information, they have been suggested to employ these under far more limited circumstances than humans, with less intrinsic motivation to engage in social learning (Herrmann et al. 2007). While there is evidence that chimpanzees possess a portfolio of different social learning mechanisms, the use of these is constrained by parameters such as the complexity and transparency of the task at hand: there are clear differences between the application of these learning processes in humans and chimpanzees, with humans having a greater tendency not only to use social information but to predominantly rely on high-fidelity mechanisms, such as imitation.

There is evidence that chimpanzees share some social learning strategies with humans, notably from whom to selectively copy and when to do so (Laland 2004), such as a preference to copy behaviors exhibited by a majority of conspecifics (Haun et al. 2012) and a proclivity to copy high-prestige individuals (Horner et al. 2010). However there are also important interspecies differences. For example, Marshall-Pescini and Whiten (2008) found that chimpanzees did not build on an existing tool-use technique to adopt a more complex method they saw others use to achieve greater rewards so long as their simpler, well-rehearsed solution produced some payoff. It was suggested that chimpanzees might rely on a copy-when-dissatisfied social learning strategy and so did not show cumulative learning in this study. However, recent studies have found contrary evidence that chimpanzees will relinquish a working solution (i.e., one that reliably produces reward) to adopt an alternative, higher payoff solution (van Leeuwen et al. 2013). Another explanation for Marshall-Pescini and Whiten’s findings is that chimpanzees are often conservative learners; that is, when chimpanzees have mastered a sufficiently rewarding behavior, they lack the behavioral

flexibility to modify that solution, with obvious consequences for the cumulative capabilities of the species.

All this being said, it is plausible that some behavior exhibited by wild chimpanzees is the result of a limited cumulative process. Boesch (2003) argues that nut cracking using an anvil stabilized by supplementary stones is an elaboration on an ancestral hammering method. Similarly, Sanz et al. (2009) argue that simple, unmodified tools were likely the precursors of more complex fishing tools with design features such as brush tips made by pulling stems through their teeth. Complex tool kits are also employed by wild chimpanzees involving the use of several, multifunctional tools in sequential order, indicative of some form of accumulation (Boesch et al. 2009; Sanz et al. 2010). Boesch (2012) offers further candidate examples of cumulative culture in wild chimpanzees. That chimpanzees have the relevant capabilities for such limited cumulative change is supported by recent experiments with captive chimpanzees which have found some evidence of cumulative build up in solution complexity (Davis et al. 2016; Vale et al. 2017). However, there is of course a lack of direct historical evidence that modern wild chimpanzees’ forebears used any less elaborate tool-based solutions than those seen today, and thus the argument of technological accumulation remains speculative in this respect (Dean et al. 2013).

### Cumulative Culture: Other Species

While chimpanzees (as well as humans) are by far the most well-studied species with regard to cultural capabilities and particularly cumulative culture, studies of other animals have recently provided evidence of such cumulative capabilities. For example, on a touch screen task, baboons improved the efficiency of their solutions to a pattern reproduction task along a chain of social learning episodes (Claidiere et al. 2014). Initially, 15 baboons were trained to memorize and recall the randomized location of four red squares in a grid of 20, where the other 16 squares were white. An iterative chain system was then implemented

whereby the behavior of the current participant then became the target behavior for the next baboon (instead of the presentation of randomized squares). Through generations, a systematic, cumulative pattern of behavior emerged, resulting in improved task performance. These results echo those in earlier studies that showed similar effects in human artificial language learning transmission experiments. In this case, for both human language learners and the baboons, the cumulative changes are in efficiency rather than rising complexity, for the material products actually become simpler and hence easier to remember.

Some avian species have also provided evidence of accumulation in behavior. New Caledonian crows display relatively complex tool-based foraging techniques, the distributions of which are consistent with the complex versions having arisen from modification on the simpler form (Hunt and Gray 2003). However, a role for social learning in the acquisition of these techniques remains to be clearly established. Most recently, Sasaki and Biro (2017) offered evidence from a quite different context: pigeon homing. These authors showed that pigeons would adopt more efficient homing routes across “cultural generations” generated by successively removing experienced birds from groups and replacing them with naïve birds, with evidence that performance was improved via social learning from prior such “generations” of pigeons. The context for this effect is that homing pigeons are known to devise homing routes both individually, and as part of a collective. While novice birds are guided by more experienced “leaders” within the collective, they can also contribute route innovations. To test if homing pigeons could build on their homing behaviors to iteratively improve their routes via social information, Sasaki and Biro repeatedly paired experienced and naïve birds in homing dyads to complete a navigational task. Each pair was given 12 trials to establish their route. In succeeding generations, the novice bird from the previous generation graduated to being an experienced leader and was paired with a new novice individual, and so on for five generations, giving a total of 60 trials across all the dyads. When performance of these changing dyads was

compared to controls on the same navigational task, Sasaki and Biro found that the last two dyad pairs outperformed individuals who had performed the task 60 times each, as well as pigeons who had been in consistent dyad pairs across the 60 trials (i.e., had the same partner across all 60 trials). Thus, here we see evidence of iterative improvement of a solution through social learning, a hallmark of cumulative culture. Of course, we cannot say that the best route is necessarily outside of the discoverability zone of all individuals, only that social learning across generations led to greater behavioral change and a subsequent convergence on the optimal route.

Other suggested examples of cumulative culture concern the songs of both birds (Lipkind and Tchernichovski 2011) and whales (Garland et al. 2017), which have been documented to change over time and, in that sense, evolve. The elaborate complexities of some songs suggest they may have arisen by cumulative culture; yet, as in many candidate examples other than experimentally controlled cases like those outlined above, we are handicapped by not having the historical records to confirm this.

In summary, the evidence for cumulative culture is very limited in nonhuman animals, and moreover a huge gulf lies between candidate behaviors for accumulation in animals and the technological and other complexities achieved in human culture.

## What Factors Are Limiting the Evolution of Cumulative Culture in Animals?

The core theoretical reasons for a lack of cumulative culture are commonly attributed to limited abilities to faithfully copy a behavior via observation from another individual, that is, to faithfully replicate the behavioral sequence inherent to a skill or artifact. As behaviors become more complex, an inability to copy their inherent action structure leads to errors in the replication process, and a likely failure to produce a functional result. Hence, even if complex innovations are invented in a species, without an ability to replicate them, they will remain unique to the innovators and fail

to spread to conspecifics. By contrast, humans readily learn from others' innovations through mechanisms such as imitation and teaching.

Low-fidelity social learning mechanisms may be one reason why nonhumans are limited in their cultural capabilities, but they are by no means the whole story. Other likely explanations are centered on the heuristics, or decision rules, governing when to change known solutions to a problem and adopt (or attempt to adopt) a potentially more optimal solution. This may be considered an "explore versus exploit" decision. Decisions which involve the use of social information are often referred to as social learning strategies (Laland 2004). For example, humans may employ a strategy such as "copy when better": when we observe a behavior which is superior to our own in terms of payoff or efficiency, we may choose to copy based on that comparison. This is a powerful driver of increasing behavioral complexity and leads to more productive outcomes inherent to cumulative culture (Mesoudi 2011). In contrast, nonhumans may rely on less cognitively demanding strategies, such as "copy when dissatisfied": instead of taking optimality of behavioral variants into consideration, an animal may take into consideration only whether their own current behavior is producing some satisfactory outcome. Regardless if there exists a far more productive alternative solution to a problem, the individual will persist with their own behavior. This would lead to a stall in behavioral accumulation because once a satisfactory solution is found, the individual will cease to explore the problem space, limiting the opportunities to build on behavior and enter into the realms of cumulative culture.

A further constraint on culture is the behavioral flexibility of a species, individuals' disposition or ability to relinquish or modify an existing solution. While typically a lack of behavioral change is ascribed to some suboptimal use of information, such as a failure to adopt another variant due to low-fidelity transmission or a stasis-inducing learning strategy, it is quite likely that many species may be behaviorally inflexible due to limited cognitive resources. With finite resources, an individual may struggle to inhibit the use of an old

solution while simultaneously holding in mind the new solution, and then switching to this new solution.

## The Slow Emergence of Cumulative Culture in the Human Animal

The high-fidelity social transmission processes of humans, along with the social learning strategies we employ, are thought to be responsible for allowing us to continually build upon the innovations of previous generations. When and how our ancestors acquired the ability to "ratchet" cultural complexity over time is still unclear. Although Oldowan technology exceeded the capabilities of extant wild great apes (Whiten et al. 2009), it was not for another million years that we begin to see significant advances, with the advent of Acheulean technology. It was not until between 160,000 and 40,000 years ago that we really see an unprecedented acceleration in cumulative culture. It is likely that before this time, our ancestors, although perhaps capable of halting cultural ratcheting, had reached some technological ceiling in the Stone Age. What, then, changed? Although there are several hypotheses, it has been suggested that technology eventually overtook that of other species due to changes in hominin social organization and demographics (Henrich 2004). Whether the changes in hominin cultural capabilities were driven by socio-cognitive advancements which led to changing demographics or vice versa is hard to disentangle. Either way, the increasing sociality of hominins may have led to the advancement of already existing social learning skills such that, over time, stable and complex cumulative culture became possible, as evidenced by later Acheulean technology. This is consistent with models which suggest that cultural complexity is achieved when learners have access to large social networks of individuals (Enquist et al. 2010) and is supported by experiments examining the effects of the number of available models on skill advancement and cumulative achievements (Derex et al. 2013). With increasingly sophisticated social organization, our ancestors would have been in a

position to donate technology (such that a learner could forego steps within the ratchet) and allow for specialization and division of labor within groups. Increased network size also means greater opportunities to learn from innovators via increasing the pool of innovators available, as well as sharing and collaborating in knowledge generation and technology (Tomasello et al. 2012).

Our ability to maintain, propagate, and continually build on complex knowledge, skills, and technology has afforded our species a highly advanced “second inheritance system” (Whiten 2005). Cumulative culture has allowed us to far exceed the general intelligence of any other known species, to cultivate resources in an unprecedented way, and to modify our environment to fit our needs and convenience.

## Cross-References

- Culture
- Cultural Transmission
- Social Learning

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## Curiosity

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*Oxford English Dictionary*

1. A strong desire to know or learn something
2. An unusual or interesting object or fact

*Cambridge Dictionary*

1. An eager wish to know or learn about something *to arouse/excite/satisfy someone's curiosity*

*American Dictionary*

1. An eager desire to know or learn about something

There is not a single universally accepted definition of curiosity, but research on this phenomenon is dominated by three main traditions. The first and oldest builds on the drives theory (exploratory and boredom drives). The second is linked to the ideas of D. O. Hebb, which draw on the hypothetical state of optimal arousal. The latest approach emphasizes the “informative” aspect of exploration. The most widely accepted definition is that of “epistemic curiosity,” which Berlyne described as a drive aimed “not only at obtaining access to information-bearing stimulation, capable of dispelling uncertainties of the moment, but also at acquiring knowledge” (Berlyne 1966, p. 31). Since the first two traditions specifically seek to explain exploratory behavior in animals, they will not be discussed in this paper. Regardless of the specific theoretical claims, the key element in curiosity-stimulating mechanisms is the novelty of the stimulus.

There are two aspects to the rewarding properties of novelty. The first is linked to the fundamental mechanism of sensory reinforcement, first observed in 1950s and subsequently incorporated into a theoretical system by D. O. Hebb (1955) and G. B. Kish (1955). Sensory reinforcement is a primitive mechanism in animal behavior and it is largely independent of novelty. For instance, rats may learn to push a lever in Skinner boxes by being rewarded with a weak light stimulus, but that effect does not disappear with progress in learning. When complete contingency between the behavior under study and the exposure to the stimulus is established, the reinforcement mechanism does not fade. Animals still display instrumental reactions even though there is no novelty and no element of uncertainty in a given situation. This phase of behavior can be described as stimulus-seeking behavior, which is basically driven by the second motivational component, namely, stimulation-seeking. At the heart of the controversy surrounding the rewarding properties of novelty lies the concept of novelty itself. Interpretative problems arise when analyzing animal behavior when faced with complete novelty. What needs to be



determined in this context is whether complete novelty is merely a complete change in the configuration of environmental elements, or whether it must also involve a change in the intensity of stimulation.

Regardless of the neural basis for various motivational processes, which may differ between organisms at various stages of evolutionary development, the rewarding, pleasure-inducing character of stimulus novelty is undoubtedly the most important aspect. The willingness to detect, recognize, and seek novelty must be regarded as a fundamental motivational process regulating human and animal behavior alike. Exploratory behavior, which is aimed at investigating the environment, seems to be the natural foundation for human curiosity about the world. Undoubtedly, exploration plays an important part in human and big-brained animals' behavior. Whether fairly simple or highly complex, exploratory behaviors form part of the behavioral repertoire.

D. Berlyne (1962) was the first researcher to study curiosity in a systematic manner. Although Berlyne himself did not make use of the integrative levels theory as a theoretical tool, his concept of "epistemic curiosity" may undoubtedly be regarded as the most advanced form of exploratory behavior (Pisula 1998). Berlyne saw curiosity as a product of the same processes that had shaped the evolution of human and animal exploratory behavior. He coined the term "epistemic behavior" to denote activity triggered by cognitive curiosity. Epistemic behavior comprises three categories: epistemic observation, which includes experimental and other observation-based scientific techniques; consultation, which involves asking other people questions or consulting reference books, databases, networks, and other sources of information; and directed thinking. Epistemic observation seems to be a direct product of perceptual exploration and manipulation. The purpose of this activity is to gather nonsymbolic information, which means observable indices, registered directly by our senses or with the help of scientific equipment. Observation is undoubtedly driven by symbolic processes, but in the case of

epistemic observation, the fundamental aspect is the focus on phenomena directly observable through the senses or scientific tools.

Consultation is an important advantage in the process of information-seeking in humans, when compared to other animals. Asking questions, searching for answers in online documents, databases, books, libraries, and other modern sources of information – all this helps construct the image of the modern human being as endowed with an insatiable appetite for information.

Directed thinking is a particularly intriguing and complex area. On the one hand, prolonged fixation of thought processes on a single object may be a symptom of pathology: Berlyne noted certain similarities between directed thinking and autistic thinking. However, in the first case, an individual is able to resist persistently returning to the same train of thought, to view a given issue from various perspectives, and to produce new content in a creative manner. Human curiosity is a recurrent motif in cognitive psychology and the psychology of creativity. D. Berlyne was also the first to list curiosity-arousing factors which he labeled "collative variables." These variables include: novelty, complexity, and surprise. Berlyne treated these variables as quantifiable, although he admitted that measurement could be problematic. This means that a given stimulus could be described in terms of the degree of novelty or complexity.

This part of Berlyne's analysis has come to be regarded as a lasting contribution to the body of knowledge about cognitive curiosity. Some of the ideas related to motivational processes proposed by Berlyne are debatable, but the validity of his conceptual system describing the properties of stimulation that triggers curiosity has never been challenged.

Three decades later, George Loewenstein (1994) systemized scientific knowledge about epistemic curiosity by making a clear distinction between information-seeking behaviors related to factors occurring in environmental settings, on the one hand, and intrinsic factors evoking curiosity, on the other. Many people (managers, patients wishing to find out about their prognosis and treatment options, journalists, etc.) constantly



seek information. Some of them do it as part of their professional duties, but one could hardly describe their curiosity as intrinsically motivated. Their actions are shaped by their roles, circumstances, or professions. G. Loewenstein noted another vital aspect of human curiosity: in order to become curious, the individual must realize that he/she has less information about a given subject than is generally available. The urge to close that information gap is the key factor driving curiosity. Loewenstein's reasoning is linked to *Gestalt* psychology and modern cognitive psychology.

In a more recent work, Loewenstein slightly modified his terminology. Although the term "epistemic curiosity" is widely accepted by researchers not directly involved in this field of research, experts in the field criticize it as too general and of little scientific use. The term that has gained popularity instead is "interest." In his elaboration of Loewenstein's concepts, P. J. Silvia (2008) considered the advances in modern psychology of emotions and stress. Referring to the functional analysis of emotions, he defined the function of "interest" as motivation for learning and exploration. Novelty, complexity, unexpectedness of stimulation can evoke curiosity, in accordance with Berlyne's classic theory. The prerequisite, however, is comprehensibility. Humans try to understand a novel situation. If an individual's assessment of such a situation results in a positive conclusion about the individual's ability to cope with the demands, then curiosity is aroused, which leads to learning, exploration or, as suggested by Loewenstein, to closing the information gap. However, if the conclusion from this initial assessment is that the demands of the situation are excessive (e.g., the material at hand is too difficult for the subject to learn), what follows is withdrawal and stress.

Research confirms this hypothesis. J. A. Litman, T. L. Huthins, and R. K. Russon (2005) conducted an experiment in which they manipulated the information gap from the "I know" status through "Tip of the tongue" to "Don't know." It showed that curiosity was mostly triggered by the "tip of the tongue"

situations. They corresponded to sensations described by the participants as "sense of knowing." The participants also typically defined curiosity as significant information deprivation and adjusted the intensity of exploration accordingly. The "I know" category did not arouse curiosity or exploration. The "Don't know" situations did not trigger a much curiosity defined as deprivation of knowledge about a given subject, but evoked positive attitudes characterized as "interest."

T. G. Reio Jr. J. Petrosko, A. K. Wiswell, and J. Thongsukmag (2006) verified the validity of epistemic curiosity using psychometric data. In a comprehensive study conducted on a few hundred students, they collected results from several scales measuring various forms of curiosity. The Confirmatory Factor Analysis confirmed that human adults demonstrate two main forms of curiosity: cognitive curiosity and sensory curiosity. The latter may be clearly divided into two subcategories: physical thrill seeking and social thrill seeking. Those subcategories are the main components of what M. Zuckerman called "sensation seeking" (Zuckerman 2003). Cognitive curiosity is a typically human mechanism involving hunger for information whereby the key element is the information content of stimulation. In the case of sensory curiosity, the human brain is saturated with pleasant sensory stimulation associated with physical or social activity.

Similar results were obtained by J. A. Litman and P. J. Silvia (2006), who also conducted a study on several hundred participants, using a series of tests measuring various forms of curiosity. They obtained a similar main effect of a factor which they called Epistemic Curiosity, after Berlyne (1962), and a second factor called Curiosity Deprivation. Despite the differences in the theoretical approaches adopted by the aforementioned authors, the structure of the dimensions they proposed involves some stable model of information-oriented curiosity (epistemic or cognitive) and sensory, or stimulation-oriented curiosity (sensory/deprivation). There are solid grounds for believing that the perceptual exploration observed in higher animals is a prerequisite for the development of

sensory curiosity, which in turn is the basis for the development of the typically human curiosity, which we may call “information curiosity” or “information hunger.”

There have been many publications about the role of curiosity in animal and human behavior, which clearly suggests that its importance must not be underestimated. Satisfying one’s curiosity is a powerful reward in itself. For this reason, it would seem that our knowledge about sensory reinforcement, curiosity, and exploration may provide sufficient basis for developing a friendly and stimulating educational environment. As recently pointed out by Kidd and Hayden (2015), however, there are several basic questions that still require more definite answers. The four crucial ones are:

- In what ways does curiosity resemble other basic drives? In what ways is it different from those drives? To what extent is curiosity fundamentally different from drives like hunger and thirst?
- What is the most useful taxonomy of curiosity? How well does Berlyne’s categorization hold up? Which factors are common to the various distinct forms of curiosity?
- How is curiosity controlled? Which factors govern curiosity, and how does the brain integrate these factors into decision-making to produce decisions? To what extent is curiosity context-dependent?
- To what extent does curiosity in nematodes overlap (if at all) with curiosity in children? How useful is it to think of curiosity as being a single construct across a broad range of taxa?

Curiosity is therefore an intriguing aspect of regulating human and animal behavior which merits further research.

## Cross-References

- [Exploratory Behavior](#)
- [Neophobia](#)
- [Novelty](#)

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## Cutis and Its Derivative

- [Integumental System](#)

## Cylinder Task

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### Synonyms

[Detour-reaching task](#); [Detour task](#)

### Definition

A task that measures inhibitory control – the ability to inhibit inappropriate or disadvantageous responses – using a reward placed within a transparent cylinder. Subjects must inhibit moving directly toward visible reward and instead reach through one of the cylinder openings at either end.

### Introduction

A lioness spots a gazelle several meters away on a hill, but a line of tall savannah grass separates her from her prey. She can proceed directly toward the gazelle, but crashing through the grass would alert the prey to her presence. Alternatively, she could inhibit the impulse to run straight toward the prey and detour around the tall grass to a better location from which to launch her attack. Similarly, a subordinate chimpanzee may inhibit its desire to mate or forage when in view of a dominant conspecific but seek those opportunities when out-of-view behind a barrier. Animals face many problems that require them to inhibit an action in lieu of a different, more goal-consistent behavioral strategy.

Inhibitory control is the ability to inhibit a powerful, almost automatic (prepotent) response. Since prepotent responses often run counter to one's goals, inhibitory control is a core feature of

executive functioning – the top-down cognitive control processes that allow individuals to remain on track and achieve desired goals. In the case of the lioness, she must inhibit the prepotent desire to move directly toward visible prey.

Researchers have used many tasks to measure inhibitory control (Table 1). Detour tasks require subjects to detour around an obstacle or barrier to reach a desired location. The cylinder task is a specific form of detour task in which subjects must retrieve a reward, typically a food item, from within an opaque or transparent cylinder. This task, along with other detour tasks, requires subjects to first inhibit the prepotent motor response to move directly toward the visible reward. Instead, they must detour around the barrier walls to obtain the reward through an available opening.

Other tasks require less motor action by focusing on choice or the withholding of responses. In reverse contingency and A-not-B tasks, subjects attempt to obtain a reward by choosing between a set of limited choices, with the prepotent choice not providing the reward. Similarly, Go/no-go tasks train subjects to respond to a frequently presented stimulus, but this prepotent responding must be inhibited in certain situations. In delay of gratification tasks, individuals must inhibit taking a reward that is available immediately or after a short delay to obtain a more desirable reward available after a longer delay.

### Cylinder Task Procedure

The basic procedure of the cylinder task involves three phases:

- **Habituation phase:** Subjects habituate to the testing environments. This often involves exposure to elements of the task that subjects have never, or rarely, encountered, such as exposure to human experimenters, tracking hand movements, and the presence of opaque cylinders.
- **Training phase:** An experimenter baits an opaque cylinder by placing a desired reward in the center (Fig. 1a). To correctly respond,

subjects must detour around the opaque cylinder and reach through one of the openings to obtain the reward. Touching any part of the opaque wall first counts as an incorrect response. To proceed to the next phase, subjects often must reach a certain criterion level of success, typically 80% correct responses in consecutive trials.

- **Testing phase:** This phase is the same as the training phase, except with a transparent cylinder (Fig. 1b). Subjects must inhibit their

prepotent response to reach directly for the desired reward, hitting the transparent wall. Instead, they must continue around to the ends of the cylinder to acquire the reward. Researchers often measure performance as the proportion of correct responses or the number of test trials required until the first correct response.

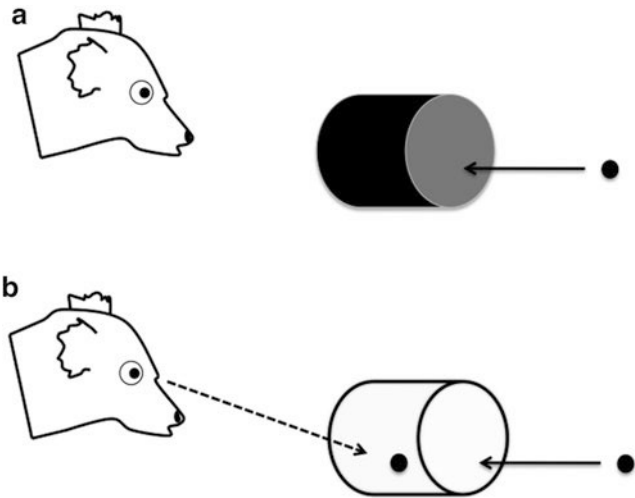
**Cognitive Capacities for Inhibitory Control**

Correctly avoiding the barrier and detouring through one of the openings requires several cognitive capacities. In the training phase, the subject must maintain a memory of the object after it is hidden inside the opaque cylinder (object permanence). In the testing phase, the subject must understand the nature of physical barriers. In particular, they must understand the solidity principle in which one solid object cannot pass through another solid object. This is particularly relevant to transparent barriers where a subject’s visual and tactile cues conflict. Lastly, the subject must combine knowledge and solve the problem at hand to achieve the goal of obtaining the reward. Subjects can see the reward through the transparent barrier, but they cannot directly access the food; therefore, they must move around the barrier to reach the reward. To succeed in this task, subjects must understand the physical state of the world

**Cylinder Task, Table 1** Inhibitory control tasks

| <i>Detour tasks</i>           | <i>Example reference</i>    |
|-------------------------------|-----------------------------|
| <b>Cylinder task</b>          | Boogert et al. (2011)       |
| Other shapes (cube/box)       | Diamond (1981)              |
| Fence/barriers                | Köhler (1925)               |
| <i>Choice tasks</i>           |                             |
| Reverse contingency           | Boysen and Berntson (1995)  |
| A-not-B                       | Piaget (1954)               |
| Go/no-go                      | Mishkin and Pribram (1955)  |
| Serial reversal               | Mcculloch and Pratt (1934)  |
| <i>Delay of gratification</i> |                             |
| Delay maintenance             | Grosch and Neuringer (1981) |
| Accumulation                  | Beran et al. (1999)         |
| Exchange                      | Ramseyer et al. (2006)      |

**Cylinder Task, Fig. 1** The cylinder apparatus. The training phase involves obtaining a reward from within an opaque cylinder (a). After reaching criterion, the testing phase involves the same procedure, except with a transparent cylinder (b). Subjects must inhibit the prepotent response to move directly forward and instead detour through one of the cylinder openings (Used with permission from MacLean et al. 2013)



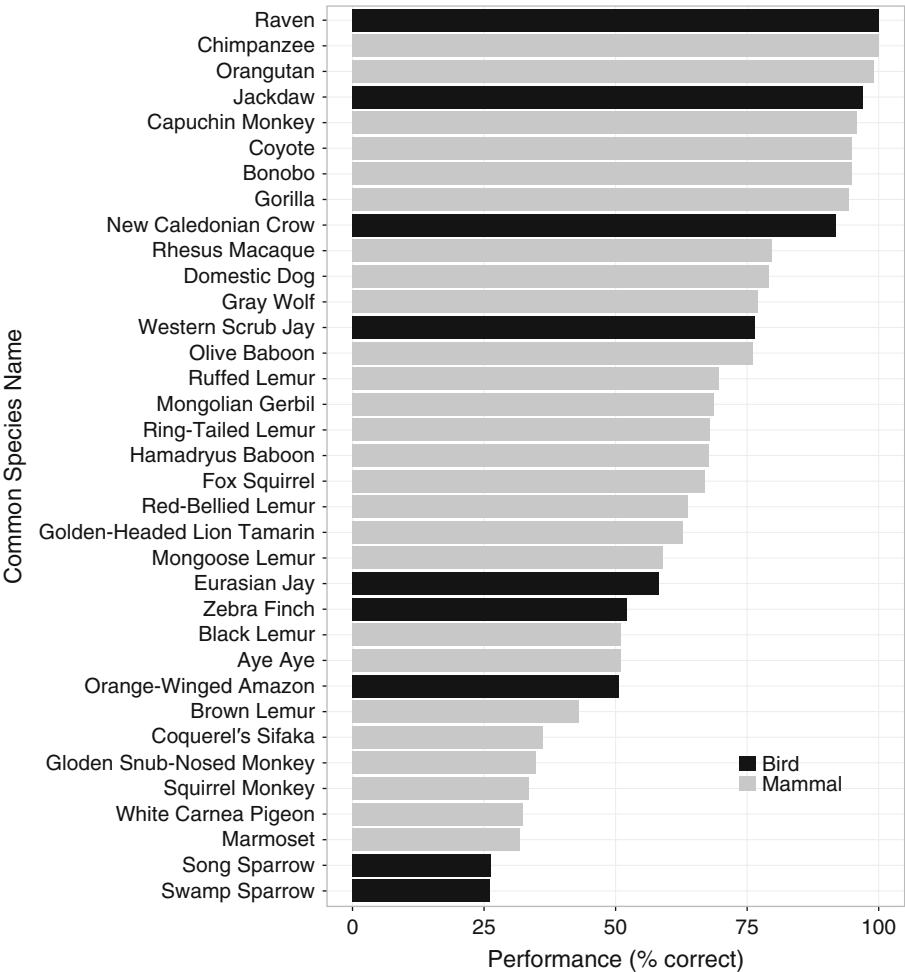
(object permanence and solidity principle) and exhibit an appropriate behavioral response (detour-reaching).

Behavioral Results

The simplicity of the cylinder task makes it easily amenable to comparative studies. Indeed, researchers have tested several dozen species, ranging from pigeons to primates. Overall, great apes, capuchin monkeys, rhesus macaques, canids, and corvids perform the best with greater than 70% correct responses (Fig. 2). Interestingly,

some corvids match or even surpass the performance of great apes.

Researchers have examined several evolutionary factors that may account for these species differences in performance. Phylogenetic comparative methods indicate that absolute brain volume predicts species differences in performance, along with relative brain volume and dietary breadth. However, species differences in performance may also result from how the animals engage in the task. Factors such as a subject’s motivation, prior experience with opaque/transparent barriers, amount of habituation and training trials prior to testing, and the degree of experimenter



Cylinder Task, Fig. 2 Species performance in cylinder task. MacLean et al. (2014) and Kabadayi et al. (2016) tested a combined 36 species of birds and mammals in the

cylinder task. They report each species’ mean percentage of correct trials during the testing phase

involvement during the task can influence performance. Therefore, without further investigation into the various contextual factors that impact performance, species differences should be interpreted with care.

The cylinder task is one of a suite of inhibitory control tasks. To assess whether inhibitory control is a unitary construct, researchers have tested the same subjects in multiple inhibitory control tasks. In general, within-individual performance across inhibitory control tasks, e.g., A-not-B and the cylinder task, does not correlate. These findings suggest that inhibitory control is multifaceted and that different inhibitory control tasks vary in the precise mechanisms activated.

## Conclusion

Inhibitory control is a critical component of executive functioning, ensuring that individuals maintain appropriate, goal-directed behavior. Detour tasks, such as the cylinder task, test an individual's ability to inhibit a prepotent desire to move directly toward a visible reward. Species vary in their propensity to correctly solve the detour task, and there may be evolutionary reasons for the species differences. Yet, we currently do not have a clear understanding of the contextual factors influencing performance on the detour task. Such data would be useful in elucidating the proximate mechanisms subjects use during task performance and could clarify why results across multiple inhibitory control tasks do not always correlate.

## Cross-References

- A-Not-B Problem
- Associative Learning
- Behavioral Flexibility
- Behavioral Variation
- Canine Cognition
- Comparative Cognition
- Comparative Psychology
- Correlation
- Corvids
- Delayed Gratification
- Detour Task
- Go/No-Go Procedure
- Goal-Directed Behavior
- Intelligence
- Learning
- Michael J. Beran
- Passerine Cognition
- Platyrrhine Cognition
- Primate Cognition
- Problem-Solving
- Proboscidea Cognition
- Prosimian Cognition
- Reversal Learning
- Rodentia Cognition
- Species-Specific Behavior
- Transfer of Learning

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## Darwinian Fitness

- [Inclusive Fitness](#)

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## Dassie

- [Hyracoidea](#)

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## Data-Driven Processing

- [Bottom-Up Processing](#)

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## Dauer

- [Developmental Arrest](#)

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## Daughter Chromosomes

- [Chromatid](#)

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## Daughter Guarding

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### Synonyms

[Daughter-guarding hypothesis](#); [Parent-offspring conflict](#)

### Definition

A hypothesis designed to describe parental control of sexual behavior and mate choices of daughters.

### Introduction

Human mating decisions are not made in a social vacuum; rather, members of the local community and external surroundings, especially close kin and coalitional allies, affect them. Parents can be particularly powerful influencers of their children's mating decisions because of their unique position in their children's lives. Parents are typically proximately close and may provide

substantial resources to children that are required to pursue mating choices, giving parents special leverage over children compared to others (Apostolou 2007, 2010; Perilloux et al. 2008). In anthropological investigations of marriage types across hunter-gatherer societies, parent-arranged marriages are the most common, occurring in 69% of societies. Close kin arranged marriages (marriages arranged by family members other than the parents) were the next most common, occurring in 18% of societies (Apostolou 2007). These two types of marriage were the most common marriage types in all geographical areas surveyed.

Parents are particularly motivated to influence their offspring's mate choice because of the closely linked reproductive consequences. Parents share a genetic relatedness coefficient of 0.50 with their offspring, meaning that decisions by offspring greatly impact parental fitness, including in the form of grandchildren with whom they share a genetic relatedness coefficient of 0.25. The parents, particularly the mother/maternal grandmother, will be certain that the grandchild is related to them. Investing in their daughter and daughter's children may be more profitable than investing in a son and son's children as there is more certainty of genetic relatedness in the former than in the latter (Apostolou and Papageorgi 2014; Perilloux et al. 2008; Trivers 1974).

Additionally, successful mating decisions may lead to myriad benefits including high-quality genes, resources, protection from threats, social alliances, social status enhancement, and psychological support required for survival and reproduction. These benefits give parents motivation to intervene in their children's mating behaviors (Apostolou and Papageorgi 2014). Anthropological studies indicate that fathers more than mothers attempt to control their children's mating choices, and this control is more focused on daughters (Apostolou 2012). Fathers may have more to gain than mothers from marrying their daughters to other men, including social status, powerful allies, and riches obtained from suitors and their families (Apostolou 2012; Perilloux et al. 2008). This can affect father's successes if they are able

to obtain new wealth or become more reproductively valuable as a consequence.

While parents guide their offspring to make particular mating choices, conflict arises as the two parties (parents and offspring) often do not agree. Conflict between parents and offspring about mate choice occur in many domains, including valuations of a prospective mate's traits. Parents and children are genetically related, but not genetically identical; their genetic interests overlap but also diverge (Trivers 1974). The desires of children compared to parents differ in terms of which traits are viewed as most valuable in a mate. Adult children more than their parents prefer characteristics signaling genetic quality (i.e., physical attractiveness and intelligence), while parents more than children value characteristics signaling future investment in grandchildren and in-group cooperation (i.e., similar religious belief, similar social status, or ethnic background) (Apostolou 2010; Fugère et al. 2017, Perilloux et al. 2011). These findings are robust across cultures. To improve their own fitness, offspring seek mates of high genetic quality; while to improve parent's fitness, parents are interested in in-group cooperation and investment in future children (Dubbs et al. 2013; Fugère et al. 2017).

Across cultures, parents behave differently toward sons and daughters in their attempts to influence mate choices and sexual behaviors. The consistent trend is that parents perform more behaviors to dissuade, manipulate, reduce, or thwart sexual behaviors of daughters compared to sons (Perilloux et al. 2008). The research conducted by Perilloux et al. (2008) led to the Daughter-Guarding Hypothesis. This hypothesis states that humans have adaptations that motivate protecting their daughter's sexual reputation, preserve their daughter's mate value, and prevent their daughters from being sexually exploited (Perilloux et al. 2008). Perilloux et al. (2008) administered questionnaires to parents asking how likely they would be to allow their children to engage in various behaviors. These questions ranged from clothing choice, mate choice, driving behaviors, and curfews. The results indicated that parents were much stricter with their daughters than with their sons in the majority of

circumstances. This survey also included four questions focused on parental attitudes related to guarding, asking about parent approval of their child's sexual activity. Once again, daughters were held to stricter standards and caused greater parental upset than sons performing the same acts (Perilloux et al. 2008). Children of these parents also completed a survey and daughters reported significantly less parental approval of each of the four acts compared to sons.

Manipulation is a common tactic that parents use to influence the mate choice of their offspring in Western, postindustrial societies, because in the modern environment, resources are more equally distributed among offspring and fewer arranged marriages occur in Western societies (Apostolou and Papageorgi 2014). Manipulation is used more often on daughters than on sons (Apostolou and Papageorgi 2014). In addition, mothers more than fathers report use of more manipulation tactics on their children to influence mate choice (Apostolou and Papageorgi 2014). Children also use manipulation tactics to persuade their parents to accept their mate choices or to persuade them to change their assessment of particular mating relationships. Daughters use manipulation tactics against parents more than do sons (Apostolou and Papageorgi 2014). Daughters' manipulation of parents may be designed to secure a mate that possesses more characteristics signaling high genetic quality rather than future-oriented commitment and investment.

Daughter guarding may occur to protect the fitness interests of the daughter as well as parental fitness interests. When comparing sons and daughters, parents are more likely to guard daughters than sons because of asymmetries between the sexes (Perilloux et al. 2008). Sexual asymmetries in reproductive biology produce sex differences in costs from recurrent adaptive problems such as rape, sexual victimization in other forms, and unwanted pregnancy. Women incur more costs from each of the aforementioned adaptive problems (unwanted pregnancy, violence and pain, or tarnished reputation) leading to more protection from parents (Trivers 1974). An early example of daughter guarding was identified by Flinn (1988), who documented that

fathers living in a Trinidadian village required their daughters more than their sons to take chaperones with them wherever they went, thus restricting their daughter's movements more than their son's. These fathers also threatened other men who came to visit their daughters (Flinn 1988).

## Conclusion

Daughter guarding is executed by parents to protect their daughters from sexual exploitation and from making mating decisions that parents perceive as mistakes. Protection manifests in many forms, including vigilance, strictness, forbiddance, curfews, chaperones, and dress codes. Daughters are subjected to greater parental guarding than sons as the certainty of relatedness of parents to resulting offspring by daughters is greater than to offspring by sons, in addition to the greater harm that daughters (and therefore parents) face from sexual exploitation of women by men.

## Cross-References

- ▶ [Parental Investment Theory](#)
- ▶ [Parent-Offspring Conflict](#)

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## Daughter-Guarding Hypothesis

### ► Daughter Guarding

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## David Attenborough

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David Frederick Attenborough, born in 1926, on the 8th of May is best known as a naturalist and as a broadcaster. Within his career, spanning over 60 years, he came to be known as one of the most popular experts on animals. He has penned and presented a natural history documentary which comprises a set of 24-disc DVD box set, which was named the Life Collection. This collection was released on 5th December in the United Kingdom and the episodes covering all domains of life like Life on Earth, The Living

Planet, The Trials of Life, and Life in the Freezer and throws light on The Private Life of Plants, The Life of Birds, The Life of Mammals, and the Life in the Undergrowth.

## Early Life

David Attenborough was born in Isleworth in Middlesex but was brought up on the campus of University College in Leicester. He thus spent his initial years in College House on the campus, and his father Frederick Levi Attenborough was the principal of the University College. Academy award-winning actor-director Richard Samuel Attenborough was his elder brother, and Alfa Romeo motor executive and then financial advisor John Michael Attenborough was his younger brother. Son of Frederick Attenborough and Mary Attenborough, David Attenborough is the second of the three sons and currently, the only one surviving.

Attenborough's fascination with nature has its origin in his formative years, which he spent collecting natural specimens, bird eggs, fossils, and stones. In 1938, during the build-up to the Second World War, Sir David's parents helped some of the many children fleeing from Germany. They have left their families behind and could bring almost nothing with them. One of them once gave Sir David a piece of amber that had some creatures embedded in it. Fifty years later, he wrote and presented the BBC documentary, *The Amber Time Machine* based on that.

In Leicester, Sir David was a student at the Wyggeston Grammar School for Boys and having secured a scholarship, he went on to pursue his degree in natural sciences as a student of Geology and Zoology from Clare College, Cambridge. In 1947, he did national service in the Royal Navy.

## Early Career

In 1950, David Attenborough worked in a training program at British Broadcast Corporation (BBC). The same year, he got married to Jane Elizabeth Ebsworth Oriell. He edited children's textbooks

after leaving the Navy before applying for his next job in BBC as a talk producer on the radio. He was rejected for the job but the head of Talks department of BBC, Mary Adams, got drawn into his CV and this soon gave Sir David his full-time job at BBC in the year 1952. He joined BBC at a time when there were almost no programs dedicated to natural sciences. Starting at such a juncture, he went on to embark on a multitude of projects, starting from a quiz show named *Animal, Vegetable, Mineral?* David Attenborough also worked on a folk music series named *Song Hunter*.

## Style and Nuances

Sir David was averse to the idea of deracinating animals from their natural habitats and transporting them to the harsh environment of TV studios. He pioneered the trend in filming animals by sending out crews into the wild to capture the images on location. Along with Sir David, Julian Huxley, another well-known naturalist, featured animals from the London zoo; explaining courtship, aposematism, camouflage, and their use. This three-part series named *Animal Patterns* was presented and produced by Attenborough, and it was through this studio-bound natural history program that David Attenborough met Jack Lester. Together, they made a series about an animal-collecting expedition, named *Zoo Quest*. Jack Lester was the curator of the reptile house of the zoo. This series was first broadcasted in 1954. The huge success of the show resulted in BBC establishing its Natural History Unit (David Attenborough n.d.).

In the early 1960s, Attenborough parted ways with the BBC, resigning from his permanent staff position in early 1960s to get his postgraduate degree in Anthropology from the London School of Economics. He joined BBC again, even before he could complete his degree, as the controller of BBC Two, the second flagship television channel of BBC.

He continued to be instrumental in making pioneering content with series such as *The Ascent of Man* and *Civilization*. In 1965, even though he was the controller of BBC Two, due to a clause in

his contract that allowed him to produce films, he was able to film Tanzania's elephants, while in 1969 he produced a series consisting of three parts on the Island of Bali in Indonesia depicting its cultural history. The following year, he was honored with Desmond Davis Award by British Academy.

He went to a New Guinea to a remote highland valley to seek out a lost tribe. This was for the television documentary *A Blank on the Map* released in 1971. Attenborough also helmed other famous series like *The Trials of Life*, *The Living Planet*, *The Life of Mammals*, *Life in the Undergrowth*.

Sir David changed the schedules as BBC Two was not doing very well. As a controller, he changed the mascot of the channel which was a quirky kangaroo and introduced programs related to drama, sports, science, natural history, entertainment, art, music, travel, archaeology, and even experimental comedy for viewing.

## Breaking New Ground

Some programs he commissioned are *The Old Grey Whistle Test*, a British music show, *The Money Program*, a finance and business affairs program, and many others like *Life*, *Monty Python's Flying Circus*, *Call My Bluff*, *Chronicle*, etc. Televised snooker and rugby league were introduced by Sir David as a controller when BBC Two became the first British television channel to broadcast in color.

BBC Two started offering an Ultra High-Frequency color television service. Sir David ordered a 13-part series to be made on Western art history. This decision was very significant. Another documentary series named "Civilisation" written and presented by Kenneth Clark was produced by BBC in 1969 that aired on BBC2. Attenborough, in 1969, controlled the output of both the BBC television channels as he had been promoted to the post of director of programs. He left his post and returned to program-making, which meant he had free time to invest in writing and presenting the natural history epic that he had planned. One of his landmark successes came



when his 96-episode program *Life on Earth* released, which employed advanced filming techniques, garnering hundreds of millions of viewers.

In the subsequent years, he produced a host of other series, aimed at documenting animal behavior. The 10-part series won him the Peabody Award. *Wildlife on One* aired from 1977 to 2005, having 250 episodes. Planet Earth was the first High-Definition show aired on BBC in 2006 and it is also the first extensive wildlife documentary ever made.

## Awards and Fame

Throughout his life, Attenborough has won several awards and accolades and has received immense fame and recognition. He was featured on a list of 100 great British heroes in a 2002 poll conducted by BBC, wherein people of Britain were asked to pick a person who, according to them, epitomized greatness. The list included scientists, inventors, and even royals. In 2006 Reader's Digest poll, he was named the most trusted celebrity. He was knighted in 1985 and holds several honorary degrees from British Universities. Several species of birds, animals, and insects have been named in Attenborough's honor. Some of them are *Pristimantis attenboroughi* (frog species from Peru), *Sitana attenboroughii* (fan-throated lizards found in coastal region of Kerala, India), *Sylvicanthon attenboroughi* (dung beetle from South America), *Euptychia attenboroughi* (butterfly), *Trigonopterus attenboroughi* (flightless weevil from Indonesia), Plesiosaur Attenborosaurus conybeare (type of prehistoric sea reptile) and *Zaglossus attenboroughi* (long-beaked echidna living in New Guinea) (Fossil named after Sir David Attenborough – BBC News [n.d.](#)).

## Views and Activism

In Blue Planet, his recent nature documentary on marine life, he portrayed the life-threatening consequences of anthropogenic activity on oceans

and in turn, the ecosystem. The series generated continuing large-scale awareness and garnered tremendous attention – a phenomenon termed the “blue planet effect” (The Attenborough effect [n.d.](#)). Andrew Dykes, founder of Global Sustainability Trust said that the effect created a trend of socially beneficial investments. The show even propelled Queen Elizabeth II to bring a ban on plastic bottles across the royal estates (“Blue Planet effect” gives boost to sustainable investment [2018](#)).

Sir David has been a staunch advocate of environmental causes both on and off screen and believes that the catastrophe of environmental destruction can be contained: “real success can only come if there's a change in our societies and our economics and in our politics.” In a 2018 interview, he said that the key to saving the planet is controlling the population. Speaking to delegates at COP24 held in Katowice, Poland, he said that humanity was in throes of a manmade disaster of global scale: climate change. “The Garden of Eden” is no more, he said, imploring the people and the leaders across the world to rise to the occasion and bring the pledges of 2015 Paris Climate deal to fruition (Carrington [2018](#)). In an interview with Prince Williams, Attenborough said that mankind could “wreck the natural world” but fortunately wields the power to live in harmony with nature (David Attenborough and Prince William take world leaders to task on environment | Environment | The Guardian [n.d.](#)). Attenborough is agnostic and believes that evolution best explains the diversity of life.

## On Animal Behavior

In the three-part documentary, Tiger-the spy in the jungle (2008), Sir David's team with the use innovative wooden spy cameras carried by elephants captured the intimate portrait of tiger's life. In this documentary, he showed the life of a tiger mother and her four cubs from Pench Tiger Reserve of India. In the same documentary, his team showed the day time foraging activity of the Sloth bear (*Melursus ursinus*) which are the most nocturnal

among the bears. His team showed the sloth mother carrying her young one on her back. Sloth bear is the only bear to carry its young on the back.

In his documentaries, Sir David has illustrated the behavior of many animals in a way that can be understood by the common man. Orangutan using axe on the wood log, nest building behavior of the Australian bowerbird, wild crows inhabiting the city and use it to their advantage in a Japanese city, mating ritual of hedgehogs, food sharing behavior of vampire bats, utilization of bioluminescence by animals, effect of cordyceps parasitic fungi on insects extraordinary hunting technique of bolas spider (orb-weaver spider), and Dam building behavior of beavers are a few examples.

## Books by Sir David

Sir David's documentaries are mostly accompanied by a book with the same name. The books by Attenborough are given below:

- Zoo Quest to Guyana (1956)
- Zoo Quest for a Dragon (1957)
- Zoo Quest in Paraguay (1959)
- Quest in Paradise (1960)
- People of Paradise (1960)
- Zoo Quest to Madagascar (1961)
- Quest Under Capricorn (1963)
- Fabulous Animals (1975)
- The Tribal Eye (1976)
- Life on Earth (1979)
- Discovering Life on Earth (1981)
- The Living Planet (1984)
- The First Eden: The Mediterranean World and Man (1987)
- The Atlas of the Living World (1989)
- The Trials of Life (1990)
- The Private Life of Plants (1994)
- The Life of Birds (1998)
- The Life of Mammals (2002)
- Life on Air: Memoirs of a Broadcaster (2002) – autobiography, revised in 2009
- Life in the Undergrowth (2005)
- Amazing Rare Things: The Art of Natural History in the Age of Discovery (2007) –

with Susan Owens, Martin Clayton and Rea Alexandratos

- Life in Cold Blood (2007)
- David Attenborough's Life Stories (2009)
- David Attenborough's New Life Stories (2011)
- Drawn from Paradise: The Discovery, Art and Natural History of the Birds of Paradise (2012)
- Adventures of a Young Naturalist: The Zoo Quest Expeditions (2017)
- Journeys to the Other Side of the World: Further Adventures of a Young Naturalist (2018)
- Dynasties: The Rise and Fall of Animal Families with Stephen Moss (BBC Books, 2018)

## Cross-References

- [Friendships in Animals](#)
- [Personality in Animals](#)
- [Zoo](#)

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## David Buss

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David Buss is one of the co-founders of the modern field of evolutionary psychology. He is widely known for his scientific contributions to understanding human mating strategies, subsumed under *sexual strategies theory*. He has made contributions to personality psychology, personality and social interaction, adaptive individual differences, tactics of manipulation, sexual conflict, stalking, sexual violence, and homicide. He authored or co-authored three other evolution-based theories: *strategic interference theory* (Buss 1989a), *error management theory* (Haselton and Buss 2000), and *homicide adaptation theory* (Buss and Duntley 1998; Duntley and Buss 2011).

In 1976 when Buss sought a PhD program, there existed no evolutionary psychologists and no field called evolutionary psychology. After receiving his PhD in 1981 from the University of California, Berkeley, in personality psychology, Buss accepted a position as Assistant Professor at Harvard University.

In 1984, Buss published his first paper on evolutionary psychology, entitled "Evolutionary Biology and Personality Psychology: Toward a Conception of Human Nature and Individual Differences" in *American Psychologist*. Although naïve and ill-informed in many ways, it signaled Buss's enduring commitment to understanding species-typical psychology and profound individual differences within a unified evolutionary framework.

In 1984, Harvard promoted Buss to Associate Professor, but he simultaneously received an offer from the University of Michigan of Associate Professor. Shortly after starting his position at Michigan, he and six other professors formed the *Evolution and Human Behavior* (EHB) group in 1986, funded with a generous internal grant from a prescient Dean. In 1986, Buss was

honored to Chair a symposium with the invited speakers Richard Alexander, W.D. Hamilton, George C. Williams, Mildred Dickemann, Martin Daly, and Napoleon Chagnon. Yearly meetings eventually led to the formation in 1989 of the *Human Behavior and Evolution Society* (HBES) with W.D. Hamilton serving as its first President.

In 1987, Buss was elected to be a Fellow at the *Center for Advanced Studies in the Behavioral Sciences* at Stanford. While there during 1989–1990, he co-led with Leda Cosmides a special project, "Foundations for Evolutionary Psychology," which included Martin Daly, John Tooby, and Margo Wilson.

## Evolved Mate Preferences

Buss launched a study of 37 cultures, involving 10,047 participants from six continents and five islands. The first wave of results was published in a target article in *Behavioral and Brain Sciences* (Buss 1989b). The findings that received the most attention were the discoveries of universal evolved sex differences. Men more than women valued cues to fertility. They placed greater importance on physical attractiveness. Appearance contains a bounty of cues to fertility. Men universally also desired younger spouses, supporting a second evolution-based prediction. Fertility is steeply age-graded among women, more so than among men, so youth is a powerful cue to fertility and future reproductive potential. Women more than men universally prioritized financial resources, economic prospects, and nearly universally prioritized cues that lead to resources, such as ambition/industriousness and social status.

These basic findings provided the first massive cross-cultural support for a key set of evolutionary psychological hypotheses. In 1989 when they were published, evolutionary hypotheses were widely regarded as speculative, lacking an empirical basis. These findings rendered that view no longer tenable. Those findings remain among the most robust psychological sex differences ever documented across cultures. It was an early

“success story” for the emerging field of evolutionary psychology and helped spur others to get into the field. The study became a “citation classic” and as of 2019 has received roughly 5,000 scholarly citations.

### **Tactics of Mate Competition: Mate Attraction and Competitor Derogation**

According to sexual selection theory, the mate preferences of one sex should establish the ground rules for intrasexual competition in the other. Buss developed the first taxonomy of tactics of mate attraction, which includes 23 distinct tactics, including displays of kindness, devotion, resources, grooming, physical strength, and so on (Buss 1988a; Schmitt and Buss 1996). These studies also discovered unpredicted tactics, such as the display of humor, a topic that has subsequently received much research attention and theorizing.

Because mate competition is a zero-sum game in which one person’s gain in mating comes at a loss to a rival, one can conceive of two general strategies – enhancing one’s own attractiveness relative to rivals (tactics of attraction) and rendering rivals less attractive to mates relative to oneself. This logic led Buss to conduct the first empirical studies of derogation of competitors – the tactics that people use to impugn the desirability of their rivals. He developed the first taxonomy of derogation of competitor tactics, which included 28, such as questioning a rival’s fidelity, spreading false rumors about sexually transmitted infections, derogating a rival’s intelligence, and questioning a rival’s sexual orientation (Buss and Dedden 1990). The studies supported the evolution-based predictions about sex-differentiated tactics. Men more than women derogated their rival’s resources (e.g., “He drives a poor car”) and physical prowess (e.g., “He told others that his rival was physically weak”). Women more than men derogated their rival’s physical appearance (e.g., “She made fun of the size and shape of her rival’s body”) and ability to remain sexually loyal (e.g., “Told others that her rival slept around a lot”).

### **Tactics of Mate Retention**

Mates gained must be retained to reap the reproductive potential inherent in long-term mate selection. Buss launched the first set of studies on tactics of mate retention in dating couples and married couples, as well as the first taxonomy of mate retention tactics (Buss 1988b; Buss and Shackelford 1997). Tactics ranged from *vigilance* (e.g., “He called her at unexpected times to see who she was with”) to *violence* (e.g., “He hit the guy who made a pass at his girlfriend”).

### **Mate Poaching Tactics**

Mate poaching – attempting to lure someone who is already in a mating relationship for either a short-term sexual encounter or a long-term relationship – turns out to be quite common (Schmitt and Buss 2001). Together with David Schmitt, Buss conducted the first studies of human mate poaching and developed a taxonomy of its main tactics. Many tactics turned out to be similar to tactics of attraction. But some are unique to the mate poaching contexts, such as befriending the couple in a platonic guise. Another is derogating one partner to the other (e.g., “He doesn’t appreciate you” or “You are too good for him”), implying a mate value discrepancy. Mate poaching represents a domain previously unexplored prior to the Schmitt and Buss (2001) study, and the term “mate poaching” has now entered the mainstream scientific lexicon ([http://tierneylab.blogs.nytimes.com/2009/08/27/why-poach-anothers-mate-ask-an-expert-or-brangelina/?\\_r=0](http://tierneylab.blogs.nytimes.com/2009/08/27/why-poach-anothers-mate-ask-an-expert-or-brangelina/?_r=0)).

### **The Emotion of Jealousy**

Jealousy is a commonly experienced emotion in romantic relationships. Yet it was largely ignored by emotion researchers. Buss sought to test hypotheses about the functional design of jealousy. He collaborated with Drew Westen, Randy Larsen, and Jennifer Semmelroth, and together, they discovered strong evidence for hypothesized sex differences in the weighting given to triggers

of jealousy. They posited that emotional infidelity was a cardinal cue to the loss of a partner's commitment for women, whereas sexual infidelity was a key cue to compromised paternity certainty. Although both sexes clearly become upset about both sexual and emotional infidelity in a partner, when forced to choose which is more upsetting the predicted sex differences emerged. Moreover, men showed greater physiological distress to imagining a partner committing sexual infidelity, whereas women showed greater physiological distress to imagining a partner committing emotional infidelity (Buss et al. 1992).

### Strategic Interference Theory

Buss saw the functional emotion of jealousy as part of two larger theories. The first was strategic interference theory (Buss 1989a). He proposed that emotions such as jealousy, anger, and upset become activated when a person's strategy for achieving a goal was impeded or blocked. A strategy of securing a partner's sexual fidelity, for example, was impeded by attempts by mate poachers or rivals trying to lure one's partner for sex or romance. To take another example, a woman's strategy of exercising "female choice" about when and with whom she consents to having sex would be impeded by a man who pursued a strategy of sexual force or aggression. Strong negative emotions such as anger, jealousy, and upset serve several key functions, according to strategic interference theory: (1) they alert someone to the source of the interference, (2) motivate action to curtail the interference, and (3) help to store interfering events in memory, which in turn functions to (4) avoid future episodes of strategic interference.

### Error Management Theory

Jealousy turned out to be illuminated by error management theory (EMT), originally developed by Martie Haselton, Todd DeKay, and Buss (Haselton and Buss 2000). EMT is a theory of selection, so can be applied to any domain of

psychology from perception to social interaction. EMT logic can be stated syllogistically: (1) we live in an uncertain world; (2) we experience cues that are only probabilistically related to cost-inflicting or benefit-bestowing events; (3) there are two ways to err – by inferring the existence of an event when it has not in fact occurred and by inferring the nonexistence of an event when it in fact has occurred; (4) if there are recurrent cost-benefit asymmetries in making these two types of errors, selection will favor adaptively biased inference procedures that function to minimize committing the more costly error, even at the cost of experiencing more frequent inferential errors of the less costly variety.

Jealousy illustrates EMT logic. Buss argued that the cost of missing a sexual infidelity that has occurred is typically greater than the cost of mistakenly suspecting an infidelity when none has occurred (Buss 2000). Because infidelities are typically conducted underneath a cloak of intentional secrecy, their existence must be inferred from probabilistic cues. Empirical evidence supports EMT logic applied to jealousy and infidelity (e.g., Buss 2000). Haselton and Buss also used EMT to illuminate design features of the male sexual over-perception bias and the female commitment skepticism bias (Haselton and Buss 2000). EMT logic has been used to illuminate a raft of other psychological phenomena, such as the auditory looming bias, the vertical descent illusion, and adaptive biases in a number of domains of social functioning. EMT logic has also been invoked to explain inferential biases about homicidal intent (Buss 2005).

### The Evolution of Aggression and Murder

Because differential reproductive success necessarily hinges on reproductive competition, conspecifics are necessarily rivals, albeit in the context of some levels of intertwined reproductive fates and win-win situations ("gains in trade") that select for adaptations for cooperation in certain contexts. Enhancing oneself relative to rivals is one generic strategy. A second is inflicting costs on rivals. Buss documented these two generic



strategies in the context of mate competition – tactics of attraction and derogation of competitors. In collaboration with Joshua Duntley, Buss extended this argument to murder. They argued, contrary to the Daly-Wilson claims that murder is a by-product of adaptations designed for nonlethal ends (Daly and Wilson 1988), that humans have adaptations for murder (Buss 2005; Buss and Duntley 1998; Duntley and Buss 2011).

Homicide adaptation theory (HAT) proposes that humans have evolved a number of distinct homicide adaptations, such as infanticide, intrasexual rival murder, and coalitional killing (warfare). Simply put, killing a rival, killing a rival's offspring, or killing a rival's kin has been extremely an effective way of inflicting massive fitness costs on intrasexual competitors. The accumulating evidence of adaptations for conspecific killing in chimpanzees leads to the conclusion that some of these homicide adaptations predate the evolution of *Homo sapiens*.

Buss and Duntley believe that there is sufficient evidence – from the paleontological skulls and skeletons riddled with unmistakable marks of murder to the psychological and behavioral footprints of “special design” for murder – to conclude that it is far more likely than not that humans have experienced a long coevolutionary arms race that created adaptations for murder and defenses to prevent being murdered.

## Authored Books

In an effort to reach a broader audience for evolutionary psychology, Buss has authored several books. These include *The Dangerous Passion: Why Jealousy Is as Necessary as Love and Sex* (2000), *The Murderer Next Door: Why the Mind Is Designed to Kill* (2005), and *Why Women Have Sex* (2009; co-authored with Cindy Meston). His two most influential books are *The Evolution of Desire: Strategies of Human Mating* (1994, 2003, 2016) and *Evolutionary Psychology: The New Science of the Mind* (1998, 2004, 2008, 2012, 2015).

*The Evolution of Desire*. This book represented the culmination of a decade of research by Buss

and a conceptual synthesis of hundreds of studies on human mating by other scientists. It elaborated on sexual strategies theory (Buss and Schmitt 1993) and included chapters on what women and men wanted in long-term and short-term mates; strategies of casual sex; tactics of attraction; causes of sexual conflict and breakups; mating over the lifespan; and harmony between the sexes. The book was first published in 1994; two new chapters were added to a new edition published in 2003; and the book was totally revamped in a thoroughly updated and revised edition, published in 2016. It has been translated into ten languages and continues to be widely used in college courses worldwide.

*Evolutionary Psychology: The New Science of the Mind*. While evolutionary psychology began to emerge as a cogent metatheory for psychology in the late 1980s and early 1990s, professors began to offer courses in it. There existed no textbook. One was urgently needed. After getting encouragement from a handful of people to write such a text, and being approached by publishers, Buss signed a contract. He produced the first textbook in the field in 1998. The text provided historical reviews of evolutionary theory and psychological science that converged on their synthesis (Chapter 1) and a chapter on the conceptual foundations of this new science of the mind, heavily influenced by the theoretical work of Leda Cosmides and John Tooby (Chapter 2). Subsequent chapters were organized logically around adaptive problems – challenges of survival, mating, parenting, kinship, and social group living (e.g., cooperation, aggression, status hierarchies). The final chapter called for the evolutionizing of all subdisciplines within psychology, such as cognitive, social, personality, developmental, and clinical; reviewed evolutionary empirical work within each; and ended with a call for a unified field of psychology that eventually could dissolve these somewhat artificial subdisciplinary boundaries.

Through this text, Buss helped the field of evolutionary psychology to grow and flourish, educating undergraduates, informing professors, and attracting new scholars to the field.



## Edited Volumes

Buss has edited six volumes, including *Personality Psychology: Recent Trends, Emerging Directions* (Buss and Cantor 1989), *Biological Approaches to Personality* (Buss 1990), *Sex, Power, Conflict: Evolutionary and Feminist Perspectives* (Buss and Malamuth 1996), and *The Evolution of Personality and Individual Differences* (Buss and Hawley 2011). His most influential edited volume, however, is *The Handbook of Evolutionary Psychology* (Buss 2005), logging in at more than 1,000 double-column pages and some 35 chapters. This led to a 2nd edition of the *Handbook* (Buss 2016), which expanded to more than 50 chapters. Both editions contained a Foreword by Steven Pinker, a special essay by Don Symons, and an Afterword by Richard Dawkins.

## Teaching and Mentoring PhDs in Evolutionary Psychology

Throughout his career, Buss has devoted considerable effort to mentoring the future generation of scientists. Of his 27 PhD students, roughly two-thirds have obtained tenured or tenure-track professorial positions. The Association of Psychological Science (APS) honored Buss with the *2017 Mentor Award for Lifetime Achievement*. His former students such as Todd Shackelford, Martie Haselton, and David Schmitt, in turn, have produced a number of PhDs in evolutionary psychology and themselves have made major contributions to the field.

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## David Hume

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David Hume (1711–1776) is considered one of the most important philosophers of the United Kingdom, since his philosophical, political, and economic works have permeated an important part of modern thinking.

## About His Life

Hume was born on April 26, 1711, in Edinburgh, Scotland. His father's family is a branch of the Earl of Hume, and his mother was the daughter of Sir David Falconer (President of the College of Justice). However, his family had little economic power, and as the youngest son, his patrimony was small. His father died when he was still a baby; his mother had to take charge of the upbringing, basic education, and religious training of him and his two siblings (Hume 1826).

He showed great interest in studies from a very young age, because of which his family considered that he should become a lawyer; however, Hume considered everything except the study of philosophy and knowledge in general to be aberrant. Unfortunately, his economic resources were not sufficient for his life plans; thus, at age 23 he began working in Bristol as a merchant, while increasing his knowledge of literature and

philosophy. After just a few months, he went to France, where he decided to dedicate himself exclusively to his studies, living and eating frugally to make his little money last. In this period he wrote his first work, the *Treatise on Human Nature*, which was published in London in 1738. Although it is now considered one of his greatest works, it did not achieve great distinction at the time (Hume 1826).

After this first publication he returned to his family's house in Edinburgh, where he began to write and publish his first works on morals and politics, which were well received. As he mentions in his autobiography, in 1745, after receiving an invitation from the Marquis of Annandale, Hume served for a year as his tutor, since the health and mental state of that young nobleman required it. He then received an invitation from General St. Clair to act as secretary in an expedition, and later to serve him in his military embassy in the courts of Vienna and Turin. Although his studies stopped during these years, he increased his capital considerably (Hume 1826).

Wishing for better success of his first work, while still in Turin he re-issued the first part of the *Treatise on Human Nature* as *An Enquiry Regarding Human Understanding*, which at first did not have much more success than the initial publication. After this he lived with his brother in the family house in Edinburgh for two years, where he wrote *Political Discourses* (1752), and republished the second part of his first work as *An Enquiry Concerning the Principles of Morals* (1752), while his other writings were attracting the attention of intellectuals (Hume 1826).

Hume moved from the country to the city in 1751, where he became the librarian of the Faculty of Advocates at the University of Edinburgh. During this time he began to write about the history of Great Britain, as well as the natural history of religion and other smaller texts. The great success of his writings allowed him to accumulate considerable money, thus he returned to his native city with the intention of stopping all activity; however, he began to receive work offers from several nobles, which he did not reject. He returned definitively to Edinburgh in 1769, where he remained until his death on August 25, 1776, as a result of a gastrointestinal disease (Hume 1826).

## Hume's Treatise of Human Nature

Hume is one of the so-called British empiricists, who postulated that human knowledge comes from experience. The ideas that Hume put forward in the *Treatise on Human Nature* (and the books derived from it), in which he expressed his theory on the content and functioning of the mind, were a great contribution to this movement. Many authors have recognized this as a consequence of an epistemological, ontological, and methodological viewpoint of the phenomena studied (Stepukonis 2019).

According to Hume, the perceptions and contents of the human mind may be classified as *simple* or *complex*. Complex perceptions are those which can be decomposed into multiple elements; for example, a forest may be composed of trees, soil, and rocks; there are also different color, odors, and sounds present. One of the main divisions Hume makes to understand the perception of the mind is that of *impressions* and *ideas* or *thoughts*; both may be simple or complex. One of the main differences is that impressions are experienced more strongly and vividly than ideas or thoughts. This is because impressions are those which are experienced when the senses are capturing the objects, while ideas or thoughts come from the impressions and are experienced once the objects are not present, and often become weaker when there is more distance between these objects (Hume 1960, 1999).

Impressions are separated into two classes: *sensation* and *reflection*. Impressions of sensations are those which excite the senses, allowing us to receive colors, sounds, heat, thirst, hunger, pain, or pleasure. These impressions produce an idea or thought which remains after the impression has ceased. When objects are again presented to the senses, the ideas of pleasure or pain generate the impressions of reflection, which are those of passions and emotions (e.g., desire, aversion, hope, fear), for which the corresponding ideas will be created (Hume 1960).

Ideas may be classified as *memory* when impressions are recalled, both simple (e.g., the color red, happiness) and complex (e.g., an entire city, amorous passions), and *imagination*, complex ideas for which there has been no

experience as such, but there are impressions of its simplest parts. An example of imagination can be the idea of a Pegasus, which is formed by the ideas of horses and of wings, or by imagining an ancient city with the descriptions provided by writers. Hume also affirms that there are moments when memory and imagination mix (e.g., when we don't remember all the facts, the imagination can act to supplement the memory); the only limit to imagination is that it cannot create simple ideas for which there is no experience, such as new colors, sounds, or passions. For this reason, Hume reached the conclusion that the best way to know if an idea is real or fictitious is to find its corresponding impression (Hume 1960, 1999).

Hume believed that ideas are mainly associated by three connecting principles: (1) *space-time contiguity*, since one idea may evoke another if they are united in time and space (e.g., sand and sea, coffee and cream); (2) *similarity*, when two or more ideas may be compared, either by their similarity or difference; and (3) *cause and effect relations*, with which what will happen or has happened may be inferred. For example, if we observe a campfire we may infer that soon only ashes will be left, and conversely, if we observe ashes, we may infer that there was a campfire in this place. However, Hume observed a problem in cause-effect relations. Although we observe that fire burns wood and leaves ashes when it extinguishes, the fire, heat, and later ashes are what the impressions capture, but it is not possible to capture the "power" that the cause has to produce the effect, and also the cause and effect often are not similar (Hume 1960, 1999).

According to Hume, the idea of cause and effect is generated due to the principles of contiguity and similarity. For cause and effect to be established as such, the cause must be followed by the effect, thus these must be united contiguously in time and space, and this connection must also happen recurrently (regularity). Once we notice that eating an apple (cause) is sweet and nutritious (effect), the similarity that this apple has with others will make us expect the same effect by eating other apples; while if we observe a difference between one apple and another, it is expected that the effect will also change proportionally,

thus forming a habit or custom (Hume 1960, 1999).

Hume observed a close relation between space and time, since we cannot perceive one without the other, and recognized that these relations have behaved regularly in the universe, giving origin to the habit that maintains the cause-effect relation, but given that we have neither experience nor impressions of the future, nothing can assure that these regularities will be maintained, due to which he classified the cause-effect relation as a belief (Hume 1960). This reasoning is also extended to the *substance/essence* of objects, the soul and the idea of God, given that these elements cannot be perceived by the senses and also does not come from an impression of reflection (Hume 1960).

The extreme of the relevance that Hume gave to the senses may be seen in his idea of *morality*, which would also come from experience. When we perceive that something does good for someone, the impression of well-being or happiness is generated, while when we observe that some behavior does bad to the other, we generate an impression of discomfort or bother. Hume thus suggests that what is morally correct should be based on these impressions (Hume 1960).

Hume's ideas on human nature have had a strong influence on other important philosophers such as Kant, who added to the discussion on human knowledge (De Boer 2019), and positivist epistemologists such as Popper, who take into account the problem of the cause-effect relation (Wettersten 2016), and have also influenced experimental psychology and learning theories (Waldmann et al. 2006), establishing the bases to understand associative processes.

## Cross-References

- Aristotle
- Associative Learning
- Associative Mechanisms
- Cartesian Dualism
- Clark L. Hull
- Classical Conditioning
- Ebbinghaus
- Episodic Memory
- Experience Projection

- Immanuel Kant
- Instrumental Learning
- Intelligence
- Ivan Pavlov
- John B. Watson
- Pattern Learning
- Perceptual Learning

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## David Premack

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## Introduction

David Premack was a prolific scholar who made major theoretical contributions, advancing the study of many comparative psychological topics. Following the cognitive revolution, he

successfully traversed the transition from his focus on behaviorism to become an active cognitive theorist and investigator. Within behaviorism, he proposed reversibility of the reinforcement relation. Later in his career, Premack raised the question of chimpanzees having a theory of mind; this early questioning has since inspired decades of research. Premack's ingenious experiments and creative approaches are widely acclaimed and serve as examples to many aspiring comparative psychologists.

## Background and Contributions

David Premack (October 26, 1925, to June 11, 2015) was an American psychologist who achieved empirical and theoretical excellence in advancing studies of associative learning and comparative cognition. He received his academic training at the University of Minnesota, obtaining a Bachelor of Arts degree in chemistry and liberal arts in 1943, a Master of Arts degree in Experimental Psychology and Statistics in 1951, and a doctoral degree in Experimental Psychology and Philosophy in 1955. He first began conducting primate research in 1954 at the Yerkes Primate Biology Laboratory in Orange Park, Florida. He held faculty positions at University of Minnesota, University of Missouri at Columbia, University of California at Los Angeles, University of California at Santa Barbara, and Harvard University. In 1990, he retired as professor emeritus of psychology from University of Pennsylvania.

### Premack Principle

By demonstrating that reinforcers were more relative and dynamic than previously considered, Premack challenged the traditional absolute value of reinforcers (Premack 1959). For any pair of responses, he asserted that the more probable response would reinforce the less probable response. He predicted that the responses themselves were reinforcing and the relation between them was reversible (Premack 1962). By testing this principle, it was demonstrated when more probable behaviors are made contingent upon less probable

behaviors, less probable behaviors are more likely to occur. Informally, this had already been widely applied by making a desirable "reward" (such as playing a game) contingent upon the occurrence of a less desirable behavior (such as completing a chore), this contingency increases the overall likelihood of the less desired behavior's exhibition. The Premack Principle stands as a major contribution to the psychology of learning.

### Theory of Mind

Premack and Woodruff (1978) introduced the concept of "theory of mind" as an individual's ability to impute mental states to one's self and others. As many others began investigating theory of mind in nonhuman apes, Premack and Woodruff presented Sarah (a female chimpanzee with experience in laboratory and language training) with video recordings of human actors attempting to solve various problems but encountering obstacles, they then assessed Sarah's ability to choose photographs of appropriate alternative solutions. Their results indicated that Sarah understood the problem, the human actor's purpose, and chose alternatives compatible with that purpose. Premack followed this initial research with innovative experiments to examine chimpanzee attention and intentions, as well as one's understanding of others' knowledge and beliefs. Subsequent to these early investigations, the ability of an individual to infer the mental states of others has been an active area of research and debate among scholars.

### Effects of Enculturation

In *The Mind of an Ape*, David Premack and his wife Ann Premack (1983) describe teaching several chimpanzees to use a token-based language system. They noticed marked performance differences across other cognitive tests by chimpanzees that were trained to use this form of symbolic communication compared to those that were not. Premack (1983) suggested exposing chimpanzees to enculturated language training could improve their abilities in abstract judgment. In particular, he discussed enhanced use of an abstract propositional code could improve their abilities to



represent and judge relations. Premack's discussions on chimpanzee enculturation and symbolic language were important contributions to investigations of cognitive ability. Relative to other ape language studies of this time, Premack was one of the first to relate an individual's abilities with past experience and learned cognitive skills.

### Human and Animal Cognition

Based on extensive comparative studies of intelligence (such as Premack 1976), Premack suggested that human and animal cognition had different evolutionary origins (Premack 2007). Human cognitive abilities are domain-general, serving many goals, whereas animal cognition represents more limited adaptations, serving a single goal. Although there are similarities, Premack rejected equivalence between animal and human cognition. He cited enduring differences in the domains of teaching, short-term memory, causal reasoning, planning, deception, transitive inference, theory of mind, and language. Throughout his career, Premack attempted to synthesize the evolutionary significance of his comparative research. For example, he thoughtfully contextualized the ape language studies (Premack 1983) and addressed the anthropological implications of cognitive differences between humans and apes (Premack and Premack 2003).

### Conclusion

David Premack's research and legacy continue to have a major impact on psychological research. In recognition of his academic achievements, he was awarded the Fyssen Foundation International Research Prize in 1988, the Medal of the College de France in 1991, and the William James Fellow Award by the American Psychological Society in 2005.

### Cross-References

- [Reinforcement](#)
- [Theory of Mind](#)

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### David Washburn

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David Alan Washburn (October 5, 1961–) is an American experimental psychologist known for studies of attention, learning, and other cognitive processes in rhesus monkeys and human adults. He is an Emeritus Professor of Psychology and Neuroscience at Georgia State University, former chairperson of its Department of Psychology, and retired as Director of its Language Research Center. He is currently a Professor of Psychology at Covenant College.

### Personal and Professional History

David Washburn was born in Birmingham, Alabama, USA to Earl Derward and Constance Joan Washburn. He has one sibling, a younger



sister named Karen Renee. In 1970, the Washburn family moved to Smyrna, Georgia, where David would spend most of his childhood. His youth and adolescent years were primarily filled with church activities, sports, and reading. Deeply religious even as a child, David was enrolled in Smyrna Christian Academy for his junior high and high school years, and graduated in 1980 as valedictorian of a graduating class of just five seniors!

Washburn became interested in counseling in the 7th grade, and so enrolled as a psychology major at Covenant College, located just one mile inside the Georgia border, near Chattanooga, Tennessee. Covenant is a small liberal-arts college affiliated with the Reformed Presbyterian Church, and offered a psychology curriculum, in-state tuition, the opportunity to play junior-varsity soccer, and a spectacularly scenic campus perched atop Lookout Mountain. The college's most recognizable building is the so-called castle in the clouds, originally constructed as a luxury hotel, but the psychology department itself occupied the loft floor of what had once been a stable for the hotel. The "psych barn" housed a classroom, several laboratory rooms, a vivarium, and offices for the two faculty members in the psychology department. Douglas R. Sizemore had earned his Ph.D. (1974) from Northern Colorado University in statistics, which was the primary subject he taught during those years at Covenant. Michael J. Rulon is a general experimental psychologist who earned his Ph.D. (1975) working with D. D. Wickens at the Ohio State University. He was department chairman, and taught the bulk of psychology courses (including General, Developmental, Learning, Physiological) including several innovative offerings that would dramatically reshape Washburn's interest. One such course was called "Psych Tour." To give psychology majors at Covenant and similar small schools exposure to the breadth and depth of the discipline, Dr. Rulon organized summer road trips to some part of the country, where the students would travel by van from school to school, reading about the psychological work taking place at each, visiting laboratories or clinics, and interviewing prominent psychologists. Because Washburn knew he wanted to major in psychology when he arrived

at Covenant, he was able to take many required courses his freshman year, and registered for Psych Tour the following summer. The intensive 3-week course featured visits with many psychologists from San Francisco to Los Angeles, including memorable visits with Drs. James Dobson, Richard Gorsuch, Ernest Hilgard, Arthur Jensen, Bruce Narramore, Robert Ornstein, Karl Pribram, Warren Brown, a sleep lab, an EEG lab, a biofeedback lab, and much more. Washburn had entered Covenant to learn more about counseling troubled teenagers, but by the end of his first year he was completely committed to psychological science and the study of learning and other behavior.

In those days, every General Psychology student at Covenant adopted a rat and learned the principles of conditioning by completing exercises using psychology's operant chambers. Washburn's work-study assignments throughout his time at Covenant included animal care, maintaining the Skinner boxes, and helping new students to shape their animals. It was in this latter role that David, then a senior, met freshman psychology student Catherine Childs. The couple would marry in 1984, and often recount that they were introduced to one another by a laboratory rat.

Before graduating with his B.A. in psychology, Washburn spent a year as a transient student at Georgia State University, where he took additional psychology coursework and volunteered in the cognitive research laboratory of R. Thompson Putney. Putney had earned his Ph.D. (1966, Missouri) working with Robert S. Daniel, who had in turn been a student of Indiana University psychophysiological R. C. Davis. Washburn would return to Georgia State for graduate study, after being accepted into the Psychological Sciences doctoral program to work with Dr. Putney. Professor Duane M. Rumbaugh, chairman of the psychology department, phoned to convince David to return to GSU and to offer an assistantship as a computer programmer for the Language Research Center (LRC), where Rumbaugh was the founding Director. With a new Commodore-64 computer in hand and some knowledge of the BASIC programming language, Washburn returned to Atlanta to write game-like computerized tasks, on which the LRC apes (Lana, Sherman, Austin,

Kanzi) would respond by manipulating a joystick so as to control a cursor on the screen. His own research was conducted with humans as part of the memory research in Dr. Putney's laboratory.

In those days, Dr. Rumbaugh or Dr. Sue Savage-Rumbaugh would periodically invite Washburn to collaborate on a research project with the chimpanzees; however, he consistently declined, insisted that his intention was to study human cognition, preferring to program for other people's studies than to establish the intensive social relationships required for working with the apes. This changed in 1986, however, with the acquisition of two rhesus monkeys (Abel and Baker) at the LRC. When the Animal Welfare Act was amended that year to require researchers to "provide a physical environment adequate to support the psychological well-being of nonhuman primates" (United States Code, Title 7, Chapter 54, Section 2143, a.2.B), primate researchers around the country scrambled to understand how best to promote and to assess psychological well-being. With cognitive enrichments like the ape-language keyboards and game-like computer tasks, the LRC was well positioned on this issue. Accordingly, it was logical that Duane Rumbaugh would be consulted by groups like the National Aeronautics and Space Administration (NASA) for guidance on how to provide enrichment for the monkeys that they were studying – and were planning to study aboard the Space Shuttle. Although he knew that rhesus monkeys might not be able to master the remote cause-effect relations required to use the game-like computer tasks written for the chimpanzees, Rumbaugh reasoned that the benefits would be great if the monkeys could be successfully taught to use the joystick test system. NASA agreed to fund a feasibility project to investigate this possibility.

Washburn and fellow doctoral student William D. (Bill) Hopkins were invited to join a research team that included Drs. Duane Rumbaugh, E. Sue Savage-Rumbaugh, and Kirk Richardson. Although Washburn was hesitant, Rumbaugh argued convincingly that training the monkeys would not require the physical and social intensiveness of chimpanzee testing, but rather would be much more like testing human participants, or even

rats in operant chambers. If the monkeys could be shaped to manipulate joysticks (or to use touchscreens, as the project began with two monkeys learning the joystick and one monkey, working with Dr. James King in Arizona, using a touchscreen), then all subsequent training and testing of the animals would be automated. Some additional negotiation with Rumbaugh ensued, but the end result was Washburn and Hopkins sharing an "office" with rhesus monkeys Abel and Baker, and working to determine whether the monkeys could learn cursor-control skills.

The monkeys' success in mastering the computer test system resulted in a flurry of publications and a new comparative focus to Washburn's nascent research program (e.g., Washburn et al. 1989a, b). Whereas his M.A. thesis (1987) was an examination of functional cerebral asymmetries in undergraduate students' recognition of the chimpanzees' visuographic language symbols (called lexigrams), his dissertation for the Ph.D. (1991) was a comparative study of the effects of stimulus movement on macaques' and humans' attention, learning, and memory (Washburn 1993).

By the time Dr. Washburn earned his Ph.D., the NASA-funded behavior and performance project had grown from a demonstration study on psychological well-being to a central component of the international research collaboration on the effects of spaceflight on rhesus monkeys' physical and psychological health. The LRC research team was preparing for a Shuttle flight in which rhesus monkeys, from a colony of macaques at the NASA-Ames Research Center being joystick-trained under Washburn's supervision, would fly as payload for 2 weeks, performing a range of game-like computer tests before, during, and after the mission. Rather than leave before this spaceflight, Dr. Washburn remained at the LRC in a postdoctoral position. By the time the project actually flew in space in 1996 (aboard a Bion Russian biosatellite rather than the Space Shuttle; Washburn et al. 2000), Washburn had additional grants of his own that kept him in Atlanta and at the LRC. Among these awards were a series of grants from various Department of Defense agencies as a principal investigator (1992–2000) at the Center of Excellence for Research on Training at Morris

Brown College, a historically black college in Atlanta.

On the strength of this productive and well-funded research program, Dr. Washburn was appointed a Georgia State University faculty member at the rank of Academic Professional in 1996. In 2001, he moved to the tenure track as Associate Professor of Psychology, and was promoted to Professor with tenure in 2005. The following year he began a 4-year term as psychology department chair.

Duane Rumbaugh retired from Georgia State University in 2001, and David Washburn was appointed as the LRC's second Director. Under his leadership, the LRC secured continued support through a series of program-project grants from the National Institute of Child Health and Human Development, and saw growth in its team of investigators (faculty, staff, and graduate students), its physical space and resources, and its resident-animal colony. With respect to nonhuman primates, the LRC provided continuing care and stewardship of chimpanzees Lana, Mercury, and Panzee until their respective deaths; facilitated the transfer of Kanzi and his family of bonobos to the Great Ape Trust (now Ape Cognition and Conservation Initiative) in Iowa; and acquired multiple groups of capuchin monkeys to support the growing research program with those animals.

## Significant Contributions

In addition to his leadership of this internationally recognized research center, Dr. Washburn is best known for his role in developing and promoting the LRC's computerized test system (also known as the video-task system, the psychomotor test system, and the Rumbaughx; Rumbaugh et al. 1989; Washburn et al. 2012) for comparative cognition research. The apparatus has been used with a wide range of primate species, and with other animals ranging from pigeons and rats to bears and elephants. Washburn and others have also reported data showing that it serves, as originally intended, as an environmental enrichment that supports the psychological well-being of nonhuman primates (Washburn 2015).

Dr. Washburn's other contributions to the literature largely pertain to the topic of attention and its relation to other cognitive constructs. His studies with human and nonhuman primates of the stimulus movement effect, Stroop-like effects, visual search, and similar attention-related phenomena have illuminated the competition between stimulus control and cognitive control in attention and behavior (e.g., Washburn 1993, 1994, 2016).

Washburn has also contributed to the comparative-cognition literature on relational versus associative learning, reflecting the long-time collaboration with Duane Rumbaugh, and featured in their coauthored book, *The Intelligence of Apes and Other Rational Beings* (2003). His interest in relational learning (and why it sometimes fails to emerge) is also reflected in studies of numerical cognition, metacognition, and memory – research that benefitted from extensive collaboration with many of the most outstanding scholars in the field of comparative cognition, particularly Michael Beran, William Hopkins, and J. David Smith. Many of these collaborators contributed chapters to *Primate Perspectives in Behavior and Cognition* (2007), edited by Dr. Washburn and based on a festschrift in Duane Rumbaugh's honor.

Dr. Washburn served as President of several regional and national scholarly organizations (Southern Society for Philosophy and Psychology, Society for Computers in Psychology, Southeastern Psychological Association, and Divisions 3 and 6 of the American Psychological Association). He is a Fellow of the Society for Experimental Psychology and Cognitive Sciences, the Society for Behavioral Neuroscience and Comparative Psychology, the Association for Psychological Science, and the Psychonomic Society and has been recognized with awards from the Southern Society for Philosophy and Psychology, Psi Chi, the American Psychological Association, and Georgia State University.

## Cross-References

- ▶ [Ape Cognition and Conservation Initiative \(ACCI\)](#)
- ▶ [Attention](#)

- [Classical Conditioning](#)
- [Cognitive Control](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Counting](#)
- [Discrimination Learning](#)
- [Duane Rumbaugh](#)
- [Georgia State University's Language Research Center](#)
- [John David Smith](#)
- [Kanzi](#)
- [Lexigrams](#)
- [Michael J. Beran](#)
- [Operant Conditioning](#)
- [Sarah, Lana, Sherman, and Austin](#)
- [Stimulus Control](#)
- [Stroop Effect](#)
- [Sue Savage-Rumbaugh](#)
- [Uncertainty Paradigm](#)
- [William Hopkins](#)

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## Dawn Singing

- [Dawn Solo/Chorus](#)

## Dawn Solo/Chorus

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## Synonyms

[Dawn song](#); [Dawn singing](#)

## Definition

The dawn chorus is a period of vocalization that occurs during twilight before the sun rises.

## Introduction

The dawn chorus is a prominent acoustic display that begins during the twilight period characterized by a high rate of vocalization by many species. Whereas the most studied species are birds, mammals, insects, and anurans also may chorus at dawn. The focus of the entry is on birds with a

summary of other species at the end. The order in which participating species begin to chorus is predictable. In resident species, the dawn chorus may occur year-round, whereas, in migratory species, the dawn chorus begins within the first weeks following arrival on the breeding grounds.

## Research on the Dawn Chorus

Due to the striking nature of the cacophony of chorusing species at daybreak, the dawn chorus has been described historically for its beauty. Research on the dawn chorus began in earnest in the 1900s with efforts to characterize the timing and composition. In the 1970s, functional hypotheses began to be explored; yet, little progress was made initially due to the difficulty of recording the complex display. With the advent of new recording techniques and the ability to easily and quickly produce large numbers of sonograms, studies of the dawn chorus have proliferated.

Studies at dawn use a mix of observational and experimental approaches. Observational approaches involve describing the timing of the chorus and the rate and type of songs produced. Observational studies traditionally involved transcribing the chorus start time and the properties of choruses of individuals in the field. Currently, most observational studies also use field recordings, which include both focal recordings of individual birds using a directional microphone and recordings of the entire chorus using omnidirectional microphones, often in association with automated recording units. Experimental techniques include using song playback, mate or neighbor removal, food supplementation, or physiological manipulations.

## Environmental Factors

In most cases, the start of the dawn chorus closely tracks the increasing light levels during the twilight period; however, in other species, the timing of song may drift further from twilight towards the middle of the breeding season (Leopold and

Eynon 1961). At northern latitudes, with nearly continuous daylight, the chorus may instead track the time when light intensity is at its lowest value (Brown 1963). Factors that influence the light level detected thus influence the timing of the chorus (e.g., Thomas et al. 2002). Meteorological conditions that may inhibit sound transmission or cause energetic stress have been shown to influence both dawn chorus timing and song output (e.g., Bruni et al. 2014). Henwood and Fabrick (1979) modelled environmental conditions at different times of day and determined the early morning (dawn) is optimal for sound transmission though empirical support for improved acoustic transmission is mixed. Noise at dawn can also influence the timing of the chorus, for example, urban noise can result in earlier singing (e.g., Arroyo-Solis et al. 2013), whereas habitat disturbance or pollution can also influence chorus properties (e.g., Van Oort et al. 2006).

McNamara et al. (1987) proposed that conditions at night are unpredictable such that birds will have energy reserves remaining at dawn that are used for singing. Alternatively, Kacelnik proposed that birds sing at dawn because foraging success is likely to be low at low light levels (Kacelnik 1979). Models varying in overnight energy requirements or foraging profitability over the morning both have support and may influence different components of the chorus (Hutchinson 2002).

## Physiological Factors

We understand very little about physiological control of the dawn chorus. There is a correlation between dawn song output and testosterone level; however, territory occupancy and dawn chorusing precedes this spike in testosterone so the seasonal pattern is not controlled by testosterone (Foerster et al. 2002). Implantations that impair estrogenic and androgenic pathways result in an increase in the number of males not chorusing or lower song rates and males with high testosterone levels have longer dawn chorus songs (van Duyse 2004). Hormones involved in circadian cycles also appear to influence song type choice (Goodson 1998).

## Functions

Song is considered to function to communicate with both mates and rivals. As such, there is considerable research focusing on both these functions. First, recent work shows support for Staicer's et al. (1996) social dynamics hypothesis that males sing at dawn to adjust their social relationships with neighbors. At dawn, males engage in vocal interactions that extend to multiple individuals (e.g., Foote et al. 2010). Males sing near territory boundaries and removal of neighbors results in chorus cessation, which resumes when the neighbor is reintroduced (Liu 2004). High male density leads to earlier singing, higher song rates, and longer choruses (e.g., Xia et al. 2014). Recent work also shows that the dawn chorus clearly plays a role in territory defense. Males begin to sing earlier at dawn when a simulated intrusion begins earlier than typical species specific song (Foote et al. 2011) or sing at higher rates following a simulated intrusion on the previous day (e.g., Amrhein and Erne 2006). The activity of territory prospecting males is also centered around sunrise; thus, there is a value for territory holders to proclaim ownership and for prospecting birds to assess territory occupancy and rival quality (Amrhein et al. 2004).

In terms of social mate attraction, there is mixed support for this function of the dawn chorus. First, the dawn chorus persists after pairing and the chorus may not vary between mated and unmated males (Kunc et al. 2005). Second, Females do not appear to actively search for mates at dawn (Roth et al. 2009). Finally, female removal results in no change in song rates (Otter and Ratcliffe 1993). There is evidence, however, that song could advertise to fertile females for within-pair and extra-pair copulations (Double and Cockburn 2000) or that females would benefit from eavesdropping on vocal interactions of males at dawn as they do during the daytime.

Staicer et al. (1996) proposed that males may sing to stimulate their mate's reproductive development or to guard mates. Both hypotheses predict high song rates or earlier singing near or when females are fertile. Mated males of some species

do begin to chorus earlier or increase song output when mates are fertile compared to during other breeding stages while others do not (e.g., Bruni and Foote 2014; Kunc et al. 2005). Female arrival often results in chorus termination and delaying female emergence results in longer choruses (Otter and Ratcliffe 1993).

The dawn chorus is an honest indicator of quality for both mates and rivals. Male dawn song or chorus properties reflect other measures of male quality and are correlated with pairing date (Murphy et al. 2008), extra-pair mating success (e.g., Kempenaers et al. 1997), are preferred by females in choice-trials (Hoeschele et al. 2010), and are repeatable (e.g., Murphy et al. 2008). Male dawn chorus properties are also correlated with responses to simulated intrusions later in the day (e.g., Poesel et al. 2004). Short-term supplemental feeding studies support the concept of the chorus being an honest indicator of quality limited by energy supply (e.g., Cuthill and Macdonald 1990).

## Heterospecific Interactions

Tropical species that sing at the same time have songs that are more similar to one another than expected by chance and that typically these species are also closely related suggesting that the chorus involves communication between species that compete for resources (e.g., Tobias et al. 2014). However, during the chorus, species avoid overlap by singing after another species stops singing (Popp et al. 1985).

## Chorusing in Other Groups

The chorus of non-avian or non-vocal species appears to similarly be important for territory defense and is affected by similar meteorological conditions (e.g., Whitten 1982). Among anurans, some *Eleutherodactylus* species chorus at dawn and may give more aggressive call types at this time again suggesting an intrasexual function (Stewart and Rand 1991). Cicadas produce a pronounced dawn chorus in the tropics, which is



partitioned by calling height, song frequency, and timing (e.g., Sueur 2002).

## Conclusion

The dawn chorus is influenced by circadian cycles linked to variation in light levels. The main function of the dawn chorus may be intrasexual, but rich information for intersexual assessment is likely also an important component.

## Cross-References

- Aggression
- Auditory Signals
- Biological Clocks
- Chorus
- Chorus
- Communication
- Countersinging
- Day/Night Cycle
- Dear Enemy Effect
- Dominance Hierarchy
- Environmental Influences
- Extra-Pair Copulation
- Foraging
- Intersexual Selection
- Light/Dark Cycle
- Mate Guarding
- Passerine Vocal Communication
- Predation Risk
- Sexual Selection
- Sound Spectrogram
- Territoriality
- Territory Defense

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## Dawn Song

### ► Dawn Solo/Chorus

## Day/Night Cycle

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## Synonyms

Circadian rhythms; Sleep cycles, Related: Biological rhythms; Internal clocks; Timing

## Definition

An organism's internal physiological and behavioral responses to the predictable 24-cycle of planetary rotation (Adapted from Shettleworth 2010). Foundational work on this topic was done in rodents in the mid-1970s showing that these animals have an endogenous cycle slightly longer than 24-h as measured by an activity wheel

(Rusak and Zucker 1975; Zucker 1976). In the absence of external cues, the animals are said to be free-running, i.e., maintaining their own cycle, which will often be longer or shorter than 24 h. These rhythms to the day/night cycle allow animals to optimize behavior adaptively. Diurnal animals will know when it is day to hunt prey, and nocturnal animals will know when the night arrives in order to avoid becoming prey, if the case may be. These endogenous clocks allow animals to anticipate changes to the day/night cycles even if they live in a darkened cave or burrow. In mammals, it is believed that the suprachiasmatic nucleus (SCN) of the retinohypothalamic pathway drives the biological clock as lesions of this area interfere with rhythms associated with eating and drinking behavior in rats (Stephan and Zucker 1972). Given that animals may be active during the day, night, or throughout various times in a 24-h cycle, we will characterize the changes to both brain and body activities as defined by when animals are active rather than just day and night.

### The “Rest” Cycle

The first few hours of sleep are typified by a release in growth hormone, while thyroid hormone is common at the end of the sleep cycle (Institute of Medicine (US) Committee on Sleep Medicine 2006). The mammalian brain enters two distinct phases of neurological activity during sleep, non-rapid eye movement (NREM), and rapid eye movement (REM) sleep. In humans, NREM sleep is further divided into four stages starting with low amplitude mixed frequency theta waves and progressing to the high amplitude low frequency delta waves associated with slow-wave sleep (SWS). REM sleep was first found in infants and differs from NREM sleep in the low amplitude fast waves accompanied by atony in most warm-blooded animals including cats and humans (Aserinsky and Kleitman 1953; Hodes and Dement 1964; Jouvet 1967; Jouvet and Michel 1959). We can look at sleep as an adaptive state, decreasing our activity at times of increased predator risk, and allowing for activity during

times of optimal foraging, prey availability, or minimizing predator risk (Siegel 2017). A major function of REM may be to allow a rapid arousal from sleep with alertness by means of periodic brainstem activation, and this could account for why the majority of REM takes place in the last third of many mammals’ sleep (Siegel 2017). Memory consolidation is another hypothesis for the function of this pattern of sleep in the rest cycle (Boyce et al. 2016; c.f. Siegel 2001), while sensorimotor system development represents a third hypothesis for REM sleep (see Peever and Fuller 2016).

### The “Awake” Cycle

It is hypothesized that mammals awaken thanks to a hormone-mediated process called the cortisol awakening response (CAR). CAR represents a predictable and marked contrast to the regular functioning of the hypothalamic-pituitary-adrenocortical axis over the diurnal cycle and begins within the first hour after awakening from sleep (Steptoe and Serwinski 2016). Significantly less is known about the processes of the brain that maintain wakefulness throughout the day. Sleep behavior in *Drosophila* can be measured using infrared beams traveling through glass tubes housing the fruit flies. These studies reveal that the circadian neuropeptide pigment-dispersing factor (PDF) plays a role in keeping the animals awake and is regulated through dopaminergic neurons (Potdar and Sheeba 2018). The suprachiasmatic nucleus maintains wakefulness most probably by sending alerting signals. Melatonin induces sleep by inhibiting this portion of the brain, and the chemical’s release is triggered by a decrease in light as the diurnal animal enters the night cycle (Parker and Dunbar 2005).

### The Evolutionary Loss of Regular Day/Night Cycles

In fully aquatic mammalian species, the loss of the penial gland indicates a resultant loss of

melatonin-bases circadian rhythmicity (Lopes-Marques et al. 2018). This is seen behaviorally in beaked whales, where their foraging behavior remains unchanged relative to the day/night cycle (Baird et al. 2008). While bihemispheric slow-wave (BSWS) and REM sleep have been observed in all terrestrial species that have been studied (denoted by traditional body posture, closed eyes, distinctive electroencephalographic [EEG] waves, decreased motor activity, and increased sensory threshold associated with traditional forms of sleep), certain marine mammals and species of birds exhibit unihemispheric sleep (Mascetti 2016; Siegel 2017). These animals have adopted a different strategy for their specific environmental needs, with unihemispheric slow-wave sleep (USWS) in marine mammals and unihemispheric-monocular sleep (Un-Mo sleep) in some birds. In USWS, wakefulness and sleep alternate between the two hemispheres of the brain, and there is no NREM or REM. In the absence of a bilateral high-voltage EEG, SWS (EEGs consisting of low frequency high amplitude waves) is confined to one hemisphere for two or more hours, while the other hemisphere exhibits high and low amplitude waves associated with an awakened state. Un-Mo sleep is defined as alternating states of both unilateral and bilateral eye closure and is considered relevant for anti-predation vigilance (Mascetti 2016; Siegel 2017). In non-cetaceans (namely, seals and birds), unihemispheric sleep is a transitory sleep event mingled with bihemispheric sleep (Mascetti 2016). It has proven difficult to know whether the first whales evolved USWS directly from BSWS/REM sleep (typical of most terrestrial species) or if there was an intermediary evolution with a pattern more closely resembling those of pinnipeds and birds (Lopes-Marques et al. 2018).

## Light Pollution and Its Effects on the Day/Night Cycle

Artificial light has often been associated as a direct cause for insomnia (difficulty initiating or maintaining sleep) in diurnal mammals (Stenvers

et al. 2016). The main trigger for the hypothalamic SCN is light, and it is the SCN that coordinates the sleep-wake cycle (Stenvers et al. 2016). With an increase in light pollution, we are starting to see long-term impacts on many species. Wistar rats introduced to dim light at night were found to significantly reduce SCN output strength causing a reduction in feeding-fasting behavior and the daily amplitude of sleep-wake (Stenvers et al. 2016). It was found that in six species of sea turtles, artificial light had deterred nest seeking on what would have been preferred beaches (Witherington 1997). In cases where nesting did occur on lit beaches, hatchlings that emerged nocturnally would wander inland toward the light sources as they were unable to locate the sea (Witherington 1997). Although many negative effects have been observed as a result of artificial light, other species like bats and birds have used artificial light to improve their performances in prey capture by feeding on the various insects drawn to these light sources (Sol et al. 2013). Other diurnal birds, like gulls and pigeons, have increased their foraging times, expanding their ability to meet daily food requirements (Sol et al. 2013). In blue tits (*Cyanistes caeruleus*) males who sing earlier in the day, by virtue of the presence of artificial light, have increased reproductive success (Kempnaers et al. 2010). Hence, light pollution has long-term consequences leading to both positive and negative fitness effects.

## Cross-References

- [Biological Clocks](#)
- [Biological Rhythms](#)
- [Circadian Rhythms](#)
- [EEG](#)
- [Sleep](#)

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## Day-Active

### ► Diurnality

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## Day-Night Activity

### ► Cathemeral



## Dead Reckoning

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*Dead Reckoning*: An animal's inability to see, smell, echolocate, or feel its way around an environment does not necessarily preclude successful navigation. Instead an animal may use a mechanism called dead reckoning to navigate. A navigator's phrase, *dead reckoning*, is also synonymous with *path integration*, meaning the organism uses cumulative information about its distance and direction to find a way back to the origin of the journey (Shettleworth 2010). Dead reckoning, as described by Gallistel (1990) is defined as an egocentric mode of navigation (see ► [Egocentric Frame](#)) that is based on the individual localizing with respect to itself. Egocentric navigation explains how a human can move around an unfamiliar darkened room with some limited success, capable of returning to a starting point after fumbling around the space for a few minutes. In these instances, an organism may use self-referential vestibular cues (Etienne et al. 1986), sensory input from leg mechanoreceptors (Seyfarth and Barth 1972), or external visual flow patterns that change with respect to the individuals' speed and heading (Saint Paul 1982; Ugolini 1987). Self-referential cues are best exemplified by the use of vestibular senses by nocturnal mammals [in gerbils: (Mittelstaedt and Mittelstaedt 1982); in hamsters: (Georgakopoulos and Etienne 1994)] to identify distance and direction. External cue usage in dead reckoning is also seen in diurnal species like bees (Ugolini 1987) and geese (Saint Paul 1982) and relies on patterns of visual flow to determine displacement. Dead reckoning as a form of egocentric navigation is in contrast to allocentric or geocentric modes of navigation that emphasize the environment's unique features and the animal's localization within an external frame of reference. External cue usage in dead reckoning differs from external cue usage in allocentric or geocentric modes because features of

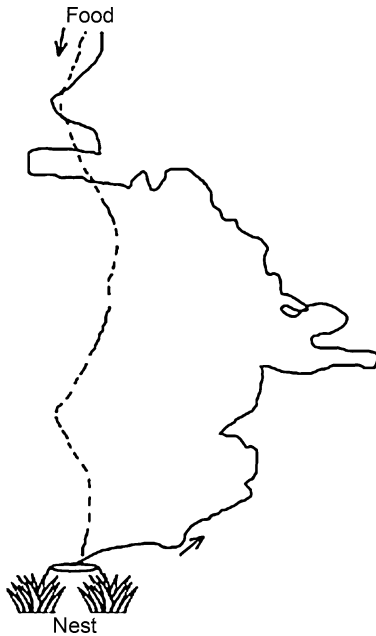
the environment are not attended to in the egocentric frame. It is helpful to picture a high-speed camera over a busy city street at night with cars moving so fast that all one sees is the blur of the lights. Features of objects are indistinguishable, but an individual can identify distance and direction traveled simply by the flow of light.

Shettleworth (2010) characterized egocentric navigation as relying on a short-term memory system, processing information related to internal cues collected on a current "expedition," and reset upon the completion of that particular track and the beginning of another. However, care must be made to not see egocentric navigation as precisely synonymous with dead reckoning, as vestibular senses can mediate the route-style navigation typified by tunneling species (Bruck et al. 2017). Theoretically, a nocturnal organism using dead reckoning can wander about in the absence of any external cues but still be able to go from any point on a trip and return to the starting place (Fig. 1). In contrast, route-navigation mediated by egocentric cues does not necessarily see the subject returning to a starting point.

So far, scientists have identified evidence for vertebrate dead reckoning in golden hamsters (Georgakopoulos and Etienne 1994), gerbils (Mittelstaedt and Mittelstaedt 1982), rats (Dudchenko and Bruce 2005; Shettleworth and Sutton 2005; Watson 1907), pigeons (Sutton and Shettleworth 2005), geese (Saint Paul 1982), and possibly voles (Eilam et al. 2003). Invertebrate examples include desert ants (Wehner and Srinivasan 1981), wasps (Ugolini 1987), and bees (Dyer 1996) to name a few.

By no means is dead reckoning a perfect system. In most cases, this is not a true mathematical integration (as the term path integration might suggest); therefore, errors tend to accumulate over time. This makes long-distance movement using dead reckoning dangerous. Some animals have mechanisms to adjust for the problem. For instance, desert ants use a wider spiraling search pattern upon return to the nest after longer journeys (Wehner and Srinivasan 1981). These wider search loops are possibly a consequence of less certainty with the exact location of the nest entrance. Another disadvantage of dead reckoning





**Dead Reckoning, Fig. 1** Foraging with dead reckoning. An organism's foraging journey in a featureless environment with the solid line representing the outgoing path in search of food and the dashed line representing the fairly direct successful return trip to the home nest mediated by dead reckoning. (Adapted from Wehner (2003) with permission from the author)

is that it usually does not compensate for slow to moderate course alterations that are uninitiated or undetected by the organism. Such events may result from wind, shifts in sand, or experimenter movement (Mittelstaedt and Mittelstaedt 1982). Dead reckoning is also subject to limitations in memory, so far as the process is cognitive. As distance travelled increases, the probability of getting lost also increases due to a higher likelihood of the animal forgetting. Without using external visual cues, there is no way for an animal to consolidate referential units of memory or to correct for errors inherent to path integration.

Experimentally, egocentric navigation can be studied using two broad methodologies. One method incorporates open field designs in what is considered a test of true dead reckoning. Here an animal's ability to return to a starting point is tested in the absence of allocentric and geocentric cues. Often this can involve using rotating platforms that turn too slowly to be perceived by the

subject's vestibular senses or experimenter translocation of animals' part way through their journey to see if errors are reflective of the distance they were moved (see Shettleworth 2010 for review of studies). One can also use mazes to study egocentric route navigation (Benhamou 1997; Bruck et al. 2017; Shettleworth 2010). In these cases, again, it is not dead reckoning that is necessarily assessed (because the animals do not necessarily travel to a location and then return to start), but rather sensory mechanisms used in dead reckoning, integrated with cognitive map formation, that are of interest. This is not to say that route-based egocentric navigation does not inform our understanding of dead reckoning, as one may be studying many of the same underlying perceptual systems an organism uses in dead reckoning.

In considering the evolution and neurological basis of egocentric navigation, it is interesting to note that impairment of the interpeduncular nucleus affects both landmark navigation and egocentric navigation but not beacon navigation (Clark and Taube 2009). Both beacon and landmark navigation are examples of allocentric navigation (Shettleworth 2010), yet it seems the landmark and egocentric modes may share brain structures. This might be explained by the associative nature of beacon navigation (navigate to perceptible target) and the integrative natures of egocentric and landmark navigation (where multiple cues are needed to orient a navigator).

## Cross-References

- ▶ [Arthropod Navigation](#)
- ▶ [Egocentric Frame](#)
- ▶ [Insect Navigation](#)
- ▶ [Navigation](#)
- ▶ [Navigation by Honey Bees](#)
- ▶ [Rodentia Navigation](#)

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## Dear Enemy Effect

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## Synonyms

Dear enemy phenomenon; Neighbor-stranger discrimination

## Definition

Reduced aggression between established territorial neighbors relative to strangers

## Introduction

Territorial animals defend resources needed for survival and reproduction. Animals advertise their ownership of territories through conspicuous signals; birds and frogs vocalize, mammals and salamanders scent mark, lizards display colorful patterns, and fiddler crabs wave their oversized claws in the air. If advertisement is not enough, animals may have to fight off intruders to maintain territory ownership. However, animal fights are relatively rare, even when territories are spatially clumped resulting in frequent interactions between neighbors. Once territories are established, individuals in neighboring territories typically respect territorial boundaries and withhold aggression from their neighbors. This makes sense because aggression can be costly, and if a neighbor already has a territory, they might not represent a threat to a territory holder. However, territory holders will often maintain a readiness to be aggressive toward unfamiliar individuals,

showing more aggression to strangers than to familiar neighbors. This phenomenon of reduced aggression between established neighbors relative to strangers is called the “dear enemy effect” and is thought to allow animals to minimize the costs of territory defense (Wilson 1975).

The term “dear enemy” originates with observations made by James Fisher (1954) that songbirds often establish territories in clusters and have relationships with their neighbors that are not strictly competitive. Fisher wrote that “the effect of the holding of territory . . . is to create “neighbourhoods” of individuals which are masters of their own definite and limited property, but which are bound firmly, and *socially*, to their next door neighbours by what in human terms would be described as a dear enemy or rival friend situation.” Much of the early research on the dear enemy effect was conducted on territorial songbirds, which often respond less aggressively to the familiar songs of their neighbors than they do to the unfamiliar songs of strangers. Since this early work on birds, the dear enemy effect has been documented in many different taxonomic groups, including insects, crustaceans, fish, amphibians, reptiles, and mammals.

### Adaptive Significance

Individuals must balance the benefits and costs of defending a territory. The primary benefit of holding a territory is the exclusive access to resources that may be limited in the environment. Defended resources may include feeding grounds, areas to advertise to and court mates, reproductive resources such as oviposition or nesting sites, and shelter. However, aggressively defending these resources from conspecifics incurs costs, such as energy spent on aggressive encounters, missed opportunities to feed or mate, risk of injury during fights, and decreased vigilance against predators. We should generally expect that evolution has equipped territorial animals with decision rules that allow them to maximize the difference between the benefits and costs of territory defense. The dear enemy effect is the product of such a decision rule, but why, exactly, is it adaptive to treat neighbors and strangers differently?

There are two hypotheses to explain the adaptive value of behaviorally discriminating between neighbors and strangers. The “relative threat” hypothesis (Getty 1987) rests on the assumption that strangers pose a greater threat to territory holders than do neighbors. The idea is that strangers are likely to be non-territorial “floaters” that are looking to establish a territory by taking over an existing territory or inserting themselves into a network of territories. Territory holders thus risk either losing their territory to a stranger or gaining an additional competitor if a stranger settles nearby. In contrast, a neighbor already has a territory of its own; neighbors may compete for mates or food but they do not pose a threat to territory ownership. By maintaining high levels of aggression toward strangers and tolerating nearby neighbors, territorial animals can both reap the benefits of possessing a limited resource and minimize the costs of defending that resource. Along a different line of reasoning, Ydenberg et al. (1988) proposed that a dear enemy effect functions to minimize the costs of escalated conflicts between neighbors and is possible because familiar neighbors have established dominance relationships. This “familiarity” hypothesis rests on the assumption that the relationship between neighbors is established through repeated conflicts, and once dominance relationships are established, individuals are less likely to make role mistakes in future conflicts. Strangers, however, do not have established relationships and need to escalate conflicts to determine dominance roles. Thus, interactions are more likely to escalate to higher levels of aggression between unfamiliar individuals than they are between familiar neighbors.

While the “relative threat” and “familiarity” hypotheses are not mutually exclusive, they do make different predictions about when a dear enemy effect should be adaptive. The “familiarity” hypothesis predicts a dear enemy effect any time neighbors can become familiar with each other. The “relative threat” hypothesis predicts a dear enemy effect only for situations in which strangers pose a greater threat than neighbors, regardless of how familiar neighbors may be. Temeles (1994) reviewed studies of the dear enemy effect and found that the results are

generally consistent with the “relative threat” hypothesis. Among birds, the dear enemy effect is typically observed in species that defend multi-purpose breeding territories, where neighbors may compete for mates or food, but strangers threaten complete territory takeover. It is often not observed in species that defend single-purpose feeding territories or nest sites, where neighbors and strangers both represent equivalent threats to food or nesting resources and are treated the same by territory holders. Some of the best evidence for the relative threat hypothesis actually comes from situations in which neighbors are more of a threat than strangers, and territory holders correspondingly direct more aggression toward neighbors (Temeles 1994).

## Neighbor Recognition

Many researchers are interested in the dear enemy effect because it allows them to study social recognition. Learning to recognize familiar neighbors allows territorial animals to direct aggression toward strangers, producing a dear enemy effect. However, the dear enemy effect and neighbor recognition are not synonymous. A dear enemy effect could be produced in the absence of neighbor recognition. For example, if individuals that do not possess territories behave differently than individuals that have territories, the behavioral cues of non-territorial strangers could be perceived as more threatening and elicit stronger aggressive responses from territory holders. On the other hand, one could observe neighbor recognition in the absence of a dear enemy effect if, for example, territory holders are more aggressive toward neighbors than strangers. Finally, a lack of observed behavioral discrimination between neighbors and strangers cannot rule out the possibility that a territory holder recognizes a neighbor but simply treats neighbors and strangers with equal levels of aggression.

Nevertheless, many studies of the dear enemy effect are also tests of neighbor recognition. The pioneering work on neighbor recognition was conducted on songbirds (Stoddard 1996). Territorial male songbirds often respond more

aggressively to the songs of strangers than the songs of neighbors played from the direction of the neighbor’s territory, showing that they learn to recognize the vocalizations of their neighbors. Further, territory holders often respond more aggressively to their neighbor’s songs played from an unfamiliar location than from their neighbor’s territory, suggesting that these birds have the capacity to recognize multiple individual neighbors based on vocalizations and location (Stoddard 1996). Similar results have been obtained in territorial bullfrogs (Bee et al. 2016) and damselfish (Myberg and Riggio 1985). Some studies have demonstrated individual recognition of neighbors independent of location. For example, though male bullfrogs are more aggressive to the vocalizations of a neighbor played from an unfamiliar location, they still show less aggression to neighbors in an unfamiliar location than to strangers in an unfamiliar location (Bee and Gerhardt 2002). Another experimental approach uses a neutral arena; Husak and Fox (2003) showed that male collared lizards are less aggressive toward familiar neighbors in the field and in staged interactions in a neutral arena, demonstrating individual recognition independent of location.

The dear enemy effect has allowed researchers to investigate a variety of perceptual and learning mechanisms that allow animals to recognize familiar individuals. In order to recognize familiar neighbors, territorial animals must be able to perceive the differences in signals produced by different individuals. Experiments in sparrows and bullfrogs have shown that territorial individuals can perceive individual differences in frequency of vocalizations, allowing them to recognize the vocalizations of familiar neighbors (Brooks and Falls 1975; Bee et al. 2016). Research on the dear enemy effect has also revealed that territorial animals can learn to recognize familiar neighbors through habituation, a common form of learning in which animals gradually decrease response to a stimulus with repeated exposure to that stimulus. Neighbors may initially be aggressive with each other during territory formation, but their aggression gradually habituates as territory boundaries are established. Because habituation is specific to a certain stimulus, habituation to the signal

properties of a familiar neighbor can allow a territory holder to recognize a particular individual by those signal properties (Bee et al. 2016). Other forms of learning are certainly involved in neighbor recognition in some species. For example, song sparrows have dear enemy relationships with their neighbors, and neighbors interact with each other by singing songs that they share in common (Beecher et al. 1996).

## Conclusions

The dear enemy effect occurs when territorial animals direct less aggression toward established territorial neighbors than toward strangers. This is a common phenomenon among territorial animals and has been documented in many different taxonomic groups. By withholding aggression from neighbors, animals can minimize the costs of territory defense. The general consensus of research on the dear enemy effect is that animals are more aggressive to strangers because strangers pose a greater threat to territory holders than do neighbors. The dear enemy effect is often made possible by the ability to recognize familiar neighbors and has allowed researchers to understand some of the perceptual and learning mechanisms that underlie this common form of social recognition.

## Cross-References

- [Aggression](#)
- [Habituation](#)
- [Individual Recognition](#)
- [Territoriality](#)

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## Dear Enemy Phenomenon

- [Dear Enemy Effect](#)

## Death

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## Introduction

The scientific study of death responses is the central agenda of the field of comparative thanatology. Within primates, humans are peculiar for

**Death, Table 1** Burying behaviors in nonhuman animals

| Taxon            | Frequency  | Sensory modality | Underlying causation         |
|------------------|------------|------------------|------------------------------|
| Termites/ants    | Very often | Chemosensory     | Pathogen avoidance           |
| Naked mole rats  | Often      | Scent            | Pathogen avoidance           |
| Rats             | Often      | Scent            | Defensive burying            |
| European badgers | Occasional | Scent/other cues | Misdirected caching behavior |
| Canids           | Rare       | Scent/other cues | Misdirected caching behavior |
| Elephants        | Very rare  | Multimodal cues  | Testing for life signs (?)   |
| Chimpanzees      | Very rare  | Multimodal cues  | Testing for life signs (?)   |

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the fact that they have been burying their dead as early as 120 Kya; however, they are not the only animal to do this. In reality, other species in the animal kingdom engage in “burying behavior,” while the underlying causes vary substantially (see Table 1). In humans, the concept of death develops from ages 3 to 10 with subcomponents being grasped at different ages. In our lineage, burials came from the realization something had to be done with the corpse, as suggested from their deliberate rather than instinctive/accidental/incidental nature in nonhuman animals. Corpses can be a source of critical information; they can signal predation events, food resource, or pathogen hazard. In this regard, a constellation of behaviors can ensue around dead conspecifics and their sensory cues; fishes/rodents avoid corpses of conspecifics due to the presence of death-associated odors, corvids alarm call/gather around their dead, while elephants investigate the bodies/bones of dead conspecifics, and nonhuman primates carry dead infants. By looking at our closest living relatives and further down the evolutionary lines, we can begin to glimpse what came before elaborate ways of treating/conceiving the dead and understand the evolutionary pressures behind it.

**Animacy Detection Malfunction**

Upon detection, corpses present a conundrum; having both inanimate and animate attributes they are uncanny, defying expectations and provoking confusion among the living. Like *agents*, they exhibit *static cues* to *animacy* (shape and texture), but like *objects* they lack *dynamic cues* to *animacy* (self-propelled motion and contingency). Gonçalves and Biro (2018) proposed the

term *animacy detection malfunction*, understood as the conflicting cognitive processes brought about by such perceptual mismatches causing violations of expectation when a corpse is detected. Hypothetically, such conflict stems from the activations of two different cognitive systems in the brain, one dedicated towards agency detection and another for object detection. This is illustrated by many accounts of social nonhuman animals displaying approach/avoidance and exploratory/fearful responses when encountering a corpse, in some cases a conspecific which they recognize and interacted with throughout their lives.

**Thanatological Interactions**

Thanatological responses (behaviors towards the dead) are often observed in many animal species, but only few are interpreted as epimeletic (helping) behaviors (Gonçalves and Biro 2018). Among mammals, and to some extent birds, they include mothers stationing around, physically interacting, and/or carrying their dead offspring. The main reason lies in phylogenetically ancient caregiving mechanisms mediated by oxytocin and its homologues continuing to function even after the offspring has died. In vertebrates, these hormones originally served a function for “basic” reproductive behavior (vocalizing, courtship behavior, nest building) and then extended to more “advanced” reproductive behavior (pair bonding and parental care) culminating in social bond formation and maintenance (Knobloch and Grinevich 2014) (Fig. 1).

From a proximate perspective, the mother perceives her infant’s condition as unclear,





**Death, Fig. 1** Similarities of dead offspring carrying behavior. Left: a female African bush elephant (Photo credit: Anna Ritenour). Right: a female Eastern chimpanzee. (Photo credit: Charlotte Richardson)

anticipating that it will still recover, thus continuing to invest in it. From an ultimate perspective, the constant caretaking behaviors result from error management, since the fitness cost of abandoning a temporarily unresponsive infant would be higher than continuing investing for a limited period. Such deaths are followed by a transitional phase that can vary extensively depending on taxa, individual, or external factors (from hours, days to weeks or months) whereupon the mother will stay in close proximity and physically interact with the corpse (e.g., inspecting/licking, grooming). These responses decrease over time always culminating in the abandonment or loss of the corpse.

In nonhuman primates, the most common response is dead infant carrying. There are currently many hypotheses explaining not only the occurrence but also the maintenance of this behavior ranging from anatomical (handling and carriage ability), physiological/emotional (hormones and grief management), perceptual/cognitive (error management, infantile cues), to life history (parity, individual differences) and ecological factors (climate, arboreality/terrestriality) (Gonçalves and Carvalho 2019). One issue is that some are not mutually exclusive; the mother may not fully comprehend the infant's state is final, she might be guided by her postpartum hormones, holding the infant may act as a buffer to grief, and drier climates and easier

locomotive habitats might facilitate and prolong such responses. Nonetheless, the motivations to station around a corpse versus carrying it are the same, the primary distinction for the latter being a physical one; non-primates have dexterous limbs that permit such carriages when other vertebrates do not. Cetaceans and, to a lesser degree, elephants have also been observed carrying dead offspring (Fig. 1), the first due to buoyancy in aquatic environments and the second owing to a dexterous trunk. Other reports suggest this carrying behavior is more widespread among taxa, including wolves (using the mouth) and hippopotami (in water).

Concerning interactions towards adult conspecifics, three main behavioral responses can occur: *guarding*, *vigils*, and *visitations*. *Guarding* is expressed through alarm calling, harassment responses, and rescue attempts, whereupon the individual defends the corpse from perceived threats. *Vigils* are defined as physical proximity towards the corpse for extended periods. *Visitations* are characterized as returns to the place where death ensued or the corpse was last seen. These responses share behavioral traits with sympathetic concern and empathetic targeted helping as usually they are performed by kin or closely bonded individuals. While these behaviors are mainly found in nonhuman primates (Gonçalves and Carvalho 2019), with the aid of camera traps, they have been recorded in other close-bonded

animals such as elephants and collared peccaries (de Kort et al. 2018; Hawley et al. 2018).

Most parsimoniously, these responses reflect a limited/implicit awareness of death (agency cessation) that requires constant status updating. Emotional motivations underlying such responses are temporarily overruling more cognitive aspects of death recognition as evidenced by the responses of individuals less bonded with the dead who cease their interactions sooner than strongly bonded individuals. From an evolutionary perspective, this makes sense as with dead infants, caretaking activities directed towards other group members would be advantageous if unresponsive individuals would recover.

### Grief-Like Responses

In describing grief, Charles Darwin made a distinction between two states: *excessive grief* and *sorrow*. The former was categorized as “frantic” and “energetic,” whereas the latter was “languid” and “dull.” Because our closest primate relatives do not weep nor show the facial expressions associated with sadness, Darwin concluded grief to be a typically human response. Nevertheless, later research on depression in both humans and monkeys similarly recognized these two states as protest (active) and despair (passive) which alternated back and forth.

The study of emotions, particularly attributing grief to nonhuman animals, is a matter of ongoing debate, as many researchers place emphasis on either the unobservable nature of mental aspects of grief or the uniqueness of human grief and it being inextricably tied to the concept of death. However, considering grief is predominantly associated with behavioral and physiological changes in the individual (sleep disturbances, decreased social activity, decreased appetite, increased self-directed behaviors, stress hormone elevations), it is important to point out such changes have been documented both in humans and nonhuman primates (Gonçalves and Carvalho 2019). Moreover, research in macaques shows the neurobiological foundations in these depressive states (gene-environment interactions and

serotonin) are the same as in humans. And although the majority of behavioral reports comes from nonhuman primates, there is convergent evidence from other animals including both mammals and bird species.

### Notable Empirical Research

Necrophobic behaviors, exhibited by aversion to death scents (cadaverine/putrescine), appear to be a highly conserved response, either innate or acquired quickly through learning. These are adaptive and would have been selected in terms of predator evasion or pathogen avoidance. In experimental settings, zebra fish, lampreys, sharks, but also mice typically avoid scent from decaying conspecifics. Experiments conducted in corvids show that when detecting a dead conspecific or similar-sized heterospecific, they tend to engage in cacophonous aggregations, likely as a form of mobbing and alarm-calling behavior, and will usually avoid the places where dead conspecifics were, apparently because of predation hazard (reviewed in Gonçalves and Biro 2018).

Studies demonstrating the strong influence of caretaking in birds showed that passerines will still incubate dead chicks placed in the nest even when they exhibit clear signs of injury (Leniowski et al. 2013). Additional observations of failed nests due to predation show species of passerine parents coming back to the nests (engaging in incubation and food provisioning), again, likely due to a strong caretaking drive that is not immediately switched off after nest predation. Notably, they found this maladaptive response was impacted by chick age at death; the older the offspring, the sooner parents abandoned the nest (Henschke et al. 2016). Collective experiments from mice show that multiparous females retrieve and show more caretaking behaviors than nulliparous females and, apparently, either group does not differentiate between live and dead pups as they retrieved them suggesting, with mediation from post-parturition hormones, visual/scent cues suffice to elicit this response rather than auditory stimuli (ultrasound pup vocalizations) (Gandelman et al. 1970).

*Contra* previous claims that nonhuman primates rarely console bereaved group members, Goldsborough et al. (2020) showed that, after a captive chimpanzee mother lost her infant, group members showed high levels of reassuring behaviors the same day and increased affiliative responses towards her following the loss. These and similar studies emphasize the role of empathy in managing social relationships.

## Conclusion

There is a strong argument for some thanatological responses indicating attachment relationships and operating on the expectation the dead conspecific could recover. Seemingly maladaptive, they may, however, serve an evolutionary purpose. By engaging in the abovementioned thanatological behaviors, socially bonded animals are gathering information on the conspecific's state. Additionally, they promote a faster recategorization from living to dead and reduce costly caregiving responses, may be essential to grief management, updating ranks in the hierarchy, and accelerating the formation of new social bonds. More empirical research is needed and is currently being done targeted at these and other questions relating to animal grief and awareness of death that will be fundamental in expanding our knowledge of how animals respond towards death.

## Cross-References

- [Attachment](#)
- [Bear Life History](#)
- [Curiosity](#)
- [Empathy](#)

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## Decaying

- [Cognition](#)

## Deceit

- [Cheating](#)

## Deception

- [Cheating](#)

## Deciduous Teeth

- [Dental Formula](#)

## Decision-Making

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### Definition

The process used to choose between different options.

### Introduction

Animals face multiple choices throughout a day and therefore must make decisions on a daily basis in several areas. Decisions can include choosing when to feed, when to sleep, where to go, and what path to use to reach a destination, to simply decide to continue or change the current activity. In each case, animals have to take into consideration a variety of factors, including the physiological needs of themselves and of conspecifics, as well as the characteristics of their environments such as the location of resources or the presence of predators. Since the outcome of a decision can be critical for the survival and the reproductive success of an individual, a decision-making process has evolved to determine which choice should have the priority at a particular time (McFarland 1977). In addition to this process, a collective decision-making process has also evolved within groups, where different mechanisms are involved to make decisions as a group.

### Animal Decision-Making

Decision-making is the process by which an animal makes decisions by choosing between different options. Such process includes different stages with different mechanisms involved, where choices emerge from the combined action of sensory integration, cognitive mechanisms, and decision rules. Animal decision-making process begins with the acquisition of information gained

through their senses. Information can come from different sources such as the environment in which they evolve or the inner state of an individual, which can provide information on the level of satiety or the level of fatigue. Individuals invest time and energy to collect various information and to evaluate and integrate it, via cognitive processes, to create a set of sensory data. These data allow the individual to reach an “informational state,” where all the information that is known can be taken into consideration in order to make a decision (Blumstein and Bouskila 1996). Decisions are then made based on this informational state using decision rules and strategies, which result in behavioral actions that change or maintain the state of the decision-maker. The consequences of a decision can then be re-evaluated to consolidate the experience into a memory that can influence future decision-making (Owen et al. 2017).

The informational state used to make a decision is not a binary state where an individual is informed or uninformed. It is rather a state where the information that is known by an individual cumulate to form a relative knowledge, where individual integrates information from multiple sources, each with different levels of accuracy and precision. When collecting information, animals can use a variety of non-mutually exclusive processes that can range from self-acquired to socially acquired information. Indeed, animals can gain information by direct detection via sensory systems, where information is based on environmental cues detected within an individual's perceptual range. In the animal realm, a variety of sensory systems have evolved to access information at different spatial scales with varying levels of accuracy. By combining inputs from different systems, animals may be able to increase the detection, accuracy, and quality of the information they can obtain (Spiegel and Crofoot 2016). Animals can also rely on their own experiences to gain information, which take the form of memories. Evidence of the use of memory as an information base to make a decision can be found in studies looking into foraging strategies, for example, repeated visits by animals to particular locations are often seen as the evidence of

memory use (Bracis et al. 2015; Merkle et al. 2014). Animals can also rely on others to obtain information about their habitat, either relying on conspecific or hetero-specifics. Socially acquired information can be based on others' sensory systems or memories. Indeed, by living in groups, individuals can gain access to the sensory information detected by other members, which can increase their detection range beyond their own physiological limitations and help improve the quality and accuracy of an individual's knowledge. Predator detection is a perfect example of such a situation as more individuals have more chances to detect a predator. On the other hand, member of a group can benefit from the experience of older members that possess more information about the habitat. For example, such reliance on others' memory can be seen in-group movement when older individuals lead the group movement toward a foraging destination (Teichroeb et al. 2012).

In addition to the different processes by which animals can reach an informational state, a set of decision rules have evolved to guide animals' decision-making (Owen et al. 2017). For example, a decision could be made using an absolute valuation rule, where the decision-making process includes an independent assignment of a fixed value to each option and where the decision is based on a trait meeting a specific criteria value taking the form of a "must have" (Jennions and Petrie 1997). For example, when choosing a mate, a decision based on an absolute value could take the form of a female assigning a fixed value to the weight of each male and then choosing the male that has the desired weight. A decision could also be made using comparative valuation, where a decision is based on the simultaneous comparison of the relative value of a trait on two or more options (Reaney 2009). In this case, the value assigned to each option is dependent on those it is compared with, rather than being an absolute value of its underlying characteristic. In this case, a female would simultaneously compare the attributes of two or more males and choose the one that has the desired weight in comparison to the others. Another rule that could be used is best-of-N choice. In this case, a comparison of a fixed

number of options is made, and the decision result on the choice of the "best" quality option is evaluated (Janteos 1980). A threshold can also be used, where a sampling of option is continuously made until a threshold value of a particular trait is found. In such case, a decision takes the form of a "must at least have" where the decision-maker would continue to search until it found what it was looking for. Finally, heuristic rules of thumb are used when a decision is made on incomplete information, which makes it a fast and frugal approach to information gathering (Owen et al. 2017). Indeed, heuristics are cognitive processes that provide a shortcut to animal decision-making via gathering partial information from all that is available (Hutchinson and Gigerenzer 2005). Since it is impossible for animals to evaluate all the possible options when facing a choice or to acquire all the information available in their environment, heuristic rules of thumb may be adaptively advantageous as it limits the amount of time and energy an organism has to invest to gather information and make a decision. Therefore, heuristic rules could enhance decision-making efficiency but limit its accuracy (Gigerenzer and Geismmaier 2011). Moreover, while heuristic rules of thumb allow one to make decisions based on partial information, simple rules of thumb can be followed to make a decision and can take the form of following simple rule such as "always forage when your resources drop below a threshold or when the other animal forages" (Conradt and Roper 2005).

## Collective Decision-Making

While solitary animals often make decisions by themselves on a daily basis, members of a group in social species often make collective decisions. To do so, a group can use different types of decisions that can use different processes and mechanisms. Two types of decisions have been proposed to occur within a group (Conradt and Roper 2005). The first one being a combined decision where group members choose individually, but not necessarily independently, between two or more options without the goal to reach a



consensus. In this case, the group's action emerges from the combined results of the decision of each member, which affect the group as a whole. A combined decision could take the form of task allocation in eusocial species, where insects allocate themselves tasks according to the local necessity (Beshers and Fewell 2001) or individuals deciding to either stay or leave a group in fission-fusion societies (Sueur et al. 2011). In such a case, the processes used by a single individual to make a decision could be involved in the decision-making process of the group. In contrast, the second type of decision, a consensus decision, occurs when members of a group choose between two or more mutually exclusive options with the specific aim to reach a consensus. In such a case, more than one individual can participate in the collective decision-making, which can involve different decision-making processes and mechanisms than the one used by an individual alone. For example, this type of decision can occur when a group has to decide which activity to engage in and at what time, as well as when and where to travel.

## Consensus Decision

Consensus decision plays an important role in social species as it allows the group to make decisions as a whole. This enhances cohesion and avoids a split that could result in the loss of the advantages of group living. To reach a consensus decision, all members of a group are not always involved in the decision-making process. Different configurations exist in terms of the number of decision-makers, ranging from one member to all members of the group. Three types of configurations have been proposed in the literature: (1) an unshared decision where a single (usually dominant) individual imposes its choice on the group; (2) an equally shared decision, where all group members have the same opportunity to contribute to the decision, independent of their identities or social status and where consensus is usually reached via a quorum or a vote; and (3) a partially shared decision, which can range from "little" to "widely" shared, where several group

members contribute more than others or make the decision for the group (Conradt and Roper 2005). In partially shared decisions, a subgroup is typically a demographic subset of members such as all males, all females, or all adults.

In addition to the configurations that can affect the decision-making process, Conradt and Roper (2005) highlighted two important aspects to consider in consensus decisions as they can also affect how a decision is made: the presence of conflicts of interest and the type of communication found in a group. Indeed, if a decision involves conflicts of interest, it can influence which members contribute to the decision-making process and affect the fitness consequences of different group members. The type of communication, either global, where all members can communicate together, or local, where a group is too big and only communication with near individual is possible, can influence group members' contributions to the decision as well as the type of decision-making mechanism involved.

In a group, conflicts of interest about the outcome of a decision emerge from the existence of consensus costs. Individuals differ in their characteristics like age, sex, and internal states, such as their level of satiety or reproductive status (Petit and Bon 2010). This can create differences in their personal needs and make them differ in their optimal timing of activities and location preferences. Thus, consensus costs emerge from the necessity to compromise with other group members (Conradt and Roper 2005), where the fitness costs will increase with the difference between the optimal timing and movement location of an individual and the actual timing and destination of its group (Conradt and Roper 2010). Because consensus costs exist and are distributed unequally within a group, conflicts of interest can emerge. These conflicts can cause different actors to attempt to participate in and influence group decisions to their own advantage, which in return can influence which mechanisms are used to make collective decisions and which group members contribute to the process. The presence or absence of conflicts could influence the exchange of decision-related information between group members (List 2004), the degree of



cooperation during decision-making (Couzin et al. 2005), and the fitness consequences of the decision outcome to individual members (Conradt and Roper 2005).

As for communication, it can affect the participation of members or the mechanism available to reach a consensus. Groups with local communication usually have to rely on what is called self-organizing rules, while in a smaller group that can rely on global communication more complex negotiating behavior can occur (Conradt and Roper 2005). Indeed, on the one hand, small groups such as those found in social primates, carnivores, or ungulates can usually use direct communication with all group members. Therefore, complex negotiating behaviors and coalitions could occur during consensus decision-making, taking the form of a vote or quorum, as the needs for such strategies are met. Direct communication can allow the opportunity for all group members to vote and be taken into consideration in the “counting of votes,” as well as allowing them the possibility to influence the decision of other members. Some examples of “voting” in animals include the use of specific vocalizations (Boinski and Campbell 1995), ritualized signals (Black 1988), body orientation (Conradt and Roper 2003), and following an initiator that propose a change of activity at the start of a group movement (Byrne 2000). Counting the vote could be done by adding up to a majority of votes or the integration of voting signals until an intensity threshold is reached (Conradt and Roper 2003). However, the voting system seems to be following a majority of “vote” rules, where consensus decision is reached via a quorum. A quorum is then the minimum number of group members that need to take or favor a particular option for the whole group to adopt this action (Conradt and Roper 2005). For example, in collective movement, decision-making starts with the departure of the first individual, called the initiator, that moves a distance exceeding a fixed threshold away from the group, sometimes including a specific posture (Bourjade and Sueur 2010). This initiator proposes a time and a direction for the group movement, and others can take part in the decision-making process by deciding to follow or not

(Petit et al. 2009). The need to actively recruit and the speed with which individuals follow can be influenced by factors such as their relationship with the initiator, and these will decrease as the number of followers increases until a quorum is reached and the group movement takes place.

On the other hand, in large groups, such as large flocks of birds, shoals of fish, herds of mammals, or colonies of social insects, direct communication between group members is likely to be impossible, which brings the individual to depend on local communication with their direct neighbors to reach a consensus decision as a group. In such context, complex voting behaviors are unlikely to occur forcing members to rely on self-organizing rules as a mechanism to reach a consensus. Self-organizing rules include simple rules of thumb and thus are behavioral rules that individuals can follow using only local information, and these result in an organized group behavior without the need for global control (Conradt and Roper 2005). More specifically, self-organizing rules arise from members of a group following relatively simple rules like staying close to one another or mimicking the behavior of others, which create an organization within the group where a group can move in coordination or start an activity without the need to communicate with every member of the group. Indeed, in movement, to reach cohesive group navigation, simple rules of interaction can be used as a general mechanism. Examples of simple rules include alignment, where individual aligns their direction with other members, or attraction at long range and avoidance at short distance. A consensus and shared decision between all group members can be achieved without the need for complex mechanisms or advanced cognitive abilities, even in very large groups (Conradt and Roper 2005). Therefore, a collective decision can be reached in the absence of leader or global information in certain circumstances but can instead rely on the rapid propagation of local information about the motion, activity, or interest of the nearest neighbors (Petit and Bon 2010).

In addition to these decision-making mechanisms, other processes have evolved within groups to facilitate the reach of a consensus.

Indeed, local interactions are an inherent characteristic of group living and are an underlying mechanism of collective decision-making processes. Local interaction between individuals allows the extraction of information about group members' activity at a short range (Petit and Bon 2010), which in return facilitates synchronization of a group allowing members to reach a consensus. Being able to extract information from other group members may also induce an increase in the probability of performing behavior already present in the group by allowing anonymous mimetism between individuals. Anonymous mimetism is the propensity for an animal to act like their congeners, which increases with the number of individuals performing an activity. The occurrence of anonymous mimetism means that a single individual can influence all members of the group (Meunier et al. 2006), whatever their identity (King and Sueur 2011; Petit and Bon 2010). However, in social species, individual identity and social relationships can have an influence on mimetism and create a selective mimetism whereby some individuals, due to their age, status, knowledge, or relationships, will be imitated more often (King and Sueur 2011). Mimetic behavior is well known in animals' group (Petit and Bon 2010) and implies a positive feedback loop (Sumpter 2006) on collective behavior that allows the amplification of an activity. Thus, this mechanism can amplify the decision made by a few individuals and may be decisive when a quorum in a small group is needed to reach a consensus (Meunier et al. 2006; Petit and Bon 2010) or when local information has to spread within a larger group.

## Conclusion

Decision-making is the process by which animals choose between different options. Individuals can integrate different types of sensory information, cognitive mechanisms, and decision rules to reach a decision, whereas the collective decision of a group can include more complex mechanisms ranging from self-organization rules to complex negotiation behaviors. The variety of sensory

system, social organization, and environment found within animals has created a multitude of configuration of decision-making, which challenges your understanding of such a critical process.

## Cross-References

- [Communication](#)
- [Costs of Group Living](#)
- [Fission-Fusion](#)
- [Group Living](#)
- [Information Processing](#)
- [Predator Detection](#)
- [Sensory Receptors](#)
- [Social Behavior](#)
- [Susan D Healy](#)

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## Declarative Memory

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## Synonyms

Explicit memory

## Definition

Declarative memory is a long-term memory system where the processes of acquisition, storage, and retrieval are activated voluntarily and consciously.

## Introduction

The study of psychological processes such as learning and perception or memory, among others, has been of interest to many authors throughout history. A considerable amount of theories have been proposed about how these

processes work, each of them having more or less empirical support, in many different areas of knowledge. Historically one of the most studied psychological processes that has remained relevant to this day to many researchers is memory. Memory could be defined as a neurocognitive capability that allows for encoding, storing, and retrieving of information (see Tulving 2000, for more information on the term memory). According to this view, the use of memory implies an initial encoding of information (acquisition), the storage of this information during a determinate time, and its posterior retrieval and use (Anderson 2000).

Although these three components seemingly participate in all memory tasks (Neath and Surprenant 2003), there are two main viewpoints aiming to explain the nature of memory. On one hand, some authors define memory as a unitary process and assume that it adapts its functionality depending on the situation (Masson and MacLeod 1992). In other words, these authors supported the idea that memory is a single system that could operate differently depending on the task at hand, the kind of information, the time available, the subject condition, or the instructions given. On the other hand, it has been argued that memory is composed of different systems and that each one is, or is not, activated in any given situation (Squire 1995). Beyond this theoretical debate (see Foster and Jelicic 1999, for a revision), the study of memory since the middle of the twentieth century supported the idea that, although there are common processes to all memory systems (Neath and Surprenant 2003), it is composed of different and relative independent systems and that each of them have their own characteristics.

## Systems of Memory

One of the first distinctions among the different systems that compose memory was made based on the amount of information stored and the time that this information remains (Hebb 1949). Firstly, short-term memory is defined as the kind of memory that stores information for a brief time lapse. The exact amount of information and the time that

it is stored depends on the task at hand, the participant's status, the kind of material used, and many other variables. However, it is accepted that short-term memory could store sets of five to nine elements during a time span of 15–30 s. On the contrary, long-term memory stores a great amount of information, indefinitely. The study of a list of randomly generated numbers, for example, 2-4-5-2-9-7-0-1-1-6-5, and its immediate retrieval could be an example of a short-term memory task. In contrast, long-term memory is used to remember, for example, the name of an old school friend or our telephone number. The distinction between long-term and short-term memory has been supported by studies in many different areas as experimental psychology, neuroscience or studies of patients, to name a few. A third memory system that could be differentiated in accordance with the time that information remains stored is sensory memory. This system keeps the information stored for whatever amount of time needed to be transferred from the perception of the stimuli to its arrival to short-term memory. This process takes just a few hundredths of a second (Walsh and Thompson 1978).

Atkinson and Shiffrin (1968) proposed a well-known memory model in which these three memory systems are integrated. These authors assumed that the information accesses memory through sensory memory, and only some of these pieces of information are transferred to short-term memory. This transfer of information seems to be mediated by an intentional process, and it only selects a small part of the information that is received from the world. Information in short-term memory can be forgotten by decay or replaced by new information. However, rehearsal can keep it active in this memory system. According to this model, the only information that could generate responses is the one that remains activated in short-term memory. An elaborate rehearsal can allow information to pass from short-term to long-term memory and be stored indefinitely. Finally, information can also be retrieved from long-term to short-term memory and, as it has been mentioned, generate a response. Although the model proposed by Atkinson and Shiffrin (1968) had a deep impact

on the study of memory, some data has been found to question some of its assumptions, such as the fact that transference of information through short-term memory is not needed for long-term storage (Shallice and Warrington 1970).

Furthermore, these three systems of memory, namely, sensory, short-term, and long-term memories, have been subdivided into other systems accordingly to some factors such as the type of information stored, the processing of the information, or the way in which the information is acquired, among others. Firstly, there are three systems, specifically sensory memory, iconic, echoic, or haptic, depending on whether the information is visual, auditory, or tactile, respectively. It has been also noted the difference between short-term memory and working memory. It is assumed that while working memory could operate with the stored information, short-term memory only stores and retrieves information without modifying it (Cowan 2008). Adding numbers could be an example of working memory because it requires the individual to keep the information active and operate with it. Finally, a division of long-term memory has been proposed which attends to the kind of processes that carry out the acquisition, storage and retrieval of the information. Moreover, a division of long-term memory has been made depending on whether these processes are activated automatically or if participant's will is required. Following that criterion, long-term memory could be divided into two different systems: non-declarative memory and declarative memory.

### **Declarative Versus Non-Declarative Memory**

Non-declarative memory, also known as implicit memory or procedural memory, is defined as the system of memory that does not allow the conscious access of information stored; it has a slow acquisition process and is relatively inflexible. Non-declarative memories are acquired and used unconsciously and automatically but, despite this, can have a broad impact in our behavior. Implicit memory could also be divided into other minor

systems like the system needed for learning skills and habits or the system for the conditioning of emotional responses. Nonetheless, the most noted implicit memory system is the priming one. In a broader sense, the priming effect consists of the influence of a stimulus previously presented in response to other stimuli without the participant's awareness (see Geva et al. 1997). For example, knowing how to read or ride a bike is a model of non-declarative memories, more specifically procedural memories.

In contrast, declarative memory, also known as explicit memory, is defined as the long-term memory system in which the process of acquisition of information, storage, and retrieval is carried out consciously and voluntarily. These processes are learned rapidly and are more flexible than implicit memory. Declarative memory acquisition and information retrieval are made intentionally, and the information stored could be formulated as propositions or images. Knowing a phone number, a recipe, or the way home or to work is an example of declarative information.

The distinction between declarative and implicit memory has been supported by several studies. For example, different authors argue that amnesic patients who present problems acquiring or storing declarative memories do not present problems to acquire motor (Brooks and Baddeley 1976), perceptive (Cohen and Squire 1980), or cognitive skills (Squire and Frambach 1990). It has also been found that the priming effect appears in amnesic patients (Musen and Squire 1992). In the view of these findings, it could be argued that non-declarative memory is less prone to forgetfulness than declarative memory. Finally, some authors have proposed that the brain areas that are activated in both systems are different. The most well-known study on this matter is the description that Milner (1966) made about H.M. This patient presented significant deficits in retrieving events that occurred after a brain operation. He could however learn some procedures such as motor skills although he did not remember having learned them. During the operation, H. M.'s hippocampus, hippocampal gyrus, and amygdala were removed. These structures seem to affect the declarative but not the non-



declarative memory. This case reveals that the brain areas involved in both systems of memory are different and, also, suggests that those systems are independent. Taking all these studies into account, it can be supported that both systems, declarative and non-declarative, are quite different.

## Two Kinds of Declarative Memory: Semantic and Episodic Memory

More than the memory division exposed above, a distinction has also been proposed between two subsystems of explicit memory depending on the kind of information stored (Tulving 1972). These criteria differentiate between episodic and semantic memory.

Semantic memory stores general information, that is, information that has been learned in the course of our lives and that represents reality and general knowledge. The color of lemons, the order of the numbers, and the name of the capital city of a country are examples of semantic memories. In contrast, episodic memory is a type of declarative memory that stores information such as events, where, how, and when they occur. The most well-known definition of episodic memory was provided by Tulving (2002) who defined this memory system as “a travel back in time.” Examples of episodic memory are the memory of a birthday party, a trip made in holidays, or a match played by your favorite team.

A kind of declarative memory is an autobiographical one. It is defined as the storage of information about ourselves, and it is composed of episodic and semantics memories. Autobiographical memory stores all events that have occurred in our lives and all the information about us. However, although some authors have formulated theories about the principles and functions of autobiographical memory (e.g., Conway 2005), nowadays it is not clear whether autobiographical memory is really different from episodic memory (Markowitsch and Staniloiu 2011), whether it is a subtype of episodic memory (Fivush 2011) or an independent system of memory on its own (Conway and Pleydell-Pearce 2000).

Some authors have criticized the distinction between episodic and semantic memory (McKoon and Ratcliff 1986). However, the distinction of these two systems has been supported through several studies. For example, Spiers et al. (2001) described 147 amnesic patients that presented problems with retrieving episodic memories but not semantic ones. On the contrary, patients have been described to have deficits in semantic but not in episodic memory (for a revision, see Kapur 1999). Despite this, it is usually assumed that, as declarative memory is more sensitive to forgetting than implicit memory, episodic memory is also more easily forgotten than semantic memory. For example, it is more difficult to retrieve the memory of a moment or the context in which the meaning of a word was learned than the meaning of that particular word. Moreover, neuroimaging studies have found that the acquisition of episodic and semantic memories are not activated in the same brain areas, the same way that retrieval episodic or semantic memories are (Wheeler et al. 1997).

However, despite this distinction, it has also been argued that these two kinds of long-term memories are not totally independent from one another and that they could operate jointly. One of the earliest authors proposing this idea was Tulving (1972) who argued that the acquisition of new episodic memories were affected by the information stored in semantic memory. Other authors have proposed a different relationship between semantic and episodic memory. For example, Baddeley (1988) defined semantic memory as the information abstracted and dissociated from various episodic memories (for more studies that propose interdependence between semantic and episodic memory, see Reder et al. 2009; Mayes and Roberts 2001). In light of these studies, it is clear that these two memory systems operate, to a certain extent, jointly and that memories stored in both declarative memory systems are related in some way.

Finally, keeping in mind that the division of the different memory systems is not supported by all authors, declarative memory could be defined as the kind of long-term memory that is acquired, stored, and retrieved consciously and voluntarily.



Declarative memory could be divided into three subsystems: semantic, episodic, and autobiographic memory, each of them storing general knowledge, information about events or the information about ourselves.

## Cross-References

- Long-Term Memory
- Memory
- Priming
- Short-Term Memory
- Working Memory

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## Deep Understanding

- Insight in Rats

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## Defended Food/Encapsulated Food Processing

### ► Nut-Cracking

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## Defense Polygyny

### ► Scramble Defense Polygyny

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## Defensive Burying

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### Synonyms

Conditioned defensive burying paradigm; Shock probe defensive burying; Shock prod defensive burying

### Definition

The defensive burying test is used by researchers to measure an animal's naturally occurring anxiety-like behaviors toward an aversive stimulus.

When an animal encounters a potentially threatening stimulus, the animal engages in a variety of behaviors to distance themselves from or reduce the risk of interacting with the noxious stimulus. A common behavior that rodents exhibit to reduce the threat of a potentially harmful stimulus is to bury the stimulus; this behavior is referred to as defensive burying. Rodents display this behavior in their natural environments, using their forepaws and heads to shovel available materials (e.g., leaves, bedding) onto or near the noxious object. Scientists have simulated this ethological behavior in the laboratory by exposing the animal to a noxious stimulus and measuring subsequent behaviors. The defensive burying test provides valuable knowledge regarding

emotional states and has been used as a screen for potential therapeutic treatments for anxiety-related pathologies (De Boer and Koolhaas 2003; Pinel and Treit 1978).

Burying behavior toward an aversive stimulus has been studied since 1950, when rats were observed covering an electrified food cup with available wood shavings (Hudson 1950). Over decades of testing, laboratory studies have used electrified shock probes, noxious odors, or noxious tastes as the harmful stimulus, although novel, non-threatening objects, like marbles, may also provoke burying behavior (Pinel and Treit 1978). In the laboratory, a standard defensive burying procedure occurs in a rodent's cage with a shock probe inserted through the cage wall. Upon touching the shock probe, the rodent receives a single electric shock and subsequently engages in behaviors to avoid further interaction with the shock probe, most commonly burying the shock probe with any materials available, such as cage bedding (Korte et al. 1992; Pinel and Treit 1978).

The defensive burying test has been useful in research to understand certain emotional states (e.g., state or trait anxiety, fear). The central behaviors assessed during the defensive burying test are frequency of and duration spent burying the shock probe with increases in either indicative of greater levels of anxiety (De Boer and Koolhaas 2003; Pinel and Treit 1978). The height of the bedding pile is frequently measured with taller bedding piles also suggesting greater anxiety. The latency to begin burying the probe following the shock can be measured as well, but the interpretation is less clear as there is a great degree of individual variability in burying versus freezing behavior (discussed below). Moreover, many additional behaviors can be assessed during the test and therefore, the defensive burying test provides researchers with multiple measures of assessing an animal's anxiety-like behaviors. The rich array of behaviors can provide researchers with a more complete picture of the rodent's behavioral repertoire, such as risk assessment/probe exploration (approach and withdrawal movements directed towards the shock probe), immobility/freezing as a measure of passive avoidance, grooming as a conflict behavior, and

rearing as a measure of escape attempts (for review see De Boer and Koolhaas 2003).

The behaviors displayed by the rodent to reduce the threat of a noxious stimulus can be categorized into active and passive coping behaviors. Active behaviors such as the time spent burying compete with passive behaviors such as freezing; and the two behaviors cannot be exhibited simultaneously but both may be indicative of an anxiety-like state. A lack of burying behavior does not necessarily indicate a lack of anxiety or fear in the animal; the animal may simply be engaging in other behaviors to cope with the stimulus, like freezing. By assessing the entirety of the animal's complex behavioral repertoire, the defensive burying test provides a more nuanced method for assessing highly specific behaviors and the timeline of the behavioral responses. The degree to which an animal expresses these active and/or passive behaviors can be indicative of adaptive coping responses and/or maladaptive behaviors. The test is typically utilized as an unconditioned measure of anxiety-like behaviors within a single day of testing in the animal's home cage. The test is flexible, however, because further trials on subsequent days can be conducted to assess the conditioned response to the shock probe; conditioned testing may provide alternative information of anxiety and fear-related pathologies (De Boer and Koolhaas 2003).

The use of the defensive burying test to assess anxiety-like behaviors in rodents has been validated by pharmacological evidence with known anxiolytic and anxiogenic agents and therefore can be utilized for screening pharmacological agents with therapeutic potential. In humans, treatment for anxiety commonly includes anxiolytic agents such as diazepam or other benzodiazepine compounds. The same types of drugs (e.g., diazepam, benzodiazepine, midazolam, and pentobarbital) administered acutely decrease rats' defensive burying behavior toward a shock probe and increase contacts with the probe compared to control animals (Treit 1990; Tsuda et al. 1988). On the other hand, known anxiogenic pharmacological agents increase burying behaviors. For example, rats injected with yohimbine, an  $\alpha_2$ -adrenergic antagonist known to induce anxiety in humans (Charney et al. 1983), spent significantly more time engaged in burying behavior compared to

control rats (Tsuda et al. 1988). Together, the effects of anxiolytic and anxiogenic drugs provide evidence that behaviors displayed in the defensive burying tests are appropriate indices of anxiety.

The shock probe defensive burying test has also been validated by physiological measures associated with a sympathetic response to a dangerous/harmful stimulus and comparable to human-state anxiety. Rats engaged in defensive burying behaviors towards a shock probe have higher plasma catecholamines and corticosterone than control, non-shocked rats (Sgoifo et al. 1996). This parallels the data that demonstrates that human states of anxiety have been positively correlated with urinary excretion of norepinephrine and cortisol as well as increased blood pressure (Charney et al. 1983; Hughes et al. 2004). It is important to note that the heightened stress response during the defensive burying test is not solely an acute physiological stress response to the shock itself. In a multiple trial defensive burying experiment, Korte et al. (1992) demonstrated that on the day following the shock, rats displayed a stress response when presented with a non-electrified probe. The stress response to the presence of the probe, rather than a stress response to the shock itself, provides evidence that the rats exhibited an increased anxiety-like state following shock probe exposure. This data parallels anxiety-like states in humans, which represent an unpleasant emotional response to a threatening or harmful stimulus.

In conclusion, the shock probe defensive burying test assesses an animal's complex behavioral repertoire in response to a harmful or threatening stimulus. Overall, the pharmacological and physiological research supports the use of the shock probe defensive burying test to measure anxiety-like behaviors in rodents and test the efficacy of potential anxiolytic therapeutic compounds. The use of this test in rodents provides clinical value in its usefulness of modeling human coping towards an adverse stimulus or states of anxiety.

## Cross-References

- [Fear Response](#)
- [Stress](#)
- [Tonic Immobility](#)

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- kinds of behavior ranging from complex tea ceremonies, to mimicking body movements are due to a sophisticated imitation capacity, or rather reflects a more general learning mechanism (Heyes 2016). This entry explores the distinction between immediate and deferred imitation to discuss the notion of a specialized imitation system versus a more general action-perception matching system from a developmental, neuroscientific, as well as a comparative perspective.

In the literature, a distinction has been made between immediate, or also-called on-line imitation where the imitator repeats the model at the same time, and deferred imitation, where the action repetition between model and imitator is delayed. Cognitive theorists highlight deferred imitation as a way of investigating long-term memory in preverbal infants (Meltzoff 1988). Deferred imitation is relevant to theorists because the infant or child will not always be able to reproduce each adult action as soon as it is demonstrated; thus, for imitation to fulfill its socio-cultural utility, the infant or child must be capable of initiating imitation in the absence of the model. Finally, Piagetians focus on deferred imitation as a developmental milestone that first emerges at about 18–24 months, as part of a general emergence of the “symbolic function” enabling representational behavior beyond sensorimotor control (Piaget 1952). For both immediate as well as deferred imitation, we first have to define what counts as imitation. Whereas some theories stress the fact that the movements of the model and the imitator have to share the same topographical characteristics to be labeled as imitation (Brass and Heyes 2005), other theories have stressed that imitation can also be seen as a more goal-directed copying behavior, where imitators copy the goal of an action rather than the movement themselves (Bekkering et al. 2000; Wohlschläger et al. 2003). Below, I will outline how this distinction might be less clear-cut than what has been argued before.

Imitation has a long tradition in developmental psychology and was used as a mean to get insights in cognitive human development. Guided by findings from Meltzoff and colleagues, it was stressed that topographical imitation is an inborn mechanism (Meltzoff and Moore 1977), newborns can

## Deferred Imitation

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Our rich and diverse cultural landscape has arisen not only from our ability to innovate but also because we can copy others and build upon the knowledge of previous generations. This unique human ability to so diversely imitate has been coined *Homo imitans*. However, a debate has taken place whether our capacity to copy all

imitate facial and manual actions by means of an active intermodal matching systems in which proprioceptive information is matched in the observer from perceptual input to motor output. The notion of an inborn imitation mechanism was supported by neurological findings of so-called mirror neurons, i.e., neurons that fire both when an animal acts and when the animal observes the same action performed by another (Rizzolatti and Craighero 2004). As referred earlier, findings of Piaget indicate that deferred imitation can only take place around the second year of life, when children start to cook meals or are driving toy cars in similar manners as their parents do with their adult-size toys (Piaget 1952). Unfortunately, this division in development does not seem to hold. There is abundant evidence that newborns do not imitate in a topographical manner (Ray and Heyes 2011), and it has also been shown that we have limited capacities to imitate elementally novel actions over the whole lifespan (Heyes 2016). Also, follow-up studies of the mirror-neuron mechanisms showed that firing was not dependent on topographical characteristics but rather on goal-directed characteristics (Umiltà et al. 2001). Many cells fire in an effector-independent as well as a perceptually multimodal manner (Kohler 2002). In line with the notion that imitation serves the initiation of already known behavior, rather than learning novel actions, mirror neurons also typically respond to actions that are in the primate's motor repertoire, as is the case when they have learned to use pliers to grasp a peanut (Umiltà et al. 2008), although suggestions that mirror neurons can also derive from solely visual observations are also reported (Ferrari et al. 2005). To summarize, there is little evidence supporting the claim that an inborn mechanism serves imitation in newborns. Rather, on the basis of sensorimotor experiences, human infants learn to imitate immediately, or in a deferred manner. Clearly, the ability to imitate more complex actions depends on general cognitive capacities like working memory, and deferred imitation is used clinically to test amnesic patients for their loss of declarative memory (McDonough et al. 1995). The latter can be taken as evidence that imitation is not based on a

simple stimulus-response (S-R) association between model and imitator akin to topographical imitation accounts. However, contemporary associative learning theory will still stress that an imitative action can be produced in the absence of the stimulus on the basis of what observers have observed earlier (Heyes 2016). As a consequence, a certain motivational urge to produce an action when observing an acting model can be based on the expected consequences of performing a specific action rather than reproducing the specific action observed. Such an outcome-based view on imitation includes the observation that when children are confronted with an extraordinary action, i.e., somebody touches his ear with her contralateral hand, this might evoke a different action, activating the ipsilateral hand, to touch the ear (Bekkering et al. 2000).

There is little doubt that humans are more skilled and prolific imitators than other animals, but the question is whether this is related to a special, inborn "intermodal matching" mechanism that integrates representations of others with representations of the self, or if it reflects more general cognitive capacities is still open. There is ample evidence that other animals have some capacity for imitation and also that this is experience dependent. Chimpanzees, for instance, have been found that after learning a strict set of actions, they are well able to imitate novel but related arbitrary gestures (Custance et al. 1995). Interestingly, deferred imitation has also been found. Deferred imitation of novel actions was also found in dogs with retention intervals of 1.5 min and memory of familiar actions with intervals ranging from .40 to 10 min. In other animals, deferred imitation is not only based on sensorimotor-related stimuli. For example, observer budgerigars accessed a stopper immediately or 24 h after the observers had watched a video of a con-specific model either pecking or stepping on the stopper to obtain access to food. The observers performed the action they had observed, pecking or stepping, with higher frequency in both immediate as well as deferred imitation, suggesting that budgerigars are capable of "deferred imitation" or "imitation from memory (Richards et al. 2009)," a



capacity previously thought to be uniquely human (Meltzoff and Moore 1994).

In summary, this entry has briefly discussed important topics in the light of underlying mechanisms of deferred and immediate imitation. First, there is little evidence that a specialized imitation system enables immediate imitative behavior, while deferred imitation is based on more complex cognitive behavior. Rather, imitation always includes perceived outcomes of actions beyond simple S-R mappings. Additionally, evidence is lacking that early immediate imitation is initiated before active experiences are collected. Second, the supposed underlying mirror neuron mechanism is not serving immediate imitation only. The system includes higher cognitive representations such as outcome expectancies and also heavily relies on experiences. Finally, findings from comparative studies suggest that imitation goes beyond simple S-R mappings. Birds as well as other animals are found to be sensitive to rewards like food, which modulate immediate as well as deferred imitation. To conclude, humans are gifted imitators, and the capacity to defer imitation in the absence of the observed model marks us as members of particular cultural groups and contributes to cultural evolution, the accumulation of knowledge and improvement of skills over generations. However, the mechanisms that make imitation possible are not likely to be an inborn, special imitative system. Rather, we are great imitators, *Homo imitans*, as we can use previous experiences in a given situation to create the likely consequences of performing the action observed in others.

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## Degenerated Organ

- Vestigial Organ

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## Degree of Relatedness

- Coefficient of Relatedness

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## Deimatic Behavior

- Secondary Defenses

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## Delay Activity

- Delay Neurons: Comparative Overview

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## Delay Cells

- Delay Neurons: Comparative Overview
- Matching-to-Sample: Comparative Overview

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## Delay Neurons

- Delay Neurons: Comparative Overview

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## Delay Neurons: Comparative Overview

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## Synonyms

Delay activity; Delay cells; Delay neurons; Entopallium; Inferior temporal cortex; Matching-to-sample; Memory; NCL; PFC

## Definition

The development of microdrives capable of recording electrical activity of individual neurons allows researchers to step away from the traditional method of brain lesions to examine brain function. Importantly, electrophysiology allows researchers to examine the ways in which information may be represented and maintained in neurons across different species and different regions of the brain. Many behavioral tasks designed to examine such mechanisms include a period of delay in which the subject is required to maintain task-relevant information to later guide successful behavior. Any neuron with changes in neural activity in either an “inhibitory” (decreased activity) or “excitatory” (increased activity) manner during a delay period when memory is engaged, relative to a period that does not require memory, is regarded as a delay neuron. Generally speaking, delay activity is considered a memory trace of either a stimulus that must be maintained, a position to which the animal must respond, or some upcoming plan of action, be it motor or non-motor.

Delay neurons are found not only in humans, but also in all nonhuman species examined, including primates, birds, and rodents. In all species, delay neurons have been identified in sensory-specific regions such as visual and auditory areas, areas that are important for processing

elements of stimuli to be remembered. As delay neurons are thought to represent memory, much research has also focused on sensory integration regions thought to be crucial for executive functioning, such as the prefrontal cortices, hippocampus, and their homologues in other species.

## Delay Neurons in Primates

Two early studies that adopted single-unit electrophysiology in nonhuman primate species found evidence of what we now call delay neurons. Kubota and Niki (1971) trained monkeys on a delayed alternation task to press either a right or left lever after a delay period that was opposite to the side they pressed before the delay period. Similarly, Fuster and Alexander (1971) trained monkeys on a delayed response task in which, after a delay, the monkeys had to displace the object over either the right or left food well that corresponded to where the object had been placed prior to the delay. Both studies reported neurons that fired during the delay period; however, despite the popular current view that delay activity represents the storage of information necessary to bridge the delay period, neither Kubota and Niki (1971) nor Fuster and Alexander (1971) favored the view that the delay activity represented a neural correlate of memory. In the case of Fuster and Alexander (1971), the reason was that they did not find any delay activity that was able to differentiate between a required left response and a required right response.

From the early work of Kubota and Niki (1971) and Fuster and Alexander (1971), primate research spawned two lines of delay neuron studies, one exploring the role of delay activity in the context of oculomotor-based delayed-response tasks, and the other exploring the role of delay activity in the context of delayed matching-to-sample (DMS) tasks. For a full review of the oculomotor-based response task literature, the reader is directed to a review by Funahashi (2017).

One of the most popular tasks used in studies examining the neural basis of memory is the delayed matching-to-sample (DMS) task. In a

standard DMS task, the subject is shown a sample stimulus, which is followed by a delay period. Following the delay period, the subject is typically presented with two comparison stimuli and must respond to the comparison stimulus that matches the sample stimulus it saw prior to the delay. In order to solve the task, the subject should remember the sample stimulus during the delay period. In the context of a DMS task, delay neurons in the inferior temporal (IT) cortex have been shown to be highly selective for a range of abstract stimulus features even across delays as long as 16 s (Miyashita and Chang 1988). In the Miyashita and Chang (1988) study, for example, delay activity occurred after some sample stimuli and not after other sample stimuli.

In IT cortex, a region dedicated to processing visual information, the delay activity is not surprisingly modality specific. Gibson and Maunsell (1997) trained monkeys on four DMS tasks simultaneously. The first was a standard visual DMS task with visual sample and visual comparison stimuli (visual-visual DMS). The second was a standard auditory DMS task with auditory sample and auditory comparison stimuli (auditory-auditory DMS). The remaining two DMS tasks were cross modal such that visual sample stimuli were symbolically matched to auditory comparison stimuli (visual-auditory DMS), or the auditory sample stimuli were symbolically matched to visual comparison stimuli (auditory-visual DMS). There were many selective delay neurons that were encountered in IT cortex, but only on the visual-visual DMS, visual-auditory DMS, and auditory-visual DMS tasks, and not the auditory-auditory DMS task. The fact that monkeys can solve visual-visual DMS, auditory-visual DMS, and visual-auditory DMS tasks (but not an auditory-auditory DMS task) by using visual memory confirms that delay activity in IT cortex is related to the processing of modality-specific visual information.

In the prefrontal cortex (PFC), delay activity is a code not only of working memory for the sample stimulus but also more abstract concepts essential in DMS and delayed nonmatching-to-sample (DNMS) task performance. For example, Nieder and Miller (2003) found many delay neurons that

coded complex numerical information. Monkeys were trained on a go/no-go DMS task using different arrays of 2–6 dots as stimuli. In their go/no-go procedure, the comparison stimuli appeared one at a time, and the subject was required to refrain from responding until the correct comparison stimulus appeared. The number of dots in the sample and correct comparison array were the same, but the position of the dots in the array were different, meaning the monkey could not rely on remembering the sample by remembering the arrangement of dots, but rather had to remember the number of dots in the array. A number of neurons in PFC were selective to specific numerocities (e.g., three dots) regardless of how the dots were arranged in the array. Such a finding demonstrates that delay neurons in PFC can code the value or number of dots rather than a specific arrangement of dots.

In addition to coding numbers, PFC delay neurons have also been shown to code the value of an anticipated reward. Watanabe (1996) trained monkeys on a spatial delayed-response task with differential outcomes (DO), such that the reward contingencies associated for one sample-comparison stimulus pairing was different to that of another sample-comparison stimulus pairing. Watanabe (1996) found neurons in the PFC that fired during the delay period of, for example, trials associated with a grape reward but not during the delay of trials associated with a potato reward. Later, Watanabe (1996) switched the reward contingencies such that the stimulus pairing associated with the grape reward was now associated with the potato reward and vice versa. After the switch, delay neurons appeared to continue to encode the identity of the upcoming reward (e.g., grape) regardless of the stimulus pairs that predicted it. Given that the stimulus pairing itself remained the same and only the upcoming reward had changed, the delay activity is indicative of a neural correlate for the upcoming reward.

PFC delay neurons have also been shown to code the rule that the animal must employ to solve a task. Much like a standard DMS task, in a DNMS task, the subject needs to use working memory to bridge the delay period in order to successfully respond during the comparison

period. However, the two tasks differ in that, in a DMS task, the rule is to respond to the comparison that matches the sample, whereas in a DNMS task, the rule is to respond to the comparison that does not match the sample. Wallis et al. (2001) trained monkeys on both DMS and DNMS tasks with a cue accompanying the sample presentation to indicate which rule was currently in operation, matching or nonmatching. For one monkey, either a drop of juice or a blue background signalled the match rule, and no juice or a green background signalled the nonmatch rule. For the other monkey, juice or a low frequency tone signalled the match rule, and no juice or a high frequency tone signalled the nonmatch rule. Delay neurons in the PFC selectively coded the rule such that activity during matching trials differed significantly from that of nonmatching trials, regardless of the stimuli used. Overall, neurons in the PFC are clearly involved in coding abstract concepts that underlie the successful performance of complex cognitive tasks.

## Delay Neurons in Birds

Unlike primates, avian species have eyes located on the side of their heads, making oculomotor tasks extremely difficult. Instead, delay activity in birds has been examined exclusively in the context of DMS tasks. Despite architectural differences, the avian entopallium is considered similar in function to part of the primate extrastriate cortex. Johnston et al. (2017a) found delay neurons in the entopallium during a DMS task, a finding that is consistent with the view that, much like delay neurons in IT cortex, delay activity in entopallium represents a sensory code of the sample stimulus.

With respect to higher order cognitive regions, the nidopallium caudolaterale (NCL) is thought to be equivalent to the PFC, with both regions sharing many similar cellular and projection patterns, as well as an impairment in cognitive flexibility and memory when lesioned (Güntürkün 1997). Johnston et al. (2017b) found that, much like the primate PFC, neurons in the pigeon NCL remain active throughout a delay period of a DMS task,

providing evidence that delay activity in NCL represents a neural correlate for the to-be-remembered sample stimulus. Similarly, Veit et al. (2014) trained crows on a basic DMS task and found that neurons in the NCL displayed differential activity during the delay period for each of the sample stimuli.

Neurons in the NCL, much like neurons in the PFC, code for reward as well as memory. Johnston et al. (2017a) found that NCL delay neurons tended to occur following the rewarded stimulus but not the nonrewarded stimulus, suggesting delay activity in NCL represents a code of the possibility of an upcoming reward, at least when reward outcomes can be used to bridge the delay period of a DMS task. Similarly, in a directed-forgetting version of a DMS task, where after the sample stimulus the subject is either told to remember or forget what they just saw, both Rose and Colombo (2005) and Browning et al. (2011) found delay activity in NCL following the remember cue but not the forget cue. Although such a finding could be interpreted as the sustained activation reflecting a neural correlate of the animal remembering the sample stimulus, the presence of delay activity following remember cue and the absence of delay activity following the forget cue could also reflect the fact that, after a remember cue, there exists the possibility of obtaining a reward, whereas, after the forget cue, no reward is forthcoming.

Like in PFC, NCL delay neurons also code abstract concepts essential for performance of a DMS task. Wagener et al. (2018) demonstrated that many delay neurons in the crow NCL not only code the sample stimulus but also selectively code numerical values from complex stimuli in a DMS task, even when untrained on numerical matching. Much like the procedure used in Nieder and Miller (2003), crows were presented with stimuli containing different dot arrays. The crows were trained to match the color of the dot arrays while not needing to remember how many dots were in the array. While the crows appeared to be behaviorally selecting based on color of the dot arrays, neurons in the NCL were spontaneously and selectively coding the different numerical values of the stimuli. Such selective activity during a

delay period, similar to that found in primate studies with comparable procedures, provides the strongest evidence that delay neurons represent a neural correlate of the to-be-recalled sample stimulus.

Finally, similar to the Wallis et al. (2001) study showing that PFC neurons can also code abstract rules, Veit and Nieder (2013) isolated delay neurons in the crow NCL during an abstract rule DMS task. For each rule, either a visual cue or an auditory cue was presented and indicated whether the crow would be required to solve the DMS task on the basis of a matching rule or a nonmatching rule. As for PFC, many delay neurons in NCL selectively coded the behavioral rule and did so irrespective of the modality of the cue signalling the rule. Furthermore, cue selectivity was weaker during incorrect trials, indicating the neuronal coding was somewhat predictive of the bird's behavioral responses. Overall, the delay neuron findings for birds closely mirror those reported for primates.

## Delay Neurons in Rodents

The poor eyesight of rodents and their quadrupedal body makes it difficult to use picture stimuli on touchscreens for DMS/DNMS tasks like those used in primate and bird experiments. However, a variety of tasks to probe working memory of a stimulus or past event in rodents have been developed. One such task is the delayed spatial alternation task. Generally, rodents are placed in a T- or Y-shaped maze in the central stem for some delay. After the delay, rodents must travel up the stem and choose the opposite arm they travelled on in the previous trial. Thus, rats must keep their previous choice in working memory to successfully complete the task. A second variety of widely used working memory tasks for rodents has a series of levers and utilizes some sensory cues, such as lights or auditory tones, that indicate which specific lever must be pressed in order for the rodent to receive a reward. Rodents wait in a holding area while the cue is given, then are held there for a delay period before they are able to make their choice. Other simplified setups involve

two levers, where rodents are presented with one of the levers and, after some delay, are presented with both levers and must choose the opposite lever (DNMS) to what they were presented as the sample. Following the discoveries of delay neurons in the primate brain (Kubota and Niki 1971; Fuster and Alexander 1971), researchers utilized these rodent-designed tasks to investigate whether rodents also possessed delay neurons.

Sakurai and Sugimoto (1986) pioneered rodent working memory tasks and the neurophysiology necessary for optimal performance. They developed a DNMS task where a pure tone indicated to the rats that they could make a “go” or “no-go” response on a small panel. In order to be rewarded, rats had to carry out the opposite response (nonmatch) from the previous trial. Following primate work (Fuster and Alexander 1971; Kubota and Niki 1971) showing that the PFC and thalamus contained delay neurons, Sakurai and Sugimoto (1986) found single units in both brain regions in rats that responded during the delay period. These units responded differently whether or not the rat was going to make a “go” or “no-go” response. Strikingly, DNMS delay activity was predictive of the rats making correct or incorrect responses. A subsequent study by Batuev et al. (1990) confirmed the presence of delay neurons in the PFC in a cued DMS task where delay neurons also encoded the upcoming choice based on the cue during a delay. These data demonstrated that rodents not only have delay neurons but that the delay neurons in these regions maintain upcoming action plans.

A number of delay neuron studies have also recorded activity from the hippocampus. The hippocampus is a well-known brain region for its vital role in memory encoding and long-term consolidation. Following the discovery of delay neurons in the PFC and thalamus, researchers investigated the role of the hippocampus in working memory tasks and if it too possessed delay neurons. Sakurai continued his rodent delay neuron investigation by recording hippocampal units (CA1, CA3, and dentate gyrus subregions) along with neurons from the motor cortex (Sakurai 1990b) and auditory processing brain regions (Sakurai 1990a). In an auditory tone-cued

continuous DNMS task, neurons in the hippocampus, auditory, motor cortices, and medial geniculate body (MGB) showed sustained activity during the 3 s delay. Auditory cortex and MGB likely encoded sensory traces of the tone the rats had to keep in working memory (Sakurai 1990a). Furthermore, motor cortical units likely encoded upcoming motor plans as these units were especially active on trials where rats had to respond. However, despite Sakurai (1990b) finding some hippocampal delay neurons, these neurons were quite rare (<20% of recorded hippocampal units). Rather, hippocampal single unit activity was most active just before the rats initiated their responses on correct trials. This may indicate hippocampal retrieval of mnemonic information from the past trial to compare to the current trial and make the appropriate response.

Others continued to build on Sakurai’s work investigating the role of the hippocampus in working memory. Otto and Eichenbaum (1992) conducted a similar experiment that utilized odors instead of auditory tones and used a longer 6 s delay between stimulus presentations. They too recorded hippocampal CA1 single units during the task and found that approximately 20% of recorded CA1 units displayed delay-related activity. However, only 13% of these delay neurons had differential firing on future correct versus incorrect responses. Many subsequent studies, primarily carried out by Hampson and Deadwyler, have confirmed that the hippocampus (CA1 and CA3) was sparsely populated with delay neurons whose individual activity poorly predicted correct or incorrect responses (Hampson et al. 1993). However, subsequent investigations into CA1 and CA3 units using simultaneously recorded large populations of neurons showed that hippocampal population activity during delay periods was indeed predictive of correct versus incorrect responses (Hampson and Deadwyler 1996). Furthermore, during incorrect long delay ( $\geq 15$  s) trials, hippocampal population activity decayed and carried less information about the past cue and upcoming response. This decay of information maintained in hippocampal ensembles was correlated to the rats’ poor performance on long delay trials. Overall, these data indicate that ensembles

of hippocampal neurons encode and maintain task-relevant information, which may aid in successful decision making when previous stimuli must be maintained in working memory.

## Delay Neurons in Humans

A number of early studies in humans implanted with depth electrodes for identifying the locus of epileptic seizures for subsequent surgical resection reported that stimulation of various regions in and around the medial temporal lobe resulted in the recall of auditory and visual events (Penfield and Perot 1963). Later studies took advantage of more modern scanning techniques. For example, Maguire et al. (1997) used PET to examine the neural basis of topographical memory retrieval and found that recalling complex routes resulted in the activation of the right hippocampus. Similarly, fMRI Studies revealed that maintenance of a percept results in activation of the prefrontal cortex and hippocampus, whereas perception of the same percept results in activation mainly in occipito-temporal areas (Portas et al. 2000).

Despite the enormous number of studies that have explored the neural basis of different types of memory using a variety of different scanning techniques, few have examined the neural basis of memory at the single-neuron level using techniques and tasks similar to those encountered in studies with monkeys, birds, and rodents. Perhaps the one study most similar in format to those conducted with nonhuman species was by Halgren et al. (1978) who recorded from single neurons in the hippocampus and amygdala while patients performed a DMS task. Halgren et al. (1978) did find delay activity, although unlike the situation that has been noted for monkeys, birds, and rats, in none of their 267 units was there a case where the activity was restricted to the delay period compared to the other periods.

It is possible that the difficulty in encountering delay neurons in the aforementioned studies may be due to the fact that most recordings have been conducted in the medial temporal lobe region, whereas most reports of delay activity in monkeys and birds (but not rats) have been conducted in

visual cortex, prefrontal regions, and auditory regions. Indeed, although the tasks and procedures were slightly different to those used with nonhuman subjects, a number of studies have reported neural correlates of memory when the recordings were made in the lateral temporal (visual) cortex of patients (Haglund et al. 1994).

## Contemporary Issues in Delay Neuron Research

Animals are typically tested on DMS tasks for many trials within a daily session. The common convention for examining delay neurons is to pool activity across all trials. It has recently been argued, however, that delay activity should be examined on a single trial basis. At the core of the debate is how information is maintained in delay periods, and whether information is stored in bursts of spiking activity (asynchronous bursts) or persistent activity (spiking maintained across the entire delay) (Constantinidis et al. 2018; Lundqvist et al. 2018).

Those in favor of spiking activity argue that, although it is possible to see persistent activity on a single neuron basis, for many neurons, the spikes are not consistent throughout a delay period (Lundqvist et al. 2018). Furthermore, of the few neurons that do show persistent activity on a single trial basis, those selected as example neurons are cherry picked and not representative of the group of neurons as a whole. Additionally, individual neurons do not always maintain activity levels that occur in response to sensory inputs from sample stimuli, suggesting that single neurons do not respond to stimuli and maintain a neural correlate for that stimulus throughout the delay (Lundqvist et al. 2018). The argument to examine bursts of spiking activity in single trials is that information is thought to be coded in a larger network of neurons, each contributing to the maintenance of task relevant information. Maintenance is therefore more robust and less likely to be interrupted, and the brain is able to conserve energy when each neuron is not continually spiking (Lundqvist et al. 2018). Importantly, single trial analysis retains temporal information,



which can be lost when activity is pooled across trials, allowing researchers to examine how networks of neurons coordinate to maintain information when using modern multichannel electrodes (Lundqvist et al. 2018). In summary, those in favor of spiking activity argue that the “seemingly” persistent delay activity is an artifact of averaging, and by averaging, the intricacies of neuronal networks and what information is being conveyed by delay neurons can be lost.

According to those that favor persistent activity, trouble with examining spiking bursts arises when spiking activity is sparse and variable between trials (Constantinidis et al. 2018). Without averaging across trials, one might not see the impact of the neuron as they do not have enough spikes in a single trial for a comprehensive analysis. Furthermore, proponents of persistent activity argue that varying patterns of persistent activity have frequently been predicative of behavioral outcomes, and that such an effect is much harder to determine in the sparsely firing spiking activity analysis (Constantinidis et al. 2018).

Averaging across trials for persistent activity is a completely reliable and robust method for analysis that has continually yielded consistent measures of delay activity. However, there is merit in examining spiking activity, as it allows for a more comprehensive analysis of temporal information in neuronal recording. As such, both techniques yield important information as to how and when information is coded in delay neurons.

## Summary

Delay neurons have been isolated in many species and across many different brain regions. Generally speaking, what the delay neurons represent tends to be largely influenced not only by the brain region in which the neurons originate but also by the parameters of the experiment. In sensory regions, delay neurons appear to represent a neural correlate of the working memory of the sample stimuli. In sensory integration regions, or regions implicated in higher-order cognitive functions, delay neurons appear to code more complex

aspects of the task. In simple DMS tasks, delay neurons in higher-order cognitive regions may reflect a neural correlate of the sample stimuli. However, more neurons in such regions seem to prospectively code reward anticipation, abstract rules, and go/no-go behaviors. Furthermore, for many of the experiments demonstrating such neurons, the delay activity levels often correlate with the behavioral performance of the subjects. Although task parameters are adapted to suit different species, properties of delay neurons appear to be remarkably similar across species, suggesting the delay function of neurons to be evolutionarily preserved.

## Cross-References

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## Delay of Reinforcement

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Delay discounting · Response acquisition ·  
Response maintenance

### Definition

*Delay of reinforcement* occurs when a period of time has elapsed between the response and the administration of the reinforcer.

Reinforcement is defined as the presentation or removal of a stimulus following an organism's response that results in an increased probability that the response will reoccur. For example, when a rat presses a lever and receives food, the rat learns that pressing the lever produces a desired result (food). The presentation of food (the reinforcer) increases the likelihood that the rat will press the lever again in the future. There are a number of factors that impact the efficacy of reinforcement, one of which is the delay of reinforcement. *Delay of reinforcement* occurs when a period of time has elapsed between the response and the administration of the reinforcer. For example, if a rat presses a lever that instantly releases food, the rat receives immediate reinforcement since no time has elapsed between the response and the reinforcement. The passing of any time between the lever press and the delivery of food would qualify as delayed reinforcement.

## Parameters of Delayed Reinforcement

There are several important parameters of delayed reinforcement. One parameter of delay of reinforcement is the contiguity between the stimulus and the reinforcement. As the delay of reinforcement increases, the contingency decreases, thus leading to a reduction in the response rate. An immediately reinforced response leads to a strong association between the target response and the contingency (i.e., the reinforcer). When reinforcement is delayed, there is a weak association between the target response and the reinforcer. Oftentimes the response(s) that precedes the reinforcer has a stronger association with the reinforcer than the target response, thereby decreasing the perception of a contingency between the target response and the reinforcer. However, very short delays (0.5–2 s) of reinforcement have been found to lead to similar response rates, if not higher response rates than immediate reinforcement (Dews 1981; Sizemore and Lattal 1978). A rat that is immediately reinforced for pressing a lever is not only more likely to press the lever in the future but also more likely to press it at a higher rate than a rat that is on a 10-second (s) delay of reinforcement.

In addition to contiguity, delayed reinforcement can be affected by the delays being fixed or variable. *Fixed delayed reinforcement* (Sizemore and Lattal 1977) requires that the amount of time between the response and the reinforcement stays constant throughout the experiment. Delay of reinforcement could be fixed at 10 s, meaning the organism will not receive the reinforcer until 10 s have elapsed following each response. *Variable delayed reinforcement* (Sizemore and Lattal 1977) allows the time between the response and the reinforcement to potentially vary across trials. Variable delayed reinforcement of 10 s means the average elapsed time across all trials is 10 s; however, one trial of delayed reinforcement could involve a 1-s delay, while another trial could involve a 19-s delay.

Another parameter of delayed reinforcement is whether the delay is signaled or unsignaled. A *signaled delay of reinforcement* (Ferster and Skinner 1957) involves the presentation of an

additional stimulus to indicate a delay period preceding reinforcement. Take a pigeon that is on a 10-s delayed schedule of reinforcement for pecking a green light when it is presented. In a typical signaled delay of reinforcement study, the pigeon will peck the green light, the cage will be blacked out during the delay (the signal is the blackout), and the pigeon will receive the reinforcer after the 10-s have elapsed. A signaled delay of reinforcement can be understood as a chain schedule because it presents an additional stimulus during the delay period, thereby creating a chain of stimuli. An *unsignaled delay of reinforcement* (Ferster and Skinner 1957) is when a delay period is not preceded by additional stimuli to indicate its onset. In the aforementioned example, the pigeon would not experience the blackout; rather, only the stimuli that were presented before the pigeon pecked the light would be present after the pecking response. An unsignaled delay of reinforcement can be conceptualized as a tandem schedule, which means that each component (i.e., stimulus, response, delay, and reinforcement) follows another.

A fourth parameter of delayed reinforcement is the occurrence of a superfluous response during the delay of the reinforcer. A response during the delay period may cause the organism to be penalized, resulting in the restarting of the delay period. This is known as a *resetting delay* (Lattal 1987). In a 10-s resetting delay, a pigeon that pecks the green light within that 10-s delay period will cause the delay period to restart. The pigeon must not respond during the 10-s delay in order to receive the reinforcer at the end of the delay. A *non-resetting delay*, on the other hand, will not be affected by a response during the delay period (Lattal 1987). Once the organism has made the reinforcing response, any responses that occur during the delay period will have no effect on reinforcement.

## Efficacy of Delayed Reinforcement

The ability to continue engaging in behaviors that are maintained by delayed reinforcement is often difficult. Organisms are more likely to engage in

immediately reinforced behaviors than behaviors that are reinforced after a delay period. For example, many individuals struggle to not eat the last piece of pie (immediate reinforcement) despite knowing the health benefits of refraining from doing so (delayed reinforcement). The ability to choose long-term benefits over short-term benefits is directly related to the concept of *delay discounting* (Mazur 2013). Delay discounting is the tendency to devalue a reinforcer as the delay of obtaining it increases, thereby leading individuals to place greater emphasis on smaller immediate reinforcers (a piece of pie) over larger delayed reinforcers (health). Delay discounting is an important concept for understanding self-control in humans because it points to the propensity for immediate rewards (piece of pie) over those delayed rewards that often take time to obtain (a healthy lifestyle).

To further understand delay discounting, it is important to understand how preferences toward immediate rewards over larger delayed reinforcers shift as a function of time. For instance, let's assume that a sweepstakes provides the option of choosing between a lump sum of \$10,000 in a year or choosing \$5,000 now. The choice of waiting a year for the \$10,000 seems like a much more lucrative option. Now imagine that instead of \$5,000 now, the sweepstakes provides the option of choosing between a lump sum of \$10,000 in a year or choosing \$8,500 now. The preference of originally waiting a year (larger delayed reinforcer) for the \$10,000 has now shifted to perhaps accepting the \$8,500 now (immediate reinforcer). This is what is referred to as the indifference point. An *indifference point* is when the delay and the amount/value of the reinforcer are considered equally preferable; in this example that point is the \$8,500. This can result in the preference switching between the two options; thus, there are moments when the same individual may actually choose the larger delayed reinforcer (health) over the immediate reward (piece of pie), but there are also moments when the reverse is true.

The *Ainslie-Rachlin Theory* explains how the value of a reinforcer is discounted as a function of the amount of time that passes between the choice

and receipt of the reinforcer (Ainslie 1975; Rachlin 1974). Specifically, the first assumption of the theory indicates that as the delay between making the choice and receiving the reinforcer increases, the value of the reinforcer decreases. The second assumption states that, at decision time, the reinforcer with the *highest* value will always be chosen. Therefore, despite the high value of a larger reinforcer (health), the delay of the reinforcer ultimately reduces the value that one places on their health. Moreover, when the individual is required to make a choice, the value of the piece of pie (immediate reinforcer) has significantly increased because of its close proximity. In the end, the piece of pie is considered greater than that of the healthy lifestyle. This line of research has helped explain impulsive choices that are often tied to maladaptive behaviors, such as drug/alcohol addiction.

The efficacy of delayed reinforcement depends on a variety of factors. Delayed reinforcement can decrease a behavior, increase a behavior, or leave the response rate unchanged. One factor that impacts its effectiveness is the purpose of delayed reinforcement. Delayed reinforcement is *primarily* used to maintain a response, also known as *response persistence* or *response maintenance* (Lattal 2010). Most studies involving delay of reinforcement examine the effects of the delay on response persistence, whereby a steady response rate was initially obtained via a schedule of immediate reinforcement. Another possible aim of delayed reinforcement is *response acquisition*. Here, delayed reinforcement is used to foster a response despite the absence of a learning history.

The length of the delay period preceding the presentation of the reinforcer is another factor that influences the efficacy of delayed reinforcement. In examining response acquisition, Skinner (1953) found that he was not able to condition a pigeon to peck a key with a 10-s delay preceding reinforcement, but he was able to do so with immediate reinforcement or a 1-s delay. This suggests that reinforcement following a 1-s delay was able to change a pigeon's behavior, but a 10-s delay was too long. Despite Skinner's observation, Lattal and Gleeson (1990) found that they

were able to shape rats' and pigeons' behaviors using a 30-s delay. Since then, the study has been replicated several times and has expanded to include different species, including humans. These works are important, as they demonstrate that delayed reinforcement can lead to response acquisition, even if it generally occurs at a slower rate than immediate reinforcement. In fact, a 0.5-s delay of reinforcement leads to higher rates of responding than immediate reinforcement. The ability to wait for a delayed reinforcement is very adaptive and useful for a species.

In terms of response maintenance, several studies have shown that as the delay of reinforcement increases (say from 1 to 10 s), the response rate decreases. An organism is less likely to perform the behavior that produces reinforcement when there is a larger delay preceding reinforcement. In addition, studies have repeatedly found that delay of reinforcement following a steady response engendered by immediate reinforcement produces a lower response rate than if the behavior was maintained by immediate reinforcement. In other words, while delay of reinforcement can maintain behavior, it is likely to result in a lower response rate. It is also important to understand that an increase in the delay of reinforcement will produce more variation in responding, potentially interacting with the existing contingencies.

Signaled and unsignaled delays also affect the efficacy of delay of reinforcement. While unsignaled and signaled delays are both likely to result in response acquisition and persistence, signaled delays maintain a higher rate of responding; however, the response rates are still lower compared to immediate reinforcement. Similarly, resetting delays are more likely to lead to response acquisition than nonresetting delays, albeit at a lower response rate than immediate reinforcement.

## Conclusion

As mentioned above, there are two main functions of delayed reinforcement: response maintenance or response acquisition. The primary function of delayed reinforcement is response maintenance:



to perpetuate a previously established behavior. Delayed reinforcement for this purpose is most commonly used when the response was previously established by immediate reinforcement. Contrary to previous beliefs, recent research has demonstrated that delayed reinforcement can also lead to response acquisition with a delay period as long as 30 s. In fact, 0.5-s delay was found to consistently produce higher rates of responding than immediate reinforcement.

Skinner and Thorndike were two of the first researchers to explore reinforcement. They believed that the behavior must be “closely followed by” the reinforcer in order for the behavior to be acquired. Although much research has been conducted on delayed reinforcement, it is still unclear how the phrase “followed closely by” should be operationalized. Part of the challenge lies in the dynamic relationships of the parameters of delayed reinforcement. The effect of delayed reinforcement on response acquisition and response maintenance varies with the different combinations of parameters. Current research is focusing on how to better predict the interactions of the parameters.

## Cross-References

- [B.F. Skinner](#)
- [Behaviorism](#)
- [Contingency](#)
- [Delayed Gratification](#)
- [Learning](#)
- [Operant Conditioning](#)
- [Positive Reinforcement](#)
- [Reinforcement](#)
- [Schedules of Reinforcement](#)

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## Delayed Gratification

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Delayed gratification, a form of self-control, is defined as the ability to tolerate longer delays in order to obtain a more preferred reward as opposed to a more immediate, lesser preferred reward. Humans and nonhuman animals must weigh the costs and benefits associated with immediacy or delayed action in several contexts such as mate choice, food retrieval, and environmental conditions in which they live (e.g., Stevens et al. 2011). The uncertainty of the future may play an important role in choices to delay gratification or not. For example, how confident



someone may be that a more productive food source will be available in the future may directly affect whether that individual stays or moves on from the current food source. Delayed gratification also is crucial in contexts regarding planning for the future and goal-oriented behavior. For example, in an economic context, individuals must inhibit impulsive buying behaviors in order to save money for future purchases. For all of these reasons, understanding the psychological mechanisms that support delayed gratification has been a goal of developmental and comparative psychology.

Early developmental work on children's ability to delay gratification focused on whether children could abstain from taking a less preferred food reward in order to obtain a more preferred reward. In these tests, children usually were given a smaller reward such as one marshmallow, and told that they could eat that, but if they waited, they would get another marshmallow. This work demonstrated that preschool-aged children often were able to wait surprisingly long amounts of time, sometimes over an hour, in order to obtain a preferred reward. In other cases, delay was much shorter, showing that there was great variability across children, and also across testing contexts (e.g., Mischel and Ebbsen 1970; Mischel et al. 1972). Thus, the basic paradigm was one of inhibiting immediate consumption to gain a better, future reward. Extensions of this approach demonstrated that the ability to delay gratification is related to other self-control abilities and also to some degree with general intelligence (e.g., Duckworth et al. 2013).

The "marshmallow test" and other similar approaches in developmental psychology drew attention from those working with animal models of self-control behavior. Traditionally, animal models focused more on intertemporal choice tasks, in which animals such as pigeons chose between a smaller-sooner reward and a larger-later reward, with the latter choices then leading to a forced delay, rather than the need to continuously inhibit taking a reward (as in the marshmallow test). Pigeons typically showed strong discounting of the future, with heavy biases to take the smaller-sooner rewards. However, when

given a task in which they could peck to end a trial with a lower preference reward (like taking the one marshmallow) or avoid pecking to get a larger reward (the equivalent of the two marshmallows), pigeons showed many of the same environmental effects as children regarding how long they could delay, such as presence versus absence of rewards, having access to alternative responses, and having other stimuli present (Grosch and Neuringer 1981). Other approaches to making animal-friendly delayed gratification tasks involved having chimpanzees sit in front of one reward, which they could receive if they pressed a button, but if they waited, another reward would come later. In this test, chimpanzees avoided pressing the button when the lower preference food was the immediate reward, although they pressed the button immediately when the higher preference food was the one they could have immediately for such responding (Beran et al. 1999). These results, and others, led the way to the development of other tests of delayed gratification with animals (see Beran 2018).

Delayed gratification often has been studied in nonhuman animals using two approaches. The first involves having participants make a discrete choice between two rewards: one less preferred, yet more immediate, and one more preferred, yet more delayed. This intertemporal choice paradigm allows for a commitment to a higher, delayed payoff, because choice of the delayed reward forces the participant to experience the full delay (e.g., Addessi et al. 2011; Amici et al. 2008; Rosati et al. 2007; Stevens et al. 2005). Alternatively, tests can involve an aspect of having to continuously maintain a commitment to delaying gratification because participants can still choose the immediate reward or they can choose to continue to delay gratification. In this approach, subjects can stop waiting for the better reward at any point in time, resulting in varying amounts of final reward given how long they maintain that delay.

One of these latter tests is known as the accumulation test (Beran 2002). It was based on another developmental design (e.g., Toner and Smith 1977) in which children postponed gratification during a period in which they observed

rewards growing over time. The novelty of this approach was that, unlike the marshmallow task, in which delayed gratification occurred in the presence of only a static, immediate reward, in the accumulation test the immediate reward gets better over time. In this kind of test, the possibility of that reward continuing to get better is predicated on the subject not giving in and taking the accumulating reward. Toner and Smith (1977) showed children between 33 and 120 months old that M&M's candies would be placed one by one on the table in front of them until the child instructed the experimenter to stop and they could receive the candies. This design lends itself nicely to comparative work, because it does not necessarily require any verbal instruction and can be presented in an intuitive fashion to a variety of species. The first use of this task was with chimpanzees and an orangutan (Beran 2002), in which they too watched as M&M's candies accumulated in a bowl that was within reach. As long as they waited, more would be added, but taking and eating any items ended the trial. These apes were able to wait to get all of the items that could accumulate, and other studies also showed that great apes can successfully delay gratification in order to receive the higher amounts of reward following a period of accumulation (e.g., Parrish et al. 2014; Stevens et al. 2011). Additionally, recent research shows that, similar to humans, delay of gratification in chimpanzees is closely linked to their general intelligence (Beran and Hopkins 2018).

The accumulation task can be adapted in a number of ways to ask questions about environmental factors that might impact delayed gratification. For example, visibility of rewards makes a big difference for children. Similar tests with chimpanzees manipulated the visibility of the reward source by obscuring the preferred reward from subjects' visual field. When chimpanzees were shown the quantity of rewards before visual access was blocked, they were still successful in delaying gratification (Beran and Evans 2006). Beran and Evans (2006) also reported that chimpanzees were successful even in the absence of a human experimenter as the agent of the ongoing accumulation. An automated dispenser that

delivered foods to the accumulation pile did not lead to decreased delay performance. In addition, chimpanzees were successful when the accumulation that occurred was not for immediate, real food rewards but instead was for tokens that could be traded for rewards at a later time (Beran and Evans 2012). This research demonstrated that in multiple variations of accumulation tasks, great apes have a high capacity for inhibiting impulses to receive an immediate reward in order to obtain a higher value or greater amount of reward.

Delaying gratification is about waiting to get something better. However, a lot of factors can impact how well one can do this. Successfully delaying gratification often includes engaging in behavioral tactics that aid in the waiting process or what is sometimes called *delay maintenance*. It is during delay maintenance that one can see the effects of environmental features interacting with strategic efforts by a subject. Some of those strategies are effective, and some are ineffective. One highly effective strategy involves directing attention away from the rewards through self-distraction. For example, children's ability to delay gratification is increased when the preferred reward is absent and therefore unattended to (Mischel and Ebbsen 1970), when distractions such as playing with a toy are available or when participants are encouraged to think about something positive or "fun" (e.g., Mischel et al. 1972). Delay is better when children verbally repeat phrases either irrelevant to the task or about the goodness of waiting (Toner and Smith 1977). These results all beg the question as to whether nonhuman animals also might engage in behavioral strategies to aid delay of gratification.

Mixed results on distraction tactics have been found in the comparative work with great apes. Early tests with the accumulation task in chimpanzees did not observe any changes in delay periods as a result of attending to the rewards or having the opportunity to distract themselves with a computerized task (Beran 2002; Beran and Evans 2009). Similarly, behaviors that either directed attention to or away from the delayed reward (such as self-grooming or touching the bowl in front of them, respectively) resulted in no difference in ability to maintain delay (Beran

and Evans 2006). However, when toys were made available as a distraction tool, chimpanzees tended to wait longer periods of time before ending accumulation of candy rewards, and the results highlighted a special aspect of what the chimpanzees were doing (Evans and Beran 2007a). Whereas it was true that chimpanzees waited longer when they had toys compared to when they did not, this was not, in itself, evidence of strategic self-distraction. What was more convincing was a comparison of two conditions, both of which involved toys being available. However, the difference was that in one condition, the accumulating food rewards were within reach of the chimpanzees, and thus they had to leave those food items alone if more were to accumulate. In the other condition, food rewards still accumulated in view of the chimpanzee, but they were out of reach, and thus the chimpanzees did not have to show delayed gratification. Despite toys always being available in these two conditions, the chimpanzees played with the toys for more time when they were in the delayed gratification condition, suggesting that they selectively used the toys for those trials where they had to maintain delay versus a condition where the delay was imposed upon them. This study suggested that humans are not the only species to distract themselves from the task at hand in order to aid in impulse inhibition. Other research (reviewed below) would also support this contention.

Comparative work with nonhuman primates also has explored the ability of monkeys to delay gratification. While some species have shown varying degrees of success, such success typically is less than that seen in great apes. In an accumulation task like that described earlier with consistent transfer of items, only three of nine Rhesus macaques consistently maintained delay of gratification. However, seven of those nine monkeys showed increased delay of gratification when the accumulation task introduced reward inequalities and high-preference rewards were presented last in the accumulation (Evans and Beran 2007b). Capuchin monkeys and squirrel monkeys also were only able to maintain delay when accumulating food items increased in size or with large

amounts of experience in the task (Anderson et al. 2010), and in this case only two of four capuchin monkeys and two of four squirrel monkeys demonstrated this ability for delay periods of only 1–5 s. However, in another experiment, capuchin monkeys showed no improvement over time on a discrete choice test between smaller-sooner and larger-later rewards, but evidence of improvement was found for several monkeys in an accumulation task (Addessi et al. 2013). This result not only shows the variability in performance across tasks as well as between individuals but also calls into question the equivalence of self-control measures that are often taken to be interchangeable. A nice example of this comes from research with rats in which animals engaged in either a delay discounting task, where the smaller-sooner and larger-later reward choices were adjusted but choice of the delayed reward led to automatic delay periods, or a delay of gratification task where choice of the larger reward was something the rats could “bail out” of during the delay. This study found no significant relation among rats in the rates of discounting delay (making an irreversible choice to delay) and delay gratification (maintaining a choice to delay without defecting; Reynolds et al. 2002). Such results have important implications for understanding how consistently different tasks, that should reflect a common self-control capacity, actually do so.

Evans et al. (2012) tested capuchin monkeys and chimpanzees on a task in which the accumulating items were tokens instead of actual food items. This task required the animals to learn the meaning of the tokens as they related to actual food rewards. The question was whether monkeys and apes exhibited similar levels of self-control when non-food rewards accumulated versus actual food rewards. If they understood that tokens represent amounts of reward they could receive, their ability to delay gratification for tokens should match their performance on tasks in which food items accumulate. However, capuchin monkeys accumulated significantly fewer tokens than food items, indicating that they struggled to generalize the value of symbolic items to the value of a food reward. Chimpanzees,

however, were able to accumulate items regardless of whether or not the items were tokens or food items. The results of this study highlighted an important difference between great apes and monkeys, in that apes more easily recognized the value of tokens in accumulating delayed rewards.

Another widely used approach to assessing delay of gratification in animals involves exchange tasks, which also highlight species differences in nonhuman primates' ability to initiate and maintain delays. In exchange tasks, animals must willingly trade items in their possession to obtain more preferred rewards, and thus necessarily delay gratification. This involves the choice to initiate a delay and also the ability to physically give up the immediate reward as part of a trade. Chimpanzees, long-tailed macaques, Tonkean macaques, brown capuchins, and domestic dogs are among those who have demonstrated successful delay maintenance in exchange tasks (e.g., Beran et al. 2016; Dufour et al. 2007; Pelé et al. 2010, 2011; Leonardi et al. 2012). These experiments, like the accumulation task, also have demonstrated the effects of varying the delay duration, the quantity of delayed reward, and the quality of delayed reward. For example, Pelé et al. (2010, 2011) reported that when they allowed monkeys the option to immediately trade their food items (rather than having to constantly inhibit their impulses to eat available food by holding onto food until the chance to exchange came), delay periods increased from just seconds up to 20 min for capuchins and about 40 min for rhesus macaques. This astonishing increase in delay maintenance highlights how large a role consumption inhibition plays in monkeys' ability to maintain delay. When they must hold on to a reward and restrain themselves from eating it, it is substantially harder to delay gratification as opposed to when they can immediately trade the food and no longer have the option to consume it. Pelé et al. (2010, 2011) also compared monkeys' delay periods in the exchange task to their subsequent performance on an accumulation task. This showed that monkeys typically delayed reward in the accumulation task for time periods similar to those for the exchange task (in which

subjects had to wait before they traded), despite the quantity of final rewards being substantially smaller in the accumulation task. In other words, monkeys chose to delay for similar periods of time given varying amounts of their final reward. There were also individual and species differences, indicating that capuchins did not maintain delay periods and inhibit impulsivity for as long as macaque species.

When tested with a similar exchange paradigm, 2-year-old children were unable to wait longer periods for larger rewards, but 3- and 4-year-old children could. All children were able to increase their initial delay periods when the final reward was much larger than the reward they initially were given (Steelandt et al. 2012). Here, older children were also able to anticipate longer delay periods with smaller rewards, choosing to end those delay periods sooner. This reflected their ability to weigh the costs and benefits given the length of delay and size of reward, which has also been demonstrated in chimpanzees and rhesus monkeys (Dufour et al. 2007; Pelé et al. 2010, 2011).

Although much of the research on animal delayed gratification has been conducted with nonhuman primates, other species have been studied. More recent efforts have focused on the ability of bird species to inhibit impulsivity. Specifically, corvids (including ravens and crows) were more likely to delay gratification when the preferred reward involved a higher quality food item than a higher quantity of the immediate, lesser-preferred reward (Hillemann et al. 2014). Similar to results from nonhuman primates, these results indicate that some birds delay gratification and resist impulsivity for an immediate reward. Similarly, a Grey parrot was able to maintain delay of gratification both when the less preferred, more immediate reward was within reach or was out of sight (Koepke et al. 2015). However, this study differed from the comparative research described earlier, in that this parrot was language trained and was specifically told the command to "wait" and not eat the immediate reward in return for a preferred reward. During a different accumulation task with other

Grey parrots, birds displayed limited levels of delayed gratification. Those individuals were unable to obtain the maximum number of rewards (five) and showed little to no improvement over the course of 30 test trials (Vick et al. 2010). These tests, like those given to nonhuman primates, highlight the importance of different testing paradigms and other factors such as rearing conditions when testing certain nonhuman species. Additionally, this research with non-primate species underscores the importance of testing a broad range of species in order to better understand how individual differences and species' characteristics may impact delay of gratification and other forms of self-control.

Overall, comparative research investigating nonhuman animals' delay of gratification provides promising evidence that animals can indeed endure long periods of delay in return for a larger reward payoff. This evidence contradicts past notions that only humans possessed these abilities. The impressive levels at which great apes can delay gratification draws clear evolutionary connections between humans and our great ape cousins. But, the success of monkeys and of non-primate species in some tasks shows that delayed gratification is a capacity widespread in the animal kingdom, even if it is often limited and fallible in some contexts. Like humans, animals have complex lives that require complex cognitive skills. It is critical for survival to make well-informed decisions, some of which involve waiting for longer periods of time for a better reward of some type – whether that is access to better food, better chances to mate, or increased safety by avoiding predators. Research investigating humans' and animals' abilities to inhibit impulsivity and show delayed gratification continues to increase our understanding of the similarities and differences of human and animal cognition and behavior.

## Cross-References

- [Anticipation of Future Events](#)
- [Executive Function](#)
- [Irene M. Pepperberg, PhD](#)
- [Michael J. Beran](#)

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## Delayed Implantation

- [Developmental Arrest](#)
- [Mustelidae Life History](#)

## Delayed Matching-to-Sample

- [Delayed Match-to-Sample](#)
- [Matching-to-Sample: Comparative Overview](#)

## Delayed Match-to-Sample

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## Synonyms

[Delayed matching-to-sample](#)

## Procedure

The delayed match-to-sample procedure (commonly abbreviated as DMTS) is a modification of the basic match-to-sample procedure (also known as match-from-sample and choice-from-



sample), which was first used as early as 1799 (see Weinstein 1941). With the match-to-sample procedure, the subject is presented with a visual sample stimulus and is then also presented with two or more additional comparison stimuli, one of which matches the original stimulus. The subject must then choose the comparison stimulus that matches the original sample stimulus. The subject is usually rewarded for correct matches. With the DMTS procedure, the sample stimulus and comparison stimuli are not presented simultaneously. Instead, there is a delay between the removal of the sample stimulus and the appearance of the comparison stimuli. To begin, the subject is first shown the original sample stimulus for a specified amount of time or until the sample is touched or otherwise responded to by the subject, and then the sample stimulus is removed. After a delay lasting a predetermined amount of time, usually seconds or minutes, the subject is presented with two or more additional comparison visual stimuli, one of which matches the original sample stimulus. The subject must then choose the comparison stimulus that matches the original sample stimulus. For example, imagine the subject is shown an image of a circle for 3 s, after which time, the image is removed followed by a 10-s delay. Next, the subject is shown two comparison stimuli, a circle and a triangle. In this case, the matching comparison stimulus would be the circle, as it matches the sample stimulus.

This procedure, as well as the basic match-to-sample procedure, is commonly used in cognitive research with humans and animals to investigate topics relating to learning and memory. The delayed match-to-sample procedure can also be used as a tool to investigate more complex phenomenon such as perception of the passage of time (Zentall and Smith 2016) or as a measure of cognitive function (Kangas et al. 2011). One advantage of these procedures is that they can be conducted without the use of language, making them ideal for studies involving animals (Zentall and Smith 2016) and human infants (Hochmann et al. 2016). However, both procedures depend on the subject's ability to understand or learn the concepts of same and/or different (Hochmann et al. 2016). The delayed match-to-sample

procedure also requires the use of memory, as the subject must be capable of remembering, either consciously or unconsciously, the original sample stimulus after it is no longer visible.

## Variations

The simplest form of matching, known as identity matching, requires the subject to identify the comparison stimuli that is an exact match to the sample, but there are other forms of matching as well. Instead of an exact match, the stimuli may conceptually match the sample in a variety of ways including color, size, number, form, function, symbolic relationship, or any other possible association. Thus, the delayed match-to-sample procedure can be used to investigate topics such as concept formation (Zentall and Smith 2016). For example, if the sample stimulus was a red circle and the comparison stimuli were a blue circle and a green triangle, the matching comparison stimulus would be the blue circle because, even though the colors do not match, they are the same shape (Vonk 2003). A more advanced example would be if the sample stimulus was a hammer and the comparison stimuli were a saw and a tree. In this case the matching comparison stimulus would be the saw, as the hammer and saw are both tools. One modification of this task is the delayed non-match-to-sample (DNMTS) task in which the subject is reinforced for choosing the comparison stimulus that does not match the original sample stimulus (oddity). Various other modifications of this procedure can be made to investigate other aspects of memory and cognition.

## Cross-References

- [Short-Term Memory](#)
- [Working Memory](#)

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## Delboeuf Concentric Circles

### ► Delboeuf Illusion

## Delboeuf Illusion

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## Synonyms

Delboeuf concentric circles; Geometric illusion;  
Size illusion

## Definition

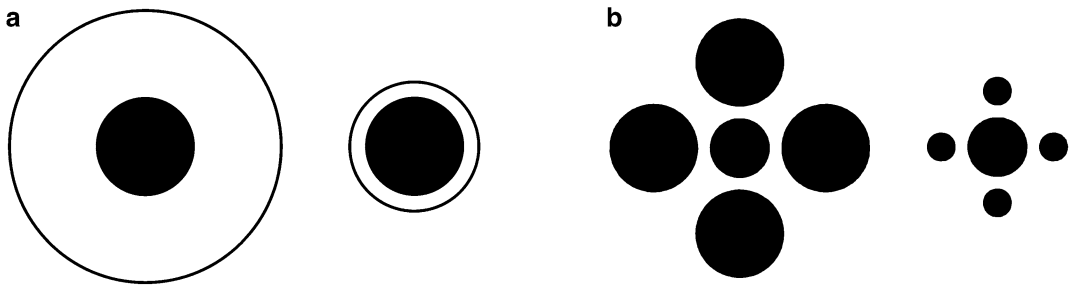
The Delboeuf illusion is a geometric visual illusion that emerges when the size of a central dot is misperceived as a function of the diameter of a concentric ring that encircles the dot. A larger outer ring leads to underestimation of central dot size relative to a smaller outer ring which leads to overestimation of central dot size. The Delboeuf

illusion is similar to the well-known Ebbinghaus-Titchener illusion in which central dot size is misperceived as a function of contrast and assimilation mechanisms. The Delboeuf illusion has been studied extensively within the human literature and recently has been extended to a variety of animal species.

## The Delboeuf Illusion

The Delboeuf illusion emerges when the size of a central target dot is overestimated if encircled by a small concentric ring and, alternatively, underestimated if encircled by a relatively larger concentric ring (Fig. 1). Joseph Delboeuf, a trained experimental psychologist, mathematician, and philosopher, first documented this size illusion in the late 1800s amidst a boom of experimental reports on related geometric visual illusions. Our current understanding of the phenomenon is posited by the assimilation-contrast theory in which the central dot is contrasted against the larger concentric ring due to the increased distance between the dot and the ring, leading to underestimates of dot size. Alternatively, the smaller concentric ring is perceptually integrated with the central target dot due to the close spatial proximity of the dot and the ring, leading to overestimates of dot size. The Delboeuf illusion, similar to other misperceptions of size such as the Ebbinghaus-Titchener illusion (Fig. 1), more readily emerges when the target dot and concentric ring are holistically (or globally) processed such that the stimuli are perceived simultaneously.

Visual illusions, in general, provide an excellent tool for investigating the perceptual systems of a wide range of species via noninvasive testing procedures. Whether a given species (or specific individuals within a species) experience geometric size illusions highlights important similarities and differences in sensitivity to contrast and assimilation effects as well as perceptual processing mode. Perceptual processing mode refers to whether an individual first perceives the global configuration of a stimulus array (e.g., dot plus ring) or the individual elements that comprise the



**Delboeuf Illusion, Fig. 1** The Delboeuf illusion (a) and Ebbinghaus-Titchener illusion (b), in which central dot size is underestimated when encircled by larger inducers

(at left) and overestimated when encircled by smaller inducers (at right). (Adapted from Parrish et al. 2015)

figure (e.g., dot then ring, or vice versa). Perceptual processing varies across species with some demonstrating a human-like global-to-local precedence and others demonstrating a local-to-global precedence. For example, a global-to-local precedence would lead to the simultaneous or global processing of the concentric ring plus central dot as a single unit, whereas a local-to-global precedence would lead to the individuation of ring and dot prior to processing its global configuration. Whether individuals process the Delboeuf array globally (along with other multi-element arrays) also is a by-product of stimuli presentation. Methods that enhance the individual features of the array as separate units (i.e., via different color cues – black dot, red ring – or presentation style, sequential presentation of dot then ring) may disrupt global processing, which is fundamental to the emergence of illusory perception.

A variety of testing paradigms are employed to investigate sensitivity to visual illusions, including the spontaneous choice task (also known as a free choice test) which requires animals to select the larger of two food quantities. This paradigm requires little to no training as it mimics a naturalistic choice setting in which animals are typically motivated to maximize by selecting the largest or highest-quality food set available. Foods are arranged to reflect the illusory arrays to test for perceptual sensitivity of the illusion under investigation. To dissociate the role of motivation and to carefully control for external cues and stimulus design, visual illusions also are presented using two-dimensional stimuli. The stimuli (e.g., black

and white renderings of illusory arrays) are presented either manually or via computerized testing. Animals are trained to select the larger or smaller of two stimuli (a relative discrimination task) or are trained to classify a single stimulus as large or small relative to a predetermined criterion (an absolute classification task). Stimuli are presented using the illusory-inducing context (e.g., central dot plus illusory ring) to determine whether subjects are sensitive to the illusion once trained on the task parameters (via reinforcement for correct responding). Comparative results have led to interesting similarities and differences in perception of the Delboeuf illusion using these paradigms, shedding light on continuities and divergences in perceptual mechanisms, quantity estimation abilities, and the role of methodology in assessing visual illusions.

### Comparative Assessments of the Delboeuf Illusion

The Delboeuf illusion has been studied extensively in the human literature, primarily using two-dimensional stimuli as described above. The impact of this geometric size illusion on choice behavior in the consumer domain also has been explored. The Delboeuf illusion appears to impact real-world decision-making scenarios including food judgments and consumption behavior. In a study with human adults, participants misjudged food portions (mimicking the central Delboeuf dot) as a function of the dishware (mimicking the outer ring) on which they were served.

Participants routinely overestimated food portions plated on smaller dishes and underestimated food portions plated on larger dishes akin to the illusory effect when judging two-dimensional dots encircled by rings (e.g., Van Ittersum and Wansink 2012). Misperceiving food portions has obvious implications for consumption behavior, with an increase in calorie intake as a function of plate size and portion estimation.

In the first study to assess the Delboeuf illusion among animals, Parrish and Beran (2014) employed the spontaneous choice task featuring edible stimuli to assess how this visual illusion may impact food choice behavior among chimpanzees (*Pan troglodytes*). Chimpanzees first were presented with control trials that pitted two different quantities of food against one another when both food portions were plated on the same-sized dishes (either both on small plates or both on large plates). A critical first step in utilizing the spontaneous choice task to assess illusory perception is to demonstrate proficiency in control trials with a true difference in food quantities presented in a non-illusory inducing context (in the case of the Delboeuf illusion, on same-sized plates). Failure to maximize in control trials may reflect low motivation or the inability to discriminate quantities at a given ratio, which may be necessary to perceive the illusion under investigation in critical test trials. Thus, the ability to reliably and effectively discriminate the size of central target dots (or food portions) in the absence of the illusory context is a pre-requisite for assessing the emergence of the Delboeuf and other size illusions.

In the spontaneous choice task, chimpanzees excelled in control trials, selecting the larger of two food portions when presented on same-sized plates (Parrish and Beran 2014). Similar to misperceptions made by humans, chimpanzees preferred food portions presented on a small plate to an equal-sized food portion plated on a larger plate. Thus, objects with a small surround appeared to be perceived as larger than the same-sized object with a large surround, in line with the Delboeuf illusion. Some chimpanzees also erroneously selected a smaller food portion on a small plate relative to a larger food portion on a large

plate, leading to the consumption of an overall smaller amount of food. These results are striking in that chimpanzees, who are highly proficient in discriminating very small differences in food amounts, performed sub-optimally in terms of maximizing the amount of preferred foods in illusion trials that they chose and ultimately consumed. This occurred for different food types and across repeated trials, and for animals that were highly motivated to maximize in spontaneous choice tasks of this nature, suggesting continuity in perception of the Delboeuf illusion across species.

Several other animal species have been presented with the Delboeuf illusion using the spontaneous choice paradigm. Positive evidence for the illusion has been documented in a variety of taxa, including domestic cats (*Felis silvestris catus*: Szenczi et al. 2019), bearded dragons (*Pogona vitticeps*: Santacà et al. 2019), and damselfish (*Chromis chromis*: Fuss and Schluessel 2017), which also fall prey to the highly similar Ebbinghaus-Titchener illusion (Fuss and Schluessel 2017). Alternatively, lemurs (*Lemur catta*) were not sensitive to the Delboeuf illusion using the spontaneous choice task, showing indifference in illusion trials with equal likelihood to select food presented on a large or small plate. It is important to note that the lemurs did not reliably discriminate food portions during control trials, suggesting that they may have failed to discriminate quantities at a given ratio necessary to perceive the Delboeuf illusion (Santacà et al. 2017). A similar finding was reported for red-footed tortoises (*Chelonoidis carbonaria*) who also failed to maximize in control trials, limiting the interpretation of illusory performance (Santacà et al. 2019).

Domestic dogs (*Canis familiaris*) have been reported to show no sensitivity to the Delboeuf illusion using the spontaneous choice task (Miletto Petrazzini et al. 2017) and have even demonstrated reversed perception of the Delboeuf illusion when judging two-dimensional stimuli (Byosiére et al. 2017). Bamboo sharks (*Chiloscyllium griseum*: Fuss and Schluessel 2017) and guppies (*Poecilia reticulata*: Lucon-Xiccato et al. 2019) also perceived a reversed Delboeuf illusion. Male guppies have dots located

on their body flanks that vary in size and coloration that are sometimes encircled by an outer ring, making this species an interesting subject for Delboeuf studies. In Lucon-Xiccato et al.'s (2019) study, guppies successfully learned to approach the larger of two orange dots suspended in their fish tank for a variety of ratios in control trials. However, they did not show evidence for the Delboeuf illusion when the dots were encircled by an outer ring. When presented with the spontaneous food-choice task, guppies again performed well in the control trials, yet preferred food encircled by a large ring versus a small ring (i.e., a reversed illusion). These results are interesting in light of the positive evidence for a human-like susceptibility to the Delboeuf illusion and the highly similar Ebbinghaus-Titchener illusion by other teleost fish (e.g., damselfish: Fuss and Schluessel 2017). Guppies may be more sensitive to assimilation effects which could lead to a reversed illusion in that the ring, regardless of its size, would be incorporated with the dot leading to overestimates (rather than underestimates) of dot size when encircled by large rings.

Such discrepancy in perception of the Delboeuf is not uncommon for geometric visual illusions, which often emerge variably across species and even produce high rates of individual differences within the same species. In addition to quantity discrimination abilities and perceptual processing mode, the methodological procedures for presenting illusions to subjects play a critical role in their emergence. When presented with a computerized version of the Delboeuf illusion, capuchin monkeys and rhesus monkeys demonstrated proficiency in discriminating a range of central dot diameters in control trials using the relative discrimination task (i.e., select the larger of two central dots encircled by the same-sized rings or in the absence of rings; Parrish et al. 2015). However, a number of monkeys from both species perceived the Delboeuf illusion in a reversed manner as described above for guppies (Lucon-Xiccato et al. 2019) and some individual dogs (Byosiére et al. 2017). However, when presented with an absolute classification task, both species of monkeys performed similarly to human adults completing the same task – overestimating

the central dot as a function of outer ring size, such that progressively smaller rings led to progressively greater overestimates in perceived central dot size. These results underscore the effects of methodology – the large-ring bias that led to a reversed illusion in the first experiment using the relative discrimination task may have reflected a bias to selecting the larger overall array (central dot + outer ring) versus discriminating on the basis of the central dot only. The absolute classification task was an important contrast within this study as it potentially reduced attention to either element in the array (dot or ring), instead presenting a range of the central dots and outer rings at equal rates throughout training and testing. This is particularly important for locally oriented species including capuchin monkeys and rhesus macaques, as a local-to-global precedence results in the initial perception of individual elements that comprise an array (dot and ring, for the Delboeuf array) prior to holistic processing, which may reduce sensitivity to geometric illusions. These results highlight the interconnectedness of species' perceptual processing mode and the methods used to investigate illusory phenomena.

## Summary

Assessing whether nonhuman animals perceive visual illusions provides a unique means for establishing similarities and differences in the perceptual and visual systems of a variety of species. Geometric size illusions in particular have played an important role in the history of comparative psychology and perception studies, with an increasing breadth of species and illusory arrays under investigation. The Delboeuf illusion and the related Ebbinghaus-Titchener illusion have attracted particular attention in that they result in interesting differences both within and across species. Null results and evidence of reversed patterns of illusory perception may reflect true differences in the perceptual experiences of animals and various populations. Such variability may stem from differences in perceptual processing mode, quantity discrimination abilities,

or sensitivity to contrast and assimilation mechanisms. It also is important to develop tests that allow for full exploration of these issues while parsing out the role of methodology (e.g., stimulus design, presentation, training procedures, reinforcement contingencies, etc.) in the emergence (or not) of illusory experiences. The Delboeuf illusion has proven to be an important tool to explore these issues in comparative psychology.

## Cross-References

- [Ebbinghaus-Titchener Illusion](#)
- [Size Illusion](#)

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## Deliberate Self-Harm

- [Self-Injurious Behavior](#)

## Dendrites

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## Synonyms

[Dendrons](#); [Nerve fiber](#)

## Definition

Dendrites are branched fibers that stem from the cell body (soma) of a neuron.

## Introduction

The dendrite was first discovered by Swiss anatomist Wilhelm His (Mall 1905). He's made the discovery in 1889 when he coined the term dendrite to refer to the "protoplasmic processes" connected to a neuron. From this initial discovery, we now understand that dendrites are branched fibers that stem from the cell body (soma) of a neuron. Dendrites receive electrochemical messages, usually in the form of neurotransmitters, from other neurons via specialized receptors



located on the surface of the dendrite (Urbanska et al. 2008). When the dendritic receptors receive the electrochemical messages from other nerve cells, the cell membrane of the neuron will passively change in polarity, dependent on the nature of the neurotransmitters received. The polarity change will move from the dendrites toward the axon. If an action potential is not reached, which would generally be due to the dendritic receptors receiving more inhibitory neurotransmitters than excitatory, the neuron will not fire, and the electrochemical message will end (Barnett and Larkman 2007). If an action potential is reached, however, the electrical message will be sent from the dendrite, through the axon hillock, down the axon, and to the terminal button. At the terminal button, the electrical message will change into a chemical message, whereby exocytosis will occur and neurotransmitters will be released into the synapse between the presynaptic and postsynaptic neuron. Once released into the synapse, the released neurotransmitters will potentially connect to the receptors on the dendrites of the postsynaptic neuron, starting the electrical stimulation paradigm over again (Barnett and Larkman 2007).

The amount of electrochemical messages a dendrite can receive is dependent upon its surface area and the number of receptors located on the dendrite (Tvonsanis 2012). In general, the larger the surface area of the structure, the more messages the dendrite can receive from other neurons. The shape of the neuron can influence the surface area available for the reception of electrochemical messages. There are three main types of neuronal shapes: multipolar, bipolar, and unipolar. Multipolar neurons consist of one axon and many branches of dendrites. Bipolar neurons have one axon and dendritic trees at both ends of the axon. Unipolar neurons have an axon that separates into two ends, one that has dendrites and the other that contains terminal buttons. The different types of neurons are responsible for different behaviors. Dendritic spines, projections that extend from the base dendritic structure of all neurons, can increase the surface area of the dendrites. The growth of dendrites is called dendritic branching which is a process that allows nerve cells to make new dendritic trees which in turn creates new

synapses with surrounding neurons (Tvonsanis 2012).

Initially, however, it was believed that dendrites could not change and that their structure was set by the adolescence of the organism. This, however, has been countered with the idea that dendrites do, indeed, have a certain amount of plasticity, specifically in the branches and dendritic spines (Koleske 2013). This changeability of the dendrites is linked to learning, as it is believed that experiences guide the growth of neurons (Yang et al. 2009). Neuronal experiences equate to increased neural stimulation. The more stimulation a dendrite receives from other neurons, the more growth will occur, even in species other than humans (Coss et al. 1980). An experience such as learning causes the stimulation of neurons and the creation of stronger synaptic connections between pre- and postsynaptic neurons. This increased stimulation can occur due to the induction of the process known as long-term potentiation (LTP). The ability of the organism to engage in LTP is linked to learning and memory formation and the subsequent growth of dendrites (Sjöström et al. 2008).

## Conclusion

Dendrites are a part of the neuron that have many responsibilities such as receiving and propagating excitatory messages from presynaptic to postsynaptic neuron. They are attached to different shapes and types of neurons and are changeable based on the conditions they are in. When a dendrite is stimulated, it becomes plastic – it grows. When a dendrite grows, it creates new synapses with both new and old neurons which allows for additional electrochemical messaging to occur.

We know that learning and memory formation can lead to the growth of dendrites and the strengthening of synaptic connections. By understanding the role of the dendrite in learning and memory, we might be better able to not only realize how our brains work but also create paradigms to study new treatments for memory-related diseases such as Alzheimer's disease and other forms of dementia.

## Cross-References

- ▶ [Action Potentials](#)
- ▶ [Axon](#)
- ▶ [Cell Membrane](#)
- ▶ [Long-term Potentiation](#)
- ▶ [Nerve Cells](#)
- ▶ [Neural Impulse](#)
- ▶ [Neuroanatomical Plasticity](#)
- ▶ [Neuron](#)
- ▶ [Neurotransmitters](#)

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## *Dendrohyrax arboreus*

- ▶ [Hyracoidea](#)

## *Dendrohyrax dorsalis*

- ▶ [Hyracoidea](#)

## *Dendrohyrax validus*

- ▶ [Hyracoidea](#)

## Dendrons

- ▶ [Dendrites](#)

## Dental Formula

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## Synonyms

[Deciduous teeth](#); [Dentition](#); [Permanent teeth](#); [Primary dentition](#); [Secondary dentition](#)

## Definition

(Dental formula) is an abridged expression for the number and kind of teeth of mammals... and the number in each jaw is written like a fraction .... (Merriam-Webster 2018)

Different species of mammals have different amounts of teeth, and therefore, different dental formulas. The dental formula has been developed to help practitioners easily and accurately express the number of and positions of animals' teeth. The dental formula will change over the life of an animal as it matures from adolescence into adulthood and the number of teeth change. Practitioners and scientists can use the dental formula of an animal, or animal remains, to determine age or to identify the species.

Primary dentition, also known as deciduous teeth, is the teeth mammals have during adolescence. Deciduous teeth will be shed as the animal grows and matures into adulthood (AVDC 2018).

In their place, permanent teeth, or secondary dentition, will grow. The number of deciduous teeth is less than the number of permanent teeth. This means the deciduous dental formula will consist of fewer teeth than the permanent dental formula for a given species.

Along with the dental formula, the types of teeth also vary between mammalian species. Animals that are carnivores (meat eaters) or omnivores (varied diet) have teeth that are adapted to perform specific functions in the process of obtaining and chewing food. Herbivores (plant eaters) have teeth that are more uniform in appearance and are adapted to eating plant material. Ruminant species (cattle, sheep, and goats) lack upper incisor teeth. Instead, these animals have a dental pad, which is modified, toughened skin, in the center of their upper jaw. Ruminants use their tongues to pull food into their mouths instead of biting plants with their front teeth. Equine species (horses, zebras, donkeys) and rodents have teeth that continually erupt throughout the life of the animal. They also have a gap between the front and back teeth known as a diastema (Easley 2018). These animals use either their lips (horses) or front paws (rodents) to pull food into their mouths and use mainly the back teeth for chewing.

There are four basic types of teeth in mammals. Each kind of tooth has developed to perform a certain function in the process of mastication (obtaining and chewing food). Below, the types of teeth and the corresponding function are described:

- Incisors are the teeth in the front of the mouth. They have developed to act like chisels or shovels. Incisors function mainly to bite off pieces or slabs of food into an appropriate size for chewing (Myers and Espinosa 2018).
  - The dental pad is a special structure in the mouths of ruminants that replaces the upper incisors. Ruminants use their tongue to hold food against the dental pad and bite the food into smaller pieces with their lower incisors (Hall and Silver 2009).
- Canine teeth are the sharp, pointed teeth just behind the incisors. These teeth are used to stab and hold food. Canine teeth may be exaggerated in size in some species as a form of social or sexual display.

- Premolar teeth are those in between the canine teeth and molars. Premolars vary from molars because they are present in the mouths of adolescent animals, whereas, molar teeth are not. Premolars function to crush food.
- Molar teeth are those in the very back of the mouth. Molars are the last teeth to erupt and are present only when an animal has reached adulthood. The molars perform the function of crushing and grinding food (Myers and Espinosa 2018).

The dental formula is written as a fraction, where the tooth on the top jaw is written over the corresponding tooth on the bottom jaw. However, only one half of the mouth is written, therefore, the values must be doubled to obtain the total number of teeth. The dog is used as an example to explain the process for writing a dental formula.

In the dog, there are 3 incisors on the upper jaw and 3 incisors on the lower jaw on each side of the mouth. Using the letter I to represent the incisors, the incisor teeth of the upper and lower jaw are noted as  $I_3^2$  in the dental formula. Next, the canine teeth are denoted with C. The dog has 1 upper and 1 lower canine on each side of the mouth. Therefore, the canine teeth are written as  $C_1^1$ . For the premolars (P), the dog has 4 upper and 4 lower, so they are written as  $P_4^4$ . For the canine molars (M), there are 3 upper and 2 lower and are written as  $M_3^2$ . The sections beginning at the midline of the mouth and moving towards the back of the mouth are strung together to construct the complete formula:  $(I_3^3C_1^1P_4^4M_3^2)$ . When denoting permanent or secondary teeth, the letters are capitalized. When denoting deciduous or primary teeth, the letters are lower case (Muyllle 2018). When representing a full mouth of teeth, the number two is placed in front of the formula, such as for the dog,  $2(I_3^3C_1^1P_4^4M_3^2)$ , to represent the entire mouth.

Some adult, or permanent, dental formulas for common domestic species are below (Muyllle 2018):

|       |                           |     |                           |
|-------|---------------------------|-----|---------------------------|
| Dog   | $2(I_3^3C_1^1P_4^4M_3^2)$ | Cow | $2(I_3^0C_1^0P_3^3M_3^3)$ |
| Cat   | $2(I_3^3C_1^1P_2^2M_1^1)$ | Pig | $2(I_3^3C_1^1P_4^4M_3^3)$ |
| Horse | $2(I_3^3C_1^1P_3^3M_3^3)$ |     |                           |

**Dental Formula,**  
**Fig. 1** “The Triadan  
 Numbering System” by  
 David Crossley for the  
 Royal Veterinary College  
 2002

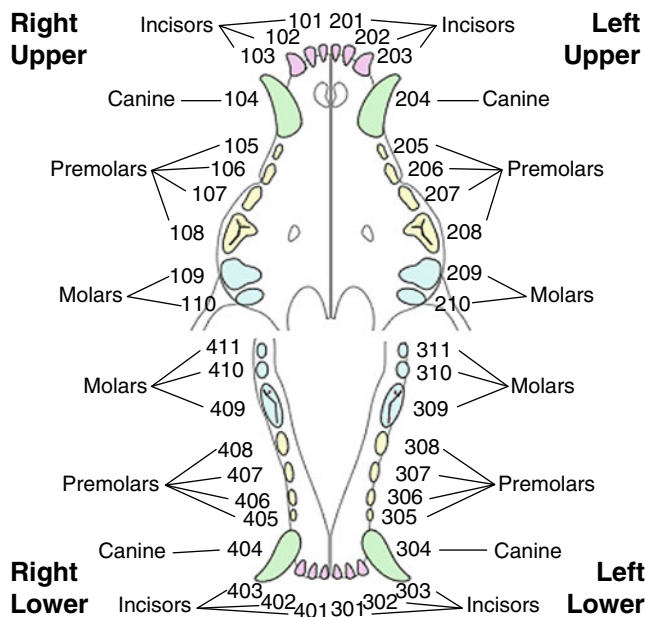


Image by David Crossley for the Royal Veterinary College, 2002

Another method to identify the teeth of mammals is the Modified Triadan Numbering System. The mouth is divided into four quadrants: a right and left side of each top and bottom jaw. A dividing line is drawn down the center between the two front incisors. Each quadrant is assigned a number series in a counterclockwise fashion. The upper right quadrant is assigned to the 100's. The upper left quadrant is assigned to the 200's. The bottom left quadrant is assigned to the 300's, and the bottom right quadrant is assigned the 400's. To specify a certain tooth within each quadrant, a predetermined number is added to the assigned 100 series number. The incisor immediately adjacent to the dividing middle line is tooth number 1, so the first incisor of the upper right quadrant is known as 100 (the quadrant number) + 1 (the tooth number) = 101. The teeth are noted in numerical order from the front incisor to the last molar. If there is a tooth missing, or a species naturally lacks a tooth in a particular position, the number is skipped or omitted. Two easy anatomical markers for numbering teeth are the canine and molar teeth. The canine tooth in a quadrant is always known as X04 (the upper left quadrant is 204; the bottom left quadrant is 304; etc...). The first molar is always known as X09

(the upper right quadrant is 109; bottom right quadrant is 409; etc...) (AVDC 2018) (Fig. 1).

The dental formula is a helpful tool in aging animals and identifying species of skeletal remains and fossils. By using an organized and widely accepted dental numbering system, scientists and practitioners are able to easily communicate information about the teeth of mammalian species. The dental formula and Modified Triadan Numbering System are important tools in the practice of veterinary medicine and the science of biology.

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## Dentate Fascia

### ► Dentate Gyrus

## Dentate Gyrus

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## Synonyms

Dentate fascia; Fascia dentata hippocampi; Gyrus dentatus

## Definition

It is the segment of the neocortex that constitutes a part of the hippocampal formation and is involved in crucial processes of learning, memory, and neurogenesis.

## Introduction

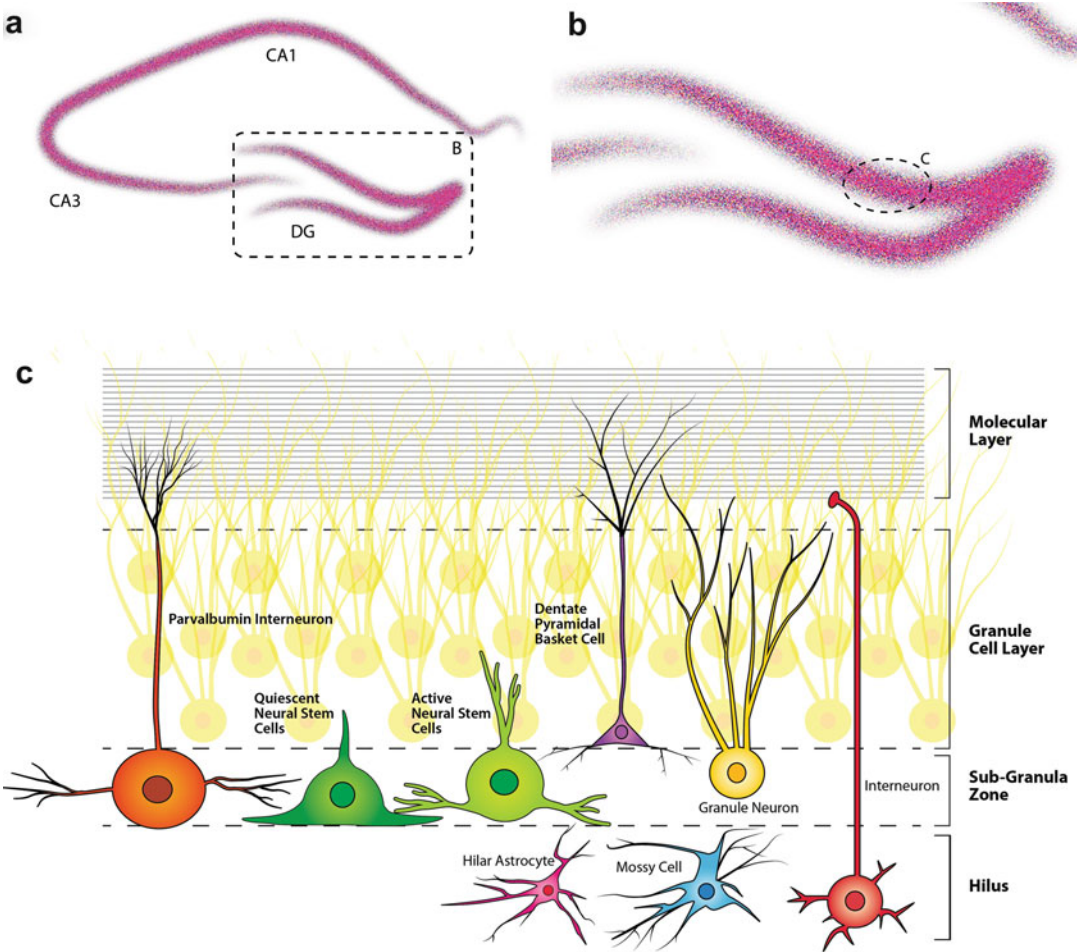
Dentate gyrus is composed of gray matter and makes an important part of hippocampal formation. It is tooth shaped and located between the fimbriae of the hippocampus and the parahippocampal gyrus (Snell 2010). It is located underneath the temporal lobe. The hippocampus formation consists of three elements, namely, the *cornu ammonis* (collectively known as the hippocampus), the dentate gyrus, and subiculum (Barrett et al. 2009; Kandel et al. 2000; Nicholls et al. 2001). The hippocampal formation forms the floor of the temporal horn of the lateral ventricle, along with other associated regions (Kandel et al. 2000). The dentate gyrus interlocks with the hippocampus, and forms a C-shaped structure, the subiculum adjoining it (Nicholls et al. 2001).

The dentate gyrus consists of three layers, each of which has an assortment of cell types (Fig. 1). Superficially, there is a relatively cell-free layer known as the *molecular layer*. It contains dendrites of the dentate granule cells. Projections from extrinsic sources such as the entorhinal cortex, through the perforant pathway, are also observed.

The middle layer is known as the *granular or principal cell layer*. It contains the hallmark cells of the dentate gyrus, the dentate granule cells. They are elliptical or rounded cells having spiny apical dendrites. These cells are densely arranged together without glial intervention. Unmyelinated axons known as mossy fibers extend from the granule cells. They project primarily to the CA3 pyramidal neurons. Dentate granule cells are primarily glutamatergic and therefore, excitatory in function. Dentate pyramidal basket cells are present where the granular layer transitions into the polymorphic layer. These cells are large and have a single, aspiny dendrite. They form pericellular plexus that gives its basket appearance. They are the inhibitory GABAergic interneurons.

The innermost layer, known as the *polymorphic layer* or *hilus*, is composed of mossy cells. They are large, stellate or triangular cells, having dendrites that bifurcate further (Amaral et al. 2007).





**Dentate Gyrus, Fig. 1** The dentate gyrus is part of the hippocampal formation that is known to contribute to the formation of new episodic memories along with other important functions. (a) Section of the hippocampal

formation, (b) magnification of the C-shaped dentate gyrus region in the hippocampal formation, and (c) the three layers of dentate gyrus, also depicting the various cells types found in the respective layers

## Neuroanatomy and Neurophysiology

Information from the entorhinal cortex reaches the CA1 region through two excitatory pathways, namely, direct and indirect. The principal output route of the entorhinal cortex is known as perforant pathway. In the indirect pathway, inputs from the entorhinal cortex synapse with dentate granule cells (axons of which are known as mossy fibers). These cells further transmit information to the CA3 pyramidal neurons via the mossy fibers. The axons of CA3 neurons (known as the Schaffer collaterals) extend to the CA1 neurons. From

here, the CA1 neurons project back to entorhinal cortex completing the trisynaptic loop (Bear et al. 2007; Kandel et al. 2000).

Adult neurogenesis is seen in the two regions of active proliferation, namely, the subventricular zone and the dentate gyrus (Purves et al. 2014). New granule cells within the dentate gyrus are produced from neural progenitor cells (Barker et al. 2017). These precursor cells are present in the basal aspect of the granular layer and give rise to neuroblasts. Postmitotically, these neuroblasts move apically and differentiate into inhibitory interneurons. Later on these neurons get



incorporated into the local neural circuits and play a critical role in learning and memory (Purves et al. 2014).

Learning and memory involves long-term changes in synaptic plasticity. Long-term potentiation (LTP) and long-term depression (LTD) has raised a lot of interest among researchers. LTP is an enduring alteration in synaptic strength succeeding a high-frequency afferent activity. In 1973, LTP was first demonstrated by Bliss and Lomo at the perforant synapses with dentate granule cells (Bear et al. 2007; Nicholls et al. 2001). They observed a consequent increase in excitatory synaptic potentials that lasted hours to days, depending on the stimulation parameters. LTP mediated by granule cells is input specific and highly dependent on NMDA receptor activity. Mechanisms that allow the reversal of LTP, for example, LTD are also displayed by the same synapses. LTD is an enduring depression in synaptic transmission. This depression could persist for days and is accompanied by an increase in calcium concentration postsynaptically (Derrick 2007). The dentate gyrus displays competitive modes of learning, specifically the homosynaptic LTP and heterosynaptic LTD (Nicholls et al. 2001). The dentate gyrus plays an important role in the efficient storage of information within the hippocampal formation. This is due to prolonged changes in neurotransmitter release, construction of new synaptic contacts, and the phenomenon of adult neurogenesis (Derrick 2007).

Pattern separation is the ability to separate two closely related images, objects, spatial configuration, etc. It plays an important role in storage and recall of explicit memory. This type of memory comprises semantic (facts) and episodic memory (episodes). It has been demonstrated that there exists a correlation between pattern separation and dentate gyrus. Absence of functional NMDA receptors in the granule cells hamper in performing a pattern separation (Kandel et al. 2000). Kindling is a process wherein an electrical or chemical stimulus is amplified until a seizure occurs. This hyperexcitability induces axonal sprouting, which refers to synaptic reorganization

in the mossy fibers (projections of granule cells in dentate gyrus). The vice versa is also true as studies in animals having focal seizures of hippocampal origin or after kindling show such reorganization (Kandel et al. 2000). One of the major hallmarks of temporal lobe epilepsy includes lack of mossy fiber innervation in the molecular layer (sprouting). Thus, the dentate granule cells play a pivotal role in the pathogenesis of epilepsy.

It has been observed that in an ageing brain, the number of granule cells is preserved. Hence, neuronal degeneration is not responsible for cognitive decline. Axo-dendritic synapses from the entorhinal cortex to the granule cells (perforant pathways) are substantially lost. The weakening of the harmful effects of ageing is intervened by certain factors such as strengthening of pre-existing connections among granule cells. Despite these compensatory alterations, granule cells are relatively more vulnerable than hippocampal cells. MRI studies show that the selective changes in the dentate gyrus can be correlated with memory decline (Chawla and Barnes 2007).

## Comparative Biology

Dentate gyrus is present in the higher-order vertebrates. Extensive research has been conducted on mammals to characterize the dentate gyrus. Generally, brain size and body mass vary proportionately, but some species have a higher brain to body mass ratio, for example, rodents and primates. Studies indicate that the number of granule cells present is dependent on the size of the brain. However, this correlation is not proportionate. Many differences occur even across species of the same class. Morphological and anatomical features, numbers, neural circuits, neurochemical content, etc. of the cells, are some parameters that discriminate them. Several deep convolutions of the dentate gyrus are observed in both human and monkeys. Rodents exhibit uniformity in the morphology of granule cells. In contrast, primates have varying width of granule cells, length of principal apical dendrites, and variable thickness of the molecular layer. Humans have the longest

thorny excrescences of mossy cells, followed by monkeys and rodents (Seress 2007). Cetaceans (whales, dolphins) have a much smaller dentate gyrus with decreased convolutions (Hevner 2016).

Dentate gyrus is a prominent component of the archicortex, which is the oldest brain system. The nonmammalian vertebrates, especially the sauropsids (reptiles and birds), have homologs of the dentate gyrus. These are the medial cortex and medial pallium in reptiles and birds, respectively. The medial cortex is very much like the mammalian cortex. Neurogenesis is observed here thus, it fulfills a role in learning and memory. It has a trilaminar organization and contains the granule neurons with several projections. They project to CA1 and dorsal cortex, unlike the mammalian dentate gyrus. The medial pallium is unilaminar and is characterized by absence of granular cells. Scientists have a divided opinion on the notion that the “avian dentate gyrus” exists where neurogenesis has been observed. It also plays an integral role in spatial learning necessary for flight and migration (Hevner 2016).

## Conclusion

Dentate gyrus is a critical region situated within the hippocampal formation. Adult neurogenesis is crucial for the proper functioning of the brain and it occurs here. It accounts for many fundamental functions such as memory formation and learning, through plasticity. Two types of synaptic plasticity – LTP and LTD are observed in the dentate gyrus. Hyperexcitability in granule cells of dentate gyrus is a core concept in the pathogenesis of epilepsy. It is a part of one of the oldest brain systems and is present in most vertebrates, if not its homolog. Evolution of the dentate gyrus is heavily dependent on the adaptations that the species acquires. It has fascinated the scientific community since time immemorial and still holds great research prospects. Many intricacies of this simple yet complex cortical structure are yet to be discovered.

## Cross-References

- [Entorhinal Cortex](#)
- [Episodic Memory](#)
- [Hippocampus](#)
- [Long-Term Memory](#)
- [Long-Term Potentiation](#)
- [Memory](#)
- [Neocortex](#)
- [Neurogenesis](#)
- [Neuron](#)
- [NMDA Receptors](#)
- [Parahippocampal Cortex \(PHC\)](#)
- [Perirhinal Cortex](#)
- [Short-Term Memory](#)
- [Temporal Lobe](#)

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## Dentition

- [Dental Formula](#)

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## Dependence

- [Correlation](#)

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## Depressive Disorder

- [Anaclitic Depression](#)

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## Deprivation of Liberty

- [Restraint](#)

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## Depth Cues

- [Depth Perception](#)

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## Depth Illusion

- [Ponzo Illusion](#)

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## Depth Information

- [Depth Perception](#)

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## Depth Perception

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## Synonyms

[Auditory perception](#); [Binocular vision](#); [Depth cues](#); [Depth information](#); [Gibsonian approach to depth](#); [Haptic perception](#); [Motion parallax](#); [Motion perception](#); [Perception for action](#); [Shape perception](#); [Space perception](#); [Tactile perception](#); [Three-dimensional \(3D\) perception](#); [Two-dimensional \(2D\) retinal images](#)

Edwin Abbott Abbott takes us to a journey into the two-dimensional world in his 1884 novella, “*Flatland: A Romance of Many Dimensions*.” The third dimension, commonly considered as depth, is missed physically as well as perceptually in Flatland; besides that perception of the second dimension for the dwellers of Flatland is at some point between nowhere to bind. In fact, this situation could be generalized as impracticability of perceiving all the dimensions precisely in a physical environment unless you get out of all those dimensions composed the environment and look from a new dimension. For instance, imagine a piece of paper is resembling Abbott’s Flatland. While looking from the third dimension, all dimensions of a geometrical shape (i.e., triangle, rectangle, or circle) drawn on the paper, so the objects and residents belong to Flatland, are evident to us. Thus we can comfortably define the shape drawn on the paper and tell its location along with the direction. Unfortunately, it is not as easy for Square, a resident of Flatland who gets stuck in two dimensions, as it is for us. Square, the narrator of the book, makes the point as follows:

You, who are blessed with shade as well as light, you, who are gifted with two eyes, endowed with a knowledge of perspective, and charmed with the

enjoyment of various colours, you, who can actually see an angle, and contemplate the complete circumference of a circle in the happy region of the Three Dimensions – how shall I make clear to you the extreme difficulty which we in Flatland experience in recognizing one another's configuration? . . . All beings in Flatland, animate or inanimate, no matter what their form, present to our view the same, or nearly the same, appearance, viz, that of a straight Line. How then can one be distinguished from another, where all appear the same? (Abbott 1884, p. 19)

Returning back from such a journey to our homeland, we live in a physical environment (or world) consists of three-dimensions: commonly called width, height, and depth. The spatial locations of all the objects in our environment and their relative positions to each other, and their shapes are defined in terms of a three-dimensional structure. Perceiving our environment in this way allows us to accurately recognize the shapes of objects and surfaces surrounds us, as well as successfully plan and coordinate the various actions we perform in everyday life. If the third dimension, also known as depth, were not available to our perception, tasks as simple as walking on the ground, grasping a coffee cup, coordinating a knife while chopping or a fork while eating spaghetti, driving a car, catching a ball, threading a needle, reaching out for hugging or kissing a loved one, and so on, would be a pain in the neck. Lack of depth perception would even have vital consequences: for instance, without depth perception you cannot discern whether you are about to step on or jump over a dangerous deep hole or simply a manhole cover, exact shapes of surfaces and objects would not be available. Without depth perception, you cannot accurately estimate whether the approaching car will crash you before you safely cross a road, in fact, you cannot even cross a road, direction of navigations would not be available. Without depth perception, a frog cannot catch flies with its tongue while starving, planning and coordinating actions would not be available.

Unlike occupants of Flatland, animals of our homeland, are equipped with perceptual systems such as tasting, smelling, haptic, auditory, and visual systems (Gibson 1979), and they live

in harmony with their environment. Such symphony saves animals from travelling to the fourth dimension to perceive their physical environment as it is in three-dimensional structure.

There are three different perceptual systems that are directly related to depth perception. The first one is the haptic system that requires information to be gathered directly from the environment by touching. Touching along with reaching is especially critical for infants while learning three dimensional structures of objects and developing depth perception. It is not surprising that infants are used to love touching every single object and all surfaces with full of curiosity but this habit fades away as they are growing up. Infants' miserable sight might be one reason of that. They cannot visually focus on objects that stand out of 8–10 inches (20–25 cm) distance from their face. Their eyes are not well coordinated, and they do not have the control of their eye-movements, neither eye-body coordination skills do they have. It takes 2 years for infants to develop a normal vision and 7 years for a fully skilled vision. On the other hand, infants start touching while in the womb, and they are born with highly sensitive skin; around 3 months of age they also start reaching. In such sense, touching is in favor for depth perception and understanding three-dimensional structure of the objects and surfaces around during childhood. Unfortunately, one handicap of haptic perception is that touching is only available within arm-length distance. Because of this boundary, haptic perception is not really practical on evaluating the long distance or the three-dimensional shape of giant objects. Touching takes a step back in the adult's process of depth perception although it still contributes in some way. There is indeed some exceptional cases where touching is still a blue eyed boy for adult, just like for children; for example, in the case of blind people. Eşref Armağan, who is a congenitally blind painter lives in Turkey may set the best example of it. He challenged scientists' knowledge about depth perception they had had until run into Eşref Armağan and saw his art. He uses pictorial information in his paintings to reflect depth that thought to be available only through vision by

then, but haptic. Eşref Armağan has never had vision to understand such information; he is used to see all details by through his fingers.

The illusions for sighted people due to depth information in Eşref's drawings are striking. Inaccuracy in touch may be less to do with depth information than vision, and more to do with grouping areas in 2D [two-dimensional]. Heller (2003) reports many tactile illusions for the blind, but no effects that can with certainty be ascribed to pictorial depth information. In contrast, studying grouping, Heller et al. (2003) found flat forms embedded in larger forms hard to discern in touch; they were grouped with the embedding form. (Kennedy and Juricevic 2019, p. 11)

Auditory is the second perceptual system that contributes to depth perception at a considerable degree. Unlike haptic, auditory is not much convenient on discovering the three-dimensional shapes of objects and surfaces; that is not because it is impossible but it requires to develop an exclusive skill to do so like bats and dolphins do. Yet, auditory has an edge on haptic in detecting spatial location of objects that are farther away from arm-length distance. Auditory could certainly be a reliable guide to determine the relative direction of the objects along with the distance from the perceiver. Otherwise a bell on the collar would not be able to help you to find your little playful kitty while it is hiding from you. Objects which somehow get our attention in the environment do not always fall within our visual field or arm-length distance. When that is the situation, auditory system takes all responsibility in evaluating the relative position of the object. For example, imagine you are camping in a jungle, and while resting in your tent at midnight, you hear kind of a strange sound that could be made by a hostile person or a wild animal. You have nothing to defend yourself and you are about 3 miles (5 km) away from your car. You, now, have two options ahead of you: either you decide to stay in your tent quietly which is the shrewd reaction to do if the beast is just right there around the tent. If you decide the beast is not really close, you may choose to sneak off to your car. Then, you have to make sure that the beast is not in the same direction you run towards. Otherwise, you end up falling

into the lap of the beast. The sound you hear is the all source of information on your hand to make such a life matter decision; if you listen to it carefully, your auditory system will reveal every detail you need like how far the beast is from you, in which direction it is moving, and how fast.

What haptic and auditory systems mean to depth perception have been discussed, so far. Each one has different advantages favorable for different aspects of depth perception. They are counterparts each of which completes deficient part of the other for a completed depth perception. In general, neither one is better than the other. However, the third one, visual system, is capable enough to be able compensate in the absence of both haptic and auditory systems by its own for the depth perception in all respect. Visual system is the one we most rely on among all perceptual systems we have and the one we are most afraid of losing.

RECENTLY, I ASKED a group of friends which sense they would miss the least if they had to lose one. Most people chose smell. No one chose vision.

If you lose vision, you lose your most important sense for knowing where things are. Vision allows us to perceive the shape of objects and their arrangement in the world around us, an ability that impacts nearly everything we do . . . Among all our sensory systems, vision's contribution is uniquely important for the brain's assembly of a sense of space. (Groh 2014, p. 7)

Visual system is important to us as playing a major role in our understanding and identifying the environment, and interacting with it. Considering the vision's essential functioning in perception, it is understandable that vision is not a simple process. The studies that dedicated to understand visual perception dates back in time until the era of philosophers lived in ancient Greece. Not alone has it been interest of neuroscientists and psychologists, but philosophers, mathematicians, artists, and astronomers, too. Democritus, Plato, Euclid, Alhazen, Leonardo da Vinci, Rene Descartes, Johannes Kepler are only a few famous historical figures who paid attention to explain vision. People from all over the world (i.e., India, China, Arabia, Anatolia, and Europe) in different disciplines have

cumulatively formed today's understanding of vision (Groh 2014; Howard 2012).

During the early stage, even the source of the information that enabled the vision and its direction between eye and perceived object or a target point was a mystery. It was mid-eleventh century in the Common Era when the first time Alhazen pointed out that the light reflecting from object to eye contains all the information needed for the vision. Albeit he revealed the obligation of one-to-one relation between the eye and the perceived object or target point, he claimed that the perception should be formed in the lens; otherwise we would perceive the world in upright position. It took until seventeenth century when Kepler's work revealed the optical basis of visual perception that is the discovery of the retinal image (Gilchrist 2014; Groh 2014; Howard 2012).

Today, common knowledge has it that vision starts when ambient light hits the retina of the eye. The retina captures only two-dimensional images of the three-dimensional world. Yet, we clearly perceive the world as being three-dimensional. What allows the visual system to reconstruct its view of the three-dimensional world from those two-dimensional retinal images? Though not a comprehensive explanation is revealed yet, there are some justifications that could be counted as the answer. Before continue with those notes, the heart of the problem with two-dimensional retinal image needs to be clarified further.

It is quite problematic to perceive the three-dimensional world through two-dimensional retinal images because the two-dimensional retinal images could be inherently ambiguous. The ambiguity basically arises from the missing third dimension (depth); different objects in different sizes, positions, or distances sometimes could be projected onto very similar retinal images; in other words, although they have differences in the real world, they may be conflated in the retinal images. Such ambiguity is called the *inverse projection problem* (Palmer 1999; Pizlo 2001).

The inverse projection problem causes failures in depth perception at the level of the retinal

images. Luckily, our visual systems are capable of preventing or at least decreasing such failures by resolving the ambiguity of the inverse problem on the retinal images. Our visual system relies on different types of depth cues to make up for the losses of depth due to the inverse projection problem. In the following part, those cues are briefly noted along with their meanings in the order they generally classified. Depth cues are mainly divided into two broad categories: oculomotor and visual.

### Oculomotor Cues

The term "oculomotor cues" refers to the information the brain receives from eye muscles while fixating the eyes on a target point, usually that is specifically an object. Such information is practically usable only for arm's length distance. For example, if you fixate your eyes on an object you are holding at eye height within arm's length, your visual system will benefit from the oculomotor information cue to decide where the position of the object is, depth-wise. If you slowly move the object towards and away from you, you can feel it through oculomotor feedback. There are two types of oculomotor information cues:

#### Accommodation

The ciliary muscles, which are located in the ciliary body around the iris of the eye and innervated by oculomotor nerves, accommodate the lens in order to focus on an object at different distances within about an arm's length radius. When an object is nearby, the ciliary muscles contract and hence make the lens rounder. In contrast, when the object is more distant, the ciliary muscles relax and hence make the lens flatter. By doing so, the ciliary muscles, on one hand, allow us to focus on objects for clear vision; on the other hand, they provide useful feedback to our brain for the depth interpretation about the object.

#### Vergence

Movements of the two eyes in opposite directions (when both of them move either inwards or outwards; towards or away from each other) are called vergence eye movements:



To be able to fixate our eyes on an object moving toward our face, we move the eyes inward; this is called convergence. On the contrary, eyes diverge as an object gets farther away from our face; this is called divergence. Vergence eye movements help to maintain a single image in binocular vision of an object moving in the depth dimension. Moreover, the feedback from the muscles that control vergence eye movements provides depth information about the object (Mon-Williams and Tresilian 1999; Mon-Williams et al. 2000). Accommodation by the ciliary muscles (as described above) is connected to vergence eye movements – both usually happen together when an object is moving in depth. Yet, vergence provides more accurate estimations of depth perception as compared to accommodation.

### Visual Cues

While oculomotor cues are considered to be internal cues, visual cues have a more external source: usually physical, psychological, and pictorial information cues. Visual cues can be categorized into two groups as binocular and monocular.

#### Binocular Cues

Binocular cues are taken to be the most essential cues for depth perception. Because these cues are the most powerful among other cues, our visual system primarily relies on this information as planning and performing actions (for a review, see Goodale 2011).

When we fixate both eyes on one object (or at a single point), two eyes see the same object from slightly different perspectives because of the space between them, known as the interpupillary distance (IPD), which averages about 2.5 inches (6.3 cm) for an adult human. As a result, we have two retinal images, which differ slightly from one another. Although we have two different retinal images, we experience only one visual image (under normal conditions); the brain forms a single, three-dimensional visual image from two different two-dimensional retinal images. The differences found between the two retinal images serves as a source of information for depth perception (Bishop 1970; Julesz 1971). For a better understanding of this source of

information, it is necessary to first understand the geometry of the “*horopter*.”

When we fixate both eyes at a single point, the fixation point, together with centers of the lenses of both eyes, all lie on an imaginary circle. On this imaginary circle, we can picture two arcs with the centers of the lenses of two eyes being endpoints; the one that contains the fixation point midway along its length is called the horopter. All images along the horopter are projected onto corresponding retinal points in the two eyes, thus the horopter is also known as the set of points with zero disparity (Von Noorden 1996). All the points in the visual field that are off the horopter fall on analogous (noncorresponding) retinal points in the two eyes. Moreover, as the distance from the horopter increases, image difference between noncorresponding points in the two retinæ also increases. This difference between the two retinal images is called retinal disparity. There are two types of diplopia, or double-vision: crossed disparity and uncrossed disparity. Crossed disparity is created by the images located between the horopter and the observer; these images are usually projected on the temporal hemiretina points (the outsides of the retinæ). On the other hand, uncrossed disparity is created by the images that are located behind the horopter; these images are usually projected on the temporal hemiretina points (Von Noorden 1996).

The retinal disparity causes diplopia. Yet, we usually do not experience the diplopia so it is called physiological diplopia – it happens on the retinæ, but not in our minds. The reason we do not experience this diplopia is that our brains fuse the retinal disparity within Panum’s Fusional Area. It is a specific area around the horopter that allows fusion. This area is narrowest at the fixation point and getting wider towards the periphery. The process of fusion is called stereopsis (Von Noorden 1996).

#### Monocular Information Cues

Although binocular vision is very powerful for depth perception, we can perceive depth even in the absence of binocular vision by relying on monocular information cues.

**Dynamical Cues** Motion provides depth information that is available even to monocular vision. Goodale (2011) described studies which revealed that one-eyed people seemed to use retinal motions resulting from head movements during reaching actions. This suggests that dynamical cues are the second most reliable depth information cues after binocular cues. Consistent with Goodale, Boring (1942) found motion parallax, which is a kind of dynamical cue, to be the most important cue after binocular cues. On the other hand, Nakayama and Loomis (1974) considered both to be primary information cues for depth perception in their comparison of binocular cues and optical velocity information, which is a specific kind of dynamical cue. They claimed that binocular cues might be more useful for actions, such as reaching, that take place in the near environment whereas optical velocity information might be more useful for more distantly directed actions such as throwing or observing.

*Motion Parallax* Motion parallax is the term used to describe optical displacement of an object in the visual field while the observer is in motion. Helmholtz's (1925) definition of motion parallax is two-fold: first, he asserted that motion parallax information allows us to judge absolute distance of the object from our own position. While an observer moves in one-direction, points, relatively fixed in the observer's visual field, provide a sense as if they are moving in the opposite direction and their apparent angular velocity to the observer is inversely proportional to their real distance. Thus, their real distance to the observer can be inferred from their angular velocity. Subsequently, Gibson and his colleagues (Gibson et al. 1955) showed that this is true only if the speed and direction of the observer are known. The second part of Helmholtz's definition claims that motion parallax information allows us to discriminate objects sitting in different positions in depth. Helmholtz (1925) used a foliage and branches example: it is almost impossible to distinguish a tangle of foliage and branches if viewed in stillness. Yet immediately upon the presence of motion, we can appreciate the separation of each

leaf and branch and become aware of their relations to each other in space. Gibson (Gibson et al. 1959) suggested these two approaches were independent and needed to be studied separately.

Later on Nakayama and Loomis (1974) explained how to extract depth information from optic flow based on a formula that describes the pattern in the optic flow. Optic flow is a related but broader notion than motion parallax. Nakayama and Loomis emphasized the distinction between motion parallax and optical flow information: motion parallax refers to only a small number of focal objects; optical flow information, however, is the totality of optical motions (Gibson 1950). The relative motion between an observer and the environment produces optic flow information. Because optical flow refers to all points in the visual field rather than a single focal point, it is represented by what is called a velocity field. Each vector, in the velocity field, is associated with optical motion of a point and the magnitude of the vectors is inversely correlated with the distance of the point. In other words, closer points move with greater velocity. Variation in distance generates motion parallax gradients. Hence, motion parallax provides information about the relative depth of the points.

Another inference that can be made from optical flow structure occurs when two adjacent points in the image have significantly different velocity magnitudes; if those adjacent image points are associated with two distinct points in depth, then the difference between their velocity magnitudes will be greater. Such information is a useful cue regarding the separation of distinct surfaces. Yet this information usually accompanies cues such as accretion and deletion that will be explained shortly after expansion and contraction.

*Expansion and Contraction* Imagine you are moving towards an object with an angular position of 0—straight ahead. The angular velocity of the object will be 0, and so the magnitude of angular velocity will be useless for depth perception. In such a case, expansion and contraction information helps to provide depth perception. While an observer moves closer to an object, the object will appear as if it is expanding because

of the change in the retinal image size of the object. Contrarily, while moving further away from the object, the object will appear as if it is contracting within the retinal image. The degree of expansion or contraction will be inversely proportional to the distance between the object and the eye. For example, assume you are in the middle of your room and looking at a tree outside the window. You are able to see only part of the tree. With each step you take towards the window, a bigger part of the tree will be available to your sight. Eventually, you will be able to see the whole tree when you reach the window. This experience could be explained as follows: while you are moving towards the window, the expansion degree of the window is greater than the expansion degree of the tree because the window is closer to you. You can use such information to infer the depth *order* between two objects. If you know your speed, you can also infer the absolute distance of the objects.

*Accretion and Deletion* When two opaque objects are located at different distances in depth, the nearer object partially or wholly covers over or reveals the more distant object as the observer moves. (Gibson 1979). Imagine that you are sitting in a theatre, in the seventh row of seats, and trying to see the picture on the scene. Unfortunately, the head of the person sitting in front of you in the sixth row blocks the scene. If you try to lean forward, the person's head will cover a greater part of the picture. Is his/her head getting bigger as you are leaning forward? Of course not. Actually what is happening here is exactly the same as with the window-tree example: as you are leaning forward both the picture and the person's head are expanding however because he/she is closer to you, the degree of expansion of his/her head is greater than the degree of expanding of the picture. Therefore, you are experiencing deletion in the picture on the scene. If you lean backward rather than forward, you experience accretion of the picture on the scene. Moreover, if he/she sits further from you and closer to the scene, the difference between the expansion/contraction degrees of the head and the picture will be smaller;

so, the accretion/deletion will occur more slowly. Hence, the rate of accretion or deletion is able to provide relative depth information about objects. Accretion or deletion will occur not only during backward/forward movements of the observer but also during sideways movements. However, with accretion and deletion information revealed by sideways movements, you can still easily infer depth order.

**Static Cues** While you are looking through a peephole to see what there is on the other side of the door or wall, binocular vision is not available at all and motion is very restricted as you are not allowed to move backward-forward or side to side. Nonetheless, thanks to static cues, so you can still experience the depth in your view.

Static cues are also called pictorial cues and often used by visual artists in two-dimensional paintings and photography to reflect the depth sense. From time to time, you may run into such paintings or photographs that make you strongly feel as if you are a part of the environment via the sensation of depth depicted in the picture. If you think you have never come across one of those, just take a break from reading this entry and check these paintings: *The Dance Class* by Edgar Degas (1874), *A Sunday Afternoon on the Island of La Grande Jatte* by Georges Seurat (1884), *Cafe Terrace at Night* by Vincent Van Gogh (1888), *Paris Street; Rainy Day* by Gustave Caillebotte (1894), and *The School of Athens* by Italian Renaissance artist Raphael (1511).

*Occlusion* Considering Edgar Degas's painting, "The Dance Class," which ballerina is closest to you in the painting? Although it is a two-dimensional picture with no dynamical cues, you can easily say that the ballerina who wears a big red ribbon barrette on her hair on the left hand side is closest with no doubt. Your confidence relies on a basic depth cue called "occlusion": some part of the girl, which seems closer, is partially occluding the other girls. Occlusion indicates the relative distance but not absolute distance. It is hard to tell the absolute distance between people in the picture based only on their occlusion cues.

*Relative Size* If one of two similar or identical objects in an image looks bigger than the other one, it will give the impression that the one that looks bigger is closer. Reconsidering your answer above to the question regarding the closest ballerina in the painting, “The Dance Class,” the occlusion is not enough by itself to say that the ballerina who wears a big red ribbon barrette on her hair on the left hand side is closest with no doubt. She is not occluding the dancers on the right hand side but she is the biggest in terms of size although they should be around same size. Thus, your confidence relies on both depth cues called “occlusion” and “relative size.”

Note that the logic of relative-size information applies to expansion and contraction in motion, and, together with occlusion, it is also related to accretion and deletion.

*Familiar Size* Our knowledge about objects can help in depth perception too. For example, if we see a toothpick, a baby, and the Eiffel Tower, all appears to be the same size, in a picture, we will think that the toothpick is closest and the Eiffel Tower is the furthest object. Moreover, we can infer that the distance between the toothpick and the baby is smaller than the distance between the baby and the Eiffel Tower.

*Distance from Horizon Line* Objects and surfaces appear closer to the horizon as their distance becomes greater. Picture a moment at a beach, you are watching people swimming in the sea; you do not hesitate to assume that the person looks closest the horizon is the furthest away from the beach.

*Shadows, Shading, and Lightning* Shading and lighting patterns on an object or surface provide powerful cues as to the three-dimensional structure of the object or surface. You can make a circle appear as convex or concave simply changing the lightning and shading. The characteristics of cast shadows help us to determine the position of objects and the shapes of the environment. For example, a cast shadow of a flying bird cannot be connected to the bird. The cast shadow of a telephone pole does not look same on a

stone as it is on a street; the stone has a convex surface whereas the street is flat.

*Atmospheric Perspective* Because of the atmospheric effect, objects that are further away appear bluer and less distinct than nearer objects.

*Linear Perspective* Parallel lines appear to converge towards a vanishing point on the horizon or close to the horizon. A railroad, viewed from one standing upon the tracks looking along them, might be the best example to clarify linear perspective. You can also visit and see some paintings in the gallery of Esref Armagan who is the congenital blind painter mentioned above.

*Texture Gradient* Considering a walkway and a wall, two different surfaces both are consisting of similar cobblestones. Indeed both surfaces have a homogenous spatial texture. But, in the real world, we see a heterogeneous spatial structure on the walkway. Based on the rate of change in the density of the pattern, we can easily distinguish a walkway from a wall, which has a homogeneous pattern. The increasing density of the pattern indicates an increasing angle from the eye and that increasing angle yields increasing depth information.

If we express this in a more general way: the volume of gradient specifies the slant of a surface in the world with respect to the line of sight. Furthermore, simple changes in gradient can define corners and/or edges. If the change of gradient of density is smooth, it yields a corner; if there is a jump in the gradient of density, it yields an edge or, in other words, two separate surfaces (Reed 1988).

## The Gibsonian Approach to Depth Perception

Earlier theories attempted to explain visual perception as a sensation-based phenomenon that found the retinal image to be central to visual perception. Those theories struggled, however, to explain three-dimensional vision based in two-dimensional retinal images. Some early

theorists (e.g., George Berkeley) suggested that depth perception could not be explained based purely on the senses *per se*; sensation was impoverished to explain perception without relying on resource to knowledge about the world such as provided by experience. These theorists explained depth perception as occurring by first having the sensation and then inferentially constructing the space.

Gibson rejected this sensation-based approach to visual perception. Instead he introduced the information-based approach. According to the information-based approach, visual perception cannot be explained based on retinal images; perception is detecting information, which exists as invariant variables in the optical array. Optical array is the pattern of structured light reaches the eye with respect to point of observation and contains all the information for visual perception directly without need for any mental representation or memory. Retinal images are just a sampling from the optical array. Hence, information is not a static two-dimensional image on the back of the eye. Instead, it is available to be detected in the optical array and specific to surfaces and lay-outs. Depth is not really lost (Braund 2008).

Although Gibson eventually rejected the sensation-based approach, he had had missteps and confusions before developing his final theory. In his early studies, Gibson tested slant perception based on different texture gradients (Reed 1988). In the experiment, subjects sat in front of an aperture in a wall. Through the aperture, they were able to see the texture of an upright screen behind the wall though the edges of the screen were occluded from their sight by the wall with the aperture. The upright screen was painted different texture gradients. These gradients allowed Gibson to manipulate the patterns of retinal images in his participants. The task of the subjects was to decide the optical slant they observed on the screen. The hypothesis behind the experiment was that the gradient of texture density with no other clues available would yield an impression of a receding surface. Results revealed that subjects thought they were seeing slanting surfaces despite the fact that the surface in the back was

always upright. Moreover, greater changes in the texture density resulted in greater perceived slants. However, there was a problem: the slant was always underestimated, even though texture gradients co-varied with perceived slant.

Subsequently Gibson decided to focus on perceptual psychophysics rather than sensual psychophysics. In his optical tunnel experiment, he was studying the optical conditions that give rise to surface and space perception. This was neither a physical tunnel nor a special retinal image; you will read more about what an optical tunnel is, in a moment. Gibson was no longer attempting to control the formation of retinal images but instead was controlling the stimulation available to observers' visual systems that enabled them to obtain retinal images.

In the optical tunnel experiment, Gibson attempted to manipulate and studied optical transitions. The tunnel apparatus controlled the gradient of optical transitions in the available stimulation by different arrangements of the transitions and different observation positions. The optical tunnel was in two arrangements. Plastic sheets are arranged with alternating smooth black and white coloring, with central holes cut out carefully so that each sheet acts as an aperture for the sheets behind it. First, the tunnel creates a constant density of optical contrast, a heterogeneous, inverse gradient in the world. This looks flat, canceling gradient in the optics, homogeneous. Second, the tunnel creates an increasing density of constant, no gradient in the world, homogeneous. This displays a visual tunnel, yields gradient in the optics, heterogeneous.

In the tunnel experiment, Gibson provides the information of a surface even though there is no real surface there. The optical structure tells the same thing as optic flow structure. The gradient in the optic flow is identical. He distinguished the world and the optical structure and studied the relation between them. The optical structure is different than the world structure but they are uniquely related. Depth is not lost; there is enough information in the structure of light.

The significant change in Gibson's methodology was that he was no longer trying to make retinal images replicate surfaces; instead, he was



trying to control the stimulation available to the eyes of his observers.

## Conclusion

Depth perception is perceiving the environment as in three-dimensional coordinate systems. It is all about knowing where things are, what they are, and what we can do with them. In this manner, depth perception provides two critical aspects of understanding our environment: clarifying the shapes and evaluating the spatial locations of the objects. Neither haptic nor auditory system alone is capable of encompassing the two aspects of depth perception. The nature of haptic confines its employability within arm-length distance. Yet, haptic system is proficient on evaluating the shapes of the surfaces and objects, so it can precisely tell us what they are and what they afford. Haptic is primarily used by infants and blind people. Auditory system is a counterpart of the haptic system; they are integral part of each other for the sake of depth perception with no strings. In other words, haptic system is strong where the auditory system is weak and vice versa. For example, haptic system works well within arm-length distance, and auditory system steps in while the distance getting greater than arm-length. Haptic clearly state what the object is whereas auditory confidently decides where the object is with respect to our position. Visual system is not affected in the absence of either one or both of haptic and auditory systems; vision still capable of promising a fully completed depth perception.

## Cross-References

- ▶ Auditory Processing and Perception
- ▶ Cognition
- ▶ Goal-Directed Behavior
- ▶ Locomotion
- ▶ Perception
- ▶ Perception-Action Theory
- ▶ Tactile Perception
- ▶ Visual Perception

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## Derma and Its Derivative

► [Integumental System](#)

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## Desensitization

► [Habituation](#)

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## Desire

► [Need Reduction](#)

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## Deterioration

► [Pollution](#)

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## Detour Task

► [Cylinder Task](#)

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## Detour-Reaching Task

► [Cylinder Task](#)

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## Deutero-learning

► [Learning to Learn](#)

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## Developed Embryo

► [Fetus](#)

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## Developing Infant

► [Fetus](#)

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## Development

► [Budding](#)

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## Developmental Arrest

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## Synonyms

[Dauer](#); [Delayed implantation](#); [Embryonic diapause](#); [Embryonic quiescence](#); [Postimplantation delay](#); [Quiescence](#); [Torpor](#)

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## Definition

A temporary period of reversible, suspended development that can occur in some invertebrates, and in mammalian and nonmammalian embryos. It is commonly induced as either a response to unfavorable environmental conditions or as a mechanism to separate the timing of mating and the length of pregnancy.

## Introduction

Developmental arrest is a widespread phenomenon occurring in a diverse range of species at a multitude of different life stages and in response to a large variation of stimuli. Much of the diversity is species-dependent. However, all forms confer some sort of selective advantage that enables the species to maximize its reproductive success. In general, there are two main forms of developmental arrest: diapause and quiescence (or torpor). Diapause is a gradually induced arrest and involves a downregulation or arrest of cell division and suppression of metabolism. It may be hormonally regulated and generally occurs prior to the onset of predictable, unfavorable conditions (e.g., in response to seasonal changes). In contrast, quiescence occurs in response to an unexpected change in environmental conditions which are not conducive to growth and/or survival. Some species are also able to delay hatching in response to environmental conditions, but this does not normally involve a reduction in metabolism or a delay in development.

In mammals, diapause occurs during pregnancy and has been classified into two types, embryonic diapause and postimplantation diapause. During embryonic diapause, the arrest occurs prior to the embryo attaching to the uterus (implantation), while postimplantation diapause or delay occurs after the embryo has attached to the uterus. Both types of arrest can be induced by either facultative mechanisms (lactational or nutritional availability) or seasonal mechanisms (photoperiod, temperature, or rainfall).

Members of three orders of nonmammalian vertebrates are able to undergo forms of developmental arrest, namely, fish, reptiles, and birds. These species undergo diapause in response to environmental factors and in the oviparous (egg-laying) reptiles, diapause can occur either prior to or postoviposition. In addition, the embryos of most species of reptile, and some fish, can employ torpor (quiescence), at any stage during egg incubation, while the majority of oviparous species can undergo delayed-hatching. Diapause also occurs in several viviparous (live-bearing) species of reptiles and fish.

In invertebrates, developmental arrest can take two forms, diapause and quiescence, and can occur at many different stages of the life cycle. Diapause may be hormonally regulated and/or occur in response to signaling cues that are predictive of forthcoming environmental change (e.g., photoperiod). Quiescence is a common reproductive strategy which allows invertebrates to respond to adverse environmental changes (e.g., anoxia or desiccation), which, depending on the species, they can survive for periods of weeks to years.

## Embryonic Diapause in Mammals

Embryonic diapause has been identified in over 130 species of mammals in eight different orders. It occurs early in pregnancy, when the embryo consists only of a ball of cells (between 30 and 500 cells, depending on the species) and is free-floating in the uterus prior to implantation. During diapause, the cell cycle of the embryo is either arrested or greatly retarded, while maintenance of a basal metabolism and low levels of RNA and protein synthesis ensure the embryo remains viable. Depending on the species, embryonic diapause can be either lactationally or seasonally induced and can last for anywhere between a few days to 11 months. In general, seasonal diapause is the predominant form of diapause in mammals with only the rodents and the macropods (kangaroos and wallabies) undergoing lactation-induced diapause. The tammar wallaby (*Macropus eugenii*) is unusual in that diapause can be both lactationally and seasonally induced, dependent on the time of year. Along with the tammar, the best understood diapause mammals are the mouse, *Mus musculus* (lactationally induced diapause) and the mink, *Neovison vison* (seasonally induced diapause) (Fenelon et al. 2014).

In the mouse, mating occurs within 24 h after giving birth, and it is the metabolic stress of suckling the young that causes the embryos to enter into a lactationally induced embryonic diapause for a period of 2–7 days on average but can be up to 14 days. This is dependent on the number of

suckling young and is postulated to delay birth since lactation in the mouse last for only 19 days while pregnancy is 20 days long. Diapause can also be experimentally induced in the mouse by ovariectomy and daily progesterone injections with reactivation occurring after injection of estradiol (Fenelon et al. 2014).

In the mink, embryonic diapause is obligate, occurring in every pregnancy and is dependent on photoperiod and controlled by the relative levels of melatonin and prolactin. In the Northern Hemisphere, mink mate in early March and the embryos are in diapause during periods of short photoperiod. Embryos then remain in diapause until after the spring equinox (21st of March in the Northern Hemisphere) when day length begins to increase and the embryos reactivate. This allows pregnancy in the mink to be extended by a number of weeks ensuring the separation of mating and parturition so that young are born when conditions are more favorable to survival (Fenelon et al. 2014).

### Postimplantation Diapause in Mammals

To date, postimplantation arrest has only been reported in the order Chiroptera (bats). The arrest normally occurs at a specific stage of development, either just after implantation, at gastrulation, or at primitive streak formation. Depending on the species, the period of delay can be either similar for all females or highly variable in others and can last for anywhere between 10 days and 8 months. Many species of bats have two pregnancies each year and only one of these tends to be arrested. For the majority of bats, the period of arrest often coincides with winter hibernation and may be due to either a decline in food availability or temperature. However, the precise stimuli and physiological regulation remain unknown. Schreiber's bent-winged bat (*Miniopterus schreibersii*) is unique in that it exhibits both embryonic diapause and a period of postimplantation diapause when the bats are in hibernation (Krishna and Bhatnagar 2011).

### Developmental Arrest in Nonmammalian Vertebrates

In the nonmammalian vertebrates, developmental arrest can occur at multiple time points in development, depending on the species. In addition, the environmental stimuli that arrest and restart embryonic development are species-specific and vary widely.

In fish, there are currently two confirmed species of Chondrichthyes (cartilaginous fish) in the subclass Elasmobranchii that undergo diapause, the bluntnose stingray, *Hypanus say*, and the Australian sharpnose shark, *Rhizoprionodon taylori*. In these species, ovulation and fertilization take place immediately after mating and development is arrested at the blastodisc stage for a period of 7–10 months. The control mechanisms are currently unknown (Waltrick et al. 2012). Developmental arrest also occurs in the Osteichthyes (bony fish) and is particularly predominant in the killifish, (order Cyprinodontiformes), which occupy temporary aquatic habitats. For example, in the turquoise killifish (*Nothobranchius furzeri*), seasonal drying of their habitats kills the adults and juveniles but the eggs can enter into diapause and remain arrested until the return of the rainy season, thus ensuring survival of the species (Hu and Brunet 2018). Delayed hatching is also a very common phenomenon in killifish embryos while quiescence normally occurs in response to anoxia (Martin and Podrabsky 2017).

In reptiles, developmental arrest is common in oviparous species and can occur at three different stages in the life cycle, either early preoviposition, late gastrulation (most common), or in the pre-hatching embryo, with some species able to undergo all three forms. Although diverse, the main environmental influences that affect whether arrest occurs are oxygen tension, temperature, or rainfall. In several viviparous species, delayed parturition can also occur, but this is at the end of embryonic development.

In oviparous reptiles, diapause can be either preovipositional or postovipositional. Preovipositional diapause ensures that all eggs are laid at the same developmental stage. It normally

occurs during early embryogenesis but can occur during gastrulation in some species. Resumption of normal development then occurs after the eggs are laid (Andrews 2004). Postovipositional diapause occurs, while the embryos are gastrulae and can be obligate in some species or dependent on environmental factors in others (Andrews 2004). There are also two additional forms of post-ovipositional arrest, delayed hatching, and torpor. Delayed hatching keeps the embryo within the egg in response to adverse environmental conditions and permits synchronization of hatching to optimal environmental conditions. In Australia, many frog species lay their eggs on land in areas that later flood, and hatching may be delayed for weeks if the eggs are not submerged. Alternatively, torpor is used by embryos, at any stage prior to hatching, to survive brief periods when temperatures are too low to support development (Rafferty and Reina 2012).

Many avian species are also able to undergo developmental arrest but this is only post-ovipositional and is primarily through the use of torpor after oviposition to prevent development of embryos until all eggs in the clutch have been laid to allow synchronization of the development and hatching of the clutch.

## Developmental Arrest in Invertebrates

Developmental arrest is widespread among the invertebrates with representatives in all families except Echinodermata (starfish and sea urchins). The most common form of developmental arrest in invertebrates is diapause, which can occur at various stages of the life cycle, depending on the species. There is considerable diversity in the various environmental conditions under which diapause can be induced in invertebrates, with the most common cues being photoperiod, temperature, and overcrowding. Two of the most well-studied examples of diapause in the invertebrates are the nematode, *Caenorhabditis elegans* and the brine shrimp, *Artemia franciscana* (Hand et al. 2016).

Many nematode species are able to undergo diapause, but while many parasitic species

undergo diapause as an obligate part of their life cycle, many free-living species are able to undergo diapause only in response to environmental triggers. During development of the larval stages in the free-living nematode *C. elegans*, exposure to unfavorable growth conditions arrests development and the larvae enter into a reversible diapause stage known as dauer. Dauer larvae are characterized by numerous morphological changes which result in an extended life span and confer an increased resistance to stress. Once conditions improve, the dauer larvae recover and continue normal development (Padilla and Ladage 2012).

In the brine shrimp, females can shift from giving birth to live young (eggs hatched internally) to oviparous reproduction (eggs develop and hatch outside maternal body), depending on the time of the year. In oviparous reproduction, the eggs are released when the embryos are at the late gastrula stage. The eggs then remain arrested with a greatly suppressed metabolism until environmental conditions improve. The cue to shift from live births is a change in photoperiod, signaling the onset of winter, and ensuring the survival of the young as diapause eggs (Hand et al. 2016).

## Conclusion

In summary, the biological mechanisms of developmental arrest are diverse and wide-ranging depending on both the species and their habitat. There have been a number of theories postulated for the evolution of development arrest. In part, this depends on the mechanism via which the arrest is induced, and in insects at least, diapause is thought to have evolved independently multiple times given the wide variation and occurrence of diapause at different life stages even in the same genus (e.g., egg, larval, and adult diapause forms exist in the mosquito genus *Anopheles*). However, a number of generalizations can be made on the selective advantage developmental arrest concurs in all species. First, developmental arrest synchronizes the production of young with environmental conditions conducive to survival and growth. In many species of mammals, diapause enables the

separation of mating and birth to suit the conditions. Second, it often serves to help individuals survive environmental conditions that are lethal to developing embryos. In the invertebrates, this can also be a mechanism to reestablish future populations; either when conditions are too harsh for the adults and juveniles to survive or via the transport and dissemination of the species to new locations. Finally, quiescence (or torpor) allows embryos to respond to, and survive, adverse environmental conditions.

## Cross-References

- [Alternative Reproductive Tactics](#)
- [Bear Life History](#)
- [Carnivora](#)
- [Embryo](#)
- [Environmental Influences](#)
- [Fetus](#)
- [Hatching](#)
- [Hibernation](#)
- [Incubation](#)
- [Insect Life History](#)
- [Insect Sensory System](#)
- [Interbirth Interval](#)
- [Light/Dark Cycle](#)
- [Marsupial Life History](#)
- [Mating](#)
- [Mustelidae Life History](#)
- [Parental Investment](#)
- [Parturition](#)
- [Pinniped Life History](#)
- [Reproduction](#)
- [Reproductive Synchrony](#)
- [Rodentia Life History](#)
- [Squamate Life History](#)
- [Suckling/Nursing](#)
- [Testudines Life History](#)
- [Torpor](#)

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## Diallel Design

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## Synonyms

[Combining ability](#); [Twin study method](#)

## Definition

The term diallel implies all probable crosses among a collection of set of animals. According to Hayman, a diallel cross can be defined as the set of all possible crosses between several genotypes, which may be individuals, clones, homozygous lines, etc. (Hayman 1954a, b). Diallel cross is the most balanced and systematic approach to analyze continuous variations among the genotypes of individual taken for

study. Since almost all the genetic information are available in the parental population so the propensity to carry out diversified breeding techniques can be done within a very short span of time.

## Background Description

The diallel mating design has been successfully applied in the plant breeding studies over more than 50 years. Not only in plant mating analysis but in many cases this technique is extended to analyze genetic mating combination in animals study. Since, 1950 this study was further aggravated to estimate genetic variance in different components like plant breeding and animal genetics. Though the analysis suffered a major drawback and criticism on validating the usefulness of its applicability, researchers use diallel design to evaluate the indispensability of the mating pattern taken for consideration (Griffing 1956).

The diallel mating design generally estimates the variation of quantitative characters in the genetic components like assessment of plant seed quality. The estimation is also performed to deduce the combining ability of the different inbred lines which participate in the different crosses taken into consideration.

## Types of Diallel Mating Design

The diallel mating design methods can be classified as follows (Griffing 1956).

1. **Partial Diallel Design** – This is a type of diallel design where a portion of required cross is made. This means in this study design each parent is not mated with every parent in the group leading incomplete or partial genetic cross.
2. **Systematic or Progressive Mating Scheme** – In this design the crosses which are made, they generally fall in particular diagonals. The diagonals are chosen in such a way that no one parent is interfered in more than few crosses.
3. **Disconnected Diallel Scheme** – This pattern of design is characterized by the parents who are categorized into tiny groups and diallel or

half diallel matings are done within each individual group.

## Methodologies for Studying DD

Griffing (1956) and his coworkers have analyzed the DD elaborately using different models. The mating ability of a particular species is initially portrayed in a tabular form then combining abilities are identified accordingly.

Two types of combining abilities are present:

### 1. General Combining Ability (GCA)

The ability of the inbred line is the mean performance of the hybrids that this line reproduces with other lines chosen from a random mating population. It is estimated from half-sib families.

### 2. Specific Combining Ability (SCA)

This refers to a pair of inbred lines which are involved in a cross. In this cases certain combinations might do relatively better or inferior than would be predicted on the basis of GCA effects on two lines involved in the study. It is generally deviation of a particular cross from the expectation on the basis of average GCA effects of the two lines involved. It is equivalent to an interaction result of a factorial experiment (Falconer and Mackay 1996; Acquah 2012).

## Diallel Design Analysis

According to Griffing (1956) there are four different methods for diallel design based on whether the parents, their reciprocal F1 crosses, or both, are included in the evaluation with the F1 crosses:

**Method I or Full Diallel Design:** The method I or full diallel design consisted by parents, one set of F1's and reciprocal F1's. The system gives  $n^2$  genotypes (Griffing 1956).

**Method II:** This method encompasses parents and one set of F1's without reciprocal F1's. This design gives  $n(n+1)/2$  genotypes.

**Method III:** Here, one set of F1's and the reciprocals are investigated. This design provides



the equation  $a = n(n - 1)$  different number of genotypes.

**Method IV:** Here, it only includes F1 crosses. This design provides the equation  $a = n(n - 1)/2$  different number of genotypes.

## Application

- The DD study estimates the genetic makeup of variation of a quantitative character.
- It also estimates the combining efficacies of different inbred lines involved in the cross.
- A random model involves parents that are random members of a random mating population.
- A random model is useful for estimating GCA and SCA variances. These effects only apply to the set of parents in the diallel.
- It is also widely used for developing breeding populations for recurrent selection (Acquaah 2012). In addition, Johnson and King (1998) reported that diallel mating designs are deployed to provide the maximum opportunity to manage coancestry in breeding population and maximize selection differential.

## Drawbacks

- The diallel design is the most mislead of all mating designs as acquired from various genetic information (Hallauer et al. 2010). Much of its limitation might be due to the presence of two models for its analysis, i.e., one is random and other is fixed (Griffing 1956).
- In reality, a diallel design with self and reciprocals is neither practical nor it is sustainable for utility.
- In extensive mating patterns, the number of parents that can be bred this way is limited (Johnson and King 1998).

## Concluding Remarks

These kinds of experimental studies may not provide a conclusive statement on the effects of non-independent distribution of gene patterns in the parents. The diallel mating design should only be

used to evaluate genetic variance components when the parents of the diallel have been randomly selected from a population subjected to linkage equilibrium.

## Cross-References

- [Combining Ability](#)
- [Diallel Design](#)
- [Twin Study Method](#)

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## Dian Fossey

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## Introduction

Dian Fossey (January 16, 1932, to December 26, 1985) was an American primatologist who dedicated her career to studying and conserving

mountain gorillas (*Gorilla beringei ssp. beringei*). In 1967, she established a research site at Karisoke in the Virunga Mountains of Rwanda to study mountain gorillas. Karisoke is currently the longest running field study of wild gorillas and internationally recognized for its scientific outputs and conservation efforts.

## Early Years

During her first trip to Africa in 1963, Fossey visited Olduvai Gorge and met Louis Leakey. Leakey's descriptions of Jane Goodall's pioneering studies of wild chimpanzees at Gombe intrigued Fossey and left a lasting impression. From Olduvai, Fossey traveled to the site where George Schaller had conducted a study of mountain gorillas at Mt. Mikeno in Democratic Republic Congo (then Zaire). In 1966, Fossey returned to Africa and traveled to Mt. Mikeno with the aim of establishing a research project focused on mountain gorillas. She would eventually identify and habituate several groups of gorillas in the Kabara Region. Fossey was also making progress documenting the behavior of the mountain gorillas when she was evacuated to Uganda due to political unrest in Congo. Not to be deterred from her study of mountain gorillas, Fossey would establish the Karisoke Research Center in the Rwandan portion of the Virunga Mountains in 1967.

## Research Contributions

Fossey obtained her doctoral degree in animal behavior from Cambridge University under the supervision of Dr. Robert Hinde (Fossey 1976) and would make several seminal contributions to understanding gorilla behavior and ecology throughout her academic career. She published many of the first reports of mountain gorilla behavior, including descriptions of their ranging (Fossey 1974), reproduction (Fossey 1982), vocalizations (Fossey 1972), feeding (Fossey and Harcourt 1977), male emigration and female transfer (Harcourt et al. 1976), and ontogeny

(Fossey 1979). Many of these publications continue to be relevant and are cited by current publications. Through her popular writings, she was very effective in sharing the rich social lives and individual personalities of the mountain gorillas with not only the academic community but to a large public audience. Fossey was a visiting associate professor at Cornell University while writing a book entitled "*Gorillas in the Mist*" (Fossey 1983) which remains one of the most widely read books about gorilla behavior. This book provides remarkable insights not only into the daily lives of mountain gorillas but also a riveting first-hand account of the challenging field research conditions and conservation context in which Fossey worked.

## Conservation

Throughout her 20 years studying gorillas in the wild, Fossey was increasingly confronted by the myriad of threats to gorilla survival. The impacts of poaching, the pet trade, and habitat destruction were devastating gorilla populations in the Virunga Mountains and beyond (Harcourt and Fossey 1981). Fossey was outspoken in her conservation efforts, but her "active conservation" tactics were controversial and often aggressive to local people. In December 1977, a male gorilla named "Digit" who Fossey had known for many years was killed by poachers when defending his group. He was speared several times before succumbing to his wounds, which provided time for his family group to flee. This would prompt Fossey to launch the "Digit Fund" to raise funds for conservation and antipoaching efforts in the region. The Digit Fund would later be renamed the Dian Fossey Gorilla Fund International.

## Conclusion

Dian Fossey's murder shocked the world and the identity of her assailant still remains unknown. Although her personal contributions were cut short by an untimely death, there is no doubt that

her research and conservation efforts have had a lasting impact on generations of aspiring scientists and improve the survival prospects of wild apes. The Karisoke Research Center is internationally renowned for its research and continued vigilance of the dwindling numbers of mountain gorillas in the Virungas. The Dian Fossey Gorilla Fund International has been extremely successful in raising awareness about the plight of wild gorillas and also supports the conservation of many populations of wild gorillas.

## Cross-References

- [Bushmeat Trade](#)
- [Home Range](#)
- [Jane Goodall](#)
- [Observational Methods](#)
- [Robert Hinde](#)

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## Diaspora

- [Migration](#)

## Diathesis Stress

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## Definition

The diathesis stress is a psychological theory which relates diathesis (susceptibility) and stress in order to develop psychopathological disorder.

## Stress

Stress is a psychological state marked by imbalance in the psych functioning of mind resulting from “unfavorable” or “not desirable” circumstances. Stress is linked to several psychopathological disorders and even considered as a major etiological factor for their occurrence. Different models have been suggested which aim to draw the relationship between the stress level and occurrence and degree of the disorder, which also depends on the individual’s psychological and biological characteristics. The majority of individuals suffering from depression must have been the victim of severe stress in the immediate past, where as some individuals after facing extreme stress do not show any trait of depression.

Some people who have experienced the stress but do not develop a disorder suggest that susceptibility is an important component of psychopathology.

## Diathesis

The terms “diathesis and susceptibility” are used interchangeably, which mean predisposed factors making an individual susceptible to the

development of disorder. The factors could be biological or psychological.

Ingram et al. (1998) suggested that diathesis is a trait which is *stable* but can change, and is usually latent and *endogenous* to the individual.

- Stability does not mean permanence, as the concept of therapy is sprouted from the possibility that positive alteration in a stable variable may occur and revert to the normal condition.
- Endogenous to the person means whether arising due to biological or psychological factors, but resides within the person. So this differentiates diathesis from external factors such as stress. But it may require some sort of activation (external factor; stress) to develop the disordered state, pointing to the feature of latency.

## Diathesis Stress Models

### Dichotomous Diathesis Model

Dichotomous diathesis describes that if there is no diathesis, not even severe stress can lead to the development of the disorder whereas, when it is present, occurrence of disorder depends on the level of stress (Fig. 1).

### Quasi-Continuous Diathesis Model

In this model, it is said that once the threshold for diathesis is crossed, the continuous effect of diathesis is seen, thus it is called as quasi-continuous, though minimal level of diathesis may not result in the disorder even after facing high stress.

### Threshold Model

The synergistic effect of diathesis and stress results in an effect beyond their combined separate effects, which is termed as threshold model.

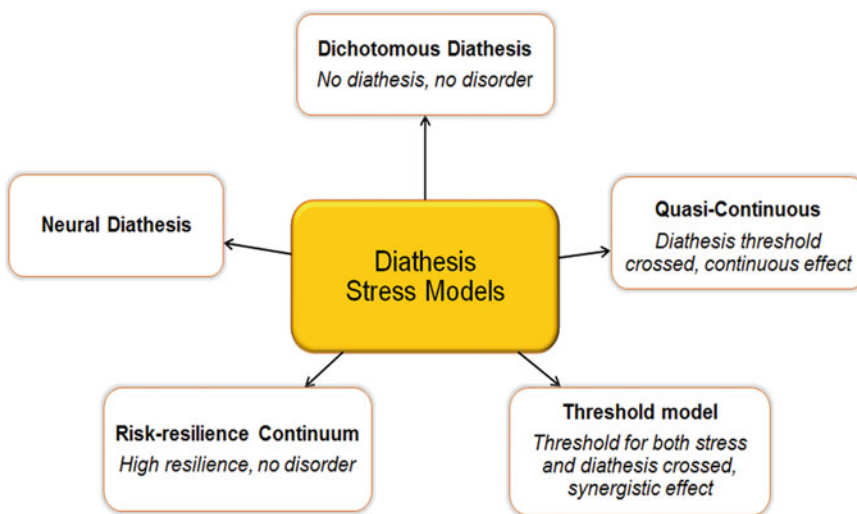
With the increase in the intensity of the trauma, the risk for psychopathology also aggravates. So, the threshold which decides the occurrence of the disorder is different for every individual (Monroe and Simons 1991).

### Risk-Resilience Continuum Model

Invulnerability, competence, protective factors, and resilience are considered to be antonyms of diathesis or susceptibility. These are the factors which enhance the resistance to the stressors. They may include personality traits, social skills, environment, and coping style.

### Schizophrenia: A Neural Diathesis-Stress Model

This model mainly proposes that stress affecting the neural system may lead to the onset and/or



**Diathesis Stress, Fig. 1** Different proposed Diathesis-models

worsen the symptoms of schizophrenia in susceptible individuals.

Schizophrenia is a serious neurodevelopmental disorder in which the person has the difficulty in distinguishing real and virtual world. Stress and schizophrenia have been linked since many years. Stress responsivity in schizophrenic individuals is addressed at two levels:

1. Behavioral
2. Biological

#### Behavioral Response

The occurrence of stressful events contributes in worsening of schizophrenic symptoms, suggesting a relationship between the two. The exposure to stressors can exacerbate premorbid behavioral dysfunction or may fasten the onset of first episode of psychosis (FEP).

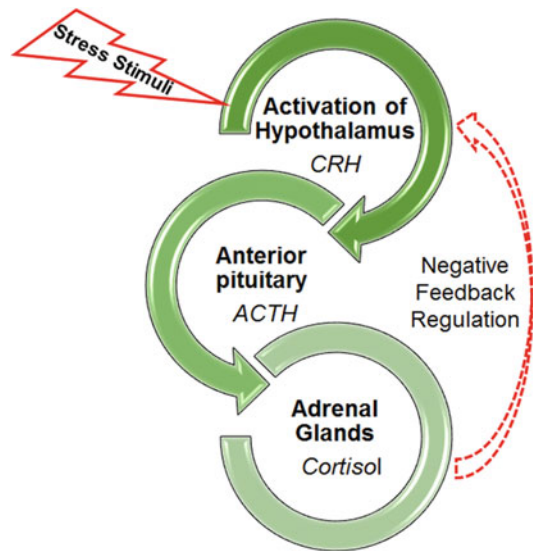
Children with high risks for schizophrenia (parents are schizophrenic) show greater behavioral dysfunction, if parenting has not been proper in their developing days. The adoption studies have revealed that the amplitude of worsened schizophrenic symptoms increased in the biological offspring of schizophrenic parents whose upbringing is done in dysfunctional adoptive family (Tienari 1991).

The above findings focus on the effects of psychosocial stressors on the symptoms of schizophrenia, but there is an interactive effect of stressors and susceptibility. High-risk children (high diathesis) are susceptible to manifest the disorder than the controls on exposure to parental maltreatment. The probability of occurrence of schizophrenia is increased in offspring of women who have experienced severely stressed events (e.g., death of a spouse during pregnancy) (Huttunen 1989). These events interfere with normal functioning of the HPA (Hypothalamic-Pituitary-Adrenal) axis which results in the impairment of neurological system.

#### Biological Response

##### 1. *The HPA Axis*

There are various neurological systems which can be activated by the stressful events, but significant among them are the



**Diathesis Stress, Fig. 2** The schematic diagram of (Hypothalamic-Pituitary-Adrenal) HPA axis

sympathoadrenal medullary system (SAM) and HPA axis (Fig. 2) (Joëls and Baram 2009), which release some secretagogues (neurotransmitters, enzymes, and hormones) that help in maintaining homeostasis and have the ability to alter brain function.

The periventricular nucleus of the hypothalamus releases CRH (corticotropin releasing hormone) under the influence of stressful stimuli which in turn stimulates the pituitary to release ACTH (adrenocorticotropin releasing hormone). This activates the adrenal glands to release glucocorticoids, cortisol being the prominent one in primates and corticosterone in rodents. Brain has the receptors for glucocorticoids, which regulates the levels of these hormones through negative-feedback check. The levels of glucocorticoids need to be maintained, their hypersecretion or poor negative feedback regulation can affect the brain functions and behavior adversely. The presence of CRH receptors in the cortical region of the brain, which includes locus coeruleus, the periventricular nucleus of the hypothalamus, the bed nucleus of the stria terminalis (BNST), and the central nucleus of the amygdala, can lead to free-forward activation resulting in allostasis.

The effects of exposure to stressors can be addressed by measuring the glucocorticoids in cerebrospinal fluid (CSF) plasma, urine, or saliva. The HPA axis function is examined using two indices among psychotic patients and high-risk individuals:

- I. Baseline cortisol
- II. The cortisol awakening response

#### *Baseline Cortisol*

The term “baseline” refers to the initial measurement of a variable in the absence of any exposure. Recent studies indicated elevated plasma/serum cortisol levels among people experiencing the first episode of psychosis (FEP) (Dogan Bulut et al. 2016).

#### *The Cortisol Awakening Response (CAR)*

It is an increase in the cortisol levels which occurs after awakening in the morning in some people. The reason is not known, but it might be linked to the preparation of the HPA axis. Though no strong finding has been reported till now, but in some cases, a blunted CAR among FEP has been observed (Mondelli et al. 2010).

Genetic and environmental (stressors) factors both act in isolation or synergistically in dysregulation of the HPA axis. For example, serotonin transporter gene (Caspi et al. 2010), FKBP5 gene (Klengel et al. 2013), and the glucocorticoid receptor gene (also called

NR3C1) are involved in modulation of the HPA axis following stressful events.

## 2. *Structural Abnormalities*

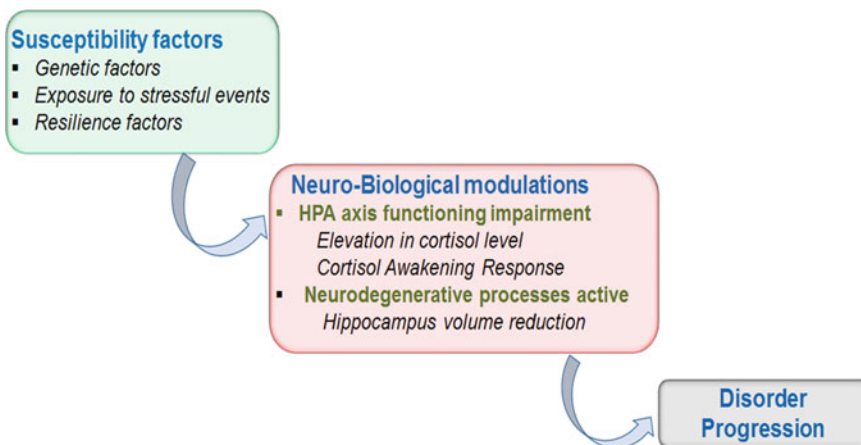
### *Hippocampus Abnormalities in Schizophrenia*

The volume of hippocampal region is reduced in schizophrenic patients, suggesting the dysfunctioning of the HPA axis.

## 3. *Dopamine Activity*

An increase in dopamine (DA) release and synthesis have been observed in psychotic patients in response to stressors (Howes et al. 2012). Dopamine has been positively related with worsening of symptoms (hallucinations and delusions) and possibility of relapse in psychosis. The varying magnitude of stress modulates the HPA axis, resulting in the cortisol release which in turn enhances the DA receptor densities as well as DA release. This suggests that it can also be viewed as a moderator of the expression of the diathesis.

To summarize, the degree of the association between diathesis and psychiatric outcome may alter on the basis of the varying level of the HPA axis activation or sensitization. Thus neural diathesis-stress model (Fig. 3) focuses on both diathesis as one factor and biological and behavioral changes due to stress as another factor.



**Diathesis Stress, Fig. 3** The neural diathesis-stress model



## Conclusion

The several diathesis models aim to draw the relationship between the external stressor and the individual which actually varies according to the person and the degree of stress. The individual who is vulnerable is more prone to develop the disorder than the control one. Not only external factors play a role in the onset of psychotic symptoms, but also the neurological system leads a pivotal role. The neural diathesis-model of schizophrenia proposes that stress, through the effect of cortisol production which further affects downstream processes, in turn, results in developing or worsening of psychopathological symptoms. But susceptibility or diatheses is an important etiological factor in the development of the disorder.

## Cross-References

- ▶ [Amygdala](#)
- ▶ [Coping Style](#)
- ▶ [Corticosterone](#)
- ▶ [Death](#)
- ▶ [Dopamine Receptor](#)
- ▶ [Hippocampus](#)
- ▶ [Homeostasis](#)
- ▶ [Hypothalamus](#)
- ▶ [Neurotransmitters](#)
- ▶ [Nucleus](#)
- ▶ [Parenting](#)
- ▶ [Sensitization](#)
- ▶ [Serotonin](#)
- ▶ [Stress](#)

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## Dichotomous Stress

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## Synonyms

[Stress dichotomy](#)

## Definition

Dichotomous stress represents bidirectional effect (+/–) of stress in various biophysical and biochemical responses and thus the behavioral outcome of an animal under the presence of stressors.

## Introduction

Mechanism of homeostasis is the key by which an organism maintains its integrity, i.e., it helps in maintaining the constant internal milieu irrespective of variant environmental influences (Goldstein 2013). Firstly, used by Selye, H., in 1956, the word “Stress” describes the physiological condition of an organism in presence of stressors (element causing the threat to homeostasis, can either be the psychosocial or the physical agent) leading to functional outcome termed as “Stress Response” (Selye 1956). Three major neuroendocrine systems which majorly mediate components of stress response are Hypothalamus-Pituitary Axis (HPA axis), Sympathomedullary Axis, and several other modulatory peptides like, Orexin-A, Ghrelin, etc.

Under different conditions of stress and respective physiological and psychological status of the subject, different patterns of biological responses are displayed by the animals termed as, “Situational Stereotypy.” Based on the severity of situations animals tend to choose from two states of responses whether it be, “Aversive Vigilance” or the “Active Coping.” Numerous studies on animal models have shown that different individuals behave differently in presence of stressors and this has been linked to the differences in their genetic makeup, defined under a term “Response Stereotypy” (Lacey and Lacey 1958; Lacey 1967). Heritability ( $h^2$ ) considering role of both the environment as well as genetic makeup of an organism defines well the stereotypy in behavior shown by the individuals.

Stress responses are just not unidirectional when linked with their net outcome, whether as behavioral changes (eating behavior), psychopathologies (suicidal tendency), or the degenerative pathologies (anovulation, muscular atrophies, etc.). Stress dichotomy represents the duality shown by stress whether by the different scales of stress or due to the interaction between stress and the preexisting internal status of an organism, biophysically, biochemically, as well as psychologically.

## Obesity and the Stress Dichotomy

Stress has the dichotomous effect on the energy balance of the body. Adaptive thermogenesis and Brown Adipose Tissues (BAT) supports the dual nature of stress, explaining its effect, considering obesity versus weight loss/obesity resistance. In presence of chronic stress, individuals have different outcomes, stress-induced obesity has been shown linked with the interaction of stress-hyperphagia-unchanged BAT, while considering obesity resistance the stress-hypophagia/hyperphagia + BAT recruitment-enhanced thermogenesis is inferred. This duality in nature of stress considering physiological conditions of an animal presents the inferences explaining the interaction between psychological/physical stress with the physiological involvement of moieties. Semantically psychogenic and metabolic stressors are different but they present themselves as two sides of the same coin (Bartolomucci and Razzoli 2016).

Little stress has been observed to engender a compensatory increase in appetite, but the severe stress has usually been studied resulting, anorexia. This represents the dual nature of an acute stress for the behavioral outcome on the basis of stress's severity (Yau and Potenza 2013).

## Acute Stress Responses Versus Chronic Stress Response

Acute stress leads to responses which are adaptive in nature, but with repeated/continuous facing of an acute stress, the stress responses will become maladaptive. In the acute stress conditions, stress hormones promote the dispersal of an energy store for their immediate use, site-specific allocation of the energy and activation of immune system thus helps to maintain an internal milieu. In the case of chronic stress, e.g., chronic sympathetic nervous system (SNS) activation leads to vascular hypertrophy and thus chronic rise in blood pressure (Schneiderman et al. 2005). Further elevated basal levels of stress hormones associated with chronic stress does suppress the immunity by directly affecting cytokine profiles; an increase in Th2 cytokines relative to Th1 cytokines

suppressing cellular immunity in favor of humoral immunity, Segerstrom and Miller, found that pro-inflammatory, Th1 and Th2 cytokines become dysregulated under chronic stress leading suppression of both humoral and cellular immunity (Segerstrom and Miller 2004).

## Conclusion

The dichotomous behavior of stress, in particular towards obesity, provides us with the general idea of how the psychogenic and physical stressors differentially interact with individual's physiological milieu leading to variant stress responses and behavioral outcomes/phenotypic variations. Though not yet well explored, the dichotomy in stress is required to be dealt through well explanatory electrophysiological experimentation in animals and neuroimaging studies in animals/humans for acute as well as longitudinally for the chronic stress-induced behavioral changes, psychopathologies, or the degenerative pathological conditions.

## Cross-References

- [Stress](#)
- [Vertebrate Nervous System](#)

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## Dictator Game

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## Synonyms

[Prosocial choice test](#)

## Definition

The dictator game is a paradigm used in behavioral economics where an actor (sometimes labeled as donor) has the power to distribute a predetermined set of rewards among themselves and at least one recipient. Typically, the actor's choices are identical but the recipient either receives an identical reward or no reward. Unlike the ultimatum game, the recipient has no choice regarding receipt of the allocated reward.

## Introduction

Humans are unique for the extent to which they engage in prosocial behaviors that benefit others, including nonkin, at some cost to themselves (de Waal and Suchak 2010). The dictator game is a well-known tool for assessing prosocial preferences in humans (Kahneman et al. 1986; Forsythe et al. 1994). It was first adopted for use with nonhuman primates when Silk et al. (2005) presented captive chimpanzees with the

opportunity to choose between two food rewards in what has become known as the “prosocial choice task.” Each choice for the actor simultaneously delivered one of two reward options for a recipient; either the recipient received no reward (1/0) or a reward equivalent to that of the actor (1/1). This became known as the 1/1, 1/0 distribution with the first number within each pairing representing the option for the actor and the second number representing the option for the recipient.

The paradigm has been widely adopted for use with young children and various other primate species (Burkart and Rueth 2013; Claidière et al. 2015; Cronin 2012; House et al. 2012; Messer et al. 2017; Vonk et al. 2020), and even non-primates (e.g., bottlenose dolphins, Nakahara et al. 2017; domestic dogs, Dale et al. 2016; jackdaws, Schwab et al. 2012; Long-Evans rats, Hernandez-Lllement et al. 2015) with various other reward distributions being presented. It is still most commonly used with primates. The paradigm allows investigators to assess which species behave prosocially when there is little cost to themselves for doing so. That is, they receive the same reward regardless of their choice and effort, but with a little more attention, they can choose to be generous rather than selfish.

In the original version, chimpanzees pulled one of two food trays toward themselves, which simultaneously caused an attached food tray to move away from the actor toward the recipient housed in another enclosure and facing the actor (Silk et al. 2005). In a follow-up study, a bar-pull apparatus was instead used so that actor chimpanzees could choose a top or bottom tray to pull, which distributed food to themselves and a recipient housed in an adjacent (rather than opposing) enclosure. Importantly, “no recipient” trials were interspersed with “recipient” trials to provide a comparison of “prosocial” choices when there was a recipient to benefit and when there was not. This manipulation allowed experimenters to differentiate between ostensive prosocial behavior that was not motivated by prosocial concerns because the actor could simply be demonstrating a bias to choose the option that contained the greater amount of food, possibly without the

realization that the reward earmarked for the recipient was inaccessible. Unfortunately, not all studies using the dictator game have implemented a “no recipient” condition, but it is critical to understanding the underlying motivations of the subjects.

In most dictator game studies with nonhumans, the actor and recipient exchange roles over the course of the study so that researchers can keep track of whether they tend to exchange rewards more frequently with individuals that behave prosocially towards them. This can be done in a “contingent choice” protocol where the actor and recipient trade roles on each trial (Brosnan et al. 2009), but this is more challenging to implement. Brosnan and colleagues found no evidence that chimpanzees behaved reciprocally in such a setup. Yamamoto and Tanaka (2010) obtained similar null results even when testing mothers and offspring. Of course, it is possible that chimpanzees reciprocate across other contexts outside of the experiment, as in allogrooming and tolerated theft. A review of prosocial choice tests in primates revealed that primates tended to attend to dominance relations although some species shared up the hierarchy whereas others tended to share down the hierarchy (Cronin 2012).

Initially, results of the tests suggested that non-human primates were not predisposed to behave prosocially. Although they seemed largely unconcerned with whether recipients received rewards even when recipients protested loudly and begged for food (Silk et al. 2005; Vonk et al. 2008), chimpanzees did not appear to behave spitefully by choosing to remove food rewards from recipients when given the opportunity to do so (Jensen et al. 2006). In these studies, chimpanzees appeared sensitive only to their own rewards. They appeared indifferent to outcomes that either benefited or were detrimental to conspecifics. However, studies began to reveal some suggestive evidence for prosocial motivations in other primates (long-tailed macaques, Massen et al. 2011), especially cooperative breeding primates, such as common marmosets (Burkart et al. 2007) and brown capuchins (Brosnan et al. 2009; Claidière et al. 2015; de Waal et al. 2008; Lakshminarayanan and Santos 2008; Suchak and

de Waal 2012; Takimoto et al. 2010). Capuchins behaved prosocially specifically when there was no reward for themselves and their choices determined only whether a recipient would receive a reward or not using a 0/1, 0/0 distribution (Lakshminarayanan and Santos 2008). On the other hand, tamarins have not always behaved prosocially (Cronin et al. 2009). Even chimpanzees appeared more likely to distribute rewards to recipients when they could not view the food rewards (Horner et al. 2011) and when tokens were presented to represent food choices rather than having actors directly work to procure the food. However, obscuring the visibility of the food and allowing actors to consume their own rewards before making an additional decision to offer a reward to a conspecific did not result in prosocial behaviors in an “extinction task” variant. In fact, chimpanzees declined to make the “prosocial” response more quickly when recipients were present versus absent (Vonk et al. 2008). It is important to note that the lack of prosocial choices in prosocial choice tests occurs even when actors and recipients are close associates and engage in otherwise affiliative behaviors, such as allogrooming. Therefore, it has been difficult to identify consistent factors predicting prosocial responses in prosocial choice tests.

Follow-ups to the original studies manipulated the quality and amount of the available rewards, asking whether actors could distinguish between preferred and less preferred rewards. Importantly, some studies manipulated the status of the recipient although it would be most important to demonstrate that actors attended to need states such that they were more generous to those that could most benefit from their actions (Liebal et al. 2014). Fewer studies have focused on the relationships between actors and recipients in these studies. Mendonca et al. (2018) tested mother-offspring chimpanzee dyads using a touchscreen version of the task and five of these six chimpanzee mothers made prosocial choices. However, another study failed to find evidence of prosocial food choices between mother and offspring chimpanzees (Yamamoto and Tanaka 2010). Another exception allowed a female orangutan to behave prosocially toward her sister or her

mother or to both simultaneously using tokens that represented various options (Emigh et al. 2020). The orangutan appeared to choose differently depending on who was able to benefit from her choices, and often behaved prosocially. Unfortunately, due to constraints in the testing environment, the “no recipient” condition was not presented to clarify the motivations for her choices or her comprehension of the options.

It is interesting, however, that orangutans, deemed the least socially oriented of the great apes, have demonstrated prosocial preferences in other studies (Amici et al. 2014b) whereas the more gregarious chimpanzees, gorillas, and bonobos have not typically behaved in a prosocial manner (Amici et al. 2014a; Tan et al. 2015). Of course, orangutans have not always behaved prosocially in such studies either (Kim et al. 2015). Furthermore, bonobos and chimpanzees have demonstrated somewhat inconsistent preferences across studies (Amici et al. 2014a, 2014b; Liebal et al. 2014; Pelé et al. 2009; Tan and Hare 2013; Tan et al. 2015). It is recognized that the dictator game may not be the “acid test” of prosocial preferences in nonhumans (Marshall-Pescini et al. 2016), with the escape and instrumental helping paradigms potentially more likely to elicit demonstrations of concern for others’ welfare. Sometimes subtle aspects of the testing methodology appear to influence the pattern of results (Dale et al. 2016), making it yet unknown the exact mechanisms that control choices in such tasks.

## Conclusion

The dictator game has proven to be an incredibly useful and flexible tool for probing prosocial preferences, particularly in primates, at least within the context of food provision. Despite some challenges with the methodology, the task has provided a framework for exploring prosociality in nonhumans – a topic that was once considered unworthy of study due to the belief that prosocial preferences were unique to humans. Since its extension to nonhuman primates (Silk et al. 2005), comparative research into prosocial



preferences has exploded. Although the prosocial choice task has been extended for use in other species, its utility has not been fully exhausted.

## Cross-References

- [Altruism](#)
- [Prosociality](#)
- [Ultimatum Game](#)

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## Dictator's Game

### ► Ultimatum Game

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## Diel Activity

### ► Cathemeral

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## Difference

### ► Oddity Learning in the Rat

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## Difference of Form

### ► Morphology

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## Differential Reinforcement of Other Behavior

### ► Punishment

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## Differential Splicing

### ► Alternative Splicing

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## Differentiation of a Response

### ► Shaping

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## Diffusion

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## Synonyms

Dispersal; Spreading

## Definition

**Diffusion** is derived from the word of *Latin* origin, *diffundere*, meaning “to spread way out.” It is a physical process involving the net movement of molecules (solute) from a region of its high concentration to lower concentration. The process whereby the spontaneous movement of the particles of liquids, gases, or solids causes them to intermingle and spread uniformly throughout a region of higher concentration to one of lower concentration. It can involve either the spreading of a material through a medium or the transport of a particle across a membrane.

## Explanation of Diffusion in the Context of Different Disciplines

The concept of diffusion is widely used in: physics, chemistry, biology, sociology, economics, and finance (diffusion of people, ideas, and of price values). However, in each one of them, the object

(e.g., atom, idea, etc.) that is undergoing diffusion is “spreading out” from a point or location at which there is a higher concentration of that object to the region where it is in low concentration.

There are two ways to introduce the notion of *diffusion*: either a phenomenological approach starting with Fick’s laws of diffusion and their mathematical consequences, or a physical and atomistic one, by considering the *random walk of the diffusing particles*.

In the phenomenological approach, according to Fick’s laws, *diffusion is the movement of a substance from a region of high concentration to a region of low concentration without bulk motion* (Philibert 2009).

From the *atomistic point of view*, diffusion is considered as a result of the random walk of the diffusing particles. In molecular diffusion, the moving molecules are self-propelled by thermal energy. Random walk of small particles in suspension in a fluid was discovered in 1827 by Robert Brown. The theory of the Brownian motion and the atomistic backgrounds of diffusion were developed by Albert Einstein (Mehrer and Stolwijk 2005).

## Aim of Diffusion

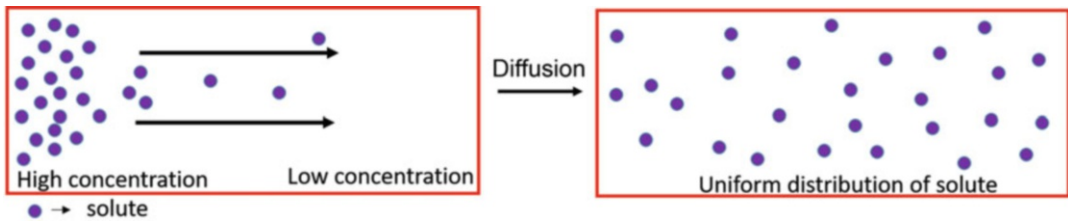
Diffusion occurs with the aim of reaching to a state of equilibrium. Equilibrium is when the amount of the particles is the same throughout a solution or is dispersed equally through a given area.

## Factors that Affect Diffusion

Diffusion is altered by the temperature, distance travelled, area of interaction, and particle size. Each of these factors, independently and collectively, can change the extent and rate of diffusion.

## Temperature

In any system, particles are moving with a certain amount of kinetic energy. This movement of molecules can appear random. It is usually not directed in any particular manner. When these particles collide with one another, there is a



change in the direction of their movement as well as momentum and velocity. With an increase in temperature, the kinetic energy of all particles in the system increases. This increases the rate at which all the molecules (both solute and solvent) move, increases their collisions with one another, thus, increasing their diffusion rate.

### Area of Interaction

Increase in the area of interaction increases the rate of diffusion. For example, this factor can be observed even better if the gas has an odor or color. When they are confined to the smaller surface area within the crucible, the rate of diffusion remains low as compared to when they are in larger surface area, indicating that molecules diffuse better when the area of interaction increases.

### Particle Size

Depending on the mass of the molecules and its surface area, at any given temperature, the diffusion of a smaller particle will be more rapid than that of a larger-sized molecule. A heavier molecule with a larger surface area will diffuse slowly, while smaller and lighter particles will diffuse more quickly.

### Role of Diffusion

Diffusion is an important part of many biological and chemical processes. In biological systems, diffusion occurs at every moment, across lipid bilayer membranes in every cell as well as through the body. Some examples are given below:

1. Gaseous Exchange: Respiration produces waste carbon dioxide, causing the amount of carbon dioxide to increase in the cell such that eventually

its concentration in the cell is higher than that in the surrounding blood. The carbon dioxide then diffuses out through the cell membrane and into the blood (Spaeth and Friedlander 1967).

2. Nerve Impulses: Neurons communicate with other cells by sending electrical signals along their cell membrane. At rest, the inside of the neuron's membrane is negatively charged, while the outside is positively charged. An electrical signal is generated when the membrane lets ions from outside flow into the cell. This inflow changes the charge on the inside of the membrane from negative to positive. This switch in charge is an electrical signal that moves down the length of a neuron's arm. The movement of ions is guided by diffusion (Bromberg and Dill 2002).
3. Olfaction: The chemical senses of olfaction and taste such as the detection of hazards, pheromones, and food are very different from vision and hearing, which detect the energy of different wavelengths in the form of light and sound. Chemical senses rely on the physical movement of molecules from the signaler to the sense organ of the receiving animal. This requires either diffusion or flow of currents (Wyatt 2014).
4. Digestion: Diffusion helps in the absorption of digested food materials in the alimentary canal. End products of digestion such as amino acids and glucose diffuse through facilitated diffusion with the help of transporters across the wall of the ileum into the blood for transport to other parts of the animal body.

### Conclusion

Diffusion in the animal body is necessary as it is a feature of number of processes which control and

supply vital substances to the body in order for basic survival. As already noted above, it is important for the absorption of digested nutrients, gas exchange, and the propagation of nerve impulses, the movement of hormones, and other metabolites towards their target organ and for nearly every event in embryonic development.

## Cross-References

- [Digestive System](#)
- [Lipid](#)
- [Neural Impulse](#)
- [Neuron](#)

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## Diffusion Studies

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## Synonyms

[Social diffusion](#); [Experimental social learning](#);  
[Experimental cultural diffusion](#)

## Definition

Experimentally controlled innovations in behavior are seeded into groups of individuals, and the spread (or otherwise) of the innovation is tracked and documented (Whiten and Mesoudi 2008).

## Introduction

One of the most famous examples of a new behavior spreading through a group of animals is undoubtedly the case of tits in England opening milk bottle left on doorsteps. The first reports came in around 1921 in the south of England that tits would flip or pierce open the aluminum cap of milk bottle to drink the cream on top. Many years later this behavior was reported all over England, Wales, Scotland, and continental Europe, in multiple species of birds (Fisher and Hinde 1949; Lefebvre 1995; Aplin 2013b). Another famous example of the diffusion of a novel behavior is the potato and wheat washing of Japanese macaques living on an island off the coast of south-east Japan. Researchers fed the monkeys with sweet potatoes on a beach of the island regularly to habituate them to human presence and to observe them more readily. A young female started to wash sand-covered sweet potato pieces in a stream on the beach before eating them. In this case too, several years later, what had started as the spontaneous behavior of a young female had spread widely within the group (Kawai 1965; Hirata et al. 1987). Regardless of the mechanisms involved in their spread – and the debates taking place among scientists about them – these novel behaviors were adopted by new individuals through specific pathways. In other words, the diffusion patterns of these behaviors were nonrandom.

The spread and persistence of these behaviors in local populations, as well as the manifestation of variation across individuals in their performance, indicated that animals could display elements of culture and tradition (Whiten and van Schaik 2007; Hoppitt and Laland 2008; Galef 2012). Since these seminal studies, an overwhelming amount of research in a great variety

of taxa has shown that animals can acquire and use novel information to modify their behavior and guide their decisions pertaining to exploiting their environment, be it social or ecological (Laland 2004; Kendal et al. 2005; Galef 2012; Hoppitt and Laland 2013; Whiten et al. 2016). This capability is often called social learning, as opposed to asocial learning, which relies on trial-and-error learning or self-exploration and experimentation of the surrounding environment. More broadly, the behaviors learned from conspecifics are said to be transmitted socially.

A fundamental development in the field of animal social learning involves diffusion studies, which aim to characterize diffusion patterns of socially transmitted behaviors within a group or aggregation of individuals (Whiten and Mesoudi 2008; Whiten et al. 2016; Duboscq et al. 2016). Typically, diffusion studies are experimental: new behaviors – “controlled innovations” – are seeded into groups of naïve individuals, for instance, an individual model is made to learn a new behavior, and other individuals are given opportunities to observe her performing the new behavior. Innovations can also be observed spontaneously in wild animals, and long-term field studies have allowed researchers to track the diffusion of novel behaviors over generations of animals and in multiple contexts (mating, foraging, social). The aim is then to track the progressive acquisition of the new behavior in terms of pathways (from whom to whom), speed, or accuracy while investigating the characteristics of individuals/pairs/groups involved as compared to controls or variants (Whiten and Mesoudi 2008; Whiten et al. 2016; Duboscq et al. 2016). For instance, transmission pathways can be characterized as vertical if the information is transmitted from parent to offspring, horizontal if it is from peer to peer, or oblique if it is from a non-kin adult to a young. Through this paradigm, social diffusion of novel behaviors has been linked to environmental or living conditions, individual features, and social characteristics (Morand-Ferron et al. 2010; Dukas and Ratcliffe 2009). For instance, in a feeding context, bumblebees (*Bombus impatiens*) choose the same-colored flowers as those chosen by

conspecifics (e.g., Leadbeater and Chittka 2005). In a social context, client fish (*Scolopsis bilineatus*) spend more time near cooperative cleaner fish (*Labroides dimidiatus*) than cleaner fish of unknown cooperative level (e.g., Bshary and Grutter 2006). In a breeding context, flycatchers (*Ficedula albicollis*) use others’ breeding outcomes (offspring quantity and/or quality) to select a breeding habitat (e.g., Doligez et al. 2002) (see Whiten and Mesoudi 2008; Whiten et al. 2016; Duboscq et al. 2016 for other examples).

## Social Diffusion and Environmental Conditions

Sometimes, whether or not a behavior is transmitted from an individual to another has little to do with the capacities animals have or with the task at hand. It can instead be linked to whether or not acquiring the new behavior is relevant in a given context (see below). For instance, in the wild, keas (*Nestor notabilis*) failed to perform a novel task although they had the opportunity to observe a knowledgeable individual and to engage with the experimental apparatus. In captivity however, most birds solved the task after observing a proficient model (Huber et al. 2001; Gajdon et al. 2004). Similarly, spotted hyenas (*Crocuta crocuta*) in captivity solved foraging tasks better than those in the wild (Benson-Amram et al. 2013). In contrast, a novel foraging behavior (piercing a lid to access food) spreads more quickly among groups of free-ranging urban pigeons (*Columba livia*) than among captive groups (Lefebvre 1986). In natural settings too, novel behavior might fail to percolate through a group even when opportunities for social learning exist, as seen in dental flossing in Japanese macaques, for instance (Leca et al. 2010). The lack of diffusion of a novel behavior might have to do with the value of the social information provided, the relevance of the task proposed, the degree of necessity for innovation, or social, cognitive, or physical constraints, among others (Duboscq et al. 2016; Rieucan and Giraldeau 2009; Giraldeau et al. 2002).

## Social Diffusion and Individual Features

Because each individual has its own experience and personality, numerous studies have looked at the characteristics of proficient and naïve individuals and their influence on diffusion processes. In blue tits, naïve young females and subordinate males with higher problem-solving abilities were more likely to solve the novel task than others, showing that sex, age, and personality are important factors for acquiring and using social information and hence for its diffusion (Aplin et al. 2013a). Sometimes, the diffusion depends on the proficient individual's features instead: in vervet monkeys, social transmission is mostly dependent on kin relationships, i.e., it occurs vertically, from mother to offspring (van de Waal et al. 2014). But, when transmission is horizontal or oblique, individuals are also more likely to copy the new foraging technique of an adult female compared to an adult or subadult male (van de Waal et al. 2010). Similarly, monkeys do pay more visually attention to higher-ranking individuals than to lower-ranking individuals (e.g., McNelis and Boatright-Horowitz 1998; Deaner et al. 2005) and to strong affiliates compared to average affiliates (Bonnie and de Waal 2006; Micheletta and Waller 2012). This preferential attention to a particular proficient model is attached to its experience, reputation, or social tolerance (Nicol and Pope 1999; De Waal 2008; Schwab et al. 2008). Nevertheless, the best innovators, i.e., the individuals that are more likely to start using a novel behavior, are not necessarily the best models. For example, male canaries (*Serinus canaria*) were better at solving a foraging task than females, but they were also highly intolerant of other individuals in proximity, and their higher aggressive tendencies prevented them from being good models (Cadieu et al. 2010).

## Social Diffusion and Social Characteristics

Animals living in groups or aggregations do not interact randomly with one another; they have

preferred associates or affiliates. The structure of the social network of the group/aggregation – and thereby the diffusion of information between individuals – is thus heterogeneous and nonrandom (Krause et al. 2009; Croft et al. 2008). Particularly, so-called central individuals in a social network – those that are more social and/or interact with more partners than others – are seen as more influential in social diffusion processes. Social diffusion is therefore more likely to occur along “lines of affiliation” (Galef 1992). The development of network-based diffusion analysis and modeling has allowed great progress to be made in tackling underlying decision rules and transmission pathways (Franz and Nunn 2009; Hoppitt 2010) in, for instance, directed social learning, in which information is transmitted at different rates depending on association patterns between individuals (Coussi-Korbel and Fragaszy 1995). Humpback whales (*Megaptera novaeangliae*) summering in the Gulf of Maine were 6 to 23 times more likely to use the lobtail feeding technique when in association with other individuals compared to cases where there would be no or little association, which overwhelmingly supported social diffusion (Allen et al. 2013). In tits, the successful discovery of new food patches was linked to individual centrality in the flock association network: more central individuals were more likely to locate and use novel foraging patches than those with limited social connections (Aplin et al. 2012). In contrast, a simulation study showed that information spreads faster in well-mixed groups compared to more structured groups (Voelkl and Noë 2008). In structured social networks, information also spreads faster when the frequency of interactions was either disregarded (unweighted or topological networks) or distributed randomly among interacting individuals (Voelkl and Noë 2008). This shows that sociality itself has costs and benefits regarding information diffusion: on the one hand, being social greatly enhances one's potential to adapt faster and/or better to its environment; on the other hand, it might also either exclude individuals from innovation or induce individuals to adopt nonadaptive behavior by getting little or incorrect information.



## Other Fields of Diffusion Studies

Other fields have used diffusion studies to track transmission patterns and pathways, notably epidemiology and health but also cognition. A diffusion model paradigm has recently been applied to a wide range of cognitive processes related to decision-making (Ratcliff 2016), social perception (Parkinson et al. 2017), and neuron connectivity (Basset and Mattar 2017). In the latter field, so-called functional brain networks or structural brain networks can be built by considering connections between brain regions, either through, e.g., their functional connectivity or through, e.g., white matter tracts. Both network types can then be used in the investigation of intrinsic and task-evoked neurophysiological processes or baseline function and its adaptability in response to task demands, for example (Basset and Mattar 2017).

In epidemiological studies, the equation computing the diffusion patterns of socially transmitted parasites and pathogens among hosts has recently incorporated the chance that a contact opportunity between hosts occurs. This parameter takes into account with whom each individual is in contact as well as how frequently and is given by a network of contacts or proximities or space/resource sharing (Godfrey 2013; Craft 2015; Schmidt-Hempel 2017). Network epidemiology thus uses social patterns to infer potential transmission routes and can provide key insights into how parasites spread through a host population (Rushmore et al. 2017). In Japanese macaques, *Macaca fuscata*, high-ranking adult females, which were also more central in their social network, showed higher fecal gastrointestinal parasite egg counts than lower-ranking less central females. In males too, differences in sociality between fully grown adult males well integrated in their social group and young males often roaming away from social groups paralleled differences in fecal egg counts, the former showing higher latent parasitism than the latter (MacIntosh 2014). A mathematical model investigating patterns of infection transmission in Japanese macaques also revealed that infection would spread faster and to a larger number of individuals

if it started with a central individual (Romano et al. 2016).

Overall, diffusion studies are widespread and do not only concern social learning processes. Nevertheless, their development in this particular field brought about extraordinary insights into relationships between the social and ecological environment of individuals while accounting for their cognition, physiology, and behavior. Ultimately, a diffusion process is the passage of “something” from one point to another along a certain pathway. Investigating each step and characteristics of this process can help understanding how animals deal with their environment, be it social or ecological, as well as bring about insights into the evolution of sociality in all its complexity and variation.

## Cross-References

- [Andrew Whiten](#)
- [Artificial Fruit](#)
- [Cognition](#)
- [Cultural Transmission](#)
- [Culture](#)
- [Innovation](#)
- [Learning](#)
- [Neural Network](#)
- [Problem-Solving](#)
- [Social Learning](#)
- [Social Network Analysis](#)

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## Digestive System

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## Human digestive system

Digestive system is a group of organs, which helps in the digestion of food and absorption of macro/micronutrients. Digestion is the process in which our body breaks the complex food

material into smaller molecules via mechanical and chemical method (Pastor 1995). Human digestive system includes the: alimentary canal (mouth, pharynx, esophagus, stomach, small and large intestine, and anus) and accessory organs (teeth, tongue, salivary glands, liver, gall bladder, and pancreas) (Davenport 1966).

### Alimentary Canal Organs

**Mouth:** It is also known as oral or buccal cavity and first orifice through which body receives food and air. The primary function of mouth is food intake and helps initial digestion of food. Apart from its primary function, its structure also helps in the formation of speech. Mouth is able to produce saliva from salivary glands, which contains digestive juices and acts as a lubricant for the food. A digestive juice contains various enzymes like salivary amylase, lysozyme, kallikrein (proteases), and lingual lipase. Major functions of these enzymes are given below:

Amylase: Breaks starch into small sugar molecules

Lysozyme: Breaks lipopolysaccharide membrane of bacteria

Lipases: Breaks fatty acids

Kallikrein: Breaks proteins found throughout the body

**Pharynx (throat):** It is the cone-shaped passage-way, where the ventrally located oral cavity can pass food bolus to the dorsally located esophagus for further digestion of food while the dorsally located nasal cavity can conduct air to the ventrally located larynx and trachea for respiration.

**Esophagus:** It is the connecting tube between mouth and stomach. It is the about 25.4 cm length and which is lined by mucosal layer for the food bolus sliding via peristalsis movement.

**Stomach:** Chewed food is deposited into the “J” shaped expandable pouch known as stomach. It secretes gastric acids and digestive enzymes which aid in the digestion of food. Gastric acids contain hydrochloric acid (HCl),

potassium chloride (KCl), and sodium chloride (NaCl), which is produced by the glands present in the lining of the stomach. The pH of the gastric acid is 1.5–3.5, which helps in the activation of digestive enzyme pepsinogen into pepsin. Stomach acidity is maintained by  $H^+/K^+$ ATPase and kills the bacteria. Acidity of the stomach is maintained by bicarbonate produced by other cells of the stomach.

**Small intestine:** Small intestine is 6–7 m long, and it includes duodenum, jejunum, and ileum. Major function of small intestine is chemical digestion and absorption of nutrients.

|               |                          |                                         |
|---------------|--------------------------|-----------------------------------------|
| Proteins      | Trypsin,<br>Chymotrypsin | Smaller peptides, amino acids, peptides |
| Triglycerides | Lipases                  | Free fatty acids and Monoglycerides     |
| Carbohydrates | Amylase                  | Simple sugars and Monosaccharides       |

Digested or indigested foods are now available in the lining of small intestine for absorption of micronutrients nutrients via simple/passive diffusion, facilitated diffusion, primary active transport, or secondary active transport. Water, electrolytes, and vitamins are also absorbed by the plicae circulares of the intestine.

**Large intestine:** Large intestine is approximately 1.5 m long and 6–7 cm in diameter and absorbs basically water and micronutrients from undigested food. Major function of large intestine is conversion of undigested material into feces. It includes cecum, colon, rectum, and anal canal. It also helps in the reduction of acidity via production of bicarbonate and protection of infections via production of antibodies. Undigested waste material is transferred to the rectum in solid form known as stool. Stool basically contains undigested waste food debris and bacteria.

**Rectum and Anus:** Rectum is the chamber which connects the colon and anus. When stool or gas received in the rectum then, sensory nerves send the message to the brain. Brain decides it is defecated from the body and transferred in the anus. Anus is the last part of digestive system and approximately 2 inches long. It helps in the process of stool removal from the body.

### Accessory Organs

**Teeth:** It helps in the chewing, cutting, tearing, grinding of food before entering into the digestion. There are four types of teeth in the mouth according to their function. Incisor cuts the food like a scissor, whereas canine tears the food and molar, premolar grinds the food.

**Tongue:** Tongue helps in the mastication and swallowing the food. Tongue has four taste buds: sweet, sour, bitter, and salty flavor. A fifth taste “Umami” results from tasting monosodium glutamate.

**Salivary glands:** It produces saliva, which keeps the mouth and food moist.

**Liver:** It is the largest gland and has excellent regeneration property. Liver has many functions such as bile production, fat, protein, and carbohydrate metabolism, adsorption and metabolizing of bilirubin, vitamin and mineral storage. It also helps in blood filtration and performs some immunological function such as clearing of foreign particles in the gut (Yen 2001).

**Gall bladder:** It stores and concentrates the bile which helps in the emulsification of fatty acids.

**Pancreas:** It is also part of the digestive system. It produce insulin and glucagon, which are very important in controlling blood levels of nutrients, such as glucose and amino acids, and somatostatin, and may inhibit growth hormone secretion.

### Digestive System Process

There are seven processes which involve in the digestion of the food:

1. **Indigestion:** It is the process of food intake via swallowing or absorbing it.
2. **Propulsion:** It is the movement of chewed food into the esophagus, and it is a series of alternating contractions and relaxations of smooth muscle, which cover the inner lining of digestive organ.
3. **Secretion of digestive enzyme:** Digestive enzymes (such as renin) and other substances (e.g., digestive juices) help in the adjustment of the pH in food material and chemically break the food material.
4. **Mechanical digestion:** Chewing and muscular churning of food are the two important processes for physically breaking down food into smaller pieces. Chewing occurs in the mouth and muscular churning occurs in the stomach, small intestine.
5. **Chemical digestion:** Food is chemically breakdown into smaller pieces via enzymes present in stomach and small intestine.
6. **Absorption:** It is the process where digested food is entered into the body. It is the movement of molecules from digestive tract to adjacent vessels and blood.
7. **Defecation:** It is the process of elimination of undigested material from the body via anus.

### Digestion of Food

Digestion of food is of two types: (1) mechanical digestion via mastication and mixing of food in the buccal cavity and (2) chemical digestion via digestive enzymes (Farner 1960).

**Chemical Digestion of Food:** It is the catabolic process in which large and complex molecules are chemically breakdown into smaller ones, i.e., breakdown of covalent bond in organic molecules via digestive enzymes.

**Carbohydrate digestion** begins in the oral cavity and then stomach followed by duodenum along with small intestine via various digestive enzymes. Large polysaccharide chains such as starch and glycogen is first digested by salivary amylase into disaccharides. Some polysaccharides, disaccharides are digested by gastric amylase, gelatinase, and pancreatic amylase. In the intestine, covalent bond of disaccharides for conversion of monosaccharide is breakdown via different types of enzymes like sucrase, lactase, maltase, and isomaltase.

**Protein digestion** begins in the stomach, pancreas, then followed by intestine. Proteins are large and complex polypeptide chain of amino acids, which are breakdown by pepsin, trypsin, chymotrypsin carboxypeptidase, aminopeptidase, and peptidase.

**Lipids digestion** is same as the protein digestion like it starts in the stomach, pancreas, then



followed by intestine. Lingual and gastric lipases, lipase, esterase are the digestive enzymes, which breaks lipids into glycerol and fatty acids.

**Nucleic acid** is converted into pentose sugars, N-containing bases, and phosphate ions via pancreatic ribonucleases, deoxyribonucleases, intestinal nucleosidases, and phosphatases.

### Functions of Digestive System

The primary function of the digestive system is to transfer nutrients, water, and electrolytes from the digested food material into the body's internal environment (Jones et al. 2012). Along with the primary functions, it involves in three other functions:

**Avoiding autodigestion:** Digestive enzymes are used by the body for breakdown of complex molecules into smaller one. But at the same time, these digestive enzymes are not able to digest the GI tract cells. This pathological condition is known as peptic ulcers.

**Mass balance:** Another challenge to the digestive system is maintaining mass balance by matching the fluid input to the fluid output.

**Defense:** Another important function to the digestive system is to protect body from the foreign invaders which is entered via food.

### Crosstalk Between Endocrine and Digestive System

Endocrine system involved in the regulation of the various glands in the body and the secretion of hormones. One important function of the endocrine system is to control stomach acidic environment. Other functions are control of appetite, ease in the digestion of food, the regulation of energy balance, and the maintenance of blood glucose levels. These hormones are known as gastrointestinal hormones, which are secreted from enteroendocrine cells in the stomach, pancreas, and small intestine (Ziswiler and Farner 1972). Based on the structure, it is divided into three groups:

(a) Gastrin–cholecystokinin family: gastrin and cholecystokinin

(b) Secretin family: secretin, glucagon, vasoactive intestinal peptide, and gastric inhibitory peptide

(c) Somatostatin family

(d) Motilin family

(e) Substance P

**Gastrin family:** Gastrin family includes a family of homologous peptides, which are frog skin peptides (cionin), caerulein and phyllocaerulein, but cholecystokinin CCK and gastrin are the only known members of the family in mammals. Gastrin family is able to induce gastric secretion, stimulate pancreatic secretion, increase blood circulation and water secretion in the stomach and intestine, stimulate smooth muscle contraction, pancreatic enzyme secretion and growth, gallbladder contraction, intestinal motility, satiety, and inhibit gastric acid secretion. Apart from classical function, this family is also involved in the neurotransmission. From phylogeny, these peptides C-terminal domain is evolutionary conserved “Tyr-Met-X-Trp-Met-Asp-Phe-NH<sub>2</sub>” (where X in most mammalian species is a glycyl residue). One or two positions downstream, there is a conserved sulfated tyrosine residue (Lewis and Southern 2000).

**Secretin family:** It regulates the activity of G-protein coupled receptor, which includes secretin, calcitonin, glucagon, parathyroid hormone/parathyroid hormone-related peptides, and vasoactive intestinal peptide receptors. These peptides inhibits gastric gland secretion and gastric motility, increases the output of pancreatic juice rich in bicarbonate ions, stimulates insulin secretion, inhibits HCL production, increases bile output, stimulates buffer secretion, dilates intestinal capillaries, and relaxes intestinal smooth muscle.

**Somatostatin family:** It affects various parts of gastrointestinal tract (GI) such as stomach, small intestine, pancreas, gall bladder, and liver. Functionally, it inhibits gastric acid and pancreatic secretion, inhibits GI blood flow, and inhibits gallbladder contraction



and bile release. It is a regulatory peptide produced by neuroendocrine, inflammatory, and immune cells in response to ions, nutrients, neuropeptides, neurotransmitters, thyroid and steroid hormones, growth factors, and cytokines. It works when stomach gets emptied, then acidic environment need not to be maintained through negative feedback mechanism, and it inhibits the secretion of HCl.

**Motilin family:** Motilin family includes ghrelin and motilin peptide hormones that resemble 50% sequence similarity. Ghrelin is popularly known as “hunger hormone” and stimulates appetite, increases gastric emptying. Motilin works in a similar fashion, which works in a similar fashion as ghrelin.

**Substance P:** It is an undecapeptide neuropeptide which acts as vasodilator and regulates inflammation.

## Crosstalk Between Endocrine and Digestive System

Nervous system is also involved in the regulation of the internal organs and glands of the digestive system (Chapman 1985).

Functionally, it is divided into two parts:

### The sympathetic nervous system (SNS):

Its primary function is to stimulate “rest and digest” activities. SNS regulates vasoconstriction of blood vessels; inhibits gastrointestinal secretions, motility, and peristalsis; stimulates glycogen breakdown in the liver; and decreases pancreatic enzyme production and insulin release.

### The parasympathetic nervous system (PNS):

Its main function is to stimulate “fight and flight” activities. PNS performs reverse function as SNS.

**Digestive System, Table 1** Common disorders related to digestive system

| S.No. | Affected organs             | Disorders                                                             | Affected function                                                                                                     |
|-------|-----------------------------|-----------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------|
| a.    | <b>Tongue</b>               | <b>Ankyloglossia</b>                                                  | Tongue movement is restricted                                                                                         |
| b.    | <b>Salivary glands</b>      | <b>Mumps</b>                                                          | Inflammation in the parotid glands; disturbed chewing and swallowing of food                                          |
| c.    | <b>Esophagus</b>            | <b>Gastroesophageal reflux disease</b>                                | When acidity of the stomach juices, food, and fluids back up from the stomach into the esophagus                      |
| d.    | <b>Stomach</b>              | <b>Peptic ulcer</b>                                                   | Open sores present in the mucosal lining of the gastrointestinal tract and the upper portion of your small intestine. |
|       |                             | <b>Hiatal hernia</b>                                                  | Upper part of the stomach bulge through diaphragm                                                                     |
|       |                             | <b>Hypertrophic pyloric stenosis</b>                                  | Blocks food from entering the small intestine                                                                         |
|       |                             | <b>Vomiting</b>                                                       | Empty the stomach from mouth                                                                                          |
| e.    | <b>Intestinal disorders</b> | <b>Inflammatory bowel disease/ Crohn’s disease/ulcerative colitis</b> | Localized inflammatory degeneration                                                                                   |
|       |                             | <b>Irritable bowel syndrome</b>                                       | Abnormal intestinal mobility                                                                                          |
|       |                             | <b>Malabsorption syndrome</b>                                         | Abnormal nutrient absorption                                                                                          |
|       |                             | <b>Enteritis</b>                                                      | Any inflammation in intestine                                                                                         |
|       |                             | <b>Colon cancer</b>                                                   | Abnormal cell proliferation in colon                                                                                  |
|       |                             | <b>Constipation</b>                                                   | Slow movement of feces                                                                                                |
|       |                             | <b>Duodenal ulcer</b>                                                 | Inhibition of the duodenal gland secretion                                                                            |
|       |                             | <b>Appendicitis</b>                                                   | Acute inflammation of the appendix                                                                                    |
| f.    | <b>Liver</b>                | <b>Hepatitis</b>                                                      | Inflammation of the liver                                                                                             |
|       |                             | <b>Cirrhosis</b>                                                      | Progressive inflammation in the liver due to alcoholism                                                               |
| g.    | <b>Gallbladder</b>          | <b>Gallstones</b>                                                     | Due to presence of large amount of cholesterol salts in the gallbladder, obstruction of the flow of bile              |
| h.    | <b>Pancreas</b>             | <b>Pancreatitis and pancreatic cancer</b>                             | Inflammation of the pancreas and abnormal proliferation of pancreatic cells                                           |

## Digestive System Disorders

Digestive system disorders are very common. Some are acute and some are chronic. These disorders many caused by eating bad quality of food followed by inflammation (Smith and Morton 2011). Some common digestive disorders are charted in Table 1 with respective affected organ.

## Cross-References

- [Diffusion](#)
- [Energy](#)
- [Nutrients](#)

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## Digit Spans

- [Cognition](#)

## Diminution

- [Need Reduction](#)

## Dioecy

- [Gonochorism](#)

## Diploid

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## Definition

Diploid term defines two complete sets of chromosomes or copies of genome in a cell or an organism.

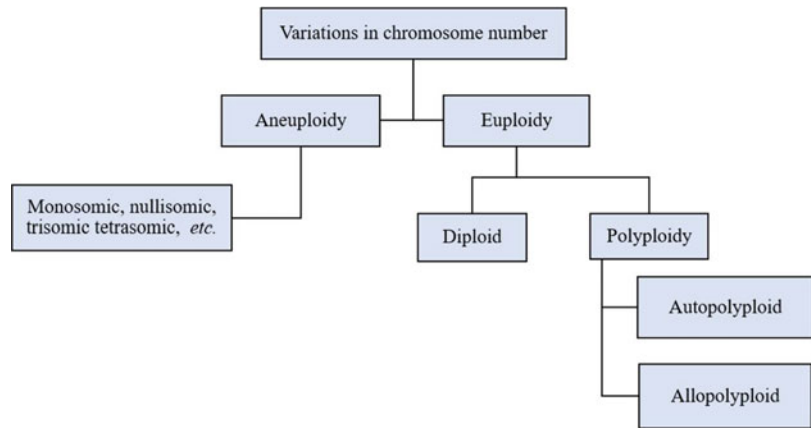
## Introduction

The organisms involved in sexual reproduction have two sets of chromosomes contributed by two sexually different parents *i.e.*, male and female parent. These two parents contribute haploid (n) set of chromosomes present in their gametes or sex cells to reproduce a diploid (2n) progeny (Fincham, 2001). Sexually reproducing plants and animals may have different diploid numbers. For instance, humans have 46 as diploid number (2n) and 23 as haploid number (n) of chromosomes. Similarly, the diploid number for chimpanzees is 48, for rhesus monkeys is 42, for zebra fish is 50, for Arabidopsis is 10, for peas is 14, for yeast is 32, for maize is 20, for mango is 40 and for rice is 24.

## Chromosomal Aberrations Due to Change in Ploidy Level

The number of chromosomes in a single basic set is called the monoploid (x) value. The chromosome number is termed as ploidy of organism and

**Diploid, Fig. 1** Flowchart showing aberrations in chromosome number due to variation in the ploidy level



the number of a complete set of chromosomes in an organism may increase or decrease. Changes in ploidy level can be categorized in two *i.e.*, euploidy and aneuploidy, which can be demonstrated by the flowchart given in Fig. 1. Euploidy involves variation in the complete set of chromosomes in a cell or an organism, which can lead to the increase in the copies of whole genome of that cell or organism for example,  $2n + n = 3n$ . However, aneuploidy occurs when there is an insertion or elimination of one or a few chromosomes for example,  $2n - 1$ : monosomic,  $2n - 2$ : nullisomic,  $2n - 1 - 1$ : double nullisomic,  $2n + 1$ : trisomic,  $2n + 2$ : tetrasomic,  $2n + 1 + 1$ : double trisomic (Griffiths et al., 1999).

Aneuploidy is caused due to segregational errors of chromosome participating in meiosis cell division. Aneuploidy in human may lead to changes in either autosomal or sex chromosomes resulting in fatal syndromes. Some examples of syndromes in humans caused by autosomal aneuploidy where the diploid number becomes 47 are Down syndrome (trisomy of 21st chromosome), Edward's syndrome (trisomy of 18th chromosome), Patau's syndrome (trisomy of 13th chromosome). Likewise, aneuploidy of sex chromosomes in humans may cause Turner syndrome (diploid number: 45, single copy of X-chromosome), Klinefelter syndrome (diploid number: 47, extra copy of X or Y- chromosome).

Euploidy is further classified into two cases: diploid and polyploid. As the name suggests, the diploid case is found in those organisms that

comprises two copies of the basic set of chromosomes. However, multiple copies of monoploid sets in an organism is identified as a condition called polyploidy. Polyploidy can be of two different types *i.e.*, autopolyploidy and allopolyploidy. Repetition of the same set of genomes in an organism causes autopolyploidy whereas multiplication of different sets of genomes in an organism results in allopolyploidy.

## Cross-References

- [Chromatid](#)
- [Chromosomes](#)
- [Gametes](#)
- [Genes](#)

## References

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## Direct and Indirect Fitness

- [Fitness](#)

## Direct Perception

- [Perception-Action Theory](#)
- [Social Affordance](#)

## Directed Movement

- [Cetacean Navigation](#)

## Directed Versus Averted Gaze

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### Definition

Directed and averted gaze refers to behavioral cues that provide information about where someone is looking. Gaze can be directed toward or averted away relative to someone or something. These gaze orientations can also refer to an individual's response to observing another's behavior. Gaze cues are used in social as well as anti-predation contexts.

### Introduction

Providing gaze cues and responding to gaze orientation are behaviors many of us engage in on a daily basis. We may have experienced being in a public area such as a train or bus and inadvertently looked toward a stranger, who, upon noticing that someone is looking at them, directs their gaze back. Immediately we tend to avert our own gaze so as to avoid any further eye contact with an unfamiliar person. In another scenario, we may have entered a busy room full of people and spotted a friend across the other side. We look directly toward them to catch their attention, causing them to look back, allowing us to greet one

another through mutual gaze. These two examples demonstrate how attention toward and sensitivity to gaze cues – either averted or directed – can be used to communicate information or to avoid confrontation. Gaze sensitivity typically presents in two forms: gaze following, whereby an individual tracks where the other is looking, and gaze aversion, whereby an individual avoids the gaze of another. Gaze following is especially prominent in social contexts in humans and many other animals. Gaze aversion is often found in predator-prey interactions, whereby prey avoids direct gaze, but also in social contexts such as the train scenario described above. Understanding the socio-ecological contexts in which humans and animals respond to gaze cues provides insight into how gaze sensitivity has evolved across species and the cognitive mechanisms that underpin it (Davidson et al. 2013).

### What Constitutes Directed and Averted Gaze?

Directed and averted gaze can refer to the cues that elicit gaze sensitivity responses and/or the responses themselves. For example, direct gaze (the cue) toward a stranger causes them to avert their gaze (the response). Gaze cues include the orientation of the head, the eyes, or both, and they may be in line with one another, or in opposing directions, such as the head directed straight but with eyes directed to the side. Gaze can be directed toward or averted away from someone or something.

### Why Are Individuals Sensitive to Gaze Cues?

Being sensitive to other's gaze can have many functional purposes. Gaze following can be used in several contexts including communication, competition, and avoiding predation. For example, looking someone directly in the eye and then averting gaze toward their shirt may communicate to the person that they have a button undone. Two builders working on a project may share mutual

gaze through direct eye contact, while they coordinate the movement of large equipment together. Animals living in social groups may benefit from attending to group members if they direct their gaze toward the sky, as this may be an indication of an aerial predator, or if a group member directs their gaze behind a bush, as this may be an indication that a food source has been discovered. Gaze aversion, by contrast, refers to avoidance behaviors in response to directed gaze. While most humans are comfortable sharing mutual gaze, people diagnosed with autism spectrum disorder typically avoid eye contact (Hadjikhani et al. 2017). In many primates, mutual eye gaze with another individual is considered a threatening display, causing subordinate individuals to avert their own gaze from dominant members to avoid aggression (Altmann 1967). Gaze aversion is also important for predator avoidance as forward-facing eyes and/or faces may represent a predator and therefore indicate whether it intends on initiating a pursuit. Fearful responses to eyes have been reported across a broad range of vertebrate taxa including fish, reptiles, birds, and mammals (Davidson et al. 2013).

### **Gaze Cues as a Paradigm for Testing Cognition**

In humans, eye gaze is at the heart of social cognition. Sharing gaze toward the same object (joint attention) or each other (mutual gaze) facilitates communication and demonstrates our capacity to recognize that others have mental representations of the external world because of what they can see and that these perspectives may be the same or different than our own. Through direct eye gaze, we recognize that we are sharing our attention toward each other and working toward the same goal, a cognitive mechanism known as joint intention (Tomasello and Carpenter 2005). These behaviors and underlying cognitive mechanisms are advantageous for communication within a cooperative society, and it is thought that the shape and appearance of the eye in humans are unique and have evolved to expose the white sclera around the iris, making eye

orientation conspicuous and easy to detect (Kobayashi and Kohshima 1997).

Gaze cues can be manipulated in experimental paradigms to test several questions related to gaze sensitivity including the features of the cues that elicit responses and the cognitive mechanisms that underpin these responses. Both human and nonhuman animals attend to gaze cues, but it is not always clear to what extent they share underlying cognitive mechanisms associated with behavioral responses to directed and averted gaze. For example, in the object-choice task, a human experimenter directs their gaze toward one of two cups to indicate the location of hidden food to the test subject (e.g., Anderson et al. 1995; von Bayern and Emery 2009). If the subject chose the correct cup more often than by chance, this demonstrates that they are following human-directed gaze to find food. In a test of gaze aversion, a human experimenter either looks toward or away from food, and a prey species, such as a bird, has to feed (e.g., von Bayern and Emery 2009). If the bird is more wary when the gaze is directed toward rather than averted away from the food, this is an indication that the subject is attending to and avoiding direct gaze. In the broadest sense, there are two interpretations with regards to cognitive abilities underlying gaze following and gaze aversion, which are often referred to as “low-level” and “high-level” interpretations. In the low-level model, animals respond to directed and averted gaze because they have learned that those cues are associated with predictable outcomes. In the high-level model, animals recognize that gaze cues indicate that another individual can see something, and some interpretations may go so far as to claim that this provides evidence that animals can reason about the minds of other social agents (i.e., theory of mind), albeit the latter is a rich and less accepted interpretation as animals may be responding to the cues, not to internal mind states.

### **What Gaze Cues Are Most Salient?**

Studies have shown that species vary in how sensitive they are to eye orientation compared to

head orientation (Tomasello et al. 2007; reviewed in Davidson et al. 2013) and that sensitivity to eye direction emerges after sensitivity to head direction in human infants (Corkum and Moore 1995). Some authors suggest that being more sensitive to eye direction as opposed to head direction may indicate an animal's ability to understand the relationship between eyes and mental representations of the world, but this interpretation is not robust because animals can still learn that eye direction is associated more predictably with certain outcomes than head direction. This is especially true when many experiments are performed on captive animals using human gaze cues, for example, to indicate the location of hidden food. Captive and hand-reared animals may have learned that human eyes always orient toward objects of interest. Moreover, because the visual systems of animals vary, including the positioning of the eyes on the head and the field of vision, directed or averted eye gaze may be irrelevant if eye movement within the optical orbit is restricted and gaze orientation occurs only through head movement (Davidson et al. 2013). Nevertheless, categorizing how animals respond to directed and averted gaze cues across a wide range of taxa enables us to understand the evolution and function of gaze sensitivity.

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Cognition](#)
- ▶ [Comparative Cognition](#)
- ▶ [Joint Attention](#)
- ▶ [Object-Choice Test](#)
- ▶ [Theory of Mind](#)

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## Directional Selection

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## Synonyms

[Positive selection](#)

## Definition

Directional selection can be defined as selection of the organisms with traits underlying at the end of trait spectrum in nature.

## Introduction

Evolution takes place by many factors in any environment. Natural selection is one of the important evolutionary forces that act on organisms and create variation among them. Natural



selection is of three types: stabilizing selection, directional selection, and disruptive selection.

Directional selection is the most common form of natural selection observed in any trait during the course of evolution. It is a type of selection in nature that causes a population to evolve toward one end of a trait spectrum. Traits are found in two forms which are either discrete (e.g., eye color) or continuous (e.g., height); in discrete, only one form will be selected (e.g., black eye color), and in continuous, either the highest or lowest value for a trait is selected (e.g., tall people). Directional selection mostly occurs when a population migrates to new environment conditions, and the trait most favorable for their fitness is selected, and therefore this selection is often referred to as positive selection (Charlesworth and Charlesworth 2010). It mostly leads to selection for the extreme phenotype over the mean or another extreme.

Directional selection also occurs due to human activities. For example, bigger animals are being hunted either for meat or ornamentation, so small-sized animals are selected in nature. Similarly slow-moving animals are killed by their predators, which leads to the selection of mostly fast-moving animals in nature.

## Methods to Assess Directional Selection

There are different methods to assess directional selection like QTL sign test, Ka/Ks ratio test, and relative rate test. QTL sign test confirms whether any trait is due to directional selection or genetic drift (see ► [QTL Linkage Analysis](#)). It measures number of quantitative trait loci involved in the formation of a different phenotypic trait from one form to the other (Orr 1998). In Ka/Ks ratio test, Ka depicts nonsynonymous substitutions and Ks denotes synonymous substitutions. If this ratio is greater than 1, it depicts directional selection. In relative rate test, evolutionary rate between two closely related species are compared by taking a third one as a reference species.

The introduction of any allele in nature takes place by mutation. When an allele is introduced in a new environment, its frequency is very less, but

as the environment becomes favorable and the organism is adapted in the new condition, the frequency of that allele is increased (see ► [Gene Frequency](#)). Suppose there are two alleles for a trait, A1 and A2, which have frequency  $p$  and  $q$ , respectively, in nature, and both the alleles are found in three forms of genotype: A1A1, A1A2, and A2A2 with frequency  $p^2$ ,  $2pq$ , and  $q^2$ , respectively. For allele A1 to fix in the environment, the fitness of the organism being homozygous for A1 should be equal to or greater than any other genotype in the environment.

However the time taken by any allele to get fix depends on following factors:

If A1 is completely dominant over A2, then it will take many generations for A1 to get fixed, because the other allele A2 remains present in the heterozygous form without any effect on the fitness of the organism and therefore unexposed to natural selection, and by this, the recessive allele remains present in nature for long time period.

But if A1 is incompletely dominant over A2, then the heterozygotes have reduced fitness and they will not be able to survive leading to reduction in the frequency of A2. So A1 will be fixed in nature in less number of generations (Futuyma 1998).

There are many examples of directional selection found in nature.

Haldane (1924) estimated the strength of selection of a trait by observing the change in allelic frequency in the two forms of *Biston betularia* (peppered moth). In Northern Europe, before the advent of the Industrial Revolution, the density of light form of peppered moths was far more than the dark-colored form of the moths. But as the number of industries increased in number and pollution increased the concentration of carbon in the environment, it caused blackening of tree barks; the light form of moths was not able to adapt accordingly and decreased in number, and this form was replaced by the dark form of *Biston betularia*. It occurred because the light form was not able to hide themselves against the dark-colored barks and was killed by their predators. The black form was thus selected in the new environment.

DDT resistance reported in mosquitoes is one of the examples. This insecticide was introduced

to kill mosquitoes which are responsible for malaria. When DDT was used for first few times, it was found to be very effective as it declined the mosquitoes' population rapidly, but after many continuous uses, the small number of resistant mosquitoes multiplied, and no further effect of DDT could be observed after any further application. This indicates the selection of the resistant mosquitoes against the application of DDT. Another example of drug resistance had been reported in HIV-1 virus where it was found that the virus acquired drug resistance mutations (DRAM) with the application of antiviral drugs (Murrell et al. 2012).

Directional selection was reported to shape the oral jaw apparatus in Lake Malawi cichlid fishes. Cichlid fishes have three general modes of feeding, and depending on the mode of feeding, they have different head shapes (Liem 1991). Further specialization of jaws and teeth depends on the specific foraging niches (e.g., biting fins or biting algae) (Kocher et al. 1993). It was analyzed that diversion in the shape of jaw in these fishes is due to directional selection and not genetic drift and that analysis was done through QTL test (Albertson et al. 2003).

## Kin Selection

The concept of kin selection is an important part underlying directional selection. It is mostly observed in many eusocial insects like that of Hymenoptera (honeybees, wasps, and ants) and termites and in a few mammals such as the naked mole rat (Frank 1998). Eusociality means an organism gives up its fitness in order to increase the fitness of its relatives. This behavior is called altruistic behavior. Hamilton (1964) gave a rule that explains the survival and selection of these altruistic organisms which exhibit this extreme level of "selflessness." The rule is as follows:

$$C < r \times B$$

According to this rule, the cost ( $C$ ) incurred by giving up self-fitness by altruistic individual should be less than the product of genetic

relatedness ( $r$ ) of the altruistic organism with its relative and the benefit ( $B$ ) obtained by the individual for whom altruism had been done.

In kin selection, allelic variant that causes its carriers to lose its fitness has the advantage to increase the fitness of related individuals, and this variant thus increases among organisms. Suppose the altruistic behavior is controlled by a gene and it is randomly distributed in a group of genetically related individuals. In this group few may be donors in altruism and others are recipients. Whenever donor sacrifices its fitness, the gene for altruism is lost with it but increases with high frequency in the recipient organisms. Genetic relatedness is not the only responsible factor for the selection of this trait; interactions between the donor and recipient are also necessary for both to memorize the past behavior of the other and to punish those who had cheated (Charlesworth and Charlesworth 2010).

## Cross-References

- [Adaptation](#)
- [Gene Frequency](#)
- [Natural Selection](#)
- [QTL Linkage Analysis](#)

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## Disassortative Mating

### ► Assortative Mating

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## Discourse

### ► Turing Test

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## Discovery

### ► Learning

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## Discrete Trial Fixed-Interval Schedule

### ► Peak Procedure

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## Discrete Trials

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## Introduction

Discrete trials (DT) procedures are frequently used to study nonhuman animal behavior and

cognition in a laboratory setting. For example, discrete trials can be used to examine behavioral and cognitive processes such as drug self-administration (e.g., Stretch and Gerber 1977), memory (e.g., delayed matching to sample tasks; Berry and Odum 2014), delay discounting (thought to measure impulsive decision-making, e.g., Woolverton et al. 2007), and stimulus control (Hinson and Higa 1989). Many schedules of reinforcement exist that define the presentation of a reinforcer following a given behavior (e.g., lever pressing or key pecking), from simple fixed ratio schedules to complex concurrent or chain schedules. Discrete trial procedures allow the experimenter to precisely control the timing of trials and earned reinforcers across a session following a given behavior (Dobrin and Roberts 2012). While discrete trial paradigms can be used to understand behavior and cognition among human subjects, the focus of this piece will be on the use of discrete trials in nonhuman animal research.

## On the Mechanics of Discrete Trials

Discrete trials procedures involve dividing a session into multiple trials so that there are individual distinct trials and intertrial intervals (ITI; the time period immediately following a discrete trial in which reinforcers are not available) (Dobrin and Roberts 2012). Specifically, each trial begins at a fixed point in time within a session, lasts for a prespecified period of time, and is then followed by a predefined ITI time period. For example, a session may begin at 8:00 a.m. and end at 9:00 a.m., with three discrete trials within the session. A trial may last for 15 min, with a 5-min ITI following the trial. When described in terms of discrete trials per hour, this is referred to as a DT3. Each discrete trial might be associated with exteroceptive stimuli signaling the beginning of the trial (e.g., house light, key light, light above a lever). During the ITI, these stimuli may change or extinguish to signal the end of that trial and the onset of the ITI.

In intravenous self-administration research, controlling the timing of drug delivery is crucial,

as free access to drug over long periods (e.g., 23-h sessions over several weeks) can result in toxicity and can be lethal (Johanson et al. 1976). To provide a specific example from a discrete trial drug self-administration paradigm, a dose of 1.0 mg/kg of cocaine per infusion might be delivered to a rat over the course of three discrete trials per hour (DT3). The infusion might be earned on a fixed ratio 1 (FR 1) schedule of reinforcement, in which a single lever press results in an infusion (see Roberts et al. (2002), for an example of several discrete trial self-administration preparations).

Discrete trials are also commonly used to examine memory processes. One example is a delayed matching to sample (DMTS) task (Blough 1959). In this task, a sample stimulus is presented (e.g., a blue key light), and then removed for some amount of time (e.g., 30 s). Then the same stimulus, along with a “distractor” stimulus (referred to together as comparison stimuli) is presented again. The organism chooses one of the two comparison stimuli presented. If the choice matches some physical property (e.g., color) of the previously presented sample stimulus, then the response is correct, and a reinforcer (e.g., food) is provided. Thus the organism is required to remember the first stimulus to accurately respond and receive reinforcement. Accuracy of remembering tends to decrease with increased time between the sample and choice stimuli. Following the DMTS trial, an ITI is presented as in other discrete trials procedures to standardize the overall timing of each trial across the session.

The types of discrete trials outlined above (i.e., discrete trials used in self-administration research or memory research) allow for assessment of behavior when exposed to discrete trials compared to other procedures, or the effects of various independent variables that might be of interest to the experimenter. For example, an experimenter might be interested in differences between patterns of drug self-administration in discrete trial paradigms compared to free access to the drug. Or a researcher may be interested in drugs or manipulations that enhance memory performance.

## Discrete Trials Data Analysis

Data from discrete trials procedures can be analyzed and displayed in numerous ways. The behavior of interest – such as how much drug is self-administered, or memory performance – can be aggregated within a session and compared across sessions to examine how behavior changes over time. For instance, one way to analyze discrete trial data would be to examine percentages over time (e.g., percentage of the available infusions taken over time, percentage correct of memory performance over time). A researcher could also analyze percentages before or after a manipulation or introduction of an independent variable.

## Conclusion

Discrete trials (DT) procedures are frequently used to study a wide range of nonhuman animal behavior and cognition under controlled laboratory conditions. Discrete trial procedures offer a way to control the precise timing of events within a session (e.g., reinforcer delivery, onset timing of each trial).

## Cross-References

- [Behaviorism](#)
- [Cognition](#)
- [Contingency](#)
- [Delay of reinforcement](#)
- [Discrimination Learning](#)
- [Extinction in Learning](#)
- [Free operant response](#)
- [Self-Administration](#)

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## Discreteness

### ► [Cognition](#)

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## Discriminated Avoidance

### ► [Avoidance](#)

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## Discrimination Learning

### ► [Entopallium](#)

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## Discrimination of Emotion

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## Synonyms

[Cognitive empathy](#); [Emotion detection](#); [Emotion recognition](#)

## Definition

Emotion discrimination is the ability to perceive differences between the emotions of others as expressed in facial expressions, body postures, sounds, chemical signals, and other observable cues. The ability to discriminate between emotions implies only that an organism recognizes differences between these physical cues and can potentially predict different behavioral outcomes on the basis of these cues (Waller et al. 2016). However, the capacity to discriminate between the unique external cues of different emotions is not equivalent to the capacity to represent the internal emotion states of others – an ability sometimes labelled as “cognitive empathy” (see Nieuwburg et al. 2021).

## Adaptive Value

It is adaptive for many organisms to attend to the signals of emotion in others. Arguably, fear, anger, and disgust are the most important emotion cues to recognize because they signal potential threats to the organism. For example, recognizing signatures of fear in others can encourage an organism to take cover or retreat from a potential threat. Recognizing the cues of anger can encourage an organism to deescalate a potential rise in conflict that could result in physical aggression. Recognizing that another individual is likely to aggress can encourage self-protective behaviors against potential harm. Recognizing the cues of disgust might discourage an organism from entering an area or interacting with an object that contains pathogens or from consuming a spoiled or toxic substance. Although it may be most useful to read emotion cues in conspecifics, this is a skill that has utility beyond the social group. For example, sympatric species can recognize and respond to alarm calls in members of other species (Carlson et al. 2020; Palmer and Gross 2018), and even solitary animals may leave an area where scents or released chemicals signaling fear/danger have been left behind by other organisms (McKillup and McKillup 1995). Therefore, despite the focus on studying emotion

discrimination in social species, it is important that the study of this topic is extended to less social animals as well.

It is unclear the extent to which animals might recognize other basic emotions like happiness, sadness, and surprise. Several species recognize and respond appropriately to signals of play, for example, dogs, primates, and bears (Taylor et al. 2019). Play faces or postures can signal to a conspecific that the intent of an individual is to play rather than to harm, even though the ensuing behavior may mimic an aggressive behavior. Recognition of happiness and sadness may be important to humans and other altricial social species to encourage bonding because infants depend upon extensive care from adults (Palagi et al. 2019). Smiling emerges early in human infants and is postulated to increase bonding. Crying, on the other hand, signals some essential need that is currently unfulfilled and may be crucial in allowing the altricial infant's needs to be met. Later in life, recognizing when another is sad allows for the provision of comfort and may be important for empathy. Although controversial, some have argued that other species, in addition to humans, are capable of affective empathy, which involves the internalization of emotions detected in others or feeling what another is feeling (de Waal 2004).

The secondary emotions, such as guilt, shame, embarrassment, pride, and jealousy, are more difficult for even humans to discriminate in the facial expressions of other humans compared to the basic emotions (Ekman 1993). Recognition of these emotions plays an important role in moderating social interactions but may be less directly critical for survival. Therefore, we might expect recognition of these emotions to be restricted to species that form long-term bonds, but this is not necessarily restricted to large social groups. Recognition of these emotions may be important for animals that pair-bond or whose offspring have long periods of dependency. However, there is little research indicating whether other species recognize the expression of these emotions, and in fact, it is controversial whether other species even experience secondary emotions.

## Modalities

It is also important to recognize that although researchers have tended to focus on the recognition of facial expressions, probably because facial expressions are one of the most important ways in which humans convey emotion, animals use a much richer range of sensory modalities to detect cues of emotion. For example, sounds, chemical signals, postures, and tactile cues may signal another individual's emotion state. For some animals, aggression or affiliation can be predicted from the position of the ears; the movement of the tail; the overall posture; hissing, growling, or snarling sounds; and piloerection. It is likely that animals convey emotion in other ways not recognized by humans. This entry will focus on the recognition of emotion in visual displays, especially facial expressions, because this is the modality that has undergone the most experimental study (see also Nieuwburg et al. 2021). In addition, almost all of the experimental work has been conducted with nonhuman primates, with some work on domestic species and their understanding of human emotion. There is less research focused on how animals understand the emotions of their conspecifics and virtually no work in non-mammals or less social species.

## Experimental Tests of Emotion Discrimination

Human faces can convey a range of emotions due to the flexibility of movement of facial muscles. Even in other apes, the movement of the facial muscles is more restricted, limiting the range of expressions that can be conveyed solely through facial movements. However, there are enough similarities that allow humans to recognize characteristics such as the sneer as conveying threat and the relaxed mouth as conveying playfulness or friendliness (Waller and Micheletta 2013). It has been suggested that domestic dogs have evolved the ability to communicate with humans by adopting expressions that humans recognize. For example, eyebrow movements convey fear and sadness, which evoke sympathy and



compassion from humans (Kaminski et al. 2019). Humans can also categorize expressions of emotion in cats, such as frustration, fear, and relaxation. Interestingly, cats seem to intensify these expressions when interacting with humans, suggesting that these emotion expressions have also been influenced by the process of domestication (Bennet et al. 2017).

### Hidden Object Paradigm

The hidden object task has been a popular paradigm for testing the discrimination of emotions in animals. In this paradigm, humans direct their attention while expressing different emotions to different objects, such as closed containers. Studies have been conducted with happy, neutral, fearful, and disgust expressions directed toward boxes. Both domestic dogs and chimpanzees chose to receive the contents of a box to which humans had directed positive emotions rather than disgust expressions, but they did not discriminate between positive and neutral emotions in this context (Buttelmann et al. 2009; Buttelmann and Tomasello 2013). Unlike the dogs and chimpanzees tested in the object choice task with human experimenters, capuchins did not discriminate based on human experimenters' cues. However, they were able to make use of the emotional responses of conspecifics to preferentially open boxes to which groupmates had directed positive expressions (Morimoto and Fujita 2012).

Merola et al. (2014) tested domestic dogs in a similar task and found that dogs preferred to investigate a box that caregivers had directed happy emotions toward in comparison to neutral or fearful emotions. However, they did not show preferences between boxes that caregivers had directed fearful versus neutral expressions. These researchers speculated that dogs had learned to attend to owner's positive expressions because they were often associated with reward. This interpretation emphasizes that it is not necessary to postulate underlying mental representation of others' emotions on the basis of successful discrimination of emotion expressions.

### Social Referencing

In a different paradigm, the same research team investigated whether domestic dogs and cats

could read the cues of human caregivers to signal whether a novel object was safe or dangerous. They found that both dogs and cats engage in social referencing, meaning that they gaze back to their caregivers and study their emotional and postural cues before deciding whether to interact with an ambiguous novel object or situation. Both dogs and cats behaved differently depending on whether their owners displayed positive or negative expressions and vocal cues (Merola et al. 2015). However, only dogs mirrored their caregivers' responses to these objects, again leading the investigators to postulate that they were engaged in observational conditioning (Merola et al. 2012). Similarly, Yong and Ruffman (2015) found that dogs were more attentive to caregivers that displayed fearful or confused expressions compared to those that displayed happy expressions, but they interpreted these findings as suggesting that dogs seek more information in ambiguous situations, not that the dogs necessarily understood their caregivers' emotional states. Cats also looked more to their caregiver than an unfamiliar human when the two humans engaged in antagonistic conversations. They showed a similar but nonsignificant preference to look at their caregiver during friendly conversations between the same humans as well (Galvan and Vonk 2016). The stronger effect of social referencing for negative conversations supports the conclusions of Yong and Ruffman (2015) that such differences reflect learning rather than understanding of the meaning of emotions.

### Matching Experiments

In one of the earliest studies to explore nonhuman primates' representation of emotion, Dittrich (1990) successfully trained long-tailed macaques to select a target facial expression from three line drawings of different emotional expressions. In another groundbreaking study, chimpanzees successfully matched images of chimpanzees conveying positive or negative emotions to videos of negative or positive scenarios such as veterinary needles or favored rewards (Parr 2001). Although the chimpanzee's performance was impressive, it might reflect associations between facial expressions witnessed during experienced

events similar to those depicted in the test stimuli. That is, the chimpanzees did not need to represent the scenarios as evoking a particular underlying emotion in order to associate the correct emotional expression with the matching scenario. It may not be possible to tease apart mechanisms that involve representations of emotions as mental states from mechanisms that involve representations of the observable manifestations of those emotions because the former depend upon the latter and cannot be separated in experimental tests with nonverbal organisms. Nonetheless, the matching-to-sample paradigm has been useful for demonstrating which other primate species can differentiate emotional expressions and which emotions can most readily be differentiated (reviewed in Nieuwburg et al. 2021).

Cross modal matching tasks have also been used to demonstrate that animals associate verbal cues linked to certain emotions with their corresponding facial expressions – at least hinting at a unified representation of individuals experiencing particular emotions. In these tasks, animals are not required to explicitly select a stimulus that matches the sample as in Parr's (2001) study. Instead, researchers make use of looking time to determine whether animals look longer when the vocal cue is a match compared to when it is a mismatch with the visual stimulus presented. For example, dogs looked longer at images of happy or angry dog faces that matched positive or negative auditory stimuli of dog vocalizations and showed a similar pattern with human voices and vocalizations (Albuquerque et al. 2016). Similarly, Quaranta et al. (2020) found that cats looked longer when cat and human vocalizations matched the valence of facial expressions presented simultaneously compared to when they mismatched. However, the cats did not show this pattern when presented with cats expressing positive emotions. Thus, the results, at least for the cat stimuli, indicated that the cats were particularly attentive to whatever image was shown when the auditory sample of cats hissing was presented. The study also involved a small sample (ten cats) and presented very few stimuli (one trial with each human and cat stimulus for a total of four stimuli), so it is difficult to know whether the results would generalize.

Interestingly, in both of these studies, subjects looked longer at congruent stimuli (where the vocalization matched the valence of the visual stimulus). However, this contrasts with the typical interpretation of data from the well-established violation of expectation paradigm where subjects are expected to look longer at surprising stimuli. In this case, one would consider the results indicative of understanding emotion if animals looked longer at incongruent rather than congruent stimuli. Indeed, horses showed exactly that pattern in two similar studies, looking longer during the incongruent trials (Nakamura et al. 2018; Trösch et al. 2019). Thus, opposing patterns of results were interpreted as reflecting the same underlying ability, which is problematic.

Similar to studies with cats (Galvan and Vonk 2016) and dogs (Merola et al. 2015) that showed greater attention and differentiation when responding to their caregivers, the horses in Nakamura et al.'s study showed this typical effect only when presented with the voices of their familiar caretakers, but not with strangers' voices. Horses also reacted more negatively when angry human vocalizations were presented compared to joyful vocalizations (Trösch et al. 2019). Furthermore, Yong and Ruffman (2016) found a null result where dogs did not look differently at congruent versus incongruent stimuli in a similar task. However, these authors did find that dogs showed a general preference to view angry or happy human faces compared to sad faces, which does suggest that they differentiated between emotions. Other studies, in contrast, failed to show differences in dogs' viewing time as a function of human emotion expression (Correia-Caeiro et al. 2020). The fact that dogs' visual scanning was more rigid than in humans and that not all companion dogs and cats are sensitive to caregivers' or unfamiliar humans' expressions suggests that their processing of emotional information differs from that of humans.

### Neural Correlates of Discrimination

In addition to examining looking time and scanning patterns, researchers have examined physiological outcomes, such as heart rate and functional asymmetries in the processing of emotional stimuli. For example, left-gaze biases are a recognized

lateralized response to negative stimuli. Dogs showed a bias to turn their heads to the left (implicating the right hemisphere) when shown human faces expressing anger, fear, and happiness, whereas they showed a bias to turn their heads to the right if the human faces expressed surprise (Siniscalchi et al. 2018). Horses show the same left-gaze bias to negative stimuli of angry human faces, along with an increase in heart rate (Smith et al. 2016). Horses also show a left-hemisphere (right ear) bias when listening to positive human vocalizations (laughter) extending the findings to auditory stimuli (Smith et al. 2018). However, when Smith et al.'s (2016) data was reanalyzed using more sensitive measures (heart-rate changes between baseline and test, maximum heart rate, or recovery time), the evidence that horses differentiated between emotions disappeared (Schmoll 2016). Although these results do not demonstrate that animals differentiate between different emotions, they do indicate a general sensitivity to human facial expressions and vocalizations in both dogs and horses. Thus, this is a promising area of further research.

### Behavioral Differentiation

Studies of behavior have also supported the idea that various domestic species can differentiate human emotions. For example, cats engaged in more positive behaviors and spent more time with their primary caregiver when the caregiver expressed happiness compared to anger (Galvan and Vonk 2016). However, the same cats did not differentiate between an unfamiliar human expressing the same emotions, suggesting a role of learning to associate owners' positive expressions with positive outcomes as was suggested for dogs by Merola et al. (2012) and Yong and Ruffman (2015). Cats do not seem to learn to associate characteristics to humans through watching third-party interactions, even those involving different emotional responses (Leete et al. 2020). Horses, on the other hand, respond differently to humans that laugh versus growl and behave with increased freezing and vigilance to negative emotional vocalizations of humans (Smith et al. 2018). Horses also respond differently to videos of positive and negative interactions

between humans and other horses and even choose to touch the negative experimenter significantly more than the positive experimenter. Although the direction of this effect is counterintuitive, the fact that horses differentiated in their responses supports the conclusion that they discriminated the negative and positive contexts of the interactions. The authors suggested that the preference to touch the negative experimenter may reflect attempts at appeasement (Trösch et al. 2020). Proops et al. (2018) additionally demonstrated that horses could remember the emotions expressed in photographs of unfamiliar humans and behaved in a manner that matched the valence of the individuals' faces in the previously presented photographs when they later met those individuals. The sensitivity of horses to human emotions may reflect a more selective domestication process by humans and a stronger selection pressure for group-living in horses compared to solitary and self-domesticated cats. Of course, highly social species, such as crows, that do not have close relationships with humans might not be expected to differentiate human emotions (Clucas et al. 2013), but it will be important to learn what they understand of each other's emotions in future studies.

### Conclusions

Thus far, it appears that domestic species and non-human primates are capable of differentiating between emotional expressions in both their conspecifics and in humans. Although it appears that social species may be more adept at discriminating emotion compared to nonsocial species like cats, many more species need to be tested. It is important to keep in mind that facial expressions, and other cues of emotion, have likely evolved to be species specific, and thus, failure to recognize emotions in other species, including humans, should not be taken as evidence that animals cannot recognize and discriminate emotions in members of their own species. Much more data is needed using naturalistic paradigms in which animals with appropriate early socialization to members of their own species use expressions of emotion to adjust their behavior appropriately. Studying

emotion discrimination in a more diverse group of animals will contribute to a better understanding of the evolution of these abilities. Several recommendations for future research directions are described in Nieuwburg et al. (2021).

## Cross-References

- Emotional Contagion
- Empathy
- Human-Animal Interaction
- Jealousy
- Shame and Guilt

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## Discriminative Parental Solicitude

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## Synonyms

Interbrood conflict; Intra brood conflict; Mother-fetus conflict; Parent-offspring conflict

## Definition

Parents are expected to differ in the amount of investment allocated to offspring as a function of a multitude of factors including resource availability and offspring health.

## Introduction

Across species, conflict between parent and offspring is routine. The notion that parent and offspring – as a result of the former relying on the latter to achieve reproductive success – should exist in harmony may be intuitive. However, not all offspring are created equal; each individual offspring can vary in its reproductive value (e.g., health, probability to reach reproductive age). Each situation for parents can also vary from one context to the next (e.g., resource availability). This review will start with the logic of parent-offspring conflict theory. The focus will then shift to a very brief summary of the empirical work on discriminative parental solicitude (where the preponderance of work is specific to avian species).

## Parent-Offspring Conflict Theory

Trivers' (1974) original formulation of parent-offspring conflict theory (POCT) is based on Hamilton's rule, the fundamental formulation of kin selection theory (Hamilton 1964):



$$rB > C$$

In this formulation, the relatedness coefficient ( $r$ ) can range from 0 to 1. This coefficient, a representation of the probability that any two individuals share the same allele at any given locus, is critically important to understanding discriminative parental solicitude. The relatedness between a parent and offspring is  $r = 0.5$ : An individual allele present in a parent has a 50% probability of ending up in any of their given offspring. Parents and their offspring are expected to share the same alleles (across *all* loci) 50% of the time. Critically, while a parent shares 100% of its alleles with itself ( $r = 1.0$ ), an individual parent only shares 50% of its alleles with a given offspring. The optimal level of investment from the parent's perspective differs from the optimal level of investment from the perspective of the offspring.

There is a conflict of interest between parent and offspring. Parent-offspring conflict theory proposes that a battle over resources between offspring and its parent is ongoing. Parents (often mothers) seek to preserve resources for their own survival as well as retaining sufficient resources to invest in additional offspring (current or future).

### Intrabrood and Interbrood Conflict

Among some birds, multiple offspring can be produced simultaneously. This leads to intrabrood conflict. Each offspring in a given clutch can benefit from attempts at eliciting a disproportionate amount of resources toward itself at a cost to its siblings. Mothers, equally related to each bird, might be expected to resist such bids and be motivated to invest in each offspring equally. However, if mothers can distinguish which offspring have relatively greater odds of surviving (and thus reproducing), the return on investment for each unit of investment can be maximized. From this perspective, some offspring will receive a greater share of investment than its siblings.

In those species that raise multiple dependent children of *different* ages, each offspring competes for investment with current and with future offspring. This *interbrood* conflict leads to the

prediction that offspring will be selected to force parents to supply resources that the parent would prefer to withhold for future reproduction. Parents should be equipped with mechanisms that can facilitate discriminative solicitude (for an example in humans, see Daly and Wilson 1988) to allow parents to make “informed bets” on a given offspring by sampling a variety of informational cues (e.g., reliable cues that can indicate availability of resources and/or reproductive value).

Offspring in utero do not directly compete with existing siblings for energetic resources. However, energy invested toward fetal development does so at a cost to existing offspring. Parents tend to invest slightly more than optimal but still less than what would optimal for a given offspring.

### Examples

A range of factors influence the cost-benefit calculation of investing (or not) in a given offspring. These include (among others) resource availability and offspring reproductive value.

### Offspring Reproductive Value

Parental investment will be more effective when restricted to offspring likely to survive. Parents must discriminate among offspring according to the expected reproductive success of that individual. Informative cues reliably associated with the probability of surviving can be markers of the offspring's quality like size, health, and competitive ability. Resources are finite. The ability to gauge the probability of an offspring's reproductive prospects would be adaptive. Offspring that are unhealthy or unlikely to reproduce would have been unwise investments for any parent. Across species, infants who show cues to low quality (e.g., small birthweight, physical deformity) would have been unlikely to survive (much less reproduce). Mothers with low resources are particularly at increased risk to abuse or neglect their low reproductive value offspring (Daly and Wilson 1988).



### Environmental Condition

In environments where resources are scarce, parents have to be increasingly cautious in their resource allocation decisions. In birds, scarce energetic resources lead to mothers biasing their (caloric) investment toward larger, more competitive offspring. At times, this comes at a cost to their smaller offspring who will sometimes starve as a result (Gottlander 1987; see Royle and Rubenstein 2004 for a comprehensive review).

### Reproductive Value and Environmental Condition

Investing in offspring has diminishing returns. Investment beyond a certain level will begin to yield reduced returns per unit of investment. A mother has two options when confronted with a low reproductive value child: (1) decrease investment – a strategy that is lower in risk (lower cost) and increases a mother's ability to divert resources to “safe bet” offspring at a direct cost to low reproductive value offspring fitness; (2) increase investment – a risky strategy but, if able to meet the offspring's amplified needs, parents may pay these high costs in exchange for the promise of increasing their own reproductive success.

This contingent model of parental investment predicts that mothers utilize cues of resource availability *and* child reproductive value to calibrate an investment strategy that maximizes a parents' reproductive success. When resources are scarce, mothers serve their reproductive interests best by investing in healthy offspring (see above). However, when resources are more plentiful, the contingent model *uniquely* predicts that mothers will invest disproportionately in high-risk offspring since resources are ample to allow all children to survive. Even in times of abundance, mothers face tradeoffs. At excessively high levels of parental investment, recipient offspring may be unable to take advantage of investment over and above a threshold. When mothers have ample resources, investment in high-risk offspring (as opposed to the diminished returns from concentrating investment exclusively in high value offspring) is part of a diversified investment

strategy that can pay dividends in terms of reproductive success for a mother.

Empirical support for this “if:then” pattern comes from a range of sources. Davis and Todd (1999) conducted a computer simulation study in which they made a test of the reproductive benefits offered by different parental investment strategies with different offspring (among birds). A simple heuristic emerged: When resources were scarce, the most successful strategy was to feed the chick with the greatest reproductive potential first. However, when resources were more plentiful, the most successful strategy was to feed the smallest chick first. Support for this pattern of investment comes also from evidence obtained regarding parental investment strategies from observations of some birds (Gottlander 1987) and some nonhuman primates (Nakamichi et al. 1996). It is important to recognize that parents show (automatic) decision processes that reflect the relative costs and benefits of their offspring as well as the accessibility of resources in their local environment.

### Weaning Conflict

One arena (out of many) for conflict that appears across mammals is that of weaning conflict – an example of discriminative parental solicitude that operates concurrently with parental cognitive machinery. The duration of breastfeeding and the specific timing of weaning have significant relevance to the developmental outcomes of children. In primates, weaning processes coincide with the resumption of mating (Maestripieri 2002). The amount of weaning conflict is expected to increase around the time when mothers begin to reallocate investment toward producing new offspring. Some primate infants increase nipple solicitation when mothers resume fertile ovulatory cycles, a solicitation that mothers must resist. Spotted hyena mothers wean offspring at approximately 12 months of age when resources are available but often delay weaning until 18 months of age when resources are scarce or predators are present (Hofer and East 1995). Weaning conflict is a good example of mothers monitoring and strategically responding to the reproductive value of

their current offspring and current environmental conditions.

## Conclusion

Discriminative parental solicitude is expected to be ubiquitous across species. Much of the evidence for this expectation comes from research on birds and some research on humans. In understanding the logic of discriminative parental solicitude, one can begin to understand the predictors of such behaviors that, on the surface, seem maladaptive such as infanticide – a strategy that appears across a range of species including humans (see Daly and Wilson 1988). The application of discriminative parental solicitude to understanding the adaptive functions of specific decisions made by parents will continue to be a fruitful area of research for generations to come. As research progresses on fields of study such as genomic imprinting, prenatal development, and epigenetics, there exists the potential for burgeoning empirical work that integrates models uncovered through the predictive nature of discriminative parental solicitude.

## Cross-References

- [Maternal Behavior](#)
- [Parental Investment](#)

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## Discussions

- [Referential Communication](#)

## Disease-Causing Agent

- [Pathogen](#)

## Disgust

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“The term ‘disgust’, in its simplest sense, means something offensive to the taste. It is curious how readily this feeling is excited by anything unusual in the appearance, odour or nature of our food”. Charles Darwin: *The Expression of the Emotions in Man and Animals*, 1872 (p. 256)

## Introduction

Do animals have emotions, as people have emotions? Current research in comparative psychology and affective neuroscience certainly suggests

that at least some nonhuman animals experience a range of basic emotions, including anger, fear, disgust, happiness, and sadness (Panksepp and Biven 2012). Emotions in animals were first described by Charles Darwin in his book of 1872 entitled *The Expression of the Emotions in Man and Animals*. In line with his evolutionary theory on the origin of species, Darwin argued that there was no fundamental or qualitative difference between people and animals in their affective responses to emotional events, suggesting that emotions are adaptive and serve communicative and motivational functions. This entry concerns the emotion of disgust in animals. It focuses on the behavioral (facial) expressions accompanying this fundamental emotion, the measurement of hedonic impacts of taste stimuli, as well as the brain systems that mediate the learning and expression of disgust reactions. Finally, the contribution of animal models of disgust for therapeutic treatments for nausea in humans is examined. Disgust can be defined as a marked aversion toward something distasteful, an adaptive reaction to potentially harmful foods accompanied by physiological and behavioral changes in the organism. As described by Darwin, “extreme disgust is expressed by movements round the mouth identical with those preparatory to the act of vomiting” (Darwin 1872, p. 257). Formal investigations have confirmed Darwin’s observation and demonstrate that orofacial reactions provide a key way to measure disgust in nonhuman animals.

### Affective Expression of Disgust

In natural environments, food poisoning is a substantial threat. Many species (including humans) readily learn to avoid foods or fluids paired with toxins that have previously caused them gastrointestinal malaise by acting on the emetic system of the midbrain and brainstem. This phenomenon is termed conditioned taste aversion and potentially represents a key behavioral mechanism for toxin avoidance as well as providing a useful model for the study of disgust in humans (Reilly and Schachtman 2009). According to Garcia’s

seminal demonstration of taste aversion learning in rats (Garcia et al. 1955), pairing a novel taste with nausea (e.g., produced by the administration of emetic drugs as lithium chloride) not only results in a reduction in consumption of that taste but also produces a reduction in its hedonic value or palatability that can be revealed by means of different techniques which allow the assessment of the animal’s affective reactions to taste stimuli. One of these techniques is the taste reactivity test (Grill and Norgren 1978) which is selective to disgust, in contrast to decreases in the voluntary intake of the taste which may simply reflect taste avoidance without a change in hedonic responses. In this test, rats are infused with a flavored solution via a cannula implanted in their oral cavity, and the orofacial reactions – stereotyped oral motor and somatic consummatory responses – elicited by the flavor are analyzed. These responses can be classified as aversive (i.e., disgust responses) such as gaping, chin rubbing, and paw treading (elicited, e.g., by unpleasant sour or bitter tastes) or appetitive reactions such as tongue protrusions and paw licks (elicited, e.g., by pleasant sweet tastes). It is important to note that some components of these patterns of taste reactivity are universal across many species including human infants, primates, and the rat (Berridge 2000). Figure 1 shows the most characteristic components of the orofacial reactions to sweet tastes (tongue protrusion) and bitter tastes (gaping response) in different species.

When infused with a palatable taste previously paired with lithium-induced nausea, rats display aversive orofacial reactions reflecting a shift in the hedonic value, or palatability, of the flavor from positive (appetitive) to negative (aversive). The taste reactivity test has revealed that rats display disgust reactions – being gaping the most sensitive and predominant aversive reaction – to flavors paired with drugs as lithium chloride, cyclophosphamide, or apomorphine that produce vomiting in species that are capable of vomiting (Parker 1998). Furthermore, pharmacological treatments with drugs that alleviate nausea (serotonin antagonist, cannabinoid agents) interfere with the establishment of disgust reactions to a nausea-paired flavor without affecting the



**Disgust, Fig. 1** Examples of affective responses to taste stimuli by human infants, primates, and rats (*top*, tongue protrusion (appetitive); *bottom*, gape (aversive)) (Based on Berridge and Kringelbach 2015)

amount consumed of the flavor (Limebeer and Parker 2000; Parker et al. 2011). Moreover, rendering a flavor familiar through simple exposure prior to aversion conditioning attenuates the acquisition of disgust reactions if that flavor is subsequently paired with nausea (López et al. 2010). Therefore, a reduction in taste palatability, as reflected by disgust reactions in the taste reactivity test, appears to be correlated with the acquisition of a nausea-induced taste aversion (Parker 2014).

Critically, not all types of aversive events have the same effects. Pairing a flavor with pain produced by either footshock (Pelchat et al. 1983) or the injection of hypertonic saline (Dwyer et al. 2017) results in a reduction in subsequent voluntary reduction of that flavor, but no increase in aversive taste reactivity responses indicative of disgust. Further evidence that taste aversion is mediated by internal nausea linked to disgust reactions includes the fact that rats can suppress the intake of flavors paired with rewarding drugs, such as cocaine or amphetamine, that do not result

in the production of orofacial aversive reactions to the flavors (Parker 1995). These dissociations in the impact of different classes of aversive events support the suggestion that a reduction in the voluntary consumption of a taste previously paired with aversive consequences may be motivated by two different processes: taste aversion, where the association of a flavor with nausea leads to acquisition of disgust reactions and a change in the hedonic value of the flavor, and fear-based taste avoidance based on the anticipation of a potential danger as that produced by a novel change in animal's physiological state (Parker 2014).

An alternative method for assessing taste palatability in rats involves analyzing the microstructure of licking behavior during voluntary consumption (Dwyer 2012). The ingestive behavior of rats consuming fluids consists of sustained runs of licks separated by pauses of varying length (clusters), and the mean number of licks in a cluster (lick cluster size) is directly related to the nature and concentration of the solution ingested.

Lick cluster size shows a positive monotonic relationship to the concentration of palatable sweet solutions, while lick cluster size decreases monotonically with increasing concentration of unpalatable quinine solutions. In the context of taste aversion learning, pairing an otherwise palatable taste with nausea results in a reduction of lick cluster size similar to that produced by exposure to quinine. In addition, the pattern of licking behavior is sensitive to changes in the hedonic value of taste stimuli produced by physiological and pharmacological treatments known to modulate palatability in humans. For example, sodium depletion elevates the palatability of sodium chloride, and the administration of benzodiazepines drugs, which increase appetitive responses in the taste reactivity test, enhance lick cluster size. However, while the size of licking clusters is particularly sensitive to changes in flavor palatability, it does not clearly select between disgust-based aversions and fear-based avoidance in the same way as the taste reactivity analysis. Pairing flavors with either pain or drugs of abuse can result in a lowering of lick cluster size, albeit that there are some suggestions that these effects are smaller and more transient than those produced by emetic drugs (Dwyer et al. 2017). These findings reinforce the idea that, while acquired disgust might result in reductions in consumption of particular foods, reductions in consumption cannot be unambiguously attributed to disgust in the absence of careful observation of orofacial behavioral responses directly indicative of that particular emotional response.

## Brain Mechanisms of Disgust

By using brain lesions and electrophysiological and pharmacological techniques, research in affective neuroscience has provided new findings on the brain regions and the neurochemical systems that mediate the hedonic impact of taste stimuli (Berridge and Kringelbach 2015). Neuroanatomical studies have identified a number of cortical (e.g., insular cortex) and subcortical structures (e.g., nucleus accumbens; ventral pallidum) that play critical roles in the hedonic reactivity to taste

stimuli and in the production of hedonic changes during the establishment of a taste aversion. For example, it has been reported that rats lacking gustatory cortex learn to avoid a fluid paired with lithium-induced nausea, but they fail to display disgust (i.e., aversive) reactions as assessed by the taste reactivity method (Kiefer and Orr 1992). Also, it has been found that depletion of serotonin by selective serotonergic lesions of the insular cortex (IC) attenuates the production of disgust reactions to a flavor previously paired with nausea (Tuerke et al. 2012). In addition, studies using *in vivo* optical imaging have found plastic changes in the insular cortex after inducing a reduction in the hedonic value of a taste stimulus by pairing with nausea. Taken together, these findings suggest that the insular cortex mediates the production of affective reactions to taste stimuli.

Other studies have suggested an important role of the nucleus accumbens (NAc) in hedonic reactivity to gustatory stimuli. It has been proposed that the appetitive and aversive value of taste stimuli is encoded by opposite changes in NAc neural activity (Carlezon and Thomas 2009). Specifically, decreased activity of NAc has been related to rewarding events (palatable stimuli), and in contrast, increased activity has been linked with aversive events. This suggests differences in the role of the NAc depending on the nature of the taste stimuli and their hedonic value. Using electrophysiological methods to examine neural activity during the acquisition of a taste aversion, an increase in the firing rate of NAc neurons in response to an intraoral infusion of a previously nausea-paired flavor has been reported (Roitman et al. 2010). Interestingly, a similar shift toward excitatory responses in NAc neurons is observed after the infusion of an unpalatable taste such as quinine. Conversely, the infusion of a palatable sugar solution induces a reduction in firing rate of NAc neurons, suggesting that inhibition of nucleus accumbens activity is associated with positive hedonic reactions to taste stimuli, whereas that excitation is associated to a reduction in the hedonic value or palatability of a taste stimuli.

Finally, the ventral pallidum (VP), which receives projections from the nucleus accumbens,



has been proposed to be a region that can mediate various aspects of reward and to be related to the hedonic impact of taste stimuli. The temporary inactivation of the ventral pallidum induced by pharmacological microinjections eliminates appetitive orofacial reactions to sweet tastes and replaces them with disgust reactions (Ho and Berridge 2014). Moreover, electrophysiological studies have found an increase in the firing rate of VP neurons following the intraoral administration of a sucrose solution but do not respond after the infusion of a concentrated salt solution. However, under a physiological state of sodium deficiency, the VP neurons now respond to the concentrated salt solution with an increase in firing rate similar to that produced by the infusion of sucrose (Tindell et al. 2006). Also, the neural activity in ventral pallidum is reduced when the hedonic value of a sweet taste changes from positive to negative after the establishment of a taste aversion by lithium injections (Itoga et al. 2016). Thus, like nucleus accumbens, activity in ventral pallidum neurons changes in response to the hedonic value or palatability of taste stimuli.

Pharmacological studies have identified several neurochemical systems that modulate the affective reactions to taste stimuli. There is considerable evidence suggesting that opioid neurotransmitter system mediate positive hedonic palatability. Using the taste reactivity method, it has been reported that intracranial microinjections of morphine (a pure opioid agonist) in the medial shell region of nucleus accumbens enhances the number of appetitive orofacial reactions to sweet tastes and reduces disgust reactions to bitter quinine (Pecina et al. 2006). Similarly, the firing rate of VP neurons increases when the hedonic value of a sweet taste is enhanced by opioid stimulation. Interestingly, opioid microinjection into the nucleus accumbens enhances also neural activity in the ventral pallidum, suggesting that these two brain areas act together in a coordinated hedonic circuit (Smith and Berridge 2007). Supporting this functional interaction, it has been found that microinjection of opioid antagonists in either the nucleus accumbens or the ventral pallidum prevents enhancement of appetitive responses to sweet taste. The benzodiazepine system also has

been identified by taste reactivity studies as a mechanism of positive hedonic taste affect. It has been reported that the intracranial administration of benzodiazepine agents (diazepam) enhances appetitive reactions to sweet tastes just as morphine does (Berridge 2000). Conversely, disgust reactions elicited by sucrose are reduced following the temporary inactivation of benzodiazepine receptors in the VP neurons. Finally, it has been suggested a possible role for serotonin system in hedonic reactivity to taste stimuli. For example, the intracranial administration of serotonin receptor agonists in the insular cortex increases disgust reactions and reduces appetitive responses in the taste reactivity test. Conversely, the administration of serotonin receptor antagonists attenuates the production of nausea-induced disgust reactions. Also, reduction of serotonin in the insular cortex by pharmacological lesions interferes with the expression of disgust reactions, suggesting that serotonin is mediating a shift in taste palatability from positive to negative (Tuerke et al. 2012). Recently, it has been reported that endocannabinoids interact with the serotonergic system in the control of disgust reactions. Pharmacological agents that reduce serotonin activation or that activate the cannabinoid system both interfere with the establishment of disgust reactions by emetic drugs (Parker et al. 2011). Taken together, these findings indicate that hedonic reactivity to taste stimuli is mediated by multiple neurochemical systems.

## Animal Models of Disgust in Clinical Settings

Research on animal disgust has contributed not only to know the behavioral and brain mechanisms mediating affective responses to taste stimuli but also provides a useful model for therapeutic treatments for nausea in humans (Rock et al. 2014). Nausea is one of the most distressing symptoms reported by patients receiving chemotherapy treatment for cancer. After receiving several sessions of chemotherapy, patients frequently display a range of learned effects based on the nausea induced by



chemotherapy: these include a loss of appetite and aversion to particular foods as well as the development of anticipatory nausea and vomiting that occurs when the patient return to the clinic for a further session of treatment (Stockhorst et al. 1993). Food aversions and appetite loss following chemotherapy can easily be understood in terms of the acquisition of conditioned disgust to flavors experienced prior to nausea. Moreover, the fact that animal studies have shown that conditioned disgust forms more readily for novel than familiar flavors has already led to the development of the “scapegoat” technique of providing novel foods prior to chemotherapy to prevent the acquisition of taste aversions to the main foods in patients’ normal diets (Andresen et al. 1990). Anticipatory nausea and vomiting may also be explained in terms of conditioned disgust when it is remembered that the complex of cues present in the clinic (e.g., sights, sounds, and smells) can become associated with the toxicosis effects of the chemotherapy drug (Stockhorst et al. 1993). Unfortunately, antiemetic pharmacological treatments (such as ondansetron) that block serotonin receptors reduce acute nausea and vomiting produced by the toxic drug, but they are ineffective in reducing anticipatory nausea and vomiting. Thus, there is an unmet clinical need to develop new therapeutic pharmacological drugs for prevent the side effects of nausea in cancer patients – a need that animal models of disgust can make a valuable contribution to meeting.

It has been demonstrated with the taste reactivity methodology that rats not only display disgust reactions to flavors paired with nausea, but they also display conditioned orofacial disgust reactions to environmental cues previously paired with emetic drugs as lithium chloride (Limebeer et al. 2006). It is important to note that the administration of serotonin antagonists, which attenuates the development of disgust reactions to nausea-paired flavors, does not interfere with the acquisition and expression of disgust reaction to a context paired with lithium-induced nausea (Parker et al. 2006). Therefore, contextually elicited conditioned disgust can serve as model to investigate in animals the antiemetic and

antinausea properties of new drugs. There are preclinical trials in humans suggesting that the administration of cannabinoids may be an effective treatment of chemotherapy-induced nausea (Parker et al. 2011; Rock et al. 2014). For example, the psychoactive component of cannabis, delta-9-tetrahydrocannabinol (THC), reduces acute nausea in rats by its action on cannabinoid receptors CB1 located in the insular cortex. It has been found that THC also attenuates the disgust reactions elicited by context cues paired with nausea (Limebeer et al. 2012). Likewise, other non-psychoactive cannabinoids as cannabidiol (CBD), which does not act at CB1 receptors, reduce contextually elicited disgust reactions in rats, an effect that is reversed by the action of cannabinoid antagonists (Parker et al. 2011). Together, these findings show that the rat model of anticipatory nausea provides a valuable tool for evaluating the effectiveness of antinausea treatments.

## Conclusion

Disgust in nonhuman animals is both real and readily measured through the observation of orofacial reactions. Studies of acquired disgust in laboratory rodents have made a considerable contribution to the understanding of the basic behavioral and brain mechanisms underpinning this process. Moreover, conditioned disgust provides a valuable model for investigating nausea and vomiting in clinical settings. Behavioral interventions have already been developed based on these animal models to reduce chemotherapy-based food aversions, and future pharmacological interventions for anticipatory nausea and vomiting are currently being assessed.

## Cross-References

- [Associative Learning](#)
- [Classical Conditioning](#)
- [Comparative Psychology](#)
- [Neurotransmitters](#)

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## Dishabituation

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### Definition

Dishabituation is defined as the immediate restoration of responding to a habituated stimulus that follows the presentation of a non-habituated stimulus.

### Introduction

The term habituation is used to describe the decremental effect of repeated presentations of the same stimulus upon the reflex response that this stimulus originally elicited. Habituation has been reported in a wide range of organisms, from single-celled animals to primates (Tighe and Leaton 1976). Once responding to a stimulus is habituated, presentation of a different stimulus right before presenting the stimulus that is already habituated results in a restoration of the habituated response to the original stimulus that it is called dishabituation (Thompson and Spencer 1966). The dishabituation phenomenon is one of the phenomena that allows for differentiating habituation from other decremental processes of behavior unrelated to learning such as fatigue.

Thus, dishabituation is found as a recovery of responding to a habituated stimulus as a consequence of presenting a new, different stimulus before the presentation of the original one. The amount of dishabituation decreases upon repeated presentations of the dishabituating stimulus in a phenomenon called habituation of dishabituation (Thompson and Spencer 1966). The fact that dishabituation disappears when the dishabituating stimulus habituates suggests that the dishabituating stimulus should be somehow unexpected and that it loses its power as novelty disappears (Rankin et al. 2009). Traditionally, the stimulus used to produce dishabituation has been a strong one, though some reports in the

literature show that at least in some cases the use of a weak stimulus may play even a better role as a dishabituating stimulus than a strong one (Marcus et al. 1988).

### Theoretical Approaches

Dishabituation has been traditionally explained within the framework of the dual-process theory of habituation (Groves and Thompson 1970; Thompson 2009). This theory assumes that two independent processes underlie responding to repeated stimulus presentations: A habituation process affecting the reflex-arch that mediates response decrements, and a sensitization process affecting the general state of the organism that mediates response increments. These two processes combine to produce the observed behavior. Dual-process theory of habituation suggests that dishabituation is caused by the superposition of an increase of a general responsiveness of the organism produced by the added stimulus (sensitization) that does not disrupt the process of habituation to the original stimulus, but reduces the general threshold for responding, facilitating the observation of the habituated response to the original stimulus.

The interpretation of dishabituation as an independent facilitation superimposed upon habituation suggested by the dual-process theory of habituation has accrued an important support over years of research in both, human (e.g., Kaplan and Werner 1986) and nonhuman animals (e.g., Carew et al. 1971; Kandel 1976). However, recent research seems to suggest that, at least within the field of the electrodermal orienting reflex in humans, dishabituation may also involve a disruption of the habituation process, with magnitude determined by the current arousal level (Steiner and Barry 2014). This is in agreement with the idea that dishabituation being considered as a disturbance of the habituation process as suggested by Sokolov (1963) in his neural-model comparator theory. However, these isolated results do not compromise the idea that, in general terms, dishabituation is due to the sensitization produced by presentation of the new stimulus

rather than by a disruption of the habituation process that seems to remain intact in most cases.

## Conclusion

Dishabituation, understood as the response recovery from habituation that follows the presentation of a non-habituated stimulus (dishabituation) is a broad phenomenon found in a wide range of species, and it seems generally due to the non-habituated stimulus increasing the general level of arousal of the organism (sensitization).

## Cross-References

- [Habituation](#)
- [Sensitization](#)

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## Dishonesty

- [Cheating](#)

## Dishonorable

- [Restraint](#)

## Dispersal

- [Diffusion](#)
- [Mustelidae Navigation](#)

## Dispersal Ability

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## Synonyms

[Dispersal mechanisms](#)

## Definition

The ability of an individual to relocate in order to acquire the resources needed for reproduction and survival.

## Introduction

Dispersal ability is measured by the ease with which an animal can move to acquire the resources needed for reproduction and survival (Tschamtkke et al. 2002). Ability is based on environmental pressures and the locomotive capabilities and adaptations of the species (Sekar 2012). Dispersal ability influences the geographic range of animals historically, as different ecological barriers impact species differently depending on their locomotion (Lester et al. 2007). With an increase in habitat fragmentation and the impact of climate change, the dispersal ability of a species is critical to determining survival of a population (Sekar 2012).

## Locomotive Capabilities

Animal locomotive abilities help to shape dispersal ability by determining the distance and habitat type that can be traversed (Croteau 2010; Cushman and Landguth 2012). For example, the dispersal ability of an island-dwelling individual that cannot swim or fly will be limited by the ocean barrier. Dispersal can be divided based on locomotive capabilities to active dispersal and passive dispersal (Croteau 2010).

**Active dispersal** is when animals disperse through their own locomotion. The larger the dispersal distance, the higher the dispersal ability (Croteau 2010). Flight gives many animals including birds, bats, and butterflies highly efficient dispersal ability, as they can travel larger distances and overcome barriers (Croteau 2010; Sekar 2012). In many marine animals, especially fish, dispersal occurs during the larval stage (Lester et al. 2007); however, active dispersal can occur in the adult period in other animal species (Croteau 2010).

**Passive dispersal** is when immobile or mobile animals disperse using disseminules through other vectors. This is common in aquatic invertebrates such as corals and sea anemones (Croteau 2010). Disseminules disperse through environmental vectors such as wind or by attaching themselves to other mobile animals (Croteau 2010).

There can also be a mobile larvae stage in which juveniles of a species are able to disperse to new areas by drifting to the surface and traveling on the water current (Grantham et al. 2003; Croteau 2010). This mobile larvae dispersal method can be seen in pelagic fishes and zooplankton (Lester et al. 2007).

## Habitat Connectivity and Quality

Habitat fragmentation can negatively impact the dispersal ability of a population by limiting the gene flow between populations separated by disconnected patches (Cushman and Landguth 2012). In general, larger animals are able to travel longer distances and cross larger barriers to maintain a higher degree of population connectivity (Cushman and Landguth 2012). Locomotion can mitigate the negative influence of habitat fragmentation on dispersal ability as flying animals are able to travel over some of the barriers that limit terrestrial animals (Croteau 2010). In contrast with recently changed and fragmented habitats, highly stable environments can result in the evolution of a lower dispersal ability (Lester et al. 2007). For example, some insects will lose their flight capabilities at higher altitudes resulting in lower dispersal ability (Wagner and Lieberr 1992).

## Conclusion

If locomotive capabilities are essential for determining the dispersal distance, then habitat quality and connectivity are the limiting factors to dispersal ability (Croteau 2010; Cushman and Landguth 2012). If the barriers to dispersal are restrictive enough to prevent dispersal from occurring, the result may be habitat loss and eventual population extinction (Cushman and Landguth 2012).

## Cross-References

- [Dispersal Patterns](#)
- [Migration](#)

## References

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## Dispersal Mechanisms

### ► Dispersal Ability

## Dispersal Patterns

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### Definition

Patterns of how and when individuals disperse within and between populations.

### Introduction

Dispersal is any movement of an animal from one location to another that has a chance of impacting gene flow (Ronce 2007). Dispersal can be divided

into two categories: **natal dispersal** when a juvenile leaves the parental range for a new area and **breeding dispersal** when an adult animal moves to a new area to increase breeding success (Clobert et al. 2012). Due to the dangerous nature of dispersal – the mobile individual has a higher risk of mortality during the dispersal period – the benefits must outweigh the fitness costs (Ronce 2007). Most importantly, dispersal allows for gene flow which maintains healthy, genetically diverse populations. This is essential for the survival of species in fragmented habitats (Clobert et al. 2012). Dispersal patterns define how and when individuals disperse within and between populations and may be affected by ecological composition, population demographics, and the individual (Clobert et al. 2012).

### Conditional and Unconditional Dispersal

There are two other dispersal patterns: conditional and unconditional dispersal. **Conditional dispersal** is a common pattern characterized by an individual only dispersing in response to pressures such as a lack of resources, increased mate competition, or excess population which forces the individual out of the natal range (Fattebert et al. 2015; Clobert et al. 2012; Gros et al. 2008). Conditional dispersal based on excess population is also referred to as density-dependent dispersal whereby the habitat fragment or patch is incapable of supporting the current population size (Fattebert et al. 2015; Clobert et al. 2012). **Unconditional dispersal** is the simplest form of dispersal (Gros et al. 2008). Based on the theory of inbreeding avoidance, individuals will leave the natal range at a constant rate, independent of resource availability, habitat quality, and population size, to avoid mating with kin (Fattebert et al. 2015; Gros et al. 2008).

### Sex-Biased Dispersal Patterns

Sex-biased dispersal patterns – when only one sex disperses – can be explained by inbreeding avoidance and kin competition levels (Ronce 2007).



In other words, if a single sex disperses, there is little chance of breeding between siblings (Gros et al. 2008), and there is little chance of competing with kin for resources/mates (Ronce 2007). Sex-biased dispersal patterns can also result when there is a difference in dispersal cost between the sexes. The sex with a lower dispersal cost should disperse at higher levels (Gros et al. 2008). Mate competition or competition for reproductive resources can also lead to sex-biased dispersal if there is a higher level of competition for one sex (Gros et al. 2008).

## Change to Patterns over Time

Dispersal is impacted by both ecological conditions and demographic differences resulting in patterns that can change over time (McPeck and Holt 1992). In leopard populations, where the group size fluctuates with human activity, male dispersal distances and timing have changed with males relocating next to their parental home range instead of dispersing farther away (Fattebert et al. 2015). Males will settle closer to related females, potentially increasing the rate of inbreeding and negatively impacting the genetic health of the population (Fattebert et al. 2015). Environmental changes can also influence dispersal patterns, causing them to evolve to reflect the new ecological conditions (McPeck and Holt 1992). Slow growth populations, such as density-dependent dispersers that engage in contest competition for resources, may struggle to adapt to habitat pressures caused by climate change or human activity. Their low population levels and slower growth rates will result in lower dispersal rates and reduced habitat connectivity and gene flow (Best et al. 2007).

## Current Methods

Dispersal patterns can be determined through indirect and direct methods. **Direct methods** such as tracking devices – GPS radio collars, mark-recapture, individual marking, and live trapping – are used to measure animal movement

between and within populations (Croteau 2010). These methods are both expensive and labor intensive and often result in a smaller sample size due to individual death (Croteau 2010). Genetic analysis is used in **indirect methods** by providing information on gene flows between and within populations to identify alleles and genetic markers. Patterns in genetic markers can infer relatedness and allow for a larger sample size than through direct methods (Croteau 2010). Despite these advantages, indirect methods do not provide any conclusive information on behavior (Croteau 2010).

## Conclusion

Dispersal patterns vary spatiotemporally as different populations experience unique ecological pressures that result in the evolution of varying dispersal patterns (Clobert et al. 2012).

## Cross-References

► [Home Range](#)

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## Displacement

### ► Cognition

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## Display

### ► Touch Screen

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## Displays

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### Definition

Displays are ritualized behaviors performed by an individual in order to communicate information to another.

### Introduction

Communication is a vital feature in the lives of animals. It involves an individual relaying information to others with the intent of changing their behavior. Receivers of this information may be of the same or of a different species to the signaller. Displays are repeatedly used patterns of signals which over time have evolved to become more conspicuous, often losing their original function and simply acting to communicate information (Smith 1977). These behaviors show a wide degree of variation in their

presentation and intention. Displays may be visual, chemical, vocal or postural, or multimodal and serve to communicate information relating to an individual's territory, fitness as a potential mate, or parent-infant interactions. Displays may also be used to deceive or intimidate predators. This entry reviews the contexts in which displays are used, various forms of displays across taxa, what impacts on their use, and how these behaviors evolved in detail.

### Antagonistic

Many displays are used in antagonistic situations, such as defending a territory, to dissuade predation, or in relation to conflict with other members of the same species. Some species use displays to defend their territories. This has been seen in territorial male goitered gazelles, *Gazella subgutturosa*, which roar and press horns during encounters with other males (Blank et al. 2015). The authors suggest these displays may function to communicate male endurance, avoiding the need for fighting during a time of decreased body mass and increased mortality for males. When fights do occur, many species perform post-conflict displays. Grafe and Bitz (2004) observed post-conflict victory displays after conflicts between pairs of tropical boubous, *Laniarius aethiopicus*, proposing that these vocal displays are used to show their victory to other pairs nearby. On the other hand, those who lose conflicts may use displays to try to appease their opponent. An example of this behavior can be seen in crayfish, *Orconectes rusticus*, which whip their antennae to appease dominant individuals after conflicts (Bruski and Dunham 1990). Displays can also be used to communicate information about an individual's social ranking within a group. Oystercatchers, *Haematopus ostralegus*, perform displays involving piping calls in order to maintain their position within the dominance hierarchy. These displays were used by lone birds in order to maintain feeding ranges and in groups to contest these areas (Ens and Goss-Custard 1986). Additionally, high-ranking individuals used a “butterfly flight” in

which they circled an area before landing (Ens and Goss-Custard 1986). When threatened by a predator, some species use deimatic displays to scare off potential attackers. Species using these displays are often camouflaged or mimicking another species or inanimate object, for example, mountain katydids, *Acripeza reticulata*, raise their wings and expose the bright colors on their body in order to shock predators (Umbers et al. 2015). Overall, displays are used to communicate a variety of messages in antagonistic situations, including territory ownership, social ranking, appeasement, and victory, as well as to avoid predation and physical confrontations.

## Mating

Courtship displays consist of a multimodal collection of behaviors which are performed in order to attract or maintain a mate. These displays are usually seen in male individuals; however, they may also be performed by females, or by both sexes in mutual displays. Additionally, both socially monogamous and polygamous species have been recorded using courtship displays. These displays are thought to act to allow for the recognition of individuals of the same species and opposite sex. This can be seen in the male courtship songs of fruit flies, *Drosophila* sp., in which song traits such as length and frequency of song pulses differ between species (Saarikettu et al. 2005). Another function is to synchronize mating behaviors, stimulating females to mate in species that do not take environmental cues for breeding. For example, male wolf spiders, *Stegodyphus lineatus*, perform vibrating behavior in order to encourage mating (Maklakov et al. 2003). Similarly, shuddering behaviors in male orb-web spiders, *Argiope keyserlingi*, serve to help prevent cannibalism from the female during mating (Wignall and Herberstein 2013). In female courtship displays, behaviors are suggested to honestly indicate an individual's reproductive potential and proximity to spawning time, as is seen in the rush and twitching displays of the Banggai cardinalfish, *Pterapogon kauderni* (Kolm 2004).

The mutual courtship displays of socially monogamous blue-capped cordon-bleus, *Uraeginthus cyanocephalus*, involve calling and dance behaviors and are suggested to have several functions. One purpose is to advertise the pair bond and signal commitment to others of the same species, while on the other hand may also serve to find mates outside of the pair (Ota et al. 2015). Overall, courtship displays are found across various species and can be performed in many different forms such as song and movement. These displays may serve multiple purposes such as species recognition, synchronization of mating, advertising reproductive potential, or reinforcing pair bonds.

## Parent-Offspring Interactions

Displays from offspring aimed at their parents are often seen in bird species, typically when requesting food. These displays often involve posturing, exposing colored mouth gapes, and repeated calling from nestlings. It is suggested that this display functions to resolve parent-offspring conflicts, in which an individual nestling aims to receive more investment from the parents than current siblings (intra-brood conflict), as well as future broods (inter-brood conflict) (Trivers 1974). To accomplish this, displays may act to persuade parents to offer more food to the nestling through signalling that they are in good condition and so worth extra investment, or by showing an honest need for food. Examples of these displays can be seen in nestling tree swallows, *Tachycineta bicolor*, which posture more intensely in relation to increased hunger, resulting in preferential feeding from the parents (Leonard et al. 2003). They also found that nestling calling rates related to where nestlings were located in the nest, with higher rates from those in more difficult to reach positions for parents, possibly to attract their attention. In barn swallows, *Hirundo rustica*, hungry nestlings called more often, and those in good condition called at a lower frequency (Sacchi et al. 2002). Displays exposing nestling mouth gapes are also proposed to suggest nestling condition, as those in better health are able to devote more resources to maintaining a

brighter gape (Saino et al. 2000). Other forms of display include wing shaking and gape-colored patches on the wings of brood-parasitic species such as the Horsfield's hawk-cuckoo, *Hierococcyx hyperythrus*. It is suggested that wing shaking may serve as an indicator of nestling condition, while wing patches may function to imitate the gapes of several nestlings, encouraging more feeding from parents (Tanaka and Ueda 2005; Grim 2008). Components of begging displays are thought to act together to communicate various aspects of nestling condition, such as the intensity of hunger and quality of the individual begging.

### Influences on Display Behavior

Several factors can affect the use of displays. Many of these influences are environmental, such as wind, light levels, distance from receiver, and perceived predation risk. Peters et al. (2007) found that the Jacky lizard, *Amphibolurus muricatus*, perform their aggressive tail flick displays for longer and in an intermittent pattern in stronger wind conditions. They propose that this may be due to the lizards timing their flicks for visibility among moving plants, increasing the likelihood that their display is seen by the receiver. Male guppies, *Poecilia reticulata*, use a visual display involving colored spots of varying sizes in courtship. When light levels within the streams they occupy are low, males reduce their distance to females in order to best show spot contrast and brightness, which are features preferred by females (Long and Rosenqvist 1998). Distance is an influence for male fiddler crabs, *Uca perplexa*, during their claw-waving courtship display, in which they shorten the duration and lateral movement involved in the display with reduced distance to females. This is suggested to reduce the energetic cost of displaying and appear less aggressive (How et al. 2008). Similarly, distance is a factor for male zebra finches, *Taeniopygia guttata*, who perform their vocal courtship display at a higher amplitude when females are further away in order to best transmit the signal (Brumm and Slater 2006). Another environment factor

is predation risk. Su and Li (2006) found that when female jumping spiders, *Jacksonoides queenslandicus*, perceive a higher risk of predation, both courting males and females respond by reducing the duration of their displays. Additionally, male túngara frogs, *Engystomops pustulosus*, were found to reduce the rate and amplitude of mating calls when confronted with a model predator (Ryan 1985). Social factors can also influence how displays are used. In whitethroats, *Sylvia communis*, courting males perform a display involving vocal and diving components. Female calls (dscharps and ze-calls), as well as short jumps around males have been observed to influence their display, causing an increase in songs and copulation (Balsby and Dabelsteen 2002). Brooke et al. (2000) examined the effect of others on the calling of ornate nursery frogs, *Cophixalus ornatus*, finding that males would use the calling of others to determine when they should call. Social facilitation of displays has also been seen in lesser short-tailed bats, *Mystacina tuberculata*, in which lekking males displaying alone would sing more than those in groups (Toth et al. 2018). An individual's physical features can also play a role in display behavior. Male dunlins, *Calidris alpina*, display more frequently and spend more of their displays hovering when they have a smaller body size (Blomqvist et al. 1997). In conclusion, displays are complex behaviors which can be affected by several factors, including environmental, social, and physical influences.

### Evolution of Displays

There are multiple theories as to how these display behaviors evolved over time across various contexts. For antagonistic displays between members of the same species, the cost of a physical fight is suggested to be the cause for their evolution. Displays offer an opportunity to weight up the likelihood of winning a physical fight and allow for avoiding a fight completely (Maynard Smith 1982). Deimatic displays are thought to have co-evolved alongside predator behaviors, developing the display in response to predators

becoming better at seeing through the first level of defense that species has, for example, camouflage (Umbers et al. 2015). Sexual selection is believed to have played a role in the evolution of courtship displays, with two main hypotheses to suggest how. One proposes that displays communicate good genes and so are chosen as mates in order to pass these onto offspring (Maynard Smith 1991). The other suggests that it is instead the display itself that is chosen, as this makes them appealing mates (Fisher 1930). Nestling begging displays are thought to have evolved due to competition between siblings, as displays increase in intensity and frequency with increased competition (Kim et al. 2011). On the other hand, other studies suggest that begging displays evolved to honestly communicate nestling condition, which in turn allows parents to invest the optimal amount of time in that individual (Sacchi et al. 2002). In terms of specific behaviors, Grim (2008) hypothesizes that nestling display behaviors such as wing shaking developed from behaviors shown during restlessness and over time became ritualized for begging. Overall, there are several evolutionary paths that led to the development of display behaviors, many of which are not yet fully understood.

## Conclusion

In conclusion, animals across multiple taxa use behavioral displays in order to share information with others, including amphibians, reptiles, birds, arthropods, and mammals. Displays may be used in antagonistic, mating, and parent-offspring interactions, involving visual, vocal, postural, or chemical signals. In many cases, such as nestling begging displays, multiple modes of signalling are used to communicate with the parents. Additionally, these displays can be influenced by factors within the environment such as predation risk, light levels, wind conditions, and distance to receiver. Social influences can also impact on and facilitate display behaviors. These can affect how long or intense displays are in an effort to best communicate to a receiver. There are currently several hypotheses on how and why displays

have evolved, including as a mechanism to avoid physical confrontations and predation, communicate good health and genes, and deal with sibling competition. However, there is still further research needed to fully understand the evolutionary mechanisms behind display behaviors.

## Cross-References

- [Auditory Signals](#)
- [Chemical Cues](#)
- [Communication](#)
- [Courtship Rituals](#)
- [Honest Signaling](#)

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## Disposition

### ► Temperament

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## Disruptive

### ► Zigzag Display

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## Disruptive Coloration

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## Definition

A set of markings that creates the appearance of false edges and boundaries and hinders the detection or recognition of an object's, or part of an object's, true outline and shape.

## Introduction

The threat of predation has driven the evolution of diverse anti-predator adaptations in nature, of which camouflage – or concealment – is widespread. One striking form of camouflage is disruptive coloration, in which contrasting markings



are used to break up and obscure an object's appearance. First alluded to by the naturalist Poulton (1890), and later formalized by Thayer in *Concealing Coloration in the Animal Kingdom* (1909) and Cott in *Adaptive Coloration in Animals* (1940), the efficacy of disruptive coloration has been convincingly demonstrated across the natural world. From the banded wings of tropical butterflies, to the bold spots of isopods, to the changeable patterns of cuttlefish (Merilaita 1998; Hanlon et al. 2009), the study of disruptive coloration has advanced our broader understanding of adaptive coloration and predation-prey interactions and has also inspired developments in human technologies.

## Mechanisms

Disruptive coloration functions by creating the appearance of false boundaries (Stevens and Cuthill 2006). This may occur both within an object to disrupt its internal shape or at its edges to confuse the distinction between an object and its background. Numerous sub-principles have been proposed that detail the mechanisms underlying the efficacy of disruptive coloration, though five appear to capture the key processes of interest (Stevens and Merilaita 2009), namely:

1. *Differential blending* occurs when parts of a color pattern match the viewing background, while others are strongly contrasting, thereby breaking up an object's contours.
2. *Disruptive contrast* describes the use of highly conspicuous, contrasting pattern elements set adjacent to one another, with the expectation that a higher degree of contrast will be more effective in inducing disruptive effects.
3. *Disruption of surface through false edges* occurs when contrasting internal markings generate illusory boundaries on the surface of an object, thereby masking its true shape.
4. *Disruptive marginal patterns* are those which make contact with an object's edge, to blur the distinction between parts of an object and its background and/or generate the impression of discontinuity.
5. *Coincident disruptive coloration* describes the geometry of disruptive color pattern elements, which may spread across distinct body regions to confuse the otherwise clear boundary between them.

These principles are nonexclusive and typically act in concert to achieve their full effect. Marginal patterns, for example, are often combined with differential blending, to engage the viewing background itself in breaking up an object's form (Cuthill et al. 2005). Similarly, coincident disruptive coloration is particularly effective in conjunction with strong disruptive contrast, to both mask the boundaries between regions and the overall form of an object (Barry et al. 2015).

## Technological Applications

Like so much in the natural world, the cryptic color patterns of animals have served as inspiration for varied applications in human affairs. The work of Thayer (1909) directly inspired early efforts at military camouflage during World War I, and disruptive patterns are now a defining feature of many military uniforms (Newark et al. 2002). As in nature, however, the use of such a strategy has proven challenging under dynamic real-world conditions, as the efficacy of disruption is severely reduced, for example, against variable backgrounds, while in motion or in unfavorable viewing conditions. And just as an animal's visual camouflage is less effective against predators that draw on diverse sensory input, the development of radar has rendered the use of disruptive coloration largely redundant for larger-scale military structures, such as planes and ships. More recent efforts have also seen the principles of visual disruption applied to everyday situations, such as in conspicuously colored "shark-repellent" wetsuits and surfboards. These rely on boldly contrasting patterns to inhibit the identification of swimmers as potential food sources by sharks which, incidentally, are largely color-blind.

## Conclusion

Disruptive coloration hinders the detection and recognition of an object's form by creating false internal and/or external boundaries with contrasting markings. It is a common mode of camouflage in nature and is a highly active area of research in the study of adaptive coloration.

## Cross-References

- [Adaptation](#)
- [Camouflage](#)
- [Cryptic Coloration](#)
- [Predator Defense](#)
- [Visual Recognition of Prey and Predators](#)

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## Distance Effect

- [Symbolic Distance](#)

## Distraction Display

- [Broken Wing Display](#)

## Distributive Coding

- [Cognition](#)

## Diurnality

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## Synonyms

- [Day-active](#)

## Definition

Diurnality is a type of daily (or diel) activity pattern in which most of the activity occurs during the light hours of the day.

## Introduction

A day in an animal's life typically alternates states of rest and activity. A variety of behaviors are performed when the animal is active, such as foraging, territory defense, exploration, and mating. The time when activity occurs is crucial to an animal's survival, since these are the moments in which it is most vulnerable to predators and harsh weather conditions. The alteration between the states of activity and rest during the 24-h daily cycle results in a temporal pattern called daily, or diel, activity pattern (Halle and Stenseth 2000). These patterns are commonly classified as diurnal (i.e., most of activity occurs during the light phase of the day), nocturnal (i.e., most activity occurs during the dark phase of the day), crepuscular (i.e., most activity occurs during dawn and dusk), and cathemeral (i.e., activity occurs during both light and dark phases of the day) (Daan 1981).

Daily activity patterns are accompanied by daily rhythms in many physiological variables. Diurnal animals not only allocate most of the behavioral activity during the light hours of the day, but it is also during this phase of the day that they display higher body temperature, higher heart rate, higher digestive function, and peak of hormones such as glucocorticoids.

## Physiological Mechanisms Behind Diurnality

The 24-h rhythmicity of behaviors and physiological processes is not merely a reaction to daily environmental cycles, such as light intensity, temperature, or food availability. This rhythmic expression persists even when the organism is exposed to conditions in which all environmental variables are held constant. In this situation, the period of the expressed rhythm (i.e., the interval of time each cycle takes to complete) is always different, although close to 24 h, which is why this rhythm is called circadian, a Latin term meaning "around one day." Persistence under constant conditions is evidence that these rhythms are generated endogenously by circadian oscillators (Moore-Ede et al. 1982).

Circadian rhythms are present in all taxa of living beings, from protists to multicellular eukaryotes (Dunlap et al. 2004). The basic structure of the circadian system in animals consists of a circadian oscillator, which generates the rhythm; efferent pathways, which transmit the rhythmic signals of the oscillator to the various organs and tissues of the organism; and afferent pathways, which receive, process, and transmit the temporal information from the environment to the oscillator (Moore-Ede et al. 1982).

In mammals, the central circadian oscillator is located in two small hypothalamic nuclei located above the optic chiasm, the suprachiasmatic nuclei (SCN). The daily light-dark cycle is the main environmental cycle involved in the synchronization of the circadian oscillator. Light is perceived by the retina, which has direct nervous projections to the SCN, through the retinohypothalamic tract. The SCN have many nerve projections to other areas of the hypothalamus and the brain and chains of neurons connecting them to peripheral organs. These projections can serve as efferent nerve pathways, which transmit the oscillator signals. In addition to these pathways, there is also evidence of neurosecretory efferences (Dunlap et al. 2004).

Despite the opposite temporal patterns in behavior that define diurnality and nocturnality, the neural activity of the SCN of diurnal mammals is very similar to the one in nocturnal mammals, with the highest metabolism and electrical activity always occurring during the light hours of the day (Yan et al. 2018). This similarity suggests that the mechanism defining the timing of behavioral activity (i.e., diurnality or nocturnality) occurs downstream from the central circadian oscillator. To date, evidence indicates that there is no single "switch" controlling the timing of activity, but rather diurnality results from the interrelationship of several mechanisms in the efferent pathways from SCN that regulate behavior and physiology (Yan et al. 2018).

## Evolutionary Aspects of Diurnality

Diurnality is widespread among all major groups of animals. In vertebrates, it is the predominant

activity pattern in fish, reptiles, and birds. Mammals and amphibians, on the other hand, are predominantly nocturnal (Daan 1981). The switch to nocturnality in mammals is believed to play an important role in the radiation of mammals in the Mesozoic, according to the “nocturnal bottleneck” hypothesis (Gerkema et al. 2013). Nevertheless, diurnality reappeared, independently, in several groups of mammals. Recent phylogenetic studies suggest that diurnally started to resurface in mammals during the Cenozoic, with simian primates being among the earliest mammals to be diurnal (Maor et al. 2017).

There are several morphological and physiological specializations related to diurnality. Many of them involve the visual system, such as eye size and shape; high concentration of ascorbic acid in the eyes, which protects them from solar radiation; and photoreceptor distribution in the retina, which usually has more cones in diurnal animals than in nocturnal ones (Kronfeld-Schor and Dayan 2008). Other specializations include dark pigmentation of the skin and physiological adaptations related to maintenance of the water balance, specially in desert animals.

## Flexibility of Activity Patterns

Characterization of a species as diurnal seems straightforward under controlled, narrow, laboratory conditions. This standard characterization, together with anatomical and morphological specializations, can lead to the conclusion that diurnality is an inherent and fixed characteristic of the species. However, activity patterns are much more plastic in nature. Many species that are classified as nocturnal because of their activity pattern under standard laboratory conditions switch to diurnality when exposed to a variety of environmental and social factors, such as energetic challenges, changes in light intensity, introduction of a running wheel, and presence of inter- or intraspecific competitors and predators (Hut et al. 2012). Switches of typically diurnal species to nocturnality can also occur in response to high ambient temperatures, competitors, or predators. Moreover, many species switch their

activity patterns across seasons, being diurnal in the winter and nocturnal during summer, for example (Levy et al. 2019).

## Final Remarks

Diurnality is a widespread activity pattern in the animal kingdom. Nevertheless, classifying an animal as diurnal is not straightforward, since many species switch their activity patterns under certain environmental conditions. Although characterization of activity patterns in natural settings is challenging due to the need of continuous measurement of activity during several days, it can shed light on the ecological and evolutionary significance of diurnality and the flexibility of activity patterns.

## Cross-References

- Biological Clocks
- Biological Rhythms
- Cathemeral
- Circadian Rhythms
- Crepuscular
- Day/Night Cycle
- Foraging
- Internal Clocks
- Light/Dark Cycle
- Photoperiod

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## Divergent Evolution

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### Definition

Divergent evolution represents the evolutionary pattern in which species sharing a common ancestry become more distinct due to differential selection pressure which gradually leads to speciation over an evolutionary time period.

### Introduction

Earth as we see today in its present form with diverse life forms is the result of evolution that has been in action since its inception. Evolution is the biological process through which

characteristics of a species changes gradually over time with the help of the forces of natural selection (Gregory 2009). It is a common belief that all the life forms that exist have gradually developed from a single common ancestor through the process of evolution (Ashraf and Sarfraz 2016). The main driving force behind evolution is better adaptation and reproductive success of species in its changing environment. Genetic variations present within the populations acts as a raw material on which various forces (like natural selection, genetic drift, etc.) act that results in a gradual change in the characteristics of present forms from their ancestors. The ultimate source of these variations is mutation and genetic recombination (Barton 2010). The process of evolution is dynamic and occurs at different rates and patterns. The mechanisms that are instrumental in evolution process are natural selection, genetic drift, gene flow, and biased mutation (Ashraf and Sarfraz 2016). Under the influence of differential selection pressure, evolution over time follows several different patterns which forms the basis for its classification. Based on this four main types of evolution are: divergent, convergent, parallel, and coevolution (Stearns and Hoekstra 2000). When organisms belonging to two or more lineages evolve similar features independently in an attempt to adapt to similar environmental conditions or same selective pressure, the evolutionary process in action is Convergent evolution (Stayton 2015). Wings of insects and of birds (analogous structures) are an example of convergent evolution. Parallel evolution is the evolutionary process through which different species belonging to closely related lineages show evolution of similar traits/attribute in an independent manner while adapting to the same kind of environmental selection pressure (Bailey et al. 2017). Parallel evolution is exemplified by the similarity between marsupials of Australia and placental mammals of other continents. Coevolution is instrumental when closely interacting species exert selective pressures on each other, as a result they adapt and evolve together. Most common examples include prey-predator relationship, host-parasite interaction, and symbiotic relationship (Thompson 2010).

The term divergent evolution was first introduced by J. T. Gullick. Divergent evolution occurs when differential selection pressure or evolutionary driving force (both biotic and abiotic) acts on a subgroup of species which leads to accumulation of variations that favors better adaptation (Schluter 2001). The buildup of these adaptive traits makes this subgroup more and more distinct from their ancestor. Thus, divergent selection eventually leads to speciation over an evolutionary time period (Rundle and Nosil 2005). Divergent evolution is mandatory to achieve best chances of survival in changing environment. In the consecutive sections, various aspects associated with divergent evolution are covered in detail.

## Forces Behind Divergent Evolution

Divergent evolution or evolutionary branching occurs in response to selective pressure like changes in biotic factors (e.g., species interactions) and abiotic factors (environmental factors like climate, nutrient status, physical structure, and niche divergence) which drive natural selection. These sources have been discussed in detail under separate headings (Schluter 2001).

### Species Interactions

The major biotic factor that leads to divergent selection is inter- and intraspecific interactions among organisms present mainly in sympatric populations. Species interactions in the form of competition, predation, mutualism, etc., play role in divergent evolution (Doebeli and Dieckmann 2000). However, they may or may not lead to speciation. Many studies suggest that interspecific competition is the predominant factor playing role in divergent evolution (Schluter 2001; Rundle and Nosil 2005). Weak species interactions do not play much role in evolution dynamics; however, they can bring about minor changes in population sizes (Barracough 2015). Strong species interactions are major players that bring about profound changes in evolution dynamics. Various positive (commensalism, symbiosis) and negative (competition, predation) species interactions

among different organisms in a community alters population size and in doing so also alters evolutionary rate. Smaller populations show lesser adaptability in changing environmental conditions leading to greater fluctuations and size reduction whereas huge stable populations adapt better and show better reproductive fitness bringing about change in evolutionary outcomes (Johansson 2008). Species interactions can also lead to co evolution across communities due to selection pressure on species by mutualists, predators, and competitors. Species interaction works synergistically with abiotic pressures (environmental changes) and promotes evolutionary responses with the help of ecological network.

### Environmental Differences

Various abiotic stresses in the form of changing environmental conditions are one of the primary sources of divergent evolution (Schluter 2001). Divergent selection normally arises among populations of same species allopatrically separated in different environmental conditions or in populations (sympatric) inhabiting different niche existing in the same geographical region (Mayr 1947). While adapting to these differing environmental gradients (climate, available resources, physical structure, etc.), different populations might develop barrier to gene flow and become reproductively isolated over an evolutionary time period leading to speciation (Nagel and Schluter 1998). Some species respond better to a certain environmental condition by the virtue of specific phenotypic traits whereas their fitness reduces in another environment, insinuating divergent selection in action (Rundle and Nosil 2005).

### Sexual Selection

Sexual selection is another potent source behind divergent evolution. It is a constituent of natural selection and arises due to variability in fertilization rate (Ritchie 2007). Sexual selection can act as a powerful evolutionary source in achieving reproductive isolation as it directly interacts with traits associated to mate recognition (Panhuis et al. 2001). The reason behind sexual selection is that in a population, individuals exhibit differential reproductive success due to variation in



secondary sexual characteristics and mating choices. Thus, sexual selection might contribute to speciation by achieving divergence in mating choices and signals (Panhuis et al. 2001). In certain scenarios sexual selection might lead to co-evolutionary divergence of traits that mutually influence partner's evolution (e.g., female select mate on the basis of their mating signals) (Ritchie 2007). Sexual selection can lead to divergence within isolated populations either independently or synergistically along with environmental differences (Ritchie 2007).

### Natural Selection

The most crucial process of evolutionary change that is responsible for the adaptability of living world is natural selection (Gregory 2009). The differential selective pressures discussed in the section above drive natural selection and compel the organisms to evolve. In order to adapt to varying conditions generated by selective pressures (environmental differences, species interaction, and sexual selection), organisms change and through the mechanism of natural selection, trait fittest for the survival of organism is selected and propagated further. It increases the frequency of genetic traits that are better suited to natural environment and eliminates the less suited ones. The origin of genetic variant through mutation is a random and directionless process; however, their propagation in next generation through natural selection is nonrandom and directional due to its pivotal role in survival and reproduction (Gregory 2009). Natural selection leads to differential survival among organisms of same species and is carried out in three ways namely directional, stabilizing and disruptive selection (Losos 2017). Under changing environmental condition when either one of the extreme phenotype is favored or average is eliminated, selection is directional and it changes the mean value of the population's trait. An example of directional selection is industrial melanism. Similarly, when both the extreme phenotypes have greater fitness and intermediates or average phenotypes are eliminated, selection is known as disruptive selection. It leads to fragmentation of population into various adaptive forms and may lead to speciation (Boddum 2008). On

the contrary, stabilizing selection favors intermediate or average phenotypes and eliminates extreme phenotypes, thereby increasing homozygosity in nonvariable environment (Boddum 2008).

### Evidence of Divergent Evolution

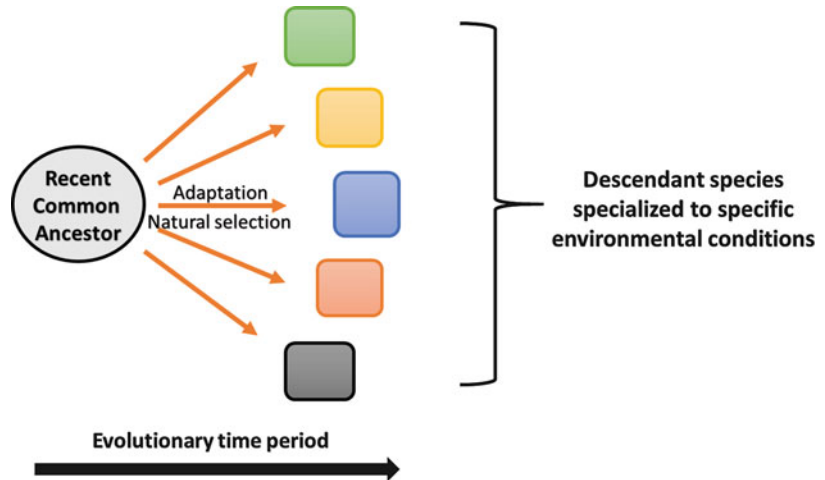
A better understanding of the process can be developed by studying the examples of divergent evolution.

#### Darwin's Finches and Adaptive Radiation

Divergent evolution is best exemplified and discussed through the study of Darwin's Finches. Darwin's finches actually show adaptive radiation which is a form of divergent evolution. It was Darwin who first introduced the concept of adaptive radiation. The process through which a recent ancestral species diversify into a number of descendant species while adapting to changing environmental conditions like availability of new resources or new niches (niche divergence) is known as adaptive radiation (Losos and Mahler 2010). Through the process of speciation and phenotypic adaptation species with different physiological and morphological traits evolve from a recent common ancestor. Adaptive radiation deals with microevolution occurring over a shorter time period, whereas divergent evolution deals with species evolution from their ancestors over a larger time period. Adaptive radiation was observed in finches of Galapagos and Hawaiian island. Galapagos Island is basically an archipelago consisting of a group of major and minor islands which is geographically isolated from mainland of South America and is inhabited by 15 different species of Darwin's finches belonging to tanager family (Losos and Mahler 2010). Each of these bird species evolved from a single common ancestor of mainland and then diverged in order to adapt to the different kinds of habitat, available food resources, and local conditions of the new island (Neige 2015). Through the forces of natural selection in action, genes that favored better dietary adaptation accumulated and lead to remarkable diversity in shape and sizes of beaks

**Divergent Evolution,**

**Fig. 1** Figure depicting formation of new species through adaptive radiation



D

of these birds. Species divergence increases with greater accumulation of structural differences. The major categories of Darwin's finches that diverged are ground finches, warbler finches and tree finches. In Fig. 1 the formation of new species through adaptive radiation has been depicted.

### Forelimbs of Mammals and Homologous Structures

An astounding example of divergent evolution is the forelimbs of mammals. In order to fill in the variety of niche available, mammals diversified from a recent ancestor by accumulating different adaptive traits which eventually led to speciation. This divergence (adaptive radiation) can be clearly seen in the various modifications of the forelimbs of different mammals like whale's fin, human arm, elephant's leg, and bat's wings (Weatherbee 2008). Although each of these structures is specialized for different function, the basic anatomy of forelimbs, that is, bone structure, is similar indicating they evolved from a recent common ancestor. Thus, divergent evolution might lead to formation of homologous structures as is in the case of forelimbs of mammals. Thus, homologous structures are organs or bones showing functional diversity but similar anatomical features indicating a shared common ancestry resulting from divergent evolution. In conclusion, greater accumulation of structural differences among related species indicates that species divergence has been in action for a longer time period.

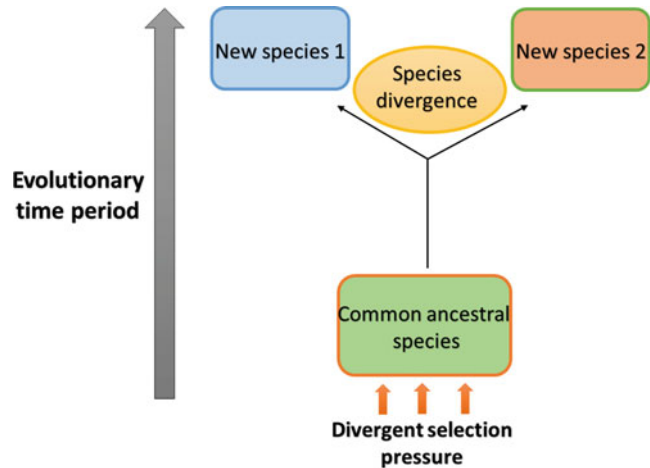
### Other Common Examples of Divergent Evolution

- (a) Human and apes evolved from a common primate ancestor. Similarly, woolly mammoth and elephants have diverged from a common ancestor.
- (b) Divergent evolution is exemplified in the diversity of orchids with different adaptive traits.
- (c) Another example of homologous structure (resultant of divergent evolution) is observed in thorns of Bougainvillea and tendrils of cucurbits as both are modifications of axillary bud.
- (d) Kit fox (*Vulpes macrotis*) adapted to desert environment and arctic fox (*Vulpes lagopus*) adapted to cold climates diverged from a recent common ancestor to adapt to their varying extreme habitats.

### Speciation

The most important and concluding consequence of divergent evolution is speciation (Schluter 2001). Figure 2 depicts the occurrence of speciation event through divergent evolution. Genesis of new and separate species as a result of the lineage splitting evolutionary process is speciation. Many environmental agents of differential (divergent) selection pressure acts upon the variations (source being mutation and genetic

**Divergent Evolution,**  
**Fig. 2** Divergent evolution  
 leading to speciation



recombination) present in the gene pool (Barton 2010) and might bring about major differences or accumulation of a number of minor differences in adaptive traits which would eventually lead to change in structure or phenotype. The aim behind all this work is survival, adapting to change and achieving reproductive success. When ecological basis of divergent selection leads to speciation then it is known as ecological speciation (Rundle and Nosil 2005). Ecological speciation is the development of gene flow barriers or reproductive isolation in response to divergent selection pressure (ecological in nature) like environmental differences, sexual selection, and species interaction. Although there are other ways or chance events like polyploidization, genetic drift, founder effect, hybridization, and bottleneck effect that could lead to speciation (Coyne and Allen Orr 1998). Sexually reproducing organisms undergo speciation due to development of reproductive barrier through evolutionary process which restricts gene flow between populations (Turelli et al. 2001). Thus, reproductive isolation (premating or postmating isolation) is the critical requirement for speciation in sexually reproducing organisms. Geographical isolation is contributory in diversification of populations leading to speciation.

Modes of speciation are commonly categorized by making use of geographical context that results in reproductive isolation (restricted gene flow) among populations (Mayr 1947). Thus, according to geographic classification, four

means of speciation are allopatric, sympatric, parapatric, and peripatric (Mayr 1947; Schluter 2001). For the speciation process to occur, there are certain prerequisites that need to be fulfilled and they are prezygotic isolation mechanism, source of divergence (including spatial divergence leading to geographical isolation), source of divergent (including disruptive) selection, transmission of divergent selection or evolutionary forces (genetic drift, mutation, natural, and sexual selection) on reproductive isolation traits and presence of variation in gene pool to increase isolation (Kirkpatrick and Ravigné 2002). These forces work in unison and lead to speciation. Pleiotropism (direct selection) and linkage disequilibrium (indirect selection) are two processes that are instrumental in transmission of divergent selection of ecological characteristics/traits to genes developing reproductive barriers (Kirkpatrick and Ravigné 2002). Speciation event is continuous and generally extends over many generations (Coyne and Allen Orr 1998). In the subsequent section, different modes of speciation have been discussed in detail.

### Allopatric Speciation

*Allopatric speciation* is the most familiar form of speciation. Allopatric speciation arises when restricted gene flow occurs among populations because of physical isolation generated due to geographical barrier. Thus, spatial separation or physical isolation triggers divergence and leads to

development of gene flow barriers. Until and unless reproductive capability is restored through certain selective forces, the isolated subpopulations will become more incompatible with time (Turelli et al. 2001). Geographical isolation or some kind of physical barrier between two subpopulations is mandatory for allopatric speciation to occur. Natural selection and genetic drift acts independently on each separated population thereby producing varied evolutionary outcomes. In isolated small population, genetic recombination leading to new combination of traits or random mutation gets fixed by chance. Natural selection acts distinctively on these differences and leads to evolution of subpopulation differently from parent population (Boddum 2008). This type of speciation emphasizes upon the importance of geographical isolation and ecological adaptation.

### Peripatric Speciation

*Peripatric speciation* is quite comparable to allopatric speciation. The only distinction is that it occurs when from a much larger population a very small subpopulation with smaller gene pool isolates which is more responsive to natural selection and genetic drift. This greater sensitivity of smaller population (smaller gene pool) to selective forces is known as Founder effect, which leads to rapid divergence and speciation (Lawson et al. 2015). Like allopatric speciation, physical isolation between founder peripheral population and parent population forms the basis of restricted gene flow in peripatric population. Due to the selective forces like genetic drift and natural selection, the isolated smaller population differs in allelic frequency from origin population. Further, spatial/geographical separation leads to accumulation of new additional genetic variations that might cause reproductive isolation between parent population and smaller founder population (Lawson et al. 2015). This may or may not lead to speciation.

### Sympatric Speciation

*Sympatric speciation* is the form of speciation in which gene flow is blocked due to intrinsic factors like nonrandom mating or chromosomal changes

(Boddum 2008). This form of speciation is most debated because it lacks any physical form of isolation. The steering force behind sympatric speciation is disruptive selection (Turelli et al. 2001). It occurs in cases where populations are within geographical reach of each other or share same habitat/environment and do not have extrinsic barrier to gene flow. Due to the reproductive barriers among individuals of a population, new species evolve within the geographical reach of parent population. In allopatric speciation, complete isolation is achieved, whereas in case of sympatric speciation continued gene flow might occur for generations even after populations separate or diverge (Schluter 2001).

### Parapatric Speciation

*Parapatric speciation* is rare and occurs when a small subpopulation starts diverging from its parent population when it enters an extreme different niche while remaining within its original habitat (Yamaguchi and Iwasa 2017). The subpopulation develops reproductive barrier because of intrinsic factors rather than geographical isolation and might lead to speciation. Since the diverging subpopulation is small (smaller gene pool) the selective forces (founder effect, genetic drift and natural selection) can also play pivotal role in speciation.

### Conclusion

Divergent evolution is a universal and complex process. A better understanding of divergent evolution can solve many questions pertaining to evolution of diverse life forms on Earth. Divergent evolution plays primary role in generating the diversity of species (biodiversity) through the process of speciation. Different species thrive in diverse habitats by adapting to them. Divergent evolution or selection confers adaptive ability to ancestral species to evolve in new/changing habitats and environment. This adaptability causes accumulation of diverging traits that makes them dissimilar from their ancestor and leads to speciation, the most important consequence of divergent evolution. Development of homologous structures is the most important manifestation of

divergent evolution. The development of homologous structure is the evidence that divergent evolution confers ability of ecological adaptation in varying environment to different species with same ancestor. Thus, divergent evolution is the key player in maintaining the biodiversity, structural, and functional integrity of ecosystem.

## Cross-References

- [Adaptation](#)
- [Adaptive Radiation](#)
- [Allopatric speciation](#)
- [Bottleneck Effect](#)
- [Coevolution](#)
- [Common Ancestor](#)
- [Convergent Evolution](#)
- [Directional Selection](#)
- [Disruptive Coloration](#)
- [Evolution](#)
- [Gene Flow](#)
- [Genetic Drift](#)
- [Genetic Variation](#)
- [Homology](#)
- [Homoplasmy](#)
- [Intersexual Selection](#)
- [Mutations](#)
- [Mutualism](#)
- [Natural Selection](#)
- [Niche Divergence](#)
- [Origin of Species](#)
- [Pleiotropy](#)
- [Reproductive Fitness](#)
- [Sexual Selection](#)
- [Speciation](#)
- [Species](#)
- [Stabilizing Selection](#)
- [Symbiotic Relationship](#)

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## Divided Attention

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## Synonyms

[Simultaneous attention](#)

## Definition

Attention is a fundamental cognitive process by which some inputs are selected for preferential processing. Divided attention specifically refers to situations in which two or more channels are attended simultaneously. The attended channels may be within the same or different sensory modalities. For example, a foraging bird might attend to a pile of seeds while simultaneously listening for the sound of approaching predators. While divided attention can be useful and can support a range of complex behaviors, it is often accompanied by a decrement in performance relative to selective attention, or focus on a single input.

## Introduction

Divided and selective attentions have been extensively studied by cognitive psychologists. For example, in dichotic listening tasks (e.g., Cherry 1953), participants are simultaneously played two

auditory messages and asked to monitor one or both. Participants can usually report the contents of one message, though accuracy is often impaired relative to when a single message is presented in isolation. More importantly, the contents of the other channel are significantly but not completely attenuated, with only major physical changes (such as changes in pitch or voice) and subjectively important messages (such as the listener's name or taboo words) being recognized. This has been dubbed the “cocktail party effect,” in reference to the challenge faced by a conversant in a crowded ballroom.

While dichotic listening tasks are among the most widely utilized, similar results have been obtained from parallel visual procedures (Neisser and Becklen 1975), indicating that divided attention is not a purely auditory phenomenon. The results of such experiments have had profound theoretical implications and led to popular characterizations of attention as a bottleneck or selective filter (Broadbent 1958) that reduces inputs to an amount that can be managed by a limited capacity working memory. Though there is still debate about the nature of this filter and whether it applies relatively early or late in processing, most theories agree that attention to multiple inputs results in relatively poorer performance.

The complexity of the natural world and the corresponding diversity and sensitivity of many animals' sensory systems would suggest that a similar attentional filter would be quite useful for many nonhuman animals. Consequently, there have been efforts to apply similar logic and methods to study divided attention in nonhuman animals.

## Methods of Studying Divided Attention in Nonhuman Animals

One of the most useful and direct procedures for studying divided attention uses a variation on the classic matching to sample task (e.g., Maki and Leith 1973). An animal is presented with a sample stimulus on a center response key, followed by two comparison stimuli on adjacent side keys. On single-element trials, the sample and comparison stimuli are all of the same type (e.g., all colors or



all line orientations), and a response to the comparison stimulus that matches the sample is reinforced. On compound trials, the sample features two element types (e.g., a color and a line orientation), while the comparison stimuli still consist of single elements. A response to the comparison stimulus that matches either of the elements present in the sample is reinforced. Because the matching comparison stimulus could feature either of the elements present in the sample, an animal must divide attention between both sample elements in order to support accurate responding. Typical results indicate that there is an accuracy cost to divided attention: matching to sample performance is worse on trials with compound samples than on trials with single element samples. This result is consistent with bottleneck theories of attention: dividing attention between elements results in fewer resources allocated to each and thus poorer performance.

Divided attention also factors into other cognitive processes of interest to comparative psychologists. Categorization, for example, allows an animal to respond to a range of category exemplars with the same appropriate response, as when a pigeon recognizes a never-before-seen hawk as a dangerous predator and executes the appropriate evasive action. Given that the members of many natural categories vary immensely, and multiple perceptual dimensions may be simultaneously and jointly diagnostic of category membership, successful categorization frequently requires divided attention. While the numerous mechanisms underlying categorization are still being clarified, researchers have specifically investigated the role of divided attention in categorization. Herbranson et al. (1999) created artificial categories that varied continuously on two dimensions. Individual exemplars were rectangles that varied in height and width, and the relevance of each dimension to category membership was varied across conditions. In some conditions, only one dimension (either height or width) was diagnostic of category membership, whereas the other varied randomly and was unrelated to category membership. In other conditions, both dimensions

were jointly diagnostic of category membership, and thus accurate categorization required attention to both dimensions. Pigeons' responses were mathematically analyzed to assess attention to the two stimulus dimensions. Results indicated that pigeons were capable of selectively attending to a single dimension or dividing attention between two dimensions, as demanded by the category structures in effect.

Another example of a cognitive process influenced by divided attention is visual search. Many animals can effectively scan their environment to identify specific targets based on visual features. Foragers, for example, use a specific searching image to spot prey at a rate greater than would be expected by their distribution alone (Tinbergen 1960). Cryptic prey in turn protect themselves by using natural camouflage that forces predators to search for a conjunction of features, rather than a single visual feature (e.g., a combination of shape and color, rather than shape or color by itself). Conjunction searches require that attention be divided between multiple visual features and consequently are more difficult than single-feature searches (Treisman 1986). Cook (1992) investigated this in the lab by presenting pigeons with texture displays on a video screen. Pigeons were trained to peck a small odd region of an otherwise uniform array of elements. On feature search trials, the odd region was differentiated by a single feature such as color (e.g., a small blue region among green elements) or shape (e.g., a small region of circles among squares). On conjunction search trials, the odd region was differentiated by a conjunction of color and shape (e.g., a small region of blue squares and green circles among green squares and blue circles). Conjunction searches required divided attention and resulted in lower accuracy than feature searches, though both were above chance. These visual search results further elaborate on the nature of divided attention by indicating that attention is not distributed exclusively across spatial locations. It can be divided among features within the same sensory modality and even in the same spatial location and yield the same pattern of results.

## Conclusion

Animals have a limited processing capacity, yet live in a world where many aspects of the environment may be simultaneously relevant. In such cases, the ability to divide attention across multiple channels can be useful. Nevertheless, divided attention usually comes at a cost and results in poorer performance relative to situations that utilize selective attention. This ability to divide attention supports many critical cognitive abilities, including but not limited to categorization and visual search.

## Cross-References

- ▶ [Attention](#)
- ▶ [Camouflage](#)
- ▶ [Categorization](#)
- ▶ [Cognition](#)
- ▶ [Foraging](#)
- ▶ [Matching-to-Sample: Comparative Overview](#)
- ▶ [Perception](#)
- ▶ [Search Image](#)
- ▶ [Visual Search](#)
- ▶ [Working Memory](#)

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## Division 6, American Psychological Association (APA)

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## Synonyms

[Division of Physiological and Comparative Psychology](#); [Society for Behavioral Neuroscience and Comparative Psychology](#)

Throughout its 76-year history, the mission of Division 6 of the American Psychological Association (APA) has been to promote research and education in physiological psychology, behavioral neuroscience, and comparative psychology. Other goals are to support communication and coordination between scientists, both within and beyond the Division, and to build psychology as a science more broadly. Since its inception, scholars identifying as animal psychologists, behavioral neuroscientists, comparative psychologists, or physiological psychologists have affiliated with Division 6, recognizing several common characteristics of these subfields. Division 6 members focus on the biology of behavior – either directly through experiments on the neural and physiological systems that underlie and/or are influenced by behavior, or indirectly through the study of similarities and differences across species that might reflect biobehavioral adaptations. Accordingly, many Division 6 members have a common interest in nonhuman animals, whether in their own right or as models for human biopsychology.

Thus, physiological psychologists, behavioral neuroscientists, and comparative psychologists generally shared the need to advocate for animal research, with respect to policy, funding, regulation, acceptance, and representation in psychology broadly. Finally, scientists from the various subfields of psychology that affiliate with Division 6 are similar in their commitment to experimental psychology. This overlap with experimental psychology has resulted in a disrupted history for Division 6, the first five decades of which were described definitively by Professor Donald Dewsbury (1996).

But the history of Division 6 began before 1944 when the APA introduced its current divisional structure. The focus on biology and the use of animals toward empirical, academic, and basic-research oriented interests were evident in the early days of psychology as a science, and of the APA as the professional home for the science and practice of psychology. Among the early Presidents of the APA, there were pioneers in American physiological or comparative psychology such as Boring, Dashiell, Dunlap, Ladd, Lashley, McDougall, Sanford, Stone, Thorndike, Tolman, M. F. Washburn, Watson, Woodworth, and Yerkes. Thus, it is unsurprising that a Division of Physiological and Comparative Psychology (Division 6) was one of the 19 charter divisions of the APA upon the organization's move to a division-based model (Olson 1944). The division was relatively small, but strong by every other metric. As Dewsbury (1996) discussed, Wolfle (1948) rated APA divisions on various measures of size and commitment and found that only the Clinical Psychology division ranked as highly across measures as Division 6; although few in number, the division's members were very loyal in paying dues, active in convention programming, willing to be nominated for leadership positions, and responsive in voting. When the Division was formed, Clifford T. Morgan was its temporary chairperson and B. F. Skinner was its temporary Secretary. Donald G. Marquis was the first elected chairman, followed by Donald Lindsley. The office was changed to President in 1947, when Morgan was elected.

Between 1948 and 1963, APA Divisions 6 and 3 (the Division of Theoretical-Experimental Psychology) voluntarily merged (Dewsbury 1996; Peak 1948). Thus, there was no "Division of Physiological and Comparative Psychology" within APA, although members from these subdisciplines continued to participate in APA through Division 3 (which changed its name to the Division of Experimental Psychology in 1949). Led by Sydney Weinstein, however, APA members representing these specializations successfully petitioned to reestablish the Division of Physiological and Comparative Psychology as a new Division 6 in the APA (Dewsbury 1996; Newman 1962). In 1995, the division leadership elected to adopt a new moniker as the Division of Behavioral Neuroscience and Comparative Psychology (Dewsbury 1996). Twenty years later, in 2015, this name was adjusted into its current form as the Society for Behavioral Neuroscience and Comparative Psychology.

Table 1 lists the names of Presidents (including the chairmen, prior to 1947) and other officers of Division 6 throughout its history. Note that Division leadership has consistently reflected both the comparative psychology and the physiological psychology / behavioral neuroscience constituencies. Over the course of the division's history, its focus areas and leadership have drawn from the diversity of psychologists who use the study of animals as a critical component of their research programs. Some early leaders, such as Donald Lindsley, studied animals using neurophysiological methods to index reflexive behaviors and their neural bases (e.g., Lindsley et al. 1950). Others, such as Austin Riesen, studied perceptual learning and development of perceptual faculties using animals as a model species (e.g., Riesen 1947). Later leaders would build upon these trends, studying the neuronal embodiment of learned behaviors (e.g., Thompson and Spencer 1966) and the psychophysiology of arousal and startle responses (e.g., Weisbard and Graham 1971). The growing influence of cognitive sciences and comparative cognition in animal research can be seen in the research programs of more recent figures (e.g., Rumbaugh et al. 1987; Young and Wasserman 1997; Zentall et al. 1996).

**Division 6, American Psychological Association (APA), Table 1** Division 6 presidents, secretaries, secretary-treasurers<sup>a</sup>, and treasurers

| Year | President            | Secretary         | Treasurer        |
|------|----------------------|-------------------|------------------|
| 2021 | Jonathon Crystal     | Jeremy Bailoo     | Cynthia Crawford |
| 2020 | Mark Krause          | Jeremy Bailoo     | Cynthia Crawford |
| 2019 | Michael Beran        | Jeremy Bailoo     | Cynthia Crawford |
| 2018 | Allyson Bennett      | R. Nicole Mathews | Lisa Savage      |
| 2017 | Mary E. Cain         | R. Nicole Mathews | Lisa Savage      |
| 2016 | Stan Kuczaj          | R. Nicole Mathews | Lisa Savage      |
| 2015 | David A. Washburn    | R. Nicole Mathews | Michael Domjan   |
| 2014 | Lisa Savage          | R. Nicole Mathews | Jesse Purdy      |
| 2013 | Chana Akins          | R. Nicole Mathews | Jesse Purdy      |
| 2012 | Mauricio R. Papini   | Mary E. Cain      |                  |
| 2011 | Gordon Burgardt      | Mary E. Cain      |                  |
| 2010 | Mark Bouton          | Mary E. Cain      |                  |
| 2009 | Nancy Dess           | Chana K. Akins    |                  |
| 2008 | William Timberlake   | Chana K. Akins    |                  |
| 2007 | Karen Hollis         | Chana K. Akins    |                  |
| 2006 | Thomas R. Zentall    | Chana K. Akins    |                  |
| 2005 | James Grau           | Chana K. Akins    |                  |
| 2004 | Edward Wasserman     | Nancy Dess        |                  |
| 2003 | Norman Spear         | James Grau        |                  |
| 2002 | David C. Riccio      | James Grau        |                  |
| 2001 | Herbert Roitblat     | James Grau        |                  |
| 2000 | Michael Domjan       | James Grau        |                  |
| 1999 | M. S. Fanselow       | Molly V. Wagster  |                  |
| 1998 | MaryLou Cheal        | Molly V. Wagster  |                  |
| 1997 | Arnold A. Gerall     | Molly V. Wagster  |                  |
| 1996 | Stewart H. Hulse     | Karen L. Hollis   |                  |
| 1995 | Bartley G. Hoebel    | Karen L. Hollis   |                  |
| 1994 | Evelyn Satinoff      | Karen L. Hollis   |                  |
| 1993 | Donald A. Dewsbury   | Karen L. Hollis   |                  |
| 1992 | Russell M. Church    | Karen L. Hollis   |                  |
| 1991 | J. Bruce Overmier    | Karen L. Hollis   |                  |
| 1990 | Frederick King       | W.P. Smotherman   |                  |
| 1989 | Linda Bartoshuk      | W.P. Smotherman   |                  |
| 1988 | Duane M. Rumbaugh    | W.P. Smotherman   |                  |
| 1987 | Martha H. Wilson     | Mimi N. Halpern   |                  |
| 1986 | George H. Collier    | Mimi N. Halpern   |                  |
| 1985 | Ethel Tobach         | Mimi N. Halpern   |                  |
| 1984 | Robert W. Doty       | Mimi N. Halpern   |                  |
| 1983 | Allan F. Mirsky      | M. Oscar-Berman   |                  |
| 1982 | William A. Mason     | M. Oscar-Berman   |                  |
| 1981 | Richard L. Solomon   | M. Oscar-Berman   |                  |
| 1980 | Byron A. Campbell    | H. C. Lansdell    |                  |
| 1979 | Frances K. Graham    | H. C. Lansdell    |                  |
| 1978 | Richard M. Held      | H. C. Lansdell    |                  |
| 1977 | Elliot S. Valenstein | J. M. Warren      |                  |
| 1976 | Philip Teitelbaum    | J. M. Warren      |                  |
| 1975 | Donald R. Meyer      | J. M. Warren      |                  |

(continued)

**Division 6, American Psychological Association (APA), Table 1** (continued)

| Year | President                                                     | Secretary          | Treasurer |
|------|---------------------------------------------------------------|--------------------|-----------|
| 1974 | Brenda A. Milner                                              | Robert L. Isaacson |           |
| 1973 | Brenda A. Milner                                              | Robert L. Isaacson |           |
| 1972 | Richard F. Thompson                                           | Robert L. Isaacson |           |
| 1971 | James Olds                                                    | Martha H. Wilson   |           |
| 1970 | John I. Lacey                                                 | Martha H. Wilson   |           |
| 1969 | Mortimer Mishkin                                              | Frances K. Graham  |           |
| 1968 | Karl H. Pribram                                               | Frances K. Graham  |           |
| 1967 | Austin H. Riesen                                              | Frances K. Graham  |           |
| 1966 | Hans-Lukas Teuber                                             | Frances K. Graham  |           |
| 1965 | Harry F. Harlow                                               | Frances K. Graham  |           |
| 1964 | Sidney Weinstein                                              | Frances K. Graham  |           |
|      | Division 6 is a part of division 3, without separate officers |                    |           |
| 1948 | Frank A. Beach                                                | Harry F. Harlow    |           |
| 1947 | Clifford T. Morgan                                            | Harry F. Harlow    |           |
| 1946 | Donald B. Lindsley                                            | Harry F. Harlow    |           |
| 1945 | Donald G. Marquis                                             | Roger B. Loucks    |           |
| 1944 | Clifford T. Morgan                                            | B. F. Skinner      |           |

<sup>a</sup>From 1950 to 2012, the secretary position was called “Secretary-Treasurer”

Among the efforts to support the fields it represents, Division 6 gives several awards annually. The current awards include recognition of the best paper published in each of the two APA journals most closely associated with the Division’s mission. The author or authors of an outstanding paper published in the *Journal of Comparative Psychology* are recognized each year with the “Frank A. Beach Comparative Psychology Award.” The author(s) of the best paper published each year in the journal *Behavioral Neuroscience* receives the “D. G. Marquis Behavioral Neuroscience Award.” Both of these awards are selected by the editorial boards of the respective journals. Additionally, the Division annually recognizes a scholar who has provided significant theoretical and empirical advances to these subfields with the “Donald O. Hebb Distinguished Scientific Contributions Award.” The “Brenda A. Milner Award” honors an author for an outstanding paper in the field of behavioral neuroscience or comparative psychology, and the “Clifford T. Morgan Distinguished Service Award” recognizes continuing exceptional service contributions to the Division. An “Early Career Investigator Award” is also conferred each year. These honors

and recognitions are announced at the annual APA convention, in which Division 6 regularly provides a strong program of science presentations and posters.

Despite this legacy of scholarship and leadership, Division 6 has long occupied a precarious position in the APA. Always a small group, the proportion of the total APA membership affiliated with Division 6 has declined steadily since it reemerged from Division 3. Dewsbury (1996) traced these membership trends through 1995, and those declines have continued to the present writing. Some of this trajectory is to be expected for any division that has been steadfast in its experimental and academic focus as the APA has become increasingly applied, clinical and political. But more structural issues are also likely to be in play. Since the late 1980s, the actual count of Division 6 members has fallen annually (from 806 members in 1986 to 405 in 2017, the most recent year for which data are available). Few indicators of future growth are apparent, with the demographic profile of Division 6 suggesting loyal retention of the division’s previous generation of members until death, but there is little evidence of attracting a new generation of

psychologists to the society (e.g., 73% of Division 6 members were aged 60 or older in 2017, with only 26% identified as female, and only 5% identified with a specific race or ethnicity other than white). Division 3 (the Society for Experimental Psychology and Cognitive Science) and some other divisions are experiencing these same trends. One might wonder whether this reflects a general decline in the subdisciplines that comprise Division 6. Psychologists have eulogized comparative psychology since at least the early 1970s (e.g., Lockard 1971; see also Abramson 2015; Galef 1987), to mixed reviews (e.g., Adler and Tobach 1971; Boice 1971); however, there are other signs that comparative psychology – particularly comparative cognition – is alive and growing. For example, the number of publications on “comparative psychology” or “comparative cognition” since 2000 is more than double the number from the previous 20 years, reflecting in part the increase in outlets for such work. In any case, certainly no claim can be made for the general demise of behavioral neuroscience. Together with cognitive neuroscience, social neuroscience, and clinical neuropsychology, these areas of scholarship are on the ascend. Specialty professional associations such as the Comparative Cognition Society, the Psychonomic Society, and particularly the Society for Neuroscience appear to be healthy and growing. Rather, the Division 6 membership trends discussed here appear to reflect ongoing challenges of attracting scholars from these subdisciplines to the APA. Its new identity as the Society for Behavioral Neuroscience and Comparative Psychology – affiliated as a division within APA but open also to members who choose not to join that larger organization – may determine what future role Division 6 plays in the subfields of psychology that it endeavors to promote.

## Cross-References

- [B.F. Skinner](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [David Washburn](#)

- [Duane Rumbaugh](#)
- [Edward Thorndike](#)
- [Ethel Tobach](#)
- [Frank Ambrose Beach](#)
- [Gordon Burghardt](#)
- [Harry Harlow](#)
- [J Bruce Overmier](#)
- [John B. Watson](#)
- [Jonathon Crystal](#)
- [Karen Hollis](#)
- [Margaret Floy Washburn](#)
- [Michael Domjan](#)
- [Michael J. Beran](#)
- [Robert Mearns Yerkes](#)
- [Stanley Kuczaj](#)
- [Tom Zentall](#)
- [William Timberlake](#)

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all levels in biological systems, from cooperative associations of organelles in some eukaryote cells and microbes, to associations of specialized cells in simple animals (e.g., sponges), varied organs in complex unitary organisms, and specialized individuals in animal societies (Crespi 2001; Simpson 2012). Division of labor is thought to be one of the principal factors underlying the major evolutionary transition from solitary to social living, and key to the spectacular success of highly social organisms such as the social insects (Hölldobler and Wilson 1990; Wilson 1971).

Division of labor in social organisms can be considered an emergent group-level property of local interactions at the individual level and arises from variation among, and interactions between, the individuals comprising the group, without top-down control. In some cases, individuals may specialize predominantly on certain tasks because the propensity to perform different tasks differs among individuals. In other cases, individuals may constantly shift between tasks as a fluid solution to ever-changing group requirements, without necessarily specializing on any particular task (Robinson et al. 2009).

## Division of Labor

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### Definition

The partitioning of tasks among individuals in a group, such that some individuals focus on one task while other individuals focus on another.

### Introduction

Economists have long recognized that dividing tasks among cooperating individuals can lead to improved efficiency, as this allows individuals to specialize on particular tasks while also reducing the costs of switching between tasks (Smith 1776). Division of labor is also widespread at

## Reproductive and Nonreproductive Division of Labor

The most fundamental form of division of labor is the skewed distribution of reproduction among members of a group: some individuals specialize in reproduction while others undertake nonreproductive tasks. In social insects, reproductive skew can be extreme, with colonies comprising a single reproductive queen and tens of thousands of nonreproductive workers. In cooperatively breeding mammals and birds, reproduction is typically monopolized by a breeding pair, aided by one or more “helpers” who perform a range of nonbreeding tasks. Division of labor is also found in microorganisms: slime molds, for example, usually exist as free-living individual amoeboid cells, but can aggregate on starvation into multicellular slugs, which then develop into a fruiting body consisting of (reproductive) spore cells and (nonreproductive) stalk cells.

Division of labor can also exist among non-reproductive individuals. The effective functioning of an ant colony, for example, requires a wide range of different tasks to be performed. Leaf-cutting ants of the genus *Atta* possess one of the most complex systems of division of labor in insects, associated with the elaborate process of harvesting leaves to tend the fungus gardens on which they feed. In *Atta sexdens*, no less than 29 distinct tasks have been identified, and these are performed by workers with four distinct morphological castes (Wilson 1980).

### Flexibility in Division of Labor

Division of labor can arise facultatively among undifferentiated individuals. In such cases, the role assumed by any given individual may change with context during that individual's lifetime. Cooperatively breeding vertebrates, for example, are typically totipotent (capable of all tasks) but choose social life over independence because of the benefits of social living and/or the costs of solitary life. As a member of a cooperatively breeding group, they may switch between dominant (breeder) and subordinate (helper) roles depending on various physical and socio-ecological factors. Similarly, many facultatively social wasps form dominance hierarchies maintained by aggression or other criteria such as relative age. Subordinate individuals perform foraging tasks while the dominant individual monopolizes reproduction, though once again these roles may change over time.

Division of labor can also be obligate. In queens and workers in many social insects, for example, roles are highly specialized and associated with morphological castes. While these castes allow individuals to perform their assigned role with greater efficiency and efficacy, they also mean a loss of totipotency, and thus dictate that any given individual is only capable of a limited range of the tasks essential for survival. Social insect queens, for example, are often specialized to produce large numbers of eggs but are incapable of basic labor tasks. Workers on the other hand have in many cases lost the ability to mate and/or reproduce, and instead are adapted for performing

a wide range of labor tasks, making these two roles mutually and obligately interdependent. This is also true for individuals in colonial scyphozoans. These animals form colonies of differentiated zooids in which individuals are not only obligately mutually interdependent, but also permanently physically connected. In this sense, scyphozoans perhaps most closely resemble the division of labor among organs systems in unitary multicellular organisms.

### Mechanistic Basis of Division of Labor

A group comprising individuals which vary in their propensity to perform different tasks can self-organize into an effective cooperative unit. While many societies are comprised of highly related individuals, these are not clones, and factors such as multiple reproductive individuals and multiple mating can result in increased genetic diversity among members of the workforce, which can itself lead to higher group efficiency (Smith et al. 2008). Individuals also vary in a wide range of factors including age, condition, morphology, and experience. The combination of these factors defines the propensity of an individual to perform a particular task (Oster and Wilson 1978; Wilson 1971), and individuals having lower "response thresholds" for certain tasks are more likely to perform those tasks. For example, many insects change role as they age, typically moving from less-hazardous roles within the nest to external roles such as foraging.

The propensity for individuals to perform certain tasks is subject not only to internal state but also external signals, such as changes in group-level requirements or environmental conditions. While individual caste, age, or genotype may largely define which tasks a worker is likely to perform, individuals may also vary their roles depending on the activity of other individuals and the needs of the group. For example, inside workers in an ant colony are likely switch to external foraging roles if they are unable to obtain food after soliciting nestmates, as this is likely to indicate a general lack of food in the colony. Effective division of labor thus depends on both variation between individuals in the tasks they are

likely to perform and flexibility within individuals to effect responses to variable environments (Beshers and Fewell 2001).

## Cross-References

- [Altruism](#)
- [Social Behavior](#)
- [Sociobiology](#)

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## Division of Physiological and Comparative Psychology

- [Division 6, American Psychological Association \(APA\)](#)

## Dizygotic (DZ)

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## Synonyms

[Monochorionic dizygotic twins](#); [Twins](#)

## Definition

In the course of fertilization, when two sperms fertilize two mature ova due to multiple ovulation under the control of hypothalamo-pituitary-ovarian axis promoted by different physiological, genetic, and other environmental factors, including the use of advanced reproductive technologies to maximize reproductive success.

## Introduction

The word “twins” originates from old English: “*twi*” means two or “*twin*” means double. Twin babies are although less frequent but not rare in parallel with the single child. Dizygotic (DZ) or fraternal twins are produced from two different ova fertilized by two different sperms whereas monozygotic (MZ) or identical twins derive from a single ova dividing into two separate embryos. Conjoint twins are also identical but not separated. Compare to the prevalence of monozygotic twins which is almost constant, the prevalence of dizygotic twins varies over time across the different places in the world. In animal society, twins are also prevalent and diversified like as reported in 2016 in South Africa, the world first twin puppies of Irish Wolfhound named Cullen and Romulus were born as the identical twin. Armadillo is another example to give birth to monozygote. Callitrichines, or clawed New

World monkeys, always give birth to twins because they produce multiple ova in their reproductive cycle.

History and Background of Twin Studies

The history of twin studies began with Galton’s study (Galton 1876); thus, he is considered as the father of twin studies and also the founder of the eugenics movement. The term “eugenics” means “well-born” and was coined by him. Galton failed to explain the cause of observed behavioral similarities in twins. In 1905, the first twin study with psychological testing was published by E. L. Thorndike. He also stated the influence of nature and nurtured on mental abilities for twins. To answer the question of the important role of common environment and experience on the mental development, he reasoned that:

- a. Twins should be more alike with increasing age.
- b. Similarity of ordinary siblings not more than 4–5 years apart should resemble the similarity of twin pairs.
- c. If experience influences mental abilities, then twins should be more similar for abilities that require training compared to those less subject to training.

He disputed the fact of the effect of experience on mental illness.

In the mid-1920s, two kinds of twins, MZ and DZ were first recognized. In 1924, Herman W. Siemens from Germany first proposed that the role of genetic factors for diseases or traits can be compared by comparing identical to fraternal twins reared together, thus introducing the classic twin method. In 1934, Wilson questioned the environmental impact on twins. In the same year, Helmut von Bracken found that identical twins experienced a higher degree of attachment compared to fraternal twins. Rosanoff and colleagues (1938) conducted their studies on schizophrenia, criminality, and delinquency in twins to conclude the role of social factors in developing abusive attitudes.

Weinberg was a popularizer of the “differential method,” which uses a simple calculation to estimate the number of expected identical pairs in a given population of twins. He also created the first “morbidity tables” used in medical statistics, as well as an age-correction method subsequently used by several twin researchers. Germany also contributed to twin research immensely. In 1928, Hans Luxenburger published the first schizophrenia twin study followed by another study performed by Johannes Lange in 1929. The most unethical practices were performed during World War II by some German physicians notoriously labeled as “Nazi Medical Experiments.” During that time, the prisoners in the camp were experimented upon without their consent. The Auschwitz and Roman twins were infested with bacteria and other pathogens for genetic studies. Following this sad history of twin studies, several animal and clinical studies were performed throughout the decades.

Beside all these studies, the most well-known twin study was Minnesota Studies of Twin Reared Apart (MSTRA) conducted by Thomas Bouchard and his colleague between the year 1979 and 2000. In 1990, Buchard and his colleague reported the correlation of physical variable, IQ, and personality test scores in monozygotic twins reared apart (MZA) and reared together (MZT). In brief, the result was tabulated below.

| Features               | Correlation for MZA | Correlation for MZT |
|------------------------|---------------------|---------------------|
| IQ                     | 0.69 (48 pairs)     | 0.88 (40 pairs)     |
| Personality test score | 0.50                | 0.50                |

Based on the result in the context of psychology and sociobiology, the team of MSTRA concluded that this is because of strong genetic influence and the similarity in the score is not due to shared family environment. The study was published in Science in the year 1990 where they mentioned that monozygotic and dizygotic twins who were separated early in life and reared apart are a nature’s experimental beauty and also provide the ample and powerful opportunity to study the influence of environment and genetics on human characteristics.

## Importance of DZ Study

Despite some methodological and ethical issues, twin research continued beyond this unfortunate history due to several reasons, including due to failure of molecular approaches in describing psychiatric disorders, genetic theories for economic and political needs, and few important publications on twin research between 1961 and 1970 (as published by Jay Joseph in his book “The Gene Illusion” and “The Trouble with Twin Studies”).

Twin study is one of the most potent and valuable tools in genetics research to assess and analyze the importance and influence of genetic factors on phenotypic and trait variation in humans. Understanding which genes are responsible for natural twinning and to know how they control ovarian functions is critical for applications in female fertility and infertility.

## Epidemiology and Prevalence

During the seventeenth century, birth registration was recorded in church registries and was officially introduced in 1749 in Sweden and Finland (Erikson 1962). From statistics recorded therein, it was possible to calculate twinning rates (TR). The TR (number of twin maternities/1000 maternities) varies geographically across Europe/North Africa, Sub-Saharan Africa, and Asia. The highest TR is observed in sub-Saharan Africa (23/1000) and the lowest in Asia (5–6/1000, Bulmer 1970). Based on international variation in TR, Little classified it as low prevalence (2–7/1000, e.g., Hawaii, Japan, and Taiwan), intermediate prevalence (9–20/1000 North Africa, America, Asia, Oceania, and Europe), and high prevalence ( $\geq 20/1000$  Nigeria, Seychelles, Transvaal, Zimbabwe) TR countries. Among the high prevalence countries, Yoruba is reported as the highest prevalence of TR (33–66.5/1000) where 1 in every 12 families has twins (Nylander 1971, 1978). In 1900, TR decreased, and from 1970 onwards, it increased steadily in most countries (Imaizumi 1997). Such demographic variations arise due to several reasons, which can be the environmental, physiological, feeding habit, genetic, etc.

**Twinning Promoting Factors:** From the TR found all over the world, it has been documented that there is an increased TR in the last two decades. The contributing factor that promotes the TR includes the use of various fertility treatments like in vitro fertilization (IVF), intracytoplasmic sperm injection (ICSI), intrauterine insemination (IUI), and ovulation induction (OI).

## Factors Affecting Twinning Rate

Principal factors that affect the twinning rate are maternal age, parity, and genetic inheritance. Several factors contributing to alteration of twinning rate are:

- (A) Increased maternal age: for example, a four-fold increase in TR from age 15 to 35. Maternal age and parity are well correlated and increase the risk of dizygotic twins (Bulmer 1970).
- (B) Body type: for example, tall women ( $\geq 165$  cm) with high BMI ( $\geq 30$ ) are much more at risk (1.5–2 times) of giving birth to twins than women of small stature ( $\leq 155$ , Basso et al. 2004; Bortolus et al. 1999; Nylander 1981).
- (C) Smoking: Women who smoke are at higher risk of giving birth to twins compared to non-smokers (Parazzini et al. 1996).
- (D) Seasonal variation: Conception during summer and autumn are reported to contribute higher rates of DZ in several countries (Eriksson and Fellman 2000). The seasonal variation in day length causes the alteration in hormonal level, which may be the cause of multiple ovulations. Seasonal foods and food supply were considered as contributing factors for DZ (Eriksson and Fellman 2000).
- (E) Iatrogenic factors: Oral contraceptives and Folic acid also influence DZ (Li et al. 2003). Folic acid consumption during conception increases the risk of DZ (Vollset et al. 2005). Soon after stopping oral contraceptives, conception leads to increased risk of DZ (Rothman 1977). Although there are some contradictory findings regarding the

association between oral contraceptives and DZ, the overall pattern can be described as recovery from exogenous steroids causing an increase of FSH level temporarily via hypothalamo-pituitary-ovarian axis (HPO), which leads to multiple ovulations (Jernstrom et al. 1995).

- (F) Genetic factors: Because height is correlated with dizygote births as the first link of twinning with heredity, Weinberg (1901) reported that mothers, sisters, and daughters of the mother with twins had an increased risk of having twins and the percentage probabilities are 39, 95, and 30%, respectively. Despite the concept of the female line contribution in DZ as supported by other scientists strongly (Bulmer 1970; Wyshak and White 1965), Greulich (1934) reported the contribution of paternal hereditary factors in DZ also. Meullemens and colleagues (1996) reported an autosomal monogenic dominant model by analyzing pedigree of 1422 Dutch and Flemish families with DZ twins, which supports inheritance from both parents. Semen quality may influence DZ twinning (Askund et al. 2007).

births. Two hypotheses have been put forward to explain the twinning rate of humans.

- A. The insurance ova hypothesis: The hypothesis states that increased production of multiple ovarian follicles will increase the probability of survival and at least one of them being fertilized. Therefore, conceiving twins is the by-product of encouraging fertility (Anderson 1990).
- B. Natural selection hypothesis: This hypothesis consults the effect of environments that promote twins or singletons as the reproductive output.
  1. In an experiment conducted by Lumma and colleagues (1998) in the archipelago of Åland, Åboland, and the mainland of Finland, to their surprise, they found that enriched food source islands were inducing twinning frequency whereas, in the poorer mainland environment, singletons are preferred to maximize the reproductive success.
  2. Similarly, during World War II, the scarcity of foods provokes singleton births, and again in subsequent years, food enrichment encourages twin births (Bulmer 1970).

D

## Hypotheses

From the previous research, four hypotheses are developed.

1. Increase in multiple ovulation frequencies leading to an increase in the frequency of spontaneous DZ.
2. The concentration of FSH is above a certain threshold by extending the time or by increasing the number of responding antral follicle to FSH during follicle selection.
3. Women with a family history of multiple births are already predisposed to multiple ovulations.
4. Gene mutations affecting multiple ovulation rates are most likely from FSH pathway of synthesis, maturation, and release of the dominant follicle.

Although during pregnancy, complications are prevalent in producing twins rather than singleton

## Mechanism

Mechanism of controlling dizygotic twinning is a complex phenomenon and still obscure. Multiple ovulations due to improved nutrition and particular gene mutations are reported in animals. Increasing follicular recruitment was found in those mothers who give birth to twins (Martin et al. 1991b). There are mainly two ways by which the control mechanism works.

1. Hypothalamo-pituitary-ovarian axis is the complex regulatory network that controls the ovulation. Two important gonadotrophin hormones, follicle-stimulating hormone (FSH) and luteinizing hormone (LH), secreted from the pituitary alter the pattern of the menstrual cycle. In the characteristic pattern of the menstrual cycle, in the early phase, FSH concentration begins to increase and, in a feedback manner, the hormone secretes from growing



follicles, (Inhibin) inhibits hypothalamus and pituitary to secrete FSH – causing FSH levels to fall. Development of one dominant follicle takes place when the concentration of FSH exceeds the threshold level, and for multiple follicle developments, FSH (independent of LH pulse) is more, or FSH exceeds the threshold for too long.

2. Ovarian follicular control – Although this pathway responds to the external FSH and LH signals and ensures the oocyte development, two closely related growth factors expressed specifically in the oocyte, bone morphogenetic protein 15 (BMP15), and growth differentiation factor 9 (GDF9) play another major role (Shimasaki et al. 2004). These two factors bind to the receptor expressed on ovarian cells, which ensures oocyte growth and development.

## Genetic Variants and DZ

Apart from these two control mechanisms, genetic variants of FSH receptor (e.g., Thr307Ala and Asn680Ser), causing the increase in sensitivity towards FSH, contributes to variation in DZ (Ayman et al. 2000). The genetic variant's contribution to DZ is still contradictory (Montgomery et al. 2001). Bone morphogenetic protein receptor1B (BMPRI1B, Duffy et al. 2001) and methylenetetrahydrofolate reductase (MTHFR, Montgomery et al. 2003), Inhibin alpha (INHA, Montgomery et al. 2000) are also enlisted among those genes that play a role in DZ. Female carriers of Fragile-X syndrome (FRAXA) are also reported to have an increased risk of DZ (Kenneson and Warren 2001). Carriers of FMR1 permutation are also at risk of DZ (Welt et al. 2004). Substitution of C to T in PPRAG gene (encoding peroxisome proliferator-activated receptor (PPAR $\gamma$ )) is also associated with DZ (Busjahn et al. 2000).

## Sex of Twins

Because DZ is more common than MZ throughout the world, the question arises of the frequency

of same-sex (SS) DZ and opposite sex (OS) DZ. French statistician Jacques Bertillon (1874) first speculated that the  $DZ = 2OS \text{ twins} + MZ \text{ twins}$ . Later Weinberg (1901) formalized Bertillon data and proposed two assumptions known as Weinberg's differential rule (WDR). The WDR states that (a) probability of conception of the male and female fetus are equal ( $P = 0.5$ ). (b) The sexes of DZ twins are determined independently. So,  $DZ = \text{equal number of } (OS+SS)$ . But the ratio is slightly more towards boys (105:100). The Trivers Willard hypothesis pointed at some doubt with the second hypothesis of WDR and stated that parental conditions have an impact on sex ratios. According to this hypothesis, parents in enriched food and other physiological conditions give birth to males, and, in poor environmental and physiological conditions, to females. Similar effects for OS and SS have been observed; if conditions are good, both are male, but if conditions are poor, both are female (Trivers and Willard 1973). OS is considered evolutionarily and developmentally disadvantageous compared to SS; then, the WDR hypothesis of independent sex determination for DZ is violated, and SS will be produced more than OS.

## Chimerism

When an organism contains cells derived from more than one zygote, this is referred to as chimerism. Although chimerism is a rare event, monochorionic dizygote (MC/DZ) twin is a comparatively new area of research. Blood chimerism has been found commonly in MC/DZ. Monochorionic twin pregnancies have complications related to vascular anastomoses, which cause twin-twin transfusion syndrome. There are many such cases; for example, at birth, male recipient twins have two bloodlines, 30% 46XY and 70% 46XX, whereas female donors have 18% 46XY and 82% 46XX (Chen et al. 2013). No anomaly in reproductive growth has been reported except few cases like a girl having Down syndrome with blood chimerism (Bogdanova et al., 2010). She was a normal female with normal genitalia and fallopian

tubes, but aplasia in the uterus, which may be due to the Mullerian inhibiting substance (MIS).

## Conclusion

In the course of multiple ovulations, when two sperm fertilizes two ova, dizygotic twins are formed. The worldwide variation of twin frequency reflects that South African Yoruba people have a high probability of having twins. Several assisted reproductive technologies like IVF, ICSI, IUI, and OI contribute to increasing the frequency of DZ production. The enriched environment and different factors like folic acid consumption, smoking, high BMI, and increased maternal age favor the process of DZ. Because enriched food sources promote DZ, the natural selection hypothesis comes forward along with insurance ova hypothesis to increase the chance of fertilization. The search for mechanisms behind multiple ovulations establishes the hypothalamo-pituitary-ovarian axis. Several genes like GDF9 and BMP15 control the ovarian follicles. Other gene variants that contribute to the DZ processing are BMPR1B, MTHFR, INHA, FRAXA, and PPARG. Twin research continues in spite of ethical issues because of its potential impact on behavioral genetics, psychology, and different diseases.

## Cross-References

- [Behavioral variation](#)
- [Hypothalamus](#)
- [Zygote](#)

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## DNA

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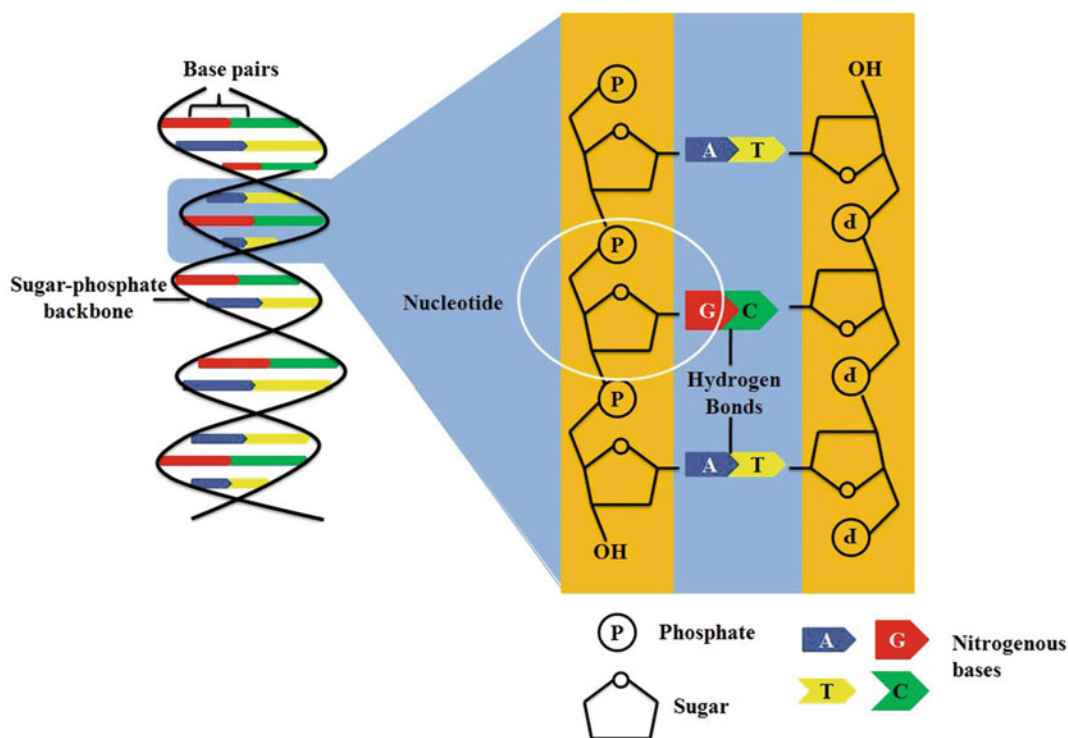
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## Definition

Deoxyribonucleic acid (DNA) is a polymer of nucleotides containing nitrogenous base, deoxy-ribose sugar, and phosphoric acid which stores and transmits genetic information.

## Introduction

DNA is a macromolecule that carries the genetic information for biological functions of living organisms. It is made up of two strands of polynucleotides coiled around each other to form a double helix. Nucleotides are the basic building blocks of nucleic acids formed of two components, nucleosides and phosphate groups, where phosphate group attaches to the 5' position of a nucleoside by ester linkage. Nucleosides are also composed of two elements, a five-membered pentose sugar and a nitrogenous base. Further, nucleotides join together by the formation of a second ester bond by reaction between the phosphate of one nucleotide and the 3' hydroxyl of another, thus generating a 5' to 3' phosphodiester bond between adjacent sugars; this process repeats indefinitely to give a long polynucleotide molecule. DNA has two such polynucleotide strands having free 5' hydroxyl group at one end and 3' hydroxyl group at another end in each strand. Therefore, each strand is having a polarity and directionality in opposite directions and known as antiparallel strands. Nitrogenous base in DNA is basically of two types – purines consisting of adenine (A) and guanine (G) and pyrimidines consisting of thymine (T) and cytosine (C) (Fig. 1).



**DNA, Fig. 1** Simplified structure of DNA

## DNA Structure

James Watson and Francis Crick (1953) identified the correct structure of DNA existing as a double helix on the basis of Chargaff's chemical data and Wilkin's and Franklin's X-ray diffraction data. The double helix model of DNA molecule further suggested the mechanism of transmission of genetic information. Watson and Crick proposed that DNA exist as right-handed double helix in the cells in which two polynucleotides are coiled around each other in spiral manner. These polynucleotide strands are held together by hydrogen bonds between bases of opposing strands and thereby maintain their helical configuration. The base pairs are stacked between the two chains perpendicular to the axis of molecule. This base pairing is specific as adenine always joins with thymine by double hydrogen bond and guanine binds with cytosine by triple hydrogen bond. Thus, all the base pairs consist of one purine and one pyrimidine and these two strands of the DNA

are complementary. The complementarity of the two strands of the double helix makes DNA suitable to store and transmit genetic information from one generation to another.

The base pairs in DNA are stacked about 3.4 Å apart, with 10.4 base pairs per turn of the double helix. The angle between the two adjacent residues in the same chain is 360. The distance of the phosphorus atom from the fiber axis is 10 Å. The twisting of two strands around each other forms double helix with a minor groove (~12 Å across) and a major groove (~12 Å across). This double helix structure is right handed as the turns run clockwise along the helical axis.

## DNA Forms

DNA exist in three conformations, B-DNA, A-DNA, and Z-DNA (Wang et al. 1979). The Watson-Crick double helix structure is called B-DNA. DNA remains in the B-DNA conformation

under physiological conditions (aqueous solution having low salt concentrations). B-DNA appears to have an average of 10.4 nucleotide pairs per turn. Further, the structure of DNA molecule change as a function of their environmental conditions and interaction with its surrounding molecules. Under high salt concentration (state of dehydration), DNA exists in A-DNA conformation. It is also a right-handed helix like B-DNA but with 11 nucleotide pairs per turn. It is a shorter, thicker double helix with a diameter of 2.3 nm. DNA does not exist in this conformation in vivo. However, DNA-RNA heteroduplexes exist in this conformation in vivo. Certain DNA sequences exist in a left-handed double helical form known as Z-DNA. It is also found in double helices which are GC rich and contain alternate purine and pyrimidine rings. It differs from A and B conformations in having 12 base pairs per turn, with a diameter of 1.8 nm and a single deep groove. The function of Z-DNA in living cell is still unclear.

## DNA Organization

Functional DNA molecules in living cells display a very high level of organization, i.e., supercoiling (Gilbert and Allan 2014). Supercoils are introduced into a DNA molecule when strands are cleaved and the complementary strands at one end are rotated or twisted around each other with the other end held fixed in space and thus not allowed to spin the DNA molecule. The DNA is maintained in a tightly coiled conformation as a consequence of supercoiling. The DNA molecules of almost all organisms exhibit negative supercoiling in vivo which helps in several biological functions. Supercoil in DNA molecules is further maintained by enzymes that play essential roles in DNA replication and other processes.

## Conclusion

DNA usually exists as a right-handed double helix with the two strands held together by hydrogen bonds between the complementary bases in which

adenine is paired with thymine and guanine is paired with cytosine. The complementarity of the two strands of a double helix makes DNA unique to store and transmit genetic information. The two strands of a DNA double helix have opposite chemical polarity as they are antiparallel. Further, the functional DNA molecules in cells are negatively supercoiled.

## Cross-References

- [Base Pair](#)
- [Chromosomes](#)
- [DNA Marker](#)
- [DNA Pooling](#)
- [Electrophoresis](#)
- [Gene Expression](#)
- [Genes](#)
- [Methylation](#)
- [Nucleus](#)
- [Primer](#)

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## DNA Array

- [Microarray](#)

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## DNA Chip

- [Microarray](#)



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## DNA Marker

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### Synonyms

[Genetic marker](#); [Molecular marker](#)

### Definition

DNA, genetic, or molecular markers are known as clearly distinguishable DNA, gene or molecular sequences on specific locations on chromosomes.

### Introduction

Mutations or alterations in genomic loci (positions on chromosome) lead evolutionary to polymorphisms (genetic variations) between species and individuals which can nowadays be quickly examined and compared. DNA markers are employed for various purposes. They are mainly used for genealogical DNA testing, evolutionary taxonomy (phylogenetics), and genetic traits underlying (inherited) diseases. Through identification of known and clearly distinguishable DNA, gene, or molecular sequences it is possible to create a physical and/or linkage map and allow for differentiation of traits and identity. In addition, the allelic status (variant form of a gene) can be detected (mono-, bi-, or polyallelic).

Historically the first employed DNA markers were allozymes (allelic variant form of enzymes coded from the same locus) and mitochondrial DNA (mtDNA).

### Types

DNA marker can vary in length from very short sequences like single nucleotide polymorphisms (SNPs) to long fragments like minisatellites

(repetitive DNA with certain motifs). In general, they can be divided into molecular and biochemical markers. Molecular markers are variations in the DNA like deletions, insertions, inversions, and/or duplications. Biochemical markers use variations in the gene products (e.g., proteins). Markers are either dominant/recessive or codominant regarding their mode of inheritance. Codominant markers are more valuable because they are able to distinguish between homo- and heterozygotic patterns (Liu and Cordes 2004). All the DNA markers naturally have their pros and contras. Therefore, it is important to know what exactly the underlying objective for the use of which specific DNA marker is.

### Examples of Application

DNA markers allow for a variety of applications. One of their main functions is to allow for the identification of the relationship between inherited diseases and their underlying genetic causes.

For example, a genome-wide association study (GWAS) is an epidemiologic survey of common genetic variants within a given population. The aim is to search for single nucleotide polymorphisms (SNPs) within individuals that are correlated with a trait or disease. SNPs are variations in the DNA common to the population, as opposed to mutations, which are changes in the DNA away from the normal allele, and are only found in rare instances. Therefore, a phenotype-first approach is normally employed where the genetic sequences of diseased (called case) and healthy (called control) patients are compared, by scanning using a SNP array for sequence variations. So far almost 150 million SNPs have been identified (Sherry et al. 2001). Alleles (variants) more frequent in cases are seen to be more associated with a disease (Manolio 2010; Pearson and Manolio 2008). While polymorphisms within a population have been identified as increasing risk for a disease, the studies are merely association studies, and do not provide functional evidence towards disease development or progression.



Another example emerged during the examination of the transmissible agent of canine transmissible venereal tumor (CTVT). Two hypotheses competed against each other where one postulated that virus-like particles induced cell transformation versus allograft infection (transplantation of cells from a nonidentical donor) as the second hypothesis. The employment of genetic markers identified that the tumor cells themselves evolved into the transmissible parasite (natural transmission) and further were able to elucidate the age of the tumor and its phylogenetics through its breed of origin (Murgia et al. 2006).

Conclusion

DNA markers are powerful tools with a broad variety of purposes and serve either to examine known molecular sequences or to determine unknown fragments close to them. Depending on its application it is possible to choose from a broad range of different marker (see Table 1) which have emerged more and more recently with the technical progression. Therefore, nowadays it is possible to exactly analyze the molecular

identity, differences and origins of various species and between individuals.

Cross-References

- [DNA](#)
- [Microsatellite Marker](#)
- [Mitochondrial DNA](#)

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DNA Marker, Table 1 Examples of DNA marker

|          |                                                           |
|----------|-----------------------------------------------------------|
| AFLP     | Amplified fragment length polymorphism                    |
| Allozyme | Allelic variant form of enzymes coded from the same locus |
| ASAP     | Allele-specific associated primers                        |
| CSI      | Conserved signature inserts and deletion                  |
| DArt     | Diversity Arrays Technology                               |
| EST      | Expressed sequence tags                                   |
| ISTR     | Inverse sequence-tagged repeats                           |
| mtDNA    | Mitochondrial DNA                                         |
| OP       | Oligonucleotide polymorphism                              |
| RAD      | Restriction site associated DNA markers                   |
| RAPD     | Random amplification of polymorphic DNA                   |
| RFLP     | Restriction fragment length polymorphism                  |
| SFP      | Single feature polymorphism                               |
| SNP      | Single nucleotide polymorphism                            |
| SSLP     | Simple sequence length polymorphism                       |
| SSR      | Simple sequence repeat – microsatellite polymorphism      |
| STR      | Short tandem repeat                                       |
| VNTR     | Variable number tandem repeat                             |

DNA Methylation

- [Epigenesis](#)
- [Genomic Imprinting](#)

DNA Pooling

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Definition

DNA pooling is an approach where DNA from multiple individuals is pooled into a single DNA mixture for library preparation and sequencing.

## Introduction

DNA pooling methods are subdivided into two categories. The first category comprises the non-overlapping pooling methods where each individual is put in only one pool and each pool has a limited number of individuals. Whereas the overlapping pooling methods insert each individual in multiple pools to recover the genotype of each of them. DNA pooling decreases the costs for genotyping in large-scale association studies and was first introduced by Erlich et al. (2009).

## Application

The cost of sequencing the genotype of single individuals has strongly decreased in recent years due to high-throughput sequencing (HTS) technologies. For example, a genome-wide association study (GWAS) is an epidemiologic survey of common genetic variants within a given population. The aim is to search for single nucleotide polymorphisms (SNPs) within individuals that are correlated with a trait or disease. SNPs are variations in the DNA common to the population, as opposed to mutations, which are changes in the DNA away from the normal allele, and are only found in rare instances. Therefore, a phenotype-first approach is normally employed where the genetic sequences of diseased (called case) and healthy (called control) patients are compared, by scanning using a SNP array for sequence variations. So far almost 150 million SNPs have been identified (Sherry et al. 2001). Alleles (variants) more frequent in cases are seen to be more associated with a disease (Manolio 2010; Pearson and Manolio 2008). The identification of putative susceptibility genes for various diseases (e.g., diabetes, schizophrenia, Crohn's disease) are examples of the functionality of this approach (Wasson 2007). While polymorphisms within a population have been identified as increasing risk for a disease, the studies are merely association studies and do not provide functional evidence toward disease development or progression. In order to perform GWAS and detect common and rare SNPs, it is necessary to collect large cohorts of

cases. Whole genome sequencing in general would be the method of choice but is still very expensive for large cohorts. The costs for sequencing come down to two parts. The first is the most labor-intensive and the so-called library preparation cost consisting of the DNA sample preparation. The second part is the sequencing itself as per-base cost. Due to technological advances the costs for sequencing are becoming less over time, whereas the library preparation costs are quite stable. Multifold studies employed overlapping DNA pools to determine rare casual SNPs with high accuracy. The problem in these cases is the assumption that all individuals show the same abundance level in the pools which might lead to falsified associations. This could be eradicated by a probabilistic modelling of individual abundance levels (Hormozdiari et al. 2012). Nevertheless, this procedure is the main application for large-scale association studies usually without the addition of probabilistic modeling.

## Conclusion

DNA pooling is a cost reducing approach for the sequencing of large cohorts of individuals in order to identify common and rare SNPs among individuals. The SNPs are associated with traits or diseases and therefore could be used for detection and prevention. In addition, advances in technology make this method more and more affordable for broad application.

## Cross-References

- DNA
- DNA Marker

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## DNA Repair Hypothesis

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### Synonyms

[Evolution of sex](#); [Sexual adaption](#)

### Definition

To repair the genetic material is the primary function of sex, and this is known as “DNA repair hypothesis.”

### Introduction

Sexual reproduction is necessary for our evolution. In sexual reproduction, progeny is similar to their parents, not the same due to genetic variation in each generation. The genetic variation facilitates adaptation. Progeny after sexual reproduction is young and genetically different from their parent. This young progeny went through different sequential gene regulation (upregulation/downregulation), i.e., on or off of different gene

during different development phases. This young progeny does not reflect the age of their parent because it is from germ cells, not from somatic cells (aged cells) (Bernstein 1979) (Gensler et al. 1987). Lack of aging in germ cells is because of cell arrest ( $G_0$  phase) and mitotic recombination. To repair the genetic material is the primary function of sex, and this is known as “repair hypothesis.”

### Hypothesis

In biological system (DNA or RNA), noise reflects damage or mutation in the genome, and this is a serious problem. Sexual reproduction is selected in evolution to avoid mutation and damage in DNA/RNA. Before sexual reproduction and during gametogenesis, germ cells undergo meiosis (cell division) and in this process recombination of the gene by homologous recombination. This homologous recombination leads to the selection of genes, and during this recombination process, a mutation leads to a new allele in populations (Felsenstein 1974).

If you compare damage versus mutation, the damage is any alteration in genetic material (DNA/RNA) which can be recognized by enzymes and repaired. DNA damage is caused by any high-energy radiation, free radicles, addition or deletion of any functioning group on nucleotides, single- or double-strand break, thymine dimer caused by UV cross-linking, and others. This damage blocks replication and leads to cell arrest, then the repair protein tries to repair it, and it is repaired, and then division continues; otherwise, cell leads to apoptosis. These damages are not inherited to the next generation because these are lethal to the cell and not replicable (Bernstein 1979), whereas in mutation are changes in the coding sequence of DNA/RNA. Due to a change in coding sequence either a change in protein expression level increases or decreases, truncated protein which in non-functional and this leads to reduce or sometimes rarely increase fitness. These are mutations not detected by enzymes, so, with the change in the genetic material, therefore, they are replicable and transfer to the next generation. Low frequency of

mutation is required for evolution to acquire new adaptive information (Bernstein et al. 1987). Mutation in one copy of genomes is masked up by homologous copy which is known as complementation. If the mutation has negative effect, the individual gets eliminated from the population by natural selection because of less fit.

There are two fundamental benefits of sexual reproduction explained by repair hypothesis. First is the recombination and to understand we need some background. Recombination is the major repair pathway in the diploid organism. Each diploid cell has two copy of genome: one is paternal, and the other is maternal. Entire genome segmented in chromosomes and each chromosome have coding as well as the noncoding region. This noncoding region helps in the regulation of the gene. In the territory of the chromosome defined in the nucleus, during meiosis I, the homologous sets of chromosome come closer and align parallel to each other. After alignment, the recombination process starts, and there is a huge shuffling of genes or chromosomal regions. This recombination process is required to the selection of genes from two different individuals (parents), and that is why the progeny has characters from both parents (H. Bernstein et al. 1985). Recombination proves the repair hypothesis in germ cells. The second fundamental is outcrossing which is required for the complementation of mutation that occurred in the homologous chromosome. This outcross is also required to increase genetic diversity and reduce the probability of carrying any hereditary disease or genetic abnormality. Finally, the two fundamental pillars of sexual reproduction are recombination and outcross which help in the repair of genetic material and complementation of genetic disease (Kodric-Brown and Brown 1987).

## Conclusion

Sexual reproductions are selected during the evolution because it gives similar progeny, not the identical one, and it also gives enough time to repair DNA. If the reproduction is by the asexual method, then a mutation carried to next generation never gets repaired in the same or next generation.

While in case of sexual reproduction, these mutations may be repaired by the recombination process (meiosis). The other copy that repairs the mutated copy is the same cell, i.e., the maternal copy repaired by paternal or vice versa. If a mutation is given fitness to population, then this has to accumulate in the population which is done by outcross and it distributed into the population.

## Cross-References

- [Evolution](#)
- [Mutations](#)
- [Natural Selection](#)
- [Recombination](#)

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## DNA Transfer

- [Conjugation](#)

## DNA Typing

- [Restriction Fragment Length Polymorphism](#)

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## Dog Behavior

- [Canine Cognition](#)
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## Dog Cognition

- [Canine Cognition](#)
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## Dog Communication

- [Canine Communication](#)
- 

## Dog Gaits

- [Canine Locomotion](#)
- 

## Dog Intelligence

- [Canine Cognition](#)
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## Dog Locomotion

- [Canine Locomotion](#)
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## Dog Racing

- [Greyhound Racing](#)
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## Dolphin

- [Cetacean Cognition](#)
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## Domain Specificity

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### Introduction

A domain-specific view of the mind describes cognition as consisting of mental computations specialized in handling selective inputs in order to achieve a particular purpose. Such a “mental toolkit”-like characterization of our minds is contrasted with theories of domain generality that claim that all-purpose learning mechanisms can sufficiently account for all cognitive abilities. Related to the view of domain specificity is the theory of modularity (Fodor 1983). Mental modules invoke the idea of domain specificity and take it one step further by committing to their innateness, neural specificity, automaticity, and encapsulation (i.e., independence from other modules).

Perhaps the most intuitive way of illustrating domain specificity is through examples of instinctive behavior in both humans and nonhuman animals. Instincts are often broadly defined as automatic, fixed behaviors and responses shared by all members of a particular species (i.e., genetically predetermined). We think of behaviors such as a spider’s ability to spin a web, a bird of paradise’s mating dance, a koala’s selective consumption of eucalyptus leaves, and a human baby’s laugh or cry as being instinctive. Each of these behaviors is innate (not learned through experience), elicited only in particular situations, involves a particular set of behaviors, and serves a particular purpose for the organism. Although instincts were initially thought to be independent from cognition, this distinction is gradually being blurred as scientists gain more insight into the cognitive underpinnings of animal behavior, on one hand, and the instinctive nature of human cognition, on the other.

Domain-specific theories provide biologically and psychologically consistent explanations of

functionally specialized mental processes that have been selected over the course of evolution. However, they are often criticized for the degree of “hard-wiring” they invoke and the apparent lack of emphasis they put on experience and plasticity.

## Core Cognitive Domains

Developmental psychologists coined the term *core knowledge* to refer to the domain-specific cognitive mechanisms that humans innately possess from infancy that are evolutionarily ancient and shared with other species (Kinzler and Spelke 2007). Four main domains of core knowledge have been characterized in detail thus far: objects, space, numerosity, and social agents. Language is sometimes referred to as another core domain, but its origins are still debated (Tomasello 2008).

*Objects.* The core domain of objects concerns macroscopic, inanimate objects and their physical behavior. Young animals and newborn human infants treat objects as solid and spatiotemporally continuous, expecting object parts that move together to be connected (Spelke 2003). They track such individual objects through space but are limited in the number of objects that they can track at once. This set size limit of about four, which can also be found in adult subjects in tasks of multiple object-tracking, has led researchers to link the core domain of objects with the mid-level object attention system in adults (Feigenson et al. 2004). In infants, this system allows babies (both human and nonhuman) to organize the perceptual world into bounded wholes and to learn to associate them with various features, concepts, and behaviors.

*Animate agents.* There are entities in the world that are not subject to constraints on their physical characteristics (as in the domain of objects) – animate agents. We are endowed with a predisposition to look at and attend to other animate beings who are potential social partners, competitors, predators, or prey. There are several specific physical and behavioral properties associated with agents, including face-like inverted

triangular arrangements of features, presence of eyes, contingent behavior, intentionality, causality, and self-propelled movement (Kinzler and Spelke 2007). Such properties are thought to guide our attention to our social companions, as well as potential threats, and to guide our learning to be able to expertly discriminate each individual from another. Studies of neural specificity in mechanisms underlying the conceptual organization of animate beings and face processing have made major contributions to the scientific discussion surrounding domain specificity (see next section).

*Number.* The ability to track a small number of individuals can be said to be a part of the core object system, but a different system is responsible for the ability to estimate numbers of elements in a set and perform mathematical operations over them. The core system of number is often referred to as an approximate magnitude representation system with properties such as scalar variability (i.e., larger numbers have larger errors) and ratio-based distinguishability (Feigenson et al. 2004). It allows us to represent, compare, and remember numerical quantities of sets of objects regardless of the individual identity (e.g., quantity of berries on a bush or number of people in a rival tribe) or modality of input (e.g., either through seeing, touching, or hearing). The accuracy and precision of the core number system has been linked to mathematical competence in both children and adults (Bugden et al. 2016).

*Space.* The first three core domains concerned representations of entities in space. But we also have a core representation of space itself, which allows us to mentally map our surrounding environment and navigate through it. Decades of research in both animal models and humans have established a detailed understanding of the neural basis of the cognitive map in the hippocampus. Core spatial representations consist of directional and distance relationships among locations and are particularly attuned to 3D environmental boundary structures (Lee 2017). The strong influence of boundary geometry on behavior (and the brain) has been well-documented across both humans and nonhuman animals, and researchers have debated for decades over the



existence of a “geometric module” underlying spatial navigation.

## Neural Specificity

Humans have known for many years that damaging certain parts of the brain can often result in the selective loss of specific mental functions. For instance, most of us have heard about memory deficits following damage to the medial temporal lobe, or the loss of verbal abilities after damaging fronto-temporal cortical regions such as Broca’s area. Some of the most powerful evidence for domain specificity in studies of human cognition come from studies of brain-damaged patients with selective conceptual category deficits. For example, damage to a particular area of the left temporal lobe can impair a person’s ability to recognize or name animate beings (e.g., animals) but not inanimate objects (e.g., artifacts) (Caramazza and Shelton 1998). This selective deficit has been shown to occur at the conceptual level, independently of the perceptual modality of presentation (e.g., both visual and auditory).

The advent of neuroimaging techniques in the past few decades has made it possible for cognitive neuroscientists to spatially localize and analyze human brain activity in response to particular types of stimuli and tasks. For instance, visual processing of faces, objects, and scenes has been correlated with activity in areas such as the OFA/FFA (occipital/fusiform face area), LOC (lateral occipital complex), and OPA/PPA (occipital/parahippocampal place area), respectively (Grill-Spector et al. 2001). Such findings have generally been taken as evidence in favor of a domain-specific organization of concepts in the brain.

## Domain Specificity and Learning

A common mischaracterization of domain specificity is that it is a deterministic view of human mental capacity. Although it is true that the roots of domain specificity lie in the evolutionary origins of mental adaptations, by no means does it

undermine the importance of learning and experience. In fact, core representations can be said to direct our attention and intention to ward specific things in specific situations so that we can *learn* the right information for the right purposes from the earliest days of development.

Taking face recognition as an example, it is possible that domain-specific mechanisms can be a result of a combination of innate predisposition and experience. An example of such a case is in the origins of face preference and face recognition (Kanwisher 2010). Although infants prefer faces over non-faces from birth, they become experts at discriminating faces of the social category (e.g., race, species) that they are perceptually exposed to over the course of development. Furthermore, the FFA has been shown to activate, in some cases, for non-face stimuli that people learn to expertly differentiate (Gauthier et al. 2000). Therefore, if both behavioral and cortical specialization in facial recognition could be a result of experience, it follows that some domain-specific processes may not *necessarily* be innate. Further research in cognitive neuroscience will lead to clearer insight as to the origins of domain specificity in behavior and the brain.

## Conclusion

Just like other organ systems of the body, the brain has adapted to perform specific functions. Domain-specific mechanisms provide animals with the basic tendencies, biases, and cognitive abilities that allow them to interpret relevant sensory input and respond to it quickly and precisely. Domain-general processes, then, may add associative data to the existing structure that allows individuals to modulate their behavior in accord with their experience. In particular, humans start out equipped with the basic domain-specific processes that we share with other animals, we overcome their limitations across development to create abstract, symbolic human knowledge systems that can be flexibly applied across conceptual domains (Carey and Spelke 1994). How this happens is a major

challenge for the fields of developmental and cognitive science to address in the future.

## Cross-References

- [Biological Preparedness](#)
- [Comparative Cognition](#)
- [Constraints on Learning](#)
- [Precocial](#)

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## Domestic Pig

- [Swine Cognition](#)

## Domestic Swine

- [Swine Cognition](#)

## Domestication

- [Self-Domestication Hypothesis](#)

## Domestication Hypothesis

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## Definition

The domestication hypothesis was developed by Hare et al. (2002) in an effort to explain the seemingly innate ability for dogs to follow human social cues to find food. The hypothesis predicts that domestic dogs should be better at using human social cues in goal-oriented tasks than wolves because domestication selected for the ability to read human communicative cues. Therefore, experience should not affect performance on tasks requiring such communication. Since its inception, the domestication hypothesis has stood against a series of alternative hypotheses and continues to be one of the most prevalent and widely held hypotheses on the topic.

## Introduction

It has long been observed that there is a unique connection between domestic dogs and humans. “Man’s best friend” is often applied to describe

the close bond between the two species. This bond is accentuated by dogs' ability to seemingly understand human communication cues – notably, their ability to understand pointing (Udell et al. 2010). This ability has long fascinated scientists, as few animals are able to understand human gestures. There have been numerous hypotheses presented in attempts to explain how and why this ability evolved in dogs. One of the most generative hypotheses was presented by Hare et al. (2002) and is known as the “Domestication Hypothesis.” Generally, it asserts that, during the process of domestication, humans specifically selected for traits that enabled dogs to perform tasks requiring communication with humans, which allowed dogs to evolve the capacity to understand and react to human-produced directional cues (i.e., pointing) in goal-oriented contexts (i.e., foraging) that their non-domesticated counterparts do not possess.

More specifically, the hypothesis can be broken down into two main tenets. The first is that “dogs should be more skillful than wolves” (and other non-domesticated species) on human-based, goal-oriented tasks; the second is that “variations in experience with humans should not affect the performance of either species” in using human communication cues (Hare et al. 2002, p. 1634). In their flagship paper introducing the domestication hypothesis, Hare and colleagues outline the results of a series of studies they conducted. There were three main takeaways from the results.

First, Hare et al. (2002) compared domestic dogs and chimpanzees on their ability to use human social cues to find hidden food. They found that, while domestic dogs were easily able to find the hidden food, chimpanzees were less skillful at applying the social cues. Similarly, they also found that domestic dogs performed better than wolves on a similar task (Hare et al. 2002). These results lend credence to the first tenet of the domestication hypothesis that dogs should be more skillful than their non-domesticated counterparts. They also studied the performance of dog puppies at a variety of ages to explore whether developmental stage or ontogeny affected their performance. In line with the hypothesis, they found that the puppies' ability to use human social

cues did not vary with their age, but rather it was consistent at a high level across ages. This finding supports the second tenet of the hypothesis that variations in experience should not affect performance. Each of these findings, taken together, supports the main tenets of the domestication hypothesis. However, since its conception, there have been a series of alternative hypotheses presented to explain deviations from these tenets.

## Domestication

To fully understand the domestication hypothesis, it is important to first outline domestication. Hare and Tomasello (2005) broadly suggested that it was the result of convergent evolution of complex social skills in dogs and humans in response to social pressures that allow dogs to understand human gestures. Other researchers have alternatively suggested that this capacity in domestic dogs comes from their acceptance of humans as social companions (Hare et al. 2002; Hare and Tomasello 2005; Udell et al. 2010). Both propositions agree with the overarching process by which domestication came about: artificial selection.

Artificial selection is the process through which dogs are selectively bred for certain traits. Through this process, individuals with the desired traits are mated with one another, artificially inflating the incidence of those traits. Notably, individuals that were more attuned to human communicative cues were bred, progressively producing individuals that excelled at reading human cues, as the genes controlling that behavior pattern has been magnified over generations (Agnetta et al. 2000). Hare and Tomasello (2005) postulated that artificially selecting for individuals with the desired temperament and social skills presented the necessary pressures for human-like social intelligence to develop. They paralleled this with a type of self-domestication in modern human societies, wherein selection for a more tolerant and cooperative nature resulted in the evolution of a “tamer” human temperament.

Communication is crucial to effective cohabitation and cooperation, which is why dogs that

were able to use human-produced social cues were at a selective advantage. Not only did it increase the likelihood of their genes carrying on to the next generation through selective breeding, but it also created a new niche for them in humans' lives (Hare et al. 2002; Hare and Tomasello 2005). This increased interaction between dogs and humans allowed for enculturation, which is a process by which opportunities for individuals to communicate and interact with humans enhance their cognitive skills, particularly on social tasks involving humans (Call and Tomasello 1996). In other words, through the process of artificial selection, domestic dogs evolved enhanced communication abilities that were specifically tailored to human cues.

### Alternative Hypotheses

The studies conducted by Hare et al. (2002) provide evidence in support of their hypothesis, but it is not these results that provide the most compelling argument in favor of the domestication hypothesis. Instead, it is the rebuttals of alternative hypotheses that lend the most credence to this hypothesis. There have been a number of alternative hypotheses proposed both before and after the domestication hypothesis that attempt to explain the unique link between domestic dogs and humans.

The canine cooperation hypothesis was proposed by Range and Viranyi (2013) and is predicated on the idea that dogs' ability to use human social cues is a form of dog-human cooperation; and since wolves have demonstrated the ability to cooperate with one another, that constitutes the basis for dogs evolving the ability to cooperate with humans. Through the process of artificial selection, these traits increased over the course of many generations, resulting in domestic dogs having high levels of social attentiveness and tolerance. The most notable issue with this hypothesis is that, if the only trait that is necessary to use human communicative cues is the ability to cooperate, then wolves should be able to use human-directed cues in the absence of experience with humans. As outlined above, wolves were

able to perform comparably only following extensive socialization; they do not innately demonstrate the ability to follow human gestures or gazes (Hare et al. 2010).

Another hypothesis that draws on behaviors seen in wolves to describe those in domestic dogs is the canine generalization hypothesis, which suggests that non-domesticated canids should perform at least as well as dogs on social tasks, as they do on nonsocial tasks (Frank and Frank 1982). The logic underlying this hypothesis is based on the general flexibility of canids in the types of social information that they are able to use (Hare et al. 2002). Lampe et al. (2017) found that wolves that had been extensively socialized by humans were able to follow both a human's point and gaze to a food reward with similar proficiency to dogs. Whereas the researchers acknowledged that the success of the wolves in their study does not eliminate the possibility that domestic dogs evolved a predisposition to learn about human social cues faster, they argued that the wolves' performance was sufficient to disprove the first tenet of the domestication hypothesis.

In a similar study, Udell and colleagues (2008) found that wolves actually outperformed domestic dogs in an object choice task, while using human pointing cues. Hare et al. (2010) issued a rebuttal of the results, reanalyzing the data from Udell and colleagues (2008). The reanalysis showed that the initial results were artifacts of the wolves being more willing to participate in trials. Thus, when looking at participation and correct choice separately, the wolves and dogs performed similarly. It is possible to then say that, regardless of the reanalysis, wolves still performed comparably to dogs, which supports the canid generalization hypothesis. But Hare et al. (2010) emphasized that these wolves had also been extensively socialized, whereas dogs are able to use human-based cues independent of their experience with humans. This suggests that the canid generalization hypothesis is based more on individual ontogeny, rather than evolution of certain abilities through the process of domestication.

The same group of researchers presented their alternative to the domestication hypothesis – the

Two Stage Hypothesis (Udell et al. 2010). It posits that the ability for canids to understand human social cues depends on two ontogenetic experiences: interaction with humans during a sensitive period and learning ability that is not restricted to a specific developmental phase. It presents itself as a more parsimonious explanation for dogs' abilities to use human social cues and provides four interesting critiques for the domestication hypothesis. First, they call into question the presupposition of the development of some advanced cognitive ability in domestic dogs, pointing to Coppinger and Coppinger's (2001) results that domestic dogs have smaller brains than wolves, as potential evidence to the contrary. Second, they draw on their earlier results, showing that wolves were able to perform comparably to dogs after extensive socialization, suggesting that the ability is not the result of some evolutionary adaptation, but rather ontogenetic in its origins (Udell et al. 2008). Third, they argue that it is unlikely that dogs could have an innate ability to exploit human communicative skills because they are different species. Finally, they point to Scott and Fuller's (1965) results that outlined the critical role of experience in the development of social interactions in canids.

In addition to the above critiques of the domestication hypothesis, the Two Stage Hypothesis has seemingly been able to side step the counterargument that dogs as young as 4 months old have demonstrated the capacity to use human-based cues. Udell and colleagues (2010) pointed out that domestication is associated with closeness to humans, a relationship that is not addressed by the domestication hypothesis, and thus the Two Stage Hypothesis predicts that experience with humans will positively correlate with object-choice task performance (Udell et al. 2010). They further argued that, even at 4 months old, it is incredibly unlikely that puppies have had no conditioning to human gestures prior to testing, even if unintentional. They also highlighted the difference in development speed between domestic dog and wolves; domestic dogs develop slower, which allows for the sensitive period for socialization to be extended, whereas wolves have a relatively fast

development and a small socialization period. They argue that, even if both dogs and wolves were socialized with humans for the same amount of time at the same age, by virtue of their different development speeds, domestic dogs would have spent more time socializing with humans during that sensitive period. The Two Stage Hypothesis thus suggests that both domestic dogs and their wild counterparts are equipped with the necessary cognitive abilities to understand human-directed cues and any observed differences are the result of different critical periods and exposure to humans.

The framework of the Two Stage Hypothesis, in conjunction with its critiques of the domestication hypothesis, brings awareness to some of the shortcomings of the domestication hypothesis. Additionally, it seems to have found an alternative conclusion for the earlier results with the 4-month-old puppies (Agnetta et al. 2000). However, an often-overlooked element of Agnetta et al.' (2000) study showed that the puppies were readily able to use a variety of novel human-directed cues to find food. This ability to spontaneously use novel cues conflicts with any purely ontogenetic hypotheses, as it does not rely on previous experience.

## Conclusion

The domestication hypothesis (Hare et al. 2002) is one of many explanations for how dogs developed the ability to follow human social cues to find food. While the hypothesis is not without detractors, it has withstood scrutiny over the years. The domestication hypothesis is an evolutionary explanation for why dogs can follow gestures. It predicts both that dogs should perform better on human-guided, goal-oriented tasks compared to non-domesticated species and that experience should not affect performance. In a follow-up, Hare and Tomasello (2005) asserted that dogs and humans experienced the convergent evolution of complex social skills due to similar social pressures. It is through this process that both human and dog temperaments became tamer and better suited for interspecific cooperation. There is still

much to learn about the domestication process and how it yielded the unique behaviors we see today.

## Cross-References

- ▶ [Canine Cognition](#)
- ▶ [Canine Communication](#)
- ▶ [Domestication](#)
- ▶ [Self-Domestication Hypothesis](#)

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## Domestication Syndrome

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Domesticated animals are so intertwined with the lives of modern humans, it is often difficult to imagine how we lived without them; for much of our evolutionary history, however, we did just that. Not until roughly 12,000 years ago did early humans discover agriculture and change everything. They learned how to domesticate certain edible plants, as well as certain animals, like cows, sheep, pigs, goats, and horses (Barker 2009). Of course, these livestock and food animals were not the first to find themselves cohabitating with humans, that title goes to the dogs. Perhaps the way dogs changed and molded into the loving pet they are inspired early humans to try to replicate that in other animals. But dogs were the first.

Though still uncertain, some put dog domestication as far back as 40,000 years ago (Hare and Woods 2013). One thing is for sure, however: Dogs were fully domesticated by 14,000 years ago. By this time they had even reached a point in the household where they were honored enough to be buried their owners (Janssens et al. 2018). Dogs were the prototypical domesticated animals, and rightfully earned their place as “Man’s Best Friend,” but what lead up to this transition from wolf to dog?

The story that is often told is of a group of early humans stealing some wolf cubs and raising them as their own, then slowly but surely breeding them over generations until they became the dogs we see today (Clutton-Brock 1977). As oft repeated as it may be, this explanation doesn’t account for the animosity that has always existed between humans and dogs, nor does it address how widespread dogs became. Instead, ancient wolves likely began by eating the trash of early humans. They likely got closer and closer to human camps, their offspring getting more and more tolerant of humans, then one day they were allowed into the camp. This began the domestication of wolves



into dogs, and it may be happening to even more species around the world now (Hare and Woods 2013).

Scholars have long observed some key similarities between those animals that humans have domesticated. These animals often had floppier ears, spotted coats, curlier tails, shorter snouts, and reached sexual maturity younger. Some scientists tried to argue that these things had been intentionally bred for; perhaps splotchy coats were easier to see in a field, or that domesticated animals needed to be able to give birth to more offspring in less time (Tchernov and Horwitz 1991). They posited that, in many ways, domesticated animals were bred to be dumber than their wild counterparts; that these animals had smaller brains because there was no need for them to be intelligent (Diamond 2002). Scientists up to this point were looking at domestication as a collection of specific traits bred by humans for specific purposes, but no one wanted to look at the whole picture. This is where Russian scientist Dmitry Belyaev comes in.

Belyaev began his research with the belief that there was yet more to know about how domestication happens. The best way, he thought, to find out how domestication truly works would simply be to domesticate an animal from scratch. Thus began one of the most influential and prolific studies on domestication in history (Dugatkin and Trut 2017).

Starting under Soviet Rule in 1958, Belyaev began his research under the guise of simply trying to breed better foxes for the fur trade. At the time, genetics research was all but outlawed, with many geneticists (including Belyaev's older brother) being executed for their research (Dugatkin and Trut 2017).

In order to create this experiment, Belyaev, with the help of young aspiring scientist Lyudmila Trut, selectively bred generations of foxes. In order to determine which foxes to breed, Trut would simply reach into the fox enclosure with her heavily gloved hand. Those foxes who were least fearful or aggressive towards the keepers' hand were bred with each other. Astonishingly, after only three generations of following this same procedure with all the fox kits, selectively bred

foxes began to show slightly more docile, tolerant traits than their freely bred counterparts (Trut 1999).

In just a few short generations, and over the course of only 40 years, the foxes who had been bred simply for tolerance towards humans were remarkably different. Beyond just being a bit friendlier towards humans, these new foxes began exhibiting more dog-like traits: Wagging tails, shorter snouts, and spotted coats (Dugatkin and Trut 2017). Where randomly bred foxes growled or cowered at the back of their enclosures, these new foxes ran to the front and begged for pets (Dugatkin and Trut 2017; Hare and Woods 2013; Trut 1999).

Past researchers had simply looked at each of the symptoms of domestication separately (Diamond 2002; Tchernov and Horwitz 1991), but this new experiment provided clear evidence that those symptoms were byproducts of simply breeding for tolerance towards humans. This discovery was coined *Domestication Syndrome*, which describes a set of traits that arise in an animal when that animal becomes domesticated. These are traits we see in many domestic animals, they include: floppier or reduced ears, shorter muzzles, smaller teeth, smaller brain, more frequent fertility, higher levels of serotonin, and, of course, higher levels of docility (Hare and Woods 2020).

It must be noted here as well that while the case of these Siberian foxes is the most longitudinal and famous, other scientists have sought to replicate the findings with other animals. One researcher sought to domesticate chickens in just the same way that Belyaev domesticated his foxes. In order to do this, Red Jungle fowl (the species from which all chicken are said to derive) were collected in a group and bred exclusively for tolerance (i.e., lack of fear) towards humans. In just eight generations, the Red Jungle fowl had increased hatch weight, increased growth, higher metabolism, higher food intake, higher serotonin, higher boldness, more dominance, smaller brains and other organs, and increased plumage (Agnvall et al. 2017). Though these changes are not identical to those seen by Belyaev, the similarities are hard to dismiss, particularly when two species

with such incredible differences at start are compared.

There is still very much to learn from those doing research on domestication and on the effects that it could have and is having on the animals who most often interact with humans. In pursuit of that knowledge, Trut has taken over since Belyaev's death in 1985, and she and her team continue to publish articles and books on the important work being done there (Dugatkin and Trut 2017; Trut 1999).

## Cross-References

- Behavioral Genetics
- Canine Communication
- Self-Domestication Hypothesis

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## Dominance

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## Synonyms

Peck order

## Definition

Dominance is an attribute of the pattern of repeated agonistic interactions between two individuals, characterized by a consistent outcome in favor of the same dyad member and a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and the loser is subordinate (Drews 1993).

## Introduction

The term dominance was first introduced by Thorleif Schjelderup-Ebbe in 1922, when he observed the behavior of domestic hens, describing their agonistic behavior (mainly pecking) and the formation of a dominant hierarchy. Schjelderup-Ebbe describes dominance in order of pecks: if A pecks at B and B never or seldom reciprocates, then A is dominant to B and B is subordinate to A.

Since that, the study and our understanding of dominance in social animals had increased a lot. Dominance among individuals in social groups is typically defined in terms of agonistic behavior,

with offensive or aggressive attack characterizing the dominant, and defensive or submissive behavior, the subordinate (Blanchard et al. 1993). To characterize a true dominance relationship, the subordinate should have a response other than escalation of the aggressive behavior toward the dominant.

Drews (1993) reviewed the literature about dominance, and proposed the definition as a relationship between individual animals, established by aggression and submission, and, dominance does not exist until one of the individual defers. Most of the time, the dominant individual has a priority access to multiple resources, such as food, mates, and territory. It is important to point that, although some authors observed a heritability in dominance, relating it to personality traits (David et al. 2011), most authors agreed that dominance is a relative measure and not an absolute property of animal (Drews 1993), being, highly context dependent.

The dominance relationship is first established with fighting and agonistic behavior. However, for maintenance of the relationship, submissive and avoidance behavior, as well as displays, is normally the most common behavior. This will normally reduce aggression (see below). Individual recognition is not a necessary condition to produce the behavioral pattern of dominance (Drews 1993).

## Function

There are two points of views about the function of dominance in social animals. First one, dominance have the function of reducing aggression and potential awareness in agonistic relationship, as well as the cost related to agonistic interactions. Reduction in aggression is normally observable in natural and modeling studies, which could be due to an internal mechanism (e.g., Pagel and Dawkins 1997) or due to a spatial reorganization and an expanding distance among individuals (Hemelrijk 2000). The second point of view states that the main function of dominance is to portioning resources, determining which individual will have a priority to access them. As dominance

predicts the individual that will have priority in this access, individuals will seize all the opportunity to reach it (e.g., Robinson et al. 2011).

## Measurement

To determine the dominance relationship, the outcome in encounters between individuals in a period of observations should be observed. The most simple and straightforward way is:

- A is dominant to B if A wins more encounters from B than B from A
- A and B are equidominant if A and B have an equal number of wins and losses
- If no encounters have been observed, their relationship is unknown (De Vries 1998)

An important observation is that not all types of aggressive/agonistic behavior are suitable for determining the dominance relationship, and, the suitable behavior must vary among species. However, as a rule, submissive behavior, which occurs when one animal recognizes another as the dominant, is a clearer indication of the dominance relationship rather than aggressive behavior (De Vries 1998; Van Dierendonck et al. 1995).

## Conclusion

Dominance is a relationship between individual animals, established by aggression and submission, and is only considered true when one of the individuals defers, which reduces the cost of aggressive interactions. Most of the time, dominant individual has a priority access to multiple resources, such as food, mates, and territory.

## Cross-References

- [Agonistic Behavior](#)
- [Alpha](#)
- [Beta](#)
- [Dominance Hierarchy](#)

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## Dominance Hierarchy

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## Synonyms

[Pecking order](#); [Rank order](#)

## Definition

Social organization in which animals interact most of the time with aggressive or submissive behaviors, leading to the creation of a rank system.

## Introduction

Dominance hierarchies were first cited by Thorleif Schjelderup-Ebbe in 1922, when he described the social organization of domestic chickens. The so-called pecking order describes the order in which individuals have access to food. This order was maintained by aggressive interactions, mainly pecking, in which the chicken that gives pecking to another one was called dominant and was never pecked by others. The dominant also has more access to food. The chicken that was pecked was called subordinate.

## Function

The emergence of dominance hierarchies in social animals is very common in nature and has the function to reduce costs and risks on injury during resource (mainly food, territory, or mates) acquisition and defense. In an ultimate view, dominance hierarchies are supposed to increase fitness of all individuals involved in this social organization, mainly the dominant. Rank in the hierarchy influences behavior, physiology, health, and ability to mate.

## Hierarchy Properties

The most basic property of hierarchies is stability. It occurs when one animal in a pair consistently delivers all or at least most of their aggressive acts, and the other one performs all or most of the submissive acts over a period of time (Chase et al. 2003).

Another desired property of dominance hierarchies is transitivity. This means that among three animals, A, B, and C, if A dominates B, and B dominates C, then A dominates C (Appleby 1983).

## Types of Hierarchy

Dominance hierarchies are generally divided in two types: linear and nonlinear hierarchy.

A linear dominance is achieved when (a) there is any unknown or undefined relationship, for every dyad A and B in the group, either A dominates B or B dominates A, and (b) the dominance order is completely transitive (de Vries 1995). A nonlinear dominance hierarchy will happen if (a) there is at least one unknown or not defined relationship and (b) there is at least one circular relationship (e.g., A dominates B, B dominates C, and C dominates A) (Appleby 1983).

## How Dominance Hierarchy Is Set Up and Maintained

There are two main hypotheses to explain how linear hierarchies are set up and maintained: they are predetermined by differences in the attributes of animals, or they are produced by the dynamics of social interaction.

The first hypothesis are also called the “prior attribute hypothesis” (Chase et al. 2002). It states that the social linear hierarchy is explained by another linear rank in an attribute that is indicative of their dominance ability (Drews 1993). For example, the larger animal takes the highest position in the hierarchy, the second larger takes the next position, and so on. Attributes that are related to dominance ability can vary depending on study species, relying on physical, physiological, and behavioral characteristics.

The second hypothesis is that social interactions among members of the groups per se generate the hierarchies (Chase 1982). This is called the “social dynamics” hypothesis (Chase et al. 2002). The social dynamics that can generate hierarchies are (a) the so-called winner and loser effects, in which individuals that win one contest have a higher probability to win later ones, and individuals that lose one contest have a greater probability to lose the next one, and (b) the “bystander,” when individuals observe others encounters and adjust their behavior according with what they are seeing, learning with it.

## Conclusion

Dominance hierarchy emerges in social animals to organize priority of access to limiting resources. The dominance order is maintained by aggressive and submissive acts, and the rank order could be determined by physical attributes or social dynamics within the group.

## Cross-References

- Basic Rank
- Dominance
- Pecking Order

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## Dominance Rank

- Basic Rank

## Dominant

### ► Alpha

## Dominant/Subordinate Relationship

### ► Aggression

## Donald Griffin

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## Introduction

If you start with his first scientific publication as a Harvard freshman, Donald Griffin spent nearly seven decades doing scientific work. Over the course of his career, he accomplished two things that few scientists achieve in their lifetimes (Gross 2009). He discovered a previously unknown natural phenomenon that he named echolocation. Later in life, he accomplished something greater than that. He changed the way we understand the minds of nonhuman beings. He did neither of these things alone, but his intellectual prowess and unflagging dedication to mustering evidence convinced many of us, including some of the skeptics that inevitably raise objections as science progresses.

## Early Life

Born in Southampton on Long Island in 1915, Donald Griffin was an only child (Griffin 1998). His family moved to the countryside near Scarsdale, New York, then, after his father's retirement for health reasons, to Barnstable, Massachusetts. Griffin's early education combined

stints of home schooling and attending nearby private schools. His uncle, a Harvard comparative physiologist who helped found the Woods Hole Oceanographic Institution, stirred his curiosity about biology. Young Griffin became a trapper and before long was studying the skins of his prey by reading scientific journals when monthly orthodontic appointments permitted post-treatment stopoffs at Boston's Museum of Natural History (Griffin 1998; Gross 2009). At age 17, a visit to a private bird research station on Cape Cod taught him about banding birds to track their migrations. Soon he was catching and banding little brown bats for the same purpose. An investigation of their homing abilities after displacement led to his first publication (Griffin 1934). By that time he had begun his first year at Harvard.

## Education and Early Career Accomplishments

As an undergraduate, Griffin was a B student. His precollege background drew him into a biology-centered curriculum, but he reluctantly took E. G. Boring's introductory psychology course to fulfill a requirement (Griffin 1998). We can only wonder whether psychology à la Boring planted a seed about cognition that would take many years to sprout. Nevertheless, the arrival of Karl Lashley at Harvard in 1935 with a joint appointment in psychology and biology allowed Griffin to pursue his real interest – animal behavior.

Despite an overall second-rate academic start, Griffin's interest in bat behavior soon paid off handsomely. Having familiarized himself with the scientific literature on bats, including Lazzaro Spallanzani's eighteenth century report on experimentally blinded bats, Griffin identified an unresolved question. No one had fully explained bats' remarkable ability to sightlessly navigate. Speculation that they might sense high-frequency sounds provided a direction to pursue, but investigating that question required specialized equipment. Fortunately, Harvard physics professor, George Washington Pierce, had the necessary instruments (Griffin 1980; Griffin 1998; Gross 2009) and readily agreed to assist. Pierce's background in



top-secret sonar research for the US Navy uniquely qualified him as a collaborator. Pierce and Griffin (1938) demonstrated that bats indeed vocalized high above the range of human hearing, which is about 20,000 cycles per second (i.e., 20 kHz). However, they cautiously refrained from concluding that bats' ultrasonic calls served a spatial orientation function.

With Lashley's support, Griffin entered Harvard's biology graduate program. There he met Robert Galambos, a fellow graduate student, who was measuring the hearing of guinea pigs with cochlear electrode implants. When Galambos tested Griffin's bats using Pierce's ultrasound generator, the bats' cochleae responded up to 98,000 cycles per second (i.e., 98 kHz), at the upper limit of Pierce's equipment. In short order, the two graduate students published findings, controversial at the time, that bats heard their own reflected ultrasonic vocalizations to dodge wires hanging from the ceiling of an experimental room (Griffin and Galambos 1941). Galambos based his dissertation on the bat research, but the topic of Griffin's dissertation was bird homing. Later, Griffin (1944) invented the term echolocation when others documented its existence in humans and secret wartime technology based on reflected energy waves became public knowledge.

The timing of Griffin's doctoral degree roughly coincided with the entry of the United States into World War II. In 1942, he began war-related post-doctoral research in Harvard's Psychoacoustic Laboratory under the supervision of S. S. Stevens, a founder of modern psychophysics and the inventor of the scales of measurement we now use to determine appropriate statistical tests. In Stevens's lab Griffin worked to improve the clarity of voice telecommunications in noisy military environments, but his stature as a bat expert presently involved him in one of the most unusual episodes of wartime research ever to be declassified.

A secret weapon development program, eventually dubbed Project X-Ray but more commonly known as the "bat bomb," began with Griffin's input (Couffer 1992; Gross 2009). In 1942, the National Defense Research Committee (NDRC) asked Griffin to evaluate a proposal submitted by a Pennsylvania dental surgeon, Lytle S. Adams, who knew Eleanor Roosevelt. Adams had seen

millions of bats take wing at dusk from Carlsbad Caverns just before he heard about Pearl Harbor on his car radio. Outraged by the sneak attack, Adams drafted a proposal to use bats in retaliation against the Japanese. It made its way to the NDRC with White House approval. The plan entailed airborne release of thousands of bats equipped with small incendiary explosives timed to ignite after the bats took roost in the wood-frame buildings of Japanese cities. The subsequent conflagration would cripple the Japanese homeland. Griffin reversed his initial favorable assessment of the plan's feasibility after determining that bats could not bear the weight of the incendiary payloads. Nevertheless, the military proceeded to try to develop the project until abandoning it in 1944.

After the war, Griffin joined Cornell University's zoology faculty but returned to Harvard in 1953, eventually becoming chair of the zoology department (Gross 2009). During this time, he either collaborated with or inspired other researchers to refine the research on bat echolocation, including its neurophysiological basis (Gross 2009). His long-standing interest in bird navigation inspired several methodological innovations to study it, including the use of aircraft, high-altitude balloons, and radar. Gross (2009, p. 256) summarized Griffin's postwar endeavors as contributions to "...the discovery of other 'new animal senses' such as infrared vision in snakes, infrasonic signals in elephants, and orientation and discrimination in electric fish." Griffin also invited to America the European ethologist, Karl von Frisch, who had decoded the sophisticated dance language of honeybees. Motivated by skepticism, Griffin replicated and reported von Frisch's findings in the foreword of the eminent ethologist's English translation (von Frisch 1950). These accomplishments merely highlight Griffin's trajectory along a successful, albeit traditional, academic career. He did change his institutional affiliation once more, moving to Rockefeller University in 1965.

## Later Career

It was at Rockefeller University that he broke with the orthodoxy that then dominated the

science of animal behavior. In retrospect, Griffin's heresy seems inevitable. By the 1970s, a new zeitgeist in psychological science had emerged. European ethology had earned the respect of American psychology (Dewsbury 1984) and its founders, von Frisch, Lorenz, and Tinbergen, were awarded a Nobel Prize in 1973. The cognitive revolution was well underway, displacing behaviorist agnosticism regarding mental events, at least in humans. Against such a backdrop, Griffin (1976) proposed a parallel revolution that opened nonhuman cognition and awareness to scientific investigation.

Predictably, Griffin's proposal was attacked by skeptics (Gould 2004), but the times were indeed changing, and Griffin persevered in the face of adversity. He published a seminal article in the respected journal, *Behavioral and Brain Sciences* (Griffin 1978), which also publishes scholarly responses. Some of those responses were favorable. His subsequent books (Griffin 1984, 1992) advanced the cognitive ethology paradigm shift, and a body of research under this new paradigm grew. He also clearly enjoyed the controversy he set off (Griffin 1998).

Griffin retired to emeritus status at Rockefeller University in 1986 but remained an active scholar. Research with a variety of species ranging from bats to bees to beavers occupied his time as an associate of zoology at Harvard's Concord Field Station. His second wife, Jocelyn, who, according to Gould (2004), may have compelled him to seriously consider animal cognition, preceded him in death in 1998. Griffin died at home in Lexington, Massachusetts, on November 7, 2003. His death coincided with the acceptance of a manuscript reviewing the most recent evidence of consciousness in nonhumans (Griffin and Speck 2004).

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## Donald O. Hebb

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## Introduction: The Education of Donald Olding Hebb

Donald Olding Hebb was born in Chester, Nova Scotia, Canada, on 22 July 1904, the first of four children. Both of his parents were physicians; his mother was the third woman to receive her MD from Dalhousie University (1896). Donald was taught at home by his mother until he entered the Chester School in the second grade. He stayed at this small rural school until he completed the eleventh grade and then finished high school at the Halifax County Academy in Halifax, Nova Scotia. He entered Dalhousie University in 1921

and majored in English and Philosophy. He was exposed to Psychology in two classes: Philosophy 1, which used William James's *Textbook of Psychology*, and Philosophy 9, which used Langfield and Allport's *Elementary Laboratory Course in Psychology* as textbooks. After graduating in 1925, he obtained a teaching certificate from the Provincial Normal School in Truro, Nova Scotia, and taught at his old school in Chester for a year until he moved to Montreal (Hebb 1980). Hebb was teaching at Verdun High School in Montreal when he met Professor W. D. Tait, the head of the Psychology Department at McGill, and attended Dr. Tait's night school class in psychology. From 1928 to 1930, he was a part-time MA student in Psychology at McGill under the supervision of Professor Chester Kellogg.

During the 1930–1931 school year, Hebb was bedridden with tuberculosis of the hip, which left him with a permanent limp. He convalesced at his father's home in Dartmouth, Nova Scotia, where he studied Sherrington's *Integrative activity of the nervous system* and Pavlov's *Conditioned reflexes*, and wrote a theoretical MA thesis which contains his first thoughts on the nature of synaptic activity during conditioning (Brown and Milner 2003). After the completion of his MA, Hebb began to work on his PhD at McGill, studying Pavlovian conditioning in the laboratory of Professor Boris P. Babkin, a former student of Pavlov. But he became disillusioned with Pavlovian conditioning procedures and his graduate studies at McGill and decided to complete his PhD under the supervision of Karl S. Lashley at the University of Chicago (Dewsbury 2002). Only a year after Hebb arrived in Chicago, however, Lashley moved to Harvard University and Hebb completed his PhD thesis at Harvard on the visual abilities of rats reared in the dark.

## **Hebb's Research Interests and Major Contributions to the Study of Animal Cognition and Behavior**

### **Human Neuropsychology and Intelligence**

Following his PhD, Hebb was appointed as a research fellow at the Montreal Neurological

Institute (MNI), under the supervision of Wilder Penfield. He administered psychological tests to patients who had temporal lobe and frontal lobe surgery (Hebb and Penfield 1940). Hebb's experience in testing patients at the MNI led him to develop a theory about the nature of intelligence and how it should be tested. With professor N. W. Morton of McGill University, Hebb developed two new tests: the verbal adult comprehension test and the nonverbal picture anomaly test. Hebb had also observed that lesions of different brain areas produced different cognitive impairments, and he developed the theory that intelligence was not unitary but a complex phenomenon, with multiple components that were differently affected by brain damage. He suggested that the different components of intelligence should be tested using specific neurological tests and came to believe that the age at which brain injury occurred was important in determining its effects on intelligence. He concluded that intelligence had two components, a fixed or innate component and a variable component that could be influenced by environmental experience, and he called these Intelligence A and Intelligence B (Hebb 1942). Cattell later renamed these as fluid and crystallized intelligence (Brown 2016). In 1939, Hebb became a lecturer in Experimental Psychology at Queen's University in Kingston, Ontario, and published his work on the effects of brain lesions at different ages and a review of frontal lobe function. He also designed a variable path maze and this Hebb–Williams maze has since been used in a number of studies of learning in animals and humans.

### **Primate Research**

In 1942, Hebb became a research associate with Lashley at the Yale Primate Laboratories at Orange Park, Florida. During this time, Hebb completed a number of studies on emotionality in chimpanzees and related these findings to human emotionality (Hebb 1947). In addition he continued his work on the development of rat intelligence. To determine the effects of early experience on learning, Hebb reared rats as pets at home and showed that enriched experience during development resulted in improved maze

learning in adulthood. These studies formed the basis of studies on the effects of environmental enrichment on behavior and neural development and have stimulated research on the effects of environmental enrichment on the brain (Nithianantharajah and Hannan 2006).

### The Organization of Behavior

During his years in Florida, Hebb completed the first five chapters of his 1949 book, *The Organization of Behavior*, in which he outlined a new way of understanding behavior in terms of neural function. Hebb became a professor of Psychology at McGill University in 1947, and during his first year in Montreal, he wrote the final chapters for *The Organization of Behavior* in which he proposed a neurophysiological theory for the explanation of psychological concepts such as attention, perception, and learning. He proposed two concepts, synaptic plasticity and cell assemblies, which have since become central tenants in neuroscience (Cooper 2005). Hebb discussed how he came to write *The Organization of Behavior* in his two autobiographical memoirs (Hebb 1959, 1980).

### Hebb's Students and Their Research

Hebb used the theories that he had developed in *The Organization of Behavior* to direct the research of his students at McGill. The publications of his students illustrate how Hebb's theories influenced his later research. For example, Rabinovitch and Rosvold developed a standardized procedure for the Hebb–Williams maze and tested rats with cortical damage and rats reared in a “free environment.” Other students used the Hebb–Williams maze to test the effects of environmental experience and lesions, thalamic stimulation, and the effects of environmental enrichment on learning and memory. Rosvold and Mishkin looked at the effects of prefrontal lobotomy, and Brenda Milner looked at the intellectual function of the temporal lobes. This research led to the groundbreaking work on patient HM, which revolutionized the study of the neural basis of memory. Hebb also continued

his studies of fear and emotionality using pure-bred Scottish terriers to examine the effects of early-rearing experience (enriched and isolated) on learning and in studies of emotional behavior and the development of social behavior. Some of the most famous work from Hebb's lab was that of Olds and Milner on electrical stimulation of brain reward pathways in the brain and the work on sensory deprivation. See Brown (2007) for detailed references.

### Hebb's Writings After *The Organization of Behavior*

With the completion of *The Organization of Behavior*, Hebb became a major theorist in the field of physiological psychology and reviewed the field for the first *Annual Review of Psychology*. In “The role of neurological ideas in psychology,” Hebb discussed his theory of behavior in comparison to the theories of Tolman, Krech, Hull, and the Gestaltists. In a 1953 lecture to the British Animal Behavior Society, he examined the problem of separating genetic and environmental components of behavior. In his presidential address to the Canadian Psychological Association, he argued that human thought was the central problem for psychology (Hebb 1953). With Thompson, Hebb wrote a chapter on the social significance of animal studies for the Handbook of Social Psychology which suggested that emotionality and psychopathology result from breakdowns in cell assemblies. In his presidential address to Division 3 of the APA, Hebb (1955) discussed the concept of motivation in terms of the CNS (conceptual nervous system). In this paper, Hebb presented the idea of an inverted U-shaped curve for the optimal arousal of behavior. Hebb wrote this paper in response to B. F. Skinner who wrote that the letters CNS should “be regarded as representing not the Central Nervous System, but the Conceptual Nervous System.” In his presentation to the American Psychiatric Foundation, Hebb again discussed the importance of environmental stimulation during development, relating it to levels of adjustment at maturity. Hebb taught the introductory psychology course at McGill for many years and wrote his *Textbook in Psychology* in 1958.

## The Long-Lasting Influence of Hebb's Ideas

In 1977, Hebb retired to Chester, Nova Scotia. He became a professor emeritus at Dalhousie University and wrote his third book, *Essay on Mind*, a summary of his ideas on the biological basis of behavior, in 1980. After Hebb died in August 1985, a number of obituaries were published which described his legacy in every area of psychology and neuroscience (e.g., Harnad 1985; Klein 1989). Hebb's influence on research in psychology and neuroscience is now greater than ever (Brown 2017). His ideas continue to stimulate research in neural and behavioral epigenetics, the long-term effects of environment on health and cognition, the physiological mechanisms of learning and memory, memory span, and language learning. Hebb's influence is also pervasive in studies of computer modeling of the brain and in robotics in which Hebbian learning rules are used to control brain–robot interfaces (Tetzlaff et al. 2015). Posner and Rothbart (2007) have gone as far as to suggest that Hebb's ideas could be used to integrate the cognitive, behavioral, and physiological approaches in psychology.

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## Donkey

### ► Equine Cognition

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## Dopamine Receptor

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## Synonyms

DRD



## Definition

A class of G-protein-coupled receptors whose endogenous agonist is the neurotransmitter dopamine.

## Introduction

The neurotransmitter dopamine plays a significant role in influencing locomotor activity, attention, motivation, positive reinforcement, cognitive functions, and hormonal regulation as it interacts with a family of G-protein-coupled receptors. The main dopamine systems arise from the midbrain and the hypothalamus. Dysregulation of dopamine is suggested to be at the root of a number of major neuropsychiatric disorders (Daly and Salloway 1994).

## The Dopamine System

The cells of the midbrain that involve dopamine can be divided into the three groups: A8 in the retrorubral field, A9 in the substantia nigra, and A10 in the ventral tegmental area. Neurons found in the retrorubral field and the substantia nigra ascend to the striatum to form sections of the extrapyramidal system, a network that governs and coordinates involuntary movement. Neurons in the ventral tegmental area project to the limbic and cortical areas, forming the mesolimbic and mesocortical tracts. These neurons may be involved in emotional expression and cognitive functioning (Daly and Salloway 1994).

## Subtypes

There are five different types of dopamine receptors, divided into two classes, activation (D1 and D5) or reduction (D2, D3, and D4) of cyclic AMP (adenosine 3':5'-monophosphate; cAMP) (Binder et al. 2009). cAMP, or cyclic AMP, is an intracellular second messenger generated by adenylyl cyclase and deriving from ATP (Offermanns and Rosenthal 2008).

## D1-like Family (Activation)

### D1

Dopamine receptor D1 is by far the most abundant subtype in the brain, found in elevated concentrations in the substantia nigra pars reticulata, the caudate, the putamen, the nucleus accumbens, the olfactory tubercle, and both the front and temporal lobes (Daly and Salloway 1994). It is encoded by the DRD1 gene and is found postsynaptically on such dopamine-receptive cells as the GABA-ergic medium spiny neurons (MSNs) in the striatum (Beaulieu and Gainetdinov 2011). D1 receptor activation on postsynaptic neurons is especially associated with a stimulatory effect on locomotor activity. As a whole, D1 receptors regulate neuronal growth and development, mediate some behaviors, including reward, and also modulate D2 receptor-related events (The National Center for Biotechnology Information 2017).

### D5

The roles of the D5 receptors remain less clear than the roles of the D1 and D2 receptors. However, the D5 receptors can be found at low levels in a variety of brain regions, including the pyramidal neurons of the prefrontal cortex, the premotor cortex, the cingulate cortex, the entorhinal cortex, substantia nigra, hypothalamus, the hippocampus, and the dentate gyrus. A very low level of expression has also been observed in the MSNs of the caudate nucleus and nucleus accumbens. It is thought that D5 might have some slight control over movement, and even possible control over cognitive functioning that involves the hippocampal regions (Beaulieu and Gainetdinov 2011).

## D2-like Family (Reduction)

### D2

Along with D3 receptors, D2 receptors are expressed both postsynaptically on dopamine target cells and presynaptically on the dopaminergic neurons. At its highest levels, D2 receptors are found most in the striatum, the nucleus accumbens, and the olfactory tubercle. Additionally, they are found in significant quantities in the substantia nigra, the ventral tegmental area, the



hypothalamus, the cortical areas, the septum, the amygdala, and the hippocampus (Beaulieu and Gainetdinov 2011). D2 is also expressed in the retina and the kidney.

D2 receptors play a role in a number of bodily processes, including locomotor activity. Activation of the D2-like family of autoreceptors on the presynapse causes a decrease in dopamine release that reduces locomotor activity, whereas a corresponding activation on the postsynapse leads to the stimulation of locomotor activity. D2 receptors appear to be heavily involved in the presynaptic regulation of the firing rate, synthesis, and release of dopamine (Beaulieu and Gainetdinov 2011). Importantly, the two splice variants of D2 receptors, D2S and D2L (“Short” and “Long” respectively), have differing neuronal distributions: D2S is largely found presynaptically, while D2L is mainly postsynaptic. D2, in tandem with D1, is responsible for learning and memory functions, as related to the prefrontal cortex. D2 receptors also mediate prolactin secretion as well as take on a variety of other roles outside the central nervous system (Beaulieu and Gainetdinov 2011).

#### D3

Receptor D3 is similar yet distinct from D2 in that it is only a presynaptic receptor. It is found in the olfactory tubercle, the nucleus accumbens, the striatum, the substantia nigra, and the hypothalamus, and may in fact play the role of an “autoreceptor” as suggested by its presynaptic location and high affinity for dopamine. It can then be said that D3 may monitor the amount of synaptic dopamine in the brain (Daly and Salloway 1994).

D3 receptors are also found in the islands of Calleja, in the temporal lobe of the brain. Due to their mentioned role as autoreceptors, it seems that D3 moderately inhibits locomotor activity and, moreover, may be involved in cognitive functions that are mediated by the hippocampal regions, just as has been found with D5 (Beaulieu and Gainetdinov 2011).

#### D4

The D4 receptor is distributed across the frontal cortex, the medulla, the hypothalamus, and to a

lesser degree across the basal ganglia (Daly and Salloway 1994).

D4 has the least amount of expression of all the receptors. Like D5, D4 has only a minimal influence on movement, and like D3, it may play a role in the cognitive functioning mediated by the hippocampus. Along with both D3 and D5, the physiological role of D4 remains rather unclear (Beaulieu and Gainetdinov 2011).

## Links to Pathology

### Attention-Deficit-Hyperactivity Disorder

It is hypothesized that people with Attention-Deficit-Hyperactivity Disorder (ADHD) may have inefficiency in processing dopamine in the frontal lobes and within the frontostriatal neuronal circuitry to such an extent that a significant amount of dopamine is removed from their brain by way of a high instance of dopamine transporter levels (Ferrell 2010; Hedlund 2013). This seems to play a role in causing the hallmark symptoms of impulsivity, hyperactivity, and inattention (Ferrell 2010). Dopamine receptors D4 and D5 have been especially implicated in this pathological process (Miller 2011).

### Substance Abuse and Addiction

The mechanisms behind the action of drugs such as cocaine, amphetamines, and nicotine have been said to involve dopamine (Bough et al. 2015).

Cocaine binds to the dopamine transporter and blocks its functioning, causing dopamine to accumulate within the synaptic cleft. This results in extended and enhanced dopamine signaling. After sustained cocaine use, decreased dopaminergic signaling may be the culprit in depressed mood disorders and the sensitization of the meso-dopaminergic circuit toward cocaine’s reinforcement, leading to dependency (Bough et al. 2015).

Amphetamines cause the release of dopamine from the mesocorticolimbic system and the nigrostriatal neurons, inhibiting some metabolic enzymes and acting as a direct agonist on serotonin receptors (Bough et al. 2015).

Nicotine consumption, such as through tobacco use, increases dopamine levels and

stimulates the reward and pleasure pathways as nicotine receptors bind to the brain. After long-term exposure to nicotine, addiction may become an issue (Bough et al. 2015).

### Schizophrenia

Schizophrenia is a severe mental illness, notable especially for its psychotic symptoms, diminished affect, and cognitive abilities. The dopamine hypothesis as proposed by Arvid Carlsson in 1963, which states that elevated dopamine transmission contributes to schizophrenia's symptoms, is still well-regarded today and came about through experimentation with first-generation antipsychotics. More modern revisions to the hypothesis have specified locations of hyperactive dopamine transmission in the mesolimbic areas and prefrontal cortex, as well as the amygdala (Brisch et al. 2014).

A decrease of D1 receptors in the prefrontal cortex is seen in schizophrenia patients, which contrasts with the elevated expression of D1 in the parietotemporal cortex. A significant increase of D2 in the striatum of schizophrenia patients has been noted as well. The decrease of D2 in the thalamus and anterior cingulate cortex may point to abnormalities in transmission from these regions to the prefrontal cortex. Both types of neuroleptics, typical and atypical, increase the expression of high-affinity D2 receptors, as do dopamine antagonists and agonists. High-affinity D2 expression in large amounts has been seen as an indicator for psychosis. In this way, antipsychotic treatment may be seen to fail in some patients because it elevates this sort of D2 expression that is associated with the increase of psychotic symptoms themselves (Brisch et al. 2014).

It is clear that every effective neuroleptic that has been formulated has had some connection to the neurotransmitter dopamine as it interacts with other neurochemicals such as glutamate, GABA, serotonin, and acetylcholine (Brisch et al. 2014).

### Parkinson's Disease

Parkinson's is primarily considered a neurodegenerative movement disorder as it involves resting tremors, rigidity, postural instability, and freezing, among such other complications as depression,

sleep disturbance, and dementia, the last one occurring especially in the late stages. Dopamine is thought to be at the root of this symptomatology, though the disease affects multiple systems (Prediger et al. 2014). The degeneration of dopaminergic neurons in midbrain nigrostriatal pathway, and thus the decline of midbrain dopamine transmission, has been pointed out as a particular focal point of the disease's etiology (Prediger et al. 2014; Double and Finberg 2016). The work of Arvid Carlsson and the prescription of L-Dopa, a medication that elevates dopamine levels, contributed greatly to the advancement of knowledge on the neurobiology behind Parkinson's (Double and Finberg 2016). Agonistic activity on D2 receptors through medication contributes to the reduction of Parkinson's symptoms, but may lead to side effects such as the vomiting, hallucinations, and hypotension associated with elevated dopamine levels (Prediger et al. 2014).

### Dopamine and the Animal Kingdom

Dopamine controls locomotor activity in animals and other vertebrates just as it does in humans. Additionally, the reward mechanism that involves dopamine has been identified through single-cell recording of dopamine neurons in animals, and dopamine has been implicated in the biology of depression in animals. However, dopamine's role in depression has been found less in humans (Blanco 2017). It is with studies involving D2 receptor-deficient mice that dopamine involvement in locomotion and reward systems has been substantiated (Oak and Van Tol 2008).

In speaking about the confluence of dopamine, animals, and reward, it is important to mention temporal difference learning. Temporal difference learning is a reinforcement-learning algorithm that learns to predict future rewards through a reward-prediction error signal, and is especially used as both a model for animal learning and dopamine activity (Seel 2012). The algorithm is an estimation tool in a way, in that it compares the prediction of a future reward to the observed reward and the estimated value of the next state. In a series of important studies, Wolfram Schultz

and his colleagues found that during classical conditioning with monkeys, dopamine neuron firing corresponded strongly with the temporal difference learning model in that dopamine neurons fired to unexpected rewards that have no precedent. This is due to a significant prediction error, as expressed by temporal difference algorithm. Dopamine neurons stopped firing after exposure to a consistent reward as suggested by the model, i.e., when subjects' predictions matched reward outcome. The temporal difference model is the dominant theory of the dopamine response to learning and has since been suggested as the basis for other models of learning beyond classical conditioning. Investigation has branched out to other subject models, including humans and rats, and other fields beyond reinforcement learning, including the burgeoning realm of neuroeconomics. The outlook is bright for further studies on this topic (Ludvig 2012).

Mice lacking in dopamine transporter show signs of hyperactivity, possibly due to a hyperdopaminergic state, and animals deficient in D2 receptors show dopamine autoreceptor-mediated cell firing inhibition (Harsing 2008). The dopamine overflow, caused by the stimulant methylphenidate, that leads to greater potentiation in dopaminergic drugs was first demonstrated in animal testing (Harsing 2008).

## Cross-References

- [Hippocampus](#)
- [Hypothalamus](#)
- [Locomotion](#)
- [Medial Striatum](#)
- [Neuron](#)
- [Neurotransmitters](#)
- [Nucleus Accumbens](#)
- [Parkinson's Disease](#)

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## Dormant

### ► Recessive

## Dorothy Cheney

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## Introduction

Through their use of playback experiments on wild primates, Dorothy Cheney and collaborator Robert Seyfarth inspired cross-disciplinary scholars of animal behavior for decades. Cheney and Seyfarth are not only pioneers in questions about the social lives and minds of animals, they also revolutionized the methods we use to investigate these questions.

## Background

Dorothy L. Cheney was born on August 24, 1950, in Boston. She received her Bachelor's degree from Wellesley College in 1972, her Ph.D. in Animal Behaviour from Cambridge under Robert Hinde in 1977, and completed a postdoctoral position with Peter Marler at Rockefeller Center in 1979. After a tenure-track stint at Rockefeller Center and UCLA, she joined the University of Pennsylvania in 1985, where she remained as a Professor of Biology until her retirement in 2016. Cheney is a fellow of the Animal Behavior

Society (1997) and American Academy of Arts & Sciences (1999) and was elected to the US National Academy of Sciences (2015). She holds an honorary Ph.D. from University of Neuchâtel, Switzerland (2013), received the Distinguished Primatologist Award from the American Society of Primatologists (2016), and accepted the Distinguished Animal Behaviorist Award from the Animal Behavior Society (2016).

Cheney married Robert Seyfarth in 1971, and the couple had two children, Caroline and Lucia. Cheney and Seyfarth conducted joint field research together throughout their careers (frequently joined by their daughters), focusing on communication, cognition, and social behavior of wild monkeys. Their award-winning book *How Monkeys See the World: Inside the Mind of Another Species* (Cheney and Seyfarth 1990) is an engaging summary of their 11 years spent studying vervet monkeys in Amboseli National Park. Similarly, *Baboon Metaphysics: The Evolution of a Social Mind* (Cheney and Seyfarth 2007) describes their 16 years of research on baboons in the Okavango Delta. Counted among its many accolades, *Baboon Metaphysics* was runner up for The Diagram Prize for Oddest Book Title of the Year by *The Bookseller* magazine, losing to *The 2009–2014 World Outlook for 60-milligram Containers of Fromage Frais*. Combining careful science with their clever writing style, Cheney and Seyfarth develop an argument in both of their books for the adaptive value of social cognition. They encourage the reader to look behind the curtain to explore the many surprising ways these animals are so similar to ourselves and, perhaps more importantly, where they differ in their cognitive and communicative abilities.

Cheney and Seyfarth have published over 200 articles, commentaries, and book chapters – 90% of these written together – on their original empirical work (many in collaboration with colleagues and students) or that review the implications of such work. Their major contributions are in social cognition and vocal communication. We focus on social cognition in this entry, but to understand Cheney's impact on communication, see Robert Seyfarth's entry in this series. Tales of Cheney and Seyfarth's narrow escapes from

hippos, lions, and malfunctioning vehicles are best communicated by the authors themselves.

## Contributions to Social Behavior and Social Cognition

As an undergraduate History major, Cheney was not particularly captivated with biology, until a course in the history of science piqued her interest in the evolution of sociality. After spending a year helping Seyfarth with his graduate fieldwork studying primate social relationships, she shelved her plans to attend law school and focused instead on figuring out what monkeys know about each other and their world.

A fortuitous result in what seemed a straightforward experiment in individual vocal recognition (Cheney and Seyfarth 1980) led to a career focused on social cognition. In the experiment, Cheney and Seyfarth played the recorded screams of juvenile vervet monkeys to a group of females with juvenile offspring, including the screamer's mother. They expected that, if vervets can recognize the vocalizations of other individuals, the mother of the screaming juvenile would respond more strongly to the playback (for example, by quickly looking toward, staring at, and/or approaching the hidden speaker) than would the control females. That is exactly what they found; however, they also recognized that they had a much more interesting result. Many of the control females had looked not at the speaker, but toward the screaming juvenile's mother, even before the mother had made any obvious response. Cheney and Seyfarth recognized the value of the unexpected finding – it demonstrated that vervet monkeys could associate a juvenile's scream with its mother, suggesting that the monkeys could make complex classifications of vocalization based on social relationships. Although identifying relationships between others (3rd party relationships) is second nature to humans, at the time, there was very little evidence that animals had similar abilities.

Further studies of vervets and baboons provided additional evidence that monkeys could indeed recognize 3rd party relationships. For

example, Cheney and Seyfarth (1989) observed female vervets for half an hour before and after fights to compare their behavior toward relatives of their opponents. They found that, after a fight, females were both more likely to threaten and more likely to behave affiliatively toward the relatives of their opponent than they were in the control period before the fight. Similarly, kin of the two opponents were also more likely to threaten or be friendly toward each other following a fight than in the control period. The vervets acted as though they recognized the similarity between their own close relationships and those of others. Although the vervets' differential treatment of kin could be explained as simple associative learning based on frequently observing kin together, Cheney and Seyfarth noted that kin relationships among the vervets were not necessarily characterized by frequent interactions. Instead, they posited that the monkeys might understand kin relationships as an abstract category that could not be entirely explained by close bonds. The ability to classify relationships in this way could be highly adaptive, since it could allow the monkeys to predict the likely behavior of others.

An elegant playback experiment by Cheney and colleagues (Bergman et al. 2003) produced strong evidence that baboons classify individuals by both rank and kinship. Female baboons have a linear dominance hierarchy, and they "inherit" their mothers' ranks. That is, young females typically attain dominance ranks immediately below those of their mothers. As a result, entire matriline can be organized in rank-order. For example, if female A1 has two offspring, A2 and A3, they rank above female B1 and her offspring, B2 and B3, such that  $A1 > A2 > A3 > B1 > B2 > B3$ . Bergman and colleagues took advantage of this structure to test whether baboons reacted differently to simulated rank reversals within compared to between matriline. In their experiment, they mimicked fights in which an aggressor threatens and a victim screams. In the control scenario, they simulated a normal interaction, with a high-ranking aggressor threatening a lower-ranking victim (A3 threatens, B1 screams). They compared the responses of females to the control scenario to their responses to simulated



within-family rank reversals (A3 threatens, A2 screams) and between-family reversals (B1 threatens, A3 screams). Even though the magnitude of the rank difference was similar in both within- and between-family reversals (in this example, the ranks are adjacent), the baboons reacted more strongly to the between-family reversal than to the within-family reversal or the control. The results made it clear that baboons were sensitive not only to the rank relationships of other individuals, but also to membership in higher-order groups, such as matriline.

In a similar vein, Cheney and colleagues (Crockford et al. 2007) demonstrated that baboons are well aware of even short-term changes in the quality of others' relationships, taking advantage of the transient nature of baboons' mating relationships. High-ranking male baboons frequently form consortships with estrus females in which the male closely follows and guards the female from other males' sexual advances. The consortships are short-lived, usually lasting several hours to several days. Crockford and colleagues mimicked broken consortships by playing the friendly grunts of a male from one speaker immediately followed by the mating call of his consort partner from another speaker positioned 40 m away – far enough apart that it seemed as though another male must have elicited the consort's mating call. They compared the responses of males to these simulated breakups to their responses to two controls. In the first control, they combined the friendly grunts of a nonconsorting male with the distant mating calls of the consorting female (consistent with an intact consortship). The second control was identical to the experimental condition, but it was played within 24 h after the consortship had ended. The males looked longer and were more likely to approach the speaker playing the mating call in the simulated breakup than in either control condition. The males' lack of response to the second control (post-breakup) was especially revealing, as it demonstrates that, even though some playbacks occurred as little as 4 h after a consortship broke up, they were already aware of the breakup. This provided evidence that baboons can recognize and categorize different types of

relationships – not just the long-term relationships of relatives but also the short-term associations of mating partners.

Though much of Cheney's cognition research focused on uncovering how monkeys categorized one another, she also ventured into even more complex cognitive processes, such as causal reasoning and theory of mind. To test whether baboons were able to identify causal relationships, Cheney and Seyfarth (1995) compared the responses of baboons to simulated anomalous social interactions to a logically consistent control. Anomalous interactions were mimicked by pairing the friendly grunts of a low-ranking female with the fear barks of a high-ranking female, as if the higher-ranking female were deferring to the lower-ranking female. Control playbacks were identical to the anomalous playbacks, except that the friendly grunts of a third female, dominant to both of the others, were included in the sequence, creating a causally consistent scenario in which the high-ranking female appeared to be deferential to an even high-ranking individual. The baboons responded more strongly to the logically inconsistent call combinations than toward the controls, suggesting that they could recognize cause-effect relationships in the social domain. Previous studies (reviewed in Cheney and Seyfarth 1995) had found monkeys incapable of recognizing cause-effect relationships; however, those studies focused on monkeys' understanding of physical relationships. Cheney and Seyfarth's results emphasized the importance of using socially relevant stimuli in experiments involving highly social, non-tool-using species.

In addition to uncovering what monkeys know about each other, Cheney and colleagues have also examined the impact of social relationships on stress hormones. For example, Beehner et al. (2005) found that female baboons had elevated glucocorticoid (GC) levels when a potentially infanticidal male took over the troop's alpha male position, but only if they had, or were pregnant with, an infant at risk of infanticide. These same females did not have elevated GC levels when a natal male who was unlikely to commit infanticide took over, or when they had friendships with males who might protect their infants.



Cheney and colleagues' more recent work has returned to her original interest in the evolution of sociality, with a focus on the adaptive value of social behavior. Using behavioral and demographic data collected over a 15-year period, Silk et al. (2009, 2010) found that female baboons who had strong, long-lasting bonds with other females lived longer and had offspring who were more likely to survive to adulthood than did females with weaker bonds. Females with high scores on a composite behavioral index of friendly behaviors were more facile at developing and maintaining bonds with other females. In addition, those friendly females showed stronger anticipatory responses to male immigration, increased the number of grooming partners after the death of a close relative, and reacted more strongly to playbacks than did other females (Seyfarth and Cheney 2013). In other words, individuals who are highly attuned to social interactions and engage in prosocial behaviors appear to have a selective advantage over less social and unfriendly individuals.

Although it is quite clear that monkeys do not have a full-blown theory of mind – that is, they are not fully aware that other individuals have different knowledge, emotions, and intentions (Cheney and Seyfarth 1990), there is some evidence that they can use their knowledge of relationships combined with memory of recent interactions to predict the likely behavior of others (Engh et al. 2006). Seyfarth and Cheney (2013) posit that selection favoring prosocial behavior may have produced a very rudimentary or functional theory of mind. Rather than knowing how other monkeys feel, monkeys have evolved to *act as if* they know how other monkeys feel.

Cheney and Seyfarth have had a profound impact on studies of social cognition. They used detailed knowledge of vervet and baboon behavior to design elegant experiments using socially relevant variables. By manipulating vocalizations and social scenarios that were familiar to the monkeys, they were able to ask clear questions about what the monkeys knew. Their own thorough research gave us a window into the rich mental lives of vervets and baboons, and their methods, adopted by other researchers, have provided

insights into the cognitive abilities of many other animals.

## Cross-References

- ▶ [Comparative Cognition](#)
- ▶ [Friendships in Animals](#)
- ▶ [Post-conflict Resolution](#)
- ▶ [Primate Cognition](#)
- ▶ [Primate Communication](#)
- ▶ [Primate Social Structure](#)
- ▶ [Reconciliation](#)
- ▶ [Robert Hinde](#)
- ▶ [Robert Seyfarth](#)
- ▶ [Social Behavior](#)
- ▶ [Social Intelligence Hypothesis](#)
- ▶ [Theory of Mind](#)

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## Dorothy Fragaszy

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Dorothy Munkenbeck Fragaszy grew up on a small farm in a rural part of New York, where the family kept horses, sheep, chickens, and occasionally other livestock. She spent much of her free time riding her horse in the woods and fields and trying to help her father (a mechanical engineer and devoted do-it-yourselfer) to construct and fix things. Her professional interests in animal behavior and problem-solving reflect these early experiences. She earned a BS in Psychology at Duke University (1972) and PhD (1978) in Psychology at the University of California, Davis. Her first research, as a graduate student with W. A. Mason in the 1970s, compared the behavior of captive squirrel monkeys (*Saimiri*) and titi monkeys (*Callicebus*) in novel spaces or facing other unfamiliar challenges. One of the more adventurous studies she conducted involved releasing pairs of monkeys one at a time into a fenced one-acre enclosure, where she had constructed aboveground paths in the center area, and retrieving the pair at the end of an hour by offering them a ride home in their familiar travel-box (Fragaszy 1979). Her studies with squirrel and titi monkeys convinced her that one must interpret a nonhuman species' behavior in a captive setting in relation to that species' behavior in natural settings. In the case of squirrel

and titi monkeys, this meant understanding their distinctly different social systems and foraging ecology, among other things. Titi monkeys form monogamous pairs and live in small territories, traveling together during the day to feed on familiar resources in known locations. In contrast, squirrel monkeys live in large groups, travel in large home ranges, and search for food visually. Monkeys of these two species display different priorities for remaining with a pairmate (titis) versus exploring independently (squirrel monkeys), and remaining in familiar places (titis) versus traveling to new places (squirrel monkeys).

In preparation for studying captive capuchin monkeys, she wanted to learn about these monkeys' lives in a natural setting. Accordingly, she studied foraging behavior and time budgets of weeper capuchins *C. olivaceus* in the llanos of Venezuela as a postdoctoral project (Fragaszy 1990). Subsequently, she established a colony of tufted capuchins in 1982 at San Diego State University, where she held her first faculty position. She took the capuchin monkeys with her to Washington State University in 1984, and finally to the University of Georgia in 1990, where she served as Chair of the Behavioral and Brain Sciences graduate program (and its predecessors) in the Psychology Department from 1995 to 2017, and is currently Professor of Psychology. Her research participants from 1980 to the present are primarily humans, capuchin monkeys, and chimpanzees, the latter species with the help of collaborators at the Language Research Center of Georgia State University and the Primate Research Institute of Kyoto University. She has collaborated extensively with Elisabetta Visalberghi, with whom she authored, together with Linda Fedigan, *The Complete Capuchin* (a scholarly book about capuchin monkeys).

Dr. Fragaszy's research contributions to the field of animal cognition concern the genesis and expression of behavioral variability and adaptability. The majority of her publications can be grouped into four domains: behavioral development, problem-solving (with an emphasis on spatial problems), motor skills, particularly manual dexterity and skilled actions with objects, and social influences on learning, including traditions.

Her studies revealed how young primates (monkeys, apes, humans) explore objects and surfaces using species-typical action routines that adults use to find and extract food and to solve instrumental problems (Fragaszy and Adams-Curtis 1991; Takeshita et al. 2005) and how young monkeys in natural settings become proficient foragers, finding and processing sometimes hidden foods, such as beetle larvae hidden under leaves or inside branches, or snails or shelled fruits that must be cracked open. Her work has sometimes indicated similarities in the actions of nonhuman primates and humans with objects and sometimes revealed striking differences. For example, Dr. Fragaszy has shown that capuchin monkeys and chimpanzees can seriate nesting cups effectively using a motor strategy: placing a cup on another and then removing it if it does not fit into the receiving cup, and repeating the sequence until each cup is contained within the one immediately below (i.e., the set is nested). Her subjects could fit a sixth cup, given after they had seriated a set of five cups, into its position in the middle of the set. This finding calls into question the hypothesis that seriating nesting cups necessarily reflects comprehension that a single cup has dual properties (larger than one, and smaller than another), as this task had been conceptualized in the human developmental literature. Perhaps children, when they first begin to seriate cups, begin with a motor strategy as well, only later developing comprehension of abstract properties of the component objects (Fragaszy et al. 2002). Similarly, capuchins and chimpanzees align the long axis of a rod or a cross-shaped object to a cutout using a motor/haptic strategy, essentially moving the object across the surface until they feel it drop into the cutout. In this case, however, even two-year-old children can align the long axis of a rod or a cross-shaped object to a cutout, apparently relying on vision to do so (Fragaszy et al. 2015). This finding suggests one reason why monkeys and apes use objects as tools in more limited ways than humans. Nonhuman primates can bring one point of a long object to a point on a surface, as in probing a stick into a hole, but it seems that they cannot precisely align even one axis of one object to an axis in another object, such as the end of a screwdriver with the notch in the head of a screw.

In the domain of manual dexterity, her studies revealed that capuchin monkeys achieve precision grips in diverse forms, occasionally use compound grips (holding two or more objects in one hand using two or more different grips). These are unexpected achievements for New World monkeys because these monkeys' thumbs do not rotate to face the palm, as do the thumbs of Old World monkeys, apes, and humans. While they use precision grips routinely, she has shown that capuchin monkeys do not use in-hand movements (translating or rotating an object wholly with the fingers of one hand) as do chimpanzees, and both species differ considerably from humans in this domain (Craet et al. 2009). Her work on skilled actions with objects also includes studies of tool use, notably by wild capuchin monkeys using stones to hammer open resistant palm nuts. In a series of field experiments conducted with colleagues at the EthoCebus field site in Brazil, she showed that wild monkeys place nuts on an anvil surface in a predictable orientation, so that the more symmetrically curved sides of the nut face the edges of the hemispheric pit in the anvil, and they use exploratory actions before initiating a strike with a hammer stone, strike with accuracy, and control the stone after the strike. These skills apparently depend on haptic perception more than visual perception. They select nuts to crack and hammer stones with which to crack them taking into account the resistance of the nut to fracture and the composition and mass of the stone (Fragaszy et al. 2010). Kinematic analyses of the striking actions revealed that monkeys modulate features of their movements, such as velocity and amplitude of their striking motions, to accommodate to the demands of the task (whether the nut is starting to crack, for example; Mangalam and Fragaszy 2015) but that they do not control some outcomes of their movements that are characteristic of human skilled percussion (such as regulating the momentum of the stone at impact). Apparently the monkeys can perceive velocity and amplitude of their strikes directly (kinesthetically), as movements of their arms, whereas momentum is a joint function of velocity and the mass of the hammer stone, and cannot be perceived through kinesthesia alone. Taken together, her studies in this area have enriched our

understanding of the perceptual foundations of actions with objects, and of the different constraints faced by different species of nonhuman primates in these actions compared to humans. Her work frames the phenomenon of manipulating objects as a problem of movement coordination and management of degrees of freedom of movement, thus linking the phenomenon of using objects as tools to biology, anatomy, and related fields, such as archaeology and robotics.

Finally, Dr. Fragaszy has contributed to our understanding of how nonhuman animals learn with and from others (“socially biased learning”), leading sometimes to the establishment of traditions in the absence of overt teaching or imitation (Fragaszy 2003). She has argued that we need to recognize the power of social coordination of activity in time and space to support young animals’ learning, and that we need to understand the temporal dynamics of social influence and the role of artifacts on learning to advance theory in social learning and cultural evolution (Fragaszy et al. 2013). In this work, capuchin monkeys provide an interesting case. Adult capuchins are highly tolerant of young monkeys remaining near them as they forage and eat, and the adults’ activity strongly influences the young monkeys’ explorations of food and of areas where adults eat (including where they crack nuts with stones and anvils). Their social dynamics and activity, and the artifacts that the adults produce, support young monkeys’ frequent practice of diverse foraging skills, including using stones and anvils to crack nuts. Practice of relevant actions hones specific motor skills, and it also likely strengthens attentional and memory processes related to these activities. Thus adults scaffold young monkeys’ skilled activity in direct and indirect ways.

Throughout her career, Dr. Fragaszy has consistently sought explanations of behavior in accord with species’ perceptual biases, motor propensities, social proclivities, and motivation to coordinate behavior with others in time and space. Her thinking draws on concepts and methods from developmental psychology, movement science, embodied cognition, niche construction theory, ecological psychology, and dynamical systems theory, as well as ethology. She has pioneered, often together with Elisabetta

Visalberghi, new methods of collecting behavioral data in natural and captive settings.

Dr. Fragaszy maintains national and international research collaborations, most notably codirecting the EthoCebus project in northern Brazil since 2005 with Patrícia Izar (University of São Paulo), and Elisabetta Visalberghi (National Research Council, Italy). Her international outlook is evident in her long service to the International Primatological Society in which she held several elected offices, including Secretary General and President, between 1989 and 2004. Subsequently she served as President of the American Society of Primatologists, and as Editor of the *Journal of Comparative Psychology*. She has served as doctoral advisor to about two dozen PhDs, mentored several postdoctoral scholars and hundreds of undergraduate research assistants, and hosted many visiting international students and researchers.

## Cross-References

- [Activity Budget](#)
- [Behavioral Flexibility](#)
- [Cognition](#)
- [Comparative Cognition](#)
- [Elisabetta Visalberghi](#)
- [Embodied Cognition](#)
- [Goal-directed Behavior](#)
- [Learning](#)
- [Nut-Cracking](#)
- [Perception-Action Theory](#)
- [Planning](#)
- [Platyrrhine Cognition](#)
- [Primate Cognition](#)
- [Primates](#)
- [Problem-solving](#)
- [Social Learning](#)
- [Stone Tools](#)
- [Tool Use](#)

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## Dorsal Pathway

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## Synonyms

[Dorsal stream](#)

## Definition

The dorsal pathway is a visual system that stretches from the primary visual cortex in the occipital lobe to the posterior parietal cortex. Also known as “where” or “how” stream, it seems to be responsible for the location of objects in space and for the guidance of actions (Binkofski and Buxbaum 2013). It has been defined as anatomically and functionally separated from another pathway, known as “what” stream, which is located in a more ventral position and has been related to perception of objects.

## Structural Organization of Visual System

To understand the anatomy and functionality of these two pathways, we must first know the way in which the visual system is organized. More specifically, it is necessary to understand how visual information flows from the retina to the visual cortex and what visual mechanisms exist in the cerebral cortex.

## Visual Processing from Retina to Visual Cortex

The specialization of the ventral and dorsal pathways described above start in the retina instead of in V1. In fact, the visual signals are first captured by the eye through the retina, where two different types of photoreceptor cells are activated: cones and rods. While cones have conical shapes and are indispensable for color processing, rods have a cane shape and are related to the processing of dynamic aspects of the world such as movement. Once cones and rods are activated, they respond stimulating the ganglion cells.

Ganglion cells are also located in the retina and could be divided, as a function of their anatomy and functionality, in magnocellular and parvocellular cells (or M and P cells, respectively) (Purves et al. 2001). M cells represent the 95% of the ganglion cells, have a large receptive field, receive information from rods (i.e., they are necessary for movement and depth processing), and emit rapid and transient responses. By contrast, P cells represent the 5% of the ganglion cells, are characterized by having small receptive field that



receive information from cones (i.e., they are related to color and shape processing), and produce slow and sustained responses. In any case, both M and P ganglion cells are responsible for sending the information from the retina to the lateral geniculate nucleus.

The lateral geniculate nucleus (LGN) is the first relay center for visual information processing in the brain. Each lateral geniculate nucleus consists of six layers that receive information from both eyes (Lynch and Corbett 2013). The two inner layers 1 and 2 receive information from the M-cells and the remaining four layers 3 to 6 receive information from the P-cells. From LGN, M and P cells axons are directed through two independent streams to the primary visual cortex. In this sense, M-cells axons project to layer 4C $\beta$  of the primary visual cortex through the Magnocellular pathway and P-cells axons project to layer 4C $\alpha$  by means of the Parvocellular pathway.

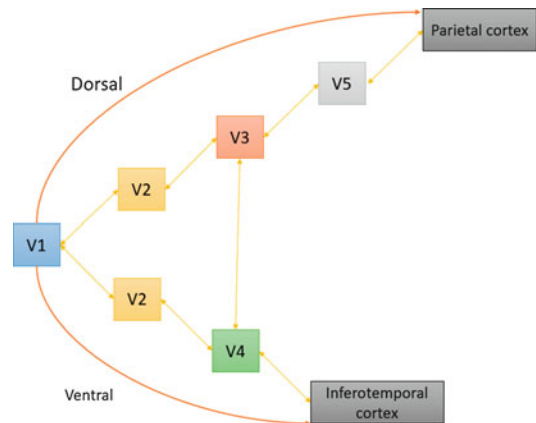
### Cortical Mechanisms for Vision

As already mentioned, visual information reaches the visual cortex from the lateral geniculate nucleus for processing to occur. More specifically, information is first processed by the primary visual cortex, also known as striate or, according to the more recent nomenclature, V1. This cortex is located on the medial surface of the occipital lobe, along the superior and inferior sides of calcarine fissure and corresponds to 17 Brodmann area (Zilles and Amunts 2012). V1 is organized into six horizontal layers and vertical columns with neurons specialized in the processing of specific characteristics of stimuli such as edges, depth, orientation, motion, and color (Remington 2012). “Striate cortex” takes its name from the layers and columns formed in this region. Moreover, V1 is retinotopically organized, so each part of the visual fields is processed by a specific part of the cortex.

From V1, information is directed toward secondary visual cortex, also known as extrastriate, which includes the occipital lobe areas located around the primary visual cortex and corresponds to 18 and 19 Brodmann areas. First, 18 Brodmann area (also known as V2) is

composed by two distinct regions: the prestriate and the inferotemporal cortex. Prestriate cortex is located around the primary visual area and receives input from this and other cortical regions and also from the thalamus. Similarly to V1, V2 process all qualities of the stimuli (color, shape, movement, etc.). Inferotemporal cortex is located in the lower part of the temporal lobe and has been related to agnosia. Second, 19 Brodmann area is composed by V3, V4, and V5, which seem to respond to specific aspects of the stimuli. In this sense, while V3 is sensitive to orientation and binocular disparity, V4 plays a role in color and form analysis of visual stimuli, and V5 is specialized in processing motion and depth.

Once the information has been processed by the primary and secondary cortex, it continues to the association areas, which encompass adjacent parts of the posterior parietal lobe and much of the posterior temporal lobe (see Fig. 1). In fact, from V1 and V2 two separate primary visual systems (i.e., the ventral and dorsal stream) emerge, which are anatomically and functionally independent and go to different areas of the secondary and associated visual areas. Specifically, while ventral stream begins in V1, goes through V2 and V4, and ends in the inferotemporal cortex, dorsal stream begins in V1, goes to V2, V3, and V5, and ends in the posterior parietal lobe (Carlson 2014).



**Dorsal Pathway, Fig. 1** Representation of ventral and dorsal streams



## The Dual-Visual Systems Hypothesis

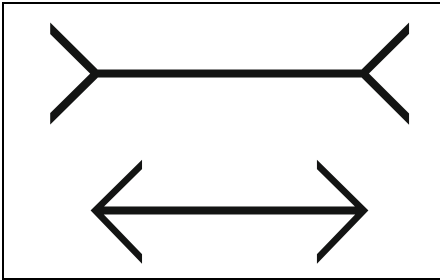
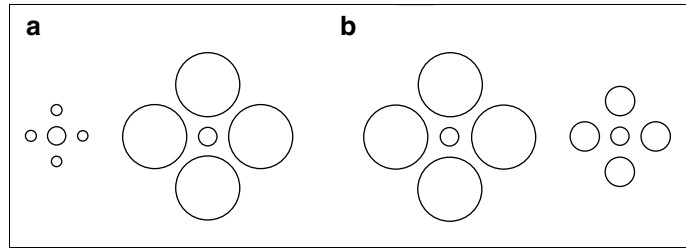
The existence of the two primary separate visual systems described above was first proposed by Mishkin and Ungerleider (1982) who define multiple visual areas in the cortex of nonhuman primates that are organized into two anatomically and functionally specialized pathways. More specifically, they observed that monkeys with inferior temporal cortex lesions had problems in the recognition and discrimination of visual shapes and objects, while monkeys with parietal lobe lesions had difficulties in analyzing the spatial location, shape, and orientation of objects. Considering the above results, these authors propose a model for visual processing composed by two separate visual pathways, one specialized for “object vision” (i.e., ventral pathway or “what” stream) and other for “spatial vision” (i.e., dorsal pathway or “where” stream). From an anatomical point of view, while the first is originated in the primary visual cortex and ends in the temporal lobe, the second also begins in the primary visual cortex but is directed towards the superior parietal region (Mishkin et al. 1983).

A decade after the appearance of this model, Goodale and Milner (1992) refined the distinction about an “object and spatial vision” systems proposing that both the perception of objects and the analysis of spatial location are processed by both the ventral and dorsal pathways, but in different ways and with different purposes. Specifically, they considered that ventral pathway uses the visual information to create a perceptual representation focused on the objects, with information about their shapes, sizes, colors, orientations, and spatial relations. The aim is to transform the visual inputs into representations that collect the enduring characteristics of the objects and their spatial relationships. On the other hand, dorsal pathway uses visual information to create a perceptual representation focused on the viewer with information about objects’ spatial location in relation to the person, in order to mediate the visual control necessary to act upon these objects. In this way, ventral stream is associated with the identification of goal objects (“vision for perception”) and dorsal stream is associated with the implementation of action directed at these goal objects (“vision for action”).

In sum, this model gives less importance to possible differences in the information received by the ventral and dorsal pathways (visual inputs), but focusses in the way they used it (visual output).

The distinction between two separate visual systems has been confirmed by neuropsychological and neuroimaging studies (Herbart and Hesselmann 2012). In this sense, the distinction between dorsal and ventral processing stream emerged from experimental works exploring neurological patients with lesions in various parts of the cerebral visual pathways that provided evidence of a dissociation between the ability to perceive an object and the ability to direct a movement toward that object. On one hand, it has been observed that patients with damage in parietal cortex who present optic ataxia, a severe impairment related with a difficulty to use the visual information to guide grasping, maintain the ability to recognize this information (Goodale and Westwood 2004). On the other hand, patients with lesions in temporal cortex who present agnosia, an impairment in the perception of objects, have an intact ability to reach these unidentified objects (Goodale et al. 1991).

These results had been confirmed by psychological studies in healthy subjects. For example, Aglioti et al. (1995) showed that automatic and metrics calibrations required for visually guided actions are independent of visual perception. Specifically, they used the “Titchener circles” illusion, also known as Ebbinghaus display, consisting of two target circles of equal size that are surrounded by other neighboring circles, which may be larger or smaller (see Fig. 2a). According to the results, subjects tend to report that the target circle which is surrounded by smaller neighboring circles is bigger than the target circle which is surrounded by larger neighboring circles. Aglioti and colleagues also used a variation of this illusion that consists on the presentation of two target circles of distinct size surrounded by other larger neighboring circles (when target circle is the smallest) or smaller (when target circle is the largest) (see Fig. 2b). In this case, subjects tend to report that target circles were perceptually equivalent when the largest is surrounded by smaller neighboring circles and vice versa. The use of this methodology confirms that participants are affected by this size-contrast

**Dorsal Pathway,****Fig. 2** The “Titchener circles” illusion**Dorsal Pathway, Fig. 3** The Müller-Lyer illusion

illusion. However, the authors also observed that regardless of the judgments made by subjects about circles' size, participants made the correct grip aperture in their hand when they are asked to pick up the target circles.

In the same line, van Doorn et al. (2007) concluded that vision for perception contributes to the selection of an action mode but not to the action itself. These authors used the Müller-Lyer illusion, which consist on an optical illusion in which two or more segments of equal size appear larger or smaller depending on whether the arrows at their ends point inwards or outwards (see Fig. 3). Specifically, they instructed subject to give, among others, a verbal judgment on the segment's size, a manual estimation of the segment's length and a manual grasp to the segment. They observed that subjects' verbal judgment and manual estimation were influenced by the Müller-Lyer illusion. However, the illusion had only a minor influence on the manual grasp.

Other, more recent, evidence of the functional division between these two pathways comes from fMRI studies. For example, James et al. (2002) showed that ventral, but not dorsal, pathway is activated when subjects view the same object from different viewpoints. In contrast, Culham

et al. (2003) observed that dorsal, but not ventral, pathway is activated when subjects made a visually guided grasping. Moreover, it has been observed a dissociation between ventral and dorsal fMRI activation during objects and action recognition (Zachariou et al. 2013).

### Processing Along the Dorsal Pathway

In spite of the great acceptance of the dual-visual systems hypothesis, the distinction between a ventral pathway that mediates object perception and a dorsal stream that supports spatial information processing and visually guided action (Goodale and Milner 1992; Mishkin and Ungerleider 1982) has been revised substantially in recent years (Binkofski and Buxbaum 2013).

Some authors have proposed that the ventral and dorsal pathways are not as independent as the classic model has postulated, but they work coordinately, especially in complex movement. In this sense, when an individual performs a complex movement, the dorsal stream needs to access to the ventral pathway store with the aim of obtaining detailed information about the object. Also, the ventral stream requires obtaining the information with which the dorsal stream works in order to adjust, as much as possible, the internal representation of the object. Different neuroimaging studies have been confirmed this hypothesis showing the existence of direct connections between dorsal and ventral streams (e.g., Cloutman 2013). In addition, some studies with patients and normal control have confirmed this interaction. With respect to the first, it has been shown, for example, that patients with agnosia who present impairment in objects perception with an intact ability to reach these unidentified

objects are unable to grasp objects in more complex task (McIntosh et al. 2004). Regarding the second, some reviewers and meta-analyses have shown that optical illusions like Müller-Lyer or Tichnerer do not influence the dorsal pathway (that is, the manual grasp) because subjects make corrections based on online feedback (e.g., Bruno and Franz 2009; Franz and Gegenfurtner 2008).

Other authors go beyond this interaction and propose that dorsal regions are not only engaged in guided actions but also in the representation of the object shape, even when actions are not required (Freud et al. 2005). More specifically, it has been suggested that dorsal stream is relevant to semantic categorization rather than simply reflecting spatial information processing and visually guided action. For example, Mahon et al. (2010) investigated the neural response associated with different category of objects and observed that dorsal stream was activated during the recognition of tools, but not during the recognition of other objects' categories. They concluded that the ability to recognize manipulable objects associated with specific hand movement (like tools) may also depend on activity of dorsal stream.

With the aim of confirming that the results described above actually reflect the involvement of dorsal pathway in semantic categorization and not only the interaction between the two streams, some authors have employed the Continuous Flash Suppression (CFS), an interocular suppression technique used to manipulate visual consciousness disrupting the ventral stream activation while leaving the dorsal pathway intact (Herbart and Hesselmann 2012). To achieve this, a static picture is presented in an eye, while a set of dynamic pictures appear in the other eye. Using this technique, Almeida et al. (2008) designed a task in which a visible target picture (a tool or an animal) was preceded by a prime picture (congruent or incongruent with the target one) rendered invisible under CFS. Results showed that while congruent primes suppressed facilitated categorization of tools (manipulable objects), they had no effect on animals (nonmanipulable objects).

To explain the variety of function within the dorsal pathway, it has been proposed the differentiation between two anatomically and functionally

different streams: the dorso-dorsal and the ventro-dorsal streams (Binkofski and Buxbaum 2013). While the dorso-dorsal stream projects to the superior parietal lobe and is engaged in the control of actions "on line," the ventral-dorsal stream goes to inferior parietal lobe and is related to space perception and action understanding.

## The Dual-Streams Approach in Other Sensory Systems

The idea of two separate visual processing pathways widely influenced the study of the organization of other sensory processes such as attention, somatosensory, and language processes.

In the case of attention, it has been proposed the presence of a dorsal system responsible for guiding voluntary attention to features or locations and a ventral system related to the detection of unexpected stimuli. From an anatomical point of view, while dorsal system is composed of the intraparietal sulcus and the frontal eye field, the ventral system comprises the temporoparietal area and the ventral frontal cortex. Moreover, it has been described that while dorsal system is organized bilaterally, the ventral system might be more lateralized to the right hemisphere (for a revision, see Vossel et al. 2014). However, it has been suggested, based on empirical findings from human neuroimaging experiments and studies in stroke patients, that these two routes streams do not seem to function completely independently, but there is a flexible interaction between them enabling the dynamic control of attention (Vossel et al. 2013).

With respect to the somatosensory system, different models have been proposed to explain its anatomical and functional organization. For example, Reed et al. (2005) proposed that while form, color, and features are processed in a ventral pathway, which runs from primary sensory cortex to the inferior parietal lobe and the prefrontal cortex, spatial characteristics and motion depend on a dorsal pathway that projects from primary sensory cortex to the superior parietal lobe. Moreover, James et al. (2007) concluded that we can distinguish between a ventral stream specialized

in material properties, including texture, and a dorsal stream related to geometric properties or shape. While ventral stream starts in the primary somatosensory cortex and ends in the lateral occipito-temporal cortex, the dorsal one projects from the primary somatosensory cortex to the posterior parietal cortex.

Finally, the existence of two different streams in language function from the superior temporal gyrus has also been proposed. In this sense, authors have described a ventral stream, which projects to the middle and inferior temporal lobe and is related to meaning, and a dorsal stream, which is directed toward inferior parietal and posterior frontal lobes and has been defined as important to articulation (Hickok and Poeppel 2004). Moreover, it has been proposed that while ventral stream is bilaterally organized, the dorsal stream is more lateralized to the left hemisphere (Hickok and Poeppel 2007). In any case, as it also happens with the visual system, more recent studies have suggested that dorsal stream is also related to syntactic processing, particularly in complex sentences. For this reason, it has been proposed, as in the case of the visual system, the existence of two different dorsal stream (Friederici 2012).

In sum, emerging data from neuroimage and behavioral studies (with healthy and clinical population) reflect the highly complex organization of various sensory processes (not only of the visual system). Future studies should examine in detail the components of different sensory systems, their functions, and the interactions that are established between them.

## Cross-References

- Attention
- Depth Perception
- Language
- Occipital Lobe
- Parietal Lobe
- Perception
- Perception-Action Theory
- Temporal Lobe
- Vision
- Visual Recognition in Birds

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## Dorsal Pigmentary Darkening

### ► Countershading

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## Dorsal Stream

### ► Dorsal Pathway

### ► Top-Down Processing

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## Dorsolateral Striatum

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## Synonyms

Sensorimotor striatum

## Introduction

The dorsolateral striatum (DLS) is a subcortical structure in rodents, that is homologous to the putamen in primates (Amaya and Smith 2018). DLS is involved in the execution of motor responses (Tang et al. 2007; Costa 2007) and is considered a key brain region for habit formation and the regulation of stimulus-driven behavior



(Balleine et al. 2007; O'Hare et al. 2018). DLS is a crucial part of a wider neural circuitry that integrate environmental cues and generate appropriate behavioral responses to those cues, based on previous experience (Amaya and Smith 2018; Balleine et al. 2009; Peak et al. 2019). Dysfunction in the formation or perseverance of stimulus-response associations has been implicated in Parkinson's disease (Costa 2007) and addiction (Yin et al. 2006) in humans.

## Habitual Behavior

DLS is primarily associated with habit formation and execution of automated stimulus-response behavior (Balleine et al. 2007; O'Hare et al. 2018). Automated stimulus-response behavior develops when an individual is repeatedly exposed to and consistently responds to the same stimulus-response-outcome contingency, leading the individual to form a strong association between the stimulus, response, and expected outcome (Balleine et al. 2007). In a rodent operant conditioning paradigm, the conditioned stimulus could be the presentation of a lever, the conditioned response would be the rodent pressing the lever, and the outcome could be the delivery of a sugar pellet. At the early stages of acquisition, the rodent will focus its attention on producing the behavior that aids it in obtaining a beneficial outcome, i.e., the behavior is goal-directed. This goal-directed stage of acquisition is strongly dependent on activity in dorsomedial striatum (DMS) (Peak et al. 2019). As a task is learned, the response time to pressing the lever gradually decreases as the stimulus-response becomes automatic or habitual (Tang et al. 2007). The change from goal-directed to automated behavior is associated with responding becoming less dependent on DMS and increasingly dependent on DLS (Balleine et al. 2009). The development of automated stimulus-responses are often adaptive, as it decreases response time, and the automatization of routine behavior also allows allocation of attention to other cognitive processes (O'Hare et al. 2018). However, once a stimulus-response has become automatic, it is difficult to

change the behavior, even when it is no longer adaptive. Rats that are overtrained on a lever pressing task become insensitive to changes in outcome value and continue pressing the lever even when the reward is devalued (Yin et al. 2006; Balleine et al. 2009). However, if DLS is lesioned after the task has been learned, sensitivity to outcome value is reinstated (Balleine et al. 2009). In addition, inactivation of DLS disrupts performance of well-learned tasks but does not affect the acquisition of new tasks (Costa 2007). This occurs because when DLS is lesioned or inactivated, the DMS resumes its previous role in mediating striatum-dependent behavior, and as a consequence, the behavioral output becomes more goal-directed (Peak et al. 2019). Similarly, if DMS is lesioned or inactivated, habitual responses increase (O'Hare et al. 2018; Balleine et al. 2009). These studies demonstrate how DMS and DLS form part of parallel and competing neural networks that organize goal-directed and habitual behavior, respectively (O'Hare et al. 2018; Amaya and Smith 2018; Peak et al. 2019; Balleine et al. 2009). Adaptive behavior is achieved by optimizing the balance between automated stimulus-response behavior mediated by DLS and reflective goal-directed behavior mediated by DMS.

## Motor Response

DLS also plays a crucial part in the initiation and fine tuning of motor responses and the majority of neurons in DLS respond to movement (Costa 2007; Amaya and Smith 2018; Tang et al. 2007). With repeated training on a movement-dependent task, motor related neurons in DLS decrease their activity, whereas the smaller population of nonmovement-related neurons increase or maintain their firing rate (Tang et al. 2007; Costa 2007). This suggests that as an automated response is learned, the response moves from being facilitated by a large number of neurons to being modulated by a smaller population of task-specific neurons within the DLS (Tang et al. 2007). In this way, DLS plays a crucial role in the fine tuning of precise motor responses (Amaya



and Smith 2018) which, through repeated pairings of stimulus-outcome associations, optimize motor-dependent behavior toward achieving a desired outcome (Amaya and Smith 2018; Balleine et al. 2009; Peak et al. 2019).

## Corticostriatal Circuitry

The striatum is the main input structure to the basal ganglia and DLS receives strong projections from both primary motor and sensory cortex and is part of a corticostriatal re-entrant circuit, linking cortical, basal ganglia, and thalamic brain regions (Peak et al. 2019; Balleine et al. 2009). Through these connections, DLS-mediated behavior is influenced by changes in this wider neural circuitry. As rats learn an operant task, neuronal activity in primary motor cortex and DLS as well as synchrony between these brain areas increase (Costa 2007; Koralek et al. 2013). Furthermore, neuronal connections within the corticostriatal circuit that are activated or inhibited during the task acquisition are strengthened or weakened to optimize the behavioral output (Peak et al. 2019). The striatum forms a crucial node within this neuronal circuitry and rather than simply conveying information from cortical and thalamic areas, DMS and DLS integrate sensory, cognitive, and motor feedback input to form associations and facilitate adaptive behavior (Peak et al. 2019).

## Dopamine

The majority of neurons in the striatum express dopamine receptors, and fluctuations in dopamine receptor activity within the striatum play an important role in mediating behavioral output (Peak et al. 2019). Neurons in the corticostriatal re-entrant circuitry project through the striatum via two different routes. Neurons in the direct pathway express predominantly D1-like dopamine receptors and project from the striatum to the internal segment of the globus pallidus and the substantia nigra pars reticulata (Peak et al. 2019; Jin et al. 2014). Neurons in the

indirect pathway predominantly express D2-like receptors and project from the striatum to the external segment of globus pallidus which connects reciprocally to the subthalamic nucleus, which in turn project to the internal segment of the globus pallidus (Peak et al. 2019; Jin et al. 2014). Whereas dopamine modulation of D1 dopamine receptors in the direct pathway is thought to facilitate movement, dopamine modulation of D2 dopamine receptors in the indirect pathway is thought to inhibit it (Jin et al. 2014). However, movement initiation is associated with increased activity in both the direct and indirect pathways, which suggests that the roles of the direct and indirect pathways may not be quite so strictly divided (Jin et al. 2014) and activity in both pathways is required to optimize stimulus-response behavior (Amaya and Smith 2018). Activation of dopamine receptors within the striatum plays an important role in both task acquisition and habit formation (Costa 2007; Amaya and Smith 2018), and habitual behavior correlates with increased DLS output to both the direct and indirect pathways whereas suppression of habitual behavior correlates with decreased output to the direct pathway (O'Hare et al. 2018).

## Cross-References

- [Acquisition](#)
- [Dopamine Receptor](#)
- [Goal-Directed Behavior](#)
- [Learning](#)
- [Medial Striatum](#)
- [Neuron](#)
- [Operant Conditioning](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Dorsomedial Area

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## Synonyms

Third-tier visual areas

## Definition

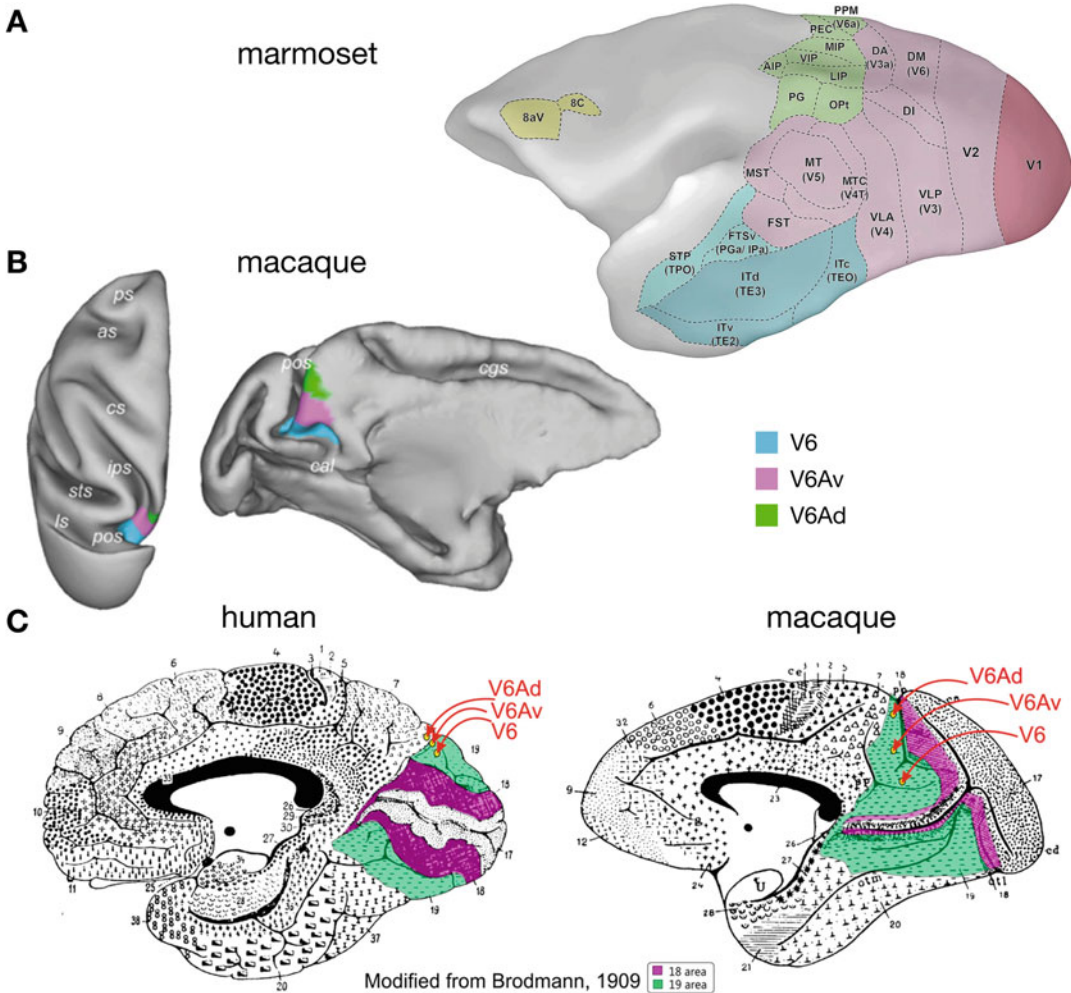
A region of the primate visual cortex that approximately corresponds to the dorsomedial part of Brodmann's area 19.

## Introduction

Since the nineteenth century, when scientists started to recognize that the cerebral cortex is a system consisting of multiple functional modules (or “cortical areas”), the systematic study of how the cerebral cortex is divided into areas (“parcellation”) has been one of the main challenges of systems neuroscience. The visual cortex, being one of the largest cortical systems in many species of mammals, has served as a model system for understanding the basic organizing principles of the cerebral cortex.

In Brodmann's 1909 landmark study of the organization of the cerebral cortex, the visual cortex is situated at the posterior end of the primate cerebral cortex, and it is divided into three areas: 17, 18, and 19 (Fig. 1c, d). Area 17 is positioned at the posterior pole and is surrounded rostrally by the belt-like area 18, which, in turn, is surrounded rostrally by the belt-like area 19. While Brodmann's areas 17 and 18 approximately correspond to the modern concept of the primary (V1) and the secondary (V2) visual areas, contemporary researchers view Brodmann's area 19 as a region consisting of multiple areas. This entry focuses on the current views of the organization of the dorsal and the medial part of Brodmann's area 19 – a region that will be referred to collectively as the dorsomedial visual cortex. Sandwiched between area V2 and the posterior parietal cortex, areas in dorsomedial visual cortex are thought to be part of the “dorsal stream” (or the “where” stream) of visual processing – important for extracting information about motion and spatial relationships in the visual field. The information is then distributed to the parietal cortex to mediate visually driven actions, such as eye movements and goal-directed reaching.

The dorsomedial visual cortex is one of the least explored sectors of the primate visual cortex, and its organization is one of the most controversial. This entry provides a succinct summary about the current state of knowledge about this region, as well as some of the controversies.



**Dorsomedial Area, Fig. 1** (a) Lateral view of the marmoset cortex, showing the parcellation of the visual cortex according to Paxinos et al. (2012). Names within parentheses indicate the names of likely homologous areas in macaque brain. Area 19M mentioned in the entry is located on the medial surface and therefore is hidden from view. (b) The location of the dorsomedial visual cortex in the macaque brain, in dorsal (left) view and medial (right) view. Abbreviations of anatomical landmarks: *pos* parieto-occipital sulcus, *cal* calcarine sulcus, *cgs* cingulate

sulcus, *ips* intraparietal sulcus, *sts* superior temporal sulcus, *ls* lunate sulcus, *cs* central sulcus, *as* arcuate sulcus, *ps* principal sulcus. (c) Medial views of the brains of human (left) and macaque (right) to illustrate the locations of the dorsomedial cortex, with respect to Brodmann's area 17, 18, and 19. In (a) and (b), the figures illustrate left hemispheres. In (c), the figures illustrate right hemispheres. The figures are not shown to scale (Sources: (a) Solomon and Rosa (2014), (b) Pitzalis et al. (2013), (c) Pitzalis et al. (2015))

## Mapping the Visual Cortex

Neurons in the visual cortex respond only to localised regions in the visual field, called their receptive fields. *Visuotopy* is the systematic, point-to-point relationship between the locations of neurons on the cortical surface and the locations of their receptive fields in the visual space.

Visual areas are said to contain *representations* of the visual field because the visual field is mapped onto the cortical surface according to their visuotopy.

Visuotopic mapping is typically accomplished by measuring the electrophysiological responses of single neurons to patterns displayed at different positions in the visual field. More recently,

functional imaging methods are increasingly being used to map large proportions or even the entire visual cortex of individual subjects. In particular, functional magnetic resonance imaging (fMRI) is now routinely used to study the human visual cortex noninvasively.

Although visuotopic mapping is essential for identifying areas, they are not defined solely by their visuotopic maps. Instead, the convergence of multiple lines of evidence is usually needed. In addition to visuotopy, visual areas are also identified by their architectonics (i.e., the cellular composition of the tissue), their connectivity patterns (i.e., the cortical networks that they participate in), and the physiological characteristics of their constituent neurons.

### The Dorsomedial Visual Cortex in New World Monkeys

Although the dorsomedial cortex has been studied in detail in a number of primate species, the precise boundaries of the areas, or even the precise number of areas in this region, have remained open to interpretation. Central to the uncertainty is the extent to which a common scheme applies to all primate species. To understand the origin of these issues, it is useful to review the organizations of the dorsomedial cortex in animals on different branches of the primate evolutionary tree separately.

New World monkeys represent one of the two branches of the family tree of simian primates. Their evolution diverged from that of Old World monkeys and apes about 40 million years ago. The cortical surfaces of many smaller New World monkeys are lissencephalic, meaning that they are smooth, lacking the deep sulci found in the brains of larger monkeys. The simple geometry of lissencephalic brains makes these monkeys ideal models for brain mapping studies, because the entire visual cortex is accessible for electrophysiological recordings, and the results can be interpreted more easily without the need to reconstruct the convoluted 3D geometry of a non-lissencephalic brain.

The nocturnal owl monkey and the diurnal marmoset monkey are the two most well-studied New World monkeys in visual neuroscience. In both species, the dorsomedial cortex is largely occupied by an area called the dorsomedial (DM) area (Fig. 1a; Angelucci and Rosa 2015). Straddled between the dorsal surface of the occipital cortex and the medial wall, DM is adjacent to the rostral border of dorsal V2. Interestingly, whereas in areas caudal to DM, namely, V1 and V2, the representations of the upper and the lower visual fields are separated on the ventral and the dorsal surface of the occipital lobe, in DM, both visual fields are represented in the dorsal surface. DM is therefore situated in a region where the belt-like structure of early visual areas (V1 and V2) makes a transition to a more complex organization, where one area shares boundaries with multiple neighboring areas.

Area DM is surrounded by a number of additional areas, which have been identified as area 19M (also known as the parieto-occipital medial area, or P<sub>Om</sub>), the dorsointermediate area (DI), and the dorsoanterior area (DA) in the marmoset monkey (Fig. 1a). Similar areas also have been identified in the owl monkey (Serenio et al. 2015). Very little is known about the organization and functions of these areas, except that they appear to form a functional network with DM.

An alternative view on the organization of the dorsomedial cortex for the marmoset monkey was proposed by Lyon and Kaas in 2001. This hypothesis is described in a later section.

### Old World Monkeys

In the macaque monkey (*Macaca*), the most well-studied Old World monkey, the dorsomedial cortex corresponds approximately to a region in the parietal-occipital cortex, where three deep sulci meet: the lunate sulcus, the intraparietal sulcus, and the parieto-occipital sulcus (Fig. 1b). The complex geometry of the cortical surface in this part of the brain contributes to a long history of controversy about its organization.

It is well established that the dorsal arm of V2 is located along the caudal bank of the lunate and

the intraparietal sulcus, extending into the medial surface of the hemisphere along the dorsal bank of the calcarine sulcus. As in New World monkeys, it represents the lower visual field. The critical question is: what area(s) lies immediately rostral to V2?

While earlier researchers (Zeki 1969) envisioned a belt-like area V3 adjoining the entire length of V2, subsequent studies indicated that the dorsal branch of V3 does not extend medially into the medial surface of the hemisphere. Instead, starting at the junction of the lunate and the intraparietal sulcus and extending into the medial surface of the hemisphere, V2 is adjoined rostrally by an area called V6 (Gamberini et al. 2015). A noteworthy characteristic of the V6 visuotopy is that the representation of the central visual field is not magnified, meaning that most of the surface area of V6 is devoted to the presentation of peripheral visual field. The emphasis on the peripheral visual field suggests that the functions of V6 have less to do with the fine analyses of the information at the center of gaze, but instead are more associated with navigation and relating the objects at the center of gaze to the environment.

In addition to V6, at least two areas in this region of the macaque brain have been identified: V6A and V3A. Dorsal to V6 on the rostral bank of the parieto-occipital sulcus is a visuomotor called V6A. V6A is divided into a dorsal (V6Ad) and a ventral (V6Av) component, with the ventral part containing more visual neurons than the dorsal part. V6Ad and V6Av do not have precise visuotopy, although the visual neurons in V6Av primarily represent the peripheral visual field, while those in V6Ad primarily present the central visual field. Area V3A is located on the rostral bank of the lunate sulcus, adjoining V3 caudally and V6 medially.

Similar to area DM in New World monkeys, V6 is located in a region where multiple areas share borders with each other.

## Humans

fMRI studies have revealed broad similarities between the organization of the parietal-occipital

cortex in humans and in macaques. An area identified as the human V6 is located in the parieto-occipital sulcus, occupying both banks (Fig. 2a, b; Pitzalis et al. 2015). As in the macaque monkey, the human V6 emphasizes the peripheral visual field and shares borders with multiple areas (V2, V3, and V3A; Fig. 2c, d).

fMRI mapping also has identified a representation of the lower visual field in the dorsal part of the parieto-occipital sulcus, which corresponds to the macaque V6Av. In addition, human V6Ad has also been identified in experiments where the subjects were asked to make finger or arm movements to reach visual targets.

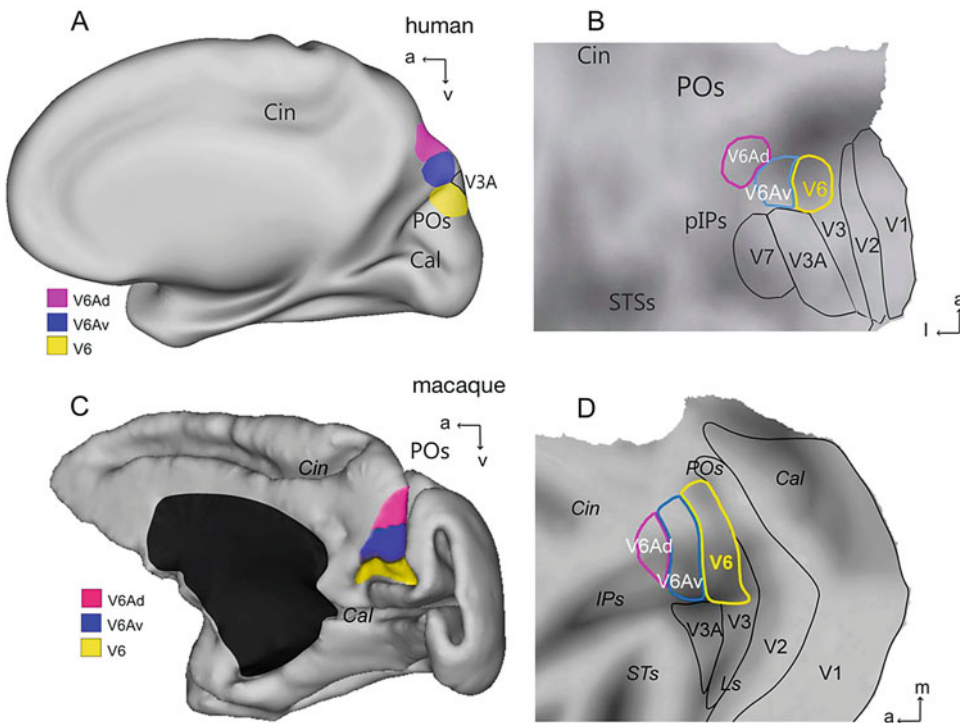
## A Common Organization for All Primates?

The broad similarities observed in the organizations of the dorsomedial cortex for different primate species have motivated efforts to unify them under a common scheme.

One approach is to interpret Old World monkeys and humans data in light of the organization described for New World monkeys. The rationale is that the lissencephalic cortices of New World monkeys are more amenable to high-resolution mapping, and the maps obtained tend to be more complete. The most significant challenge in this approach is that area DM is not commonly accepted as a visual area in macaque monkeys and in humans. A possible solution to this problem was proposed by Rosa and Tweedale (2005), who observed that the union of macaque area V6, the dorsomedial part of V3, and part of the upper quadrant representation in V3A constitutes a visuotopic map similar to the visuotopy of marmoset DM. This region might be interpreted as the homolog of the marmoset DM in Old World primates.

It's also possible to take the opposite position. Lyon and Kaas (2001) proposed a unifying scheme based on the idea that the organization of the dorsomedial cortex in the New World monkey is in fact similar to that of Old World monkeys. Under this view, area DM does not directly adjoin the rostral border of V2. Instead, a





**Dorsomedial Area, Fig. 2** The locations of area V6 in relationship to surrounding areas in humans (**a, b**) and in macaques (**c, d**). In (**a**), the medial view of the inflated human cortical surface (right hemisphere) is illustrated. In (**b**) and (**d**), the cortical surfaces of the human and the macaque brains are “flattened” by a computational

algorithm so that areas in sulci can be viewed. *Light gray* and *dark gray* indicate gyri and sulci. Abbreviations: *a* anterior, *v* ventral, *l* lateral, *m* medial, *cal* calcarine sulcus, *pos* parieto-occipital sulcus, *Cin* cingulate sulcus, *ips* intraparietal sulcus, *sts* superior temporal sulcus (Source: Pitzalis et al. (2015))

previously unidentified thin strip of cortex representing the lower quadrant is sandwiched between V2 and DM. This strip of cortex extends laterally and ventrally to form a complete representation of the visual field surrounding V2, called area V3. A belt-like area V3 that approximately adjoins the rostral border of V2, with a visuotopy that mirrors that of V2, is therefore proposed to be a common feature shared by all primates.

Whether if the theories discussed above successfully explain existing data remains a controversial issue. A third approach recognizes the differences observed in different primate species as genuine organizational variations. In particular, Gattass et al. (2015) observed that the organization of the dorsomedial cortex in the capuchin monkey, a New World monkey with a large and convoluted brain, is more similar to what has been

described for the Old World macaque monkey than those described for the lissencephalic owl monkey and marmoset monkey. He contends that the organization of the dorsomedial visual cortex in lissencephalic monkeys underwent reorganizations in the process of evolution, which resulted in different cortical areas, in comparison to monkeys with larger, gyrencephalic brains.

## Functions

The primate visual cortex can be approximately conceived a hierarchical system, whereby information in a lower-level area is sent to a higher-level area via feedforward connections for more elaborated processing in the higher-level area. V1 receives the majority of inputs from the visual thalamus, and therefore it is considered an entry-



level area in the hierarchy, whereas V2 is considered a second-order area because it receives most of its inputs from V1. Both area DM (in marmosets and owl monkeys) and area V6 (in macaques) receive strong inputs from V1 and V2, suggesting that they can be considered second- or third-order areas mediating relatively low-level visual functions.

Furthermore, the primate visual cortex is commonly conceived as having two main “streams” of processing: areas in the dorsal stream (also known as the “where” pathway or the “how” pathway) are associated with functions related to spatial relationship, motion, disparity, navigation, and guidance for action, whereas areas in the ventral stream (also known as the “what” pathway) are associated with functions related to the analysis of textures and shapes, and the recognition of objects. Area DM in New World monkeys and area V6 in macaques and humans are closely associated with the dorsal stream, as evidenced by the fact that both areas receive strong connections from layer 4B of V1, a layer with many direction-selective neurons and projects primarily to dorsal stream areas. Furthermore, DM and V6 are directly connected with other dorsal stream areas, such as the middle temporal (MT) and the medial superior temporal (MST) areas. As well as areas in the posterior parietal cortex, which mediates functions associated with eye movements and reaching.

The response characteristics of neurons in the macaque V6 have been investigated in some detail. As expected for a dorsal stream area, the majority of V6 neurons are selective to the directions of moving patterns, as well as to the patterns of coherent motion generated when a person moves in a complex environment (optic flow fields). Similar responses have also been demonstrated in human V6 using fMRI, which provide strong evidence for the homology between V6 in the two species. Selectivity for patterns of optic flow fields is a response characteristic found in neurons in other areas in the dorsal pathway, such as area MST. It is important for visual functions such as determining the direction of heading as one moves in the environment and for inferring

the distances to objects in the environment during locomotion.

Area MT has been traditionally considered the central node of the dorsal pathway, due to the prominent presence of a large population of direction-selective neurons in this area. In recent years, however, studies of V6 have motivated the recognition of two major motion areas in the dorsal pathway – area MT, the lateral motion area, and area V6, the medial motion area. Although the two areas are heavily interconnected and must have overlapping functions, their roles in vision appear to have different emphases. For example, V6 is more involved in the processing of self-motion, due to its more expanded representation of the peripheral visual field and its selectivity to flow field patterns. MT, on the other hand, has an expanded representation of the central visual field and therefore is more important in the processing of object motion.

In addition, V6 is directly connected to V6A and areas in the posterior parietal lobe, which contain visuomotor neurons that are activated during the movements of the arm, head, and eyes. It is therefore likely to have important functions in visually guided actions.

Clinical studies have provided valuable information about visual areas surrounding the parieto-occipital sulcus. Patients with lesions in this region of the visual cortex have been reported to exhibit optic ataxia – a condition where the patients misreach objects under visual guidance. Some patients have been reported to have motion recognition deficits. Epileptic seizures originating in this region can also produce hallucinations of self-motion. These symptoms are consistent with the known function of areas V6 and V6A.

Very little is known about the functions of the dorsomedial cortex of the marmoset monkey. Although the overall connectivity pattern of the marmoset DM is very similar to that of the macaque V6, DM is connected to ventral stream areas, but V6 is not. DM therefore is expected to mediate a mixture of dorsal stream and ventral stream functions. In accordance to this expectation, populations of DM neurons that are selective to the orientation and the direction of gratings have been reported.

## Cross-References

- [Dorsal Pathway](#)
- [Neocortex](#)
- [Primate Sensory Systems](#)
- [Primates](#)
- [Vision](#)

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## Dorsomedial Neostriatum

- [Medial Striatum](#)

## Dorsomedial Striate Nucleus

- [Medial Striatum](#)

## DRD

- [Dopamine Receptor](#)

## Drive State

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## Synonyms

[Energy](#); [Motivation condition](#)

Among many other ordinary meanings not relevant here, the English Oxford Living Dictionary defines “drive” (<https://en.oxforddictionaries.com/definition/drive>) as a verb meaning “Propel or carry along by force in a specified direction,” “provide the energy to set and keep,” “Urge or force (animals or people) to move in a specified direction,” and “Cause (something abstract) to happen or develop.” The dictionary also includes the following meanings as a noun in psychology: “an innate, biologically determined urge to attain a goal or satisfy a need” and “determination and ambition to achieve something.” Among the synonyms are listed “motivation” and “energy.” Lemon’s 1783 dictionary of English etymology lists the following meaning for “drive:” “to thrust, push, shove before one.”

In the same dictionary, “state” (<https://en.oxforddictionaries.com/definition/state>) is mostly used as a noun to mean “the particular condition that someone or something is in at a specific time” and “a physical condition as regards internal or

molecular form or structure.” Thus, focusing on the above meaning for psychology, “drive state” could be defined as a “particular condition that is innate and biologically determined, and which urges, pushes, energizes, or moves an animal to attain a goal or satisfy a need.”

This definition captures typical uses of the expression “drive state” in psychology, although some details vary across different uses. Uses also include a close relation between drive and motivation but not quite the aforementioned synonymy. For example, Young (1936) began the chapter entitled “The energetics of behavior” with the following quote that he attributed to child psychologist Florence L. Goodenough (1886–1859): “The literal meaning of motivation is the process of inducing movement” (p. 48). Throughout his book, Young views drive and motivation as closely related but not identical:

... motivation is the process of producing movement. ... it is the liberating of “bound” energy so as to induce reaction. The greater the amount of energy liberated in a given situation, the greater the degree of drive. *Drive is energy.* (p. 78, emphasis added)

Young attributed the first use of the term “drive” in psychology to Woodworth (1918), who identified “the problem of drive” as raising the “Why” questions in psychology. The other kind of problem central to psychology, according to Woodworth, was “the problem of mechanism,” which raised the “How” questions. Woodworth related the two kinds of questions thusly: “This distinction between drive and mechanism may become clearer if we consider it in the case of a machine. The drive here is the power applied to make the mechanism go; the mechanism is made to go” (p. 37). According to Young, Woodworth “derived the term [“drive”] from mechanics; a machine must be driven if it is to move, and the drive of a machine is the supply of energy that puts the mechanism in motion” (Young 1936, p. 71).

Woodworth was influenced by Sigmund Freud. Indeed, shortly before Woodworth’s book, Freud (1915) used the German word “trieb” – translated as “drive,” “impulse,” or “urge” – to characterize human motivation. In Freud’s theory of motivation, instincts were the

causes of animal behavior, but he reserved the term “instinct” for nonhuman animals and rarely applied it to humans, using instead the term “drive” to refer to the cause of humans’ behavior.

Thus, contrary to ordinary uses, early psychologists did not quite use the two terms as equivalent. They used “drive” to refer to energy and “motivation” to refer to the result of a drive as energy, although this result is not the same as an animal’s movement. Movement is overt behavior, whereas “motivation” presumably refers to an internal, covert condition. Thus, it is not entirely clear how drive and motivation differ as internal conditions. Energy, of course, is a central concept in physics, especially *thermodynamics*, the branch of physics concerned with how energy relates to temperature and *entropy* (roughly, a measure of the disorder of a system, which is internal to it as well). If drive is energy, perhaps motivation could be analogous to entropy.

Freud (1895), in an unfinished work, was the first to try to apply Hermann von Helmholtz’s (1821–1894) thermodynamics concepts of free and bound energy to theorize about human psychological phenomena. This work was the beginning of what came to be called “psychodynamics” and went later on by the more familiar name of “dynamic psychology” (precisely, the title of Woodworth’s book). The term “dynamic” in this label thus likely comes from “thermodynamics.”

As is also well known, Freud called psychological drive “libido” and reduced it to sex drive, surely too restrictive a concept of a psychological drive. More importantly, Freud built his theory on assumptions that were soon discredited in biology, specifically, Haeckel’s biogenetic doctrine (“Ontogeny recapitulates phylogeny”) and Lamarckian inheritance of acquired traits (see Gould 1977, pp. 155–164). Freud’s drive theory thus soon became a dead end in the scientific study of drives.

Thermodynamics, however, was much more than just von Helmholtz’s concepts of free and bound energy, and nothing in it implied (or presupposed) Freud’s discredited assumptions. Alas, no other early drive theorist in psychology after Freud delved into thermodynamics as further developed by others (e.g., Boltzmann,

Gibbs, Maxwell, Planck, etc.). Who knows how the concept of drive in psychology, and the theories based on it, might have developed had early drive theorists after Freud used amore developed thermodynamics, without following his lead in reducing psychological drive to sex drive and adopting those assumptions. Much later, Krebs and Kornberg (1957) in biology seized the opportunity, initiating the very fruitful area of biological thermodynamics (see Haynie 2008).

In a landmark paper almost a decade before Krebs and Kornberg's seminal book, Shannon (1948) proposed his famous information theory, based on the thermodynamics concept of entropy. This theory has been very influential in biology (although it is nowhere to be found in Krebs and Kornberg's seminal book). The theory has also been very influential in information-processing approaches to cognitive psychology, but this influence never quite reached traditional theorizing about drives and motivation in psychology. At least, contemporary information-processing approaches to learning (e.g., Gallistel and Balsam 2014) do not include theorizing about drives or motivation. Nor have theories of drive and motivation in psychology (e.g., Baumeister 2016; Bolles 1975) made much use of information-theoretic concepts either.

None of this is surprising, given that information theory was designed for symbolic systems, and it is far from clear how drives can be conceived as symbolic in nature, beyond the all-too-easy metaphor that they “inform” or “tell” the animal it is time to, say, eat. Fortunately, nothing in thermodynamics *implies* that thermodynamic systems (heat engines) are symbolic in nature (of course, they *could* be conceived as symbolic, but this, in and of itself, is hardly a strong reason to do it; the issue is not whether it *can* be done, but *why* do it). Nor does information theory, as successful as it has been, imply that all systems to which thermodynamics is applied are symbolic in nature either. Thus, a nonsymbolic thermodynamics approach to drives, and how they relate to and differ from motivation is entirely possible. But then again, early drive and motivation theorists in psychology never explored this possibility. What if they had? How would their concepts and

theories have developed had they used thermodynamics? These are interesting questions in counterfactual history better left for another occasion.

Counterfactual history aside, uses of “drive” in early psychology remained standard for decades. Such uses attempted to explain behavior in terms of *internal* efficient causes, the factors that mechanically *pushed* animals, seemingly often purposefully, towards particular aims or goals (see “Goal,” this volume). The concept has often been related to that of *homeostasis*, a biological equilibrium or balance towards which animals supposedly strive. Thus, drive states have been often conceived as means for animals to restore homeostasis (Bolles 1975). As such imbalances become more severe, the concomitant drive states become stronger, which supposedly increases the likelihood that an animal will respond in certain ways under certain conditions.

Some biologists during the 1950s and 1970s viewed drives as *instincts* and proposed them as the main proximate (ontogenetic, as opposed to distal or phylogenetic) causes of animal behavior in their natural environments. This view dominated the works of European biologists Lorenz (e.g., 1966) and Tinbergen (e.g., 1951), who received the Nobel Prize in 1973. They and others ushered the beginnings of ethology, literally “study of behavior,” framing it squarely within biology, with an emphasis on innate behavior. Such framing, of course, was strongly Darwinian, where drives qua instincts were viewed as *adaptations*, phenotypic traits that were present in current animals for having increased their ancestors’ reproductive success. The conditions under which such ancestral adaptive value obtained constituted distal causes of animal behavior.

The notion of an instinct also favored explanations of adaptive behavior in terms of “biological programming”: Animals behaved in the way they did because they were biologically programmed to do it. However, criticism quickly ensued (see Lehrman 1953). According to one criticism, it was impossible to estimate a priori how many instincts operated as determinants of behavior. It seemed that each new response pattern could be attributed to an unknown instinct. Another criticism was that there were no precise criteria to distinguish what

was an instinct and what was not. More importantly, because instincts were biologically fixed, they made behavior invariant instead of an evolved expression of adaptive actions (Strassmann 2014). In sum, appealing to instincts did not help much to address several issues about the causes of behavior.

The concept of a drive state had several advantages over the concept of an instinct. Although instincts and drives were supposed to have a physiological basis, this basis seemed easier to study experimentally for drives, as they were defined more clearly and precisely. Additionally, research indicated that biological correlates of drives could be more precisely measured. A remarkable attempt to do this was reported by Jenkins et al. (1926), who developed an apparatus to measure specific drives, and suggested that these measures should be distinguished from the measurement of general and random activity.

Experimental results using such measurements supported the characterization of a drive as a dynamic central state. During the first half of the twentieth century, it was broadly accepted that an increase in drive was associated with an increase in general activity (Dashiell 1925), provoked by an alteration of the organism's homeostasis. Richter (1927) reported that activity increased with biological needs. Therefore, drives did not specifically direct particular behaviors to satisfy the underlying need. Rather, the effects of a drive seemed to be broad and coarse. All these results led to a distinction between the exogenous stimulus that had the potential to provoke a response, and the subject's internal drive (see Pecoraro 2005).

American psychologists thus proposed the drive theory of motivation as an alternative to the instinct theory that dominated in European ethology. This alternative proposal was central to classical learning theories between 1930s and 1950s, primarily from Clark Hull and Kenneth Spence. Hull (1943) viewed drives as "typical intervening variables" (p. 57), symbolized as  $D$  in his famous (abridged) equation  ${}_SE_R = {}_SH_R \times D$ , where  ${}_SE_R$  denoted the reaction potential (probability of response  $R$  to stimulus  $S$ ) and  ${}_SH_R$  denoted the learning-dependent habit ( $S$ - $R$  associative) strength. Hull hypothesized that  $D$  was "produced" by a need (see "Need Reduction," this volume).

More specifically, Hull viewed the "hunger drive" as "primary" and a "function of *observable* antecedent conditions, i.e., of the need which is measured by the number of hours of food deprivation" (ibid.). Somewhat less abstractly, Seward (1956) viewed a drive as an "excitatory state produced by a homeostatic disturbance" (p. 195). This definition is largely consistent with the one used by Hull, Spence, and other classical learning theorists. However, talk of "drive state" is not commonly found in the works of these authors. It thus is unclear whether they would have made a conceptual distinction between drives and drive states. Perhaps, by "drive" they referred to a general *type* of condition, whereas "drive state" could be used to refer to a more specific condition (more on this distinction later on).

Still, the expression "drive state" makes it clear that a drive typically, if not always, is a *temporary condition* of an animal. Sometimes an animal is *in* a drive state, sometimes it is not (or it is but to a lesser degree). When *all* of an animal's needs are satisfied, the animal supposedly is not in any drive state (or it is to a small degree). The notion of a state as a temporary condition, of course, is widespread in all natural sciences, beginning with physics. For example, the notion is central to the concept of entropy, defined in terms of the number of a system's possible microstates. The essentially temporary character of a state makes being in a drive state *dynamic* in nature, which facilitates viewing all phenomena that involve drives as *processes* that can be mathematically described through differential (or, if time is viewed as discrete, difference) equations.

Hull's (1943) theory was partly inspired by Edward L. Thorndike's "Law of Effect." One of Thorndike's works (1932) cited by Hull provides the following formulation of the law as a "principle of connection-forming": "... what happens as an effect or consequence or accompaniment or close sequel to a situation response, works back upon the connection to strengthen or weaken it" (p. 6). Such talk of "connection" made Thorndike call his view "connectionism," which he submitted as a "new associationism" that "differs deeply and widely from that older British associationism" (p. 4). A key notion in this law was that "repetition

of a situation” played a key role in the formation and strengthening (or weakening) of situation-response connections.

Hull based his theory on a wide variety of experimental data. For example, one of his many laboratory assistants (Williams 1938) studied the effects of the number of reinforcements and food deprivation level on resistance to extinction (rate of response reduction upon discontinuation of reinforcement) of bar-pressing in rats in a Skinner box. The data showed that resistance to extinction increased as a negatively accelerated function of the number of reinforcements and a positively accelerated function of the number of hours of deprivation. The basic explanation in Hull’s theory is that the number of food deprivation hours increases  $D$  in a positively accelerated fashion, whereas the number of reinforcement increases  $sH_R$  in a negatively accelerated fashion. Both increases interact multiplicatively to produce a joint effect on resistance to extinction.

Hull viewed the presence of a drive, mathematically expressed as  $D > 0$ , as necessary for the behavioral expression of habits (i.e., for  $sE_R > 0$ ). Clearly, according to his equation, if  $D = 0$ , then  $sE_R = 0$ , for any value of  $sH_R$ . In this view, if there is no drive, there is no reaction potential either, even if there has been learning (i.e.,  $sH_R > 0$ ). According to Hull, if the animal has learned just the one habit,  $D > 0$  allowed for the behavioral expression of that habit. If the animal has learned several habits,  $D > 0$  evoked the strongest one.

Hull also distinguished between primary (or innate) and secondary (or learned) drives. Primary drives bear most directly and immediately on the organism’s biological survival. Although his research on maze learning focused almost entirely on hunger as a primary drive, he admitted other primary drives such as thirst, sex, and social interaction. Secondary drives, in contrast, are learned and do not directly bear on the animal’s biological survival, although they can certainly help the animal deal with environmental conditions that could eventually bear more directly and immediately on its survival. Learned drives became conceptually necessary to account for the persistence of behavior in the temporary absence of reinforcement. Related notions in learning research are second-order

reinforcers in Pavlovian conditioning and secondary reinforcers in operant conditioning.

After playing such a central role in theories of motivation and learning during the 1940s and 1950s, the concept of a drive state gave way to the concept of an incentive, an external stimulus that can create a need and *pull* (as opposed to the *pushing* effect of drives) the animal towards the stimulus. For example, someone could get hungry (or just come to want to eat) upon seeing food. Typically, incentive theories focus on situations where animals must behave in certain ways to obtain the incentive, which implies that they must be able to somehow anticipate the consequences of their behavior. However, this focus applies more clearly to instrumental than Pavlovian conditioning, where, strictly speaking, there is no explicit instrumental contingency or consequence of any behavior. Thus, it is most unclear how incentive theories can account for Pavlovian conditioning, unless the adventitious response-reinforcer relation that occurs during the maintenance of Pavlovian conditioning is postulated to “reinforce” that response in an “operant” way. Additionally, incentive theories still have to come up with plausible *mechanisms* that explain exactly how incentives affect the behavior that occurs to obtain them. If someone is told they will get \$5 (incentive stimulus) for whistling (required response), and then they whistle, how did the incentive make the whistling happen in the first place?

Despite these limitations, the concept of an incentive is thought to solve some difficulties with the drive-reduction hypothesis. For example, it is unclear exactly how secondary reinforcers such as lights and tones (or, in the more complex situation of a maze, contextual cues such as corners and walls) reduce drives. Perhaps such reinforcers function in a different way, other than changing drive states. But exactly what it is remains elusive for classical drive-reduction theories. Another difficulty is that animals quite often engage in behaviors that do not seem to lead in any obvious way to a change in a drive state. Behaviors such as seemingly spontaneous exploratory activity and pleasure-seeking (Brown 1955) do not seem to have a clear drive-reduction value.



Animals quite often eat just because they want to, not because they are hungry. And when hungry, animals often show preferences for certain kinds of foods over others, a phenomenon that becomes inexplicable under drive-reduction theories, insofar as, classical drive theory views all foods as equally effective to quench hunger.

Nowadays, despite the waning of the concept of a drive in the psychology of learning, strong interest remains in studying the effects of food or water deprivation, as well as other primary drives. For example, Stephens (1981) has studied the effects of food deprivation on risky choice. He observed that the level of food deprivation, relative to the subject's energetic requirements, determined the probability of choice of a constant but insufficient (nonrisky choice) over a variable but perhaps sufficient (risky choice) source of food. More recently, Kacelnik and colleagues (e.g., Pompilio et al. 2006) have studied the level of food deprivation on the value attributed to a response alternative in a choice task, a phenomenon they have called "state-dependent valuation learning." Their evidence suggests that food deprivation when an animal faces a response option for the first time increases the probability that the animal will choose that option when presented with another that delivers the same consequences.

There are plausible substitutes for the concept of a drive state and all the theories based on it. Learning, theorizing, or, as it has come to be more customarily and humbly known, "modeling," has made great advances. Recent models have risen to the occasion of explaining phenomena that are unexplainable in terms of changes in drive state. Among the most impressive phenomena, discovered after the golden age of drive learning theories, are blocking, latent inhibition, misbehavior, and autoshaping, just to name a few.

In blocking, previous Pavlovian conditioning of a conditioned stimulus (CS) A interferes with the conditioning if another CS X if both are paired in compound with the unconditioned stimulus (US). From the perspective of a drive theory of learning, it is unclear why conditioning to X is weak despite being paired with the US. Latent inhibition is a significant retardation of conditioning to X after X has been preexposed alone. Drive theories of

learning predict the opposite effect: The drive after preexposure should be higher (as there was no need satisfaction during the preexposure phase), for which acquisition should be faster.

Drive theories of learning face similar difficulties with other phenomena. Misbehavior is the occurrence of collateral, adjunctive behaviors that significantly delay instrumental reinforcement. Auto-shaping is the acquisition of an instrumental response (e.g., keypecking) through purely Pavlovian contingencies where a visual cue is paired with response-independent food. These last two phenomena have led to question traditional ways to understand the instrumental-Pavlovian distinction.

There also has been a proliferation of more sophisticated models that have incited much further empirical, theoretical, and conceptual work, which has promoted a healthy scientific competition that can only result in progress. The Rescorla-Wagner model (Rescorla and Wagner 1972), as impressive and numerous as its successes have been, also suffers from important failures. For instance, the model does not predict latent inhibition. As a result, many other models have been proposed, all of them with successes and failures. As part of this proliferation, some modeling efforts (e.g., Sutton and Barto 1981) have joined the connectionist revolution in psychology, a sort of revival (with important modifications, to be sure) of Thorndike's old connectionism. Contemporary connectionism (see Rumelhart et al. 1986) is better characterized, not as a school of thought, but as a cross-disciplinary movement that seeks to explain adaptive behavior in terms of artificial neural networks, abstract neural circuits where representations are distributed and processed in parallel. These models are inspired by brain structure and functioning, for which they are said to be "subsymbolic." Despite this subsymbolic character, or perhaps because of it, these models have been very successful in simulating many different kinds of complex adaptive behavior. Such success demonstrates that adaptive systems such as animals need not be conceived as symbolic to be successfully explained.

None of these models uses the concept of drive state and related concepts like need and motivation. This commonality suggests that it is

time to dispense with these concepts altogether, at least as traditionally defined in psychology. But perhaps there is no need to be so extreme. The possibility could be explored of redefining these concepts in thermodynamic terms, as suggested above, and see what results from this redefinition. A model formulated in this direction is the so-called “Boltzmann machine” (Hinton and Sejnowski 1986), an artificial neural-network with fully, symmetrically connected, stochastically activated units. This model is squarely framed within thermodynamics. The model also is subsymbolic, which proves the possibility of a nonsymbolic (noninformation-processing) thermodynamic model of adaptive behavior. However, it is unclear whether and how the types of phenomena that learning psychologists study, especially instrumental and Pavlovian conditioning, can be simulated with Boltzmann machines as we know them today. It might be possible to build a Boltzmann machine for these phenomena, and where the concepts of drive state, motivation, and need, suitably redefined, play a renewed role.

## Cross-References

- [Associative Learning](#)
- [Autoshaping](#)
- [Blocking](#)
- [Clark L. Hull](#)
- [Classical Conditioning](#)
- [Dynamic Systems Theory](#)
- [Edward Thorndike](#)
- [Energy](#)
- [Goal](#)
- [Homeostasis](#)
- [Information Processing](#)
- [Innate Behaviors](#)
- [Instinct](#)
- [Intervening Variables](#)
- [Latent Inhibition](#)
- [Motivation](#)
- [Need Reduction](#)
- [Neural Network](#)
- [Satiation](#)

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## Drug Withdrawal

- [Withdrawal](#)

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## Drug Withdrawal Syndrome

- [Withdrawal](#)

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## Dual Sexuality

- [Hermaphrodite](#)

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## Duality

- [Cognition](#)

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## Dual-Store Model

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### Definition

A model of memory proposed by Atkinson and Shiffrin (1968) that features memory as being comprised of three major components: sensory memory, short-term memory, and long-term memory. Also known as the Multistore Model of Memory.

### Introduction

In their proposal of the Dual-Store Model, Atkinson and Shiffrin (1968) claim that memory processing involves a series of sequential processes that lead to the input, storage and usage of information. This model of memory breaks down memory processing into three distinct components known as *sensory memory*, *short-term memory*, and *long-term memory*. Information is first processed in the form of sensory memory, and subsequent processing leads this information to be stored in short-term memory and later transferred to long-term memory.

## Sensory Memory

In the initial phase of memory processing, stimuli from the environment are detected via the senses and the information provided is stored in the form of *sensory memory*. The existence of such a form of memory is supported by studies in which participants were quickly shown a matrix of words on a machine that briefly displays images, known as a tachistoscope (Sperling 1960, 1963). Immediately after viewing the matrix of words, participants were asked to write down as many letters that they remember seeing, with the average number of letters remembered being six. Subsequent studies involved the presentation of a matrix of letters on a tachistoscope where after viewing the matrix, participants were told to report back the letters in a particular row (Averbach and Coriell 1961; Sperling 1960, 1963). Participants were able to correctly identify the letters in each particular row, indicating the existence of a complete, visual image that is briefly stored in memory.

Sensory memory is further broken down into two subcategories, with *iconic memory* being comprised of memories from the visual system and *echoic memory* being comprised of memories from the auditory system. The memories formed during this stage last only a very short duration and are forgotten or decay if not transferred into short-term memory soon after they are formed. While the senses detect a large quantity of information from the surrounding environment, only some of this information is paid attention to, a process known as *selective attention*. Through selective attention, information that is paid attention to in sensory memory is able to transfer on to short-term memory, while unattended information is forgotten.

## Short-Term Memory

Compared to sensory memory, short-term memory lasts for a somewhat longer duration, with memories lasting approximately 18–20 seconds. Short-term memory can hold approximately five to nine separate memories, with the average capacity of items being seven (Miller 1956).

While approximately five to nine separate memories can be stored in short-term memory, the amount of information stored can be increased through a process known as *chunking*, where multiple pieces of information can be grouped together into a single memory or “chunk.” An example of chunking includes remembering a telephone number, where a ten-digit phone number can be remembered as two chunks of three digits and one chunk of four digits (i.e., xxx-xxx-xxxx). Short-term memory consists of memories that are within one’s consciousness and is described by Atkinson and Shiffrin (1971) as “a store in which decisions are made, problems are solved, and information flow is directed” (p. 83), earning it the nickname of *working memory*.

Because of the short duration and low capacity of short-term memory, its memories can be forgotten or displaced by new information. In order to retain information in short-term memory, the memories that contain this information must be rehearsed. This process, known as *maintenance rehearsal*, helps keep memories in short-term memory and simultaneously prevents the information from being forgotten.

## Long-Term Memory

In order for information to transfer from short-term memory to long-term memory, a process known as *encoding* must occur. Though the use of simple repetition via maintenance rehearsal can lead to the encoding of memories in long-term memory, a more complex type of rehearsal process known as *elaborative rehearsal* is more effective. During elaborative rehearsal, memories in short-term memory are associated with information already stored in long-term memory. An example of elaborative rehearsal is the process involved in remembering a boat as a form of transportation and connecting “boat” to forms of transportation already in long-term memory, such as “car” and “plane.”

As a result of its creation of deep associations between short-term and long-term memory, information that undergoes elaborative rehearsal is more likely to be encoded into long-term memory

to the simpler techniques provided through maintenance rehearsal. Similar to the process of transferring memories from sensory memory to short-term memory, whether or not a memory is encoded in long-term memory also depends on the amount of attention placed on it; memories that are rehearsed for a greater amount of time are more likely to be encoded into long-term memory, while memories that are rehearsed to a lesser extent are forgotten. Long-term memory is the most stable of the components of the Dual-Store Model, with memories lasting in long-term memory from several minutes to a lifetime.

While memories in short-term memory are within one's conscious, memories in long-term memory are within one's unconscious and are not readily accessible. In order to access information from long-term memory, information must be brought back up to short-term memory through a process known as *retrieval*. There are two forms of retrieval, known as *recognition* and *recall*. Recognition involves the recognition of a cue, usually related to the memory, to trigger the retrieval of the memory. Recall involves the retrieval of information from long-term memory without the use of a cue, such as answering a free-response question. Because it does not have assistance from a cue, recall typically requires more effort to retrieve memories than recognition; this difference explains why multiple-choice questions on a test, which involve recognition, are usually easier to answer than fill-in-the-blank questions, which involve recall. Unlike short-term memory, long-term memory has no definite limit to its storage capacity, and the availability of memories from long-term memory depends on whether or not a memory can be accessed through retrieval.

Long-term memory can be further classified into two types of memory, known as explicit memory and implicit memory (Tulving 1972). *Explicit memory*, also known as declarative memory, is comprised of memories that are based off of information that can later be recalled. There are two types of explicit memory, known as semantic memory and episodic memory; semantic memory is comprised of memories based on facts such as the names of colors or the meaning of words, and

episodic memory is comprised of memories based on personal experiences such as remembering someone's appearance or what happened during an event. While explicit memory involves memories that are consciously recalled, *implicit memory* is comprised of memories of skills and procedures that can be learned and performed unconsciously, such as driving a car, riding a bike, or playing a musical instrument.

### Evidence of a Dual-Store Model

The existence of a Dual-Store Model of memory gained support through studies involving *free recall*, where an individual listens to an instructor read a list of words and is then asked to recall the items on the list in any order (Murdock 1962). When recalling a list of words, individuals tend to remember more words presented at the beginning of the list and at the end of the list, but forget words presented in the middle of the list. Words at the very beginning of the list are often remembered well because they are rehearsed the most, thus having more time to be encoded into long-term memory, a phenomenon known as the *primacy effect*. On the other hand, words at the end of the list are often remembered well because they are the most recently learned and are still in short-term memory, referred to as the *recency effect*. The words in the middle of the list are often forgotten because they are not encoded into long-term memory or are displaced by incoming new words into short-term memory. This group of phenomena, collectively referred to as the *serial positioning effect*, and the findings from studies involving free recall support the idea that memory is comprised of two distinct stores, with a short-term store for short-term memory and a long-term store for long-term memory.

The majority of free recall tests have individuals recall a list immediately after the items are read, known as an immediate free recall, but some studies have participants recall the list after a short duration of time has passed. This type of test, known as a delayed free recall, have participants complete a distractor task, such as a series of math problems, in between being read the word list and the recall period. Compared to immediate free recall, the number of words remembered from

the end of the list during delayed free recall tends to be lower (Glanzer and Cunitz 1966). This observation is due to the fact that newly acquired information during the distractor task displaces words from short-term memory, thus reducing the intensity of the recency effect by decreasing the amount of words available in short-term memory during the recall period. Experiments involving free recall have also determined that the format memories are stored in during short-term and long-term memory affect recall performance. Information in short- and long-term memory is typically stored, or *coded*, using one of three methods: auditory coding (by sound), visual coding (by appearance), or semantic coding (by meaning). However, information from any particular sense does not need to be stored in the same format that it is detected via the senses, such as a person remembering a conversation with another person by visualizing the words that they heard (Atkinson and Shiffrin 1968). Short-term memory is thought to prefer coding information acoustically, as immediate free recall performance has been better for groups of words that are phonetically similar, such as “play, clay, day.” Long-term memory, on the other hand, has been shown to prefer to code information semantically, as delayed free recall test performance has been shown to be better for groups of words with similar meanings, such as “large, tall, huge” (Conrad 1964; Baddeley 1966).

### Case Study of “H.M.”

In support of their Dual-Store Model, Atkinson and Shiffrin looked at a now iconic case study of brain damage involving man identified as “H.M.” (Milner 1959; Milner et al. 1968). Following a bicycle accident at a young age, H.M. developed epilepsy and suffered from regularly occurring seizures. In an attempt to treat H.M.’s epilepsy, doctors localized and surgically removed a majority of H.M.’s left and right medial temporal lobes, which included the hippocampi. Following the surgery, H.M. developed severe anterograde amnesia, meaning that he was unable to recall memories occurring after the surgery, as well as

mild retrograde amnesia, where he could not remember most events occurring 1–2 years prior to the surgery. H.M. was unable to store new information in explicit memory and could only remember events that occurred prior to 1953, the year that he had the surgery. While H.M. had impairments involving long-term memory following the surgery, his short-term memory remained intact, as he was able to perform tasks that involved recalling information stored in short-term memory. While “H.M.” was able to perform previously acquired skills, he was unable to remember recently taught information regardless of rehearsal.

The case of H.M. further suggests the separation of long-term and short-term memory processes and supports the idea that the processing and storage of the various types of short- and long-term memories are separate from one another.

### Baddeley’s Model of Working Memory

While Atkinson and Shiffrin’s concept of a Dual-Store Memory Model helped promote interest for research in memory processing, it received criticism from the scientific community. One of the largest areas of criticism for the model concerned how it suggests that information from sensory memory is stored and processed into short-term memory in the same manner for all of the senses. In contrast to Atkinson and Shiffrin’s idea of a singular store for all of short-term memory, Baddeley and Hitch created a model that features short-term memory being comprised of processes and storage areas specific for different types of sensory information, known today as *Baddeley’s Model of Working Memory* (Baddeley and Hitch 1974).

The original version of the model consisted of a “head” *central executive* system and two “slave” components, the *phonological loop* and the *visuo-spatial sketchpad*. The central executive is involved in problem solving and coordinates activity within the “slave” components through task switching, information retrieval, and selective attention. The phonological loop is



responsible for recording and processing information regarding auditory stimuli and is involved in the nonverbal rehearsal of how a word sounds and the order of words in a sentence. The visuospatial sketchpad is responsible for processing and storing visual stimuli and works by creating a mental image of what is seen. The separate processing and storage of auditory and visual memories prevents the phonological loop from interfering with the visuospatial sketchpad, allowing both components to work simultaneously without affecting each other's performance. Baddeley later revised the model to include a third component under the control of the central executive, known as the *episodic buffer*, which organizes multiple types of visual, auditory, verbal information into a chronological order (Baddeley 2000).

Evidence for such a model of working memory came from studies involving dual-task paradigms in which participants had to complete two tasks simultaneously (Baddeley Hitch 1976). The tasks involved in the dual-task paradigms were a digit span task, where participants did a digit span that involved repeating back a list of numbers, and a verbal reasoning task that involved answering True/False questions. As the number of digits to be remembered in the digit span task increased, the number of errors made on the verbal reasoning task remained unchanged. From this finding, Baddeley and Hitch concluded that participant performance was unhindered because the two tasks involved different forms of working memory, with the digit span task utilizing the phonological loop and the verbal reasoning task using the central executive system. Additional support for Baddeley and Hitch's model came from a case study of a man identified as "K.F." who suffered from impaired short-term memory due to brain damage resulting from a motorcycle accident (Shallice and Warrington 1974). K.F. had impairments in his verbal short-term memory yet intact visual short-term memory, indicating the existence of separate components involved in visual information (visuospatial sketchpad) and verbal information (phonological loop) in short-term memory.

In addition to the separation of short-term memory into separate components, the Baddeley

model also proposed the idea for separate stores for long-term memory. After being processed by one of the three "slave" components in short-term memory, information from each component is stored in a different form. Information from the phonological loop is stored in the form of language, while information from the visuospatial sketchpad is stored in the form of visual semantics and in the form of episodic memory for information from the episodic buffer.

### Separation of Long-Term Memory

Another part of the Dual-Store Model that received criticism was the methods that the model used to for coding memories during short- and long-term memory and the lack of the model's specialization for storage of different types of memories. Edmund Tulving (1972) stated that different types of information in long-term memory, such as procedural memory, semantic memory and episodic memory, are stored in different fashions through different types of encoding processes, rather than one universal method. An example of these principles can be seen through the case study of H.M. After undergoing surgery to treat his epilepsy, H.M. was regularly visited by a research team who taught him a mirror-drawing task, where one draws an image by looking at the reflection of their drawing, a task which becomes better with practice. While H.M. was able to retain his motor skills involved in the mirror-drawing task and subsequently began completing the task at faster speeds, he was unable to recall how or when he learned how to do the task (Milner 1965; Milner et al. 1968). In addition to his inability in remembering how he learned how to do the mirror-drawing task, H.M. was also unable to remember the meaning of vocabulary words. H.M.'s intact ability to encode and retrieve implicit, procedural memories from long-term memory despite having severe impairments in explicit memory suggests that different types of memories are stored and processed in different areas of the brain.

## Encoding Specificity

In addition to his comments on the Dual-Store Model's universal storage system for long-term memory, Tulving also suggested that there are additional factors that influence the effectiveness of memory retrieval rather than the format information is coded in (Tulving and Thomson 1973). According to Tulving, the retrieval of information is best when the conditions are similar to those during encoding, such as the context in which information was learned, the environment that something was learned in, as well as the mental and physical state that one is in when encoding and retrieving. An example of this is the idea that by studying for a test in the classroom that one will take the test, the scenario where the memories were encoded (during studying) will be the same as that during recall (while taking the test), thus allowing more memories to be recalled (Smith et al. 1978). This concept, known as the *encoding specificity principle*, states that contextual factors play a role in the effectiveness in memory retrieval more than the form that the memory is stored in.

## Levels of Processing Effect

Another model of memory that was developed as an alternative to Atkinson and Shiffrin's Dual-Store Model involved memory functions being based on the amount, or depth, of processing that is placed on pieces of information. This model, referred to as the *levels of processing effect*, claims that the processing of memories is divided into two categories known as shallow processing and deep processing (Craik and Lockhart 1972). Memories that undergo *shallow processing* are processed at the surface level using the senses, such as remembering a word by how it is pronounced, while memories that undergo *deep processing* are analyzed at a deeper, more elaborative level and are processed by the meaning behind it, such as the definition of a word. The strength of memories depends on the level of processing placed on them, with shallow processing

producing memories that are fragile and less memorable and deep processing producing memories that are stronger and more likely to be remembered over time. This model builds off of the concept already in place by the Dual-Store Model in terms of rehearsal methods, in which maintenance rehearsal helps temporarily retain information in short-term memory, while elaborative rehearsal leads to the encoding of information in long-term memory.

## Conclusion

The Dual-Store Model of memory helped pave the way to a better understanding of how the human memory system functions. While more complex models of memory have taken favor among the scientific community since its introduction, the Dual-Store Model promoted the idea that memories are contained in a short-term store and a long-term store. Atkinson and Shiffrin's Dual-Store Model led to an increased interest in memory research, leading to subsequent theories and developments on memory storage and processing.

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## Duane Rumbaugh

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Duane M. Rumbaugh (July 4, 1929 – June 22, 2017) was an American comparative psychologist known for computer-based ape-language research with a chimpanzee named Lana, for developing the Transfer Index procedure for assessing intelligence across species, and for his conception of emergent forms of learning that reflect recognition of salient regularities in experience rather than stimulus-response conditioning. He served on the faculty of San Diego State College and of Georgia State University, where he chaired the psychology department and was the founding Director of the Language Research Center.

## Personal and Professional History

Duane Rumbaugh was born on the 4th of July, 1929, to Reverend Arthur and Ida (Traudt) Rumbaugh in the small rural town of Maynard, Iowa. Except for a brief period in the early 1930s in which the Rumbaughs (including two sisters born in 1919 and 1927) lived in the even smaller town of Alexandria, Nebraska, Duane spent the first two decades of life on and around the farms of Iowa. Growing up during the Great Depression in the Dust Bowl Midwest was hard, and Rumbaugh spent many hours tending to animals, haying, milking cows, and other farm activities, even as a youth. Too young for World War II, there was more than enough work to do back home, with so much of the workforce in the military. Strenuous farm jobs have motivated many bright young men and women to pursue higher education, and so it was that Rumbaugh headed to college after graduating as class President from Ackley High School in 1946, just a few months after the end of the war.

Duane studied psychology at the University of Dubuque, where he earned a baccalaureate degree

in 1950; however, he spent his entire senior year enrolled at the University of Iowa to strengthen his qualifications for graduate study. Duane was greatly influenced at Iowa both by the faculty from whom he took courses and also by some of his fellow students. It was on the recommendation of one such friend, a doctoral student named Anthony Cacioppo (who would himself have an accomplished career in engineering psychology), Rumbaugh enrolled in Kent State University to pursue a master's degree.

With the emerging conflict in Korea threatening military service, Duane was motivated to complete his thesis as quickly as possible. He worked under the direction of Charles C. Perkins, and was also influenced by Martin R. Baron and Raleigh M. Drake. All three had completed doctoral training at Iowa, two directed by Kenneth W. Spence and Drake supervised by Carl Seashore. Accordingly, it is unsurprising that Rumbaugh's thesis project was a maze study with rats, contrasting place learning with response learning. He received his M.A. in 1951, and continued his doctoral education with another former Spence student, Maurice P. Smith at the University of Colorado. Rumbaugh's 1955 dissertation was titled, *An Investigation of the Relationship Between Drive Intensity and the Growth of Habit Strength*, reflecting his theoretical orientation within the Hull-Spence framework.

Dr. Rumbaugh accepted a one-year Instructor position at San Diego State College (now University) in 1954, which became a tenure-track faculty appointment. Rumbaugh would remain at San Diego State until 1969, moving steadily through the academic ranks as an assistant, tenured associate, and professor. It was during this period that research in comparative psychology would begin in earnest, although the transition from general-experimental psychology to comparative studies was a product of good fortune at least as much as master plan. In early 1955, Dr. Rumbaugh met with his department chairperson to discuss teaching assignments. Flipping through the course catalog, Chairman Walcott Treat found one course that was not already "owned" by another faculty member: Comparative Psychology, which had not been

offered for some time. With his experience studying learning by rats and his background with farm animals, Dr. Rumbaugh jumped at the chance to be the department's resident comparative psychologist!

To obtain animals and laboratory facilities for this new interest, Rumbaugh approached the San Diego Zoo. Because of his experience, he gained access to rats and space to test them. The rats were from the breeding colony that provided food for the reptiles, but were otherwise fully available for learning research before being returned to the colony and the circle of life. Other animals, including pigeons, cats, chickens, and the occasional monkey, were also available in these early days.

With the Suez Crisis of 1956, Dr. Rumbaugh was again at risk of military service. He obtained a commission in the U. S. Naval Reserves as an officer in the medical service corps, and spent a summer in Bethesda, Maryland, at the Naval Medical Research Institute (now Center). He was assigned to work under the direction of Lt. Robert B. Voas on a project to determine whether a primate could survive flight aboard a Jupiter Intermediate Range Ballistic Missile – an important precursor to manned spaceflight. Dr. Voas (who would later become an astronaut training officer for the National Aeronautics and Space Administration's Mercury program) and Dr. Rumbaugh trained a squirrel monkey named Gordo for the 15-min suborbital missile flight, which launched in December, 1958. Biosensors indicated that the monkey tolerated the launch and flight with no ill effects; however, failure of the parachute system caused neither the monkey nor the missile to be recovered after crashing into the sea.

Dr. Rumbaugh returned to his academic position with renewed interest in nonhuman primates. He requested and was granted 90-sq. ft. of laboratory space where he could test apes and monkeys on discrimination-learning problems, in the fashion of Harry Harlow's classic learning set research. Among the animals that Rumbaugh attempted to test was the gorilla Albert, who expressed his displeasure with the situation by smashing the apparatus with his huge fist. Albert

was excused from further testing, but fortunately other animals were more willing to participate, and publications on primate (especially squirrel monkey) learning began to flow from the Rumbaugh laboratory.

Between 1963 and 1969, Dr. Rumbaugh held the administrative title of Associate Division Chairman, Life Sciences Division, San Diego State College. In 1969, he was recruited by Geoffrey Bourne, Director of the Yerkes Regional Primate Research Center at Emory University (Atlanta, GA, USA), into the position of Associate Director and Chief of Primate Behavior. In 1971, Dr. Rumbaugh left this position to join the faculty of nearby Georgia State University (Atlanta, GA, USA) as tenured professor and chairman of the psychology department. He chaired the department for 18 years, and remained on the faculty of Georgia State until his 2001 retirement as Regents' Professor of Psychology and Biology.

In his personal life, Duane Rumbaugh married twice. In 1952, he wed Phyllis Foresman, with whom he had a daughter. He subsequently married E. Sue Savage in 1976, and adopted her son. Duane and Sue Savage-Rumbaugh remain close collaborators long after their marriage ended.

## Significant Contributions

In a productive career that has spanned more than half a century, Duane Rumbaugh was a creative scholar, a visionary leader, and a skillful administrator. His many contributions to comparative psychology include several important innovations for methodology and theory. For example, his studies in San Diego suggested differences between species in the rate of two-choice discrimination learning; however, Rumbaugh recognized that there were many reasons other than intelligence itself that might contribute to performance differences. He developed the Transfer Index (TI) as a way to control for these other variables, producing an assessment of each animal's capacity to learn and to transfer learning to new situations. TI scores were found to vary systematically across primate species, with larger-brained primates

showing better transfer-of-learning and more rule-like relational (vs. associative) learning than the smaller-brained prosimians and monkeys (Rumbaugh and Washburn 2003).

Relational learning on the TI and its variations was cited by Rumbaugh as one example of what he termed "emergent" – a category of learning distinct from respondents (i.e., classical or Pavlovian conditioning) or operants (i.e., operant or instrumental conditioning). Emergents reflect the organism's perception of salient, rule-like regularities in experience (Rumbaugh 2002, 2013). They appear as complex and generalized competencies that have not been previously reinforced. Respondent, operant, and emergent behaviors constituted a framework that Rumbaugh called "rational behaviorism" to contrast with the radical behaviorism of B. F. Skinner and others.

Other examples of emergent competencies are found in language comprehension and production. When Geoffrey Bourne recruited Duane Rumbaugh to the Yerkes Center, he challenged Rumbaugh to study language learning by chimpanzees. Rumbaugh was hesitant, but finally capitulated, envisioning a fully automated language-training environment, in which apes could interact with a computer by means of a specially designed keyboard. Dr. Rumbaugh assembled a team of scientists and engineers, and the Language Analogue Project was born. One chimpanzee (Lana) and one orangutan (Biji) were selected for the study, but Lana's eagerness to engage the apparatus soon made her the focus of training. A vocabulary of visuographic symbols ("lexigrams") was developed, and each lexigram functioned as a word on the computerized keyboard. A grammar was also developed for the combination of these symbols, and Lana learned a variety of grammatical stock sentences that could be used to communicate with the computer and, more critically and effectively, with the human researchers who interacted with her. The work garnered considerable attention from the media and from scholars within the field, and was reported in numerous publications including 1977s *Language Learning by a Chimpanzee: The LANA Project*, edited by Duane Rumbaugh (1977). On the strength of Lana's impressive results, additional apes and special-



needs human children were subsequently trained to communicate with computer-based keyboards embossed with lexigram symbols.

The success of the ape-language work with Lana also led Dr. Rumbaugh, working with Sue Savage-Rumbaugh and other collaborators, to establish Georgia State University's Language Research Center (LRC). A series of laboratory and animal-housing buildings were constructed on more than 55 acres of forest, and the ape-language project was moved from the Yerkes Center to the LRC in 1981. Rumbaugh served as the LRC's first Director until his retirement in 2001, and oversaw expansion of the language-acquisition work to new chimpanzees (Sherman, Austin, Panzee) and a second ape species (bonobos, or *Pan paniscus*; Kanzi, Panbanisha); introduction of a language intervention project, headed by Dr. MaryAnn Ronski, in which children and young adults with intellectual disabilities were trained to use the keyboard-based language system that Rumbaugh had developed; expansion beyond language to studies of many other cognitive competencies, including numerical cognition, attention, memory, and cognitive control; and continuous support from the National Institute of Child Health and Human Development and other funding agencies.

Much of this cognitive work was facilitated by another methodological innovation. The introduction of the personal computer was rapidly changing the way human participants were tested in the late 1970s and early 1980s. After observing the chimpanzees elbowing Dr. Savage-Rumbaugh aside to gain access to a joystick and to respond to a computer game, Dr. Rumbaugh saw great possibilities for testing apes and even monkeys on game-like computerized tasks, and for using the test paradigm to provide environmental enrichment to support the psychological well-being of nonhuman primates. His publication of a hardware and software "computerized test system" that was used effectively with rhesus monkeys established a new testing paradigm that has revolutionized the comparative study of cognitive competencies (Rumbaugh et al. 1989).

For his many contributions – only a few discussed here – Duane Rumbaugh has been honored as a G. Stanley Hall lecturer by the American

Psychological Association (APA), as a Distinguished Professor by Georgia State University, with Outstanding Alumnus awards from Dubuque and Kent State, as Distinguished Member of the international honor society of psychology (Psi Chi), with the Donald O. Hebb Distinguished Contributions Award from APA Division 6 – Behavioral Neuroscience and Comparative Psychology, with the Lifetime Achievement Award from the Society for Experimental Psychology and Cognitive Science (APA Division 3), and with other recognitions. He has served as President of the Behavioral Neuroscience and Comparative Psychology Division of the APA, and of the Southern Society for Philosophy and Psychology.

## Cross-References

- ▶ [B.F. Skinner](#)
- ▶ [Clark L. Hull](#)
- ▶ [Classical Conditioning](#)
- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)
- ▶ [Counting](#)
- ▶ [David Washburn](#)
- ▶ [Discrimination Learning](#)
- ▶ [Georgia State University's Language Research Center](#)
- ▶ [Harry Harlow](#)
- ▶ [Intelligence](#)
- ▶ [Kenneth Spence](#)
- ▶ [Language Research: Great Apes](#)
- ▶ [Lexigrams](#)
- ▶ [Operant Conditioning](#)
- ▶ [Reversal Learning](#)
- ▶ [Sarah, Lana, Sherman, and Austin](#)
- ▶ [Sue Savage-Rumbaugh](#)
- ▶ [Yerkes Primate Research Center](#)

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## Ducks

- [Waterfowl](#)

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## Dugong

- [Sirenia Navigation](#)
- [Sirenia Sensory Systems](#)

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## Dugong Diet

- [Sirenia Diet](#)

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## Dugong Movement

- [Sirenia Locomotion](#)

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## Duplicating

- [Reproduction](#)

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## Duplication

- [Reproduction](#)

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## Duty Factor

- [Gait](#)

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## Dynamic Systems Theory

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### Definition

Dynamic systems is a theoretical framework that is used to understand and predict self-organizing phenomena in complex systems that are constantly changing, reorganizing, and progressing over time. Often mathematical formulae are used to capture processes of change within a given system.

### Introduction

The term “dynamic systems” is used to refer to a variety of phenomena in nonliving and living systems that display nonlinear behavioral changes over time. Behavioral change can occur in clouds formations in the sky or in a chemical reaction; it can reflect a sudden transition of gait pattern in a biological system, or a shift in flying pattern formation in a flock of birds. Dynamic systems aim to study the complex processes driving those changes. They are complex because whether occurring in a single system/organism, or a group of individuals, change occurs as the product of multileveled interactions between the various elements constituting these systems. Collectively, these dynamic interactions between elements of the system can lead to sudden transitions or the emergence of new forms in the behavior of the system. This encyclopedia entry provides a short history of the origins of this dynamic systems framework; it discusses its main tenets and

principles along with a number of examples focusing mainly on the behavior of biological systems.

## A Brief History

Dynamic systems theory originated in mathematics and physics. It is credited to Henri Poincaré (1854–1912) who developed the foundations of modern chaos theory, a precursor to dynamic systems. Chaos theory, and subsequently dynamic systems theory, began when Poincaré sought to understand the three-body problem. In this problem, he aimed to determine the final position of three celestial bodies, given an initial starting point and their relation to and effect upon one another. Several decades later, scientists found that the prevailing formulae of mathematics and physics, grounded in linear theory, did not explain the seemingly randomness associated with some experimental observations at the time. This randomness, initially considered as noise, was then seen as a crucial element that impacted the outcome of studies and observations. For example, Edward Lorenz (1917–2008), while working on weather forecasting, found an error that expressed the importance of taking “noise” into consideration when performing calculations or experiments. He found that minor differences in systems seemingly identical at their starting point, could result in two completely different systems given enough time.

The dynamic systems theory soon found applications to the fields of psychology and biology as a useful theoretical framework to capture and better understand behavioral change in living systems. To cite a few examples, dynamic systems theory has been used to capture transitions in movement coordination in humans and animals, such as fingers coordination (Schöner and Kelso 1988), gait transitions from walk to run in humans (Diedrich and Warren 1995), or trot to gallop in quadrupeds (Vilensky et al. 1991). It has been used in human development to comprehend how the seemingly erratic limb behaviors of newborn infants develop over time into functional behaviors such as reaching for objects and walking

(Thelen 1995). It has also been used to capture and model group dynamics such as the movement of crowds in public areas (Moussaïd et al. 2010), the complex interaction networks of ant colonies (Gordon 2010), or the thermoregulation of rat pups (Alberts 1978).

## Tenets of the Dynamic Systems Theory

### Multilevels and Multicausality in the Study of Change

The central quest of dynamic systems is to capture and understand how patterns evolve over time and transition from one mode of functioning (or state) to another. Often, pattern formation does not follow a predetermined, linear process. Biological systems, as many other systems, are complex and composed of a multitude of extremely varied elements inherent to the system corresponding to multiple levels (i.e., neural system, organs, functional characteristics, level of experience, energetic status, to cite a few) that continuously interact with each other in the most varied ways. Systems are also open to interactions with other elements that are external to the system (such as the physical environment, niche, group peers, social context, etc.). These interactions between elements from multiple levels of the systems can modify the elements themselves and their interactions, thereby altering the overall dynamics of the system’s behavior. Thus, change occurs as the product of these multiply interacting processes between multileveled elements.

This key tenet of the dynamic systems theory – that multiple, interacting processes can affect outcomes – is also referred by some as a multicausal process (Thelen and Smith 2006). The processes can be pressing on the individual from external sources present in the environment, but they can also stem from within the individual itself. For example, growth spurts in adolescence, weight gain, or drop in blood pressure can alter one’s physiology, mood, self-esteem, energy level, and so on. All these elements are connected and interact in time with the multiple levels of the system, entraining unique, sometimes unexpected changes in the system.

Good illustrations of multicausality in behavioral change come from infant studies. Before the introduction of dynamic systems to the field of developmental psychology, behavioral changes in infants were mainly viewed and studied independently of one another. Different behaviors within the infant system (i.e., perceptual development, body growth, reaching skill, walking, language, etc.) were assumed to follow independent developmental paths, and to grow as the product of a unicausal factor (often maturation of the central nervous system). There was little or no regard to the effect that each developing individual behavior had upon another. But infants are complex systems consisting of numerous subsystems, each developing at different rates, and studies in the last decades have shown how each newly emerging and existing subsystems can affect and can be affected by every other subsystem. This dynamic relationship between subsystems (or elements of the system) requires that the system be viewed as a whole organism with multicausal influences (not just one) driving developmental change. A first example of this was provided by the disappearing step reflex that was originally described in the early 1940s by Myrtle McGraw (1943). At the time, it was believed that the reflex was suppressed by neuromuscular maturation (a single causal factor). By applying a dynamic systems approach to this phenomenon, Thelen et al. (1984) discovered that other subsystems, in this case the rapid gain in weight and slower rate of leg strength of the infant, played a defining role in the suppression of the reflex.

Another well-documented example stems from Corbetta and Bojczyk (2002), who found that the emergence of bipedal walking (but also other forms of self-produced locomotion) can trigger temporary changes in reaching behavior. When infants produce their first independent steps, they have already developed fine reaching skills. They can use finger grasps for picking up cheerios, and they can anticipate grasping by shaping and orienting their hand ahead of contact with the object. Nonetheless, when they are beginning to walk upright, infants with extensive experience at reaching revert to two-handed reaching for

small objects while sitting – a behavior that is more typical of 4–6 months novice reachers. Corbetta and Bojczyk (2002) observed that during this critical period of motor learning, reaching, and walking, which have been typically considered as two functionally independent behavioral skills, in fact interact closely to allow the integration of the novel walking skill into the existing motor repertoire of the infants. When learning to walk, infants couple their upper arms intensely to maintain postural balance and generate steps. This upper arm coupling transfers to reaching, yielding this temporary return to two-handed reaching around walking onset. However, when infants become better walkers and do not need their arms so much anymore to maintain balance, the two-handed responses dissolve and infants show again more adapted reaching responses to objects in their environment. More recently, Corbetta et al. (2014) revealed that these walking-onset related changes did not uniquely incur in reaching, but affected cortical reorganizations as well. Thus, this example illustrates well how a change in the system (the emergence of walking) interacts with other multiple levels of the system (i.e., reaching, brain connections) to create a new form of behavior (the return to two-handed reaching). Extension of this work shows that this process is multicausal because walking is not the only behavioral form associated with an increase in two-handed reaching in the first year of life; scooting while sitting (Corbetta et al. 2006) and the onset of cruising onset (Atun-Einy et al. 2014) can lead to similar increases in bimanual reaching behavior, while other forms of self-produced locomotion such as belly crawling or hands-and-knees crawling are more linked to one-handed reaching responses.

Development is often thought to be an upward linear trend; however, it is a dynamic process that fluctuates with the different demands of the system. In many cases, development and behavioral formation unfold in a “seesaw” pattern, where the organism reaches periods of cost-effective functioning, alternating with periods of behavioral regressions, before continuing a trend of upward development. This has been seen in motor skills development as discussed above

(Corbetta and Bojczyk 2002; Corbetta et al. 2014), but occurs also in cognitive development such as in language development (Gershkoff-Stowe 2001). In language development, toddlers can begin to correctly map labels onto objects during their second year of life, and around 18–20 months old, they begin to go through a rapid period of productive vocabulary expansion. However, during this time of vocabulary expansion, the amount of labeling errors increases – production increases, yet children’s ability to accurately label words regresses. If this were to be a unicausal system, then the regression would be viewed as an unexplained decrease in the ability to produce object labels, or an overload of new words resulting in confusion and labeling errors. Gershkoff-Stowe (2001) supports that the system is more complex and dynamic; a child can correctly label a duck, yet when they are presented with a shoe immediately after, they label the shoe “duck.” This is an error in retrieval, not in the knowledge of the word. This is believed to be due to the child’s inability, at this stage, to overcome the priming effect and correctly produce the known label (Gershkoff-Stowe 2001). One of the major tenets in this example is the idea of coupling; language itself is a dynamic system with multiple processes linked together, or coupled. At this stage of development, retrieval and prior activation of the previously labeled word are tightly coupled such that the previously activated label interferes with the production of a new label. As the child continues to develop, there is a shift in the system where the dynamic between retrieval and prior activation is no longer tightly coupled, and therefore prior activation no longer interferes with accurate production.

The same principles of multicausality can be applied to the larger scale of group behavior, not just changes in behaviors of single individuals. For instance, in Zebrafish, shoal cohesion – the distance between neighbors in a group of fish – can be impacted by either aspects of their physical environment, social factors of the group, or both (Shelton et al. 2015). One factor of shoal cohesion is the density of the shoal (relative to the space available in the tank); however, shoal cohesion can also be modified by the social factor of

group size within the varying shoals. If the group size is different, but the density within the tank remains consistent, then there is no difference in the cohesion of the shoal; it is only when density and group size have a specific combination that there is an impact on the behavior of the shoal. If group cohesion were to be considered a result of a unicausal process, such as only the density in the tank, then the unique relationship between group size and density would not have been captured.

### **Self-Organization, Emergence of New Forms, and Nonlinearity**

How do systems transition from one mode of functioning (or state) to another? Given the intrinsic complexity of behavioral systems, with their large numbers of elements and interactions between elements, how do systems “know” how to reorganize? And how do they form stable patterns of functioning? Self-organization is the concept at core here. Systems evolve and move through discrete states (or behaviors) that form and dissolve continuously over time. These states can be stable or unstable depending on the interactions that are taking place between the elements in and/or out of the system. It is through the cooperation or assembly between these elements that states or behavioral patterns in the system emerge. However, given the intrinsic complexity of the systems, the formation of such new patterns or behaviors are often considered the product of self-organization or self-assembly. In complex systems, it is difficult to establish a hierarchy or order that dictates which element will entrain a change in the system’s behavior and how the ensuing interactions among elements will unfold. The changes occurring also cannot be considered as prescribed, preexisting, or preprogrammed. They are the direct product of the multileveled dynamic interactions occurring between elements of the system. For example, decades of studies in cognitive science have assumed that the brain was the ultimate organ receiving information, making decisions, and deploying responses, but from a dynamic systems perspective, the brain is only one piece of the complex process of making decisions and producing actions. The brain, the body,

the developmental history, the experience level of the system, and the existing constraints intrinsic to the system and the environment all partake in concert to the produced behavioral outcome of the system at a specific point in time (Chiel and Beer 1997).

Because of the patterns of interaction between elements and the way they self-assemble, systems are in perpetual state of change and transformation, and these transformations only exist as a function of time (this is certainly true for biological systems). Thus, behaviors are in constant evolution, second by second, minute by minute, creating new forms, dissolving those forms, reassuming old forms, or transitioning between forms. And often, these changes are nonlinear. Nonlinear changes typically reflect qualitative, sometimes sudden transitions in the behavior of the system, and again they result from modifications in the patterns of interaction between elements.

These concepts of self-organization, emergence of new forms, and nonlinearity can be best illustrated using crowd dynamics as an example. In humans, we are able to observe the spontaneous self-organization and emergence of new behavioral forms in pedestrian crowds. Pedestrian crowds illustrate the dynamic relationship that can exist between elements of a system (i.e., single pedestrian and/or grouped individuals). Similarly, to the shoal example described above, the size and density of the crowd are affected by the surrounding environment such that as the size of the crowd increases, the distance between elements decreases, and the members of the crowd also move slower. But large crowds were also found to be composed of 70% of its members belonging to smaller social groups within the crowd. These subgroups of pedestrians walk abreast to one another and are likewise affected by the environment. However, as the density of the overall crowd increases, it was found that the formation of the group changes into a “v-formation” around a central member in the crowd (Moussaïd et al. 2010). These changes are systematically arranged but not consciously decided. There is no central driving force that dictates the movements of all other members of

the crowd, but rather each individual, which is a system unto itself, interacts, affects, and is affected by the other surrounding individuals of the crowd. No one person expresses the need to change the group’s formation; it is an automatic reaction to the surrounding crowd’s density. This is a self-organizing system.

This is further illustrated when opposing flows of pedestrians meet on a walkway. When bidirectional streams of pedestrians meet, the two groups of pedestrians will narrow their overall size and pass one another on opposing sides rather than blending into one another. This turns out to be the most energy-efficient and effective way for the opposing streams to pass one another (Helbing et al. 2005). There is no “leader” in the two crowds of pedestrians or a specific protocol that dictates the actions of the groups; thus, the different crowds self-organize in a manner that most effectively circumnavigates one another.

More specific features of the environment can also be a significant factor in generating self-organization in systems’ behaviors. Research by Jeffrey Alberts (1978) countered the previously held view that rat pups were incapable of regulating their temperature, therefore deemed “helpless,” by examining group behavior while manipulating the ambient temperature. The goal of each pup, while forming huddles, is to reduce the amount of heat loss and the consumption of oxygen, thereby reducing metabolic use and saving energy. This is achieved by huddling into groups that dynamically interact in response to ambient temperatures. The surface area of the huddle expands and contracts in warmer and cooler temperatures, respectively. The composition of the huddle continuously changes, with pups cycling from the outer exposed surface area, a more metabolic costly area of the huddle, to inward toward the warmer, less costly inner portion of the huddle. Therefore, the huddled group temperature is self-regulated through the competitive actions of each individual pup as it moves to the warmer center of the huddle. Therefore, the rat pups share the costs of maintaining low metabolic expenditure. This example illustrates how a seemingly simple behavior such as rat pup huddling is actually a self-organizing

dynamic system that can only be truly understood when taking into account the different aspects and relationships that interact and produce the observed behavior.

### Attractor as a Metaphor for States and Transitions

Changes in patterns and self-organization create states that can be identified to describe the behaviors or patterns that are being produced by the system and its interacting elements at a given time. The word “attractor” is used to define these states in their given situations. In living organisms, observed and recurrent behaviors are called attractor states. These behaviors can be stable (this can refer to established forms of behavior such as walking or running in a human or animal) or unstable (meaning that the behavior is subject to imminent change). Transitions can occur when a current attractor state becomes unstable or is no longer viable, and the system as a result shifts to a more stable attractor. Transition in gait patterns is a classic illustration of such shifts from one behavioral state to another. Take the example of increasing speed in walking. As we walk increasingly faster, there is a point prior to the transition, where the state attractor – walking – becomes energetically costly, no longer efficient, and unstable. At this point, if we continue to increase speed, the system transitions to a more stable attractor state – running. This new state is more stable and energy efficient at the higher speed compared to the unstable state of walking at faster speeds. Such transitions are also frequently seen in the animal world, e.g., in horses, cats, dogs, and monkeys (Farley and Taylor 1991; Vilensky et al. 1991), where transitions to a new gait supersedes their previous gait that was no longer ideal for the amount of energy being spent. These changes are not only influenced by self-regulated actions, as walking speed in this example, but can also be affected by external forces from the environment. For example, walking against strong winds or walking over an iced surface will make running unstable and energy costly, pushing the system to adopt another locomotor pattern as a preferred one.

### Embedded Multiple Timescales and Developmental Trajectories

Most of the examples presented above corresponded to changes in behavior occurring within relatively short timescales. But what dynamic systems also brought to our understanding of change over time is that one change occurring in a system at a given moment in time (short timescale) can alter the broader developmental trajectory of the system over the more extended timescale (larger timescale). Biology, for instance, has already offered several examples of how, from initially identical conditions, organisms can form and develop quite different phenotypes depending on the system developmental history and interacting elements. Gottlieb (1992), as one example, has reported the case of two identical twins raised apart who developed to very different heights and body composition when they reached adulthood. It is easy to consider how factors such as diet, exercise, medical history, climate exposure, and probably many other environmental influences may have interacted with the genes to alter physical development.

Examples applying more specifically to behavior have been documented as well. For instance, in recent decades, it was discovered that the position in which a baby sleeps can alter the developmental timing of its subsequent motor milestones (Davis et al. 1998; Pin et al. 2007). Following the “Back-to-Sleep” campaign which was initiated in the 1980s in an attempt to reduce the rate of sudden infant death, it was noticed that the age at which infants began to perform a number of motor milestones, including crawling on hands-and-knees, was being delayed, and that in some cases, babies even skipped the crawling milestone altogether. Because infants were now sleeping on their back and side more often and for longer periods of time (than on their tummies), they were less enticed to use their arms and legs to push their body upward to be able to see their surroundings. Push-up behavior from laying prone was discovered to be an essential behavior to help babies transition to subsequent motor milestones and facilitate their discovery of crawling. As a result, pediatricians began recommending “tummy-time” during playtime to entice babies to push-up from a prone



position. This example illustrates how multiple timescales are embedded over time to alter the rate and form of developmental trajectories. As demonstrated here, a local change in the initial state (sleeping in supine or prone) can have extended cascading consequences for the development of future motor milestones.

Another example is stemming from animal behavior and the hatching behavior of domestic chicks (Casey and Martino 2000). This example also illustrates how a short timescale change introduced at an early stage of development can change the development of more protracted behaviors. When a chick hatches from their egg, they need to chip away the egg by kicking holes with their right foot 360 degrees, counter clockwise around the egg to emerge. After they hatch, if they are put in a T-maze where there is a forced choice of walking left or right, they overwhelmingly choose to turn left. They also display footedness preference of their right foot. The chicks appear to have a set laterality preference. In their study, Casey and Martino (2000) controlled the conditions of the nursery to maintain all conditions comparable to prior studies, but introduced unique modifications in the hatching behavior of the chicks. They manipulated the egg such that the chick only needed to peck around for a portion of the 360 degrees to hatch, thus reducing hatching behavior. When the chicks were tested later on, they found that the strength of their typical laterality preferences decreased significantly. Thus, again, the course of development, in this case laterality formation, was altered due to a shift in the hatching behavior performed earlier in life.

Embedded timescales are important in dynamic system theory as they illustrate how change occurring in the spans of seconds and minutes can impact the organization of the behavior over the span of hours, months, or years.

## Conclusion

Dynamic systems theory allows for the understanding of seemingly random nonlinear behavior and other phenomena observed in both living and nonliving systems. The basis of dynamic systems

theory is change – over time, through self-organization, within the individual, or in the environment. Just as the nonliving complex systems (i.e., chemical reactions, water currents, and weather forecasting) are affected by small changes, living organisms are also complex systems that are affected by the ever changing, self-organization, and reorganization of the subsystems that constitute them. Observed behavior of living organisms can more thoroughly be explained when viewed through the lens of the dynamics systems theory. As the systems within an individual reorganize, they can affect change in the behavior displayed by the individual, e.g., ambient temperatures influencing huddle formations (Alberts 1978) or the onset of walking creating a shift in reaching patterns exhibited by human infants (Corbetta and Bojczyk 2002). These reorganizations occur at multiple levels of the system (i.e., the development of infants language and motor skills), across different timescales (i.e., transitions in gaits over minutes and transitions in development over months and years), and are self-organizing (i.e., bird flocks and pedestrian crowds). Though dynamic systems theory originated in the fields of mathematics and physics, its applications in the area of animal and human research are invaluable.

## Cross References

- ▶ [Behavior Systems](#)
- ▶ [Behavioral Variation](#)
- ▶ [Correlation](#)
- ▶ [Epigenesis](#)
- ▶ [Learning](#)
- ▶ [Ontogeny](#)
- ▶ [Perception-Action Theory](#)
- ▶ [Sensitive Periods](#)
- ▶ [Twin Studies](#)

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# E

## E.O. Wilson

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Edward Osborne Wilson, Jr., born in Birmingham, Alabama, on June 10, 1929, grew up in many cities mostly within Alabama and Florida. He graduated with a B.S., M.S. (biology) from the University of Alabama in 1949, 1950 and a Ph.D. (biology) from Harvard University in 1955. He married Irene Kelley in 1955. Throughout his career he held multiple professorships at Harvard University, 1955–1997.

Many, perhaps most, children have a bug period during which they are fascinated by small living things. Wilson says he never grew out of his own bug period. At the age of 10, he decided that when he grew up he would be an entomologist. And he has never changed.

Butterflies were his first passion. Later, while living in Mobile, Alabama, his passion turned to ants. Close to his home, he found what proved to be the first colony of the imported fire ant (*Solenopsis invicta*) recorded in North America. He soon figured out that it belonged to a small population transported from Argentina or Paraguay to the docks of Mobile, Alabama, which were less than a mile from his family's house. From this site, the imported fire ant was destined to become a major pest across the southern United

States and thence onward to the West Indies, China, and Australia.

By 1942, the imported fire ant had spread widely through Lower Alabama and into Mississippi and the Florida Panhandle. Then a 19-year-old senior at the University of Alabama, and a dedicated myrmecologist (specialist on ants), and the world authority on the imported fire ant, Wilson was hired by the State of Alabama to study all aspects of the ant's biology and recommend a way to control it if possible. The result was his first scientific publication. He also found a new species of ant, the first of what was to be about 450 such novelties during his 70-year scientific career. He also became aware of a new kind of miniature beetle that rides on the backs of army ants, feeding on their oily secretions.

A year later, as a Ph.D. student of the University of Tennessee, he began to deepen his studies of the classification and natural history of ants in general, into what he was later to call sociobiology. Many species have multiple castes, beginning with the universal system of queen and workers (all female, incidentally) and extending to various combinations of soldiers, minors, supersoldiers, and intermediates. Tracing the most likely pathways of evolution leading to these arrays, he discovered that their origins can be mostly explained by changes in as few as two properties: allometry, the differences between the castes depending on size (e.g., big individuals have proportionately large heads), and the size frequency distributions. Both are colony-level

traits. It was immediately apparent that these traits arose by group selection, a process in time to become controversial.

In 1951, Wilson was invited to apply to the Ph.D. program in biology at Harvard. He enthusiastically accepted: Harvard had the largest collection of ants in the world, accumulated by the great myrmecologist William M. Wheeler. In 1953, he was elected to the Society of Fellows, which supported eight new scholars a year to go anywhere in the world and conduct research on any subject. There was only one requirement, which was read at the induction dinner: "Do something extraordinary."

And so, he submerged himself in the classification and biology of ants, traveling to Cuba, Mexico, New Caledonia, New Guinea, Australia, and Sri Lanka. He visited the major ant collections of the museums of Europe. All this travel was equivalent to Alabama writ large – very large. On settling back at Harvard, he married, worked hard, was appointed assistant professor in 1956 and given tenure in 1958.

The classification and biology of ants and other social insects were wide open at that time. In 1959, he and a few other researchers discovered the first glandular sources of pheromones in ant communication. Using ants and insects as models, he then worked with the mathematician William H. Bossert to create the first general account of physical and chemical properties of pheromones (1963). With Robert H. MacArthur, he made the data on ants acquired in the Pacific as an element of a theory of island biogeography (1963). This research eventually led many years later to Wilson proposing the Half-Earth project in global biodiversity conservation.

The pivotal event in the origin of sociobiology, however, occurred in January 1959. It occurred during a visit with Wilson's first Ph.D. student, Stuart Altmann (1930–2016), to the semi-wild rhesus macaque colony maintained on Cayo Santiago, an island off the coast of Puerto Rico. Altmann had chosen the social organization of this species for his thesis research.

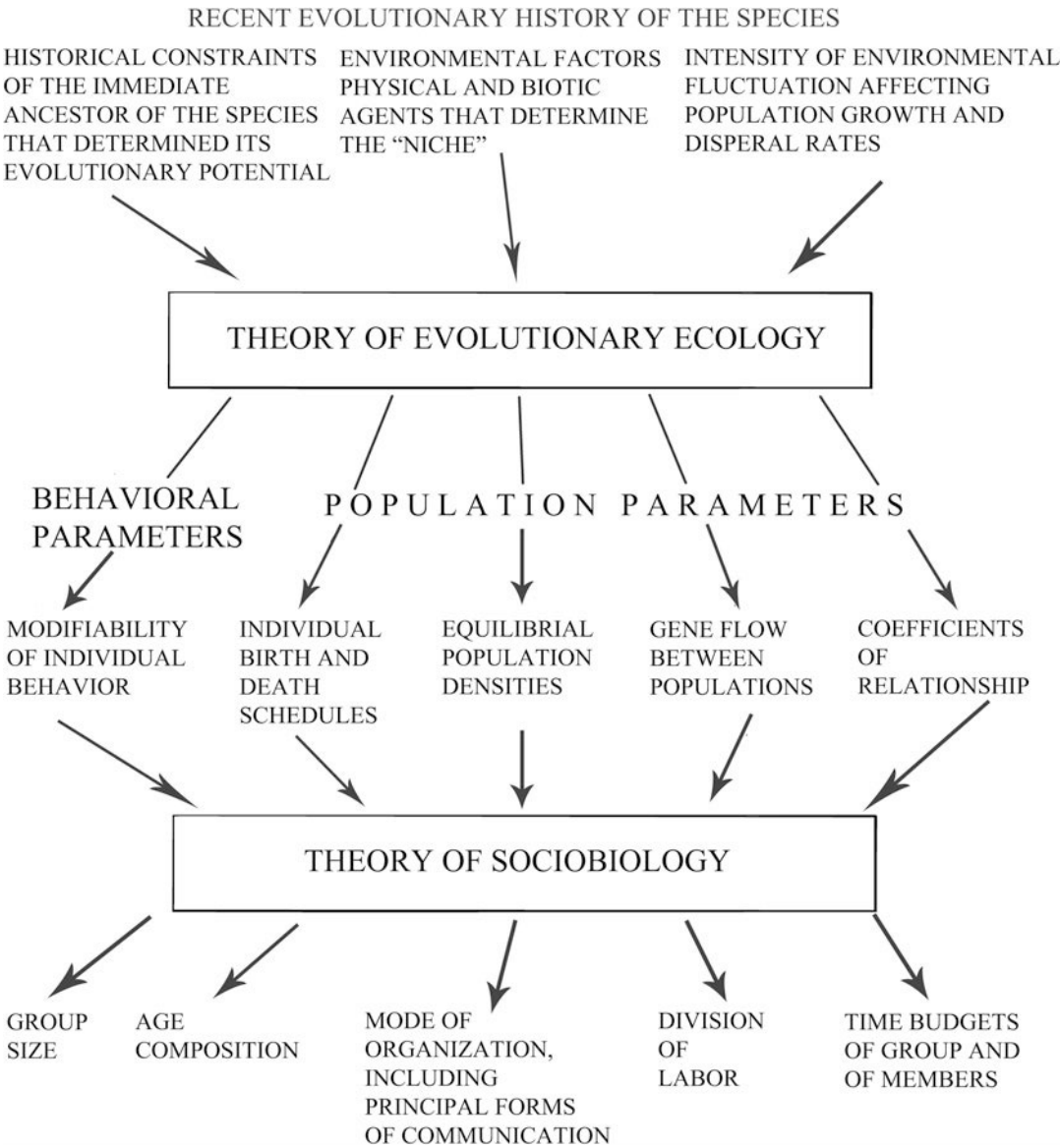
Wilson was stunned by the complex patterns of dominance, alliances, leadership, and division of

labor he witnessed in each of the several groups present. In the several days he was on the island, insect and primate social organizations held their attention leading to the key questions: *What are the basic differences and similarities between the otherwise radically different species? And what principles about the origin and maturity of social behavior might they illustrate?* They saw that this body of research and knowledge could form a new discipline of biology. Altmann and he agreed that it should be called "sociobiology."

Through the 1960s, Wilson spoke often, both informally and at seminars, on the content of the new discipline. Toward the close of the decade, he decided to summarize the rich but still unorganized literature on the social insects that had accumulated during the past half century – primarily with social wasps, social bees, and termites. His idea was to make this widely scattered information available to students and researchers – and further, to use its generalizations to formulate as much as possible the principles of sociobiology.

His book, *The Insect Societies* (Harvard University Press, 1971), met these goals and formally introduced the discipline of sociobiology. It became the standard reference on the social insects, and was moreover a popular success, selected as a finalist for the National Book Award in 1972. For the first time, in addition he was able to connect sociobiology intellectually with other scientific disciplines (Fig. 1).

*The Insect Societies* also highlighted the genetic theory of inclusive fitness, introduced in 1964 by the British geneticist W. D. Hamilton. Based on earlier work by Ronald A. Fisher and J. B. S. Haldane, it posited that altruism in animal societies evolves when trade-offs made in personal sacrifice are more than compensated by benefits provided relatives. An individual may lose some of its genes in future altruistic behavior, but genes identified by common descent can be increased by its altruism, leading to a genetically based altruism among relatives. This attractive idea eventually faded away due to its flawed logic, among which is making the unit of natural selection the individual group member rather than the genes prescribing altruism. This approach has never



**E.O. Wilson, Fig. 1** The 1971 diagram of the connections that can be made between phylogenetic studies, ecology, and sociobiology, published in Wilson (1971)

worked in general population genetics, nor, as it turned out, can it be fitted to the origin of altruism.

*The Insect Societies* proved a considerable success in stimulating research theory on the social behavior of both animals and human beings. While lecturing on the subject at the University of California at Berkeley in the spring of 1972, Wilson decided to expand the synthesis to the organization

of vertebrate societies, as well as colonies of siphonophores and other primitive invertebrates, in other words all eukaryotic animals.

The result was the book *Sociobiology: The New Synthesis*, published by Harvard University Press in 1975. The work was intended to be encyclopedic – heavily illustrated, thoroughly documented, and complete in its coverage of the

scientific literature. It soon was recognized as the founding document of sociobiology as a scientific discipline, defined as “the systematic study of the biological basis of all forms of social behavior.”

*Sociobiology: The New Synthesis* succeeded. In 1975, however, a serious interruption occurred. With near unanimity, social scientists believed that humans lack instinct, and that instead all social behavior is culturally derived. Similarly, 1975 saw the end of the Vietnam War, and a widespread lingering belief among protest groups that any notion of a human instinct, entailing genetic causation, was intrinsically racist and pro-war. One of Wilson’s close colleagues at Harvard, Richard C. Lewontin, identifying himself as a devoted Marxist and “socialist biologist,” devoted his energies to discrediting the entire book *Sociobiology* as racist, and Wilson as an unintended purveyor of racism. There followed disruption of Wilson’s classes by angry students and mobs forming around Harvard calling for his dismissal. “Sociobiology” became, briefly, a political epithet.

What was labeled as the “controversy of the decade” in fact lasted only a year or two. In 1976, Wilson was awarded the US National Medal of Science for *Sociobiology* and his research programs that led to the book. In 1978, he followed *Sociobiology* with *On Human Nature*, which expanded on the full powers of sociobiology to help explain innate human behavior. This book was widely acclaimed, receiving the 1976 Pulitzer Prize for nonfiction. For *The Ants*, coauthored with Bert Hölldobler, and organized around the themes of sociobiology, he received a second Pulitzer Prize for nonfiction in 1991.

There is no question that *Sociobiology*, followed by *On Human Nature* played a definitive role in the rise of the discipline of evolutionary psychology, which was taking shape at the time. Some of its founders denied the influence, saying that evolutionary psychology sprang autonomously from independent novel combinations of evolutionary biology and psychology. A more convincing explanation is the desire by its authors in the late 1970s to avoid the stigma attached to sociobiology during the early turbulent years of its controversy.

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## Early Learning

- [Human Infancy and Childhood](#)

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## Earth Pig

- [Aardvark](#)

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## Ebbinghaus

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Hermann Ebbinghaus (1850–1909) is considered one of the experimental psychologist’s pioneers. He was one of the first to investigate memory using an experimental paradigm, heavily contrasting with the predominant unscientific approaches used by psychologists of his era. Despite the lack of proper control procedures in his work – relative to what we know today – he demonstrated that memory is a phenomenon that can be measured and studied scientifically.

## About His Life

Ebbinghaus was born on the 24th of January of 1850 in the former Kingdom of Prussia, specifically in the city of Barmen which belongs to the



province of Rhine. Son of a prestigious and wealthy merchant (Carl Ebbinghaus), he had a traditional evangelical education, and as soon as he was able, he joined the University of Bonn and later the University of Berlin and Halle (Shakow 1930). He studied history and philology at first, but quickly gained an interest in philosophy. Nonetheless, his studies were interrupted by the Franco-Prussian war in 1870, when he enlisted to serve his country at the age of 20.

Ebbinghaus resigned to the Prussian Army in 1871 and continued his studies in philosophy, obtaining his Ph.D. degree (1873) from the University of Bonn with a dissertation over the “Philosophy of the Unconsciousness” in a time in which he moved constantly between England and France taking the role of the teacher as well as the role of the student (1875–1878). During this period, he planned to return to Berlin and apply to an academic position, but this did not happen. Instead, he kept teaching as a tutor in England and France to finance himself. As an important side note in his life, in 1879 he became the French tutor of the young and ill Prince Waldemar of Prussia (Shakow 1930).

During his travels between London and Paris, Ebbinghaus acquired a book written by Gustav Fechner, which became one of his biggest inspirations. The book was titled *Elements of Psychophysics* (Fechner 1948), and its scientific approach to human behavior deeply moved Ebbinghaus to pursue a life researching the field of human memory (Shakow 1930; Roediger 1985). Specifically, Fechner’s book helped Ebbinghaus in designing a mathematical model for the study of memory and motivated him to follow the study of human behavior from an experimental point of view. Nonetheless, it must be noticed that the equations used by Ebbinghaus differ significantly from the ones used by Fechner (Roediger 1985).

Eventually, Ebbinghaus came back to the University of Berlin, wherein 1880 he founded the third laboratory of experimental psychology in history, after Wundt’s and Müller’s laboratories (Shakow 1930). During his time in Berlin, Ebbinghaus published one of his most significant works, titled “Memory: A contribution to experimental psychology” (Ebbinghaus 1913) where he

detailed his experiments and advances to the study of memory.

In 1894 Ebbinghaus was expecting to fill a vacant place as the head of the Department of Philosophy at Berlin and to become a full-time professor, nonetheless, most likely due to lack of publications, the promotion was given to Carl Stumpf instead. And as result, Theodor Lipps left his position at the University of Breslau – nowadays Warsaw, Poland – to replace Carl Stumpf in his former post at the University of Berlin. Due to the latter, and after receiving a formal invitation from the University of Breslau, Ebbinghaus left the University of Berlin and traveled there to fill the position left open by Theodor Lipps (Shakow 1930).

During 1894, his first year in Breslau, Ebbinghaus once again founded a laboratory for the experimental study of psychology and was invited to commission to study the decline of children’s mental ability during 5-h school sessions (Shakow 1930; Roediger 1985).

During his last years, Ebbinghaus published yet again some important books to psychology, *Fundamentals of Psychology* (1902) – *Grundzüge der Psychologie* – and *Psychology: An elementary text-book* (1908) – both books being a success for years even after Ebbinghaus death – (Shakow 1930). In these books, he presents a big part of his experimental works on memory. In his studies, Ebbinghaus tried to control the greatest number of variables that might be interfering with his observations, nonetheless, he was the only participant in most of his experiments, which in present days would not qualify as highly controlled studies.

Ebbinghaus died of pneumonia on February 26th of 1909. He was described as an ever caring and joyful person to his fellow students, presenting himself as always helpful and encouraging the diversity of opinions among his students (Shakow 1930). He was the father of Julius Ebbinghaus, who later became a well-known Ph.D. in Philosophy dedicated to studying the ideas of Immanuel Kant. Julius Ebbinghaus served his country during World War I and II, and during the latter, he also worked as a psychologist for the German army. After the war, Julius

Ebbinghaus occupied a high academic position as a philosopher for the University of Marburg (Herb 1989). Lastly, Julius Ebbinghaus's son, Ernst Albrecht Ebbinghaus did not get into philosophy or psychology as his father and grandfather did, instead, he dedicated his life to the study of American German's history, linguistics, and literature.

## About His Work

Ebbinghaus's memory experiments lacked external validity and the capability to generalize its results, mostly because Ebbinghaus himself was the only experimental participant of them. However, in an era where the scientific view of psychology was not the predominant stance of the discipline, he showed to the world that memory, a psychological process, could be studied with a scientific and experimental methodology (Murdock 1985).

Despite Ebbinghaus being interested in many topics like history, philology, and philosophy, and even given lectures on these topics, his main interest always was psychology and memory. In retrospect, he was one of the main scholars working to emancipate psychology from its philosophical roots and bring it to the scope and methodology of formal sciences.

Additionally, Dr. Ebbinghaus made a great service to the discipline by founding and editing along with Arthur König – a physicist and astronomer with interests in the color wave spectrum – the journal *The Psychology and Physiology of the Sense Organs* – *Zeitschrift für Psychologie und Physiologie des Sinnesorganes* – in 1890. The volumes of this journal were printed between 1890 and 1910 – until the moment of his death – representing an interesting portrait of the psychology of the change of century (Shakow 1930).

In its fifty volumes, we have a complete view and depiction of the psychology of two decades (Shakow 1930; Roediger 1985; Holling and Erdfelder 2007), especially because Ebbinghaus was very open to publishing the opinions of diverse groups into the journal. Thus, making it the most important psychological outlet in Germany, and consequently one of the most important

at the time in the entire world (Shakow 1930), considering it was the second psychology journal ever to be founded (Holling and Erdfelder 2007). Furthermore, it must be noted that when this journal was founded, German was the de facto language for scientific publications, which made it one of the main sources to publish empirical work in the field of psychology. It was the psychological analog of *Annale der Chemi* or *Annale der Physik* – both world-known media for scientific publications in chemistry and physics, respectively.

Such was Ebbinghaus's journal importance that the most influential works of Raymond Dodge, David Katz, Kurt Lewin, Hugo Münsterberg, and Charles Spearman were published in the journal. And more specifically, the pioneering and classical works of Schumann's and Lewy's early work on auditory, visual, and tactile short-term memories, Müller's and Schumann's classical experiments on episodic memory, Netschajeff's explorations of memory development in school children, Müller and Pilzecker's famous work on retroactive inhibition, Jost's laws on effects of relearning after different intervals, and Cohn's pioneering research on the detrimental effects of articulatory suppression on phonological short-term memory (Holling and Erdfelder 2007). Additionally, in contrast with the psychology of Ebbinghaus' times, the methodology and language in which he presented his work and in which the journal was written was one that resembles the writing of today's psychology and its methods (Roediger 1985).

Also, it can be noted that Ebbinghaus was a person who encouraged and engaged in discussion with different points of view related to psychology. He defended and promoted the scientific approach to the discipline, but he also encouraged others to have different opinions. Now, despite his gentle and caring personality to deal and discuss with people about psychology, and even considering his effort for the foundation of a couple of experimental laboratories in the universities where he taught, he never got really interested in the training of pupils who could continue his work after him. He was a magnificent teacher, but as a researcher, he never got interested in developing a

future legacy for his laboratory work (Shakow 1930).

Regarding Ebbinghaus's experimental work, it is easy to say that he will be especially remembered for his contribution to the forgetting curve, which is first described in his publication "Memory. A contribution to Experimental Psychology" (Ebbinghaus 1913). The forgetting curve describes the exponential loss of information while passing a certain amount of time. The decrease is exponential, and there are two sharp decline points in the curve, one occurs after 20 min (being the largest decline) and the second occurs an hour after learning a seriation list. After that, the curve stabilizes its decline following the first day (Postman 1968; Murdock 1985).

Specifically, the experiment consisted of learning and recalling many times, in the most complete way possible, a series of syllables until the sequence would be completely forgotten. These syllables or nonsense syllables were later put in a box from which sixteen were extracted, written down in a notebook, and then memorized for the experiment.

These syllables or combinations of nonsense syllables were used as a method of control and validity, because Ebbinghaus believed that by using proper words this could create an inference in the measurement of a proper recall due to words being associated with one another, thus facilitating the recall process. Additionally, Ebbinghaus noted that it seems that humans tend to look for words close enough to the nonsense syllable to make it more meaningful. Nonetheless, he did not go deeper into this topic (Roediger 1985).

The forgotten curve was mathematically modeled, explained by a logarithmic equation developed by Ebbinghaus. This fact made him one of the first psychologists to mathematically model his theory. Additionally, he reported that learning was more difficult after certain hours in the afternoon compared to the morning. This was an early indication of the influence of circadian cycles on memory. Furthermore, followed by the discoveries related to the forgetting curve, an interesting fact about learning was found. When Ebbinghaus attempted to review and restudy the sequence of syllables, he noted that the process of

relearning the same seriation task was faster than previous attempts (Roediger 1985). Now, the mathematical model of the forgetting curve was later picked and reviewed by Kjerstad in 1919. He disagreed with Ebbinghaus work, specifically due to lack of experimental subjects. But he used Dr. Ebbinghaus's findings to further develop the concept of learning curve (Kjerstad 1919).

In what regards to the learning curve, further development in the field of psychology is scarce, but some resemblance can be found in the error-correction expectancy of the model proposed by Rescorla and Wagner (1972) and the error-reduction present in the overtraining effect (Witnauer et al. 2014). Nonetheless, the concept was picked and popularized worldwide, especially in the field of production optimization, due to the work of Wright (1936) in the aviation industry, proposing a further development of the mathematical formula behind learning to calculate the cost of production. Additionally, the concept of a learning curve was also picked by machine learning to explain the performance increase due to experience in machines, with both terms being the least number of errors due to the increase in the number of trials, respectively (Newell and Rosenbloom 1981; Sammut and Webb 2010).

In addition to Ebbinghaus experimental work, the combination test he developed to measure children's intellectual fatigue was not very successful in comparison with the other test presented by the commission in which he worked when he was at Breslau in 1894 (Shakow 1930; Roediger 1985). Nonetheless it resulted very valuable to measure the general intellectual capacity by correlating the results with the scholarship level of the students, laying the ground for further research on this field, like the future development of the Healy Picture Completion Test and the Trabucce Sentence Completion Test (Shakow 1930).

It can be clearly said that compared to Wilhelm Wundt – who is recognized as the founder of the first formal experimental laboratory for psychology, and one of the main influences in the development of modern psychology as a science – Ebbinghaus was not an equal in matters of scientific publications, with a considerably smaller list of published works and without a systematic way

of publication. It seems that Ebbinghaus was contemptuous and satisfied with his studies and interpretation of memory. Nonetheless, it must be mentioned that he made his experiment with great care and careful methodology, he repeated his experiments on memory until he was sure to be satisfied with the results. His memory work was completed in 1880, but he did not publish it until 1885 (Ebbinghaus 1913), after repeating the experimental processes in its entirety (Shakow 1930).

Despite the criticisms that could be made to Ebbinghaus's work, especially related to certain aspects of his methodology (e.g., being himself the only participant of his studies), it has to be noted that his work remains relevant until today. His findings are robust, and despite not having a proper external validity, he pioneered many of the fundamental pillars of today's psychology (Murdock 1985; Postman 1968).

Finally, it is important to highlight that Ebbinghaus was a pioneer in the scientific study of psychology, and as many of his kind, he did his best to provide a proper and elaborated method of study and research with what he had. He may not be the one who established the bases of today's modern psychology, but he made the first steps towards that direction. He did not foresee many of the problems and methodological mistakes that we know today, but he remains an important landmark in an age in which psychology as we know it was still emerging, and in which a scientific and methodological approach to psychology was not popular or highly accepted (Postman 1968; Murdock 1985; Roediger 1985).

Dr. Hermann Ebbinghaus did not form a so-called school of psychology, nor a field of research (Shakow 1930). Nonetheless, the legacy of his work showed us something of great relevance to psychology. Is not the fact that he was the first to suggest the discovery of the forgetting curve. It is the fact that he showed us that complex organic functions of human beings, like memory, could be instrumentalized, subjected to a method, and thus granting us scientific knowledge of a process that was believed that it could only be discussed philosophically. His pioneering

incursion in the experimental study of memory set the bases of an upcoming trend in the rise of cognitive and behavioral sciences.

## Cross-References

- [Associative Learning](#)
- [Associative Mechanisms](#)
- [Clark L. Hull](#)
- [Classical Conditioning](#)
- [David Hume](#)
- [Declarative Memory](#)
- [Ebbinghaus Illusion](#)
- [Edward Thorndike](#)
- [Episodic Memory](#)
- [Immanuel Kant](#)
- [Laboratory Research](#)
- [Latent Learning](#)
- [Learning](#)
- [Long-Term Memory](#)
- [Memory](#)
- [Morris Water Maze](#)
- [Perceptual Learning](#)
- [Prospective Memory](#)
- [Radial Arm Maze](#)
- [Short-Term Memory](#)
- [Working Memory](#)

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## Ebbinghaus Illusion

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### Synonyms

Ebbinghaus-Titchener illusion; Geometric illusion; Size illusion; Titchener circles

### Definition

The Ebbinghaus illusion is a geometric size illusion that emerges when two identically sized circles are misperceived on the basis of surrounding circles due to contrast effects. Larger surrounding circles lead to an underestimation of the central circle, whereas smaller surrounding circles lead to an overestimation of the central circle. The Ebbinghaus illusion, like many other visual illusions, has been used to assess similarities and differences in the perceptual systems of a wide range of species including humans, nonhuman primates, dolphins, dogs, birds, and fish.

### The Ebbinghaus Illusion

Geometric visual illusions emerge when the true physical properties of a stimulus (e.g., overall area, length, height, color, orientation, brightness) are misperceived on the basis of illusory-inducing features of surrounding stimuli. The Ebbinghaus illusion (Fig. 1), also referred to as the Ebbinghaus-Titchener illusion, is a classic geometric size illusion in which a central target circle (or dot) encircled by larger circles (or dots) is perceived as smaller than a central target dot of the same diameter encircled by smaller dots. Importantly, susceptibility to geometric illusions is contingent upon perceptual grouping mechanisms, in which the target stimulus (central dot) and its surrounding stimuli (outer dots) are assessed simultaneously. Geometric illusions have gained increasing popularity with comparative psychologists as a tool for investigating mechanisms of perception, including perceptual grouping.

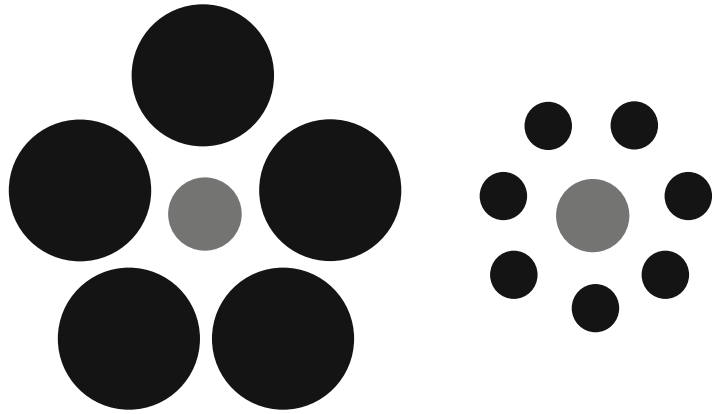
### Ebbinghaus Illusion Studies with Humans

The Ebbinghaus illusion is one of the most well-studied and robust size illusions in the human literature. In the Ebbinghaus illusion and related arrays such as the Delboeuf illusion, contrast effects lead to overestimates in size if a target



**Ebbinghaus Illusion,**

**Fig. 1** The Ebbinghaus illusion. The gray central target dot in the array at left (encircled by larger surrounding dots) is perceived as smaller than the identically sized gray central target dot in the array at right (encircled by smaller surrounding dots)



stimulus is contrasted with smaller stimuli and underestimates in size if a target stimulus is contrasted with larger stimuli. Because size illusions emerge when stimuli are perceived within the context of surrounding stimuli (as opposed to when perceived in isolation), susceptibility to the Ebbinghaus often is discussed in light of perceptual processing mechanisms. As global processors, humans readily perceive multiple elements within a visual scene as a cohesive group prior to assessment of each individual element (i.e., perceiving the whole before the parts). For the Ebbinghaus array, this would mean that the central target dot is assessed in light of the surrounding dots.

Susceptibility to the Ebbinghaus illusion can be weakened or even diminished if grouping of the central target and surrounding dots is disrupted. For example, when the gap between the central target dot and the surrounding dots is increased, the illusion is weakened in human adults. The Ebbinghaus illusion also can be eliminated or weakened if the surrounding dots are diminished in any way so that they are less salient (e.g., decreased brightness, altered shape). Environmental or cultural influences on perceptual processing mode also have been examined using the Ebbinghaus illusion. In a cross-cultural study with human adults, researchers documented a decrease in the strength of the illusion among Himba tribesmen who are known to perceptually prioritize local elements versus global features (de Fockert et al. 2007). Thus, there is a direct relationship between susceptibility to the

Ebbinghaus illusion and perceptual grouping of the individual elements that comprise the array.

### Comparative Ebbinghaus Illusion Studies

In contrast to humans, who show fairly consistent Ebbinghaus illusion effects, comparative studies yield greater variability in perception of this size illusion among nonhuman species. Evidence suggests that damselfish, dolphins, domestic 4-day-old chicks, and redbellied splitfin also are susceptible to the Ebbinghaus illusion (*Chromis chromis*: Fuss and Schluessel 2017; *Tursiops truncatus*: Murayama et al. 2012; *Gallus gallus domesticus*: Rosa Salva et al. 2013; *Xenotoca eiseni*: Sovrano et al. 2015). Alternatively, evidence of either a reversed illusion (in the opposite direction of humans) or no illusory susceptibility (perception of the central target dots as equal despite the differing sizes of surrounding dots) has been documented in dogs, gray bamboo sharks, pigeons, domestic chickens, and baboons (*Canis familiaris*: Byosiére et al. 2017; *Chiloscyllium griseum*: Fuss and Schluessel 2017; *Columba livia*: Nakamura et al. 2008; *Gallus gallus domesticus*: Nakamura et al. 2014; *Papio papio*: Parron and Fagot 2007). The majority of these studies report individual differences with variability in illusory perception across animals (or species) tested under identical circumstances (e.g., Fuss and Schluessel 2017: damselfish vs. gray bamboo sharks). These



irregularities may emerge as a by-product of species-level differences in visual pathways (see Rosa Salva et al. 2013, for a discussion on mammalian vs. avian visual pathways) and perceptual processing mechanisms as well as differences in the methodologies used to test for susceptibility of the Ebbinghaus illusion.

Fundamental differences in species' ability to perceptually group stimuli may partially account for the variance in comparative results. Unlike most humans who are known to display a global-to-local precedence as discussed above, some species instead display a local-to-global precedence. This means that baboons, pigeons, and chickens, all of which are known to display a local precedence, may perceive a weaker or an even reversed Ebbinghaus due to an orientation toward local elements prior to perceptual grouping. Alternatively, evidence for the Ebbinghaus illusion in a human-like direction was documented in redbill splitfins (Sovrano et al. 2015) and a dolphin (Murayama et al. 2012), both of which have demonstrated a global precedence. Nakamura et al. (2008, 2014) proposed that rather than experiencing the Ebbinghaus illusion as a contrast illusion in the typical human fashion, locally oriented species may instead perceive a reversed Ebbinghaus illusion due to assimilation effects. Assimilation occurs when two items close in proximity or size are integrated together, which typically leads to overestimation of size. Concerning the Ebbinghaus illusion, locally oriented species may assimilate the central target dot of the display with the nearby surrounding circles, creating a reversed effect of the illusion.

The procedures used to test for the Ebbinghaus illusion also may lead to variability in its perception across studies. Because animals cannot simply be instructed to respond to central target dot size only (i.e., "choose the larger central dot"), they must be trained to do so. This is particularly important for size illusions with multiple stimuli as the animal must respond to the target alone rather than erroneously responding to the surrounding dots or even total area of the target plus surrounding dots. In the case of the Ebbinghaus array, researchers may present differently colored target and surrounding dots or gradually fade in the surrounding dots to train

animals to respond to the target dot alone. Or, the surrounding dots may be present during training as they appear in testing but positioned at a distance from the target dot. While isolating the target dot is vital during training, this may inadvertently bias a subject to ignore the surrounding dots even during the critical test phase. This would lead to either no illusory experience (if outer dots are ignored altogether) or a reversed illusion (if outer dots are assimilated with the central target dot). Evidence of the Ebbinghaus illusion was documented in redbill splitfins, damselfish, chicks, and a dolphin, in studies that presented the surrounding stimuli used in the test phase as part of the training phases (Murayama et al. 2012; Rosa Salva et al. 2013; Sovrano et al. 2015). In contrast to this, a gradual exposure technique in which the surrounding dots were gradually introduced led to either no illusion in pigeons and domestic chickens or a reversed illusion in baboons (Nakamura et al. 2008, 2014; Parron and Fagot 2007). A particularly interesting avenue for future research would be to use multiple techniques for training within the same subjects to isolate the role of methodology in illusory perception.

The method by which an animal makes a choice among stimuli in these tasks may impact the strength and direction of the Ebbinghaus illusion. As discussed by Sovrano et al. (2015), chickens and pigeons indicated their choice between target dots via pecks to the desired stimulus in Nakamura et al. (2008, 2014) (e.g., versus using a joystick-controlled cursor or touch screen). Pecking may shift focus to the local elements of the stimuli as it necessitates a closer viewing angle of the illusory arrays. As demonstrated in the human literature, participants perceived a reversed Ebbinghaus effect when viewing the stimuli from a close perspective (e.g., Oyama 1960). To control for this potential confound, Rosa Salva et al. (2013) introduced an observational-learning technique with 4-day-old chicks, in which these animals approached the stimuli from a distance to facilitate a further vantage point which may have aided the perceptual grouping of stimuli and subsequent perception of the Ebbinghaus illusion. Thus, differences in training, choice modality, and stimuli design

likely play an important role in the emergence and strength of visual illusions.

## Summary

The role of perceptual processing mode (grouping mechanisms), experimental procedures (training techniques, choice modality, stimuli design), and species' unique evolutionary histories all play a vital role in the perception of the Ebbinghaus illusion. A comparative approach has provided interesting insights about the nature of this illusion as it emerges in different species. Experimental work with more species and individuals across the lifespan will continue to shape our understanding of the mechanisms governing both perceptions and misperceptions of visual stimuli.

## Cross-References

- [Computerized Testing Paradigm in Primates](#)
- [Corridor Illusion](#)
- [Ebbinghaus](#)
- [Pigeon \(\*Columbidae\*\)](#)
- [Ponzo Illusion](#)
- [Primate Cognition](#)
- [Size Illusion](#)
- [Visual Perception](#)

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## Ebbinghaus-Titchener Illusion

- [Ebbinghaus Illusion](#)

## Ecdysis

- [Molting](#)

## Echidna

- [Monotreme Sensory Systems](#)

## Echolocation

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## Synonyms

- [Biosonar](#)

Introduction

Echolocation (biosonar) is a specialized behavior which allows animals to use echoes from self-produced sounds to assess their environment for the purposes of orientation and foraging.

The term echolocation was coined by Donald R. Griffin (1944) to describe how bats orient using the differences between acoustic signals they produce and the echoes of these signals they receive from objects in their paths. Echolocation resolved what had been known as “Spallanzani’s bat problem” (the fact that bats could fly around a completely dark room but owls could not), because it described how bats could ‘see with their ears’ (Griffin 1958; Au 1993). A polyphyletic group of species uses echolocation (Table 1), including most species of bats, all toothed whales (e.g., dolphins), some shrews and tenrecs, some birds, and even some blind humans (Fenton et al. 2017; Surlykke et al. 2014; Thomas et al. 2004). Although animals such as tiger moths, seals, and dormice have been proposed as echolocators, we lack convincing evidence that this is correct. Many animals vocalize as they move but by itself, this behavior does not demonstrate echolocation.

Most of what we know about echolocation comes from studies on captive bats and toothed

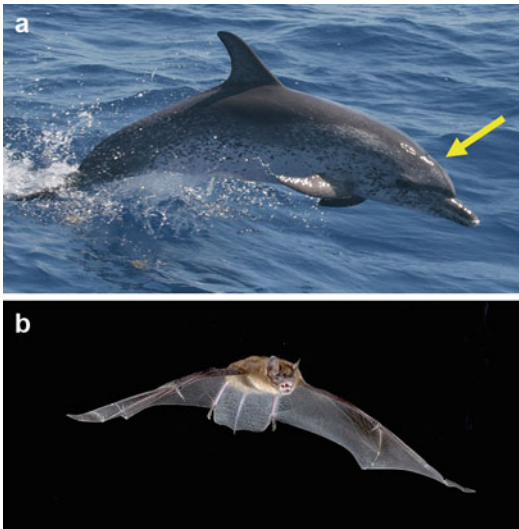
whales (Fig. 1). Experimental protocols generally involve observing animals deprived of other cues (visual, olfactory, tactile, passive acoustic) successfully orienting around obstacles or correctly identifying objects (e.g., Au 1993; Buchler 1976; Griffin 1958; Kellogg 1961). Captive studies are increasingly supplemented by studies of free-ranging animals (e.g., Surlykke and Kalko 2008; Simard et al. 2010). Several recently published reviews provide a great deal of information about echolocation (e.g., Fenton et al. 2017; Surlykke et al. 2014). There are interesting levels of convergence in the range of behaviors associated with echolocation (e.g., Au and Simmons 2007; Teeling 2009).

Signal Production

Echolocation signals are usually produced in the larynx or mouth (Table 1). Among the bats known as flying foxes (family Pteropodidae), a few species echolocate with tongue clicks, as do echolocating blind humans (Fenton and Simmons 2015). Laryngeally echolocating bats, as the name implies, produce their echolocation calls in their larynges (Veselka et al. 2010; Yovel et al. 2011). Echolocating birds produce their clicks in the syrinx (Suthers and Hector 1982, 1985), the

**Echolocation, Table 1** Echolocating animals (Au 1993; Gould 1965; Gould et al. 1964; Griffin 1958; Kellogg 1961; Griffin 1958)

| Taxa                                   | Total number of species | Number of echolocating species | Type of signal    | Source of production |
|----------------------------------------|-------------------------|--------------------------------|-------------------|----------------------|
| Class Aves, Order Caprimulgiformes     | ~ 120                   |                                |                   |                      |
| <i>Steatornis caripensis</i> (Oilbird) | 1                       | 1                              | Clicks            | Syrinx               |
| Class Aves, Order Apodidae             | ~ 93                    |                                |                   |                      |
| <i>Aerodramus spp</i>                  | ~ 35                    | ~ 10                           | Clicks            | Syrinx               |
| Class Mammalia, Order Eulipotyphla     | ~ 360                   |                                |                   |                      |
| <i>Sorex spp.</i>                      | ~ 142                   | ~ 5                            | Clicks            | Unknown              |
| <i>Blarina spp.</i>                    | 4                       | 1                              | Clicks            | Unknown              |
| Class Mammalia, Order Cetacea          | ~ 89                    |                                |                   |                      |
| Suborder Odontoceti (toothed whales)   | ~ 75                    | ~ 75                           | Clicks, FM sweeps | Phonic lips          |
| Class Mammalia, Order Chiroptera       | ~ 1260                  |                                |                   |                      |
| Family Pteropodidae                    | ~ 170                   | ~ 10                           | Clicks            | Mouth                |
| Other Chiropteran families             | ~ 1090                  | ~ 1090                         | Clicks, tones     | Larynx               |
| Class Mammalia, Order Primates         | ~ 256                   |                                |                   |                      |
| <i>Homo sapiens</i>                    | 1                       | Some individuals               | Clicks            | Mouth                |



**Echolocation, Fig. 1** (a) An Atlantic spotted dolphin (*Stenella frontalis*), an example of a toothed whale with arrow indicating the location of the melon and nasal passages. (b) A big brown bat (*Eptesicus fuscus*). Photos by Peter Simard, taken under NMFS research permit no. 10038 (a) and M. Brock Fenton (b)

vocal organ of birds. However, toothed whales produce echolocation signals in their nasal passages, specifically with a pair of phonic lips (often referred to as the Monkey Lips Dorsal Bursae (MLDB) complexes (Cranford et al. 1997)). The sperm whale (*Physeter macrocephalus*) has a modified but similar sound production anatomy (Cranford et al. 1996). While the sound production mechanism is well understood in the toothed whales, bats, birds, and humans, there are few data about production of echolocation sounds by shrews and tenrecs.

In air, echolocation signals are broadcast through the open mouth (birds, shrews, some bats) or nostrils (other bats). In water, the similar acoustic impedance between environment and biological tissues has led to the evolution of a series of reflective structures (air sinuses and a concave frontal region of the skull). The directionalization of echolocation signals also is facilitated by the melon (Fig. 1), a fatty structure located anterior to the phonic lips channels from which sounds move forward and away from the animal (Au 1993).

## Signal Types

### Clicks

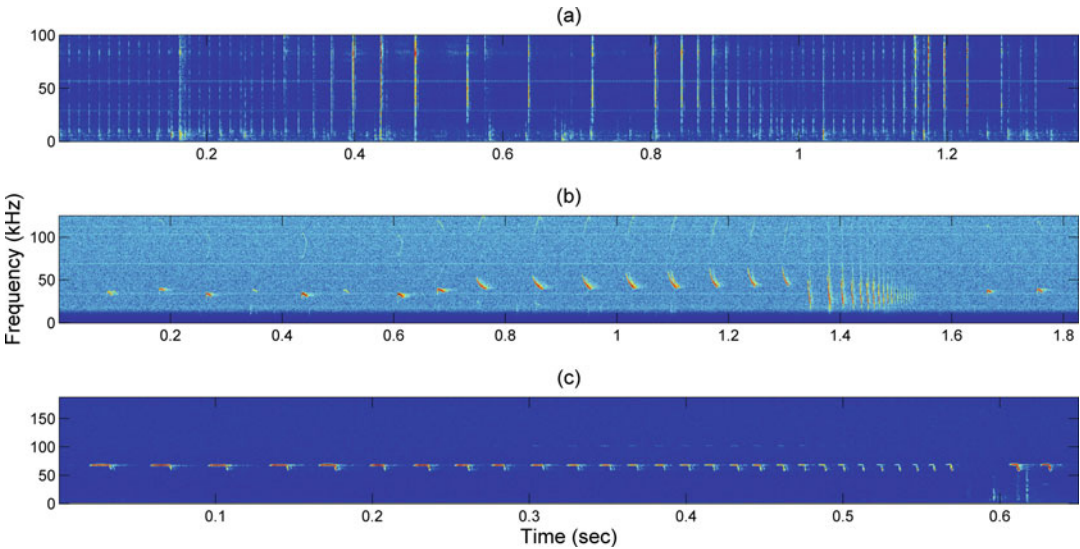
Most animals echolocate with clicks (Table 1) which provide detailed information about objects in the echolocators' paths (Bucher and Mitz 1980). Clicks are short in duration (e.g., 40–70  $\mu$ sec for bottlenose dolphins, *Tursiops truncatus* (Au 1993)), broadband (Figs. 2a and b, 3a and b, and 4d and e), and often cover a range of frequencies. In water, sounds travel about five times faster than they do in air, therefore all toothed whales use short duration signals to avoid pulse overlap (Au and Simmons 2007).

### Tonal Signals

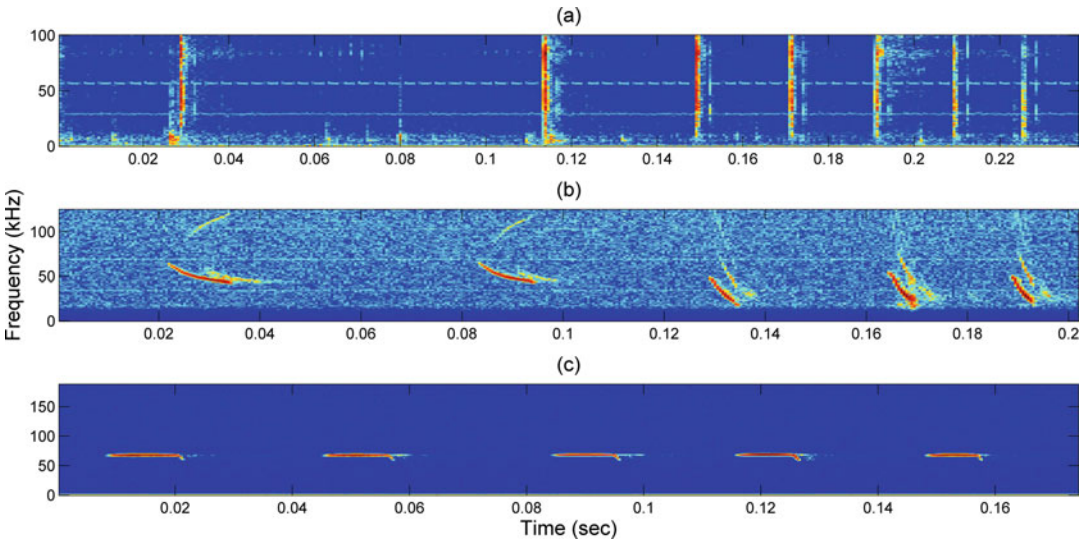
Unlike clicks, tonal signals (Figs. 2c, 3c, and 4f) show structured changes in frequency over time. Tonal signals are commonly used by most laryngeally echolocating bats (Schnitzler and Kalko 2001). They range in duration from  $\sim$ 1 ms to  $>50$  ms. The tonal signals are usually frequency modulated (FM) signals and, in bandwidth, can be broad (tens of kHz) to narrowband (a few kHz) to constant frequency (CF – by definition, 0 kHz bandwidth). Most bats use search phase echolocation calls that are some combination of broad and narrowband components (Fenton and Simmons 2015). Some species in four families (Rhinolophidae – the horseshoe bats, Hipposideridae – the old world leaf-nosed bats, Rhinonycteridae – the trident bats, and a few Mormoopidae – the mustached bats) use signals dominated by CF components.

## Frequency

Among echolocators, peak frequencies (frequencies with maximum amplitude) of signals range from  $<5$  kHz to over 100 kHz (Fig. 4d–f). Higher frequency signals (shorter wavelengths) provide more details about targets (Fenton and Simmons 2015). Many species of laryngeally echolocating bats regularly add harmonics (overtones) to their signals (Bates and Simmons 2011). Although it is common to read about “ultrasonic” echolocation, ultrasonic is not synonymous



**Echolocation, Fig. 2** Spectrograms of (a) bottlenose dolphin echolocation (*Tursiops truncatus*, 1024 point resolution, sample rate 200 kHz), (b) black mastiff bat echolocation (*Molossus ater*, 1024 point resolution, sample rate 250 kHz, 15 kHz high-pass filter), (c) Mesoamerican moustached bat echolocation (*Pteronotus mesoamericanus*, 1024 point resolution, sample rate 375 kHz). Sound files from Natalija Lace (a) and M. Brock Fenton (b, c)

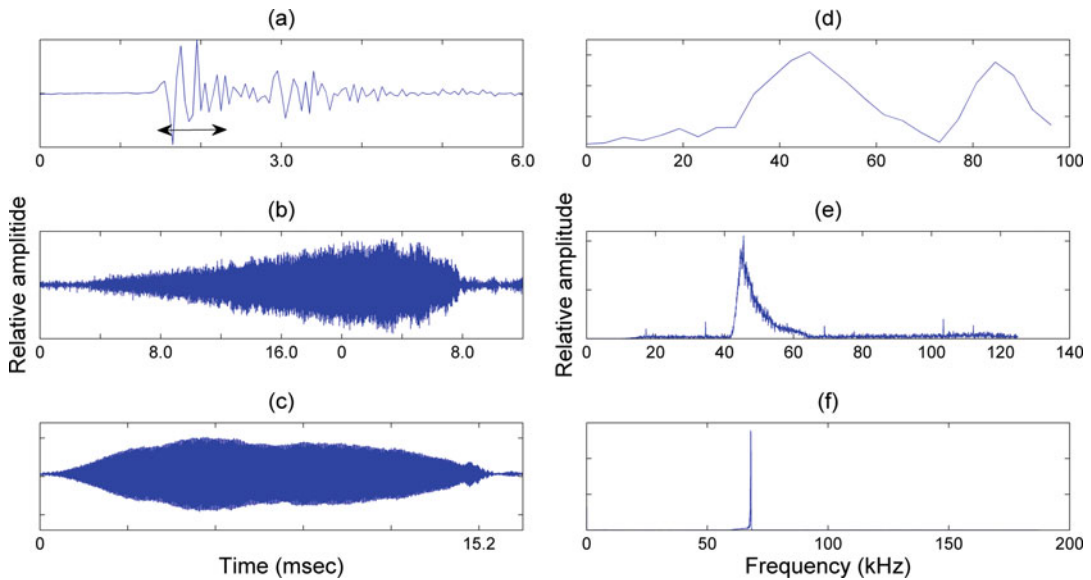


**Echolocation, Fig. 3** Close-up spectrograms of (a) bottlenose dolphin echolocation (*Tursiops truncatus*, 512 point resolution, sample rate 200 kHz), (b) black mastiff bat echolocation (*Molossus ater*, 512 point resolution, sample rate 250 kHz, 15 kHz high-pass filter), (c) Mesoamerican moustached bat echolocation (*Pteronotus mesoamericanus*, 512 point resolution, sample rate 375 kHz). Sound files from Natalija Lace (a) and M. Brock Fenton (b, c)

with echolocation. Ultrasonic refers to sounds above the range of human hearing, theoretically those above 20 kHz (20 kilocycles per second)

although most adult humans cannot hear sounds above 10 kHz. The difficulty with the human-based definition is that what is ultrasonic to one





**Echolocation, Fig. 4** Waveforms (sound pressure) of single echolocation signals from (a) bottlenose dolphin (*Tursiops truncatus*, note that signal itself is indicated by arrow, and waveforms after are from echo reverberation), (b) black mastiff bat (*Molossus ater*), (c) Mesoamerican moustached bat (*Pteronotus mesoamericanus*). Energy spectra of single echolocation signals from (a) bottlenose

dolphin (note that plot is only of echolocation signal itself as indicated by arrow in (a), and that dolphin echolocation commonly has energy above 100 kHz (Au 1993)), (b) black mastiff bat, (c) Mesoamerican moustached bat. Sound files from Natalija Lace (a, d) and M. Brock Fenton (b, c, e, f)

individual might be quite audible to another. The bats that Spallanzani and later Griffin studied (Griffin 1958) used ultrasonic signals, accounting for their silent (to humans) flight. Many other bats use echolocation signals entirely audible to most humans. These signals have most acoustic energy down to 8 kHz. Many toothed whales have echolocation pulses that are largely ultrasonic; however, broadband echolocation signals often have considerable energy at frequencies audible to humans. At the other end of the spectrum are bats whose echolocation calls are dominated by energy at 212 kHz (*Cloeotis percivali*), and echolocation pulses of the porpoises and *Cephalorhynchus* dolphins whose echolocation clicks only contain energy above 100 kHz. However, high frequency sound by itself does not signify echolocation.

### Patterns of Pulse Production

Echolocating animals typically produce trains of pulses as they move through their environment

(Fig. 2) and adjust the timing (cadence) of the pulses in response to the distance between themselves and the target(s). Most echolocating animals separate the outgoing pulse and returning echo(es) in time in order to avoid overlap between the high-amplitude outgoing pulses and the low-amplitude incoming echoes. This results in the decreasing inter-pulse interval (and often pulse durations) observed in bats and toothed whales as they approach a target (Au 1993; Griffin et al. 1960). In engineering terms, most echolocators are low duty cycle because the signal is on for only a brief period in any time frame (short signals separated by long periods of silence; Fig. 2a and b). A few bats separate pulse and echo in frequency, using Doppler shifted echoes to exploit changes in frequency associated with relative movements of echolocator and prey (Schuller and Pollak 1976). These are high duty cycle echolocators because signals are on for longer periods of time in any time frame (Fig. 2c).

High duty cycle echolocators produce long signals separated by short intervals of silence.



The only high duty cycle echolocators described to date are species in the bat families Rhinolophidae, Hipposideridae, Rhinonycteridae, and a few species in the Mormoopidae. This approach to echolocation is associated with Doppler shift compensation behavior and distinctive echolocation calls. These bats also have an “acoustic fovea” in their cochlea (inner ears); consequently, their hearing is most sensitive at the frequencies dominated by Doppler shifted echoes (Schuller and Pollak 1976).

Bats adjust the durations and frequencies of their echolocation signals (e.g., Fig. 4). Griffin et al. (1960) described the feeding buzzes of echolocating closing with flying insect prey. In these situations, interpulse intervals range from around 200 ms when bats search for targets to 5 ms as they close with prey. Toothed whales can also adjust the frequency content of their echolocation signals (e.g., Houser et al. 2005).

### Pulse Production and Echo Reception

In terrestrial echolocators, echoes arrive at the auditory bullae via the ears (in mammals the pinnae). The faces of laryngeally echolocating bats are often specialized for sound transmission and/or echo reception (Fig. 4). Facial features such as noseleaves may affect the structure of the outgoing signal or the cone of transmission associated with the calls (e.g., Zhang and Mueller 2006). Echolocating toothed whales receive echoes through their lower mandibles which are filled with lipids like those found in the melons. In this way, echoes are transmitted to the auditory bullae.

The data used in echolocation are the differences between what the animal says (outgoing signal) and what it hears (received echo). These differences include information in time and frequency domains. The timing of the return echo encodes information on the distance from the object (i.e., the two-way travel time of sound), while the frequency spectra of the echo contains information on the composition of the object. For echolocation to work, the outgoing signal must be registered in the animal’s brain for future comparison with returning echo(es) (Au 1993).

### Advantages and Disadvantages of Echolocation

Echolocation allows animals to orient themselves and to detect objects when light is unpredictable or absent. This is obviously advantageous to any organisms with this capacity. For example, echolocation gives oilbirds and cave swiftlets access to underground nest sites (Brinklov et al. 2013). Many species of laryngeally echolocating bats not only gain access to dark roosts but also can hunt prey in situations where vision is unreliable. Furthermore, the echolocation calls of some bats echo strongly from some plants that bats pollinate (e.g., von Helversen and von Helversen 1999). Much of the aquatic environment has reduced light levels, and many species of toothed whales forage at depths below the maximum light penetration. However, echolocation can be costly. Both oilbirds and swiftlets stop echolocating when they emerge into lighted areas. In bats, evolutionary development evidence suggested that species of Pteropodidae lost an earlier capacity for laryngeal echolocation (Wang et al. 2017), implying that echolocation was an ancestral trait. This suggests a cost associated with echolocation. The question of whether echolocation or flight was ancestral in bats remains a point of active discussion (e.g., Gunnell and Simmons 2012; Simmons et al. 2008; Veselka et al. 2010).

Information leakage likely is a primary disadvantage of echolocation. Biologists use the echolocation signals of bats and toothed whales to monitor patterns of activity and distribution. In air and in water, some potential prey for bats and toothed whales have ears that detect echolocation signals and allow the prey to avoid echolocating predators. For example, mammal-eating “transient” killer whales (*Orcinus orca*) use echolocation sparingly in comparison to fish-eating “resident” communities of killer whales, which is thought to be a behavioral adaptation to the superior high-frequency hearing of the mammal prey (Barrett-Lennard et al. 1996). Eavesdropping on the echolocation of foraging echolocators could also be an effective way for animals to detect and exploit ephemeral concentrations of prey (e.g., Wang et al. 2016). This underscores

the reality that one animal's echolocation signals can and do serve in communication (e.g., Dechmann et al. 2009) and contribute to inter-individual learning (e.g., Page and Ryan 2006).

## Evolution of Echolocation

Arguably, echolocation allowed the ancestors of bats and toothed whales to detect and track prey in situations where vision was not dependable. In either case, echolocation opened a new adaptive zone for these animals. The ability to echolocate has evolved repeatedly among birds (two orders) and among mammals (at least five orders). Echolocation can permit access to food sources and shelters not readily accessible to animals mainly restricted to vision. Echolocation by blind people indicates that echolocation can develop facultatively. This also is suggested by the appearance of some level of echolocation in some pteropodid bats (Boonman et al. 2014).

Among living pteropodids, echolocation seems most developed in some species of *Rousettus*, while species in other genera show more rudimentary echolocation (Boonman et al. 2014). It is obvious that in *Rousettus aegyptiacus* at least, echolocation with tongue clicks is sophisticated and well developed. High duty cycle echolocation has evolved independently in two lineages of bats (Teeling 2009). These bats are very effective at detecting fluttering targets, perhaps increasing access to flying prey in cluttered habitats. Toothed whales are thought to be a monophyletic group, suggesting that echolocation evolved only once in this group, approximately 35 million years ago (Steeman et al. 2009).

As noted above, many species that are potential prey for echolocators have ears tuned to the frequencies predators use in echolocation. In this realm, we know most about the interactions between bats and their insect prey (e.g., ter Hofstede and Ratcliffe 2016; Cocoran et al. 2009; Roeder 1967). However, it is clear that marine mammals (e.g., seals) can hear the echolocation of their killer whale predators (Barrett-Lennard et al., 1996) and the same abilities are

shared by at least some fish (e.g., Mann et al. 1997).

## Conclusion

As Donald R. Griffin noted, echolocation is one of the most significant modern discoveries about animal behavior. Echolocation has allowed certain animals to occupy spatial and temporal niches unavailable to those without the ability, and the sophisticated echolocation abilities of the bats and toothed whales has likely led to the ubiquity and diversification of these groups.

## Cross-References

- ▶ [Auditory Signals](#)
- ▶ [Cetacean Navigation](#)
- ▶ [Cetacean Sensory Systems](#)
- ▶ [Megachiroptera Sensory Systems](#)
- ▶ [Microchiroptera Cognition](#)
- ▶ [Microchiroptera Sensory Systems](#)
- ▶ [Sound Spectrogram](#)

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## Eclosion

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## Synonyms

[Hatching](#); [Spawning](#)

## Definition

Eclosion is the act of emerging from the egg.

## Introduction

Oviparity is by far the widest way for an individual to brood in animal kingdom; with some exceptions, invertebrates, lower vertebrates (amphibians, reptiles, fish), and birds are oviparous. From a cognitive standpoint, embryos in eggs are generally much more exposed to external sensory information than in viviparous species, the embryos of which receive buffered inputs through their mother. To adequately respond to environmental pressure at hatching (relevant abiotic conditions, finding food, and avoiding predators), siblings of oviparous species have three sources of information: (1) from their mother (from egg formation to incubation and hatching),

(2) from their own prenatal sensory experience, and (3) from their own perception of surroundings at eclosion. In addition, direct parental guidance in the peri-hatching period would enhance the development of cognitive skills in numerous oviparous species.

## Parent Effects on Hatchlings' Behavior

Parents have direct influence on neonates' cognitive architecture through genes. There is an extensive literature showing that behavioral response of the young to external stimuli depends on the species history. Some sensory inputs make sense to hatchlings, without previous sensorimotor experience; this can be considered, in cognitive ethology, as an “innate representation.” Sea turtles follow visual signals for sea-finding at hatching, ducklings will recognize mother call, even when devocalized and coming from eggs kept in artificial incubators (Gottlieb 1980). Influences of parents are also epigenetic; they can choose and arrange the laying site in response to their own knowledge of the environment. In many species, it is likely that location of egg mass or building-nest may be chosen carefully in safe sites (e.g., in Siberian jay, Eggers et al. 2006) where food is available for neonates and that adaptive social interactions are possible. These processes occur basically in all oviparous species in which the females lay their eggs in the site where they hatched themselves (eel, salmon, turtles, etc.) or resembling those they come from (e.g., ant queens with odor cues). Adaptive behaviors of hatchlings can also be influenced by information provided by mothers via the hormones deposited in the egg. For example, stressed mother of some birds and fish can produce yolk with modified concentrations of sex steroid hormones and cortocosteroids (e.g., in birds, for a review see Henriksen et al. 2011). These compounds will alter learning/memory skills of hatchlings and potentially their behavioral profiles. These parental investments to siblings are part of “parental effects” together with “parental care” *per se*. These post-mating parental cares are present from insects to birds.

Direct parental influence on embryo's perception of environment may also occur in case of egg attendance, nest building or burrowing, egg brooding, or ovoviviparity (see Royle et al. 2012, chapters 1, 4, and 5 for reviews).

### Embryonic Experience, Hatchlings Behavior and Cognition

As embryos develop in their egg, they get more and more information from their surrounding environment whatever the opacity of the egg capsule. Indeed, in vertebrates and in some invertebrates, the onset of sensory functioning follows an invariant sequence, the visual system being the last to develop. Given the relatively buffered nature of the prenatal environment, it is likely that the developing embryo is primarily exposed to unimodal stimulation and has relatively fewer opportunities to experience multimodal stimulation. Several studies showed that embryos react to these stimuli by reducing or increasing their heart-rate or ventilation. Such exposure can have profound effects on behaviors at hatching, in the feeding, social or defensive realms. Direct embryonic exposure to a chemosensory stimulus, or through the maternal diet, alters subsequent chemosensory preferences in favor of the familiar stimulus after hatching (e.g., in mite: Quesada and Schausberger 2012). When eggs of ringed salamanders (*Ambystoma annulatum*) were exposed to chemical cues from predators, post-hatching larvae showed reduced activity and greater shelter-seeking behavior (Mathis et al. 2008). Prenatal auditory learning also has been reported in birds. As mentioned before, ducklings will prefer their mother's calls when they have heard them as embryos; this learning will drive the duck's social preferences. In the superb fairy wren (*Malarus cyaneus*), embryos will learn the incubation call produced by their mother. After hatching this begging call will serve for nestling discrimination by the female and hence detection of intruder nestling, in this species parasitized by cuckoos (Colombelli-Negrel et al. 2012). In the cuttlefish, *Sepia officinalis*, juveniles that have

been showed crabs before hatching will alter their innate shrimp preference for a crab preference (Darmaillacq et al. 2008); this is the only evidence of prenatal visual learning. Besides exposure learning, embryos are also capable of other simple learning like habituation or association learning. Fairy wren embryos are able to learn to discriminate between the vocalizations of conspecifics and to habituate to a familiar call (Colombelli-Negrel et al. 2014). Wood frog embryos can learn to recognize unfamiliar predators by associating the odor of the predator with a conspecific alarm cue (Mathis et al. 2008). This recognition of the familiar stimulus could lead to a number of behavioral adaptations, such as modifications of habitat choice at settlement or of prey preference depending on the abundance of food. These factors could affect development and behavior in postembryonic individuals, all of which may increase their chance of survival.

In several oviparous species, from mollusks to birds, the peri-hatching period is a sensitive window during which individuals can learn and store a great amount of information that will serve in subsequent behaviors. Studies of these widespread and trans-specific processes have been one of the roots of modern ethology through the detailed description of imprinting in precocial birds and basic questionings about its biological significance (Immelmann 1975). Interestingly, associative structures of the brain are particularly immature at hatching. Since long-term memory is based on the capacity of the nervous system to be plastic, it is likely that neural plasticity of developing brain in hatchlings could allow easier recording and storage of information.

### Is Eclosion a Cognitive Disruption?

At the behavioral level, the question of continuity-discontinuity of hatching has been extensively debated in Ethology, at least in bird models. Factually, in most oviparous species, emerging from an egg corresponds to the appearance of specific motor patterns (which are more or less transformations of embryonic spontaneous



motility). From a sensory standpoint, hatching potentially provides the young animal with a big flow of new information (i.e., visual information in birds and many amphibians and fishes), potential disappearance of chemical inputs from the embryo's perivitelline fluid/yolk, and substantial changes in auditory and proprioceptive information. This is especially important in precocious species, the sensory systems of which are mature very early in life. However, both pre- and post-hatching information from the environment will be combined and processed by hatchlings to orient their early behaviors: respond to potential threats, recognize available food items, and interact with social partners. As a consequence, even if eclosion implies a severe sensory-motor discontinuity in sensory ecology of the organism, embryonic learning and memory of egg-surroundings will familiarize and prepare hatchlings to their post-embryonic environment. Cognition in embryo will help the newly hatched organisms to adaptively respond to their behavioral needs. To conclude, perinatal memory, if any, enables the young to mentally bridge the prenatal and the postnatal environments and hence ensures a perceptive continuum through eclosion.

## Cross-References

- [Embryo](#)
- [Imprinting](#)
- [Incubation](#)
- [Innate Behaviors](#)
- [Konrad Lorenz](#)
- [Molting](#)
- [Nest Construction](#)
- [Ontogeny](#)
- [Precocial](#)

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## Ecological Index

- [Indicator Species](#)

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## Ecological Psychology

- [Plantae](#)
- [Social Affordance](#)

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## Ecological Stimuli

- [Naturalistic Stimuli](#)



Ecology

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Definition

|                         |                                                                                                                                                                                                                                                                                      |
|-------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Adaptive                | A trait that increases fitness is adaptive.                                                                                                                                                                                                                                          |
| Behavioral machinery    | Causes the immediate behavior. Typically the central nervous system (brain) reacting to specific stimuli by producing the observed behavior.                                                                                                                                         |
| Ecology                 | The science studying the interactions between and among organisms and their environment.                                                                                                                                                                                             |
| Environment             | All biotic and abiotic factors surrounding an organism, including individuals of the same species (social environment), other species, habitat, and weather.                                                                                                                         |
| Evolution               | Change of the heritable characteristics of a population or species over time.                                                                                                                                                                                                        |
| Fitness (evolutionary)  | This is a relative measure of reproductive success. Individuals with a high reproductive success have a higher fitness than individuals with a low reproductive success. If this difference in reproductive success is due to genetic differences, then this will lead to evolution. |
| Function (evolutionary) | Describes how a trait leads to an increase of fitness via natural or sexual selection.                                                                                                                                                                                               |
| Ontogeny                | Individual development from the fertilized egg over the                                                                                                                                                                                                                              |

|           |                                                                                                         |
|-----------|---------------------------------------------------------------------------------------------------------|
|           | juvenile stage, adolescence, and adulthood until senescence and death.                                  |
| Phylogeny | Evolutionary history, typically shown as a tree of life.                                                |
| Proximate | The mechanisms that cause a trait such as behavior. It refers to ontogeny and the behavioral machinery. |
| Ultimate  | Refers to the evolution of a trait, i.e., how and why it evolved (function and phylogeny).              |

Introduction

Ecology is a relatively recent science in biology. The idea that everything in nature is connected with each other was first emphasized by the German naturalist Alexander von Humboldt, in his *Naturgemälde* from 1807, showing both the biotic and abiotic aspects of the South America volcano Chimborazo. Throughout his published books, von Humboldt emphasized the complexity of nature and that species can only be understood if one considers their natural environment with all possible interactions with other species and climate (von Humboldt 1845–1862). In 1842, the then 73-year-old von Humboldt met the 32 years young Charles Darwin in England. Unfortunately von Humboldt was talking so much that it was impossible for Darwin to explain him his ideas about evolution (Wulf 2016). Nevertheless, the work of von Humboldt significantly influenced Charles Darwin as he was developing the modern theory of evolution. But even though both scholars realized how important interactions of individuals with their environment were, it was only in 1866 when the German scientist Ernst Hackel (an admirer of both von Humboldt and Darwin) used the word *Oecologie* for the first time to name the science of the interactions among organisms and their environment (Hackel 1866). The word *Oecologie* comes from Greek οἶκος, “house”, or “environment”, and -λογία, “study of,” and is translated in English as ecology. Interestingly, Hackel also invented the terms ontogeny and phylogeny, which later became

very important in animal behavior, as outlined below.

Ecologists study the influence of the environment on the individual, but environment and ecology are not perfect synonyms. Ecology refers to interactions in the natural environment, but the environment can also be artificial. Thus, in biology one typically differentiates between field studies in natural environment and studies in the laboratory under artificial conditions. However, laboratory experiments can also be used in ecology to test the effect of specific aspects of the environment on a trait. In ecology, one differentiates between aspects of the nonliving or abiotic environment and aspects of the living or biotic environment. The soil and weather (temperature, rainfall, etc.) are typical factors of the abiotic environment and other plants and animals of the biotic environment. All these environmental factors can also influence behavior. For behavior, the social environment (part of the biotic environment) can be especially important, i.e., individuals of the same species that live together in the same group or the same area.

### The Four Questions of Tinbergen and Ecology

In the field of animal behavior, first studies were often done in zoos, then with free-ranging tame animals under seminatural conditions, for example, by Konrad Lorenz during the 1930s and 1940s. At the same time, his Dutch colleague Nikolaas Tinbergen, who together with Lorenz got the Noble Prize for medicine in 1973, studied animals in their natural environment, testing often experimentally the influence of specific stimuli of the environment on behavior. Extensive field studies started in the 1950s and 1960s, leading in the 1970s to the establishment of behavioral ecology, for example, by E.O. Wilson (1975), and many field studies continue today (Schradin and Hayes 2017).

While the field of behavioral ecology always had a strong focus on the evolutionary function of behavior but neglected the proximate mechanisms of behavior, ecology plays an important role both

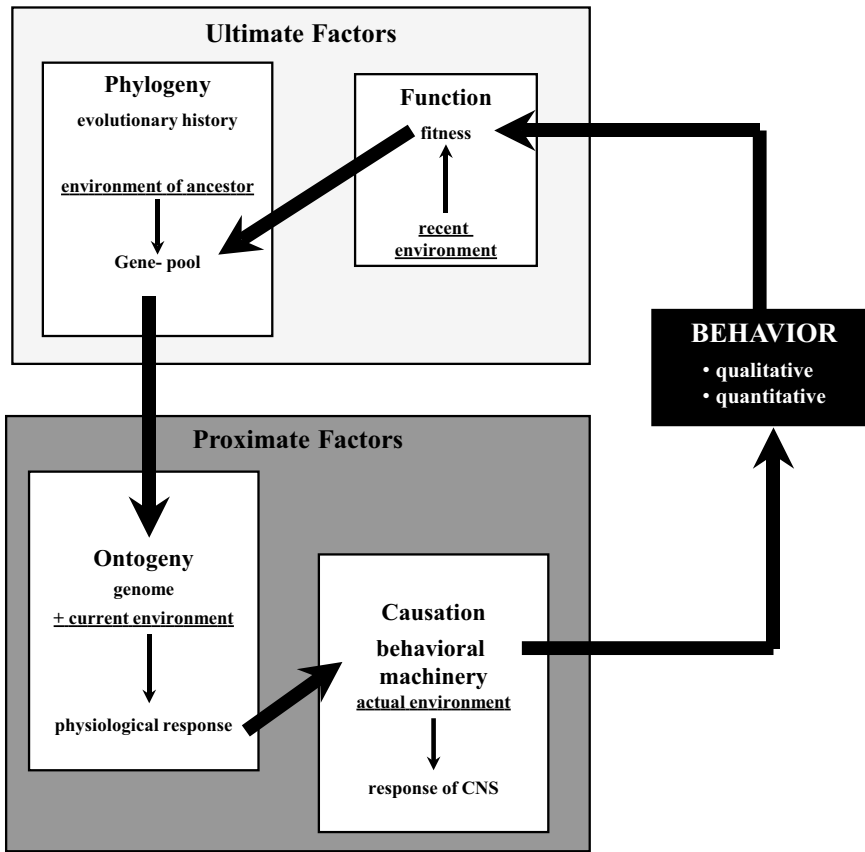
for ultimate function and proximate mechanisms. This was already made clear by Tinbergen, who formulated in 1963 four questions that form the basis of research in animal behavior (Tinbergen 1963) (Fig. 1). After Tinbergen, to fully understand behavior, one has to address questions about (1) ontogeny, the question about individual development; (2) causation, the question about the behavioral machinery causing behavior, i.e., normally the central nervous system; (3) function, the question about the fitness consequences of behavior; and (4) phylogeny, the question about the evolutionary history of behavior.

The questions about ontogeny and the behavioral machinery of behavior refer to the proximate mechanisms of behavior, while the questions about the phylogeny and function address the ultimate consequences of behavior. Importantly, the environment does not only influence the ultimate function of behavior but also its proximate mechanisms (Fig. 1). As such, the question of how ecology influences behavior and cognition can best be addressed by asking the four questions of Tinbergen and what the role of ecology is in finding answers to these questions. Hereby it is useful to first differentiate the influence of abiotic and biotic factors. Especially for social behavior, one also has to take the social environment into consideration. Addressing in this way the role of ecology for all four questions helps to understand the interplay of these factors and leads to the insight from von Humboldt that everything in nature is connected with each other.

### Ecology and Function

Behavior represents an evolved trait which has a heritable and genetic basis. For example, the deer mouse *Peromyscus maniculatus* is closely related to the oldfield mouse *Peromyscus polionotus*, but both species differ in social behavior. While males of the deer mouse mate polygynously with several females, males of the oldfield mouse live monogamously. Only males of the monogamous oldfield mouse but not of the polygynous deer mouse show high levels of paternal care. These differences in paternal care are heritable, and 12 regions in the

# Integrative Understanding of Behavior



**Ecology, Fig. 1** Integration of the four questions of Tinbergen to come to a comprehensive understanding of behavior and the role of the environment. We describe and measure behavior (black box on the right). Behavior is caused by the CNS (central nervous system = behavioral machinery) which developed during ontogeny in an individual specific manner. The behavior itself has fitness consequences (function) which changes the gene pool (genes and gene controlling DNA that regulates gene expression) of future generations (phylogeny). The gene pool determines potential genotypes of individuals. The

genotype and the environment determine the development of an individual (ontogeny) including its behavioral machinery. The environment (underlined) plays a critical role for all four questions: stimuli of the actual environment cause the behavioral machinery to express the observed behavior (causation); its fitness consequences depend on the recent environment in which the behavior is shown (function); it evolved in the environment of the ancestor (phylogeny); and it develops as gene-environment interaction (ontogeny).

genome have been identified that affect paternal care (Bendesky et al. 2017). Whether these heritable differences are due to the species having different genes, or whether there are species differences in gene activation, is unknown. Therefore, a modern definition of genetic differences includes all heritable differences, whether these are due to different genes or differences in gene activation. The burrowing behavior of the two species also differs,

leading to different forms of tunnel systems, and these differences are also genetically determined (Hu and Hoekstra 2017). Thus, behavior including social behavior has a genetic basis and represents traits evolved by natural selection that changes the gene pool of populations.

Whether a behavioral trait spreads in a population depends on its fitness consequences. Individuals that have a higher reproductive success have

a higher evolutionary fitness. If their reproductive success increases due to a specific behavior, then the genetic basis of this behavior will spread in the population. In the last decades, the main question in behavioral ecology was: what are the fitness consequences of a specific behavior?

The fitness consequences of a trait depend on the environment! For example, in many small mammals, basking in the sun to passively warm up is an important behavioral strategy to reduce energy consumption, which is believed to have fitness benefits (Scantlebury et al. 2010). African striped mice (*Rhabdomys pumilio*) live in the Succulent Karoo semidesert of South Africa, where food availability is low during the dry season. Accordingly, basking is especially important in the dry season and leads to reduced energy consumption. It is like the sun is switching striped mouse activity on in the morning: as soon as the sun illuminates a shrub in which a group of striped mice is nesting, the striped mice become active and leave their nest to start sun basking. Striped mice with a nest which are illuminated 3 min later than another nests because of the shadow of a mountain will also become active 3 min later (Schradin et al. 2007). And as sunrise starts later during the course of the year (from summer to winter), the mice also start their activity a few minutes later from week to week. This is an example of how the abiotic environment can influence adaptive behavior.

Important aspects of the biotic environment that influence behavior are food and predators, both also being factors that influence population dynamics (predators: top-down; food: bottom-up regulation). Animals behave adaptively by foraging in a way that optimizes energy intake per time and simultaneously reducing the risk of death by predation. Thus, the distribution and abundance of both food and predators significantly influence animal behavior. Optimal foraging theory has been very successful in predicting how animals maximize energy intake per unit of time. How animals can remember their variable environment was experimentally tested using artificial flowers providing food to rufous hummingbirds (*Selasphorus rufus*), with the flowers being either refilled every 10 or every 20 min. This resembles natural

differences between plant species in nectar production. The hummingbirds were able to recognize the different artificial flowers, and they remembered where the flowers were and which flowers they had last drunk from (Henderson et al. 2006). Another example is provided by stickleback, small fish, which prefer areas with many daphnia, their own prey, as long as the areas are safe. But when one presents them the silhouette of a kingfisher, a stickleback predator, they prefer areas with few daphnia, probably because there they can increase their vigilance against their potential predator (Milinski and Heller 1978). In sum, animals evolved behavioral strategies to maximizing their individual fitness given the current ecological situation such as the limited food supply and the presence of predators and conspecifics (mates and competitors).

For most species, one of the most important aspects of their environment concerns their social environment. This consists of all conspecifics they encounter, which means potential mates, potential competitors such as same-sex neighbors, and their own offspring. Thus, a social environment does not only exist for group-living species but also for solitary species which have to find a mate and defend a territory. Defended territories contain important resources for survival and reproduction, which is why territories are aggressively defended against conspecifics. Territorial neighbors often recognize each other and show reduced aggression toward each other than to unfamiliar conspecifics. Thus, neighbors respect each other as “dear enemies” and as such each other’s territories, while floating and dispersing individuals which have no territories are heavily attacked (Temeles 1994). However, sometimes the territorial neighbor is a stronger competitor than the non-territorial floater. For example, in African striped mice, territorial males defend a group of two to four females with which they breed. In striped mice, extra-group paternity is high, and females especially mate with the familiar neighbors and not with the floating males. This can explain why in striped mice territorial males are much more aggressive toward their “nasty neighbor” than toward unfamiliar males, as this aggressive strategy could significantly reduce the amount of

extra-group paternity and thus increase their fitness (Schradin et al. 2010).

Living in groups creates its own, special social environment. This leads to significant costs, such as increased competition for food and mates and increased risk of the spread of disease. Group-living has evolved in species in which these costs of group-living are on average lower than the benefits group-living provides (Krause and Ruxton 2002). Benefits of group-living mainly fall into two categories: foraging and avoidance of predation (Krause and Ruxton 2002). Living in groups can make it easier to find good food sites, to catch prey, and to avoid competition for renewable food sources. Possible advantages of group-living referring to predator avoidance are (1) increased vigilance: A group will discover a predator sooner than a single animal. The sooner the prey is alerted, the faster the predator's chance of success will decline. (2) Dilution effect: When a predator attacks a group of ten animals and captures one, the probability of one individual being captured is ten times lower (10%) than if the individual would have been alone. (3) Encounter effect: Decreased probability of predator encounter per individual as detection of larger groups does not increase proportionally with group size. In other words, a predator is less likely to detect a group of ten than to detect ten single individual. (4) Group defense: A group may be able to defend itself against predators while a single individual may not. (5) Confusion effect: Predators take more time to capture a single prey individual if it is surrounded by other moving conspecifics than if it is on its own. Thus, the environment determines whether the costs or the benefits of group-living are higher. Group-living is expected to have evolved especially in environments in which food availability is high or can be increased by foraging in groups (low competition for food) and where predation pressure is high.

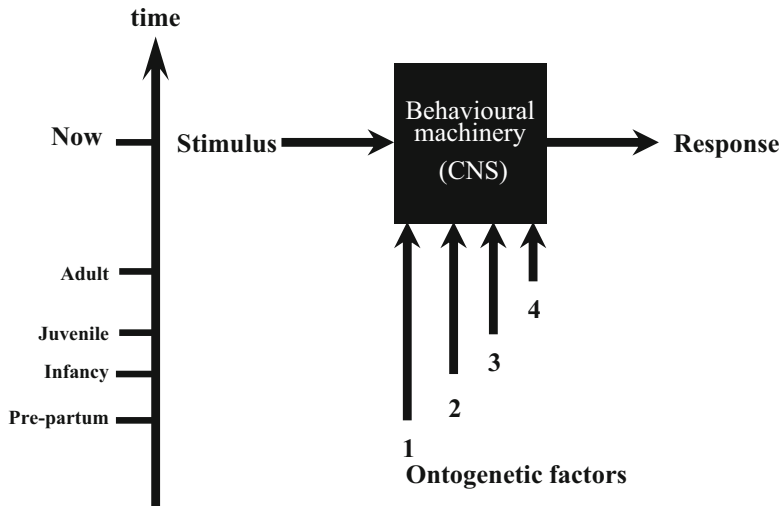
Apart from the function of behavior, which means how it increases fitness, the second ultimate question is about the phylogeny or evolutionary history of behavior. From an ecological point of view, here the question about the environment of the ancestor is important, because the trait evolved in this environment: what was the

function in previous generations, how did it increase fitness? In other words, the current environment in which we are measuring fitness consequences of behavior depending on abiotic, biotic, and social factors represents the previous environment for the next generations, an aspect of a species phylogeny. It is especially important to consider the ancestor's environment when it differs from the current environment. For example, this could explain why an observed behavior doesn't seem to lead to fitness benefits, because of an evolutionary mismatch due to environmental change. This is especially important in our current period of accelerated global change: will behavior (and physiology) that is now adaptive still be adaptive in future generations that might have to survive and reproduce in a different world with a different climate (Rymer et al. 2016)?

## Ecology and Evolved Mechanisms

The ultimately oriented field of behavioral ecology (including sociobiology) sometimes created the impression that ecology is only important to understand the ultimate, but not the proximate reasons of behavior. This is wrong for two reasons: (1) proximate mechanisms of behavior are evolved mechanisms that increase fitness; and (2) the proximate mechanisms work in the environment in which the individual shows its behavior; thus, the ecology is an important component of the proximate mechanisms. In sum, why specific mechanisms exist can only be understood when considering the ecology of a species.

Tinbergen (1963) regarded the responding central nervous system (CNS) as the behavioral machinery. He defined ontogeny of behavior as the "change of behavioral machinery during development." Thus, the question addressing causation is the question about the behavioral machinery leading to the observed behavioral pattern, and the question about ontogeny asks how this machinery develops until the observed behavior is shown. One point of confusion has been that ontogeny itself has a causal impact on the observed behavior: otherwise it would not make sense to study it! Although both ontogeny and the



**Ecology, Fig. 2** The difference between ontogenetic factors and the behavioral machinery. Ontogenetic factors occur over time before a behavioral response is shown, whereas the behavioral machinery (central nervous system, CNS) is directly connected in time with the behavior. Ontogenetic factors can occur at different times before

the behavior occurs, while the factors of the behavioral machinery occur together with the observed behavior. Arrow 1 represents a possible ontogenetic factor pre-partum, arrow 2 a factor occurring during infancy, arrow 3 a factor during the juvenile phase, and arrow 4 a factor during adulthood.

behavioral machinery cause behavior, there is a clear difference concerning the time when this occurs (Fig. 2). While ontogenetic factors occur before the behavioral response is shown, the behavioral machinery is directly connected with the behavior in time. When we observe a special behavioral pattern, the question concerning causation is “What is happening to induce the animal to show this behavior at this particular moment?,” whereas the ontogenetic question is “What previous circumstances have caused the animal to respond at this moment in this way?” For both questions, the environment in which ontogeny and causation take place plays an important role (Fig. 1).

During ontogeny, the individual develops its behavioral machinery that will later produce the observed behavior. The behavioral machinery mainly consists of the brain (central nervous system), but also the endocrine system, which influences the brain via its hormones. Importantly, the endocrine system itself is regulated by and as such part of the brain. In fact, the brain is the largest endocrine gland of the vertebrate body, secreting both traditional hormones and especially from the hypothalamus and the pituitary releasing hormones which influences the secretion of other endocrine glands. The development of the brain

and the endocrine system starts with the fertilized egg. Especially important periods occur during embryogenesis and infancy, when sensitive periods can occur. During these sensitive periods, hormones can have permanent organizational effects on the brain which influences adult behavior. Thus, the environment during early development is especially important for the development of the behavioral machinery. But ontogeny continues during adulthood and senescence, and the brain and endocrine system also change during adulthood. For example, learning represents a change of the brain that occurs throughout life. Thus, the process of ontogeny is continuous from fertilization of the egg until senescence and death, though sensitive periods occur that are especially important (West-Eberhard 2003).

How an individual develops depends on both its genotype and the environment in which it lives, representing the gene-environment interaction. For example, in many reptiles, the abiotic factor of temperature influences whether the embryo in the egg develops into a male or a female (Yatsu et al. 2015). Of course this also has very strong effects on the behavior of the adult, as many behaviors are sex specific. Biotic aspects influencing early development include hormones



circulating in the blood of pregnant mammalian females or in the eggs of birds, which influence the later behavior of the offspring. In Mongolian gerbils, males that developed between two male fetuses in utero were reported to show less paternal care than males that developed between two female fetuses, because they experience higher testosterone levels in utero (testosterone diffusing from the neighboring male fetuses), leading to the development of a more masculine and a less parental brain (Clark et al. 1997). The environment experienced as an infant or juvenile can also influence paternal response as an adult. Growing up in a family group and experiencing paternal care leads to higher levels of paternal care in adult rodents (McGuire 1988). In rodents, maternal effects significantly influence stress response and social behavior of the offspring, which is an adaptive response to specific environments. For example, when female rats show increased levels of licking and grooming toward their pups, this decreases the stress response of her offspring when they are adult and as such also influences their behavior (Weaver et al. 2004). In sum, abiotic, biotic, and social factors influence the development of individuals, including the development of their behavioral machinery and, thus, their behavior.

The environment plays an important role in causing the brain (behavioral machinery) to show a specific behavior. It is stimuli from the environment that trigger a behavioral response. One simple abiotic stimulus that has great consequences on behavior is weather. For example, activity of African striped mice is delayed or even inhibited on cold rainy days when they remain in their nests instead of leaving for foraging (Schrader et al. 2007). The study of stimuli triggering behavior was one main focus at the start of the studies of animal behavior (Tinbergen 1966) but receives very little attention in current research. For example, early studies in the field of animal behavior tried to identify the so-called Schlüsselreize (sign stimuli) that triggered very fixed behavioral responses, the so-called fixed action patterns. Fixed action patterns are behaviors believed to be hard wired into the nervous system, representing instinctive and inherited behavior. Tinbergen studied the red belly of male

sticklebacks as a sign stimulus triggering aggression in territorial male sticklebacks. For this he created a series of simplified dummies representing sticklebacks, identifying that it is not the form of the dummy but only the presence of a red belly that triggers aggression (Tinbergen 1966).

Environmental stimuli are important for animals to show their behavior at the appropriate time and appropriate place. For example, parental care has to rely on appropriate stimuli indicating where and when individuals (and thus the parental brain) should respond with caregiving behavior, allowing them to recognize their young and their needs. Males might recognize young as their own if they are associated with their mate. Male laboratory mice (*Mus musculus*) are more likely to kill their own pups in the nest of a strange female than to kill strange pups in the nest of a familiar female. Male deer mice respond paternally to strange pups that are together with their mate but kill their own pups when these are associated with a strange female (Brown 1993). Males might recognize young as their own offspring when they are associated with a special place. Male mice show paternal care toward pups in their own home cage but show infanticide toward pups in the home cage of a strange male (Elwood and Kennedy 1991). Many bird parents take care of any chick in their own nest, as has been shown experimentally by placing additional strange chicks in a nest. However, they often ignore their own young if they are placed just a few centimeters away from the nest. The monogamous and biparental desert wood louse (*Hemilepistus reaumuri*, Isopoda) recognizes its own young from family-specific odors and kills and eats strange young (Linsenmair 1972), while king penguin chicks recognize their parents coming back from sea by their individual calls (Jouventin et al. 1999). Thus, multiple and different stimuli from the environment such as the place, the smell, or the sound trigger adaptive behaviors to be shown.

## Ecophysiology of Cognition

How smart does an animal have to be? A penguin knows everything it has to know and can do everything it needs to do. It won't be more

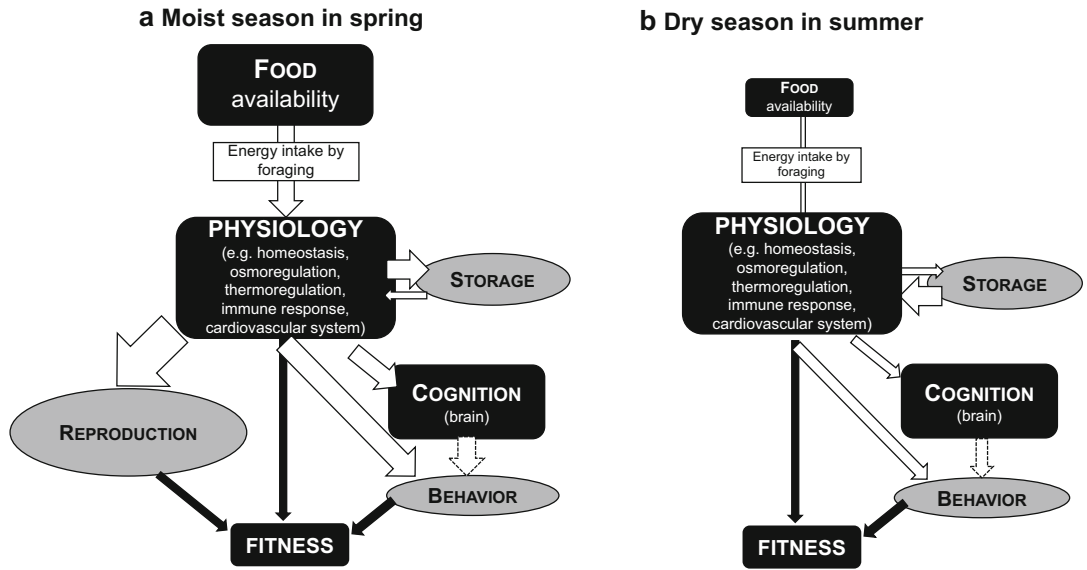
successful if it would have the intelligence of a monkey or of a human being! Thus, the cognitive abilities of a species depend on the environment in which it lives. Cognition is a product of evolution. Cognitive traits are selected to closely match the cognitive demands posed by each species' environment. Thus, specialized cognitive abilities evolved as a response to specific environmental demands while general cognitive abilities are present in most or all species. As such, cognitive performance can differ between species due to evolutionary adaptation. But cognitive performance can also differ between populations due to phenotypic plasticity and within populations and individuals due to phenotypic plasticity. A specific cognitive trait only evolves if the benefits are higher than its costs. To understand cognition, one has to find answers to the four questions of Tinbergen, and each depends on the environment. The proximate causes, including the physiological state of an individual, influence cognition, have ultimate fitness consequences.

While one field of cognitive research has focused on variation in cognitive abilities of animals in its ecological context and how this increases fitness (Healy and Braithwaite 2000), another has focused on the influence of physiology on cognition (the proximate mechanisms) under highly standardized laboratory conditions (e.g., Neese and Schantz 2012). Few field studies have addressed the relationship between metabolism, hormones, and cognitive traits under natural conditions. Seasonal changes in hormone secretion might have pronounced effects on cognitive performance, as do seasonal changes in blood glucose levels. For example, low blood glucose level during periods of low food availability might negatively influence both behavior and cognition, because insufficient energy is available to optimally run these processes (Fig. 3). Low food availability in the environment leading to starvation can also affect cognition. Whether starvation has a positive or a negative effect on cognition might depend on the phase of starvation. As starvation first activates glycogen stores, it can first improve cognition, but as starvation continues, reduced energy availability will negatively affect cognition (Maille and Schradin 2017). This is especially the case in free-ranging animals. In

contrast, obese humans and obese domestic and zoo animals might have improved cognitive abilities when been food deprived, as this can increase their health status.

Cognition is a function of the central nervous system, which consumes a significant amount of energy. For example, in humans, 20% of the resting metabolic rate is due to the metabolic costs of the human brain although it represents only 2% of the body mass (Laughlin 2001). The generation and propagation of neural signals increase energy consumption, and the storage of information requires additional neural tissue, either in the number of neurons or in the number of connections between these neurons, which further increases the energetic demands of the brain. The supply of metabolic energy is supposed to constrain the growth and function of the brain and consequently the cognitive performance. The capacity of the brain to store energy is very limited. As such, an ecological decrease in food availability, for example, due to seasonal changes, is likely to affect brain functions and cognition and behavior as well (Fig. 3).

In sum, cognitive performance is based on brain functions, which have energetic demands and are modulated by physiological parameters such as metabolic hormones. As both environmental demands and environmental energy availability change seasonally, cognitive performance in free-living animals can also change seasonally. Environmentally induced changes in physiological traits, such as blood glucose and hormone levels, influence cognitive performance in free-living animals. Individuals spending more energy than they can currently obtain from their environment face a trade-off of investing energy into cognition, into other life sustaining processes, or into reproduction. Selection pressures such as predation risk, mate choice, or social demands act on the trade-off between energy-saving and cognition. Different environmental conditions can lead to three different trade-off outcomes: cognitive impairment, resilience, or enhancement (Maille and Schradin 2017). If cognition is very important, then the organisms will still allocate the same amount of energy to cognition, while reducing energy spent for other processes, such as reproduction. Further, not only food



**Ecology, Fig. 3** Energy flow in the African striped mouse (*Rhabdomys pumilio*) from a semidesert habitat in South Africa, during (a) the moist breeding season in spring with high food availability and (b) the dry non-breeding season in summer with low food availability. The African striped mouse can only reproduce in the moist season when sufficient food and thus energy is available. Black arrows indicate effects on fitness. White

arrows represent energy invested in one process: thickness represents amount of energy. Energy availability in the environment influences both behavior and cognition. This figure illustrates how the environment influences both proximate factors and ultimate consequences of cognition and behavior via its changes in food availability (Figure adapted from Maille and Schradin (2017))

availability but also other aspects such as predation pressure can change seasonally. Cognitive impairment occurs when periods of food shortage are also periods of low cognitive demands. Cognitive resilience occurs when cognition helps to stabilize or improve the physiological state in challenging environments (Buchanan et al. 2013). Cognitive enhancement occurs when cognition allows a net benefit in the energy budget. Thus, the environment has a significant influence on cognitive performance, and this influences an individual's fitness. The emerging field of eco-physiology of cognition studies how physiological changes affect cognition in free-living animals exposed to natural environmental variation, such as seasonal variation in food availability and temperature (Maille and Schradin 2017).

## Conclusion

Behavior and cognition cannot be understood without taking the ecology into account. The

environment in which an individual lives influences the development, causation, and fitness consequences of its behavior and cognition, and as such also the phylogeny of behavioral and cognitive traits of future generations. Animals have evolved physiological mechanisms that allow them to maximize their evolutionary fitness giving the environment in which they live. Thus, they have evolved to deal with ecological problems, especially food availability and predation pressure. While nothing in biology makes sense except in the light of evolution, evolution and behavior cannot be understood without taking the ecology of a species into account.

## Cross-References

- [Adaptation](#)
- [Behavioral Flexibility](#)
- [Comparative Cognition](#)
- [Ethogram](#)
- [Evolution](#)

- ▶ Evolutionary Psychology
- ▶ Homeostasis
- ▶ Hormones and Cognition
- ▶ Intelligence
- ▶ Natural Selection
- ▶ Nikolaas Tinbergen
- ▶ Ontogeny
- ▶ Phylogeny
- ▶ Reproductive Fitness
- ▶ Social Behavior
- ▶ Sociobiology
- ▶ Ultimate Causation

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## Ectopic Nipple

### ► Supernumerary Nipple

## Ectostriatum

### ► Entopallium

## Edward B. Titchener

Nancy Digdon  
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Canada

## Introduction

Titchener, Edward Bradford (1867–1927) is best known for his system of psychology called structuralism. It was an experimental psychology that studied the structure of human consciousness by identifying its smallest elements.

## Early Years and Education

Titchener was born in Chichester, England, on January 11, 1867 to John and Alice (nee Habin) Titchener. His ancestors had lived in Chichester since the 1500s and many had been wealthy and influential (see Boring 1927 for more detail). But

Titchener's paternal grandfather lost the family fortune and died poor. Financial hardship persisted and was exacerbated when Titchener's father died while still in his 30s.

Without financial assistance from family, Titchener attended elite schools on academic scholarships. He graduated from the prestigious Malvern College before entering Oxford University at the age of 18 to complete an A.B. degree (1885–1890). He studied philosophy, classics, Greek, and Latin and conducted supervised research in physiology. Titchener was also active in extracurricular hobbies. He was an accomplished musician, a skilled tennis player, an avid naturalist, and a voracious reader of diverse writings in several languages. His reading of Wilhelm Wundt's German publications about a new science of psychology that investigated human consciousness in the laboratory peaked Titchener's interest and shaped the direction of his career.

In 1890, Titchener moved to Leipzig, Germany, for 2 years where he completed a PhD under Wundt's supervision. After finishing his PhD, Titchener's goal was to move back to his homeland so that he could establish experimental psychology at a British university; however, none were hiring experimental psychologists. While in Wundt's lab, Titchener met American students and one of them (Frank Angell) suggested Titchener apply for an experimental job at Cornell University in Ithaca, N. Y. In 1892, 25-year-old Titchener crossed the Atlantic to become the Director of the psychology laboratory at Cornell University, and he remained at Cornell until retirement.

## Structuralism System of Psychology and Laboratory Science

Titchener's structuralism system of psychology was a pure experimental science conducted in the laboratory with specialized equipment (like that used in Wundt's lab). Titchener had a six-room laboratory and he immediately purchased or made the necessary equipment for his scientific investigations.



In his research, Titchener used a method of introspection that required scientists to direct their observation inward on their own consciousness in order to record the smallest elements of sensations, images, or feelings that they experienced under various controlled conditions. Titchener argued that his method of introspection was scientific because it was a form of systematic observation. But he cautioned that “when we introspect, we must be absolutely impartial and unprejudiced. . . We ought to be ready to take the facts precisely as they are. . . Impartiality is a necessary condition of all scientific observation” (Titchener 1896, p. 45). Titchener’s introspection required expert training in order to detect the elements in consciousness. Introspection experts avoided the “stimulus error,” which was to say the name of the stimulus, such as saying “rose” when shown one, rather than correctly saying the sensory elements involved in the conscious experience of it (e.g., “red,” “softness,” and “silkeness”). Titchener believed that the work of well-trained introspectionists would reveal the structure of the generalized human mind.

Titchener likened his analysis of the elements in consciousness to the analysis that physical scientists had done when constructing the periodic table of the elements of the physical world. By 1896, Titchener had already discerned more than 44, 435 elementary sensation qualities, including 32,820 related to the eye; 11,600 to the ear (audition); 4 to each of the tongue and skin; 2 to the muscle; 1 to each of the ear (static sense), sex organs, tendon, and joint; and possibly other sources of elements that he was uncertain about, including the alimentary canal, blood-vessels, lungs, and tongue (Titchener 1896). Titchener wrote extensively about his structuralism between 1893 and 1900, publishing 62 research articles and 2 books about it. Most research articles are in *The American Journal of Psychology*, which Boring (1927) dubbed the “mouthpiece” for psychology at Cornell. Titchener served as Associate Editor (1895–1920) and Editor (1921–1925) of this journal, and had some control over what was published therein. Titchener quickly rose through the academic ranks, being promoted to full Professor in 1898 when he was only 28-years-old.

In Titchener’s 1898 article, titled *The Postulates of Structural Psychology*, he contrasted structuralism with alternative psychologies in the USA at that time. According to Titchener, the other psychologies were problematic because they investigated the function of consciousness (without being sufficiently informed about its structure), focused on individual differences (instead of using science to understand the generalized human mind), or attempted to apply psychology (e.g., mental testing), which Titchener believed detracted from psychology’s status as the pure experimental science of the structure of human consciousness.

Titchener was a powerful figure at Cornell, and his structuralism defined the psychology department for the 35 years that he was there. But Titchener’s structuralism was not popular among American psychologists who had no ties to Cornell. The use of a psychology laboratory and specialized equipment, however, did become the norm for teaching psychology at other American universities. Thus, when Titchener (1901) published his student and instructor manual for laboratory practice, it was widely adopted by other universities even though the adoptees did not accept structuralism. As one reviewer of Titchener’s manual exclaimed,

Professor Titchener has here placed at the disposal of his colleagues the result of years of very special and successful devotion to the problems of psychology susceptible to treatment by the experimental methods, and for this service so admirably accomplished he is entitled to the honors and privileges attaining to the distinction of carrying through so difficult and important piece of pioneer work. (Jastrow 1901, p. 743).

Titchener further promoted laboratory research by publishing another textbook (see Titchener 1910) and by organizing his Experimentalist Group. This group met annually in psychology laboratories across the country to have frank discussions about new research or research still in progress. Attendance at these events was by Titchener’s invitation only. He barred women so that the male attendees had the liberty to behave in ways considered unsuitable for female audiences. Titchener, however, did not exclude women from Cornell’s PhD program or from his own



laboratory, in contrast to other prominent universities that were male only at that time (e.g., Clark University and Harvard University). Titchener's first PhD student was Margaret Floy Washburn. When she earned her PhD in 1894, she was the first woman to have a PhD in psychology from an American university.

## Titchener's Ties to Comparative Psychology

Titchener was clearly interested in comparative psychology even though he did not include it as part of his structuralism system of psychology. Indeed, Margaret Floy Washburn's PhD was based on animal research. And Titchener helped Washburn publish her 1908 book, *Animal Mind*, with the company that published his own books (i.e., Macmillan Company).

Although rarely cited today, Titchener has 10 short publications about comparative psychology/biology topics that are in the journal *Nature* between 1889 and 1894. See Dewsbury (1997) for a list of these references. In these publications, Titchener reported his observations that the color of bird eggs seemed unrelated to the color of the nest and its surroundings; his experiments on the palatability of different insects fed to mice and other small animals; his observations of which birds had a serrated edge on the third digit of their claws (called pectination) and how the birds used it; and his observations of mate preferences in birds and insects.

In addition to these publications in *Nature*, Titchener authored and co-authored English translations of Wundt's works, which included the 1894 lectures on *Human and Animal Psychology* and their revisions in 1896 and 1901 (see Boring 1927 for these references).

## Adjustment to Life in America

Two years after moving to America, Titchener married Sophie K. Bedlow from Portland Maine. As their children grew, the Titchener family hosted Sunday evening orchestral performances by family and musical people affiliated with

Titchener's laboratory, as told by Titchener's former PhD. student, Edwin Boring. Titchener lived in America for 35 years, up until his sudden death from a brain tumor in 1927 at age 60. However, Titchener never became "Americanized" or an American citizen. As Heidbreder (1933) tells it,

...only two years at Leipzig had Germanized him. He even looked like a German and was sometimes mistaken for one; the science for which he labored was German to the core; and it what must have seemed to him a crude university on the wrong side of the Atlantic, he preserved with sturdy and punctilious devotion the ceremonial with which he had seen psychology surrounded in a German university. (p. 114).

Boring (1927) noted that Titchener became isolated from his laboratory in his later years. Boring recalled that "In June Titchener came to the Laboratory for doctors' examinations, but I do not think that in seven years (perhaps seventeen) he was once in the Laboratory between June and February. Graduates saw him at the house and not often" (p. 501).

From 1917 to 1927, Titchener published on a wide range of topics that went beyond his structuralism system of psychology. See Dallenbach (1928) for a bibliography of Titchener's writings during that period. Titchener also developed expertise in deciphering the meaning and significance of the inscriptions on ancient Greek, Roman, Chinese, and Mohammedan coins, and collaborated with Howland Wood, the curator of the American Numismatic Society.

Late in life, Titchener worked on a book titled *Systematic Psychology*, in which he questioned the utility of structuralism and the breaking down of consciousness into elements. Instead, he argued for what he called a phenomenological or existential approach, which examined consciousness as it occurred without breaking it down. Titchener died before finishing this book, but his writing-in-progress was published after his death (see Titchener 1929).

In closing, Titchener's significance to psychology was summed up in his obituary:

The death of no other psychologist could so alter the psychological picture in America. Not only was he unique among American psychologists as a personality and in his scientific attitude, but he was a cardinal point in the national systematic orientation. The clear-cut opposition between behaviorism and

its allies, on the one hand, and something else on the other hand, remains clear only when the opposition is between behaviorism and Titchener, mental tests and Titchener, or applied psychology and Titchener. His death thus, in a sense, creates a classificatory chaos in American systematic psychology. (Boring 1927, p. 377).

Titchener's system of structuralism dwindled at Cornell after his death. However, a piece of him remained; his brain is in the Wilder Brain Collection managed and displayed by the Department of Psychology.

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## Edward C. Tolman

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Edward Chase Tolman (1896–1959) developed purposive behaviorism. He studied rats in mazes and the routes they chose to get to the end of the

maze. The rats behaved as though they had a mental map of the maze. The rats' performance in the maze also varied depending on whether they got desirable foods at the end of the maze.

## Early Years and Education

Edward Chace Tolman was born and raised in West Newton, MA. His family was committed to humanitarian causes, social justice, and pacifism, which reflected the values of their Quaker and Unitarian Church ancestors (see Carroll 2017 for a detailed biography of Tolman and his ancestors). After high school, Tolman earned a BSc in electrochemistry from Boston Tech [which is now called the Massachusetts Institute of Technology (MIT)]. He chose this program because he was good at high school math and science and because his father wanted him to get appropriate training so he could contribute to the family business, J. P. Tolman & Co., which was known for manufacturing quality hemp cord. But after finishing his BSc in 1911, Tolman was uncertain about his career path. He read William James's (1890) *Principles of Psychology*, which sparked an interest in academic philosophy as a possible career, and this prompted him to take two summer courses at Harvard, one in philosophy and the other in psychology. These summer courses helped Tolman crystalize his career plans. In his autobiography, he writes, "I decided then and there that I did not have brains enough to become a philosopher. . . but that psychology was nearer my capacities and interests. It offered, at that date, what seemed a nice compromise between philosophy and science" (Tolman, 1952, p.323).

Tolman completed a PhD in psychology at Harvard in 1915, with the support of his father, who respected his son's intention of using psychology for the betterment of human lives. Tolman's dissertation was on human memory and was supervised by Hugo Münsterberg. The dissertation had an appendix with supplementary research on the effects of a change of purpose on memory, which foreshadowed Tolman's later development of purposive behaviorism (which is described in the next section). Importantly, the dissertation research used the method of

introspection, which relied on people's verbal accounts of their mental experiences. The results were unreliable and uninterpretable. Tolman's dissertation research caused him to doubt the utility of introspection as a scientific method. Moreover, in his final year, he took a comparative psychology course taught by Robert Yerkes. Tolman was introduced to behaviorism and animal research via the course's textbook, which was John B. Watson's (1914) book, *Behavior: An Introduction to Comparative Psychology*. While a graduate student, Tolman also became familiar with Gestalt psychology and Kurt Lewin's field psychology, whose influences are evident in Tolman's later work.

Tolman's first academic job was teaching at Northwestern University in Evanston, Illinois from 1915 until his dismissal in 1918. In his autobiography, Tolman writes that he was let go because he had.

a compulsion for research and writing, although it did not result in a large output at the time, (it) interfered with my learning to become much of a teacher. . . Further, this was just before we got into the first World War and my pacifist training, plus my own problems about aggression, kept me in a terrific emotional turmoil so that I did a still poorer job. (Tolman 1952, p. 327).

In 1918, Tolman was already married (to Kathleen Drew) and had an infant daughter (Deborah). He and his family moved back to his parents' home in Newton, and Tolman worked briefly as a laborer in a garden market until he received a job offer from Berkeley in California.

## Research Career at Berkeley and the Development of Purposive Behaviorism

In 1918, Tolman and family moved to Berkeley where Tolman was to produce his major works in the ensuing decades. In 1919, Tolman acquired his first white rats and shifted his research from human studies to laboratory studies of how rats behave when placed in different mazes under controlled conditions and experimental manipulations. As a result of this research, Tolman became skeptical of Watson's version of behaviorism that focused on the specific muscle

movements in a conditioned reflex as being the central units of behavior. Tolman published a theoretical paper in 1922, in which he argued that what a behavior accomplished, or the function it served, were more important than the specific muscle movements used in carrying out the behavior. Tolman called his version of behaviorism "purposive behaviorism." Moreover, he argued that behavioral methods could be devised to study "mental concepts" such as thinking, consciousness, learning, ideas, and emotions in an objective way that did not involve references to mental states or the use of introspection. Tolman's 1932 book, *Purposive Behavior in Animals and Men*, further articulated this argument and introduced the concept of "molar behaviorism" to denote that a behavior's purpose (or function in terms of meeting a goal) were important emergent properties that were missed when the study of behavior was restricted to a fine grained molecular analysis of each of the small, specific muscle movements involved in doing the behavior.

Tolman's lab produced several clever studies in support of his version of behaviorism. One example is the empirical demonstration of "latent learning," meaning that learning could occur without an immediate change in performance. In this research, rats were randomly assigned to one of three groups. All rats were partially food deprived when they navigated the same maze on multiple trials, but each group did so under different conditions. Group 1 rats always encountered food at the end of the maze. They gradually made fewer and fewer wrong turns and "errors" in getting from the start of the maze to the food at the end. Group 2 rats received no food at the end of the maze, and their rate of wrong turns and errors did not improve across trials. Group 3 rats received no food on the first ten trials, and their performance was similar to that of the group 2 rats. But after the 10th trial, group 3 rats encountered food at the end of the maze on every trial. The key finding is that group 3 rats had a sharp drop in wrong turns and errors once trials were associated with food at the end of the maze. Their performance improved at a faster rate across trials compared to the rate of improvement seen in the group 1 rats who had encountered food since the start of the study. Other examples of innovative research pertain to

the concepts of “insight,” “sign-gestalts” and “cognitive maps.” Tolman (1932) gives a detailed account of these other topics.

Tolman achieved national prominence when he was elected president of the American Psychological Association in 1937. In his presidential address (see published version in Tolman 1938), he contrasted his behaviorism with that of a contemporary rival, Clark Hull. Tolman took issue with Hull’s strategy of reducing behavior to stimulus-response connections and the mathematical learning laws that govern them. Tolman argued that a rat’s behavior at a “choice point” in a maze was determined in part by a host of intervening variables that operate between the stimulus and the response, which Tolman believed Hull’s theory neglected. Examples of these intervening variables are the rat’s hereditary makeup, past training/experiences, and the rat’s current motivational state in terms of appetites or aversions. Tolman conducted most of his research using rats as subjects, but he believed that many phenomena found in rats were general enough to apply to other species including humans.

## Social Issues and Social Activism

In addition to developing purposive behaviorism and conducting experiments, Tolman was an active member of the Society for the Psychological Study of Social Issues (SPSSI), which was established in 1936. This society gave psychologists an opportunity for united efforts against major social issues of the day, including world hunger, racism, labor union/management friction, the rise of fascism, and the threat of a second world war. Tolman was Chairman of SPSSI when the USA entered World War II, and he published a paper about SPSSI’s relevance (see Tolman 1941) and a book on psychological insights into the causes and the prevention of war (see Tolman 1942).

After World War II, the USA was embroiled in the cold war over nuclear arms and concerns that communism could infiltrate and supplant American culture. Berkeley, like other American universities, required its professors to sign a loyalty oath

proclaiming they had no ties to communism. Faculty refusing to sign were fired (see detailed account in Carroll 2017). Although Tolman had no ties to communism, he refused to sign the loyalty oath on the principle of faculty rights. Tolman emerged as a leader in the non-signers’ fight against the university. Ultimately the California Supreme court ruled in favor of the non-signing faculty and they were reinstated.

Toward the end of his life, Tolman reflected upon his life’s work and his system of purposive behaviorism:

The system may not well stand up to any final canons of scientific psychology. But I do not much care. I have liked to think about psychology in ways that have proved congenial to me. Since all the sciences, especially psychology, are still immersed in such tremendous realms of the uncertain and the unknown, the best that any individual scientist, especially any psychologist, can do seems to be to follow his gleam and his own bent, however inadequate they may be. In fact, I suppose that actually this is what we all do. In the end, the only sure criterion is to have fun. And I have had fun. (Tolman 1959, p. 152.)

## Cross-References

- [Behaviorism](#)
- [Clark L. Hull](#)
- [Latent Learning](#)

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## Edward L. Thorndike

► [Edward Thorndike](#)

## Edward Lee Thorndike

► [Edward Thorndike](#)

## Edward Thorndike

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## Synonyms

[Edward L. Thorndike](#); [Edward Lee Thorndike](#)

## Introduction

Edward Lee Thorndike was born 31 August 1874 in Massachusetts. Thorndike was introduced to psychology during his junior year (1893–1894) at Wesleyan University, during which he read chapters of William James' *The principles of psychology*. Thorndike subsequently attended Harvard University, with the intention of taking courses on English literature and the French language and earning a master's degree in teaching. During his first year (1895–1896), he attended courses taught by Josiah Royce and William James, and thereafter psychology increasingly became his focus. By the

time he earned his master's degree (1897), Thorndike had begun to research animal learning and had decided to earn a Ph.D. and teach psychology. Thorndike completed his doctoral dissertation in 1 year at Columbia University, under the direction of James McKeen Cattell. His dissertation (*Animal Intelligence: An Experimental Study of the Associative Processes in Animals*) was an instant classic and described the puzzle box experiments for which he is best known. After graduation, he taught for 1 year at the College for Women at Case Western University. He spent the remainder of his career at the Teachers College at Columbia University. Thorndike is most famous for his contributions to learning theory, but his interests were wide-ranging. He wrote several seminal books on educational psychology and classroom instruction. He assisted the United States Army during World War I in developing aptitude tests for recruits and selecting aviators for flying schools. After the war much of his research was concerned with human learning, intelligence, and intelligence testing. During the 1930s and 1940s, he additionally completed a number of studies concerned with social psychology and personality. Thorndike served as the president of the American Psychological Association (1912) and the Psychometric Society (1937). He retired from Columbia in 1940, but continued scholarly writing. Thorndike died 9 August 1949 in New York. By the time of his death he had amassed more than 500 publications. He is one of the most influential psychologists of the twentieth century (Hagbloom et al. 2002) and arguably the greatest of all the learning theorists (Olson and Hergenhahn 2009).

## Initial Animal Research

At Harvard Thorndike began performing research with chickens under the direction of William James. He is thought to have been the only student performing animal research at Harvard at the time; he chose this research, he wrote, “not because I knew animals or cared much for them, but because I thought I could do better than had been done” (Joncich 1968, p. 89). Chickens offered several advantages over other species: they were



relatively easy to acquire, they required little room or expense, and they quickly matured. Thorndike studied chicks' instinctive reactions at different ages to a range of aversive or potentially aversive stimuli (such as water, the presence of a live kitten or a stuffed owl, candle flames, or a football thrown into the chicks' pen).

## Puzzle Box Experiments

Thorndike's most famous research is the dissertation he completed at Columbia (1897–1898), especially the section describing how cats learn to escape from puzzle boxes.

The subjects in this research were 12 cats (strays that he had caught), and all but one was under a year in age. He tested the cats in 15 boxes he constructed. In each box it was possible for the cat to escape through a door, otherwise the boxes were differently configured. For example, in one box the door could be opened by depressing an external bar that held the door in place. The cat could reach this bar by placing a paw through the wooden slats near the door. In another box the door could be opened by pulling on a string inside the box that was connected to a bolt holding the door closed. The simplest box required a single act to open the door; the most complex required three actions. After the cat opened the door, it was able to eat food that had been placed outside the box.

On each trial, Thorndike placed the subject in a particular box and recorded the time until escape occurred. He observed that the cat's behavior was initially variable. The subject would appear to wander around the box and meow, seemingly looking for a way to escape. Thorndike (1898) wrote:

It tries to squeeze through any opening; it claws and bites at the bars or wire; it thrusts its paws out through any opening and claws at everything it reaches; it continues its efforts when it strikes anything loose and shaky; it may claw at things within the box. It does not pay very much attention to the food outside, but seems simply to strive instinctively to escape from confinement. The vigor with which it struggles is extraordinary. For eight or ten minutes it will claw and bite and squeeze incessantly. (p. 13).

At some point the subject would make, seemingly by accident, the response that opened the door. He observed that on subsequent trials the time until escape occurred tended to decrease. In Thorndike's (1898) words:

Starting, then, with its store of instinctive impulses, the cat hits upon the successful movement, and gradually associates it with the sense-impression of the interior of the box until the connection is perfect, so that it performs the act as soon as confronted with the sense-impression. (p. 15)

In other words, the cat learned to connect the situation (a stimulus) to a particular response. He reasoned that the stronger this connection became, the more quickly escape would occur. When he examined how latency to escape varied across trials, he observed that the data appeared to follow an irregular curve. Thorndike (1898) argued that this "time-curve" provides "a fair representation of the progress of the formation of the association. . ." (p. 16).

Subjects were studied in the simplest boxes first. All cats learned to escape from boxes that required only a single response. Thorndike found that cats were less consistently able to learn to escape when multiple responses were required.

Thorndike found little evidence that the cat's learning was affected by insight. He reasoned that if the cat could act based on an idea of how the door was opened, then once it obtained this idea there would be an abrupt shift from long escape latencies to short escape latencies. Instead, Thorndike observed only gradual and irregular time-curves. He additionally observed that a cat's "instinctive impulses" (e.g., meowing, clawing at different parts of the box) were slow to disappear when they did not aid in escape; this also seemed inconsistent with the cats having an idea of how the puzzle boxes worked.

Thorndike considered animals' cognitive abilities. For example, he tried to show the cat how to make the response by holding its paw and putting it through the proper motions, but this did not change the subject's behavior. He gave novice cats the opportunity to observe experienced cats make the appropriate response, but this also did not facilitate learning. He also observed how cats adjusted to being placed in a new box. He



observed that the cats would attempt to make a response that had worked before, even if the response was not available in the new box. For example, if a cat had learned to escape by pulling on a loop inside the box, it would continue pawing at that spot even if the loop was not there. Based on these observations, Thorndike concluded that a cat's learning was mostly or solely based on the incremental development of a stimulus-response (S-R) connection.

Thorndike also placed three dogs in puzzle boxes (which of course were larger than those used with cats). In so doing, the puzzle box experiments contributed to the nascent field of comparative psychology. Thorndike quickly found that dogs differed from cats both in their "instinctive impulses" and in learning. He observed, for example:

A dog... is not nearly so vigorous in his struggles to get out as is the young cat... He paws or bites the bars or screening, and tries to squeeze out in a tame sort of way. He gives up his attempts sooner than the cat, if they prove unsuccessful. Furthermore his attention is taken by the food, not the confinement. He wants to get *to* the food, not *out of* the box. (1898, p. 32).

Thorndike's dogs succeeded in learning to escape from the simplest boxes, but they were less successful than cats in learning to escape from more complex boxes. He attributed this difference to motivational factors rather than to a difference in how learning occurred in dogs. He noted, "It was... a practical necessity that the dogs should be kept from howling in the evening, and for this reason I could not use as a motive the utter hunger which the cats were made to suffer" (1898, p. 32).

## Other Animal Studies

Thorndike believed there may be an abundance of methods that can be used to study animal learning. Thorndike followed his puzzle box experiments with studies performed with chicks, fish, and Cebus monkeys. The chicks were placed in simple mazes built chiefly from books that were set on end. Escaping from the maze caused the chick to

return to its home pen (where there were food, water, and the other chicks). The fish learned to find an opening in a barrier that led to a part of an aquarium where there was food and shade. The monkeys learned to open a box set next to their cage in order to obtain a piece of food. In all three cases, Thorndike obtained "time-curves" that resembled those from cats and dogs in puzzle boxes.

Thorndike (1901) observed instances in which a monkey showed "a rapid, often apparently instantaneous, abandonment of the unsuccessful movements and a selection of the appropriate one which rivals in suddenness the selections made by human beings in similar performances" (p. 15). In other words, it appeared that monkeys *could* learn from an idea of the task. However, he was reluctant to accept this interpretation because gradual time curves characterized the more difficult tasks and he felt there was no reason why ideas would affect how subjects learned simple tasks and not complex ones. Thorndike concluded that the rapid learning was more likely due to other factors. He noted that "monkeys obviously form more associations and associations in a greater variety than do the other mammals" and that they have an "instinctive curiosity or tendency to fool with all sorts of objects" (1901, p. 18), which would facilitate learning to open a box.

## Connectionism

Thorndike ceased conducting animal research after taking positions at Case Western University and Columbia University. However, Thorndike continued to write about the apparent nature of animal learning and to describe this learning in terms of general principles and laws.

Thorndike stated that there are general laws controlling behavior. Firstly, he maintained that that behavior is predictable; "Every response or change in response of an animal is then the result of the interaction of its original knowable nature and the environment" (1911, p. 242). The original nature of an animal includes "instinct," that is, "inherited... connection-and action-systems" (Thorndike 1911, p. 243). How these connections

functioned depended on circumstances, along with motivation, fatigue, illness, aging, and other variations in the state of the organism.

Thorndike believed that when an organism encounters a novel situation, its behavior will be varied (he termed this the principle of varied reaction). If the subject's initial action does not produce satisfaction, then a change occurs within the organism that makes a different action more likely. When an action finally occurs that leads to satisfaction, a connection will form between the situation and the response. The strength of this connection determines how likely the situation will lead to a repetition of the action in the future.

Thorndike believed several factors affect an acquired S-R connection. One factor is whether the outcome is "satisfying" or "dissatisfying" to the subject. (He also used "reward" in place of satisfaction and "discomfort" or "annoyingness" in place of dissatisfaction). Thorndike believed that more satisfying outcomes produced stronger S-R bonds and that more dissatisfying outcomes produced weaker S-R bonds. He termed this principle the law of effect. Thorndike also believed that the connection became stronger every time a stimulus led to a particular response and that it became weaker every time a response failed to occur when a particular stimulus was present. He termed this principle the law of exercise.

A third factor that Thorndike emphasized was the "readiness" for a connection to occur. Readiness, he believed, is in part innate. For example, an organism is generally more ready to eat than vomit, or laugh than hiccup. Readiness is also affected by the state of the organism. For example, an organism becomes more ready to eat when it is hungry, or less ready to play when it is tired. In addition, readiness is affected by features of the situation that cause the organism to anticipate that a stimulus-response connection will be activated. For example, Thorndike (1913a) wrote, "When a child sees an attractive object at a distance, his neurons may be said to prophetically prepare for the whole series of fixating it with the eyes, running toward it, seeing it within reach, grasping, feeling it in his hand, and curiously manipulating it" (p. 126). Thorndike believed that readiness helps determine how the organism is affected by

activation of a stimulus-response connection. According to the law of readiness, satisfaction comes from activity among neurons that are ready for activity, and annoyingness comes from an absence of activity for which the organism is ready, or activity for which the organism is not ready. Thorndike (1932) also believed that "learning may consist in changing the readiness of connections as truly as in changing their strength" (p. 329).

While effect, exercise, and readiness largely determined the strength of a connection, he acknowledged that the particular manner in which the stimulus was presented and the response occurred were also factors in learning. Learning was facilitated, for example, if a response and its effect were temporally contiguous. Learning was also affected by the attention that the subject gives to its actions. For example, Thorndike suggested that if a cat accidentally made the response leading to escape with its nose while trying to claw at an opening, then the S-R association will develop more slowly than it would if the response had been made intentionally (Thorndike 1911, p. 249). In addition, he attributed importance to a somewhat nebulous concept termed "set," which involved an organism's attitude or determination to act in a particular circumstance. For example, he believed that a person who is interested in topic and motivated to learn will learn differently than someone who is neither of those things. In animal experiments, set may be affected by physical maturation, hunger, fatigue, and prior learning. For example, a cat that has succeeded in learning to escape from a series of puzzle boxes in the past is more likely to show greater determination to escape when placed in a novel box than are other, inexperienced cats. The differing "set" of the experienced cat might cause it to attend differently to the parts of the puzzle box, or to make more definitive movements when, say, depressing a bar or pulling on a string inside the box.

Finally, Thorndike described factors affecting the transfer of learning from one situation to another. He believed that a situation may consist of a number of different stimuli or elements and that certain elements may be more important in producing the response than others (he termed

this the principle of prepotency of elements). In a new situation, an S-R connection will be activated so long as the new situation resembles a situation in which a response occurred before (the law of assimilation); this is especially true if prepotent elements are present in the new situation. He also believed that the transfer of learning could be facilitated through a principle termed associative shifting. According to this principle, when there is a relationship between some set of stimuli and a particular response, it is possible to gradually replace certain elements of the stimulus set with others without eliminating the response. In this way, an entirely new set of stimuli can be made to produce the response. “Thus, what was at the start utterly without power to evoke a certain response may come to do so to perfection” (Thorndike 1913b, p. 15–16).

Thorndike generally attributed the formation of S-R connections in animals to “learning by trial and accidental success” (Thorndike 1901, p. 2). Although his research had yielded little evidence that animals can learn through observation or by reasoning and using ideas, he thought it obvious that these forms of learning occurred in humans. Indeed, he attributed to learning by ideas “practically all the advances in civilization” (1901, p. 2). In later years he became less certain and suggested that “higher forms of learning” might be found to be reducible to readiness, the action of connections, and other S-R concepts (Thorndike 1932).

In total, Thorndike’s theory came to be known as “connectionism” (e.g., Olson and Hergenhahn 2009). However, the term also was used to describe other theorists’ ideas (e.g., Medler 1998), and Thorndike did not attempt to popularize this view as a distinct school of thought (Joncich 1968).

## Applications to Education

Thorndike’s appointment to a faculty position at the Teacher’s College at Columbia University unsurprisingly caused a shift in his interests. Thorndike observed how much of educational practice depended on tradition and assumption

rather than on science. As was the case with the field of animal learning, he held a conviction that it was possible to do better. Therefore, Thorndike began to focus on how psychology informed education. Thorndike (1906) wrote:

Anyone of good sense can farm fairly well without science, and anyone of good sense can teach fairly well without knowing and applying psychology. Still, as the farmer with the knowledge of the application of botany and chemistry to farming is, other things being equal, more successful than the farmer without it, so the teacher will, other things being equal, be the more successful who can apply psychology, the science of human nature, to the problems in school. (p. 10).

Thorndike identified many ways in which education could be improved. He was critical, for example, of the lecture style of teaching, writing, “The commonest error of the gifted scholar, inexperienced in teaching, is to expect pupils to know what they have been told. But telling is not teaching” (1912, p. 61). He also argued that lectures limit education to what students can be told or shown. Another problem was that lectures did not promote critical reasoning; instead:

[Teachers] frankly present the student with conclusions, trusting that he will use them to learn more. They ask of him only to attend to, and do his best to understand, questions which he did not himself frame and answers which he did not himself work out. They try to give him an educational fortune as one bequeaths property by will. (Thorndike 1912, p. 188).

Another area in which Thorndike felt that education could be improved concerned the transfer of learning from one situation to another or one task to another. Thorndike felt that transfer of learning shouldn’t be assumed. Instead, transfer occurs only to the extent to which one situation resembles another. If the tasks students are asked to complete in school are unlike the “real-world” tasks to which learning must be applied, then transfer will likely be poor. Thorndike observed that a teacher could better prepare students by teaching students skills in school that closely match the skills those students are expected to need in the future. Similarly, Thorndike recommended that the problems students are given in the classroom should resemble the problems they will face in the real world. In line with

these views, he was a proponent of apprenticeships, internships, and other forms of experiential learning.

Thorndike frequently referred to the principles of learning when making recommendations concerning educational practice. For example, Thorndike viewed much of learning in S-R terms and believed a teacher can help a student connect a certain situation to the appropriate response by ensuring that the student is ready for the connection to be made and by ensuring that the appropriate response is followed by satisfaction to the learner.

## Revisions to Connectionism

Thorndike continued to study learning throughout his career and over time came to be influenced by the work of Pavlov, Tolman, and other learning theorists. Eventually, he began to revise portions of his theory and propose additional factors in learning (cf. Olson and Hergenhahn 2009; Thorndike 1932). The most notable revisions involved the law of effect and the law of exercise. Thorndike revised the law of effect to state that rewards strengthen a connection, while punishment has no comparable effect (indeed, may have no effect on the strength of a connection). The law of exercise lost its status as a major component of learning. Instead, Thorndike concluded that neither use nor disuse may have much of an effect on the strength of an S-R connection.

Among the new principles added to connectionism were belongingness, impressiveness, and polarity. Belongingness is concerned with whether there is by nature or experience a tendency to perceive one stimulus as “belonging” in some way to some other stimulus or to some response, in which case a connection more readily occurs. Impressiveness is roughly concerned with how intensely the stimulus affects the learner. A bright light is relatively “impressive” as are more emotionally charged words, such as “love,” “kiss,” “insane,” and “vomit” (Thorndike 1932, p. 131). Thorndike found that using more impressive stimuli leads to stronger S-R connections. Polarity is concerned with the normal sequence in which a series of actions are

performed. Each step in the sequence is associated with the step that precedes it; there is little “backward association” among the steps (Thorndike 1932, p. 152). Therefore, for example, it is easier to perform a skill in a forwards manner than in a backwards manner (e.g., a musician playing the notes in a song).

## Conclusion

Thorndike began his research in an era in which claims about animal learning commonly rested on isolated cases. Thorndike pointed out:

Dogs get lost hundreds of times and no one ever notices it or sends an account of it to a scientific magazine. But let one find his way from Brooklyn to Yonkers and the fact immediately becomes a circulating anecdote.

Thorndike sought to replace this approach with a systematic study of learning and behavior under controlled conditions. He considered the history of the subject, attempted to control motivation, and repeated observations by using multiple subjects and multiple conditions. In his experiments, he wrote:

...the work done by one investigator may be repeated and verified or modified by another. No personal factor is present save in the observation and interpretation. ... The curves showing the progress of the formation of associations, which are obtained from the records of the times taken by the animal in successive trials, are facts. ... They are absolute, and whatever can be deduced from them is sure. (Thorndike 1898, p. 7)

Thorndike’s puzzle-box experiments lacked methodological rigor and employed primitive analyses compared to modern research (Chance 1999), nevertheless they represent a seminal moment in the study of animal learning and behavior. At the time he began his research, it was unclear to what extent animal behavior was the result of instinct or reason. He discovered that animal learning was best described by something else entirely: trial and error learning, or rather, “trial and accidental success” (Thorndike 1898, p. 105). He also either discovered or anticipated many other concepts important to the psychology of learning or cognitive psychology; for example,

“associative shifting” anticipates the discovery of shaping procedures, the “law of assimilation” describes stimulus generalization, the principle of “the prepotency of elements” describes a form of selective attention and claims that “readiness” can be partly innate anticipates the discovery of biological preparedness in learning.

By taking a science-based approach to the field of education, Thorndike demonstrated how one could study best practices in teaching and free the field of education of questionable assumptions about student learning.

It is difficult to overstate Thorndike’s importance to the psychology of learning, especially during the first half of the twentieth century. For example, B. F. Skinner admired Thorndike and saw himself as continuing the work Thorndike had started (Joncich 1968, p. 506). Perhaps none were as complementary as Tolman, who wrote:

The psychology of animal learning—not to mention that of child learning—has been and still is primarily a matter of disagreeing with Thorndike, or trying in minor ways to improve upon him... all of us in America seem to have taken Thorndike, overtly or covertly, as our starting point. And we have felt very smart and pleased with ourselves if we could show that we have, even in some very minor way, developed new little wrinkles of our own. (Tolman 1938, p. 11)

## Cross-References

- [Associative Learning](#)
- [B.F. Skinner](#)
- [Comparative Psychology](#)
- [Edward C. Tolman](#)
- [Feline Cognition](#)
- [Intelligence](#)
- [Law of Effect](#)
- [Learning](#)
- [Operant Conditioning](#)
- [William James](#)

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## EEG

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## Synonyms

[Electroencephalogram](#); [Electroencephalography](#)

## Definition

EEG stands for both electroencephalogram and for electroencephalography. While electroencephalography is the name of a *test* (see below), electroencephalogram is the resulting signal from that



test. Electroencephalography measures the electric field that is naturally elicited by brain activity, usually recorded at scalp level. However, in animal research and in some medical applications, invasive intracranial recording is sometimes used.

## What is Registered by the EEG Test?

Neurons communicate each other through so-called nerve impulses or *action potentials* (see ► [“Action Potentials,”](#) this volume). EEG signal is rarely produced by these action potentials themselves. On the contrary, EEG electrodes register the electrical activity produced by the chain of biochemical processes originated as a consequence of the *action potentials*. Without getting in too much detail, action potentials produced neurotransmitters that bind to receptors, what changes the extra- and intracellular ionic flow of neurons, in what is known as *postsynaptic potentials*. During *postsynaptic potentials*, the ionic concentration outside neurons becomes unevenly distributed, what makes them a dipole with positive and negative charged ends (or poles) (for more detail see Buzsáki et al. 2012). Dipoles generate an electromagnetic field. EEG electrodes can detect this electric signal, while *magnetoencephalography* devices are able to detect the magnetic field.

The electric signal elicited by one neuron is too weak to be detected by EEG, especially when the EEG signal is noninvasively measured at scalp level. Only when a large number (millions) of neurons are active at the same time, the sum of all these small electric fields forms a dipole strong enough for being detected by the EEG electrodes placed at the scalp. Importantly, electric fields only add each other when they have the same orientation (otherwise, they cancel each other). For this reason, EEG signal is produced by brain structures in which neurons share the same spatial alignment. Brain areas with such regular structures are mostly in the cerebral cortex. For this reason, the EEG test is useful for the study of cortical brain activity, and it is considered not suitable for the study of subcortical regions (see Luck 2005). Thus, in brief, we could say that the

EEG test measures the electric field produced by the sum of millions of postsynaptic potentials in the cerebral cortex.

## Advantages and Disadvantages of the EEG Test

One of the greatest advantages of using EEG is its great temporal resolution, in the range of the millisecond (or even better for intracranial measurements). Therefore, the use of EEG is especially appropriate if you are interested in knowing *when* certain brain activity occurs (see ► [“Event-Related Potentials \(ERPs\),”](#) this volume). However, EEG spatial resolution is low as compared with other neuroimaging techniques (e.g., fMRI). The reason for this is that, given a specific EEG distribution at scalp level (i.e., a 2D map of differences in voltage), there are an infinite number of possible combinations of dipoles (in a 3D space) that could cause it. This has been known as the *inverse problem in EEG*, and, although several mathematical tools have been proposed to solve it (see Grech et al. 2008), it is still advisable to combine EEG with other neuroimaging techniques (e.g., fMRI) if you are interested in the neural generators of the EEG signal. The other important limitation of EEG is that it cannot register neural activity from subcortical brain areas.

However, the EEG test has advantages that make it very popular in both research and medical contexts. The EEG test is relatively inexpensive and is noninvasive, and it can be easily combined with other techniques, such as eye-tracking or fMRI.

## Most Common Uses

EEG is used for both research and medical purposes. In research, EEG is widely used in the form of *event-related potentials* (see ► [“Event-Related Potentials \(ERPs\)”](#)). In addition, sleep research has been greatly benefited of the use of EEG. For instance, EEG is used to discriminate and study sleep stages. In medical context, EEG is



used in several clinical circumstances, for instance, for epilepsy diagnosis and monitoring and for monitoring brain activity of patients in a coma or a vegetative state.

## Cross-References

- [Action Potentials](#)
- [Event-Related Potentials \(ERPs\)](#)
- [Evoked Response Potentials](#)

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## Effect Size

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## Definition

An Effect Size (ES) is a statistic or a parameter that reflects the quantitative magnitude of a phenomenon or the intensity of an association among two variables in a meaningful way. Furthermore, it is focused on describing the size of the difference

or the association rather than confounding this with sample size (Coe 2002). It is precisely for this reason that today there is a clear push for ES to be reported and used for discussing the importance of the results obtained in research studies (Kelley and Preacher 2012). For example, quantifies how fast a rat solves a maze when an experimental training is used vs. a control group.

## Introduction

Traditionally, statistical analyses in scientific research have taken the form of significance tests. Fisher developed the Null Hypothesis Significance Testing (NHST), guided by the idea of falsifying the scientist's hypothesis, in line with Popper's falsificationism. Although at first he set the  $\alpha$  at .05 (i.e., the probability to make a false positive, point out that there is an effect when there is not), later he argued against the idea of using threshold probabilities and pointed out that probabilities can be used as a continuous measure of strength of evidence against the null hypothesis (Fisher 1973); nevertheless, he was mistaken as it does not say anything about the value or the magnitude of that evidence.

Additionally, null hypotheses are almost always false (Kirk 2015), i.e., although trivial, a variable always has an effect over others. Therefore, trivial differences can be labeled as statistically significant with a big sample size and conversely, a limited sample size can output a nonsignificant result, although the difference exists. These lead researchers to control for type I error (reflected in  $\alpha$ ), neglecting type II error (i.e., a false negative, not finding an effect that exists; Kirk 2015).

Finally, Null Hypothesis Significance Testing approach goes in another direction than scientific inference (Kirk 2015). The first one is concerned with the probability of obtaining a set of data (or more extreme) if the null hypothesis is true, while the latter has to do with the probability that the null hypothesis is correct based on available data. These two probabilities rarely coincide (Falk 1998).

Criticisms about the Null Hypothesis Significance Testing have led quantitative psychologists

to search manners to complement it. One of them is the effect size. Despite the successive calls from the American Psychological Association (APA; e.g., APA 2020) encouraging its use, the reporting of ES keeps being limited (Barry et al. 2016).

In the literature, there are several definitions of effect size (we presented a general one above). For instance, for Kelley and Preacher (2012) is a quantitative reflection of the magnitude of a phenomenon used for addressing a question while for the APA and the AERA (American Educational Research Association) is a population-based parameter that can be estimated from samples with uncertainty and reflects the index of the effect or the relation between variables (Peng and Chen 2013). According to Kirk (2015), it can be a statistic or a parameter that allows to quantify the size of a phenomenon of interest in an interpretable way. As can be noticed, APA and AERA definition emphasizes the function while others the statistic to be used. Nevertheless, all of them point to the same idea.

Commonly, it has been pointed out that ES are free-scale measures. That is not totally true because some are standardized while others don't. Using a standardized ES allows you to compare data from different scales of the same conceptual variable. The use of an effect in the original metric is easier to interpret.

As has been noted above, hypothesis testing is very sensitive to the sample size. In contrast, ES does not depend on the sample size; however, it can be better estimated with bigger sample sizes.

ESs are very useful in behavioral science. Besides its uses as a report of the quantitative magnitude of a phenomenon, it also allows calculating the required sample size to achieve an acceptable power (i.e., the capacity of the study's to find the phenomenon, inversely related to type II error), integrate the literature from different experiments and reports about the same question by meta-analytic techniques, and determine the practical significance of research results.

## Effect Size Estimates

There are a lot of effect size measures and most of them can be grouped in two categories:

differences between groups (the *d* family) and measures of association (the *r* family).

### Difference Between Groups

The procedures that belong to this family estimate difference of parameters like differences in means or proportions. The group's comparison can be done on continuous and dichotomous variables.

#### Continuous Data

The first effect size measure explicitly labeled as such is part of this family and was introduced by Cohen (1969) is the parameter  $\delta$ , given by:

$$\delta = \frac{\mu_E - \mu_C}{\sigma}$$

where  $\mu_E$  stands for the population mean of experimental group and  $\mu_C$  is the population mean of the control group.  $\sigma$  represents the common population standard deviation. Given that the numerator can be influenced by the scale of measure of the means, is divided by  $\sigma$  to rescale it in units of the amount of error variability in the data (Kirk 2015). For that reason, it is recognized as a standardized measure.

To estimate  $\delta$ , Cohen's *d*, Glass's *g*, and Hedges's *g* had been developed. They have in common that are standardized ES estimators and assume normality of the distribution of data and homoscedasticity (i.e., similar variance between the groups; Peng and Chen 2013; Kirk 2015).

Of these, Cohen's *d* is perhaps the most commonly reported. It ranges from negative infinity to infinite, where the sign – positive or negative – indicates the direction of difference between groups. It is calculated as follows:

$$d = \frac{\bar{X}_1 - \bar{X}_2}{\sigma_{\text{pooled}}}$$

where  $\bar{X}$  stands for sample mean of each group and  $\sigma_{\text{pooled}}$  is calculated as:

$$\sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2}}$$

With  $n$  = sample size and  $s^2$  is the variance statistic.

Cohen (1988) proposed that Cohen's  $d$  of 0.2 is a small effect size, while 0.5 and 0.8 are medium and large, respectively. However, an effect size must be interpreted as small or large linked to the research area, the methods employed and the outcome.

Despite its widespread use, Cohen's  $d$  has some problems. In the first place, it is a biased estimator of  $\delta$ . Also, the estimation of  $\sigma$  depends on the groups size. In the third place, it must be said that if the population variances are not equal, it is problematic estimate  $\delta$  from Cohen's  $d$  because the parameter itself is undefined. Finally, this estimator is sensitive to outliers.

Another estimator of  $\delta$  is Hedges  $g$ . It only introduces a little change in the way of estimating  $\sigma_{pooled}$  respect to the formula just presented: to  $n_1 + n_2$  is subtracted the value of two (i.e.,  $n_1 + n_2 - 2$ ; Hedges 1981)

Finally, we present Glass's  $g$ , which was developed for meta-analysis in the context of an experimental study with one control group and an experimental one. Glass reasoned that comparisons of different experimental groups with control could lead to differing estimates of  $\sigma_{pooled}$ . Due to this, instead of dividing by  $\sigma_{pooled}$  as in Cohen's  $d$ , the mean difference is divided by control's group sample standard deviation (Glass 1976). Depending on the research design, it could be estimating different parameters, so researchers must be cautious. It is traditionally recommended when the homoscedasticity assumption is violated.

### Dichotomous Variables

When the groups are compared on two-level variables (e.g., solve vs. fail to solve a recognition task), comparisons can be based on the probability that the members of a group will be classified in one of the categories.

The two measures that we present here, risk ratio and odds ratio, compare how possible is the occurrence of an event in one group relative to the other group. The first one understands likelihood in terms of probabilities while the second does it in terms of odds. These indexes will be explained using a fictional example.

Imagine that a group of researchers conduct an experiment to learn if the maternal consumption

**Effect Size, Table 1** Number of descendants able to solve a memory task

|        | Solve the task | Fail to solve the task | Total |
|--------|----------------|------------------------|-------|
| THC    | 27 (0.9)       | 3 (0.1)                | 30    |
| No-THC | 7 (0.2)        | 28 (0.8)               | 35    |

*Note:* In the table is shown the number of descendants of mothers treated with Tetrahydrocannabinol (THC) and non-treated rats able to successfully solve an object recognition task and those who failed.

of THC affects the recognition ability of its descendants (measured in an object recognition task, widely used in the study of rodentia memory and the study of memory and learning other species). They obtain the following results, expressed as row data (probabilities) (Table 1):

The risk ratio is calculated dividing the probability of the outcome in one group ( $p$ ) over the probability of that outcome in the other group. In this example, the outcome is the number of rats that solved the task and the groups are THC (i.e.,  $p$ ) and No-THC (i.e.,  $q$ ). In this case it is 4.5.

To calculate the odds ratio, the other measure of this group presented here is needed to compare the odds of certain outcome for each group. The formula is as follows:

$$OR = (p/(1 - p))/(q/(1 - q))$$

Replacing the values with the outcomes from Table 1, we have:

$$OR = (0.9/(0.1))/(0.2/(0.8)) \Rightarrow 36$$

If the result of this division were smaller than one, then the outcome is more likely in the second group. If it is one, then there is no difference. If it were larger than one, then the outcome is less likely in the second group. In this case, the odds ratio is 36, which means that the likelihood of descendants able to solve the task is minor in the group treated with THC.

### Association Measures

The ES of this family includes measures of association among two or more variables.

Pearson's  $r$  (developed in 1896) is probably the most known and several of the other members of this groups are variations of  $r$ . Indicates the degree of linear association between two variables and ranges from  $-1$  to  $+1$ , where  $|1|$  means perfect association. It must be taken account that the scale is not linear (e.g., 0.2 is not twice 0.1). When it is squared, we have the coefficient of determination used in bivariate regression analysis and indicates how much of the variance of one variable can be attributed to the other. It is measured in terms of percentages.

In the context of multiple regression analysis, when one variable can depend on a set of predictors, it is used the coefficient of multiple determination ( $R^2$ ). However, it can be inflated through the sample size and the number of predictors in the model. One alternative developed to deal with this is the adjusted  $R^2$ .

$\eta^2$  or correlation ratio also can correct the resulting inflation of  $R^2$ , although partially. It is more common in psychology that  $R^2$ , allowing to know how many of the dependent's variable variance is accounted by the group membership of the subjects.  $\eta^2$  is also associated to – one-way – Analysis of Variance (ANOVA; i.e., there are more than two groups).

Finally, we present the Cohen's  $f$ . It is used in the context of multiple regression but also in ANOVAS as  $\eta^2$ . In the last case, it can be considered as an extended version of Cohen's  $d$  and it is used to measure the dispersion of means among three groups or more.

## Reporting and Interpreting ES

Although standardized effect size measure makes easier the processes of meta-analysis and power analysis (for example, Cohen's  $d$  can be transformed to Pearson's  $r$ ), the literature suggest the use of ES in the original metrics of the variables in the context of primary research. Both may be useful.

It may be obvious, but the ES reported must be specified. Also, given the lack of agreement on names for estimates of  $\delta$ , for example, its

suggested to inform how ES was calculated (Appelbaum et al. 2018).

Additionally, it is recommended to provide a confidence interval (Steiger 2004). This allows to quantify the accuracy of the point estimate. This must be considered when interpreting. The wider the confidence interval, less mature is a research paradigm. Thus, the research and historical context must be taken account in the interpretation.

## Cross-References

- Fisher
- Odds Ratio

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## Egalitarianism

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## Definition

Egalitarianism is a term used variously in political philosophy, sociology, anthropology, and evolutionary psychology to describe socially organized groups that do not possess hierarchies of universal dominance by a leader or ruling set over all of the remaining members (Fried 1967; Boehm 1999). This entry focuses on anthropological and evolutionary psychological research on the presence and structures of egalitarianism in both human and nonhuman primate groups. It does not address philosophical arguments on egalitarianism.

## Tolerance and Egalitarianism in Nonhuman Primate Societies

To this date, Flack and de Waal's taxonomy of power (2004) in nonhuman primates is considered by some researchers (cf. Watts 2010) as the most comprehensive attempt to classify the distribution of power, and its correspondent political behavior, in societies of nonhuman primates. According to their perspective, dominance style is classified into (1) despotic, (2) tolerant, (3) relaxed, and (4) egalitarian. The distribution of social power associated with a despotic style is uniformly distributed and often found in hierarchical social systems where access to resources is specified by the individuals' social rank. In this type of political organization, coalitions and alliances tend to reinforce the hierarchical system. Alternatively, the distribution of power in societies displaying a tolerant dominance style is relatively equal among most individuals. This dynamic, however, does not entirely preclude some group members from exerting greater social power over others. Tolerance is found in constrained political systems where leveling coalitions, policing, and mediation regulate the frequency and intensity of internal conflict. The distribution of power in societies exhibiting a relaxed dominance style is ephemeral based on occasional differences in individuals' social power. Group members live under an equal outcome system enforced by several coalitions destined to protect and mediate the relations between subordinate and dominant conspecifics. Hence, third-party policing facilitates the equal distribution of resources. Lastly, in egalitarian organizations, some group members act more influentially or powerfully than others, with most individuals not differing across time in their social power. An egalitarian style is often associated with an equal opportunity political system and with the punishment of free riders and non-punishers.

Other authors have also developed similar classifications. Plavcan (2004), for example, ranked numerous extant primate species based on the reported intensity and frequency of intrasexual competition. The author operationalized the intensity dimension as the degree to which individuals



live under strict social hierarchies being based on the outcomes of agonistic interactions and the degree of social tolerance. Under this scheme, species are classified as featuring either low or high intensities of conflict. Alternatively, the dimension of frequency of conflict entailed the probability of intrasexual agonistic interactions based on the number of breeding individuals of the same sex. Hence, the author assigned primate species living in societies with multiple adult males as high-frequency taxa. In contrast, low-frequency primates featured a single breeding male or had a short mating season with several males competing with each other for copulations. Consequently, Plavcan generated a 4-point competition scale based on the combination of intensity and frequency of conflict (level 1, low intensity and low frequency; level 2, low intensity and high frequency; level 3, high intensity and low frequency; and level 4, high intensity and high frequency). Plavcan's scale featured considerable convergent validity with canine size dimorphism, a metric often interpreted as a proxy for the magnitude of intrasexual competition. The author's evaluation revealed that only a small number of primate species fall under the first competition level, whereas the vast majority of primates live in societies featuring some degree of social despotism. Evolutionary researchers, such as Boehm (1999) and Turchin (2016), have developed theoretical and mathematical models for understanding the evolution of egalitarianism in human societies. Per Boehm (1999), prehistoric human communities evolved an array of social mechanisms leading to the establishment of an antihierarchical structure wherein a large coalition holds upstarts and despots at bay.

## Egalitarianism in Human Societies

Prior to a time approximately 12,000 years ago, humans were essentially egalitarian in political structure. Human egalitarianism is commonly found in bands or tribal societies but is often starkly contrasted by despotic behavior. The presence of egalitarianism in a society implies relatively universal equality in the authority of

individual members in relation to others. It is not, however, associated with other potentially unequal traits separating group members. Early work on egalitarianism by Fried (1967) noted substantial individual differences in male strength, prestige, influence, and even authority. Although those differences were openly viewable and acknowledged by other group members, in egalitarian societies, Fried observed that they do not culminate in an organized hierarchy that preferentially benefits individuals with such advantages (Boehm 1999).

Several authors have proposed different explanations of the social and environmental roots of egalitarianism in humans. Sharp (1973), studying Australian Aboriginal societies, proposed the presence of intertwined dominance-submission networks that suppress the possibility for hierarchy. These networks ensured that every male was both submissive and dominant to some other males, thus promoting egalitarianism (Boehm 1999). Turnbull (1965) found, when studying Mbuti Pygmies, that constant demographic modifications to band composition appeared to decrease the effectiveness of control by potential authority figures. Gluckman (1965) pointed to specialization as the leading cause, claiming that nonspecialized systems of production would decrease hierarchy, noting that most nomadic foraging tribes are generalists. Lastly, Slobodin (1969) and Cashdan (1980) both claim that nomadic forms of subsistence place limits on the ability of the group to accumulate vast amounts of resources, acting as a leveling mechanism on social inequality.

Though each of the theories above successfully presented evidence corroborating their view, Guenther (1991) pointed out the heavily localized bases of these theories, noting that none attempted to make universal claims beyond the tribe or band they were studying. Boehm extends Guenther's critique by describing these theoretical viewpoints as not only limited in scope but also sometimes contradictory with observations from nonliterate agricultural societies who are not nomadic, do not practice widespread sharing of food and resources, have many material goods, are economically specialized, and exhibit stability in



group demographics. In such groups, strikingly similar forms of egalitarianism have been observed to that normally remarked upon in the cases of hunter-gatherer societies. Alternatively, Fried (1967) and Boehm (1999), among others, suggest a theoretical importance for a range of leveling mechanisms in explaining egalitarianism. Boehm (1999), for instance, developed a taxonomy of antiauthoritarian sanctions destined to curb the rise of despots and upstarts. Per Boehm, public opinion, criticism, and ridicule operate as mild forms of punishment where the goal is for the target to feel ashamed and rectify his behavior. Alternatively, individuals may also disregard the wishes of upstarts attempting to coerce other group members or abandon the community as a form of avoiding a confrontation with the despot. If, however, the defector's transgressions are thought to threaten the rest of the community members' livelihoods directly, the group can adopt more severe sanctions, including expulsion or execution. In contrast to other forms of punishment, the decision to execute a defector requires the upstart's kin and allies to either participate or at the very least agree with the community's determination. Carrying through an execution without the consent of friends and relatives of the target may lead to a chronic state of internal blood feuds jeopardizing the group's cohesion. It is worth noting that the effectiveness of these mechanisms varies depending on the community's size and the probability of recurrent interactions. Hence, the larger the group and the greater the anonymity among co-residents, the less likely sanctions such as criticism and ridicule will successfully maintain within-group cooperation.

In studying egalitarian societies, Fried noticed the presence of multiple high-status positions replacing that of a single leadership role. This was present across a range of roles, from hunters to shamans, and resulted in a dilution of competitiveness that allowed rivalries formed over status to be resolved in non-zero-sum ways. The study of human universals has continued as a necessary entry to the topic of egalitarianism and its evolutionary significance. Boehm (1999) combines the often separated universals of an innate tendency toward domination and another toward avoiding

being dominated. The favoring of anti-authoritarian political tactics is one such form of avoidance. The second tendency is one that promotes the formation of egalitarian structures. The first does not promote such structures but is not always actively opposing them either. Further, Boehm views such universals as nested within forms of cultural conditioning that can substantially alter their expression. Both individuals and groups, depending on the structure of decision-making in a society, can alter their environments through niche construction, favoring either more egalitarian or more autocratic structures. One possible interpretation of Fried's (1967) and Boehm's (1999) works concerns the fact that forms of cultural conditioning involving the surrounding physical ecology, which controls the degrees of specialism and generalism present in a society, can act as a leveling mechanism. As a result, human egalitarianism differs from nonhuman forms in several ways, which will be discussed further here, most notably avoiding relaxed structures.

## Discussion

Egalitarianism is studied in numerous social contexts. In nonhuman primates, egalitarian social structures strongly influence subsequent behaviors, sometimes species-specific ones, in intrasexual competition and group power relations more generally. In egalitarian political systems, as opposed to despotic ones, individuals distribute power evenly throughout the social group, with punishment expected for those who do not cohere. Additionally, punishment is expected from those who do, as members who do not punish nonconforming members can also be viewed negatively. Although nonhuman primates generally live in systems with some degree of despotic rule, those that do live in egalitarian structures appear to follow these general rules uniformly. Human egalitarianism, however, does differ from nonhuman forms through its stability in expression. In particular, human egalitarianism is marked by universal patterns that appear to be observable exclusively in human social groups

and not other primate species. Additionally, a substantially larger literature has been amassed on human egalitarianism than nonhuman egalitarianism because of the political and sociological emphasis placed on the concept by numerous theorists and philosophers. These approaches have differed from standard operational uses of the term in the empirical sciences that culminate in the observations documented here.

## Cross-References

- [Agonistic Behavior](#)
- [Agonism and Social Status](#)
- [Coalition Enforcement](#)
- [Dominance](#)
- [Dominance Hierarchy](#)
- [Tolerance](#)

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## Egg Brooding

- [Incubation](#)

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## Egg Deposition

- [Spawning](#)

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## Egg Rejection

- [Cuckoo Brood Parasitism](#)

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## Egg Release

- [Spawning](#)

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## Eggs

- [Ova](#)

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## Egocentric Frame

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## Synonyms

[Linear egocentric spatial information](#)

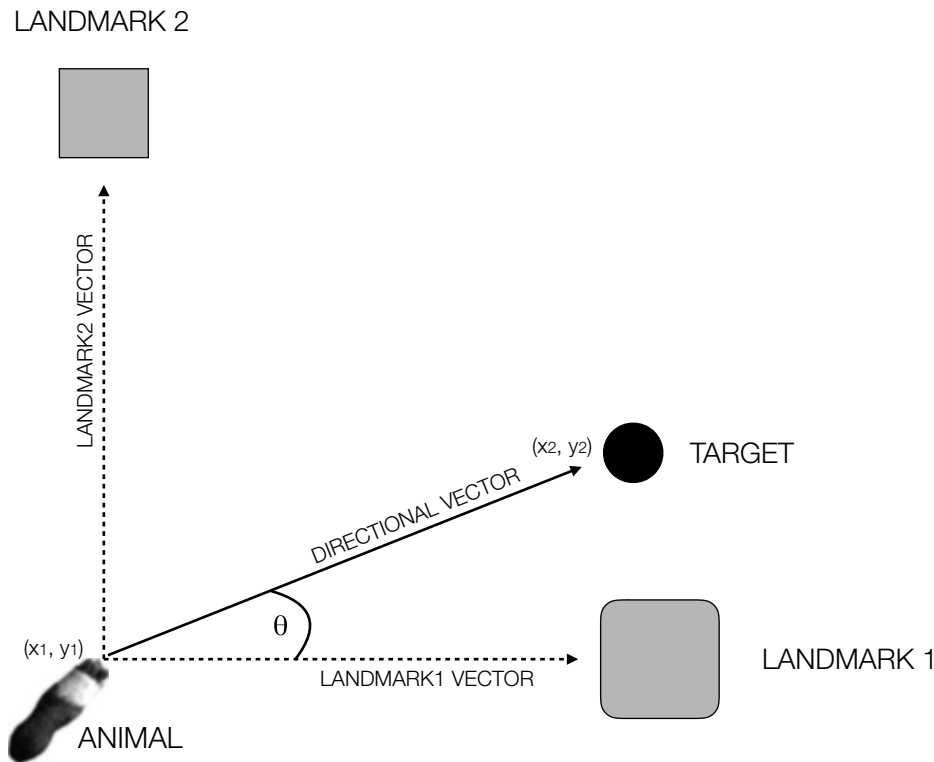
In animal literature, egocentric frames of references have historically been associated with the concept of response learning. However, unlike egocentric information, which is a mental representation of space, response learning is the learning of a motor act. For instance, response learning has been used to describe animal spatial learning abilities in various experimental conditions like the T-maze, in which they learn to discriminate the right and left arms of the maze based on position of their body axis (*e.g.*, see Blodgett and McCutchan 1947). Egocentric spatial information is a much more complex form of spatial cognition than response learning and should be dissociated from it. More specifically, an egocentric frame of reference refers to the directional information derived from the spatial coordinates of an organism within its surrounding environment (Bremner 1998; Fiset et al. 2006). The simplest form of egocentric spatial information is known as linear egocentric information (Fiset and Doré 1996; Fiset et al. 2000), which is used by animals to plan and maintain a single direct trajectory towards a specific location. Dead reckoning, also known as path integration, is a more sophisticated form of an egocentric frame of reference (Étienne and Geffery 2004; Wallace et al. 2002). Animals use this to keep track of their displacements and reorientations through space by encoding vestibular information to return to a desired location. The current definition of an egocentric frame of reference is limited to the linear form of egocentric information.

A linear egocentric frame of reference is best described with a Cartesian coordinate system. In a Cartesian plane, a vector is a line between two points in space: its length represents the distance and its angle represents the direction. Thus, a linear egocentric frame of reference can be defined as a vector between two points in space (see Fig. 1): one point ( $x_1, y_1$ ) is the current spatial coordinate of the animal, and the second point ( $x_2, y_2$ ) is the spatial coordinate of the target location. However, before determining a vector in the direction of the target position, an animal must first establish its current position relative to its own spatial location. This can only be done if the animal constructs a cognitive map of its environment. The concept of a cognitive map (see Gallistel 1990) suggests that an animal encodes

and uses the geometric components of distance and direction (vectors) between landmarks to navigate. Thus, the animal positions itself within its cognitive map by encoding a series of vectors emanating from its current location and pointing to some prominent landmarks (see Landmark 1 and Landmark 2 in Fig. 1). By establishing its position relative to these landmark vectors, the animal now has the liberty to reorient itself relative to its own position without losing track of its position or of the desired location. From these landmark vectors, the animal then determines a directional vector from its current position to its target location. Once this directional vector has been specified, the animal can mentally determine the angular deviation ( $\theta$ ) and the distance between its own spatial coordinates in the environment and those of the target location. It is this last form of spatial representation that corresponds to linear egocentric spatial information.

It is also worth mentioning that egocentric frames of reference are highly vulnerable. Indeed, if the directional vector is broken due to environmental circumstances, such as strong winds that shift an animal off course or some obstacles must be bypassed by the animal, it is highly probable that the animal will lose track of its direction and distance. Nevertheless, when environmental conditions are stable, the use of an egocentric frame of reference is well adapted and suitable.

From a comparative perspective, the domestic dog is a nice model to illustrate the use of a linear egocentric frame of reference in animals. Indeed, a few studies have shown that the domestic dog strongly relies on a linear egocentric frame of reference to search for objects (conspecific, toys, prey) that it has seen disappear (see Fiset et al. 2000, 2006). In these studies, the dogs' task was to search for an attractive object they have seen disappear behind one of the screens placed in front of them. After the disappearance of the object, an opaque panel was introduced in front of the dog for a short retention interval (*e.g.*, 10 s). During this interval, the walls of the testing room as well as the screens were systematically shifted to the right or to the left. At the time of searching, although, from the dog's perspective, the visual properties of the room had drastically changed and that the dogs' body/head orientation did not



**Egocentric Frame, Fig. 1** Illustration of an egocentric frame of reference with a Cartesian coordinate system.  $(x_1, y_1)$  represents the coordinates of the encoding position of

the animal (a dog), and  $(x_2, y_2)$  represents the coordinates of the target location.  $\theta$  represents the estimated angle of the directional vector

correlate with the hiding position, the dogs systematically searched at the initial hiding location. These results therefore support the hypothesis that the domestic dog encodes and uses a directional vector associated with an egocentric frame of reference for finding hidden objects. Additional studies (Fiset 2007, 2009) have also revealed that the domestic dog positions itself in the environment by encoding the distance and the direction from local and global landmarks. These later studies therefore suggest that the domestic dog encodes and uses a metric cognitive map, which is used to determine its egocentric frame of reference.

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## Egotistical Attributions

► [Self-Serving Bias](#)

## Ejaculate

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## Synonyms

[Semen](#)

## Definition

Insemination package of sperm and other compounds produced by the male to facilitate transfer of sperm to the site of fertilization

## Introduction

An ejaculate is composed of male genetic material housed within sperm cells and fluids containing chemical compounds that improve male fertilization success. Sperm is produced in the testes and travels out of the male's body through a system of ducts connected to the accessory reproductive glands (ARGs). The accessory reproductive glands add fluids to the ejaculate for sperm nourishment and protection while inside the female reproductive tract.

## Sperm Production

Spermatogenesis, or the process of sperm production, occurs within microscopic tubules within the testicles. Mature sperm cells develop from

spermatogonia, the undifferentiated male germ cell, and are matured and stored within the male reproductive tract prior to ejaculation. Sperm cells are haploid, meaning they contain only half of the genetic material present in all other cells in the body. As such, sperm cells are recognized as “nonself” and targeted by the immune system. In order to avoid this unwanted immune response, males down-regulate immune activation in the testes through the excretion of androgens. Immune compromised males have less scope for immune suppression and will therefore have compromised sperm production, making sperm quality a reflection of male health (Folstad and Skarstein 1997).

## Sperm Morphology

Although sperm size and shape is remarkably diverse both within and between taxa, most sperm cells are generally composed of four main constituents: the acrosome, nucleus, mitochondria, and flagellum. Sperm are generally minute compared to the size of the egg and typically do not contribute nutrition to the zygote. A proportion of ejaculates typically contain non-viable, morphologically aberrant sperm. The proportion of morphologically normal sperm in an ejaculate can be highly influenced by the environment (e.g., chemical pollutants), pathogens, and degree of sperm competition (Pitnick et al. 2009).

Sperm heteromorphism, typically in the form of dimorphism, occurs when males produce morphologically discrete types of sperm cells. This occurs across a wide taxonomic range and generally results in a genetically functional “eusperm” morph and a nonfertilizing “parasperm” morph (Pitnick et al. 2009). Parasperm are hypothesized to improve fertilization success in many different ways, such as by transporting eusperm, provisioning eusperm, assisting in eusperm capacitation, disabling the sperm of previous mates, or delaying remating in the female, though there is limited evidence supporting any one hypothesis. At present, there is only a rudimentary understanding of the adaptive value of diverse sperm morphologies.

## Accessory Reproductive Glands

The composition and organization of male accessory reproductive glands (ARGs) varies both within and between classes of organisms, but collectively they provide fluid to transport and nourish sperm on their journey to the egg. In internally fertilizing species, these fluids are generally alkaline to buffer the sperm in the acidic environment of the female reproductive tract and commonly possess a mixture carbohydrates, lipids, and amino acids for sperm nourishment (Gillott 2003). In addition to its role in transporting and nourishing sperm, ARG fluids can also change female behavior and physiology. In *Drosophila*, male ARG fluids increase rate of female egg-laying, reduce female receptivity to further matings, and destroy the sperm of previously mated males (Chapman et al. 1995).

## Sperm Competition

Sperm competition intensity has consequences for the composition of the ejaculate, reproductive behavior, and morphology of the male. Sperm competition is the competition that occurs between sperm of different males to fertilize the same egg. Sperm competition theory predicts that when females mate with multiple males, selection would favor males producing the largest number of viable sperm. Supporting this prediction, the number of sperm contained in an ejaculate is positively associated with the intensity of sperm competition in a wide breadth of animals. Larger testes can produce sperm at faster rates and store larger reserves of mature sperm, so larger relative testes size is also consistently associated with degree of sperm competition (Møller and Briskie 1995).

In addition to sperm number, the outcome of sperm competition is also influenced by sperm form and function. Sperm length, velocity, and longevity have consequences for male fertilization success (reviewed in: Snook 2005). Species that engage in sperm competition are commonly observed to have longer sperm capable of swimming at higher velocities (Gage 1994). Sperm longevity declines with sperm length due to the

increased energy demands of a longer tail, thereby increasing the need for multiple ejaculations to ensure paternity in competitively mating species. Quality control of sperm morphology is also more subject to selection in species with intense sperm competition. In a comparative study of seven pairs of closely related insect species, the presence of sperm competition was associated with a larger proportion of normal live sperm per ejaculate (Hunter and Birkhead 2002).

Along with sperm anatomy, mating patterns have had evolutionary consequences for ARG morphology and fluid production. Species that engage in sperm competition have larger ARGs that secrete larger volumes of fluid per ejaculate. Chemicals in the seminal fluid can coagulate after ejaculation and form what are called copulatory, or sperm plugs. Tendency to produce sperm plugs is related to degree of sperm competition and is higher in species engaging in polygynandrous mating systems and lower in species engaging in polygynous or monogamous mating systems (Dixson and Anderson 2002). There are numerous hypotheses for the function of sperm plugs, including chastity enforcement, storage of sperm, prevention of sperm leakage, inducement of pseudopregnancy, and stimulation of sperm transport (Birkhead and Møller 1998). Sperm plug function is likely to vary between species, due to differences in plug density, longevity, and composition.

## Ejaculate Allocation

Though the cost of producing one sperm cell may be tiny, each ejaculate can contain millions of gametes, the production of which amounts to non-trivial energetic costs. As such, males are limited in the number of ejaculates they can produce related to the length of time it takes to restore depleted sperm reserves. This is observed in the diminished amount of both sperm and ARG fluids in successive ejaculates of a wide range of species, a condition which can persist for a considerable amount of time (reviewed in: Dewsbury 1982). Therefore, in species that engage in multiple successive ejaculations, strategic ejaculate allocation would be prudent.



Differential ejaculate allocation is observed in the context of mate quality and perceived sperm competition. Female quality, measured by body size, fecundity, or novelty, can be positively associated with the number of sperm per ejaculate (Spence et al. 2013). Perceived amount of sperm competition, manipulated through the density of rival males at the time of copulation, is also positively associated with sperm expenditure in a variety of insects, fish, and mammals (reviewed in: Parker and Pizzari 2010). For example, male Norway rats copulating in visual proximity to a rival male ejaculate significantly more sperm than those copulating with no other males present (Pound and Gage 2004).

The type of reproductive tactic a male engages in can also influence relative investment in an ejaculate. Males can ensure paternity by investing in features that prevent female copulation with other males, such as large body size and weaponry to win in competitive male interactions (bourgeois males), or males can opt out of direct competition and gain paternity through sneak copulations (parasitic males). Bourgeois males invest less in sperm quality because they experience less sperm competition than parasitic males, as is shown in Atlantic salmon, where small morph males have relatively larger testes, and produce ejaculates with a higher percentage of motile sperm that remain viable longer within the female reproductive tract (Gage et al. 1995).

## Conclusion

An ejaculate is made in the testes and accessory reproductive glands of males, is composed of male gametes and accessory fluids, and is costly to produce. Due to its integral role in reproduction, ejaculate properties are likely to be under strong selection. However, the adaptive significance of the diverse sperm morphologies observed in different species is still not fully understood. Sperm competition has marked evolutionary effects on sperm production, morphology, longevity, and allocation. The study of sperm allocation provides support for the little-studied role of male mate choice as a mechanism of intersexual selection.

## Cross-References

- [Alternative Reproductive Tactics](#)
- [External Fertilization](#)
- [Internal Fertilization](#)
- [Sperm Competition](#)
- [Spermatogenesis](#)

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## Alternative Words

► [Sensing](#)

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## Electric Organ Discharge

► [Electroreceptors](#)

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## Electroencephalogram

► [EEG](#)

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## Electroencephalography

► [EEG](#)

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## Electrogenic

► [Electroreceptors](#)

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## Electromagnetic

► [Electromagnetic Fields](#)

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## Electromagnetic Fields

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## Synonyms

[Electromagnetic](#); [Electromechanical](#); [em](#); [Magnetic](#)

## Definition

Electromagnetic (*em*) field is a property of free space which is caused due to the interaction of oscillating electric and magnetic field when an electric charge is in motion. This *em* field can be considered as a continuous field propagating like a wave at the velocity of light, carrying *em* energy.

## Introduction

Over the years, *em* waves have found applications in various fields such as wireless communications, bioelectronics, RADAR, EMI/ EMC, agriculture, remote sensing, etc. The design of the *em* devices used for such applications are based on the laws and principles of *em* waves. Within the *em* spectrum, an *em* wave is assigned different names based on their frequency of oscillation or its wavelength. Radio waves, microwaves, ultraviolet rays, X-rays, and gamma rays are the *em* waves having frequency in increasing order in the spectrum. The motion of an electron can be assumed to be in uniform electric field or uniform magnetic field or a uniform *em* field. The electric and magnetic fields which can be static or dynamic govern the *em* fields.

## History

In 1845, Michael Faraday studied the effect of magnetic field on the propagation of light and observed that there is a relationship between electromagnetism and light. It was then in the year 1873 when James Clerk Maxwell formulated the essentials of electromagnetic theory based on mathematical considerations derived from electromagnetic wave propagation and the concept of light being a form of *em* energy. During the period 1887–1891, Heinrich Hertz, a German physicist validates Maxwell's theory of *em* waves by carrying out a set of experiments. Until the development of RADAR during World War II in the 1940s, the

growth in *em* technology had not proliferated. During that period, research had started to develop RADAR in practice. Communication systems initiated to be established soon after the birth of radar systems (Pozar 2005).

## Maxwell's Equations

The discovery of *em* wave propagation by Hertz and Marconi is the basis of electric and magnetic phenomena at macroscopic level which is summarized by Maxwell (Pozar 2005; Jordan and Balmain 2013). Maxwell's work was based on empirical and theory established by Gauss, Ampere, Faraday, and others.

Electric and magnetic fields are independent of each other in static *em* fields, whereas the fields are interdependent in dynamic *em* fields, i.e., a time-varying electric field essentially includes a corresponding time-varying magnetic field. The general form of time varying Maxwell's equations or *em* field equations in phasor form

$$\nabla \times \bar{E} = -j\omega \bar{B} \quad (1)$$

$$\nabla \times \bar{H} = j\omega \bar{D} + \bar{J} \quad (2)$$

$$\nabla \cdot \bar{D} = \rho \quad (3)$$

$$\nabla \cdot \bar{B} = 0 \quad (4)$$

where  $\bar{D} = \epsilon \bar{E}$ ,  $\bar{B} = \mu \bar{H}$ ,  $\bar{J} = \sigma_s \bar{E}$ .

$\bar{E}$  is the electric field intensity (V/m),  $\bar{H}$  is the magnetic field intensity (A/m),  $\bar{D}$  is the electric flux density (Coul/m<sup>2</sup>),  $\epsilon$  is the permittivity,  $\bar{B}$  is the magnetic flux density (Wb/m<sup>2</sup>),  $\mu$  is the permeability,  $\rho$  is the electric charge density (Coul/m<sup>3</sup>), and  $\bar{J}$  is the electric current density (A/m<sup>2</sup>), due to an external field, and  $\sigma_s$  is the conductivity.  $\mu_0 = 4\pi \times 10^{-7}$  Henry/m is the permeability, and  $\epsilon_0 = 8.854 \times 10^{-12}$  farad/m is the permittivity of free space.

## EM Field in Material Media

When an electric field *E* is applied to a dielectric material, the polarization of the atoms or molecules

of the material occurs to create electric dipole moments that increases the total flux, *D*. This additional polarization vector is called electric polarization ( $\bar{P}_e$ ), and the electric flux is given as

$$\bar{D} = \epsilon \bar{E} + \bar{P}_e \quad (5)$$

The applied electric field is linearly related to the polarization in a linear medium by  $\bar{P}_e = \epsilon \chi_e \bar{E}$ , where  $\chi_e$  is the electric susceptibility and  $\epsilon = \epsilon_0 \epsilon_r$ . The relative permittivity,  $\epsilon_r$ , of the medium is complex and expressed as  $\epsilon_r = \epsilon'_r - j\epsilon''_r$ ,  $\epsilon'_r$  and  $\epsilon''_r$  being the real and imaginary parts. When an electric field interacts with a dipole, the dipole rotates to align itself according to the polarity resulting in energy loss through the generation of heat. The degree to which the dipole is out of phase with the incident electric field is a characteristic of the material and depends on the frequency of the oscillating electric field. This determines the magnitude of the imaginary part of the permittivity. The larger the imaginary part, the more is the energy dissipated. Thus, the imaginary part of the relative permittivity relates to loss in the system.

Similarly, an applied magnetic field may align magnetic dipole moments in magnetic materials producing magnetic polarization or magnetization ( $\bar{P}_m$ ), and the magnetic flux is given as

$$\bar{B} = \mu \bar{H} + \bar{P}_m \quad (6)$$

The applied magnetic field is linearly related to the magnetization in a linear medium by  $\bar{P}_m = \chi_m \bar{H}$ , where  $\chi_m$  is the magnetic susceptibility and  $\mu = \mu_0 \mu_r$ . The relative permeability,  $\mu_r$ , of the medium is complex in general and expressed as  $\mu_r = \mu'_r - j\mu''_r$ ,  $\mu'_r$  being real part, while  $\mu''_r$  is imaginary.

Equations (1) and (2) can be rewritten as

$$\nabla \times \bar{H} = j\omega \left( \epsilon' - j\epsilon'' - j \frac{\sigma_s}{\omega} \right) \bar{E} \quad (7)$$

$$\nabla \times \bar{E} = -j\omega \left( 1 - j \frac{\mu''}{\mu'} \right) \bar{H} \quad (8)$$

The terms  $\tan \delta_e = \frac{\omega \epsilon'' + \sigma_s}{\omega \epsilon'}$  and  $\tan \delta_m = \mu'' / \mu'$  describe the amount of energy supplied by an

external *em* field that gets dissipated during dipole alignment.

## Uniform Plane Waves

Considering the case of *em* phenomena in free space and solving the field equations, the following equations are obtained as

$$\nabla^2 \bar{E} = \mu\epsilon (j\omega)^2 \bar{E} = -\omega^2 \mu\epsilon \bar{E} \quad (9)$$

$$\nabla^2 \bar{H} = \mu\epsilon (j\omega)^2 \bar{H} = -\omega^2 \mu\epsilon \bar{H} \quad (10)$$

Equations (9) and (10) are known as the wave equations or Helmholtz equations. The electric field intensity or the magnetic field intensity must satisfy the wave equation.  $k = \omega\sqrt{\mu\epsilon}$  is a constant which is called as the wavenumber or propagation constant of the medium.

## Plane Waves in a Lossless Medium

$\epsilon$  and  $\mu$  are real in a lossless medium, so  $k$  is also real. Considering an electric field with no variation in  $x$  and  $y$  directions, the wave equation reduces to

$$\frac{\partial^2 E_x}{\partial z^2} + k^2 E_x = 0 \quad (11)$$

The solutions to the above equation is in the form

$$E_x(z) = E^+ e^{-jkz} + E^- e^{jkz} \quad (12)$$

where  $E^+$  and  $E^-$  are the arbitrary amplitude constants. The first term and the second represent wave traveling in the  $+z$  direction and  $-z$  direction.

The velocity of the wave at which a fixed phase point on the wave travels is called the phase velocity and is given by

$$v_p = \frac{1}{\sqrt{\mu\epsilon}} \quad (13)$$

In free space,  $v_p = 1/\sqrt{\epsilon_0\mu_0} = 3 \times 10^8$  m/s, which is the speed of light.

The wavelength,  $\lambda$ , defined as the distance between two successive maxima or minima on a wave at a fixed instant of time is given as  $\lambda = v_p/f$ .

Similarly,

$$H_y(z) = \frac{1}{\eta} [E^+ e^{-jkz} - E^- e^{jkz}] \quad (14)$$

where  $\eta = \omega\mu/k = \sqrt{\mu/k}$  is the ratio of the  $\bar{E}$  and  $\bar{H}$  fields which is known as wave impedance or intrinsic impedance of the medium. In free space,  $\eta_0 = \sqrt{\mu_0/\epsilon_0} = 377\Omega$ .  $\bar{E}$  and  $\bar{H}$  are orthogonal to each other and orthogonal to the direction of propagation ( $z$ ) and thus a transverse electromagnetic (TEM) wave.

## Plane Waves in a Lossy Medium

For a lossy medium, if it is conductive, then the field equations take the form as

$$\nabla \times \bar{H} = j\omega\epsilon \bar{E} + \sigma_s \bar{E} \quad (15)$$

$$\nabla \times \bar{E} = -j\omega\mu \bar{H} \quad (16)$$

The wave equation for  $E$  then becomes

$$\nabla^2 \bar{E} = -\omega^2 \mu\epsilon \left(1 - j \frac{\sigma_s}{\omega\epsilon}\right) \bar{E} \quad (17)$$

Comparing the above equation with the wave equation for  $\bar{E}$  in the lossless case, it is observed that the wave number  $k^2 = \omega^2 \mu\epsilon$  is replaced by  $\omega^2 \mu\epsilon (1 - j\sigma_s/\omega\epsilon)$  which is known as propagation constant ( $\gamma$ ):

$$\begin{aligned} \gamma &= j\omega\sqrt{\epsilon_0\mu_0}\sqrt{\epsilon_r\mu_r} \left(1 - j \frac{\sigma_s}{\omega\epsilon}\right) \\ &= j \frac{2\pi f}{c} \sqrt{\epsilon_r\mu_r} \left(1 - j \frac{\sigma_s}{\omega\epsilon}\right) = \alpha + j\beta \end{aligned} \quad (18)$$

$\alpha$ , is the attenuation constant which defines the rate at which the fields of the electromagnetic wave attenuates, and  $\beta$  is the phase constant representing the phase change as the wave propagates.

Considering an electric field with no variation in  $x$  and  $y$  directions, the wave equation reduces to

$$\frac{\partial^2 E_x}{\partial z^2} - \gamma^2 E_x = 0 \quad (19)$$

which has solution in the form

$$E_x(z) = E^+ e^{-\gamma z} + E^- e^{\gamma z} \quad (20)$$

The wave traveling to the positive direction has a propagation factor of the form

$$e^{-\gamma z} = e^{-\alpha z} e^{-j\beta z} \quad (21)$$

which in the time domain take the form as  $e^{-\alpha z} \cos(\omega t - \beta z)$ .

A wave is traveling in the +z direction with a phase velocity  $v_p = \omega/\beta$ , a wavelength  $\lambda = 2\pi/\beta$ , and an exponential damping factor. If the loss is removed,  $\sigma_s = 0$ , then  $\gamma = jk$ , and  $\alpha = 0$ ,  $\beta = k$ , and also

$$\gamma = j\omega\sqrt{\epsilon_0\mu_0}\sqrt{\epsilon_r\mu_r} \quad (22)$$

The associated magnetic field can be given as

$$H_y(z) = \frac{j}{\omega\mu} \frac{\partial E_x}{\partial z} = \frac{j\gamma}{\omega\mu} [E^+ e^{-\gamma z} - E^- e^{\gamma z}] \quad (23)$$

The wave impedance,  $\eta$ , is given as

$$\begin{aligned} \eta &= \frac{j\omega\mu}{\gamma} = \frac{j\omega\mu_0\mu_r}{j\omega\sqrt{\epsilon_0\mu_0}\sqrt{\epsilon_r\mu_r}} = \sqrt{\frac{\mu_0}{\epsilon_0}} \sqrt{\frac{\mu_r}{\epsilon_r}} \\ &= Z_0 \sqrt{\frac{\mu_r}{\epsilon_r}} \end{aligned} \quad (24)$$

Equation (23) can be rewritten as

$$H_y(z) = \frac{1}{\eta} [E^+ e^{-\gamma z} - E^- e^{\gamma z}] \quad (25)$$

### Plane Waves in a Good Conductor

In case of a good conductor, the conductive current is much greater than the displacement current, which means  $\sigma_s \gg \omega\epsilon$ . The propagation constant is given as

$$\begin{aligned} \gamma &= j\omega\sqrt{\epsilon_0\mu_0}\sqrt{\epsilon_r\mu_r} \left( \frac{\sigma_s}{j\omega\epsilon} \right) \\ &= (1+j) \sqrt{\frac{\omega\mu\sigma_s}{2}} = \alpha + j\beta \end{aligned} \quad (26)$$

The depth of penetration or skin depth,  $\delta$ , is that depth at which the amplitude of the fields in the conductor is attenuated to  $1/e$  or

approximately 37% of its original value, after traveling a distance of one skin depth, since  $e^{-\alpha z} = e^{-\delta z} = e^{-1}$ :

$$\delta = \frac{2}{\omega\mu\sigma_s} \quad (27)$$

For low loss microwave components, only a thin plating of a good conductor is sufficient, and most of the current flow in thin region near the surface of the conductor.

The wave impedance inside a good conductor is given as

$$\eta = \frac{j\omega\mu}{\gamma} = (1+j) \frac{\omega\mu}{2\sigma_s} = (1+j) \frac{1}{\sigma_s\delta} \quad (28)$$

### Energy and Power in em Field

As *em* waves propagate, the rate at which the energy is transferred from source to receivers is related to the amplitudes of electric and magnetic field strengths of the *em* wave. This energy is either transmitted or dissipated as loss. This rate of energy flow over any closed surface is given by Poynting theorem as

$$\bar{P} = \bar{E} \times \bar{H} \quad (29)$$

having the dimensions as watts per square meter. The direction of flow of energy is perpendicular to  $\bar{E}$  and  $\bar{H}$  in the direction of  $\bar{E} \times \bar{H}$ .

The total power flow is given by the integration of the Poynting vector over any cross-sectional surface as

$$W = \int_S \bar{E} \times \bar{H} \cdot d\mathbf{a} \quad (30)$$

### Application: Wearable Antenna

Increased mobility of human beings and requirement of good and reliable communication systems have added a new dimension to antenna design where convenience in carrying communication gadgets has acquired significant importance. Wearable computing systems are getting popular day by day due to the potential application in health

monitoring, physical training, tracking, etc. Antenna plays a major role in transmitting and receiving of data or signals among short- and long-range wireless communication systems. The design and development of low profile, light weight, low-cost, miniaturized flexible planar antennas are critical for wearable wireless communication systems (Hall and Hao 2012; Khaleel 2014). As the antenna is within a close proximity to the human body, the radiation from the wearable antenna should obey the guidelines of specific absorption rate (SAR) inside the human tissue for safety requirements. A kind of structures known as electromagnetic bandgap (EBG) structures is included in wearable antenna designs to provide isolation from the human body and reduce the SAR in the tissues (Zhu and Langley 2009; Velan et al. 2015).

An EBG structure design exhibiting an operating bandwidth of 27% and a gain of 7.8 dBi at 2.4 GHz has been proposed having low SAR values following the limit specified in the FCC regulations (Ashyap et al. 2017). The antenna which is of low profile integrated with EBG structure is capable enough to be used for wearable medical applications.

### Application: Nanocomposites for Shielding

Electromagnetic emissions are usually generated and transmitted during operation of wireless and electronic devices. Beyond a certain level, these emissions cause operational interferences and are classified as electromagnetic interferences (EMI). Growth in modern high-speed electronic devices packaged alongside the electromagnetic wave emitting sources in devices such as cellular telephony, Wi-Fi, Bluetooth, etc. are posing newer challenges for the designer. In addition, these multitudes of applications have created an even more congested electromagnetic environment leading to operational challenges of systems in close proximity (Tong 2009; Ren et al. 2016).

The em vulnerability and radiation hazard have to be controlled for obtaining an electromagnetically compatible (EMC) environment by reducing EMI. Electromagnetic shields are generally used

for sufficiently reducing EMI. Sandwich composite structures due to their strength, low weight, and good thermal insulation are being used in aerospace, automobiles, consumer industries, etc.

A sandwich structure consisting of carbon woven fabric as surface layer and a mixture of carbon particles/epoxy matrix as a binder is proposed (Novotna et al. 2018). The carbon particles were fused in epoxy in order to enhance the dielectric properties so that the electromagnetic shielding (EMI) properties and sound absorption properties of sandwich composites are improved. All of these properties are important so the application of developed composites could be beneficial in protection of equipment.

### Cross-References

- [Communication](#)
- [Electromagnetic Spectrum](#)
- [Energy](#)

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## Electromagnetic Spectrum

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### Definition

Radiation set of different frequencies composed of waves of radio, microwave, infrared radiation, visible spectrum (or light), ultraviolet radiation, X-rays, and ray's gamma.

### Introduction

Just like several physiscal phenomena, it is not possible to define a starting point for the studies of electricity and magnetism. In 600 BC, the Greek philosopher Thales of Miletus discovered that a bar of amber would be attracted to straw if they were rubbed together. This phenomenon was later called *electricity* because the Greek word *elektron* means “amber.” There are also reports that a shepherd wearing sandals with metal nails used to feel his feet “attached” to the ground as he walked on a mountain. Once the mountain was formed by a stone known as magnetite, this effect was called *magnetism*.

In the nineteenth century, with Maxwell's equations (James Clerk Maxwell, 1831–1879), it was

shown that electricity and magnetism corresponded to the same force, that one could not exist without the other. Therefore, the study of the two forces received the name of electromagnetism. Maxwell's equation also shows that light is an electromagnetic wave, instead of the prediction of Newton's theory that light had a corpuscular character, i.e., composed of “tiny bodies,” like atoms. For more details, see “A Dynamical Theory of the Electromagnetic Field” by Maxwell (1864).

Electromagnetic waves may have different lengths (i.e., measure from a crest – the highest point of a wave) and consequently different frequencies (i.e., number of wave oscillations over time), as this relation can be seen in Fig. 1a and b. The set of these frequencies compose the *electromagnetic spectrum* (Fig. 2). Visible and invisible light are both forms of electromagnetic radiation of different wavelengths. More details about the electromagnetic spectrum can be verified in *Introduction to Electrodynamics* by Griffiths (2017).

The vision and delimitation of colors is a characteristic of each ► [species](#) eyes. For example, the spectrum range corresponding to the human eye, called *visible spectrum*, starts with violet (larger wavelengths, 760 nanometers (nm)) and ends with red (smaller wavelengths, 360 nm) (Slinye, 2016). Thus, any light with wavelengths below violet (<360 nm, e.g., ultraviolet, X-ray, gamma rays) or above red (>760 nm, e.g., infrared, microwave) cannot be seen by humans but may be possible for other animals (*for details*, see brief examples below and a chapter ► [“Evolution of Animal Color Vision”](#) by Jacobs, in this volume).

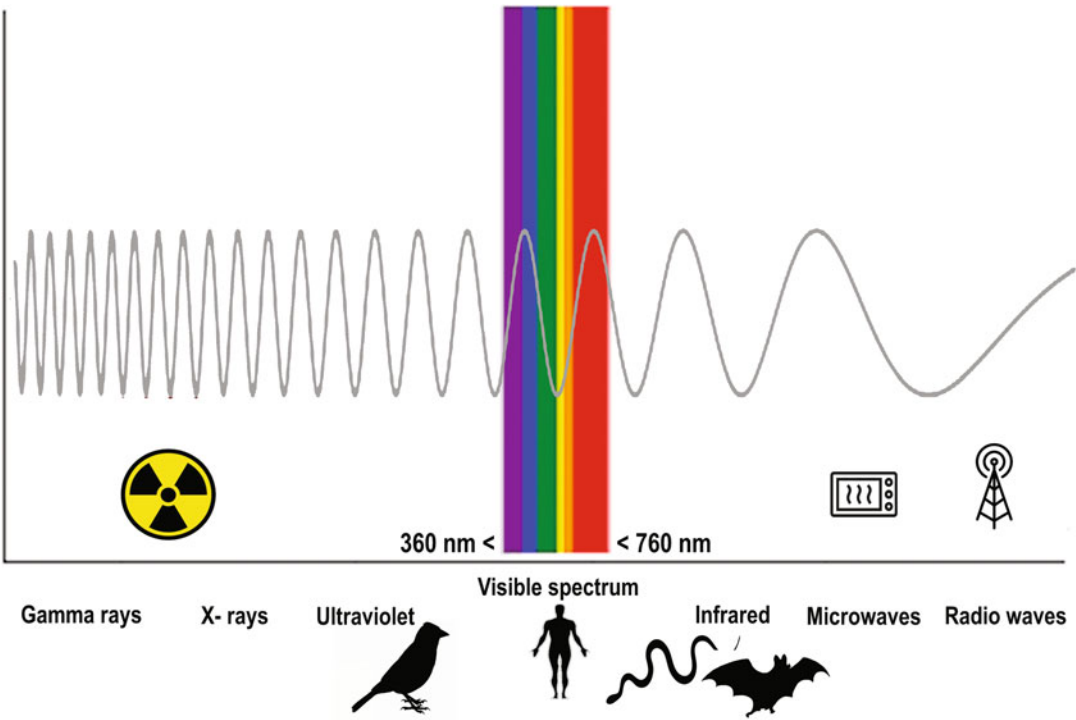
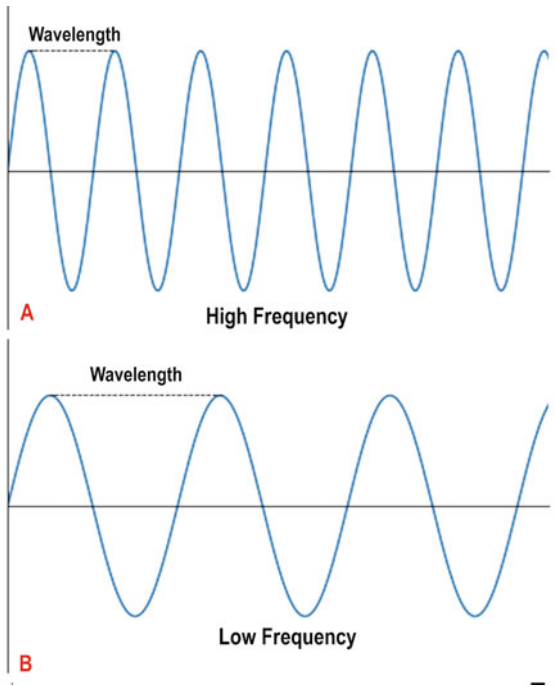
### Biological Examples

#### Humans: Visible Spectrum and Color

This range is composed of the following colors: red, orange, yellow, green, blue, and violet, with electromagnetic wavelengths from about 360 to about 760 nanometers (nm) (*for details*, see Slinye, 2016). The human eye has photon receptor cells called cones and rods that transmit information to the optic nerve, and finally to the brain, which create the image. Human vision is trichromatic, i.e., composed of three types of cones –

**Electromagnetic Spectrum,**

**Fig. 1** Relation between wavelength and frequency. (a) Shorter wavelength and higher frequency; (b) higher wavelength and shorter frequency



**Electromagnetic Spectrum, Fig. 2** The electromagnetic spectrum with different wavelengths and frequencies. Visible spectrum and biological examples of detection

longwave (L) sensitive to red (R) colors, mediumwave (M) sensitive to green (G) colors, and shortwave (S) sensitive to blue colors (B). By varying the amount of red, green, and blue light, and mainly by the interaction of these L, M, and S cones, the perception of all the colors in the visible spectrum can be possible to humans. The sensitivity of the human eye is varied according to the cone interactions, and the colors are classified according to the frequency of the light.

#### ► **Birds: Ultraviolet Vision**

Bird eyes are sensitive to different wavelengths through receptor cells, permeable lenses, and corneas. Unlike humans, avian vision is tetrachromatic: they have four single cone types that have peak sensitivities, L, M, and S, as human eyes, and ultraviolet (UV). UV is a radiation with a wavelength less than human visible light, with about 380 nm to 1 nm. This UV-sensitive cone makes birds see a greater diversity of colors than that detected by humans, and it can be used for food detecting and in feeding strategy, as in *Birds of Prey*. Also, most bird families show some UV reflectance in feathers, with an important ecological significance, acting on partner choice mechanism and communication (*for details*, see Rajchard, 2009).

#### **Bats and Snakes: Infrared Detection**

Infrared radiation is the portion of electromagnetic radiation characterized by wavelengths greater than 700 nm, or the longest wavelengths of visible light. Some snakes of the families Boidae, Pythonidae, and Viperidae have specialized receptors on the face to detect and locate ► [prey](#) and predators. Boidae and Pythonidae snakes may have scattered innervations or pits in the labial scales, and some Viperidae snakes (the subfamily Crotalinae) have only one pit on each side of the face, called pit organs. These innervations can be stimulated by infrared radiation and transmit that information to the optic tectum, by the trigeminal nerve. Snakes may create a unique image from the eyes and infrared radiation receptors. As a result, snakes can identify the size and position of prey.

Some vampire bats (*Desmodus* genus) have sensors specialized for infrared radiation in their nasal pads and nose-leaf. This sensory mechanism is connected to the trigeminal nerve, and it allows

to locate and prey on homeothermic animals, because it is possible to detect the vessels of their prey beneath thick skin. This is the main difference between bats and snakes on infrared detection; bats have ability not only to detect body heat but also for the detection of vital blood meals (*for details*, see Jones et al., 2013).

### **Cross-References**

- [Birds](#)
- [Evolution of Animal Color Vision](#)
- [Photoreceptors](#)
- [Prey](#)
- [Species](#)

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### **Electromechanical**

- [Electromagnetic Fields](#)

### **Electrophoresis**

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### **Definition**

Electrophoresis is the migration of charged particles in a liquid medium under the influence of an electrical field.

## Introduction

The term electrophoresis describes the migration of a charged particle under the influence of an applied electric field. Many important biological molecules, such as amino acids, peptides, proteins, nucleotides, and nucleic acids, possess ionizable groups and, therefore, at any given pH, exist in solution as electrically charged species either as cations or anions. Under the influence of an electric field, these charged particles will migrate either to the cathode or to the anode, depending on the nature of their net charge.

Charged molecules in an electric field migrate at a speed determined by their charge-to-mass ratio. According to Coulomb's law of electrostatics, an ion with charge  $Q$  in an electric field of strength  $E$  will experience an electric force:

$$F_{\text{electrical}} = QE$$

The resulting migration of the charged molecule through the solution is opposed by a frictional force:

$$F_{\text{frictional}} = Vf$$

where  $V$  is the rate of migration of ion and  $f$  is frictional coefficient.

Frictional coefficient depends on the size, shape, and viscosity of the solution. In constant electric field, the force on ion balances each other:

$$QE = Vf$$

So each ion moves with a constant characteristic velocity. Thus the rate of migration is directly proportional to the field strength and to the net charge of the molecule.

An ion electrophoretic mobility,  $\mu$ , is defined as the rate of migration (cm/s) per unit field of strength (volt/cm):

$$\mu = V/E = Q/f$$

So according to the equation, if two molecules have the same mass and shape, the one with the greater net charge will move faster toward an electrode (Stellwagen 2009).

When a mixture of proteins is applied to a gel and an electric current is applied, smaller proteins migrate faster than larger proteins through the gel. The rate of movement is influenced by the gels' pore size and the strength of electric field. The pores in a highly cross-linked polyacrylamide gel are quite small. Such a gel could resolve small proteins and peptides, but large proteins would not be able to move through it. SDS-PAGE is rapid, sensitive, and capable of a high degree of resolution. SDS denatures proteins, causing multimeric proteins to dissociate into their subunits, and all polypeptide chains are forced into extended conformations with similar charge-to-mass ratio. SDS treatment gives negative charge to all proteins, so the molecular weight of protein becomes the sole determinant of the migration rate of proteins in SDS-PAGE. Bands resulting from electrophoretic separation can be located by a variety of staining techniques like Coomassie staining or silver staining (Fig. 1).

## Two-Dimensional Gel Electrophoresis

In 2D electrophoresis, proteins are separated in two sequential steps: first by their charge and then by their mass. During first dimension, protein samples are run on an immobilized pH gradient gel which separates them according to their isoelectric point. In the second dimension, proteins separated according to their molecular weight by SDS-PAGE (Fig. 2).

## Native PAGE

If a particular protein (e.g., enzymes) has to be separated on the basis of its biological activity, then SDS-PAGE cannot be used as the protein is denatured by the SDS. In native gels, non-denaturing condition is used. Since all the proteins in the sample being analyzed carry their native charge at the pH of the gel, proteins separate according to their different electrophoretic mobilities.

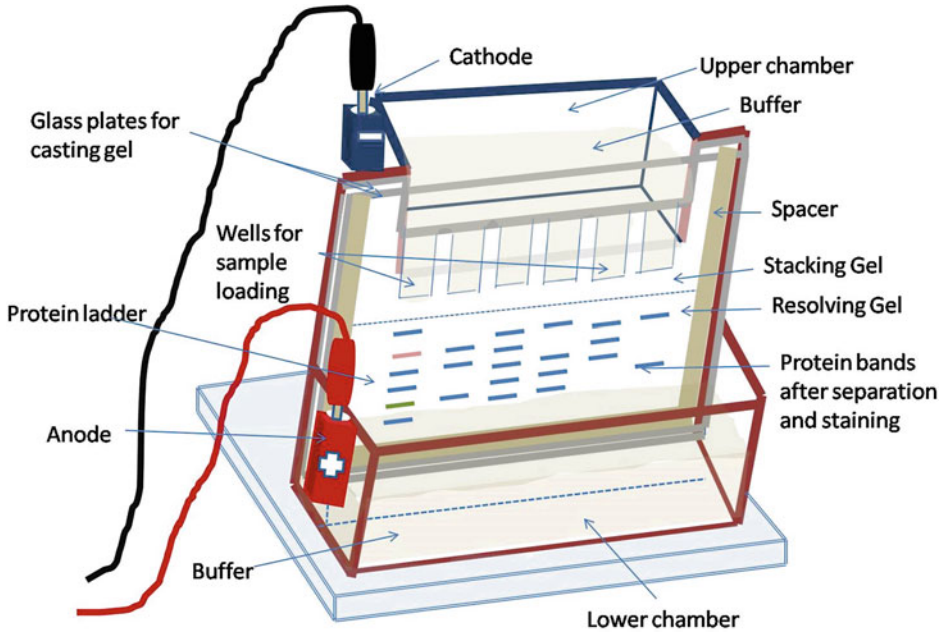
## Electrophoresis of Proteins

### Sodium Dodecyl Sulfate-Polyacrylamide Gel Electrophoresis (SDS-PAGE)

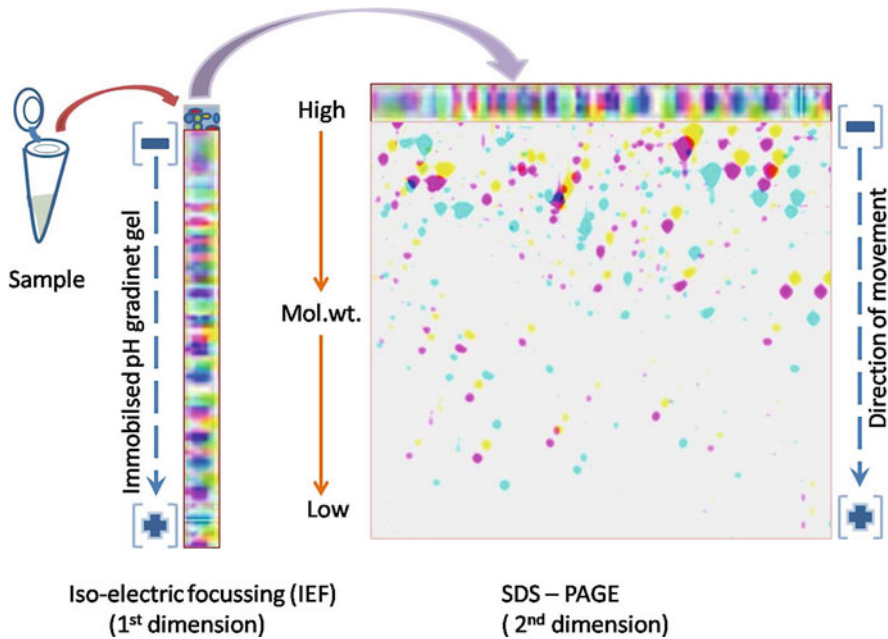
Electrophoretic separation of proteins is most commonly performed in polyacrylamide gels.

## Electrophoresis of Nucleic Acids

Gel electrophoresis is the process by which pieces of DNA of different sizes can be resolved. An agarose or polyacrylamide gel is loaded with the DNA fragments, and current is passed through the



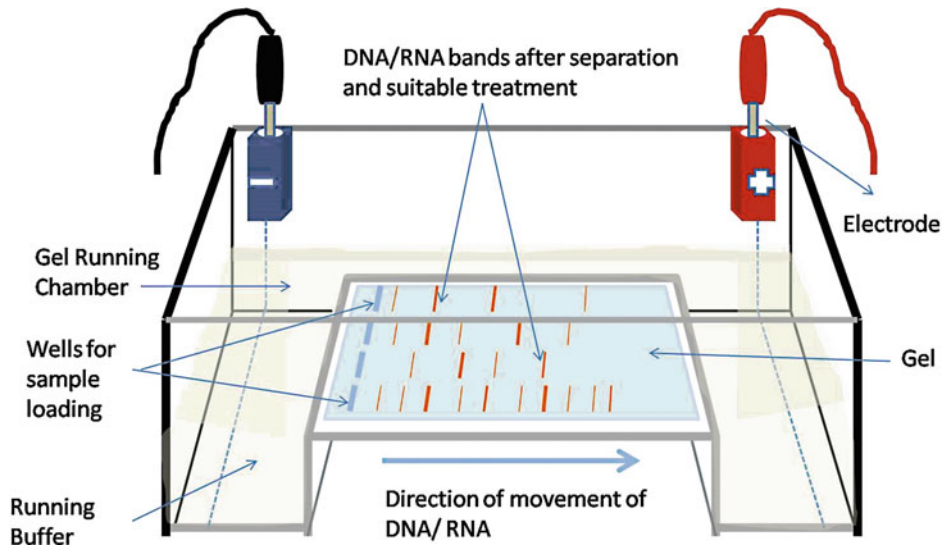
**Electrophoresis, Fig. 1** Schematic representation of polyacrylamide gel electrophoresis of proteins



**Electrophoresis, Fig. 2** Schematic representation of 2D gel electrophoresis of proteins

gel. Since DNA is negatively charged, it will migrate toward the positive pole. However the DNA will not migrate at the same rate. Larger

pieces of DNA collide with the gel more often and are slowed down, while smaller pieces of DNA move through more quickly. The following



**Electrophoresis, Fig 3** Schematic representation of agarose gel electrophoresis of nucleic acids

factors determine the rate of migration of DNA through agarose gels:

- Molecular size of DNA
- Concentration of agarose
- Conformation of the DNA
- Presence of ethidium bromide (EtBr) in the gel and electrophoresis buffer
- Applied voltage (Sambrook et al. 2001)

DNA or RNA bands can be visualized under UV transilluminator by using EtBr in the gel (Fig. 3).

### Pulsed-Field Gel Electrophoresis

Pulsed-field gel electrophoresis (PFGE) is a technique used for the separation of large deoxyribonucleic acid (DNA) molecules by applying to a gel matrix an electric field that periodically changes direction.

While in general small fragments can find their way through the gel matrix more easily than large DNA fragments, a threshold length exists above 30–50 kb where all large fragments will run at the same rate and appear in a gel as a single large diffuse band. However, with periodic changing of field direction, the various lengths of DNA react to the change at differing rates. That is, larger pieces of DNA will be slower to realign their charge when field direction is changed, while

smaller pieces will be quicker. Over the course of time with the consistent changing of directions, each band will begin to separate more and more even at very large lengths. Thus separation of very large DNA pieces using PFGE is made possible.

### Cross-Reference

- [DNA](#)
- [DNA Marker](#)
- [Protein](#)
- [RNA](#)

### References

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### Electroreception

- [Cetacean Sensory Systems](#)
- [Monotreme Sensory Systems](#)



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## Electroreceptor

### ► [Electroreceptors](#)

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## Electroreceptors

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### Synonyms

[Ampullae of Lorenzini](#); [Electric organ discharge](#); [Electrogenic](#); [Electroreceptor](#); [Tuberous electroreceptor](#)

### Introduction

All living organisms maintain homeostasis, which necessitates that the concentration of ions within the body differs from the outside environment. As a result, a voltage develops across the skin. In an aquatic environment, this voltage has the potential to leak out and create a charge distribution around the body. These charges can be detected by specialized organs known as electroreceptors. Because electroreception relies upon a conductive medium in which to operate, it is restricted to aquatic species, or species that forage in moist environments.

### Prevalence

Electroreception is an ancient sensory modality that arose at the base of the vertebrate clade (Albert and Crampton 2005). It remains widespread among extant taxa but has been largely lost among the most speciose groups, the amniotes and actinopterygian (ray-finned) fishes. Among the agnathans, it is found in the Petromyzontiformes (lampreys) but is absent in the Myxiniiformes (hagfish). Among the

gnathostomes, it is present in the Chondrichthyes and most of the Osteichthyes, with the exception of the Holostei (gars and bowfin) and the Euteleostei. Despite its loss in the Euteleostei, it has re-evolved within the Ostariophysi (catfishes and knifefishes). In addition to its reappearance within some members of the euteleost lineage, electroreception has also independently re-evolved within two amniote lineages: the monotremes (platypus, echidna) and most recently in a single species of cetacean, the Guiana dolphin, *Sotalia guianensis*. Among the amphibians, electroreception is identified in the aquatic larval forms of caecilians and some urodeles (salamanders), but not the anurans (frogs). Although electroreception is taxonomically widespread, the total number of extant species that are electroreceptive is only about 10% of the total number of species within the vertebrate clade (Albert and Crampton 2005).

Despite the diversity of species that have been documented to be electroreceptive, the majority of research on electroreception is devoted to either the electrogenic mormyrid and gymnotid fishes or the largely non-electrogenic elasmobranch fishes (sharks and rays). Both groups utilize ampullary electroreceptors, which are tuned to low-frequency stimuli, to passively detect the bio-electric fields of prey. Ampullary electrosensory organs were first described in the sixteenth century from sharks and rays, and the elasmobranchs are renowned for their acute electrosense.

### Structure

Electroreception in elasmobranchs is mediated by a sensory system known as the ampullae of Lorenzini. The ampullae of Lorenzini consist of hundreds to thousands of glycoprotein-filled tubules which extend from pores on the surface of the head and body of elasmobranchs to blind-ending ampullae within the head that are lined with sensory hair cells. The glycoprotein gel is highly conductive with a conductivity almost equal to that of seawater (Murray and Potts 1961). In contrast, the cells that comprise the walls of the tubules are bound by tight junctions, which serve

to insulate the gel in the tubules from the surrounding tissues within the head (Waltman 1966). Compared to the walls of the tubules, shark tissue and the skin offer a relatively low electrical resistance, which means that the basal surface of the electrosensory cells in the head will be at nearly the same voltage as the surrounding seawater immediately adjacent to the head in that region. In the presence of an environmental electric gradient, the apical surface of the electrosensory cells facing the lumen of the ampulla will be at the same potential as the pore opening of the insulated tubule. The difference in electric potential from the pore opening on the surface of the head to the basal surface of the electrosensory cells lining the ampulla is a function of the position of the pore and length of the tubule with respect to the electrical voltage gradient across the head. This likely enables the animal to derive magnitude and direction information from environmental electric fields, which provides it with a richly detailed electric landscape.

## Function

The ecological function of the ampullae of Lorenzini remained uncertain for many years because electrophysiological experiments demonstrated that the system responded to a variety of stimuli, including mechanical pressure, temperature changes, salinity changes, and electrical stimuli. Behavioral experiments finally determined that the ampullae of Lorenzini act as electroreceptors, which can detect the presence of prey (Kalmijn 1971). Subsequently, electroreception was demonstrated to be used for mate detection (Tricas et al. 1995) and predator detection (Sisneros et al. 1998). It is also hypothesized that elasmobranchs can utilize their electroreceptors to detect the electric fields induced around their body as they swim through the earth's magnetic field (Kalmijn 1974). An extension of this hypothesis is that sharks might use their electroreceptors to enable them to orient to geomagnetic anomalies on the sea floor (Klimley 1993). Although there is a theoretical basis for support of these magnetic-induction-based hypotheses, definitive empirical data are lacking.

## Tuberous Electroreceptors

In addition to passive electroreception mediated through the ampullary electroreceptors, which respond best to low-frequency (<50 Hz) stimuli, electrogenic species, such as the gymnotids and mormyrids, also possess specialized tuberous electroreceptors, which are best tuned to higher-frequency stimuli of 50–2000 Hz (von der Emde 1998). The tuberous electroreceptors work in conjunction with the electric organ discharge (EOD) in these electrogenic species to detect the active EOD of other electrogenic individuals (electrocommunication). Sympatric species produce species-specific EODs, which facilitate identification of conspecifics for mating. The tuberous electroreceptors are also used to detect environmental distortions of their own self-generated electric fields (electrolocation). This enables these species to successfully navigate their environment by sensing and avoiding the presence of conductive and resistive objects. Thus, the tuberous electroreceptors can serve dual purposes, electrocommunication and electrolocation, and, when combined with ampullary electroreceptors for prey detection, can provide the animals with a comprehensive survey of their electrical environment.

Because humans lack an electric sense, we fail to appreciate the wealth of electrical information available in the environment. All living organisms in an aquatic medium generate an electric field around their body, which varies in the range from microvolts to millivolts, and these bioelectric fields provide an important sensory cue that can serve to inform electro-sensitive species. The persistence of electroreception throughout the vertebrate clade, and its reappearance in numerous lineages, illustrates the evolutionarily adaptive value of electroreception.

## Cross-References

- ▶ [Caudata Cognition](#)
- ▶ [Caudata Sensory Systems](#)
- ▶ [Chondrichthyes Morphology](#)
- ▶ [Chondrichthyes Navigation](#)
- ▶ [Chondrichthyes Sensory Systems](#)
- ▶ [Electromagnetic Fields](#)

- Electromagnetic Spectrum
- Homeostasis
- Mechanoreceptors
- Sensory Receptors

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## Elektrokardiography (EKG)/ Electrocardiography (ECG)

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## Historical Perspectives

Elektrokardiography (EKG), or electrocardiography (ECG), is a technique that records the

electrical activity of the heart. The early work of Italian physician and physicist Dr. Luigi Galvani laid the foundation for the field of electrocardiography when he discovered and recorded electrical currents in frog leg skeletal muscles, thus demonstrating that muscle is an electrically excitable tissue. Galvani's seminal findings were published in *De viribus electricitatis in motu musculari commentaries* (Translation: *Commentary on the Effect of Electricity on Muscular Motion*) in 1791 (Galvani 1791). In 1842, Carlo Matteucci observed that electrical currents accompanied each heartbeat in frog experiments. The works of Galvani and Matteucci provided a foundation for study of the electrical and mechanical events of the cardiac cycle. In 1887, Augustus Desire' Waller recorded the first electrocardiogram using a Lippman capillary electrometer and electrodes placed on a human subject's torso (Besterman and Creese 1979). The resulting electrocardiogram was of little clinical value, as the tracings showed only two deflections. Yet, Waller's contributions to the field of electrocardiography were invaluable, as he was first to demonstrate that the heart's electrical activity could be recorded. It was Willem Einthoven, Dutch professor of physiology at the University of Leiden, who was credited with the "discovery of the mechanism of the electrocardiogram" and his achievement earned him a Nobel Prize for Physiology and Medicine in 1924, 2 years after Waller's death. Einthoven initially utilized the Lippman capillary electrometer but made a mathematical correction accounting for inertia. By doing so, Einthoven was able to record five deflections on the electrocardiogram, which he named PQRST, perhaps to follow Descartes tradition (though no one knows for certain). At the 1893 Dutch Medical Meeting, Einthoven coined the term "elektrokardiogram," yet he attributed it Waller as a token of respect (Snellen 2015). In contemporary scientific discourse, the term electrocardiogram (ECG) is also used to refer to the "elektrokardiogram" (EKG) named by Einthoven. It was also Einthoven who first speculated that there may be differences in the electrocardiograms of healthy and diseased hearts. This prompted Einthoven to improve the fidelity of electrocardiogram

recordings. In 1901, Einthoven developed a string galvanometer capable of producing high-quality electrical recordings (Einthoven 1903, 1964). Sir Thomas Lewis, a British cardiologist, was another prominent figure in the history of the early electrocardiogram. Lewis' notable accomplishment was using the ECG for the characterization of cardiac arrhythmias; he first identified atrial fibrillation and flutter on the ECG (Lewis 1921). Others also worked to use the ECG for clinical applications. In 1906, Willem Einthoven was the first scientist to observe heart block on the ECG (Cooper 1986). Frank Norman Wilson receives recognition for using the ECG to observe bundle branch block (Wilson et al. 1932).

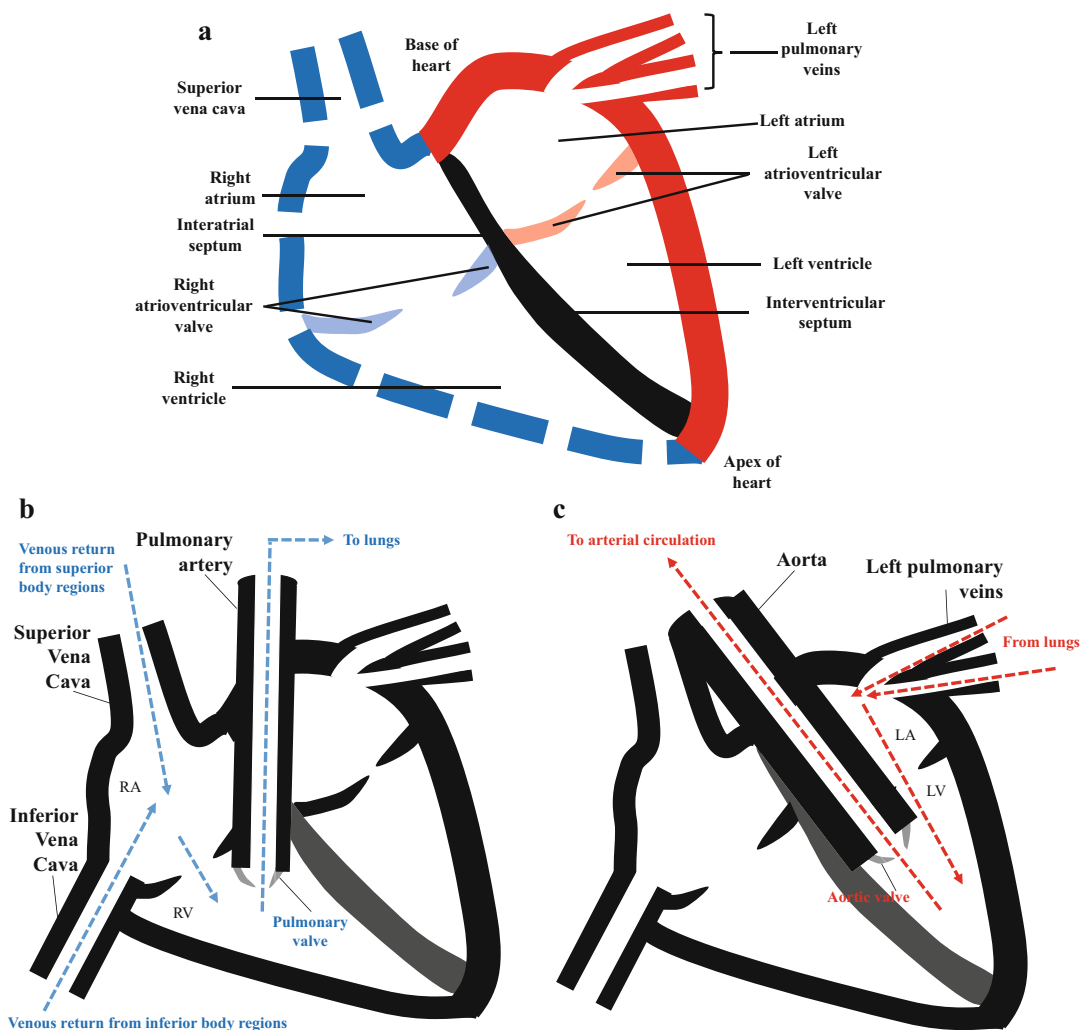
### Brief Overview of Heart Anatomy

The heart is a valved, muscular structure responsible for pumping blood through the blood vessels of the body (Fig. 1a). The heart is a critical component of the nutrient and gas delivery system of the mammalian body. The mammalian heart contains four chambers. The two superior blood-receiving chambers are called atria, while the inferior blood-pumping chambers are termed ventricles. The two atria are separated by the interatrial septum, while the two ventricles are separated by the interventricular septum. The septa of the heart ensure that blood on the left and right sides of the heart are isolated from each other. The heart also contains two atrioventricular valves and two semilunar valves. The atrioventricular (AV) valves are located in between the atria and ventricles. The AV valves are able to open and close, thereby regulating blood flow between the atrium and ventricle. When the AV valves open, blood moves into the ventricles from the atria. When the AV valves close, the atria relax and fill with blood from the systemic circulation (right atrium) or pulmonary circulation (left atrium) while the ventricles contract and pump blood to the lungs (via right ventricle and pulmonary arteries) or systemic circulation (via left ventricle and aorta). The heart also contains valves called semilunar valves,

which are found between the ventricles and great vessels (pulmonary artery on right side; aorta on left side) of the heart. The semilunar valve between the right ventricle and pulmonary artery is called the pulmonary semilunar valve. The semilunar valve between the left ventricle and aorta is called the aortic semilunar valve (Saladin 2017).

### Path of Blood Flow Through Heart and Role of Pressure

The right side of the heart receives oxygen-poor blood from the systemic venous circulation (and coronary veins). The superior and inferior vena cavae drain oxygen-poor blood into the right atrium (Fig. 1b). As the volume of blood increases in the right atrium, the pressure climbs within the right atrium. When pressure in the right atrium exceeds the pressure in the right ventricle, the right AV valve opens and blood moves into the right ventricle. As blood moves into the right ventricle, the volume and pressure increase in the right ventricle. When the pressure in the right ventricle exceeds the pressure in the right atrium, the right AV valve closes and the right ventricle contracts. As the pressure in the right ventricle exceeds the pressure in the pulmonary artery, the pulmonary valve opens and blood moves into the pulmonary artery. The oxygen-poor blood is carried to the lungs by way of the left and right pulmonary arteries. After the blood undergoes gas exchange in the lungs, dropping off carbon dioxide and picking up oxygen, it returns to the left side of the heart via the left and right pulmonary veins (Fig. 1c). The pulmonary veins drain into the left atrium. As the left atrium fills with blood, the pressure inside the left atrium increases. When the pressure in the left atrium exceeds the pressure in the left ventricle, the left AV valve opens and blood moves into the left ventricle. As blood collects in the left ventricle, the pressure increases. The left AV valve closes and the left ventricle contracts. As the pressure in the left ventricle exceeds the pressure in the aorta, the aortic valve opens and blood moves into the aorta. Blood traveling through



**Elektrokardiography (EKG)/Electrocardiography (ECG), Fig. 1** (a) Overview of heart chambers, septa, and atrioventricular (AV) valves. (b) Path of blood flow through right side of heart. Arrows indicate movement of oxygen-poor blood through right side of heart. RA = Right

atrium. RV = Right ventricle. (c) Path of blood flow through left side of heart. Arrows indicate movement of oxygen-rich blood through left side of heart. LA = Left atrium. LV = Left ventricle. Right pulmonary veins are not shown

the aorta continues through the systemic arterial circulation, thereby delivering nutrients and gases while picking up waste materials, in the cells and tissues of the body. It is important to note that the events occurring on the right and left sides of the heart are occurring nearly simultaneously. The ventricles contract as a unit, while the atria relax. The atria contract as a unit, while the ventricles relax. The timing of contraction/relaxation events is coordinated by an electrical

system of the heart called the cardiac conduction system (Fox 2016; Saladin 2017).

## The Electrical Activity of the Heart

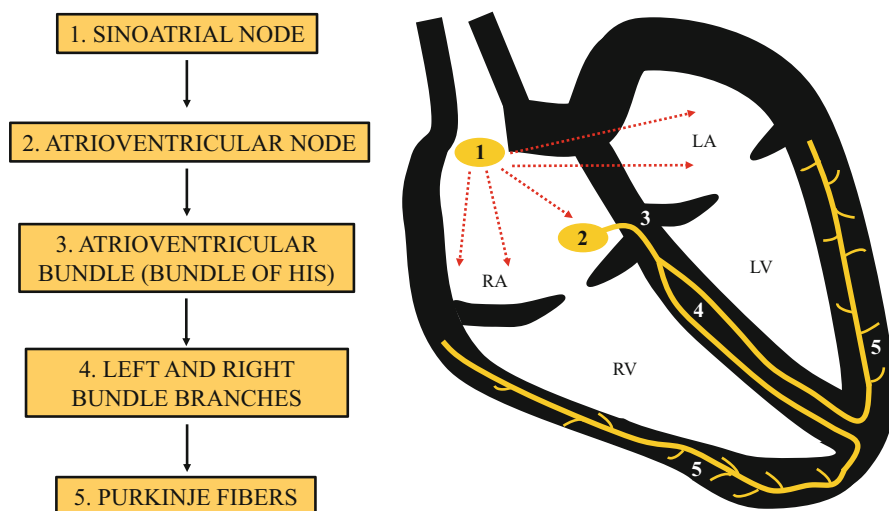
The cardiac cycle consists of contraction and relaxation events, named systole and diastole, respectively. In each instance of systole, the

contraction event is preceded by an electrical signal. Thus, the electrical events occurring in the heart serve as precursors for the mechanical aspects of cardiac function (i.e., pumping blood); a deviation in normal electrical function in the heart can translate to a mechanical deviation from normal. The structures which generate the rhythm of the heart are part of the cardiac conduction system. The cardiac conduction system is comprised of electrically excitable pacemaker cells and nerve fibers which extend throughout the myocardium (muscle) of the heart. The pacemaker of the cardiac conduction system may be neurogenic (made of neurons) or myogenic (made of modified muscle cells). Invertebrates, such as decapod crustaceans (shrimps, crabs, etc.), utilize a neurogenic pacemaker (Wilkins 1999). Vertebrates, including primates, utilize a myogenic pacemaker. In vertebrates, the cardiac conduction system is comprised of a sinoatrial (SA) node, atrioventricular (AV) node, atrioventricular (AV) bundle, left and right bundle branches, and Purkinje fibers (Fig. 2). The sinoatrial node, the atrioventricular node, and Purkinje fibers all have the capacity to serve as the pacemakers of the cardiac conduction system, but the pacemaker that fires action potentials with the highest frequency will set the heart rate by overriding the

electrical activity of the slower pacemakers (Boron and Boulpaep 2012; Saladin 2017).

### Sinoatrial (SA) Node

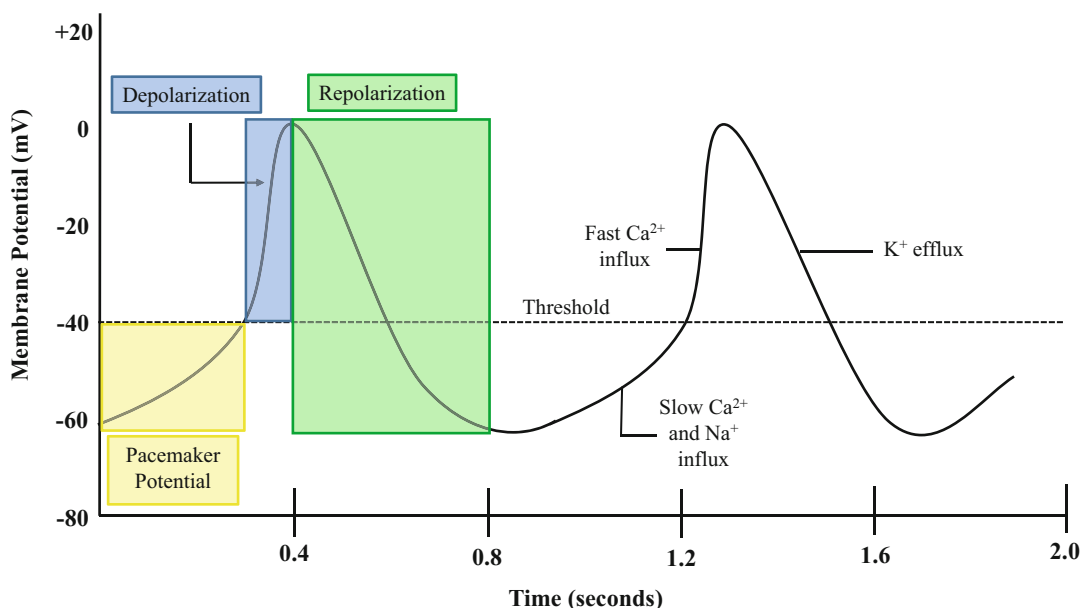
The SA node is the fastest pacemaker in the heart and fires at a rate of approximately 60–100 action potentials per minute, compared to the AV node's 40 action potentials and the Purkinje fibers' 20 action potentials per minute. Because it is the fastest pacemaker, the SA node acts as the primary generator of cardiac rhythm in a healthy mammalian heart. The SA node is located in the right atrium near the superior vena cava. The SA node is comprised of pacemaker cells which are automatic, meaning the cells fire action potentials spontaneously and at regular intervals without need for nervous system stimulation. Unlike neurons and skeletal muscle cells, SA node cells do not have a stable resting membrane potential; rather the pacemaker cells undergo a steady depolarization from  $-60$  mV towards threshold. This depolarization is called the pacemaker potential. The cells of the SA node have a low threshold for action potential firing, approximately  $-40$  mV. Once threshold is reached, voltage-gated calcium open, allowing rapid influx of calcium producing



**Elektrokardiography (EKG)/Electrocardiography (ECG), Fig. 2** Path of electrical excitation in cardiac conduction system. The action potential propagation pattern of

the cardiac conduction is shown, starting with the sinoatrial node and terminating at the Purkinje fibers





**Elektrokardiography (EKG)/Electrocardiography (ECG), Fig. 3** Sinoatrial node action potential. The phases and ionic movements of the sinoatrial node cell action potential are shown in this figure

a fast depolarization (Fig. 3). Following depolarization, voltage-gated potassium channels activate and a steady outward potassium current causes the cell to repolarize. The SA node pacemaker action potential duration (APD) is approximately 0.8 s. Although the SA node generates cardiac rhythm independent of nervous system function, it is innervated and regulated by both divisions of the autonomic nervous system (ANS). Under “rest and digest,” the parasympathetic division of the ANS releases acetylcholine onto the SA node, lowering the rate of action potential firing. The vagus nerve, a major parasympathetic nerve, continuously releases acetylcholine onto the pacemaker cells (called vagal tone), thus driving down the intrinsic firing of the SA node to 70–80 action potentials per minute. Acetylcholine, by decreasing the action potential firing rate in the SA node, lowers heart rate. The sympathetic division of the autonomic nervous system, by way of postganglionic sympathetic neurons, releases norepinephrine onto the SA/AV node cells. Norepinephrine, as well as epinephrine from the adrenal medulla, decreases action potential duration and increases the action potential firing rate of SA/AV node cells. It is

predominantly the effect of norepinephrine that drives the increases in heart rate observed under the sympatho-adrenal (“fight-or-flight”) stress response (Boron and Boulpaep 2012). When the SA node generates an action potential, the electrical excitation spreads throughout the atrial myocardium and stimulates the AV node.

### Atrioventricular (AV) Node

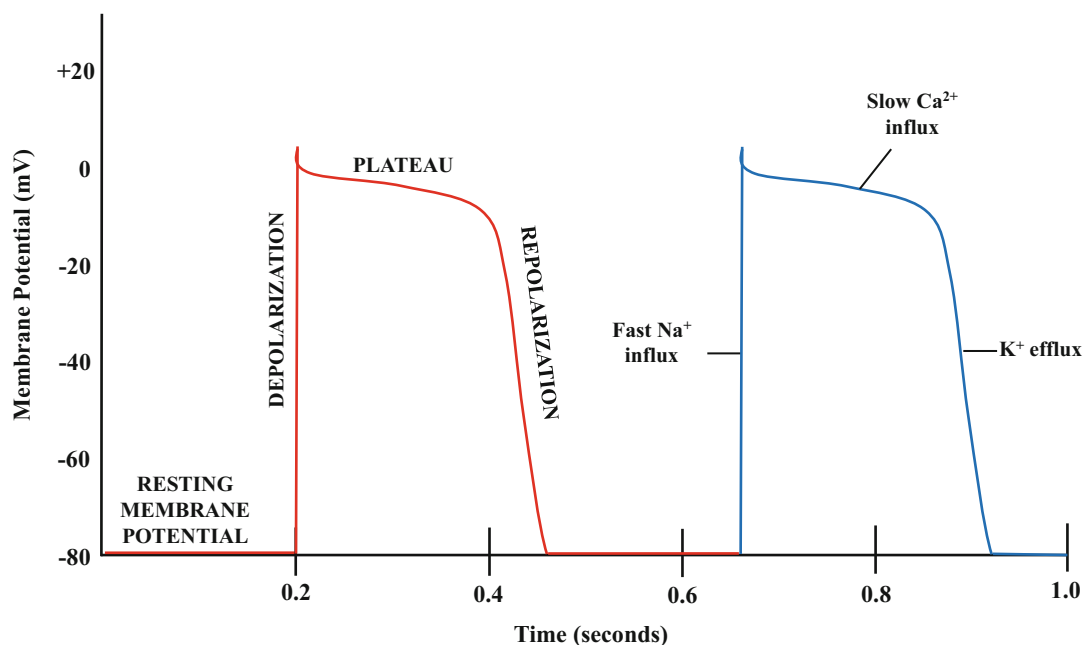
The signal from the SA node electrically stimulates the second part of the cardiac conduction system, the atrioventricular (AV) node. The atrioventricular node is located superior to the right atrioventricular valve and it shares many physiological traits with the SA node. In the event that the SA node is damaged, the AV node will generate the heart rhythm at a rate of approximately 40 beats per minute. The AV node also has the same conduction velocity as the SA node (0.05 m/s). Additionally, the action potential waveform of AV node pacemaker cells is very similar to that of the SA node cells. The AV node is important in that it serves as the electrical gateway between the atria and the ventricles,

and all signals traveling through the atria must pass through the AV node to reach the ventricles. Due to the presence of a fibrous skeleton between the atria and ventricles, the AV node serves as the only electrical access point between the atria and ventricles. Like the SA node, the AV node is innervated by the parasympathetic and sympathetic nervous systems, and it exhibits similar physiological responses to acetylcholine, norepinephrine, and epinephrine (Boron and Boulpaep 2012; Hall 2016).

### His-Purkinje Network and Ventricular Muscle

The atrioventricular bundle, bundle branches, and Purkinje fibers are part of the His-Purkinje system that begins after the AV node. The atrioventricular bundle (Bundle of His) is located at the inferior interatrial septum near the right atrioventricular valve. The electrical signal moves slowly through the AV bundle, allowing time for ventricular filling. The AV bundle branches into left and right bundle branches. The left bundle branch

supplies the left ventricle with innervation, while the right bundle branch supplies the right ventricle with innervation. The left and right bundle branches enter the interventricular septum and terminate at the apex. The electrical signal is carried into the ventricular myocardium by the Purkinje fibers. The Purkinje fiber cells have the slowest intrinsic pacemaker firing rate (only 20 beats per minute) and in a healthy heart, do not set the cardiac rhythm (Saladin 2017). In a healthy individual, the Purkinje network acts a conduction relay to rapidly conduct signals to the ventricular myocardium. The cells of the Purkinje network have a conduction rate of 4 m/s, 80 times faster than the SA/AV nodes. However, the Purkinje fibers can serve as a pacemaker for the heart in the event that the SA and AV nodes are nonfunctional (Boron and Boulpaep 2012). The Purkinje fibers directly innervate the ventricular myocardium, and they stimulate the ventricular muscle cells to generate an action potential (Fig. 4). Ventricular myocytes have a resting membrane potential of  $-80$  mV. When the electrical signal from the cardiac conduction system stimulates the myocytes, voltage-gated



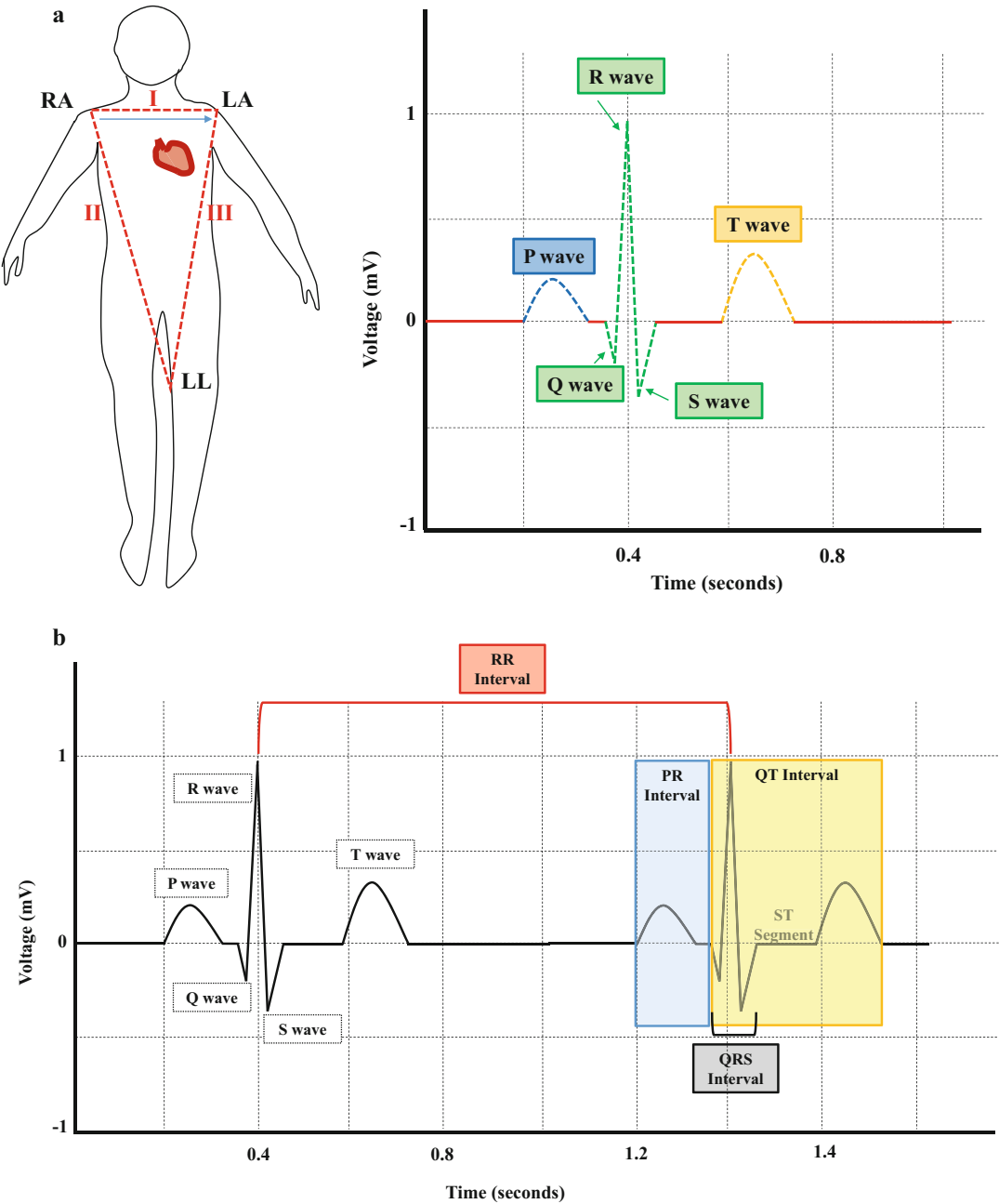
**Elektrokardiography (EKG)/Electrocardiography (ECG), Fig. 4** Ventricular muscle action potential. The phases and ionic movements of the ventricular myocyte action potential are shown in this figure

sodium channels open, activating a fast inward sodium current responsible for the depolarization phase of the action potential. At depolarized values near the peak of the action potential, voltage-gated sodium channels inactivate while voltage-gated calcium channels activate and open. Calcium influx through these channels produces the plateau phase of the myocyte action potential. Importantly, the calcium entering during the plateau phase will be utilized to liberate calcium from intracellular stores (in sarcoplasmic reticulum of myocyte) to use for contraction. At the end of plateau, voltage-gated calcium channels inactivate while voltage-gated potassium channels activate and open. The resulting outward potassium current drives repolarization. The ventricular myocyte action potential duration (APD) is approximately 250 ms. Ventricular muscle cells are functionally connected by gap junction channels. Thus, when a ventricular muscle cell is stimulated via Purkinje fiber, the wave of electrical excitation will pass through functionally connected cells in a given chamber of the heart. Additionally, the ventricular myocardium is innervated by the sympathetic, but not the parasympathetic nervous system. The effect of epinephrine and norepinephrine on ventricular muscle is to increase intracellular calcium and therefore force of muscle contraction (Widmaier et al. 2016).

## The Electrocardiogram

In 1901, Einthoven found that when electrodes are placed on a human or animal subject, a tracing can be produced of action potentials spreading between the negatively and positively charged electrodes. He utilized an additional electrode to ground the current. The tracings varied according to the location of the electrodes, and Einthoven subsequently described three angles or leads which formed a triangle with the heart in the middle. Today, this is known as Einthoven's Triangle; the three electrodes are known as the limb leads I, II, and III (Fig. 5a) (Becker 2006). There are also six leads called precordial leads (V1–V6) placed on the chest wall (Noble et al.

1990). The patient is instructed to relax with hands in the supine (facing anteriorly) position. Simultaneous recordings are made from the electrodes, and the resulting ECG is a composite of all the electrical activity of the heart (VanPutte et al. 2014). It does not represent a single action potential, but it is rather a representation of all action potentials occurring during the cardiac cycle. Figure 5a shows a typical electrocardiogram of an individual in sinus (normal) rhythm. The P wave is produced when an electrical signal from the sinoatrial (SA) node is generated by the pacemaker cells, depolarizing the left and right atria. The P wave is produced during the depolarization phase of the pacemaker action potential. Atrial contraction occurs approximately 100 ms after the P wave during the PQ segment. The electrical signal, as it travels through the AV bundle, bundle branches, and Purkinje fibers, does not produce any discrete waves on the ECG. The QRS complex is the result of ventricular myocyte depolarization. The QRS complex is large because the ventricles of the heart have the most muscle mass and generate the greatest amount of current. Atrial repolarization and relaxation also occur during the QRS complex, but the electrical event is obscured by the QRS complex. The T wave represents ventricular repolarization, which immediately precedes diastole. The T wave is produced by the repolarization noted on the myocyte action potential waveform. The repolarization process takes longer than depolarization, which accounts for the wider T wave (as compared to the QRS complex). In rare instances, the U wave is noted on the ECG. The U wave follows the T wave and represents repolarization of papillary muscle which attach to AV valves within the ventricle (Boron and Boulpaep 2012). There are also several intervals and segments that are physiologically relevant (Fig. 5b). The PQ segment indicates how long it takes the signal to propagate from the SA to AV node. The PR interval is a measurement of the how long it takes for the signal to propagate through the AV node to the ventricles. The QRS interval allows one to measure how long it takes the electrical signal to spread throughout the ventricles. The QRS complex represents ventricular



**Elektrokardiography (EKG)/Electrocardiography (ECG), Fig. 5** The electrocardiogram. (a) This figure shows Einthoven's Triangle and the relationship between electrical vectors (left) used to create a typical

electrocardiogram (right). Roman numerals I, II, and III denote the limb leads I, II, and III, respectively. RA = Right arm. LA = Left arm. LL = Left leg. (b) Intervals and segments are shown on the ECG

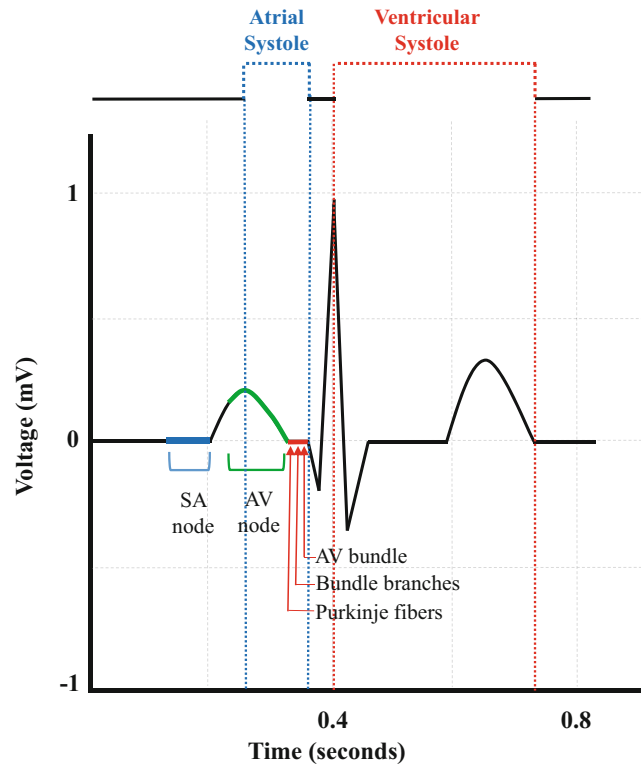
myocyte depolarization (see Fig. 4). Additionally, atrial repolarization and relaxation occur during the QRS interval. Ventricular contraction begins

immediately after the QRS complex. The plateau phase on the ventricular myocyte action potential waveform is represented by the ST segment,

## Elektrokardiography (EKG)/

### Electrocardiography (ECG), Fig. 6

Cardiac conduction system and the ECG. This figure shows the relationship between the events occurring in the cardiac conduction system and the ECG. This figure also notes atrial and ventricular systole events



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which also signifies ventricular contraction. The QT interval represents how long the ventricular remain in a depolarized state. This interval gets shorter as heart rate increases. The RR interval is the time between ventricular depolarization events and is used to measure heart rate. The cardiac conduction system, discussed above, is responsible for producing the waves, intervals, and segments of the ECG. A summary of the path of electrical excitation of the cardiac conduction system and its relations to the waves, intervals, and segments of the ECG is reflected in Fig. 6. Systole events are also noted in Fig. 6. In addition to evaluating waves, intervals, and segments, the ECG is also used to determine the electrical axis of the heart (Goldberger et al. 2018). All of the action potentials, including the magnitude and direction of each, occurring in the heart are represented by vectors. The vectors for individual myocytes can be summed to create a mean electrical axis for the heart. Deviation from the normal electrical axis occurs during pathological states such as cardiac hypertrophy

(enlarged heart) (Kashou and Kashou 2018) or myocardial infarction.

## Diagnostic Value of the ECG

The ECG is a powerful tool used in the diagnosis of pathological conditions. Heart pathologies such as myocardial infarction, arrhythmias, conduction block, and heart enlargement may be reflected on the ECG. However, pathological states of other organ systems can cause deviations in the ECG. For instance, hormone and electrolyte imbalances can have cardiovascular consequences which are reflected on an ECG. Any deviation in the normal sinus rhythm of the heart is called an arrhythmia. Most arrhythmias are discernable on the ECG; thus the ECG serves as an invaluable diagnostic tool for clinicians. Some arrhythmias are more serious than others. For instance, ventricular fibrillation refers to a condition in which the ventricles do not contract in a coordinated, unified manner. The ventricular muscle cells

depolarize quickly and irregularly. As a result of ventricular fibrillation, the heart is unable to pump blood, because it cannot generate a unified, productive contraction. Ventricular fibrillation also means that there is no coronary blood flow, and the myocardium dies of ischemia (lack of blood flow). The ECG of a fibrillating heart shows small, erratic waves with no discernable pattern. Ventricular fibrillation can be fatal if not reversed. Defibrillation is a life-saving procedure that aims to shock the conduction system back into a sinus rhythm (Hall 2016). Atrial fibrillation occurs when the atria depolarize approximately 300–600 times per minute, yet the action potentials are of such low magnitude that discrete P waves are not discernable. The signals generated in the atria will reach the AV node; however, the AV node will limit the impulses traveling to the ventricles and will attenuate the signal rate. The ventricles will be stimulated 100–200 times per minute under atrial fibrillation. The ECG will also show elevated but erratic heart rate. Other cardiac arrhythmias involve the use of a non-SA node pacemaker to set the heart rhythm. For instance, if the SA node is damaged, the ECG may show an absent P wave indicating a nodal rhythm. A nodal rhythm occurs when the AV node assumes the role of setting heart rhythm. An individual experiencing a nodal rhythm will also have a heart rate of approximately 40–50 bpm. If the AV node is damaged, electrical signals from the SA and AV nodes will not reach the ventricles. In this state, the ventricular myocardium is solely responsible for generating the cardiac rhythm. A cardiac rhythm generated by the ventricular myocardium is called an intrinsic ventricular (idioventricular) rhythm. An individual experiencing intrinsic ventricular rhythm will have a resting heart rate of 20–40 bpm. Arrhythmias may also be categorized as partial or complete conduction block disorders. Partial conduction block disorders include first-degree AV block, second-degree AV block, intermittent block, and bundle branch block. First-degree AV block is characterized by a long PR interval. Physiologically, a first-degree AV block refers to a slower than normal conduction of impulses through the AV node. Intermittent block is a partial conduction disorder in which only some

electrical signals are conducted. Second-degree AV block has two subtypes, Mobitz type I block and Mobitz type II block. Mobitz type I block is characterized by the PR interval that gets progressively longer until the AV node fails and the ventricles skip depolarization cycles. In Mobitz type II blocks, the PR interval does not change, but an occasional QRS complex/T wave is missing nonetheless. The ECG will show a P wave but remain flat until the next P wave. Bundle branch blocks are typically characterized by failure of the Bundle of His or Purkinje fiber system. Both left and right bundle branch blocks are discernable on the ECG by a wide QRS interval. The ST segment is of great clinical importance, as an elevation in the ST segment can be indicative of a myocardial infarction. Cells near the sight of ischemia experience anoxic injury and remain in a depolarized state. Additionally, coronary artery spasms during a MI can trigger a ST segment elevation. Additionally, the ECG will often appear abnormal in instances of electrolyte imbalance. Potassium imbalances (see “Homeostasis” entry for normal potassium levels) can prove deadly if not reversed. Potassium efflux drives repolarization and relaxation of excitable muscle tissue. If extracellular (plasma) levels of potassium are elevated, excitable tissues will struggle to repolarize. If plasma levels of potassium are elevated (hyperkalemia), changes in the ECG will occur if the plasma potassium levels continue to rise. Initially, a person may exhibit a prolonged PR interval and tented T wave at slight deviations (6 mM). As hyperkalemia progresses, the QRS complex can become prolonged, obscuring the P wave (8 mM). At dangerously high levels of plasma potassium (10 mM), ventricular fibrillation can occur (Boron and Boulpaep 2012). Hyperkalemia rarely occurs in healthy individuals. Hypokalemia, or low levels of plasma potassium, is reflected by a flat T wave and large U wave on the ECG. Potassium can be lost via sweating mechanisms on hot days where dehydration is a concern. Additionally, some individuals may have low dietary intake of potassium, causing hypokalemia. The electrocardiogram has greatly enhanced the clinician’s ability to diagnose cardiac disorders using this safe, noninvasive technique.



## Cross-References

- [Action Potentials](#)
- [Circulatory System](#)
- [Diffusion](#)
- [Vasal-Vagal Stimulation](#)

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## Elemental and Configural Perception

- [Olfactory Perception](#)

## Elephant Communication

- [Proboscidea Communication](#)

## Elephant Life History

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## Synonyms

[Proboscidea](#)

## Introduction

Elephants are the largest land-dwelling mammals alive today. They are long-lived (living into their 60s or 70s) and highly social animals with slow life histories. Their lives have frequently overlapped with human societies, and thus their ecology has been affected greatly by habitat

fragmentation, legal and illegal hunting, and human-elephant conflict. Thus, investigations of behavior are at times subject to the confounding effects caused by human interference. Additionally, collecting long-term data on the life history of elephants can be challenging and, at times, fragmented due to their slow physical development and long life spans.

There are two well-established species of elephants alive today of the order Proboscidea – *Loxodonta africana* and *Elephas maximus*. More commonly, these elephants are referred to as the African and Asian elephant. The African elephants can be divided into two subspecies (or species, depending on the source (Blanc 2008; Hart et al. 2008)), *Loxodonta africana cyclotis* (African forest elephant) and *Loxodonta africana africana* (African bush elephant). There is debate in the scientific community with regard to the African savannah and forest elephant and whether these two populations should be considered distinct species within the genus *Loxodonta*.

African savannah elephants are found in eastern, southern, and western Africa, while forest elephants are found in the central and western regions of the continent (Sukumar 2003). African elephants have been classified as “vulnerable” by the International Union for Conservation of Nature (IUCN) with a rising population (Blanc 2008). An enormous amount of research on African savannah elephants has arisen from Amboseli National Park, specifically produced by Dr. Cynthia Moss. Moss’ study of African elephants is the longest continuous, official study of any elephant species. The data collected at Amboseli, however, cannot speak across all ecological conditions in which *Loxodonta africanus* live. Though the Amboseli population has been comparatively undisturbed by human activity over the course of the data collection, these elephants were by no means isolated from human interaction; the primary cause of death in adult elephants in this study population is related to human activity (Moss 2001). Further, the span of the presented research does not contain the full life span of a single elephant. All this being said, the data collected at Amboseli certainly gives a better understanding to the life history of both

African and Asian elephants, providing richer information than a captive population could replicate (Moss 2001).

Asian elephants live primarily in India (around 60% of wild Asian elephants) but also in a variety of other countries in Southeast Asia – primarily Myanmar, Indonesia, Sri Lanka, Thailand, and Malaysia (Sukumar 2006). This slightly smaller species is currently thought to be divisible into three subspecies – *Elephas maximus indicus* (living primarily in India), *maximus* (Sri Lanka), and *sumatranus* (Indonesia) (Choudhury et al. 2008). Unlike the African elephant, Asian elephants are listed as “endangered” by the IUCN and have been since 1986 (Choudhury et al. 2008). It is estimated that the Asian elephant has been eliminated from as much as 95% of its original range (Sukumar 2006). Much of the data regarding Asian elephants has been synthesized by Dr. Raman Sukumar, an ecologist working in the Center for Ecological Sciences at the Indian Institute of Sciences.

African and Asian elephants, though similar in a variety of their life history traits, are distinct both behaviorally and physiologically. Additionally, they face very different challenges with regard to their conservation. The different statuses across the three species have led to discrepancies in their study, especially given the numerous challenges of studying elephants even in the best of circumstances.

## Reproduction

Female elephants begin estrous upon reaching sexual maturity. Each species varies in the exact number of days and manner of signaling while in estrous. Estimates of the estrous cycle in a population of Asian elephants in Sri Lanka found Asian elephants go into their estrous cycle for 18–27 days and begin at sexual maturity between the ages of 11 and 14 – though this varies significantly per population (Sukumar 2003). Their gestation period is extremely long as well, lasting between 20 and 22 months. When in estrous, females will signal their state to surrounding males. This signaling has been recorded in

both African and Asian elephants. Specifically, a number of auditory and chemical signals in addition to behavioral indicators of estrous have been noted in African savannah elephants living in Amboseli (Sukumar 2003).

Behaviorally, female elephants go through the following four stages during estrous: (1) a wariness period during which females are hesitant in nearing bulls and are intolerant of their approaching, (2) the estrous walk during which the female will walk with her head held up in reaction to an approaching male, (3) a chase period during which she will run away from or in an arc around approaching bulls, and (4) the courtship period. Here, physical proximity is decreased and the female closes in on a chosen bull while the bull turns away other competing males. This period can last multiple hours while the actual mating is comparatively short. The couple may then mate multiple times over the course of the day or more (Sukumar 2003).

It is not just females that signal their readiness to mate. Males go through periods known as *musth* during which their sexual interest peaks, as does their aggression. Musth is defined by the enlargement and secretion of the temporal gland, increased aggression and sexual activity, and dribbling of urine (Vidya and Sukumar 2005). This period can last days or months. The musth phenomenon was discovered originally in observations of Asian elephants, though it has been found to occur in African elephants as well (Sukumar 2003). Relatively recently Poole and Moss (1981) described the same process with a few small differences between species. Similar to the female estrous signaling, they have detailed the behavioral components of musth for the Amboseli population; while the general outline of these behaviors applies to both the Asian and African elephant, there are a few noted differences (Sukumar 2003). To begin, the male begins with a musth walk where he walks with his head high, chin tucked, and ears spread. He also will swing his head and tusks. He then moves into a tusking phase where he goes to his knees and tusks at the ground. As he does so, he will throw lumps of mud and grass while discharging fluid. This tusking behavior, however, has not been seen

universally across populations (Sukumar 2003). The male will also scent mark more frequently, rubbing his temporal glands against trees (Poole and Moss 1981). Additionally, there is an auditory communicatory signal of musth named the “musth rumble.” This sound is of very low frequency and garners a specific auditory response from females. Lastly, the male will urinate with a sheathed penis at a very slow rate for an hour or more. He may also urinate with his penis retracted in order to spray urine on his back legs (Poole and Moss 1981). Aside from the tusking behavior, these behaviors have been noted – at least anecdotally – across species. In African elephants, however, musth may also be accompanied by an “ear wave” during which the male will move (wave) one ear at a time (Sukumar 2003; Poole and Moss 1981).

Though musth is always a postpubertal phenomenon, the age of first musth is variable across populations and species. In Asian elephants, musth will begin from about 15 years of age. In the Amboseli population of African savannah elephants, however, elephants are at least 24 years of age upon first musth, and the average age is closer to 29 years of age. Further, regular onset of musth will not begin until the age of 35 (on average) (Lee and Moss 2002; Moss 2001; Sukumar 2003).

## Life Span and Mortality

In the Amboseli population, median age of first birth is 14.11 and the mean 13.67. The youngest known first birth in the population was recorded at 8.9 years and the oldest 21.6 years. On average, however, most elephants will have their first birth between 11 and 13 years. Additionally, though there are calves born year-round, the majority of calves (81%) are born between the months of November and May with an average interbirth period of one calf every 4.5 years. These elephants can reproduce well into old age, though their fecundity declines after around 50 years of age (Moss 2001).

Mortality in adults was still primarily caused by human activity throughout the

30 years of observation. In juveniles, however, 80% of mortality occurred from natural causes. It should be noted, however, that only 231 of the 691 deaths had causes that could be determined with certainty. Furthermore, though the sex ratio at birth between males and females was not far from 1:1, juvenile mortality is significantly different between the sexes (Moss 2001). In the Amboseli population, males had a 75% chance of living to age 10, whereas for females it was an 85% chance. More strikingly, because on average males don't enter musth regularly until the age of around 30, their chances of surviving to this point of reproductive maturity were only 39%. Whereas females, who on average reach reproductive maturity at age 14, have a much higher percent chance of living until they are reproductively mature – 82%. Overall (perhaps in part due to the age of reproductive maturity), females have a 70% chance of living to produce at least one offspring, whereas males only have a 50% chance of living to regularly enter musth (Moss 2001).

Estimating the life span of truly wild Asian elephants has been a greater challenge. Much research dealing with the life span of Asian elephants has been done using semi-captive populations who face different environmental obstacles regarding longevity. These semi-captive elephants are allowed to “intermingle” with wild elephants and forage independently. They are also used, however, as workers in the Myanmar timber industry. These individuals make up the largest captive population of Asian elephants. A portion of the elephants here are captive born, and the others are wild-caught (though this is now forbidden). Of the wild-caught elephants, the longest lived is 83 years. Further, the earliest age of first birth was 5.28 years with an average interbirth interval of 5 years (Robinson et al. 2012). Previously, Sukumar reported the average age of first birth to be closer to 17–18 years in Asian elephants living in Biligirirangans, whereas the Myanmar semi-captive elephants had an average first birth between 18 and 23 years of age (Sukumar 2003). Lastly, studies have found

that probabilities of survival remain relatively constant up to age 25 after which they decrease (Robinson et al. 2012).

## Social Structure and Cognition

Elephants have prolonged development periods and exhibit a great deal of social learning. All species of elephant produce precocious offspring that rely on their smell, touch, and sound to find mothers for suckling. The calves will remain dependent on the mother's milk until their 3rd month. In the 4th month, however, they are generally able to use their trunk for foraging on a variety of greenery though they continue to nurse at least into their 9th month. Though at the age of 1 year, the calves are nutritionally independent and take part in grooming, there remain behavioral and social skills that are undeveloped. To continue developing these skills, calves spend a great deal of time with their mothers, in addition to spending time playing with other calves (Sukumar 2003).

In African elephants, males grow faster and continue growing for more time than do their female counterparts. Further, unlike the females, males will disperse from their mother between 9 and 18 years of age (Vidya and Sukumar 2005). Though bulls do disperse, they are not completely solitary – Moss and Lee have calculated that Amboseli bulls spend less than one-third of their time alone (Lee and Moss 2002; Moss 2001). They are accompanied often by other males or in the presence of female groups. In Asian elephants, males will also disperse around the age of sexual maturity, though the age range is closer to 10–15 years of age. Further, it has not been clearly determined whether this dispersal is locational or social (Vidya and Sukumar 2005).

Female African elephants do not disperse and instead stay in matriarchal groups. The female social structure is far more dynamic than that of the males. They form highly complex social networks among different family

groups known as “bond” or “kinship” groups (Vidya and Sukumar 2005). Over 80% of their time is spent in the family group, and their behaviors are highly coordinated. The structure of these groupings varies across species and subspecies of elephant. In contrast, groups of African forest elephants consist of single adult females and their dependent offspring – they have not been found to form the same kinship/bond groups as African savannah elephants. Asian elephants, however, have been seen to form family groups similar to those of the African savannah elephants; however there is no long-term study confirming this observation. A recent analysis on Asian elephant haplotype, however, has shown maternal relatedness within the groups, suggesting a similar group structure to the African elephant (Vidya and Sukumar 2005).

Furthermore, elephants are extremely intelligent beings. Though not advanced toolmakers like the great apes, relatively recent research has elucidated various manifestations of their intelligence in the form of long-term social and spatial memory. Though some of this data is anecdotal, it is supported by multiple experts in the field who have documented occurrences of such behaviors repeatedly. In one case, it was found that during a drought, only elephant groups with older matriarchs knew to leave their normal grounds to find a different watering hole. Additionally, in a playback study, it was found that elephants could recognize up to 100 different individual elephant calls from up to 1.5 km away (Hart et al. 2008). Lastly, whether elephants possess a “theory of mind” – meaning the animal is self-aware and can act based on the well-being of another – has been brought up for questioning. Evidence in favor cites elephants attuned focus on elephant bones, mirror recognition, and response to distressed group members. Their highly sophisticated social and emotional processing skills have been the subject of much scientific and public conversation, often in the context of elephant welfare in captivity (Hart et al. 2008).

## Cross-References

- Animal Welfare
- Life History
- Reproduction
- Social Behavior

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## Elephant Locomotion

### ► Proboscidea Locomotion

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## Elephant Seals

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### Synonyms

*Mirounga angustirostris*; *Mirounga leonina*;  
*Miroungini Mirounga*

### Introduction

Elephant seals, known colloquially as sea elephants, are part of a group of marine mammals called Pinnipeds, which means “fin-footed” (Wyss 1989). Pinnipeds are found globally and can be divided into three sections: true seals, eared seals, and walruses. Elephant seals fall under the true seal category and contain two sub-categories: southern and northern. The two elephant seal species were discovered to be taxonomically different species in 1866 (Stewart et al. 1994). The southern elephant seal’s Latin name, *Mirounga leonina*, means lion and may be a reference to the loud roaring vocalizations they emit when they want to warn off breeding competition. For the northern species, the Latin name, *Mirounga angustirostris*, means “narrow snout” and refers to the namesake, characteristic nose of adult males. Those of northern elephant seals are discernably thinner than

those of their southern cousins. They are sexually dimorphic, meaning males and females are physically distinguishable as adults.

While the northern elephant seals are the largest pinniped species in the Northern Hemisphere, the southern elephant seals are the largest in the world. All individuals have the same light to dark brown coloration and molt once a year. The males are easily differentiated from females, as they can grow up to five times larger and have the characteristic elongated snout that founded their common name (Folkens and Reeves 2008). Females can gestate and have one pup per year. Physical adaptations enable these animals to dive to extreme depths for up to 30 min, withstanding great pressure and freezing temperatures (Folkens and Reeves 2008).

### Description

Seals are built to exist on land but are most well-equipped for life in the water. True seals and fur seals look generally alike to the untrained eye but have some small key differences. Elephant seals have rounded, sleek bodies, sizable heads, small tails, and four flippers. Typically females will sexually mature by 3 years of age in the northern species, while the other species and sexes will take between 4 and 6 years (Geraci and Lounsbury 2005). Males grow their eye-catching, long snouts called a proboscis when they reach puberty. Their large, round bodies are kept warm by a layer of blubber just under their skin and coat of fur. They have large heads respective to their bodies and broad, thick shoulders and chests. This feature is more exaggerated in males than females, but both sexes have tapered torsos that end in long hind flippers. These hind flippers propel them in the water, moving laterally side to side and expanding in a fan shape to utilize more surface area (Folkens and Reeves 2008). Front flippers are used for steering underwater. Like other true seals, elephant seals do not have a rotating hip bone, which means they are unable to walk on all four limbs while on land. Instead, their terrestrial locomotion is scooting on their bellies, in an inchworm-type fashion (Geraci and Lounsbury



2005). Their fore-flippers may be used for occasional boosts but are otherwise not utilized on land. Elephant seals do have claws, and unlike fur seals, they have front flipper digits that are not entirely covered with skin and are separated by webbing (Folkens and Reeves 2008).

Northern elephant seals express more sexual dimorphism than their Antarctic cousins. Southern seals are sexually distinguished by their physical appearance, but the northern species' sexes differ in foraging behavior and molting season. Southern seals, being the largest, grow to be 5 m in length, while the northern species grows to just over 4 m (Geraci and Lounsbury 2005). Males can weigh up to 5000 and 2000 kg, respectively, with females weighing up to 900 and 600 kg (Folkens and Reeves 2008). Both species of elephant seals are tan to dark brown in color. Other than their greater size and characteristic noses, males can be identified by their robust, thick necks. They become thicker and calloused with size and age, collecting pink scars and mottling from years of fighting and molting (Folkens and Reeves 2008; Geraci and Lounsbury 2005). Females are generally between three to four times smaller than their male counterparts and do not have lengthy noses (Folkens and Reeves 2008). Females and pups are similar in appearance. After pups lose their silver or gray newborn fur, they too become dark brown dorsally with some lighter tan coloration on their ventral belly side (Folkens and Reeves 2008).

Northern seals' mouths hold eight pairs of teeth in the lower and upper jaws. Southern seals only have seven pairs in the bottom jaw. The largest and most intimidating of the teeth are the canines, growing to be 20 cm in the northern and 15 cm in the southern species (Folkens and Reeves 2008). Teeth located further in the mouth, behind the canines, are all the same peg shape and known as "post-canines" (Folkens and Reeves 2008; Geraci and Lounsbury 2005).

Elephant seals are the deepest divers in the pinniped family, and their foraging takes place where they cannot rely on much light (Le Boeuf and Laws 1994). The large size of their eyes hints that they rely heavily on eyesight to detect prey. True to form, their eyes are capable of adjusting to dark surroundings faster than other pinnipeds and

can perceive bioluminescence in the dim, unlit reaches of the subarctic oceanic hunting grounds (Folkens and Reeves 2008; Levenson and Schusterman 1999).

As true seals, sea elephants have no external, visible ear flaps. Their hearing thresholds above and under water are comparable to other true seals, with the exception of low frequencies under water, which suggests their hearing is actually very well adapted, particularly for hearing under water and at high pressures (Kastak and Schusterman 1999; Macdonald 2009). This marine adaptation comes at the expense of aerial hearing, though, as their auditory sense out of water is not sharp by comparison (Kastak and Schusterman 1999).

## Habitat and Locations

Northern elephant seals are only found in the Northern Hemisphere of the Pacific Ocean. Much of their distribution is unknown prior to the time of widespread hunting that diminished their prior population size (Stewart et al. 1994). Colonies are located in southern and central coastal California, as far north as Point Reyes and as far south as Isla Natividad in Mexico (Stewart et al. 1994). The largest colony is on the Channel Islands.

Southern elephant seals, as the name suggests, are only found in the Southern Hemisphere, but unlike their northern counterparts, their range is circumpolar. They span the southern Atlantic, Indian, and Pacific Oceans. Large breeding colonies have been established respectively on South Georgia, the Kerguelen Islands, and Macquarie Island (Boyd et al. 1996). Other than the coasts of Antarctica, exploratory and migrant seals have been seen in the most southern reaches of Australia, South America, and South Africa.

When southern elephant seals haul out, they prefer beaches of gravel or sand (Folkens and Reeves 2008; Le Boeuf and Briggs 1977). Southern elephant seals can dive up to 1500 m but generally stay at depths between 180 and 600 m (Folkens and Reeves 2008). Migration for foraging purposes will occur throughout the year,

outside of breeding season, and spans from the Antarctic coast to northern edges of the Southern Ocean. Outlying individuals have been reported as far north as Western Asia (Folkens and Reeves 2008).

Adults of both species are solitary; the only time they see conspecifics is during mating or molting (Folkens and Reeves 2008).

When they are not hauled out for molting or mating season, northern seals will range a grand span of the northeastern part of the Pacific Ocean. Unlike southern seals, northern seal migrations are sexually dimorphic and will differ in locale based on the sex of the animal. In the past, northern seals have been sighted as far west as Japan (Folkens and Reeves 2008). Average foraging dives of northern elephant seals are down to depths between 330 and 800 m and also last half an hour (Folkens and Reeves 2008). However, individuals have been noted to dive for up to 2 whole hours. They forage and avoid land for 8–10 months between the combined molting and breeding period.

## Diet

Population and individual diets will vary based on preferences and availability due to geographic location. All seals are carnivorous and have been known to eat birds and other seal species (Le Boeuf as cited in Riedman 1990). Their diet mainly consists of free-swimming fish, octopus, and squid, the size and species of which correlate to the age and size of the seal (Folkens and Reeves 2008; Clarke and Macleod 1982; Field et al. 2007). As suggested by their propensity to also spend time at sea floor depths, elephant seals may also forage for benthic creatures, notably elasmobranchs and amphipods (Folkens and Reeves 2008; Field et al. 2007). They hunt for prey that exhibits bioluminescence, which are more easily detectable in depths where little to no sunlight is able to penetrate (Folkens and Reeves 2008).

Southern elephant seals find most of their prey at depths between 180 and 600 m. They generally go after pelagic, or free swimming, fish and squid that reside there. Individuals have been tracked

diving repeatedly to benthic depths in subantarctic waters, suggesting that some seals will forage on the ocean floor for food as well (Folkens and Reeves 2008).

## Threats and Predators

Elephant seals will live to be in their mid to late teens (Folkens and Reeves 2008). The most accurate age estimation is accomplished by counting the layers of tooth growth that are the results of annual dentine deposits (Hohn 2009). Natural limiting factors of seal populations are comprised of natural predators (e.g., sharks, bears, cougars, and wolves), intense storms or weather, variability in food availability, and causes of disease like lungworm parasites and bacteria (Brownell et al. 2000; Geraci and Lounsbury 2005; Gulland et al. 1997).

Anthropogenic threats include human interaction (e.g., fishery entanglement or legal shooting), ocean contamination (e.g., organic contamination and trash pollution), territory encroachment or loss of habitat, and ocean contamination in the form of trash and organic pollution that lead to fatal skin diseases (Beckmen et al. 1997; Folkens and Reeves 2008; Geraci and Briggs 2007). However, infectious diseases are always evolving just like their hosts. Notably, population development near human-associated regions can allow for transfer of disease where there was no prior concern for such predating the bottlenecking event (Brownell et al. 2000).

General pinniped pup survival rate is low within their first year (Geraci and Lounsbury 2005). Whether it be due to mother inexperience, overcrowding, or weather events, primary cause of newborn death is accidental separation or early desertion from the mother, the cascading results of which being targeted by predators, trampling from adult males, and eventually starvation (Le Boeuf and Briggs 1977). A pup has a higher likelihood of death when its harem, or group of females that bred with a single male, is larger (Le Boeuf and Briggs 1977). Death rates in seals are very high in pups and juveniles. This decreases with age into adulthood and then will eventually increase as old

age and its accompanying complications come into play (Geraci and Lounsbury 2005).

## Physiology

Elephant seals undergo what is called a catastrophic molt, meaning that instead of only shedding fur, the top, epidermal layer of skin will detach in mats with the fur on top (Ling 1978). Molting happens in late summer to autumn for southern elephant seals and takes up to a month to complete. The seals will haul out on shore at a safe location and stay there for the entirety of their molt (Folkens and Reeves 2008). Molting season occurs in spring and early summer months for northern seals, earlier for the females and juveniles, then later for the males. Northern seals do not engage in much activity during actual molting. Aggregated groups will huddle together and pass most of the molt sleeping (Folkens and Reeves 2008). After a recent molt, pelage of adults will take on a silver sheen, pups, too, after weaning (Folkens and Reeves 2008). Within several weeks, this coloring will change to the characteristic tan or dark brown (Folkens and Reeves 2008).

They also have special internal adaptation to regulate their body temperature and circulatory system for deep diving. They can hold their breath for up to 2 h, though standard foraging dives last around half an hour, by inducing bradycardia, a slowing of the heart rate (Folkens and Reeves 2008). Elephant seals are so adept at warming their bodies for underwater conditions; they have a greater chance of overheating on land (Noren 2002).

## Reproduction

Both species of elephant seal are extremely polygynous, meaning that one male will breed with many females, and breeding season occurs once a year (Folkens and Reeves 2008). Adult males will make landfall before the females, who are pregnant from the previous year's mating. They will give birth after spending a week on land. Pups

will be weaned and self-sufficient within 3 to 4 weeks, having grown nearly five times their weight at birth (Folkens and Reeves 2008; Le Boeuf and Briggs 1977). Males will challenge each other through vocal and physical posturing for the right to mate with females (Folkens and Reeves 2008). When posturing aggressively against other competitors, males will inflate their snouts to emit roaring vocalizations (Folkens and Reeves 2008). Damage from teeth can be extensive but not usually fatal. A hierarchy is created based on these confrontations and the relative size and age of the present males (Folkens and Reeves 2008). While young males may become sexually mature, they may not achieve successful mating for years later (Geraci and Lounsbury 2005). If a male does not achieve enough rank status, he will not be allowed to mate with any females. While the breeding season haul out is still enacted, the established hierarchy will remain in place through vocal reinforcement of the most dominant males (Folkens and Reeves 2008). When mating is over, adults will return to their ocean habitats to forage for food. Females will need to regain weight lost through pup bearing and milk production. Newly weaned pups must fend for themselves (Folkens and Reeves 2008).

Seals are capable of a neat trick called delayed implantation. It allows them to mate, undergo egg fertilization, and then delay the fertilized egg from attaching to the uterine wall by causing temporary dormancy, thereby suspending embryo development until the mother is able to physically and nutritionally withstand the pregnancy and hormone levels promote the continuation of the pregnancy and time of the birth of the offspring to coincide with the next year's haul out period (Geraci and Lounsbury 2005). This is known as obligate diapause. It enables the successive pairing of birthing and mating periods, therefore limiting the amount of time individuals need to be out of their foraging habitats (Geraci and Lounsbury 2005).

Before mating can begin, males of both species will develop a hierarchy of dominance to determine who can mate with females. Vocal threats used by males in these challenges are called "clap-threats" and resemble a clapping sound (Folkens

and Reeves 2008). They are deafening and can reach for miles. Juvenile males may play-fight to practice using the same posturing, rearing their head and chests with mouths open.

Southern seals breed in the months of October and November (McConnell et al. 1992). After molting, the birthing and breeding periods occur subsequently, and respectively, during the same haul out (CDC). Gestation can last for 10 months.

The height of northern seal breeding season occurs in January and occurs in regions of Baja California and Oregon (Le Boeuf and Briggs 1977; Le Boeuf as cited in Le Boeuf and Laws 1994). Females typically give birth midwinter, in mid-December or early January (Le Boeuf and Briggs 1977). For 28 days, they care for and nurse their newborn pups, fasting the whole time (Le Boeuf and Briggs 1977). Concurrently, females will also bite and vocalize to ward away other pups and females in the event of wayward milk-stealing or feeling that their own pup is being threatened (Folkens and Reeves 2008; Le Boeuf and Briggs 1977). Twins and adoptions are possible but rare, due to the high-energy cost of pregnancy and nursing (Le Boeuf and Briggs 1977). Gestation lasts 11 months in northern seals (Folkens and Reeves 2008). After this time of nursing, females will mate with a dominant male and promptly leave their newly weaned young to forage in the ocean and regain lost fat stores.

## Conservation Status

Northern elephant seals underwent a severe bottlenecking event due to hunting in the 1800s (Brownell et al. 2000). They were commercially hunted thoroughly in the 1800s that they were believed extinct (Folkens and Reeves 2008). Population numbers have steadily risen since the hunting termination. Instances of such astounding rebounds are uncommon (Stewart et al. 1994). This resulted in the limitation of genetic diversity of the species. However, the population sizes have been estimated to have recovered from less than 100 animals to close to 130,000 (Le Boeuf and Laws 1994).

Threats to elephant seals are led by habitat loss from pollution and climate change and decrease in prey species availability. Natural predators of the

northern elephant seal are no longer as widespread terrestrially, and laws have recently been adopted that protect seals and their habitats. These are leading reasons for the recent regrowth of northern populations (CDC).

Aboriginal uses for seals included sources for clothing material, food, and tools (Folkens and Reeves 2008). Aboriginal and indigenous people traditionally hunted elephant seals for hundreds, if not thousands, of years (Folkens and Reeves 2008). The population reached its lowest numbers in the 1800s and 1900s when sealing was a commercial business spurred by demand of blubber for its many uses. Sealing ended in the 1960s, concurrently with whaling that took place along shorelines (Folkens and Reeves 2008). In 1972, the Marine Mammal Protection went into effect in the United States. The Convention for the Conservation of Antarctic Seals was globally implemented in 1978. These regulations prohibit the interference with and hunting or capture of seals and other marine mammals, with some exceptions. According to stock assessments conducted by the National Oceanic and Atmospheric Association, which do not include southern elephant seals, northern elephant seal populations have shown increases since their enforcement (National Oceanic and Atmospheric Association 2015). Elephant seals are currently categorized under least concern regarding their conservation status as of 2014 (Hofmeyr 2015).

## Cross-References

- [Adaptation](#)
- [Bottleneck Effect](#)
- [Carnivora](#)
- [Circulatory System](#)
- [Dentition](#)
- [Foraging](#)
- [Life History](#)
- [Locomotion](#)
- [Molting](#)
- [Pinniped Cognition](#)
- [Pinniped Communication](#)
- [Pinniped Life History](#)
- [Pinniped Morphology and Locomotion](#)
- [Polygyny](#)

- Reproductive Synchrony
- Sexual Dimorphism
- Species
- Thermoregulation
- Vertebrates (Chordata)

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## Elephants

- Proboscidea Morphology

## Eliciting Stimulus

- Unconditioned Stimulus

## Elisabetta Visalberghi

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## Introduction

Elisabetta Visalberghi (Senior Research Associate, CNR) retired in 2017 from the position of Research



Director at the Istituto di Scienze e Tecnologie Cognizione of the Consiglio Nazionale delle Ricerche (CNR) in Rome, Italy. She is best known for her contributions to our understanding of primate cognition, particularly in the areas of tool use, responses to novel foods, and social influences on learning. Both her experimental techniques in the laboratory and her observational/documentary methods in the field have established approaches to animal cognition that have been innovative and influential.

### **Overview of Dr. Visalberghi's Academic Career and Major Contributions**

Born in Aosta, Italy in 1952, Visalberghi studied at the University of Rome and then at the Scuola Normale Superiore of Pisa under the supervision of Professor Floriano Papi, a renowned ethologist. Although Visalberghi is one of the world's foremost experts on capuchin monkeys, she has also studied other species such as homing pigeons, rats, wolves, titi monkeys, squirrel monkeys, and chimpanzees.

Throughout her career, Visalberghi has published extensively in a variety of high quality journals and edited volumes. As of 2017, she has published seven single and co-authored books, 146 journal articles, 52 book chapters, and an additional 20 articles in Italian journals. She is a frequent consultant on television and radio programs, has acted as a scientific advisor to several public institutions, has been a visiting scientist at academic institutions in Brazil, Germany, Japan, Ivory Coast, Guinea Conakri, and the United States, and is the former President of the Italian Ethological Society and the Italian Primatological Association and Secretary General of the International Primatological Society. Over the course of her career, she supervised 49 theses to completion (31 Laureates, 7 Masters, 11 PhDs).

Visalberghi began her academic career in ethology with a thesis on the cryptic and warning colorations of grasshoppers. From there she went on to study navigation in homing pigeons and neophobia in rats. However, a turning point came early in her career when she was invited to

establish a small primate center for the CNR inside the Rome Zoo. Determined to train herself first in primatology, she won a NATO fellowship to study at the California Primate Centre. It was there, working with titi and squirrel monkeys under the supervision of the experienced primate psychologist William Mason, that Visalberghi designed the first of her long line of inventive and effective laboratory experiments to elucidate how monkeys solve problems (Visalberghi and Mason 1983).

When Visalberghi returned to Rome, she started to study the capuchin monkeys she obtained for the newly established Primate Center and began her lifelong focus on their cognitive abilities, an interest prompted by her first experiment on capuchin tool use (Antinucci and Visalberghi 1986). It was in this period that Visalberghi met and began her lifelong teamwork with Dorothy Fragaszy, who also focuses on the cognitive abilities of capuchins. In the 1980s, they began a productive and continuing collaboration of designing experiments for captive capuchins that examine the tool using capacities of these monkeys as a window into the functioning of their minds.

Two particularly significant experimental contributions developed by Visalberghi are called the "tube task" in which the subject must learn how to acquire a food item out of a clear tube by pushing it through with the appropriate tool from a variety of options and the "trap-tube test" in which the subject needs to avoid the hazard of the trap (Visalberghi and Limongelli 1996; Fragaszy et al. 2004) by choosing into which side of the tube to insert the tool. Visalberghi has performed these experiments separately with capuchins, chimpanzees, and human children and compared their performances. Results indicate that all species learn to select and use the correct tool, but do so at different speeds. In particular, capuchins need more extensive experience to appreciate what makes a tool effective. Visalberghi also tested whether naïve individuals of the three species can take advantage of observing a proficient individual solving the tube task. She found that adult capuchins were unable to replicate the model's behavior with the tool shortly after



observing the proficient individual. In contrast, when chimpanzees above a certain age, and even more so children above a certain age, observe a proficient model, they more quickly acquire the new behavior. Finally, in the “trap tube task,” some chimpanzees and most children above 3 years of age were able to appreciate the consequences of pushing the reward in such a way as to avoid the trap, whereas capuchins were not, unless they could use another arbitrary predictive cue (see ► “Trap-Tube Problem” in cross-references). The results of these and many other experiments led Visalberghi to her signature conclusion that monkeys do not learn complex behaviors by imitation but rather by trial and error in a social context that facilitates acquisition of the new behavior. She and Frigaszy have published numerous articles on socially biased learning, continuing through their most recent paper in PNAS (Frigaszy et al. 2017). Their more recent studies on wild capuchins who have many years of experience using stone tools to crack open palm nuts proved that capuchins can acquire stone tool-using skills resembling those of wild chimpanzees. Since these behaviors have been considered sophisticated only when chimpanzees perform them and field observations are not powerful enough to disambiguate this issue, Visalberghi and co-authors proposed creative field experiments (Visalberghi et al. 2015).

From her years of examining the tool-using abilities of captive capuchins, Visalberghi had predicted that capuchins in the wild would be most likely to use tools in an environment where they spent a lot of time on the ground and where there would be an availability of hard-shelled nuts and appropriate stones that can function as hammers and anvils (Visalberghi 1987). In 2004, Visalberghi and Frigaszy, and colleagues Patricia Izar and Eduardo Ottoni, found precisely such a site – Fazenda Boa Vista in northeastern Brazil. In 2005, the “EthoCebus” research team began to study the behavioral ecology of the bearded capuchins (*Sapajus libidinosus*) living in an open woodland habitat, where these monkeys routinely use stones to crack open palm nuts that they have placed on stone or wood anvils (<http://EthoCebus.net>). The work of this research team has resulted

in an outpouring of notable scientific publications on how and why these monkeys are such prolific and successful tool users (e.g., Visalberghi et al. 2005, 2009, 2015) plus a great deal of popular science press and attention. Though counterintuitive, they found that the routine tool use of these monkeys is not due to food scarcity (Visalberghi and Frigaszy 2013). Their images and video footage of capuchins strategically placing nuts on anvils and lifting heavy stones to shoulder or head height and then pounding the stones down on the fruits (actions that look similar to the “clean and jerk” move of weight lifters) is so eye-catchingly remarkable as to have been exhibited on the covers of several journals and books, and repeatedly shown in the popular scientific media. In 2012/2013, Visalberghi and Alessandro Albani made a documentary on the bearded capuchin monkeys of Fazenda Boa Vista, a film that they regard as a needed correction to the less rigorous/scientific interpretation of primate behavior that is typical of most nature documentaries. Their documentary, called “The Bearded Capuchin Monkeys of Fazenda Boa Vista,” has won several awards. The trailer and information can be found at: <http://www.ucp.istc.cnr.it/index.php/news/124-the-bearded-capuchin-monkeys-of-fazenda-boavista>

## Conclusion

In recognition of her outstanding achievements in research, Visalberghi has won numerous awards, such as the Frassetto Award for Physical Anthropology from the Italian Academy of Science, the Prix Geoffroy Saint-Hilaire given by the French Society for the Study of Animal Behavior, and the Career Award from the Italian Primatological Association. There are other aspects of Visalberghi’s research interests, such as capuchin sexual behavior, facial displays, responses to novel foods, social influences on food consumption, action synchronization, and affiliation (many of these projects carried out in collaboration with her students) that have resulted in important insights into primate behavior. But the enduring characteristic of her work is that she begins with

careful observation of the animal and then applies various ingenious experiments to illuminate how the animal solves problems, learns new tasks, and is affected by controlled variables. And she is willing to defend a parsimonious interpretation even when her findings are counterintuitive to popular assumptions and prevalent scientific views. Her empirical, inductive approach has led to a wealth of new understandings in the field of primate behavior and cognition that will surely stand the test of time.

## Cross-References

- [Categorization](#)
- [Cognition](#)
- [Comparative Cognition](#)
- [Dorothy Fragaszy](#)
- [Inequity Aversion](#)
- [Neophobia](#)
- [Nut-cracking](#)
- [Platyrrhine Cognition](#)
- [Primates](#)
- [Problem-Solving](#)
- [Social Facilitation](#)
- [Social Learning](#)
- [Stone Tools](#)
- [Tai Chimpanzees](#)
- [Tool Use](#)
- [Transitivity](#)
- [Trap-Tube Problem](#)

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## em

- [Electromagnetic Fields](#)

## Embodied Cognition

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## Synonyms

[Situated cognition](#)

## Introduction

Psychology's mid-twentieth century cognitive revolution viewed thinking as information processing. This information processing hypothesis was inspired by the digital computer, and by

demonstrations that this new device could perform many tasks that were assumed to require intelligence (Feigenbaum and Feldman 1963). In other words, when cognitive psychologists hypothesize that cognition is information processing, they view “information processing” as being analogous to the operations of a digital computer: the rule-governed manipulation of stored information. Traditional cognitivists therefore assume the existence of mental representations and presume that thinking is manipulating these representations using a mental programming language (Fodor 1975; Gardner 1984).

In general, traditional theories elaborate this view of cognition into a three stage process. First, information from the environment is sensed. Second, this information is used to construct a model of the external world (i.e., a mental representation of the world) that can then be manipulated to plan actions to perform. Third, once an appropriate plan of action is developed (and once inappropriate plans are discarded), this action is executed. Thus, cognition is treated as a sense-think-act cycle called the classical sandwich (Hurley 2001) because thinking is sandwiched between sensing and acting. According to the classical sandwich, thinking necessarily stands between sensing and acting: one cannot act without first thinking, and that the purpose of thinking is to plan action. Importantly, while the classical sandwich assumes three different processing stages, traditional cognitive theories almost invariably emphasize the “thinking” stage, and underemphasize “sensing” or “acting” (Dawson 2013).

Traditional cognitivism has led to many successful theories and is the dominant school of thought within psychology and cognitive science. However, this approach has also faced many setbacks. Cognitive theories of human thinking, or computer simulations of human cognition, have often been successful for simple or small problems but have performed poorly when scaled up to deal with more complicated situations (Dreyfus 1972, 1992). In domains where real-time action on the world is critical, such as robotics, traditional theories are often flawed because they encounter a “thinking bottleneck: Far too much

time is spent updating and manipulating a representation of the world before actions are performed (Brooks 2002). Some have argued that traditional cognitivism’s emphasis on internal representations prevents it from developing adequate accounts of phenomena like understanding language, because such phenomena arise from rich interactions between the bodies of agents and the ways in which these bodies can sense and act upon the world (Winograd and Flores 1987).

Such problems have led some researchers to develop new perspectives on cognition that adopt assumptions that are radically different from those adopted by traditional cognitivism. Embodied cognition is one such reaction (Clark 1997; Dawson 2013; Dawson et al. 2010; Shapiro 2011). The purpose of this article is to introduce the major characteristics of embodied cognition and to contrast these characteristics with the basic assumptions of traditional cognitivism.

## Characteristics of Embodied Cognition

In very general terms, the theories of embodied cognition depart from those of traditional cognitivism by considering cognition to be a sense-act cycle instead of a sense-think-act cycle. This departure has two crucial consequences. First, there is a move away from emphasizing mental representations. This is because the external world is viewed as its own representation; it is accessed by being sensed instead of being modeled in the mind. Second, there is a move towards emphasizing sensing and acting. This in turn requires considering the rich relationship between both the world and the agent. How the world can be sensed, and how it can be manipulated, depends crucially on the structure of an agent’s body.

While traditional cognitivism aims to explain complex behavior by appealing to the complexities of mental representations, embodied cognition is more likely to explain complex behavior as emerging from the complexities of the environment interacting with (simpler) properties of an agent. Let us briefly consider some of the key

assumptions that provide the foundation for embodied cognition.

### Environment

One key characteristic of embodied cognition is its recognition of the importance of the environment. While traditional cognition explains complex behaviors by appealing to complex mental representations, embodied cognition recognizes that environmental properties are critical contributors to this complexity. This is perhaps best reflected in Herbert Simon's parable of the ant (Simon 1969). To explain the complex shape of an ant's path as it moves along a beach, Simon famously noted that "viewed as a geometric figure, the ant's path is irregular, complex, hard to describe. But its complexity is really a complexity in the surface of the beach, not a complexity in the ant" (Simon 1969, p. 24).

The parable of the ant is nicely illustrated by the 1940s autonomous robot, called the Tortoise, invented by William Grey Walter (Grey Walter 1950, 1963; Holland 2003a, b). The Tortoise displayed a variety of complex, life-like behaviors. The Daily Mail reported that "the toys possess the senses of sight, hunger, touch, and memory. They can walk about the room avoiding obstacles, stroll round the garden, climb stairs, and feed themselves by automatically recharging six-volt accumulators from the light in the room. And they can dance a jig, go to sleep when tired, and give an electric shock if disturbed when they are not playful" (Holland 2003a, p. 2090).

However, such varied behavior was not produced by complicated internal mechanisms. The internal structure of the Tortoise was surprisingly simple: two sensing mechanisms, one for light and the other for physical contact, controlled two motors, one for moving and the other for steering. As the values detected by the sensing mechanisms changed, so too did the speeds of the two motors. The complexity of Tortoise behavior emerged from interactions between these simple mechanisms and the Tortoise's environment (e.g., light sources, obstacles). To generate more complex behavior, Grey Walter left the Tortoise's internal mechanisms unaltered and instead increased the complexity of the robot's environment by adding

multiple light sources, new obstacles, obstacles that reflected light, moving sources of light, and so on.

Importantly, one reason that complex behavior can emerge from the interactions between a complex environment and a simple agent is the fact that these interactions are generally nonlinear. For example, there is a nonlinear relationship between light level and steering motor speed in Grey Walter's Tortoise. In low light, the steering motor runs slowly; in medium light, the steering motor stops; in bright light, the steering motor runs at a higher speed.

### Situatedness and Embodiment

If complex behavior emerges from the nonlinear interactions between the world and the environment, then additional assumptions must follow. First, agents must be able to sense properties of the environment. In embodied cognition, this ability is called *situatedness*. As the sensors of an agent become more sophisticated, or greater in number and variety, the agent will become capable of producing more and more complicated behavior provided that it is placed in an interesting environment (Braitenberg 1984). In this context, an interesting environment is an environment in which various qualities that can be sensed are distributed unevenly.

In embodied cognition, agents are considered to be *situated* – and not merely as "sensing" – because their ability to respond to properties of the environment is fundamentally related to the structures of their bodies. *Situatedness* is closely related to the early twentieth century theoretical biology of Jakob von Uexküll. He coined the term *umwelt* to denote the "island of the senses" produced by the unique way in which an organism is perceptually engaged with its world (Uexküll 2001). Von Uexküll realized that because different organisms experience the world in different ways, they can live in the same world but at the same time exist in different *umwelten*. One can only describe an *umwelt* by describing the properties of both a world and an agent. For instance, it can be easily demonstrated that the behavior of a simple robot can be changed by repositioning its light sensors by moving them further away from

the center of the agent, or by changing their physical orientation (Dawson et al. 2010). Furthermore, in embodied cognition it is frequently assumed that agents actively explore their world to seek out new information as it is needed (Noë 2004); the nature of such exploration depends upon the structure of agents' bodies.

A second assumption that follows from the view that complex behavior emerges from the interactions between agents and environments is that agents must be embodied. To say that an agent is embodied is, in the most general sense, simply to say that the agent is physically present in the world. More sophisticated notions of embodiment drive embodied cognition. It can be argued that there is a continuum of embodiment, and that even if an agent physically exists this does not mean that it is completely embodied. Instead, embodiment is reflected in the degree to which the agent can affect or manipulate its environment (Fong et al. 2003). The more embodied an agent is, the more it can alter the world in which it is situated.

This notion of embodiment is therefore strongly related to Gibson's ecological theory of perception (Gibson 1979). Gibson's theory relied upon the coupling between an agent and the world, and emphasized that this coupling depended upon the nature of an agent's body. "It is often neglected that the words *animal* and *environment* make an inseparable pair" (Gibson 1979, p. 8). One reason for this was because Gibson's theory was an argument that the purpose of perception was to deliver affordances. Affordances are the possibilities for action that a particular object permits a particular agent. Affordances require an integral relationship between an object's properties and an agent's ability to act on these properties. Furthermore, an agent's ability to act depends upon the structure of its body. In short, an affordance must be defined in relation to an agent's body.

In short, in embodied cognition's emphasis on situatedness and embodiment, we see modern researchers endorsing two older notions, *umwelt* and affordance, as they emphasize the dynamic, nonlinear relationship between agents and their environments.

## Feedback

In embodied cognition, agent behavior is driven by sense-act connections based upon situatedness and embodiment. An agent is viewed as being embedded in a dynamic relationship with its environment; its environment triggers particular actions from the agent. Importantly, if an agent's actions can change the world, then these changes in turn can influence the agent's future actions. Cyberneticists called this dynamic relation between agents and environments feedback (Ashby 1956; Wiener 1948). Ashby (1956, p. 53) noted "'feedback' exists between two parts when each affects the other," when "circularity of action exists between the parts of a dynamic system." Feedback is an important source of behavioral complexity in embodied cognition, particularly in cases where an agent's environment includes other agents.

For example, consider the dynamics of a bat pursuing a moth. Many species of bats hunt by emitting ultrasonic sounds and by using their echoes to detect the location of targets. This enables bats to detect and to intercept targets as small as fruit flies or mosquitoes from distances of between 50 and 100 cm (Griffin et al. 1960). However, moths do not passively wait to become meals. Some moths have evolved transducers that permit them to hear bat echolocation signals (Fenton and Fullard 1979; Roeder and Treat 1961; Rydell et al. 1995). As soon as such a signal is heard, a moth will execute a power dive towards the ground; this dive often includes a series of evasive maneuvers that involve tight turns, loops, and climbs (Roeder and Treat 1961). In addition, some moths emit their own ultrasonic sounds to cause bats to turn away from their prey (Dunning and Roeder 1965). In short, bats and moths are clearly in a feedback relationship with their environment. The bat's actions – both in terms of its flight and in terms of the kinds of sounds that it generates – depend upon the distance between the bat and its prey. Furthermore, when a moth detects this attack, it begins evasive maneuvers, which represents a change in the world caused by the bat's ultrasonic probing. In turn, this change in the world produces changes in the bat's behavior, as it alters its flight path to foil

the evasion. The feedback relationship between these two agents – which are each dynamic components of the other's environment – is required to explain the complexity of the behavior of either agent as predator pursues prey.

It is important to note that the dynamic interactions between bats and moths occur over exceedingly short periods of time. Bats are usually hunting targets that are less than a meter away, are flying speeds of 1–6 m/s, and have only a few milliseconds to process the echo from any given target (Horiuchi 2005). Embodied cognition researchers would argue that bats simply do not have time to construct a mental model of their world to be used to plan the trajectory of their pursuit. Embodied cognition's emphasis on sense-act processing is to eliminate the "thinking bottleneck." "Models of the world simply get in the way. It turns out to be better to use the world as its own model" (Brooks 1991, p.139).

### Sense-Act Mechanisms

The notions of situatedness, embodiment, and feedback are all tied into embodied cognition's emphasis on sense-act processing as an alternative to traditional cognitivism's preference for the sense-think-act cycle. As a result, it is not surprising that embodied cognition seeks support for its position by discovering evidence for neural mechanisms that directly link sensing to acting.

For one example, neuroscientists studying bat echolocation have discovered a circuitry that is consistent with sense-act processing. Auditory processing in the bat brain is tightly coupled with motor processing, particularly with motor circuits responsible for bat vocalizations (Moss and Sinha 2003). This might reflect a sense-act system for modulating ultrasonic signals as a function of echolocation feedback.

Cognitive neuroscientists are also providing evidence for existence of sense-act mechanisms in the human brain (Goodale and Humphrey 1998). Goodale and Humphrey argue that the dorsal stream in the human brain, with connections from visual cortex to parietal cortex, mediates the visual control of action. They propose that the dorsal stream converts visual information directly into motor commands. This proposal is

supported by double dissociation evidence obtained from clinical patients. Patients with damage to their ventral stream are unable to describe the orientation or shape of any visual contour (Goodale et al. 1991). However, while this information could not be consciously reported, it was available and could control actions. The patient could grasp objects, or insert objects through oriented slots, in a fashion indistinguishable from control subjects, even to the fine details that are observed when such actions are initiated and then carried out. In contrast, damage to the posterior parietal cortex – part of the dorsal stream – can cause optic ataxia, in which visual information cannot be used control actions towards objects presented in the part of the visual field affected by the brain injury (Jakobson et al. 1991). Optic ataxia, however, does not impair the ability to the orientation and shapes of visual contours.

### Scaffolding and Control

Embodied cognition views agents as being dynamically embedded in environments and as being capable of acting upon and altering their worlds. The ability to change the world permits agents to use their environment to support or extend cognition. Using the world in this way is called cognitive scaffolding. For instance, using external devices (pens and notebooks, computers, etc.) to take notes during a lecture demonstrates the scaffolding of memory. More elaborate examples of scaffolding come from studies that examine practical problem solving activities in real world environments.

One famous example is Sylvia Scribner's study of problem-solving strategies exhibited by different types of dairy workers (Scribner and Tobach 1997). For example, workers assembled orders by converting information from computer printout into the required number of cases and partial cases of dairy products to be loaded onto each truck. However, the printout represented an order's information in a format that required the worker to convert it into more practical numbers of to-be-loaded products. Scribner found that novice workers solved this problem using mental arithmetic. In contrast, expert workers scaffolded the solution of this problem by working directly



from the visual appearance of cases of dairy products. One of the expert participants in this study reported that “I walked over and I visualized. I knew the case I was looking at had ten out of it, and I only wanted eight, so I just added two to it ... I don’t never count when I’m making the order, I do it visual, a visual thing you know” (Scribner and Tobach 1997, p. 303).

The external world can not only be used to store information but can also be used to manipulate it. Examples of this are provided by a variety of navigational tools that permit the results of computations to simply be inspected after data is recorded on them (Hutchins 1995). “It seems that much of the computation was done by the tool, or by its designer. The person somehow could succeed by doing less because the tool did more” (Hutchins 1995, p. 151).

There are also interesting examples in which computations are performed by the shapes of agent bodies. For instance, let us briefly return to bat echolocation. With echolocation, the horizontal position of a prey insect is uniquely determined by the difference in time between the echo’s arrival to a bat’s left and right ears. However, this information is not sufficient to uniquely specify the vertical position of the target. Evidence suggests that the extravagant shapes of the pinna and tragus of bats external ears are important for computing a target’s vertical position. These shapes cause returning echoes to strike the ear at different angles of entry, causing specific distortions in the sound signal (Muller et al. 2008; Obrist et al. 1993; Reijniers et al. 2010). These distortions provide additional auditory cues that vary systematically with the vertical position of the target (Wotton et al. 1995; Wotton and Simmons 2000). In other words, the shape of a bat’s ear alters sound in such a way that information about a target’s vertical dimension is added to the incoming signal. The bat’s body computes a solution to the vertical positioning problem before sound signals even reach the bat’s brain.

Finally, scaffolding also provides an external means of systematically controlling action to achieve complex goals. For instance, entomologists have long been interested in explaining how

social insects can build large and complex structures such as termite mounds. One important idea about the “plan” for the construction of social insect nests is the notion of *stigmergy* (Grasse 1959; Theraulaz and Bonabeau 1999). With stigmergy, the actions of a group of agents are controlled via a shared environment. Environmental cues cause an agent to act upon and change the world. These changes in turn alter the later actions of this agent, or those of other members of an insect colony. Grassé’s notion of stigmergy is the proposal that termite building behavior is not planned or regulated by the insects themselves but is instead controlled externally by the changing appearance of the mound.

### The Extended Mind

We have seen that one consequence of embodying cognition is that an agent’s environment can be actively exploited or modified to scaffold cognition. This in turn leads to a radical and controversial hypothesis: that the mind extends into the world (Adams and Aizawa 2008; Clark 1997; Clark and Chalmers 1998; Wilson 2004). According to the extended mind hypothesis, the mind and its information processing is not separated from the world by the skull. Instead, the mind interacts with the world in such a way that information processing is both part of the brain and part of the world – the boundary between the mind and the world is blurred, or has disappeared.

Where is the mind located? The customary view – typified by traditional cognitivism – is that thinking is inside the individual, and that sensing and acting involve the world outside. However, if cognition is scaffolded, then some thinking has moved from inside the head to outside in the world. “It is the human brain *plus* these chunks of external scaffolding that finally constitutes the smart, rational inference engine we call mind” (Clark 1997, p. 180). As a result, Clark describes the mind as being extended, because it spreads from inside our skull to include whatever is used as external scaffolding. In other words, one key difference between traditional cognition and embodied cognition concerns where minds are located.

## Conclusion

Traditional cognitive theories emphasize sense-think-act processing, presuming that the purpose of cognition is to construct models of the external world that can be used to plan future behavior. Embodied cognition is a reaction against this view and assumes that mental models of the external world are not required, because the world can serve as its own model. Embodied cognition therefore attempts to replace the sense-think-act cycle with sense-act processing that permits the world to directly control action. This view places a greater emphasis on the nature of the environment, and on the structure of agents' bodies, than is found in traditional cognitivism. Agents are taken to be situated and embodied in an environment. What can be sensed in the environment, and how the environment can be altered by agents, depends critically on the interaction between worlds and bodies. The complex behaviors of agents may be explained by appealing to feedback between agents and environments that are mediated by sense-act mechanisms, and which permit critical components of the mind to extend into the world by means of cognitive scaffolding.

## Cross-References

- Cognition
- Embodied Perception
- Perception-Action Theory
- Plantae

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## Embodied Perception

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## Synonyms

Action perception; Enactive perception

## Introduction

Embodied perception, sometimes called enactive perception, reacts against the traditional view that the purpose of perception is to construct mental representations of the external world. Embodied perception does this by adopting a key position of behavior-based robotics: that it is unnecessary to create costly mental representations of the world when the world can serve as its own representation (Brooks 1999, 2002). Embodied perception further argues that perception is not a representational process but is instead a motor skill concerned with actions upon the world (Noë 2004, 2009). This casts embodied perception as a modernization of James Gibson's ecological approach (Gibson 1966, 1979).

This entry introduces embodied perception. It begins by briefly describing the main assumptions underlying traditional, representational, theories of perception. It then uses problems associated with these assumptions to introduce the properties of theories of embodied perception. Different kinds of evidence supporting these assumptions are briefly reviewed, as are the links between embodied perception and some modern theories of vision.

## Against Representational Theories of Perception

Our phenomenal experience of visual perception gives rise to a simple notion that seeing is like photography: the eyes transmit visual information

to an inner screen that is mediated by some spatial layout of neurons (Frisby and Stone 2010). Our everyday experience is that visual perception is effortless, that we simply look at the visual world and automatically experience its layout. This inner screen theory necessarily defines visual perception as a representational process. This is because whatever the nature of the “inner screen,” it differs from the visual world outside the head, and therefore must stand for or represent the world’s visual properties.

With the current prevalence of cognitive theories in psychology (Dawson 2013), the view that the purpose of visual perception is to create meaningful representations of the world is widely accepted (Marr 1982). This position in turn dictates that theories of visual perception must explain the nature of these representations and how they are created and manipulated. Explorations of perceptual representations have led to two different issues that have fueled research questions, but that have also produced reactions against this representational approach.

The first issue is that visual perception is underdetermined (Marr 1982). Visual perception can be conceived as beginning when a distal stimulus (the layout of surfaces in the external world) provides visual information that creates a proximal stimulus (such as a pattern of stimulation on the retinae). Cognitivism implies that the task of vision is to create a mental representation of the distal stimulus that caused the proximal stimulus. The problem, though, is that for a variety of reasons information about the distal stimulus is lost when the proximal stimulus is created (Grimson 1981; Hildreth 1983; Marr 1982; Richards 1988; Ullman 1979). This means that there is a poverty of the proximal stimulus: on its own it does not contain sufficient information to uniquely recreate the distal stimulus that produced it. In principle, the proximal stimulus by itself is consistent with an infinite number of different distal stimuli. Vision is underdetermined because there is not a one-to-one mapping from a proximal stimulus to a distal stimulus.

Many different representational theories have arisen to deal with the problem of underdetermination. These theories propose

various means by which information missing from the proximal stimulus can be added by additional processes in order that a unique and correct representation of the visual world can be constructed. These theories range from the top-down addition of knowledge of the world (Bruner 1957, 1992; Gregory 1970; Rock 1983) to the bottom-up application of natural constraints (Marr 1982; Richards 1988; Ullman 1979).

Importantly, the additional processing that is required to create unique representations from underdetermining proximal stimuli leads to a second key issue: that creating representations of the distal world is costly. The relevance of this issue was revealed in early research on autonomous robots, machines that navigated by planning routes and actions by using representations of the world (Brooks 2002; Moravec 1988; Nilsson 1984). In general, these machines were stationary most of the time they were operating because they were busy updating and manipulating their internal representation of the world to plan actions before these actions could be carried out. Brooks (2002) has noted that one famous robot, Nilsson’s Shakey, would take hours to move to a goal location a few meters from its starting position. “Most of the time Shakey, the robot shell, sat idle while its remote brain contemplated a long series of moves to accomplish its ultimate goal” (Brooks 2002, p. 23).

Brooks’ response to this problem was to abandon representations. He developed robots that did not require internal models of the sensed world. Instead, these robots directly converted sensed information into actions upon the world, making the behavior of these robots fast, responsive and adaptive. This approach has been called behavior-based robotics or new wave robotics (Brooks 1999; Sharkey 1997). The defining feature of this approach is replacing representation with reaction; embodied perception is also characterized by this feature. Accordingly, visual perception becomes construed as a sensorimotor skill that accesses information in the world as it is needed. Rather than building detailed internal models of the world, embodied perception – like behavior-based robotics – considers the world to be its own representation; we don’t construct an

internal model of the world, because we can act upon the outer world, and inspect it, when required (Noë 2002, 2004, 2009).

Embodied perception involves more than merely assuming that information in the world is inspected, and not represented. It also abandons representations because it assumes that perception has a quite different goal: guiding bodily actions upon the world. “Perceiving is a way of acting. Perception is not something that happens to us, or in us. It is something we do” (Noë 2004, p. 1). This view of perception arises because embodied theorists are inspired by Gibson’s ecological approach to perception as is discussed later (Gibson 1966, 1979).

Acting upon the world plays multiple roles in the theory of embodied perception (Noë 2004). First, the purpose of perception is not viewed as building internal representations of the world, but instead as controlling action on the world. Second, and related to the importance of controlling action, our perceptual understanding of objects is sensorimotor, much like Gibson’s (1979) notion of affordance, as is discussed below. That is, we obtain an understanding of the external world that is related to acting on an object, or by moving to a new position. Third, perception is presumed to be an intrinsically exploratory process. Perceptual objects are virtual – we have access to properties in the world when needed, and only through action. “Our sense of the perceptual presence of the cat as a whole now does not require us to be committed to the idea that we represent the whole cat in consciousness at once. What it requires, rather, is that we take ourselves to have *access*, now, to the whole cat” (Noë 2004, p. 63).

## Evidence for Embodied Perception

Clearly there are dramatic differences between the basic assumptions of embodied perception and those found in more traditional representational theories. The discussion in the previous section highlights some of the theoretical motivations for the new sets of assumptions that are adopted in the study of embodied perception. There is also growing empirical evidence that supports these

assumptions. The purpose of this section is to briefly provide some examples of such support.

Representational theories of visual perception seem plausible because we experience our visual world as a rich, stable panorama that is present in its entirety. However, this experience is illusory. Evidence suggests that we only experience fragments of the distal world a glance at a time, which is consistent with the basic assumptions of embodied perception (Noë 2004, 2009).

One example of evidence that our perceptual experience is fragmentary is that we are subject to change blindness, and fail to notice substantial visual changes even though they occur in plain sight (O’Regan et al. 2000). We are also prone to a related phenomenon, inattention blindness, in which we do not detect obvious visual information because our attention is not directed to it. Inattention blindness is demonstrated by one famous experiment in which subjects watched a video of a basketball game, and counted the number of times that the teams changed possession of the ball (Simons and Chabris 1999). In the midst of the game, a person dressed in a gorilla suit walked out onto the court and danced a jig. Amazingly, most subjects failed to notice this highly visible event because they were attending to the ball.

Embodied perception not only assumes that perception is fragmentary (because it is not representational), but also assumes that there is a fundamental link between perception and action. This emphasis on actions on the world was also central to Gibson’s (1966, 1979) ecological theory of perception. Gibson proposed that perceiving agents “picked up” the affordances of objects in the world. Critically, the affordances of an object are the possible actions that a particular object makes available a particular agent. “The *affordances* of the environment are what it *offers* the animal, what it *provides* or *furnishes*, either for good or ill” (Gibson 1979, p. 127, his italics).

Crucially, the view that affordances are potential actions leads to the assumption that affordances emerge from an integral relationship between an object’s properties and an agent’s embodiment. This is because an agent’s embodiment defines its abilities to act. “Note that the four



properties listed – horizontal, flat, extended, and rigid – would be *physical* properties of a surface if they were measured with the scales and standard units used in physics. As an affordance of support for a species of animal, however, they have to be measured *relative to the animal*. They are unique for that animal. They are not just abstract physical properties” (Gibson 1979, p. 127).

Given that affordances are defined in terms of an organism’s potential actions, which in turn are defined by an agent’s embodiment, it would be expected that perceptions of the world can be affected by the states of an agent’s body, as well as by changes in these states. Evidence indicating that this is indeed the case provides additional support for embodied perception.

For instance, in a task where participants point to objects with their index finger versus pointing with a conductor’s baton, objects are viewed as being nearer in the latter condition (Proffitt 2006). Furthermore, Proffitt has also demonstrated that perception is also altered when changes in bodily state alter the cost of actions on the world. For example, slopes are viewed as being steeper, and distances are viewed as being longer, when one’s body is made heavier and therefore more costly to move. Similarly, the size of objects appears to be judged relative to the shape of body parts used to manipulate them (Linkenauger et al. 2011). Linkenauger et al. found that the apparent size of objects became smaller when participants experienced their hand size as being modified. Interestingly, such hand-size manipulations did not affect size perception when the object being judged was too large to manipulate with the hand. In a related study, when goggles are used to make the apparent size of objects larger or smaller, this apparent size modification vanishes when one reaches for an object with one’s hand – if the appearance of the hand is similarly modified (Linkenauger et al. 2010). However, the apparent size modification does not vanish if one views the object being manipulated by someone else’s hand, even if the appearance of this other hand is manipulated in the same way as the object.

It was noted earlier that embodied perception’s emphasis upon action links it to behavior-based robotics. Brooks’ robots are controlled by what he

calls the subsumption architecture (Brooks 1999). This architecture is a set of modules or operators that can each be described as a sense-act mechanism. That is, each module senses information in the world and then directly converts this information into action by altering the behavior of an actuator. Is there any evidence for this type of architecture in biological perceptual systems?

Evidence does suggest that sense-act modules that provide the foundation of the subsumption architecture also appear to exist in the human brain (Goodale 1988, 1990, 1995; Goodale and Humphrey 1998; Goodale et al. 1991; Jakobson et al. 1991). This has led to the duplex theory of vision (Goodale and Humphrey 1998). One characteristic of the duplex theory is its reworking of a standard perspective on the neuroscience of vision. According to this standard perspective, there exist two distinct physiological pathways in the human visual system, one (the ventral stream) for processing the appearance of objects, the other (the dorsal stream) for processing their locations (Livingstone and Hubel 1988; Maunsell and Newsome 1987; Ungerleider and Mishkin 1982). In contrast, the duplex theory proposes that while the ventral stream creates perceptual representations, the dorsal stream mediates the visual control of action in a fashion quite similar to the modules in Brooks’ subsumption architecture. “The functional distinction is not between ‘what’ and ‘where’, but between the way in which the visual information about a broad range of object parameters are transformed either for perceptual purposes or for the control of goal-directed actions” (Goodale and Humphrey 1998, p. 187).

Double dissociation evidence from cognitive neuroscience has been used to support the duplex theory. The study of one brain injured subject (Goodale et al. 1991) revealed normal basic sensation. However, the patient could not describe the orientation or shape of any visual contour, no matter what visual information was used to create it. While this information could not be consciously reported, it was available and could control actions. The patient could grasp objects, or insert objects through oriented slots, in a fashion indistinguishable from control subjects, even to



the fine details that are observed when such actions are initiated and then carried out. This pattern of evidence suggests that the patient's ventral stream was damaged, but that the dorsal stream was unaffected and controlled visual actions. "At some level in normal brains the visual processing underlying 'conscious' perceptual judgments must operate separately from that underlying the 'automatic' visuomotor guidance of skilled actions of the hand and limb" (Goodale et al. 1991, p. 155).

Other kinds of brain injuries produce a very different pattern of abnormalities, establishing the double dissociation that supports the duplex theory. For instance, damage to the posterior parietal cortex – part of the dorsal stream – can cause optic ataxia, in which visual information cannot be used control actions towards objects presented in the part of the visual field affected by the brain injury (Jakobson et al. 1991). Optic ataxia, however, does not impair the ability to detect the orientation and shapes of visual contours.

Healthy subjects can also provide support for the duplex theory. For instance, in one study subjects reached to an object whose position changed during a saccadic eye movement (Pelisson et al. 1986). As a result, subjects were not conscious of the target's change in location. Nevertheless, they compensated to the object's new position when they reached towards it. "No perceptual change occurred, while the hand pointing response was shifted systematically, showing that different mechanisms were involved in visual perception and in the control of the motor response" (Pelisson et al. 1986, p. 309). This again supports the existence of sense-act modules in the human brain. Similar evidence exists for other perceptual modes. For example, a great deal of evidence supports the claim that neural circuits for motor actions are critical components for the understanding of spoken and written language (Pulvermuller and Fadiga 2010).

The evidence cited above focuses upon the relationship between action and perception. The embodiment of an agent can affect perception in other ways as well. For instance, consider some evidence concerning how bats echolocate prey. Bats emit a high-frequency sound and detect the

location of targets by processing the echo (MacIver 2008). The horizontal position of a target (e.g., a prey insect) is uniquely determined by the difference in time between the echo's arrival to the left and right ears. However, this information is not sufficient to specify the vertical position of the target. The physical nature of bat ears solves this problem. The visible external structure (the pinna and the tragus) of the bat's ear has an extremely intricate shape. This shape causes returning echoes to strike the ear at different angles of entry. This provides additional auditory cues that vary systematically with the vertical position of the target (Wotton et al. 1995; Wotton and Simmons 2000). Furthermore, if the shape of the bat's ear is physically manipulated, then there is a substantial decrease in its echolocation abilities (Chiu and Moss 2007; Lawrence and Simmons 1982). In other words, the bat's body – in particular, the shape of its ears – is critical to its perceptual abilities.

## Integrating Representational and Nonrepresentational Theories of Perception

Embodied theories in cognitive science vary in their degree of radicalness. More radical embodied theories attempt to completely eliminate mental representations (Chemero 2009). Less radical theories combine both nonrepresentational and representational processes in an attempt to generate more complete, hybrid theories (Clark 1997). In certain respects, the growing acceptability of embodied perception is revealed by theories that attempt to integrate its nonrepresentational ideas with more traditional representational accounts of perception.

One such theory that we have already briefly encountered is the duplex theory (Goodale and Humphrey 1998). It is integrative in the sense that while the ventral stream in the human brain mediates traditional representational processing, at the same time the dorsal stream is presumed to implement sense-act modules of the type to be found in theories of embodied perception. In this section, we briefly consider another hybrid theory,

Zenon Pylyshyn's theory of seeing and visualizing (Pylyshyn 2003, 2007). The hybrid nature of this theory is intriguing because its author is a noted critic of a position that is central to embodied perception, Gibson's ecological theory (Fodor and Pylyshyn 1981). Discovering elements of embodied perception in Pylyshyn's theory provides strong evidence for the growing importance and acceptance of embodied ideas.

Pylyshyn's theory of seeing and visualizing emerged from his interest in explaining how diagrams were used in reasoning (Pylyshyn 2007). Pylyshyn recognized that a system for performing such reasoning required two core abilities: to be able to individuate visual entities and to be able to track or maintain the identities of visual entities over time. His account of these core abilities adds a strongly embodied flavor to his theory. He argues that one of the primitive processes of early vision is individuating a visual object as being distinct from others. In his theory, this is accomplished by preattentively tagging an object with an index called a FINST (for finger instantiation). A FINST only provides access to the individuated object, so that its properties can be inspected when needed. Once assigned to an object a FINST remains attached to it even as the object changes its location or other properties.

FINSTs individuate visual objects without delivering a description of them. Pylyshyn (2007) argues that this is the visual equivalent of using indexicals or demonstratives in language. "Think of demonstratives in natural language – typically words like *this* or *that*. Such words allow us to refer to things without specifying what they are or what properties they have" (Pylyshyn 2007, p. 18). FINSTs are visual indices that operate in exactly this way. They are analogous to placing a finger on an object in the world, and (while not looking) keeping the finger in contact with it as the object moved or changed (thus the term "finger instantiation"). As long as the finger is in place, the object can be referenced ("this thing that I am pointing to now"), even though the finger does not deliver any visual properties.

FINSTs are linked to embodied perception in two important ways. First, in traditional

representational theories of perception an object's features are first detected, and then the object is identified and individuated by combining these features into a description (Treisman 1986; Treisman and Gelade 1980). In contrast, in Pylyshyn's theory object individuation occurs before its features are processed or combined. In this sense, FINSTs are much less representational. Second, the purpose of a FINST is to provide access to an object in the world when needed, so that the properties of the object can be inspected when required. This is consistent with embodied perception's view that perception is fragmentary and that perceptual experience is constructed by examining parts of the world when needed.

There is a growing literature that provides empirical support for Pylyshyn's FINST hypothesis, which in turn provides additional evidence in support of embodied perception. Some of this evidence comes from a multiple object tracking paradigm in which a set of moving objects are treated as targets, and are indistinguishable from other moving distractors. Human participants are capable of tracking the target objects even when all of the objects move randomly through the visual field. This process is parallel, because up to four objects can be tracked, and tracking results cannot be explained by a model that shifts a spotlight of attention serially from target to target (Pylyshyn and Storm 1988). However, the fact that no more than four targets can be tracked also shows that this processing has limited capacity. FINSTs are assigned to objects, and not locations; objects can be tracked through a locationless feature space (Blaser et al. 2000). Using features to make the objects distinguishable from one another does not aid tracking, and object properties can actually change during tracking without subjects being aware of the changes (Bahrami 2003; Pylyshyn 2007). Thus, FINSTs individuate and track visual objects but do not deliver descriptions of the properties of the objects that they index.

Of course, FINSTs make up only one component of Pylyshyn's theory. Other aspects of this theory are representational because once FINSTs are used to access visual objects, the features made available via inspection are then used to

create mental representations of the visual world. However, the fact that mechanisms that are consistent with embodied perception define an important part of early visual processing in this hybrid theory indicates embodied perception's growing influence in the discipline.

## Cross-References

- [Cognition](#)
- [Embodied Cognition](#)
- [Perception-Action Theory](#)
- [Visual Perception](#)

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## Embryo

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## Synonyms

Fertilized egg; Unborn child/baby

## Definition

Embryo is the earliest prenatal phase of development *in utero* between the fertilized egg and the end of eighth week of gestation (in human), after which it is termed as fetus.

## Introduction

In the simplest form, embryo can be defined as a collection of cells generated from the fertilized ovum after implantation in the uterine wall till the eighth week of gestation (in human). Therefore, embryo defines the phase of development between fertilized ovum and fetus. It is the derivative of zygote that is intended to become the offspring (fully developed both anatomically and physiologically and able to survive as a separate organism) (Gould 1977).

Generally, embryo as a term for vertebrates correlates differently for different animals. It can belong to the developmental stage anytime before birth/hatching or till it becomes fetus or until it structurally resembles the adult form (Harrison 1969, 1988). Most rapid growth is

observed during the embryonic stage in most of the animals.

## Embryogenesis

The study of the development of an embryo is called embryology. When a sperm of the male fertilizes an egg cell (ovum) in the female, it forms a zygote containing DNA from both the parents (Gilbert 2010). The zygote then divides mitotically to produce a multicellular organism, which is known as embryo. This transition from zygote to embryo occurs through explicit discernible stages of blastula, gastrula, and organogenesis. A fluid filled cavity (blastocoel) is formed which is surrounded by a spherical sheet of cells (blastomeres) in the blastula stage. During gastrulation stage, single layered blastula is reorganized into a multilayered gastrula forming distinguishable germ layers (ectoderm, mesoderm, and endoderm; as in triploblastic organisms) (Stern 2004). After gastrulation, various molecular interactions between the germ layers result in differentiation of organ-specific cell types and this process is known as organogenesis. Different tissues are formed during process like myogenesis (muscle), neurogenesis (brain, spinal cord, and peripheral nerves), etc. In this way, the embryo is formed (Gilbert 2010) (Fig.1).

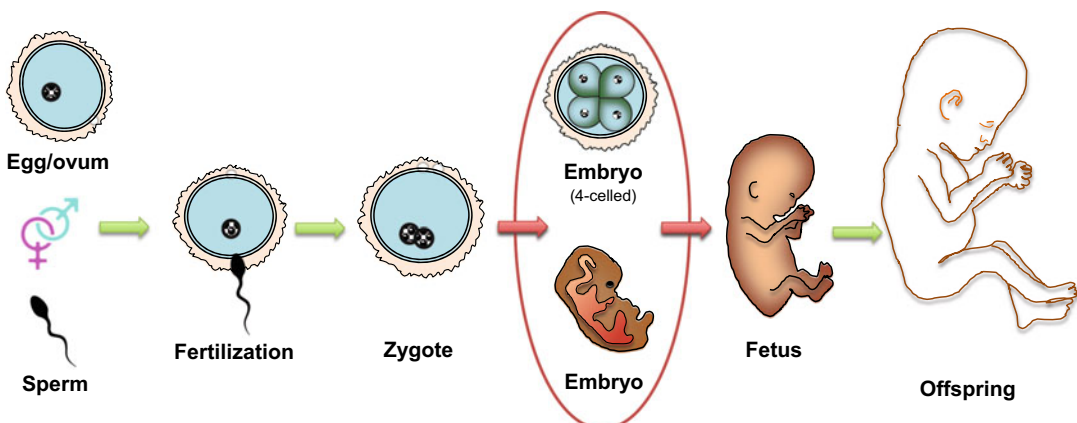
## Terminology for Embryo on the Basis of Appearance of Somites

1. **Presomite embryo:** When the embryo is at any stage before the appearance of the first somite, it is known as presomite embryo.
2. **Previllous embryo:** It is the embryo till the placental chorionic villi grow.
3. **Somite embryo:** The embryo between the appearance of the first and the last somites is called somite embryo.

## Stages of Human Embryonic Development

The human embryonic period (*i.e.*, the first 8 weeks of gestation, postovulation) is divided into 23 distinctive developmental steps, known as Carnegie stages (Hill 2017). It is named after Carnegie Institute of Washington, USA, which collected and classified embryos. These stages of the embryo are distinguished from each other on the basis of external or internal morphological development, independent of size or age.

The Carnegie stages can be grouped into different weeks. First week has Carnegie stages 1–4, whereas week 2 has stages 5 and 6. Similarly third week has 7–9, fourth week has 10–13, fifth week has 14 and 15, sixth week as 16 and 17, seventh



**Embryo, Fig. 1** Embryogenesis. An embryo develops from the zygote and reaches fetus stage before becoming a fully grown up offspring which is ready to take birth. This

includes the most complex physiological and morphological changes in an organism



week has 18 and 19, and finally the remaining stages 20–23 come under eighth week (Hill 2017).

On day 1 of first week (stage 1), the size of fertilized oocyte or zygote is between 0.1–0.15 mm, which increases up to 0.2 mm by the end of 15th day. On second and third day (stage 2), there is reduction in cytoplasmic volume forming morula, after which blastocyst is formed. There is a loss of zona pellucida and the blastocyst is found free till day 5 (stage 3). During days 5–6 (stage 4), the blastocyst gets attached and implantation occurs between days 7 and 12 (stage 5). This is followed by the appearance of extra embryonic mesoderm, primitive streak, and gastrulation between days 13 and 15 (stage 6). Gastrulation continues and notochordal process appears in week 3 between days 15–17 (stage 7) and the size of the embryo at this stage is around 0.4 mm. The embryo grows rapidly to size of 1.0–1.5 mm between days 17 and 19 (stage 8) when the primitive pit is formed and notochordal canal appears. This growth is followed by somitogenesis, where different somites are formed as follows: (a) somite 1–3, neural folds, cardiac primordium, and head fold are formed (embryonic size = 1.5–2.5 mm, stage 9), (b) somite 4–12 are formed and neural fold fuses (embryonic size = 2–3.5 mm, stage 10), (c) somite 13–20 are formed and rostral neuropore closes (embryonic size = 2.5–4.5 mm, stage 11), (d) somite 21–29 are formed and caudal neuropore closes (embryonic size = 3–5 mm, stage 12), and (e) somite 30 is formed with appearance of leg buds, lens placode, and pharyngeal arches (embryonic size = 4–6 mm, stage 13). By now the embryo reaches a size of 5–7 mm at stage 14 in the week 5 where between days 31 and 35, lens pit and optic cups are formed. Then in stage 15 between days 35 and 38, lens vesicle, nasal pit, and hand plate are formed with embryonic size of 7–9 mm and then the nasal pits move ventrally in the stage 16 (week 6, days 37–42, size 8–11 mm) along with the development of auricular hillocks and foot plate. Between days 42 and 44 at the stage 17, embryonic size becomes 11–14 mm and finger rays can be clearly seen. At stage 18, ossification starts during days 44–48 with size reaching 13–17 mm. Straightening of trunk can be seen at the stage 19 (days 48–51, size

16–18 mm) and then during 51–53 days (in week 8, size 18–22 mm) the upper limbs become longer and get bent at the elbows. At stage 21, during days 53–54 the embryonic size is 22–24 mm and the hands and feet turn inwardly. Between days 54 and 56 (stage 22), overall size becomes 23–28 mm, and eyelids and external ears can be clearly observed. Finally at stage 23, between days 56 and 60 the embryo reaches a size of 27–31 mm and rounded head, body, and limbs are observed. After this stage, the embryo turns into a fetus, which grows till birth that occurs in around 37 weeks (Hill 2017).

## Conclusion

Embryo is the developmental stage between the zygote and fetus where highest growth and differentiation (cellular and molecular) occurs.

## Cross-References

- [Fetus](#)
- [Internal Fertilization](#)
- [Zygote](#)

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## Embryonic Diapause

- [Developmental Arrest](#)



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## Embryonic Quiescence

- [Developmental Arrest](#)
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## Emotion Detection

- [Discrimination of Emotion](#)
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## Emotion Recognition

- [Discrimination of Emotion](#)
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## Emotional Arousal

- [Arousal](#)
- 

## Emotional Contagion

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Emotional contagion is the process leading to the emotional state matching between two interacting subjects: the individual experiencing a particular emotional state and the observer. Emotional contagion is considered a basic building block of empathy and makes individuals able to share emotions. Empathy, in its most complex definition, is a phenomenon that implies the ability to perceive and interpret what another person is feeling and understand their needs (de Waal and Preston 2017).

Emotional contagion is so influential and pervasive in driving the feelings of people (fear, sadness, joy, surprise, etc.) that it has become of interest not only to the academic disciplines

(anthropology, psychology, sociology, neuroscience, ethology, etc.) but also to the working, marketing, entertainment, and political domains (Decety 2012). In the working context, emotional contagion can significantly influence individual attitudes and group processes. For instance, positive emotional contagion between group members was found to improve cooperation, decrease conflict, and increase perceived task performance at work (Barsade 2002). Advertisement, politicians, and film or theatre scenes often fake emotional sharing to enhance involvement, increase motivation, and boost audience approval and support. For example, when watching scenes involving laughter or cry, we are aware that the actors are emoting (cognitive consciousness) and still we are often infected by faked feelings and internally reproduce real emotions. This reveals that our emotional responses are unconscious and unstoppable, and cognition has limited control over our immediate reactions.

The reason why emotional contagion has been naturally selected over the course of evolution is under debate. The most accepted explanation that accounts for the evolution of emotional contagion is social living. Humans live completely nestled in an emotional network that makes us socially interdependent beings. Obviously, in this social world, we are not alone and also other animal species are able to experience and express emotions. Unveiling emotions is essential to communicate with conspecifics and synchronize many social activities. A large bulk of research has been recently devoted to understand how emotional contagion comes into play, how humans and other animals get to share emotions, and what are the proximate and ultimate causes of this phenomenon (de Waal and Preston 2017).

## Rapid and Spontaneous Mimicry

One of the most fertile fields of research is the facial and bodily motor expression of emotions, including how human and nonhuman animals are able to perceive the emotions of others by mimicking the same motor pattern that makes such emotion manifest. Emotional contagion

and resonance occur when an observer pre-consciously activates shared emotional representations during the perception of an action or of a facial expression. This activation response, known as perception-action coupling, is a basic requirement of empathy because it leads individuals to automatically experience others' affective states (Christov-Moore et al. 2014; de Waal and Preston 2017). Literature indicates that the ability to emotionally empathize involves the mirror neuron system and different brain areas (the inferior frontal gyrus (IFG) especially, but also the inferior parietal lobe (IPL); the anterior cingulate cortex (ACC); and the anterior insula (AI); Shamay-Tsoory 2011).

One of the mechanisms that informs emotional contagion is rapid and spontaneous mimicry, the fast (less than 1 s), unconscious, and unintentional imitation of behavior shown by two interacting partners leading to motor facial and bodily resonance (Hess and Fischer 2013).

According to some definitions (e.g., Whiten et al. 2009), true imitation requires that the observer both recognizes the goal of the demonstrator and reaches that goal by exactly copying the observed sequence of actions. Mimicry, on the other hand, does not involve any recognition of the goal (for review: Palagi and Scopa 2017). The process that links mimicry and emotional contagion involves two steps. Firstly, the perception of others' expressive behavior automatically induces the observer to mirror such behavior. Secondly, the mimicry of others' behavior can induce the observer to share the emotional state underpinning such behavior (Dezecache et al. 2015). It is in order to specify that rapid mimicry and emotional contagion, although possibly interacting, are distinct concepts, because each can occur independently (Nakahashi and Ohtsuki 2015; Palagi et al. 2015). This is, for example, the case of consolation, explained better below.

From a functional point of view, mimicry regulates dyadic relations and favors the formation of strong, enduring social bonds, which in turn enhance reproductive success. Mimicry is an honest signal of affiliation whose perception informs the demonstrators on the ongoing emotional synchronization (Kavanagh and Winkielman 2016; Niedenthal et al. 2010). This emotional sharing

makes individuals more inclined to interact in a positive way, which opens the way to strong long-term social bonds. Therefore, the value of mimicry relies on the fact that it is a true signal of emotional contagion (Kavanagh and Winkielman 2016).

Considering the importance that mimicry plays in sharing emotions and regulating social interactions, it is not surprising that this phenomenon is more widespread in mammals than previously thought. The presence of emotional contagion has also been demonstrated in birds. In an elegant playback experiment, Schwing et al. (2017) showed that New Zealand parrots (*Nestor notabilis*) are emotionally infected by the playful vocalizations of conspecifics. During the administration of the play calls, the authors recorded an increase of play frequency and duration in the receivers that started to play with nonplaying birds, thus demonstrating that play vocalizations can act as positive emotional contagion.

In the last decades, many researchers have become increasingly aware that the only possibility to understand even the most complex forms of human empathy is to look at other branches on the evolutionary tree. As a result of this new interest, some convincing data emerged on similar phenomena in nonhuman species. In primate and nonprimate species, rapid mimicry is a good regulator of social interactions and reliable predictor of emotional closeness.

Play provides researchers with the opportunity to investigate the relationship between rapid mimicry and emotional contagion because play is punctuated by a unique, behaviorally specific facial expression, the relaxed open mouth display (ROM), which is unequivocally associated to a positive emotion. The possibility to use ROM, homologous to human laughter, is particularly important in the study of nonhuman animals in which deciphering the emotional state is not trivial. In geladas (*Theropithecus gelada*), the presence of rapid facial mimicry involving ROM allowed the players to engage in longer play sessions by enhancing emotional synchrony (Mancini et al. 2013a, b). A similar phenomenon was found also in chimpanzees (*Pan troglodytes*), lowland gorillas (*Gorilla gorilla gorilla*; Palagi

et al., submitted), and domestic dogs (*Canis lupus familiaris*; Palagi et al. 2015). Interestingly, rapid facial mimicry was found in the tolerant Tonkean macaque but not in the despotic Japanese macaque (*Macaca fuscata*) (Scopa and Palagi 2016). Hence, rapid mimicry appears to be sensitive to the relationships established via emotional bonding rather than via dominance power. In geladas, it was also observed that in the first months of life, the highest levels of rapid facial mimicry were present between mothers and their offspring (Mancini et al. 2013a), thus supporting the empathic gradient hypothesis, which predicts that the emotional involvement is maximum between closely bonded subjects (de Waal and Preston 2017).

Facial mimicry is a visually-based form of emotional contagion. Nevertheless, other sensory cues can vehicle emotions from a subject to another. In humans, it was demonstrated that listeners were able to discriminate whether American English people laughing together (collaughter) were friends or not with one another. The listeners, who belonged to 24 different societies from all over the world, were capable to do so just by hearing a short audio-record without receiving any visual indication. The level of laughter contagion in the listener was highest when hearing friends laughing. Hence, vocal mimicry represents a valuable communicative signal of relationship quality, independent of the sociocultural background. While discussing their results, the authors pointed out that the emergence of articulate language did not erase our ability to use unconscious facial/vocal signals of affiliation (Bryant et al. 2016). They posited that during the evolution of our species, those individuals who were able to decode nonverbal communicative exchange between others and understand their level of social bonding, probably obtained advantages in terms of fitness.

## Yawn Contagion

In 1872, Darwin defined yawning as a wide gaping of the mouth, until the acme is reached, followed by a passive closure of the jaws, with all phases accompanied by respiratory

components. Yawning has often been considered a *stereotyped action pattern* due to its consistency in duration, morphology, and frequency (*Homo sapiens*, Provine 2005). The yawning motor pattern is an ancient (plesiomorphic) facial display that can be unambiguously recognized (Baenninger 1997). Yawning can be spontaneous or triggered by another yawn. In particular, yawn contagion occurs when someone yawns in response to someone else's yawn (Provine 2005). Even though the way to exactly quantify the phenomenon is under debate, yawn contagion has been demonstrated in human and nonhuman primates and even in dogs and wolves (de Waal and Preston 2017). Similarly to mimicry, contagious yawning is a preconscious response and it is therefore scarcely affected by cognitive biases (Provine 2005). As mimicry, it relies upon the perception-action mechanism involving the mirror neuron system (de Waal and Preston 2017) and recruits different neuronal networks involved in empathic processing, including the inferior frontal gyrus (IFG) and other mirror neuron areas (Arnott et al. 2009; Cooper et al. 2012; Haker et al. 2013; Nahab et al. 2009). Yawn contagion is biased by the same variables that affect emotional contagion, the basic layer of empathy (de Waal and Preston 2017). As empathy, yawn contagion increases with age starting at 3–5 years when the ability to identify others' emotions is being acquired and declines with old age when empathic abilities also decline (Hoogenhout et al. 2013; Millen and Anderson 2011; Saxe et al. 2004).

Yawn contagion is present between strangers in both humans and bonobos (Norscia and Palagi 2011; Tan et al. 2017) and this is in line with findings demonstrating that the subjects of both species can provide help to unfamiliar individuals and not just to familiar ones (Tan and Hare 2013; Raihani and Bshary 2015). Nevertheless, yawn contagion follows the empathic trend because it is more frequently observed between familiar than between unfamiliar individuals in both humans (Norscia and Palagi 2011) and non-human primates (monkeys, Palagi et al. 2009; apes, Demuru and Palagi 2012). A study considering both humans and bonobos showed that familiarity is the factor that most influence the likelihood of observing yawn contagion, being

this factor even more salient than the biological species the individuals belong to (Palagi et al. 2014b). In humans, within the population susceptible to yawn contagion, women respond more frequently to others' yawns compared to men (Chan and Tseng 2017; Norscia et al. 2016). Consistently, psychological and neurobiological studies converge in indicating that women are more responsive to others' emotions than men, possibly because women are hardwired for maternity and parental care (for a review, see Norscia et al. 2016).

Although the issue is still a matter of lively discussion within the scientific community, the above reasons suggest that yawning after perceiving others' yawns is driven by emotional contagion.

## Consolation

In humans, the act of providing comfort via spontaneous affiliation offered to a distressed subject is widely accepted as a crucial behavior that can reveal the empathic potential of individuals. In nonhuman primates, third-party affiliation is behaviorally described as the first affiliative contact occurring between the recipient of an aggression (namely, the victim) and a bystander not involved in the aggression (de Waal and van Roosmalen 1979). More generally, consolation is a reassurance behavior directed at a distressed subject and it is driven by the emotional contagion experienced by the consoler in response to victim's anxiety. In particular, consolation is probably triggered by the transfer of negative affect from the victim to the observer. Consolation has been found not only in primates (including apes and tolerant monkey species), but also in canines, elephants, rodents, and corvids (de Waal and Preston 2017).

The witness of a fight can affiliate with the victim either spontaneously or upon the request of the victim. The comparison between these two forms of third-party affiliation can reveal why only the spontaneous consolatory behavior is driven by emotional contagion. In bonobos, a long-term study showed that both spontaneous

and solicited affiliation led to increased protection of the victim against further aggression. However, the victims experienced anxiety reduction only after receiving spontaneous affiliation. Hence, the improved emotional state in the victim was not the mere by-product of risk reduction but the consequence of the perceived the genuine emotional involvement of the consoler. The spontaneous comforting gesture relying on the motivational independence of the consoler (de Waal and Preston 2017) may hold a greater significance to the victim as it was initiated by the consoler who, most frequently, was an individual the victim shared a good relationship with.

As it occurs with rapid mimicry, also consolation seems to be affected by the levels of social tolerance between subjects. In the same group of *Macaca tonkeana* in which facial mimicry had been found, consolation was present. In the group of *Macaca fuscata*, the absence of facial mimicry was associated with the lack of consolation (Palagi et al. 2014a; Scopa and Palagi 2016). This is consistent with the strict linkage that both phenomena have with emotional contagion, and with the influence that social tolerance has on it.

In summary, emotional contagion is based on the ability to internally reproduce the feelings of others. It can be expressed through behavioral patterns, such as mimicry, yawn contagion, and consolation, provided that the social context allows their expression. To date, no case study has been able to disentangle social modulation and emotional contagion.

Because it is the basic building block of complex forms of empathy, such as perspective taking and targeted helping, emotional contagion must be taken into account when approaching the study of such forms of empathy whatever the studied species may be.

## Cross-References

- [Consolation](#)
- [Contagious yawning](#)
- [Empathy](#)
- [Imitation](#)
- [Mimicry](#)

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## Empathy

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## Introduction and Definition

Many of us experience empathy, yet this feeling eludes the direct measurement often required for scientific understanding. Empathy cannot be quantified by a functional MRI scan of the brain, yet we can use relatively simple language to describe it. The purpose of this entry is to delve into the various features of empathy and how we can use scientific approaches to infer its properties. For the most part, empathy will be discussed in the context of experiments with non-human animals. While so doing, we will explore the differences between motivation and behavior, affect and cognition, and empathy and compassion.

The modern concept of empathy originated in the late 1700s, introduced as the German word *Einfühlung* and referring to the human extension of oneself into the “consciousness” of the natural environment. *Einfühlung* was also used to describe the viewer’s active participation in a work of art, of “feeling into” the perceived object (Nowak 2011). In 1909, the term was adopted into the English language as “empathy” and rapidly embraced by psychologists.

Empathy is a subjective experience, not a behavior. Subjective experiences include feelings (affective experiences), thoughts (cognitive experiences), and sensory perceptions (what we see, hear, smell, feel, or taste). At its core, empathy refers to the feelings engendered by witnessing the situation of another individual. For instance, imagine that you are a bystander who witnesses a child falling off a moving bicycle and skinning her knee on a concrete driveway. Seeing the fall, you might feel a wincing sensation. When I imagine her fall, I feel a sharp tingling on the inside of my arms. The sensation might vary from person to person, even from time to time, but the sensation would likely be direct and immediate and evoke an emotional response. Your affective experience might be even more salient if you had also skinned your knee against concrete.

In other instances, empathy might include cognitive function, such as the experience you might feel upon learning of the aftermath of the 1890 Massacre of Wounded Knee. If I describe to you the strewn dead bodies of native American women and children who just hours earlier were waking up to a peaceful cold winter morning, the scene might arouse in you a feeling of loss or anger at the cavalry who massacred them. You might imagine the din of report and smoke from the cavalry guns and the screams of children in a massacre that occurred well over a century ago. You might never have seen an actual slain human body or a native village. Your cognitive process – of imagining from my description of a scene of strewn bodies – might evoke in your emotions something akin to what the few surviving natives might have felt when they looked over their destroyed village on that cold morning on the American plains.



A modern definition of empathy encompasses both affective and cognitive contributions but asserts that affective experience resides at empathy's core: "the generation of an affective state more appropriate to the situation of another compared to one's own" (Hoffman 1975; Preston and de Waal 2002). Empathy is adopting the feelings of another: their fear, joy, pain, anxiety, appreciation, or disdain.

In current popular usage, "empathy" has often been jumbled with feelings of compassion or with behaviors associated with compassion, such as helpful or altruistic acts or displays of sorrow for a victim. Compassion is a feeling related to helping behavior that includes empathy or an awareness of another individual's distress, *but compassion also includes a desire to alleviate that distress*. Indeed, helping behavior can arise from compassionate feelings. For the sake of scientific inquiry and the ongoing need for precision in language, strict boundaries on the term empathy can help us to understand its evolution and neurobiology. So again, empathy is not compassion or a compassionate act because it does not require a desire to alleviate the distress in others.

## Empathy and Affective States

A close relationship exists between subjective experience and behavior, so these terms are often confused. In our daily lives, we commonly infer one another's motivations from behaviors. Often times, different people make different inferences. A woman might shade her eyes with sunglasses. I might infer that the sunlight hurts her eyes. You might infer that she'd like to hide her eyes. Someone else might think she's showing off her new sunglasses.

We also infer subjective experiences from language. We commonly assume that if we use identical words to describe our experiences, we share identical experiences. Bertrand Russell argues that words can evoke unreliable inferences to subjective experience. For instance, two people might look at the same object and use the same word to describe its color, yet neither one of them can know whether they both experience the same

color (Russell 1912). We might both look at the same ripe apple, and you might see it as crimson while I might see it as magenta, yet we both would say that we see the apple as "red." I might see the apple as what looks like purple to you – yet by calling it red – we still would be ignorant to the discrepancy between our experiences.

How can we observe a behavior and infer subjective experience? To answer this question, it is helpful to consider the seminal contributions of Theodore C. Schneirla regarding the psychology of motivated behavior (Schneirla 1959). An individual animal might be motivated to move toward or away from a setting, an object, or another individual. How can we infer whether an approaching behavior indicates that the individual is seeking a certain experience? Likewise, how can we infer that a withdrawing behavior indicates an intention to avoid a particular setting, object, or individual? I might seek an orange sphere in my environment with a particular weight, texture, and fragrance because I associate it with the rewarding experience of peeling its rind and eating its wedges. Likewise, we both might withdraw from a situation where we expect an aversive experience, like the sting felt when we touch the nettles of a certain green plant.

Our affective experiences of seeking and avoidance are the proximal mechanisms that often underlie our approach and withdrawal behaviors. But we must be careful. Not all approach and withdrawal behaviors result from psychological experiences. For instance, if we watch an amoeba move across a petri dish, we cannot infer that the single-celled organism *wishes* to cross the plate. An amoeba lacks a central nervous system.

The critical scientific problem with empathy is that while we can understand what empathy is and how it emerges as a feeling, we are asking about a subjective feeling experienced by one individual that is responsive to the subjective experience of another – and all this seems remarkably inferential and outside the realm of scientific inquiry.

To tackle this problem, we must return to what we know. Empathy occurs in the context of a social interaction, even if that interaction is with a historical or fictional character. In these social interactions, behaviors signal the emotions of

others in the words spoken and their intonations and in facial expressions and gestures. These emotions can be intentionally directed toward one another or not be intentional at all. For instance, when an individual animal vocalizes, emotions can moderate the acoustic parameters of the vocalization, such as loudness and pitch (Scherer 1986). Emotions can be conveyed by vocal utterances that may not be intended for communication, such as a laugh, a sigh, or a grunt. Visual cues can also convey emotions, often as body movements, such as the redirection of eye gaze, an extra bounce in a step, the hair that stands on end along the backbone of a frightened dog, or the slow slumped pace of a person walking home from work. In a social interaction, we attend to eye movements, facial expressions, hand gestures, and gait to gain some clue to the internal experiences of the individual we interact with. Intended or involuntarily, each behavioral expression of an emotion is then either correctly or incorrectly perceived and can pivot the direction of a social encounter.

We consider empathy as an affective experience. Although we commonly use the word “emotion” interchangeably with “affective experience,” emotions are one of several affective experiences that occur during a human or non-human social encounter. Others include moods, interpersonal stances, and attitudes. Some occur in an instant. Others endure over much longer periods. Affective experiences influence what each participant of a social interaction anticipates when meeting another individual and what they might perceive correctly or incorrectly in another’s motives and emotions (Scherer 2003). An *emotion* is a relatively brief, in-the-moment response to an external or internal stimulus that is valued as being of major significance (anger, sadness, joy, fear, desperation). A *mood* is a more diffuse but still labile affective state, experienced as a change in subjective feeling, of low intensity but relatively long duration, often without apparent cause (cheerful, gloomy, irritable). An *interpersonal stance* is a feeling associated with another specific individual that colors the interpersonal exchange in that situation (cold, warm, supportive, contemptuous). We might consider whether dominant-subordinate relationships are

interpersonal stances. An *attitude* is more enduring than an interpersonal stance: affectively colored beliefs, references, and predispositions toward objects or persons (liking, loving, hating, desiring). We might ask whether the male-female pair bonds of a variety of species are behavioral expressions of attitude. How pinyon jays make transitive inferences about dominance hierarchies by watching the hierarchical interactions of others (Bond et al. 2004) might reflect an adjustment of attitude. *Personality traits* are not affective experiences, per se, but they are emotionally laden, stable dispositions and behavioral tendencies of an individual (nervous, anxious, hostile, jealous) that have been demonstrated in studies of mice (Caramaschi et al. 2008). A personality trait might dictate how a social encounter is experienced or might explain why certain affective experiences are predictably experienced in particular situations.

While affective states are not directly measurable, we can use these terms to dissociate their various attributes across a range of possible social encounters. With this framework of affective experiences transpiring during a social encounter, empathy might be responsive to changes in emotions and moods. The behaviors expressed during a social encounter are moderated in part by these emotions and moods and correctly or incorrectly perceived through the context of interpersonal stance, attitude, and personality trait. With this background, we can now turn our attention toward experimental techniques that allow us to infer a subjective experience of empathy.

## Experimental Considerations

How can we infer that an individual has acquired *an affective state more appropriate to the situation of another compared to one’s own*? If we are inquiring about humans, we might ask how a person feels after witnessing someone else experience a change in mood or emotion. But, as mentioned earlier, language has its shortcomings. Words are labels or tags we use to convey our emotions, but it is impossible to know whether one person’s feelings of anger or sadness match

those of another person who is describing feelings with the same words.

How can we infer an affective experience of empathy? One approach used by scientists to gain inferences about empathy in rodents is to use a modification of a tool employed in many learning experiments called “fear conditioning.” The first step in these experiments involves “conditioning,” whereby the rodent learns that when it experiences a particular environmental cue or context, it will experience an aversive stimulus. The environmental cue might be a tone or a small light that turns on and off. An environmental context might include different visual patterns on the walls of the chamber where the rodent is placed. The aversive stimulus might be an electrical shock or an air puff.

When a laboratory mouse experiences an electrical shock, it vocalizes at a frequency that is audible to the human ear and sounds like a squeak. These vocalizations do not resemble the ultrasonic vocalizations emitted for communication (Chen et al. 2009) or the precise overtone frequency modulations used for alarm calls by other rodent species (Kiriazis and Slobodchikoff 2006). They are harsh and audible. When a laboratory rat is administered a shock, it vocalizes at a frequency of approximately 22 kHz (Atsak et al. 2011), which is above the frequency audible to the human ear. These 22 kHz calls are often emitted by rats placed under aversive conditions.

During the conditioning phase, the rodent is exposed to an aversive experience, such as a shock (what scientists call an unconditioned stimulus), administered in conjunction with exposure to an otherwise innocuous cue or context (conditioned stimulus). For instance, in *context-dependent* fear conditioning, a rodent might be placed inside a chamber with horizontal stripes on the walls where it does not receive any shock. Placement of the rodent in this context is alternated with placement in a different chamber with vertical stripes on the walls where the rodent is delivered an electrical shock. With repeated exposures to both chambers, one with shock and one without, the rodent begins to express freezing behavior inside the chamber where it is administered the shock. With each successive pairing of the chamber with the

shock, the rodent’s freezing behavior becomes more prolonged and more frequent. In the control condition, in the chamber with the horizontal bars, the rodent does not freeze express an increased level of freezing behavior. In this example of *context-dependent* fear conditioning, the rodent learns that the patterns of the stripes on the walls of the chamber are predictive of the presence or absence of an impending electrical shock.

In *cue-dependent* fear conditioning experiments, the rodent is exposed to a temporal cue, such as a tone, that is paired with the aversive experience. In the testing that follows fear conditioning, the rodent is exposed to the tone (the conditioned stimulus) without the associated aversive experience of the shock (the unconditioned stimulus), and we measure the frequency and duration of freezing behavior in response to the tone.

Freezing behavior appears as a nearly motionless trembling in place and may be the expression of fear in anticipation of an imminent shock. We cannot infer with absolute scientific certainty that freezing behavior is a manifestation of fear. However, physiological, anatomical, and ethological responses of rodents to fear conditioning bear a strong resemblance to correlates of human fear, suggesting that freezing behavior manifests this highly salient affective experience.

To test for empathy, this experimental paradigm is slightly modified. The test subject is no longer the rodent undergoing fear conditioning but a different rodent that witnesses the rodent that undergoes fear conditioning. In many cases, empathy experiments use cue-dependent fear conditioning. The cue is often a tone. In this experimental model, the rodent that is administered the electrical shock is called the “object” or the “demonstrator.” The rodent that witnesses the conditioning is the test subject and is often called the “observer” or “witness.” While the demonstrator undergoes fear conditioning, the witness resides inside an adjacent chamber where it can hear the tone and the demonstrator’s vocalizations in response to shock.

In our experiments, both the demonstrator and the witness are subjected to a 30-s tone. For the demonstrator, the tone co-terminates with a 2-s electrical shock. During this 2-s period, the

demonstrator vocalizes in response to the shock. For the witness, the tone co-terminates with this 2-s vocalization emitted by the demonstrator. Following the 30-s tone, both the demonstrator and witness mice experience 90 seconds of silence. The tone is then played again and co-terminates with a shock. Then there is silence. With repeated tone-shock pairings, demonstrator mice inside the shock chamber freeze when they hear the tone. After conditioning, the test subjects that witnessed the demonstrators undergo conditioning are then placed inside the shock chamber. If they freeze when they hear the tone, we can infer that they have learned from the demonstrator mice that the tone predicts an aversive experience (Chen et al. 2009). We know from playback studies that the vocalizations emitted by demonstrator mice during the shock are sufficient to generate a freezing response by witness mice to the tone once they are placed inside the shock chamber (Chen et al. 2009).

In these “vicarious” fear conditioning experiments, researchers typically administer to the test subject (the witness) a single exposure to the aversive experience (Chen et al. 2009; Atsak et al. 2011; Sanders et al. 2013; but see Jeon et al. (2010). For example, in the experiments described above, prior to the conditioning of the demonstrator, the witness is administered an aversive shock. Critically, *the shock is not co-administered with the cue or context*. This pre-treatment is thought to give the witness a sense of the adversity of the shock experience. Interestingly, when investigators temporarily deafen the witness before administering the aversive stimulus, so that it cannot hear its own vocalization in response to the shock, the witness subsequently fails to learn from the vocalizations of others that the tone predicts the shock (Jeon et al. 2010). Like rodents, humans who have experienced a specific adverse experience in the past are more likely to feel empathy for another individual undergoing a similar trial (Batson et al. 1996; Eklund et al. 2009; Preis and Kroener-Herwig 2012).

What should be highlighted here is that animal researchers who use ethologically relevant stimuli, such as threats relevant to the evolution of a mouse, may not require that the subject have

direct experience with the aversive stimulus. For instance, mice can learn from others to bury themselves in cage bedding to escape from biting flies after they observe a single successful escape (Kavaliers et al. 2001).

It is also important to recognize that “vicarious” fear learning is only one kind of “observational” learning. In the example above, the test rodent learns to become fearful of a stimulus that another rodent finds painful, or at least unsettling. Vicarious fear conditioning experiments can be used to identify the biological correlates of empathy inside the brain. Indeed, the brain activity patterns of rodents that witness demonstrators bear aversive conditions show a remarkable resemblance to brain activity patterns of humans under similar conditions. For instance, rodent and human subjects that witness a pain response in demonstrators express increased circuit activity in the anterior cingulate cortex and the amygdala (Jeon et al. 2010; Kim et al. 2014; Singer et al. 2004, 2006).

Some forms of observational learning may not require empathy, such as some behavioral tasks that are motivated by access to a food item. In this case, observational learning requires that the test subject have the ability to learn the sequence of behavioral movements necessary to obtain the reward. The subjects are evaluated for their ability to perform a task after witnessing demonstrators perform a set of behavioral movements to gain access to the reward.

In empathy experiments that use fear conditioning, test subjects are not learning to reproduce the mechanics of a behavior. Further, we find that nuclei of the amygdala are activated during the freezing responses in these experiments and since these activities can correlate with fearful experiences, these biological findings support the inference that the learned freezing responses of the test subjects are behavioral expressions of fear.

A different measure of socially related behavior allows experimenters to assess “contagion,” a behavior that may, at least in some cases, involve empathy. Contagion might include adults yawning or babies crying in unison. In a classic experiment of contagion, mice are brought together after they have been injected with different

concentrations of irritants, either into the peritoneum (acetic acid) or into the paw (formalin). When these mice are separated, they show differences in their levels of writhing and paw licking behaviors proportional to the concentrations of irritant injected into their peritoneum or paw. However, when mice are injected with different concentrations of irritant and placed next to one another, their behavioral responses converge such that differences in their writhing or paw licking behaviors diminish (see Langford et al. 2006). This convergence of behaviors may suggest empathy, but we cannot infer the affective experience from the behavior because the test does not separate the social stimulus from the behavioral response.

We can infer empathy from conditioning experiments because the tested behavior is an expression of retained affective experience. The witness learns to associate an otherwise innocuous environmental cue or context with pain by witnessing another rodent undergo the painful experience. The rodent witnessing its conspecific undergo conditioning embodies this affective experience and retains it through subsequent testing when it also freezes in response to the tone. Since the test phase occurs at a separate time and place from the conditioning phase, we are measuring the influence of this retained affective memory on the witness' subsequent behavior. By so doing, we capture the contribution of an affective experience, in this case, vicarious fear, on behavior.

The tests described above use adverse stimuli to measure empathy. When compared with the poverty of experience afforded to rodents living inside standard laboratory cages, repeated shocks may be a minor aversive stimulus. Biomedical research would be more ethical and, in many cases, more relevant to aspects of human health were it to provide laboratory animals with ongoing challenges that can be overcome. The home environment should include a complexity of social and non-social contexts that offers both pleasurable and aversive stimuli (Lahvis 2017a, b). Empathy should also work in both directions, serving to predict both aversive and enjoyable conditions. To better understand empathy, we

should also develop tests that measure rodent responses to pleasant vicarious affective experiences.

## Why Empathy Is Adaptive

A capacity to feel into the moods and emotions of others allows an individual to sense from others emerging dangers or rewards that are not perceived directly. And since empathy is, in part, a vicarious affective experience, it can exert a much more pronounced effect on behavioral responses than what might be perceived only by cognitive understanding. An individual fearful from what it senses in another is likely to express a robust behavioral response. For instance, it is near axiomatic that while hearing an orator speak about an injustice with an angry voice, an audience is more likely to become angry and take action than would be an audience hearing an orator outline the same injustices with a dry and indifferent voice. Likewise, we would expect that the capacity to feel into the emotions of another individual (e.g., anticipation, fear, interest) would engender high levels of arousal that are appropriate for the situation versus the modest arousal that might be evoked by cognitive discernment.

For species that rear their young, a capacity for empathy also has adaptive value for parents. It can help them to adjust their behaviors to moderate the comfort of their offspring. Similarly, empathy may help offspring learn from a parent what aspects of the environment to fear or seek. After young captive-trained prairie dogs witness an experienced adult avoid a predator, they are more likely to survive release into the wild than are their unschooled controls (Shier and Owings 2007). Social learning includes imitation, where an action is copied, and emulation, where the goal of the action is understood and the mechanics of the behavior are then reproduced after subsequent trial-and-error learning. Rodents are capable of emulation (Zentall and Galef 1988; Galef 2013) and to the extent that an observer experiences the intent of the demonstrator in emulation, empathy may be involved in social learning.

Empathy is also thought to aid in rough-and-tumble play or play fighting, a behavior that is commonly expressed by young mammals. Play fighting requires that each participant be sensitive to the moment-by-moment situation of the playmate. If a move or a bite is too vigorous or not vigorous enough, play fighting ends. Drugs that dull changes in affective experience can moderate play fighting (Vanderschuren et al. 1997), suggesting that the behavior requires a responsive affective state. Play fighting promotes normal brain development (Gordon et al. 2003; Pellis and Pellis 2007) and is believed to confer adaptive advantages that include better emotional responsiveness to unexpected events (Nunes et al. 1999; Spinka et al. 2001), familiarization with self-handicap and fair behavior (Bekoff 2004), improved social coping abilities (Van den Berg et al. 1999a), and refined abilities to respond to subtle and ambiguous social signals (Pellis et al. 2010).

### **Empathy and Altruism: The Camaraderie Effect**

One of the most provocative questions regarding wild animal behavior is why wild animals often help others even at their own personal cost. A prediction arising from the theory of evolution is that individuals that successfully compete against others for limited resources would be more likely to survive and reproduce than individuals that share resources at their own expense. A corollary to that hypothesis might be that we expect a competitive psychology among wild animals because they are singly motivated to acquire resources for themselves and their progeny.

Contrary to these predictions, scientists including Darwin have observed “biological altruism” in the wild: individuals helping others, incurring upon themselves costs to their own survival and reproduction. Also observed in the wild are the related behaviors of “cooperation,” in which individuals coordinate their behaviors to acquire resources that they would not be able to obtain by acting alone. Some altruistic behaviors are expressed by only a few species. Vampire bats

risk starvation when they regurgitate their blood meals to share them with others (Wilkinson 1984). Other altruistic behaviors are expressed among many species, such as prey species that engage in mobbing of their predators (Templeton et al. 2005; Krams et al. 2006; Graw and Manser 2007).

Behaviors expressed in the wild can be explained by either ultimate or proximal mechanisms (Tinbergen 1963). Ultimate explanations attempt to reconcile altruistic behaviors with the pressures of natural selection and include kin selection, direct and indirect reciprocity, and multilevel selection (Nowak 2006). Proximal explanations attend to their underlying mechanisms and include the psychological and biological correlates of these behaviors. Experiments that examine proximal correlates of behavior are often conducted in the laboratory.

Like wild animals, laboratory animals also express helping behaviors at the expense of their own well-being. In an experiment conducted over 50 years ago, laboratory rats were given a choice between pushing a lever to gain access to a chocolate chip and a different lever to release a nearby rat that was hanging in a harness just above a cage floor. The rats chose to push the lever relieving the distressed rat over gaining access to a food reward (Rice and Gainer 1962). In a more recent experiment, rats were presented with a similar dilemma, in this case, the opportunity to release a rat from inside an uncomfortably small container versus personal access to a food reward. Rats again choose to relieve the distressed rat and share the chocolate (Bartal et al. 2011, 2014). In yet a different experiment, rats were found to free other wet rats from a pool and share their access to a food reward (Sato et al. 2015). In this last experiment, rats that had previously been soaked themselves were more likely to help, a pattern of behavior that bears resemblance to the empathy experiments described earlier.

While a capacity for empathy might partly explain why rats help other rats, empathy is not by itself sufficient. As mentioned at the beginning of this entry, helping behavior and perhaps the underlying feeling of compassion likely include an awareness of another individual’s distress, but compassion also includes a desire to alleviate that



distress. In this regard, helping behaviors may require both empathy and a motivation to be with others (that an individual finds social encounter to be a pleasurable experience).

Like empathy, the experience of finding social interaction rewarding can be experimentally inferred from conditioning experiments. The social condition place preference (SCPP) test can be used to infer whether a rodent, such as a particular strain of mouse, seeks and derives pleasure from a social encounter (Panksepp and Lahvis 2007). Laboratory rodents typically express strong preferences for environments that have been “conditioned” by their association with access to other rodents versus environments that have been paired with social isolation (Calcagnetti and Schechter 1992; Van den Berg et al. 1999b). A rodent’s response to conditioning allows us to infer an affective state, in this case, the positive affective experience associated with access to a social reward (Panksepp 1998; Burgdorf and Panksepp 2006).

The psychological motivation for a social reward can be adaptive if it serves to catalyze opportunities for affiliative social interactions and promotes communication with others. To the extent that social motivation engenders greater attentiveness to the communication and behaviors of others, it likely enhances social learning. An individual attending to another would be more apt to learn from that conspecific. Social motivation would also promote group living, which may not be adaptive when local resources are depleted or colony parasitism is high but can be adaptive if it increases the likelihood for predator detection and improves the likelihood of identifying foraging opportunities (Hoogland 1979). Evidence that group living can be adaptive also comes from studies of animal dispersal: emigration from a colony can be associated with very high survival costs (Koopman et al. 2000; Pocock et al. 2005). As social reward brings individuals into closer proximity, this affective experience becomes adaptive too in its service to another affective experience, empathy, because it is more likely to amplify the individual’s detection and embodiment of the emotions of a conspecific, such as a threat that is not perceived directly. For individuals that derive pleasure and survival benefits

from social interactions, ostracism would be devastating.

Indeed, ostracism from colonies is well-described for adolescent mammals (see Barash 1974; Festa-Bianchet and King 1984) and has been observed among adult mammals that fail to cooperate. For instance, a wolf pack may ostracize subordinate wolves that are found mating in the pack (Peterson 1979), chimpanzees shun individuals appearing abnormal (Goodall 1986), and female rats can reject males found to have copulated with anestrus females (Galef et al. 2008).

Both social reward and empathy are heritable affective states (Panksepp and Lahvis 2007; Chen et al. 2009) and, because they may each be adaptive for survival, could thereby persist as stable population traits. The finding that captive juvenile ground squirrels express social reward suggests that positive affective experiences in a social context can be felt by wild animals (Lahvis et al. 2015), not just domesticated mice and rats that may have been selected for their affinity for social interactions by living for many generations in close quarters. Natural selection could act upon the alleles that promote the capacity for affective experiences of social reward and empathy and, as a result, increase the prevalence of interactions between these experiences in any species where social reward and empathy are heritable.

What if an individual enjoyed social reward and had a capacity for empathy? What if it could feel the affinity, indifference, or enmity of other members of the colony? Such an individual might be motivated to behave in a way that minimizes group feelings of indifference and enmity and maximizes their affinity. This combination of empathy and social reward could engender the *camaraderie effect* that, at both proximal and ultimate levels, could explain why biological altruism exists in the context of natural selection (Lahvis 2016b). Empathy of another’s stance toward one’s self, whether amicable, dispassionate, or hostile, might predict a future of ongoing social acceptance, indifference, or ostracism from the colony.

In addition to the physical risks of ostracism from a colony in the wild, the *subjective* experiences associated with social isolation might contribute to physiological detriments that

jeopardize survival and reproduction. Among humans, social rejection can increase correlates of anxiety (Blackhart et al. 2007). Among laboratory rodents, social isolation impairs brain development (Black and Greenough 1998; Champagne and Curley 2005; Wiedenmayer 2009), immune reactivity (Shanks et al. 1994; Boissy et al. 2007; Tuchscherer et al. 2010), healing from burns and wounds (Detillion et al. 2004; İşeri et al. 2010), response to ischemia (Norman et al. 2010), recovery from social defeat (Ruis et al. 1999), resiliency to metastasis (Wu et al. 2000), and competence within social hierarchies (van den Berg et al. 1999a). Subjective feelings of the hostile sentiments of other colony members would engender expectancy of social ostracism and would increase levels of anxiety. These feelings might thereby foment the physiological correlates of social isolation and compromise immune function and wound repair. By contrast, a sense of general social affinity might contribute to the physiological health of an individual in response to disease and injury. Altruistic behaviors would promote well-being in others and feelings of camaraderie from others and thus general colony-wide improvements in physiological well-being.

Taken together, the camaraderie effect could promote the expression of altruistic behavior at both proximal and ultimate levels and could serve as an essential stake in others. This stake in others is thought to be necessary for the evolution of altruistic behavior (Roberts 2005).

## Ethical Implications of Empathy

Empathy exists as a relationship between the brain and social environment, arising from the interplay between the molecules, cells, and circuitry of the brain and the social dynamics that exist outside. In this sense, empathy is an emergent property, a quantum step beyond what we can measure and manipulate in the circuitry of the brain, beyond what is genetically pre-programmed, such as knowing how to walk or how to swallow.

In this context, we must reconsider the ethics of studies of captive animals raised inside laboratory

cages. They live with few social experiences and environmental risks, adversities, and rewards, and they lack opportunities to make decisions, what they would be naturally afforded in a natural environment. Indeed, young laboratory mice that are raised without their peers lack the capacity for empathy (Panksepp and Lahvis 2016). Inside cages, research animals lack the natural substrates of brain development (Lahvis 2016a) and mental and physical activity (Lahvis 2017b). Mental activity allows an individual with a specific genetic background to adjust to his or her social and physical environment. In this sense, is it ethical to deny laboratory animals complex environments that sufficiently nourish their mental activities and offer them opportunities to engage with challenges that they can overcome? Is there possibility for scientists to give laboratory animals greater agency to make choices about who to mate with, what microenvironment to explore, or what to eat? If we fail to acknowledge the subjective experiences of laboratory animals, are we limiting our own abilities to understand human psychosocial well-being and illness?

In a broader global view, knowing that animals of other species, like our own, place value on their social interactions and can feel empathy for the conditions of others, do we have an ethical responsibility to treat them better in the context of our daily lives? We use domesticated animals for our food and comfort. We displace wild animals and clear their land for our agriculture, energy, transportation, and shelters. Should we consider how human consumption and population growth impinge on the well-being of individuals belonging to other species? Are wild animals “natural resources” or is this term no longer relevant?

In a more uplifting sense, we can live more fully with the knowledge that we are not the only sentient species on our planet. It is ironic that the concept of empathy has its roots in how humans experience their natural environments. With the discovery of empathy in other animals, we can have empathy for their situations and experiences and perhaps reestablish our own emergent psychological connection with the natural environments we live within.

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## Emulation

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## Definition

Emulation is a form of social learning in which an observer achieves the same goal as an expert they observe, but do not copy the bodily actions of the demonstrator, as when imitating.

## Introduction

Wood (1989) provided an early definition of emulation learning when he noted that “...children not only attempt to impersonate others by imitating their actions but also try to emulate them by achieving similar ends or objectives” (p.71). Following Wood’s original description, emulation has become to be considered to encompass more meanings. For example, Byrne (1998) proposed that, in addition to Wood’s “goal directed” sense of emulation, it could also include learning the physical properties of objects; learning relationships among objects; and learning what can be done with an object. Specifically, he noted that “having seen a change of state effected, the observer knows more about the physical nature of an object: that nuts crack, that rocks are heavy and hard, that fruit peduncles are flimsy. . . [and/or that] having seen an object manipulated, the observer knows more about the structural relationships that make it up or into which it meshes: that nuts are hollow and contain food, that rocks can cover food, that lids are threaded . . . [and/or that] having seen an object used in a particular way, the observer knows that this functional use is possible for this sort of object: a stick can be used as a rake, the lid of a jar can be unscrewed, nuts can be smashed by striking them with rocks, a rod can be slid through a hole, fruit can be knocked down by swiping at it with sticks” (Byrne 1998, p. 604–605).

More recently, Whiten et al. (2009) provided definitions for three distinct forms of emulative learning: object movement reenactment, end-state emulation, and affordance learning. Affordance learning relates most closely to Byrne’s (1998) description of emulation, in which an individual learns about the physical properties of a task or elements within the environment, so they are then able to manipulate them in their own manner to reach a goal and can apply that knowledge to related tasks. End-state emulation more closely matches Wood’s (1989) original definition, in which an observer recreates the end-state of another’s actions, but through their own methods. As with body mimicry, object movement reenactment refers to an observer replicating the movements shown by a demonstrator, but in this case,



the movements of a task or tool, without the need to achieve the same goal. (Note, this entry does not expand upon it, but it is worth considering that an “end-state” is a more objective element to measure than a “goal,” as goals may be subjective, and vary by the actor, whereas end-states refer to physical changes in the environment. See Gattis 2002 for a more detailed discussion on this topic.)

## Emulation and Culture

Although emulation may involve less complex copying than imitation, it may represent a more efficient form of social learning in which the observer achieves the same goal but without “blindly” copying all the actions of a demonstrator (Horner and Whiten 2005). Additionally, although it was originally proposed that high fidelity transmission of information via teaching or imitation was required for behavioral traditions that evidenced cumulative culture, more recent experimental work with humans has revealed that emulative learning is sufficient (Caldwell et al. 2012; Zwirner and Thornton 2015, but see Morgan et al. 2015). It is also unlikely that species are either “emulators” or “imitators,” but rather that they have an arsenal of social learning mechanisms at their disposal that they can employ depending on the complexity of the task to be learned, as well as the completeness of their own personal information (Whiten et al. 2009).

## Testing for Emulation

To test for emulative learning, researchers have used a number of techniques including apparatuses that occlude the causal relationship of the demonstrator’s actions in achieving the goal (e.g., Horner and Whiten 2005); ghost control or end-state conditions (reviewed in Hopper 2010); or tests in which the method used by the demonstrator is not available to the observer when it is their turn to attempt to solve the task (e.g., Tennie et al. 2010). Such tests have been run with both humans and nonhuman animals, providing a phylogenetic

perspective on whether and when individuals are likely to emulate (Hopper 2010).

## Cross-References

- ▶ [Andrew Whiten](#)
- ▶ [Canine Cognition](#)
- ▶ [Cecilia Heyes](#)
- ▶ [Cognition](#)
- ▶ [Cognitive Imitation](#)
- ▶ [Comparative Psychology](#)
- ▶ [Copying](#)
- ▶ [Cultural Transmission](#)
- ▶ [Culture](#)
- ▶ [Cumulative Culture](#)
- ▶ [Diffusion](#)
- ▶ [Ghost Control](#)
- ▶ [Goal-Directed Behavior](#)
- ▶ [Imitation](#)
- ▶ [Learning](#)
- ▶ [Ludwig Huber](#)
- ▶ [Michael Tomasello](#)
- ▶ [Mimicry](#)
- ▶ [Primate Cognition](#)
- ▶ [Rational Imitation](#)
- ▶ [Rodentia Cognition](#)
- ▶ [Social Learning](#)
- ▶ [Stimulus and Local Enhancement](#)
- ▶ [Tom Zentall](#)

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## Enactive Perception

### ► Embodied Perception

## Encapsulated Nerve-Cell Bodies

### ► Ganglion

## Encephalization

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## Synonyms

Brain evolution; Corticalization

## Definition

Encephalization is an evolutionary increase in the complexity or relative size of the brain, involving a shift of function from non-cortical parts of the brain to the cortex.

## Introduction

The term encephalization has been frequently associated with the evolution of the brain and intelligence. Present explanations for encephalization derive from Marsh (1886), who described the evolution of brain size in reptiles, birds, and mammals. Marsh proposed general law of brain growth as (1) relative brain size gradually increased through geological time, (2) the increase was largely confined to the cerebral hemispheres, and (3) the increase was accompanied by an increase in the complexity of cerebral convolutions.

As per first law of Marsh, Northcutt (1984) stated that the term encephalization was used earlier to describe an increase in brain size with time. Weiskrantz (1961) defined *encephalization* as an evolutionary process in which the neocortex progressively takes over functions previously handled by the tectum and striatum (i.e., lower brain regions). This was consistent with Marsh's second law. In 1985, Jerison explained that encephalization is the increase in brain size larger than that required for control of basic body functions.

Encephalization is not a common morphological phenomenon in evolutionary biology. It is rare in “lower vertebrates” and is primarily a feature of avian and mammalian evolution. The fossil evidence suggests that encephalization is more prominent in primates (Hodos 1988).

## Understanding Encephalization Through Human Fossils

The study of brain evolution by studying endocasts of human ancestors is done under the branch of paleoanthropology known as hominin

paleoneurology. Here, the paleoneurologists have focused on analyses of cranial cavities and endocranial casts (endocasts), which were prepared from the interiors of fossilized braincases and reproduce details of external brain morphology. Sometimes, these endocasts occur naturally, but traditionally these are prepared by casting the insides of braincases with latex or some other molding material. Recent technology has made this considerably easier. For example, “virtual endocasts,” created by various 3D imaging techniques, allow researchers to reconstruct, manipulate, and measure simulated endocasts (Falk 2012).

Endocasts are facsimiles of general brain shape, but they include some details such as the location of blood vessels, cranial nerves, and cranial sutures. They can also reproduce information about the convolutions of the brain that were imprinted on the inner walls of the braincase during life. The convolutions, or folds of gray matter on the brain’s surface, consist of bulges (gyri) and the grooves (sulci) that separate them. Although hominin paleoneurologists study the sulcal patterns of endocasts, knowledge about them is limited. Hence, the analyses of brain evolution begin with the measurements of brain size which helps in better estimation of changes in size of its various parts (Hodos 1988).

## Encephalization and Brain Size

The vertebrate brain shares a common structure which appears during early stages of embryonic development as three swellings (the prosencephalon, mesencephalon, and rhombencephalon) at the rear end of neural tube. The brains of the vertebrates contain the same set of basic anatomical components and can be simply compared in terms of their size which increases with body size, but not in a simple linear proportion. In general, smaller animals tend to have larger brains, measured as a fraction of body size. For mammals, the relationship between brain volume and body mass essentially follows a power law with an exponent of about 0.75 (Armstrong 1983). This formula describes the central tendency, but every family of mammals deviates from it to some degree, in a

way that reflects in part the complexity of their behavior.

In kingdom Animalia, the brain becomes evident in phyla Platyhelminthes as an enlargement called ganglion. There are also some substantial differences in the shape of the brain which accounts for the differences between mammals and other vertebrates. These differences developed mainly in the forebrain in form of both size and shape. In nonmammalian vertebrates, the surface of the cerebrum is lined with a simple three-layered structure called the pallium, while in mammals, the pallium is a complex six-layered structure called the neocortex or isocortex. The enlargement of the cerebral cortex carries with it changes to other brain areas. The superior colliculus, which plays a major role in visual control of behavior in most vertebrates, is small in mammals, with many of its functions taken over by visual areas of the cerebral cortex. The mammalian neocerebellum is a large portion of cerebellum dedicated to supporting the cerebral cortex, which has no counterpart in other vertebrates (Falk 2012).

## EQ or Brain Size: Indicator of Intelligence

Among all the mammals, primate brain is three times larger than other mammals of comparable size, and the human brain is three times bigger than that of other primates of similar size in proportion to their body size (Faiq et al. 2013). To compare the brain size across species, encephalization quotient (EQ = brain to body mass ratio) is taken into account. Humans have EQ of 7.4–78, while that of an elephant is 1.13–2.36 and can be seen to be as low as 0.2 in opossum (Roth and Dicke 2005). The larger the brain relative to the body, the more the brain is available for heightened complex cognitive tasks, and this justifies the simplicity of EQ formulation by ranking of animals on the basis of their EQ that coincides better with observed complexity of behavior. Diet and social behavior are the prime factors on which EQ depends. Species with diets of energy-rich foods (meat, fish, fruits) have larger brains than those with relatively nutrient poor diets (plants, insects). Also, more social species

(humans, dogs, dolphins) consistently score high EQ (Lefebvre et al. 2004).

Recent research suggests that, for nonhuman primates, brain size is a better measurement of cognitive abilities than EQ. Factors such as different degrees of brain folding, which increases the surface area (and volume) of the cortex, are positively correlated to intelligence in humans other than brain-to-body mass ratio (Roth and Dicke 2005).

## Encephalization and Metabolic Disorders

The human brain is approximately nine times larger than other non-primate mammals. In the past four million years, the brain volume in genus *Homo* has increased from 400 cm<sup>3</sup> in australopithecines to 1300–1400 cm<sup>3</sup> in humans. Such large proportion of gray matter has high energy demands, which induced the instinct of overfeeding. The overfeeding causes consistently higher concentration of energy nutrients (like glucose) which leads to energy storage as fats (predisposition to obesity) and relatively higher amounts of insulin (for glucose uptake) and leptin (for fat storage). Reduction in size of gut was accompanied by reduction in size of energy-metabolizing organs (liver, pancreas, etc.) and hence an increase in metabolic stress due to work overload on these organs. Further, the brain develops resistance to excess amounts of insulin and leptin, rendering their appetite suppressing activity ineffective, thereby amplifying the food intake. Hence, assemblage of factors such as high food intake, the increased metabolic stress, and insulin resistance of the brain predisposes the human to an array of metabolic disorders such as obesity, impaired glucose homeostasis, lipid disorders, hepatic steatosis, and diabetes (Faiq et al. 2013).

## Cross-Reference

- Cephalization
- Evolutionarily Stable Strategies
- Evolutionary By-product
- Primates

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## Encode

- Coding

## Encoding

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Encoding is the process of storing information, such as personal experiences, visuospatial maps of the world, or semantic meaning. Encoding may be studied on a neuronal level or more abstract cognitive level, but both approaches reflect a

useful representation of the process by which new information is placed into mental storage.

## Neural Encoding

Encoding on a neural level involves a change in the interconnectivity between two or more neurons. Changes include establishing new connections or strengthening or weakening existing connections between neurons. Collectively, these changes are called synaptic plasticity. Long-term strengthening of neuronal connections, or long-term potentiation (LTP), is believed to be the primary mechanism underlying memory encoding. In early experiments studying LTP, researchers observed the strengthening of neuronal connections in the hippocampus of rabbits (Bliss and Lømo 1973) and the amygdala of rats (Clugnet and LeDoux 1990). Malenka and Bear (2004) argue that LTP may occur anywhere in the brain where one neuron connects to another.

## Encoding Effects

Much of the evidence on encoding derives from behavioral studies designed to determine the boundaries of the cognitive processes involved. For example, cognitive phenomena such as encoding specificity, levels of processing effects, and chunking demonstrate the expression of encoding effects using behavioral measures.

### Encoding Specificity

Encoding specificity refers to the phenomenon that the context in which something is learned is encoded along with the remembered exemplar (Tulving and Thomson 1973). For example, Godden and Baddeley (1975) observed improved memory in human participants when the encoding environment (in scuba gear on land or underwater) matched the retrieval environment. Concrete evidence of encoding specificity exists in non-humans as well, such as rats undergoing sensory preconditioning procedures with compound stimuli (Lin et al. 2013).

The implication of encoding specificity is that seemingly irrelevant stimuli may be associatively connected to relevant stimuli at the time of encoding, although the evidence for the impact of context effects on learning and memory processes is mixed (see Rosas et al. 2013 for a review). This appears to hold in animal learning as well. For example, Bouton et al. (2011) demonstrated the effects of context on rats for which button-pressing had been extinguished. The renewal of button pressing was stronger in a new context than in the one extinction occurred. Retrieval processes may be able to take advantage of this information in order to enhance the success of retrieval later, especially if the context is relevant to learning or remembering (Rosas et al. 2013).

### Levels of Processing Effect

The levels of processing effect is an encoding phenomenon in which to-be-remembered exemplars are better remembered when more effort is applied towards remembering the items ( Craik and Lockhart 1972). For example, in 1975, Craik and Tulving (1975) demonstrated the levels of processing effect when human participants judged items superficially (“Is the word in italics?” or “Does the word begin with the sound bee?”) or more deeply (“Can you meet one in the street?”). Evidence of the levels of processing effect in non-humans may be difficult to obtain. Nevertheless, there may be some evidence of a similar kind of processing in chimpanzees (Vonk and Mosteller 2013). Unlike with encoding specificity, the levels of processing effect suggests that the way to which information is attended matters to encoding processes. If attentional control influences encoding, this suggests that it may not be a purely bottom-up process.

### Chunking

A larger number of items may be more easily remembered when those items are grouped together, often in a meaningful way. This is called chunking, and it was described in the mid-twentieth century by Miller (1956). In humans, chunking may explain the extraordinary memories of expert chess players (Chase and Simon

1973) in recalling positions of pieces on a chessboard. Fountain (1990) demonstrated chunking in rats using patterned sequences of lights. He did this by training rats to track patterns of flashing lights and respond on one of six levers. Fountain reported the rats errors occurred most often at the boundaries of structural groupings in the pattern, reflecting chunking similar to that found in humans. Thus, in both humans and nonhumans, chunking effects suggest structure of the encoded material is important during the encoding process, enough that it may aid in retrieval later.

## Conclusion

Encoding is a critical part of the memory process. A failure to encode information fundamentally means that information cannot be retrieved later. For encoding to occur, some physical change is necessary at the neuronal level, demonstrated in the strengthening of connections due to long-term potentiation. The effects of encoding are also evident at the cognitive level, which demonstrate the subtleties of how information is structured after encoding, as well as the processes and information included in encoded memories. These processes are not unique to humans. Many nonhuman species demonstrate parallel encoding phenomena, which suggest a largely universal encoding process.

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## Endel Tulving

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Dr. Endel Tulving (1927 –) is an experimental psychologist and neuroscientist who specializes in the study of long-term memory. Tulving is particularly well known for his introduction and development of the concept of episodic memory (Habib 2009; Roediger and Craik 1989; Tulving 1972), as well as his work related to encoding specificity (Tulving and Thompson 1973; Tulving



1974), amnesia (Habib 2009; Tulving 1985), and autoeotic consciousness (Habib 2009; Tulving 1985). Overall, Tulving is one of the most influential figures in the study of human memory, and at the time of writing, Tulving has published over 200 papers and book chapters, and his work has been cited 88,000 times (Google Scholar, Sept. 2018).

In recognition of Tulving's contribution to the study of memory, he has received numerous honors and awards. For example, Tulving has been elected to the Royal Society of London (1992) and the Canadian Medical Hall of Fame (2007) and is an Officer of the Order of Canada (2006), a Foreign member of the Royal Swedish Academy of Sciences (1991), a Foreign member of Academia Europaea (1996), a Foreign member of the Estonian Academy of Sciences (2002), a honorary member of the American Academy of Arts and Sciences (1986), a Foreign Associate of the US National Academy of Sciences (1988), and a William James Fellow of the American Psychological Society (1990) (GLS Research Society 2015; Habib 2009). Tulving has also received such awards as the Howard Crosby Warren Medal from the Society of Experimental Psychologists (1992), a Guggenheim Fellowship (1987), a Killam Prize from the Canada Council (1994), a Gold Medal Award for Lifetime Achievement from the American Psychological Foundation (1994), the McGovern Award from the American Association for the Advancement of Science (1996), and the Gairdner International Award (2005) (GLS Research Society 2015; Habib 2009).

## Biographical Details

Dr. Tulving was born in on May 26, 1927 in Estonia and immigrated to Canada in 1949 (Canadian Medical Hall of Fame 2017). Shortly thereafter, Dr. Tulving enrolled at the University of Toronto to study Psychology and graduated in 1953 at the top of his class with a BA (Honors, First Class) degree in Psychology (Roediger and Craik 1989). After this, Tulving continued to study at the University of Toronto for an

additional year, and in 1954, earned a Master of Arts degree in Psychology (Habib 2009; Roediger and Craik 1989). At the time of completing his MA, Tulving was awarded a Harvard Foundation fellowship to continue his studies as a PhD student at Harvard (Roediger and Craik 1989).

At Harvard, Tulving studied under many of the foremost scholars in psychology of the time, including E. G. Boring, E. G. Heinemann, G. A. Miller, E. B. Newman, S. S. Stevens, and B.F. Skinner (Roediger and Craik 1989). Tulving's own doctoral research focused on visual acuity and accommodation (see Tulving 1958 for a publication based on Tulving's dissertation), which he completed in 1956. After earning his PhD, Tulving returned to the University of Toronto in Canada to work as a lecturer (Habib 2009; Roediger and Craik 1989).

When Tulving returned to the University of Toronto, he found it difficult to continue his research on perception due to a lack of space, equipment, and money (Roediger and Craik 1989). As a result, he sought out other research opportunities that he could complete under such constraints. Tulving thus began his work investigating verbal learning, even though he had no previous formal training in the subject (Roediger and Craik 1989).

Tulving remained at the University of Toronto for the remainder of his career, with the exception of a short move to Yale for less than a year in 1970 (Habib 2009; Roediger and Craik 1989). Tulving officially retired from the University of Toronto in 1992 (Habib 2009) and currently holds the title of Professor Emeritus (University of Toronto, n.d.). Tulving is also currently a member of the Rotman Research Institute of Baycrest Centre for Geriatric Care in Toronto (Baycrest Health Science 2016).

## Brief Overview of Work

### Episodic Memory

In 1972, Tulving introduced the term "episodic memory" to psychology. Episodic memory was conceptualized as an information processing system of explicit (declarative) long-term memory



that was functionally distinct from semantic memory. Specifically, Tulving defined episodic memory as:

[A memory system that] receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events. A perceptual event can be stored in the episodic system solely in terms of its perceptible properties or attributes, and it is always stored in terms of its autobiographical reference to the already existing contents of the episodic memory store. (Tulving 1972, pp. 385–386)

Thus, Tulving proposed that episodic memories are memories of personal experiences that contain information related to what happened, where it happened, and when it happened (what-where-when information).

However, in 2005, Tulving revised his definition of episodic memory to emphasize the need for episodic memories to contain reference to conscious experience. This requirement thus led him to claim that “only human beings possess ‘auto-noetic’ episodic memory” (Tulving 2005, p. 4, quotations in original). Specifically, Tulving’s revised definition of episodic memory includes reference to the idea of mental time-travel in which a person travels subjectively back in time to re-experience the event as part of their recollection (Tulving 2005).

### Encoding Specificity

In 1973, Tulving and D.M. Thomson published a paper that introduced the term “encoding specificity” to the psychological literature. Tulving and Thomson (1973) stated that to-be-remembered information is encoded in conjunction with other cues that are present at the time of learning, even if one is not explicitly trying to remember these other cues. For example, if you were to learn a list of items from a piece of paper, you may also store information from the surrounding environment, such as the quiet murmur of voices nearby. Thus, when asked to recall the information for the list, the surrounding environmental cues, if still present, could act as retrieval cues to aid recall. Conversely, if they were not present, there may be nothing to cue the appropriate memory, and thus the information would not be recalled (or in other

words, the information would appear to be forgotten) (Tulving 1974).

### Amnesia and Autonoetic Consciousness

Tulving is known for working with the amnesic patient K.C. (originally identified as N.N. in his 1985 work). K.C. was an individual whom, due to a traffic accident and head wound, had profound amnesia for personal events. In particular K.C., while having reasonably intact language skills and the ability to remember semantic information, could not recall “*a single event from the past*” (Tulving 1985, p. 4), and who had difficulty planning for the future. Tulving wrote that “[K.C.’s] knowledge of his own past seems to have the same impersonal experiential quality as his knowledge of the rest of the world” (Tulving 1985, p. 4). Thus, K.C. provided Tulving with evidence that there was a separation of episodic and semantic memory that may have a physical basis in the brain. Tulving’s work with K.C. also contributed to his redefinition of episodic memory to include elements of autonoetic consciousness, or in other words, to include the ability to mentally travel in time.

### Cross-References

- [Episodic Memory](#)
- [Mental Time Travel](#)

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## Endemism

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## Other Terms

### Precinctive

Endemism, a term originally described by botanist Augustin Pyramus de Condolle in 1820, refers to a species (animal or plant) which is unique to a distinct geographical area and thus an endemic species. It is, however, important to highlight the frequent lack of agreement on the exact meaning of this term due to its broad definition and use across biogeographical, ecological, and conservation contexts (Anderson 1994; Harrison 2013). Furthermore, the geographical scale can vary dramatically from specific location, such as islands, lake, mountains/volcanoes, and rivers. Some examples of species include the Amami Rabbit (*Pentalagus furnessi*), which is found on two Japanese islands in the Nansei archipelago (Yamada and Cervantes 2005), and the Wekiug bug (*Nysius Wekiucicola*), which is only found between 3415 and 4205 meters above sea

level on the dormant volcano, Mauna Kea, in Hawaii (Eiben and Rubinoff 2014). Other endemic species may be found only in specific countries or regions (e.g., the common Emu (*Dromaius novaehollandiae*) is endemic to Australia (Taylor et al. 1999)). Some sources stated that the geographical region is subject to a 50,000 km<sup>2</sup> threshold (also known as “local endemism”) and regions which have two or more endemic species are referred to as “areas of endemism” (Platnick 1991; Bibby et al. 1992). Endemism is caused by one or more phenomena evolutionary (e.g., formation of islands), ecological (e.g., specific climate), and human/social influences (e.g., deforestation).

Endemism can be categorized to highlight aspects about a species and the regions or areas in which it lives. This includes terms such as “Paleoendemism,” which refers to a species which had previously occupied a larger area but now lives in a smaller area to that they had previously occupied. For example, Martino Vole (*Dinaromys bogdanovi*) which is endemic to the western Balkans was previously found to have occupied a larger range during the Pleistocene period to that of which it currently does (Kryštufek and Bužan 2008). Furthermore, “Neoendemism” can be defined as a species which has recently evolved but is closely related to another species and not distributed further. The Behr’s sulphur butterfly (*Colias behrii*) only found in California in the Sierra Nevada mountain range and has been highlighted as a neoendemic species based on its limited genetic diversity and indicators of population expansion (Schoville et al. 2011). It has been noted that these forms of endemism can be indicators of different evolutionary timescales; for example, neoendemism is regarded as the start of evolutionary life whereas paleoendemism is seen toward the latter stages of evolutionary spectrum prior to extinction (Cowman et al. 2017). A further term is included for those species which are specifically endemic to specific soil types, this is known as “Edaphic endemism.” For example. The butterfly Muir’s Hairstreak (*Callophrys muiri*) is endemic to serpentine soil due to the plant on which it feeds are only

restricted to these soil types (Harrison 2013). Sources have defined further categories which includes more detailed terms, such as Morrone (2008) who refers to additional detailed terms such as autochthonous/allochthonous endemics and biogeographic relicts.

## Cross-References

- Biogeography
- Conservation
- Ecology

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## Endocrine System

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## Definition

It is a physiological functionary comprising of a network of the ductless glands in the animal body secreting a chemical messenger, called hormones, into blood circulation to carry to the target destinations, i.e., various organs and tissues/cells. Hormones act through the specific receptors expressed at the target destinations inducing signaling pathways involved in the crucial biological functions viz. growth, repair, reproduction, hunger, and survival behavior.

## Introduction

Animal body has the ductless glands as the distinct organs or cell groups inside an organ or a tissue, which exit their secretions called “hormones” in the blood circulation to carry to the target destinations. Hormones are involved in the

maintenance of physiological functions involved in day to day activities like sleep, feeding, and drinking etc., and also that with prolonged course of effects like reproduction, growth, aging, immunity, etc. (Kovacs and Ojeda 2012, pp. 1–3).

These hormone secreting glands are called “endocrine” which literally meant “to secrete within” indicating their mode of secretion. The target destinations of the hormones bear the specific receptors which upon binding induce signaling pathways involved in specific biological functions. There are eight such major along with many minor glands which are grossly conserved in animal kingdom (including human) and share similar morphology among mammals. Figure 1 is showing a schema of the major endocrine glands in male and female.

In general, the “endocrine system” comprises of three parts: a brain part – a nuclei of the hypothalamus, a pituitary gland part, and a target endocrine gland. Hypothalamic nuclei secrete releasing or inhibitory hormones, which either stimulate or inhibit anterior pituitary cells to secrete a stimulatory hormone, which will further act upon a target endocrine gland like adrenal, thyroid, or else, which secrete exit hormone(s) which will be taken through the blood circulation to the target organs or body parts containing

specific hormonal receptors for action. Exceptions to this three tier system are some specific cells existing inside some organs, or body parts which secrete specific hormones (Kleine and Rossmanith 2016, pp. 269–297; Kumar et al. 2018).

The endocrine system works in concert with the nervous and immune systems which also share their functionaries (Kovacs and Ojeda 2012, pp. 1–3). The branch of science dealing with the endocrine system is called “endocrinology,” which is now a well-developed branch enjoying the technological advancement for the investigatory and diagnostic tools in the field.

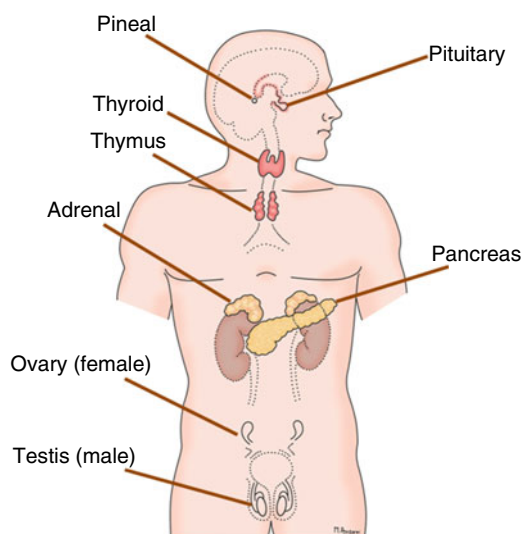
Being a physiological functionary “endocrine system” bears the sets of diseases which arise of hyper or hypo function of the specific endocrine glands or faults in their brain part regulations or receptor activation at target site. This chapter is dealing with the individual endocrine glands, their central and peripheral regulations, implied hormonal mechanisms, and related diseases/disorders to provide the readers a comprehensive view of the animal “endocrine system,” with a focus in human.

### History: A Brief Chronological Description of the Progress Made in Endocrinology

Earliest descriptions for the endocrine system are found about 200 B.C. when Chinese began isolating sex and pituitary hormones from human urine and using them for medicinal purposes. Later descriptions are from the medieval Persia by Avicenna, a legendary scientist, who provided a detailed account on diabetes mellitus in “The Canon of Medicine” (c. 1025), describing its clinical features as abnormal appetite, collapse of sexual functions, and sweet taste of urine.

In 1835 Irish doctor Robert James Graves described a case of goiter with bulging eyes (exophthalmos); the condition was later named after him as Graves’ disease.

In 1849, Thomas Addison described Addison’s disease (also known as primary adrenal deficiency or hypocortisolism). In the same year, Arnold



**Endocrine System, Fig. 1** Major endocrine glands in the human body

Berthold, who is regarded as a pioneer in endocrinology, observed that castration had negative effect on male cockerels who did not develop proper sex-specific characteristics. Later, in 1889 Brown-Séquard, a professor at the Collège de France, reported that self-administration of animal testes extracts led to enhancements in his physical strength, intellectual capacity, and sexual potency though it could not be replicated by the others. It could not be clarified further until 1904, the year Bouin and Ancel reasoned that some secretion from the Leydig cells is involved in the development of the male characteristics which were later named testosterone. Pure, crystalline testosterone was extracted not until 1935.

In 1889 when Joseph von Mering and Oskar Minkowski described hormonal etiology of the diabetes, they observed that surgically removing the pancreas resulted in an increase of blood sugar, followed by coma and eventually death.

In 1891, Murray successfully treated a female patient with myxedema with thyroid extract.

In 1894, Oliver and Schaefer described the presence of epinephrine in extracts from the adrenal medulla.

In 1902 William Bayliss and Ernest Starling in a unique experiment showed that acid instilled into the duodenum induced secretion in pancreas, even after removing any nervous connections between the two organs.

Nayliss and Starling discovered the hormone secretin in 1903 and also used the first the term “hormones” to indicate such chemical messengers.

In 1909, MacCallum and Voetlin stated an association between calcium metabolism and the parathyroid glands.

In 1913, Farmi and Von den Velden treated diabetes insipidus with posterior pituitary extracts.

In 1921 Otto Loewi first brought the idea of neurohormones and that year only growth hormone (GH) was first described by Evans and Long.

In 1922 Banting and Best discovered insulin. Insulin showed a magical effect on the health of the diabetes patients for whom otherwise no cure was available until then (Fig. 2). No later, Eli

Lilly, a chemist and owner of an American pharmaceutical company, started mass production of insulin (Fig. 3).

In 1962 Sutherland a renowned pharmacist reported that the action of epinephrine is mediated by secondary messengers like cyclic adenosine monophosphate (cAMP). It was a landmark discovery which unraveled the mechanism of the action of hormones.

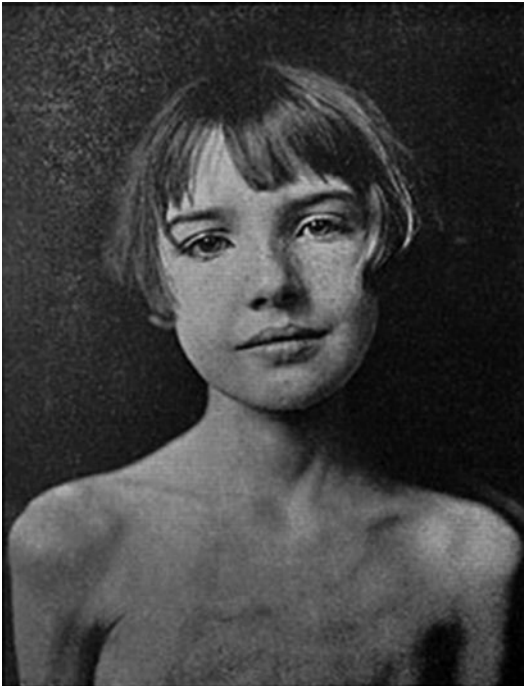
## Evolutionary and Developmental Basis

Most animals with well-developed nervous/circulatory systems essentially have an endocrine system. The endocrine system of vertebrates consists of glands and diffuse cell groups scattered in epithelial tissues. Endocrine glands develop from all three germinal tissue layers (endoderm, mesoderm, ectoderm); hence, the type of endocrine product is determined by the tissue layer a gland originated in. Glands of ectodermal and endodermal origin produce peptide and amine hormones; but mesodermal-origin glands secrete steroid or lipid hormones (Sadler and Langman 2015; Kleine and Rossmanith 2016, pp. 347–353).

## Classification of Endocrine Glands

Endocrine glands can be classified as central and peripheral. Central endocrine glands are those which are present within the cranium and are part of the brain as hypothalamus, pituitary and pineal glands. The other glands existing outside the cranial premises are called peripheral. Endocrine glands also can be classified as primary and secondary endocrine organs. Primary endocrine organs have the only function to secrete hormones (Table 1a), but secondary endocrine organs are primarily meant for the other biological functions and also secrete hormones to support and sustain their primary functions (Table 1b). In secondary endocrine organs, only specific cell groups or tissue components would be devoted for the hormonal secretion. Pancreas, though merits to be a primary endocrine organ by definition, it is only partly endocrine, as it has only a specific cell





Case VI

Before Insulin



Case VI

4 Mos. After

**Endocrine System, Fig. 2** Therapeutic effect of insulin historically demonstrated in a diabetic girl. (Image credit: Wellcome Collection, a proprietary of Wellcome Trust, UK,

available under Creative Commons Attribution International Licensing)

group (Islets of Langerhans) dispersed along whole length of organ (mainly tail part) which is endocrine, rest of the pancreas is exocrine – secretes enzymes meant for digestive functions which exit through ducts. Similarly, hypothalamus though considered as a primary endocrine organ, only neurons in the specific nuclear groups are endocrine. Table 1 enlists animal endocrine glands, exiting hormones, and their major functions.

## Endocrine Glands: Brief Anatomy and Hormone-Related Functions

### Primary Endocrine Organs

#### Hypothalamus

**Structure** Hypothalamus is the basal part of the diencephalon (its upper part is called thalamus)

making the floor of the third ventricle of the brain. The lower most part of this brain structure projects into the pituitary (infundibular) stalk making posterior or neurohypophyseal part of the pituitary gland. The specific nuclei groups of hypothalamus involved in the secretion of hormones are described below along with the functions.

**Function** Hypothalamus is the central regulator of the entire endocrine system. Hypothalamic neuronal cells secrete releasing/release inhibiting hormones which further stimulate/inhibit the synthesis of stimulating hormones from the anterior pituitary. Chiefly, arcuate nucleus of the tuberal region, and also some nuclear groups in preoptic and supraoptic regions, which control the secretion of hormones from the anterior pituitary, or the supraoptic and paraventricular nuclei (PVN) of supraoptic region of the hypothalamus which secrete oxytocin and vasopressin and corticotrophic releasing hormone (CRH)





*The First Insulin Commercially Available In the United States*

Iletin is the name that distinguishes the Insulin made by Eli Lilly and Company. It was the first Insulin commercially available in the United States.

The great demand for Iletin (Insulin, Lilly) necessitates the manufacture of large lots and has enabled us to develop methods of preparation and standardization that insure purity, stability and constant strength within narrow biological limits.

Patients who use Iletin (Insulin, Lilly) are afforded protection against disturbances which might follow a change from one lot to another if the lots in question were not uniform. A service wholesaler can supply Iletin (Insulin, Lilly) in such quantities as to help you secure a maximum turnover on a minimum investment.

*Lilly*

**Endocrine System, Fig. 3** An advertisement for Lilly Insulin (McCormick). (Image credit: Truman Library)

constitute endocrine part of the hypothalamus. Arcuate and other hypothalamic nuclei controlling hormonal secretion form the anterior pituitary

send their axons to the median eminence (hypothalamic extension which forms stalk of the pituitary gland) and emit their secretions

**Endocrine System, Table 1** Animal endocrine glands, hormones, and their major functions

| Glands/hormone                                    | Cell/tissue source                                                                  | Major functions                                                                                                | Glands/hormone                                   | Cell/tissue source  | Major functions                                                                                                                                         |
|---------------------------------------------------|-------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------|--------------------------------------------------|---------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>(a) Primary endocrine organs</b>               |                                                                                     |                                                                                                                |                                                  |                     |                                                                                                                                                         |
| <b>Hypothalamus</b>                               |                                                                                     |                                                                                                                |                                                  |                     |                                                                                                                                                         |
|                                                   |                                                                                     |                                                                                                                | <b>Pituitary</b>                                 |                     |                                                                                                                                                         |
| Corticotropin-releasing hormone (CRH)             | Paraventricular nuclei (PVN)                                                        | Stimulates release of ACTH and B-endorphin from anterior pituitary                                             | Adrenocorticotrophic hormone (ACTH)              | Anterior pituitary  | Stimulates synthesis and release of glucocorticoids                                                                                                     |
| Gonadotropin-releasing hormone (GNRH)             | Preoptic area; anterior hypothalamus                                                | Stimulates release of FSH and LH from anterior pituitary                                                       | Follicle-stimulating hormone (FSH)               | Anterior pituitary  | Stimulates development of ovarian follicles and secretion of estrogens; stimulates spermatogenesis                                                      |
| Luteinizing hormone-releasing hormone (LHRH)      | Nuclei; medial basal hypothalamus (rodents and primates); arcuate nuclei (primates) | Stimulates release of LH from anterior pituitary                                                               | Growth hormone (GH)                              | Anterior pituitary  | Mediates somatic cell growth                                                                                                                            |
| Somatostatin (growth hormone-inhibiting hormone)  | Anterior periventricular nuclei                                                     | Inhibits release of GH and TSH from anterior pituitary; inhibits release of insulin and glucagon from pancreas | Luteinizing hormone (LH)                         | Anterior pituitary  | Stimulates Leydig cell development and testosterone production in males; stimulates corpora lutea development and production of progesterone in females |
| Melanotropin-release inhibitory factor (Dopamine) | Arcuate nuclei                                                                      | Inhibits the release of MSH (no evidence of this peptide in humans)                                            | Melanocyte-stimulating hormone (MSH)             | Anterior pituitary  | Affects memory; affects skin color in amphibians                                                                                                        |
| Neuropeptide Y (NPY)                              | Arcuate nuclei                                                                      | Regulation of energy balance                                                                                   | Prolactin (PRL)                                  | Anterior pituitary  | Many actions relating to reproduction, water balance, etc.                                                                                              |
| Neurotensin                                       | Arcuate nuclei                                                                      | Regulation of energy balance                                                                                   | Thyroid-stimulating hormone or thyrotropin (TSH) | Anterior pituitary  | Stimulates thyroid hormone secretion                                                                                                                    |
| Orexin A and B                                    | Lateral hypothalamic area                                                           | Regulation of energy balance/food intake                                                                       | Oxytocin                                         | Posterior pituitary | Stimulates milk letdown and uterine contractions during birth                                                                                           |
| Thyrotropin-releasing hormone                     | Paraventricular nuclei (PVN)                                                        | Stimulates release of TSH and PRL from anterior pituitary                                                      | Vasopressin or antidiuretic hormone ADH or AVP   | Posterior pituitary | Increases water reabsorption in kidney                                                                                                                  |

|                                          |                                                       |                                                                                                                  |                                                               |                                       |                                                                                             |
|------------------------------------------|-------------------------------------------------------|------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------|---------------------------------------|---------------------------------------------------------------------------------------------|
| Histamine                                | Tuberomammillary nucleus (also from mast cells)       | Increases wakefulness, prevent sleep                                                                             | <b>Pineal gland</b>                                           |                                       |                                                                                             |
| Kisspeptin                               | Arcuate nucleus                                       | Acting on the receptors present in the anterior pituitary regulates synthesis/secretion of reproductive hormones | Melatonin                                                     | Pinealocytes                          | Affects reproductive and circadian control of bodily functions                              |
| <b>Adrenal gland</b>                     |                                                       |                                                                                                                  |                                                               |                                       |                                                                                             |
| <b>Mineralocorticoids</b>                |                                                       |                                                                                                                  |                                                               |                                       |                                                                                             |
|                                          |                                                       |                                                                                                                  | <b>Thyroid/parathyroid</b>                                    |                                       |                                                                                             |
|                                          |                                                       |                                                                                                                  | Thyroxine or tetraiodothyronine (T4)<br>Triiodothyronine (T3) | Follicular cells                      | Regulate oxidation and basic metabolic rates in tissue; learning associated neuroplasticity |
| Aldosterone                              | Zona glomerulosa of adrenal cortex                    | Sodium retention in kidney                                                                                       | Calcitonin (CT)                                               | C-cells of thyroid                    | Lowers serum $\text{Ca}^{2+}$ levels                                                        |
| 11 - Deoxycorticosterone (DOC)           | Zona glomerulosa of adrenal cortex                    | Sodium retention in kidney                                                                                       | Parathyroid hormone (PTH)                                     | Parathyroid gland                     | Stimulates bone resorption; increases serum $\text{Ca}^{2+}$ levels                         |
| <b>Glucocorticoids</b>                   |                                                       |                                                                                                                  |                                                               |                                       |                                                                                             |
|                                          |                                                       |                                                                                                                  | <b>Pancreas (Islet cells of Langerhans)</b>                   |                                       |                                                                                             |
| Cortisol (hydrocortisone)/corticosterone | Zona fasciculata and z. reticularis of adrenal cortex | Increases carbohydrate metabolism; antistress hormone                                                            | Glucagon                                                      | a-cells                               | Glycogenolysis in liver                                                                     |
|                                          |                                                       | Increased carbohydrate metabolism; antistress hormone                                                            | Insulin                                                       | b-cells                               | Glucose uptake from blood; glycogen storage in liver                                        |
| Dehydroepiandrosterone DHEA              | Zona reticularis of adrenal cortex                    | Weak androgen; primary secretory product of fetal adrenal cortex                                                 | Somatostatin                                                  | d-cells                               | Inhibits insulin and glucagon secretion                                                     |
| Epinephrine or adrenaline (EP)           | Adrenal medulla                                       | Glycogenolysis in liver; increases blood pressure                                                                | Pancreatic polypeptide (PP)                                   | Peripheral cells of pancreatic islets | Effects on gut in pharmacological doses                                                     |
| Norepinephrine or noradrenaline (NE)     | Adrenal medulla                                       | Increases blood pressure                                                                                         |                                                               |                                       |                                                                                             |
| (continued)                              |                                                       |                                                                                                                  |                                                               |                                       |                                                                                             |

**Endocrine System, Table 1** (continued)

| Glands/hormone                                      | Cell/tissue source                                                                            | Major functions                                                                 | Glands/hormone         | Cell/tissue source                     | Major functions                                                                                                                              |
|-----------------------------------------------------|-----------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------|------------------------|----------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Ovary</b>                                        |                                                                                               |                                                                                 |                        |                                        |                                                                                                                                              |
| Estrogen                                            | Follicles (also in brain regions like hippocampus, hypothalamus, prefrontal cortex, amygdala) | Uterine and other female tissue development Enhances cognition, neuroprotective | Progesterone           | Corpora lutea, placenta                | Uterine development; mammary gland development; maintenance of pregnancy                                                                     |
| Inhibin                                             |                                                                                               | .....                                                                           |                        |                                        |                                                                                                                                              |
| <b>Testes</b>                                       |                                                                                               |                                                                                 |                        |                                        |                                                                                                                                              |
| Androstenedione                                     | Leydig cells                                                                                  | Male sex characters                                                             | Testosterone           | Leydig cells                           | Spermatogenesis; male secondary sex characters                                                                                               |
| Dihydrotestosterone (DHT)                           | Seminiferous tubules and prostate                                                             | Male secondary sex characters                                                   |                        |                                        |                                                                                                                                              |
| <b>(b) Organs with secondary endocrine function</b> |                                                                                               |                                                                                 |                        |                                        |                                                                                                                                              |
| <b>Organ</b>                                        | <b>Hormone</b>                                                                                | <b>Major functions</b>                                                          | <b>Organ</b>           | <b>Hormone</b>                         | <b>Major functions</b>                                                                                                                       |
| <b>Lung</b>                                         | Leukotrienes (LT)                                                                             | Long-acting bronchoconstrictors                                                 | <b>Multiple organs</b> | Prostaglandins E1 and E2 PGE1 and PGE2 | Contraction/relaxation of smooth muscle cells in vessels, aggregation/disaggregation of platelets, sensitization to pain (and other actions) |
| <b>Heart (Atrial myocytes)</b>                      | Atrial natriuretic factor (ANF)                                                               | Regulation of urinary sodium excretion                                          | <b>Multiple organs</b> | Klotho                                 | Enhances cognition, protects against aging                                                                                                   |
| <b>Thymus (Thymocytes)</b>                          | Thymosin, thymulin and thymopoietin                                                           | Proliferation/differentiation of lymphocytes                                    | <b>Skin</b>            | Cholecalciferol                        | Modified to form Vit. D                                                                                                                      |
| <b>Kidney</b>                                       | Renin                                                                                         | Stimulates release of aldosterone                                               | <b>Liver</b>           | Insulin like growth factor (IGF-I)     | Stimulates bodily growth                                                                                                                     |
|                                                     | Calcitriol                                                                                    | Helps absorption of $\text{Ca}^{2+}$                                            |                        | Angiotensinogen                        | Raises blood pressure                                                                                                                        |
|                                                     | Erythropoietin                                                                                | Induces absorption of red blood cells in bone marrow                            |                        | Thrombopoietin                         | Causes increase in platelets                                                                                                                 |
| <b>Skeleton</b>                                     | FGF23                                                                                         | Inhibits production of calcitriol and increases phosphate excretion             |                        | Hepcidin                               | Blocks release of iron into body fluids                                                                                                      |
|                                                     | Osteocalcin                                                                                   | Increase insulin secretion                                                      | <b>Gut</b>             |                                        |                                                                                                                                              |

|                                                        |             |                                                                       |                                                 |                                                                                   |                                                                                                                                            |
|--------------------------------------------------------|-------------|-----------------------------------------------------------------------|-------------------------------------------------|-----------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Adipose tissue</b>                                  | Leptin      | Promotes satiety signals in the brain                                 | Bombesin                                        | Neurons and endocrine cells of gut                                                | Hypothermic hormone; increases gastrin secretion                                                                                           |
|                                                        | Adiponectin | Reduces insulin resistance                                            | Cholecystokinin (CCK)                           | Duodenum and CNS                                                                  | Stimulates gallbladder contraction and bile flow; affects memory, eating behavior                                                          |
| <b>Placenta</b>                                        |             |                                                                       | Gastric inhibitory polypeptide (GIP)<br>Gastrin | Duodenum<br>G-cells of midpyloric glands in stomach antrum                        | Inhibits gastric acid secretion<br>Increases secretion of gastric acid and pepsin                                                          |
| Chorionic gonadotropin (CG)                            | Placenta    | LH-like functions; maintains progesterone production during pregnancy | Gastrin-releasing peptide (GRP)                 | GI tract                                                                          | Stimulates gastrin secretion                                                                                                               |
| Chorionic somatomammotropin or placental lactogen (CS) | Placenta    | Acts like PRL and GH                                                  | Vasoactive intestinal peptide (VIP)             | Small intestine (also in central and enteric nervous system, and nerve terminals) | Inhibits gastric acid secretion and increases intestinal secretion of water and electrolytes; a neurotransmitter/neuromodulator in CNS/ENS |
|                                                        |             |                                                                       | Serotonin                                       | GI tract and blood platelets (also a neurotransmitter in brain)                   | Maintain mood, sleep, appetite, and digestion. Regulate bowel function and movements                                                       |

which get collected in the portal venous capillaries present there and through the portal veins reach to the anterior pituitary. Contrastingly, oxytocin and vasopressin are synthesized by the supraoptic and paraventricular nuclei of the hypothalamus, respectively, though are released at the posterior pituitary or neurohypophysis where their axons are ending. Hypothalamic endocrine function is regulated by the instructions from the higher cortical centers and also through the feedback received from the different hierarchical levels of the endocrine systems which are under the hypothalamic control (Kovacs and Ojeda 2012, pp. 116–148, Kleine and Rossmanith 2016, pp. 269–297). Hypothalamic endocrine regulation is further discussed in this chapter in section “Endocrine System: Physiological Regulations.”

### Pituitary Gland

**Structure** Pituitary gland is the master controller of all peripheral primary endocrine glands. This gland is located in the hypophyseal fossa (also called pituitary fossa) which is placed in the center of middle cranial fossa of base of the skull. Embryological derivation of this gland is unique. Posterior half of the gland is the extension of the hypothalamus hence neural and is called neurohypophysis. The neurohypophysis contains the axons terminals of the neurons supraoptic and PVN nuclei of the supraoptic region of the hypothalamus. Anterior part of the gland is derived from the evagination of the oral ectoderm in front of the buccopharyngeal membrane and is called adenohypophysis. Most of the pituitary hormones are

secreted from the adenohypophysis part except oxytocin and vasopressin or antidiuretic hormone (ADH) which are secreted from the neurohypophysis part (Kovacs and Ojeda 2012, pp. 116–171).

**Function** The hypothalamic releasing or inhibitory hormones regulate the synthesis of trophic hormones from the anterior pituitary through hypophyseal portal system (Fig. 4). Posterior pituitary hormones oxytocin and vasopressin regulate hemodynamic status of the body. Oxytocin is also involved in induction of the delivery and ejection of breast milk in female (Kovacs and Ojeda 2012, pp. 148–171). Both of the hormones have effect on animal social behavior, memory, and learning, especially oxytocin, which is also called social molecule (Kumar et al. 2018).

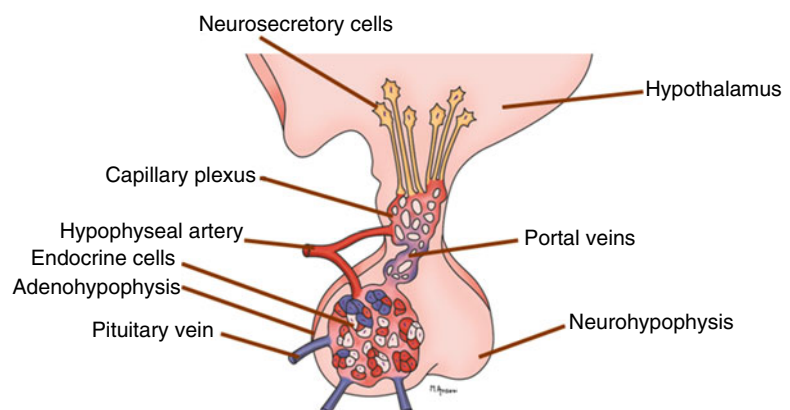
### Pineal Gland

**Structure** Pineal is a minute pine cone like gland located at the rear end of the diencephalon. The cellular elements of the gland are pinealocytes (approx. 95%) and neuroglia cells, and it is densely filled with afferent nerve terminals. The gland is highly vascular and rich in sympathetic innervations.

**Function** Pineal gland secretes (by pinealocytes) a serotonin-derived photoactive hormone melatonin which helps regulate circadian rhythm of the body (to regulate the sleep and wakefulness) in concert with the biological clock situated in the supra-chiasmatic nuclei (SCN) of the hypothalamus. It is also a known powerful antioxidant. Melatonin secretion is regulated by light exposure

### Endocrine System,

**Fig. 4** Hypophyseal portal circulation





and its intensity and shows a rhythmic secretion, being low during the daylight hours and high during dark periods.

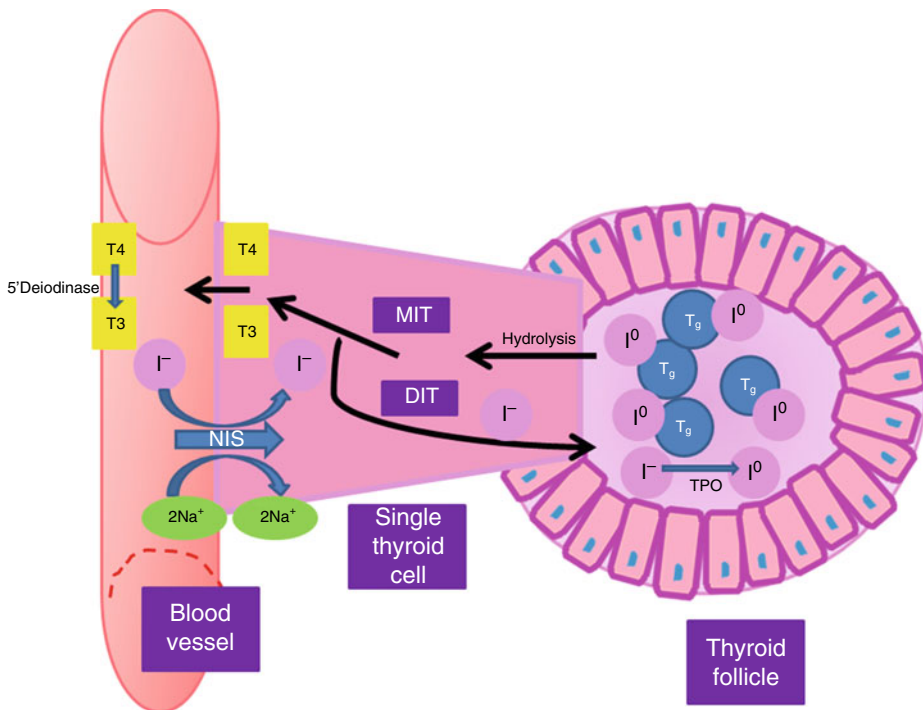
Melatonin is also believed to be involved in sexual development and reproductive functions (blocks secretion of LH and FSH), thermoregulation, cellular metabolism, and also in immune function. Though there is little evidence in human that the pineal gland plays a significant role in the neuroendocrine regulation of reproduction during either puberty or adulthood, in seasonally breeding animals, such as sheep and hamsters, melatonin secretion is said to be influenced by the day length and thus gating reproduction as a function of the season (Kleine and Rossmanith 2016, pp. 243–244).

### Thyroid Gland

**Structure** Thyroid gland is situated in the neck extending from C5 to T1 vertebrae and is related with laryngeal cartilages and upper tracheal rings. It is a butterfly-like structure having two lobes and

a connecting isthmus that lies in front of 2–4th tracheal rings. The lobes lie on either side of the larynx and trachea and whole gland is covered by pretracheal fascia. In some individuals, an extra smaller lobe of thyroid called pyramidal lobe may be present, which may extend from the isthmus up to the hyoid bone.

**Function** Thyroid gland secretes hormones Tri-iodothyronine (T3) and Tetra-iodothyronine or Thyroxine (T4) which are involved in the regulation of the basic metabolic rate of the body (influencing physiological functioning of almost each cell and the organ). Thyroid hormones are secreted from the lining epithelial cells of the follicles which further go iodination in the colloid filled in the lumen of the follicles (Fig. 5). Iodine is exclusive to and an essential component of the thyroid hormones. The term “iodine” here refers to the elemental form of the iodine (I) which will get assimilated in the hormones in the iodide form ( $I^-$ ). Ingested iodine is absorbed through the small intestine and transported in the plasma to the



**Endocrine System, Fig. 5** Synthesis of Thyroid hormones. I: ionized iodine;  $I^0$ : oxidized iodine; Tg: thyroglobulin; TPO: thyroid peroxidase

thyroid, where it is concentrated, oxidized, and then incorporated into thyroglobulin (Tg) to form intermediate mono and diad (MIT and DIT) and later final and active triad (T<sub>3</sub>) and tetra (T<sub>4</sub>) forms of thyroid hormones in the thyroid follicles, and is stored there for a variable period (Fig. 5). Further, Tg base of the thyroid hormones undergo proteolysis releasing T<sub>3</sub> and T<sub>4</sub> into the circulation to be carried by specific binding proteins to target tissues. The synthesis of T<sub>4</sub> is about 4 times more than T<sub>3</sub>. Its vast influence is mediated through differential expression of hormone receptor isoforms in tissues and conversion of thyroxine (T<sub>4</sub>) to triiodothyronine (T<sub>3</sub>), by the enzyme 5'-deiodinase (Fig. 5). The thyroid hormone secretion is controlled by thyrotropin-releasing hormone (TRH) from hypothalamus and thyroid stimulating hormone (TSH) from anterior pituitary along with nutritional signals like availability of the iodine and carrier molecules, and also by the environmental factors like radiation, chemical exposure, drugs, and temperature. Calcitonin is a small polypeptide hormone secreted by the parafollicular or "C" cells of the thyroid. Calcitonin decreases blood calcium and increases blood phosphate level by suppressing the osteoclast activity in bones and increasing the amount of calcium excreted in urine (Kleine and Rossmanith 2016, pp. 269–297).

#### Parathyroid

**Structure** The small glands (about 50 mg), two each side, are normally found on the posterior aspect of the lobes of thyroid gland.

**Function** Parathyroid gland secretes parathyroid hormone (PTH) that controls calcium and phosphate homeostasis in the body. Effect of PTH on blood calcium and phosphate levels is opposite of calcitonin for which it is known as an antagonizing hormone.

#### Adrenal Gland

**Structure** Adrenal gland is a small gland located on the top of each kidney enclosed in renal fascia (alternative name for this is suprarenal gland). It

has cortical and medullary parts which secrete steroid and amine hormones respectively. The cortex is further differentiated into pars glomerulosa, fasciculata, and reticularis. Central medullary part contains chromaffin and ganglion cells of neural crest origin.

**Functions** Its cortical and medullary parts secrete distinct hormones which are involved in maintaining important physiological functions.

**Cortical Hormones** The pars glomerulosa, fasciculata, and reticularis secreting sex steroids or gonadotrophins, mineralcorticoids, and glucocorticoids or cortisol in order. All cortical hormones are steroid compounds derived from cholesterol.

**Gonadotrophins** The adrenal cortex secretes many male sex hormones, including DHEA, DHEA sulfate (DHEAS), androstenedione, and 11-hydroxyandrostenedione, and also small quantities of the female sex hormones progesterone and estrogen. Androgens secreted from the adrenal go extra-adrenal conversion to testosterone. These androgens have a role in early development of the male sex organs in childhood. They also mediate secondary sexual characteristics during puberty in the both sexes. ACTH from anterior pituitary has a physiological stimulatory effect on androgen release by the adrenal.

**Mineralocorticoids** Aldosterone accounts for most of the mineralocorticoid activity, with some contribution from glucocorticoids. The concentration of aldosterone in blood exhibits diurnal variation, and the secretory rate is generally 150–250 µg/day. Aldosterone promotes sodium reabsorption and potassium excretion by the tubular epithelial cells of the collecting and distal renal tubules thus way maintaining normal osmolality and water balance in blood. Reabsorption of sodium is followed by passive absorption of water, leading to an increase in the extracellular fluid volume with minimal change in the plasma sodium concentration.

**Glucocorticoids** Most of the glucocorticoid activity comes from cortisol, with corticosterone having a minor contribution. The normal blood cortisol concentration averages 12  $\mu\text{g/dL}$ , with an average secretory rate of 15–20 mg/day. Cortisol secretion from adrenal gland is the output hormone in HPA axis, and also it is the chief stress hormone in body. Other functions of cortisol are like counteracting insulin secretion, stimulating gastric-acid secretion, reducing bone formation, and functioning as a diuretic. Cortisol also contributes to the maintenance of various homeostatic actions, like blood pressure, immune system, metabolism of protein, carbohydrate, and fat, and anti-inflammatory action. Its secretion is controlled by the hypothalamo-pituitary-adrenal (HPA) axis, which follows a circadian rhythm and also gets influenced by exposure to the light and hours of the sleep (vice versa it regulates sleep) (Longo 2015, Chapter 399; Kleine and Rossmanith 2016, pp. 339–346). Its regulation through HPA axis and neural and molecular basis of rhythmic secretion are further discussed in this chapter in section “[Endocrine System: Physiological Regulations](#).”

**Medullary Hormones** The chromaffin and ganglion cells in the medulla secrete epinephrine/adrenalin and norepinephrine/noradrenaline and in minute amount dopamine. These hormones are secreted into the bloodstream as a result of direct stimulation by acetylcholine release from the sympathetic nerves. Preganglionic sympathetic nerve fibers reach to the chromaffin cells of the adrenal medulla without synapsing anywhere else. These hormones are responsible for the maintenance of cardiac output, physiological vascular resistance, and stress response (Kleine and Rossmanith 2016, pp. 269–297).

#### Ovary

**Structure** Ovary is the female gonad located in the pelvis one on each side at the terminal end (fimbria) of the uterine tube. A single follicle is the endocrine unit of the ovary. Each follicle contains a germ cell/oocyte at the core surrounded by an

inner and an outer layer composed of granulosa cells and theca cells, respectively.

**Function** It secretes the hormones which are essential for the maintaining functions and health of their reproductive organs. Ovary chiefly secretes estrogen and progesterone which are, respectively, responsible for the initiation and maintenance of the pregnancy, and also secretes androstenedione and testosterone in slighter amount which can get converted to estrogen with aromatization. Estrogen also shows a terminal surge which induces secretion of the oxytocin which in turn would initiate uterine contraction to facilitate delivery of the child. Ovary also secretes minor nonsteroidal hormones as activin, inhibin, and relaxin. Nonsteroidal ovarian hormones have a contribution in regulating production of steroid hormones though chief regulation is by LH and FSH by anterior pituitary (activin enhances, and inhibin and relaxin suppress). Relaxin also relaxes the hip ligaments before delivery of the child.

Estrogens also have effect on the physiological processes other than reproduction such as bone metabolism/remodeling, nervous system maturation, and endothelial responsiveness. Estrogen also brings pubertal changes in female like breast development and enlargement and maturation of the uterus, ovaries, and vagina. Estrogen also works in concert with growth hormone and insulin-like growth factor I (IGF-I) to produce a growth spurt and stimulates the maturation of chondrocytes and osteoblasts, which ultimately leads to epiphyseal fusion. Until midpuberty, estrogen begins to exert a positive feedback on gonadotropin-releasing hormone (GnRH) secretion, leading to the progressive increase of LH and FSH production, culminating in the LH surge, ovulation, and the initiation of the menstrual cycle. In the adult female, estrogen plays a critical role in maintaining the menstrual cycle (Kovacs and Ojeda 2012, pp. 194–238, Kleine and Rossmanith 2016, pp. 269–297).

#### Testes

**Structure** Testis is the male gonad which in contrast to the female gonad, along with the external

genitalia presents in the perineal region, present bilaterally enclosed in scrotal sac.

**Function** It chiefly secretes testosterone which is necessary for the gametogenesis and also development and maintenance of the male reproductive system and male sexual behavior. Higher center regulation of testosterone synthesis is much simpler than the female sex hormones due to absence of a defined cyclic period in male. The male sex hormones secreted from adrenal gland make additional source of this hormone through conversion.

#### Pancreas (Islet Cells)

**Structure** Islet cells of the pancreas which are dispersed among the exocrine acini as clusters constitute endocrine part of this organ. Islet cell clusters are more abundant towards rear part of the organ with highest density in the tail.

**Function** Islet cells secrete three types of the hormones: alpha cells secrete glucagon, beta cells insulin, and delta cells somatostatin, respectively, which are crucial for the normal metabolic functions of the body. Insulin and glucagon control the two opposite aspects of glucose metabolism, glycogenesis and glycogenolysis, respectively, in consequent control concentration of glucose in blood. Insulin is also involved in the metabolism of many other energy storing biomolecules which finally reduce blood glucose level.

#### Organs/Tissue Components with Secondary Endocrine Function

Certain animal organs contain a tissue component or specific cell groups with endocrine functions (Table 1b). Below is being provided a brief descriptions of such endocrine structures and their functions.

#### Placenta

**Structure** Placenta is an endocrine organ of pregnancy. All female mammals other than monotremes and marsupials (most) bear placenta during pregnancy. Placenta is implanted in the uterine

wall, where it receives nutrients and oxygen from the mother's blood and passes out excretory products. It is a disc like structure. Uniquely, it has maternal and fetal components both providing a physical link between the two. Maternal and fetal components are derived from uterine decidua (functional layer of the endometrium which is shed during parturition) and chorionic frondosum (an outer trophoblast shell and inner chorionic plate made of extraembryonic mesoderm), respectively (Sadler and Langman 2015, p. 112). It is the fetal component, especially the syncytial layer of the trophoblast cells, which is endocrine, and secretes hormones to sustain pregnancy.

**Functions** Placenta secretes progestins (mainly progesterone) along with the corpus luteum. It also secretes estrogen (especially weaker estriol) which inhibit the LH along with the progesterone to help sustain pregnancy and induce growth of the breast. During initial 2 months of the pregnancy, syncytial cells of the trophoblast secrete human chorionic gonadotrophin (HCG), which helps to maintain corpus luteum until placenta takes the action of synthesizing progesterone. HCG also inhibits LH like gonadotrophins to stop further ovulations and to help sustain pregnancy. This hormone is excreted in the maternal urine in initial months of the pregnancy and is used as a gestational indicator. Another hormone secreted by the placenta is somatomammotropin (placental lactogen), which is a growth hormone like substance, providing fetus a priority on maternal glucose and inducing maternal glucose synthesis hence making the mother functionally diabetic during pregnancy. It also helps growth of the breast in mother (Sadler and Langman 2015, pp. 116–117).

#### Thymus

**Structure** The thymus is a double lobed structure located in the upper anterior part of chest directly behind sternum. It has an outer zone called cortex and an inner zone called medulla. Histologically, the organ is composed of two types of cell called lymphocytes and reticular cells. The cortex bears the immature T cells

which migrate to the medulla in order to mature (Standring 2016, pp. 1362–1365).

**Function** Thymus produces hormones like thymosin (alpha 1), thymulin, and thymopoietin, which have been stated to circulate through blood and to act on both prothymocytes and mature T-cells in the periphery which helps to maintain commitment and functions of these cells. The hormones produced by the thymus promote the maturation of the T cells prior to their release into the blood. Once these thymic lymphocytes (or T cells) have fully matured in the thymus, they migrate to the lymph nodes in the body and guard against invader microorganisms or living or nonliving foreign particles causing diseases, a biological function called immune surveillance (Kleine and Rossmanith 2016, pp. 269–297; Standring 2016, pp. 1362–1365).

#### Adipose Tissue

Adipose tissue secretes several hormones. These hormones are mainly involved in lipid metabolism and storage. Adiponectin – a hormone synthesized by adipose cells – appears to reduce cellular insulin resistance and to protect blood vessels from inflammation and atherosclerosis. Leptin, synthesized by the adipose cells, acts as an indicator of satiety. It is released in response to food and acts on the neuronal regions dealing with the energy intake and expenditure (Kleine and Rossmanith 2016, pp. 269–297).

#### Skin

The skin cells synthesize inactive form of vitamin D<sub>3</sub>, cholecalciferol from cholesterol when exposed to ultraviolet radiation. Cholecalciferol is converted to an intermediate in liver, which further is converted to calcitriol – the active form of vitamin D<sub>3</sub>, in kidney. Vitamin D is important in a variety of physiological processes, including intestinal calcium absorption and immune system function (Kleine and Rossmanith 2016, pp. 269–297).

#### Skeleton

Bone cells secrete Fibroblast growth factor 23 (FGF23). Its action is to inhibit the formation

of calcitriol from vitamin D<sub>3</sub> and to increase phosphorus excretion from kidney. Osteocalcin, from the osteoblasts, induces insulin secretion from pancreas and also promotes its responsiveness on the peripheral tissues (Longo 2015, chapter 423).

#### Heart

Specialized cells in the atrium wall secrete the peptide hormone atrial natriuretic peptide (ANP) in response to distension caused by increased blood volume or pressure. ANP has a role in maintaining hemodynamic status of the body. It reduces sodium reabsorption and, in turn, decreases accompanied water reabsorption from the urinary filtrate in the kidney, bringing down the total blood volume. It also has an inhibitory effect on the renin secretion from the specialized cells of the kidney tubules, hence initiation of the renin-angiotensin-aldosterone system (RAAS) which has an opposite effect on hemodynamic balance in the body (Kleine and Rossmanith 2016, pp. 269–297).

#### Gastrointestinal Tract

The mucosa of the GI tract, mainly the stomach and small intestine, contains specialized cell which secrete hormones meant to help in the digestion. Like, G-cells in the stomach secrete a peptide hormone, gastrin, in response to distension caused by entering food that stimulates the release of hydrochloric acid from other cells. Similarly, secretin, a peptide hormone, is secreted by the small intestine in response to the acidic chyme released from stomach. Secretin stimulates the release of bicarbonate from the pancreas, antagonizes acidic chyme, and also inhibits the further secretion of hydrochloric acid by stomach mucosa. Cholecystokinin (CCK) is another peptide hormone released from small intestine which induces the secretion of digestive enzymes from pancreas and also the release of bile from the gallbladder. Intestinal hormones are also involved in glucose metabolism, like gastrin inhibitory peptide-1 (GIP-1) and glucagon like peptide-1 (GLP-1) secreted from the small intestine induce secretion of insulin (Kleine and Rossmanith 2016, pp. 269–297; Kumar et al. 2018).

## Liver

The endocrine function of liver is highly involved in metabolic regulation of the digestive nutrients. It synthesizes various hormones such as insulin-like growth factor (somatomedin), angiotensinogen, thrombopoietin, and hepcidin. IGF-1 has insulin-like effects as its name suggests, and it can bind to the insulin receptor. Its actions are mediated through a same named tyrosine kinase receptor which presents on the surface of almost all cells and is the stimulus for growth in the body. Angiotensinogen by the action of enzyme renin secreted from the kidney gets converted to angiotensin which is a substrate of Renin-Angiotensin-Aldosterone System (RAAS) maintaining hemodynamic balance in the body. Angiotensin also causes vasoconstriction (Kleine and Rossmanith 2016, pp. 269–297). Hepcidin is small peptide hormone majorly synthesized in the liver. It is chief regulator of the extra cellular excretion of the iron in the body (Gressner and Gressner 2018).

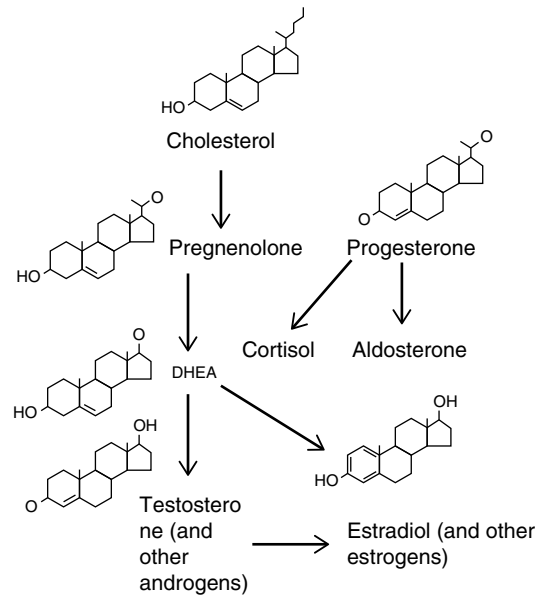
## Kidneys

Certain cells of kidney secrete hormones which are crucial for hemodynamic and electrolyte balance in the body. A decline in blood flow which is detected at the glomerular filtration system induces release of the enzyme renin, which in turn switches on the RAAS stimulating the reabsorption of sodium and water leading to increase in blood flow and blood pressure. The kidneys regulate blood calcium levels through the production of calcitriol from vitamin D<sub>3</sub>, which is released in response to the secretion of PTH. Low oxygen level in circulation induces synthesis of erythropoietin (EPO) from kidney which in turn would stimulate the production of red blood cells (erythrocytes) in the bone marrow, thereby increasing oxygen delivery to tissues (Mukoyama and Nakao 2005).

## Hormones

### Types and Structure

Hormones are mostly proteins, but some are also peptides, amines, or steroids. The protein, peptide,



**Endocrine System, Fig. 6** Cholesterol derivations of the lipid hormones

or amine hormones are water soluble, but steroid hormones are lipid soluble. Lipid-soluble hormones act slow, but their effects last longer than water soluble hormones (Kleine and Rossmanith 2016, pp. 11–17; Kumar et al. 2018). Lipid hormones have a common molecule of origin as cholesterol (Fig. 6). Most of the hormones are secreted by peripheral organs or specific tissue components. Some hormones are synthesized inside the brain which are called “neurohormones” (Table 2). Neurohormones also include some of the sex hormones (estrogen, progesterone, and testosterone) which are also synthesized by cortical neurons (Ish et al. 2007).

### Mechanisms of Action

Protein, peptide, and amine hormones (except thyroid hormones) are water soluble, hence cannot cross through the cell membrane directly. These hormones attach to the receptors present on the surface of target cells creating the hormone-receptor complex, in turn engaging a G-protein dependent secondary messenger pathway (like cAMP, cGMP, Diacylglycerol, Ca<sup>++</sup>, etc.,) to induce protein kinases/phosphorylases related to specific biological events. Steroid



hormones are lipid soluble, hence can cross through the cell membranes. They directly reach nucleus tagged with transporters or binding protein present in the cell cytoplasm, where they set free from the carrier molecule and attach to the nuclear receptors (binding sites) at DNA promoter regions for the genes assigned for forming specific

proteins (Fig. 7) (Kleine and Rossmanith 2016, pp. 263–267; Kumar et al. 2018).

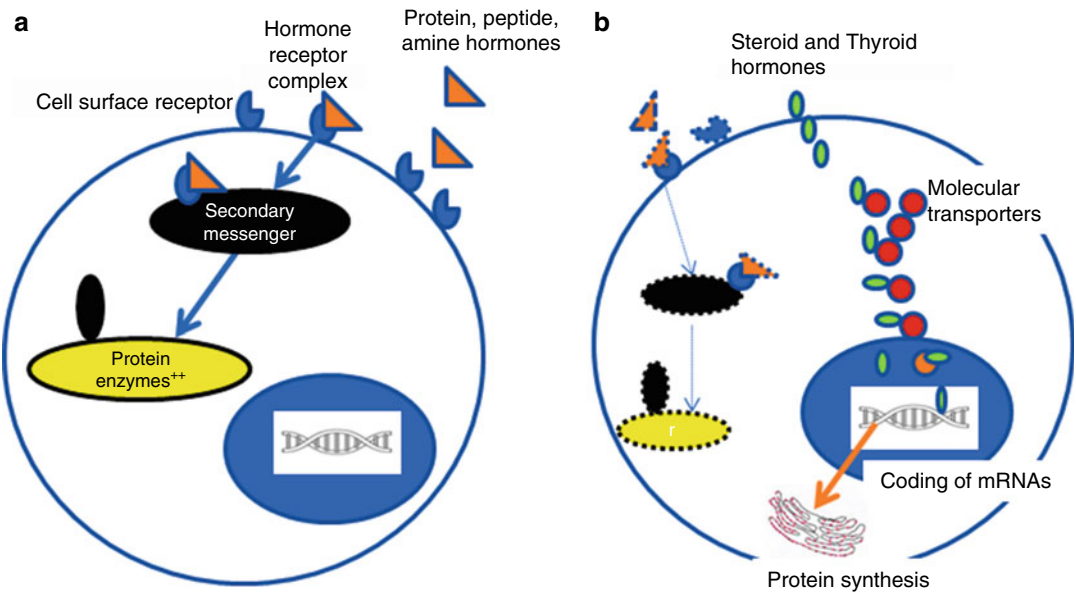
Thyroid hormones, though chemically amine, are exception to the group. Their three dimensional structure resembles that of the steroid hormones, hence can enter the cell and reach to the specific nuclear receptors with the help of specific transporters present at the cell membrane (facilitated diffusion) and in the cell cytoplasm.

Hormones are biologically active in very minute amount which get usually measured in micrograms ( $\mu\text{g}$ ,  $10^{-6}$  g), nanograms (ng,  $10^{-9}$  g), or picograms (pg,  $10^{-12}$  g). Hormone-Receptor interactions for all categories of hormones are highly specific, reversible, and satiable and follow a threshold limit for the maximal biological response (i.e., follow normal distribution curve). Also, there is differential purposing of the category of hormones depending on the metabolic processes involved. Metabolic processes which need urgent response, such as blood glucose or calcium homeostasis, are usually controlled by peptide hormones (also epinephrine), but processes for which response is slow, such as pubertal development or basic metabolic rate, are controlled by steroid hormones and thyroid

**Endocrine System, Table 2** Neurohormones

|                                                   |                                      |
|---------------------------------------------------|--------------------------------------|
| Corticotropin-releasing Hormone (CRH)             | Thyrotropin-releasing Hormone        |
| Gonadotropin-releasing Hormone (GNRH)             | Histamine                            |
| Luteinizing hormone-releasing Hormone (LHRH)      | Vasopressin or antidiuretic Hormone) |
| Somatostatin (growth Hormone-inhibiting Hormone)  | ADH or AVP                           |
| Melanotropin-release Inhibitory factor (dopamine) | Oxytocin                             |
| Neuropeptide Y (NPY)                              | Norepinephrine                       |
| Neurotensin                                       | Dopamine                             |
| Orexin A and B                                    | Serotonin                            |
|                                                   | Melatonin                            |
|                                                   | B-endorphin                          |
|                                                   | Agouti-related protein (AGRP)        |
|                                                   | Estrogen                             |

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**Endocrine System, Fig. 7** Mechanisms of action (a) Protein, peptide, and amine hormones (b) Steroid and thyroid hormones. (Reproduced with permission from

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hormones. Electrolyte homeostasis requires intermediate response speed and is regulated by peptide and steroid hormones both (Kleine and Rossmanith 2016, pp. 263–267).

**Hormone Secretion, Transport, and Degradation**

The blood level of a hormone is determined by its rate of secretion and its circulating half-life. After protein processing, peptide hormones are stored in secretory granules, from where are later released into the circulation. The stimulus for hormone secretion may be a releasing factor or neural signal that induces rapid changes in intracellular calcium concentrations, leading to secretory granule fusion with the plasma membrane and release of the hormones. In contrast, steroid hormones diffuse into the circulation as they are synthesized hence their secretory rates are closely aligned with rates of the synthesis.

Hormone transport and degradation determine the speed with which a hormonal signal may decay. Some hormonal signals are short decaying (e.g., somatostatin), whereas others are longer-lived (e.g., TSH). An understanding of circulating hormone half-life is necessary for the proper physiologic hormone replacement (Longo 2015, chapter 399).

**Crossing Blood Brain Barrier (BBB)**

Transport of a hormone through blood brain barrier (BBB) depends on whether it is water or lipid soluble. Steroid hormones are lipid soluble, hence can easily pass to and fro through the BBB (the peripherally synthesized hormones enter brain and those synthesized inside brain reach to periphery), but protein, peptide, amine, and other hormones which are water soluble can do it with help of the transporters/binding proteins only. Transport of the lipid insoluble hormones is a saturable/rate limited process due to exhaustion of the transporters/binding proteins (Banks 2012; Kumar et al. 2018).

Certain of the hormone synthesizing brain regions, called circumventricular organs, are devoid of a blood brain barrier (BBB) which facilitates the release of the stored hormones in the blood (Table 3) (Kumar et al. 2018).

**Endocrine System, Table 3** BBB free regions in brain

|                                            |
|--------------------------------------------|
| Circumventricular organs                   |
| 1. Organum vasculosum of lamina terminalis |
| 2. Subfornical organ                       |
| 3. Subcommissural organ                    |
| 4. Median eminence (hypothalamus)          |
| 5. Intermediate lobe of pituitary gland    |
| 6. Posterior pituitary                     |
| 7. Pineal gland                            |
| 8. Area postrema (4th ventricle)           |

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These BBB-free regions are also the site for receiving peripherally released hormones. These brain regions contain receptors for the peripheral hormones – presenting a unique opportunity for neuron-hormone interactions.

**Endocrine System: Physiological Regulations**

**Central Endocrine Axes and Hormonal Homeostasis**

The endocrine system is governed by the central axes which essentially connects three components of the system: a brain component – a nuclei of the hypothalamus, anterior part of the pituitary gland, and any of the endocrine glands as adrenal, gonads, or thyroid. Each axis is regulated by the feedback cycles (Fig. 8) (Kleine and Rossmanith 2016, pp. 299–338; Kumar et al. 2018). Table 4 mentions the central axes, their essential components, and secreted hormones.

Central endocrine axes run from hypothalamus to adrenal, gonads, or thyroid via anterior part of pituitary (adenohypophysis). Hypothalamus in association with anterior pituitary and adrenal gland constitutes HPA axis – which bears an influence on most of the neurophysiological functions and is crucial for the neuroendocrine adaptation to the stress. A parallel axis connecting hypothalamus and anterior pituitary to gonads (testis in male and ovary in female) constitutes HPG axis which regulates reproductive functions.

In HPG axis, releasing/inhibitory hormones are secreted from specific hypothalamic nuclei which induce synthesis/release of stimulating/ luteinizing hormones from anterior pituitary which in turn induce synthesis/release of sex

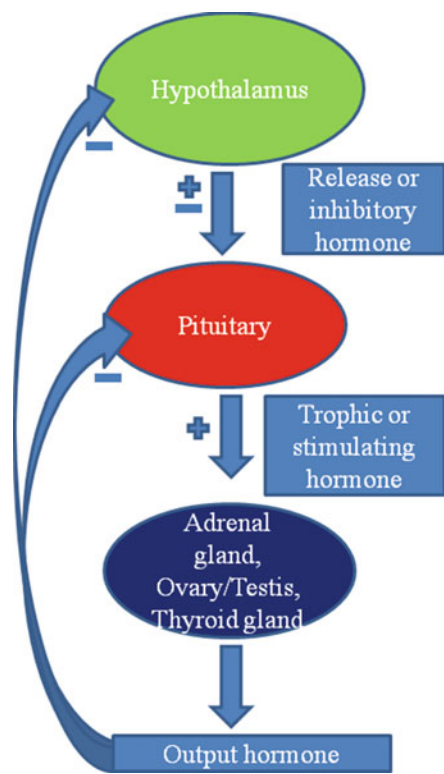
hormones from the gonads. The peripheral endocrine glands and their central regulatory centers work in coordination in an attempt to maintain a state of functional equilibrium or physiological homeostasis in the body (Kleine and Rossmanith 2016, pp. 299–338).

Feedback regulation also occurs for endocrine systems that do not involve the central axes, for example, calcium feedback on PTH, glucose inhibition of insulin secretion, and leptin feedback on the hypothalamus.

Uniquely, prolactin a hormone secreted from the anterior pituitary essential for the control of the lactation in female and many other functions has only two components in its regulatory axis- (hypothalamo-prolactin axis) which does not contain an inter-gland feedback loop. The dopamine secreted from the tubero-infundibular nuclei of the hypothalamus is inhibitory to the secretion of prolactin from the anterior pituitary and also sets auto-inhibition of its own secretion (Macleod et al. 1981).

Paracrine and Autocrine Regulation

*Paracrine regulation* refers to factors released by one cell that act on an adjacent cell in the same tissue, such as somatostatin secretion by pancreatic islet cells inhibits insulin secretion from nearby cells. *Autocrine regulation* states the action of a factor on the same cell from which it is produced, such as IGF-I acts on the cells that produce it to regulate its secretion.



**Endocrine System, Fig. 8** Feedback regulations at central endocrine axes

**Endocrine System, Table 4** Central endocrine axes in the animals (including human)

| Name                                       | Hypothalamic component/hormone                                        | Pituitary component/hormone                                                                  | Target endocrine organ/hormone |
|--------------------------------------------|-----------------------------------------------------------------------|----------------------------------------------------------------------------------------------|--------------------------------|
| Hypothalamic-pituitary- adrenal (HPA) axis | Paraventricular nucleus (PVN)/ corticotrophin releasing hormone (CRH) | Adrenocorticotrophs, anterior pituitary/ adrenocorticotrophin hormone (ACTH)                 | Cortisol/ cortisone            |
| Hypothalamic-pituitary-thyroid (HPT) axis  | Paraventricular nucleus PVN/thyrotrophin releasing hormone (TRH)      | Thyrotrophs, anterior pituitary/thyroxine stimulating hormone (TSH)                          | Thyroxine 3 and 4 (T3 and T4)  |
| Hypothalamic-pituitary-gonadal (HPG) axis  | Arcuate nucleus/gonadotrophin releasing hormone (GnRH)                | Gonadotrophs, anterior pituitary/follicle stimulating hormone (FSH)/luteinizing hormone (LH) | Estrogen/ progesterone         |

Circadian Control of Endocrine Functions

SCN and PVN nuclei of hypothalamus regulate circadian release of hormones. Pineal gland is also known to maintain circadian release of melatonin which depends on exposure of the organism to the light. The circadian release of any hormone from the hypothalamic and pineal nuclei is affected by the duration and intensity of the light exposure. The SCN and other hypothalamic nuclei are connected to the retina – screening portal of the light, through bidirectional retinohypothalamic connections. Pineal gland nuclei are also connected to this circuitry through to and fro channels. Control of circadian rhythm through hypothalamic nuclei is a complex biological process which is genetically determined and conserved among species (Tsang et al. 2014; Andreani et al. 2015). The molecular repertoire maintaining circadian rhythms (Table 5) are not present only in the endocrine organs but in many organs and tissues, which together create a complex molecular network system with a central command from SCN (Hughey and Butte 2016).

Cortisol, the HPA axis output hormone, also follows circadian rhythm, with its peak secretion in the morning at 8 AM with lesser serum values along the day, with minimum at 4 PM. A dysregulation of circadian synthesis/release of the hormones is implicated in metabolic syndromes and neuroendocrine disorders including stress-induced psychiatric disorders and sleep disorders (Kleine and Rossmanith 2016, pp. 299–338; Kumar et al. 2018).

**Endocrine System, Table 5** Molecular repertoire of SCN

|                                                                       |
|-----------------------------------------------------------------------|
| Brain and muscle ARNT like protein-1 (Bmal1)                          |
| Clock (or Npas2 in neuronal tissue)                                   |
| Cryptochrome (cry) 1,2                                                |
| Period (per)1,2,3                                                     |
| E-box                                                                 |
| Retinoid-related orphan receptor (Ror) $\alpha$ , $\beta$ , $\lambda$ |
| Rev-Erb $\alpha$ , $\beta$                                            |
| Chrono                                                                |
| Casein kinase 1 (ck1) $\delta$ , $\epsilon$                           |

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Endocrine-Nervous-Immune Cross-Regulation

Endocrine system is an autonomous but not a completely independent physiological unit. It has noted cross regulation with the nervous and immune system – which meant that hormones interact with the neuropeptides/neurotransmitters and immune cell derived cytokines. Evidence suggests that interaction between these systems is bidirectional and a dysregulation of it implicates in etiogenesis of the diseases like metabolic and psychiatric disorders (Kelley 1988).

Effects of Aging on Endocrine System

Most hormone levels decrease with aging. Salient hormones which decrease with aging are GH, IGF-1 and melatonin, and sex hormones like DHEA, estrogen, and progesterone. Decline of the melatonin may play an important role in the loss of circadian rhythms with aging. Sex hormone-binding globulin is reported to increase with age in both sexes. Levels of some hormones may also increase, like LH and FSH, and pancreatic polypeptide and gastrin (but not other gut hormones). For some hormones, their levels remain near normal with aging, these are thyroid (except T3, which is reduced possibly due to decrease conversion from T4). Parathyroid hormone shows an increase that may be due to decreased renal excretion. Adrenal cortical hormones like glucocorticoid and mineralocorticoid show higher serum concentrations with aging though the target organ for mineralocorticoid activity (kidney), however, becomes less responsive. For adrenal medullary hormones like epinephrine and norepinephrine, their baseline serum concentrations increase with aging though stimutable increases in both (as percentages of the basal concentrations) show a decrease. The circadian patterns for the hormones showing diurnal variation like cortisol, norepinephrine, and growth hormone are altered in aged.

In female, fall of the female sex hormones (estrogen and progesterone) is marked by menopause near the age of 45 years with rise of LH and FSH (LH initially may show a fall at commencement of menopause). In males, there is a gradual

fall of testosterone and increase of LH and FSH with aging called andropause. Insulin secretion is impaired and insulin resistance increases with age. Levels of androgens in female and estrogen in male may not show much change with aging (Chahal and Drake 2007).

## Endocrine Disorders

Each endocrine organ has specific disorders which may alter functions of the related physiological systems. Certain of the endocrine diseases/disorders present as the syndrome involving many organs. Endocrine disorders can result from dysfunction originating in the peripheral endocrine gland itself (primary disorders) or under stimulation or overstimulation by the central regulators of an endocrine axis as anterior pituitary, or hypothalamic nuclei (secondary disorders). The disorders can result in hormone overproduction (hyperfunction) or underproduction (hypofunction). Rarely, endocrine disorders (usually hypofunction) occur because of reduced responses from the target site receptors (Longo 2015, chapter 399; Kleine and Rossmanith 2016, pp. 357–376).

Endocrine disorders may also happen from exogenous or self-administration of a hormone, or due to a blockade in the regulatory axis for an endocrine gland (such as HPA axis), or in response of a diseased state (Longo 2015, chapter 399).

Hypofunction of a peripheral endocrine gland can be caused by congenital (like a genetic disorder resulting from deletion of a gene), or acquired disorders (like autoimmune and vascular disorders, tumors, infections, toxins, or hormone receptor hypofunction). Some hormones require conversion to an active form after secretion from the synthesizing gland, which may happen in some other glands, a dysfunction of the organ where activation has to take place, may result in hormonal hypofunction. For example, inactive form of Vitamin D is synthesized in the liver which requires further modification in kidney and skin, respectively, to become active, a disease of kidney or skin may result in hypofunction of vitamin D. Primary hyperfunction of endocrine

glands generally results from hyperplasia or neoplasia of the gland. Other reasons for this can be ectopic production of a hormone from a different tissue as may happen in cancers and autoimmune diseases (as in hyperthyroidism of Graves' disease). Table 6 provides a detailed list of endocrine diseases/disorders with anatomical and functional abnormality for each.

## Commonly Used Investigations

The concentration of hormones in blood or serum in the living animal can be investigated with the immunoassays (radio-, enzyme-, and fluorescence-immunoassay) and more recently high-performance liquid chromatography (HPLC) and mass-spectrometry combined with gas chromatography (MS–GC). The general investigations used for in vitro determination of hormones or their receptors are immunocytochemistry (ICC), autoradiography, in situ hybridization, and blotting. Medical imaging techniques (like PET scan and f-MRI) which reveal organ activation during certain actions or behaviors, paired with endocrine manipulations or monitoring, can provide important information (Fusani 2017). For human cases, taking patient history and clinical examination is the first thing to be done for an endocrine disorder, which would pave the way which tests should be conducted to reach a diagnosis. Hematology and urinalysis provide important information in diagnosing endocrine disorders. Other investigations are available to test the function of specific endocrine glands. Medical imaging like CT and MRI scans, sonography, and scintillation counting are useful for detecting change in the size of endocrine glands and the presence of tumors or cysts. Karyotyping for the chromosomal errors, or genotyping, or sequencing for mutation analysis, and genomewide association study for single nucleotide polymorphisms (SNPs) or copy number variations (CNVs) are also done for the disorders where a genetic basis is speculated (Fusani 2017; Kumar et al. 2018).

## Common Therapeutic Approaches

Control of the hypersecretion (surgical removal, radio or chemosuppression, or using a

**Endocrine System, Table 6** Major endocrine disorders, their causes, clinical features, diagnostic investigations, and management

| Glands              | Disorders                                                              | Pathology/causes                                                                        | Signs and symptoms                                                                                                   | Diagnostic investigations            | Management                                                       |
|---------------------|------------------------------------------------------------------------|-----------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------|--------------------------------------|------------------------------------------------------------------|
| <b>Hypothalamus</b> | Trauma                                                                 |                                                                                         | Symptoms caused by deficiency of pituitary, adrenal or gonadal hormones. Symptoms are also specific to the etiology  | Hormone analysis, neuroimaging       | Hormone replacement                                              |
|                     | Tumors                                                                 |                                                                                         |                                                                                                                      | Hormone analysis, neuroimaging       | Surgical removal of the tumor, radiotherapy, hormone replacement |
|                     | Kallmann syndrome                                                      | Genetic mutation                                                                        |                                                                                                                      | Hormone analysis, Genetic screening  | Gene correction, hormone replacement                             |
|                     | Anorexia Nervosa and Bulimia Nervosa                                   |                                                                                         |                                                                                                                      | Hormone analysis                     | Hormone replacement                                              |
|                     | Prader-Willi syndrome                                                  |                                                                                         | Symptoms caused by deficiency of pituitary, adrenal, or gonadal hormones. Symptoms are also specific to the etiology | Hormone analysis                     | Hormone replacement                                              |
|                     | Inflammatory and vascular diseases, malnutrition, infection, radiation |                                                                                         |                                                                                                                      | Hormone analysis                     | Hormone replacement                                              |
| <b>Pituitary</b>    | Central precocious puberty                                             | Early release of GnRH from hypothalamus may be due to brain injury or a pituitary tumor | Early onset of puberty                                                                                               | GnRH stimulation testing             | GnRH analogue therapy                                            |
|                     | Cushing's disease                                                      | Excessive production of ACTH due to some tumor                                          | Weight gain, high blood pressure, thinning of the skin, easy bruising, etc.                                          | Blood hormone analysis, neuroimaging | Surgical removal of tumor/medication                             |
|                     | Acromegaly                                                             | Excessive production of GH due to some tumor                                            | Abnormally increased height                                                                                          | Blood hormone analysis, neuroimaging | Surgical removal of tumor/medication                             |
|                     | Pituitary growth failure                                               | Due to low secretion of GH                                                              | Decreased height                                                                                                     | Blood hormone analysis, neuroimaging | Surgical removal of tumor/medication                             |
|                     | Hypogonadotropic hypogonadism                                          | Low LH and FSH<br>Leading to low secretion of testicular/ovarian hormones               | Delayed puberty                                                                                                      | Blood hormone analysis, neuroimaging | Surgical removal of tumor/medication                             |
|                     | Pituitary masses                                                       | Excessive production of some hormones, like in prolactinoma                             | Large masses may compress surrounding tissue, erode into bone, or produce excess hormone                             | Blood hormone analysis, neuroimaging | Surgical removal of tumor/medication                             |
|                     | Hypopituitarism                                                        | Surgery, radiation treatments, large pituitary tumors,                                  | Nonspecific, including weakness, fatigue, and                                                                        | Blood hormone analysis, neuroimaging | Surgical removal of tumor/hormone replacement                    |
|                     |                                                                        |                                                                                         |                                                                                                                      |                                      |                                                                  |
|                     |                                                                        |                                                                                         |                                                                                                                      |                                      |                                                                  |
|                     |                                                                        |                                                                                         |                                                                                                                      |                                      |                                                                  |



|                                |                            |                                                                                                                                                                                                                                                                             |                                                                                                                                        |                                                                                         |                                                                                                                    |             |
|--------------------------------|----------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|-------------|
|                                |                            | bleeding or loss of blood supply                                                                                                                                                                                                                                            | dizziness, headache, occasional loss of consciousness                                                                                  |                                                                                         |                                                                                                                    |             |
|                                | Central diabetes insipidus | Damage to the pituitary gland (or hypothalamus) disrupting the normal production, storage and release of ADH<br>Due to surgery, a tumor, an illness (such as meningitis), inflammation or a head injury or an inherited genetic disorder (in children), of an unknown cause | Intense thirst even after drinking fluids (polydipsia), and excretion of large amounts of urine (polyuria), electrolyte imbalance      | Urine and blood tests, water deprivation test.<br>Investigations for underlying causes  | Medication (desmopressin a synthetic ADH analogue), management of water loss, electrolyte imbalance and water loss |             |
| <b>Thyroid and parathyroid</b> | Hyperthyroidism            | Excessive production of thyroid hormones due to autoimmune conditions (Graves disease) or inflammation                                                                                                                                                                      | Restlessness, agitation, anxiety, tremors, weight loss, sweating, rapid heart rate, intolerance to heat, and, frequent bowel movements | Blood hormone analysis, tests for specific antibodies                                   | Medication, radioactive iodine therapy                                                                             |             |
|                                | Hypothyroidism             | Low production of thyroid hormones due to autoimmune conditions or inflammation, surgery, radiation, drug induced                                                                                                                                                           | Tiredness, feeling cold, weight gain, dry skin, constipation, and swelling (edema) of the face or ankles                               | Thyroid hormone analysis, increased blood TSH                                           | Thyroid hormone replacement                                                                                        |             |
|                                | Thyroiditis                | Excess/low production of thyroid hormones due to autoimmune conditions ((Hashimoto's thyroiditis) or infections, hypersensitivity                                                                                                                                           | Sign and symptoms of hyper/hypo thyroidism                                                                                             | Testing for the thyroid peroxidase (TPO) antibody in the blood/thyroid hormone analysis | Depending on the hormonal analysis                                                                                 |             |
|                                | Tumors                     | Benign and cancerous                                                                                                                                                                                                                                                        | Pressure in the neck, hoarseness of the voice, or difficulty in swallowing or breathing, metastatic symptoms                           | FNAC (biopsy), radioisotope scan                                                        | Surgical removal, radioactive iodine therapy                                                                       |             |
|                                | Hyperparathyroidism        | Excess parathyroid hormone (PTH) in the blood, caused by                                                                                                                                                                                                                    | Increased blood calcium levels can cause symptoms of                                                                                   | Blood hormone analysis                                                                  | Calcium monitoring, surgery                                                                                        | (continued) |

**Endocrine System, Table 6** (continued)

| Glands         | Disorders                                                    | Pathology/causes                                                                                                                                                                                                                                                                             | Signs and symptoms                                                                                                                                                                                     | Diagnostic investigations                                 | Management                                 |
|----------------|--------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------|--------------------------------------------|
| <b>Adrenal</b> |                                                              | tumorous growth in parathyroid gland                                                                                                                                                                                                                                                         | tiredness, poor concentration, low mood, bone pain, and stomach or abdominal symptoms                                                                                                                  |                                                           |                                            |
|                | Hypercortisolism                                             | Excess production of adrenal hormone cortisol secondary to Cushing's syndrome or an adrenal tumor                                                                                                                                                                                            | High blood pressure, weight gain, thinning of the skin, easy bruising, poor wound healing                                                                                                              | Blood and/or urine testing                                | Medication, surgical removal of the tumor  |
|                | Hyperaldosteronism                                           | Excess production of adrenal hormone aldosterone due to a tumor or nodular disease                                                                                                                                                                                                           | Low potassium in the blood and high blood pressure resistant to treatment                                                                                                                              | Blood test, <b>adrenal vein sampling</b>                  | Medication, surgical removal of the tumor  |
|                | Adrenal insufficiency                                        | Reduced hormone secretion from the adrenal gland, resulting in deficiency of all adrenal hormones, including cortisol and aldosterone. Reasons may be autoimmune destruction of the adrenal gland (Addison's disease), bleeding into the adrenal glands, or infections, such as tuberculosis | Weakness, weight loss, dizziness, and sometimes abdominal pain, nausea, and vomiting                                                                                                                   | Blood hormone analysis, screening for specific antibodies | Hormone replacement                        |
| <b>Ovary</b>   | Adrenal masses                                               | Mostly benign and rarely cancerous tumors. May produce excess adrenal hormones                                                                                                                                                                                                               | Symptoms of hyperaldosteronism and corticosisolism                                                                                                                                                     | Ultrasound, CT and MRI, histopathology                    | Clinical monitoring, surgery               |
|                | Ovarian insufficiency (sometimes called premature menopause) | Ovaries either do not develop, or are damaged hence no longer function normally                                                                                                                                                                                                              | Symptoms of low estrogen can develop in many, but not all: hot flashes, night sweats, poor sleep, and vaginal dryness. Infertility and the loss of the beneficial effects of estrogen and progesterone | Blood hormone analysis                                    | Hormone replacement                        |
|                | Polycystic ovary syndrome (PCOS)                             | Small cysts in the ovaries, increased amount of                                                                                                                                                                                                                                              | Irregular menstrual periods, loss of fertility, increased hair growth on the face, chest, or                                                                                                           | Blood tests for sex hormone, ultrasound                   | Ovulation induction by medication, surgery |

|                                  |                                                                                       |                                                                                                                                                      |                                                                                                                                              |                                                                                                                             |                                                                                                                                     |
|----------------------------------|---------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------|
| <b>Testis</b>                    |                                                                                       | androgens produced by the ovaries                                                                                                                    | abdomen, acne, and a tendency toward weight gain and insulin resistance (diabetes)                                                           |                                                                                                                             |                                                                                                                                     |
|                                  | Low testosterone levels in men                                                        | Due to testicular trauma, radiation or chemotherapy for certain types of cancer, infection or loss of blood supply to the testes                     | Reduced energy, mood, strength, and libido                                                                                                   | Blood hormone/clinical radiological evaluation                                                                              | Testosterone replacement                                                                                                            |
|                                  | Primary testicular hypogonadism                                                       | Genetic causes                                                                                                                                       | Reduced energy, mood, strength and libido, infertility                                                                                       | Blood hormone analysis/genetic screening                                                                                    | Testosterone replacement                                                                                                            |
|                                  | Androgen insensitivity syndromes                                                      | Genetic causes                                                                                                                                       | Female phenotypic features with male genetic makeup, infertile                                                                               | Blood hormone analysis/genetic screening                                                                                    | Management for functional, sexual, and psychological issues                                                                         |
| <b>Pancreas (islet cells)</b>    | Diabetes mellitus                                                                     | Dysfunction of insulin production/secretion (type 1), or the target cells' responsiveness to insulin (type 2)<br>Gestational diabetes mellitus (GDM) | Insulin resistance is related to the metabolic changes of late pregnancy, and the increased insulin requirements may lead to IGT or diabetes | Blood test for glucose level, HbA <sub>1c</sub> , insulin                                                                   | For type 1 diabetes, synthetic insulin must be administered by injection or infusion.<br>For type 2, life style changes and insulin |
|                                  | Neuroendocrine tumors like insulinoma, gastrinoma, glucagonoma, carcinoid tumor, etc. |                                                                                                                                                      | Sign and symptoms depend on the hormone involved                                                                                             | Serum hormone and analysis<br>Genetic screening, CT, MRI                                                                    | Hormone replacement, surgery, medication                                                                                            |
| <b>Multiple endocrine organs</b> | Multiple endocrine neoplasia I and II (MEN I and MEN II)                              |                                                                                                                                                      | Primary hyperparathyroidism, hypercalcemia, hypophosphatemia, increased secretion of epinephrine/norepinephrine                              | Serum calcium and PTH, adrenal hormone estimation (elevated levels of serum calcium and intact parathyroid hormone) CT, MRI | Genetic screening for mutations, surgery/medication                                                                                 |
|                                  | Polyglandular autoimmune (Pga) syndromes                                              | Mutations, inherited disorder                                                                                                                        | Sign and symptoms depend on the hormone involved                                                                                             | Serum hormone analysis<br>Genetic screening                                                                                 | Hormone replacement                                                                                                                 |

pharmacological agent as the antagonist) and replacement or correction of the deficiency (by pharmacological or dietary means, or treating the causes) are the main stream approaches for treating the endocrine disorders (Longo 2015, chapter 399–409). Recently, gene-based therapeutic approaches have shown promises for this where a genetic basis is known. Known gene-based approaches are either correction of the faulty genes through genomic editing or gene supplementation or using antisense oligonucleotides against the targeted genes. Gene therapy is considered more suitable for correcting the monogenic endocrine disorders like GH deficiency or familial hypercholesterolemia, though newer advances in gene-based therapy have also raised hope for the multifactorial diseases like diabetes mellitus or endocrine cancers, and obesity (Barzon et al. 2000). In case of autoimmune endocrine disorders, targeting the genes coding for the culprit immune molecules has been a successful approach. Suicide gene therapy (using a tumor and/or tissue specific gene which converts a pro-drug into a toxic substance which would kill the tumor cell) has been successfully used to treat endocrine tumors (Barzon et al. 2000).

## Cross-References

- Circadian Rhythms
- Estrogen
- Hormones and Behavior
- Hypothalamus
- Stress
- Testosterone
- Thyroid and Adrenal Glands

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## Endogenous Attention

### ► Top-Down Processing

## Endogenous Oscillations

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### Definition

Endogenous oscillations are rhythmic intrinsic physiological processes by which biological systems establish time.

### Introduction

Endogenous oscillations refer to the naturally occurring mechanism by which biological systems mediate a wide array of rhythmic physiological and behavioral changes in organisms. In mammals, these highly conserved rhythms/cycles assume an approximate 24-h period, in the absence of external cues (i.e., zeitgebers), such as light.

Because the intrinsic biological clock maintains its periodicity in the absence of external cues, it is said to “free run.” Though the internal biological clock can keep time on its own, it tends to synchronize or “entrain” to environmental stimuli, primarily light, hence roughly the period of one solar day. Entrainment of the biological clock to light (as well as subsequent physiological responses) is mediated by the suprachiasmatic nucleus (SCN) of the hypothalamus (Partch et al. 2014). The coordinated actions of both the suprachiasmatic nucleus and the endogenous oscillators are collectively known as the “biological clock.”

## Molecular Mechanism

The SCN is considered the “master pacemaker” of the biological clock, due to its ability to synchronize the clock to the environment. However, the concept of timekeeping is fundamental to all cells. On a transcriptional level, this is achieved through the rhythmic/oscillating expression of clock genes.

At the center of the molecular mechanism underlying this biological clock is an auto-regulatory transcription-translation feedback loop (TTFL) whose cycle duration reflects the rhythmic/oscillatory expression of clock genes over the course of a day. The rhythmic fluctuations in abundance of resulting protein products determine their participation in either the positive arm or the negative arm of the loop, where they can facilitate or inhibit their own expression, respectively.

Though first discovered in the fruit fly, *Drosophila melanogaster*, the TTFL model for circadian rhythm is highly conserved across species and cell types. In mammals, the TTFL is composed of circadian oscillator proteins, which exist as homologues of *Drosophila* counterparts: the TTFL is initiated upon the formation of a transcriptional activation complex, Bmal1/CLOCK, consisting of brain and muscle Arnt-like 1 (Bmal1) and circadian locomotor output cycles kaput (CLOCK), which drives transcription of the core clock genes *periods* (*mPer1*, *mPer2*, *mPer3*) and *cryptochromes* (*mCry1*, *mCry2*). As Per and Cry proteins accumulate, they heterodimerize to form a Per/Cry complex, which in turn feed back to repress Bmal1/CLOCK, and turn off transcription of *mPer* and *mCry* (Partch et al. 2014). Degradation of residual Per and Cry proteins then permits the recommencement of the loop. In this way, Per and Cry are considered to be negative regulators of the TTFL, which maintain the circadian periodicity of the clock and operate in a light-independent fashion. The delay/lag in gene transcription, protein translation, accumulation, modification, and dynamics account for the cyclical nature of the expression of clock genes throughout the day.

## Effect on Behavior

Precise regulation of the transcriptional and post-transcriptional mechanisms driving core clock component dynamics is essential for temporal homeostatic control. Not surprisingly, dysregulation of the TTFL and/or mutations in core clock components is associated with disruptions in sleep-wake cycle (i.e., alterations in free-running period and phase of the clock) and genetic sleep conditions.

Polymorphisms in human *Cry1* are associated with delayed sleep phase disorder (DSPD), a common variant of insomnia characterized by late sleep onset (Patke et al. 2017). In the absence of the primary entrainment cue, light, *Cry* mutant mice demonstrate altered circadian rhythms and aberrant daily activity patterns. *Cry1* and *Cry2* mutants possess shortened and increased period lengths, respectively, and result in early or delayed daily activity onset, while *Cry* knockout mice display activity patterns that are entirely arrhythmic. This suggests an antagonistic role of *Cry1* and *Cry2* in modulation of the period and alignment of the internal clock and demonstrates the necessity of *Cry* proteins for setting the endogenous/internal clock (van der Horst et al. 1999).

Disruptions in the rhythmic posttranslational modification of *Per* proteins are linked to familial advanced sleep phase syndrome (FASPS), a sleep disorder characterized by early sleep onset and early awakening (i.e., morning insomnia; see Vanselow et al. 2006).

## Conclusion

Endogenous biological rhythms represent ubiquitous and robust timekeeping systems common to nearly all organisms. Biological rhythms are generated and maintained by the temporal dynamics of molecular components of a highly conserved autoregulatory transcription-translation feedback loop (TTFL). The duration of the cycle is reflected in peripheral tissues by the time-delayed light-independent/endogenous oscillations in TTFL clock gene expression,

which can be aligned to exogenous inputs by the suprachiasmatic nucleus of the hypothalamus. The resulting phasic expression drives time-dependent physiological and behavioral processes at the organismal level. Dysregulation of this loop results in impaired sleep-wake function and poor temporal homeostatic control, thereby causing negative physiological and psychological outcomes.

## Cross-References

- Biological Clocks
- Circadian Rhythms
- Knockout Genes
- Protein
- Sleep
- Transcription

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## Endogenous Retroviruses

- Repeat Sequences



## Endoparasite

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### Definition

Endoparasite is a type of organism that harbors inside the host organism and is dependent on host organisms for their continuous source of nutrients and survival.

### Introduction

Parasitism is a type of symbiotic relationship between two same or different species where among them, one organism is known as parasite (which gets the benefit of relationship), while the other one which bears the loss in relationship is known as host (Cox, 2002). Parasites are generally host-specific and need specialized structures to invade the host. The host for parasite can be definitive or intermediate. The host which allows the parasite to attain maturity and multiply is known as definitive or primary host. However, some hosts that allow the parasite to reside for short transition period only to complete some developmental stages but not to reproduce are known as intermediate or secondary host. For instance, both malarial parasite of genus *Plasmodium* and sleeping sickness parasite of genus *Trypanosoma* have infective stages in the intermediate host cell that is further transferred to definitive host by insects' bites (Politt et al., 2011).

## Endoparasite

Parasites are classified as endoparasite and ectoparasite. The parasite residing inside the host body is termed as endoparasite, while ectoparasite is those residing outside, i.e., on the surface of the host body. Hookworms, tapeworms, and liver flukes are some endoparasites, whereas ticks,

fleas, and mites come under ectoparasites. Endoparasites are further differentiated as intercellular (inhabits spaces inside the host's body) or intracellular endoparasite (inhabits cells in host's body).

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## Endophenotype

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### Synonyms

Intermediate phenotype

### Definition

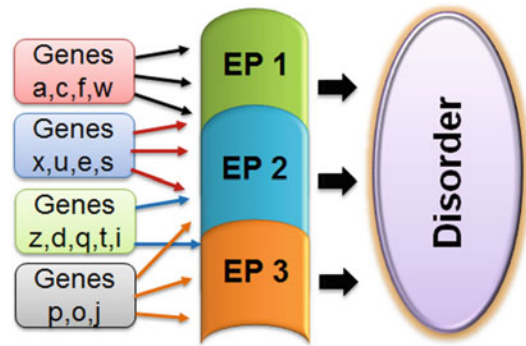
Literally, “endo” means internal or inside, and “phenotype” means immediately observable signs and symptoms. Thus, an endophenotype is a quantitative biological trait that is reliable and reasonably heritable, i.e., shows greater prevalence in unaffected relatives of patients than in the general population, but not easily observed on the surface.

### General Features of Endophenotype

Gottesman and Gould (2003) have outlined certain features of endophenotype as listed below:

1. The endophenotype is a quantitative biological trait that is heritable and associated with illness in the population.
2. Endophenotype and illness (appearance of a disorder) co-segregate within families.
3. The endophenotype is primarily state independent (always appears in an individual irrespective of the status of symptoms).
4. The endophenotype shows greater prevalence in unaffected relatives of patients than in the general population. It varies continuously in the general population.
5. Endophenotypes are associated with causes rather than effects of disorders.
6. Numerous endophenotypes can affect a given complex disorder.
7. Endophenotypes affecting multiple disorders could be found in genetically related disorders.
8. Endophenotypes should optimally be measured across several levels (genetic and or behavioral) of analysis.

In contrast to a monogenic or Mendelian disorder, a complex disorder results from a polygenic matrix whose individual components contribute only a small portion of the total risk. Researchers have found endophenotypes for many psychiatric disorders, including anorexia, autism, obsessive-compulsive disorder, and attention deficit disorder. But the most promising candidates of endophenotypes so far have come from the study of schizophrenia. A complex disorder like schizophrenia (a neurodevelopmental disorder that affects thinking, feeling, and behavior of a person) is the sum of many candidate intermediate phenotypes which used to be functionally associated with variant alleles and core clinical manifestation of the disorder quantitatively (Preston and Weinberger 2005) (Fig. 1). Some examples of such candidates are like P50 suppression, prepulse inhibition, antisaccade, mismatch negativity (MMN), and P300 event-related potential (Braff and Freedman 2002). In schizophrenia, the candidate endophenotypes are more likely to be modeled by a less complex genetic architecture than the disorder as a whole, i.e., the intermediate phenotypes have a less complex relationship to susceptibility genes (or variant alleles) than the



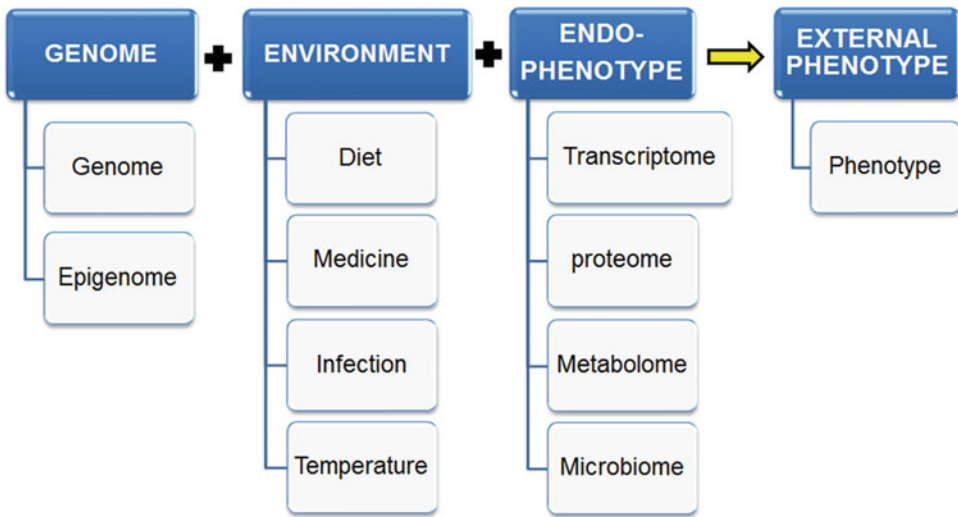
**Endophenotype, Fig. 1** Schematic diagram showing the relationship between genes, endophenotypes (EPs), and disorder

diagnostic phenotype based on statistical significance.

Importantly, the precise means by which a concentration of intermediate phenotypes might explain the clinical presentation of schizophrenia is yet to be determined. Hence, it is also conceivable that schizophrenia is more than a simple sum of distinct traits. In this view, phenotypic expression of the disorder requires the complex interaction of genetic and epigenetic matrices and, to some extent, the influence of environmental factors, acting perhaps through a final common pathway (Egan and Goldberg 2003) (Fig. 2).

## Endophenotypes of Some Common Medical Disorder

The endophenotype of some common medical disorders such as coronary heart disease (Cipollone et al. 2004), hypertension (Schwartz et al. 2004), depression (Goldstein et al. 2014), colon cancer, hereditary hemochromatosis (HH) (Pietrangelo 2004), and type 2 diabetes mellitus (Carlsson et al. 2005) has been studied. These are similar to psychiatric disorders as they arise from a polygenic matrix, each of which shows a relatively small contribution to the total risk. In the case of diabetes, insulin receptor resistance is an endophenotype because it has been viewed as an intermediate between several susceptibility genes and clinical diabetes. For



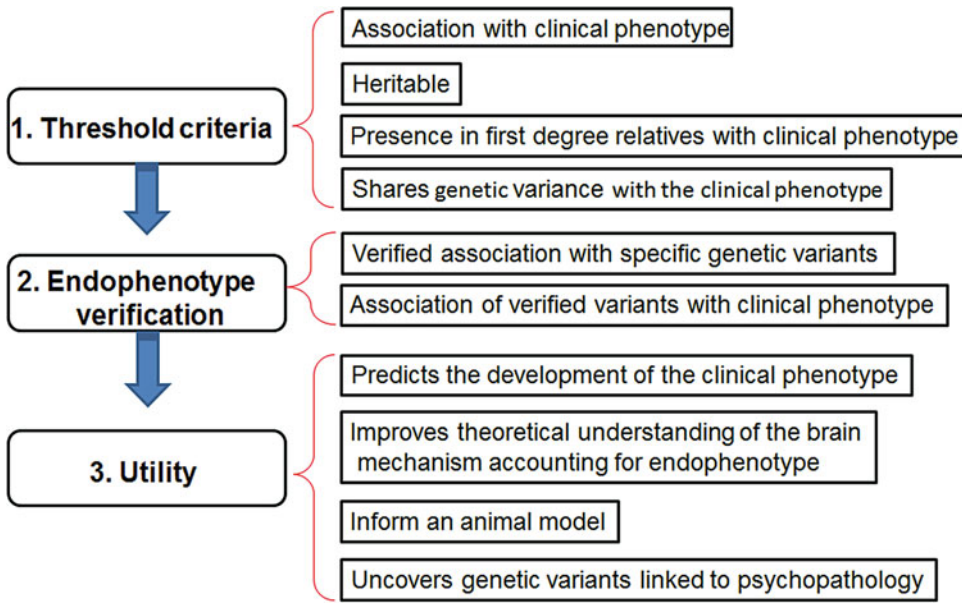
**Endophenotype, Fig. 2** Genome and environmental factors affect the endophenotype of an individual, and finally by acting through common pathway, they regulate the external phenotype, i.e., phenotypic expression of the disorder

depression, neuroticism, frontal asymmetry of cortical electrical activity, morning cortisol, reward learning, and biases of attention and memory have been found as endophenotypes. Similarly, colon polyps are intermediate phenotypes related to colon cancer. In hereditary hemochromatosis (HH), a clinical disorder of iron metabolism, studies of genetic susceptibility are good examples of the intermediate phenotype and the “gene of susceptibility” concepts. A quantitative measure of serum transferrin saturation was first to identify endophenotype in HH (Pietrangelo 2004), which led to the recognition of high prevalence of a mutation carrier hemochromatosis gene (*HFE*). The *HFE* codes a membrane protein that associates with  $\beta$ 2-microglobulin and regulates iron absorption by regulating the interaction of the transferrin receptor with transferrin. Thus, *HFE* gene is recognized as a gene of susceptibility in HH.

Since a long time, psychiatric research has interested in developing reliable biomarkers with clinically significant biological features which are associated with psychopathology. A valid biomarker could help to improve diagnosis, prognosis, and treatment as well as provide clues to the nature of underlying pathophysiology (Iacono 1985). There are many biomarkers like

neurochemical metabolites or measures of inflammatory response that have been reported for the vast majority of disorders. But, there is a lack of consensus regarding which molecule will act as the best marker target. So, identifying a valid biomarker from a vast array of putative biochemical markers is still an intimidating task. Endophenotypes have been recognized as biomarkers. To be addressed as a good biomarker for psychiatric research, an endophenotype construct should be validated by certain criteria which are grouped into three domains (Iacono et al. 2017) (Fig. 3).

1. **Threshold criteria** depict the minimum requirements for any biomarker to stand as a putative endophenotype.
2. **Endophenotype verification** identifies the requirements necessary to remove the qualifier “putative” or “candidate” from an endophenotype’s status. Compared to the first domain, there is far less endophenotype research targeting verification.
3. **Utility** shows the usefulness of an endophenotype, i.e., how a verified endophenotype can be used as a research tool to study the biological etiology of psychiatric disorder as well as identification of molecular genetic variants associated with psychopathology.



**Endophenotype, Fig. 3** Endophenotype construct validation. Steps and components involve in construct validation of an endophenotype

## Conclusions

According to the central dogma, the fundamental unit of genetic transmission is an abnormality in the structure or function of a protein. Such abnormalities in protein affect neuronal function which reflects changes in physiological functions, i.e., endophenotypes. The analysis of alone or combined contribution of different genetic abnormalities to neuronal pathophysiology of a psychiatric disorder may help in the study of psychotic illnesses in depth and point the way to new treatment approaches. The endophenotypes are measurable and heritable biological traits that are related to complex psychiatric disorders such as schizophrenia and reflective of genetically based disease mechanisms. The identification and study of endophenotype help to uncover genetically mediated risk/vulnerability factors that often interact with nongenetic factors to produce psychiatric disorder like schizophrenia. Thus, endophenotype-based strategies can play an important and informative role in diagnosis and treatment of the complex psychiatric.

## Cross-References

- ▶ [Alleles](#)
- ▶ [Attention](#)
- ▶ [Candidate Gene](#)
- ▶ [Carrier](#)
- ▶ [Epigenesis](#)
- ▶ [Genes](#)
- ▶ [Genetic Variation](#)
- ▶ [Heredity](#)
- ▶ [Learning](#)
- ▶ [Memory](#)
- ▶ [Mutations](#)
- ▶ [Phenotype](#)
- ▶ [Polygeny](#)
- ▶ [Population](#)
- ▶ [Protein](#)
- ▶ [Status](#)

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## Endoskeleton

### ► Skeletal System

## Endotherms

### ► Hibernation

## Energy

### ► Drive State

## Enlightenment

### ► Learning

## Entopallium

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## Synonyms

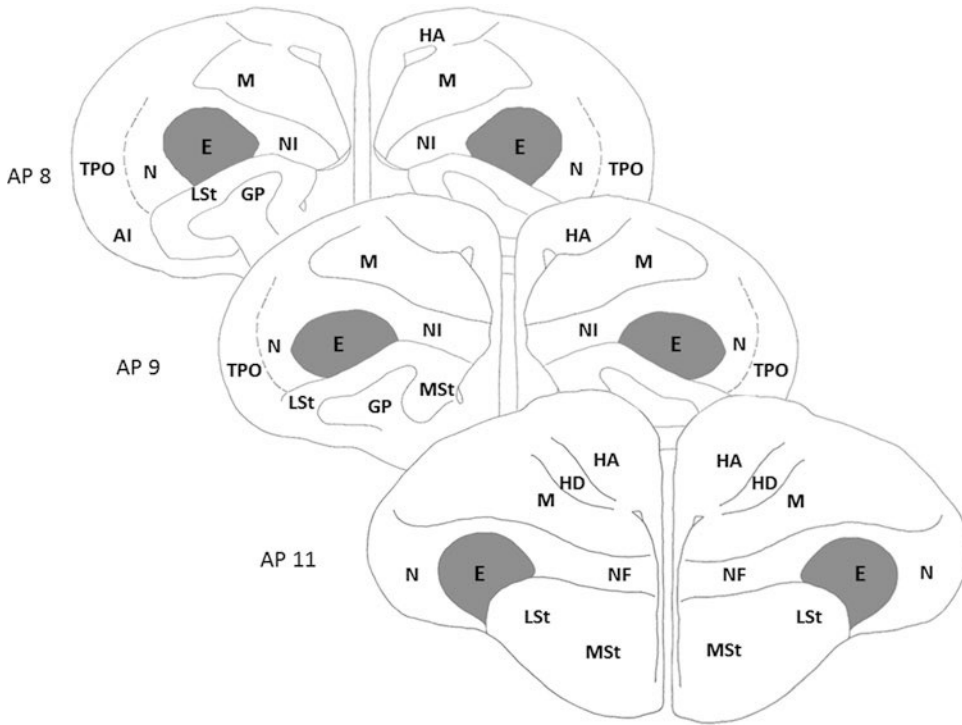
Avian; Discrimination learning; Ectostriatum; Memory; Vision

## Introduction

The dorsal ventricular ridge (DVR) is the main body of mass that forms the avian telencephalon. The DVR contains the major pallial regions of the avian brain, including the nidopallium (N), mesopallium (M), arcopallium (A) and, nested among these areas, the entopallium (E). Based on its afferent and efferent projections, the effects of lesions to the area, and single-unit electrophysiological data, the E is a higher-order visual and motion processing structure and is considered analogous to some region of the primate extrastriate cortex.

## Anatomy of Entopallium

In most avian species, the E is a large curved structure located deep within the DVR, surrounded by the N in all but the ventral position (Fig. 1). Depending on the posterior (AP8) to anterior (AP11) position, dorsal to the E is the M, hyperpallium densocellulare (HD), and hyperpallium apicale (HA). Ventral to the E is lateral striatum (LSt), globus pallidus (GP), and medial striatum (MSt) (Reiner et al. 2004). The E is a component of one of the two main pathways



**Entopallium, Fig. 1** Cross section through the pigeon brain demonstrating the location of the E (shaded gray). The following are the brain regions as defined by Reiner et al. (2004). *AI* arcopallium intermedium, *E* entopallium, *GP* globus pallidus, *HA* hyperpallium apicale, *HD*

hyperpallium densocellulare, *LSt* lateral striatum, *M* mesopallium, *MSt* medial striatum, *N* nidopallium, *NF* nidopallium frontale, *NI* nidopallium intermedium, *TPO* temporo-parieto-occipitalis

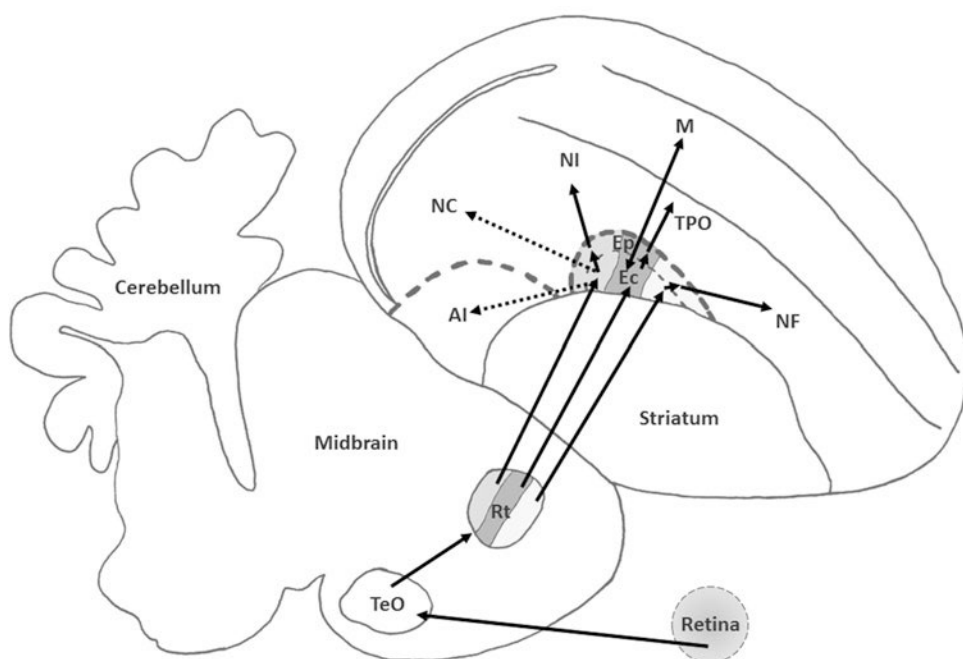
that transmit information to the telencephalon in the avian brain. The thalamofugal pathway projects from the retina to the nucleus opticus principalis thalami (OPT) and then to a region of the dorsal telencephalon known as the visual Wulst (HA and HD). The tectofugal pathway, on the other hand, projects from the retina to the optic tectum (TeO) and then bilaterally to the nucleus rotundus (Rt) and finally ipsilaterally to the E (Fig. 2; Krützfeldt and Wild 2005). The consensus from studies examining the projections from Rt to the E is that the projections are organized topographically along the anterior–posterior axis, such that neurons in the anterior Rt project to anterior E, while neurons in the posterior Rt project to posterior E.

The E can be divided into two main subregions, the core (Ec) and the peripheral belt (Ep), with Ep surrounding Ec (Karten and Hodos 1970). In the zebra finch, the outer boundary of E is

clearly defined; however, in the pigeon, the boundary appears intermittent. The cells in the two subregions can be differentiated on the basis of a number of characteristics, as well as their projection patterns. With respect to cell characteristics, Ec is populated mainly with medium-sized round cells with thick myelinated axons that are generally parvalbumin (PV) positive. In contrast, Ep neurons are characterized by smaller and longer cells with thin myelinated axons, very few of which are PV positive, the exception being the zebra finch, which has a greater number of PV-positive cells in area Ep.

With respect to afferent and efferent projections, the major projections from Ec are primarily directed to Ep and then onto Ep2 (Fig. 2), an ill-defined area immediately surrounding the Ep and that some consider similar to Ep (Krützfeldt and Wild 2005). For the current entry, Ep2 is considered to be coextensive with Ep. Much like the





E

**Entopallium, Fig. 2** The afferent and efferent projection patterns of the E. The E is part of the tectofugal pathway. Information flows from the retina to TeO and then to the Rt and from there in a topographical fashion to Ec. From Ec, information projects to Ep and then the rest of the avian pallium. Arrows in solid line represent major projection patterns, while dashed arrows represent minor projection patterns, with all arrow points indicating the direction of

the projection. Regions shaded in Rt and E represent the anterior, intermediate, and posterior divisions of each area. The following are the brain regions as defined by Reiner et al. (2004). AI arcopallium intermedium, Ec entopallium core, Ep entopallium peripheral belt, M mesopallium, NC nidopallium caudale, NF nidopallium frontale, NI nidopallium intermedium, Rt nucleus rotundus, TeO optic tectum

projections to the E from Rt, the projections from Ec to Ep, and from Ep to other pallial regions of the avian brain are also arranged in a topographical manner along the anterior–posterior axis, such that projections from the anterior portion of Ep are sent to nidopallium frontale (NF), projections from the intermediate regions of Ep to temporo-parieto-occipitalis (TPO), and projections from posterior regions of Ep to nidopallium intermedium (NI). Along with the major projections from Ep, there are minor projections from the posterior regions of Ec to arcopallium intermedium (AI) and nidopallium caudale (NC).

Although the majority of projections to the pallial regions of the avian brain originate from Ep, there are minor projections from Ec to the NF, TPO, and NI as well (Krützfeldt and Wild 2005). In the zebra finch and chickens, Ec also projects to the lateral striatum (LSt), and Ec may also have

reciprocal projections with the M in both the zebra finch and pigeon (Krützfeldt and Wild 2005).

## Functions of Entopallium: Lesion Studies

Hodos and his many colleagues extensively explored the functions of the E in a series of psychophysical discrimination studies conducted throughout the 1970s and 1980s (see Hodos et al. 1988 and references therein). Damage to the E causes a variety of visual impairments. In one study, birds were trained to discriminate between a blank uniform stimulus and stimuli with different spatial frequency gratings. After E lesions, the birds showed impairments in visual acuity, that is, elevated thresholds for detecting gratings. E lesions also cause elevated luminous intensity thresholds. Similarly, E lesions, especially medial

E lesions, cause elevated thresholds for detecting differences in the size of an annulus, a measure of low spatial frequency. Hodos and colleagues suggested that the medial E processes information about the low-spatial-frequency structure of stimuli, whereas the lateral E processes information about the high-spatial-frequency structure of stimuli.

Damage to the E also causes impairments beyond elevated psychophysical thresholds, such as in the processing of complex visual information. For example, Bessette and Hodos (1989) reported that pigeons with E damage show marked deficits in the ability to discriminate between different patterns (e.g., vertical vs. horizontal line or triangle with apex at top vs. triangle with apex at bottom) and intensities (two squares that differed in luminance) but not colors (green vs. yellow). Additionally, others have reported that E lesions cause impairments in the ability to discriminate between a number of different mirror-image and non-mirror-image stimuli that were matched on the basis of luminance. The most striking impairments after E lesions are in the ability to discriminate lateral mirror images, and this does not seem to be a function of difficulty, as the lateral-mirror-image discrimination was acquired preoperatively at the same rate as the other mirror-image and non-mirror-image discriminations.

Watanabe (1996 and references therein) conducted a series of studies in the 1990s examining the role of the E in the processing of ecologically relevant and ecologically irrelevant stimuli. Lesions of the E does not impair the ability to discriminate food items (corn, peas, buckwheat, and wheat) from nonfood items (stones, twigs, nuts, and yellow paper clips) but does impair the ability to discriminate these stimuli when they were randomly arranged into two groups (e.g., corn, peas, stones, and twigs vs. buckwheat, wheat, nuts, and yellow paper clips), a finding that likely reflects the fact that the randomly arranged discrimination is harder than the food versus nonfood discrimination. Similarly, E lesions impair the ability to discriminate between many exemplars of a triangle versus many exemplars of a line, but have little effect

on the ability to discriminate between one triangle and one line.

E lesions also cause an impairment in the ability to discriminate one pigeon from another pigeon, but do not impair the ability to discriminate one pigeon from another bird such as a quail. Although such a finding might reflect the fact that the E is important for discriminating members of one's own species from another, again it could also reflect task difficulty, with the pigeon versus pigeon discrimination more difficult and hence more sensitive to E lesions than the pigeon versus quail discrimination. Indeed, the effect of task difficulty was confirmed when in a follow-up study, Watanabe (1996) showed that E lesions also cause impairments in the ability to discriminate between a sparrow and a starling, but not between pigeons and other birds. Also related to task difficulty is the finding that E lesions do not impair the acquisition of color discrimination (yellow vs. green) but does impair subsequent reversals of the color discrimination.

In some of the aforementioned lesion studies, the impairments are correlated with the extent of damage to Ec, whereas in other studies what seems important is the total extent of the lesion to the E. As of yet, no firm functional differentiation has been uncovered for the core versus the belt regions. Some, however, report functional differences within different regions of the E as a whole. The earlier reported study by Hodos and colleagues, for example, proposed functional differences between the medial and lateral E with respect to the processing of low- and high-spatial frequency information. Nguyen et al. (2004) also report functional differentiation within the E. Birds were trained on a psychophysical procedure to perform either a pattern discrimination or motion discrimination, both with varying degrees of background noise superimposed upon the images. The authors uncovered a double dissociation, with birds with rostral E lesions impaired on the pattern discrimination and not the motion discrimination, whereas birds with caudal E lesions impaired on the motion discrimination and not the pattern discrimination. The findings of both pattern and motion impairments following lesions to the E suggest that it may serve functions similar to

the primate's extrastriate cortex, which houses areas responsible for both pattern perception (e.g., inferior temporal cortex) and motion perception (e.g., area MT).

### Functions of Entopallium: Electrophysiological Studies

Early studies reported that cells in the E display characteristics similar to those reported in extrastriate visual cortex of primates (see Colombo et al. 2001 and references therein). For example, compared to the receptive fields of neurons in visual Wulst and primate striate cortex, the receptive fields of neurons in the E and primate extrastriate cortex are generally large. Similarly, the receptive fields of cells in visual Wulst and striate cortex are retinotopically mapped, whereas those in the E and extrastriate cortex show little retinotopic mapping.

Beyond the small number of studies characterizing the basic properties of E neurons, however, few electrophysiological studies have been conducted. Those that have been conducted further add to the view that the E represents a higher-order visual processing region in the avian brain similar to the primate extrastriate cortex. Using a variety of differently shaped and colored stimuli that included pictures of pigeons, Scarf et al. (2016) reported that over 90% of E neurons are visually responsive and 20% show selective activity for one or more of the tested stimuli, numbers higher than any of the other three areas examined (nidopallium, arcopallium, and hippocampus) and numbers that are not only in line with extrastriate regions of the primate brain but are representative of what one might expect from a higher-order visual area. Some neurons in the E are also selective for the size, speed, or direction of stimulus movement, a trend thought to be associated with the large receptive fields found in the E. The findings of neurons responsive to shape and motion further add to the view that the E serves a similar function to the primate extrastriate cortex.

The E is also involved in memory for visual information. According to Johnston et al. (2017 and references therein), 70–85% of E neurons

display activity during the delay period of a delayed matching-to-sample task when the animals are required to remember visual information. Additionally, E neurons are more likely to display delay activity when the pigeons are completing the task at high (>75% correct) compared to low (<75% correct) performance levels. Johnston et al. (2017) also report that delay activity remained stable throughout the delay period. The finding of delay neurons, that encountering delay neurons is more likely when the animal is performing well as opposed to poorly, and the fact that delay activity remains stable throughout the delay period parallel the characteristics of memory cells found in the primate extrastriate cortex.

### Conclusion

The E is the pallial termination point of the tectofugal pathway. From the E, information is distributed throughout the rest of the avian brain. The E is primarily a visual structure and damage leads to impairments in visual acuity, brightness discrimination, size discrimination, as well as the ability to discriminate different shapes and naturalistic objects. Damage to the E also causes impairments in motion perception. There is little evidence at present to support a functional difference between the core and belt regions, although there is some evidence for functional differentiation along the medial and lateral extent of the E, and in particular between the rostral and caudal extent of the E, with the rostral area being more involved in pattern discrimination and the caudal area more involved in motion discrimination. The E may also play a role in visual memory and cognition. On the basis of projection patterns, the effects of lesions, and findings from electrophysiological studies, the E has functions similar to regions of the primate extrastriate cortex.

### Cross-References

- [Afferent and Efferent Impulses](#)
- [Cognition](#)

- ▶ [Comparative Cognition](#)
- ▶ [Declarative Memory](#)
- ▶ [Delay Neurons: Comparative Overview](#)
- ▶ [Delayed Match-to-Sample](#)
- ▶ [Discrimination Learning](#)
- ▶ [Episodic Memory](#)
- ▶ [Instrumental Learning](#)
- ▶ [Learning](#)
- ▶ [Matching-to-Sample](#)
- ▶ [Memory](#)
- ▶ [Neural Impulse](#)
- ▶ [Neuron](#)
- ▶ [Operant Chamber](#)
- ▶ [Pattern Learning](#)
- ▶ [Pigeon \(\*Columbidae\*\)](#)
- ▶ [Reinforcement](#)
- ▶ [Reversal Learning](#)
- ▶ [Skinner Box](#)
- ▶ [Vision](#)
- ▶ [Visual Recognition in Birds](#)
- ▶ [Working Memory](#)

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## Entorhinal Cortex

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## Synonyms

[Brodman area 28](#)

## Definition

The entorhinal cortex (EC), a brain region critical to memory processes, consists of six cortical layers located in the medial temporal lobe. Most contemporary subdivisions of the EC include a lateral and medial subfield, consistent with (1) the distribution of input fibers that this structure receives from the perirhinal and postrhinal/parahippocampal cortices (2) the distribution of its output projections onto the hippocampal formation (HF) and more recently

(3) functional differences observed in lesion and electrophysiological studies.

## Current Knowledge

### Brief Overview

The entorhinal cortex (EC), a brain region critical to memory processes, consists of six cortical layers located in the medial temporal lobe. After a series of preliminary naming conventions used in early histological reports, nomenclature shifted to emphasize the position of this structure with respect to the rhinal sulcus (Insausti et al. 1987; Witter et al. 1989). Over the course of a century of anatomical descriptions of the EC, as many as 23 subfields have been identified, depending on the criteria used to subdivide this structure (Insausti et al. 1987). Most contemporary parcellations have converged on defining lateral and medial subfields, consistent with (1) the distribution of input fibers that the EC receives from the perirhinal and postrhinal/parahippocampal cortices (Burwell and Amaral 1998), (2) the distribution of its output projections onto the hippocampal formation (HF) (Witter et al. 1989; Insausti et al. 1987), and more recently (3) functional differences observed in lesion and electrophysiological studies (reviewed in Knierim et al. 2014). Although the precise role of the EC in cognition remains obscure, results from clinical, histological, electrophysiological, and lesion studies point to its unique contributions within the system of brain regions subserving episodic memory in general, and spatial navigation in particular (Moser et al. 2008; Knierim et al. 2014).

### Structure

**Gross Anatomy.** The entorhinal cortex (EC) receives a diverse array of cortical and subcortical inputs and is bidirectionally connected with the hippocampal formation (HF) (Burwell and Amaral 1998; Insausti et al. 1987). Defining the anatomical boundaries of the EC poses a challenge due to the heterogeneity in cell type and organization, as well as the dense connectivity of the EC with adjacent regions. In order to mark the

boundaries of structurally and functionally distinct subregions, contemporary parcellations have taken into account both cytoarchitectonic appearance and distribution of input and output fibers across the rostrocaudal and mediolateral extents of the EC (Witter et al. 1989; Insausti et al. 1987).

**Inputs.** Although exact anatomical configurations differ across model species, structurally analogous connectivity patterns have been identified across rodents, bats, nonhuman primates, and humans. To date, some of the most extensively characterized connections arise from the rodent perirhinal and postrhinal cortices (perirhinal and parahippocampal cortices, in primates) (Canto et al. 2008; Burwell and Amaral 1998). In the rodent, perirhinal and postrhinal inputs largely terminate onto the superficial layers of the EC. While perirhinal projections preferentially target the lateral entorhinal area (LEA) of the EC, postrhinal projections primarily innervate the medial entorhinal area (MEA). Although the primate EC has been subdivided into approximately five areas, a homologous gradient of preferential targeting exists as perirhinal inputs predominantly innervate rostrolateral regions, while parahippocampal projections primarily impinge on caudomedial areas (Insausti et al. 1987). Several subcortical regions, such as the amygdala, the basal forebrain, and the claustrum, have also been found to reciprocally connect to various portions of the EC (Canto et al. 2008; Witter et al. 1989).

**Outputs.** The main output of the EC consists of the “perforant path.” Originally described by Ramón y Cajal, this dense bundle of fibers arises from the cells in the superficial layers of the EC and “perforates” through the subiculum to innervate each of the major subfields of the hippocampal formation (Canto et al. 2008). The distribution of perforant path terminals depends on the origin of the fibers in the EC. For instance, LEA projections preferentially impinge on the outer third of the molecular layer of the dentate gyrus, while projections from the MEA primarily innervate the middle third. Early anatomists used this topographic distribution of perforant path terminals onto the dentate gyrus as a main criterion to

mark a distinction between the lateral and medial subfields of the EC (Witter et al. 1989).

## Theories of Function

**Histological, clinical, and lesion studies.** Early functional hypotheses of the EC were prompted by reports of neural degeneration of this structure in patients diagnosed with Alzheimer's disease (AD), a neural pathology characterized by increasingly severe memory deficits. Braak and Braak (1991) examined the extent of accumulation of neurotoxic protein aggregates in the brains of patients with AD. Results revealed that neurofibrillary tangle deposits follow a characteristic spatiotemporal spread that corresponds to disease progression. Specifically, toxic deposits were consistently found in transition zones between the EC and the neocortex during early stages of the disease. Brains of patients with intermediate disease pathology exhibited dense neurotoxicity throughout the EC, followed by a gradual encroachment of neurofibrillary tangles into the HF and neocortex in later stages of pathology. These findings suggested that the etiology of this disease, and the related memory impairments, could be traced to early entorhinal pathology.

Controlled lesion studies in nonhuman primates have facilitated further examination of the role of the EC in memory. Bilateral removal of the EC has been carried out in monkeys who subsequently performed a series of tasks designed (1) to assess their ability to learn associations between pairs of objects and (2) to infer relationships between objects whose relationships were not explicitly defined during the learning phase. Although monkeys with EC lesions took longer to learn the original associations than the intact monkeys, they could reliably produce appropriate behavioral responses indicating their recognition of the relationship between paired objects. However, monkeys with EC lesions were notably unable to flexibly use previously learned associations to make inferences regarding the reward value of the familiar objects in novel configurations. This striking observation led investigators to posit that while structures other than the EC

might subserve acquisition of associations between objects, the EC might critically contribute to supporting the flexible use of an established relational framework to guide behavior (Buckmaster et al. 2004).

**Electrophysiological studies.** Although a wide array of cortical and subcortical brain regions modulate electrical activity patterns in the EC, investigators have largely based functional hypotheses on the distribution of inputs arriving from the perirhinal and postrhinal/parahippocampal cortices. A prominent theory in the field posits that perirhinal and postrhinal/parahippocampal inputs into the EC constitute largely parallel information streams, providing preferentially multimodal object information to the LEA and visuospatial information to the MEA. Investigators have hypothesized that this apparent information segregation allows the subfields of the EC to independently process information regarding the *content* of an experience (multisensory object information) and the *contextual* circumstances (visuospatial information) that scaffold and facilitate an experience. According to this classical view, the LEA and MEA would in turn further process and ultimately route this information to the hippocampus, where content and context information could be combined to encode an "episode" (reviewed in Knierim et al. 2014).

Leaders in the field are careful to note that this functional model, in its current formulation, fails to capture the plurality of inputs that the EC receives, including feedback from the hippocampus itself (see Gross Anatomy). Moreover, the reciprocal connectivity between the LEA and MEA have led some to suggest that information regarding the content and the context of an experience is integrated to some extent prior to being transmitted to the HF (Burwell and Amaral 1998; Canto et al. 2008; Knierim et al. 2014). Extracellular recordings of the electrical activity of neurons in the EC have proved invaluable in parsing through these hypotheses and probing the function of this structure and the contributions of each of its subfields to episodic memory and spatial cognition (Moser et al. 2008; Knierim et al. 2014).



**Medial entorhinal area (MEA).** Structurally, MEA cell types vary widely according to shape and connectivity. Functional differences are also apparent, as patterns of electrical activity are robustly correlated to distinct variables such as the animal's head direction or the physical borders of an environment. More recently, functionally defined "grid" cells were found to selectively increase their activity in a pattern that corresponds to the vertices of tessellated triangles (Hafting et al. 2005). The electrical activity of grid cells thus "tiles" space as an animal traverses an environment (Hafting et al. 2005). The presence of neurons tuned to head direction, borders, and a grid-like patterning of space has fueled influential hypotheses regarding the role of the MEA (and the hippocampus) in spatial cognition (Moser et al. 2008; Knierim et al. 2014). Particularly, several key investigators proposed that this network of MEA cells could integrate visuospatial and vestibular information in order to continually update the animal's position over time with respect to the boundaries of an environment. These theoretical insights were recognized with the 2014 Nobel Prize, for their potential to constitute a neural substrate of spatial navigation and cognition (Moser et al. 2008, Knierim et al. 2014).

**Lateral entorhinal area.** While less is known regarding the neural correlates of behavior in the LEA, some studies provide evidence to suggest that the electrical activity of a subset of cells in this area might contain information for the identities or locations of objects experienced within a given spatial environment. Tsao et al. (2013) recorded the LEA as rats explored an environment that contained an object in a fixed location. Consistent with previous findings, some cells responded only when the rat sampled a given object, while other cells consistently increased their activity when the rats traveled over locations at fixed distances away from particular objects. When the object was relocated within the same environment, another subset of cells selectively increased their activity as the rat traveled over the space where the object had been *previously* located. Investigators then found that as the object was moved to different locations along the environment and then subsequently removed, the

activity of these cells tracked the history of locations that the object had occupied, but not the identity of the object itself (Knierim et al. 2014; Tsao et al. 2013). Importantly, the integrity of the response fields of LEA neurons decayed once the rats encountered the familiar object in a novel context. These findings suggest that the LEA does encode some information about the contextual scaffolding of an experience, presenting subtle challenges to the classical view of information processing in the LEA (Knierim et al. 2014).

## Summary and Future Directions

Rigorous anatomical characterization has ultimately facilitated a framework in which to interpret results from clinical, lesion, and electrophysiological studies in animal models, in an ongoing effort to elucidate the contributions of the EC to memory processes. A century of study through this diverse repertoire of approaches provides some evidence to suggest that this structure critically contributes to organizing relationships between stimuli and the contexts in which experiences take place. Moving forward, behavioral paradigms designed to assess previously unexplored cortical and subcortical influence on information processing in the EC might facilitate a richer understanding of the role of this brain region in cognition and behavior.

## Cross-References

- [Amygdala](#)
- [Hippocampus](#)
- [Medial Temporal Lobe](#)
- [Neuron](#)

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## Environment

### ► Adaptation

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## Environmental Effect

### ► Environmental Influences

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## Environmental Index

### ► Indicator Species

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## Environmental Influences

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## Synonyms

Environmental effect

## Definition

External factors that affect humans or any other life form

Before the nineteenth century, the effects of the environment on an organism were not well studied. Wilhelm Johannsen, a Danish botanist, first found differences in observable physical properties of genetically identical bean plants. He coined genetic content as “genotype” and observable properties as “phenotype.” He concluded from his experiments that these variations in phenotypes are caused by environmental factors (or environmental influences; Johannsen 1911).

Genotype is not the sole factor that decides the phenotype of any organism; there are several environmental influences which possibly modify them. Researchers are particularly interested in studying effects of environmental influences on development, growth, and health over long periods of time, as well as in humans and other animal species. Understanding of this unpredictable interplay between environment and genetics may provide insight of how a person may differ from its predefined genetic makeup.

Gene, a small part of our genome (entire genetic content), is the smallest functionally heritable unit of the entire genetic content of any organism. Each gene consists of two variant forms known as alleles; at a given loci (location of gene on chromosome), two alleles are present, one contributed by the father and one by the mother. These alleles encode a specific protein that is responsible for providing a characteristic

phenotype to an individual. The combination of these two alleles will produce different phenotypic characteristics (Lewis 2002).

The environment includes everything that surrounds us and can possibly affect us in one way or another. It includes common modifiable factors like lifestyle, dietary habits, and physical activity and other non-modifiable factors like temperature, humidity, season, migration, demographics, etc. In humans and many other organisms, these environmental factors can influence the gene expression, therefore significantly affecting the phenotype with time. Growth and developmental studies in relation to various environmental influences like temperature, high altitude, seasonality, migration, and activity are already established (Schell et al. 2009). Regulation by the environment is a normal component of development and growth for all the organisms (Gilbert 2014).

### Environmental Influences During Embryo Development

Both genotype and environmental influences work synergistically to produce a phenotype. One common example is linear growth (height or length). An individual may carry a genotype of normal growth, but availability/consumption of a proper growth-promoting diet will affect the phenotype by means of metabolism and changed pattern of hormone production in the body. Tall parents can be expected to have offspring with good/tall stature. This can be solely attributed to the fact that they carry “genes for good height.” However, if offspring do not receive proper nutrition and diet during their growth years, their growth can be stunted due to the absence of proper nutrition required to express that growth genotype.

The sensitivity of animal growth and development to social and environmental conditions was established early in the modern era of growth studies (Schell et al. 2009). Environmental influences are well-known to affect development before birth; this “extent of influence” is so strong that it contributes toward fetal developmental

syndromes and congenital defects. Environmental influences affect the development of the embryo/fetus in two different ways. Some intrinsic maternal environmental features like age and external environmental features like nutritional deficiency, certain diseases, smoking, alcohol consumption, drugs, and emotional stress during pregnancy can increase the risk of miscarriage, stillbirth, premature delivery, improper development of the newborn, congenital defects, etc. These external (i.e., physical and chemical) agents with the ability to produce defects in newborns are collectively known as teratogens.

Commonly known teratogens like azaserine, alcohol, glyphosate, thalidomide, thiadiazole, triazene, and 6-aminonicotinamide are known to be teratogenic to both humans and several lab animals (Murphy et al. 1957). These teratogens mediate effect by different means. Glyphosate, thalidomide, and several other teratogens are known to mediate developmental defects in animal embryo through chromosomal abnormalities (Soukup et al. 1967). Also some are reported to block pathways responsible for developments of limbs as well (Tantibanchachai and Yang 2014).

Thalidomide was a commonly used drug in the USA in the 1950s; it was known to be one of the safest drugs available in the market. Studies confirmed that it had no side effects on healthy adults and their gene expression. However, when it was created, its teratogenic effect on fetuses was unknown. Research studies led by William McBride and Widukind Lenz reported that thalidomide was a potent teratogen. These agents are known to exert their adverse effect by changing the expression of significant genes. They are also known to exert their effect by altering the synthesis of important hormones and any other significant metabolite in the body (Jürgen and Rüther 2008).

Similarly, severe poisoning caused by mercury in Minamata, Japan, proved that, during development, exposure to undesired agents can affect fetal development. It is very well established that mercury enters into the body from fish, which is the main diet in Japan (Schell et al. 2009). Fetuses and newborns are particularly susceptible to certain environmental toxins.

## Environmental Pollution Influence on Humans and Other Living Organisms

Although fetuses, neonates, and young children are more at risk from environmental pollutants, adults are also affected by these toxins. Exposure of environmental toxins like heavy metals (lead, mercury, arsenic, etc.), toxic chemicals (several pesticides, dioxins, phenolic compounds, etc.), and many other compounds are known to increase the risk of developing human diseases like cancer, disorders of nervous system, and several other diseases/disorders as well (Bolger et al. 2002). An American community-based study showed a strong association of environmental pollutants exposure to sexual maturation, obesity, and disturbed thyroid function, which are known to severely affect growth and maturation of adults (Schell et al. 2009). One of the very recent and notable examples in this context is urban air pollution; it is so severe in some cities in developing and a few developed countries that the majority of young children and elderly adults are suffering from various respiratory disorders like asthma and other chronic airway diseases (Jiang et al. 2016). Animals are not spared from these toxins. A British study found feminization of male fishes due to industrial discharge in rivers. It is reported that certain toxins known as reproductive toxins were responsible for this sex reversal (Gross-Sorokin et al. 2006).

All living species are now facing a different kind of challenge due to artificial/man-made environments and its influence on them. It is very well established that this artificial environment that mainly includes pollution affects all living organisms. Current research is looking into the role and other aspects of the artificial, human-made environment full of pollutants and how it influences human, animal growth, and development.

## Behavior and Environmental Influences

Behavior is an important attribute of an organism; it is a response to the external environment. The study of how behavior is predetermined or influenced by the environment has long been a popular topic of research and debate among researchers and intellectuals.

Studying effects of environmental influences on behavior is difficult as each person varies genetically and thrives in different environments. However, studies on genetically identical twins or monozygotic twins provide a valuable way of understanding how the environment can affect genetically similar individuals differently. Identical twins are produced from a single cleavage of zygote (formed after fusion of female egg by male sperm), having similar genotype (100% same genes). Studies comparing identical twins reveal how environmental influences affect phenotypes among them. It is very commonly known that identical twins have different fingerprints as fingerprint patterns are affected by the environment (Choi and Kim 2007).

Although twins are known to have similar visible traits, behavior is one of the factors that is greatly influenced by the environment as well. Twins raised in the same environment are known to have strikingly different behavioral traits like personality, ability, preferences, etc. A study in 1960 indicated that twins can have different behavior right from the birth, which can be affected by factors like birth sequence and birth weight. Moreover, common social factors like parental and peer influence are known to shape behavior differently even for genetically identical individuals (Brown et al. 1967).

Proof of genetic background of behavior are limited, but factors like personality traits, IQ, social traits, and even alcoholism are strongly linked to genetic inheritance. Research fails to identify specific genes that may directly link to specific behavior, making it difficult to understand the relation. Besides, substantial evidence is present to link behavior to the environmental influences, and scientists consistently believe that non-shared environmental factors (environmental factors not shared with other children of the same family) have more impact on the behavior differences than shared factors (Brown et al. 1967).

## Environmental Influence on Animals

Light, temperature, and resource availability are the most commonly known external environmental factors. Their influence on phenotypic

development is very well established in animals ranging from insects to reptiles to mammals.

A recent study reported that environmental influence possibly affects cognition in lizard species. Temperature was found to influence brain performance and anatomical structure in young lizard (*Pogona vitticeps*). Lizards incubated at colder temperature were found to be quick social learner and performed their task quickly as compared to lizards incubated at higher temperature (Siviter et al. 2017). These findings are further supported by another study by Pike et al. (2018): they found that short-term brain plasticity (overall size and development of certain brain region) is influenced by environmental factors. Their research suggested that fishes developed under low-light/visually restricted condition have significantly smaller optical region besides significantly larger olfactory bulbs as compared with fishes from normal visual condition. Their brain preferentially uses olfactory chemoreception over visual perception.

Influence of temperature on phenotypic development is very well established in Himalayan rabbit species. Temperature strongly influences expression of skin pigment producing gene in these animals. C gene is pigments-producing gene in the rabbit body parts like eyes, fur, skin, etc. Its expression is temperature dependent. This gene is known to be inactive above 35 °C; it is highly expressive between the temperature of 15 °C and 25 °C. This temperature-regulated expression of C gene produces distinctive coat patterns among rabbits. In warm body parts, the gene is inactive and produces no pigments. Meanwhile, in other body parts like the ears, nose, and feet where the temperature is below 35 °C, it produces black pigment, making these parts darker than other body parts (Sturtevant 1913).

Optimal light is also known to affect gene expression status in butterflies, affecting their growth and development. Thomas Hunt Morgan studied caterpillars under different lights in 1917. He kept caterpillars under controlled light conditions (red, green, blue light), and some caterpillars were kept in the dark. These caterpillars exhibited drastic differences in wings. Red light exposure resulted in wings with intense color, and green light exposure resulted in dusky wings, while

darkness and blue light produced pale wings (Morgan 1917).

Whereas sex of most animals is determined by genetic factors, in some animals like all crocodile species and many species of turtles, sex is determined by temperature. In these species, temperature plays a pivotal role during certain critical developmental stage in sex determination. A common example of such temperature-dependent sex determination is red-eared slider turtles (*Trachemys scripta elegans*). If the nest temperature is below 28 °C, all the hatchings will be males. If the nest temperature is above 31 °C, all will be females. Temperatures in-between will produce offspring of both sex with equal probability (Shoemaker and Crews 2009).

Many insect species have developed strategies to properly deal with adverse environmental condition known as diapause, also known as animal dormancy. It involves suspension of development at any phase of life cycle (embryo, larva, pupa, or adult) until favorable conditions are available for supporting growth (Gilbert 2014).

These examples indicate strong environmental influences on gene expression in animal species as well. However, it is important to keep in mind that there is a very complex interaction between genes and environment that defines phenotype and who we are.

## Environmental Influences and Human Diseases

Environmental influences have great impact on our health. Lifestyle diseases are “group of diseases” that are linked to “long-term habits.” All the major lifestyle diseases (diabetes, heart diseases, cancer, asthma, obesity, and many other diseases) have a very strong environmental background (Sharma and Majumdar 2009). A person may carry a disease-causing gene or set of genes (family history of a disease), but chances of development of that disease will significantly depend on the environment. Individuals with a family history of lung cancer are less likely to develop the disease if they avoid any kind of tobacco use. Similarly, individuals with a



family background of diabetes or heart disease are less likely to develop them if their dietary habits (healthy food) and lifestyle (physical activity) are adjusted according with disease risk. People living in heavily polluted urban industrial areas will suffer more from asthma or any other respiratory disease as compared to people living in areas with comparatively less or near to nil air pollution. Similarly, lifestyle changes of diet and activity in recent times (high-calorie food and fast-food consumption and lack of proper exercise) have been responsible for a very rapid growth in obesity in developed and developing countries over the past several decades (Brantley et al. 2005). Moreover, an individual raised in a disturbed family environment is also similarly at higher risk for developing mental disorders like schizophrenia, bipolar disorder, etc. (Brown et al. 1967).

It is also important to understand that all these diseases involve controllable risk factors (lifestyle or environment) and uncontrollable risk factors (genetic factors) that cannot be changed. The interplay of both will dictate the chances of developing such diseases in any person.

## Conclusion

We wonder about the factors that affect our personality and characters. Plenty of researchers around the world are studying and debating the nature (inherited genotype or set of genes) versus nurture (environment) for a very long time. Every individual has their own unique environment that guides their overall development. Both of these factors are equally important, and either one of them cannot be downplayed in determining a person's phenotype. However, most but not all features involve environmental modification of a phenotype. Some characteristics (e.g., eye color and appearance) have higher genetic weightage on their expression and are not affected by the environmental influence. After considering all the facts, it can be safely said that environment is like a mold that will always dictate how an organism shapes itself within it.

## Cross-References

- [Phenotype](#)
- [Teratogen](#)
- [Twin Studies](#)
- [Umwelt](#)

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## Environment-Organism Systems

### ► Social Affordance

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## Envy

### ► Jealousy

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## Epigenesis

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## Synonyms

[DNA methylation](#); [Epigenetic modification](#)

## Definition

Epigenesis is a mechanism by which modifications are introduced during embryo development which does not affect the nucleotide sequence but alters the expression of genes (Russo et al. 1996). These epigenetic modifications are inherited by mitosis and can cause short-term or long-term changes in gene expression. Epigenome is the term for the epigenetic modifications to the genome of an organism. Epigenetics is required for embryo development and cell differentiation and also facilitates transcription of genes and silencing of genes. Environmental conditions also influence the epigenetic pattern, and thereby the expression pattern of genes such as adverse environmental conditions like inadequate healthcare and poor nutrition can introduce long-lasting effects in the offspring including predisposition of diseases like diabetes and heart diseases. Epigenetic modifications in the offspring are also likely to undergo trans-generational inheritance (Gong et al. 2010). Mechanisms involved in epigenetic modifications are DNA methylation, histone modifications, and small RNAs.

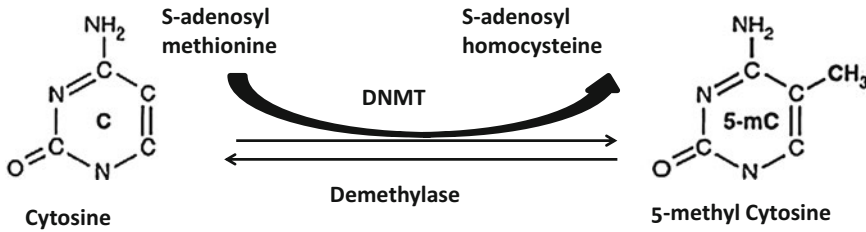
## DNA Methylation

DNA methylation is catalyzed by the DNA methyltransferases which are the class of enzymes involved in covalent attachment of methyl (CH<sub>3</sub>) group to the 5' position of the cytosine (5'-methylcytosine) in the dinucleotide sequence CpG (Bird 2002). Mostly, the CpG islands are present in the promoter region of the genes, and hypermethylation of the promoter region causes gene silencing (Fig. 1).

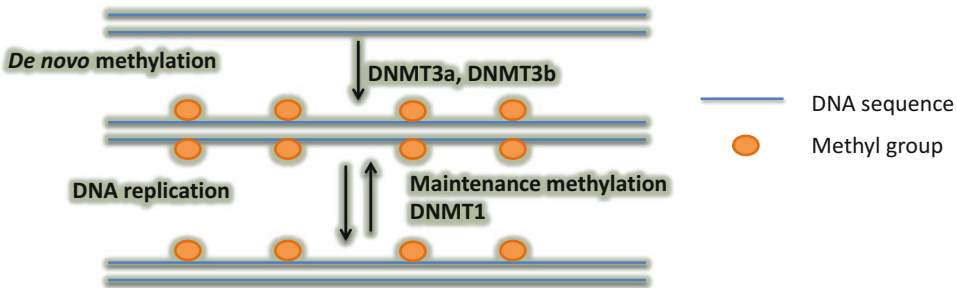
There are four types of DNA methyltransferases:

1. DNA methyltransferase 1 (DNMT1)
2. DNA methyltransferase 2 (DNMT2)
3. DNA methyltransferase 3a (DNMT3a)
4. DNA methyltransferase 3b (DNMT3b)

DNMT3a and DNMT3b are the examples of de novo methyltransferases that introduce new



**Epigenesis, Fig 1** Mechanism of methylation of the cytosine residue by DNA methyl transferase enzyme (DNMT)



**Epigenesis, Fig 2** De novo methylation and maintenance methylation of the DNA sequence

pattern of methylation in the genome particularly during early embryo development, while DNMT1 is an example of maintenance methyltransferases which after cell division maintain the methylation pattern (already introduced by the de novo methyltransferases in the parental strand) in the newly synthesized strand from the parental strand (Xu et al. 2010). DNMT2 is a putative methyltransferase with no evident activity reported (Fig. 2).

Different processes by which methylation of CpG island ensures silencing of the gene expression are unavailability of promoter region to the transcription initiation complexes, RNA polymerase inhibition, and accessibility of transcriptional repressor complexes (Murr 2010).

Addition of methyl group to the DNA changes the topological structure of it and provides binding site or domain for protein binding; for example, methyl-CpG-binding proteins (such as MBD1, MBD2, MBD3, MBD4, and MeCP2) bind to CpGs through methyl-CpG binding domains (MBD). Binding of MBPs further recruits other proteins such as DNMT1, histone deacetylases HDAC1 and HDAC2, human H3K9

methyltransferase (Suv39 h1), and heterochromatin protein 1 (HP1) (Fuks et al. 2003; Sarraf and Stancheva 2004; Stewart et al. 2005) which alter gene expression by changing chromatin structure that leads to heterochromatin state or silenced state.

DNA demethylation process is also as important as DNA methylation and involves unsuppressing the expression of the gene by removing the methyl groups from the DNA. DNA demethylation can be performed by the following two mechanisms:

**Passive demethylation:** Passive methylation occurs when DNMT1 enzyme is inhibited which causes no maintenance of the methylation pattern to the newly synthesized strand during replication.

**Active demethylation:** In active demethylation, methyl groups are either removed directly from the methylated DNA or may involve deamination or oxidation of the methyl group followed by removal by glycosylase enzyme (involved in base excision repair pathway). Active methylation is not dependent on replication.

## Important Roles of DNA Methylation

- (i) Differential DNA methylation of parental alleles which are known as differential methylated regions (DMRs) causes allele-specific expression of imprinted loci during development (Li et al. 1993).
- (ii) Chromosomal structural integrity maintenance (Chen et al. 1998).
- (iii) In defense of genome from parasitic retrotransposons (Yoder et al. 1997).

## Histone Modifications

Chromatin is composed of nucleosomes which package the long DNA molecule into compact structure with the help of basic proteins known as histones. Each nucleosome is made up of 146 base pair of DNA wrapped around histone octamer which is comprised of four subunits (H2A, H2B, H3, H4) in the core, and H1 subunit helps in the packaging of the nucleosomes (Luger et al. 1997). Histone octamer also possesses an unstructured N-terminal tail (apart from the core unit) which is subjected to different types of covalent modifications like methylation, acetylation, phosphorylation, biotinylation, sumoylation, ubiquitination, and proline isomerization in mainly four amino acid residues such as lysine, arginine, tyrosine, and serine.

Histone modification is a posttranslational modification and mainly associated with the gene expression regulation. Two major type of histone modification that regulates gene expression are methylation and acetylation of lysine residue in histone 3. Histone acetyl transferases (HATs) catalyze the transfer of acetyl group from acetyl coenzyme A to the histones, while histone deacetylase (HDACs) are the enzymes involved in the removal of acetyl groups from the histone (Fig. 3). Acetyl group is negatively charged and by binding with the lysine residue in the histone neutralizes the charge of the histone which further affects affinity with the negatively charged DNA molecule. This results in opening of the structure (euchromatin state) such that access of the transcription factors for gene activation becomes easy

and promotes gene transcription. Acetylation of H3K9 (**H3K9ac**) is an example of histone modifications associated with the activation of the gene expression. Likewise, histone methyltransferases (HMTs) catalyze the transfer of methyl group from S-adenosylmethionine (SAM) to histone. Methylation of histone (particularly at 9th and 27th lysine residue of histone 3) increases the affinity of the negatively charged DNA to the histone as methyl group is positively charged and results in the more compact form of nucleosome known as heterochromatin state which causes repression of gene expression. H3K9 trimethylation (**H3K27me3** and **H3K9me3**) is an example of gene silencing due to histone methylation. However, tri-methylation of H3K4 (**H3K4me3**) is associated with the activation of the gene expression (Davie 1998).

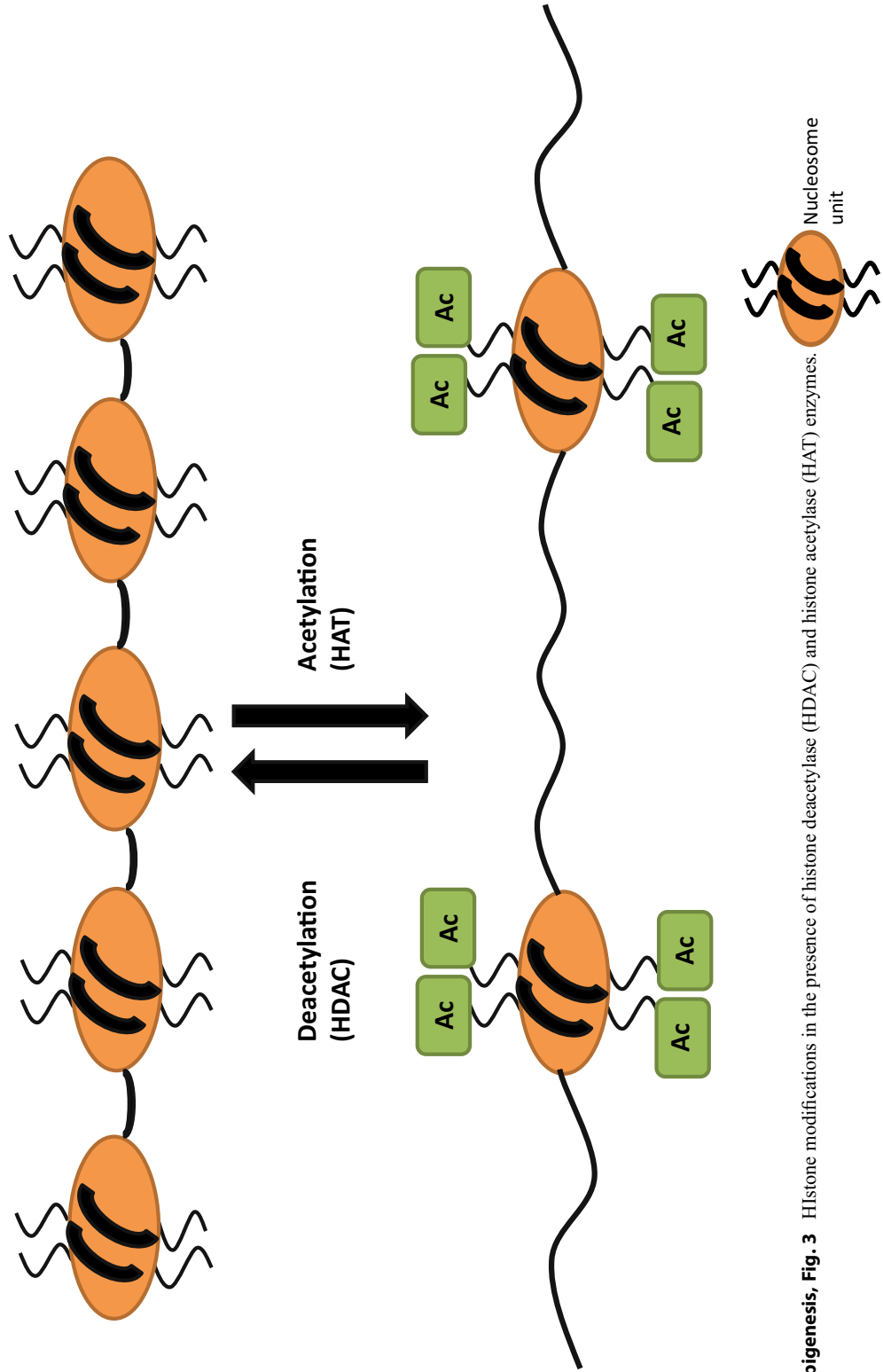
The histone modifications recruit DNA methylation enzymes, while DNA methylation recruits histone modification enzymes; thus, there is a cross talk between the epigenetic reprogramming mechanisms which is necessary for the controlled regulation of the gene expression.

## Noncoding RNAs

Noncoding RNAs are the molecules that are not translated into protein. They can be divided into short ncRNAs and long ncRNAs. Short ncRNAs can be further classified into miRNA, siRNA, and piRNA. Noncoding RNAs are reported to be involved in regulating gene expression by epigenetic modifications like DNA methylation, gene silencing, heterochromatin formation, etc.

- (i) **Short ncRNAs:** Short noncoding RNAs can be classified into three types:

**MicroRNAs (miRNAs):** MicroRNAs cleave or degrade target messenger RNA by binding to it via complementary sequence. Example of miRNA genes associated with the epigenetic-based regulation is mir-127 and mir-136 which regulate expression of Rtl1 protein essential for placenta formation in mice.



**Epigenesis, Fig. 3** Histone modifications in the presence of histone deacetylase (HDAC) and histone acetylase (HAT) enzymes.

**Short interfering RNAs (siRNAs):** It regulates posttranscriptional gene silencing by degradation of target mRNA molecule. It also promotes H3K9 methylation and heterochromatin formation by binding to the RNA-induced transcriptional silencing (RITS) complex.

**Piwi-interacting RNAs (piRNAs):** They interact with the piwi class of proteins and are involved in the suppression of transposon activity in cells by targeting and cleaving transposons.

- (ii) **Long ncRNAs:** The major group of noncoding RNA transcripts belongs to long ncRNA class. They are found to be associated with chromatin remodeling, posttranscriptional regulation, transcriptional regulation, etc. An example of the role of lncRNAs in epigenetic is X-chromosome inactivation (XCI). X-chromosome inactivation involves two lncRNAs, i.e., X-inactive-specific transcript gene (Xist) and antisense transcript of Xist known as Tsix which is a negative regulator of Xist.

## Methods to Determine Methylation Status of the Genome

There are three methods developed for DNA methylation detection:

- (i) **Bisulfite genomic sequencing:** It is based on chemical modification of the DNA sequence with bisulfite which involves conversion of cytosine residue to the uracil residue, but the 5-methylcytosine residues in the dinucleotide CpG remain unaffected. When PCR is performed on the bisulfite-treated DNA segment, non-methylated cytosine residues will convert to thymidine, while 5-methylcytosine residues will be cytosine only. Methylation pattern can be detected by direct sequencing of the PCR product. This method is used to determine methylation pattern at specific loci and can differentiate between single nucleotide polymorphism (thymidine and cytosine).
- (ii) **Methylation-sensitive restriction endonucleases:** This method is based on utilizing methylation-sensitive restriction enzymes like *HpaII* and *MspI*. Both *HpaII* and *MspI* recognize the sequence CCGG and are isoschizomer. This method identifies the methylation pattern in the DNA sequence either by enriching methylated region or by enriching non-methylated region.
- (iii) **Methylated DNA immunoprecipitation:** It is an affinity-based isolation method. In this method, genomic DNA is fragmented by sonication followed by immunoprecipitation with antibodies specific to 5-methylcytidine. The fragments of DNA bound with the antibody complex are then purified and used for identification of locus-specific (PCR) or genome-wide methylation pattern in the genomic DNA. This method is very rapid and efficient.

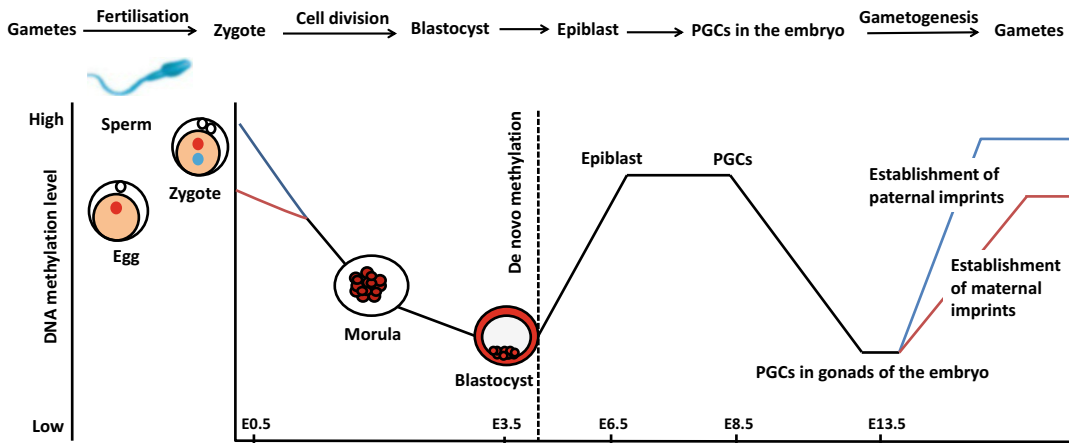
## Epigenetic Reprogramming During Embryo Development

Epigenetic reprogramming during embryo development is a bimodal DNA methylation pattern that occurs in two phases:

- (i) During the formation of the primordial germ cells (PGCs)
- (ii) During early embryo development soon after fertilization

These two events reprogram the epigenetic landscape to a basal level; i.e., demethylation and then remethylation occur on the basis of the differentiation of the lineages such that the PGCs differentiate into germ cells (sperm and eggs) and inner cell mass (ICM) of the early embryo differentiates into all the other cell types of the organism (Fig. 4).

Primordial germ cells are terminally differentiated cells that carry all the information necessary for the embryo development after fertilization. There is difference in the paternal and maternal genome due to differential expression of the paternal and maternal alleles of imprinted genes known



**Epigenesis, Fig 4** Epigenetic gene regulation during embryonic development

as genomic imprinting during development (Kobayashi et al. 2013).

Primordial germ cells are derived from epiblast cells (day 7.5) and migrate to germinal ridge (day 11.5) where differentiation of PGCs to sperm or egg occurs. PGCs are highly methylated when they enter germinal ridge and from day 11.5 to 12.5 undergo global erasure of DNA methylation in the genome including in imprinted genes as well. This is an example of active demethylation. However, it is global demethylation, but some regions of the genome avoid demethylation. Following demethylation, the de novo remethylation of PGCs of both sperm and egg initiates by day 16.5 when gametogenesis commences and ends on day 18.5 in male and before ovulation in maturing oocyte in females. Now both gametes are highly methylated and mature for fertilization event.

Second round of epigenetic reprogramming occurs between fertilization and blastocyst stage. After fertilization, paternally inherited genome undergoes rapid active demethylation within the first cycle of fertilization, while maternally inherited genome undergoes gradual passive demethylation (Smith et al. 2012). Erasure of DNA methylation pattern in the newly formed zygote continues till the end of blastocyst stage, but this demethylation does not affect imprinted gene methylation pattern. After implantation, de novo methylation of the embryo starts which

coincides with the differentiation of the embryo into the inner cell mass (ICM) and trophectoderm (TE). The inner cell mass (ICM) is hyper-methylated which forms all the tissue types, while the trophectoderm (TE) is under-methylated which is involved in placenta formation. On day 7, highly methylated PGCs arise from the extra-embryonic mesoderm of the developing embryo from the ICM.

## Reprogramming of Somatic Cell Nucleus

Somatic cell nuclear transfer (SCNT) is a nuclear cloning technique which involves transfer of somatic cell nucleus into the cytoplasm of the enucleated oocyte (Wilmut et al. 1997). The nucleus of the egg cell is removed through the process known as deprogramming of the egg cell. Somatic cell nucleus is then inserted into the enucleated egg cell which further results in the fusion of these two cells. The somatic cell nucleus inside the egg cell undergoes reprogramming due to the cytoplasmic factors of the egg cell. Dedifferentiation of the somatic cell nucleus results in the formation of new zygote; however, only 5% of the cloned embryos survive during development. The low rate of survival of the cloned embryos as compared to the fertilized embryos is because of the incomplete demethylation of the embryo before implantation and insufficient de novo



remethylation of the developing embryo. Abnormal epigenetic reprogramming results in improper methylation of some important genes (like Oct4, imprinted gene) which are essential for embryonic development. SCNT has potential importance in therapeutic cloning and reproductive cloning.

## Conclusion

Epigenetic reprogramming is the modification in the DNA such that it does not alter the sequence of the DNA fragment. Histone modification and DNA methylation are well studied and important mechanisms by which epigenetic regulation of gene expression is performed. Epigenetic reprogramming is well studied during embryo development and has essential role in embryo development as many diseases have been encountered in the last decades due to abnormality in the epigenetic reprogramming during embryo development. Understanding the exact mechanism and cross talk between different epigenetic mechanisms will provide new platform to identify many unidentified facts about genetics and developmental biology.

## Cross-References

- [DNA Methylation](#)
- [Embryo](#)

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## Epigenetic Modification

- [Epigenesis](#)

## Epigenetics

- [Genomic Imprinting](#)

## Epinephrine

### ► Adrenalin

## Episodic Memory

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## Introduction

From antiquity, memory has fascinated intellectuals such as philosophers, artists, mathematicians, and more recently psychologists and neuroscientists. The definition of memory itself has evolved through time. The twentieth century has specifically impacted the study of memory. Under the influence of eminent scientists such as Bartlett (1886–1969), memory was no longer considered as a passive trace in the brain, but instead as an active process involving the reconstruction of previously encoded features. Human memory was divided into sensory memory (very short-term memory receiving perceptual and sensitive information from environment), short-term memory (temporary storage of information), and long-term memory (long-term storage of information). It is only during the second part of the twentieth century that long-term memory was divided in several types based on its different functions. Two broad long-term memory systems differing according to their accessibility to conscious recall (i.e., the capacity to retrieve information previously encoded) were described: the non-declarative and the declarative systems. Non-declarative memories, also called implicit or procedural memories (e.g., memory of habits, skills...), are characterized by an unconscious

processing of information (e.g., cycling does not need a conscious access of previously learned motor memories). On the contrary, declarative memories (or explicit memory) are characterized by the conscious recollection of facts and events. These declarative memories are in turn divided into two forms, semantic knowledge or labels about the world (e.g., Paris is the capital of France) and episodic memories or experiences (e.g., what I wore and how I felt last time I went to Paris), a distinction first made by Tulving (1972, 1983).

Episodic memory is the capacity to travel mentally back in one's personal past. Both episodic and semantic memories imply bringing memories into conscious awareness; however consensus in the scientific community states that they differ in terms of the nature of information they convey (Tulving 1972, 1983). Semantic memory refers to general knowledge of the world (e.g., Paris is the capital of France), while episodic memory refers to the memory of *personally experienced* past events (e.g., a memory of a poignant moment spent with friends). Episodic memory involves contextual information pertaining to the previously experienced event (i.e., temporal and spatial information). The phenomenological aspects of episodic memory have been defined by Tulving (1972, 1983): namely, the personal and conscious recollection of an event that occurred in the personal past (i.e., I am aware that I am remembering a specific event from my past, and I know that I live in the present and that I can recall memories from *my* past or anticipate future events). One crucial phenomenological element is called *autonoetic* consciousness (i.e., self-knowing) and another is *chronesthesia* (an awareness of the passage of time). Together they build personal identity by accessing autobiographical information about how the self moves and changes through time while maintaining identity and integrity (e.g., *I* am different from someone else, and *my* memories belong to my *personal* past). These phenomenological elements make episodic memory a very special type of memory precisely because it is rooted in *self* (i.e., one's identity), in *time* (i.e., the past), and in *consciousness* (i.e., being aware of the external environment

and of one's internal state and how these make and maintain changes in the self through time). This definition of episodic memory in terms of consciousness has long led authors' claim that episodic memory is unique to humans.

The distinction between episodic and semantic memory arose from neuropsychological studies of amnesic patients presenting an impairment of episodic recall while semantic knowledge was preserved. In these studies, patients were not able to create new episodic memories and to retrieve episodic memories from several years before their brain damage. That is, the owner of a semantic memory will *know* one fact he encoded in his semantic memory but will not be able to recall any contextual information present at the moment of encoding (e.g., temporal or spatial information). At the opposite, the owner of an episodic memory will *remember* this memory by recollecting the specific features present when the memory was formed (e.g., perceptual, sensitive, emotional, cognitive information). From a methodological point of view, episodic memories are created after a single presentation of an event. Multiple presentations of such an event would lead to semantic information processing. The crucial notion hidden behind these statements is the "expectation of being asked." Indeed, it is now debated whether animals should be asked unexpected questions in order to eliminate rule-based (i.e., semantic) explanation of the behavior to investigate episodic cognition in animals.

Episodic and semantic memories would represent two parallel subsystems where episodic memory is embedded within semantic memory. According to Tulving (1983, p. 66), the two systems "can operate independently of the other, although not necessarily as efficiently as it could with the support of the other intact system." The two systems seem to share cerebral structures, such as the hippocampus (Suzuki and Clayton 2000). That is, even if their functioning is different, episodic and semantic subsystems interact and are part of the same memory organization.

Some researchers argue that remembering the temporal component of an episodic memory may involve retrieving contextual information instead of a specific timing, for instance, recalling which

objects were present when the memory was encoded (Eacott and Norman 2004). The specific type of memory in charge of recalling contextual features that were present when the episodic memory was formed is called source memory (Johnson et al. 1993). Episodic recollection is being triggered by contextual information; source memory tasks are designed to study episodic memory.

Episodic memory is the retrospective part of mental time travel which corresponds to the ability of re-experiencing of personal past event (remembering the past), and episodic future thinking is the pre-experiencing of future events (imagining the future) which involves the prospective nature of mental time travel. In this entry, we will assess the evidence for such systems in animals. Asking whether animals possess such episodic capacities for both the past and the future would help understand the function of the episodic cognition in an evolutionary perspective.

## Episodic-Like Memory in Animals

There is an important debate as to whether mental time travel is unique to humans or shared with other animals. Bischof-Köhler (1985) claimed, for instance, that it is impossible for animals to anticipate future states because they are bounded into a present defined by their current motivational state, and Tulving (1983) suggested that animals do not remember personal past experiences. The "mental time travel" hypothesis stated also that the ability to mentally re-experience or pre-experience one's personal event is uniquely human (Suddendorf and Corballis 1997). Even though the debate is still vivid today, opinions have evolved since 1997 (e.g., Corballis 2013), in particular through research showing sequential replay in the rat hippocampus suggesting anticipation of future paths in a maze, as they either correspond to path rats have not actually taken or path rats previously took but in a temporally reversed order (Gupta et al. 2010). It led the author to admit that the difference between human and other animal's mental time travel ability might be one of degree and not of kind.

One issue is the definition of episodic memory in terms of consciousness, i.e., of autonoesis and chronesthesia mentioned above. Phenomenological aspects of episodic memory are usually investigated through verbal tasks in humans. A classical approach is to ask whether adult humans are able to verbally express what they recall in opposition to what they know during an interview, giving details of when and where they learnt the information. As these tests are highly dependent on verbal abilities, they are not relevant for infants and toddlers, as well as animals. As no conclusive experiments have been developed to study the phenomenological aspects of episodic recollection in the absence of agreed nonlinguistic criteria, it remains impossible to ask these individuals, be they nonverbal animals or preverbal children, whether they know or remember something.

The study of episodic cognition in animals needs to rely on behavioral measures that can be objectively tested. Clayton et al. (2003a) suggested three main behavioral criteria to investigate episodic memory in animals, namely, the content (i.e., “what” happened, “when,” and “where”), structure (i.e., the three features are bound together and integrated into one and the same episode), and flexibility (i.e., cardinal features of a declarative as opposed to a procedural system) of the memory. This minimalist view, circumventing the phenomenological aspects of episodic memory, refers to “episodic-like” memory.

The **content** behavioral criterion of episodic-like memory is based on Tulving’s original definition (i.e., “a system that receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events” Tulving 1972). This definition means that an episodic memory provides information about “what” happened as well as “when” and “where” it happened. According to the authors, the “when” component is crucial as episodic memory is temporally unique, whereas the spatial component (where) and the event itself (what) can be shared by several episodic memories. The **structure** behavioral criterion of episodic-like memory implies that the content

must represent an integrated representation of the three components acquired through a unique encoding. In other words, the “what,” “when,” and “where” must represent the same episodic memory. The **flexibility** behavioral criterion of episodic-like memory states that this integrated representation should be reused flexibly when required. Indeed, episodic memory is a subpart of the declarative memory system which supports the flexible deployment of encoded information.

The description of these three behavioral criteria has allowed researchers to start investigating, at least from a behavioral point of view, whether or not this cognitive ability would possibly be present in nonhuman species. A wide range of species has been studied during the past decades using this theoretical background; it is noteworthy that researchers were differently assessing the temporal component of episodic-like memory. In the following sections, we will review some of the studies using different definitions of this component.

### Studies Using the What-Where-When Criterion

Time can be defined as a continued and linear movement occurring irreversibly from the past through the present to the future. One single exception is the capacity of mental time travel allowing one to look back into the past and look forward into the future. Episodic memory is thus deeply rooted in temporality. Measuring this temporality can be done in several ways. Friedman (1993) discusses three main different theories to consider time. The first focuses on the event’s distance from the present. The remembered event is dated based on the time expired from the actual present (distance-based theory: i.e., how long time ago). The second approach assumes that the event itself shares information about the age of the memory (location-based theory or absolute timing theory: e.g., date of the calendar). The last approach is based on the relative time of occurrence of the memory where the date of the memory is determined according to other events (order-based theory: i.e., event B occurred after

event A and before event C). In this conception, the date of the memory is determined in relation with other events (before/after judgments).

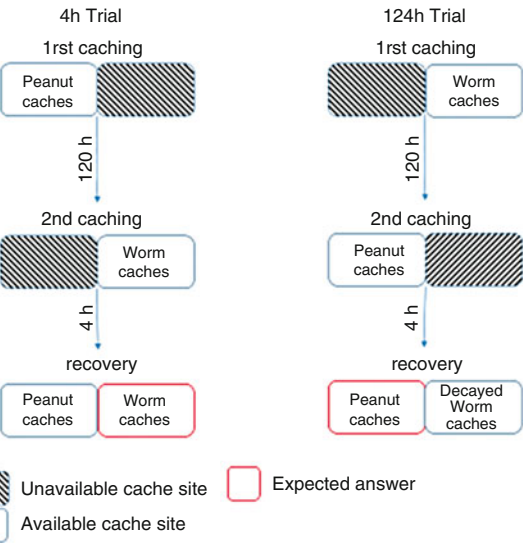
Time is a process of active, repeated construction. In the following section, we will give some behavioral examples of experiments using these different approaches to investigate episodic-like cognition in animals.

**What-Where-When (In Terms of How Long Ago)**

Clayton and Dickinson (1998) were the first to experimentally test episodic-like cognition in animals, by using the three behavioral criteria (Fig. 1). In their original experiment, California scrub jays (*Aphelocoma coerulescens*) were able to learn that wax worms (preferred food item) would degrade after a long delay (124 h) but not after a short delay (4 h) and that nonperishable food (peanuts, non-preferred food item) would be available at both delays. Birds could cache the worms and the peanuts in a tray during the study phase and then retrieve their caches after 4 or 124 h at test. After the short interval, birds searched in the area where they cached the worms, and after the long interval, the jays searched in the area where they cached the peanuts. It seems then

that these birds were able to recall what they cached, where, and when. The following studies showed that this result was not due to familiarity cues and that the birds learned the rule by which food would be degraded and how long it would be eatable, forming an integrated representation of the what, the where, and the when. This representation was also flexibly accessed as the birds continued to respond appropriately even when the rule about the delays or the food changed (Clayton et al. 2003b). Recent study showed that magpies (*Pica pica*) were also able to retrieve what was cached, where, and when (Zinkivskay et al. 2009).

The episodic-like memory about what happened, where, and how long ago was also investigated in mammals such as rats (Babb and Crystal 2006). In their experiment, the rats were trained to discriminate what, where, and when they encountered food. Rats were placed in an 8-arm radial maze where distinctive food (grape, raspberry, i.e., preferred food items) or nondistinctive food (regular chow, i.e., non-preferred food items) pellet was available. During training, rats were allowed to visit four arms and returned after a short or long interval to the maze where all the arms were open. During the study phase, the arms containing chow pellet never replenished until the next trial,



**Episodic Memory, Fig. 1** Procedure of Clayton and Dickinson (1998) what-where-when task. 4 h and 124 h training and trials experimental conditions and contents

of the caching trays. During caching, birds could cache only on one side of the tray, as the other side was covered



while the arms containing grape and raspberry replenished after a long (6 h) retention interval but not after a short (1 h) interval. The arms that were closed during the study phase were filled with chow pellet at test. Results showed that rats were more likely to revisit grape and raspberry locations after long than short delay. Moreover, rats were able to adjust flexibly their behavior when one flavor was devalued. This study showed that rodents are able to encode the content of episodic-like component. Another study showed episodic-like abilities in meadow vole (*Microtus pennsylvanicus*; Ferkin et al. 2008). Male meadow voles can detect when a female is in best disposition for reproduction, a period called postpartum estrus (PPE). In this study, male meadow voles encountered two females in two different locations. One female was pregnant and about to enter the PPE period, while the other was neither pregnant nor lactating. After 24 h, the male was replaced in the same empty maze. At this time, the pregnant female was now a PPE female. The male spent significantly more time in the location of the PPE female. Results also showed that when males encountered a PPE female and a female who was neither pregnant nor lactating during the study phase, at test, males would spend equivalent time in both locations 24 h later as the PPE female was now a lactating female. Thus, meadow vole males were able to remember which female (what) was in the best period for reproduction after a single encounter (when) and in which location he could find her (where). What-where-when abilities were also found in primates (Martin-Ordas et al. 2010).

More surprisingly, episodic-like abilities were also found in invertebrates. Cuttlefish are part of the cephalopod mollusk's family. They possess a rich behavioral repertoire making them a good model for investigating complex cognitive abilities. Following the original study of Clayton and Dickinson (1998), Jozet-Alves et al. (2013) presented cuttlefish with similar what-where-when paradigm. On every trials, two distinct emplacements in the tank of the animals were spotted with identical visual cues. When the cuttlefish went close to one of these visual cues, a crab and a shrimp were simultaneously placed in front of the cues. Cuttlefish were then allowed to catch

one of the preys. After a short delay (1 h), the non-preferred prey was still available at the previous location, while the location associated with the preferred prey was not rewarded (Fig. 2). After a long (3 h) retention interval, both locations were reinforced. Results showed that cuttlefish went significantly more close to the visual cue associated with the non-preferred prey after a short interval, while they went significantly more to the visual cue associated with the preferred prey after the long interval. Cuttlefish flexibly adapt their foraging behavior according to the delay of replenishment of different preys, which represent the first episodic-like evidence in an invertebrate.

### What-Where-Temporal Order (Relative Timing)

Another way to investigate episodic-like memory is to consider the “when” component as a relative occurrence of the event. In their study, Fortin et al. (2002) showed that rats could remember series of odors previously encountered presented without any specific spatial cues, while rats impaired with hippocampal lesions showed severe and selective difficulty to recall the sequential order of the series of odors. However, rats with hippocampal lesions were able to recall odors that recently occurred. Hippocampus is known to be involved in episodic cognition. Authors argue that hippocampal network is associated with sequential events composing an episodic memory as rats could remember which odors (what) occurred in which order (when) and in which location (where). In another study, rats were trained to remember a sequence of four odors displayed in four different locations on a platform (Ergorul and Eichenbaum 2004). According to the authors, rats were able to recall which combination of odors (“what”) was presented in which location (“where”) and in which specific order (“when”).

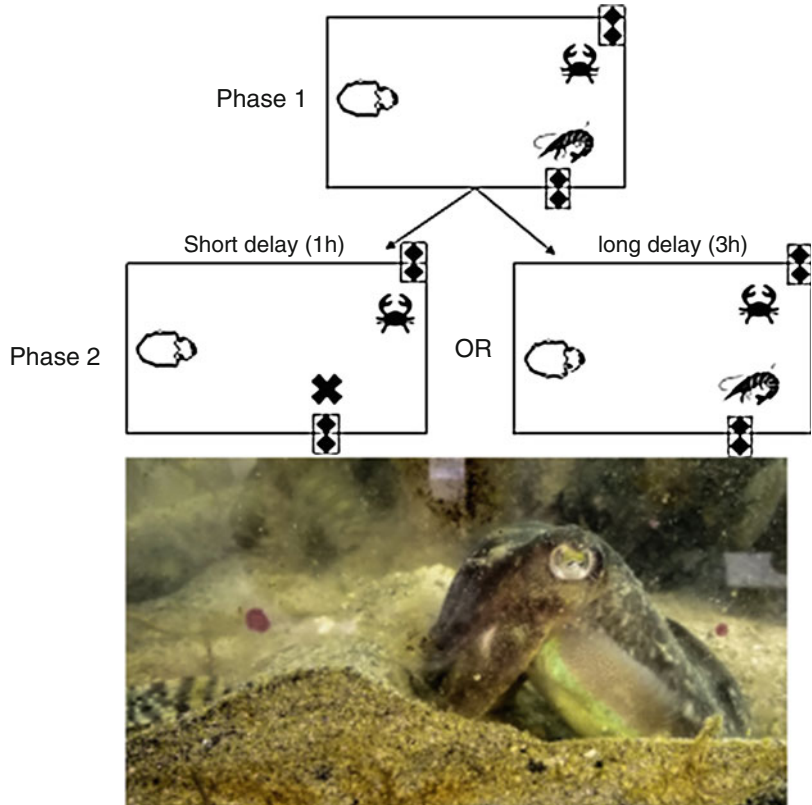
### What-Where-Which

In the original what-where-when paradigm, context was mostly defined as the place and time in which the event took place. Some researchers argue that the “when” component serves to distinguish the remembered event with similar experiences and therefore to context, as opposed to the temporal representation which is important



**Episodic Memory,**

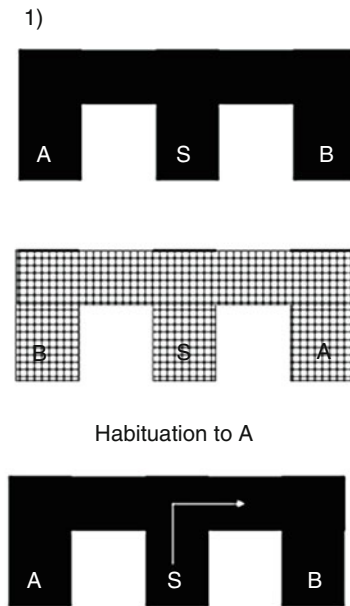
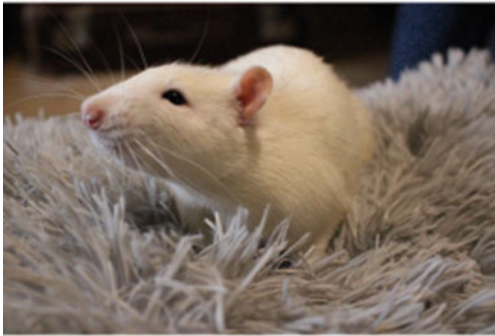
**Fig. 2** Procedure of the Jozet-Alves et al. (2013) what-where-when task. Each trial consists of two phases: during Phase 1, the cuttlefish learn which prey is associated with which visual cue; during Phase 2, the cuttlefish are tested either after a short (1 h) or a long (3 h) delay. After the short delay, the nonpreferred prey is available but not the preferred prey. After the long delay, both prey is available



E

(Eacott and Norman 2004). Thus, the “when” component can be changed into a unique “which” component retrieving contextual information and being comprised in an integrated representation of what-where-in which context episodic-like memory. Moreover, the original what-where-when paradigm relied on natural food-storing habits of scrub jays, and the adaptation of the paradigm with different species can be somewhat tricky. Eacott and Norman (2004) have based their paradigm on the natural tendency of rodents to explore novelty leading to a preference for exploring a novel object over a familiar one. Object recognition tasks are made of two main phases. In the first phase, animals are presented with several objects. In the second phase, a familiar and a novel object are presented at the same time. As rats are neophilic, they will explore significantly more time the novel object instead of the familiar one. In their study, during the test session, rats were presented with two familiar objects in a specific context and location. One of the objects was placed in the same context and

location than previously, but the other object was placed in another context and location. Results showed that rats explored more time the object placed in another context and location, showing that rats formed integrated representation of the object, the context, and the location at the encoding. In a more recent study, Eacott and Easton (2007) replicated the what-where-which experiment with another protocol. In their study, rats were placed in an E-shaped maze presented in a specific context (e.g., black). During 3 min, rats could explore the maze where two novel objects (A and B) were placed in the left and right arms. Then, rats were placed in a similar E-shaped maze in a different context (e.g., mesh). Similarly, they could explore the maze for 3 min where the same objects were placed in reverse locations. After this exploration phase, rats were placed for 8 min in habituation chamber with one of the object (e.g., A). At test, rats were placed in one of the previous contexts with objects in their context-specific location. Results showed that rats explore significantly more the unhabituated object showing



**Episodic Memory, Fig. 3** Procedure of the Eacott and Easton (2007) what-where-which task. Rats were placed in the start arm (S) in the E-shaped maze in one context. After 3 min of exploration of two novel objects (A and B), they were placed in a second E-shaped maze in a novel context,

with the same objects in reversed position for further 3 min. Rats were then transferred into a habituation chamber with the object (e.g., A) before returning to one of the previous context

that rats were able to recall what-where-which episodic-like memory (Fig. 3). This modified version of the episodic-like memory was also used in domestic animals showing that this cognitive ability is not negatively impacted by domestication. In an adapted version of the what-where-which task, domestic pigs (*Sus scrofa*) showed similar abilities to recognize the less familiar object/location/context configuration (Kouwenberg et al. 2009). Episodic-like memory for the context was also showed in zebrafish (*Danio rerio*; Hamilton et al. 2016). Fish were able to remember which object they previously encountered, in which location, and in which context they saw it.

### Other Ways to Investigate Episodic Cognition

The what-where-when paradigm is now a widely renowned paradigm to investigate episodic-like memory. However, other ways are also used

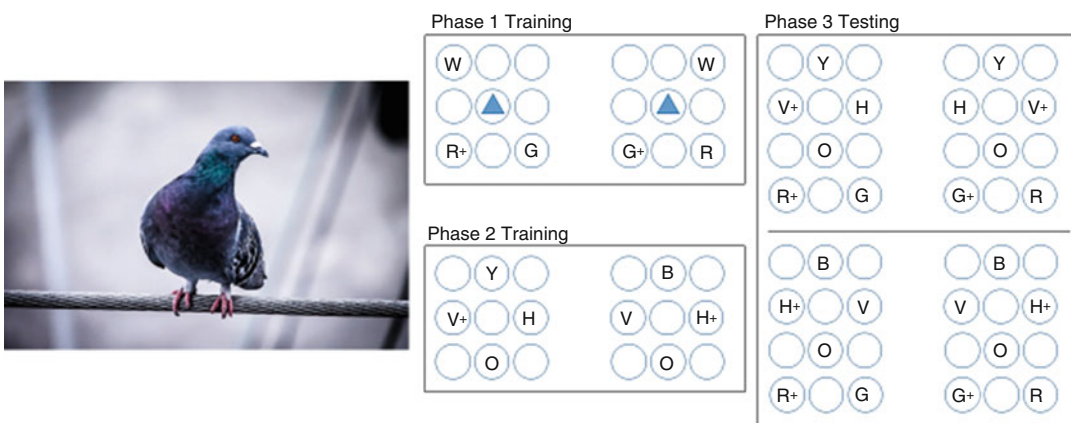
to address episodic-like memory. First, some researchers question the validity of this paradigm suggesting that it would rely on semantic rather than episodic processes. Indeed, the investigation of episodic-like cognition in animals often depends on rule learning procedures, and researchers argue that animals expect of being asked. It would then be necessary to investigate episodic-like cognition with “unexpected questions” to ensure that animals do not perform a task with semantic information processing. Another way to assess episodic-like memory is to study source memory which is the ability to retrieve the origin of a memory. Source memory specifically allows to distinguish between two episodic memories by remembering specific features of the episodic memory which were present when the memory was formed.

### Unexpected Question

To ensure that the what-where-when criterion for episodic-like memory is dissociated with semantic memory processes, Zentall and collaborators (2008) suggested to investigate episodic cognition

in animals using an “unexpected question.” They argue that most research with animals is based on rule learning procedures, such that animals are presented with classical conditional discrimination associated with retention intervals. For the authors, the what-where-when task for animals would actually rely on semantic memory or rule learning instead of episodic memory because animals expect to be asked to retrieve a specific information. In their experiment, pigeons were trained in a conditional discrimination task. Animals had to discriminate between colors (red vs. green) and positions (vertical vs. horizontal) according to an initial stimulus displayed at the beginning of the trial. Colors were associated with the position of this initial stimulus (e.g., if the initial stimulus was displayed on the left side, pigeons had to peck a red key and inhibit pecking a green key), and position discrimination was associated with the color of the initial stimulus (e.g., if the initial stimulus was yellow, pigeons had to peck the vertical key). At the end of vertical versus horizontal discrimination, if the correct comparison has been selected, pigeons were rewarded by pecking an orange key. At test, pigeons were presented with similar position

discrimination task, except that pecking the orange key was followed by red and green key choice. The red and green keys were reinforced equally. Results showed that pigeons remembered the rule associated with the red/green discrimination (i.e., choose the color according to the left/right location of the preceding stimulus) even though the question was completely unexpected. Other researchers used unexpected questions to investigate episodic memory, for instance, Skov-Rakette and collaborators (2006). They used a what-where-when paradigm asking pigeons in three separate matching-to-sample tasks (old-new recognition task: in matching-to-sample tasks, animals are rewarded if they respond to a stimulus that was encountered recently) (Fig. 4). In the “what” task, pigeons had to select the recently presented item. In the “where” task, animals had to select the location where the stimulus was recently presented, and in the “when” task, pigeons had to report how long ago the stimulus was encountered (3 s vs. 6 s). Once these tasks were learnt, the pigeons were presented with an unexpected configuration of the experiment in which pigeons had to perform the different tasks in random order. Animals could



**Episodic Memory, Fig. 4** Procedure of the “unexpected task” designed by Zentall et al. (2008). During the first phase, animals were trained to peck a side key (W) and then to peck a center triangle. If the initial side key was on the left, pigeons had to peck the red key (R+) to get a reward. If the initial key was on the right, pigeons had to peck the green key (G+). The position of the red and green comparison stimuli was counterbalanced. During the

second phase, yellow and blue keys were associated with vertical- and horizontal-line comparison stimuli, respectively. Pigeons had to peck the orange key (O) on the center, which was reinforced if the correct comparison had been selected before. Test trials replicated the second phase procedure except that a peck to the orange center key was followed by choice red and green side keys

not expect which tasks or which stimuli were going to happen next.

This “unexpected question” paradigm was also used in mammals such as rats which incidentally learned the presence or the absence of food in a radial maze and were unexpectedly asked about it (Zhou et al. 2012).

### Source Memory

Another way to investigate episodic memory is to consider the source of the memory, in other words a conscious awareness about how one knows about the informational content of the memory, for example, did I read it or did I hear it? Another way of expressing this idea is to argue that the “memory of the source” allows one to retrieve the origin of the memory by recollecting the information encoded when the memory was formed, constituting the context of the prior situation, and making the memory episodic. Source memory is essential in everyday life as it contributes to control the reliability of our beliefs, ideas, and memories (Johnson et al. 1993). Troubles in recalling the source of information can be very disturbing and, in the worst cases, lead to delusion and confabulation (the memory of the source contributes to the subjective experience of autobiographical recollection (i.e., the feeling that a memory belongs to one’s own past; Johnson et al. 1993)). Indeed, the information contained in the memory (e.g., perceptive, contextual, sensitive, cognitive, semantic, affective) allows to relive the event encoded and to recognize the memory as belonging to one’s own past. It is important to mention that source memory is not fundamentally different from episodic memory, but rather it is part of the mental time travel process. (Both are linked such as one leads to the other) When retrieving the source of a memory, the information is not simply accessed, but combined with cue information in an integrated representation, forming the episodic memory (Tulving 1983). The source-monitoring framework of Johnson et al. (1993) describes the processes involved in making attributions about the origins of a memory, knowledge, or beliefs. They postulate that during remembering, records are evaluated and attributed to a particular source through decision processes. These decision

processes would allow retrieving of specific features labeling the memory, specifying a memory’s source. The ease and the accuracy with which the source of a memory is identified would be determined by the type and the amount of the memory characteristics reactivated in memory records (e.g., spatial, temporal, social context, perceptual, sensitive stimulations, or again cognitive operations), how unique these characteristics are for given sources, and the efficacy of the judgment processes by which sources decisions are made. Some characteristics are less significant than others to recall the source of a memory, depending on the prior situation. For instance, one can remember having been to the beach because he remembers the heat of the sun, the noise of the sea, the persons he was with, or the activities he did. In other words, the perceptive, sensitive stimulations and the social context are really significant to recall the source of this information. In another hand, the cognitive operations he performed during the prior situation will be less likely remembered and evaluated to determine the source of this memory.

Jonathon Crystal’s work with rats constitutes one of the first reports about source memory in animals (Crystal et al. 2013). In this study, rats had to remember whether they had encountered a preferred food (chocolate) with self-generated cues (i.e., finding the chocolate by themselves) or experimenter-generated cues (i.e., placement of the rat at the chocolate site) cues. When rats found the chocolate by themselves, they had the possibility to retrieve it at the same location, whereas when they were placed by the experimenter in the chocolate location, the latter was not refilled afterward. Rats selectively adjusted revisits to the chocolate location based on source information. When the experimenters temporarily inactivated the CA3 region of the hippocampus with lidocaine, performances during this task were impaired. This result suggests that source memory is dependent upon an intact hippocampus.

Source memory has also been investigated in great apes with delayed matching to sample procedure where monkeys showed cross-modal recognition abilities of conspecifics (i.e., they

confused the identity of a monkey they saw with a monkey they heard; Adachi and Hampton 2011) or using item and source memory dissociation (i.e., monkeys learned to select the image from one source and to avoid the other; Basile and Hampton 2017). However, the study of source memory in animal is really underrepresented in the scientific community, and there is an urgent need to design behavioral tests to investigate it.

## Episodic Future Thinking

In this entry, we have focused on the retrospective component of episodic cognition. Episodic future thinking (or episodic foresight) is the ability to pre-experience (i.e., imagine) or anticipate future personal events. At first, it seems that episodic memory and episodic future thinking represent two opposite sides of mental time travel. However, there is growing consensus that episodic memory is intrinsically linked with episodic future thinking. Scientists argue that the real function of episodic memory would be to increase survival and fitness in present situations and future potential scenario. Thus, episodic memory would not be a memory of the past only but would actually be turned toward the future. Memories are made for the future: that's why they are so labile and flexible and forward-looking.

Investigating episodic foresight requires behavioral criterion as well. Behavior will have to be independent of current motivational state to be considered as demonstrating episodic foresight. This criterion is crucial because two identical behaviors can have totally different meaning in terms of episodic foresight. As an example, this morning I went to buy some food because I was hungry; it does not represent an anticipation on future needs as my behavior answers a current motivational state (i.e., hunger). However, if I went to buy food while being satiated because I know that I will be hungry in the evening, it can be considered as an episodic anticipation of future needs.

The Bischof-Köhler hypothesis postulates that animals always act following current motivational goals, leaving the ability of episodic foresight

unique to humans. However, studies demonstrate that animals show future-thinking abilities in a wide variety of domains. As an example, recent studies have shown that rats mentally pre-experience navigation and route planning, where hippocampal activations were similar when the rodents travelled through the routes and when they were about to pursue them (Pfeiffer and Foster 2013). Emery and Clayton (2001) showed that jays were able to adjust their caching strategies to reduce the risk of being stolen by a conspecific. Birds could cache food either in private or being observed by another bird. The interesting finding was that birds that have stolen another bird's caches previously then re-cached their food at recovery when they had the opportunity to do so in private, whereas naïve birds that had not experience of stealing from another bird did not re-cache their food. This result shows that re-caching behavior is triggered by previous personal experience of stealing. In other words, birds having stolen from another bird rely on their previous experience of stealing to adjust their caching strategies, which constitutes evidence for future-oriented behavior. After all the only point of re-caching the food is if one is able to recover it at some point in the future.

Other studies have shown that Californian scrub jays (*Aphelocoma californica*) would cache the food type that they wished to eat at the time of recovery as opposed to at the time of caching (i.e., their current need is not the same at the time of caching), thereby demonstrating that they could cache with the future in mind and dissociate current from future motivational states (Correia et al. 2007). Subsequent studies with Eurasian jays (*Garrulus glandarius*; Cheke and Clayton 2012) demonstrated that these birds could also cache for two future motivational states. Studies of tool use and forethought showed that chimpanzees (*Pan troglodytes*) and orangutans (*Pongo abelii*) were able to select a convenient tool to obtain a food reward in the future independently of their current motivational state (Osvath and Osvath 2008). Recently, similar findings were found in ravens (*Corvus corax*; Kabadayi and Osvath 2017) and in New Caledonian crows which were able to plan ahead on sequence of



tool behavior in metatool problems (Gruber et al. 2019). Taken together, these studies show that corvids can remember specific past events about what happened where and when and can also plan ahead, flexibly adjusting their strategies based on what they predict about what the future will hold, and that they can make these cognitive decisions independently of current desires.

## Conclusion

According to Tulving's definition, episodic memories consist of recollections of what, where, and when a past event occurred (Tulving 1972). Based on this conception, Clayton and Dickinson (1998) suggested three behavioral criteria for assessing episodic-like abilities in animals, devoid of the complications of the phenomenological characteristics that accompany human episodic memory and are evaluated through verbal report. Clayton and Dickinson (1998) were the first to demonstrate episodic-like behavior in a nonhuman species by developing this what-where-when behavioral paradigm. Subsequent studies have shown that episodic-like memory is found in a wide range of species including mammals, birds, fish, or invertebrates. Although all of these studies have used a what, where, and when paradigm of some sort, the "when" component has been investigated in multiple ways. Some studies have focused on how long ago the event was encountered following Clayton and Dickinson's original paradigm, while others have studied the relative occurrence of the stimulus (i.e., temporal order; Fortin et al. 2002; Ergorul and Eichenbaum 2004) or the context encoded with the event ("which"; Eacott and Norman 2004; Eacott and Easton 2007; Kouwenberg et al. 2009; Hamilton et al. 2016). Contextual information is specifically investigated in source memory studies, as source memory is the capacity to recall the origin of a memory, that is, recalling specific features pertaining to the encoded event (e.g., temporal and spatial location, perceptual, sensitive, cognitive information). Source memory raises the question of the link between episodic and

semantic memory as it involves decision-making processes and judgments about the episodic memory. Some researchers suggest that the what-where-when paradigm involves no more than semantic process, and it has been proven to be difficult to create a what-where-when experiment without rule learning explanation. A possible alternative would be to add an unexpected question as proposed by Zentall et al. (2008) whose aim is to provide animals with a novel configuration of the task, where animals have to use previously acquired incidentally encoded knowledge to formulate an answer (i.e., encoded without the expectancy of being asked).

Young children, just like animals, cannot verbally relate their previous past experiences, and researchers need to use a similar behavioral approach to investigate their episodic cognition. Some researchers, for example, Russell and Thompson (2003), have done just this by applying the food caching paradigm (Clayton and Dickinson 1998) and testing preverbal children aged between 14 and 25 months. Their results showed that children between 22 and 25 months could perform the task above chance, reproducing scrub jay performance. Other behavioral studies were used to investigate deferred imitation and source memory in preverbal children. Interestingly, these studies show that nonverbal animal tasks can be reliably used with preverbal children, which can help to follow the ontogenetic trajectory of episodic cognition. Taken together, these studies provide evidence that animals do have episodic-like memory. At issue is whether and to what extent episodic-like memory is like episodic memory, in other words whether the ability to remember unique past experiences about what happened where and when involves mental time travel with all its associated phenomenological construes. It is a question that remains controversial, but it is fair to say that the behavioral components of episodic memory, in particular the what-where-when methodology, have led to the development of a comparative cognition approach, from corvids to cephalopods and chimpanzees and from the nonlinguistic to the preverbal.



## Cross-References

- Cognition
- Comparative Cognition
- Comparative Psychology
- Corvids
- Declarative Memory
- Encoding
- Endel Tulving
- Hippocampus
- Jonathon Crystal
- Long-Term Memory
- Memory
- Nicola Clayton
- Primate Cognition
- Rodentia Cognition
- Stuck-in-Time Hypothesis

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## Epistasis

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## Synonyms

Epistatic interaction; Gene interaction

## Definition

Epistasis is a genetic phenomenon in which the function of one genetic locus is affected by the product of another genetic locus.

## What is Epistasis?

### Introduction

The term epistasis has originated from the Greek root words “epi” meaning “upon” and “stasis” meaning “stopping.” This terminology highlights the essence of the genetic phenomenon epistasis; the ability of one gene to bring about stoppage or affect the functionality of another gene’s function. Or to put it in a different perspective, it is the dependency of one gene’s functionality on the modifying effect of other regulatory “epistatic” genes (Alberts et al. 2014).

Usually, epistasis takes place due to the interconnected nature of the pathways on which the gene products operate (Sanders and Bowman 2014). Often, the final phenotype is produced by combinatorial effect of gene products from multiple loci. An alteration in a pathway at one place can have far-reaching effects, such as rendering downstream effectors nonfunctional (Watson 2014).

## How to Detect Epistasis?

The traditional and simplest way to detect the presence of epistatic interactions between two genes is by examining the phenotypic ratios of the F2

generation offspring of a dihybrid cross (Phillips 2008). In the first generation, homozygous parents differing in allele composition at two loci are mated. The F1 generation is heterozygous at both the loci, inheriting alleles from both parents. Mating between heterozygous individuals of F1 generation is the actual dihybrid cross and it produces F2 generation offspring. In absence of epistatic interactions, the phenotypic ratio of F2 generation is expected to be 9:3:3:1, as can be easily demonstrated by the punnet square (Russell 2005).

How to Interpret the Punnet Square?

The punnet square is used to diagrammatically represent the possible outcome of a cross, such as a dihybrid cross (Snustad and Simmons 2003). As it is evident from Table 1, the dominant alleles are expressed without any epistatic interference and give rise to the 9:3:3:1 ratio of phenotype among the offspring. Nine genotypes have at least one copy of each dominant allele and express the dominant phenotype of both loci. Three genotypes have at least one dominant allele of gene A and two recessive alleles of gene B. Hence they show dominant phenotype of gene A and recessive phenotype of gene B. Three genotypes have at least one dominant allele of gene B and two recessive alleles of gene A. Hence they show dominant phenotype of gene B and recessive phenotype of gene A. One genotype has two recessive alleles for both loci and thus shows recessive phenotype for both genes.

Distinguishing Linkage and Epistasis

A shift from the expected 9:3:3:1 ratio indicates epistasis or linkage (Russel 2009). Linkage can skew the expected phenotypic ratio. The extent of

shift in linkage is dependent on the intergenic distance between the loci under consideration and is a continuous phenomenon. On the other hand, epistatic interactions give rise to definite fixed ratios of offspring phenotypes, depending on the type of epistasis. Epistasis also causes clubbing of two or more phenotype classes into one. Thus a reduction in phenotype classes is an indicator of epistatic interactions. By studying the observed ratio, one can draw inferences about the type of epistasis in play. Some of the most important epistatic interactions are described as follows:

Dominant Epistasis

In dominant epistasis, the dominant allele at one locus masks the phenotype of both alleles at the second loci.

For example in foxgloves, allele B produces dark-red pigment and allele b produces light-red pigment in flowers. At loci A, recessive allele a causes pigment distribution in flowers while dominant allele A restricts pigment distribution. As a result, the presence of dominant allele A renders flowers colorless irrespective of the allele composition at loci B.

It is characterized by a 12:3:1 phenotypic ratio. Twelve genotypes have at least one copy of allele A and therefore would produce colorless flowers. This is dominant epistasis at work. Rest four genotypes have two copies of allele a and thus they are colored. Three of them have at least one copy of dominant B allele and are dark red while one is light red due to presence of two copies of recessive allele b.

Recessive Epistasis

In recessive epistasis, the presence of two recessive alleles at first locus masks the phenotype of both alleles at the second loci.

For example, gene A is responsible for eumelanin synthesis and gene B controls eumelanin distribution in certain dog breeds. In the presence of allele B, eumelanin distribution is complete while allele b reduces eumelanin distribution. As long as at least one copy of allele A is present coat color is either black due to presence of allele B or chocolate due to reduced distribution by two copies of allele b. In recessive homozygous offspring having two

Epistasis, Table 1 Punnet square showing offspring genotype of a dihybrid cross

|              |    | Female gametes |      |      |      |
|--------------|----|----------------|------|------|------|
|              |    | AB             | Ab   | aB   | ab   |
| Male gametes | AB | AABB           | AABb | AaBB | AaBb |
|              | Ab | AABb           | AAbb | AaBb | Aabb |
|              | aB | AaBB           | AaBb | aaBB | aaBb |
|              | ab | AaBb           | Aabb | aaBb | aabb |

copies of allele a, no eumelanin is synthesized and hence coat color is yellow, irrespective of allele composition at loci B, which control distribution of allele A generated eumelanin.

It is characterized by 9:4:3 phenotypic ratios. Four genotypes contain two copies of recessive alleles of a and thus have yellow colored coat. These are the individuals in which the recessive epistasis is operative. Recessive allele a in homozygous state masks the phenotype at locus B.

Nine genotypes possess at least one copy of allele A and at least one copy of allele B and hence are black. Three genotypes have at least one copy of allele A and two copies of allele b. Therefore they have reduced pigment distribution and have chocolate coat color.

### Duplicate Recessive Epistasis

This is also known as complementary gene interaction. Dominant functional alleles at both loci are required for the resultant phenotype. Presence of homozygous recessive alleles at either locus masks the phenotype.

For example, allele A and allele B produce enzymes which act on a biosynthetic pathway to produce purple flower color. Precursor X is converted to precursor Y by allele A. Allele B converts precursor Y to product Z, which gives purple color to the flower. In the absence of either dominant allele, product Z would not be formed and the flowers would be colorless.

This interaction is characterized by a 9:7 phenotypic ratio. Seven genotypes lack either dominant allele A or B or both and are thus colorless due to lack of complementarity between allele A and allele B products. The rest nine genotypes have at least one copy of dominant allele at each locus. As a result they can form the purple color-generating product Z and the flowers are colorful.

### Duplicate Dominant Epistasis

This is also known as duplicate gene interaction. In this case, dominant alleles at both loci have the same function. Hence, the presence of functional dominant allele at either locus is sufficient to give rise to the resultant phenotype. This is an example of redundancy in the biological systems.

Petal colors in snapdragons are governed by duplicate gene interaction. Both dominant allele

A and B can convert the precursor into functional pigment that gives color to the petals. It is characterized by a 15:1 phenotypic ratio. Only the double recessives are colorless. Rest of the 15 genotypes possess at least one copy of dominant allele on at least one locus and are thus capable of producing colored petals.

### Dominant Gene Interaction

In this interaction, dominant allele at either locus produces an identical phenotype but gives rise to a different phenotype when both dominant allele products are present.

For example, in squash fruit, double recessives give rise to long fruit shape. Dominant allele at only one locus gives rise to spherical fruit, irrespective of whether it is allele A or allele B. Both allele products seem to synthesize proteins which can produce spherical shaped fruit. Interestingly, in presence of dominant alleles at both loci, disk-shaped fruit is produced. Both allele products interact to produce this new phenotype.

It is characterized by a 9:6:1 phenotypic ratio. Nine genotypes have at least one dominant allele at both loci and thus interact to form disc shaped fruit. Six genotypes have dominant allele at only one locus and thus give rise to spherical fruits. One genotype is double recessive and produces long fruit.

### Dominant Suppression

In case of dominant suppression, the dominant allele at one locus suppresses the dominant allele phenotype at the second locus.

For example, feather color in chicken requires the dominant allele A that converts colorless precursor to colored pigment. Recessive allele a is unable to cause this conversion and hence recessive homozygous condition for allele a causes chicken to be colorless. Dominant allele B at the second locus causes inhibition of allele A function. As a result, the presence of copy of allele B suppresses allele A phenotype and chicken have colorless feather.

This is characterized by a 13:3 phenotypic ratio. Thirteen genotypes show colorless feathers. Nine out of 13 genotypes have at least one copy of dominant A allele but the simultaneous presence of at least one copy of dominant B allele masks the allele A phenotype. These nine are the offspring in which the actual dominant suppression is taking

place. Rest of the four genotypes are recessive homozygous for allele a and hence are anyways going to produce colorless phenotype, irrespective of presence (three genotypes) or absence (one genotype) of allele B. Three genotypes show the colored feather phenotype. These have at least one copy of functional allele A and no copies of functional inhibitor allele B, i.e., recessive homozygous for allele b.

### Epistasis in Humans

Just like in other organisms, epistasis is seen in humans too. The Bombay phenotype is an example of epistatic interaction.

ABO blood group is coded by gene I of which allele  $I^a$  and  $I^b$  are codominant. Allele products of  $I^a$  and  $I^b$  are glycosyltransferases and they act on the precursor oligosaccharide (H-antigen) to add N-acetyl galactosamine or galactose respectively to form antigen A or antigen B. The nonfunctional allele  $I^o$  produces no functional enzyme and hence does not modify the precursor oligosaccharide.

For the effect of  $I^a$  and  $I^b$  to be observed, the formation of the precursor is essential. Gene H controls the formation of precursor H-antigen by adding a fucose to its precursor. Dominant allele H is required for addition of fucose to the precursor of H-antigen. In recessive homozygous individuals containing two h alleles, no H-antigen is formed. As a result,  $I^a$  and  $I^b$  allele products cannot act in absence of H-antigen and the phenotype is similar to that of nonfunctional  $I^o$  allele. Thus the gene locus H has an epistatic influence on the gene locus I (Snustad and Simmons 2003).

### Conclusion

It may be concluded that epistatic interactions are highly prevalent in all forms of life. Understanding the epistatic relation between genes is essential for unravelling the complex network of interactions that take place at the molecular level to bring about the phenotypes visible to us.

### Cross-References

- Additive Genetic Variance
- Alleles

- Crossover
- Frequency Distribution of Phenotypes
- Genes
- Genotype
- Heredity
- Homozygosity
- Mendel's Laws
- Mendelian Crosses
- Recessive

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### Epistatic Interaction

- Epistasis

### Equal Environments Assumption

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### Synonyms

Twin study method

## Definition

The equal-environment assumption (EEA) is a biometric model that predicts how far the monozygotic (MZ) and dizygotic (DZ) twins are correlated to each other upon their exposure to environmental effects which are of etiologically significance to the trait/traits under consideration (Kendler et al. 1993).

If EEA is not accurate in assessing the extent of correlation between MZ and DZ, then the considered additional similarities or traits based on genetic factors might be alternatively explained by environmental impacts.

The basic principal postulation of the twin method has been attributed by the fact that both MZ and DZ twin pairs are reared together experience similar environmental effects (Siemens 1924).

## Background Description

In 1968, Scarr introduced a test of EEA which assesses the influence of phenotypic similarity in twins of assumed versus true zygosity. After his discovery in course of time, numerous research innovations have been proposed to measure the heritabilities of wide variety of traits like height (Visscher et al. 2006) to autism (Liu et al. 2010) and even food preferences (Breen et al. 2006). However, many assessments for twins are based on twin pair analysis. Therefore, it is dependent on strong assumptions about the relative environmental likeness and its impact on modulating the development of identical (MZ) and fraternal (DZ) twins.

Since 1920, scientists in psychology and psychiatry also have employed the “classical twin method” to assess genetic elements governing psychological traits such as IQ and personality (Joseph 2004). This is because of the fact that fostered-together MZ pairs share 100% of their segregating genes, whereas under similar circumstances DZ share only 50%. Twin researchers have argued over the fact that MZ pairs resemble each other more for behavioral characteristics and disorders than do same-sex DZ twin pairs. This is mainly caused by the former’s greater genetic

similarities over the other. At the same time, most reviewers of the twin method have claimed that MZ pairs experience much more alike environments than DZ pairs, and consequently this greater environmental parity surprises genetic interpretations of twin method data (Joseph 2004). Looking back in time during 1960s most critics and many twin researchers agreed that MZ twin pairs experience more or less similar environments. They are treated more alike and are socialized to be more identical than DZ counterparts (Joseph 2004).

Societal connections impose a potential influence on shared physical features of MZ twins. MZ twins on an average are much closer to each other than DZ twins by a number of measures. Both this suggested closer bond between MZ twins and similar reactions from the family or society to the identically featured MZ twins could well encourage the behavioral enrichment of the children in the direction of greater similarity. In such conditions the incorrect acceptance of the EEA could lead to heritability estimations in twin studies that would be highly exaggerated, despite the fact that the characters under consideration were strongly environmentally influenced.

## Methodologies for Analyzing EEA

There are four major methodologies to test the weight of the EEA in twin studies (Kendler 1983).

1. In the first method the EEA predicts that resemblance in twins is governed by the similarity of impact by social environment which in turn reflects their degree of physical attributes.
2. The second method encompasses direct observation of twins in a social or family background where the behavior of other entities is divided into those which are self-initiated and which take place in response to twin behavior. In a study, it was found that very young twins and their parents hold excess resemblance in the parental treatment of MZ vs. DZ twins. The assessment was entirely directed to parental behavior which was in response to twin behavior.



3. The third method based on observations that definite and quantifiable parameters of the childhood and adult environments of MZ twins are more or less alike than that for DZ twins. As for example it has been surveyed that MZ twins generally share same dress or use similar kind of dresses, etc. which is not observable in case of DZ twins (Loehlin and Nichols 1976; Kendler et al. 1986, 1992c).

Moreover, as it has been found that adult MZ twins are much frequent in contact with each other than that of the same sex DZ ones (Kendler et al. 1986, 1992c; Rose et al. 1990). Now the problem arises, on account of the fact that if all the environmental experiences affect twin similarity then this might violate EEA interpretation. So in this case, the detection may be done by using correlative study by separating each of the zygosity group and assuming the degree of environmental influence on both childhood and adulthood (Loehlin and Nichols 1976). In this regard, Kendler and his group found that there were no observable association between childhood and adulthood environmental similarity for assessing certain psychological disorders. Therefore, this kind of study has certain limitations like the frequency of connection between adults to that of phenotypic similarity between twin pairs are very much unpremeditated and casual as addressed by Lykken et al. (1990). He also pointed out the fact that the degree of phenotypic resemblance may directly or indirectly impart relation with frequency of contact should considered as an influential factor.

4. The fourth method suggests a comparison of trait similarity as a function of both “real zygosity” as assessed by investigators and “perceived zygosity” as observed by twins and their parents (Scarr 1968). This study method has a definite advantage over the previous ones. In the previous studies, only one potential source is taken for assessment like dress used by twins but in this case investigators incorporate global test for all potential environmental factors that influence the zygosity associated attitudes and expectations.

## Application

- Twin study methodology is generally applied on the examination of physical similarity in different psychiatric disorders like major depression, generalized anxiety disorder, phobia, alcoholism, and bulimia.
- The applicability of EEA for MZ and DZ twin study may extend to both prenatal and postnatal environment.
- In utero, twins are distinguished in terms of whether they share a chorion, and thus have a single placenta. MZ twins can be of two types, like monochorionic (MC) or dichorionic (DC) depending on the timing of their division. On the other hand, DZ twins are always DC. MC twins always share the same placenta and if this makes them more similar than DC and DZ twins then a specific example of violation of the trait-relevant EEA (Prescott et al. 1999).
- Twins do not differ in terms of their disease-related features (Andrew et al. 2001). An entire issue of the journal *Twin Research* was based on the fetal origin of disease hypothesis (Lambalk and Roseboom 2001) whereas none of the articles dealt with behavioral phenotypes.

## Drawbacks

- Critics have debated over years that twin study method cannot unravel the potential roles of genetic and environmental influences on each other.
- On the other hand, geneticist from other disciplines like political science couldn't furnish convincing opinions than their predecessors in psychology and psychiatry in figuring out the inter-effect of environment and genes on each other (Joseph 2010).
- The study principle also could not nullify the tenet that EEA should be tested “trait-by-trait,” or rather specifies the evaluation, very similarly in a way that most of the behavioral geneticists currently assess the family studies.

## Concluding Remarks

The traditional twin method study between MZ and DZ is generally assumed by EEA. The associative environmental impacts correlative to MZ and DZ are also considered for the study. Numerous diseases and genetic disorders exemplifying the MZ/DZ conditions are basically assessed by EEA. Many of the MZ-DZ pedigree studies interpret several doubtful scientific outcomes thereby giving the entry to nonviable accesses of EEA study. Thus, sometime makes gateway to mislead operational definition, which would rather have been called “heritability.”

## Cross-References

### ► Heritability

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## Equality

### ► Inequity Aversion

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## Equational Division

### ► Mitosis

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## Equatorial

### ► Tropics

## Equestrianism

- [Horseback Riding](#)

## Equids

- [Equine Cognition](#)
- [Perissodactyla Cognition](#)

## Equine Cognition

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## Synonyms

[Cognitive ecology](#); [Donkey](#); [Equids](#); [Horses](#); [Human–horse interaction](#); [Social cognition](#); [Zebras](#)

## Introduction

The equids (Equidae) comprise zebras, donkeys, and horses. They are not considered to be independent taxa and can be crossbred, with wild animals sometimes crossbreeding in overlapping habitats. In general, the resulting equid hybrids are called zebroids (zebra and any other equid), mules (male donkey and female horse), or hinnies (male horse and female donkey). Other informal

labels include zebrules, dedonks, and zorses. The hybrids are usually infertile.

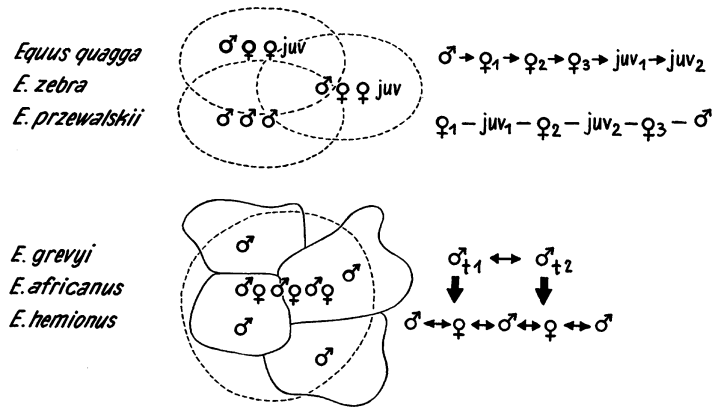
Equids differ in their social organization and have different habitats (Klingel 1972; Fig. 1). Some species are exclusively wild, and some include domestic types. In evaluating their cognitive capacities, it is important to consider the species' social and environmental challenges (Griffin et al. 2017). Only by knowing the conditions to which animals have to adapt can their cognitive capacities be compared in relation to other species. For example, if feral and wild equids do not encounter humans on regular basis, they may not need to learn how to read human-given cues, even though they may be able to do so when living close to humans. They may, however, need to learn to read cues given by other species with which they cohabit. Therefore, the equids' social systems and environments will briefly be described. The state of the art in cognition research will follow.

Cognition research is scarce in the wild species, the Przewalski's horse, zebras, and wild asses. This is mostly due to the fact that these species are difficult to observe because they avoid contact with humans, they live in remote areas, and because only a few animals are left in nearly extinct zebra and wild ass species. During the last two decades, cognition research in domestic horses has advanced in giant steps. For horses, only milestones in cognition research and some interesting approaches which are worth following up with are presented.

## The Zebras

### Social Organization

Zebras comprise three exclusively wild species, plains zebra (*Equus burchelli*), Cape mountain zebra (*E. zebra zebra*), and Grevy's zebras (*E. grevyi*). Zebra species can be assigned to type I and type II social systems (Klingel 1972; Fig. 1). Plains zebra (*E. burchelli*) and Cape mountain zebra (*E. zebra zebra*) live in the African Savanna and form type I social systems. They live in harem groups with several females, their offspring, and usually one or a few mature males.



**Equine Cognition, Fig. 1** Equid social systems. In type I social organizations, depicted above, females (♀), offspring (juv), and males (♂) live in mostly stable groups with usually one alpha male and several females and their offspring. Whereas in type II organizations depicted below,

males protect particular habitats and dominate loosely bonded females and males that travel through these areas (Klingel 1972). In recent publications *Equus quagga* is termed *Equus burchelli*, *Equus zebra* is *Equus zebra zebra*, and *Equus africanus* is referred to as *Equus asinus*

Surplus males gather in bachelor groups. Several of these subgroups may form herds of about 200 up to 1,000 animals (Klingel 1972). Mostly linear hierarchies are formed within and between subgroups, and animals are bonded with fellow group members, so they form so-called social bonds. The linearity of the hierarchies and the numbers of social bonds between group members varies from group to group (Fischhoff et al. 2007).

Grevy's zebras (*E. grevyi*) live in remote African mountains with little vegetation or water. They form type II social systems (Fig. 1). Solitary males defend a territory around a water source and mark the borders with feces (scent marks). The males claim mating rights over the females within their territory. Whether females form social groups depends on the resource availability. When food and water is scarce, females live alone with their offspring, but in periods with plenty of food and water, they form small groups.

### Social Cognition

Plains zebras protect their social bonds by intervening in the interactions of others (i.e., third-party intervention). Foals, yearlings, and adult mares intervene when certain group members exchange friendly (affiliative) behaviors. For example, they chase away an animal which grooms with their preferred group member.

Furthermore, yearlings and foals intervene when their mothers are attacked by stallions. They show submissive-type behavior, the so-called “snapping” or tooth clapping, which usually stops the aggression of the stallions immediately. Finally, stallions, in multi-male, bachelor groups, intervene in the courtship behavior of others, especially when females which are bonded to the intervening males are involved (Schilder 1990).

### Spatial Cognition and Movement Decisions

Abilities in spatial cognition allow plains zebras to find distinct paths for short- and long-distance movements (Brooks and Harris 2008). The exact mechanism is not certain. They use spatial memory to orientate on landmarks, but orientation on magnetic fields may also play a role.

Plains zebra group movements appear to arise out of a mix of cognitively undemanding self-organized movements and cognitively demanding decision-making. When movements are self-organized, group members synchronize their movements with other group members in their vicinity, mostly without making any decisions on whom to follow. However, zebras appear to decide whether to follow particular group members to some extent. For example, lactating females initiate movements toward water more often because of their enhanced need for water. Some zebras may

just follow more or less unconsciously, by movement synchronization. But, as the number of followers depends on the quality and the quantity of the initiating animal's social bonds within its group, it appears that zebras do make decisions about whether they follow all or just preferred group members (Fischhoff et al. 2007).

When Grevy's zebra females have to walk long distances to water sources, they have been described as leaving their sleeping offspring behind, while one or two mature animals stay with the "kinder garden" (Klingel 1972).

## The Donkeys

### Social Organization

Donkeys comprise the African wild ass (*Equus asinus*), Asian wild ass (*E. hemionus*), the Kiang (*E. kiang*), and domestic types (*E. asinus asinus*). Wild asses are close to extinction. All form type II social organizations (see above; Fig. 1). Some individuals in donkeys and wild asses appear to mark their territory with urine and feces (Klingel 1972). They avoid contact with humans and roam in steppe or semidesert habitats in very remote areas where they are not threatened by heavy hunting. In the past, herds comprised more than 1000 individuals, but this is now reduced to a few extant herds with less than 200 individuals.

### Social Cognition

So far, there has not been any research on cognition in wild asses, but some has been conducted in domestic donkeys. Anecdotal reports on strong bond formation between domestic donkeys have been scientifically confirmed. Donkeys recognize the individuals with which they are bonded and prefer to stay close to them (Murray et al. 2013).

### Spatial Cognition

Donkeys appear to have a good working memory for locations, for example, the point where food was removed from view through a barrier, and they demonstrated an understanding of object permanence, i.e., the understanding that objects which are not perceptible may still be present. They searched for a food bucket, which was

removed from view through a hole in the center of a simple V-shaped barrier by detouring around the barrier after ten and 30 seconds (Baragli and Regolin 2008). In a comparative approach, mules were superior to donkeys and horses in learning the position of a gap in a barrier. When the gap was moved from location A to location B, horses kept returning to the old, now closed gap (A), while mules and donkeys approached the old and the new gap (A and B) randomly (Osthaus et al. 2013). Mules and donkeys, therefore, showed a higher plasticity in reasoning about spatial conditions, i.e., in spatial cognition, than horses.

### Object Discrimination

When donkeys, mules, and horses were tested on how many pairs of particular patterns on paper cards they would learn to discriminate within 25 sessions. Five out of six mules, but only one out of six horses and none of the six donkeys achieved three different pattern pairs (Proops et al. 2009b). It has been suggested that the superiority of mules in discrimination learning is a matter of hybrid vigor. However, it remains a matter of debate whether the horses' gradual, and the donkeys' fast, decline in performance is due to attention loss rather than to discrimination learning capacities.

## The Horses

### Social Organization

The domestic horse (*Equus caballus*), the feralized domestic horse (*E. ferus caballus*), and the wild Przewalski's horse (*E. ferus przewalskii*) all form type I social organizations (Fig. 1), and they build social bonds with up to three partners. In contrast to the teaching of some traditional textbooks, harem and group stability varies considerably between groups. Some show stable core groups, but all-male "bachelor" bands are unstable in feral horse populations with only a few exceptions. Ninety to 100% of the male and 80–90% of the female offspring disperse from their natal groups when they reach maturity. Some females disperse and later return to their

original harems. Animals which frequently change groups are termed “switchers” (see for review: Linklater 2000).

### **Social Cognition**

Female horses form alliances for offspring protection. Their success in raising the offspring is higher when they are bonded to another female. Furthermore, horses protect social bonds through third-party intervention and seek for conflict resolution within their group. They intervene when horses are bonded to groom with others, and they chase aggressors away, especially when horses they are bonded to are challenged (Krueger et al. 2015). Horses even show post conflict resolution, by consolidating group members that were objects of aggression from others in the group. Uninvolved third parties (horses) stay close to and show friendly interaction toward recipients of previous agonistic interactions, i.e., winner–loser interactions, from which the challenged participant had to retreat (Cozzi et al. 2010).

The horses' social system can be described as a fission–fusion society. A fission–fusion society is characterized by frequent animal departures and returns within groups and within herds. Living in such a constantly changing system calls for the ability to identify departing and returning group members. In fact, horses identify their group members individually. They recognize group members by their whinnies, especially by calls which are used to stay in contact over long distances (Proops et al. 2009a). Furthermore, they recognize their group members by their outer appearance and the smell of their fecal marks (Krueger and Flauger 2011).

### **Humans: Part of the Horses' (Social) Environment**

The domestication of horses 3000–6000 years ago may have shaped interspecies communication abilities with humans (Fig. 2). Scientific evidence is yet to be established for the so-called domestication hypothesis in horses; this would require comparison between wild horses, domestic horses, and horses of different domestication durations and purposes, for their interspecies communication abilities. However, horses' skills

in responding to human facial and gestural cues have been known since the early twentieth century through the case of Clever Hans.

Clever Hans was claimed to have the arithmetic skills of a 12-year-old child. He presented the solutions to mathematical problems by tapping the number with his hoof. Although subsequent observations revealed that he could not count, he was, nevertheless, extremely skilled in reading subtle human facial expressions and body movements, which he used to decide when to begin tapping and when to stop. He even generalized the cues from his trainer to unfamiliar persons (Pfungst 1907).

The discovery of Clever Hans' “shortcut” to solving mathematical equations stigmatized cognition research in domestic animals, especially in horses, for about 100 years. Nobody dared to approach the evaluation of whether Clever Hans' skills in reading human given cues were unique or common in horses. Only in the last decade was research conducted in this area.

Today, we know that horses identify humans individually. Domestic horses are able to use human hand pointing gestures and human head and body orientation to find food. They orientate on the direction of human attention, for example, when humans turn away and stare in a particular direction. They distinguish between familiar and unfamiliar persons, generalize positive and negative experiences with humans from one person to another, and infer emotional states of humans from photographs. Some horses may have negative or positive expectations of human behavior acquired from previous encounters with humans. These expectations may even inhibit their performance in experiments. They may refuse to participate in a test if they believe humans will solve the task for them or if they are waiting for distinct signals to direct them to what they are expected to do (for human-horse interaction, see Hausberger et al. 2008; Schuetz et al. 2016).

### **Spatial Cognition and Movement Decisions**

Research in spatial cognition in horses is still puzzling. On one hand, short-term memory for the placement of objects and food has been said to be limited to 10–30 s. Furthermore, horses have been said to have a limited understanding of



object permanence, i.e., the understanding that objects which are not perceptible are still present, and limitations in some horses' spatial reasoning may hamper their performances in simple detour tasks (Baragli and Regolin 2008; Osthaus et al. 2013).

On the other hand, horses need cognitive capacities to stay with group members, to protect offspring, and to flee from predators together. Landscape cues have to be memorized for decisions on where to flee to and where to move the group to. A recent study on pattern discrimination showed that horses have a good spatial memory, and they prefer spatial cues over visible object-specific cues. They were better at memorizing the position of a food bucket and distal spatial cues in the experimental arena than at memorizing patterns on the food bucket (Hothersall et al. 2010).

Horses actively move other group members into a chosen direction. Group movements can be initiated by the despotic herding of alpha males, for example, in dangerous situations, when a larger or more dominant, competing group approaches the stallion shows herding posture and drives his whole group away. On the other hand, any group member may initiate movements by departure in Przewalski's horses and in feral horses (Kruger et al. 2014b). Movement initiations by departure are not exclusive to any particular individual, as has been claimed for so-called "lead" mares. Instead horses show a limited form of distributed

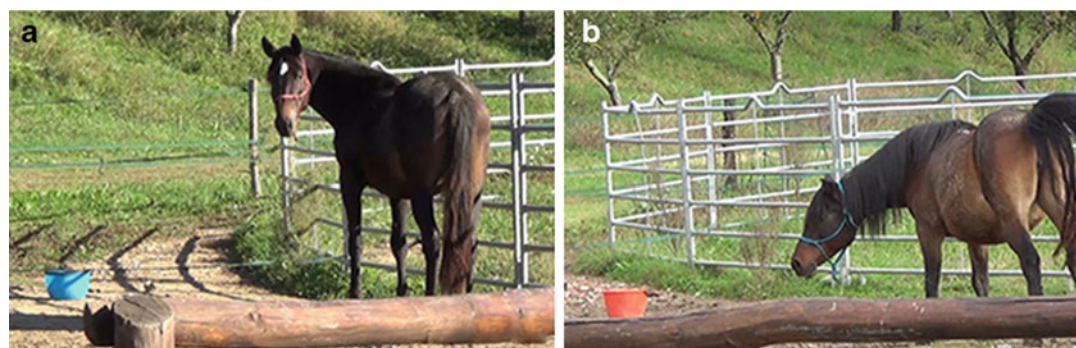
leadership, such that higher-ranking animals are followed more often, but no one individual has unique or permanent control over movement initiation (Kruger et al. 2014b).

Most horse movements appear to be self-organized, with individuals responding to the movement of other horses in their direct vicinity and with little need for cognitive decision-making. However, as in baboons, movement initiations of high-ranking, older horses may be perceived as being more reliable and therefore more advantageous to follow. The fact that social rank affects whether animals are followed or not implies that decision-making on the reliability of the potential initiator takes place (Kruger et al. 2014b). So far, recruitment of group members to join in the movement of an individual has not been observed in horse to horse interactions, despite expectations.

However, horses appear to recruit humans. Horses have shown distinct recruitment behavior toward humans when trying to direct humans to open a gate to allow access to food (Malavasi and Huber 2016; Fig. 2).

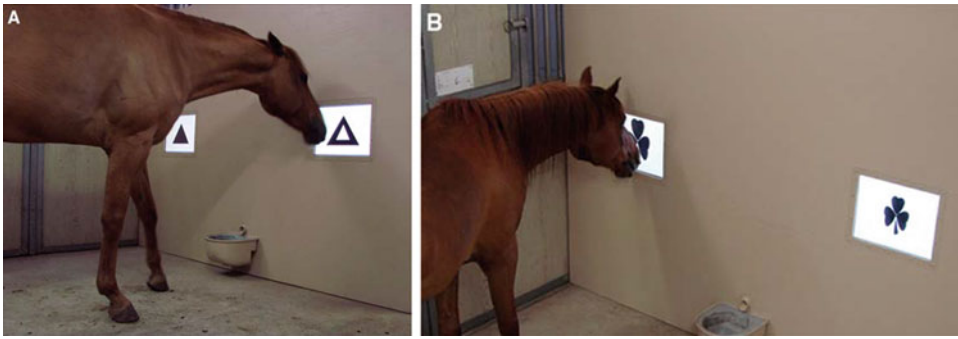
### Object Discrimination, Categorization, and Generalization

Object discrimination is the basis of recognizing landmarks for orientation and useful for recognizing food and predators. Some studies have shown horses to be able to discriminate precisely between



**Equine Cognition, Fig. 2** Human-animal referential communication in horses. Horses try to recruit humans to help them to get access to food, by (a) gazing to the experimenter or (b) pointing at a bucket with food behind a fence. The fence, a blue rope, is difficult to see. They

communicate their interest in the bucket to an experimenter facing in their direction, but showed less referential communication when the person turned around or walked away after releasing them into the experimental arena (Malavasi and Huber 2016)



**Equine Cognition, Fig. 3** Horses discriminate objects on computer screens. Horses were able to understand (a) the categories filled versus open center and (b) the concept small versus large (Hanggi and Ingersoll 2009)

objects. Horses learn object categories and concepts and even generalize them to unknown objects. For example, they learn the categories “filled versus open objects” and concepts of “always choose the smallest object” (Fig. 3). The horses applied the learned categories and concepts to test situations with unknown objects, and they generalized the categories and concepts. Two horses have also shown impressive long-term memories of 7 and 10 years for object categories and concepts (Hanggi and Ingersoll 2009).

Recently, it was demonstrated that Shetland ponies can distinguish numbers up to 5, by keeping pictures with different numbers of object apart, e.g., different numbers of dots of different sizes in different arrangements. This indicates that they have a concept of numbers. Some of the ponies were able to transfer the “number concept” to different symbols, such as triangles, rectangles, rhombs, and crosses (Gabor and Gerken 2014).

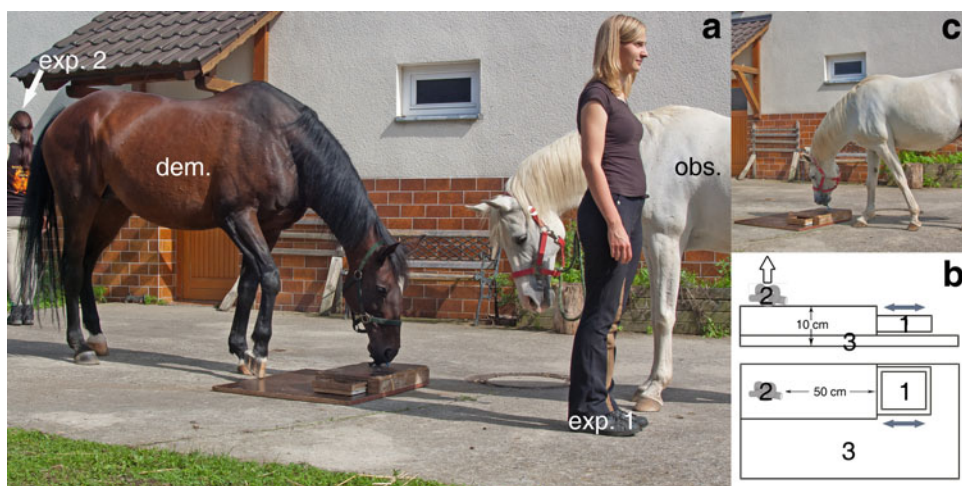
### Social Learning

Finally, the social intelligence hypothesis claims that animals that live in complex social systems face higher cognitive demands. They need to identify group members and deal with conflict. Horses are capable of both. Furthermore, animals would benefit from learning socially, from learning from others, in a complex social setting. For decades researchers had difficulties demonstrating social learning in horses, but now it has been established that horses can learn by observing other horses and from humans (Krueger et al. 2014a; Fig. 4; Schuetz et al. 2016).

An interesting finding has set the stage for further investigations into the topic. It started with the idea that imprinting training, in which humans confronted passive foals with stimuli of different qualities right after birth to decrease their fear, is ineffective. At the age of 3, horses which were imprinted when they were foals reacted as aversively to the presented stimuli as non-imprinted horses. However, grooming the dams for only 10 min a day caused the foals which observed this to show less aversive behavior toward humans (Haupt 2007; Hausberger et al. 2008).

Horses copy the social behavior of other horses, for example, they copy the following of a person, they adapt to the expectations of other horses when crossing a carpet, and they are fearful when others are fearful and confident when others are brave. They can learn to open a feeding box by watching another horse pulling a rope to open it (Krueger et al. 2014a; Fig. 4), and they can learn to open a feedbox by pushing a light switch after watching a familiar person doing it (Schuetz et al. 2016). Interestingly, horses learn from higher-ranking, older horses in their social group (Krueger et al. 2014a), which raises interesting, and so far unanswered, questions about their perception of familiar and unfamiliar persons.

Apart from individual trial and error learning, stimulus and local enhancement have been discussed as the primary social learning mechanism in horses (Krueger et al. 2014a; Schuetz et al. 2016).



**Equine Cognition, Fig. 4** Social learning in horses. (a) shows the situation in which a demonstrator horse (dem) opens a feedbox by pulling a rope. An observer horse (obs) watches the demonstration and the resulting opening of a

drawer with food. (b) depicts the feeding apparatus in detail: (1) is the opening drawer and (2) the rope which has to be pulled and (c) shows the successful observer (Krueger et al. 2014a)

### Effects on the Performance in Cognition Tasks

The performance of horses in cognition tasks may be hampered by environmental, individual, and social factors.

#### Environmental Factors: Housing and Management Conditions

Unsuitable housing and management conditions may cause severe stress and result in altered behavioral responses and cognitive capacities. Housing and management conditions hampered the learning efficiency in a test where horses learned to open a food box by lifting a lid. Horses with stereotypies, which are usually developed under unsuitable housing and management conditions, had poorer performance and also spent less time lying down and sleeping. The reduced resting and sleeping time may have affected the attentional state and therefore the learning efficiency of the horses (Hausberger et al. 2008). In another study, young more stressed, stabled horses took longer to complete standardized initial training on the ground and with a rider than less stressed, pasture-kept horses (Hausberger et al. 2008).

Horses under unsuitable management conditions may show depressive-type behavior, comparable to depressed humans. They “withdraw” into

themselves, and their reaction toward external stimuli, approaching humans, and other horses is altered. When confronted with auditory signals, horses with depressive-type symptoms responded on fewer occasions than control horses, but their low response rate was not reduced further by habituation to the signals. They continued responding to the signals on a low, altered level, while normal horses would stop responding after some repetitions (Rochais et al. 2016).

#### Individual Factors: Prior Experience and Temperament

Some horses may develop preconceptions regarding their participation in cognition tests which may also hamper their performance. Strong preferences for always choosing the same side of a test area (i.e., side biases) have been reported. Side biases may develop from habituation to the experimental procedure, from experiences within the test area, and from the animals’ laterality (for details see below). Apart from side preferences, decisions to go to the opposite side of the arena, when the side first approached was not rewarded, have been reported.

Such learning strategies may be affected by a cognitive bias, i.e., a bias of rating the learning

situation positively (optimistic) or negatively (pessimistic). Horses with a positive cognitive bias tend to judge uncertain situations to be rather pleasant or positive, while horses with a negative cognitive bias judge the same situation to be rather unattractive or negative. Environmental enrichment may cause a positive cognitive bias (Rogers 2010). For example, horses that were housed in single boxes experienced an environmental enrichment by the addition of turnout on pasture, in groups, during the day. This seemed to cause a corresponding positive cognitive bias. All the horses were trained to expect to be rewarded with food in a box when the box was located in specific spots in an arena and to expect no reward when it was placed in different specific spots. When the horses reached the learning criteria and consistently approached the box when it was in the “reward” positions, the box was moved to a neutral position between the trained “reward” and “no reward” positions. The horses that approached the box in the new, neutral, position were considered to have a positive cognitive bias (they had the expectation that the new position would be a “reward” one), and horses that did not approach the box in the new position were considered to have a negative cognitive bias (their expectation was that the new position was a “no reward” one). When the horses had daily turnout, they showed a positive cognitive bias that was not evident when they were fully stabled. However, the researchers suggest that this positive cognitive bias may decrease over time, possibly due to adaptation to the new housing conditions (Rogers 2010; Loeckener et al. 2016).

Animals may acquire a negative cognitive bias when they experience stressful situations while maturing (Rogers 2010). In mice, it has been shown that a strong negative cognitive bias goes along with a left shift in motor laterality, the preference for using a certain leg paw or foot. Recent studies (Marr et al. in progress) indicate that stress in maturing horses causes a left shift in motor laterality and in sensory laterality, i.e., the preference to use sensory organs on a particular side (Rogers 2010). The use of either the left or the right sensory organs and forelimbs appears to result from different responsibilities of the two brain hemispheres that are contralateral connected

to limbs, eyes, and ears. (Nerve tracts from the nasal cavities run to the brain hemispheres on the same side.) The left brain hemisphere is generally considered to be in charge of rational information processing, learning behavior, and responses to routine situations, while the right hemisphere is thought to be responsible for fight or flight reactions, processing emotions and the regulation of endocrine functions and heart rate. Changes in laterality may therefore indicate an altered emotionality and cognitive processing of information intake, i.e., a cognitive bias (Rogers 2010).

The temperament of horses has been shown to affect visual discrimination learning. Prior to a test, horses were assessed on whether they would react more or less emotionally when approaching novel objects. In the ensuing experiment, horses with a higher emotionality assessment required more trials to learn pattern discriminations in a test where yellow and black diagonal stripes indicated the place with a reward in a T-maze test (Hausberger et al. 2008). Similarly, neophobic horses had greater difficulties in learning how to open a feeding apparatus after observing a demonstrator horse (Krueger et al. 2014a). Furthermore, fearful and active Welsh ponies were most successful in learning to avoid a puff of air by jumping a fence, while the least fearful and most sensitive ponies were best in learning how to back up after a tactile or vocal command (Lansade and Simon 2010).

The exposure to particular training strategies may affect the animals' emotional state and their motivation to perform in cognition tests (Hausberger et al. 2008; Rogers 2010). The use of positive reinforcement (adding a pleasant stimulus to enhance the possibility that the behavior is shown more often), negative reinforcement (removal of an unpleasant stimulus to enhance the possibility that the behavior is shown more often), positive punishment (adding an unpleasant stimulus to reduce the possibility that the behavior is shown again), or negative punishment (removal of a pleasant stimulus to reduce the possibility that the behavior is shown again) can result in different emotional states. The animals' motivation to perform may differ depending on whether they experience a positive feeling about something pleasant when positively reinforced, a reduction of



psychological pressure when negatively reinforced, fear of something when being positively punished, or frustration when being negatively punished.

Horses with a chronic stress life history, for example, horses that were repeatedly stressed in previous management and handling, developed more exploratory behavior in a novel object test and showed a higher motivation for training, when they were positively rather than negatively reinforced while learning to be led by humans, stand still while being groomed, traverse an obstacle course, load into a trailer, and pick up their feet (Innes and McBride 2008).

### Individual Factors: Age, Breed, and Sex

Young horses learn faster in social learning tasks in which observer horses can learn how to open a feedbox by observing conspecific or human demonstrators (Krueger et al. 2014a; Schuetz et al. 2016). From a certain age (14 years in one study, see Krueger et al. 2014a), horses failed to learn the task. It has also been reported that only young horses learn to operate a feeding device in an individual learning test. However, it needs to be clarified whether older horses undergo a loss of motivation rather than a decline in cognitive capacities.

The breed may also be a factor in horses' performance in learning experiments. For example, a group of horses picked signs on paper cards to communicate whether they wanted a rug put on in windy and wet weather, a rug taken off when it was warm, or no change. Warmblood horses learned the communication faster than coldblood horses (Mendjell et al. 2016).

Interestingly, in a study which claimed horses' short-term spatial memory for the location of food declines after 10 s, differences between the breeds in behavior at the test waiting area were also reported. Warmblood horses were said to be the most patient, thoroughbred horses became nervous more quickly, and coldblood horses and ponies lost interest quickly and could not be persuaded to participate again once they had refused. Breed differences have also been reported for the performance of horses in a detour task. Ponies from semi-wild management showed an understanding of object permanence, even after a

delay of 10 s. Similar to the donkeys described above, they searched for a food bucket which had been removed from view by detouring around a simple V-shaped barrier. However, Standardbreds which were raised in traditional stabling did not succeed in the task (Baragli and Regolin 2008). A follow-up study is needed to clarify whether the differences in the performance are due to the housing and management conditions rather than to the horses' breed.

### Social Factors: Social Rank and Affiliation

Social transfer of information may be especially dependent on the relationship between observers and demonstrators. Horses appear to learn most readily from higher-ranking, older members of their own group (Krueger et al. 2014a). When horses are confronted with humans in learning tasks, prior experiences with those persons may affect their learning performance, as described above (Schuetz et al. 2016).

### Conclusion

The cognitive capacities of equids were underestimated for decades; in fact, their abilities are in line with the demands of their environment. Horses are extremely social and show highly developed social cognition abilities. They have a well-developed understanding for concepts and categories and readily generalize them to new objects, environments, social contacts, and to their interaction with humans. Humans have used the cognitive skills of horses when training them for centuries, but our understanding of the effect of domestication on these learning capacities is still in its infancy. Many more tests are needed to evaluate the full spectrum of equine cognition.

### Cross-References

- [Attention](#)
- [Attention-Getting Behaviors](#)
- [Behavioral Variation](#)
- [Categorization](#)
- [Clever Hans](#)

- ▶ Cognitive Bias
- ▶ Communication
- ▶ Cooperation
- ▶ Costs of Group Living
- ▶ Dominance Hierarchy
- ▶ Detour Task
- ▶ Domestication
- ▶ Domestication Hypothesis
- ▶ Equine Cognition
- ▶ Equine Communication
- ▶ Equine Locomotion
- ▶ Equine Locomotion
- ▶ Equine Sensory Systems
- ▶ Fission-Fusion
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- ▶ Home Range
- ▶ Human-Animal Interaction
- ▶ Human Approach Test
- ▶ Hybrid Vigor
- ▶ Imprinting
- ▶ Individual Recognition
- ▶ Landmark
- ▶ Laterality (Handedness)
- ▶ Memory
- ▶ Perissodactyla Cognition
- ▶ Perissodactyla Communication
- ▶ Perissodactyla Diet
- ▶ Perissodactyla Locomotion
- ▶ Post-Conflict Resolution
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- ▶ Scent-Marking
- ▶ Social Behavior
- ▶ Social Learning
- ▶ Social Grooming
- ▶ Social Intelligence Hypothesis
- ▶ Stimulus and Local Enhancement
- ▶ Ungulate
- ▶ Working Memory

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## Equine Communication

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### Synonyms

Behavior; Horse; Signals.

### Definition

An overview of communicative signals in the domestic horse (*Equus caballus*).

## Introduction

Communication is a social event in which a signal is intended to influence the behavior of the receiver (Seyfarth and Cheney 2003). The ability to recognize other individuals is essential to animals in a social hierarchy, territorial animals, and animals that interact with each other regularly (Scott 2005). A communication system requires (1) the operation of the signals, (2) the sensory and cognitive systems used to receive the signals, and (3) the behavior associated with the signaling. Signals evolve simultaneously with sensory and cognitive systems as these systems determine the signals that are easier to receive, distinguish, and base decisions on (Endler 1993). Animals that possess the sensory equipment necessary to receive the signal make use of all the senses that they are able to use over distances for communication in variable circumstances (Marler 1967).

Signals originally evolved for some other function but have been modified by selection to transmit information (Searcy and Nowicki 2005). Selection has favored signalers who (Seyfarth and Cheney 2003):

- Can exploit the sensory abilities of the receivers
- Accurately signal competitive skill when it is advantageous
- Deceive the receiver when it allows them to win with minimal cost
- Give acoustically different vocalizations in different situations

Simultaneously, selection has favored receivers who (Seyfarth and Cheney 2003):

- Are skilled in extracting information
- Express behavior that makes it easy for them to extract information
- Can rapidly decode signals and respond appropriately
- Can use information to represent their environment

The emission of a communicative signal is dependent on the immediate features of the social environment as well as the history of the

interactions between the signaler and receiver (Seyfarth and Cheney 2003); however, not all communication follows the form of a clear signal followed by a clear response (Manning and Dawkins 1998). Signal generation follows three steps: (1) generate and emit the signal; (2) transmit the signal through a medium, minimizing background noise and interfering signals; and (3) receive and process the signal (Endler 1993). Signal structures are designed to be diverse in order to maintain species specificity and to permit a signaler to elicit unique responses from the receiver (Marler 1967). This allows for the possibility of deception on the part of the signaler.

## Visual Communication

Horses are able to communicate via highly sensitive sensory systems. Horses, unlike humans and nonhuman primates, do not possess a fovea, but instead employ a streak of high density cells to perceive fine detail (Hebel 1976). Horses are dichromats, with visual capabilities resembling those of humans with red-green color deficiencies (Hanggi et al. 2007). Dichromats do not perceive intermediate hues; mixed colors result in either an achromatic hue or a desaturated version of one the colors (Carroll et al. 2001). However, dichromacy in multiple species has provided evidence that having dichromatic vision is more than suitable for solving visual tasks in various habitats, and color deficiencies are compensated for by visual cues such as brightness, hue variation, depth, etc. (Hanggi et al. 2007).

Horses first detect a stimulus based on its size and contrast (Saslow 1999) and highly contrasting and bright colors consistently affect behavior (Hall and Cassaday 2006). Due to the excellent vision in horses, even minor movements that are sudden or unusual can induce arousal. These movements are used to gain attention from conspecifics in threat gestures, such as quick jerks of the head, striking a foreleg on the ground, or rearing. A more subtle form of communication relays the current mood of an animal; a relaxed animal has an elongated posture, whereas an aroused horse has an arch in its back and contracted muscles. In confrontations, horses can

use signals to estimate an opponent's ability to fight (e.g., size). A dominant horse will show an increasing display of threat gestures, while a subordinate horse will either walk away or show a submissive posture (Mills and Nankervis 1999).

## Auditory Communication

Horses' hearing goes to much higher frequencies than that of humans. Therefore, it is reasonable to assume that their vocalizations, while audible to humans, also contain supplemental information inaudible to species with a lower frequency threshold. One example of a horse vocalization is the neigh or whinny. This sound is able to traverse large distances and signifies the presence of an individual, and is often used when a horse is isolated from the group. Nickers seem to encourage socialization with another horse, and are often used by mares towards their foals. Conversely, squeals act as a warning threat to unfamiliar horses or as a reaction to a painful stimulus. When threatened with extreme physical violence, horses issue roars or screams. All of these auditory signals are used in a social context, emphasizing the great importance of access to conspecifics for horses (Mills and Nankervis 1999).

Horses attend to stimuli by pointing their ears (Saslow 2002) and are able to manipulate their pinnae to point directly forward or backward. This may allow an individual to localize sound by orienting the pinnae (Heffner and Heffner 1984). They do not possess good acuity for sound localization, but are able to localize lower frequencies much better than higher frequencies. One study found that horses were able to localize 250 Hz, 500 Hz, and 1 kHz, but could not localize sounds 2 kHz or greater. In fact, they performed at chance levels for tones of 2–25 kHz (Heffner and Heffner 1986).

Vocalizations in feral horses have been hypothesized to encode information about status. Squeals could be associated with physiological ability (via lung capacity or strength of thoracic musculature) and thus provide an indication of the dominance status of an opponent. Dominant stallions emit squeals that are 20% longer than subordinate stallions. In addition, the squeals of these dominant

animals possess high-frequency sounds otherwise absent in the calls of subordinates and they maintain three strong broadband energy wavelengths to the end of the signal, whereas subordinate animals have narrower energy bands towards the end (Rubenstein and Hack 1992).

## Chemical Communication

Chemical signals are found in the form of social odors or pheromones. The horse can obtain chemical information from urine and feces, saliva, skin secretions, and breath. When two horses meet, their greeting involves the investigation of the mouth and nose, flanks, and perineal region. The urine excreted by a mare signals stallions as to whether she is in estrus. Stallions also use feces to declare their presence, and may also be used visually for orientation. Chemoreception allows an individual to identify others, and obtain information on the sex, age, and physiological state of the animal. It provides opportunity for silent alarm signaling, as well as signaling a calm state, and can also be used for navigation and orientation. Finally, chemical signals are useful in the separation of different groups and individuals within a group, as well as promoting the bond between mare and foal (Mills and Nankervis 1999).

The horse possesses a prominent vomeronasal organ, which is more responsive to large species-specific molecules such as pheromones (Saslow 2002). Odors can provide information about identity. In wild horses, stallions are able to distinguish between fecal piles of familiar and novel animals. They showed no response in scent differences of dominant or subordinate horses, but investigated the scent of an unfamiliar stallion twice as long as familiar stallion. If in fact scents are used as a basis to identify individuals, a horse could assess an opponent in a fight by associating the odor of the other horse with previous encounters and outcomes (Rubenstein and Hack 1992).

Certain odors produce a behavior in horses and several other species called flehmen. The flehmen behavior is characterized by a retraction of the upper lip, wrinkling of the nose, and baring of the gums, accompanied by deep breathing. At times the animal may also elevate and extend the

head (Weeks et al. 2002). Flehmen research has mostly been tested through the discrimination of estrus and nonestrus bodily fluids (Weeks et al. 2002). Many researchers believe that the flehmen behavior is most likely associated with sexual behavior rather than novelty (e.g., Christensen et al. 2005). Saslow (2002) reported that stallions age four and up tend to investigate piles of manure with intense sniffing and licking. Mares and geldings, however, show little interest in manure piles. Additionally, a stallion that sniffs its own manure shows a brief period of heightened aggression.

In contrast, Weeks et al. (2002) demonstrated that males and females displayed flehmen equally in response to estrus versus nonestrus stimuli and no effects of age were demonstrated. Horses have also been observed to flehmen in response to a distasteful odor (Saslow 2002). Anderson et al. (1996) discovered that the frequency of flehmen is lower when olfaction is blocked and the number of events associated with flehmen is lower when vision is blocked, indicating that both olfactory and visual cues initiate the flehmen response. Houpt and Guida (1984) support this, stating that stallions are able to use visual and auditory cues to determine if a mare is in estrus and do not rely on olfactory stimuli.

## Tactile Communication

Tactile stimulation is used in most species to provide relaxation and form or enhance relational bonds. Mutual grooming episodes may be used as a measure of social bonding (Crowell-Davis et al. 1987) and can also produce a pleasing response at certain parts of the body (Saslow 2002). Horses are very sensitive to tactile stimulation. Intraspecifically, they employ touch during mutual grooming, where a pair of horses will nibble each other's backs, manes, and limbs for a short period of time. This behavior is increased during the molt cycle and times when external parasites are prevalent (Mills and Nankervis 1999). For horse owners, tactile stimulation is used to communicate with their animals (Saslow 2002). The primary nonaversive stimuli used in training are tactile (e.g., pressure against the sides, shifting weight, lifting of reins), although aversive

tactile stimuli such as whips and spurs are also employed (Dougherty and Lewis 1993). Inexperienced riders may inadvertently deliver irrelevant tactile signals, thereby failing to teach the horse to discriminate meaningful signals (Saslow 2002).

Spier et al. (2004) demonstrated that foals that were handled neonatally were significantly more inclined to allow the researcher to pick up their back feet and handle their limbs at the age of 3 months compared to foals that had not been handled neonatally. They also observed that the mares of handled foals seemed more relaxed during the second conditioning session. Handling techniques developed by Miller (1991) include full-body rubbing, picking up each hoof, slapping each hoof until the foal ceases to respond, rub the inside of the ears, mouth, and nostrils, rub the foal with a plastic bag, and spray water near and on the foal. The goals of tactile conditioning are: (1) bonding with humans, (2) desensitization to certain stimuli, (3) sensitization to certain stimuli, and (4) decreasing the fear response (Miller 1991).

## Conclusion

Overall, communication in horses can be very complex, and may employ more than one type of sensory system at a time. Socialization depends on a horse's ability to emit signals, as well as detect and process them. From birth, foals learn the importance of such communicative signals such as the scent of its mare, meanings of different vocalizations and body postures, and grooming from others. These learned signals are vitally important to the later survival and reproductive success of the adult horse and are also important to the relationship between horses and humans. Equine sensory systems are extremely sensitive and influence the behavior of the horse in response to stimuli. Their vision picks up fine detail with the visual streak, despite lack of a fovea, but they see objects on the ground easier than raised objects. Horse hearing has a significantly higher frequency threshold compared to humans, though they have difficulty localizing sounds about 2 kHz. Olfaction is used widely by

the horse for individual identification and utilizes the behavior flehmen during scent investigation. Touch is used in horses from birth, and is used in adulthood primarily for mutual grooming. Domestic horses show reduced heart rate in response to human tactile stimulation. Horse behavior ranges from simple to complex, but every behavior along the continuum is dependent on these advanced sensory systems. Study of these systems and behavioral processes will greatly enhance human understanding of the horse and the human-horse relationship.

## Cross-References

- [Communication](#)
- [Equine Cognition](#)
- [Equine Sensory Systems](#)

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## Equine Diet

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## Synonyms

Feed; Forage; Grains; Nutrition; Oats; Roughage

## Definition

Feeding and nutrition of horses

## Introduction

Horses have been incorporated into the lives of humans throughout history and cultures in diverse roles and purposes for centuries. Horses have evolved from primarily grass-dwelling creatures (Muller 2012), and the equine diet is unique and dependent upon the role and use of the horse. The domestication of horses, as well as the popularity of equestrian sports, has led to a change in dietary standards for horses (Manso Filho et al. 2019). Although domestication has changed the foraging habits and equine diet, horses have small stomachs that cannot intake large amounts of concentrated feed and supplements at one time since they only have a capacity of approximately 2–4 gallons (Williams 2004). The implementation of equine nutrition varies across disciplines and geographic regions (Mastellar et al. 2017), and it is essential to understand proper feed and nutrition for horses as individuals with unique needs.

Nutrition is a vital component of equine care, and without appropriate management, various health problems can occur in horses (Mastellar et al. 2017). Maintaining the proper equine diet is essential for caregivers of horses, as improper nutrition can lead to a variety of health issues, such as metabolic diseases or colic (Parker et al. 2018). It is essential that the diet of the horse is related to its role, and proper nutrition supports the lifestyle of the horse. However, whereas the diet of a wild horse consists of forage or roughage, the diets for domesticated horses should consist of roughage, as well as concentrated feeds and supplements, that provides proper care and nutrition that is aligned with their lifestyle. A senior horse requires a specific diet for age and nutrition compared to the needs of a younger horse used in various competitions, such as racing, endurance, or show jumping. It is essential that the diet of the horse is related to its work and proper nutrition supports the lifestyle of the horse. Overall, the equine diet for domesticated horses consists of



roughage and various types of concentrated feed, which is dependent upon factors such as age, lifestyle, special needs, and work. Some horses are also provided additive supplements in addition to their regular equine diet for a variety of healthcare and lifestyle accommodations.

## Roughage

Although a domesticated horse has a greater range of available food than a wild horse, it is essential to remember that it is still a grazing animal (Vogel 1995). Roughage, including grazing and consumption of forage, hay, and hay-related products, is an essential part of equine diet and nutrition, which horses should have access to for most of the day. Diets consisting of low rations of roughage have contributed to an increase of digestive upsets and colic in horses, as well as increase in dental treatments for horses (Muller 2012). Digestibility is also a key factor that affects the value of feeding forage to horses (Hansen and Lawrence 2017). Horses are also known to be more selective grazers in comparison with other livestock, and research has demonstrated preferences for different types of roughage based on geographical location (Martinson et al. 2016). It is also essential to consider the seasonal nutritional value of roughage and hay for horses. The nutrients in forage vary greatly with the maturity of grasses, environmental conditions, fertilization, and management (Williams 2004). Quality hay for horses should be leafy, fine-stemmed, and green in color, as well as free of dust and mold, in order to have the best nutritional value (Hill 2007).

There are several hay varieties available for horses that are dependent upon type, cutting, and geographical location. Hay varieties include alfalfa, birdsfoot trefoil, red clover, orchard grass, timothy, and brome (Hill 2007). Alfalfa tends to be a popular choice for hay, as it is a good mineral source and more nutritious due to its large leaves (Vogel 1995). Also, each of these types of hay should be cut at specific time as roughage that is harvested at late maturity consists of a lower nutritional value and must be fed to horses in higher amounts (Muller 2012).

Generally, a mixed grass type of hay, such as meadow hay, is suitable for most horses, which is made in a permanent pasture (Vogel 1995). However, since hay can vary in nutritional quality, horse owners should also test hay before a large purchase to be sure it meets the needs of the equine diet. Additionally, hay must be stored properly to avoid retention of moisture, which causes mold and can lead to respiratory issues and illnesses in horses.

Other fibrous foods may also be part of the roughage equine diet. Silage, a compacted and fermented grass feed, must be wrapped and stored carefully to avoid causing botulism and other illnesses in horses (Vogel 1995). Straw can be chopped into tiny pieces to make chaff for horses, and grass can be vacuum packed for horses, which provides more nutritional value than hay (Vogel 1995).

## Feeds: Parts of a Balanced Diet

Although a horse should be fed mostly roughage, grass and hay usually cannot supply the energy required for work (Vogel 1995). Each horse is an individual and requires a unique, balanced diet. Effective planning for the equine diet includes providing energy through a balance of food and work based on the individual horse. A horse that does little or no work may require a diet consistently mostly of roughage, but the diet of a horse that engages in two or more hours of hard work, including galloping or competing, must include approximately 45% of concentrated feed (Vogel 1995). A vast array of concentrated feeds is available to meet the equine diet and nutrition of horses according to breed, work, special needs, and age. The feeds are part of a balanced diet for horses that includes protein, carbohydrates, fat, vitamins, and minerals, as well as water (Vogel 1995).

Protein is important as the building blocks of muscles. Soybean meal and alfalfa are good sources of protein and may be used for higher protein consumption in lactating mares and growing foals (Williams 2004). Most adult horses require 8–10% protein in their feed ration.



Carbohydrates are the main energy source used in most feeds (Williams 2004) and are also an essential part of the horse's diet. Carbohydrates consist of simple sugars, starches, and cellulose, but many horses, particularly those with metabolic issues, can benefit from a diet without sugar or molasses (Hill 2007).

Fats are associated with healthy coats for horses and are necessary for metabolic functions (Hill 2007) and can be added to increase the energy density in the horse's diet (Williams 2004). Most concentrated feeds have a 2–6% of fat, but some higher fat feeds fill contain 10–12% of fat (Williams 2004).

Horses typically have adequate amounts of vitamins in their diet if they are consuming fresh green, leafy forages (Williams 2004). Vitamin E is found in leafy greens, and Vitamin D is obtained through sunlight. Horses that are provided with fresh fruits and vegetables are receiving Vitamin C.

Minerals are required in the equine diet for electrolytes, body structure, nerve conduction, and muscle contraction (Williams 2004). Macro-minerals, such as calcium, sodium, magnesium, and potassium, are required daily in small amounts (Williams 2004). Minerals, such as salt, are absorbed by horses when grazing and through salt lick blots (Hill 2007; Vogel 1995).

There are a variety of concentrated feeds available to meet the diverse nutritional needs of domesticated horses consistent with their age, work, and lifestyle. Concentrated feeds can be loose or processed into pellets or grains, which provide a balance of nutrients (Vogel 1995). One of the most popular types of feed is oats, which has a low-energy content. Feed is also available in the form of pellets, which is manufactured to suit different horses, but coarse feed mix is more appetizing and takes longer to eat and digest (Vogel 1995). Barley, oats, and corn are also included in concentrated feeds for horses. These types of feed are lower in fiber and higher in energy than roughages (Hill 2007), but flaked corn is processed further so that it provides less energy (Vogel 1995).

Another popular feed option for horses is alfalfa pellets, which consists of a strong

concentration of vitamins and minerals similar to grass. Additionally, various forms of beets, which is rich in protein and energy, can be part of concentrated feed, including beet pulp, beet cubes, and soaked beet. It is essential that each form of beet pulp is soaked in water as it expands rapidly and may cause the horse to choke or colic. Beet-related feeds are also an excellent source of fiber for horses, and some horse owners add beet products as a supplement to concentrate feeds dependent upon individual horse's needs. Additionally, supplements and treats can also be included as part of the equine diet.

## Supplements

The equine market includes a wide variety of supplements to aid equine diet and nutrition. Supplements are used for a variety of purposes, including weight management, parasite control, joint support, and hoof and coat enhancement. Supplements can be provided to horses in different forms, such as salt lick blocks and rations. It is essential that horse owners clearly understand the needs of their horses, as well as the purpose and effects of supplements. If a horse owner is unsure of which supplements will be necessary or effective, a veterinarian should be consulted for guidance.

Various oils can also be included as supplements in the equine diet and mixed with feed. Oils, such as corn or vegetable oil, are a rich source of energy and can be added to the diet of competition horses to supply their energy needs (Vogel 1995). Additionally, oils, such as cod-liver oil, are also a good source of calories for weight gain, as well as contributory to a healthy skin and hair coat (Hill 2007). Linseed is also a supplement used to help produce a shiny coat, but the seeds can be toxic for horses if not boiled for many hours and prepared properly for horses (Vogel 1995).

In addition to oils, molasses is also a popular supplement for horses. Molasses are a common ingredient in treats for horses, as well as some beet pulp feeds. However, although it is a palpable supplement, horses with metabolic issues should

have a reduced intake of molasses so as not to incur digestive or laminitis issues. When not being used as a supplement, molasses can also be mixed directly with medicines and put directly into the horse's mouth (Vogel 1995).

When many people think about what horses eat, carrots and apples are common responses. Although these roots and fruits are ideal healthy treats for most horses, they must be cut lengthwise as opposed to circles to prevent choking (Vogel 1995). Carrots may be fed in larger quantities but do not have great nutritional value (Vogel 1995).

## Water

Water, naturally, is an essential part of the equine diet. Water is necessary for horses to avoid colic, dehydration, and death, and the average horse will intake 5–10 gallons of water each day (Swinker 2014). Horses should have free access to water at all times. Water must be clean and unpolluted (Vogel 1995), as well as clear of algae and insects, such as mosquitoes, which carry diseases that can be fatal to horses. Horses grazing in a pasture may also have access to natural water sources, such as a clean running stream or creek. Horses grazing in pastures are also able to consume water through the intake of grasses, which is decreased during the winter months when the equine diet consists of roughage (Swinker 2014). Some horses are also less active during the winter months. Therefore, it is essential to be more mindful of the horse's water intake during winter months and to consistently check that water buckets and troughs are full, clean, and unfrozen.

## Conclusion

Equine diet and nutrition will continue to develop with new knowledge, technology, and the use of horses. Research has demonstrated that knowledge of equine nutrition is not always reflected in management practices and that the understanding and application of equine nutrition concepts can be improved (Mastellar et al. 2017).

Additionally, each horse is a unique individual and requires a feeding regimen based on their age, breed, geographic region, special needs, and work.

## Cross-References

- [Feeding](#)
- [Forage](#)
- [Nutrients](#)

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## Equine Gaits

- [Equine Locomotion](#)

## Equine Locomotion

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## Synonyms

Equine gaits; Horse gaits; Horse Locomotion

## Definition

Movement used by equine species to traverse their environment.

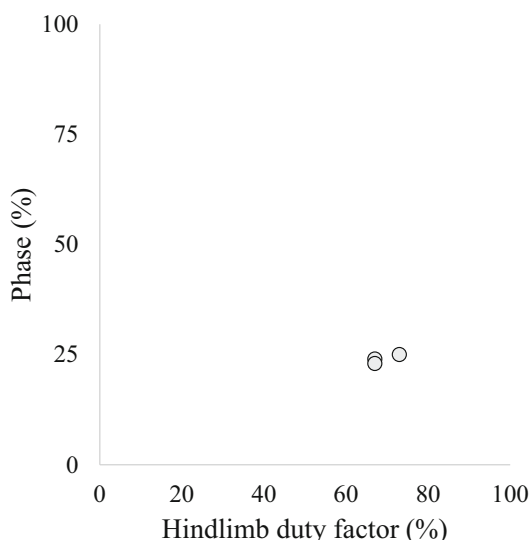
Horses belong to the order Perissodactyla, a group of odd-toed ungulate mammals, which are characterized by the enlargement of the third digit on each extremity (Bowling and Ruvinsky 2000). Horses fall under the family Equidae and the genus *Equus*. It is likely that horses, donkeys, and zebras all evolved in North America and spread when the Bering land bridge was open into Africa, Asia, and Europe (Bowling and Ruvinsky 2000). Why equids eventually became extinct in North America is unknown, but the last of them was perhaps exterminated by the first human inhabitants some 12,000 years ago (Bowling and Ruvinsky 2000). Wild horses survived into historic times. Unfortunately, both the Tarpan (*E. ferus ferus*) and the Przewalski horse (*E. ferus przewalskii*) are now either extinct or critically endangered. The extinction of the Tarpan came about when the last wild Tarpan was killed in December 1879 in Ukraine and the last living purebred Tarpan living in the Moscow Zoo passed in the late 1880s (Bowling and Ruvinsky 2000).

Horses domesticated around 6000 years ago in the steppes area of Russia and Ukraine gave rise to

the modern-day horse (*E. ferus caballus*) (Bowling and Ruvinsky 2000). The earliest evidence of domestication came from an excavated settlement in southern Ukraine which dated back to 4200–3800 BC (Bowling and Ruvinsky 2000). Horses are recognizable by the long-haired tail, a mane that is both long and thick and tends to fall on one side, and an elongated snout. The metacarpus is short compared with the metatarsus so the horses' hindlegs are longer than their forelegs (Bowling and Ruvinsky 2000). Horses have played a crucial role in the expedition of social progress. Horses have contributed to military campaigns, the development of transport systems, and the improvement of agriculture. Even with the advent of modern technology, the use of horses in sports, including racing, is wildly popular. The speed of the horse has hardly increased under traditional artificial selection methods since the nineteenth century suggesting the horse may have reached its physiological speed limit through natural selection and evolutionary pressures (Bowling and Ruvinsky 2000).

## Gait Patterns

Equine locomotion is divided into natural and acquired gaits, each of which has their own sub-classifications. Natural gait patterns include walk, trot, canter, and gallop, which are differentiated by footfall patterns, speed, and gait beats. It is classically accepted to describe gait patterns starting with the footfall of the left hind limb (Hildebrand 1989). The walk pattern is traditionally categorized as a lateral sequence lateral couplet (i.e., left hindlimb to left forelimb, right hindlimb, right forelimb; Fig. 1). It is considered a four-beat gait, which means each foot strikes the ground at a different moment in time, but two feet are always in contact with the ground (Ball 2006). The trot is a two-beat gait where the limbs work as diagonal pairs, the left hindlimb and right forelimb move together, and the right hind limb and the left forelimb move together. Canter is a three-beat gait which sees one diagonal pair moving at the same time, while the opposite diagonals move independently. For example, if the left hind limb



**Equine Locomotion, Fig. 1** “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in equines ( $n =$  three species)

strikes independently, the right hind limb and left forelimb will strike together next, followed by the right forelimb. This is called a right lead since the right forelimb is moving independently. A left lead canter would be the same sequence on the other side. The gallop is a four-beat gait, similar to canter, except diagonals do not strike together (Ball 2006). Two types of gallops exist, a rotary gallop where the feet fall in a circular pattern (left hindlimb, right hindlimb, right forelimb, and left forelimb) and a transverse gallop in which the weight is transferred on a diagonal axis (i.e., left hindlimb, right hindlimb, left forelimb, and right forelimb). Both types of gallops have two forms, clockwise and counterclockwise for rotary, and left and right lead for transverse (Leach et al. 1984) (Fig. 2).

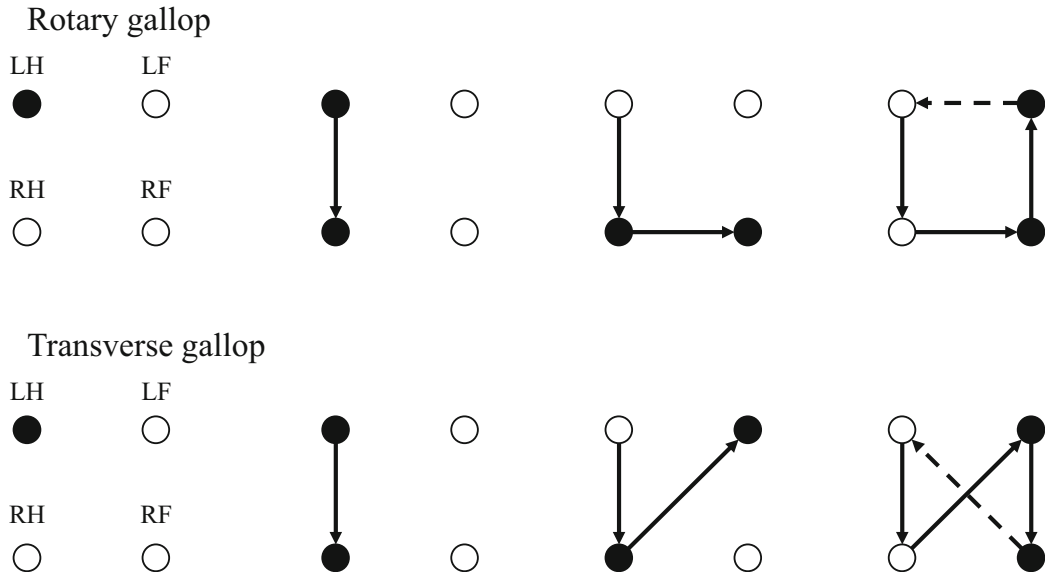
Additional gait variants are possible, but not universal across breeds. The ability to perform these additional gaits properly has been linked to a gene mutation of the *DMRT3* gene affecting spinal neurons. The *DMRT3* gene was found to play a pivotal role in the development of spinal circuits that control strides and limb movements. The mutation allows a greater variety of gait patterns to emerge, by coordinating left and right limb movement, as well as forelimb and hind

limb movement. Icelandic horses are well known for their characteristic gait pattern, known as Tölt, and have a high heritability of the genetic mutation: 0.6–0.73 (Andersson et al. 2012).

Although gaits are distinctly named and classified, the classifications are varied and difficult to properly differentiate. The different gaits are seen more as a continuous spectrum rather than different set points of motion, and boundaries set to differentiate the gaits are somewhat arbitrary. They tend to vary heavily based on the species of the horse, rather than by the general movement of the limbs (Hildebrand 1965).

## Limb Loading

The study of the limb loading (i.e., the external forces acting on the limbs) has increased practical detection of horse lameness (abnormal gait or stance due to a locomotor dysfunction) and has thus enabled better treatment of these animals (Bobbert et al. 2007). Several methods have been developed to study the limb loading forces during various gaits, such as force plates in the ground, treadmills with force sensors under the support structure, instrumented horse shoes that capture the work output, and an indirect method where force vectors are calculated based off of the kinematics of the horse during gait. Each of these techniques presents their own advantages and disadvantages. Ground force plates can measure the strike in its full force, with several force vectors analyzed, but are unable to measure several steps in sequence. Data is also harder to gather since the hoof strike has to occur exactly on the plate and horses have a natural tendency to avoid the plates (Bobbert et al. 2007). Treadmills are able to capture several strides in sequence, but their measurements are sometimes incomplete, and the horse has to be habituated to treadmill walking (Bobbert et al. 2007). Horseshoes with embedded transducers are able to measure several strides in series with no training of the horse; but have limitations in the data they gather, are sensitive to shock, and weigh more than natural shoes, thereby slightly altering gait (Bobbert et al. 2007). The method based on kinematics works by recording and



**Equine Locomotion, Fig. 2** Foot fall diagram representing the two types of gallops found in horses. *LH* left hindlimb, *LF* left forelimb, *RH* right hindlimb, *RF* right forelimb

measuring the movements with tracers on the limbs, with the assumption that the distal limb acts as a linear spring with a consistent stiffness. In reality, each horse differs slightly in regard to the spring like capacity of their musculoskeletal system, with one research group listing ranges as great as  $101\text{--}156\text{ N}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ . This means that to accurately measure ground forces via kinematics requires some calibration of the tendon spring capacity before accurate results can be obtained, but once calibrated, can provide accurate measurements over sequential strides (Bobbert et al. 2007).

Merkens and Schamhardt (2010) analyzed kinematics and the ground reaction forces occurring in the forelimb and hind limbs of horses during different gait patterns, with ground plate and kinematic analysis assisted by the presence of photodiodes (tracers) on the limbs. They found that the ground impact occurring in both walk and trot were similar in each limb, but that overall, the forelimbs had a higher ground force reaction than the hind limbs. Further research into this showed that the forelimbs carry approximately 60% of the body weight at rest and have greater vertical forces when moving (Merkens and Schamhardt 2010) (Fig. 3). However, the hindlimbs

experience greater horizontal forces during locomotion, as they generate more of the propulsion for the animal (Payne et al. 2005).

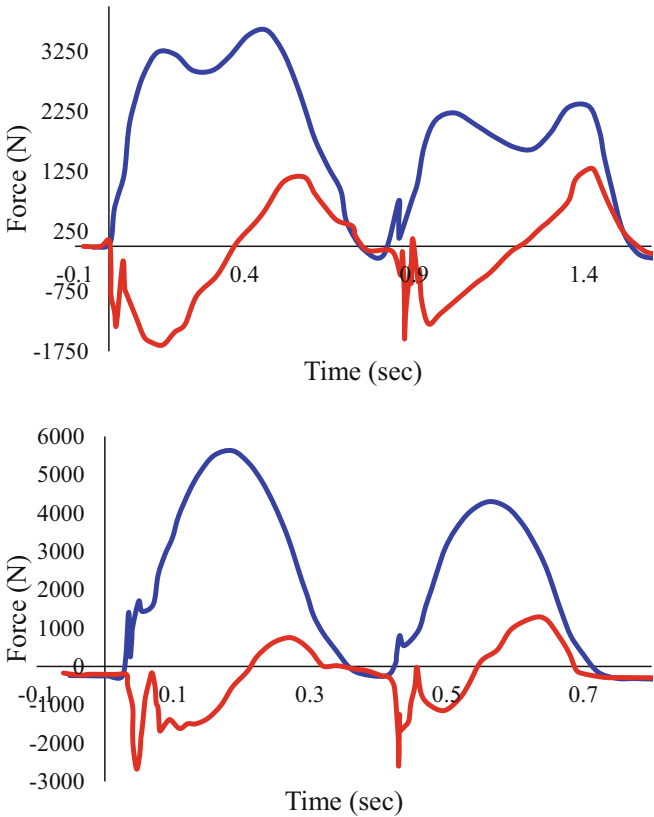
During locomotion high external forces act to hyperextend the fetlock joint in horses. Hyperextension of the fetlock joint (Fig. 4) causes high levels of stress in the *m. interosseus medius* (suspensory ligament) and deep digital flexor and superficial digital flexor tendons. The high forces get built up within the tendons as stored potential energy, allowing the limb to act in a spring-like manner, releasing the stored energy as kinetic energy for high-efficiency gaits. However, the high stresses in these tendons increase with speed, and thus, the tendons become more prone to injury with increased speeds (Harrison et al. 2010).

## Kinematics

The kinematics of horse movement is largely defined by the specialized anatomy of the joints in their lower extremity. While horses share similar skeletal arrangements to other mammals due to common descent, the evolution of their bones and joints has adapted them for efficient gait

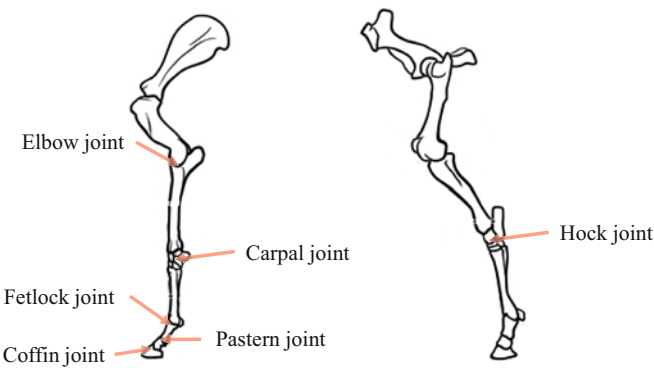
**Equine Locomotion,**

**Fig. 3** Force plate recording of the horizontal (red) and vertical (blue) ground reaction forces of the right fore and hind limb at walk (top panel) and trot (bottom panel). Data from Merkens and Schamart (2010)



**Equine Locomotion,**

**Fig. 4** Forelimb (left) and hind limb (right) joints of the horse mentioned in text



patterns. Starting distally (Fig. 4), the equivalent of the distal interphalangeal joint is the coffin joint, located directly above the hoof (Budras et al. 2012). This joint is classified as both a hinge and saddle joint, due to the unique articulation of the bones' joint surfaces. The fetlock joint is a hinge joint located proximal to the coffin joint and corresponds to the human metacarpophalangeal joint. Most proximally is the

carpal joint, also known as the hock joint in the hind limbs. In horses, this joint resembles the human equivalent of the elbow or knee. Altogether, these joints allow for flexion and extension of the hoof, pastern, and canon (Holmström et al. 1990).

The coffin joint absorbs energy (negative work) received into the limb during the initial strike with the ground, and a large burst of



positive work (generated by the musculoskeletal system) extends the joint during push off. The fetlock joint produces the largest burst of positive energy of the three lower joints mentioned. The positive work occurs during the swing of the contralateral limb, originating from stored energy across the musculotendinous structures travelling through the joint (Colborne et al. 2010). The main negative work occurring in this joint is in the early stance, as it is flexed against extensors. There are also small periods of both positive and negative work occurring in the joint while in mid-stance. The carpal joint's main function is negative work, much like the human knee. In early stance the carpal joint works against a flexor moment and then oscillates to work against an extensor moment in the end stance, which facilitates transition to the swing phase (Colborne et al. 2010).

Horses are most often used for riding, driving, or working, all of which are activities that increase the workload in the limbs and can thereby alter the kinematics of locomotion. To adjust to the added weight, work horses increase the time spent in stance phase and increase extension in the fetlock joint to optimize the stability and work output. In driving conditions (pulling a carriage or sleigh), horses at trot increase the range of motion of their carpal, fetlock, and elbow joints (Miró et al. 2006). The greatest increase in range is in extension of the fetlock joints of the forelimbs, which occurs with no significant change in the ground forces through the limb. This indicates that there may be a compensatory measure to adapt to the added weight or stress. In addition to the increase in the joint angles, there are significant decreases in the speed, stride length, and swing duration in both walk and trot when in driving conditions (Miró et al. 2006).

Correlations between angles of joints and performance in show and jump have also been found. Larger hock angles are found in elite performers, indicating that smaller hock angles might lead to more injury and decreased ability to properly perform at higher levels due to inability to support their weight when stepping under themselves (Holmström et al. 1990). Similarly, a correlation was also found between increased performance in show and dressage horses and the slope of the

scapula. Elite dressage performance horses had greater inclinations of their scapulae, allowing for better performance of gaits, whereas “underachieving” horses had a straighter scapular slope (Holmström et al. 1990).

A longitudinal study done over 15 years with more than 5000 horses indicated that all of these variables are not only greatly affected by the gait pattern and velocity but also by the age and sex of the animal. When comparing groups differentiated by age and sex for length versus velocity, it was found that these features share a positive linear correlation; as velocity increased, stride length increased. With this study, it was noted that older males had the longest stride per velocity, and young females had the shortest strides per velocity. This also showed that inversely young females had the highest stride frequency to make up for the decreased length, and older male horses had the lowest stride frequency (Seder and Vickery 2003).

## Energetics

The size and speed of large running mammals require substantial energetic demands. Among large mammals, horses consume less metabolic energy than expected based on body mass even when moving at relatively fast speeds (Butcher et al. 2009). Much of this extra locomotor capacity may result from the effective utilization of elastic strain energy (Butcher et al. 2009). Muscles and tendons serve as springs, alternately storing and releasing elastic strain energy as the animals bounce along at a constant speed (Heglund and Taylor 1988). Strain energy recovery is most effective when animals use bouncing gaits at faster running speeds (Butcher et al. 2009).

Tendon strain energy storage is defined as the energy that can be stored within a muscle-tendon unit complex as that muscle-tendon complex is elongated during an eccentric contraction, that is, when the limb acts as a strut and the animal's momentum loads the limb (Butcher et al. 2009). Energetically favorable use of strain energy requires that tendons allow strain energy storage under a given load and that the muscles of these tendons produce adequate resisting force in a

metabolically economical manner (Butcher et al. 2009). Short fibered, multipennate muscles with long tendons are specialized for economical high force and enhanced elastic energy storage (Butcher et al. 2009; Dutto et al. 2006). For force production alone, short, pennate fibers are the most metabolically economical organization for muscle. High force is provided by a large number of sarcomeres in parallel (multipennate architecture) while the volume of active muscle, a reliable predictor of metabolic cost, is minimized via short fibers with fewer sarcomeres in series (Butcher et al. 2009). Lengthening contractions of slow, multipennate fibers result in high force production with relatively large tendon strains and substantial strain energy storage (Butcher et al. 2009). This is especially evident during trotting, where moderate trotting can store mechanical work by tendon elastic strain (Dutto et al. 2006). Active eccentric contraction results in substantial force enhancement while maintaining a relatively lower metabolic energy investment (Butcher et al. 2009). Short, multipennate muscle fibers facilitate this function because a small absolute stretch of the muscle results in force enhancement while limiting the number of sarcomeres that must be activated (Butcher et al. 2009). Short-fibered pennate muscles with long, thin tendons have been shown to provide economical high force production and enhanced elastic energy savings in the bouncing gaits, reducing the metabolic cost of locomotion in horses (Butcher et al. 2009; Dutto et al. 2006).

The cost of locomotion in horses is determined primarily by two factors: the cost of activation of muscle determined by pumping calcium into the sarcoplasmic reticulum and the cost of force generation determined by cross-bridge cycling (Heglund and Taylor 1988). Both costs increase directly with increasing stride frequency. The cost of activation will vary directly with stride frequencies because the muscles will be turned “on” and “off” once per stride necessarily increasing with higher stride frequencies. The cost of force generation will also vary directly with stride frequency. The same mass-specific force will have to be generated and decay once per stride. The greater frequency requires increased rates of force

generation and decay which in turn requires faster rates of cross-bridge cycling (Heglund and Taylor 1988). Thus, the energetic cost of locomotion in equine species at a given speed is almost directly proportional to the stride frequency (Heglund and Taylor 1988).

Stride frequency increases nearly linearly with increasing speed during a trot in all quadrupeds; however, energy cost per stride also increases with speed (Heglund and Taylor 1988). The metabolic rate when locomoting increases when the length of time the hoof is in contact with the ground decreases (Wickler et al. 2003). The increase in energy cost per stride with increasing speed may be related to differences in mechanical advantage of the limb muscles. Changing mechanical advantage requires higher muscle forces for the same ground force reaction as stride length increases both in the trot and in the gallop (Heglund and Taylor 1988). In both a trot and a gallop, stride length during the time the foot is in contact with the ground increases with speed. In other words, when traveling at greater speeds the length of each stride the horse takes increases, yet the amount of time the hoof is in contact with the ground does not increase. Thus, the limb excursion angle increases with increasing stride length (Heglund and Taylor 1988). This increase will change the average mechanical advantage between the limb and muscles and the ground and will require that a greater average force be developed (Heglund and Taylor 1988). In the trot, the increase in stride frequency nearly matches the increase in the rate of energy consumption. Most of the increase in cost with speed could be explained by the higher costs associated with higher stride frequencies. The remainder can be explained by increasing average muscle force associated with increasing stride length (Heglund and Taylor 1988). In a gallop, the stride frequency only increases by about 10% for every twofold increase in speed. Thus, the increase in speed is necessarily driven by an increase in stride length. Therefore, the mechanical advantage will change more dramatically for the higher average muscle force this entails (Heglund and Taylor 1988).

The trot-gallop transition is defined as the transition point between the maximum trotting

speed and the minimum galloping speed (Wickler et al. 2003). The stride frequency is the same whether animals trot or gallop at this speed (Heglund and Taylor 1988). If stride frequency is the same, then what determines gait transition? Several theories have been proposed and substantiated yet the prevailing two hypotheses for gait transition revolve around the metabolic economy and force-triggered transitions (Wickler et al. 2003). Horses transition from walking to trotting at an energetically optimal transition speed (Wickler et al. 2003). Likewise, horses transition from a trot to a gallop when it is energetically favorable, but see Granatosky et al. (2018). However, horses will also transition gaits when it is energetically unfavorable to do so when carrying a given load. Therefore, forces acting on the bones have been identified as a potential trigger for the trot–gallop transition (Wickler et al. 2003). As complex as gait transitions may be, it has been observed that terrestrial animals exhibit a clear preference for the speeds and frequencies used within each gait in nature (Heglund and Taylor 1988). Preferred speeds fall in the middle of the speed range within each gait, and at the minimum sustained galloping speed, the gallop is more economical than the trot (Wickler et al. 2003).

One of the major evolutionary adaptations of survival for the wild equid is a swift retreat from threatening circumstances (Back and Clayton 2013). Consequently, the horse has an efficient locomotor system designed to move a relatively large mass with great speed and endurance. Animals that are highly adapted for aerobic endurance, such as horses and dogs, have much greater speed ranges than less aerobic animals, such as goats and cattle (Heglund and Taylor 1988). Horses not only have high intramuscular stores of glycogen for quick bursts of energy but also have large intramuscular concentrations of mitochondria for sustained aerobic metabolism (Back and Clayton 2013). Large intramuscular energy stores combined with the ability to increase oxygen-carrying capacity through splenic contraction allow horses to have a high aerobic capacity for sustained locomotion (Back and Clayton 2013).

## Jumping

Jumping plays a major role in many equestrian sports. Equine jumping is an asymmetrical activity with three phases: the approach, the jump stride, and the move off (Clayton 1989; Meershoek et al. 2001). The stride before the jump stride is referred to as the approach stride. Normally, the horse approaches the object to be jumped in a transverse canter or gallop in which the leading forelimb and hindlimb pair is ipsilateral. The jump stride is the stride in which the horse jumps and is subdivided into the take-off, jump suspension, and landing. The take-off is the period from impact of the first hindlimb to liftoff of the last hindlimb in the jump stride. During the take-off, both hindlimbs function similarly to the single take off leg of bipeds. Therefore, take-off may be considered the stance phases for the hindlimbs. The jump suspension is the period from lift off of the last hindlimb at take-off to the impact of the first forelimb at landing. The landing is defined as the period from the impact of the first forelimb after the jump suspension to the next impact of the trailing hindlimb (Clayton 1989). During landing, the leading forelimb is placed down later and more forward than the trailing forelimb. This placement variance results in a difference in tendon loading between the forelimbs, with the flexor tendons in the trailing forelimb more loaded than in the leading forelimb. In addition, the extensor tendon in the leading forelimb is also loaded (Meershoek et al. 2001). The move-off is the period when the transition to forward movement is completed, balance is regained, and the normal stride pattern is reestablished. The strides following the jump stride are called move-off strides (Clayton 1989).

## Bioinspired Robotics

Knowledge of equine locomotion has spurred innovation in the field of robotics. In fact, several biomimetic robots have been designed using the principles of equine limbs and joints. One such model defines five key elements of the equine limb (effective leg length, leg kinematics, limb mass distribution, actuator power, and elastic

energy recovery) as the determinants of the animals' agile and powerful locomotion, and then applies these elements to a robotic leg prototype (Garcia et al. 2011). Another similar model relies on the analysis of equine joint trajectories while walking, trotting, and galloping to describe a set of four kinematic Motion Primitives that are used to generate viable and stable gaits in a quadruped robot (Moro et al. 2013). Conversely, a dissimilar model uses the mechanical stiffness of a dual-spring structure inspired by an equine distal forelimb (low-stiffness spring at touchdown and high-stiffness spring during the support phase) to improve the gait stability of a hydraulic quadruped robot when it travels over uneven terrain (Park et al. 2015). However, the impact of understanding equine locomotion in the realm of robotics is not just limited to biomimetic robots. Exotendons have also been developed based on the polyarticular elastic mechanisms of equine locomotion and can be used to aid in human locomotion. These unpowered assistive devices can significantly reduce the muscle forces as well as the metabolic energy needed for walking and may even allow for the independent movement of human patients with substantial deficits in muscle function (van den Bogert 2003).

## Conclusion

The equines share common structures to humans that have evolved differently over time to allow them specialized movement and gait patterns. These specializations allow horses to travel at high speeds efficiently due to energy storage within the spring like musculotendinous structures of their distal limbs and high-power output from the proximal limbs. Information about the gait patterns, kinematics, limb loading, and energetics of horses can be used to influence human advancement in bioinspired robotics.

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)

- [Adaptedness of Behavior](#)
- [Artificial Selection](#)
- [Basal Metabolic Rate \(BMR\)](#)
- [Cognition](#)
- [Common Ancestor](#)
- [Domestication](#)
- [Ecology](#)
- [Equine Communication](#)
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- [Taxa](#)
- [Terrestrial](#)
- [Zoo](#)
- [Zoology](#)

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## Equine Sensory Systems

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### Synonyms

Hemispheric specialization; Horses; Lateralization; Perception

### Definition

*Umwelt.* J. von Uexküll used the term “Umwelt” (meaning subjective universe) to characterize the particular perceptual world of a species or even an individual. The subject’s Umwelt is divided into two parts, the Merkwelt and the Wirkwelt, both forming a coherent entity. Merkwelt (“perceptual world”) refers to everything a subject perceives. Wirkwelt (“active world”) refers to everything a subject does. To be perceived by a subject, objects have to possess a feature (Merkmal) that matches a subject’s receptor. The perceived stimulus is then processed in the Merkgorgan (“sense organ”), for example, the brain, where a meaning is attributed to each stimulus. This meaning can change depending on the context or the subject’s internal state. Thus, a stimulus can have different meanings to the subject. We thus have to keep in mind that the horse’s perceptual world differs strikingly from that of humans (Leblanc 2013).

### Introduction

Horses have adapted to natural conditions where they live mostly in groups in large open spaces. They spend most of their time grazing or eating a

variety of diverse plants or fruits. Although horses have disappeared from the wild, Przewalski horses have reproduced in captivity and have been successfully reintroduced in various areas from where they originated. Escaped or released domestic horses have successfully expanded in various parts of the world such as North America, Australia, and even Namibia. These observations show that domestic or captive-raised horses retain some of the adaptations arising from evolutionary pressures. Being able to survive in a given environment depends fundamentally on perceptual abilities, whether to escape predators, choose the right food, or memorize where resources can be found. They must thus be able to detect constantly danger while foraging which is their major activity (Waring 2003). They must also be able to associate plant characteristics (shape, odor, flavor, energy content) with immediate or delayed consequences. Horses also have a clear social organization that relies upon both social affinities and hierarchy and ensures restricted energy expenditure and risks. Socialization in stable groups occurs through ritualized communication signals that prevent aggression escalation (e.g., Waring 2003; Fureix et al. 2012a). Communication signals may thus be very subtle and involve individual identity, group membership, and/or social status. Perceiving these signals, which can be unimodal (e.g., auditory) or multimodal (e.g., visual and auditory), is therefore an important part of the individual’s ability to be part of a well-functioning group (e.g., Lemasson et al. 2009; Proops et al. 2009).

Information on the perceptual world of horses arises from two major fields of study: (1) anatomical studies that inform us on the morphology of sensory systems, from the peripheral sensory organs (e.g., ear) to central areas (e.g., primary auditory cortex) where the brain processes sensory information, and (2) behavioral studies where the horse’s reactions and perceptions of stimuli are assessed. Both approaches have advantages and limits. Anatomical data give us an idea of how the animal may perceive stimuli (e.g., presence of typical cells and their density) where any inference is biased by the human perceptual system. Moreover, the properties perceived are not necessarily



the “real” properties of the objects detected: the brain constructs perception on the basis of the information provided by the sensory organs but also its own memories and characteristics. For example, kittens raised in a uniform environment are unable to perceive stripes and will perceive something else (Hubel and Wiesel 1963). Behavioral reactions are an expression of perception but individuals may not react just because they lack attention or motivation, especially in cases where experiments involve conditioning learning. Conditioning learning is the most used procedure where individuals are trained to respond to one type of stimulus through positive reinforcement (e.g., if a circle appears on a screen) and to neglect others (e.g., if a triangle appears on a screen). Appropriate responses guarantee that the animal has discriminated, and thus perceived, the two types of stimuli. Stimuli properties can be modified to become very close which can inform on the limits of perception (i.e., acuity).

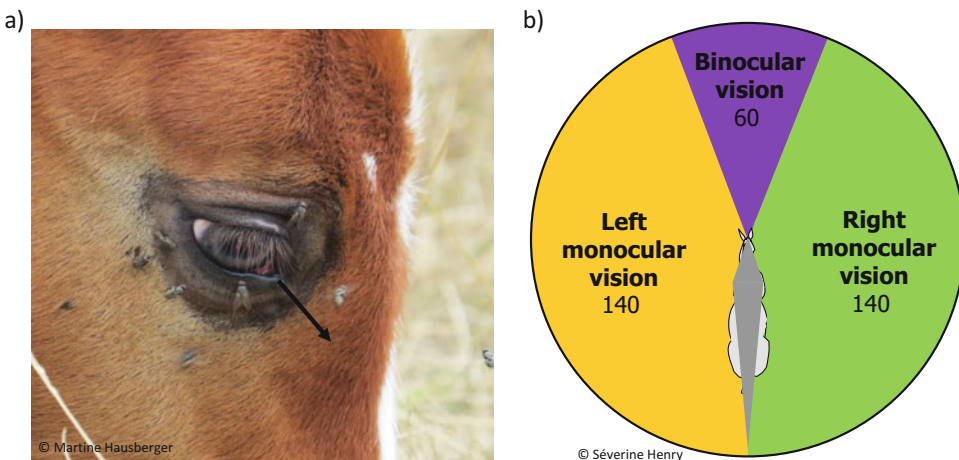
## Visual Perception

This is the most studied modality, probably because it seems the easiest to test and horses react clearly to visual communication signals, novel or moving stimuli (e.g., Waring 2003). The eyes of horses are very large (more than 7 times the size of a human eye) and the

circumference of the retina is greater than that of most mammals, which means that the images are magnified compared to those perceived by humans. The eyes are laterally placed (on each side of the head), prominent, and turn slightly in the orbit if necessary. This lateral position provides the horse with 180° **panoramic vision** in the vertical dimension and 140° **monocular** vision on each side (Hanggi and Ingersoll 2012). The 60° **binocular overlap** is restricted compared to humans (i.e., 120°) (Fig. 1a).

Binocular vision allows horses, like humans, to **perceive depth**. Since both eyes are spatially separated, the two images of the same object seen from different angles are combined by the brain in constructing the perception of a single 3D image (stereopsis) (Timney and Keil 1992). Horses also use binocular vision when they are especially attentive toward a neutral stimulus (e.g., Rochais et al. 2017). There are however two “blind” spots: one behind the horse, and one immediately in front (from eyes to nose) when the neck is horizontal and the head straight, but a slight head movement is enough to observe objects in these areas.

The optical axis of each eye diverges at a 40° angle from the body’s horizontal axis and is oriented toward the ground at 20° (Fig. 1b). This means that horses can see the ground 2 m ahead. Thus, grazing horses can observe grass available in front of them and what is happening in their



**Equine Sensory Systems, Fig. 1** (a) The horse’s eye and its optical axes; (b) The horse’s visual fields

### Equine Sensory Systems,

**Fig. 2** When grazing, horses must look down at their feed and be able to detect danger in the environment



surrounding environment, a clear adaptation to both feeding and awareness of potential dangers, respectively (Harman 1998) (Fig. 2). Because of this axis, they must however raise the head to observe distant objects. This means they need the freedom to move the head when directing toward an obstacle they will have to jump. Neck hyperflexion (rollkür), as seen in some dressage competitions, may prevent the horse from seeing where it is going. The pupil becomes horizontal when it retracts and the pupillary reflex to light is slow. Almost half an hour is required to adapt from full light to darkness. This explains common observations such as the reluctance of horses to enter dark corridors (or trailers).

Retinal cells transform light energy (visual stimuli) into electric impulses that are transferred to the brain (visual primary cortex) along the visual pathway. Horse retinas have a narrow band of high cell density, which seems to be responsible for visual acuity (Timney and Wright 2007). Visual acuity corresponds to the smallest perceived space between two dark points on a white background and is measured on the basis of human visual perception. Conditioning studies where horses were confronted with parallel vertical black and white stripes, that were progressively made thinner and less spaced, have allowed an estimation of horse visual acuity; horses see object details at 9 m that humans

perceive at 6 m (Timney and Keil 1992). Unless they have visual problems, horses have, therefore, a **fairly good visual acuity** (better than in most mammals; e.g., Timney and Wright 2007). It is worth noting though that out of 333 horses examined in the UK (retinoscopy), one third had visual alterations (e.g., myopia; Bracun et al. 2014). As in other mammals, two types of cells are present, i.e., rods and cones, which have pigments that absorb particular wavelengths. In horses, rods are 20 times more numerous than cones. Because rods are more than 100 times more sensitive to light than cones they are important in scotopic (crepuscular) vision. Horses also have, just behind the retina, a reflective surface (“*tapetum lucidum*”) that amplifies light, a characteristic shared with nocturnal species. Behavioral experiments have shown that they are able to **perceive** objects **in relative darkness** (under starlight in a moonless night sky) or can even move in a dark night (no star and no moon), although their acuity is then low. Rods are also involved in **movement perception**, which may explain both horse reactivity to moving objects and the ability to detect subtle movements. The famous example is Clever Hans, who was able in cognitive tests to associate involuntary cues from his owner with the expected response (see ► “Clever Hans”).

Cones, on the other hand, can only be stimulated in bright light and are responsible for color



**Equine Sensory Systems, Fig. 3** Horses are able to detect visual communication signals (a) and may recognize if another horse is attentive (b)

vision and perceiving object detail. Much contradictory information has circulated regarding color vision (or rather its absence) in horses. Anatomical studies indicate that horses, like all nonprimate mammals, have two types of cones, compared to primates that have three (Carroll et al. 2001). Since the brain constructs color perception by combining the information provided by two types of cones, this suggests that horses do indeed have color vision, but, compared to humans, of a daltonian type. Behavioral studies have proved particularly useful, although factors like luminance, or brightness, make it difficult to test “pure” colors. An early study of Grzimek (1952), using discrimination tests based on colored panels, mentioned that horses saw yellow best. Since then, different studies have been performed, involving reluctance to approach colored surfaces (Hall and Cassaday 2006). Also, discrimination testing shows that horses are able to discriminate all basic colors (red, green, yellow, blue) from gray but that they have greater difficulties where red and green are involved. There is no doubt now that **horses do have color vision**, and there seems to be a consensus now to say that horses best perceive yellow, and at least blue and green and red just as well (Blackmore et al. 2008). However, with dichromate vision, the color world of horses remains less rich than that of trichromate primates.

Visual perception has been shaped to respond to survival requirements and horses’ panoramic vision, associated with movement perception, makes them ready to react appropriately (fleeing or attack) to the approach of a hunting predator. In addition, visual acuity may help them learn about the visual characteristics of the best plants to consume.

Thanks to their visual abilities, horses have also developed the ability to detect subtle postural changes of other group members (Fig. 3) and thus avoid overt aggression (Waring 2003). This detection occurs through subtle cues in detecting changes in the attentional state of other horses (from ears and eyes positions; Fig. 3; Watham and Mc Comb 2014), or humans (they may detect gaze direction even if it is “distracted”; Sankey et al. 2011b). Even foals may observe their dam’s reactions and use them to learn about their environment (Henry et al. 2005).

## Auditory Perception

Contrarily to visual stimuli, acoustic stimuli can be perceived in variable light conditions. Sounds correspond to vibrations that travel at 340 m/s in the air. Sound frequencies correspond to the number of oscillations in cycles/sec (Hertz), and sound intensity is measured in decibels. Horse audiograms (curves based on responses in discrimination studies at different frequencies and

intensities) reveal that they perceive a **broad range of frequencies** (5 Hz–33 kHz vs. 20 Hz–17 kHz in most humans), **including ultrasounds** (Heffner and Heffner 1983). The best frequencies are very similar for horses and humans.

In all terrestrial mammals, sounds are first received by ears. The external ear includes the pinna and the auditory canal. The middle ear includes the tympanic membrane, the Eustachian tube, and the inner ear includes both the vestibule (equilibrium) and the cochlea. Ciliar cells in the cochlea transform the sound vibrations into electrical impulses that pass via the auditory nerve to the brain (primary auditory cortex).

Horses have particularly very mobile ears, with 16 different muscles that enable orientation in many directions. The direction of sound can then be detected from the front, the side, or from behind. Sudden sounds elicit the “Pryer” reflex where one or both ears turn immediately toward the sound (Fig. 4) (e.g., Basile et al. 2009). If the sound is of interest, the horse will then turn the head or even its whole body toward the general direction of the sound. Indeed, while the “horn” structure of horse ears may act as sound amplifiers and identifying sound location, horses are not very good at locating sounds. For horses to distinguish two sounds, the sounds need to be at least 25° apart (1° in humans) (Heffner and Heffner 1983).

Reactions to sounds are thus a clear representation of the importance of multimodality (involving different sensory modalities). When horses hear a sound, they will direct their visual attention toward it, probably to locate it but also to

confront both sources of information. They will show more visual attention if the sounds come from an unknown horse (Lemasson et al. 2009) or is incongruent with the visual information (Proops and McComb 2009) or situation (Sankey et al. 2011b). Here, **distant interactions will involve more bimodal (visual/auditory) perceptions.**

## Olfactory Perception

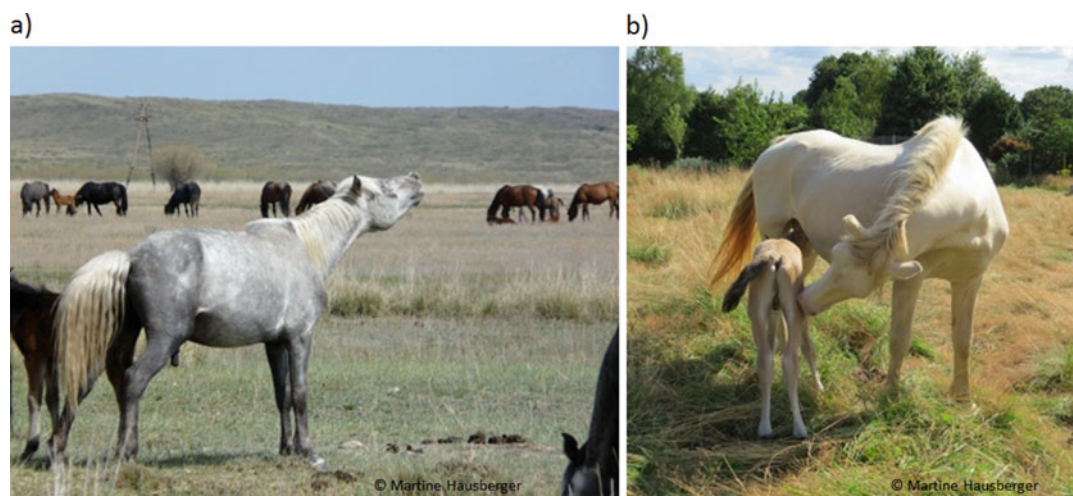
Odors are received through the nostrils to the olfactory epithelium where olfactory cells generate action potentials in response to the binding of molecules on the receptors. Olfactory information is then transmitted to the olfactory bulb and then the primary olfactory cortex. To this is added the “secondary” olfactory system, the vomeronasal organ, which is very well developed in horses where it uniquely opens in the nasal cavity. The vomeronasal epithelium also includes different types of cells. Information is then transmitted to a secondary olfactory bulb and then thalamus and amygdala. The respective functions of these two systems are poorly known. Chemical perception (olfaction and gustation) is difficult to test, as it is difficult to extract pure molecules, construct right composite odors, or to identify pertinent molecules. There is behavioral evidence that horses perceive complex odors, but the extent of their abilities remains under question. The flehmen behavior (Fig. 5a) is supposed to allow molecules to reach the vomeronasal organ better and has been thought to characterize sexual responses of stallions to sexual stimuli. Observations show that it is present in many species and that in horses both sexes may do it for detecting a diversity of odors that also include food stimuli.

Sniffing conspecifics is an important part of social encounters, sexual displays, and pre-copulatory behavior and is part of mare-foal bonding (Fig. 5b). Stallions spend time sniffing other stallions and mare feces for olfactory cues (Marinier et al. 1988). Behavioral experiments suggest that horses may discriminate sexes from urine (Hothersall et al. 2010) and determine familiarity (Péron et al. 2014). Individual recognition through odor is quite possible as horses, like the few other



**Equine Sensory Systems, Fig. 4** The “Pryer reflex”: an unusual or sudden sound induces the rotation of the ear on the corresponding side





**Equine Sensory Systems, Fig. 5** (a) A typical flehmen posture with the head and the nostrils raised, right; (b) mares spend time sniffing their newborns during the bonding process

species tested, appear to have an individual odor profile, being more similar between related individuals (siblings, parents-offspring) (Deshpande et al. 2017).

Olfaction may be associated to other modalities in multimodal representations, and **horses may associate the visual representation of a familiar human to its odor** (Lampe and Andre 2012).

A recent study has confirmed that horses, like other animals, do not have an innate recognition of predators. Odors of wolf or lion urine did not increase the heart rate of stalled horses and the odor of a wolf skin had a limited effect on vigilance. However, if blood of a stressed horse (waiting in a slaughterhouse) was associated with that of a wolf skin, vigilance increased. If then the wolf skin was associated with an unusual noise, flight reactions appeared (Christensen and Rundgren 2008). The sensory system of horses may have had some predispositions to learn a stimulus range corresponding to predator characteristics, but their functional significance requires learning. This reveals that horses are sensitive to other horses' stress odors, which may be present in a range of situations. Whether this stress level needs to be intense remains to be investigated.

Finally, odors probably play a role, together with gustation in food preferences. Horses may

eat up to different plant types per day in natural conditions and seek diversity in food ingested (Hansen 1976). Their chemical characteristics must be important. Horses do discriminate odors such as anise, coriander, and ginger (Bonde and Goodwin 1999).

## Gustation

Gustation is difficult to separate from the complementary sense of olfaction because of mixing processes involved. The back of the tongue has gustatory papilla where gustatory buds are grouped. Horses perceive the four basic flavors of sweet, salt, bitter, and sour, although with different thresholds from humans. It is probably important for horses to be able to associate flavors of food items with their postingestive consequences in order to guide food selection. Horses kept in naturalistic conditions (Fig. 6) generally avoid poisonous plants, but cases have been found of poisoning. It has been shown in horses that aversive conditioning (associative learning between a food item and postingestion sickness) requires that no more than half an hour has elapsed (Pfister et al. 2002).

Horses seem to prefer fenugreek, banana, or cherry over carrot or peppermint flavors,

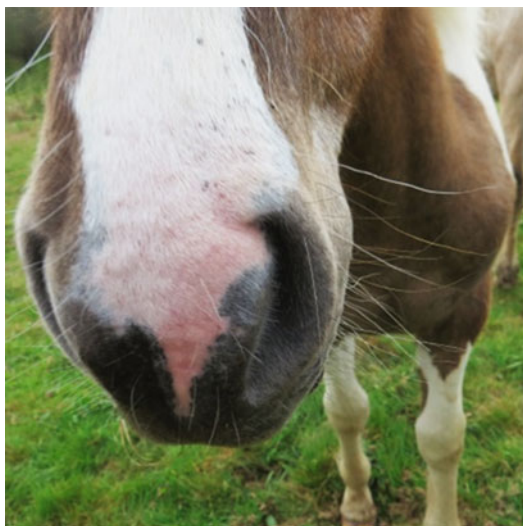


**Equine Sensory Systems, Fig. 6** Horses use gustation to explore their environment

demonstrating that they clearly discriminate these flavors (Goodwin et al. 2005). Nevertheless, overall chemical perception also remains poorly known.

## Tactile Perception

The skin presents numerous receptors that transmit information about pressure, and heat/cold, contact. In horses, the skin is very thin (a few mm), but it is thicker in some areas such as the back, near the mane, and tail. Additional information is given by some hairs such as the vibrissae around the mouth, nose, and eyes (Fig. 7) which help horses detect objects or obstacles they may not have seen. The mouth mucous membrane is also highly sensitive. Horses are able to detect a fly sitting on its skin, which can be recognized by a slight movement of the skin. In a study using von Frey thin filaments (consisting of a hard plastic body extended by a



**Equine Sensory Systems, Fig. 7** Horses' vibrissae around the nose increases its tactile perception

nylon thread and calibrated to exert a specific force on the skin) applied at the base of the withers, 67% of the horses could perceive a filament of 0.02 g/m density while none of the persons tested were able to do so (Lansade et al. 2008). Tactile sensitivity is certainly largely under evaluated as riders' actions through legs and hands (conducting to the bit and thus the mouth) may be quite rough considering these thresholds.

Some parts of the body are favored for social allogrooming and their stimulation may induce a reduction of heart rate. This has induced authors to suggest that particular regions of the body relate to positive perceptions (Feh and De Mazières 1993).

Clear individual variations are evident in the reactions to tactile contact (e.g., Rochais et al. 2014). However, compared to other mammals, horses exhibit little social contact, with group proximity best predicting social affinities (Waring 2003).

## Perceptual System Asymmetry

Laterality is the systematic preference for the use of one side of the body over the other to realize motor or perceptual tasks involving paired limb or perceptual organs. In other words, laterality



manifests both on the motor (hands, feet) as well as the perceptual (eyes, ears, nostrils) level. Such behavioral laterality emerges from hemispheric lateralization, i.e., the left and right cerebral hemispheres are specialized in controlling distinct neural functions or cognitive processes. Since the late-nineteenth century, hemispheric specialization was believed to be a human specificity, but studies over the last 30 years have provided increasing evidence for lateralization in non-human mammals, including birds and even lower vertebrates (Rogers and Andrew 2002). Hemispheric specialization is assumed to confer advantage to the functioning of the brain. Among other advantages, cerebral lateralization can enhance neural capacity by allowing parallel and separate processing in the hemispheres: thus, in lateralized individuals, several cognitive tasks that demand the simultaneous but different use of both hemispheres can be performed more efficiently (Rogers and Andrew 2002). In mammals and birds, transfer of information and coordination between both cerebral hemispheres are allowed by the *corpus callosum*, the major neural pathway that connects homologous cortical areas of both sides in mammals. More recent studies in animals converge on the conclusion that stimuli, and in particular visual and auditory stimuli, with different emotional valences induce different lateralized responses. Such asymmetrical processing of emotion was largely assessed by the literature in humans leading to the establishment of two dominant theories: “the right hemisphere theory” and “the valence theory” (Davidson 1995). The right hemisphere theory defends a predominance of the right hemisphere for the processing of any stimuli expressing high emotional value. The valence theory defends rather a differential implication of the left and the right hemisphere to process stimuli depending on their emotional valence: thus, positive emotional stimuli would be preferentially processed by the left hemisphere, while the right hemisphere would be specialized for the processing of negative emotions.

Research on either motor or perceptual laterality are still scarce in equines (e.g., less than 20 scientific publications since the 2000s), but an increasing interest has been given to side bias in perceptual processing. Visual laterality

and, to a lesser extent, auditory, tactile, and olfactory have been thus demonstrated in (mostly domestic) horses.

Horses with their eyes placed laterally used them in an asymmetrical way. Due to an almost complete decussation (i.e., 80–90% vs. 50% in humans) of the optic fibers, the visual input from each eye is processed primarily by its contralateral hemisphere (e.g., Harman et al. 1999): thus, using the left (or right) eye means that the right (or left) hemisphere is used. As in other species, asymmetrical processing of visual stimuli according to emotional valence has been clearly demonstrated: when experimentally exposed to an object with a negative emotional valence (such as a veterinary shirt associated with stress-inducing situations or a novel fear-inducing object), horses use predominantly their left eye (i.e., involving the right hemisphere) rather than their right eye (i.e., involving the left hemisphere) to glance at it (Larose et al. 2006; De Boyer Des Roches et al. 2008). The tendency to look at a novel object with the left eye is even correlated to the emotional level of the horse (Larose et al. 2006): the more emotional in presence of novelty (i.e., active locomotion, increased vigilance, reluctance to approach item) the horse appears to be, the greater the proportion of time spent looking at the object with the left eye. However, novelty is not forcefully associated with a left bias in visual processing: it depends on how horses perceive the novel situation (De Boyer Des Roches et al. 2008).

Interestingly, horses can also show visual laterality in different contexts of interaction with conspecifics (with a predominant left eye use during agonistic encounters; Austin and Rogers 2012) and humans (e.g., Austin and Rogers 2007; Sankey et al. 2011a). Adult horses displayed a greater reactivity (i.e., larger flight distance) toward a “threatening” person (i.e., a person opening an umbrella and then approaching) presented in the left compared to the right monocular visual field (Austin and Rogers 2007). Similarly, 1-year-old untrained horses display asymmetrical responses to an approaching human, with more negative reactions (escapes, threats) when approached from the left side, while approaches toward the right shoulder

elicited more positive behaviors (Sankey et al. 2011a). Such visual laterality could provide important clues regarding horse perception of a particular person, or humans in general, or even work/training sessions. It is worth noting that horses trained with positive reinforcement, well known to improve horse–human relationships (e.g., Sankey et al. 2010), show no negative behavioral responses when they are approached by the left (contrary to the year-old untrained horses mentioned above). On the contrary, horses trained with more stressful approaches (such as the round-pen technique in which the horse is chased repeatedly) show a left eye preference for viewing at the trainer. Similarly, horses trained with negative reinforcement turned their heads to the right when the experimenter agitated the stick in front of them, thus looking at it with their left eye (Sankey et al. 2010).

Studies to date in other sensory modalities are scarce in equines. However, a recent study (Basile et al. 2009) revealed in the domestic horse a preponderant processing of familiar conspecific (i.e., group members and familiar neighbors) whinnies by the left hemisphere (i.e., responses with right head turning) compared to the whinnies of unfamiliar conspecifics, suggesting that the degree of familiarity influences the laterality of the auditory response. Similarly, it has been shown that the degree of novelty influences the laterality of the olfactory response, with a preponderant processing of new odors (i.e., odor of unfamiliar conspecifics) by the right hemisphere (i.e., the use of the right nostril; McGreevy and Rogers 2005).

Data in horses all converge toward a specialization of the right hemisphere for the processing of stimuli that elicit negative emotional responses, and raise questions concerning the classical practice that consists in approaching and manipulating horses on their left side.

## Individual Variations and Factors of Influence

In horses, like in any other species, individual differences exist in the reactions toward sensory stimuli. It has been proposed that sensory

sensitivity is considered a temperament trait (Lansade et al. 2008). However, if individuals do not react to a given stimulation, it may be that they do not perceive it, or that they do not react because they lack motivation or are inhibited. Thus, apathetic horses have been described in different studies on horses whose welfare was compromised or were in pain. A lowered visual and tactile reactivity was found in “depressed” horses (Fureix et al. 2012b), and stereotypic horses show opposite responses to a wither grooming to nonstereotypic horses (Normando et al. 2007). Horses may also not show reactions because of an inhibition (e.g., taught not to move). This is where behavioral observation may reach its limits and neurophysiological data are needed. Finally, developmental plasticity may influence the developmental sensory trajectory of individuals; deprived social and sensory environments during development (e.g., early individual stall housing) may well impair the development of brain sensory areas as found in other species (Hubel and Wiesel, 1963; Cousillas et al. 2004, 2006). Adult plasticity has been demonstrated in other species and would be worth investigating in equines: brain lateralization may vary with the arousal state or season in birds for example (Karino et al. 2016). Promising approaches, such as electrophysiological recordings of brain activity in free-moving horses, will help fill the gap between anatomy and behavior (Cousillas et al. 2017).

## Cross-References

- [Attention](#)
- [Behavioral Lateralization](#)
- [Cerebral Asymmetry](#)
- [Clever Hans](#)
- [Cognition](#)
- [Equine Cognition](#)
- [Hemispheric Specialization](#)

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## Equity

### ► Inequity Aversion

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## Erasmus Darwin

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The grandfather of both Charles Darwin and Francis Galton, Erasmus Darwin was born in Elston, UK, on December 12, 1731. Trained as a physician at the University of Edinburgh, Darwin had a successful medical practice based in Lichfield, in the midlands of England. By some accounts, he was the finest physician in England at the time (King-Hele 1977). He declined the opportunity to move to London as royal physician to treat King George III for his bouts of mental illness. A compassionate man of unending curiosity, he was an enthusiastic amateur natural philosopher. After forming the Botanical Society of Lichfield, he translated the works of Linnaeus from Latin to English and published the taxonomic work as “*A System of Vegetables*” and “*The Family of Plants*” from 1783 to 1787 (Darwin 1782–1783; Darwin 1791). Because Linnaeus had classified plants based on the structure of their flowers, Darwin converted this into a long poem, “*The Loves of the Plants*” which was shocking for the times, because it was so sexually explicit. For example, grapevine (*Vitis*) is described as “Seductive harlot” because the flowers have 5 stamens (male parts) and 1 pistil (female); Rose campion (*Lychnis*), with 10 stamens and 5 pistils as “Wanton beauties in gay undress” (Browne 1989). In this way, Darwin popularized science. *The Botanic Garden* sold well, was translated for European audiences, and Darwin became well-known as a writer and poet.

Erasmus was a founding member of the Lunar Society (which met near full moons), a group of politically progressive scientists, industrialists, and inventors that included among others the potter Josiah Wedgwood; developer of the steam engine, James Watt; and the chemist Joseph Priestly. Darwin was also a friend of Benjamin Franklin. The society was anti-slavery, promoted the Industrial Revolution and supported the French and American Revolutions (positions which would later get some members in trouble with society and the law). Darwin also belonged to the Derby Philosophical Society, which promoted experiments with gases to treat diseases such as cancer and infections. The author of *Frankenstein*, Mary Shelly, attributed some of Darwin's experiments as inspiration for her novel (Shelley 1818).

Although he did not patent his ideas, Darwin invented a horizontal windmill (used at Wedgwood's pottery to grind pigment) and after being injured in a carriage accident that damaged his knee, invented a stabilizing system to prevent carriages from tipping and a steering mechanism that was later used in automobiles. He also envisioned a speaking machine, a canal lift, a copying machine, a rocket engine, weather monitors (which were used for many years), and even a mechanical bird. While convalescing from his accident, Darwin began to consider theories about the relationship between mind and body, about medical practice and theory, and even about the origin of the Earth and the history of life. These ideas led to the publication of his most controversial and famous work, *Zoonomia: The Laws of Organic Life* (1794–1796) (Darwin 1796).

*Zoonomia* was a massive work (586 pages). In it, Darwin covered his theory of disease and classified various illnesses in charts. The book was used as a medical text. Darwin was influenced by the medical doctor and philosopher David Hartley (1705–1757), who suggested that vibrations detected by the five senses became ideas. This was a materialistic (some argued atheistic) view that linked humans with animals. Darwin suggested that the human body was composed of fibers and nerves, and that “motions” were detected by the senses, translated into ideas in the brain, and that patterns of experience could

be passed down generations (associationism). The most controversial ideas were presented in a chapter called *Generation*.

In *Generation*, Darwin suggested that the earth was ancient and that life formed from minute filaments in prehistoric seas. From this early form of life, Darwin suggested that the environment had caused organisms to evolve adaptations to satisfy their “*perpetual endeavor to supply the want of food*.” Erasmus Darwin's driving force for evolution (change through time) was not natural selection but an innate drive caused by needs to meet environmental challenges. He thought that fossils provided evidence of descent and that humans were animals and a part of the vast array of life. He made no attempt to reconcile his views with standard biblical interpretations. Darwin also went on in a book published after his death, “*The Origin of Society*” to reiterate his ideas for the origin and history of life and suggested that human societies evolved from monarchies to democratic/republican systems (Darwin 1803).

After publication, *Zoonomia* was greeted with severe criticism (Garfinkle 1955). It was considered subversive, a horror, a monstrosity, atheistic and that it degraded humans and exalted animals. One reviewer despised Darwin's “*total denial of any interference of a Deity in the creation and preservation of everything that exists*” (Hardin 1959). The ideas expressed by Erasmus Darwin were considered to menace the social order in England. The publisher of *Zoonomia*, Joseph Johnson was imprisoned. Because of the heretical nature of *Zoonomia*, it was placed on the papal index of prohibited books in 1817. A long parody poem of *The Loves of the Plants*, called “*The Loves of the Triangles*” led to widespread ridicule of Darwin and his eccentric ideas (Fara 2012).

Nevertheless, many of the ideas in *Zoonomia* resonated. In France, Jean Baptiste de Lamarck adopted the same idea that organisms responded to the environment by changing over time from generation to generation (evolution) due to needs (*besoins*) and that these had created new species (*Philosophie Zoologique* 1809). Lamarck, however, was not aware of Darwin's work (Mayr 1982).



Because of the ridicule directed at Erasmus Darwin, the term “*Darwinism*” became a derogatory expression for fanciful speculation, which was later applied to his grandson’s work. Charles Darwin read *Zoonomia* twice and concepts such as the old age of the Earth, vestigial organs (“wounds of evolution”), sexual selection, analogies and homologies, hereditary diseases, and inbreeding, among others, which appear in *Origin of the Species*, occurred in germinal form in *Zoonomia* (Darwin 1859). Charles did refute the idea that his grandfather’s writing directly influenced his work on natural selection and

decried the fact that *Zoonomia* offered little concrete evidence to back up the theories it presented (Stott 2012). It is likely that one of the reasons that Charles Darwin took so long to publish *Origin of Species*, and assembled so much supporting evidence for natural selection, was because of the scorn that his grandfather had incurred (Hardin 1959).

Although there were some similarities and many differences between grandson and grandfather (see Table 1), Erasmus Darwin deserves to be better known for his historical role as a progressive free-thinker who was not afraid to challenge established

**Erasmus Darwin, Table 1** Erasmus Darwin compared with grandson, Charles Darwin

|                           | Erasmus Darwin (1731–1802)                                                                                                                                                                                                                                                     | Charles Darwin (1809–1882)                                                                                                                                                                                                                            |
|---------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Personal Life             | Promiscuous, licentious                                                                                                                                                                                                                                                        | Faithful, conservative                                                                                                                                                                                                                                |
|                           | Fathered at least 16 children with two wives and a mistress                                                                                                                                                                                                                    | Married once and had 10 children                                                                                                                                                                                                                      |
|                           | Never left England and Scotland but did travel often within the midlands                                                                                                                                                                                                       | Travelled around the world but became sedentary and settled after marrying                                                                                                                                                                            |
|                           | A large, portly man; very outgoing with many friends                                                                                                                                                                                                                           | A large man, reclusive with a close group of a few trusted good friends                                                                                                                                                                               |
|                           | Suffered with a permanent limp after a carriage accident; stammered when he spoke                                                                                                                                                                                              | Mostly healthy and hardy until 1838 when he started to have many health complaints (which may have been due to Chagas’ disease or to psychosomatic issues); stammered                                                                                 |
|                           | Agnostic – “THE FIRST GREAT CAUSE” gave a living filament animality                                                                                                                                                                                                            | Trained in theology but later was probably an atheist or agnostic                                                                                                                                                                                     |
|                           | Died at age 70                                                                                                                                                                                                                                                                 | Died at age 73                                                                                                                                                                                                                                        |
| Professional Life         | Medical doctor (Univ. of Edinburgh) with a successful medical practice, poet and author                                                                                                                                                                                        | Dropped out of medical school (Univ. of Edinburgh), trained in Theology (Cambridge), author and scientist.                                                                                                                                            |
| Natural History Interests | Botany, Geology and fossil collecting. Experiments with gases as treatments for diseases                                                                                                                                                                                       | Botany (experiments with seeds, climbing plants and orchids), Entomology, Geology, Fossils, Marine invertebrates (especially barnacles) and experiments with earthworms                                                                               |
| Political Interests       | Anti-slavery, promoted women’s education, supported republican democracy                                                                                                                                                                                                       | Anti-slavery but otherwise made few comments regarding government                                                                                                                                                                                     |
| Main Work                 | <i>Zoonomia</i> – was very cautious about publishing because of political and social implications. Theoretical with little supporting evidence presented                                                                                                                       | <i>Origin of Species</i> – was very cautious about publishing because of scientific and societal-religious implications. Theory presented (evolution by natural selection) was supported by a great amount of experimental and observational evidence |
| View of Evolution         | Evolution explained the history and diversity of living things. The main agent of change was an innate drive to adapt to environmental challenges. Lamarckian evolution by the inheritance of acquired characters<br>Evolution was goal directed toward constant “improvement” | Evolution explained the history and diversity of living things. The main agent of change was natural selection due to the non-random survival of randomly generated varieties. Evolution was not goal directed                                        |



ideas (King-Hele 1999, 2003, 2007). He used his great observational skills (honed to diagnose and treat patients) to observe the natural world. He linked the practice of medicine to broader ideas about the substance of life, where and how life arose, and its history. He tried to explain how sensations could mechanistically be transformed to ideas. He was a social activist who provided medical care to the poor for free, promoted education for women, and opposed slavery. Samuel Taylor Coleridge is said to have stated that Erasmus Darwin had a "... greater range of knowledge than any other man in Europe" at the time (Barber 1980; Chancellor 1976). William Goodwin in 1797 claimed Darwin as "so extraordinary a man" in his list of "lions" of the day (Hardin 1959). However, Erasmus Darwin has been accused of not being original – that he merely synthesized and popularized the ideas of others (Mayr 1982), an accusation his grandson would also face. Erasmus Darwin died of a heart attack at Breadsall, UK, on April 18, 1802 (King-Hele 1977).

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## Error Rate

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## Definition

Error rate may refer to a variety of methodological and statistical procedures used within experimental studies. With respect to the former, error rate is typically characterized as a performance criterion used for assessing a variable of interest, for example, learning. In regards to statistics, error rate refers to the significance level, alpha, utilized in null hypothesis testing.

## Introduction

At a basic level, error rates can be understood as occurring within the signal detection schematic outlined in Fig. 1. If we consider a simple task in

|                                        | Flashing light is present | Flashing light is absent |
|----------------------------------------|---------------------------|--------------------------|
| Response: “There is a flashing light”  | Correct detection         | False-Positive           |
| Response: “There is no flashing light” | False-Negative            | Correct rejection        |

**Error Rate, Fig. 1** Schematic of signal detection theory for a light discrimination task

which a subject must indicate the absence or presence of a flashing light, two types of errors can occur, false negatives and false positives. False negatives occur when the subject identifies the light as being absent when in fact the light was actually there, while false positives occur when the subject indicates the presence of the flashing light in its absence. Combined together, these two measures can provide insight into sensory processes related to detection and discrimination, as well as other cognitive processes.

**Error Rate as a Performance Criterion**

As a performance measure, error rate refers to behavior that deviates from a stated criterion. Consider a prototypical experiment in which a rat is trained to turn left within a T- maze in order to obtain a sugar pellet. Within this setup there is a performance criterion identified as “turning left” in the maze. Alternatively, “turning right” within this setup is conceptualized as committing an error. By analyzing the behavior of the rat placed within the maze over multiple time points to the criterion of “turning left,” an overall rate of errors committed or error rate can be determined.

Typical studies of animal behavior and cognition utilize the above defined error rate as a means of analyzing how animals learn and perceive their environment. For example in reinforcement learning, the error rate functions as an index of the associative strength between a stimulus and particular response contingency (Sutton and Barto 1998). As the animal learns the association between a stimulus and a specified response–reward contingency, they become

more likely to engage in the specified response. Within this setup, as the error rate decreases, the animal can be said to have learned the relationship between the stimulus and reinforcement contingency.

Error rates can also provide insight into the cognitive capacities of animals. Within reversal tasks where the pairing between stimuli A1 A2 with rewards R1 R2 is reversed after stable performance (i.e., A2 now signals R1 and A1 now signals R2), the error rate or amount of responding on the now unrewarded stimulus provides insight into the cognitive flexibility of the organism in recognizing and adapting to changing environmental contingencies (Bond et al. 2007) as well as the underlying neural circuits (Guise and Shapiro 2017). Likewise, cognitive capacities related to working memory and metacognition are often assessed by examining error rates for false negatives and positives in memory recall tasks and investigations of metacognition (Smith 2009).

**Error Rate Within Null Hypothesis Testing**

Within null hypothesis testing, error rates refer to two main types of conclusions regarding the plausibility of the null hypothesis a researcher may arrive at, termed type I and type II errors. A type I error is characterized by an incorrect rejection of the null hypothesis and is related to the significance level of the test or alpha ( $\alpha$ ) value. In simple terms, a type I error occurs when a particular relationship between the dependent and independent variable is reported, when in fact no

relationship exists (this corresponds to a false positive in Fig. 1). Conversely, a type II error is characterized by an incorrect failure to reject the null hypothesis, akin to failing to detect a relationship between the independent and dependent variables (this corresponds with a false negative in Fig. 1). As with type I errors, type II errors are related to statistical power and are defined as beta ( $\beta$ ).

As a general convention, the type I error rate specified by alpha is typically set at or below .05. This value represents the likelihood of observing the data given the null hypothesis is true. One consideration when conducting multiple statistical tests is the compounding of type I errors that arises when examining each additional hypothesis, known as the family-wise error rate. In order to avoid this potential pitfall, it is wise to adjust the alpha level using a statistical procedure, such as the Bonferroni correction (Kirk 2008).

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## Escape Behavior

► [Escape Response](#)

## Escape Motion

► [Escape Response](#)

## Escape Response

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## Synonyms

[Escape behavior](#); [Escape motion](#)

## Definition

An escape response is a coordinated response by an animal to end exposure to a noxious stimulus or potentially dangerous experience. Escape responses may be innate or learned and function to improve the survival of the animal.

## Introduction

An escape response functions to terminate a negative experience or exposure to a hazard. It will take a form likely to produce this outcome, which may be fleeing, hiding, or releasing materials. For example, a marine mollusk such as an octopus may release ink (Derby 2007), or an insect such as an aphid may drop from a branch (Gish and Inbar 2006). Many animals will flee rapidly from a threat along an unpredictable trajectory or zig-zag path. Predator escape is one of the most commonly studied escape responses; however, it may be shown in response to a range of stimuli such as temperature extremes, a source of pain, or any sudden intense stimulus.

Escape responses with a known and predictable form may have a specific name. For example, the “C-start” is a sudden turn and acceleration shown by fish avoiding a predator (Eaton and Emberley 1991) and is named after how the fish’s body appears from above as it makes its sudden turn. Crustaceans such as shrimp rapidly escape predators with a tail-flipping motion called

the caridoid escape reaction (Faulkes 2015; Heitler et al. 2000).

As some escape responses can be reliably elicited, they are convenient models for assessing how the nervous system evolved, how the behavior is elicited and performed, and how environmental variables and various types of learning modify the response. For example, the tail-flipping escape response circuit of crustaceans such as shrimp, which is relatively simple and mediated by giant interneurons, appears to be ancestral to all decapods (Faulkes 2015).

### **As Distinct from Avoidance**

If a behavior allows an animal to prevent its exposure to a stimulus that would otherwise elicit an escape response, this constitutes an avoidance response. However, the distinction between escape and avoidance is less clear when considering the role of the stress or anxiety felt in anticipation of a predictable or signaled danger. That is, a behavior that prevents the animal from encountering a hazard may be maintained through escape behavior that occurs as soon as the animal experiences a conditioned fear response provoked by stimuli that indicate the hazard may be nearby. These conditioned fears are seen as animals acquire fear of predators but then also of conditions where predators hunt more effectively such as open or brightly lit areas (Griffin et al. 2000).

### **Absence of Escape Behavior and Learned Helplessness**

When animals find they are unable to escape a noxious stimulus, they may stop performing escape behavior, and this passivity may persist into situations where an escape response would be effective. This failure to perform an available escape response due to prior learning is referred to as “learned helplessness” (Maier and Seligman 1976). This conditioned absence of an escape

response is associated with chronic negative welfare states such as depression (Maier 1984).

### **Marginal Cases**

The status of some behaviors as escape responses is speculative or disputed. For example, some researchers suggest that self-mutilation behavior may function to end stressful demands or unpleasant internal states or to cope with unstimulating environments (Carr 1977). And bar-chewing by rats and mice, once considered a stereotypy, is now widely considered to be an escape-motivated behavior (Lewis and Hurst 2004). Where the response is not rapid and clearly elicited by an observable stimulus, or is not effective in the animal’s current environment, its role as an escape response may be more difficult to establish.

### **Modifications**

Escape responses are modified by many variables. For example, animals in groups may show an escape behavior without ever experiencing the eliciting stimulus if they imitate the escape responses of conspecifics (Herbert-Read et al. 2015). And there is evidence that animals show reduced or absent escape responses to predators when influenced by parasites that rely on predation to complete their life cycle (Holland and Cox 2001; Libersat and Moore 2000).

### **Conclusion**

Escape responses are a class of behaviors that remove an animal from an aversive or dangerous situation. Due to the high survival value of this behavior, it can often be reliably produced and systematically studied. For this reason, the study of escape behaviors has contributed to knowledge of the neural and psychological basis for behavior in many different species.

## Cross-References

- [Avoidance](#)
- [Habituation](#)
- [Learned Helplessness](#)

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## Essentialism

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## What Is Psychological Essentialism?

Much of human cognition is characterized by psychological essentialism (Gelman 2003). In its broadest form, psychological essentialism is a conceptual framework that defines our naïve-metaphysical perspective on the structure of objects and categories. Its basis is the distinction between two kinds of properties: Objects of a given kind can have many *accidental* properties: These are properties that the object in question can but need not have, and in respect to which it can change without becoming a different kind of object. *Essential* properties (Essential properties are sometimes called “defining,” and accidental ones “characteristic.” Research in cognitive development, for example, suggests that children’s lexical semantics undergo a “characteristic-to-defining” shift in the preschool years such that children initially base word meaning on superficial features associated with prototypical instances of a given kind, and only later focus on the defining features underlying the category and its prototypical as well as less prototypical members alike (Keil and Battermann 1984)), in contrast, are those properties that make an object the kind of object it is and that thus define its very identity.

Whether something is a piece of gold is a question of its deep, essential (chemical) properties. If you change these properties, the object in question is no longer a piece of gold. Pieces of gold, on the other hand, usually have some prototypical surface features like looking golden. But these are merely accidental, not defining or essential, features. You can change them, for example, by painting the piece green, without altering the very identity of the object.

Importantly, psychological essentialism is a rather general and abstract framework and we often do not need to know what exactly the essential properties in question are in order to assume that there are some. This is particularly clear in the case of many of our natural kind concepts. No layperson has any idea about the essential properties of being a tiger, elm, or piece of gold (Kripke 1972; Putnam 1975). We are often able to refer to and pick out objects of these kinds demonstratively (“This is a tiger”), and we assume that there must be a deep, underlying essence (its tiger-ness) that defines its natural kind, but mostly we either defer to authority (“zoologists know”) or future research (“they’ll find out”) when having to explain what this essence may be. Our concepts of “tiger”, “elm,” and “gold” function, as it were, as *essence placeholders* (Medin and Ortony 1989).

### The Scope of Psychological Essentialism

The most obvious domain of application of psychological essentialism is thought about natural kinds, and in particular biological kinds. Typically, adult humans share the intuition that biological natural kinds, such as tigers and elms, are constituted by shared, deep essential properties that are largely unknown to the folk, but may be specified by scientists or other experts (Atran 1998). Some form of psychological essentialism, however, seems also to be at work in our categorization of artifacts – whose essences have to do with history of invention, production, and use (Bloom 1996; Gelman 2013). Another prominent area in which psychological essentialism features prominently is social categorization: For many social categories, for example, gender, ethnicity, race, or social class, adult humans tend to posit deep, underlying essential properties (even if they are unknown) that contrast with merely superficial accidental properties (Rhodes and Mandalaywala 2017).

### Signatures of Psychological Essentialism

From a logical point of view, at the heart of psychological essentialism lies the distinction

between deep essential and superficial accidental properties. Typically, in human adults this distinction has a characteristic signature or pattern of manifestations:

- Categories to which psychological essentialism applies are seen as natural kinds that – unlike merely nominal kinds (such as Tuesdays) – are real and objective and out there in the world even if we (still) do not know what their essence is.
- Though considered as radically different, essential and accidental properties are seen as causally related in characteristic ways: Members of a given kind have many of their accidental properties in virtue of their hidden essence that somehow produces patterns of perceivable characteristic features (tigers look like tigers because of their tiger-hood).
- At a given time, membership in such categories (and thus the identity of a given object as object of this kind) is a binary rather than fuzzy matter.
- Over time, membership in the category remains stable even over major transformations of accidental properties (as long as these changes do not affect the essential properties).
- Within the category, there is a tendency to see its members as more homogenous than they really are (like in categorical perception, where analogous stimulus differences are underestimated within and overestimated between categories).

### Virtues and Vices of Psychological Essentialism

From a pragmatic point of view, psychological essentialism has many virtues: It is, above all, a powerful cognitive framework for inductive learning and the development of naïve theories. It has been argued, however, that it also comes with cognitive and moral detriments. Cognitively, a rigid overapplication of essentialist assumptions of the stability and unchangeability of natural kinds stands in the way of understanding the dynamic picture of species and their evolution



according to Darwinian theory, for example (Gelman and Rhodes 2012; Mayr 1982). Morally, psychological essentialism with regard to social kind can tend to foster racism, sexism, and other evils (Haslam and Whelan 2008).

### **Empirical Indicators of Psychological Essentialism in Human Adults and Older Children**

The signatures of psychological essentialism mentioned above can be tapped empirically in various ways. Studies on category-based induction, for example, have widely documented that subjects make inductive inferences from some sample objects to other objects based on essential properties rather than their surface accidental properties (Gelman and Davidson 2013). Most prominent, and most relevant for the evolutionary and ontogenetic question in focus here, have been studies that address subjects' intuition of identity and stability of kind membership over time and over various dramatic property changes (Keil 1989). In one kind of vignette, for example, animals of a given kind (say, piglets) are adopted and raised by animals of another kind (say, tigers) and learn to behave like them, etc. In another kind of vignette, an animal of a given kind (e.g., racoon) is superficially transformed by being shaved, painted or even by surgical treatments to look (and even smell) like an animal of a different kind (e.g., skunk). In both cases, the target question is what the original animal will end up and turn out to be (Keil 1989). In both cases, human adults and children from age 4 to 5 are very firm in their intuition: You can adopt or superficially transform animals as much as you want to, but this will never turn them into animals of a different kind.

### **Roots of Psychological Essentialism**

While psychological essentialism has been amply documented in adult humans and older children, little is known so far about its origins, both ontogenetically and phylogenetically. This is partly

due to methodological reasons: Most studies on psychological essentialism heavily rely on language as dependent measure (participants are asked to make explicit identity and category judgments such as “Will this animal end up as a racoon or a skunk?”), and are therefore not suitable for testing nonverbal animals or preverbal infants. This may, however, also partly be due to theoretical reasons. It has been argued that psychological essentialism is a “late and sophisticated achievement” (Fodor 1998, p. 159), both historically and ontogenetically, that heavily rests on linguistic and technological foundations. According to this argument, it simply would not make sense to even look for basic forms of psychological essentialism in infants or nonhuman primates.

### **Sortal Object Individuation**

However, recent research in developmental and comparative psychology has begun to use alternative, nonverbal methods in order to explore ontogenetic and phylogenetic roots of psychological essentialism. This research is based on the assumption that psychological essentialism need not come as an all or nothing package. Rather, it may develop in steps, and there may be more basic and foundational forms of essentialism in which not all of the characteristic adult signatures (see above) are present yet. Quite plausibly, the most basic form of essentialism builds on basic object cognition, namely on intuitions about the identity and stability of objects as members of a given kind – without necessarily including other signatures such as understanding the causal relatedness of essential and accidental object properties. And quite plausibly, the primordial form of such intuitions is found in sortal object individuation (Xu and Carey 1996).

Sortal concepts are kind concepts, linguistically typically reflected in the form of count nouns, such as “tiger,” “car,” or “duck.” Sortal concepts supply criteria of individuation and countability (whenever one can reasonably ask “How many Xs are in the room?” “X” is a sortal concept), and identity (such that one can ask and answer questions of the form “Is this the same X as the one that was here a while ago?”). Sortal object individuation is the capacity to use such

sortal concepts to individuate, identify, and track objects. The crucial point for present purposes is the following: Given their role in identity judgments, sortal concepts already involve a basic distinction between essential properties that do preserve identity (even if they are unknown) and merely accidental properties that are irrelevant to identity questions.

Sortal object individuation has been studied in human infants, since a pioneering study by Xu and Carey (1996), with designs like the following: The infant is confronted with a box into which an object of kind A enters at time 1, followed by an object of kind B that comes out of the box at time 2. The central dependent variable is subjects' numerical expectation as to how many objects are in the box, as indexed by their looking and searching behavior. If they individuate the objects as objects of distinct kinds that cannot turn into each other, they should expect that there must be still (at least) one object, the object of kind A, in the box. Basic versions of such tasks in which an object of kind A (e.g., a ball) and an object of kind B (e.g., a toy duck) are used that differ both in essential and superficial properties are mastered by human infants from around 12 months (Xu 2007). Interestingly, this is the age at which children begin to acquire serious language competence and, indeed, some studies found that sortal object individuation and language development go hand in hand: The children who solve a given sortal individuation task tend to be those children who already understand the requisite words ("ball," "duck"), and children generally perform better when the objects are explicitly labeled (Xu 2002). This has led to speculations, in line with a long philosophical tradition (e.g., Quine 1957), that sortal object individuation may be basically a linguistically grounded phenomenon (Xu 2002).

However, subsequent comparative studies with analogous tasks amply documented the very same capacities in nonhuman primates (Mendes et al. 2008, 2011; Phillips and Santos 2007; Phillips et al. 2010; Santos et al. 2002). And some studies with dogs and birds even suggest that sortal object individuation may be more ancient and widespread beyond the primate lineage (Bräuer and

Call 2011; Fontanari et al. 2011, 2014). Therefore, on the premise that these kinds of tasks really tap sortal object individuation, this capacity seems to be older than language and clearly not uniquely human.

But is this premise justified? Does one really need to use sortal concepts in order to solve these tasks? The basic methodological problem is that in these scenarios, information about the kinds of objects (their essential properties) and information about their merely superficial properties are necessarily confounded (balls and toys ducks are different kinds of objects, but they also look very different). And so success in these tasks could be more parsimoniously explained on the basis of tracking superficial (rather than essential) properties.

Another set of studies, therefore, combined the logic of such individuation studies with the logic of verbal transformation stories (used in research on psychological essentialism) in order to investigate whether infants and nonhuman primates really make use of sortal (and not just property-based) object individuation. In one study, 14-month-old infants saw events of the following structure: at time 1, an object with appearance A (e.g., a toy bunny) entered into a box, and at time 2 infants either saw an object with appearance A (same bunny) or with appearance B (e.g., toy carrot) come out of the box (Cacchione et al. 2013). The two appearances, in real fact, belonged to one and the same object (a soft toy that could be turned inside out, with carrot-appearances on one side, and bunny-appearances on the other). Crucially, there were two groups of infants: One had been previously familiarized with such dual-aspect objects, while the other one had not. The ignorant infants took the difference in superficial appearance as diagnostic for questions of numerical identity (they searched longer in the bunny/rabbit condition than in the bunny/bunny condition). The infants in the other group (familiar with such dual-identity objects), in contrast, ignored the superficial differences for their judgment of numerical identity (they did not search differently in the two conditions). That is, given the requisite background knowledge, infants disregard the superficial feature differences in much the same

way as older children disregard the superficial feature differences between a normal racoon at time 1 and a skunk-looking racoon at time 2 (after it has been painted, etc.), when it comes to the question of the animal's identity.

In another study with a slightly different approach, great apes saw a food item of kind A (e.g., slice of banana) enter into a box and a food item either of kind A or of kind B (e.g., slice of carrot) come out of the box. Crucially, in some conditions, the food item entering the box was first changed in its superficial properties (e.g., the banana slice was painted orange) so that it was perceptually more similar to items of kind B than to other items of kind A. The findings were very clear: Apes treated kind information as more valuable than surface feature information when inferring the number of objects present in the box. They searched longer in conditions involving a difference in kind between the object placed and the object retrieved from the box (as compared to conditions involving only surface feature differences) (Cacchione et al. 2016).

### **Distinguishing Deep/Inside from Superficial/Outside Features**

Converging evidence for a systematic distinction between deep and superficial features in 14-month-old human infants comes from a study by Newman and colleagues (Newman et al. 2008): When trying to figure out the sources of behavior of a self-propelled object (e.g., a toy cat), infants searched more for its internal (deep) rather than its external (superficial) features. That is, they seem to appreciate that the self-generated movement of agents is more likely to be caused by deep internal properties than by more accidental external features.

### **Summary and Outlook**

Psychological essentialism marks a fundamental way of human thinking about the natural and the social world. The workings of psychological essentialism and its underpinnings have been extensively studied in research in cognitive and social psychology. From an evolutionary and

ontogenetic point of view, however, still little is known about its origins and roots. It has sometimes been assumed that essentialism crucially builds on sophisticated linguistic and cultural influences, and should thus emerge relatively late both phylo- and ontogenetically. Recent comparative and developmental research, in contrast, highlights the possibility that precursors and/or basic forms of essentialist thought develop early in humans and are shared with other species in the primate lineage and possibly beyond. In particular, sortal object individuation – the capacity to keep track of a given object as object of a certain kind over time – may be a primordial form of essentialist cognition. It may be the first clear form of fundamental distinguishing between essential properties of objects that determine their identity over time and merely accidental properties that can be changed without altering the object's identity.

Many open questions remain for future research, of course: Is sortal object individuation merely a precursor to or rather already an early form of psychological essentialism? Resolving this question may be largely a terminological matter: If psychological essentialism is conceived in such a way that its core is the distinction between essential and accidental properties and that it can otherwise come in degrees, sortal object individuation appears as one (perhaps even the) basic form of essentialist cognition. If, however, psychological essentialism is seen itself as an all-or-nothing matter that necessarily involves all the different signatures found in adults, then sortal object individuation may be merely a precursor.

What is currently largely unknown is how other signatures typically associated with psychological essentialism (such as assumptions about the causal relations between essential and accidental properties) develop(ed) through ontogeny and evolution. Relatedly, how do children develop the barebones of essentialist sortal object individuation into the full-fledged adult framework of essentialist reasoning? Finally, what other potential foundations of essentialist cognition may there be, and how do they relate to sortal object individuation? It has been suggested, for example, that human essentialism develops out of

a fundamental cognitive tendency to explain events and patterns by focusing on inherent features of the relevant constituents, the so-called inherence heuristics (Cimpian and Salomon 2014). Future research will need to clarify whether such a heuristic is an additional and complementary building block out of which full-fledged psychological essentialism finally develops; or alternatively, whether it is even the most basic cognitive foundation that underlies psychological essentialism.

## Cross-References

- Categorization
- Reasoning

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## EST

### ► Gene Expression Profiling

## Estrogen

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## Introduction

Over the past 30 years, evidence has revealed that estrogen effects on behavior transcend that of sexual behavior and in fact have profound effects on cognitive function in animals and humans. This entry briefly summarizes the effects of estrogen on the central nervous system, including structural and local synthetic effects, and how these actions modify cognitive differences between sexes, menstrual phases, and the

menopausal transition. Finally, this entry will explore implications for estrogen therapy as it relates to cognitive dysfunction and aging.

## Mechanisms of Estrogen Action on the Central Nervous System

Estrogen is a steroid hormone best known for sexual differentiation and reproduction. Estrogenic modulation of brain regions and cognitive function first begins in utero, continues through adolescence, and reaches its highest impact in adulthood when regular hormone secretions reach their highest levels before rapidly plummeting with aging. Estrogen-dependent effects on cognition have largely been attributed to both classic, genomic mechanisms – hormone binding to nuclear receptors and modification of gene transcription. The receptors mainly responsible for such ligand-activated transcription are estrogen receptor ER- $\alpha$  and ER- $\beta$ . Both are distributed throughout the body, including several areas of the central nervous system that coordinate cognitive function, including the cortex, amygdala, hippocampus, basal forebrain, cerebellum, locus coeruleus, raphe, and central gray matter. The ER subtypes differ in localization, binding affinities for ligands and modulators, and effects on cognition (Luine 2014).

Subcellular localization of ERs to the plasma membrane of neurites, soma, dendritic spines, and axon neurons suggests another role for estrogens as a mediator of synaptic transmission (McEwen and Alves 1999). Estradiol can also bind to a G-protein coupled receptor (GPR30) which is expressed in the hippocampus. The role of this receptor remains unclear, but it is thought to promote cell signaling (Brailoiu et al. 2007). Finally, there is evidence for in situ production of estradiol, likely resulting from conversion of other steroids (i.e., testosterone or cholesterol), by aromatase in discrete brain regions. Local accumulation may represent a neuromodulatory role for estrogen as neurosteroid, potentially mediating synaptic connectivity (Balthazart and Ball 2006). In summary, estrogen effects on the brain are complex and regulated through an array of



cellular mechanisms that likely work in concert to influence cognition.

## Estrogen and Cognition

The role of estrogen in sex-specific events (menstruation, pregnancy, and menopause) is outside the scope of this review. To summarize briefly, gonadal production of testosterone begins in utero and directly masculinizes the male genitalia. In the central nervous system, testosterone is aromatized to estradiol and together these hormones program sexual behavior. In many animal species, sexual behaviors are strikingly different. Males exhibit mounting, while females exhibit lordosis. What is less apparent is that there are also sex-differences in nonsexual behaviors. For example, male rodents immediately outperform females on tasks requiring spatial memory, while females tend to take longer to acquire visual representation of spatial cues, but once they do they retain task performance even after environmental alterations (Luine 2014; Williams et al. 1990).

Similar sex differences in cognition are evident in human studies. As with rodents, men tend to outperform women in tasks require spatial cues. Women, however, are superior to men in aspects of verbal abilities, including spelling, grammar, and speech acquisition. Women also tend to outperform men in tests of perceptual speed and accuracy and exhibit better short-term memory. Overall sex differences in cognitive function in rodents and humans is small in magnitude, but it is important to note that differences in spatial abilities are present in children and become larger at puberty suggesting that differences are driven by both organizational and activational hormone effects (Luine 2014).

Further demonstrating activational effects of estrogen are differences in cognitive performance throughout the estrous and menstrual cycles. Physiological fluctuations in ovarian hormones across cycles allow for noninvasive studies of the effects of estrogen on cognition. During proestrus, when estrogen peaks in rodents, females

demonstrate better recognition and spatial memory compared to those in different phases of the estrous cycle (Frick and Berger-Sweeney 2001; Frye et al. 2007; Walf et al. 2006). One reason for this may be estrogen effects on the stress-experience. The majority of rodent learning and memory tests introduce stress via negative (shock) and positive (food deprivation prior to reinforcement) reinforcement, as well as extensive handling. Estradiol administered to ovariectomized rats has been shown to decrease anxiety and depression in laboratory tests, making it difficult to determine cycle-related changes to cognition independent of stress effects (Frye et al. 2007). Nevertheless, human studies have reported menstrual cycle effects on tasks specific to spatial and working memory. However, the results are inconsistent and seem to be specific to spatial tasks (Luine 2014).

The majority of evidence for a role for estrogen on cognitive function comes from ovariectomized rodent studies. Ovariectomized rats show impaired performance on tasks requiring spatial working memory that can be improved by estradiol treatment. Other evidence suggests that estrogen replacement specifically enhances acquisition, but not reference memory. Such activity may be explained by estrogen enhancement of cholinergic function and increasing dendritic spine density. In monkeys, ovariectomy reduces, while estrogen and progesterone replacement restores the density of axons related to acetylcholine and dopamine neurotransmission in the prefrontal cortex (Kritzer and Kohama 1998). In humans, this region plays an important role in information processing, thus decreased estrogen levels may play critical role in age-related declines in cognitive function, especially short-term memory, seen in postmenopausal women.

## Estrogen and Cognitive Loss

One of the most important areas of study in the estrogen and cognition field is age-related cognitive decline. While it is difficult to ascribe a



specific role for estrogen in the neurogenerative due to other factors associated with the aging process, the potential impact of the hypo-estrogenic state following menopause is an important area of study. There is a clear sex-difference in the development and pattern of neurodegenerative disease. For example, females are more likely to develop Alzheimer's disease than males although the mechanism is unknown. Studies in rodents propose that decreased spine density in the prefrontal cortex and hippocampus are decreased following ovariectomy, but less significantly so with normal aging (Luine 2014). Structural changes along with impaired spatial memory in these animals suggest synaptic reorganization resulting from low estrogen levels.

Whether connectivity and working memory can be restored by estrogen treatment is a critical unanswered question. During the 1980s and 1990s estrogen therapy was demonstrated to promote memory during aging in several observational studies. However, longer trials using hormone replacement therapy in women suffering from Alzheimer's disease found no cognitive benefit (Luine 2014). Several expert sources have tried to pin the critical period hypothesis as a reason for inconsistencies in the literature on estrogen therapy and neuroprotection. According to the critical period, estrogen therapy will only have an effect on aspects of cognition if it is initiated soon after menopause. It has been suggested that exogenous estrogen effects are impaired by already existing adverse modifications such as reduction in brain volume, synaptic connectivity, and neurotransmitter systems; thus delayed neuroprotective effects are putative. There is some evidence for this theory in rodents (reviewed in Daniel 2013). For example, rats given estrogen replacements immediately after ovariectomy at middle age demonstrated superior learning in old age compared to animals ovariectomized at the same age but receiving no therapy. These rats, which were given estrogen for a short period also showed similar learning and memory as ovariectomized rats that received continuous replacement therapy thus indicating

the need for studying the regimen of replacement therapy.

Finally, premenopausal women experience cyclic fluctuations in estradiol, as specific hormone, 17 $\beta$ -estradiol. These fluctuations co-occur with fluctuations in another hormone, progesterone. Therefore, there is still work to be done to determine how specific hormonal interactions and delivery may affect normal and pathological changes in cognition (Luine 2014). Currently, the main confounder in existing studies is the use of conjugated equine estrogen (CEE) as hormone therapy. CEE is a mixture of conjugated estrogens, including sodium estrone sulfate and sodium equilin sulfate, among others, and only trace amounts of estradiol. For this reason, it is difficult to correlate the results of hormone replacement therapy using CEE to estradiol replacement. Interestingly, since its approval in 1942, the marketed version of CEE – Premarin, has been the only available compound for hormone replacement therapy. While new routes of administration have been developed, no novel estradiol-based compounds have been brought to the market. In the past two decades, selective estrogen receptor modulators (SERMS) have been developed for the treatment of other estrogen related conditions, such as osteoporosis and breast cancer (Luine 2014). The ability of SERMS to directly target specific estrogen receptors represents an exciting new avenue to research the role of estrogen on cognition and potential therapeutic targets.

## Conclusions

Awareness of estrogen effects on cognition has grown immensely over the past several decades (Luine 2014); however, the neural action of estrogen is still not well understood. Estrogen receptors are now known to be nuclear, localized to the plasma membrane, and function via G-protein coupled signaling pathways. Local synthesis of estrogen is another potential way by which estrogen may function as a neuroprotectant. There is

still much to uncover regarding the neural mechanisms for estrogen action, including the effects of specific isomers, timing, and delivery. Future research is necessary for understanding estrogen effects on cognitive function and identifying pharmacological treatments for the reversal of age-related decline.

## Cross-References

### ► Psychopharmacology of Sex Steroids

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## Estrous

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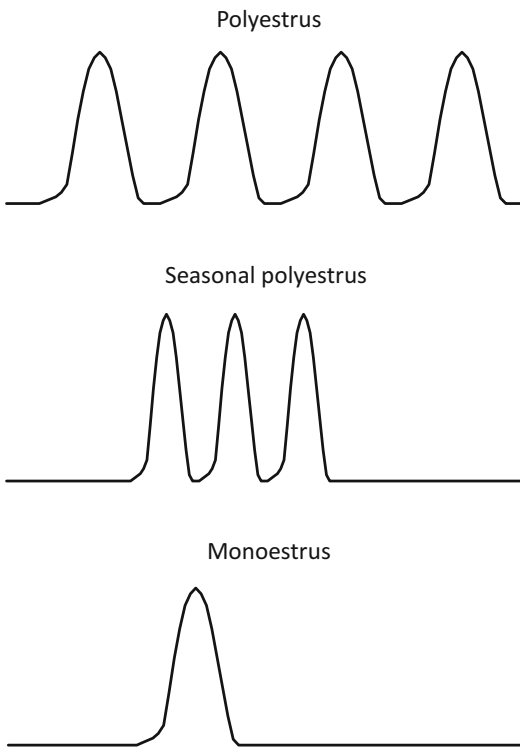
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## Synonyms

Oestrous

## Introduction

Reproduction can be an energetically expensive, complex, and risky phase within a female's life history cycle (Hazlerigg and Simonneaux 2015). To assist during these demanding periods, the adult female reproductive system has evolved numerous mechanisms to enhance reproductive success (Weems et al. 2015). One such mechanism in female mammals, excluding the old world monkeys, great apes, and humans, is estrus. Estrus is defined as “the periodic state of excitement in the female of most mammals that immediately precedes ovulation and during which the female is most receptive to mating; heat” (The American Heritage Stedman's Medical Dictionary 2004) and includes a number of endo- and exogenous factors, as well as behavioral components. The occurrence of estrus can be divided into three categories: polyestrous, seasonal polyestrous, and monoestrous. Polyestrous species have a succession of estrous periods throughout a single sexual season, while seasonal polyestrous species display estrous events in “clusters” during a specific period within a sexual season (Fig. 1).



**Estrous, Fig. 1** The graphical representation of seasonal polyestrous, polyestrous, and monoestrous

Finally, monoestrous refers to a single estrus event during a sexual season (Vasanthi 2016). During each estrus event, a number of fixed parameters are observed: the activation of the **central nervous system** (CNS) by environmental and endogenous cues, the resulting stimulation of the **hypothalamic-pituitary-gonadal** (HPG) axis and its regulation of estrus, the activation of estrus behaviors to assist in reproductive activity, and finally, the termination of the estrus event.

### External and Internal Cues Which Activate the Estrous Cycle

Ovulation, i.e., the release of an egg from the ovary, and the mating event required to ensure conception, are important components of estrus. However, as both components are energetically costly and time consuming, females aim to partake in this only if environmental conditions, and social dynamics, allow for successful mating,

conception, and pregnancy (Hazlerigg and Simonneaux 2015). As a result of this, ovulation in mammals has evolved into two distinct patterns, namely spontaneous and induced ovulation.

**Spontaneous ovulators** are known to display a constant cycle of reproductive hormones (e.g., polyestrous, Fig. 1), behavioral estrus and ovulation, irrespective of the presence of physical stimuli by a male (van Sandwyk and Bennett 2005). To ensure that the most favorable conditions are present when raising young, spontaneously ovulating females display a strong coupling of mating activity and date of parturition (Larivière and Ferguson 2003). Chemical, visual, photic, thermal, and/or tactile cues have all been shown to trigger reproductive activity in females, indicating the ideal time for mating and conception, and thus ensuring that young are born during favorable periods (Goldman 1999). For example, the use of photic cues (photoperiodism) allow an organism to use the annual progression of day length as a cue for determining the precise time of year and, thus, successfully regulate an individual's biological rhythm (Goldman 1999).

Another external cue involves the availability of food sources to initiate mating activity. In the natural environment, food resources are often limited or seasonally fluctuating, and as such, play an important role in regulating an organism's ability to reproduce successfully (Bronson 2009). To cope with this, organisms have evolved a number of strategies to ensure optimal energy acquisition and allocation to enhance reproduction. One such strategy involves capital and income breeders; **capital breeders** are species that build up energy reserves during periods of resource abundance but only reproduce at a later stage of the season. In contrast, **income breeders** allocate available resources directly to reproduction (Jönsson 1997). Nonseasonal regions, where resource availability remains constant, are advantageous to income breeders, as postponing reproductive activity does not lead to better environmental conditions.

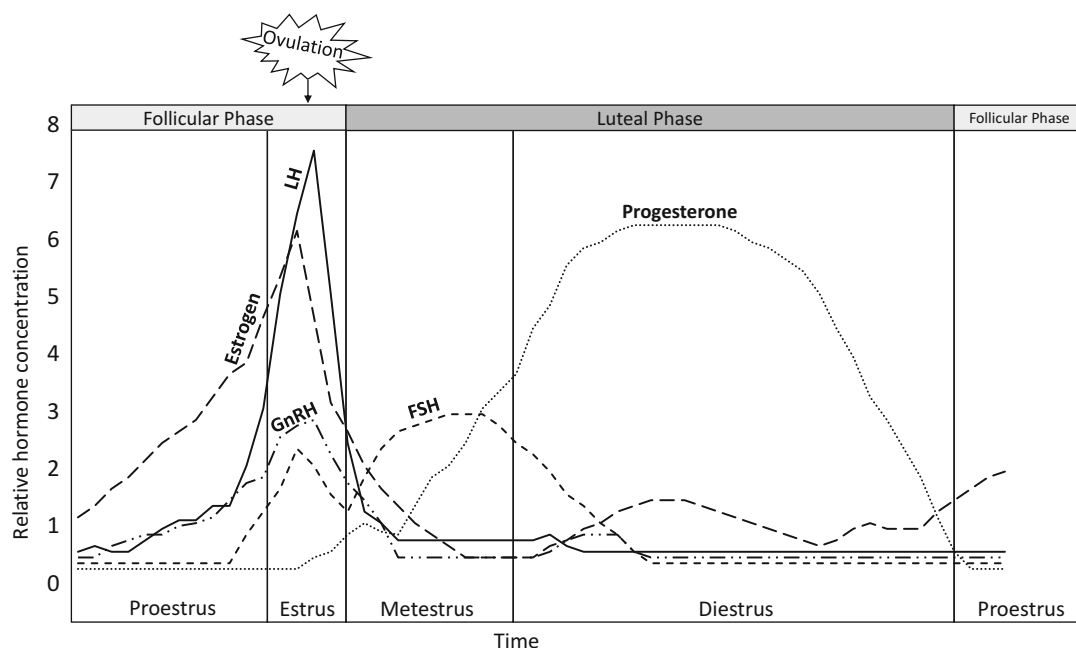
In animal species where environmental cues are not a primary determining factor in driving mating activity, social cues may be a primary driver of reproductive activity. In contrast to

spontaneous ovulators, **induced ovulators** do not ovulate spontaneously and require direct copulatory stimulation to induce ovulation (Clemens and Weaver 1985). Here, the presence of a male acts as a cue for a female to initiate behavioral, physical, and physiological aspects of estrus. This mechanism allows females of solitary species, where male–female interactions are limited, to conserve energy, only investing in reproduction when a viable mate is in close proximity (Larivière and Ferguson 2003). Despite the different mechanisms driving ovulation in spontaneous and induced ovulators, similar pathways, in terms of the CNS and HPG axis, are present.

### The Neuroendocrine Control of the Estrous Cycle

Hormones are defined as chemical messengers that are excreted by an endocrine gland into the bloodstream, ultimately reaching a target cell and exerting a physiological regulatory action

(Woolley and Schwartzkroin 1998). The most well-known hormones include those that are produced and secreted by the thyroid, adrenal gland, and ovaries/testes. Of these, the reproductive hormones have been shown to underlie and regulate reproduction, forming an important part of the female estrus cycle (Wielebnowski and Watters 2007). The estrous cycle represents the cyclic patterns of ovarian hormone secretion (Fig. 2) and facilitates the transition of a female from a nonreproductive to a reproductive state (estrus), allowing for successful mating and conception (Forde et al. 2011). However, in order for the HPG axis to secrete the necessary reproductive hormones, along with their behavioral components, the initial activation of the CNS, through the applicable external and endogenous cues, is required. In **spontaneous ovulators**, factors such as photoperiodism act as a cue for CNS activation. In this regard, the photic stimuli is sent to the reproductive neuroendocrine system via the neurohormonal pathway, starting with the retinal projection (photoreceptors). From here, the stimuli is



**Estrous, Fig. 2** The relative hormone concentrations of gonadotrophin-releasing hormone, luteinizing hormone, follicle-stimulating hormone, estrogen, and progesterone during a single estrous cycle. The cycle is divided into two

main periods, namely follicular and luteal phase. Within the follicular phase, both proestrus and estrus are observed, while metestrus and diestrus are found during the luteal phase of the estrous cycle. The ovulation event is indicated

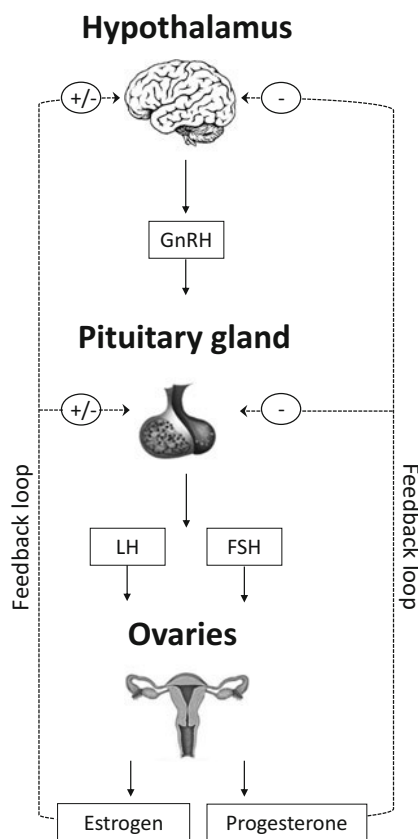
sent to the suprachiasmatic nucleus and finally through a multisynaptic circuit which is composed of neurons found in the paraventricular nucleus, intermediolateral spinal cord, and superior cervical ganglion, before reaching the pineal gland (Weems et al. 2015). The resulting production of melatonin by the pineal gland plays an important role in conveying specific photoperiod information to the hypothalamus and other regions of the brain. In **induced ovulators**, the activation of the CNS is controlled by the receipt of genital somasensory stimuli (Bakker and Baum 2000). In both spontaneous and induced ovulators, the stimuli from the CNS activates the HPG axis, resulting in the secretion of a number of reproductive steroid hormones such as gonadotrophin-releasing hormones (GnRH), luteinizing hormones (LH), and follicle-stimulating hormone (FSH), as well as estrogen and progesterone (Fig. 2; Vasantha 2016).

### Phases of Estrus

The estrus cycle can be divided into the follicular and luteal phases, both of which have a number of specific substages defined as proestrus, estrus, metestrus/diestrus, and anestrus (Fig. 2).

#### Proestrus

Following the activation of the CNS by the specific environmental or endogenous cue, the hypothalamus secretes GnRH in pulsating bouts, which is transported to the pituitary gland (Christensen et al. 2012). In order for GnRH to apply both trophic and regulatory effects on the HPG axis, it interacts with the G-protein-coupled GnRH-receptors located in the pituitary gland, forming a hormone-receptor complex (Naor 2009). **Hormone receptors** are molecules found in target tissues which interact with hormones, altering the biological activity of the receptor, and ultimately changing gene expression and cellular activity (Pfaus et al. 2015; Sinchak and Wagner 2012). This binding event results in the production and secretion of the glycoprotein hormones, LH and FSH. Both LH and FSH stimulate and enhance ovarian follicle maturation and development, as part of the follicle phase (Fig. 2). Furthermore, LH and FSH bind to their



**Estrous, Fig. 3** A representation of the hypothalamic-pituitary-gonadal axis in female mammals. Hormonal production, secretion, and paths are indicated by solid arrows. The positive and negative feedback loops are indicated by dashed lines

respective G-protein-coupled hormone receptors found on the thecal and granulosa cells of the ovary (Hillier 1994). This binding results in the production and secretion of cholesterol derived androgens, which in turn are aromatized by the granulosa cells to produce estrogen and progesterone (Fig. 3). As a result of the high lipophilic nature of both ovarian hormones, they are able to easily cross the blood-brain barrier and diffuse through cell membranes, ultimately altering cell activity (Woolley and Schwartzkroin 1998). The increase in estrogen concentration during this period results in the activation of a positive feedback loop between estrogen, the brain, and the pituitary gland (Fig. 3). This positive feedback loop promotes an increase in GnRH, and its

receptors in the pituitary gland, which enhances pituitary responsiveness to GnRH, and leads to a LH secretion surge (McCarthy and Becker 2002). The LH surge, along with FSH secretion, plays an important role, during the ovulatory phase, to ensure follicle maturation, ovulation, and a further increase in estrogen secretion (Hillier 1994). The increase in concentration of the respective hormones described (GnRH, LH, FSH, estrogen), along with **reproductive behaviors (attractivity, proceptivity)**, form an important component of the **proestrus** period in females (McCarthy and Becker 2002).

#### Estrous

The continuous increase of circulating estrogen and progesterone has two important functions. Firstly, the sequential increase of estrogen, along with secreted progesterone, act upon reproductive tracts to prepare the uterine endometrium for copulation and embryo implantation (Sinchak and Wagner 2012). Secondly, circulating estrogen, and to a lesser degree progesterone, bind to receptors within the brain and are vital to the initiation of sexual activity during the estrus cycle (Pfaus et al. 2015). Although an estrogen-only steroid regime is capable of activating reproductive behaviors, a delay in activation is seen herein compared to an estrogen-progesterone steroid regime (Sinchak and Wagner 2012). Although mostly facilitative in nature, progesterone can also inhibit reproductive activity in certain species (Lipschitz 1997). As different steroid regimes are capable of activating, or inhibiting, reproductive behaviors, it is clear that multiple neural pathways may mediate similar behaviors. Of great physiological importance is the synchronization of the estrogenic increase of GnRH and LH, along with the ovulation event, to the activation of reproductive behaviors allowing for successful conception during estrus. Receptive behaviors are limited to the estrus period during the estrus cycle.

#### Metestrus and Diestrus

Following the ovulation event, LH causes the terminal differentiation of the ovulated follicle into the corpus luteum (CL) through the process

of luteinization (McCarthy and Becker 2002). The CL is a transitory endocrine gland responsible for the production and secretion of progesterone and, to a lesser degree, estrogen (Stocco et al. 2007). The secreted progesterone, along with estrogen, activates a negative feedback loop on the hypothalamus and pituitary gland, inhibiting GnRH, LH, and FSH production and secretion (Fig. 2). As a result of this, a decrease in secreted estrogen occurs, which ultimately leads to the termination of reproductive behaviors following ovulation. In the event of successful conception, the CL remains functional and secretes steroid hormones throughout pregnancy. Should conception not occur, the CL will continue to secrete progesterone throughout the luteal phase until the CL undergoes degradation during diestrus (McCarthy and Becker 2002). With this, the negative feedback loop is terminated and GnRH secretion is initiated, starting a new estrus cycle. In certain mammal species, a period of sexual inactivity follows diestrus and the parturition event, known as anestrus. During anestrus, the HPG axis secretes low hormone levels, thus inhibiting ovulation and reproductive activity.

### Reproductive Behaviors During the Estrous Cycle

Beach (1976) proposed that female sexual behaviors be divided into three components: attractivity, proceptivity, and receptivity. **Attractivity** is defined as the stimulus value of a female to a male, which is measured by male preference of a female, and often calculated by the extent to which a male prefers to be in close proximity to a female conspecific. The stimuli basis of attractivity can be both behavioral and non-behavioral (visual, chemosensory; Thomas 2011). **Proceptivity** refers to a range of female solicitation behaviors towards male conspecifics which might lead to an increase in male mountings (Blaustein and Kiesecker 2002). In contrast to attractivity, proceptivity is largely focused on female preference and includes activities such as female–male grooming and/or female pacing and



presenting to name a few. Such affiliation behaviors play an important role in establishing a close proximity of females to a selected male, increasing the chance of intercourse. A well-known example of this is lordosis behavior, where females lower their forelimbs, extending their rear limbs and arch their spine in order to attract and facilitate mating (Pfaus et al. 2015). Both attractivity and proceptivity are limited to the **proestrus** period of the estrus cycle. **Receptivity** reflects the stimulus value of a female individual for eliciting an intravaginal ejaculation from a male (Nelson 2011). During this activity period, female individuals display a specific set of behaviors which assist, and are often necessary, for fertile copulation with male conspecifics. In the majority of mammals, receptive behaviors are initiated shortly prior to the ovulation event and continue until shortly thereafter; this period is referred to as estrus (Fig. 2). In a number of species, proceptivity and receptivity frequently overlap, with females engaging in male soliciting, directly followed by female posturing and copulation (Nelson 2011).

### Postpartum Estrus

**Postpartum estrus** (PPE), a subsequent reproductive period immediately following parturition, can be a major reproductive strategy employed by mammals to ensure maximum reproductive output; this is especially true for small bodied mammals with a short lifespan (Conaway 1971). Despite the obvious advantages of including PPE, it can be energetically expensive and costly for females in two ways. Firstly, the activation of reproductive activity during PPE coincides with lactation and raising of young, both of which constitute an energetically expensive life history stage in a female (Speakman 2008). As a result of this, females must increase the time spent on foraging behaviors to account for the additional energy requirements or face a decrease in body condition and survival likelihood. Secondly, females must divide their time and attention during PPE between two mutually exclusive activities, raising young and mating activities. As maternal care is directly linked to survival rate of

newborns, entering PPE while younglings are still dependent on a female can be a costly endeavor which leads to litter loss (Witt et al. 1990). Thus PPE will only be activated should the necessary environmental and social factors be present to support it. For example, prairie vole females (*Microtus ochrogaster*), will activate PPE only if a reproductively active male is present (Carter et al. 1986). PPE requires the activation of the HPG axis and the secretion of reproductive hormones to prepare the uterine endometrium for copulation and embryo implantation. In the absence of such activation, females may be unable to enter estrus and successful mating may be absent (Scheun et al. 2016). In contrast to increased reproductive output, PPE may also be used as a back-up/fall back mechanism should litter loss occur (Steyaert et al. 2014). The flexibility with which certain mammal species engage in PPE indicates that PPE acquisition or loss may be one of the most easily made reproductive adjustments in mammals (Witt et al. 1990).

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## Estrous, Oestrous

### ► Polyestrous

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## Estrus, Oestrus, Heat

### ► Polyestrous

## Ethel Tobach

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Ethel Tobach (née Idels) was born on November 7, 1921, and passed away on August 14, 2015. Her passing brought to a close an important era in comparative psychology. This essay is not intended to be an obituary, but rather a biography and a paean to a scientist, a scholar, a social activist, and despite her curmudgeonly side (something familiar to all who knew her), a genuinely good person. She was my friend and mentor for over 25 years following the completion of my doctoral degree at Kansas State University in 1971.

(Much biographical material in what follows has been adapted from Greenberg 2015; Lewis 2010; Unger 2009). Born in Ukraine, the pogroms of Russia's White Army forced Ethel's family to move to Palestine soon after her birth. Following the death of her father when she was 9 months old her mother emigrated with her to Pennsylvania, USA. They did not stay there long, finally settling in New York City when Ethel was 10. She remained a New Yorker the rest of her life, living for many years just a short walking distance from the American Museum of Natural History, where she was to spend her entire career.

She inherited her social and political activism from her mother and this was to be one of her lifelong defining characteristics, a result of which was her cofounding in 1971 of Psychologists for Social Action which later morphed into Psychologists for Social Responsibility (Miller 2008) described at this website (<http://www.psysr.org/>). Important in her life's work was her leadership in psychology activist groups through which she sought and worked for constructive public policies, nuclear disarmament, and peace building. She was, in this regard, the epitome of a socially responsible scientist. The award she received from the American Psychological Association in 2003 (Gold Medal Award for Lifetime Achievement in Psychology in the Public Interest carried

this citation: "[Dr. Tobach] has exposed the unsound science and social damage of genetic determinism institutionalized as racism and sexism." She was, indeed, one of her generation's ardent and widely recognized spokespersons against the pernicious ideas of the genetic determinism of behavior.

Interestingly, she came to psychology late in her education. Her bachelor's degree was from Hunter College of the City University of New York in 1949. Not surprising she was a Phi Beta Kappa student. At Hunter her interests were in English, economics, pre-med, and educational psychology. It was only later that she switched her interests to comparative psychology, the focus of her productive career. Professors tried to steer her away from psychology telling her that there were no women in that field. Her response, in her typical style, was, "I don't care about that." Charles Tobach, an independent photo journalist, whom she married in 1949, encouraged her to pursue doctoral work at New York University (NYU). Characteristic of the times, NYU was wary of accepting married women. It was there that she met and was supervised by T. C. Schneirla, at the time among the preeminent comparative psychologists of the day. She completed her doctoral work with him in 1957.

Tobach began her career at the Department of Animal Behavior at New York's American Museum of Natural History (see Greenberg et al. 2004) joining Schneirla who was working there at the time. She spent her entire career there and though retiring as Curator Emerita in 1991, she worked and maintained her association with the Museum almost until the time of her passing. Her laboratory at the Museum was a warren of equipment and animals. She had worked at various times with rats, mice, gerbils, spiny mice, and the marine mollusk, *Aplysia*. Schneirla, famous for his work with ants, championed working between naturalistic field settings and laboratories, an approach favored as well by Tobach. I had accompanied her on three field trips to Puerto Rico to study and collect *Aplysia* for shipment back to her laboratory in New York. The photo accompanying this essay shows her transcribing field notes on one of those field trips (Fig. 1).



**Ethel Tobach, Fig. 1** Ethel Tobach transcribing field notes after a full day observing *Aplysia* in waist-deep water (La Parguera, Puerto Rico. Early 1980s. Photo by the author)

While her base was at the Museum at various times she held academic positions at New York University, Yeshiva University, City College of New York, State University of New York, and several other institutions, some outside the USA. She had visiting research assignments at numerous international laboratories. Ethel Tobach was famous for mentoring high school students in her laboratory as well as promising undergraduate and graduate college students and occasional postdoctoral students, of which I was one (Greenberg 2015). In this regard, she was known to be an exciting teacher and lecturer (Miller 2008), something I can attest to.

Her activism began to show itself in her early 1920s during WWII when she was employed making lenses for bombsights. It was then that she became active in her lifelong promotion of trade unions. Despite her pacifism her anti-Nazi feelings impelled her to join the Women's Army Corps and was assigned to a New York psychiatric

hospital. The bombings of Hiroshima and Nagasaki firmly cemented her tireless and lifelong peace activist activities.

Tobach was a Fellow of several divisions of the American Psychological Association including 6 (Physiological and Comparative Psychology, President 1984–85) and 48 (The Society for the Study of Peace, Conflict, and Violence, President 2004). She held membership in several organizations which reflected her many interests: member and president (later president emerita) of the International Society for Comparative Psychology (which she founded), the Animal Behavior Society, the American Association for the Advancement of Science, the Association for Women in Science, and several others. She held elective offices in the New York Academy of Science, the American Psychological Association, the international Union of Psychological Sciences, the Eastern Psychological Association, the Association for Women in Psychology to UN/DPI/NO, as well as other scientific and social activist organizations. In her service to the profession of psychology she held editorial positions on publications such as *Animal Behavior*, *Biological Psychiatry*, *Journal of Comparative Psychology*, *Advances in Comparative Psychology*, and also edited the book series *Genes and Gender* and the *T. C. Schneirla Conferences*.

Her several awards and recognitions include the Kurt Lewin Award from the American Psychological Association's Society for the Psychological Study of Social Issues, which acknowledged her "outstanding contributions to the development and integration of psychological research and social action" and the American Psychological Association's Gold Medal Award for Lifetime Achievement in Psychology in the Public Interest (2003).

Her body of scholarly and research work was impressive, with over 117 professional articles, books, and book chapters. She believed her major contributions to comparative psychology to include demonstrating that susceptibility to TB is directly related to behavioral stress; that the olfactory system plays a role in newborn rats; that the inking response of *Aplysia* is not an instinctive defensive reaction; and that serotonin

deficiency in fawn-hooded rats is related to taste. However, all who were familiar with her and her work acknowledge that she was known for far more significant contributions to scientific understanding than that. Beyond her research publications and essays on various aspects of psychology she had edited several important books: The *Genes and Gender* series (Gordian Press); The *T. C. Schneirla Conference* series (Erlbaum Press); *Selected Writings of T. C. Schneirla* (W. H. Freeman); and *Development and Evolution of Behavior: Essays in Memory of T. C. Schneirla* (W. H. Freeman). [See Unger (2009) for a list of Tobach's publications and see Lewis (2010) for a list of references about Tobach.]

The publication and popularity of *Sociobiology*, Wilson's (1975) attempt at biologizing the social sciences, represented in her words that "the study of the evolution of behavior as a psychological discipline [had] been eclipsed by recent developments in evolutionary biology" (Innis 2000, p. 54). This coupled with her outstanding international reputation as a psychologist provided the impetus for her to found the International Society for Comparative Psychology (ISCP) in 1980 (Innis 2000). In the letter of invitation to join the society sent to comparative psychologists around the globe Tobach said, "[w]e aim toward an openness of theoretical orientation in comparative psychology and so the 'psychology' of comparative psychology may be defined variously. The 'comparative,' however, is firmly based on evolutionary principles" (Innis 2000, p. 54). The first meeting, held in Canada in 1983, brought together psychologists from the USA, Japan, Italy, Germany, and Colombia. It was again her global reputation that gained the ISCP almost immediate acceptance as an affiliate organization of the important International Union of Psychological Sciences at a 1984 meeting of the International Congress of Psychology in Acapulco, Mexico. The ISCP still holds biennial meetings around the world and publishes a journal also founded by Tobach, the *International Journal of Comparative Psychology*.

To be sure, Ethel Tobach was well known and well respected in global science circles. This anecdote provided by Howard Topoff (2016,

Personal communication), one of her close colleagues and coworkers at the Museum of Natural History, is a fitting way to sum up her career and provides a glimpse into the kind of person Ethel Tobach was. Topoff was Schneirla's last doctoral student – they shared that relationship in common.

The 1973 Nobel Prize in Physiology or Medicine was awarded jointly to Karl von Frisch, Konrad Lorenz and Nikolaas Tinbergen "for their discoveries concerning organization and elicitation of individual and social behaviour patterns." During lunch in the Seminar Room of the Department of Animal Behavior at The American Museum of Natural History, Ethel had an idea. Since the Museum's Animal Behavior program was a collaboration with the City University of New York, let's have CUNY invite Konrad Lorenz to come to New York to give a presentation. I said great idea, and that I would contact the office of the President to make an appointment. Ethel said "nah. I know him very well. Let's just go there after lunch." We did, he was in his office, and when he heard that Ethel Tobach was waiting to see him, he ushered us right in. So, she was great friends with the President of The City University of New York. Actually, not so surprising, Ethel seemed to know everyone, everywhere. Politicians, union leaders, deans – wherever she went, people would recognize her, wave, and yell "hi Ethel." And she would say "hi" back, calling out their name. You would think that all of New York City was her family. "Who was that" I once asked her when leaving the theater. "Oh, just the New York Commissioner of Cultural Affairs but, we don't know each other that well." I said "Ethel, you're not SO famous that you have to be modest."

## Cross-References

- [Approach/Withdrawal Theory](#)
- [Behavioral Levels](#)
- [Comparative Psychology](#)

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## Ethics

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## Introduction

The moral status and treatment of 17 macaque monkeys, used for experiments in neuroplasticity and housed at the Institute of Behavioral Research in Silver Spring, Maryland, became the center of attention between 1981 and 1991 (Sideris et al. 1999). As one author put it, the case of these monkeys is responsible for “launching” the Animal Rights Movement in the United States (Guillermo 1993). The Silver Springs monkeys incident raised questions about the limits on what can and should be done to research animals, and the quality of both veterinary care and husbandry that is owed to research animals. Public outcry along with the efforts of the animal rights group PETA (People for the Ethical Treatment of Animals), including the release of its self-produced 26 min film, *Unnecessary Fuss*, led to an amendment in 1985 to the US Animal Welfare Act (introduced as the *Improved Standards for Laboratory Animals Act* as part of the Food Security Act (Farm Bill) of 1985), changes to the US Public Health Service Policy, and the formal introduction in 1986 of Institutional Animal Care and

Use Committees (IACUC) (Sideris et al. 1999). Per the direction of Congress, an information service to provide resources to both the general public and the research community on the care and welfare of animals and alternatives as expressed by the 3Rs (reduction, refinement, and replacement) was established at the National Agricultural Library (now the Animal Welfare Information Center).

The Silver Springs monkeys case highlights the importance of having the highest ethical standards for governing how we manage, care, house, and treat animals, especially those whom we have invited to be part of our families as companions or pets, and animals in the laboratory, agricultural, or clinical settings. While a good deal of common ground in making ethical judgments about how we should treat animals and promote their welfare have emerged since the 1980s (DeGrazia 1999), there is still no universal agreement regarding the moral status of animals, and ways to strengthen the ethics behind human-animal relationships continue to be debated. While we continue to struggle over claims that there is something distinctive about human beings that justifies difference in moral significance or treatment from members of other species, advances in philosophical, ethical, and legal arguments challenging the status of animals as mere property, research instruments, or mere resources are more frequent and warrant serious moral consideration (see, for example, Quebec's Bill 54 (2015) that officially recognizes animals as sentient beings with biological needs, and the EU's Lisbon Treaty (2009)).

Below, a discussion related to important developments in the study of ethics and animals follows, as well as other ways to think philosophically about animals and their interests.

## What Is Animal Ethics?

This entry has been developed with a view to aid nonphilosophers (e.g., scientists who are sensitive to the philosophical complexities regarding animal consciousness, cognition, and their moral status) navigate some of the main highlights in the philosophical literature on ethics



and animal ethics, with a view to references that might be most relevant to their own research and scholarship.

*Ethics* concerns beliefs or attitudes regarding right and wrong actions, and the rules or standards for governing conduct. It also concerns what constitutes good and bad persons or character. Ethics helps us to better understand human nature and the proper scope of our moral obligations to other individuals, groups, and entities. Ultimately, ethics involves the study of how to live well, to be good at being human, if you will. Ethical inquiry on a particular subject helps us to deliberate and make judgments about the nature of right and wrong and to reflect on the norms or standards of acceptable behavior that support right relationships with others during the course of our day or a lifetime, including whether or not to accept the moral claims or arguments of others and what ethical commitments to value. Our ethical commitments promote respectful and caring actions towards others, and proscribe unfair distributions of benefits to the already disadvantaged or actions that would increase harms or burdens to others. Ethics also help us aspire towards laudatory behavior and activities, such as helping those in need, whether or not they are distant to us temporally, spatially, or species-wise. Ethics addresses issues around health and well-being, pain and suffering, rights and freedoms, hope, and life and death and circumscribes actions that are morally obligatory, permissible, forbidden, and supererogatory.

*Animal ethics* refers to the ongoing project to understand our relationship to nonhuman animals. Animal ethics brings together the above-mentioned ethical underpinnings and applies them to human-animal relationships. Animal ethics highlights ethical challenges that can constrain healthy human-animal interactions, especially in cases where animals are treated as resources or when interspecific conflicts of interests persist. Animal ethics is a sub-branch of applied ethics that specializes in animal issues. In particular, animal ethics debates the bases of moral consideration of animals (i.e., membership into the moral community and moral considerability) and justification for certain treatment

or use, which may or may not involve inflicting pain, suffering, and death upon them. Philosophers working in animal ethics are concerned about animal husbandry and their welfare, the use of animals in agriculture and medicine, and the impacts of environmental policies, biotechnology, and precision or networked technologies on animals. Animal ethics informs our treatment of animals and seeks answers to a range of ethical questions regarding how we ought to deliberate about their welfare and dignity, and when we have to utilize practices that cause them pain, suffering, or death, do we have defensible reasons for doing so. More broadly, this area of applied ethics is concerned with whether:

- Animals have moral standing in their own right. And if so, what kind of responsibilities do human beings have towards them
- We have responsibilities to only individual animals or also to species or populations of animals
- The grounds for human uses of animals is defensible

Philosophers working in animal ethics strive to promote healthy human-animal relationships and offer guidance to humans, qua moral agents, on how they should treat animals in our “mixed communities” (Midgley 1983). Animal ethicists struggle with how we should balance our duties to animals against other kinds of duties (to other humans and the planet) as well as basic questions like whether animals should be used in biomedical research, teaching or entertainment, and if they should be raised for food or kept as pets.

Today, animal ethics questions have also fallen to both experts and laypersons alike – scientists, veterinarians, farmers, pet owners, food consumers, and policy makers. Though the core of animal ethics is still moral philosophy, fully informed animal ethics must be performed with a competent grasp of the relevant empirical facts and other nonmoral issues (Fraser 1999), including, but not limited to, the veterinary, cultural, scientific, legal, and technological domains that inform us about the capacities of animals and how human action may harm animals. Progress in

addressing healthy human-animal relationships require interdisciplinary work by philosophers and scientists alike, namely, finding novel ways to integrate emerging empirical details about what matters to animals with philosophical arguments regarding just what evidence (e.g., phenomenological, epistemological, and metaphysical) should be employed to establish their place in the moral community with moral claims on human beings, including proper treatment.

Returning to the nature of ethics, our view of which ethical standards are laudatory is connected inextricably to our moral beliefs and values. Here, values are ideas that direct our actions. Values guide us by giving meaning to our lives as well as by providing the blueprint of how to be good and live well with others. Values impress on us what matters and why they do. Values suggest both an inevitability and inescapability regarding facing ethical issues and meeting our ethical commitments. This includes reflecting on what to value, the shape of moral concepts themselves, addressing pressing ethical questions, like fair distribution of scarce health care and ecosystem resources and environmental stewardship, and how we should treat each other. Duties to pets or companion animals (Ellingsen et al. 2010), the permissibility of using animals in teaching and biomedical research (Greek and Greek 2010; Tannenbaum and Rowan 1985), and the moral status of raising animals for food are among notable “pressing issues” that seem to have gained ethical currency and prominence and captivated our public imagination and moral consciousness (Riffkin 2015; Loveridge 2013; Prickett et al. 2010; Fraser 2008b; Sandøe and Christiansen 2008).

Moral judgments, principles, and rules direct conduct and shape moral practices and provide benchmarks for assessing the moral worth of others. Our moral judgments, rules, principles, and standards regarding animals are informed by religion, political ideology, law and public policy, level of education, economics, family and peers, societal factors like customs and norms, our relationship to technology, how animals promote personal aspirations and self-efficacy, and how we judge benefits and harms (Guerrini 2016; Deemer

and Lobao 2011; Naald and Cameron 2011; Kendall et al. 2006). Ethical standards inform professional codes of conduct and processes, such as those that might govern Institutional animal care and use committees (IACUCs), which are tasked with ensuring ethical oversight of research employing animals. These standards have also influenced OIE Animal Welfare principles, the leading intergovernmental organization responsible for improving animal health worldwide, and form the basis of numerous other governance initiatives about animals (e.g., Article 13 of Title II, of The Lisbon Treaty) (2009), ([https://ec.europa.eu/food/animals/welfare\\_en](https://ec.europa.eu/food/animals/welfare_en)) and national or state/provincial animal protection laws.

Ethical theories that apply in the human case (e.g., deontology, utilitarianism, virtue ethics, feminist ethics, contractarianism) have been used to provide justification for respectful treatment of animals. Ethical approaches under the heading of “animal welfare utilitarianism,” for example, require that we choose actions resulting in the best possible balance of benefit versus harm for all sentient beings, including some animals. In the research setting, this choice advocates for the now familiar 3Rs of reduction, refinement, and replacement (Russell and Burch 1959). A rights-based approach, on the other hand, requires that we respect the inherent worth of certain animals (Regan 1983; Russow 1990, 1999; Sideris et al. 1999).

Empiricists like sociologists, anthropologists, historians, and psychologists also study matters concerning ethics and provide descriptive accounts of what people actually believe, what preferences they hold, what customs they practice, which moral standards they support, and catalogue how people behave (e.g., Herzog 2011; Bradshaw 2009; Arluke and Sanders 1996). The scientific method is employed to carry out these investigations, and is used by these researchers to uncover links between beliefs, attitudes, and action or to understand the causal reasons why people hold the beliefs, attitudes, and preferences that they do that influence their actions. A key difference between the normative work that ethicists do and scientific

investigations undertaken by scientists is that while ethicists are concerned with normative matters such as “how ought we to live” or “how should we treat sentient beings,” scientists are concerned about empirical matters, i.e., what is the case. For example, animal scientists might study what husbandry conditions are suitable for goats to thrive (e.g., pen size, enrichment opportunities, including exposure to conspecifics).

## Ethics and Animals: A Glance at Where We've Been

Since the 1970s, the academic community has given more and more attention to the ethical nature or shape of the relationship between human beings and animals. Much of this has been spurred on by greater interest in the inner lives of animals, including the distribution of animal consciousness across various species, and research regarding animal emotion, pain, behavior, and cognition, from both laypersons and those working directly with animals in the sciences (Boly et al. 2013; Allen and Bekoff 1997; Pepperberg 1999). In 1964, Ruth Harrison's *Animal Machines*, preceded by Rachel Carson's *Silent Spring* (1962), helped to fuel both public concern and academic interest over human responsibility over the plight of animals and the environment. Standing on the shoulder of Carson and Harrison, Godlovitch, Godlovitch, and Harris at Oxford University published a series of philosophical essays in *Animals, Men and Morals* (1971) that highlighted the ethical terrain involving animals. Subsequently, in 1975, Australian philosopher, Peter Singer, published the first edition of *Animal Liberation: A New Ethics for Our Treatment of Animals*, which raised both public awareness and moral critique regarding then “current day practices” involving animals. Since then, there have been a number of influential philosophical and ethical expositions on animals and human-animal interactions. They have been inspired by and have in turn inspired the thinking of some of the professionals in direct proximity to animals, namely, researchers and animal scientists, cognitive ethologists, and veterinarians.

Philosopher Lilly-Marlene Russow (1999), for example, in *Ethical Implications of the Human-Animal Bond in the Laboratory* invites researchers to consider bolstering the ethical norms in the laboratory setting. Russow advocates for an “ethics of caring” as engendered by human-animal interactions to supplement “impartial” theories such as utilitarianism and deontological ones. Her concerns for more a nuanced animal ethics have been echoed most recently by essays in Bovenkerk and Keulartz's (2016) *Animal Ethics in the Age of Humans: Blurring Boundaries in Human-animal Relationships*. Philosophers and other scholars are invested now in studying not just the ethics of animal welfare but also why we consider the death or intentional termination of an individual morally concerning (e.g., Višak and Garner 2015; Meijboom and Stassen 2016). Concerns for the ethical treatment of animals have also led to revisions of professional codes of conduct and greater interest in animals by veterinary and animal science organizations all across the world (e.g., Lord et al. 2017; Phillips et al. 2012; Heleski et al. 2004, 2005). Animal scientist, David Fraser in *Animal Ethics and Animal Welfare Science: Bridging the Two Cultures* (1999) and again in *Understanding Animal Welfare: The Science in its Cultural Context* (2008b) issued a challenge to both the scientific and animal ethics communities. For the former, he argued for greater awareness and self-reflection of and engagement with the norms and values that guide their research on animal cognition, welfare, and behavior. For the latter, he emphasized the need for ethicists and philosophers to be informed about the circumstances of animal husbandry and use and to grapple with the on-the-ground constraints of animal scientists and veterinarians so that ethical recommendations that are made can lead to practical solutions. Philosopher, Paul Thompson has encouraged philosophers to transcend traditional forms of “humane moralisms” and embrace collaborations at the intersectionality of philosophy and science so that those working in various animal industries can exact effective guidance from the relevant academic research (2004).

In contemporary Western society, an anthropocentric outlook is seemingly pretty entrenched.

Human beings are inclined to give themselves priority over members of other species. Those still resistant to the idea that animals matter morally in their own right and should not be given membership in the moral community can be considered “exclusivists” or “human exceptionalists.” They exclude animals from the moral community because animals do not bear certain moral qualities that are deemed morally significant. Historically, influential philosopher and the professed “father of modern philosophy and modern natural science,” Rene Descartes (Descartes 1637/1988), for example, argued that animals were limited in their hardwiring. While they are capable of “sensation,” and possessed memory, perception, fear, joy, and hunger, Descartes argued that these experiences were not conscious in the relevant sense. A leading exponent of the mechanistic view that emerged after the middle ages, Descartes argued that only human beings were “thinking beings.” Animals or “brutes,” Descartes contended, failed to count morally since they lacked human language and rationality. Based on these omissions, Descartes argued that they could be subjects of experimentation and dissection. By his lights, animals are but nature’s complex automata akin to biological robots. They do not demonstrate actions that suggest inner thinking. Pierre Gassendi, a contemporary of Descartes’ who was priest and logician, focused not on reason but on animals’ perceptive abilities and ability to suffer. He went on to write that “There is no pretence in saying that any right has been granted to us by [the Moral Law] to kill any of those animals which are not destructive or pernicious to the human race.” Contra Descartes, Gassendi called for compassion towards animals.

Another influential exclusivist is philosopher Immanuel Kant (1724–1804). Kant denied that human beings had direct duties to animals (only duties *about* them) for they lacked higher-order cognitive capacities and thus, *moral personhood*. In his *Lectures on Ethics* (1963), Kant argued that we should treat animals well since treating animals inhumanely could likely lead to mistreatment of other human beings and was a sign of weak character. “If a man shoots his dog because the animal is no longer capable of service, he does

not fail in his duty to the dog, for the dog cannot judge, but his act is inhuman and damages in himself that humanity which it is his duty to show towards mankind. If he is not to stifle his human feelings, he must practice kindness towards animals, for he who is cruel to animals becomes hard also in his dealings with men” ([1784–5] 1997, p. 212).

These sentiments found in Descartes and Kant still prevail in some circles in more nuanced instantiations. Christine Korsgaard, for example, argues that animals while (unlike Kant) proper objects of moral consideration do not possess a reflective mind and thus are not sources of normativity (i.e., cannot convert their desires to reasons for moral actions, for the lack both “practical” and moral identities (Korsgaard 1996, 2007, 2015)).

A variant of exclusivism today is contractarianism (see also Carruthers 1992; Rowlands 2011). Canadian philosopher Jan Narveson is a main exponent of this approach. According to Narveson (1983) and following the tradition of Thomas Hobbes, morality is a function of certain conventions or contracts between members of a political community, i.e., contractors of comparable abilities or political-ethical “powers.” Animals lack certain morally valuable qualities such as metacognitive capacities (e.g., linguistic capabilities, or the ability to form and give reasons) that disqualify them from being able to make, keep, and understand the implications of promises, the basis of contracts. For Narveson, it would be foolish to make promises with “lower animals” since they cannot reciprocate morally for they are fixated on mere conscious activities – responding to and satisfying immediate perceptions and desires, respectively. Human contractors may have indirect obligations to animals by way of how animals stand to other human contractors. This relational link gives animals indirect moral significance but it still does not generate direct concern for animals’ welfare, suffering, or dignity.

In contrast to proponents of human exceptionalism, inclusivists challenge the underlying premise that only and all human beings matter morally. They also call into question the rational basis of personhood since not all human beings

are rational. They offer other criteria for moral considerability. Two animal ethics philosophers who have gained prominence as inclusivists are Peter Singer and the late Tom Regan. Both philosophers argued that animals merit direct moral consideration in their own right. Much of recent philosophical animal ethics, since the 1980s at least, has been framed (i.e., the “animal welfare-right” debate) by Singer and Regan.

Both Singer and Regan challenge the view that all and only human beings have moral status by raising concerns regarding “marginal case” (an unfortunate term in the literature) human beings who lack properties associated with human exceptionalism. Human infants and certain mentally challenged human beings would be excluded from being the recipients of direct moral respect in their own right if reason, rationality, or higher order cognition became predominant moral status defining properties. Singer seeks to secure higher levels of protection for nonhuman animals who can suffer by reforming current systems of animal use. Regan, on the other hand, sought to overcome the view that human persons deserve greater priority over animals simply because they are human.

Singer’s ethical commitment is rooted in the moral theory utilitarianism. Utilitarians seek to bring about the best outcomes for all the relevant parties. Singer extends coverage to all *sentient* animals. Singer’s view is informed by utilitarian progenitor Jeremy Bentham who argued that there is no good reason to exclude animals from the group of constituents that could be harmed morally (1789, *Introduction to the Principles of Morals and Legislation*). While Bentham focused on pain and pleasure, Singer emphasizes preference satisfaction and frustration. As a preference utilitarian, Singer (following in Bentham’s footsteps) contends that, “[t]here can be no moral justification for regarding the pain (or pleasure) that animals feel as less important than the same amount of pain (or pleasure) felt by humans” (Singer 1990, 1975). On Singer’s view, moral agents ought to maximize preference satisfaction (including the conscious desires, projects, and goals of agricultural and research animals) or minimize preference frustration. We should limit

harms to sentient beings who can conceive of their own futures and have the capacity for forward looking desire satisfaction.

Singer is an outspoken critique of *speciesism*, a concept coined by Richard Ryder (1971) (see Waldau 2001) which translates to the discrimination against animals (or privileging human interests) *merely* on the basis of species identity. Speciesism is as indefensible as racism or sexism (Singer 1979a). There is a slight nuance to Singer’s view in that for some animals (those that may just have an immediate interest in suffering avoidance but not a future directed interest in continued existence), killing does not constitute a moral harm in utilitarian terms if they are euthanized painlessly, replaced, and overall welfare is preserved (Singer 1979b, 2011). Under the current forms of animal use, Singer concludes that we ought to strive to adopt moral vegetarians or minimize use of animals in medical research (Singer 1990), since the benefits of current animal use to humans and animals do not justify the harms done to animals. Singer’s utilitarian argument allows some degree of moral toleration of animal use, since humans have a wider range of interests that animals do not, and if the practice promotes happy lives and painless deaths for the animals.

While Singer’s criterion, sentience, has been instructive in making moral claims on us, it has been criticized for being too simplistic and failing to recognize important moral differences in the quality and richness of life between humans and animals (e.g., moral culpability, reciprocity, and self-respect). Singer’s initial call to boycott industries of animal agriculture and biomedical research has not brought lasting changes. Other strategies have proven to be more effective in the long run to inform change, such as active citizen-producer participation in public policy making, engagement with certain animal industries and animal science communities, and consumer pressure and citizen ballot initiatives (Appleby 1999). Singer has also been criticized for failing to acknowledge structural impediments (e.g., market and cultural forces, willingness to pay, and operating costs) that hinder reform of animal industries and the adoption of higher standards of care and



welfare practices by caregivers of animals such as farmers (Stuart et al. 2013; Fraser 2001).

Tom Regan, in contrast to Singer's utilitarianism, defends animals as moral rights bearers as he launches against the instrumentalization or commodification of animals as mere resources. According to Regan, "...animals are treated routinely, systematically as if their value were reducible to their usefulness to others, they are routinely, systematically treated with a lack of respect, and thus are their rights routinely, systematically violated" (Regan 1985, p. 24). As a non-consequentialist, Regan argued that the basis of making ethical judgments should be to ensure that we treat others with dignity and respect regardless of the outcome (e.g., if it would maximize utility to harm them). Animals, in the spirit of Kant's rational personhood argument, should be treated as ends in themselves. Direct moral consideration should be afforded to all "subjects-of-a-life" (SOL) and not just to human persons or moral agents. According to Regan, some animals are subjects-of-a-life (SOL), have inherent worth, and deserve moral respect/have rights (Regan 1983). Even if the good outcomes outweigh the badness, Regan contends that it is unethical to exploit animals in order to benefit others. SOL "possess an integrated inner life," i.e., that there is something to be that individual that includes having desires, a sense of the future, expectations and goals, and mental continuity that grounds the bases of interspecies respect. Regan's abolitionist view regarding animal use is nuanced. He offers the mini-ride principle (where comparable harms are concerned, we ought to override the protected interests of the fewest number of individuals) and the worst-off principle (where noncomparable harms are concerned, we ought to avoid injuring the individual who will be worse-off) as attempts to arbitrate how moral claims made against moral agents should be assessed or to adjudicate conflicting ones.

Russow (1988) criticized Regan's definition of subjects-of-a-life for its lack of specificity and usefulness as a moral category. Anthony (2009) has argued that Regan's strong animal rights, which aims to emphasize species similarities and egalitarianism, puts animals into an amorphous

group with the same moral identity and does not appreciate the uniqueness and diversity of capacities in the animal kingdom that make for different bases for moral treatment.

In recent years, Christine Korsgaard has developed a different Kantian cum rights-based alternative to Regan's subjects-of-a-life approach. She acknowledges that "we have obligations to animals" and that their pain is "not a trivial fact" (1996). She argues that human beings ought to respect the dignity of animals. The basis of human duties towards animals on Korsgaard's (2011) view is recognition of their behavioral drives or natural inclinations. This view, which draws from Nussbaum's (2006) notion of capacities and Rollin's (1981) concept of *telos*, deemphasizes human characteristics as the basis of moral significance of animals' moral claims on human beings. Instead, they give ethical priority to natural species prerogatives, diminishing the significance of countervailing elements in the process. Under Nussbaum's capabilities approach (an extension of her work on human rights), certain capacities of animals define their agency or good of their own, and delineate the contours of their moral claims on moral agents. "[T]here is waste and tragedy when a living [nonhuman animal] has the innate, or 'basic' capacity for some functions that are evaluated as important and good, but never gets the opportunity to perform those functions" (Nussbaum 2004, p. 305). Further, as a matter of justice we should be concerned with the quality of an animal's life, its dignity and free movement, and affiliations with conspecifics (Nussbaum 2006). More pointedly, "The general aim of the capabilities approach in charting political principles to shape the human-animal relationship would be ... that no animal should be cut off from the chance at a flourishing life and that all animals should enjoy certain positive opportunities to flourish. With due respect for a world that contains many forms of life, we attend with ethical concern to each characteristic type of flourishing and strive that it not be cut off or fruitless... Human beings affect animals' opportunities for flourishing, pervasively... Respect for other species' opportunities for flourishing suggests [a more]... robust, positive political



commitment to the protection of animals ...” (Nussbaum 2004, p. 307).

While many philosophy and ethics courses have employed the philosophies of Singer and Regan (i.e., the animal welfare-rights debate) to showcase the theoretically important aspects of traditional ethical theories like utilitarianism and rights-based approaches, of late, more nuanced approaches to improving the lot for animals have gained currency. Many of these approaches are informed by empirical details involving animals’ capacities (Rollin 1995a; Nussbaum 2006; Varner 2012; Thompson 2015) and are responsive to problems faced by those working with animals on a daily basis (Korthals 2016). Many of these approaches, generally speaking, reflect the view that our treatment of animals should be grounded both in empirical fact and reflect normative ideals or human virtues regarding interspecies equity and stewardship. They aspire to determine respectful practices that are based on a more intimate understanding of animals’ points of views or animal-based measures and mutual dependencies between the species (Bovenkerk and Keulartz 2016). Examples of these proponents of these approaches include relational (feminist) theorists, Mary Midgley (1983) and Josephine Donavon and Carol Adams (2007), proponents of the ethics of care approach, and Bernard Rollin (1995a) (communitarianism).

On the relational or ethics of care approach, the relationships we have with others help to carve out our responsibilities to “the other.” Thus, our actual fellowship with animals forms the basis of our care, compassion, respect, and empathy towards members of our mixed communities (Midgley 1983; Gruen 2015). Elizabeth Anderson has argued that, “Moral considerability is not an intrinsic property of any creature, nor is it supervenient on only its intrinsic properties, such as its capacities. It depends, deeply, on the kind of relations they can have with us” (Anderson 2004, p. 289).

Enduring bonds can be formed between humans and animals and these relationships acquire moral significance (Donovan and Adams 2007; Anthony 2003; Russow 1999). This view recognizes that moral obligations are necessarily

multifactorial. That is, our moral obligations are determined by different kinds and strengths of needs, the kinds and contents of interests that are associated with the one cared for, and the context (e.g., urgency, preferences, clinical indications) of both caregiver and recipient of care. Concerns related to this view mainly have to do with the notion of community and strength of the bond between human beings and animals. Animals regarded as “pests” or which do not belong to a “charismatic” species or those with whom we may not have a strong emotional attachment may not show up on our moral radars as deserving of moral concern and hence require supplemental protections.

On communitarianism or the social ethics approach à la Bernard Rollin, technology and economics have usurped the traditional prudential relationship between humans and animals that underscored a kind of interspecific contract: “If one’s animals did not fare well, then you did not either.” The commodification of animals is correlated to their invisibility in our communities and limited exposure to them, e.g., in terms of their final form as packaged protein at grocery stores or delivered vittles. For many of us, animals are “absent referents” (Adams 2000). Rollin’s view focuses on meeting the evolutionarily inherited species endowments or adaptations of farmed animals, i.e., their *teli* or distinctive natures. *Telos* is, “a nature, a function, a set of activities intrinsic to [an individual of a particular species], evolutionarily determined and genetically imprinted.” For those of us who interact with animals, we know that “[they] have natures – the pigness of the pig, the cowness of the cow, ‘fish gotta swim, birds gotta fly’ – which are essential to their well-being. Common sense tells us that animals who are built to move need to move to feel good; there is no point in trying to prove that they are fine if kept immobile.” Being respectful to animals is tantamount to ensuring that animals have access to natural elements in their environment so that they can express their evolutionarily shaped species endowments and adaptations (1995a). Rollin’s emphasis on according intrinsic value to evolutionarily established species typical “natures” or behaviors has been critiqued for

being ambiguous and unscientific. Also, in the wake of advances in modern molecular biology, e.g., Dolly the sheep cloned from an adult somatic cell or the AquaAdvantage salmon, there is some question over just what weight “*telos*” bears morally if we can enhance an individual animal’s welfare by transcending its “nature” through genetic modification or other forms of technological enhancements. Rollin has attempted to address this issue by employing the conservation of welfare principle (Rollin 1995b). By his lights, genetic alteration is morally problematic if it would worsen an animal’s well-being relative to unaltered fellow creatures or if the individual in question would have enjoyed a better life without the intervention.

These approaches highlight a plethora of ways we experience animals morally and provide additional arguments to challenge poor or disrespectful treatment of animals. When we consider our relatedness to animals as morally significant, we are able to acknowledge the impact of the moral claims made on us (Gruen 2015). Treating animals poorly, for example, may not be a function of violating rights they possess or a failure to attain an optimistic balance of good outcomes over bad ones. Instead, it may be a function of insensitivity, lack of compassion, and immaturity towards members of the moral community. The relational and communitarian views bring to light virtues and qualities of character that align with attitudes of compassion and mindfulness that underlie our relationship with animals and alternative ways of seeing animals. This is echoed by Hursthouse, a virtue theorist:

“I began to see [my views] that related to my conception of flesh-foods as unnecessary, greedy, self-indulgent, childish, my attitude to shopping and cooking in order to produce lavish dinner parties as parochial, gross, even dissolute. I saw my interest and delight in nature programmes about the lives of animals on television and my enjoyment of meat as side by side at odds with one another...Without thinking animals had rights, I began to see both the wild ones and the ones we usually eat as having lives of their own, which they should be left to enjoy. And so I changed. My perception of the moral landscape and where I and

the other animals were situated in it shifted” (Hursthouse 2000, pp. 165–166).

These approaches also highlight the importance of empirical evidence in revealing how animals actually are. Animal scientists and cognitive ethologists have an important role to play in filling in the actual relationship between species-specific behaviors and how animals’ interests are frustrated or rewarded when they are actualized. For example, it is unclear that animals are harmed morally or have their “rights” violated in every instance in which their natures or species-specific behaviors are frustrated. Animals may have other adaptive capacities that can offset momentary frustration or discomfort (Fraser et al. 1997). Here, those in the empirical sciences can help philosophers understand the links between frustrated behaviors or psychological distress and diminished welfare, and good welfare and the expression of “natural” behaviors as well as reveal the relationship between the behaviors’ evolutionary and physiological antecedents and their impacts on animals’ welfare (Fraser 2008a).

As philosophical animal ethics advances, philosophers and scientists alike are increasingly interested in transcending the seemingly inherent individualism that has plagued philosophical animal ethics (Swart 2016; Dubois and Fraser 2013; Fraser 2010). Rather than focus on the impact of intrinsic or innate properties of individual nonhumans as the basis of their moral considerability, improving arguments regarding the moral recognition and value of species, (including conservation or management strategies and the permissibility of altering the genome) will be an important frontier in human-animal relationships.

## **Beyond Animal Ethics: Investigations into the Inner Lives of Animals**

Although a lot of attention has been given to the ethical shape of our relationship to animals in the philosophical literature, philosophers have also been interested in the capacities of animals, such as their inner lives as its own field of inquiry. Philosophers working on animal issues, for their part, have availed themselves of the empirical

research in animal consciousness, language, memory, emotion, behavior, and cognition in exploring animals' minds. Research in the philosophy of mind or consciousness studies, while connected to work in animal ethics, is also intriguing in itself. Philosophers of mind are interested in animal consciousness and cognition, the nature of sentience, animal emotions, and other phenomenological experiences or "qualia," i.e., the something it is like to be it, for example, is there something it is "like to be a bat?" (Nagel 1974). Noted philosophers of mind, Tom Nagel (1974) and Peter Carruthers (1989) have been interested in "theories of mind" or the inner lives of animals and have spawned much interest in extending metaphysical approaches and categories of mind-brain to animals, including paradoxes of consciousness, psychopathologies, and higher-order thought processes (Gennaro 2009). Furthering the ground that Descartes laid, Carruthers (1989) initially denied that animals possessed experiences that are conscious because they lacked the requisite hardwiring found in humans. In a version of Descartes "biological automata," Carruthers argued that animals are on "autopilot" since they lack proposition language, a prerequisite for having beliefs and desires. Carruthers also echoes Donald Davidson (1982) here who argued for the necessity of propositional language in higher order capacities like having future-oriented beliefs and desires, and being able to plan and execute certain projects that did not hinge on gratifying immediate affective states (see also Gennaro 2004; Robinson 1997). Carruthers has since changed his view (2006), citing that different physiology and anatomy from that possessed by human beings can also give rise to conscious phenomenal experiences. David DeGrazia, (1996) in *Taking Animals Seriously: Mental Life and Moral Status*, makes the vivid case for "animal mentation" and its connection to attributions of moral considerability to animals.

Many of the philosophers identified above like Singer and Regan who work in animal ethics rely on factual or empirical details about animals' mind to either justify or debunk human exceptionalism (Andrews and Beck 2017; Varner 2012; Lurz 2011; Beauchamp and Frey 2011). Animal

scientists, for example, animal welfarists and cognitive ethologists (e.g., Duncan 2006; Weary et al. 2017; Dawkins 1993), have and continue to provide important evidence regarding the mentality of animals and their capacities. Knowing about consciousness and capacities for pain and suffering intersects with real-world concerns such as best practices for performing euthanasia (<https://www.avma.org/KB/Policies/Documents/euthanasia.pdf>), or for minimizing unpleasant effects on research animals (<https://grants.nih.gov/grants/olaw/guide-for-the-care-and-use-of-laboratory-animals.pdf>) that veterinarians and scientists are also invested in. Animal scientists either assessing or working on improving the quality of lives of animals through frameworks like the Five Freedoms (Brambell 1965) or Fraser's Three Domains model of experiential and physiological welfare and opportunities to express species typical behaviors (Fraser 2008b; Fraser et al. 1997) also appeal to the inner lives of animals to promote better quality of life for animals. Philosophers like Singer and Varner appeal to evidence regarding which animals are able to experience states of satisfaction and frustration in making utilitarian style moral arguments. Regan style ethical arguments regarding subjecthood and mental complexity (1983) depend on evidence of biographical existence and future-oriented desires. Rollin is concerned if animals are temporally fixed in the present (1998). New frontiers in animal ethics, like fish cognition and welfare (Allen 2013; Braithwaite 2013) and the impacts of emerging (bio or neuro) technological manipulations on animals (Takala and Häyry 2014), also rely on the latest science regarding animal minds. Interdisciplinary collaboration is thus essential to curtail concern for anthropomorphism, the projection of human qualities onto nonhuman entities (Daston and Mitman 2005; Bekoff and Allen 1997; Fisher 1990).

Beyond matters of ethics or normativity, there is much opportunity for cross-pollination between cognitive ethologist and animal scientist and philosophers to probe together and carve out new research trajectories regarding the inner lives of animals (Andrews 2015). The work of

philosophers, like Allen and Bekoff (1997), Varner (2012), and Lurz (2011), have shaped the way animal scientists (e.g., Braithwaite 2010; Ian Duncan 2006) and cognitive ethologists (Griffin 1976) think about the mental capacities of animals and vice versa. Animal scientists, ethologists, and cognitive and neuroscientists have already helped to provide evidence supporting higher cognitive state in animals including higher order capacities for planning and execution and emotions (Panksepp 2005). Birds, fish, and other non-mammalians have been shown to have the capacity to learn from past experiences (Allen 2013; Braithwaite 2010; Allen and Fortin 2013). Beyond showing that pain, suffering and positive affective states are widespread throughout the animal kingdom; recent scientific evidence is highly suggestive that human beings no longer have a monopoly on “theory of mind,” higher order thought, and that episodic memory, self-consciousness, joy, empathy, desires and beliefs about the(ir) future, and fulfilling projects or “mindreading” others’ intentions or the capacity for deception are also distributed in other species (Gennaro 2016; Varner 2012; Bekoff 2007).

New opportunities are afoot (e.g., Buller 2014) to broaden existing metaphysical views (Dennett 1996) regarding the richness of animal minds especially, as greater attention is devoted to resolving debates regarding what morally relevant capacities of animals should be taken into account in our treatment of them and in our quest to improve the welfare of other species in our sphere of influence. Rethinking the morality of human-animal relationships and metaphysical and scientific connections regarding animal minds will not only benefit animals in the long run but also afford us the opportunity to reflect on our own humanity and its trajectory (Gruen 2015; Bradshaw 2009).

## Conclusion: Ethics, Animals, and Science

Ethical inquiry into the philosophical bases of respectful human-animal interactions and relationships provides a systematic way of examining and assessing the merits of different viewpoints

and theories regarding these interactions in a structured way. This process appears to be the cornerstone of the 1985 US Animal Welfare Act and the basis of the 1986 establishment of IACUCs in the wake of the Silver Springs macaque incident. Ethical and philosophical inquiry can be critical in probing the attitudes, prejudices, misunderstanding, biases, and assumptions that motivate how we should regard and treat animals. They can help us reveal and gauge our attitudes regarding animals and highlight possible implications of different perspectives that influence public and disciplinary attitudes on human duties towards animals (Appleby and Sandøe 2002). The work of ethicists and philosophers to interpret our ethical judgments and values about animals and how the latter should influence practice and policy can reveal central points of tension and internal inconsistencies within the perspectives we hold, and remind us that the moral considerability of animals and the significance of their interests should be balanced alongside other relevant and vital projects that deserve our critical attention. While respect and proper treatment of animals is a weighty norm, our moral lives also consist of other duties we have towards ourselves, others, and the natural world (Bovenkerk and Keulartz 2016; Jamieson 1998). Thus, in thinking ethically about whether and how to use animals, due consideration should be given to when our duties to animals may be overridden by other important moral or practical concerns. If our moral judgments regarding human-animal interactions are to have any weight at all, they should be backed by the best of reasons. Here, they ought to be the result of careful reflection in which we have arrived at good reasons for accepting them. These reasons should be in a format that can be recognized as action guiding by any other conscientious and reasoning person.

The dominant debate in philosophical animal ethics for the last half decade or so has assumed the form of discovering the terms of membership of the moral community and then debating whether that membership affords full or equitable moral significance and protection to moral agents and subjects alike (Garner 2013). Today, philosophers

recognize that there are multiple ways in which ethical norms and concepts exert a pull on our reason and emotions, and good reasons for justifying healthy human-animal interactions requires integrating philosophical work on animal ethics with research by animal scientists and others dedicated to improving the welfare of animals. Objective norms and standards for respectful treatment of animals need not be relative to cultural or individual whim. Important gains in information about what animals need and are feeling or thinking either by direct or indirect means have been made that have enhanced our experiences, moral imagination, and sensitivity regarding what matters to various animals. A fairly solid body of science is available now about the capacities of animals beyond experiences such as fear, pain, and frustration. Gaps in knowledge remain on states of pleasure such as joy and happiness in animals and just where during an individual's ontogenesis or during the evolutionary development and history of a species morally significant capacities like sentience, self-consciousness, and other higher order thoughts emerge (Gennaro 2016; Bovenkerk and Keulartz 2016; Boly et al. 2013).

Animal and cognitive science have contributed immensely to ethical inquiry into the nature of our obligations to animals. A deeper appreciation of phylogenesis, biological functioning, anatomical similarity, and "animal mentation" have all contributed to a better understanding of how animals can be benefited and harmed as a result of human actions and omissions. Ethical inquiry coupled with philosophical and scientific engagement on the viewpoint of animals will continue to illuminate how to improve human-animal interactions and animal welfare (Fraser 2009; Thompson 2004). Opportunities for improvement lie in the ways in which we handle, house, and manage animals (individually or at the group level), and what different philosophical conceptions and arguments regarding their moral status and measurements of animal welfare mean to the animals themselves.

Partnership between ethics and science is vital in helping us discover which animals are capable of experiencing morally relevant states such as pain or self-consciousness. As moral agents, we

are obliged to take all morally relevant features into account in our treatment of animals, including their minds, natures, and experiential and physiological welfare. Just how we should take these features into account falls to both members of the philosophical and scientific communities. Weighing probabilities of harm and benefits and relative weight given to other features of our moral lives is a shared project. Finding ways to match concerns about why animals matter with how they matter in light of what threatens to cause animals harm given the capacities they possess is a shared project.

## Cross-References

- [Animal Welfare](#)
- [Aristotle](#)
- [Cartesian Dualism](#)
- [Cognition](#)
- [Consciousness](#)
- [Donald Griffin](#)
- [IACUC](#)
- [Immanuel Kant](#)
- [Theory of Mind](#)

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## Ethogram

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### Synonyms

[Behavior catalogue](#)

### Definition

A descriptive inventory or catalogue of all behaviors used by a particular species of animal.

### Introduction

One of the fundamental issues in any branch of science is how to measure the components (objects, entities, and events) studied by that branch of science. The discoveries in a branch of science can be no better than the quality of the measurements used in that field. In the study of animal behavior and cognition, the events that are studied are the behaviors of animals; the components of animal behavior are measured according to an intellectual construct called an *ethogram*.

The construct of an ethogram originated in the field of ethology in the 1930s, derived from the Greek *ethos*, meaning “nature” or “disposition,” and *gram*, meaning “writing or drawing.” The term is now a common tool in all areas of the study of animal behavior, regardless of theoretical orientation. In its simplest form, an ethogram is an exhaustive list of all the behaviors exhibited by individuals belonging to a particular species. Each behavior is operationally defined, meaning that it is defined by the criteria that must be satisfied before that behavior can be said to have occurred.

### Ethogram Requirements

The basic requirements for the development of an ethogram are that it must include an exhaustive

list of behaviors, and those behaviors must be defined in ways that are mutually exclusive. The term exhaustive means that anything the animal might possibly do – its entire behavioral repertoire – can be classified somewhere in the catalog; mutual exclusivity means that no action can simultaneously meet the criteria for more than one of the behaviors represented in the list. This requirement is logically necessary, so that no matter what behavior occurs, there is one and only one way to classify that behavior.

The term ethogram was originally applied only to behavioral catalogs that were believed to be comprehensive; over time, however, the term has come to be used to describe more limited behavior catalogs. For example, a particular investigator may have been primarily interested in courtship behavior; such an investigator might, through extensive study and detailed analysis, develop a complete and nuanced list of behaviors for only those behaviors found in the particular context of courtship and reproduction. Animals do, however, engage in behaviors other than courtship and reproduction. The requirement that the catalog be comprehensive could be satisfied in this situation by the inclusion of a broad category (e.g., “other behavior”) into which all noncourtship-related behaviors would be classified. The requirement that all behaviors be classifiable somewhere in the catalog is satisfied, without the investment of time and resources required to develop detailed operational definitions for behaviors that are not of interest in this particular context.

Before the ready availability of video recording and electronic recordkeeping, it was necessary to conduct behavioral observation in real time; this circumstance dictated that behavioral classification systems be straightforward even sometimes to the point of oversimplification. The availability of technologies that allow the examination of behavior in slow motion or stop-action, as well as observing the same instance multiple times, has permitted the collection of data concerning complex streams of events, which has in turn permitted the development of richer,

more complex systems (e.g., Renner and Seltzer 1991).

Video capture and analysis technologies have made it possible for this concept of mutual exclusivity to evolve, recognizing the existence of multiple semi-overlapping behavior streams in an individual animal. These behavior streams are coded in ways that can be separated for some analyses and recombined for others, allowing the coding to capture the layering of different component behaviors that occurs in nature (Renner and Seltzer 1994).

To illustrate, behaviors can occur as events (i.e., meaning that they are of very brief duration, or punctate, functionally occurring at a single point in time, such as a canine bark) or states (having an indefinite duration, such as lying down). Although it is certainly possible to construct a coding system that includes “barking while lying down” as a behavior distinct from “sneezing while lying down” and “lying down without making noise,” it is simpler to understand an ongoing state of “lying down” that may or may not have embedded events such as “bark” or “sneeze.”

Nevertheless, for ethogram to successfully describe the behavior of a species, any action that can be displayed by any individual member of that species must fit into one, and only one, category in the ethogram.

### Defining Behavior

Two approaches to defining behaviors (and through definition, measurement) are always in dynamic tension. The first approach is to determine what behaviors can be easily and reliably quantified and then to measure those behaviors, with a likely eventual goal of assigning functional significance to the behavior patterns detected in this way. A behavior may be defined in strictly physical terms by describing the positions and movements of specific body parts over time (c.f., Eshkol and Wachman 1958). This approach is often useful when the function of the target behavior is poorly understood or disputed. Because such definitions are based on objectively observable phenomena, they require relatively little context-specific knowledge of the species' habits and

ecology. For example, one could define “sniffing an object” in a quadruped as follows:

Interaction with an object that is anterior to the plane perpendicular to the spinal column at the level of the animal's ears, and within a sphere centered on the tip of the animal's nose with a radius of the distance between the tip of the nose to the plane of the ears.

This definition, although sterile, does not require the observer to make judgments about the animal's intent.

The second approach is to determine what is interesting or important on theoretical or conceptual grounds, and then to attempt to develop methods to measure, however imprecisely, those behaviors. This approach is often accompanied by the assertion or assumption that successive iterations of the measurement technique will produce improved precision. One example of this approach is often called a functional definition, which defines a behavior by observing the outcome of the interaction between the animal and its environment. One might define eating as follows:

Interaction between an animal's mouth and some object or substance that results in the ingestion of the object or substance.

This definition makes no attempt to specify whether or how the object or substance is chewed, only that interaction occurs with the net outcome of ingestion. More generally, functional definitions allow for variation in specific motor patterns, grouping behaviors together if they achieve a common result.

### Ethogram Uses

Once a usable ethogram exists for a particular species, it becomes possible to empirically determine the time budget for that species. A time budget reports how individuals of the species typically allocate time among possible behaviors. Although there is considerable interindividual variability in behavior within a species, as well as circadian and seasonal changes in behavior patterns, the behaviors used to solve the basic problems of life (e.g., finding food, shelter, mates, etc.) do not vary, and so these variations likely occur as deviations from a characteristic or default time budget for a species.

Such a time budget can also serve as a useful baseline reference in evaluating the behavior of animals under captive management. The absence of opportunity to exhibit particular species-typical behaviors reflected in the ethogram can lead to stress, which may result in, or be indicated by, the presence of stereotypic behavior. Similarly, captive animal management standards now require a program of environmental enrichment, the implied goals for which include the absence of abnormal behavior (i.e., stereotypies) and the behavioral expression of the full ethogram for that species (Renner et al. 2000; Renner and Plebani Lussier 2002). A known time budget for is a powerful reference point in such work.

An ethogram is conceptualized as concerning a single animal's behavior, but it is possible that the catalog for an individual's behavior may well include interactions with one or more other individuals. Social behaviors can include those in which the subject animal is the agent (e.g., a facial grimace directed toward a conspecific), the object or recipient (e.g., defensive behaviors), or one of an obligatory pair (e.g., one actor in a mutual courtship display sequence, where both animals must act for the sequence to exist).

### Observational Methods

An ethogram can be used as the basis for recording behavior through any of several observational methods. The choice of method dictates some of the characteristics of the data that can be collected, and constrains the types of generalizations and inferences that can be drawn from the data (Altmann 1974).

Instantaneous sampling is the practice of classifying which behavior is occurring a single point in time; this is commonly applied periodically (e.g., making one observation per minute). This method is akin to capturing a series of still images; it produces data that are relatively easy to analyze, but this type of data tends to underrepresent short-duration behaviors (i.e., events) and thereby overrepresent behaviors that have variable duration (i.e., states).

An alternative is one-zero sampling, in which the observation period is divided into a series of time periods, which are sometimes referred to as

time bins. The observer records which behaviors from the ethogram occur during each of these time periods; within each time period each behavior is classified as present (1) or absent (0). There is no attempting to record either the duration of any behavior or the number of times that a particular behavior occurs during the time period. One-zero sampling captures short-duration behaviors (i.e., events) more effectively than instantaneous sampling. The tradeoff, however, is that multiple behaviors can occur within a single time period; information about the durations and sequences of behaviors is lost.

The most complete record of behavior for a defined period of time is known as continuous recording, in which every behavior of an individual is recorded and its duration timed. This approach captures states, events, and order of behaviors. However, it is complex and difficult or impossible to accomplish with precision in real time. It requires highly trained observers, is more susceptible to error, and is far more labor-intensive than other methods because it generally requires analysis of video records after the fact.

### Measuring the Behavior of Multiple Individuals

There are two methods available for measuring the behavior of animals living in groups. Focal animal sampling involves recording the behavior of an identified individual from the group over a period of time. To represent the behavior of the group, multiple observers can be employed during a single time period, or a single observer can observe different individual animals at different times. Scan sampling involves surveying the entire group at a point in time in order to count the number of individuals that are engaged in each of the behaviors from the ethogram; these instantaneous samples are repeated at defined intervals. Such a survey of the group provides what amounts to a behavioral census; over time, this type of data this reflects the distribution of behaviors across the entire group.

### Instrumentation and Reliability

Some behaviors, although they may not be amenable to measurement by automated methods, can



be measured by proxy measures that can be automated. For most ethological study, however; the application of human judgment is necessary to properly categorize behavior. Therefore, detailed study of animal behavior requires human observers and remains highly labor intensive. As scientific models of behavior become more sophisticated, and as technologies advance (in particular pattern-recognition, image analysis, and the identification of physical events that can serve as reliable proxies for behaviors or sequences), it is likely that more types of behavior observation will become amenable to automation.

The measurement of behavior through observation raises the question of whether the judgments of different observers are equivalent. This is addressed in ethology through measures of interobserver reliability, using calculated or statistical techniques to assess whether the observations of two or more distinct observers may be treated as interchangeable (Martin and Bateson 2007). In many research programs, a period of apprenticeship or training, followed by extensive evaluation of interobserver reliability and additional training, is required before a new member of the research team begins to collect data that become part of the project's corpus of data.

## Cross-References

- [Behavioral Variation](#)
- [Focal Animal Sampling](#)
- [Observational Methods](#)
- [Species-Specific Behavior](#)

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## Euchromosome

- [Autosome](#)

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## Eugenics

- [Social Darwinism](#)

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## Eukaryota

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## Synonyms

[Eukaryotes](#); [Eukaryotic organisms](#)

## Definition

Eukaryota is a major group of organisms, defined by the sophisticated cellular organization. The term “eukaryote” itself means “true nut” or “true kernel” in Greek: the “nut” refers to the nucleus of the eukaryotic cell. The group eukaryota includes all the organisms with a cellular structure that



consists of a nucleus, membrane-bound organelles, and a network of cytoskeleton.

## Introduction

In order to facilitate a systematic study of organisms, the organisms are classified into multiple groups based on their various defining features. The most fundamental level of these classifications is based on the cellular architecture, and at this level all the organisms have been divided into three groups, or domains: Archaea, Bacteria, and Eukaryota. While the bacteria and the archaea are invariably single-celled (unicellular) organisms, the eukaryotes span a vast range: from unicellular protozoans to giant multicellular mammals and trees, and all those in between. In fact, all the organisms visible to the naked eye are eukaryotes, though not all the eukaryotes are visible to the naked eye. This reflects the sheer heterogeneity of the group eukaryota.

## Defining Features of Eukaryota

The eukaryotic organisms can be generally recognized on the basis of the following common features:

**Larger size of cells:** Most conspicuously, the eukaryotic cells are larger than the prokaryotic cells. While the diameter of prokaryotic cells ranges between 1 and 10  $\mu\text{m}$ , the size of eukaryotic cells is a thousand times greater and typically they are between 10 and 100  $\mu\text{m}$  (Cooper and Hausman 2016).

**Multicellularity:** The eukaryotes can be single-celled (i.e., unicellular) or many-celled (i.e., multicellular). Most of the life forms familiar to us are multicellular plants or animals. The life cycle of the multicellular eukaryotes requires several additional features like adhesion of cells together to form tissues, intercellular communication, and differentiation of cells into multiple kinds in order to facilitate division of the labor. Those features are not shared by the unicellular, free-living eukaryotes.

**Presence of membrane-bound intracellular structures:** While the prokaryotes have simple, uncompartimentalized cells in which all the molecular processes take place within the confines of one envelope, the eukaryotic cells have specialized compartments for distinct functions, each one separated by a membrane analogous to the one covering the cell. These intracellular structures are called “organelles.” The most prominent of these structures is the nucleus which houses the genetic material.

Besides the nucleus, the eukaryotic cells have organelles such as mitochondria (for respiration and energy production), Golgi complex, lysosomes, peroxisomes, endoplasmic reticulum, and supporting structures like cytoskeleton.

**Genetic material:** The genetic material of a eukaryotic cell, which is deoxyribonucleic acid (DNA), is folded with the help of histones and some non-histone proteins and gives rise to compact structures, called “chromosomes.”

## Taxonomic Status

According to the three-domain classification system (Woese et al. 1990), all the life forms can be divided into Archaea, Bacteria, and Eukarya domains. This system puts all the eukaryotes within the Eukarya and divides the prokaryotes into Archaea and Bacteria domains.

The credit for proposing the prokaryotic-eukaryotic distinction goes to the book *Titres et Travaux Scientifiques* (1937) by a French marine biologist Edouard Chatton (1883–1947) (Sapp 2005). As the classification system underwent gradual refinement, by 1970 all the living organisms were classified into five kingdoms: Animalia, Plantae, Protista, Fungi, and Monera (Prokaryotae). In this five-kingdom system, the first four encompassed the eukaryotic organisms. In 1977, by comparing the nucleotide sequences of the small subunit of ribosomal RNA (known as 16S rRNA), Carl Woese et al. were able to derive a global molecular phylogeny of cellular organisms. As a consequence of the insights derived through his work, the prokaryotic group was divided into eubacteria and archaea, leading to

the formation of a six-kingdom system. This new system overturned the eukaryote-prokaryote dichotomy and resulted in three most fundamental units, “domains” of life.

The six kingdoms, Archaea, Bacteria, Protista, Fungi, Plantae, and Animalia have been organized under three domains: Archaea, Bacteria, and Eukaryota. According to this system, the kingdoms Protista, Fungi, Plantae, and Animalia fall within Eukaryota. Thus, all the animals, plants, fungi, and protists are the members of Eukaryota group. According to one of the classification schemes, these members of the eukaryota group have been classified into the following clades: Opisthokonta, Amoebozoa, Excavata, Plantae, and “SAR” (Stramenopila, Alveolata, and Rhizaria) (Katz 2012). Opisthokonta, here, includes animals, fungi, and their microbial relatives. Within the “Amoebozoa” clade are included amoebae like *Amoeba proteus*, the slime molds, *Entamoeba histolytica*, and so on. The members of “Excavata” group, for example, the human parasites *Giardia lamblia* and *Trichomonas vaginalis*, are characterized by the occurrence of an excavate groove.

## Cellular Architecture of Eukaryota

The eukaryotic cell is characterized by its sophisticated intracellular organization. Each eukaryotic cell is enveloped by a selectively permeable plasma membrane composed of protein-lipid bilayer. In plants and fungi, there is an additional external layer of a rigid cell wall. Cells connect to and exchange materials with their environment and the neighboring cells through specific adhesions/junctions and transporters embedded in the membrane. Communication of a plant cell with its exterior takes place through numerous plasmodesmata.

The inside of the cell is made up of the fluid, cytosol, and membrane-bound “organelles” (Fig. 1). The membranes enclosing the cell or the organelles have distinct properties which enable them to protect the integrity of its content and facilitate the processes performed by the cell or the organelle. The nature of the membrane may

vary based on the lipid and protein content. Due to the presence of specific receptors, transporters, etc. membranes around different cells or organelles respond differently to their surroundings and help the cell/organelle perform specific functions. For example, while the outer membrane of mitochondria is highly permeable for movement of solutes across it, the internal membrane is very selective and only specific substances can cross it.

## Intracellular Organelles

### Nucleus

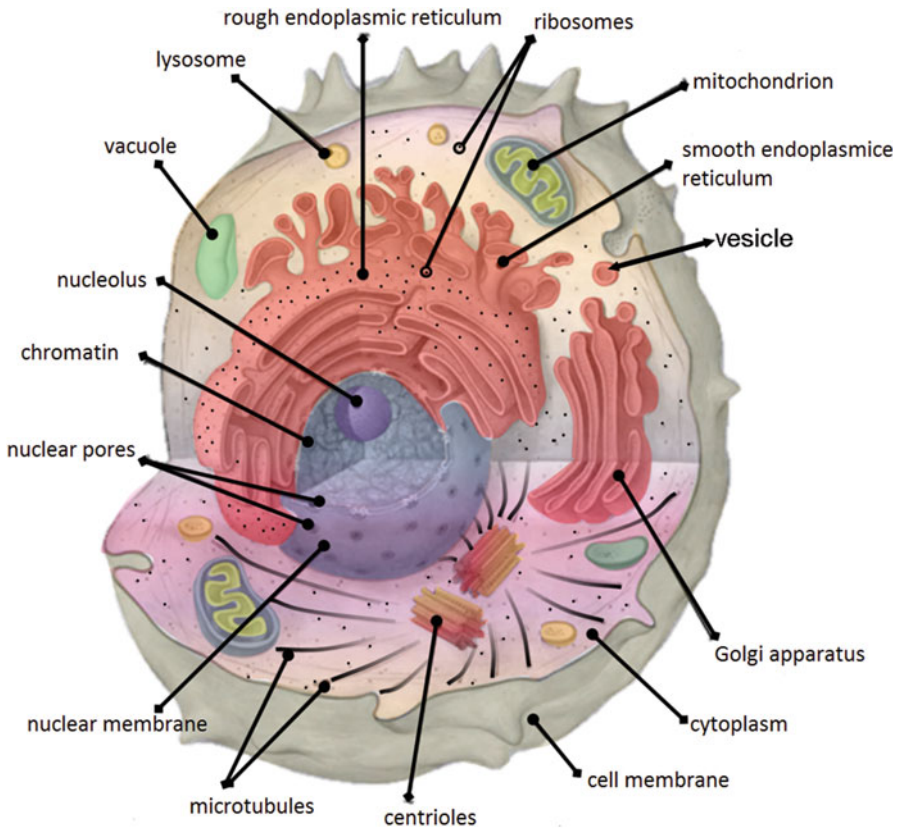
Among the intracellular organelles, the nucleus, mitochondria, and chloroplast are double-membrane structures, while the remaining are single-membrane. Nucleus is the largest organelle of a eukaryotic cell. The genetic material of a eukaryotic cell, DNA, is stored inside the nucleus, and processes like replication of DNA, transcription, and RNA processing take place herein. Certain cells, such as mammalian RBCs, lack the nucleus.

The contents of the nucleus are kept isolated from the cytoplasm through a “nuclear envelop” which is made up of double membranes. The exchange of material between the nucleus and the surrounding intracellular material, cytoplasm, happens through large nuclear pore complexes. The space between the outer and inner nuclear membranes extends into the cytoplasm and forms the endoplasmic reticulum. Underneath the inner nuclear membrane, a meshwork of “nuclear lamina” is attached. This lamina is made up of fibrous proteins called “lamins” and provides structural support to the nuclear envelope.

Inside the nucleus, there are a number of different sub-organelles, known as “nuclear bodies” involved in various functions. Nucleolus is one such nuclear body which is associated with ribosomal RNA transcription, processing, and ribosome formation. These nuclear bodies are not membrane-bound structures and are dynamic in nature.

### Mitochondria

The mitochondria are the sites where the breakdown of carbohydrates and fatty acids takes place



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**Eukaryota, Fig. 1** The cellular organization of a typical eukaryotic cell

to extract energy and ATP is produced through the process of oxidative metabolism. The initial breakdown of glucose, known as glycolysis, occurs in the cytosol. The end product of glycolysis, pyruvate, is transported to mitochondria where it is completely oxidized into  $\text{CO}_2$ . Processes known as citric acid cycle and oxidative phosphorylation, which take place at the mitochondrial matrix and inner membrane, respectively, result in extraction of energy from glucose and its storage in ATP molecules.

### Chloroplasts

Chloroplasts are found in cells of plants and green algae. These are larger and more complex than mitochondria. The primary function of chloroplasts is to carry out photosynthesis and convert  $\text{CO}_2$  to carbohydrates. In addition, these are also sites for synthesis of amino acids, fatty acids, and

lipid constituents of their own membrane. Unlike mitochondria, chloroplasts have an additional third membrane inside the organelle and this membrane, known as “thylakoid,” is the site of ATP generation.

Mitochondria and chloroplasts possess their own genomes. These genomes consist of circular DNA molecules which occur in multiple copies. The organelle genomes encode tRNAs, rRNAs, and some organelle-specific proteins (essentially involved in oxidative phosphorylation). The genomes of chloroplasts are larger and more complex than the mitochondrial genomes.

### Lysosomes

Lysosomes are organelles meant for the digestion of various intracellular and extracellular substances. These contain about 60 different enzymes capable to hydrolyze DNA, RNA, proteins, lipids,

carbohydrates, etc. (Cooper and Hausman 2016). Most of these enzymes act at acidic pH (~5).

#### Peroxisomes

Peroxisomes are the sites of oxidative reactions and many other metabolic processes. These too can replicate by division like the mitochondria and chloroplasts.

#### Cytoskeleton

The shape of the eukaryotic cell is maintained by a scaffold, a skeleton arising out of a network of protein filaments extending throughout the cytoplasm. These filaments are anchored to the cell membrane through a variety of accessory proteins. There are three main types of the protein filaments: (i) microfilaments, made up of actin subunits, (ii) microtubules, made up of tubulin subunits, and (iii) intermediate filaments, made up of various proteins.

The cytoskeleton is a dynamic structure. As per the requirement and the status of the cell, rapid re-organizations of the cytoskeleton enable the cell in shape change, motility, etc. Besides its structural role in maintaining cell shape, and effecting cell motility, the cytoskeleton is also essential in correct positioning of intracellular organelles, and intracellular movement of organelles and other structures. The cytoskeletal protein filaments also play crucial roles in the processes like muscle contraction, and the formation of the spindle apparatus, which separates the chromosomes during mitosis.

#### Flagella

Flagella are long threadlike structures. These facilitate the movement of an organism or cell through liquid medium. The eukaryotic flagellum is a bundle of nine pairs of microtubules surrounding a central pair (the so-called 9 + 2 structure). The eukaryotic flagellum emanates from a microtubule organizing center, or MTOC.

#### Endoplasmic Reticulum

The endoplasmic reticulum, or ER for short, is a complex network of membranes that provides a transport system within the cell. There are two types of endoplasmic reticulum, rough and smooth – the two are contiguous parts of the

same network, distinguished by the presence or absence of ribosomes. The rough ER (studded with ribosomes) is the site of protein formation and transport. The smooth endoplasmic reticulum is the site of lipid formation. The proteins that are destined for organelles like ER, the Golgi apparatus, the plasma membrane, or lysosomes, or for extracellular secretion are synthesized on ribosomes attached to RER, in contrast to other kinds of proteins which are synthesized on free, cytosolic ribosomes. The proteins synthesized on ribosomes on RER are processed within the lumen of the RER and further sorted in the Golgi apparatus, if necessary.

#### Golgi Apparatus

The Golgi apparatus, or Golgi complex, is composed of flattened membrane-enclosed sacs (cisternae) and vesicles outwards to the ER. This structure is responsible for processing, followed by sorting and packaging into vesicles of proteins received from the ER for their transport to their final destinations. The Golgi apparatus is also involved in lipid metabolism, in particular the synthesis of glycolipids and sphingomyelin.

#### Ribosomes

Ribosomes are the sites of protein synthesis. These large complexes of ribosomal RNAs and proteins are composed of two subunits. The eukaryotic ribosomes are larger than the prokaryotic ribosomes and more complex with greater number of proteins and rRNAs. While the bacterial ribosomes are designated as 70S (based on their sedimentation coefficient), the eukaryotic ribosomes are 80S. These 80S macroparticles are made up of 60S and 40S subunits (the subunits of prokaryotic ribosomes are 50S and 30S). Around 46 proteins take part in forming the 60S subunit, along with 28S, 5.8S, and 5S rRNAs. On the other hand, the smaller, 40S subunit is formed by 33 ribosomal proteins and 18S rRNA (Cooper and Hausman 2016).

A key feature of the eukaryotic ribosomes is that a large pool of them is found associated with the endoplasmic reticulum, giving rise to the rough endoplasmic reticulum.

## Vacuoles

In the plant cells, multiple reservoir organelles of large size are present. These are known as “vacuoles.” The vacuoles are involved in digestion of macromolecules and storage of waste products and nutrients.

## Genomic Features

The genomes of eukaryotes are not only larger than prokaryotic genomes, the former are also more complex. The larger size of eukaryotic genomes is not accounted for by a greater number of genes. On the other hand, the eukaryotic genome contains many non-genic regions, like introns, repetitive sequences, regulatory regions, etc. The variations among these regions lead to a huge diversity in genome sizes of eukaryotes. The observation of this discrepancy between number of genes and genome size has been referred to as the “C-value paradox.”

The DNA of eukaryotes is packed inside the nucleus in the form of a DNA-protein complex called “chromatin.” The formation of chromatin reduces the DNA length and facilitates efficient packaging. The major protein constituents of chromatin are histones, with five major types H1, H2A, H2B, H3, and H4. The basic structural unit of chromatin is referred to as “the nucleosome.” The extent to which DNA is condensed to form chromatin varies between different regions and also temporally, resulting in the division of chromatin into euchromatin and heterochromatin regions.

## Origin of Eukaryotes

The oldest sign of eukaryotes is found at least 2.7 billion years ago (Cooper and Hausman 2016). Many features of the eukaryotic cells, including its genome, reveal that the eukaryotes are chimeric, with traits derived both from bacteria and archaea. According to the most widely accepted theory, the eukaryotic cells evolved from a symbiotic association between an archaean host and prokaryotic cells, such as  $\alpha$ -proteobacteria and cyanobacteria. The theory is known as endosymbiosis. The acquisition of aerobic proteobacteria gave rise to

mitochondria of the eukaryotic cells, while the photosynthetic cyanobacteria evolved as the chloroplasts of the green plants and algae. The mitochondria and chloroplasts share features similar to bacteria. These are similar to bacteria in size, have their own circular DNA, and ribosomes similar to bacteria.

The idea of endosymbiosis may be traced to the Russian biologist Constantin Mereschkowsky. Mereschkowsky (1905) was the first to postulate that chloroplasts resemble cyanobacteria and the occurrence of chloroplasts in plant cells was a result of symbiosis between a cyanobacterium and a heterotrophic host. The origin of mitochondria was attributed to an event of endosymbiosis by the French microbiologist Paul Portier (1918). However, the theory of the endosymbiotic origin of cell organelles received serious attention around 1970 by the American microbiologist Lynn Margulis (Margulis 1981). Currently, there are multiple models of the endosymbiosis theory which attempt to explain the various aspects of the eukaryotic origin and evolution (Martin et al. 2015).

## Conclusion

Eukaryota is a vast and diverse group of organisms. It includes all the multicellular animals, plants, fungi, along with unicellular protists. All these members of the eukaryota group are united by their advanced cellular features, which are lacking in bacteria and archaea. The evolution of eukaryotic life involved many innovations like advanced cytoskeleton and multicellularity, which conferred eukaryotes much adaptive advantage leading to their flourishing. The mechanisms which led to such innovations are still matters of debate.

## Cross-References

- ▶ [Algae](#)
- ▶ [Archaea](#)
- ▶ [Bacteria](#)
- ▶ [Cell Membrane](#)
- ▶ [Chromosomes](#)
- ▶ [DNA](#)
- ▶ [Fungi](#)



- [Mitosis](#)
- [Plantae](#)
- [Transcription](#)
- [Woese's Three Domains of Cellular Life](#)

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## Eukaryotes

- [Eukaryota](#)

## Eukaryotic Organisms

- [Eukaryota](#)

## Eureka Effect

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## Definition

The feeling of positive affect one experiences during problem-solving events where a previously incomprehensible problem suddenly becomes clear.

## Introduction

Imagine someone faced with solving a complicated new problem. This problem-solver tries several strategies to find a solution and then tries again when a new strategy does not work. The individual may experience a bit of frustration or feel as though the task at hand is impossible, until that moment when a solution suddenly comes to mind. A surge of excitement rushes over him/her and in that moment the individual cannot help but exclaim “Yes, that’s it!” This feeling of positive affect specifically as a result of one’s own achievements has been coined the “Eureka Effect.” In human terms, this refers to the feeling one experiences the moment he or she suddenly understands a previously perplexing problem, concept, or task. Evidence at hand suggests that animals may also experience this emotional reaction to their own achievements. Experiments focusing on the intrinsic reinforcing properties of problem-solving and the emotional consequences of responding to challenge for nonhuman animal species are rare, however the handful that are available provide clear evidence in support of the phenomenon. As it is not possible to ask most animals directly how they are feeling during their problem-solving experiences (as one can with humans), it is necessary to use proxy measures to better understand the emotionality around problem-solving. Key studies investigating the Eureka Effect specifically in species ranging from cattle to dogs involve use of a yoked control design to assess whether animals respond emotionally to their own achievements and to tease these emotions out from responses to rewards themselves (e.g., Hagen and Broom 2004; McGowan et al. 2014). These studies have found that animals who master a task in order to control their own access to rewards demonstrate more behavior indicative of excitement than control animals that received the same reward without the opportunity to learn the relationship between the task and gaining access to the reward.

Take for example the study by McGowan et al. (2014) which examined the emotional response to problem-solving in dogs by assigning dogs to matched pairs allowing them to serve as both an experimental and control animal at different stages



of the study. In this case, the dogs were trained to perform distinct tasks on specific devices (e.g., press a key on a toy piano) and were also exposed to additional devices to which they were not trained (to be used in the control scenario). Weeks after this initial training dogs were tested with the same devices in a completely new context. When acting as an experimental dog, access to a reward was granted immediately upon completion of the trained operant tasks via a swinging door that would pop open only after successful completion of the task. When acting as a control dog, access to the reward was independent of the dog's actions and was instead granted after a delay equal to their match partner's latency to complete their task. In this regard, only dogs in the experimental situation had the opportunity to learn that their actions could control the door. Thus any differences in the dogs' behavior between the two situations could be attributed to experimental dogs having the opportunity to learn to control access to the reward. McGowan et al. (2014) noted distinct differences in the behavior of the dogs when they were acting as experimental animals versus when they were acting as controls. Experimental dogs who had the opportunity to learn that their actions were controlling the door (and access to the reward) showed signs of excitement including increased tail wagging and activity, whereas control dogs showed signs of frustration such as chewing of the operant device (never seen with dogs in the experimental condition) in response to the unpredictability of the situation. In this regard it seems that problem-solving opportunities are intrinsically rewarding and that an understanding of personal achievement generates a state of positive affect in both human and nonhuman species alike.

### What's in a Name?

Anecdotally, the phenomenon derives its name from an old tale of Archimedes suddenly solving a problem on how to use water displacement to measure the volume of an object (Eureka is a word from Ancient Greek meaning "I have found it"), where he was so excited by his discovery that he ran through the streets yelling "Eureka!" It is difficult to determine the validity of this tale, but

it paints a perfect picture for illustrating the notion. While the act of suddenly finding a solution to a problem is referred to as an epiphany or insight, the term Eureka Effect describes the positive "Aha!" feeling immediately following the moment of epiphany or insight when a previously unsolvable conundrum becomes unmistakably clear. In general, theoretical accounts of experiencing an epiphany include four defining characteristics: (1) the realization appears suddenly to the individual; (2) the newfound solution seems obvious to the individual and so he/she processes the solution with relative ease; (3) the moment of understanding elicits a positive affective state within the individual; and (4) the individual experiencing the epiphany is convinced that the solution that has suddenly come to him/her is true and thus the solution transforms his/her perspective of the problem (Topolinski and Reber 2010). Typically, immediately prior to the Eureka moment the problem solver is stumped and even though he or she may have explored all the possibilities that have come to mind, he or she is still unable to come up with a solution to the problem at hand. After experiencing some level of frustration the problem solver is able to take a break from his/her mental fixation, stepping back to re-evaluate the problem, and "Voila!" the answer appears suddenly (epiphany). In this instant, this transition from not understanding to spontaneous clarity is accompanied by the Eureka moment, a manifestation of joy or extreme satisfaction.

### Mapping the Moment

Recent studies utilizing brain imaging technologies to investigate neural activation around problem-solving events, where a sudden insight or epiphany are involved in the subject coming to a solution, highlight the emotional connection to such achievements (e.g., Shen et al. 2013). In general, problem-solving activities employ a vast cortical network within the brain. However, insightful solutions elicit distinct neural and cognitive processes that enable problem solvers to suddenly make connections that previously were not apparent (Jung-Beeman et al. 2004). Though a

variety of specific areas of the brain have been implemented in studies of the Eureka moment, heightened activity in the amygdala, which is generally associated with emotion, accentuates the emotional connection to the experience. As noted above (point 3 of the theoretical framework), theory behind insight includes the experience of positive affect as a key component of the occurrence. This positive emotional experience is considered by many as definitive, or at least a clear characteristic, of insightful problem-solving and today serves as the best behavioral indicator to tease out problem-solving that involves sudden insight or an epiphany from other forms of problem-solving (Shen et al. 2015).

### **Why Is Problem-Solving So Emotional?**

From an evolutionary perspective, it makes sense that problem-solving should be emotionally rewarding as the positive emotional response (intense feelings around achievement) should help to solidify memories of the process and/or solution. In this sense, problem-solving achievements should evoke an immediate positive affective state in animals as a means to motivate them to explore, solve problems, and gain insights about their environments, even if the true benefit of these behaviors is in the long term (just as play serves as training for the unexpected). Studies of insight in humans demonstrate that better recall of information results when the solving of problems involves an “Aha!” moment where the solution suddenly comes to the subject by their own accord. This is evidenced through numerous studies examining insightful problem-solving where subjects were presented with a wide range of problems including everything from word problems involving sentence comprehension (e.g., Auble et al. 1979) to video clips of magic tricks (e.g., Danek et al. 2013) and those subjects who reported a positive affective feeling of achievement when they solved the problem through insight had better recall of the information than those subjects who were provided some clues toward the solution and solved the problem through reason or trial and error. Thus, it seems

that the positive feeling associated with the mind’s process of moving concepts from incomprehensible to comprehensible facilitates better recall. In fact, there is ample evidence to suggest that recall is greater for solutions that are generated by an individual versus solutions that are presented to them. In terms of the Eureka Effect in dogs described by McGowan et al. (2014), dogs who were acting as experimental animals, and had the opportunity to realize the connection between their actions and a reward, seemed to better remember the task at hand and be more eager to re-enter the test arena than when acting as control animals. Hence, there may be a memory advantage when individuals are able to produce an answer themselves. This concept is further supported by the fact that dopamine release within the brain has been implemented in the process by which learnings are permanently stored (Bethus et al. 2010; Chowdhury et al. 2012). Thus, it makes sense that animals should react emotionally to their own achievements during problem-solving tasks as, to some degree, heightened states of positive emotion can facilitate learning and memory. Just like for humans other animals can experience cognitive bias, where one’s underlying emotional state can influence one’s cognitive processing of even ambiguous stimuli (Mendl et al. 2009). These ideas come to life on a daily basis when humans are interacting with and training animals. In general animals are much more responsive to positive training that is done in a very playful and rewarding way than they are to negative training techniques. Positive affective feelings around problem-solving may help animals to better identify behaviors that are biologically useful, encourage animals to carry out these behaviors to their benefit in the long term, and help to cement memories around the insights learned through problem-solving.

### **Eureka! In a Nutshell**

There is more to problem-solving than facts, skills, and meeting basic needs; problem-solving has an emotional side and the realization of one’s own achievements elicits positive affective states.

The surge of positive emotions occurring specifically during the moment of understanding, the “Aha!” moment, is a powerful motivator. Given the association between realization of achievement and positive emotions, it may be that opportunities to solve problems, make decisions, and exercise cognitive skills are key to emotional well-being in humans and animals alike.

## Cross-References

- [Innovation](#)
- [Insight](#)
- [Insight in Pigeons](#)
- [Insight in Rats](#)
- [Problem-Solving](#)
- [Serendipity](#)

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## Evasion

- [Zigzag Display](#)

## Eve gene

- [Mitochondrial DNA](#)

## Even-Toed Ungulate Biology

- [Artiodactyla Life History](#)

## Even-Toed Ungulate Locomotion

- [Artiodactyla Locomotion](#)

## Even-Toed Ungulates

- [Artiodactyla Diet](#)
- [Artiodactyla Morphology](#)
- [Artiodactyla Navigation](#)

## Event-Related Potentials (ERPs)

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### Definition

Event-related potentials, or ERPs, are the resulting of average the *EEG* signal (see ► “*EEG*,” this volume) locked to a specific event. Therefore, the main function of ERPs is to *study* the brain activity that is elicited because of that event, while it is discarded, the brain activity elicited for everything else. The event under analysis typically is the perception of a stimulus (e.g., an image or sound) (e.g., Thorpe et al. 1996), or the emission of an overt response (e.g., Gehring et al. 1993), although the *EEG* signal can be locked to covert (internal) responses as, for instance, inner speech (Ford and Mathalon 2004).

### Advantages and Disadvantages of the ERPs Technique

Because ERPs are generated from the *EEG* signal, the use of ERPs has the same advantages and disadvantages described for the *EEG* test (see ► “*EEG*,” this volume). In brief, *EEG* is good for studying cortical brain activity with great temporal resolution and is noninvasive and inexpensive. On the other hand, the most important disadvantages of using *EEG* are its poor spatial resolution and that it is not appropriate for studying subcortical brain areas.

We might add another drawback for the ERPs technique. ERPs work under the assumption that the *EEG* signal locked to an event contains both a “true” signal from the brain and some degree of noise. The noise is not elicited because of the event and therefore should take different values each time that the event takes place. Therefore, given a sufficient number of repetitions of the event or *trials*, the average data from all these trials should reflect only *event-related* true signal,

since recordings of noise should cancel each other. The number of event repetitions that you need in order to wipe out all the noise depends on the signal/noise ratio. In most of the cases, the number of event repetitions needed for proper ERPs analysis is relatively high, although it depends on the *components* under study (see below). Consequently, ERPs experiments are usually very long and need many trials. This makes the ERPs technique hard to use for the study of some topics. That is the case, for example, if you are interested in the brain activity associated with the first learning episode of some specific content (you can only learn something for the first time once, although see Luque et al. 2012).

An important advantage of using ERPs is that you can use it for studying *covert* events. That is, you do not need overt responses to register your dependent variable. This feature, plus the great temporal resolution of *EEG*, makes ERPs a great tool for studying the first stages of perceptual/attentional processing (Luck et al. 2000).

### Components

ERPs signal, after the averaging process described before, takes the form of a sequence of positive and negative deflections in voltage. Importantly, this sequence is usually the same for events of the same type (visual events, overt responses, etc.). These deflections are usually called peaks, waves, or *components*. ERPs components were named depending on whether the peak is positive or negative and reflecting the approximate latency of the peak (from the onset of the event). For instance, the N200 component stands for a negative wave (hence the *N*) with its maximal amplitude (peak) at 200 ms after the onset of the event. The latency of each component is only approximate, what makes components’ names sometimes confusing (it is not rare to find a P300 component peaking at 500 ms). To make things more complicated, sometimes the ordinal position of the component in the sequence of peaks is used to name the component, instead of the latency in milliseconds (e.g., P3 would be the third positive peak).

Numerous ERPs studies have investigated the psychological meaning of these components, with variable success. In general, there is agreement that early components (peaking sooner than 200 ms) are easier to relate with underlying psychological processes. For instance, the P1 and N1 components reflect rapid deployment of attention and the first stages of perceptual processing (Hillyard and Anllo-Vento 1998).

The more important ERPs components in cognitive neuroscience are (among others) the aforementioned P1 and N1, the N2 and the mismatch negativity (which might reflect the detection of a perceptual deviant), the P3 (which has been related with working memory), and the N400 (elicited by semantically incongruent stimuli) (for more information, see Luck and Kappenman 2011).

## Cross-References

► EEG

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## Evoked Response Potentials

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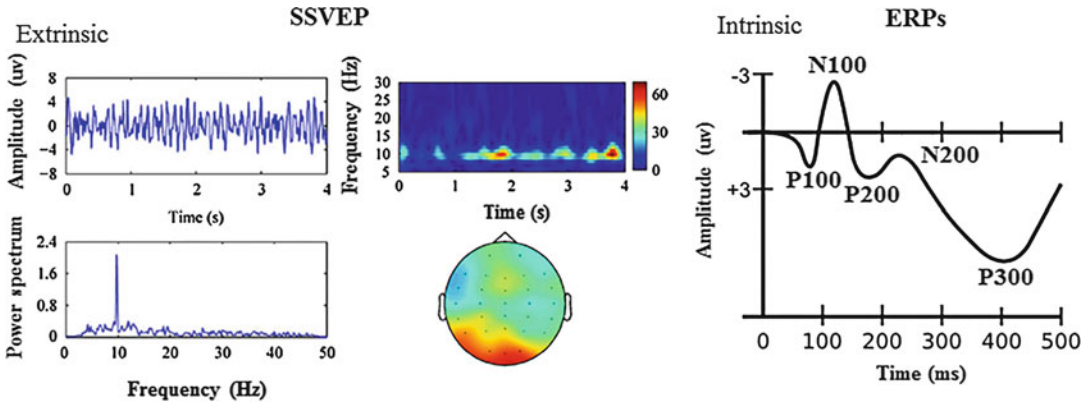
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Evoked potentials (EPs) or evoked responses are electrical potentials recorded from a human (or an animal) of the nervous system following presentation of a specific variety of stimuli (visual, auditory, somatosensory), as distinct from spontaneous potentials as detected by electroencephalography (EEG), magnetoencephalography (MEG), electromyography (EMG), or other electrophysiologic recording methods.

Stimuli are characterized by intensity (strength of stimulus), duration (length of stimulus), rate (number of times a stimulus is administered), and repetitions/sweeps (number of stimuli presented to). Evoked potentials are characterized by amplitude, polarity, inter-peak, latency, and morphology (see Fig. 1).

In this session, we focused on the EPs which were recorded by EEG. The EPs are too weak to be seen directly in EEG signals, which are always submerged in noises and ongoing activity of the brain (Misulis and Fakhoury 2001). We employ multiple responses averaged to extract the signal from noise and randomly generated brain activities. In other words, we extract responses to time-locked to stimulus from ongoing background activity (noise and random activities of the brain).

There are mainly three kinds of evoked potentials: steady-state evoked potentials, sensory evoked potentials, and motor evoked potentials.



**Evoked Response Potentials, Fig. 1** EPs

## Steady-State Evoked Potentials

Steady-state evoked potential (SSEP) can be steady-state visual evoked potential or steady-state somatosensory evoke potential, which could be evoked by flicking lights or vibratory stimulation with a certain frequency. The amplitude and phase of the frequency components of SSEP are approximately constant over time. The SSEP-based brain-computer interface (BCI) was presented based on this phenomenon. Steady-state visual evoked potential (SSVEP)-based BCI was firstly presented by Vidal in 1973 (Vidal 1973), which was improved significantly in information transfer rate (Chen et al. 2015) recently. The SSVEP-based BCI could be further improved by combining with other brain patterns. Wang et al. presented a new SSVEP and P300 hybrid BCI system to enlarge the user group. In this system, SSVEP and P300 stimuli would not affect each other (Wang et al. 2015). Steady-state somatosensory evoked potential (SSSEP)-based BCI was implemented for the patients who have weak vision or who cannot control their eye movements. Compared to the SSVEP-based BCI, this BCI system provides lower fatigue and is less annoying. However, the classification accuracy and information transfer rate of SSSEP-based BCI are considerably lower compared to the SSVEP-based BCI.

## Sensory Evoked Potentials

Sensory evoked potentials are usually evoked by visual, audio, and tactile stimuli, which are widely used in clinical diagnostic medicine and intraoperative neurophysiology monitoring. Since sensory evoked potentials can be reliably and stably induced and recognized with classification machine learning methods, they are widely used in brain-computer interface to help disabled patients.

### Visual Evoked Potentials

The first work that applied visual evoked potential (VEP) to BCI system was presented by Farwell and Donchin who used a stimuli matrix of letters or graphical symbols to evoke brain potentials for a speller system (Farwell and Donchin 1988). Recently, VEP-based BCI system has been considerably improved by color stimulus, moving stimulus, face stimulus, and other carefully designed smart stimulus. In 2016, a speller system based on VEP with the relatively high information transfer rate was presented by Townsend and Platsko (2016).

### Auditory Evoked Potentials

Auditory evoked potentials (AEPs) are generated in the cochlea and goes through the cochlear nerve, through the cochlear nucleus, superior olivary complex, and lateral lemniscus, to the



inferior colliculus in the midbrain, onto the medial geniculate body, and finally to the cortex. The patients who have weak vision or who cannot control their eye movements but keep audition could not use visual-based BCI system; however, the audio-based BCI system using AEP could be adopted by them. Hill et al. (2004) presented one of the earliest AEP-based BCI system (Hill et al. 2004). Recently, many studies have been performed to increase the targets and information transfer rate and to develop user-friendly AEP-based BCI systems.

### Somatosensory Evoked Potentials

Somatosensory evoked potential (SEP) is usually evoked by tactile and vibratory stimulus. Brouwer and Van Erp (2010) presented the SEP-based BCI which have some advantage over the visual or auditory systems (Brouwer and Van Erp 2010). This kind of BCI system was applied to the ALS patients with visual/auditory impairment and the stroke patients for recovery of somatosensory function. Recently, it was used for consciousness detection in disorders of consciousness (DOC) patients.

For example, auditory brain stem *evoked* response or *potential* (ABER or ABEP), as very small EP in response to a complex auditory stimulus which contains a range of frequencies. Somatosensory *evoked* response or *potential* (SSER or SSEP), occurs when the nervous system is stimulated by electrical pulses and vibrations.

### Motor Evoked Potentials

Motor evoked potentials (MEPs) could be induced by transcranial magnetic stimulation (TMS), which has been widely used in experiments in cognitive neuroscience. They offer a quantitative way to test the role of various types of intervention on the motor system (pharmacological, behavioral, lesion, etc.) because of the correlation between MEP amplitude and motor excitability. MEPs have not been used in brain-computer interface directly; however, it

was used to assess the treatment function of brain-computer interface.

In summary, evoked potentials are widely used for understanding the relationships between physical stimuli, brain activity, and human cognition. Brain-computer interface is used to build a new bridge between human brain and computer through recognizing the brain activities related to specific stimuli (Jin et al. 2015). Evoked potentials could be evoked by visual, audio, electrical, and tactile stimuli, which are widely used in the BCI systems by designing the stimuli characteristics and sequences according to a special code (Jin et al. 2013). The study of EPs will bring new pathways to improve the BCI systems.

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## Evolution

- ▶ [Adaptation](#)
- ▶ [Fisher](#)
- ▶ [Hominoidea Morphology](#)

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## Evolution of Animal Color Vision

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### Introduction

How and why do we see color? Isaac Newton's early studies of light provided a fundamental insight into the "how" question. His observations implied that color is not an inherent property of light or objects, but rather represents a perceptual experience resulting from the effects of light on an active visual system. In his words, "the Rays, to speak properly, are not Coloured. In them there is nothing else than a certain power and disposition to stir up a sensation of this or that Colour" (Newton 1730). Much of the scientific study of color since Newton's time consists of behavioral and biological experiments designed to reveal the nature of the linkages between the characteristics of light reaching the eye and the biological changes and visual experiences that ensue. Significant progress has also been made toward understanding the manner in which color vision may have evolved, thus beginning to illuminate the

"why" question. That process has been facilitated by recent discoveries about visual system biology, and by an expansion of knowledge about the nature and distribution of color vision across a broad range of animal species (Cronin et al. 2014; Kelber and Jacobs 2016).

### Definition of Color Vision

Color is an intimate feature of human experience so it is natural to talk about it using the richly descriptive language of everyday life. The scientific study of color vision, however, requires precise definitions. Fundamentally, light reaching the eye of a viewer from various locations in visual space can vary in its distribution of spectral energies (wavelength variation) and in its total photon flux (intensity). The presence of a capacity to see color – color vision – is formally defined as the ability of a viewer to discriminate variations in wavelength content irrespective of variations in intensity (Wyszecki and Stiles 1982). From a practical point of view this means, for example, that objects differing only in the wavelengths they reflect to the eye must remain fully discriminable irrespective of their relative intensities. Note this definition carries with it an implication about the underlying biology: visual systems capable of supporting color vision must contain an organization that allows some disambiguation of the effects of variations in the intensity and wavelength of light. Beyond this simple criterion for establishing the presence of color vision, many more derived features of color vision can and have been extensively studied.

### Dimensionality of Color Vision and Its Biology

The observations that Newton made on color mixing – the appearances produced by the superimposition of lights having different spectral contents – yielded another fundamental discovery. He found that additive mixtures of various spectral lights (called primaries) produced colors that often differed dramatically in appearance from

that of the primaries themselves. He further showed that results obtained from a variety of combinations of such lights could be economically summarized by plotting them on a circular surface where the primaries are located around the circumference of the circle and the perceptual results of the mixtures then positioned within; the latter falling along straight lines that interconnect the various mixture components. A critical point of this demonstration is that the same perceived color can be produced through the mixture of different primary lights. That fact implies that color vision must have a limited dimensional quality. A century later, Herman von Helmholtz and others expanded color-mixing experiments and found that various mixtures of only three appropriately-chosen primaries are sufficient to match in appearance all other spectral lights so normal human color vision must be three dimensional, i.e., it is *trichromatic*.

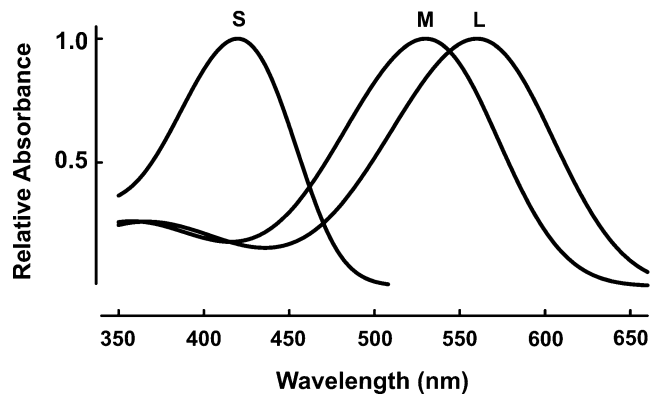
The simplest explanation for the trichromacy of normal humans was that there must be a visual system organization that supports a three-way sorting of light-elicited signals. Although there was much theorizing about the nature of such a mechanism, it was not until about 1960 that it became technically possible to show that there are three separate classes of photopigments located in the cone receptors of the human retina. The absorption properties of these three photopigments are sketched in Fig. 1. In such plots, the height of the curve represents the relative probability that light will be absorbed as a function of the wavelength of the stimulating light.

Those absorption events produce an electrical signal in the photoreceptor that is proportional in size to the total amount of absorbed light, independent of the wavelengths of that light. The result is that stimulating the eye with light generates a neural response that is distributed across the three types of cone in accord with the spectral distribution of the incoming light. The outputs from these three are then compared and contrasted in the neural networks of the visual system so as to yield the complete palate of visual percepts, including those features that we describe as colored.

Progress toward understanding the biology of color vision also emerged from another early discovery: within human populations there are some individuals whose color vision differs dramatically from that of most others. Although commonly referred to as being “color blind,” such individuals are better described as having defective color vision. Prominent among them are those who in the basic color matching task are able to match all other spectral stimuli using only two primary lights. Accordingly, their color vision is two-dimensional rather than three-dimensional and they are therefore considered to be *dichromats*. When it became possible to examine their cone photopigments directly, it was discovered that they possess two rather than three types of cone pigment, thus affirming the idea that the dimensionality of human color vision seems tightly linked to the number of cone pigment types. Dichromacy varies in nature among color defectives depending on which of the three types of cone pigment (S, M, or L) is missing. In

# Evolution of Animal Color Vision,

**Fig. 1** Absorption curves for the three cone photopigments found in the human retina. S, M, and L are shorthand designations used to indicate short-wavelength, middle-wavelength, and long-wavelength sensitive photopigments



addition, there are still other color defectives that require three primaries to complete the color matching task, but to do so they select aberrant proportions of the three. Such people are trichromatic, but since they differ significantly from the normal, they are described as being *anomalous trichromats*. Measurements of their cone pigments show that they indeed have three types, but that the spectral positioning of their pigments along the wavelength axis is different from those with normal color vision. Finally – and very rarely – there are individuals who lack color vision completely; they are truly color blind. In a color matching task they can match the appearance of any spectral light with the light from only a single primary and so are classified as being *monochromatic*. The underlying biology of monochromatic color vision includes some complicated individual variations, but in most cases there is only a single active photopigment.

Another long-established fact is that color-defective vision is inherited as a sex-linked trait such that those affected are predominantly male. The total incidence of defective color vision in the population is significant – somewhere around 8% of all males have a color vision defect. The condition is much rarer among females and that difference provided an early key to uncovering a basic feature of color vision biology.

## The Ubiquitous Opsins

Photopigments play a unique role in supporting color vision and thus an understanding of the evolution of color vision requires a little closer look at those remarkable devices.

All animal photopigment molecules consist of two linked components. One is a chromophore, an aldehyde of Vitamin A; the other a protein, opsin. Absorption of the energy from incoming light causes a structural alteration in the chromophore initiating a series of steps that result in an electrical signal from the photoreceptor. It had long been hypothesized that small variations in the structure of the photopigment molecule are responsible for the spectral positioning of their absorption functions, but verification awaited the

development of molecular biological techniques. In 1986, the genes that specify the three human cone opsins were first isolated and sequenced (Nathans et al. 1986). The results showed the structures of the cone photopigment genes are all greatly similar with only small changes in the primary structure of these genes being linked to differences in the absorption spectra of the three cone pigments. For example, only three amino acid substitutions in the cone opsins – out of a total of 365 amino acids – are sufficient to shift the spectral absorption curves across total range encompassed by the middle (M) and long (L) pigments of Fig. 1 (Neitz et al. 1991). This intimate coupling between gene alterations and the spectral properties of the photopigments means that mutational events must have played a critical role in shaping the evolution of color vision.

The opsin gene complements of hundreds of different animal species have now been documented and thus the links between the structure of these genes and photopigment absorption spectra are well established. A consequence is that genetic studies by themselves can yield an indication of the number of photopigment types an animal has and they can provide inferences about their spectral absorption properties. This in turn allows predictions about the nature of vision – including color vision – in animals which have not been otherwise studied. Such results also provide tools for generating hypotheses about the evolution of color vision.

## Opsin Histories

Opsins belong to a large family of proteins (G-protein coupled receptors, GPCRs) that collectively serve as cell-surface receptors whose functions are to detect external inputs and convert these into cellular signals. Comparisons of gene sequences have fostered significant advances in understanding the evolutionary history of opsins. It appears that the ancestral opsin evolved from GPCR precursors about 700 million years ago (Mya) (Feuda et al. 2012). Subsequent gene and whole genome duplications led to the emergence

of several opsin-gene families. Vertebrate and invertebrate visual opsins arose from two of these families (Lamb 2013).

The opsin gene that gave rise to the vertebrate visual opsins duplicated at a time close to the first appearance of vertebrates (~525 Mya). Shortly thereafter, four cone-opsin gene groups emerged. Representatives from these four (identified by the acronyms SWS1, SWS2, Rh2 and LWS) encompass all contemporary vertebrate cone opsins. A fifth group, Rh1, emerged somewhat later from a gene duplication in the SWS1 gene family. Rh1 specifies the photopigment opsins found in the other type of vertebrate photoreceptor, rods. Rods do not normally contribute to color vision. The spectral positioning of the photopigments associated with these opsins depends on the details of their amino acid sequences and on the identity of the chromophore to which these are bound. Photopigments are designated according to the spectral location of their peak sensitivity ( $\lambda_{\text{max}}$ ). For example, when conjoined to retinal-1, a common chromophore, the  $\lambda_{\text{max}}$  ranges covered by the vertebrate photopigments drawn from the cone-opsin groups are: SWS1 (355–440 nm), SWS2 (440–470 nm), Rh2 (480–530 nm), and LWS (500–565 nm).

Broad-scale comparisons of opsin gene sequences allow the construction of opsin-gene phylogenetic trees. One such tree for vertebrate opsins is shown in Fig. 2 where a small number of contemporary vertebrate species drawn from among all those that have been studied are shown to the right. The figure reinforces the point that all vertebrate cone photopigment opsins are representatives from four opsin-gene families. Another fact that emerges from analyses like this, as well as from direct measurements of photopigments, is that not all vertebrates derive opsins from each of the four cone opsin-gene families. Note, for example, that although chicken and zebrafish have opsin genes from all four families, frogs lack representation from the Rh2 gene family and the mouse has opsins from only two of the four (SWS1 and LWS). If all species derived only a single cone pigment from each of the gene families, that arrangement

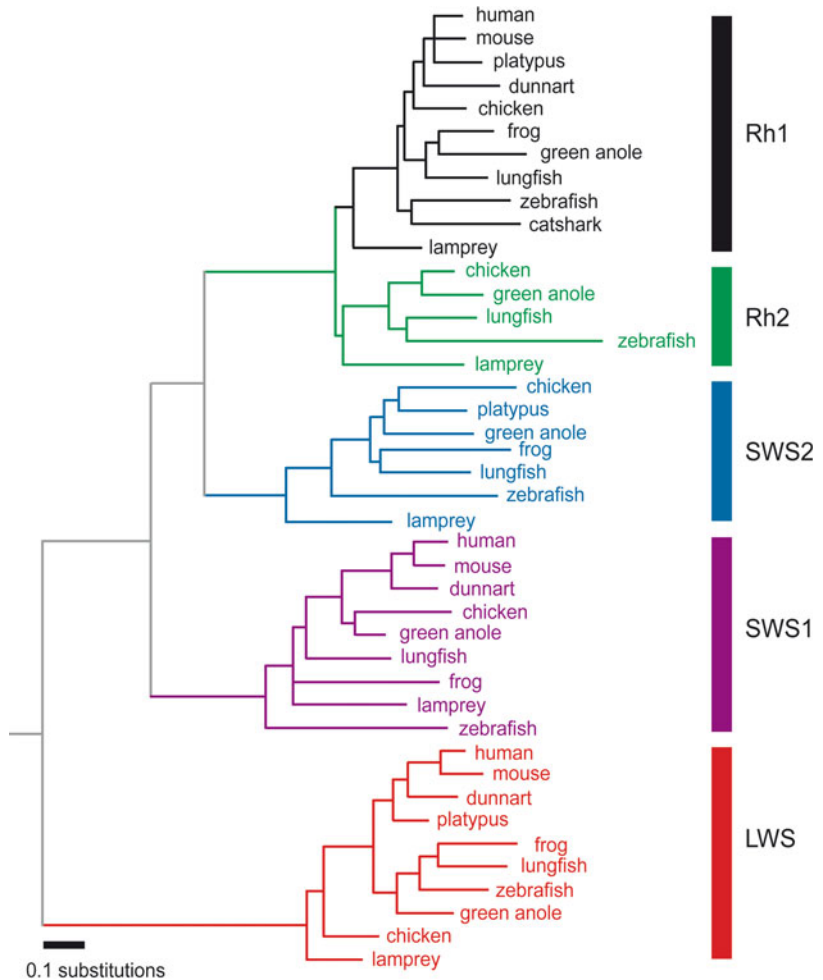
would predict that chicken and zebrafish have four different cone photopigments, whereas frogs have three, and the mouse only two. Although that inference can be the correct – in fact is for all of those named species – other animals may derive more than a single opsin gene (and a corresponding cone photopigment) from a single gene family. That is what has happened in humans who, thanks to an ancestral gene duplication event, have two separate opsin genes from the LWS family yielding the M and L pigments of Fig. 1. The converse has also happened such that a species may have an opsin gene that fails to express a functional photopigment. That occurred for example in the common hamster, a species whose genome contains opsin genes from both SWS1 and LWS families, but due to the presence of fatal mutations in the SWS1 opsin gene expresses only a single photopigment from the LWS family.

Principally because of the great disparity in their relative numbers, the evolution of invertebrate opsins is less well established than that for the vertebrates. Among the invertebrates, the opsins of arthropods have been the most thoroughly studied (Cronin and Porter 2014). In that group, the visual opsins also fall into four families that specify visual photopigments whose  $\lambda_{\text{max}}$  values occupy different spectral ranges. Many of these invertebrate species have highly diverse photopigment complements, some examples of which are given below.

The phylogenies derived for the opsin genes of different groups of animals reveal rich histories of gene addition and gene loss. These changes have been brought about through the classical mechanisms of gene mutation and gene duplication. These processes allowed various lineages to end up with greater or fewer than the number of genes that might be predicted from the presence of four gene families alone. Additionally, mutational changes in gene structure have served as a primary means to alter opsin spectral tuning and thus change the photopigment absorption properties. All of these events working in concert have fostered a rich range of possibilities on which natural selection operates to shape the complement of photopigments of a species.

# Evolution of Animal Color Vision,

**Fig. 2** Phylogeny of the five vertebrate opsin-gene families. The Rh2 genes specify opsins used for rod photopigments; the other four are for the cone opsin genes. See text for further details (Figure reprinted by permission from Kelber and Jacobs (2016))



## Multiple Functional Roles for Photopigment Signals

To appreciate how the number of photopigment types an animal possesses links to color vision requires understanding the varied roles that photopigment signals play in supporting vision. As noted, photopigments signal the total amount of light absorbed, irrespective of its wavelength. A single photopigment is thus blind to wavelength variation independent of intensity variation – as is required for color vision – and, consequently, an animal possessing only a single photopigment is by definition normally absent of all color vision. Among contemporary species numerous such animals exist; for example, some sharks, whales, mollusks, and deep sea fishes have only a single

photopigment and thus are without a capacity for ordinary color vision. Opsin phylogenies, such as that shown in Fig. 2, imply that ancestral animals acquired multiple types of photopigment at a time early in evolution. A consequence is that contemporary species without any color vision must have lost the potential for that capacity sometime during the evolution of their particular lineages.

The presence of two or more photopigments is usually a prerequisite for having a color vision capacity. But although necessary, the presence of two photopigments is not by itself sufficient to assure color vision. In order to generate signals that can be used to support color vision, the outputs from the two different types of photopigment must be compared in the nervous system. These comparisons occur through the actions of



chromatic-opponent neurons in the visual system that effectively subtract the two photopigment signals one from another (Jacobs 2014). The operation of these cells accomplishes a disentangling of wavelength- and intensity-related changes, thus satisfying the criterion for supporting color vision. Such comparisons made between the signals from two types of photopigment can support a single dimension of color vision (dichromacy). If the two signals are simply added together in the nervous system, these signals may support other visual behaviors but they cannot provide for a color-vision capacity.

Adding photopigments to the eye beyond the minimal two sets the stage for the presence of additional interactive comparisons between different pigment types and those changes serve to increase the dimensionality of color vision. In humans, for example, the presence of three types of cone photopigments allows an additional type of cone photopigment comparison and adds a dimension of color vision, making normal human color vision trichromatic. Adding still further cone pigments beyond three, and increasing the number of appropriate nervous system comparisons, can further increase dimensionality so animals could potentially become tetrachromatic, pentachromatic, etc.

The important point is that although knowing the number of photopigment types an animal possesses can provide predictions about the limits of color vision, that information is not, by itself, a necessarily reliable indicator of the nature of its color vision. To fully understand the nature of an animal's color vision requires results from appropriate behavioral tests.

## Evolution, Photopigments, and Color Vision

There is a large literature covering various aspects of visual photopigments, photopigment evolution, and animal color vision (Briscoe and Chittka 2001; Kelber et al. 2003; Jacobs 2012; Kelber and Jacobs 2016). Although there are still major gaps in our understanding of these topics individually, as well as to how each may interrelate to the

others, several organizational themes can be discerned.

1. *Photopigment evolution and color vision established.* For a number of species, the dimensionalities of their color vision and its evolution have been reasonably well established. Mammals, considered separately below, fall into this group. Among other vertebrates, the opsin gene phylogeny of Fig. 2 shows that a representative bird (chicken), fish (zebrafish), and reptile (green anole) all inherited visual opsin genes from each of the four cone opsin families. That is also the case for many other representatives of each of these three groups of animals. An arrangement like this provides such animals with a total of four cone photopigments. Although there are significant variations in the spectral positioning of these pigments across species, as well as in other features of their visual systems, this arrangement can support tetrachromatic color vision. Actual color vision tests on such species have been relatively infrequent, but in the several instances where these tests have been performed tetrachromacy was in fact established. Well-known examples of tetrachromats in these groups include chickens, pigeons, parrots, goldfish, and turtles.

A number of insects have opsins from three gene families providing the potential for eyes that contain three photopigments and support trichromatic color vision. One such case where trichromacy has long been established is that of the honeybee (Hempel de Ibarra et al. 2014). The three photopigments underlying honeybee trichromacy are all significantly shifted toward the shorter wavelengths, allowing honeybee color vision to extend well down into the ultraviolet wavelengths, a portion of the spectrum invisible to the human eye.

2. *Photopigment swapping.* A recent discovery is that the opsin gene arrays of some animals allow for the production of more types of photopigments than are actually expressed in the eye at any given time. The best examples come from studies of cichlids – small, colorful fishes that inhabit the Rift Lakes of East Africa

(Carleton 2014). As a result of earlier gene duplications, cichlids derive a total of seven distinct cone-opsin genes from the four vertebrate-opsin gene families. Yet only three of these genes are expressed in the retina at any given time. These three can vary across species and also may change in individual animals as a function of their stage of development or in response to the details of the local photic environment. Although thus apparently being limited to having trichromatic color vision, the nature of the trichromacy in these fish shows considerable plasticity. Similar opsin gene/photopigment swapping arrangements seem likely to be more common than is currently appreciated.

3. *Photopigments for specific occasions.* The genomes of some invertebrates have been found to contain significant numbers of different visual opsin genes. This allows the eyes of such animals to contain photoreceptors that feature multiple combinations of photopigments. In some cases, there may be 15 or more such receptor arrangements. The roles played by all of these photopigments often remain unknown, but in some cases the signals derived from these receptors have been shown to support a variety of highly specific behaviors. For example, the eyes of the Japanese yellow swallowtail butterfly contain eight different photoreceptor arrangements (Koshitaka et al. 2008). The outputs from four of these photoreceptor types are used to provide general-purpose tetrachromatic color vision. In addition, signals derived from some of the receptors, taken either singly or in various combinations, are used to trigger stereotyped species-specific behaviors. For example, in many butterflies egg laying on a surface is preferentially triggered in the presence of some spectral lights (typically greenish in appearance to humans), but not in other illuminations. These are usually categorized as being “wavelength-specific” behaviors and they constitute a kind of hard-wired color vision that is distinct from the color vision capacities supported by dimensional color vision (Kelber and Osorio 2010). Wavelength-

specific behaviors are common among invertebrates.

4. *Special case of mammals.* Mammals are special, not just because that is our class, but also because there is a plausible scenario for the evolution of mammalian color vision (Jacobs 2009). Mammals first emerged ~200 Mya. Like other vertebrates, the earliest mammals had representation from all four opsin gene families and thus likely had photopigment arrays sufficient to support color vision, potentially a tetrachromacy. The subsequent evolution of mammalian opsin genes is mostly a story of loss. The timing of most losses is traced to the long period during which mammals were principally nocturnal (from ~200 to 150 Mya), a circumstance where the predominant visual environments (dim to dark) would not have been well served by elaborate color vision capacities. The Rh2 gene family disappeared prior to the divergence of three mammalian subclasses (monotremes, marsupials, eutherians) such that the crown mammal probably had three cone opsin genes with a potential for trichromacy. Subsequently, SWS1 representation disappeared in the monotremes, while SWS2 genes were lost in both marsupial and eutherian lines. A consequence of these losses is that, unlike other vertebrates, the opsins of all contemporary mammals are from only two gene families. Another early event of significance for color vision is that opsin genes of the LWS family were translocated from an autosome to the X chromosome in both marsupials and eutherians. That evolutionary step explains why human color defectives are mostly males.

Eutherians make up most (~94%) of contemporary mammals and with the exception of the primates all these species are limited to having two active opsin genes (from SWS1 and LWS gene families, respectively.) That arrangement predicts that if color vision is present at all, it should be a dichromacy. To the extent that good behavioral evaluations exist that seems to be true. At the same time, many contemporary mammals are either nocturnal or crepuscular and thus

probably enjoy only a limited color vision capacity (Jacobs 2010).

Color vision in primates is unique among that of the mammals. Although many primates acquired a third cone pigment and with it trichromatic color vision, others have two cone pigments and dichromatic color vision (Jacobs 2008). Old World primates (humans, apes and monkeys) added a second LWS gene on their X chromosomes from an early (30–35 Mya) gene duplication and it is normal for such animals to have trichromatic color vision. New World monkeys are different, having polymorphic X-chromosome LWS genes. This arrangement allows those females who are heterozygous at the X-chromosome opsin-gene site to gain two middle-to-long wavelength cone pigments and enjoy trichromatic color vision while males having a single X-chromosome are uniformly dichromatic. There are some notable exceptions to these two basic arrangements, including those nocturnal primates that have only a single LWS photopigment and a nonfunctional SWS1 opsin gene and so lack color vision.

### Utility of Color Vision

A complete account of the evolution of color vision requires both documentation of heritable changes in visual systems that support new capacities and details about how such capacities have yielded adaptive advantages and thus have been maintained in the population.

Over the years, there has been much speculation about the roles that color vision might play in supporting behavior. Two general approaches are currently being used to examine the utility of color vision. One is basically computational, employing detailed measurements of individual photic environment as inputs to models of how visual systems process color signals. The outcomes from variations in model parameters, for example, the spectral positioning of the recipient photopigments, can then be evaluated to see how well the model system performs and from the results determine what arrangements seem most advantageous to support particular visual needs. The

second approach is behavioral, involving either the direct observations of animals as they deal with potential color signals in their environments (for example, as an aid in the harvesting of fruit) or the testing of animals in contrived experimental settings to see how well they perform in the presence of carefully supplied color cues. A particularly useful variant of such behavioral techniques involves comparisons of the performances of individuals of the same species that differ in their color vision, e. g., dichromatic and trichromatic conspecifics such as that seen in the New World monkeys. To date these two approaches are only just beginning to reveal information about the utility of color vision, but it seems likely that they will eventually make major contributions to our further understanding of the evolution of color vision (Jacobs 2015).

### Cross-References

- [Genes](#)
- [Mutations](#)
- [Photoreceptors](#)
- [Polymorphic](#)
- [Visual Perception](#)
- [X-linked Trait](#)

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## Evolution of Sex

### ► DNA Repair Hypothesis

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## Evolutionarily Relevant Stimuli

### ► Naturalistic Stimuli

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## Evolutionarily Stable Strategies

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## Definitions

- *Strategy*: set of (behavioral) phenotypes or decision rules having evolved under natural selection.
- *Evolutionarily stable strategy*: strategy that, when resident (i.e., adopted by most members a population), cannot be invaded by an initially rare alternative strategy (also referred to as mutant).
- *Darwinian fitness*: expected reproductive contribution to future generations.
- *Frequency dependence*: dependence of the fitness payoffs of a strategy on the frequency of the other strategies in a population.

## Introduction

The concept of evolutionary stable strategy (ESS) is an essential part of the behavioral ecologist's toolbox. It belongs to the general field of game theory, which is extensively used to describe and analyze the evolution and the maintenance of (behavioral) phenotypes in a population. Such formal analysis is particularly relevant due to the complex interdependence between the members of a population. The adaptive value of a behavior can rarely be assessed on its own merit irrespective of the behaviors of the individuals from the rest of the population. For instance, the

efficiency of a fighting technique could depend upon its scarcity. While left-handedness does not provide intrinsic mechanical or cognitive benefits in noninteractive sports, being a rare left-handed opponent offers a strategical advantage in many sports involving direct interaction between players as in combat sports, tennis, or cricket (Llaurens et al. 2009). This could be explained by a surprise effect, their opponents being more accustomed to practicing against right-handed players. Consequently, left-handed players are overrepresented in these sports compared to their proportion in the general population. Their frequency increases until their opponents have enough opportunities to be accustomed to their playing style. The proportion of left-handed and right-handed players reaches an equilibrium characterized by the fact that no handedness is advantageous compared to the other.

Such cases of frequency dependence are ubiquitous in nature. For instance, in *Perissodus microlepis*, a small cichlid fish from Lake Tanganyika which feeds on scales of other fish, some individuals are specialized in attacking their prey from the left side, while other are specialized on the right side. The proportions of these two strategies oscillate around 50%. The rarer morph temporarily benefits from lower vigilance by their prey which is more often attacked on the other side by the more abundant morph (Hori 1993). Frequency dependence is not restricted to discrete strategies; it is also relevant for continuous strategies such as the level of selectivity during mate choice. Even when the individuals gain direct benefits from pairing with the highest quality partners, the evolution does not necessarily lead to very selective strategies. Being picky would theoretically allow a female to find a high-quality male if she was the only chooser in the population. But if there are other females competing for the same pool of males, the female would be better accepting even a mediocre partner. A greedy female trying to outsmart her unselective competitors by increasing her choosiness exposes herself to the risk of losing the mate race, all the males being progressively removed from the

pool of potential partners by less selective females while she is unsuccessfully searching for her ideal, yet no longer available, male (Dechaume-Moncharmont et al. 2016). The average partner quality that a female can expect when following a given decision rule cannot be calculated as an absolute value. It is strongly dependent upon the frequency of the other strategies in the population through the background distribution of the remaining male's quality. Searching for the optimal sampling strategy of a given individual thus requires to explicitly consider the behaviors of its competitors.

## Nash Equilibrium

The kind of problems described above, with complex interdependent decision-making, belongs to the general field of game theory, which started to attract considerable attention from mathematicians and economists when von Neumann and Morgenstern's published their seminal book *Theory of Games and Economic Behavior* (1944). Among the family of game theory, one is particularly relevant in biology, the noncooperative game in which the players are not assumed a priori to cooperate or to form binding agreements. The cooperation between the players can emerge from such games as a consequence of the interaction but not as a prerequisite. The central assumption is that the players act rationally and try to maximize their payoffs. The difficulty is to find the possible outcomes from the interactions between the players. A decisive result has been formulated by John Nash (1950), which earned him the Nobel Prize in Economics in 1994. He characterized the solution of a noncooperative game as an equilibrium, which is now referred to as "Nash equilibrium." He gave a very concise definition of this concept which can be summarized as: an equilibrium point is reached when the strategy of the players cannot be strictly outperformed by another strategy. In other words, no player would be tempted to switch strategies because he would not increase his payoffs by unilaterally deviating from the equilibrium point.



## Evolutionary Game Theory

A very strong assumption of the classical game theory is that each player acts rationally, which means that they purposely behave in order to maximize a criterion of self-interest. Yet, the existence of rational decision-making has been challenged many times in experimental psychology. The ecologists considered the problem from a completely different perspective than the economists or the psychologists. William Hamilton and Robert Trivers were among the first biologists to acknowledge the relevance of game theoretical framework in evolution, but the field of evolutionary game theory was founded by John Maynard Smith and George Price (1973). They introduced the concept of *evolutionarily stable strategy*, which is closely related to the Nash equilibrium. The key idea behind the concept of ESS is that the individual behaviors directly affect its Darwinian fitness, namely, its probability to survive, reproduce, and contribute to future generations. The best strategies lead to higher reproductive success, and thus, their frequency increases in the population across generations. On the contrary, the least efficient strategies are progressively washed away by the natural selection. This evolutionary perspective is an elegant way to escape the questionable assumption of perfect rationality in classic game theory, which assumes that agents are able of complex calculation to determine the appropriate action. Evolutionary game theory does not require any cognitive skills for the players. It is the natural selection itself which performs the decision-making procedure: strategies are favored provided they performed well in the environments in which they evolved. This hypothesis of *ecological rationality* is a decisive improvement because the process of natural selection is a clearly defined mechanism. The term strategy could even to be understood in a very broad sense as any set of phenotypes affecting the Darwinian fitness of the individual, as long as they are able of replication: they are heritable and can be transmitted to the next generation. Following that definition, plants, fungus, or microorganisms can perfectly adopt an ESS without any rational thinking. For instance, in bacteria, one can describe the probabilities to

cooperate with neighboring cells and contribute or not to the collective defense as strategies which can be analyzed in a game theoretical framework (Frey 2010).

The concept of ESS is grounded on the existence of mutation which randomly appears in the population. In the evolutionary biology jargon, a mutant is any alternative strategy challenging the resident strategy and trying to invade the population. A strategy is said to invade if, when rare, it does better than the prevailing strategy and so spreads in the population and become the new resident strategy. An ESS is characterized by its stability, i.e., its ability to resist the invasion by a mutant. This property can be formulated in mathematical terms (Maynard Smith, 1982). Write  $W(p, q)$  the fitness of a player following the strategy  $p$  in a population of players following the strategy  $q$ . If  $p$  is the ESS, no rare mutant strategy  $q$  can outcompete  $p$  when it is resident in the population:

$$W(p, p) \geq W(q, p), \text{ for all } q. \quad (1)$$

This first condition corresponds to the Nash equilibrium. It is, however, possible that the rare mutant strategy  $q$  does as well as the resident strategy:  $W(p, p) = W(q, p)$ . While it is not strictly favored by natural selection, the frequency of the mutant may increase by the neutral process of genetic drift. In other words, the average resident strategy in the population is likely to change. In such case, the Nash equilibrium condition verifying that the strategy  $p$  cannot be outperformed (Eq. 1) is not sufficient. To ensure its evolutionary stability, the ESS should also be able to invade other strategies:

$$\begin{aligned} &\text{if } W(p, p) = W(q, p), \\ &W(p, q) > W(q, q), \text{ for all } q \neq p. \end{aligned} \quad (2)$$

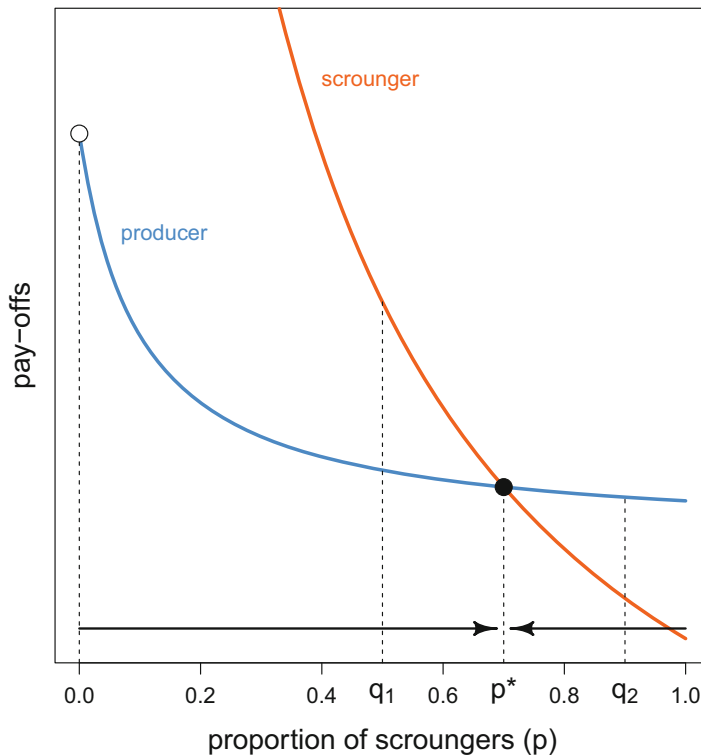
The only best response to an ESS is the ESS itself. Note also that the concept of ESS is more restrictive than the Nash equilibrium: every ESS is a Nash equilibrium, but all Nash equilibrium is not necessarily an ESS.



# Evolutionary Stable Strategy and Population Optimality

The concept of ESS has an important heuristic value in biology because it is a powerful argument against group selection as a major mechanism for the evolution of cooperation: most collectively optimal strategies are very fragile and highly unstable when confronted to selfish mutant strategies. To illustrate this point, one can consider the classical example of the producer-scrouter game (Giraldeau and Caraco 2000). In many species, the foraging strategy of the individuals can be categorized in two contrasted

behaviors: the producers actively search for food on their own, while the scroungers try to steal a portion of the food discovered by the producers. Consider a population with proportion  $p$  of scroungers, and  $1 - p$  of producers. The producers are bearing all the costs of active food searching. A scrounger takes advantage of the active food searching of the producers and thus negatively affects its foraging efficiency. The total amount of food per individual, which can be used as a proxy of the fitness payoffs, decreases as the proportion of scroungers increases (Fig. 1). The optimal situation at the group level (group optimum) that would



**Evolutionarily Stable Strategies, Fig. 1** The fitness payoffs of the producers and scroungers are frequency-dependent: they both decrease with  $p$  the proportion of scroungers in the population. The plot should be read vertically: a given state of the population corresponds to a given proportion of scroungers, which allows comparison on both fitness payoffs. For any proportion of scroungers  $q_1 < p^*$ , the scroungers have higher fitness payoffs, and their proportion should therefore increase over time. On the contrary, for any proportion  $q_2 > p^*$ , the producers have higher fitness payoffs, and thus,

$p$  decreases. The only evolutionary stable strategy (ESS) is the proportion  $p^*$ . Any mutant trying to deviate from this proportion will be counter-selected, and the population comes back to the stable point (solid circle). The “group optimum” (in that order), which maximizes the individual payoffs, corresponds to a population of pure producers  $p = 0$  (open circle), but it is an unstable optimum: a scrounger mutant would largely benefit from the producers’ efficiency to locate food and will therefore quickly invade the population up to the ESS point

maximize the payoffs for all the individuals is thus a pure population of producers ( $p = 0$ , open circle in Fig. 1), but it is not a stable state. Indeed, an individual which begins to play as a scrounger largely benefits from its rare behavior, and its expected fitness payoffs are much larger than those of the producers. Consequently, it will have a greater probability of contributing to the next generation, and its behavior quickly spreads in the population. The proportion of scroungers increases up to  $p^*$  (solid circle in Fig. 1) which is the ESS: any deviation from this proportion would be counter-selected. A remarkable feature of such a game is that the ESS (Fig. 1; solid circle) leads to much higher payoffs than the population optimal strategy (Fig. 1; open circle). Evolution does not necessarily comply with the general interest. This idea is very similar to the “tragedy of the commons” in economy (Hardin 1968).

## Future Directions

Since the seminal book by John Maynard Smith (1982), the concept of ESS is not only considered as a central concept in evolutionary biology, but it also attracted the attention of economists (Hammerstein and Hagen 2005; Weibull 1997). The field of evolutionary game theory has developed in many directions. The analysis described above essentially focused on the ESS because it is easier to analyze the equilibrium than the dynamical trajectories leading to the equilibrium. Yet, the ESS is essentially a question of stability around the equilibrium point: the population can both resist the invasion by mutants and move back to the ESS after a perturbation. But the definition of ESS does not guarantee that any potential ESS can evolve in the first place, i.e., when it is the rare mutant itself. The background environment might not be favorable enough to ensure its initial spread. This particular question is specifically addressed by the field of *adaptive dynamics* (Diekmann 2004; Waxman and Gavrillets 2005).

Another important concern about the concept of ESS is related to its heuristic value in animal behavior. Evolutionary game theory essentially

aims at proposing normative models about the outcome of complex interactions between agents and the resulting equilibrium strategy, with limited assumption about the underlying decision-making processes. It is a powerful mechanism to describe the evolution of phenotypes across generation, allowing the application of game theory analysis to any living organisms, regardless of their cognitive abilities, as long as they are submitted to the evolutionary processes of replication, mutation, and selection. It is a convenient way to escape the demanding assumption of classical game theory about the players' capacity to understand the rules of the interactions and to think rationally. It is however important to note that the evolutionary time scale is measured in a number of generations. In other words, the convergence toward the ESS is based on the very slow process of selection of the most efficient strategies across generations. This mechanism is not relevant for most behaviors of interest. The animals constantly make short-term adjustments of their behaviors in response to changes in the social context. These adjustments can occur through learning, reinforcement, trials and errors, copying, or cultural transmission. Superficially, these mechanisms appear consistent with the fundamental mechanisms at the very basis of the evolutionary game theory: if a new behavior (mutation) performs well (selection), it could be adopted by other members of the population (replication). But they also assume advance cognitive skills such as memory, ability to compare the frequency-dependent payoffs, learning, and behavioral flexibility. The apparently simple ecological mechanisms invoked in the definition of the ESS had led many behavioral ecologists to disregard the question of the underlying decision-making process. At most, they assumed that the underlying cognitive machinery itself should evolve by natural selection in order to generate behaviors close to the ESS. It is still an open question whether the limited learning skills allow the convergence toward strategies close to the ESS (Fawcett et al. 2013; Hagen et al. 2012). Even if the concept of ESS has an enormous interest as a normative model, it might be of very limited interest as a descriptive model

because it fails to encapsulate the underlying processes of decision-making. Hopefully, these mechanisms are currently the object of a growing interest in behavioral ecology (Fawcett et al. 2014), and this research could, in turn, spawn new development in game theory.

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## Evolutionary By-product

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## Synonyms

Spandrels

## Definition

Biological and psychological traits can have an adaptive function (i.e., adaptation) or appear as a (nonadaptive) by-product of another adaptation (i.e., spandrels or by-product).

## Evolutionary Psychology

Evolutionary approaches have become very popular in many areas of the behavioral and social sciences. Evolutionary psychology argues that

most human behaviors can be explained by internal psychological mechanisms and claims that the reason for these mechanisms to have emerged in our evolutionary past is to provide solutions to the adaptive problems our ancestors have faced. In other words, many of these psychological mechanisms exist because they provided a solution to problems related to survival and reproduction in the past. The main purpose of evolutionary psychology as a research program is to identify these psychological mechanisms directing behavior that are the product of evolutionary processes. What we mean by a psychological mechanism are mental capacities like the ability to acquire language, the ability to detect cheating, the tendency to make moral judgments, the tendency to learn about the fear of snakes, the ability to recognize relatives, the tendency to find certain characteristics of the opposite sex attractive, and the ability to identify others' cognitive and emotional states.

According to this view, human behavior is not a direct product of natural selection; instead, psychological mechanisms evolve as a result of natural selection (and other evolutionary processes) and behavior emerges as a result of an interaction between these mechanisms and environmental conditions. The brain is a kind of computer that has developed to collect inputs from the environment. Programs in the brain are adaptations. All of these adaptations may not be adaptive at present, but they were adapted to the environmental conditions in which our ancestors lived (Tooby and Cosmides 2005). In this sense, evolutionary psychology differs from cognitive psychology. While both address the importance of internal mechanisms in influencing behavior, evolutionary psychologists also focus on what ultimately explains these behaviors; that is, whether they contributed to the survival and reproductive success of our ancestors. Cognitive psychologists, on the other hand, are content with providing only proximal explanations of these behaviors.

A second assumption in evolutionary psychology is that the mind is modular. That is, different adaptations have emerged in humans to solve many different adaptive problems they encounter in the environmental conditions they evolved. Therefore, according to this point of view, the

mind should consist of many different modular mechanisms for solving specific problems rather than a single mechanism for solving general problems. In other words, just as there are different organs in the body having different functions, the mind may also consist of different adaptations of this kind.

In evolutionary psychology, there are two different levels of explanation. The first is the ultimate explanation that reveals the evolutionary roots of behavior (explains why and how it evolved) and reveals its underlying foundations. For example, the proposal that the reason language evolved is that it promotes interhuman cooperation is a kind of ultimate explanation. The proximate explanation, on the other hand, deals with elucidating the psychological and neurobiological underpinnings of that behavior. For example, the proposal that the reason we help our sibling is our emotional closeness to him/her is a kind of proximate explanation.

Although evolutionary psychology has been subjected to quite a bit of criticism from both philosophers and biologists to date (e.g., Buller 2005; Richardson 2007; for responses, see Hagen 2015; Confer et al. 2010), it has become quite popular in recent years. One of the reasons for its popularity is the theoretical developments in evolutionary biology, especially in the second half of the twentieth century. These developments include William Hamilton's idea of inclusive fitness and kin selection; George Williams's books that led to the drop of the idea of group selection off the map; Robert Trivers's reciprocal altruism, parental investment, and parent-offspring conflict theories; and game theory and the concept of evolutionarily stable strategy that John Maynard-Smith carried from economics to evolutionary biology. In addition to these advances in biology, evolutionary psychology has also gained tremendous popular support over the past 20 years. In addition to the theoretical developments listed above, Edward Wilson's *Sociobiology* book, which is an excellent synthesis of the evolutionary foundations of social behavior, and Richard Dawkins' book *The Selfish Gene* popularized all these ideas and presented them in a new perspective (Buss 2012).

## Adaptation and By-product

According to the adaptive view of the modern evolutionary approach based on Charles Darwin's theory of natural selection, biological features can have an adaptive function (i.e., adaptation) or appear as a by-product of another adaptation (i.e., spandrel or by-product). Although evolutionary by-products do not directly lead to adaptive advantage, they emerge as a derivative of another adaptation that leads to adaptive advantage. To give an example of by-products in this situation, the umbilical cord can be taken as a typical example of adaptation due to its function of allowing nutrient exchange between the placenta and the embryo. As far as we know, the belly button, which does not directly lead to adaptive advantage, is a by-product of another adaptation (i.e., umbilical cord) because everyone who has an umbilical cord has a belly button. This explains why, although not adaptive, by-products persist in the population for generations.

In addition to adaptations and by-products, there are individual differences that occur entirely by chance, as far as we know, which we will define as a random product. In other words, although the belly button appears in all members of the species, the shape of the belly button varies from person to person, and this can be defined as the accidental variation due to the by-product that does not have any adaptive function.

One of the main difficulties in evolutionary approaches is the process of deciding what is an adaptation and what is a by-product. Especially in the field of evolutionary psychology, this ambiguity is more tangible than in evolutionary biology because one of the preconditions to be able to call something an adaptation is that trait have a genetic basis. However, we have very limited knowledge about the genetic basis of many psychological processes and behaviors, because psychological behaviors are generally not affected by a single gene as they are complex structures, but are formed as a result of the interaction of many genes. This makes it difficult to identify the genetic origins of many psychological processes underlying behavior. Apart from having a genetic basis, adaptations should be seen in all members

of the species, except for those specific to gender. The fact that this feature is seen in all members is an important indicator that distinguishes adaptations from other features, as it is a direct reflection of the evolutionary process and gives species-specific functionality. The third criterion is that adaptations arise in the process of development and therefore do not have to be innate. Another important feature of adaptations is that it solves a problem in the past environment effectively and economically (see Schmitt and Pilcher 2004, for an in-depth discussion of the criteria to be used in identifying psychological adaptations).

## Adaptation or By-product?

In this final section, we will illustrate the adaptation-by-product debate on the basis of several proposed psychological mechanisms. It has been argued, for example, that religious belief is an adaptation that arises due to its promotion of intragroup cooperation through the fear of supernatural punishment (Johnson 2015). In other words, according to the adaptationist view of religion, religion provides a very effective solution to the problem of free-riding due to its reliance on belief in supernatural agents, which has the capacity to punish every moral transgressor by monitoring every human behavior. According to this view, often referred to as *the supernatural punishment hypothesis* (Johnson 2015), interindividual punishment involves a potential risk (e.g., the risk of retaliation), but belief in a supernatural observer who is always watching people and punishing norm violations, solves this evolutionary problem. Because when someone violates traditional moral norms, the idea of supernatural monitoring will encourage people to stay in line. Overall, according to this view, religion emerged as an adaptation as it fostered interpersonal cooperation.

However, an opposing view claims that religion emerged as a by-product of other adaptations (Boyer 2001). According to this view, there are certain evolved adaptive cognitive features and abilities in our mind which emerged as adaptation such as the ability to mentalize. As a by-product of

believing that other people have independent minds, belief in nonphysical supernatural agents has emerged. According to this idea, we can mentalize supernatural beings such as jinn, angels, and devils in our minds, just as we are aware that other human beings have mental states. When Gould and Lewontin (1979) first proposed the idea of evolutionary by-products (i.e., spandrels) in their famous article written in 1979, they claimed that it may not be a secondary feature. Instead, they claimed that a feature that emerges as a by-product could later come to have an adaptive function, often referred to as “exaptation.” According to this idea, even if religious belief has emerged as a by-product, it can be construed as an exaptation since it later gains an adaptive function and encourages cooperation among people.

One of the most popular disputes on adaptation/by-product distinction has taken place in the area of the evolution of language. Noam Chomsky has argued that language and universal language faculty emerged as a kind of by-product (Hauser et al. 2002). According to this view, language emerges as a kind of by-product of the development and complexity of the brain. However, a group led by Steven Pinker and Jack Jackendoff argue that Chomsky’s statement is not very convincing, and language can be an adaptation itself due to its various adaptive benefits (Pinker and Jackendoff 2005). According to this view, language has emerged as an adaptation on its own in terms of its functional solutions in issues such as low-risk punishment (i.e., gossip), interpersonal cooperation, and child-rearing. Therefore, it can be concluded that deciding what is an adaptation and what is a by-product is difficult, especially in evolutionary psychology.

The moral foundations theory (Haidt 2012), which led to a paradigmatic change in the field of moral psychology, also explains morality through evolved adaptations. According to the moral foundations theory, there are five different intuitive foundations (harm, justice, loyalty, authority, holiness), each of which has its own evolutionary function. The care/harm foundation is defined as the behavior shown by other group members to the weaker group member in need of

protection or care. The fairness/cheating, on the other hand, is the moral sensitivity that is required to ensure justice and maintain order within the group. The loyalty/betrayal has been defined as protecting the interests of the group without betrayal. The authority/subversion is defined as another moral sensitivity that is important for mammalian groups living a hierarchical social structures. Finally, the sanctity/degradation describes a moral sensitivity that is thought to have evolved due to a sensitivity to disgust. This alleged evolutionary adaptation, protecting the environment necessary for clean living in natural life and keeping group members away from diseases caused by microbes and bacteria, also affects the moral sensitivity of people. However, since the mechanisms proposed by evolutionary psychologists rarely meet the necessary criteria of identifying a trait as an adaptation, future empirical work, especially in genetics, are warranted to reach a clear conclusion.

## Cross-References

► [Adaptation](#)

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## Evolutionary Determinism

### ► Ultimate Causation

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## Evolutionary Ladder

### ► Scala Naturae

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## Evolutionary Psychology

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Evolutionary psychology is a discipline of psychology that examines psychological mechanisms from an evolutionary perspective. Some authors do not consider it to be a distinct branch of psychology, but rather a “theoretical lens that is currently informing all branches of psychology” (Buss 1998). The central aim of evolutionary psychologists is to identify which psychological traits

can be considered adaptations – functional products of natural or sexual selection in human evolution.

## History of Evolutionary Psychology

Evolutionary psychology, albeit relatively new as a scientific discipline, dates back to Charles Darwin. In his book *The Origin of Species* published in 1859, Darwin predicted that “psychology will be based on a new foundation, that of a necessary acquirement of each mental power and capacity by gradation” (Darwin 1859). As an academic discipline, evolutionary psychology developed on the basis of cognitive psychology and evolutionary biology, but its beginnings were also influenced by behavioral ecology, ethology, genetics, anthropology, paleoanthropology, and biology. More specifically, the evolutionary thinking in psychology was prompted by the animal behavior studies of Nikolaas Tinbergen, Konrad Lorenz, and Karl von Frisch in the 1930s and 1940s; William D. Hamilton’s research on inclusive fitness in the 1960s; Robert Trivers’s work on reciprocity and parental investment, and John Maynard Smith’s evolutionary game theory and introduction of the evolutionary stable strategy in the 1970s. Edward O. Wilson combined evolutionary theory with studies of animal behavior and sociality, earning his name as “the father of sociobiology.” Stemming from ethology, sociobiology was first defined as “a systematic study of the biological basis of all social behavior” (Wilson 1975). An additional branch that emerged from ethology is behavioral ecology, the focus of which was on the ecological and evolutionary basis of behavior. George Williams’ 1966 book *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* outlined a gene-centered view of evolution, later popularized by Richard Dawkins’s *The Selfish Gene*, published in 1976.

One of the first publications in which evolutionary concepts were shown to be applicable to humans is “The Evolution of Human Sexuality” by Donald Symons, published in 1979. Herein the author discusses how various aspects of human

sexual anatomy and behavior, such as ovulation, female orgasm, homosexuality, promiscuity and rape, are results of human evolutionary history and can be viewed as adaptive traits (Symons 1979). Despite some criticism, the book is by many considered the most important book on human sociobiology.

*The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, published in 1992 by Jerome H. Barkow, Leda Cosmides, and John Tooby is widely regarded as the foundational text of evolutionary psychology. This is an edited volume of commissioned, empirical research papers on topics such as cooperation, mating and sexual behavior, parental care, perception and language as adaptations, environmental aesthetics, intrapsychic processes, and cultural phenomena (Barkow et al. 1992). According to the authors, the goal of the publication was to introduce the field of evolutionary psychology to a wider scientific audience, as well as to clarify how this field will supply the necessary connection between evolutionary biology and complex social and cultural phenomena. Some of the most prominent evolutionary psychologists, such as Steven Pinker and David Buss, are among the 25 authors who have contributed to the book.

The publication includes an essay by Donald Symons entitled “On the use and misuse of Darwinism in the study of human behavior.” Using the examples of human reproductive strategies and sexual attractiveness, Symons pointed out that Darwin’s theory of evolution by natural selection only explains human behavior as well as it explains its adaptive value. From his point of view, the link between Darwinian theory and behavior is psychology, especially evolutionary psychology. One of the most influential parts of “The Adapted Mind” is the highly-cited essay by Tooby and Cosmides entitled “The psychological foundation of culture.” Herein the authors discuss the social sciences’ lack of progress, which they blame on these disciplines’ insufficient exploration and acceptance of their logical connections to the other sciences. The authors suggested an abandonment of the so-called Standard Social Science Model (SSSM) – a dominant paradigm in the social sciences during the twentieth century,

which they described as “the consensus view of the nature of social and cultural phenomena that has served for a century as the intellectual framework for the organization of psychology and the social sciences and the intellectual justification for their claims of autonomy from the rest of science” (p. 23). Instead, they argued that it should be replaced by a new framework, which they have named the “Integrated Causal Model” (ICM). They believed this would enable progress through acceptance and exploitation of the natural connections that exist among all branches of science.

As outlined in the essay, the SSSM is based on several assumptions, the majority of which are in opposition to the considerations of the ICM. For instance, the SSSM proposes that humans are, apart from the capacity to learn, born as “blank slates” (Hampton 2004). When they are born, infants lack complex adult behaviors, which are only acquired during the course of development, and are products of exposure to the cultural and social elements. Because the individuals are molded by these external sources, they are the creations of the social world. Ideas, values, behaviors, and even the complex emotions are cultural products and can only be explained by the social conditions. The ICM counterargument states that humans are born with numerous emotional, motivational, and cognitive adaptations. While the SSSM sees human brain as a “general purpose” computer, considering all mechanisms and processes of the human mind to be content-free and content-independent, the ICM argues that the brain is a collection of domain-specific modules. Domain specificity entails these modules being evolved to only solve problems in particular domains, which makes them unsuitable for solving problems of other domains.

According to the SSSM, genetic variation does not explain why many human behaviors are shared within groups, but not between groups. As stated by the so-called *psychic unity of human-kind* postulate, formulated by Adolf Bastian, a German ethnologist, all humans, regardless of culture and race, share the same psychological and cognitive make-up. While infants’ behavior does not cross-culturally differ, behavior of adults can differ to a great extent. The inability of

genetics to explain the major differences between thought and behavior of human groups across the world is the only feature of the SSSM that the authors consider to be correct, and which they have thus incorporated into the ICM. They, however, believe that the reason behind this lies in the complex psychological and physiological adaptations that SSSM denies. The ICM acknowledges the role of interactions between the external influences of culture and environment on one side, and the evolved psychological influences on the other side in forming human behavior.

Building from the notion of content-free nature of the human mind, the SSSM views human culture as free to develop in any direction. The ICM, however, argues that the foundations of culture lie on and are constrained by the universal human nature. This illustrates the contrasting views on biology held by the SSSM and the ICM supporters. While SSSM believes biology to be of relatively low importance in understanding human behavior, the ICM accentuates the relevance of understanding the interactions between nature and nurture.

The SSSM-ICM disjunction encountered some criticism, with some authors accusing Tooby and Cosmides of creating a false dichotomy, and arguing that the SSSM was introduced as a term solely for the purpose of pleading in favor of the ICM and evolutionary psychology. However, the success of the SSSM validated its characterization as a paradigm, and it has since been adopted by numerous researchers (Hampton 2004).

## Central Premises of Evolutionary Psychology

### The Massive Modularity Hypothesis

To better understand the discipline of evolutionary psychology, it is necessary to consider the concepts, principles, and hypotheses from which it stems. One of the central premises of evolutionary psychology is that the human mind (or the brain) is an information processing device which produces behavior in response to external and internal inputs. This approach, common in cognitive psychology, stems from the *computational*

*theory of mind*. Evolutionary psychologists propose that brain is composed of modules, which account for all sophisticated human behavior and are units of mental processing designed by natural selection. The so-called *functional architecture* of mind has historically been divided into two different theories: *horizontal* – viewing mental processes as interactions between various faculties that are not domain-specific (such as memory or perception), and *vertical* – claiming that the mental faculties are genetically determined, associated with particular neurological structures, computationally autonomous, and can be distinguished based on their domain specificity. This kind of adaptationist view of physiological mechanisms comprising different modular adaptations that serve different functions is common in evolutionary biology. Evolutionary psychologists believe the human mind has been shaped by natural and sexual selection. For this reason, the many cognitive modules it comprises are specialized for solving particular adaptive challenges that occurred in humanity's evolutionary past. Examples of these modules include language acquisition, incest-avoidance, cheater-detection, mate preferences, foraging, and intelligence.

### Environment of Evolutionary Adaptedness

Another core assumption of evolutionary psychology is that brain is, just like all the other parts of human body, designed and adapted to the conditions of the ancestral environment in which it has evolved. Much of the modern human behavior is considered to be a product of psychological *adaptations* that have evolved to solve problems that were recurrent in the species' *Environment of Evolutionary Adaptedness* (EEA). Evolutionary psychologists develop and examine hypotheses deriving from the idea that conscious as well as unconscious behaviors have evolved to maximize the inclusive fitness of the individual performing them.

Since the human brain has evolved to deal with problems that were recurrent in the EEA, it can have difficulties comprehending and dealing with situations that did not exist in the ancestral environment. This concept is also known as the *Savanna Principle* (Kanazawa 2004). Due to the

insufficient stability of the human environment, the human brain has not experienced significant changes since the Pleistocene (Kanazawa and Perina 2012). According to the Savanna Principle, the brains of modern humans are, in respect to the ability to deal with the challenges that were present in the EEA, similar to those of the species' ancestors. Such issues are referred to as *evolutionary familiar*, and among others, include mate choice and food preference. The adaptive behaviors that provided an advantage in survival and reproduction in the EEA are the ones that humans have retained to this day. However, besides the recurring trials that human ancestors encountered daily, the EEA would occasionally present new and unusual problems. Certain individuals were better able to understand and deal with such non-recurring stimuli that are now commonly referred to as *evolutionary novel*. According to the *Savanna-IQ Interaction Hypothesis* (Kanazawa 2004), those individuals were endowed with higher general intelligence. This hypothesis suggests that intelligence is a domain-specific psychological adaptation that evolved to solve evolutionarily novel problems. The individuals with higher general intelligence should therefore be better able to understand and deal with situations that were not present in the EEA. Since better understanding of a stimulus encompasses an increased likelihood of its preference, this ability also affects values and preferences.

### Adaptiveness of Modern Humans' Behavior

The behavior of nonhuman animals, as well as humans can be interpreted at four levels of analysis, which are jointly called *Tinbergen's Four Questions* (Tinbergen 1963). These questions divide behavioral explanations into two categories – *ultimate* and *proximate*. Ultimate or evolutionary explanations focus on the function of behavior in terms of its adaptive value for survival, and phylogeny, or how a behavior evolved. These types of explanations are based on the comparison of behavior between closely related animal species, or that of different species living

in the same environment, as well as the study of selection on the evolution of behavior. They answer the “why?” questions. Proximate explanations concentrate on behavioral mechanisms and causes of particular behaviors, as well as their ontogeny or development during organism's lifespan. They aim to answer the “how?” questions. Evolutionary psychology primarily focuses on the former, explaining behavior in terms of the processes and the forces of evolution. Function or the adaptive value of a behavior describes the contribution of a particular behavior to animal's reproductive fitness or survival.

Tinbergen argued that behavior is no different from physiological characteristics, in that it has evolved as a means for survival. Just as selective pressures over time alter the physiology, they also alter the behavior. If a behavioral strategy is adopted by an entire population inhabiting a particular environment and cannot be replaced or invaded by any other strategy through the means of natural selection, it is considered an *evolutionarily stable strategy* (ESS) (Taylor and Jonker 1978). ESS rests on two conditions: an individual employing such strategy must do better than an individual employing a different strategy, and should a new strategy evolve, the individual employing the initial strategy must still do better than an individual employing the newly evolved one.

Not all traits can be considered adaptive. Some would be more accurately defined as *exaptations* – “preexisting traits that take on new beneficial effects without being modified by new selection pressures” (Buss 1998, p. 125). This term, introduced in 1982 by Stephen J. Gould and Elisabeth Vrba refers to the characteristics that were originally shaped by natural selection for a particular function (an adaptation), but were later co-opted for another use. They are common in both anatomy and behavior. Conversely, as the environment changes, some of the originally adaptive mechanisms can also become unsuitable. *Evolutionary mismatch*, or *evolutionary trap*, refers to the evolved traits that were once advantageous becoming maladaptive in the current environment (Lloyd et al. 2011). The mismatch hypothesis often attributes this transition to rapid

environmental change. This has been observed in humans, as well as in nonhuman animals. In human evolution, an evolutionary mismatch occurred after the transition from a hunter-gatherer lifestyle to an agricultural one – about 10,000–12,000 years ago. This changed the way humans interacted with the environment, but the evolution of human bodies was too slow to cope with the advancement of the Western cultures. As a result, the adaptations to the previous foraging lifestyle have persisted. Some of the consequences of this mismatch are obesity, metabolic syndrome, osteoporosis, and the increase in allergies and autoimmune diseases. Furthermore, the reward system of dopaminergic pathways of the human brain programs that are programmed for continual pleasure seeking, while adaptive in hunter-gatherer societies is over stimulated and abused in the present environment by activities such as gambling, drug use, and overeating, leading to addictive behaviors.

Another example of an evolutionary mismatch are the responses to *supernormal stimuli* – exaggerated versions of stimuli to which there are existing response tendencies, but which elicit the reaction more strongly than the ones for which it has evolved. The term was coined by Nikolaas Tinbergen. Dr. Deirdre Barret, a psychologist, argued that human behavior is just as influenced by supernormal stimulation as is the behavior of other animals. In her 2007 book *Waistland: A (R) evolutionary View of Our Weight and Fitness Crisis*, the author explained that human instincts are designed for the African savannah in which the species evolved. She further explained how junk food exploits the cravings for salt, sugar, and the fats. She provided another example of a supernormal stimulus in television, which comprises many amplified social cues – like laughter, smiling faces, or attention-grabbing action (Barret 2007). In 2010, Barrett published another book, *Supernormal Stimuli: How Primal Urges Overran Their Evolutionary Purpose* (Barrett 2010). Herein the author applied the concept of supernormal stimuli to the disassociation between human instincts and the current environment to which they have not had the time to adapt to. According to Barrett, this dissociation is the

reason behind the appeal of television, pornography, and video games, as well as being at fault for many of the problems humanity is faced with, such as obesity and warfare.

## Areas of Research in Evolutionary Psychology

In response to evolutionary pressures, humans have developed complex social behaviors and the elaborate brain structure that supports them. The neocortex of humans is larger than that of other primates or mammals of similar size and comprises many areas thought to be involved in higher social cognition – for example, language, regulation of behavior and emotions, empathy, and theory of mind. A lot of research within the field of evolutionary psychology has been done on the various aspects of human social lives and the adaptations that enable their complexity.

### Sociality and Altruistic Behavior

Humans are highly social and many of the adaptive problems the species has faced are linked to social interactions. Social exchange of goods, services, or kindness is considered the very basic fact of human sociality, and although present in only a small number of species, it is present across numerous human cultures (Cosmides and Tooby 2005). Providing benefits to others who will later reciprocate is beneficial to the individual originally providing the benefit. As a result, both individuals are better off. For the social exchange to evolve, the species that engages in it must be able to detect cheaters – i.e., individuals who obtain benefits without reciprocating them. *Cheater-detection mechanism* has evolved to solve the evolutionary problem of detecting cheaters in situations of social exchange. This mechanism looks for cheaters themselves, as opposed to the behavior of cheating, as the behavior itself could be a result of a mistake. Despite the high sociality of the human species, some evidence suggests there is a cognitive limit to the number of stable social relationships an adult can maintain. This number is called *Dunbar's number*. It was proposed by a



British evolutionary psychologist and anthropologist Robin Dunbar (Dunbar 1992). Extrapolating from the results obtained from studying non-human primates and using the average human brain size, he projected that humans can only maintain 150 stable relationships, and that groups of larger sizes will likely require more restrictive rules to maintain their cohesion.

*Altruism* occurs when an instigating individual suffers a fitness loss while the receiving individual experiences a fitness gain. Altruistic behavior will be positively selected for if the benefit to the recipient multiplied by the genetic relatedness of the recipient to the performer is greater than the cost to the performer of a social act. This is known as *Hamilton's rule*, and it stems from research carried out by William D. Hamilton. A failure to satisfy the Hamilton's rule leads to selfish behavior. *Kin altruism* is altruistic behavior, the evolution of which has been driven by *kin selection* – an evolutionary strategy favoring the reproductive success of an individual's genetic relatives, even at a cost to the individual's own survival and reproduction. It is an example of *inclusive fitness*. Inclusive fitness is the number of *offspring equivalents* an individual rears or otherwise supports through its behavior. A direct offspring carries 50% of each of their parents' genes and is considered to be one offspring equivalent. An offspring of a sibling with whom an individual only shares 50% of genes only carries 25% of said individual's genes and is considered 1/2 offspring equivalent. From the gene's perspective, evolutionary success will increase as a function of the number of copies of the gene in the population. This is achieved not only through leaving a maximum number of viable offspring – or increasing personal fitness – but also through increasing the fitness of genetic relatives, as they are likely to carry copies of the same genes. This is called *kin selection theory*. In evolutionary psychology, a degree of genetic relatedness can be used to predict altruism. Relatives who share more genes invest more resources. Furthermore, there is a preferential investment in more certain kin. Mothers' mothers invest the most, followed by mothers' fathers, then fathers' mothers, and finally fathers' fathers. These differences have

been explained by theories of paternal uncertainty (Buss 1999).

When an organism acts in a way that temporarily reduces its own fitness, while increasing that of another, with the expectation that the favor will be returned at a later time, such behavior is considered *reciprocal altruism*. This concept was introduced by Robert Trivers to explain the evolution of *cooperation*. When organisms work together towards a mutual benefit, it is considered cooperation. Any adaptation that has evolved to increase the reproductive success of the acting individual's social partners, at least in part, can be regarded as cooperation. It carries direct fitness benefits (by-products of cooperation) and indirect fitness benefits (resulting from cooperation with genetically similar individuals). *Multi-level selection theory* posits that selection for cooperation happened on multiple levels – from the level of atoms and cell molecules, to the level of individual organisms, community level, and finally the level of the species. Drawing from the classic example of cancer spreading through an organism through the success of individual (cancer) cells that prevail in their efforts to multiply, which ultimately diminishes organism's chance at survival, and hence reproduction, this theory explains that this type of cooperation causes individuals to avoid behaviors that would ensure short-term benefits for themselves, but would be detrimental to the community in the long term.

The most famous example of cooperation comes from the *game theory*, and it is called the *prisoner's dilemma*. It explains why two rational individual might not cooperate, even if such cooperation would seemingly be in the best interest of them both. It was developed by Merrill Flood and Melvin Dresher in 1950, but named by Albert W. Tucker. It describes a situation of two prisoners who have been caught and are individually presented with an opportunity to either betray their partner or cooperate with them. If both choose to cooperate, each will receive a sentence of 1 year in prison, and if both betray their partner, both will receive a doubled sentence of 2 years in prison. However, if one of them betrays their partner, while the other cooperates, the cooperating one will receive a 3-year sentence, while the betrayer



will be freed. As betrayal carries a greater reward than cooperation, all rational “prisoners” should betray each other, but results often show a systemic bias towards cooperation.

While the complexity of the brain structures that guide social behavior implies many benefits, maintaining the size and the high level of sophistication also brings many costs. Development of such a complex system to full capacity takes a long time, which is reflected in a comparatively prolonged developmental period. Providing a stable social environment from responsive and caring adults during individual’s childhood is of high importance for the development of a secure attachment style, which can persist throughout the lifespan.

### Language and Communication

Evolution of human communication is one of the most intriguing areas of research within this discipline. Despite being researched for several centuries, the consensus on the exact origin and age of human language still has not been reached. Due to a lack of direct evidence, a lot of research involves a comparative approach and investigation of communication systems used by other animals, especially nonhuman primates. There are several hypothesis and theories explaining the evolution of language, mainly proposing that language developed from ancestral vocalizations, or that it developed from gestures.

According to a theory put forward by Robin Dunbar, human gossip serves a purpose similar to grooming in other primate species, allowing for the maintenance of relationships and alliances based on reciprocity (“if you scratch my back, I’ll scratch yours”). In his grooming hypothesis, Dunbar proposes that as human groups became increasingly bigger, manual grooming became too time-consuming. An energetically cheaper form evolved in the shape of vocal grooming, which gradually evolved into vocal language (Dunbar 1996). This hypothesis, however, has trouble explaining how meaningless sounds developed into complex syntactical speech.

The *ritual-speech co-evolution theory* argues that language is not a separate adaptation, but an internal aspect of symbolic culture. Verbal

communication is easy to fake, and in many early cultures, trust was established in collective rituals. To understand how language evolved, it is necessary to address the emergence of symbolic culture.

The *gestural theory* suggests language developed from nonverbal, gestural communication, which preceded vocal communication. It is hypothesized that bipedalism played an important role, as it made both hands available for gesturing. The switch to vocal communication was selected for because it freed the hands for other functions.

The evidence for this theory often comes from comparative and biological psychology. For example, nonhuman primates use numerous gestures as means of communication, many of which resemble those used by humans. Gestural communication, especially pointing, is an important part of teaching children to use language. Furthermore, both gestures and spoken language are processed by a common, modality-independent neural system, which links meaning with symbols, and therefore plays a more general role in human communication.

Unlike the vocalizations of many animal species, human words are unreliable signals because they are easy to fake. For a language to fulfill its purpose, listeners need to be able to distinguish lies from honesty. William Tecumseh Fitch, an American evolutionary biologist, proposed the *mother tongue hypothesis*, according to which language initially evolved for communication between mother and the offspring and has later been expanded to include other relatives (Fitch 2004). This explanation is similar to the Darwinian principle of kin selection: genetic interest led individuals to trust the unreliable signals of human words. Simon Baron-Cohen argued that evolution of language was preceded by the evolution of *theory of mind*. Empirical evidence from developmental and cognitive psychology supports this notion.

### Emotions

According to Darwin’s evolutionary theory, emotions are products of natural selection. Recurrent encounters with situations such as escaping predators, falling in love, or recognizing sexual



infidelity selected for adaptations that guided the processing of relevant information and response behavior. Over many generations, those emotions that contributed the most to individual fitness became more prevalent in the population. Modern day emotions are therefore well-designed for solving the adaptive problems of the ancestral environment. They are responses to probabilistic clusters of situational cues that were reliable enough to allow for such detectors to evolve. Situational cues trigger emotions, and with them, a perspective of seeing the world in a way similar to the ancestral cluster of situationally present elements.

The evolutionary theory of emotions states that situations relevant to emotions are those which recurred ancestrally, could not be handled successfully without a superordinate level of program coordination, had a reliable and rich repeated structure, had recognizable cues that signaled their presence, and in which an error would have resulted in large fitness costs (Cosmides and Tooby 2000). Emotions are viewed as superordinate programs which mobilize and direct subprograms such as goal planning, motivation and prioritizing, information-gathering, perception, memory, attention, physiology, communication and emotional expressions, behavior, specialized inference, reflexes, learning, effort allocation, and others. They detect evolutionarily reliable cues that a particular situation is occurring, and then activate a specific set of subprograms chosen as the most useful for dealing with that particular situation during the process of natural selection.

To identify an emotion as an adaptation, it is necessary to identify the adaptive problem, establish the evolutionarily recurrent situation in response to which an emotion has evolved, and describe cues that signal the presence of such situation, as well as situation-detecting algorithms (emotion programs), algorithms that assign priorities (i.e., a type of a supervisory system that decides on the order in which simultaneously arising situations should be dealt with), an internal communication system (sending a situation-specific signal to all relevant mechanisms), and algorithms that regulate responses to each

emotional signal (i.e., switching the mechanism on and off) (Cosmides and Tooby 2000).

Facial expressions associated with basic emotions served an adaptive function for the individual and their social surroundings. However, alongside the physiological function, emotion expressions also have a social-communicative function of, in the example of fear, a nonverbal warning of the other group members of an immediate threat. Expressions of emotions are highly recognizable, and in the case of the basic or primary emotions (happiness, sadness, fear, surprise, disgust, and anger), cross-culturally universal. While emotional responses of infants tend to be uniform, emotional expression of adults can be highly variable, due to a large number of open parameters on which emotional programs depend.

### Mate Choice

Mate choice or intersexual selection is an evolutionary process relating to the selection of a potential partner. Along with intrasexual selection, it is one of the two components of sexual selection. Modern humans' mate preferences are, from the perspective of evolutionary psychology, a result of evolutionary pressures and represent answers to adaptive problems associated with mate acquisition. These problems are often gender-specific, which means that the principles that apply to men do not necessarily apply to women. The consequences of this are the differing strategies of mate acquisition employed by the two sexes. The overarching reason behind these strategies may lie in the differential parental investments of women and men.

According to Trivers's *Parental Investment Theory*, parental investment is any parental expenditure that benefits an offspring and increases its chances of surviving at a cost of its parents' ability to invest in other aspects of their own fitness (Trivers 1972). Parental investment can be split into mating investment (i.e., the sexual act and the sex cells invested) and rearing investment (i.e., the time and energy invested into raising the offspring). One of this theory's main assumptions is that parental investment also affects sexual behavior. Reproduction is costly and each individual has limited time and resources available to produce

and raise their offspring. In regard to human reproduction and parental investment, a woman's investment in both mating and rearing the offspring surpasses that of the man. According to Bateman's principle of *Lifespan Reproductive Success* (LRS), the LRS variance is smaller in women due to their high obligatory parental investment. Women have a shorter reproductive life cycle than men, and their number of sex cells is much smaller. While men produce sperm cells at a rate of 12 million per hour, women are born with a finite supply of around 400 egg cells (Buss et al. 1992). Furthermore, both the fertilization and the 9-month-long gestation occur in a woman's body. After the birth, the woman is responsible for breastfeeding, and much like the pregnancy, lactation is a highly energy-demanding task. Since women are the more investing sex, evolution has favored those who are more selective of their mates. As a result, women are generally speaking more discriminating in choosing a partner.

Finding a partner involves using different *sexual strategies* – evolved solutions to adaptive problems associated with mate acquisition that have been faced by women and men during the evolutionary history of the human species. They are employed with no consciousness or awareness. According to the *Sexual Strategies Theory* proposed by David M. Buss and David P. Schmitt, there are two different types of reproductive strategies, which are used by both sexes: *short-term*, and *long-term*. While non-evolutionary psychologists sometimes still treat short-term mating as dysfunctional or even pathological, evolutionary psychologists consider both reproductive strategies to be adaptive. In order to understand human sexual strategies, it is necessary to consider evolutionary pressures that shaped them.

During the evolutionary history of the human species, both women and men have employed both the short-term and the long-term sexual strategies, depending on the conditions they were in. Either of the strategies solves different adaptive problems. Since the parental investment of women is disproportionately larger than that of men, women tend to allocate more effort in long-term mating. On the other hand, men invest more

in short-term mating than women do. There are many sex-related differences in both the reproductive opportunities and constraints in both contexts.

## Male Selection Pressures and Mate Preferences

From an evolutionary perspective, the reproductive success of men has been constrained by the number of available fertile women, as well as the difficulty of identifying the fertile women and women that are sexually accessible. Men employing a short-term sexual strategy encountered adaptive challenges of finding as many potential partners as possible, identifying women that were sexually accessible, and women that were fertile, while also trying to minimize their own risks, commitment, and investment. The main way in which men increased their reproductive success has been through an increase in the number of sexual partners. However, that approach carries many costs. The higher the number of women with whom a man achieves sexual contact, the higher is his risk of contracting a sexually transmitted disease. Another cost associated with high numbers of sexual partners is a gain of negative social reputation, which could impair a man's value as a potential long-term mate for women of high mate value, as such behavior signals a low likelihood of parental investment, an important preference to women looking for a long-term partner. Men employing long-term strategies were faced with challenges of identifying reproductively valuable women, women with quality genes, women with good parenting skills, and women who are willing and able to commit to a long-term mating relationship. The success in dealing with these problems presented them with a final problem of ensuring certainty in paternity.

Short-term strategies are more prevalent in men than women. As one of the main adaptive challenges men have faced is gaining sexual access to as many women as possible, they have evolved a strong desire for sexual access to a large number of women (Symons 1979). This trait is accompanied by employing comparatively lower

standards for what constitutes an acceptable short-term partner. Woman's age, intelligence, or personality are in this context of lesser relevance, and the time men are willing to invest before trying to obtain sexual contact is shorter. Men seeking a short-term mate are also likely to more intensely pursue women who are sexually accessible than those that are not. Promiscuity, although highly undesirable in a long-term mate, is likely to be desired in a short-term mate, as it signals accessibility. This implies a higher likelihood of discrimination against women with traits such as prudishness, sexual inexperience, conservativeness, or a lower sex drive.

Another adaptive problem men have faced is identifying women who are fertile. There are two different angles to tackling this challenge – assessing women's fertility and *reproductive value*. Fertility refers to the probability of present reproduction for a given age and sex, while reproductive value is the extent to which people of a given sex and age are likely to contribute, on average, to the ancestry of future generations (Fisher 1930). Female fertility typically peaks in the early to middle twenties, while their reproductive value is the highest in the middle teens (Thornhill and Thornhill 1983), and both show a steep decline with age. According to this, men seeking a short-term mate are more likely to prefer women of higher fertility, while those among them who are seeking a long-term mate should be more interested in their prospective partner's reproductive value. However, it is nearly impossible to know a person's fertility or reproductive value. Younger and healthier women are more likely to have higher reproductive capacities, but since age or health are also not always directly observable, men have evolved preferences for features that act as cues of a woman's age and health. Examples include physical characteristics such as facial symmetry, clear and smooth skin, clear eyes, full lips, shiny hair, and good muscle tone, as well as behavioral characteristics such as youthful gait or high activity level, and a woman's social reputation.

As a man's reproductive success depends on his number of sexual partners, one of the adaptive challenges men faced was avoiding commitment.

A large investment into a single partner meant fewer number of total partners. One of the answers to this problem is avoidance of women who desire long-term commitments.

Despite the many advantages of pursuing a short-term sexual strategy, men have also evolved long-term strategies. Prior to engaging in sexual intercourse, women seek out reliable signals of long-term commitment. Since men might fake the long-term interest, women have evolved psychological mechanisms to detect deception and mechanisms that allow a reliable prediction of actual long-term commitment potential. Additionally, women look for commitment signals that are more costly to forge, thus forcing men into long-term relationships. This has, however, brought benefits to men. Commitment to a single partner decreases the costs of repeatedly pursuing short-term mates, while increasing the opportunity for developing cooperative relationships, due to a mutual interest in the same children. This allows for more efficient care, decreasing the necessary effort per offspring. Willingness to dedicate all resources to one partner also increased men's chances of obtaining a partner of higher-quality phenotypic attributes or genes, which could later be passed down to their offspring (Gangestad 1989).

The main cost of pursuing long-term strategies is a decreased number of potential partners. By committing to a single long-term partner, men are jeopardizing their reproductive success. They therefore needed to find a way to maximize their reproductive success with a sole partner. Unlike many other mammalian species, women have a concealed (cryptic) ovulation. For men, this creates a problem of decreased certainty of paternity. As they cannot be sure when a woman is ovulating, formation of long-term relationships was selected for in men. Men who monopolized a woman during longer time periods gained a selective advantage by an increased probability of paternity of children conceived in that relationship. For this reason, men show a preference for women who provide them with evidence that, if the relationship results in offspring, their paternity will be certain. Traits such as faithfulness and sexual loyalty are highly preferred in long-term

mates, although they are seemingly irrelevant when it comes to the selection of short-term partners (Buss et al. 1992). Sexual jealousy is stronger in men than in women (Buss et al. 1992), and it evolved in response to the problem of paternity uncertainty. It elicits mate guarding, so as to decrease intrasexual competition and lower the likelihood of another man fathering an offspring.

### Female Selection Pressures and Mate Preferences

Reproductive success of women has been constrained not by the quantity of the available potential partners, as is the case with men, but by their quality. Mate quality is assessed in terms of the external resources that such union would bring the women and their shared offspring, as well as a man's genetic makeup. Within a short-term mating context, these constraints can be summarized as the problem of immediate resource extraction and the problem of assessing a man's genetic quality. As women are the more investing sex, the importance of selecting the correct long-term partner is higher, as is the cost associated with making the wrong choice. Because of this, women sometimes engage in short-term relationships to assess men as prospective long-term mates.

As women pursue short-term sexual strategies in a different way than men, they also desire different attributes in their short-term mates. However, some of the risks women are faced with are similar to those that are faced by men. By having multiple partners, women increase the risk of contracting sexually transmitted diseases, as well as being physically or sexually abused, in the attempts of men to control them reproductively. Short-term strategies may also impair their value as long-term partners. This is, however, more detrimental to women than it is to men due to the paternity certainty problem men have faced. As a result, the social status of sexually promiscuous women is likely to decrease. Women of high mate value tend to be more discriminating than women of lower mate value, which leads to promiscuity being regarded as an

indicator that a woman is not capable of securing a quality long-term mate (Buss and Schmitt 1993).

Women are less inclined to short-term strategies, but they still carry reproductive benefits (Gangestad 1989). For example, pursuing shorter relationships with high-quality mates that are not available for long-term relationships is a way for women to obtain better quality genes that can be passed on to their offspring, increasing their survival or reproductive success, as well as for women to obtain material resources. Beyond the obvious example of prostitution, which involves a direct exchange of resources for temporary sexual access, men bringing gifts to women whom they sexually engage with is a cross-culturally stable finding (Shostak 2014). Women who pursue short-term sexual strategies are more likely to show a preference for traits that signal immediate provision of resources, such as ambition, intelligence, industriousness, material possessions, lack of existing commitment, high income, and generosity. However, these characteristics are also desirable in prospective long-term partners.

Because women use short-term relationships as a way to assess potential long-term partners, their short-term preferences are much more similar to their long-term preferences than is the case with men. Although short-term encounters may provide women with better quality mates who would otherwise be inaccessible to them, they seek out long-term partners so as to ensure male parental investment. Social and economic benefits, such as high social status and provision of resources, are advantageous for the offspring. Furthermore, if traits that lead to acquiring better social status and more resources are heritable, mating with men who possess these features may also give the resulting offspring a reproductive advantage. Additionally, long-term partners may provide food and protection to the woman, which is especially important in periods when the woman is especially vulnerable, such as during pregnancy and lactation.

Pursuing a long-term sexual strategy does not limit women's reproductive success in the way that it does men's, as the number of potential offspring a woman can have in a given amount of time is restricted by her own biology, and not

her partner's. The adaptive problems women had to solve to pursue a long-term mating strategy have been identifying men who are able and willing to invest resources in both them and their potential children on a long-term basis, men with quality genes, men with good parenting skills, men who are able and willing to commit to a long-term mating relationship, and men who would be able to grant them and their children physical protection from aggressive conspecifics. Due to these differences, men and women have evolved distinct psychological mechanisms, to help them pursue short-term and long-term mating strategies.

Female sexual selection is evident from the sexually dimorphic phenotypic features that are selected for, but which would otherwise serve very little purpose, such as beards, lower voice pitch, and greater height. These are indications of good genes, which will be passed on to the offspring, increasing their chances of survival or reproduction. However, as male reproductive capacity declines less steeply with age and cannot be as accurately assessed from their physical appearance, characteristics that indicate reproductive capacity are comparatively less valuable to women than they are to men. Phenotypic traits' relative importance is therefore second to that of personality characteristics, social and financial status, which signal the likelihood of a successful and long-lasting relationship with a potential partner, as well as his ability to take care of offspring.

## Research Methods in Evolutionary Psychology

Evolutionary psychologists use several methodological approaches to test whether a particular psychological trait could be an evolved adaptation. The *Cross-cultural Consistency* approach focuses on the characteristics that were found to be universal across cultures, such as facial expressions. *Function to Form* ("Problem to Solution") direction of analysis is used when the psychological mechanism is known, and an attempt is made to discover its evolutionary benefit – for example, gender differences in sexual versus emotional jealousy (with the former being more

characteristic of men, while the latter is more typical of women) thought to originate in men's higher risk of misidentification of offspring (the so-called "paternity insecurity"). The reversed, *Form to Function* ("Solution to Problem") approach is used when some behaviors or traits seemingly carry the characteristics of adaptations. For example, women's morning sickness during pregnancy and aversion to certain types of food are both complex and universal, and have been hypothesized to have the function of avoiding the ingestion of toxins that could damage the fetus (but would be harmless to nonpregnant women). *Corresponding Neurological Modules* approach combines evolutionary psychology and neuropsychology. The former is used to identify the ultimate evolutionary functions of psychological mechanisms regarded as adaptations, while the latter helps identify their proximate manifestations. The *Current Evolutionary Adaptiveness* approach is used to study the impact of psychological adaptations in the current environment. This type of research can be useful in studying evolutionary psychopathology. Evolutionary hypotheses can be tested experimentally, in observational studies, using archaeological records, neuroscience data, self-reports and surveys, public records, mathematical models, or using computer simulations.

## Criticism of Evolutionary Psychology

One of the main critiques of evolutionary psychology is the problem of testability of evolutionary hypotheses. Some of the hypotheses are very difficult or even impossible to test, which challenges the discipline's status as an empirical science. Many traits considered to have been adaptive in the EEA now serve different functions, and they can frequently be explained by entirely opposite hypothesis, as often the only evidence for their adaptiveness is their own internal logic. Moreover, many traits originally considered universal have later been found to be culturally dependent or products of historical circumstances. Evolutionary psychologists are often accused of ethnocentrism, and of believing that their own current cultural context is representative of



universal human nature. However, their main defense is that they are simply focusing on commonalities rather than variation, in order to help identify cultural universals.

Many evolutionary hypotheses are criticized for being based in the assumptions made about the EEA, of whose features there is often insufficient evidence. Evolutionary psychology assumes that the EEA was uniform, but critics contend that it is possible that there were multiple EEAs, which makes presumptions about specific traits' adaptiveness unsubstantiated (Plotkin 2008). A counterargument to this critique states that although a lot of information about the EEA is missing, considerable information about the lives of ancestral humans and the environment in which they lived is available, and hypotheses are only made regarding psychological mechanisms related to those certainties, for example, kinship, female-exclusive pregnancy and lactation, cooperation in hunting and predator avoidance, and others (Buss 1999).

Evolutionary psychologists are at times criticized for reductionism and genetic determinism, as well as limiting environmental influences to that of a trigger, or a predetermined developmental instruction encoded in the genes. According to the critics, evolutionary psychology has trouble differentiating between cultural and environmental explanations on the one side, and adaptive, evolutionary explanations on the other, which leads to a discrediting of social processes, cultural artifacts, and dialectical explanations. A counterargument to this claim lies in the historical importance of reductionism to many scientific discoveries, as well as the importance of assessing different phenomena on all levels, including that of genes and environmental pressures. Moreover, while genes do not cause behaviors, they predispose for them, allowing other, external factors to further affect their expression.

## Cross-References

- [Adaptation](#)
- [Charles Darwin](#)
- [Ecology](#)
- [Evolutionary By-product](#)

- [Evolutionarily Stable Strategies](#)
- [Fitness](#)
- [Kinship](#)
- [Konrad Lorenz](#)
- [Memory](#)
- [Mismatch Hypothesis](#)
- [Natural Selection](#)
- [Nikolaas Tinbergen](#)
- [Origin of Species](#)
- [Parental Investment](#)
- [Richard Dawkins](#)
- [Robert Trivers](#)
- [Sexual Selection](#)
- [Sociobiology](#)
- [William Donald Hamilton](#)

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## Evolutionary Radiation

### ► Adaptive Radiation

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## Evolved Interaction

### ► Symbiotic Relationship

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## Exact Number

### ► Cardinality

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## Exchange Behavior

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## Synonyms

[Interchange](#); [Reciprocity](#); [Trading](#)

## Definition

Behaviors exchanged between individuals belonging to the same group or society.

## Introduction

A particular feature of primate species is that most of them live in groups or societies. Within these societies, individuals do not seem to interact at random with other group-members; instead, they appear to selectively interact more with some individuals than with others. Further, the type of social behaviors display towards group members may differ depending on the identity of a given individual. This arrangement of social interactions gives rise to complex patterns of social behavior. For instance, in many primate societies, individuals appear to exchange social behaviors, e.g., grooming for the receipt of support in fights. The exchange of social behaviors has been extensively studied during the last 30–40 years. Empirical support for the exchange of behaviors comes mainly from studies that usually find a statistically significant positive correlation between the number of behavioral acts given and the ones received. These studies usually distinguished between the

exchange of the same kind of behaviors (hereafter reciprocity) or between different kinds (hereafter interchange). This entry revises studies on behavior exchange in species of great apes and New and Old World monkeys. It is focused on these taxa, given the great amount of research that has been conducted on them. It will start by defining the three main types of social behaviors being exchanged in primate societies. Then, it will review the evidence that has been accumulated during the last 30–40 years, supporting the exchange of behaviors. Thereafter, it will focus on the ultimate functions and proximate mechanisms that gave rise to the exchange of behavior. Lastly, it will address the biological market theory.

## Behaviors Exchanged

Three behaviors have usually been the focus of studies investigating reciprocation and interchange of behaviors in societies of primates: allo-grooming, support in fights or coalitions, and food sharing.

Grooming is possibly the most common behavior in primates. It is defined as the brushing and picking at the hair of the fur. Grooming can be self-directed (auto-grooming) or directed towards another individual's fur (allo-grooming). Allo-grooming (hereafter grooming) is thought to serve many different functions such as hygienic, reduction of tension, establishment and maintenance of social bonds, etc. Grooming thus is considered a valuable commodity for primates, and it may be used as a currency to exchange for itself or other commodities (Henzi and Barrett 1999).

Support in fights or coalitions are defined when one individual intervenes in an ongoing conflict between two opponents and supports one against the other (Schino 2007). Following this definition, this kind of social interactions are triadic with the intervening individual being the “supporter,” the individual being helped the “recipient of support,” and the individual being attacked the “target of aggression.” Coalitions with more than three participants have also been described. Studies on interchange of support, however, have usually focused on triadic interactions.

Food sharing is defined as the transfer of food from one individual, “the possessor,” to another, “the recipient.” Food sharing can be passive, the possessor allowing the recipient to take pieces of food, or active, in which the possessor actively hands a piece of food to the recipient (Gilby et al. 2010). The vast majority of food sharing in primates is passive, i.e., above 95% of the instances in which food sharing has been recorded (Jaeggi and Van Schaik 2011).

## Exchange of Same Type of Behaviors: Reciprocity

Reciprocity of grooming and support has been commonly reported in primate societies. The evidence for the exchange of grooming given, for that of grooming received, is compelling. A meta-analysis that included 48 different primate groups belonging to 22 species and 12 genera (Schino and Aureli 2008a) found that individuals directed more grooming to those from whom they also received more grooming, i.e., grooming was reciprocated. Similarly, many studies have reported a significant positive correlation between the amount of support given in fights and that received. In a review on support in fights, Smith et al. (2010) found that individuals gave more support in fights to those from whom they also received more support, in 61% of the studies revised (19 out of 31 studies). In contrast, evidence for reciprocity of food sharing is scarce among monkey species; perhaps due to the fact that food sharing outside the mother-offspring context is not a common behavior in monkeys (Jaeggi and Gurven 2013). Only studies on capuchin monkeys (*Cebus apella*) have reported significant positive correlations between the acts of food given and those received (de Waal 2000). Regarding great apes, most studies on food sharing have focused on chimpanzees (*Pan troglodytes*). In this species, individuals indeed seem to reciprocate food sharing (Boesch and Boesch-Achermann 2000; de Waal 1997; Mitani 2006; Silk et al. 2013). The few studies on bonobos (*Pan paniscus*) (Goldstone et al. 2016; Jaeggi et al. 2013) and orangutans (*Pongo* sp.) (Kopp and

Liebal 2016; van Noordwijk and van Schaik 2009) on the other hand have found no evidence for reciprocation of food sharing.

## Exchange of Different Types of Behaviors: Interchange

### Interchange of Grooming

Studies on the interchange of grooming have mostly focused on the correlation between grooming given and support in fights received and vice versa, support in fights given and grooming received. Evidence for this kind of interchange is moderate. In their review on support in fights, Smith et al. (2010) report that ~53% of the primate studies revised present evidence for the interchange of grooming and support, and in a meta-analysis of 36 primate studies from 14 different species, Schino (2007) found a weak but significant positive correlation between grooming and agonistic support. Further, in studies on different groups belonging to the same primate species, evidence has been found for some groups but not for others.

Besides being interchanged for support, grooming seems to be interchanged for some other behaviors as well. For instance, Tiddi et al. (2012) found that individuals interchanged grooming for tolerance during feeding time in wild tufted capuchin monkeys (*Cebus paella nigrinus*). Other studies have found an interchange between grooming and access to handle infants (e.g., chacmababoons, *Papio cynocephalus ursinus*, (Henzi and Barrett 2002)). Further, a study by Gumert (2007) found that male long-tailed macaques interchange grooming for sex with females. Moreover, several studies on macaques (Puga-Gonzalez et al. 2016; Schino et al. 2005) have found a positive correlation between aggression given and grooming received, a finding interpreted as an extortion of grooming (Schino et al. 2005).

### Interchange of Food

Reciprocity and interchange of food outside the mother-offspring context has rarely been reported in species of primates other than great

apes (Jaeggi and Van Schaik 2011). Thus, the focus below is on studies investigating interchange of food in great apes and especially on chimpanzees.

Chimpanzees are frequent hunters, male chimpanzees have been regularly observed to prey on monkeys (e.g., red colobus – *Procolobus* spp.) and other small mammals, and they often share the meat obtained from these hunts (Gilby et al. 2010). Besides sharing meat, chimpanzees also share other types of food such as plants or fruits, although to a lesser extent than meat. Several interchange-based hypotheses have been put forward to explain this kind of behavior. Food for grooming, food for support, and food for sex are usually invoked as an explanation. Others, however, suggest that food sharing has nothing to do with interchange. Instead, they suggest that chimpanzees share food to reduce begging/harassment from other group members, i.e., the “sharing under-pressure” hypothesis. According to this hypothesis, food sharing is a form of tolerated theft.

Some of the best evidence for the interchange between food and grooming comes from studies by Mitani and colleagues (Mitani 2006) on chimpanzees’ communities at Ngogo, Kibale National Park in Uganda. Studies on these communities have been carried out several times over a time span of over 4 years. In all cases, researchers have consistently found positive correlations between food shared and grooming received and vice versa. It seems thus that individuals in these communities interchange food for grooming. Further evidence comes from experimental studies on captive chimpanzees at the Yerkes National Primate Research Center, USA, in which it was shown that individuals were more likely to share food with others after being groomed (de Waal 1997). Studies on chimpanzees’ communities of Gombe in Tanzania, however, have failed to find evidence of the trade between food and grooming (Gilby et al. 2010). Regarding the interchange between food and support, studies on communities of wild chimpanzees at Ngogo and at Tai National Park in Cote d’Ivoire have found positive correlations between these two behaviors (Mitani 2006). Hence, in these communities,

individuals appear to share more meat with those from whom they received more support in fights.

Most research on the interchange of food has focused on the interchange of food for sex. In chimpanzees, males are the usual hunters and are often observed to share meat with females. Thus, it has been hypothesized that, as in human hunter-gatherer communities, males chimpanzees may trade meat for sex with females (Gomes and Boesch 2009). Evidence in support of this hypothesis is, however, mixed. Initial studies suggested that the presence of estrus (fecund) females in the group influenced the motivation of male chimpanzees to hunt (Sánchez-Amaro and Amici 2015). More recently Hockings et al. (2007) showed that when chimpanzees raided crops, males were more likely to share their food with a cycling female; Gomes and Boesch (2009) found that males who shared meat with females increased their mating opportunities with them in the long-term but not in the short-term. In contrast, several other studies have failed to find evidence in support of the “food for sex” hypothesis. For instance, Hemelrijk and colleagues found that sharing food was not correlated with the probability of copulating (Hemelrijk et al. 1992), nor with siring offspring with a specific female (Hemelrijk et al. 1999). And Gilby et al. (2010) found that Gombe males were not more likely to share food with estrus than with anestrus females, that the presence of estrus females did not increase the probability of hunting, and that sharing meat with females did not increase the probability of mating in the short-term. Gilby and coauthors (Gilby et al. 2010) thus have suggested that meat sharing in chimpanzees is better explained by the sharing under-pressure hypothesis. The sharing under-pressure hypothesis suggests that individuals share food in order to stop the harassment of other group-members begging for food around them (Gilby et al. 2010). Several studies have indeed found a correlation between the amount of begging received and the amount of food shared (Silk et al. 2013). In sum, evidence supporting the “food for sex” hypothesis remains circumstantial at most.

Few studies have investigated food sharing in other great ape species. In contrast to

chimpanzees, bonobos and orangutans share primarily fruit. Studies that focused on these two great ape species have found little evidence in support of the “food for grooming,” “food for sex,” or “sharing under-pressure” hypotheses (Goldstone et al. 2016; Jaeggi et al. 2013; Kopp and Liebal 2016; van Noordwijk and van Schaik 2009). Instead, researchers suggested that bonobos share food with those with whom they have a good relationship (Jaeggi et al. 2013; Kopp and Liebal 2016), and that individuals may beg for food, to gain information about the aggressiveness or relationship status with the food possessors (Goldstone et al. 2016; van Noordwijk and van Schaik 2009).

## Ultimate Causes of Behavior Exchange

When an individual displays altruistic behaviors (a behavior that provides a benefit to the recipient, while incurring a fitness cost to the actor), it is thought that the actor must somehow receive a benefit in return; otherwise, natural selection would not have allowed the evolution of such behaviors. Grooming, support in fights, and food sharing, are behaviors considered altruistic, and thus, if individuals display these behaviors towards others, it is because they also obtain a benefit (de Waal and Brosnan 2006). Evolutionary theory suggests that altruistic behaviors can evolve via two different processes: kin selection or reciprocal altruism. According to the kin selection theory, altruistic behaviors may evolve, when actors direct their altruistic behaviors towards their own kin because by helping their kin, they increase their own inclusive fitness (Hamilton 1964). Hence, altruistic behaviors are expected to occur mostly among kin-related individuals. Reciprocal altruism on the other hand suggests that altruistic behavior may evolve even if individuals direct beneficial behaviors towards nonkin-related individuals. In this case, however, individuals should restrict their altruistic acts to those, from whom they are certain to receive an altruistic act in the future, i.e., altruism must be reciprocated. In this way, the fitness of altruistic individuals is increased (Trivers 1971). Indeed, as



suggested by both theories, in many primate studies, it has been shown that altruistic behaviors such as grooming, support in fights, and food sharing are usually directed towards kin-related individuals (Jaeggi and Van Schaik 2011; Schino 2007; Schino and Aureli 2008a). Further, in studies in which the effect of kinship could be controlled, individuals still directed more altruistic acts towards those from whom they also received altruistic behavior (Mitani 2006; Schino 2007; Schino and Aureli 2008a). It seems, thus, that kin selection and reciprocal altruism have played a key role in the evolution of behavior exchange in primate societies.

### Proximate Mechanisms of Behavior Exchange

The proximate mechanisms underlying reciprocity and interchange of behaviors are still controversial. Three mechanisms, varying in their degree of cognitive demands, have been proposed: symmetry-based reciprocity, attitudinal reciprocity, and calculated reciprocity (de Waal and Brosnan 2006).

Symmetry-based reciprocity is the mechanism requiring the least cognitive capacity. This mechanism assumes that positive correlations between behaviors given and received may result from a common symmetrical variable within a dyad of individuals, e.g., proximity, kinship, age, and rank. For instance, when individuals direct most of their behaviors towards those partners with whom they spent most in proximity or to those of similar age or rank, reciprocation and interchange should automatically emerge (de Waal and Brosnan 2006). Symmetry-based reciprocity, however, seems insufficient because when symmetrical variables are removed from the correlations, the correlations remain still statistically significant (Gomes and Boesch 2009; Mitani 2006; Schino 2007; Schino and Aureli 2008a). This suggests that reciprocity and interchange are not entirely explained by symmetry in common variables between dyads, and that other mechanisms must underlie the behavior exchange.

Calculated reciprocity is the mechanism requiring the most sophisticated cognition. This mechanism assumes that, to avoid being cheated, individuals keep track of the number of behaviors given to and received from each group member, respectively. Hence, it requires long-term memory of past events (de Waal and Brosnan 2006). Calculated reciprocity has been criticized because keeping track of acts given and received over the long-term is a task that is difficult, even for humans (Stevens et al. 2011). Therefore, several studies have investigated whether reciprocation and interchange of behaviors occur on a short-term rather than on a long-term basis. These studies, however, did not find evidence of short-term reciprocity or interchange (Amici et al. 2014; Gilby et al. 2010; Gomes and Boesch 2009; Jaeggi et al. 2013). The lack of evidence for short-term reciprocity and interchange has shifted the focus from “calculated reciprocity” to more parsimonious mechanisms, such as “attitudinal reciprocity” (de Waal 2000) or “emotional book-keeping” (Schino and Aureli 2009).

Attitudinal reciprocity was first proposed by de Waal (2000) as a mechanism mediating food sharing reciprocity in brown capuchin monkeys (*Cebus apella*). He suggested that individuals may reciprocate behaviors by mirroring the attitudes of their social partners in recent interactions, i.e., “if you are nice, I’ll be nice” (de Waal 2000). This idea was then further developed by Schino and Aureli (2009) to explain reciprocity and interchange of behaviors over the long-term. They proposed emotions as the basis of the individuals’ behavioral decisions. Whether an individual reciprocates or interchanges a behavior with a specific partner depends on the type of emotion the individual associates with that partner. The frequent receipt of beneficial behaviors (e.g., grooming) from a specific partner over long periods of time elicits the association of a positive emotion with that partner. This emotion may then subsequently motivate the individual to behave positively towards this specific partner as well (Schino and Aureli 2009). Emotions, thus, enable individuals to preferentially interact with those group members that have provided them with most benefits over a long-term period, rather



than on a short-term basis (Schino and Aureli 2009). This mechanism, called “emotional book-keeping,” is nowadays the leading hypothesis regarding the proximate mechanism giving rise to reciprocity and interchange of behaviors. Indeed, several empirical studies have shown that individuals reciprocate and interchange behaviors in the long-term rather than in the short-term, and that they do so with those partners, with whom they form long-lasting “social bonds” (Gilby et al. 2010; Jaeggi et al. 2013; Kopp and Liebal 2016; Silk et al. 2013).

### Biological Market Theory

Biological market theory attempts to explain not only how individuals exchange behaviors but also the variation in the degree of exchange. In some primate societies, researchers have consistently found a correlation between grooming given and the individuals’ dominance rank, i.e., individuals direct grooming up the dominance hierarchy. To explain this finding, Seyfarth (1977) reasoned that individuals use grooming as a “currency” to interchange for the receipt of support in fights and because individuals ranking high in the dominance hierarchy offer the best support, individuals should aim at interchanging grooming for support with them. Individuals, thus, should direct their grooming toward high ranking individuals. In some societies, however, the correlation between grooming given and dominance rank is either weak or absent, and in other societies, agonistic support is rare or absent but individuals still direct grooming up the hierarchy (Sánchez-Amaro and Amici 2015). Thus, to explain the differences in the distribution of grooming behavior observed in groups and species of primates, Henzi and Barrett (1999) introduced biological market theory into the primates’ social system.

Nöe and Hammerstein (1994) developed biological market theory to explain how individuals trade commodities in any given biological system. The theory assumes that whenever commodities cannot be acquired by force and are under the control of individuals, individuals may interchange commodities for their mutual benefit.

The theory assumes that, similar to human markets, in any given biological market there are two classes of individuals, producers and consumers; it also assumes that the rate of exchange of commodities is determined by the laws of supply and demand, i.e., when the commodity offered is rare, its value (and price to pay) should be higher than when it is common (Nöe and Hammerstein 1994). The theory, thus, assumes that individuals are able to choose trading partners according to the type of commodities they offer and the current rate of exchange. Henzi and Barrett (1999) extended this theory into primate societies. They argue that in primate societies, grooming is a valuable commodity that can be either traded for itself or for other commodities. If the dominance hierarchy in a primate society is steep, high-ranking individuals are able to monopolize resources; and in this case, subordinates may benefit by trading grooming for rank-related benefits, e.g., support, tolerance, food, etc. In shallow hierarchies, on the other hand, resources cannot be monopolized and, consequently, high-ranking individuals have no commodities to trade for. In this case, grooming would be exchanged only for itself, i.e., reciprocated. Grooming directed up the dominance hierarchy should then be expected when the dominance hierarchy is steep, but not when it is shallow (Henzi and Barrett 1999).

Several studies hinted at the operation of biological market theory in primate societies. For instance, in a meta-analysis on grooming reciprocation, Schino and Aureli (2008b) found that primate groups with steeper dominance hierarchies were associated with a higher tendency to groom up the dominance hierarchy and a lower degree of grooming reciprocation. Similarly, Barrett et al. (2002) studied a troop of Chacma baboons (*Papio ursinus*), in which the competitive regime differed at two different time periods. In period one, when the dominance hierarchy was steeper than in period two, the degree of grooming reciprocation was lesser than in period two. This finding was interpreted in support of biological market theory, arguing that individuals in these societies adjust their distribution of grooming to the fluctuation in the competitive regime of the group. Perhaps the best evidence in support of

biological market theory comes from an experimental study on two groups of wild vervet monkeys (*Chlorocebusaethiops*) by Fruteau et al. (2009). In their experiments, researchers first taught an individual to open a food device and provide food to its group members. Then, they measured the amount of grooming the food provider received in the hour after food was provided. In a second step, they taught another individual to open a second food device and provide food to others. Again, they measured the amount of grooming received by the food providers. Their findings showed that food providers received more grooming after being taught to manipulate the device and provide food to others, than at baseline levels. More interestingly, the amount of grooming the first provider received decreased after the introduction of the second food provider, but, nevertheless, this amount remained still higher than the baseline levels. The authors concluded that, as suggested by biological market theory, in these groups, grooming was fine tuned to the laws of supply and demand (Fruteau et al. 2009).

Despite these results, some researchers are skeptical about biological market theory. In a recent review, Sánchez-Amaro and Amici (2015) identified several issues, which according to them, need to be addressed to firmly confirm that primates trade behaviors as suggested by biological market theory. A first issue is that in all studies on behavior exchange, the time frame of interchange is undefined. Experimental studies find that individuals may interchange grooming for food within periods of 1–2 h (de Waal 1997; Fruteau et al. 2009). Observational studies on the other hand, find that interchanges happen in the long-term. Chimpanzees, for instance, reciprocate grooming and interchange meat for sex over periods that span up to 15–22 months, respectively (Gomes and Boesch 2009). This raises questions such as why primates interchange some behaviors in the short-term and others in the long-term? What is the biological significance of this? Is it valid to use different time frames across different studies/populations of primates (Sánchez-Amaro and Amici 2015)? Another

issue is the type of behaviors being exchanged. Grooming is usually thought to be the “currency” to be exchanged for several other behaviors. Thus, how do individuals know what grooming is being interchanged for (itself, food, support, etc.)? Similarly, how can researchers know what grooming is being exchanged for? (Sánchez-Amaro and Amici 2015). All these questions need to be answered, so that careful predictions can be formulated and tested with empirical data. Finally, besides the cognitive challenges previously identified (e.g., keeping records of behaviors given and received), there are some other cognitive skills that seem necessary for the biological market theory to be plausible. Individuals, for instance, should be capable to assess the number of producers and consumers in their group over time and adjust the relative value of the behavior being interchanged according to laws of supply and demand. Whether primates have the cognitive skills to do so or whether emotional bookkeeping can account for these, complex interchanges remains to be investigated (Sánchez-Amaro and Amici 2015).

## Conclusion

There is good correlational evidence that individuals in primates’ societies reciprocate and interchange different kind of behaviors (grooming, support in fights, food). It also seems likely that evolutionary processes such as kin selection and reciprocal altruism may have given rise to behavior exchange in primate societies. It remains unclear, however, what the proximate mechanisms underlying interchange and reciprocation of behaviors are, and whether these interchanges operate as predicted by biological market theory.

## Cross-References

- [Allogrooming](#)
- [Altruism](#)
- [Begging](#)
- [Behavioral Flexibility](#)

- Cooperation
- Counting
- Dominance Hierarchy
- Grooming
- Individual Recognition
- Kin Selection
- Long-Term Memory
- Nonhuman Primates
- Primate Cognition
- Reciprocity
- Short-Term Memory
- Social Grooming
- Tai Chimpanzees

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## Excretory System

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## Introduction

The excretory system is a vital biological system that removes excess and waste products from the body to maintain ► [homeostasis](#). Most of these products are in fact used and broken down components of metabolism that leave the body in the form of urine, sweat, or feces. While many organs are linked indirectly to the removal of metabolic waste, the term excretory system refers to those organs that are used strictly for the elimination and excretion of these broken-down components; this limits the focus of a discussion of the excretory system to mainly the urinary, or renal, system, which consists of the kidneys, ureters, a bladder, and a urethra. While there is a specific set of organs generally referred to as the excretory system, there are several auxiliary organs that play roles in other major body systems that help in the excretory system's function.

## The Central Role of the Kidneys in the Urinary System

The excretory system is largely associated with the urinary, or renal, system. This system consists of various organs that produce and then excrete the urine out of the body: the kidneys, ureters, the bladder, and the urethra. While many might assume that the urinary systems of males and females are incredibly different, they are in fact largely the same; the major difference between the two genders is the length of the urethra. The system has multiple functions: to eliminate metabolic waste matter, to regulate the pH of the blood, to regulate blood pressure and volume, and to control the levels of metabolites and electrolytes such as sodium, potassium, and calcium (Marieb and Hoehn 2001). To put it succinctly, urine is

formed in the kidneys and travels through the ureters to be stored in the bladder until it is expelled from the body through the urethra.

To begin the process of urine formation, the two kidneys remove nitrogenous wastes from blood that is supplied from the renal arteries. The right and left renal arteries are blood vessels that transport blood flow in the body into the kidneys (Fine and Keen 1966). Each artery splits into multiple branches before reaching the hilum, which is the center region of the kidney that recesses into itself. The renal veins drain the kidneys of blood after it has been filtered and send it through to the inferior vena cava. The inferior vena cava carries deoxygenated blood from the lower and middle body into the right atrium of the heart (Saladin 2007).

The basic functional unit in the kidney is known as the nephron, which acts as a filter and regulates water concentration and soluble substances such as sodium, filters blood, and controls the pH of blood (Jones et al. 2013). The kidney contains a varied range of nephrons from 500,000 to nearly two million nephrons in humans (Douglas-Denton et al. 2006). A glomerulus capillary and the Bowman's capsule lie where the nephron begins at the renal corpuscle. An afferent arteriole, basically a small blood vessel leading towards the glomerulus, supplies the glomerulus with blood. Because the efferent arterioles that lead away from the glomerulus are narrower than the afferent vessels leading towards the glomerulus, a hydrostatic pressure gradient is created that helps force water and solutes in the blood to be filtered into the Bowman's capsule. The afferent arteriole has a higher blood pressure, while the efferent arteriole has a lower blood pressure (Marieb and Hoehn 2001; Jones et al. 2013; Saladin 2007). The membrane is impermeable to larger molecules such as proteins (Marieb and Hoehn 2001).

The filtrate travels into the renal tubule and then into the collecting ducts. In the collecting ducts, the normally water impermeable duct becomes permeable due to antidiuretic hormones, or ADH, that affect aquaporins, membrane proteins that facilitate water transport while preventing passage of other solutes. ADH

leads to the reabsorption of water through osmosis. Osmosis occurs when the concentration of a solute is higher in one region than it is in another; solutes go down the gradient into the region with a lower concentration to equal out (Nielsen et al. 2002). Solute in the filtrate, such as water, glucose, amino acids, and other ions like sodium, are reabsorbed by nephrons, excreting what is not needed as urine. Excess water and nitrogenous waste products such as urea, uric acid, and creatinine are not reabsorbed (Marieb and Hoehn 2001). This means that antidiuretic hormones control the concentration of urine. During dehydration, ADH levels increase when the individual is dehydrated to retain water. Conversely, ADH levels decrease when the individual has had plenty of water, leading to the dilution of urine. Urine leaves these collecting ducts into the renal calyces and then the renal pelvis on its way into the urinary bladder (Marieb and Hoehn 2001).

The renal pelvis is at the mouth of the ureter and acts as a funnel to flow urine into the ureter, collecting urine from the surrounding renal calyces (Marieb and Hoehn 2001). The calyces are chambers of the kidney; urine travels from the kidneys into minor calyces that come together to form a major calyx. The walls of the calyces all lined with smooth muscle fiber that undergo peristalsis, or rhythmic constriction and relaxation to create wavelike movement that pushes the urine through the renal pelvis into the ureters to the bladder (Longrigg 1975; Saladin 2007). Urine is stored in the bladder and then released through the urethra in a process known as urination (Saladin 2007).

## Kidney Stones

When substances that normally dissolve in urine do not, they can build up and form kidney stones composed of calcium, cysteine, oxalate, and uric acid that normally do dissolve in urine. Kidney stone classification is determined by their location of ► [occlusion](#) or their compositional makeup. When they are in the kidney, they are referred to



as nephrolithiasis, in the ureter they are called ureterolithiasis, and in the bladder, they are called cystolithiasis. Kidney stones get stuck in the urinary tract but are usually small enough to pee out. Sometimes, however, the kidney stones get lodged in the ureter and begin to grow even more. The larger a stone becomes, the less likely it is to pass through the urine spontaneously (Stoller and Meng 2007). This can cause great discomfort and pain as it blocks the flow of urine. The excruciating pain that people experience when they do not pass through the urine stream due to their large size can last up to an hour as the ureter contracts and relaxes to push the stone out. It can also cause nausea or vomiting (Coe et al. 2005).

A urologist often treats kidney stones with shock wave lithotripsy, a procedure that involves using a laser to shock the large kidney stone into several smaller pieces that can be more easily urinated (Stoller and Meng 2007). Major risk factors are obesity, high fructose consumption, dehydration, and a surplus of calcium, oxalate, sodium, and animal protein in the diet (Romero et al. 2010). The pH of urine is an underlying factor that can cause supersaturation of urine. Supersaturation occurs when the urine contains more solvents than it can hold, resulting in buildup. Once nucleation, when molecules begin to stick together and crystalize, has begun, it begins to form much quicker. There is heterogeneous and homogenous nucleation. Heterogeneous nucleation requires less energy because it involves an existing surface on which to grow, while homogenous nucleation of a kidney stone must grow in the urine alone. For kidney stones formed due to uric acid or cysteine, the pH of urine plays a larger role than for calcium-based stones. As the pH of urine decreases, the solubility of uric acid in urine decreases as well (Coe et al. 2005). A higher solubility means something dissolves more easily; in this more acidic environment, the lower solubility means that uric acid begins to accumulate and solidify much easier in urine. Kidney stone prevention can involve alkalinizing agents to raise urine pH to over 6.5 to avoid the formation of stones (Worcester 2002).

## The Liver

The liver performs a variety of vital functions. It produces bile, which is secreted into the small intestine to emulsify fat and promote digestion. It performs various tasks in carbohydrate metabolism, such as the creating and storing glucose in glycogen until needed. With regards to excretion, the liver metabolizes amino acids and converts the ammonia that results into urea, which is a nitrogenous waste, found in urine (Saladin 2007). In birds, the liver also excretes uric acid, the white pasty substance that can be seen in the excrements of birds (Kotz et al. 2008). The liver excretes excess cholesterol and calcium using bile. In addition, the liver can detoxify alcohol, antibiotics, and other drugs. Bilirubin is metabolized from red blood cell breakdown and excreted as bile pigments as well (Saladin 2007).

## The Role of the Large Intestine in the Gastrointestinal Tract

When many people think of the excretory system, they do not always picture the urinary system. For many people, the excretory system is largely embodied by the role of the large intestine, which mainly absorbs water. The large intestine, also known as the large bowel, consists of the cecum, colon, rectum, and the anal canal. It makes up the final part of the gastrointestinal tract and is around 5 ft long. The gastrointestinal tract is responsible for food digestion and the extraction and absorption of energy and nutrients. The remaining waste is removed as either feces or urine, so the gastrointestinal tract is closely linked to the excretory system (Saladin 2007).

The ► **digestive system** is comprised of the mouth, esophagus, stomach, and the large and small intestines. This entry focuses on the gastrointestinal tract, a term which refers to small and large intestine, due to the more direct role in excretion these organs play. The small intestine is an organ that absorbs digestion products like carbohydrates, proteins, and vitamins into the bloodstream. It comprises three sections that in order are called the duodenum, the jejunum, and



finally the ileum. In the first section, the stomach's contents, pancreatic juice and bile secreted from the liver are mixed. The pancreatic juice neutralizes stomach acid, while the bile emulsifies fat. The jejunum is where most digestion and nutrient absorption into the bloodstream occurs, while the rest continue to the ileum (Saladin 2007). The ileum absorbs vitamin B12, bile acids, and other nutrients that remain in the waste product as it continues to the large intestine (Van der Heide 2016).

The large intestine's cecum starts attached to the small intestine's ileum. As it ascends into the abdomen and then moves laterally to the other side of the abdominal cavity, it is referred to as the colon and then the transverse colon. The transverse colon then descends, forms an S-shape known as the sigmoid colon, and turns into the rectum and then to the anal canal. The lower region of the large intestine extracts usable water from the waste before it is removed as solid brown feces during defecation. The large intestine neither produces nor contains digestive enzymes, as digestion is completed in the small intestine. The brown color comes from a compound called urobilinogen (Saladin 2007). A pigment urochrome is the cause of the yellowish tint of urine (Marieb and Hoehn 2001).

The first section of the colon contains the cecum and the appendix and is involved in digestion. The ascending colon is attached to the cecum and is responsible for removing water and recycling nutrients from waste material as it leaves the small intestine (Saladin 2007). Peristalsis is responsible for pushing waste material up towards the transverse colon that runs latitudinal to where it turns by the spleen. At this point, fecal matter is largely liquid due to the immense secretions during digestion, but as the waste material moves forward the excess water is extracted and the fecal matter begins to solidify as it moves towards the descending colon for storage. The sigmoid colon is S-shaped and connects the descending colon to the rectum. Lined with muscle, the walls of the sigmoid colon contract and move the stool into the rectum that holds it until defecation through the anus (Saladin 2007).

Once again, peristalsis is the method of transportation in the process called defecation (Saladin

2007). Frequency of defecation can vary from a few times daily to a few times weekly. Waste fills the rectum and encounters mucosa in the lower rectum, acting as a signal that it is time to defecate. When humans feel a need to defecate, it is because of rectal muscles contracting reflexively, the internal anal sphincter relaxing, and the external anal sphincter contracting (Biggs and Dery 2006; Nurko and Zimmerman 2014). The internal anal sphincter is an involuntary muscle that is nearly always contracted to prevent the leakage of waste matter. Fecal matter enters the anal canal when the internal sphincter relaxes as the rectum shortens due to peristaltic waves that push the feces out, and the external sphincter contracts to defecate (Shafik 1987; Penninckx et al. 1992). If an individual does not defecate in a timely manner, reverse peristalsis moves the waste product back into the colon where even more water is absorbed. As expected, prolonging defecation can lead to feces hardening, resulting in constipation (Nurko and Zimmerman 2014). Diarrhea occurs from the opposite, when people defecate waste material too fast and excess water has not yet been reabsorbed (Saladin 2007).

When people expel solid waste, it has been noted that urination often occurs simultaneously, despite being involved in two separate processes with separate organs. This is because the anal and urethral muscles are linked and can only contract together. When the external sphincter muscles relax during defecation, the urethral sphincter relaxes as well, releasing urine from the bladder. Normally, both the internal and external urethral sphincter is contracted, sealing the urethra and preventing urination. The internal urethral sphincter is a smooth muscle that is under involuntary control and is responsible for inhibiting urination. The external sphincter is made up of skeletal muscle, allowing for voluntary control over urination (Marieb and Hoehn 2001; Saladin 2007).

The large intestine plays another minor role of excretion but of the third phase of matter. While feces embody solid waste and urine expels liquid waste, the bacteria present in the large intestine help produce gaseous waste. Flatus, the gas that is generated in the intestinal tract because of bacterial activity, can contain gases such as

nitrogen, carbon dioxide, methane, hydrogen, and hydrogen sulfide (Calloway et al. 1966).

## The Skin and Sweat Glands

Sweat glands excrete sweat throughout the body to help cool the body when it gets warm in a process called perspiration. Sweat is therefore another form of waste, and it tastes salty because of the presence of sodium chloride, or NaCl, a salt that helps in evaporation (Saat et al. 2005). Sweat is a dilute electrolyte solution that also contains mainly water but also urea, fatty acids, lactic acid, proteins, and various other components (Draeos 2011).

In humans, the release of sweat helps to regulate levels of salt as well as to remove urea from the body (Huang et al. 2002). In reabsorption, sodium and chlorides pass through ducts such as a Na/K ATPase pump or the chloride channel cystic fibrosis transmembrane conductance regulator, or CFTR (Wilke et al. 2007). Epithelial sodium channels located on eccrine gland membranes also perform the task of reabsorbing sodium ions that are secreted in sweat (Stutts et al. 1997). A deficient epithelial sodium channel, such as in the case of cystic fibrosis, results in salty sweat because the sodium ions are not reabsorbed into the body and remain in the sweat (Di Sant'Agnese et al. 1953). While sweat contains urea, its small concentration suggests that the role of sweat is primarily to regulate body temperature and not to excrete harmful substances from the body (Huang et al. 2002).

There are two main types of sweat glands: eccrine and apocrine sweat glands. Eccrine glands are found throughout the body, especially on the palms and soles of the feet, and help secrete excess water from the body. Eccrine sweat glands play a central role in ► [thermoregulation](#) and are vital to life and are functional from birth. All the sweat glands in the human body together would resemble the size of a kidney. Humans can perspire, or sweat, nearly 10 liters a day (Wilke et al. 2007; Sato 1977). Sweat gland activity is controlled by the central ► [nervous system](#) and the ► [hypothalamus](#) (Wilke et al.

2007). Eccrine sweat contains sodium, chloride, potassium, calcium, lactate, ammonia, amino acids, urea, bicarbonate, as well as proteins (Wilke et al. 2007).

The scent of sweat comes from bacterial activity on apocrine sweat gland excretion. Apocrine sweat glands are larger than eccrine glands and are commonly found in the armpit and between the anus and genitals, and other hairy sites on the body. This is because they secrete into the hair canal rather than onto the skin itself. They do not play a role in the excretory system and only begin functioning during ► [puberty](#) due to hormonal changes (Wilke et al. 2007). The secretions of apocrine glands contain nutrients for bacteria on the skin, and when the sweat decomposes it creates an odor. A third type of sweat gland is the apoeccrine gland, which is a mixed gland that is thought to also be found in hairy areas. They are believed to develop from eccrine glands once an individual hits puberty, since the proportion of eccrine glands decreases as people get older. Due to their origins, they also secrete sweat with a similar composition when it comes to concentrations of molecules like sodium and potassium to that of the eccrine glands. Apoeccrine glands have higher overall sweat rates and so are believed to contribute heavily to sweating in areas like the armpits (Wilke et al. 2007).

## Summary

The excretory system consists of several organs that aide in the removal, secretion, or elimination of metabolic waste products and other harmful substances that are created in the body as a means of achieving homeostasis. The kidneys and their nephrons filter blood using a semipermeable membrane as it makes its way through the body as a part of the circulatory system. The filtrate that is produced travels through the urinary system and is expelled from the body out the urethra during a process known as urination. Kidney stones served as an example of the dangers of what occurs when material that should be dissolved into the urine is not. The liver performs a variety of functions, including the production of

bile and the creation of urea or uric acid. Urea is a major component of urine. The large intestine is a part of the digestive system and gastrointestinal tract that is responsible for extracting water from solid waste matter passing through from the small intestines. This waste matter exits the body as feces or stool out of the rectum or anal canal during defecation. When waste matter is not released or released too early, these are signs of constipation as the stool hardens too much or even diarrhea as excess water is not removed properly. Finally, the skin and sweat glands help to release hazardous elements such as urea. However, the minute levels detected of these suggest that the larger role of sweat and perspiration is thermoregulation.

## Cross-References

- Digestive System
- Homeostasis
- Hypothalamus
- Nervous System, The
- Occlusion
- Puberty
- Thermoregulation

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## Executive Function

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## Introduction

Executive function (EF) is a heterogeneous construct widely used to refer to a conspicuous number of higher-order cognitive processes devoted to the monitoring and control of thoughts and actions. EF is generally regarded as being particularly important in novel or unfamiliar situations in which thoughtful and cautious behavior, instead of automatic and impulsive response, is required (Diamond 2013). The functioning of executive processes is thought to rely on the prefrontal cortex (PFC) in both humans and non-human animals, regardless of the anatomical variations existing across different species (Robbins 2000).

Despite the fact that EF is still often mentioned as a unitary system, there is growing consensus that regards it as a multidimensional construct including separable components. A possible clarification on the architecture of EF comes from factor analyses conducted on human populations (school-aged children, adolescents, and adults), which have identified three core components (Miyake et al. 2000). First, inhibitory control, defined as the ability to suppress a prepotent

response in order to achieve a relevant goal. Importantly, individuals can exert inhibition by not only suppressing an impulsive response, but also initiating a subdominant (conflicting) action at one time. Second, working memory, which refers to the cognitive processes designated to hold information in mind in order to recall and work with it at some point in the future. Third, cognitive flexibility, which facilitates adjustment to changes and perspective shifting to solve a problem. Evidence from neuroimaging studies gives further support to the non-unitary organization of EF, showing that different areas of the PFC subserve different EF components in both humans and nonhuman animals. However, a clear distinction between EF components is pretty challenging in experimental practice, since a task that is supposed to purely examine a given EF component is concurrently likely to elicit other nonrelevant cognitive processes.

In humans, EF and its neural correlates were discovered in brain-injured patients in the nineteenth century. Later on, research focused on war veterans with brain injuries and on patients affected by neuropsychiatric disorders such as attention-deficit/hyperactivity disorder (ADHD), obsessive compulsive disorder, and schizophrenia. Poor EF is associated with overeating, substance abuse, and social problems, whereas good EF predicts success in school and overall quality of life. Over the past two decades, EF has been the object of notable comparative studies, which have mainly involved nonhuman primates and rodents. In particular, behavioral and neurobiological investigations in animal models allowed us to comprehend the relative contribution of the different areas of the PFC to the diverse EF components. In the ensuing sections, a brief overview of the most up-to-date literature on EF in human and animal populations is presented, with a special focus on comparative approaches.

## Inhibitory Control

In humans, inhibitory control is considered a highly adaptive ability, as it involves voluntary control over some of the most important processes for an individual's social adjustment, such as

internal states (e.g., intentions, emotions, and beliefs) and behavior. This ability emerges early in development and starts to become evident and measurable in the first years of life. However, inhibitory control is subject to noticeable improvements during the preschool period, between 3 and 6 years of age, and becomes more specialized throughout adolescence. The preschool age is a crucial period for the development of inhibitory control as, if children are more able to exert self-control at this age, they are more competent in social situations, less prone to risky behavior, and more likely to show better academic performance later in life. In comparative research, human beings show better inhibitory control than nonhuman animals and, among the latter, considerable interspecific differences, which are likely related to their feeding ecology, have been reported (MacLean et al. 2014). Two classes of tasks are generally used to assess inhibitory control: conflict and delayed gratification tasks. In conflict tasks, individuals are required to suppress a dominant response and to concurrently provide a subdominant response. In delayed gratification tasks, individuals are required to wait in order to obtain something pleasant in the future.

Examples of conflict tasks are the A-not-B task, the detour-reaching task, and the reverse-reward contingency task. In the A-not-B task, the subject repeatedly observes the experimenter hiding an object at location A; then, after a few trials, the experimenter hides the object at location B. Incorrect attempts of retrieving the object by searching at location A denote prepotent motor responses. Children begin to succeed in this task by 10–12 months of age (Diamond 2013). Among nonhuman primates, considerable interspecific differences have been observed, with apes showing a better performance than several monkey and lemur species (MacLean et al. 2014). In the detour-reaching task (or object-retrieval task, Diamond 2013), the subject has to inhibit from reaching directly for a visible reward, which is placed behind a clear barrier or inside a transparent container with open ends. To obtain the reward, the subject must detour around the barrier and reach from the side. Very young infants show a prepotent tendency to reach directly for the visible reward, and they begin to succeed around

their first birthday. As with the A-not-B task, in the detour-reaching task children and apes show a better performance than several monkey and lemur species (MacLean et al. 2014). Importantly, in all species tested so far, a better performance is achieved when the barrier blocking the reward is opaque rather than transparent. In the reverse-reward contingency task, the subject is faced with a series of choices between different quantities or types of reward and has to select the smaller/less preferred option to receive the larger/more preferred one, thus inhibiting the spontaneous tendency to reach toward the larger/more preferred reward. All the populations tested so far (preschool children, lemurs, monkeys, and apes) were more successful when appetitive rewards were replaced by symbolic stimuli, which decrease the attractiveness of the options and the consequent impulsive responses toward them.

Delayed gratification tasks include delay choice and delay maintenance tasks. In delay choice tasks, the subject is presented with a series of choices between a small/less preferred reward, immediately available, and a larger/more preferred reward, available after some delay. Individuals often prefer the immediate option, demonstrating a devaluation of future outcomes: a process known as delay (or temporal) discounting. In delay maintenance tasks, after an initial choice to delay gratification, the subject is required to actively maintain the decision to wait for the large/more preferred reward throughout the delay, since the immediate, small/less preferred option remains continuously available. Importantly, the few studies that have tested the same subjects in delay choice and delay maintenance tasks (within human, nonhuman primate, and rodent samples) have found modest or scarce correlation between performances, as these tasks tapped different components of inhibitory control (Addessi et al. 2013).

## Working Memory

In 1974, Baddeley and Hitch proposed a theoretical model of working memory, which includes the ability to retain information no longer present in the environment into short-term storage and to



mentally manipulate a limited number of items during complex cognitive tasks. Working memory consists of three components: (i) the central executive, which provides processes of attention and control of information, (ii) the phonological loop, specialized in verbal information processing, and (iii) the visuospatial sketchpad, specialized in nonverbal information processing. Since then, working memory has been theorized in increasingly sophisticated forms, underlining its central role in important cognitive processes, such as language, reasoning, problem solving, and academic success (Towse and Cowan 2005). Baddeley (2000), for instance, has proposed a fourth component of working memory, the episodic buffer, which provides temporary storage of information held in a multimodal code.

Human infants, beginning from 9 to 12 months of age, can hold few items in mind. Then, working memory develops gradually over childhood and adolescence, probably due to an enhancement in the speed of information processing and in the capacity to inhibit interferences, and considerably declines in older adults, likely due to the higher vulnerability to interferences and to a decreased inhibitory control (Diamond 2013).

In humans, working memory is often assessed through the dual-task paradigm, which requires individuals to complete a memory span task and a processing task at the same time. In nonhuman animals, working memory is evaluated by means of tasks that require the subject to choose a reward location after a delay. The spatial delayed response task is used to investigate working memory in both humans and nonhuman primates. In this task, the subject observes the experimenter baiting one of two (or more) locations. Then, all locations are covered with identical objects, and a barrier is placed between the subject and the food locations. After a delay, the barrier is raised and the subject is allowed to choose the baited food location. As in humans, also non-human primate individuals are less accurate as delay increases; moreover, performance critically depends on dorsolateral PFC functioning and declines with age. The delayed alternation task is used to assess working memory in rodents by means of a T- or Y-maze apparatus. On the first trial, rats are

rewarded for entering either of the choice arms. From the second trial on, rats are only rewarded if they enter the arm which was not chosen on the previous trial and working memory is assessed by varying the delay between successive trials.

## Cognitive Flexibility

Cognitive flexibility, also known as set shifting or mental set shifting, involves the capacity to rapidly switch between different perspectives and implement novel strategies to cope with adverse situations or changed circumstances. In humans, cognitive flexibility emerges later and improves more slowly than the other EF components; as working memory, it also declines with age (Diamond 2013).

In most tasks used to assess cognitive flexibility, participants are required to switch from one mental set to another, according to the feedback provided by the experimenter. A classical task used to investigate cognitive flexibility is the Wisconsin card sorting task. This task requires the subject to sort a deck of cards according to a certain feature (color, shape, or number), which is learnt by trial and error through the feedback provided by the experimenter. Then, during the experiment, the sorting criterion changes without notice, and the participant is required to infer the new sorting criterion on the basis of the experimenter's feedback and to flexibly switch to sort cards according to the new perceptual feature. Performance in this task depends on dorsolateral and orbital PFC functioning (Dias et al. 1996). Attentional set-shifting tasks can be used to compare cognitive flexibility between humans and nonhuman species. In these tasks, an extra-dimensional shift occurs when the participant is initially trained to respond to one of the two dimensions of a stimulus composed of two dimensions and is subsequently required to respond to the alternative stimulus dimension. In contrast, an intra-dimensional shift occurs when the participant is required to respond to different stimuli characterized by the same dimension. Extra-dimensional shifting takes significantly longer to be learnt than intra-dimensional shifting



(Chudasama 2011). Three-year-old children can pass tests where they need to invert a rule while the features of the stimuli remain unvaried (*response shifting*). In contrast, they encounter difficulties when perceptual aspects of the stimuli change (*attention shifting*). Such distinction is well supported by neuroimaging studies indicating that, in both humans (children and adults) and nonhuman animals, response and attention shifting are linked to different areas of the brain, with the first being connected with the medial frontal areas and the second involving the lateral frontal areas (Garon et al. 2008). In a particular version of the attentional set-shifting task adapted for rodents, individuals are required to discriminate between stimuli that differ on odor and texture in order to retrieve the reward (Birrell and Brown 2000). The reversal learning task is also widely used to evaluate cognitive flexibility in humans and nonhuman animals (Chudasama 2011). In this task, the subject initially learns that the response to one of two stimuli is consistently rewarded. Then, the stimulus-reward contingency is reversed, and the subject must flexibly switch to select the alternative option in order to be rewarded. Performance in this task is highly sensitive to orbital PFC lesions and to serotonin depletion, but not to dopamine depletion.

## Cross-References

- [A-not-B Problem](#)
- [Delayed Gratification](#)
- [Detour Task](#)
- [Working Memory](#)

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## Executive Monkey Study

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## Historical Development of “Psychosomatic Medicine”

The “executive monkey” study, which was published over 60 years ago in 1958, remains in all probability the most well-known experiment in a field referred to as Psychosomatic Medicine. Given its prominence in this field, we will therefore consider the definition and historical development of the concept of Psychosomatic Medicine before describing the details of the “executive monkey” experiment and its findings. That mental or psychological events could

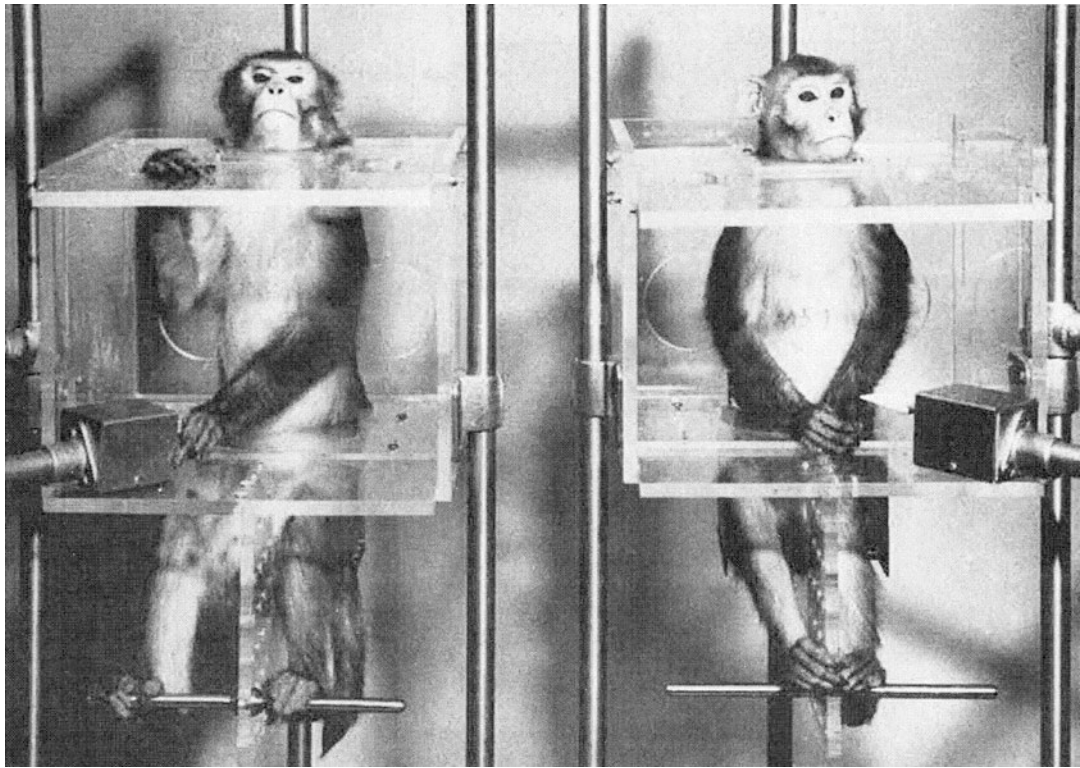
influence disease was known as far back as the early Greeks, as Hippocrates and Galen proposed that mind and body were inseparably linked and that physical wellbeing was tied to psychological wellbeing (e.g., Coxe 1846). Similar sentiments were expressed during the centuries that followed, so that by the eighteenth and nineteenth centuries one finds definitive pronouncements that psychological factors profoundly influence disease. For instance, Daniel Hack Tuke, the prominent British physician and psychiatrist, published a volume in 1872 titled “Illustrations of the Influence of the Mind Upon the Body in Health and Disease” (Tuke 1872) in which he described thought processes and emotions both causing/exacerbating disease as well as ameliorating it (for a detailed quotation from Tuke in this regard, see introductory section Weiss 1972). The relationship between psychological processes and bodily function (symptoms and disease) soon received new attention with the studies and writings of Sigmund Freud at the end of the nineteenth century when he hypothesized that psychic conflicts could find expression as physical disabilities in hysteria (Freud, 1890–1893; translated by Strachey, 1955).

The early to mid-twentieth century saw a renaissance of interest in what came to be known as psychosomatic medicine – the relationship of psychological events to somatic disease. An excellent recounting of this history can be found in an article by Lipowski (1984). He finds the term “psychosomatic medicine” to have been first used in 1922. Important events thereafter were the publication in 1935 of Helen Flanders Dunbar’s book titled, “Emotions and Bodily Changes: A Survey of Literature on Psychosomatic Interrelationships” (Dunbar 1935), followed by the founding of the Journal “Psychosomatic Medicine” in 1939. Psychoanalytic analysis introduced by Freud reached perhaps its highest development in relation to somatic disease in the work and writings of Franz Alexander, who saw a variety of different diseases as resulting from specific intrapsychic conflicts (Alexander 1950). In the case of peptic ulcer, Alexander posited that this pathology resulted from the ulcer patient’s unconscious desire to be dependent and taken care of while at the same time adhering to the compulsion

to act independently and assertively, with the unconscious desire resulting in the need to be constantly fed causing chronic hypersecretion of stomach acid and eventual ulceration. Needless to say, it is difficult, if not impossible, to see how this intrapsychic conflict could explain the duodenal ulcers that were found in the “executive” monkeys, and as the result of challenges such as this as well as other psychoanalytic explanations were soon viewed as conjectural and unlikely to be correct. Meanwhile, controversy raged within Psychosomatic Medicine as to whether mental events could actually cause disease (called “psychogenesis”) or whether mind and body were really inseparable and that disease resulted from physiological processes necessarily involving interplay of psychological and somatic factors. While the field has settled on the latter view (as evidenced in the Lipowski article), even at the present time the term “psychosomatic” is commonly used to mean that psychological influences lead to disease. For example, in 2016, author Claudia Kalb described Charles Darwin’s continuing gastrointestinal problems, asking whether these problems might have been caused by an infectious tropical bug picked up in his travels aboard the ship *Beagle* or “were Darwin’s lifelong symptoms psychosomatic – physical manifestations of ongoing mental stress?” (Kalb 2016).

### **The “Executive Monkey” Experiment: Description and Findings**

Turning now to the “executive monkey” experiment, this experiment utilized pairs of rhesus monkeys, ultimately four pairs of monkeys. The two monkeys of each pair were restrained in chairs as shown in Fig. 1. The monkeys were subjected to intermittent electric shocks that one member of each pair, shown at the left side of the figure, could control by pressing a lever in front of it which postponed occurrence of the next shock, so that shock only occurred when this monkey, dubbed the “executive monkey,” failed to activate its lever. The second member of the pair also had a lever mounted at the front of its chair but the lever was inactivated so that this monkey received the



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**Executive Monkey Study, Fig. 1** A pair of rhesus monkeys in chairs as used in the “executive monkey” study. The monkey on the left is controlling (avoiding) delivery of shock to its feet by pressing the lever mounted at the front of its chair, while the monkey on the right (yoked

monkey) receives the same shocks as the avoidance, or “executive,” monkey at the right. The yoked monkey also has a lever mounted at the front of its chair, but this lever is inactive and the yoked monkey is not attending to it. As shown in Brady (1958) Scientific American article

same shocks as did the “executive” but did not have any control over shock occurrence. Thus, one monkey of the pair exerted control over the occurrence of shock while the other monkey, called the “yoked” monkey, had no control, with both monkeys receiving the same shocks throughout the experiment.

This experiment attracted so much attention because, when the monkeys were maintained in these experimental conditions for many days, the “executive” monkeys eventually died apparently as a result of gastrointestinal pathology including lesions and perforating ulceration, while the “yoked” monkeys developed no such pathology and lived on. It thus appeared that being the “executive” and exerting control caused pathology and death, whereas not exerting control avoided this detrimental outcome.

The history of how the experiment unfolded is important for understanding and interpreting the results. The first report of the procedure described above appeared in the Journal “Psychosomatic Medicine” in 1958 in an article for which R.W. Porter was the first author (Porter et al. 1958). Titled “Some Experimental Observations on Gastrointestinal Lesions in Behaviorally Conditioned Monkeys,” the article describes that in various behavioral studies being undertaken with rhesus monkeys at Walter Reed Army Medical Center in Washington, DC, gastrointestinal pathology leading to death began to show up in many of the animals. The procedures performed on monkeys confined in chairs as shown in Fig. 1 involved conditioned anxiety (shock paired with a signal) and punishment (shock given for performing a response otherwise rewarded with

a sugar pellet), as well as a combination of such procedures. Eleven of nineteen animals undergoing such procedures died during the experiments, and on autopsy gastrointestinal pathology was discovered as the likely cause of death.

The paper by Porter et al. concludes with a description of the first two pairs of monkeys that eventually constituted the “executive” monkey study. In an attempt to determine that behavioral conditions led to the pathology seen in the 11 monkeys described above – which the investigators strongly believed to be the case – and perhaps gain insight into what conditions could do this, two monkeys were subjected to a shock avoidance paradigm, this being the lever press contingency whereby these two animals were made to avoid/control shock by pressing the lever at the front of their chair. The avoidance procedure, however, leads to animals receiving electric shocks, so that any pathology eventually observed could be simply a result of the physical stressor of electric shock being given to the monkeys and not because of the behavioral condition of performing an avoidance response. In order to rule out the possibility that electric shocks alone might produce the pathology eventually seen, this aspect of the experiment included a “yoked” animal for each avoidance monkey, these yoked animals having no control over shock and not engaging in avoidance responding but receiving the same shocks as the monkeys performing the avoidance response. If these yoked animals did not develop pathology, it would be evident that the electric shock itself did not cause such pathology. It is of note, therefore, that the “executive” monkey experiment was not designed to determine the effects of having control versus not having control in a stressful situation, as subsequent scientific and popular perception seized upon, but included yoked animals (i.e., animals having no control) to rule out electric shock as the cause of pathology. That the yoked animal was included in the study to exclude electric shock as being responsible for development of pathology is explicitly stated in the subsequent summary article that appeared in *Scientific American* (Brady 1958).

A second important paper appeared later that year in which findings from “executive”-yoked pairs reached  $n = 4$  (eight monkeys); similar

results were seen with the addition of two pairs of monkeys as reported in the first paper described above. Thus, in the total of four pairs, which constituted all of the animals eventually reported for the “executive monkey” study, all four “executive” monkeys died of gastrointestinal pathology whereas the four yoked animals showed no behavioral impairment, and, when sacrificed, showed no G.I. pathology (Brady et al. 1958). Following this, the most famous article describing these results – “Ulcers in ‘Executive’ Monkeys” – appeared in *Scientific American* and presented the data from the four pairs of monkeys (Brady 1958).

That receipt of electric shock was not the cause of the pathology seen in these monkeys becomes even more evident when the schedule for delivery of shock and the avoidance behavior it generated is examined (Brady et al. 1958; Porter et al. 1958). The avoidance schedule to which the “executive” monkeys were subjected is called a “Sidman avoidance schedule” named after its developer, Dr. Murray Sidman. In this schedule, shocks were not preceded by any warning signal, and brief shocks (5.0 mA intensity, 0.5 s in duration) were given every 5.0 s (shock delivered to the feet of the animals) unless the active lever is pressed in which case the next shock was delayed for 20 s. Thus, unsignaled shocks occurred in a train of one brief shock every 5.0 s unless an avoidance response was made which then delayed the onset of the next train of shocks for 20 s. When this schedule was in place, “executive” monkeys (i.e., avoidance monkeys) proved remarkably proficient at acquiring and practicing the lever press response to avoid (i.e., postpone) shock. The investigators report that within a few hours of the beginning of training, stable avoidance responding emerged, the avoidance monkey making approximately 15–30 responses per minute. This response rate remained essentially unchanged during the entire experiment. As a result, shocks received by the monkeys never exceeded 2 per hour and typically averaged less than 1 per hour. Thus, very few shocks were received by the monkeys throughout the course of the experiment; shocks occurred so infrequently it is not surprising that the results revealed (by inspection of yoked animals) that this physical



stressor did not generate gastrointestinal pathology.

Describing the course of the experiment and the development of pathology, the animals were confined in the chairs as shown in Fig. 1 continuously. Each day of the study was divided into “time-in” periods lasting 6 h during which shocks would occur (and the executive [avoidance] monkey therefore was going to respond to control shock and the yoked monkey also received shock if the avoidance monkey did not avoid shock) and “time-out” periods also lasting 6 h when no shocks would occur. These periods alternated, so that a 24-h day consisted of two 6-h “time-in” periods and two 6-h “time-out” periods. The presence of the “time-in” phase was signaled by illumination of a red light in full view of both animals of the pair. Regarding development of gastrointestinal pathology and death of the “executive” animals, one died after 9 days of this procedure while the other three died after 23, 25, and 48 days. Pathology found in the “executive” monkeys was gastric hemorrhage and erosions as well as duodenal ulcers that perforated in two instances. When the yoked monkeys were sacrificed shortly after the death of their matched “executive” partners, yoked monkeys showed no evidence of any gastric pathology.

In the *Scientific American* article by Brady (1958), a brief description is given of other testing conditions (described as being “still in progress”), such as prevention of social interaction between the two monkeys and exposure to different time-in, time-out intervals for responding. However, the details of these studies were not given nor, more importantly, were these procedures and their outcome described in any subsequent formal publication, so the number of monkeys that comprised the “executive monkey” study remains four pairs of animals.

### **Subsequent Research: Being Able to Control Found to Reduce Stress and Pathology**

Popular press and scientific researchers quickly realized that the “executive” monkey study compared animals that had control over a stressor (i.e.,

monkeys able to perform the avoidance response) with yoked animals that did not have any such control, and so the effects observed were viewed as the consequences of exerting control versus not having that ability, or, as the results suggested, that responsibility/burden. The study was thenceforth seen in this light, despite the fact that, as explained above, the investigators who carried out the experiment did not intend to study effects of having control versus no control but, instead, included yoked monkeys to set up what is called a “control condition” to rule out the possibility that shock alone produced pathology. Regardless, the “executive monkey” study was thereafter seen as demonstrating the effect of having control versus no control.

While the pathological findings of the “executive monkey” study seemed plausible given the amount of responding by the avoidance monkeys versus the nonresponding of the “yoked” monkeys, other data looking at the consequences of having control versus noncontrol, though extremely limited in amount and scope, did not point to the same conclusion. In 1948, O. Hobart Mowrer and his student P. Viek had found that rats able to control (terminate) an electric shock by jumping into the air showed less subsequent fear (i.e., were more willing to approach and eat food) than were rats that received equal shocks but could not terminate them (Mowrer and Viek 1948). Though it was obvious that the conditions of the “executive monkey” study and the experiment by Mowrer and Viek were very different, the contrasting findings suggested that the consequences of having control versus no control might not be described comprehensively by what was seen in the “executive monkey” study. Following publication of the “executive monkey” findings, however, no additional experimental results looking at consequences of having control versus no control appeared for approximately 10 years, but then new findings were reported at this time.

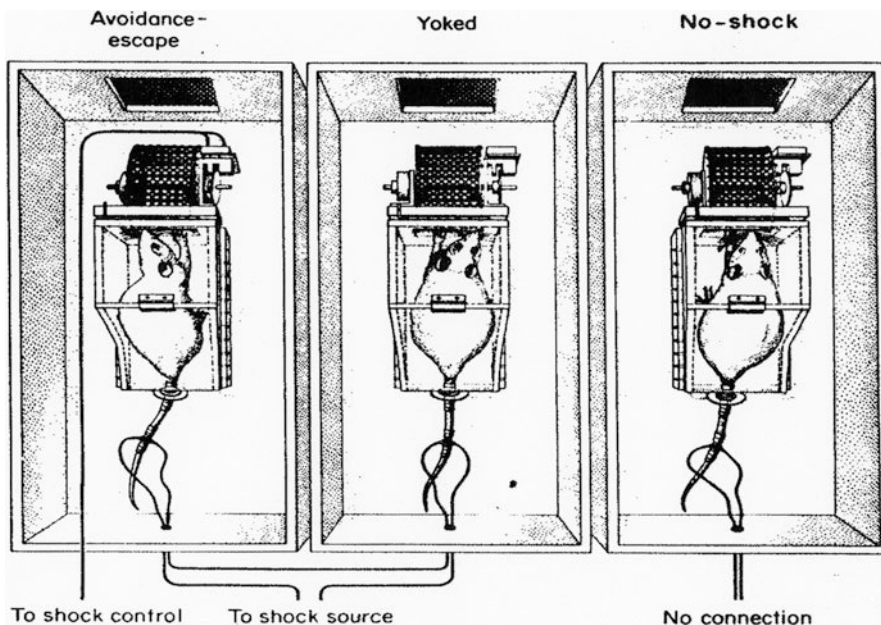
In 1968, 10 years after publication of the “executive monkey” study, the findings of my Ph.D. dissertation research were published in which rats were the subjects (Weiss 1968). These data also pointed to a conclusion opposite to that suggested by the “executive” monkey study,



indicating that control over a stressful event lessened consequences of stress and stress-induced pathology. This study examined effects of having control versus no control over electric shocks on (a) body weight and food/water intake, (b) fearfulness as measured by willingness of the rats, when thirsty, to drink in the control versus no control environment, and (c) development of gastric pathology (gastric erosions). Using matched triplets of rats in which one rat could avoid and escape electric shocks (i.e., control occurrence and duration of any shocks received), a “yoked” animal that received the same shocks but had no control over them, and a nonshock subject that simply remained in the apparatus and received all stimuli as the other two animals but did not receive any shocks, differences between these three types of animals were observed. The experimental design for a triplet is shown in Fig. 2,

although the particular apparatus shown in this figure was used in a later experiment and differs somewhat from the apparatus employed in Weiss (1968) (apparatus used in Weiss 1968 is shown in that article).

A highly important detail in these studies, which can be seen in Fig. 2, was that electric shocks received by the rats were delivered through electrodes affixed to the rat’s tail, a procedure prompted by the insight of my brilliant Ph. D. advisor, Professor Neal E. Miller. (Neal Miller was a member of the National Academy of Sciences and first recipient of the National Medal of Science in the field of Social and Behavioral Science [1964], receiving this award in the third year after the Medal was established by President John F. Kennedy.) Miller had criticized the original Mowrer and Viek experiment on the basis that the animals were given shocks via a grid floor.



**Executive Monkey Study, Fig. 2** The experimental design paradigm for matched triplets of animals as used in Weiss (1968) and Weiss (1971a, b, c). The Avoidance-escape animal shown at left could control shock by performing a response (wheel-turn shown in this figure); this is noted as connection of wheel “To shock control.” Both the Avoidance-escape and the Yoked animal shown at center which is unable to perform a response to affect shock received exactly the same shocks via tail electrodes, with their tail electrodes wired in series into the same

electrical circuit; electrode connection is noted as “To shock source.” The third animal shown at right (“No shock”) receives all stimuli throughout the procedure as the other two animals of the triplet except that it receives no shocks as its tail electrodes are not connected (“No connection”). Apparatus shown here was used in Weiss (1971a, b, c), while apparatus and responses to control shock were different in Weiss (1968) (see text), but all aspects of triplet design shown here were the same in all of these experiments

Miller pointed out that on a grid floor, rats can change their bodily posture to lessen shock and/or jump completely off the floor to momentarily avoid shock, so that using this method to deliver shock cannot insure that the two matched animals (i.e., avoidance-escape animal and yoked animal) will get exactly the same shocks. Consequently, differences seen between these conditions might be due to the animals learning different postural maneuvers to consistently receive different amounts of shock. When I originally proposed to Miller to study control versus noncontrol for my dissertation research, he called attention to this problem and urged me to try to develop shock electrodes that could be affixed to the animal's body to eliminate the ability of the rat to make postural changes that would alter shock. Fortunately, I was able to accomplish this during the next few months, and the method used has been published (Weiss 1967). Consequently, all experiments using the triplets as described and shown above employed tail electrodes affixed to the rats for delivery of shocks. With each matched pair of avoidance-escape and yoked animals having their shock electrodes wired in series into the electrical circuit for all of the experiments, shocks received by these two animals were necessarily exactly the same in number, duration, and intensity.

The results reported in Weiss (1968) were briefly described as follows: in the first experiment, animals were exposed to avoidance-escape versus yoked conditions for a session lasting 2.5–3.0 h (i.e., avoidance-escape rats could avoid tail shock or terminate it by jumping onto a shelf while yoked animals received the same shocks but could not control them). Twenty-four hours later, avoidance-escape rats were found to be significantly heavier in body weight than the yoked animals, having eaten more food during the night after the stress session than did yoked animals. Yoked animals also weighed less than matched no-shock animals, while avoidance-escape animals were only slightly lighter than the no-shock subjects. In the second part of this study, all rats were made thirsty by water deprivation and placed into the shock environment where a water tube was now present. Yoked animals were considerably more reluctant to approach

the drinking tube than were avoidance-escape or nonshock subjects, thereby showing that yoked rats, as a result of exposure to shocks over which they had no control, were now more fearful in that environment than the other two groups. Finally, to assess gastric pathology as was measured in the “executive monkey” study, a second experimental situation was used in which animals were mildly restrained in a tube wherein avoidance-escape rats could control shock to its tail by a nose-poke at the front of its tube, “yoked” rats could nose-poke but without effect on shocks and received equal tail shock as their matched avoidance-escape partners, and no-shock rats did not receive shocks in this condition. When gastric pathology was assessed after rats had been in these conditions for 48 h, “yoked” rats developed clearly more gastric erosions than were seen in the other two groups.

Thus, the first foray into examining effects of control versus noncontrol on various physiological indices after appearance of the “executive monkey” study yielded results consistently opposite to its findings, including what was observed when development of gastric pathology was assessed. However, it was the next series of experiments that led to the most illuminating results; these findings will now be described.

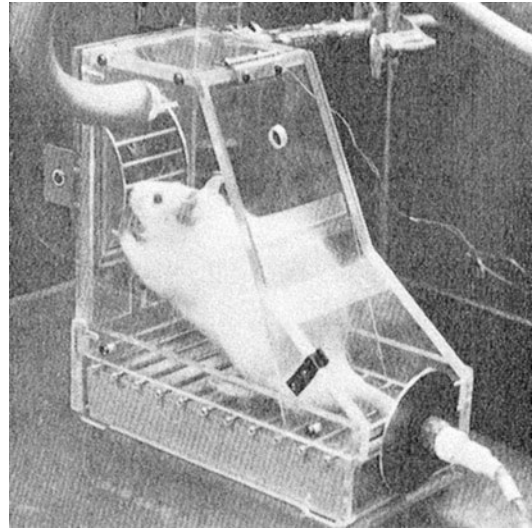
### **Addressing the “Executive Monkey” Findings: Assessing the Importance of Signals Before Shock**

The next experiments attempted to determine why the findings in Weiss (1968) differed from what was seen in the “executive monkey” study. As described earlier, the “executive monkey” procedure required the animals controlling shock to respond in a “Sidman” avoidance procedure in which all shocks occurred without any signal preceding them; responses simply postponed a train of shocks before which no warning signal had occurred. In contrast to this, in Weiss (1968), shocks had always been preceded by a warning signal. In those experiments, therefore, a warning signal informed the rats that shock onset was imminent, and also responses made during the

warning signal not only avoided shock (i.e., caused shock not to occur) but terminated the warning signal to convey additional external information for the animal exercising control. Was a key factor in producing the difference the presence of a warning signal before shock as used by Weiss versus simply postponing shocks that had no warning signal preceding them as was the case in the “executive monkey” study?

To test this, the importance of warning signals was examined (Weiss 1971a). In this large study, rats were exposed to electric shocks that were (1) unsignaled, or (2) preceded by a warning signal (“beeping” tone auditory signal beginning 20 s before shock), or, additionally, (3) preceded by a series of auditory warning signals (different tones) even more elaborate than a usual single warning signal (i.e., the “beeping” tone). As previously, matched triplets of rats were used; the design as well as the apparatus for this study is shown in Fig. 2, and an animal in an enclosure with the wheel mounted at the front is shown in Fig. 3. In all three warning-signal conditions, a response by the avoidance-escape rat – turning of the wheel at the front of its apparatus – postponed the onset of shock, which consisted of a train of brief, rapidly-occurring shock pulses, for 200 s (i.e., this was an avoidance response). If the shock train had begun, the response immediately terminated shock and shock did not occur again for 200 s (i.e., this was an escape response). Thus, the avoidance-escape rat exerted control over shock, avoiding/postponing shock or terminating shock if it had begun, and the effect of a response by this animal on shock – postponement of the next shock for 200 s – was exactly same in the three warning-signal conditions.

What therefore differed in the three warning-signal conditions was (a) how much external information rats got as to when shock would occur, and (b) how much external information rats got when the avoidance-escape rat responded. In the unsignaled shock condition, these rats, like the “executive monkeys,” got no external feedback informing them when shock would occur, and also they did not experience any stimulus change in their environment when they made an avoidance response postponing shock. For these



**Executive Monkey Study, Fig. 3** The Plexiglas enclosure used in Weiss (1971a) and also Weiss (1971b, c). Each rat was placed in this Plexiglas chamber where it was able to turn the wheel mounted at the front of the enclosure. Electric shock could be delivered to the rat’s tail protruding through the rear end of the enclosure via electrodes attached to the tail. Each of these enclosures was placed into a separate soundproof chamber so that each animal was isolated and separated from other two animals of its triplet. The white tubing leading from the top of the wheel-turning enclosure is an air exhaust that provided constant ventilation of the enclosure. The graduated cylinder seen at the rear contains water; a spout from the cylinder protruded into the enclosure through a small hole thereby providing the rat access to drinking water throughout the procedure

animals, only an escape response produced any external change because in this case the shock train terminated. For signaled shock animals, rats knew when shock was imminent (i.e., the “beeping” tone warning signal sounded), and if the avoidance-escape animal responded during this warning signal (avoidance response), an external stimulus change occurred because the warning signal immediately terminated. For the third warning-signal condition, even more information was provided; this condition essentially provided an external clock leading up to shock. In this condition, called Progressive signal, a succession of warning signals was initiated 30 s after a shock had occurred, and consisted of five tones that became higher in frequency pitch and louder every 30 s until the “beeping” tone warning signal then began 20 s before shock. Note that the yoked

and nonshock animals of each triplet heard exactly the same external tone signals as the avoidance-escape animal, and yoked animals experienced the same shocks and shock terminations as well. Animals were exposed to these conditions for 48 h, at which time they were sacrificed and the presence of gastric pathology (gastric erosions) was determined and quantified.

### **Findings from This Analysis: Exerting Control Reduces Stress and Ulceration in All Signal Conditions. Subsequent Analysis Leads to a Promising General Formulation**

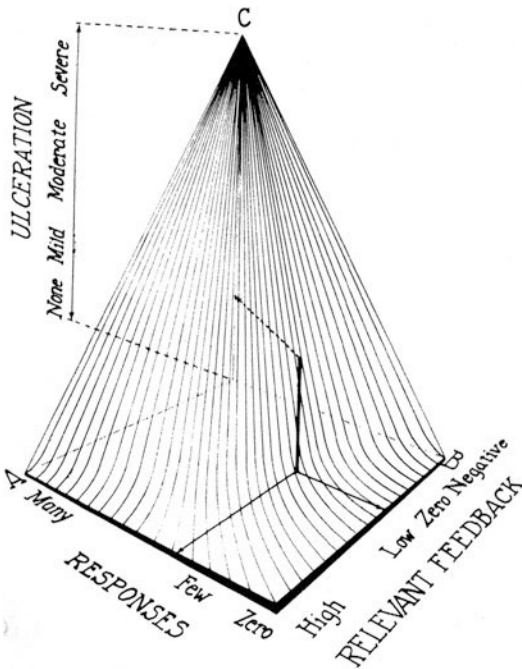
The results of this study did not indicate that the simple presence or absence of warning signals was the key to understanding the “executive monkey” findings. In all three conditions – Unsignaled shock, Signaled shock, and the more elaborate warning signal condition called Progressive signal – the avoidance-escape rats able to exert control over shock developed less pathology and evidence of stress than did their matched yoked animals that could not control shock (Weiss 1971a). Differences in gastric ulceration between avoidance-escape and yoked rats were statistically significant in all three signal conditions, favoring avoidance-escape animals over yoked animals. On its face, therefore, the “executive monkey” study appeared to be an anomaly, and writings between 1958 and the beginning of the 1970s that emphasized the negatives of having the burden of being in control were left lacking empirical support.

However, detailed analysis of the large amount of data generated by this study (20 matched triplets were included in each signal condition) led to a theoretical formulation that to this day appears to be valid and subsequently led to a potential explanation for the “executive monkey” findings. Examining the wheel-turning behavior of the rats, particularly the animals in the unsignaled shock condition, revealed that rats which made the most responses tended to develop the most severe gastric ulceration. **This led to the first leg of the hypothesis: As coping attempts (i.e., responses)**

**by the animal increases, stress and pathology tends to increase.** However, this relationship between the amount of responding and development of pathology was observed to be much weaker in avoidance-escape animals of the Signaled shock condition, and, in particular, was weakest in avoidance-escape rats of the Progressive signal condition. Why? The idea emerged that the response rate of animals could be high but if the amount of information they received about the success of their responses was also high, pathology would be prevented from developing. What was the relevant information? In a stress situation, the relevant information that the animal wants is that the danger/stress situation is over, it has ended, it has gone away. In other words, it seeks stimuli not associated with danger/stress/electric shock; i.e., it wants a stimulus condition that represents safety. When shock is signaled, and even more so in the Progressive signal condition, wheel-turning responses by the avoidance-escape animal often terminate warning signals to immediately bring about silence which is a safety period insofar as silence for these animals is present when shock is not occurring or imminent. Consequently, warning signal terminations produce a large amount of relevant information that the animal seeks. This “good information” from a response was called “relevant feedback.” **This led to the second leg of the hypothesis: As relevant feedback from coping attempts (i.e., responses) increases, stress and pathology tends to decrease.**

Thus the consequences of being in a stressful situation are a function of two factors: adverse effects increase as the number of coping attempts (responses) increases, but then these adverse effects are held in check by the outcome of the coping attempts, decreasing (or failing to increase) as the relevant feedback resulting from coping attempts (responses) increases. The combination of these two functions has been presented graphically, which is shown in Fig. 4 (from Weiss 1971a). This figure shows the prediction of adverse effects generated by the convergence of the two functions (adverse effects in this case labeled “ulceration” insofar as this is what was measured in the experiment described above). The

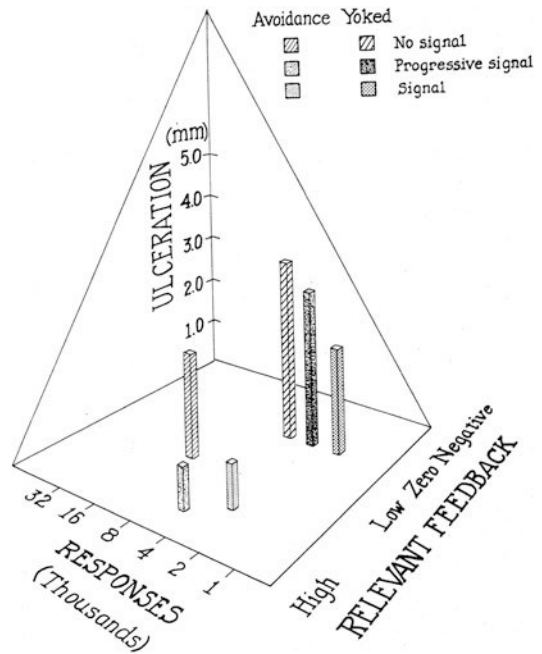




**Executive Monkey Study, Fig. 4** The three-dimensional plane describing the proposed relationship between the two independent variables – “Responses” (coping attempts) and “Relevant Feedback” from such coping attempts – and how this is related to the severity of stress and/or pathology (labeled here “Ulceration”). As Responses increase and Relevant Feedback decreases, stress/pathology increases. For ease of reading, the axes for Responses and Relevant Feedback are labeled in the foreground; customarily, these labels are placed on these axes in the background. Also presented in this figure is a hypothetical example showing the amount of pathology resulting from (A) a low number of responses being made (B) when these responses generate a low amount of relevant feedback

figure includes a hypothetical example indicating how much pathology will occur when a certain number of responses are made in a given situation and these responses produce a certain amount of relevant feedback.

Figure 5 shows how the results of exposure to the three different warning signal conditions in Weiss (1971a) conformed to the formulation shown in Fig. 4. Wheel-turn responses were counted, so this was known for all groups. Regarding relevant feedback, this could be estimated as well. For the avoidance-escape groups, those in the Signal condition received a moderate amount of



**Executive Monkey Study, Fig. 5** Results found in Weiss (1971a) for the Avoidance (Avoidance-escape) and Yoked groups of the three different signal conditions. For each group, the amount of gastric ulceration observed (height of bar) is shown at the point where the amount of responding observed in that group and the amount of relevant feedback from responding in that condition intersect. Note that for Yoked groups, amount of relevant feedback in all conditions is zero, which is necessarily the case when animals have no control over the stressor

relevant feedback for responding, resulting from signal terminations and escape responses, whereas those in the Progressive signal condition received even more relevant feedback because of the presence of more auditory signals that responses terminated. The lowest amount of relevant feedback was experienced in the unsignaled (No Signal) condition. Here avoidance responses postponed shock but changed nothing in the external environment; only escape responses (shock terminations) produced relevant feedback in this condition. These three conditions are represented appropriately in Fig. 5. The most interesting and informative groups, however, are the yoked groups. *This formulation tells us why it is so detrimental to have no control over a stressor. For these animals, relevant feedback from any response is always zero – all responses have no effect on the environment or the*



*stressor*. That is, in fact, what it means to be without control – relevant feedback from any coping attempt is zero. In this condition, adverse effects of stress are a direct function of the number of coping attempts made – the higher the response rate in this condition, the more the pathology. This relationship can be seen in the three yoked groups shown in Fig. 5.

### Tests of the Formulation and Explaining the “Executive Monkey” Findings

The validity of the formulation presented in Fig. 4 was then tested in two experiments. First, it is noted above that having no control is a condition where relevant feedback from any coping attempt is zero. But what would happen if the value of relevant feedback might fall below zero, becoming negative? This could occur if a coping attempt (avoidance-escape response) produced some aspect of the stressor rather than leading to a stimulus condition indicating absence of the stressor. In the first test experiment, avoidance-escape animals were required to perform a wheel-turning response to avoid and/or terminate a train of shocks but then negative relevant feedback for such responding was introduced by giving one brief pulse of shock immediately following any wheel-turning response. The results of this study, reported in Weiss (1971c), made clear that this condition was very detrimental; so much pathology developed when animals were forced to respond when relevant feedback from coping attempts becomes negative that animals could hardly survive this condition for 24 h. Next, as noted above, avoidance-escape responding in an unsignaled shock condition produces a low level of relevant feedback. Therefore, a manipulation was preformed to greatly increase relevant feedback in this condition. To do this, a brief auditory signal was added after every avoidance-escape response; because this signal is a stimulus always removed in time from the occurrence of shock, it represents a safety signal and greatly increases relevant feedback from responding in the unsignaled shock condition. The results of this study, reported in Weiss (1971b), showed that

simply adding this auditory signal for relevant feedback essentially eliminated gastric pathology, reducing it almost to the level seen in no-shock subjects that received no shocks at all. In summary, findings of these two experiments strongly supported the formulation shown in Fig. 4 and the underlying reasoning that led to it. Incidentally, these studies established that the rat’s receiving uncomfortable or even painful electric shocks throughout the procedure had almost no influence on the development of stress/gastric pathology; the severity of stress and pathology was shown to depend almost entirely on behavioral and psychological factors attending the shock situation and did not result from the shocks themselves.

The formulation shown in Fig. 4 can be used to account for the results seen in the “executive monkey” study. As described earlier, the “Sidman” avoidance schedule used in that experiment administered unsignaled shocks to the monkeys, and, for the monkey controlling the shock by pressing its lever, the relevant feedback from responses was therefore low. In fact, because shock in that experiment consisted of a train of very brief shock pulses each pulse given 5.0 s apart, the animal controlling shock could not even perform a clearly-defined escape response that demonstrably terminated shock – in contrast, every lever press by this monkey just postponed shock without producing any stimulus change in its environment, a condition of very low relevant feedback. Thus, a high rate of responding in such a condition is prone to high stress and pathology.

Additionally, an important detail regarding how the “executive monkey” study was conducted adds to its pathogenic potential. As also discussed earlier, the “executive monkey” study was not designed to examine the effect of having control versus no control, but, rather, was conducted to establish that preforming an avoidance response could lead to gastric pathology. Consequently, no attempt was made to equate the avoidance and yoked monkeys of each pair; instead, a yoked subject was simply paired with each avoidance monkey to insure that an animal not performing the avoidance response would receive an equal number of shocks in order to rule out the electric shock as having produced

the gastric pathology. Because of this, the experimenters used an unfortunate procedure: they set up both animals of each pair with an active lever at the outset of training, and let the animal that became the avoidance subject self-select itself by taking over avoidance responding. Within the first hours of the experiment, one monkey of the pair responded at a much higher rate than the second monkey, and so the high-rate responder was made the avoidance subject and the other monkey's lever was deactivated so that it became the yoked subject. This anomaly is crucial – as a result of this procedure, the “executive monkey” was designated as such because it responded at a high rate, and higher than its yoked subject. Thus, the monkeys that were made the “executive” were, because of their response tendencies, more prone to develop pathology than the yoked monkeys from the outset. And then these “executive monkeys” were placed into an ongoing situation where their responding produced very low relevant feedback. Consulting Fig. 4, this set of circumstances – high response rate, low relevant feedback from responding – is precisely the kind of situation that will result in pathology, and this is what indeed was observed in the “executive monkey” study.

More than 45 years have now elapsed since publication of the Scientific American article in 1972 titled “Psychological Factors in Stress and Disease” (Weiss 1972) which was relevant to the “executive monkey” experiment that had been published in the same Journal in 1958. Since then, a number of significant developments have occurred. First, the principles proposed in that article – i.e., that stress and pathology increases as (a) responses increase and (b) relevant feedback from responses decreases – has been embraced, applied, and reiterated in a number of fields, including, notably, industrial psychology (e.g., Karasek 1979; Siegrist 1996). Second, a large amount of research has established that having control over a stressful situation is more beneficial – i.e., results in less stress – than having no control, which is opposite to what the “executive monkey” study suggested (e.g., Gray 1998; Payne 2013; Sherman et al. 2012). This is now accepted as an accurate general conclusion. Third, it is often said that the

“executive monkey” results now have been falsified, debunked, as a result of the selection factor used to choose the “executive” monkey. For example, this is what was stated recently by Sherman and colleagues in Proceedings of the National Academy (Sherman et al. 2012). I respectfully disagree. The results of the “executive monkey” study have not been debunked; they are not erroneous. They are highly lawful and exactly what one would predict given the conditions that generated them. These findings are clearly explained in accord with the formulation shown in Fig. 4. What is correct to say is that the executive monkey experiment does not describe what one would expect to be the normal consequence of exerting control versus no control, but, rather, represents a highly unusual situation where exerting control was detrimental – because of the resulting high response rate, augmented by the avoidance monkeys being selected because of their high response proclivity, and the low relevant feedback from responding. Consequently, we now understand the findings in the “executive monkey” experiment and why negative consequences occurred for animals “in control,” and therefore these findings can be appropriately integrated into our knowledge.

## Concluding Comments

First, with the discovery, in the 1980s, of the pathogen *Helicobacter pylori* as an important factor in peptic ulcer disease, and the successful treatment of the disorder by antibiotics (Marshall and Warren 1984; Marshall et al. 1985), initially it was thought that any association of this disorder with stress was now disproven, and decades of previous study and theorizing in this regard were erroneous. However, (1) it was subsequently discovered that ulcer could develop and also recur in the absence of *H. pylori* (e.g., Laine et al. 1998; Tsuji et al. 1999), (2) it has been proposed that *H. pylori* is not the primary cause of ulcer but, rather, is responsible for a secondary infection that accounts for chronicity of ulcer disease (Tovey et al. 2001; Vikram et al. 2013), and (3) while prevalence of *H. pylori* infection is high across the

world (for example, present in 35% of the population in the U.S. [Hooi et al. 2017]), peptic ulcer disease is found in a much lower percentage of people (for example, present in 1.1–1.5% of the population in U.S. [Sung et al. 2009]), so other factors clearly must be present for peptic ulcer disease to occur. Thus, *H. pylori* infection is neither necessary nor sufficient for development of peptic ulcer. Also, stress has been shown to decrease bodily defenses against pathogens by decreasing protective immune responses including phagocytosis that controls gram-negative bacteria such as *H. pylori* (e.g., Glazer and Kiecolt-Glazer 2005), so stress may influence infection by *H. pylori*. Research throughout this period has continued to show that development of peptic ulcer disease requires hypersecretion of stomach acid. Fifty years earlier, Wolf and Wolff had shown that emotional upset led to gastric engorgement and increased stomach acid secretion in humans (Wolf and Wolff 1947). In summary, discovery of the significance of *H. pylori* for ulcer disease does not rule out an important role for stress in development of gastric and duodenal ulcer.

Second, while the writings of psychoanalysts on the topic of ulcer have been pushed aside for many years, this writer suggests that perhaps the work of perceptive psychoanalytic colleagues should not be summarily dismissed. Franz Alexander, in theorizing that many ulcer patients were hard striving individuals whose unconscious desire was, instead, to be passive and nourished, describes a high response rate, low relevant feedback condition leading to gastric pathology. Experimental research on animals described in this chapter provides a framework indicating that this particular condition is one of high stress and conducive to development of gastric pathology. That framework may integrate the data from these different sources; perhaps there is a surprising agreement here.

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## Exemplar Theory

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## Introduction

Understood psychologically, a category is a memory store that lets organisms behave consistently and adaptively toward ecologically equivalent objects that may have imperfect perceptual similarity. Animals' capacity for categorization has conferred fitness advantages on them for hundreds of millions of years. Indeed, some animals (e.g., vervet monkeys) have developed calls that denote or “name” members of threatening categories, thus warning conspecifics and allowing them to respond appropriately. Exemplar theory is an entrant into the sharp theoretical competition to provide the best psychological description of these category-knowledge stores.

## Definition

Exemplar theory's idea is that animals store separately the category exemplars they encounter (e.g., exemplars of predator eagles or durian fruits) as whole, individuated memory traces. Then they compare new items to these multiple memory reference standards and include the items in the category if they are similar enough to the stored exemplars. The key point is that the organism need not have, and may not have, a unitized, summary idea of predator eagle. Rather, it may have a slide carousel of eagles, a Rolodex of eagles, an iPhone playlist of eagles. It is an intriguing psychological theory that warrants careful consideration and evaluation.

## History of Exemplar Theory

Exemplar theory came to dominate the human literature in the 1970s, given a confluence of research findings and a particular scientific aesthetic. At the time, Rosch and others had developed the prototype comparison theory of family-resemblance categorization (Rosch & Mervis, 1975). Its idea was that minds average their experiences with natural-kind categories (like eagles) to produce a memory representation that is the central tendency or prototype of the category. This theory fit admirably the case of eagles, durian fruits, and many other natural kinds that are coherent families of perceptually similar objects. Indeed, as we will see, this theory may be the appropriate psychological account of animal categorization. However, Medin and his colleagues (e.g., Medin & Schaffer, 1978) realized that not all categories are organized by family resemblance and prototypy. Categories can also be defined logically (e.g., exclusive-or categories), randomly (who is in my foraging group today?), or for ad hoc reasons (items to pack in the car for a road trip!). Furthermore, Medin's research showed that humans can somewhat learn (but see below) logical, random, and ad hoc categories for which prototype-averaging processes will not work. Thus, we might need different psychological explanations for explaining the learning of different kinds of categories, ending with a messy, unparsimonious model of mind. Bear in mind that human and animal minds could be messy in just this way.

Defending parsimony, Medin proposed instead that one representational system might serve all categorization. Their elegant proposal was as already described, with many individuated exemplar memories used as the memory reference standards for categorization. It is not required in exemplar theory that *all* experienced instances be stored in memory. However, in many formulations of the theory, and in nearly all of exemplar theory's formal models, the allness assumption is obeyed. Over a lifetime, a vervet monkey's eagle playlist could grow quite large (leave aside humans' playlist of French fries).

Exemplar theory's dominance lasted for about 20 years (sustained especially through work by Nosofsky and his colleagues, e.g., Nosofsky, 1986). One can see why. The theory instantiated well the attractive aesthetic of parsimony in science, just as did the associative construct in comparative psychology. Exemplar theory made categorization unitary – categories of all kinds could be learned in the same manner by the same unitary system. There was only one exemplar-comparison process to understand. This unity possibly obviated the need to consider different kinds of categories, different category tasks, different learning strategies, different brain circuits, and possibly even different categorization capacities across species. In essence, all categories could be deemed equivalent and learnable. The exemplar theorists in particular fought the idea that family-resemblance categories were somehow better structured, more natural, more learnable, or psychologically privileged. This period in categorization science is intriguing because it shows how salient and guiding the principle of parsimony can become, perhaps even slowing empirical progress and veiling the psychological truth of the matter.

## Evaluation of Exemplar Theory

Exemplar theory has been evaluated along two dimensions: by the goodness of fit of formal exemplar models to categorization data and by the learnability of poorly structured categories unfriendly to prototype processes. Considering these two in turn, one sees that exemplar theory met with serious difficulties almost immediately.

### Model Fits

Regarding model fitting, exemplar theory's early successes that fed its popularity were limited in several ways. First, the categories tested contained small numbers of exemplars that were easily memorized, making them most amenable to exemplar processing. Possibly these "categorization" tasks were really stimulus-identification tasks, with participants rotely associating stimuli



to arbitrary labels with no sense of coherent categories (Blair & Homa, 2003). Second, the categories were poorly differentiated in similarity terms. Sometimes items were more perceptually like items in the opposing category than like items in their own category (Medin & Schwanenflugel, 1981). These categories – impoverished in family resemblance – possibly showed what humans do denied their natural approach to categorization, rather than showing their preferred exemplar approach at work. Third, the early studies used the scarce computational resources available (computers were just arriving on the scene) to fit the aggregated performance of whole participant groups. Averaging across individuals changes the character of psychological data – for example, by homogenizing away the high and low extreme performance levels on individual items produced by individual participants (Smith et al., 1997). For reasons beyond the scope of this entry, fitting averaged data systematically biases outcomes toward the exemplar model's good fit.

### **Learnability of Poorly Structured Categories**

Regarding learnability, humans performed very poorly on these early tasks that favored exemplar theory. In many experiments, about half of all participants never reached the learning criterion. Murphy (2003) warned categorization researchers about this problem. This failure to learn was problematic because it suggested that exemplar theorists were expressing the wrong psychology, or expressing a psychological competence that humans lack, or testing poorly structured categories in which humans cannot show their true categorization competence.

Accordingly, Smith and Minda conducted research (e.g., Smith & Minda, 1998) using well-structured family-resemblance categories that humans found more learnable. Now, many participants' data were fit better by a prototype model than by a closely matched exemplar model. In fact, the exemplar model made large, essentially disqualifying errors in these cases, in part because it mispredicted how strongly humans resonate to category prototypes. These results reminded the field that Rosch and others might have been

expressing an important insight about prototype processes in human categorization.

This was an important crossroads. The field might have acknowledged that alternative theoretical explanations like prototype theory still needed to be part of categorization's overall theoretical explanation. It might have narrowed the role of exemplar theory so that it applied to poorly structured categories with small, memorable exemplar sets. However, the attraction of the unitarian exemplar principle was too strong. Instead, mathematical variations and amplifications were added to the exemplar model to make it more powerful. In particular, modelers adopted the additional free parameter – gamma – that let the exemplar model manage more heterogeneous (spiky) data produced by individual participants. In some situations, gamma essentially enabled the exemplar model to imitate by mathematical artifice a prototype model. Readers must judge whether resuscitating mathematically a theory that is failing psychologically is a strong scientific approach.

### **Comparative Psychology Enters the Debate**

More recently, comparative research has made a transformational contribution to the evaluation of exemplar theory by rebalancing the theoretical literature back toward prototypes. One aspect of this contribution has been to illuminate the fundamental flaw with exemplar theory. The theory proposes the representation of multiple, disparate, and separate predator-eagle exemplars. These eagle exemplars – perceptually dissimilar – will be spread out like a cloud in the mind's psychological space. Therefore, exemplar theory predicts that even a perfectly typical item (e.g., a platonically ideal eagle) – precisely at the center of the category space – may still not be maximally endorsed into the eagle category, because it will still not be similar to all the stored eagles arrayed around it in memory space. Instead, it will always be close (similar) to some regions of the cloud but far (dissimilar) from others. Therefore, exemplar theory predicts that

even the prototype eagle will not generate a dramatically strong Eagle!-Hide! response.

## Monkeys

Rhesus macaques (*Macaca mulatta*) tested this prediction in Smith et al. (2008). The monkeys learned shape-distortion categories as shown in Fig. 1. These are family-resemblance categories (like eagles) – perceptually coherent, containing mutually similar instances and prototypical, typical, and less typical items.

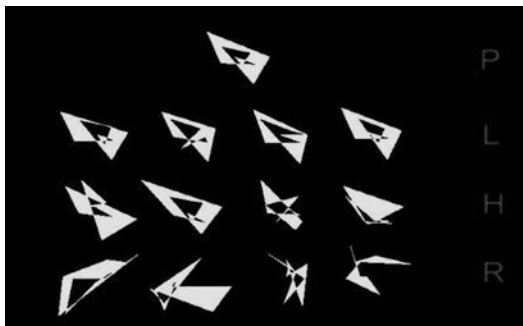
Figure 2 (circles) shows the proportion of times a macaque accepted (endorsed) different instances into the category. We fit these data using a standard model instantiating exemplar processes. The model (Es) predicted lower performance on even the most typical item types, as dictated by the inherent geometry of exemplar memory spaces described above. It fit the monkey's data poorly – for example, sharply underpredicting the monkey's maximal endorsement of prototype items. The monkey apparently was not referring items to whole clouds of exemplars. Humans produce the same result as monkeys, disconfirming exemplar

theory in this task for both species (e.g., Smith & Minda, 2000).

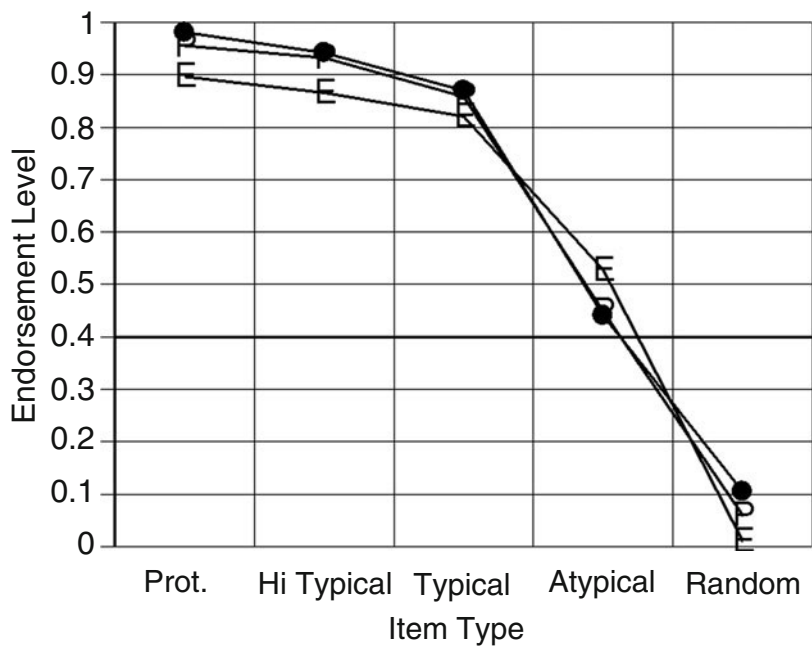
If not exemplar comparisons, a competing possibility is that macaques average their exemplar experience to produce the category's central prototype. Then, when they experienced that prototypical eagle in nature, it would be indefinitely similar to their represented prototype and resonate terrifyingly strongly as an eagle. Testing this idea in Smith et al. (2008), a prototype model emulated a monkey's prototype processing. It was closely matched to the exemplar model except for assuming a unitary prototype comparison standard. The model's predictions (Ps in Fig. 2) were so precisely right that the Ps are hidden by the data points. Probably something like a prototype was the macaques' cognitive reference point, a conclusion reinforced by other studies (e.g., Aydin & Pearce, 1994).

Researchers have also tested exemplar theory by testing primates in prototype-exception tasks as described now. In Fig. 3, the eight shapes to the left and right are rewarded as Categories A and B, respectively – even though in each case the two bottom stimuli appear to belong to the opposing category. If exemplar theory is correct, monkeys should simply memorize the typical and exception items and categorize both item types correctly. However, if monkeys naturally assume prototype categories organized by family resemblance, they will systematically miscategorize the exceptions, placing them wrongly into the categories that maximize perceptual similarity and family resemblance. This tendency should result in poor, even below-chance exception-item performance.

Figure 4a–c shows three macaques' performance in this task (Smith et al., 2010). The macaques systematically miscategorized the exceptions, performing them below chance for thousands of trials. They did so even given hundreds of attempts at these trials – there were only four exceptions to memorize. To the contrary of exemplar theory's prediction, they exhibited a very weak capacity to store individuated exemplars and respond to them appropriately. This may imply that their exemplar capacity is not nearly developed enough to be relied on for all the

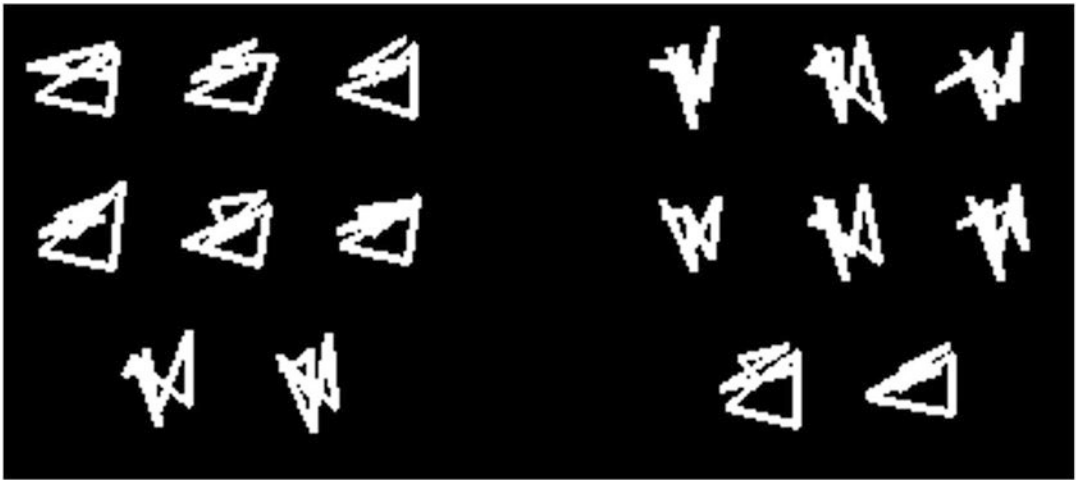


**Exemplar Theory, Fig. 1** Dot-Distortion Category. (Note. The originating prototype (P), low-level distortions (L), high-level distortions (H), and random-unrelated shapes (R) in the top to bottom rows, respectively. This category illustrates the idea of a family-resemblance category, with a typicality gradient running from the central prototype outward. Adapted with permission from "Prototype Abstraction by Monkeys (*Macaca mulatta*)," by J. D. Smith, J. S. Redford, and S. M. Haas, 2008, *Journal of Experimental Psychology: General*, 137, p. 391. Copyright 2008 by the American Psychological Association. Reprinted with Permission)



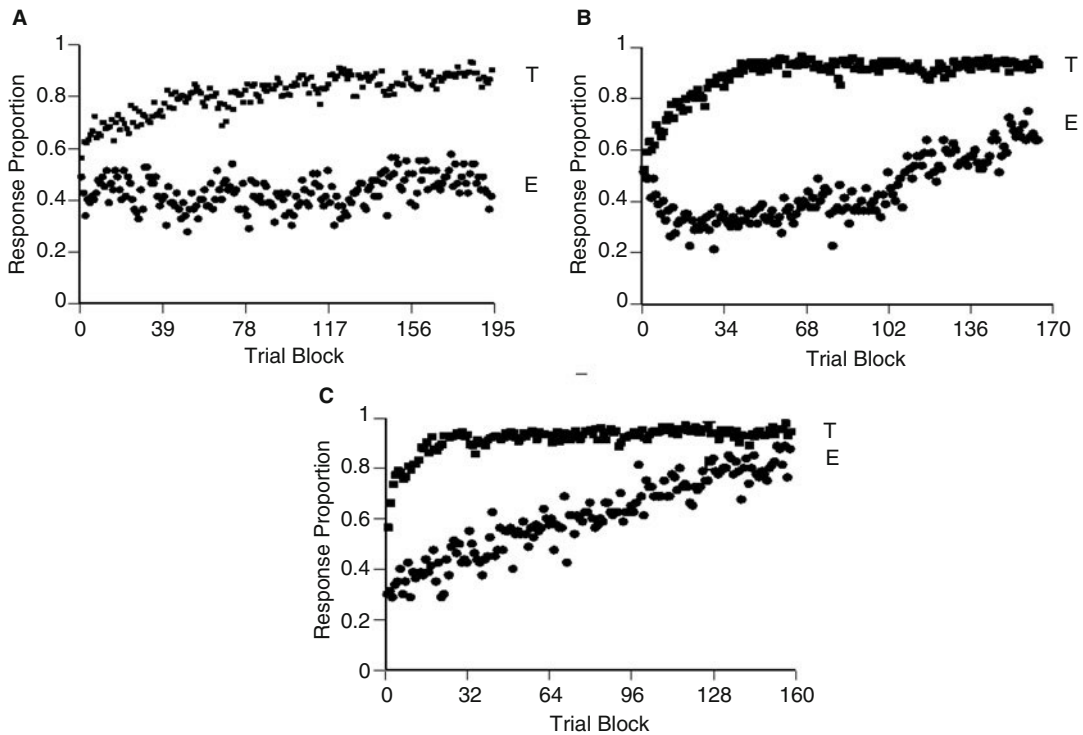
**Exemplar Theory, Fig. 2** The Proportion of Times a Macaque Endorsed Items as a Category Membe. (Note. Decreasing typicality was a function of increasing shape distortion from the prototype. Exemplar and prototype models fit the macaque’s performance as well as they could (E and P symbols, respectively). The models differed only in assuming multiple, specific-exemplar cognitive

reference points for categorization or a single, central cognitive reference point. Adapted with permission from “Prototype Abstraction by Monkeys (*Macaca mulatta*),” by J. D. Smith, J. S. Redford, and S. M. Haas, 2008, *Journal of Experimental Psychology: General*, 137, p. 395. Copyright 2008 by the American Psychological Association. Reprinted with Permission)



**Exemplar Theory, Fig. 3** Examples of Categories and Stimuli Used in Smith et al. (2010). (Note. The 8-shape groupings are two categories A and B. The 6 shapes in the top rows of each category are variations on the theme of the category prototype. The bottom row contains exception items that are variations on the theme of the opposing

prototype. From “Stages of Category Learning in Monkeys (*Macaca mulatta*) and Humans (*Homo sapiens*),” by J. D. Smith, W. P. Chapman, and J. S. Redford, 2010, *Journal of Experimental Psychology: Animal Behavior Processes*, 36, p. 43. Copyright 2010 by the American Psychological Association. Reprinted with permission)



**Exemplar Theory, Fig. 4** (a, b, c) Performance by Three Macaques in the Category Task of Smith et al. (2010). (Note. Curves T and E, respectively, show the proportion of correct responses made to the six typical and two exception items in each category. From “Stages of Category Learning in Monkeys (*Macaca mulatta*) and Humans

(*Homo sapiens*),” by J. D. Smith, W. P. Chapman, and J. S. Redford, 2010, *Journal of Experimental Psychology: Animal Behavior Processes*, 36, p. 48. Copyright 2010 by the American Psychological Association. Reprinted with permission)

important tasks of categorization. Instead, they apparently chose a persistent strategy based on prototypes and family resemblance. In this strategy, miscategorizing the exceptions *technically* is categorizing them *correctly* according to family resemblance. Humans produce similar results (Smith & Minda, 1998). Smith (2014) described the important evolutionary and fitness implications that follow from primates’ default strategy.

Yet one also sees that two macaques finally showed some mastery of exceptions. So we can grant them some late-breaking exemplar competence and acknowledge some role for exemplar memory in primate categorization. In the end, more than one process may support animals’ and humans’ categorization. Categorizing minds may actually be messy minds, an idea with which this entry began.

## Pigeons

Cook and Smith (2006) extended these findings and conclusions further across the vertebrates and by possible implication farther back through vertebrate evolution. They gave pigeons (*Columba livia*) prototype-exception tasks. The tasks presented color disks (not reproducible in this volume) with sectors of six different colors. The disks within a category had six typical colors (the category prototype), five typical colors (the typical items), or one typical color (this exception disk contained five typical colors of the technically opposing category). Cook and Smith found that pigeons – exactly as rhesus monkeys – systematically cross-categorized the exception items into the categories that would maximize perceptual family resemblance. A standard exemplar model fit pigeons’ data poorly. For reasons already

discussed, it could not predict how strongly they performed the prototypes or how poorly they performed the exception items they should just have memorized. Wasserman et al. (1988) found a converging result that they also supported through formal modeling.

Late in learning, the pigeons did develop some competence in learning/memorizing the exceptions so as to get them technically correct. Humans showed the same pattern of results early and late in learning. In fact, the cross-species graphs in Cook and Smith (2006) reveal a striking continuity in the processes of categorization across far-separated vertebrate species. Broadly across species, vertebrates seem to present with the same default prototype approach to category tasks, with a residual and weak exemplar capacity after extended training. However, in this consistent pattern, exemplar theory has only a narrow application and plays only a minor role.

In fact, this minor role may not even be biologically or fitness relevant. If the world contained exception eagles as tested in Cook and Smith (2006) or Smith et al. (2010), vervet monkeys would never survive the hundreds of error attempts they seem to need to memorize them. They would not survive a week. But there apparently are not exceptional eagles (i.e., eagles in sheep's clothing). Smith (2014) described the beautiful convergence between primates' true categorization competence (a prototype and family-resemblance competence) and the structure of natural kinds in the natural world (a prototype and family-resemblance structure). Perhaps this convergence is not accidental. It could have been sculpted by cognitive evolution.

### Exclusive-Or Tasks

Finally, researchers have tried to isolate the exemplar-memory process, forcing the animal's reliance on it so that its potency can be directly assessed. To that end, Smith et al. (2011) tested macaques in exclusive-or tasks. In this task, Category A and B items are split into subcategories and placed into opposite diagonal corners of their perceptual space (e.g., Category A members bottom-left and top-right in the space; Category B members top-left and bottom right). Here,

averaging the exemplars experienced into prototypes will fail because the A and B prototypes will be coincident in the center of the stimulus space. The prototypes will be useless to A vs. B categorization. Moreover, the two subgroups of A items (and B items, too) will not be perceptually similar to each other at all, defeating strategies based on family resemblance. So, this task structure leaves standing alone the forced categorization strategy of exemplar memorization.

Smith et al. (2011) gave macaques two-, three-, and four-dimensional XOR tasks. They found these tasks lacking prototypicality and family resemblance very difficult. Monkeys only reached about 75% accuracy. They erred on about a third of all trials. They received 15,000 20-s timeouts during this experiment. Contrary to the predictions of exemplar theory, and even when the task really only allowed the exemplar strategy, monkeys showed a minimal capacity to memorize and respond differentially and appropriately to individual exemplars. The exemplar capacity was absent without theoretical leave.

### Conclusion

In the end, human and animal evidence disconfirms an exemplar theory that purports to be a sufficient psychological explanation of categorization. Humans and animals display a robust prototype-abstraction capability. This prototype capability has apparently spanned more than 100 million years of vertebrate cognitive evolution encompassing birds and primates. It is likely that this prototype approach to categorization must carry the theoretical weight in explaining animal categorization. In contrast, exemplar-memorization processes in categorization – to the extent they are seen – are weak, hesitant, late-developing, and perhaps not biologically relevant. Murphy (2016) concluded that important phenomena in the psychology of concepts have no proposed exemplar explanation and that it is difficult to understand how an exemplar theory could be adequate. He wondered: "Is there an exemplar theory of concepts?" And yet there will certainly be times when animals face the need for



individuated exemplar traces, as when they learn their social group's dominance hierarchy. Therefore, it is premature to write exemplar-memorization processes off altogether for some cognitive purposes (although identifying alpha individuals is more specific-item recognition than it is categorization). Accordingly, the working consensus in the literature is that exemplar theory is discredited, but exemplar processes are sometimes in play. We can tentatively adopt a mixed idea of categorization that humans and animals have multiple categorization processes that manage the cognitive demands of multiple kinds of categories.

## Cross-References

- [Categorization](#)
- [Cognition](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Declarative Memory](#)
- [Episodic Memory](#)
- [Family Resemblance](#)
- [Primate Cognition](#)

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## Exodus

- [Migration](#)

## Exon

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## Synonyms

### Coding DNA

## Definition

Exons are the coding part of genome, which retained in the finally processed transcript and being translated into protein.

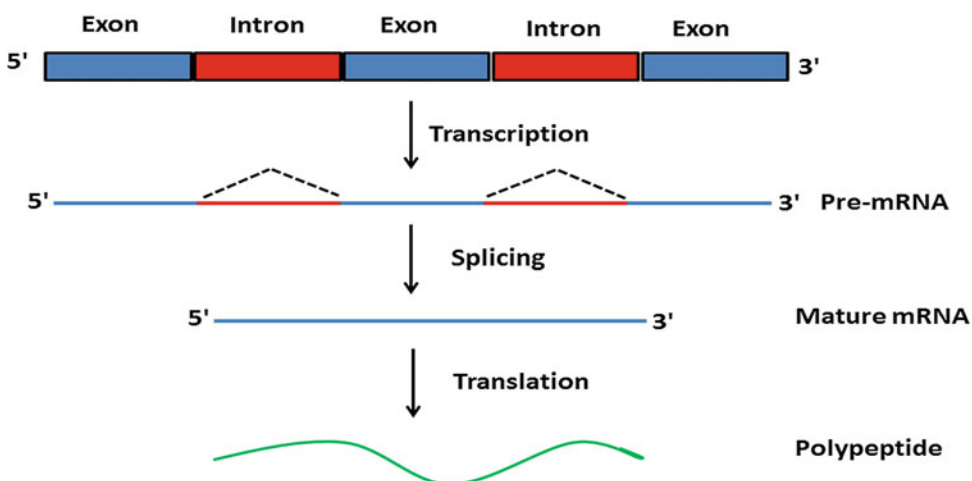
## Introduction

Exon is a part of the nucleic acid that is finally spliced together in the mature transcript and has the information for protein synthesis. The term “Exon” was first used by American biochemist Walter Gilbert in 1978. Richard J. Robert and Phillip A. Sharp independently discovered the split gene in the year 1977. The split or interrupted genes (in most of the eukaryotic genes) are those

genes in which the noncoding part, i.e., intron is present in between coding exons (Alberts et al. 2015; Gilbert 1978; Watson et al. 2004). The term “exon” is also used for rRNA, tRNA, and different genomic regions which are ligated by the transsplicing. Both the intron and exon part of the DNA are transcribed into the RNA which is heterogeneous and nonfunctional. This pre-mRNA undergoes the process of splicing in the nucleus in which noncoding part or introns are removed and the coding exons are ligated into a functional RNA. Exons of a gene are joined covalently in functional mature mRNA (transcript). The transcript after splicing is exported to the cytoplasm for translation. Exons are present in the genes of all eukaryotic organisms but absent in the genome of prokaryotes. New exons are originated by the mutation in the existing intronic sequence, termed as exonization, which is evident in the genomes of human, mouse, etc (Fig. 1) (Alberts et al. 2015; Gilbert 1978; Karen et al. 2010).

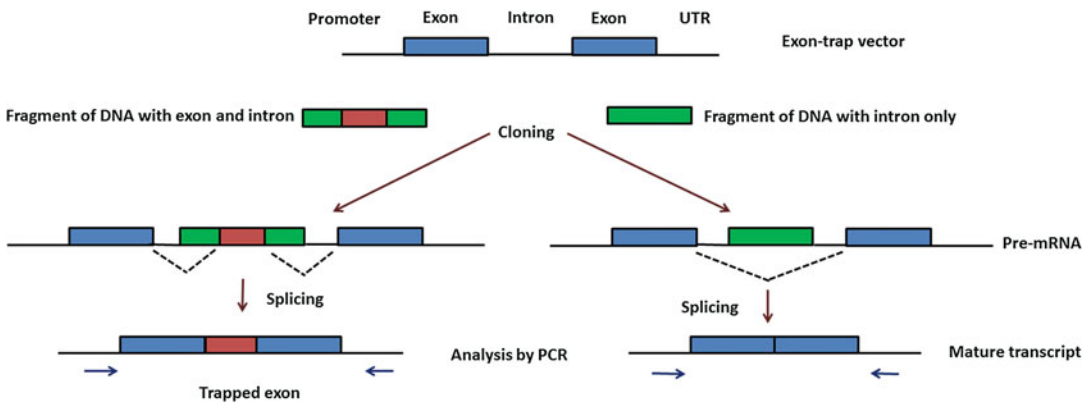
## Molecular Tools for the Characterization of Exon

1. **Exon Trapping:** Exon trapping is a technique to identify expressed part, i.e., exon in any fragment of DNA. In this technique, DNA



**Exon, Fig. 1** Upper panel shows organization of split gene with exons (coding DNA) interrupted by introns (noncoding DNA) which transcribed into primary transcript (pre-mRNA), contains exons and introns. By

splicing, noncoding introns are removed and coding exons ligated to form mature transcript which is being translated into polypeptide chain



**Exon, Fig. 2** Figure showing the cloning of DNA fragment (with and without exon) in a splicing vector. After splicing only exon parts trapped in the final transcript while the intron parts spliced out

fragment of analysis first cloned in between two exons in a splicing vector (exon trap vector). If the cloned part contains intron only then will be spliced out in the final transcript. The exon part will retained which can be analyzed by PCR (Fig. 2) (Wapenaar and Dunnen 2001).

2. **Exon Array:** Exon array is the type of microarray in which specific oligonucleotide probes are used to target specific exon combination or alternative splicing pattern in the mixture of transcripts. The probes are designed in such a manner that a particular transcript can be picked up if it is undergoing alternative splicing. This method is also used to study tissue specific expression of protein isoforms of a gene. Different labelling protocols in exon array method are required to avoid contamination from the other RNA species as rRNA and tRNA (Majewski 2009).
3. **Exome Sequencing:** Exome term refers to the entire set of exons of an individual. In the human genome, only 1% part constitutes the exons, remaining part is noncoding intron and intergenic DNA, thus exome sequencing is cheaper and convenient than whole genome sequencing. Exome sequencing is useful to study gene expression and pathology of various diseases but it is not suitable to study regulation of gene expression by the noncoding RNA and DNA (Warr et al. 2015).

**Exon Shuffling:** Exon shuffling is the recombination between noncoding introns which results

in assorting of exons from different gene, leading to the formation of new gene structure. Exon shuffling occurs by three modes, i.e., exon duplication within the same gene, exon insertion, and deletion from the different gene. Exon shuffling is another mode of generation of new genes as around 19% of exons have been reported for exon shuffling. The exon shuffling was first reported by Walter Gilbert in 1978 in blood coagulation factors, which is now evident in many multidomain proteins. Exon shuffling also results in the altering the function of proteins and evolution of new protein family. The recombination generally occurs in the noncoding intron as they are longer and contains transposable elements and repetitive sequences. Existence of mosaic proteins in which protein domains from a gene are present in another gene product provides evidences of exon shuffling (Jonathen 2013; Hillstrom).

**Exitron:** Exitron are exon-like intron retained in the final transcript and translated into protein part. The splicing of exitron impaired the protein structure and function. They are well reported in plants and metazoan transcriptome. Exitron are produced due to alternative splicing (Marquez et al. 2015).

## Conclusion

Exons are the protein coding part of DNA and its transcribed RNA which are interrupted by the noncoding introns. These noncoding introns are

spliced out and coding exons are ligated by the process of splicing during posttranscriptional processing. Thus the exon is the section of genome which is expressed into proteins. Exon trapping is a technique of gene identification and characterization. By exon trapping we can identify whether an expressed part, i.e., exon present in any fragment of DNA or merely an intron sequence. In exon shuffling, recombination occurs between intronic regions so that coding exons from different part of genome come together and translated into mosaic proteins. Sometimes mature mRNA may contain retained intron within the exon termed as exitron which functionally affect the outcome of the gene expression. Splicing can be targeted or modulated by the use of morpholino or blocking snRNPs so that different combination of exons can be included in the final mature transcript.

## Cross-References

- ▶ [Alternative Splicing](#)
- ▶ [Gene Expression](#)
- ▶ [Intron](#)

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## Expanded Triple Repeat

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## Synonyms

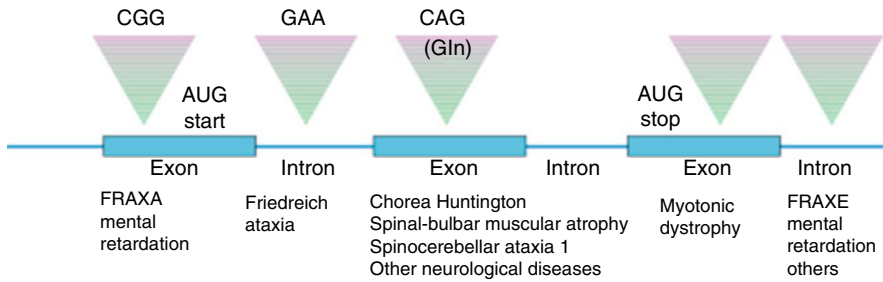
[Trinucleotide repeat expansion diseases](#); [Trinucleotide repeat expansion](#); [Triple repeat disorders](#)

## Definition

Dynamic instability of trinucleotide repetitive sequences (CAG or CGG) in the coding or non-coding regions of the genome and its expansion and epigenetic changes followed by paternal or maternal transmission to the next generation cause different neurological and muscular diseases.

## Introduction

In the large human genome, different stable repeat sequences are present at different levels with its significant role. Since 1991, the potential for apparent genomic instability was unsolved when an expansion of one of these repeats, a trinucleotide (CAG) repeat (TNR) in the gene encoding androgen receptor, was discovered in patients with spinal and bulbar muscular atrophy



**Expanded Triple Repeat, Fig. 1** Unstable TNR in different diseases (Science Daily Nadine Ben, 4 Jan 2017)

E

(a neurodegenerative disorder) (La Spada and Wilson 1991). In normal condition, there are 13–30 CAG repeats, whereas in patients, it lengthens up to 40 or more. In the progressive year, more than 20 disorders have been reported with the TNR expansion. Unlike other conventional mutations, this mutation is dynamic because the expanded repeats undergo further changes in subsequent generations. The magnitude of the expansion is related to parental repeat length. Although mammals have developed different systems to resist the unexpected rapid deleterious repeat sequences in their genome, beyond a crucial threshold length, this TNR breaks down the barrier and expands during parent-child transmission and the progeny development (Fig. 1).

## Classification

Disorders of this repeat expansion can be either in the (a) noncoding region of the genome or (b) coding region of the genome. Noncoding region repeat expansion causes a loss of gene function or toxic effect at the mRNA levels, and in case of coding regions, it results in an expansion of polyglutamine or polyalanine tracts in the protein product causing the protein to become toxic with or without loss of function.

Loci that undergo repeat expansion can be classified into two groups based upon their repeat, either the CGG repeats or CAG repeats. The CGG/CCG repeats are found in noncoding region and associated with chromosome fragile site whereas CAG/CTG repeats are most often found in coding region and associated with

neurodegeneration (exception myotonic dystrophy). CGG repeat can be of massive expansion of thousands of normal length of 30 repeats, whereas CAG repeat is of more modest two- to threefold of normal length of 20 repeats (Fig. 2).

## Noncoding TNR Expansion

Noncoding TNR includes CGG, GCC, GAA, CTG, and CAG. The pathophysiology of the related disorders lies on its particular repeat types and its location in the gene.

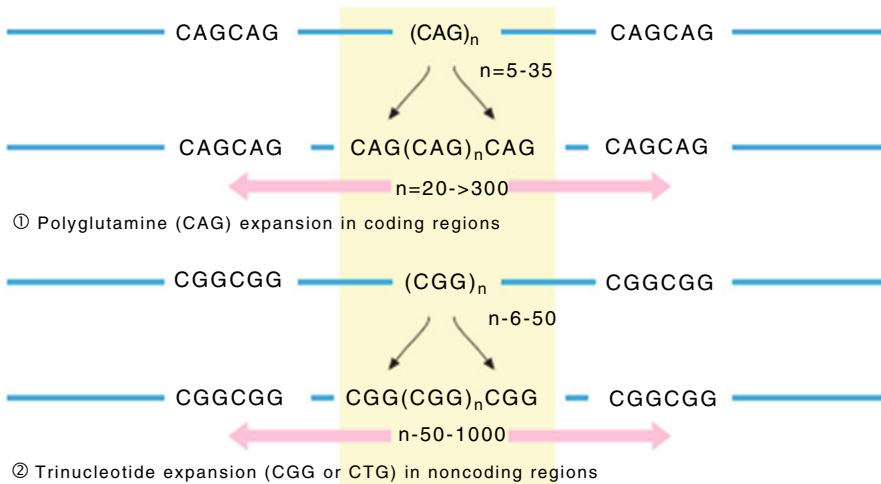
### Friedreich Ataxia (FA)

The most common hereditary ataxia (autosomal recessive) bears homozygous GAA repeats in intron 1 of the gene frataxin (210aa Frataxin) resulting in abnormal mRNA and protein production. Accumulation of mitochondrial iron (Fe-S cluster deficiency) causes increased susceptibility to oxidative stress due to decrease in oxidative phosphorylation. Clinical features include cardiomyopathy, renal failure, diabetes, myocardial infarction, thinner spinal cord, selective atrophy of large neurons, synaptic modification, etc. Diagnostic criteria are ataxia of the limb and gait, dysarthria, extensor plantar response, type I hereditary sensory, and motor neuropathy.

### Fragile X Syndrome (FMR1/FRAXA)

This is caused by an expansion of CGG repeat (230–1000 in full mutation compared to 6–52 copies with interspersed AGG repeats in normal) in the 5'UTR of fragile X mental retardation (FMR1) gene. Nonstaining gap of fragile sites on human metaphase chromosome (Xq27.3) which are cytogenetically visible is known as





**Expanded Triple Repeat, Fig. 2** Different types of TNR expansion (Science Daily Nadine Ben, 4 Jan 2017)

FRAXA (fragile site, X chromosome A site). This is most frequently associated with mental retardation. In an X-linked dominant inheritance pattern, it is showing reduced penetrance of 80% in male and 30% in female (Sherman paradox) (Sherman et al. 1984, 1985) where normal allele and permuted alleles are unmethylated, whereas full mutation CCG repeats are methylated, and this methylation is the most sensitive indicator of penetrance. Learning disabilities and mental retardation (IQ level 20–70) with ataxia or tremor are diagnostic clinical features. 20% male and 5% female patients show seizure, and some of them show obsessive compulsive disorder and self-injurious activity.

Other folate-sensitive FMR1 but negative FRAX includes **fragile X E, F (FRAXE, F)** and **fragile 16A, 11B (FRA16A, 11B)**.

#### Myotonic Dystrophy (DM)

In an autosomal dominant fashion, human chromosome 19q13.3 was identified for displaying length variation like 50–3000 CTG repeats in the 3'UTR of serine-threonine kinase (DMPK, DM kinase) in DM patients (Brook et al., 1992) compared to 5–37 in normal caucasian. This repeat is associated with muscular dystrophy in those patients. Altered chromatin structure associated with DM TNR and unusual nuclear sequestration

has been reported from muscle biopsies and affected fibroblast (Taneja et al. 1995).

#### Coding TNR Expansion (CAG/CTG)/ Polyglutamine Expansion

The CAG expansions are present in the coding region of a gene, which when transcribes and translates produces polyglutamine which is misfolded due to aberrant protein interaction and acquired toxic features by losing protein degradation via ubiquitination causing selective neuronal loss.

#### Spinal and Bulbar Muscular Atrophy (SBMA)/ Kennedy's Disease

It is an X-linked recessive adult-onset motor neuropathy (Kennedy et al. 1998; La Spada and Wilson 1991). In the Xq12 site, the androgen receptor (AR) contains a TNR (38–66 CAG) within the first exon encoding polyglutamine tract (PGT) compared to the normal 11–33 causing meiotic instability in transmission (La Spada et al. 1992). In affected sperm, there is 60% expansion, and 15% contraction in AR has been found (Zhang et al. 1995). Altered AR gene expression causes neuron degeneration and incomplete androgen sensitivity including gynecomastia, reduced fertility, and testicular atrophy as well as gain of function resulting in

selective motor neurotoxicity due to lower motor neuron degeneration (loss of brainstem nuclei resulting in proximal muscle weakness and fasciculation, bulbar muscle dysfunction like dysphagia).

Spinocerebellar Ataxia, Type 1 (SCA1)

SCA1 is an autosomal dominant neurodegenerative disease. A CAG repeat (41–81 in comparison with normal individual 6–39 repeats) on chromosome 6 was identified in the SCA1 (codes for 87 kD ataxin protein) region by Orr et al. (1993). An inverse correlation between repeat length and age of onset has been documented, whereas direct correlation between repeat length and severity of disease is present. Juvenile cases are mostly due to paternal along with maternal transmission. The presence of cryptic interrupting CAT repeats in 13th and 15th position of CAG repeats in normal population is important for maintaining the genomic stability. Clinical features include progressive limb and gait ataxia, dysarthria, dysphagia, ophthalmoparesis, muscle wasting, and peripheral neuropathy including loss of Purkinje cells of the cerebellar cortex, atrophy of the brainstem, and neuronal loss in the cerebellum, brainstem, and spinocerebellar tracts.

SCA6, 7, 8, 12, and 17 are the other few types of spinocerebellar ataxia.

Huntington’s Disease (HD)

Huntington’s disease is an autosomal dominant movement disorder characterized by neuronal

loss (primarily of medium spiny neurons) in the caudate and putamen. Following the description by George Huntington in 1872, this disease is named as Huntington’s disease. An unstable CAG repeat (36–121) in HD patients, encoding a PGT in the It15 gene (348 kD huntingtin protein), is present compared to 10–35 (normal). Predominant paternal transmission in juvenile cases is very common with the presence of permutation allele like FXMR. Characteristic features include progressive cognitive decline, chorea, and movement impairment.

Huntington’s disease like2 which is another CTG TNR expansion related to neurological abnormalities is also reported.

Dentatorubral-Pallidoluysian Atrophy (DRPLA)

DRPLA is an autosomal dominant disease named for the neuropathological findings of atrophy of the dentate nucleus of the cerebellum and its projections to the red nucleus (rubro) combined with atrophy of the lateral segment of the globus pallidus and its projections to subthalamic nuclei. 7–25 CAG repeats (normal) with expansion to 49–75 repeats in affected individuals and repeat expansions are more frequently observed in paternal transmissions. Clinical features include cerebellar ataxia, choreoathetosis, and dementia, although patients <20 years old show progressive myoclonic epilepsy and mental retardation.

**Expanded Triple Repeat, Table 1** Polyalanine repeat (Di Prospero and Fischbeck 2005)

| Disease                                                            | Symptoms                     | Gene   | Protein                         |
|--------------------------------------------------------------------|------------------------------|--------|---------------------------------|
| Oculopharyngeal dystrophy                                          | Weakness                     | PABPN1 | Poly(A)-binding protein 2       |
| Congenital central hypoventilation syndrome                        | Respiratory difficulties     | PHOX2B | Protein paired-like homeobox 2B |
| Infantile spasms                                                   | Mental retardation, epilepsy | ARX    | Aristaless-related homeobox     |
| Synpolydactyly                                                     | Limb malformation            | HOXD13 | Homeobox D13                    |
| Cleidocranial dysplasia                                            |                              | RUNX2  |                                 |
| Holoprosencephaly                                                  |                              | ZIC2   |                                 |
| Hand-foot-genital syndrome                                         |                              | HOXA13 |                                 |
| Type II blepharophimosis, ptosis, and epicanthus inversus syndrome |                              | FOXL2  |                                 |

**Haw River Syndrome (HRS)**

It is an autosomal dominant neurodegenerative disorder (CAG TNR 63–68) prevalent in a single African-American family from Haw River, North Carolina (Farmer et al. 1989).

**Machado-Joseph Disease (MJD/SCA3)**

The disease was initially described in individuals of Portuguese-Azorean descent (Nakano et al. 1972), now recognized as SCA3. The CAG

TNR (12–37) is present in MJD1 gene in normal, whereas affected individuals contain 61–84 repeats. Degenerative changes have been noted in the neurons of the substantia nigra, dentate nucleus of the cerebellum, spinocerebellar and pyramidal tracts of the spinal cord, and peripheral neurons. Clinical features like cerebellar ataxia and extrapyramidal features include dystonia-rigidity reminiscent of parkinsonism, peripheral

| Target                              | Drugs                                                                                                                            | Purpose                                                                   | Effects                                                                 |
|-------------------------------------|----------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------|-------------------------------------------------------------------------|
| Mitochondria (FA)                   | Idebenone, mitoquinone (antioxidant)                                                                                             | Decreases lipid peroxidation and enhances mitochondrial energy production | Neurological function improvement                                       |
| Iron accumulation                   | Pyridoxal isonicotinoyl hydrazine (PIH)                                                                                          | Chelation therapy, mobilizing mitochondrial iron                          |                                                                         |
| Enhancing frataxin gene expression  | Cisplatin, hemin, and sodium barbiturate (histone deacetylase HDAC inhibitor)                                                    |                                                                           |                                                                         |
| Increasing FMR1 mRNA level          | 5-azadeoxycytidine (5-aza), L-carnitine or acetyl L-carnitine, %aza + HDAC inhibitor                                             | DNA demethylation                                                         |                                                                         |
| Symptomatic treatment for DM1       | Phenytoin, carbamazepine, tocainide, imipramine, and DHEA-S                                                                      |                                                                           | Clinical benefit                                                        |
| Polyglutamine protein aggregation   | a) Geldanamycin, benzothiazoles, Congo red, and trehalose<br>b) Cysteamine (competitive transglutaminase inhibitor)              | Reduction of polyglutamine protein aggregation                            |                                                                         |
| Caspase activation                  | Minocycline, tauroursodeoxycholic acid                                                                                           | Reduction                                                                 | Benefit in mitochondrial stability and behavioral deficit               |
| Excitotoxicity                      | Amantadine, riluzole                                                                                                             | Reduction                                                                 | Reduced chorea in HD patients, but motor performances were not improved |
| Neuroprotection                     | Ascorbate, BN8245, creatine, coenzyme Q10 with remacemide, and $\alpha$ -lipoic acid                                             | Oxidative stress reduction                                                |                                                                         |
| Transcription factor overexpression | CREB-binding protein (CBP or CREBP), p300/CBP associated factor (PCAF), TBP associated factor 4 (TAF4), and SP1                  | Transcriptional regulation of PG                                          |                                                                         |
| HDAC inhibitors                     | Phenyl acetate, phenylbutyrate, Valproic acid, suberoylanilide hydroxamic acid, depsipeptide and MS-275, polyphenol, resveratrol | Transcriptional regulation of PG                                          | Phases I and II clinical trial                                          |
| Neurotrophic factors                | BDNF, NGF, CNTF, GDNF                                                                                                            | Protection                                                                | Benefit in transgenic HD model                                          |
| Antisense RNA technology            | Antisense RNA against CAG repeat                                                                                                 | Translational regulation                                                  | Tested in cell-based SBMA model                                         |

neuropathy, facial and lingual fasciculation, and external ophthalmoplegia (Table 1).

#### Polyaspartic Acid Repeat

Mutations in the COMP (cartilage oligomeric matrix protein) gene in patients with multiple epiphyseal dysplasia.

### Therapeutic Approach

The development of therapeutics also varies for the noncoding and coding disorders. For noncoding disorders, restoring gene function or compensating for the loss of function is the major focus, whereas coding is directed toward ameliorating the consequence of the toxic protein.

### Conclusion

An acute and sophisticated mechanism maintains the stringency and stability of human genome and also in subsequent generations. Disruption of stability in the genome causes malfunctions and executes its effect in the form of disease. Repeat sequences are present in the genome normally in the form of micro- or minisatellite, triple repeats, etc. After exceeding a certain threshold level, the triple repeat can be toxic for the cell. Triple repeat can be in either noncoding or coding region in the form of CCG or CAG repeat, respectively. These repeats are expanded in subsequent generations and execute their effect when it transmits paternally or maternally, in the form of mental retardation, movement disorder, reduced fertility, etc. Different therapeutic interventions are under clinical trial targeting the pathomechanism of the disease. Most of the drugs are either in the form of antioxidant, transcriptional suppressor, demethylating agent, apoptosis inhibitors, etc. The in-depth knowledge of the pathomechanisms and the cryptic genetic mechanism related to these diseases will help in the further progression of the amelioration of these diseases.

### Cross-References

- Exon
- Genetic Code
- Heredity
- Intron
- Methylation

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## Experience Projection

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### Definition

Experience projection is the ability to use our own past experiences to attribute experiences to others in similar situations. A task proposed by Cecilia Heyes to test the ability has become a landmark for investigating mind-reading abilities in other species.

### Introduction

Suppose you look out the window and see a new car in the driveway. Moments later you notice me looking out the same window, and you draw a conclusion: that I must be able to see the new car in the driveway. In doing this, you are using your past experience to draw a conclusion about what I can see. You have “projected” your experience of looking out the window to me. Since seeing is a mental state, such an attribution is a form of “mind-reading” – the activity of discerning the mental states of others. It has become a focal point for psychologists aiming to establish mind-reading in other species.

### Knowing About Other Minds

How do we figure out what is going on in others' minds? The striking thing about other minds is that we can have no direct experience of them ourselves – they are “invisible” (Locke 1690/1975 111.ii.1). All that we have to go on is the

behavior of others to decide what, if anything, they are thinking. For this reason, an early account of how we generate beliefs about other minds is that we do so through an “analogical inference” from our own experience (Mill 1865). On this view, when we see others behave in familiar ways, we attribute to them the mental states (experiences, beliefs and desires) that we ourselves have when we behave in those ways. We could say that this straight-forward account of mind-reading amounts to a description of what has more recently been called experience-projection.

In experience-projection, we take our own past experiences and use them to form beliefs about others' experiences. The notion of “experience” is broad here and can include a whole range of mental states including what someone can see, what they can hear, what they might believe, or what they might desire. Since this kind of reasoning involves mental state concepts like “sees” or “believes,” experience-projection is a kind of mind-reading. In addition to being central to the “analogical inference” account of mind-reading, experience-projection plays a central role in “simulationist” accounts of mind-reading (Goldman 2006), while “nativist” accounts (Leslie et al. 2004) or theory-theory accounts (Gopnik and Meltzoff 1997) do not assign a central role to this kind of reasoning.

The fact that all we have to draw on when mind-reading is the behavior of others, however, generates substantial philosophical puzzles for our knowledge of other minds. For example, since behavior is only indirect evidence of mental states, some have doubted whether our beliefs in other minds can ever be properly justified (Ryle 1949, 15); and since we can have no direct experience of others' mental states, we can also doubt whether the concepts we use to think about others' mental states are ever appropriate (Nagel 1974). That all we have to draw on is others' behavior to engage in mind-reading also generates difficulties for experimentally testing mind-reading abilities in other species. If every instance of mind-reading is also an instance of behavior-reading, then any observation of apparent mind-reading in another species will also be an observation of behavior-reading. This raises the worry that any experiment



that appears to illustrate mind-reading in another species may always be interpretable as illustrating no more than behavior-reading.

To see the problem, consider the “guesser-knower” paradigm, designed to experimentally illustrate mind-reading in nonverbal creatures (Povinelli et al. 1990). Here, participating chimpanzees (*Pan Troglodyte*) are presented with two agents, one with a bag over her head (the guesser) and one without (the knower). Food is hidden in containers by a third agent, in such a way that the “knower” sees the hiding but the guesser does not. All of this is observed by the participating subject. The guesser and knower now each point to different locations, and the participant can pick one of these locations to search for food. After a number of trials, the apes reliably prefer to search the location indicated by the “knower.” The authors took the results to illustrate a recognition of the difference between a knowledgeable and an ignorant agent on the part of the apes, and hence to illustrate mind-reading. However, the setup is vulnerable to a clear behavior-reading alternative. The “guesser” and “knower” are visually distinct – the guesser wears a bag over her head, the knower does not. And so the results are ambiguous, as the authors came to recognize. On the one hand, they might show that the apes understood that one agent could see the food being hidden and the other could not – a “mind-reading” interpretation; but they could also simply show that the apes learned that the agent without a bag on her head was more likely to be pointing at the location of food – a “behavior-reading” alternative (Heyes 1998, 106).

### Experience Projection as a Solution to the Behavior-Reading Confound

To disentangle mind-reading from behavior-reading, Heyes (1998) proposed an “experience projection” paradigm. The aim of the paradigm is to capture subjects evaluating the behavior of an agent differently depending on what they have themselves experienced in the past. In one condition, subjects have had the experience of being in the position of the agent they observe, and in the other condition they have not had that experience.

If subjects form different expectations depending on their own past experience, it seems that this can only be explained by the subjects projecting their own past experience to the agent they observe. Particularly, since the observed agent’s behavior would be identical in both conditions, it seems that there is no behavior-reading alternative that participants could be using to form their expectations.

Heyes presented the idea as a hypothetical paradigm we can call “the goggles experiment.” In this setup, subjects first get to have experience with two pairs of goggles. Both pairs of goggles look as though they are opaque from far away, but when worn, one of the pairs turns out to be see-through. Participants now get to watch someone else wearing the goggles. This agent provides the participant with pointing gestures to indicate the location of hidden food, while wearing either the opaque or the see-through goggles. What we should expect is that participants who have had experience with the goggles and can attribute states of “seeing” or “not seeing” to the agent will follow the gestures of the agent wearing the see-through, but not the opaque goggles. A control group of subjects is also presented with the pointing behavior from the agent wearing goggles, but has no prior experience with the goggles themselves. Participants who have had no experience should not make this distinction.

If the participants who have had experience pay more attention to the agents wearing the transparent goggles than the agent wearing the opaque goggles, there seems to be only one explanation for how they could do this. This is that they have drawn on their own past experience with the goggles, and they have used this experience to attribute states of “seeing” or “not seeing” to the agent. Since the concept “seeing” is a mental concept, this would illustrate mind-reading on the part of the subjects. And since the behavior of the agents the participants observe is identical, we seem to have demonstrated mind-reading while eliminating the behavior-reading confound.

In addition to promising to eliminate the behavior-reading confound, the paradigm has the potential to capture the most intuitively clear kind of mind-reading – the “analogical inference” articulated by Hume, which is really what

experience-projection amounts to. Heyes' proposal is therefore both experimentally and conceptually very appealing.

## Experimental Progress

Meltzoff and Brooks (2008) conducted a study along the lines of this proposal with 18-month-old infants. They used blindfolds that both looked opaque from a distance, but one of which blindfold could be seen through when held close to the face. Children participated who either had experience with the properties of the blindfolds or had no experience. The authors found that children who had experience with the "see through" blindfolds would follow the gaze of an experimenter wearing one of these more than they would follow the gaze of an experimenter wearing one of the opaque blindfolds; while the children that did not have experience with the two kinds of blindfolds showed no preference to follow experimenters wearing the transparent blindfolds. This seems to indicate that at 18 months, children can engage in mind-reading by experience-projection.

Vonk and Povinelli (2011) report a similar experiment with chimpanzees, but found no positive result. This time buckets were used, either transparent or opaque. Apes with experience of the see-through buckets displayed no preference to follow the gaze of an experimenter wearing a see-through bucket over one wearing an opaque bucket. Karg et al. (2015) also found a negative result for chimpanzees in a similar gaze following task. However, these authors then introduced a competitive element to the experiment, drawing on the finding that chimpanzees are often more motivated and skillful in competitive than cooperative contexts (Hare and Tomasello 2004). Chimpanzees were given the opportunity to interact with two boxes. Both boxes have lids that are opaque when viewed from an angle; but the lid of one of the boxes, when viewed directly, is transparent. The chimpanzees are now placed opposite an experimenter who will remove food from a box that the chimpanzee tries to extract food from – in effect acting unhelpfully or competitively. The experimenter is viewing the lids of the boxes

directly and hence can see through one of them, while from the chimp's position both lids appear opaque. What was found is that the chimps that had experience with the see-through lid avoided taking food from the box fitted with that lid, apparently to avoid taking food that an experimenter can see. This indicates that the chimps are indeed drawing on their own prior experience to make a decision about which box to try to take food from, and are attributing mental states of being able to see or not being able to see to the experimenter.

We also have evidence for the convergent evolution of experience projection in other species beyond our close cousins the chimpanzees. Emery and Clayton (2001) have found that corvids can also pass a version of the experience-projection task. Scrub Jays (*Aphelocoma coerulescens*) were given the opportunity to "cache" or hide food when a second bird is either watching them or not. They were then allowed to subsequently return to the enclosure to retrieve their food, without the observing bird. It was found that the birds who had been watched by another bird were more likely to re-cache their food in a new location when they had the chance than those who had not been watched. Importantly, the authors found that the birds who had themselves previously played the role of observer and then attempted to pilfer another's food were more likely to move their food to a new location when in private than those who had never played the role of observer. This suggests that having had the experience of observing another bird caching food, Scrub Jays can draw on this experience to pick a strategy when hiding their own food. This would again count as an instance of experience-projection, since it would appear to require the birds to evaluate what the observing bird can see on the basis of what they saw themselves in the past.

## Criticism of the Paradigm

Lurz (2009) argues that the experience projection task is flawed – that there remains a behavior-reading alternative that is not ruled out. The

behavior-reading alternative is that a participant might solve the task by simply tracking whether another either has or lacks a “line of sight” on some object. Since a line of sight is simply a geometric line in space between an agent’s eyes and some target, the concept is not essentially mental, and hence if the task can be solved in this way, it would count as a behavior-reading alternative. Lurz argues that the task could be solved in this way by the agent who gains experience with the goggles by recognizing that when the transparent goggles are worn, the wearer has a direct line of sight on objects in her environment. When the opaque goggles are worn, on the other hand, there is no direct line of sight. This should be enough to get the subject to follow an agent’s gaze when the agent wears the transparent but not the opaque goggles, or to steal food when the opaque but not transparent goggles are being used. But it would not involve any mental concepts on the part of the subject.

Whether this critique is sound is unclear. It requires us to believe that the subject takes the agent she observes as having nothing occluding her vision when she is wearing the transparent goggles. But this is hard to believe – it is immediately obvious that an agent wearing transparent goggles has something occluding her vision – namely the goggles. The reason we understand that an agent wearing the transparent goggles can see is not because she has nothing in her line of sight, but rather because the object in her line of sight is transparent. And the very idea of transparency is itself a notion that cannot be separated from the mental concept of seeing: “transparent” simply means “see-through.” Doubtless, we will benefit from having further experimental setups that can illustrate mind-reading in other ways, as multiple lines of evidence are always more convincing than just one. Recent success with implicit false-belief tasks in chimpanzees illustrate that other ambitious mind-reading experimental setups can indeed succeed (Krupenye et al. 2016; Buttelmann et al. 2017). But the experience-projection paradigm remains an extremely important contribution to this family and should not be discarded just yet.

## Cross-References

- ▶ [Guesser-Knowner Paradigm](#)
- ▶ [Social Cognition](#)
- ▶ [Theory of Mind](#)

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## Experimental Cultural Diffusion

### ► Diffusion Studies

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## Experimental Social Learning

### ► Diffusion Studies

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## Explicit Memories

### ► Cognition

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## Explicit Memory

- Declarative Memory
  - Long-Term Memory
- 

## Exploratory Behavior

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Exploratory behaviors in animals involve various activities, such as moving antennae or raising ears, fixating gaze, moving from one place to

another in space, manipulating objects, sniffing, sensing, etc.

The best known and the most widely accepted definition of exploratory behavior was first put forward by Berlyne (1962), who defined exploratory behavior in terms of its function: “The function of exploratory responses is to change the stimulus field” (p. 286).

Marler and Hamilton (1966, p. 159) began their chapter on *Exploration, Aggression, Conflict and Play* with the following statement: “Animals spend much of their time in motor activity, the function of which is often difficult to identify.” Twenty-eight years later, when writing about exploration, Keller et al. (1994, p. 3) stated: “. . . we have not attempted to arrive at a definition of curiosity and exploratory behavior upon which every contributor to this volume would agree. Given the state of the art in research and theory on curiosity and exploratory behavior, we thought to attempt to do so would be counterproductive.” It seems that the difficulties with defining exploration are due to the many forms of behavior that different authors label as “exploration.” Some of these behavioral forms are described below from the least to the most complex.

**Taxes and Orienting Reflex.** These terms describe any turning of the body in relation to the position of the specific stimulus. Orienting reflex is synonymous with taxis. This term, however, is most often used with reference to less advanced organisms. In Pavlovian terms, an orienting response means any response involving paying attention to a stimulus, such as head turning or ear raising. Any reference to information seeking stresses the animal's own activity. However, any organism's fundamental reaction to external information is responsive in nature, since it involves a reaction to a stimulus received from the environment. This is a characteristic feature of the taxis and the orienting reflex observed in vertebrates. This reflex is released by a sudden, unexpected stimulus (“unexpected” from the point of view of the organism concerned). Information seeking in response to a stimulus is mostly aimed at finding its source: it is a strictly short-term response of an organism to a clear, unexpected sensory stimulus. The

orienting reflex is a behavior typical of vertebrates.

**Perceptual Exploration.** This refers to a prolonged perception, by any sensory system, of a specific stimulation – a direct extension of the orienting response. Perceptual exploration is strictly linked to focusing attention on the object perceived.

**Locomotor Exploration.** This refers to a situation where an organism is moving within or approaching a novel environment. The term “patrolling,” on the other hand, is often used to describe movements through a well-known area, usually the animal’s own territory. It involves “covering” the area available to the animal, while its main purpose is to obtain topographical information about the animal’s surroundings. This manner of gathering information develops in animals with the ability to form representations of the space that they inhabit.

Locomotor exploration is a one of the three main forms of exploratory behavior, along with orienting and investigatory reflexes. This general categorization inevitably places many different forms of behavior under one category. One of the forms of locomotor exploration is patrolling behavior, which involves systematic traversing of a familiar space, usually the animal’s own territory. An animal that inhabits a given environment forms a representation of its surroundings. Such mental representations may have varying degrees of complexity and include objects with well-recognized features. They can also include poorly defined objects, in which case the structure of representation will be very simple. Tolman (1948) put forward a hypothesis that the function of exploratory behavior is to construct a cognitive map. This was probably the first scientific attempt at analyzing animal behavior in terms of gathering information at the cognitive level.

Later studies by Tinbergen (1951) further illuminated the issue of cognitive maps. In his seminal research on digger wasps, Tinbergen demonstrated that animals seek specific information. They usually look for “landmarks” in terms of spatial orientation and subsequently shape their behavior in relation to those spatial cues. Locomotor play is also sometimes associated with

exploration, but it is found in fewer species than locomotor exploration. It provides a different type of information.

**Investigatory Behavior.** This term refers to various behavioral activities, such as interaction with the object being examined, manipulation of the object, investigation of a particular area (prolonged sniffing), etc. This is done through the mental representations an animal creates of the objects it examines. Learning the properties of these objects and their relationship to other elements in the environment takes place via perceptual exploration coupled with investigative responses. These two forms of activity allow the animal to enrich its existing representations of objects with their properties and attributes. Perceptual exploration makes it possible to replenish the existing representation of an object or area with information about its stimulatory properties. Manipulatory responses allow the animal to add information about the weight and structure of the object being explored. They also allow for the creation of contingencies between a given behavior and the environment. Both forms of information gathering are shaped by the animal’s ability to construct complex cognitive representations of objects. They are therefore a prerequisite for more advanced information seeking: knowledge seeking at the cognitive level.

An important new aspect at this level of information seeking is that the properties of an object become crucial to the regulation of the behavior in question. Complex novel stimuli (objects) become powerful incentives to begin exploratory and manipulative activities. There is also another dimension to novelty which involves not only relocation of a familiar object in space or the introduction or removal of a new object. Exploration may simply be triggered by a change in the object’s properties. Investigatory responses are induced in reaction to a change in a familiar environment (Pisula et al. 2019).

**Cognitive Curiosity.** This term covers seeking novelty and information at a cognitive level. Daniel Berlyne was probably the first to notice the close relationship between exploratory behaviors and cognitive activity (Berlyne 1962). He coined the term “knowledge-seeking behavior” and



emphasized the symbolic character of knowledge acquired in this manner. Berlyne attributed the highest level of complexity to the following basic types of activity: epistemic observation, consultation, and directed thinking. Within the integrative levels framework (Pisula 1998, 2009), epistemic observation must be categorized as a sophisticated form of perceptual exploration. Consultation, on the other hand, forms part of information seeking, as does directed thinking. This modification does run counter to Berlyne's intended classification, as he placed directed thinking at a privileged position in terms of behavior regulation. This modification, however, takes into account the integrative levels and the ecological approach (Gibson 1979) that stress the dependence of the meaning of a certain stimulus on the individual's perceptual abilities.

### Motivation to Explore

Research on the motivational mechanisms of exploration has been inhibited by the absence of a precise definition of these behaviors. Whether exhibited spontaneously or in response to (often quite intense) environmental stimulation, these behaviors have been analyzed collectively. Multiple studies have looked at forced (i.e., extrinsically motivated) exploration and spontaneous (intrinsically motivated) exploration (Renner 1990). There is no doubt that every behavior of an organism is closely related to the stimulation present in its environment. It is important, however, to determine which component plays the key part in a given situation. A comparative psychologist would naturally be more interested in intrinsically motivated exploration, as it reveals the complexity of an animal's psychological processes. However, for technical reasons, tests commonly used in laboratory experiments are usually designed to study forced exploration. Studies that successfully measure spontaneous exploration are much less common, although they are currently considered to be the most promising.

As early as 1958, M. Glanzer presented a comprehensive summary of studies on exploratory behaviors. His review included more than

70 research projects on the subject. The results of these studies yielded the following conclusions:

1. Places in which there are complex or multiple stimuli are explored more intensely than places without such properties.
2. The intensity of exploration drops rapidly with time spent by the animal in a given situation.
3. The intensity of exploration decreases with repeated experiences of a given situation.
4. Lack of exposure to an experimental condition or a prolonged time of waiting for a stimulus intensifies exploration.
5. An opportunity to engage in exploration is rewarding and, as such, can be used as reinforcement in the operant conditioning procedure.
6. A decrease in exploratory behavior in a familiar experimental condition is generalized onto similar situations, and the degree of similarity between those situations is a good predictor of exploration intensity.
7. To a large extent, exploration is independent of the amount of effort it requires. Thus, rats press levers offering various levels of resistance with a similar amount of effort, as long as this is an element of exploratory activity.
8. Exploration is not related to the ability to engage in motor activity in general: there are no differences in exploration between rats given access to a running wheel in their home cage and those deprived of such an opportunity.

In the summary of his article (which is exceptionally comprehensive given the early stage of research in that area), Glanzer lists key issues to be studied in the context of exploration:

1. Learning. What and how does an exploring animal learn? There is no question that it does in fact learn through exploration.
2. Exploratory drive. What is the nature of the exploratory drive? Is it similar to the hunger drive?
3. Stimuli controlling exploration. What attributes of stimulation arouse or inhibit

exploratory behavior? Are they stable or subject to change?

4. Fear of a novel stimulus. A high-intensity novel stimulus will not arouse stimulation but provoke escape or ceasing of all locomotor activity. What mechanisms determine the change in the function of a stimulus?

Research focused on the above issues has shaped our current understanding of exploratory behavior. There is not a single universally accepted definition of curiosity, but research on this phenomenon is dominated by three main traditions. The first and oldest builds on the drives theory (exploratory and boredom drives). The second is linked to the ideas of Hebb (1955), which draw on the hypothetical state of optimal arousal. The latest approach emphasizes the informative aspect of exploration.

The hypothetical drives of curiosity and boredom may be analyzed together, since, as noted by Russel (1983), they are compatible. The boredom drive hypothesis (Myers and Miller 1954) assumes that as the situation of monotonous stimulation persists, an organism generates drive tension. The curiosity drive hypothesis (Montgomery 1953) predicts that tension is generated as a result of the absence of access to varied stimulation. It can be easily demonstrated that these two concepts are reversible. The drive theory exerted a lasting influence on the psychological theories and therefore merits a more detailed analysis.

When analyzing theoretical concepts, it is vital to formulate predictions on the basis of a given model. Research hypotheses based on the above model would be as follows:

- With the passage of time and with no access to stimuli that could trigger a drive behavior, the threshold of sensitivity to these stimuli decreases, while the intensity of the triggered behavior increases.
- After a long time spent in an environment devoid of stimuli triggering drive behaviors, elements of the drive behavior chain will occur in the absence of the triggering stimulus (“releaser”) due to the accumulation of “drive energy.”

Analyses of the experimental data on exploratory behavior reveal no solid evidence in support of the drive theory. Birke and Archer (1983) obtained results that contradicted the first hypothesis and found that sensory deprivation does not always provoke an increase in exploration. Subsequent studies have shown that the increase in exploration following sensory deprivation is consistent with the expectations of the drive theory. The increase in the activity of rats subjected to sensory overload, however, suggests a more complex mechanism regulating exploration.

In summary, deprivation or sensory overload may lead both to an increase and to a drop in the intensity of exploratory behavior. This is probably due to the fact that there are other variables involved in the regulation of these behaviors, unaccounted for in the exploratory drive theory.

Another hypothesis arising out of the single-drive theory of exploration is that since various forms of this behavior are triggered by a common mechanism, they should be covariant. However, Barnett and Cowan (1976) published results demonstrating that the correlations between various forms of exploration are relatively weak. A theoretical analysis (Pisula 1998) also shows that different forms of exploration must be driven by different control mechanisms characterized by various levels of complexity and organization. Thus, despite the advantage of simplicity and apparent universality, the drive theory (of boredom or curiosity drive) does not explain exploratory motivation sufficiently well.

Since the early 1950s, the search for the mechanisms that control exploration gravitated towards systems based on maintaining an optimal level of nervous system arousal. Although the same concept was considered by multiple authors, it was presented in its most mature form by Hebb (1955). To mark its importance, the article was reprinted in Fowler’s (1965) collection of essays on exploration. Hebb opens his analysis of motivational processes by listing two central aspects of sensory experience: the cue function and the arousal function. He defines arousal as the most general drive and emphasizes its energizing aspect: “the drive is an energizer, but not a guide; an engine but not a steering gear” (Hebb 1955, p. 249).

The analysis of the relationship between cue effectiveness and cerebral cortex arousal prompted Hebb to propose the inverted “U” hypothesis, according to which there is an optimal level of cerebral cortex arousal for every activity. Thus, depending on arousal level, a given stimulation may improve the performance of a specific activity when the arousal level is low or deteriorate it when the level is too high.

This process is central to our understanding of motivation in higher animals and humans. An organism seeks to maintain the optimal level of arousal. Even though Hebb uses the term “drive,” his concept is in stark contrast to theories based on the classical drive theory. In the traditional approach (e.g., Lorenz), an organism is motivated to act when drive anxiety is reduced. According to Hebb, an intensification of drive anxiety may have the same effect. This difference has important consequences, including an impact on learning. In the classical drive theory, the positive rewarding value is assigned to those events that reduce the drive. In Hebb’s approach, it is ascribed to those that move the arousal level (through the stimulation they provoke) to its optimal value. Thus, the same response may be rewarded or punished depending on the state of the organism at the time of its occurrence. Exploration is undoubtedly a source of new stimulation and, as such, it increased arousal. Thus, according to Hebb’s theory, exploratory behavior occurs when the organism seeks to increase its arousal. This hypothesis laid the foundations for developing an area of research on exploratory behaviors that treated them as symptoms of a wider class of activities resulting from the need for stimulation.

The final conclusion is that there is a certain relationship between exploratory behavior, on the one hand, and the need for sensory stimulation driven by the Hebbian mechanism of optimal arousal, on the other. The relationship is positive, that is, individuals with a strong need for stimulation tend to explore more than those with a low need for stimulation, albeit by no means straightforward. While it must be taken into account in the theory of exploratory behaviors, it does not explain them. The results show that the mechanism described by Hebb does indeed play some

role in controlling exploration, but it is neither the only nor the most prominent factor in that process.

An alternative to the “drive” and “arousal” approaches to the factors underlying exploration was explored by researchers focusing on its information-seeking function. This function has two components: the informative (signal) value of stimulation and the content of the information warehouse (however understood) at the organism’s disposal. As indicated above, Glanzer (1958) proposed a system for analyzing exploration that must be regarded as one of the first theories explaining this class of behaviors. He was among the first authors to emphasize the role of information gathering in the regulation of these behaviors. Glanzer based his reasoning on the indisputably correct assumption that an organism is a system that processes information from the environment. This system requires a certain amount of information to be received in a given space of time. If the inflow of data is insufficient, it is actively increased through exploratory activity. If, on the other hand, the amount of incoming information is excessive, it is reduced by avoidance and freezing. Information needs are determined by earlier experience: an animal that experiences an inflow of a significant amount of information puts high demands on itself (raises its standards). Conversely, an animal kept in conditions of information scarcity sets itself low requirements in this respect. Though very neat, Glanzer’s theory has not gained many supporters due to problems with the operationalization of the variables studied, which resulted in conflicting empirical results (cf. Inglis 1983).

The search for a mechanism based on the informative content of stimulation resulting from exploratory behavior has developed towards analyzing the relationships between exploration and changes in stimulation. Novelty and complexity of stimulation are both psychological functions of the stimulus itself and of the state of the organism. The same stimulus can thus be more or less novel/complex, depending on the preexisting experience-based expectations of the organism. For the same reason, objectively different stimuli may have similar subjective values. This approach to the attributes of stimulation in the context of

exploratory behavior has become a constant feature in the analysis of animal behavior when encountering a novel stimulus. The idea that the organization of animal and human behavior may, to a large extent, be based on the comparisons between what is expected with what is actually observed is not new. One of the first authors to examine this mechanism was Salzen (1970, 1991).

In his analysis, Salzen pointed out that the mechanism underlying exploration is based on a comparison of the neural environmental model that is constructed as the organism gathers experience with the present stimulation from that environment. The discrepancy between the two is what prompts the animal to engage in actions aimed at reducing and ultimately eliminating that discrepancy. A small discrepancy triggers exploration, while a significant one triggers a flight response. The discrepancy between the observed stimulus situation and its neural representation is often cited in the attempts to explain the motivational basis of behavior. Archer (1976) developed an essentially analogous theory of agonistic behavior regulation. The appearance of another animal is a novel stimulus, which results in a discrepancy between the current neural model and the sensory input of the organism. A small discrepancy leads to aggression, while a bigger one to flight. Both categories of behavior serve to reduce this discrepancy.

The concept of motivation for exploratory behavior that took into account the mechanism of comparing the representation of the stimulus situation and the actual input was put forward by Inglis (1983, 2000). His model is also the most advanced – making use of the ideas derived from cognitive psychology. In short, it consists of the following hypotheses:

- Animals tend to form representations of their surroundings.
- These representations modify their behavior by generating expectations towards the current stimulation received from the environment.
- Attention processes are focused on stimulation, which differs from these expectations. They result from the mechanism comparing

the stimulation from and the representation of the environment.

- The intensity of biological needs modifies expectations towards stimulation by affecting the comparator mechanism.
- The strength of response to a stimulus is the function of the activity of the comparator mechanism triggered by this stimulus.
- The efficiency of assimilation of new stimulation and its integration into the existing representation depends on the ability to accommodate a stimulation deviating from the model and on the complexity of the existing representation.
- Whether the animal engages in exploring new stimulation or escapes depends on the intensity of the comparator mechanism response related to the particular efficiency of stimulation assimilation at a given point in time.

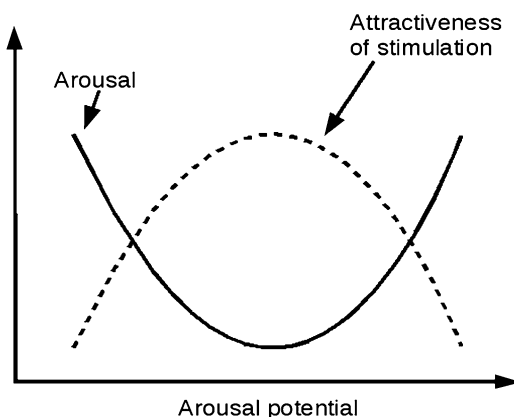
The mechanism operates as follows: an organism receives a specific input from the environment. The filtering mechanism (operating as part of the analyzer) isolates a set of potentially significant stimuli through automatic stimulation processing. This set is analyzed further by a hypothetical comparator mechanism. As a result of the analysis, appropriate behavior is triggered. If the expectations and the stimulus match, this triggers behavior aimed at satisfying a given biological need. If there are discrepancies, the orienting reflex is triggered first, followed by exploration (or flight) aimed at reducing the disparity.

In his comprehensive article, Inglis (1983) expressed his hope that the above theoretical idea would prompt extensive empirical research. This wish, however, has never materialized for a number of reasons. One problem is the complexity of this model, which makes it difficult to use as a basis for predicting the behavior of a given animal in a specific situation. It is even more difficult to determine what findings would be “prohibited” by this theory, that is, their occurrence would effectively be tantamount to a refutation. Furthermore, all theories based on the concept of discrepancy between the expected and the observed states have a common

methodological problem: discrepancy cannot be quantified with any precision. When discussing theoretical assumptions, terms such as “large” or “small” discrepancy make sense. Nevertheless, when researchers attempted to verify the presence of the theoretical processes empirically, the mounting difficulties often forced them to abandon their projects altogether. However, this theoretical framework for describing the relationship between the organism and its environment undoubtedly provides a tool for formulating hypotheses regarding the ways of coping with environmental change.

Berlyne's theory (1962) was a serious attempt at a synthesis. Berlyne analyzed two basic concepts related to the motivational mechanisms of exploratory behavior: arousal (interpreted as drive) and arousal potential. Arousal potential is a variable describing the relationship between the expectations regarding the stimulation properties of a given environment and the actual properties of that environment. Any departure from these expectations (although Berlyne did not use such a term himself), in any direction, results in increased arousal (curiosity drive). The relationship between arousal and arousal potential is therefore a U-shaped curve (Fig. 1).

Arousal potential is influenced by affective stimuli, strong stimuli, and internal stimuli. Their effect is modified by the following cognitive variables: novelty, complexity, and uncertainty. The



**Exploratory Behavior, Fig. 1** D. Berlyne model of the relationship between arousal potential and the attractiveness of stimulation and arousal. (Reprinted by permission)

exploratory behavior motivation theory proposed by Berlyne is probably the most frequently quoted one. In hindsight, Berlyne's theoretical model was an important contribution to the understanding of the mechanisms regulating exploratory behavior. While its predictive value is not particularly impressive, Berlyne's theory is important owing to the synthesis of elements derived from many different theoretical traditions: elements based on the curiosity/boredom drive, optimal arousal, and concepts derived from information theories. Creating such a theory is no easy task, and Berlyne took the first step in the right direction.

Ethologists were critical of the psychologists' efforts. In a monograph summarizing the achievements of ethology, Konrad Lorenz (1982) formulated some important hypotheses for the issues discussed here. First, he pointed out that exploratory behaviors differed from other behavioral classes: their uniqueness was due to the fact that an animal exploring an object employs a variety of locomotor patterns belonging to multiple drive categories and switches between them easily. When exploring a completely novel object, an animal may approach it as it would a dangerous enemy, attack it as a potential victim, try biting or carrying it, etc. Lorenz believed that exploration performed in this manner is objective in the literal sense of the word. The object becomes familiar in many respects, and the knowledge of its properties is stored for potential future use. As regards the motivational mechanisms, Lorenz emphasized their distinctiveness. This hypothesis is supported by the important finding that exploration comes to an end immediately when arousal of another kind occurs, for example, fear, pain, or hunger. Exploration occurs only in a field devoid of tension.

The foundations for modern ethological theory were laid by Buchholz and Persch (1994). These authors make use of the fundamental concepts of ethology. Stimulation received by an organism may be divided into two basic kinds: specific stimulation, that is, stimulation “targeted” at a specific release mechanism (RM), and nonspecific stimulation. The concept of the release mechanism was put forward by Tinbergen and Lorenz (1938). Lorenz (1982) presented a comprehensive analysis of this concept. According to Lorenz, the



release mechanism is a functional unit that belongs to afferent processes. It was originally referred to as the innate release mechanism (IRM) (Lorenz 1982; Tinbergen and Lorenz 1938). This term denotes a hypothetical mechanism enabling the animal to recognize biologically significant stimuli without prior learning. Recognition, in turn, triggers action readiness. This state, where stimulation is still being received, may transform into the arousal of the motoric coordination center (MCC), which controls a given behavior. Stimuli recognized by the release mechanism for exploration are frequently recognized by the release mechanism for flight. The action readiness system linked with exploration is inhibited by the flight readiness system. This results in behaviors that are typical of conflicts between drives, such as alternating exploration and flight (ambivalence) and displacement behavior (Tinbergen 1951). Which system becomes dominant in a given situation depends to a large extent on the modifying effect of memory, the influence of nonspecific stimulation and internal stimuli. The dominance of action readiness leads to the activation of appropriate motoric coordination centers and the launch of the exploration program.

It would be difficult to compare a theory based on an ethological approach with strictly psychological models. The differences in the conceptual frameworks used to describe the phenomena are too vast. The ethological theory, however, is undoubtedly an attempt at integrating exploration (while maintaining its distinctiveness) into the overall system of behavior regulation. This is where a clear advantage of this model of exploration lies. On the other hand, it would be exceedingly difficult to formulate verifiable hypotheses based on this theory. Detailed hypotheses could be proposed only if concepts such as “memory storage” or “external factors” were defined using psychological concepts, that is, if there was a description available of how these elements affect action readiness and the release mechanism. These improvements would bring the model closer to information-based theories.

Action readiness concept is compatible with the non-specific arousal of the central nervous

system (CNS), a concept employed by Berlyne (1962), and Hebb (1955). The ethological approach to exploratory behaviors thereby complements the psychological analysis with an important and comprehensive perspective but does not exhaust the potential scope of that analysis. There is still uncharted ground between the two approaches waiting to be illuminated by means of an integrated theory of exploratory behaviors.

Regardless of the internal regulatory mechanisms that determine the exact form of exploratory behaviors, there is no doubt that the novelty of a stimulus functions as a critical reinforcement (reward).

## Cross-References

- ▶ Curiosity
- ▶ Neophobia
- ▶ Novelty

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## Expressed Sequence Tags

### ► Gene Expression Profiling

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## External Fertilization

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### Definition

**External fertilization** or “the ancestor of internal modes of reproduction” is generally a widespread reproductive approach of aquatic animals including both invertebrates (coelenterates, annelids, mollusks, echinoderms) and vertebrates (fishes and amphibians) in which male and female gametes are released into the aquatic environments and fertilization occurs outside of the body (Giese and Kanatani 1987; Jigersten 1972; Parker 1984; Wray 1995; Rouse and Fitzhugh 1994).

### Introduction

Fertilization is the combination of haploid male and female gametes forming diploid zygote to begin a new life. Fertilization may occur inside the body of a female (internal fertilization) or outside the internal milieu (external fertilization). Our focused area is external fertilization which usually ensues in water or a humid area to ease the travels of sperms to the egg. Females and males spawn freely into the environment which might be triggered by various factors such as water temperature or the length of daylight. The trigger for spawning causes the egg and sperm to be in a small area, enhancing the likelihood of fertilization. This is not only the environmental triggers that signals and controls the spawning process; other male and female physiological components and phenomena also regulate the

entire process. Due to the presence of different types of species in the same environment with same breeding season and having same kind of environmental triggers, they face various challenges such as to address the right chance of contact of the gametes of the same species as well as on prevention of getting fertilized by sperms of another species. Thus, to overcome these encounters, these organisms have evolved several mechanisms which we are discussing below.

- (a) **Environment:** Gamete concentration is the primary factor for either a male or a female spawner which regulates the probability of external fertilization. Several field experiments have documented that in an aquatic milieu gamete can diffuse and rapidly convert diluted resulting in declined fertilized egg ratio. This depends on various aquatic environmental situations such as high-wave-intensity shores, increasing water flow, or increasing water velocity. These environmental factors are responsible for the very fast diffusion of gametes that sometimes males set apart greater than 10 cm up current from a female have deposited her eggs which in turn increase the rate of mixing. This situation come up with bigger gamete clouds, more gamete diffusion and plunging the probability of gamete contacts which abridged the fertilization achievement (Pennington 1985; Denny and Shibata 1989; Levitan et al. 1992; Petersen et al. 1992).
- (b) **Population:** At the populational viewpoint, gamete concentration and the probability of sperm-egg meetings are also matriculated by following four factors, i.e., the distance between folks, richness of folks, rate of gamete release, and timing of gamete release. These four factors have strong impact on the local concentration of gametes followed by fertilization success. The distribution and richness of concurrent spawners are determined by the group behaviors such as accumulation and synchronization of spawning. Various experimental studies documented previously that fertilization declines to about 20% at 1 m and about 1% at 10 m (Pennington 1985; Yund 1990; Levitan et al. 1991; Yund and McCartney 1994; Levitan and Young 1995). Spawning in natural environment also shows that female spawning occurs from the distance of several meters from a male, possess very low levels of fertilization. Thus, fertilization success depends on the male and female richness which ensures the female distance from a spawning male.
- (c) **Individual's behavior:** Individuals also can have impact on the gamete dispersal in the aquatic environment. Individual of the population can generate fluctuations in the frequency and timing of gamete release, spawning behavior, and the expanse of energy investment during reproduction. The dispersal of gametes in the environment depends on the rate of gamete ejection from the gonopore. A high spawning rate increases the gamete concentration (Denny and Shibata 1989) but decreases the spatial extent of the gamete cloud. A high spawning rate again allied with high spawning synchrony, close male-female pairing, and intense sperm race.
- (d) **Production of gametes:** These organisms harvest massive quantity of gametes. The occurrence of the fertilized eggs and emerging young in the water provides prospects for predation, ensuing in a forfeiture of offspring. Hence, millions of eggs must be produced by folks. The offspring produced over this way must be developed rapidly. The endurance rate of eggs produced over broadcast spawning is truncated.
- (e) **Sexual selection:** It seems like sexual selection may not appear to arise during external fertilization, but it can by few ways. Two types of external fertilizers are classified, i.e., nest builders and broadcast spawners. Female nest builders mainly focus on the location finding to lay her eggs. A female mainly picks a nest adjacent to the male she desires to fertilize her eggs, which is not guaranteed that any of the eggs will be fertilized by the favored male. Due to the randomness of releasing gametes, broadcast spawners possess very feeble assortment (Robalo et al.

2012). Alonzo et al. (2016) performed an experiment to investigate the outcome of female choice on external fertilization; an in vitro sperm race experiment was done from where they found declined importance of sperm amount but amplified the importance of the sperm velocity resulting in changed sperm race outcome. Interestingly they also found that the ovarian fluid possesses impacts on the increased paternity for the favored male as they release fewer and faster sperm. The achievement of an external fertilization thus relies on the aptitude of a male's sperm to outcompete other sperm that is beholding to fertilize the same egg which is mostly governed by sperm chemotaxis, i.e., the chemical signals which gives sperm the capacity to navigate an egg and hence possess vast aids to reproductive success (Hussain et al. 2016).

- (f) **Species-specific sperm attraction:** Species-specific sperm attraction has been reported in all species which encounters external fertilization, such as cnidarians, mollusks, echinoderms, fishes, amphibians, and urochordates (Miller 1985). As we discussed above about chemotaxis, i.e., a chemical gradient secreted by the eggs, it basically attracts sperms toward eggs of their own species. After reaching maturity, these oocytes release the chemotactic factor, governs not only the type of sperm they appeal but also the time of sperm attraction. This chemotactic factor creates a gradient surrounding the eggs. This species-specific chemotactic factors recognizes and binds to the specific receptor situated at the outer surface of the sperm head or acrosomal sac. The mechanism of chemotaxis is diverse among species, and chemotactic molecules are different even in closely inter-related species. For example, the gonadal pH of *Arabica punctulata* is kept low (about pH 7.2) by the high concentrations of CO<sub>2</sub>, and thus the sperm cells inside testes show no movement and motility is acquired only after spawning (Eisenbach 2004). Once sperms are spawned into seawater, the pH raise to about 7.6, resulting in the stimulation of the dynein

ATPase which splits ATP, providing the energy for the flagella to wave, and thus sperms commence vigorous swimming (Christen et al. 1983). The sperm movement in *Arabica punctulata* also needs the right direction to swim, and this direction is governed by a small chemotactic peptide, i.e., Resact, a 14 amino acid peptide, which diffuses radially from the outer jelly layer of the egg and makes a gradient (Ward et al. 1985). This sea urchin-specific chemotactic peptide can only be recognized and bind with its specific receptor situated on the sperm head which then gives the direction toward the gradient and finally allows to attach with egg (Kirkman-Brown et al. 2003).

- (g) **Success of fertilization:** In external reproduction, the close proximity of egg and sperm doesn't occur because animals always scatter their gametes through a body of water. This scattering reduces the possibility to the meeting of sperms and eggs resulting in many of the sperms and eggs dying before attaining fertilization. Hence, this low achievement rate of external fertilization puts aquatic-free spawning animals at a reproductive drawbacks compared to internal fertilization.

## Examples of External Fertilization

### Invertebrates

Most invertebrates are benthic sessile animals, maintaining their progeny by external fertilization that depends on ambient water motion which gives the proper atmosphere to meet the sperm and eggs together. Other invertebrates like the sea urchin also fertilize externally in the restricted to shallow burrows on bare shores where turbulent flows aid in gamete transports (Costa et al. 2016). The efficiency of fertilization in invertebrates is primarily governed by the spawning properties (i.e., gamete quality, gamete proximity, and spawning time) and its hydrodynamic environments (i.e., turbulence, water current, water velocity, etc.) which influence the rate of water mixing in the gamete cloud (Thomas et al. 2013). For example, increased turbulence in the water dilute

sperm and egg due to rapid mixing of water resulting in lower probability to fertilize (Costa et al. 2016). Sessile adult invertebrates prefer a synchronized production and release of gametes in the water column which helps increasing fertilization rates due to lack of share mobility of these organisms (Mercier and Hamel 2010). Before synchronized release of gametes, these animals also choose a place where all future survival factors such as the presence of food, resources, and favorable environmental conditions and the lack of predators is present for of the next generation, and then they go for gamete release (Forrest and Miller-Rushing 2010). To enhance the fertilization probability, they also rely on turbulent mixing and sperm mobility (Costa et al. 2016). Before a mass reproductive event, i.e., when multiple females are producing and releasing eggs in the water body, they accomplish predator satiation (Kelly and Sork 2002). The Great Barrier Reef is known as the place for “mass spawning” where a mass reproductive event of almost 130 species occur, starting from the week after the full moon in October and continues from dusk to midnight (Harrison et al. 1984; Willis et al. 1985). In some cases, fertilization can also ensue on the surface of a spawning animal and when the animals are in the turbulent wake (Thomas et al. 2013). Although, this fertilization on the surface of spawning animal does not follow traditional short-term external fertilization process due to the possibility of gametes being engaged on the surface of an animal for a prolonged time period (Marshall 2002). With the purpose of release an egg or sperm over time, gamete clusters are formed that drift in the water column which gives a variation in fertilization of the same invertebrate by changing locations and time differences (Thomas 1994; Thomas et al. 2013).

### Vertebrates

- **Amphibians:** External fertilization in vertebrates started till 300 million years ago. From Anura (Browne et al. 2015) to Caudata. Among the amphibians, anurans lack tail like frog and toad (Browne et al. 2015; Arak 1983). Due to the large, easy to manipulate eggs, fast developmental rate, high fecundity rate, no

parental involvement, and capability of external fertilization, anurans are used to be the common model organisms. In the mating season, males approach females by producing species-specific mating call from the “calling station,” i.e., near the lake or pond, where they gather at the mating season before approaching. Females firstly judge those approaches coming from different males and the move toward that male whom she chooses, and this is how the anurans ensure their sexual selection. The selection also depends on the body size of the male which has been supported by another observation that sperm number is associated with testes size which in turn depends on the body size (Browne et al. 2015; Bruning et al. 2010). For example, the larger the body size, the larger the testis size with increased number of sperm. During copulation, male anuran hops on the back of the female and moves toward the chosen spot where they simultaneously release their gametes. Fertilization is not necessarily done with the hopped male; other males of that area can also release their sperm to attempt fertilization. In this kind of situation sperm competition increase through agonistic behavior and spawning in groups because anuran sperms have high longevity and osmotic tolerance (Browne et al. 2015). Sometimes females don’t want to fertilize her eggs by the hopping male, and in that situation, she waits until the male leaves her back and moves to another place (Zhao et al. 2016). When preferable pairing occurs, the pair tries to release their gametes in close proximity, so that sperms get the best chance to enter the gel layer of the eggs followed by successful fertilization. If the gametes are not in enough proximity males occasionally release their sperm into oocyte containing foam nests to go precisely to the gel coat of the oocyte to release their sperm (Browne et al. 2015). Males target a female who is about to spawn along with releases their sperm anywhere he finds unfertilized eggs over the passage of a breeding season while females can only release their eggs once per breeding season (Zhao et al. 2016).



*Cryptobranchidae* (giant salamanders) Sirenidae, and Hynobiidae are the amphibians of the order Caudata that have tails (Browne et al. 2015). These external fertilizers group animals also possess almost the same kind of factors and processes to achieve their successful fertilization. Here, the males become protective toward the eggs after copulation and starts to hover over the eggs to reduce the sperm competition. In some cases, males become overprotective toward the eggs to ensure paternal success that they even latch onto the female during her egg laying (Houck and Arnold 2003).

- **Fish:** All fishes are the external fertilizers, among the every common examples are salmon, cod, trout, and char. The fertilization protocol is common to all other external fertilizers, i.e., release of male and female gametes into the water which diffuses and meets to form a new life (Stoltz and Neff 2006). Like in amphibians, the success of an external fertilization in fish also depends on the lower water velocity or turbulence along with closer proximity between gametes which in turn increases the chance of penetration of the sperms into the gel layer of eggs, leading to a successful fertilization (Browne et al. 2015). Sometimes the timing of gamete release also can be an important factor, i.e., suppose the male release his sperm too early, then sperm got diluted and die before the reach to egg and thus it gives the higher chance to other sperms from other fishes to fertilize the eggs. Same thing happens if they lost the proximity. Also, higher sperm velocity and larger sperm amount increase the probabilities of fertilization (Stoltz and Neff 2006). There are examples where males build habitats to monopolize females and upsurge his paternal success (Browne et al. 2015). Mostly fishes are iteroparous, and spawn more than once, but exceptions are always in the nature such as semelparous fishes, i.e., which spawn once before death. Within iteroparous fishes, they show no parental care (Murua 2014). The sperm motility depends on the environmental conditions. For example, a salmon sperm motility depends on the decrease of potassium in fresh water, or a

cyprinid fish's sperm motility depends on the decrease in osmolality after spawning in fresh water (Dzyuba and Cosson 2014).

## Conclusion

As discussed above, the success of external fertilization depends maximally on the environmental factors such as pH of water, water turbulence, water velocity, osmotic pressure, mineral level, presence of predators, etc. Some biological factors related to parents like gamete longevity, gamete proximity, timing of gamete release, etc. also controls the probability of external fertilization. Although a successful external fertilization faces several environmental and biological hindrances, this is still a strong natural fertilization process where a large number of offspring is produces with low parental energy investment. Due to the lower probability to be fertilized, both male and female produces large number of gametes. In contrast, external fertilization shows less survival rate of offspring due to lack of parental care as well as higher risk of being predated by other species along with their own parents. Still external fertilization is an evolutionary selected fertilization procedure for a large amount of aquatic species due to its sexual selection strategies, sexual dimorphism, limitation to become overpopulated, and higher probability of genetic variations.

## Cross-References

- [Gametes](#)
- [Sperm Competition](#)

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## Extinction in Learning

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The term extinction was coined by Russian physiologist Ivan Pavlov who became the first to employ a classical conditioning procedure, also known as a Pavlovian conditioning learning paradigm, through his study of dogs (Dickinson and Mackintosh 1978; Domjan 2010; Pavlov 1927). Extinction can either refer to an associative learning procedure where the reinforcer is removed or a decline in responding as a result of an absent reinforcer (Pavlov 1927). In order to conceptualize extinction, it is important to understand learning processes such as classical conditioning and instrumental conditioning, which both utilize associative learning procedures. During a classical conditioning procedure, a biologically relevant or unconditioned stimulus (US) is paired with a previously neutral or conditioned stimulus

(CS) to produce a conditioned response (CR). In classical conditioning, the innate or unconditioned response (UR) to a biologically significant stimulus becomes evoked by the pairing of the conditioned or previously neutral stimulus with the unconditioned stimulus. When the unconditioned stimulus is presented in the absence of the conditioned stimulus, the conditioned response is expected to diminish, a process known as extinction. In other words, extinction refers to the gradual decrease in a response due to the removal of a conditioned stimulus.

While classical conditioning refers to how an organism adapts to uncontrollable changes in their environment, instrumental or operant conditioning is a type of learning in which stimuli encountered are a result of an organism's behavior (Bouton and Swartzentruber 1991; Pavlov 1927). In instrumental learning, the organism's behavior is instrumental in producing a particular outcome, which either serves as a reinforcer or a punishment for such behavior in the future. Extinction in learning can occur subsequent to the learning of both classically and instrumentally conditioned behaviors. However, as noted by Pavlov (1927), extinction only produces a temporary loss of conditioned responses; following a passage of time, originally learned associations are likely to recover.

## Extinction in Classical Conditioning

Classical conditioning is a form of learning that allows for human and nonhuman animals to learn about relations between one event and another through the pairing of a biologically relevant stimulus with a biologically neutral stimulus (Pavlov 1927). During a classical conditioning procedure, the experimenter is expected to create a relationship between the stimulus and the reinforcer through repeated pairings of the two. This is known as the stimulus-reinforcer contingency, where the conditioned stimulus (CS) is paired with an unconditioned stimulus (US). In Pavlov's famous experiments with dogs, he paired food, which served as the biologically significant stimulus, with a previously neutral stimulus (e.g., the

sound of a metronome) to create a conditioned response (e.g., salivation). Pavlov noticed that the dog learned to salivate at the sound. However, the response became weakened when the stimulus-reinforcer contingency was removed; that is, when the bell was no longer paired with food, a significant decrease in the conditioned response occurred over time.

When the unconditioned stimulus or reinforcer is omitted and the conditioned stimulus is consistently presented in isolation, this is referred to as extinction (Pavlov 1927). While it may appear that the loss of the conditioned behavior observed in extinction may imply forgetting, it is important to note that it does not equate to forgetting or unlearning. Extinction is different from memory loss in that it is an active process that occurs due to the absence of the unconditioned stimulus. It is also referred to as an active inhibitory process because the conditioned response reemerges following extinction when tested after a prolonged period of time has elapsed; this is a phenomenon that occurs as a result of exposure to the conditioned stimulus, without any additional training. The ability for the previously extinguished conditioned stimulus to elicit a conditioned response is a strong indication that the original CS-US association still remains post extinction.

## Extinction in Instrumental Conditioning

While studying animal intelligence, Edward Lee Thorndike (1911) serendipitously began some of the early laboratory and theoretical analyses of instrumental conditioning (Bouton and Swartzentruber 1991). He was interested in understanding if animals possessed human intellectual capacities and to what magnitude. He studied this through the use of a puzzle box in which a hungry animal (e.g., cat, dog, or chicken) was placed in the box and had to determine how to get out of the box in order to obtain food. Each box he created required different responses to get out; some were more complex than that of others. While one box required the pulling of a ring, another box required a lever to be pushed. Although the animals took a while to

learn the associations, with more exposure, their latencies to get out of the box became much shorter. Thorndike believed that as the association between being in the box and the escape response became stronger, the hungry animal learned which behaviors led to favorable outcomes much quicker. He interpreted his findings as a stimulus response form of learning, which simply put means that a stimulus or cue is directly associated with an outcome. This is also referred to as an instrumentally conditioned response. In instrumental conditioning, extinction occurs when the behavior that was previously reinforced no longer produces reinforcing outcomes. In the experiment described above, if the hungry animals were to learn that food was no longer associated with escape, their stimulus response association would weaken. This would serve as an example of extinction in instrumental conditioning.

## Recovery of Responding After Extinction

Recovery of responding following extinction has been demonstrated in various experiments (Hermans et al. 2005; Leung et al. 2007; Lovibond et al. 2008; Norrholm et al. 2006). Following successful extinction, classically learned responses have a tendency to recover. Several studies have shown that conditioned fear is likely to return following the passage of time, a change in context or an aversive event. The way in which this recovery of responding occurs can be classified into several categories such as spontaneous recovery, renewal, or reinstatement. Recovery of responding following extinction demonstrates that extinction does not lead to unlearning and can be explained by the Rescorla-Wagner (1972) model of learning. This model suggests that the strength of the conditioned response is dependent on the strength of the CS-US association. According to the Rescorla-Wagner model, extinction results in the loss of the associative strength gained by the CS during conditioning. Various experimental findings on conditioning and extinction can be explained through the Rescorla-Wagner model (Bouton and Bolles 1979; Bouton and King 1983; Huff et al. 2009; Norrholm

et al. 2006; Zimmer-hart and Rescorla 1974). As a result, this model has been used as a reference point for subsequent learning theories (Siegel and Allan 1996). Overall, the recovery of responding following extinction supports Bouton's (1993) failure to retrieval theory which suggests that contextual and temporal cues play a role in the retrieval of extinction memories.

## Extinction and Spontaneous Recovery

Several studies have found that the time between extinction and testing impacts the long-term effectiveness of extinction in animals (Costanzi et al. 2011; Maren and Chang 2006; Myers and Carlezon 2010). While extinction produces a decline in conditioned behavior, this effect is weakened over time. When the previously extinguished response recovers following a rest period, this effect is called spontaneous recovery. Spontaneous recovery is a term that was originally identified by Ivan Pavlov. In a Pavlovian conditioning experiment by Rescorla (1997), rats in one group paired noise (CS) with food (US), while those in another group associated food (US) with light (CS). The CS in both groups, which served as a previously neutral stimulus, came to elicit conditioned responses more quickly over repeated presentations. Subsequently, 16 extinction trials occurred in both groups, followed by four test trials. In one group, testing occurred immediately, while there was an 8-day interval between extinction and testing in the other group. Although responding was suppressed for the group tested immediately after conditioning, responding recovered for the group tested 8 days after extinction. This recovery of responding is referred to as spontaneous recovery.

## Reinstatement

Recovery of responding can also be observed through the reintroduction of the CS-US relationship, where additional conditioning trials are administered post extinction, which primes the originally acquired association to recover

immediately. This phenomenon is referred to as reacquisition and tends to be more robust under fear conditioning (Bouton and Bolles 1979). The unconditioned stimulus is more likely to reinstate fear because it may serve as a retrieval cue for conditioning memories. Responses that have been successfully extinguished can recover following exposure to the unconditioned stimulus (Bouton and Bolles 1979; Rescorla and Heth 1975). In a study by Norrholm et al. (2006), participants were exposed to a fear conditioning paradigm where colored lights (CS) were paired with an air blast to their throat (US). Post 24 h of fear conditioning, participants received extinction trials. When the unexpected US was presented, participants demonstrated significant reinstatement of fear.

## Renewal

Another process known to produce a recovery of the originally learned association is renewal. Renewal provides evidence that conditioned responding is not context specific but can occur in contexts outside of the one in which conditioning originally occurred (Bouton 1993). When the extinguished conditioned stimulus is encountered outside of the extinction context, renewal of conditioned responding is observed. Studies have found that renewal of fear can be observed when an organism encounters the CS in a novel or familiar environment (Bouton 1993; Bouton and King 1983; Bouton and Swartzentruber 1991). For example, research on conditioned suppression found that fear of an extinguished CS can be affected by the excitatory strength of the context, but it is not context driven and can reemerge in any context (Hermans et al. 2005).

## The Importance of Extinction Training in Therapy

Cognitive behavioral therapies such as exposure therapy are a common treatment for psychological conditions like specific phobias, anxiety, and traumatic stress disorders (Barlow 2008; Craske et al. 2014). In exposure therapy, a person is exposed to



the feared stimulus or context without exposure to the US or the feared contingency. This exposure occurs either through in vivo (e.g., real life) or virtual reality (e.g., computerized CBT) exposure therapy. As previously mentioned, several animal and human learning studies have found that conditioned responses tend to recover following successful extinction treatment (Hermans et al. 2005). This effect has been observed in cognitive behavioral therapies such as exposure therapy, where conditioned fear has returned in up to 30–50% of individuals who have received successful treatment for an anxiety disorder, an effect also referred to as relapse in clinical practice (Choy et al. 2007; Craske and Rachman 1987). The return of fear following successful extinction serves as a manifestation that extinction creates an inhibitory memory which temporarily suppresses fear-related expressions until the passage of time, change in context, or reexposure to the US (Bouton 1993). Clinically speaking, this return of fear following extinction contributes to relapse when using exposure-based therapies for anxiety- and trauma-related conditions (Bruce et al. 2005).

While several studies have found evidence of fear recovery following extinction (Bouton and Bolles 1979; Hermans et al. 2005; Norrholm et al. 2006; Rescorla and Heth 1975), recent studies looking at the neural mechanisms of Pavlovian conditioning have since challenged this notion (Quirk et al. 2010). The neuroscience literature has found that extinction may erase some aspects of fear memory at a neural level, particularly in the amygdala (i.e., area of the brain involved in emotions), although fear may still be presented behaviorally. Research by Quirk et al. (2010) has found that altering the timing of extinction trials in both animals and humans has allowed for extinction training that has shown evidence of unlearning. These researchers have found that there are different neural circuits that mediate extinction of conditioned responses depending on the stage of development. In rats 24 days postweaning, extinction is dependent on the medial prefrontal cortex (mPFC), similarly to that of adult rats. However, in fear extinction at 17 days of age, the mPFC does not impact extinction. Rats that received extinction training at 17 days of age did not

exhibit a return of fear when tested in a different context (i.e., renewal) or following exposure to a stressor (i.e., reinstatement), like that of that of rats who received extinction training at 24 days of age. Therefore, these findings suggest that extinction-induced erasure is much more likely to occur in younger rats as opposed to older rats.

Recent findings suggest that the same effect is possible in human beings (Myers et al. 2006). It is possible for extinction training to update previously learned behaviors if it occurs within a specific timeframe, which would essentially reduce the risk for recovery of fear responses according to this research. Myers et al. (2006) found that when extinction training occurs immediately after fear conditioning, the fear memory is less likely to be consolidated. This implies that if extinction can be facilitated during the reconsolidation phase, fear associations can be reestablished as safe. Due to limitations in human causal learning, many studies have demonstrated that the time between extinction training impacts the effectiveness of extinction using animal models of fear (Corley et al. 2012; Maren and Chang 2006; Robbins 1990).

## Conclusion

Extinction is one of the most popular topics in the area of cognition and behavior theory (Domjan 2010). It offers transferable research that seeks to improve clinical practice based on findings from the laboratory (Bouton and Nelson 1998; Craske et al. 2014; Craske and Rachman 1987). Extinction has been very instrumental in providing implications for exposure therapy and relapse by looking at the factors that contribute to the persistence in responding, conditions that encourage a decline in responding, or the circumstances in which responses spontaneously recover (Craske et al. 2014). While extinction produces a diminished response to originally learned associations as a result of the removal of either a conditioned stimulus or reinforcer, following a rest period, the preexisting association returns. Other phenomena that lead to the return of fear include renewal or reinstatement. Renewal occurs when the CS-US

association is introduced in a new context (e.g., renewal), while exposing the organism to the CS post extinction in the absence of the US is likely to encourage reinstatement of responding. These phenomena serve as evidence that extinction does not lead to unlearning or forgetting. Although extinction was originally coined by Pavlov (1927), much of what we know about extinction today has been informed by research in the past few decades.

## Cross-References

- ▶ [Classical Conditioning](#)
- ▶ [Extinction in Learning](#)
- ▶ [Fear Response](#)
- ▶ [Operant Conditioning](#)
- ▶ [Unconditioned Response](#)
- ▶ [Unconditioned Stimulus](#)

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## Extra-Pair Copulation

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## Synonyms

Cuckoldry; Cuckquean; Extra-pair copula; Extra-pair fertilization; Extra-pair mating; Extra-pair paternity; Infidelity; Sneaky matings

## Antonyms

In-pair copulation; Mate fidelity

## Definition

A paired individual opportunistically mates with an individual other than its social mate within pair bond.

## Evolutionary Context

According to Trivers (1972), there will be uneven investment in offspring related to the gender roles. At one end, is the sex that invests less in the offspring (the competitive end), and, at the opposite side, the sex that invests more (the choosier end). If both sexes invest a great deal in offspring, then both should be choosy. This high level of biparental care is unusual among animals, where female consistently holds a larger proportion of care for the young. Biparentalhood is, thus, more common among monogamous species, in which both parents form a pair bond and stay together for at least one breeding season in order to raise the young together, sharing the workload. Others form lifelong pairs (lifetime monogamy), sticking together for consecutive breeding seasons and successive broods or litters. Yet, monogamous species do not necessarily exhibit sexual fidelity.

## Extra Nipple

► [Supernumerary Nipple](#)

## Extractive Foraging Hypothesis

► [Technical Intelligence Hypothesis](#)

## Extra-Pair Copula

► [Extra-Pair Copulation](#)

Many pairs do not present exclusive sexual relationships, resulting in extra-pair copulation (EPC). Thus, the mating strategies of species are now separated into social monogamy, as defined by an exclusive living arrangement, and genetic monogamy, in which cohabitation is accompanied by exclusive parentage (see Lack 1968; Lukas and Clutton-Brock 2013).

EPC is expected to occur in both sexes depending on the reproductive strategy of the species. The large investment towards the raising of young increases the costs of extra-pair copulation, although it also renders increased benefits to the cuckold. In many species, the male pursuit of EPC is associated with its “gender role,” copulating with as many females as possible and investing little in offspring. Yet, he must also reduce the possibility of having his paternity stolen somehow. In turn, a female will pursue EPC to obtain benefits to her offspring and/or herself (Westneat and Stewart 2003). Female infidelity is the most important generator of sperm competition and, why not, generator of mate guarding in monogamous species.

Which benefits is the female looking for? Petrie and Kempenaers (1998) listed a few for birds, such as (i) seeking “good genes” (high genetic quality that will improve the survival or reproductive chances of their offspring); (ii) reduction of costs of mate loss (they will be able to find another partner quicker in the event of partner loss or death); or (iii) direct benefits (e.g., increased foraging opportunities, defense against predators and additional mates).

As for mammals, Solomon and Keane (2007) listed benefits of mating with multiple males that is similar to those for birds: (i) assurance of fertilization (nullifying effects of empty copulas); (ii) gaining material benefits (more paternal investment from males); (iii) better genes for offspring (probability of mating with high-quality males); (iv) mate compatibility; (v) increased genetic variability of offspring; (vi) prevention of harassment by males; or (vii) prevention of infanticide.

Many studies addressing mate guarding also address EPC, in that mate guarding and the pursuit of EPC are mutually exclusive (e.g., Lukas and Clutton-Brock 2013; Westneat and Stewart 2003).

For instance, highly synchronous estruses hinder the male ability to guard his partner and simultaneously seek for EPC. In some species, EPC overlaps the concept of group guard/monogamy (e.g., one male mating with or paired with multiple females as seen in the anemonefishes *Amphiprion akallopisos*, Fricke 1979). Yet, mate guarding is not always an effective mechanism to prevent extra-pair copulations. Some species with no obvious mate guarding maintain genetic monogamy. Many species described under mate guarding also have been reported to show EPC. However, Westneat et al. (1990) correlated monogamy, pair bonding and EPC, stating that, in order to EPC to occur, the bond needs to be long lasting. Thus, many examples should not be considered as EPC because they are related to brief associations between males and females. The maintenance of long lasting and equitable bonds is more common among birds and social mammals. Thus, EPC descriptions hereafter will focus on those two groups.

## Extra-Pair Copulation Examples

### Birds

Many birds are monogamous (around 90% of species), a mating system sometimes considered as an extended mate guarding. Therefore, extra-pair copulation has been described primarily for this group and later extended to others. Frequency of extra-pair paternity varies from zero in willow warblers *Phylloscopus trochilus* to more than half of the brood with extra-pair paternity in superb fairy-wrens *Malurus cyaneus*. For Westneat et al. (1990), who conducted an extensive review of EPC in birds, in communally breeding birds such as Acorn Woodpeckers *Melanerpes formicivorus*, matings with auxiliaries are not EPC because each male in the group has a long-term social association with the female. Consequently, they also do not consider polyandry as EPC if the female is normally part of a social unit that contains both her primary and secondary partners, such as dunnocks *Prunella modularis*. These authors also disregard lek-breeding birds, such as sage grouse *Centrocercus urophasianus* because they do not form pair bonds.

Males that present paternal care need to ensure paternity to reduce risks of expending parental investment on the offspring of other males. Communal species are more likely to present extra-pair copulation than solitary nesting ones. This scenario is even considered as the main disadvantage of colonial breeding. The bank swallow males (*Riparia riparia*) pursue extra-pair mates and spend more time at neighboring territories while females are incubating, although he guards her when she is sexually receptive.

Male birds have evolved an elaborate array of tactics to avoid cuckoldry, such as frequent mating and mate guarding. The regular copulation increases the amount of sperm introduced inside the female reproductive tract and, consequently, displaces any possible sperm from another male. Yet, frequent copulation also favors females as it depletes sperm storage and leads the male to exhaustion, reducing his chance to copulate with other females. Females will engage in EPC only if outside the view of her partner. Otherwise, paternal care will be sharply reduced if the proportion of offspring is sired extra-pairly. Thus, extra-pair copulas need to be unseen by the male mate so that he is misled as being the only father of the subsequent offspring and helps care for the young.

### Mammals

Monogamy is rare among mammals (3–9% of species, Lukas and Clutton-Brock 2013) and EPC has been widely studied in social species, such as primates and carnivores. In dwarf mongoose *Helogale parvula*, dominant males sired 75% of offspring; in African wild dogs *Lycaon pictus*, dominant males sired 80–90%; mountain gorillas *Gorilla beringei beringei*, dominants sired 75% of offspring; and in meerkats *Suricatta suricatta* dominant males sired around 86% of offspring. In some other highly social mammals, such as cetaceans, males use coercion to prevent the female from seeking EPC. Male bottlenose dolphins *Tursiops truncatus* sequester females and use force to deter her from extra-pair copulations and Humpback females *Megaptera novaengliae* resist consorting attempts.

Highly social mammals frequently present reproductive skew, in which a dominant pair monopolises reproduction. It is important to

emphasize that, in groups with highly skewed reproduction, EPC will not be as successful for the subordinate female as it would be for the subordinate male, as subordinate females will fail in their reproductive attempts. Subordinates will fail to conceive, reabsorb their embryos, or will lose their offspring to infanticidal resident/dominant females. In alpine marmots *Marmota marmota*, resident males have been cuckolded by their own subordinate males, satellite males and neighboring families. Subordinate females, on the other hand, did not succeed in many attempts. Conversely, a subordinate male may copulate with high-ranking females of his own group when the dominant male is occupied, or rove to neighboring families and copulate with the local dominant female. Although motivations vary among the species, one feature seems to be underlying: the genetic relatedness between social mates, with dominant females using EPC as a strategy to avoid the negative effects of inbreeding. Sometimes, the male meerkat that rose to dominance within a meerkat group is related to the dominant female (sons or nephews). Hence, the extra-pair males are no more distantly related than the social mate, but they are more heterozygous (Young et al. 2007). However, according Westneat et al. (1990), these examples may not constitute true EPC because females live in social groups where both the primary and secondary partners live together.

Regardless, EPC provides many benefits. For instance, multiple-paternity in the European badger *Meles meles* provides fitness advantages such as fertilization assurance, reduced harassment, decreased infanticide, genetic benefits by promoting sperm competition, increased litter genetic diversity, reduced genetic incompatibilities, compensation for poor-quality mates, and obtainment of good genes. Similarly, many primate species uses multiple matings to generate paternity confusion and entrust as many males as possible in the care of the young and prevent infanticide. By mating with potential invaders, these females might reduce risks of future infanticide, and encourage paternity confusion, as suggested for Old World primates, long-tailed macaques *Macaca fascicularis* and Hanuman langurs *Semnopithecus entellus*, but also New World



primates, such as howler monkeys. In red howler monkeys *Alouatta seniculus*, females that indulged in EPC had experienced infanticide previously (Agoramoorthy and Hsu 2000). For other species, such as rodents, there is evidence that multiple copulation and, therefore, possibly extra-pair copulation, provides the female with extra set of nutrients by the absorption of unused sperm. These motivations are in tune with those observed in birds (see above).

EPC in humans are particularly interesting. In human lineage, males seek high partner variety due to their “gender role”. As a counterstrategy, females present what is called “concealed ovulation” and it is suggested that this evolved to obtain a high quality sire without the detection by both EPC and primary partners (Benshoof and Thornhill 1979). Yet, women are not good themselves at detecting their own fertility so that they will cryptically pursue EPC. Humans are particularly susceptible to the negative effects of cuckoldry as parental investment failure is measured in years and some women have only one child throughout her entire life. Sometimes EPC has complex social consequences in Western cultures, such as diminished virility (for males) or decreased femininity (for females) and dwindled overall social reputation, decreasing his or her status. Conversely, for some cultures, the concept of “EPC” is meaningless as all men within a village help care for the babies (e.g., Bari people, in Venezuela, Hrdy 2001). For some other cultures, gender roles are interchangeable (e.g., African Aka tribe). However, whilst men can pursue other partners if he is cuckolded, the costs for a woman are lower as genetic cuckoldry will never happen to her: she will always be the mother of her child, regardless of the strategy of her culture or her partner’s unfaithfulness for those cultures in which it matters.

## Conclusions

Among animals, the female usually holds the large proportion of care for the young. Yet, in pair bonding species, biparental care is high and

both parents invest a great deal in the offspring. Biparentalhood is, thus, more common among monogamous species. Conversely, the formation of pair bonds yielded a breach for extra-pair copulation (EPC). EPC is common among birds, in which the majority of species are monogamous, and particularly common among carnivores and primates groups in mammals. EPC motivation is similar for birds and mammals, namely, fertilization assurance, reduced harassment, decreased infanticide, genetic benefits, by promoting sperm competition, increased litter genetic diversity, reduced genetic incompatibilities, compensation for poor-quality mates, obtainment of good genes, and pursuit of high partner variety. Both sexes will benefit or suffer from EPC advantages and costs depending on the reproductive strategy of the species and on the mating tactics of each sex.

## Cross-References

- [Facultative Polyandry/Strategic Pluralism](#)
- [Mate guarding](#)
- [Sexual selection](#)
- [Sneaky Copulator](#)
- [Sperm competition](#)

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## Extra-Pair Fertilization

- ▶ [Extra-Pair Copulation](#)

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## Extra-Pair Mating

- ▶ [Extra-Pair Copulation](#)

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## Extra-Pair Paternity

- ▶ [Extra-Pair Copulation](#)

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## Extrastriate Cortex

- ▶ [Face-Selective](#)      [Neurons:](#)      [Comparative Perspectives](#)

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## Eyesight

- ▶ [Hominoidea Sensory Systems](#)

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## Face Cell

► Face-Selective      Neurons:      Comparative  
Perspectives

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## Face Processing in Different Brain Areas and Face Recognition

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### Introduction

Face-selective neurons were discovered in the inferior temporal visual cortex by Perrett et al. (1982), in the amygdala by Sanghera, Rolls, and Roper-Hall (Sanghera et al. 1979; Rolls 2011) and Leonard et al. (1985), and in the orbitofrontal cortex by Rolls et al. (2006). These neurons respond 2–20 times more to the best face compared to the best nonface, and different brain regions provide the basis for face recognition and for emotional responses to faces. These neurons are described here.

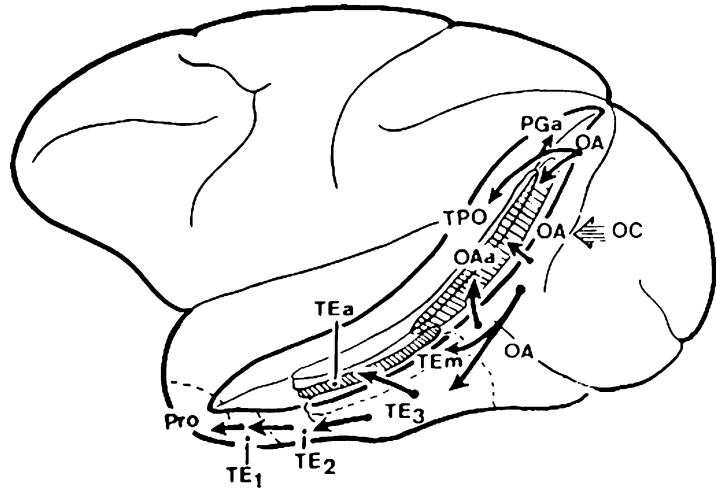
## Neuronal Responses to Faces in Different Temporal Lobe Cortex Visual Areas

Visual pathways project by a number of cortico-cortical stages from the primary visual cortex until they reach the temporal lobe visual cortical areas in which some neurons that respond selectively to faces are found (Perrett et al. 1982; Rolls 2007, 2011, 2012, 2016a). The inferior temporal visual cortex, area TE, is divided on the basis of cytoarchitecture, myeloarchitecture, and afferent input into areas TEa, TEm, TE3, TE2, and TE1. In addition, there is a set of different areas in the cortex in the superior temporal sulcus (Seltzer and Pandya 1978; Baylis et al. 1987) (see Fig. 1). Of these latter areas, TPO receives inputs from temporal, parietal, and occipital cortex; PGa and IPa from parietal and temporal cortex; and TS and TAa primarily from auditory areas.

Considerable specialization of function was found in recordings made from more than 2600 neurons in these architectonically defined areas (Baylis et al. 1987). Areas TPO, PGa, and IPa are multimodal, with neurons that respond to visual, auditory and/or somatosensory inputs (though not typically with corresponding bimodal auditory and visual responses (Sliwa et al. 2016)); the inferior temporal gyrus and adjacent areas (TE3, TE2, TE1, TEa, and TEm) are primarily unimodal visual areas; areas in the cortex in the anterior and dorsal

### Face Processing in Different Brain Areas and Face Recognition,

**Fig. 1** Lateral view of the macaque brain (*left*) and coronal section (*right*) showing the different architectonic areas (e.g., TEm, TPO) in and bordering the anterior part of the superior temporal sulcus (STS) of the macaque (see text; after Seltzer and Pandya 1978)



part of the superior temporal sulcus (e.g., TPO, IPa, and IPg) have neurons specialized for the analysis of moving visual stimuli; neurons responsive primarily to faces are found more frequently in areas TPO, TEa, and TEm, where they comprise approximately 20% of the visual neurons responsive to stationary stimuli, in contrast to the other temporal cortical areas in which they comprise 4–10%. Moreover, neurons with responses related to facial expression, movement, and gesture are more likely to be found in the cortex in the superior temporal sulcus, whereas neurons with activity related to facial identity are more likely to be found in the TE areas (Hasselmo et al. 1989; Rolls 2007). Indeed, we can think of the cortex in the superior temporal sulcus as being a more dorsal face processing stream than the stream in the inferior temporal visual cortex (Baylis et al. 1987; Rolls 2012).

Using fMRI in macaques, the segregation of face cells into 6 face patches has been described: 1 posterior (PL), 2 middle (ML, MF), and 3 anterior (AL, AF, AM) (Tsao et al. 2008a, 2014). Neurons in ML and MF are view-specific; neurons in AL are tuned to identity mirror-symmetrically across views, thus achieving partial view invariance; neurons in AM, the most anterior face patch, achieve almost full view invariance and provide a sparse representation of face identity. Neurons in ML/MF respond to both monkey and human faces, whereas in AM many cells are selective for either monkey or human faces.

Human subjects showed 4 face areas or patches (occipital, fusiform, anterior to fusiform, and superior temporal sulcus face areas (Tsao et al. 2008a). In human fMRI studies, evidence for specialization of function related to visual processing in areas similar to those in macaques has been described (Spiridon et al. 2006; Said et al. 2011; Vul et al. 2012; Weiner et al. 2017). The fusiform face area, which corresponds to part of the macaque inferior temporal cortex, is implicated in the processing of face identity. The cortex in the superior temporal sulcus and just above it in the middle temporal gyrus, which corresponds to the macaque cortex in the superior temporal sulcus, is implicated in face expression and gesture (i.e., moving faces) (Critchley et al. 2000), and has reduced functional connectivity in autism (Cheng et al. 2015). An area that may correspond to the macaque inferior temporal cortex has a highly developed representation of objects (Rolls 2012, 2016a). A parahippocampal area is implicated processing spatial scenes and probably corresponds to the macaque parahippocampal gyrus areas in which neurons are tuned to spatial view and to combinations of objects and the places in which they are located (Georges-François et al. 1999; Rolls et al. 2005, 2016a; Kesner and Rolls 2015). This parahippocampal spatial scene area may receive input from an occipito-temporal lateral place patch (Kornblith et al. 2013).

Some of the key discoveries about face-responsive neurons in the anterior parts of the temporal lobe, and in the amygdala and orbitofrontal cortex, are described next.

### The Selectivity of One Population of Neurons for Faces

The neurons discovered as having responses selective for faces are selective in that they respond 2–20 times more (and statistically significantly more) to faces than to a wide range of gratings, simple geometrical stimuli, or complex 3-D objects (Perrett et al. 1982; Rolls 1984, 2007). These neurons are specialized to provide information about faces in that they provide much more information (on average 0.4 bits) about which (of 20) face stimuli is being seen than about which (of 20) nonface stimuli is being seen (on average 0.07 bits) (Rolls et al. 1997a, b, 2007). These information theoretic procedures provide an objective and quantitative way to show what is “represented” by a particular population of neurons (Rolls and Treves 2011).

### Neurons Selective for Individual Face Features or for Combinations of Face Features

Masking out or presenting parts of the face (e.g., eyes, mouth, or hair) in isolation reveal that different cells respond to different features or subsets of features, and some require all the features to be present in the correct spatial configuration (i.e., not jumbled) (Perrett et al. 1982; Rolls 2007).

### Distributed Encoding of Face Identity

An important question for understanding brain function is whether a particular object (or face) is represented in the brain by the firing of one or a few gnostic (or “grandmother”) cells, or whether instead the firing of a group or ensemble of cells each with different profiles of responsiveness to the stimuli provides the representation. It has been

shown that the representation of which particular face is present is distributed. For example, in a study using 23 faces and 45 nonface natural images a distributed representation was found, with rather few stimuli producing high firing rates, and increasingly large numbers of stimuli producing lower and lower firing rates (Rolls and Tovee 1995) (see Fig. 2). Indeed, the firing rate probability distribution of many neurons is approximately exponential (Franco et al. 2007).

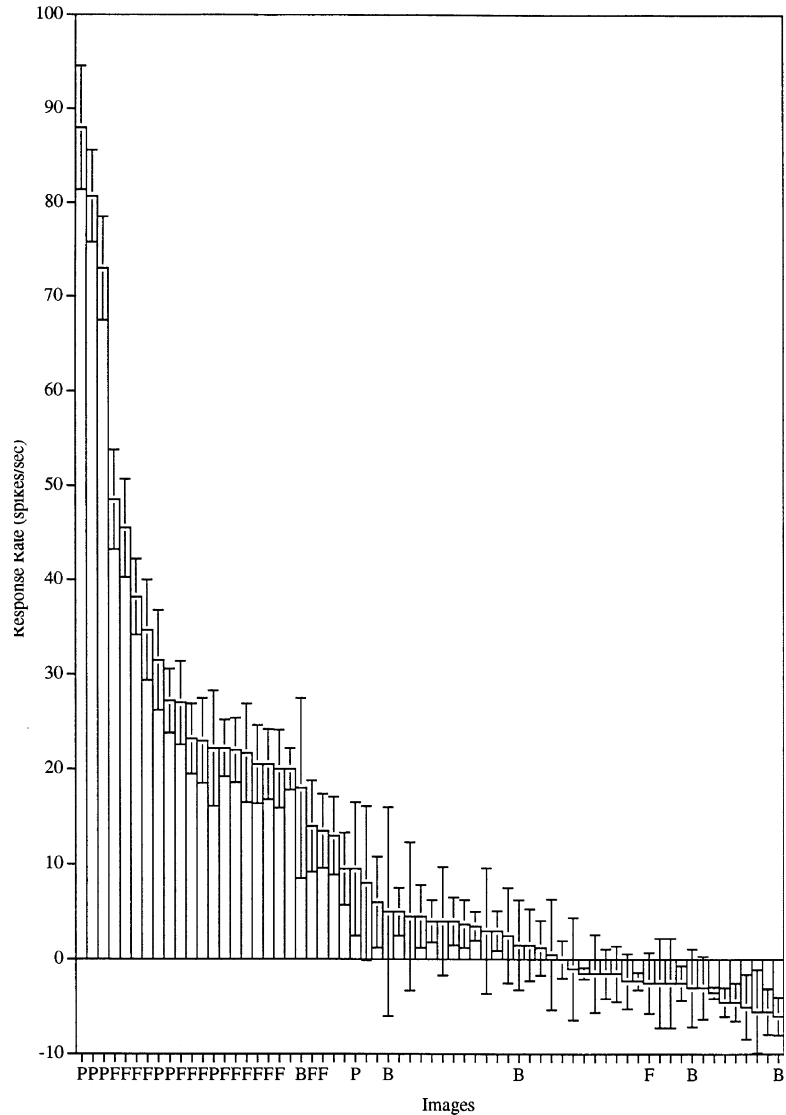
Complementary evidence comes from applying information theory to analyze how information is represented by a population of these neurons. The information required to identify which of  $S$  equiprobable events occurred (or stimuli were shown) is  $\log_2 S$  bits. (Thus 1 bit is required to specify which of two stimuli was shown, 2 bits to specify which of 4 stimuli was shown, 3 bits to specify which of 8 stimuli was shown, etc.) The important point for the present purposes is that if the encoding was local (or grandmother cell-like), the number of stimuli encoded by a population of neurons would be expected to rise approximately linearly with the number of neurons in the population. In contrast, with distributed encoding, provided that the neuronal responses are sufficiently independent, and are sufficiently reliable (not too noisy), the number of stimuli encodable by the population of neurons might be expected to rise exponentially as the number of neurons in the sample of the population was increased. The information available about which of 20 equiprobable faces had been shown that was available from the responses of different numbers of these neurons increases approximately linearly with the number of neurons in the population (see Fig. 3), and thus the representational capacity increases exponentially with the number of neurons in the ensemble (Fig. 4) (Rolls et al. 1997a; Rolls and Treves 2011; Rolls 2016a). This is further evidence for distributed encoding, and for the power of the code used.

The code that is used in the inferior temporal visual cortex is primarily the number of spikes from each neuron (i.e., a rate code), for very little (not more than approximately 5% of the total information) was available from stimulus-



### Face Processing in Different Brain Areas and Face Recognition,

**Fig. 2** Firing rate distribution of a single neuron in the temporal visual cortex to a set of 23 face (*F*) and 45 nonface images of natural scenes. The firing rate to each of the 68 stimuli is shown. *P* indicates a face profile stimulus, *B* a body part stimulus such as a hand (After Rolls and Tovee 1995)



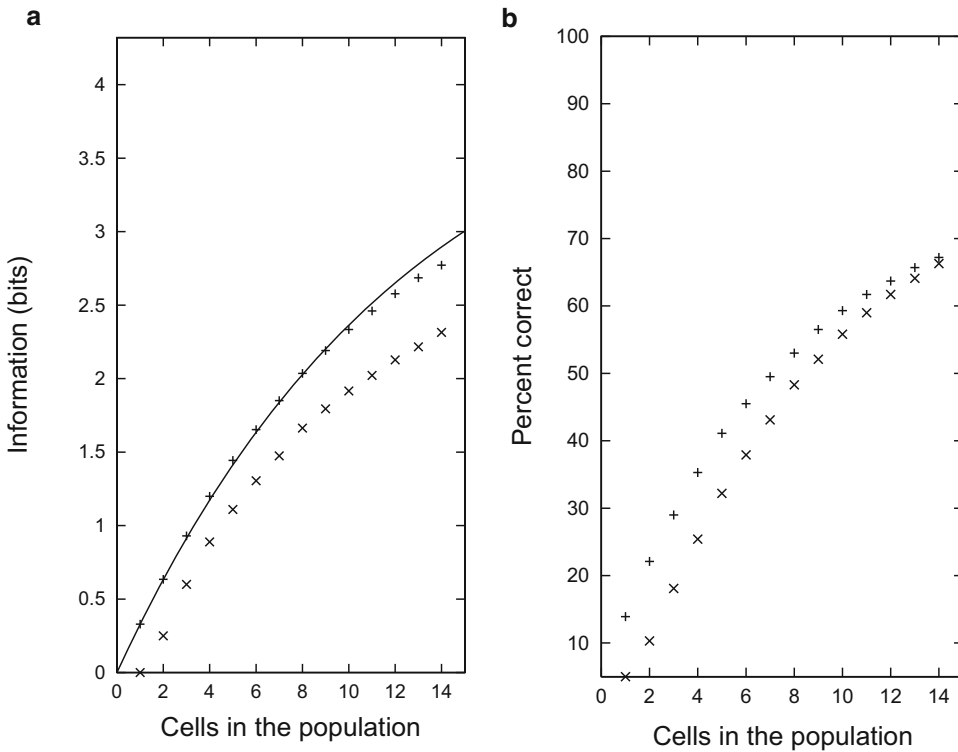
dependent synchrony (Rolls and Treves 2011; Rolls 2016a). The same result was found in natural scenes in which two test images had to be segmented from a complex background, the features of each object had to be bound together, and the monkey had to use top-down attention to search for one of two images in a complex scene (Rolls and Treves 2011; Rolls 2016a).

The advantages of the code that has been found include exponentially high coding capacity, readability by a neuronally plausible (synaptically) weighted sum of the firing rates of different neurons, resistance to noise, generalization,

completion, graceful degradation or fault tolerance, and speed of readout of the information, as described elsewhere (Rolls and Treves 2011; Rolls 2016a).

### Invariant Representations

One of the major problems that must be solved by a visual system is the building of a representation of visual information which allows recognition to occur relatively independently of size, contrast, spatial frequency, position on the retina, angle of



**Face Processing in Different Brain Areas and Face Recognition, Fig. 3** (a) The values for the average information available in the responses of different numbers of these neurons on each trial, about which of a set of 20 face stimuli has been shown. The decoding method was dot product (DP, x) or probability estimation (PE, +), and the effects obtained with cross validation procedures utilizing 50% of the trials as test trials are shown. The remainders of

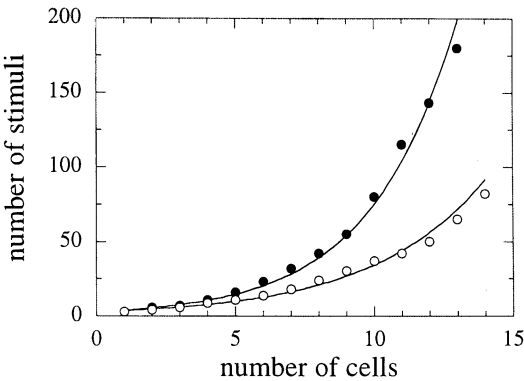
the trials in the cross-validation procedure were used as training trials. The *full line* indicates the amount of information expected from populations of increasing size, when assuming random correlations within the constraint given by the ceiling (the information in the stimulus set,  $I = 4.32$  bits). (b) The percent correct for the corresponding data to those shown in Fig. 3 (After Rolls et al. 1997a)

view, etc. This is required so that if the receiving associative networks (e.g., the amygdala, orbitofrontal cortex, and hippocampus) learn about one view, position, etc. of the object, the organism generalizes correctly to other positions, views, etc. of the object. It has been shown that the majority of face-selective anterior inferior temporal cortex neurons have responses that are relatively invariant with respect to the size of the stimulus, and the exact position of the face on the retina (translation invariance) (Rolls and Baylis 1986; Rolls 2007, 2016a). Interestingly, the receptive fields become smaller (and still include the fovea) when faces or objects are seen against a complex natural background, and this helps with the binding problem (Aggelopoulos

et al. 2005). It makes the interface to action simpler, in that what is at the fovea can be interpreted (e.g., by an associative memory in the orbitofrontal cortex or amygdala) partly independently of the surroundings, and choices and actions can be directed if appropriate to what is at the fovea (Rolls 2007, 2016a). Some neurons have view invariant responses to faces (which would be useful for face recognition, and indeed these neurons tend to be tuned to face identity) (Hasselmo et al. 1986; Rolls 2000). Other neurons have view-specific responses, and indeed are found in the cortex in the superior temporal sulcus where some neurons are tuned to face expression, and typically to face motion and face gesture (change of expression), all of which are important

in social interactions (Hasselmo et al. 1989; Rolls 2007, 2016a). These discoveries have been confirmed (Said et al. 2011; Polosecki et al. 2013; Tsao 2014).

A computational model of how invariant representations for faces and objects are built in the ventral visual system can account for the responses of many of these neurons. The model,

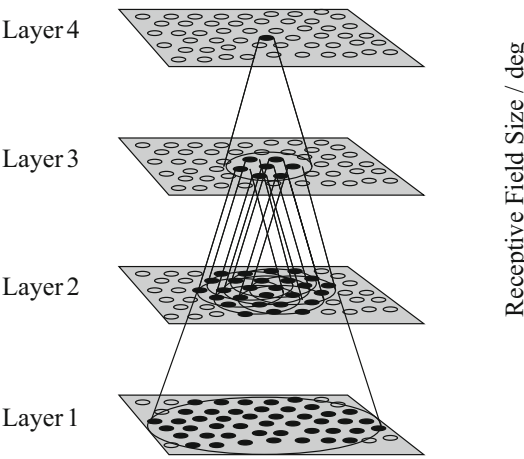


**Face Processing in Different Brain Areas and Face Recognition, Fig. 4** The number of stimuli (in this case from a set of 20 faces) that are encoded in the responses of different numbers of neurons in the temporal lobe visual cortex, based on the results shown in Fig. 3. The decoding method was dot product (DP, open circle) or probability estimation (PE, filled circle) (After Rolls et al. 1997a)

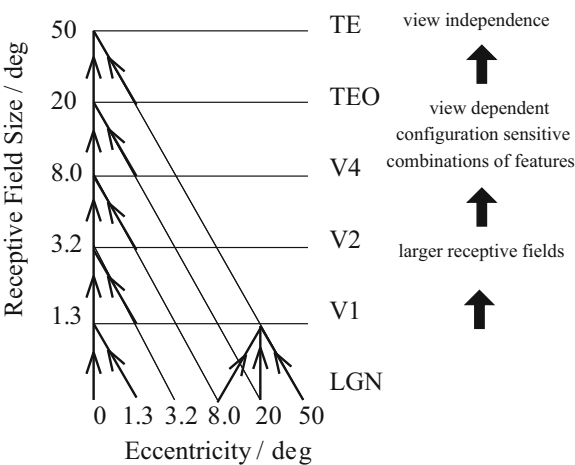
VisNet, utilizes competitive learning at each stage of the hierarchy of visual cortical areas in the ventral visual system with convergence from stage to stage to form feature combination neurons, and slow learning implemented by an associative synaptic learning rule with a short-term trace memory of previous activity to enable the learning of invariant representations (Wallis and Rolls 1997; Rolls 1992, 2012, 2016a) (Fig. 5). Consistent with this, macaque face cells respond to combinations of several metric properties of human faces (Chang and Tsao 2017). VisNet can locate and identify objects and people in complex scenes by adding an emulation of the dorsal visual system to foveate salient stimuli (Rolls and Webb 2014). VisNet can also learn deformation-specific representations of pose, which are likely to be useful for the emotional and intentional interpretation of faces and people (Webb and Rolls 2014).

**A Representation of Faces in the Amygdala**

Outputs from the temporal cortical visual areas reach the amygdala, and evidence is accumulating that these brain areas are involved in social and



**Face Processing in Different Brain Areas and Face Recognition, Fig. 5** Right. Schematic diagram showing convergence achieved by the forward projections in the visual system, and the types of representation that may be built by competitive networks operating at each stage of the system from the primary visual cortex (V1) to the



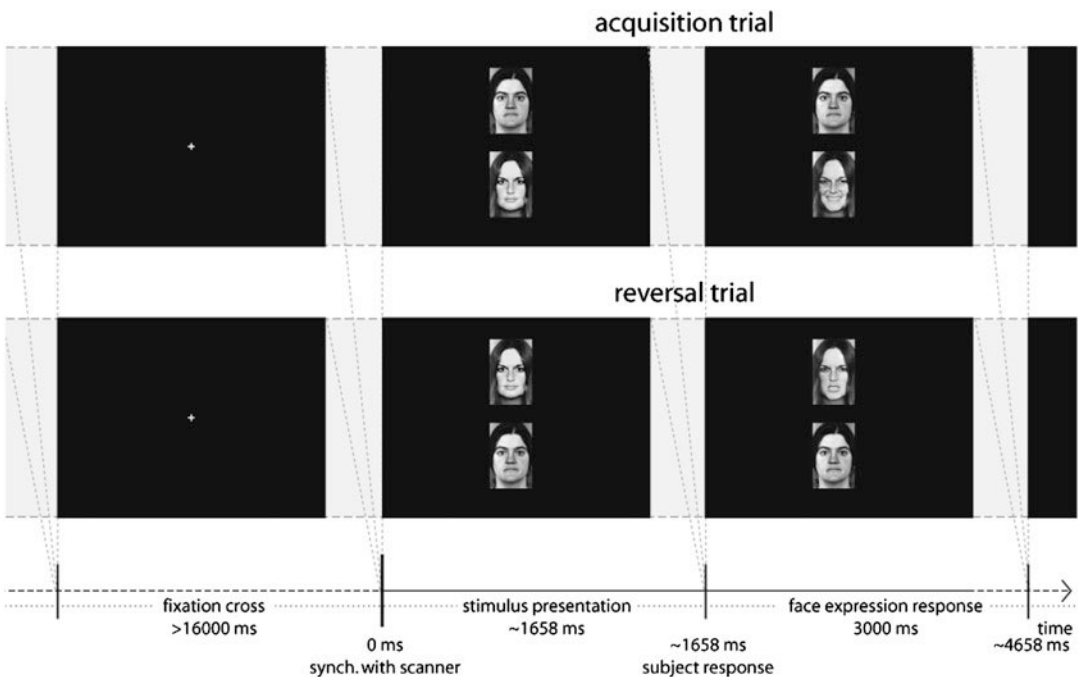
inferior temporal visual cortex (area TE) (see text). LGN lateral geniculate nucleus. Area TEO forms the posterior inferior temporal cortex. The receptive fields in the inferior temporal visual cortex (e.g., in the TE areas) cross the vertical midline (not shown). Left. Hierarchical network structure of VisNet (See Rolls 2012)

emotional responses to faces (Rolls 2014). For example, we have identified a population of neurons with face-selective responses in the primate amygdala, some of which may respond to facial and body gesture (Leonard et al. 1985). In humans, amygdala damage can impair the recognition of fear face expressions, and extraversion influences whether activations will be found to happy faces (Rolls 2014).

## A Representation of Faces in the Orbitofrontal Cortex

Rolls et al. (2006) have found a number of face-responsive neurons in the orbitofrontal cortex, and they are also present in adjacent prefrontal cortical areas (Rolls 2007, 2016a). The orbitofrontal

cortex face-responsive neurons, first observed by Thorpe et al. (1983), tend to respond with longer latencies than temporal lobe neurons (140–200 ms typically, compared with 80–100 ms) and can convey information about which face is being seen, by having different responses to different faces. Some of the orbitofrontal cortex face-selective neurons are responsive to face gesture or movement and others to face expression (Rolls et al. 2006). The findings are consistent with the likelihood that these neurons are activated via the inputs from the temporal cortical visual areas in which face-selective neurons are found. The significance of the neurons is likely to be related to the fact that faces convey information that is important in social reinforcement, both by conveying face expression, which can indicate reinforcement, and by encoding information about



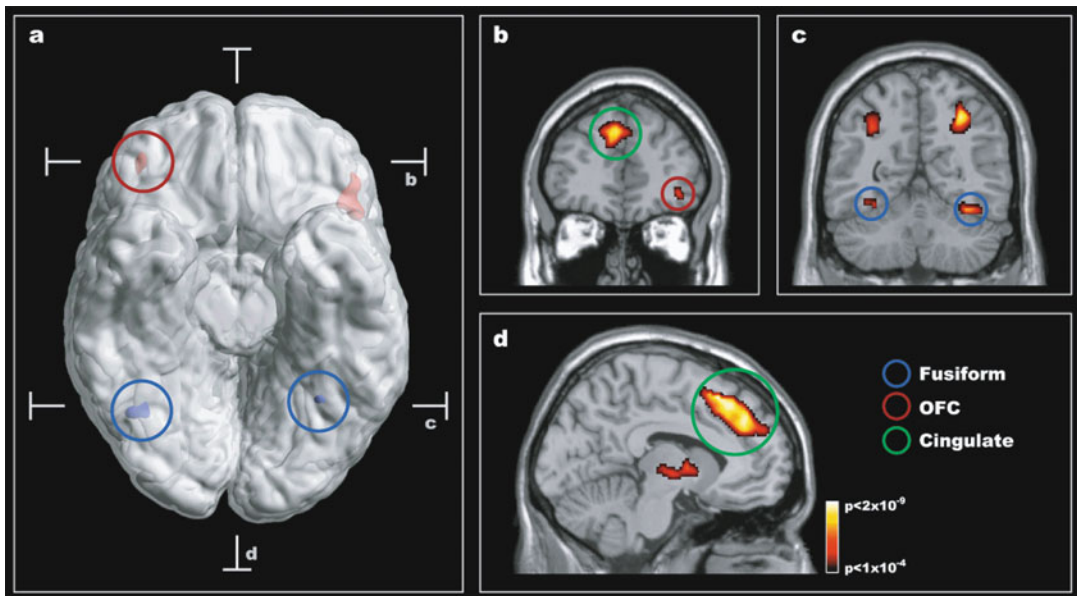
**Face Processing in Different Brain Areas and Face Recognition, Fig. 6** Social reversal task: The trial starts synchronized with the scanner and two people with neutral face expressions are presented to the subject. The subject has to select one of the people by pressing the corresponding button, and the person will then either smile or show an angry face expression for 3000 ms depending on the current mood of the person. The task for the subject is to keep track of the mood of each person

and choose the “happy” person as much as possible (*upper row*). Over time (after between 4 and 8 correct trials) this will change so that the “happy” person becomes “angry” and vice versa, and the subject has to learn to adapt her choices accordingly (*bottom row*). Randomly intermixed trials with either two men, or two women, were used to control for possible gender and identification effects, and a fixation cross was presented between trials for at least 16,000 ms (After Kringelbach and Rolls 2003)

which individual is present, also important in evaluating and utilizing reinforcing inputs in social situations (Rolls 2014). The existence of these neurons has been confirmed using fMRI (Tsao et al. 2008b).

We have also been able to obtain evidence that nonreward used as a signal to reverse behavioral choice is represented in the human orbitofrontal cortex (see Rolls 2014). Kringelbach and Rolls (2003) used the faces of two different people, and if one face was selected then that face smiled, and if the other was selected, the face showed an angry

expression. After good performance was acquired, there were repeated reversals of the visual discrimination task. Kringelbach and Rolls found that activation of a lateral part of the orbitofrontal cortex in the fMRI study was produced on the error trials, that is when the human chose a face, and did not obtain the expected reward (see Figs. 6 and 7). The investigation reveals that the human orbitofrontal cortex is very sensitive to social feedback when it must be used to change behavior (Rolls 2014) and that provides some evidence for the theory that



**Face Processing in Different Brain Areas and Face Recognition, Fig. 7** Social reversal: Composite figure showing that changing behavior based on face expression is correlated with increased brain activity in the human orbitofrontal cortex. (a) The figure is based on two different group statistical contrasts from the neuroimaging data which are superimposed on a ventral view of the human brain with the cerebellum removed and with indication of the location of the two coronal slices (b, c) and the transverse slice (d). The red activations in the orbitofrontal cortex (denoted OFC, maximal activation:  $Z = 4.94$ ;  $42, 42, -8$ ; and  $Z = 5.51$ ;  $x, y, z = -46, 30, -8$ ) shown on the rendered brain arise from a comparison of reversal events with stable acquisition events, while the blue activations in the fusiform gyrus (denoted Fusiform, maximal activation:  $Z > 8$ ;  $36, -60, -20$  and  $Z = 7.80$ ;  $-30, -56, -16$ ) arise from the main effects of face expression. (b) The coronal slice through the frontal part of the brain shows the cluster in the right orbitofrontal cortex across

all nine subjects when comparing reversal events with stable acquisition events. Significant activity was also seen in an extended area of the anterior cingulate/paracingulate cortex (denoted cingulate, maximal activation:  $Z = 6.88$ ;  $-8, 22, 52$ ; green circle). (c) The coronal slice through the posterior part of the brain shows the brain response to the main effects of face expression with significant activation in the fusiform gyrus and the cortex in the intraparietal sulcus (maximal activation:  $Z > 8$ ;  $32, -60, 46$ ; and  $Z > 8$ ;  $-32, -60, 44$ ). (d) The transverse slice shows the extent of the activation in the anterior cingulate/paracingulate cortex when comparing reversal events with stable acquisition events. Group statistical results are superimposed on a ventral view of the human brain with the cerebellum removed, and on coronal and transverse slices of the same template brain (activations are thresholded at  $P = 0.0001$  for purposes of illustration to show their extent) (After Kringelbach and Rolls 2003)



depression is related to overactivity in a lateral orbitofrontal cortex nonreward attractor network (Rolls 2016b).

To investigate the possible significance of the neurons in the orbitofrontal cortex with face-related inputs, we also tested the responses to faces of patients with orbitofrontal cortex damage. We included tests of face (and also voice) expression decoding, because these are ways in which the reinforcing quality of individuals is often indicated. Impairments in the identification of facial and vocal emotional expression were demonstrated in a group of patients with ventral frontal lobe damage who had socially inappropriate behavior (Rolls 2007, 2014). The expression identification impairments could occur independently of perceptual impairments in facial recognition, voice discrimination, or environmental sound recognition. The face and voice expression problems did not necessarily occur together in the same patients, providing an indication of separate processing.

To obtain clear evidence that the changes in face and voice expression identification, emotional behavior, and subjective emotional state were related to orbitofrontal cortex damage itself, and not to damage to surrounding areas which is present in many closed head injury patients, we performed further assessments in patients with circumscribed lesions made surgically in the course of treatment (Hornak et al. 2003). We found that some patients with bilateral lesions of the orbitofrontal cortex had deficits in voice and face expression identification (Hornak et al. 2003). (The same group of patients had deficits on a probabilistic monetary reward reversal task, indicating that they have difficulty not only in representing reinforcers such as face expression but also in using reinforcers (such as monetary reward) to influence behavior.) Some patients with unilateral damage restricted to the orbitofrontal cortex also had deficits in voice expression identification. Patients with unilateral lesions of the anteroventral part of the anterior cingulate cortex and/or medial prefrontal cortex area BA9 were in some cases impaired on voice and face expression identification.

## **“Concept Cells” Recorded in Humans: Correspondence with Object-Place Memory-Related Neurons in Macaques**

Some neurons in the human medial temporal lobe, in structures that include parahippocampal regions, respond to the faces of particular individuals, such as Jennifer Aniston (Quiroga 2012). These neurons are multimodal, in that they may respond to the voice of the person, and to the place associated with a person, and have been termed “concept cells” (Quiroga 2012). These neurons thus appear to correspond to the hippocampal/parahippocampal system memory-related neurons in macaques, which respond to an object or the place in which it is located, and which are part of an episodic memory system (Georges-François et al. 1999; Rolls et al. 2005; Kesner and Rolls 2015; Rolls 2016a). These neurons, like face neurons, use sparse distributed encoding, and are not grandmother cells (Quiroga et al. 2008).

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## Face-Selective Neurons: Comparative Perspectives

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### Synonyms

Extrastriate cortex; Face cell; Facial recognition; Grandmother cell; Visual processing

### Introduction

Of all the biologically relevant visual categories that surround humans and other animals,

faces convey the most information required to successfully navigate the social environment. For instance, recognition of a conspecific or an approaching predator, interpretation of emotional expressions, the direction of eye gaze, and selection of an appropriate mate are all critically dependent on facial cues. Indeed, specialized neural circuits have evolved for the processing of faces within the visual systems of a number of species (see Freiwald and Tsao 2010, and references therein). For example, many animals attend preferentially to faces from birth or, at least, exhibit the neural foundations required to recognize a face during the earliest stages of development (Srihasam et al. 2014). Such predispositions to faces evoke the notion of “grandmother cells,” hypothetical neurons that code for a single complex stimulus across changing viewpoints, such as one’s grandmother (Gross 2002). As we shall see, although face cells do respond in a highly selective manner to faces as a stimulus category (Gross 2008), and while they may be mediating animals’ remarkable abilities of facial perception, face-selective neurons are not quite these hypothesized, highly invariant “grandmother cells.”

## The Origins of the Grandmother Cell Hypothesis

Jerzy Konorski, a Polish neuroscientist, expanded on the theories of William James, who postulated that certain cells within the brain may represent conscious experiences or percepts (James 1890). Firstly, Konorski (1967) capitalized on the findings of Hubel and Wiesel (1965) that there was a progressive increase in the complexity of a cell’s receptive field from the retina to area V3 and reasoned that higher visual areas beyond V3, such as the inferior temporal (IT) cortex, would continue the trend of increasing complexity (see Gross 2002, and references therein). Secondly, Konorski (1967) noted that only IT cortex lesions correlated specifically with visual abnormalities in recognition and discrimination learning. Finally, Konorski (1967) inferred from his own clinical work that prosopagnosia, a difficulty in recognizing faces, was also associated with IT

cortex damage (Konorski 1967). These three lines of evidence lead Konorski to predict that “perceptions experienced in humans’ and animals’ lives, are represented not by the *assemblies* of units but by *single units* at the highest levels of particular analyzers” (Konorski 1967, p. 74). Konorski named the specialized cells “gnostic units” and suggested that they were organized in areas called “gnostic fields,” that these fields were located in the ventral temporal lobe, and that each field represented a different biologically relevant perceptual category, such as emotional expressions, locations, hands, and faces (Konorski 1967). Konorski asserted that destruction of a gnostic field dedicated to faces in IT cortex would manifest as prosopagnosia (Konorski 1967). Konorski’s (1967) early speculations on the location of the facial processing circuitry were astoundingly similar to our modern understanding (Gross 2002).

In parallel to Konorski’s (1967) work, Jerry Lettvin pioneered single-cell recording in the frog retina, found that certain cells only responded to small dark spots in the visual field, and hypothesized these cells to be acting as specialized bug detectors (Lettvin et al. 1961). Interested by these neuron’s selectivity and the related work of Hubel and Wiesel (1965), Lettvin predicted the existence of “grandmother cells” that could represent the highest order of perceptual categories (Gross 2002, and references therein). Therefore, much as Konorski (1967), Lettvin asserted that cells in the visual system must exist that respond to a single individual, despite changes in viewpoint, color, and other arbitrary features (Gross 2002, and references therein).

### “Where” and “What” Visual Pathways

To understand how face-selective neurons function in facial recognition, it is necessary to understand the structure of the mammalian visual system. Prior to the late 1960s, vision was regarded as a functionally homogenous system, with object and location coding occurring across the same regions of visual cortex (Ungerleider and Haxby 1994). Schneider (1969) was the first to challenge the prevailing view by training

Syrian hamsters on two tasks, one requiring orienting to a sunflower seed held overhead, the other requiring discrimination between two differently patterned doors in a two-arm maze. The hamsters were then given bilateral lesions to the superior colliculus and visual cortex. Superior colliculus lesions impaired the ability to spatially localize the seed but did not impair performance on the pattern discrimination task. Visual cortex lesions, on the other hand, disrupted pattern discrimination learning but not performance on the spatial localization task. The double dissociation suggested that two separate subcortical pathways exist in the hamster: a colliculo-pulvinar-cortical pathway processing “where” information and the geniculostriate pathway processing “what” information. The colliculo-pulvinar-cortical pathway projects from the retina to the pulvinar nucleus of the thalamus and finally propagates to the extrastriate visual processing areas (Ungerleider and Haxby 1994). In contrast, the geniculostriate pathway projects from the optic nerve to the lateral geniculate nucleus of the thalamus and finally to the primary visual cortex (V1) (Ungerleider and Haxby 1994, and references therein). Similar findings were made by Ungerleider and Mishkin (1982), who showed that IT cortex lesions impaired performance on an object discrimination task, but not a spatial localization task, whereas parietal lesions impair spatial localization but not object discrimination.

Schneider’s (1969) discovery of separate subcortical routes from retina to cortex is now recognized as a universal organization of the mammalian visual system. The double dissociations noted by Schneider (1969) and Ungerleider and Mishkin (1982) have led to the proposal that visual information is processed along two different cortical streams: a dorsal (“where”) pathway that projects from the primary visual cortex to the inferior parietal lobe and is responsible for spatial localization and a ventral (“what”) pathway that projects from the primary visual cortex to IT cortex and is responsible for pattern perception (Ungerleider and Haxby 1994, and references therein).

## Face-Selective Neurons in Nonhuman Primates

Charles Gross performed pioneering electrophysiological recordings in IT cortex and the adjacent dorsal bank of the superior temporal sulcus (STS) of macaques in the late 1970s and early 1980s, revealing populations of neurons that responded selectively to faces (see Fig. 1) and body parts (see Gross 2008, and references therein). The receptive fields of face-selective neurons in IT cortex encompassed most of the visual field and were always localized within the fovea, consistent with their role in complex pattern recognition. Many face cells in IT cortex were sensitive to a face's orientation. For example, some units fired only or maximally to faces viewed in portrait or profile viewpoints (viewer centered), while others responded to faces in both viewpoints (object centered). Removal of facial features such as the eyes and mouth or the presentation of a line-drawn caricature of a face elicited reduced responses from face cells, suggesting that face cells summate incoming visual information about the components of faces.

While the aforementioned studies indicated that the primary role of face cells in IT cortex is in the recognition of an individual, whereas face cells in STS work in parallel to interpret emotional expression and the direction of eye gaze, it remained unknown if face cells were casual in the perception of faces. To examine the notion of causality, Afraz et al. (2006) applied electrical microstimulation to sites that contained clusters of face cells and non-face cells within IT cortex of macaque monkeys during a categorization task that required discriminating between images of face and non-face objects. Stimulation applied to face-selective sites, but not non-face-selective sites, biased the monkeys' decisions heavily toward the face category, thereby establishing a causal role for the activity of face-selective neurons in mediating the perception of faces.

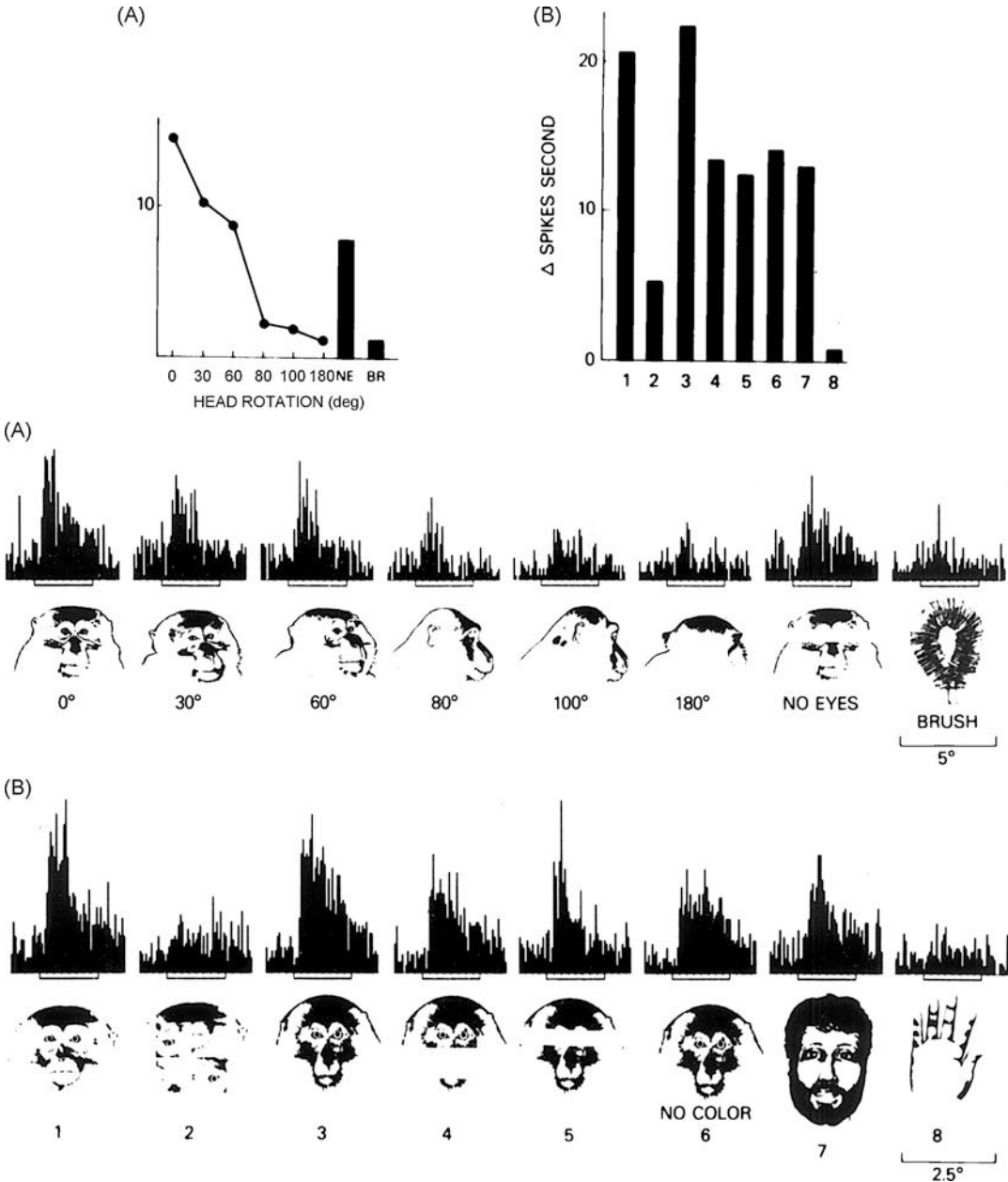
The next challenge was to determine the spatial location of face-selective sites in IT cortex and if these sites were in conserved locations across all primates. Freiwald and Tsao (2010) used fMRI to reveal that face-selective neurons in IT cortex

reside in a series of six anatomically and functionally connected clusters, known as "face patches." A similar series of six face patches were subsequently discovered in IT cortex of the marmoset (a New World monkey), suggesting that the foundations of the face processing system were present in our anthropoid primate ancestors over 35 million years ago (Hung et al. 2015). Examining the role of face patches further, Chang and Tsao (2017) demonstrated that face-selective neurons in most of the face patches represent a combination of facial features (e.g., eyes, nose, and mouth shape) in a specific viewpoint. In contrast, face-selective neurons in the face patch at the final output of IT cortex represent a combination of facial features across any viewpoint. Thus, the face patches work together to build a point-by-point 3-D representation of a face, allowing primates to recognize an individual across changing viewpoints. Chang and Tsao's (2017) discovery demonstrates that face-selective neurons are face-component neurons. As such, face cells are not really "grandmother cells" as originally conceived. Rather, each face cell performs a specific analytic role within an ensemble across IT cortex, synthesizing the emergent property of facial identity.

## Face Processing in the Human Brain

Given the wealth of evidence in nonhuman primates documenting a specialized circuitry for the perception of faces, it was natural to wonder whether a corresponding series of areas exist in the human brain. Initial investigation using fMRI revealed a distinct area in the right fusiform gyrus, now known as the fusiform face area (FFA), that was reliably activated specifically to face stimuli (Kanwisher et al. 1997). Subsequent fMRI work determined that the FFA is homologous with the face patch at the final output of IT cortex in macaques, the patch that facilitates individual recognition across changes in viewpoint (see Freiwald and Tsao 2010, and references therein). In addition to the FFA, the STS is also highly responsive to faces, and is likely responsible, as in monkeys, for the processing of emotional





**Face-Selective Neurons: Comparative Perspectives, Fig. 1** Example of an IT cortex neuron that responded more strongly to the front view of faces than to any other stimulus tested. The stimuli were interleaved colored slides projected onto the fovea for 2.5 s, as indicated by the horizontal lines under each histogram. **(a)** Responses of an IT neuron to a monkey face in different degrees of rotation (bottom), and a line graph (top) depicting the firing

rate to each of the different rotations of the monkey face, as well as the firing rate when the eyes were removed (NE) and to a brush (BR). **(b)** Responses of an IT neuron to altered faces, faces with components removed, a human face, and a hand (bottom) and a bar graph (top) depicting the firing rate to each of the different stimuli (Reprinted with permission from Gross 2008)

expression and direction of eye gaze (see Kanwisher et al. 1997, and references therein).

Unlike in nonhuman primates, in humans there are far fewer opportunities to analyze the activity of single cells within the extrastriate visual cortex. Nevertheless, Schalk et al. (2017) performed a landmark case study to determine if neurons in the FFA were specifically involved in facial recognition. Electrical stimulation was applied to face-selective and non-face-selective visual areas of a neurosurgical patient while viewing the experimenter's face, as well as a series of non-face objects (a box, ball, or kanji symbol). Stimulation of face-selective areas while viewing the experimenter's face elicited consistent reports of changes in the appearance of the experimenter's facial features. Stimulation of face-selective areas while viewing non-face objects resulted in the patient reporting hallucinations of a whole or partial face (known as facephenes) superimposed over the non-face objects; these facephenes did not occur when stimulation was applied to non-face-selective visual areas. Schalk et al.'s (2017) case study established that the activity of face-selective neurons in the FFA of humans are, much like in nonhuman primates, causal in the perception of faces.

## Face-Selective Neurons in Other Mammalian Species

The only reports of face-selective neurons other than in primates are from the extrastriate visual cortex of sheep (Kendrick and Baldwin 1987). Face-selective neurons were isolated across the temporal cortex and exhibited very similar basic response properties to those found in primates. A subpopulation of the face cells were tuned to the size of a sheep's horns, a feature that conveys information on gender and position in a sheep's dominance hierarchy. Most face cells responded preferentially to conspecifics faces, while a smaller number also fired to human and sheepdog faces. Interestingly, the neuronal responses to familiar sheep, human, and sheepdog faces were significantly greater than to unfamiliar faces

(Peirce et al. 2001, and references therein). Landi and Freiwald (2017) determined that familiar faces also cause significantly greater activation of face-selective neurons in the face patches of macaque IT cortex. The strikingly similar effect of familiarity on the neuronal responses to faces in sheep and macaques suggests both species possess separate mechanisms for general and familiar face recognition.

Regions sensitive to faces have also been observed in dogs. Cuaya et al. (2016) used fMRI imaging to reveal an area in the ventral temporal cortex of domestic dogs that exhibited significantly greater activation to human faces than non-face visual stimuli. Dogs are easily able to visually discriminate between different human faces, as well as detect subtle changes in eye gaze direction and emotional expressions based on human facial cues. It is possible that dogs' long history of mutual attachment with humans has facilitated the appearance of neural circuits that process human faces. It is currently undetermined whether the same area of temporal cortex active to human faces in dogs is also active to dog faces. Given that face-selective areas in the sheep temporal cortex contain neurons that respond to the faces of other species (Kendrick and Baldwin 1987), it seems likely that a general face processing system has evolved in the temporal cortex of all mammals.

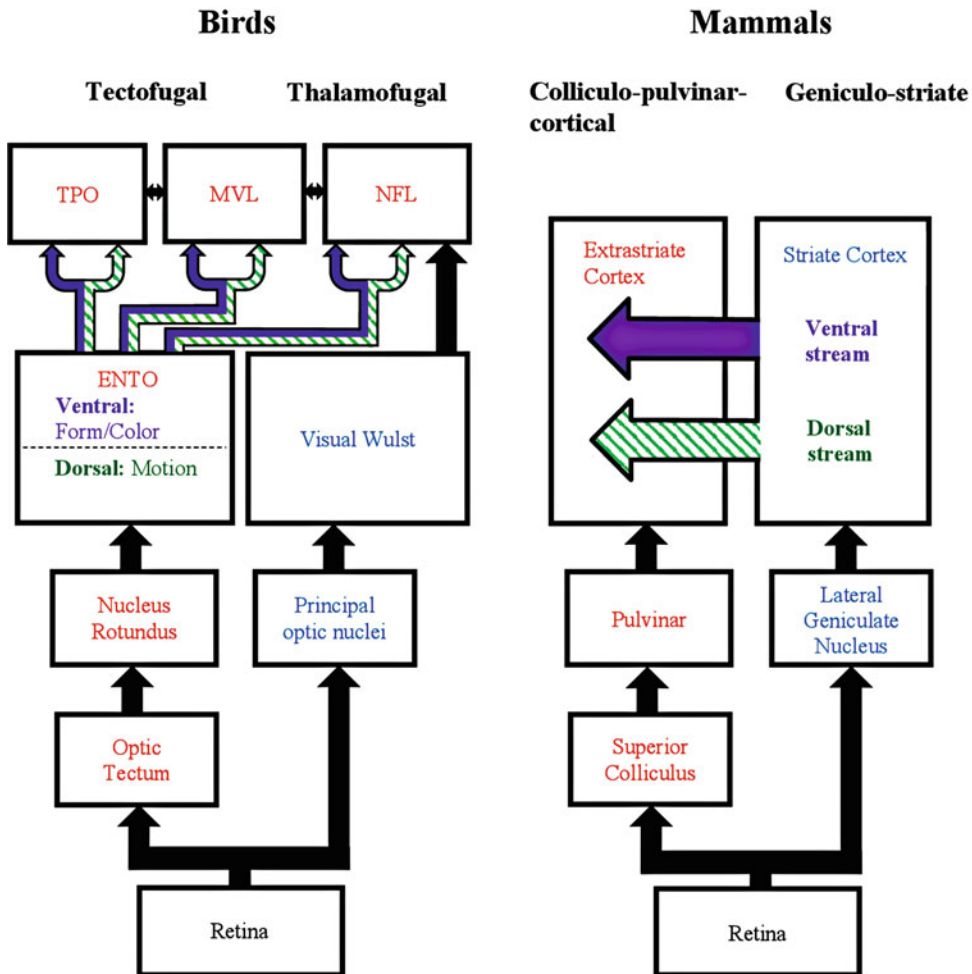
## Do Birds Possess Face-Selective Neurons?

Birds are one of the few classes of vertebrates that possess a visual system comparable to primates in complexity. Despite the fact that the last common ancestor of mammals and birds existed around 300 million years ago, many structures of the avian visual system are considered functionally homologous to areas of the mammalian visual pathways (Stacho et al. 2016, and references therein). For example, as in mammals, there are two main visual pathways in the avian brain. The thalamofugal pathway, similar to the mammalian geniculostriate pathway, projects

from the retina to the principal optic nuclei and then to the visual wulst in the telencephalon (Fig. 2; Stacho et al. 2016, and references therein). The tectofugal pathway, similar to the primate colliculo-pulvinar-cortical pathway, travels from the retina to the optic tectum and then to the nucleus rotundus of the thalamus, and from there to a structure known as the entopallium (ENTO), and finally to three visual association areas: the mesopallium ventrolaterale (MVL), area temporo-parieto-occipitalis (TPO), and the

nidopallium frontolaterale (NFL) (Fig. 2; Stacho et al. 2016, and references therein).

Lesions to the ENTO cause an array of visual deficits, consistent with a complex visual processing structure (Nguyen et al. 2004). For instance, ENTO lesions impair performance on psychophysical tasks of visual acuity, intensity threshold discriminations, and pattern and color discriminations, with the magnitude of the deficits correlated with the extent of damage (see Bessette and Hodos 1989, and references therein). As in



**Face-Selective Neurons: Comparative Perspectives, Fig. 2** Anatomical and functional similarities of the thalamofugal and tectofugal pathways in birds (left), and geniculo-striate and colliculo-pulvinar-cortical pathways in mammals (right). The entopallium (ENTO) is comparable with the early extrastriate regions of the mammalian

visual system. Area temporo-parieto-occipitalis (TPO), the mesopallium ventrolaterale (MVL), and nidopallium frontolaterale (NFL) receive projections from the ENTO and are likely involved in processing higher-order aspects of form, color, and motion information

mammals, there is segregation of incoming visual information into separate form, color, and motion parallel processing streams in the ENTO (Nguyen et al. 2004) that is likely maintained into the higher visual areas MVL, TPO, and NFL (Stacho et al. 2016). Fewer studies have been conducted on the MVL, TPO, and NFL, but those that have (Stacho et al. 2016; Koenen et al. 2016) further support the view that these areas are functionally similar to areas of the mammalian extrastriate cortex.

A plethora of behavioral studies using pigeons and Japanese quail suggest faces play a critical role in conspecific recognition and social signaling for birds (Shimizu et al. 2010, and references therein). Likewise, as a bird's face comprises a series of distinct local features, such as the beak, eyes, plumage, and cere (exposed skin on the upper beak), it is possible that a corresponding series of neural circuits in the avian brain analyses these local facial features within their global configuration. Indeed, ENTO lesions in pigeons impair the ability to discriminate between two conspecific pigeons or between two separate avian species (Java sparrow vs. gray starling), but not the ability to discriminate between food/nonfood object categories, or between a pigeon and a different avian species (see Watanabe 1996, and references therein). Despite the aforementioned evidence that processing faces is important for birds, the only study that has investigated face cells in the avian visual system failed to find any evidence of face-selective neurons (Scarf et al. 2016). It is possible that neural circuits dedicated to the processing of faces in birds reside upstream of ENTO in higher visual association areas, such as NFL, MVL, and TPO. Indeed, Marzluff et al. (2012) demonstrated significant neuronal activation of the NFL and MVL of crows in response to viewing human faces using positron emission tomography (PET) brain imaging. However, as the crows were not presented with any non-facial stimuli, or indeed even crow faces, it is unclear if the activity is representative of areas specialized for face perception as opposed to processing complex visual information, as would be expected from regions functionally similar to extrastriate cortex.

## Lateralization of Face Processing

Across all vertebrates that rely on vision for social recognition, there are significant differences in the ability of the left and right cerebral hemispheres to process face information. Nonhuman primates (Freiwald and Tsao 2010), humans (Kanwisher et al. 1997), sheep (Peirce et al. 2001), and domesticated dogs (Cuaya et al. 2016), all exhibit greater right hemisphere activation when viewing faces, an effect that is associated with the global processing of faces as a combination of local component features (Chang and Tsao 2017). In support of global processing, the ability of nonhuman primates, humans, and sheep to recognize faces (Brecht et al. 2017, and references therein) is significantly impaired when viewing an inverted face, suggesting that all mammals process faces in a global manner.

Interestingly, pigeons categorize visual stimuli based on their local features over their global configuration, an effect associated with a left hemispheric dominance of visual discrimination and learning in birds (see Scarf et al. 2016, and references therein). The predisposition to attend to local features over the global configuration also appears to extend to faces. For instance, it was recently demonstrated that a crow's ability to discriminate between upright and inverted images of crow and human faces was unimpaired by the inversion of the faces, a finding that stands in contrast to that observed in mammals (Brecht et al. 2017, and references therein). Thus, in contrast to mammals, birds may process faces more at the level of individual features and that might explain why Scarf et al. (2016) failed to find any face-selective neurons. The study of face-selective neurons in the avian brain is still in its infancy, and further studies examining how cells in higher association areas of the avian visual system respond to faces are required.

## Concluding Thoughts

In summary, over 50 years of research into the extrastriate visual areas of the vertebrate brain has unequivocally shown that face-selective neurons

mediate facial recognition. Face-selective neurons do not represent “grandmother cells,” but nevertheless respond with astounding specificity to faces over any other complex stimulus. The computational goal of such neurons in the visual system is not to encode particular individuals, but rather to create a flexible neural code representative of a given face that is forwarded downstream for further mnemonic and cognitive appraisal. Most of our current understanding of face-selective neurons comes from functional imaging and electrophysiological studies in nonhuman primates. While there have been preliminary investigations in other mammalian and avian species, the absence of sufficient comparative data makes it difficult to assess the evolutionary origins of the face processing system across vertebrates. Birds are of particular interest in the search for face-selective neurons, given their highly developed visual system and divergent cortical organization from mammals. While there is much we do not understand of visual processing and beyond, the stage has been set to determine whether face-selective neurons represent a universal individual recognition solution across the animal kingdom.

## Cross-References

- Corvids
- Dorsal Pathway
- Entopallium
- Evolution of Animal Color Vision
- Face Processing in Different Brain Areas and Face Recognition
- Familiarity
- Hemispheric Specialization
- Individual Recognition
- Laterality Effect (Face Perception)
- Neocortex
- Nerve Cells
- Neural Impulse
- Neuron
- Occipital Lobe
- Parietal Lobe
- PET
- Pigeon (*Columbidae*)
- Primate Sensory Systems

- Primates
- Prosopagnosia
- Spatial Orientation
- Superior Temporal Sulcus
- Temporal Lobe
- Vertebrate Nervous System
- Vertebrates (Chordata)
- Visual Perception
- Visual Recognition in Birds
- Visual Recognition of Prey and Predators
- Visual Self-Recognition

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## Facial Expression

### ► Catarrhine Communication

## Facial Recognition

### ► Face-Selective Neurons: Comparative Perspectives

## Facilitation

### ► Mutualism

## Facultative Polyandry/ Strategic Pluralism

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### Synonyms

Alternative reproductive strategies; Context-dependent strategies; Extra-pair copulation

### Facultative Polyandry

Traits that are expressed in contexts in which they are potentially advantageous, and suppressed at other times, are referred to as **facultative** traits. In mating systems with female **polyandry** (from Greek: poly- “many” + andr- “male”), females mate with multiple males within a breeding period (Barrows 2011). **Facultative polyandry** is therefore a female mating strategy wherein normally monogamous females mate with multiple males within a breeding period. In a large number of species, including many birds and mammals, pair-bonded females practice facultative polyandry (e.g., birds, Yezerinac et al. 1995; humans, Scelza 2011; marmots, Graziani et al. 1998).

### Flexible Mating Systems

Facultative polyandry is an example of behavioral flexibility in animal mating systems. **Strategic pluralism** theory posits that such flexibility is adaptive because it allows animals to pursue alternatives to their primary strategies when social or environmental factors change (Gangestad and Simpson 2000). Males’ and females’ primary mating strategies are generally attributed to differences in reproductive potential: due to sex differences in the biology of reproduction, males may benefit from mating with multiple females by producing more

offspring, whereas females generally cannot increase their reproductive output by mating with more than one male (Andersson 1994). This fundamental biological difference has led to two widely accepted assumptions: females should form long-term pair-bonds, and males should mate with as many females as possible. However, as suggested by strategic pluralism theory and the occurrence of facultative polyandry, animals’ mating behavior can be highly flexible, and alternative mating strategies may, under certain ecological conditions, be preferable to primary strategies.

### Monogamy, Polyandry, and the Ecology of Facultative Polyandry

Sexually monogamous females ensure that the offspring they produce will be sired by their primary mates. Males can provide direct benefits, such as parental investment, and are more likely to do so when they are certain of paternity (Arnqvist and Kirkpatrick 2005). They are also far less likely to intentionally injure or kill their own offspring and may even protect them from threats by conspecifics or predators. However, if the primary mate of a monogamous female dies, invading males are unlikely to protect, and may be more likely to kill, the dependent offspring of her former mate. In addition, by being limited to a single mate, females risk choosing a male of low genetic quality and passing low-quality genes on to their offspring (Clutton-Brock 2016).

Under polyandry, the costs and benefits are reversed. By mating with multiple males, females may incite sperm competition, potentially leading to fertilization by a male with relatively high genetic quality (Zuk 2003). Furthermore, the total risk of infanticide may be reduced when females are polyandrous, as killing an infant that he may have sired risks a substantial reduction in a male’s reproductive success. Because no particular male can be especially confident of paternity, however, paternal investment is less prevalent in polyandrous species (Clutton-Brock 2016; Kappeler 2012).

In most species, neither strict monogamy nor extreme polyandry is the ideal strategy. Females may be primarily monogamous to secure direct benefits such as paternal care but seek extra-pair copulations when they have mates with low genetic quality. In this way, facultative polyandry serves as an intermediate strategy that may allow females to secure the social benefits of monogamy while also seeking the genetic benefits of polyandry on an opportunistic basis.

## Cross-References

- [Alternative Reproductive Tactics](#)
- [Extra-Pair Copulation](#)
- [Facultative Trait](#)
- [Mating](#)
- [Parental Investment](#)
- [Paternal Behavior](#)
- [Polyandry](#)
- [Polygynandry](#)
- [Postcopulatory Selection](#)
- [Sneaky Copulator](#)
- [Sperm Competition](#)

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## Facultative Trait

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## Definition

The word “facultative” originated from the New Latin word *facultātīvus* which means “optional,” the process in which an organism could perform optionally in response to a particular situation rather than by nature (<http://www.dictionary.com/browse/facultative>).

In biology, “facultative trait” can be defined as the efficiency of an organism to survive into more than one specific set of environmental conditions (<http://www.dictionary.com/browse/facultative>).

## Introduction

The facultative trait evolves according to a change in the surrounding environment at a particular time. The first example is that in bright light, a person's eyelids shrink together tightly to protect the eyes until unless he cannot adjust to that light. Another example is that in a colder atmosphere, person's nails turn purple. These two examples are showing facultative adjustments because in both situations, the body adjusts its phenotype according to the particular environment.

In other words, we can say that the facultative trait is a general competent character of any organism, which is not restricted by particular function or mode of life. Facultative trait may be used in many ways at different places. Some examples are as follows, to understand more about this aspect.

### Examples of Facultative Trait

1. **Facultative anaerobe** – Facultative anaerobes are organisms which use oxygen for energy production but also capable to survive in anaerobic condition due to having anaerobic methods of energy production.
2. **Facultative biped** – Facultative biped is an animal that can walk or run on two legs as well as on four limbs according to own specific situation.
3. **Facultative carnivore** – Facultative carnivores do not depend merely on animal flesh for food. They also can survive on nonanimal food. We can compare omnivores with facultative carnivores.
4. **Facultative heterochromatin** – Heterochromatin is a supercoiled structure of DNA or condensed DNA which is less or not active. Facultative heterochromatin is also tightly packed but in the form of non-repetitive DNA which may lose its condensed structure and become transcriptionally active like a euchromatin (Volpe et al. 2002).
5. **Facultative parasitism** – Depending on a particular environmental condition, facultative parasites can survive in both free-living and parasitic condition. This kind of trait shows competitive intermediate state among both the free-living and fully parasitic way of life (Luong and Mathot 2019).

It has been reported that facultative parasites are those who can live their entire life without a host but can also seize the opportunity of hosts and can be parasitic under favorable conditions. For example, some moribund juveniles of nematodes having parasitic characters similar to that of dauer larvae generally formed under tough

situations like high nematode density, low food availability, heat stress, etc. Simultaneously under favorable conditions, these parasites can also live entirely free without a host (Viney 1996; Stasiuk et al. 2012).

6. **Facultative pathogens** – Some bacterial species which are pathogenic and may reproduce in environmental resources such as water, soil, etc. On the other hand, they can also cause disease after getting entry into the vulnerable host. Such kinds of pathogens are known as facultative pathogens (Alberts et al. 2002).
7. **Facultative parthenogenesis** – Parthenogenesis is a mode of asexual reproduction in which female reproduces their offspring without any genetic involvement of a male, e.g., squamate (Snakes and Lizards). Sexually reproducing species like Komodo dragon and several species of snakes are also capable of parthenogenesis in the absence of male partner via mechanism known as half-cloning (a haploid polar body formed due to normal female meiotic divisions fuses with the egg to form a diploid nucleus); this ability is known as facultative parthenogenesis (Ross et al. 1997; Lampert 2008; Laurie and Caldwell 2013).
8. **Facultative parental care** – According to Kolliker (2007), the survival of offspring totally depend on parental care as offspring cannot survive in the absence of their parents, but there are several animals including insects like *N. pustulatus* which appear to be facultative in parental care. Earwig belonging to order Dermaptera show higher variation in maternal care as some of them furnished and defend their nymph, but others terminate care soon after hatching, and even some of them support only at the time of eclosion (Costa 2006; Capodeanu-Nägler et al. 2016).

### Conclusion

From the above discussions, it can be concluded that facultative trait is a special kind of phenotype that might be applied to any organism at any specific time due to changes in environment. It

can be in the form of behavior, different ways of feeding and reproduction for subsistence or any genotypic phenomenon, and many more to survive or to be the fittest. Basically facultative trait is an efficiency to perform optionally in response to particular situation for existence.

## Cross-References

- [Omnivore](#)
- [Pathogen](#)

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## Fairness

- [Inequity Aversion](#)

## Falcon Locomotion

- [Falconiformes Locomotion](#)

## Falconiformes Cognition

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## Introduction

The order Falconiformes are represented by the diurnal birds of prey belonging to the Falconidae family, with three recognized subfamilies: Falconinae with 46 species (i.e., falcons), Herpetotherinae with 8 species (i.e., laughing falcon and forest falcons), and Polyborinae with 11 species (i.e., caracaras) (Fuchs et al. 2015). Even though originally this order also included the families Accipitridae, Cathartidae, Sagittariidae, and Pandionidae, recent analyses showed that Falconidae are not a sister taxon of Accipitridae (and the rest of the diurnal bird of prey families), but rather a separate lineage in the terminal landbird clade which includes Psittaciformes and the Passeriformes (Jarvis et al. 2014; Prum et al. 2015).

These raptors species represent a highly versatile group of predatory birds with a broad range of sizes and lifestyles: there are species with a weight close to 2000 g, like the Gryfalcon (*Falco rusticolus*), as well as sparrow-size raptors, like the White-fronted Falconet (*Microhierax latifrons*) or the Black-thighed Falconet (*Microhierax fringillarius*). The habitat type used is also variable, which goes from rain forests



to arid steppes and savannas, and many species have also successfully colonized urbanized environments. Moreover, this raptor order includes species with diverse trophic habits and techniques, which ranges from highly specialized species, like *Ibycter americanus* feeding almost exclusively on hymenopterans, to those that show a remarkable broad diet, like the generalist Caracaras, which food and feeding habits can include a spectrum and breadth exceeding the rest of the Falconiformes species (Ferguson-Lees and Christie 2001). With so many different adaptations, this order, along with the rest of the raptors, has attracted the attention of scientists and people in general for long time. Thus, it is not surprising that extensive research about almost every aspect of their biology and ecology, as well as avian medicine and health, has been performed during the last decades in this group of predators.

One issue in raptor research that has been scarcely studied until now relies on the realm of animal cognition. Cognition is the mechanisms that enable animals to acquire, process, store, and act on information from their environment, which include perception, learning, memory, and decision-making (Shettleworth 2010), processes that determinate behavioral responses. There are numerous recognized cognitive abilities that are underpinned by these processes (Shettleworth 2010), which cannot be directly observed in the phenotype of an individual, so they are evaluated through changes in behavior. These are commonly studied using robust experimental methods designed to measure specific cognitive abilities while keeping under control any other factor extraneous to the question of interest, thus reducing the possibility that performance variability on a cognitive task is due to some other cognitive or noncognitive factors than the investigated ability *per se* (Rowe and Healy 2014). Possibly related to this experimental requirement, raptors have not been considered as a good model taxon for cognitive research mainly because they can be challenging for capturing and handling due to their relative big size and apparently low “docility”; also many of these predators occur at low densities, with wide territories, and some are quite secretive or elusive,

all of which make them difficult to mark and track. Additionally, because raptors are placed in the top of the food-chain, they are considered particularly sensitive to the rapidly human-induced environmental changes, so the effort has been put mainly on their ecological role and requirements to the correct planning of conservation and management strategies. Notwithstanding the above, in last few years there was an increase in the studies about raptors’ cognitive abilities and the role of cognition in helping or hindering the adjustment of these predatory birds to a human-dominated world. These works are described in the next sections.

## Individual Learning

The way an animal reacts to a certain stimulus can be the result from a preexisting bias or predispositions, which are also known as innate or genetic controlled behaviors. Learning is a form of plasticity, described as the capacity to modify behavioral patterns based on individual experience, and involves forming internal representations of new information obtained from the current external and internal environments (Shettleworth 2010). Thus, the ability to learn is an evolutionary adaptation that allows many animals to make short-term behavioral adjustments to changing environments. Both preexisting or innate behaviors and learning operate together to produce many behaviors. The link between these two sources of behavioral outcomes relies on the fact that genes and prior environment influence how an animal is affected by specific experiences, thus determining the possibility of learning (Shettleworth 2010).

Raptors are generally considered as capable of showing highly complex behaviors, from which the best-known and detailed documented are those related to their hunting and feeding techniques (e.g., Newton 1979; Ferguson-Lees and Christie 2001). Much of these are considered as representing species-specific preexisting behavioral patterns, which are perfected through maturation (i.e., cognitive, morphological) and, to a different degree, by experience (e.g., trial and

error learning) (Newton 1979). Nevertheless, as occurs with the majority of the behavioral systems in Falconiformes species, we lack detailed studies about the role of learning in the development of their hunting and feeding techniques.

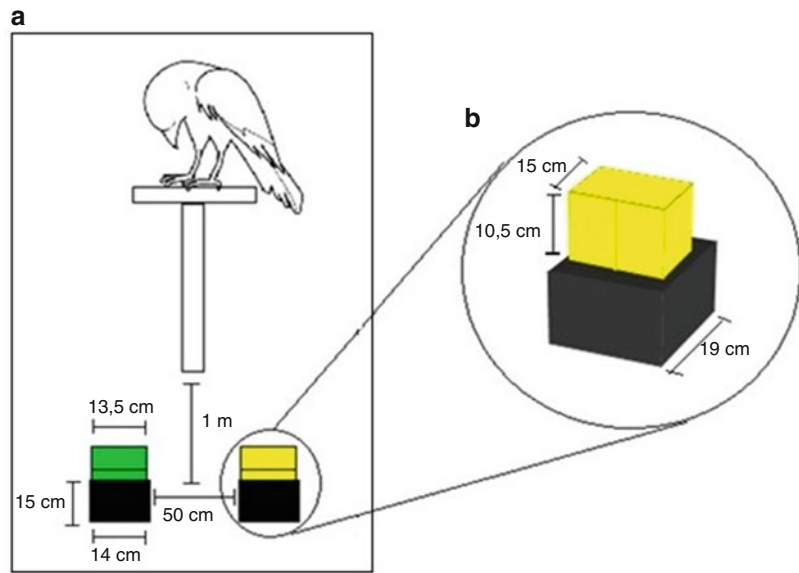
In this sense, the first ones explore and exploit the learning capability of raptors where people involved in the “art” of falconry, or falconers. This practice (i.e., the hunting of wild animals in their natural state and habitat by means of a trained raptor) has been in existence for more than 3000 years, originating in the Middle East and then spreading throughout all over the world. Thus, this discipline or “art” has a history in almost every continent and culture. Today, falconry is also commonly used as a tool in wild raptors’ rehabilitation and in educational programs. Yet, the basis of the raptor’ training has remained practically unchanged since the earliest days of falconry and involves both classical and instrumental conditioning (Jones 2001). These two methods have been proved highly useful for the analysis of associative learning, which occurs when there is a change in the behavior of an animal as a result of one event being paired with another (Pearce 2008). In classic (or Pavlovian) conditioning, two events that are paired together are a neutral conditioned stimulus (CS) and a biologically significant unconditioned stimulus (US). This pairing of a CS-US results in the CS causing a conditioned response (CR) in the animal, which is the natural respond to the particular US presented (Pearce 2008). In the context of falconry, for example, the trainers can use a visual or acoustic cue (CS) which once released the birds respond by coming to the trainer glove (CR) for a portion of meat (US). Operant or instrumental conditioning is a learning method that occurs through rewards and punishments for behavior. Through operant conditioning, an individual makes an association between a particular behavior and its consequence. This consequence acts as a reinforcement that causes a behavior to occur with greater frequency, or as a punishment which decrease the occurrence of such behavior. In this way, for example, trainers can strengthen a falcon’s behavior of flying until certain height before strike a prey, by releasing the quarry only when

such height is reached. Thus, the behavior of taking an appropriate height is then positively reinforced (Jones 2001).

Instrumental conditioning has also been used as an experimental paradigm to assess the visual acuity in several raptor species (Potier et al. 2020 and references therein). The most commonly used method is a 2-choice discrimination task. An animal is trained to choose between two different simultaneously presented stimuli, usually a grating of black-and-white stripes and a uniform gray field. Once the animal is trained to select the patterned display, the reward trials are repeated using patterns with progressively thinner bars, until the point is reached at which the animal chooses the patterned display no more than 50% of the time respect to the other. The spatial frequency of the grating, which cannot be reliably resolved and discriminated from the uniform gray gives the visual acuity threshold. The analysis of the visual acuity of Falconiformes using this learning method has only been performed in several species (reviewed in Potier et al. 2020), and the data about the speed of association between the correct stimulus and the reward is not available, which is not surprising considering that this work did not have the aim to evaluate the variability of learning ability *per se*. The only study that directly assessed the variability in associative learning in Falconiformes was carried out by Guido and collaborators (Guido and Biondi 2017) in the species *M. chimango*, a highly generalist Falconiformes species. These authors compared the performance during the acquisition of a stimulus-reward association and the posterior capacity of reversing this previously learned association. This experimental approach, known as reversal learning paradigm, represents one of the most common methods used to evaluate cognitive flexibility in animals. First, the authors trained the birds to discriminate between two containers of different color (green and yellow, Fig. 1), with only one of them associated with a reward (meat). When the birds reached a learning criterion of five correct consecutive trials, the color-reward contingency was reversed, and the raptors had to reach the same learning criterion to successfully finish the reversion phase. The

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**Fig. 1** Experimental set-up used during the reversal learning test (**a**) relative location of the boxes in the aviary; (**b**) frontal view of the box showing the two inward swinging doors. (Extracted from Guido et al. (2017))



measurements of learning speed used were the quantity of trials and errors committed before reaching the learning criterion. Furthermore, the authors analyzed the type of errors performed during the reversion phase; that is, perseverative errors, which reflected the capacity to inhibit the previous learnt color-reward association, and the regressive errors, which measure the ability to learn and maintain a new choice after initially shifting away from the previously correct choice. The results from this work showed that all individuals of *M. chimango* were able to acquire a color-reward association and to reverse this previously learnt association, adults and juveniles performing similarly in both learning tasks. Moreover, for this raptor species, reversal was a harder task compared to the initial acquisition phase, being the perseverative errors those that lasted for longest, which indicated that reversal learning speed in *M. chimango* was mainly conditioned by the ability to inhibit a previously acquired response, rather than to produce a new alternative behavioral choice. The authors suggested that this type of reversal learning performance might be of great advantage to the highly generalist lifestyle of this predatory bird, which frequently make use of anthropogenic resources (e.g., garbage), whose spatial and temporal predictability does not follow a natural variation but rather is subject to human

activity, so they must be able to react rapidly to changes in the value of the environmental cues that indicate food and others biologically relevant resources.

### Behavioral Innovation and Problem-Solving

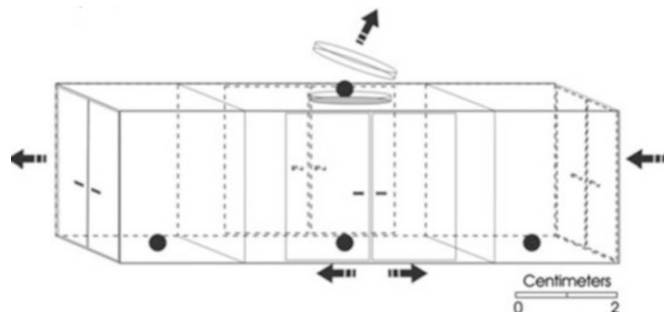
In nature, animals frequently have to confront a range of potential problems that they have to solve to achieve different vital goals, like the access to a valuable food source, find safe shelters, suitable nest sites, etc. Many of these problems may involve situations with certain level of novelty, for which animals may adapt the behavioral patterns already present in their species' repertoire, or develop completely new ones (e.g., novel skills, preferences, behavioral strategies). The capacity of behavioral innovation is widespread across the animal kingdom and is assumed to be a fundamental attribute facilitating animals' adjustment to novel or changing environments, allowing them to invade new habitats, exploit novel resources, and cope with habitat modifications (Griffin and Guez 2014). One of the approaches for the study of innovations that evaluates its functional implications is represented by large-scale multitaxa correlational analyses between

anecdotal reports of novel behavioral patterns, ecological characteristics, and evolutionary parameters (Lefebvre 2011). These studies have shown, for example, that Falconiformes and Accipitriformes represent highly innovative orders, characteristic that also correlate with their high relative forebrain size, a brain structure assumed to play a role in higher cognitive functions (Lefebvre et al. 1997). From a mechanistic approach, the novel problem-solving paradigm (or innovative problem-solving) provides an ecologically meaningful assay for measuring the natural proclivity of animals to innovate (Griffin and Guez 2014) and commonly involves a novel extractive foraging task that has to be solved to reach a valuable reward (e.g., puzzle box with food inside). Although this experimental paradigm has been applied to a taxonomically broad array of species (reviewed in Griffin and Guez 2014), only one Falconiformes species, the Chimango caracara, has been explored regarding their capacity to innovative problem-solving and behavioral flexibility in general. In a series of investigations, Biondi and collaborators (Biondi et al. 2008, 2010a) analyzed the capacity of solving a novel puzzle box containing food, as well as the role of cognitive (i.e., learning) and non-cognitive (age, object neophobia, and explorative behavior) factors known to underpin innovation propensity, of wild-caught adults and juveniles chimangos. The test apparatus was made of a transparent Plexiglass material and has four isolated sections containing pieces of food. Each section could be opened by lifting, pushing, pulling, or sliding the lids, respectively (Fig. 2). The authors first characterized the individuals according to their neophobic response and

exploration tendency. Neophobia, or the level of aversion to novel situations, was measured by recording the latency to feed in close presence of a novel object (Greenberg 1983), whereas explorative behavior was investigated by presenting the chimangos with a number of natural and artificial objects and quantifying the time the birds took to approach and contact these objects, and the time they spend exploring them. A day after the end of these two tasks, the authors tested the chimangos with the puzzle box once per day, during five consecutive sessions. The repetition of the box presentation had the main objective of evaluating the possible improvement in chimangos' performance with experience (i.e., learning). The results from these works evidenced a low neophobic response, a high explorative tendency, and a remarkable capacity of innovative problem-solving in this raptor species. During the box solving attempts, the birds used both the beak and talons to contact the different areas of the box, actions that are highly common in the majority of raptors species during prey manipulation. Also, juveniles were less neophobic, more explorative and showed in general better performance in the innovative problem-solving task than adult chimangos. Regarding this last result, a lower neophobia and a higher solving persistence were the factors that most contributed to the enhanced performance observed in young raptors. Furthermore, individual performance improved with experience, as indicated by the progressive reduction in feeding latency across days and by the increase of success in lids opening during subsequent sessions. Although more controlled studies on the cognitive mechanisms involved are needed, the authors suggested that following the

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**Fig. 2** Diagram of the clear Plexiglas box used for the problem-solving test. Black dots represent the pieces of meat and the arrows indicate the movement direction necessary to open each lid. (Extracted from Biondi et al. (2010a))



first experience with the novel task, a process of learning occurred, that is, individuals behaved randomly until by trial and error the correct responses (those that allowed access to food) were performed and then repeated and improved during the next sessions. More recently, Solaro and Sarasola (2019) used the same experimental protocol and test apparatus as Biondi and collaborators (Biondi et al. 2008, 2010) to compare the problem-solving capacity between chimangos occurring in suburban and rural habitats. They found an enhanced solving performance in raptors coming from more urbanized areas, a result that was already observed in a considerable number of other bird species (reviewed by Griffin et al. 2017).

Although not belonging to the Falconiformes order, another study on raptor cognition worth mentioned belongs to Colbert-White and collaborators (2013), who investigated the ability of Harris's Hawk, *Parabuteo unicinctus* (Accipitriformes) to solve a string-pulling task, an experiment test that has been used to evaluate avian problem-solving capacity and, more specifically, insight or folk physics (Pearce 2008). This species is recognized for its complex social behavior reflected in its cooperatively hunting behavior, so the link between this attribute and their potential cognitive abilities is straightforward. In accordance with this claim, Colbert-White and collaborators found that this raptor species was able to successfully solve the string-pull task with a relatively fast time of first solution, and then enhancing their techniques with experience. Although this capacity could rely on simple operant learning mechanisms (i.e., trial-and-error learning), the evidence of this general problem-solving skills in two non-closely related raptors species highlights the need for more research on the evolution of the underlying cognitive abilities in birds of prey.

## Social Learning

Social learning can be defined as any modification of the behavior that is acquired at least to some extent, by paying attention to the behavior of

another animal or its products (Heyes 1994). Thus, social learning involves an observer (naïve) and a demonstrator, who performs the behavior that later will be reproduced in whole or part by the observer. To be classified as learning rather than facilitated behavior, the observer's performance must occur at a later time, without the influence of the demonstrator. By copying others, for example, naïve animals can learn about novel resources, the location of food and water sources, how to identify and avoid predators, and how to move safely around their environment, minimizing at the same time the cost linked to asocial or individual learning (Heyes 1994; Galef and Laland 2005). Social learning can be found in numerous taxa and behavioral domains, and theoretical works indicate that it will be advantageous mostly in changing environments where genetic change is too slow and asocial learning too costly to cope with change (Reader 2016).

Raptors have traditionally been considered as solitary predators. However, it is well known now that the majority of them show at least some degree of gregariousness, relying to varying extents on social information about feeding behavior, mate choice, nest location, and other habitat resources. For example, different types of social foraging can be found in this avian group, from true cooperative searching and hunting (e.g., pack hunting by Harris' Hawks) to opportunistic aggregations in response to high concentrations of prey (see Ellis et al. 1993). Moreover, several species of Falconiformes show communal roosting and colonial breeding behaviors (Ferguson-Lees and Christie 2001), which enhance the opportunity and adaptive value of using social information and learning from it. In spite of these characteristics, few attempts have been made to analyze the behavioral and ecological factors that determinate the probability of social learning in these predatory birds.

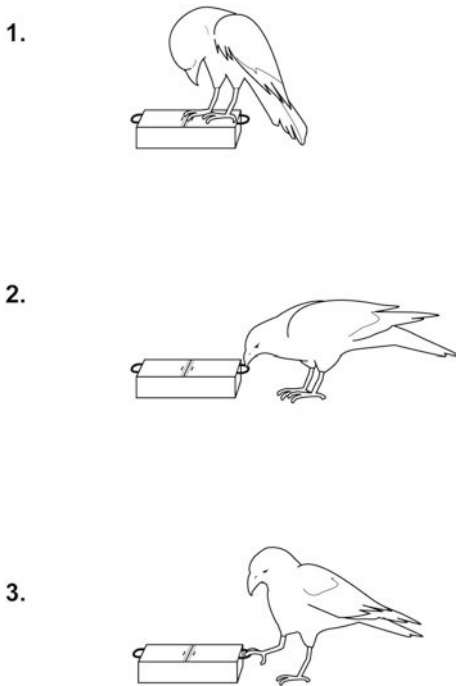
One of the most common documented cases in raptor behavior in which social learning is invoked is regarding the development the hunting and flight skills of in young raptors. This learning (both social and asocial), which occurs mostly during the postfledging period when parent-



offspring dependence is highest, is assumed to be of key importance in the survival of juveniles after independence (Newton 1979). In this sense, for example, adults of some raptor species are considered to have an active role in the development of flight and hunting behavior of its offspring, by training or “teaching” the young birds while hunting within view of the nest and through aerial food-passes, sometimes of live prey (e.g., Meinertzhagen 1954; Kitowski 2005). This is the case, for example, of adults of ospreys (*Pandion haliaetus*), a fish specialist species of Accipitriformes, that have been observed dropping caught fish to their offspring allowing them to dive and catch the prey, behavior that has been considered to be part of a parents’ teaching strategy, to allow their young to practice their hunting skills (Meinertzhagen 1954). However, more recent studies have suggested that this raptor species did not teach their offspring at the nest to hunt they prey, as previously thought (Howard and Hoppitt 2017). Social hunting involving siblings and parents, or only juveniles, is another example in which social learning (i.e., observational learning) has been proposed as the mechanism underlying the improvement of hunting skills in young raptors (e.g., *Falco sparverius*: Varland et al. 1991, *Circus aeruginosus*: Kitowski 2009). Nevertheless, there are also several documented cases in which young raptors were observed to carry out hunting attempts during the postfledging dependence period, without its parents or adults present (Kross and Nelson 2013; Ruaux et al. 2020 and references therein) indicating that postfledging individuals can train its foraging techniques alone, without the necessary presence of an experienced demonstrator. In all of these works, there is no certainty about the extent to which asocial and social learning are involve in the hunting behavior development of different raptors species, so there is a great need for controlled and experimental studies to determine their relative importance.

Regarding social learning about novel adaptive behaviors, only one study has been done that explore this phenomenon throughout an experimental approach. This is the case of Biondi and collaborators (2010b), who evaluated the ability

to socially acquire a novel feeding behavior in wild-caught individuals of Caracara Chimango. This is a gregarious species, with communal roosting and colonial breeding habits, also forming feeding aggregations in sporadic food sources, like carcasses and waste landfills (Ferguson-Lees and Christie 2001). Biondi and collaborators had already shown the notable capacity of innovative problem-solving in this raptor species (see previous section) and what factors determinate the individual variability in its performance. However, the innovation process also includes the spread of its product through the population, and the transmission of such innovation between generations, via social learning (Tebich et al. 2016). On these grounds, Biondi and collaborators tested whether the ability to solve a novel extractive feeding task was improved by observing the behavior of a trained demonstrator, assessing the age of both observers and demonstrators on the probability of social learning in the chimango. The authors first trained a group of chimangos (juveniles and adults) to reach the food hidden inside an opaque Plexiglas box with two lids, using the successive-approximations method. This group of trained birds was then used as demonstrators to perform the learned box opening behavior in front to an unexperienced bird (observer). Each of these observer birds was exposed to a demonstrator during several trials and then tested with the same experimental box but in isolation. The authors compared the box opening success and performance between the observer group and a control group, made up of chimangos that did not have the chance to previously observe a demonstrator opening the experimental box. Also, they recorded the opening techniques used by the observer individuals to then compare it with those shown by its demonstrators (Fig. 3). These authors found that individuals in the observer group outperformed control individuals both in solving speed and success and that this performance was maintained and/or enhanced during the subsequent session days only in the observer group. These results represent direct evidence of the capacity of this raptor species to learn a novel feeding task by observing the behavior of an



**Falconiformes Cognition, Fig. 3** Schematic drawing of the three opening techniques used by the control and observer individuals during the social learning test. (Extracted from Biondi et al. (2010b))

experienced conspecific. Also, in the observer group, juveniles opened the box faster than adult observers, which may reflect the higher persistence of juveniles during a problem-solving task and their higher propensity to rely on social clues to make a behavioral response, thus reducing the need for time-consuming and costly trial-and-error individual learning. Finally, the opening techniques used by observers did not always match the motor actions of their demonstrators. The authors suggested that some form of non-imitational social learning, such as stimulus enhancement or emulation, was probably involved.

## Conclusion

Until now, raptors are represented in an extremely low percentage of the cognitive studies performed in birds. The works presented here indicate

significant cognitive capacities of this group of predatory birds, which in part reflect their already shown relative brain size, comparable in some cases with that found in corvids. However, taking into account that this is a highly diverse group with different ecological strategies and life-styles, it would be necessary to evaluate how these characteristics influence, and are influenced by, their cognitive attributes.

## Cross-References

- [Accipiters](#)
- [Associative Mechanisms](#)
- [Behavioral Flexibility](#)
- [Cognition](#)
- [Discrimination Learning](#)
- [Evolution](#)
- [Falconiformes Locomotion](#)
- [Falconiformes Sensory Systems](#)
- [Innovation](#)
- [Instrumental Learning](#)
- [Intelligence](#)
- [Memory](#)
- [Neophobia](#)
- [Operant Conditioning](#)
- [Problem-Solving](#)
- [Reversal Learning](#)
- [Social Behavior](#)
- [Social Learning](#)

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## Falconiformes Flight

### ► Falconiformes Locomotion

## Falconiformes Locomotion

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## Synonyms

Caracara locomotion; Falcon locomotion; Falconiformes flight

## Definition

Movement used by members of the family Falconidae (i.e., falcons and caracaras) to traverse their environment.

The order Falconiformes is made up of approximately 60 species of diurnal birds of prey. Clades within Falconiformes include families Falconidae (falcons, caracaras, *Polihierax*, and *Neohierax*) and Herpetotheridae (laughing falcon and forest falcons). Falconiformes are estimated to have been around for 60 million years, with extant genera ranging from 2 to 19 million years (Mindell et al. 2018). The family has a cosmopolitan distribution with the exception of central Africa, and some parts of the Arctic and Antarctica. They inhabit a range of environments, such as tundras, rainforests, and deserts. Species like peregrine falcons (*Falco peregrinus*) are found in a wide array of habitats while species like the Mauritius kestrel (*Falco punctatus*) are restricted to island habitats (Tardoff 2002).

Falcons and caracaras range in size from small to medium-sized birds. They have hooked bills, sharply curved talons, and excellent eyesight. Falcons and caracaras are carnivorous, and they feed on birds, reptiles, insects, and small mammals

such as bats. (Mikula et al. 2016). The genus *Falco* are fast-flying predators while other species, particularly the *Caracara*, are more sedentary in their feeding style (Collopy 1977).

## Flight Biomechanics in Falconinae

The main method of locomotion for the order Falconiformes is flight with some exceptions. The modes of flight include flapping, gliding, soaring, and diving. The family Falconidae consists of three recognized subfamilies, Falconinae, Polyborinae, and Herpetotherinae (Picasso and Mosto 2018), each with different flight behaviors (Mosto et al. 2018). The peregrine falcon (*Falco peregrinus*) and the merlin (*Falco columbarius*) rapidly flap their wings to locate and hunt prey. They strike their talons to kill their prey (Mosto 2016). The falcons and merlins belong to the genus *Falco*, and these birds generally require more energy expenditure to sustain such fast-flying flapping flight. A result, these species have a larger muscle mass (Siewwright and Macleod 2012), particularly the *m. pectoralis* and *m. supracoracoideus*. The larger muscle mass inherently generates a greater force that allows the birds to rapidly change the position of their wings and facilitate rotation of the wing (Bribiesca-Contreras et al. 2019). In contrast, gliding and soaring birds selectively utilize the muscles that maintain an outstretched horizontal wing position to balance two types of force: a gravitational force and an aerodynamic force generated by air flowing over the body and wings (Tucker 1998) (Fig. 1). These birds keep a varied extended wing posture depending on their speed (Bribiesca-Contreras et al. 2019). At low speeds, the gliding birds spread their wings entirely, and they decrease their wingspan as their speed increases (Tucker 1998). Soaring birds maintain or gain altitude by flying upward and accelerating air currents (Tucker 1998). Soaring flight can be static or dynamic. A static soaring bird maintains its flight by the upward velocity component of air equal to or greater than the bird's sinking speed, whereas a dynamic soaring bird utilizes changes in horizontal wind velocity component to stay aloft.



**Falconiformes Locomotion, Fig. 1** Gliding flight in the peregrine falcon (left) and elongated hindlimbs of the caracara (right). (Photo credit for peregrine falcon by Juan Lacruz – own work, CC BY-SA 3.0, [https://](https://commons.wikimedia.org/w/index.php?curid=20851640)

[commons.wikimedia.org/w/index.php?curid=20851640](https://commons.wikimedia.org/w/index.php?curid=20851640). Photo credit for caracara by Thomas Fuhrmann, CC BY-SA, <https://creativecommons.org/licenses/by-sa/4.0>)

The two primary muscles of flight are the *m. pectoralis* and *m. supracoracoideus* muscles, which depress and elevate the wing, respectively (Bribiesca-Contreras et al. 2019; Tobalske 2007). Both muscles insert on the humerus (Tobalske 2007). The two main phases of flapping flight are the upstroke and downstroke (Dial et al. 1988), and it is mediated by different movements of the humerus through depression, elevation, protraction, retraction, and rotation (Picasso and Mosto 2018). The downstroke provides the majority of the propulsive force needed to generate lift and thrust, and upstroke prepares the wing for downstroke (Dial 1992; Picasso and Mosto 2018).

Geometric morphometric techniques show that variation in humeral morphology is associated with different flight speeds and flight styles. For instance, the deltoid crest is a key feature in differentiating fast and slow fliers as well as differentiating the different modes of flight. The deltoid crest serves as an attachment point for *m. deltoideus minor* and *m. pectoralis minor*. Fast-flying flapping birds require a large attachment area to the deltoid crest for the pectoral

muscles compared to the slower, soaring fliers. This increased area of attachment serves to prevent excessive muscle strain and bone breakage. Slow soaring fliers require a steady force from the pectoral muscles and require a smaller area of attachment to the deltoid crest (Sievwright and Macleod 2012).

Falcons attack prey in the air at the end of a high-speed, high-altitude dive (Tucker 1998). Peregrine falcons have been known to fly up to  $320 \text{ km h}^{-1}$  during a dive making them the fastest animal in the world (Ponitz et al. 2014a, b). The peregrine falcon beats its wings before the dive to accelerate and folds its wings close to its body to begin the dive. The closer the wings are to the body, the faster it moves as drag is decreased. There are two criteria that must be met for a bird to dive. First the bird's gliding path must be straight. Second, its wingspan must be less than 70% of its maximum length (Tucker 1998). Peregrine falcons can fine-tune their body during a dive through wing morphing which changes the shape of the wings to resemble a diamond shape. The changes in wing positioning correspond with the three phases of diving: acceleration/diving



phase, transient phase, and deceleration phase. At the beginning of the dive, the wings are close together and they gradually open up as the dive progresses (Ponitz et al. 2014a, b).

During the accelerating phase, peregrine falcons (*Falco peregrinus*) increase speed by moving the frontal portion of its wings into a cupped formation to reduce drag and increase lift. The cupped wing shape occurs when the outer edges of the wings point inward and downward to create a streamlined body shape that helps reduce drag (Ponitz et al. 2014a, b). The streamlined body shape resembles a diamond and allows the flow separation of the air during the dive to flow towards the tail rather than over the wings (Ponitz et al. 2014a, b). During the transient phase, the speed at which the falcon is traveling is constant because the drag has equalized to the constant gravitational force. The speed remains constant until the deceleration phase, which is at the end of the dive. Falcons control their speed during a dive by changing the amount of drag. However, it must be done without increasing their lift as that could result in falcon pulling out of a dive prematurely (Tucker 1998).

As the falcon nears the end of the dive, it opens its wings to slow down. This increases drag and generates lift (Ponitz et al. 2014a, b), enabling the falcon to pull out of the dive. During this time, the bird transitions from a straight flight path to a curved flight path, producing large external forces on the body amount of and wings of the bird. Due to the high amount of force placed on *F. peregrinus* during a high-speed dive and pullout, these birds require bones that are resistant to fracture (“solid bones”). Thus, *F. peregrinus* have thick-walled humeri and high bone mineral density in the humerus, radius, ulna, and sternum, allowing the falcon body to withstand forces that are three times its body weight especially during the pullout of a dive (Schmitz et al. 2018).

### Polyborinae Locomotion

Caracara have a varied foraging diet that consists of invertebrates, vertebrates, carrion, and garbage (Picasso 2018). These birds exhibit erratic and

slow flight behavior by alternating between flapping and gliding (Mosto et al. 2018). The forelimb muscles of caracaras have relatively small mass resulting in require less energy expenditure and contributing to their gliding flight pattern (Picasso and Mosto 2018). This subfamily is unusual compared to the other Falconiformes, due to the increased time spent on the ground rather than in the air. These ambulatory birds are known to have longer hindlimbs to allow them to efficiently ambulate on the ground (Mosto et al. 2018) (Fig. 1). The long hindlimbs are due to an elongation of the tarsometatarsus that serves to increase stride length making locomotion on land more energetically effective (Mosto 2016).

The musculature of the hindlimbs in Polyborinae is also distinct compared to the rest of the Falconidae. The *m. flexor cruris lateralis* is an important hip extensor that prevents hyperextension of the knee while walking and is typically absent in the rest of the species in Falconidae. The presence of this muscle means that caracaras can walk, run, and jog on land for extended periods of time (Mosto 2016). Conversely the hip extensor *m. flexor cruris medialis* is present in all species within Falconidae but is twice as big in caracaras (Mosto et al. 2018). Such an increase in size may provide additional muscular propulsion during striding locomotion. *M. fibularis longus* is an ankle joint extensor that is responsible for generating the propulsive force for the bird to lift off the ground and is found in all the species with Falconidae. However, in caracaras the muscle is larger and more developed than in other falcons (Mosto 2016). By possessing different morphological features in their limbs and muscles, these species have adapted to a more terrestrial environment.

### Falconry

Falconry is the hunting of wild animals in their natural state by means of a trained bird of prey controlled by its trainer. Falcons used are the “longwings,” including peregrine falcons, kestrels, gyrfalcons, and Saker falcons (Kenward et al. 2001). While falconry was initially

developed for purposes of subsistence hunting, today other utilitarian uses have taken advantage of the falcons' locomotor abilities, such as recreational hunting and pest control. Peregrine falcons have been used to disperse pest birds that frequently strike aircrafts, which might make for a hazardous flight situation for the aircrafts. They have also been used in dispersing pest birds that feed upon agricultural crops, which limits the produce, and thus economic continuity of farming and agriculture (Erickson et al. 1990).

Falconry is also used as a biodiversity tool to keep birds of prey healthy and improve their survival. Historically, falcons were protected by falconers preserving their nests, but more recently, decline in falcons has been observed, particularly the Saker falcon in Asia and the Peregrine falcons, in part due to pesticides such as Dichlorodiphenyltrichloroethane (DDT), and electrocution by voltage lines. Remnants of DDT accumulates in the food chain, and in addition to health consequences in the raptors, it also deregulates calcium thinning the shells of falcon eggs. As such, eggs are crushed by nesting mothers, leading to an even further decline in surviving numbers. Falconry in this context acts to reintroduce falcons to areas that have suffered severe decline, or even complete extinction, of the falcons. This is achieved by training falcons that are a few months old by experienced falconers, and that ensures that the falcons stay healthy and in good condition. Additionally, their plumage is maintained by falconers, which is vital for the locomotion of the falcon and its hunting success (Kenward 2004; Kenward and Gage 2008).

## Adaptation to Urban Environments

Peregrine falcons have been increasingly settling into urban environments, as these provide an advantage for the raptors both in terms of hunting behavior and food resources. Falcons seem to prey most often on feral pigeons, but other prey species are observed seasonally. Peregrine falcons have been noted to hunt at night near the Empire State Building in Manhattan, New York City. The

falcons are attracted to tall, well-lighted, anthropogenic structures. The platforms allow the falcons to perch at or above the level of migratory birds, especially nocturnal migrants, allowing the falcons to swoop down to hunt. The lights of these buildings act as a disorienting element to the migrants, which generally result in bird-to-skyscraper collisions annually, but for the falcons, it is advantageous, allowing for higher hunting success rates (Gahbauer et al. 2015).

## Conclusion

The order Falconiformes is made up of around 60 species of diurnal birds of prey that are colloquially known as falcons and caracaras. The falcons are fast-flying predators that attack their prey in the air while caracaras are foragers that spend much of their time on land. Falcons have many modes of flight while caracaras fly when necessary and mainly alternate between flapping and gliding modes. This difference in locomotion has led to differences in osteology and myology within the different subfamilies of the order. The peregrine falcon is known for its diving abilities, which is achieved through carefully timed shape changes its wings to achieve maximum speeds. Falconry has been used for millennia to hunt wild animals using a trained bird of prey. More recently, falconry has become largely recreational, but the birds are also used as a biodiversity tool to keep birds of prey healthy and improve their survival. Due to their global distribution, falcons, especially peregrine falcons, are common in urban environments where they have been able to establish high perches and gain easy access to prey in the night.

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Radiation](#)
- [Arboreality](#)
- [Basal Metabolic Rate \(BMR\)](#)

- Captivity
- Carnivore (Diet)
- Common Ancestor
- Dispersal Ability
- Dispersal Patterns
- Diurnality
- Ecology
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- Extinction in Learning
- Falconiformes Cognition
- Falconiformes Sensory Systems
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- Homoplasy
- Locomotion
- Morphology
- Muscular System
- Natural Selection
- Navigation
- Paleontology
- Phylogeny
- Species
- Taxa
- Terrestrial
- Territoriality
- Vertebrate Nervous System
- Zoo
- Zoology

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## Falconiformes Sensory Systems

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### Synonyms

Hearing; Magnetoreception; Mechanosensation; Olfaction; Taste; Vision

### Definition

The order Falconiformes has evolved around 60 million years ago and comprises two families, *Herpetheridae*, the laughing falcon and forest falcons (eight species), as well as *Falconidae*, falcons, pygmy falcon, falconets, and caracaras (66 species; Mindell et al. 2018). Falconiformes occur on all continents except Antarctica, they are carnivorous birds with sharply curved talons and hooked bills and range in size from the sparrow-sized *Microhyrax* falconets to the medium-sized species of the genera *Falco* and *Caracara* (Fuchs et al. 2015).

Sensory systems allow animals to receive information on physical and chemical properties of their environment, including conspecifics, predators and food sources, and retreats. Birds have access to information from the magnetic

sense, vision, olfaction, gustation, hearing, and mechanosensitive cells associated with specialized feathers.

## Introduction

Sensory systems are adapted to the ecology and behavioral needs of animals, specifically their habitats, feeding habits, mate finding strategies, locomotion, diurnal activity range, and predator avoidance strategies. These will be introduced shortly, before turning to the sensory systems and abilities of falconiform raptors. Falconiformes inhabit a wide range of habitats, including tundras, rainforests, and deserts. While species such as the Peregrine falcon (*Falco peregrinus*) are found in many habitat types including cities, others, such as the Mauritius kestrel (*Falco punctatus*), are restricted to islands.

Being raptors, falconiforms feed on birds, reptiles, insects, and small mammals such as bats (see, for instance, Mikula et al. 2013). *Ibycter americanus* is a specialist predator of social wasp nests (McCann et al. 2015), and *Herpetotheres cachinnans* is feeding on snakes (Costa et al. 2014), but most species are more generalists. The genus *Falco* are fast-flying predators, attacking prey in the air, after a high-speed dive from high altitude. The peregrine falcon can reach speeds of up to 320 km/h during such dives, making them the fastest of all animals (Ponitz et al. 2014). Cruising speeds of falcons are slower, between 35 and 45 km/h, in several species of falcons (*F. naumanni*, *F. tinnunculus*, *F. vespertilius*, *F. subbuteo*, *F. eleonora*, *F. peregrinus*; Alerstam et al. 2007). Caracaras are opportunistic foragers that spend a lot of time walking on the ground hunting small animals like insects, but also scavenging on carcass or eating fruits and even garbage (Picasso and Mosto 2018).

Even though Falconiformes generally are diurnal, almost a third of the species can also be active in dim light or at night (see Mitkus et al. 2018 for references). Red-throated caracaras (*Daptrius americanus*) are active before sunrise and after sunset, hunting prey by walking on the ground,

and Pygmy-falcons (*Polihierax* spp.) as well as Forest-falcons (*Micrastur* spp.) hunt in dim light, under the canopy of tropical forests. Other falcons using open landscape regularly hunt on the wing migrant passerines or nocturnal seabirds, insects, or bats at crepuscular times after sunset: Eleonora falcons (*Falco eleonorae*), Sooty falcons (*F. concolor*), four species of hobby (*F. subbuteo*, *F. cuvierii*, *F. severus*, *F. longipennis*), Dickinson kestrel (*F. dickinsoni*), Bat falcon (*F. rufigularis*), Merlin (*Falco columbarius*), Peregrine falcon (*F. peregrinus*), and Lanner falcon (*F. biarmicus*). Common kestrels (*F. tinnunculus*), Lesser kestrels (*F. naumanni*), and Peregrine falcons, living in cities, which are illuminated at night, can increase their foraging time by being active at night (see Mitkus et al. 2018).

Intraspecific communication is poorly studied in Falconiformes. Little is known on acoustic communication in falconiforms, but vocalizations tend to cover a broad frequency range between 0.6 and 10 kHz, with dominant frequencies between 1 and 4 kHz (Jurisevic 1998). Sexual dimorphism, potentially indicating the use of visual signals for intraspecific communication, is only found in few falconiforms including some kestrels (*Falco* spp.; Sarasola et al. 2018). In the Chimango caracara (*Phalcoboenus chimango*), there are no plumage differences, but the adult male has pigments, vascular red coloration with the pumping of blood to the exposed skin bright yellow cere and legs, whereas the female and the juvenile of both sexes present either pinkish or bluish coloration in those areas (Sarasola et al. 2018). Skin flushing also occurs in Southern caracaras (*Caracara plancus*). In many species of falcons and kestrels, the cere of the beak and the feet are colored yellow, orange, or, more rarely, red, as in the Red-footed falcon (*Falco vespertinus*) and Amur falcon (*Falco amurensis*).

Like other birds, falcons and caracaras have well-developed senses of vision and hearing. The general belief that birds have a poor olfactory sense is in the process to be refuted, and little is generally known about mechanical senses allowing flying birds to sense air flow. The following sections will deal with these senses in detail.

## Vision

Falconiformes, as all raptors, are known for their outstanding visual abilities. Their two large lens eyes provide them with close to panoramic vision, leaving a blind sector of only slightly more than 60° behind the head (Potier et al. 2017). Of the two species studied to date, the Saker falcon had a smaller binocular field (max 37° width) than the Southern caracara (*Caracara plancus*; max 47° width).

Visual acuity, or spatial resolution of vision, has been determined in three species using behavioral experiments. The Brown falcon (*Falco berigora*), the largest studied species, was able to resolve gratings with 76 cycles/° visual angle, the smaller American kestrel (*Falco sparverius*) could resolve 40 cycles/° and the Chimango caracara (*Milvago chimango*), on average 30 cycles/° (see Potier et al. 2020b for details and additional references). Anatomical studies confirm a similar value for the Common kestrel. The high spatial resolution of falcons is supported by a high density of retinal neurons, specifically the cone photoreceptors and the retinal ganglion cells, in a small specialized part of the retina, the fovea (Potier et al. 2017). The Southern caracara has only one such specialized region of high resolution in the central retina, the central fovea. All investigated falcons, by contrast, have an additional fovea in the temporal part of the retina, which looks forward and is thought to help the birds in handling prey while the opportunistic caracaras lack the second fovea (Mitkus et al. 2017; Potier et al. 2017; Potier et al. 2020b).

Like the majority of birds, Falconiformes are well adapted to see in color using four spectral types of cone photoreceptors sensitive to violet, blue, green, and red light, with narrow spectral sensitivities (Wu et al. 2016). They also have double cones with a broader sensitivity and rod photoreceptors adapted to see well in dim light, but both these are absent from the fovea, at least in the studied species, the Peregrine falcon (Mitkus et al. 2017).

Being the fastest flyers in the animal kingdom, falcons also have the ability to see fast, they can see the flickering of a light at temporal



frequencies up to 102 Hz (in the Saker falcon) and 129 Hz (Peregrine falcon; Potier et al. 2020a), thus twice as fast as humans. Such fast vision is, however, only possible in very bright light conditions.

All the mentioned adaptations allow falcons to successfully aim for flying prey. Both the acuity and speed of vision, however, are clearly diminished in dim light (Reymond 1987; Potier et al. 2020a), again, making falconiforms best adapted to hunt during the day. However, their vision in crepuscular conditions or in a nightly illuminated city seems good enough to occasionally catch prey (see above).

## Hearing

Birds mainly use acoustic information for communication and prey and predator detection. Sounds of low frequency can propagate over long distances while high frequencies can be used for more private communication. The outer ear of birds is a tube positioned just behind and below the eye, thus making directional hearing important. Many birds thus have highly directional tympana, due to their interaural canal. Sound frequency and location of a sound source are coded in the avian auditory midbrain nucleus (nMLD). In the Brown falcon (*Falco berigora*), omnidirectional cells and hemifield cells were found (Calford et al. 1985). Unlike the barn owl, where such units have circumscribed receptive fields, falcon cells sensitive to specific stimulus locations had large receptive fields, which were restricted in azimuth but not in elevation (hemifield units). These cells could not provide an acoustic space map representing azimuth and elevation, but cells with contralateral borders found more superficially in the tissue and those with ipsilateral borders were situated deeper in the nucleus. Units in the central region of nMLD were sharply tuned to stimulus frequency, arranged in tonotopic sequences, and were omnidirectional, whereas units in the lateral region of nMLD were less frequency specific and had hemifield receptive fields in the contralateral sound field (Calford et al. 1985).

All units were most sensitive to frequencies of less than 5 kHz, and no units responded to tones above 6 kHz. The spatial properties of cells in the raptor nMLD are probably primarily determined by the directional properties imparted upon the auditory system by the interaural canal.

## Chemical Senses: Olfaction and Taste

The sense of smell – allowing for detection of chemicals from the distance – has long been neglected by researchers studying sensory biology of birds. Birds lack the vomeronasal organ known from many other vertebrates, but the olfactory system of many species is well developed, and the number of functional olfactory receptor genes generally quite high (Steiger et al. 2008).

Little is known about olfaction in Falconiformes specifically. The nostrils, positioned above the bill, are always open, and inhaled air passes through three chambers or conchae (Roper 1999). The first concha filters out small particles and warms the air, the second concha also filters the air, but the third concha is lined with olfactory epithelium, from which the olfactory receptor cells send their axons directly to the olfactory bulb. Only 63 olfactory receptor genes have been found in the Peregrine falcon and the Saker falcon, and less than half of these genes were considered to be functional (Zhan et al. 2013). This is fewer than in other birds, which can have between around 100 (in the galah, *Eolophus roseicapilla*) and more than 600 (kakapo, *Strigops Habroptila*) olfactory receptor genes (Steiger et al. 2008).

Maybe more importantly, in behavioral tests, Potier et al. (2016) have shown that, in the absence of other cues, the Southern caracara *Caracara plancus* can find food using smell exclusively. Compared to visual cues, olfactory cues did not seem to be prevalent. There is also some evidence that the foul-smelling secretion of the Great spotted cuckoo, *Clamator glandarius*, may act as an olfactory repellent for different species of falcons. Falcons refused to eat chicken meat after it was sprayed with a synthetic mixture of juvenile cuckoo secretions (Röder et al. 2014). Almost no information on chemical

communication or the use of olfactory cues for navigation in raptors is available.

The sense of taste – allowing for the detection and discrimination of chemical and nutrients in food – is even less studied in falconiform birds. The taste buds of birds are distributed in the oral cavity, more frequent on the palate, the lower mandible, and the pharyngeal floor than the tongue. They are not associated with papillae and are connected with the surface by a taste canal (Erdoğan and Iwasaki 2014; Rowland et al. 2015). Genomic studies on the peregrine falcon have revealed that falconiforms, like other birds, have lost one of the three G-protein coupled taste receptors that mediate the perception of umami and sweet resulting in a loss to sense sugars (Baldwin et al. 2014). They have two functional genes for bitter receptors, compared to three in the common ancestor of birds (Wang and Zhao 2015). Sour and salt receptors are presumed to be ion channels rather than G-protein-coupled receptors, and present in all birds including falconiforms.

### Somatic and Magnetic Senses

Like other birds, falcons have additional senses, but these are barely studied (Martin 2017). The somatosensory system includes receptors distributed over the body to allow the birds to detect, thermal, noxious, and mechanic stimuli such as vibration, pressure, or air flow (Gottschaldt 1985). Two types of somatosensory receptors are found in the dermis: Herbst (lamellar) corpuscles sensitive to vibration and Grandry corpuscles that respond to rapidly acting movement (Gottschaldt 1985). They are important for behavioral control for flight, feeding, and other tasks but have not been studied in Falconiformes specifically. Of specific interest are rictal bristles that, similar to the whiskers of mammals, may have various functions including protection of the eyes from airborne particles, preventing the soiling of facial feathers during feeding or aiding in navigation (Delauney et al. 2020).

While it has been proven for a number of bird groups including passerines and pigeons, the ability to sense the magnetic field of the earth has not been studied in falcons. It is thus possible but not

sure that falcons can use this modality to navigate in their surroundings. The anatomical and histological basis of the magnetic sense has not been understood for birds yet even though hypotheses exist (Wiltshko and Wiltshko 2019).

### Conclusions

Falconiformes comprise falcons, the fastest-flying animals on the globe, which have excellent visual abilities with high spatial and temporal resolution. Other falconiforms, such as caracaras, predominantly move more slowly, but share many sensory traits. While falconiform vision has been studied to some degree, other sensory modalities are still barely understood in these fascinating birds.

### Cross-References

- ▶ [Accipiters](#)
- ▶ [Auditory Processing and Perception](#)
- ▶ [Carnivore \(Diet\)](#)
- ▶ [Diurnality](#)
- ▶ [Ecology](#)
- ▶ [Falconiformes Cognition](#)
- ▶ [Falconiformes Cognition](#)
- ▶ [Falconiformes Locomotion](#)
- ▶ [Falconiformes Sensory Systems](#)
- ▶ [Navigation](#)
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- ▶ [Optic Flow](#)
- ▶ [Predator](#)
- ▶ [Vertebrate Nervous System](#)
- ▶ [Visual Search](#)

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## Fallacy of Origins

### ► Genetic Fallacy

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## Fallacy of Virtue

### ► Genetic Fallacy

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## False Perception

### ► Appearance Reality Tests

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## Familiarity

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## Synonyms

Feeling of knowing

## Definition

The feeling that an item has been recently experienced without clear recollection of other contextual information about the experience.

## Introduction

In everyday life, the word familiarity gets used in many ways. For instance, one might discuss their familiarity with animal cognition, their friend Susan, or the name Navalny. One is referring to knowledge about a topic, the second their relationship with an individual, and the last their sense

of a previous encounter. These are very different cognitive experiences with the only overlap being an involvement of previous experience. Unfortunately, the use of the term familiarity in animal cognition is similarly broad. It is used to discuss the effects of previous experience on perception (e.g., Talbot et al. 2015), social behaviors (e.g., Wickberg et al. 2014), categorization (e.g., Stephen et al. 2013), and memory judgments (e.g., Basile and Hampton 2013).

Unlike everyday life, in cognitive memory research, the term familiarity has a specific definition. Familiarity is the “feeling” that an item has been recently experienced without clear recollection of other contextual information about the experience. It is a noncontextualized “sense” of memory. Familiarity is contrasted with recollection, the specific memory of an item tied to other information about the context. In this case, the memory not only includes the item but also associated information such as time or place. Familiarity can also be contrasted with fluency. Fluency is the ease of processing an item, and fluency is often increased by recent experience. Some theories assume that fluency is the primary cue underlying feelings of familiarity. However, even when this relationship is assumed, the definitions of fluency and familiarity are not interchangeable, and there is clear evidence that perceptual fluency can happen without an accompanying sense of familiarity (for review see, Yonelinas 2002).

## Theories of Familiarity

There are two primary classes of theories to explain the experiences of familiarity and recollection. The first class assumes that feelings of familiarity and recollection are tapping different cognitive processes requiring different areas of the brain that can be dissociated and understood independently. There are a number of different dual process theories that vary substantially in their assumptions about the underlying mechanisms of familiarity. However, they all assume that familiarity is qualitatively distinct from recollection. They also assume that familiarity is a

faster and more automatic process relying on different parts of the medial temporal lobes than recollection. The most common neurophysiological assumption is that hippocampal involvement is necessary for recollection, while parahippocampal cortex mediates feelings of familiarity (for review, see Yonelinas 2002).

The other class of theories assumes that differences in familiarity and recollection are explained by differences along a continuum such as memory strength. These single process theories also tend to assume differential involvement of the parahippocampal cortex and the hippocampus in judgments of familiarity and recollection, but they assume these differences reflect the requirement for hippocampal input for “stronger” memories (for review, see Yonelinas 2002). Because the differences in the theories’ predictions about brain-area involvement are subtle, the search for appropriate animal models of familiarity and recollection has been considered vital to distinguishing between them.

### Tasks Used to Examine Familiarity in Nonhuman Animals

In animal cognition, the delayed match to sample (DMS) and delayed non-match to sample (DNMS) are generally used to assess memory. Though specific methodologies can vary across species, the basic idea behind DMS and DNMS is that if an animal behaves differently toward items based on previous experience, then they are expressing memory. These tasks are akin to recognition memory tasks in humans because the items are present. Comparative researchers have usually assumed that performance on these tasks reflects the animal’s sense of familiarity with the items, and they have been used to try to determine the role of different parts of the medial temporal lobes in familiarity (e.g., Hölscher et al. 2003). However, in human research, recognition memory clearly involves both familiarity and recollection (for review, see Yonelinas 2002). Therefore, this assumption about nonhumans may not be correct. In human research, task-dissociation procedures and process estimation techniques have been used

to try to determine the relative contributions of familiarity and recollection to recognition memory. Some of these techniques have been applied in comparative studies as well.

*Task-Dissociation Procedures with Nonhuman Animals.* In the human literature, there is an assumption that recall performance always reflects recollection. However, successful recognition could reflect a sense of familiarity or a recollective experience. Therefore, many researchers have used the subtraction of recalled items from recognized items as a measure of pure familiarity.

Recall tasks are relatively rare in the animal cognition literature because designing tasks that allow animals to behaviorally show memory for items that are not present is difficult. However, to dissociate recall and recognition, researchers developed a paradigm where rats (*Rattus norvegicus*) learned to associate two objects with particular locations in a maze in different contexts (e.g., Eacott and Easton 2007). They were then habituated to one object and released into the context-dependent maze. The object location they went to first and the time spent exploring each object was measured. They hypothesized that if the rat recalled the objects associated with the context-dependent locations, they would go to the non-habituated object first, and if they recognized the habituated object, they would spend less time exploring it. With these measures of recall and recognition, the authors explored the involvement of different areas of the medial temporal lobes in the different measures.

Another task-dissociation method relies on the assumption that recollection is necessary in associative recognition memory tests. In contrast, familiarity, because it reflects memory for items untethered from context, is less useful in these tests. Thus, tests of associative recognition have been used as an index of pure recollection. As with comparisons of recall and recognition tasks, a subtraction of associative recognition from item recognition is used to measure familiarity. An advantage of the item/associative method over the recall/recognition method is that the test cues and required responses are more similar to each other (for review, see Yonelinas 2002).



Cross et al. (2013) used this item/associative recognition task dissociation to determine the role of different brain regions in recollection and familiarity. They measured the rat's ability to perform multiple tasks. One was a DNMS task testing recognition for experienced objects. One was a DMS task where the rat chose previously experienced locations. In a third task, they tested whether rats could distinguish objects that retained their place in an array compared to those that had switched, testing recognition for item-place associations. They found different regions involved in the association task compared to the object or location tasks.

Because familiarity is assumed to be faster than recollection, response speed should be useful for separating the contribution of familiarity and recollection. Faster responses should reflect familiarity and slower responses recollection. Basile and Hampton (2013) tested this speed assumption with rhesus macaques (*Macaca mulatta*) by examining the types of errors made at different latencies. They split the monkeys' responses into three latency categories (fast, medium, slow) and examined the errors. At fast latencies, most of the errors were false alarms to familiar lures, but at medium latencies these errors were greatly reduced. The authors concluded that this pattern reflected familiarity-mediated fast responses and recollection-mediated medium responses. At long latencies, monkeys performed at chance.

*Process Estimation Procedures.* Each of the task-dissociation methods makes assumptions about the nature of familiarity and recollection, and their general limitation is their imprecise estimates of familiarity and/or recollection. Though subtraction or time cutoff methods may give an approximation of how many items are familiar, there is always likely to be some items that are incorrectly categorized. To develop more precise measures, process estimation techniques were designed to mathematically distinguish familiarity from recollection.

Process estimation procedures arose in research with humans where complex verbal instructions and verbal reports are ubiquitous. Because of this, the most common procedures like remember/know judgments (after

recognition, the participant classifies the item as something they remember from the learning context or they just know) and process dissociation procedures (compares item recognition to the ability to exclude items on the basis of a contextual cue) are simply not possible with nonhuman animals.

However, there is one process estimation technique that has been adapted with nonhuman animals. Receiver operating characteristic (ROC) analyses assume that measuring the effect of varying response criterion on hits and false alarms can allow estimations of familiarity and recollection's contribution to memory. In human research, varying response criterion is usually measured by confidence ratings. This method is difficult with nonhumans. However, ROC analyses can also be used when response criteria (willingness to call something old) are manipulated by instructions or payoff ratios (for review, see Yonelinas 2002).

Fortin et al. (2004) examined ROC curves for rats' odor memory manipulating difficulty and payoff ratio to produce varying response criteria. They found that rats showed the classic ROC curved pattern assumed to measure separate contributions of familiarity and recollection. They also found that rats with ablated hippocampi did not show these bi-process curves.

Wu et al. (2020) combined the speeded response method used by Basile and Hampton (2013) and ROC analyses to compare human and macaque familiarity and recollection measures in the speeded response paradigm. They found that both species had the same fast and slow error patterns, and both showed ROCs consistent with familiarity-driven fast responses and recollection-driven slower responses. They concluded that the simpler speeded response methodology was adequate for separating the contributions of recollection and familiarity in nonhumans.

## Conclusions

In human research, the term familiarity has a precise definition based on the "sense" of previous experience that is not concretely tied to context.

Without language to self-report this “feeling,” it can be difficult for animal cognition researchers to disentangle familiarity from recollection or fluency. However, this ability is vital both for understanding similarities and differences between human and nonhuman memory and for adequate animal models of the role of different brain regions.

Creative research using task-dissociation methods and ROC curve process estimates with rats and monkeys (e.g., Basile and Hampton 2013; Cross et al. 2013; Eacott and Easton 2007; Fortin et al. 2004; Wu et al. 2020) have helped to bridge this divide. These methods have substantially contributed to understanding mammalian familiarity processes and their neural underpinnings. Hopefully, future research will extend these methodologies to other vertebrates to explore the evolutionary trajectory of memory processes.

## Cross-References

- [Animal Models](#)
- [Categorization](#)
- [Cognition](#)
- [Comparative Cognition](#)
- [Declarative Memory](#)
- [Delayed Match-to-Sample](#)
- [Entorhinal Cortex](#)
- [Episodic Memory](#)
- [Hippocampus](#)
- [Long-Term Memory](#)
- [Priming](#)
- [Reaction Time](#)
- [Recall](#)

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## Family Resemblance

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## Introduction

Categorization is a crucial skill that allows animals to manage their environment. Inaccurate categorization would be detrimental to the life of the animal. A vervet monkey must decide to alert their troop of an approaching bird. Is this a safe bird?

A categorization error would result in a poor outcome for the vervets. The decision must be made quickly, and there is little room for error. Unfortunately for the vervet, different species of predator birds, for instance, eagles and hawks, do not look exactly alike. Even eagles of the same species will not be identical to each other, though they share definite similarities. Many of the world's natural categories (like predatory birds) follow a family resemblance category structure (e.g., Rosch & Mervis, 1975). Family resemblance category members share an overall similarity, but no criterial attributes define all members of the category. In other words, members of the category tend to share several features with other members of the category, but there is not necessarily a single feature common to all category members. Therefore, when trying to classify these family resemblance categories, it would make sense for the vervet to make its decision by comparing the bird's overall similarity to either their representation of a typical predatory bird or the other examples of predators that they have experienced.

## Prototype Versus Exemplar Strategies of Classification

The two primary theories of how animals are able to classify family resemblance categories are the prototype and exemplar comparison theories. Prototype comparison theory hypothesizes that we average our experiences with category members (exemplars) into a single schema or prototype. We can then make categorization judgments by comparing the similarity of a new object to the prototype. In prototype comparison theory, the prototype is centrally located in a cloud of similarity, and members of varying similarity lie around the prototype. Those members most similar to the prototype will lie more closely to it in psychological space. However, the exemplars do not fall in a straight line leading away from the prototype, because the exemplars themselves can vary in similarity to each other. Instead, the exemplars form a cloud of similarity around the prototype (Smith, 2002). Figure 1 shows the prototype (P) in the center of this cloud, as it is the most representative of the category. Exemplars (E) can

### Family Resemblance,

**Fig. 1** Example of  
Prototype and Exemplars in  
Psychological Space.

(Note. A schematic drawing of hypothetical to-be-classified items (8 to 1) that are made to approach the psychological space of a category system containing a central prototype (P) and a shell of training exemplars (E). Reprinted from "Exemplar theory's predicted typicality gradient can be tested and disconfirmed" by J. D. Smith, (2002), *Psychological Science*, 13, p. 439. Copyright 2002 by the Association for Psychological Science. Reprinted with permission)

### Approaching A Category System



then fall at varying distances on any side of the prototype. Two exemplars may be equally similar to the prototype, but they are perceptually very different from one another as the psychological space can have many dimensions, leaving them to fall equal distances away from the prototype but far from each other.

On the other hand, exemplar theory suggests people categorize a novel object by comparing similarity to the memory representations of *all* previous exemplars from each relevant category and then summing that similarity to decide membership (e.g., Nosofsky, 1987). Therefore, no single member is more representative of the category than the next.

Examining Family Resemblance Category Learning

Family resemblance category learning is often tested by using polymorphous categories or prototype distortion tasks. In polymorphous categories, several stimulus features are partially informative about category membership, but no single feature is present in all members (Couchman et al., 2010). Table 1 presents an example of two, binary-feature polymorphous categories, with the first line representing the best example of the category, the prototype, and the following five lines representing potential exemplars of that category. Each dimension corresponds to types of features with 0 and

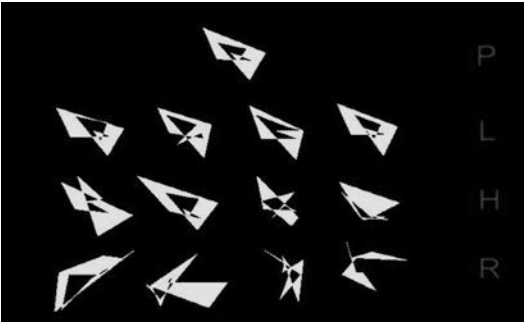
1 corresponding to the value on these dimensions. D<sub>1</sub> could represent shape, in which 0 might correspond to circle and 1 to square. D<sub>2</sub> could represent color, in which 0 corresponds to blue and 1 corresponds to yellow. Looking at within-category similarity of the family resemblance categories, all category members share three features with each other and four features with the prototype. Looking at between-category similarity, members from different categories do not share more than one feature with the opposing category’s prototype.

Prototype distortion tasks create exemplars along a distortion continuum by *randomly* distorting the category prototype to controlled degrees instead of exchanging different specific features (Posner & Keele, 1968). As with polymorphous categories, no single feature is fully informative of category membership, but rather overall similarity decides category membership. The most common example consists of dot patterns, often connected by lines to create polygon shapes (see Fig. 2). Category members are created from an initial prototype dot pattern that can then be distorted spatially to have varying degrees of similarity. Often the category members are then

Family Resemblance, Table 1 Example of polymorphous categories

| Category A                                                  | Category B                                                  |
|-------------------------------------------------------------|-------------------------------------------------------------|
| D <sub>1</sub> D <sub>2</sub> D <sub>3</sub> D <sub>4</sub> | D <sub>1</sub> D <sub>2</sub> D <sub>3</sub> D <sub>4</sub> |
| 0 0 0 0 0                                                   | 1 1 1 1 1                                                   |
| 1 0 0 0 0                                                   | 0 1 1 1 1                                                   |
| 0 1 0 0 0                                                   | 1 0 1 1 1                                                   |
| 0 0 1 0 0                                                   | 1 1 0 1 1                                                   |
| 0 0 0 1 0                                                   | 1 1 1 0 1                                                   |
| 0 0 0 0 1                                                   | 1 1 1 1 0                                                   |

Note. The first row under Categories A and B represents the prototypes; the five following rows represent category members. Each D<sub>#</sub> column represents a different dimension



Family Resemblance, Fig. 2 A Dot-Distortion Category. (Note. Illustration of the idea of a family-resemblance category, with a typicality gradient running from the central prototype outward. The originating prototype (P), low-level distortions (L), high-level distortions (H), and random-unrelated shapes (R) in the top to bottom rows, respectively. Adapted from “Prototype Abstraction by Monkeys (*Macaca mulatta*),” by J. D. Smith, J. S. Redford, and S. M. Haas, 2008, *Journal of Experimental Psychology: General*, 137, p. 391. Copyright 2008 by the American Psychological Association. Reprinted with permission)

mixed with random shapes, and the participant must decide if the shape belongs to the category or not. Figure 2 presents a prototype, low-level distortions, high-level distortions, and random shapes.

Prototype and exemplar comparison theories each have their own predictions for how participants will perform in this task. These predictions can be tested using formal modeling (Fig. 3). Prototype comparison emphasizes a strong resonance to the prototype, so it will be endorsed into the category at maximally high levels (Smith, 2002). Exemplar theory does not predict this, because the prototype is being compared to a bunch of exemplars that may be far away from it in psychological space.

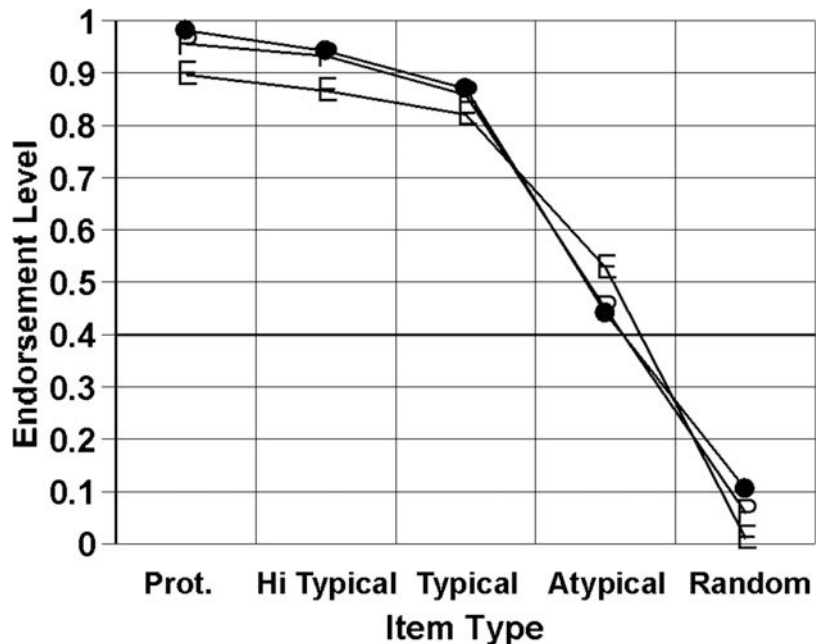
### Evidence for Prototype Comparison in Family Resemblance Category Learning

Prototype and exemplar comparison in family resemblance category learning have been studied in several animal species. The majority of research has been with rhesus macaques and humans. Studies with rhesus macaques (*Macaca mulatta*) have consistently shown that they have

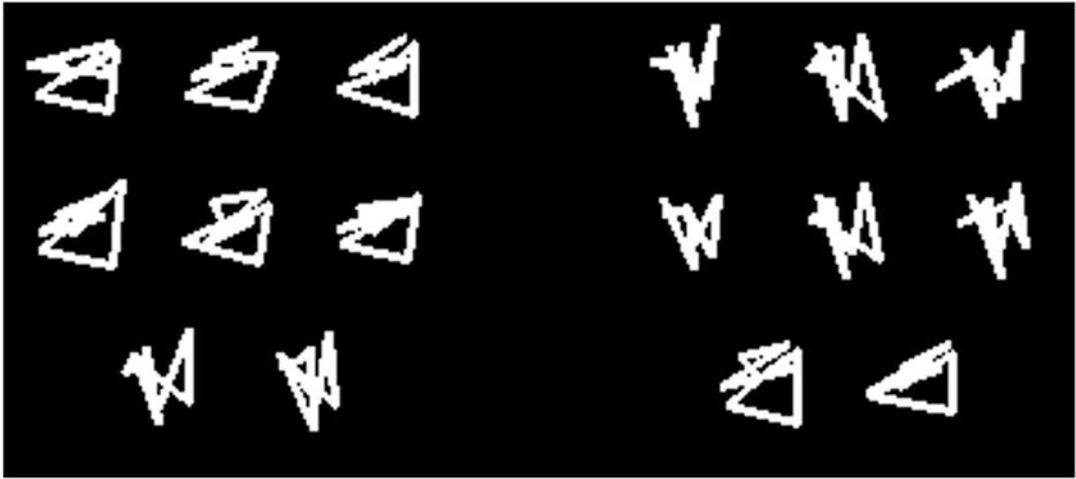
strong preferences for prototype comparison. For example, in a prototype distortion task, the macaques had nearly perfect performance with the prototype, and when the data were fit using a standard prototype and exemplar model (P, E symbols in Fig. 3), the exemplar model was a poor predictor of performance (Smith et al., 2008). However, the prototype model (P symbols) fit so well that it became nearly impossible to see the symbols in the figure because they overlapped so closely the macaques' endorsements (circle symbols).

In another study, Smith et al. (2010) tested macaques in a prototype-exception task to see whether they would continue to assume a family resemblance category structure even when feedback directly signaled otherwise. If the macaques learned categories by abstracting and comparing to a prototype, they would be unable to learn exceptional category members. The researchers created eight low-level distortions from two prototypes. Six of these distortions were then kept together to constitute a prototype-based family of exemplars, and then two of the distortions produced from each prototype were crisscrossed into the opposing category. This produced two, eight-exemplar categories containing six typical

**Family Resemblance,**  
**Fig. 3** *The Proportion of Times a Macaque Endorsed Items as a Category Member. (Note. Exemplar and prototype models fit represented by the E and P symbols, respectively. Adapted with permission from "Prototype Abstraction by Monkeys (*Macaca mulatta*)," by J. D. Smith, J. S. Redford, and S. M. Haas, 2008, *Journal of Experimental Psychology: General*, 137, p. 395. Copyright 2008 by the American Psychological Association. Reprinted with permission)*







F

**Family Resemblance, Fig. 4** *Examples of Two Categories from a Prototype-Exception Task by Smith et al. (2010). (Note. The 8-shape groupings are two categories, A and B. The 6 shapes in the top rows of each category are variations on the theme of the category prototype. The bottom row contains exception items that are variations on the theme of the opposing prototype. Adapted from*

*“Stages of Category Learning in Monkeys (*Macaca mulatta*) and Humans (*Homo sapiens*),” by J. D. Smith, W. P. Chapman, and J. S. Redford, 2010, *Journal of Experimental Psychology: Animal Behavior Processes*, 36, p. 43. Copyright 2010 by the American Psychological Association. Reprinted with permission)*

exemplars and two exceptions that could have been a typical exemplar of the other category (Fig. 4). If macaques assume family resemblance categories, then they should respond B to the exceptions on the left and A to the exceptions on the right. The macaques performed below chance with the exception items for thousands of trials. The macaques showed minimal capacity to memorize and respond appropriately to exception items even when there were only four items to memorize. However, after thousands of trials, two of the three macaques were partially able to learn the exceptions. The rhesus macaques clearly defaulted to a family resemblance assumption, and they found it difficult to learn items inconsistent with this assumption. They kept this approach, in direct opposition to the feedback, for thousands of trials.

One study with baboons (*Papio papio*) has examined their family resemblance category learning. The baboons were tested to see if they would discriminate prototypes of polymorphous categories more accurately than less typical exemplars (Dépy et al., 1997). Their performance with the prototypes was significantly greater than with novel non-prototype stimuli.

Research with pigeons (*Columba livia*) has shown similar results. Cook and Smith (2006) examined family resemblance category learning in pigeons also using a prototype-exception task. Results showed that pigeons had difficulty learning to correctly categorize the exception items, just as the macaques did. Formal modeling confirmed that pigeons' data were fit poorly by an exemplar model. Similarly to the macaques, the pigeons made a transition to exemplar memorization late in learning. Eventually, exception performance improved, and the exemplar model fit well. This transition suggests some residual capacity to finally learn/memorize exceptional items. Research using polymorphous categories has also supported the idea that pigeons use prototype comparison to learn family resemblance categories (Jitsumori, 1996).

While prototype comparison has not been directly studied in rats, Vermaercke et al. (2014) incidentally found evidence of rats using a prototype comparison strategy in a visual water-maze task using rule-based and information-integration categories. The performance of rats was consistent with a nondimensional, similarity-based categorization strategy. They found that the more

distant from the trained prototype, the worse the performance, supporting a family resemblance category structure assumption and a prototype comparison strategy.

## Conclusion

The research suggests that animals may default to a prototype comparison strategy rather than an exemplar comparison strategy for categorizing new objects. This indicates that animals assume categories are based on overall similarity or a family resemblance structure. From an evolutionary standpoint, prototype comparison may be the most efficient strategy, as one only needs to store a single memory representation as opposed to many, and it could allow for faster comparison as there is only one comparison to be made. Because family resemblance categories are common in nature (Rosch & Mervis, 1975), it makes sense that cognitive evolution might naturally move animals toward a strategy that allows them to easily and quickly learn these family resemblance category structures.

## Cross-References

- [Categorization](#)
- [Cognition](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Exemplar Theory](#)
- [Primate Cognition](#)

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## Farrowing Crate

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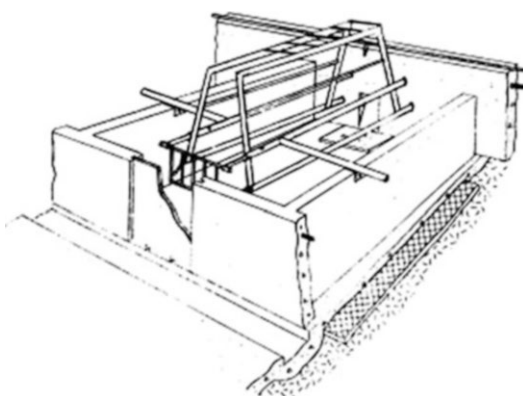
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Farrowing crates are metal stalls in which sows are typically housed from a few days before parturition until weaning (21–28 days). In the 1960s,

when intensive farming was considered as the way to improve pork production, farrowing crates were developed (Robertson et al. 1966). This was also in response to genetic improvements in pig production leading to sows being larger in size, producing more piglets per litter, and increasing the risk of piglets being crushed. Farmers and researchers reported a reduction in crushing of the piglets by the sow following adoption of farrowing crates when compared to farrowing pens (Blackshaw et al. 1994). Apart from increasing productivity, farrowing crates also helped management of the sow and her litter during routine husbandry activities such as castration of piglets and giving iron injections to piglets enabling them to be performed in a safe manner. Farrowing crates confine the sow to one place, and thus her dung is deposited in one area, at the back of the crate. This helps to keep the pen clean and increases pen hygiene for the piglets.

A standard farrowing crate provides a space allowance of around  $2.2 \text{ m} \times 0.60 \text{ m}$  (7.2 ft by 2 ft) for the sow. However, there are small size variations between manufacturers. Initial designs were made with minimal space allowance for sow along with additional pen space to contain the litter of piglets (Fig. 1). As Fig. 1 illustrates, farrowing crate “footprint” includes the pen space available for the piglets, apart from the metal crate for the sow. Therefore, the total space allowance is around  $2.3 \text{ m} \times 1.8 \text{ m}$ . Modern crate designs offer the ability to increase the width of the crate, to accommodate large sows, and facilitate lying postures (Fig. 2). Standard farrowing crates do not allow sows to turn around and limit the sow’s interaction with her piglets (Harris and Gonyou 1998). This restriction of movement at a time when sows are highly motivated to perform nesting behavior (Jensen et al. 1993) has been an ethical debate for some time now. Sniffing and nose-to-nose contact between sow and piglets are common in unrestrained conditions (Watson and Bertram 1983). Standard farrowing crates prevent turning, inspection, and reduce sow-initiated nose-to-nose contact (Blackshaw and Hagelsø 1990).

Whilst the advantages of farrowing crates were based on financial benefits and ease of animal management, the disadvantages surrounds welfare



**Farrowing Crate, Fig. 1** Farrowing crate design developed by Canada Plan Service, Saskatchewan, Ministry of Agriculture Draftsman: Don Sproule in 1976



**Farrowing Crate, Fig. 2** A well-designed farrowing crate which can be adjusted to increase the space allowance for the sow by widening one side of the wall of the crate (photo credit: Karunasena Bandarlage, Prairie Swine Centre)

concern for the sow. In many countries with a developed economy, there is an increasing consumer pressure for the farming sector to adopt methods that do not involve animal confinement systems. Consequently, in the pig farming sector, there is ongoing discussion surrounding farrowing crate use and the behavioral restrictions they bring. Identifying whether viable alternatives can be found that improve sow welfare, yet continue to protect piglet welfare and farmer safety is a goal. As new housing provisions are developed to better accommodate the natural behavior of the sow, any such system also needs to protect the piglets from being crushed (Baxter et al. 2011). Any farrowing

housing system adopted without careful consideration for piglet mortality will have obvious negative welfare consequence for the piglets (Baxter et al. 2012) and will likely also not be economically viable in the long run as a result.

Currently there are efforts to improve the design of the farrowing crate. In many European countries there is increased interest in free farrowing pens (the sow is loose during farrowing and lactation). Some of the different types developed in Europe are PigSAFE (Piglet and Sow Alternative Farrowing Environment), the Danish designed Free Farrower, FAT systems, comfort pen designed by Norwegian University of Life Sciences and WelCon (Welfare for animals and convenience for farmers) designed by Institute of organic farming and farm animal biodiversity, Austria. ([www.freefarrowing.org](http://www.freefarrowing.org)) In North America, some certification programs such “Certified Humane” are promoting the discontinuation of farrowing crates ([www.certifiedhumane.org/farrowing-systems/](http://www.certifiedhumane.org/farrowing-systems/)).

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## Fascia Dentata Hippocampi

► [Dentate Gyrus](#)

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## Father of Modern Genetics

► [Gregor Mendel](#)

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## Father's Behavior

► [Paternal Behavior](#)

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## Fats

► [Lipid](#)

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## Fear Learning

► [Passive Avoidance Learning](#)

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## Fear Response

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The conditioning of emotional responses has been a major area of focus by Pavlovian conditioning researchers (Fent and Fanslow 1999; Leaf and Muller 1965). Pavlovian conditioning simply refers to a form of associative learning in which

a biologically relevant or unconditioned stimulus (US) is paired with a previously neutral or conditioned stimulus to produce a conditioned response. This area of research preceded studies by Watson and Rayner (1920) who studied infants through the use of Pavlovian or classical conditioning. The researchers conditioned a fear response in a 9-month-old infant named Albert through the use of a white laboratory rat which first served as a neutral stimulus (NS) or unconditioned stimulus. Albert was first exposed to a variety of stimuli, but it appeared that there was hardly anything that he was afraid of. Watson and Rayner found that Albert had a startle response when he heard the noise of the steel bar being hit by a hammer. The loud noise of the hammer was used as an unconditioned stimulus (US), while the white rat, which was first a neutral stimulus, became the conditioned stimulus (CS) after successful conditioning. During the Pavlovian conditioning trials, Albert was exposed to the white rat, followed by the striking of the steel bar. Although Albert reached out to touch the rat at first showing no fear, after about a few conditioning trials, he became reluctant to do so. Eventually Albert displayed a conditioned emotional response of crying, whimpering, and leaning as far away from the rat as he could or even attempting to escape by crawling away.

Watson and Rayner's (1920) work on Pavlovian conditioning with Albert provided a foundation for future studies in this area. Research interest in how fear and anxiety is acquired, what the neural mechanisms of fear are, and how fear is reduced through pharmacological and behavioral treatments have been intriguing topics in this area of research (Charney and Deutch 1996; Craske et al. 2014). However, many of these questions cannot be fully explained through the sole use of human participants. In studies that model fear in animals, the aversive stimulus used is a brief shock (Fendt and Fanselow 1999). The reason that shock is used is because it can be easily regulated and calibrated to cause no harm. It serves as an aversive and unconditioned stimulus because it is both alarming and novel to the animal. While humans such as Albert show fear through crying and whimpering, rats show their fear by freezing.

## Freezing as a Fear Response

Freezing is a species typical defensive response to fear among many species, because lack of motion reduces the probability of being detected by predators (Carlson 2010; Domjan 2010). The magnitude of the conditioned response to freeze has served as a measure of conditioned fear in neurobiological studies of fear (Fendt and Fanselow 1999). Two indirect measures of freezing used by researchers have been conditioned suppression and conditioned emotional response procedures (Leaf and Muller 1965). In the conditioned suppression, the measured behavior is licking a drinking spout that contains water in an experimental chamber. When a fear conditioned stimulus such as a tone is introduced, the animal's licking behavior becomes suppressed (Leaf and Muller 1965; Urcelay and Miller 2008).

On the other hand, the conditioned emotional response is a classically conditioned response that occurs when a neutral stimulus is followed by an aversive stimulus (Annau and Kamin 1961). In the conditioned emotional response procedure, rats learn to press a lever for a reward of food in an experimental chamber. The lever pressing much like the licking behavior in the conditioned suppression task serves as the baseline for the measurement of fear. Fear conditioning, which consists of a tone or a light paired with a brief shock, is introduced only after rats have become accustomed to lever pressing. As they acquire the conditioned fear, the lever pressing becomes suppressed. The conditioned suppression procedure has also been adapted for research with humans, in which the behavioral baseline has been provided through video games (Arcediano et al. 1996; Nelson and Carmen Sanjuan 2006).

## Fight, Flight, or Freezing Response

The fight or flight response, also referred to as the fight, flight, or freezing response, is a physiological reaction to a perceived environmental threat (Leaton 1976; Seyle 1936). This response was coined by Walter Bradford Canon, who explained how animals react to threats through an activation



of their sympathetic nervous systems, which then primes the animal to either fight, escape, or freeze during a potentially harmful event or attack. The sympathetic nervous system helps the body prepare for fight or flight by releasing adrenaline, increasing heart rates and breathing rates, dilating pupils, increasing blood supply to muscles, and enhancing the organism's reflexes. If the perceived threat is intense enough, it can activate a freezing response, which is what happens in conditioned analgesia.

Conditioned analgesia is a way of inducing a fear response such as freezing. Research by MacLennan et al. (2013) found evidence of greater conditioned analgesia in rats as a result of re-exposure to initial shock conditions following test than those who were not re-exposed to the initial shock environment prior to testing. This response is referred to as the first stage of a general adaption syndrome, which is responsible for the regulation of stress responses among human and nonhuman animals (Seyle 1936).

## The Role of the Amygdala

The fight or flight response is initiated in the amygdala, which is an integrative center in the brain for emotional processing (Gazzaniga et al. 2014; Goldstein 2010; Seyle 1936). Emotional responses involve consolidative components of behavioral, autonomic, and hormonal processes, which are controlled by the amygdala. The amygdala is able to detect fear and assist in preparing for emergency events. This brain region can process sensory information and encourage a behavioral response before the information is processed by other areas of the brain. Therefore, the identification of what startled an organism often occurs post the fight or flight reaction. While the amygdala plays a key role in emotional reactions, there are other brain regions that provide pathways to the amygdala. The hippocampus is the area of the brain associated with memory and provides the amygdala with contextual information. Stimuli that have triggered emotional reactions in the past are likely to initiate a heightened sensitivity to the present situation. Emotionally significant stimuli

based on the organism's past experiences are more likely to intensify the fight or flight response.

## Startle Response

The startle response, also known as the startle reflex, is a part of an organism's unconscious response to an abrupt or threatening stimulus such as a sudden noise or sharp movement (Fendt and Fanslow 1999). This response consists of a sudden jump, tensing of upper muscles (e.g., back and neck), and eye blinking; it is evident across species. Much like the fight or flight response, the startle reflex is activated by the sympathetic nervous system. This reaction has been studied mainly due to its pivotal role in fear responses and defensive behaviors. It can be measured by placing an organism on a surface that measures sudden movements (Leaton 1976). Studies on the fear response have helped to bridge gaps in knowledge on the neurobiology of fear and the understanding of which pharmacological treatments are most effective for anxiety as well as trauma and stressor-related disorders (Charney and Deutch 1996; Craske et al. 2014).

## Conclusion

Organisms can display a multitude of reactions to fear, with freezing being one of the most common species typical responses (Fendt and Fanslow 1999; Leaf and Muller 1965; MacLennan et al. 2013; Seyle 1936). Freezing has been studied by researchers through conditioned suppression and conditioned emotional response procedures in which researchers were able to suppress a behavior by inducing fear in the animal. Other responses to fear include the fight or flight response and the startle response. The fight or flight response is a physiological reaction to a perceived or real environmental threat. This response activates systems such as the sympathetic nervous system and is processed through the amygdala or the brain's emotional processing center. On the other hand the startle reflex differs from the other two responses to fear in that it occurs unconsciously

in response to an unexpected or threatening stimulus in the environment. The organism displays a hyperarousal or startle reflex reaction where they jump and tense the muscles at the upper part of the body. Other physiological reactions that occur at this time are pupil dilation and increased heart rate to name a few. Fear reactions among animals can vary depending on how the fear was acquired and whether or not it is expected.

## Cross-References

- [Amygdala](#)
- [Classical Conditioning](#)
- [Operant Conditioning](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Feather Damaging Behavior (FDB)

- [Feather-Plucking](#)

## Feather Picking

- [Feather-Plucking](#)

## Feather-Plucking

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## Synonyms

[Feather damaging behavior \(FDB\)](#); [Feather picking](#); [Pterotillomania](#)

## Definition

A maladaptive, self-mutilating behavior involving excessive plucking, chewing, fraying, and/or biting resulting in feather loss or damage.

## Introduction

Naturally, birds are driven to preen (groom feathers through beak) to remove dust, dirt, and foreign objects and reset feather position. Parrots and exotic birds also have an uropygial gland (a.k.a. “preen gland”) near the base of their tail that secretes oil onto the skin surface to protect feather structure and skin health; preening allows the oil to spread from the tail to the rest of the body (Encyclopaedia Britannica 2017).

Feather damaging behaviors occur in other birds, such as feather pecking in commercial poultry. Feather-plucking occurs mainly in pet African grey parrots (*Psittacus erithacus*); however, it can occur in other captive birds, like ostriches, conures, *Amazona* spp. parrots, cockatoos, and more. It is similar to trichotillomania in humans.

Feather-plucking begins when the bird reaches sexual maturity and is rarely observed in the wild. Prevalence in pet birds ranges from 1.3% to 17.5% depending on if the bird was raised by other birds or hand-raised by humans. Most affected areas are areas easily accessible by the beak, including the chest, rump, and under wing regions. Denuded birds risk infection, hypothermia, or hemorrhage, if the blood feathers are plucked (Grindlinger 1991).

## Feather Pecking

Not to be confused with the self-mutilation behavior in pet birds, commercial poultry exhibit redirected foraging behavior involving pulling or removing conspecific's feathers. Feather pecking is detrimental to birds and economically significant to poultry producers, as it leads to increased mortality if it escalates to cannibalism.

## Behavioral Causes

Inadequate diet, environmental stimuli, and early weaning are thought to attribute to feather-plucking (Costa et al. 2016). Feather-plucking may be a coping strategy for negative affective states like stress or boredom. Unable to properly cope with its environment, the bird

develops the maladaptive behavior of feather-plucking to reduce anxiety, even if the outcome is nonproductive. Birds that feather-pluck often have three times the cortisol levels of non-feather-plucking birds, indicating high levels of stress.

Pet parrots are more frequently hand-reared by the handler or breeder, resulting in birds that imprint on humans and are socially dependent on them. It is not clear whether any one method of hand-rearing results in less negative behaviors; however, all hand-rearing is associated with aggressiveness, feather-plucking, and stereotypies. The age of removal from the nest is inversely correlated with stereotypical behavior.

Feather-plucking is more heritable than in other stereotypies, and birds susceptible to stressful situations (i.e., in view of a constantly opening door) are more likely to develop severe feather-plucking (Garner et al. 2006).

## Treatments

Clomipramine has been shown to improve feather-plucking behaviors in placebo-controlled double-blinded studies (Seibert et al. 2004). This treatment is not completely effective, and severely affected birds often will not respond to treatment.

Mechanical prevention (i.e., collars, physical restraint devices) is not recommended as a lone treatment, as it is considered inhumane. Punishment for the behavior often leads to increased or exaggerated behavior caused by stress and fear of being punished (Jenkins 2001).

Early treatment and prevention remains the best method. Providing sufficient environmental enrichment and introducing novel enrichment to the cage environment can increase meaningful activity and allow the bird to perform normal activities such as chewing, foraging, nesting, and socializing.

## Cross-References

► [Self-Mutilation](#)

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## Feature Integration Theory

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## Synonyms

Pop-out; Saliency; Vision; Visual attention; Visual search

## Definition

Feature integration theory models how attention is guided, for example, when the visual field needs

to be searched for a particular target. At its foundation, feature integration theory first employs separate but parallel, preattentive, and unconscious registration of basic visual features, and later on their integration to conscious controlled perception based on a master map of retinal locations. Attention can be guided (to facilitate object detection, for example) during either phase depending on the visual properties of the target compared to other items in the stimulus, a process that allows either fast pop-out of the target or its detection via a slower serial attentional deployment process. Conceived originally for human vision, there are many ecological reasons, and now ample evidence, to support the argument that feature integration theory is universal and relevant to many animal species too.

## Introduction

Visual attention is one of our fundamental behavioral features. As seeing creatures, humans continuously scan the visual world around us and focus our visual attention on important visual objects. From searching for our friends in a crowd to looking for a car key in a drawer, from seeking a ripe fruit on a tree to looking for a foe in a computer game, such visual search tasks often (but not always) require much visual attention. But clearly, this visual behavior cannot be unique just to humans, as most nonhuman species could benefit tremendously from guided attention for survival, including mating, hunting, navigation, and predator avoidance. How visual attention is guided also in nonhumans species is thus crucially important and can inform us a great deal about universal behavioral principles and information-processing strategies across the animal kingdom.

## Feature Integration Theory in Humans

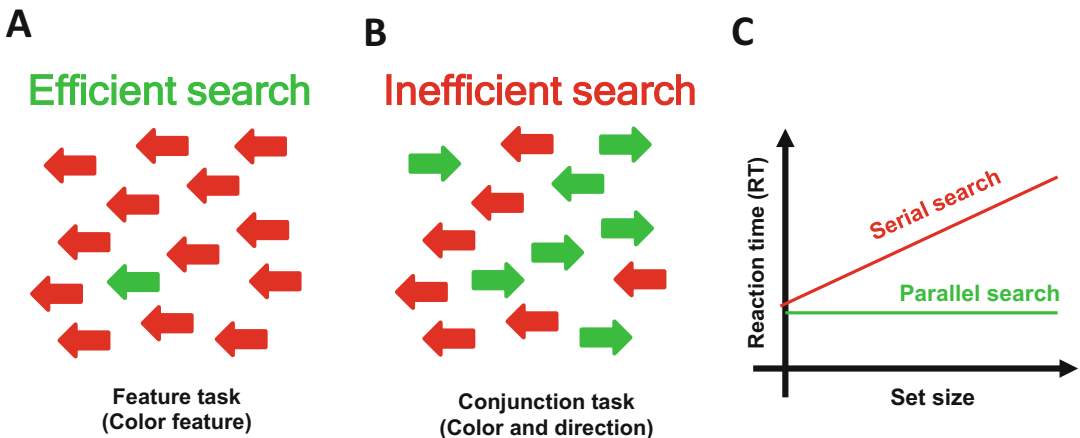
Introduced by Treisman and Gelade in the early 1980s (Treisman and Gelade 1980), Feature Integration Theory is one of the most influential theories that accounts guided attention. According to this theory, visual stimuli are processed in two

consecutive stages. First, the visual system processes the visual stimulus to yield separate spatial maps of the distribution of basic visual features (such as color, orientation, motion, etc.). This first stage is called *preattentive* since it is performed before attention is deployed and before the organism becomes conscious of what it is looking at. The second stage is termed the *attentive* stage where the organism focuses its attention on a certain object or location in the visual field. This occurs within a master map of stimulus locations where features have been represented after processing of the individual maps from the first phase. After attention selects a certain location to focus on, the individual features at that location are integrated to facilitate the conscious perception of the relevant visual information.

Testing Feature Integration Theory and its applicability is typically done using controlled visual search experiments. In a typical experiment, subjects are asked to detect the presence or absence of a target in a display as quickly and as accurately as they can, where the target is characterized by a certain combination of features that distinguish it from other nontarget distracting items around it. Using this methodology, and

under the classic framework of Feature Integration Theory, Treisman and her associates characterized two distinct visual search modes, which they dubbed *parallel* and *serial* (Treisman and Gormican 1988; Treisman and Gelade 1980).

The parallel search mode occurs in the preattentive stage where certain visual features are processed immediately throughout the entire visual field and in a massively parallel fashion. If any of these features uniquely characterizes the target, the latter pops out to complete the search. This automatic process is reflected in a reaction time that is relatively unaffected by the number of items (a.k.a. the set size) such that the slope of its reaction time graph as a function of the number of distractors is around zero (Treisman and Gelade 1980; Wolfe 1998). This is illustrated in Fig. 1a where the green item pops out from the group of red distractors due to the difference in their color/luminance feature. While the green arrow would continue to pop out regardless of the number of red distractors, a target defined by a unique conjunction of features would not pop out similarly, forcing the observer to scan the displayed visual items one by one until it is found, as shown in Fig. 1b. Naturally, in such a scenario, the time to



**Feature Integration Theory, Fig. 1 Efficient and inefficient visual searches.** (a) When a target is defined by a unique color/luminance feature (the green arrow), it pops out regardless of the number of distractors, a result of a highly efficient search that appears to process all items in parallel. (b) Other searches, in particular, conjunction searches, are much more difficult to resolve, requiring the observer to scan each item separately until it detects the

unique target (in this case, a left pointing green arrow, just as in panel A). (c) Efficient search does not require more time with growing number of distractors, while inefficient search grows linearly. This behavior signals parallel vs. serial processing of the stimulus, expressed clearly by a zero vs. positive slope of the reaction time to target, respectively



find the target will grow (typically linearly) with the number of distracting items, where the performance slope depends on how efficiently the visual system can process the visual features that contribute to the detection. Figure 1b illustrates the expected performance graphs in these two modes.

Following the above, the features of the target and the distractors, as well as their interrelation, determine the visual search mode that is ultimately exhibited in a search task (Nakayama and Silverman 1986). For instance, a considerable amount of evidence indicates that if a target is defined *uniquely* by either color, size, orientation, or motion, it will “pop out” of the display (Wolfe and Horowitz 2004). According to Feature Integration Theory, this is because such features are accessible efficiently to the human visual system during the preattentive stage and their uniqueness signals the location of the target already in the preattentive maps. In other visual search tasks, where targets are defined by less accessible properties or nonunique combinations of properties, the target does not always pop out, forcing the observer to serially search for the target (Wolfe and Horowitz 2004). Hence, which features drive visual attention in visual search scenarios is one of the fundamental questions addressed when conducting visual search experiments. A significant body of research and a variety of theoretical models have been studying this and other aspects of visual search in humans for more than two decades now, and new ways for running countless visual search trials for additional insights have been emerging in recent years. Additional properties of Feature Integration Theory in humans are discussed in recent surveys on this subject (Wolfe and Horowitz 2004).

## Feature Integration Theory Beyond Humans

Indeed, although the research effort mentioned above had followed the ideas of Feature Integration Theory, it has been restricted almost entirely to humans, leaving interesting questions open. Are Feature Integration Theory and its contemporary variations applicable beyond humans? If so,

what features facilitate pop out in different animals? If a preattentive stage occurs in nonhuman animals, do different animals maintain different feature maps? And perhaps first and foremost, since visual search in humans is considered a cortical function, could animals that lack a fully developed cortex be able to perform efficient visual search, and if so, how? These questions are especially interesting given the numerous nonhuman species that depend on vision, and specifically on guided attention, for their survival.

Notwithstanding the extensive research into the visual systems, visual ecology, and visual behavior of nonhuman species, including the type of visual cues that drive their vision, relatively little work has explicitly addressed the features that guide attention, enable pop out, or otherwise affect the efficiency of visual behavioral tasks. Thus, many questions relating to Feature Integration Theory in nonhuman species remain unanswered. And yet, certain studies *have* examined visual search in selected nonhuman species after all. In these studies, the efficiency of visual features is typically determined by the target selection rate (i.e., how often the animal actually finds and selects the designated target), but sometimes also by the reaction time and occasionally by both. Interestingly, many of these studies imply a great deal of similarity in the visual search behavior of humans and nonhumans in both feature search and conjunction search tasks, as this entry discusses below.

But before discussing these details, it is worth mentioning that like many other types of experiments, visual search tasks are far more complicated to perform with animals than with humans. Clearly, it is overwhelmingly simpler to communicate the task to human subjects while animals must be trained to implicitly understand what constitutes the target before it can participate in experiments. Such training can last up to several months (e.g., (Orlowski et al. 2018)) for a single type of experiment, a procedure that much care and patience (by all parties). Furthermore, in the lack of verbal communication, training is required for every new target or visual search experiment. This entails a very time-consuming, multiple-training procedure, if the same animal is to be

tested in multiple types of visual search tasks (as is usually the case in most studies). Another complication in nonhuman visual search tasks relates to the number of consecutive trials a typical subject can participate in. In humans this number is typically determined by cognitive capacity (such as boredom, fatigue, focus, motivation). Animals, on the other hand, are typically rewarded for participation by food portions (unlike payment, course credit, or no reward at all in humans), a mechanism that critically limits the number of trials based on the animal's food intake capacity. Indeed, in reality, an hour's worth of experimentation with human participants might require weeks or months to run on certain animals. Overall, visual search experiments with nonhumans are thus challenging and requires much ingenuity to extract quality behavioral data while preserving the wellbeing of the subjects.

### Feature Integration Theory in Insects

Owing to the methodological difficulties involved, Feature Integration Theory and visual search in general was studied in insects relatively scarcely, where one of the most investigated species in the context of visual search being bees, especially their performance in color feature search tasks. As mentioned above, bees too must be trained for certain behavior in order to allow overt observation of their visual decision, in this case by visit a sucrose solution feeder placed inside an experimental arena near the hive. In a typical experimental trial, the bee enters the arena through a small entrance (Fig. 2a) and then faces a visual search task composed of various visual items (e.g., colored disks) located on the opposite wall. Each such item is equipped with a reward feeder attached to its back and accessible to the bee through a small opening (black dots in Fig. 2a). The bee is required to make a visual decision to obtain the reward while the location of the target and reward feeder change each trial.

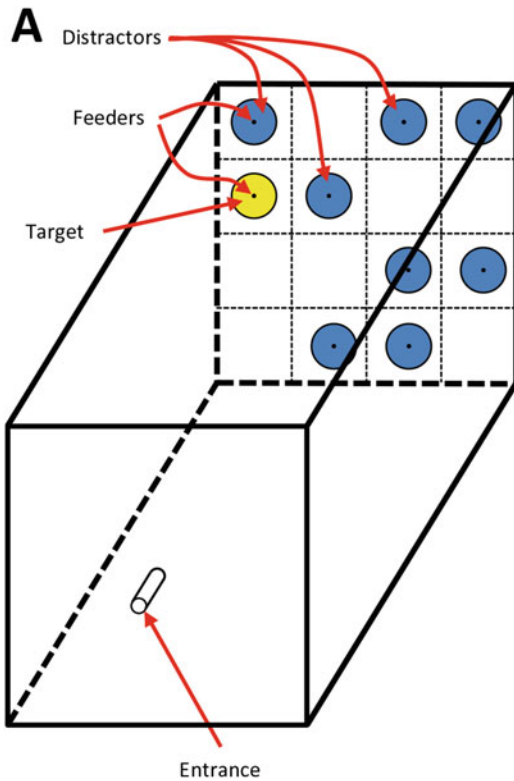
The animal's decision, success rates, and response time are documented for the analysis and based on results in such experiments it was

shown that performance in bees varies between species (Morawetz and Spaethe 2012). Specifically, error rates increased as a function of set size but only in honeybees and not in bumblebees (Fig. 2b). At the same time, response time in bumblebees was approximately 30% longer than honeybees (Fig. 2c), although neither species seems affected by set size in a significant way. These findings suggest that the speed-accuracy trade-off to detect the target is species dependent, which the authors attributed to ecological pressure. Given both decision time and error rate, color feature search elicits serial-like search in honeybees and parallel-like search in bumblebees.

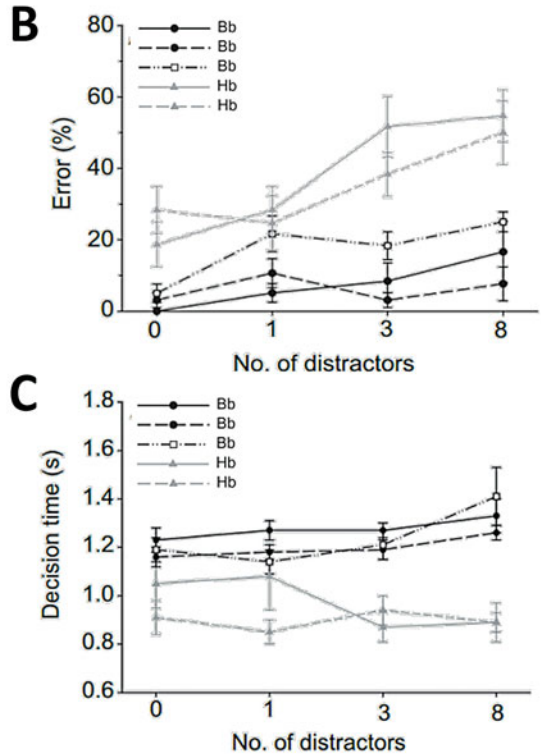
### Feature Integration Theory in Birds

Among the earliest nonhuman visual search investigation, even before FIT was conceived, was carried out in the 1970s on pigeons, leveraging the fact that they are relatively easily trained to peck at a selected visual item on a monitor (Blough 1977). Read in the language of the then forthcoming Feature Integration Theory, results indicated that both geometric shape or letters (Blough 1977) were inefficient features that led to longer reaction times and drops in target selection rates as the set size increased. Moreover, pop-out and search asymmetries related to line terminators (Harmening et al. 2011; Orłowski et al. 2015, 2018) were shown to not exist in pigeons (Allan and Blough 1989), unlike in humans. Based on by target selection rates, however, it was shown that pigeons are more efficient at processing color, size, orientation, or shape feature searches conjunction search (Cook et al. 1996).

Using similar pecking response methodology in an operant conditioning chamber, it was later shown that visual search behavior of blue jays incorporates a fundamentally serial component (Bond and Kamil 1999). Trained to detect an image of cryptic moth (namely, the target) embedded in different backgrounds with different levels of crypticity, it was found that reaction time increased and the accuracy decreased as a function of stimulus complexity. However, instead of



**Feature Integration Theory, Fig. 2 Visual search in bees.** (a) A typical experimental arena includes an array of visual items mounted around the access points of reward feeders (Sketch adapted from (Morawetz and Spaethe 2012)). The item in front of the feeder to which bees first approach are considered their visual decision (with some tolerance and decision lines, such as the dotted grid shown, typically employed by the experimenters). (b) Error rate as

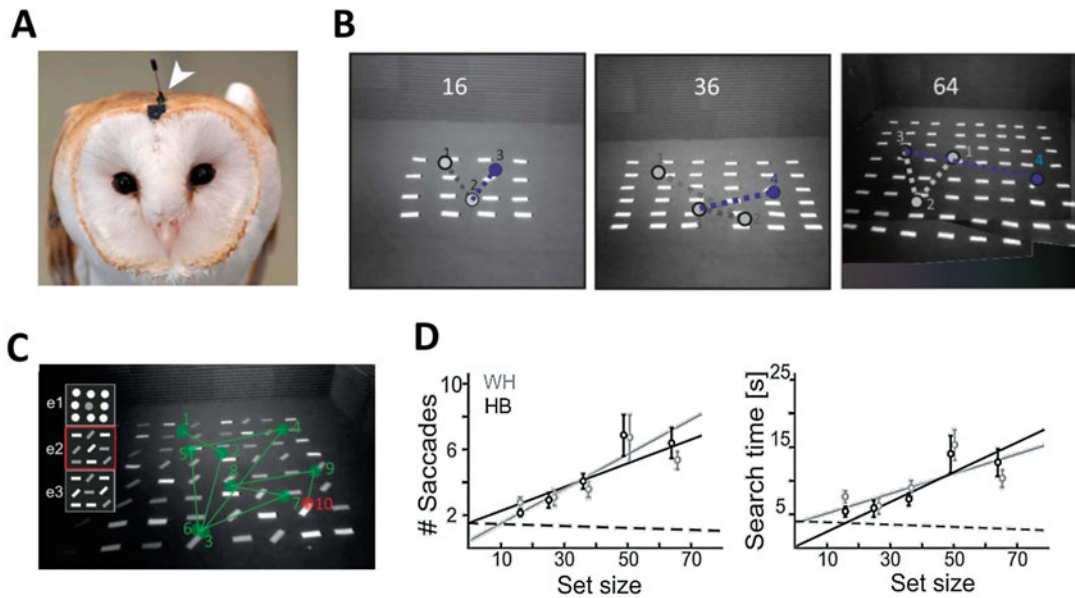


a function of set size does not seem to change for bumblebees (dashed and solid black lines) but increases for honeybees (dashed and solid gray lines) (c) The decision time (as a function of set size) of bumblebees (dashed and solid black lines) is approximately 30% longer than for honeybees (dashed and solid gray lines). Values in both graphs are means  $\pm 1$  standard error of the mean (Morawetz and Spaethe 2012)

increasing the number of distracting objects as in a classic visual search experiments, the difficulty level of discriminating between the target and background was increased. In this sense, these results may fit less naturally into FIT. Also, rather than testing how the target's and distractor's features affect visual search per se, the study was aimed to test how the latter is influenced by different procedures (such as cuing and sequential priming) to attain initial focal attention (Bond and Kamil 1999; Goto et al. 2014).

A significant progress using more robust methodology has been achieved in the last decade on what has become a major animal model in nonhuman visual search and saliency

research – the barn owl (Harmening et al. 2011; Orłowski et al. 2015, 2018). Unlike most species, barn owls virtually lack eye movements, which in fact facilitates the overt observation of their visual behavior through gaze tracking from a head-mounted camera, dubbed the OwlCam (Fig. 3a). By using proper image processing and automatic computer vision analyses, it is possible to identify the “functional fovea” and thus the spatial and temporal order of the items that the bird fixates on during free behavior, including flying (Fig. 3b,c), just like the scan path that modern eye trackers would extract from human observers. A series of studies that employed this methodology (Harmening et al.



**Feature Integration Theory, Fig. 3 Visual search in barn owl.** (a) The OwlCam is a tiny wireless video camera that is mounted on the owl's skull and enables a bird's view of its frontal field of view. With proper processing it is possible to generate a panoramic field of view and identify the locations/items that the owl fixates on during search or other visual tasks (Image adapted from (Harmening et al. 2011)). (b) Examples of panoramic scene reconstructions, scan paths (dash lines), and fixations (circles) until the target was first fixated (blue disk) during an orientation task. The numbers near the circles indicate the fixation number. The stimulus arrays contain (from left to right) 16, 36, and 64 items. Note that the number of saccades to the target hardly varies despite the change in set size, indicating that the orientation feature elicits pop-out in

the barn owl (Images adapted from (Orlowski et al. 2015)). (c) A similar panoramic image and scan path during a conjunction search task (in this case, of a target defined by a particular contrast and orientation as illustrated in inset e2). Note the high number (10) of saccades till the target was found, indicating a much more challenging search task for the bird (adapted from Orlowski et al. 2015). (d) Number of saccades and search time as a function of set size clearly shows differences between serial search behavior (solid lines of positive slopes) in a conjunction task (in this case, conjunction of high contrast and orientation) vs. parallel search behavior (dashed lines of virtually zero slope) in feature search task (in this case, high contrast feature search). Data adapted from Orlowski et al. (2018)

2011; Orlowski et al. 2015, 2018) have shown that barn owls exhibit both parallel and serial search modes in a fashion extremely similar to humans. Stimuli in these experiments were either projected or physically organized as real objects on the floor in front of animal subjects, and the dependent variables employed were the number of saccades and search time until the target was found. Both indicators, when examined as a function of set size, have indicated that orientation and luminance-contrast search tasks elicit pop-out and parallel search mode (Harmening et al. 2011; Orlowski et al. 2015) while low-contrast feature tasks and certain conjunction tasks elicit serial search (Orlowski et al. 2018) (Fig. 3d).

## Feature Integration Theory in Fish

In the aquatic world, one of the most extensively studied species for its visual search behavior is the archerfish. This fish is especially well-known for its incredible hunting skill of *terrestrial* insects that rest on foliage and low-lying branches by shooting them with a strong accurate jet of water from his mouth. This extremely fantastic behavior is often attributed (in part) to excellent eyesight and unique neural computations (Ben-Tov et al. 2018; Vasserman et al. 2010), and since it is possible to train the archerfish to shoot at artificial objects presented on a monitor, it allows controlled behavioral experiments where the fish's visual decisions can be easily observed.

Using this animal model, it was first shown that the archerfish exhibits both parallel and serial search modes (Ben-Tov et al. 2015, 2018; Mokeichev et al. 2010; Rischawy and Schuster 2013). Since initial work sought to leverage the high responsiveness of the archerfish to movement, stimuli typically incorporated moving bars. However, more recent work showed that the archerfish not only exhibits pop-out behavior, but that the latter is facilitated by four common visual features known to elicit the same behavior in humans, namely color, size, orientation, and motion (Reichenthal et al. 2019). That was also an early demonstration that shape tasks elicit serial search, with reaction time that grows, and target selection rate that decreases, with the number of distractors. Additionally, it was also shown that conjunction search tasks of size and color are asymmetric. Parallel search was elicited in the archerfish when a large blue target was embedded in a field of small blue and large black distractors, but serial search was elicited for a small blue target amidst small black and large blue distractors.

A very recent follow-up (Reichenthal et al. 2020) has further extended these findings and explored the possibility that fish performance exhibits the same continuum found in human vision (Wolfe 1998). Unfortunately, at the time of this publication, the relatively small total number of trials in the literature that have tested archerfish in visual search still prohibits comparable conclusions, but given these scant data, and inspired by Feature Integration Theory, Reichenthal et al. (2020) have been able to categorized archerfish performance based on the classical bimodal (easy/efficient/parallel vs. difficult/inefficient/serial) Feature Integration Theory division (Treisman and Gelade 1980) in a rigorous fashion, concluding that ~45 ms/item is a proper threshold between the two behaviors (as depicted by the black dashed line in Fig. 4b), compared to 5 ms/item attributed to humans. Apart from this expected species-dependent response time threshold, performance of humans and archerfish was found qualitatively similar, and in particular all features of color, size, orientation, and motion elicited the same type of visual search behavior in both (Reichenthal et al. 2020). Similar

behavioral similarity between the species also was observed in conjunction search tasks (in that case of size and color), both in the type of performance (i.e., parallel vs. serial) and in terms of performance asymmetries (i.e., when switching the role of targets and distractors. Note that as discussed above, these findings also match those in birds, where behavior was found qualitatively similar to humans, differing quantitatively only in the scale of response time (Harmening et al. 2011; Orłowski et al. 2015, 2018).

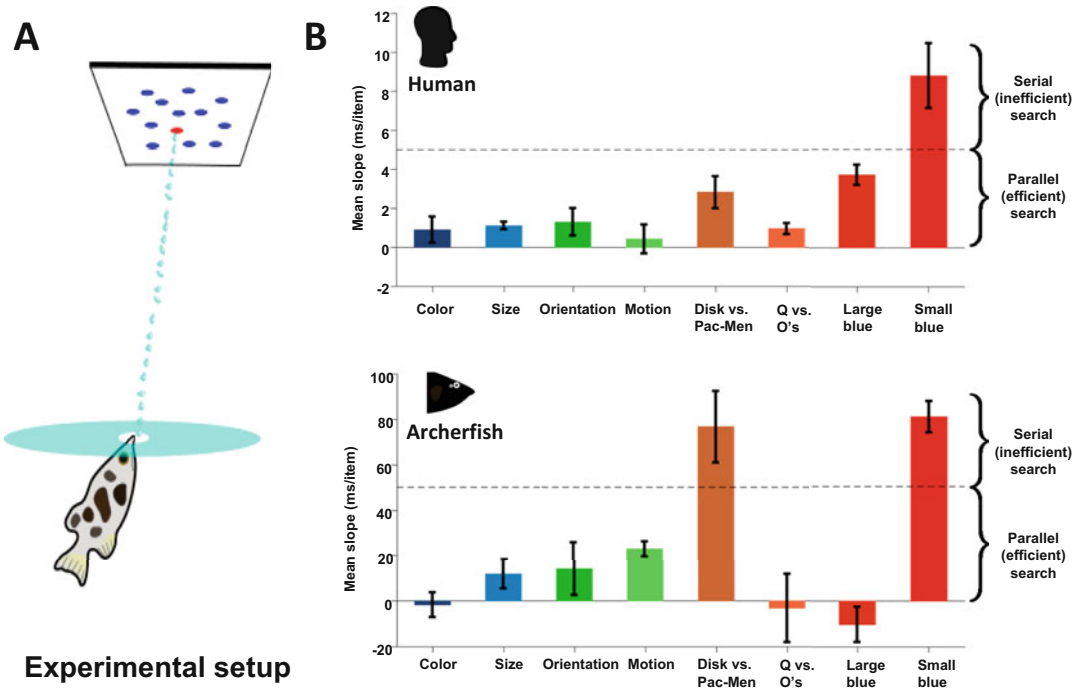
That being said, the same experimental methodology used to study the archerfish revealed qualitatively different behaviors compared to humans when the search is governed by target shape. For example, while searching for a solid disk amidst Pacman like distractors is easy (parallel) for humans, it was found difficult (serial) for archerfish. Yet, when the targets were Q-like shapes amidst full disk distractors, performance was qualitatively similar again, that is, parallel in this case. This inconsistent comparison in different cases could arise from the difference in familiarity of the species to certain shapes and/or to negative shape associations (e.g., due to fear, see e.g., Öhman et al. (2001), that certain shapes could generate in each species.

Overall, taken as a primary animal model, the archerfish indicates that Feature Integration Theory is indeed applicable to fish and humans alike, except when it depends on shape processing that may be species-dependent. While the archerfish provides an excellent platform for such research, exploring visual search (or any other visual) behavior in other (more “traditional”) species of fish clearly requires other means of probing their visual decisions, for example by training them to approach the target. Using such methods, it was indeed demonstrated that zebrafish exhibits pop-out in color feature visual search (Proulx et al. 2014).

## Feature Integration Theory in Nonhuman Mammals

Given findings as described above, one would expect visual search in mammals to lead the





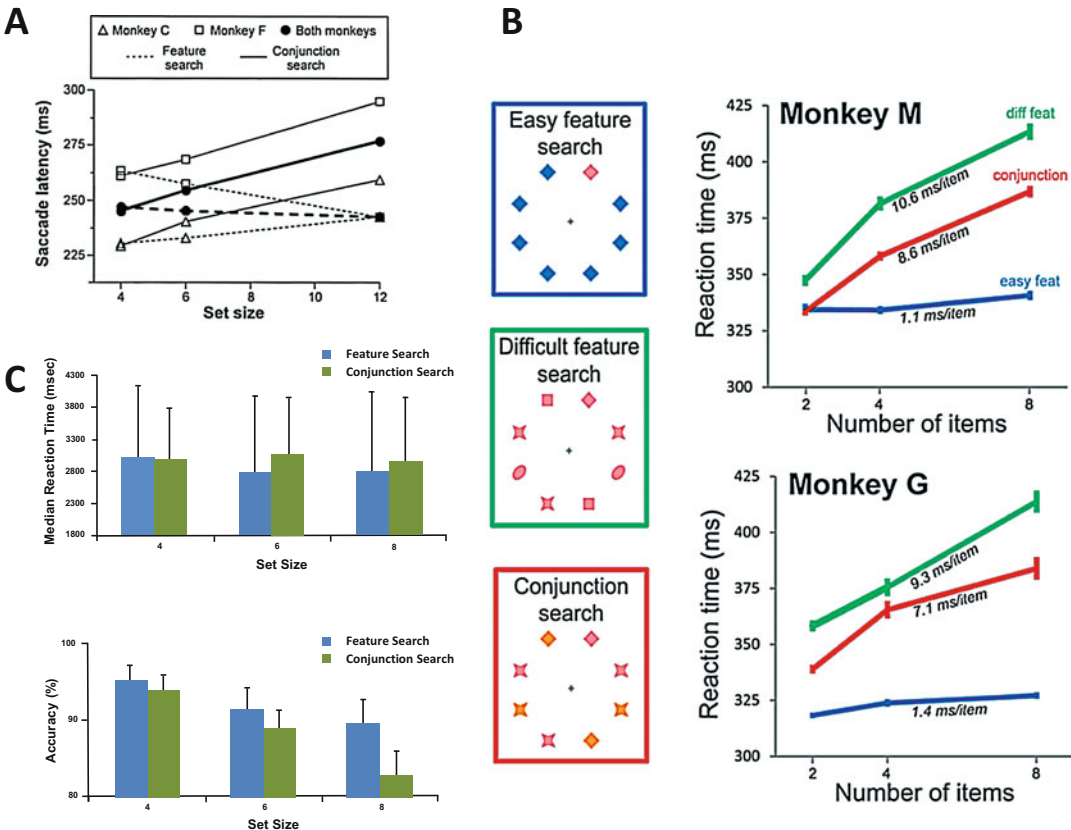
**Feature Integration Theory, Fig. 4 Visual search in fish.** (a) Archerfish can be trained to perform visual search tasks on a monitor, very much like human subjects. Their visual decisions are observed overtly (and recorded with a video camera) based on the target that the fish shoot at. (b) A summary of archerfish vs. human performance in various visual search tasks that were performed *identically* on the two species. The sole difference in the analysis is based

on the scale of response times that cannot be identical for both species. However, the threshold between parallel and serial modes can be determined by the same method for both species (as described in Reichenthal et al. 2020) and is marked by the dashed horizontal lines. Search mode that was elicited by both species is identical in virtually all search tasks, except for one specific case that involves shape processing (disk vs. Pacmen)

way. It is thus surprising that nonhuman terrestrial mammals have not been widely studied in the context of visual search, with primates, and especially monkeys, being by far the most studied animal in this group. The methodologies employed in these studies vary significantly.

In the classic visual search experiment by Bichot and Schall (1999), both saccade latency slope and error rates were measured in macaque subjects as a function of the set size, to demonstrate that color and simple shape searches are more efficient than their conjunction counterparts (Fig. 5a). Such insights were further supported by a forced-choice target detection paradigm that indicated that time-to-detection for targets defined by color does not depend on

set size (hence, they pop out), whereas targets defined by shape, or a conjunction of shape and color, lead to reaction times that increase with set size (Buračas and Albright 1999; Wardak et al. 2012) (Fig. 5b). Unlike Bichot and Schall (1999), the latter used a more direct procedure where the task of the monkey was to press a lever only when the stimulus contains a target, and to abstain from response in target-absence trials. While more difficult to analyze from Feature Integration Theory's perspective, other visual search experiments also demonstrated influence of emotional aspects, like threat, of the efficiency of visual search (Shibasaki and Kawai 2009) as well as the capacity of monkeys to perform serial visual search based on more complicated



**Feature Integration Theory, Fig. 5 Visual search in mammals.** (a) Saccade latency as a function of set size in macaques (Bichot and Schall 1999) suggests that feature search tasks elicit pop-out while conjunction searches lead to serial search. (b) Searching for the pink diamond in these tasks led monkeys exhibit pop-out (parallel search mode) in color feature searches, but serial mode in complex shape or conjunction searches (graph colors code the same

experiments as the panels on the left; adapted from (Wardak et al. 2012). (c) Visual search response time in rats did not change with set size in a feature task (dark gray) or a conjunction task (light gray). Accuracy, on the other hand, did decrease as a function of set size (Botly and De Rosa 2012), leaving the evidence so far ambiguous regarding the search mode or even the search goal employed

combination of feature. Furthermore, monkeys also demonstrate the classic speed-accuracy tradeoff found also in human visual search (Tomonaga and Imura 2015).

Unfortunately, very little visual search exploration has been performed thus far on nonprimate mammals, perhaps a result of methodological complexities. A notable exception involving rats has demonstrated that unlike monkeys this species exhibits a somewhat mixed performance, with essentially fixed reaction times but error rates that increase with set size, all for targets defined

by luminance, shape, and certain conjunctions (Botly and De Rosa 2012) (Fig. 5c).

## Epilogue: Is Animal Advantage Possible?

To date, the literature on Feature Integration Theory in animals that has been summarized above supports (at least implicitly) the idea that visual search behavior is similar in humans and in many animals, and in particular that whatever pops out to animals also pops out for humans. The

converse, however, is not always true and a few experiments have indicated that while certain shape tasks pop out to humans, they do *not* do so for animals. This “one way” advantage in performance may be explained by the fact that the human visual system is much more developed and facilitates complex processing much faster and better than animals, whereas many basic pop-out features are universal in nature and thus affected many species in the course of evolution. This intuition thus raises a simple but interesting question of whether there are any visual tasks on which animals outperform humans. Clearly, Feature Integration Theory neither excludes nor necessitates this possibility, and to date this question remains largely open.

And yet, some speculations can be made. Obviously, visual properties that humans cannot observe at all will naturally give animals (that can sense them) an edge when such properties define the target. For example, if the target is composed solely of the polarization of the light it reflects or by wavelengths outside the visible spectrum, it may pop out to certain animals but not for humans. Naturally, our open question does not refer to such cases. But in the spirit of ecological vision, and hard evidence about the effect of the natural environment on neural processing, a habitat abundant with a certain visual cue, feature, or property that are rare in human life could pop out to certain animals living in that environment but not to humans. For example, it is tempting to hypothesize that certain visual search experiments based on unique shapes would elicit effective (parallel) search in a particular animal but serial search in humans. This type of experiment would need to revolve around a typical shape from the animal’s habitat, which rarely exists or completely absent in human environments. For example, human face targets, but not animal faces, pop out to human observers when presented amidst non-face objects, and this is despite the many similarities one can draw between animal and human faces (Hershler and Hochstein 2005). If such effect also generalizes to other species, one may that a fish figure or fish face would pop out for fish and not for humans. Recent preliminary

investigations in this direction have yet to generate a suitable demonstration of such animal advantage and dedicated research is needed to resolve this open question.

## Cross-References

- [Attention](#)
- [Bottom-up Processing](#)
- [Operant Chamber](#)
- [Saccadic Eye Movement](#)
- [Visual Perception](#)
- [Visual Search](#)

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## Fecundity

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## Synonyms

Fertility; Reproductive output; Reproductive potential

## Definition

The number of gametes produced by an organism

## Introduction

For all animals, fecundity is a measure of gamete production expressing the number of eggs or sperm produced by females and males, respectively. In that respect, fecundity is a quantitative variable differing from “fertility” and “reproductive potential” which are more general and qualitative terms expressing an individual’s reproductive success and its capacity to produce gametes and viable embryos, respectively. Fecundity measurements are of particular importance in animal biology and ecology since they are used for assessing population reproductive dynamics and energetics and for estimating their annual reproductive output and how it is linked to recruitment and population growth (Stearns 1992). In addition, measurements of fecundity can be

implemented in the appraisal of biomass of ecologically or socially important species, especially in commercial fishes. There are several measures of fecundity such as the daily or the (potential) annual fecundity, the absolute or the relative fecundity, the determinate or the indeterminate fecundity, etc. (Hunter et al. 1992). Given that individual cells of young embryos all originate from the zygote – the fertilized egg – most focus in fecundity assessments in population biology and ecology has been given to reproductively active females.

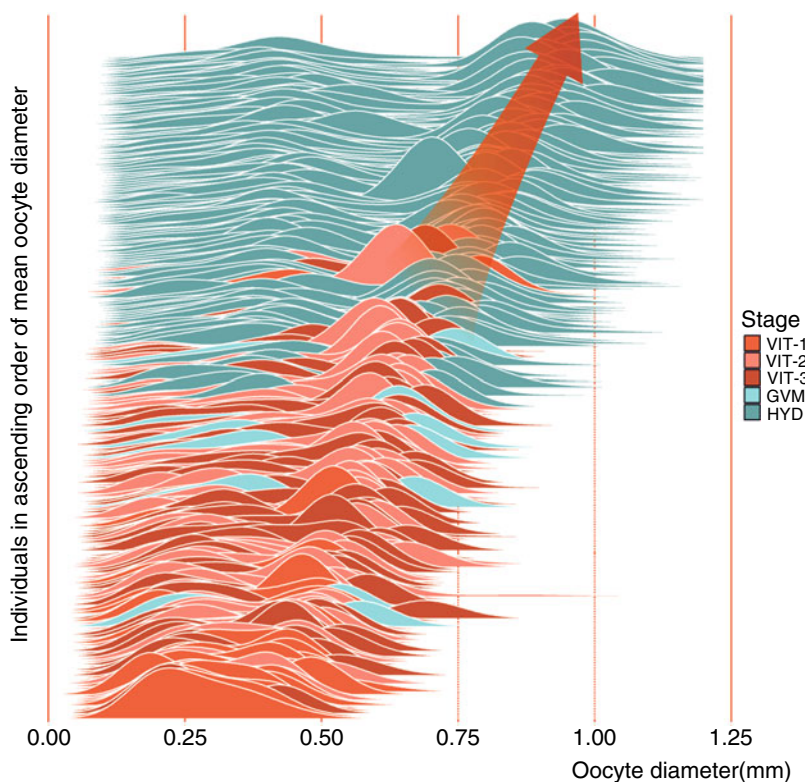
## Fecundity Measurements

Fecundity measurements vary based on the modes of reproduction animals use to produce their young. In viviparous organisms, like placental mammals, fecundity is usually measured as the number of litters per year while in humans approaches to measuring fecundity include the

assessment of time to pregnancy and day-specific probabilities of conception (daily fecundities) indexed to a day of ovulation. On the other hand, in oviparous animals, fecundity measurements are typically performed through direct counting of eggs in oviposition sites such as nests. In broadcast spawners – most aquatic animals, except for aquatic mammals and reptiles – which release their gametes into the water, fecundity measurements should rather be based on oocyte counts in spawning capable females. In highly fecund spawners, like most teleosts, fecundity measurements are carried out in smaller fractions of ovarian tissue of known weight/volume and resulting oocyte densities are extrapolated to the total weight/volume of the ovary (gravimetric or volumetric method respectively).

Apart from their number, the size of oocytes can also be important in fecundity assessments. The resulting oocyte size distributions (Fig. 1) provide an illustration of the fecundity production process which is particularly helpful for

**Fecundity, Fig. 1** Oocyte size frequency distributions from a marine teleost fish (sardine, *Sardina pilchardus*) arranged in ascending order of mean oocyte size. The plot illustrates the gradual growth and separation of the spawning batch (arrow) from the smaller oocytes of the ovary in sequential stages of development. *VIT-1 to 3*: various stages of true vitellogenesis; *GVM* germinal vesicle migration stage, *HYD* hydration stage (typical in marine teleosts).



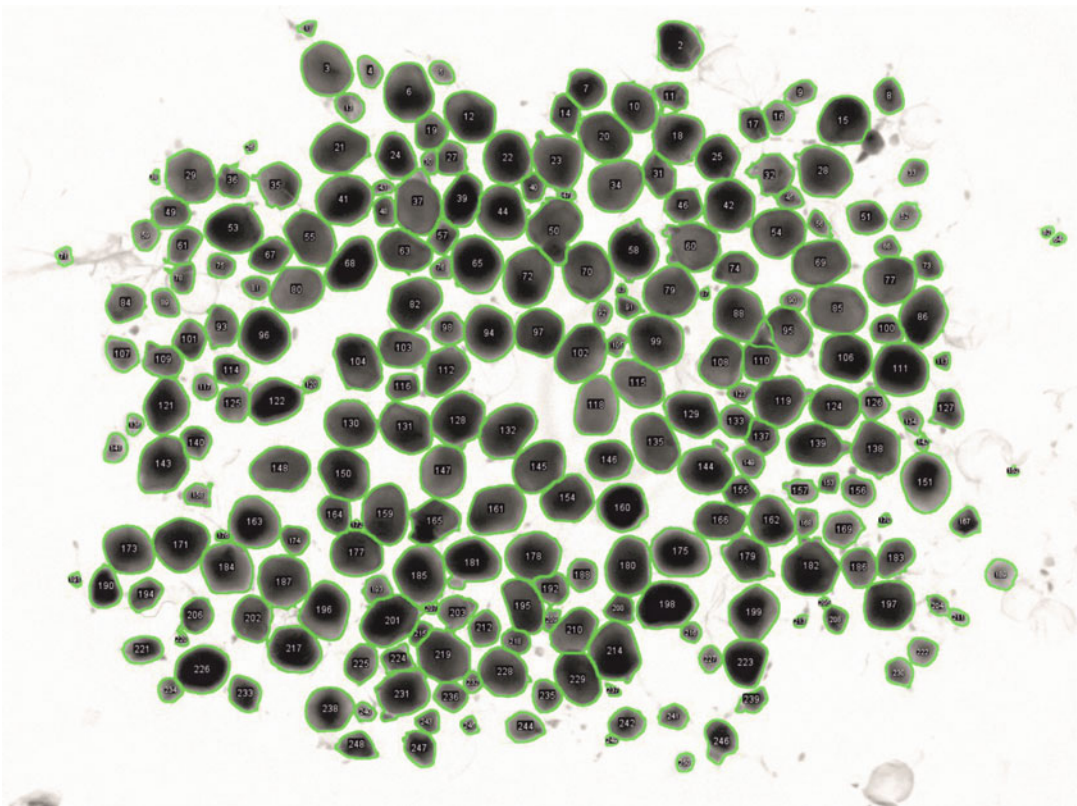


disentangling total fecundity from batch size in fish. Traditionally, these measurements are performed by averaging the maximum and minimum axes in a number of oocytes through direct observations under dissecting microscopes. However, these traditional methods not only are painstaking and labor-intensive but can also be inaccurate due to biased selection of oocytes, repeated measurements, etc. Undoubtedly, one major improvement in fecundity assessments was the automation of the process of measuring and counting oocytes through image analysis systems which is a friendlier and more cost-effective means to estimate fecundity (Fig. 2). Another important advance deals with the quantification of various follicular types such as previtellogenic oocytes, atretic and postovulatory follicles that may only be identified through ovarian histology through stereological methods.

## Fecundity Production and Temporal Dynamics

For a reproductive event to occur, oocytes must be recruited to the appropriate developmental stages at the right time so that species can breed when there is potential for reproductive success. There are three key fecundity recruitment events (Wallace and Selman 1981): (1) from oogonial nests to primary growth oocytes; (2) from primary to secondary growth oocytes; and (3) into oocyte maturation. Recruitment to primary growth is responsible for populating the ovary with primary growth oocytes which are seldom taken into account although clearly play a role in the process of sexual maturation. Recruitment to oocyte maturation is indicative of an individual's commitment to imminent egg laying. However, it is the frequency and patterns of recruitment to

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**Fecundity, Fig. 2** Measurement of oocyte size and number in a small sample of a fish ovary (whole mount) by means of particle analysis.

secondary growth which are commonly used in assessments of fecundity production.

Fecundity temporal dynamics commonly occur at four temporal scales (Lowerre-Barbieri et al. 2011; Ganas and Lowerre-Barbieri [accepted](#)): lifetime, annual, intra-seasonal, or diel. At the lifetime temporal scale, the number of breeding opportunities (i.e., semelparous vs. iteroparous) is dependent on whether recruitment from primary to secondary oocyte growth is “complete” or “partial.” At the annual scale, fecundity production is performed in two distinct breeding patterns: single and multiple breeding. Single breeders lay all their eggs in one event or over a very short time period within the reproductive cycle while multiple breeders develop and release more than one batch of eggs within a spawning season. Fecundity type (determinate or indeterminate) is determined at the intra-seasonal scale by whether oocytes to be spawned in a given breeding period continue to be recruited to secondary growth within the breeding period or not. Species with determinate fecundity exhibit “restricted” recruitment, recruiting all oocytes which will complete vitellogenesis and be released in a reproductive cycle prior to the beginning of the breeding season. Recruitment to oocyte maturation is usually performed at the diel scale and as said above is indicative of imminent breeding event.

## Fecundity Dependencies and Trade-Offs

Life history theory predicts that fecundity in animals is interdependent with maternal size, offspring size, and egg mass. Such dependencies and trade-offs are reflected in patterns of parental care, recruitment, population growth, and mortality that profoundly affect the ecology of the species. However, it is the trade-off between fecundity and individual size of the offspring that mostly dominates the allometry of those variables and the analysis of gross patterns among different animal groups shows two distinct modes with strong taxonomic effect (Visman et al. 1996): low fecundity and large offspring size which is a general characteristic of amniotes (mammals, reptiles, and birds), and high fecundity

and small offspring size which is mostly prominent in anamniotes (fish and amphibians) and other lower taxonomic groups such as crustaceans. For example, fecundity in fish increases with age and size of the female both within species (Blaxter 1969) and among species (Duarte and Alcaraz 1989), while among amniotic organisms fecundity is only loosely, and negatively, related to female mass (Visman et al. 1996). It is interesting to point out that viviparous or ovoviviparous anamniotic organisms such as most elasmobranchs (e.g., chimaeras, sharks, and rays) deploy the low fecundity and large offspring strategy (Goodwin et al. 2002), clearly suggesting that the evolution of strategies mostly deals with parental investment and survival rates of individual offspring (Winemiller 1989). For example, again amongst fish, fecundity tends to be higher in marine fish than in freshwater fish (Duarte and Alcaraz 1989), while multivariate methods across a wide range of species identified that high fecundity is generally grouped together with delayed maturation, fewer reproductive events, shorter breeding season, and vice versa (Winemiller 1989). Physiological constraints, e.g., the trade-off between oocyte number and size within the finite abdominal cavity, geographical trends such as latitudinal clines, and genetic variation may also affect animal fecundity (Stearns 1992).

## Cross-References

- [Fertility](#)
- [Ova](#)
- [Ovaries](#)
- [Reproduction](#)
- [Spawning](#)

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## Feed

- ▶ [Equine Diet](#)
- ▶ [Feed Industry](#)

## Feed Industry

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## Synonyms

[Animal feed industry](#); [Feed production](#); [Feed](#); [Nutrition](#); [Feedstuff manufacturing](#); [Livestock feed](#)

## Definition

The feed industry refers to the production of feeds and feedstuff for consumption by animals,

whether production, companion, or managed wild and exotic species. The feed industry is also responsible for the production of feedstuff for use in aquaculture.

## Introduction

The **feed industry** is a global, multibillion-dollar industry that is critical for both human and animal nutrition. The feed industry is typically viewed as distinct from the food industry which produces food and foodstuff for human consumption, although both industries are clearly linked, with the feed industry supporting the production of animal products destined for the human food chain. In livestock production systems, feed constitutes the major expense associated with output, typically exceeding 50% of total costs involved. For this reason, the feed industry must consider the economic viability of feed production, from individual raw materials to diet and ration formulation. Equally, the feed industry typically also benefits from the utilization of co-products and by-products from the human food industry that are not otherwise used or consumed due to reasons of choice or culture.

Consequently, as it is responsible for providing safe, nutritious, sustainable, suitable, cost-effective, and accessible feedstuffs for animal consumption either directly or indirectly, the feed industry is one of the most responsive and important global industries. However, the feed industry is increasingly facing challenges in many forms, and issues of sustainability are driving rapid and specific changes. As a result, the feed industry heavily relies on scientific and technological advances to ensure currency, economic security, and environmental sustainability.

The feed industry researches, develops, formulates, and produces feedstuffs suitable for a range of species, from production, companion, zoo, and even managed wild species when supplemental feeding might be initiated. Developing feedstuffs for production animals is, however, a key component of the feed industry. Food (and ancillary) products derived from cattle, sheep, pigs, poultry, and aquaculture continue to comprise a large

proportion of the Western diet (Sapkota et al. 2007), highlighting the link between the feed industry and human food production. Furthermore, as the global human population continues to expand and the demand for animal-derived protein increases as a result, the feed industry is tasked with finding ways to maximize production in a safe, sustainable, affordable, and ethical way.

## The History and Development of the Feed Industry

All organisms need food for survival. Food supplies key nutrients to support growth, activity output, recovery/regeneration, and production. For organisms that do not acquire their own food through free grazing or predation, the feed industry is essential for ensuring that suitable feedstuffs are available and accessible. The feeding of production animal species particularly has seen dramatic changes in the last century and continues to meet new challenges in the sustainable provision of feeds and feedstuffs. Animal nutrition as a scientific discipline first began to develop in the early 1800s (Coffey et al. 2015), and the modern-day feed industry is now responsible for the production of nutritious and safe feedstuffs to feed production animals such as cattle, sheep, pigs, poultry, and farmed fish and for use in other aquaculture systems.

The feed industry is also involved in the research, manufacture, and provision of feedstuffs for other species such as companion animals that, while not necessarily destined for human consumption, still require safe, nutritious, and effective feeds. Notably, there has been an increase in the humanization of pet diets (Clemens 2014), concurrent with increased owner awareness of their own health and diet. This leads to additional challenges for the feed industry, to meet owner-driven demand for dog and cat diets, to be rich in animal-derived protein (Okin 2017).

The development of the feed industry on a large scale has been gradual, and early beginnings in the production of animal feeds and feedstuffs, in concert with specific animal management practices, likely date to approximately 12,000 years

ago (Coffey et al. 2015). As the human population gradually moved from a nomadic, hunter-gather existence to an agrarian, settled existence, the reliance on hunting as a source of nourishment decreased, and instead, crops were grown, and animal species domesticated as food sources. At this point, the agricultural production of food became important, for nourishing the animals used as a source of milk, meat, wool, and hides and thus to support human nutrition and survival. The evolution of modern agricultural practices and the increased intensification of animal production have necessitated the development of an industry that can support both nutritional and production requirements of fed species. Indeed, the development of the feed industry is closely linked with the development of intensified agricultural production, notably the movement of animal production from open, expansive grazing to confinement and intensive housing practices (Coffey et al. 2015). This has coincided with the global expansion and technological development of the human population, in addition to a move toward a more urbanized existence.

Historically, feed production would have been on a small scale, with individual farmers growing and producing enough food for themselves, their animals, and perhaps their small, local community. As populations expanded, however, such subsistence production became less viable, and economies of scale started to have an impact. Farms have steadily increased in size and rates of production output have increased substantially. The increased urbanization of the human population has further reduced the proportion of the human population employed or involved directly in food production, necessitating more intensive feed and food production practices to be adopted (Satterthwaite et al. 2010). As a result, the feed industry is under substantial pressure to meet increasing demands of a growing human population and an increased reliance upon and desire to consume animal-derived products. This is combined with commercial pressure to feed the global human and animal population safely and sustainably, from both economic and environmental perspectives. Indeed, by 2050, it is estimated that the human population will exceed nine billion and

that the required food will be 60% higher than that at present (IFIF 2019), highlighting the need for an efficient and effective feed industry. Food safety continues to be a significant consideration, with the quality of animal-derived end products being related to how those animals were originally fed and managed (e.g., see (Zaghini et al. 2005)), so the feed industry must strive to balance demands from a production and consumer perspective.

Indeed, the feed industry is significantly affected by issues and concerns relating to human consumers. The consumption of animal-derived products is directly affected by the wealth of the human population (McDonald et al. 2011), with wealthier populations typically demonstrating increased consumption and utilization of animal products. Indeed, global inequalities, natural disasters, conflict, and other crises continue to affect the provision of human-destined foodstuff, and it is estimated that 800 million people remain chronically hungry, with approximately 2 billion suffering from various micronutrient deficiencies (FAO 2017). Culture and religion also play a part in determining specific animal production, and increasingly, consumers are making consumption choices based on ethical, moral, or health concerns (McAfee et al. 2010). This is also observed in the choices that human caregivers are making in companion animal diets, with increased humanization and perceived quality choices leading to diets for cats and dogs being formulated to meet human demands rather than animal nutritional requirements (Clemens 2014). These factors all impact on the feed industry and further challenge it to respond to environmental, health, welfare, safety, and integrity concerns.

## The Scientific and Technological Development of the Feed Industry

The feed industry has benefitted significantly from scientific advances in the understanding of animal nutritional requirements and how nutrition can impact upon performance output. Nutrition is widely viewed as a controllable variable that can support an animal reaching its genetic potential

for a given production output and has seen significant scientific advances since the early 1800s (Coffey et al. 2015). Genetic advances in livestock have also meant that there is increased homogenization of breeds/types and the required nutrient provision for consistent production output. The first commercial, compound feeds were developed for feeding horses and mules in the 1800s. These animals were critical for providing transport and draft power and, as such, required consistent and quality feedstuff (Coffey et al. 2015). As the production of livestock continued to expand and develop, with improvements in feed conversion rates and efficiencies in different species, the feed industry has further developed via consolidation, automation, scientific research, and technological innovations, to support altered rates of growth, nutrient requirements, and specific production targets of livestock species. The modern feed industry is now highly automated and specialized and functions on large economies of scale.

As livestock species have developed, the feed industry has had to respond. The broiler chicken demonstrates an extreme example of intense selection for production traits since the 1950s, with the modern-day broiler now reaching slaughter weight in significantly fewer days and thus with less feed intake than historic forms (Tallentire et al. 2016). Indeed, the broiler chicken has demonstrated an increased growth rate of over 400% between 1950 and 2005 (Zuidhof et al. 2014), revealing the extent of livestock genetic improvements. As a result, nutrient provision for livestock by the feed industry is under constant review, with research and innovation driving advances.

Technology within the feed industry is also critical for developing effective manufacturing and feed provision strategies, to reduce spillage, wastage, and contamination. Improvements in how animals are fed directly reduce waste and improve overall efficiency (Svihus et al. 2004). It has also been observed that more commercial, heavily selected breeds of broilers have reduced levels of feed wastage and spillage (Zuidhof et al. 2014), in addition to increased growth rates and voluntary food intakes (Schmidt et al. 2009).



Maximal utilization of feed is just one way of managing and meeting sustainability targets by the feed industry.

## Feed Ingredients, Safety, and Production

The feed industry relies on raw ingredients that are both animal and plant in origin. The target animal to be fed and its nutrient requirements, as well as its digestive strategy, will determine what ingredients will be utilized. Typically, national and international organizations also regulate what ingredients are acceptable within animal diets and at what levels, identifying those that are legally permitted for animal consumption. This is necessary to ensure safety and suitability.

For many production species, diets are formulated to be compound feeds, consisting of several raw ingredients, combined to create a complete and balanced diet. Cereals, grains, and other plant-derived materials (including by-products from human food production, such as fruit pomaces) will provide ready sources of protein, fats, fiber, and other nutrients. Care must be taken to ensure the quality of many plant ingredients, notably cereals that can be contaminated with mycotoxins, potentially hazardous to both animal and human health (Hussein and Brasel 2001). Maximum levels of key mycotoxins in finished feed products are identified, but monitoring is critical, especially due to geographical and seasonal variation in their occurrence.

Ingredients derived from animal products and by-products (such as rendered meat meals, feather meals, and blood meals) can also be incorporated into feeds for certain species, again providing rich sources of key nutrients, especially protein. Similarly, in some countries, animal waste products are incorporated into animal feeds as a protein-rich, sustainable raw material, although this is not endorsed by the US Food and Drug Administration (FDA), with concerns about pathogen and drug residue transfer (Sapkota et al. 2007).

Indeed, the inclusion of animal-derived products within animal feedstuffs, especially for target

species that are not omnivorous or carnivorous, is an area of interest, with concerns relating to pathogens, heavy metals, and dioxins being present. A significant example of this is the prion-mediated disease, variant Creutzfeldt-Jakob disease (vCJD) in humans (Collinge 1999), that was transmitted to humans via the consumption of prion-infected meat and linked to historic practices of feeding cattle rendered animal protein, containing prions from cattle infected with bovine spongiform encephalopathy (BSE).

Other pathogenic agents can be transmitted via feeds and foodstuffs, such as *Salmonella* spp. (Crump et al. 2002), *E. coli* (Dargatz et al. 2005), and antibiotic-resistant bacteria, this having become especially problematic and of concern in some raw meat-based companion animal diets (Nüesch-Inderbilen et al. 2019). Dry pet foods have also been associated with *Salmonella* infection risk (Barton Behravesh et al. 2010), highlighting the importance of high production and safety standards within the feed industry to minimize contamination of finished products.

Contamination of animal feed with such pathogens can occur at many stages of production, but their potential impact on both human and animal health highlights the importance of balancing efficiency and sustainability with safety and ensuring active collaboration between relevant regulatory bodies and food/animal health professionals (Sapkota et al. 2007).

## New and Alternative Ingredients in the Feed Industry

The pressure for the feed industry to remain both economically and environmentally sustainable means that the industry is increasingly researching and examining the use of alternative, novel, and by-product ingredients within the manufacture of feedstuffs. Since the 1970s, the feed industry has benefitted from several advances in feed production, both nutritional and technological (Coffey et al. 2015). The intention is threefold: to minimize and reduce waste, to enhance nutrition, and to ensure economic and feed efficiency where possible. This is where previous lessons

learned from including ingredients into animal diets are critical (such as the prion diseases vCJD and BSE). However, novel algal, plant, and insect ingredients are being explored for use in feedstuffs (Coffey et al. 2015; van der Spiegel et al. 2013), although queries regarding aspects of safety, legislation, and nutritional value for some novel ingredients remain and further research is needed. However, in the pursuit of economic and dietary efficiency, it is likely that novel additives and ingredients will form an increasingly large portion of the animal feed industry in the future.

## Feed Analysis and Standards

In order to produce nutritionally appropriate and adequate feedstuffs, the feed industry is dependent upon the ability to analyze both raw ingredients and finished feed products. Early systems of feed analysis and standards related to the development of comparative measures, allowing different feeds to be compared. The “proximate analysis system” which remains in use for basic analytical comparisons of feedstuff even today (crude protein, crude fiber, crude fat, ash, and moisture) was developed in Germany in the mid-1800s and permitted nutritional values to be ascribed to feeds, based on chemical analysis. Awareness of digestibility of nutrients gradually developed, and the energy content (from fats, proteins, and carbohydrates) of a given diet could be determined via analytical techniques. The determination and definition of calorie equivalence of fat, protein, and carbohydrate was pioneered by the US scientist, W.O. Atwater (Nichols 1994). Atwater is also credited with the general introduction of the term and definition of the calorie in an 1887 article (Hargrove 2006). Indeed, Atwater was pivotal in the analytical determination of the physical energy of feed and proximate analysis, and his work continues to underpin proximate analytical techniques in the modern feed industry.

The development of feed standards and associated analytical techniques was further supported by accumulating evidence regarding the specific nutrient requirements of individual species, including vitamin and mineral requirements.

This information was primarily generated in the mid-twentieth century, concurrent with increased intensification of agricultural animal production systems and commercialization of the feed industry. One key development was the publication of nutrient requirement tables for individual species by the Committee on Animal Nutrition of the National Research Council in the USA, in 1944. The NRC nutrient requirements for species as diverse as cattle, poultry, horses, dogs, and cats are regularly updated and continue to remain as key global animal nutrition resources and standards for diet formulation and animal nutrition research.

The feed industry has also had to remain responsive to advances in the genetic management of the raw materials produced and target species fed. Heavy genetic selection for both crop and animal species that demonstrate enhanced levels of productivity, environmental resilience, improved health and disease resistance, and in the case of many animal species from cattle to poultry, significantly improved levels of feed conversion efficiencies has resulted in the feed industry having to adapt.

Genetic improvements and enhancements of crops and other raw materials incorporated into diets can also impact on the mineral density and other nutrient characteristics. Diet formulation consequently needs to be dynamic and capable of assessing this impact and managing overall utilization of such raw materials. The application of fertilizers and other substances to crops can also impact on their value as raw ingredients, with the potential of increasing levels of substances (such as nitrates), that can be toxic to fed species at certain levels. Consequently, monitoring is critical to ensure safety at all levels of the feed chain.

## Diet Formulation

The feed industry is dependent upon the application of nutritional science in both the formulation of effective diets for target species and the safe, effective, and efficient production of such diets. Depending on the target species and ingredient availability, formulated diets will vary in

composition. For many production species, compound feeds are prepared from several ingredients, including vitamins, minerals, and other nutritional and technological additives such as antioxidants and preservatives. For other species, notably those predominantly consuming browse, fodder, or forage material, the material itself will be analyzed and that information used to develop supporting diets to ensure nutritional adequacy.

Diet formulation is typically achieved *in silico*, whereby fundamental nutritional knowledge regarding the nutritional requirements of the target species for specific production levels is met by selecting dietary ingredients at the correct levels (often on a “least cost” basis) to meet daily nutrient needs. Formulations can be developed either as “fixed” or “variable” formulas, with fixed formulas being consistent in the ingredient composition and amount, and variable formulas differing in fundamental composition, but consistent in analytical nutritional content. Economic pressures often mean that variable formulas are more viable as they permit alternations of ingredients on a cost basis while still meeting the required nutritional analytics.

Conversely, fixed formulas are often viewed as more desirable, although they can be problematic from the perspective of raw material variation between batches and can be affected by price fluctuations in raw materials. This lack of flexibility can also negatively impact upon the nutritional content and performance of the finished product. However, notably in the pet food industry, fixed formulation diets are typically regarded as preferable and attract a premium, in contrast to variable formulation diets. This is largely a consequence of the humanization of the pet food market and a perception of quality and consistency that is not necessarily based on sound nutritional science.

## Pressures on the Feed Industry

The global feed industry increasingly must meet several challenges. The sustainability of food production and allied agricultural systems is under intense scrutiny because of increasing pressures

on limited global natural resources. Land, water, and other natural resources are under threat, despite technological and productivity enhancements. Deforestation, depletion of soil integrity, and the climate change crisis are creating a situation where increased yield is expected and required, from both crops and animals, but is hampered by natural and anthropogenic factors limiting output potential. This is combined with the prediction that the world’s population is anticipated to reach 10 billion by 2050 (FAO 2017) and the pressure on the feed industry to support the human demand for animal products, especially, is clear.

Consequently, the feed industry is facing a future with substantially increased demands on production output while balancing the utilization of land and other natural resources in a safe and sustainable way. Organizations such as the International Feed Industry Federation (IFIF) respond to these demands by recognizing the need to manage the industry in an effective way. For example, the IFIF identifies three pillars as underpinning the strategic objectives of the industry: sustainability, regulatory and industry standards, and education and the sharing of best practice (IFIF 2019). Recognizing the global responsibilities of the industry is critical to its continued success and ability to meet demand while ensuring safety, integrity, and sustainability.

Sustainability is a key responsibility of the feed industry, and with the wider human population increasing taking a more critical stance over the global impact that animal and feed production has, there is a real need to demonstrate progress and improvements. Notably, the genetic advancement of both crop ingredients and fed livestock is a significant part of this. Where crops have been selected for improved yield, desiccation tolerance, and resistance to pests and diseases, this leads directly to efficiency savings and reduced environmental impact. Similarly, species, such as the broiler chicken, that demonstrate improved feed conversion efficiencies and time to slaughter, will need less nutrition and food intake over their lifespan, excrete less, and have less indirect environmental impact through fossil fuel use (Pelletier 2008). These factors are integral to the ongoing

development of sustainability actions within the feed industry.

From a global perspective, the feed industry must also remain responsive to demands and regulations from individual and collective governments, relating to aspects of feed safety, feed quality, and feed integrity. The safety of feedstuffs relates to the potential health hazard that ingredients or compound feeds could pose to fed animals, or indeed the subsequent products intended for human (or other animal) consumption (Hoorfar et al. 2011). Feed quality reflects the nutritional value of ingredients and feedstuff to support the physiological and health and welfare demands of fed animals. Consequently, feed quality will have a direct impact on the quality of end products also. Finally, feed integrity is essential to ensure the traceability and provenance of feed materials, an aspect of increasing importance given the consumer desire for specific characteristics such as organic origin as opposed to conventional feed and food production (Hoorfar et al. 2011).

## Conclusion

The global feed industry is a rapidly evolving industry and is under increasing pressure to respond and adapt to the requirements of high feed conversion efficiency, sustainability, affordability, and technological and scientific advances in terms of animal nutrition. Consumer demand for safe, nourishing, and appropriate foodstuff for their direct consumption and for feeding production, companion, and wild species similarly drives industry developments to ensure efficiency, integrity, safety, and sustainability.

Production animal nutrition has been the cornerstone of the development of the feed industry and remains a significant driver of technological advances. As the global human population continues to increase and the corresponding requirement for animal-derived products increases, the feed industry needs to continue to identify ways to enhance productivity and feed conversion efficiencies while remaining sustainable and cost-effective. Ensuring animal health and welfare is also an important aspect of the feed industry,

and progress continues to be made about understanding specific nutritional requirements of individual species, as well as advances in nutritional science. It is likely that the feed industry will continue to adopt enhanced technologies and utilize novel ingredients and additives in the drive to meet sustainability, welfare, and feed conversion efficiency goals in the future.

Feeding companion animal species involves additional challenges, notably the increased humanization of “pet” species. Consumers choosing foods for their companion animals are increasingly aware of ingredients, processing, transparency, traceability, and potential safety issues. The feed industry has a responsibility to meet these demands with a strong evidence base. Consequently, the sector of the feed industry concerned with companion animal nutrition must acknowledge the human-animal bond and how this affects consumer behavior and purchasing choices. Balancing robust scientific knowledge in the formulation and development of foodstuffs, alongside meeting the marketing requirements for a competitive and highly commercial industry, is a significant challenge for the feed industry moving forward while still factoring in affordability and sustainability.

## Cross-References

- [Bovine Diet](#)
- [Canine Diet](#)
- [Digestive System](#)
- [Husbandry](#)
- [Nutrients](#)
- [Pathogen](#)
- [Pets](#)

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## Feed Production

### ► Feed Industry



**Feeding**

- ▶ [Chondrichthyes Diet](#)

**Feeding Behavior**

- ▶ [Artiodactyla Diet](#)
- ▶ [Bovine Diet](#)
- ▶ [Marsupial Diet](#)

**Feeding Habits**

- ▶ [Bear Diet](#)
- ▶ [Mustelidae Diet](#)

**Feedstuff Manufacturing**

- ▶ [Feed Industry](#)

**Feeling of Knowing**

- ▶ [Familiarity](#)

**Feigning Death**

- ▶ [Tonic Immobility](#)

**Felidae**

- ▶ [Feline Life History](#)

**Feline Cognition**

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**Synonyms**

[Cat behavior](#); [Cat cognition](#); [Cat intelligence](#);  
[Cat-human bond](#)

**Definition**

Feline Cognition: A wide range of feline experiences that inform behavior including sensing, perceiving, learning, remembering, and reasoning.

**Introduction**

Felines are a diverse group of carnivores that belong to one of two classifications – either the big cats, *Pantherinae*, or small cats, *Felinae*, to which the domestic cat belongs. Felines inhabit a range of environments from jungles and savannahs to human homes. The domestic cat has been particularly successful in its social relationship with humans and has lived in association with humans for thousands of years, with the first domestication of cats hypothesized to have begun around 9000 years ago (Ottoni et al. 2017). Despite human’s long-standing association with both wild and domesticated cats, relatively little is known about feline cognition, especially the cognition of non-domestic feline species. However, the research that does exist provides evidence of a family of mammals that has evolved to successfully perceive and navigate their surroundings, learn about their environment, and display an array of social relationships with both asocial and social species represented.

**Perception**

Perception is the process by which an individual becomes aware of stimuli in the environment

through their senses. Domestic cats (*Felis silvestris catus*) have served as a model species for perception research over the last century, informing much of what we know about both the cat and human perception systems.

Domestic cats have several senses equipped to bring in information about the surrounding environment. Tactile and olfactory systems are functional at birth indicating these senses are vital in the early days of a kitten's life. As kittens age, their auditory system develops and kittens begin to orient to auditory stimuli at 11 days old and follow auditory stimuli at 15 days old. Slightly later, kittens begin to orient to visual stimuli, around 16 days old, and follow visual stimuli at 18 days old with the ability to complete more complex visual tasks occurring after 25 days of age (Norton 1974).

One such visual task includes the use of a visual cliff test, which assesses the animal's ability to use visual cues in their environment to perceive depth. For example, domestic kittens are placed on a raised apparatus of which half is covered in a checkerboard pattern (shallow side) and the other half is covered in Plexiglas, with a checkerboard pattern underneath at ground level (deep side). If kittens are able to determine depth, they should not cross over into the Plexiglas area, as this would be perceived as a drop-off. Indeed, kittens displayed the ability to discriminate depth at around 27 days (Walk and Gibson 1961).

Does domestication influence the perception of stimuli on these visual tasks? Another study examined the behavior of kittens of several species including tigers (*Panthera tigris*), jaguars (*Panthera onca*), and snow leopards (*Panthera uncia*) on the visual cliff test. Researchers found that just like domestic kittens, non-domesticated felines also display depth perception. However, these non-domestic kittens were slightly older than the domestic kittens tested, being between the ages of 35 and 70 days old – so it is unknown if these feline species are able to perceive depth at earlier ages. Additionally, the researchers found some differences between the *Panthera* species. Compared to the other species, snow leopards spent the longest amount of time gazing over the side of the cliff and were the only species to spend

all of their time on the shallow side of the cliff (Routtenberg and Glickman 1964). Because snow leopards are the only of these species to live in a rocky mountain habitat, this behavior may be due to differences in behavioral ecology, or differences in traits selected for in response to the environmental contingencies that species has encountered.

Similarly, as a cat navigates its environment, what it perceives is dependent, in part, on the stimuli it encountered as a kitten during the early development of its sensory systems. Several seminal experiments with the domestic cat visual system have highlighted the importance of early experience in shaping brain development and perception of the environment. For example, kittens that were reared in environments with only vertically oriented lines or, alternatively, only horizontally oriented lines, were unable to detect the alternative line orientation when tested later (Blakemore and Cooper 1970).

Cats also display flexibility in their ability to compensate for a lost sense. Blind domestic cats show more precision in locating an auditory stimulus and significantly sharper tuning of cortical neurons to auditory cues than cats with normal vision (Rauschecker and Kniepert 1994). This suggests a cat's brain can adjust in response to the loss of one sensory function by the sharpening of another modality.

Prior experience is also important in the perception of olfactory stimuli and cats appear to readily be able to distinguish between different sources of scents (for review see Vitale Shreve and Udell 2017). Normally reared domestic kittens are able to orient to their family nest region and typically show reduced distress in the presence of their family nest area. However, kittens that are initially isolated at birth from their mother and littermates, and therefore unable to learn the scent of their family, are unable to orient to their family nest region and emit distress vocalizations in response. This indicates that recognition of the family scent is dependent on experience with that olfactory cue. Adult cats also behave differently in the presence of scents from familiar and unfamiliar cats. Cats will spend significantly longer sniffing the feces or urine marks of unfamiliar

conspecifics than that of familiar conspecifics. This indicates that familiarity of the scent stimulus influences the degree of the behavioral response.

Together, research with felines, specifically the domestic cat, indicates that a fully functioning perceptual system is not only dependent on the genetic makeup of the animal but also the stimuli encountered during development of the individual.

## Learning

Skinner's (1938) influential work on the behavior of organisms would suggest significant species continuity with respect to classical and operant conditioning. Therefore, once a cat has perceived a stimulus in its environment, it is likely that similar basic learning principles apply across species. However, it is possible that variation in some aspects of learning including reinforcer preference or imitation may vary between species, populations, and even individuals.

In pioneering experiments, Thorndike (1898) placed food-deprived domestic cats in puzzle boxes in which they could escape and receive a food reward by engaging in some behavior, such as pulling a cord loop to open the door of a puzzle box. Although initially cats tended to try to escape the box through spontaneous behaviors such as clawing or biting the bars of the box or trying to squeeze through the bar slots, over repeated exposure to the box, the cat's behavior changed. Eventually, the cat may pull the cord by accident, the door to the box opens, and the cat is rewarded with both escape from the box and food. Therefore, when placed in this situation, the cat makes an association between engaging in the cord-pulling behavior and the consequences of escaping the cage (the removal of an aversive stimulus, which increases a behavior or negative reinforcement) and receiving a food reward (the addition of an appetitive stimulus which increases a behavior or positive reinforcement). These early experiments highlight the ability of cats to make associations between a behavior and a consequence, the basis for operant conditioning.

Increasingly, domestic cats are trained for entertainment outlets and to participate in discrimination tasks in scientific settings. Many zoos and sanctuaries also train captive wild felines in order to make health care procedures easier for animal caretakers and reduce stress for the felines involved. In scientific settings, domestic cats can learn to differentiate between stimuli with different characteristics, such as rectangles of varying colors, white or black, and varying orientations, horizontal or vertical (Mumma and Warren 1968). Cats can also be trained to discriminate between visual quantities of two and three groups of dots (Pisa and Agrillo 2009). Felines as a whole may have the ability to learn quantity discrimination, as lions (*Panthera leo*) also have the ability to discriminate between the vocal recordings of an individual lion compared to a group of three lions (McComb et al. 1994). However, the exact features of the stimuli being used to assess quantity in felines are unknown. For example, in dot quantity comprehension, cats could be using the spatial area covered by the dots as a discriminative cue, instead of the actual numerical values. Additionally, laboratory-reared domestic cats, which have experienced a limited range of stimuli in their environment, often display impairment on discrimination and associative learning tasks as compared to free-roaming cats, which have encountered a broader range of stimuli (Żernicki 1999). Again, this knowledge indicates that providing species-appropriate experiences, such as access to the outdoors and enrichment, is vital in increasing the welfare of felines in captivity and reducing cognitive impairment.

In tests examining what characteristics of stimuli are most salient in facilitating learning on cognitive tasks, there appear to be differences between individual cats. In one study, although the majority of domestic cats preferred use of the visual cue over the olfactory cue, one individual displayed reliable preference for the olfactory cue (Mayes et al. 2015). This finding indicates there is individual variation in what sensory cues are used in learning tasks, with this preference for one cue over another potentially shaped by that individual's prior learning experience with those cues.

Cats can also gather knowledge via observational learning, in which learning occurs by viewing the actions of another individual. In order to receive a food reward, domestic kittens had to learn to press a lever in the presence of a light, which served as the discriminative stimulus. Kittens that were able to observe their mother engaging in the task both discriminated the task and acquired the response sooner than kittens that observed a stranger cat engaging in the task. Kittens that did not observe an adult engage in the task, and were thereby left to engage with the task by trial and error, never acquired the behavioral response at the same success rate as the observational group (Norton 1974). Just like kittens, several experiments have shown adult cats can benefit from observing another individual complete the task.

It appears that not only domestic cats are capable of observational learning. Preliminary research indicates lions are also capable of social learning (Borrego 2017). Although the majority of lions were able to solve a puzzle box task independently, some were initially unsuccessful at the task. However, after the unsuccessful lions were paired with a successful lion, all but one lion was able to successfully solve the task, indicating that observation of a social companion can facilitate learning, at least in a social species. To date, no one has examined the observational learning abilities of an asocial feline species. However, with social interactions still occurring in asocial species, especially during mating and kitten rearing, social learning may still be an important aspect of learning in more solitary species, especially during early interactions with the mother and littermates.

## Social Cognition

Social cognition is one of the most understudied areas of feline cognition. One reason for this disconnect may in part be due to the misconception that felines are not especially social. Instead, research from free-roaming cats indicates that social living in domestic cats is flexible and dependent on both life experience and the

distribution of food, shelter, and mate resources (Bradshaw and Cameron-Beaumont 2000; Turner 2014). Domestic cats are a facultatively social animal, meaning they can live socially or solitarily, and therefore display a wide range of nonobligatory social behavior toward conspecifics and humans. Additionally, although only two other feline species, lions and cheetahs (*Acinonyx jubatus*), commonly live in social groups, other asocial species still engage in social behavior with one another during breeding, kitten rearing, and territorial defense, and much of this social behavior has gone unstudied (Elbroch et al. 2017).

Because of the ability of cats to discriminate between stimuli in the environment, it is no surprise domestic cats can discriminate between both conspecifics and humans. Free-roaming cats have preferred associates within the colony, or individuals a cat prefers to spend time near and displays affiliative interactions toward (Crowell-Davis et al. 2004). This indicates that domestic cats can not only differentiate individual conspecifics within a colony but also form social relationships with certain individuals over others. Similarly, lions, which form socially complex associations with one another, also have this ability. Male lions are able to differentiate between roars produced by males and females, and female lions are able to discriminate between roars of familiar resident males and unfamiliar males (Borrego 2017). Overall, it appears that felines, at least social species, have the capacity to differentiate between conspecifics.

Domestic cats also appear to behave differently in response to familiar and unfamiliar humans. Behaviorally, cats display a significantly higher body orienting response (movement of ears and head) to their owner's voice compared to a stranger's voice (Saito and Shinozuka 2013). Physiologically, cats exhibit significantly higher blood pressure rates in the presence of their owner compared to an unfamiliar human, which in other species has been suggested to indicate anticipation of interaction with a bonded individual (Slingerland et al. 2008). However, some studies have found that domestic cats spend more time in association with an unfamiliar human, indicating

that familiarity is not the only mechanism influencing social behavior; novelty may also be a factor (Podberscek et al. 1991).

Humans provide a variety of attentional, emotional, and gestural cues during interaction with cats, and research has begun to explore the sensitivity of domestic cats to these cues. One such study examined how cats behaved in the presence of an unfamiliar human who was either sitting passively, ignoring the cat and reading a book, or interacting freely with the cat. Cats displayed more social behaviors such as allorubbing and playing during the interactive phase, indicating the attentional state of the human can directly influence the social behavior of cats (Mertens and Turner 1988).

More recent research has examined if pet cats can detect the emotional state of a human and adjust their behavior in response. Using a social referencing paradigm, the cats are placed in the presence of an unfamiliar, potentially frightening stimulus, often a desk fan with streamers attached. The cats are then exposed to one of two human emotional groups, with some cats experiencing their owners providing a positive emotional message toward the fan and the other cats experiencing a negative emotional message to the fan. Cats were found to gaze at their owner's face and the unfamiliar stimulus at similar rates found in domestic dogs and also adjusted their behavior in response to their owner's emotional message to some extent. Cats in the negative group more frequently gazed at the room exit (the only way out of the room), were active and more quick (potentially preparing for escape), and interacted with their owner more frequently (potentially indicating security-seeking behavior) than cats in the positive emotional group (Merola et al. 2015).

Further evidence that domestic cats are sensitive to human cues has come from research that presented cats with human facial, postural, and vocal cues that expressed happiness or anger from both an unfamiliar human and their owner. Although the researchers found cats were not sensitive to the vocal cues and were only moderately sensitive to the visual cues, they found cats were most sensitive to the happy visual cues given off by their owner and were significantly more

likely to interact with their owner when they displayed happy visual cues over angry cues, although no difference was seen with the unfamiliar human (Galvan and Vonk 2016). Cats also appear to be proficient in following pointing gestures, another physical human cue, and are able to follow human pointing to successfully find the location of a food reward (Miklósi et al. 2005). Overall, domestic cats seem to be able to pick up on human cues and adjust their behavior to some extent, although the familiarity of the human providing the cues, and possibly the reinforcement history of the cues given off by this individual, may influence the degree to which cats pick up on these cues.

Cats appear to be able to use gazing at the owner's face as a way to pick up social information and adjust their behavior accordingly. However, cats may use gazing differently depending on the situation presented. For example, when presented with an unsolvable food task, cats persisted and engaged with the task for longer periods of time and infrequently gazed at their owners, as compared to dogs that gazed at the owner earlier and for longer periods of time (Miklósi et al. 2005). Therefore, cats may use gazing in social situations, such as when presented with an ambiguous stimulus or using physical human cues, but may be less likely to gaze at the owner for help on tasks involving physical problem solving.

What happens when non-domesticated feline species encounter humans? As would be expected, non-socialized big cats do not have the same response to humans as a domestic cat. Although understudied, preliminary research indicates that big cats kept in captivity are more stressed when they see human visitors through their enclosure. However, affiliative behavior toward humans can be seen in socialized, non-domesticated *Felidae* species. Researchers found several socialized *Felidae* lineages, including the domestic cat, caracal, lynx, and ocelot lineages, display affiliative behavior such as allorubbing, licking, and tactile contact toward zookeepers (Cameron-Beaumont et al. 2002). Interestingly, the highest proportion of affiliative behavior came from the ocelot lineage, which diverged



from the domestic cat lineage millions of years ago. This indicates that *Felidae* as a whole may have a preadaptation for domestication if other environmental criteria are met.

Finally, the individual characteristics, or personality, of a cat may influence the way they behave toward social companions. Personality can be defined in many ways, but broadly it is a prolonged state in which behavioral responses are relatively stable over time and circumstances (Gosling 2001). Many scientific studies have indicated domestic cats do indeed display relatively consistent behavioral patterns, with individual differences between kittens within a litter being detected as early as 5 days old and behavioral patterns stabilizing around 3–5 weeks old (for review see Vitale Shreve and Udell 2015). Indeed, the individuality of the cat is one of the largest factors influencing how they behave socially with humans (Mertens and Turner 1988). Cat personality is influenced by a combination of both genetics and life experience; therefore domestic cats exist on a continuum of social cognition.

Research with lions has also demonstrated individual variation within the species, finding substantial variability in how lions respond to conflict. When presented with the roar of a possible intruder, female lions behave in various ways, with some females consistently cooperating and other lions only cooperating when it is absolutely necessary (Heinsohn and Packer 1995). Additionally, this behavioral response appears early in life and persists into adulthood, indicating it is a relatively stable behavioral pattern and thereby potentially an aspect of lion personality.

This individuality of domestic cats in response to humans can be seen in a recent study examining the preferences of cats. Cats underwent a preference assessment in which they were placed with several categories of stimuli – items in human social interaction, food, toy, and scent categories. Individual cats displayed a range of preferences within these categories. Some cats most preferred to be pet in the human interaction treatment, whereas others most preferred playing, while again some did not prefer the social stimulus at all. For each category cats displayed a range of preferences, forming a list of most preferred items

unique to each individual (Vitale Shreve et al. 2017). This research indicates that individual variability for preferences exists in cats and, just like personality, is most likely due to a combination of genetic, experiential, and motivational mechanisms. Additionally, in a final treatment, where each individual cat's most preferred social interaction, food, toy, and scent item were presented simultaneously, the majority of cats displayed a preference for the social stimulus – even when presented with their most preferred food, toy, and scent item, thereby foregoing interaction with those items. The next most preferred category was food, followed by toys, then scent. Again, this research suggests that preference for social interaction may lay on a continuum, but does the sociality of an individual influence any other cognitive abilities?

Although not well studied, research indicates that the sociality of a species may indeed influence their cognitive abilities. Several feline species and one non-feline species were compared on their ability to solve a puzzle box task. Researchers found that lions and spotted hyenas (*Crocuta crocuta*), both social species, outperformed leopards (*Panthera pardus*) and tigers, asocial species. Although the puzzle box task did not contain a social component, it may be that sociality influences the cognition of a species (Borrego 2017). Future research could utilize the facultative nature of the domestic cat, which exists in both solitary and social states, to further examine this hypothesis and assess if sociality has a direct influence on cognitive abilities such as problem solving tasks.

## Conclusion

With domestic cat ownership growing every year, it is no surprise that more research is being conducted on their cognition in the recent years. However, there is still much to learn about how cats of all species sense and learn about the world around them and decide to act upon the individuals and experiences they encounter. Not only will future research provide more information as to the cognition of the cats we share our homes with; comparisons of domestic and non-domestic feline

species may also address the extent to which domestication alters the cognition of a species and how living socially or solitarily influences other aspects of cognition.

## Cross-References

- [Affiliative Bond](#)
- [Allogrooming](#)
- [Associative Learning](#)
- [Cognition](#)
- [Discrimination Learning](#)
- [Edward Thorndike](#)
- [Facultative Trait](#)
- [Familiarity](#)
- [Feline Communication](#)
- [Feline Sensory Systems](#)
- [Human-Animal Interaction](#)
- [Learning](#)
- [Perception](#)
- [Personality in Animals](#)
- [Pets](#)
- [Problem-Solving](#)
- [Reinforcement](#)
- [Social Intelligence Hypothesis](#)
- [Social Learning](#)
- [Visual Cliff, The](#)
- [Visual Perception](#)

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## Feline Communication

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## Synonyms

Cat communication

## Definition

Cats communicate by visual, vocal, olfactory, and tactile signals. Among carnivores, cats are considered as relatively less social, but they still have a rich signaling repertoire. They communicate directly in social contact, as well as by leaving long-term messages. Domestic cats have to communicate efficiently with conspecifics as well as with human caretakers.

## Introduction

Domestic cats (*Felis catus*) are solitary hunters, but, at the same time, they have a potential to live as social animals. Therefore, cats have flexible social behavior like other carnivores (Macdonald 1983). Indeed, a human-made environment provided cats with ample and secure food resources, so, during domestication, they started to live at higher densities, unlike their ancestral species (*Felis silvestris lybica*), which are solitary animals. By entering human settlements, the cats formed groups with high intraspecific tolerance. These changes in the social organization and group density led to an evolutionary change in the communication system used by the domestic cat. Indeed, solitary and group-living individuals may choose different modalities of communication (Bradshaw and Cameron-Beaumont 2000). Furthermore, the relationship with humans has generated additional communication signals specific to cat-human interactions (Crowell-Davis 2005). Cats can communicate their mood and intention (Crowell-Davis 2005). Information can

be conveyed as visual, vocal, olfactory, and tactile signals (e.g., Beaver 2003; Bradshaw and Cameron-Beaumont 2000).

## Vocal Communication

The domestic cat is one of the most vocal carnivores (Bradshaw 1992; Crowell-Davis et al. 2004). Vocalization may be partly inborn and partly developed by auditory feedback that cats get through ontogenetic development (Hubka et al. 2015). In home-raised cats, Moelk (1944) described 16 different voice patterns and divided them into three main categories with relation to the mouth opening. The first category is “murmurs,” i.e., sounds produced while the mouth is kept closed. The second category is “vowel-patterns” – sounds produced while the mouth is opened and then slowly closed. The third category includes sounds produced while the mouth is opened in a constant position (Beaver 2003; Moelk 1944).

“Murmur” patterns are generally considered as indicators of a friendly or relaxed emotional state and contentment, because they include acknowledgment, call, grunt, and purr (Beaver 2003; Stanton et al. 2015). However, cats can purr in any conditions, pleasant and unpleasant, and in many different contexts, such as when they are happy, content, or aroused. Therefore, purr may be related to high emotional arousal, regardless of situation (Casey 2007).

Cats purr when they are petted by their owners, when they are rubbing against an object, rolling on the ground, or when falling asleep. Furthermore, the queen is purring during nursing, and a purr is a part of a friendly greeting and care-soliciting call. Hence, in these cases, the purr can be considered as a sign of contentment. On the other hand, cats will also purr when they are distressed or in pain, such as during birth or before death following a chronic disease, so maybe the purr has a self-soothing and healing function (Casey 2007; Crowell-Davis 2005).

Finally, sometimes cats purr while they are trying to seek something from their owners, e.g., food, attention, or access to the outdoors. This is called a solicitation purr, and it sounds more like

cry: it is lower pitched, harsher, and quicker or more urgent, so it differs from the natural low-pitched purr (McComb et al. 2009).

The purr is unique to the family Felidae. While purring, domestic cats are able to produce between 25 and 150 vibrations per second. Depending on the context, purrs have different forms. Cats purr during inhalation and exhalation, but the inhalation sound is usually louder, longer, and a lower-pitched component of the purr (Beaver 2003; Case 2010).

“Vowel patterns” are the second group of sound produced by cats. They are produced when the cat’s mouth is first open and then slowly closed. According to Beaver (2003), “vowel patterns” are anger wail, bewilderment, complaint, demand, mating cry produced by estrus females, Siamese vocalizations, and ultrasonic variations. These sounds are more articulated and are related to particular situations such as those involving goal-seeking or frustration with goal seeking, as well as when a cat is soliciting the help of the owner (Moelk 1944).

The third group is the “strained-intensity patterns,” which are vocal patterns produced with the mouth open. “Strained-intensity patterns” are growl, hiss, mating cry of a tomcat, refusal, scream, and snarl (Beaver 2003). They are noisy and expressed in intensely emotional circumstances, such as when a cat is nervous, angry, ready to attack or withdraw, and as a mating demand. In dockyard cats, females in estrus were not heard to call but toms that were seeking estrus females emitted a characteristic cry (Dards 1983). They may be expressed in aggressive confrontations, such as growls, yowls and snarls, or in defense, such as a hiss and a spit (Casey 2007).

Vocal communication is very important for mother-kitten relationships. Kittens can distinguish their mothers’ vocalization, “greeting chirps” and “meows,” from the vocalization of other cats by 3 weeks of age (Szenczi et al. 2016). On the other hand, kittens use several special calls that diminish as they get older, and the mother responds to these calls by a chirp kind of trill. Therefore, certain vocalizations are responsible for maintaining connections between them (Casey 2007).

Interestingly, cats living in feral colonies tend to be much quieter than domestic cats but can be loud during breeding season. Shimizu (2001) described three distinct types of vocalization in feral cats: rutting cry, yowl, and mew. The rutting cry can be heard only in breeding seasons, and it is frequently produced by males. Furthermore, in laboratory cats, which are less socialized with humans, the vocal repertoire is extremely limited (Rosenblatt and Schneirla 1962).

It is therefore considered that the meow is something that cats mostly use to communicate with humans and not for communication with other cats. As every cat learns the best way to communicate with its owner, huge individual variations can be observed in vocalizations. Cats' vocalizations towards their owners are shaped by operant learning, so the cat will adapt the sound that works best on their owner (Casey 2007). Domestic cats do not have a context-specific repertoire of human-directed vocalization as such, but cat owners with experience can become successful in context classification of their cats' meows (Ellis et al. 2015; Nicastro and Owren 2003). When vocalizing, cats vary their intonation to indicate different emotions, and humans can distinguish them based on signals used to express emotions in human speech (Schötz 2014).

In comparison of meow vocalizations by domestic cats (*Felis catus*) and African wild cats (*Felis silvestris lybica*), human listeners considered domestic cat meows as more pleasant sounding than wild cat vocalizations, what may be considered as a consequence of domestication pressure on meows from people (Nicastro 2004).

Finally, being more or less vocal is a part of a cat's personality (Litchfield et al. 2017). However, some cat breeds are a lot more vocal than other cats, as for example, oriental breeds, such as the Burmese and Siamese (Beaver 2003; Landsberg et al. 2003).

## Olfactory Communication

For cats, communication with odor means leaving long-term messages with urine, feces, by scratching and by rubbing alongside their body,

as well as direct smelling of another cat (Bradshaw and Cameron-Beaumont 2000). Cats have an excellent sense of smell and the capacity of cats' olfactory communication is still not fully understood (Crowell-Davis 2005). Furthermore, general body odor is important for mother cats to recognize their kittens from others (Bánszegi et al. 2017).

Having a solitary wild ancestor, domestic cats still have evolutionarily driven motivation to defend and demarcate the hunting territory. They mark the boundaries of their territory with their scent in the form of urine and feces, as well as by scratching to leave scent from interdigital glands (Crowell-Davis 2005). For solitary animals, remotely messaging by scent-marking is an important aspect of their behavior because they can maintain distance between each other. Furthermore, it permits a delay of several hours or days between the deposition of the signal and its reception. In this way, they can maintain the territory without the risk of potentially dangerous encounters and conflicts with conspecifics (Bradshaw and Cameron-Beaumont 2000; Casey 2007).

Olfactory messages are left in prominent places or places where other cats are expected to pass. These messages can have different meanings to the recipient animal, such as which individual left the scent, particularly with regard to reproductive status and, possibly, the emotional state of the signaler, and the time when the message was left (Casey 2007; Crowell-Davis 2005).

Cats can urinate in two different postures, one is when they squat and the other is when they intentionally scent-mark by spraying. After urination in squatting position, cats cover the urine with soil or litter, but other cats may still sniff it. Squatting is observed in kittens, juveniles, and adult females (Bradshaw and Cameron-Beaumont 2000; Case 2010).

Spraying behavior is mainly used by intact male cats as sexual marking behavior but is naturally performed by all cats, regardless of their gender and sexual status. When a cat is spraying, it backs up to a vertical object, and urine pulses backwards, while its tail is raised and quivering. In this way, cats mark their home range, especially



on pathways, crossings, and boundaries, and leave a scent message to other members of their social group, cats from outside the group, but also for itself (Bradshaw and Cameron-Beaumont 2000; Casey 2007; Crowell-Davis 2005).

When cats are kept permanently inside the house, urine spraying may occur as a sign of social conflict among cats or as a sign of stress and anxiety. Cats can be in conflict with the cats in the same home in a multiple-cat household or with outdoor cats that walk and spray around the house. In cats, stress and anxiety can be caused by some environmental changes, such as when owners are moving house, having a new baby, or are visited by some guests (Case 2010; Landsberg et al. 2003). Therefore, for cats, chemical cues can serve as a coping strategy because they can reduce stress and anxiety as well as increase feelings of self-assurance. When an individual cat leaves messages for herself, scent marks could be a reminder of something unpleasant or make her feel more secure in her environment (Casey 2007; Vitale Shreve and Udell 2017).

Therefore, spraying behavior is a complex signal, where the scent is left as a long-term signal, while display can be a visual signal meant to draw attention of others. Cats show a great interest for urine marks left from other cats and investigate it by sniffing (Bradshaw and Cameron-Beaumont 2000). When cats smell the urine mark of another, they are not intimidated and they do not tend to cover it with their own scent, and they spend a lot of time investigating the smell of urine of unknown individuals (Beaver 2003; Case 2010).

The odor of sprayed urine is strong and sharp and consists of different chemical compounds. Maybe the two most important compounds are feline and isovalthene, whose microbial and oxidative degradation increase odor after deposition. Intact male urine odor is stronger than that of females, and it changes with age (Bradshaw and Cameron-Beaumont 2000). However, the chemical composition of urine can differ, so the urine may not always be giving the same signal. For example, it may comprise different pheromones, which are deposited in the spray mark, and this may vary with the emotional state of the signaler (Casey 2007).

Before defecation, domestic cats dig a small hole, and afterwards they bury the feces. However, occasionally they may leave feces uncovered at certain locations probably as a territorial marker for another cats (Crowell-Davis 2005; Macdonald et al. 1987).

Rubbing behavior is another way in which cats use scent marks. They rub against other individuals, cats, or human companions, and different objects. Cats have scent producing glands on their skin: enlarged sebaceous glands at the corners of the mouth, on the chin, temporal glands on the side of the forehead, in the ear canals, in the perianal area, at the base of the tail, and all along the length of the tail (Beaver 2003; Case 2010). When cats are rubbing (or bunting) against others, such behavior suggests a social relationship. Cats like to rub against others, as well as when they are stroked on the gland areas – and deposition of odors on others suggests friendly relationships (Crowell-Davis 2005). Cats sometimes purr when they are rubbing their heads on each other or against human companions, so this may also be a composite signal.

Furthermore, object rubbing is how cats deposit and pick up some scents. Specifically, head rubbing (bunting) seems to happen in the core areas of a cat's territory, performed on the visually prominent objects. This behavior seems to be highly correlated with comfort activities, the solicitation of social attention, and positive emotional state (Bradshaw and Cameron-Beaumont 2000; Casey 2007).

Scratching is another composite signal that has multiple functions for cats, where they leave scent marks from the glands in the paws. Additionally, the resulting visual signal includes leaving long-term scratches on the surface of trees, fences, sofas and other furniture, as well as on special cat scratching posts (Case 2010). In general, scratching is very important for cats because it allows them to trim their claws, to stretch front legs, shoulders and back but also to exercise the muscles and tendons involved in claw protraction and retraction, which they need for hunting (Casey 2007). Cats may scratch horizontal or vertical surfaces

that have a rough texture, such as wood bark or heavy cloth, and they frequently use the same site (Case 2010; Crowell-Davis 2005).

## Visual Communication

Living in social groups places an additional evolutionary pressure on cats to communicate more by visual signals given by body positions and movements. However, cats are solitary predators, so they lack the complex visual signaling repertoire that can be seen in social predators. In comparison with some other carnivores (e.g., wolves), cats have immobile flat faces, with less facial muscles that enable subtle changes in expression. Furthermore, the coloration of cats' fur is not specifically adapted for signaling (Bradshaw and Cameron-Beaumont 2000).

Cats can use several communicative body postures for maintaining harmony in a social group, but they are probably less important for the cat than for more social animals (Beaver 2003). They have a capacity to communicate some emotions to each other and to human companions. Their visual signals may include the orientation of the cat's whiskers and ears, the size of a pupil, a position and movement of the tail, and the whole body posture. Having limited body language to a certain degree, cats do not have a range of appeasement signals for resolving the social conflict, so they tend to display either defensive or offensive aggression or avoidance when faced with aggressive individuals (Case 2010; Casey 2007).

Facial expressions in cats are subtle, but it can be estimated how the cat is feeling by paying attention to the eyes, ears, and whiskers. The ears and whiskers will be pointed forward when the cat feels friendly and when she is interested in a particular person or an object. However, if the cat feels scared or threatened, her ears will be pressed back and down, while the whiskers will be pulled back. When cats are frustrated or angry, their ears are pulled backwards and the whiskers can be protruded from the face (Beaver 2003; Bradshaw and Cameron-Beaumont 2000).

The cat's eyes can also signal pleasure or agitation. For example, relaxed cats may softly gaze with their eyes half closed and slow blinking eyelids. On the other hand, when the cat is anxious, fearful or highly aroused, her pupils will be dilated. Cats can perceive direct gaze as a threat, and therefore, gaze aversion is a signal that a cat is avoiding a conflict. Constricted pupils are a signal that a cat feels tense and potentially aggressive (Case 2010).

In agonistic encounters, cats may display offensive or defensive threat and fear. Additionally, cats can experience conflicting emotions, such as fear and anger at the same time, and then it is more possible that they will show the arched body posture. Some postures adopted by a cat can be considered as the cat's efforts to look bigger. An aggressive, attacking cat in offensive threat will stay in full height, with a rigid body posture, piloerected coat, straightforward view, and the tail is up. In defensive threat, the cat will turn side-on to the opponent, with arched back, ears flattened back, bared teeth, and wrinkled nose (Beaver 2003). On the other hand, a fearful cat that wants to withdraw from an agonistic encounter will crouch on the ground, have a low and tucked body posture, and flattened ears (Bradshaw and Cameron-Beaumont 2000). Offensive and defensive threatening cats can be described as "active responders," while fearful individuals are "passive responders" (Casey 2007).

A relaxed and content cat may stretch out, lie on its side with visible tail, but it may also roll over and expose its abdomen as a sign of trust. By rolling on its side or back, cats expose abdomen, i.e., the most vulnerable part of their body (Beaver 2003). In addition, cat may expose its belly to solicit play by their owners, when rolling to rub its back on a ground or as a part of aggressive display (Case 2010; Stanton et al. 2015). While Crowell-Davis et al. (2004) consider rolling over as submissive behavior, Case (2010) states that this is learned behavior and not sign of submission.

In visual communication, the tail postures and movements can be important for sending a message. In fact, the tail may be the most expressive part of the cat's body and the easiest one for

humans to read (Casey 2007). A usual tail position is roughly flat. An arched tail or inverted-U posture tail may be seen during aggressive encounters or conflicts, while an anxious or fearful cat will lower and tuck the tail closely in between her legs or around its body (Beaver 2003).

In greetings and friendly encounters, the cat will raise the tail vertically. The tail up is displayed when an adult individual meets another one as a “friendly” signal (Cafazzo and Natoli 2009; Casey 2007). Furthermore, kittens greet their mother and other adult individuals in this way. The whole greeting behavior with tail up of kittens, including rubbing their forehead and then upper part of the head against mother’s chin, may be considered as a display that should inhibit the potential aggressiveness of adult cats. Additionally, during domestication, this juvenile behavior might have been conserved in the adult cats (neoteny) to inhibit aggressive encounters because of the increased number of social interactions (Cafazzo and Natoli 2009).

The movement of the tail can also be very expressive and quite subtle, too. When a cat is flicking tail, she is signaling that she is in uncomfortable situation. An angry cat will thrash with a tail, while a swishing tail will be seen in a cat that is frustrated. The function of the twitching tip of the tail is still not fully understood (Casey 2007).

## Tactile Communication

This form of communication is important for feral cats of the same colony and can be observed in cats from the same household as well. Tactile communication includes resting together (lying or sitting together), allorubbing (cat-cat rubbing their heads, flanks, or tail), allogrooming (one cat licking another), nose touching, or a simple tail contact (Bradshaw and Cameron-Beaumont 2000; Van den Bos 1996). Furthermore, cats use their tails to stroke each other or wrap their tails together. This may enhance social bonding and social harmony within a group (Crowell-Davis et al. 2004).

When allorubbing, cats wipe their heads, bodies, and tails against each other and repeat this for several minutes. It is speculated that this behavior has multiple functions. Because allorubbing cats often purr, this behavior may have social significance similar to human hugging. Furthermore, in this way, cats exchange their scent, which may be important for group cohesion (Barry and Crowell-Davis 1999).

Allogrooming can be observed in cats, where in indoor cat colonies, usually individuals that are more aggressive groom less aggressive individuals more frequently (Van den Bos 1998). On the other hand, Barry and Crowell-Davis (1999) observed indoor-only altered domestic cats, and they did not find differences in this behavior display in cats of different gender, between household types, or between recipients of the affiliative behaviors.

Finally, it is important to notice that most of the communicative signals are in fact composite, and their meaning should be explained in the context of all body signaling. Indeed, animals have the flexibility to combine signals in patterns that carry particular meaning. For example, when different body postures are explained, they may include signaling by ears, eyes, and tails, while this body display is accompanied by a vocalization and the odor of the whole body. Similarly, scratches are obvious composite signals with a visual and olfactory message.

## Feline Behavioral and Welfare Problems Due to Incomplete Understanding of Communication

There are several behavioral problems that cat owners report and that are related with cat communication. However, more important is the influence on cat’s welfare because sometimes people relinquish their cats to shelters or they simply leave them on a street. It is particularly sad that some of the complaints are due to the cat’s normal behavior, such as scratching. In some countries, it is still permissible to declaw cats to stop furniture destruction (Beaver 2003). Because scratching is important for cats as a visual and olfactory signal, such a procedure has to reduce cats’ welfare.

Sometimes cats are accused of aggressive behavior toward humans, while owners do not understand and appreciate the cats' communicative signals, such as tail flicking, the way cats signal that they are uncomfortable with a situation, and that the owner needs to retreat. On the other hand, cat-cat aggression occurs because humans dictate which cats have to live together.

Moreover, leaving "pee-mails," i.e., spraying vertical surfaces, is a behavior that cats use to communicate between each other but also to make it easy for themselves when they are stressed (Vitale Shreve and Udell 2017). However, cats' urine has a pungent smell for humans and may be the reason why some cats lose homes or are even euthanized. This problem behavior may be more frequent in Bengal and Birman cat breeds, while it is less present in Maine coon cats (Wilhelmy et al. 2016).

Finally, some cats may vocalize extensively, which is also considered a nuisance for pet owners. Because this is more frequently present in oriental breeds, the breed standards should be reconsidered to reduce the problem. In Tonkinese cats, this behavioral problem is more prominent, and less present in Abyssinian and Birman cats (Wilhelmy et al. 2016). Finally, increased vocalization occurs most commonly in elderly cats and can be a symptom of some physical illness (Landsberg et al. 2003).

## Conclusion

Cats have made an extraordinary adaption from solitary animals that mostly used distant communication signals, to social group members that are able to exchange information in close proximity. They have also succeeded to develop a communication catalogue for humans, as well as for other animals that they have to live with in human households. However, human beings can probably comprehend the meaning of vocal and visual signaling, but olfactory communication is often overlooked in cat-human communication. Future research may bring more understanding and consequently higher quality of life for domesticated cats.

## Cross-References

- [Animal Welfare](#)
- [Feline Cognition](#)
- [Feline Diet](#)
- [Feline Life History](#)
- [Feline Locomotion](#)
- [Feline Morphology](#)
- [Feline Navigation](#)
- [Feline Sensory Systems](#)
- [Pets](#)
- [Pheromone](#)
- [Scent-Marking](#)
- [Socialization](#)
- [Territory Defense](#)

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## Feline Cult

### ► Sacred Cats

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## Feline Diet

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## Synonyms

Cat diet

## Definition

The necessary foods commonly eaten to provide nourishment and sustenance specific to species within family Felidae.

## Introduction

Forty-one extant felid species exist today, grouped within two subfamilies of the Felidae family: *Pantherinae* and *Felinae* (Kitchener et al. 2017). These species possess a multitude of physical



characteristics, each combining into a singular morphology that is considered similar among all cats. Many shared physical characteristics among felids can be attributed to an overall morphology adapted and evolved for hunting to meet the specialized hypercarnivorous diet which all cats thrive upon (Sunquist and Sunquist 2002). Individuals within felid species require a much higher percentage of diet from protein and possess a morphology that reflects an ability to hunt, capture, and kill live prey (Sunquist and Sunquist 2002).

Though a singular morphology exists as a result of diet similarities in felids, felid species also exhibit distinctive diet differences. As sea levels dropped and land bridges appeared millions of years ago, ancestral individuals of modern-day felids dispersed and emigrated from Asia to other continents (O'Brien and Johnson 2007). These migrations allowed for the formation of new lineages in which individuals could adapt to new environments and, over time, evolve into today's existing unique felid species (O'Brien and Johnson 2007). As a result, felid species vary in size and are exposed to differing prey options, both of which have allowed for the establishment of variations in diet.

## Diet Nutritional Requirements

Although numerous carnivorous felid species exist, most research on dietary nutritional needs have been conducted on the domestic cat, *Felis catus* (Howard and Allen 2007; Morris 2002). Therefore, nutritional requirements for diets composed of commercially prepared raw-meat diets for captive nondomestic felid species are determined utilizing information previously studied and discovered regarding domestic cats (Howard and Allen 2007). The nutritional information gleaned through studies of the domestic cat has proven successful in providing the necessary nutritional requirements for captive nondomestic felid species (Howard and Allen 2007). For the purposes of this entry, the general nutritional requirements determined to date for domestic cats will be discussed and applied for all felid species.

Felids are “obligate,” or “strict,” carnivores, meaning they require meat in order to survive (Case et al. 2011; Gates 2019). The felid diet must be primarily composed of high-protein meat due to nutritional requirements that can only be satisfied through consuming animal tissue (Case et al. 2011). The highly specific nutrient requirements of the high-protein meat diets felids consume are believed to have evolved as a result of adaptations due to evolutionary pressures acting upon metabolic enzymes in cats (Morris 2002). Eisert (2011), however, postulated that the high-protein nutritional requirement noteworthy in hypercarnivorous felid diets may actually be a secondary phenomenon. Eisert (2011) hypothesized that the required diet in felids may be the result of high glucose demands from high glucose-requiring tissues, including the brain, that is fulfilled using amino acids supplied by protein to synthesize glucose through a process known as gluconeogenesis.

Aside from the high-protein requirement that only animal tissue can satisfy for strictly carnivorous cats, felids also require multiple nutrients that can only be obtained from animal sources due to an inability to synthesize such nutrients (Case et al. 2011; Morris 2002). These nutrients include arginine, taurine, water-soluble B vitamins, vitamin A, vitamin D, and arachidonic acid (Case et al. 2011; Morris 2002; Zoran 2002). Arginine, an amino acid necessary in the urea cycle, is considered a highly essential nutrient in the felid diet, with the lack of arginine in a single meal observed to induce hyperammonemia, acute ammonia intoxication, and hyperglycemia in cats, resulting in swift death (Morris 2002; Morris and Rogers 1978). Taurine, a highly studied amino acid in the felid diet, is necessary for bile salt formation and must be obtained by felids from outside dietary sources due to an inability to endogenously produce sufficient amounts (Howard and Allen 2007). Water-soluble B vitamins, including niacin, thiamin, and pyridoxine, are unable to be stored in the body and must be continuously supplemented using diet as well (Zoran 2002).

Necessary for healthy vision, skin, bone growth, and reproduction, vitamin A can be

converted into its active form from carotenoids, such as beta-carotene, in plants using an enzyme found in the intestines of certain animal species (Case et al. 2011). As felids do not possess this specific enzyme, referred to as beta-carotene 15,15'-dioxygenase, they are unable to convert plant-based carotenoids into vitamin A and therefore require animal-based dietary sources that can supply preformed active vitamin A (Case et al. 2011; Lakshmanan et al. 1972). Vitamin D, important for well-balanced calcium and phosphorus within the body, is also required from dietary sources for felids due to an inability to synthesize the vitamin endogenously (Morris 2002; Zoran 2002). Aside from fat providing energy and food palatability for felids, essential fatty acids, such as linoleic acid and arachidonic acid, are crucial for skin and coat condition, kidney function, and reproduction (Howard and Allen 2007). Unlike most animal species, felids lack sufficient activity of necessary enzymes for converting the essential fatty acid known as linoleic acid into a necessary essential fatty acid known as arachidonic acid, though they can obtain it from animal sources as well (Howard and Allen 2007; Zoran 2002). Felids are capable of meeting dietary requirements for arachidonic acid, vitamin A, and vitamin D through the consumption of animal fats which contain ample amounts of each (Case et al. 2011; Zoran 2002).

## Form of Diet

To satisfy the high-protein, obligate, hypercarnivorous diet composed almost solely of meat with the highly specialized nutritional requirements discussed above, felid species eat food in several different forms. Domestic cats are typically fed commercially produced dry foods, though a canned-food or even raw-meat diet has been advocated for in recent years due to negative health effects that have been associated with eating a commercial diet (Bernard 2004; Pierson 2013). As previously noted, captive nondomestic felid species, housed in North American zoos, are typically fed frozen or canned commercially prepared raw-meat diets, composed of horse or beef,

and enhanced nutritionally with vitamin and mineral additives, though some captive felids are also fed supplemental meat diets composed of skeletal muscle meat from horse, beef, deer, or turkey, and added vitamins (Bechert et al. 2002; Howard and Allen 2007). In contrast, "whole-prey diets," sometimes used in zoos and composed of carcasses, provide a well-balanced diet that more closely resembles the diets of wild felids (Howard and Allen 2007). The commercial diets mentioned above are nutritionally similar to consuming whole prey; however, captive felids eating whole-prey diets and wild felids eating whole prey are also exposed to hide, hair, and hooves that their captive counterparts eating commercially prepared diets are not (Howard and Allen 2007).

Felid species hunt a variety of prey as a result of differences in size and environmental location. For example, leopards (*Panthera pardus*) located in Africa typically hunt prey including young wildebeest, impala, varying small antelope species, warthogs, young baboons, small animals, and small birds (Fraser 2012). In contrast, snow leopards (*Panthera uncia*) found in Asia typically prey upon blue sheep and ibex and unlike other felid species will eat carrion (Fraser 2012). A smaller species comparatively to both leopard species previously mentioned, the bobcat (*Lynx rufus*) located in North America primarily hunts hares, rabbits, and occasionally small domestic livestock (Fraser 2012). As shown by the abovementioned species, the diet spectrum ranges greatly among felids due to the respective environment and prey that each species is exposed to.

## Diet Preferences

Multiple studies have found nutritional profile to be a large determining factor, potentially even over taste, when felids choose foods to eat or include in their diets (Watson 2011). When given dietary choices, felids have shown preference for fat- and protein-rich foods comparatively with foods of lower fat and protein content and also avoided diets high in casein (Beauchamp et al. 1977; Cook et al. 1985). Similarly, Hewson-

Hughes et al. (2011) noted that felids can regulate macronutrients within their diets, consistently seeking out food combinations equating to a daily intake of 420 kJ (kilojoules) of protein, 280 kJ of fat, and 100 kJ of carbohydrate, or 52% protein, 36% fat, and 12% carbohydrate, when provided with various wet and dry foods (Hewson-Hughes et al. 2011). Hewson-Hughes et al. (2011) also noted a “carbohydrate intake ceiling” in which cats would restrict dietary intake of carbohydrates to a maximum of approximately 300 kJ per day.

However, dietary preferences are not only affected by nutritional profile as olfactory and gustatory sensing impact food preference as well. Felids partially rely upon both taste and smell for determining what food to ingest or if the food is considered ingestible (Fraser 2012). Not unlike numerous other species within Carnivora, the taste buds of a felid, located on the frontal portion of the tongue, show no preference for carbohydrate sweeteners due to genetics resulting in a lack of sweet taste receptors (Beauchamp et al. 1977; Fraser 2012; Jiang et al. 2012; Li et al. 2006). This lack of sweet taste receptors is also hypothesized as one of the reasons felids are strictly carnivorous (Li et al. 2006). Though lacking in sweet taste receptors, cats, specifically housecats, have been found to prefer ingesting some amino acids over others, especially avoiding those with mildly bitter to strongly bitter flavors (White and Boudreau 1975). Even with housecats likely discerning bitter taste differently than that of humans, this is likely as a result of the bitter taste receptors housecats possess (Lei et al. 2015; Sandau et al. 2015).

## Diet-Related Health Issues

A strong link exists between diet and the development of health issues and related health diseases in felids. As noted above, specific nutritional requirements exist for felids that must be met for prime health. For example, arginine, taurine, water-soluble B vitamins, vitamin A, vitamin D, and arachidonic acid must be consumed through dietary sources for a felid to remain healthy (Case et al. 2011; Morris 2002;

Zoran 2002). Without the inclusion of the abovementioned nutrients, various important bodily functions would be unable to be performed in felids and are therefore extremely important for survival. As previously mentioned, diets without arginine were observed to produce rapid death after ingesting a single meal without the nutrient (Morris and Rogers 1978). A diet low in taurine is associated with cardiomyopathy, retinal degeneration, and reproductive issues in felids (Hayes et al. 1975; Pion et al. 1987; Sturman et al. 1987). As is apparent from the issues noted from the lack of a few of the above nutrients, diet can have huge impacts on felid health through nutrient exclusion.

Beyond the inclusion of necessary nutrients, certified veterinarian Lisa Pierson (2013) noted that diet is believed to both impact and help manage such diseases as diabetes, kidney disease, cystitis, bladder/kidney stones or crystals, urethral blockage, inflammatory bowel disease, obesity, hepatic lipidosis (fatty liver disease), dental disease, and even feline asthma. Commercially produced dry cat foods are believed by some to be detrimental to the health of cats due to high plant-based protein content unable to supply the correct nutrition for cats, high carbohydrate levels in the food that cats are not adapted for, and low water content (Pierson 2013). Domestic cats, as a result of ancestry, are adapted for dry desert environments and are also adapted to acquire most of the water in their diets from prey, making water content another very important aspect of managing diet in domestic cats (Zoran 2002).

## Conclusion

Diet is extremely important in the lives of felids and can be found in numerous forms dependent on domestication and captivity exposure for various species, as wild felids, captive felids, and domestic cats all exhibit obvious differences in diet. Differences in diet are even more widespread among wild felids due to prey accessibility as a result of individual size and environmental location. Despite the differences associated with diets in felids, species within family Felidae share some dietary characteristics, most notably the

hypercarnivorous, obligate carnivore diet required for survival. Without the consumption of specific nutrients and sustenance provided from animal tissues within the high-protein diet consumed by felids, individuals suffer dire health consequences and are unable to survive and thrive within their respective environments, indicating the large impact diet has on the lives and well-being of felids.

## Cross-References

- [Animal Welfare](#)
- [Canine Diet](#)
- [Carnivora](#)
- [Carnivore \(Diet\)](#)
- [Evolution](#)
- [Feeding](#)
- [Feline Cognition](#)
- [Feline Communication](#)
- [Feline Life History](#)
- [Feline Locomotion](#)
- [Feline Morphology](#)
- [Feline Navigation](#)
- [Feline Sensory Systems](#)
- [Hunting](#)
- [Lipid](#)
- [Nutrients](#)
- [Pets](#)
- [Predator](#)
- [Prey](#)
- [Protein](#)
- [Quadrupedal](#)
- [Sensory Judgment](#)
- [Sensory Receptors](#)
- [Water Balance](#)
- [Zoological Association of America \(ZAA\)](#)
- [Zoology](#)

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## Feline Dispersal

### ► Feline Navigation

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## Feline Gaits

### ► Feline Locomotion

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## Feline Life History

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## Synonyms

Cat family; Felidae; Felis; Panthera; Pantherinae; Reproduction; Survival

## Introduction

Felids are made up of two families of cats, the Pantherinae and the Felinae, from the order Carnivora. Extant Pantherinae species, generally referred to as “big cats,” include tigers (*Panthera tigris* spp.), lions (*Panthera leo*), jaguars (*Panthera onca*), leopards (*Panthera pardus*), snow leopards (*Panthera uncia*), and clouded leopards (*Neofelis nebulosa*; *Neofelis diardi*) and diverged from the Felinae between six and ten million years ago (Johnson et al. 2006). Felinae, the “small cats,” is comprised of 36 extant species from 12 genera: cheetahs (*Acinonyx jubatus*); caracals and African golden cats (*Caracal caracal* and *aurata*); bay cats and Asian golden cats (*Catopuma badia* and *temminckii*); Chinese mountain cats, domestic cats, jungle cats, Martelli’s cat, sand cat, black-footed cat, and wildcats (*Felis bieti*, *catus*, *chaus*, *lunensis*, *margarita*, *nigripes*, *silvestris*); jaguarundis (*Herpailurus yagouaroundi*); pantanal cats, colocolos, Geoffroy’s cat, kodkods, southern



tiger cats, Andean mountain cats, pampas cats, ocelots, oncillas, margays (*Leopardus braccatus*, *colocolo*, *geoffroyi*, *guigna*, *guttulus*, *jacobitus*, *pajeros*, *pardalis*, *tigrinus*, *wiedii*); servals (*Leptailurus serval*); Canadian lynx, Eurasian lynx, Iberian lynx, bobcats (*Lynx canadensis*, *lynx*, *pardinus*, *rufus*); Pallas's cats (*Otocolobus manul*); marbled cats (*Pardofelis marmorata*), leopard cats, Sunda leopard cats, flat-headed cats, rusty-spotted cats, fishing cats (*Prionailurus bengalensis* spp., *javanensis*, *planiiceps*, *rubiginosus*, *viverrinus*); and pumas (*Puma concolor*). Of these species, almost all are endangered at some level, with only 12 listed as Least Concern (LC).

The felids emerged in the Oligocene, originating in Eurasia (Johnson et al. 2006). The current eight main lineages emerged, *Panthera* first, 11.3 million years ago (Wei et al. 2011), and then the Felinae: bay cat, caracal, ocelot, lynx, puma, leopard cat, and domestic cat lineages (Johnson et al. 2006).

Felids live on every continent but Antarctica (and are native to all but Antarctica and Australia), although most of the small species are found in closed forest or woodland habitats (Nowell and Jackson 1996) – because of this diversity of environment, they feature differences in life history but also, as expected from a family group, many similarities.

## Reproduction

Felids have four phases of estrus: proestrus (presence of ovarian follicles and increased estrogen), estrus (advanced follicle development, increased estradiol, and behavioral changes such as lordosis, vocalizing, rubbing, and rolling), diestrus (elevated progesterone), and anestrus (low estrogen; Brown 2011). All species are induced ovulators (they ovulate when an external stimulus is present, in this case, mating), but some spontaneous ovulation (which can occur at any time) is present in some species as well, such as clouded leopards, fishing cats, and margays (Brown 2011). Estrus lasts 3–10 days (and can differ not only among species, but between individuals, possibly

due to differences in environment; Brown 2011). Some species reproduce seasonally (domestic cat, tiger, clouded leopard, Pallas's cat, lynx, and snow leopard), while some are not influenced by seasonality (lions, leopards, bobcats, pumas, margays, ocelots, oncillas, jaguars, and fishing cats; Brown 2011).

For solitary species, scent marking is vital to finding mates. There is some evidence that female cheetahs will choose the best mate by interpreting scent marks (Mossotti 2010) in terms of relatedness. Similarly, female domestic cats will leave their home range to find mates if they are related to the cats around them (Liberg 1983). However, mate choice other than for relatedness seems to be absent in females and only present in males (Natoli et al. 2000) – but there is little published work on this subject. Both females and males of most species will mate with more than one cat given the opportunity. In lions, one male will mate with the females in his pride – here, mate choice is related to Dominance, where dominant males have the ability to take over and defend a pride from other males, therefore giving them the opportunity to mate. Male lions that take over prides will practice infanticide in order to spur estrus in females (Nowell and Jackson 1996).

Gestation lasts anywhere from 58 to 108 days (for species that have been recorded; Brown 2006; Gittleman 1986). Litter size varies from 2 to 3.8 kittens/cubs, with birth weights varying from 65 to 1650 g (Gittleman 1986). Weaning age can be as little as 25 days (for leopard cats) and as much as 165 days (in tigers). Kittens/cubs reach puberty and therefore become independent from 4 months (in domestic cats) to 3 years (in lions). Most kittens/cubs are raised by their mothers, with the males playing no part or only a small part in raising young (in lions). As adults, cats range in size from very small to quite large (see ► “Feline Morphology”).

## Survival

Felids range in size from 1.1 kg (rusty-spotted cat) to 306 kg (Amur tiger; Nowell and Jackson 1996), with most species showing sexual dimorphism –

the females are smaller than the males. This vast difference indicates a wide variety of habitats and diet – cats are very well adapted to many ecosystems. As might be expected, felids have a wide variety of home range sizes as well, from 1 (domestic cat) to 2,075 km<sup>2</sup> (African lion; Gittleman and Harvey 1982), although lions more typically seem to range from 26 to 226 km<sup>2</sup> (Viljoen 1993). In addition, semino-madic solitary cheetahs can have much larger territories than smaller coalitions, with the former ranging from 800 to 1500 km<sup>2</sup> (Caro 1994) and the latter from 12 and up to 150 km<sup>2</sup> (Frame 1980; Caro and Collins 1986). In some species, male and female home ranges will overlap, but male territories rarely do. As with many predator species, home range is often dependent on prey availability (MacDonald et al. 2010). All cats scent mark, which allows them to outline their territories and also avoid unnecessary conflicts with other cats.

All felids are obligate carnivores (see ► “[Feline Diet](#)”) and are therefore hunters. However, while cats are predators, the smaller ones are not apex predators and therefore may be preyed upon. In addition, interspecific competition occurs where prey is similar and not plentiful (Macdonald et al. 2010). While the largest of the cats don’t have other animals to fear as adults (cubs may be preyed upon by other big cats, hyenas, jackals, etc.), death is often caused by humans – from habitat destruction, to revenge killings, to trophy hunting, to poaching for fur, teeth, and other body parts believed to promote healing.

The felid social structure can be social or solitary, with fewer species being completely solitary as once thought. Lions, the only fully social species of felid, live in a fission-fusion social group led by one or more males and a group of females and their offspring; young males disperse at puberty (some females also disperse; Packer and Pusey 1987). Males form coalitions, both within the pride and without, allowing them both to hunt and to take over prides. Male cheetahs are known to form coalitions as well (Caro and Collins 1986). Domestic cats will stay in the same area if there is a common, plentiful resource, and females have been known to

alloparent (help raise young that are not their own, although may be related) and form matriarchal groups (Bradshaw 2016; Voith and Borchelt 1986).

## Personality

Personality has not been assessed in all species of felids, but in those that have, there is a remarkable similarity. Generally felids seem to have three dimensions of personality: Neuroticism, Impulsivity, and Dominance, with some traits related to Openness and Agreeableness in some species (Gartner et al. 2014). Differences emerge on the trait level, which explains some behavioral differences, such as sociality in lions. Overall similarities are reflected in similarities in behavior, from hunting to home range establishment, as well as mating, and indicate that personality most likely evolved early in cat species, with later trait development.

Personality has effects on health and in turn is affected by age and sex (see ► “[Personality in Animals](#)”). For example, in cats, well-being is negatively related to Neuroticism – that is, an animal rated higher in Neuroticism will have lower well-being. In addition, while some cat species become more agreeable as they age (Scottish wildcats), some become less so (clouded leopards; Gartner et al. 2014). Impulsivity seems to decrease with age in certain species. Female lions are rated as more Impulsive than males, which makes sense given their society, in which females are the hunters and therefore would rate higher in such traits as active and excitable. Personality also affects strategies of survival. For example, animals that rate higher in Dominance may mate more often, but may also be preyed on more often, whereas animals that rate lower in Dominance may mate less but live longer.

## Special Adaptations

It was long thought that cats could either roar or purr, due to differences in physiology (see

► “[Feline Morphology](#)”). Cats that roar include lions, tigers, jaguars, and leopards. With an increase in research and technology, there is now some debate on this point, with some arguing that the two are not mutually exclusive, others that only lions can truly roar, and some that the original differences are still correct (Kitchener et al. 2010; Peters and Hast 1994; Weissengruber et al. 2002).

Special adaptations for hunting include pelage (see ► “[Feline Morphology](#)”), hearing and eyesight (see ► “[Feline Sensory Systems](#)”), skeletal build (see ► “[Feline Morphology](#)”), paws/claws, whiskers, and teeth, jaws, and tongue (see ► “[Feline Morphology](#)”; Kitchener et al. 2010).

Cats mainly use sight and sound for hunting. As crepuscular hunters that may be active at night and during the day as well, their eyes are adapted for both dark and light (see ► “[Feline Morphology](#)”). They can see six times better than humans can, both in light and dark (Kitchener et al. 2010). While some cats feature especially large ears to aid in hunting animals they can’t necessarily see (e.g., servals), all cats can hear over three times better than humans. This aids in hunting in the smaller cats because rodents communicate on the ultrasonic level (Kitchener et al. 2010). Big cats can hear fainter lower-frequency sounds better than small cats (Huang et al. 2000) – this is likely because their prey is larger, and, in the case of lions, they communicate using low-frequency roaring (Kitchener et al. 2010).

All cats have claws for traction and hunting. Cheetahs are the only cat with nonretractable claws (excepting the dew claw; Hudson et al. 2011). This feature enables them to pursue prey, rather than the typical stalking and ambush style that other felids use, giving them more traction and support (Russell and Bryant 2001). Their soft paw pads allow them to tread quietly while hunting.

Whiskers are one of the most well-known adaptations in cats, who have three sets – above the eyes, on the cheeks, and on snout. Whiskers allow killing bites to appropriately oriented (Kitchener et al. 2010).

Penile spines, present in a number of mammals, are an adaptation of felids as well, but their morphology differs across species – they are thought to stimulate ovulation and are therefore adaptive (Swanson et al. 2003; see ► “[Feline Morphology](#)”).

## Longevity

Felids can live from 10 to 30 years, depending on the species (Kohler et al. 2006). Species in captivity (at zoos or shelters) tend to live longer, due to a lack of predation, a prevalence of food, and attention to physical health.

## Conclusion

Cats are some of the most widespread, adaptable, mammals in the world. While they have a vast amount of features that are similar across the taxon, small differences allow them to adapt to different habitats and prey. However, their adaptability does not protect them from habitat destruction, poaching, and hunting, and most of their numbers are in decline.

## Cross-References

- [Feline Diet](#)
- [Feline Morphology](#)
- [Feline Sensory Systems](#)
- [Personality in Animals](#)

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## Feline Locomotion

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## Synonyms

Cat locomotion; Feline gaits

## Definition

Movement used by members of the felid family (e.g., jaguars, cheetahs, lions, domestic cats) to traverse their environment.

Within this chapter, feline is the colloquial term given to members of the family Felidae in the order Carnivora. This includes wild cats, such as the jaguar (*Panthera onca*), the cheetah (*Acinonyx jubatus*), and the lion (*Panthera leo*), and domestic cats (*Felis catus*) (Lamberski 2015). The Felidae family has the largest body size range in the order Carnivora (Lamberski 2015). Felids dwell in diverse habitats, such as forests, bushlands, and deserts, and are found naturally throughout the world, except for polar regions and places such as Madagascar, New Zealand, and Australia, where their presence is a result of anthropogenic introductions (Sicuro and Oliveira 2010).

Felids possess short- to medium-length limbs and utilize digitigrade locomotion. Most felids have retractable claws that are used for climbing trees and capturing prey (Lamberski 2015) and use a “stalk and ambush” approach to hunting (Sicuro and Oliveira 2010). One notable exception is the cheetah, which, unlike most felids, uses its agility and speed to hunt down its prey at incredible speeds (twenty-nine meters per second; Hudson et al. 2012). The cheetah’s claws are not retractable, and are likely used to increase traction while running – thereby creating a functional “cleat.” Felids are carnivorous and their body size and environment impact their diets, which primarily consist of large and small mammals, birds, and occasionally fish (Sicuro and Oliveira 2010).

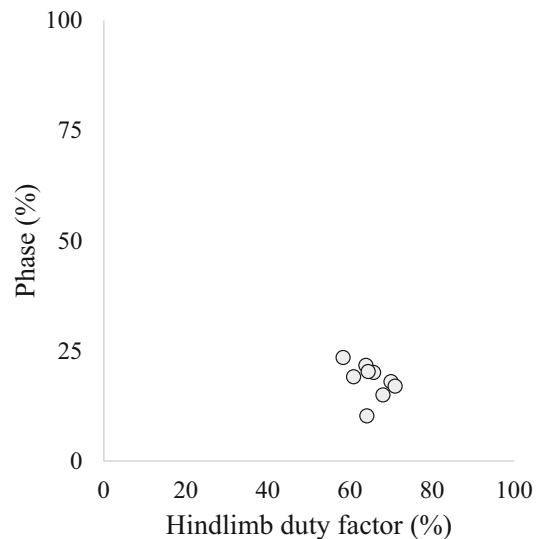
## Major Locomotor Modes

### Quadrupedal Gaits

Felids use symmetrical walking gaits when moving at slow speeds. Symmetrical gaits occur when footfalls between the forelimb and hindlimb are evenly spaced in time (i.e., walk, pace, or trot) (Granatosky 2018; Miller et al. 1975; Vilensky et al. 1991; Wetzal and Stuart 1976). This is different from asymmetrical gaits, which occur when the forelimb and hindlimb are unevenly spaced in time (e.g., bound, gallop; see below). These symmetrical gaits are further subdivided based on sequence gaits and limb coupling patterns

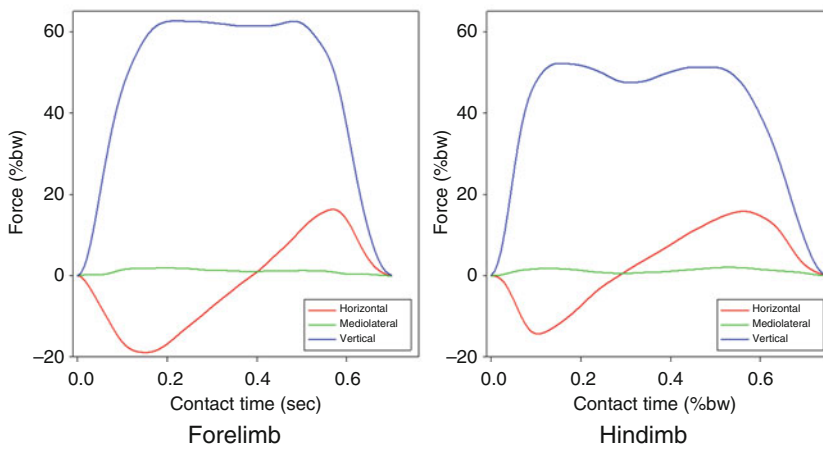
(Granatosky 2018). A lateral-sequence gait is when each hindlimb footfall is followed by an ipsilateral forelimb footfall. A diagonal-sequence gait is when each hindlimb footfall is followed by a contralateral forelimb footfall. During walking, the forelimbs and hindlimbs of a felid travel in a slight asynchronous couplet. A lateral couplet is when ipsilateral forelimbs and hindlimbs move together, while a diagonal couplet is when contralateral forelimbs and hindlimbs move together. It is very rare for limbs moving together in perfect synchrony (Granatosky 2018). As a whole, felids tend to use either lateral sequence diagonal couplet gaits or lateral sequence lateral couplet gaits (Fig. 1).

Limb-loading for felids (i.e., the external forces acting on the limbs) is quite “standard” for parasagittal mammals. Limb-loading during locomotion can be broken down into mediolateral, horizontal, and vertical components (Granatosky et al. 2018; Fig. 2). The vertical force component is usually of highest magnitude and has been used in numerous studies to understand how animals load their limbs. Felids show a slight forelimb bias for peak vertical magnitude and a characteristic “double-peak” force trace for each limb that is usually associated with limb stiffness.



**Feline Locomotion, Fig. 1** “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in felines (n = 9 species)





**Feline Locomotion, Fig. 2** Representative force trace collected from a tiger (*Panthera tigris*) during quadrupedal walking. Force is presented as a proportion of the animal's body weight (%bw) over a single forelimb and hindlimb

stance phase. Vertical force is presented in blue, horizontal (fore-aft) in red, and mediolateral in green. Data originally published in Granatosky et al. (2018)

The horizontal force component allows us to explore how animals accelerate and decelerate by examining at the distribution of braking and propulsive forces within a stride. As with most quadrupeds, felids show a distinct braking role for the forelimb and a propulsive functioning hindlimb. Throughout a stride, mediolateral forces are generally low and measure the side-to-side movement of the center of mass (COM) and/or muscular forces applied by the animal to maintain stability. The felids show quite small mediolateral forces (Granatosky et al. 2020).

For many felids, “stealthy” locomotion is essential for capturing prey. Biomechanically, this “stealthy” behavior is achieved by

maintaining a flexed limb posture and flattening the COM trajectory during locomotion. For most striding animals, their COM fluctuates between kinetic energy and potential energy, similarly to an inverted pendulum. During this fluctuation, kinetic energy is temporarily stored as gravitational potential energy, as the COM rises and shifts over the stance leg. It then becomes kinetic energy once again. This exchange between kinetic energy and potential energy reduces the amount of muscle activity needed to accelerate and decelerate the COM. Thus, the costs of locomotion are reduced. However, during “stealthy” locomotion, the flexed limb posture and flattened limb trajectory result in low energy recovery resulting in

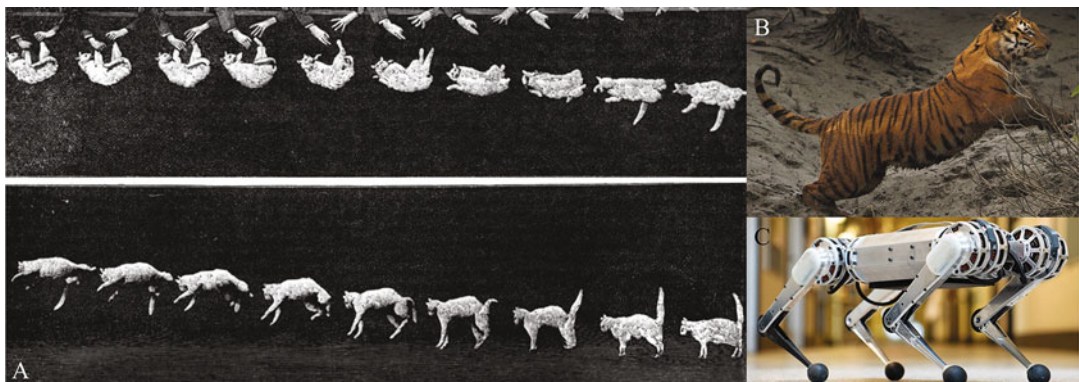
increased locomotor costs. The “stealthy” locomotion in felids adds further evidence against the almost axiomatic assumption that energetic economy is the most important target of natural selection, and animals will choose gaits and postures that maximize energetic efficiency (Bishop et al. 2008).

At higher speeds, felids engage in trotting and galloping gaits. During trotting, a felid’s diagonal limbs are in synchrony, and each limb contacts the ground for less than 50% of the locomotor cycle (Vilensky et al. 1991). Trotting allows for the maintenance of stability by decreasing the overall movement of a felid’s COM. As such, the trotting gait has been proposed to conserve energy, and therefore may be the most efficient gait when travelling over long distances (Fig. 3).

Gallop is most often seen when a felid engages in hunting or evasion behaviors. Among the felids, no species is more specialized for speed than the cheetah, which can reach velocities up to ninety-three kilometers per hour. This remarkable speed can be attributed to its use of the rotary gallop, also referred to as a double suspension gallop (Bertram and Gutmann 2009). The double suspension gait is a four-time, asymmetrical gait where the feet fall in a circular sequence around the body, and gets its name from the two aerial phases: a gathered aerial phase, where the back is flexed and the hindfeet pass in front of the forefeet, and an extended aerial phase, where the feet

are stretched away from the body and the back is extended (Bertram and Gutmann 2009; Hudson et al. 2012). Compared to other felids, the cheetahs have hindlimbs that are longer, heavier, and thicker in diameter when scaled to their body mass (Day and Jayne 2007). This has been proposed to allow for increased bone strength and safety to manage the higher magnitude loads during high-speed pursuits (Hudson et al. 2011).

As part of the normal locomotor repertoire, felids must make speed-induced gait transitions. The most common gait transition seen in felids is trotting to galloping. Transition duration and speed are heavily dependent on body size. Moreover, felids use rotary and transverse gallop mechanisms to aid transitions across different speeds (Miller et al. 1975; Vilensky et al. 1991). Rotary transitions highlight changes during hindlimb swing phases, while transverse transitions focus on diagonal limb swing phases (Vilensky et al. 1991). While this gait transition has been described as abrupt in direction and magnitude, some studies have shown that transverse gallops have the potential to occur gradually through smooth forelimb-forelimb and forelimb-hindlimb phase changes (Vilensky et al. 1991). Numerous studies have determined that most transitions occur in the swing phase, are completed within two to three steps, and can occur in normal and decerebrate cats (Miller et al. 1975; Vilensky et al. 1991). During these transitions, there is a defined



**Feline Locomotion, Fig. 3** Illustrative demonstration of (a) the air-righting reflex and (b) feline jumping behavior. (c) The Pneupard is a bio-inspired robotic model used to develop a stronger understanding of feline locomotion,

particularly the cheetah and its fast speeds. Images fall under Creative Commons Attribution-Share Alike 4.0 International

elongation of the feline trunk as well as a strong thrust from the hindlimbs that allow for upward and forward movement (Vilensky et al. 1991).

### Jumping

As a group, the cats are quite well-known for their ability to jump to and from great heights and land safely on all four limbs. Propulsion, or jumping, is a bilateral synchronized movement that involves predominantly hindlimb action (Zajac et al. 1981). However, the starting position of propulsion will vary between different species. Some cats will crouch with both forelimbs touching the ground, while others will crouch with only one forelimb touching the ground and the other flexed. For this reason, forelimbs are not considered to contribute significantly to jumping, but rather are necessary for static stabilization and landing (Zajac et al. 1981).

There are three phases of propulsion during jumping: preparatory, launching, and heel-off (or lift-off). In the preparatory phase, the felid first secures its footing to the ground. It then contracts its forelimb extensor muscles bilaterally to push itself off and throw its body upward. Once the forepaws are off the ground, it keeps its forelimbs in a fully flexed position until it is about to land. During launching, the felid's hindlimb remains in contact with the ground, allowing for the COM to shift toward the hindlimbs from the heels to a point directly over the toes. In heel-off, the hindlimb extensor muscles contract bilaterally, pushing off against the ground, and project the animal's entire body into the air, thus shifting the COM upwards. Once the hindlimbs lose contact with the ground, they also go into flexion. During launching and heel-off, the cat will shift its COM again to allow for further propulsion. This shift in its COM is achieved through extension of the cat's trunk. During launching, the trunk will extend vertically and horizontally, and after heel-off, it will extend vertically. The head and tail do not assist with propulsion. During the jump, the head is maintained at a fixed angle relative to the target and the tail is always pointed upward and never touches the ground (Miller et al. 1975; Zajac et al. 1981; Zomlefer et al. 1977).

During propulsion, the joint angles of the hips, knees, and ankles undergo changes. From the preparatory phase to the launch phase, the hip angle extends from 90° to a maximum of 175°. The knees undergo continuous extension starting from 45° in the preparatory phase until approximately 160° throughout the launch and lift-off phases. The ankle, on the other hand, will start off at 80° and flex to about 60° during launching. The ankle will stop flexing at heel-off and will follow a similar extension trajectory as the knee (Zajac et al. 1981).

When landing, the central pad of the felid's forepaws is the first to contact the ground, providing initial support. The long tendons in its forelimb muscles and the flexibility of its spine allow for the absorption of the rapid and high force impact. This ability of dissipating forces during landing prevents injuries. Two additional factors that are important for landing are height and time. Cats jumping from higher heights have more time to adjust the magnitude of the prelanding limb muscle activity that is appropriate for that height (Wang et al. 2019). Other factors such as hindlimb length and body weight will also affect the height and velocity of the jump. Felids with longer hindlimbs and lower body fat mass relative to lean body mass will achieve higher velocities and greater vertical forces (Zomlefer et al. 1977).

Another key ability that allows cats to land successfully is the air-righting reflex. The air-righting reflex is described as the "ability of cats to turn in the air without pushing against anything and to land upright upon their feet when falling from an inverted or askew position" (Cremieux et al., pg.564). Kittens typically develop this reflex around 33 days. Sensory information is taken from the visual and vestibular systems to perform this reflex. It has been observed that blindfolding a normal adult cat does not prevent the air-righting reflex. Instead, removing their vision affects the accuracy of their landing, likely because they are unaware of the height of the fall (Cremieux et al. 1984). Immediately after mid-air release, the cat will bend its spine first forward, then to one side, then backward, then to the other side, and finally forward again. Rather than "twisting," the bending of its torso and spine

allows the cat to turn over (Manerikar and Anandpara 2015). In addition to bending, cats can project or tuck in their forelimbs and hindlimbs to reorient the pelvis, spine, and torso, and thus still land upright.

### Pacing in Captive Cats

There is a long history of interaction between felids and humans. Apart from the domestication of house cats, humans have also kept larger and wild felids captive in zoos and observation centers. When housing wild cats in smaller and confined areas, wild cats engage in stereotypies and abnormal repetitive behaviors. Stereotypies include licking walls and tongue flicking, while abnormal repetitive behaviors include aggression, self-biting, mutilation, and, most relevant to this chapter, pacing (Breton and Barrot 2014). Pacing behavior is continuous walking back and forth or in a circle, following the same path. Signs of regular pacing include definite paths worn in the ground. Typically, pacing serves no actual function and may be triggered because the felid cannot forage or hunt for their meals (Breton and Barrot 2014; McPhee and Carlstead 2010).

Some studies also demonstrate that these wild cats are under stress, which has negative implications on brain development and reproduction (Breton and Barrot 2014). Prolonged periods of distress can cause high levels of hypothalamic-pituitary-adrenal activity, which can lead to immunosuppression, atrophy of tissue, and maladaptive behaviors (McPhee and Carlstead 2010). For example, a study demonstrated that Siberian tigers (*P. tigris altaica*) at a Bucharest zoo developed gastroenteritis because they could not adapt to their new environment and stress (McPhee and Carlstead 2010). Several other studies on clouded leopards (*Neofelis nebulosa*) and leopard cats (*Felis bengalensis*) found that high levels of glucocorticoids and abnormal behaviors were positively correlated to public displays, proximity of predators, and a lack of different environmental factors (McPhee and Carlstead 2010). Moreover, offspring growing up in captive environments can develop alternative learning behaviors, which can be introduced to the population and reproduced into newer generations of captive felids.

### Bio-inspired Robotics

Bio-inspired robotics has utilized cat models based on both the domestic cat and cheetah. These robotic models not only provide veterinarians and researchers with a deeper understanding of biological parameters of the cat, but also mitigate unethical harm to cats used for research. One such example is the PneuPard model, which has been based on extensive studies performed on real domestic cats, cheetahs, and other quadruped robots (Kajiwara et al. 2018; Nakatsu et al. 2014). Engaging in feline biomimicry, PneuPard models can walk on rough terrain with stability as well as jump and gallop similarly to cheetahs (Rosendo et al. 2013). Moreover, the models can alternatively shift body load and engage in relatively smooth gait transitions (Nakatsu et al. 2014). PneuPard models have informed researchers on how animals perform adaptive locomotion, how muscles contribute to stable gait, and how the spine and limbs influence different gait patterns and transitions (Rosendo et al. 2013). In more recent years, the PneuPard has been used to study how cheetahs can achieve fast speeds.

The PneuPard model has changed rapidly throughout the years, going from a model with two active muscles on each hindlimb to a model with 28 muscles on each hindlimb and 10 muscles on the spine (Rosendo et al. 2012, 2013). Researchers have also begun to focus on the role of monoarticular and biarticular joints in developing computer simulations and robots (Rosendo et al. 2012). It has been found that monoarticular joints generate lateral forces, while biarticular joints transfer forces between the joints, especially during jumping, galloping, and gait transitions (Nakatsu et al. 2014; Rosendo et al. 2013). Researchers have recently developed better robotic landing positions for the PneuPard through different combinations of monoarticular and biarticular joint activation (Rosendo et al. 2012).

### Feline Locomotion in Medicine

Felids have long served as mammalian models for human locomotion after spinal cord injuries (SCIs) (Rossignol et al. 2002; Frigon 2012). Dorsal lesions have been induced in a variety of quadrupeds to examine the impacts on locomotion

(Rossignol et al. 2002). When large lesions were induced into cats, recovery occurred within 10 days, and there were increases in both the cycle and swing phase duration (Kuhtz-Buschbeck et al. 1996; Frigon 2012). Partial lesions of the spine have shown quicker and stronger recovery rates than complete lesions (Kuhtz-Buschbeck et al. 1996). Ventral lesions have not been studied extensively due to harder selectivity constraints, but few studies have demonstrated hindlimb locomotion and weight support recover gradually while lateral stability does not (Frigon 2012). Some studies have highlighted that with extensive treadmill training, felids were able to use their hindlimbs for locomotion after incomplete SCIs because of spinal CPGs (Rossignol et al. 2002).

Both humans and cats have similarly organized spinal cords, including spinal CPGs (Frigon 2012). Spinal CPGs are neuronal networks composed of interneurons that generate movement (Rossignol et al. 2002). These networks interact with sensory systems that stem from the limbs and allow for humans and cats to adapt to their surroundings, such as correcting posture during environmental changes (Rossignol et al. 2002). The spinal CPGs seen in human infants are most similar to feline spinal CPGs because when infants crawl, they exhibit quadrupedal locomotion. However, these human spinal CPGs still retain unique properties that allow for bipedal locomotion (Rossignol et al. 2002; Frigon 2012).

Spinal CPGs are malleable and are important for neuroplasticity, as seen in feline partial SCI studies (Rossignol et al. 2002; Frigon 2012). These CPGs can be generalized between humans and cats, and lesions may help explain motor deficits seen in human patients with SCIs. Studies have implemented intense treadmill training in partial lesioned cats and serve as research designs for human locomotion training and neuroplasticity regeneration in SCI patients.

## Conclusion

Since many cats have been domesticated and wild felids are kept in zoos, researchers have

extensively studied *feline locomotion*. Over time, both domestic and wild cats have adapted to a variety of different environments to stalk and hunt their prey. These quadrupedal animals can locomote with either symmetrical gaits, such as walking and trotting, or asymmetrical gaits, such as galloping. As they move through the environment, conserving their energy is especially important when hunting prey or escaping from predators. However, “stealthy” walking in the felid is costly, and highlights that not all locomotion is optimized for energetic expenditure. In addition, felids also possess impressive jumping abilities and a remarkable air righting reflex. When compared to their wild counterparts, changes in captive feline behavior have been observed and result from the increased stress caused by zoos and closed off environments. When studying feline gait patterns, we gain more insight into their agility, postural balance, and, especially in the case of the cheetah, their speed. Moreover, we can apply this knowledge into the development of bio-inspired robotics and possible clinical treatments for human SCIs.

## Cross-References

- ▶ [Activity Budget](#)
- ▶ [Adaptation](#)
- ▶ [Arboreality](#)
- ▶ [Basal Metabolic Rate \(BMR\)](#)
- ▶ [Canine Locomotion](#)
- ▶ [Carnivora](#)
- ▶ [Domestication](#)
- ▶ [Ecology](#)
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- Muscular System
- Natural Selection
- Navigation
- Paleontology
- Pets
- Phylogeny
- Predator
- Quadrupedal
- Taxa
- Terrestrial
- Zoo
- Zoology

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## Feline Morphology

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## Synonyms

Cat morphology

## Definition

The shared and unique physical characteristics of felid species contributing to similarities and variations in bodily form.

## Introduction

Forty-one extant felid species exist today, grouped within two subfamilies of the Felidae family:

Pantherinae and Felinae (Kitchener et al. 2017). These species possess a multitude of physical characteristics, each combining into a singular morphology that is considered similar among all cats. This morphology comprised of shared physical characteristics is likely due to a shared genetic lineage among all existing cat species today, dating back 10.8 million years ago to a common ancestor, in the form of a panther-like *Pseudaelurus* species located in Asia (O'Brien and Johnson 2007). The singular morphology that has persisted across time, environment, location, and species within the Felidae family includes similarities in overall body shape, foot and claw structure, facial form, teeth, and presence of coat color patterns, to name a few (Fraser 2012; Sunquist and Sunquist 2002). Many, if not all, shared physical characteristics among felids can be attributed to an overall morphology adapted and evolved for the specialized hypercarnivorous diet that cats thrive upon (Sunquist and Sunquist 2002). Individuals within felid species require a much higher percentage of diet from protein, therefore requiring and showcasing a morphology that reflects an ability to hunt, capture, and kill live prey (Sunquist and Sunquist 2002).

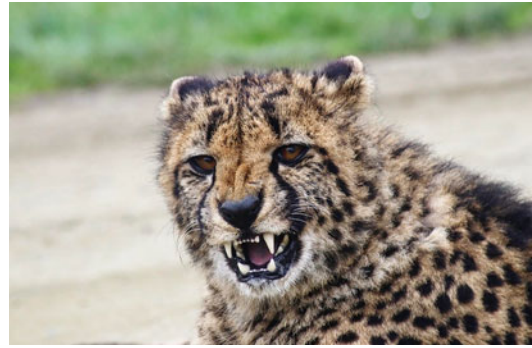
In addition to the aforementioned similarities and an overall singular morphology discussed above, individual felid species also exhibit distinctive characteristics. As sea levels dropped and land bridges appeared millions of years ago, individuals within the *Pseudaelurus* species dispersed and emigrated from Asia to other continents (O'Brien and Johnson 2007). These migrations allowed for the formation of new lineages in which individuals could adapt to new environments and, over time, evolve into today's existing unique felid species with specialized physical characteristics suitable for their respective habitats (O'Brien and Johnson 2007).

## Head

Individuals within family Felidae share defining skull characteristics including a domed shape, a

shortened muzzle, and the presence of a sagittal crest to which strong jaw muscles attach (Sunquist and Sunquist 2002). The presence of the sagittal crest coupled with the shortened muzzle in feline individuals allows for an increased bite force when using canine teeth during hunting (Sunquist and Sunquist 2002). In addition to an increased bite force, felids also have less teeth as a result of the shortened muzzle, with a total of 28 or 30 teeth in the mouth (Sunquist and Sunquist 2002). The teeth are typically comprised of six small incisor teeth located on the top and bottom jaw, four large canine teeth toward the front of the mouth, and molars located at the back of the mouth on the top and bottom jaw referred to as carnassial teeth (Fraser 2012; Sunquist and Sunquist 2002). Each type of tooth is important for different reasons, as incisors are used for holding objects, carnassial teeth are useful when tearing and shredding meat, and canine teeth are relied upon for killing prey (Fraser 2012; Sunquist and Sunquist 2002). The canine teeth are especially important during hunting as prey is rendered inactive and ultimately killed through throat biting and strangulation or cutting of the spinal cord (Fraser 2012; Sunquist and Sunquist 2002). The tongue in felid species is also specialized as a result of the feline diet, as the surface of the tongue is comprised of horny papillae which not only feel rough to the touch but also provide the ability for cleaning flesh off the bone (Fraser 2012). Additionally, felid species possess differing morphology in the structure and positioning of the larynx, pharynx, and hyoid apparatus located below the skull (Hast 1989; Weissengruber et al. 2002). It has been hypothesized that these differences explain why certain felid species (i.e., lion, tiger, jaguar, and leopard) can roar, while all other felids are incapable (Hast 1989; Weissengruber et al. 2002) (Fig. 1).

Felid species also possess vibrissae, most commonly referred to as whiskers. Whiskers are thick sensory hairs deeply rooted beneath the skin that are located in multiple locations on the body including near the eyes, on the chin, and on the legs (Sunquist and Sunquist 2002). However, whiskers are most notably located on both the left and right side of the muzzle on a cat



**Feline Morphology, Fig. 1** The image of a cheetah above showcases the typical dentition observed in felid species: front incisors, large canines, and carnassial teeth at the back of the mouth. (Photo by Brittany D. B. Greene)

(Sunquist and Sunquist 2002). Whiskers are more than just hairs, as they are sensitive to minute movement, touch, and even changes in air currents (Sunquist and Sunquist 2002). As a result, whiskers are invaluable when hunting, especially at night, as the vibrissae move forward when an individual moves in on prey, providing the cat with tactile information regarding the location of the prey relative to itself (Sunquist and Sunquist 2002).

Felid species have large eyes relative to body size and are believed to be able to see the colors green, blue, and red due to the presence of rods and cones within the retina of the eye (Fraser 2012; Sunquist and Sunquist 2002). As individuals in the Felidae family are exclusively hunters, eyesight is very important for prey capture in both light and dark conditions within the environment (Sunquist and Sunquist 2002). Felid species have pupils similar to other species, which can contract and dilate in the presence or absence of light (Sunquist and Sunquist 2002). However, individuals within the Felidae family also possess a reflective tissue in the eye, referred to as the tapetum lucidum, which provides advantageous eyesight that has been hypothesized to be six times more sensitive to light than the human eye (Sunquist and Sunquist 2002). Felid sight is especially well-equipped for navigation, with well-developed peripheral and binocular vision due to high-set, forward-facing eyes (Sunquist and Sunquist 2002). Even so, cat

eyesight does vary depending upon body size, as smaller species of felids, especially the domestic species of cat, *Felis catus*, require and therefore have evolved to have better eyesight for closer objects (Fraser 2012). In contrast, larger felid species, adapted for locating distant prey in larger environments, have evolved to have better long-range sight (Fraser 2012).

## Body

All felids are similar in body shape, with an agile, limber, and muscular body; however, high variation in body size exists both between species and within species (Sunquist and Sunquist 2002). For example, body size ranges drastically in felid species with females of “very large” categorized felid species, such as lions and tigers, weighing approximately 120–130 kg and females of “very small” categorized felid species, such as leopard cats, black-footed cats, and rusty-spotted cats, weighing approximately 1–2.8 kg (Fraser 2012). In addition to body size variation between species, variation in body size and form also exists within species due to factors including geographical location and sexual dimorphism (Pitakarnnop et al. 2017; Sunquist and Sunquist 2002). In fact, Pitakarnnop et al. (2017) noted significant differences in size and shape of bones between male and female domesticated cats.

Similar to variation in body size and form, coat color and pattern are also highly variable between felid species (Sunquist and Sunquist 2002;). Felid coats can contain various markings including rosettes, blotches, spots, and stripes or appear solidly colored (Sunquist and Sunquist 2002). These various markings on felid coats are believed to have evolved from a primitive “fleck,” or spot, pattern in ancestral felid species (Werdelin and Olsson 1997). The high variability observed in coat pattern and color is likely due to the behavior of each species within its environment as well as the need for each species to camouflage into its respective environment (Allen et al. 2011). Allen et al. (2011) determined that species with more “complex” flank markings were more likely to be arboreal and

found in closed environments, such as forested habitats. In addition, Allen et al. (2011) noted “especially irregular” flank markings were also most prominent on nocturnal hunters, arboreal hunters, and tropical-forest dwelling cats.

## Appendages

Felid species have five toes on their forepaws and four toes on their hind paws and present themselves as limber creatures due to their muscular forelimbs and hindlimbs as well as possessing the pedal quality referred to as digitigrade (Fraser 2012; Sunquist and Sunquist 2002). All felid species are digitigrade, meaning all individuals within felid species walk on, and distribute their weight onto, their highly sensitive toe and paw pads (Fraser 2012; Sunquist & Sunquist). This locomotive characteristic allows for weight distribution to the balls of the feet, enabling the signature agile movement observed in cat species (Sunquist and Sunquist 2002).

All felid species possess sharp, curved claws that are typically protected by sheaths within the toes of each paw (Fraser 2012). These claws are retractable when an individual is at rest due to a flexible ligament, though can be released quickly using a specialized muscle referred to as the flexor profundus perforans (Fraser 2012; Sunquist and Sunquist 2002). Though all species within family Felidae possess the same morphology allowing for the ability to retract their claws, certain species including the cheetah, the serval, and the flat-headed cat have claws that remain visible and appear nonretractable, even at rest (Sunquist and Sunquist 2002). This is due to the presence of claws that extend further than the fur on the paws for all species previously mentioned, though cheetahs additionally lack the previously mentioned sheaths protecting the claws (Sunquist and Sunquist 2002). The claws in felid species are an important morphological trait, as they provide individuals with the ability to scratch, climb, and, most importantly, hold prey (Fraser 2012; Sunquist and Sunquist 2002). In fact, within the order Carnivora, felids are the only carnivores known to use the claws on their forepaws to





**Feline Morphology, Fig. 2** The above image details the paws of a cheetah, including the paw pads all digitigrade felid individuals walk upon, as well as the uniquely cheetah characteristic of seemingly unretractable claws

restrict prey movement prior to administering a lethal bite at the throat (Sunquist and Sunquist 2002) (Fig. 2).

Tails are a prominent feature typically observed in felids as well and are a highly flexible anatomical trait that can aid individuals in balance and changing direction rapidly (Fraser 2012; Sunquist and Sunquist 2002). The majority of felids possess long tails ranging from 1/3 to 1/2 of the combined length of the head and body (Sunquist and Sunquist 2002). Even so, exceptions exist to this rule, as species such as the margay, clouded leopard, and marbled cat have unusually long tails, and bobcat and lynx species have very short tails (Sunquist and Sunquist 2002).

## Conclusion

Felid species possess multiple physical characteristics and traits that are shared among individuals within family Felidae, thus producing an overall recognizable singular morphology within the family. Though similar in overall form, felid species vary greatly in size and physical characteristics that developed over time due to survival requirements put forth in each species' respective environment. This similar morphology interspersed with adaptive traits and physical characteristics specific to each species has allowed for the development of a simultaneously uniformly

congruous and richly diverse grouping of species within family Felidae.

## Cross-References

- Carnivore (Diet)
- Evolution
- Feline Cognition
- Feline Communication
- Feline Diet
- Feline Life History
- Feline Locomotion
- Feline Navigation
- Feline Sensory Systems
- Hyoid Bone, The
- Pets
- Predator
- Quadrupedal

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## Feline Navigation

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### Synonyms

[Cat navigation](#); [Feline dispersal](#)

### Definition

The process in which individuals within family Felidae identify their location relative to, and move throughout, the surrounding environment.

### Introduction

Navigation in nonhuman animal species, including the cat, has long been, and in some ways still remains, a mystery to scientists (Belluck 2013; Kluger 2015). However, strides have been made recently to further understand nonhuman animal navigation. Nonhuman animal species, such as sea birds and dung beetles, are believed to navigate using the sun and stars, dogs are believed to rely upon scent for navigation, and baby sea turtles are believed to use magnetism when migrating and navigating after hatching (Kluger 2015). Felids are believed to navigate similarly to baby

sea turtles, relying upon Earth's magnetic fields to navigate within their environments, possibly due to the presence of iron within their ears (Kluger 2015). This ability to navigate using Earth's magnetic field may explain the uncanny ability of felid species to move around within their environments. This renowned ability has been referred to as a “homing ability” or “homing powers” in felids and has been noted throughout history, including multiple examples of various house cats traveling between 200 and 1000 miles to return home after traveling for months (Belluck 2013; Herrick 1922). This seemingly effortless “homing ability” in felids can be attributed to physical characteristics and related to movement capabilities. Physically, felids possess a morphology ideal for navigating within their respective environments. Additionally, felids must also be capable of dispersing and establishing territories or home ranges within their respective environments that they can move within and return to using their “homing ability.”

### Felid Morphology Aiding in Navigation

In addition to iron within their ears that may contribute to their impressive navigation skills, felid species also possess a multitude of physical characteristics and sensing systems that aid in navigation within their respective environments. For example, within familiar locations, cats are hypothesized to memorize locations using their olfactory and visual senses (Belluck 2013). This is but one reason that sight is an important sense for a feline when navigating within the environment. In addition, several felid species are nocturnal or exhibit nocturnal behaviors (Fraser 2012). Therefore, they require, and possess, morphological traits capable of navigating in low light conditions. Felid eyesight is highly responsive in varying light conditions, as felid eyes are dominated by “light-sensitive” rod cells within the retina that aid in eyesight in darker conditions (Sunquist and Sunquist 2002). In fact, felids are believed to have much better eyesight than humans in low light conditions (Fraser 2012). Felid pupils are capable of contracting and dilating in the presence or absence of light, thereby

controlling the amount of light that enters the eye (Sunquist and Sunquist 2002). Felids also possess a reflective tissue in the eye, referred to as the tapetum lucidum (Sunquist and Sunquist 2002). This “mirror-like” structure, located behind the retina, aids in dispersing and reflecting light, providing cats with eyesight that has been hypothesized to be six times more sensitive to light than the human eye (Fraser 2012; Sunquist and Sunquist 2002). These adaptations allow for the ability to hunt in varying light conditions ranging from bright daylight during the day to obscuring darkness at night (Sunquist and Sunquist 2002).

Just as eyesight is important in navigation, olfactory sensing is also helpful in navigating the socially constructed territories possessed by individual felids within their respective environments. Olfactory sensing is used a great deal in the social lives of felids, as scent is used abundantly for communicating intraspecifically and interspecifically within the environment of felids (Sunquist and Sunquist 2002). Scent-marking is commonly conducted where felid ranges overlap, and female individuals have been observed increasing urine-spraying prior to fertile periods with the hopes of attracting a mate (Sunquist and Sunquist 2002). Scents and odors produced by felids are believed to indicate such information as sex, status, breeding condition, temporal details, and identity (Sunquist and Sunquist 2002).

Auditory sensing can aid in navigation for hunting as well. Felids, especially the serval species (*Leptailurus serval*), utilize the outer ears, referred to as the pinnae, to both amplify and locate sound (Sunquist and Sunquist 2002). Felids can also hear ultrasonic sounds, though they do not communicate through ultrasonic sound (Sunquist and Sunquist 2002). It has been hypothesized that the ability to hear at ultrasonic levels in felids is likely specialized for hunting, especially in smaller felid species that hunt rodent prey that communicate using sounds within the range of 20–50 kHz (Sunquist and Sunquist 2002).

Tactile sensing is also beneficial for navigation. Felid species possess vibrissae, most commonly referred to as whiskers, to aid in tactile sensing. Whiskers are thick sensory hairs deeply rooted beneath the skin that are located in multiple

locations on the body including near the eyes, on the chin, and on the legs (Sunquist and Sunquist 2002). However, whiskers are most notably located on both the left and right side of the muzzle on a cat (Sunquist and Sunquist 2002). Whiskers are more than just hairs, as they are connected to nerve endings, thereby making them quite sensitive to minute movement, touch, and even changes in air currents (Sunquist and Sunquist 2002). The tactile sensing from whiskers helps cats better understand their location and proximity to objects within the environment (Hanlon 2016). As a result, whiskers are invaluable when hunting, especially at night, as the vibrissae move forward when an individual moves in on prey, providing the cat with tactile information regarding the location of the prey relative to itself (Sunquist and Sunquist 2002).

## Felid Dispersal and Navigation Within the Environment

Location within the environment can also have a huge impact on feline navigation. Most felids undergo a process known as dispersal, in which recently matured individuals socially disengage from family members, leave their mothers' territories, and embark on a journey in search of their own respective territories (Fraser 2012). This period of dispersal is markedly asocial, with individuals in various felid species able to potentially disperse over 100 km and males typically traveling farther than females in search of a territory (Fraser 2012). Though this behavior is common in wild felids, domestic cats have not been observed to exhibit obvious dispersal impulses, likely due to the restrictive nature of a living in a home with a continuous food source (Fraser 2012).

After eventual establishment of a territory or home range, wild felids have been known to travel back to those territories or home ranges when removed and translocated, likely using the “homing ability” previously discussed. For example, following translocation to locations nearly 310 miles from their home ranges, two separate male pumas returned to their respective home ranges. One male traveled a total of 288 miles (465 km) back to his home range over a period

of 469 days, while the other male traveled a total of 305 miles (490 km) over a period of 166 days (Sunquist and Sunquist 2014). In addition to traveling back to a home range or territory, navigation can impact the behavior of wild felids within their territories as well. Within their home ranges, wild felids have been observed to frequent man-made structures, including roads and trails, for movement throughout the environment. Sunquist (1981) noted that tigers (*Panthera tigris*) not only frequented roads and trails but that they were considered an important source for movement within the ranges of the tigers. Sunquist (1981) also noted that the movements of the tigers along the roads and trails were highly directional and likely used for facilitating quick navigation within the tigers' home ranges. Similarly, though less frequent, leopards (*Panthera pardus*) were also observed using roadways for travel within the same national park in Nepal (Sunquist 1981).

Unfortunately, increased frequency of felids using human-made structures also puts those individuals at increased risk of entering into potential situations of conflict with humans. Inskip and Zimmerman (2009), after reviewing 349 literature sources regarding human-wildlife conflict involving 37 felid species, noted that habitat availability, impacted by the need to navigate extensive home ranges overlapping with human-dominated areas, was one of six main determinants of conflict between humans and felids. However, studies, such as that conducted by Haidir et al. (2020) examining Sunda clouded leopards (*Neofelis diardi diardi*), Asiatic golden cats (*Catopuma temminckii*), and marbled cats (*Pardofelis marmorata*), have been conducted to research corridor land use in felid species, with the hopes of identifying and protecting safe passages for navigating felid individuals in an uncertain future.

## Conclusion

Navigation capability is an important trait for wild felid individuals and domestic individuals alike. Individuals within family Felidae can be exceptionally adept at navigating within their environments as a result of morphological traits. Felids possess an extraordinary homing ability, likely as

a result of morphology adapted for successfully moving around within the environment. Location can be highly impactful on navigation as well, as felid individuals entering adulthood disperse, establish their own territories or home ranges, and move around within those areas. Human-made structures, including roads and trails, have been observed to be utilized, sometimes frequently, by felid species as a means of navigating within their home ranges; however, though these human-made structures are important for felid navigation, increased interaction of wild felids and humans has contributed to conflict in areas where human and carnivore habitat overlap. Nonetheless, there is hope for the future, as researchers work to identify, and advocate for, safe navigable routes for felids within their home ranges.

## Cross-References

- ▶ [Auditory Processing and Perception](#)
- ▶ [Carnivora](#)
- ▶ [Dispersal Ability](#)
- ▶ [Dispersal Patterns](#)
- ▶ [Evolution](#)
- ▶ [Feline Cognition](#)
- ▶ [Feline Communication](#)
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- ▶ [Memory](#)
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- ▶ [Olfactory Perception](#)
- ▶ [Pets](#)
- ▶ [Predator](#)
- ▶ [Prey](#)
- ▶ [Quadrupedal](#)
- ▶ [Sensory Receptors](#)
- ▶ [Spatial Orientation](#)
- ▶ [Tactile Perception](#)
- ▶ [Territoriality](#)
- ▶ [Translocation](#)
- ▶ [Visual Perception](#)

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providing for social interspecific and intraspecific interaction within the surrounding environment.

## Introduction

Forty-one extant felid species exist today, grouped within two subfamilies of the Felidae family: *Pantherinae* and *Felinae* (Kitchener et al. 2017). These species possess a multitude of physical characteristics, each combining into a singular morphology that is considered similar among all cats. Many, if not all, shared physical characteristics among felids can be attributed to an overall morphology adapted and evolved for the specialized hypercarnivorous diet which cats thrive upon (Sunquist and Sunquist 2002). Individuals within felid species require a much higher percentage of diet from protein, therefore requiring and showcasing a morphology with sensory systems equipped for hunting live prey (Sunquist and Sunquist 2002). Such sensory systems are also important for individual feline well-being (Fraser 2012). These sensory systems are comprised of visual, olfactory, gustatory, auditory, vestibular, and tactile sensing.

## Visual Sensing

The visual sensory ability is the primary sense used by individuals within family Felidae when hunting prey (Sunquist and Sunquist 2002). Felids possess advantageous evolutionary adaptations in eye morphology that allows superior eyesight and the capacity to successfully hunt and catch prey. Felid eyesight is highly responsive in varying light conditions, as felid eyes are dominated by “light-sensitive” rod cells within the retina that aid in eyesight in darker conditions (Sunquist and Sunquist 2002). In fact, felids are believed to have much better eyesight than humans in low light conditions (Fraser 2012). Felid pupils are capable of contracting and dilating in the presence or absence of light, thereby controlling the amount of light that enters the eye (Sunquist and Sunquist 2002). Felids also possess a reflective tissue in the eye, referred to as the tapetum lucidum (Sunquist and Sunquist 2002). This

## Feline Sensory Systems

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## Synonyms

Cat senses; Cat sensory systems

## Definition

Developed visual, olfactory, gustatory, auditory, vestibular, and tactile senses in felid species resulting from evolved morphological traits ideal for supporting the ability to hunt as well as

“mirror-like” structure, located behind the retina, aids in dispersing and reflecting light, providing cats with eyesight that has been hypothesized to be six times more sensitive to light than the human eye (Fraser 2012; Sunquist and Sunquist 2002). These adaptations allow for the ability to hunt in varying light conditions ranging from bright daylight during the day to obscuring darkness at night (Sunquist and Sunquist 2002). In addition to a sensitivity to visible light, felids, among other mammals, are also believed to be sensitive to UV light (Douglas and Jeffery 2014). Eye lenses of domestic housecats (*Felis catus*) were observed to let in significant amounts of UVA, between 315 nm and 400 nm, proposing the argument that felids may also be able to see within the UV spectrum (Douglas and Jeffery 2014).

In addition to a sensitivity to light, felid eyes also are believed to be able to detect such colors as green, blue, and red in bright light conditions (Sunquist and Sunquist 2002). Even so, it is believed that felids are unable to detect fully saturated colors or as many colors as humans due to an insufficiency in color-detecting cones within the retina (Sunquist and Sunquist 2002). Felids, however, have enhanced binocular vision that is believed to be superior to all other species in order Carnivora due to high-set, forward-facing eyes (Sunquist and Sunquist 2002). Felids can focus eyesight, and swiftly adjust that focus, exceptionally well due to the location of the lens further back in the eye (Fraser 2012). Interestingly, even with superior binocular vision, cat eyesight does vary depending on body size (Fraser 2012). Smaller species of felids, especially domestic housecats, require and therefore have evolved to have larger eyes coupled with better eyesight for closer objects (Fraser 2012). In contrast, larger felid species, adapted for locating distant prey in larger environments, have evolved to have smaller eyes coupled with better long-range sight (Fraser 2012). All felid species also have enhanced peripheral vision, resulting in individuals rarely focusing eyesight when at rest (Sunquist and Sunquist 2002).

## Olfactory and Gustatory Sensing

Olfactory (smell) and gustatory (taste) sensing function similarly, with chemical stimuli interacting with receptors, such as taste buds, located on a mucous membrane, such as the tongue or nasal membrane (Fraser 2012). Both senses are considered “chemical senses,” as they are reliant upon and responsive to chemical stimuli, in contrast to all other senses responsive to light, vibration, and pressure (Fraser 2012). In fact, olfactory receptor cells within the nose can integrate smell and taste together when sensing a stimulus (Fraser 2012).

Olfactory and gustatory sensing impact food preference, as felids partially rely upon both taste and smell for determining if a food is considered ingestible (Fraser 2012). Even so, multiple studies have found nutritional profile to be a large determining factor, potentially even over taste, when choosing diet (Watson 2011). Nonetheless, taste does have an impact on food preference to some degree. Not unlike numerous other mammal species within Carnivora, the taste buds of a felid, located on the frontal portion of the tongue, show no preference for carbohydrate sweeteners due to genetics resulting in a lack of sweet taste receptors (Beauchamp et al. 1977; Fraser 2012; Jiang et al. 2012; Li et al. 2006). This lack of sweet taste receptors is hypothesized as one of the reasons felids are strictly carnivorous (Li et al. 2006). Though lacking in sweet taste receptors, housecats have been found to prefer ingesting some amino acids over others, especially avoiding those with mildly bitter to strongly bitter flavors (White and Boudreau 1975). Even with housecats believed to potentially discern bitter taste differently than humans do, this is likely as a result of the bitter taste receptors housecats possess (Lei et al. 2015; Sandau et al. 2015).

Gustatory sensations are also important in intraspecific interactions, such as licking other feline individuals (Fraser 2012). It has been hypothesized that taste sensing is even useful for a mother cat after giving birth (Fraser 2012). The gustatory sense is believed to be utilized while



cleaning neonatal kittens, aiding in a mother cat developing kin recognition (Fraser 2012).

Though less understood, the significance of olfactory sensing in the lives of felids is still acknowledged. Olfactory sensing is conducted through the nasal membranes and olfactory bulb, with odor information believed to be ascertained in the olfactory area of the cerebral cortex of the brain (Fraser 2012). Though not as sensitive as canines, felids are believed to have a keen sense of smell, with mother cats able to differentiate between the scent of their own young and “alien offspring” (Bánszegi et al. 2017; Sunquist and Sunquist 2002).

Olfactory sensing is used a great deal in the social lives of felids, as scent is used abundantly for communicating intraspecifically and interspecifically within the environment of felids (Sunquist and Sunquist 2002). Scent-marking is commonly conducted where felid ranges overlap, and female individuals have been observed increasing urine-spraying prior to fertile periods with the hopes of attracting a mate (Sunquist and Sunquist 2002). Scents and odors produced by felids are believed to indicate such information as sex, status, breeding condition, temporal details, and identity (Sunquist and Sunquist 2002). In fact, odor from anal-sac secretions in housecats is believed to provide conspecifics with an individual’s identity information, versus species level or even sexual information (Miyazaki et al. 2018).

Felids also possess a vomeronasal organ, also referred to as the Jacobson’s organ, which is comprised of two small tubes located in the nasal passages and specialized for aerosolized scent uptake of pheromones (Fraser 2012; Verberne 1976). When a pheromone is detected, a response referred to as flehmen is typically observed, in which an individual’s mouth opens, upper lip raises, and tongue-flicking occurs (Pageat and Gaultier 2003). Flehmen, though a strange observation to witness firsthand, aids in the uptake of pheromones into the vomeronasal organ (Pageat and Gaultier 2003). The vomeronasal organ is believed to be primarily utilized for detection of

sexual pheromones and potential breeding prospects (Fraser 2012). Felids possess six significant areas for secreting pheromones (Pageat and Gaultier 2003). Pheromones are produced from pheromone-secreting glands located in the facial area, the pedal complex (all four legs), the perianal complex, the genital complex, and the mammary complex and can also be found in feces and urine (Pageat and Gaultier 2003).

## Auditory and Vestibular Sensing

The auditory sense, or ability to hear, is highly developed in felids when compared with humans and even canines (Fraser 2012; Sunquist and Sunquist 2002). Felids, especially the serval species (*Leptailurus serval*), utilize the outer ears, referred to as the pinnae, to both amplify and locate sound (Sunquist and Sunquist 2002). Additionally, felids have been categorized as one of the mammals most able to perceive sounds made at middle frequencies within the range of 1–20 kHz (Bradshaw et al. 2012). Felids can also hear ultrasonic sounds, in the range of 60–80 kHz, compared with humans, which are only capable of hearing sounds up to 15–20 kHz (Sunquist and Sunquist 2002). As felids do not communicate through ultrasonic sound, the ability to hear at ultrasonic levels is likely specialized for hunting, especially in smaller felid species that hunt rodent prey that communicate using sounds within the range of 20–50 kHz (Sunquist and Sunquist 2002). Though it can aid in hunting prey, ultrasonic hearing can also be detrimental to the well-being of cats as loud noises can be harmful to hearing in felids (Fraser 2012).

Balance, brought about by the inner workings of the vestibular system within the inner ear, is also an important sense in felids (Bradshaw et al. 2012). This sense is especially developed in felids as a result of specialized inner ear morphology (Bradshaw et al. 2012). The heightened sense of balance as a result of the vestibular system aids felids in successful hunting, carefully navigating narrow walkways, landing right side up following

a fall, and staving off motion sickness (Bradshaw et al. 2012; Fraser 2012).

## Tactile Sensing

Tactile sensing, or touch, is also important in individual well-being and function for felids (Fraser 2012). Felids are believed to possess 15 different types of receptors related to tactile sensing (Bradshaw et al. 2012). These receptors are partitioned into three groupings including mechanoreceptors responsive to touch and pressure, thermoreceptors responsive to temperature, and nociceptors believed to be responsive to pain (Bradshaw et al. 2012). The mechanoreceptors can be further partitioned into two groupings based on responsiveness to the presence of maintained versus inconsistent touch or pressure (Bradshaw et al. 2012). Felid species contain varying amounts of mechanoreceptors all over the body, with abundant mechanoreceptors found in the nose and front paw pads (Bradshaw et al. 2012). The abundance of mechanoreceptors in the front paw pads aids in hunting, while the sensitive nose is believed to be used for examining temperature in newborn kittens (Bradshaw et al. 2012; Fraser 2012).

Felid species also possess vibrissae, most commonly referred to as whiskers, to aid in tactile sensing. Whiskers are thick sensory hairs deeply rooted beneath the skin that are located in multiple locations on the body including near the eyes, on the chin, and on the legs (Sunquist and Sunquist 2002). However, whiskers are most notably located on both the left and right side of the muzzle on a cat (Sunquist and Sunquist 2002). Whiskers are more than just hairs, as they are connected to nerve endings, thereby making them quite sensitive to minute movement, touch, and even changes in air currents (Sunquist and Sunquist 2002). As a result, whiskers are invaluable when hunting, especially at night, as the vibrissae move forward when an individual moves in on prey, providing the cat with tactile information regarding the location of the prey relative to itself (Sunquist and Sunquist 2002).

In addition to moving forward while hunting, whiskers also notably move forward when an individual is aggressive or backward when an individual is fearful (Fraser 2012).

## Conclusion

Species within the Felidae family have evolved visual, olfactory, gustatory, auditory, vestibular, and tactile senses ideal for supporting the ability to hunt as well as provide for social inter-specific and intraspecific interaction within the surrounding environment. While all the aforementioned senses in felids function at a high-level individually, it is the integration of these senses as part of a singular morphology that has allowed felids to navigate throughout their respective environments, thriving as uniquely successful predators.

## Cross-References

- ▶ [Accipitriformes Sensory Systems](#)
- ▶ [Auditory Processing and Perception](#)
- ▶ [Bear Sensory Systems](#)
- ▶ [Carnivora](#)
- ▶ [Carnivore \(Diet\)](#)
- ▶ [Catarrhine Sensory Systems](#)
- ▶ [Caudata Sensory Systems](#)
- ▶ [Cephalopod Sensory Systems](#)
- ▶ [Cetacean Sensory Systems](#)
- ▶ [Chemical Cues](#)
- ▶ [Chondrichthyes Sensory Systems](#)
- ▶ [Crocodilian Sensory Systems](#)
- ▶ [Equine Sensory Systems](#)
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- [Hunting](#)
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- [Olfactory Discrimination](#)
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- [Platyrrhine Sensory Systems](#)
- [Predator](#)
- [Primary Somatosensory Cortex](#)
- [Primate Sensory Systems](#)
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- [Psittaciformes Sensory Systems](#)
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- [Scent-Marking](#)
- [Sensory Judgment](#)
- [Sensory Receptors](#)
- [Sirenia Sensory Systems](#)
- [Squamate Sensory Systems](#)
- [Tactile Perception](#)
- [Visual Perception](#)

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## Felines in Religious Ritual

► [Sacred Cats](#)

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## Felis

► [Feline Life History](#)

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## Female Choice

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### Synonyms

[Intersexual selection](#); [Mate choice](#)

### Definition

Process by which females can bias paternity of their offspring to certain categories of males.

### Introduction

Sexual selection acts on variation in traits that affect reproductive success. Sexual selection can occur via competition between members of the same sex for reproductive opportunities with members of the opposite sex (intrasexual selection) or through mate choice for attractive members of the opposite sex (intersexual selection). Whereas intrasexual selection has traditionally been thought to act more strongly on males via male-male competition leading to male weaponry and body size dimorphism (direct competition) and large testis volume (indirect competition), intersexual selection has been thought to act more strongly on females choosing males due to differences in life history and parental investment between the sexes. Female choice is a form of

intersexual selection by which females can increase their reproductive success by biasing paternity of their offspring toward certain males (Andersson 1994).

Here, different types of female mate choice in relation to male attributes are described with examples. The benefits that these choices might confer to females are also discussed. This description is limited to examples between members of the same species and does not cover mechanisms of mate choice that might act to create and maintain isolation between species. This entry is organized into four non-mutually exclusive types of female choice in relation to the timing of mating and type of female discrimination: direct precopulatory choice, indirect precopulatory choice, direct postcopulatory choice, and indirect postcopulatory choice. Precopulatory choice happens before the act of mating, and postcopulatory choice occurs during or after the act of mating. Direct female choice occurs via active discrimination between males based on male attributes. Indirect female choice is a process whereby females elicit male-male competition, as an indirect mechanism for discriminating between males.

Although the terminology associated with female choice can sometimes imply reasoning and higher-level cognition, female choice does not refer to any type of conscious decision-making regarding preference. Whereas females of certain species may have the capacity for top-down modulation of reproductive behavior, most examples of female choice are thought to be the product of affective state and arousal in response to different males and their exhibited signals.

### Direct Precopulatory Choice

Direct precopulatory choice occurs when females influence male mating success by behaviorally discriminating between particular categories of males. This type of female choice received the most attention from Darwin and other early evolutionary biologists, due to the vibrant ornamentation and courtship displays that may evolve in males in response to such choice. Direct

precopulatory female choice is best described in aquatic and avian species, where females tend not to live in large aggregations and can escape male coercive tactics more easily across three dimensions. There is relatively less evidence for direct precopulatory female choice in terrestrial mammals, where females commonly live in monopolizable groups to avoid predation and in which marked sexual dimorphism has commonly evolved to facilitate male coercion (Clutton-Brock and McAuliffe 2009).

Selection favors females that can perceive informative cues to assess male attractiveness and alter their behavior accordingly. Females perceive mate quality through multiple communicatory modalities, including visual, auditory, and olfactory channels. Color vision is hypothesized to have evolved in a feeding context; however, females may exploit this adaptation to assess cues of male quality, such as plumage or skin color. Signal symmetry is another trait hypothesized to be assessed by females during mate choice due to its reflection of an individual's ability to cope with environmental stressors during development. Male vocalizations can be helpful in locating a male, but females have also evolved the capacity to gain information about male quality, such as body size, from these vocalizations. The assessment of olfactory cues may be especially important for females to ensure the genetic quality of their offspring. The sensory systems most affected by selection on female perception of male attractiveness will depend on the ecology of the species, including issues related to signal bandwidth and noise structures in the environment.

Female perception of male genetic characteristics and subsequent mating preferences can favor males possessing "good genes," or males with genetic compatibility to the female. Genetic compatibility refers to the interaction between the male and female genome, whereby females may prefer males possessing alleles that complement their own, as opposed to males possessing particular genotypes, or overall diversity. Genetic compatibility is implicated in inbreeding avoidance, which decreases the probability of disadvantageous recessive alleles being inherited and expressed and increases overall heterozygosity.

Heterozygosity throughout the genome is known to increase survival in numerous species through enhanced disease resistance, growth rate, and developmental stability (Allendorf and Leary 1986; Brown 1997). Female discrimination between kin and non-kin may occur based on familiarity during development, or through multiple hypothesized mechanisms of phenotypic matching, including via olfactory signals.

One area of the genome that may be especially important in female choice is the major histocompatibility complex (MHC), a highly polymorphic area of the genome that is involved with pathogen identification and immune response regulation. The "good genes" hypothesis predicts that females will prefer males with specific or diverse MHC types, causing mate choice between females to converge on certain types of males. This is observed in the great snipe (*Gallinago media*), a lekking bird species, where males with certain MHC alleles experienced higher mating success, regardless of female MHC type (Ekblom et al. 2004). Conversely, mate choice for genetic complementarity appears to be important in many other species. In sticklebacks (*Gasterosteus aculeatus*), females mate non-randomly in a manner that optimizes the number of MHC alleles that her offspring will inherit, and, in sand lizards (*Lacerta agilis*), females prefer the odors of males more distantly related at the MHC class I loci (Aeschlimann et al. 2003; Olsson et al. 2003). There is growing evidence that females perceive genetic characteristics via olfactory signals, due to the MHC's influence on the gut microbiome and associated volatile molecules related to body odor (Ziegler et al. 2005).

Once preferred mating partners are identified, females can facilitate mating with proceptive behaviors. Proceptive behaviors refer to active initiation and maintenance of sexual encounters and are distinct from receptive behaviors, which indicate only a willingness to copulate. Proceptive behaviors can include bodily postures, facial expressions, and locomotor patterns aimed to encourage male sexual arousal. Female-initiated reproductive behaviors, even in the most sexually dimorphic species with the largest scope for male sexual coercion, can have fitness consequences.



For example, female mandrills maintain proximity and engage in sexual presentations to males with the most brightly colored faces, which translates into higher mating success for brightly colored males, independent of dominance rank (Setchell 2005).

Female perception of male attractiveness and directed proceptivity has numerous documented effects on male morphology, physiology, and behavior. Male ornamentation and courtship displays are secondary sexual characteristics hypothesized to have evolved through female mate choice. The “good genes” hypothesis predicts that exaggerated secondary sexual traits convey honest information about male quality (Andersson 1986). Many male secondary sexual characteristics develop in correlation with increased production of androgens, such as testosterone, leading to sexual maturation. Androgens are associated with suppression of the immune system, and secondary sexual traits are hypothesized to develop in a trade-off with a male’s immunological status, so helping to maintain signal honesty (Hamilton and Zuk 1982). Conversely, the “runaway selection” hypothesis posits that exaggerated male secondary sexual characteristics do not communicate aspects of male quality and instead may simply be the result of the coevolution of male phenotype and a female preference for male traits based on female preexisting sensory biases (Fisher 1915). The challenging nature of explicitly demonstrating that a male trait does not communicate any aspect of male quality leaves the process of runaway selection difficult to substantiate.

Male qualities that are influenced by the local environment and provide direct fitness benefits, such as fertilization ability and paternal investment ability, can also be communicated via male secondary sexual characteristics and used to inform female mating decisions. Sperm depletion after successive matings is well known in many species to influence female mate choice. For example, female lemon tetra (*Hyphessobrycon pulchripinnis*) preferentially mate with males that have not spawned recently and avoid males with reduced sperm supply (Nakatsuru and Kramer 1982). Sperm supply may be communicated through physical or behavioral changes,

such as the extent of courtship. Courtship success in *Drosophila* is reduced after sperm depletion, and there is a correlation between male courtship display rate and sperm supply in smooth newts (*Triturus vulgaris*) and checkered white butterflies (*Pieris protodice*) (Halliday 1977; Markow et al. 1978; Rutowski 1979).

In species with paternal care, a male’s ability to invest in offspring can also be an important factor influencing female mate choice. Male nutritional state and parenting experience are important aspects of male quality impacting male parental ability. In moorhens (*Gallinula chloropus*), females compete for access to fat males with large energy reserves which allow them to incubate eggs for longer (Petrie 1983). Red-winged blackbird females (*Agelaius phoeniceus*) prefer experienced fathers who tend to feed their offspring more and are able to identify them based on their larger song repertoires and longer courtship displays (Yasukawa 1981). Courtship is also an honest indicator of subsequent paternal investment in the bicolor damselfish (*Stegastes partitus*). Males with larger body fat reserves perform longer courtships, guard eggs for longer periods of time, and are less prone to cannibalizing eggs (Knapp and Kovach 1991).

In some species of birds and insects, males provide females with nutrition during courtship. The size of nuptial gifts can impact the probability of copulation and be indicative of future paternal investment, as in the common tern (*Sterna hirundo*), where the rate at which a male feeds a female during courtship is correlated with that male’s later rate of feeding to the resultant offspring (Nisbet 1973). These types of gifts can benefit the female in two ways. In species where finding prey is dangerous, nuptial gifts increase a female’s survival probability by reducing her hunting time. Females also gain increased resources to invest in increased fecundity. In species exhibiting individual discrimination, exchanging food or other types of support (e.g., protection from predators, grooming) for mating opportunities may happen on longer timescales, although evidence for this is limited (Gomes and Boesch 2009).

## Indirect Precopulatory Choice

Indirect precopulatory choice occurs when male contest competition and female choice work in combination. Under this scenario, females bypass the need to actively discriminate between males based on attractiveness and instead incite male-male competition, with mating access then granted to the male that wins. Multiple species achieve this by signaling fertility in different communication modalities. Swelling of the perineal skin in multiple species of primates around the fertile phase of the cycle is hypothesized to have evolved because it stimulates competition among males (Nunn 1999). Acoustic signals of fertility work in the same manner and have been documented in the estrus calls of a number of different mammalian species and groups, such as African elephants, Old World monkeys, and bovids (Gouzoules et al. 1998; Poole 1989; Pradhan et al. 2006; Yeon et al. 2006). Delivering a call during times of peak fertility advertises the female's sexual receptivity and encourages dominant males to supplant subordinate males and engage in mating and subsequent mate guarding.

Evasive behaviors are another method by which a female can ensure that she mates only with males of a certain type without needing to discriminate between them. Ducks, barn swallows, and tree squirrels all engage in indirect female choice by running away from potential mates (Koprowski 1993; McKinney et al. 1983; Møller and Gregersen 1994). The first male that is able to catch the female has the opportunity to mate with her, which may limit mating partners to those males in top physical condition.

Female aggregation, sometimes at predetermined locations, has also been suggested to act as a means of indirect female choice. Grouping of receptive females facilitates herding by males and promotes competition between males for exclusive access. In some Caribbean fish, females return to the same location year after year to spawn, and males compete for access to females in these areas (Domeier and Colin 1997). Although these areas do have advantages, such as abundant food or protection from predators, the locations are chosen relatively arbitrarily

(i.e., there are many locations with similar food and predator densities) and are learned from previous generations. Many species of insects engage in a similar kind of behavior called "hill-topping." Males compete among each other for access to the highest elevated areas, and females mate with those males possessing those territories, thereby mating with males of the highest competitive ability without actively discriminating between male qualities (Alcock 1987).

Indirect female choice can also be related to resource holding in males. For example, female Grevy's zebras (*Equus grevyi*) late in gestation will restrict their ranges to areas with watering holes to sustain lactation (Rubenstein 1986). Males holding these areas in their territory have exclusive mating access to lactating females during their post-estrus cycle. As such, females are more likely to mate with males that are able to defend high-quality territories, a preference constrained by their need for water. Some researchers have classified this type of assortative mating as indirect precopulatory choice, while others have referred to it as "coincidental" mate choice (Clutton-Brock and McAuliffe 2009).

## Direct Postcopulatory Choice

Postcopulatory choice, also termed cryptic female choice due to the cryptic nature of processes occurring inside the female reproductive tract, is a mechanism of sexual selection that occurs during or after copulation. Direct postcopulatory choice occurs when females behaviorally or physiologically discriminate between the seminal products of different males, thereby influencing the likelihood of male fertilization after mating has already occurred. Most simply, this can be achieved by preventing complete intromission and ejaculation but can also occur after insemination through modification of the amount of sperm retained or stored in the female reproductive tract, or preferential usage of particular sperm.

Sperm ejection from the female reproductive tract is documented in many species, such as jungle fowl, rattlesnakes, parrots, and many species of insects. This can be a large portion of

the inseminate, such as in the soil nematode (*Caenorhabditis elegans*), where 42% of copulations resulted in active ejection of the ejaculate from the female's body (Barker 1994). Sperm ejection can also be more subtle, such as the gravitational flow back of only a portion of the seminal fluid. Coagulations of seminal fluids, called sperm plugs, are produced by many species in many taxa exhibiting polygynandrous mating and are used to retain the ejaculate within the female reproductive tract. There is ample evidence of females removing sperm plugs, thereby facilitating flow back. The peristaltic contractions of the vaginal walls that occur during female orgasm are also implicated as a mechanism by which females can influence the amount of sperm that flows back out of the vagina after mating. This process is noted in humans, and many nonhuman mammals, such as rabbits, cattle, and dogs. Differential sperm transfer within the reproductive tract to the location of sperm storage or ova fertilization is also a suggested mechanism of cryptic female choice.

Remating with a different individual soon after insemination is expected to decrease the probability of paternity in the first mating male, and the latency to remating is often associated with male quality. For example, female rats remate sooner after copulation with a low-ranking male than with a high-ranking male (McClintock et al. 1982). The order in which females mate with multiple males is well-documented to have significant effects on paternity in birds and insects, with the last mated male usually receiving a majority of paternity (Birkhead and Møller 1992; Thornhill and Alcock 1983). Once remated, female postcopulatory choice can occur through differential sperm storage, transport, or preferential use of the new male's sperm.

Throughout the process of fertilization, implantation, gestation, and after parturition, females can modify or terminate investment in ways that modify their reproductive success as well as that of their mate. Male traits that increase the probability of ovulation, or the number of eggs produced, would increase a male's reproductive success and be passed on to offspring. In mammals, hormonal changes within the female prepare

the uterus for implantation, which can also be differentially triggered by male behaviors. Once a zygote has been formed, spontaneous abortion (termed the "Bruce effect") can occur. This process is well characterized in mice following the introduction of a novel male but has also been observed in a wild setting in the gelada, a large-bodied, long-lived primate (Bruce 1960; Roberts et al. 2012). Finally, in species with parental care, females can differentially invest or terminate investment in offspring after parturition based on the quality of their mate; however, there are limited concrete examples of this mechanism of cryptic female choice occurring.

The genetic composition of sperm both within the same ejaculate and between the ejaculates of different males can also be the target of postcopulatory female choice. The "sperm receptor selection" hypothesis posits that receptors on the surface of sperm that lack self-reactivity will respond to chemical stimulation in the reproductive tracts of genetically dissimilar females, improving the probability of oocyte fertilization by sperm of dissimilar genetic composition (Ziegler et al. 2002). For example, in the gray mouse lemur (*Microcebus murinus*), researchers found that males with higher amino acid distances and fewer MHC supertypes shared with their mate sired more offspring (Schwensow et al. 2008). In addition to complementarity, certain genetic makeups may be favored regardless of female genetic composition. This preference for "good genes" is also suggested in the gray mouse lemur. All females favored sperm with greater microsatellite heterozygosity and more absolute total MHC alleles. In this case, however, it is difficult to determine whether this effect is due to intrinsic qualities of sperm with those genetic makeups or cryptic female choice.

## Indirect Postcopulatory Choice

The most commonly recognized mechanism of indirect postcopulatory female choice is that of sperm competition (Birkhead and Møller 1998). Sperm competition refers to the race that ensues between sperm from different males to fertilize the

egg in a multiply mated female. Females can play an active role in the extent of sperm competition occurring within their reproductive tract. Vocalizations given after copulations are hypothesized to communicate fertility and incite male-male competition for future matings. In primates, copulation calls appear to encourage mate guarding by dominant males, thereby decreasing sperm competition; however, copulation calls may also have the capacity to increase sperm competition by stimulating the interest of distant males and promoting promiscuous mating (Maestriperi and Roney 2005).

Female mating patterns and sperm competition have well-documented morphological and behavioral consequences for males. The relatively larger testis size observed in male primates living in polyandrous and polygynandrous mating systems is attributed to their increased need for sperm production as a consequence of sperm competition within the female reproductive tract (Harcourt et al. 1995). Selection on enhanced sperm production, semen coagulation, ejaculatory frequencies, and penile morphology are all likely influenced by the extent of sperm competition in the species. As a counter-strategy to sperm competition, males can produce a physical barrier to prevent the sperm of subsequent mating partners from fertilizing the females' eggs. In the Australian redback spider (*Latrodectus hasselti*), the male breaks off a portion of his copulatory organ inside of the female, blocking the entrance to her sperm storage organ from subsequent mating partners' sperm (Snow et al. 2006). Males can also engage in prolonged associations with fertile females, called consortships, to prevent mating and decrease sperm competition with other males.

Along with the quality of the sperm cells themselves, nutrients provided to the female by the male during or after mating may also correlate with paternity allocation and female fecundity. The hangingfly (*Hylobittacus apicalis*) female allows males to copulate with her only for as long as it takes for her to consume the male's food gift, with a larger food item equating to longer time spent in copulation, greater sperm transfer, and increased paternity (Thornhill 1976). The most drastic display of male

nutritional donation occurs when females cannibalize the male after copulating. In these species, females experience increased fecundity after copulations in which the female consumes the male. Larger males are more likely to be able to escape consumption after copulation, thereby females indirectly bias paternity toward smaller males (Thornhill and Alcock 1983).

## Conclusions

Even though this entry has organized female choice into four separate processes, it is likely that multiple mechanisms of female choice are present in the behavioral and psychological repertoire of any given organism. Both pre- and post-copulatory mechanisms may be at play, as seen in the female katydid (*Metaplastes ornatus*) that approaches only males with the most attractive calls, but stores ejaculate based upon the number of genital couplings the male performs (Helvesen and Helvesen 2004). Similarly, females can employ strategies of both direct and indirect choices. For example, female elephant seals (*Mirounga angustirostris*) modify their rate of calling depending on the dominance rank of their partner, so, while the call indirectly benefits the female by advertising fertility and inciting male-male competition, females are also actively adjusting their behavior based on male quality. In addition, if copulation calls incite mating by more than one male, indirect postcopulatory choice may then also subsequently occur via sperm competition (Cox and Le Boeuf 1977).

Much of what is known about female choice has been best explored in fish, insects, birds, and other organisms that are conducive to manipulatory experimental studies. Creativity in the design of experimental studies, particularly those in natural settings, will be needed in order to explore how intersexual selection acts on many animal groups. It will continue to be difficult to tease apart the extent of female choice relative to male coercion, especially when these tactics favor the same paternity outcome as seems to be the case in many mammalian species. Additionally, visual and auditory communication of mate quality has

been a major focus in studies of female choice, leaving a dearth of knowledge on the role of olfactory signals outside of a few taxa. As methods allowing exploration of genomic information become more efficient, the genetic underpinnings and consequences of female choice will be an especially interesting avenue of research. Until this information is available, it would be smart to assume that the processes observed in experimental studies of insects and other small organisms are likely not confined to those classes of organisms and are probably present in species of other taxa too.

## Cross-References

- ▶ [Cryptic Mate Choice](#)
- ▶ [Intersexual Selection](#)
- ▶ [Major Histocompatibility Complex](#)
- ▶ [Runaway Selection](#)
- ▶ [Sperm Competition](#)

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## Female Defense Polygyny

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## Synonyms

[Harem defense polygyny](#)

## Definition

Individual males control access to a large group of gregarious females.

## Introduction

There exists a range of potential mating systems among all species. These various mating systems have been classified to organize the terminology to better understand the evolution of mating systems (Emlen and Oring 1977). One of the overarching categories in this classification system, polygyny, includes any mating system where an individual male monopolizes access to a group of females. The grouping of females may occur by many means, such as behavioral or environmental pressures. Included in this category are resource defense polygyny, female defense polygyny, and male dominance polygyny. These categories are separately defined, but the distinction may not be straightforward in real-life scenarios.

## Female Defense Polygyny

Of the three types of polygyny, female defense polygyny is defined as when females gregariously group together and one male is able to monopolize these females from other males (Emlen and Oring 1977). The grouping of the females is possibly due to any number of reasons but does not include reproduction purposes. In this type of polygyny, the males may herd or retain the females within their territory through aggressive actions toward other opposing males. They must stop all opposing males' attempts in order to control access to the cluster of females.

## Distinguishing Female Defense and Resource Defense Polygyny

An issue observed in many species is that female defense polygyny often occurs in combination with male resource defense polygyny (Emlen and Oring 1977). Therefore, it can be difficult to distinguish between the two types of polygyny. It has been suggested that even though these may occur in combination, one may still be able to distinguish the value of the role that each system may play (Ostfeld 1987). It is first critical to assess if the males are in contact with the grouping females without being near any critical resources. If this is true, one may exclude resource defense polygyny. If it is not, then one must assess if the males will monopolize a resource in both the presence and absence of females. If males attempt to control this resource in the absence of females, then resource defense polygyny is the system employed. However, one must not rule out female defense polygyny if males adjust their territory after the arrival of females. Although female defense polygyny and resource defense polygyny may not be mutually exclusive, the classifications are still of empirical value.

## Conclusion

Female defense polygyny is a system of polygyny that requires individual males to monopolize the

access to a grouping of females. It is possible that this system may exist in conjunction with resource defense polygyny, but experimental evidence should be acquired to distinguish each system's role.

## Cross-References

- [Costs of Group Living](#)
- [Facultative Polyandry/Strategic Pluralism](#)
- [Group Living](#)
- [Mate Guarding](#)
- [Mating](#)
- [Monogamy](#)
- [Pair Bond](#)
- [Polyandry](#)
- [Polygamy](#)
- [Polygynandry](#)
- [Polygyny](#)
- [Polygyny Threshold Model](#)
- [Resource Defense Polygyny](#)
- [Scramble Competition Polygyny](#)
- [Scramble Defense Polygyny](#)
- [Sneaky Copulator](#)

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## Female Gametes

- [Ova](#)

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## Feral Pigeon

- [Pigeon \(\*Columbidae\*\)](#)

## Fertility

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## Synonyms

Productiveness; The ability to conceive children

## Definition

Fertility is the ability of an individual to produce the offsprings by natural means. The root word of fertility is fero, which means “to carry, to bear.”

## Fertility

Fertility is the ability of an individual to produce the offsprings by natural means. The root word of fertility is fero, which means “to carry, to bear.” The term fertility is sometimes confused with fecundity, which defines the capacity of reproduction. Although fertility is a general term for all of the organisms, including plants, here we focused on human fertility. Louis Henry coined a term “natural fertility” which applied to the population where contraception is not used depending on the number of children that families have. The inability to conceive a child within a year or more with regular sexual intercourse is defined as infertility. The rate of fertility is an important factor to keep a close eye in the societies as many modern societies are going through fertility crisis (Caldwell and Schindlmayr 2003). The rate of fertility is a measure of health of a population, and to sustain a population, the balance of fertility rate is very important. The measurement of fertility rate is also important for policy makers and family welfare. Therefore the factors involve in modulation of fertility and indexes to measure a fertility rate are important to be discussed. The rate of fertility

can be influenced by various factors such as economic factors, social factors, cultural beliefs, and natural factor (Fernandez and Fogli 2006). One such social and cultural factor is gender division of labor in a family or household. Many studies found direct correlation between gender division in household and fertility rate. In one such study, it was found that women feel the burden of having a child in the household (Dommermuth et al. 2014). Altogether the factors that influence fertility can be categorized into mainly two types: proximate (direct) factors and background (indirect) factors (Bongaarts and Potter 2013).

## Proximate Factors

These variables influence fertility directly and also are intermediate factors. The ten different fertility variables, proposed by Davis and Blake (1956), which influence infertility, are directly given below and also can be categorized in 3 main groups, and each of them is described briefly.

- A. Factors affecting the exposure to intercourse:
  - (i) Age of marriage and entry into sexual unions
  - (ii) Reproductive period
  - (iii) The celibacy
  - (iv) Coital frequency
  - (v) Voluntary and involuntary abstinence
- B. Factors affecting exposure to conception:
  - (vi) Infertility
  - (vii) Contraception
  - (viii) Lactational infecundability
- C. Factors affecting parturition:
  - (ix) Miscarriage and fetal mortality
  - (x) Induced abortion

## Factors Affecting the Exposure to Intercourse

The higher exposure to intercourse increases the chance of becoming pregnant and results in higher fertility rate. In human society, childbirth is mainly considered after marriage. The average age of marriage differs in societies. The age of the marriage would be a major factor for the percentage of the reproducing female in a sexual

union in a population. If marriage age is lesser, then the more proportion of the female would enter in sexual unions, and that's how the year of the reproductive age also increases. There are many factors influencing the age of marriage such as education, economic development, cultural factors, etc. (Becker 1960).

Women can conceive for a short period of time called reproductive period. The culture factors also influence age of marriage and the time spent for regular intercourse. In many societies, there is a number of females who never enter into sexual unions and intently live in celibacy. All these factors influence the proportion of reproductive unions in a population and hence influence the fertility rate.

The fertility rate is influenced by the rate of coital frequency. Although the estimate on actual coital frequency is hard to find for a population, they have high impact on fertility. The higher the coital frequency, the higher the chance to conceive that leads to high fertility rate. The educated and working couples spend most of their reproductive time in separation due to separate work space and hence reduce the chance of pregnancy.

### Factors Affecting Exposure to Conception

Infertility is the inability to conceive child after having regular intercourse for at least a year and is considered a major factor which influences the exposure to conception. About 15% of couples are infertile, around the world. The infertility which is responsible by male and female's factors is almost 50–50%. The infertility is caused by different factors such as environmental toxicity, life habits, sexual diseases, and genetic factors. There are only 20–30% cases with known genetic factor; otherwise about 70% cases are idiopathic. One such factor which covers 15% genetic factor is Y chromosome microdeletions.

Contraception is a method which reduces the frequency of conception. Contraception is another factor that contributes to the exposure to conception which clearly can reduce the birth rate and clearly affect the rate of fertility of the society. In the late twentieth century contraceptions, mainly condom, hormone-based contraceptive pills, and germ cell sterilization, become tools to reduce birth rate. The revolution of the use of

contraception is highly correlated with decrease in fertility rate around the world. The use of contraception is also influenced by different factors such as education, sociocultural factors, and availability. The use of contraceptive methods is higher in educated women and higher in women who are living in urban areas. The use of contraceptive increases among women having enough number of children, but the criteria of enough number of children changed with different societies. There are also cultural factors such as some societies still think that children are god's gift and refuse to use contraception (Hayford and Morgan 2008). The methods used for contraception are also a concern for individuals for future risk of not conceiving a child. This fear reduces the use of hormonal-based contraception in many societies and was correlated with high birth rate. These factors influence the use of contraception in different societies and influence the fertility rate.

After delivery, women remain unable to conceive for a certain period of time. The duration of infecundability is dependent on the duration and the quantity of breastfeeding. The long duration of lactation delayed the normal menstrual cycle, and ovulation of breastfeeding mother differs among societies. The period of breastfeeding is lower in economically developed populations. The length of infecundability is longer in rural area and uneducated women (Campino et al. 2001). This is an addable factor which affects the conception and the rate of fertility among different societies.

### Factors Affecting Parturition

Miscarriage is a loss of pregnancy before 20 weeks of gestation. About 15% of pregnancies are unsuccessful because of miscarriage. The problem of miscarriage is correlated with different factors such as economic development, lifestyle, reproductive health, and pathological infections. Some women face recurrent miscarriage due to some known and idiopathic genetic disorders such as immunological disorders and chromosomal abnormalities, and its prevalence is approximately 5–8%. Induced abortions are another factor, which affects fertility rate. Its occurrence mainly depends on the practice to restrict childbearing and availability of contraception. Induced abortion is

practiced in almost all societies with different proportions. Induced abortion is motivated by different factors such as cultural and socioeconomic factor. One such cultural factor is dowry system which induces burden on girls' parents and leads to motivation of induced abortion of girl child. This gender-biased abortion leads to decrease in women proportion in a population and plays a meaningful effect on fertility (Hayford and Morgan 2008).

## Background Factors

This factor does not affect fertility rate directly. These factors are cultural, socioeconomic, and demographic variables such as age and marital status, place of residence, literacy status, occupation, religion, mass media exposure, wealth status, knowledge, the number of children already born, employment status, and income.

## Fertility Rate Measurement

Fertility can be measured by different methods in a population which refer to as fertility rate. Fertility rate is mainly estimated by two ways: first is periodic measure during a given period of time, and second is cohort measure within a given population.

The periodic measures include different estimates of the rate of fertility:

1. Crude birth rate (CBR) is defined as the number of live births during a year in a population of 1000 during the middle of the year.
2. General fertility rate is the number of live births stated in a time period per number of women aged 15–49 in the same period and expressed in 1000 women.
3. Total fertility rate is the total number of child born or likely to be born to a woman in her lifetime if she was to experience the prevailing age-specific fertility rates of women.

The abovementioned parameters are considered as proximate determinants (direct effect on fertility) such as union patterns, contraception, lactational amenorrhea and postpartum abstinence, pathological sterility, and abortion.

Bongaarts and Potter (2013) developed a model to establish the relationship between the total fertility rate and the proximate determinants of fertility and model known as Bongaarts model of proximate determinants. In this model total fecundity rate (TF) of women is considered the same, but their actual reproductive performance is modified by four major proximate determinants, marriage, contraception, induced abortion, and postpartum infecundability, i.e., denoted by  $C_m$ ,  $C_c$ ,  $C_a$ , and  $C_i$ , respectively. So, the equation is as follows:

$$TFR = C_m \times C_c \times C_a \times C_i \times TF$$

where TFR = total fertility rate

$C_m$  = index of marriage ( $C_m = 0-1$ ; equals 1 if all women of reproductive age are married and 0 in the absence of marriage)

$C_c$  = index of contraception ( $C_c = 0-1$ ; equals 1 in the absence of contraception and 0 if all fecund women use 100% effective contraception)

$C_a$  = index of induced abortion ( $C_a = 0-1$ ; equals 1 in the absence of induced abortion and 0 if all pregnancies are aborted)

$C_i$  = index of postpartum infecundability ( $C_i$  ranges from 0 to 1; equals 1 in the absence of lactation and postpartum abstinence and 0 if the duration of infecundability is infinite)

TF = total fecundity rate

Total fertility rate of India is 2.33 births per woman (2016). Africa and Somalia have high TFR (6.95 children per woman), whereas South Korea has low TFR (1.1 children per women).

## Conclusion

Fertility has a major impact on the socioeconomic condition of a country. To regulate the fertility rate in a country, it is very important to study the direct and indirect parameter carefully (Mahjabeen et al. 2011). The following methods could be used to regulate fertility:



- (a) Contraception-related information and campaigning should be re-emphasized, as it is a direct parameter that affects fertility rate.
- (b) After achieving the desired number of children, couples should be encouraged for sterilization to avoid unwanted pregnancy.
- (c) Awareness-raising programs should be undertaken in order to prevent female child or adolescent marriage – especially among illiterate people and in the rural areas which will help to increase the age at marriage of women.
- (d) Due to traditional sociocultural background, open consultation about reproductive health issues should be encouraged. Education system and media can play important role in overcoming this problem.

## Cross-References

- [Fecundity](#)
- [Gametes](#)
- [Mating](#)
- [Population](#)
- [Reproduction](#)

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## Fertilized Egg

- [Embryo](#)

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## Fertilized Ovum

- [Zygote](#)

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## Fetus

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## Synonyms

[Developed embryo](#); [Developing infant](#); [Unborn young](#)

## Definition

The term fetus can be defined as the unborn offspring in the uterus representing the post-embryonic stage of development until birth.

## Introduction

Fetus is a Latin word that symbolizes “pregnancy, childbirth, offspring.” Fetus is the unborn vertebrate that has reached later stages of development exhibiting distinctive features of a mature animal. In a fetus all major structures (organs and their precursors) are already formed and they keep growing, differentiating, and developing.

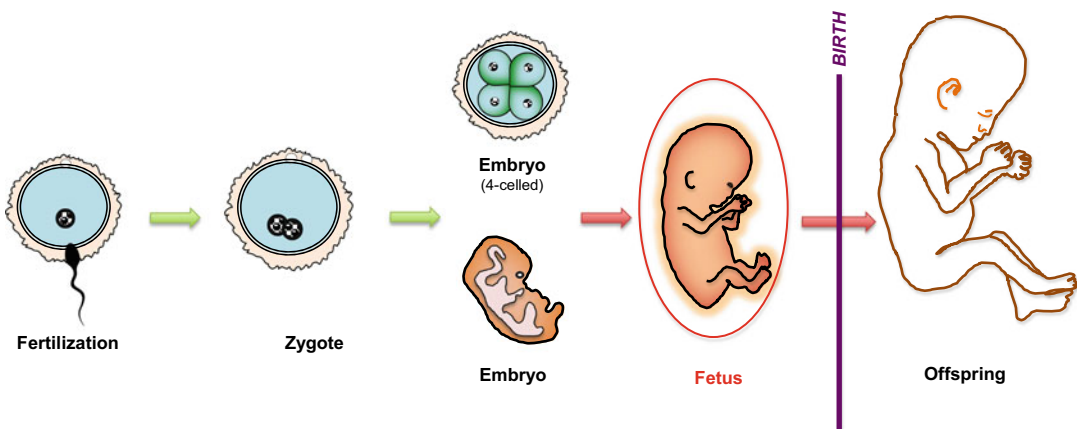
Among glands, thyroid is known to develop first by 4th week of gestation when adrenal cortex can be seen and parathyroids begin to develop (Gardner and Shoback 2011). At the same time, fetal pancreas starts to develop but insulin secretion begins around 12th week of gestation. Reproductive system starts developing from 4th to 5th week of gestation. During this duration, a cavity of ectodermal cells of the oropharynx known as Rathke’s pouch forms and later gives rise to the anterior pituitary gland. Hematopoiesis starts in the yolk sac and then by 10th week of gestation, the function is transferred to liver. Later, it goes to spleen and bone marrow subsequently. Early in development fetal erythrocytes are megaloblastic which later become normoblastic near parturition. Fetal RBCs live for about 80 days. Leukocytes production in fetus begins at 8 weeks of gestation from thymus and spleen (Percival et al. 1980; Evans and DeFranco 2014).

Development of brain starts with neurulation (formation of neural tube from ectoderm) just after gastrulation in all vertebrates. During gastrulation the

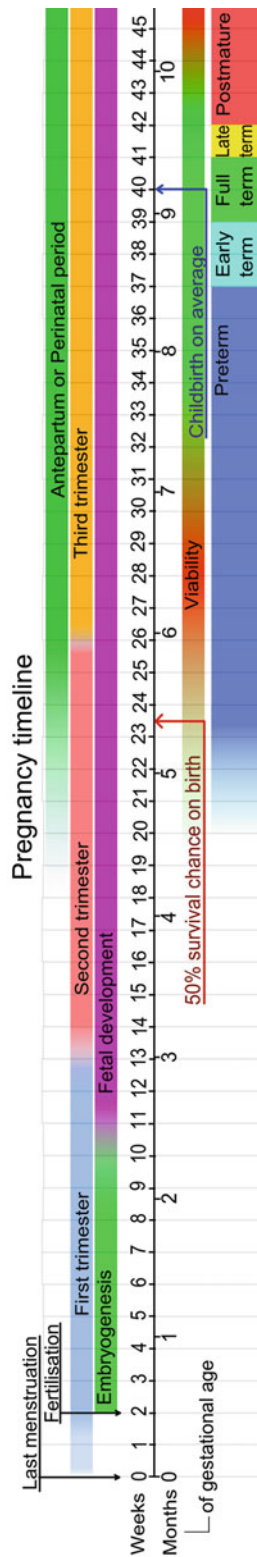
three germ layers are formed namely the endoderm (the inner layer, which gives rise to the gut), ectoderm (the outer layer, which gives rise to skin and the nervous system), and mesoderm (the middle layer, which later gives rise to rest of the organs). A group of cells from the mesoderm forms notochord (notogenesis). In the gestational week 3, underlying notochord induces the ectodermal cells just above it to become neuroectoderm. This forms neural stem cells giving rise to neural plate, from where the complete nervous system emerges (Fig. 1).

## Fetal Development in Humans

In humans, fetal period is four times longer than the embryonic period, *i.e.*, between weeks 9–37 following fertilization. In clinical context, it is delineated as second and third trimester. During this period highest rate of growth occurs *per se* as well as in various organs. The organ systems that started to form (organogenesis) during embryonic phase persist to develop and differentiate further in an age-dependent manner. Different molecular switches control organ system development in the fetus. For example, a DNA-binding protein, known as sex-determining region Y (SRY) protein, encoded by *SRY* gene initiates male sex determination. During fetal period, the urogenital system differentiates into either male or female pattern accordingly. Additionally, the



**Fetus, Fig. 1** Perinatal development showing the stage of fetus. A fetus develops from the embryo and after birth it is called as offspring. During fetal period most organs get fully developed and functional



**Fetus, Fig. 2 Human pregnancy timeline.** Embryogenesis precedes fetal development, which occurs since week 9 till the birth of the offspring. On an average, childbirth occurs after completion of 9 months but one can see, birth classification states it to be preterm if occurs around 7th or 8th month whereas it is called postmature if it is around 10th month of gestation (Hägström 2014) (Reproduced with permission)

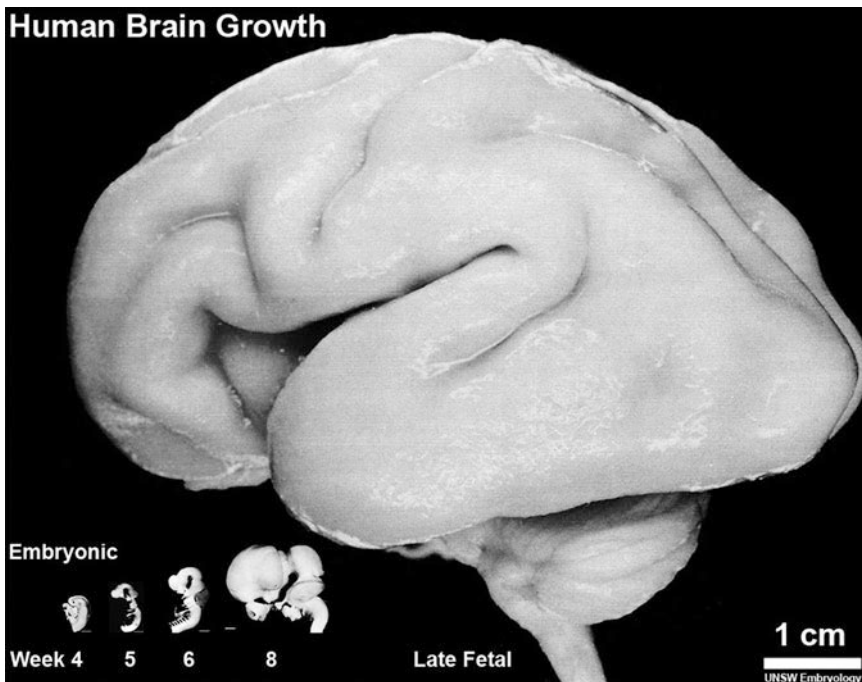
gastrointestinal tract and endocrine system starts functioning during this period. Brain keeps on growing and differentiating into more complex structure during the fetal period. While the brain keeps improving itself in the postnatal period, respiratory system completes the differentiation process just before birth (Moore and Persaud 2003) (Fig. 2).

## Fetal Brain Development

Brain is one of the first organs to start forming in an embryo and certainly the last to completely develop functionally. This long duration is required for neural differentiation, making complex network of neurons and interconnecting neural pathways controlling all organ systems. The nervous system continuously grows and increases in its complexity. By week 3 of embryonic development (gestational week 5), neural groove and folds are visible and hence

neurogenesis commences. During 4th week, the development of central nervous system (also known as CNS) initiates as a neural plate which folds to form a groove and then the neural tube (Hill 2017). The stem cells from the neural tube give rise to majority of cells in the nervous system namely neurons and glia. Later on these cells differentiate into different types with varied shape, structure, and function according to the microenvironment milieu. At cellular level different neurons are born that migrate and differentiate, extend processes, and few die (programmed cell death) during fetal period to accommodate different functions and rectify the assembly of nervous system.

By the end of week 4, spinal cord and the primary brain vesicles are formed namely Prosencephalon (forebrain), Mesencephalon (midbrain), and Rhombencephalon (hindbrain). By next week the secondary vesicles are formed: prosencephalon gives rise to telencephalon and diencephalon; mesencephalon remains same as secondary



**Fetus, Fig. 3 Human fetal brain in the later stage.** *Left* dorsolateral view of a human fetal brain at crown-rump length (CRL) of 240 mm. Few major gyri and sulci start appearing as compared to the embryonic brain and hence

the Sylvian fissure becomes prominent. The scale bar shows 1 cm length (Hill 2017) (Reproduced from [https://embryology.med.unsw.edu.au/embryology/index.php/File:Human\\_brain\\_growth\\_01.jpg](https://embryology.med.unsw.edu.au/embryology/index.php/File:Human_brain_growth_01.jpg))

vesicle; and rhombencephalon gives rise to metencephalon and myelencephalon. These secondary vesicles give rise to different adult brain structures and the major ones are: Telencephalon gives rise to cerebrum (cortex), amygdala, hippocampus, hypothalamus, pituitary, basal ganglia, lateral ventricles whereas, diencephalon differentiates into epithalamus, thalamus, subthalamus, pineal and third ventricle. Mesencephalon forms the cerebral peduncle, tectum, pretectum, and cerebral aqueduct. Metencephalon differentiates into cerebellum and pons whereas medulla oblongata evolves from myelencephalon (Hill 2017) (Fig. 3).

## Factors Affecting Fetal Development

The development during the embryonic and fetal stages of gestation is called prenatal development. By 11th week of gestation, an embryo acquires its basic form and from then it is known as fetus. At this stage of fetal development many of the organs are fully developed. If there are any genetic abnormalities in the embryo/fetus, it gets spontaneously aborted in the first trimester. Fetus drives all of the requirements from the mother therefore, perinatal nutrition is very important. A pregnant woman needs an increase of calories by 300 kcal/day and proteins by 70–75 g/day as compared to regular diet. For proper neural development and avoiding neural tube defects, a mother should also increase the dosage of vitamin B12 and folate. Such supplementation helps in proper growth of the fetus. At this stage the concept of fetal origins (programming) of adult disorders (FOAD) (Barker 1990; Last 2007) is very crucial to understand. Evidences show nutritional insufficiencies during fetal development, program for metabolic syndrome in later life (Lakshmy 2013; Ghosh et al. 2017).

Prenatal developmental period, that is critical for the growth and development of the embryo and fetus, is susceptible to exposures to various internal or external factors, like:

1. Nutritional insufficiencies, *e.g.*, vitamin B12, folate, *etc.*
2. Drugs (substance) of abuse and alcohol (fetal alcohol syndrome), *e.g.*, cocaine, amphetamines, lysergic acid diethylamide (LSD), phencyclidine (PCP), *etc.*
3. Toxins, *e.g.*, lead, polychlorinated biphenyls (PCBs), tetrachloroethylene (PERC), bisphenol A (BPA), dichlorodiphenyltrichloroethane (DDT), phthalates, chlorpyrifos, arsenic, mercury, fluoride, *etc.*
4. Radiation exposure above 200 mSv, *e.g.*, x rays, fluoroscopy, or radiation therapy
5. Infections, *e.g.*, candidiasis, cytomegalovirus, rubella, *etc.*

## Conclusion

Fetus is the postembryonic stage in the prenatal development of viviparous animals and lasts till the birth of the organism.

## Cross-References

- Embryo
- Internal Fertilization
- Zygote

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## Fibril

► [Cilia](#)

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## Fidelity

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### Definition

The exactness with which an agent reproduces the observed behavior of another individual or group. Copying (also called imitative) fidelity can be thought of as a spectrum from high to low and encompasses various social learning strategies.

Copying fidelity and imitation have been characterized in a variety of ways throughout the literature on social learning. Research on social learning has primarily come from comparative programs focusing on how children, and other species (primarily apes and monkeys) learn from others to acquire problem-solving, instrumental skills. Much of the previous literature has examined the physical-causal information required to allow children, and other animals, to accurately copy an instrumental action sequence. The focus on the role of physical-causal reasoning in social learning led to attempts to define social learning mechanisms based on what features of an action sequence children, and other animals, accurately replicate. Much of this literature has ascribed a central role to children's ability to read a demonstrator's intentions toward a physical-causal end-goal. There are alternative theories that

diminish the role of intention reading in copying fidelity as well as evidence that copying fidelity is increased or decreased based upon the nature of the observed task. When an action sequence is interpreted as conventional and based in social stipulation, copying fidelity is increased, and when an action sequence is interpreted as instrumental, copying fidelity may be decreased when a clear goal is present. The tendency to copy conventional behavior with high fidelity may be a uniquely human trait associated with the importance of engaging in conventional behavior for group membership.

### Theories of Social Learning Strategies Associated with Copying Fidelity

Tomasello and colleagues (Tomasello 1990, 1996; Tomasello et al. 1993, 2005) proposed a distinction between social learning via imitation and social learning via emulation based upon what an observer is proposed to be attending to when replicating behaviors: the behavior of another (imitation) or the changes in the environment caused by the behavior of another (emulation). An individual who is emulating will seek to reproduce the same change in the environment with little attempt to copy the actual actions of a model. In this way, the observer may be said to be learning something about the causal effect of another's actions, which they may seek to reproduce using their own strategy. Early research in this field sought to examine the differences between social learning strategies used by young children and apes.

One of the first paradigms used to examine differences in imitation and emulation between children and chimpanzees was the artificial fruits task (Whiten et al. 1996) in which a demonstrator opened a "fruit" by removing components of the apparatus using one of two possible techniques. Results demonstrated that even through chimps would copy observed methods of removal on the artificial fruit, young children (18–24-months-old) imitated the demonstrated action with higher fidelity. More recently, Tennie et al. (2006) used an apparatus that could be opened either by

pushing or pulling a door to retrieve a reward. They tested children (12–24-month-olds) and great apes in one of four conditions: (1 & 2) watching a demonstrator either push or pull the door to retrieve the reward or (2 & 3) watching the door open by itself either inwardly or outwardly on its own (“ghost” control). They found that apes tended to retrieve the reward using their own strategies and children tended to use the method they saw demonstrated. These results were taken to indicate that children more readily use demonstrated actions to inform their goal-directed behavior.

In the framework of this research, imitation requires an understanding of another’s intentions and goal-directedness including attention to and replication of the model’s actions used in attaining the goal. This intention understanding also distinguishes imitation from mimicry in which reproduction of body movements is said to occur at the sensory-motor level and not to involve cognitive processes of intention attribution. Imitation, involving an understanding of another’s goal and the actions used to attain the goal, can be employed as an efficient learning strategy even when causation is not apparent. Alternatively, Heyes (2001) has argued that proposing a dichotomy between mimicry and imitation conflates a model’s intention and the observable outcome of the model’s actions as goals. Heyes and colleagues (Bird et al. 2007; Leighton et al. 2010) have presented evidence in support of the argument that imitation is not reliant on the coding of goals, either as physical end-states (Bird et al. 2007) or as mental states or intentions (Leighton et al. 2010).

Imitation has also been described as a process in which aspects of an action sequence are selectively reproduced based upon a rational assessment of the physical-causal information available (Gergely and Csibra 2003, 2006). This requires an understanding of the means, goals, and subgoals in a hierarchical manner (Bekkering et al. 2000). If end-states or “final goals” are present, these become the most salient aspects to be copied and copying fidelity will be low. When end-goals are not apparent or salient, however, an observer will copy the action styles, seemingly because they

view the action styles as the only apparent goal and copying fidelity will be high (Carpenter et al. 2005).

Whiten and colleagues (Whiten and Ham 1992; Whiten et al. 2004) have termed the phenomenon of copying the end-state, or goal at the top of the action hierarchy, “goal emulation.” Goal emulation involves an observer seeking to replicate a model’s goal, while not necessarily using the same means to attain the goal. Imitation, end-state emulation (including both result and goal emulation), and object movement reenactment (OMR) constitute forms of copying the behaviors of others. Imitation is defined as copying the form of an action. Object movement reenactment involves an observer attending to and copying what an object does, or what is done with an object. End-state emulation includes emulation of results and goals. Heyes (2001) distinguishes “imitation” from “emulation” as involving the copying of body movements and copying of object movements, respectively. Copying can be viewed as a continuum containing end-state emulation, moving to object movement reenactment, with the extreme end of the continuum involving copying body movements (Whiten et al. 2009).

When an observer emulates, they must understand and work out the causal links involved in a behavioral sequence in order to attain the same results as the model using individual means. When using an imitative strategy, however, the observer need only reproduce the model’s actions closely enough to replicate the results, without needing to fully appreciate the causal links involved. This would be a good strategy to employ when the causal links of an action sequence are difficult to discern, and possibly when there is no apparent end-goal, or result, to achieve (Horner and Whiten 2005).

In a series of experiments (Horner and Whiten 2005), the availability of causal knowledge was manipulated across conditions to assess the strategies children and chimpanzees use in reenacting demonstrated actions. Children and chimpanzees were shown a demonstration of how to use a tool to retrieve a reward from a puzzle-box. The action sequence demonstrated both causally relevant and

irrelevant actions in retrieving a reward from the box. In one condition, the subjects were shown the demonstration on a transparent puzzle-box, in which it was clearly visible which actions were relevant and which were irrelevant to retrieve the reward. In the second condition, the subjects were shown the same actions on an opaque puzzle-box, in which it was not clear which actions were necessary to retrieve the reward. Chimpanzees were more likely to discard the irrelevant action in the transparent condition and were more likely to include the irrelevant actions in the opaque condition. The authors concluded that chimpanzees are likely to employ an emulative strategy when causal knowledge is available and an imitative strategy when causal knowledge is absent or ambiguous (Horner and Whiten 2005).

Importantly, children were found to reproduce both causally relevant and irrelevant actions with a high degree of fidelity in both the transparent and opaque conditions (Horner and Whiten 2005), demonstrating what has come to be termed “over-imitation” (McGuigan et al. 2007; Lyons et al. 2007) or “overcopying” (Whiten et al. 2009). These findings indicate that children are likely to imitate regardless of their knowledge of the causal relations involved in a problem-solving task. These results may be due to children’s selective attention to the actions, and therefore intentions and goals, of the demonstrator (Horner and Whiten 2005). Thus, the children may have carried out all of the demonstrator’s actions, even if they were aware that some of the actions were causally irrelevant, because they viewed the demonstrator’s actions as purposeful (Horner and Whiten 2005; Williamson and Markman 2006). Research suggests that knowledge of the causal relationships involved in a problem-solving task does not detract from the fidelity of copying in young children’s matching behavior.

The main argument in the majority of the social learning literature is that imitation affords the highest level of copying fidelity, which is required for the transmission of behavior and cultural evolution. Whereas there is evidence that children can copy based on goal hierarchies and intention reading, much of human culture consists of not only causally, but also cognitively, opaque practices.

Therefore, there must also be a mechanism that allows for imitation that is not reliant on the identification of goals based on an inference of intentions.

### **Copying Fidelity and Conventional Versus Instrumental Interpretations of Behavior**

Much cultural learning in human societies is motivated by affiliative goals that guide the acquisition of conventional, ritualistic behavior rather than instrumental behavior. Many of the conventions children need to learn to become competent members of their cultural community involve high-fidelity copying and the replication of behavior for which physical-causal rationales are never provided and never sought. High-fidelity copying is crucial for learning basic socially stipulated behavior. Young children often implicitly engage in the gestural, postural, and overt (yet opaque) actions of older children and adults. Children navigate social learning opportunities by using physical, situational, and social cues to determine when actions are based in physical-causal reasoning and when actions are based in conventionality and social stipulation (Legare et al. 2015; Legare and Watson-Jones 2015; Watson-Jones and Legare 2016).

Whereas previous research has demonstrated that intention reading likely plays a part in determining why an individual may imitate in a given situation (Horner and Whiten 2005; Tomasello et al. 2005), there is evidence that there is not a special relationship between imitation and intention reading (Leighton et al. 2010). The associative sequence learning (ASL) model (Heyes 2001, 2005, 2013; Heyes and Ray 2002) proposes a direct connection between a visual and a motor representation of any given action. The ASL model allows for imitation that is often not deliberate or “rational” and will often result in over-imitation – high-fidelity copying. This concept of imitation does not require an understanding, or inference, of a model’s goal (Heyes 2013).

Research has demonstrated that when children are presented with an action sequence that has no

clear end-state, or physical causal rationale, copying fidelity is increased. Children were either presented with a demonstration of an action sequence that contains a distinct end-state that is different from the start-state (instrumental condition) or a video demonstration of an action sequence in which the start- and end-states are equivalent (convention condition). Both of the action sequences used in the study were causally opaque. The presence of an end-state that was different from the start-state in the instrumental condition, however, cued the children to the possibility of a potentially knowable causal structure. The start- and end-state equivalency of the convention condition biased the children's interpretation of the action sequence towards an interpretation of conventionality and significantly increased copying fidelity. These results indicate that when physical-causal goals are absent, children may be more likely to interpret actions as socially stipulated behavior (Legare et al. 2015; Watson-Jones et al. 2014).

Children use cues, such as the presence or absence of end-states, consensus between actors, synchrony, language, etc., to navigate cultural learning and determine when actions are based in instrumentality and when they are based in social convention (Clegg and Legare 2016; Herrmann et al. 2013). Therefore, "overimitation" may not even be an appropriate term for copying social convention, in which strict adherence is typically expected and observed. High-fidelity copying is plausibly driven by social motivations, more specifically a propensity to engage in affiliative interaction with group members. Humans have relied on group living for survival throughout evolutionary history (Brewer 2007; Buss and Kenrick 1998) and engage in unique forms of collaborative interactions that require a motivation to maintain affiliation and good standing within a group. Research has demonstrated that when affiliative goals are increased, children increase their copying fidelity (Over and Carpenter 2009), especially of action sequences cued as conventional and associated with an in-group (Watson-Jones et al. 2014, 2016). Whereas social motivations likely play a role in

children's copying fidelity of instrumental skills, socially motivated copying may be essential to learning the social conventions of one's group (Legare and Watson-Jones 2015; Watson-Jones and Legare 2016; Wen et al. 2016).

## Cross-References

- [Affiliative Behaviors](#)
- [Copying](#)
- [Culture](#)
- [Emulation](#)
- [Group Living](#)
- [Goal](#)
- [Imitation](#)
- [Means-End Reasoning](#)
- [Mimicry](#)
- [Rational Imitation](#)
- [Social Learning](#)

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## Fighting Ability

### ► Resource Holding Potential

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## Filament

### ► Cilia



## Filial Imprinting

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### Definition

Shortly after birth or hatching, the young of some animals, usually of **precocial** species, learn to recognize their mother and/or other social partners (e.g., siblings) by simply being exposed to them, and subsequently exhibit affiliative responses to them. Filial imprinting is thus a form of perceptual learning that serves to confine social preferences and social attachment to a specific object (or class of objects) as a result of exposure to that object (Bateson 1990).

### Introduction

Filial imprinting was known from antiquity and exploited by farmers and breeders. It was originally described in the scientific literature by Douglas Spalding and later studied and popularized by the ethologist **Konrad Lorenz** (1935).

Although imprinting phenomena have been described in mammals, they have been mostly studied in birds. Filial imprinting is most readily apparent in **precocial** species, i.e., those whose young are relatively mature and mobile soon after birth or hatching. Domestic chicks and ducklings have thus been mainly used for research on filial imprinting, though it has been described also in altricial species.

Lorenz (1935) believed that filial imprinting determines adult sexual preferences. Actually, filial and **sexual imprinting** appear to be two different (though partially overlapping) processes. Apart from the difference in the expression of behavior (approach and affiliative responses in filial imprinting versus courtship

and sexual behavior in sexual imprinting) they differ in timing, for sexual preferences are expressed later than filial preferences and have a longer period of exposure. Moreover, sexual preferences are affected by experiences occurring after filial imprinting is completed (review in Bolhuis 1991).

Lorenz (1935) also believed that the function of imprinting was to develop species recognition but it has become apparent that the main outcome of imprinting is the formation of a recognition memory of the specific individual (either a living animal or an artificial object) to which the animals have been exposed to. This is not necessarily in contrast with the fact that imprinting mediates species recognition, for evidence suggests that the two hemispheres of the chick's forebrain could attend separately to these functions (below).

### Imprinting as a Learning Phenomenon

Imprinting has been traditionally considered different from associative learning because of the absence of an explicit reward and because it is irreversible. There have been attempts, however, to argue that the imprinting object itself, or some of its features (e.g., motion) may act as reward or as unconditioned stimulus (as in Pavlovian associative learning). However, evidence suggests that phenomena observed in associative learning are small (e.g., blocking) or absent at all (e.g., overshadowing) in filial imprinting. Besides, neurobiological studies in which brain areas involved with filial imprinting were lesioned (see below) revealed a dissociation: chicks unable to imprint on an object because of the brain lesion were nonetheless capable of associative learning on the same object (i.e., to press a pedal in order to see the object as a reward) (see Bateson 1966).

As to irreversibility of imprinting, it has been shown that "secondary imprinting" can be observed. After learning on a particular object, chicks can, for instance, reverse their preferences for that object following exposure to a new one. However, it seems that memory of the original object ("primary imprinting") is not lost and can reappear under certain conditions, thus showing

that there is indeed some irreversibility, though in a less strong form as originally theorized.

Imprinting differentiated from observational learning as well because, instead of being available throughout the lifespan, it is exhibited in a limited period of life, what Lorenz (1935) called a **critical period**. In the youngs of domestic fowl (*Gallus gallus domesticus*), for instance, imprinting usually occurs within 24–48 h from hatching. However, this time window can extend for few more days, in case a proper stimulus is not immediately available (Bolhuis 1991). For instance, if domestic chicks are maintained in the dark, imprinting can be obtained up to about day 8 after hatching. This flexible period, that has the characteristics of a self-terminating process, is known as **sensitive period**. It has been discovered that the thyroid hormone  $T_3$  is implicated in controlling the timing of the sensitive period. In domestic chicks, imprinting causes fast inflow of  $T_3$  in the vascular endothelial cells in the brain. In non-imprinted chicks whose sensitive period is ended, administration of  $T_3$  allows imprinting to occur, re-opening the sensitive period (Yamaguchi et al. 2012).

Bateson (1990) argued for a basic difference between imprinting and associative learning, with the associative learning being mainly involved in extracting the causal structure of the world and imprinting implicated in building up perceptual categories. While timing is crucial to establish cause-effect relationships (for causes should come before effects), the order of the stimuli should not be important to establish categories in filial imprinting. Order could be important, however, if associated with different probability of occurrence. Recent evidence shows a sensitivity of chicks to ordered transitional probabilities of different stimuli images during imprinting (Santolin et al. 2016). As Bateson (1990) noticed, in a natural environment chicks must recognize their social partners independently of the visual perspective and, given that different views of social partners likely follow one another over short periods of time with a certain ordering, these abilities can be useful to build up a representation of the whole social companion.

Although imprinting can be obtained with either naturalistic (resembling to a conspecific) or artificial objects, evidence has accumulated for the existence of biological predispositions that act as a sort of guidance or canalization system to direct the newborn animals' attention, and in turn exposure important to determine imprinting, towards the objects that are more likely to be social partners. Predispositions for animacy cues (that make apart animate vs. non-animate objects) have been described in newly-hatched chicks and comprise preferences for face-like stimuli, biological motion stimuli, self-propelled objects, and objects that move with changes of speed (review in Di Giorgio et al. 2016).

## Neural Bases of Imprinting

A restricted part of the forebrain, the intermediate and medial mesopallium (IMM), has been identified in the domestic chick as a plausible memory store for visual imprinting. Ablation of the IMM before exposure to an imprinting object prevents imprinting, ablation after exposure makes chicks amnesic, i.e., unable to discriminate between the exposure object and a novel object. Imprinting is also associated with pre- and postsynaptic changes in the IMM, and neurons that respond selectively to the imprinting object have been described in this area (Horn 2004).

Auditory imprinting, with acquired preferences following exposure to the maternal call of a hen, seems to be associated with activation of a closed area, the medio-rostral nidopallium/mesopallium (MNM). Changes in synapses and electrophysiological activity related to imprinted acoustic stimuli have been documented.

A **brain lateralization** has been described in the neural bases of imprinting memory, with respect to both the temporal and the functional aspect (Rogers et al. 2013). It appears that three different storage systems are formed following exposure to an imprinting object: one in the left IMM, one in the right IMM, and a third one in an unknown location after about 6 h from exposure. The left IMM appears to be responsible for the long-term storage of information about the

imprinting stimulus, whereas the right IMM would act as a sort of buffer store to permit storage in another site outside IMM. Studies with domestic chicks tested under monocular conditions of vision (which in birds with laterally placed eyes largely confine information processing to the contralateral hemisphere) and single cell recordings in the IMM suggest functional differences between storage sites in the two hemispheres. It has been suggested that encoding of the general and invariant features of the imprinting object occurs in the left hemisphere, whereas encoding of the unique and variant features of individuals is carried out in the right hemisphere (Rogers et al. 2013). This would guarantee both fast responses to social partners as distinct by other types of stimuli (e.g., food, predators) and considered responses within the category of social partner (e.g., individual recognition of a sibling).

## Imprinting as a Tool to Study Animal Cognition

Other than being an important scientific topic in itself, imprinting has recently proven to be useful to investigate a variety of early knowledge mechanisms in young birds. For instance, it has been employed to study early knowledge of the intuitive physics of objects, geometry, and arithmetic (see Vallortigara 2012). It has also been shown that newborn chicks (Versace et al. 2017) and ducklings (Martinho and Kacelnik 2016) are able to extract abstract patterns present in the imprinting object. For instance, chicks imprinted using either patterns with two identical items (XX) or patterns with two different items (XY), were able to extract and generalize the abstract XX or XY relation presented in the imprinting stimuli to novel objects. All this suggests that, in spite of its apparent behavioral simplicity, filial imprinting is associated with quite abstract conceptual reasoning.

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## Finding

► [Learning](#)

## Finding Out

► [Learning](#)

## First digit

► [Opposable Thumb](#)

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## First Diploid Cell of New Organism

► [Zygote](#)

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### Fisher

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### Synonyms

[Evolution](#); [Genetics](#); [Natural selection](#)

Ronald Aylmer Fisher (1890–1962) was the most original evolutionary biologist of the twentieth century. Fisher was also the greatest statistician of all time, and the majority of his publications were devoted to statistics rather than to evolution or genetics. His life and work have been the subject of many articles and a full-length biography (Box 1978). This entry summarizes his major contributions to evolutionary biology.

There was, of course, a strong connection between his statistical and biological interests. His first major paper on genetics (Fisher 1918) applied the principles of Mendelian genetics to measures of the resemblances between relatives with respect to continuously varying traits (regression and correlation coefficients), which had been developed by Francis Galton and Karl Pearson (Provine 1971). Fisher showed that (contrary to claims by Pearson), the values of these measures for traits like human height were compatible with the hypothesis that variability is caused by the joint effects of multiple Mendelian loci and nongenetic causes.

While this problem was independently studied by Wilhelm Weinberg in 1910 and Sewall Wright in 1921 (Provine 1971), Fisher's formulation formed the basis for most subsequent theoretical work on the genetics of quantitative traits. He

introduced the term “variance” for the mean of the squares of deviations from the mean, and the concept of breaking the total genetic variance down into its component parts, with the “additive” component playing the main role in resemblances between relatives, whereas the “dominance” and “epistatic” components (referring to nonadditive effects of alleles at the same genetic locus and among alleles at different loci, respectively) make smaller contributions. As enshrined in Fisher's famous and much-debated “Fundamental Theorem of Natural Selection” (Fisher 1930b, 1941), the additive genetic component of variance in fitness determines the rate of change in mean fitness of a population due to allele frequency changes.

In 1922, Fisher made several pathbreaking contributions to population genetics theory, in a paper motivated by his wish to understand the causes of quantitative trait variability (Fisher 1922). First, he studied the stable equilibrium in allele frequency in a large population that arises when the heterozygote at a locus with two alternative alleles has a higher fitness than the two homozygotes. This was the first demonstration that selection could act to preserve variability, as opposed to causing one type to replace another, a very important shift in thinking about the workings of natural selection. He also analyzed the dynamics of allele frequency change when one allele has a net advantage over the other, for some special cases with respect to the level of dominance of the fitness effects of the alleles. In addition, he introduced the use of probability generating functions for analyzing the survival of a new mutant gene in a large population, later employed by J.B.S. Haldane to derive the widely used result that a mutation with a small selective advantage of  $s$  over the prevailing type has a probability of approximately  $2s$  of surviving random loss from the population (Provine 1971).

Fisher also introduced the diffusion equation method for studying the probability distribution of allele frequencies, generated by the random sampling of alleles in a finite population (now called “genetic drift” following Wright's terminology), analyzing both purely neutral cases and cases with selection, and asking how much variability could be maintained with a given supply of new

mutations. Fisher made an error in using a transform of the allele frequency, incorrectly assuming that the expected change in the transformed variable due to drift was zero. This led him to claim that the rate of loss of variability due to drift is  $1/(4N)$ , where  $N$  is the size of the breeding adult population of a diploid, randomly mating organism. Wright was stimulated by Fisher's work to initiate his own study of the problem and found the rate to be  $1/(2N)$ , leading to an extensive correspondence with Fisher (Provine 1971).

In his 1930 paper, Fisher reworked and extended his approach, in what is one of the most brilliant papers in population genetics (Fisher 1930a), providing results that form the theoretical basis for current studies of molecular evolution and variation. Of especial general significance was his formula for the probability of fixation of a mutation in a finite population of size  $N$ . Fisher's conclusion was that a very weak intensity of selection (of the order of  $1/N$ ) is sufficient for a new mutation to behave as though the population is infinitely large. This was of considerable historical importance in combatting the then widely held view that natural selection was not capable of explaining adaptive evolution (Provine 1971).

His early work was synthesized in *The Genetical Theory of Natural Selection*, the most important book on evolution after *The Origin of Species* (Fisher 1930b). It opens with a discussion of the importance of Mendelian, particulate inheritance for evolution, pointing out that the Mendelian mechanism preserves genetic variability. This removes the difficulty faced by Darwin, whose belief in blending inheritance led him to postulate a high rate of input of new variability each generation by the inheritance of acquired characters, in order to counteract the loss of variability under blending inheritance. Fisher argued that random mutations in Mendelian genes provide a sufficient supply of variability on which selection can act, a fundamental tenet of what has become known as the Modern Synthesis of evolution. This set the stage for a series of chapters exploring the consequences of Mendelian inheritance for the evolutionary process.

Together with contemporary work by Haldane and Wright (Provine 1971), Fisher's ideas provided a coherent theory of the mechanism of

evolution, forming the core of research in evolutionary genetics down to the present day. His concepts of a "runaway process" of the evolution of female mate choice of male secondary sexual characters, and selection for equal investment by mothers into male and female offspring, have been extremely influential. Several of Fisher's other important conclusions were communicated in a few sentences, such as his anticipation of the theory of kin selection, and arguments for the evolutionary advantages of sexual reproduction and for the evolution of close linkage between polymorphic genes that interact in their fitness effects; they are thus often overlooked.

In discussing the evolution of mimicry as an example of the evolution of a complex adaptation involving coordinated changes in several traits (Chapter 7), Fisher proposed that the effects of alleles at a segregating locus could be modified by mutations at other loci, so that a relatively small initial difference between polymorphic mimetic and nonmimetic forms would become much greater over time. This greatly influenced subsequent empirical research into mimicry. Fisher was the first to propose the idea of the inverse dependence of the fitness of a genotype on its frequency in the population as a mechanism for maintaining genetic variability, noting that this occurs when predators have to learn to avoid eating members of a harmful species that is being mimicked by a harmless, edible species. Not surprisingly, Fisher was probably the most explicit advocate of the neo-Darwinian view of stepwise adaptive evolution. He developed a geometric model of the fitness effect of a mutation affecting a multidimensional trait, which he used to argue that mutations with small effects are more likely to confer a selective advantage than ones with large effects (Chapter 2); again, this model is widely used in contemporary research.

Fisher's theory of the evolution of dominance also involved modifiers; he proposed that mutations with deleterious fitness effects when heterozygous with the wild-type allele at the same locus would create selection on modifier loci to reduce these fitness effects, explaining the fact that mutations with major phenotypic effects are usually recessive. This led to a controversy with Wright, who proposed an alternative explanation based on



enzyme kinetics (Provine 1971). Most current researchers believe that Wright's view has been validated with regard to rare, deleterious mutations, although dominance modification probably plays a role in the evolution of genetic polymorphisms that involve major phenotypic differences, such as mimicry.

Fisher also disagreed with Wright about the importance of drift in a species divided into many small subpopulations, which formed the basis of Wright's "shifting balance" theory of adaptive evolution. Fisher rejected the possibility that genetic drift could be a significant evolutionary process on the grounds that most species have population sizes in the millions or thousands of millions, so that even minute average selective effects should be able to control the frequencies of variants. Later, Kimura argued that much variation and evolution at the DNA and protein sequence level reflects the action of drift on selectively neutral or nearly neutral mutations. A good deal of current research into molecular variation and evolution seeks to test the predictions of neutral models against alternative models that invoke selection – the Fisher-Wright controversy thus continues to resonate in modern evolutionary biology.

Most of Fisher's general views on evolution were developed by 1930, with some additions in the 1958 second edition of *The Genetical Theory of Natural Selection*. These included an attack on the idea that adaptive traits can evolve because of an advantage to the species rather than the individual, which had unfortunately become widely accepted because of the writings of C.D. Darlington and G.L. Stebbins on the evolution of genetic systems and breeding systems. He continued to make characteristically ingenious contributions to evolutionary genetics theory throughout his life, the most notable probably being his analysis of the wave of advance of a favorable mutation through a population occupying a linear habitat (Fisher 1937). He was the first to understand that there can be selection on a trait such as the frequency of self-fertilization purely through its effect on the transmission of alleles from one generation to the next (Fisher 1941). He also invented the theory of "junctions" in the composition of chromosomes, reflecting sites where a recombination event in an ancestral

individual causes a switch from maternal to paternal material (Fisher 1954). This has recently become an important tool for statistical analyses of DNA sequence data from natural populations.

Fisher was involved in establishing the "ecological genetics" approach to studying evolution, using conspicuous color and pattern polymorphisms for detecting selection in nature, especially in Lepidoptera, in collaboration with E.B. Ford (Fisher 1953). This was paralleled by the collaboration between Wright and Theodosius Dobzhansky on studies of natural populations of *Drosophila pseudoobscura*. Both sets of investigations were important in demonstrating that natural selection can be detected on traits that might superficially seem unimportant, leading eventually to thousands of studies demonstrating the action of natural selection in wild, domestic and human populations. Fisher also made important contributions to research on human blood groups, the earliest source of biochemical genetic markers in population genetics (Fisher 1953).

This brief summary of Fisher's major contributions to evolutionary biology cannot do justice to his originality, depth of thought, and mathematical virtuosity. But it should provide some idea of how important his work has been for the development of modern evolutionary biology.

## Cross-References

- ▶ [Additive Genetic Variance](#)
- ▶ [Alleles](#)
- ▶ [Balanced Polymorphism](#)
- ▶ [Epistasis](#)
- ▶ [Frequency-Dependent Selection](#)
- ▶ [Gene Frequency](#)
- ▶ [Heterozygote Advantage](#)
- ▶ [Mendel's Laws](#)
- ▶ [Modern Synthesis](#)

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## Fisher's Principle

### ► Sex Ratio

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## Fisherian Selection

### ► Runaway Selection

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## Fission-Fusion

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## Synonyms

[Fission-fusion dynamics](#); [Fusion-fission](#)

## Definition

Fission-fusion is a property of many animal groups that split in temporary aggregations or subgroups. First described in hamadryas baboons (*Papio hamadryas*; Kummer 1971), it has been found in an ever-larger number of species, including elephants, hyenas, dolphins, chimpanzees, and several other primates. *Fission-fusion dynamics*, as the term is currently used, consist of the temporal variation in the spatial cohesion between group members, who form subgroups that can also vary in size and composition over time, due to splitting and coming together with other subgroups. Because different species show a different extent of temporal variation in these three dimensions (spatial cohesion, subgroup size, and subgroup composition), they can be characterized by their *degree* of fission-fusion dynamics (Aureli et al. 2008). Resulting in part from the benefits of foraging in variable environments, these dynamics are an important part of social complexity. Fission-fusion dynamics influence the opportunities for individuals to interact, introducing uncertainty about the whereabouts of other group members and the social relationships they hold with each other. As such, they are relevant for the study of the cognitive and communicative mechanisms used to deal with this social uncertainty. It is believed that early hominid societies also showed fission-fusion dynamics, as do contemporary hunter-gatherer societies and even urban populations (Rodseth et al. 1991). Thus, the study of the cognitive mechanisms underlying fission-fusion dynamics is relevant for the study of the evolution of cognitive abilities according to the social intelligence hypothesis, which posits that complex cognitive skills and large brains may be directly related to the complexity of the social realm (Humphrey 1976).

## History of the Term

In his 1971 book Hans Kummer used for the first time the term “fusion-fission” to explain the social system of some group-living primates, but the inverted order “fission-fusion” became the

standard term. This term was introduced to describe the social system of chimpanzees, geladas, and hamadryas baboons, that change the size of their groups by means of fission into and fusion of subunits (called parties or subgroups) according to their activities and the availability and distribution of resources. Different types of fission-fusion patterns can be recognized depending on their subunit (Rodseth et al. 1991). Two main types of subunit were recognized, borrowing terminology from chemistry. In “atomistic communities,” the smallest unit is the individual (like an atom) that moves from one subgroup to another, whereas in “molecular communities” the smallest unit is a stable one-male unit that may include several females (like a molecule formed by several atoms). Atomistic communities, which are typical of chimpanzees, bonobos, dolphins, and spider monkeys, were also called “fission-fusion societies.” Molecular communities are typical of elephants, geladas, hamadryas baboons, and snub-nosed monkeys and are also called “multilevel societies,” in which different grouping levels are recognized, from large night aggregations to small foraging one-male units with a fixed composition (Grueter et al. 2012).

The terminology used by Kummer (1971) also entered anthropology as it became clear that human societies also show fission-fusion patterns, having elements of the atomistic communities during the day, as it is the single individual that moves from one subgroup to another (Rodseth et al. 1991). However, at night individuals tend to return to the same fixed unit, resembling molecular communities. Later on, it was shown that species other than primates, such as elephants, dolphins, spotted hyenas, bats and parrots, also show fission-fusion patterns, each with their peculiarities (e.g., Bradbury 2003; Willis and Brigham 2004; Smith et al. 2008). Recently, the modal fission-fusion types were called into question about whether they can actually capture the pronounced variation in the fission-fusion patterns documented across and within species. Thus, a fundamental change in terminology was proposed.

Aureli et al. (2008) proposed the use of the term “fission-fusion dynamics” to refer to the

extent of variation in spatial cohesion and individual membership in subgroups over time. As a consequence, any animal social system can be characterized by its degree of fission-fusion dynamics, varying from highly cohesive with fixed membership to highly fluid with flexible membership. This perspective fits Kappeler and van Schaik’s (2002) degree of spatiotemporal cohesion as a key component of social organization. The revised concept offers the opportunity for comparative studies of socioecological factors that affect the degree of fission-fusion dynamics as a key component of social systems across species. Aureli et al.’s (2008) article generated a revival of research on fission-fusion patterns. In more than 30 years since the publication of Kummer (1971)’s book fewer than two articles on fission-fusion patterns were published each year. This changed dramatically after 2008 with a more than 10-fold increase in the yearly publication rates of such articles.

### Scientific Relevance of Fission-Fusion Dynamics

Fission-fusion dynamics are relevant to the social intelligence hypothesis, which posits that complex cognitive skills and large brains may be directly related to the complexity of the social realm (Humphrey 1976). Indeed, many of the species with high degrees of fission-fusion dynamics have a relatively large neocortex, including dolphins, elephants, and chimpanzees (Barrett et al. 2003). While the study of early hominid ancestors reveals little about their grouping patterns, a high degree of fission-fusion dynamics may have acted as a selective pressure on the evolution of human cognitive abilities, if we assume that the common ancestor of humans, bonobos, and chimpanzees shared the grouping patterns of the three existing species (Grove et al. 2012).

Fission-fusion dynamics are also relevant to foraging efficiency (Kummer 1971). High degrees of fission-fusion dynamics allow species to efficiently exploit food resources that vary in abundance and distribution, both in space and

time. One way of coping with this variability is forming flexible subgroups that can change in size according to resource availability at a given location or period in time. As a consequence of this flexibility, animals need to coordinate when spatially separated, so there is a role for long-distance vocalizations and other forms of communication that can maintain contact between highly separated group members (Ramos-Fernandez 2005).

Fission-fusion dynamics are also relevant to the study of group coordination and decision-making (Sueur et al. 2011). When deciding where to forage, for example, groups with low degrees of fission-fusion dynamics have to reach a consensus on where to go or follow a single leader. For example, during their morning departures, chacma baboons follow the adult males (Stueckle and Zinner 2008), while Tonkean macaques seem to reach a consensus on the direction where all of them will go before they initiate a collective movement (Sueur and Petit 2008). On the contrary, groups with high degrees of fission-fusion dynamics can split in subgroups when not reaching a consensus. Such is the case of colonies of Bechstein's bats, which increase their fission rates when their members have conflicting information about suitable communal roosts (Kerth et al. 2006). In spotted hyenas (*Crocuta crocuta*), an individual with high dominance rank will be found in larger subgroups and feeding at higher rates than low-ranking individuals, suggesting that low-ranking individuals avoid others more often in order to avoid feeding competition (Smith et al. 2008). Thus, in groups with high fission-fusion dynamics we find a greater flexibility in how individual behavior relates to group dynamics, as animals have the alternative to split from others in addition to simply following a leader or trying to impose a decision on the rest of the group.

## Adaptive Features

Fission implies a reduction of group size by forming smaller subgroups. If everything else stays the same, this reduction carries potential

costs and benefits. For fission-fusion dynamics to be adaptive, the potential costs need to be outweighed by the benefits.

A possible cost associated to fissioning into smaller subgroups is the increased predation pressure. While difficult to measure, this cost can be important in species in which being in a large group serves as a protection against predation, due to increased vigilance, dilution effects, or cooperative mobbing (Beauchamp 2017). Another possible cost is the reduction in strength of cooperative defense of group resources against other groups. In chimpanzees and spider monkeys, certain individuals form subgroups that patrol the group's territorial boundaries and defend it from neighboring groups, sometimes even raiding the territories of neighboring groups. The size of these subgroups may determine their success in aggressive encounters with subgroups from the neighboring group (imbalance of power: Manson and Wrangham 1991).

The main benefit of fissioning is the reduction of local resource competition. When food is scarce, individuals fission into smaller subgroups that exploit several small food patches, reducing competition with other group members. For example, during the dry season, when less food is available, spider monkeys do not increase their aggression rates, probably because they form smaller subgroups which effectively reduce competition (Asensio et al. 2008).

Fissions can also be effective in managing social conflicts (Asensio et al. 2008). Avoiding other group members who have been aggressive in the past by fissioning can be a strategy by victims of this aggression (Smith et al. 2008). Fusions, in turn, can create potential conflict. Aggressive interactions between individuals that were previously in different subgroups are higher after fusion than at other times (Aureli and Schaffner 2007).

One important consequence of adjusting subgroup size to local resource availability and thus reducing the intensity of contest competition is that dominance relationships between females (the sex whose fitness is more closely related to foraging success) are often not particularly pronounced in species with a high degree of fission-

fusion dynamics. However, potential differences in reproductive outputs across females of the same group may result by their use of areas with different quality within the group's home range (Emery Thompson et al. 2007; Asensio et al. 2015).

In general, individuals in larger groups incur in higher ranging costs than those in smaller groups living in similar environments because they need to travel farther to obtain sufficient resources for each group member. Fission-fusion dynamics deal with these ranging costs as larger subgroups occur mainly when resources are abundant. As a result, there are no differences in ranging costs between larger and smaller subgroups of spider monkeys (Asensio et al. 2009).

Another important benefit of fission-fusion dynamics in heterogenous environments is that individuals can take advantage of more foraging sites, discovering and exploiting them more effectively than a single, cohesive group would. As evidence for this, the spatial dispersion of subgroup members, as well as the rate of fission and fusion are higher in more heterogenous environments (Pinacho-Guendulain and Ramos-Fernandez 2017).

Fission-fusion dynamics have also been shown to provide effective means to deal with large-scale environmental disturbances, such as hurricanes (Schaffner et al. 2012). When two hurricanes passed through the home range of a group of Geoffroy's spider monkeys (*Ateles geoffroyi*) in the Yucatan peninsula in 2005, they left most trees without branches. As a consequence, fruit production was very poor for several months. The highly frugivorous spider monkeys reduced fusion rates and stayed in small subgroups. By doing so, they travelled less and invested more time in foraging, which was needed because their diet was mostly made of young leaves.

Different benefits of fissioning and fusing may apply to different species and to groups of the same species depending on different circumstances. Still, in each case fission-fusion dynamics allow flexible responses to environmental changes. Such flexibility can also have consequences for a species geographical distribution. For example, there is evidence that a high degree

of fission-fusion dynamics may allow spider monkeys and chimpanzees to live in habitats that would otherwise not be able to sustain them in their typically minimum viable group size (Korstjens et al. 2006).

## Mechanistic Basis

While there is evidence that the flexible adjustment of the size of subgroups to the current food availability is one of the main benefits of fission-fusion dynamics, how animals actually implement this adjustment is less well known. One possibility is that aggression over resources at the patch level simply limits the number of individuals that can feed in a given patch. Indeed, spider monkey subgroups in which aggression occurred were larger relative to the patch size than those subgroups where aggression was not observed (Symington 1988). Thus, individuals might be better off fissioning and searching for alternative patches than staying in a larger subgroup and face high rates of aggression. Whether they find an alternative patch depends on the abundance of these patches in the habitat. Fusions, on the other hand, can result from several individuals coinciding at the same foraging patch. Therefore, subgroup size and the rate of fissions and fusions may depend on food availability at the patch and habitat levels.

A simulation model aimed at uncovering some of these mechanisms (Ramos-Fernández et al. 2006) found that simulated foraging agents can coincide in preferred feeding patches, forming variable-sized subgroups, even in the absence of specific rules for social interactions. These foraging agents, who have knowledge about the location of feeding sites and their history of previous visits, would also split in smaller subgroups, while avoiding already visited patches. The largest subgroups, with the most variable composition, were found when large patches were neither too abundant nor too scarce, that is, when heterogeneity was maximal. This approach is useful for finding the minimum mechanisms that would give rise to a pattern resembling fission-fusion dynamics, in which subgroup size can be adjusted to the



availability of food in the environment (Aureli et al. 2008).

Environmental heterogeneity may also influence the flow of information about the location of foraging sources. If by virtue of splitting in different subgroups individuals gain information about different foraging sources, their decisions on whether to join others or split may be influenced by this different knowledge (Ramos-Fernández and Morales 2014). Additionally, they could be exchanging information about the location of available feeding patches by leading and following others at different times. Collectively, the group might thus have a more complete knowledge of the environment than any single individual. It is possible that, during food-limited periods, individuals decide to fission and fuse with those particular group members that have information about the location of fruiting trees.

A key feature of fission-fusion dynamics is that, by being away from other members of their own group, individuals may have fewer opportunities to interact than those in more cohesive groups. In groups with high degrees of fission-fusion dynamics as well as high levels of cooperation among group members, the differentiated and long-term social relationships must be regulated and maintained using partial information and through less frequent social interactions than in groups with lower degrees of fission-fusion dynamics. Thus, there are several mechanisms that have been hypothesized to play a role in facilitating fission-fusion dynamics, both at the behavioral and cognitive levels (Aureli et al. 2008).

At the behavioral level, interactions aimed at avoiding conflict, such as appeasement or greeting behaviors, seem to be important when group members reunite after being in different subgroups. These behaviors may reduce uncertainty and reinforce social relationships between individuals even when opportunities for interaction may be interrupted by the frequent fission in different subgroups. In spider monkeys, such greetings in the form of embraces greatly reduce post-fusion aggression (Aureli and Schaffner 2007). The use of some form of greeting between group members joining at fusion has also been

reported in other species, such as spotted hyenas and bonobos (East et al. 1993; Hohmann and Fruth 2000). Long-distance signals, such as vocalizations, or long-lasting signals, such as olfactory marks, play a relevant role in maintaining contact between closely associated group members that may nevertheless spend time in different subgroups (Janik and Slater 1998; Ramos-Fernandez 2005). The information transmitted by these signals may simply be about the signaler's identity, which receivers may interpret depending on their own relationship with the signaler. Additionally, these signals may also aid in distinguishing group members from individuals of neighboring groups.

At the cognitive level, inferential skills, like transitivity (i.e., the capacity to infer the linear order of magnitudes based on partial information), or relational concepts, like dominance hierarchies, may allow individuals in groups with high degrees of fission-fusion dynamics to keep track of their own relationships and the relationships between others and predict other group members' behavior using partial information (Aureli et al. 2008). However, simpler emotion-based mechanisms could instead play a role. For example, animals can make their behavioral decisions on the basis of the emotional states associated with each potential partner, which are affected by previous social interactions. Such an emotional bookkeeping may allow individuals to monitor each relationship they hold, albeit they have only intermittent contact with other group members (Schino and Aureli 2009). Other abilities, like inhibitory control (Amici et al. 2008), may allow individuals to suppress certain behaviors depending on the social contexts, which are always changing in groups with high degrees of fission-fusion dynamics.

## Prospect for Future Research

If we conceive fission-fusion dynamics as a property of any social system (Aureli et al. 2008), then it is necessary to develop metrics of the degree to which this property is present in any particular situation, group, or species. These metrics would

allow researchers to compare different species to test hypotheses about the evolution of social behavior and the mechanisms underlying it. Among these, the social brain or social intelligence hypothesis can be tested using quantitative metrics of the degree of fission-fusion dynamics and relating them with quantifications of the particular cognitive abilities that are supposed to be useful for dealing with the complexity of the social environment.

The temporal variation in spatial cohesion, one of the dimensions of fission-fusion dynamics, is particularly hard to measure. Not only are there practical limitations in monitoring the exact position of all group members, but it is also challenging to determine how dispersed is a given configuration, from the perspective of the animals themselves. For example, identifying significant clusters of individuals based on their interindividual distances can be challenging (Aureli et al. 2012), moreover if they are involved in a collective movement (cf. Farine et al. 2017). Ideally, these measures should take into account the fact that two individuals, even if separated by a relatively long distance, might still be in contact through visual or auditory means and therefore remain as part of the same cluster or subgroup of individuals. As telemetric data of animal movement accumulates, it will be possible to develop accurate measures of cohesion and definitions of subgroups based on each species' within-group spatial distribution.

Given the diversity of species in which high degrees of fission-fusion dynamics have been reported (Aureli et al. 2008), it is clear that such dynamics appeared multiple times in different evolutionary lineages. Investigating both the functional and mechanistic aspects of fission-fusion dynamics should therefore consider the evolutionary history, without necessarily assuming that high degrees of fission-fusion dynamics serve the same function or that the same mechanisms are in place in all lineages of interest. At the same time, comparative studies should explicitly consider the role of phylogeny when finding differences or similarities between fission-fusion dynamics and their underlying mechanisms in different taxa.

Investigating the underlying mechanisms of fission-fusion dynamics can profit from two complementary approaches: experiments and agent-based models. In the former, cognitive abilities or behavioral interactions are explored in experimental settings in order to examine expected differences between species with different degrees of fission-fusion dynamics (e.g., Amici et al. 2008). This approach is promising because it uses clear hypotheses that are rigorously tested. Modeling approaches explore the most parsimonious rules of behavior or cognitive mechanisms that could give rise to a particular grouping pattern, via simulations in which fission-fusion dynamics arises depending on the behavior of individual agents (e.g., Ramos-Fernandez et al. 2006). This approach is promising as a proof of concept that can fruitfully complement empirical results or even be used to generate hypotheses that can be tested via new observations in the study system.

Individuals living in groups with high degrees of fission-fusion dynamics clearly face a higher social uncertainty than those living in more cohesive groups with more stable membership. This uncertainty can be simply about the whereabouts of other group members, but it can also be about the current status of the social relationship individuals hold with each group member, which is updated only when they are in the same subgroup. Capturing this social uncertainty through the appropriate metrics should aid the development of hypotheses about the particular cognitive and behavioral mechanisms that have evolved to cope with the uncertainty that results from flexible social dynamics.

## Conclusions

The study of the mechanisms and adaptive properties of fission-fusion dynamics is an increasingly important field within the behavioral sciences. The ability to form variable-sized subgroups allows animals to forage in variable environments, reducing feeding competition. At the same time, this variability introduces challenges for the maintenance of social relationships, which may need to be dealt with using increasingly

sophisticated cognitive mechanisms. Because the human lineage is likely to have lived in groups with high degrees of fission-fusion dynamics for a long time, the study of fission-fusion dynamics may shed light on the origins of human social intelligence.

## Cross-References

- [Foraging](#)
- [Social Behavior](#)
- [Social Intelligence Hypothesis](#)

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## Fission-Fusion Dynamics

### ► Fission-Fusion

## Fitness

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## Synonyms

[Adaptation](#); [Direct and indirect fitness](#); [Inclusive fitness](#); [Individual genotype growth](#); [Kin selection](#); [Leslie matrix](#); [Lifetime reproductive success](#); [Survival](#)

## Definition

*Fitness*: the change in frequencies of alternative forms of an organismal trait over time in a population. Change can be within a generation, in which case transmission to the next generation depends on genetic and nongenetic inheritance, or among generations, in which case inheritance is implicit.

## Introduction

Fitness is central to Darwin's theory of evolution by means of natural selection, and the concept of fitness is intimately tied to that of adaptation (Darwin 1859; Fischer 1930). What Darwin called the “struggle for existence,” later referred to as “survival of the fittest” by H. Spencer (1866), is the idea that the *fittest entities* in nature are those best *adapted* to prevailing environmental conditions. Fit entities are better at surviving and reproducing in given environments, spreading higher numbers of copies of their characteristics (or, rather, traits) through generations and in the population. The above highlights three important points:

1. Natural selection acts on entities that exhibit variations in traits (i.e., different forms of those traits) that can be passed on from parents to offspring. It is *heritable trait forms* (not necessarily genetic) that lead to greater overall fitness of individuals, and it is the trait forms that endure through generations and spread or decline in the population.
2. Fitness depends on the environment. A trait form can be adaptive (conferring high fitness) in a given environment but maladaptive (conferring low fitness) in another.
3. Darwinian fitness is a *relative*, frequency-based measure, that is, characteristic of a population of individuals. It is the fitness of a given trait form relative to others that matters to the individuals that carry the trait form. This is because natural selection operates in terms of changes in frequencies, not absolute numbers (Poulton 1884; Clarke 1979). Thus, the key concept of fitness for natural selection is the “fitness difference” among alternative forms of a trait (Endler 1986).

Defining and refining the concept of fitness has been an ongoing exercise in the field of evolutionary ecology (Hamilton 1964; Caswell 1980; Grafen 1982, 1984; Lucas et al. 1996; Queller 1996; McGraw and Caswell 1996; Hunt and Hodgson 2010). Here, we provide a condensed overview of the concept for graduate students, academics, and practitioners.

## Unit of Selection in Defining Fitness

Most evolutionary biologists view fitness as the property of an entity that is a biological characteristic of individuals: a genotype or group of genes (Hamilton 1964; Williams 1966; Grafen 2009). Successful genotypes under selection have high fitness and will proportionally increase at a higher rate in the population. A problem from this general viewpoint is that each genotype is unique and is diluted by inheritance, since only half of a genotype can usually be passed on to offspring. An alternative viewpoint is that selection occurs at the level of the single gene (Dawkins 1976). In

this case, the individual phenotype – and its interactions with the environment – is viewed as a competitive vehicle shaped by the gene (and its interaction with other genes), to ensure the gene’s journey through generations to immortality (Dawkins 1976, 1982). Here, fitness is theoretically measured at the level of the gene (Gardner and Welch 2011). However, this concept also appears impractical, since most phenotypic traits in real-world organisms are governed by the additive effects of an infinite number of loci distributed all over the genome, each having an infinitesimally small effect on a character (Hill and Kirkpatrick 2010). As emphasized by Mameli (2004), one issue with current views of evolution is the premise that natural selection acts on genetic variation or genetically caused variation. Yet, the modern evolutionary synthesis is currently undergoing a profound paradigm shift with growing evidence that not all forms of inheritance are genetic, and evolutionary models need to account for both sources of genetic and nongenetic inheritance in predicting evolutionary change (Helanterä and Uller 2010; Danchin et al. 2011; Danchin 2013). An example of nongenetic inheritance is maternal care behavior (licking and grooming) in rodents (Champagne 2008). Maternal care behavior is related to variation of specific (epigenetic) factors that modify the expression (not the DNA sequence) of given genes, themselves related to the expression of maternal behavior (Weaver et al. 2004; Champagne 2008). Such epigenetic trait forms may be passed on through generations with important implications for how we think about natural selection (Danchin 2013).

Because trait variation (whether anatomical, physiological, behavioral) is shaped by heritable sources of variation that are both genetic and nongenetic, fitness differences are likely best measured at the level of the phenotypic trait – integrating all sources of phenotypic variation. Empirically, this approach further provides the advantage of practicality, since measuring phenotypic characters (e.g., height) is straightforward and does not require making assumptions about the genetic and nongenetic architecture underlying trait variation. Measuring selection on traits often makes the assumption that traits are



independent with respect to change between generations, disregarding the fact that some traits coevolve or are genetically (or nongenetically) linked (Falconer 1981; Lande and Arnold 1983; Charmantier et al. 2014). However, refinements in statistical methods and computing algorithms are progressively allowing us to parse out sources of variation underlying phenotypic traits (Kruuk 2004; Kruuk and Hadfield 2007), including between correlated traits (Lane et al. 2011; Bize et al. 2017). Those models provide promising avenues for understanding the importance of genetic and nongenetic sources of variation in evolution (Charmantier et al. 2014).

### A Caveat: Inclusive Fitness

One of the most significant advances in defining Darwinian fitness came from Hamilton (1964) and his concept of inclusive fitness. First advanced by Darwin (1859), and later discussed by Fischer (1930) and Haldane (1932), Hamilton laid out the mathematics for explaining how apparently altruistic behavioral traits might evolve, i.e., traits favoring the reproduction of others at a cost of one's own reproduction and survival. Such an evolutionary strategy, termed kin selection by Maynard Smith (1964), results if the net fitness benefits of expressing cooperative or helpful traits, weighed by the degree of relatedness to the helped individual, outweigh the costs suffered by the helper. This breaks fitness into direct and indirect components, inclusive fitness being the summation of the two. An indirect component to fitness due to helping behavior comes about according to Hamilton's rule:  $rB - C > 0$ . Here,  $B$  is the fitness benefit of the cooperative behavior to the recipient,  $C$  the fitness cost of the behavior the donor, and  $r$  the degree of relatedness between the donor and recipient (not the intrinsic rate of natural increase of a population, but unfortunately given the same symbol). Inclusive fitness reduces to direct fitness when there is no helping behavior, that is, when the indirect component is zero. A similar argument can be applied to behaviors that appear spiteful: behaviors that hinder unrelated individuals more

than kin (Dobson et al. 2000; West and Gardner 2010).

### Measuring Fitness in Practice: Annual Measures

As a practical matter, fitness differences among alternative forms of a trait can only be measured from the reproductive success of the individuals that exhibit the particular trait forms. Reproduction and survival each contribute to the number of successful offspring that individuals with a particular trait form produce. Thus, if we ignore the effects of genetic (and epigenetic) architecture, the task seems fairly simple: simply add up the number of offspring that each individual produces and average individuals that exhibit each trait form. The point is to use the success of individuals relative to others to estimate the fitness of trait forms.

The simplest measure of fitness in an experiment, or in populations where individual life histories are known (e.g., annual schedules of reproduction and survival), is to consider individual annual reproductive success and individual annual survival separately as components of fitness. More comprehensively, both measures can be combined by counting the number of gene copies present in a population from 1 year to the next, for each individual in the population (Qvarnström et al. 2006). For example, this approach was used in common terns, *Sterna hirundo*, where the timing of egg laying was studied with respect to annual number of fledglings, annual survival to the next year, and a combined annual fitness measure (Dobson et al. 2017). The annual fitness measure was the number of individual gene copies surviving to the next year: for a given individual, this represented half the number of the fledglings it produced (because young carry half of each parent's genes), plus its survival to the next year (0 or 1). Perhaps the most comprehensive approach to measuring annual fitness is to consider both the combined fitness measure and concurrently break it down into its fecundity and survival components (see also Raveh et al. 2015).

## Measuring Fitness in Practice: Lifetime Measures

The drawback of annual and shorter-term fitness measures is that they do not account for effects that last longer during the lifespan. For example, an advantageous environment during an individual's developmental period can lead to improved reproduction and survival over the lifetime (for an example in bighorn sheep, *Ovis Canadensis*, see Pigeon et al. 2017). Capturing such effects requires working at the scale of an individual's lifetime. This is termed "lifetime reproductive success" or LRS, and it has been extensively applied (we know of no detailed review, but a search of the Web of Science for the term "lifetime reproductive success" brings up about 1000 articles at the time of writing). While it would be preferable to measure offspring production as those that go on to reproduce themselves, offspring production is most often measured at an earlier stage (such as eggs laid or juveniles produced), usually because of the complexity in natural history studies to tease apart whether juvenile disappearance from the population is due to emigration or death.

Lifetime reproductive success suffers from an important drawback: fitness differences depend on the timing of reproduction, not just the number of offspring. Timing is especially important for organisms with long lifespans, so that survival becomes a critical aspect of any measure of fitness (e.g., in seabirds; Jouventin and Dobson 2002; Reed et al. 2008). Reproduction cannot occur without survival to reproductive age, the number of times that an individual reproduces requires extended survival, and the rapidity of offspring production may itself influence survival patterns. For all of these reasons, two measures of fitness have been commonly used, net reproductive rate (usually symbolized as  $R_0$ ) and the intrinsic rate of population increase (symbolized as  $r$  or the related  $\lambda = e^r$ ,  $\lambda$  is called the "finite rate of population increase") (de Jong 1994). These practical measures are applied to subgroups in a population in which individuals express alternative forms of a trait.  $R_0$  is not standardized by generation time, which might differ among different trait forms.

Thus,  $r$  or  $\lambda$  are preferred fitness measures that take the timing of reproduction into account (Stearns 1992).

The usual procedure is to separate a population into groups representing alternative trait forms and then treat the groups as though they were independent populations themselves. Life tables with information on reproduction and survival are commonly used to calculate rates of population growth, assuming that vital rates will not change. A life table can also be constructed for individuals, treating each individual as a population that exhibits the trait form (for examples of individual fitness at different ages at maturity in sparrow hawks and blue tits, see McGraw and Caswell 1996). The reproductive rate is simply the reproduction for the individuals, and the survival rate is 100% throughout life. A measure of population growth such as  $\lambda$  can then be calculated from an algebraic matrix that reflects the individual's success at reproduction and survival. Individuals with different trait forms are then averaged as separate subpopulations within the larger population. The alternative trait form with the greater average  $\lambda$  value is judged to have greater fitness and thus at an advantage during natural selection.

The individual matrix approach (McGraw and Caswell 1996; Oli and Armitage 2008; Viblanc et al. 2010) uses individuals to estimate the fitness benefits of different forms of the trait and should provide a good comparison of alternative trait forms, if all individuals lived the same lifespan and were born in the same year. In real populations, however, individuals are often born at different times. This leads to a problem, because individual fitness measures will be higher when a population is growing and lower when a population is declining. Because natural selection produces changes in gene frequencies, fitness must be considered relative to what others in the population are doing. In an increasing (or decreasing) population, an individual with an individual fitness value of 1.0 is below (or above) average, and the trait forms that the individual carries will decline (or increase) in frequency. The solution to this problem is methodological: one should take changes in population size into account. This can

be done by comparing individual fitness to how the population is changing during the lifetime of the sampled individuals. For instance, in Columbian ground squirrels (*Urocitellus columbianus*), changes in population size during each individual's lifetime were used to calculate an "individual" estimate of population change over the lifespan (Viblanco et al. 2010). In an unpublished study (Dobson et al., manuscript), individual fitness was also compared to changes in population size during an individual's lifetime using a traditional "Leslie matrix" measure of population growth (after Leslie 1945; for details of methodology, see Caswell 2001). In both approaches, individual fitness estimates can then be adjusted for population growth during the individual's lifetime using regression analyses to provide an individual fitness estimate that is stripped of the influences of changes in population size.

fitness can be estimated from females that have no close kin nearby that can help them. For the indirect component, it is necessary to estimate the individual fitness of females that received help and subtract (strip) away the estimate of direct fitness, leaving the residual fitness due to the help of their relative. When this procedure was applied to ground squirrels, the direct component of fitness accounted for about 60% of a female's estimated fitness and the indirect component the other 40%. This result suggests that individual fitness was much higher when helping was present, and significant differences in the actual fitness estimates bore this out. This example shows the advantage of studying the fitness of trait forms, even when the basis of genetic variation is unknown or in question. If genetic variation in helping behavior had been present, it would have had a strong fitness advantage.

## Return to the Inclusive Fitness Concept

The above annual and lifetime practical fitness measures are suitable for traits when there is no indirect component to inclusive fitness. But if the traits influence the success of other individuals, such as close kin, then additional care is necessary. In a study of fitness effects of the presence of close kin in cooperative females of the Columbian ground squirrel, an attempt to estimate inclusive fitness and its direct and indirect components was made (Dobson et al. 2012). The specific behavioral traits were estimated from the presence or absence of female close relatives in this matrilineal species, but evidence suggested that the beneficial trait was the propensity or rate of aggressive behavior. Individual fitness measures relative to population size were calculated as described above for 70 females (after Viblanco et al. 2010).

The major difficulty for calculating direct and indirect components of individual fitness is to count each fitness component only once (Grafen 1982; Creel 1990; Lucas et al. 1996; Queller 1996). Hamilton (Hamilton 1964, well explained by Oli 2003) described a process of "stripping away" the effects of help so that they are singly counted. In practice, the direct component of

## Caveat Emptor

Fitness is a complicated topic because it applies to trait forms, but can most easily be measured from the individuals that carry the trait forms. And this is "fitting," since it is the individuals that survive and reproduce. But this means that each trait form is embedded within the other traits that the individuals exhibit. Thus, when there are interactive effects among trait forms, as is likely, current methods of measuring fitness will have to be modified. Current models of natural selection take associations and interactions among trait forms into account by examining a genetic variance-covariance matrix for the traits involved (Houle 1991; Stepan et al. 2002). Thus, in the future, the fitness of individual trait forms may have to be modeled within a matrix of organismal traits, as well as for its genetic and nongenetic components.

## Cross-References

- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Additive Genetic Variance](#)

- Alleles
- Allelic Association
- Artificial Selection
- Bear Life History
- Charles Darwin
- Coevolution
- Convergent Evolution
- Directional Selection
- Divergent Evolution
- DNA
- Evolution
- Fisher
- Frequency Distribution of Phenotypes
- Frequency-Dependent Selection
- Gene Flow
- Gene Frequency
- Gene Pool
- Genes
- Genetic Drift
- Genetic Variation
- Genotype
- Green Beard
- Heredity
- Heritability Estimate
- Kinship
- Methylation
- Modern Synthesis
- Natural Selection
- Origin of Species
- Phenotype
- Quantitative Genetics
- Richard Dawkins
- Robert Trivers
- Runaway Selection
- Sexual Selection
- Stabilizing Selection
- William Donald Hamilton

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## Fitness Relevance

- [Adaptive Memory](#)
- [Survival Processing](#)



## Fixation

### ► Cognition

## Fixed Action Patterns

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## Synonyms

### Modal Action Pattern (MAP)

A fixed action pattern (FAP) is a species-specific, stereotyped behavior pattern that once triggered by an environmental stimulus continues to completion without further modification by the initial stimulus. The behavior is innate and not subject to individual learning.

The genesis of the FAP can be traced to the works of Charles Otis Whitman and Oskar Heinroth, two members of the emerging school of European ethologists, who independently proposed the concept of “species-specific units of behavior” (Lorenz 1981; Schleidt 1974). However, it was Konrad Lorenz who further developed the concept and became its most vocal advocate. The term fixed action pattern was first used as the moniker for this type of behavior in Thorpe (1951), a report published following the 1949 symposium for the Society for Experimental Biology on Animal Behaviour (Schleidt 1974). Prior to this several different terms were employed. Konrad Lorenz’s own writings illustrate the changing descriptor, as documented by Schleidt (1974). Initially, Lorenz adopted Heinroth’s term “*arteigene Triebhandlung*” (species-specific action drive), before switching to the term *Instinkthandlung* (instinctive action), then *Instinktbewegung* (instinctive movement), and finally *Erbkoordination* (hereditary coordination). When writing in English, Lorenz used the terms “innate

behavior pattern” and “fixed motor pattern” (Schleidt 1974). Lorenz’s collaborator Nikolaas Tinbergen proposed the use of the term “fixed pattern” (Tinbergen 1951, p. 87), but used the term “typical form” when describing signaling behavior (Tinbergen 1964, p. 223). This flux in terminology seems to have reflected the ongoing development of the concept by its authors, although, perhaps not surprisingly, it often caused confusion (Barlow 1977). Despite this variable terminology, the development of the FAP concept provided a framework with which ethologists could articulate the broader concept of instinctive behavior. Central to ethological thinking was the idea that many behavior patterns occurred without prior experience or learning and were therefore under the influence of genes. Such instinctive behaviors could be compared across species and lead to hypotheses about their evolution.

Following its initial inception, Lorenz (1970) and others (see Dewsbury 1978) identified several criteria/characteristics that could be used to identify a behavior as a Fixed Action Pattern. Schleidt (1974) articulated Lorenz’s development of these criteria, while Gadbois et al. (2015) provide a summary of their criteria using modern terminology. They can be summarized as follows:

1. Stereotypy: FAPs are composed of a ridged predictable sequence of components that are not altered by novel environmental conditions.
2. Species specificity: The behavior pattern is genetically determined and all individuals of the species respond the same way.
3. Spontaneity: The longer an animal has gone without performing the FAP, the more likely it is to occur in the absence of its triggering stimulus (vacuum behavior), while the more recently it has occurred the less likely it is soon to occur again.
4. Not goal-oriented: The actor is not aware of the purpose of the FAP.

Schleidt (1974) noted that Lorenz settled on these first four criteria in his later writings, with stereotypy being the most important defining criteria. Additional criteria include:

5. Stimulus specific: A FAP is typically triggered by a specific stimulus (sign stimulus), but cannot be subsequently modified by it.
6. Context specific: A FAP typically occurs within a specific context or situation. However, as noted in 3, this is not always the case.
7. Nonmodifiable: Once triggered by the appropriate stimulus, a FAP is obligatory and will continue to completion without modification by conscious or cognitive input.
8. Innate: Learning and experience do not influence the expression of the FAP. Fixed action patterns are developmentally fixed and predetermined.
9. More than a reflex: FAPs are more complex than a reflex, although they are often similar in appearance.

The criteria described above have resulted in no single accepted definition, with different authors emphasizing different characteristics when trying to define the concept of a FAP. The lack of consistency in defining the term prompted Dewsbury (1978) to analyze ten major sources of FAP definitions to determine the main defining and secondary attributes that each ascribed to the term in the hope of developing a single unambiguous definition. Unfortunately, Dewsbury concluded “the term ‘FAP’ cannot presently be used in effective scientific communications” (Dewsbury 1978, p. 311). Despite this pessimistic conclusion and a general decline in its use since the 1970s, the concept of the FAP continues to persist. Recent papers follow Lorenz’s initial criteria when defining fixed action patterns. For example, Dixon et al. (2008) define a FAP as “unlearned (innate), repetitive movements in response to external stimuli that are relatively unaffected by feedback, influenced by underlying motivation and species-specific,” while Gadbois et al. (2015, p. 3) define FAPs as “predictable, genetically predetermined and rigid sequences of behavior.” Therefore, although there may be variation in the exact criteria used in defining the term, there appears to be a consensus on what types of behavior constitute a FAP.

The classic, and most frequently cited, example of a fixed action pattern is the egg retrieval

behavior exhibited by female greylag geese in response to an egg rolling out of the nest. Lorenz and Tinbergen (1970, pp. 329–330) described the behavior as follows: “When the brooding goose sights an egg lying not too far away outside the nest-cup, the egg-rolling movement definitely does not emerge immediately as a ‘decisive’ action. Instead, the goose – on first sighting the stimulus-transmitting object – briefly gazes at the egg and then looks away. When the goose’s gaze returns to the egg, it is fixated for a longer interval, and it is possible that a mild movement of the head towards the egg may be performed at this stage. After a brief series of intention movements of rapidly-increasing intensity, but of highly-variable length, the goose will stretch its neck towards the egg lying in front of its head, without moving the rest of its body. The goose frequently remains squatting in this position for a number of seconds, ‘as if spell-bound’, until rising slowly and hesitantly from the nest (without altering the posture of the head and neck) and walking towards the egg with a particularly careful gait characteristic of all locomotion in the neighbourhood of the nest-cup. . . . When the goose has approached the egg sufficiently, the egg is first touched with the tip of the beak at the point on its surface nearest the goose. . . . The lower side of the beak is then passed slowly forward over the upper surface of the egg, maintaining continuous contact, until it has extended beyond the egg and approaches the substrate on the side furthest from the goose. At this point, the bird’s entire body is seized with a peculiar tension; the neck becomes taut and the head begins to quiver quite noticeably, this delicate quivering motion persists while the egg is slowly pushed or rolled towards the goose and into the nest-cup by means of a movement of the lower side of the beak accompanied by a strangely stiff and awkward-looking curved posture of the neck. The egg finally arrives on the goose’s toes, and if it has by then passed the highest point of the nest wall it will roll into the nest-cup to join the other eggs.”

Lorenz and Tinbergen (1970) were careful to distinguish this FAP from the accompanying lateral movements of the head, neck, and beak which

allowed the goose to guide the egg back to the desired position following deviations to either the left or right. They regarded these movements as the products of a taxis. This distinction between the FAP and the accompanying taxis (orientation) movements was reiterated by Tinbergen (1951, p. 87). The distinction is important in that the FAP was considered stereotyped and independent of the triggering stimulus, while the taxis movements of the behavior pattern could be further modified by the triggering stimulus and therefore variable in their expression.

One of the driving motivations behind the development of the FAP concept was the desire, by ethologists, to understand how behavior evolved. Anatomical structures, which are discrete and readily quantifiable, had been the focus of comparative and evolutionary studies since Darwin's monumental work *On the Origin of Species* (Darwin 1859). Behavioral studies lagged behind those on morphology (although Darwin 1872 himself used the comparative method in his book *The Expression of the Emotions in Man and Animals*) with respect to the comparative method. The formulation of the fixed action pattern provided a discrete unit of behavior that could be analyzed using the comparative and phylogenetic methods applied to anatomy. In 1939 Konrad Lorenz articulated his thoughts on behavioral elements as taxonomic characteristics (Lorenz 1957) and produced, in 1941, one of the earliest phylogenetic studies using behavioral units when he analyzed the courtship displays of the Anatinae (Lorenz 1971). Later, Baerends (1958) discussed the application of comparative methods to studying the evolution of behavior, with special emphasis on identifying behavioral homology. The use of the comparative and phylogenetic analysis in animal behavior has continued to develop, although use of the classical concept of a FAP has diminished (e.g., Martins 1996).

The concept of the fixed action pattern as a definable unit of behavior found initial support from European ethologists. However, mounting criticism of the concept followed from both the comparative psychology and ethological schools of animal behavior. The focus of much of this

criticism was on the ideas that FAPs were highly stereotyped and completely innate units of behavior.

Lorenz's emphasis on the stereotypy of FAPs was questioned by a number of ethologists (e.g., Barlow 1968; Schleidt 1974). Schleidt (1974), although supportive of the FAP concept, discussed the degree of variability of FAPs and proposed methods to quantify it statistically. In concluding his paper on "How 'fixed' is the fixed action pattern," he states (Schleidt 1974, p. 207) "the adjective 'fixed' in the term FAP refers to a superficial rather than a fundamental property of such behavioral units, even if we refer to fixed as being relative, i.e., meaning 'highly' stereotyped or having low degree of variability. . . . My hope is that the acronym FAP will persist and its actual meaning will be gradually forgotten so that this abbreviation will change its meaning with the changes in the concept." The latter part of this statement was in response to the term Modal Action Pattern (MAP) that had previously been suggested by Barlow (1968). Barlow (1968) had also evaluated the concept of FAPs as a fundamental unit of behavior and concluded that most FAPs had some degree of variability and were not rigidly stereotyped. He therefore suggested fixed be removed from the term and replaced with modal. The term "modal" explicitly recognized that variation within a behavior pattern will cluster around a mode. In a subsequent paper, Barlow (1977, p. 99) provided the following definition of a MAP: "(1) A Modal Action Pattern is a recognizable spatiotemporal pattern of movement that can therefore be named and characterized statistically. (2) It usually cannot be further subdivided into entirely independently occurring subunits, although some of its components may occur independently or in other MAPs. (3) It is widely distributed in similar form throughout an interbreeding population." He then provided a guide to recognizing and analyzing MAPs before applying the concept to communication (Barlow 1977).

The use of the term "innate" was criticized by both comparative psychologists (e.g., Lehrman 1953) and some ethologists (e.g., Jenson 1961). Lehrman (1953) was one of the most vocal critics of this concept and argued against the

idea that behavior patterns could be defined as being innate or instinctive. His main point was that learning could not be ruled out when examining behavior because it is not possible to determine if learning does not occur during development in utero or within the egg. While acknowledging that “learning processes” can take place in the egg or uterus, Lorenz (1965) responded to Lehrman and other critics of the use of innateness by arguing that it was not possible to learn a behavior response for one environment while developing within another environment (the egg or uterus), that the ability to learn is itself an evolved feature and that behavior is a function of “(a) the adaptive process of evolution and (b) by individual acquisition of information” (pp. 18–19), and that neither component should be dropped from consideration when trying to understand the origins of a behavior.

As the field of ethology developed, the what some might consider simplistic concept of FAP was superseded by other more complex concepts of behavioral systems. For example, Fentress and colleagues proposed that behavior be studied in terms of “action sequences” that are determined by a system of rules and can be described probabilistically (Fentress and Gadbois 2001; Gadbois et al. 2015). However, they do not dismiss FAPs as nonexistent but recognize them as a discrete type of behavior unit that may occur (Gadbois et al. 2015). Others have made use of the highly stereotypic nature of FAPs to study their underlying control. Recently a series of papers (D. H. Kim et al. 2015; Y. J. Kim et al. 2006) have studied the role of ecdysis-triggering hormones (ETH) and peptidergic ETH receptor neuron ensembles in the central nervous system on the ecdysis FAP of pupal *Drosophila*. Through genetic manipulation of these neurons, they demonstrated that they were under the direct influence of ETH and determined the timing of behavioral steps in the ecdysis FAP sequence. These studies begin to provide insight into the mechanistic neural control of FAPs, what Lorenz and Tinbergen (1970) referred to as the *innate releasing mechanism*. Although the FAP has been marginalized to a historic footnote, these recent studies suggest that the concept continues to have relevance.

## Cross-References

- [Innate Behaviors](#)
- [Innate Releasing Mechanism](#)
- [Konrad Lorenz](#)
- [Nikolaas Tinbergen](#)
- [Sign Stimulus](#)
- [Species-Specific Behavior](#)

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## Flesh-Eater

### ► Carnivore (Diet)

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## Flight

### ► Migration

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## Floor and Ceiling Effects

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Every time an experimental design is proposed, several pragmatic constraints (i.e., fixed variables) are decided and implemented at the same time. When dealing with new problems in a research area, where most of the results are uncharted territory, some of these fixed variables may pass unnoticed at first. Thus, good control groups are not always trivial to be defined.

When analyzing experimental data, *spurious effects* may supervene, affecting the quality of the conclusions (Cohen 1995). In psychobiology experimentation, three common spurious effects are Ceiling, Floor, and Order Effects. Order Effects – when performance depends on the order of presentation of the task components – should be easy to detect and avoid, but the same is not always true about ceiling and floor effects.

A *Ceiling Effect* takes place every time many experimental subjects reach the maximum performance allowed for the measured variable of choice. If most of the subjects in both control and experimental groups reach this score, it may be impossible to detect significant differences between them, and the experimental setup should be considered unfit to decide if the hypothesis under scrutiny is true or false. Notwithstanding this particularly bad experimental setup, sometimes it is necessary to allow some (or even most) tested subjects to reach the maximum level in order to observe certain expected outcomes (see below). Thus, while Ceiling Effects may plague poorly designed tests, they may be tolerated and managed in situations where a practical upper limit of whatever property being quantified (e.g., time to perform something) must be imposed (in this case: session duration). The same situation may happen on the other extreme of the



**Floor and Ceiling Effects, Table 1** summarizes the main aspects of ceiling and floor effects

|                                      | Ceiling Effect          | Floor Effect                 |
|--------------------------------------|-------------------------|------------------------------|
| <i>Basic characteristic</i>          | Test is too <i>easy</i> | Test is too <i>difficult</i> |
| <i>Control and. treated subjects</i> | <i>Excel</i> alike      | <i>Fail</i> alike            |
| <i>Increased risk of</i>             | False negatives         | False positives              |

performance scale, when a minimum value is obtained by all groups: this is called *Floor Effect*, the siamese twin of the Ceiling Effect (which is sometimes called *Basal* or even *Basement Effect*).

It is easier to grab these concepts in the context of human psychological tests, may them be employed for scientific or applied (clinical) purposes: Ceiling Effects take place when the task is not challenging enough (say, too easy), and most outcomes reach the maximum defined level. This sample of subjects would neither lead to a conclusion about the general trend in a population, nor allow the gauging of one specific individual. Floor Effects are just the opposite, usually appearing when the test is too difficult for the experimental subjects. Extreme scores, either above the higher (ceiling) or below the lower (floor) level, also increase the risk of, respectively, false negatives, or false positives (Banks 2011a; Page 2017). Table 1 describes floor and ceiling effects.

Ceiling (or Floor) Effects may be circumvented by a better, revised experimental design, frequently with an adequate adjustment of the controlled variables. The following example, taken from the behavioral pharmacology of memory research should illustrate these possibilities in an animal model. There are two versions of the Inhibitory Avoidance task (IA), step-down IA or step-through IA (sometimes both are inaccurately named “passive avoidance” – Netto and Izquierdo 1985). In the Step-down IA task, for instance, training sessions are typically very short (seconds to 1 min mostly), ending when the animal climbs down the platform and receives the shock (for more details, see Quillfeldt 2016). When testing aversive memory with this task, if the stimulus – a foot shock in the grid floor – is too intense, most or all animals will never step down the platform during the test session. They tend to “remember” so well the experience that has

reached a maximum response under those experimental conditions. Notice that the *duration* of the test session will be decisive to define the results: moderate shocks applied during IA training imply that a 3–5 min test session would be more than enough, and no better results would come out from a longer session. However, since the avoidance time is proportional to the shock intensity, in an experiment with a stronger shock we *might observe a different response* if the test session is extended till, say, 10 min. The arbitrary decision of imposing a smaller time, e.g., 5 min, for the session would simply render the alternative, opposite response undetectable (a false negative): it might or might not be there, we will never know. But there are other aspects to be considered, since too long test sessions would both put an unnecessary burden upon the experimental animals and consume lab time and resources: the decision rests on the two aspects, choosing the shock intensity and setting test session duration.

When there is no way to avoid certain practical constraints upon the experimental variables, important methodological consequences rise, in particular, regarding possible statistical models. In the above example, since *time* is both the measured (step-down latency) and the constrained variable (session duration) – and a test session ceiling time of 180 or 300 s is assumed – the random distribution of animal performances would hardly conform to a Gaussian curve, and data *should not be analyzed* by Parametric Statistics due to the risk of reaching false conclusions. Non-parametric tests should be used instead, and results should be presented as median [interquartile range] (a clear example of this: Izquierdo et al. 1997).

It is widely known that if a parametric test can be applied, more statistical *power* will be available, but this is valid (and reliable) *only if at least two* strong assumptions are met: (1) Normality of

data distribution, and (2) homoscedasticity (same variances in all groups). Parametric statistical tools may be richer and simpler to use (and beware of fancy software packages literally offering a *buffet* of statistical tests!), but they are also more demanding in terms of needed conditions. Ignoring that increases the chance of failure. Actually, statistical *power* should never be confused with statistical *robustness*, i.e., the capacity to resist to errors in analysis that result from deviation from (necessary) assumptions (Huber 2009). Non-Parametric statistics does not make assumptions related to any specific statistical distribution, being really more robust as a procedure. Depending on the characteristics of the data obtained, it may be the only reliable approach.

One simple way to avoid facing this annoying analytical limitation (and not appeal to data transformation) would be, in the example above, simply reduce the shock intensity to a level at which all animals will perform under the cut-off time of, say, 180 (or 300) secs. Now the collected data may conform to a normal curve, possibly displaying equal variances per group, and parametric analysis may not be so risky (see an example of this in Quillfeldt et al. 1994). Yet, a note of caution: since behavioral pharmacology usually employs a few animals per group to keep their size “as low as reasonably viable” – studies rarely use more than 15 animals/group – sample data, according to the Central Limit Theorem, would barely fit a Normal Distribution out of pure chance (Zar 1998). Considering that behavioral research employs experimental animals, the number of animals used must be kept to a minimum in order to ensure animal welfare compliance (not to mention keep costs reduced). This is why, even if data *appears to be normally distributed*, it is always necessary to check for the two assumptions, normality (e.g., employing Kolmogorov-Smirnoff or Shapiro-Wilke tests) and homoscedasticity (e.g., using Levene test for equality of variances), before jumping into parametric analysis.

Thus, as a general rule, *Ceiling Effects* usually take place in tasks that are *too easy for the subject*, i.e., when the amount of information required to process is low. Conversely, Floor effects appear with difficult tasks. In animal models, it is easier

to observe Ceiling Effects in aversive tasks such as IA (above), but they may also be present in other behavioral tasks, even nonaversive/spatial ones (Buccafusco 2001; Levin and Buccafusco 2006). Some examples: Fear-Potentiated Startle (FPS), in which setting baseline startle responses too high may result in hardly detecting differences in the following test sessions; Delayed matching-to-sample (DMTS), in which defining the retention intervals must be based on the baseline performance (accuracy) of the same subject in order to avoid a Ceiling Effect in the case of the proficient ones; Radial Arm Maze (RAM) – that may be used to study either working or reference memory – can be made more difficult in different ways, e.g., more arms being presented, longer-time delays between training and retention tests, and the complexity of the sequences of arm choices. On the other side, Contextual Fear Conditioning (CFC), another popular aversive behavioral task, compared to IA has no explicit constraints upon time because healthy animals rarely display freezing during 100% of the duration of the test session: for this variable at least, parametric statistics could be used without risk (see, e.g., De Oliveira Alvares et al. 2010).

Finally, notice that Ceiling Effects are a problem only when the variable you choose to measure is expected to *increase* its value after some interference or treatment (e.g., pharmacological or behavioral) compared to the control group, being less critical in the opposite situation, unless the effect size obtained is too small. For experimental designs in which you expect the measured variable to *decrease* compared to controls, Floor Effect may be the main problem. Obviously, when measuring more than one variable in the same experiment, there may be the case that one is plagued by these effects while the other (s) don't: thus their data can still be useful, provided the clean variable is shown to be independent from the limited one.

## Cross-References

- [Avoidance](#)
- [Biological Preparedness](#)

- [Contrast Effects](#)
- [Effect Size](#)
- [Fear Response](#)
- [Joint Attention](#)
- [List Memory Effects \(Primacy and Recency\)](#)
- [Reaction Time](#)

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## Florence Merriam

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## Synonyms

[Florence Merriam Bailey](#)

## Definition

Florence Merriam was an ornithologist and naturalist.

## Introduction

Florence Merriam was a pioneering woman in science who built a career on her passion for birds and her desire to end the practice of wearing deceased birds or bird feathers as fashion accessories. She is celebrated for the accessibility of her works for people both within and outside of academia, and her legacy is one of inspiring people to embrace nature, rather than seeking to become masters over it.

## Her Life

Florence Augusta Merriam was born on August 18, 1863, in Locust Grove, New York (Oehser 1952). Her father, Clinton Merriam, was a businessman who later served two terms as a Republican Congressman, and her mother, Caroline Hart, was a graduate of Rutgers College (Kofalk 1997). Merriam was the youngest of four children. She had two older brothers – Charles and Clinton Hart, who was referred to as C. Hart or simply Hart – and an older sister, Gertrude, who died one day before Merriam’s birth (Kofalk 1997; Tayebi 2008).

Merriam’s innate interest in naturalism and science was impacted by her family members. Her mother inspired and encouraged her

relationship with nature through her own passion for astronomy, exposing her daughter to scientific pursuits at an early age (Kofalk 1997). Her paternal aunt was a botanist who maintained an herbarium and spent time studying and collecting samples of local plants (Tayebi 2008). Clinton, Merriam's father, was a friend of well-known naturalist John Muir and was himself interested in natural history, but it was his stories about hearing the birdsong of robins at his parents' farm that inspired Merriam's love of birds and her later career (Kofalk 1997; Oehser 1952; Tayebi 2008). Merriam was extraordinarily close to her brother Hart, who remained one of her dearest friends throughout their lives, and it was his interest in taxidermy and collection of animal specimens that further inspired Merriam's love of nature while simultaneously revealing her preference for observing and studying live animals (Kofalk 1997).

Because of her relatively fragile health and struggle with what is believed to have been tuberculosis, much of Merriam's education took place at home, during which time her interest in naturalism continued to be cultivated through long walks in the forest with her father and Hart (Kofalk 1997; Tayebi 2008). After brief periods of attending public schools, including a preparatory school in Utica, New York, Merriam was permitted to study at Smith College in Massachusetts under the condition that she did so as a nondegree student who would receive no formal degree upon the completion of her education in 1886 (Kofalk 1997; Oehser 1952). Despite her successes, Merriam remained without a degree until 1921, when Smith College officially awarded her a Bachelor of Arts degree, followed by a Legum Doctor degree given to her by the University of New Mexico in 1933 (Kofalk 1997).

As an adult, Merriam's beloved brother Hart relocated to Washington, D.C., where he became the head of the United States Biological Survey – the nation's first federal program focused on natural sciences as a field (Kofalk 1997). Hart's assistant, Vernon Bailey, maintained a friendship with Merriam for nearly a decade before they were married on December 16, 1899 (Kofalk 1997). Bailey went on to become the US

Biological Survey's foremost field naturalist – a position he occupied for over 40 years that afforded he and Merriam an opportunity to travel and conduct the fieldwork that would characterize their respective careers (Kofalk 1997). While Merriam and Bailey never had children of their own, they enjoyed close relationships with their nieces and nephews and remained faithfully married (Kofalk 1997).

Bailey and Hart both died in 1942 and, having lost the two people she loved the most within such a short period of time, Merriam retired afterward to the home she had shared with her husband in Washington, D.C., where she remained until her death in 1948 (Kofalk 1997).

## Her Work

Throughout her life, Merriam's focus was on birds and ornithology. Even while matriculating at Smith College, Merriam continued to conduct ornithological fieldwork and wrote journal articles on the subject (Oehser 1952). After marrying Bailey, the couple spent the majority of their life together traveling across the United States conducting fieldwork, which was their mutual specialty, though Bailey and Merriam focused on mammals and birds, respectively (Kofalk 1997). Like many women of her day, Merriam capitalized on the freedom to travel, taking to wagons and horseback to explore the areas where trains could not take her during her explorations alongside Bailey (Kofalk 1997).

During her final year of study at Smith College, Merriam was made aware that George Bird Grinnell was founding an Audubon Society (Kofalk 1997). She set out to raise awareness and gain members, which she did so successfully that shortly thereafter, nearly one third of the college's student body had become involved, earning her a position as one of the chapter's founding members (Kofalk 1997; Oehser 1952). Though this initial chapter later dissolved, it was reborn in Massachusetts and resulted in the National Audubon Society that exists today (Kofalk 1997). Additionally, in 1885, Merriam became the first woman to be made an associate

member of the American Ornithologists' Union (AOU), which was founded in part by her brother, Hart (Kofalk 1997; Oehser 1952). She went on to become the AOU's first woman fellow in 1929 and the first woman recipient of the AOU's Brewster Medal in 1932, as a result of her rise to prominence following the release of *Birds of New Mexico* (Kofalk 1997).

Over the course of her career, Merriam wrote nearly a dozen books and over 100 journal articles (Tayebi 2008). Despite traveling and conducting fieldwork alongside one another for decades, Merriam and Bailey collaborated on only two books, preferring to keep their work separate from one another's (Kofalk 1997). The articles Merriam wrote as a student at Smith College appeared in such publications as "Audubon Magazine," and they were later compiled into her first book, *Birds Through an Opera Glass*, in 1889, which provided means of recognizing different avian species while also detailing many of her bird-watching experiences (Oehser 1952; Tayebi 2008). Her most significant work *Birds of New Mexico* consisted of over 800 pages and was published in 1928, earning her attention and acknowledgments from the AOU, as it was the first comprehensive account of avian life in that region of the United States (Kofalk 1997; Oehser 1952). For these reasons, it is widely considered to be her *magnum opus*. Her book *Birds of Village and Field* was published in 1898, and it is regarded as the first popular bird-guide book in America, with its noteworthiness being partially due to the illustrations by celebrated artists such as Louis Agassiz Fuertes contained therein (Oehser 1952). Alongside Bailey, Merriam continued to write ornithological articles which were published by notable mediums such as *The Auk* and *The Condor* (Oehser 1952). In 1902, her *Handbook of Birds of the Western United States*, which contained several hundred illustrations by Louis Agassiz Fuertes, was released; it was the first of her works to feature technical, scientific terminology and detailed descriptions of the appearances, reproduction, and behavior of various avian species (Oehser 1952; Tayebi 2008). Merriam continued to work and write into late adulthood, and her final significant work,

"Among the Birds in the Grand Canyon National Park," was released in 1939, when she was 76-years-old (Oehser 1952).

Unlike other women in her day, Florence Merriam always published her works under her own name, and it is this independence that, when coupled with her impressive career, affords her a place as one of the most prominent women naturalists and writers of the nineteenth century (Kofalk 1997). Her writings are likewise unique because they are written more for laypeople than academics or scientists, which showcases her desire to educate people about the birds and the natural world around them, as she believed that possessing such awareness and knowledge was key to protecting and celebrating nature as it deserves (Kofalk 1997). Merriam possessed the necessary knowledge and technical vocabulary to write for fellow ornithologists, but her passion was such that she chose instead to focus on lay readers, who might be inspired to go outdoors, view nature differently than they did before encountering her works, and discover for themselves the wonders that had eluded them previously (Kofalk 1997).

Decades later, her legacy lives on; she is still considered one of the most prominent sources of information on avian behavior (Oehser 1952).

## Cross-References

- Bird Migrations
- Owls
- Pigeon (*Columbidae*)

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## Florence Merriam Bailey

► [Florence Merriam](#)

## Florida Manatee

► [Sirenia Diet](#)

## Fluctuating Asymmetry (FA)

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## Introduction

Developmental stability is referred to as an “ideal” form of an organism to respond against random perturbations during development under a set of conditions (Palmer and Strobeck 1986). As such, abrupt deviations from the ideal condition, when stability in development is disturbed, produce a range of forms that depart from normal phenotypes. Under normal conditions, those outcomes of stability are widely known in bilateral organisms. Even though bilaterally symmetrical

organisms have been extensively used as a calibration point to assess deviations from the norm, these organisms also present developmental instability (DI), especially between the left and right sides of certain characters, and thus they have been of interest to evolutionary biologists.

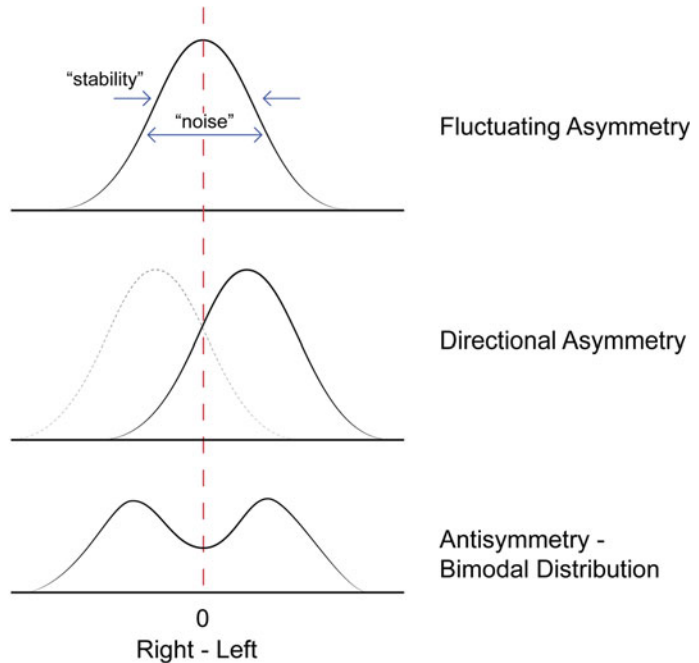
Developmental instability (DI), also known as developmental noise, or treated as an outcome of that, implies subtle deviations from symmetry, which usually exhibit one of three types: fluctuating asymmetry (FA, imprecisely determined path during development); directional asymmetry (DA, general tendency in which one side shows greater development); and antisymmetry (AS, equal frequency of variation) (Fig. 1). These terms refer to patterns of variation in a particular characteristic displayed by a sample of individuals. Fluctuating asymmetry is the most studied and has become a measure of DI, especially because it is the easiest to visualize in populations due to differences in the left-right sides (L-R). However, it is a matter of debate which stressors trigger DI during ontogeny and whether genetics alone, or together with the environment, play a role in producing such variation in chirality. Despite extensive efforts to discover the development basis of FA, the underlying causes of heterogeneity are still unclear. Here, we will highlight the current state of knowledge on FA, measurements, and its applications in evolutionary biology.

## The Definition of FA

Fluctuating asymmetry is characterized by small, random departures from the symmetrical form in bilateral organisms. During DI, individuals are unable to overcome extrinsic (e.g., habitat fragmentation, thermal noise) and intrinsic (e.g., inbreeding depression, bottleneck event) stressors, exhibiting nonidentical forms on both sides of a given trait. Because phenotypes are not identical within populations, as FA implies imprecise pathways during development, FA can be used as a measure of developmental (in)stability, estimating the sensitivity of development from genetic and environmental stresses. Therefore, FA has been the subject of a lot of attention for

# Fluctuating Asymmetry (FA), Fig. 1

Three most common potential distributions of the right-left means in bilateral organisms. Fluctuating asymmetry in a population exhibits a normal distribution of the difference between the sides with a mean of zero ( $R-L = 0$ )



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generating valuable outcomes for assessing the biological effect of stress at the population level and its impacts on fitness and heritability (see Van Dongen 2006; Benítez et al. 2020).

The search for features notably under FA is quite simple: these traits will be asymmetrical on the right-left sides and can be measured separately, considering the right-minus-left in each individual in a population (Fig. 2). These measures reflect the usual normal distribution with a mean around zero, characterized by a leptokurtic (i.e., when the distribution has an excess of kurtosis, with tails larger than the normal distribution) curve in FA. Although it is well-known to affect the behavior of populations, particularly sexual behavior, and have genetic bases still to be discovered, FA does not have adaptive biases. Basically, this claim is underpinned by the idea that symmetrical traits are the ideal form and, thus, highly genetically controlled (Tomkins and Kotiaho 2002).

## Measuring FA

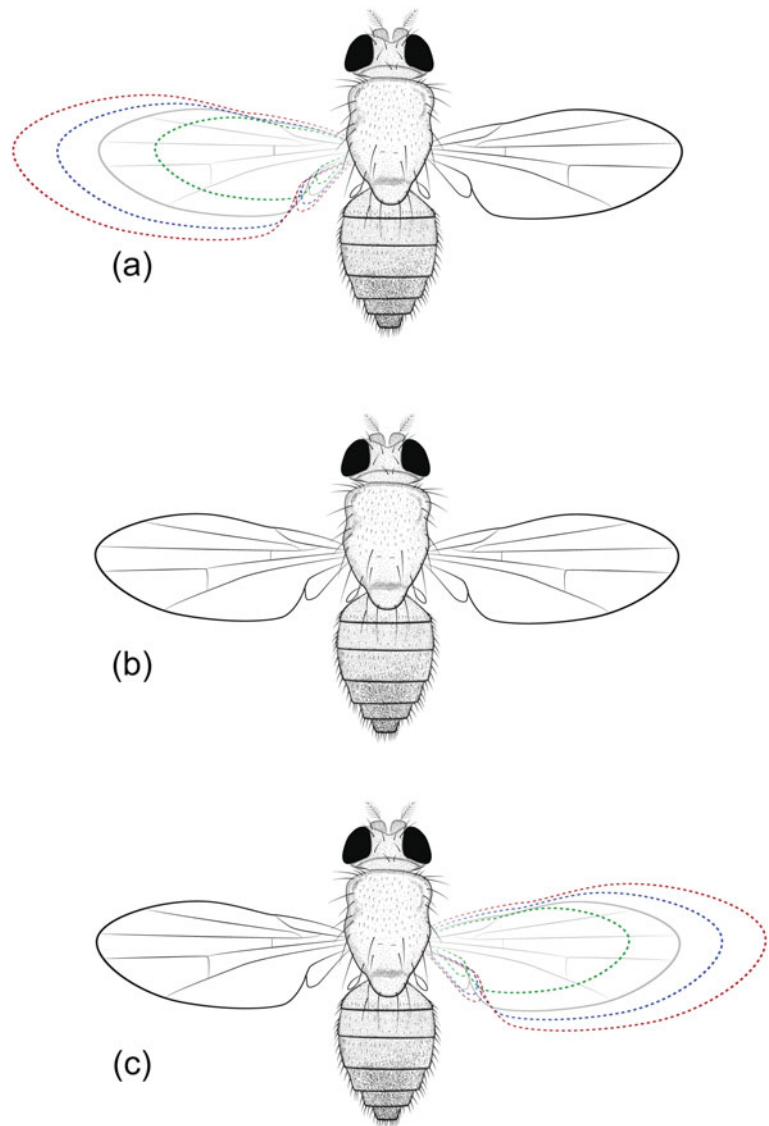
Fluctuating asymmetry can be achieved as simply as measuring the size of a given bilateral trait in

the left-right sides and assigning the difference between the absolute value of both afterwards, although other indices can also be used to assess this variation (e.g., morphometrics; see Palmer and Strobeck 2003). Therefore, more symmetrical traits are those whose difference is closer to zero. However, quantifying FA among individuals can be a troublesome task, as the magnitude of FA is usually the same as the measurement error (Palmer and Strobeck 1986). Measurement error reinforces variance in a sample, especially in mean absolute deviations, which often generate apocryphal associations (Graham et al. 2010). To avoid spurious information, a statistical analysis must be included in FA observations, and the most widely used is the mixed model analysis of variance (ANOVA).

In this regard, most experts have repeatedly measured the same character on both sides to ensure accuracy in their analysis, also applied to estimate the extent of the variation during counting the focal character, which accounts for measurement error. These measurements must be taken under the same conditions (e.g., stereomicroscopy), guaranteeing the same manipulation in achieving the measures. Repeatability is of

**Fluctuating Asymmetry**

**(FA), Fig. 2** Hypothetical scheme of a *Drosophila* showing R-L wing size variation: (a) right wing size variation; (b) symmetric form; (c) left wing size variation. In fluctuating asymmetry, it is expected that small deviations from symmetry in a sample of individuals should have a larger or smaller right side (a, positive asymmetry) or should have a larger or smaller left side (b, negative asymmetry). Measurements can be taken using morphometry methods (e.g., wing width versus wing height) to estimate the fluctuating asymmetry of a population by the average of the absolute differences between both sides



paramount importance in every trait that will be analyzed, mostly because it is the principal input for the statistical analysis for both measurement error (ME) and traits (ANOVA), which will indicate if the observed asymmetry is significantly different from ME and whether it reaches a normal distribution (Graham et al. 2010). A thorough statistical procedure is available and detailed in Palmer and Strobeck (2003).

Regarding the accuracy of FA as an estimator of DI, estimated DI is rather difficult to generalize to a population, especially because FA is usually measured from two sides of a given bilateral trait

(i.e., with one degree of freedom), which reflects the DI of that individual (Leamy and Klingenberg 2005), and not the whole population, resulting in low precision as an estimator of DI variability. Therefore, to have confidence that differences in L-R sides in a population are due to FA, sampling variation should rely on many FA values. For this, FA and DI should be standardized by *hypothetical repeatability* (HR), an estimator that correlates how much of the difference observed by FA corresponds to differences in DI (Van Dongen 1998). However, even when estimating HR for a huge number of traits and values of FA, it is difficult to

establish that high values of HR express high DI, mainly because different traits may be upon different selective pressures on its symmetry. Therefore, there is a common observation of low values of HR, stressing the difficulty in estimating the degree of DI in a trait.

### More Common Than It Seems: The Evolutionary Significance of FA

Fluctuating asymmetry has been correlated with a number of evolutionarily relevant issues, such as sexual selection, mate choice, fitness, and heritability (Carter and Houle 2011; Ishihara and Miyatake 2020; Leung and Forbes 1996; Møller and Pomiankowski 1993). Most of these studies focus the attention on a particular aspect of FA at the population level, a feature that can be inferred by the degree of FA. In terms of sexual selection, for example, researchers have raised the idea that FA is a possible indicator of individual quality, a consequence of FA that directly affects individuals' behavior in natural populations. For instance, males with secondary sexual ornaments may be negatively affected by FA, as asymmetrical males indicate to potential mates that they are unable to cope with environmental stress during development, reflecting male quality (Møller and Zamora-Muñoz 1997). As such, females may benefit from choosing symmetrical males according to the “good gene” model of sexual selection.

Individual quality, especially in males, is thought to be sensitive to FA under the assumptions of three main hypotheses: (i) secondary sexual ornaments are costly to produce; therefore they are more sensitive, suffering more from environmental stress, decoupled from other highly costed, and more functional important, symmetric traits; (ii) selected traits are dependent on their expression, and the tiniest modification in that pathway triggers phenotypic deviations; (iii) symmetry is repeatedly observed in characters with a selective advantage, which makes it tempting to assume a genetic component underlying this pattern. Along with these, asymmetry in secondary sexual traits may be under recent directional selection (Møller and Swaddle 1997).

Convincing studies have demonstrated that females are biased toward choosing symmetrical males as mates, which raises the idea that females may have strengthened sensorial biases according to sexual selection models (i.e., sensory bias model). There is growing evidence that female mate choice shapes sexual selection, with empirical demonstration in birds, insects, and spiders. In insects, fireflies display a unique, and widespread, range of variation in both the left-right antennae, with cases up to 80% of asymmetry in a population (Nunes et al. 2020). Complex mate finding (i.e., using chemical components or light signals) may maintain unusual variation among taxa, which may benefit them from having extra antennomeres (i.e., more antennal surface). Another example is also reported in cerambycid beetles *Stenurella melanura* (Linnaeus 1758) in which males with symmetrical antennae were chosen more often than asymmetrical ones, reflecting that this trait has been sexually selected. However, these asymmetries characterized a sharp asymmetry between mated and unmated males, instead of slight deviations from the ideal form – which is a common form of FA (Møller and Zamora-Muñoz 1997).

Studies using tetrapods as a model system consistently show results in FA mean values among more functionally important traits in anurans and turtles (Didde and Rivera 2019; Rivera and Neely 2020). These findings agree with a growing current of thought that more useful and biologically important morphological traits may display lower degrees of FA. Especially in vertebrates, large differences in FA in limbs may decrease the performance of terrestrial animals (Trivers et al. 2013) and aerial organisms (Swaddle 1997), as well as aquatic tetrapods (Rivera and Neely 2020). This handful of examples highlight that different FA plays a different role and has evolved at different rates, according to the trait.

### What Is the Role of Environment and Genetics in FA?

An organism's development is constantly under epigenetic phenomena (i.e., molecular alterations that occur on DNA but not within DNA

sequencing, producing heritable phenotype changes), being subject to huge intrinsic perturbations. These perturbations give rise to the opportunity for unpredicted phenotypes, culminating in nondirectional departures of paired structures for perfect symmetry (i.e., fluctuating asymmetry). Environmental and genetic factors are the main drivers of FA, and their roles have been investigated in depth (Leamy and Klingenberg 2005; Mabrouk et al. 2020; Sandner 2020). Published evidence seeking signatures of both stressors upon individual development showed that FA arises whenever the environment presents higher concentrations of distinct contaminant exposure. In aquatic environments, ecotoxicological monitoring of several species of anurans and fish suggests that developmental instability increases as a result of exposure to pollutants (Seixas et al. 2016; Guo et al. 2017). As such, higher levels of FA are often found in these environments. These patterns also point to the importance of conservation policy, given that high rates of FA are found with chronic exposure to a range of pollutants, from metals to chemical components. Furthermore, these parameters are closely related to individual and environmental quality – polluted environments and higher levels of FA are suitable and reliable biomarkers for ecotoxicological studies, conservation, and prediction of FA (Leary and Allendorf 1989).

On the other hand, the role of genetics in shaping FA is still unclear and contentious. Some studies have found heritability in morphological characters (Carter and Houle 2011) while others have found no such relationship (Kruuk et al. 2003). In order to search for the role of genetics in developmental instability, researchers have focused on candidate genes (Batterham et al. 1996) and quantitative trait loci (Leamy et al. 1997, 1998). However, a consensus on whether the genetic architecture is conditional to certain characters to ensure symmetry in organisms' development awaits further investigation.

More generally, a better understanding on how the genetic pool affects the degree of FA under environmental stressors and the extent of phenotypic variation among populations is elusive. Heritable variation of FA has been reported for

artificial selection of outbred populations in the fruit fly *Drosophila melanogaster* (Meigen 1830) (Carter and Houle 2011), although natural selection has not fixed all the extant phenotypes found during artificial selection. Noteworthy, according to these findings, natural selection tends to decrease levels of FA in evolutionarily relevant traits in all wild populations, such as locomotor appendages (e.g., legs, limbs, and wings). Therefore, it is assumed that FA (and DI) is deleterious to fitness.

## Summary

Fluctuating asymmetry plays a pivotal role in mate choice, sexual selection, heritability, and conservation. To date, a broadly available literature portrays the importance of environment and genetics as a trigger of developmental instability, thus leading to higher degrees of FA in bilateral organisms. However, the mechanisms underlying FA remain to be investigated.

## Cross-References

- [Bilateral Symmetry](#)
- [Brain Asymmetry](#)
- [Radial Symmetry](#)

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## Focal Animal Sampling

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## Synonyms

[Focal sampling](#); [Focal sampling methods](#); [Focal observation](#)

## What is animal focal sampling?

Focal animal sampling is a method commonly used in the study of animal behavior, such as for the elaboration of ethograms (Altman, 1974). According to Altman (1974), observers using this method should sample the behaviors of only

one individual at a time, regardless of the number of individuals that could be sight during sampling. When using focal animal sampling, individuals are observed for a period of time each, recording their behaviors in intervals of pre-established duration. This method allows a more detailed behavioral sampling if compared to other sampling methods. Despite its usual application to one individual at a time, adaptations of the method to sample groups of few individuals spatially restricted have been reported (Anciães and Prum 2008; Bosholn et al. 2016).

Ideally, before beginning observations, the observers should define the recording rules. Three recording rules can be used for record behavior in focal animal sampling: continuous recording (all occurrences in the interval), instantaneous sampling (occurrences in the beginning of the interval), and one-zero sampling (first occurrence in the interval) (Martin and Bateson 1986). Subsequently, it is important to determine the duration of the time interval in which the focal individual will be observed (Altmann 1974). Observation interval duration depends on multiple factors (Altmann 1974), including characteristics intrinsic of the focal species such as mobility and habit. For species that are very active or highly mobile, such as birds, a short observation interval can be efficient to quantify the behavior of the focal individual using either recording rule (e.g., Anciães and Prum 2008; Bosholn et al. 2016; Durães 2009). In these cases, longer observation intervals would prevent recovering accurate information regarding when the behaviors were observed. On the other hand, in species with little activity or low mobility, it is suggested that the duration of observation intervals be longer. The three-toed sloth, for example, can remain inactive for many minutes and, for this reason, longer observation intervals are considered sufficient for good behavioral sampling (e.g., Urbani and Bosque 2007). In order to determine the duration of the observation interval it is also necessary to consider the number of behavioral categories that will be sampled. If the goal is to observe many categories (e.g., vocalizations, displays, agonistic interactions), short observation intervals might

not be appropriate for accurately sampling all intended behaviors. However, if observation intervals are too long, it might turn out to be difficult for the observer to concentrate during the entire sampling interval, which may affect the accuracy of the collected data (Altmann 1974).

Before beginning observations using focal animal sampling, it is important to determine which individuals will be observed. This choice will depend on the research goals. For example, if the research aims to study behavioral variation among adult females in a particular species, the observers should give priority to individuals of that sex and age category. Observers should then, ideally, observe as many individuals of the intended sex and age with equivalent sampling effort. This would allow more robust comparisons among individuals. After all, results would possibly be skewed by observing one individual for only 10 intervals while observing another for 120 intervals, which could compromise data comparison between individuals.

To determine the duration of the observation intervals, the most appropriate recording rules, and the number of individuals that can be sampled, it is recommended that observers conduct a pilot study before beginning the behavioral data collection using focal animal sampling. Without appropriate planning, many behavioral data might be in fact useless or obsolete. Besides that, pilot studies might be important both for the habituation of the focal individuals and for acquaintance of observers with the studied species. Additionally, they are essential to (i) correct minor errors referring to data collection not detected in the project proposal; (ii) observe the mobility of focal species and frequency/duration of behavioral categories, besides adjusting the duration of the observation intervals; and (iii) determine the total time of observation that will be necessary to obtain a complete sampling of the behavioral repertoire, besides obtaining enough replicates of the behaviors, for each sampled individual. From these pilot studies, the observers can elaborate the spreadsheet that will be used to quantify the different behaviors of focal individuals. This spreadsheet will vary according to the needs of

Local:Date:Observer:

Individual:Sex:Age:

| Time     | behavioral<br>element 1 | behavioral<br>element 2 | behavioral<br>element 3 | additional<br>considerations |
|----------|-------------------------|-------------------------|-------------------------|------------------------------|
| 06:00 am |                         |                         |                         |                              |
| 06:05 am |                         |                         |                         |                              |
| 06:10 am |                         |                         |                         |                              |
| 06:15 am |                         |                         |                         |                              |

**Focal Animal Sampling, Fig. 1** Spreadsheet template to quantify behavioral data. Page header should contain general information such as localization of study area, date of observation, and observer identification among others if necessary. It is also essential to record the identification,

sex, and age of the focal individual. In the first column of the spreadsheet, the captions referring to the behavioral elements and additional considerations should be placed. In the lines, the durations of observation intervals should be placed

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each observer and according to the characteristics of the focal species (Fig. 1). However, the observer should be aware that the data collected during the pilot studies should not be used in the posterior analyses. Even if the observer felt that little has been modified from the pilot study, the habituation of the observer with the object of study requires some time (1–3 days in simplest cases).

One of the advantages of focal animal sampling is a more detailed sampling if compared to other sampling methods (Altmann 1974). The amount of information sampled with focal animal sampling is relatively similar to that collected through other methods (e.g., ad libitum). However, the accuracy of the collected data is generally greater with focal animal sampling because it is possible to specify at which time the behaviors occurred. This method is thus recommended when observers intent to sample specific behaviors performed by each individual in a group (e.g., courtship ritual, parent/offspring conflict, female choice). Brodt et al. (2013), for example, used focal animal sampling to determine the dominance hierarchy of one lekking bird species. While, Anciães and Prum (2008) used focal animal sampling to study whether display behavior of some bird species changes with temporal changes in light conditions. Another advantage is that little information is lost when an individual is

observed through this method. However, focal animal sampling also has some disadvantages (Altmann 1974). This method requires a higher number of sampling records, inflating the required sampling effort in studies of large groups of individuals. In addition, during observations of free wild animals, the individual being observed might disappear. In these cases, the observer has two options: find again the focal individual or observe another individual (if the observer chooses the second option, observation data of the lost individual need not be discarded). Therefore, it is very important to consider that, despite the numerous advantages, focal animal sampling will not always be appropriate. In species which are very active and participate in large groups, for example, other observational methods (e.g., ad libitum, scan sampling, behavior sampling) can be used to maximize behavioral data sampling (e.g., termites, *Nasutitermes corniger* (Pequeno 2017); the pied tamarin monkey, *Saguinus bicolor* (Sobroza et al. 2017)).

Cross-References

- Courtship Rituals
- Ethogram
- Female Choice
- Observational Methods

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## Focal Observation

- [Focal Animal Sampling](#)

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## Focal Sampling

- [Anecdote](#)
- [Focal Animal Sampling](#)

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## Focal Sampling Methods

- [Focal Animal Sampling](#)

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## Folk Physics

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## Synonyms

[Intuitive physics](#); [Naïve physics](#); [Physical causality](#); [Physical cognition](#)

## Definition

Controversial (see below): People’s and other animals’ commonsense or naturally-occurring understanding of the physical world (e.g., properties of objects, causality), especially as it relates to the manipulation of objects using tools. Of particular interest is whether this understanding consists of reasoning about unobservable physical mediators (e.g., transfer of force) or is based on observable features of physical events.

## Introduction

When a chimpanzee stands on a wooden crate and uses a pole to reach bananas suspended from the ceiling, what does the ape understand about its actions, the crate and pole, and the bananas? Does the ape think about the necessary conditions for the pole to function as a tool that can be used to get the bananas? Does this animal understand why these same objects (i.e., the crate and pole) cannot be used to procure water? When a capuchin uses a stone hammer to crack a nut placed on a stone anvil, what does the monkey understand about its actions, nuts, hammers, and anvils? Does this animal think about the conditions necessary for the hammer to crack the nut? Does the capuchin understand the concept of “hardness?” And when a child uses scissors to cut paper, what does she understand about her behavior, scissors, and paper? Does she think about the necessary conditions for the scissors to cut the paper? Does she understand that the

same effect cannot be achieved if a tool lacked “sharpness?”

These are the sorts of questions that interest anthropologists, biologists, philosophers, and psychologists who study folk physics. For these scientists and scholars, the proximate purpose of studying folk physics is to gather information about how people and other animals think about objects in their physical worlds and about physical causes and their effects (i.e., physical causality). Some of the dimensions of the physical world and causality that interest researchers are distance (how far), time (how long), quantity (how many), magnitude (how much), and frequency (how often). Some of the dimensions that are not directly observable include transfer of force and gravity. Although researchers want to discover if and how humans and nonhuman animals think about unobservable physical constructs, the domain of folk physics consists of those physical events that can be observed without sensory aids such as cameras, telescopes, microscopes, oscilloscopes, and the like. Phenomena of an astronomical, chemical, magnetic, and electrical nature are thus normally excluded from the study of humans’ and, for obvious reasons, animals’ folk physics. The ultimate purpose of studying folk physics is to develop a theory about the evolution of cognitive abilities.

The pursuit of evolutionary goals requires comparative methods, and the study of folk physics is no different. Although primates such as chimpanzees, gorillas, and capuchin monkeys are the animals whose folk physics is most often compared with that of humans, the folk physics of tool-using avian species such as New Caledonian crows and woodpecker finches also have been compared to the folk physics of people and other primates. Folk physics is studied in controlled laboratory experiments (e.g., Chappell and Kacelnik 2002), using naturalistic observation in field studies (e.g., Hunt 1996), by observing the behavior of captive animals (see Haslam 2013), and through computer simulations of animal robots (e.g., Chappell and Hawes 2012). But discovering what nonverbal

animals know about their physical world is not easy. The root of the problem is that it is unclear what folk physics is (a conceptual problem) and how it should be studied (a methodological problem).

## Conceptual-Methodological Challenges in the Study of Folk Physics

There are several challenges in the study of folk physics that fall along a conceptual-methodological continuum. At the conceptual end is a lack of clarity about the definition of folk physics: People’s and other animals’ commonsense or naturally-occurring understanding of the physical world. At the methodological end is a lack of clarity about how to study folk physics.

### What is “Understanding?”

The definition of folk physics is itself a source of two major conceptual challenges. The first concerns the term “understanding,” which is not a well-defined scientific concept (Pear 2001). As a result, a seemingly simple question such as, “Do chimpanzees understand weight?” or a more specific question such as, “Do chimpanzees form mental representations of unobservable causal mechanisms?” are difficult to answer. What counts as evidence of understanding weight? What counts as evidence that a chimpanzee formed a mental representation of an unobservable causal mechanism? In studies of concept learning, if a person or another animal makes a common response in the presence of stimuli that share specifiable characteristics, that is evidence that the subject understands the concept or class. Learning a concept thus depends on appropriate discrimination (i.e., identifying stimuli that are not part of a class) and generalization (i.e., identifying stimuli that are part of a class). For example, a child shows that he understands what “red” is if he says or writes “red” after someone asks, “What color is that?” while pointing to the red feature of various objects. Learning the concept “red” requires discriminating between red and other colors, as well as generalizing across varieties of red (e.g., burgundy, maroon, crimson). In relation



to folk physics, a chimpanzee that chooses rakes that are long enough to retrieve out-of-reach objects and does so while avoiding holes that can trap the object may be showing an understanding of the relations among a tool's length and an object's distance, that holes cannot support objects (and thus trap them), and perhaps even unobservable constructs such as transfer of force and gravity. Similarly, a chimpanzee that routinely tries to obtain water using pails, cans, and other containers instead of pails and cans without bottoms (which are thus merely tubes) may be showing an understanding of containment. But what counts as evidence of understanding has not been agreed upon. At a minimum, proof that a concept has been learned requires making a correct response across different situations.

### **What is "Common Sense" or "Naturally-Occurring" Understanding?**

The second conceptual challenge in the definition of folk physics is the adjective "commonsense," as in "commonsense understanding." Common sense is also not a well-defined scientific concept, and how it could apply to animals is even more ambiguous. According to Kuipers (1984), "commonsense causal reasoning is qualitative reasoning about the behavior of a mechanism which can be done without external memory or calculation aids" (p. 170). Davis (1990) defined common sense as "the common knowledge about the world that is possessed by every schoolchild and the methods for making obvious inferences from this knowledge" (p. 1). Entire articles have been written about commonsense reasoning without defining what it is.

Perhaps because of the difficulty of defining common sense, especially as it relates to animals, some researchers define folk physics in terms of naturally-occurring understanding instead of commonsense understanding. For example, Povinelli (2000) defined folk physics as understanding about the physical world that "develops naturally and spontaneously" (p. 2) in the course of development. A problem with this variant of the definition is that programmatically training animals to assess their folk physics disqualifies such research as studies of folk physics,

which is about naturally-occurring understanding or understanding that develops without explicit training.

A problem with restricting folk physics to naturally-occurring understanding is that the distinction between naturally-occurring (on the one hand) and explicitly-trained (on the other hand) may be artificial or unimportant. To illustrate, consider the following question: Is the understanding that results from teaching children to identify shapes programmatically trained or naturally occurring? Teachers and parents are a part of most children's natural environments. Teachers and parents may provide explicit feedback to a child's labeling of a shape, such as when a parent says, "That's right" or "No, that's a triangle." Is the child's eventual understanding naturally occurring or explicitly trained?

One solution to the problematic aspects of the adjectives "commonsense" and "naturally-occurring" is to eliminate them from the definition of folk physics. "Physical causality" and "physical cognition" are often used interchangeably with "folk physics." When researchers study physical causality, they are trying to discover if and how people and other animals reason about events that are associated with one another in space and time; specifically, whether organisms reason about unobservable mediating physical forces (e.g., gravity) or whether an organism's understanding is based on directly observable features of the events (e.g., a desired object falls out of reach) (Visalberghi and Tomasello 1998). Unlike the study of folk physics, the study of causal understanding in the physical domain (i.e., physical causality) has no restrictions about the conditions under which this understanding develops. Similarly, physical cognition refers to "how an organism understands and manipulates its physical world" (Parrish and Brosnan 2012, p. 174), again, without any restriction on how this understanding is acquired or that it relates only to causality. At present, though, there is no consensus as to whether physical causality, physical cognition, and folk physics are the same or different, or whether the definition of folk physics should contain the adjectives commonsense, naturally-occurring, or intuitive.

### Why Does the Definition of Folk Physics Matter?

The definition affects the methodology used to study folk physics and the interpretation of the results of experiments that purport to study it. To see how, consider that the study of folk physics is characterized by two approaches. In one approach, researchers specify an aspect of folk physics that adult humans possess, such as knowing that objects fall because of gravity or that a rigid rake is necessary to retrieve a heavy object. These researchers then devise physical puzzles to test if nonhuman animals or children possess the same knowledge. Relative to a variety of control problems, solving the puzzles should only be possible if the subject possesses the relevant knowledge. Without this knowledge, subjects should make many errors or otherwise be incapable of solving the problem. For example, pigeons do not seem to have knowledge of “insideness.” When presented with 80 images of simple curves with a single dot either inside or outside a curve, these birds had a great deal of difficulty categorizing the two types of images: those of curves with a dot on the inside versus a dot on the outside (Herrnstein et al. 1989). Had the pigeons spontaneously sorted the two types of images or, after extended training, been able to sort novel images of curves with a dot on the inside or outside, researchers would have concluded that the pigeons understood insideness.

In the second approach, which is exemplified by Povinelli’s (2000, 2012) studies of folk physics, researchers also specify an aspect of folk physics that adult humans possess, devise physical puzzles to test if animals or children possess the same knowledge, and use a variety of control problems. But unlike studies that fall neatly into the first approach, in the second approach, explicit training is kept to a minimum and consists of what is normally considered pretraining – trials to familiarize the subjects with the testing environment, procedures, and equipment (e.g., tools). Attempts to explicitly train understanding invalidates, by definition, an examination of a subject’s naturally-occurring understanding of its physical world. “Determined to demonstrate similarity [between humans and other species], many researchers train on, without ever seriously

considering the possibility that the very extent of the efforts required to produce human-like behaviors in their animals undermines the very claims they wish to make in the first place” (Povinelli 2000, p. 338). Also unlike the first approach, the second approach relies on testing subjects using increasingly difficult variations of the physical puzzles to discover the limits of the subjects’ understanding. These limits are then compared to adult humans’ purported understanding of similar or related phenomena.

These two approaches can come into conflict. If a study used the second programmatic-training-not-allowed approach and failed to find evidence of abilities in animals comparable to those of adult humans, researchers who use the first programmatic-training-allowed approach could argue that the absence of evidence could be because the animals lacked the relevant concept, because of a lack of motivation, because of the subjects’ experiences prior to testing, because of poorly designed tests, or because of many other reasons (see Buckner 2013; Machado and Silva 2003). In short, researchers who use the first approach would not necessarily conclude that absence of evidence is evidence that the ability is absent. Proponents of the second approach, though, could conclude that absence of evidence is evidence of absence.

Similarly, if animals trained to learn a concept seemed to possess an understanding comparable to that of humans, proponents of the programmatic-training-allowed approach could conclude that they discovered a similarity between humans’ and animals’ understanding. But proponents of the programmatic-training-not-allowed approach may disagree. They could argue that what was demonstrated was that animals can be trained to behave like humans on a particular task or set of tasks, not that the people’s and animals’ folk physics were similar.

The cost of these conflicting approaches, which are rooted in different definitions of folk physics, is that it is unclear what scientists and scholars know about different species’ folk physics. Proponents of the programmatic-training-allowed approach, which is rooted in a definition of folk physics without the terms commonsense or

naturally-occurring, can claim that, “Because Species A behaved similarly to Species B across several tasks, we conclude that these two species have a similar understanding of physical concept X.” Proponents of the programmatic-training-not-allowed approach, which is rooted in the definition of folk physics that contains the terms commonsense or naturally-occurring, could claim that, “Because the two species behaved similarly only after extensive training, the results do not show that these species’ folk physics were the same.” In sum, what is known about the comparative study of folk physics depends on who you ask, this person’s preferred definition of folk physics, and this person’s preferred approach to the study of folk physics.

## Folk Physics: Contrasting Evidence

### Weight

Chimpanzees and other primates (e.g., capuchin monkeys) use hammers and anvils to crack nuts so that the desired kernel can be obtained. One variation of this nut-cracking behavior involves placing the nut on a stone anvil and then hitting the nut with the flat side of a hammer stone. Mastering nut cracking requires that the animal “attends to the properties of the tool that are relevant for reaching the goal of cracking the nut” (Schrauf et al. 2012, p. 1). Wild chimpanzees select hammers of a particular size, shape, and material that can be used to effectively crack the nut. Wild capuchins select stones that are best suited for cracking nuts.

To answer the question, “Do chimpanzees use weight to select hammer tools?” Schrauf et al. (2012) presented captive chimpanzees with cuboid-shaped (one experiment) and spherical (another experiment) hammers identical in every way except their weights. Although the chimpanzees did not have an initial preference for the weight of the hammer they used to crack the nut, they eventually developed a preference for heavier hammers that required less time and fewer hits to open the nuts. Because all hammers in a given experiment differed only in terms of their weights, the results showed that chimpanzees learned to attend to a key property of the tool

(namely, its weight) relevant to the problem (i.e., cracking nuts).

These results suggest that chimpanzees’ folk physics consists, at least to some extent, of an understanding of weight. At a minimum, their understanding consists of being able to perceive and differentiate weight as a property of objects. But the significance of these results is unclear because the ability to discriminate objects by weight required many trials (learning), which leads to questions about the animals’ *naturally-occurring* understanding of weight. Also, without generalization (transfer-of-training) tests to determine whether the chimpanzees can use what they know about weight to solve novel problems, it is difficult to say what they understand about weight. Analogously, if a psychologist was investigating what a child understood about colors, and the results of an experiment showed that the child could, after many trials, reliably select a red object that was associated with a reward instead of green or yellow objects that were not, few psychologists would conclude that the child understood the property “color.” Before concluding that the child understood color, psychologists would test if the child could identify the correct color in a variety of circumstances, across many problems. That is, psychologists would test for evidence of concept learning. Without generalization tests, the strongest conclusion is that the child can differentiate objects on the basis of color, or that the child can associate different colors with different outcomes. This is one reason why after more than 30 experiments to determine what chimpanzees understood about weight, Povinelli (2012) concluded that, although these animals understand many aspects of weight, they do not reason about it as an abstract concept.

In the absence of programmatic training, New Caledonian crows, a tool-using avian species, do not differentiate between heavy objects, which could be dropped into a tube to trigger the release of food, and lighter objects, which lacked the weight to produce the force needed to release the food. After explicit training, though, the birds learned to select the heavier objects that caused the release of food (Neilands et al. 2016). These results suggest that New Caledonian crows’ folk

physics consists of the ability to differentiate objects on the basis weight. But, again, the importance of these results is hazy because the ability to discriminate between heavy and light objects required programmatic training. If folk physics is about naturally-occurring, commonsense, or intuitive understanding, then training to produce that understanding undermines the target of the investigation (Povinelli 2000).

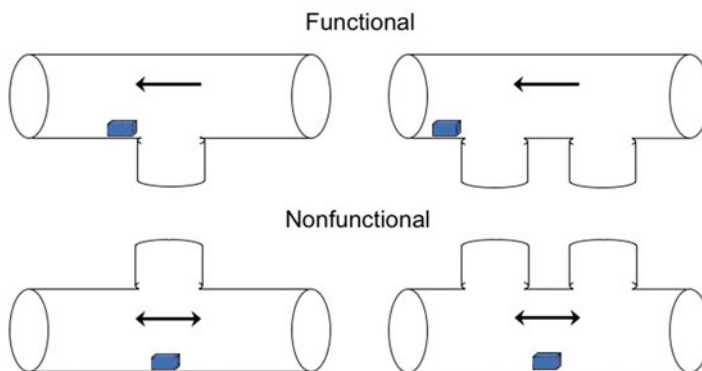
### Gravity

Rooks are birds that are not known to use tools in the wild. They can, however, in laboratory settings use tools to obtain a desired reward. For example, rooks can shape wire to produce a hook, and use several tools in a sequence to obtain a reward (e.g., picking up a stone and dropping it into a vertical tube to obtain access to food). These birds may even “possess an understanding of tools rivaling habitual tool users such as New Caledonian crows and chimpanzees” (Bird and Emery 2009, p. 10370).

Rooks’ understanding of gravity has been tested using a trap-tube task, a problem that is commonly used to study chimpanzees’ and other primates’ folk physics. The trap-tube consists of a clear tube from which animals can extract a reward if they can avoid pushing or raking it into a trap. The most commonly used trap-tubes have one or two traps (see Fig. 1, top panel). An experimenter can disable a trap by inverting it (see Fig. 1, bottom panel). In this position, a trap

does not function as a trap. What an animal understands about the task is often measured in terms of how many trials it takes the animal to avoid a functional trap and whether the animal will continue to avoid the trap when it is inverted into a nonfunctional position. “The rationale is that, if they understand that unsupported items fall under gravity, they will also understand that an inverted trap cannot endanger the item” (Chappell 2006, p. R244).

Using a programmatic-training-allowed approach, rooks learned to solve the trap-tube problem by pulling a stick that retrieved the reward; pulling the wrong stick caused the reward to fall into the trap (Seed et al. 2006). To see if the birds could transfer what they learned about the trap-tube to new circumstances, the experimenters presented the rooks with two novel problems. When the new problem consisted of a relatively minor variation of the initial trap-tube, the rooks solved the problem (i.e., avoided the trap). However, when the new problem was more dissimilar to the initial trap-tube that the rooks had learned to solve, most of the birds failed to avoid the trap. Because most of the rooks did not transfer what they learned about one physical task (i.e., the initial trap-tube) to this novel task which had the same underlying causal structure and unobservable construct (i.e., the role of gravity), the researchers concluded that “it seems unlikely that they [the rooks] had an understanding of the unobservable causal properties of the task” (Seed



**Folk Physics, Fig. 1** Schematic of the trap-tube problem. Top panel illustrates tubes with functional traps. The arrow indicates the direction that the desired object (blue cube)

must travel to be retrieved. Bottom panel illustrates tubes with inverted (nonfunctional) traps. The desired object can be retrieved by moving it in either direction

et al. 2006, p. 700). Based on the success of the one rook that successfully solved both novel problems, the researchers suggested that although physical cognition may involve reasoning about unobservable forces, it could also consist simply of forming rules based on strictly observable features of a problem (Seed et al. 2006).

Great apes (gorillas, chimpanzees, bonobos, orangutans) presented with similar tasks designed to assess their understanding of the properties of the trap also learned to solve the problems, but did not transfer what they learned to novel tasks. The researchers concluded “that nonhuman great apes may know more about the relation between traps, rewards and tools than previously thought. This knowledge, however, may be task specific and may not easily permeate across tasks, perhaps due to a limitation in apes’ analogical reasoning abilities” (Martin-Ordas et al. 2008, p. 430).

These and other studies show that nonhuman animals can learn to solve problems with a trap whose action depends on gravity. What these studies demonstrate about nonhuman animals’ naturally-occurring understanding of their physical worlds is debatable. In most cases, animals are first trained to solve a problem, and doing so undermines the study of folk physics according to proponents of the programmatic-training-not-allowed approach. Also, adult humans who supposedly understand the underlying causal structure of simple tool-use tasks sometimes behave like other animals, which raises questions about the conceptual foundations of some studies of folk physics and the methods used to study it (see Silva and Silva 2006). In addition, although transfer tests are important methods for ascertaining what subjects have learned, the inability to generalize from one problem to another with similar unobservable properties may not reveal much about what an animal understands (Machado and Silva 2003). Generalization is often unlikely, even in humans, without explicit generalization training (Stokes and Baer 1977).

### Support

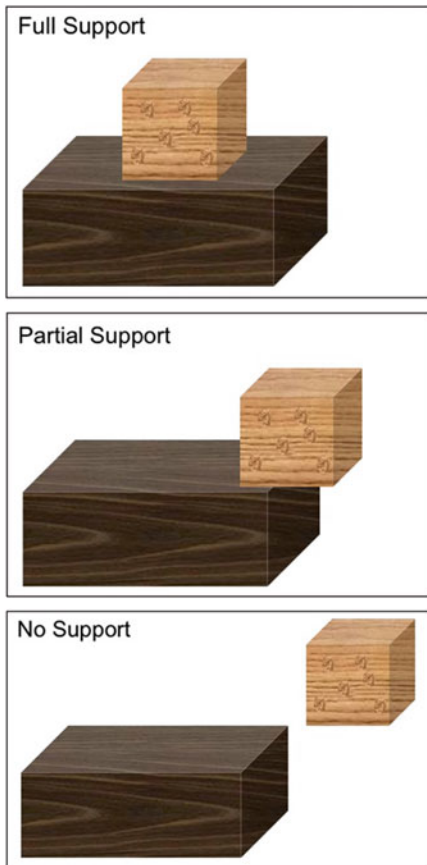
Jean Piaget’s (1952) support problem has been used to study both humans’ and animals’ understanding of means-end connections as related to physical support. This sort of problem consists of

a desired but out-of-reach object (e.g., a toy) that is placed on a supporting object (e.g., a blanket) that is within a subject’s reach. The desired object can thus be obtained by the subject pulling the blanket and dragging the object so that it is within reach.

In one variation, a chimpanzee is presented with the choice of pulling a blanket with a piece of food on it or pulling a blanket with a piece of food beside it. The ape should pull the first blanket if it understands the necessary relation between the supporting object and obtaining the desired object. Although some chimpanzees will make the correct choice without having been trained to do so, their behavior is controlled by what they see. As a result, these animals fail to solve transfer of training tests that are perceptually dissimilar but causally similar to the task they previously solved (Povinelli 2000). And the same appears to be true of dogs. Using a programmatic-training-allowed approach and novel tasks to assess the canines’ understanding of support, researchers discovered that dogs learn to solve support problems based on perceptual cues (i.e., what they see), not an understanding of the underlying (unobservable) causal structure (Müller et al. 2014). But, again, depending on a scientist’s or scholar’s definition of folk physics and the methods used to study it, the veracity of these conclusions is questionable.

People’s and animals’ understanding of support relations have also been studied using a violation-of-expectation paradigm, an approach that relies on habituation – a comparatively simple form of learning, but explicit training nonetheless. To test children’s folk physics related to support, a psychologist could present children with a stimulus that consists of a target object (e.g., an attractive box or a toy) and a platform (e.g., an inverted crate) that could support the target object. The target object might be placed completely on the platform (i.e., fully supported), partially on the platform (i.e., partially supported), “magically” floating next to the platform (i.e., unsupported), and in various other combinations to determine what children understand about the physical aspects of support (e.g., amount of contact, center of gravity) (see Fig. 2). What infants understand is assessed using a violation-of-expectation





**Folk Physics, Fig. 2** Schematic of support relations configurations. Top row: The target object (light cube) is fully supported by the platform (dark cube). Middle row: The target object is partially supported. Bottom row: The target object is unsupported

paradigm. The key feature of this paradigm is, after some training that consists of habituation, the measurement of the cumulative amount of time that a subject looked at several presentations of different configurations. If what a subject is looking at is inconsistent with her expectations about the physical world, she will be surprised by what she sees and will thus stare longer at the scene than if what she is looking at is consistent with her expectations. In the latter case, the configuration of the target object and the platform will not elicit surprise and thus the subject will spend less time looking at this scene. In short, because impossible configurations violate children's expectations, these configurations are more surprising and novel than possible configurations; the

more novel and surprising an event, the more time the child will spend looking at it.

Based on differences in looking times at different configurations (possible vs. impossible), psychologists have concluded that by 3 months of age, children's understanding of support is that the target object can be supported as long as it is in contact with the platform. Between 3 and 6.5 months of age, children become aware that the locus and amount of contact between the object and the platform are important determinants of the whether the object can be supported. Thus, by about 6.5 months of age, children expect the object to fall if a significant portion of its bottom surface is not in contact with the top of the platform (Baillargeon 1994).

When chimpanzees were shown video clips of objects in physically possible (e.g., a banana supported by a box) versus physically impossible (e.g., a banana floating in the air near a box) support relations, these animals spent more time looking at the impossible relations (e.g., Cacchione and Krist 2004). These results and others led Cacchione and Krist to conclude that chimpanzees have some expectations about support relations that are "based on the perceived contact relation between two objects, both qualitatively (contact vs. no contact) and quantitatively (sufficient vs. insufficient amount of contact)" (p. 147). Although these studies of people's and other animals' understanding of support deviate somewhat from the two major approaches for studying folk physics, there are questions about the validity of the violation-of-expectation approach (e.g., Clearfield and Westfahl 2006).

## Conclusion

The study of folk physics is controversial and fractious (Buckner 2013). The sources of these divisions are many: conflicts between camps of researchers characterized accurately or inaccurately as "overestimators" or "killjoys" of non-human animals' abilities, tensions about what is folk physics, disputes about the value of naturally-occurring learning versus programmatically-trained understanding, disagreements about the significance of understanding based on inferences

about what is seen versus what is unseen, debates about what are the right tests to assess different species' understanding of their physical worlds, and arguments about whether the existence of reasoning about unobserved forces can be reduced to simple "yes" or "no" answers. Add to this list philosophical debates about the role of language: Is it even reasonable for a nonverbal creature to infer abstract causes such as gravity or transfer or force (Machado and Silva 2003)? The philosopher Wittgenstein (1958) remarked, "We say a dog is afraid his master will beat him; but not, he is afraid his master will beat him tomorrow. Why not?" (p. 166e). It is because it seems impossible to learn the concept "tomorrow" effectively without language. The same may be true of concepts such as weight, gravity, and support. But folk physics need not be primarily about reasoning about unobservable forces (Seed et al. 2006). "Rule abstraction and the formation of representations based on observable features" [emphasis added] may explain why some animals "have the ability to form sophisticated cognitive solutions to physical problems in the absence of causal understanding of unobservable forces" [emphasis added] (Seed et al. 2006, p. 700). This sort of emphasis on reasoning about observable features provides a means of studying physical cognition using established methodologies from the study of concept learning and associated frameworks from which to compare the results (e.g., Vonk and MacDonald 2002; see also Zentall et al. 2014).

## Cross-References

- [Stone Tools](#)
- [Tool Use](#)
- [Trap-Tube Problem](#)

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## Follitropin Alfa

### ► FSH

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## Follitropin Beta

### ► FSH

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## Food

### ► Chondrichthyes Diet

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## Food Calls

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## Synonyms

Food-associated calls; Food-associated vocalizations; Food-related calls

## Definition

Vocalizations that are produced while foraging and/or feeding.

Food calls, also known as food-associated calls, occur in several animal species and are emitted upon discovering food and during foraging/feeding bouts (primates: *Cebus capucinus*, Boinski and Campbell 1996; *Cebus apella*, Di Bitetti 2003; *Ateles geoffroyi*, Chapman and Lefebvre 1990; *Saguinus oedipus*, Cleveland and Snowdon 1982; Roush and Snowdon 2000; *Saguinus labiatus*, Caine et al. 1995; *Callithrix jacchus*, Vitale et al. 2003; *Callithrix geoffroyi*, Kitzman and Caine 2009; *Leontopithecus rosalia*, Benz et al. 1992; *Cebuella pygmaea*, Pola and Snowdon 1975; *Macaca mulatta*, Hauser and Marler 1993; *Macaca sinica*, Dittus 1984; *Pan troglodytes*, Hauser et al. 1993; Wrangham 1977; *Pan paniscus*, van Krukowski et al. 1996; *Gorilla g. gorilla*, Luef et al. 2016; naked mole rats: *Heterocephalus glaber*, Judd and Sherman 1996; dolphins: *Tursiops truncatus*, Janik 2000; greater spear-nosed bats, *Phyllostomus hastatus*, Wilkinson and Boughman 1998; avian species: *Gallus domesticus*, Marler et al. 1986; Evans and Marler 1994; *Passer domesticus*, Elgar 1986a; *Hirundo pyrrhonota*, Brown et al. 1991; *Corvus corax*, Heinrich 1988; Heinrich and Marzluff 1991). In some species, food calls are a distinct call in the vocal repertoire (e.g., Geoffroy's marmoset, domestic chickens), whereas in others, the calls emitted in a feeding/

foraging context are also emitted in other nonfood-related contexts (e.g., toque and rhesus macaques, spider monkeys, red-bellied and golden-lion tamarins, bottlenose dolphins, and greater spear-nosed bats among others).

Food calls across species have a range of different functions (Clay et al. 2012). Only a few species have what are traditionally labeled “functionally referential” food calls. To be “functionally referential” (Macedonia and Evans 1993), calls first must be given exclusively in a feeding context and have a unique acoustic structure relative to other calls in the vocal repertoire (production criterion). Second, animals who hear the calls show feeding-related behaviors even in the absence of food (perception criterion). Calls of domestic chickens (Evans and Evans 1999) and Geoffroy’s marmosets (Kitzman and Caine 2009) fit the production and perception criteria for functional reference. Domestic chickens who hear playbacks of food calls will fixate downwards and search the substrate, both of which are anticipatory feeding behaviors (Evans and Evans 1999). Similarly, Geoffroy’s marmosets show more foraging and feeding behaviors following playbacks of food calls compared to control calls (Kitzman and Caine 2009). The question of whether calls contain information and/or are functionally referential has long been debated and there has been recent renewed interest in this issue (see Clay et al. 2012; Carazo and Font 2010; Rendall et al. 2009; Seyfarth et al. 2010; Wheeler and Fischer 2012).

## Function of Food Calls

There are a number different hypothesized functions of food calls. The information-sharing hypothesis suggests that calls attract individuals who are out of visual contact to inform others about the presence of food (Dittus 1984; Brown et al. 1991; Evans and Evans 1999; Hauser and Marler 1993; Vitale et al. 2003). In socially foraging species, such as cliff swallows (*Petrochelidon pyrrhonota*; Brown et al. 1991), it makes sense to inform others about food for group foraging; food calls attract conspecifics, which

results in more insects becoming available as they are stirred up by increased activity of more birds and tracking the swarm is more effective (Brown et al. 1991). Food calls also function to attract others who, in turn, help to monopolize food (ravens: Heinrich and Marzluff 1991; Wilkinson and Boughman 1998). For example, in ravens, “haa” food calls attract others who, in turn, help to cooperatively defend the food source (Heinrich and Marzluff 1991; see also Bugnyar et al. 2001). In these species, it is beneficial to attract others to increase efficient and successful foraging.

In other species, it is less clear why individuals would share information about food, given that it can come with a cost; experiments in tufted capuchins (*Cebus apella*) showed that individuals who called more quickly after finding food ultimately consumed less than individuals who had a longer latency to call (Di Bitetti and Janson 2001). In addition, in white-faced capuchins (*Cebus capucinus*), aggression can be high in feeding contexts; dominants can displace or attack subordinates to steal food or drive them from a feeding source (Perry 1996, 1997; Gros-Louis 2004a). Therefore, other functions of food calls have been proposed to explain the benefits to the signaler of calling.

Studies that have assessed why signalers produce food-associated calls has revealed a number of possible functions: to attract mates (bonobos: van Krunkelsven et al. 1996; chimpanzees: Kalan and Boesch 2015; domestic chickens: Evans and Marler 1994; Pizzari 2003; Marler et al. 1986b), to decrease predation risk (house sparrows: Elgar 1986b; red-bellied tamarins: Caine et al. 1995; Newman and Caraco 1989), and to regulate spacing between foraging individuals (big brown bats, *Eptesicus fuscus*, Wright 2014; pied babblers, *Turdoides bicolor*, Radford and Ridley 2008). For example, in white-faced capuchins, nearest neighbor distance increases following food calls, suggesting that food calls help to regulate spacing during foraging (white-faced capuchins, *Cebus capucinus*, Boinski and Campbell 1996). Furthermore, experimental studies found that calls are produced more in the presence of a higher ranking individual, which decreases the likelihood of the caller receiving aggression and/or

experiencing food theft. These findings were corroborated with focal observations (Gros-Louis 2004a). Thus, calls may serve to announce ownership, thereby decreasing aggression (see also Hauser and Marler 1993).

Recent studies that have explored social factors associated with calling have revealed more subtle functions. Male chimpanzees emit more food calls when social partners, particularly those who are higher ranking, are nearby and are proposed to serve to maintain affiliative relationships (Schel et al. 2013). Furthermore, individuals who hear food-associated calls (“receivers”) were more likely to remain in the food patch, suggesting that the calls function to maintain cohesion during prolonged feeding bouts with preferred partners (Fedurek and Slocombe 2013). By contrast, in Western chimpanzees (*Pan troglodytes verus*), researchers (Kalan and Boesch 2015) found that males produce more food calls when oestrus females are nearby, which serves to attract females to food sources thus increasing mating opportunities. Therefore, there might be different functions of food calls in different populations, which suggests flexibility in pragmatic use of calls, a new and fruitful research topic in primate communication (Scott-Phillips 2010; Wheeler and Fischer 2012).

Regardless of the possible function of food calls for signalers, individuals who hear the call can benefit by knowing the presence and location of a food source. This distinguishes different functions for signalers and recipients: if the probability of listeners hearing call A in context X is very high and, conversely, context X rarely occurs in the absence of call A, call A comes to have high predictive value of context X (for further discussion, see Seyfarth and Cheney 2003). Playback studies in white-faced and tufted capuchins demonstrated that individuals were more likely to approach when they heard food calls than when they heard control calls (Gros-Louis 2004b; see also Di Bitetti 2003). Observations in other species also support these findings (e.g., primates: *Ateles geoffroyi*, Chapman and Lefebvre 1990; *Macaca sinica*, Dittus 1984; dolphins: *Tursiops truncatus*, Janik 2000; greater spear-nosed bats: *Phyllostomus hastatus*, Wilkinson and Boughman

1998; avian species: *Gallus domesticus*, Marler et al. 1986a; *Passer domesticus*, Elgar 1986; *Corvus corax*, Heinrich 1988). Food calls thus can be considered a source of public information that indicates the presence of food (Valone 1996; Janik 2000).

## Effects of Food Quantity, Preference, and Quality

Studies have shown that food call rate and acoustic structure can vary as a function of food quality and food quantity. It is more common for call rate to vary rather than acoustic structure, suggesting that food calls may reflect arousal related to food quantity or quality, rather than something specific about the type of food. For example, East African chimpanzees call more when encountering large divisible food sources (Hauser et al. 1993). In addition, New World monkeys have been shown to produce more calls when encountering larger quantities of food and when they encounter fruit compared to other food types (Benz 1993; Caine et al. 1995; Elowson et al. 1991). These observations are consistent with findings in different species of capuchins (Boinski and Campbell 1996; Di Bitetti 2005; Gros-Louis 2004a; Robinson 1982), suggesting that call rate can increase with both food quantity and/or food quality. Rhesus macaques call at higher rates in the presence of high-quality food and call less for lower quality food (Hauser and Marler 1993). Ravens also produce a specific call (“haa” call) at higher rates when meat is discovered compared to other items. Therefore, calls may reflect a preference for presumably higher quality food, possibly mediated by arousal. Similarly, domestic chickens and white-tailed ptarmigan call more when they encounter better quality food (Marler et al. 1986a; Clarke 2010). In white-tailed ptarmigan, food calls are given proportionally more to higher protein foods, and chicks eat more of the items that receive food calls, suggesting a role in the development of diet selection (Clarke 2010; see also Wauters and Richard-Yris 2002).

Food call acoustic structure can vary as a function of individual food types and/or size of



feeding patch, although this pattern of call variation is less common (or less well studied). West African chimpanzees produce higher pitched calls for smaller trees, but also for preferred fruits. Furthermore, the pitch of calls produced for presumed preferred fruits varied as a function of patch size. Lower pitch calls were produced in larger patches and conspecifics tended to approach low-pitched calls (Kalan et al. 2015). Captive studies have also demonstrated that acoustic structure of food calls vary as a function of preference, with higher fundamental and peak frequencies also being produced in the presence of preferred food items (Slocombe and Zuberhubler 2006); however, the study on food preference associated with call variants has not been replicated in the wild. A recent study has also shown that rather than emitting different acoustic variants of a single call, bonobos combine calls into sequences in patterns that reflect individual food preferences and relate to the quality of food (Clay and Zuberbuhler 2009).

In summary, in a few species, food calls are a unique call in the vocal repertoire; more commonly, food calls are associated with feeding contexts but also occur in other contexts. Food calls rate and/or acoustic structure has been shown to vary with food quantity, quality, or preferences. In the few species in which food calls are produced only in feeding contexts, individuals perform specific foraging and feeding-related behaviors after they hear the call, whereas, in other species, food calls attract others, regulate spacing between foraging individuals, or relate to affiliative relationships. Because of the variability in call production and responses to food calls in different species, there are a range of hypothesized functions for food calls across taxa (see Clay et al. 2012).

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## Food Neophobia

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Food neophobia is a term established by Barnett (1958) for the fear of eating new food and hesitation to ingest it. It is common in many species, e.g., rats, mice, dogs, turtles, domestic ruminants, nonhuman primates, and some species of birds, such as crows or blue jays. This phenomenon was first observed and documented as early as in the eighteenth century, when a certain rat catcher observed that rats need to familiarize themselves with the food-bait before accepting it as food. Food neophobia is a specific type of neophobia, which is a fear-like response to a novel stimulus. However, this reaction to the novelty of edibles plays a crucial role in animals' survival. It is particularly relevant to omnivores/generalists, whose diet may be very broad but which need to distinguish between edible and inedible food. This problem is called "the generalist's dilemma" (Rozin 2000). Researchers claim that many animals will not eat unfamiliar food, when they first encounter it. This behavior may persist for several days and may be more pronounced in an unfamiliar environment. When an animal notices a novel object in its environment, it has to overcome the

initial fear of novelty and assess the properties of the object. Next, it has to recognize it as potential food and determine the consequences of consuming it. Novelty of food may be due to changes of food location, a container in which the food is presented, and food properties. The fear of a new container may be significantly stronger than food neophobia itself, which may suggest that animals assess any new food in two steps: first by assessing the novelty of an object and only then by assessing the food itself. Therefore, animals' responses to novel food result from an interaction of behaviors motivated by curiosity about the novel object's potential value and fear of possible threat or toxicity. However, if an animal overcomes its neophobia and the new food does not become associated with adverse bodily symptoms, the intake of food increases, and the preference for the particular feed persists (Barnett 1963, 2009). The hungrier the animal, the quicker it starts to eat unfamiliar food. Animals can develop an aversion to foods that cause illness even after a couple or dozen hours. It should be stressed, however, that food avoidance may be due not only to neophobia but also to the low palatability of a specific food item or individual food preferences. Food neophobia may be also mediated by prior subsequent food-related illness or conditioned taste aversion toward similar odors or flavors.

Although the neural mechanisms of food neophobia are still unknown, the brain structures that most probably take part in regulating its occurrence may be the gustatory cortex, the gustatory thalamus, and the medium nucleus of the amygdala.

Caution toward unfamiliar foods and preference for known sources of nutrition have an adaptive value. Individuals that enrich their diet with new items display an advantage over species specializing in one type of food only. However, while the environment offers many potential food sources, some food may be toxic or unpalatable. Studies carried out on wild-type rats (Modlinska et al. 2015; Modlinska and Stryjek 2016) show that the level of food neophobia depends on the developmental history of a specific individual.

It seems that animals that experience high levels of environmental variability on a daily basis do not develop food neophobia to the extent observed in animals living in stable conditions. Some researchers have suggested that pest control activities may have enhanced food neophobia in rats (Barnett 2005; Taylor and Thomas 1989). For example, food neophobia seems to be absent in Norway rats inhabiting landfills, where constant environmental changes provide ubiquitous contact with novelty of varying character and value (Barnett 1963). Absence of food neophobia has also been reported in a group of *Rattus norvegicus* that lived on an isolated island for over a century (Taylor and Thomas 1989). Therefore, the variability of the environment may result in a lower threshold for food neophobia. The behavioral plasticity in rats, as a response to changeable environmental conditions, suggests that the mechanisms underlying food neophobia must originate in ontogenesis and relate to ecological impacts. It may be concluded that environmental variability prompts omnivorous animals to reduce their food neophobia. In other species, however, the mechanisms underlying food neophobia may be related to the level of the animal's cognitive complexity, the group's social structure, and the level of complexity of social relations.

Relying on others' knowledge about palatability of foods, copying ingestive behaviors of other individuals, and following them to food sources reduce food neophobia by decreasing the uncertainty linked to food novelty. Food preferences of other group members provide information on which foods are safe to eat. By adopting those preferences, an animal decreases the risk of eating new foods and reduced the cost of individual learning by saving time that would otherwise be spent collecting information already accessed by other group members.

In animal ontogenetic development, the process of learning how to distinguish between food and other objects and selecting foods that are palatable is a key step. Studies on rats show that food neophobia in young individuals is expressed by avoidance of foods which they do not know.

At an early stage of an animal's life, it is one of the parents (the mother in most species) that provides information about palatable foods. In mammals, the first contact with the mother's diet occurs already in utero. By swallowing the amniotic fluid, these animals become familiar with the flavors and odors of food eaten by the mother. In this way, they obtain information about the types of food that are safe to consume and develop specific food preferences. This process continues at the suckling stage. The mother's milk is rich in flavors and odors of food she consumed. What is more, the odor of food the female ingested lingers on her mouth and fur.

After the weaning period, offspring stay in close proximity to their parent or parents and follow them to food sources. Consequently, young individuals ingest the same food as the parents and avoid foods that are not eaten by them. However, it must be stressed that juveniles do not learn which foods to avoid but rather develop preferences for the foods their parent ingest and are cautious toward any other potential feeds. Moreover, other adult group members have a major influence on food preferences in young animals by providing access to food sources and cues about properties of the types of food preferred by the group (Galef 1981). For example, in monkeys, youngsters spend most of their time close to adults, which, in addition to allowing them to passively familiarize themselves with foods consumed by the group, enables them to feed on other individuals' leftovers and to snatch pieces of food from other group members. In these species, adult individuals may also share their food with their offspring. Studies on capuchin monkeys show that the influence of the group on reducing the level of food neophobia is positively (asymptotically) correlated with the number of other individuals that are eating. An individual that has observed the behavior of the group eats more of the new food if the group is bigger (e.g., Visalberghi and Addessi 2000). A similar result was obtained in studies on rats (e.g., Galef et al. 1990).

Although neophobic behaviors may be triggered by basic phylogenetically shaped

mechanisms, the process of reducing or overcoming food neophobia seems to originate in learning, including various forms of social learning.

## Cross-References

- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Behavioral Flexibility](#)
- [Bennett G. Galef](#)
- [Maternal Behavior](#)
- [Neophobia](#)
- [Social Learning](#)
- [Taste Aversions](#)

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## Food Patch

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## Synonyms

[Artificial food patches](#); [Artificial foraging trays](#); [Foraging patches](#); [Foraging trays](#)

## Definition

Patch used to quantify one of an individual’s three foraging costs.

Artificial food patches have a wide variety of uses in the study of animal behavior. Optimal foraging theory (Charnov 1976; Stephens and Krebs 1986), specifically patch use theory (Brown 1988, 1992), provides a conceptual framework for understanding how food patches can be used to assess an individual’s foraging costs. Assuming an individual experiences diminishing returns while foraging in a depletable food patch, Brown’s (1988) model predicts that an optimal forager should cease foraging, in lieu of exploiting other patches or engaging in other activities, when its instantaneous patch harvest rate is equal to the sum of its metabolic, missed opportunity, and predation costs, which together form its foraging costs. When the amount of food within a patch is proportional to an individual’s harvest rate, the giving-up density (i.e., the resource density at the point at which an individual quits foraging in a patch) provides a surrogate of the patch quitting harvest rate. Therefore, the variation in giving-up densities across multiple food patches can be used to quantify changes in one of an individual’s foraging costs by holding two of the three foraging costs constant, often through experimental manipulation.

Proper construction and collection of artificial food patches is critical to ensure the giving-up densities collected are representative of the quitting harvest rate of the targeted species or



individual. Use of a substrate within the patch itself is necessary to generate diminishing harvest rates as the tray is depleted by the forager. In addition, all nontarget species must be excluded from foraging from patches either through physical construction or temporal availability. A habituation period where the targeted foragers are given time to locate and begin foraging within the food patches is required. The experimenter should the habituation period to ensure all nontarget species are excluded and, if necessary, to adjust the amount of food and/or substrate that is necessary to ensure the target forager is unable to forage the patch down to a zero density.

The use of artificial food patches to quantifying different aspects of an individual's foraging cost has been varied and widespread. Giving-up densities from artificial food patches have been shown to change appropriately in response to a forager's metabolic (Kotler et al. 1999), missed opportunity (Brown 1988), and predation costs (Schmidt et al. 2008).

## Cross-References

- [Foraging](#)
- [Optimal Foraging Theory](#)
- [Predation Risk](#)

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## Food Preference

- [Canine Diet](#)

## Food-Associated Calls

- [Food Calls](#)

## Food-Associated Vocalizations

- [Food Calls](#)

## Food-Caching Birds

- [Susan D Healy](#)

## Food-Related Calls

- [Food Calls](#)

## Footfall

- [Gait](#)

## Footlet

- [Cilia](#)

## Forage

- [Equine Diet](#)

## Foraging

- [Bovine Diet](#)
- [Crocodilia Diet](#)
- [Mustelidae Navigation](#)
- [Plantae](#)
- [Squamata Diet](#)
- [Susan D Healy](#)

## Foraging by Honeybees

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### Introduction

The foraging behavior of a honeybee colony (*Apis mellifera*, L.) represents one of the most sophisticated examples of cooperative behavior in the animal kingdom and has arisen as the evolutionary product of an unusual and highly complex social system. Honeybees are advanced eusocial insects, defined by overlapping generations, cooperative brood care, and reproductive division of labor. In each colony a single queen is almost always responsible for the vast majority of the reproductive output, with the functionally sterile workers (her daughters) helping to rear their sisters (other workers and new queens) and brothers (drones). The colony therefore functions as a single reproductive unit, with the workers sharing a common goal: to optimize foraging effort in a manner that allows the colony to grow in size until the entire group can reproduce by splitting, in a process known as swarming. Seeley (1989) and others have thus described the colony as a “superorganism” – an individual entity with many of the attributes of an organism, but itself composed of individual organisms. Consequently, a discussion of foraging behavior in this species must include both the behavior of the individual units, the workers, and the colony-level behavior of the “superorganism” as a whole as it efficiently

exploits the surrounding resources to sustain itself.

Honeybees are central place foragers. Although domestic colonies reside in hives that are managed by beekeepers, such hives mimic the hollow tree cavities that are the species’ natural nest sites. Inside the nest, the workers build sheets of vertical wax comb made up of hexagonal cells in which food is stored and brood (young bees) are reared. From that base, a subset of the workers, the foragers, leave to collect resources from the environment and bring them back to the nest. Tasks in the colony are allocated by age, with younger bees performing less risky tasks inside the nest such as nursing brood and food processing and switching to the more hazardous task of foraging toward the end of the lifespan. Foragers can travel up to approximately 14 km to collect food, although typically 95% of foraging trips are within 6 km in a temperate environment. This represents a foraging area of 100 km<sup>2</sup>, partially reflecting the enormous requirements of a colony typically comprising around 30,000 animals. This demand represents a considerable foraging challenge: a honeybee colony in a temperate climate must collect approximately 120 kg of nectar, 20 kg of pollen, 25 l of water, and 100 g of resin each year (Seeley 1995).

Nectar is the energy currency of the colony and is collected both to fuel the current activity of the bees and to store for the winter and other times of dearth (Abou-Shaara 2014). Nectar is concentrated by evaporating off much of the water content, then mixed with salivary enzymes and stored as honey. If nectar is freely available, a colony will continue to collect and store as much as its labor and space resources allow. Pollen provides the protein source, as well as containing lipids and vitamins, but can only be processed by nurse bees. These young bees digest the pollen collected by foragers and convert it to a protein-rich secretion called brood food from the hypopharyngeal glands in the head and fed to other bees by trophylaxis (transfer of liquid via the proboscis). In contrast to nectar, the colony does not collect pollen indefinitely, but instead maintains a stable amount that is sufficient to buffer the colony through periods when forage is unavailable.

Water is collected for honey dilution, particularly early in the season when the colony is utilizing stored honey and pollen, and for nest cooling by evaporation. Collected in much smaller quantities, resin is mixed with saliva to form a sticky substance called propolis and used to seal cracks in the nest cavity.

The main forage substances, nectar and pollen, are collected primarily from flowers (although sugar may also be collected from fruit, honeydew, or robbing other honeybee colonies). Floral resources are transitory, characterized by a constantly varying patchwork of profitable locations that change over time. Some species of plant only produce nectar at certain times of the day, different species come into bloom at different times, and patches may be depleted and replenished over varying periods. To efficiently exploit the resources available to it, a colony must track the locations and profitability of the forage landscape as it changes over time. Patches that have ceased to be rewarding must be abandoned, additional foragers must be recruited to more rewarding patches and a scouting effort must be maintained to gather information on new forage sites. In addition, a colony must preserve a sufficient amount of stored food as a buffer during times of dearth such as bad weather or poor nectar flow, balancing this against current nutritional demands of brood and adults and available storage space and processing labor. How honeybees have evolved to respond to this foraging challenge, both at the individual and colony level, is discussed below.

## Individual Foraging Behavior

In one foraging trip, a bee collects up to 15 mg of pollen or 30 mg of nectar (or a combination of both), often requiring visits to over 100 flowers. Efficient foraging at the individual level requires the integration of learning, sensory perception, adaptable flower handling behavior, and navigation.

### Locating and Collecting Forage Resources

Honeybees rely primarily on visual and olfactory perception to locate flowers in the environment. Bees have compound eyes made up of several

thousand functional units called ommatidia, resulting in visual resolution 100 times poorer than that of the human eye (Chittka and Raine 2006). Bee color vision is determined by the presence of three different color receptors in the ommatidia (ultraviolet [UV], green, and blue), allowing bees to perceive a visible spectrum spanning 300–650 nm, encompassing UV but not red light. Green light is particularly important for motion vision and detection of small targets. The polarization pattern of light can also be detected by bees using a narrow band of photodetectors on the dorsal region of the eyes (Kraft et al. 2011). Honeybee antennae contain at least 130 olfactory receptors, resulting in highly developed odor perception.

Learning about the visual and olfactory cues that identify the most rewarding flowers plays a critical role in maximizing honeybee foraging efficiency (Menzel and Muller 1996). Bees are able to quickly learn to associate the characteristics of flowers, such as color, shape, pattern, and odor, with reward, and will preferentially visit flower types that they learn to be more rewarding. In the laboratory, it has been shown that individuals are capable of learning not just about the physical properties of these cues, but also about the relationships between them. For example, individuals can learn concepts such as “the same as,” or “above/below.” Although the extent to which such abilities are put to use in the field has not yet been fully explored, it is clear that such “nonelemental learning” abilities have potential applications in optimizing foraging efficiency. Individuals also respond to information provided inadvertently by conspecifics in the field, including the visual presence of other feeding bees, which they use to identify both rewarding inflorescences and rewarding flower species. To minimize visits to flowers that other bees have recently drained, individuals typically avoid inflorescences where they detect cuticular hydrocarbons that have been inadvertently deposited by other foragers. Finally, there is some evidence that volatiles produced by stressed conspecifics might lead bees to avoid dangerous areas where other bees have been injured, since such volatiles have been shown to induce both aversion

responses and future avoidance of contextual stimuli in laboratory settings.

Although honeybees are generalist foragers, feeding from a broad range of species, a single individual commonly prefers one species during a foraging trip (Grüter and Ratnieks 2011). This may clearly be beneficial for the plant, increasing the probability that pollen from a conspecific will be transferred to its stigma resulting in pollination, but flower constancy may also be advantageous for the bee, increasing flower handling efficiency through honing skills on a specific floral morphology, or distributing a colony's foragers across different resources. However, visiting only one species in a mixed patch of flowers may have energetic costs associated with increased flight distance between flowers, and it has been suggested that flower constancy is a constraint due to limited memory capacity for floral characteristics. Nevertheless, the behavioral flexibility of flower constancy – for example, increasing fidelity when rewards are higher – suggests an adaptive basis.

As central place foragers, individual bees must find their way home at the end of a foraging bout. Foragers use a combination of path integration, celestial compass orientation, and landmark learning to navigate to resource patches and back to the nest (De Marco and Menzel 2005). Path integration involves integrating each successive vector of travel during a flight to produce a continuously updated distance and direction from the hive. Distance is measured by the bee using optic flow, i.e., the amount of visual information that passes the eye per unit time, on the outbound flight to the resource (Si et al. 2003), while the direction is measured using celestial cues from the sun and polarized light. Bees also use memory of landmarks as a spatial reference of nest location or as checkpoints along a route.

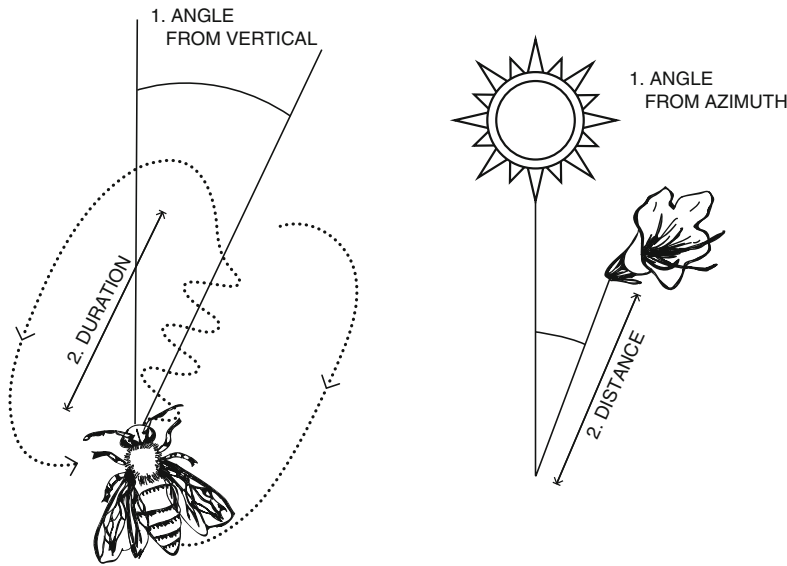
### Communicating Forage Information

In 1946, the Austrian ethologist Karl von Frisch made a discovery that would later lead him to be awarded a Nobel Prize in Physiology or Medicine (shared with Niko Tinbergen and Konrad Lorenz): that honeybee foragers can communicate to their nestmates the location of the resource which they have visited, in order to recruit other foragers to

exploit the same resource (von Frisch 1967). This highly evolved behavior, known as the waggle dance, represents perhaps the only known example of symbolic communication in a nonprimate species. On returning to the nest with pollen, nectar, or water from a particularly profitable source, a forager navigates to a part of the comb near the entrance, the “dance floor,” where unemployed foragers are waiting for information on the day's forage. Here she performs a distinctive figure-of-eight dance on the comb, vibrating her body laterally 12–15 times per second as she walks in a straight line (the waggle phase), then ceases vibrating and veers alternately to the left or right, looping back to the start (the return phase) to repeat the waggle run (Fig. 1). This dance encodes three pieces of information about the resource: distance, direction, and quality (Couvillon 2012).

The vector (distance and direction) information is contained in the waggle phase. The distance of the resource from the nest is encoded in the length of time that the bee vibrates her body, with a linear relationship between duration and distance. Dances for locations that are very close to the hive elicit such short waggle runs that often no vibration is present, resulting in an erratic truncated dance called the round dance, now widely accepted as an extremely short waggle dance rather than a separate behavior (Gardner et al. 2008). Bees have a gravity-proprioceptive system involving sensory neurons in the neck hair plates, allowing the bee to direct her waggle run at a specific angle relative to gravity. This corresponds to the angle from the current solar azimuth at which the resource is located, measured from celestial compass information. A bee may continue dancing over sufficient time for the sun's position to have moved, rendering the original dance angle inaccurate; however, the integration of endogenous circadian clock information allows a dancer to extrapolate the current azimuth without leaving the nest, modifying her angle to track the sun's position over time.

A combination of tactile input via antennation of the dancer's abdomen and perception of directional jet air flows produced by the oscillation of the dancer's wings allow bees following the dance to determine the angle and duration in the



**Foraging by Honeybees, Fig. 1** The honeybee waggle dance. A forager returning from a profitable resource such as a flower patch informs her nestmates of the location of the resource by performing a distinctive figure-of-eight dance on the comb (*left*). Two pieces of information are encoded in the dance (*right*): (1) the angle from the solar

azimuth, encoded in the angle of the waggle run with respect to gravity; and (2) the distance from the nest, encoded in the length of time for which the bee vibrates her body. This forms a vector allowing unemployed foragers following the dance to locate the resource

darkness of the hive (Gil and De Marco 2010; Michelsen 2003). These two pieces of information form a vector that is theoretically sufficient for nestmates to locate the resource. However, there is considerable variation between different runs within a single dance, meaning that the dance does not signify a precise location. Could this error be adaptive? Floral resources rarely consist of a single point in space, and researchers have theorized that the error has evolved to optimally spread foragers across large patches of flowers. Accordingly, angular variation decreases with increasing communicated distance, consistent with recruits being spread across even-sized patches at near and far distances. Yet there is also considerable evidence to the contrary, suggesting that dance angle variation is driven by biophysical constraints: for example, error is reduced when dancers have a direct view of the sun, when dancing parallel to gravity or when return phases are longer (Preece and Beekman 2014). To minimize the effects of this error, it appears dance followers take an average of several

runs, with recruits that follow more runs locating the site more accurately.

Not all foraging resources are of equal quality: nectar concentration and volume, distance from the nest, floral density, and risk of predation or competition all contribute to the profitability of a resource (Abbott and Dukas 2009). The third piece of information encoded in the dance concerns resource quality, primarily in the form of the number of waggle runs performed. Bees may perform between 1 and 100 runs within a single dance, with a linear relationship between number of runs and resource quality. The rate of waggle runs per unit time, modified by altering the duration of the return phase, is also correlated with quality. A forager's measure of profitability is based on two sets of variables: features of the resource itself and the current forage supply and demand of the colony. For nectar sources, resource variables include sugar concentration; while all bees show a linear relationship (up to the point where viscosity limits profitability) between runs and sugar concentration, individual



assessment varies widely between bees, reflected in differences in the slope of the relationship and the concentration threshold that elicits dancing. Sugar concentration is combined with the energetic cost of the flight (related to distance, but not measured using optic flow) to calculate the energy efficiency of exploiting a resource and it is this in addition to risk that informs a bee's assessment of the objective quality of a resource.

In contrast to nectar, it is likely that bees cannot assess the protein content of pollen (Beekman et al. 2016). Assessment of relative profitability in the context of current overall forage influx into the colony and processing capacity is discussed below. Combining these variables results in a final integrated assessment of quality encoded in the run number and intensity. However, unlike the vector information, this is not directly perceived by dance followers, who only follow a small proportion of the runs of any dance. Instead, this forms part of the elegant system of feedback loops regulating forage intake at the colony level described below.

### Colony-Level Foraging Behavior

We have seen that the individual forager possesses a suite of complex behavioral traits that allow her to efficiently locate flower patches, collect resources, and communicate their location on return to the nest. How are these individual endeavors integrated at the colony level, to spread labor across the foraging landscape, tightly control the influx of resources and regulate the balance between collection and processing of food? Like the human body, a honeybee colony must regulate its energy intake and expenditure, maintaining a complex array of homeostatic processes that depend upon extensive information flow between its units, the individual bees. No single individual or group possesses global information about all the processes occurring in the colony. Rather, each individual responds to local information according to a set of simple rules, resulting in a self-organized system that is capable of responding flexibly to environmental conditions and making adaptive decisions in its own

right. Information flow in the colony consists of a combination of signals (behaviors that have evolved specifically to convey information) and cues (provided inadvertently, as a byproduct of other behavior) (Seeley 1998). One example of a signal, the waggle dance, has already been discussed; in the following section, we present a further array of signals and cues involved in the regulation of foraging at the colony level.

### Spreading Labor Across the Foraging Landscape

At its strongest, a honeybee colony may contain up to 60,000 workers. This labor market must be effectively distributed across the major behavioral roles – cleaners, nurses, food storers, and foragers – and even across subdivisions within those groups, such as pollen or nectar foraging, scouting, or dance following. The proportion of workers involved in each task must be balanced with the supply and demand of brood and forage, and coordinated with other roles; it does not work to have large numbers of successful nectar foragers returning if there are insufficient food storers to receive their loads. At the highest level, behavioral tasks are allocated by age: newly emerged bees clean cells, the second youngest care for brood, middle-aged bees process food and perform other in-nest tasks and the oldest bees forage. This age polyethism potentially maximizes worker longevity, with the task involving the highest associated mortality, foraging, allocated to bees close to the end of their natural lifespans. The age of transition is flexible and can respond to changes in colony requirements. Within the forager caste, an individual's propensity to collect pollen, nectar, or water is associated with sensitivity to sucrose; bees with low, medium, and high sucrose response thresholds preferentially forage for water, pollen, and nectar respectively. This variation is thought to be adaptive at the colony level, facilitating division of labor.

At any one time, around a quarter of the colony workforce are foragers. Those not currently employed in exploiting a resource, due to the abandonment of a no longer rewarding patch or just beginning their foraging career, may be

allocated to a patch in a number of ways. A small proportion of foragers will be scouts, exploring the environment in search of novel food sources. The remaining foragers may use memory of previously visited patches, or social information to locate resources. Social information about foraging locations comes in the form of waggle dances or via olfactory information from floral odor carried on dancers' bodies or in nectar samples transferred to followers (trophallaxis). At any time on the dance floor, several dancers may be advertising multiple different locations. How does a forager choose which location to visit? As previously described, the dancer encodes the profitability of the resource in the number of waggle runs performed. One solution would be for a follower to survey many of the dances and select the one communicating the highest quality. However, such a system would not only require extensive dance sampling effort on the part of dance followers, but also necessitate measurement and comparison of the number of runs that each dancer performs. Instead, a much simpler self-organized system has evolved to achieve the same end, based on each worker responding to a small amount of local information rather than collecting global information. A dance follower has no perception of the quality encoded in the dance, and thus she may well select and follow a dance not advertising the most profitable site available. However, because dances for higher quality sites contain more runs, the number of bees that encounter these dances is higher. As such, the number of recruits to a resource is proportional to the number of waggle runs performed for it. In addition, more profitable resources are more likely to elicit dances in the first place. This ensures an appropriate distribution of foragers across sites, relative to their quality, and allows the colony to rapidly track changes in profitability.

A surprisingly low proportion of dance followers visit the advertised site. The location encoded in the waggle dance (a signal) is not the only piece of information provided by dancing bees, and the floral odor carried by dancers (a cue) may take precedence over the location information conveyed by the dance (Grüter and Farina 2009). If the odor is from a flower species a

follower has experience with, this can reactivate the memory of a previously visited forage patch, creating a conflict between personal memory and social information about forage locations encoded in the dance (Grüter et al. 2008). There is evidence that in this scenario bees preferentially rely upon their own location memories, but increase their use of waggle dance information when those sites become unrewarding. As foragers age, they rely less on waggle dance information and more on private memory. Unemployed foragers may also follow a dance for confirmation of the continued profitability of a previously visited site. In practice, only 12–25% of dances are followed for the discovery of new sites, with the remaining associated with reactivation to known resources (Biesmeijer and Seeley 2005).

### Regulating Nectar Influx

Collection of resources must be coordinated with the colony's current requirements. Returning nectar foragers must decide whether to recruit additional foragers to a patch, given the current availability of other sources. Rather than collecting direct, global information about the entire colony's nectar influx, returning foragers use an indirect cue in the form of the time it takes to unload their nectar load. If nectar influx is currently low, there will be several unemployed food-storer bees waiting to receive nectar, so unloading time will be short. If nectar influx is high, a returning forager may have to queue to unload. The precision of this measurement is increased by making multiple transfers of portions of the load; the average unloading delay informs the forager about the colony's nectar influx. Although her objective assessment of the quality (sugar concentration, distance, and risk) of the resource does not change, this information about nectar influx alters the quality threshold that elicits a dance and the intercept of the relationship between quality and number of runs. Therefore, a low-quality resource that would elicit many waggle runs during a time of dearth may not elicit any dancing at all during peak nectar flow.

In addition to the waggle dance, several other movement signals have evolved to regulate the balance between nectar collection and processing.

Unloading delay is also used by returning foragers to perceive a need for increased food processing effort. A long delay increases the probability that the returning forager will subsequently perform a “tremble dance,” which stimulates nest bees to become food-storers and inhibits waggle dances in other returning foragers (Biesmeijer 2003b). A bee shaking a nestmate by grasping her with her legs and vibrating her body forms a more general, context-dependent signal to encourage reassessment of current activity (Biesmeijer 2003a). An inhibitory signal, the stop signal, is also now known to be used by foragers and dance followers to interrupt dancers advertising a site known to be associated with danger from predation or competitive aggression or to be no longer rewarding (Nieh 2010).

### Homeostatic Control of Pollen Stores

As discussed above, the only limits to the amount of nectar a honeybee colony extracts from its environment are the labor available to collect and process it and the space available for storage. In contrast, a colony maintains a limited stable pollen store that requires precise homeostatic control (Schmickl and Crailsheim 2004). Thus, instead of being driven primarily by supply, pollen foraging is also driven by demand. Pollen demand changes with the amount of brood present and supply changes with the foraging conditions; regulation needs to integrate both these variables. How pollen stores are homeostatically controlled has been subject to considerable debate and research effort, with two main theories posited: (1) the direct, independent hypothesis, and (2) the brood food hypothesis.

The direct, independent hypothesis suggests that the global status of pollen supply and demand are measured directly by returning foragers. Quantity of stored pollen (supply) may be measured by the time taken to find an empty cell; unlike nectar, pollen is deposited directly into cells by foragers. Amount of brood (pollen demand) may be measured by brood pheromone levels in the nest, which may be either an evolved signal or an incidental cue. According to this theory, foragers integrate these pieces of

information to assess the need to collect pollen. Some evidence in support of this exists: brood pheromone has been shown to affect pollen foraging activity and returning pollen foragers perform cell inspections (Dreller et al. 1999). The alternative theory suggests that an indirect cue – the protein content of the hypopharyngeal secretions (“brood food”) fed by nurse bees to all workers – gives information on the combined pollen supply and demand. In times of protein scarcity, either due to increased brood or reduced pollen stores, low protein content in the brood food fed to foragers would stimulate increased pollen foraging. Research has shown that separating foragers from the pollen stores with a screen does not disrupt pollen store homeostasis (Camazine 1993), suggesting that direct contact with stores is not required, and an inhibitory effect of trophallaxis on pollen foragers has also been found (Camazine et al. 1998). However, experiments using a protease inhibitor to artificially lower brood food protein content have found no evidence for the brood food hypothesis (Sagili and Pankiw 2007). The two hypotheses are not mutually exclusive, and it is likely that a combination of direct and indirect cues are involved in regulation of pollen storage.

### Conclusion

In any animal species, foraging behavior is under intense selection pressure. The ability of an individual to successfully extract energy and nutrition from its environment while minimizing hazards and metabolic costs is a strong driver of fitness. The honeybee is no exception: natural selection has shaped individual foraging behavior such that a bee can locate flower patches, efficiently collect nectar and pollen and remember the locations and characteristics of profitable resources. However, the honeybee differs from most other taxa in that selection has also acted strongly upon foraging behavior at another level of biological organization: the colony. The behavior of the “superorganism” has evolved such that the colony acts as a static reproductive unit from which

individual parts can be deployed to collect resources from its surroundings. As such, selection has favored maximizing the energy balance and nutritional regulation of the colony as a whole. Intricate networks of information flow via communication signals and cues coupled with a suite of behavioral rules at the individual level in response to local information results in a highly complex self-organized foraging system. In this way, the honeybee colony provides an intriguing comparative model for nutritional regulation and sensory perception in analogous self-organized systems such as the human body, on a macroscopic scale.

## Cross-References

- ▶ [Altruism](#)
- ▶ [Central Place Foraging](#)
- ▶ [Cooperation](#)
- ▶ [Feeding](#)
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## Foraging Patches

- [Food Patch](#)

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## Foraging Trays

- [Food Patch](#)

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## Force

- [Newton’s Third Law](#)

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## Forced Copulation

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## Synonyms

[Rape](#); [Sexual coercion](#)

## Definitions

Forced copulation occurs when a male forces sexual intercourse on an apparently resistant female. Gang rape occurs when two or more males force copulation on a female at the same time. Sexual coercion refers to unwanted copulations within an established pair-bond. Extra-pair copulations refer to matings that occur outside of a pair-bond.

## Introduction

Forced copulation occurs in many species, including birds, insects, and mammals – including humans (Baker 2020/1996; Baker and Bellis 2014/1995; Goetz and Shackelford 2006; McKinney et al. 1983). Gang rape also occurs in many species, including birds, butterflies, and humans (Baker 2020/1996; Baker and Bellis 2014/1995; McKinney et al. 1983). Rates of forced copulation typically increase during times of stress, such as during warfare in humans (Baker and Bellis 2014/1995). Forced copulation may have evolved because it increased the coercive male’s reproductive success (Baker 2020/1996; Baker and Bellis 2014/1995; Cheng



et al. 1982; Goetz and Shackelford 2006; McKinney et al. 1983), or forced copulation may be a by-product of male adaptations that motivate desire for sexual variety and the use of aggression to secure desired resources (Goetz and Shackelford 2006).

### Tactics Used in Forced Copulation

Males attempt to force females to copulate using various tactics such as chasing after or confronting the female. For example, in many species of birds, males chase the female before mounting her, apparently against her will (Cheng et al. 1982). Once the male has the female in possession, he grasps part of the female's feathers with his beak and places his wings on both sides of the female's body to prevent her from escaping (McKinney et al. 1983). Male minks that engage in forced copulation initiate physical fighting with the female because pre-copulatory fighting may induce ovulation, increasing the likelihood of conception (Baker and Bellis 2014/1995). In several species of birds, males are more likely to pursue forced copulation with more fertile females that recently produced a healthy clutch with another male. The male perpetrator typically attacks the female in the mornings, shortly after she lays her eggs and when she is most fertile, and early in the breeding season (Baker 2020/1996; Cheng et al. 1982).

In some species, males may compensate for smaller-than-average body size by utilizing specialized body parts that aid in trapping the female for copulation. Male scorpion flies, for example, use a special hook on their wings to grip and secure the female and then force copulation (Baker 2020/1996). In some species, including ducks, birds, and butterflies, males engage in gang rape when they are unsuccessful at mating without the assistance of other males. Gang rape involves males coordinating different roles and rotating for sexual access to the female. For example, some male ducks chase the female, other males guard her from escaping, and one male forces copulation with the female (Baker 2020/1996).

### Reasons for Forced Copulation

Males of some species apparently force copulation as a reproductive strategy. In many species, most males that engage in forced copulation do not fail at consensual copulations and neither are they disadvantaged; rather, these males pursue forced copulation and gang rape as additional copulations and select and pursue females that are attractive and at peak fertility (Baker 2020/1996; Baker and Bellis 2014/1995). However, males in other species, such as in scorpion flies, force copulation as a reproductive strategy to compensate for disadvantages such as small size or failed mating success (Baker and Bellis 2014/1995). Reproductively disadvantaged males are more likely to engage in gang rape because the female is less likely to escape than if the male were to attempt to force copulation on his own (Baker and Bellis 2014/1995).

Males are more likely to force copulation via sexual coercion when infidelity occurs or the male suspects his long-term partner's infidelity. Sexual coercion occurs in many socially monogamous species, such as humans, birds, and a few mammals, in which males force copulation with their regular partner in response to threatened paternity. Females that engage in extra-pair copulations promote sperm competition among the males they mate with, thereby threatening their regular partner's paternity certainty – the degree to which a male is certain that his partner's offspring are genetically his own. Sperm competition occurs when more than one male's sperm is present in a female's reproductive tract and compete to fertilize available ova (Goetz and Shackelford 2006). Thus, a mated human male may force his partner to copulate if he suspects an extra-pair copulation occurred to increase his paternity certainty, punish his partner, or prevent future infidelities (Baker 2020/1996; Baker and Bellis 2014/1995; Goetz and Shackelford 2006).

### Costs and Benefits for the Perpetrator

Various types of forced copulation, such as gang rape and sexual coercion, involve sexual conflict

and entail costs. For instance, males who force females to copulate risk being injured or killed by the female if she resists (Baker 2020/1996). Furthermore, the male's safety is threatened by other individuals who discover the female is in danger and attack the perpetrator (Baker 2020/1996; McKinney et al. 1983). Regarding gang rape, males risk losing the competition to inseminate and fertilize the female (Baker 2020/1996; Baker and Bellis 2014/1995; McKinney et al. 1983).

Although forced copulation can be a reproductive strategy, males may fail to reproduce using this tactic. On the other hand, males may successfully produce offspring by forcing copulation. Females may be more likely to conceive via forced copulation than consensual copulation, and considering males typically target victims of higher reproductive value, offspring are more likely to inherit "good" genes, survive, and be successful at mating, thus benefiting the reproductive success of the male that forced copulation (Baker 2020/1996; Baker and Bellis 2014/1995; Cheng et al. 1982; McKinney et al. 1983). Considering males often abandon the female after forcing copulation, males who successfully reproduce via this strategy incur the benefits of not having to invest time or resources in the female and her offspring (Baker and Bellis 2014/1995), thus allowing the male more opportunities to increase his reproductive success.

### Costs and Benefits for the Victim

Female victims of forced copulation are at risk for being injured or killed by the perpetrator (Baker 2020/1996; Baker and Bellis 2014/1995) and human victims often suffer negative psychological and physical health outcomes (Goetz and Shackelford 2006). Females may incur the costs of rearing resulting offspring with no paternal investment if the perpetrator abandons her after forcing copulation (Baker 2020/1996), thereby reducing her reproductive success. A female's reproductive success may also be hindered if her offspring inherit low-quality genes (Baker 2020/1996), because the offspring may be less likely to survive or be less successful at producing

offspring and thereby fail to transmit the mother's genes. However, females also may benefit reproductively by producing offspring sired by forced copulation, because these offspring may also be successful at transmitting genes through forced copulation (Baker and Bellis 2014/1995).

### Conclusion

Among many species, forced copulation by the male is not uncommon and may be used as a reproductive strategy. Tactics for successfully forcing copulation include chasing, holding down, and harming the female. Males that force copulation may be disadvantaged for success in mating, sperm competition, or infidelity. Male perpetrators risk being physically harmed and not producing offspring by forcing copulation but may sometimes be reproductively successful by producing offspring without the costs of investing time and resources in the female or resulting offspring. Female victims are at risk of harm by being forced into copulation, and then abandoned, but may benefit by producing offspring who are successful at transmitting their genes.

### Cross-References

- Aggression
- Benefits for Aggression in Humans
- Extra-Pair Copulation
- Mate Guarding
- Reproduction

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## Forced Desynchrony

- [Free-Running Cycle](#)

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## Form

- [Canine Morphology](#)

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## Fowl

- [Waterfowl](#)

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## Framing

- [Metacommunication](#)

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## Framing Effects

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### Introduction to Framing Effects

The way that information is presented systematically changes perceptions of and reactions to that information, even when the details remain objectively equivalent. These perceptual shifts subsequently alter judgments and decisions. Traditional

models of decision-making suggest that people make rational choices based on showing consistency and coherence in their decision making (cf. Kahneman and Tversky, *Journal of the Econometric Society*, 47(2), 263–291, 1979; Tversky and Kahneman, *Science*, 211(4481), 453–458, 1981). In other words, rational models propose that people will select the same choice option across different contexts. However, a vast literature has shown that *framing effects*, where different message frames change and even reverse people's judgments and decisions about equivalent choice problems, aid in our understanding of the decision process (cf. Kahneman and Tversky, *Econometrica: Journal of the Econometric Society*, 47(2), 263–291, 1979; Kahneman and Tversky, *American Psychologist*, 39(4), 341–350, 1984; Levin et al., *Organizational Behavior and Human Decision Processes*, 76(2), 149–188, 1998; Tversky and Kahneman, *Science*, 211(4481), 453–458, 1981).

Much of the literature on framing effects has dealt specifically with people's evaluations of risky choice options (e.g., gambles) and how differences in the framing of these options influence the way that risk is evaluated in decision-making. Risky choice problems require the decision maker to choose between either a sure outcome (i.e., certain to win or lose a specific amount) or a risky gamble where the outcome is uncertain (i.e., there is a chance you could either win or lose). When faced with a risky choice context, individuals evaluate the available information relative to a reference point. Individuals systematically become more risk-averse or risk-seeking based on whether the decision problem is framed as a gain or loss, relative to that reference point. However, other judgment and choice contexts that do not necessarily involve risk are also susceptible to the influence of framing (cf. Levin et al., *Organizational Behavior and Human Decision Processes*, 76(2), 149–188, 1998).

This entry outlines some of the essential literature on framing effects in judgment and decision-making. In doing so, it explores how framing influences risky decisions, explores the influence of emotions on framing effects, examines the neural correlates of framing effects and how framing effects have been demonstrated in nonhuman

animals, addresses framing beyond risky choice problems, and discusses real-world situations in which people may be susceptible to framing effects.

## Framing Effects in Risky Choice: Gain and Loss Frames

Framing effects have traditionally been studied in the context of gain and loss messages. A message is believed to be in a “gain frame” when an outcome is portrayed in terms of benefits (e.g., number of lives *saved*), whereas a “loss frame” describes when that outcome is portrayed in terms of costs (e.g., number of lives *lost*). For example, in a traditional risk task known as the Asian disease problem (cf. Kahneman and Tversky 1979, 1984; Tversky and Kahneman 1981), people are presented with the following scenario:

Imagine that the U.S. is preparing for the outbreak of an unusual Asian disease, which is expected to kill 600 people. Two alternative programs to combat the disease have been proposed. Assume that the exact scientific estimates of the consequences of the programs are as follows:

Half of subjects are presented with a *gain frame*:

- If Program A is adopted, 200 people will be saved. (*Sure gain*)
- If Program B is adopted, there is a one-third probability that 600 people will be saved and a two-thirds probability that no people will be saved. (*Risky gamble*)

Half of subjects are presented with a *loss frame*:

- If Program C is adopted, 400 people will die. (*Sure loss*)
- If Program D is adopted, there is a one-third probability that nobody will die and a two-thirds probability that 600 people will die. (*Risky gamble*)

Note that the proportion of lives saved versus lives lost is equivalent in both the gain and loss frame scenarios (i.e., the expected value of selecting either option is the same). However, people who view the Asian disease problem in the “gain frame” become more risk averse because they focus on how many lives will be saved (Kahneman and Tversky 1984). In other words, viewing the problem in a gain frame increases the likelihood that the decision-maker will select Program A, where 200 people will be saved for

sure. On the other hand, individuals who view this problem in the “loss frame” tend to focus on the sure losses incurred and consequently become more risk seeking. That is, the decision-maker in the loss frame is more likely to select the risky gamble outlined in Program D, where there is a 2/3 probability that nobody will die but also a 1/3 probability that all 600 people will die (Kahneman and Tversky 1984).

This choice reversal, termed the “reflection effect,” is also observed in simple numeric gambles involving risk (cf. Kahneman and Tversky 1979). These seemingly counterintuitive effects arise because people exposed to a loss frame are more willing to gamble in order to avoid a sure loss (i.e., become more risk seeking) (cf. Kahneman and Tversky 1979). This also highlights the concept of loss aversion, whereby people tend to prefer avoiding a loss over acquiring equivalent gains. Consequently, in a gain frame, people will avoid the gamble to ensure that they gain something (i.e., become more risk averse).

## Emotion and Framing Effects

Emotion interplays with decision-making to influence behavior in a variety of ways (cf. Lerner et al. 2015), and several behavioral studies have shown that emotions modulate framing effects. Research examining the relationship between affective valence (i.e., positive or negative feelings) and framing effects suggests that inducing positive feeling states reduces loss aversion, and this ameliorates framing effects such that people no longer change their choice based on whether the decision problem is framed as a loss or a gain (Cassotti et al. 2012).

Other work examining discrete emotions suggests that distress (Druckman and McDermott 2008) and fear (Lecheler et al. 2013) increase framing effects, whereas anger decreases framing effects (Druckman and McDermott 2008; Lecheler et al. 2013). Contentment has also been found to reduce framing effects (Lecheler et al. 2013), and enthusiasm produces mixed results where for some scenarios it decreases framing

effects (Druckman and McDermott 2008; Lecheler et al. 2013) and for others it does not (Druckman and McDermott 2008). Thus, to gain a more complete understanding of the interplay between emotion and framing effects, it is critical to study not only positive or negative valence but to also investigate how discrete emotions differentially influence people's reactions to message frames.

Future behavioral examinations will be critical as discrete emotions often vary based on perceptions of situational certainty. For example, fear is marked by low situational certainty appraisals, and anger is marked by high situational certainty appraisals (cf. Lerner and Keltner 2001). Seeing a snake can make people feel uncertain about the safety in the situation and thus lead them to experience fear. On the other hand, when encountering a rude person, an individual may feel certain that the rude person's behavior was unjust and consequently experience anger. The "cognitive appraisal" of certainty is especially useful in the assessment of risk (cf. Lerner and Keltner 2001), as fear has been shown to systematically increase risk aversion (e.g., run away from the snake) and anger to systematically increase risk-seeking behavior (e.g., yell at the rude person). Examinations of the influence of emotional states on the framing of risky choice options warrant additional research.

## Neural Correlates of Framing Effects

A growing literature within the field of decision neuroscience has sought to uncover the neural mechanisms underlying framing effects. Consistent with behavioral findings, neural regions associated with emotion and reinforcement learning have also been implicated in framing effects (De Martino et al. 2010; Deppe et al. 2007; Windmann et al. 2006; Zheng et al. 2010). For instance, De Martino and colleagues (2006) found that framing effects were associated with amygdala activity. The amygdala is a region of the brain commonly associated with salience, value-related prediction and learning, and the processing of emotional information (cf. De Martino et al.

2006), and so this finding supports a link between the framing of risky choices and neural systems related to emotion. However, more recently, a study found that lesions to the bilateral amygdala did not significantly alter framing effect behavior (Talmi et al. 2012). These inconsistent findings suggest that the relationship between amygdala activation and framing effects warrants further exploration.

Greater activity of the orbital and medial prefrontal cortex (OMPFC), associated with reward processing and the integration of emotional information into decisions, was linked to lower susceptibility to framing effects (De Martino et al. 2010). Further, activation of the ventral medial prefrontal cortex (vmPFC), another region associated with the use of emotion in decision behavior, was correlated with people's susceptibility to message frames (Deppe et al. 2005). A similar pattern was found in activation of the anterior cingulate cortex (ACC), a neural region associated with the processing of information about positive and negative reinforcements (Deppe et al. 2007). Deppe et al. (2007) revealed that greater activation in the anterior cingulate cortex (ACC) predicted increased susceptibility to framing effects, suggesting a critical role for reinforcement learning in our understanding of framing effect biases. Taken together, these findings further support the importance of emotion systems in the processing of risky choice frames.

Other work has suggested that framing effects rely on a trade-off between the cognitive effort required to calculate expected values and the affect (e.g., emotion) associated with a particular choice option (Gonzalez et al. 2005). Results indicate that the cognitive effort required for participants to select a sure gain (e.g., in the Asian Disease problem described above, the 200 lives saved for sure) was less than for a risky gain (e.g., 1/3 chance of saving 600 lives, 2/3 chance of saving 0). However, the effort expenditures were equivalent for sure losses (e.g., 400 lives lost for sure) and risky losses (e.g., 1/3 chance nobody will die, 2/3 chance 600 will die). Gonzalez et al. (2005) further described neural associations between regions of the prefrontal and parietal cortices while people were making decisions



involving framing, which are brain regions typically involved in working memory and imagery processing.

Windmann et al. (2006) also examined the link between the medial and lateral orbitofrontal cortex (OFC) and sensitivity to information frames. Activation of the medial OFC has been associated with the detection of positive and negative affective valence, whereas activation of the lateral OFC is believed to represent the extent to which outcomes change (e.g., a gamble where lives are either saved or lost) or stay the same (e.g., lives are always lost or always gained). The lateral OFC was indeed found to be sensitive to the steadiness of outcomes and showed effects above and beyond activation of the medial OFC. These data indicate that both the processing of valence and outcome steadiness are important to our understanding of the neural mechanisms underlying framing effects (Windmann et al. 2006).

### **Risky Choice Framing Effects in Nonhuman Animals**

One consideration in understanding framing effects is whether the observed behaviors are specific to humans. For instance, it could be that cultural influences have led to an increased sensitivity to framing effects. It is, however, also plausible that contextually sensitive framing effect biases have more of a biological basis. One way to address this problem is to examine whether similar behaviors exist in nonhuman animals. Initial investigations suggest that framing effects are not limited to humans and can be observed in nonhuman primates (i.e., capuchin monkeys; Chen et al. 2006; Lakshminarayanan et al. 2008, 2011) and in birds (i.e., starlings; Marsh and Kacelnik 2002).

For example, in a recent demonstration, Lakshminarayanan et al. (2011) presented capuchin monkeys with tokens that could be traded for apple slices. Monkeys in the loss frame condition were presented with three apple slices as a reference point. Experimenter 1 always deducted one apple slice when given a token (i.e., sure loss), whereas Experimenter 2 either deducted two

apple slices or deducted no apple slices, at an equal rate (i.e., risky loss). Monkeys in the loss frame condition showed a preference for giving a token to Experimenter 2 (the risky loss), indicating risk-seeking decision behavior that parallels that of humans in a loss frame condition. In the gain frame condition, monkeys were presented with one apple slice as the reference point. Experimenter 1 always added one apple slice when given a token (i.e., sure gain), and Experimenter 2 either added two apple slices or added no apple slices, at an equal rate (i.e., risky gain). As with humans, monkeys in the gain frame showed a preference for giving the token to Experimenter 1 (the sure gain), indicating risk-averse decision behavior for gains.

Framing effects have also been observed in research on European starlings. Marsh and Kacelnik (2002) demonstrated that training birds to peck a symbol in exchange for food led to more risk-seeking behavior in the loss treatment. The starlings were more likely to peck the risky loss symbol that resulted in a loss of either one or five (out of a total of seven) pellets at an equal rate, over pecking the sure loss symbol where three (out of seven) pellets were always lost. Like the research on capuchin monkeys described earlier, the loss frame results parallel that of human choice behavior. In the gain frame treatment, however, where pecking one symbol always led to receiving three pellets (sure gain) and pecking an alternative symbol led to a gamble of receiving either one or five pellets, with equal chance (risky gain), there were no significant differences in the amount that starlings pecked one symbol over the other. Thus, unlike humans and capuchin monkeys, European starlings faced with a gain treatment were not more risk seeking.

Despite the lack of strong evidence for framing effects in the gain condition, starlings' response in the loss frame condition still suggests that a sensitivity to loss is present across species. Thus, changes in risk preference, particularly for losses, are indeed observable in nonhuman animals. Future mechanistic accounts of framing effects would benefit from continuing to explore this and other decision biases using both animal and human models.

## Framing Effects Beyond Risky Choices

While framing is critical to decisions involving risky choice probabilities, other information in a decision problem is also susceptible to framing effects. Levin et al. (1998) presented a taxonomy of framing manipulations organized into three distinct categories: risky choice framing, attribute framing, and goal framing.

**Risky Choice Framing.** As described throughout this entry, risky choice framing involves the consideration of choice options that differ in their level of risk. Risky choices include the comparison of simple monetary gambles or other risk scenarios, like the Asian disease problem, where framing the message to highlight gains or losses influences how risk averse or risk seeking the individual becomes.

**Attribute Framing.** In this type of framing, components of a decision (i.e., an attribute or feature) become the focus of the frame rather than the level of risk. For example, Levin and Gaeth (1988) showed that framing the quality of a ground beef as 75% lean (positive frame) versus 25% fat (negative frame) changed how positively or negatively people evaluated the beef on the attribute of its quality. Attribute framing highlights specific attributes as relatively “good” or “bad” and can be applied either to risky or to non-risky attributes in a decision problem (Levin et al. 1998).

**Goal Framing.** In this category, the goal of an action or behavior becomes the focus of the frame, and goal framing is commonly used in persuasion attempts. Goal framing becomes most relevant in contexts where the persuader aims to encourage people to engage in a behavior. The message of the goal can either take a positive frame and focus on the benefit of the action (e.g., women who do regular breast self-examinations (BSEs) have an increased chance of finding a tumor early; cf. Meyerowitz and Chaiken 1987) or take a negative frame and focus on its potential to prevent or avoid a loss (e.g., women who fail to do regular breast self-examinations (BSEs) have a decreased chance of finding a tumor early). Meyerowitz and Chaiken (1987) found that the negative goal frame is often more influential than the positive goal

frame in critical contexts, such as those often encountered when making healthcare decisions.

All three types of framing effects systematically influence decision behavior. Goal and attribute framing are distinguishable in that goal framing typically focuses on achieving the action or behavior (e.g., BSE), whereas in attribute framing, the attribute is framed as either good (75% lean) or bad (25% fat).

It should be noted, however, that framing effects have been shown to be more reliable for risky choice and attribute framing than for goal framing (Levin et al. 2002). Levin et al. (2002) suggest a plausible explanation that different processes underlie goal framing, such that goal frames will be less effective in cases where the goal is less critical or self-relevant to the decision maker.

## Framing Effects in Other Translational Settings

Framing effects also lead to differences in how people navigate decisions involving healthcare, politics, and financial decisions. Within the framing of risky medical decisions, gain-framed persuasion appeals are more effective when the message targets behaviors that prevent the onset of some disease, whereas loss-framed appeals are more effective when targeting behaviors that detect the presence of an existing disease (Rothman et al. 2006). Thus, the framing of risky health information critically depends on whether the decision is framed as being about prevention or detection of a health condition.

Politics are another critical choice domain in which a variety of message frames are used. Framing effects in political settings are important because the way a message is framed can influence long-term political candidate and policy voting decisions. In an investigation of the difference between message framing and persuasion in mass political communication, Nelson et al. (2001) provided empirical evidence of how framing and persuasion messages are differentially effective, depending on whether the goal is to activate or alter a person's belief system. Specifically,

framing was shown to function mostly by activating pre-existing cognitions and beliefs. Persuasion appeals, on the other hand, seek to add to or change something about a person's beliefs. Distinctions such as these are important to our understanding of how message framing affects decisions above and beyond basic persuasion attempts.

Choice diversification (i.e., diversifying across several choice options) in financial decision-making is also susceptible to the effects of framing. For example, Fox et al. (2005) examined the implications of choice diversification using a framing technique called "partition dependence." In partition dependence, if the choice/option sets are subjectively partitioned in different ways, then choices and allocations will vary systematically with those partitions. For example, when an individual donates to a charity that is grouped (i.e., partitioned) by domestic and international, they might diversify by allocating half of their charitable contributions based on this grouping. If, however, these same charities are grouped by local, national, and international, a person who allocates their money evenly across the three groups will consequently donate more to domestic than to international causes. Fox et al. (2005) found that partition dependence occurs across domains, particularly when decision-makers lack expertise or strong intrinsic preferences. These partition effects are observed even in competitive prediction markets (i.e., financial, sports, weather), including when informed traders are incentivized to bet on their beliefs about events (Sonnemann et al. 2013).

## Conclusion

In sum, framing effects systematically influence judgments and decisions across a variety of contexts. The findings described in this entry, although not comprehensive, are meant to provide an overview of research on framing effects within the literature. Framing effects have consequences not only for hypothetical monetary gambles and risky choice scenarios but can have very real outcomes for how people make judgments and

decisions in daily life. Future research should continue to explore when and how framing effects influence behavior and provide more evidence for how translational contexts like healthcare and political decisions are influenced by message framing.

## Cross-References

- ▶ [Cognition](#)
- ▶ [Cognitive Bias](#)
- ▶ [Decision-making](#)
- ▶ [Judgment Bias](#)
- ▶ [Primate Cognition](#)
- ▶ [Rationality](#)

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## Frank Ambrose Beach

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Frank Ambrose Beach, Jr., was the doyen of modern behavioral endocrinology, the study of the influence of hormones on behavior. His text, “Hormones and Behavior,” published in 1948, is the seminal volume on the subject and to this day remains a major source of information. While research on hormones and their effects received a significant impetus early in the twentieth century, especially with Rowan’s studies on the induction of migratory behavior in birds (which, of course, had been anticipated by Aristotle; Rowan 1931, *The Riddle of Migration*, Williams and Wilkins Press), it was Beach more than any other scientist of his generation who brought the discipline into full flower.

Beach was the son of Frank Ambrose Beach and Berthe Robinson Beach, the first of three offspring. His birthday was on 13 April 1911. His education was at Emporia State University, in Kansas, his home state, and Antioch College,

from which he graduated in 1932. With several stints as teacher behind him, he eventually completed a doctorate at the University of Chicago and then spent a year with Carl Lashley before joining the staff of the American Museum of Natural History in 1937. Almost a decade later, he moved from New York and the American Museum to Yale. Yet another decade later, in 1957, he spent a year at Stanford's Center for Advanced Study, moving from there to the University of California at Berkeley, where he remained until his death. He married three times and, with his second wife, raised two children. (His biography is fully detailed in Donald Dewsbury's "Portraits of Pioneers in Psychology.")

Beach clearly confounded many who encountered him. He could appear in a neighborhood bar as a blue-collar laborer or enthrall a group of distinguished Cambridge dons with his incisive discourses. As a young and inexperienced graduate student, I first met him when my professor insisted I cross town and present my thesis plans to Professor Beach. I timidly knocked on Beach's office door and was then tempted to flee when a booming voice ordered me to hurry on in. It was a warm spring day in New Haven, and Beach was casually dressed, lounging in his reclining chair with a can of cheap beer in his hand. The walls of his office were adorned with photos of the penises of various animals, most of them erect. Except for Beach's broad smile and gentle assurances, I would never have had the nerve to speak, but, with his encouragement, I outlined my plans. He quickly reached for the phone, explaining as he did so, that he wanted his student, Julian Jaynes (who later, as a professor at Princeton, was the author of "The Bicameral Mind"), to participate in our discussion. Julian soon appeared and we adjourned to a local pizza parlor for food, beer, and friendly discourse. This was a pattern which repeated itself in one form or another for decades: Beach was the consummate mentor, though also exceedingly demanding of precision and clarity.

As his long list of publications reveals, he had an exceptional breadth of interests and knowledge, a critical approach to empirical science, and deep understanding of the philosophical implications of his work. More than any other

biologist or psychologist of the 1950s and 1960s (except perhaps for Dan Lehrman at Rutgers), he countered the deterministic position of the European ethologists as represented by Konrad Lorenz (and cf. Klopfer 1994). His puckish humor is also evident in much of his writing, for example, in "The Snark is a Boojum," an argument against genetic determinism.

Beach died in Berkeley on 15 June 1988. A biographical memoir by Donald Dewsbury provides a more detailed picture of his life (Dewsbury 1998).

Dewsbury also provides a list of his more important publications, to wit:

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- [Aristotle](#)
- [Konrad Lorenz](#)

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## Frans de Waal

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Contemporary students of animal cognition move fluidly through doorways to fascinating capabilities – peacemaking, justice, fairness, morality, and empathy – to name just a few. So unimpeded is their progress that few may fully realize how briefly these doors have been open. They may not fully realize how much work and courage it took to systematically *wedge those doors open* with one persuasive discovery after another over the last few short decades.

The world of animal cognition we enjoy today, which this encyclopedia showcases so well, was unimaginable not long ago. For example, this author did her PhD under Frans de Waal on the development of reconciliation – studying how capuchin monkeys learn to apologize as youngsters. Capuchins were a good model because they grow up faster and are not quite as conscious of being studied as are apes and humans. During the final defense, this author was repeatedly questioned by a committee member about the role of personality in the capuchins' peacemaking behavior. "But we don't talk about personality in monkeys!" was her startled defense, as she cast entreating glances to Frans to help her out. The questioning committee member was a human psychologist. He was incredulous that animal behaviorists dared not invoke personality or emotion in the animals we studied (if they wished to avoid professional crucifixion). Denying things like personality and emotions was very hard and always awkward. Yet that denial was still largely the tenor

of the time. Where did the invisible wall that completely blocked legitimate investigation of fascinating possibilities of animal cognition come from?

There is little question where it came from. René Descartes was wrong when he claimed that animals were stupid machines – organic automata without thoughts or feelings. But that did not stop three centuries of people from believing him. Descartes' application of logic when seeking to understand the natural world produced many cutting edge contributions to philosophy, mathematics, and science. For example, it was Descartes who introduced skepticism as an essential part of the scientific method, which includes the contemporary practice of methodological skepticism. These contributions gave him great credibility. If Descartes said animals were stupid machines, then they must be.

Descartes' simple assurance of the superiority of humanity over animals even effectively silenced countless centuries of lessons, we had learned about animal behavior before his notorious birth in 1596. These lessons extended far back to our dim past as "Man the Hunter" whose survival depended on his knowledge of prey behavior, but of the behavior of the predators that stalked him as well. These lessons are accumulated through the domestication of animals, discovery of agriculture, and establishment of farms and farm animals. They accrued through the age of grand estates – think cheetahs lounging in ancient Egyptian palaces – and more recently in animal collections on private estates and in zoological gardens, the latter in name only, because of the small, hard, empty cells we gave the animals to live in.

The point is that Descartes' simple proclamation that animals were stupid machines erected a wall that has been simultaneously invisible and omnipresent for the past three centuries. Those walls even surrounded universities, despite scholars' best efforts to study animal behavior objectively. Contemporary scholars of all forms of animal behavior have all been thoroughly basted and baked in the Cartesian animals-are-stupid-machines attitude, a reality that demands their most profound consideration.

In this author's own lifetime, a few intrepid individuals dared to scale those tall and terrible Cartesian walls. One was a boy born in 1948 in the land of tulips and windmills (Den Bosch, the Netherlands). His mother taught him that the saddest sight was a bird in a cage. This kind of thinking, along with exposure to the brilliant ethologists of his day, gave the boy his special sympathy for animals. He henceforth developed a single-minded desire to understand animals clearly and realistically on their own terms. Unbeknownst to the earnest lad who went on to study biology in Nijmegen and Groningen, the Netherlands, his single-minded desire meant spending his life slamming his shoulder against Descartes' invisible wall.

He did his PhD project at Utrecht University. As he patiently recorded aggressive behavior among macaques, he saw the glimmerings of the other side of aggression: peacemaking. To earn some money, the sprouting young man helped the psychologists in Nijmegen, the Netherlands, who worked with chimpanzees. When Frans de Waal saw the chimps, it was love at first sight.

It is hard to doubt someone you love. But Frans knew for himself what Descartes said famously aloud, "If you would be a real seeker after truth, it is necessary that at least once in your life you doubt, as far as possible, all things." Frans has done exactly that – doubt – systematically and empirically across his entire career. Frans used Descartes' own methodological skepticism against his terribly unjust invisible walls by questioning the claim that animals were stupid machines.

So Frans studied chimpanzees with fresh eyes, questioning the answers. Could all this bowing, bravado, kissing, and alliance shifting really occur without the chimps grasping at least the basics of planning, social calculations, and consequences? Did conflict *really* disperse opponents? Frans' discovery of chimpanzee politics and peacemaking was his first big shoulder shove against that invisible Cartesian wall. The wall creaked.

And he gave the rest of us a foothold. He refined the technique of providing empirical evidence for reconciliation when he designed a user-friendly, empirically elegant method. This

wedged open a sliver of a slit in that invisible Cartesian wall. It has since widened considerably with the passage of scores of investigators who used Frans' PCMC method to reveal peacemaking in other species, including my own demonstration of reconciliation in bottlenose dolphins.

The author met Frans when he came to study the bonobos at the San Diego Zoo, where she worked. He was just the "guy from Europe." He was fun. He did not fanfare the guts it took to put "chimpanzee" and "politics" together in the title of a book. Nor did he complain that the tenor of the times insisted that his use of the word reconciliation (to describe peacemaking gestures after two chimps fought) was inevitably attended by the caveat "heuristic label" because, after all, animals were not exactly robotic automatons, but almost.

Frans kept heaving his shoulder against that invisible Cartesian wall. He led contemporary students of animal behavior and cognition in another direction with cross-fostering experiments. These not only demonstrated that peacemaking has a strong learning component. They encouraged animal behaviorists to conduct observation-based experiments. No Skinner box is needed.

Frans heaved his mighty shoulder against that invisible Cartesian wall again when he demonstrated how mere observation could be used to reasonably correlate behaviors that were staggered in time: I groom you this morning. You share food with me this afternoon. Who thought animals were paying attention like that? The chimps taught Frans that social interaction was a transaction. No exchange was without impact. This time, a couple of big boulders tumbled out of those invisible Cartesian walls.

Frans kept heaving. In turning Cartesian skepticism around, Frans invoked possibilities of animal behavior that few others dared consider: planned social strategies that included third party interventions, cooperation, reciprocity, and peacemaking, but also justice, altruism, fairness, consolation, food sharing, and generosity. With such a tool chest, social interaction becomes a series of transactions with consequences. Animals had to remember and to think ahead.

Citing parsimony, Frans argued for evolutionary continuity with empirical evidence that empathic and cooperative tendencies are continuous across species. He argued that empathy is one of the emotional roots of morality. It had evolutionary roots far deeper than our own. Equitable attitudes are universal mammalian characteristics. Though the idea remains unwelcome in many quarters, one conclusion had to be that nonhuman great apes and humans are simply different types of apes. Nonetheless, humans are more systematically brutal than chimps and more empathic than bonobos. "Our societies are never completely peaceful, never completely competitive, never ruled by sheer selfishness, and never perfectly moral," Frans pointed out when calling us the bipolar ape!

No one familiar with Frans' work has to be persuaded that he has unique vision. His penetrating views of the cognitive basis of animal behavior have given us a rich vocabulary for seeing animal behavior the way digital glasses give a 3D image in profound depth, color, and realism.

Little wonder that Frans is C. H. Candler Professor of Psychology at Emory University and the Director of the Living Links Center at the Yerkes National Primate Research Center and has been a University of Utrecht Distinguished Professor since 2014. In 2007, *Time* magazine included him in the "TIME 100: The People Who Shape Our World," a list of the 100 most influential people. He was elected to the Dutch Academy of Sciences in 1993 and to the National Academy of Sciences in 2004. His books have been translated into over 20 different languages, and he probably wrote one in the time it took me to write this biography. He is married and lives close to Atlanta, where he and his wife Catherine throw generous parties so their graduate students can enjoy a moment of misty equality.

Frans told this author that he thought his greatest contribution to animal behavior and cognition studies was probably his discoveries of conflict resolution and empathy. To this author, Frans' greatest contribution was role modeling *how* to tease evidence out of benign observation by designing experiments that did not traumatize anybody involved – except Lance the capuchin,

whose tantrum-like recognition of the unfairness of getting a cucumber reward when his compatriot got a grape went viral on the Internet!

Frans has worked single mindedly to put animals in a whole new light and reverse the appalling Cartesian sanction to brutalize them with impunity. Frans is not the only animal behaviorist to assault those invisible Cartesian walls with an academic battering ram, as this encyclopedia amply portrays. It was just that Frans' ram grew huge with time, and he hit those walls harder and more often than most. The last time this author saw Frans, she thanked him for casting such a bright light that so many of us could bask in his reflected glory. Frans' greatest contribution to animal cognition was to storm those Cartesian walls open. Because of his work, contemporary students of animal behavior and cognition are free today to actually explore these fascinating topics without the constraints of the past.

Frans, how does it feel to be your very own personal paradigm shift?

## Cross-References

- [Agonistic Behavior](#)
- [Primate Cognition](#)

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## Fraternal Birth Order Effect

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## Synonyms

[Birth order](#); [Male androphilia](#); [Male sexual orientation](#); [Maternal immune hypothesis](#); [Older brother effect](#)

## Definition

The *Fraternal Birth Order Effect* (FBOE) is the well-established finding that each biological older brother a male has increases the likelihood that he will be same-sex attracted.

## Introduction

In humans, having a greater than average number of biological older brothers is reliably associated with an increased probability of male homosexuality. The Fraternal Birth Order Effect (FBOE) is among the most consistently established correlates of male sexual orientation (Blanchard 2017), being linked to male homosexuality in diverse populations throughout the world. These include Western samples drawn from the United States, Canada, the United Kingdom, Italy, and the Netherlands, as well as non-Western cultures such as Brazil, Turkey, and Samoa (reviewed in Blanchard 2017; Blanchard and VanderLaan 2015). Some studies have reported that homosexual males also have an elevated number of older sisters relative to heterosexual comparison groups. It is important to note that homosexual males tend to have larger families in general than heterosexual males (Bailey et al. 2016). Additionally, no plausible mechanisms exist for an older sister effect, and only older brothers predict male homosexuality after controlling for overall number of siblings. As such, this “older sister effect” is simply due to the fact that having more older brothers is correlated with having more older sisters as well (Blanchard 2014, 2017; VanderLaan and Blanchard 2015). Similarly, many studies that found no FBOE in their original analyses *do* reveal an effect of older brothers when properly controlling for family size (Blanchard 2017). Some studies have also looked for a possible birth order effect in the origins of female homosexuality, but female sexual orientation appears to be unaffected by sibling characteristics (see Blanchard 2004).

The FBOE for male sexual orientation has been established in modern populations and in decades old archival samples, among both homosexual males who identify as men and homosexual males who identify as transgender women (or culturally specific third-gender categories), and even among individuals with sexual attraction to prepubescent and pubescent males. Although the FBOE is related to sexual attraction specifically, a recent meta-analysis has shown that it may be implicated in gender expression as well.

The FBOE appears to be stronger in homosexual males who are transgender, as compared to the strength of the effect among homosexual men (Blanchard 2017). The reasons for this difference are currently unclear. It is possible that the FBOE feminizes both sexual preference (i.e., attraction to males) along with traits associated with a feminine gender presentation, or that the FBOE is in some way more “feminizing” than other mechanisms leading to male homosexuality, such as genetics or hormone exposure in utero. Despite the varied populations examined, numerous replications of the FBOE confirm the same general pattern – each older brother that a natal male has increases the probability of homosexual attraction.

Specifically, each biological older brother that a male has increases the odds of same-sex attraction by approximately 33% (odds ratio = 1.33) over the baseline rate of male homosexuality (~2–4%) (Cantor et al. 2002; Blanchard 2014; VanderLaan and Vasey 2011). Given this increase, and assuming a linear effect, a male with 10 older brothers would stand roughly a 50% chance of being homosexual (i.e., odds ratio \* number of brothers \* base rate of homosexuality =  $1.33 * 10 * 0.04 = 0.532$ , or 53.2% chance of being homosexual). It is estimated that overall, 14–29% of homosexual males owe their sexual orientation to the FBOE (Blanchard and Bogaert 2004; Cantor et al. 2002), meaning that at least one in seven homosexual males owes their sexual orientation to the FBOE.

Work on the FBOE was pioneered in the early 1990s, spurring numerous studies into both its existence and possible mechanisms by the original investigator (Canadian psychologist, Dr. Ray Blanchard), as well as others. Independent replications of the FBOE are numerous, and persist even in meta-analyses that specifically exclude scientific reports published by Blanchard and his usual collaborators (see VanderLaan and Blanchard 2015). Nonbiological siblings have no impact on male sexual orientation, nor does time spent with these siblings, meaning that the FBOE is specific to *biological* older brothers (Bogaert 2006). Indeed, the FBOE persists whether individuals are raised together with, or separately



from, their biological older brothers (Bogaert 2006). Such evidence is consistent with the suggestion that male homosexuality is biological in origin, the result of pre-natal, rather than post-natal influences (Bailey et al. 2016; Bogaert 2006). The causal mechanism of the FBOE is pre-natal in origin, with the most likely explanation involving the influence of the maternal immune system impacting the neural development of her male fetus.

The most prominent explanation for the FBOE is the Maternal Immune Hypothesis (MIH). While there is currently no direct laboratory evidence, ample circumstantial evidence converges on the MIH being the most likely causal mechanism underpinning the FBOE (Blanchard 2004; Bogaert and Skorska 2011). The MIH proposes that each male fetus a woman carries heightens the probability that she is exposed to male-specific antigens produced by the Y-chromosome, which are foreign to her immune system. Increased exposure to male specific (Y-linked) antigens provokes a progressively stronger immunological response, which in turn can cross the placental barrier, impacting the brain development of a male fetus. As such, every male fetus a mother carries increases the likelihood of exposure to Y-linked antigens, and in turn makes it more likely that a subsequent male fetus will be exposed to maternal antibodies. The heightened immunological response of a mother to Y-linked antigens is hypothesized to disrupt the sexual differentiation of a male's brain, including key regions linked to sexual orientation such as the hypothalamus (Blanchard 2004; Bogaert and Skorska 2011; Blanchard 2017). At least four candidate antibodies have been identified as specific mechanisms of the MIH (PCDH11Y, NLGN4Y, TBL1Y, SMCY) (Bogaert and Skorska 2011), but confirmation that these specific proteins are directly responsible for the FBOE awaits further histological confirmation in the laboratory.

## Conclusion

In summary, a greater than average number of biological older brothers is consistently associated

with male homosexuality across numerous diverse populations. Reliable effects emerge across studies, especially when controlling for family size (Blanchard 2017). While the existence of the fraternal birth order effect (FBOE) is firmly established, the exact causal mechanism requires further investigation. The FBOE is most likely caused by maternal antibodies that target male-specific proteins, disrupting the typical neural development of the male fetus. Future work on the FBOE could include both laboratory studies of candidate proteins (Y-linked antigens) that are targeted by maternal immune factors, as well as longitudinal studies examining pre-natal factors in pregnant mothers and the post-natal outcomes of their male children's sexual orientation.

## Cross-References

- Chromosomes
- Homosexual
- Immunology
- Interbirth Interval
- Overdominance Hypothesis for Male Homosexuality
- Protein
- Sex Ratio

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## Fraud

### ► Cheating

## Free Operant Response

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## Synonyms

[Instrumental behavior](#)

## Introduction

Typically studied in the laboratory using an operant chamber (or “Skinner box”), operant, or instrumental, behavior can be generally described as a freely emitted behavior that has an effect on the environment. For example, a rat might learn to press a lever in order to produce a food outcome or produce an intravenous injection of a drug such as

cocaine (see “Self-Administration”). Thus, operant conditioning is a relatively simple and straightforward method used to study variables that influence voluntary behavior. Free operant behavior refers to an operant behavior that has a schedule of reinforcement (see “Operant Conditioning”; Ferster and Skinner 1957 for an extensive review on reinforcement schedules) that is in effect for the duration of the time the animal is in the operant chamber with no constraint on the number of responses the animal can emit while in the chamber. Thus, responding and reinforcement schedules in a free operant design are not limited to discrete periods or trials. Free operant behavior can be contrasted with discrete trial operant behavior, in which only one response can be made per trial (e.g., performance on a maze task). Further, discriminated operant procedures, in which the schedule of reinforcement is in effect only in the presence of a discrete discriminative stimulus, or  $S^D$ , such as a tone or the illumination of a panel light can be differentiated from standard free operant procedures in that the reinforcement schedule is not in effect when the  $S^D$  is not present, whereas the reinforcement schedule is not constrained to a discrete period in free operant procedures (Skinner 1938).

## Association Formation During Free Operant Conditioning: What Learning Underlies Responding?

Traditionally, the role of the reinforcer (an outcome that increases the likelihood of future responses) or a punisher (an outcome that decreases the likelihood of future responses; see “Operant Conditioning”) in free operant behavior was thought only to strengthen or weaken (respectively) the response, making it more (or less) likely to occur in the presence of the stimuli available when the response was reinforced (or punished). Thus, the counterintuitive prediction made by this view is that the consequence does not actually get encoded into the associative structure that promotes instrumental responding. In other words, responses were thought to be performed mindlessly without explicit knowledge or in pursuit of the outcome. However, given that responding is lawfully tied to

outcome delivery, the associative structure should thus depend in part on knowledge of the outcome. To test for this, the so-called “reinforcer devaluation method” is used. In a standard version of this paradigm, an animal is taught to perform a behavior (e.g., a lever press) for a food outcome. Once this behavior is established, the animal has the reinforcer “devalued” in some way, typically, through pairing its presentation with a lithium chloride induced illness (which conditions a taste aversion to the outcome) or through a satiation procedure in which the animal is allowed to consume as much of the outcome as he wants. Then, in a crucial test, the animal is placed back in the chamber and responding is tested without any outcome presentations. If the animal has knowledge of the outcome produced by the response (i.e., the animal has knowledge of a response–outcome, or R – O, association), then behavior should be suppressed for an outcome that has been devalued. This demonstrates that responding is goal-directed in nature. Overall, research suggests that responding is typically goal-directed early on in training (i.e., responding is suppressed following devaluation) but that following extensive training in which the response is paired with the outcome, the reinforcer devaluation effect on responding is not observed and behavior is described as habitual. This suggests that behavior is initially dependent on an R – O association for expression, but gradually comes to rely on an S – R association (Dickinson 1985).

### **Contextual Control of Free Operant Responding: Associations Between the Context and the Response**

Although, as previously discussed, in standard, nondiscriminated free operant procedures there is no discrete stimulus or  $S^D$  that signals that responses will be reinforced, free operant responding depends crucially on the acquisition context for expression. Thus, a change to a new context (i.e., a new operant chamber with different tactile, visual, and olfactory cues) consistently results in a decrement in operant performance. This suggests that the context is an important

part of the associative structure that underlies instrumental learning. The context can come to signal the response–outcome association in a hierarchical Context – (R – O) relationship in which the context signals that a certain response will produce an outcome. The context can also come to elicit the response directly in a Context – R association. In the case of free operant behavior, the context is likely the stimulus (or S) that supports habitual S – R performance (see Trask et al. 2017, for a review).

### **Influence of Stimuli on Free Operant Responding: Pavlovian-Instrumental Transfer**

Free operant responding that does not involve learning to perform a response in the presence of a discrete stimulus or  $S^D$  can still be influenced by stimuli in a paradigm known as Pavlovian-Instrumental Transfer, or PIT, in which a stimulus associated with a reinforcer can invigorate instrumental responding. A typical PIT experiment involves training of an instrumental response to produce an outcome and pairing of a conditioned stimulus with the same outcome in separate phases. Following this training, the response is available (but not reinforced) and tested with the conditioned stimulus. The typical result is that, despite never having been trained as an  $S^D$ , the conditioned stimulus will elevate responding. The opposite is also true; a conditioned stimulus paired with an aversive unconditioned stimulus (e.g., a shock) will result in a suppression of the response. In this way, Pavlovian stimuli can guide or motivate instrumental responding despite a lack of explicit training (Bouton 2016).

### **Operant Extinction and Relapse**

Previously reinforced free operant behavior can become inhibited or suppressed when the response no longer produces a reinforcer in a process known as extinction (note that, although both procedures cause a reduction in responding, extinction differs from punishment in that a punisher is a consequence of a response; extinction is programmed such that responses explicitly have no consequences). While, behaviorally, this

initially looks as though the original behavior is erased, several “relapse” phenomena suggest that the original behavior remains intact and responding can return under certain circumstances (Todd et al. 2014). Briefly, these relapse phenomena are renewal (a return of extinguished responding due to a removal from the physical context where extinction occurred), spontaneous recovery (i.e., a return of extinguished responding due to the passage of time), reinstatement (i.e., a return of extinguished responding due to exposure to the reinforcing outcome), and resurgence (i.e., a return of extinguished responding due to the removal of alternative reinforcement contingent upon a second response). It has been hypothesized that operant behavior results in formation of an inhibitory stimulus-response association between the context in which extinction takes place and the response. Thus, the animal learns not to perform a response in the extinction context (Rescorla 1997; Trask et al. 2017).

## Conclusion

Free operant behavior (and operant conditioning more generally) provides a useful method to study the variables that influence voluntary behavior. While this method is theoretically interesting and a fruitful area of investigation in its own right, it also provides a useful laboratory model for understanding maladaptive voluntary behavior, such as over-eating, smoking, and drug-taking. Further, this training can contribute to our understanding of the mechanisms that produce relapse of these behaviors following procedures that reduce responding, like extinction and punishment.

## Cross-References

- ▶ Acquisition
- ▶ Avoidance
- ▶ B.F. Skinner
- ▶ Discrete Trials
- ▶ Extinction in Learning

- ▶ Extinction in Learning
- ▶ Goal-Directed Behavior
- ▶ Inhibition
- ▶ Instrumental Learning
- ▶ Learning
- ▶ Negative Reinforcement
- ▶ Operant Chamber
- ▶ Operant Conditioning
- ▶ Positive Reinforcement
- ▶ Punishment
- ▶ Reinforcement
- ▶ Schedules of Reinforcement
- ▶ Self-Administration
- ▶ Skinner Box
- ▶ Spontaneous Recovery
- ▶ Stimulus Control
- ▶ Taste Aversions
- ▶ Unconditioned Stimulus

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## Free-Operant Avoidance

- ▶ Avoidance

## Free-Running Cycle

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## Synonyms

Forced desynchrony; Nonentrained

## Definition

An endogenous circadian rhythm or behavior that is not synchronized to any external cue.

## Introduction

In 1938, Dr. Nathaniel Kleitman and his graduate student, Bruce Richardson, spent 32 days deep within the Mammoth Cave in Kentucky. Their goal was to understand what happens to daily circadian cycles (derived from the Latin terms *circa*: approximately, *dies*: day) in the absence of daily environmental cues (i.e., without the normal daily changes in light and temperature caused by the Earth's rotation). The cave was ideal for this experiment as it was always dark, it had a constant temperature, and it was isolated from outside noise and human interaction. To separate the normal sleep and wakefulness cycle from any internal circadian rhythms, the investigators chose to live on a 28-h day-length (i.e., one sleep bout every 28 h), and they recorded their body temperatures at regular intervals. After over a month of living in the cave, they found that body temperatures can

keep a near 24-h rhythm, suggesting that humans have an endogenous time-keeping system which is self-sustained in the absence of environmental time cues, and even persisted when the sleep and wakefulness cycle had a different period (28 h). After recreating this cave-like environment with different day-lengths (e.g., 20-h or 28-h “days”) in controlled laboratory settings (dim-lighting, constant temperature, equally distributing behaviors across the entire circadian cycle), we now know that this circadian timing system has an endogenous period that is close to but not exactly 24 h, and that this period is slightly different between people, averaging around 24.2 h (Czeisler et al. 1999). In the absence of time-cues, the circadian rhythm will cycle with this endogenous period; in these conditions, it is known as a “free-running” circadian rhythm. This type of protocol – free of environmental time-cues and of differing day-lengths – has been important because it has helped to uncover the endogenous nature of the body clock, the quantification of the endogenous circadian period, and has allowed investigators to assess the circadian rhythms of many physiological and behavioral variables, and their interactions independent of outside influence. Further, these discoveries have allowed us to understand why certain populations, such as some blind individuals, have trouble maintaining a 24-h schedule as they lack the pathway to synchronize to the 24-h day and thus exhibit free-running circadian rhythms.

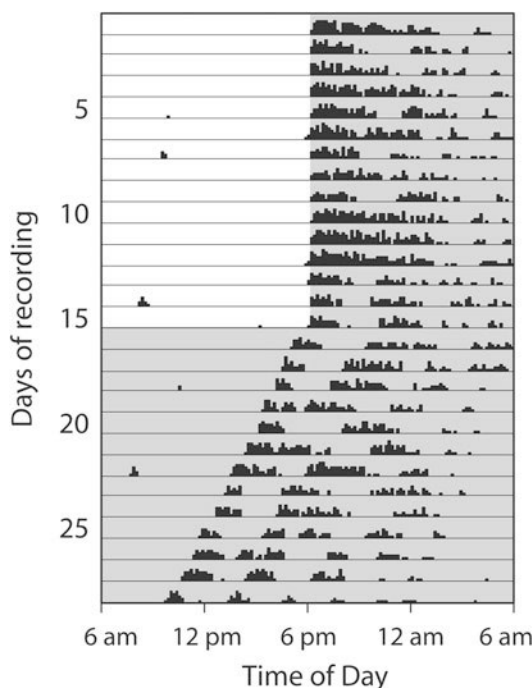
## The Circadian System, Entrainment, and Free-Running Cycles

In mammals, the circadian timing system is controlled by a central pacemaker, or master clock, located in the suprachiasmatic nucleus (SCN) of the anterior hypothalamus. The SCN is composed of approximately 20,000 neurons; among these, many are individual autonomous oscillators. When studied in a dish – the “Mammoth Cave” for cells where external timing cues can be eliminated – SCN neurons exhibit free-running rhythms of electrical activity and gene expression



with periods close to 24 h (Welsh et al. 1995). SCN neurons use both neuronal and humoral outputs to communicate timing information to peripheral clocks located throughout the body (e.g., kidneys, gut, pancreas, etc.), synchronizing these peripheral clocks with the master clock to organize biological functions for anticipation of changes in the environment (e.g., promote wakefulness, feeding, and motor activity for the daytime, and promoting sleep or resting behavior for the nighttime) (Schibler and Sassone-Corsi 2002). The duration of the rhythm produced by the SCN, however, most often does not exactly match the Earth's 24-h rhythm and thus must be synchronized or entrained on a daily basis to match physiology and behaviors with the Earth's 24-h light-dark cycle. Circadian entrainment is the process of achieving a stable phase relationship between the timing of a circadian marker (e.g., peak cortisol secretion, melatonin onset, core body temperature minimum, etc.) and a periodic environmental time cue (e.g., lights-on, lights-off). When entrainment does not occur, rhythms will instead free-run at their own endogenous period (Fig. 1).

Circadian clocks are ubiquitous on Earth and they are phylogenetically diverse, having been studied in all branches of life. The mechanisms that encode circadian rhythms are diverse as well, and differ between bacteria, fungi, plants, and animals (Edgar et al. 2012). Animals may be broadly categorized as being active during the day (diurnal), night (nocturnal), or twilight (crepuscular). Though exceptions exist, diurnal animals tend to have free-running periods greater than 24 h and nocturnal animals tend to have free-running periods less than 24 h (Aschoff 1981). The average circadian period in humans is ~9 min longer than the Earth's 24-h light-dark cycle (Czeisler et al. 1999), while a typical laboratory mouse may have a free-running period closer to 23.5 h. Thus, these circadian rhythms must be continually entrained to 24 h by exogenous stimuli. Although nonphotic cues can synchronize circadian rhythms, in most animals, including humans, light is the primary zeitgeber ("time-giver") for the circadian system (Czeisler and Wright 1999). In mammals, light is detected by



**Free-Running Cycle, Fig. 1** Simulated wheel running record of a nocturnal rodent that is entrained to the 24-h day and then placed into a dim-lighting environment, whereby entrainment no longer occurs and the activity rhythm free-runs at the rodent's endogenous circadian period (<24 h in this example). *White bars* represent room lighting and the *gray bars* represent dim-lighting. The *black ticks* indicate wheel-running activity

photoreceptors in the retina. A specific set of retinal ganglion cells, which contain melanopsin and are intrinsically photosensitive, transmit this photic information through direct projections to the SCN via the retinohypothalamic tract (Hattar et al. 2002). The response of the circadian system to light depends on the timing of exposure. Light exposure in the early biological night causes the circadian clock to shift to a later time (phase delay); light exposure in the early biological morning causes the circadian clock to shift to an earlier time (phase advance) (Khalsa et al. 2003). Thus, to remain entrained to the Earth's 24-h environmental cycle, individuals or species with a circadian period that is longer than 24 h require a daily phase advance and those with a circadian period that is shorter than 24 h require a daily phase delay.

The eyes are necessary for entrainment of free-running circadian rhythms in mammals, but this is not the case for other branches of life. Circadian rhythms of reptiles and birds can be entrained by light that penetrates the skull and activates deep-brain photoreceptors. For single cell cyanobacteria, light entrains their circadian clocks by changing the ratio of ATP to ADP. This last example highlights the close connection between clocks and metabolism, which is a hallmark across phylogeny (Asher and Schibler 2011).

Maintaining an appropriate relationship between the phase of the internal clock and the timing of the external environment and behaviors (e.g., the sleep/wake) is vital for healthy cognitive and physiological functioning. Individuals with a free-running rhythm, common in blind individuals lacking an entraining photic pathway, typically have difficulty as their non-24-h clocks drift in and out of phase with work, social, and sleep schedules dictated by the Earth's 24-h day (Sack et al. 2007). In this regard, one particular non-photic zeitgeber deserves mention: the hormone melatonin is synthesized and released during the night; it is also a chronopharmacologic agent that advances the clock in the evening and delays the clock in the morning (opposite to the effects of light). For free-running blind people, evening or morning melatonin (depending on whether the person's free-running rhythm is longer or shorter than 24 h) can therefore entrain them to the 24-h day. The consequence of a free-running period that is not exactly 24 h is that the daily behaviors, such as sleeping and eating, must shift each day relative to the external time (e.g., GMT) or else result in a state of almost permanent "jet lag," when the daily behaviors occur at suboptimal circadian times. This condition is called circadian misalignment and is most noticeable as the acute nausea and sleepiness that often accompanies jet travel across many time zones or when changing work schedules, such as starting night shift work. Indeed, poor health has also been attributed to the chronic occurrence of circadian misalignment, which testifies to the importance of the internal circadian system in optimizing our physiology and behaviors.

## Conclusion

Most animals have an endogenous circadian clock that is not exactly 24 h, and thus require a daily entraining stimulus (e.g., light) to remain synchronized to the Earth's 24-h rotation. When this entrainment is interrupted either by scientific manipulation or disruption of the entrainment pathway, the organism's endogenous circadian rhythm will become a free-running rhythm and express its intrinsic circadian period.

## Cross-References

- Circadian Rhythms
- Light/Dark Cycle
- Sleep

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nervousness, altruism, etc.) which may vary person to person. Further such variable traits may be discrete (or categorical, or discontinuous) which do not bear range of phenotypes and will be either present or absent (as blood group or physical characteristics as skin color or built or a disease as albinism, cystic fibrosis, or sickle cell anemia), or continuous (as height, weight, or blood pressure) which can be measured and can bear any value in a defined range on a scale.

## Frequency Distribution of Phenotypes

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### Definition

Relative distribution of the specific observable traits, or “phenotypes,” in the individuals of a population like physical characteristics (i.e., height, weight, skin color, etc.) or the behavioral features (i.e., attitude, aggression, nervousness, altruism, etc.), which may vary individual to individual.

### Introduction

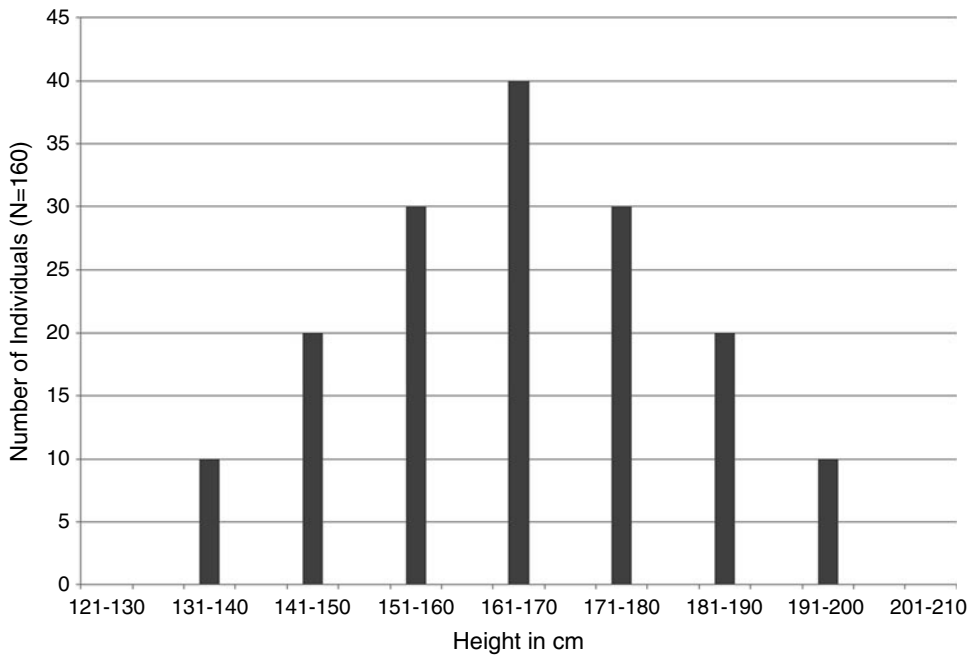
To study the frequency distribution of a specific observable trait or a “phenotype” in a population is an important aspect of quantitative genetics (Halliburton and Halliburton 2004). The phenotype meant an expressed characteristic of an organism, like physical characteristics (i.e., height, weight, skin color, etc.), or a particular behavioral feature (i.e., attitude, aggression,

## Relative Phenotype Frequency

The number of individuals in a population bears a specific observable trait or phenotype is called as “relative phenotype frequency.” The relative phenotype frequency for a phenotype can be calculated by counting the number of times a particular phenotype appears in a population and dividing it by the total number of individuals in the population. The relative frequency of the observed phenotypes in a population can be assembled together to show the frequency distribution of the set of phenotypes (“[The Variety of Genes in the Gene Pool Can Be Quantified within a Population | Learn Science at Scitable](#)”).

## Graphical Representation of the Phenotypic Frequency Distribution

Frequency distribution of a phenotype is studied in a population and presented in bar graphs or histograms. For discrete or discontinuous traits, a qualitative statistical test as Chi-square test is applied and the frequency distribution is presented in line or bar graphs, or pie diagrams. A continuous trait can be measured on a set scale and charted in histograms. As continuous trait may bear any value in a defined measuring system, all statistical tests using central tendencies (i.e., mean, median, mode) can be applied to it and show a typical bell-shaped standard curve if measurement values are presented in a histogram (Minter 2003). Figure 1 shows the example of the frequency distribution histogram for a continuous trait as height in an assumed population. At the extreme values



**Frequency Distribution of Phenotypes, Fig. 1** Frequency distribution for the height of individuals in an assumed population

towards both ends, there are minimum numbers of individuals, and the higher numbers of individuals are at the mid-values progressively, mimicking the frequency distribution of trait in a natural population which will give a typical bell-shaped standard curve in the histogram.

allele would not be convertible into a phenotype if the organism is not carrying all alternative forms. Genotype or allelic frequency distribution for a phenotype is a quantifiable property and can be estimated using Hardy-Weinberg principle if the dominance or recessive traits for the alleles are known.

## Phenotype Versus Genotype Versus Allele

Phenotype depends on the genetic makeup or “genotype” of an organism at a particular gene locus. Genotype is the particular allelic combination at a gene locus which will give rise to a trait. Alleles are the alternative forms a gene present at a specific locus.

Phenotype frequency distribution can be also derived from the genotype or allelic frequency or vice versa for a particular trait in a population. But a genotype is not always equal to a phenotype, as some characteristics only express in the organism depending upon that allelic combination for the trait is either dominant or recessive. A recessive

## Hardy-Weinberg Equilibrium Principle

Hardy-Weinberg equilibrium principle is used to predict the frequencies of alleles and genotypes in a population. It states that genotypic or allelic frequencies in a population remains constant or maintain a state of equilibrium in the absence of any disturbing factors, i.e., the sum of all possible outcomes must be equal to one. For example, if “p” and “q” are the two alleles for a particular gene, then  $p + q = 1$ , or if there are three alleles (p, q, and r) for a particular locus of a gene, then  $p + q + r = 1$  (Halliburton and Halliburton 2004).

The disturbing factors to the Hardy-Weinberg equilibrium can be many including mutations,

natural selection, nonrandom mating, genetic drift, and gene flow. The mutations disturb the equilibrium of allele frequencies by introducing new alleles into a population. Similarly, natural selection and nonrandom mating may disturb the Hardy-Weinberg equilibrium by changing gene frequencies due to bias for a favorable trait (“[Hardy-Weinberg equilibrium | Learn Science at Scitable](#)”).

Contrary to the assumption, the desired state of equilibrium in – Hardy-Weinberg principle, which is used as a model for studying real populations – can never be achieved in a real population but only can be approximated in the laboratories in ideal conditions. There are certain criteria which need to be fulfilled so a population ideally can achieve Hardy-Weinberg equilibrium (Box 1).

#### Box 1 Criteria to be fulfilled for Hardy-Weinberg equilibrium

- Population is large
- Mating is random
- Allele frequencies are equal in the sexes
- There is no migration, mutation, or selection

### Genotype, Allelic, or Phenotype Frequency Estimation Using Hardy-Weinberg Equilibrium Principle

How to calculate genotype or allelic frequency if relative phenotype frequency for an observable trait is known or vice versa can be understood from the following sample problem.

#### Sample Problem

1. Let us assume a mice population where individual bears either of two color phenotypes black or white. Black mice are 36% and remaining is white. Now calculate the allelic and genotype frequencies using the Hardy-

Weinberg equation (assuming that population is at equilibrium).

- (a) Let us consider the gene for color trait has two alleles A (dominant) and a (recessive)
- (b) The frequency of allele A is represented by p
- (c) The frequency of allele a is represented by q
- (d) The frequency of genotype AA =  $p^2$
- (e) The frequency of genotype Aa = pq
- (f) The frequency of genotype aa =  $q^2 = 36\% = 0.36$  (so  $q = 0.6$ )

### Alleles and Allelic Frequency

|                                   |   |
|-----------------------------------|---|
| Frequency of dominant allele (A)  | p |
| Frequency of recessive allele (a) | q |

Hardy-Weinberg equation for allelic frequency:  
 $p + q = 1$ .

### Genotype Frequency

| Observed Trait       | Genotype | Frequency | Phenotype |
|----------------------|----------|-----------|-----------|
| Dominant homozygous  | AA       | $p^2$     | White     |
| Heterozygous         | Aa       | pq        | White     |
| Recessive homozygous | aa       | $q^2$     | Black     |

Hardy-Weinberg equation for genotypic frequency:  $p^2 + 2pq + q^2 = 1$ .

### Steps in Solving Problems Using Hardy-Weinberg Equation

1. Assign the frequency of dominant and recessive alleles (dominant as p and recessive as q).
2. Calculate q by taking the square root of the number of homozygous recessive individuals.
3. Calculate p ( $p + q = 1$ , so  $p = 1 - q$ ).
4. Using values of p & q, calculate the genotype frequencies ( $p^2$  – frequency of dominant homozygous genotype,  $2pq$  – frequency of heterozygous genotype,  $q^2$  – frequency of recessive homozygous genotype).



**Step 1**

Let us assume that dominant allele “A” which bears frequency “p” stands for white color, and recessive allele “a” which bears frequency “q” stands for black color.

**Step 2**

The key to solving frequency distribution problems lie in the number of homozygous recessive individuals because they can be easily identified.

$$q^2 = 36\%, 0.36, \text{ so } q = 0.6$$

**Step 3**

$$p + q = 1, \text{ so } p = 1 - q$$

$$\text{So } p = 1 - 0.6 = 0.4$$

**Step 4**

$$p = 0.4, \text{ so } p^2 = 0.16 \text{ or } 16\%$$

$$2pq \text{ (heterozygous)} = 2 \times 0.4 \times 0.6 \\ = 0.48 \text{ or } 48\%$$

Verifying the values with the original equation for genotype frequency estimation,

$$p^2 + 2pq + q^2 = 1 \text{ or } 0.16 + 0.48 + 0.36 = 1$$

Using the Hardy-Weinberg equation, if genotype or allelic values and dominant/recessive traits are known, phenotype frequency distribution can be also derived.

**Cross-References**

- Alleles
- Base Pair
- Crossover
- DNA
- Gene
- Gene Expression
- Genetic Variation

- Genotype
- Homozygosity
- Mendel's Laws
- Recessive

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**Frequency-Dependent Selection**

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**Synonyms**

Antipostatic selection; Minority advantage;  
Rare-type advantage

**Definition**

Frequency-dependent selection occurs when the fitness of genotypes vary as a function of the genotypic composition of the population.

**Introduction**

Frequency-dependent selection is a type of natural selection where the fitness of a given genotype depends on its frequency in the population.

Frequency-dependent selection is operated via **negative frequency-dependent selection (rare-type advantage)**, where the fitness of a genotype/phenotype increases when its frequency in the population is rare, and **positive frequency-dependent selection**, where the fitness of a genotype/phenotype increases when its frequency in the population is abundant.

In the development of the concept of frequency-dependent selection, interest was clearly focused on negative frequency-dependent selection because of its theoretical importance. Suppose that there is an allele  $A_1$  which is dominant over  $A_2$  and  $A_1A_1$  and  $A_1A_2$  have the same fitness, which is different from that of  $A_2A_2$ . If the fitness of  $A_1A_1$  and  $A_1A_2$  is higher than that of  $A_2A_2$  when  $A_1$  is rare, but becomes lower when  $A_1$  is frequent, so that, a stable polymorphism can exist (Charlesworth and Charlesworth 2010). Thus, this type of selection mechanism is essential for maintaining the genetic variability in population.

### Examples of Frequency-Dependent Selection

Many examples are available which confer that negative frequency-dependent selection occurs more commonly. One example is **apostatic selection**, in which there is selection by predators that learn while they hunt; this favors rare forms of prey (Clarke 1969). Vertebrate predators, such as birds, tend to form search images of their prey. For example, if a snail with a particular shell color is encountered, and is found to be good to eat, the bird will look out for more of the same. Rare color variants that differ from the majority of the population will tend to be ignored and experience lower predation rates. This will cause them to rise in its frequency, but the birds will then start to encounter them more frequently. The selective advantage will then decrease, possibly resulting in a stable equilibrium with both forms present. Similar studies have shown that the strength of the observed selection is affected by prey density, palatability, coloration, and conspicuousness. When the prey density is very high, sometimes

selection becomes “**antiapostatic**”: predators preferentially remove rare prey.

Another very important example is a system in which frequency-dependent selection causes the maintenance of polymorphism in self-incompatibility in hermaphroditic species of plants (Wright 1939; Vekemans and Slatkin 1994; Schierup et al. 1998). Genetic studies of plant species with an inability to self-fertilize have shown that these are often controlled by one or a small number of “ $S$  loci,” which are among the most highly polymorphic genes known in terms of numbers of alleles (Richman et al. 1996; Sato et al. 2002). The simplest such system involves a single gametophytic self-incompatibility locus, found in plants. Pollen grains carrying an allele  $S_i$  at the  $S$  locus cannot fertilize ovules of plants that also carry  $S_i$ , and these pollen grains tubes usually fail to grow down the stigma to the ovary. This means that all plants in the population are heterozygous for two different  $S$  alleles, and that there must be at least three of these for the plant to be able to cross-fertilize each other and allow the population to survive. Usually, at least a dozen or more  $S$  alleles are found in a population. A mutation that creates new  $S$  alleles will have a selective advantage, since pollen carrying a new variant can fertilize any plant in the population, whereas pollen carrying an established allele cannot fertilize the fraction of the population that carries that allele. This selective advantage will decline as the new allele increases in frequency; if the alleles have no other effects on fitness, equilibrium will be achieved when all possible heterozygotes have equal frequencies.

In *Drosophila*, the phenomenon of rare male mating (minority male mating) is an example of negative frequency-dependent selection (Singh and Sisodia 2000). It occurs when two types of males are present in unequal proportions and the females preferred that type of male whose frequency is relatively low.

A recent example of negative frequency-dependent selection in *Drosophila melanogaster* describes the maintenance of behavior polymorphism which is directly linked to naturally occurring functional alleles of the foraging (*for*) gene (Fitzpatrick et al. 2007). “Rover” (*for<sup>R</sup>*) larvae move more than “sitter” (*for<sup>S</sup>*) larvae when

foraging within a food patch, and they are also more likely to explore new food patches than are sitters. However, when they are raised in low-nutrient conditions, both of the naturally occurring alleles of foraging gene (*for<sup>R</sup>* and *for<sup>S</sup>*) have their highest fitness when rare. This effect disappears at higher resources level demonstrating the role of larval competition.

Frequency-dependent selection also arises from the relation between hosts and parasites (Haldane 1949). Possibly, many amino acid polymorphisms in the major histocompatibility complex (MHC) loci of vertebrate are maintained by frequency-dependent selection.

### Evolutionary Significance of Frequency-Dependent Selection

Balanced polymorphism is essential for maintaining the genetic variability in the natural population. This can be achieved by either heterozygote advantage or frequency-dependent selection. With constant fitness, selection acting at a single locus always maximizes the mean fitness of a randomly mating population, even though homozygotes with lower fitness are present when there is heterozygote advantage. On the other hand, when fitnesses are not constant, even if there is no heterozygote advantage, genetic variability can be maintained by other forms of balancing selection, i.e., frequency-dependent selection.

### Cross-References

- [Genetic Variation](#)
- [Heterozygote Superiority](#)

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## Friendliness

- [Xenophilia](#)

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## Friendships in Animals

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### Synonyms

[Animal social relations](#); [Relationship quality](#)

### Introduction

Friendship in animals has long been considered an anthropomorphism, and the use of the term was

consequently a taboo. Joan Silk, while advocating the use of term, even referred to it as the “F”-word in primatology (Silk 2002). The debate about animal friendship originates, at least partly, by the lack of a proper definition. The Oxford dictionary of English defines friendship as *a relationship between friends* and more broadly as *the emotions or conduct of friends*. Whereas the former provides little help as to compare the social relationships of humans and other animals, the latter is rather subjective, be it while comparing the emotions involved in friendships of humans and other animals, or even when comparing the emotions involved in friendships of different people. Rather than discussing semantics, however, it may be useful to first have a look what friends, be it human or non-human, are actually doing.

From a more behavioral point of view, Robert Hinde (1976) defined a relationship as a series of interactions in time, and based on the nature of these interactions, in their specific context, these relationships can be defined as good or bad. Good relationships are thus defined as a series of positive interactions, and the measures that are often used to quantify such good relationships are (tolerance for) close proximity and social grooming or other forms of gentle body contact (e.g., embracing and preening) (Massen et al. 2010). As these objective measures are comparable for humans and other animals, first primatologists, and later also researchers that work on different species, have started to adopt the term friendship for such good relationships or close social bonds.

In an attempt to reconcile “costly” investments such as grooming with the theory of evolution, Hans Kummer (1978) recognized that such differential relationships do not emerge randomly, but that specific relationships have specific value. In particular, the value of a relationship may be the support or protection of the individual with whom one has such a good relationship. Later, this value of a relationship has been integrated in a more detailed and overarching description of relationship *quality* that also includes the security or consistency of a relationship, and the compatibility of a relationship (Cords and Aureli 2000). Nevertheless, this value of relationships has incited a long-

lasting debate among biologists, as well as between biologists and psychologists about the comparability of human friendships and those of other animals. Because, such short-term “business partnerships” (Barrett and Henzi 2002) are *clearly* different from the unconditional friendships of humans. In fact, Hinde’s definition of a relationship as a series of interactions *in time*, makes it inevitably dynamic and subject to short-term changes. Consequently, it is indeed important to distinguish short-term relationships that only cater current needs from long-term stable social relationships.

Many relationships of animals, including those of humans, are short-term, and interest and investment in particular relationships may follow economic market forces like supply and demand (a.k.a. biological markets: Noë and Hammerstein 1994). For example, males start entertaining affiliative relationships with females only when they are in estrous, and their investment in that female (e.g., the amount of time they groom them) depends on how many other females are in estrous (supply) and how many other males are interested (demand). Nevertheless, not all relationships follow such patterns. Some relationships remain stable over long periods of time, and these are what we call friendships, at least in humans. However, not only humans have such long-term stable affiliative relationships with others, and by now we know that, for example, chimpanzees can have stable friendships that last at least 10 years (Mitani 2009), and similar patterns have been observed in other primates, but also in elephants (Moss et al. 2010), dolphins (Connor et al., 2000), and several bird species (Bugnyar and Massen 2017). With evidence accumulating that animals do not merely have short-term goal-orientated relationships but also show long-term stable relationships, by now the term animal friendship has been accepted in the academic world (e.g., Seyfarth and Cheney; 2012).

## The Adaptive Value of Friendships

If these enduring friendships are not contingent on current needs, why do we humans and all those

other animals nonetheless entertain such costly long-term investments? A common answer to that question is that a friendship is rewarding in itself; i.e., we experience joy when spending time with friends. Indeed, such emotional responses to proximity to friends can easily be detected, yet from an evolutionary point of view such endorphin peaks do not constitute any fitness benefit (i.e., ultimate causation), but instead provide “merely” the system (i.e., proximate causation) that entices us to form such friendships (c.f. Tinbergen 1963). However, for a behavior like forming and maintaining friendships to evolve it should also have direct (i.e., an increase in survival/longevity and/or reproductive success) or indirect fitness benefits.

Many of the long-term and stable relationships we observe in both animals and humans alike are among kin; by helping our relatives (i.e., nepotism), we *indirectly* promote the contribution of (part of) our own genes to the next generation (i.e., kin-selection: Hamilton 1964). Nevertheless, some of the friendships we observe among humans and other animals are with unrelated conspecifics, or even with individuals of a different species (e.g., human bonds with their dogs), and recent research has elucidated that those friendship also have fitness benefits. In fact, having friends is shown to increase people’s odds of survival by an equal amount as quitting to smoke does (Holt-Lunstad et al. 2010). In non-human animals having friends may be paramount to, for example, surviving a harsh winter (MacFarland and Majolo 2013) or to gain access to mating opportunities (Schülke et al. 2010). Indeed, in the last decade, evidence for fitness benefits of friendship has been accumulating; be it increased access to food or mates, or protection for both the animal itself or its offspring against extreme weather conditions, predators or aggressive conspecifics. Moreover, this evidence does not just include studies on humans and other primates, but encompasses a range of species including, for example, horses, elephants, hyraxes, dolphins, hyenas, kangaroos, but also birds like, for example, geese and ravens.

## Cooperation

Many of the fitness benefits related to friendship arise through cooperation. For example, animals may cooperate while hunting, thereby gaining access to high-value food sources, or team up to fight conspecifics in competition over resources, be it food or mates, or to fend off predators or aggressive conspecifics. Long-term studies on a range of species have now shown that it is specifically friends that form such alliances and support each other in conflicts (e.g., Schino 2007). Additionally, several behavioral experiments testing cooperation in a range of species have shown that the strength of the social bond is indeed the main predictor for success in such cooperation tasks, and that, if given the choice, animals prefer to cooperate with friends rather than with just anybody (e.g., Asakawa-Haas et al. 2016). Relying specifically on friends while cooperating may be beneficial as your long history with them makes them more predictable and trustworthy. Consequently, not only humans but also, for example, chimpanzees place greater trust in their friends than in non-friends (Engelmann and Herrmann 2016).

Trust in a partner becomes really important when the benefits of cooperation are not acquired at the same time for both partners; i.e., when one individual helps another now, and the other reciprocates that help when the former individual needs it at a different point in time (i.e., reciprocal altruism: Trivers 1971). Such an interaction carries a form of uncertainty because you do not know if the other keeps up to his/her part of “the deal,” as there is the possibility of freeriding. To prevail, one needs to keep track of such cheaters and not interact with them anymore and only maintain interactions with those that reciprocate. However, the cognitive requirements underlying such tit-for-tat reasoning have been subject of debate (e.g., Brosnan and de Waal 2002), as many animals are considered unable to keep track of everything given and received from all their group members, especially when living in large groups. Whereas humans may be able to do so (which can be debated considering the large-scale societies we live in), in fact, humans tend not to revert to such “calculated reciprocity” (see Brosnan and de



Waal 2002) in their everyday interactions. Instead, in their decisions on whether to invest they rely on the feelings they have for a certain interaction partner. Such emotionally based reciprocity (Schino and Aureli 2010) relies on series of interactions with a partner to create such specific emotions and is not necessary contingent on the short-term but rather on the long-term. Whereas such a system may be exposed to short-term inequality, it is constantly updated, and that friend that never buys a round of drinks may slowly become less of a friend and consequently will also receive fewer drinks from his/her “friends” after a while. Observational data on exchange patterns among a variety of species shows that also among non-human animals, these exchanges are mostly not contingent on the short-term but rather on the long-term. Moreover, it has been shown experimentally that animals base their decisions of, for example, food sharing on the more long-term qualities of a relationship, rather than on immediate reciprocation.

## The Requirements of Friendships

In contrast to when we interact with strangers, when dealing with friends we do not seem to actively keep track of what is given and received (Massen et al. 2010). Consequently, having friends may sound like one of the simplest things there is. Nevertheless, creating and maintaining such unique social bonds does require some cognitive skills and some biochemical regulations. However, by now many studies have shown that not only humans have the cognitive requirements for friendships, and moreover, that the biochemical mechanisms that allow for such relationships seem evolutionary old and are shared among many animal species (Brent et al. 2014).

### Cognitive Requirements

To have friends, you need to know who they are; i.e., distinguish them from other individuals. Individual recognition may seem a given, but not all animal species have it, or at least for some there is no proof so far (Sheehan et al. 2014). Nevertheless, it is widespread in the animal kingdom with examples in both vertebrates and invertebrates,

which are using either visual, vocal, or olfactory cues or a combination of those to distinguish individuals from each other (Tibbetts and Dale 2007). Next you need to understand your relationship with that other and, if separated for a while, also remember the nature of that relationship. Because it could be harmful if you start treating your former enemies as friends, many species do indeed remember and understand the nature of their relationships with others.

Besides knowing who your friends are, it may also be beneficial to know who the friends of your enemy are. For example, you don’t want to pick a fight with someone, if at that moment that individual has multiple friends standing next to him/her. Thus, to have an understanding of the relationships of others can be very important for surviving in large social groups, and it is the need for such social intelligence that is hypothesized to be the driving force in the evolution of large brains (Byrne and Whiten 1999). Having such knowledge may be particularly beneficial if used to ones own advantage in a Machiavellian way (see ► “Machiavellian Intelligence”). For example, ravens seem to monitor the affiliative relationships of their conspecifics, and when they notice that others attempt to become friends and thus potentially form a powerful competitive alliance, they intervene in the affiliative behaviors of those two birds thereby preventing them from forming that bond (Massen et al. 2014).

### Biochemical Mechanisms

As mentioned before, friendships seem to be regulated, at least partly, by emotions. The emotions involved in friendship do not only have a behavioral and cognitive component, but also, like any emotion, require a certain physiological infrastructure. Not surprisingly, oxytocin (which has sometimes been dubbed the “love hormone,” but see De Drue and Kret 2015) does seem to play a major role. Oxytocin, mesotocin (the oxytocin homologue in amphibians, reptiles, and birds), or isotocin (the oxytocin homologue in fish) promote and facilitate different aspects of social bonding like for example trust and cooperation, in both humans (De Drue and Kret 2015) and other animals (Young and Wang 2004). Additionally,

$\beta$ -endorphins, which are involved in the reward system, are released during certain social behavior. As these  $\beta$ -endorphins induce positive affect, this mechanism may be a crucial driving force in the initiation of friendships (Keverne et al. 1989). In contrast, a lack of social contact may be stressful (e.g., Stocker et al. 2016), and the avoidance of associated high cortisol levels, may form an alternative reason for the initiation of friendships. Finally, a combination of different biochemicals and their interactions with each other play important roles in, for example, the perception of social stimuli and social memory but also in aggressive behavior (see Brent et al. 2014 for a nice overview).

## The Development of Friendships

Relatively little is known about how friendships start and develop over time, as it is rather difficult to pinpoint the exact start of “a series of interactions” and to check whether there is actual partner choice at play. Many social relationships seem structured by the society the animal lives in. For example, in societies that are based around matrilineal friends are often kin. Also, just by avoiding aggression, hierarchical societies are structured such that dominance status leads to spatial centrality in the group (Hemelrijk 2000). Thus, dominant individuals spend most of their time close to each other in the center of the group, whereas more subordinate individuals spend most of their time with other subordinates at the periphery of a social group. As a consequence, many friendships are based on similarities in traits like dominance rank, but also for example age (e.g., Silk et al. 2006). Likewise, having similar interests can influence the spatial structure of a social group in such a way that you end up next to each other. For example, curious individuals are always at the forefront of a population and just by association may become friends (Croft et al. 2009). Alternatively, you may actively choose to spend your time with individuals that have similar interests and or personality. Similarity increases predictability (as you know what you would do in a given situation) and could consequently increase

trust in cooperation. Recent research does indeed show that, like humans, animals choose their friends based on similarity in personality (Massen and Koski 2014).

## Conclusions

After some controversy in the early days of animal cognition and behavior studies, by now the term animal friendship is accepted across the field. Studies on a multitude of species show that animals entertain differentiated relationships with their group members, and like human friendships, the affiliate relationships between animals are not just short term “business deals” but instead can be stable over long time periods.

Friendships of humans and other animals are adaptive as they provide clear fitness benefits, be it survival or increased reproductive success. Most of these benefits are acquired by cooperation, and animals indeed do cooperate more often and more successfully with their friends in comparison to with other conspecifics, and consequently, also seem to actively choose to cooperate with their friends. If cooperation concerns the reciprocal exchange of goods and services, animals, and in particular friends, do not keep an active count of what has been given and received. Instead, they rely on an emotionally based mechanism, in which decisions to give are based on the long-term qualities of the relationship with the interaction partner.

To have friends requires some cognitive capacities. First off you need to be able to recognize and differentiate individuals from each other, and second, you need to recognize and remember the specific relationship you have with certain individuals. Additionally, understanding the relationships of others may also be beneficial when maneuvering in a complex social world. From a physiological perspective, friendship concerns a mix of biochemicals that operate different systems within the brain. And like the cognitive aspects, these systems seem evolutionary old and shared among a range of different species.

Finally, the ontogeny of friendship is relatively understudied, particularly because it is difficult to

observe the actual start of a friendship. Nevertheless, some retrospective studies are showing that many friendships are based on homophily; i.e., love of the same. Friends may be similar with regard to rank or age simply by association. Alternatively, animals actively choose to befriend individuals that are similar with regard to personality, since these are more predictable and may consequently be trustworthier in future cooperation. As the saying goes, it does indeed seem like that “birds of a feather flock together.”

## Cross-References

- ▶ [Altruism](#)
- ▶ [Andrew Whiten](#)
- ▶ [Dorothy Cheney](#)
- ▶ [Frans de Waal](#)
- ▶ [Kin Selection](#)
- ▶ [Machiavellian Intelligence](#)
- ▶ [Oxytocin](#)
- ▶ [Primate Social Structure](#)
- ▶ [Reciprocity](#)
- ▶ [Richard Byrne](#)
- ▶ [Robert Hinde](#)
- ▶ [Robert Seyfarth](#)
- ▶ [Robert Trivers](#)
- ▶ [Sarah Brosnan](#)
- ▶ [Social Behavior](#)
- ▶ [Social Grooming](#)
- ▶ [Social Intelligence Hypothesis](#)
- ▶ [Social Network Analysis](#)
- ▶ [Sociobiology](#)
- ▶ [Ultimate Causation](#)
- ▶ [William Donald Hamilton](#)

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## Frog Locomotion

### ► Salientia Locomotion

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## Frugality

### ► Parsimony

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## Fruit Bat Locomotion

### ► Megachiroptera Locomotion

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## Frustration Effects

### ► Contrast Effects

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## FSH

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## Synonyms

Follitropin alfa; Follitropin beta

## Definition

Follicle-stimulating hormone (FSH) is a glycoprotein hormone that acts primarily at the gonads to regulate multiple aspects of reproductive physiology in both males and females, including gametogenesis, follicle maturation, and steroidogenesis.

## FSH Structure

FSH, and the closely related luteinizing hormone (LH) and chorionic gonadotropin (CG) form a class of hormones called the gonadotropins that

regulate the physiology and function of the gonad. FSH and LH are produced and secreted by gonadotrope cells in the anterior pituitary gland and all gonadotropins are composed of two distinct subunits, an alpha subunit that is common to FSH, LH, CG, and thyroid-stimulating hormone, and a beta subunit that differs among these four hormones and confers specificity of function to each. The alpha and beta subunits are bonded noncovalently and each contain numerous oligosaccharides attached to the amino acid backbones. Different patterns and classes of attached oligosaccharides result in multiple alpha and beta subunit isoforms that differ in circulating half-life, receptor binding properties, and bioactivity (Mullen et al. 2013). These moieties also differ across life-history stages, such as during puberty and pregnancy, resulting in altered FSH dynamics across the lifespan (Mullen et al. 2013).

## Regulation of FSH Synthesis and Release

### HPG Axis

In both sexes, synthesis and release of FSH is tightly regulated by a multi-tiered, negative-feedback system called the hypothalamic-pituitary-gonadal axis (HPG axis). In this system, reproductively relevant information from the brain and periphery is integrated by a population of neurons in the hypothalamus that express the peptide gonadotropin-releasing hormone (GnRH). GnRH is released from axon terminals into the pituitary blood supply to activate gonadotropes that produce and release both FSH and LH into the general circulation. Together, these gonadotropic hormones regulate steroidogenesis – the production of steroid hormones, particularly estradiol and testosterone – and gametogenesis in both sexes. The newly produced gonadal steroids, along with a number of other gonadotropin-stimulated gonadal peptide hormones, feedback to the hypothalamus and pituitary to inhibit further gonadotropin release. This negative feedback system maintains circulating concentrations of FSH and LH appropriate to the animal's life-history stage and reproductive status.

## FSH Function Across Life-History Transitions

Given its critical role in reproductive physiology, FSH production and release tends to coincide with periods of reproductive competence or heightened gonadal steroidogenesis across the lifespan (with the notable exception of reproductive decline/senescence, see below).

### Adulthood

#### Females

FSH is critical for the maturation of female gametes. Prior to ovulation, FSH serum concentrations are high and contribute to recruitment and maturation of a new cohort of ovarian follicles each reproductive cycle (Hall 2016). After ovulation, FSH decreases until it rises at the initiation of the next round of follicular maturation.

FSH also prepares the ovary to initiate and respond to factors regulating ovulation from the mature follicle. Specifically, FSH increases ovarian expression of the LH receptor and aromatase, an enzyme necessary for the synthesis of estradiol. The latter event is critical because elevated estradiol initiates ovulation by stimulating a surge of LH from the anterior pituitary. Thus FSH and LH complement each other to promote normal reproductive competency during female reproductive cycles.

#### Males

FSH, in conjunction with locally synthesized testosterone, helps to initiate and maintain spermatogenesis (Plant and Marshall 2001). FSH receptors are localized to, and induce proliferation of, Sertoli cells that are located within the blood-testis barrier. Each Sertoli cell is responsible for supporting a finite number of germ cells, resulting in a direct relationship between FSH-induced proliferation of Sertoli cells and maximum adult spermatogenic capacity (Liu and Veldhuis 2016). FSH is not thought to contribute directly to testosterone production; however, FSH does stimulate production of estradiol and a complement of proteins that may act locally to regulate intratesticular physiology and steroidogenesis (Gnessi et al. 1997).



### Fetal/Neonatal Period

In placental mammals, the HPG axis is active shortly after birth, resulting in high circulating concentrations of FSH during early infancy. During this time, FSH contributes to proliferation of Sertoli cells in males (Liu and Veldhuis 2016) and supports FSH receptor expression and follicular development in ovarian follicles, both of which set the stage for activation and maintenance of normal reproductive function in adulthood.

### Puberty

During the juvenile period of development, the HPG axis is quiescent and FSH levels decrease to basal concentrations. At the onset of puberty, HPG quiescence declines and FSH concentrations rise in both sexes. The elevation in FSH induces the initial stages of folliculogenesis in females (Hsueh et al. 2015), while in males it initiates sperm production and a second round of Sertoli cell differentiation (Plant and Marshall 2001), which is subsequently maintained by high local concentrations of androgens. Thus, in both sexes the pubertal rise in FSH increases fecundity, coincident with steroid-mediated maturation of pubertal reproductive behavior, and somatic physiology.

### Pregnancy, Parturition, and Lactation

In mammals, normal ovarian cyclicity is eliminated during pregnancy, resulting in a virtually complete decline in maternal circulating FSH and LH for the duration of pregnancy. Upon parturition, FSH concentrations rise and are maintained at normal follicular phase levels. In women, varying durations of lactational amenorrhea may occur; however, FSH continues to stimulate follicular growth during lactation, even though ovulatory cycles are prevented due to decreased steroidogenesis (Velasquez 2006).

### FSH and Fertility: Menopause, Andropause, and Infertility

Some species outlive their periods of maximal fertility, resulting in either reduced fertility or

complete cessation of reproduction with aging. In women, one of the earliest hormonal harbingers of menopause is an increase in FSH, due to the loss of negative feedback that results from decreased ovarian steroidogenesis (Hall 2015). Further decline in circulating gonadal steroids, but maintenance of normal hypothalamic and pituitary function, leads to decreased negative feedback and a chronic ~15-fold increase in circulating FSH after menopause (Hall 2015). Males also experience a decline in reproductive competence with aging, though it is neither as abrupt nor as drastic, resulting in a gradual two- to threefold increase in circulating FSH in elderly men (Snyder 2016).

### Evolution

Glycoprotein alpha and beta subunits arose in early metazoan evolution. However, the FSH beta subunit, marking the origin of FSH, likely diverged from this ancestral gonadotropin sometime during the early evolution of jawed fish, resulting in the presence of an FSH beta homologue throughout jawed vertebrate phylogeny (Kawauchi and Sower 2006).

Within a given species, the FSH beta subunit tends to show low genetic variation, purportedly because its critical role in the maintenance of reproduction places significant constraints on its evolution. Across species, a high degree of similarity in the three-dimensional structure of FSH likely results from the conservation of the locations of cysteine residues and disulfide bridges (Mullen et al. 2013).

In females, the function of FSH has been largely conserved across jawed vertebrates but its role in initiating spermatogenesis is more labile across species. In fish, the FSH receptor is localized to both Sertoli cells and Leydig cells (which are the primary steroidogenic cells of the testis), while in mammals and birds the FSH receptor is localized to Sertoli cells alone (Huhtaniemi 2015). Notably, in fish the FSH receptor binds to both LH and FSH, providing a mechanism by which either gonadotropin may

initiate and maintain spermatogenesis and steroidogenesis in males.

## Environmental Influences on FSH Secretion

In temperate areas, avian and mammalian species commonly display seasonal variations in behavior and physiology that allow them to restrict the production and rearing of young to warmer, resource-rich times of year. During the reproductively inactive period, individuals show cessation of breeding behaviors and maintain low levels of circulating steroid hormones and gonadotropins, as well as regressed gonads (Ball and Bentley 2000). In a taxonomically diverse range of species (including rodents, ungulates, and songbirds), these changes are mediated by the transduction of photoperiod cues to the GnRH system and, in at least some species, the more recently discovered gonadotropin-inhibiting hormone (GnIH) system (Kriegsfeld et al. 2015). Notably, the specific impacts of day length on these systems and the timing of annual reproductive changes can vary considerably across species, depending in part upon whether they are long or short day breeders. However, in general, the reductions in LH and FSH secretion are observed during the non-breeding season and lead to suppressed gametogenesis and sex hormone production (Kriegsfeld et al. 2015).

## Conclusion

Work across many decades has done a great deal to clarify the critical role of FSH in reproduction. However, additional FSH functions may exist. For instance, as recently as 2001, it was thought that FSH receptors did not exist in the brain and that FSH influenced reproductive behavior indirectly via its impact on sex steroid production. However, both FSH receptors and locally produced FSH have been identified in several brain regions and a diverse number of organs and tissues (Harvey et al. 2012), suggesting that FSH

may serve diverse functions across the brain and body that are not directly related to reproductive physiology.

## Cross-References

- [Estrogen](#)
- [Reproduction](#)
- [Testosterone](#)

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## Function

### ► Proboscidea Morphology

## Functional Genomics

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### Keywords

Genomics · High-throughput assays ·  
Microarray · Proteomics

## Definition

Functional genomics is one of the fields of molecular biology that is attempting to make use of the vast wealth data produced by genome sequencing projects to describe genome function.

## Background

Over a decade, several conventional biology methods like Southern analysis, Northern analysis, PCR, RT-PCR, RNase protection assay, and in situ hybridization detecting DNA or RNA that enabled to assess gene expression levels over

a multitude of paradigms including normative conditions, development, experimental manipulations, and pathological states. These well-accepted methods typically quantitate the abundance of individual transcripts or molecules one or few at a time.

Proteomics reveals complex protein expression, function, interactions, and localization in different phenotypes of neuron. As proteomics, considered as a highly complex screening technology, moves from a theoretical approach to practical reality, neuroscientists have to determine the most appropriate applications for this technology. In proteomics, protein fractionation and separation use two-dimensional gel electrophoresis (2-DGE) as well as multi-dimensional liquid chromatography (LC) followed by mass spectrometry (MS). For qualifying relative gene product expression between samples (e.g., two-dimensional difference in gel electrophoresis (2D-DIGE), isotope-coded affinity tag (ICAT) and iTRAQ methods have been utilized. The possible coverage of the proteome has ability to detect unique cell components such as post-synaptic densities and membrane proteins, resource requirements, and quantitative as well as qualitative reliability of different investigative approaches. While there are many challenges in neuroproteomics, this field promises many returns in the future.

Neuroscientists found it challenging to overcome difficulties particular to the research in neuroscience and behavioral genetics, such as limited sample amounts, heterogeneous cellular compositions in samples, and the fact that many proteins of interest are hydrophobic proteins. The necessity of exclusive technology, sophisticated software, and skilled manpower itself is the big challenge.

Developments in high-throughput functional genomic technologies enable the assessment of dozens to hundreds to thousands of genes simultaneously in a coordinated and potentially stochastic fashion (Schena et al. 1995; Lockhart et al. 1996; Brown and Botstein 1999; Eisen and Brown 1999). Transcriptome profiling experiments using microarrays are data-driven approaches with the potential power to uncover

unanticipated relationships between gene expression alterations and experimental manipulations or neuropsychiatric/neuropathological conditions.

Whenever, when we discuss that how the environment, particularly the social environment, does influence brain and behavior of animals, we ask and what are the underlying physiologic, molecular, and genetic mechanisms? The changes in social or physical environment leads to the adaptations by brain and behavior and expressed either as short-term or as long-term modifications in behavioral or physiologic properties in animals. Because living systems depend on their environment, the evolution of environmental adaptability is inseparable from the evolution of life itself (Pross 2003).

To explore and understand the complex relationship between genome and environment, functional genomics approach has been implemented. It determines the genes, under environmental control, which facilitate the study of interrelationship between an individual's gene expression profile and its social phenotype in a given environmental condition. In this chapter we will discuss, how functional genomics played important role in cognition and behavioral aspects of animals. It was outlined the advantages as well as some of the potential challenges of applying high-throughput functional genomic technologies toward a better understanding of neural and behavioral features.

## Introduction

According to EMBL-EBI, functional genomics is the study of how genes and intergenic regions of the genome contribute to different biological processes. Typically it studies genes or regions on a “genome-wide” scale (i.e., all or multiple genes/regions at the same time), with the hope of narrowing them down to a list of candidate genes or regions to analyze in more detail. It describes gene function, gene expression patterns, and control of gene expression of all genes in a genome and their interaction with different

cellular processes and phenotype. It is also helpful in investigation of gene expression change in various diseases or following a treatment.

The goal of functional genomics is to understand the complex relationship between an organism's genome and its phenotype. Functional genomics focuses on the dynamic expression of gene products in a specific context, for example, at a specific developmental stage or during a disease. It focuses on the high-throughput techniques like DNA microarrays at RNA level (transcriptomics), proteomics at protein level, epigenomics at DNA level, metagenomics at metagenome level while metabolomics at metabolite level and mutation analysis to describe the function and interaction of genes. Functional genomics typically utilize large-scale, high-throughput assays like DNA-microarray, RNAi analysis, or proteomics with samples from patients and healthy individuals to measure and track many genes or proteins in parallel. This “genome-wide” approach allows the function of different parts of the genome to be discovered by combining information from genes, transcripts, and protein.

## Functional Genomics in Cognition and Behavior Analysis

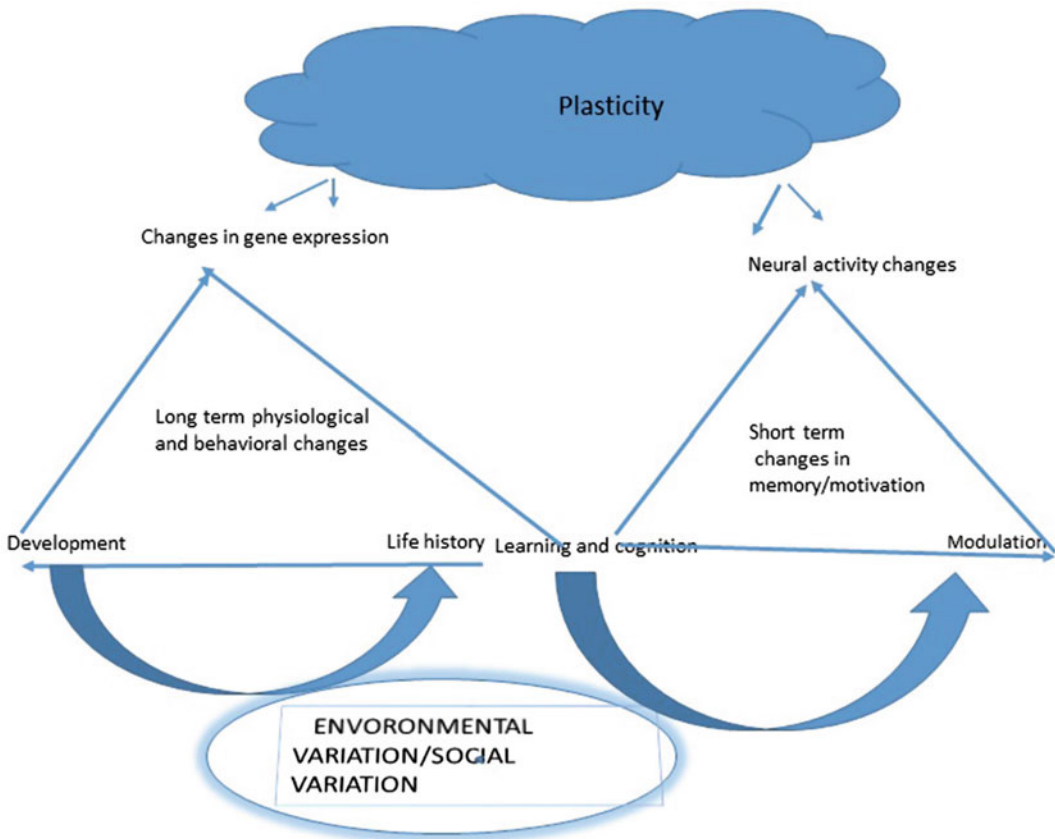
Living organisms adapt and survive in varying environments with the ability of their complex survival strategies. Diurnal or seasonal fluctuations of abiotic environmental factors such as temperature, oxygen availability, and salinity affect the life history strategies, physiologies, and behavior of organisms. In humans, social environment is an unavoidable factor deeply influencing the behavior and development of individual. One of the grand challenges in animal biology is to understand the influence of genes on the development of phenotypic and behavioral traits. Just like any other phenotypic trait, behavior is commonly influenced by both environmental and epigenetic factors (Pigliucci 2001). Because of this intricate relationship between genes and environment, the genetics of behavior and of the most common diseases requires the dissection and analysis of complex phenotypes or traits.

In cases where the frequency of the environmental change (the stimulus) is high or when immediate action is required, nervous systems can respond quickly by means of modulation or through learning. Those dynamic changes of the internal state of an animal (e.g., motivation, memory trace) are usually achieved, at least initially, by changes in neural activity and excitability or by endocrine responses.

Short-term changes will then often lead to subsequent changes in brain and behavior (e.g., memory formation) through differential gene expression as well as structural and physiologic changes. Environmental stimuli that are slow or relatively infrequent can alter developmental trajectories and shift neural functioning throughout life history, even in adult animals (e.g., seasonal and use-dependent changes). (See Fig. 1.)

By integrating concepts from neurobiology, ethology, and evolutionary biology with powerful genomic technologies, functional approach facilitates a more comprehensive understanding of the roles that genes and environment play in the dynamic and plastic sculpting of brain and behavior throughout life.

In fact, behavioral genetics has provided us with a wealth of information regarding the roles of individual genes in the implementation of behavior. Genetic and functional genomic studies have already yielded important insights into neuronal diversity and function, as well as disease. The major challenges facing the genetic study of behavior is intricate relationship to dissect and analysis of complex traits involve genetic, epigenetic, and environmental traits whose interactions are often unpredictable.



**Functional Genomics, Fig. 1** Conceptual diagrammatic representation of phenotypic plasticity of brain and behavior (Modified figure referenced from Hoffmann 2003)



One of the most exciting and challenging frontiers in neuroscience involves harnessing the power of large-scale genetic, genomic, and phenotypic data sets and then development of tools for data integration and mining for better understanding of the genetic mechanisms underlying behavior.

The functional genomics revolution allowed neuroscientists to provide a more integrative understanding of nervous system function. It allows the detailed study of individual molecules of interest to an understanding of interacting signaling or metabolic pathways within cells, by combining these data to achieve a systems-level understanding of brain circuit function in health and disease.

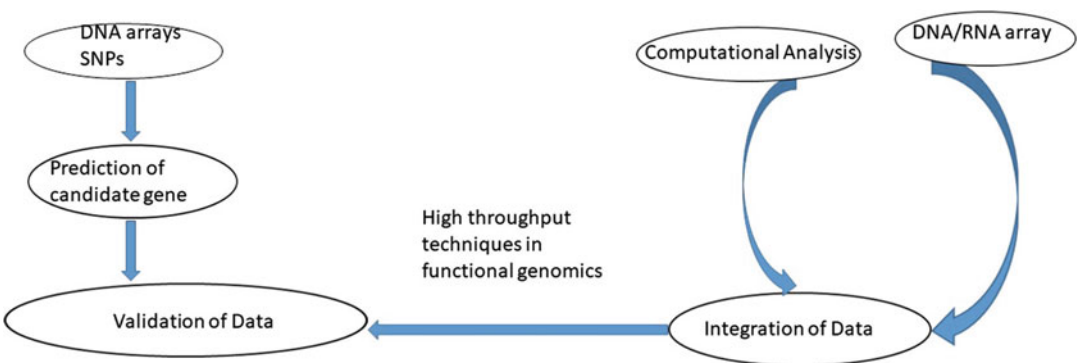
Animal's brain is complicated structure with heterogeneous neuronal and non-neuronal cell types with interconnected circuits. The advances in technical and experimental methods for accession of tissues, RNA amplification, and improved downstream genetic methodologies including microarray analysis and RT-quantitative PCR opened the door of informative studies pertinent to understanding brain structure and function thoroughly. However, transcriptome profiling by microarrays having the potential power to uncover unanticipated relationships between gene expression alterations and neuropsychiatric or neuropathological conditions. It also provides an affordable, simultaneous assessment of expression levels of a sample preparation in a single experiment. For example, in the

hippocampus and basal ganglia for a variety of downstream genetic analyses in animal models, including studies of alcohol consumption (Saito et al. 2002), aging (Blalock et al. 2003), amyloid overexpression (Dickey et al. 2003; Reddy et al. 2004), and antidepressant administration (Drigues et al. 2003), microarray analysis has been utilized.

Henceforth, modern functional genomics with the inputs of large-scale high-throughput analysis of gene expression enabled the quantitative assessment of dozens to hundreds to thousands of genes simultaneously in brain regions and individual cell populations. Thus, functional genomics approach facilitates the dynamic measurement of gene products in a parallel manner, coupled with an underlying systems-level knowledge of the organization of these gene products (see Fig. 2).

## Functional Genomics in Psychiatric/ Behavioral Disorders

The complete raw data obtained by high-throughput microarray or mass spectrometry technologies among others permits specialized computational methods for data analysis leading to the development of biomarkers, for example, biomarker discovery for neurological diagnosis and prognosis. By extracting significant genomic and proteomic biomarkers in controlled experiments, one can understand how biological



**Functional Genomics, Fig. 2** Presentation of a potential high throughput framework for functional genomics (Modified figure referenced from Ding and Lawrence 2001)

mechanisms contribute to neural degenerative diseases such as Alzheimer's and how drug treatments interact with the nervous system. The recent development of microarray technologies has made possible the simultaneous measurement of mRNA levels for thousands of genes and a new genomic method termed gene expression profiling. The application of this approach to animal models provides a powerful tool for the discovery of novel genes involved in psychiatric disorders. This approach has an efficiency to complement to another genomic method for gene discovery, positional cloning. Microarray technologies and their application to animal models of bipolar disorder were reviewed. A novel approach termed convergent functional genomics, which integrates gene profiling and positional cloning in order to rapidly identify candidate disease genes, was also described.

One of the difficulties of applying microarray and related genomic studies to neuroscience-based disciplines was that many classes of transcripts as well as individual genes tend to be expressed at relatively low levels (with corresponding low copy number for specific genes). In addition, gene expression patterns, or mosaics, often are cell-type specific and reflect the intricate connectivity of the brain, making global studies of gene expression patterns difficult to interpret, and the relevance of performing these types of studies comes into question (Galvin 2004; Ginsberg et al. 2004).

The power of functional genomics in neuroscience is highlighted by several successful demonstrations of the strength of such methods to identify the molecular basis of neuronal diversity synaptogenesis, disease biomarkers, disease mechanisms and pathways, and the development of user friendly genome-scale resources (Geschwind and Konopka, 2009)

Ayalew et al. (2012) reported regarding translational convergent functional genomics (CFG) approach to identify and prioritize genes involved in schizophrenia.

This study involved gene-level integration of genome-wide association study data with other genetic and gene expression studies in humans and animal models. The polyevidence scoring and pathway analyses, and identified top genes

in brain development, myelination, cell adhesion, glutamate receptor signaling, G-protein-coupled receptor signaling and cAMP-mediated signaling are utilized as key to pathophysiology and as targets for therapeutic intervention.

The top candidate genes for Schizophrenia, obtained from this analysis compared with top candidate genes for bipolar disorder and anxiety disorders from previously done CFG analyses, as well as findings from the fields of autism and Alzheimer. Overall, this work plots the genomic and biological landscape for schizophrenia, leading toward a better understanding of illness, diagnostics, and therapeutics.

Further, translational Convergent Functional Genomics (CFG) approach has been also applied to discover genes involved in alcoholism by using gene-level integration of genome-wide association study (GWAS) data from human and animal model studies.

By taking together, these results suggested that stress-reactive DBP animal model helped to validate and prioritize the key behaviorally relevant genes for alcoholism from the CFG-discovered genes.

These genes fall into a series of biological pathways involved in signal transduction, transmission of nerve impulse (including myelination), and cocaine addiction. Overall, this work provided a better understanding of illness, diagnostics, and therapeutics, including treatment with omega-3 fatty acids.

Also examined the overlapping between the top candidate genes for alcoholism from this work and the top candidate genes for bipolar disorder, schizophrenia, anxiety from previous CFG analyses conducted by us, as well as cross-tested genetic risk predictions. This finally revealed the significant genetic overlap with other major psychiatric disorder domains, providing a basis for comorbidity and dual diagnosis and placing alcohol use in the broader context of modulating the mental landscape.

Levey et al. (2014) studied about bipolar disorder in low mood vs high mood in blood samples from mouse and separately measured whole-genome gene expression differences in blood samples as well as changes in gene expression in

the brain and blood of a mouse as pharmacogenomics model.

The integration of human blood gene expression data with animal model gene expression data, human genetic linkage or association data, and human postmortem brain data has been called convergent functional genomics, especially performing cross-validating and prioritizing the findings.

Out of a list of 11 candidate blood biomarker genes, it was found that 5 genes involved in myelination (Mbp, Edg2, Mag, Pmp22 and Ugt8) and 6 genes involved in growth factor signaling (Fgfr1, Fzd3, Erbb3, Igfbp4, Igfbp6, and Ptpm). All of these genes have prior evidence of differential expression in human postmortem brains from mood disorder subjects. A predictive score of ten top candidate biomarkers (five for high mood and five for low mood) shows sensitivity and specificity for high mood and low mood states, in two independent cohorts. This study suggested that blood biomarkers might offer an unexpectedly informative window into brain functioning and disease state.

## Conclusion

The functional genomic methods permit, dynamic measurement of gene products in a parallel manner, coupled with an underlying systems-level knowledge of the organization of these gene products, has the potential to provide a more integrative understanding of nervous system function. The functional genomics approach has provided the better understanding of the complex relationship between an organism's genome and its phenotype. It focuses on evaluation of the dynamic expression of gene products in a specific context, by determining a specific developmental stage or during a disease.

Functional genomics employs high-throughput or microarray techniques to perform the dynamic studies. A microarray experiment has been thought appropriate but still demands much consideration needs to go into sample size and preparation, tissue and/or cell quality, and, importantly, input amount of RNA that would

likely to be generated. Sample preparation, RNA amplification, array hybridization, and array analysis usually require a long-term commitment; many investigators found out this method is frustrating.

Therefore, it was suggested that a combination of multidisciplinary approaches is ideal for verification and broad application of gene expression level alterations, with the explicit knowledge that the sum of the evaluations may be more informative and reflect the actual biology of the system than an individual method.

The revolutionary techniques of functional genomics permitted neuroscientists to get enhanced integrative understanding of nervous system function. It allows neurologists and behaviorists to thoroughly study individual molecules of interest to an understanding of interacting signaling or metabolic pathways within cells. By combining these data, researchers achieve a systems-level understanding of brain circuit function in health and disease.

## Cross-References

- [Bioinformatics](#)
- [DNA](#)
- [Genes](#)
- [Microarray](#)
- [Transcriptome](#)

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## Functionalism

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In this entry, we examine functionalism, which is often proposed as, and taken to be, a proper philosophical underpinning for the study of human cognition. We consider two important points. First, does functionalism actually provide a good underpinning for the study of human cognition? Second, does functionalism serve well as an underpinning when extended to the study of non-human animal cognition? We will suggest that the answers to these questions are no and suggest that there are other philosophical positions that provide a better, more integrated underpinning for the study of both human and nonhuman cognition. In particular, we will suggest that an Aristotelian-Thomistic (A-T) approach, recently proposed in cognitive psychology itself (Spalding and Gagné 2013; Spalding et al. 2014) and within the philosophy of mind (Feser 2006, 2014; Madden 2013), should be explored. We begin by reviewing the history of how functionalism came to be adopted by much of cognitive psychology and then discuss some of functionalism's weaknesses for human cognition. We then attempt to see what it would

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mean to extend functionalism fully to the study of nonhuman animal cognition. Finally, we present a brief argument that the A-T approach might be a better philosophical underpinning for the study of cognition, both human and nonhuman.

Confidence in logical positivism and operationism waned in both philosophy and psychology during the 1960s. At about the same time, psychology experienced the cognitive revolution, which reinstated mental states and processes as central to theory building and explanation. As Levin (2013) points out in her review, cognitive psychologists turned to the functionalist theory of mind as a philosophical underpinning for all aspects of cognition. This interchange produced psycho-functionalism, the dominant subtype of functionalism for cognitive science. As described by Levin:

A second strain of functionalism, psycho-functionalism, derives primarily from reflection upon the goals and methodology of “cognitive” psychological theories. In contrast to the behaviorists’ insistence that the laws of psychology appeal only to behavioral dispositions, cognitive psychologists argue that the best empirical theories of behavior take it [behavior] to be the result of a complex of mental states and processes, introduced and individuated in terms of the roles they play in producing the behavior to be explained. . . . All versions of functionalism, however, can be regarded as characterizing mental states in terms of their roles in some psychological theory or other. (p. 7)

Hence, as Levin sees it, functionalism in all its aspects is intertwined with cognitive psychology at both the philosophical and psychological levels.

## Analytic Philosophy and Functionalism

Analytic philosophy, spawned in Britain as a reaction to idealism, dominates English-speaking philosophy to the present time. As Preston (2007) demonstrates in his review of the history of analytic philosophy, the movement was initiated by Russell and Moore, refined as logical atomism by Russell and Wittgenstein (see Wittgenstein 1922), elaborated by the Vienna Circle as logical positivism (Ayers 1952), seriously questioned by Quine (1951), and later reinvented by Wittgenstein (1953). Preston

characterizes contemporary analytic philosophy, the home of the philosophy of mind, as eclectic and interested in limited metaphysical problems, as still grounded in language analysis and semantics, and as interested in the kinds of thought experiments often used by philosophers of mind. Although current philosophers of mind are split along property dualist (e.g., Chalmers 1996) and materialist (Armstrong 1968) lines, all agree that cognitive processes, from sensation and memory through all of the higher-order phenomena of thinking, reasoning, categorization, planning, etc., can be explained by the doctrine of functionalism. In fact, Chalmers (1996), though a property dualist, asserted this about functionalist cognitive models:

Cognitive models are well suited to explaining psychological aspects of consciousness. There is no vast metaphysical problem in the idea that a physical system should be able to introspect its internal states, or that it should be able to deal rationally with information from its environment, or that it should be able to focus its attention first in one place and then in the next. It is clear enough that an appropriate functional account should be able to explain these abilities, even if discovering the correct account takes decades or centuries. (p. 31)

In her review, Levin (2013) points out that functionalism has antecedents (e.g., Wittgenstein 1953) but emerged as a definitive philosophical position in the last 35 years of the twentieth century. Feser (2006, Chap. 3) provides a brief and readable explanation of how functionalism developed in response to problems with other strictly materialist philosophies, such as philosophical behaviorism and identity theory. Several major strains of functionalism developed: machine functionalism, psycho-functionalism, and analytic functionalism. So, far from being monolithic, functionalism itself is divided, with arguments in favor of and attacking the various strains.

Machine functionalism was the first of the three developed and appeared to answer a number of problems with behaviorism, for example, critiques pointing out that behaviorists seemed to undervalue internal mental states, such as beliefs and desires, when those constructs contributed implicitly to their theories. Machine functionalism postulated that any “mind” can be regarded as a



finite digital computer, one that receives inputs (14), while in a certain state (S1), goes into other states (Sx), and produces output (0). The person with a mind is viewed as a probabilistic automaton, so for each state and sets of inputs, the machine (mind) will enter a subsequent state and produce output according to certain probabilities. These internal mental states were called representations, and the nature of these representations was and is disputed. Over time, early machine functionalism's ties to a "machine table" or program came to be seen as inadequate. However, the basic idea involving inputs, lawful interactions of internal states, and final outputs has been retained in later functionalist approaches.

Psycho-functionalism is closely tied to the emergence of cognitive psychology in the late 1960s and maintains that mental states and processes are entities (constructs) that are defined by the role they play in cognitive psychological theories. They may be tied to brain structures and processes, but this is not a requirement. However, there does seem to be a trend toward attempting to ground these constructs in neuroscience (see Stedman et al. 2009). These constructs can include mental states and processes easily identified with common sense (folk psychology) or can go beyond common sense to incorporate more refined constructs identified by laboratory findings, thus replacing folk psychology constructs.

Analytic functionalism (e.g., Armstrong 1968) asserts that all mental states, such as pain, hunger, belief, desire, consciousness, and so on, are constituted by their functional role, that is, to quote Chalmers (1996): "On this view, a mental state is defined wholly by its causal role: that is in terms of the stimulation that tends to produce it, the kind of behavior it tends to produce, and the way it interacts with other mental states" (p. 14).

In spite of these different forms of functionalism, advocates of functionalism hold for the following commonly: (a) functionalism offers a comprehensive ontological account either of all mental states or at least the psychological portion of mental states but not the phenomenal (Chalmers 1996); (b) some mental states, according to Chalmers and others, are primarily psychological and are fully accounted for by

functionalist ontology, including learning, memory, categorization, perception, and higher-order cognitive processes; and (c) some mental states, such as belief, desire, and hope, are referred to as intentional mental states in that they refer to something about the world. Many functionalists regard these states as primarily psychological and, hence, fully accounted for by functionalism. Chalmers (1996) views mental states as mixed. However, whatever in these states is psychological, he asserts, can be accounted for by a functionalist ontology.

As mentioned above, the models of cognitive psychology rest on functionalism as a philosophical foundation, specifically psycho-functionalism. Hence, cognitive psychology, via psycho-functionalism, is subject to all the ontological strengths and weaknesses of analytic functionalism.

Contemporary cognitive psychology theories are grounded in psycho-functionalism, expressed as models and/or mechanisms: for example, perceptual binding, working memory, category formation, and so forth. Some theories incorporate brain structures and processes and others do not. All postulate multiple, interacting mental states and processes that play definite roles in the theory. All are grounded in stimuli at the beginning and behavioral outcome at the end. Various psycho-functional cognitive theories compete, and their truth claims are established by empirical observations.

For example, consider the exemplar model of concept formation. The exemplar model claims that category (concept) formation occurs when people compare new information to exemplars stored in memory. This version of concept formation states that exemplars are learned through repeated presentations and naming of category members and the repeated naming allows the pairing of a common name with a set of exemplars, which in turn allows generalization over those exemplars when the name (or other similar cue) is presented. The exemplar model requires a number of psychological constructs: sensation, perception, learning (of exemplars), many constructs in the area of memory and recall, some mechanism accounting for comparing new stimuli

to exemplars, and an account of language to perform the response. Because cognitive psychology is increasingly linked to neuroscience, interactions with brain structures must also be factored in. Similar examples could be offered for all content areas of current cognitive psychology, and psycho-functionalism is expected to serve as the ontological and epistemological underpinning for all of cognitive psychology.

### **Problems with Functionalism as a Theory of Human Cognition**

As mentioned earlier, both property dualist and materialist philosophers of mind agree that functionalism is sufficient to account for all the “psychological” components of cognitive psychology. However, functionalism, as a philosophical position, has been challenged by philosophers of mind almost from its inception. Two of these objections will be presented in some depth.

A general objection to functionalism, well known in the philosophy of mind, is the “damn/darn problem,” brought forth by Block and Fodor (1972). Their objection lies within the broader theory of mental holism, which claims that the meaning of a belief (or a sentence expressing that belief) is determined by its place in a network of beliefs (or sentences) making up a whole theory or even a group of theories. They point out that a functional account of mental states must take into consideration any difference in stimuli or responses. Joe smashes his finger in the door and says, “Darn”; Clyde smashes his finger in the door and says, “Damn.” We have two equivalent stimuli but different responses. However, functionalists claim that outputs are related to all or many of the agent’s internal mental states, so two people who have pain but produce different outputs must share little, if any, common mental states. But this conclusion appears absurd. Hence, Block and Fodor believe that functionalism leads to an extreme and undefendable version of mental holism.

This critique is also important in that one of the presumed advantages of functionalism was that it would allow one to avoid the type/token problems

that arose in identity theories. In particular, a problem with identity theories is that if the mind/thought is taken to be identical to the brain/brain state, then there must be lawful relations between given brain states and thoughts, but there seem clearly to be logical relations among thoughts, but only physically (efficiently) causal relations among brain states. This difference calls into question rather strongly the whole notion of identity between brain states and types of thought. Functionalism works around this problem by defining states with respect to their functional (including logical) relations to other states. However, if, as Block and Fodor (1972) claim, differences in response (including between individual tokens of a particular type of thought) dictate large differences in mental states, the mental holism implied by this removes this purported advantage of functionalism. In short, functionalism does not avoid a similar kind of problem as that identified in identity theories.

A second, and perhaps more damaging, critique asserts that functionalism, as an ontological claim, is trivial, that is, that functionalism’s internal structures (constructs), anchored by stimulus inputs and behavioral outputs, are not unique but can be present in many complex and less complex systems. This criticism has been stated recently by Godfrey-Smith (2008). These arguments all point out that the functionalist realization of a complex mental system is present when the set of mental states maps or corresponds to physical states of the system. These systems are known as combinatorial state automata (CSA) and can occur in a large number of formats, including a properly manipulated bucket of water! Godfrey-Smith (2008) asserts the following:

If a normal human’s functional organization over some interval is represented by a CSA, then our designer could build a transducer device that perturbs the bucket of water in specific ways in response to every possible sequence of inputs that a human might receive, and another transducer device that maps the water’s responses to appropriate behaviors. So a bucket of sea water could act as control system for a humanoid robot, provided that our designer was extraordinarily knowledgeable about the object’s contingency tree and skilled in the building of input and (especially) output transducer devices. (p. 23)

The triviality argument, as mentioned, is very complex, and only this brief sketch will be presented here. It is important to recognize, however, that the import of the critique goes beyond the fact that it seems to lead to strange outcomes in which a bucket of water might have a mind. In particular, the issue is that if these kinds of arguments go through, then there is no guarantee, in functionalist terms, that any mental or intentional state actually bears the meanings that we ordinarily assign to them (see, e.g., Madden 2013, Chap. 5). In sum, there is a real possibility that a consistently functionalist account of thought collapses upon close inspection (see also Feser 2006). For example, functionalist treatments of intentionality tend to lead to a denial of, or eliminative reduction of, intentionality. But the functionalist treatment itself is presented and argued for in intentional terms. Similar problems arise in functionalist treatments of logical reason and other topics.

Other general objections to functionalism include how to characterize the inputs and outputs of a functional system (Block 1990), problems in accounting for what appear to be the causal effects of our mental states (Kim 1989), and introspective belief (Armstrong 1968). All of these objections and more have been put forward, many from functionalism's early days. In summary, functionalism as a philosophical ontology has met with serious objections. It should be noted that these objections apply to all functionalist positions, including psycho-functionalism and analytic functionalism.

Within cognitive psychology, functionalism has often failed in the task of theory building and theory discrimination. A recent example of this failure was presented by Spalding and Gagné (2013). They pointed out that none of the three predominant models of concept formation (exemplar, prototype, and theory-theory) has emerged as superior, and all have approximately the same amount of empirical support (this problem occurs in many areas of psychology). In fact, they note that recent studies of psychological essentialism, generics, K-properties, and perceptual symbol systems/embodied concepts challenge the validity of all three probabilistic models mentioned above.

It should be noted that all three theories of concept formation meet the criteria demanded by functionalism. All commence with stimulus conditions, postulate interacting internal cognitive constructs, and produce behavioral outcomes. However, years of research have not led any of the three theories to dominance. In fact, Spalding and Gagné (2013) made this comment about the current state of affairs:

Given the diversity of representations and processing systems suggested by recent research results, it is unclear whether there can be a theory of concepts at all (e.g., Machery 2009). How can concepts be both essentialist and yet not involve necessary and sufficient features?... How can they be both sensory-based and abstract/universal? (p. 71)

Hence, we see that this level of theory building and theory discrimination has failed. Of course, it is possible that there will be a new, functionalist-based, theory that will account for human concepts, though Machery (2009) makes a strong case that this is unlikely. However, this conspicuous failure can also be taken to suggest that a more fundamental re-thinking of concepts is in order, and, since failure of theory discrimination is common in most areas of cognitive psychology, perhaps functionalism is simply not up to the task of theory building.

## Functionalism and Animal Cognition

Given that philosophical functionalism arose in the first instance as a way of understanding what constitutes mental states, it is unsurprising that its primary application was to human cognition. Interestingly, in the wake of the "cognitive revolution" in psychology, research in animal cognition took on much of the vocabulary and the theoretical method of human cognitive psychology, with a move away from "pure" behavior and toward the study of memory, perception, etc., in nonhuman animals. In particular, much work on animal cognition took on functional analyses of processes presumed to intervene between stimulus and response, in much the same way as seen in the so-called cognitive revolution. Interestingly,

although animal cognition work took on the vocabulary and theoretical method associated with human cognition, it is unclear that it truly took on the notion of functionalism as a philosophical underpinning. It is unclear to what extent work in animal cognition generally claims that there are “mental states,” and if there are, it is unclear to what extent those mental states are actually constituted by the states’ position in the functional chain (note that it is this quite radical claim that mental states just are the functional connections that makes functionalism the kind of thing that could claim to serve as an account of mental states, philosophically). To our knowledge, there is no existing, full-scale exposition of philosophical functionalism with respect to nonhuman animal cognition.

Lacking an existing clear statement of how functionalism can serve to underpin research on animal cognition, we will attempt to describe how functionalism might be extended from human cognition to nonhuman animal cognition and then to evaluate the resulting construct in terms of whether it provides a convincing account of the relationship between human and animal cognition. As noted above, we find functionalism lacking in its ability to truly undergird the study of human cognition, but the ability to have a single philosophical underpinning (even with some weaknesses) that could profitably be applied to both human and animal cognition would be a boon to psychology as a whole, and this could outweigh functionalism’s weaknesses (at least in the absence of more effective competitors).

We begin considering the extension of functionalism from human to animal cognition by noting that the functionalist is more or less required, by the internal logic of functionalism, to hold that animals have mental states and that those mental states just are functional relationships. That is, because the functionalist holds the highly abstract view of what constitutes mental states (input, state transformations, output) described above, any system having such characteristics (or analyzable into such characteristics) is more or less compelled to have mental states in the functionalist’s view. As noted above, any properly constituted functional system (whether human,

animal, computer, or whatever) thus has “mental” states. So the simplest approach to functionalism and animal cognition is just to say that both human and nonhuman animals have mental states constituted by the functional relationships among those states.

There are both strengths and weaknesses to this extension of functionalism. On the one hand, we have, potentially, a unified underlying philosophical approach that accounts for both human and nonhuman animal cognition. This would, certainly, be an admirable outcome. On the other hand, all the weaknesses of functionalism for human cognition would seem to extend to animal cognition as well. Furthermore, this simplistic extension would seem to require a completely continuous relation between the abilities of nonhuman animals and humans (and, indeed, among all of the nonhuman animals). Functionalism, as such, appears to provide no help in understanding the relationships among the differing abilities of different species (or for that matter, the common abilities of different species), making it, perhaps, not a particularly helpful philosophical underpinning for comparative psychology’s concerns. Finally, it is unclear whether functionalism actually adds anything to the understanding of animal cognition. Recall that functionalism arose specifically as a way of thinking about mental states in humans because those mental states had shown themselves to be resistant to other philosophical accounts (see, e.g., Madden 2013). But there is a real question about the extent to which there is a need for such an approach in order to understand the cognition of nonhuman animals, and further there is a real question about whether it is appropriate to extend intentional notions such as beliefs or hopes to nonhuman animals, even if such notions are appropriate to humans (which is, of course, a question of its own).

In short, the study of animal cognition reveals interesting and principled continuities and discontinuities of behavior and abilities among various species, including in comparing many of those species to humans. While it is certainly possible to extend functionalism from human cognition to nonhuman animal cognition, it is unclear what benefits this extension actually provides, as it

does not seem to offer a clear way of understanding any of the seemingly principled continuities and discontinuities of abilities among the various species. Of course, as we said above, we do not know of any fully developed, clear version of functionalism that has attempted to cover the broad field of animal cognition, so it is certainly possible that such a version could be developed. However, given the concerns we have raised about functionalism as a philosophical underpinning for human cognition, we wish now to suggest an alternative approach that might have more promise.

### The A-T Alternative

As mentioned in our statement of purpose, both philosophers of mind and psychologists have recently proposed Aristotelian-Thomistic alternatives to functionalism. We will consider philosophers of mind first. Madden (2013) has written a thorough review of the major approaches to the philosophy of mind, including functionalism. In fact, he is rather enthusiastic about functionalism, as noted in the following quote:

Functionalism is a powerful theory. It seems to provide an account of psychological states without even a hint of anything left to be explained by supposed nonphysical states, while at the same time allowing for mental causation without raising problems of mind body interaction. . . It is, whatever its vices, a very good idea. (p. 131)

Although Madden concedes that functionalism has many merits, he argues that its shortcomings outweigh its merits as a philosophy of mind. His arguments against functionalism are those covered in the previous section, plus issues regarding intentionality, beliefs, and thoughts in general.

As an alternative, Madden proposes Aristotelian-Thomistic hylomorphic theory as applied to human and animal sensory and cognitive processes as the best solution to the observed phenomena of mind. His argument for this position is indeed complex and is marshaled against materialist positions, property dualism, and substance dualism; all fail as explanatory systems for mind. For the purposes of this essay, we will not

present any further detail regarding these purely philosophical arguments raging among the philosophers of mind but will leave it to the reader to investigate the arguments in the works cited below (As mentioned in our statement of purpose, both philosophers of mind and psychologists have proposed an Aristotelian-Thomistic (A-T) account as an alternative to functionalism. Readable recent descriptions of A-T approaches to metaphysics (Feser 2014), philosophy of mind (Feser 2006; Madden 2013), and other specific relevant topics, such as induction (Groarke 2009) or essences (Oderberg 2007), as well as overall systematic descriptions of Thomistic philosophy (e.g., Feser 2009; Stump 2003), and older descriptions specifically relating to the application of A-T ideas to philosophical and experimental psychology (e.g., Maher 1909), are available. Feser (2014) is particularly interesting in the current context as he takes a compare/contrast approach with many recent developments in analytic philosophy.).

Returning to functionalism's adequacy as an account of cognitive psychology, we have seen that functionalism has deficits as an ontological system. These deficits also apply to functionalism as an underpinning for cognitive psychology. Recognizing problems with functionalism and particularly incoherence in cognitive psychology's account of concept formation led Spalding and Gagné (2013) to propose an Aristotelian-Thomistic alternative model to account for concept formation. At about the same time, Stedman (2013) published a paper demonstrating parallels between modern cognitive psychology and neuroscience and Aristotle's hylomorphic theory. He showed that these parallels exist at all areas of interest to cognitive psychology and neuroscience, including sensation, perception, memory, and higher-order cognitive functions, such as concept formation, theory of mind, reasoning, and so forth.

The details of the A-T model have been elaborated in three recent publications (Spalding and Gagné 2013; Spalding et al. 2014; Stedman 2013) and so will be outlined here only briefly and mostly in order to shed light on how the A-T model presents animal cognition, especially



so-called “higher animals” with complex cognitive lives like wolves, cats, horses rather than, say, sponges, or oysters. In the A-T framework, human and nonhuman animal cognition are fundamentally similar, at least until concept formation is accounted for. Sensory cognition in both humans and nonhuman animals commences with the sensation of particular objects in the environment. Importantly, this account of cognition is conditioned by certain metaphysical commitments, especially that objects in the environment are composed of form and matter, which are correlates to the actuality and potentiality of a thing. Thus, the form of a thing, which is paramount in the account of cognition, is a way of speaking about its actuality, i.e., what the thing is currently doing.

Now, in sensation, the form of the object is received by the appropriate sense organ(s) and is then communicated to the “internal senses” via the production of a “phantasm.” The phantasm is a sort of internal image of the externally sensed object (the technical A-T language here is that the phantasm has the “form” of the external sensed object but not its matter), and these internal senses deal with phantasms in various interconnected ways. On Aquinas’ account, there are 4 internal senses: (1) the “common sense,” which allows for the subject to distinguish between what is presented through different senses and to be aware that external sensing is occurring; (2) the “imagination,” which is the “storehouse of forms” and allows for the animal or human to recall things when the object is not actually present and, in humans, allows for the mental combination and separation of sense images to produce fictional objects; (3) the “estimative sense,” which is called the “cognitive power” for humans (the estimative sense in animals is instinctive and what allows animals to pursue or flee or ignore an external object; in humans, this internal sense compares individual intentions in various sorts of deliberation); and (4) the “memory,” which retains intentions that are held by the estimative/cognitive power. Aquinas says that these internal senses occur in an organ in “the middle part of head,” i.e., the brain.

As noted, sense cognition for humans and non-human animals are fundamentally similar: there is a thing in the external world that is sensed and then communicated internally. Through various internal powers, which are basically the same in humans and nonhuman animals, these sense images are unified into a holistic experience, and those images can be recalled, manipulated, and are the means by which the animal navigates the world. Unlike the functionalist model, cognition in the A-T model does not simply break cognition down to a description of inputs and outputs, but is an internalization of exterior objects. This internalization is not the “representation” of some early modern thinkers, in which the representation is a sort of degraded copy of the external thing, but the formal existence of the exterior thing existing internally or mentally. Thus, the basic metaphysical structure of the external world – wherein objects are composed of form and matter – is reflected internally but only at the formal level. The matter is left out in the external world, while the form is propagated via sense organs and internal senses internally. The result is a particular intention of the external object.

It is axiomatic for the A-T framework that sensation is always of particular things, whereas understanding, via concepts, reaches to universals. As such, the sensory process just explained only touches upon particulars and the sensory process only has particular intentions. As such, on the A-T model, nonhuman animals only ever sense and cognize particulars. So-called “higher animals” can, in a way, recognize an external object as being a member of a class, but this is accounted for through the estimative power, i.e., instinct. Thus, if a wolf falls into the field of vision of a sheep, the sheep immediately recognizes a threat and will pursue an instinctual course of action. This response does not cognize the wolf as a wolf, but as a threat (whereas the converse will hold for the wolf that sees a sheep, which will be seen as an object of desire). This is the closest to some sort of universal cognition that the A-T model will afford animals, for at this point the cognitive story for humans and nonhuman animals diverges, and the A-T model will turn to account of concept formation by way of a process

of abstraction, which accounts for the move from a particular to a universal intention or concept.

It is beyond our current purposes to explain in detail the complex process by which concepts are formed on the A-T model, for that process speaks to what is conceived as a conceived as a uniquely human process. It should be noted, however, that Spalding and Gagné (2013) surveyed several varieties of concepts research and showed that the results, though seemingly completely incompatible from the viewpoint of modern concept theories, all appear to be at least compatible with, and in most cases directly expected by, the A-T view of concepts. On the basis of this strong correspondence between the A-T view and the empirical results, Spalding and Gagne suggest a serious investigation into the A-T view as a possible high-level framework within which the scientific investigation of the psychology of concepts can proceed. Most importantly for the present purposes, Spalding and Gagné's presentation of the A-T view should be taken as a kind of existence proof that an A-T approach is compatible with modern scientific psychological research (see also Gagné et al. [in press](#), for an example applying an A-T approach to a specific experimental research program within the field of concepts research).

## Functionalism, the A-T Model, and Animal Cognition

Animals have sensation, perceptual organization of that raw sensation, and memory. They can learn and many assert that they also have "higher-order" cognition that parallels human thought, reasoning, and problem solving, at least to a degree. As Aristotle noted, a living organism's abilities are known by observing its behaviors and certainly animals, especially primates, manifest these behaviors. It is not the purpose of this essay to debate the "higher-order" cognitive abilities of human vs. animals (see George 2003, for a thorough discussion of this topic). Our task is to consider whether the A-T model is superior to functionalism in accounting for animal cognitive behaviors.

The shortcomings of functionalism, as a general theory and as a metatheoretical underpinning for psychology at every level, have already been discussed and will not be repeated. The A-T model offers an explanation of all animal cognition based on an analysis of the external and internal senses. The external senses are those we are all familiar with, such as hearing and sight, and there is a vast animal psychology literature investigating these phenomena. The internal senses, discussed previously, account for perception, memory, and "higher-order" cognitive events in animals. A-T theory holds the following: (1) these abilities are brain based, (2) these abilities are shared by humans and animals, and (3) these four internal senses can explain all of animal behavior, including what many believe to be acts of reasoning and problem solving in mammals (see Cates 2009; George 2003, for an elaborate discussion of these issues).

Some may react to the presentation above and conclude that the A-T model and the functionalist model are very similar in their accounts of animal cognition, such that one is no better than the other. Indeed, both depend on external sensory input; postulate mechanisms to account for sensory integration, memory, and such; and look at behavior outcomes for proof. We claim that the A-T model is superior because it offers a better and more detailed account at the animal level and an integrated account of both animal and human cognition.

## Conclusions

The major outlines of A-T and functionalism as ontological and epistemological systems have been presented here and in the recent publications mentioned above. We have also considered some of the philosophical strengths and weaknesses of both functionalism and the A-T model. While much thought has been devoted to philosophical critiques of both systems, we have not attempted to summarize that material in a few lines. We simply assert that, in a head to head comparison, the A-T hylomorphic model is better than functionalism as a scientific realist account of human

and animal cognition. Arguments for this assertion are found throughout this essay, in the three recent publications cited (Spalding and Gagne 2013; Spalding et al. 2014, and Stedman 2013) and specifically in Stedman et al. (2016). Functionalism claims to be an adequate ontology to explain all cognitive events from sensation to all higher-order cognition. However, as pointed out above, functionalism has been seriously challenged as an adequate general ontological theory. Spalding and Gagné (2013) and Stedman (2013) both make a reasonable case for A-T ontology as a meta-theory that provides at least as good a philosophical underpinning for cognitive psychology as functionalism does, in that (a) the A-T approach is compatible with the existing cognitive psychology research results and (b) the A-T approach is capable of accounting for many aspects of the concepts literature that are deeply surprising if one takes a functionalist approach. Finally, we have shown that there are also philosophical reasons to prefer the A T approach and have shown that some of the common objections to such an approach are misguided and often based on a misunderstanding of the A-T approach.

## Cross-References

- Aristotle
- Behaviorism
- Cognitivism
- Representation

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## Functionally Relevant

### ► Naturalistic Stimuli

## Fungi

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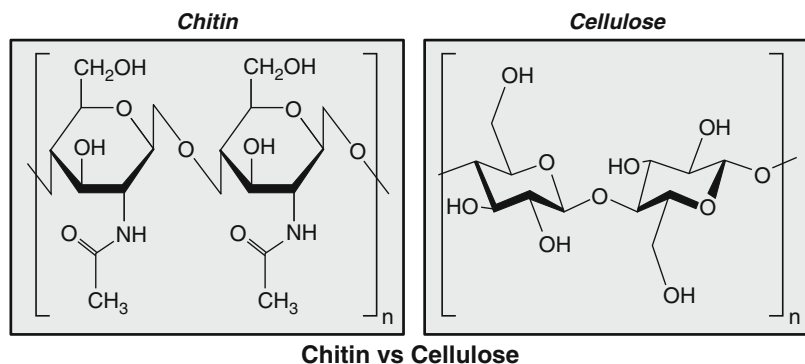
Fungi are present in almost all habitats. At present about 99,000 known species of fungal organisms, including yeasts, rusts, smuts, mildews, molds, and mushrooms exist on earth. They are

eukaryotic organisms which have been placed in a separate kingdom from “Animals” and “Plants” (Ruggiero et al. 2015). Fungi are only second to the plants with respect to biomass on land, and unlike plants, are devoid of chlorophyll. They are more closely related to animals than plants. Most peculiar feature about the fungi is their cell wall which is composed of glucan or chitin, unlike cellulose in plants (Bowman and Free 2006). The difference between chitin and cellulose sub-unit has been shown in Fig. 1 (<http://www.easybiologyclass.com/kingdom-fungi-general-characteristics-key-points-with-ppt/>) and the image of the fungal cell wall has been provided in Fig. 2 (<https://byjus.com/biology/fungal-cell-wall/>).

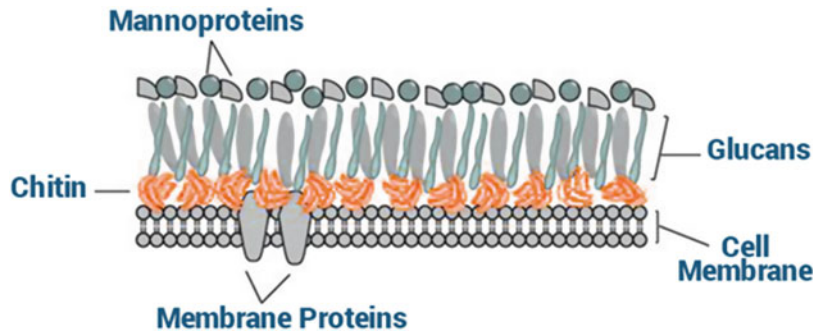
Fungi are aerobic in nature depicting both sexual and asexual reproduction. Unlike plants, they are heterotrophs which have the ability to form diffuse bodies comprising of an extended network of very narrow, tubular, branching filaments termed as hyphae. These filaments secrete enzymes and also absorb the food at their growing tip. They are chiefly found growing on dead and decaying material. Some of them are useful as food, source of medication, and recycling, mycorrhizae and plant growth, and others are less desirable, such as mold on food or spores that cause diseases (Kendrick 2011).

Fungi can exist in two forms: yeasts and molds. The important identifying characters of yeast are that they are single, small, and oval cells, whereas hyphae are the characteristic feature of the mold form. Apart from this, another group of fungi exist which has the ability to exist in both form and require a stimulus such as temperature to switch

**Fungi, Fig. 1** Structural difference between the chitin and cellulose present in fungal and plant cell wall respectively



**Fungi, Fig. 2** Structure and composition of the fungal cell wall



between the two forms (McGinnis and Tyring 1996; Gow et al. 2002).

Fungi have three major roles to play in the environment: (1) as saprobes, (2) as pathogens/parasites, and as (3) mutualistic symbionts. In the terrestrial ecosystem, the saprophytic fungi play a vital role in order to decay the dead material. Plant debris comprising of lignin, cellulose, and animal debris constituting of chitin and keratin needs to be degraded in order to release the basic constituents back into the biosphere, otherwise due to continuous piling up of the dead material, the soil would become unfertile and impoverished. Next, the fungus also plays the role of a parasite and pathogen. Not all fungi can cause diseases but a few of them can cause serious and fatal infections in both plants and animals. Generally, fungi are opportunistic in nature and infect immunocompromised (suffering from AIDS, undergoing radiotherapy or chemotherapy, undergone a transplant, etc.) individuals (Neelabh and Singh 2018).

Finally, the most interesting aspect of the fungal ecology is the mutualistic symbiosis. Fungi are known to live in close co-operation with a variety of organisms such as cyanobacteria (blue-green “algae”) and chlorophycota (green algae) (in lichens), with bryophytes, pteridophytes, gymnosperms and angiosperms (in mycorrhizae), and with coleopteran, dipteran, homopteran, hymenopteran, and isopteran insects (Read et al. 2000).

## Conclusion

Fungi have multitudinous roles to play in the environment, primarily the role of saprophytes.

They are both advantageous and harmful in many respects. A broad range of their use especially in the field of agriculture and medicine makes them very useful for the mankind but in contrast to this the deleterious effects of some fungi in the storage of food grains and human health can be devastating. However, these ill effects of the fungi can be curtailed to a certain extent if proper storage methodologies are employed and suitable measures regarding diagnosis and treatment of the fungal diseases are executed.

## Cross-References

► [Eukaryota](#)

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## Fusion-Fission

► [Fission-Fusion](#)

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## Future Planning

► [Stuck-in-Time Hypothesis](#)

# G

## Gait

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## Synonyms

Center of mass; Duty factor; Footfall; Limb phase; Locomotion; Tetrapods

## Definition

A locomotor pattern typical of legged animals that can be described either by the sequence of footfalls or movements of the center of mass over a stride.

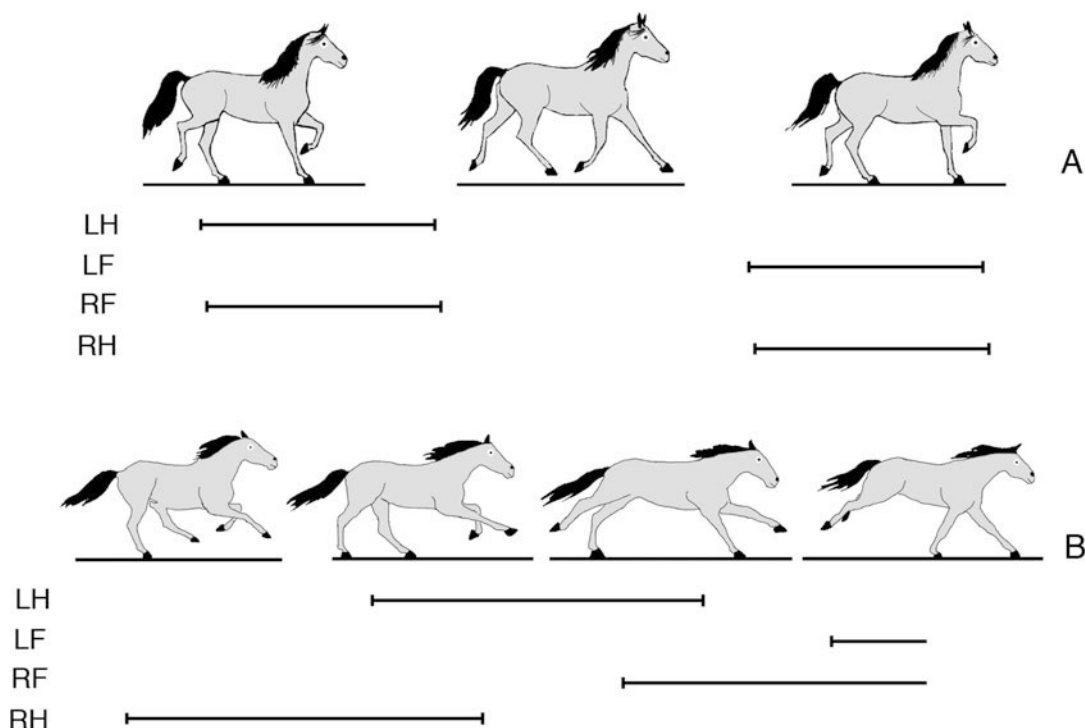
## Defining Gaits: Duty Factor and Limb Phase

The “gait” of four-legged land vertebrates (known as tetrapods) involves a precise sequence and coordination of the limbs as forward movement takes place. It is the sequence and timing of the limb contacts that essentially define different gait types. As tetrapods move forward, each limb

touches the ground, moves backward, is lifted off the ground, and brought forward again. This pattern results in a contact phase (called the support or stance phase) and a noncontact phase (called the swing phase), which together represent a locomotor cycle or *stride*. A few animals like birds, fast-moving reptiles, some nonhuman primates, and humans most obviously adopt a bipedal gait in which the entire weight of the body is supported solely by the hind limbs with right- and left-foot contacts alternating evenly during the stride (see “► [Bipedalism](#)” entry).

There is an obvious relationship between speed and the proportion of the stride for which the limbs are on the ground (the technical term for this is known as *duty factor*). At higher duty factors, when the limbs spend more than 50% of the stride on the ground, an animal is walking; at lower duty factors, when the limbs spend less than 50% of the stride on the ground (and are all off the ground at some point during the stride), an animal is running. This is easiest to observe in a biped like yourself. During walking, right and left footfalls alternate with at least one foot remaining on the ground at all times. During running, in contrast, both feet are off the ground at some point during the stride, and an aerial phase is introduced.

Walks and runs are examples of what are known as *symmetrical* gaits (Howell 1944; Hildebrand 1985; Cartmill et al. 2002, 2007). Gaits are considered to be symmetrical when pairs of limbs (front or back pairs) touch the ground at even time intervals (Fig. 1a). In other



**Gait, Fig. 1** Symmetrical and asymmetrical gaits in the horse. During a symmetrical step (**a**), left and right hind limbs (RH and LH) and forelimbs (RF and LF) contact the ground at even time intervals (horizontal bars in figure). In this particular symmetrical gait known as a running trot, there is a whole-body aerial phase (no bars), and the limb phase is nearly 50%, resulting in contralateral pairs of limbs (LH and RF; RH and LF) striking the ground almost simultaneously (see text for more details). During an asymmetrical step (**b**), pairs of hind limbs and forelimbs touch

the ground at irregular time intervals. In this particular asymmetrical gait known as the transverse gallop, the leading hind limb and forelimb (i.e., the limb of a fore and hind pair still in the air when the other limb of that pair strikes the ground) are on the same side (LH and LF are the leading limbs in this sequence). The whole-body aerial phase that follows touchdown of the forelimbs (last panel on the right) is not shown. (All images redrawn and adapted from Gambaryan (1974))

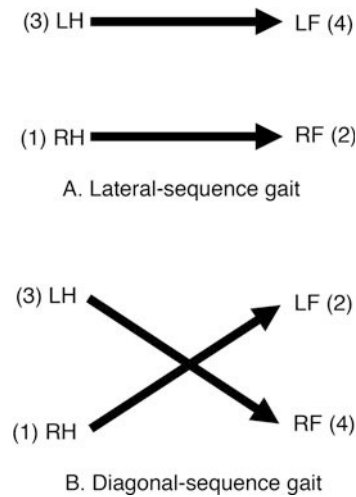
words, the time elapsed between the touchdowns of the right and left hind limbs should equal half of the stride total time. When pairs of limbs touch the ground at uneven time intervals, this results in *asymmetrical* gaits (Howell 1944; Hildebrand 1985; Fig. 1b). Put differently, symmetrical gaits are generally sequenced front to back. In symmetrical gaits like a walk, the contact of a hind limb is followed by that of a forelimb, or the contact of a hind limb/forelimb pair is effectively simultaneous as in the trot (Fig. 1a). Asymmetrical gaits are generally sequenced side to side. For such gaits, the contact of a hind limb is often simultaneous or immediately followed by that of the contralateral (opposite side) hind limb and then followed by a forelimb (Fig. 1b). Gaits such as the

bound, half bound, and gallop are all considered asymmetrical (Howell 1944; Gambaryan 1974; Hildebrand 1985). The bound, which is repetitive and appears symmetrical, is actually asymmetrical because two simultaneous hind limb contacts are followed by two simultaneous forelimb contacts. The half bound involves simultaneous contact of the hind limbs followed by sequential contact of the forelimbs. The most characteristic and best-known asymmetrical gait, the gallop, involves sequential contact of the hind limbs followed by that of the forelimbs (Fig. 1b). During the gallop, the limb of a pair of hind limbs or forelimbs that lands first is known as the trailing limb, while the other limb still in the air is defined as the leading limb. When leading hind limb and forelimb are

ipsilateral (same side), a transverse gallop results; contralateral leading hind limb and forelimb are found in a rotatory gallop (Howell 1944; Hildebrand 1985). All these asymmetrical gaits are characterized by an aerial phase (also known as suspension), either between hind limb and forelimb contacts or at the end of the stride. Interestingly, the canter, an asymmetrical gait equivalent to a slow gallop, has sometimes no aerial phase (Howell 1944; Schmitt et al. 2006).

Thus, it is clear that the sequence at which the limbs strike the ground or footfall sequence during a stride (referred to as the *gait cycle* [Cartmill et al. 2002, 2007]) defines specific gait types. A footfall sequence can be expressed as a percentage by calculating the time taken between the fore footfall and hind footfall on the same side during a stride (Hildebrand 1985; Cartmill et al. 2002, 2007). The technical term of this measure of interlimb coordination during forward movement is known as the *limb phase*. Terms such as “diagonality” and “gait number” have also been used and are essentially treated as synonymous.

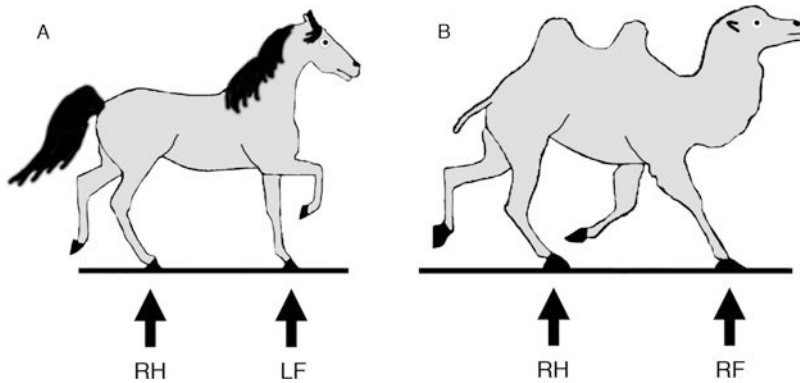
Limb phases are known to vary quite a bit between quadrupedal animals and even within a single species (e.g., different horse breeds). This variation results in a broad spectrum of interesting gaits. Here are a few examples. At limb phases approaching 0% or 100%, the fore- and hind limbs on the ipsilateral side of a quadrupedal animal strike the ground pretty much at the same time. This is known as a *pace*. At limb phases closer to 50%, the fore- and hind limbs on contralateral sides of the same quadrupedal animal strike the ground almost simultaneously. This is known as a *trot*. As limb phases deviate from that 50% mark, either lower or higher, the limbs strike the ground in a specific order known as *lateral sequence* or *diagonal sequence* (Hildebrand 1985; Cartmill et al. 2002, 2007). In a lateral-sequence gait, the footfall of a forelimb (F) follows that of the hind limb (H) on the ipsilateral side (RH, RF, LH, LF); in a diagonal-sequence gait, the footfall of a forelimb (F) follows that of the hind limb (H) on the contralateral side (RH, LF, LH, RF) (Hildebrand 1985; Cartmill et al. 2002, 2007; Fig. 2). As the limb sequence proceeds with forward movement,



**Gait, Fig. 2** Sequence of footfalls for lateral-sequence and diagonal-sequence gaits. In a lateral-sequence gait (a), the footfall of a forelimb (F) follows that of the hind limb (H) on the ipsilateral side, which results in the following sequence: RH, RF, LH, LF. In a diagonal-sequence gait (b), the footfall of a forelimb (F) follows that of the hind limb (H) on the contralateral side, which results in the following sequence: RH, LF, LH, RF

some limbs are on the ground (in stance phase); others are off the ground (in swing phase). Unless the speed is really slow, only two limbs provide body support at some point of the walking stride. When contralateral limbs provide body support (e.g., RH and LF), this is known as a diagonal bipod; when ipsilateral limbs provide that support (e.g., RH and RF), it results in a unilateral bipod (Cartmill et al. 2002, 2007). Diagonal bipods are inherently more stable than unilateral bipods, and most animals seem to optimize periods of diagonal bipedality over unilateral bipedality (see Cartmill et al. (2002, 2007) for in-depth modeling and theory).

When walking, most tetrapods including most mammals adopt a lateral-sequence footfall sequence with diagonal couplets (i.e., a pair of contralateral forelimb and hind limb swings forward, while the other contralateral pair supports the body; Fig. 3a) or LSDS gaits (Hildebrand 1985; Cartmill et al. 2002, 2007). Such limb sequence is thought to result in greater stability during walking (i.e., forward motion without falling or stumbling) as a wider base supports the



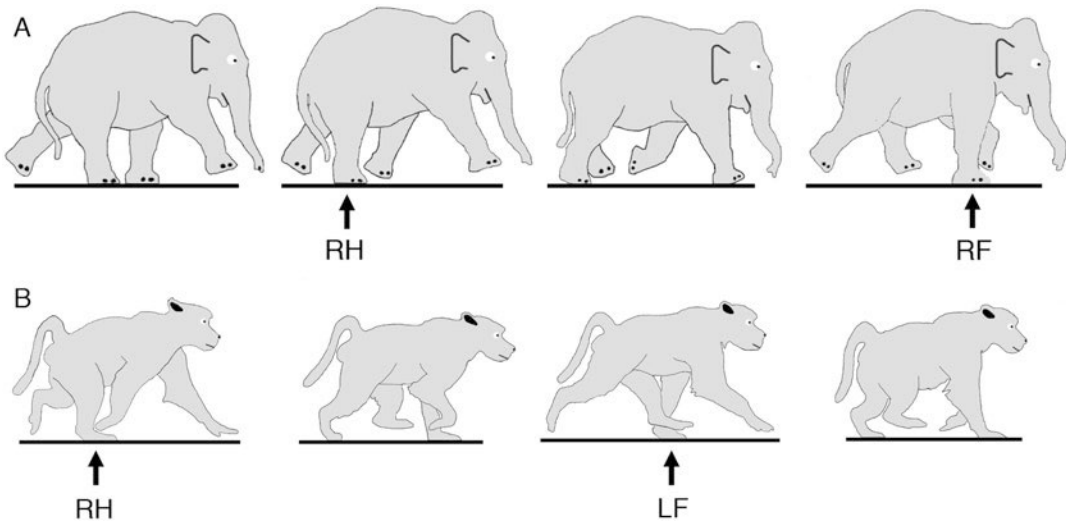
**Gait, Fig. 3** Couplets used during different gaits. When a pair of limbs on the opposite side (contralateral) swings forward while the other contralateral pair on the other side supports the body, this is known as a diagonal couplet shown by the horse (a). When a pair of limbs on the

same side (ipsilateral) swings forward while the other ipsilateral pair supports the body, this is known as a lateral couplet shown by the camel (b). (All images redrawn and adapted from Gambaryan (1974))

body center of mass when three limbs are on the ground (Hildebrand 1985; Cartmill et al. 2002, 2007; see following section on movements of the center of mass during locomotion). There are exceptions in the mammal world, however. For example, some long-legged mammals (e.g., camels) or certain horse and dog breeds prefer lateral-sequence footfall sequence with lateral couplets (i.e., a pair of ipsilateral forelimb and hind limb swings forward, while the other ipsilateral pair supports the body; Fig. 3b) or LSLC gaits commonly known as pacing (Hildebrand 1985; Cartmill et al. 2002, 2007). Another important exception is the adoption by virtually all nonhuman primates of a diagonal-sequence footfall sequence with diagonal couplets or DSDC gaits during quadrupedal walking (Hildebrand 1967; Vilensky and Larson 1989; Cartmill et al. 2002, 2007). Outside of nonhuman primates, DSDC gaits are also common in the woolly opossum (genus *Caluromys*) and the kinkajou (genus *Potos*) (Hildebrand 1985; Cartmill et al. 2002, 2007; Lemelin et al. 2003; Lemelin and Cartmill 2010), which like nonhuman primates move and forage in the trees, particularly where thin and pliable branches abound. This complex fine-branch environment is believed to have played an important role in the evolution of diagonal-sequence gaits (Cartmill et al. 2002, 2007; Lemelin et al. 2003; Lemelin and Cartmill 2010).

Nonhuman primates are also unusual in the way they run. A typical run in a quadruped involves a whole-body aerial phase for which all limbs are off the ground at some point during the stride (think of a running trot in a horse). Primates almost never trot, and some species prefer the canter instead of galloping (Schmitt et al. 2006). In lieu of trotting, primates rely on the *amble*, a symmetrical running gait characterized by only pairs of limbs (forelimbs or hind limbs) undergoing an aerial phase (identified by Muybridge 1887 and Howell 1944 and later described in detail by Schmitt et al. 2006). In other words, there is no whole-body aerial phase as at least one limb contacts the substrate at any time of the ambling stride. Elephants rely on a similar running strategy, although their ambles have a lateral sequence compared to the diagonal sequence of nonhuman primates (Gambaryan 1974; Schmitt et al. 2006; Fig. 4). Despite adopting the amble, the functional reasons why nonhuman primates and elephants rely on such running gaits are quite different. Nonhuman primates maximize contact with an unstable branch (a very good thing to avoid a fall), while elephants maximize contact with the ground and avoid a whole-body aerial phase, possibly in order to moderate stresses on their limbs (a very good thing to avoid a bone fracture). Since the body never undergoes a complete aerial phase during an amble compared to a trot, the vertical





**Gait, Fig. 4** Ambling gaits in the Asian elephant (a) and baboon (b). A forelimb (F) or hind limb (H) remains in contact with the ground at all times during the step. Note

the lateral sequence in the elephant (RH, RF) compared to the diagonal sequence in the baboon (RH, LF). (All images redrawn and adapted from Gambaryan (1974))

oscillations of the body center of mass (and resulting force) are also less pronounced, which is again advantageous for moving on an unstable, pliable branch or mitigating limb stresses (Schmitt et al. 2006).

### Defining Gaits: Movements of the Center of Mass

Defining gaits visually is effective and relatively straightforward; it tells us a lot about what animals are doing. Another way to define gaits is by the movements of the animal's center of mass (COM). During walking and running, the movements (acceleration and deceleration) of the COM follow different patterns, and the vertical movements can differ between gaits (see Cavagna et al. 1977). When an animal walks, it tends to maintain relatively stiff limbs (limited joint flexion and limb compression), and because of the angles of the arc the leg sweeps, the COM of the body will rise and fall like an upside-down pendulum. At its highest point (which corresponds to mid-support of the contact phase when the hand or foot is directly below the shoulder or hip), this inverted pendulum has the greatest amount of gravitational

potential energy. As the COM falls, that energy is converted into kinetic energy and is used to drive the COM downward and forward. Using the limb as a relatively stiff pivot, it will “push” the COM back up, restoring potential energy to be used again in the next stride. During running, animals often allow their limbs to flex more deeply, and the COM is at its lowest point at mid-support. In doing so, the COM behaves more like a bouncing ball than a pendulum, stretching muscles and tendons and storing energy in them. Recent research has suggested that discontinuity in the path of the COM (i.e., the redirection of the COM from downward to upward or so-called collisions) is a more important variable to consider and represents an alternative way to envision locomotion that unifies all gaits under a single model (see Bertram 2016 for a thorough review). The costs of different gaits are thought to relate to the level of energy exchange or the cost of redirecting the COM, and that specific footfall sequences are chosen to minimize the latter (see Griffin et al. 2004). The question of why animals shift gaits as a result of changes in energetic costs, loads, or other factors remains an active area of research and discussion, but far beyond the limits of this entry. Suffice it to say that gait choice

appears to be profoundly complex and context specific.

## Conclusions

As animals move, they adopt specific gaits or sequences of footfall contacts with the substrate. A wide variety of gaits exist and are used by tetrapods. Gaits can be defined visually based on (1) the sequence of footfalls and the presence or absence of an aerial phase or (2) by movements of the center of mass during a stride. Gaits can be further subdivided into patterns with sequenced limb contacts (such as the walk, amble, canter, or gallop) or simultaneous limb contacts (such as the pace, trot, or bound). Regardless of the way gaits are defined, they represent the fundamental unit of motion for legged animals. The gaits that animals select represent their mechanical needs in specific situations and reflect both selective and situational priorities.

## Cross-References

- [Adaptation](#)
- [Arboreality](#)
- [Artiodactyla Locomotion](#)
- [Bear Locomotion](#)
- [Bipedalism](#)
- [Bovine Locomotion](#)
- [Canine Locomotion](#)
- [Catarrhine Locomotion](#)
- [Crocodilia Locomotion](#)
- [Equine Locomotion](#)
- [Evolution](#)
- [Feline Locomotion](#)
- [Hominoidea Locomotion](#)
- [Insectivore Locomotion](#)
- [Lagomorpha Locomotion](#)
- [Locomotion](#)
- [Marsupial Locomotion](#)
- [Mustelidae Locomotion](#)
- [Perissodactyla Locomotion](#)
- [Pinniped Morphology and Locomotion](#)
- [Platyrrhine Locomotion](#)
- [Proboscidea Locomotion](#)
- [Prosimian Locomotion](#)
- [Quadrupedal](#)
- [Rodentia Locomotion](#)
- [Salientia Locomotion](#)
- [Squamate Locomotion](#)
- [Swine Locomotion](#)

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## Galactin

### ► Prolactin

## Galago

- Prosimian Cognition
- Prosimian Communication
- Prosimian Life History

## Galliformes Locomotion

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## Synonyms

Chicken-like bird locomotion; Land fowl gait

## Definition

Movement used by the members of the Galliformes order (chicken, quail, partridges, pheasants, turkeys, peafowl, grouse, quail, and guineaowl) to traverse their environment.

Galliformes is an order of terrestrial birds divided into three families, Phasianidae or Old World Quail (chicken, quail, partridges, pheasants, turkeys, peafowl, and grouse), Odontophoridae (New World Quail), and Numididae (Guineaowl). Until recently, two other families, Cracidae (Chachalacas and Curassows) and Megapodiidae (Malleefowl and brush turkeys), were also included under the order of Galliformes; however, they have now been placed in a separate order known as the Craciformes (Coles 2009). This chapter will discuss only the species included under the three families of Galliformes. There are approximately 290 species found worldwide on every continent, except Antarctica. Gallinaceous birds inhabit a variety of habitats including forests, farmlands, grasslands, woodlands, mountains, meadows, savannas, riverbanks, sand dunes, deserts, and city parks (Crespo et al. 2018; Coles 2009). These birds are important to humans as several species, including chickens and turkeys, have been domesticated for meat and eggs. Humans also hunt game birds, such as wild turkeys, quail, partridges, and pheasants, for sport (Howard 2004).

Galliformes vary in size ranging from the small king quail, which weighs 28–40 g to the large North American wild turkey weighing up to 14 kg (Crespo et al. 2018). Most are medium sized birds that have similar body forms and behavioral characteristics to domestic chickens. These birds generally have short rounded wings, short bills, large stout legs and feet, three forward pointing digits, and a fourth digit directed caudomedially (Coles 2009). Some species, such as the wattles and casques, have elaborate head and neck ornamentation. Their plumage coloration can be cryptic to dark to brightly colorful depending on the species and gender (Howard 2004). Galliformes are mostly granivorous to slightly omnivorous. They feed on the ground and search for seeds, fruits, nuts, roots, and invertebrates with their feet (Coles 2009; Crespo et al. 2018).

While these birds have wings, most are incapable of long, sustained flights, and are able to fly only short distances. Thus, Galliformes are considered resident birds and a majority are non-migratory. There are a few species known to be

capable of making extensive flights and migrating such as grouse and guineafowls. Altitudinal migration is also common in species living in high altitudes, such as the Ptarmigan (*Lagopus mertus*), Willow grouse (*Lagopus lagopus*), crimson horned pheasant (*Tragopan satyra*), and Eurasian quail (*Coturnix japonica*), as they must fly to reach their foraging areas (Coles 2009).

## Terrestrial Locomotion

Domestication of chickens, turkeys, and quail has made these gallinaceous birds more accessible for studying their locomotion. Therefore, most of this chapter's discussion will focus on these species. Birds in general, "inherited bipedalism and many hindlimb morphological features from theropod dinosaurs, an ancient lineage that first appeared around 230 million years ago" (Daley 2018, p. 884). During terrestrial locomotion, Galliformes use alternating hindlimbs to support their body (Gatesy 1999). In bipedal walking and running, the feet alternate half a cycle out of phase with each other. Such gaits are generally classified as walking if the duty factor (the fraction of the time for which each foot is on the ground) is greater than 0.5 and running if it is less than 0.5 (Alexander 2004).

When walking, the hindlimb movements of chicks can be broken down into two phases, swing and stance, which together create one stride. Swing phase is the period when the foot is lifted above the ground, and the stance phase is the period when the foot is in contact with the ground. The swing phase begins with swing flexion as the hips, knees, and ankle joints are flexed and the foot is lifted off the ground. The three muscles that are mainly responsible for swing flexion are the *m. sartorius* (hip flexor and knee extensor), *m. iliofibularis* (hip extensor and knee flexor), and *m. tibialis anterior* (ankle dorsiflexor). Then during swing extension, the knee extends by use of the *m. femorotibialis*, while the hips and ankles are kept in flexion, bringing the foot forward with respect to the body. At the end of the swing phase, the lateral and medial *m. gastrocnemius* plantarflex the ankle, and the foot is placed on the ground, initiating stance

phase. During stance phase, the knee and ankle flex, while the hips extend slightly. The amount of flexion on the ankle is minimal and is maintained at a relatively constant joint angle for most of stance phase. Stance phase involves continuous activity of many hindlimb muscles, including lateral and medial *m. gastrocnemius*, *m. iliotibialis posterior* (hip and knee extensor), *m. ilirotrochantericus posterior* (medial rotator of thigh), and *m. ischiofemoralis* (lateral rotator of thigh). Towards the end of stance phase, when the chick's trunk has moved ahead of the point of contact with the ground, the ankle extends. This backward movement of the limb with respect to the body aids in supporting and propelling the chick forward (Jacobson and Hollyday 1982). When the foot is planted on the ground during the stance phase, the ground produces an equal and opposite reaction force that passes through the center of mass (COM). This balance of forces supports the body and helps with either deceleration or propulsion (Morrison et al. 2018).

An inverted pendulum model is used to describe the energy mechanics involved in walking. Walking is considered to be energetically efficient because of the exchange between potential energy (PE) and kinetic energy (KE). In the middle of the stance phase, the leg acts as a solid strut, allowing for the body's COM to reach its maximum height. Here, PE is maximized, while KE is minimized. As the body moves in front of the leg, the COM falls converting PE into KE as PE decreases and KE increases. When both limbs are equally weight bearing, the COM is at its lowest and the forward velocity is at its highest, thus PE is minimized and KE is maximized. As the opposite leg begins its stance phase, bringing the COM upwards, the KE is then converted back in PE (Muir et al. 1996).

Due to their long and powerful hindlimbs, Galliformes are excellent runners (Morrison et al. 2018). As they increase their speed, these birds transition from a walking gait, to a grounded running (without an aerial phase), to a running gait (with an aerial phase) (Granatosky et al. 2018). Just like walking, running consists of a stance phase and a swing phase, forming one stride (Gatesy 1999). To move faster, birds

increase their stride length and stride frequency. Stride length is increased by further extending the hip, knee, and ankle at the end of stance phase. To increase stride frequency, stance duration is decreased by reducing the amount of time that the foot is in contact with the ground, thus leading to an aerial phase. As speed increases, there is greater muscle shortening rather than greater muscle force, causing an increase in joint movements (Morrison et al. 2018).

Changes in the movement of the hip and knee joints allow for changes in speed. When the feet contact the ground (touchdown), the hip flexes slightly followed by a period of hip extension throughout the stance phase. To draw the leg up and forward in the swing phase, the hip is flexed again before re-extending for touchdown. At low speeds, the hip joints remain relatively stable. At higher speeds, the arc of stance phase hip extension increases to over 40 degrees at 3.0 m/sec. At the fastest running speeds, the hip angle peaks at approximately 90 degrees. After toe contact, the knee joint flexes and the limb compresses, drawing the foot backwards. At low speeds, the knee continues to flex throughout ground contact. As speed increases, the knee extends later into the stance phase, and at the beginning of the swing phase, it flexes more rapidly to bring the foot off the ground. During the swing phase, the knee extends, projecting the foot forward for the following step. At all speeds, the arc of knee flexion during stance phase is relatively large averaging between 45 and 65 degrees. Pelvic rotations are relatively small but gradually pitch forward with speed. Overall, movement at higher speeds is initiated by knee flexion and then amplified by hip and knee extensions later in the stance phase (Gatesy 1999).

In contrast to walking, PE and KE simultaneously increase and decrease during running, making this exchange impossible. Instead, running is a spring-like gait that involves exchanges between elastic energy and KE (Muir et al. 1996). The leg serves as a spring during running. In the beginning of the stance phase, the leg is compressed, absorbing KE and storing it as elastic energy in the leg muscles and tendons (Muir

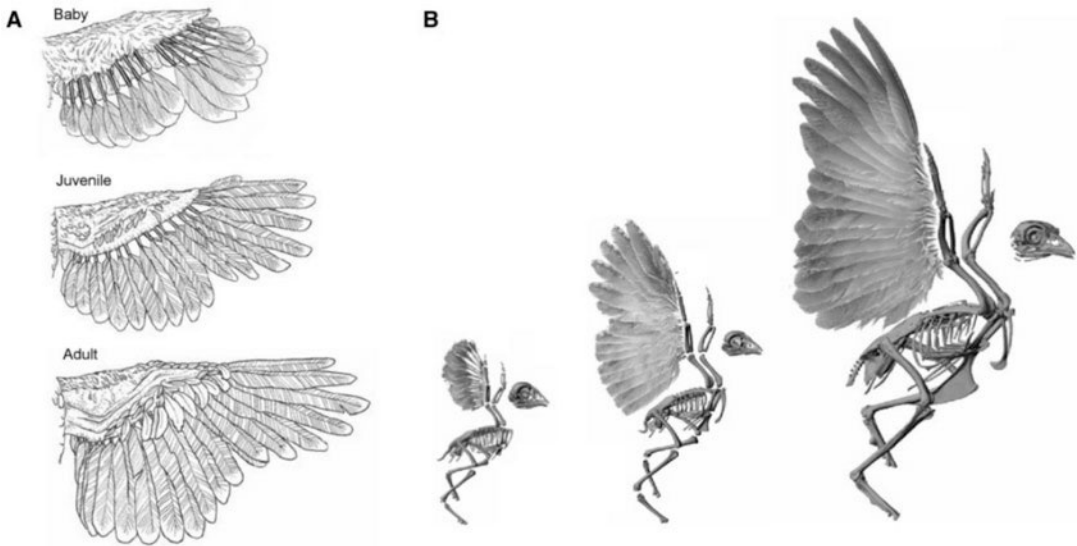
et al. 1996). In the latter half of stance, the tendons recoil and the elastic energy is released as KE, propelling the body upward and forward. This stretch and recoil of the tendons helps conserve energy while running (Morrison et al. 2018). The body's COM is lowest at mid-stance and highest during suspension, when forward velocity is also the greatest (Muir et al. 1996).

## Aerial Locomotion

The majority of Galliformes, such as pheasants, partridges, grouse, and turkeys, fly only short distances and cannot disperse far from their environment. This is due to these species being short-winged, heavy-bodied, and ground dwelling (Fig. 1). The *Cortunix* quail is an exception. As a result of their small body size and high aspect-ratio wings, these birds can disperse far and travel long distances. Among the partridge genera, the *Margaroperdix* of Madagascar and *Anurophasis* of alpine New Guinea can also travel long distances; however, their body type is similar to that of short-distance fliers (Hosner et al. 2017).

In Galliformes, a certain type of flight known as fast flapping with tip reversal is employed. In small birds, fast flapping is used during takeoff and landing, but in larger birds, it is seen just prior to landing. There are two phases involved in flapping: downstroke and upstroke. During downstroke, the wing starts off fully extended followed by rotation of the wings around the shoulder joint. When this occurs, the wing tips are horizontal, and the downstroke finishes off with the wings forming in front of the body. The second part of the cycle involves the upstroke, which begins with the wings extended ventrally. After this, the humerus is flexed and rotated. Then, the wing tips separate, and the wings start to extend and produce a rapid, propulsive flick (Brown 1963). An important part of developing flight is this "wing-stroke," which is employed by ground birds shortly after hatching. Although hatchlings have yet to form functional wings, the wing-stroke is important because it allows birds to navigate habitats and eventually helps them fly (Dial et al. 2008).





**Galliformes Locomotion, Fig. 1** Wing morphology (a) and skeletal morphology (b) in different age classes of the Chukar partridge (*Alectoris chukars*). Figure adapted from Tobalske et al. (2017) with permission

Field observation reveals that the ability to fly decreases with increasing body size in birds. One explanation for this is that the maximum power formed by the flight muscles could be limited by wingbeat frequency, which depends on mass. Another contribution for shorter flight time in these birds is the low-myoglobin content and glycolytic fibers found in the pectoral muscles, which provides bursts of energy for short-distance flight. In comparison, birds such as doves contain oxidative muscle fibers, allowing for longer flight times. Other factors that can affect how much power is available for flight are the proportion of time spent shortening and timing muscle activation and deactivation (Tobalske and Dial 2000).

Many birds in the Phasianidae family, the largest family in the branch of Galliformes, utilize rapid takeoff. These birds include northern bobtail (*Colinus virginianus*), chukar partridge (*Alectoris chukar*), ring-necked pheasants, and turkeys. These species use a similar wingbeat during take-off, which is a vortex-ring gait with tip reversal. The backward flick at the end of a tip reversal increases lift production during the downstroke. For ground dwelling birds with rounded wings, using tip reversal is unusual, but it could provide rapid acceleration during takeoff (Tobalske and Dial 2000).

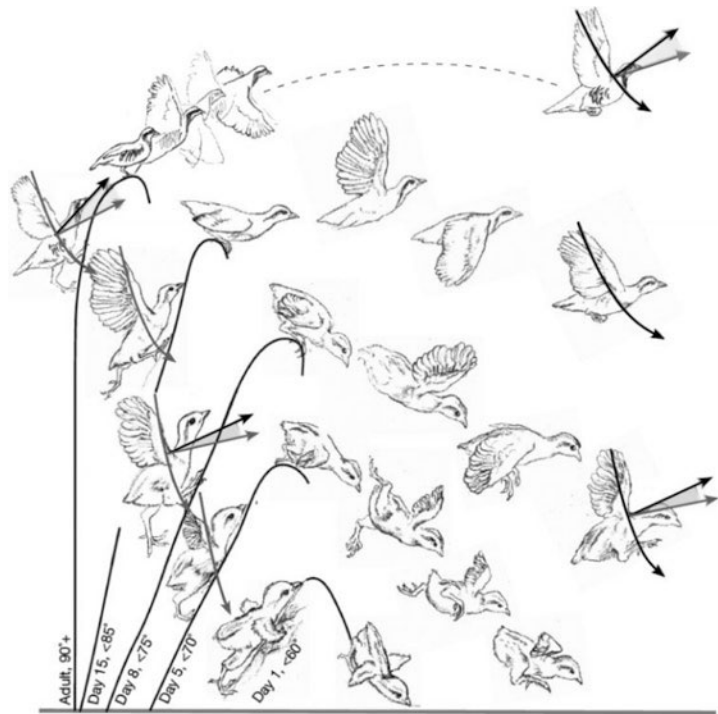
The vertical acceleration needed for rapid take-off is achieved by jumping and is critical for many ground-dwelling birds such as phasianids. Jumping is an integral part of flight because it helps birds escape from predators and helps initiate flight. The musculature in the legs of these birds are adapted for walking and running as ground-dwelling birds, but also must be able to provide high power outputs to jump into the air. This is due to the energy requirements after take-off to maintain an upward trajectory after leaping into the air. Immediately after takeoff, the flight muscles in these birds produce large amounts of power to continue climbing (Henry 2005).

Prior to flying, birds must first develop wing-flapping. Wing-flapping is essential in both flying and walking. It can occur without flight and can be seen in young birds that have not developed wings. For example, in White Leghorn chickens, Red Jungle fowl, Japanese quail and Cornish Rock Chickens, wing-flapping is evident immediately after hatching (Provine et al. 1984). Wing-flapping can occur without flight. Flight-flapping requires a significant amount of mechanical power that occurs due to the contraction of the pectoral muscles (Jackson et al. 2011).

Other than flying, Galliformes also utilize wing-assisted incline running (WAIR), which is

**Galliformes Locomotion,**

**Fig. 2** Locomotor development of Chukar partridge (*Alectoris chukars*) from hatching to adulthood. Fledglings begin using their wings 5 days post hatch to ascend inclines in wing-assisted incline running (WAIR) and to slow their fall from elevation. “Stroke curves represent the trajectory of the wing. Vectors indicate average lift during WAIR and estimated lift during slow level flight and descent.” Figure adapted from Tobalske et al. (2017) with permission



a behavior that consists of flapping wings and running with legs to climb sloped structures like trees, cliffs, etc. It is typically used as a form of escape from predators by ground dwelling Galliform birds. For example, chukar partridge can run up on vertical inclines when utilizing WAIR. Also, chukar hatchlings as young as three days old can use their partially formed wings to ascend (Fig. 2). When utilizing WAIR, birds experience different vectors of acceleration during downstroke. During the first part of the downstroke, the acceleration of the bird's COM is oriented in the direction of travel. In the later stages, the COM receives an acceleration towards the substrate. These aerodynamic forces produced by their wings aid their legs in climbing up higher and steeper terrain. In precocial hatchlings, these birds utilize their underdeveloped wings to move up small inclines (Bundle and Dial 2003). As they grow older and engage in more WAIR, the aerodynamic forces from the wings also increase due to the maturation of feathers, skeletal structures, neuromuscular control, and muscle contractile properties (Tobalske et al. 2017).

There are a variety of different directions birds can take during WAIR; however, the basic wing path remains the same. Specifically, in the wing joints, the glenohumeral joint controls most wing movements. The acrocoracohumeral ligament (AHL) goes across the glenoid from the acrocoracoid process to the transverse sulcus of the humerus. The AHL restricts humeral pronation and controls the pitch of the body in between the wings. It also stabilizes the glenohumeral joint to prevent dislocations. During WAIR, the humeral head rolls in a complex pattern but is restricted to the dorsal side of the joint surface. In addition, the distal joints are responsible for changing the wing shape (Baier et al. 2013).

Wing-assisted incline running only requires a fraction of the muscular effort compared to level flight. As such, chukar partridges and other ground-dwelling birds preferentially use WAIR compared to other forms of flight when placed on an inclined obstacle. There is also minimal neural activity when using WAIR and only recruitment of a few regions of the pectoral

muscles. By also recruiting the hindlimbs and forelimbs during WAIR, it reduces the strain on the pectoral muscles and allows energy to be conserved for more energy consuming flight (Jackson et al. 2011).

## Impact of Domestication

Domestication of Galliformes, such as chickens and turkeys, has a significant impact on their gait. The broiler chicken (*Gallus gallus domesticus*) is a major part of the human food supply. These chickens have been selectively bred for hundreds of years for increased size and growth rate (Paxton et al. 2013). High growth rates, stocking density, diseases, nutritional deficiencies, air quality, light, age, and genetics are factors associated with lameness in broiler chickens (Granquist et al. 2019). Birds with leg weaknesses are prematurely culled or have an increased incidence of mortality, which then affects the farm's profitability. The most common leg pathologies seen in broiler chickens include bacterial chondronecrosis with osteomyelitis and rotational and angular deformities. These pathologies are observed at high incidences in chickens at all developmental stages, which highlights the problem of maintaining high growth rates and muscle masses (Paxton et al. 2014).

Compared to their wild counterparts, broiler chickens have a much larger body mass. This increase in mass places greater stress on their hindlimb muscles during standing and movement. Therefore, to support their bodies, these chickens must increase their hindlimb muscle mass especially in their hip and knee extensors. Larger feet are also necessary to help improve their stability during the stance phase. However, larger feet affect the broiler chicken's ability to accelerate and decelerate the limb during swing phase. As the birds continue to grow, more metabolic energy is required to accelerate and decelerate. This energy cost may be a factor contributing to the reduced activity levels seen in broiler chickens.

Although domestic chickens rely more on hindlimb muscles for terrestrial locomotion, their breast muscles have also increased in response to artificial selection for meat production. Breast

muscle mass increases faster than body mass. However, there is no significant change in wing mass, which is consistent with decreased flight frequency and ability observed in broiler chickens (Tickle et al. 2014). The growth of pectoral muscles is observed between 4 and 6 weeks of age and this increase in muscle mass causes a shift in the COM position from a caudodorsal to a craniodorsal position. This shift in COM then requires an increase in muscular force to balance it out. Increase pectoral mass also compromises the efficacy of the chicken's respiratory apparatus (Paxton et al. 2014).

As a result of selective breeding, in comparison to other Galliformes, broiler chickens move slower and more carefully to compensate for their large sizes (Paxton et al. 2013). Changes in limb orientation are observed in these chickens. When standing, their limbs are more flexed and when walking, their limbs are more extended (Paxton et al. 2014). When walking, these birds place their feet at a more lateral position, providing an increased potential for medial lateral motions around the COM. While one limb is in swing phase, the body is moved laterally over the contralateral limb in stance phase. For stability, they fine tune their step length and width to control their COM. These exaggerated medial and lateral motions suggest broiler chickens may share more in common biomechanically with waddling birds such as penguins, geese, or ducks, than the wild Galliformes (Paxton et al. 2013).

Similarly, domesticated turkeys have been bred to be larger than their wild counterparts. Without proper limb compensation for their increased body mass, the COM is altered and the stance is wider, leading to changes in gait. Unlike wild turkeys, domesticated turkeys walk with emphasis in the mediolateral forces, similar to a waddling gait. These birds may also have a long stance duration with high frequency strides, leading to a shuffling gait. This shuffling gait increases stability but reduces the speed. Furthermore, as turkeys are bred for meat production, especially the breasts, these large pectoral muscles can interfere with their legs while walking (Stover et al. 2018).

## Influence in Understanding Human Locomotion

Although there are numerous differences between humans and birds, the principle similarity is that both are strictly bipedal (Müller et al. 2016). As a result, ground dwelling birds can serve as animal models when studying the integration of mechanics and neuromuscular control for bipedal locomotion (Daley 2019). Digitigrade posture in birds versus plantigrade posture in humans is a significant difference affecting locomotor mechanics. Birds have digitigrade posture due to their near horizontal femurs and elongated tarsometatarsal (proximal foot bones in humans) segments. Humans are plantigrade and have a vertically oriented femur during quiet standing (Müller et al. 2016). However, this difference does not exist in the early locomotor development of children. Children initially learn to walk in a digitigrade pattern and gradually transform to an adult-like plantigrade pattern after 1–2 years. Many of the changes seen during locomotor development in humans are also observed in chicks but over a shorter period. Both chicks and children must eventually be able to stabilize and support their bodies on one leg to develop a bipedal gait. This developmental change to a single leg support as well as changes in duty factor occurs in humans around 6–7 years of age (Muir et al. 1996). Comparing the development of bipedal locomotion between ground dwelling birds like Galliformes and humans can further our understanding of human locomotor development.

Bipedal animals avoid falls, collisions, and injuries, when moving across varied terrain through precise control of limb substrate interactions (Daley 2019). The adaptations used by birds and humans when running on uneven terrain are quite similar. The conservative spring mass model is used to describe both human and bird running. When adjusting to drops or downward steps, the leg angle at touchdown and the initial leg length are increased. When adjusting to obstacles and upward steps, the leg angle at touchdown and the initial leg length are decreased. Due to morphology, birds have a greater range of leg angle

and leg length adaptations than the restrictive straight leg of humans. The major difference between humans and birds is the leg angle at touchdown. On level ground, the leg angle in birds is usually between 40 and 68°, while in humans it is steeper at around 60–80° (Müller et al. 2016). The human leg instead is better adapted for leg stiffness changes when running on uneven ground. While birds lengthen their legs to cope with level discrepancies, humans not only adjust the leg angle and leg length but can also reduce their leg stiffness. If humans needed to increase their range of leg lengthening, they would move in a less upright posture. It has been theorized that early humans walked bipedally in a crouched position with more flexed hips and knees, similar to birds (Müller et al. 2016). This understanding of how ground-dwelling birds traverse terrain can be applied to designing and controlling bioinspired robotics and human-assisted devices.

## Conclusion

As a result of the domestication of chickens and turkeys, the locomotion of the Galliformes is exceptionally well-studied. Galliformes are predominantly ground dwelling birds that move by foot because it is energetically favorable. In bipedalism, the inverted pendulum model and the conservative spring model are used to describe the energy mechanics involved in walking and running, respectively. Only a few species of Galliformes fly long distances. Most of the other species fly short distances due to their large body size and low myoglobin containing glycolytic muscle fiber type. Fast flapping, rapid take off, jumping, and WAIR are used for traveling, avoiding predators, and searching for food. By domesticating some of these birds for meat and eggs, humans have altered their gait in comparison to their wild counterparts. As the evolution of bipedalism is shared among humans and Galliformes, studying locomotor behavior in these species can provide insight on the development of bioinspired robotics for clinical application.

## Cross-References

- Activity budget
- Adaptation
- Adaptedness of behavior
- Adaptive radiation
- Artificial selection
- Basal metabolic rate (BMR)
- Captivity
- Common ancestor
- Dispersal ability
- Dispersal patterns
- Diurnality
- Domestication
- Ecology
- Evolution
- Extinction in Learning
- Gait
- Home range
- Homology
- Homoplasy
- Husbandry
- Locomotion
- Morphology
- Muscular system
- Natural selection
- Navigation
- Pets
- Phylogeny
- Species
- Taxa
- Terrestrial
- Vertebrate nervous system
- Zoo
- Zoology

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## Gambling Fallacies

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## Definitions

**The Monte Carlo or Gambler's fallacy** – The erroneous belief that if, in the recent past, a particular event occurs more frequently than expected, and it is less likely to happen in the future because probabilities should even out.

**The near miss fallacy** – A near miss (or more accurately near hit) is a special kind of failure to reach a goal, one that fails but comes close to being successful.

**Chasing losses, entrapment, or sunk cost** – Trying to win back money one has already lost, by gambling more.

## Introduction

Gambling fallacies are thought to result from the misunderstanding of probabilities: what it means for a series of events to be random and from the mistaken understanding of the effects of past events on future events (fairness and equity). As such, they may be unique to humans and probably do not apply to other animals. That is, they may be culturally determined. In other cases, however, animals like pigeons show evidence of having similar biases, and those are likely to result from basic behavior processes.

## The Monte Carlo or Gambler's Fallacy

Certain fallacies, like the *Monte Carlo fallacy*, are unique to humans because they are based on what we believe to be characteristic of the fair distribution of random events. If one flips a coin four times and each time it comes up heads, many people would believe that the probability that it will come up heads again is much less than 50%, to make up for the unlikely outcome of four heads in succession. But coin tosses are

independent – the coin has no memory of its past behavior. As most animals live in an unpredictable world, one in which purely random events would be very rare, animals become sensitive to short-term changes in the probability of events. Thus, if animals are exposed to random events in which a particular event occurred four times in succession (e.g., left and right turns in a maze), they would be more likely to show a greater tendency to make that same response again. That is, because they live in a world in which the probability of events typically changes over time, they likely learn that the repeated event is now more likely to occur. Thus, if an animal were exposed to the coin flipping example, it would likely to act as if the coin was biased.

This phenomenon is related to *probability matching* in which humans are presented with two alternatives, but the probability of one being correct is greater than the other (e.g., 70% vs. 30%). Humans suboptimally tend to match those probabilities, responding 30% of the time to the lower probability event (Humphreys 1939). However, rats (Bitterman et al. 1958) and monkeys (Wilson and Rollin 1959) tend to choose the higher probability event, exclusively, thereby maximizing reinforcement. In both cases, humans attempt to do better than the experienced probability of the random events, whereas most animals do not.

## The Near Miss Fallacy

The *near miss fallacy* (more accurately referred to as the *near hit fallacy*) can most easily be seen in the way that slot machines function. Historically, slot machines have three reels, and the player wins when the pictures on the three reels match. The near hit outcome occurs when the first two reels match but the third does not. Curiously, when the probability of a win is equal, people prefer to play a slot machine with a higher rate of near hit outcomes (MacLin et al. 2007). Reid (1986) suggested that a near hit appears to be more similar to a hit than the other forms of losing because it is the only loss that is not apparent when the second reel stops.

Unlike humans, however, when pigeons are trained on a task, equated for losses, in which they can choose between an alternative with *near hit* trials and another alternative with other patterns of losses, they tend to avoid the alternative with the *near hit* trials (Fortes et al. 2017; Stagner et al. 2015). Apparently, for pigeons the similarity of the near hit losses to trials representing a win actually devalues the effects of a win. That is, because those losses look more like wins than other losses, they generalize to win trials.

What accounts for the difference between pigeons and humans? Humans tend to have considerable experience with tasks in which losses similar to a near hit actually represent progress towards a goal. Consider trying to get a basketball into a hoop. Initially, one might miss the hoop entirely. With practice one might get closer to putting the ball into the hoop but still not get it in. That incremental improvement would be evidence that one is making progress. The *near hit* in basketball represents an improvement. In the slot machine task, in which there is no skill, however, the near hit does not represent progress. But to a human, who has had considerable experience with tasks involving skill, it may feel like an improvement. Unlike a coin flip, the *near hit* is more closely related to skill tasks because in the sequence of the three events, the signal of a loss is delayed.

## Chasing Losses, Entrapment, or Sunk Cost

When gamblers start to lose, there may be a tendency to keep gambling to recoup the money that they have lost. This behavior comes under the larger category of *sunk cost*. *Sunk costs* are expenses that cannot be retrieved and, thus, should not factor into future investment decisions. But people will often invest additional funds in a failing business to try to make up for those losses, a behavior that typically results in additional losses. Gamblers who are losing will often do the same.

Research with animals suggest that pigeons, too, show a *sunk cost effect* (Pattison et al. 2012). In that study, pigeons were trained to peck a green button 30 times for food. They

were also trained to peck a red button 10 times for food. The pigeons were then tested with a choice. After they had pecked the green button a variable number of times, the pigeons were given a choice to continue pecking the green button or to switch to the red button. Regardless of the number of times that they had pecked the green button (e.g., only 10 times), the pigeons almost always chose to stay with the green button (see also Magalhães and White 2014; Navarro and Fantino 2005).

The research with pigeons suggests that the *sunk cost effect* does not result from not wanting to “give up” or the potential social consequences of failure. Instead, it may result from a tendency to misperceive that the consequence of persistence is more predictable of reinforcement than the consequence of switching to an alternative behavior. This behavior may be predisposed because in nature, it is likely that giving up on the current search may involve increased uncertainty, greater travel time, and the potential danger associated with travel.

## Conclusion

Examining the similarities and differences in the way that humans and other animals approach probabilistic learning tasks can identify which fallacies can be attributable to cultural information about the task and which can be attributed to basic behavioral processes, perhaps attributable to evolution.

## Cross-References

► [Suboptimal Behaviors in Gambling-Like Tasks](#)

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## Game Theory

► [Ultimatum Game](#)

## Gametes

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## Synonyms

[Ovum](#); [Reproductive cell](#); [Spermatozoa](#)

## Definition

Gametes are sex cells of organisms, haploid in chromosome content that fuse with other haploid

cells during fertilization in sexually reproducing organisms.

## Purpose of Gamete Formation

Gametes or reproductive cells are always haploid in sexually reproducing organism in order to maintain the chromosomal number constant in the species after getting combined with the gamete from the other partner. The new organism has half the chromosomes from its mother and half from its father. Sexual reproduction also helps in the maintenance of genetic diversity of organisms because each organism has a different combination of genes than either of its parents. For example, in humans, a sperm cell gets fused with an egg cell, producing a zygote that has a unique set of genetic information and correct number of chromosomes.

## Types of Gametes

There are two types of gametes in humans, male and female gametes. The male gamete is called sperm and has chromosome structure XY. The female gamete is called the ovum and has chromosome structure XX.

## Spermatogenesis

Spermatogenesis is a process of formation of male gametes that occurs in the seminiferous epithelium of the adult testis. The process of spermatogenesis gets completed in four phases and includes (1) the proliferation and differentiation of spermatogonia, (2) meiotic divisions of spermatocytes, and (3) the transformation of haploid round spermatids arising from the second meiotic division into spermatozoa (spermiogenesis), which (4) are released into the lumen of the seminiferous tubules (spermiation). Spermatogonia are the diploid ( $2n$ ) stem cells of spermatogenesis and can be divided into type A and type B. Type A spermatogonia have an oval euchromatic nucleus in contrast to type B spermatogonia, which have a round heterochromatic nucleus (ref

1). It is the type B spermatogonia that get differentiated and enter the process of meiosis. Meiosis starts with DNA synthesis of type B spermatogonia which lose contact with the basal lamina (preleptotene). After completion of DNA synthesis, each chromosome consists of two chromatids (C). These cells are named primary spermatocytes, and the DNA content is tetraploid ( $2n;4C$ ). Primary spermatocytes undergo the first meiotic division that results into the formation of haploid secondary spermatocytes with diploid DNA content ( $1n2C$ ). Secondary spermatocytes undergo the second meiotic division after a short interphase of about 6 h in the human without DNA synthesis. By this division, chromatids are finally separated leading to round spermatids with a haploid number of chromosomes and DNA content ( $1n1C$ ). The transformation of conventional round cell spermatids into spermatozoa with the capacity for motility and fertilization of an egg includes a complex sequence of events: (1) formation of the acrosome, (2) condensation of the nucleus, (3) development of the sperm tail, (4) reorganization of cellular organelles such as mitochondria and centrioles, and (5) reduction of the cytoplasm. The length of the human spermatozoon measures about 60  $\mu\text{m}$ . The flat and oval head (diameter: 3  $\mu\text{m}$ , length: 5  $\mu\text{m}$ ) consists of the acrosome and the extremely condensed nucleus. The acrosome covers the head surface and contains numerous proteolytic enzymes, i.e., hyaluronidase, collagenase, neuraminidase, phospholipase A, acrosin, and others. The release of these enzymes, the so-called acrosome reaction, enables the spermatozoon to penetrate the "corona radiata" of follicle cells and the zona pellucida of the egg. Some nuclear vacuoles are common. The flagellum measures about 55  $\mu\text{m}$  in length. It possesses the central axoneme and is divided into neck piece, mid piece, principle piece, and end piece (Bergmann 2006; L'Hernault 2006; de Kretser et al. 1998).

## Oogenesis

Oogenesis occurs in the outermost layers of the ovaries. Oogenesis starts with a germ cell, called an oogonium (plural: oogonia). Oogonia undergo

mitosis to increase in number, eventually resulting in up to one to two million cells in the embryo. The cells that undergo meiosis are called primary oocytes. These cells will begin the first meiotic division but get arrested during the first prophase stage. At the time of birth, all future eggs are in the prophase stage. At adolescence, anterior pituitary hormones cause the development of a number of follicles in an ovary (Gilbert 2000). This results in the primary oocyte finishing the first meiotic division. The cell divides unequally, with most of the cellular material and organelles going to one cell, called a secondary oocyte, and only one set of chromosomes and a small amount of cytoplasm going to the other cell. This second cell is called a polar body and usually dies. A secondary meiotic arrest occurs, this time at the metaphase II stage. At ovulation, this secondary oocyte will be released and travel toward the uterus through the oviduct. If the secondary oocyte is fertilized, the cell continues through the meiosis II, completing meiosis, producing a second polar body and a fertilized egg containing all 46 chromosomes of a human being, half of them coming from the sperm (Bukovsky et al. 2005; Virant-Klun 2015). In some species, such as sea urchins and frogs, the female routinely produces hundreds or thousands of eggs at a time, whereas in other species, such as humans and most mammals, only a few eggs are produced during the lifetime of an individual. In those species that produce thousands of ova, the oogonia are self-renewing stem cells that endure for the lifetime of the organism. In those species that produce fewer eggs, the oogonia divide to form a limited number of egg precursor cells. In the human embryo, the thousand or so oogonia divide rapidly from the second to the seventh month of gestation to form roughly seven million germ cells. After the seventh month of embryonic development, however, the number of germ cells drops precipitously (Gilbert 2000).

## Conclusions

Gametogenesis is an essential process for the survival of the species. Any alteration in this process

leads to high-risk pregnancy cases. Any disturbance or alteration in the process of spermatogenesis like oligospermia, azoospermia, asthenozoospermia, and chromosomal anomalies leads to the higher percentage of male infertility. On the other hand, in the case of females, various conditions like polycystic ovarian syndrome and premature ovarian failure contribute to female infertility cases around the globe. Various research studies are in process throughout the world for solving these issues of infertility. There are many herbal products in markets for humans after their preliminary study on animal models.

## Cross-References

- ▶ Chromosomes
- ▶ Ovaries
- ▶ Reproduction
- ▶ Reproductive fitness
- ▶ Sex-Linked
- ▶ Spermatogenesis

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## Ganglion

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## Synonyms

Encapsulated nerve-cell bodies

## Definition

An aggregation or assembly of neuronal cell bodies, usually in the peripheral nervous system (forming a nerve center) is termed a ganglion. The basic function of a ganglion is to serve as a connection between the central nervous system (CNS) and peripheral nervous system (PNS). *Plural-ganglia.*

## Introduction

The human nervous system consists of CNS and PNS. Located in the PNS, the cell bodies (which are known as ganglion) occur as a relay between them. The development of the human nervous system begins from the signals sent by the

notochord, which forms the structure called the neural tube, which later forms the neural crest.

There are two types of ganglia in the PNS. They are (1) sensory ganglia that are the cell bodies of sensory neurons and (2) autonomic ganglia, which are the cell bodies of efferent neurons from the autonomic nervous system.

## Evolution

The evolution of ganglia has taken place in their own pace during the evolution of different species. The simplest species in animal kingdom are under the phylum Porifera, e.g., sponges. These species do not have any nerve net organization or development of a brain. Apart from sponges, all other animals have a neural system or correlates to carry signals in their bodies. Nervous systems in hydra consist of sensory cells and ganglionic cells. Ganglions are thought to be formed from the neuroblast's migration in CNS (Blentic et al. 2011).

The most primitive nervous system is a diffuse nervous system found in Cnidaria and in Ctenophora (Encyclopaedia Britannica 2017). Here, a nerve net is formed beneath the epidermal layer of the organism. This diffused nerve net is found in flatworms (planaria), which also develop two cerebral ganglia at the cephalic end, forming part of a more complex central nervous system (Erulkar and Thomas 2020). The nervous systems of annelids, mollusks, and arthropods consist of nerve cords and ganglia running along the length of their bodies. Nematodes have a group of ganglia placed anteriorly consisting of nerve cells with a high degree of centralization. Nerve nets are absent here. Arthropods are diverse in nature and consist of three pairs of ganglia. The functions conducted by the ganglia of arthropods are vision control, control of tactile sensations and integration of sensory information (Erulkar and Thomas 2020). Few studies have shown clusters of ganglia in mollusks in relation with the enteric nervous system. Species such as crabs and snails consist of several ganglia. As the organizational level of organisms become more complex, the level of centralization and cephalization increases.

Gradually, the functions such as feeding and locomotion become specified in certain parts of the nervous system (Erulkar and Thomas 2020; Nicholls 1992).

In the vertebrates, the neurons gather in masses forming ganglionic structures in the peripheral nervous system. The cells associated with ganglion are called the ganglionic cells. On the other hand, in the invertebrates, there is no distinctive separation between the central nervous system and peripheral nervous system. The nerve nets and ganglionic bodies branch together as a diffused nervous system.

## Types of Ganglia

There are around 24 paravertebral ganglia in each chain in the human body. In the vertebrates, ganglia are classified into three major categories:

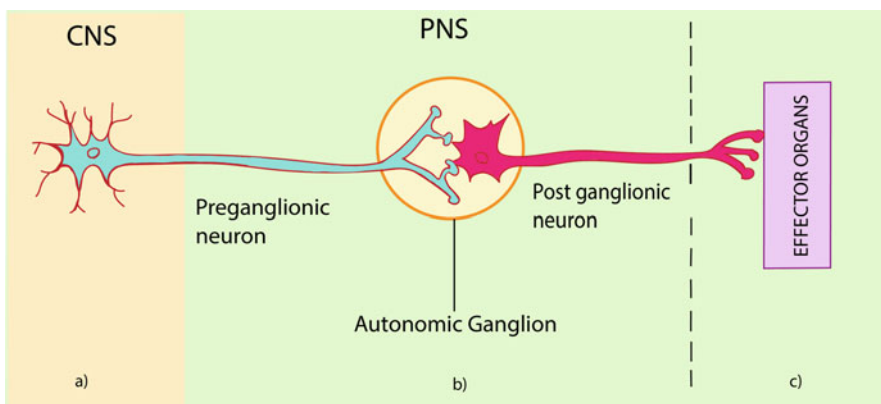
1. **Autonomic ganglia** consist of cell bodies of efferent neurons, associated with autonomic system. It has two sets of ganglia, the preganglionic neurons and postganglionic neurons.
2. **Cranial ganglia** consist of cranial nerve cell bodies.
3. **Dorsal root ganglia (spinal ganglia)** consist of afferent nerves cell bodies, associated with sensory neurons.

## Autonomic Ganglia

Autonomic ganglia are basically groups of neuronal cell bodies along with their dendrites. Autonomic ganglia consist of motor neurons and act as a connection carried by the autonomic nerves between the central nervous system and the target organs located at the periphery. Autonomic ganglia have two divisions of neurons that are antagonists to each other, i.e., the sympathetic ganglia and parasympathetic ganglia (Mai and Paxinos 2011). Both of these ganglia have sensory fibers associated with them. A set of myelinated neurons arising in the spinal cord or the brainstem are termed as preganglionic fibers, whereas the unmyelinated fibers located outside the central nervous system are the postganglionic neurons. The preganglionic neurons carrying relay information from the brainstem connect to the organs in the viscera through the postganglionic ganglia (Fig. 1). These ganglionic cells control visceral behavior, i.e., involuntary movements.

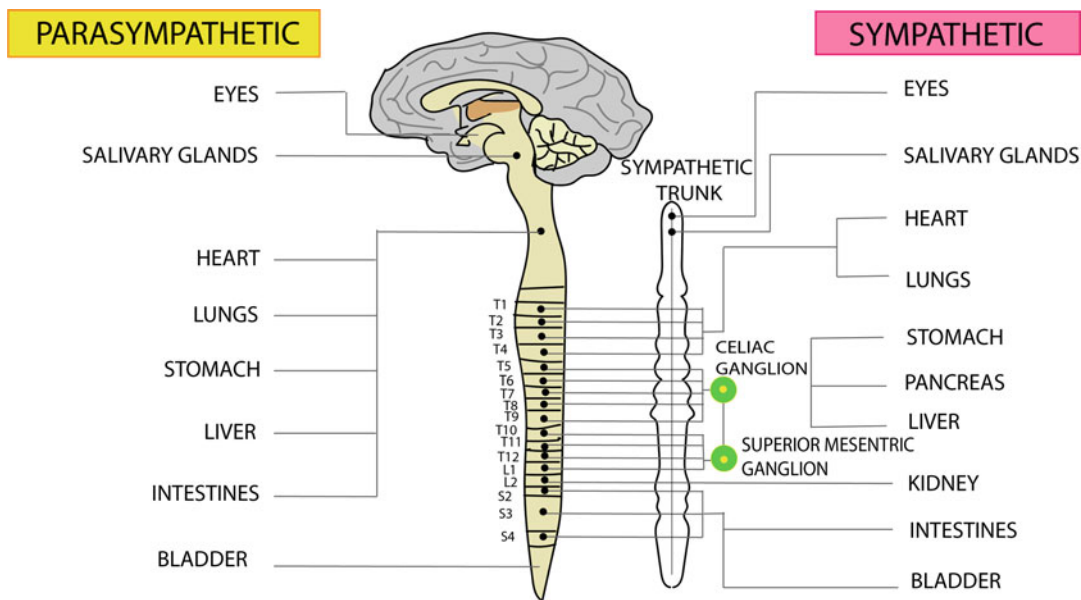
### (i) Sympathetic Ganglia

This is the ganglia associated with the sympathetic nervous system. The sympathetic ganglia are localized at distant region in front of the vertebrae from the target organ. The preganglionic sympathetic ganglia are present at the lateral horns of 12th thoracic till the second and third lumbar



**Ganglion, Fig. 1** Autonomic ganglia. Connections between the CNS and PNS occur through the ganglionic neurons. (a) Central nervous system, (b) peripheral

nervous system, and (c) effector organs: cardiac muscles, smooth muscles, or glands



**Ganglion, Fig. 2** Autonomic nervous system. Regulation and functioning of the organs carried by parasympathetic and sympathetic systems in human body. Spinal cord

segments represented as (1) T1–T12, thoracic segments; (2) L1–L2, lumbar segments; (3) S2–S4, sacral segments

region of the spinal cord. The sympathetic ganglia further have two types based on their location of cells (Fig. 2). There are 21–22 pairs of paravertebral sympathetic ganglia, present along the sides of vertebrae, and three prevertebral sympathetic ganglia (celiac, mesenteric and inferior mesenteric) located on the anterior side of aorta (Mai and Paxinos 2011). Sympathetic ganglia perform the function of carrying stress responses or danger signals.

### (ii) Parasympathetic Ganglia

The parasympathetic ganglia are associated with the PNS and present in the vicinity and adjacent to the organs it innervates. Preganglionic parasympathetic ganglia are localized at the brainstem and sacral region of the vertebral column (Fig. 3). On the other hand, the postganglionic parasympathetic ganglia are present near ear and urinary bladder. Parasympathetic ganglia are cholinergic in nature, i.e., secrete acetylcholine. Parasympathetic ganglia in association with the various cranial nerves (CN III, VII, IX, X)

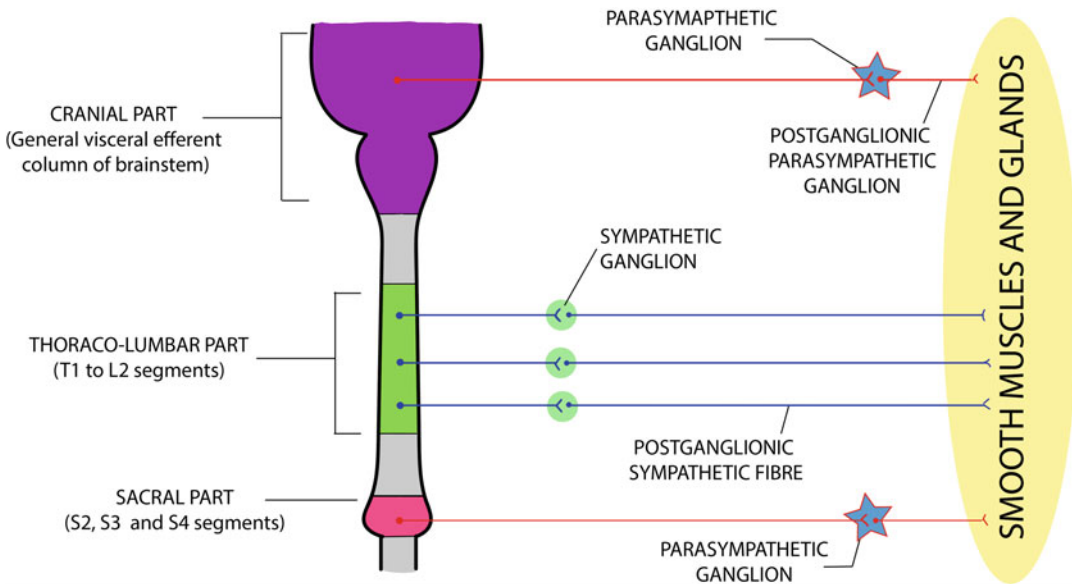
have different functions such as salivation and secretory activities.

### (iii) Enteric Ganglia

The assembly of neurons enclosed within the wall of the gastrointestinal tract comprises of the enteric nervous system. This system controls motility along with the gastrointestinal tract and secretion.

### Cranial Ganglia

These are the sensory ganglia associated with the cranial nerves. They are located at the surface of hard and dense part of temporal bone. There are 12 pairs of cranial nerves in human beings. The trigeminal nerve is the largest nerve, and the trigeminal ganglion gives rise to three large nerves: ophthalmic, maxillary, and mandibular. The cell bodies of sensory fibers are predominantly present in this ganglion. The intermediate nerve of the facial nerve consists of parasympathetic fibers. Ciliary ganglion, submandibular ganglion, geniculate ganglion, and pterygopalatine ganglion are part of this nerve. Cranial nerve ganglia serve the function of controlling reflexes for head and neck.



**Ganglion, Fig. 3** Parasympathetic and sympathetic ganglia. Segmental divisions of brainstem and spine into three regions along with the fibers projecting from each segment have been represented

The sensory input carried by the fibers includes sensations like vision, taste, smell, hearing, and balance.

### Dorsal Root Ganglia (Sensory Ganglia)

The dorsal root ganglia (DRG), also termed as spinal ganglia, is normally located along the dorsal horn of the spinal nerve, i.e., close to intervertebral foramina. It contains cell bodies of primary afferent neurons, which are pseudo-unipolar neurons. Sensory ganglia are made up of unipolar neurons that are structures in oval shape which are located on DRG (Fig. 4). These cells undertake a T-shaped bifurcation allowing one branch to descend in periphery, while the other enters the spinal cord and brain (Mai and Paxinos 2011). Many cells, such as satellite cells, macrophages, lymphocytes, and endothelial cells, are found in the DRG. DRG carries the information (temperature, harm signals) to the central nervous system.

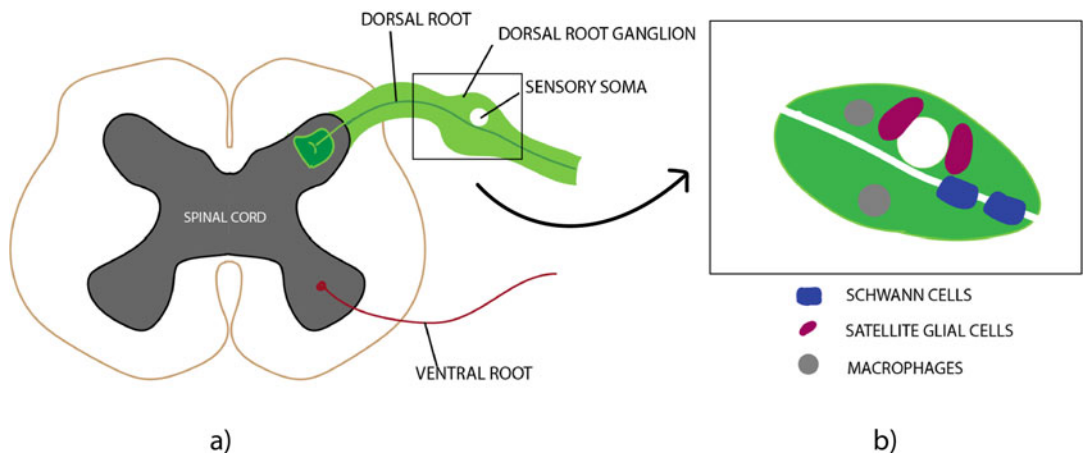
DRG consist of TRP channels and exhibit peripheral sensitization in the conditions of chronic pain. Therefore, recent studies are targeting DRG for treatment of neuropathic pain caused due to sudden and serious injuries (Berta

et al. 2017). The most common technique used is DRG radiofrequency ablation. The satellite glial cells (SGCs) found in the DRG form a tight envelope around the neuronal cells which generate response in conditions of nerve injury or inflammation (Haberberger et al. 2019). These contribute in neuropathic pain and participate in signal processing in sensory ganglia (Hanani 2005).

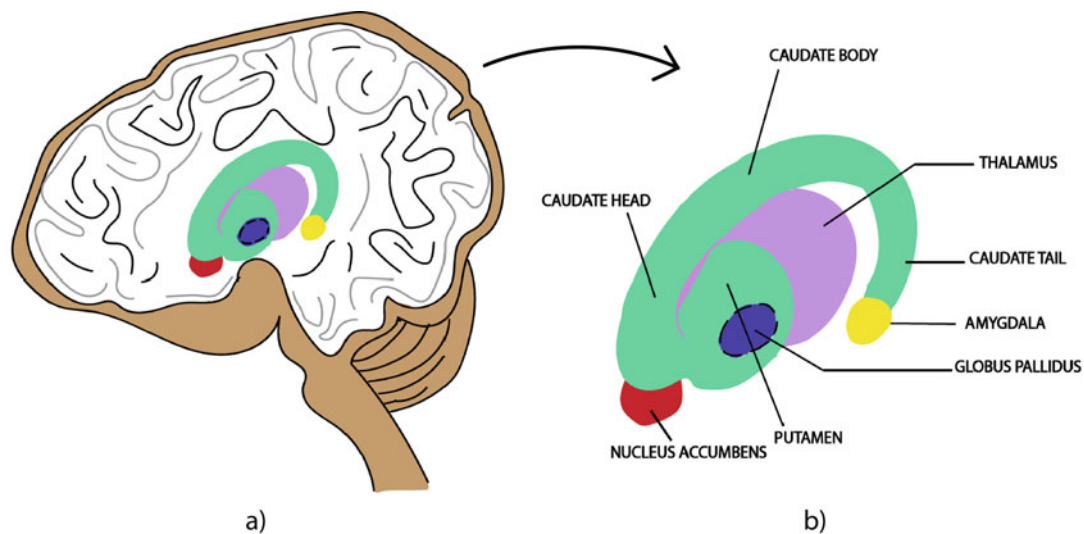
### Basal Ganglia

Basal ganglia (BG) are a set of nuclei, which is a part of gray matter in the cerebrum. Basal ganglia consist of certain structures: caudate nucleus, putamen, globus pallidus, nucleus accumbens, subthalamic nucleus and substantia nigra (Fig. 5) (Florio et al. 2018). Caudate nucleus and putamen (striatum) show excitatory activity in BG, whereas globus pallidus acts inhibitory (GABAergic neurons) sending signals to the thalamus. Dopamine plays an important role in stability of BG.

Specific regions of the striatum serve different purposes such expression and habit acquisition, which depend on the factors like DA inputs, cortical inputs and intrinsic circuitry (Florio et al. 2018). Basal ganglia are responsible for emotions



**Ganglion, Fig. 4** Dorsal root ganglion. Location and structure of dorsal root ganglion. (a) Dorsal horn of the spinal cord with pathways of dorsal root and ventral root. (b) Enlarged view of dorsal root ganglion and the types of cell involved in its structure



**Ganglion, Fig. 5** Basal ganglia. Position and parts of basal ganglia in the human brain. (a) Brain section representing location of basal ganglia, (b) structure of basal ganglia

and habit formation in humans. Along with this, it also contributes in decision-making, directional movement, and other cognitive processes.

### Conclusion

Ganglia are a set of nuclei, which either consist of afferent or efferent neurons outside the central

nervous system. These structures are located at various parts defining their particular functions in the organ. Primarily, ganglia serve as a relay for information transfer between the CNS and the PNS. Ganglionic structures have evolved along with the evolution of organisms. The sensory, autonomic, and cranial ganglia are present in the PNS, whereas an important ganglion termed basal ganglia is found only in CNS, specifically the



cerebrum. There are several studies and researches conducted on the sensory and cranial ganglia. The dorsal root ganglion and satellite ganglion cells are currently being subjected to study for treatments for neuropathic pain. Techniques such as DRG radiofrequency ablation and gene therapy are used in modern treatments (Hanani 2005).

## Cross-References

► [Peripheral Nervous System](#)

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## Gap

► [Contagious Yawning](#)

## Gause's Exclusion Law

► [Gause's Law](#)

## Gause's Law

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## Synonyms

[Gause's exclusion law](#); [Gause's principle](#); [Grinnell's axiom](#); [The competitive displacement principle](#); [The competitive exclusion principle](#)

## Definition

Gause's law is a principle in the field of population dynamics first outlined by Russian/Soviet biologist G.F. Gause, which states that two species that are competing for the same limited resources cannot coexist at constant population values, that no two species with similar ecological niches can coexist in a state of stable equilibrium, or that realized ecological niches do not intersect. It is otherwise called the competitive exclusion principle (CEP). Three different basic outcomes have been specified: competitive exclusion, local extinction, and niche differentiation.

## Introduction

Population dynamics is a field that studies the change in the prevalence of different species over time in relation to four key life-path processes: birth, death, immigration, and emigration. Prior to Gause, after the initial nineteenth-century contribution of T.R. Malthus on the consequences of exponential population growth, the study of inter-species interaction in the early part of the twentieth century had been advanced through

important work by Alfred Lotka (1925) and Vito Volterra (1931 [1928]), which together yielded the Lotka-Volterra predator-prey set of differential equations, as Gause readily acknowledged (Gause 1932, p. 389). These equations modeled the association of two separate species or two groups within a species, one of which preys on the other with deadly intent as a result of asymmetric power relations. However, inter-species interactions are not limited to the very specific case of predator-prey relations, as the significant work of G.F. Gause would go on to illustrate.

### G.F. Gause

Georgii Frantsevich Gause – Георгий Францевич Га́йзе – (1910–1986) was a Russian/Soviet biologist born in Moscow who became a Professor at the Timiriasev Institute for Biological Research and the Zoological Museum in the University of Moscow, after first studying under W.W. Alpatov. Gause worked initially as a biologist on population structure and the dynamic interactions of microorganisms and then later became a researcher on antibiotics such as Gramicidin S, which he discovered in 1942 and which was then used during WW2. He eventually received the Stalin Prize for his antibiotic discovery, and his research in this field was considered so important that he was spared the Lysenkoite persecution that affected some of his Soviet biologist colleagues.

The nineteenth-century achievements in Russian science had reached its peak in the work of D.I. Mendeleev, the inventor of the periodic table of chemical elements, but many other Russian scientists made notable contributions across both the nineteenth and the early twentieth centuries. As the work of Gause suggests, Russian contributions to experimental biology were also significant, as epitomized by the worldwide reputation of physiologist I.P. Pavlov (Vucinich 1970, pp. 298–313). Some other Russian scientists in the first half of the twentieth century also contributed to work on aspects of population dynamics such as plotting population density (Barnett 2011, pp. 61–63), and this field generally remained outside of the more politically contentious areas of Soviet science that were

negatively affected by the growth of Stalinist repression at the end of the 1920s.

### Gause's Law

In his well-known book *The Struggle for Existence* (1934), Gause attempted to provide aspects of a mathematical theory of the struggle for existence. He started from three generalizations of the phenomena of species multiplication. These were (1) multiplication occurs theoretically by geometric progression; (2) in reality, multiplication is subordinate to the rule of inertia; (3) small organisms multiply more rapidly than larger organisms (Gause 2019 [1934], p. 8).

As Gause explained about his approach to population dynamics, in his view, the growth of each species depended in part “on the unutilized opportunity for growth at that moment” (Gause 2019 [1934], p. 89): each species possessed certain specific coefficients of utilizing this opportunity in relation to the particular environment it resided in and in relation to the actions of the other species within this environment. Gause expressed his basic result as follows: the rate of growth of two species in a mixed population is determined by the absolute potential increases in the two populations multiplied by the comparative degree of realization of the increases (Gause 2019 [1934], p. 47).

Another concept outlined by Gause was the intensity of the struggle for existence, measured by the resistance needed to be overcome in order to increase the number of individuals by a unit in a given period of time. He suggested that, contrary to what might initially be expected, in many cases at least, the better were the environmental conditions for sustaining the different species involved, the more intense was the struggle for life, and the greater was the percentage of individuals of a given species who subsequently perished (Gause 2019 [1934], p. 14).

In the empirical sections of the book, Gause reported the results of several experiments that he had conducted with simple organisms undertaken in order to study how the populations of different organisms interacted with each other in specific

shared environments. For example, as has been outlined about his experiment with yeast:

Using the yeasts *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir*, Gause unequivocally demonstrated the importance of interspecific competition in the interactions between species. These yeasts differ in their relative intensities of oxidation and fermentation. *Saccharomyces cerevisiae* is able to reproduce rapidly in the absence of oxygen, while the growth of *Schizosaccharomyces kephir* under anaerobic [oxygen-deficient] conditions is exceedingly slow. In the absence of other species ... Over time, it was predicted that *Schizosaccharomyces* would be excluded by *Saccharomyces*. (Bonsall 2002, p. 923)

As Gause explained, whether the first species would supplant the second (or vice versa) in any competitive context also depended on their respective inherent rates of growth and their maximal physical masses, the latter being known from separate studies of their individual growth potentials (Gause 1932, pp. 391–392).

In addition to yeasts, Gause experimented with different species of *Paramecium* and *Didinium* (unicellular ciliates), namely, *Paramecium aurelia*, *Paramecium caudatum*, and *Didinium nasutum*. In one experiment he introduced two species of *Paramecium* into containers with a bacterial culture that was a food source. After a few days, one of the species invariably became extinct as it was not able to compete with the other for access to the bacterial culture, thus verifying Gause's law in this particular instance. As Gauss explained: "*if we know the properties of two species growing separately ... then connecting these values into a theoretical equation of the struggle for existence we can calculate in what proportion a certain limited amount of energy will be distributed between the populations of two competing species*" (Gause 2019 [1934], p. 89; italics in the original). This links to the rate of the stream by which a population completely corners the food resources.

A classic example of Gause's law in action is MacArthur's warblers, which are five species of insectivorous wood warblers in Maine and Vermont (USA) that occupy exactly the same forest breeding area, which are named after Canadian ecologist Robert MacArthur (1930–1972). Although this location-specific coexistence might appear to

violate Gause's law, in fact, MacArthur discovered that the feeding positions of the birds on the trees they inhabit are divided into 16 different zones or positions, which each species confining their feeding activities to specific designated zones (MacArthur 1958). The foraging behaviors of the warblers also differ in the same structured and specialized manner, thereby corresponding fully to the competitive exclusion principle.

## Grinnell's Axiom

Although the competitive exclusion principle is universally referred to as Gause's law, the first person to clearly specify it was Joseph Grinnell (1877–1939), an American field biologist and zoologist. Grinnell explained that "we never find two 'subspecies' breeding in the same faunal area," and "Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other" (Grinnell 1904, p. 373, 377). This was a more concise statement of Gause's law than was originally provided by Gause himself in his various publications from the early 1930s (Gause 1932, 2019 [1934]), and it has subsequently been named as Grinnell's axiom.

Grinnell maintained that which species would eventually triumph in the case of an indigenous species versus an invader species depended on the specifics of the particular case under view, and which species was best fitted to the local conditions as they existed at the time of the invasion. Small changes in local conditions could give an invader species an advantage in some instances, facilitating their victory in the competitive battle for survival, while if the indigenous species was still best adapted to local conditions due to its longer exposure to them, then they would successfully see off the competitive challenge.

## The Logical Status of Gause's Law

However, the theoretical nature or logical status of Gause's law has been subject to debate, primarily because there are various acknowledged

exceptions to it (the prevalence of natural coexistence of species in some verified instances: see the next section below). This means that it is not a strictly observed, *a priori*, or universal causal law; instead, it has been characterized variously as a broad empirical regularity, a *ceteris paribus* law, or a coexistence law.

In addition, the operation of Gause's law in any particular instance may be specific to the example under review. For instance, in one case (an invasive ant species), it was reported that there was no simple relationship between the degree of aggression exhibited by the invaded species involved and the taxonomic remoteness of the intruder species (de Vroey 1979). In some instances it might be the case that a specific homologous range of species may coexist in the same niche, but others outside this range do eventually become out-competed, or in other instances, it might be the case that closely related species can have very similar niches.

Some interesting and unusual results have also been reported regarding the expression of Gause's law. For example, one set of experiments repeatedly pitted two species of flour beetles against each other, with the result that one species always eventually eliminated the other, but it was not always the same species that had triumphed (Hardin 1960, p. 1293). This was interpreted to demonstrate that small variations in the initial conditions and/or small changes in the developing circumstances could sometimes have decisive effects on the outcome, this being a population dynamics version of the well-known butterfly effect.

Some of the various factors that have been specified as having an impact on the final outcome are initial species numbers, numerous environmental factors, comparative competitive abilities, resistance to disease, the degree of genetic diversity, and many others. As has rightly been explained on the general applicability of Gause's law:

To assert the truth of the competitive exclusion principle is not to say that nature is and always must be, everywhere, "red in tooth and claw." Rather, it is to point out that *every* instance of apparent coexistence must be accounted for. Out of the study of all such instances will come a fuller

knowledge of the many prosthetic devices of coexistence, each with its own costs and its own benefits. (Hardin 1960, p. 1297)

As is well articulated in this paragraph, the question of environment-sharing coexistent species, or apparent exceptions to Gause's law, now requires consideration in more detail.

## Exceptions to Gause's Law

The best known exception to Gause's law is the so-called plankton paradox. According to Gause's law, since all plankton species live on a very restricted set of marine resources in a given oceanic area, only a small number of plankton species should be able to coexist in this environment over the long term. In fact, large numbers of plankton species thrive together within limited regions of the open ocean (Hutchinson 1961).

One aspect of the solution to the plankton paradox may be the already-outlined notion that in a given ecosystem – in this case an ocean/marine ecosystem – a certain range of very similar species may coexist. This could be (for example) because of the prevalence of environment-specific features such as spatial heterogeneity, chaotic fluid motion, and/or equilibrium-deficient systems that produce chaotic oscillations, rather than stable equilibrium points, in given ocean/marine environments (Scheffer et al. 2003). The oceanic environment is a very different ecosystem than that occupied by most land-based animal species, so the rules underlying the competitive behavior of ocean-based species might also be very different in some instances.

Another potential exception to Gause's law is predator-mediated coexistence, which occurs when selective predation facilitates the coexistence of different prey species that would otherwise eradicate a proportion of them by means of the standard operation of Gause's law. The existence of aggregated distribution, or highly uneven and widely separated aggregated regional distribution patterns, and/or environmental heterogeneity, may also aid some competitor species exemptions from Gause's law. Character

displacement, or trait evolution to lessen resource competition, is another explanation that can be seen to apply in some instances. In general, the existence of various different exceptions to Gause's law is firmly established in the literature, but this does not invalidate the law itself as a substantiated *ceteris paribus* law.

## Gause's Law and the Evolution of Animal Cognition

A cognitively enhanced version of Gause's law could be articulated as follows: no two species with very similar ecological niches, similar morphologies, and similar food sources, but with some different cognitive abilities, can coexist in a state of stable equilibrium, as the species with the superior cognitive function in key areas of behavior will ultimately triumph. A particular species competitive advantage could also include a cognitive element but not be limited to this area alone. It can consequently be asked whether interspecies competition can sometimes act as a factor driving the evolution of cognitive function: a form of competitive co-evolution or reciprocal evolution may also lead to competitive displacement.

Certainly, co-evolution between predators and prey often involves an evolutionary arms race between predating capture skills and predator avoidance skills, these skills sometimes being partly cognitive in nature (Barnett 2019). One key set of cognitive skills in this case is the development of an understanding of individual intentionality and agency in relation to the progression of predator-prey interactions, skills such as gaze direction detection mechanisms, movement projection deception abilities, predator-prey intention awareness, and fast and frugal decision-making abilities (Barrett 2005, p. 202). Even if two closely situated species are not in a predator-prey relationship, their interactions can still involve direct cognitive competitions and subsequent neurological evolutions, and the outcomes of these iterated interactions might then in some circumstances produce the extinction of one of the species involved, in accordance with Gause's law.

An additional element to any cognitive competitions between competing species residing in the same environment or ecological niche is the hypothesized existence of the cognitive niche, or a repertoire of simple decision-making strategies that utilize regularities in the local environment to assist in the decision-making process (Marewski and Schooler 2011). In relation to predator-prey interactions, these cognitive niches can be seen to facilitate the fast and frugal decision-making abilities that are required to increase an individual animal's chances of victory and/or survival.

## The Application of Gause's Law to *Homo Sapiens*

Gause's law has in certain cases been applied to some prehistoric types of human society. For example, it has been suggested that two or more hunter-gatherer groups living within the same ecological niche will sometimes come into direct conflict over available resources, leading in some instances to the departure/vanquishing of one or more of the competing hunter-gatherer groups, in accordance with Gause's law (Fog 2017).

The theory of kin selection also predicts that contemporary minority ethnic groups will show higher degrees of in-group solidarity than is seen among the wider general population in particular countries (Salter 2007). This suggests not that ethnic groups supplant other indigenous populations via Gause's law but that ethnic nepotism is a real phenomenon that has an effect on both wider social cohesion and local business structure, for example, through the development of ethnically homogeneous housing clusters or minority-dominated trading groups (Light and Karageorgis 1994). Here the competitive exclusion principle is functioning within specific geographical areas and particular business sectors of the economy, rather than between whole population groups.

Gause's law has also been applied to the competition between very similar businesses in the same sector in a market economy, with large



companies tending to takeover or acquire smaller rival companies producing very similar products in some circumstances (Henderson 1989). However, as with all these types of extension of Gause's law to elements of human societies, the parallels that are here being posited are only very inexact ones, and various modifications to the underlying assumptions are usually necessary. Also, the various exemptions from Gause's law that have already been discussed might apply to some instances of *Homo* competitive activities.

## Conclusion

Gause's law, albeit a *ceteris paribus* law with various highlighted exceptions, has proved itself to be an important contribution to population dynamics and also to ecological thinking more generally. However, although Gause's law is now universally defined as the competitive exclusion principle (CEP), Gause himself did not initially name it as such, and it has been suggested that a loose formulation of the idea can be found in Charles Darwin's *Origin of Species*: with similarity of habits and constitutions in species, the struggle between them is generally more severe (Gause 2019 [1934], p. 15; Darwin 1872 [1859]). And it was Joseph Grinnell who had earlier specified a more concise version of Gause's law in an article that was published in 1904.

Even so, the relevance of Gause's law as a *ceteris paribus* law to the contemporary world still remains, and he was still personally defending it almost four decades after he first presented it (Gause 1970). Therefore, Gause's book *The Struggle for Existence* should be regarded as an enduring classic of mathematical biology, population dynamics, and behavioral ecology that also has significant relevance outside the narrow confines of the mathematical modeling of abstract biological processes.

## Cross-References

- Extinction in Learning
- Niche Divergence

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## Gause's Principle

- [Gause's Law](#)

## Geese

- [Waterfowl](#)

## Gender Balance

- [Sex Ratio](#)

## Gender Differences

- [Sex Differences](#)
- [Sexual Dimorphism](#)

## Gender-Based

- [Sex-Linked](#)

## Gender-Related

- [Sex-Linked](#)

## Gene

- [Behavioral Genomics](#)
- [Gene Pool](#)

## Gene Expression

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## Synonyms

[Central dogma of life](#); [DNA](#); [Post-transcriptional modification](#); [Ribosome](#); [Transcription](#); [Translation](#)

## Definitions

Gene expression is the process of decoding the information stored in the DNA (2-deoxyribonucleic acid) to its functional forms.

## Heredity and Gene Expression

In the 1860s, Gregor Mendel showed that genetic information transfers from parents to offspring in discrete units, later named genes, that confer heritable traits such as morphological features including flower color or plant height. The exact chemical nature of the genetic material was unknown until the mid-1940s. Two possible candidates, DNA and protein, were always found together in the chromosomes of the nucleus – the center of hereditary information of the cell. Genes affect phenotypic traits was known since Mendel's work. Compelling evidence also suggested that genes affect enzyme functions and control the metabolic activities of an organism. In the early 1900s, Archibald Garrod examined patients excreting homogentisic acid (alcapton) in their urine that turned black upon exposure to air. This disorder (alcaptonuria)

follows a pattern of Mendelian inheritance. Garrod concluded that in the affected individuals, the gene responsible for the breakdown of alkapton was missing or compromised. On the same note, Beadle and Tatum performed random mutagenesis in *Neurospora* and showed that genes act stepwise to drive metabolic reactions. They generated *Neurospora* mutants defective for the distinct steps of metabolic pathways involved in vitamin biosynthesis (Beadle and Tatum 1941). This sparked their “one gene-one enzyme” hypothesis.

DNA was widely accepted as genetic material in the mid-1940s and confirmed by Hershey and Chase in 1952. In 1953, a model for the structure of the DNA was proposed (Watson and Crick 1953). Two sugar-phosphate antiparallel strands of DNA pair up with each other through hydrogen bonding of nitrogenous bases. These nitrogenous bases are adenine, guanine, thymine, and cytosine. Adenine pairs with thymine with two hydrogen bonds, while guanine forms three hydrogen bonds with cytosine. The pairing of complementary nucleotides between two DNA strands provides a simple mechanism for copying the genetic information. When separated, each strand

provides the template for creating a complementary daughter molecule to pass on to the next generation (Fig. 1). It is the order of bases that has the instructions for the development of a complete organism from a single fertilized cell. In 1957, Vernon Ingram associated a defect in the hemoglobin gene which expresses a protein with a single amino-acid change, causing sickle-cell anemia. It was conclusive evidence that hereditary information in DNA is expressed via the synthesis of proteins that act to determine morphology and physiology of an organism, although it was still unclear where and how the DNA expressed proteins in the cell.

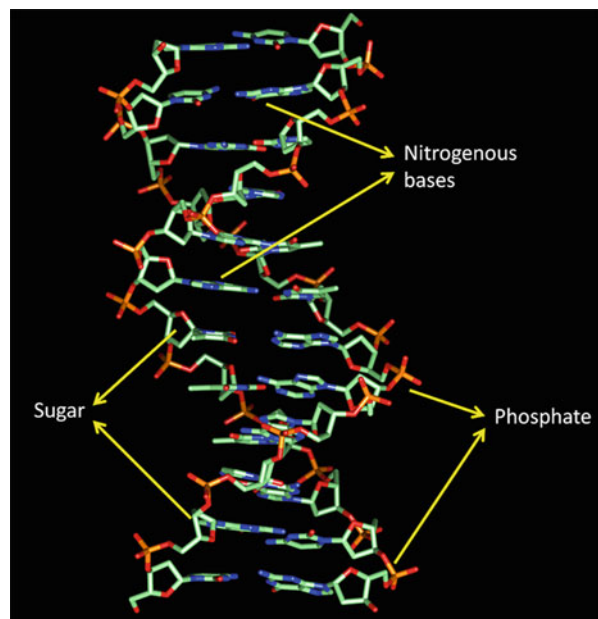
### Gene Expression: Information Flow from DNA to Proteins

In the 1950s, cellular protein synthesis was monitored by radioactively labeled amino acids. When such a cell was lysed and the contents fractionated by centrifugation, the radioactivity always appeared in the RNA-rich fraction. This fraction contains small electron-dense structures known as microsomal particles, later named ribosomes.

#### Gene Expression,

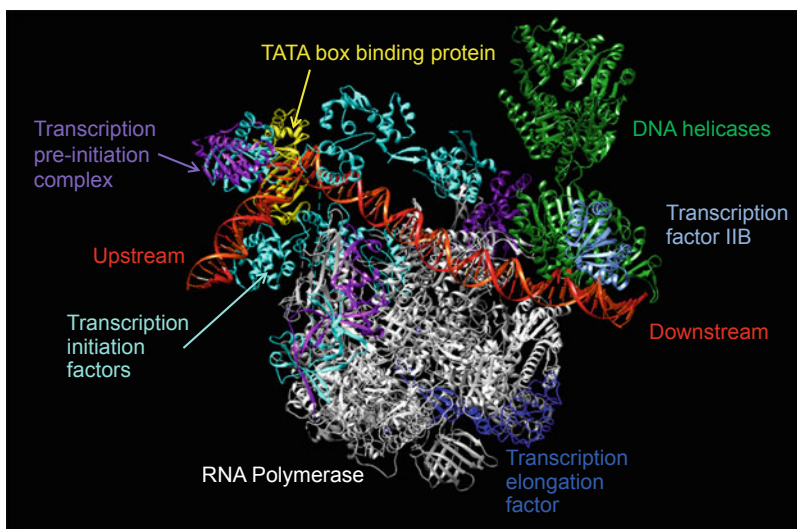
##### Fig. 1 A molecular structure of the DNA.

DNA consists of two complementary strands that are joined through hydrogen bonds and form a double helix. The hydrogen bonds are formed between the nitrogenous bases that are attached to a sugar-phosphate backbone: adenine pairs with thymine and cytosine pairs with guanine. In DNA, the sugar is 2-deoxyribose. Chimera structure visualization tool was used to draw image from Protein Data Bank (PDB) database structure, accession number – 1d65



Ribosomes were assumed to be the sites of protein synthesis (Hoagland et al. 1957) and were found to be. Obviously, ribosomal RNA (rRNA) was thought to carry information from DNA to make protein. However, this possibility was ruled out because all ribosomes have an identical rRNA composition, contrasting the variety of RNAs required for the synthesis of various proteins. Meanwhile, Francis Crick made the following suggestions on protein synthesis in his seminal paper (Crick 1958): (1) The sequence hypothesis proposes that the order of bases in the DNA determines the order of amino acids in the protein. (2) The central dogma speculates that RNA formation precedes protein formation and not vice versa. It means that once the information has passed into protein, it cannot reverse. (3) The adaptor hypothesis assumes that either protein or nucleic acid acts as adaptor to carry individual amino acids for protein formation. These ideas were based on the experimental results of the last 10 years. In 1959, Weiss and Gladstone incubated radiolabeled cytidine 5'-triphosphate (CTP) in an

extract of rat hepatocyte nuclei to find a large fraction of labeled CTP in RNA which was incorporated in a DNA-dependent manner (Weiss and Gladstone 1959). The enzyme responsible for this activity is now recognized as a RNA polymerase, and the process is called transcription (Figs. 2 and 3). In 1961, with isotopic labeling experiments on infection of *E. coli* with T4 phage, it was found that the phage proteins were made using an intermediate molecule synthesized from its DNA by employing the bacterial ribosomes. This intermediate molecule was recognized as an RNA species with a high turnover, indicating its unstable nature (Brenner et al. 1961). This special RNA is termed as messenger RNA (mRNA) since it carries a complementary sequence of the DNA template and is transported as messenger from the nucleus to the ribosomes, where its base sequence was utilized for protein synthesis in a process called translation (Jacob and Monod 1961). After protein synthesis, the mRNA would leave the ribosomes, making way for other potentially different mRNAs.

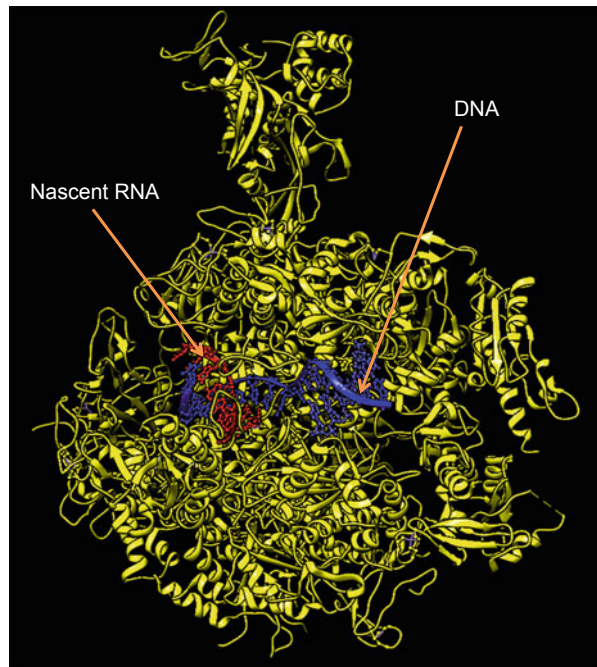


**Gene Expression, Fig. 2 RNA polymerase II in transcription pre-initiation complex.** DNA double helix (in red color) is bound by five transcription initiation factors (in cyan color) in the upstream (indicated) of TSS. TATA box-binding protein (in yellow) is bound to the promoter region. RNA polymerase II and its pre-initiation complex subunits are shown in gray and purple,

respectively. In the downstream region (indicated), DNA helicases (forest green) and other associated factors are unwinding DNA for transcription elongation. The figure reveals the tight regulation of transcription initiation by several proteins. Chimera structure visualization tool was used to draw image from Protein Data Bank (PDB) database structure, accession number – 5FMF

**Gene Expression,****Fig. 3 Ternary complex of RNA polymerase, DNA, and the nascent RNA.**

DNA is shown in *blue* and nascent RNA in *red*. RNA polymerase II subunits are shown in *yellow*. During transcription elongation, the DNA double helix is opened, and polymerization of RNA starts along the template DNA strand based on the principle of base-pairing. Chimera structure visualization tool was used to draw image from Protein Data Bank (PDB) database structure, accession number – 1ylw

**Transcription in Eukaryotes**

A typical eukaryotic cell, particularly in multicellular organisms, expresses only a subset of genes present in its genome. This expressed subset determines the cellular identity and functionality. Often the expression pattern is maintained in the daughter cells to ensure tissue homeostasis. In addition, most cells tune global gene expression in response to extracellular and intracellular signals without altering their DNA. For instance, when exposed to high temperature, cells will express genes involved in heat resistance. Gene expression is a highly energy-demanding process, and in principle, all steps involved can be regulated. However, most genes are regulated during transcription initiation by a special class of DNA-binding proteins called transcription factors (TFs), along with several other associated proteins (Fig. 2). A mechanistic detail of the transcription regulation mainly comes from the structural studies of RNA polymerase and accessory proteins by Kornberg and coworkers (Murakami et al. 2015).

The upstream regions of genes contain regulatory sequences where TFs and the RNA polymerase bound. Transcription begins when RNA polymerase gets recruited to the region of the

gene called promoter, which is generally located 25–30 nucleotide bases upstream of the transcription start site (TSS) (Fig. 2). RNA polymerase is recruited there by TFs, also called *trans*-regulatory elements, that recognize and bind to the upstream regulatory DNA sequences. One of the most common promoter regions is called a TATA box, reflecting the presence of adenine and thymine nucleotides. Mutations either in regulatory sequences (also called *cis*-regulatory elements) or the TFs may affect transcription. There is a certain variability in the promoter elements, but they are invariably bound by the general TFs needed for transcription and eventually by RNA polymerase that synthesizes the mRNA. In recruiting the transcription machinery, general TFs are often assisted by specific TFs. The latter can enhance or attenuate the transcription of a gene, even if they bind thousands of nucleotides away from the TSS. These TF-binding sequences are called enhancer elements. They mainly regulate genes that define the function of a cell, such as hemoglobin gene which must be expressed only in erythrocytes. Specific TFs rarely regulate housekeeping genes that are required in every cell for performing general functions such as metabolic maintenance



or building cytoskeletal components. Housekeeping genes are expressed constitutively.

Once the RNA polymerase is recruited, it moves along the DNA template strand in 3–5' direction and synthesizes a strand of RNA consequently in 5–3' direction complementary to the DNA (Fig. 3). RNA and DNA are very similar nucleic acids, except for the pentose sugar which lacks a hydroxyl group in DNA, and a uridine (instead of thymidine) is inserted in the RNA by RNA polymerase based on its complementarity with adenine of the DNA template.

### Posttranscriptional Processing

mRNA is short lived, distinct from other RNAs, and transported from the nucleus to the cytosolic ribosomes. It would be degraded quickly in ribonuclease-rich cytosol. Therefore, mRNA undergoes processing at both ends before leaving the nucleus. The 5' end is capped with 7-methylguanosine, and a long sequence of adenines is attached to the 3' end (poly-A tail). Poly-A tails are unique to mRNAs and absent in the DNA template. Moreover, a typical eukaryotic gene is composed of coding regions called exons and intervening regions (known as introns) that are incorporated into pre-mRNA but not translated into proteins. While the order of the exons is maintained through the removal of introns (splicing), some exons may be removed along with the introns in the process of alternative splicing. It results in different gene products from the same gene. This challenges Beadle and Tatum's one gene-one enzyme hypothesis. It creates several functional variants from the same gene, expressed in different contexts. mRNA is bound by several proteins called messenger ribonucleoprotein particle (mRNP) which are transported into cytosol through nuclear pores.

### Translation in Eukaryotes

In the cytoplasm, the mRNP will be remodeled, and binding of translation initiation factors to the 5' methylcytosine cap of the mRNA will initiate translation. The small ribosomal subunit carrying

a methionine-charged tRNA moves along mRNA until it encounters an AUG sequence also called a start codon. Subsequently, a large ribosomal subunit replaces initiation factors to elongate the polypeptide sequence. Ribosomes and amino-acid-charged tRNAs read the mRNA in a frame of three nucleotide bases (called a codon, a unit of genetic code) at a time and transfer amino acids from tRNA to the nascent peptide according to the sequence of the mRNA (Crick 1963; Nirenberg and Leder 1964). The tRNA has a base triplet, called as anticodon, that pairs with its matching mRNA codon. Upon binding of codon and anticodon, the amino acid is transferred from the tRNA to the nascent peptide. Peptide elongation stops when one of the three termination or stop codons occurs in the mRNA sequence. The nascent peptide will be folded during its synthesis with the help of chaperone proteins. Misfolded proteins are degraded immediately, while many proteins undergo posttranslational modifications. This may include their transport into specific cell organelles which require targeting sequences that are cleaved at the destination. Many proteins are covalently modified by the addition of various chemical moieties such as phosphorylation or methylation in order to function.

### Importance of Studying Gene Expression

Gene expression enables an organism to mount a high fidelity response to the existing environment by expressing a subset of genes. The various possible combinations allow great diversity in gene expression from the same piece of DNA. It is the differential gene expression which gives rise to numerous cell types from a single cell. Studying gene expression has brought on the era of biotechnology, high-yielding crops in agriculture, and diagnostic biomarkers for several diseases. Any malfunction during gene expression could manifest in a life-threatening condition. For example, several antibiotics proved to be lethal weapons against bacteria as they inhibit protein synthesis. Many diseases such as cancer result from altered functions of TFs. The modern techniques like gene expression profiling which

measure the expressions of mRNAs in the cells have been crucial in understanding cellular responses to various conditions.

## Cross-References

- [Alternative Splicing](#)
- [Base Pair](#)
- [Codon](#)
- [DNA](#)
- [Exon](#)
- [Gene Expression Profiling](#)
- [Genes](#)
- [Genetic Code](#)
- [Intron](#)
- [Messenger RNA](#)
- [RNA](#)
- [Transcription](#)
- [Translation](#)

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## Gene Expression Profiling

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## Synonyms

[EST](#); [Expressed sequence tags](#); [Gene expression](#); [Microarray](#); [Next-generation sequencing](#); [RNA sequencing](#); [Transcriptome](#)

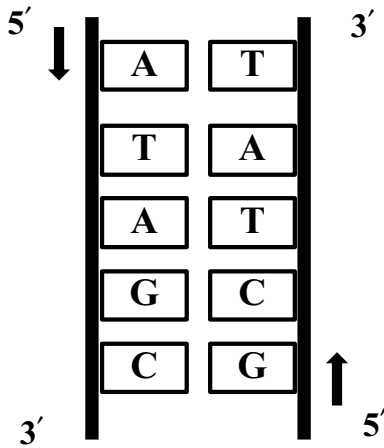
## Definitions

The measurement of the expression levels of the genes present at a particular time point in the cell.

## Introduction

In 1953, Watson and Crick proposed the structure of the DNA – the blueprint of the cell (Watson and Crick 1953). DNA is made up of two sugar-phosphate strands which run antiparallel to each other, paired up with each other through hydrogen bonding between the four nitrogenous bases which protrude from each strand (Fig. 1). DNA sequence contains functional regions called as genes, which confer phenotypic traits to an organism.

DNA transcribes its gene containing regions into various types of functional RNAs and messenger RNAs (mRNAs). mRNAs get translated



**Gene Expression Profiling, Fig. 1** A double-stranded DNA molecule. Two sugar-phosphate backbones represented by straight black lines form the side rails of the ladder-like structure of the DNA. Four nitrogenous bases: adenine (A), thymine (T), guanine (G), and cytosine (C) which protruded from these backbones and represented by rectangles are the rungs of the DNA ladder. Small arrows indicate the direction (5' to 3') of the sugar-phosphate backbones

into different types of proteins. The overall process is called gene expression (Fig. 2).

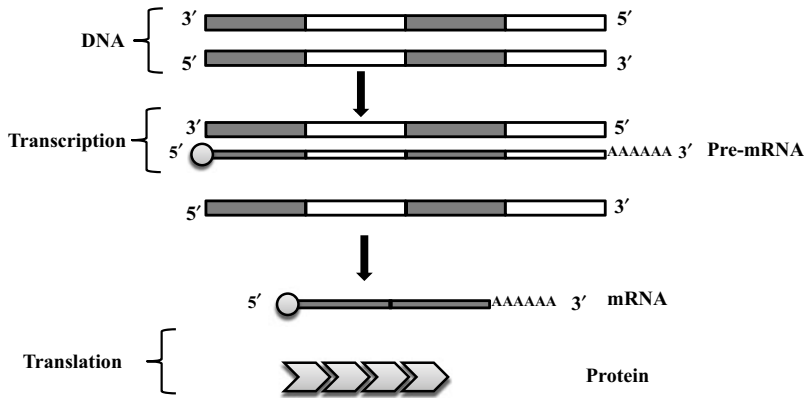
Generally, in all the cells of higher organisms like human, the DNA of each somatic cell is the same. The distinct functions and appearances of various cells in animals and plants is due to the expression of different types of proteins. For example, the cells of the human eyes are enriched in opsin proteins, which enable us to see the world, while cells of the tongue are enriched in G-protein-coupled receptors for rejoicing different kinds of food. All this happens because different genes get activated in different cell types and express different forms of proteins in spite of having the same DNA. The total number of genes expressed in an organism is called transcriptome. Measuring the expression levels of all genes by quantification of all RNA species in the cells at a particular time point is called gene expression profiling. Gene expression profiling provides a snapshot of the physiological state of the cells at a particular time point. In the tissue of multicellular organisms, gene expression will change with the age, diseases, environmental

changes, and during stress, e.g., exposure to toxic chemical compounds. Damaged or diseased cells often have very different gene expression profiles compared to their healthy counterparts. Comparison of the expression profiles of healthy and diseased/infected cells often leads to an understanding of the impaired gene functions in diseases. Therefore, gene expression profiling is changing the course of future medicine. Gene expression profiling may provide more assistance in understanding disease and cure than the biopsies (Heinloth et al. 2007).

Studies on investigating the abundance of several mRNAs at large scale commenced in the late 1970s using the Sanger sequencing technique (Sim et al. 1979). This technique evolved over time and extended to simultaneous expression profiling of almost every gene of the cell. In this chapter, we shall give an overview on the three most successful gene expression profiling techniques.

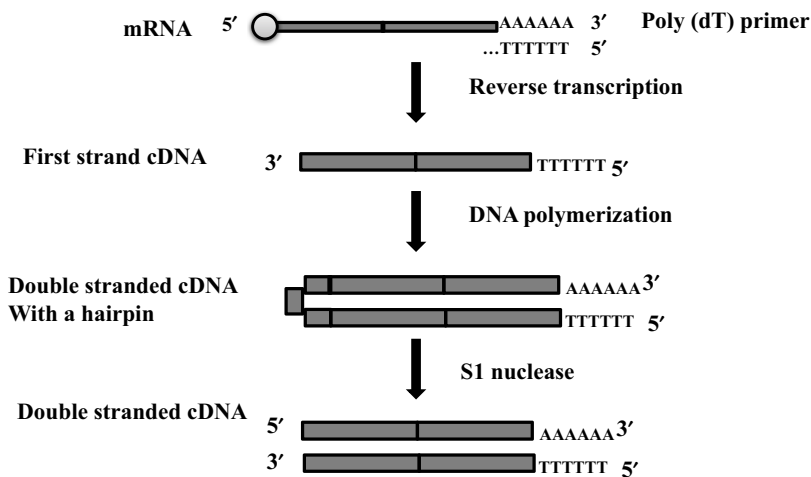
## Expressed Sequence Tags

In eukaryotes, precursor mRNA (pre-mRNA) is transcribed from the DNA template in the nucleus, and undergoes posttranscriptional modifications before being exported to the cytoplasm. Pre-mRNA is composed of the 5' untranslated region (UTR) before the transcription initiation codon, varying number of exons (coding regions), and introns (noncoding regions), and a 3' UTR after the termination codon. The 5' end is capped with 7-methylguanosine while 3' is polyadenylated (carrying a poly-A tail) (Fig. 2). Introns are removed (during splicing) to create the mature mRNA by retaining different exons for different transcript-variants by alternative splicing of exons. The cDNAs (complementary DNAs) obtained through reverse transcription of mRNAs are regarded the first-strand cDNAs. Reverse transcriptases like the one from the avian myeloblastosis virus (AMV) create a hairpin loop at the 3' end of the first-strand cDNA which can then be used as a primer for the synthesis of second strand of cDNA as shown in Fig. 3 (Efstratiadis et al. 1976). In the end, special



**Gene Expression Profiling, Fig. 2 Gene expression in eukaryotes.** The two strands of DNA are represented by a pair of grey- and white-colored thick lines. Grey represents the exon and white marks the intron. The thin grey-and-white-colored line represents mRNA. Pre-mRNA (premature messenger RNA) is having exons, introns, 3' polyadenylated or poly-A tail, and 5' methylguanosine

cap, which is shown by the circle. 5' cap and 3' poly-A tail are added into the primary transcript later on. 5' and 3' UTRs (untranslated regions) are omitted from the diagram for simplicity. mRNA (mature messenger RNA) is similar to pre-mRNA but lacks introns. Protein is represented by a bunch of arrow heads

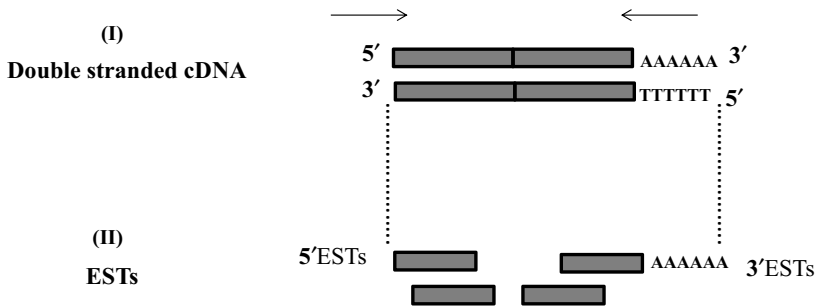


**Gene Expression Profiling, Fig. 3 Double-stranded cDNA synthesis.** The thin line represents mRNA. mRNA is shown with two exons, the 3' polyadenylated tail, and 5' methylguanosine cap, which is shown by the circle. Poly-deoxythymidylate or poly (dT) containing primer anneals

to the 3' end of mRNA and is used for reverse transcription. The 3' hairpin at the first-strand cDNA acts as primer for the synthesis of second strand of cDNA. S1 nuclease cuts the hairpin to create the double-stranded cDNA with free ends

nucleases (such as the S1 nuclease) cleave the hairpin to obtain double-stranded cDNA with free ends that can be cloned into plasmids for generating cDNA libraries. cDNA clones are sequenced arbitrarily from both 5' and 3' termini without completing the full length. Thus, the reads

output generates 5' and 3' expressed sequence tags (ESTs), respectively (Fig. 4). As mRNA is fragile, the cDNA represents its different length forms in the cDNA library. Hence, the reads of ESTs are overlapping with each other as shown in Fig. 4 (Nagaraj et al. 2007). EST was one of the best



**Gene Expression Profiling, Fig. 4 Redundancy in ESTs.** (I) The two strands of cDNA (cloned in the plasmid) are shown, representing two exons. The poly (dA) and poly (dT) tails are shown. Thin arrows indicate the direction of

the sequencing. (II) The 5' and 3' ESTs are drawn parallel (dotted lines) to the original cDNA sequence. ESTs reads are redundant and overlapping with each other

techniques in earlier days to study high-throughput gene expression and novel gene discovery (Nagaraj et al. 2007). For instance, in 1991, Adams et al. were able to identify 337 novel genes (ESTs) expressed in the human brain (Adams et al. 1991).

The number of genes studied through ESTs are limited since the procedure involves cloning of cDNAs. With the availability of many completely sequenced genomes since the late 1990s, doors were opened to another gene expression profiling technique called DNA microarray, which remains useful even through the next-generation sequencing era.

## DNA Microarrays

Through DNA microarrays, the expression of thousands of genes can be studied without much manual labor of cloning and sequencing (Schena et al. 1995). Information obtained through ESTs, genome projects, and other genomics techniques is used to create single-stranded oligonucleotides which represent known sequences of genes. These oligonucleotides can be fixed on a glass chip, literally forming microscopic spots of DNA microarrays. DNA microarrays work by the principle of hybridization of two complementary strands of DNA (Fig. 1). In short, a strand of DNA from a known gene is fixed to a particular

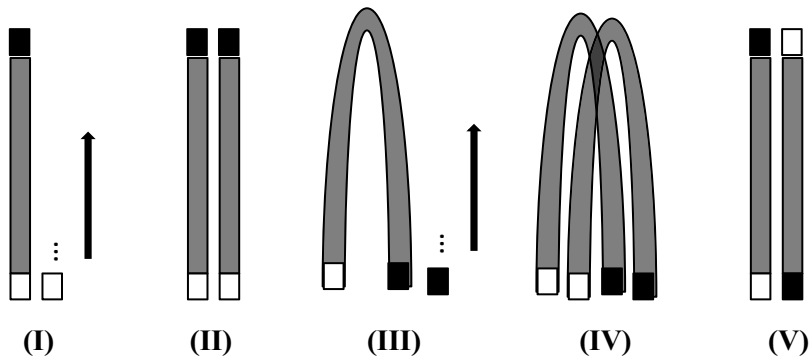
spot on the microarray chip and cDNA obtained through reverse transcription (Fig. 3) from the sample mRNA is used to hybridize with the strand fixed on the chip. Reverse transcription is performed with fluorescently labeled nucleotides, so that the hybridized DNA can emit light which can be detected and read under LASER irradiation and thus can be quantified. The unhybridized sample DNA is washed away.

Since 1995, DNA microarray was the method of choice to understand diseases and specific gene expression dynamics of cells, tissues and organs (Schena et al. 1995). DNA microarrays have also been of great help in understanding cell cycle, developmental stages, metabolism, disease diagnostics, and classification of various cancers. However, the method can be applied for profiling expression of known genes only.

## RNA Sequencing

In order to make DNA microarrays work, enough information about the sequences of genes is required. When gene information is not available for a species of interest, gene expression profiling can be performed by RNA sequencing (RNA-seq). RNA-seq utilizes next-generation sequencing technology (NGS) for gene expression profiling. NGS technology is based on massively parallel sequencing-by-synthesis of DNA,





**Gene Expression Profiling, Fig. 5 Clonal expansion in next-generation sequencing.** (I) The grey line is the cDNA and the white and black stripes at both ends of the line represent the adapters of the cDNA. At the right-hand side, the white stripe represents the oligonucleotide fixed to the solid surface which is complementary to one of the white adapter sequence. The arrow indicates the direction

of the polymerization. (II) One new strand complementary to the cDNA got synthesized. (III) The second adapter (black) pairs with its counterpart attached sequence (bridge amplification). The arrow indicates the direction of the polymerization. (IV) Another strand is synthesized. (V) During denaturation, the two strands separate

as explained below in more detail (Ju et al. 2006). The protocol for preparing the cDNAs is very similar to the one described before (and in Fig. 3) for ESTs. Depending upon the specific requirements, a particular type of RNAs (mRNA, transfer RNA, ribosomal RNA, and small noncoding RNA) is isolated. Generally, mRNA is enriched by employing polythymidylate or poly (T) magnetic beads that bind to poly-A tails unique to mRNA. The enriched mRNA is used to produce double-stranded cDNA through reverse transcription (Fig. 3). DNA adapters of known sequences are ligated to both ends of the cDNAs in a process called tagmentation. These adapters can hybridize to known complementary sequences attached in millions to a solid surface and DNA polymerase can synthesize the complementary strand of DNA (Fig. 5I and II).

In the second step of bridge amplification, the new strand complementary to the one synthesized in the first round can be assembled where the sequence complementary to the second adapter works as the primer as shown in (Fig. 5III and IV). These steps repeat and clonal expansion of the cDNAs takes place. For sequencing, the primers complementary to the adapter sequences are used for DNA polymerization with four nucleotides. Each of the four nucleotides is labeled with a fluorescent dye of a different color. Upon

incorporation of a nucleotide to the nascent strand, its fluorescence is captured by a camera, and the fluorescent tag subsequently cleaved enzymatically. Only after cleavage of the tag, the next nucleotide can be incorporated. Millions of sequences corresponding to the forward and reverse strands of DNA can be read out on the screen as the reaction progresses. Bioinformatics tools are used to assemble reads and compute the abundance of each mRNA in the initial sample using sophisticated mathematical and statistical techniques (Trapnell et al. 2012).

The advantage of RNA-seq over previous techniques is manifold. RNA-seq can be used for gene expression profiling of any organism. RNA-seq based quantification of gene expression levels highly correlates with the transcript abundance measured by low throughput experiments. This reflects the high accuracy of the method (Mortazavi et al. 2008). It has turned out to be most accurate gene expression profiling technique so far, and a real game changer in understanding the complexity of transcriptional regulation.

## Cross-References

- [Alternative Splicing](#)
- [Base Pair](#)

- [Bioinformatics](#)
- [DNA](#)
- [Exon](#)
- [Gene Expression](#)
- [Genes](#)
- [Intron](#)
- [Messenger RNA](#)
- [RNA](#)

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## Gene Flow

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## Synonyms

[Allele flow](#); [Gene migration](#)

## Definition

The migration/movement or transfer of the genetic variation from one population to another is called gene flow.

## Introduction

Gene flow is the elementary agent of evolution responsible for the dispersal of genes between two populations of the same or different species, followed by the successful establishment of the immigrant genotypes in the new population (Woodruff 2004). Gene flow between two populations of the same species is mediated by reproduction and vertical gene transfer from parent to offspring. Gene flow between two different species, for instance, from a bacteria or virus to a higher organism or an endosymbiont to the host, occurs due to horizontal gene transfer (Choudhuri 2014). Conclusively, when the gene flow occurs within a population, it can increase the genetic variation between the populations, whereas gene flow occurring between genetically distant populations can reduce the genetic variations between them (Choudhuri 2014). When gene flow is hampered, it results in an increase in inbreeding, which can be measured by the inbreeding coefficient (F). For instance, the Black Footed Rock Wallaby has several

populations that are strongly isolated due to geographical barriers and, therefore, favor inbreeding (Eldridge et al. 1999). Another example of hampered gene flow is the young female chimpanzees, which are incapable of emigration from their natal social group due to the loss of habitat in the surrounding countryside. Therefore, they would experience increased inbreeding.

A lot of events can result in gene flow; for instance, pollen is blown away by the wind to far-off regions, blue-eyed people migrating from Sweden to a city in Mexico where all brown-eyed people live, a group of women from West Africa where Malaria is present mate with a group of Europeans, etc. A diagrammatic representation of the migration of a brown-colored beetle to the population of green-colored beetles has been shown in Fig. 1.

All these events would result in the induction of genetic variations if the gene versions in question were not present at these places before (UCMP 2020). However, if the gene flow rate is high enough, then the two populations would have equivalent allele frequencies and therefore, would effectively be considered one population. Because gene flow can be facilitated by the physical proximity of the populations, gene flow can be restricted by physical barriers separating the populations. Incompatible reproductive behaviors between the individuals of the populations also prevent gene flow.

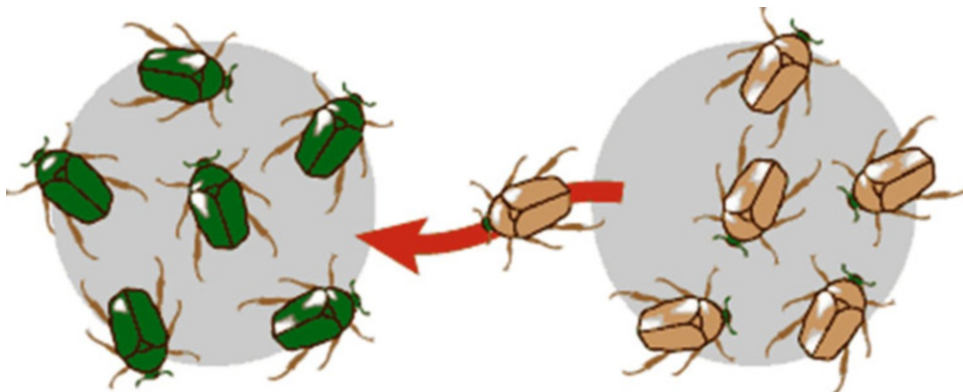
Gene flow is often gender-prejudiced and is restricted to specific stages of the life cycle.

There are several factors on which gene flow depends. It is likely to be lower in species having low mobility or dispersal, small population size, long distances between populations, and occurring in fragmented habitats (Hastings and Harrison 1994; Hamrick and Godt 1996). Mobility has a significant role to play in the migration rate. Individuals having high mobility tend to have high migration potential. However, in the case of plants, although they are less mobile than animals, yet their genetic content can be transferred to a great distance by animals or wind.

### Examples of Gene Flow

Around 15,000 years ago, all dogs were basically wolves. But, some of the pre-dogs scavenged near the human settlements and came closer to humans, whereas the wolves moved further away from the human-occupied areas. Dogs served humans with vermin control, waste removal, or a hunting guide. Humans, in turn, provided shelter and food to the dogs. Gene flow, in the case of dogs, can be assumed in a condition where one dog from a specific population can breed with other pure breeding populations. This would result in the introduction of the new alleles to the group, for example, Labradoodle, half-Beagle, Puggle, etc. (Pilot et al. 2015).

Another example can be of the red parrots having brought to a remote area of the jungle in which originally only the blue parrots lived. This



**Gene Flow, Fig. 1** Brown-colored beetle migrates from its original population to the green-colored population. (Adapted from UCMP 2020)

would introduce color variations into the gene pool of the parrots living in the jungle (Your Dictionary 2020).

Red parrots are brought on an expedition to a remote section of jungle with only blue parrots, introducing color variation into the gene pool of jungle parrots.

Bacteria have a peculiar way of gene transfer. They make use of the horizontal gene transfer when it comes to the gene flow. In this process, the DNA passes between the organisms without the need for sexual reproduction. Most of the diversity seen today is a result of these gene transfers that took place millions of years ago (Biology Dictionary 2018). An example of the horizontal gene transfer in bacteria can be the transfer of the antibiotic resistance genes from one bacterium to the other. This gene transfer is the primary reason responsible for the growing resistance in bacteria against the currently used antibiotics.

## Conclusion

Gene flow, gene migration, or allele flow is an important mechanism responsible for transferring genetic diversity from one population to the other. When there is an obstruction or no transfer of genes between two populations, then it may lead to speciation. Migration and intermarriages between national and state communities are strong forces of gene flow. Conversely, geographical isolation and reproductive isolation play an essential role in limiting the transfer of gene flow.

## Cross-References

- [Migration](#)
- [Speciation](#)

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## Gene Frequency

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## Synonyms

[Allele frequency](#)

## Definition

Gene frequency can be defined as the fraction or percentage of a population that carries allele (i.e.,

one type of a gene variant) at a particular locus (Gillespie 2004). It is also more appropriately known as allele frequency.

## Introduction

In population genetics, gene frequencies refer to the quantity of variation at a particular locus or across multiple loci. The gene frequency is different from the genotypic frequency in case of diploid organisms, although they seem to be related to each other, and gene frequencies are usually calculated from genotypic frequencies. The value of gene frequency always exists between 0 and 1. For example, if all of the alleles in the pea plant population were tall alleles (represented as “T”) and none of the alleles were dwarf alleles (represented as “t”), then the “T” allele frequency would be 100% or 1, and “t” allele frequency would be 0% or 0. However, if half of the alleles were “T” and half were “t,” then either of the alleles would have an allele frequency as 50% or 0.5.

## Calculation of Gene or Allele Frequency

Gene frequency calculations are dependent on the ploidy of the species. For a haploid organism like *E. coli*, the gene frequency of a particular nucleotide polymorphism (e.g., G vs. C) can be estimated by taking a sample of 1000 bacterial cells and analyzing them for the sequence variant of interest. Now, suppose if we found that 25 of 1000 are G, then the gene frequency of G allele =  $25/1000 = 0.025$  or 2.5% and the frequency of alternative allele C =  $975/1000 = 0.975$  or 97.5%. Moreover, another way to calculate the frequency of C allele can be simply as  $1 - p$  (where  $p$  = frequency of G allele), i.e.,  $1 - 0.025 = 0.975$ .

It is necessary to differentiate between gene and genotype frequencies in diploid organisms (Aquadro 2001), since in DNA of diploids, at a particular site, some chromosomal locus carry a G (in frequency  $p$ ) and some carry C (in frequency  $q$ ). Some individuals will have two Gs, some a G and C and some two Cs. Individuals with two copies of the same allele are called homozygotes (e.g., G/G or C/C), and

one with two different alleles is called heterozygotes (e.g., G/C). Genotype frequencies refer to the ratio or percentage of each genotype in the population sample. For one set of gene frequencies, many different types of genotypic frequencies can be possible: e.g., for  $p = q = 0.5$ , genotypic frequency could have 0.5 G/G, 0.0 G/C, and 0.5 C/C; or it could have 0.0 G/G, 1.0 G/C, and 0.0 C/C; or it could have 0.25 G/G, 0.5 G/C, and 0.25 C/C; the latter is what is expected with random mating and no selection, drift, mutation, or migration, i.e., the Hardy-Weinberg equilibrium genotype frequencies.

In a diploid, sexually reproducing organism, gene, or allelic frequencies for autosomal locus can be measured in either of two ways. The first way is simply by counting genes. Consider, for example, the phenotyping distribution of MN blood types (controlled by codominant M and N alleles) among 200 persons:

Type M (MM genotype) = 117

Type MN (MN genotype) = 69

Type NN (NN genotype) = 14

Since the homozygotes have two of a given allele and heterozygotes have only one, and since the total number of alleles is twice the number of individuals (each individual carries two alleles), we can calculate allelic frequencies in the following manner:

Frequency of M allele

$$= \text{Number of M alleles} / \text{Total number of alleles} \\ = (2 \times \text{Number of MM homozygotes}) \\ + (\text{Number of MN heterozygotes}) \\ / (2 \times \text{Total number of individual})$$

The expression “frequency of” can be shortened to  $f(X)$ . For example, the frequency of the M allele will be written as  $f(M)$ .

Then,

$$f(M) = p = 2(117) + 69 / 2(200) = 303/400 \\ = 0.76$$

and,



$$f(N) = q = 2(14) + 69/2(200) = 97/400 \\ = 0.24$$

Alternatively, because the frequencies of the two alleles, M and N, must add up to unity ( $p + q = 1$ ),  $q = 1 - p$  (and  $p = 1 - q$ ), if we know that  $p = 0.76$  and  $q = 1 - 0.76 = 0.24$ .

Another way of calculating the allelic frequencies is based on knowledge of genotypic frequencies, which in this example are:

$$f(MM) = 117/200 = 0.59$$

$$f(MN) = 69/200 = 0.34$$

$$f(NN) = 14/200 = 0.07$$

We derive an expression for calculating  $p$  and  $q$  based on genotyping frequencies as follows:

$$p = f(M) \\ = 2 \times \text{Number of MM} + \text{Number of MN}/2 \\ \times \text{Total Number} \\ = (2 \times \text{Number of MM}/2 \times \text{Total Number}) \\ + (\text{Number of MN}/2 \times \text{Total Number}) \\ = f(MM) + 1/2 f(MN)$$

$$q = f(N) \\ = 2 \times \text{Number of NN} + \text{Number of MN}/2 \\ \times \text{Total Number} \\ = (2 \times \text{Number of NN}/2 \times \text{Total Number}) \\ + (\text{Number of MN}/2 \times \text{Total Number}) \\ = f(NN) + 1/2 f(MN)$$

Thus, allelic frequencies can be calculated as the frequency of homozygotes plus half the frequency of heterozygotes as follows:

$$p = f(M) = f(MM) + (1/2) f(MN) \\ = 0.59 + (1/2) 0.34 = 0.76$$

$$q = f(N) = f(NN) + (1/2) f(MN) \\ = 0.07 + (1/2) 0.34 = 0.24$$

Allele and genotypic frequencies must always lie between 0 and 1.

## Calculation of Gene or Allele Frequency with Multiple Alleles

It employs the same rule that we used with two alleles. Suppose we have three alleles – A1, A2, and A3 – at a locus with dominance hierarchy  $A1 > A2 > A3$ . Let  $p$ ,  $q$ , and  $r$  represent the frequencies of alleles A1, A2, and A3, respectively. In this case, allelic frequency will be:

$$p = (2 \times A1A1) + (A1A2) \\ + (A1A3)/(2 \times \text{Total number of individuals})$$

$$q = (2 \times A2A2) + (A1A2) \\ + (A2A3)/(2 \times \text{Total number of individuals})$$

$$r = (2 \times A3A3) + (A1A3) \\ + (A2A3)/(2 \times \text{Total number of individuals})$$

To calculate expected genotype frequencies (if the population is in Hardy-Weinberg equilibrium), we use trinomial equation,  $(p + q + r)^2$ , which expands to  $p^2 + q^2 + r^2 + 2pq + 2pr + 2qr = 1$ .

Homozygotes will occur with frequencies  $p^2$ ,  $q^2$ , and  $r^2$ , and heterozygotes will occur with frequencies  $2pq$ ,  $2pr$ , and  $2qr$ .

## Conclusion

In nutshell, gene frequency or allele frequency is a measurement to show the genetic diversity of a population species or in other terms the abundance of its gene pool. Mathematically, it is expressed in terms of percentage or proportion. For example, *Merriam-Webster* defines this term as “the ratio of the number of a specified allele in a population to the total of all alleles at its genetic locus.” The subject of population genetics is concerned with the study of different factors or forces, which lead to the change in distribution of these gene frequencies for a given population.

## Cross-References

► [Gene Flow](#)

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## Gene Imprint

- [Genomic Imprinting](#)

## Gene Interaction

- [Epistasis](#)

## Gene Locus

- [Locus](#)

## Gene Map

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## Synonyms

[Genome mapping](#), [Linkage maps](#)

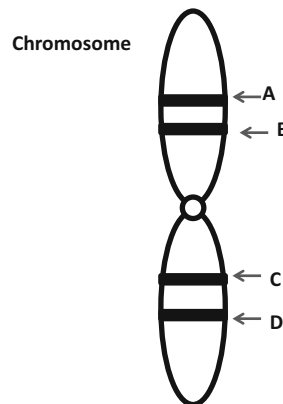
## Definition

Gene mapping is allocating chromosomal location coordinates to a gene.

## Gene Map

Gene mapping is allocating chromosomal location coordinates to a gene. Mapping a gene helps to prepare a roadmap of genome and identify milestones in form of genetic markers. The genetic map of an organism gives an overview of gene arrangement in their chromosomes (refer Fig. 1). The gene maps are composed of markers which might be genes controlling visible phenotypic traits (classical markers) or molecular markers whose phenotype is revealed by using modern molecular biology techniques (e.g., DNA markers). In case of animals, gene mapping is used for all aspects of genome analysis and their improvement for benefit of human beings. Mapping of genes in farm animals, companion animals, laboratory animals, aquatic animals, insects, and primates, including humans provides comprehensive data which is used to elucidate origin, evolution, phylogenetic relationship; position of genes; function, expression, regulation, and sequence of genes. This information has tremendous application in agriculture, medicine, and environmental sciences (Montgomery et al. 1994; Morton 1955; Litt and Luty 1989; Klungland et al. 1995; Peters et al. 2003; Chial 2008).

Gene mapping methods are divided into (a) genetic mapping and (b) physical mapping.



A,B,C,D denotes location of genes on chromosome

**Gene Map, Fig. 1** A gene map showing position of genes A–D on chromosome

## Genetic Mapping

Before sequencing of human genome, mapping of gene was carried on the basis of gene transmission in pedigree analysis and distinct phenotypes associated with different alleles of same gene. The gene sequence data was not needed to assign chromosomal location to genes.

The important factors deciding gene location were – phenotype associated with gene and cosegregation of two genes. Two closely located genes had highest chances of cosegregation or linkage. The data obtained from recombination frequencies was used to determine exact distance between genes.

Even before genome information-based mapping, many genes had already been mapped on X-chromosome due to ease with which sex-linked traits could be determined through pedigree analyses. However, gene mapping on autosomes was quite a challenge as these contain non-sex-linked genes. To some extent pedigree analysis (generation analysis) helped to solve the purpose and researchers were able to generate linkage maps of the 22 human autosomes using linkage phenotypes in pedigrees. This remarkable landmark started with research published by Donahue et al. (1968) when the group successfully proved Duffy blood group locus, involved in imparting blood heterozygosity, to be located on chromosome 1 (Klungland et al. 1995). Locus is defined as position or coordinates of a gene on chromosome.

Other than chromosome linkage, gene maps can also be based on molecular or DNA techniques such as restriction fragment length polymorphisms (RFLP), random amplification of polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR), and single nucleotide polymorphisms (SNP), which are most commonly used in genetic linkage analysis.

Recently, a comprehensive research resource Online Mendelian Inheritance in Man, OMIM<sup>®</sup> containing description of human genes and phenotypes and their relationship, is launched. OMIM is based on the published peer-reviewed biomedical literature and is used by

overlapping and diverse communities of researchers as well as students. OMIM.org has enhanced search capabilities such as genome coordinate searching and thesaurus-enhanced search term options (Amberger et al. 2015).

## Physical Mapping

Post genomic era has brought revolution in gene mapping techniques. The physical map representing a partial ordering of specific DNA sequences by their position on a chromosome is prepared to locate specific genes. There are several types of physical maps including cytological maps, restriction maps, STS content maps, radiation hybrid maps, ordered clone collections (i.e., “contig maps”), and the DNA sequence of an entire chromosome, constructed by a wide range of experimental methods without having any complete sequence information (Vaiman et al. 1996; Xiong et al. 1996; Reece 2000).

## Conclusion

Gene map describes the coordinates of gene on a chromosome. Gene maps offers a great scope of development and betterment for animals especially livestock and farm animals. With advent of more sophisticated techniques more information on gene location and the rationale will be revealed.

## Cross-References

- ▶ [Autosome](#)
- ▶ [Candidate Gene](#)
- ▶ [Gene Frequency](#)
- ▶ [Geometric Encoding](#)
- ▶ [Quantitative Genetics](#)
- ▶ [Quantitative Trait Loci \(QTL\)](#)

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## Gene Migration

### ► Gene Flow

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## Gene Polymorphism

### ► Genetic Variation

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## Gene Pool

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## Synonyms

Gene; Genotype; Heredity

## Definition

The sum of all the genes in a given population at a given time can be referred to as **gene pool**. The term gene pool is used in reference to a population which includes all individuals of the same species and includes all genes and combinations of genes (sum of all the alleles) in the population.

## Introduction

The concept of gene pool was given by Russian geneticist Aleksandr Sergeevich Serebrovskii in the 1920s as *genofond* (gene fund). The term “*Genofond*” was imported to the United States from the Soviet Union by Theodosius Dobzhansky, who translated it into English as “gene pool.” Gene pool refers to the collection of genes in an interbreeding population that includes each gene at a certain frequency in relation to its alleles. The gene pool is a measure of generic diversity. The composition of a population’s gene pool can change over time through evolution. This can occur by a variety of mechanisms such as mutations leading to genetic variation, natural selection, genetic drift, habitat diversity, and geographical isolation. Such processes can cause an altered gene pool which is attenuated to the needs of the population’s specific environment. For example,

the migration of human population from equatorial region towards north where they were exposed to lesser amount of sunlight, resulted in variations in skin color over due course of time. The genetic modifications responsible for changes in the skin color become part of this population's gene pool. In contrast to this, several endemic species of tortoise and marine iguanas of Galapagos Island and aye-aye species of lemur in Madagascar island are example of least diverged genepool.

### Changes in the Gene Pool

Gene pool changes with time, it does not always stay the same. The changes in the gene pool of a population over time that result in changes to the varieties of individuals in a population is known as **microevolution**. Example of microevolution may include bacteria that have become insensitive to antibiotic over time. Small changes in the gene pool can happen for a number of reasons; a few of these have been listed below (Windows to the Universe 2011):

- **Gene Mutation:** Mutations are the source of new allele in gene pool. If a mutation occurs in the gamete producing cells and get fixed during meiosis, then when the gamete is fertilized, this mutation will enter gene pool. Any mutation that enters the gene pool is acted upon by natural selection. Alleles that result from unfavorable mutations are selected against and remain in the gene pool only if they are recessive, while favorable mutation can lead to speciation. Neutral or silent mutations are not acted upon by natural selection.
- **Gene Flow:** Gene flow refers to inflow of new traits by the migration of new individuals of the species into or out of certain geographic location that can affect gene pool. Gene pool can shrink due to loss of certain traits from a given population due to migration or natural selection. Gene pool can be enriched due to

immigration of diverged population into certain otherwise isolated locality.

- **Genetic Drift:** It is the change in the frequency of an existing gene variant (allele) in a population over years due to chance (sampling error), which can affect the gene pool. For example, if a few individuals leave a population and establish a new one, their gene pool may not have the same frequency of genes as in the population they left. Inbreeding of such population causes reduced genetic variation, thus causing a founder effect. Sometimes, catastrophic environmental events that reduce the population size and consequently causing loss of alleles in the population lead to reduction in genepool.
- **Natural Selection:** It is the key mechanism responsible for evolution. Some genetic differences are favored by nature and improve the chance of survival of individuals that have them. For example, hawks with large sharp talons may be more likely to survive than hawks with small talons. As the surviving alleles are preferred to be passed on to next generation, the genes for large talons are more likely to be passed on. Eventually the gene pool shifts towards large talons. Population with large and diverse gene pool have better survival fitness, while population with narrow gene pool have low fitness and under the pressure of natural selection, the species may become extinct.

When the changes in the gene pool of a population occur over a very long period of time, and the changes are large enough that the population is no longer able to breed with other population, such population is then considered as a different species. This process is known as **macroevolution**.

### How to Measure Gene Pool?

For measuring gene pool, it is very important to know how many variants of a gene are present in



the given population. The size of the gene pool is a direct measure of the genetic variation in a given population. Genetic variation is generally expressed as a relative frequency. Relative genotype frequency and relative allele frequency are the two most important measures of genetic variation. The distribution of genetic variation in a population can be known by relative genotype frequency. Relative allele frequency is the percentage of all copies of a certain gene in a population that carry a specific allele. This is an accurate measurement of the amount of genetic variation in a population.

This can be achieved by:

- Simply estimating relative phenotype frequency by calculating frequency of observable trait appearing in the population
- Calculating relative genotype/allele frequency in a population, which gives accurate estimation genetic variation in a population. Allele frequency can be calculated if there are two forms of alleles known for the genotype. The relative frequency can be mathematically expressed as:  $p^2 + 2pq + q^2$  (also known as Hardy-Weinberg equilibrium), where allele frequency remains unchanged in population.

However, when distinct forms of alleles are not obvious, genotyping can be performed by sampling DNA from individuals in the given population and using RFLP, microsatellite markers, or by DNA sequencing. Further, mitochondrial DNA markers are also used to identify different variants.

## Gene Pool Centers

Gene pool centers refer to areas on the earth where important crop plants and domestic animals originated. They have an extraordinary range of the wild counterparts of cultivated plant species and useful tropical plants. Gene pool centers also contain different subtropical and temperate region species. The major gene pool centers are as under:

1. Mediterranean
2. South American

3. South West and Middle East
4. African
5. South Mexican and Central American
6. Indian
7. Central Asian
8. East Asian

## Gene Pool Concept in Crop Breeding (My Agriculture Information Bank 2015)

Gene pool of a crop includes all cultivars, wild species, and wild relatives containing all the genes available for breeding. Based on degree of relationship, the gene pool of a crop can be divided into three groups (Harland and Dewet 1971),

1. Primary gene pool
2. Secondary gene pool
3. Tertiary gene pool

These are briefly discussed below:

### 1. Primary Gene Pool (GP1)

The gene pool in which intermating is easy and leads to production of fertile hybrids is known as primary gene pool. It includes plants of the same species or of closely related species which produce completely fertile offspring's. In such gene pool, genes can be exchanged between lines simply by making normal crosses. This is also known as gene pool one (GP1).

### 2. Secondary Gene Pool (GP2)

The genetic material that leads to partial fertility on crossing with GP1 is referred to as secondary gene pool. It includes plants that belong to related species. Such material can be crossed with primary gene pool, but usually the hybrids are sterile and some of the progeny to some extent are fertile. This type of gene pool is also known as gene pool two (GP2).

### 3. Tertiary Gene Pool (GP3)

The genetic material which leads to production of sterile hybrids on crossing with primary gene pool is termed as tertiary gene pool or gene pool three (GP3). Transfer of gene from such material to primary gene pool is possible with the help of special techniques.

## Conclusion

Gene pool represents total number of genes present within a population. Populations with larger gene pool tend to have more genes and hence show more genetic diversity. Each gene has a specific purpose such as giving plants or animals specific characteristics, resistance to disease, tolerance to harsh climate, etc. So, population with a larger genetic diversity will be better adapted to deal with disease outbreaks and harsh environmental conditions. On the other hand, populations with a lesser number of genes in their gene pools will be susceptible to such problems which may cause them to become endangered. Hence populations with a large gene pool are more likely to survive, while those with small gene pool are in danger of acquiring genetic diseases, infertility, deformities, etc. Gene pool gives an idea of the number of genes, the variety of genes, and the type of genes existing in a population. It can be used to help determine gene frequencies or the ratio between different types of genes in a population (Biology Online 2008).

## Cross-References

- Genetic Variation
- Genotype
- Mutations

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## Gene Targeting

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## Definition

Gene targeting is the process of making specific changes to the DNA of a cell or an organism that can be permanent or conditional.

## Introduction

The ability to engineer biological systems holds immense potential for applications across basic science, medicine, and biotechnology. Gene targeting has been a powerful research tool for scientists that has gained and continues to gain valuable information about genetics and gene function by studying the effects of changes in DNA, by adding or removing either whole genes or single bases, or by manipulating the levels of gene expression. For a long time, geneticists used chemicals or radiation, such as ethyl methanesulfonate (EMS) and X-ray mutagenesis to cause DNA lesions (Lewis and Bacher 1968; Muller 1927). However, they had no way of controlling where in the genome the mutation would occur. By the development of new gene targeting strategies, such as the nuclease-based gene-targeting technologies (Gupta and Musunuru 2014), the potential today exists to accurately incorporate modified genetic material into the genome of several recipient organisms.

## General View

Gene targeting experiments allow for the modification of a selected DNA sequence within its

genomic locus, manipulations that can lead to gene inactivation by its complete deletion or by the creation of subtle mutations, the replacement of the gene by another gene or by any DNA sequence, or correction and creation of genetic mutations. In the best condition, the incorporated DNA fragment is accurately returned back to its homologous location in the genome and becomes inserted at the target locus; this is feasible through homologous recombination that depends on the ability to find and pair homologous DNA fragments between the target, endogenous chromosomal sequence, and the exogenous fragment, the donor. Homologous recombination is a natural process used by eukaryotic cells to repair harmful double-strand DNA breaks and to exchange nucleotide sequences between similar (homologous chromosome) or identical (sister chromatid) DNA molecules during meiosis (Sung and Klein 2006). Gene targeting can also concern the manipulation of gene expression at the mRNA level using oligonucleotides. Generally, this mechanism implicates the hybridization of the oligonucleotide fragment with the complementary mRNA sequence, followed by destruction of the hybrid by cellular enzymes.

Gene targeting led to a revolution in the ability to interrogate the function of specific genes, revealing the molecular basis of several biological phenomena from animal diversity to human pathologies. A large number of mutant cell lines and model organisms have been created to totally or partially inactivate the function of a selected gene to determine its role. A large number of human diseases result from genetic mutations that lead to the synthesis of defective proteins or to a deregulation of their expression and as a consequence can cause disturbances in fundamental molecular and cellular mechanisms. The conventional therapies are intended to treat the symptoms caused by those genetic defects. Gene therapy using gene-targeting strategies targets the origin of the pathology. This consists of incorporating a functional copy of the mutated gene, or another gene coding for a therapeutic activity, or repairing the mutation that is at the source of the physiological disorder. Therefore, gene targeting

represents an attractive genome-editing tool for not only gene function analysis but also for gene therapy applications.

## Gene Targeting Techniques

### Nuclease Systems

Several nuclease-based gene-targeting technologies have been developed (Gupta and Musunuru 2014). These technologies include zinc-finger nucleases (ZFNs) (Urnov et al. 2010), transcription-activator-like effector nucleases (TALENs) (Christian et al. 2010), and clustered regularly interspaced short palindromic repeats/CRISPR-associated sequence (CRISPR/Cas) system (Cong et al. 2013). ZNF is an artificial nuclease constructed by fusing a modular array of Cys2-His2 DNA-binding zinc fingers to the nuclease domain of the restriction enzyme *FokI* (Kim et al. 1996). This chimeric protein is usually composed of 3-6 zinc fingers that recognize three nucleotides each, providing DNA binding specificity to the nuclease. Since the *FokI* nuclease domain requires dimerization to work, a pair of ZFNs must be designed to induce the DNA cutting (Urnov et al. 2010). As ZFNs, TALENs were developed by fusing the *FokI* endonuclease domain with an array of TALE repeats. TALE proteins are major players during plant infection; they are secreted bacterial proteins that regulate the gene expression of the host cell by binding to specific DNA promoter regions (Christian et al. 2010). The CRISPR system functions as an adaptive immune system in bacteria and archaea that defends against phage infection (Mojica et al. 2005). In this system, an endonuclease is guided to specific genomic sequences by a single guide RNA (gRNA), resulting in DNA cutting near a protospacer adjacent motif (PAM) sequence. Those nucleases induce specific double-stranded breaks (DSBs) that stimulate the cellular DNA repair mechanisms by natural processes known as nonhomologous end joining (NHEJ), by directly rejoining the two DSB ends, and homologous recombination, a process that requires a repair DNA template (Haber 2000). NHEJ-mediated DSB repair can result in the

formation of small insertions or deletions into the coding sequence of a gene causing a frame shift in translation that leads to mRNA degradation or results in the production of a nonfunctional truncated protein. Homologous recombination occurs by using a DNA repair template with homology arms to replace a mutated gene directly and restore mutated gene function without modifying the regulation of gene expression. In addition, nuclease-based gene-targeting systems are being used for nongene-editing purposes such as activation and inhibition of gene expression, as well as for fluorescence tagging of chromosomal regions and individual mRNAs to track their cellular location (Bedell and Ekker 2015; Kaneko and Mashimo 2014).

### Cre-lox System

Cre-lox recombination is a sophisticated site-specific recombinase technology that allows DNA modification to be targeted to a specific cell type or to be triggered by a specific external stimulus. Cre is a recombinase protein derived from the P1 bacteriophage that catalyzes recombination between loxP sites (Sauer and Henderson 1988). LoxP sequences are formed by a consensus sequence with two palindromic sequences separated by a spacer region that is responsible for the sequences orientation. A DNA fragment with flanking loxP sites will be excised by homologous recombination in the presence of Cre, leaving a single loxP site making the point of excision and re-ligation of upstream and downstream DNA. Because the loxP sites are relatively small and placed in intronic regions, they do not typically interfere with normal gene transcription. The most important aspect of Cre-lox is its reversibility; a transgene can be inserted, expressed, studied for cellular effects, and then removed. This is possible with the modified version of Cre, Cre-ERT2, a chimeric protein that translocates to the nucleus in the presence of tamoxifen. Therefore, regardless of ubiquitous or cell type-specific expression of Cre-ERT2, the Cre-mediated recombination will only occur after tamoxifen treatment, providing sophisticated timing control capabilities.

### Viral-Based Systems

Adeno-associated virus (AAV) is a single-stranded DNA animal virus. The wild-type genome contains two open reading frames (ORFs) termed *rep* and *cap*, which encode non-structural and structural proteins, respectively. In addition to their broad potential for therapeutic gene delivery, recombinant AAV (rAAV) vectors possess the innate ability to stimulate homologous recombination in mammalian cells at high efficiencies (Ellis and Bernstein 1989). By altering the DNA sequence between the AAV homology arms, a broad range of modifications can be introduced in a targeted manner by natural recombination with the target locus, including single-base substitution (Inoue et al. 1999; Inoue et al. 2001), and site-specific integration (Hirata et al. 2002). rAAV can transduce various cell types in different species, and several studies have reported the successful application of rAAV vectors in different model organisms including mouse, rat, monkey, and other (Flierl et al. 2005).

### Oligonucleotides

The usage of oligonucleotides in gene targeting is used in the antisense field for many years to block gene expression at the mRNA level. Antisense oligonucleotide agents induce the inhibition of target gene expression in a sequence-specific manner by exploiting the ability of oligonucleotides to bind to target RNAs via Watson-Crick hybridization. Once bound, the antisense agent either disables or induces the degradation of the target RNA. There are three major categories of gene-silencing molecules: (1) antisense oligonucleotide derivatives that, depending on their type, recruit RNase H to cleave the target mRNA or inhibit translation by steric hindrance; (2) ribozymes and deoxyribozymes catalytically active oligonucleotides that cause RNA cleavage; and (3) small interfering double-stranded RNA molecules that induce RNA degradation through a natural gene-silencing pathway called RNA interference (RNAi). Specialized oligonucleotides capable of forming a third strand of the helix to block gene expression, single-stranded oligos to introduce and adduct at a specific site were also described (Haber 2000).

## Conclusion

The sequencing of human and different model organism genomes with the continuous development and performance of gene targeting techniques should be associated with a great expansion of functional genomics. Gene targeting techniques will allow the total or partial inactivation of protein function in order to determine their role or their labeling for in vivo analyses. The techniques that are used to disrupt or to restore gene function also have potential for therapeutic applications. However, considerable advances in the comprehension of their mechanisms, particularly those involved in the downstream response to the induced damage, are needed before these approaches move from bench to bedside.

## Cross-References

- [DNA](#)
- [Genes](#)
- [Targeted Mutation](#)

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## Genechip

- [Microarray](#)



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## Generic

### ► Arbitrary Stimuli

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## Genes

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## Definition

*Genes* are defined as the fundamental physical and functional units of heredity. They serve as the carriers of genetic information from parents to offspring across generations.

## Main Text

### Genes Are Inheritable Genetic Units

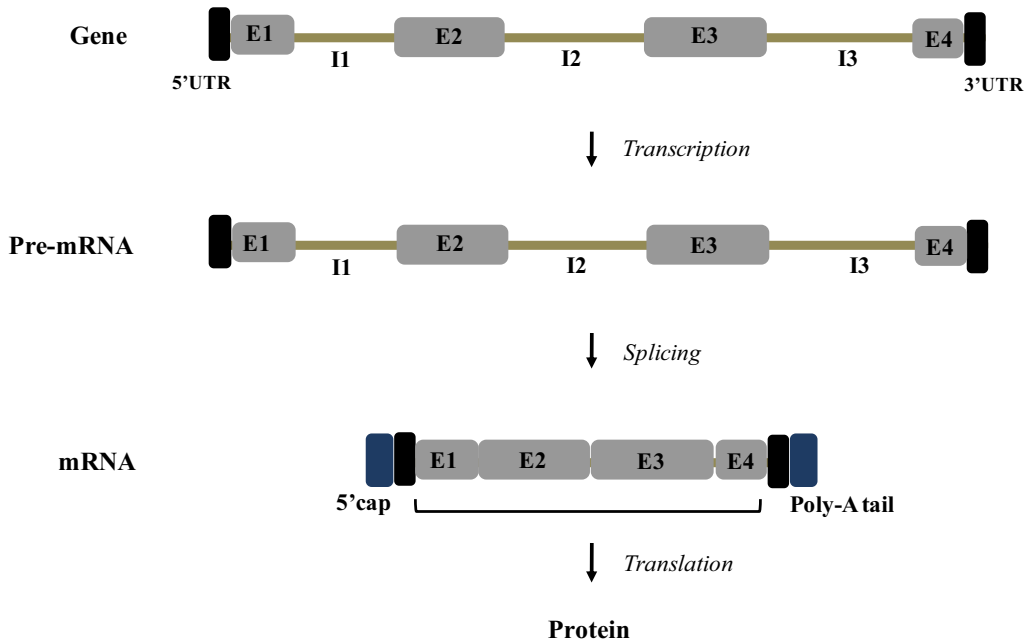
The existence of inheritable genetic units was first described by Gregor Mendel as early as 1865 and the term “genetics” was first used in 1905 by William Bateson (Keynes and Cox 2008). Genes are made up of DNA (deoxyribonucleic acid), positioned on chromosomes and code for proteins. The chromosomes comprised of autosomes and sex-linked chromosomes in entirety are known as DNA that constitutes the genetic material. Genes are made up of introns, exons, and 5' and 3' untranslated regions. Exons are the regions that code for the corresponding protein and introns are the noncoding parts that are removed during the process of mRNA splicing (Fig. 1).

Two or more alternative forms of a gene located at the same chromosomal position are known as *allele*. The position at which a gene is placed on the chromosome is often referred to as *locus*. Majority of the multicellular organisms including humans are diploid, containing a pair of each chromosome or homologous chromosomes. Thereby, every allele of a gene on a single

chromosome has its allele pair at the same locus of the homologous chromosome. The two alleles of a gene are inherited from each parent. These alleles can vary from each other if they contain mutations. Such genes made up of two different alleles are known as *heterozygous* with respect to that gene. Condition in which both the alleles are same makes that gene *homozygous*.

### Genetic Expression

Genetic information on the DNA is converted into RNA (ribonucleic acid) also known as messenger RNA (mRNA) by a process called *transcription*. This in turn gets decoded by ribosomes into the respective protein by a process called *translation*. Nucleotides are the building blocks of DNA and RNA (ribonucleic acid). Each nucleotide is composed of a nitrogenous base, a five-carbon sugar (ribose or deoxyribose) and a phosphate group. Four nitrogenous bases, adenine (A), guanine (G), thymine (T), and cytosine (C) make up the nucleotides in the DNA. Thymine is replaced by uracil (U) in mRNA. Genes therefore are constituted of nucleotides that appear similar to any other region of the genome. However, they are equipped with a feature that distinguishes them from rest of the DNA. This is the sequence specific promoter region that precedes a gene. Promoters facilitate the binding of RNA polymerase to initiate transcription. The information content on genes is read from the corresponding mRNA as a set of rules called the *genetic code*. Every triplet of nucleotide sequences known as the *codon* specifies for a single amino acid. Only 20 amino acids appear in the genetic code, a combination of which makes up all the known proteins in any living organism. The initiation codon “AUG” encodes methionine as the first amino acid in eukaryotes and a modified methionine (fMet) in prokaryotes. Some proteins of the mammalian cells, however, can also initiate translation with leucine decoded from “CUG.” Certain viruses contain RNA as the genetic material instead of DNA. They use reverse transcription by an enzyme reverse transcriptase to synthesize DNA from the RNA prior to protein synthesis.



**Genes, Fig. 1 Structure of a gene.** Gene structure representing the 5' and 3' UTRs; exons E1, E2, E3, E4; and the intervening introns I1, I2, I3. The gene gets transcribed into pre-mRNA. Splicing removes the introns and

generates the mature mRNA with a 5'cap at the 5'UTR and poly-A tail in the 3'UTR. This mRNA gets translated into the corresponding protein coded by the gene

### Inheritance of Genetic Information

Animal cells contain two types of DNA, nuclear and mitochondrial. Plant cells additionally contain chloroplast DNA. Each mitochondrion can contain 2–10 copies of the DNA and mitochondrial proteins can be coded by nuclear genes too. The human mitochondrial DNA (mtDNA) is made up of 37 genes and along with most other species is inherited exclusively from the mother. Nuclear DNA inheritance is however seemingly different. *Meiosis* of germ cells is a specialized cell division process that reduces the chromosome number ( $2n$ , representing the DNA that contains a pair of each chromosome) to half and produces four haploid cells or gametes ( $n$ ). During the process of meiosis, the homologous chromosomes pair with each other and undergo crossovers leading to *genetic recombination* that produces four gametes with unique genetic content different from the parent cell. Genetic recombination is an event that exchanges genetic information randomly between two homologous chromosomes to produce chromosomes with a new

combination of genetic information. Upon fertilization, two gametes fuse and create a diploid cell with paired chromosomes. This process results in the inheritance of genetic information from the parents that is exclusive and determined by the randomness of genetic recombination event. The genetic information is embedded in the genes. This produces individuals that can decode distinctive genetic material which makes them unique from any other individual. The human genome contains ~25,000 genes (Van Straalen and Roelofs 2006). This is a small number as compared to much simpler eukaryotes like yeast that contains 6000 genes, fruit fly made up of 14,000 genes, or *Caenorhabditis elegans* which contains 18,000 genes (Van Straalen and Roelofs 2006). However, the biological complexity of humans has been advocated to a combinatorial diversity generated at the level of *post-translational modifications of proteins* (such as methylation, acetylation, glycosylation, phosphorylation to name a few).

Certain genes follow *Mendelian inheritance* where a specific trait is determined by a single



**Genes, Fig. 2** A homologous chromosome pair representing alleles (A, a) of a gene. Alleles A and a are inherited from each parent

gene. The phenotype (observable physical and behavioral features) is determined by the genotype (the allelic combination of a gene). Mendelian inheritance underlies several genetic disorders. Alleles that determine these traits can be dominant or recessive. Dominant alleles (A) express the corresponding phenotype when paired with the same or any other allele of the same trait, i.e., in homozygous or heterozygous states (AA or Aa). Recessive alleles (a) express the respective phenotype only when paired with a same allele (aa), i.e., in a homozygous combination. With knowledge of the genotype and corresponding phenotype, the dominant allele can be easily detected (Fig. 2).

### Genes and Disorders

Depending on the chromosomes on which the genes are located and if the causative alleles are dominant or recessive, Mendelian inherited genetic disorders can be autosomal dominant, autosomal recessive, X-linked dominant, X-linked recessive, Y-linked or of mitochondrial inheritance. Genetic disorders can also result from de novo mutations that arise independently. De novo mutations usually result in severe disorders that can result in a disrupted reproductive capacity or early death and hence never get inherited. Several genetic disorders also result from polygenic contribution of more than one gene and do not follow a Mendelian inheritance. However, knowledge of the causative genes in any genetic disorders is helpful to lead to the correct research that can be used to treat these disorders. Gene therapy has been an area of great interest for several years to treat genetic disorders and only recently success has been made in this field in patients with beta thalassemia, hemophilia, and hereditary blindness.

## Cross-References

- ▶ [Allele Sharing](#)
- ▶ [Alleles](#)
- ▶ [Autosome](#)
- ▶ [Chromosomes](#)
- ▶ [Crossover](#)
- ▶ [DNA](#)
- ▶ [Mendel's Laws](#)
- ▶ [Mendelian Crosses](#)
- ▶ [Ribosome](#)

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## Genetic Carrier

- ▶ [Carrier](#)

## Genetic Code

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## Definition

Genetic code is the set of instructions in the form of linear sequences of nucleotides encoded on DNA and subsequently on mRNA in the form of triplets of nucleotides, the codons, which correspond to 20 different types of amino acids in proteins in living cells.

## Introduction

While a codon is a triplet of nucleotides, the genetic code refers to the correct sequence of the

codons which results in corresponding amino acid sequence of a protein. Each codon in the genetic code consists of three nucleotide bases arranged in a specific order, with each combination corresponding to a specific amino acid. The genetic code can be expressed as either RNA codons or DNA codons, which in living cells is translated into proteins. Translation is accomplished by **ribosome** subunits, which links amino acids in an order directed by mRNA sequences, via transfer RNA (tRNA) molecules that transport amino acids corresponding to codons and help in decoding of the genetic code into corresponding proteins. Many organisms use standard genetic code with few exceptions which include some bacteria, some single-cell eukaryotes, and mitochondria that use nonstandard code.

## Discovery

After the discovery of structure of DNA in 1953, efforts to understand how proteins are encoded in genetic material DNA began. George Gamow attempted to solve the problem of how the combination of four bases (adenine, cytosine, thymine, and guanine) in nucleotide chain directs the synthesis of proteins from amino acids. He postulated that sets of three bases must be involved to encode the 20 standard amino acids to make proteins, which would allow a maximum of  $4^3 = 64$  amino acids.

With the help of genetic studies, Crick, Barnett, Brenner, and Watts-Tobin in 1961 showed that the code is a triplet code which was later confirmed by biochemical studies. Although base compositions of codons were determined, the order of bases within the codons was still unknown. It was Marshall Nirenberg and Heinrich J. Matthaei who first determined the sequence of the codon in cell-free extract of *E. coli*. By then, base composition of 50 codons was assigned to the amino acids, but trinucleotide synthesis was still a major problem. Har Gobind Khorana and his associates after series of studies over many years were able to synthesize oligo and polynucleotides using chemical method. At that time only 20–30 trinucleotides were synthesized.

Khorana and his colleagues were able to synthesize 64 trinucleotides by chemical method. Then in 1965, Robert Holley from Cornell University deciphered the structure of transfer RNA (tRNA), an adapter molecule which carries specific amino acids corresponding to codon on mRNA template to ribosomal assembly during translation process.

Marshall Warren Nirenberg, Har Gobind Khorana, and Robert William Holley were awarded the Nobel Prize in Medicine in 1968 for deciphering the genetic code and its importance in protein synthesis (Fig. 1).

## Characteristics of Genetic Code

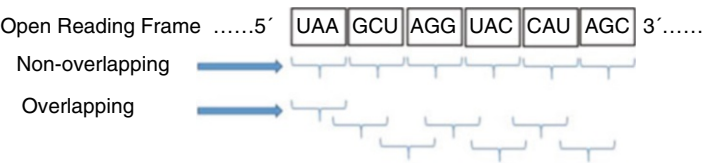
Here are mentioned some features of the genetic code (as described by F H C Crick in his article “The Origin of the Genetic Code” published in 1968) which are of such a general type that they do not depend upon the details of the code at all.

1. Each codon comprises triplet of bases.
2. Some codons function special codons like AUG as start codon which codes for methionine (Met), and UAA, UAG, and UGA are called termination codons or stop codons or nonsense codons which do not code for any amino acid.
3. The genetic code is universal (except mitochondria where AUA codes for methionine and UGA for tryptophan instead of isoleucine and stop codon, respectively, some bacteria and few single-cell eukaryotes) i.e., codons that code for specific amino acids are identical in nearly all species. To prove this, two hypotheses have been proposed.

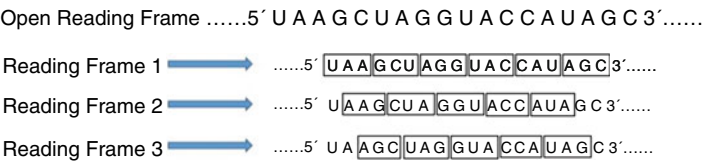
- *The stereochemical theory*: According to this theory genetic code is universal because of its stereochemical reasons, i.e., high affinity between an amino acid and its corresponding codon or anticodon.
- *The frozen accident theory*: This theory stated that allocation of codons to amino acids was merely a matter of chance. Assuming that all

**Genetic Code, Fig. 1** The standard genetic code

|              |   | Second letter                            |                                      |                                            |                                           | Third letter |
|--------------|---|------------------------------------------|--------------------------------------|--------------------------------------------|-------------------------------------------|--------------|
|              |   | U                                        | C                                    | A                                          | G                                         |              |
| First letter | U | UUU } Phe<br>UUC }<br>UUA } Leu<br>UUG } | UCU }<br>UCC } Ser<br>UCA }<br>UCG } | UAU } Tyr<br>UAC }<br>UAA Stop<br>UAG Stop | UGU } Cys<br>UGC }<br>UGA Stop<br>UGG Trp |              |
|              | C | CUU }<br>CUC } Leu<br>CUA }<br>CUG }     | CCU }<br>CCC } Pro<br>CCA }<br>CCG } | CAU } His<br>CAC }<br>CAA } Gln<br>CAG }   | CGU }<br>CGC } Arg<br>CGA }<br>CGG }      |              |
|              | A | AUU }<br>AUC } Ile<br>AUA }<br>AUG Met   | ACU }<br>ACC } Thr<br>ACA }<br>ACG } | AAU } Asn<br>AAC }<br>AAA } Lys<br>AAG }   | AGU } Ser<br>AGC }<br>AGA } Arg<br>AGG }  |              |
|              | G | GUU }<br>GUC } Val<br>GUA }<br>GUG }     | GCU }<br>GCC } Ala<br>GCA }<br>GCG } | GAU } Asp<br>GAC }<br>GAA } Glu<br>GAG }   | GGU }<br>GGC } Gly<br>GGA }<br>GGG }      |              |



**Genetic Code, Fig. 2** Schematic diagram showing that the genetic code is read in open reading frame in non-overlapping manner



**Genetic Code, Fig. 3** Schematic diagram showing that the genetic code can be read in three different possible reading frames

- organisms evolved from a single ancestor and inherited the same set of codons so they do not change and any change in the codon would be highly disadvantageous or even lethal in extreme form.
4. Most interesting feature of genetic code is its degeneracy means a single amino acid may be coded by more than one codon but one codon specifies only one amino acid.
5. Codons are read in open reading frame (ORF) and non-overlapping manner (Fig. 2).
6. Every coding sequence has three possible reading frames (Fig. 3).
7. There is no punctuation between consecutive codons, i.e., they are comma-less.



## Nonstandard Amino Acids

In general all organisms have proteins composed of 20 amino acid encoded by 61 standard codons. However, there are the cases (certain archaea, eubacteria, and eukaryotes) where amino acid in the protein is not one of the standard amino acids, i.e., selenocysteine (21st amino acid) and pyrrolysine (22nd amino acid). These two amino acids are called nonstandard amino acids and are substituted for standard stop codons, UGA that code for selenocysteine and UAG for pyrrolysine depending on signal sequences on mRNA. Here it is interesting to know that UGA is still used as a termination codon or stop codon, but the translation machinery is able to discriminate when to use UGA as stop codon and when to code for selenocysteine. However, the mechanism is still not known.

## Cross-References

- [Amino acid](#)
- [Codon](#)
- [DNA](#)
- [RNA](#)
- [Ribosome](#)

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## Genetic Compatibility and Sexual Selection

- [Genetic Compatibility/Histocompatibility](#)

## Genetic Compatibility/Histocompatibility

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## Synonyms

[Genetic compatibility and sexual selection](#); [Genomic compatibility/incompatibility](#)

## Definition

In the process of sexual selection to produce better-fitted offspring, the parental genetic combination arises the issue of compatibility because the closely related individuals along with interspecies mating provide lower fitness and even sterility of the offspring due to interaction of the genetic elements.

## Introduction

It is the basic characteristic feature of an animal to reproduce and propagate its genetic material to the next generation. In this process, selection of partner on the basis of their genetic makeup is an important feature. Up to what extent partners are biocompatible or genetically compatible is the question female faces during choosing of good genes. The model of genetic incompatibility was proposed by Dobzhansky (1936) and Muller (1942), and they found that independent evolution of two populations can generate alleles compatible in native background whereas deleterious on genetic background of other population rendering hybrid inviability or sterility. Genetic compatibility is one of the most important parameters of evolution based on which mate choice, polyandry, and extra-pair copulation also come into the scenario. Genetic histocompatibility in the form of major histocompatibility complex (MHC)

plays a significant role in the partner selection and less parasitized better-fitted offspring.

### Dilemma Between Genetic Compatibility and Genetic Dissimilarity

Selection of good genes (genetic dissimilarity) for better fitness of the offspring (genetic compatibility) put the female in dilemma. To derive the relationship between genetic dissimilarity and genetic compatibility, it has been found that highest level of fitness (genetic compatibility) achieved at intermediate level of genetic dissimilarity (Bateson 1983). Inbreeding or mating with close relative (low genetic dissimilarity) provides lower fitness (genetic compatibility) to the offspring, and even mating with different species also causes genetic incompatibility like hybrid vigor and hybrid sterility (hybrid incompatibility). Genetic compatibility furnishes as a nonadditive genetic variance (interaction between genetic elements) in fitness, whereas good gene acts as an additive genetic variance in the fitness (Neff and Pitcher 2005). Females are in dilemma of choosing good genes or compatible genes during sexual selection. The females administer both the parameters to avoid confrontation and provide optimum survival and fitness to the offspring.

### Ways to Achieve Genetic Compatibility

The intriguing puzzle in sexual mode is to avoid genetic mismatch or incompatibility and selection of partner which will provide higher fitness to the offspring. Parasite avoidance is one of the ways to get away from the genetic incompatibility, since there are many evidences like selection of mate which is healthy, parasite-free reduces parasite load, and also the less parasitized individuals have higher reproductive success. In support to this, the red queen hypothesis presumes that the new gene combination provides the platform to combat with currently dominating parasite.

During mate selection, male confronts with three demands of female, viz., (a) there is enormous variation of resistance gene in population,

(b) she knows about her immune genes, and (c) she can recognize immune gene of potential mate and choose accordingly.

For reproductive success, male ornamentation is one of the promising features of sexual selection, e.g., spur length of pheasants (*Phasianus colchicus*) which is correlated with male survival, offspring fitness, and sexual attractivity (Von Schantz et al. 1996). This spur length is also correlated with MHC (major histocompatibility complex) genotype, and the female can discriminate the MHC from the spur length of the male.

In the year 1974, Zinkernagel and Doherty explain the role of MHC in recognition and processing of foreign antigen followed by Gorer who discovers the mice MHC complex known as H-2 complex. Due to codominant expression of MHC alleles, MHC heterozygous is advantageous possessing greater resistance against different pathogens by presenting a greater variety of peptides to the T-cell receptor.

### Genetic Incompatibility Hypothesis

According to this hypothesis, the quality of an offspring depends on the interaction between paternal and maternal genes, i.e., the haplotype of each partner matters. The incompatibility may rise due to three components: homozygote disadvantage, selfish genetic elements, and coadapted gene complexes (Nordeide 2007).

### Homozygote Disadvantage

Genomic incompatibilities are theoretically because of two reasons:

- (a) Dominance – Heterozygous experiences lower expression of recessive deleterious mutations because heterozygous can bind twice as many foreign peptides as homozygotes (homozygote disadvantage) (Hughes and Nei 1992) and balances the costs of numerous MHC allele expression.
- (b) Overdominance – Certain heterozygotes are superior, produce a greater variety of gene

products, favor parasite avoidance, and decrease the risk of autoimmunity (Penn and Potts 1999).

## Coadapted Gene Complex and Genetic Compatibility

### (i) Between species

Preferences for conspecific partner are universal to all animals. In reproductive character displacement, many examples about mating with wrong species (divergence) (Butlin 1989) have been reported. Lower fitness individuals are produced in mating between species because of (a) major differences in the genetic system of two groups (chromosome structure, number, etc.) which may interrupt meiosis and result in hybrid sterility, and (b) different genomic elements are coadapted differently, and the phenotypes suffer when they mixed together (Dobzhansky 1948).

Coadapted gene complex – It is a group of traits which if present together helps to enhance the individual fitness, whereas fitness will be compromised if they don't. This coadaptation is in the form of external or internal. Externally, phenotypical adaptation is with the environment and internally compatibility of new allele with the other alleles. For example, in the case of *Heliconius erato*, hybrid butterflies are fully viable and fertile, but they are prone to predators for their extreme coloration (Mallet 1993) (external coadaptation disadvantage). Internal coadaptation may also cause hybrid disadvantage even under standard condition, e.g., if parthenogenetic strain *Drosophila mercatorum* mates, the offspring shows hybrid viability disadvantages (Templeton et al. 1976) due to interaction between alleles of unlinked gene, chromosome, and chromosome arms.

### (ii) Between population within species

At any given set of loci, recombination will prevent retention of more than one coadapted gene complex in spite of less limitation in gene exchange within species breeding. Spatial or temporal subdivision between species creates

geographical population within species. Cross population mating reduces hybrid fitness and hybrid disadvantage due to breakdown of association between genes. Due to outbreeding, in few convincing cases, assortative mating driven by selection against genetic incompatibility has been reported (Butlin and Tregenza 1997). The fact about sympatric speciation driven by mate choice for genetic compatibility is confusing. Female selection for a particular male genotype like sperm protein binding is very common in the case of *Echinometra*, where intraspecific sperm protein binding variation has been found.

### (iii) Within population

Contributing factor for the optimal balance between inbreeding and outbreeding is coadaptation gene complex. Recombination suppression is the criteria to evolve and maintain coadaptation. Further if these coadapted regions are protected from recombination, females will not exercise mate choice to maintain the coadapted gene complex and will not be a common source of variation in genetic compatibility. Ratti et al. (1995) found that in pied flycatchers (*Ficedula hypoleuca*), breeding with low genetic similarity birds has more offspring and suggests that females may be engaged in extra-pair copulation to reduce the unspecified cost of fitness.

## Selfish Genetic Elements and Genetic Compatibility

Genomic conflict or genetic incompatibility within all organisms arises because of selfish genetic elements like segregation distorters, transposable elements, inherited bacterial symbionts, autonomous replicating elements, converting elements, transmitting sex-enhancing elements, t-complex in mice, etc. In two specific rules, it determines the sexual selection and genetic compatibility. Firstly the diversity of selfish genetic elements is correlated with the outbreeding rate of that species. Secondly the phenotype is often shown in hybrids but is not observed in within-population crosses (Hurst

and Werren 2001). In spite of cost bearing by selfish genetic element, its transmission provides advantages to the individual by helping to combat with the new mutation and also with the deleterious mutation.

Different species are sensitive to different meiotic drivers which are considered as selfish elements. Mate selection depends on this sensitivity to avoid creation of genetic compatibility in the offspring. Selfish genetic elements include selfish DNA and cytoplasmic symbionts or parasites and promote their transmission in the expense of affecting other genes, e.g., female stalk-eyed flies prefer X-linked suppressor containing males (Wilkinson et al. 1998) or males who lack meiotic drivers altogether (Lande and Wilkinson 1999). In case of parasitoid wasps *Nasonia vitripennis*, sperm, which lack meiotic drive B chromosome, will fertilize the egg in competition of other driver male sperm (post-copulatory choice) (Beukeboom 1994). In some cases, selfish genetic element encourages polyandry (Martin 2009).

## Conclusion

In the course of evolution, choice of sexual mode over asexual mode provides variation to the offspring with higher viability and reproductive success. Second level of reproductive success and increasing fitness of the offspring is the selection of partner where heterozygous provides advantage. Genomic compatibility in regard with selfish genetic elements and coadaptation gene complex drive the mate choice for better fitness of the offspring. To find a good gene, mate selection depends on genotype variation, and the discrimination is based on odor which is related with MHC. Heterozygous MHC haplotype provide better fitness and immunity to the animal and also reduce the risk of fetal abortion as found in homozygous parents.

## Cross-References

► Hybrid Vigor

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## Genetic Constitution

### ► Genotype

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## Genetic Drift

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Random sampling of the organisms in a population leads to changes in the allelic frequencies. This process is termed genetic drift or allelic drift or the Sewall Wright effect (Goodhart 1963; Fisher and Ford 1950). The source of the change in frequency in case of genetic drift is just “chance.” In other words, unlike natural selection, no environmental factors influence the genetic drift to occur. Genetic drift is one of the basic mechanisms of evolution along with natural selection, migration, and mutation.

Another important feature related to genetic drift is that it is more evident in smaller populations. The reason behind this is that, in small populations, alleles that are present in lower frequencies face a greater chance of being lost than that of higher frequency alleles. Therefore, if the force of the genetic drift is strong

enough, it might result in a complete removal of those alleles, leading to a loss in the genetic diversity of the population.

Population bottlenecks and the founder effect are the favorable conditions for the occurrence of the genetic drift as they can drastically reduce population size, which is an important factor for the activity of genetic drift. The bottleneck effect can be caused by a natural event like a natural disaster that wipes out most of a large population. This results in the genetic structure of the survivors becoming the genetic basis for the entire population, which may be very different from the population before the disaster. For example, in the case of *Phytophthora infestans*, the cause of potato blight, a single clone that escaped out of Mexico and into North America resulted in the Irish potato famine and then was circulated globally (Goodwin et al. 1994). Similarly, the present population of the North American bison has resulted from a bottleneck which constricted the original population to less than a hundred (Hedrick 2009).

Another extreme example of genetic drift is the founder effect. This effect occurs when a small group of individuals separates from the large population to establish a colony. The small group of individuals might not represent the entire previous population or the alleles present might be in a different frequency than the original population (Peltonen 2001). According to Milgroom et al. (1996), the population of chestnut blight (*Cryphonectria parasitica*) in North America also shows some characteristics of a founder population due to much reduced genetic variance from the original population in Asia. The most important difference between the bottleneck effect and the founder effect is that the former involves catastrophe while the latter involves colonization.

Genetic drift is also termed as random drift because the change in the allelic frequencies occurs merely by chance and is not predetermined. The consequences of the genetic drift include the increase in inbreeding coefficients and also homozygosity in a population. The populations that regularly undergo extinction and recolonization are more susceptible to genetic drift.



## Cross-References

- [Genetic Variation](#)
- [Mutations](#)
- [Natural Selection](#)

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## Genetic Fallacy

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## Synonyms

[Fallacy of origins](#); [Fallacy of virtue](#); [Heritability fallacy \(in behavioral genetics\)](#)

## Definition

It is the practice of basing the veracity of a claim on the origins, history, genes, etc., that may be

completely irrelevant to the point in question. In the context of the science of genetics and molecular biology, it may be defined as attributing a behavioral trait to genes without any respect to the environment.

## Description

“Genetic fallacy” may refer to a line of arguments or justification/s invoking genetics that seem to be logical but are illogical, and out of context thereby erroneously attributing an observed trait or phenomenon to irrelevant causes (like origins and genes). Genetic fallacy has many synonymous connotations like “Fallacy of origins,” “Fallacy of virtue,” and cover arguments that come under the arguments of irrelevance where the conclusions about the observed phenomenon (or a behavioral trait) are based on something’s/someone’s origin, history, background, genetics, with no relevance to the actual meaning and context. The act Genetic fallacy may or may not be a biased exercise, but it always denies to evaluate a trait on the basis of merit. The origin of the term goes back to the philosophers Morris Raphael Cohen and Ernest Nagel who coined the term in 1934 in their book *Logic and Scientific Method* (Honderich 1995). A coherent argument is (and should be) based on the premise having a direct bearing on the truth or falsehood of the claim; and there should be a direct relationship between the claim and the truth/falsehood of the argument (Damer 1980). But claiming genetic basis as the solo reason for a trait (particularly behavioral trait) without consideration the context (environment) is fallacious and misleading. Conclusions drawn by such an approach are disingenuous and often wrong. The structure of a typical genetic fallacy is based on a combination of two statements. The first statement/argument is “invoking the genesis” and the second statement is a “therefore statement.” It may be born in mind that these two statements don’t have any direct relationship with each other yet in a Genetic fallacy they are speciously thought to be related. The following is how the Genetic fallacy looks like:

Statement 1: The genesis/origin of the claim is put forth.

Statement 2: Based on just an apparent “therefore,” the claim is categorized as true or false.

An example of genetic fallacy is: “His father was wealthy, therefore, he is genetically predisposed to success in business.” Anyone’s success in business does not have any direct relation to one’s father’s economic status. Children of wealthy people are not all successful businessmen neither are the children of poor people business failures. Furthermore, genetic predisposition cannot be attributed as a cause of someone’s success in business. Upbringing, value system, education, skill set, development, belief system, circumstances, opportunities and many other reasons (collectively called environment) have a bearing on a person’s success in business. Attributing it solely to somebody’s genetics qualifies for being genetic fallacy.

Genetic fallacy is a philosophical term with little connotation to behavioral genetics. But a lot of use can be made of this phenomenon in genetics because behavior is a complex combination of genetics and environment. The interaction of these components is extremely intricate and genes are not the sole players in such a context. A person’s success may be attributed to many factors like intelligence, opportunity, hardwork, training, socioeconomic status etc., and a person becoming a successful businessman cannot just be attributed to the genetics.

Since Genetic fallacy is a philosophical term, a relevant term in science of behavioral genetics and molecular biology may be the “Heritability fallacy.” (Moore and Shenk 2017). According to Moore and Shenk, this term is one of the most misleading terms in behavioral genetics. They argue that the measurability of a particular trait is not an indication of “genetic heritability” of that trait. It is not indicative of the cause and mechanism of development of the trait. Also, it is not explanatory about the relative role and nature of interaction between genes and environment in shaping a behavioral trait of an individual.

A behavioral trait is an outcome of a complex combination of genetic, epigenetic and environmental factors which range from as objective

parameters as DNA sequence to as subjective factors as belief system and value system. There seem to be two distinct paradigms (viz. Genetics and Environment) interacting through an inter-phase (epigenetics) that results in development of a particular trait in a certain way. It is, therefore, important to emphasize that genetics has a role to play and environment also does have but the mechanism and extent of contribution of each paradigm is complex and we are just beginning to unravel the mysteries.

## Cross-References

- DNA
- Genes
- Heritability

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## Genetic Fingerprinting

- Restriction Fragment Length Polymorphism

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## Genetic Inheritance

- Complementary Genes Hypothesis
- Polygenic Inheritance

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## Genetic Make-up

- Genotype

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## Genetic Marker

- [DNA Marker](#)

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## Genetic Material

- [Chromosomes](#)

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## Genetic Polymorphism

- [Polymorphic](#)

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## Genetic Translocation

- [Translocation](#)

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## Genetic Variation

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### Synonyms

[Gene polymorphism](#); [Mutations](#)

### Definition

Genetic variation (GV) is defined as the subtle genomic differences among individuals within or between populations that makes each or a group of organisms different from others.

### Introduction

Variations are found throughout the genome of an organism. However, these variations are not evenly

distributed. Instead, some regions are “hot spots” of variability like CpG islands, and some other parts are stable enough that don’t show variation (Mugal and Ellegren 2011; Xia et al. 2012) at all among the individuals. Variation in the genetic material of an organism is depicted in its phenotype. Almost every trait of an individual is affected by genetic variation. Variations in the eye color and hair color, ear lobes, height etc. are due to the genetic differences between individuals.

## Genetic Variation Drives Evolution

Genetic variation is an important evolutionary force as it provides the diversity within and between populations. Genetic variability makes an organism more adapted to its environment. Variations result in different forms of a gene (called alleles). For example, if a gene “A” is mutated to “a” and if the new allele (a) has some selective advantage for the individual either through fitness or fecundity, then the mutated allele will be transmitted to the next generation over a period of time. On the other hand, if the new allele is deleterious, then it would be selectively eliminated as the offspring carrying it will not survive. Preexisting advantageous mutations when selected will result in observation of new phenotypes. This process is called natural selection (Darwin 1859). Natural selection brings about changes in the gene frequency. Over few generations, this would result in speciation. Hence, disturbance in genetic equilibrium or Hardy-Weinberg equilibrium, i.e., change of frequency of alleles in a population would lead to evolution.

## Sources of Genetic Variation

Mutations, gene flow, and sexual reproduction are three primary sources of genetic variation.

### Mutations

Mutation is a process which produces altered DNA sequence. It may be induced by radiations and chemical mutagens in the environment or

insult from endogenous reactive oxygen species (ROS) or occur spontaneously due to endogenous factors (errors in chromosomal segregation, recombination, DNA replication and repair, and also spontaneous chemical damage to DNA). Mutations are inexorable. They may have adverse effects on organism's health and survival. Sometimes, they may have no obvious effects, or rarely, they may be beneficial for the bearer.

### Gene Flow

Gene flow is the transfer of genes from one population to another and thus affects the allele frequency. The rate of gene flow is directly proportional to the mobility of an individual and is limited by geographical barriers which may be natural or man-made. Cross-species hybridization in plants to generate new and improved varieties and gene transfer from bacteria or virus to new hosts lead to genomic variations.

### Sexual Reproduction

Somatic cells divide and multiply by mitosis that produces daughter cells, identical to the parent cell, whereas during gamete formation, a special type of cell division, i.e., meiosis, results in newer combinations of parental genotypes by crossing over and independent assortment of homologous chromosomes thus generating unique genotypes, followed by random fertilization. Sexually reproducing organisms are more diverse than the asexually reproducing ones.

## Types of Genetic Variants

Genetic variations are basically of three types, viz., single-nucleotide variations, insertion/deletions (indels), and structural variations. These variations may be rare or common depending upon their frequency in population and pathogenic or nonpathogenic.

### Single-Nucleotide Variations (SNV)

SNVs are the most common type of all variations where a nucleotide is replaced by another. It may be either transition (purine to purine or pyrimidine to pyrimidine) or transversion (purine to

pyrimidine or vice versa). When a SNV is common in a population or we can say its frequency is  $\geq 1\%$ , then it is known as single-nucleotide polymorphism (SNP). SNPs may fall within the coding or noncoding region of genes or in the intergenic regions. Coding region SNPs may be either synonymous (no change in amino acid) or non-synonymous (change in amino acid). SNPs are usually selectively neutral, but they often make an individual predispose to certain disease, e.g., SNPs in *MTHFR* (methylene tetra hydro folate reductase) predispose an individual to cardiovascular disease (Kluijtmans et al. 1996), cancer (Izmirli 2013), and neural tube defects (Botto and Yang 2000). SNPs also confer a selective advantage to individuals harboring them, e.g., Duffy blood group allele, FY(a-b-) (Duffy null phenotype), protects against malaria (Carvalho and Carvalho 2011). SNPs are cataloged in a public database, dbSNP (<http://www.ncbi.nlm.nih.gov/projects/SNP>). Coding region SNVs may affect the structural and functional aspect of a protein. They are usually deleterious and present less frequently in population ( $\leq 1\%$ ). They are known as rare variants. Rare variants which are clinically significant are cataloged in clinical variation database, ClinVar (<https://www.ncbi.nlm.nih.gov/clinvar>). SNPs present in non-coding regions are also reported to influence gene splicing and transcription factor binding. The functional effect of variants on the protein's structure and function can be predicted using in silico tools like SIFT, PolyPhen2, MutationTaster, etc. (Table 1).

### Insertions and Deletions (Indels)

Indels refer to DNA mutations involving insertion and deletion of one or more base pairs. These can have devastating effects on the gene because either translation of the gene is frame shifted or amino acids are deleted. For example, 3 bp deletion ( $\Delta F508$ ) in coding region of *CFTR* (cystic fibrosis transmembrane conductance regulator) gene is the most common cause of cystic fibrosis (Cutting 2015). However, nonpathogenic indel are often useful in mapping common ancestry in kinship and human origin studies because chances of two mutations of the same length occurring in the same genomic position are negligible.

**Genetic Variation, Table 1** List of bioinformatic tools and softwares to predict the pathogenicity of a missense genetic variant

| Tool              | Web address                                                                                                                                                                                 |
|-------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| AUTO-MUTE         | <a href="http://proteins.gmu.edu/automute/">http://proteins.gmu.edu/automute/</a>                                                                                                           |
| Align-GVGD        | <a href="http://agvgd.hci.utah.edu/agvgd_input.php">http://agvgd.hci.utah.edu/agvgd_input.php</a>                                                                                           |
| CanPredict        | <a href="http://www.cgl.ucsf.edu/Research/genentech/canpredict">http://www.cgl.ucsf.edu/Research/genentech/canpredict</a>                                                                   |
| CADD              | <a href="http://cadd.gs.washington.edu/score">http://cadd.gs.washington.edu/score</a>                                                                                                       |
| CONDEL            | <a href="http://bbglab.irbbarcelona.org/fannsdb/help/condel.html">http://bbglab.irbbarcelona.org/fannsdb/help/condel.html</a>                                                               |
| FATHMM            | <a href="http://fathmm.biocompute.org.uk/">http://fathmm.biocompute.org.uk/</a>                                                                                                             |
| FunSAV            | <a href="http://sunflower.kuicr.kyoto-u.ac.jp/sjn/FunSAV/index.html">http://sunflower.kuicr.kyoto-u.ac.jp/sjn/FunSAV/index.html</a>                                                         |
| FuzzySnps         | <a href="http://ma.gmu.edu/FuzzySnps/">http://ma.gmu.edu/FuzzySnps/</a>                                                                                                                     |
| HANSA             | <a href="http://www.cdfd.org.in/HANSA/">http://www.cdfd.org.in/HANSA/</a>                                                                                                                   |
| I-Mutant2.0       | <a href="http://folding.biofold.org/i-mutant/i-mutant2.0.html">http://folding.biofold.org/i-mutant/i-mutant2.0.html</a>                                                                     |
| LS-SNP            | <a href="http://ls-snp.icm.jhu.edu/ls-snp-pdb/">http://ls-snp.icm.jhu.edu/ls-snp-pdb/</a>                                                                                                   |
| MAPP              | <a href="http://www.ngsl.org.uk/Manchester/page/mapp-multivariate-analysis-protein-polymorphism">http://www.ngsl.org.uk/Manchester/page/mapp-multivariate-analysis-protein-polymorphism</a> |
| Mutation assessor | <a href="http://mutationassessor.org/r3/">http://mutationassessor.org/r3/</a>                                                                                                               |
| MutationTaster    | <a href="http://www.mutationtaster.org/">http://www.mutationtaster.org/</a>                                                                                                                 |
| MutPred2          | <a href="http://mutpred.mutdb.org/">http://mutpred.mutdb.org/</a>                                                                                                                           |
| nsSNPAnalyzer     | <a href="http://snpanalyzer.uthsc.edu/">http://snpanalyzer.uthsc.edu/</a>                                                                                                                   |
| PhD-SNP           | <a href="http://snps.biofold.org/phd-snp/phd-snp.html">http://snps.biofold.org/phd-snp/phd-snp.html</a>                                                                                     |
| PMut              | <a href="http://mmb.irbbarcelona.org/PMut/">http://mmb.irbbarcelona.org/PMut/</a>                                                                                                           |
| PolyPhen2         | <a href="http://genetics.bwh.harvard.edu/pph2/">http://genetics.bwh.harvard.edu/pph2/</a>                                                                                                   |
| PROVEAN           | <a href="http://provean.jcvi.org/index.php">http://provean.jcvi.org/index.php</a>                                                                                                           |
| SAPRED            | <a href="https://omictools.com/sap-disease-association-predictor-tool">https://omictools.com/sap-disease-association-predictor-tool</a>                                                     |
| SIFT              | <a href="http://sift.jcvi.org/">http://sift.jcvi.org/</a>                                                                                                                                   |
| SNAP              | <a href="http://www.bio-sof.com/snap">http://www.bio-sof.com/snap</a>                                                                                                                       |
| SNPs3D            | <a href="http://www.snps3d.org/">http://www.snps3d.org/</a>                                                                                                                                 |
| SNPs & GO         | <a href="https://snps-and-go.biocomp.unibo.it/snps-and-go/">https://snps-and-go.biocomp.unibo.it/snps-and-go/</a>                                                                           |
| SuSPect           | <a href="http://www.sbg.bio.ic.ac.uk/servers/suspect/about.html">http://www.sbg.bio.ic.ac.uk/servers/suspect/about.html</a>                                                                 |

## Structural Variations

Structural variation refers to large-scale structural differences in the DNA, originated mainly due to chromosomal rearrangements – deletion, duplication, novel sequence insertion, or inversion. They include copy number variations, variable number of tandem repeats, and chromosomal rearrangement.

## Copy Number Variations (CNV)

A CNV can be simple in structure, such as tandem duplication, or may involve complex gain and loss of homologous sequences at multiple sites in the genome. CNVs are genomic structural variants in which the number of copies of a particular segment is different in two or more different genomes as compared to a reference genome.

## Variable Number of Tandem Repeats (VNTRs)

These variations involve changes in the number of repeated DNA sequences arranged in tandem arrays. These are highly heterogeneous groups of loci. These are multiallelic markers while SNPs are generally biallelic. They are classified according to the size and number of their repeat units. They are sometimes considered as neutral markers. But there are many instances among various classes of VNTRs which shows phenotypic effects. VNTRs can be microsatellite, minisatellite, satellite, or telomere-repeat arrays.

## Microsatellites

They are also known as “short tandem repeats” (STRs) or “simple sequence repeats” (SSRs) having 1–6 bp long repeat units. Their copy number varies from 10 to 30. Microsatellites with some specific repeat units show clustering, but most are distributed throughout the genome which is useful in linkage analysis. The most common microsatellite is (CA)<sub>n</sub> repeat. Mutation at these regions may involve either increase or decrease in repeat units. Microsatellites are reported to be associated with many human diseases like fragile X syndrome (FMR1/FMR2;(CA)<sub>n</sub> repeat) and Huntington’s disease (HD; (CAG)<sub>n</sub> repeat).

## Minisatellites

Minisatellites are tandem arrays of repeat unit around 8–100 bp with a copy number of 5–>1000. They are generally GC rich. They are among most dynamic loci in our genome. Like most of the microsatellites, these are considered to be neutral markers, but there are examples that they play essential roles. A few lie in the coding regions, encoding repetitive, and highly variable proteins.



### Satellite

They are also called macrosatellite. They are large tandem arrays spanning hundreds of kilobases to megabases, composed of repeat units of wide range of sizes that can display a higher-order structure. Alpha satellite or alphoid DNA is a good example. It is 170 bp in length. Their detailed structure is difficult to study due to their size and repetitive nature.

### Telomere-Repeat Arrays

Telomeres are the structure present at the end of chromosomes having tandem arrays of hexanucleotide repeat TTAGGG, typically 10–15 kb in length. One end of this array is contiguous with subtelomeric DNA, while other is the true end of the chromosome.

### Chromosomal Rearrangements

Chromosomal rearrangement involves deletions, duplications, inversion and translocations which are caused by either breakage of DNA double helices at two different points, followed by the rejoining of the broken ends or through crossing over between repetitive DNA sequences to produce a new chromosomal arrangement of genes. Chromosomal rearrangement may lead to disruption of genes and implicated in many human

disorders particularly cancer like chronic myelogenous leukemia where balanced translocation results in fusion of the breakpoint cluster region (BCR) with the c-abl (ABL1) proto-oncogene tyrosine kinase leading to the formation of BCR-ABL fusion transcript which constitutively activates tyrosine kinase that can transform cells and inhibit apoptosis (Ren 2005). Chromosomal rearrangement is also a common mode of speciation mainly through post-mating reproductive isolation, e.g., inversion resulted in species diversity between two closely related drosophila species, *Drosophila pseudoobscura* and *Drosophila persimilis*. Gene duplication (16A) also causes bar eye phenotype in drosophila.

### Techniques for Detecting Genomic Variations

Genotyping provides a measurement of the genetic variation between members of a species. Genomic variations are often found to be the etiology of many human diseases and are of particular interest in pharmacogenomics. The increase in interest in GV has been reflected by the rapid development of a diverse range of SNP genotyping methods (summarized in Fig. 1).

### Genetic Variation,

**Fig. 1** List of techniques used for detecting genetic variations

#### Hybridization based methods

- Dynamic allele specific hybridisation
- Molecular beacons

#### Enzyme based methods

- Restriction fragment length polymorphism
- PCR based methods
- Flap endonuclease
- Primer extension

#### Methods based on physical properties of DNA

- Single strand conformation polymorphism
- Temperature gradient gel electrophoresis
- Denaturing high performance liquid chromatography

#### High throughput techniques

- Sanger sequencing
- Next generation sequencing

## Applications of Genomic Variations

### Screening for Genetic Diseases

GV can cause many diseases in humans. These diseases are usually rare but fatal, and an example is cystic fibrosis, caused by mutations in the *CFTR* gene. Many common diseases such as heart disease and cancer are genetically complex, with alleles from several genes contributing to the disease. Linkage and association studies are used to conduct genetic tests for screening of diseases which involves profiling of disease causing variants (Taylor et al. 2001).

### Pharmacogenomics

GV in patients make them respond differently to a medication. In the future, the most appropriate drug for an individual could be determined in advance of treatment by analyzing a patient's SNP profile and such kinds of treatment which are specific for an individual are called "personalized medicines."

### Biological Markers

Often GV tend to be relatively stable genetically; they serve as excellent biological markers. Constructing a chromosome map that shows the positions of known genes with genetic markers allows researchers to study and pinpoint disease traits.

### Forensic Technologies

Genetic profiling of biological material has become one of the most powerful tools for solving parental disputes and in criminal investigations. Traditional methods in DNA "fingerprinting" is now replaced by polymerase chain reaction (PCR)-based technology which detects very short polymorphic stretches of DNA.

## Conclusion

Subtle differences in DNA are the ultimate cause of genetic variation. They may include single-nucleotide polymorphisms, variable numbers of tandem repeats, and large-scale copy number variants. Both inherited and *denovo* variations could

be either advantageous or deleterious for an organism. Beneficial variations are selectively favorable and allow an organism to adapt in changing environmental conditions and hence drive evolution. Studies of these variations are directly relevant in understanding many features of human populations. The structure of populations in terms of inbreeding and reproductive isolation, the relationship of different populations to each other, and the geographical and historical origins of populations – all these aspects are illuminated by studies of genetic variation. Now with the advancement of next-generation sequencing technologies, vast amount of data is available which is being utilized for screening of genetic diseases and for designing personalized medicines. Despite of numerous technical advances, many variations still may exist in the genome which needs to be discovered to fully understand the distribution, pattern, prevalence, and evolution.

## Cross-References

- [Copy Number Variant \(CNV\)](#)
- [Evolution](#)
- [Gene Flow](#)
- [Mutations](#)
- [Single Nucleotide Polymorphism \(SNP\)](#)
- [Polygenic Inheritance](#)
- [Polymorphic](#)

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## Genetically Modified

### ► Transgenic

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## Genetics

- Behavioral Genomics
- Fisher
- Heredity

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## Genital System

- Reproductive System

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## Genome Mapping

- Gene Map

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## Genome Project

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## Genome

A genome is an organism's complete hereditary information. It is present in nucleus and also in mitochondrial DNA and present in RNA in some viruses. Human genome contains 23 pairs of chromosomes (22 autosomes and a pair of sex chromosome). Males contain both X and Y sex chromosome and females have XX sex chromosome in their genome. Coding genes and noncoding regions are identified within the genome. In 1944, DNA was shown to be the hereditary material, and in 1953, the concept of double helix was acknowledged. Genetic makeup of an organism lies in DNA sequences which differs in every individual at least at some places.

### Some Facts Regarding Human Genome

- Diploid, 23 chromosome pairs, shows biallelic expression
- $3 \times 10^9$  bases  $\approx$  30,000 genes
- Coding genes represent  $\approx$  1.5–2% of genome sequence
- Repetitive DNA  $\approx$  50%
- 8% present in large recent duplications

## Genomics

Molecular characterization including structure, function, and interaction of whole genome is termed as genomics. Contrast to genetics, where few genes are studied, genomics includes the study of several genes or entire genome of an organism. It needs complex and sophisticated methods to study the genome.

Genomes in Medical Research

By comparing genomes of pathogenic and non-pathogenic strains of a particular microorganism, it's possible to find out the determinants of virulence. Similarly we can compare the genome of virulent strains and the host in order to design drugs targeting the protein products of pathogen-specific genes that have little or no side effect on the host. In addition to this, genome sequencing has an impact on day-to-day practice of medicine and agriculture as to gather information regarding organisms that colonize, feed, and infect homo sapiens.

History of Human Genome Project (HGP): A Book of Life

The gaining of vast knowledge in genomics is attributed to human genome project (HGP). It was a global collaborative effort to clone, sequence, and map the whole human genome. With the establishment of genetic engineering techniques came the HGP, launched in 1990. It was a 13-year project launched by the US Department of Energy (DOE) and National Institutes of Health (NIH) in coordination with international partners to sequence the entire three billion bases in human genome. DOE participated in this project to study the effects of radiation (due to usage of atomic bombs during World War II) on health, more precisely at DNA level. Eighteen countries participated, and the overall budget of three billion dollars was allocated for this coordinated project. DNA of five subjects from different ethnical background were selected for sequencing. Human genome has approximately  $3 \times 10^9$ bp, so enormous amount of data expected to be generated necessitated the use of rapidly processing and DNA sequencing machines and high speed computational devices for data storage, retrieval, and analysis in mapping human genome. It was associated with additional sequencing projects of microbes, plants, mouse, fugu fish, etc. It has to assemble 12,000 bases every minute. Achieving goals of HGP would have been impossible without technological

advancement and collaborative efforts. The entire data is available in public databases in World Wide Web for free access. By 2000, Craig Venter (from Celera Genomics) and Francis Collins (from National Human Genome Research Institute, NHGRI) jointly announced the draft completion of human genome sequencing. In February 2001, the HGP consortium published the first draft of human genome sequence in the journals *Nature* and *Science* (International Human Genome Sequencing Consortium 2001; Venter et al. 2001). Craig Venter was the first named person to get his own genome sequenced. The whole sequence was deposited in GenBank, a public database of DNA sequence operated by National Institutes of Health (NIH) for free access.

Data of few Organisms Studied in Human Genome Project

| Organisms                                  | Genome size<br>Million base pairs (Mb) | Estimated number of genes |
|--------------------------------------------|----------------------------------------|---------------------------|
| <i>Escherichia coli</i>                    | 4.6                                    | 4,300                     |
| <i>Drosophila melanogaster</i> (fruit fly) | 165                                    | 13,300                    |
| <i>Mus musculus</i> (mouse)                | 3,000                                  | 30,000                    |
| <i>Homo sapiens</i> (human)                | 3,200                                  | 25,000–30,000             |

Genome sequences of >5,000 biological entities, ranging from viruses and bacteria to plants and animals, have been reported. By 2011, >180 eukaryotic, prokaryotic, and archaeal genomes had been sequenced, e.g., genomes of chicken, cat, dog, elephant, rat, rabbit, orangutan, etc.

Bioinformatics in HGP

The challenge posed by multifactorial diseases demands a quantum increase in depth of our knowledge of living organisms and we must be able to trace factors both external and internal that compromise health by analyzing genetic,



environmental, and dietary factors across entire community. So, scientists have turned to sophisticated computational tools to collect and analyze biologic information on mass scale (owing to massive size of human genome,  $3 \times 10^9$  nucleotide base pairs) through a process called bioinformatics. This includes all aspects of gathering, storing, handling, analyzing, interpreting, and spreading vast amounts of biological information in databases. The information involves gene sequences, biological activity/function, pharmacological activity, biological structure, molecular structure, protein-protein interactions, and gene expression. It provides rich information from basic metabolism to evolution to aging.

### Goals of Human Genome Project

- Identify all the app. 20,000–25,000 genes in human DNA (15,000 full-length human genes identified).
- Mapping and sequencing the genomes of model organisms like mouse, drosophila (fruit fly), the first plant *Arabidopsis thaliana* (thale cress), chimpanzee, *Caenorhabditis elegans* (roundworm), pathogens, domestic animals, etc.
- Determine the sequences of the three billion chemical bp that make up human DNA (99% human DNA sequence finished to 99.99% accuracy).
- Store this information in databases.
- Improve tools for data analysis.
- Research training.
- Transfer related technologies to other sectors, such as industries.
- Address the ethical, legal, and social issues (ELSI) that may arise from the project. With new tools in genomics, ELSI also arises, so as to use this knowledge in an appropriate and beneficial way, questions that arise are:
  - How to interpret this information and use it?
  - Who should have an access to it?
  - If not used properly, how people can be protected from the associated harm? effect on race and ethnicity should also be considered

So, based on these issues, need for certain public policies development also arises including the philosophical and ethical consequences of understanding our own DNA blueprint.

### How They Sequence DNA?

- (A) DNA polymerase binds to a single-stranded DNA template and synthesizes a complementary strand of DNA.
- (B) When DNA polymerase randomly incorporates a fluorescently labeled ddNTP base, synthesis terminates. This step produces a mixture of newly synthesized DNA strands that differ in length by a single nucleotide. Each strand is labeled at the 3' end with a fluorescently labeled ddNTP base.
- (C) The DNA mixture is separated by electrophoresis.
- (D) The electropherogram results show peaks representing the color and signal intensity of each DNA band. From these data, the sequence of the newly synthesized DNA strand is determined.

### Methodologies of Genome Project

- Genetic mapping
- Physical mapping
- cDNA sequencing
- Genomic sequencing

Major approaches utilized in HGP for sequencing and annotating DNA were:

1. Expressed sequence tags (EST) identify all the genes that are expressed as RNA. This is a blind approach of simply sequencing the whole set of genome that contained all coding and noncoding sequences and later on assigning different regions in sequence with a particular function, i.e., called sequence annotation.
2. Single nucleotide polymorphisms (SNPs)/snips. Scientists have identified around 3 million snips out of 15 million.



3. Clone by clone method: Creating a crude physical map of the whole genome by restriction mapping before sequencing. The approach involved breaking the genome into overlapping fragments and inserting them into BACs and transfecting into *E. coli*. After collecting clones using DNA recombinant technology, a genomic library is developed and physical maps were prepared after organizing these clones into overlapping groups.
4. Craig Venter, one of the leaders of the project, suggested a new method called shotgun sequencing (Venter et al. 1998) for long DNA strands as Frederick Sanger sequencing (DNA sequencing, i.e., a process of reading nucleotide sequences using dideoxy Sanger's method or chain termination method) used earlier can only be used for short DNA strands up to 100–1,000 bps. Shotgun sequencing is analogous to rapidly expanding, quasi-random firing pattern of shotgun. Two main methods are there for this fragmentation and sequencing process, using random fragments. Here, DNA is broken randomly into numerous small segments which are sequenced using chain termination method to obtain reads. Multiple overlapping reads for target DNA are then obtained which are further analyzed through various computer programs and then assembled into continuous sequence.
5. Other essential tools include features from genome map.

The whole genome was read at four- to fivefold coverage to avoid gaps and mistakes in sequence.

## Applications of HGP

1. Chromosomal mapping.
2. Linkage analysis.
3. To study the migration of different population groups.
4. Microsatellites (e.g., variable number of tandem repeats (VNTR)) study is useful for fingerprinting in forensic medicine.

5. HapMap project (International HapMap 3 Consortium & Frazer 2007) to study the SNP (more than 20 million SNP found in human genome) patterns in relation to disease pathogenesis
6. Polymorphism (SNP, copy number variants (CNV), insertions/deletions, inversions) to study risk assessment like early predisposition of disease.
7. Genome-wide association studies (GWAS) to detect common gene variants
8. Cancer genome project – DNA markers help in forming a panel/genetic profile for specific cancers.
9. Genetic counselling – To reduce the likelihood of genetic disease transmission.
10. Personalized medicine.
11. Pharmacogenomics to rationalize drug design.
12. Laboratory diagnostics.
13. Most of the model organisms (*C. elegans*, *Drosophila*) for medical research have conserved regions of genome similar to human genome in evolution (easy to maintain and quick to breed in research laboratories).
14. To identify endangered and protected species – Serves as an aid to wildlife researchers.
15. Agricultural research – To develop disease- and drought-resistant, highly productive breed of plants and seeds.

## Achievements Following the HGP Completion

ENCODE (Encyclopedia of DNA Elements) project was initiated to explore the noncoding sequence (approximately 98% of the genome). It identified many functional elements present throughout the noncoding regions of genome.

Considering the high cost spent for sequencing in HGP, few companies developed the sequencing machines with high throughput, speed, and accuracy at an affordable cost. With the advent of next-generation sequencing (NGS), the whole genome can be sequenced now within a day with much lower cost. Several genome projects like “1000 genome project”

which studied the genetic variation among genome of large number of people, “Genome 10k project” which aims at assembling genome of 10,000 vertebrate species of specific genus, and “i5k project” through which genomes of 5,000 insects and arthropods are to be sequenced in a period of 5 years were launched. Through GeneSweep, the information regarding sequence of human genome increased. So many species genome sequencings are still ongoing.

### What We Learnt Out of HGP?

Through this blueprint, it was found that only less than 2% of the genome codes for proteins. Remaining regions may contain regulatory and repetitive or junk sequences. Almost 99.9% of genome is the same in all people. Size of the genome does not correspond to the number of genes. Most of the translated regions for proteins are conserved in evolution among various organisms. Human genes are just twice in number compared to a fruit fly. ChIP-seq, DNase I hypersensitivity, RNA-seq, and DNA methylation assays were used in ENCODE project (ENCODE Project Consortium 2011).

### Limitations

Obtaining the blueprint alone may not explain the effect of other factors like environment and the role of epigenetics in multifactorial disease, where the genome sequence remains unchanged.

### Conclusion

HGP cannot be concluded, as it is constantly expanding and will be continuing further to fill the gaps and errors. It revealed the extraordinary valuable information about the role of an organism’s genome in evolution, in physiology, and in disease. The HGP was possible with the advent of newer computational and molecular technologies. The cost and time for genome sequencing are

becoming much lesser. A simple blood test to obtain the data of genome sequence will provide a complete genetic profile that predicts the individual’s susceptibility to a disease, responsiveness to a drug, etc. This elaborate database can be effectively applied in emerging field of personalized medicine, after considering the pros and cons.

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## Genome-Wide Association Studies

- [Candidate Gene](#)

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## Genomic Compatibility/Incompatibility

- [Genetic Compatibility/Histocompatibility](#)

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## Genomic Context

- [Bioinformatics](#)

## Genomic Imprinting

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### Synonyms

DNA methylation; Epigenetics; Gene imprint;  
Non-Mendelian inheritance

### Definition

Genomic imprinting is an epigenetic phenomenon which results in the monoallelic expression of a gene depending on the parental origin. Genomic imprints may be covalent (DNA methylation) or noncovalent (DNA-protein and DNA-RNA interactions, genomic localization in nuclear space) and the process of imprinting encompasses the specialized nuclear enzymatic machinery which maintains parental epigenetic marks throughout the life.

### How Imprinting Works?

All of us inherit two copies of a gene—one copy from mother and another one from father. Normally, both copies are active, whereas in some situations only one of them is turned on. Of these, some genes are active only when they are inherited from father, while others will be activated when inherited from mother. So which copy will remain active depends on their parental origin. These genes are called “imprinted genes.” Genomic imprinting is reversible: a man may inherit a particular allele with a maternal imprint from his mother, but when he passes it on to his child, it will then carry a paternal imprint (Fig. 1).

In imprinted genes, the parent of origin is often marked, or “stamped,” on the gene during the formation of egg and sperm. This stamping

process mostly involves methylation, which turns the gene off, and demethylation which makes the gene active. Most imprinted genes are developmental genes which affect fetal growth, nutrient transfer through placenta, cell proliferation, and brain development. Usually growth-related genes are maternally imprinted.

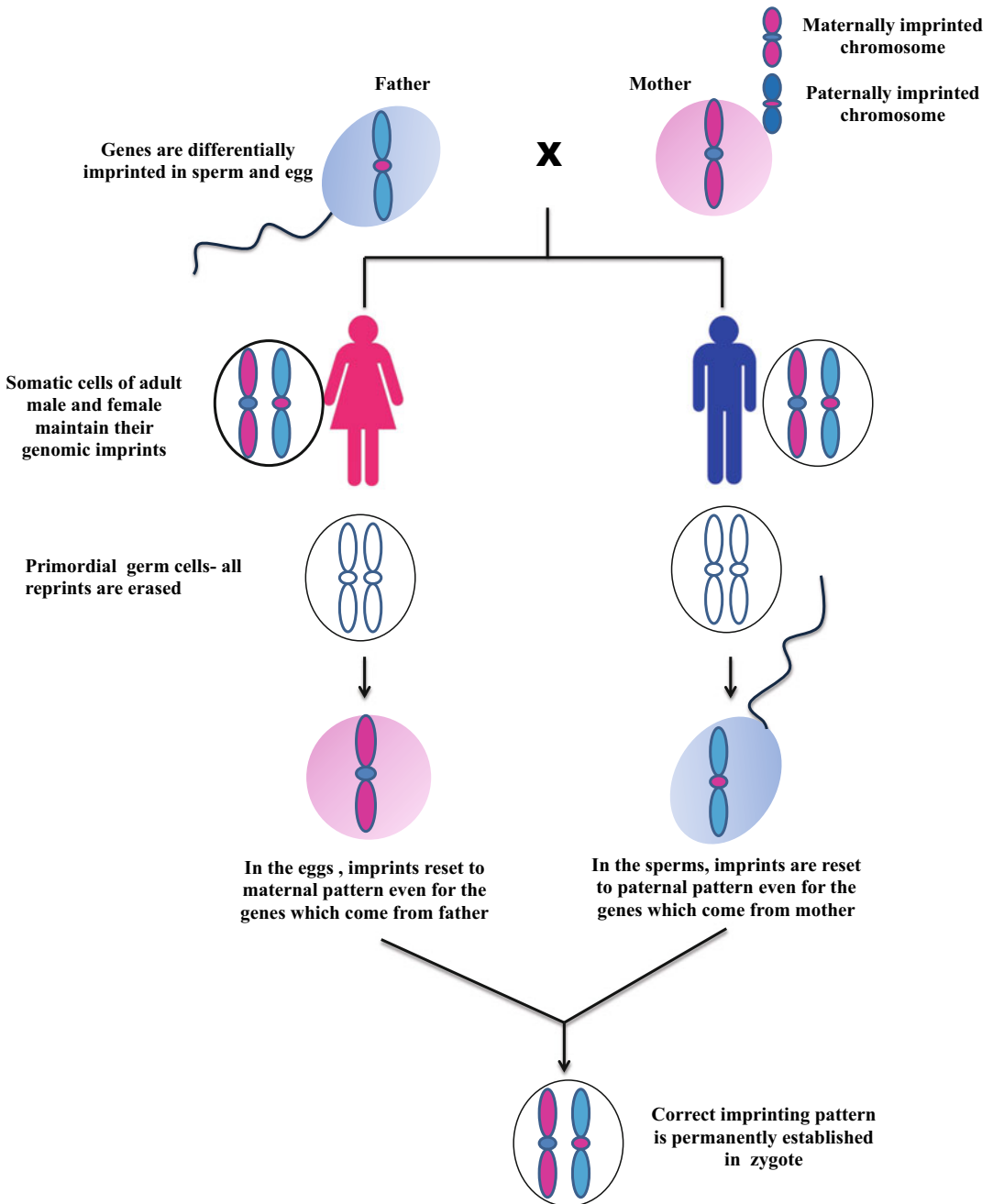
### Evolution of Genomic Imprinting

Genomic imprinting was first recognized in mammals in 1984 when pronuclear transplantation experiments showed that both maternal and paternal genomes are needed for the normal development of mouse embryos to term (McGrath and Solter 1984). In parallel, mouse genetic experiments provided strong evidence that in some regions of the genome, genes function differently when inherited maternally than when inherited paternally. This provided an explanation for earlier genetic findings (Cattanach and Kirk 1985).

This phenomenon evolved in mammals over 125 million years ago (Killian et al. 2000). The most prominent evolutionary explanation for the origin of genomic imprinting is the “Kinship Theory of Imprinting”. According to this theory, imprinted gene expression is the result of an evolutionary conflict between the maternally and paternally derived alleles within an organism to control the maternal expenditure of resources to the offspring. This battle for resources continues even after birth (Haig 1996). Paternally expressed imprinted genes are meant to promote growth while it is suppressed by maternal genes. By contrast, “Coadaptation Theory” proposes that imprinted genes act co-adaptively to optimize fetal development as well as maternal health and nutrition (Wolf and Hager 2009).

### Mechanism of Genomic Imprinting

Parental imprints are established during gametogenesis when parental imprints are erased and reset. The differential imprinting in gametes correlates with differences in the epigenetic state of the two alleles which is established by DNA

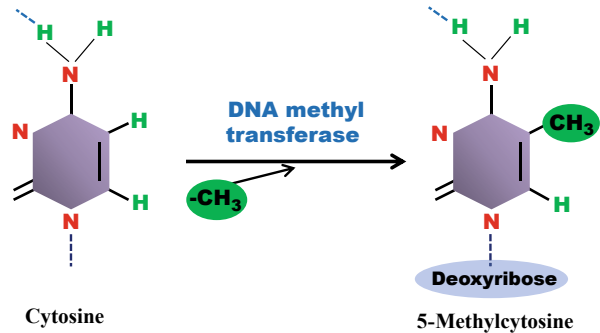


**Genomic Imprinting, Fig. 1** Inheritance of imprinted genes across generations

methylation at CpG dinucleotides, as well as histone modifications. The differential allele expression may occur in all somatic cells, or in specific tissues and stages of development. DNA

methylation is an epigenetic mechanism that occurs by the addition of a methyl ( $-\text{CH}_3$ ) group to DNA, thereby often modifying the function of the genes and affecting gene expression.

**Genomic Imprinting,**  
**Fig. 2** Mechanism of DNA  
 methylation



The covalent addition of methyl group at the 5'-carbon of the cytosine ring is the most common method of DNA methylation. As a result of this covalent addition, 5-methylcytosine (5-mC) is formed (Fig. 2). These methyl groups inhibit transcription by interfering with the major groove of DNA. Different members of the DNMT family of enzymes act either as *de novo* DNMTs (DNMT3a and DNMT3b), putting the initial pattern of methyl groups in place on a DNA sequence, or as maintenance DNMTs (DNMT1), copying the methylation from an existing DNA strand to its new partner after replication. Methylation results in suppression of gene expression, whereas unmethylated genes remain active. The promoter region of the imprinted gene is differentially methylated during gametogenesis in most of the cases.

### Imprinted Gene Organization and Regulation

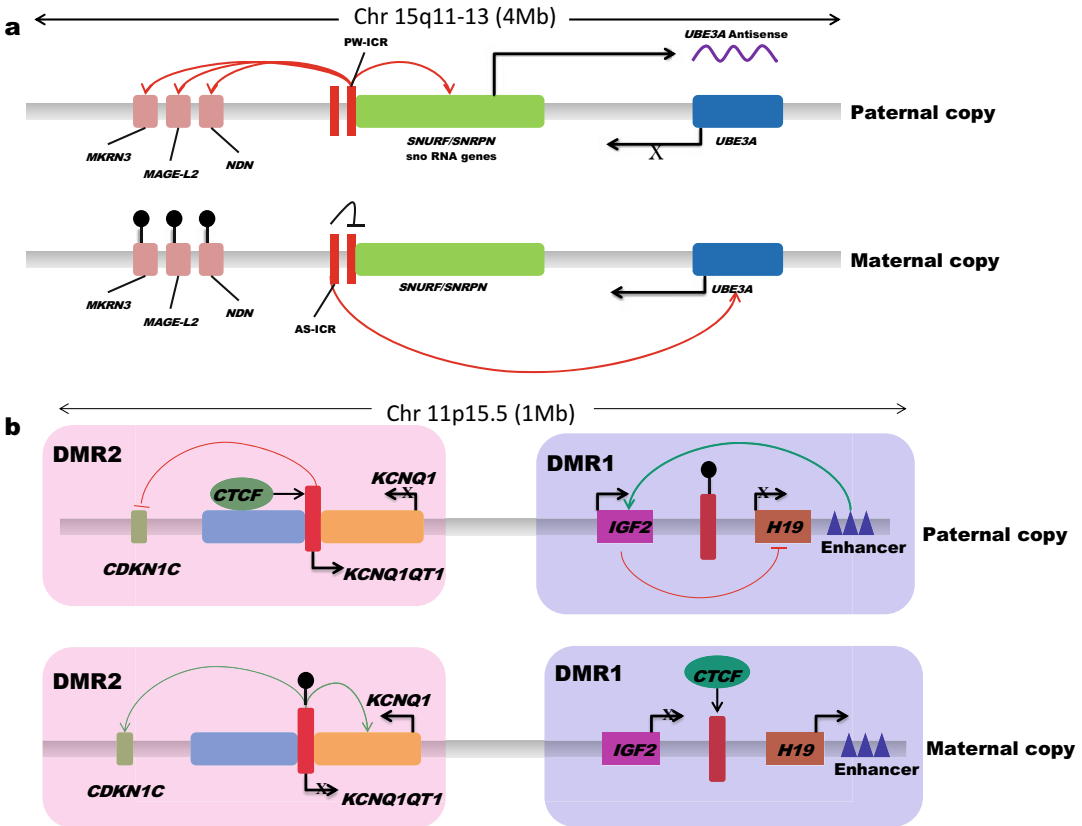
Imprinted genes are usually organized in clusters containing 2–15 genes and vary in size from <100 kb to several megabases. All clusters contain both maternally and paternally expressed genes, as well as genes that encode proteins and those that encode long noncoding RNAs. Molecular organization of two important imprinted gene clusters in human is shown in Fig. 3. Imprinted genes show exclusive or predominant expression from either the maternal or the paternal allele with an exception of growth factor receptor-bound protein 10 (*Grb10*) gene. Latter encodes an adaptor protein which is predominantly maternally expressed and acts as a growth inhibitor during

embryogenesis, but is paternally expressed in the brain and regulates adult social behavior. Imprinting is under the overall control of a *cis*-acting imprinting control region (ICR). This region shows parent-specific silencing and activation of genes. The germline methylation is robust and resistant to the extensive reprogramming of the genome that occurs in the embryo after fertilization, but is erased and reset during germ-cell development in adults. Most ICRs acquire methylation in the female germ line during oogenesis, and these ICRs typically contain the promoters of long noncoding RNA (lncRNA) genes that run antisense to at least one of the protein-coding genes within the cluster (Fig. 3). ICRs that acquire methylation in the male germ line seem to be located in intergenic regions. An ICR is active when un-methylated and inactive when methylated. The mechanisms by which un-methylated ICRs control imprinted gene expression are only partially understood and two different models, i.e., the lncRNA model and the insulator model, have been described. Only a small percentage of all human genes undergo genomic imprinting. It is still a question that why some genes are imprinted and others are not. Around 150 genes are known to be imprinted in mouse (Mouse book imprinting catalogue), and nearly 70 imprinted genes have been verified in humans (Catalogue of parent of origin effect in human).

### Genetic Mapping of Imprinted Genes

Mouse genetics experiments have shown that mouse embryos have been generated which





**Genomic Imprinting, Fig. 3** Schematic representation of molecular organization of major gene clusters in humans (a) 4 Mb region of chromosome 15 (15q11-13) with at least 10 genes of which 9 are paternally expressed and 1 maternally expressed. There are two components of ICR; one specific to Angelman Syndrome (AS-ICR) and another for Prader-Willi syndrome (PW-ICR). They are differentially methylated and govern which genes are to be paternally or maternally imprinted. The paternal allele encodes a huge transcript (up to 460 Kb and 148 exons) with multiple splice forms under PW-ICR. The first 10 exons encode two proteins, *SNURF* (*SNRPN* Upstream Regulating Frame) and *SNRPN* (Small Nuclear Ribonucleo Protein), while downstream exons lack ORF and some of the introns encode sno RNA (small nucleolar RNA). The downstream part of transcript overlaps the *UBE3A* gene (Ubiquitin ligase) on the opposite strand and possibly acts as an antisense RNA, preventing transcription of *UBE3A* from paternal allele. **Lack of paternal copies of *SNURF* and *SNRPN* is the cause of Prader-Willi syndrome, whereas lack of a maternal copy of *UBE3A* causes Angelman**

**syndrome (b)** 1 Mb region of chromosome 11p15.5 imprinted regions. It contains two differentially methylated regions (DMR1 and DMR2). CTCF (CCCTC-binding factor) binds to unmethylated alleles of both DMRs. In DMR1, there are two imprinted genes: *H19* and insulin-like growth factor 2 (*IGF2*). *IGF2* is a paternally expressed fetal growth factor and *H19* is a noncoding RNA. The *H19*-associated imprinting center (IC1) is usually methylated on the paternal chromosome and unmethylated on the maternal chromosome. Normally, the *H19* gene is expressed from the maternal allele and *IGF2* from the paternal allele. DMR2 contains several imprinted genes, including *KCNQ1*, *KCNQ1OT1*, and *CDKN1C*. DMR2 contains the promoter for *KCNQ1OT1*, a paternally expressed noncoding transcript that regulates in cis the expression of the maternally expressed imprinted genes in this region. **Disturbance of genomic imprinting due to loss or gain/loss of methylation on maternal/paternal allele is responsible for Beckwith-Wiedemann syndrome and Russell-Silver Syndrome**

contained a small proportion that were derived either from paternal or maternal source. The generation of a series of such uniparental

disomies, which simultaneously span the entire genome allowed the generation of an imprinting map. More than 50% (approximately 80%)

**Genomic Imprinting, Table 1** List of diseases associated with imprinted genes in humans

| SN | Syndrome                                    | Chromosome location              | Major features                                                                                                                                                                                                                                              | Cause                                                                                                                                                                                                                            |
|----|---------------------------------------------|----------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1. | Prader-Willi syndrome                       | 15q11-13                         | Short stature, obesity, hypogonadism and learning difficulties                                                                                                                                                                                              | Interstitial deletion of ~2Mb proximal region of long arm of paternal chr 15 or maternal UPD of chr 15                                                                                                                           |
| 2. | Angelman syndrome                           | 15q11-13                         | Epilepsy, severe learning difficulties, unsteady or ataxic gait and happy affect                                                                                                                                                                            | Interstitial deletion of ~2Mb proximal region of long arm of maternal chr 15 or paternal UPD of chr 15                                                                                                                           |
| 3. | Beckwith-Wiedemann syndrome                 | 11p15.5                          | Macrosomia (prenatal and postnatal overgrowth, macroglossia (large tongue) omphalocele, umbilical hernia diastasis recti, neonatal hypoglycemia, renal and ear abnormalities, cleft palate and predisposition to embryonal tumors particularly Wilms' tumor | Complex epigenetic error leads to loss of maternal <i>H19</i> expression and paternal biallelic <i>IGF2</i> expression along with reduction in <i>CDKN1C</i> expression or paternal UPD11                                        |
| 4. | Russell-Silver syndrome                     | 11p15.5(65% cases) MatUPD7 (10%) | Prenatal and postnatal growth retardation, triangular face with pseudohypocephalic appearance                                                                                                                                                               | Hypomethylation of <i>H19</i> DMR results in <i>IGF2</i> silencing and biallelic expression of <i>H19</i> or Maternal UPD7; <i>MEST</i> and <i>GRB10</i> are candidate genes for MatUPD7                                         |
| 5. | Pseudo-hypothyroidism type 1a               | 20q13.3                          | Dysmorphism, obesity, cognitive impairment, end-organ resistance to PTH (which results in hypocalcemia and hyperphosphatemia)                                                                                                                               | Maternal inactivating mutations of <i>GNAS</i> result in 50% expression of non-imprinted <i>GNAS</i> , which causes the dysmorphic phenotype AHO; loss of imprinted <i>GNAS</i> expression causes obesity and hormone resistance |
| 6. | Pseudo-hypothyroidism type 1b               | 20q13.3                          | End-organ resistance to PTH (which results in hypocalcemia and hyperphosphatemia) and occasional resistance to TSH                                                                                                                                          | Lack of maternal <i>GNAS</i> methylation imprinting results in loss of expression of imprinted <i>GNAS</i>                                                                                                                       |
| 7. | Transient neonatal diabetes mellitus type 1 | 6q24                             | Neonatal hyperglycemia and IUGR                                                                                                                                                                                                                             | Overexpression of <i>PLAG1</i> and <i>HYMA1</i>                                                                                                                                                                                  |
| 8. | MatUPD14 syndrome                           | 14q32                            | Prenatal and postnatal growth retardation, premature puberty and obesity                                                                                                                                                                                    | Loss of paternal expression of <i>DLK1</i> and <i>RTL1</i>                                                                                                                                                                       |
| 9. | PatUPD14 syndrome                           | 14q32                            | Dysmorphism, placentomegaly and excessive amniotic fluid (polyhydramnios)                                                                                                                                                                                   | Increased expression of <i>RTL1</i>                                                                                                                                                                                              |

imprinted genes are found in clusters, indicating a coordinated control (Reik and Walter 2001). These clusters are known as imprinting domains. Currently, genome-wide screenings identify imprinted genes by using following methodologies:

1. Differential expression of mRNAs from control fetuses and parthenogenetic or androgenetic fetuses hybridized to expression arrays (Kobayashi et al. 2009).
2. Allele specific gene expression using SNP genotyping arrays (Bjornsson et al. 2008).

3. Transcriptome sequencing (Babak et al. 2008).
4. *In silico* prediction pipeline (Luedi et al. 2007).

## Genomic Imprinting and Genetic Disorders in Humans

The growth of embryos in human is regulated by many imprinted genes which also regulate the development. Deviation from monoallelic expression of imprinted genes leads to severe developmental defects in humans (listed in Table 1). Many disorders also occur due to a unique phenomenon known as uniparental disomy (UPD) of the chromosomes having imprinted genes. If an individual inherit both homologs of a chromosome pair from one of their parent then it is called uniparental disomy. UPD leads to either loss of expression of a gene or bi-allelic expression of the gene, hence loss of genomic imprinting.

## Genomic Imprinting in Other Species

Genomic imprinting is unique to therian mammals (placental mammals and marsupials) and flowering plants. Imprinting of whole chromosomes has been reported in mealybugs (Genus: *Pseudococcus*) and a fungus gnat (*Sciara*). It has also been established that X-chromosome inactivation occurs in an imprinted manner in the extra-embryonic tissues of mice and all tissues in marsupials, where it is always the paternal X-chromosome which is silenced.

## Conclusion

Genomic imprinting is the mechanism through which a gene or a genomic domain is stamped biochemically with information about its inheritance. There is biased allelic expression due to imprinting that favors expression from one parental locus over other. Though majority of the imprinted genes code for protein, there are some which code for untranslated RNA transcripts. Genomic imprints violate Mendel's laws of inheritance, one of which stipulates that the

dominance of one genetic allele over another is an inherent function of the alleles themselves and does not depend upon the parent of origin. Loss of imprinting lies at the root of many human disorders. They may also be involved in the development of common diseases such as obesity, diabetes mellitus, and cancer. To fully comprehend the role of imprinted genes in biology and disease, a complete list of imprinted genes is needed.

## Cross-References

- ▶ [Alleles](#)
- ▶ [Gene Expression](#)
- ▶ [Imprinting](#)
- ▶ [Methylation](#)

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## Genotype

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## Synonyms

Biotype; Genetic constitution; Genetic make-up;  
Genotypic ratio

## Definition

The set of genes in our DNA which is responsible for a particular trait is referred to as genotype. Hence, it is the information stored within a gene.

## Introduction

The word genotype can be used to refer a particular gene or set of genes which are carried by an individual. Genotype of an individual is its complete heritable genetic identity, which is unique to an organism or individual. It also refers to the alleles or variants of a gene, which are carried by an organism. Humans are diploid organism, which means they have two alleles at a given locus, wherein one comes from father and the other one from mother. These alleles represent the genotype of a specific gene. Genotype, along with epigenetic factors, determines the phenotype.

Genotype is internally coded inheritable information which is carried by all organisms. This coded information is used as a blueprint for building and maintaining a living creature. This information is present in all cells and is passed on to

next generation at the time of cell division. These coded instructions control everything such as formation of protein, regulation of metabolism. In contrast to genotype, phenotype is the outward physical manifestation. It may include physical parts, energy utilization, tissues, organs, reflexes and behavior, therefore anything which is part of the observable structure, function, or behavior of living organism can be a part of phenotype.

The examples of genotype include genes responsible for the stripes on cat, size of a bird's beak, height, hair color, eye color, etc. Let us assume the eye color of human being; we have different colors like blue, brown, green, black, etc. Why we all have a different eye color? This is because of the difference in the amount of eye pigment, **melanin** which is present in iris. Eye color is an inherited trait and there have been evidences that up to 16 genes can influence the color of eye (Sturm and Larsson 2009). There are three known alleles that control the shade of eye color. These alleles assort independently during gamete formation. Every individual has four alleles for controlling their eye color; B allele (brown) is always dominant over G allele (green). The blue trait is always recessive (Table 1).

From the above Table, we can see that two or more than two different genotypes can give the same phenotype, so two different individuals having brown eyes may have different genotype. The inheritance pattern in albinism and hemophilia can also be taken into account for correlating genotype and Mendelian inheritance.

**Genotype, Table 1** Genotype and phenotype of eye color

| Genotype | Phenotype |
|----------|-----------|
| BGG      | Brown     |
| BbGG     | Brown     |
| BBGg     | Brown     |
| BbGg     | Brown     |
| BBgg     | Brown     |
| Bbgg     | Brown     |
| bbGg     | Green     |
| bbGG     | Green     |
| Bbgg     | Blue      |

## Genotypic Ratio

The number of times a genotype would appear in the offsprings after a cross between both parents will be the genotypic ratio. The value depends upon the genotype of parents. It can be calculated by Punnett square. Let us assume that two organisms with same genotype (Aa, A is dominant and a is recessive) are allowed to mate, the offsprings will have the genotype: AA, Aa, and aa and the resulting genotypic ratio will be 1:2:1, whereas the resulting phenotypic ratio will be 3:1 (Fig. 1).

## Genotyping

The process of determining differences in the genetic make-up of an individual by examining an individual's DNA sequence and comparing it to another individual's sequence or a reference sequence is known as genotyping. The most widely used methods for genotyping include polymerase chain reaction (PCR), DNA sequencing, random amplified polymorphic detection (RAPD), amplified fragment length polymorphism, allele-specific polymerase chain reaction, and hybridization to DNA microarrays. Genotyping finds its application in prenatal disease diagnosis, for which two widely used techniques are "amniocentesis" (Hessner et al. 1998) and "chorionic villi sampling." Apart from prenatal disease diagnosis, genotyping is routinely used for determining blood group, genetic counseling, and personalized medicine. Genotyping can be done right from humans to microorganisms. For

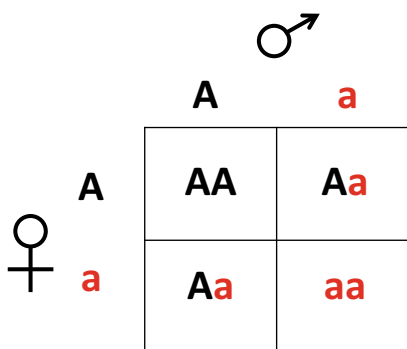
microorganisms, genotyping can be used for controlling the spreading of pathogens. Similarly transgenic organisms can also be genotyped. A transgenic mouse can be genotyped by a simple polymerase chain reaction (PCR) technique.

## Effect of Environment on Genotype

Genotype of an organism is its inherited map which is carried within its genetic code. All organisms that have the same genotype do not look or behave the same way as phenotype and behavior are modified by environmental factors. When two different genotypes respond to environmental factors in a different way, it is referred to as gene environment interaction. Such interactions can provide a better insight for the genetic epidemiology of certain diseases. We all know that every individual may have different response to a particular drug due to gene environment interactions. Here, now the term pharmacogenetics (Klotz 2007) comes into picture, which is the study of inherited genetic differences in drug metabolic pathways which generally affects the individual responses to drugs. Hence, it will allow clinicians to select the drug and its dosage more precisely.

## Conclusion

Genotype is the entire set of genes in a cell, an organism, or an individual. It depends on the genetic information which was given to an individual by their parents. An individual's genotype is indicative of their full genetic information which is determined by the genes passed on by the parents. Children born to a parent will have different genotype, the exception to this are twins or multiple births that are fertilized from same egg. Genotype determines the type of trait that a phenotype can have and it is the major influencing factor in development of phenotype. The concept of phenotypic plasticity can explain the degree to which an organism's phenotype is determined by its genotype. Phenotypic plasticity is the changes in an organism's behavior, physiology,



**Genotype, Fig. 1** Punnett square showing the genotypes of offsprings when parents have the same genotype

and morphology due to its adaptation to a unique environment. There is another contrasting term as compared to phenotypic plasticity, known as genetic canalization which explains about the extent to which an organism's phenotype allows conclusions about its genotype.

## Cross-References

- [Dominant](#)
- [Gene Pool](#)
- [Phenotype](#)
- [Recessive](#)

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## Genotypic Ratio

- [Genotype](#)

## Genus

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## Definition

**Genus** is a Latin word, which was popularized by Swedish scientist *Linnaeus* in his 1753 *Species Plantarum*. But “the founder of the modern concept of genera” is a French botanist *Joseph Pitton*

*de Tournefort* (1656–1708). “Genus” (plural “genera”) is a principle taxonomic classification, which lies in between the family above and the species below and comprising of species that are structurally or phylogenetically related to each other or an isolated species.

## Introduction

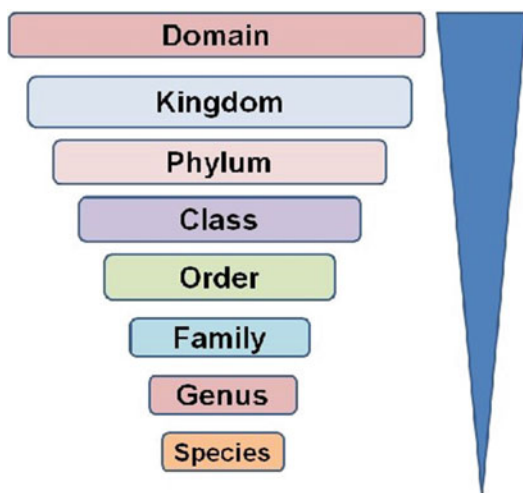
### Taxonomy/Taxonomic Hierarchy

*Carolus Linnaeus* (1707–1778), a Swedish botanist, first used the term Systematics, which is defined as the study of various organisms' identification and relationships. Later during the eighteenth century, “Taxonomic Hierarchy” was introduced by *Linnaeus*, a unique classification system of all living organisms. The classification given by him is being pursued all around the world now. Linnaeus is considered the father of modern taxonomy and classification. AP De Candolle gave the term “Taxonomy” **in the year 1813**, which is derived from an ancient Greek word “taxis” meaning arrangement and “nomos” meaning law or method (Kotpal 2013). Taxonomy is a scientific method of naming, describing, and classifying all living organisms (plants, animals, and microorganisms) in an ordered system that indicates natural relationships. In simple words, “Taxonomic hierarchy is defined as the process in which various organisms are arranged into successive levels of the biological classification either in a decreasing or an increasing order from kingdom to species and vice versa” [Fig. 1] (The Editors of Encyclopedia Britannica 2017). Taxonomy is one of the oldest most fundamental branches of biology. New species of animals and plants are being identified every day, and their classification and characters are studied with the help of taxonomy.

### Taxonomic Rank/ Category

Carl Linnaeus also developed a binomial nomenclature system of animals and plants in his first remarkable publication, “*Systema Naturae*” **in 1735** (Kapoor, 1998). This book is known as the “dictionary of classification.” Linnaeus used some taxonomic ranking or levels under this





**Genus, Fig. 1** Showing taxonomic hierarchy categories

classification, which included *kingdom*, *phylum*, *class*, *order*, *family*, *genus*, and *species* (Fig. 1). Also, Carl Woese proposed another level named the *domain*, a crucial rank now being used widely. Each level of the hierarchy is called the taxonomic category or rank, where the highest rank is given to the kingdom and the lowest rank given to the species. Before Linnaeus, the classification of organisms was somewhat arbitrary, and organisms were often given long names that could be easily altered, making it more difficult for different biologists to understand what species they were referring to. Linnaeus was the first to formulate the classification based on the organism's similarities and designate the binomial system (*genus* + *species*) to classify organisms (Kaburu 2017).

## Binomial Nomenclature

The writing system of all the organisms on earth, living or extinct, introduced by *Linnaeus* is known as "Binomial Nomenclature" or a two-term name. This nomenclature is a unique method of naming organisms and includes two Latin words. The first word of the name belongs to the genus; another word belongs to that specific animal or plant and is called species. Thus the second word is used to

**Genus, Table 1** Showing an example of taxonomic hierarchy

| Taxonomic hierarchy | Example (Human being- <i>Homo sapiens</i> ) | Example (Tiger- <i>Panthera tigris</i> ) |
|---------------------|---------------------------------------------|------------------------------------------|
| Domain              | Eukaryota                                   | Eukaryota                                |
| Kingdom             | Animalia                                    | Animalia                                 |
| Phylum              | Chordata                                    | Chordata                                 |
| Class               | Mammalia                                    | Mammalia                                 |
| Order               | Primates                                    | Carnivora                                |
| Family              | Hominidae                                   | Felidae                                  |
| Genus               | <i>Homo</i>                                 | <i>Panthera</i>                          |
| Species             | <i>Sapiens</i>                              | <i>Tigris</i>                            |

separate each of the species within the same genus. We can use some examples to understand the binomial nomenclature: a very popular bird in India called Gauraiya is named as *Passer domesticus*, the dog is named as *Canis familiaris*, the housefly is *Musca domestica*, and the scientific name of human beings is *Homo sapiens* – genus name is *Homo* ("human being" in Latin) and the species name *sapiens* ("wise"), and it designates all living humans (and their extinct direct relatives); it comes under family Hominidae (Sigwart et al. 2018) (Table 1).

There is a difference between a binomial name and a common or vernacular name. Vernacular name is not standardized and varies by location, whereas binomial name is standardized and is accepted worldwide for the nomenclature of plants and animals. There are different organizations which deal with the nomenclature of animals like ICZN (International Code of Zoological Nomenclature), and body or organization dealing with the nomenclature of plants, algae, and fungi is ICNafp (International Code of Nomenclature for Algae, Fungi and Plants); earlier it was called ICBN (International Code for Botanical Nomenclature). For prokaryotes nomenclature, it is ICNP (International Code of Nomenclature of Prokaryotes); previously, it was called ICNB, i.e., International Code for Nomenclature of Bacteria. The body for the nomenclature of viruses is ICTV (International Committee on Taxonomy of Viruses) (Narendran 2006).

## Rank: Genus

The words species, genus, and family were first used by **John ray**. In taxonomic classification, “genus” is one of the levels used to classify various organisms, including viruses (ICTV Taxonomy 2018). Genus consists of a group of related species with more characters in common than species of other genera. We can say that genera are aggregates of closely related species (Kotpal 2013). For example, potato and brinjal are two different species, but both belong to the genus *Solanum*. Lion (*Panthera leo*), leopard (*P. pardus*), and tiger (*P. tigris*) with several common features are all species of the genus *Panthera*. Genus *Panthera* belongs to the family *Felidae*. This genus differs from the genus of cats *Felis*. If we consider common characteristics, for example, in genus pine (*Pinus*), all the trees would have hard, woody cones with tough, thick scales and long, narrow needles in bundles.

According to modern biological [taxonomy](#), genus lies between species below and the family above (Fig. 1). In binomial nomenclature, each name has two components – the generic (genus) name and the specific epithet. Hence genus represents the first name in the scientific names used for naming any organism around the world. Sometimes between family and species, other categories also are used, such as subgenus (below genus) and subfamily (above genus). The genus name is always capitalized and italicized. For example, mango’s scientific name is written as *Mangifera indica*, where genus is represented by its first name *Mangifera* and second name *indica* represents species or a specific epithet. However, taxonomists define the genus composition for the scientific name of any organism.

## Genus: Two Types

- **Monotypic:** When a genus consists of only one species, then it is known as a monotypic genus. For example, the sea turtle hawksbill is the only member of the genus *Eretmochelys*.
- **Polytypic:** When a genus consists of more than one species, it is known as a polytypic genus.

For example, the genus *Panthera* includes both lion and tiger.

## Use in Taxonomy

Genus is the first name of any organism according to binominal nomenclature, which helped taxonomists to name and classify various animals and plants including viruses and prokaryotes.

### Type Genus

The type genus is the [genus](#), which determines the name of the family or subfamily in biological classification. It is the largest or best-known or earliest-described criteria, although not necessarily the most representative genus. The type genus is commonly used for zoological nomenclature and not used unofficially for the nomenclature of plants where “type genus” is used as a convenience ([ICZN Code art](#)).

### Type Species

In zoological nomenclature, type species is the name of the species, with which the name of a [genus](#) or subgenus is thought to be associated taxonomically, i.e., the species that contains the biological type specimen (International Code of Zoological Nomenclature 1999). Type species is used to describe a genus, mainly modified and expanded by the features of other included species.

## Cross-References

- [Nomenclature](#)
- [Origin of Species](#)
- [Taxa](#)

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## Geographic Speciation

### ► Allopatric Speciation

## Geometric Encoding

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## Synonyms

Global geometry; Local geometry; Spatial reorientation

Successful movement between locations first requires the determination of a direction of travel, and understanding the process of determining a direction is the central focus of orientation research. As shown in the top panel of Fig. 1, the general approach to understanding orientation involves training disoriented participants to respond to a particular location within a rectangular enclosure (left). Importantly, this location is often uniquely specified by a distinctive feature. Interestingly, tests in the absence of the distinctive features reveal that participants not only respond to the originally trained location but also to its 180° rotationally equivalent location (right).

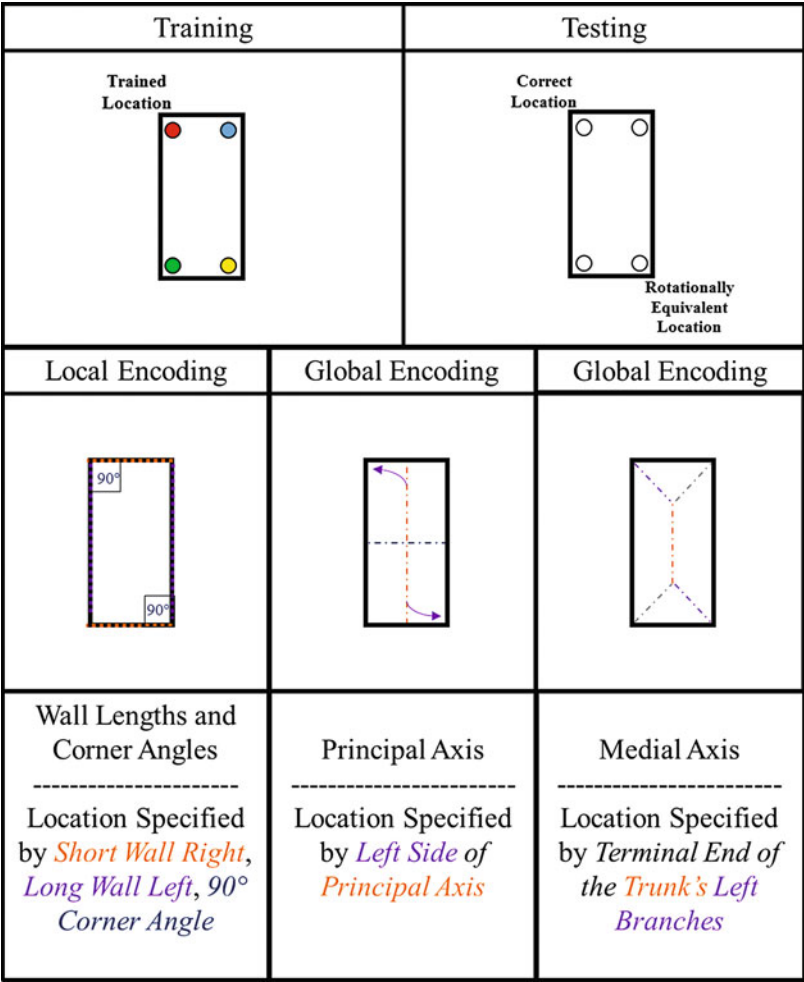
Responses to this 180° rotationally equivalent location are termed a *rotational error* (for a review, see Cheng et al. 2013).

The occurrence of the rotational error is particularly interesting because it suggests that participants learn something about the geometric shape of the enclosure itself during training, and such learning about the geometric shape of the enclosure during training is unneeded because it is neither necessary nor sufficient to determine the correct location (for a review, see Cheng et al. 2013). Specifically, the correct location is uniquely and sufficiently specified by the distinctive feature; yet in its absence, participants respond as if they learned the correct location with respect to the environmental shape, and the rotational error is suggested to occur because, in the absence of the distinctive feature, environmental geometry alone cannot disambiguate the correct from the rotationally equivalent location.

The occurrence of the rotational error has been observed in ants, chicks, pigeons, fish, and primates – including human children and human adults (for a review, see Cheng et al. 2013). In human adults, the rotational error also occurs in a sensory modality other than vision (Sturz et al. 2014). Specifically, blindfolded adults trained to respond to a particular corner of a rectangle designated by a unique texture respond to the trained and rotationally equivalent locations when the unique texture is absent. This occurrence across species and sensory modalities suggests that orientation via geometric cues may be a ubiquitous and fundamental process in the animal kingdom (see Tommasi et al. 2012). As a result, determining the nature of this geometric encoding – environmental points, lines, angles, and overall shape to determine a direction – has received considerable research attention (see Sutton 2009), and manipulations of shape from training to testing have revealed two basic categories of geometric cues used during reorientation: *local geometric cues* and *global geometric cues* (see Bodily et al. 2011; Lubyk et al. 2012; Sturz et al. 2012; for a review, see Sutton 2009). Both types of cues explain the presence of the rotational error but differ with respect to what is encoded about environmental geometry.

**Geometric Encoding, Fig. 1** *Top Panels.*

Illustration of the Training and Testing components of the reorientation paradigm. *Bottom Panels.* Illustration of local and global geometric encoding strategies



As shown in Fig. 1 (bottom left), local geometric cues are independent cues such as wall lengths and corner angles that constitute the environmental shape (see Miller and Shettleworth 2007). Thus, local geometric encoding would involve encoding the correct location during training as a location specified by short wall right, long wall left, and 90° corner angle. Such local geometric encoding during training explains the occurrence of the rotational error during testing because both the correct and rotationally equivalent locations are located at the right side of a short wall, the left side of a long wall, and at a 90° corner angle. In contrast, global geometric cues (often derived from computational geometry) are dependent on the overall shape of the environment because they must be encoded from the overall shape of the environment (see Sturz and Bodily 2012). For

example, the principal axis of space, which runs through the centroid and approximate length of the space is a summary parameter derived from the boundaries (see Sturz et al. 2011). Thus, global geometric coding with respect to the principal axis would involve encoding the correct location during training as the location specified by the left side of the principal axis. Such global geometric encoding during training explains the occurrence of the rotational error during testing because both the correct and rotationally equivalent locations are located at the left side of the principal axis. Similarly, the medial axis of space which is a trunk and branch system that captures overall shape information is also derived from the boundaries (see Kelly et al. 2011). Thus, global geometric encoding with respect to the medial axis of space would involve encoding the correct location

during training as the location specified by the terminal end of the trunk's left branch. Such global geometric encoding during training explains the occurrence of the rotational error during testing because both the correct and rotationally equivalent locations are located at the terminal end of the trunk's left branch.

Despite recent debate about which global geometric cue may be encoded (see Sturz and Bodily 2012), it is clear that both local and global geometric cues are encoded and used for orientation (see Cheng et al. 2013). As importantly, it is also clear that a sense component (i.e., left or right) is part of this encoding process (see Sovrano and Vallortigara 2006). Current research is continuing to manipulate aspects of the environment from training to testing to further illuminate the geometric cues used to reorient with respect to the environment.

## Cross-References

- [Cognitive Map](#)
- [Encoding](#)
- [Geometric Module](#)
- [Landmark](#)
- [Navigation](#)
- [Orientation](#)
- [Place Versus Response Learning](#)

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## Geometric Illusion

- [Delboeuf Illusion](#)
- [Ebbinghaus Illusion](#)
- [Ponzo Illusion](#)

## Geometric Module

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The concept of cognitive modularity is crucial to our understanding of the architecture of the mind. One view is that psychological processes such as learning, perception, memory, and judgment are *domain general* such that they are able to interact

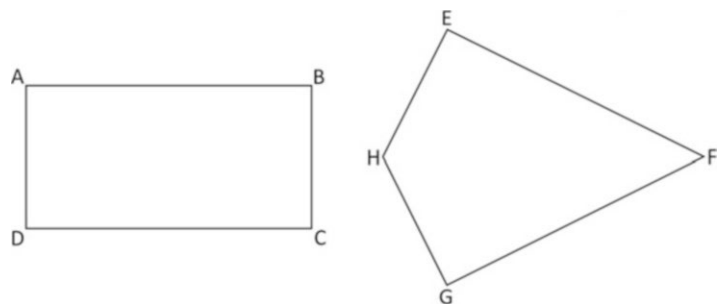
with and influence one another. Others argue, to a lesser or greater degree, that the mind is composed of independent *domain-specific* processing modules. Fodor (1983) argued that some perceptual processes follow this modular architecture but that cognitive processes were largely nonmodular. One characteristic of a module is that the information it processes is *encapsulated*; that is, the module is impenetrable to information stored centrally elsewhere, and the central store of information has limited access to the information processed by the module. Thus in an encapsulated module, processing of information is largely independent of information processed elsewhere. A classic example of this kind of modularity is in visual illusions. A person may know the reasons for the illusion but is unable to prevent themselves from experiencing it.

An apparent example of a cognitive process being under the control of an encapsulated module came with Cheng's (1986) influential study on spatial cognition in rats. Rats were placed into a rectangular box that contained food in one of its corners. After finding and eating some of the food, the animals were removed from the box before being replaced and given the opportunity to eat the remainder. In the original study, the rats were replaced in an identical box that differed in its orientation to the first (e.g., rotated 90° clockwise). In later studies, the animals themselves might be disoriented through slow rotations in the dark to achieve inertial disorientation and replaced in the same box. Despite visual and/or odor cues (termed *featural* or *nongeometric*) that could be used to distinguish the ambiguous corners of the rectangle, the rats appeared to ignore these and use only the geometric properties of the

box to relocate the food. This led to the rats searching in the correct corner and also in the diametrically opposite but geometrically equivalent corner. The result was interpreted in terms of a primacy for the use of geometric information over featural information. Because the rectangle was geometrically ambiguous, with two corners that are identical in terms of the arrangement of long and short walls (e.g., corners A and C in Fig. 1), when the animals reoriented, they chose the two geometrically equivalent corners equally – a quirk of the shape selected. This result was replicated in a wide range of taxa from fish to humans (reviewed in Cheng and Newcombe 2005) which led to the popular view that many animals possess a geometric module that serves to represent the global geometric properties of the environment. Cheng showed that with repeated training, featural cues were able to gain control over behavior, but he claimed that this representation was “pasted on” to the geometric representation such that the representation is retained without being altered by the representation of the features. Such a geometric module makes sense from an evolutionary perspective. The features of an environment (e.g., foliage on trees) are likely to change over time, but its geometric layout will not, so it may be adaptive to extract information about the broad geometric shape of the environment without interference from more transient featural cues.

Cheng's study has gone on to influence theories of how humans and other animals orient themselves and navigate with reference to the geometric properties of their environments. However, examples of the use of featural cues for reorientation or the failure to use geometric cues even when they are good indicators of a location

**Geometric Module,**  
**Fig. 1** The geometric layout of arenas in Pearce et al.'s (2004) transfer experiment





have cast doubt on the original formulation of the geometric module as a mechanism for rapid cognitively economic spatial orientation (reviewed in Cheng 2008). The geometric module hypothesis supposes that geometric cues should have primacy for control over spatial behavior, and that featural cues should be unable to interfere with learning about geometric cues. One way of testing this is to test for effects known as cue competition. In associative learning, cues that signal important events, such as the delivery of food, are said to compete for control over behavior. For example, a rat might be trained in a Pavlovian conditioning task that a light signals that food is about to be presented. When the light is illuminated, the rat begins to poke its nose into the hole where the food drops, in anticipation of the food. If another rat were to be trained similarly, but with both a light and a tone signalling the food, it would be expected to learn something about the significance of the light, and something about the significance of the tone. Crucially, however, what is learned about the light restricts what is learned about the tone, and vice versa, indicating that the cues compete for control over the nose-poking behavior. We can test this by presenting both rats with a light and recording the number of nose pokes. Cue competition is said to have occurred if the rat trained with both the light and the tone nose pokes less than the rat trained with the light only.

Attempts to examine these cue competition effects in geometry learning at first met with null results, in line with the geometric module hypothesis. Animals appeared to have learned about geometry regardless of the presence of nongeometric features. However, demonstrations of two forms of cue competition – overshadowing, as described above, and blocking, in which learning about one cue (e.g., a light) in a prior stage subsequently restricts, or blocks, learning about an additional cue (e.g., a tone) when the light and tone are presented in compound – followed in mountain chickadees (*Poecile gambeli*) and laboratory rats when a colored wall restricted learning based on geometry, compared with animals that were only able to rely on geometry (review in Cheng 2008).

Perhaps surprisingly, it was also found in rats that under some circumstances the non-geometric feature actually facilitated learning about geometry (Pearce et al. 2006). Neither of these results was predicted by the geometric module hypothesis, but the latter was also a surprise in terms of the prediction of cue competition. Subsequent work showed that non-geometric and geometric cues come to be associated with one another during training in a within-compound association. The presentation of one cue evokes a memory of the other, which drives responding. The salience of the nongeometric and geometric cues is key to whether cue competition or cue facilitation will be detected. If cue competition is weak because the nongeometric feature is not very salient, then the opposing action of the within-compound association is more readily detected and geometry learning will appear to be facilitated. If cue competition is strong, then the within-compound association will be unable to counteract its effects. Thus results from cue competition studies appear to support an associative domain-general analysis of geometry learning and not a modular account.

Another aspect of the geometric module hypothesis is its characterization of the representation of geometry. Cheng (1986) described his findings in relation to rats encoding the shape of the environment via a metric frame, which has subsequently been allied to the notion of a cognitive map that takes its inputs from the geometric properties of the environment (Doeller and Burgess 2008). A cognitive map is difficult to define, but it could be said to be an internal representation of the global geometric relations among stimuli in the environment, used for navigation through the environment. In these terms, the geometric module should be responsible for forming a representation of the overall shape of the environment. Pearce et al. (2004) tested this idea by training rats to find a submerged platform in one corner (e.g., corner A in Fig. 1) of a rectangular water maze. The water maze was surrounded by curtains and rotated by either 90, 180, or 270° between trials. The point of release also varied between trials, so rats were required to reorient

using some aspect of the geometry of the arena in order to identify the correct corner. Following this training, the overall shape was altered to that of a kite, which contained one corner with the same arrangement of long and short walls as the correct corner of the rectangle (e.g., corner E in Fig. 1), and one with the mirror opposite arrangement of walls (e.g., corner G).

Rats transferred their behavior across the arenas, searching in the corner that shared the same local geometric properties as those of the correct corner in the rectangle. Pearce et al. (2004) argued that rats had relied on a more local representation of space and claimed that an appeal to a global representation was unnecessary. However, their findings did not necessarily rule out that rats were able to use a global map-like representation because the opportunity to act on such a representation was removed by transforming the overall shape. Recently, results in humans (Buckley et al. 2016) have suggested that a global representation of shape is maintained despite performance in a transformed arena that indicated reliance on a local representation of geometry as found by Pearce et al. (2004). Buckley et al. trained human participants to navigate to a target location within a computer-generated arena in the shape of a rectangle. At the end of training, they were transferred to the outside of the arena and asked to go to the location that was closest to the target when they had been on the inside. If the arena in the test trial was the same overall shape as during training, then participants were able to perform accurately. However, if the overall shape had been transformed to that of a kite participants performed at chance, despite the same local geometric cues being present in both test trials. The results are best explained by reference to a global geometric representation. As yet, such a test has not been conducted in nonhuman animals.

The notion of a geometric module is not entirely refuted by the results described above. Evidence of a geometric module in humans is still widely debated, with some arguing that geometric cognition is one of suite of core knowledge components in human cognition (Spelke and Kinzler 2007). Spelke and her colleagues have

put forward a modified version of the geometric module hypothesis that includes information about distance and direction based on surfaces surrounding the environment, but not angle or length, which instead are processed by a landmark system that is responsible for the representation of smaller objects. Cheng et al. (2013) have challenged these claims based on the plausibility of a geometry system that is so selective in the cues that it processes, and the evolutionary advantage such a system would deliver. They also pointed to a wider range of literature than was considered by Spelke and colleagues, including findings from animals. Others have considered the neural systems that process spatial information and concluded that there is a hippocampus-based system for processing boundaries, and a separate striatal system for landmarks (Doeller and Burgess 2008). In common with the geometric module hypothesis, this account predicts that learning based on the geometry of the arena should be unrestricted by learning based on landmarks, but it differs in that it is concerned less with reorientation and more with the representation of location. Ultimately, these accounts of the role of geometric information in spatial cognition demonstrate the limited scope of the geometric module hypothesis: they either reconceptualize the hypothesis so that they constrain the type of information processed in the module, based on a limited corpus of data, or they expand the role of geometry to support a wider range of behaviors (i.e., in navigation to locations) than originally hypothesized. What becomes clear is that it is necessary to apply the role of geometry in spatial cognition more widely than is envisaged within the original modular hypothesis and to consider whether a modular cognitive architecture is necessary to explain apparent independent cognitive processes.

## Cross-References

- [Associative Learning](#)
- [Cognitive Impenetrability](#)
- [Cognitive Map](#)
- [Geometric Encoding](#)
- [Spatial Orientation](#)

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- cognition in animal species (ranging from unicellular organisms to humans). Romanes was also an innovator in the study of the anatomy and physiology of simple nervous systems in marine invertebrates including jellyfish, starfish, and sea-urchins. He suggested that the origination of new species could arise not only through Darwin's mechanisms of natural selection and sexual selection but by a third mechanism he called "physiological selection."

The first part of this entry is a sketch of Romanes's life and background. His research on the nervous systems of invertebrates and his view on physiological selection are covered in this first part. The second part is an account of his theory of the evolution of intelligence in humans, moving progressively from animal to human cognition (including language). The third part outlines some issues in the secondary literature concerning the scientific reception of his ideas.

## A Sketch of Romanes's Life

Romanes's Scottish lineage is traced back to 1586 and to a region southeast of Edinburgh. But we start in 1834, when his father, George Romanes, emigrated to Canada. Romanes was born on 2 May 1848, at 207 William Street, Kingston, Ontario. His father moved into this house in order to teach at Queen's College (now Queen's University). Prior to the move, his father was an Anglican minister in small Ontario parishes not far from Kingston. In Romanes's time, the house was part of the fledgling University that was founded in 1841, and it was here that Romanes's father was a professor of Classics. Protestant Christianity was a prominent part of Romanes's background; not only was his father Anglican, but his mother, Isabella Gair Smith, was the daughter of a Scottish Presbyterian minister. She maintained her Scottish roots and Romanes was later able to establish a laboratory for his "neuroscientific" research in her family house (called "Geanies") at Dunskaith in Scotland, located just north of Inverness, on the North Sea coast, a rich source of marine life. Romanes had three surviving siblings, namely, an older brother James, an

## George Romanes

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## Introduction

George John Romanes (1848–1894) was an illustrious member of Darwin's circle and a pioneer in the study of the evolution of behavior and

older sister Georgina, and a younger sister Ethel, who later assisted him in some of his behavioral research.

In 1849, his father received information of an inheritance, the wealth having accrued from a family business dealing in Scottish fabrics and textiles. On the same day, the house on William Street was seriously damaged by fire. The Romanes family moved back to Britain in 1850, where they settled in London.

After Romanes entered Gonville and Caius College, Cambridge, in October 1867, he studied mathematics and religion (he originally intended to become a clergyman). He turned to physiology 3 years later under the tutelage of Michael Foster (1836–1907), famed for his work on embryology and on the history of physiology. The importance of Foster's laboratory for the history of science in general has been outlined by Geison (1978). Geison explained that the founding of new laboratories for physiology, and also for physics, at the University of Cambridge was motivated by the fear that Britain was falling behind Germany in the publication and institutionalization of scientific research.

Romanes's first influential experimental research, carried out in Scotland as well as in Cambridge, was on the primitive nerve-nets of jellyfish. In his research on jellyfish, he suggested that the nerve fibres "cross and re-cross one another without actually coalescing" (Romanes 1896/1898, p. 19), a conjecture later substantiated by his physiologist friend E. A. Schäfer. These investigations were the first to establish that jellyfish had a primitive nervous system; they have also been argued by Lesch (1976, p. 517) and Geison (1978, pp. 244–249) to anticipate the discovery of the synapse in the 1890s.

In other research, Romanes investigated the effects of injuring and stimulating the nerves of starfish. He showed that the nervous system in starfish is much more sophisticated than it is in jellyfish, because injury or stimulation of the jellyfish's nerve-net caused a reaction of the whole organism, whereas injury or stimulation of the starfish's nervous system caused movements that could be restricted to a particular body part such as one of the arms. During the

course of this research, Romanes concluded that the key to an understanding of the evolution of intelligence in the animal kingdom resided in appreciating the increasingly specialized role of individual subsets of nerves. This belief, particularly, pertained to enhanced sensory discrimination and the refined coordination of movements. His various articles on invertebrate neuroscience, dating mainly from 1876 to 1881, were summarized in *Jelly-Fish, Star-Fish, and Sea Urchins* (Romanes 1885).

Romanes was also caught up in the excitement over *The Origin of Species* (Darwin 1859/2004), published when Romanes was 11. He was also inspired by its sequel, *The Descent of Man* (Darwin 1871/1899), published 1 year after Romanes had commenced his physiological investigations at Cambridge. A letter to *Nature* (Romanes 1873), written while he was engaged in marine research at Geanies, concerned the evolution of the variety of shadings found in flatfish such as plaice and sole. This letter attracted the attention of Darwin himself, who arranged for a meeting with Romanes. From then on, the two were close friends and colleagues. They frequently visited each other and, in 1881, when Darwin sensed that his death was not far off, he sent Romanes an article titled "A Study of Instincts" for publication as an Appendix to Romanes's book, *Mental Evolution in Animals* (Romanes 1883). Romanes was the last person Darwin called on in London before being confined, because of his terminal illness, to his house in the Kent countryside (Atkins 1974, p. 93).

Romanes moved to London in 1874, where he continued to study physiology under William Sharpey (1802–1880) and John Burdon-Sanderson (1828–1905) at University College. He remained in London for the next 16 years, becoming a Fellow of the Royal Society in 1879, at the age of 31. In that same year, he married Ethel Duncan (1856–1927) of Liverpool and settled into a house a few doors down from the house his father moved into in 1850; they had six children. While he resided in London, he wrote his three contributions to comparative psychology, namely, *Animal Intelligence* (Romanes 1882),

*Mental Evolution in Animals* (Romanes 1883), and *Mental Evolution in Man* (Romanes 1888).

During the last part of his life, Romanes put forward his new mechanism for animal speciation, which he named “physiological selection.” He suggested that two parents of the same species might possess, in their hereditary transmission materials, a physiological anomaly, one that by chance was roughly identical in the two parents. The offspring of such parents might then possess an anomalous anatomical or physiological characteristic. This characteristic is sufficiently divergent from the parents’ own characteristics for the offspring (who are assumed not to be sterile) to be the start point of a new species. Clearly these views predated genetic theory. It is of great interest that Forsdyke (2001), while working on viruses, came to believe that Romanes’s idea, rejected in his own time, was prescient of modern genetics.

In 1890, Romanes moved to Oxford, partly to take advantage of the new physiological laboratory there, and partly because he felt oncoming ill health. He and his family occupied a sixteenth-century house opposite the imposing gateway of the largest Oxford college, Christ Church. Later, he became a member of this college. In 1892, he was elected to be an honorary member of his old college at Cambridge, Gonville, and Caius College. At Oxford, he made friends with several clergymen including the Rev. Charles Gore and the Rev. Aubrey Moore, as well as his friend from childhood the Very Rev. Francis Paget. Shortly after arriving, he tried to persuade the university to offer an honorary degree to Francis Galton (1822–1911). He also provided funding for a Romanes Lecture to be delivered at Oxford annually.

Early warnings that Romanes was suffering from a brain disorder included headaches, disturbed vision, and a temporary left hemiplegia. Schwartz (2010, pp. 679–680) tentatively supported Forsdyke’s conclusion that Romanes suffered from a brain tumor. Romanes was advised by doctors, among whom was the neurologist Hughlings Jackson (1835–1911), to stop working. In a letter he claimed he was advised to make his “rule of life” that of a “tortoise”

(Romanes 1896/1898, p. 346). He spent time in Bohemia, Bavaria, Madeira, and the south of France in order to convalesce. During this period, he elaborated on some writings about religion he published as a student. He prepared notes for a projected book to be titled *A Candid Examination of Religion*, published under the pseudonym “Metaphysicus”; these notes were edited by Rev. Charles Gore and appeared posthumously as *Thoughts on Religion* (Romanes 1895). He also accepted frequent visits from his clergymen friends during his final months. On 23 May 1894, at the age of 46, he had a cerebral hemorrhage, from which he died within 1 h. He was buried at Holywell Cemetery (Plot E. 225) in Oxford. He is memorialized in a window in the chapel of Gonville and Caius College, Cambridge.

Summaries of his life and correspondence are provided by E. R. Romanes (1896/1898) and Schwartz (2010). An invaluable account of Romanes’s contributions to neuroscience and to genetics is provided by Lesch (1976), who lists several locations containing archival materials. Summaries of Romanes’s achievements as a comparative psychologist are provided, among others, by Boakes (1984, Chapter 2), Richards (1987, Chapter 8), Murray (1988, pp. 261–271), Wozniak (1999), and Thomas (2012). Brief outlines of his views on the evolution of language are provided by Romanes (1889/1897) himself, Carter (1899), and Kroll (1986).

## Romanes’s Theory of the Evolution of Human Intelligence

In *Animal Intelligence*, Romanes (1882) collected evidence of the kinds of problems that individuals of a wide variety of species were capable of solving. Most of the accusations that Romanes relied too heavily on anecdotal evidence, or was anthropomorphic in his explanations of animal behavior, are based on passages from the last half of *Animal Intelligence*. We know, however, that Romanes preferred to collect experimental data on animal behavior rather than rely on anecdotes. Indeed, in his wife’s biography of him, she stressed that

some anecdotes were rejected from the book because Romanes felt that the evidence was questionable (Romanes 1896/1898, pp. 200, 207). About half the book was devoted to invertebrates such as marine animals and insects. Their small size, rapidity of breeding, and ease of upkeep allowed earlier investigators to experiment on the abilities of these creatures to adapt to unusual environments or to overcome obstacles. Anderson (2001) reviewed some of this Victorian research on insect behavior. She demonstrated how it influenced the way in which some scientists conceptualized animals as being more “machine-like” than humans.

Romanes also reported on the learning and problem-solving abilities of birds and mammals, up to and including the primates. He carried out some experimental work with monkeys (both at the zoo and in his sister’s house); he was one of the first to describe how a monkey responded on seeing itself in a mirror (Romanes 1882, pp. 478–479, 495–496). In his chapter on dogs, he discussed an experiment by Darwin apparently showing that a dog could “recognize” Darwin after not seeing him for 5 years (p. 438). He also related an anecdote sent to Darwin from Canada indicating that dog teams pulling sleds would fan out over the ice on a lake in order to distribute their weight more evenly (p. 482).

In *Mental Evolution in Animals*, Romanes (1883) put forward a theory of the evolution of problem-solving behavior and of learning abilities; this theory depended on the assumption that the more sophisticated a species was at problem-solving and learning, the more highly developed its nervous system. He asserted that a high level of development in the nervous system could be displayed in terms of three main characteristics. First, there was the ability to experience a wide variety of emotions; for example, Romanes believed that more advanced animals (e.g., dogs and apes) were capable of experiencing sophisticated emotions such as jealousy, deceitfulness, or vengeance. Second, there was the ability to learn, recognize, and adapt behavior to difficult environmental circumstances; these included tool-using, detour behavior and cooperative behavior. Third, there was the ability to regulate,

control, and plan future actions; for example, whether to fight or flee when confronted by a predator.

This classification of characteristics dovetailed neatly into “emotion, cognition, and conation,” sometimes called “feeling, knowing, and willing,” that was standard in the teaching of psychology by the end of the nineteenth century (see, e.g., Sully 1888). This classification scheme was introduced in the eighteenth century by German-speaking psychologists including Moses Mendelssohn (1729–1786) and J. N. Tetens (1736–1807). Romanes’s scheme was illustrated by a pull-out chart reproduced in full by Boakes (1984, p. 29) and by Murray (1988, pp. 266–267).

The pull-out chart was divided into 50 horizontal levels. Apes and dogs were ascribed intellectual levels located at about level 28. A human baby aged 15 months was speculated to have a brain that had matured to about level 28 as well. The rationale for Romanes’s scheme was as follows. Romanes believed that life originally consisted of organisms possessing only excitability; however, because excitability had different levels of comfort (at the extremes were pain and pleasure), increasing capacities for sensory discrimination and refinement of movement emerged. Both capacities were mediated by “neurility,” that is, by the evolution of a “conductile” nervous system. In primitive animals, the nervous system operated in an essentially reflex-like way. Animals with highly developed nervous systems, thanks to the evolution of a complex brain, were capable of controlling individual body parts.

As a frontispiece to *Mental Evolution in Man* (1888), Romanes reproduced the pull-out chart of *Mental Evolution in Animals* (1883) without any changes. He presented arguments to show that language in humans had evolved naturally and gradually from its origins in animal vocalizations. There was no sharp separation between humans and animals. There was no “Rubicon,” as the Oxford philologist Max Müller (1823–1900) had called it. Müller wrote that “man speaks, and no brute has ever uttered a word. Language is our Rubicon, and no brute will dare to cross it” (Müller 1866, p. 392). The orthodox Judeo-Christian religious view, based on the book of Genesis, was that humans were created, after the animals and



separately from them, in “God’s own image.” Humans were also uniquely endowed with language. Greenblatt (2017) reviews the impact of Genesis on theories of the origin of language. The countervailing view, still unorthodox in Romanes’s time, was that humans were simply another species of animal, and that it was a challenge for science to spell out how language may have evolved in a continuous manner from the vocalizations of animals to the utterances of humans.

The gist of Romanes’s conceptualization of human language was that it differed from animal communication in three particular ways. First, although it is true that human vocal communications and animal vocal communications both use vocal articulations as “signs” that represent some event in reality, humans are able to use vocal signs as signifiers of a much wider variety of events than is the case for animals. In order to explain why this is so from an evolutionary standpoint, Romanes insisted that it was an outcome of the evolution of a human brain capable of a wider variety of cognitive processing than was possessed by the brain of any animal. He stated that the most fruitful approach to a theory of the evolution of language begins with cognitive psychology, rather than with a study of grammar or another subdiscipline of linguistics. The same viewpoint is maintained by modern writers on the evolution of mind (e.g., Paivio 2007).

Second, Romanes claimed that the human brain had attained a level of cognitive development that allowed its owner to think about (and represent in language) events and things not present in the here-and-now. Although it may appear that few animals have this capability to the same extent as humans, there is evidence that suggests that some animals (notably dogs and primates) do have an elementary form of this ability (Suddendorf and Whiten 2001). The stimuli that humans can respond to are divided into (perceptual) stimuli that are currently present and (memory) representations of stimuli that are not currently present. From a language point of view, Romanes contended that the invention of certain *words* facilitated communication between humans about present events and past events.

Third, Romanes suggested that another way in which human cognitive development differs from

that of animals concerns the conceptualization, by a human, of his or her self. The study of cognitive development in humans indicates that somewhere around the age of 2 or 3, the typical human infant develops a “sense of self,” by which is here meant “self-consciousness.” One of the effects of becoming self-conscious is that one vastly enhances the number of possible stimuli that can be represented in memory and thereby linked with one’s self-concept.

Romanes used memory as a unifying device for developing a consistent model of the above relationships between cognitive and linguistic competence. In a brain that has developed minimal memory, a sensation aroused by a present stimulus quickly dies away when the stimulation stops. Sometimes, however, the sensation persists in a form of “sensory after-effect.” At more advanced levels of development, memory becomes sophisticated enough for the animal to detect that two successive stimuli are different. Romanes believed that, at a slightly more advanced level, an animal could detect that two successive stimuli were identical. When an animal sees that two successive stimuli are identical, and also remembers the emotion associated with the earlier stimulus, a major step forward is taken in the evolution of memory. It allows a bird not to eat a particular caterpillar because, when it had seen the same kind of caterpillar before and eaten it, the experience was aversive. It allows a deer to remember that the last time it was in a certain thicket, it was threatened by a predator. When a given stimulus situation is associated with a particular emotional response, and the situation is repeated in the animal’s experience, the repeated situation (which is in the here-and-now) can elicit a learned emotion.

Romanes argued that English language was lacking a convenient scientific term for this kind of associative memory. In everyday speech, the term “percept” was appropriate for describing what an animal or human experienced while sensing events of the here-and-now. The term “concept” was appropriate for describing what a human adult experienced while thinking about events not in the here-and-now or about abstract ideas. There was, however, no convenient word to describe what an animal or pre-linguistic human

baby experienced when something in the here-and-now elicited an emotional memory. So Romanes (1888), in Chapter 3 of *Mental Evolution in Man*, invented the word “recept” to refer to this intermediate stage of ideation.

Romanes divided recepts into two broad categories. Lower recepts comprised what we now call conditioned emotional responses. They are shared by animals and by pre-linguistic human infants. Higher recepts are special cases of learned responses in which situations can evoke vocal responses that indicate that a child can remember, not only that a situation had occurred but that it was associated with the learning of one or more words. For example, a child may see her sister and a cat simultaneously in the room. She has learned words for “sister” and “cat,” and can say aloud those words. These are learned responses of a verbal, rather than an emotional, kind. This is the level of development that Romanes called “pre-conceptual” and is typically found in a 2- or 3-year-old child. It is not found in animals. The question of whether a parrot, who has learned a given sound in a given situation, is using language, was discussed in depth by Romanes; he argued that the parrot was demonstrating lower receptual behavior, rather than higher receptual or conceptual behavior. It was, therefore, inappropriate to assert that the parrot possessed “language.”

When a child has acquired the understanding that words stand for objects and starts learning words in order to label situations in the here-and-now, the child is moving into the acquisition of concepts. At this stage, the child is also becoming self-conscious. Romanes linked the “conscious” learning of new vocabulary by a child with the acquisition of a “consciousness” of herself. Moreover, her brain is developing to a level at which words that were used to label situations in the here-and-now could be used in a more sophisticated way, namely, to refer to objects that were perceived in the past but are not present in the here-and-now.

## The Secondary Literature on Romanes

Carter (1899) published a critical account of Romanes’s theory of the evolution of intelligence.

Two of her arguments deserve particular attention. First, she objected that Romanes’s invention of the word “recept,” while in some ways welcome, was not defined rigorously enough to form a solid foundation for a theoretical superstructure as detailed as was Romanes’s. It can be added that the various subclassifications of kinds of recepts that were included in *Mental Evolution in Man* were difficult for readers to grasp and retain. This was acknowledged by Romanes (1889/1897) himself.

Second, Carter (1899) pointed out that Romanes often narrated anecdotes about individual problem-solving achievements in infrahuman species. Carter suggested that this led him to imbue animals with high levels of problem-solving or emotional intelligence. Knowledge of an animal’s prior history has to be available before a claim can be made that the animal is unusually gifted at problem-solving. In many textbooks of introductory psychology, or of comparative psychology, published in the twentieth century, Romanes was castigated for being “anthropomorphic,” that is, for being too ready to ascribe human-like intelligence to animals. In the twenty-first century, however, researchers have been more lenient in accepting that anecdotal evidence can sometimes validly be used as evidence of a high level of cognitive competence in animals (De Waal 2019; Godfrey-Smith 2016, Chapter 6).

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- [C. Lloyd Morgan](#)
- [Charles Robert Darwin](#)
- [Evolutionary Psychology](#)
- [Speciation](#)

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## Georgia State University's Language Research Center

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The Language Research Center (LRC) is a primate-research facility operated by Georgia State University (GSU). Physically located on over 55 acres of forested land near Atlanta, GA, USA, the LRC has provided resources for the noninvasive, longitudinal study of behavior and cognition of nonhuman primates, primarily resident colonies of chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Sapajus apella*). These animals participate voluntarily in behavioral research (they are not deprived of food or fluid for purposes of testing, nor are they exposed to aversive conditions to make them work). Additionally, the LRC has supported comparative research with human adults and children – including intervention research, for example, with youth with developmental disabilities – throughout its history.

Scientists from psychology, neuroscience, biology, anthropology, philosophy, linguistics, computer science, and other departments within GSU, and from dozens of other universities worldwide, study the unique animals at the LRC on a wide range of topics. (Note: Humans are animals, primates, and apes too; however, these terms here will refer to nonhuman animals, primates, and apes.) What makes these animals particularly interesting to researchers are the training histories and testing experience that each possesses. This includes, in the case of some of the apes, symbolic-communication training that has yielded competencies in comprehension and production that both advance understanding of what organisms can do with language that they could not do without it, and also challenge the uniqueness of human competencies in language and other domains. Working with academic departments at GSU and other institutions, the LRC also serves an educational mission, allowing students at the undergraduate, graduate, and postdoctoral levels to learn about primates and the methods of noninvasive primate research at the behavioral, social, cognitive, neural, biological, and ecological levels of analysis. LRC student and faculty scholars have also reported findings that educate the public through the popular media (print and electronic) and in textbooks and other educational materials for children, youth, and adults, in a large number of languages and cultures. Among these findings are principles of psychological well-being in nonhuman and human primates; that is, a primary aim of LRC scientists has always been to understand and to promote psychological health in humans and in the non-human animals that partner with those scientists in the pursuit of discovery.

## History

The LRC was founded in 1981, but its roots extend a decade earlier. Two of the most important individuals in this history were a comparative psychologist named Duane M. Rumbaugh and a chimpanzee named Lana, who was the focal participant in the Language ANalog (LANA)

Project, established by Rumbaugh and a team of collaborators at the Yerkes Regional Primate Research Center, Emory University (Atlanta, GA, USA). In 1970, Rumbaugh, then the Associate Director and Chief of Primate Behavior at the Yerkes Center, proposed an innovative investigation of whether apes could learn and use a human-like language. Although this question had been studied by others (Hillix and Rumbaugh 2004), Rumbaugh believed that an unparalleled level of experimental control over training and potential confounding variables could be achieved by automating language training through the use of computers, which were still a relatively new technology. Working with a biomedical researcher, computer programmer, electronics technician, psycholinguist, research technicians, and a developmental psychologist, Rumbaugh developed a computer-based keyboard system in which each key would be a unique visuospatial symbol (called a lexigram), corresponding to an English word (Rumbaugh 1977). Pressing any key would cause it to illuminate, and the appropriate symbol also to display on a panel of projectors located above the keyboard. Dispensers, televisions, and other devices were connected to the keyboard so that the computer could automatically respond to key-presses by delivering food, dispensing juice, playing music, or whatever action was indicated by the selected keys. However, depression of single keys left too much room for interpretation and potential experimental bias: If a chimpanzee pressed the key for WATER, was the animal requesting water, labeling the liquid on the floor as water, commenting on water it previously received, or something else? To avoid this ambiguity, a grammar (called Yerkish, after Robert Yerkes) was developed to determine the rules for symbol sequences, and a series of stock sentences (e.g., “PLEASE MACHINE GIVE \_\_\_\_\_ PERIOD” where “PLEASE” and “PERIOD” were used to start and end requests, and any number of deliverable objects could be inserted in the blank) became the initial targets of ape-language training.

In 1973 and with funding from the National Institute of Child Health and Human Development (NICHD), LANA Project scientists began

training the 2½-year-old chimpanzee to use the lexigram keyboard. Lana learned to use the symbols and the Yerkish grammar to make requests, to answer questions, to ask questions, to comment, and generally to communicate with the PDP8 computer and the researchers (particularly Dr. Timothy Gill, then a graduate student who served as Lana's primary trainer). Lana's performance quickly garnered attention from both the scholarly community and the public, with reactions ranging from highly critical (e.g., "Aping language"; Wallman 1992) to extremely positive (e.g., "Computer helps chimpanzees learn to read, write and 'talk' to humans"; Rensberger 1974) and all points in between (see Hillix and Rumbaugh 2004 for a review of both reactions). In any case, the findings from Lana were sufficiently encouraging, and raised significant questions for further inquiry, that additional chimpanzees were obtained for lexigram training.

In 1975, chimpanzees Austin and Sherman were assigned by the Yerkes Center to the ape-language project. Rumbaugh, postdoctoral research Sue Savage, and their research team endeavored to build on the strengths of the LANA Project while addressing the weaknesses. The lexigram-based computer keyboard was retained, but the Yerkish stock sentences were abandoned. Interactions with human caregivers and researchers were still studied, but the emphasis was shifted to social communications between the two apes. Communicative production was still measured, but the real focus was comprehension, or what the symbols might mean to the chimpanzees. Like Lana, Sherman and Austin used the symbols in a variety of contexts; however, they showed more convincing evidence than did Lana of conceptual understanding of the lexigrams as representing referents that were not physically present, and of using the computer keyboard to solve problems that could not be solved without symbol-based communication (Savage-Rumbaugh 1986).

Although the Lana, Sherman, and Austin research of the 1970s predates the founding of the LRC, the success of the work with these apes and the investigators' success in securing extramural funding for the research were critical for the

events that would follow. On September 20, 1979, a memorandum was distributed to the various Deans and Department Chairpersons at GSU. The university had been given several hundred acres of land in nearby Dekalb County, GA, by the federal government, under the condition that the land be used for significant academic purposes. GSU was using the land for sports and recreation but was feeling pressure to expand the academic use of the property. The memorandum served as a call for proposals.

Duane Rumbaugh, who had accepted appointment as Professor and Chair of Psychology at GSU in 1971, pitched the idea of moving the ape-language project from the Yerkes Center to this property. Additionally, the complementary language-intervention work that had grown out of the LANA Project would also move from the Georgia Retardation Center to that same location. This intervention research with children and young adults with intellectual disability (what was, at the time, called mental retardation) involved training the nonspeaking youths to use and to understand keyboard-based lexigrams, applying the principles of language learning that had been gleaned from work with apes (Rumbaugh 1977). Together, the NICHD-funded ape and human "Language Formation Study" would require vivarium, laboratory, office, and support facilities adequate to continue the work in a single site. Although a requirement for any proposed academic use of the Dekalb property was that the proposals utilize available resources, Rumbaugh argued that GSU should purchase a 3,500-sq ft prefabricated building that would support the parallel research projects. In a memorandum to the GSU Associate Vice President for Academic Affairs (October 20, 1979), Rumbaugh wrote, "To have all of the work going on in the same situation would maximize our use of people, equipment, and, most important of all, it would make possible optimal communication between the chimpanzee and human child projects."

By December of that year, Rumbaugh had secured commitments from the GSU Foundation to assign more than 50 acres of land to the Language Formation Study and to commit \$130,000

to construct a building of approximately 6,000-sq ft. Shortly thereafter, construction began with foundation and university support. Fred King, Director of the Yerkes Center, agreed to allow the apes to move to the GSU property, although Yerkes would retain ownership of the animals for more than a decade. The Georgia Retardation Center at the Georgia Regional Hospital of Atlanta agreed to permit two children at a time to be transported by bus to the GSU property for training and testing. NICHD approved the relocation of the science to the new facilities. Research began on the property in the spring of 1981. A few months later, the GSU Foundation Board of Directors toured the new facility. The Board of Regents of the University System of Georgia approved the LRC as an officially designated research center, the first at GSU. A brass plaque unveiled at the Fall 1981 dedication of the center acknowledged the support from all of these parties and revealed the LRC slogan: "So that together we might learn of language."

In the dedication of the LRC, Rumbaugh, Savage-Rumbaugh, and their colleagues indicated that the center was founded on five research assumptions: (1) that there is continuity between chimpanzees and humans in learning and other cognitive competencies; (2) that it is important for research to define where the species do differ in these competencies or in the processes by which the organisms come to gain them; (3) that comparative psychological inquiry affords significant and singular power for investigating how cognitive skills emerge; (4) that biology and experience interact to produce the emergence of cognitive competencies; and (5) that computer technology is uniquely useful in the comparative approach. These five assumptions continue to underlie research at the LRC. Similarly, the original statement of LRC research goals is as accurate today as when it was written on September 15, 1981: Goal 1. To study the emergence of cognitive skills; Goal 2. To define the parameters of training or teaching that cultivate particular cognitive skills; and Goal 3. To extrapolate those principles into research with humans, particularly those with developmental delays.

## LRC Facilities

Today, the LRC is a campus comprised of four laboratory/vivarium buildings and several research-support structures, situated on more than 50 acres of forest. For much of its history, the LRC employed the forest as laboratory space as well, with researchers traveling with lexigram-trained apes through its many trails to treehouses, camp sites, the river, and other locations where food might be available and where language lessons might be conducted. The original 6,500-sq ft building constructed at the LRC (representing a significantly larger investment from GSU and its foundation than their original commitment!) was designed to support chimpanzee (and, subsequently, bonobo) research in half of the structure, with indoor/outdoor caging, laboratory, and kitchen areas. The other half of the building was originally used for the child-language project and provided workspace for LRC faculty and students. In time, the language-intervention research moved out of the laboratory and into the children's homes and schools (e.g., Ronski and Sevcik 1991), and the apes moved into new buildings constructed for them (described below), so that the LRC main building now primarily serves office and laboratory functions for the faculty, staff, and students at the center.

The Lanson Building is a dedicated laboratory and vivarium for chimpanzee research. It was named for chimpanzees Lana and the son (thus Lanson) named Mercury she delivered there. It also served as primary home to other apes. The Sonny Carter Life Sciences Laboratory (SCLSL) is a dedicated laboratory/vivarium used primarily for monkey research. It was named in 1991 for astronaut Manley L. "Sonny" Carter (1947–1991), a Georgia native and Emory University alumnus who served as the liaison for the National Aeronautics and Space Administration (NASA) to the LRC for a multidisciplinary, international research project on the effects of space-flight on rhesus monkey behavior and physiology, funded by NASA grants. The CapLab was originally constructed as a quarantine and vivarium building for bonobos, which lived and worked in



the “ape area” of the main building as well as this new laboratory. A chain-link tunnel connected the two structures, allowing the apes to move between them securely. When the bonobos moved in 2004–2005 to facilities constructed for them at the Great Ape Trust of Iowa (now Ape Cognition and Conservation Initiative), the quarantine building was converted for housing and testing capuchin monkeys.

These buildings provide over 12,000 sq ft of indoor/outdoor housing and testing space, with another 7,000 sq ft of research support (e.g., office, prep) space. Additionally, maintenance shop, cage washing, and storage buildings are also available on campus. The LRC also leases an adjacent residence that is used as rental space for students, postdoctoral fellows, and visiting scientists.

## LRC Animals

The LRC is not merely a brick-and-mortar (and caging) compound; it is also, indeed primarily, defined by the resident animals that live and work in those facilities, and by the people who work with them. Since 1981, the LRC has served as home for 5 chimpanzees, 14 bonobos, 2 orangutans (*Pongo pygmaeus*), and dozens of rhesus monkeys and capuchin monkeys. This census includes many nonhuman primates that are well known and widely represented in the literature. Already discussed were Lana (1970–2016), Austin (1974–1996), Sherman (1973–present), and Mercury (1986–2016). The chimpanzee Panzee (1985–2014) and the bonobo Panbanisha (1985–2012) were co-reared at the LRC in a study designed to disentangle the contributions of species and experience on various cognitive competencies, including lexigram use and the comprehension of spoken English (Hillix and Rumbaugh 2004). Other bonobos raised at the LRC, notably Kanzi (1980–present) also demonstrated impressive cognitive skills, including the comprehension of lexigrams and spoken English under experimentally controlled tests (Savage-Rumbaugh et al. 1993), although his adopted mother, wild-born Matata (~1970–2014) failed

to learn these skills. The two orangutans also contributed data to published studies before they retired, Mari (1981–present) to the Center for Great Apes in Florida, and Madu (1983–present) to Zoo Atlanta, where she is now a featured attraction for her skills as a surrogate mother. Rhesus macaques Abel and Baker were the first two monkeys to master the joystick-manipulation skills required to respond to computer-generated stimuli in a series of game-like computerized tasks (Rumbaugh et al. 1989), and thus were pioneer animals in the development of the computer-test system, used originally with Sherman and Austin, and discussed further below. Many other rhesus monkeys (e.g., Hank, Gale, Willie, Murph, Lou, Hans, Obi, Chewie) have also contributed data to the literature, as have dozens of capuchin monkeys (e.g., Drella, Gabe, Griffin, Liam, Lily, Nala, Logan, Wren, and others) generously transferred to the LRC from the colonies of Frans de Waal, Dorothy Fragaszy, and Stephen Suomi.

## LRC Scientists and Caretakers

As indicated above, one cannot describe the LRC without discussing the innovative and dedicated people who have invested time and effort into understanding human and nonhuman primate behavior and cognition, and who have worked to ensure that the nonhuman animals that participate in this research are as healthy and as happy as possible. Any list of faculty, staff, and students who have worked in significant capacities at the LRC will necessarily be selective, and yet one cannot fully appreciate the impact of the center without recognizing some of the individuals associated with it. The studies conducted by these researchers have frequently employed animals other than those at the LRC, but each has made important contributions to the literature with LRC animals, and most have also attracted grant support to the center. Duane Rumbaugh was the founding Director and served in this role until his retirement in 2001. For many of those years, Sue Savage-Rumbaugh functioned as Associate Director. From 2001–2019, David Washburn directed the LRC, with Michael Beran—and his

research programs on numerical cognition, memory, cognitive control, and other topics (e.g., Beran 2004; Beran et al. 2014, 2016—as the Associate Director since 2012. Additional senior researchers include Sarah Brosnan, whose creative investigations of social cognition (particularly inequity, cooperation, and economic decision making) span all four of the primate species (capuchins, rhesus, chimpanzees, and humans) studied at the LRC. Charles Menzel has directed research on memory and spatial cognition. William (Bill) Hopkins has published extensively on neural and genetic differences across species, and their relation to behavior. J. David Smith and Barbara Church examine species similarities and differences in categorization and metacognition (e.g., Smith et al. 2016a, b). Previous senior researchers at the LRC have included MaryAnn Ronski (language intervention with special populations of children and adults), Rose Sevcik (language acquisition in apes and children), Robin Morris (functional lateralization of behavior), James Pate (learning and memory), Lauren Adamson (language development), Kirk Richardson (learning), and Michael Owren (vocal communication). Many other GSU faculty have collaborated on LRC publications and grants, including Roger Bakeman, Robert Latzman, Becky Williamson, Chris Conway, Tricia King, Marise Parent, Yanqing Zhang, Mukesh Dhalama, and R. Thompson Putney. Investigators from institutions outside of the LRC have also collaborated on research at the center, including Emil Menzel (problem solving), Patricia Greenfield (language), Dennis Molfese (cognitive neuroscience), Michael Tomasello (imitation), Dorothy Frigaszy (spatial cognition), Christian Argrillo (judgment), Kimberly Espy (executive functioning), Redouan Bshary (cooperation), Franz De Waal (social cognition), Gregory Ashby (categorization), Tara Stoinski (face recognition), Andrew Whiten (imitation), Steven Shapiro (face recognition), Anika Paukner (social cognition), Bart Wilson (economic decision making), Hani Freeman (primate personality), Joan Silk (prosociality), Bob Cook (categorization), Drew Rendall (auditory communication), Jennifer Vonk (comparative cognition), Carla Krachun and

Robert Lurz (theory of mind), Nicholas Toth and Kathy Schick (tool construction), Michael Posner and Mary Rothbart (development of executive attention), and countless others. Dr. Sarah Brosnan and Dr. Michael Beran are currently co-directors of the LRC.

In partial fulfillment of the “academic use” that motivated the original center proposal, the LRC has facilitated the education and training of many students. Washburn (attention), Hopkins (lateralization), Sevcik (language), and Beran (numerical cognition) were graduate students at the LRC years before they became senior scientists. Other graduate students who completed LRC-supported doctoral research include Kim Bard (behavioral development), Tom Smith (language research), Darlene Meador (discrimination learning by children), Karen Brakke (differences between bonobos and chimpanzees), Heidi Lyn (language), Jared Taglialatela (vocal production), Krista Wilkinson (language intervention with children), Wendy Shields (judgments of knowing), Joshua Redford (study-time allocation), Laurent Pretot (social cognition), Justin Couchman (self-agency), Mariana Coutinho (uncertainty), Jonathan Gulledge (numerical cognition by macaques), Audrey Parrish (perception), Kate Talbot (face recognition), Megan Hoffman (memory), Darby Proctor (decision making), Emily Marr (numerical cognition), Timothy Flemming (analogical judgment), and Lisa Heimbauer (speech comprehension). Hundreds of other graduate and undergraduate students have benefitted from LRC research resources. Postdoctoral researchers at the LRC over the years include Shelly Williams, Kenneth Sayers, Bonnie Perdue, Dan Cerutti, Dalila Bovet, Carole Parron, Claudio Cantalupo, Samuel Fernandez-Carriba, Lydia Hopper, Marcela Benitez, Emily Klein, and Travis Smith.

This list omits many other contributors, but perhaps none so important as the staff members who have provided care for the animals. Some, like Assistant Director of Animal Resources John Kelly, Liz Pugh, Janine Murphy, Kelly Leverett, Ted Evans, and others have been recognized as coauthors on scholarly contributions, but many other people merit acknowledgment for the

animal care and research assistance they have provided. It takes a village to raise, teach, study, and care for nonhuman primates, and the LRC has been fortunate to attract and retain a highly dedicated staff.

## LRC Support

Administratively, the LRC is a unit of the College of Arts and Sciences at GSU, which provides generous support. GSU and its foundations own the land and the animals and have also supported the center extensively. With respect to extramural funding, LRC scientists have attracted grants from multiple agencies in the National Institutes of Health (NIH), the National Science Foundation (NSF), NASA, Templeton Foundation, Wenner-Gren Foundation, McDonnell-Pew Foundation, Leakey Foundation, and other agencies. Primary support for LRC research has been provided through several program-project (P01) awards from the Eunice Kennedy Shriver NICHD (HD06016, HD38051, and HD060563), representing more than four decades of continuous funding for investigations with nonhuman primates of issues related to child health and development.

## LRC Contributions

Since the LRC was founded, its research team has averaged more than 20 published articles and chapters per year. As suggested by the topics associated with the collaborators listed above, the questions reflected by these scholarly products span the comparative study of behavior (although paradoxically, the topic of language has become less central in the LRC research portfolio, as scientists have increasingly broadened their questions to other competencies). Some of the most influential findings from these studies are that apes use lexigrams to label or name objects, treat the symbols as equivalent to the objects they represent, and remember the meanings of lexigrams and other symbols, even if they have not used the symbols for many years (e.g., Savage-Rumbaugh 1981, 1986; Beran et al. 2000; Beran and Heimbauer 2015). Language-experienced apes

can also learn to recognize spoken English and may modify their own vocal production as a result of enculturation (e.g., Heimbauer et al. 2011; Savage-Rumbaugh et al. 1993; Taglialatela et al. 2003). The methods and apparatus used to provide language training to apes are also transformative when applied to human youth with language impairments (e.g., Ronski and Sevcik 1991), and there is evidence that techniques developed for nonhuman primates may be similarly effective as interventions with children for other cognitive competencies (e.g., Rueda et al. 2005). Nonhuman primates can also learn symbols that represent quantities, use the symbols to count, perform simple combinatorial operations, and judge quantities using analog representations (e.g., Beran et al. 2007; Rumbaugh 2013). The animals show other evidence of rule-like, relational learning on a variety of tasks, as well as memory performance that may suggest mental time travel to the past (i.e., episodic-like what-where-when memory) or the future (i.e., prospective memory; Beran et al. 2016). Such findings underscore the continuity of cognitive competencies; however, interesting species differences also appear (e.g., Flemming et al. 2007; Pr  t  t et al. 2016; Rumbaugh and Washburn 2003; Smith et al. 2016b). For example, humans, chimpanzees, and macaques show robust evidence of meta-cognitive monitoring of subjective cues, whereas such evidence has been elusive from capuchin monkeys (e.g., Smith et al. 2016b). Phenotypic individual or species differences in behavior may be predicted from variations in genotype, brain structure, activation (e.g., Hecht et al. 2017; Latzman et al. 2016). The importance of social variables is also revealed by the primates' performance on tests of inequity aversion, prosociality, cooperation, social recognition, deception, and economic decision making (e.g., Hall and Brosnan 2016; Talbot et al. 2016). By comparing performance across primate species, across development, and across experience, the competition between stimulus control of behavior and cognitive control is brought into focus, as are the factors that allow organisms to be more self-directed and purposive in behavior (e.g., Beran et al. 2014, 2016).

LRC scientists have also authored or edited 20 books, including *Ape Language: From*

*Conditioned Response to Symbol* (Savage-Rumbaugh 1986); *Biological and Behavioral Determinants of Language Development* (Krasnegor et al. 2013); *Primate Laterality* (Ward and Hopkins 1993); *Communicating Meaning* (Velichkovsky and Rumbaugh 1996); *Breaking the Speech Barrier* (Ronski and Sevcik 1996); *Kanzi: The Ape at the Brink of the Human Mind* (Savage-Rumbaugh and Lewin 1994); *Apes, Language, and the Human Mind* (Savage-Rumbaugh et al. 1998); *Intelligence of Apes and Other Rational Beings* (Rumbaugh and Washburn 2003); *Animal Bodies, Human Minds* (Hillix and Rumbaugh 2004); *Educating the Human Brain* (Posner and Rothbart 2007); *Primate Perspectives on Behavior and Cognition* (Washburn 2006); *The Evolution of Hemispheric Specialization in Primates* (Hopkins 2007); *Animal Acoustic Communication* (Hopp et al. 2012); *Foundations of Metacognition* (Beran et al. 2012); *Number Without Language: Comparative Psychology and the Evolution of Numerical Cognition* (Agrillo and Beran 2013); and *With Apes in Mind* (Rumbaugh 2013). Many of the scientific contributions discussed above are detailed in these publications.

The LRC has also been active in disseminating research findings through electronic media, including video documentary of methods and results, as well as interviews or brief features on websites, television, or radio programs. Noteworthy contributions include *The Amazing Apes* (1977) featuring Lana and her lexigram use; *Ape Language: From Conditioned Response to Symbol* (1986), with documentary footage of Sherman and Austin to accompany the Savage-Rumbaugh (1986) book by the same name; *Lana Chimpanzee Learns to Count by "Numath"* (Rumbaugh et al. 1989) on numerical cognition research; and *Bonobo People* (1993), including footage filmed by NHK on the research with Kanzi and his family of bonobos. Similarly, public exhibits on LRC research have been included in the American Psychological Association's centennial celebration traveling exhibit and in the American Museum of Natural History in New York.

LRC scientists have also made important methodological contributions to comparative

psychology. From apparatus innovations like the computerized language keyboard and the joystick-based computer-test system to specific testing paradigms (both automated and manual), many of the methods developed at the LRC have been adopted for comparative research at other research facilities. For example, the innovative training procedure and apparatus configuration that allowed rhesus monkeys to respond to computer-generated stimuli via joystick manipulation (Rumbaugh et al. 1989) were exported to dozens of laboratories. This computerized test system has become a standard testing paradigm for comparative research, and has been shown to provide environmental enrichment to nonhuman primates, addressing three of a (human or non-human) primate's basic dimensions of psychological well-being: challenge, control, and comfort (Washburn 2015). Given recent refinements of the paradigm for the testing of socially housed animals (Fagot and Bonté 2010; Gazes et al. 2012), the system is also compatible with the fourth dimension of well-being: companionship.

## Summary

The LRC is a facility with uncommon research and training resources. The LRC is also a resident colony of special primates with unique skills and experiences. The LRC is a team of creative and collaborative scientists who are excited about the challenges of understanding primate (including human) minds and behavior. It is a center with a rich past and with a promising future. At a time when science is becoming increasingly collaborative, increasingly interdisciplinary, increasingly about working together, the LRC embraces its partnership with nonhuman primates as it pursues its mission: "so that together we might learn."

## Cross-References

- [Categorization](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Counting](#)

- ▶ David Washburn
- ▶ Dorothy Fragaszy
- ▶ Duane Rumbaugh
- ▶ Episodic Memory
- ▶ Frans de Waal
- ▶ John David Smith
- ▶ Kanzi
- ▶ Language Research: Great Apes
- ▶ Lexigrams
- ▶ Matching-to-Sample
- ▶ Meta-cognition
- ▶ Michael J. Beran
- ▶ Panbanisha and Panzee
- ▶ Primate Cognition
- ▶ Primate Communication
- ▶ Prospective Memory
- ▶ Sarah "Sally" Boysen
- ▶ Sarah, Lana, Sherman, and Austin
- ▶ Sue Savage-Rumbaugh
- ▶ Theory of Mind
- ▶ William Hopkins
- ▶ Yerkes Primate Research Center

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## Gerald S. Wilkinson

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Gerald Wilkinson is a behavioral ecologist and evolutionary geneticist who has spent his career testing assumptions and predictions of highly debated evolutionary theories involving sexual selection and cooperation. He is best known for his work on cooperation in bats and sexual selection and meiotic drive in stalk-eyed flies.

Wilkinson was born in 1955 in San Francisco and grew up near Sacramento California. As a kid, he chased jack rabbits and kept pet reptiles he caught in the fields near his home. He fostered his naturalist curiosity further in the boy scouts and became an avid birder, but always “found it more interesting to watch what the birds were doing, than to simply count seeing a rare bird.” As an undergraduate at UC Davis, he took a course on primate behavior taught by Peter



Rodman, who later allowed Wilkinson to be the sole undergraduate in his graduate student seminar, which covered E. O. Wilson's newly published book *Sociobiology*. Wilkinson enjoyed reading, discussing, and debating the topics of the book. Less than a decade later, he himself would make substantial contributions to this new field.

While an undergraduate, Wilkinson conducted a field study with a classmate to see if industrial dumping of tomato waste increased rodent densities and hence raptor density, leading to his first publication. A few years later, he and another classmate also completed a study on predation and group size in cliff swallows.

Wilkinson also took a methods course by Rodman where he learned how to perform and analyze observational data by studying bonnet macaques at the UC Davis primate center. He would later use these methods in his classic PhD work on vampire bats. Rodman recognized Wilkinson's motivation and talent and suggested he pursue a PhD with behavioral biologists Jack Bradbury and Sandra Vehrencamp at UC San Diego, which he did. During mandatory lab rotations, he developed a method to catch roadrunners for radio-tagging, created an optimal foraging model for sea otters, wrote four short research proposals, and learned enzyme electrophoresis – another method he would employ during his study of vampire bats.

Wilkinson's PhD advisor, Jack Bradbury, was trained by Donald Griffin, who discovered echolocation in bats. By the end of the 1970s, Bradbury was the leading expert on bat sociality. At this time, inclusive fitness theory was inspiring biologists to use newly developed genetic techniques to look at the effects of kinship on cooperative behavior. At a scientific meeting, Uwe Schmidt, the world's leading expert on vampire bat behavior, described regurgitated food-sharing behavior in his captive colony of vampire bats. Bradbury wrote Wilkinson, then stationed in Costa Rica, and suggested that he study this behavior in the wild.

In Costa Rica, Wilkinson initially began a project looking at a common nectar-feeding bat, but this species would abandon their roosts after he marked them with wing bands, so he was eager to consider an alternative. He individually

marked vampire bats with bands and found he could continue observing them after slowly habituating them to small amounts of light. Wilkinson and his team of field assistants spent over 400 h observing the bats within their roosts. This process involved wearing a protective respirator while lying inside a cockroach-infested hollow tree full of vampire bat feces. Regardless, Wilkinson enjoyed his work and became quite fond of the vampires, which often groomed each other, like primates.

His findings, based on a 5-year study, including 3 years of intense fieldwork, showed that wild female vampire bats regurgitate blood to help not only their own offspring but also hungry kin and nonkin adult females of high association. Wilkinson then showed experimentally that food donations among unrelated adults were predicted by past reciprocal donations. When Wilkinson returned to the USA, the two explanations for altruism in animals were that animals help individuals based on genetic relatedness, (i.e., kin selection) or that they helped based on past experience of helping (i.e., reciprocal altruism). In the food-sharing vampire bats, Wilkinson found evidence supporting both hypotheses. A surge of interest in reciprocal altruism came from an evolutionary game theory paper (Axelrod and Hamilton 1981) showing that a strategy of reciprocal helping (“tit for tat”) could outcompete selfish strategies even under conditions that made cooperation nearly impossible (“the prisoner's dilemma”). When it was published, Wilkinson's report on food sharing in vampire bats was one of the most convincing cases for such reciprocity in nature and was highlighted in textbooks, magazines, and popular science books (e.g., the second edition of *The Selfish Gene* by Richard Dawkins). With more than 900 citations as of 2016, Wilkinson's 1984 paper on reciprocal food sharing in vampire bats is his most often-cited publication.

Later as a professor at University of Maryland, Wilkinson advised several students who studied social behavior and social learning in bats, often in collaboration with his University of Maryland colleague, Cindy Moss. One of the lab's more fascinating lines of research, led by two PhD students, first Jenny Boughman and later Kisi

Bohn, was that neotropical greater spear-nosed bats, which live in unrelated female groups, produce a group-specific “screech call” that is consistent across group members (reviewed by Wilkinson et al. 2016). These group signature calls are used for maintaining contact and are learned over time. Infants, however, make an individually distinct “isolation call” that is important because the helpless pups sometimes fall to the floor of caves where females from other groups will try and kill them. Astonishingly, unrelated females from the same group will defend them, a cooperative behavior which remains to be fully explained (Bohn et al. 2009; Wilkinson et al. 2016).

Since his PhD, the main focus of Wilkinson’s work, however, shifted from bats to stalk-eyed flies. He sought to test some of the underlying assumptions of genetic models that provide the foundation for much social evolution theory, and this would require developing skills and techniques for studying evolution more directly and rigorously in organisms that were more tractable than bats. As a postdoc at the University of Sussex and then at the University of Edinburgh, he began experiments that addressed two influential theory papers on sexual selection (Lande 1981, Kirkpatrick 1982) that described the genetic conditions leading to either an equilibrium between sexual and natural selection or a state of positive feedback, e.g., Fisherian runaway sexual selection. A key assumption of the first condition is that natural and sexual selection act in opposite directions. Wilkinson first confirmed this in fruit flies, but he really wanted a model organism with more explicit female choice.

Stalk-eyed flies seemed perfect. Their eyes are mounted on the ends of long stalks, which are dramatically larger in males, and are used to attract females and compete with males. Wilkinson heard from faculty member Arthur Ewing about stalk-eyed flies he had seen on Mount Kenya during a recent holiday. Wilkinson (2001) described his excited reaction:

Within a month, I had booked a cheap flight from London to Nairobi. The day after I arrived, just as he had described, I found stalk-eyed flies in several streams in the forests on Mount Kenya.

He brought flies back to Scotland and bred them in the lab. However, during his second postdoc at UC Boulder studying behavioral genetics and communal nursing in mice, he was unable to secure the permits to bring his stalk-eyed flies to Colorado.

In 1987, Wilkinson joined the faculty at University of Maryland, where he setup a lab to study bats in the field and to conduct artificial selection experiments with stalk-eyed flies in the lab. There, he tested a key assumption of sexual selection models: a genetic correlation between the male trait and the female preference. If such a correlation exists, then selecting on the male trait should lead to changes in female preferences in those genetic lineages. The Wilkinson lab selected males on the ratio of eyespan to body length for 2 years (or 13 generations). Then he tested female preference. As expected, females from short-stalk male lines preferred short-stalk males, whereas females from long-stalk male lines preferred long-stalk males.

In the 1990s, Wilkinson teamed up with Rick Baker (then a graduate student at Yale) to study the evolution of sexual dimorphism in stalk-eyed flies. He also conducted a large study with six species of stalk-eyed flies to measure the magnitude of change in genetic variation and covariation for traits that were either under natural or sexual selection to complement his ongoing selection experiment, which he wanted to use to directly measure changes in genetic variation. While counting the numbers of male and female offspring from half-sib families in each line, he stumbled across something astonishing.

Male flies from the short-stalk lines produced primarily female offspring, while male flies from the long stalk lines produced more male offspring. Eventually Wilkinson’s lab found that this was due to a process called sex chromosome meiotic drive, whereby one of the sex chromosomes is transmitted more often. For example, meiotic drive can lead to all of one’s offspring being 100% female. The “driving” X chromosome is a selfish genetic element that spreads itself at the expense of the other genes and the fitness of the individual as a whole. Genes on the other chromosomes are therefore selected to suppress drive. The result is an evolutionary battle of genes within the genome.

Wilkinson's lab detected this intragenomic conflict in the stalk-eyed flies he brought from Southeast Asia. By decreasing eyespan, the lab had increased the frequency of the drive X chromosome, which led to more female offspring. He faced an astonishing hypothesis: Did the females choose long-stalked males to increase their fitness by producing more males?

Indeed, a combination of models and experiments supported the notion that male stalk length advertises the presence or absence of a drive X chromosome and that meiotic drive could accelerate the process of sexual selection (Wilkinson et al. 1998). Over the next decade, the Wilkinson lab showed that the genes influencing stalk length and those causing sex chromosome meiotic drive were linked. They discovered that stalk-eyed flies possess a "neo-X" chromosome and they determined that many genes have duplicated and moved on and off of this chromosome over evolutionary time. By sequencing the genome for a stalk-eyed fly, they searched for gene duplications and sex-specific changes in gene expression across different tissues for over a dozen different species of flies. These studies continue and are providing insight into the origin and evolution of sex chromosomes.

A unifying theme of Wilkinson's work is understanding the factors that promote or prevent cooperation. He points out that meiotic drive is really a lack of cooperation among chromosomes, much like cancer is a lack of cooperation between cells in the body. Is meiotic drive a consequence of the genome's defense system not working properly? Wilkinson's work continues to ask such questions.

In reflecting on his scientific career, Wilkinson notes that some of his most influential discoveries came through recognizing something surprising in his data that were theoretically interesting. There's a lesson here: continuously check your data, and know the current theory and literature well enough to tell when a strange result is interesting. As Wilkinson (2001) explained, "future advances in the field will depend on discovering behavioral patterns that fail to conform to conventional theories. My best advice, therefore, is to be alert for the unexpected. Such discoveries may

well turn out to be more important than any preconceived ideas under examination."

## Cross-References

- [Behavioral Genetics](#)
- [Behavioral Genomics](#)
- [Evolution](#)
- [Genes](#)
- [Reciprocity](#)
- [Sexual Selection](#)

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## Gestalt

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## Synonyms

[Configurational processes](#); [Gestalt laws](#); [Perception](#); [Perceptual figures](#); [Whole](#)

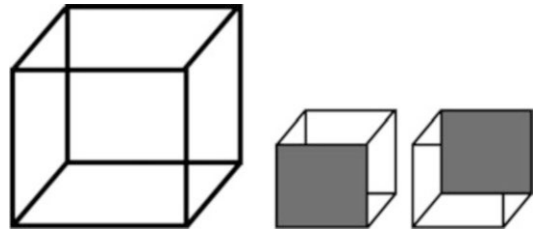
## Definition

Gestalt psychology was a school of thought originating in the early twentieth century that defended a molar view of perception. According to Gestalt principles, perception involves an active organization of stimuli that takes place within schemes of meanings. A widespread contribution of gestalt theory was to synthesize in laws the ways in which perceptual information tends to be grouped through conceptualization.

## Introduction

Essentially, Gestalt psychology defined perception as a process that organized the world of objects. According to gestalt theorists, this process is led by meanings and not by the adding of one part to others. The objective of gestalt principles was to demonstrate that perception is not simply an accumulation of information.

If we search the etymological sense of the term, Gestalt is a German noun that means form, or figure. Additionally, Gestalten is a verb that means organize, configure, or restructure. Gestalt psychology postulates an innate origin of certain categories that give rise to the schemas in which we perceive. The theory claims that perception does not come from emptiness but, as Kant stated (Oviedo 2004), perception goes beyond the literal data and builds global phenomena. Classic examples of gestalt perception include well-known optical illusions in which a visual pattern can be perceived according to multiple conceptualizations. An example of this is the Necker cube (see Fig. 1), in which two different cubes may be perceived, depending on the point where the deeper perspective is fixated. To gestalt theorists, this is proof that a molecular definition of perception is not possible. That is, the object perceived comes from a qualitative organization of stimulus characteristics. Depending on the frame of perception, object perception can change without modifying the composition or arrangement of its features. Another well-known example, characteristic of gestalt analysis, is the image



**Gestalt, Fig. 1** Necker cube. The perspective of the 3D cube can change depending on the fixation point



**Gestalt, Fig. 2** Older and young women illusion (Adapted from Boring 1930)

of the young and the older woman and its numerous versions (see Fig. 2).

In contrast to the atomistic perspective of cognition, which claims additive summation of discrete stimuli as the main function of perception (Katz 1945), Gestalt psychology suggests that perception involves forming hypotheses about stimuli in the world. Historically, taking into account the physiological trends up until the early twentieth century, Gestalt explanations in terms of meanings, wholes, and interpretations of stimuli seemed revolutionary. The Gestalt theory contrasted with the historical period in which it emerged because of its molar level of explanation, in opposition with the elementary point of view. For instance, Katz (1945) supports the idea that an atomistic perspective of perception cannot explain rhythmic auditory stimulation and, consequently, the melodic music experience as a perceptual phenomenon. Katz says, that in a succession of metronome oscillations, different

rhythm patterns can be heard depending the speed of the beat. For this author, the dynamic organization of auditory figures is essential for the experience of rhythm.

This molar view of the act of perception fits with the existence of perceptual constancies. Perceptual constancy is an invariance of meaning within a given perceptual category. Even if one discrete characteristic of a target varies, our recognition of the target category does not vary. For example, viewpoint invariance (Goldstein 2010) is the ability to visually recognize a known object, despite it being presented from different angles. Another perceptual constancy is size, seen in the capacity to recognize a moving object although it is displayed in different sizes because of changes in distance. Color constancy is another basic constancy that brings simplicity to the multiple and variable stimulus world in which we live. Color constancy brings the possibility to group different palettes of tonality (turquoise, indigo, cobalt, sapphire, azure), as the same color, blue. From a gestalt view, the whole remains separate from its specific parts.

In short, the core of Gestalt theory may be summarized by the classic slogan, “the whole is greater than the sum of its parts” (Boring 1929, pp. 588–589). This whole may be observed in everyday examples such as perception of auditory melodies, in which notes sound different in the context of the melody than if they are heard in isolation. In taste perception, the combination of several flavors results in a totally different whole than the isolated ingredients. In this regard, another example widely explored in animal learning is the taste flavor paradigm. It is a well-known phenomenon in which a two-flavor compound tastes qualitatively different from each component tasted separately (Rescorla and Cunningham 1978).

Besides the aforementioned ideas, the Gestalt perspective introduced inference into the perception process. Perception is the act of grouping the myriad stimuli in the environment into dynamic wholes (Ellis 1938). For the Gestalt psychologist, perceivers are active organizers of stimuli. Gestalt psychology defended the experimental study of perception as a flexible status to fit and adapt to

the environment, working between exteroception, interoception, and cognition in an organizational way.

The basic topics of gestalt theory (Boring 1929) include the study of principles of relativity and transposition, related with generalization and discrimination processes in different perceptual variables. In this case, differentiating indigo from other blue tonalities is a discrimination exercise. Conversely, deciding that turquoise is also blue is an example of generalization. Additionally, in early Gestalt works, other principles to explore were the underpinnings of object constancy, field dynamics, and laws of form.

The rest of the entry is divided into three sections. The first is a historical overview of the principal authors from Gestalt psychology. The second is an exposition and synthesis of the Gestalt laws. Although the majority of the examples in the literature are on visual reorganization, gestalt laws may be observed in all perceptual modalities. Thus, perception is to see, hear, touch, smell, or taste from a scheme of meaningful organization. An assortment of examples will illustrate these principles. In the third and final section, the relationship between gestalt theory and general cognition will be discussed.

## Origins of Gestalt Theory

Gestalt psychology was developed primarily by Max Wertheimer, Wolfgang Köhler, and Kurt Koffka, in the first decades of the twentieth century. These authors were German psychologists who began their careers together at the Berlin Psychological Institute.

Max Wertheimer (1880–1943) published what many consider to be the first work of Gestalt psychology in his 1912 paper on the *phi* phenomenon (Wertheimer 1912). In this phenomenon, participants perceive illusory motion when they are presented with a sequence of spatially displaced images (Wagemans et al. 2012). In the original procedure, participants were exposed briefly to a line, followed by a short delay, and then by a second line, parallel to the first, and spatially separated. When the delay was below a



certain threshold (about 30 ms), participants perceived only one, stationary line; when the delay was above a certain threshold (about 200 ms), participants correctly perceived two lines, one appearing after the other; however, when the delay was at a certain middle value (about 60 ms), participants perceived a single line in motion. This final illusory motion effect is the same one that underlies our perception of motion in films, which consist of a series of static images. Wertheimer concluded that motion perception emerged as a perceptual whole, or *gestalt*, that was qualitatively different from any of its separate elements. This finding thus served as a starting point for the development of Gestalt theory (Wagemans et al. 2012).

Wolfgang Köhler's most essential findings came from his experiments on chimpanzee intelligence, published in *The Mentality of Apes* (Köhler 1925). In these experiments, Köhler (1887–1967) set out to test the extent to which chimpanzees could manipulate the environment or use tools to obtain food that was out of reach. For instance, in one experiment, a basket of fruit was hung in the air, with some boxes placed on the ground off to the side. The only way for the chimps to reach the fruit was to stack the boxes on top of each other underneath the fruit basket and climb them. Some of the chimpanzees tested (although not all) in fact did this. In another experiment, the only tools available to the chimpanzees were a pair of short sticks that they needed to insert into each other to create a longer stick able to reach the fruit basket and knock it over. One chimpanzee in fact did this. In another experiment, the only solution was to use a short stick to reach a longer stick and then use the longer stick to knock over the fruit basket. Several of the chimpanzees were able to solve the task.

Importantly, in all these experiments, the chimpanzees received no explicit training with the tools involved. Rather, it appeared that they came upon the solution through what Köhler called insight: a mental process in which the elements in the environment came to be perceived in relation to each other as a unique stimulus whole that made the solution obvious, as in an “aha” effect. Köhler described that, when faced with

each problem, the chimpanzees initially tried to reach the food directly with their hands, but eventually gave up that futile approach and appeared to sit in thought for a while, examining the surroundings. The chimpanzees' attention eventually focused upon the available tools and, a few moments later, the chimps proceeded to use the tools more or less correctly for the purpose of obtaining the food. Köhler argued the core of this insight process was the perception of the complete environment and all of its parts in relation to each other, and a reorganization of the stimulus elements in the chimpanzee's mind to achieve a new perception that was qualitatively different from the sum of its separate parts. Köhler viewed this type of learning as fundamentally different from the mechanistic S-R learning proposed by another prominent psychologist of the time, Edward Thorndike (Ruiz and Sánchez 2014), whose theory might predict that the chimpanzees would arrive at the solutions only gradually and through trial and error. Köhler observed quite the opposite: that the solution appeared rather swiftly after a careful reflection of the situation.

Kurt Koffka (1886–1941) contributed to the development of Gestalt theory with the publication of works such as *Principles of Gestalt Psychology* (1969). As Goodwin (1999) recalled, Koffka did his PhD in Berlin exploring perceptual contrast of color and the study of rhythm in auditory stimuli (Goodwin 1999). Koffka also got involved in Wertheimer's apparent motion experiments, as did Köhler. His work built upon that of Wertheimer and Köhler and applied it to new areas such as child development. Like his colleagues, Koffka also sought to distinguish gestalt theory from the prevailing behaviorist theory of the time. He argued that while behaviorists, such as Thorndike, refused to study conscious mental phenomena, gestalt theory tackled these phenomena directly and successfully. Furthermore, Koffka spent the later part of his career as a professor in American universities such as Cornell, the University of Wisconsin, and Smith College, and as such was the main promoter of the Gestalt perspective in America.



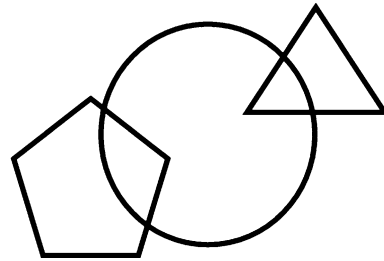
## Gestalt Laws of Form

Besides explaining perception in terms of schemas of meaning, Gestalt psychology formulated the Laws of Gestalt. These laws summarized the general trends of how we organize our perceptual world. First studied by Wertheimer between 1923 and 1967 (Goodwin 1999), Gestalt laws assumed that elements are organized as part of a meaningful whole. This organizational principle underscores the ultimate purpose of the perceptual process, to find meaning in the chaotic world of stimuli that surrounds us. Each law exposed below organizes figures through a common purpose, soft lines, symmetrical order, space distribution, similar features, or same orientation. Gestalt organization also tends to the maximum simplicity that encourages the maximum effectiveness of perceptual effort. For instance, Fig. 3 shows a simple example of gestalt organization. A plain set of two points and a line are quickly organized as a schema of a human smiling face.

As Boring first claimed (1929), Gestalt principles form the basis for 114 laws of perception. However, the main rules that appear in basic perception manuals can be grouped as follows.

1. **Good Form or Pregnancy.** This law, also known as Common Destiny or Simplicity, was formulated by Koffka (1969). This law states that elements that share a common end, following the simplest principle, tend to be considered as being from the same figure. A common end could be a meaningful category or schema. This rule helps the perceiver to differentiate parts from different objects that visually overlap with each other (Katz 1945), as Fig. 4 shows. It also operates when there are several options of figures in the perceptual field. The constellations in astronomy are pure examples of gestalt pregnancy. Figure 5 shows the basic stimulus input that comprises the Ursa Major constellation and the schema that provides the image of a bear. Another interesting example in another sensory modality is the effect studied by Benussi (in Katz 1945). In this tactile effect, the stimulation provoked by three points of pressure in

**Gestalt, Fig. 3** Example of organization

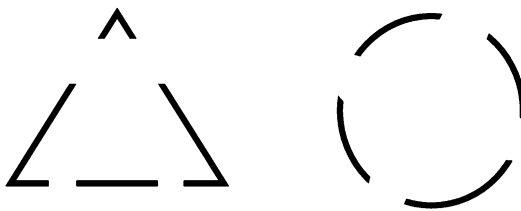
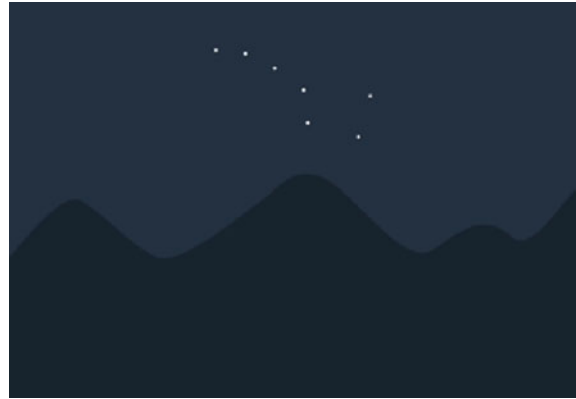


**Gestalt, Fig. 4** Delimitation of geometric figures from Good Form law. Example of delimitation of edges following the geometric schemas of pentagon, circle

the skin, delimiting a triangle, is perceived as a circle sensation.

2. **Closure.** Human perception tries to complete or close figures (Katz 1945). People prefer closed to unclosed figures (Wertheimer 1923). This tendency to complete incomplete sensorial information takes place in an automatic way. All the information provided to help to finish a contour will be selected to outline a whole, as Kanizsa showed in his varied incomplete triangles and other invisible border images (1976). A proof can be seen by removing a part of any geometric shape, a triangle for example. In Fig. 6, one can observe the difficulty of ignoring the whole shape despite being incomplete. An example from the auditory domain is known as auditory closure strength, the ability to listen to the whole message in a radiophone speech with interference (Katz 1945). An example of the same phenomenon in a visual-reading domain can be seen in Fig. 7.
3. **Continuity or Good Continuation.** Human perception tends to complete lines but also softly, and tends toward the circle shape (Wertheimer 1923). For example, motor integration involves a preference for indirect and

**Gestalt, Fig. 5** Draw Illustration of Ursa Major. Exemplification of Gestalt Pregnancy. A bear figure can be perceived from a few spots in the sky. (From: Pixabay)



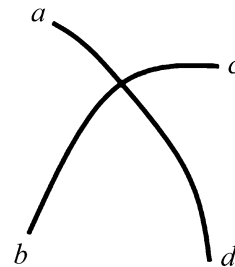
**Gestalt, Fig. 6** Examples of geometric closure. Triangle and circle are visible for the closure gestalt law

# gestalt

**Gestalt, Fig. 7** Example of Closure in reading

circular movements in the perception of human motor translation. In Fig. 8, one can see a clear example of continuity in which the viewer tends to perceive two softly curved lines, rather than pointy shapes. In another example, from ethology, there is a preference for soft and circular shapes in mammalian offspring. Lorenz (1943) showed that similarities exist in some physical characteristics of young animals, such as round faces. Maps also can be a good model of continuity; we are able to distinguish geographic delimitations from many overlapping lines.

4. **Symmetry.** Figures are usually perceived as symmetrical. Asymmetries tend to be neutralized (Katz 1945). This principle completes and emphasizes the aforementioned rules



**Gestalt, Fig. 8** Example of Good Continuation. Facing the task of determining the start and end of those two lines, Good Continuation predicts the limits of one from *a* to *d*, and the other from *b* to *c*, due to a preference for soft lines over sharp corners. The scheme of letter x in the Western alphabet may also be influencing (Adapted from Katz 1945)

and shows a perceptual preference for homogenous images and sensorial perceptions. Also, the objects that tend to be symmetrical, that is, those equally distributed around their axis, are easily perceived and selected.

5. **Proximity.** Stimuli near each other tend to form a unity (Wertheimer 1923). Good examples of this are from auditory perception of musical patterns. A piece played slowly, or “lento” in musical terms, can hardly be heard as the same piece when it is performed quickly, or “presto.” Another auditory phenomenon is that of auditory segregation, which is similar to the proximity effect (Bregman and Campbell 1971). In the original experiments, these authors presented an alternating sound sequence of low (between 350 and 550 Hz) and high tones (between

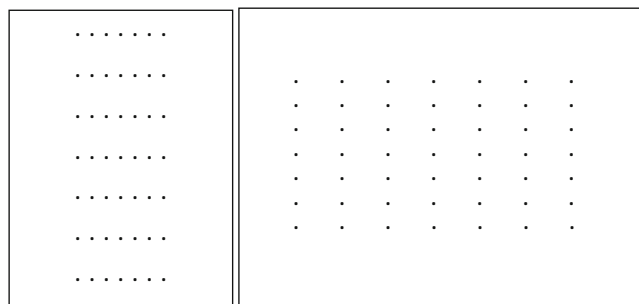
2500 and 1600 Hz). When the sequence was played slowly (interstimulus-interval of 400 ms), a pattern of successive low and high stimuli clearly appeared. When the same sequence was presented faster (interstimulus-interval of 100 ms), the perception was divided into two auditory paths: a high one and a low one. This segregation effect, due to temporal proximity between similar sounds, can be experienced in the classical music opus S. 141 study of Litz, commonly known as “Campanella.” In Fig. 9, one can also see a visual example. The elements in each set of points are the same, but they differ in its spatial distribution, creating a very different visual result.

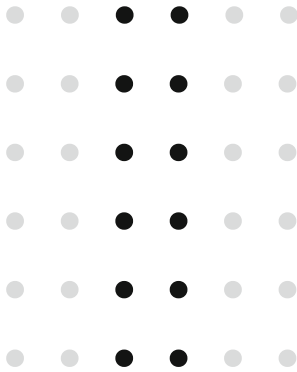
6. **Similarity.** Stimuli that share features tend to form a unity. Lightness, color, texture, size, shape, (Goldstein 2010) are possible characteristics to be grouped, as can be seen in Fig. 10. In a complex visual pattern, as a Monet painting, the figures can emerge from the similarity of color, size, and texture of the brush strokes, as can be seen in his studies of “Water Lilies.” The similarity principle is evident in the painting style of lots of impressionistic artists. Moreover, a painting technique called pointillism uses similarity and gestalt principles, using the different color points to conform the scenes, as Van Gogh and Seurat did.
7. **Good direction or Common fate.** This principle takes into account the movement or tendency to group elements in the same direction (Wertheimer 1923). Orientation and synchronicity in the static figures is relevant to define figures. In Escher’s paintings, common

fate is a clue to discern the different illusions hidden in each drawing, like in his series “Sky and Water.”

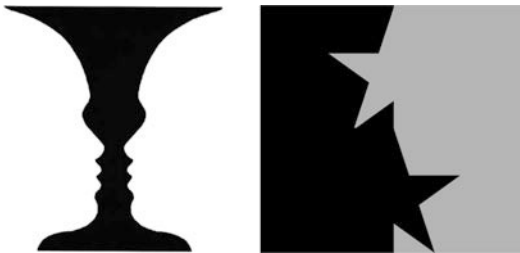
8. **Strong form.** A strong or intense stimulus tends to be differentiated from other stimuli. If a strong stimulus competes with a weak stimulus, the strong stimulus tends to attract more attention. This is the case of the reorganization process called reification, the ability to see more information than is actually provided by the physical stimuli. The subject gives additional attributes in order to organize intense meanings. This reification process is governed by powerful meaning. Something similar happens in the pareidolia phenomenon. This cognitive process occurs when perceivers are able to distinguish concrete forms in a simple environment, like an artificial apparatus or a natural phenomenon. An example of this is the common example of seeing animals, faces, and other significant figures in the clouds. Something relevant in all these processes is considering that human faces are strong stimuli for human perception. This principle is reflected in the perception of a facial expression in Fig. 3. Similarly, in Fig. 2, one image is usually more difficult to see than the other. Sometimes, familiarity gives the stronger value to one option over another. This principle supports the next law to be considered in terms of differentiating strong figures from weak ones, which sometimes can be considered as background.
9. **Figure and Ground.** Human perception tends to fixate on one main point over the background. The figure has a defined outline that stands out from the ground. This principle

**Gestalt, Fig. 9** Example of proximity. The same stimuli form different configurations (horizontal or vertical, respectively) depending on a proximal variable





**Gestalt, Fig. 10** Similarity example. Columns of points tends to be grouped by shade identity



**Gestalt, Fig. 11** On the *left* are the Rubin faces, a classic example of Figure and Ground. On the *right*, a combination of shades between Figure and Ground (Adapted from Rubin 1921)

explains why perceivers need a certain contrast to distinguish figures (Oviedo 2004). The first description of this principle was by Rubin (1921) and was illustrated by the classic faces and cup image, as can be observed in Fig. 11. Another example of the influence of ground in the perception of a figure is the visual differences depending on the color of possible backgrounds (see Fig. 11). Also, in Fig. 2, the hidden figure can be conceptualized as ground, since it is not possible to perceive both women at the same time. Koffka (1969) exposed an analysis of characteristics in which figure and ground are related, including factors such balance in color, limits of the figure contour, orientation, relative size, and feature complexity. In another perceptual paradigm, Signal Detection Theory (Green and Swets 1966) has widely developed the task of finding a figure (a Signal, in the terms of the theory) from the

Ground (Noise, in the parlance of the theory). The particularity of this theory is the systematic study of different ambiguity conditions of figure and ground. Signal Detection methodology explores the measures of probability to perceive and decide between response or no response to the signals and possible false alarms that can be confounded with the ground.

10. **Stability.** When organizations are established, they are also difficult to eliminate and tend to persist. Gestalt perception tries to conform stable objects. For example, in visual illusions like the Necker cube (check Fig. 1) and the younger and older woman (see Fig. 2), the option not seen at first sight, is usually more difficult to see.

From all these laws, Closure, Good Continuation, Proximity, Similarity, and Figure and Ground are the most general and commonly observed. In lots of everyday examples, various laws work together. Several applied fields have explored the extent of these principles, with logos and advertisements serving as good examples of this. Also, analysis of visual art has made a lot of effort to apply gestalt principles to art perception.

## Gestalt Perception Theory and Learning

Gestalt principles have served as a platform for studying animal learning and cognition in a variety of contemporary research. One manner in which this has been done is through the study of perceptual laws outlined above, in animals. Studies of the perceptual constancies have been performed in species as diverse as parrots (Pepperberg and Nakayama 2016), ants (Sakiyama and Gunji 2016), mice (Kanizsa et al. 1993), and chimpanzees (Hopkins and Washburn 2002).

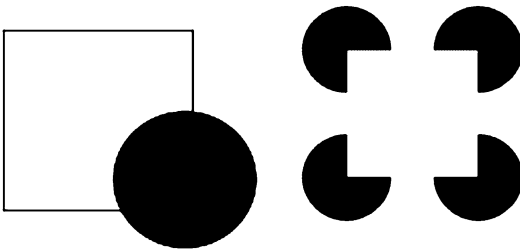
For instance, Pepperberg and Nakayama (2016) tested, in a parrot, the phenomena of amodal and modal completion. Amodal completion is the recognition of an object that is partially covered, such as the square in Fig. 12a. Modal

completion is the recognition of an object that lacks some of its boundaries, such as the square in Fig. 12b. Notice that the phenomena rely on the gestalt principles of good form and closure. Pepperberg and Nakayama tested whether a parrot could identify incomplete two-dimensional (2D) shapes similar to the ones in Fig. 6 after having been trained to verbally identify the corresponding three-dimensional (3D) shapes. They found that the parrot was indeed able to identify the incomplete 2D shapes, whether they required amodal or modal completion. Importantly, the parrot had previously been trained only with 3D shapes, and had never been tested with their 2D counterparts, let alone 2D shapes requiring completion. While the authors acknowledged that the exact mechanism underlying the results is not clear, the finding at least provides evidence that parrots might engage in a “gestalt”-style processing of the world, possibly reflecting higherorder cognitive abilities.

Another aspect of modern learning and cognition that draws a parallel from Gestalt psychology is the concept of configural, as opposed to elemental, processing (Wasserman 1997). Elemental processing refers to a bottom-up processing of the

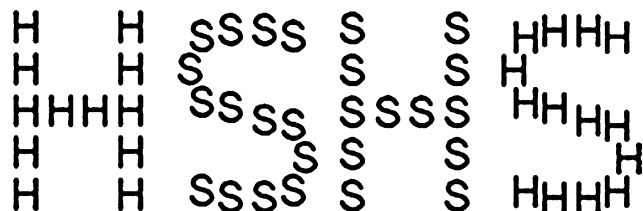
individual parts of a stimulus set, whereas configural processing refers to processing the complete stimulus set as a whole, akin to a gestalt. For instance, suppose an animal is presented with a light and tone simultaneously, followed by food. Elemental processing would be said to take place if the animal forms two distinct associations, one between the light and food, and another between the tone and food. Configural processing would be said to take place if the animal forms a single association between the light-tone configuration and food. Some modern learning theories use the concept of configural learning (e.g., Pearce 1987), and a number of findings suggest that configural associations play a role in animal learning (for a review, see Pearce and Bouton 2001). Other research suggests animals may engage in both types of processing in varying degrees (Honey et al. 2014).

A related concept in modern learning and cognition drawing inspiration from Gestalt psychology is that of global, as opposed to local, processing (Navon 1977). For instance, imagine one is asked to discriminate between hierarchical stimuli, such as those shown in Fig. 13, involving large letters made up of small letters. Local processing would be defined as focusing attention on the small letters, while global processing would involve focusing attention on the large letters, as in “seeing the forest before the trees.” Hopkins and Washburn (2002) trained chimpanzees and rhesus monkeys on discriminations between hierarchical stimuli similar to those shown in Fig. 13. The authors found that while rhesus monkeys performed better when the discrimination was between the small letters (local processing), the chimpanzees performed better when the discrimination was between the large letters (global processing). The global processing exhibited by the chimpanzees may be interpreted as a gestalt



**Gestalt, Fig. 12** On the *left*, a square requiring amodal completion; on the *right*, a square requiring modal completion

**Gestalt, Fig. 13** Local and global processing



processing of the whole stimulus. More generally, there appears to be a relationship between cognitive complexity and global processing (Neiworth et al. 2006). In a study that compared adult humans with children and adult tamarin monkeys, adult humans showed the strongest tendency towards global processing, while children and adults tamarin monkeys showed similar, lower levels (Neiworth et al. 2006).

As the preceding findings show, Gestalt-inspired principles serve as a useful basis for studying animal learning and cognition, as well as for performing cross-species comparisons. The general presumption is that the level of gestalt processing reflects the level of cognitive complexity, although the specific underpinnings of such processing remain unclear.

## Conclusion

Gestalt psychology defined perception as an active way to organize the stimuli that surround us. From first decades of the twentieth century, the primary Gestalt authors (Wertheimer, Koffka, and Köhler) experimentally studied the principles and laws which describe the general trends of how we group sensorial information. The Gestalt perspective changed the general conceptualization of the study of cognition, emphasizing that molar processing in perception could influence other basic psychological processes.

## Cross-References

- [Categorization](#)
- [Cognition](#)
- [Insight](#)
- [Pareidolia](#)

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## Gestalt Laws

### ► Gestalt

## Gestation Stall

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## Synonyms

Individual sow accommodation; Sow stall

## Definition

A metal enclosure used to house an individual breeding sow during pregnancy.

## Introduction

Pregnant sows may, in some agricultural systems, be kept in small individual pens. Sows are typically kept in these stalls until several days before their expected parturition date when they are moved to farrowing crates. Gestation stalls are made from metal pipes or bars and are often approximately 6.5 feet long by 2.5 feet wide. Food and water is provided at the front of the stall, and, at the rear, a slatted floor allows manure to be collected in a pit underneath the building. The stall is long enough for the sow to take a few steps forwards or backwards, but the width of the stall does not allow the sow to turn around.

Gestation crates are an example of a housing system of extreme confinement, epitomizing the advantages and disadvantages of this approach to farming animals for meat. Crates contribute to highly efficient systems that produce abundant supplies of meat at a relatively low cost. Crated animals can be easily controlled, inspected, fed, and protected from outside hazards such as extreme temperatures, parasites, or predation, and the potential for inter-sow competition and aggression is greatly reduced. However, this efficiency is at the cost of the animals being able to engage in normal social interaction, perform natural foraging, or nesting behavior, move more than a few steps at a time or turn around. As such, it challenges the idea of how animals should live, and whether it is reasonable to keep them in such small and barren environments.

## Alternative and Comparisons

Other systems for housing gestating sows include larger individual pens, group pens, hoop barns, and free range (outdoor pasture).

Stall housing is associated with abnormal repetitive behaviors (“stereotypies”) thought to indicate poor welfare, and animals housed in this manner are prone to certain kinds of injury such as pressure sores. However, most other objective measures of health and productivity do not differ significantly for animals housed in stalls versus

other housing systems (AVMA 2015). When sows are group housed, management practices need to be employed to control aggression and ensure that all of the sows have access to food and other resources.

## History

After World War II, Europe and the United States had moved towards raising pigs indoors to control parasites and improve efficiency. Gestation crates were widely adopted by new farms beginning in the 1970s. The housing of sows in confined, individual crates from farrowing to weaning of the piglets had already become common by this time, and extending stall housing throughout pregnancy provided farmers with a number of advantages: the sows occupied less space than in group pens and waste was more easily managed. For these reasons, crate housing often reduces the costs of production and increases productivity (McGlone 2013). Individual housing can also be justified as a method for reducing competition between animals and ensuring that all animals receive sufficient feed, protection, and other individual attention.

As stall and crates were emerging as a dominant system for commercial pig farming, confinement systems were also being challenged as inhumane “factory farming” – for example, by the book “Animal Machines” (Harrison 1964). The degree of confinement imposed by gestation crates has been further exacerbated as their dimensions have generally not been increased sufficiently to accommodate the increasing size of commercially farmed pigs (McGlone et al. 2004).

## Public Attitudes

Sow crates are a frequent subject of the broader debate about how to weigh the different aspects of animal welfare, with increasing emphasis being placed on indications of mental health and opportunities to perform natural behaviors. On this basis, in North America, a majority of the public

support banning the use of gestation crates (Tonsor et al. 2009), and, when surveyed, individuals who were taught more about how these systems are used tended to exhibit stronger disapproval (Ryan et al. 2015).

## Conclusion

Gestation crates were initially welcomed as a modern system that benefited sows’ physical health, and the safety, and cost of pork. Over time, the degree of confinement that crates impose on animals has been demonstrated to negatively impact their mental health, and the use of crates is now unpopular with consumers in developed nations in America, Europe, and Australasia.

## Cross-References

► [Farrowing Crate](#)

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## Gesture

► [Catarrhine Communication](#)

## Gestures

### ► Human Infancy and Childhood

## Ghost Control

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### Definition

An experimental technique used to differentiate social learning mechanisms.

### Introduction

The “ghost control” is an experimental technique used to tease apart social learning mechanisms (Hopper 2010). When learning from watching the actions of others, a naïve observer may faithfully copy the bodily actions of the expert (i.e., imitate them) or they may learn about the environmental changes caused by the actor and reach the same goal through their own means (i.e., emulate them) (Wood 1989). In a ghost control, the animate model is removed from the demonstration, making it look as if the task were acted upon by “a ghost.” The researcher can then measure subjects’ abilities to learn from, and replicate, methods shown in ghost control displays in comparison to observing live (often conspecific) models. Thus, the ghost control is one method that can be employed to help tease apart social learning mechanisms, namely to distinguish imitation from emulation.

### Theory

The theory underlying ghost controls is most clearly exemplified by an idea put forth by Michael

Tomasello in his book *The Cultural Origins of Human Cognition*. Tomasello asked the reader to consider the following hypothetical scenario involving wild chimpanzees: “if a mother rolls a log and eats the insects underneath, her child will very likely follow suit. This is simply because the child learned from the mother’s act that there are insects under the log – a fact she did not know and very likely would not have discovered on her own. But she did not learn from her mother how to roll a log or to eat insects; these are things she already knew how to do or could learn how to do on her own. (Thus, the youngster would have learned the same thing if the wind, rather than the mother, had caused the log to roll over and expose the ants.) This has been called *emulation learning* because it is learning that focuses on the environmental events involved – the changes of state in the environment that the other produced – not on a conspecific’s behavior or behavioral strategy” (Tomasello 1999, p. 29). Following this idea, a ghost control condition would equate to the wind rolling the log, while the experimental condition would provide a live model, akin to the mother chimpanzee in Tomasello’s example.

### Methodology

To create ghost control displays, researchers have employed a range of techniques – both digital and mechanical – to provide a demonstration without a social model. Typically, the social model is omitted altogether and a hidden mechanism is used to move the apparatus, for example via near-invisible fishing-line (e.g., Hopper et al. 2015) or with magnets (e.g., Loukola et al. 2017). In contrast, some researchers have used video manipulation either to digitally remove the actor from video footage shown to observers (e.g., Huang and Charman 2005) or to crop the frame to eliminate the actor from view (e.g., Flynn and Whiten 2013). Lastly, in tests of social learning using touchscreen interfaces, stimuli on the screen have been programmed to automatically show the required pattern of responses without the need for a social model to demonstrate them (e.g., Subiaul et al. 2004).

## Species Tested

The ghost control technique has been used extensively with human children (e.g., Thompson and Russell 2004) and nonhuman primates (e.g., Hopper et al. 2015), and also with dogs (e.g., Miller et al. 2009), birds (e.g., Fawcett et al. 2002), reptiles (e.g., Kis et al. 2015), and even insects (e.g., Loukola et al. 2017). Hopper (2010) provides a review.

## Criticisms of the Ghost Control

It has been argued that the ghost control has limitations as a test for emulation as it lacks validity (Howard et al. 2017). For example, the ghost control display might not be equally engaging to the viewer as a demonstration provided by an animate model. In turn, reduced attention to ghost displays, in comparison to animate models, might translate into reduced learning. Additionally, naïve observers may be less likely to learn from ghost control displays, than from socially provided demonstrations, because the movements shown in ghost controls may appear implausible and as if they defy the laws of physics. Therefore, to differentiate imitative from emulative learning, researchers have employed comparable but different controls, such as the end-state method (Hopper 2010), or by showing observers animate models with agency *versus* inanimate models that lack agency (Howard et al. 2017).

## Cross-References

- Andrew Whiten
- Canine Cognition
- Cecilia Heyes
- Cognition
- Cognitive Imitation
- Comparative Psychology
- Copying
- Cultural Transmission
- Culture
- Diffusion
- Emulation

- Goal-directed Behavior
- Imitation
- Learning
- Stimulus and Local Enhancement
- Ludwig Huber
- Michael Tomasello
- Mimicry
- Primate Cognition
- Rational Imitation
- Rodentia Cognition
- Social Learning
- Tom Zentall

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## Gibsonian Approach in Ecological Psychology

### ► Perception-Action Theory

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## Gibsonian Approach to Depth

### ► Depth Perception

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## Gisela Kaplan

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### Prehistory

Gisela Kaplan grew up in West Berlin and migrated to Australia in 1968. She is a field biologist and emeritus professor of animal behaviour at the University of New England (UNE), Armidale, New South Wales, and also serves as honorary professor at the Queensland Brain Institute. Her fields of research have been largely in primate and avian cognition and communication with an increasing focus on Australian avian species.

Her career in animal behaviour started rather late in life and was preceded by an entirely separate career in literature and social science (sociology and psychology, both as major study areas). As an overseas applicant, she completed a higher school certificate in Melbourne and won a coveted Commonwealth Scholarship for Excellence (top 4% of results statewide), despite

substantial hurdles of having had to learn English at the same time as taking the subjects. Kaplan came from a humanistic schooling background (a selective lyceum) in which Latin, Old Hebrew and Greek were taught but, at that time, not necessarily English. She chose to study at Monash University, and there, she completed a BA (Hons first Class) and a postgraduate diploma in education qualifying her as a secondary school teacher. At the end of that qualifying year, she was awarded a Commonwealth Postgraduate Scholarship for Excellence and enrolled in a Masters of Arts (awarded in 1978) and then in a PhD. Throughout her PhD, she taught night classes and took on projects such as translating the work by German anthropologists into English and translating Sir Monash's letters to his father for a book. On being awarded her first PhD in 1984 at Monash University, she advanced very quickly through the ranks at various universities and was appointed foundation professor of social sciences in 1990, serving as head of the newly formed school at the Queensland University of Technology. In that time, between 1989 and 1996, she published six books and many papers, working on social movements, social injustice and racism. This led also to the prestigious Gustavus Myers Human Rights Award in 2002 for the joint project of *Challenging Racism and Sexism* (1994, edited by E. Tobach and B. Rosoff) by offering explanations alternative to genetic determinism. Later, her joint book with Lesley Rogers brought together the social and the scientific critique of social and scientific biases (Kaplan and Rogers 2004).

### Changing Career

These activities and scholarly engagements seemed a long way off animal behaviour, and indeed, they were, had it not been for some exceptional opportunities that became career changing. In extensive field research of orangutans (*Pongo pygmaeus*), undertaken in team work with Prof Lesley Rogers, Kaplan began investigating innovative and cognitive behaviour, hand preferences and inter-species communication, reflected in a series of joint papers and in three books devoted

entirely to orangutans, the first being published in 1994.

Kaplan and Rogers then established a colony of common marmosets at the University of New England to enable close-up primate research on perception, lateralisation, communication and a range of welfare issues. The colony attracted many postgraduate students and produced a volume of papers and PhD theses over more than a decade. The combination of field work with orangutans in Borneo and laboratory/purely behavioural work with common marmosets enabled a broad view of great apes versus New World monkeys and raised issues of social organisation and evolutionary and cognitive questions both within primatology and in animal behaviour in general. For a considerable time, UNE became the only facility in Australia in which primate behaviour could be studied to PhD level on tertiary campus grounds well equipped and especially designed for behavioural studies. Kaplan then served on the international scientific committee of the International Primatological Society (IPS) and is a life member of that organisation.

By 2004, it became clear that the primate-centric approach to cognition had to be examined more closely. Kaplan, together with Rogers, put together a substantial edited volume asking precisely whether, indeed, primates are cognitively superior to other species. It was the first major publication on the topic (Rogers and Kaplan 2004).

Kaplan's interest in animal behaviour was more and more drawn to birds. While studying orangutans was within Kaplan's qualifications (incl. Experimental/comparative psychology), the study of bird behaviour was not. Kaplan thus enrolled in a second PhD at the Veterinary School at Queensland University, spending years acquiring a classic ethological training as well as a sound veterinary science background. Her thesis analyzed general development, vocal development and communication in Australian magpies, using data collected over thousands of hours of field-work. This detailed study, conducted beside near full-time academic work and the only study of a single Australian avian species, not only gained her a second PhD (2005) but also the coveted

Dean's Commendation of Veterinary Science for Outstanding Original Research (2007).

Kaplan started out again as a junior research scientist, moving quickly through the career stages to senior research fellow, and was appointed professor of animal behaviour in 2007 at the University of New England, by which time she already had accumulated a substantial number of publications in animal behaviour including eight books jointly authored with Lesley Rogers.

Professor Gisela Kaplan has become a very eminent voice in animal behaviour and particularly bird behaviour and cognition, reflected in substantial research papers and a substantial number of books, many of them noted internationally and bestsellers, as well as a string of awards, among them the prestigious Whitley Award for Behavioural Zoology for her book *Bird Minds* (2015). This and her latest book, *Bird Bonds* (2019a), have had strong positive international attention (e.g. reviews in *Animal Behaviour* and in one of the oldest and most prestigious American ornithological journals *The Auk*). In 2014, she was elected an honorary corresponding member of the American Ornithological Society (AOS), a society that maintains an honours list of the 100 most eminent extant avian scholars worldwide, outside the USA and Canada. In 2011, the University of New England awarded Prof Kaplan an honorary doctor of science, and in 2016, she was appointed emeritus professor in animal behaviour.

## Research Emphases

Kaplan has found a very rich field of study in Australian native birds, being inspired by the taxonomical findings between 2002 and 2011 which confirmed that modern songbirds first evolved in Australia (then East Gondwana). Indeed, some 22 lineages are said to have survived the mass extinction events of 56 million years ago, including the stem lineages for cockatoos and possibly other psittacines.

One of her major contributions to avian and cognitive studies lies partly in the reassessment



of behavioural and cognitive traits in birds from an evolutionary perspective and redressing almost single-handedly the previously held assumptions about modern birds' origins in the northern hemisphere. Australian birds thus offered her opportunities to study the original lineages from which later emigrants to other continents may have diverged and speciated (Kaplan 2015, 2019a).

Her model species became the Australian magpie, a member of the broader Corvida and widespread across Australia. Her research and ideas have focussed on this project, conducting groundbreaking research into vocal learning, communication (Rogers and Kaplan 2000) and cognition (Kaplan 2019b). The project, over a 25-year period, involved in-depth examination of their vocal and cognitive abilities, studying the song control system (Deng et al. 2001), their physiological preconditions for song performance (Suthers et al. 2010), how juveniles learn (Kaplan 2017b, 2018a) and manifestations of hemispheric specialisations in vision (Koboroff et al. 2008) and audition (Kaplan 2017a). Magpies have a number of unusual attributes such as a substantial song repertoire not typically associated with territorial songbirds, and males and females sing alike and all year round (Kaplan 2008a). Kaplan documented that both males and females are capable of extensive mimicry of other species, including human voices (Kaplan 2000, 2004). Furthermore, Kaplan uncovered the multitude of signal characteristics of magpies, including special referential signals (Kaplan 2008b; Kaplan et al. 2009; Kaplan and Rogers 2013). Kaplan's project showed that successful maintenance of territory is built on clever strategies (Koboroff et al. 2013).

Kaplan was the first to discover pointing behaviour in an avian species (Kaplan 2011) and the first to study complex cognitive and affective behaviour in Australian land birds as a whole (Kaplan 2015), inviting searching questions about the cognitive and social requirements for which biological adaptations had to be made (Kaplan 2019a, 2020). She also conducts research with other species, such as tawny frogmouths (Kaplan 2018b), zebra finches (Rogers et al.

2018), a number of psittacine species Kaplan (2020b) and even the domestic chicken (De Tommaso et al. 2019). Kaplan is a member of the International Ornithology Union (IOU) and has served on its executive.

Over both careers, Kaplan has authored more than 250 research articles and published 23 books and is a constant presence in the media. She has been called one of the most prominent science communicators in Australia. Indeed, she has brought knowledge of the behaviour and life histories of Australian birds close to the general public, be this via books and radio programmes, podcasts, speaking engagements or personal e-mails to listeners or readers. In her spare time, Kaplan rehabilitates native birds under license and has done so for the past 25 years.

## Cross-References

- [Birds](#)
- [Corvids](#)
- [Lesley J. Rogers](#)
- [Psittacine Cognition](#)

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## Global Geometry

### ► Geometric Encoding

## Go/No-Go Procedure

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## Synonyms

### Stop-Signal Task

## Definition and Specificity

The Go/No-Go (GNG) procedure is an experimental paradigm designed to probe, primarily, behavioral response inhibition. The task involves a continuously presented series of stimuli composed of frequent Go cues and less frequent No-Go cues. Subjects respond to stimuli either by executing (to Go cues) or by withholding (to No-Go cues) a behavior, such as pressing a designated key. It is essential to the GNG task that

Go cues are presented more frequently than No-Go cues so that response to the former is automatic and response to the latter is effortful. In human studies, the two types of stimuli are typically presented in the auditory or visual modality.

Tasks similar to the GNG task include the Two-Choice Task and the Stop-Signal Task (SST). In the Two-Choice Task, subjects are typically required to respond to a stimulus using one of two possible choice responses. The spread of response time (RT) distributions in the GNG task was reported to be larger than that in the two-choice task (Gomez et al. 2007), which may be of significance when RT is applied to compare individuals scoring low vs. high on some trait (e.g., Liu et al. 2015). The Stop-Signal Task (SST) is considered functionally equivalent to the GNG task in capturing individual differences in inhibiting actions and impulsive behavior (Verbruggen et al. 2019). Despite similarities, there is also an important difference; the former is used to test the ability or failure to withhold a response before its execution (action restraint), whereas the latter assesses the ability or failure to inhibit a motor response during its execution (action cancellation) (Eagle et al. 2008). In the fields of neuroscience and psychology, the SST is a well-established tool to study response inhibition across human and nonhuman populations. The paradigm combines two concurrent tasks; participants typically perform a two-choice Go task (pressing different keys depending on the provided stimuli), but on a minority of the trials, a predetermined stop signal appears requiring subjects to suppress the prepared or initiated Go response. It is important to note that direct comparison of the GNG and SST indicate distinct underlying neural mechanisms and dynamics, implying that interchangeable use of the two superficially similar inhibition tasks is unjustifiable (Raud et al. 2020).

## Design and Measured Variables

Being a relatively simple task, when designing a GNG procedure, three parameters need to be

determined; the proportion of Go relative to No-Go trials, the total number of trials, and the RT window.

There is great variability across studies with respect to both the proportion of the two types of stimuli and the total number of trials.

An underlying assumption of GNG tests is that the Go response is more automatic; as such, it can be withheld only via recruitment of inhibitory functions and processes. For the Go response to be more prepotent, the Go stimulus must be presented more frequently than the No-Go stimulus. In case of too frequent No-Go stimuli, participants might tend to wait for a No-Go trial to occur, resulting in differences in performance (e.g., slower RT to Go trials as a result of expecting those to be No-Go trials) caused by diverse strategies to anticipate No-Go trials. Although this basic principle is widely accepted, a great number of studies use equiprobable Go/No-Go trials. To test whether applying such equiprobable tasks elicit prepotent motor activity and probe inhibitory control, EEG data were recorded during four GNG tasks, varying in No-Go rate and trial duration (Wessel 2018). Findings revealed that only fast-paced GNG tasks with rare No-Go trials reliably evoked relevant brain activity. Therefore, it is suggested that in proper GNG studies a maximum of 25–40% No-Go trials are used, to reliably evoke prepotent motor activity, otherwise the inhibitory requirements of the tasks are greatly reduced, which has major implications for the usage of the paradigm in experiments. In some functional magnetic resonance imaging studies, the proportion of No-Go trials can be 10% or less, accompanied by a very high (>1000) number of total trials (e.g., Kaufman et al. 2003). Although reliability increases with the total number of trials, adding more trials than the minimum necessary is not always feasible, considering that factors other than inhibition, such as decreasing attention or motivation and/or increasing frustration, may have a confounding effect. The selected time window may also move in a wide range depending both on the given GNG procedure and the research question.

Despite its apparent simplicity, these three features of the GNG paradigm vary across studies in

ways that can affect the validity of the obtained results in comparative studies.

The basic dependent variables measured in a GNG procedure are two error types and the RTs for Go responses (and sometimes for erroneous hits to No-Go stimuli). The subject commits an omission error not executing a Go response on Go trials and a commission error making a Go response on No-Go trials. The analysis is typically based on calculating the commission error percent (the proportion of commission errors relative to the total number of No-Go stimuli), and sometimes also on the omission error percent (the proportion of omission errors relative to the total number of Go stimuli). In the most typical application of the GNG procedure, the primary function of interest, response inhibition (withholding a prepotent behavioral response), is indexed by the commission error rate, with fewer errors implying better inhibition. The secondary function of interest, attention, is indexed by the omission error rate, with fewer errors implying better attention.

RT is calculated as the average latency of correct Go responses (the elapsed time between stimulus onset and execution of a correct Go response). RTs for Go responses are informative about how the sequence of perception, decision-making, and action is organized. In a GNG task, unlike the latency of Go responses, the latency of response-inhibition cannot be directly observed. Conversely, the SST allows the estimation of the covert latency of the No-Go reaction, as the stop signal can be presented after a variable delay following the onset of the test stimulus.

## To Go or Not to Go?

That is the simple question subjects face many times in a row in the GNG procedure. However, what seems to be simple, can be pretty difficult, depending on the participant's temperament, personality, executive functioning, and attentional and motivational state.

The GNG is one of the most commonly used paradigms to assess response inhibition that is a crucial component of adaptive and goal-directed

behavior (Votruba and Langenecker 2013). It is essential for navigating everyday life without conflict and deficiencies in this ability can contribute to numerous neurological and psychiatric disorders. As described, in an experimental set up, response inhibition refers to the suppression of prepared or initiated actions and successful response inhibition results in the absence of an observable response. Research using the GNG task has revealed links between inhibitory control capacities and a wide range of behavioral and impulse control problems in everyday life (e.g., attention-deficit/hyperactivity disorder – ADHD; Barkley 1997) and revealed unique information about the underlying neurocognitive control mechanisms of impulse control. In GNG tasks, compared to typically developing peers, youth with ADHD exhibit more errors and slower RTs and their omission errors are primarily associated with inattention, whereas commission errors can be primarily associated with hyperactivity/impulsivity (Bezdjian et al. 2009).

Active choice by GNG paradigms has been also used to measure the effects of cognitive biases on emotional states and disorders (e.g., depression) in humans. Cognitive bias is a systematic pattern of responses; it occurs when an affective state or temperamental trait affects cognitive processes. This concept is based on findings that people in negative emotional states will show increased attention to negative stimuli and are more likely to make pessimistic interpretations of ambiguous situations (e.g., intermediate between Go and No-Go stimuli). Individual differences in cognitive biases in humans are related to dimensions of personality, attention, memory, and impulsivity (e.g., Marshall et al. 1992). Considering the findings on the links between response inhibition and ADHD symptoms, it should be noted that the results of GNG tasks employed to assess cognitive bias certainly reflect variations in characteristics beyond cognitive biases, such as in individual differences in attention and behavioral disinhibition.

In humans, neuroimaging techniques have also been used to find differences in brain response to Go and No-Go stimuli and thereby reveal the neural substrates of response inhibition.

The GNG procedure is relevant to assessing the association between task performance and important sociocognitive traits not only in humans. It is ideal for comparative research, as it is appropriate for assessment of human and animal subjects without considerable alterations to experimental or task design (Eagle et al. 2008).

## Application in Nonhuman Studies

Although human participants receive little to no training before GNG measurements, they do receive instructions on how to complete the task, such as to respond as quickly as they can. In contrast, animals need extensive pretraining for GNG measurements, which may have an impact on their performance. Choice tasks have been argued to be preferable to GNG tasks because they allow a general lack of motivation to respond to be distinguished from a pessimistic interpretation of an ambiguous stimulus, however, GNG tasks are usually faster to train. Animals are rewarded with food for every correct Go and No-Go response during the training sessions (Tremblay and Schultz 2000). Even during the test sessions, continuous reward might be needed for the correct choices, which can interfere with some test designs, for example, when an ambiguous stimulus is presented.

Following a classical training procedure, scent-detection variants of the GNG task involve training detection dogs to respond to the presence of a new target scent and not respond to control samples (Concha et al. 2019). In line with other animal studies, dogs are trained to sniff individual carousel arms without assistance from their handler, applying operant conditioning methods, using only positive reinforcement (food/ball reward) and negative punishment (no reward in case of false indications). Of note, in this version of the paradigm, RTs cannot be evaluated as the odor stimuli are presented simultaneously, using a multichoice carousel, which makes it impossible to apply a preset time window.

In contrast, introducing a slightly different training procedure, a more standard GNG

procedure has been used with companion dogs (Bunford et al. 2019a). Stimuli were presented by a touchscreen device, and dogs were trained to operate the touchscreen device by a step-by-step procedure using food reward but no aversive stimulus. Early on during training, owners could actively “explain” to their dogs what to do and comfort the animal in case of failure (i.e., no reward situations), to avoid loss of motivation and make the situation more similar to other training contexts. After dogs learned to respond to the Go stimulus by executing a nose poke, they were presented with the Go and No-Go stimuli simultaneously and trained to respond only to the Go stimulus. Dogs were rewarded with a treat and praise/stroke for every correct Go response but received no negative feedback for omission or commission errors. During the final phase of training, dogs were presented either with the Go or the No-Go stimulus and were rewarded for every correct No-Go response, with the time between stimulus onset and food reward gradually increased until it reached 3 s (the preset time window) to make the relatively long inhibition period less frustrating.

As the dog was recently proposed to be a promising model species to study the evolutionary background of certain human sociocognitive skills, comparative studies aim to apply similar research tools across species. Given that in humans, behavioral disinhibition is associated with personality and ADHD features, the authors of a recent study aimed to examine the associations between family dogs’ performance on a behavioral GNG paradigm and their owner-reported personality and inattention and hyperactivity/impulsivity scores (Bunford et al. 2019a). A greater proportion of commission errors was associated with greater hyperactivity/impulsivity, in accordance with what has been found in humans. Regardless of accuracy, greater confidence and extraversion and lower openness were linked to shorter RTs to correct Go responses and commission errors, and greater inattention was associated with shorter latency to commission errors.

With a diverse set of tasks and tools applied, cognitive biases have been observed in a range



of nonhuman animal species (e.g., Kis et al. 2015). Discrimination tasks are one effective method for probing cognitive bias in animals, however, a GNG procedure necessitating active choice in response to ambiguous stimuli could also be applied efficiently. In studies with discrimination tasks, animals' inner states are typically experimentally manipulated to induce cognitive bias. In one study, to assess if negative emotion induction (being housed under unstable vs. stable conditions) leads to negative bias in rats, a GNG task was applied; subjects were trained to press a lever to the Go stimulus to obtain a food reward and to withhold this behavior in response to the No-Go stimulus and avoid a burst of aversive white noise. Rats housed in a chronically stressful environment responded less quickly and frequently both to Go and to ambiguous stimuli, indicating less optimism (Harding et al. 2004).

Recently, in dogs, to assess the link between personality and naturally occurring individual differences in cognitive biases was examined (Bunford et al. 2019b). The study established a relationship between a behavioral index of more positive/negative judgments about ambiguous stimuli in a modified Go/No-Go paradigm and individual differences in owner reported personality; dogs with higher conscientiousness and extraversion scores were more likely to exhibit a Go response to ambiguous stimuli.

Despite the many advantages of the GNG procedure, there are also limitations of the method in comparative studies. Considerable pretraining is necessary, differences in food motivation can have a confounding effect, and the paradigm may not be useable in case of some focus populations, such as for example, in dogs with extreme traits such as having high scores on ADHD-like symptoms.

## Conclusions

The GNG procedure is a simple experimental set up that is especially efficient in assessing some important sociocognitive abilities of humans and nonhuman animals such as response inhibition

and cognitive bias. Analyzing the number and proportion of the two types of errors (commission and omission errors) and the RT for go responses can contribute to important discoveries about the relations between functions such as behavioral response inhibition, attention or temperament in different species and help establish, in comparative studies, boundaries of comparability for modeling human inhibition and other characteristics of which inhibition is part.

## Cross-References

- Cognitive Bias
- Stop-Signal Task

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## Goal

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## Synonyms

Aim; Objective; Purpose; Target

Like many other terms in psychology (e.g., see “Drive State,” this volume), “goal” is a term from ordinary language. In the Oxford English Dictionary (<https://en.oxforddictionaries.com/definition/goal>), the following ordinary meaning of “goal” is found (among others): “The object of a person’s ambition or effort; an aim or desired result.” Psychologists’ uses of “goal” adopt and elaborate on this ordinary meaning, where by “goal” they mean a kind of mental state that “guides” certain actions conducive to reaching the goal. Roughly equivalent terms are “purpose” and “aim.” A term that often accompanies talk of goals is “outcome,” an end-product or result of actions that are guided by the goal.

Somewhat more technically, but perhaps less intuitively, most psychologists (except for Skinnerians) view goals “as internal representations of desired states, where states are broadly construed as outcomes, events, or processes” (e.g., Austin and Vancouver 1996, p. 338), where “internal” usually means “mental” (and vice versa). A mentally represented outcome is an expected or *thought-of possible* result of certain thought-of actions. If the thought-of actions actually occur, the thought-of results may or may not actually occur. If they do, the goal is said to have been achieved.

This view is consistent with a defining feature goals share with other mental states such as expectancies, desires, needs, wants, wishes, and beliefs. Philosophers of mind call this feature “intentionality,” from the Latin noun “intentio” and verb “intendere,” meaning “to point to” or “to aim

at.” The notion was introduced by the Medieval Scholastics and revived by philosopher/psychologist Franz Brentano in his 1874 *Psychology from an empirical standpoint* (originally published in German, and translated into several other languages).

Intentionality is the property of “being about,” “being directed towards,” or “referring to” something. In more contemporary lingo, intentional states have *representational content*, or are *propositional attitudes*. Paradigmatic examples are beliefs, which makes them essentially similar to goals. All beliefs are about something, and this is their distinctive feature. For example, the belief *that* it is raining is about rain, where the term “that” is used as a function word to indicate the subject or object (rain) of verb (believing). The term “that” here thus indicates a direction, pointing to or aiming at something, the object of an intentional state (in the case of this belief, rain). However, the object of this belief is not the actual physical rain occurring externally, independently of the mind, but a mental representation of rain.

In general, Brentano maintained that an intentional state’s object (that about which the state is) was *constitutive* of or *existed in*, and hence it was as mental as, the state itself. The object is a mental representation *of* (not about) something external to the state. The belief that it is raining is about a mental representation of rain, not about the actual physical rain, *even if it is being witnessed*. If not (perhaps someone said it was raining), the mental representation which is the object of the belief cannot be of that particular rain, but of something else, most likely of previously experienced rains.

This distinction becomes clearer in the belief that it *will* rain tomorrow. Evidently, this belief cannot be about tomorrow’s rain. It seems incoherent to say that a mental representation represents (literally, “presents again”) a future event. What is represented in that belief must be something else, most likely, previously experienced rains. If the believer has never experienced rain before, the belief would be about some previously experienced verbal description, painting, or photograph of rain.

The same clarification applies to goals: The goal to get a college degree is not about some yet-to-occur future state that exists nonmentally, independently of and external to the goal. Rather, the goal is about a mental representation of something, a representation that exists in the present and only mentally, as part of the goal *qua* mental state. This something could be a variety of previous experiences (e.g., photographs or videos of people obtaining their degree, verbal descriptions of the advantages of getting a degree, photographs of actual college degrees obtained by other people, etc.), which are external to the goal and its object. This clarification avoids the absurdity that goals are determined by something in the physical future, which violates the venerable but still valid principle that the physical future cannot cause the physical present.

In theorizing about goals, psychologists often speak of “goal-oriented behavior” to refer to actions that are guided by goals *qua* mental representations (see Aarts and Elliot 2012, for a recent compilation). But then again, goal-oriented behavior is not determined by the yet-unachieved goal in the physical future. The mental representation, the object of the goal, can only be of some previous experience (e.g., having achieved a goal in the past, tales of others having achieved goals and their perks, etc.).

A desired outcome is also often said to be “anticipated” or “expected.” But how do outcomes come to be expected? Answers have revolved around the conjecture that *learning* is key to goal-formation and pursuit. During 1920s and 1940s, classical learning psychologists based their answers on observations of subjects, typically hungry rats, that learned to navigate mazes (typically T mazes) from a starting area to a finish or “goal” area with a reward in it (typically food). The more precise question here is this: How do rats learn to anticipate that navigating a maze in a certain way will allow them to reach the finish box and obtain the reward without sensing any of it from the starting box? This question, in contrast to the ordinary definition of “goal” given at the

beginning, admits the possibility of goals in non-human animals.

Hull (1930), an influential classical learning theorist, called this ability “foresight,” “*the reaction to an event which may be impending, but which has not as yet taken place*” (p. 514). But then again, it is incoherent to say that the rat reacts in the present to a future event (obtaining the food). Whatever the rat reacts to must reside in the present and/or the past. Hull hypothesized that sufficient experience with obtaining food in the finish box by navigating a maze in a certain way promoted the strengthening of *stimulus-response* (S-R) associations. The Ss were the maze’s various exteroceptive cues (e.g., visual, auditory, olfactory, tactile), and the animal’s proprioceptive cues. The Rs were the rat’s various movements through the maze.

Hull (1943) also submitted his “goal-gradient” hypothesis. According to this hypothesis, the S-R associations grew progressively stronger as the animal approached the finish box, after sufficient experience with obtaining food at the end of the maze for navigating it in a certain way, which Hull viewed as “reinforcing” S-R associations. Hull thus conceived goals as chains of S-R associations that progressively led the animal from the start to the finish box. Rather than unanalyzable, elementary constructs, Hull (1943) viewed goals as “emergents” (p. 29) that could be derived from more elementary postulates about stimuli, responses, and their associations.

Hull proposed that *need reduction*, discussed in another entry (see “[Need Reduction](#)”), was the reinforcement mechanism in maze learning. His theorizing was molecularist in that he viewed particular responses as the proper units of analysis of goal-seeking behavior. Tolman’s (1948) “purposive behaviorism,” in contrast, was *molarist* in that he viewed *acts*, long response chains, as the proper units of analysis of goal-seeking behavior. He further hypothesized that maze learning consisted in the formation of “cognitive maps” as mental representations of all the maze’s relevant spatial locations and their relative positions.

More recently, goal-directed behavior has been studied using operant conditioning chambers,

where the reward is given in a food receptacle that the animal must approach to obtain the reward. Unlike mazes, operant conditioning chambers have no paths that the animal must learn to reach the site of the reward. Animals in this apparatus have been observed to approach and engage with the site of the reward. Boakes (1977) called this behavior “goal-tracking” and defined it as behavior directed towards the location of the reward.

Typically, obtaining the reward in an operant conditioning chamber also requires a so-called instrumental response (e.g., pressing a bar in rats), which could be viewed as part of a goal-directed behavior. Some researchers have studied whether this response is affected by changes in the value of the reward. For example, Colwill and Rescorla (1985) trained rats in an operant conditioning chamber to obtain two rewards, each one dependent on a different response topography (bar-pressing vs. chain-pulling). Then, one reward was devalued through association with either illness induced by LiCl, or satiation. In a test, both instrumental responses were measured. The results showed a significant reduction in the rate of the response that had been associated to the devalued reward. This result suggests that goal-directed behavior is sensitive to S-outcome relations.

Some researchers (e.g., Dolan and Dayan 2013) also distinguish habits from goal-oriented behavior. On this distinction, a habit is automatic and insensitive to changes in the value of the reward, whereas goal-oriented behavior is directed towards reaching a reward and modifiable by such changes. This distinction is consistent with evidence that instrumental behavior trained for a long time is significantly less sensitive to changes in reward value than instrumental behavior trained for a shorter time (Adams 1982).

Others have used this distinction to explain the transition from recreational to abusive substance drug consumption (for a review, see Hogarth et al. 2013). A drug’s initially high value (due to its novelty) would explain the initial consumption (goal-oriented behavior) as involving action-outcome associations. Initial drug-seeking is goal-directed behavior determined by the drug’s

anticipated incentive value. When the drug is consumed for the first few times, it reinforces in an instrumental way the drug-seeking behavior, promoting the formation of an R-outcome association. After more extended drug consumption, chronic (abusive) consumption (habit) promotes the formation of S-R and S-outcome associations which maintain persistent drug seeking that becomes independent of the drug's initial incentive value.

Despite important theoretical and conceptual differences, most psychologists agree that brain functioning and structure are key to all behavior, goal-seeking behavior included (Hull famously cast his theory explicitly in neural terms, using expressions like “neural reactions,” “neural impulses,” “neural mediation,” and “neural activity”). Some brain regions have been linked to goal-directed behavior. For example, lesions in the medial prefrontal cortex (e.g., Ostlund and Balleine 2005) disrupt acquisition but not maintenance of reward-seeking behavior controlled by instrumental contingencies. This result and others support the view that goals as mental representations may be more profitably viewed as neural representations (activation patterns) in certain brain areas.

## Cross-References

- [Associative Learning](#)
- [Clark L. Hull](#)
- [Drive State](#)
- [Goal-Directed Behavior](#)
- [Instrumental Learning](#)
- [Intentionality](#)

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## Goal-Directed Behavior

- [Appetitive Response](#)

## Goggles Experiment

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The goggles experiment is the common name of an experimental procedure proposed by Cecilia Heyes (1998) with the aim of distinguishing the theory of mind hypothesis of behavior from non-mentalist alternatives. The theory of mind hypothesis claims that nonhuman animals, most

notably chimpanzees and other primates, have a concept of mental states like “see,” “want,” or “know” (Premack and Woodruff 1978). Heyes’ objection was that all experiments and observations supporting this claim could also be interpreted with alternative explanations like associative learning or inferences that did not require mental state attribution.

The original goggles experiment is based on a guesser-knower paradigm (Povinelli et al. 1990), and the procedure consists of three phases:

1. In the *pre-training*, chimpanzees would be trained to wear two pairs of goggles that are only distinguishable from the outside by an arbitrary cue like different rim colors. Only by wearing the goggles, chimpanzees would experience that one pair is opaque while the other is translucent. They would never experience anybody else wearing the goggles at this point.
2. In the *training*, chimpanzees would watch an experimenter hiding food underneath cups behind an occluder. One trainer would be present for the baiting, while a second trainer would leave the room and come back after the baiting. Both would then indicate one of the cups, and chimpanzees are rewarded for choosing the cup indicated by the trainer who saw the baiting (the knower) and never for choosing the cup indicated by the one who left the room (the guesser).
3. In *transfer*, training trials would be interspersed with probe trials in which both trainers remain in the room but wear the pairs of goggles from the pre-training. In this case, the trainer wearing the translucent goggles would be the knower and therefore the right choice if chimpanzees have a concept of seeing. Importantly, chimpanzees would not be rewarded differentially in probe trials to avoid associative learning.

Heyes argued that if chimpanzees take the knower’s cues in probe trials more often than the guesser’s, it would distinguish between the theory of mind hypothesis and non-mentalist alternatives

as it can only be based on using their own mental experience to infer the others’ mental states.

Other variations of the goggles experiment have been proposed. Povinelli and Vonk (2003) suggested simplifying the procedure in a way that does not involve the extra step of distinguishing between knowing and guessing. In this version, chimpanzees can choose to beg for food between two experimenters—one wearing an opaque bucket over their head and one wearing a translucent one. If the chimpanzees preferentially gestured to the latter, it would show that they understand who can and who cannot see them.

In general, a “goggles experiment” has to follow the basic structure of (1) experiencing the properties of unknown eye covers that cannot be inferred from the outside and can only be distinguished by an arbitrary cue and (2) transferring this experience to a novel situation in which others look through these covers and make inferences about their mental states.

Recently, a study based on this general structure has been conducted with chimpanzees with positive results and has therefore been suggested to support the claim of mental state attribution in chimpanzees (Karg et al. 2015). However, the interpretation of these and other results supporting the theory of mind hypothesis in nonhuman animals, including primates and corvids, still remains a debated topic of animal cognition.

## Cross-References

- [Cecilia Heyes](#)
- [Josep Call](#)
- [Michael Tomasello](#)
- [Theory of Mind](#)

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## Gonad

### ► Testis

## Gonochorism

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## Synonyms

Dioecy; Gonochory; Unisexualism

## Definition

Gonochorism is the condition of individual organisms within a species existing as one of two possible sexes, specifically male or female. Gonochorism includes distinct sex-specific reproductive strategies among sexual reproducing taxa.

## Sex in the Animal Kingdom

Within the kingdom Animalia, sexual reproduction is the norm, and asexual reproduction appears as a rare exception, and usually not in exclusion, to sexual reproduction (Avisé 2008; Schön et al. 2009). Gonochorism is likewise characteristic of the vast majority of animal species (Jarne and Auld 2006) and is almost ubiquitous among

vertebrates, with the largest variations occurring among marine organisms, especially teleost fish (e.g., Kobayashi et al. 2013). Compared to asexual reproduction, sexual reproduction necessitates the combination of gametes from two different individuals. In all known animal taxa, sexual reproduction occurs through the combination of heterogenous gametes that differ in size and shape, a condition known as anisogamy (see Kumar et al. 2019). Indeed, anisogamy appears to be common because of the costs associated with isogamy, in which gametes of all individuals are of similar size and shape (Matsuda and Abrams 1999).

The size of the gametes is the most direct means of differentiating between sexes. By definition, male gametes are smaller, and female gametes are larger (see Verma 2019). Individuals producing smaller gametes are defined as males, and individuals producing larger gametes are defined as female. Sex determination mechanisms are more stable among mammals and birds and far more variable among many marine taxa, with genes, environment, and epigenetics determining and reversing sex across numerous gonochoristic fish species (see Baroiller and D’Cotta 2016). However, it should be noted that male and female sex are more usefully defined by reproductive strategy, rather than by immutable physiological characteristics (Schärer 2017). In this way, males and females occupy distinct reproductive niches that reflect the combination of their asymmetrical gametes and results in a cascade of sex differences, such as in morphology and behavior (see Eberhard 1996; Trivers 1972).

Gonochorism can be contrasted to simultaneous hermaphroditism, which is the capacity of an individual to reproduce using either male or female gametes within its lifetime (see Rosenfield 2018). Not infrequently within simultaneous hermaphroditic species, such as marine flatworms (*Pseudoceros bifurcus*; Michiels and Newman 1998), individuals may preferentially attempt to reproduce using less costly male gametes and attempt to avoid reproducing using more costly female gametes (Michiels and Koene 2006). These species are not considered gonochoristic even though they demonstrate a preferred



sex-specific reproductive strategy, because they maintain the capacity to reproduce using male or female gametes. Sequential hermaphroditism also is a separate reproductive strategy from gonochorism, although there is some overlap such that it may be unclear whether a species is gonochoristic or sequentially hermaphroditic (e.g., *Patella ferruginea*; Espinosa et al. 2009). For sequential hermaphroditic species, individuals may change sex across the lifespan but only conserve one sex-specific reproductive capability at a time. For example, an individual of a protogynous species, such as the rock wrasse (*Halichoeres semicinctus*; Adreani and Allen 2008) may begin life producing exclusively female gametes but may undergo a transformation later in life after which it will only produce male gametes. In these cases, the individuals may appear to be gonochoristic, but because it is possible for a female to develop a male reproductive capacity, such taxa are distinct from gonochorism. Gonochorism conveys distinct benefits compared to hermaphroditism and asexual reproduction, which likely have acted as selection pressures favoring the reproductive strategy, but more data are needed to specify the evolutionary trajectory of gonochorism in the animal kingdom (Sasson and Ryan 2017).

## Cross-References

- Anisogamy
- Asexual Reproduction
- Gametes
- Hermaphrodite
- Protandrous Hermaphroditism
- Protogynous Hermaphroditism
- Reproduction
- Sex Role Reversal
- Sex-Linked
- Sexual Dimorphism

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## Gonochory

- Gonochorism

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## Good Genes Hypothesis

### ► [Healthy Mate Hypothesis](#)

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## Gordon Burghardt

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**Gordon M. Burghardt** is an Alumni Distinguished Service Professor in the departments of Psychology and Ecology & Evolutionary Biology at the University of Tennessee. He has broad interests in many aspects of animal behavior, publishing widely in several areas.

## Early Life and Educational Background

Dr. Burghardt was born on October 11, 1941 in Milwaukee, Wisconsin; he spent his early life there in the public schools, wandering in parks and fields, and attending summer camps on the many lakes in the southeast Wisconsin. Here, he nurtured his love of the natural world, especially snakes and other reptiles. Pet animals included turtles, lizards, and snakes, along with a budgerigar, raccoon, skunk, and others. He attended the University of Chicago and, although initially majoring in chemistry, received both his undergraduate and PhD degrees in biopsychology in 1963 and 1966, respectively. His most important mentor was Eckhard H. Hess who was one of the few American comparative psychologists engaged in ethological approaches to animal behavior at that time and who had close contacts with many European ethologists. Hess, though primarily working with birds and humans, encouraged his work on reptile behavioral development and chemoreception.

## Professional Career

After completing his PhD, Burghardt remained at the University of Chicago as an Instructor in Biology but in 1968 gave up a tenure track position to accept a position at the University of Tennessee in Knoxville, where William S. Verplanck, also an experimental psychologist promoting ethology, was building an impressive psychology department. Burghardt thought that getting closer to field settings and national parks and forests was beneficial after spending his life primarily in large cities. Except for professional leaves and visiting fellowships, he has remained at the University of Tennessee for over 50 years. These 50 years have seen many serpentine shifts in research topics, but his core interests remained the same and he has returned to some after a 20–30 year hiatus!

Over his career, he is very proud of the over 40 graduate students he has mentored and the development of many of their careers and accomplishments. They have gone in many different directions, which in some ways mirrors the many areas of research Burghardt has explored. Over the years, Burghardt has been active with several professional organizations and editorships. He hosted the annual meeting of the Animal Behavior Society in Knoxville in 1981, and later that decade was elected to several offices in the society, including President. More recently, he served as President of the Society for Behavioral Neuroscience and Comparative Psychology (Div. 6, APA) and received the Clifford T. Morgan Distinguished Service Award. He also developed and directed the Life Sciences Graduate Program in Ethology at the University of Tennessee. He has edited or been associate editor of several journals including *Ethology*, *Animal Learning and Behavior*, and the *Journal of Comparative Psychology* and served on many editorial boards. He is a Fellow of the American Psychological Association, Association for Psychological Science, AAAS, and the Animal Behavior Society, and received many local awards at the University of Tennessee, including the Macebearer award, the highest academic award for faculty members. Burghardt has published hundreds of journal articles, book chapters, and book reviews as well as having written or

edited seven books, including, most recently, as an Associate Editor of the 80 chapter two volume APA Handbook of Comparative Psychology (2017).

## Research Interests

Burghardt has always been interested in understanding the natural behavior of animals and all his work reflects variations of this focus. His early work was on the ontogeny of food preferences and the role of sensory cues in prey detection and selection, primarily in snapping turtles, natricine snakes, and small lizards. Upon arriving in Tennessee, where few psychology students saw reptiles as useful research subjects, the administrators of the nearby Great Smoky Mountains National Park were having to deal with escalating problems with black bears such as bear jams on the roads, tourists feeding bears, and bears wandering into picnic areas and commandeering culinary resources. He brought Park Superintendent Fry and his staff to UT to give a joint Zoology-Psychology talk and then meetings on developing a collaborative research program. This is still ongoing. Burghardt's role was getting some field observations of bear-human interactions underway with students but within a few months two orphaned bear cubs needed to be cared for, so Burghardt raised them in his house and applied for a small NIMH grant to build a research enclosure in the park. This resulted in research theses by several students in which the fine vision bears have, including color, was established along with basic information on foraging, food preferences, play, agonism, mating, learning, and so on. After many years, Burghardt is again studying bear cub behavior through analyzing den cam videos of the first months of life in natural dens of wild black bears in Minnesota with Lynn Rogers.

Burghardt, as a high school student, joined the American Society of Ichthyologists and Herpetologists (ASIH) and is a life member. All during his career at Tennessee he has continued reptile behavior research in several areas besides snake chemoreception including comparative and ontogenetic studies of constriction, antipredator

behavior, sexual dimorphism, conservation genetics, environmental enrichment, optimal foraging in monitor lizards, effects of diet on behavioral and morphological plasticity, multiple paternity, behavior of two-headed snakes, and other topics. After meeting A. Stanley Rand, scientist at the Smithsonian Tropical Research Institute in Panama, and hearing about the remarkable communal nesting behavior of green iguanas, he teamed up with Stan to study what happened during hatching, nest emergence, and their subsequent life. They discovered remarkable sociality in the hatchlings then viewed as unconceivable in a lizard. This work led to many studies with students and colleagues as well as an edited book. Again, although his main fieldwork ended over 35 years ago, he and former students are still mining important information from the data collected. Two documentaries depict this research.

Another collaborative research program began with a Japanese reptile ethologist, Akira Mori, at Kyoto University studying an unusual snake with two methods of delivering toxins. The snake is the Japanese Tiger Keelback and it is a rear-fanged animal so has a venom that can be dangerous, though the snake is generally not prone to bite. However, the species also has glands on the neck that contain toxic bufadienolides, cardio-tonic steroids sequestered from skin secretions of toads. Associated with these glands are unique defensive postures and behaviors not seen in species without such glands. Research on the biochemical, behavioral, anatomical, physiological, and ecological aspects of these animals has involved a multidisciplinary program of research with many colleagues. Burghardt has worked in Japan and Mori in the US on them. Snakes who do not eat the toads, as from toad-free islands, flee rather than deploy nuchal gland-related defensive behavior and, remarkably, snakes seem to "know" when they are defended by the toxins.

Reptile learning and cognition, including social learning (as in turtles), has also been a focus of his research and he has worked on this topic over much of his career. This focus on learning and sociality in reptiles along with the focus on development led to an interest in why reptiles do not seem to play. For many decades, he has

been studying play and many of his contributions are described in his 2005 book, *The Genesis of Animal Play: Testing the Limits*. He developed criteria for recognizing play in species and contexts where it had not been identified, documented the occurrence of play in a number of unusual species including turtles, lizards, crocodilians, cichlid fish, stingrays, and spiders, formulated a theory underlying play termed Surplus Resource Theory (SRT), developed hypotheses on the origin and evolution of play. He has also worked on phylogenetic modeling of play and SRT and has applied play concepts to creativity, religion, and ritualized behavior.

Although other empirical projects could be mentioned, Burghardt also has written extensively on ethical issues and especially on the early history of animal behavior, ethology, and comparative psychology. He has developed theoretical and conceptual ideas involving communication, critical anthropomorphism, controlled deprivation, and other topics. Besides Hess, Verplanck, Rand, and Mori noted above, the following senior people also were, along with others, extremely valuable at various times in his career: George Rabb, Charles C. Carpenter, Marc Bekoff, Carl Gans, Konrad Lorenz, and Brian Sutton-Smith. He was honored by a symposium on his career organized by former students at the 2014 annual joint meeting of the herpetological societies in Chattanooga, TN, hosted by the ASIH. The occasion was to recognize the 50 years since his first published scientific paper in 1964, a comparative study parsing the roles of prey size and movement in prey capture in lizards. His twin daughters, Karin and Liana, both now PhD biologists doing creative and important research themselves attended, and he is more proud of them than any of his scientific contributions!

## Cross-References

- [Anthropomorphism](#)
- [Bear cognition](#)
- [Chemical cues](#)
- [Chemoreception](#)
- [Play Behavior](#)

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## Gordon Gallup

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## Mirror Self-Recognition

In 1969, he conducted an experiment designed to determine if chimpanzees could recognize themselves in mirrors (Gallup 1970). Although chimpanzees initially respond to mirrors as though they were seeing other chimpanzees, after a couple of days the chimpanzees began to use the reflection to respond to themselves. As an objective test of self-recognition he developed the mark test, where anesthetized chimpanzees were marked with a red, odorless, nonirritating dye on the top half of an eyebrow ridge and the upper half of the opposite ear. Upon recovery from anesthesia, he discovered that the chimpanzees used the mirror to touch and investigate the red marks on their faces that could only be seen in the mirror.

These findings have been widely replicated with chimpanzees and extended to include orangutans and humans. Early attempts to adapt this methodology for use with children, however, were seriously flawed (Gallup 1994). The capacity for mirror self-recognition in other species is widely debated, but as yet the evidence is not conclusive (Anderson and Gallup 2015).

The mark test has been cited as the “gold standard” for assessing self-recognition, and it has survived multiple challenges, including the idea that it may be an artifact of species differences in face



touching behavior (Suarez and Gallup 1986) or an artifact of anesthetization (Povinelli et al. 1997), along with claims that failures to find self-recognition may be due to gaze aversion (Anderson and Roeder 1989), a lack of interest in superimposed body marks (Gallup et al. 1980), or that the presence of a human researcher may inhibit or distract subjects from investigating the marks (Shillito et al. 1999). Pervasive species differences in mirror self-recognition continue to prevail in spite of attempts to argue for the possibility of self-recognition in other modalities (Platek et al. 2004), along with repeated but unconvincing attempts to engineer self-recognition in other species (Anderson and Gallup 2015) and unsupported claims that self-recognition has nothing to do with self-awareness (Gallup et al. 2014).

More recently, Platek and Gallup developed a method for assessing self-recognition that involves showing people faces on a computer monitor, and they are instructed to press particular keys on the keyboard to indicate if it is a stranger's face, a familiar face, or their own face (Platek et al. 2004). Rather than an all or none (pass/fail) approach to self-recognition, this paradigm can be used to quantify individual differences in self-face identification latencies measured in milliseconds and that has led to some striking results implicating important and clinically relevant self-processing deficits (Platek et al. 2003).

Gallup's idea that self-awareness may be a springboard to being able to use your experience to model the experiences of others and make inferences about their mental states has also been controversial (Gallup 1982). The jury is still out about mental state attribution in chimpanzees and orangutans (Shillito et al. 2005), but for humans there are no documented instances of being able to take into account what others know, want, or intend to do without being able to recognize yourself. Likewise, deficits and developmental delays in self-recognition (e.g., autism) covary with mental state attribution deficits, and this also holds true for brain-damaged patients who are deficient in self-recognition as well as those who lose the capacity to recognize themselves due to mental illness (Gallup et al. 2003).

## Tonic Immobility and Open Field Behavior

Tonic immobility is triggered by the application of manual restraint, such as holding an animal down on a flat surface. Initially the animal will struggle and try to escape, but if you persist in holding the animal in place for several seconds it will go into a seemingly catatonic-like state of physical immobility which can last from a few minutes to over an hour or more after you remove your hands.

In a series of studies featuring many different species, Gallup and his students showed that laboratory procedures designed to increase fear (e.g., loud noise, conditioned aversive stimuli) prolong the response, while those that alleviate fear (e.g., handling, taming, tranquilizers) antagonize the reaction. Under natural conditions, the evidence shows that tonic immobility is one of several defensive reactions in a distance-dependent series of antipredator strategies (Gallup 1977). Tonic immobility depends on the integrity of neurological structures at the level of the brainstem, is associated with widespread autonomic involvement, and the duration of the response is related to changes in brain serotonin (Wallnau and Gallup 1977).

Examples of extreme behavioral inhibition in humans prompted Suarez and Gallup (1979) to theorize that "rape-induced paralysis" may be an instance of tonic immobility. As a result, the idea that certain states of behavioral inhibition in humans (e.g., rape, PTSD, catatonic schizophrenia) represent instances of tonic immobility has been embraced by a growing number of clinical psychologists (Marx et al. 2008). Tonic immobility is a useful means of modeling states of extreme behavioral inhibition under controlled laboratory conditions and may have important practical implications for how such states are dealt with in applied settings (Gallup and Rager 1996).

As an extension of this predator-prey model, Gallup undertook a series of studies to re-examine open field behavior. The point of departure for these studies was that what animals do when tested in an open field is a byproduct of predatory overtones associated with being contacted, handled, and tested by a human experimenter and also being socially separated from companions. This



creates a classic approach/avoidance conflict, and predictions derived from this model are surprisingly accurate across a number of mammalian and avian species.

For example, the mere presence of someone in the room when animals are tested makes animals freeze longer. The further away the experimenter is from the open field and if the subjects cannot see his/her face the amount of time spent freezing diminishes. Likewise, animals that are placed by hand into the open field freeze longer than those that are mechanically introduced into the open field. According to this model, the initiation of movement in the open field represents an attempt to reinstate contact with companions. Consistent with this analysis, animals that are tested in pairs wait longer to begin moving and show fewer attempts to escape from the open field. In contrast, animals maintained in social isolation before testing wait longer to move (Gallup and Suarez 1980; Suarez and Gallup 1981, 1982).

Results such as these raise serious questions about the validity of open field testing as it has been traditionally used as a measure of emotionality.

## Human Reproductive Competition

In the 1980s, Gallup's attention began to focus on human behavior from an evolutionary perspective. Rather than being a matter of competition for scarce resources and the survival of the fittest, evolution is a matter of competition for gaining genetic representation in subsequent generations.

Work that Gallup and others have done that was inspired by this perspective has shown that the mere sound of a person's voice contains information about their sex, age, health, fertility, body configuration, facial attractiveness, grip strength, when they lost their virginity, how many sex partners they have had, their propensity for infidelity, and where they are in their menstrual cycle (for a review see Gallup and Frederick 2010).

Work from his lab has also shown that most people have found themselves attracted to someone only to discover that, after they kiss that person, they are no longer interested (Hughes et

al. 2007). Thus, there may be hard-wired mechanisms activated at the moment of the first kiss that function to make a determination about whether this would be a good genetic/reproductive match. Sex is also a component to courtship, and sampling semen from different suitors may be analogous to kissing; i.e., either you wake up the next day head over heels in love or with feelings of regret for what you did the night before (Gallup and Reynolds 2014).

Most women have a guarantee of sharing half of their genes in common with their children. But, because of female infidelity, men have to contend with paternal uncertainty and the prospect of being cuckolded. Gallup's work on paternal assurance tactics has shown that men invest in children in relation to the presence of shared physical and psychological features (Gallup et al. 2016). Competition for paternity has even affected human genital morphology. Using laboratory simulations Gallup and his students have shown that the peculiar shape of the human penis evolved to compete with the presence of rival male semen in the woman's reproductive tract by promoting semen displacement and increasing the likelihood of paternity by the resident male (Gallup et al. 2003). This research prompted Satoshi Kanazawa to conclude that "if you want to know what women have been up to, look at the human penis." The work on human genital morphology also led Gallup to raise the question among uncircumcised men of unwittingly piggybacking rival male semen captured under the foreskin from one vagina to the next (Gallup and Burch 2004), which inspired a recent novel "The Hitchhiker's Child" (Baker 2013).

As evidence for the impact of some of this work, it is worth noting that in 2017 the journal *Evolutionary Behavioral Sciences* published by the American Psychological Association listed seven of his former students as members of the editorial board (Rebecca Burch, Michael Frederick, Andrew Gallup, Marissa Harrison, Susan Hughes, Nathan Pipitone, and Steven Platek).

Some of Gallup's more controversial work on reproductive competition involves applying evolutionary theory to homosexuality (Gallup and Suarez 1982) and attitudes toward homosexuals (Gallup 1995). According to him, homosexuality

is a byproduct of evolved differences between men and women in fitness maximization strategies and as a consequence everyone has the capacity to become homosexual. Likewise, his view of homophobia as a byproduct of natural selection implies that everyone (including homosexuals) will exhibit homophobia under certain conditions.

## Yawning as a Brain Cooling Mechanism

While most of Gallup's research continues to focus on human reproductive competition about 10 years ago he became interested in yawning, which is something we all do but was not well understood. In contemplating what happens during the execution of a yawn, it occurred to him that yawning might function as an evolved brain cooling mechanism.

Just as is true for metabolism elsewhere in the body, brain metabolism generates heat and research had shown that one of the rate-limiting steps to how big brains can get is dependent upon the development of mechanisms that function to dissipate heat and cool the brain (Falk 1990). As evidence for the idea that yawning may be one of several mechanisms that function to maintain thermal homeostasis in the central nervous system, Gallup and his son Andrew found that nasal breathing and forehead cooling antagonizes yawning in college students (Gallup and Gallup 2007). They also found that rats with temperature probes implanted in the frontal cortex exhibited consistent increases in brain temperature prior to yawning, with brain temperature returning to baseline within seconds after the execution of a yawn (Shoup et al. 2010). Additional work has confirmed the existence of a thermal window that constrains yawning at ambient temperatures that rise to body temperature or approach freezing (Gallup and Eldakar 2013). A recent comparative study inspired by Andrew Gallup found positive correlations that exceeded .9 between species differences in yawn duration and both brain weight and number of cortical neurons (Gallup et al. 2016). As brains get bigger yawns last longer.

Numerous medical problems are related to thermoregulation (e.g., multiple sclerosis) and

emerging evidence suggests that excessive yawning in humans may be a diagnostic red flag for central nervous system thermoregulatory dysfunction (Gallup and Gallup 2008).

Contrary to popular opinion, yawning is a compliment. Because yawns appear to function to cool metabolically overheated brains, if someone yawns the next time you are talking with them do not take it as an insult. Rather than a sign of boredom, yawning is an indication that mechanisms have been activated to maintain attention and promote optimal cognitive processing.

Other aspects of Gallup's research are also related to thermoregulation. His work with Jessica Ash on the impact of climate change on brain evolution suggests that global warming may be undermining the conditions that gave rise to big human brains during the last ice age (Ash and Gallup 2007). And because the scrotum functions to cool the testicles, he has theorized that descended testicles evolved to capitalize on the conditional increase to body temperature that occurs when sperm are released into the vagina which functions to induce a time-bound activation of sperm (Gallup et al. 2009).

It should be clear from this brief overview that rather than being focused and pedantic, Gallup's interests have been very broad and driven by theory construction and hypothesis testing. One of his least cited but most interesting papers involves our reliance on visual metaphors to capture different mental states, which may be a byproduct of our earlier adaptation to life in the trees as arboreal primates (Gallup and Cameron 1992).

## Cross-References

- [Self-recognition](#)
- [Tonic Immobility](#)

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**Gordon G. Gallup, Jr** was born in 1941 and held his first faculty appointment in 1967 as an Instructor at Washington State University, where he got his Ph.D. in 1968. In the fall of that year, he accepted a position at Tulane University where he was promoted from Assistant to Associate Professor in 1972 and to Full Professor in 1974. In 1975, he took a position at the State University of New York at Albany as Chair of the Psychology Department and served in that capacity for three consecutive 3-year terms. He continues to hold a position there as a faculty member. He served as the Editor of the **Journal of Comparative Psychology** from 1989 to 1994.

Most of Gallup's research has focused on the impact of evolution on behavior. Some aspects of his research are represented by work on the following four broad but not mutually exclusive categories.

## Goshawk

### ► Accipiters

## Graded Signals

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## Synonyms

### Continuous signal

## Definition of Graded Signals and Some Clarifying Examples

Signal variants, and signalling repertoires, can be described as either graded or discrete, though categorizing signals as such is often challenging and ambiguities often exist (Keenan et al. 2013; Wadewitz et al. 2015). Graded signals are those whose magnitude can vary continuously; the signal can take any value from a continuous distribution, with intermediate signal values between any two values being possible (Bradbury and Vehrencamp 1998; Marler 1975). As signals have evolved to influence the behaviour of receivers, for a signal to be considered graded, receivers must also be able to perceive signal variation as meaningful and use this variation to adjust their responses (Marler 1977; Fischer et al. 2001). Conversely, discrete signals can only take a finite number of values; intermediate values do not occur or, at least, are not perceived by receivers as meaningful, meaning that receivers perceive signal variants as qualitatively different (Bradbury and Vehrencamp 1998; Marler 1975).

Though static signals which exhibit continuous variation among individuals in a population are sometimes referred to as “graded” in the literature (Rowland et al. 1995), the label “graded” typically applies to dynamic signals within a species’ signalling repertoire that communicate something about the immediate circumstances of the signaller, such as how motivated the signaller is at that moment to attack, or the level of threat posed by a predator. An example of a graded signal is provided by warning signals given by reed warblers in response to threats to their nest. Mobbing calls were given in response to sparrowhawks and cuckoos at faster rates when threats were detected closer to the nest, i.e., when the threat was more immediate (Welbergen and Davies 2008). Additionally, mobbing calls given at faster rates elicited a greater response from conspecifics, with a greater number coming to the signaller’s aid. This demonstrates that this signal (call rate) is sensitive to immediate conditions in a graded way, and receiver responses (probability of approaching and aiding the signaller) are sensitive to graded variation in signal magnitude.

Continuous variation in many animal signals can be perceived and acted upon by receivers, but not all signals exhibiting continuous variation are typically referred to as graded. For example, in koalas, larger males produce bellows with lower-formant values, and females prefer these lower-formant bellows (Charlton et al. 2012). This suggests females use continuous variation in bellow characteristics among males to select for larger males. However, this should not be referred to as a graded signal, since anatomical constraints prevent individuals from producing a varied range of signal magnitudes. Typically, in signals considered graded, all individuals can and do flexibly express a broad range of these signals, and signal variation is not constrained by signal costs or anatomical constraints. When considering the reed warblers again, there is no indication that mobbing call rate is constrained such that only some individuals can call at certain salient rates.

### When Are Graded Signals Beneficial?

A primary benefit of using graded signals rather than discrete is that they enable animals to flexibly encode fine-grained information about the state of the world. For example, as demonstrated with the reed warbler example mentioned above (Welbergen and Davies 2008), rather than simply alerting conspecifics to the presence of an enemy, the graded dimension of the signal enables transmission of additional information regarding how serious and immediate a threat the enemy poses. This allows receivers to make more informed decisions about their participation in mobbing. Additionally, the nature of the states of the world that signallers are informing receivers about will influence whether graded signals are beneficial. For example, discrete calls are often associated with predator calls relaying information about the detection of specific predator types (Blumstein 1999). As such, the information being transmitted refers to real discrete categories in the world, making discrete calls effective. However, when communicating information about continuous states of the world (e.g., signaller arousal state or perceived urgency of a situation), graded

signals are often beneficial (but see Morris 1957; Johnstone 1994).

The flexibility afforded by graded signals may be useful in social interactions, which consist of an interplay of both interactants' signals. Graded signals allow a degree of temporal updating within a single signal type, allowing interactants to perceive and adapt to changes in one another's states in real time. In this way, they allow individuals to flexibly and gradually navigate interactions by probing one another's responses. For example, male satin bowerbirds perform vigorous courtship displays to females at their bowers, and females prefer more vigorously displaying males. However, if displays are performed too vigorously early on in the encounter, females become startled and flee (Patricelli et al. 2006). Females signal their level of comfort with a male's display intensity through crouching behaviour, with increasing crouching rates indicating a decreasing likelihood of being startled by intense displays. Males modulate the intensity of their displays in response to female crouching rates, facilitating gradual escalation of display intensity over the course of the interaction and so avoiding startling females (Patricelli et al. 2006). This example demonstrates the utility of graded signals in allowing social situations to be navigated in a flexible manner, and such flexibility can be beneficial in many contexts, including affiliative and aggressive interactions (Maynard-Smith 1982).

Graded signals also have the benefit that they can, at least partially, resolve trade-offs resulting from the need to manage different receivers at a single point in time. Optimal signal characteristics for evoking desired responses from different classes of receiver may be mutually exclusive, but in a graded signalling system, intermediate signals are possible which can allow a degree of success in managing both receiver types simultaneously. For example, in African painted reed frogs, males produce both advertisement calls and aggressive calls (Grafe 1995). These call "types" differ in that aggressive calls have a relatively greater number of pulses per call, longer call duration and a lower dominant frequency, though these call types grade into one another along a spectrum of these parameters. Advertisement calls are more attractive to



females, while aggressive calls signal aggressive motivation to rival males but are discriminated against by females. Males often call at intermediate levels, and Grafe (1995) suggested that this graded signalling system may allow males to interact aggressively with rivals while maintaining a degree of attractiveness to females. Graded signals as a solution to this aggression/attraction trade-off have been suggested in several anuran species (discussed by Owen and Gordon 2005).

Though gradedness in signals allows increased flexibility, this added flexibility has been suggested to increase the potential for ambiguity in a signal's meaning (Morris 1957). This is thought to be especially true for species living in habitats in which signals may be easily degraded by the environment, such as a dense forests in which aspects of visual and auditory signals can be distorted or obscured by surrounding trees (Marler 1975). As such, it has been proposed that such species should favour discrete signals. Conversely, species living in open habitats without such impediments to signalling may be able to alleviate any potential ambiguity due to gradedness by producing signals composed of multiple redundant components or multimodal signals, allowing the benefits of gradedness without ambiguity costs (Marler 1976; Johnstone 1996). Similar arguments regarding signal degradation and a flexibility/ambiguity trade-off should apply to the typical distances across which signals need to be transmitted, meaning social structure may play a role here too (Owings and Morton 1998). Ambiguity will be most detrimental when inappropriate responses by receivers have the highest fitness consequences for signallers and receivers. This is likely the reason that predator warning calls of many species are discrete (Blumstein 1999), particularly when animals are preyed upon by multiple predator types, each requiring different escape strategies (Seyfarth and Cheney 1990).

## How Are Discrete and Graded Signals Studied and What Has Been Revealed?

Researchers often endeavour to describe a species' signal repertoire by counting the

number of discrete signal types produced by that species, with larger repertoires considered more cognitively demanding to correctly produce and perceive (Freeberg et al. 2012). However, whether signals in a repertoire are genuinely discrete or graded can be difficult to parse. Originally, categorizations of signals as discrete or graded were purely a judgement call, as were the divisions between apparently different categories of discrete signals. These judgements were based on the experience of human observers observing through human sensory systems, which often differ drastically from those of the species under study, raising the possibility of erroneous categorizations (Von Uexküll 1909). As instruments for recording, measuring and analyzing signals have become more sophisticated, researchers have been able to employ less-biased quantitative approaches to categorizing signals and repertoires. This has been especially true for acoustic signals, as current software allows signals to be decomposed and compared along several dimensions with high precision (e.g., Wadewitz et al. 2015). This allows precise descriptions of call types and analysis of whether call types grade into one another through a series of intermediates. Obtaining precise quantitative descriptions of signals in other modalities, such as facial displays in the visual modality (Preuschoft and van Hooff 1995), currently represents a greater challenge, but advances in image analysis and machine learning techniques may enable similar advances in the future (Winters et al. 2020). When these quantitative techniques have been applied to signals, they often present a more complex and ambiguous picture than the neat distinctions between graded and discrete signals often applied by human observers (Keenan et al. 2013; Wadewitz et al. 2015), but they have also lent some support to such human categorizations (Tallet et al. 2013).

Quantitatively understanding signal structure is essential when understanding the selective forces that have shaped signals (Endler 1992). However, the presence of variation in signal parameters is only evolutionarily meaningful if receivers can perceive this variation and use that information to make decisions (Marler 1977).



Species' sensory systems will determine the granularity with which they can perceive differences in signal magnitudes of graded signals (e.g., just noticeable differences; Wysecki and Stiles 1982), meaning that not all signal variation may be perceived. Additionally, responses of receivers of a species to signal variation may deviate importantly from a simple positive linear relationship between signal magnitude and strength of response (e.g., complex preference functions; Edward 2015). As such, though gradedness of signals emitted by signallers is a prerequisite for a graded signalling system, graded perception and response by receivers must be assessed. This can be approached by investigating neurological responses to signal perception (e.g., Toscano et al. 2010), but in animals, receiver perception is primarily investigated via playback experiments (McGregor 1992). Playback experiments using acoustic stimuli have predominated due to their relative simplicity when compared to other modalities, and these have revealed graded responses in many systems (Burmeister et al. 1999; Wilson and Evans 2012; Goutte et al. 2010). More recently, innovative use of robotic models and video stimuli has also allowed graded signals and receiver responses to be demonstrated for visual signals (Ligon and McGraw 2018; Ord et al. 2002; Patricelli et al. 2006). However, as with quantitative signal analysis, playback experiments often present a complex and sometimes ambiguous picture regarding receiver perceptions and responses as graded or discrete (Fischer 1998; Fischer et al. 2001).

Empirical investigations of signalling systems, such as those mentioned above, have prompted a growing realization that signals are almost always extremely complex and are often composed of multiple components from across multiple signal modalities (Hebets and Papaj 2005). Signals seldom convey information along only a single isolated axis, and in many signals, graded and discrete elements are used in conjunction to expand the range and specificity of information transmitted. For example, meerkats have discrete calls for different predator types, but the acoustic

properties of these calls vary in a graded way which indicates the level of arousal of the signaller and the severity of the current threat (Manser et al. 2001). Thus, classifying entire signalling repertoires as graded or discrete is probably overly simplistic (Keenan et al. 2013). However, through careful application of these concepts to specific signals or separate components of multicomponent signals, these categorizations can shed light on the selective forces favouring discrete or graded signal elements and repertoires.

## Cross-References

- [Categorization](#)
- [Honest Signaling](#)
- [Information Processing](#)
- [Modality](#)
- [Primate Communication](#)
- [Receiver](#)
- [Signaller](#)
- [Umwelt](#)

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## Grains

► [Equine Diet](#)

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## Grandmother Cell

► [Face-Selective Perspectives](#)    [Neurons:](#)    [Comparative](#)

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## Grandmother Hypothesis

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### Definition

The grandmother hypothesis is a theory explaining why longer post-reproductive life span has developed in human evolution and why infertility in old age can be an evolutionary benefit for females.

### Introduction

While our ancestors – comparably to today's apes – could become 40–50 years old, modern humans may double this life span. The aging process takes place equally quickly in all human organs – with an almost paradoxical exception: ironically, the reproductive organs of women age much faster. Menopause marks the end of the fertile life span and is a universal feature of human females; up to a third of the average female's lifetime is postmenopause (Harman and Talbert 1985). This is undoubtedly in need of explanation because according to Darwinian

theory, one should expect that a shorter reproductive span would impair fitness and therefore would not be expected to provide any evolutionary benefits (Hamilton 1966). This raises the intriguing question of why evolution prolonged life altogether, but not the fertile lifetime? Why did evolution produce sterile grandmothers instead, a phenomenon extremely unusual in the rest of the animal kingdom? The grandmother hypothesis provides an adaptationist explanation for this evolutionary conundrum and builds on the previously postulated “mother hypothesis.”

According to the “mother hypothesis,” it may be more advantageous for females to renounce further reproduction at some point and to put the resources into the well-being of the already born children due to the increasing risks of late-life pregnancy (Williams 1957). This “mother hypothesis” was extended to the “grandmother hypothesis” which proposes that post-reproductive females increase their inclusive fitness by investing in their daughters' fertility and their grandchildren's survival (Hawkes et al. 1997).

Presumably, the prolonged post-reproductive life span might have evolved as a consequence of the food sharing practice in humans' ancestors and is suggested to have emerged with climate-driven changes in the late Plio-Pleistocene. These ecological changes and the prolonged juvenile dependency due to increased cranial capacities may have forced hominins to change their foraging practices and to opt for more challenging but valuable foods such as tubers that required adult skills to harvest and process. These dietary demands may have constrained female birth intervals and fertility. Thus, provisioning grandmothers who increase the foraging productivity would increase their daughters' fitness benefits, whether by increasing the number of offspring or ensuring the survival of existing offspring (Hawkes 2004).

### Evidence for

Demographic studies in humans support the grandmother hypothesis and show that the presence of menopausal females is associated with an

increase in their daughter's reproductive success and grandchildren's survival (Lahdenperä et al. 2004; Sear and Mace 2008). The most compelling evidence come from the research on Hadza, a hunter-gatherer society living in the Tanzanian savannah (Hawkes et al. 1997). There, older women contribute extra food, which increases the fertility of their adult daughters. In this ethnic group, women and children are active collectors. However, since infants are still inept when dealing with large roots, i.e., the main food component, the mother's success in foraging has a measurable effect on the nutritional status of her children. Nursing mothers, however, can spend less time looking for food, so the task of the postmenopausal grandmothers is to provide food for the newly weaned children. These environmental conditions to which Hadza is exposed emphasize the particularly important opportunity for older women to increase their fitness despite the decline in fertility, namely, if they help the newly weaned grandchildren, mothers can have shorter interval births without compromising their children's chances of survival.

### Alternative Explanations

As intuitive as the "grandmother hypothesis" is, that postmenopausal survival does not have to be a biological adaptation. It could also be that post-generative longevity is to be understood as a nonfunctional by-product of a selection for increased pre-menopausal vitality (Peccei 2001b). A spacecraft set up to reach a distant planet will continue to shoot out in space once it has served its original purpose. To install a self-destruct mechanism would be more expensive than leaving the spacecraft to its fate. Thus, post-menopausal survival would be a surplus, as a fly-by phenomenon, and a by-product of a selection that favored pre-menopausal survival (Peccei 2001b). However, such a nonfunctional interpretation in no way excludes the possibility that the years of life gained are secondarily seized by adaptive behavioral strategies, such as typical grandmother behavior. It is only doubted that the adaptive possibilities created by an increase in life span formed the motor of evolutionary

life extension. The average human longevity would, therefore, be an originally functionless evolutionary by-product, which would have gained secondarily evolutionary significance with the "invention" of the grandmother role.

### Maternal Versus Paternal Grandmothers

Interestingly, evidence suggests that maternal and paternal grandmothers' effects may be different. For instance, Volland and Beise (2001) pointed out that the helping grandmother, who helps her daughters and their children, is less likely to care for her sons and their children. Many studies report that the paternal grandmother's family support is either less pronounced, not measurable, or even negative (see Fox et al. 2010 for a review). Mother-in-law has taken on the role that the vernacular implies. One explanation for this could be the fact of latent paternity insecurity. While women can be sure of their genetic relationship with their children, there is no comparable safety for men. Maternity is directly perceptible, but paternity is assigned. The assigned paternity may or may not be genetically identical, leading to the evolutionary consequence that the probability of shared genes between grandparents and their grandchildren in the male line is always lower than in the female. The mother-in-law's interest in her daughters-in-law only goes as far as her daughters-in-law work toward the reproductive interests of the mother-in-law. The different interests of the daughter-in-law, however, find no support. From all this it follows that the grandmother's evolution cannot be thought of without the mother-in-law's evolution: there are two social strategies, namely, "helping" and "social manipulation," which could have favored the evolution of the post-generative life span.

### Toothed Whales' Grannies

As mentioned above, long female post-reproductive life spans are rare in the animal kingdom and, apart from humans, have only been confirmed to exist outside of captivity in

the short-finned pilot whales, *Globicephala macrorhynchus*; the killer whales, *Orcinus orca*; the belugas, *Delphinapterus leucas*; and the narwhales, *Monodon monoceros* (Croft et al. 2015; Ellis et al. 2018). Killer whales represent a suitable model organism for studying the potential benefits of long-lived grandmothers. Similar to humans, they are extremely long-lived compared to other highly developed mammals and have a sex-specific mortality rate, with males reaching 50 years or less, females living almost twice as long, and females having one of the most extended post-reproductive life spans in the entire animal kingdom (Olesiuk et al. 1990).

First empirical data provide evidence that, in the killer whales, the oldest females of the group pass on their experience to the next generations. For example, they can “report” on historically good hunting grounds or contribute to the dissemination of group-specific dialects (Brent et al. 2015), in other words, pass on cultural information or help with additional care. Foster et al. (2012) provided evidence that calves, at least at a certain age, benefit from the help of their grandmothers and the reproductive life span and interbirth interval of the daughters also seem to be related to grandmotherly presence. Therefore, the menopause and long post-reproductive life are by no means a peculiarity of the genus *Homo*.

## Critique of the Grandmother Hypothesis

While the grandmother hypothesis won a large following, it remains a highly controversial topic in evolutionary anthropology since the evidence from contemporary hunter-gather societies and historical data produced mixed results. Some critics have cast doubt on the hypothesis because of several reasons (for a review see Peccei 2001a). One of the fundamental flaws, however, is that it fails to explain longevity with continued spermatogenesis in males and completely ignores the contributions of other family members to offspring survival.

## Conclusions

Although there is substantial evidence that grandmothers provide significant survival and reproductive benefits to their grandchildren, the evolutionary status of menopause and prolonged post-reproductive life span is still unclear (Croft et al. 2015). Is it a biological fit to enhance the reproductive fitness or rather a nonfunctional “burden” from the mammalian tribe’s history? Is postmenopausal survival a sort of “by-product” of pre-menopausal vitality selection, or is it the care of the post-reproductive women that have driven the evolution of human longevity? Future research that looks at the grandmother effects more broadly, including grandfathers, grandmothers, fathers, uncles, aunts, and siblings, will give new insight into the evolutionary pressures that are likely to have shaped human life history evolution. Finally, the fact that long post-reproductive life has also been found in non-human mammals highlights the importance of widening the taxonomic test bed for the evolutionary theories of menopause and provides intriguing opportunities for future research.

## Cross-References

- Fitness
- Inclusive Fitness
- Reproduction
- Reproductive Fitness

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## Grasping

- [Opposable Thumb](#)
- [Parieto-occipital Sulcus \(POS\)](#)

## Grasping Hands and Feet

- [Quadrumanous](#)

## Grasping Reflex

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## Synonyms

[Clutching](#); [Grasp reflex](#); [Gripping](#); [Holding on](#)

## Introduction

The grasping reflex is a group of several primitive reflexes found in healthy newborns. Like all reflexes, they are an involuntary and unalterable motor response provoked by a stimulus. These reflexes may vary from one species to another depending on life’s conditions but are always inherited (Pedroso 2008).

## The Different Groups of Grasping Reflexes

Grasping has been studied under several names throughout time. As well mentioned by Schott and Rossor (2003), Seyffarth and Denny-Brown (1948) were able to separate these into two distinct groups: the grasp reflex and the instinctive grasp reaction:

**The grasp reflex** is composed of two phases. First, children’s fingers close when the examiner

## Grasp Reflex

- [Grasping Reflex](#)



stimulates the palm of the hand, usually by introducing a finger between the thumb and the forefinger (Berg 2014). This is called the “catching” phase. After that, if light tractions are made on the tendons of the flexor or adductor muscles, it will develop into a second phase called the “holding” phase (Futagi et al. 2012; Schott and Rossor 2003; Seyffarth and Denny-Brown 1948). The thumb may also be involved in gripping depending on the size of the object (Schott and Rossor 2003).

**The instinctive grasp reaction** is a small chain reaction performed when a stimulus is placed on any part of the palm of the hand. These movements are aimed at bringing the stimulus closer to the center of the hand in order to trigger a grasping phase. Nevertheless, it is a different catching phase from the first one in that it is induced only by a stationary presence of the stimulus (Schott and Rossor 2003; Seyffarth and Denny-Brown 1948).

The grasp reflex is already present and observable in utero. In the definition given by Berg (2014), the reflex appears from 28 weeks of gestation to become strong at 38 weeks; however, Sherer (1993) was able to observe it from 16 weeks of gestation from an ultrasound that showed the fetus retaining the umbilical cord. This reflex disappears in the first months of life and gives way to a voluntary grasp of objects by the child (Berg 2014).

The foot also has a grasp reflex when the sole of the foot is properly stimulated. Usually called plantar grasp reflex, this reflex is induced when the examiner performs pressure behind the toes, which causes flexion and adduction of the toes (Futagi et al. 2012; Schott and Rossor 2003).

## The Grasping Reflex in the Field of Medicine

These grasp reflexes should disappear during the first months of the child’s life. However, they may reappear in pathological states usually in case of lesions of the frontal lobes, which show that, although they are suppressed during the normal development of the child, reflexes are not lost (Schott and Rossor 2003). Testing the

presence of these reflexes during the maturation of the child makes it possible to determine its neurodevelopment. A primitive reflex is considered abnormal if it is absent, diminished, or exaggerated during the normal reflex period or if it does not disappear after this period of time (Futagi et al. 2012).

## The Grasping Reflex in Other Primates

The grasp reflexes are also present in newborn monkeys and apes. As well mentioned by Futagi et al. (2012), this suggests that, even if these reflexes no longer have any purpose for human species, they are rudiments of phylogenetic functions needed for juvenile monkeys in their arboreal life for support and locomotion. Indeed, the studies that Futagi et al. mention suggest these reflexes are even stronger in nonhuman primates. Richter (1931) conducted a study on five monkeys from a rhesus macaque colony and succeeded by demonstrating that the newborn macaque grasp reflex was much stronger than the reflex of the newborn human. One of the monkeys had managed to remain hooked for 33 min to a rod with one hand. According to Richter, the subject would have been able to hang for hours if it had used both of its hands. A similar study carried out by Robinson (1891) on humans demonstrated that the newborn was able to withstand his own weight hanging from a horizontal rod. The record obtained during this study is, however, only of 2 min and 35 s using two hands. Brain and Curran (1932) also support the idea that monkeys have true reflex grasping because, from their earliest days, they are able to cling to the mother’s underside with their hands and feet without any support.

## Conclusion

In conclusion, the grasping reflex is a group of several reflexes, very probably homologous across the primates, all of which lead to the grasping. They are an involuntary response to a stimulus. In the field of medicine, their presence and

their disappearance make it possible to monitor the development of the child and to establish the presence of brain damage in adults.

## Cross-References

- [Clutch](#)
- [Precision Grip](#)
- [Step Reflex](#)

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## Gravity Bias

- [Hood's Gravity Rules](#)

## Gravity Error

- [Hood's Gravity Rules](#)

## Great Ape

- [Haplorhini](#)

## Great Apes

- [Josep Call](#)

## Great Chain of Being

- [Scala Naturae](#)

## Green Beard

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## Definition

Green beards are genes that can identify the presence of copies of themselves in other individuals and cause their bearer to behave nepotistically toward those individuals (Gardner and West 2010).

## Green Beard: an Evolutionary Strategy of Cooperation

According to evolutionary biologists, evolution is an entity which functions to ensure the survival of the best fitted individual. However, sometimes nature selects the traits which are not the best survivors but unique (Haig 1996). These unique traits are selected not for the individual carrying the trait but for the benefits of the reproductive family members within the colony such as sterile workers in the insect colonies (West et al. 2010). Then the question arises that why would natural

selection choose a trait that does not benefit the immediate bearer of the trait? This could be explained with the idea that the presence of such unique traits in an individual indirectly benefits its future generations/lineages. Carrier of these unique traits would put themselves on stake for the benefits of their closely related family members (Darwin 1859). Such interactions have been previously explained with the altruism where indirect benefit is more than the personal cost (Hamilton 1964).

All these social interactions come under the category of cooperation which is an intricate evolutionary phenomenon of mutual benefits. But somehow this phenomenon is highly susceptible to exploitation when cooperative groups get invaded by cheaters, ones who get the benefits but do not reciprocate. In these conditions, cooperative systems tend to collapse (Laird 2011). In such systems, green beards function as rescuers and introduce a convenient way for cooperation to evolve and ensure that cheaters do not get any benefit from cooperative groups. The idea of green beard allele was proposed by William D. Hamilton (1964), and this term was coined by Richard Dawkins in his book *The Selfish Gene* (Dawkins 1976). Green beard is a certain gene with a particular phenotypic marker discriminately favoring the individuals with that phenotype only even if they do not share any other genes. In this case, the selected genes might or might not have an observable distinguishable phenotype but encode a characteristic behavior which ensures the discriminative selection toward the carriers of that gene. Green beards show high degree of relatedness at the green beard locus and other closely linked gene loci. Main functions of green beard gene/locus are to establish a signal, discriminative exclusion of noncooperators, and cooperative behavior favoring other green beards (Queller et al. 2003); if all of these characters are controlled by two different genes or distantly related loci, then there are more chances of them being uncoupled during evolutionary mechanisms which renders the green beard effect useless.

High degree of self-recognition at genetic locus preferentially distributes the green beard

gene/locus within green beard groups. But the probability of the presence of other genomic parts in such groups of donors and recipients (including green beard siblings) depends on its closeness to green beard locus. Also there are genetic modifiers of green beard locus whose selection will depend on their closeness to the green beard and whether they facilitate the selection of green beard locus or not. Modifiers linked in coupling and favoring the locus (enhancers) will be under high selective pressure than the ones disfavoring it (suppressors) or present on different chromosomes (Haig 1996).

Green beards are different from genetic kin recognition as green beards are social interactions that are related to the direct perception of genetic identity at a particular or closely linked locus (Dawkins 1976), while genetic kin recognition is based on the phenotypic similarity due to genealogical relationship over the whole genome (Hamilton 1964). Earlier green beards were thought to be highly unlikely in nature, but new investigations have shown that green beards are not as unusual as it was considered to be. In slime mold, *Dictyostelium discoideum*, cells containing *csa* gene, cooperatively adhere to each other to form the aggregated stalk to become fruiting bodies while excluding noncarriers of the gene (Ross 1997). In another remarkable example, green beards are observed in red fire ant (*Solenopsis invicta*) polygyny (multiple-queen) colonies where the queens with Bb heterozygous genotype (where b allele produces specific odor to determine if the prospective queen carries the b allele or not) at Gp-9 gene locus reproduce successfully, while queens with bb genotype die prematurely due to internal causes (Fletcher and Blum 1983). Queens with BB genotype are killed by the aggressive workers with Bb genotype. Identification and execution of BB queens may be due to the two signaling cues that represented queen's reproductive state and her Gp-9 locus genotype. Pheromones produced by sexually mature queen can be assessed by the workers (White and Winans 2007). Gp-9 locus linked to green beard gene can produce a chemical signal which can induce the workers to kill all sexually mature females except those carrying the same chemical

signal (Bb queens) encoded by this allele (Keller and Ross 1998).

Green beards have been distinguished into four kinds depending upon their characteristic evolutionary behaviors such as “helping” ( $rB > 0$ , Hamilton’s rule, where  $r$  is the coefficient of genetic relatedness between actor and recipient and  $B$  is benefit to recipient), “harming,” “facultative” (facultative harming, e.g., Gp-9 gene of the fire ant (*Solenopsis invicta*); facultative helping,  $b/c > 1$  (where  $b$  is benefit to recipient and  $c$  is the fitness cost to actor and if the benefit to the recipient outweighs the cost to the actor), e.g., cell surface gene FLO1 in the yeast *Saccharomyces cerevisiae* where cells adhere with other cells containing the FLO1 gene (Smukalla et al. 2008) and in slime mold *Dictyostelium discoideum* (Ross 1997) and  $b$  allele at the OBY locus in side-blotched lizards where  $bb$  males with blue coloration throat function as a mate guard of genetically similar but unrelated and protect them against yellow aggressive males (Sinervo et al. 2006)), and “obligate” (obligate helping,  $b/c > 1/p$ , i.e., where the ratio of benefit to cost exceeds the reciprocal of the green beard’s frequency in the population ( $p$ ), e.g., the tumor-inducing (Ti) plasmid in the bacterial plant pathogen *Agrobacterium tumefaciens*; obligate harming, e.g., bacteriocin-encoding genes, which are present in all main bacterial lineages and provide antimicrobial activity). Immunity from toxin is provided by clone mates of producer cells which show the tight linkage between bacteriocin-encoding gene and the gene which deactivates the bacteriocin (Sinervo et al. 2006).

Sometimes the gene gets selected in the course of evolution even if it is disadvantageous to its bearer but has sufficiently large benefits to the relatives because the relatives also carry the replicas of that gene. But this concept cannot be generalized as the probability of carrying each gene similar to your relative is questionable given into account the environment, mutations, and other genetic forces that play a role during development of an individual (Hamilton 1964). And this applies to all four different kinds of green beards. When a rare green beard will be favored, it will undergo

frequency-dependent selection which will ultimately lead to its fixation. Consecutively most of the population will display green beard, individuals will be treated equally, and it will eliminate its function as a characteristic phenotypic/behavioral marker among cooperative individuals. This would make the green beards resistant to identification in such populations. Also the requirement of single-gene/locus system in green beards increases the chance of false beards with cheating genotypes. Thus multi-allelic system of green beards was postulated in social amoeba (*Dictyostelium discoideum*) at Tgr gene locus explaining the specificity required by individuals to direct cooperative behavior toward matching partners and reduce the fitness cost caused by chimeric shifts (Gruenheit et al. 2017). Adding more loci would also prevent against disruption of linkages due to intragenomic conflict and intrusions by false beards (Haig 1996). However, this might be the reason behind numerous examples of green beards in microorganisms where relatively simpler genotype and phenotype correlation prevents the decoupling of beard and behavior. We do not find much examples of green beards in other hierarchal systems as we often look for simple ones with few genes and categorize the complex shared gene interaction as kin selection (Sinervo et al. 2006). But green beard organisms present a remarkable evolutionary picture of social interactions for the survival of species where individuals interact/cooperate with each other either for mutual or indirect fitness/benefits.

## Cross-References

- [Altruism](#)
- [Competition](#)
- [Cooperation](#)
- [Kin Selection](#)

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## Greenhouse Effect

### ► Pollution

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## Gregor Johann Mendel

### ► Gregor Mendel

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## Gregor Mendel

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## Synonyms

[Father of modern genetics](#); [Gregor Johann Mendel](#)

## Introduction

The dawn of the twentieth century witnessed an important discovery that had been biting the dust for more than three decades, and it took three independent researchers – Hugo de Vries, Carl Correns, and Erich von Tschermak – to rediscover the results from the 8-year long study of G. J. Mendel (Fig. 1), which answered the questions related to fundamentals of life. Although this came as a shock to the scientific community that a study with this kind of impact went unnoticed for such a long time, it would be a huge lie to render that Mendel’s results were



**Gregor Mendel, Fig. 1** Gregor Johann Mendel. (Pic Courtesy: MaterialsScientist, Wikimedia commons)



totally in the dark after getting published, as there had been multiple citations of his published article between years 1868 and 1900 (Brannigan 1979). After one and a half century of publishing, Mendel's results have brought us to interact at gene level, and to honor him, we refer to him as the "father of modern genetics."

The knowledge of an achiever's past and upbringing helps the subsequent generations to understand the environment and the factors that had been stitched together to have led to the achievement. Right after the rediscovery of Mendel's results, biographers have travelled up and below to know every bit about him, his family, his upbringing, and all about his history. But as the rediscovery took 34 long years which includes 16 years of Mendel's demise, it was difficult to explore the facts about his upbringing and history. Had it not been his nephew, Alois Schindler (1859–1930), the son of Mendel's sister Theresia, we would have not known Mendel's pedigree (Klein and Klein 2013). In this entry, we will learn concisely about the past of Gregor Johann Mendel from the efforts of multiple biographers.

### **Mendel's Infancy and Uncertainty About His Date of Birth, Name, Family, and Village**

Mendel was born to the peasant couple named Anton Mendel and Rosina (Schwirtlich) Mendel in Heinzendorf. The year of his birth was 1822, but there surrounds a confusion regarding the date. Two dates are to be considered: July 20 and July 22, 1822. The former is the date recorded in the parish (baptismal) register and indicated on Mendel's birth certificate; the latter is the date transmitted to us through family tradition. If the register which records baptism on the same day of birth is to be followed, then a controversial situation of a child being baptized (according to the register) before being born (according to the family tradition) arises. According to the Mendel family tradition, Johann Mendel was born on Saint Magdalene's Day, which comes on July 22 (Klein and Klein

2013). This was also confirmed by Alois Schindler who recorded that his mother Theresia, Johann's younger sister, as well as other relatives, insisted that in the family Johann's birthday was always celebrated on Saint Magdalene's Day.

The name also carries quite a bit of history along with it, while the surname was that from the father's side, the middle name also has a connection to his father's family as he was baptized Johann after his uncle, Anton Mendel's younger brother contrary to the belief that Mendel got his middle name from Saint John as he was born few days before Saint John's day. He assumed his first name Gregarious (Gregor in German, Rehor in Czech, and Gregorios in Greek, meaning "vigilant") at a robing ceremony, where he received the habit of a St. Augustine friar on October 9, 1843. It was after this ceremony he started signing as Gregor Johann Mendel (Klein and Klein 2013).

In the family apart from himself and his parents, Mendel had four sisters. The older was Veronika and three younger were Rosina, Theresia, and Rosina, in sequence of their birth order. Both Rosina died shortly after their birth, the reason to which is not known. Biographers considered Theresia to be more close to Johann than Veronika because of the fact that Theresia renounced her right on a dowry to enable Johann the continuation of his studies and later he enabled Theresia's sons to study and that it was through them that most of the information about the Mendel family has reached us (Henig 2000).

The village of Hyncice (Fig. 2) from the Odra domain was Mendel's birthplace, the German name of Hyncice is Heinzendorf. This village lies near the Moravian–Silesian border in what is now the Czech Republic (at that time part of the Austrian empire) (De Castro 2016).

### **The Childhood and Nurturing of a Naturalist**

Later in this entry, we will learn that the decision to become a priest and not return to his farm didn't had any inspiration from his upbringing as





**Gregor Mendel, Fig. 2** Mendel's home at Hynčice. (Pic Courtesy: Vit Lang)

there is no reporting that Mendel's family was religiously too forward or was there any predetermination in him to become a monk. The biographers believe that Mendel was just a normal village boy in his childhood who in his free time climbed the trees to fetch twigs, gazed the sky for birds, raided the nests, and knew where to fetch for the edible mushrooms or find the berries which were large, sweet, and juicy. All the while, being in continuous exposure of the nature would have given him the unconscious expertise to develop as a naturalist. Along with these expertise, he would have had some added advantage over other children of his surrounding which would have induced a lifelong attachment to the nature. This added advantage would have attracted his teachers, Thomas Makitta and Johann Schreiber, who must have started to nurture the talent (Bateson 1909).

Johann Schreiber was a priest and an experienced horticulturist who resorted to asexual propagation of plants by grafting as he knew that the hybrids, if propagated sexually, will produce different types of offspring and the original type may all but disappear. He usually taught religion to children, but more than anything else, he liked to spend the time with them in the garden, showing them how to prepare the scions and the stocks for grafting. Being a priest with

vast knowledge about fruit plants enabled him to become one of the founding members of the Pomological Association in Brno in 1816. On the other hand, very little is known about Thomas Makitta. He was a farmer's son, born in 1774, and later became a certified teacher. He started at the Heinzendorf elementary school either in 1795 or 1796 and taught religion as well as principles of horticulture and beekeeping, presumably until 1850 (Schwarzbach et al. 2014).

Since both his teachers were fond of trees, plants, and animals, the child's interests were too directed on the same path, leading to questions. The increment in child's interest must have pleased his instructors, and so they would have paid even more attention to him. In the end, this mutual psychological amplification of the bond between the child and his teachers led to the fixation of his interests, thus laying the foundation for the development of a future naturalist (Dunn 2003).

### **Stretch to Lipnik Followed by a Jump to Opava (or Troppau)**

Having experienced the talent of Mendel's intelligence and his eagerness to learn, Schreiber and Makitta must have thought that he should

be given the opportunity to receive a higher education. But before that, they wanted him to move to a school in Lipnik, a town 20 km from Heinzendorf, to complete the sixth year of his compulsory education. To move the boy away from his home and family, the teachers had to convince his parents. The convincing part is supposed to be done by Makitta, as recorded by Alois Schindler, and seems to make sense as he was Mendel's main teacher (Klein and Klein 2013). But, there are other arguments in Schreiber's support because being a spiritual leader of the community he was better acquainted with the individual families and also he must have had contacts in Lipnik school. To add to this in his letters to home, Mendel added frequently greetings to the priest, but never to Makitta which has been interpreted as a sign of Gregor's gratitude to the former for his help in convincing the parents. Finally, after the consent from both the parents, the 11-year-old Mendel packed his meagre belongings and said goodbye to his family, home, and childhood and moved to Lipnik in fall of 1833 (Dunn 2003).

The year passed, and in the summer of 1834, the 12-year-old Mendel became the Pramianten, i.e., the prize-winner. Considering the odds against him, this achievement was remarkable for a boy who had to adapt to being alone, away from home, and to an entirely new way of life and a new environment. Apart from everything else, this would have contributed to his father's decision to allow Johann to continue his studies in the Gymnasium in Opava (or Troppau). After Mendel's father gave his definitive decision, Makitta and Schreiber would have prepared for him the application for his admission to the Opava Gymnasium. It was also at that time that Schreiber sent to the Gymnasium the birth certificate with the wrong birth date. The teachers recommended the Opava Gymnasium because it was the closest to Hyncice or Heinzendorf and because of its good reputation. Johann was accepted and reported to school on December 15, 1834 (Klein and Klein 2013).

Opava was the capital of Czech Silesia and was the center for numerous institutions, courts, and governmental offices and had a chamber of commerce with several banks, custom offices, a

number of clerical institutions, churches, monasteries, a military battalion, a theater, a museum, hospitals, an array of schools for general and specialized education, and a rapidly growing textile, machine, and other industries. A city with a recorded history since 1224, it amounted for a lot of adjustment on the part of Mendel, a small-town boy. The Baroque building in Opava is the place where Mendel went to school from 1834 to 1840, and this is being displayed on a commemorative plaque at its entrance (De Castro 2016). Among all those years at Opava, the toughest was the year of 1838, as mentioned in his autobiography. Mendel's father met an accident leading to serious injuries to the extent that he became unable to attend to his farms from this point onward. Mendel came to know about the condition back at home on his return for the vacation, and it must have led to the thought that Mendel's wish of getting a full education might come to an end as he would now not be supported by his family and will have to look after the farm. But on the contrary Mendel's father became more resolute about the completion of his studies. To this encouraging belief from his father, Mendel moved toward self-sufficiency and got enrolled in a course for school candidates and private teachers at the Hauptschule in Opava, to obtain the permit necessary for tutoring other students. As one would expect from a bright student riding on the confidence entrusted by his father, Mendel not only cleared the course with highest marks, he was also able to find students on recommendation of the school for tutoring and thus was able to support himself through school. Mendel received Abgangszeugnis, a certificate attesting the successful completion of his studies in Opava and revealing him as a *Musterschuller*, a student whose example was given by teachers to students with lesser zeal toward studies. Along with the accolades for his diligence to studies, the city of Opava also gave Mendel the confidence of surviving on his own, and with these factors on his side, he decided to enroll at the Philosophical Institute in Olomouc, a city some 50 kilometers southwest of Heinzendorf (Klein and Klein 2013).

## Journey to Become “the Monk”

Mendel reached Olomouc in the year 1840 and spent 2.5 years. The Philosophical Institute looking into the circumstances of Mendel waived the tuition fee, but in order to pay for his rent and food, he had to earn from somewhere. In a city where the inhabitants spoke Czech and with no contacts to recommend him to parents looking for a tutor for their children, he somehow managed to keep his head above the water. The struggle continued till the end of first semester where he passed in mathematics and Latin but fell ill before completing the rest of them. He returned home where time was great as Veronika got married, and her husband, Alois Sturm, agreed to take over the Mendel farm, which Anton could no longer manage. Theresia was 11 years old and decided to forgo her part of dowry in favor of Mendel, a decision which allowed him to return to Olomouc in 1841 and complete his studies (Schwarzbach et al. 2014).

At the Philosophical Institute, religion, theoretical and practical philosophy, history, mathematics, and physics were among the obligatory courses, while pedagogy (the art and science of teaching), Austrian history, diplomacy and heraldry, numismatics, history of philosophy, classical literature, Greek philology, and agriculture were elective courses. Among the faculty, Prof. Dr. Friedrich Franz, who taught physics to Mendel, lived in the Augustinian Abbey at Brno and so came to know the friars or priests there quite well, including the Abbot Franz Cyrill Napp (Klein and Klein 2013). In 1843, Franz recommended Mendel as a suitable candidate for admission into the Augustinian (name of the religious order) order (De Castro 2016). The fact that almost all the professors Mendel knew were priests must have led to the thought that it was through priesthood that he will be able to get university level education and the post of professor; also he knew that after completion of his studies at the Philosophical Institute he could not expect of help from home and with his inability to support further studies all by himself he decided to become the priest or the monk. In his autobiography Mendel mentions that, “he found

himself forced to enter the profession and that his circumstances determined his choice to become a priest which would free him from worries about making a living” (Klein and Klein 2013).

Mendel got enrolled in the Theological Institute (officially known as *Caesario Regio ac Episcopali instituto theologico Brunensis*, translated as Imperial-Royal and Episcopal Theological Institute of Brno) in 1843. It trained candidates for priesthood and so was under the jurisdiction of the bishop. But he began his studies in September 1844. After completing 1 year as novitiate, his status at the abbey changed to juniorate; it was now that he became a candidate for priesthood. He took simple vows which did bound him to the monastery, but the bond was not quite unbreakable yet, and transgressions against the rule were pardonable (Henig 2000).

Due to the sickness, death, and incapacitation of many candidates at the abbey, there was a shortage of priests to perform the pastoral duties. This forced Napp to entrust one of the juniorate to the post of priest before completion of their studies in order to perform the pastoral duties, and obviously the choice was Mendel, who with his impressive accomplishments till date presented little risk of having the burden of pastoral work endanger the completion of his studies. However, there were two hurdles, first was Napp required the permission of the provincial government and the bishop, and second was Mendel’s age: the rules stipulated that a priest must be at least 25 years old, an age which Mendel would only reach after few months, i.e., on July 22, 1847. Napp countered the first hurdle on December 17, 1846, by asking the body of abbey’s chapter, to which they voted unanimously and asked Mendel to take the solemn vows. And so he did take the solemn vows on December 26, 1846, in a ceremony that took place in the parish Church of Virgin Mary, after preparing through a series of spiritual exercises. The second hurdle was something Napp knew couldn’t be waived. It was Napp’s good rapport with the civil authorities that helped him to obtain the approval to advance Mendel’s ordainment 1 year ahead of schedule. This struggle didn’t halt here, it

was understood that the Roman Catholic Church maintains a strict hierarchical organization where clerics have to pass through different levels of ranking order, namely, subdeacon, followed by the deacon, priest, bishop, archbishop, cardinal, and the pope, each with different sets of privileges and responsibilities. Hence, to become a priest, the order comprising of several years in between them must be followed, and a bishop should ordain a candidate ceremonially to each of these levels. However, in Mendel's scenario, the passage through the levels of subdeacon and deacon was accelerated subjected to the crisis of situation at the abbey. The bishop ordained him subdeacon on July 22, deacon on August 4, and priest on Sunday, August 6, 1847. Mendel then celebrated his first mass (the "Primiz") on August 15, 1847 (Klein and Klein 2013).

### Returning to School and String of Failure in Exams

In the year of 1848, Mendel was appointed as the full-time assistant of the parish priest, in other words he was the "man Friday" both in the church and the parish. The pressure of full-time pastoral work was immense as he had to do everything in between baptizing a newborn to burying the dead. He struggled to overcome the burden of work, but by the end of the year, he took to bed being seriously ill both mentally and physically through the entire beginning of the year 1849. Mendel's illness put Napp in a difficult situation of what to do of a priest who cannot withstand the pressure of pastoral work, especially if the ordainment of that priest was accelerated on his request. It must have been the fortunes of both Napp and Mendel that a request for an extra teacher came from the city Znojmo. Napp knew that Mendel had no teaching experience and no formal qualifications for the post (though he took the course for school candidates and private teachers at the district teachers' seminary at Opava and was highly recommended in the qualification report) but had no doubt that Mendel could handle the job. And so he recommended him for the position teacher, to which a message arrived inviting

Mendel to report immediately to Znojmo as a substitute teacher. Mendel assumed his teaching duties in Znojmo in the year 1849 and soon became popular among the students due to his vivid and lucid method of teaching, also his colleagues held him in high esteem (Schwarzbach et al. 2014).

In the same year, in order to tighten its grasp on the society and limit the autonomy of the institutes in educational field, the government directed that schools would no longer be allowed to employ substitute teachers who could not present a certificate that they were qualified to teach their particular subject. In order to obtain the required certificate, the eligible candidates had to pass a qualifying examination administered by Royal Imperial Scientific Examination Committee at the University of Vienna, established by the ministry. Mendel applied and failed in the viva portion in 1850. The very next year, he was sent to Vienna as suggested by the state examiners and Napp to continue his studies in science at the Royal Imperial University (Monaghan and Corcos 1993), the thought being that Mendel's failure seemed to be attributed to his lack of formal preparation. In Vienna, he studied physics with Christian Doppler (of Doppler effect fame) and botany with Franz Unger. Unger had been using a microscope for his studies and was meddling with a pre-Darwinian theory of evolution, both of which Mendel used particularly in mathematics to evaluate and analyze empirical data (Henig 2000). Mendel's time in Vienna was the high point of his education as up to that time he had been largely self-taught.

After 2 years of studies, Mendel went back to Brno in 1853 and was appointed as a substitute school teacher in natural history and physics. In the spring of 1856, Mendel was able to retain his position as substitute school teacher only by the virtue of being an excellent, enthusiastic educator. He failed the certification examination again even after having spent time at Vienna and having practiced as a full-time substitute teacher (Monaghan and Corcos 1993). It was from this year till 1863 that he diligently worked in his pea garden at St. Thomas Abbey in greenhouse foundation.



## Serendipity that Led to Beginning of Genetics

There has been a consensus among the biographers and researchers that by working on the peas Mendel did not set out to prove the laws of inheritance (Opitz and Bianchi 2015; Olby 1979), instead, he worked with peas to develop new color variants and to examine the effects of hybridization. Mendel paid special attention to plant breeding, a topic that fascinated him since his childhood back home, when he assisted his father or priest Schreiber as they grafted fruit trees and took care of them. At St. Thomas Abbey (Fig. 3), nurseries were established by Napp even before he became abbot. One of these nurseries was utilized by Mendel to study hybridization and develop new color variants of peas. His selection of peas was the serendipity, the reason to which is not known. Assumptions could be made for his selection as peas exist in pure, separate lines, they are hermaphrodites and able to self-fertilize before the bud opens, and great numbers can be bred in a small space (Reid and Ross 2011). Unknown to Mendel is the fact that the characters

he chose are not subject to linkage disequilibrium, and at least five out of the seven traits he used are on separate chromosomes (Blixt 1975) which made the analysis of crosses and any conclusions inferred from them straightforward. Mendel's pea experiments were carried out over 8 years and included more than 15,000 plants, and these are astounding numbers, even by today's standards. Mendel completed his work in 1863, prepared the manuscript after analysis of the data, and finally submitted his work on the laws of heredity, *Versuche uber Pflanzen-Hybriden* (*Experiments on Plant hybridization*), to the Proceedings of the Natural History Society of Brno in 1865, to be published in 1866 (Weiling 1991). His paper got few citations, but its importance was understood after more than three decades of publishing when in 1900 three botanists Erich Tschermak in Austria, Hugo de Vries in the Netherlands, and Carl Correns in Germany independently replicated his results only to find that the data and theory already had been published in 1866 by a monk named G. J. Mendel (Weinstein 1977). Mendel's article led to the foundation of inheritance theory, articulated later by Bateson and



**Gregor Mendel, Fig. 3** Panoramic View of St. Thomas Abbey. (Pic Courtesy: VitVit, Wikimedia commons)

Fisher (Fisher 1918; Bateson 1902). This also led to the birth of genetics in the early twentieth century.

### The Other Scientific Domains and His Final Years

Apart from his work on laws of heredity, Mendel also pursued other scientific domains. He was a well-trained mathematician and physicist and applied mathematical theories to interpret his biological experiments and to plan new ones (Opitz and Bianchi 2015). In 1865, he established the Austrian Meteorological Society and published numerous articles in meteorology, and he also did hybridization experiments on other plants (*Hieracium*), vegetable, and fruit tree horticulture (Walsh 1966), apiculture and agriculture in general (Weiling 1991). Mendel's data on the water table assessed from groundwater collection from a

nearby well are one of the most extensive physical and meteorological observations. Conserved in the Mendel museum in Brno are extensive records kept over the years of these data (De Castro 2016).

In 1868 Mendel was appointed as abbot of the monastery after Napp. The administration of the abbey took most of his time making him to abandon his illustrious pea experiment. In 1874, he introduced taxing of religious institutes which isolated him from his contemporaries due to public opposition. Many of his writings were destroyed in a fire to mark an end to disputes over taxation of religious institutions. Ultimately on January 6, 1884, at the age of 62, he took his last breath; the official cause of death noted in the autopsy report is Bright disease (nephritis), with heart and kidney failure (Dunn 2003).

The twentieth century was filled with discussion on the interpretation of Mendel's experiments. Few also questioned his protocols, motive, and beliefs about evolution and heredity

**Gregor Mendel,**  
**Fig. 4** Mendel's statue in  
monastery garden. (Pic  
Courtesy: Vit Lang)





(Singh 2015). His journey was filled with obstacles and disappointments, but as per the quotes of his last thoughts, “I have experienced many a bitter hour in my life. Nevertheless, I admit gratefully that the beautiful, good hours far outnumbered the others. My scientific work brought me such satisfaction, and I am convinced the entire World will recognize the results of these studies”. It took years before Mendel was given his rightful place in the field of science and very rightly was honored as “father of modern genetics” (Fig. 4).

## Cross-References

- [Mendel's Laws](#)
- [Mendelian Crosses](#)

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## Greyhound Racing

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## Synonyms

[Dog racing](#)

## Definition

An organized, competitive sport in which greyhounds are raced around a track.

**Greyhound racing** is a competitive, organized sport in which bets are placed as greyhounds run around a track (Baker 1996; Thompson 2003). There are two forms of dog racing, which include track racing and coursing. Track racing utilizes an artificial lure that travels along a rail ahead of the dogs until the hounds cross the finish line. In

contrast, coursing traditionally involves dogs chasing after a hare in a relatively open environment (Thompson 2003).

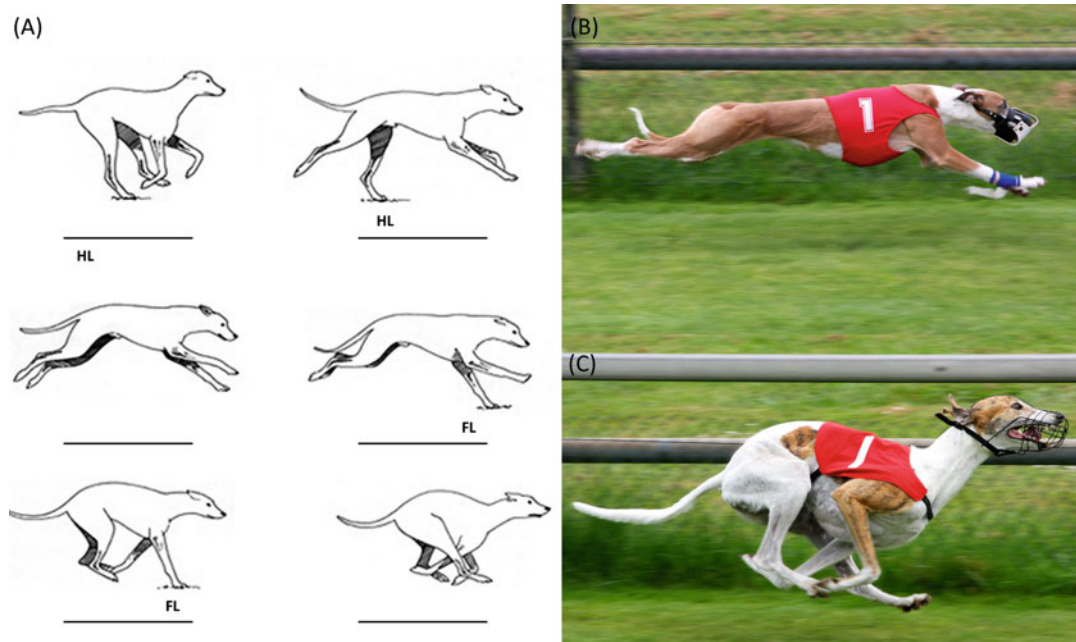
Modern **greyhound racing**, around a circular or oval track, has its origins with the invention of the artificial hare (Thompson 2003). **Greyhound racing** had its peak during the first half of the twentieth century and was particularly popular amongst a working-class audience, for whom evening races and tracks in urban centers were accessible (Ray 2001; Thompson 2003). Popularity for **greyhound racing** has waned in recent decades worldwide, and, at the time of writing of this entry, only five states in the United States still operate dog races (Baker 1996; Jackson 2001; Ray 2001; Sicard et al. 1999; Thompson 2003). Greyhound adoption programs have been wildly successful in helping to find homes for retired racing dogs, with an estimated adoption rate of over 95% in the United States.

Dog racing is dependent on the build and gait capabilities of the greyhound. Greyhounds are thought to be one of the oldest breeds of dogs, and were bred to hunt by outrunning their prey (Thompson 2003). As such, the greyhound has a number of anatomical features that allow the animal to generate remarkable speeds (Williams et al. 2008a, b). In general body form, the greyhound has long, powerful legs, a deep chest, highly flexible spine, and slim build. The greyhounds' heart is larger than similarly sized breeds and pumps blood with higher levels of red blood cells than other breeds. Since red blood cells carry oxygen, this higher level allows the hound to move larger quantities of oxygen faster from the lungs to the muscles (Herrmann 1926). The locomotor muscles of greyhounds consist of a large proportion of fast-twitch fibers compared to other similarly sized breeds, which tend to fatigue faster than other muscle types, but help to generate powerful bursts of movements like sprinting (Rodriguez-Barbudo et al. 1984).

Greyhounds are known to reach speeds of over 40 miles per hour. This remarkable capability can be attributed to its use of the rotary gallop, also referred to as a double-suspension gallop (Bertram and Gutmann 2009; Usherwood and Wilson 2005; Fig. 1). The double-suspension

gait is a four-time, asymmetrical gait, where the feet fall in a circular sequence around the body, and gets its name from the two aerial phases: a gathered aerial phase where the back is flexed and the hind feet pass in front of the forefeet and an extended aerial phase where the feet are stretched away from the body and the back is extended (Bertram and Gutmann 2009; Hudson et al. 2012). When running competitively, the greyhound is in the air 75% of the time. There are several theories as to why the rotary gallop may be beneficial for generating speed, including reducing momentum losses during stance (Bertram and Gutmann 2009) and allowing internal work to be stored in the elastic structures of the back, increasing efficiency (Alexander 1988). Despite the speed, the double-suspension gait doesn't offer much endurance (Hudson et al. 2012).

Despite similarity in size and build, the greyhound falls short of the remarkable running capabilities of the cheetah (*Acinonyx jubatus*) (Hudson et al. 2012). Three major limits have been proposed to explain an animal's maximum speed: peak limb force, minimum achievable swing time, and muscular power (Hudson et al. 2012; Kram and Taylor 1990; Usherwood and Wilson 2005). Hudson et al. (2012) observed several differences that may account for the cheetah's ability to generate faster speeds than the greyhound. The cheetah's longer limbs and back allow it to attain longer stride lengths. This, coupled with the cheetah's ability to reduce its swing times, contribute to it achieving faster maximal speeds than the greyhound. The range of swing times used by both species indicates that the minimum possible swing time was not often utilized and cheetahs in particular may attain even higher stride frequencies at greater speeds by reducing swing time. In both species, Hudson et al. (2012) observed that the forelimbs maintain a constant peak force with increasing speed, reducing vertical impulse as stance time decreases. Despite this, it seems unlikely that a peak force limit has been reached as other locomotor tasks (e.g., turning, prey capture) are likely to require the forelimbs to resist higher peak limb forces than those during straight line steady-state galloping. The hind limbs



**Greyhound Racing, Fig. 1** Gait characteristics of greyhound running. The greyhound is capable of achieving remarkable speed due to the double-suspension gallop (a), aka the rotary gallop, which is characterized by two

aerial phases: an extended aerial phase where the feet are stretched away from the body and the back is extended (b) and a gathered aerial phase where the back is flexed and the hind feet pass in front of the forefeet (c)

contributed a greater proportion of body weight support at higher speeds.

## Cross-References

- [Adaptation](#)
- [Canine Locomotion](#)
- [Canine Morphology](#)
- [Evolution](#)
- [Quadrupedal](#)
- [Zoology](#)

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## Grinnell's Axiom

- [Gause's Law](#)

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## Gripping

- [Grasping Reflex](#)

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## Grooming

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## Synonyms

[Preening](#)

## Definition

Grooming behavior is a physical process that functions to maintain the form and composition of an animal's body surface.

Grooming behavior is seen across a diverse range of animal taxa, including, for example, arthropods, birds, canids, felids, mongooses,

primates, rodents, and ungulates. Grooming is a physical process that serves the primary function of maintaining the form and composition of an animal's integument (i.e., skin, hair, feathers, or scales). Self-grooming, or auto-grooming, is the term used to describe an individual grooming its own body, and allogrooming is the term used to describe one individual grooming the body of another.

Taxa-specific differences exist in the behavioral form of grooming and the functional value it holds to those participants involved. Whereas arthropods typically groom by rubbing their own body parts with their legs or between their mouthparts, birds use their beaks to groom (otherwise known as preening), and feet to scratch, their plumage. Most mammals use either their tongues to lick, or lower incisors and canines as a dental comb to scrape, when grooming their pelage. Grooming among primates is typically a bimanual process, whereby the groomer sweeps through the pelt with their hands. Monkeys and apes are particularly skilled groomers, a consequence of the enhanced dexterity afforded by their highly opposable thumbs (“► [Precision grip](#)”). The strepsirhines (i.e., lemurs and lorises), who lack such a precise grip, more commonly rely on the use of a dental comb to scrape when grooming.

Almost all animals devote a significant amount of time to self-grooming, providing a range of taxa-specific benefits (e.g., thermal, anti-infective, hygiene, communication) that can improve individual “► [Fitness](#).” Maintaining the integument in and of itself plays an important role in “► [Thermoregulation](#).” For hair-covered mammals, grooming can prevent the hair from matting and helps distribute sebum along the hair shaft. Such maintenance facilitates piloerection and the overall thermal efficiency of the pelt, which helps animals compensate for changes in their environment without experiencing the water-loss and increased energy expenditure associated with autonomic thermoregulatory processes. In addition to its comparable role in thermoregulation, a bird's plumage plays an important role in flight, and thus maintaining its form via preening also serves an important locomotory function. Ritualized displays of preening are thought to play

a communicative role in courtship displays (“► [Courtship Rituals](#)”) among birds.

Some animals use grooming as a means to distribute secreted chemicals over their body’s surface, providing various protective functions. Where possible, most mammals will use their tongues to lick a wound to receive the antibacterial benefits of saliva that promote wound healing. Anogenital licking, observed most commonly among rodents, can facilitate sexual development and reduce the spread of certain diseases and sexually transmitted infections.

Some birds supplement preening behavior with anting, a self-anointing behavior (“► [Anointing](#)”) during which the birds rub ants on their skin and feathers. The release of formic acid, a chemical defense of the ants, is thought to help prevent parasite infestation, decrease skin irritation, and self-stimulate. Some arthropods spread antibiotic secretions over their body to protect themselves from bacterial and fungal infections. Secreted lipids or fatty acids also help protect some mammals from the cold, by absorbing radiation and providing an additional layer of insulation. Similarly, frogs use lipids secreted from specialized cutaneous glands that are then wiped across the body surface to provide a barrier against evaporative water loss. For the majority of birds, the uropygial gland, or preen gland, is an important part of preening. The uropygial gland is found near the base of the tail and produces an oily substance that when distributed over the plumage via preening, helps waterproof the feathers and keep them flexible. Some preen gland secretions also possess antimicrobial properties. Secretions distributed over the body surface via grooming are also considered to serve as chemical signals (“► [Pheromone](#)”) during foraging, social, and courtship interactions among a range of animal taxa.

In addition to maintaining the form of the integument itself, the groomer may also remove foreign material (i.e., dirt, ectoparasites, detritus, scabs, vegetative debris) from in or between the skin and its appendages (e.g., hair, feathers, and scales). Most animals are prone to various ectoparasite infestations, including lice, leaches, mites, and ticks. Ectoparasites can

negatively effect their host in a variety of ways, including blood loss, reduced appetite, nutritional deficits and weight loss, and an increased prevalence of disease transmission. Parasite infestations have a negative impact on individual health and fitness by reducing survival and reproduction, so any means by which parasite removal is possible, in this case grooming, is likely to have come under strong selection. By removing dirt and ectoparasites, grooming increases the cleanliness of the pelt and increases individual health. Indeed, grooming rates are predicted by intensity of parasite infestation and are higher on body regions of higher parasite load, and grooming is also more prevalent among populations that live in geographic regions of high parasite risk. Allogrooming tends to be directed toward body regions that cannot be reached by self-grooming. As well as maintaining the pelts form and keeping the fur clean, it feels good to be groomed. Being on the receiving end of grooming has been associated with endorphin release, lowered heart rates, and reduced social anxiety and baseline stress levels. Grooming, however, also comes with its associated costs. Grooming is a time-consuming activity and occurs at the expense of other behaviors critical for survival and reproduction, namely, vigilance for predators, feeding, resting, and mating. Allogrooming may also increase the transmission of disease and infection between social partners, which can have a negative impact on individual fitness. Repetitive self-grooming, self-scratching, yawning, and body-shaking are all forms of displacement activity, behaviors that reflect the emotional status of an individual at times of internal conflict and social uncertainty. Excessive self-grooming, or plucking, which can lead to baldness, can be seen across a wide range of animal taxa, most notably in birds.

Allogrooming is thought to have evolved primarily for its hygienic function. In some animal taxa, however, allogrooming occurs at rates that far exceed the amount needed for parasite removal alone, and can sometimes occur in the absence of parasite infestation all together. If allogrooming were to serve a purely utilitarian function, one



would expect grooming rates to be positively predicted by body size, since the greater surface area associated with larger body size would require more grooming effort to clear it of dirt and ectoparasites. Evidence that grooming rates are positively predicted by group size, but not body size, however, has led to the belief that allogrooming is not solely limited to a utilitarian function, but also serves an important role in social bonding. Social grooming is seen across a diverse range of animal taxa. Social grooming is used to service social relationships among group members. Social relationships help alleviate the negative consequences of within group competition, and individuals more socially integrated into their group experience improved health, longevity, and offspring survival, compared to those more socially isolated. The social functions of grooming are discussed in detail in the entry “► [Social Grooming](#).”

## Cross-References

- [Anointing](#)
- [Allogrooming](#)
- [Courtship Rituals](#)
- [Fitness](#)
- [Pheromone](#)
- [Precision Grip](#)
- [Social Grooming](#)
- [Thermoregulation](#)

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## Group Living

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## Synonyms

[Sociality](#)

## Introduction

The distinction of animal species between solitary and group living is rather artificial (Krause and Ruxton 2002), as even animals that spend the vast majority of their time alone engage in social interactions and/or join a group at some point in their life (Tinbergen 1953), for example, when mating, during parental care, or when a large food source attracts many conspecifics. Definitions of group living differ based on the type and frequency of social interactions that group members are expected to display with one another to form a “group,” the degree of cohesion and coordination between group members, and the stability of the group over time (Krause and Ruxton 2002). Terminology also varies depending on the taxonomic group or type of social interactions between group members. For example, a social group of fish is called a “shoal” and scientists use the term “community” to define a group of chimpanzees. However, virtually every definition of group living accepts that animals need to show some degree of spatial proximity over time to form a group. Wilson (2000, p. 585) defined a group as “any set of organisms, belonging to the same species, that remain together for a period of time while interacting with one another to a distinctly greater degree than with other conspecific organisms.”

## Evolution of Group Living

Solitary life is considered the ancestral state and group living has probably evolved independently in various taxa. Several different hypotheses have been proposed to explain the evolution of group living, some that can potentially apply to any taxonomic group and others that are more taxon-specific. Wilson (2000) argued that the prime driving forces of social evolution are phylogenetic inertia and ecological pressure; the evolution of sociality would thus result from the constraints imposed by phylogenetic inertia on genetic response to ecological pressure. Phylogenetic inertia refers to the constraints of evolutionary change (Blomberg and Garland 2002) and can

be observed when there is a mismatch between ecological conditions and behavioral responses. For example, phylogenetic inertia has been proposed as a factor determining why current ecological conditions do not explain differences in social style in the genus *Macaca*. Theories on what ecological pressures favored the evolution of sociality consider the costs and benefits of group living versus solitary life for individual fitness. According to these theoretical frameworks, group living may have evolved independently in various taxa when, over evolutionary time, the benefits of group living for the inclusive fitness of an individual outweighed the costs. Different theories have proposed a range of different ecological pressures as the main determinants of social evolution. These different ecological pressures can be grouped into three broad categories: (a) foraging (and access to other resources such as water or shelter), (b) defense from predators, and (c) access to mating opportunities (including infanticide). Each of these ecological pressures can give benefits to individuals living in groups (Majolo et al. 2008). However, group living animals can also incur in some costs when, for example, a group becomes so large that food competition within the group becomes so intense that its costs outweigh the benefits of group foraging (e.g., protection from predators). Although group size is expected to vary within species, depending on the local ecological conditions of a population or group, each species/population is expected to have an upper and lower limit of “tolerable” (or “optimal”) group size. If a group falls below the lower limit, or it grows above the upper limit for the species/population optimal group size, the costs of group living are expected to outweigh the benefits and the animals in the group can, respectively, join another group or fission into two or more groups.

### Foraging

Group living (or living in larger groups) allows group members to access and/or defend valuable resources at the expenses of solitary animals or smaller groups from the same or from different species (Packer and Ruttan 1988). Group-living predators, such as wolves and African wild dogs,

can catch large prey that they would not be able to capture if hunting alone. In the nonbreeding season, Harris’ hawks (*Parabuteo unicinctus*) form parties of two to six animals to improve their capture efficiency. Hawks in those parties also consume less energy per unit of time spent hunting. Pelagic dolphins (*Stenella longirostris*) act together to force their prey into a smaller space so that increased prey density improves capture rate. In the social spider *Anelosimus eximius*, communal living favors group defense and protection of food sources. In the blue tang surgeonfish (*Acanthurus coeruleus*) group foraging results in better defense of food from damselfish (*Stegastes dorsopunicans*) and increased feeding efficiency (i.e., increased bite rate on algal mats). Finally, the larger a group of lions (*Panthera leo*) the greater their chance of defending their prey from spotted hyenas (*Crocuta crocuta*).

Searching the environment for food is time-consuming and potentially dangerous in terms of exposure to predation risks, particularly for solitary animals. Group living gives animal the possibility to gather information from other group members, or from members of other species for mixed-species associations (i.e., two or more species moving together with some degree of coordination for a given amount of time). Such information can be about the location of food, the amount of food available, the assessment of a habitat or area (its suitability, richness, or perceived risk), or the presence of predators nearby. The advantages of foraging in groups have been shown in various taxa. Goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*) locate food more rapidly with increasing group size. Group foraging allows bats (*Rhinopoma microphyllum*) to increase their efficiency on prey detection and capture by maintaining high-levels of group density and conspecific interference.

Additional benefits of group living, not necessarily associated to foraging, are thermoregulation and reduced costs of movement. Group living allows animals to huddle together when cold, to maintain the necessary body temperature and improve thermos-regulation, with significant benefits on energy expenditure. Moreover, moving in a group allows animals to take turn at the front or

back of the group, and to travel behind other individuals reducing resistance of the medium and energy expenditure. This is particularly beneficial for migratory birds or fish.

Group living may also involve some potential foraging costs for individuals, in the form of increased within-group food competition, depending on the amount and distribution of resources. Food competition is differentiated into “contest” and “scramble” competition. Contest competition occurs when animals aggressively interact with one another to gain access over the contested resource. Such interactions may range from aggressive displays from a distance to physical contact resulting in injuries or death, and the winner of the interaction may have either full or prioritized access to the contested resource. Scramble competition describes the scenario where animals are depleting a resource without engaging in a direct contest with other animals who are similarly interested in accessing and using that same resource. For example, scramble competition would occur when two animals are feeding on the same fruiting tree but at different times, that is, without encountering each other on/near the contested resource. Therefore, even if animals do not monopolize and aggressively exclude other group members from a food patch, in larger foraging groups animals have a lower amount of food potentially available per capita, other things being equal (e.g., interindividual difference in feeding efficiency). The degree of within- and between-group food competition determines the optimal group size for a population or species. In a comparison of the ecology and behavior of 75 species of African antelopes, researchers found that species that are described as selective feeders form smaller groups than the species that are unselective feeders. Selective feeders are species where animals feed on resources that are that are difficult to find, and/or patchy in time or space, that is, species where the risk of food monopolization and competition is high. In those species, therefore, smaller groups result in lower within-group food competition. Conversely, in species with unselective feeding the cost of within-group competition is lower and thus group size is greater.

Another potential benefit/cost of foraging in groups is klepto-parasitism, where an animal steals food from another individual. Klepto-parasitism is particularly frequent when the energy required to find food is high: such a scenario makes klepto-parasitism highly beneficial for the “thief” (as that animal gets food without incurring in the energy expenditure necessary to obtain it) and costly for the target. Klepto-parasitism is common in seabirds between and within species, especially during communal nesting.

Increased risk of infection and of transmission of parasites and disease may pose significant ecological pressure on group living animals (Alexander 1974). Animals living in groups often interact and are in close proximity with other individuals so the risk of disease/parasite transmission is higher than for solitary animals. For example, in a ground-dwelling avian species, the bobwhite quail (*Colinus virginianus*), there is a positive association between flock size and intensity of infection by parasitic helminths. Moreover, parasite infection in European bee-eaters (*Merops apiaster*) decreases with increasing inter-nest distance. A high parasite burden imposes significant fitness costs to animals, such as slow growth, high winter mortality, and reduced reproduction. The extent to which the risk of parasite/disease infection constrains sociability and group size is still unclear.

### Defense from Predators

One of the main advantages of group living, in relation to predation risk, is that animals in groups are more likely to spot a predator (so-called many eyes effect) than solitary individuals. Many group living species use alarm calls and other displays to signal group members about the presence of a predator. In some species, e.g., meerkats (*Suricata suricatta*), group members take turn in performing the role of “sentinels” while the rest of the group is resting or feeding. There is a positive relationship between group size and reliable predator detection. For example, in the banked killifish (*Fundulus diaphanus*) the occurrence of false alarms is reduced in larger groups. Moreover, common starlings (*Sturnus vulgaris*) and laughing

doves (*Streptopelia senegalensis*) in flocks respond more quickly to a predator model than single birds. In mammals, the distance at which long-tailed macaques (*Macaca fascicularis*) detect predators increases with their party size. Thus, the many eyes effect allows an individual forager to spend less time on antipredator vigilance and more time on other activities, and the more so the larger the group.

Once a group living species detects a predator, it can either escape a predator attack or mob the predator. Mobbing behavior occurs when potential prey join forces together to aggressively attempt to drive the predator away. Mobbing has been observed in a range of species including, for example, in crows mobbing eagles or baboons mobbing leopards (Caro 2005). As demonstrated in the Antarctic terns (*Sterna vittata*), mobbing against South Polar skuas (*Catharacta maccormicki*) significantly reduces the costs of predation risk. Mobbing is a cooperative behavior that may depend on reciprocal altruism: in the pied flycatchers (*Ficedula hypoleuca*) birds are more likely to help their conspecific neighbors mobbing a predator if those neighbors have helped them previously.

Group living helps animals escaping predators' attacks through a "dilution effect" whereby the larger the group of prey the more difficult for a predator to focus on a single prey and the less likely is for a single animal to be caught by a predator. There is an upper limit to the number of prey that a predator can handle or consume during a certain period. Therefore, groups that maximize the synchronization of their activities and their coordination of movements can benefit the most from the dilution effect, as animals in those groups are less likely to be separated from the rest of the group. For example, redshanks (*Tringa totanus*) who live in a larger flock have lower probability of being killed by raptors than those living in a smaller flock. Reproductive synchrony can be a strategy for reducing predation rate on vulnerable offspring through a dilution effect. In snowshoe hares (*Lepus americanus*) predation risk is negatively related to the number of synchronous litters. Similarly, the mortality of pronghorn (*Antilocapra americana*) fawns during

the peak fawning period is lower than for pronghorns born during the nonpeak period.

Even though larger prey groups are more exposed and conspicuous to predators, the increased risk of being detected is outweighed by the decrease of the individual likelihood of being preyed upon as the group becomes larger. The interplay between the risk for a group to be detected by a predator and for a group member to be attacked by a predator determines the benefits/costs of group living for an animal in relation to predation. For example, although larger groups of stream-dwelling trichopteran pupae (*Rhyacophila vao*) were more likely to be attacked by planarian predator (*Polycelis coronata*) than smaller groups, the predation risk for each pupa was still lower than for those pupae who were living in smaller groups. Finally, animals in a group are not all equally likely to be attacked, as predators prefer to target individuals who are weak, ill, or slower, and/or those who are at the periphery of the group. For example, predators like the bluegill sunfish (*Lepomis macrochirus*) preferentially attempt to hunt individuals who do not coordinate their movement with the rest of the group. Therefore, there may be competition between group members over which position (center or periphery) each animal should take in the group when a predator is nearby.

### Access to Mating Opportunities

Group living animals are more likely to get access to a mate than those who live solitary and so the former has more opportunities to compare potential mating partners and for mate choice. In mammals living in groups composed of multiple males and females, concealment of estrous and estrous synchrony among group females reduce the risk of sexual coercion by males (a significant risk for females, especially in species with pronounced sexual dimorphism in favor of males), increase sperm competition, paternity uncertainty, and female mate choice.

Leks, or mating arenas, are communal mating grounds where males gather to engage in competitive displays to signal their strength to females, as the competitive ability of males in lekking species is a measure of genetic quality. For females, the

lek allows effective assessment of each male's quality and strength, and it thus provides excellent opportunities for female mate choice. Females who choose the most powerful male in the lek have lower risk of harassment from other males. Lekking is observed in a large number of species and it allows strong, dominant males to maximize their reproductive success. Several models predict that the ability to monopolize females by high-ranking males can be affected by the extent of disturbance received from low-ranking males in a lek. Therefore, lower-ranking males should have greater reproductive success in larger leks, which attract more males, and/or under a wider spatial distribution of females. Moreover, related males can join forces and out-compete unrelated males when the inclusive fitness benefits gained through reproductive success of relatives are greater than the benefits of reproduction to direct fitness (Kokko and Lindstrom 1996).

In several mammals, infanticide is a strategy used by males to increase their reproductive success. In these species, males can kill infants who they are unlikely to have sired so that females can resume estrous and become ready to resume mating. Infanticide is a potential risk for both solitary and group living species, as, for example, it may be observed in species where solitary lactating females with their infants move within the home range of a male. However, infanticide is a particularly beneficial strategy for subordinate or immigrant males, and risky for females, in species where multiple females are present in the same group and where females synchronize their estrous. In these species, several infants of roughly the same age can be present, making the group particularly "attractive" for immigrant infanticidal males who attempt to enter that group at the top-ranking position. Similarly, a group male who has a subordinate position but manages to outrank the dominant male (who sires all/most of the infants) can kill the infants to mate with the group females. Group females employ counter-strategies to avoid or limit the risk of infanticide. In some nonhuman primate species, for example, group females form alliances with one another to prevent immigration of adult males into their group. Moreover, in baboons (*Papio*

*cynocephalus*), group males protect lactating females from potentially infanticidal males. During intergroup interactions, dominant male black howler monkeys (*Alouatta pigra*) show more aggressive behavior towards potentially infanticidal intruders when vulnerable offspring are present.

## Interspecies Variation in Grouping Patterns, Mating Strategies, and Social Structure

The large number of animal species, especially those foraging nocturnally or underground, such as some marsupials and insectivores, tend to be solitary. There are, however, several exceptions to this pattern; badgers, for example, are a highly social species but are often active at night and spend the day in burrows. Many group living species are diurnal, possibly as a response to the increasing predation risk in open environments and during the day (van Schaik 1983). Group living animals inhabit a wide variety of habitats, use different ecological niches, and are exposed to a range of ecological pressures. Indeed, extensive differences exist between and within group living species and several nonmutually exclusive factors can be used to describe such differences (Clutton-Brock and Harvey 1980). These factors include mating patterns (monogamy or promiscuity), group size and composition (i.e., whether animals of both sexes and/or of every age class are present in the group or not), the rate of gene flow within and between groups, kin and dominance relationships, and social bonds between group members. In the second half of the last century, researchers have spent a growing amount of effort to try and extrapolate general patterns on the social organization and structure of group living species based on the factors described above and in response to different ecological conditions (Crook and Gartlan 1966). The resulting socioecological models attempt to explain within and between species differences in grouping patterns and explain how these may have emerged in response to the cost and benefits of group living linked to a specific ecosystem (Crook et al. 1976).



## Eusociality

Eusociality describes a social organization where individuals engage in cooperative care of the young; there are different generations in the same colony and division of labor. Colonies of eusocial species are mainly found in social insects (ants, wasps, bees, and termites) (Wilson 2000), but also in some spiders, coral-reef shrimps, and mammals. In eusocial colonies, members are often divided into two castes, one composed of the reproductive individuals and the other of the (partially) nonreproductive individuals; members of the nonreproductive caste gain inclusive fitness benefits by helping their genetically related and reproductively active members of the colony (Nowak et al. 2010). Three main evolutionary pathways to eusociality have been proposed. In haplodiploid Hymenoptera, males are haploid (i.e., have an unpaired set of chromosomes) while females are diploid (two sets of chromosomes). Therefore, females are more closely related (they share 75% of their genes) in those species than females in non-haplodiploid species (who share 50% of their genes). This can facilitate the evolution of a sterile caste of females who gain inclusive fitness benefits by helping their reproductively active sampling to reproduce (Hamilton 1964). Boomsma (2007) argued that kin selection can favor the evolution of eusociality also in non-haplodiploid species, when inclusive fitness benefits for some individuals are comparable or greater than fitness benefits obtained via reproduction (Davies et al. 2012). A third hypothesis states that the formation of eusocial colonies is a response to intense competition with other colonies and/or predators that favored the evolution of a caste of soldiers.

## Monogamy

Among noneusocial species, groups composed of a monogamous breeding pair are found in various taxa, especially in insects, fish, birds, and mammals. The breeding pair often occupies a territory and their sexual bond can last for a single breeding season or for their lifetime. Even though living in pairs reduces the chances for females to elicit sperm competition and for males to sire a large

number of females, biparental care is considered as an essential advantage of pair bonding. In species with this social organization, the cost of reproduction is too high for a female to sustain it without the help of their breeding pair so males maximize their reproductive success by providing parental care. In marmosets and tamarins, for example, females often produce twins or triplets that are very heavy, relative to the body weight of the mother; thus, males are mostly responsible for carrying the infants around and for protecting them (Gubernick and Teferi 2000). Similarly, male zebra finches (*Taeniopygia guttata*) contribute as much as females to the rearing of the infants. After artificially removing male snow buntings (*Plectrophenax nivalis*), females who were left alone could only rear fewer young with lower body mass than the females who did not lose their male partners. Monogamous pair bonding could also enhance the ecological defensibility of females and protect their offspring from infanticidal competitors. Monogamy is much more common among birds than mammals: in birds, approximately 90% of species are monogamous. However, advancements in DNA analysis are showing that many species of birds that were once considered as monogamous are in fact promiscuous. Females may mate with more than one male to increase the number of males who contribute in feeding the nestlings. Similarly, males may be able to mate with two females and raise the two broods when food is abundant. Extra-pair paternity also exists among extensively monogamous mammals, such as prairie voles (*Microtus ochrogaster*), alpine marmots (*Marmota marmota*), fat-tailed dwarf lemurs (*Cheirogaleus medius*), and white-handed gibbons (*Hylobates lar*). In mammals, although paternal care is a strategy to maximize reproductive success, it is not considered to be a precondition for the evolution of social monogamy. According to Lukas and Clutton-Brock (2013), the evolution of social monogamy is favored when there is intense feeding competition, intolerance among females, and low demographic density, because males are incapable to monopolize more female partners under these circumstances.

### Cooperative Breeding

Cooperative breeding is a reproductive system in which some group members do not reproduce (for part or all of their life) but provide alloparental care to help the breeding individuals (Arnold and Owens 1998). Together with eusocial insects, cooperative breeding is found in birds and mammals. Usually the helpers, sometimes called auxiliaries or co-breeders, may be nonbreeding subadults or adults who are related to the offspring's parents; thus, helpers gain inclusive fitness benefits by providing parental care (Stacey and Koenig 1990). The helping behavior can involve not only incubating and providing food for the infants, but also defending nest and protecting young from predators. In these cooperative groups, sometimes the older offspring remain in the group until they reach adulthood and/or until they find a breeding partner, and help their parents raise the next generation of offspring, thus forming a family unit similar to what found is in many human societies. Cooperative breeding is particularly beneficial in altricial species, where young individuals are born in an underdeveloped state and need extensive care (Wilson 2000), and/or when food is scarce. Among pied kingfishers (*Ceryle rudis*), for example, under severe food shortage the presence of helpers is significantly and positively related to infant survival. In mammals, a high level of relatedness between group members is one of the driving forces in the evolution and maintenance of cooperative breeding (Lukas and Clutton-Brock 2013). Moreover, alloparental care can help inexperienced individuals to "learn to be parent" or to gain social benefits such as agonistic support. For example, female rhesus macaques (*M. mulatta*) provide alloparental care to their higher-ranking sisters in exchange for food tolerance and alliance formation.

### Polygamy

Another type of group living is where a single individual of one sex monopolize several individuals of another sex. A classic example of this type of group living is the uni-male groups (harems) of gorillas. Both polygyny (a male with multiple

females) and polyandry (a female with multiple males) have been observed (Shultz et al. 2011). Three main hypotheses have been proposed for the evolution of polygyny, resource defense polygyny, female defense polygyny, and male dominance polygyny (Emlen and Oring 1977). Resource defense polygyny should appear when a male attempts to attract females by occupying an area or territory with abundant and high-quality resources that would be available for females. This form of polygyny mainly occurs in habitats where resources are unevenly distributed and the number of females attracted by a male is often dependent on the quality of the area a male occupies and can defend from other males. Among shell-brooding cichlid fishes (*Lamprologus callipterus*), territorial males transport and accumulate shells as substrates for females to spawn in them; the more shells the male accumulates, the more females the male mates with. Female defense polygyny appears when males try to join in a group of gregarious females and fight with other males to monopolize the females in the group; this is also defined as female guarding polygyny. In these species, related females forage and move together, while males leave their natal groups before their sexual maturity and join other female groups during the breeding seasons to mate. This pattern is observed, for example, in African elephants (*Loxodonta africana*) and sperm whales (*Physeter macrocephalus*). The male dominance polygyny is found in species where there is high synchronization of reproductive activity among females. Males aggregate in competition arenas to fight other males and display their strength to females (see lekking behavior above). Dominant males can mate with several females but usually do not provide parental care; females are responsible for nesting, incubation, and feeding of the nestlings. For example, in the lekking white-bearded manakins (*Manacus manacus*), males who engage in more aggressive displays mate with a larger number of females than less aggressive males. After mating, females leave the lek and start nesting whereas males stay and compete to mate with other females.

### Mixed-Sex and Multilevel Societies

Multimale-multifemale groups are composed of various individuals of both sexes. The presence of multiple females attracts males and, in this species, a positive correlation exists between the number of males and females in a group. The larger the number of females, the less likely dominant males are to monopolize mating. This is particularly true for seasonal breeding species and where females synchronize their estrous and increase the importance of female mate choice and sperm competition. Multimale-multifemale groups are particularly common among Old World monkeys like baboons and macaques (Wrangham 1980).

Multilevel societies are characterized by a discrete stratification of one or more stable social units (i.e., layers such as basic social unit and clans) within the group. In the basic form of multilevel societies, individuals are grouped into a basic social unit, often composed of an adult male and one or more adult females plus their dependent infants, and these units can be grouped into a larger social layer (e.g., a herd). Multilevel societies are common in mammals and can be observed, for example, in elephants, cetaceans (bottlenose dolphins, *Tursiops* spp.), plains zebras (*Equus burchelli*), and some nonhuman primates (e.g., gelada baboons, *Theropithecus gelada*). Multilevel societies have probably emerged independently in different taxa in response to a combination of environmental and demographic factors. The social organization of plains zebras, which is supposed to be one of the simplest forms of multilevel society, is composed of only two tiers where several basic breeding units form a large herd. The formation of herds is due to the presence of large and even food resources (grass) and protection from predators. In nonhuman primates, elephants and cetaceans, multilevel societies have a more complex hierarchical structure. For example, in some primates, such as gelada baboons, hamadryas baboon (*P. hamadryas*), proboscis monkeys (*Nasalis larvatus*), and snub-nosed monkeys (*Rhinopithecus* spp.), there is a complex network of social relationships within and between each social layer, which has been termed modular or nested organization. In

hamadryas baboons, societies are hierarchically structured with several embedded levels: breeding units, "clans" (where often either the males or the females are genetically related to, or have social bonds with individuals of other breeding units within the clan), bands, and troops. The bands are often followed by males who are immature or young and affiliated with some breeding units. The troop can consist of hundreds of animals who move in a rather coordinate way. In snub-nosed monkeys, societies are structurally similar to those of hamadryas baboons. However, independent breeding units are territorial and occupy a certain home range; the degree of tolerance, proximity, and coordination between breeding units varies with familiarity between members of the different units and with the quantity of food available. The threat from conspecific individuals is thought to be the selective force of multilevel societies in nonhuman primates. The ancestral species lived in multimale-multifemale groups and a modular social structure emerged in response to competition between breeding units.

### Fission-Fusion

Fission-fusion societies describe group living species characterized by a flexible and dynamic social structure: individuals within the same fission-fusion society can join different parties for a variable amount of time (from a few hours to days); the composition of these parties can vary over time and parties can merge and split repeatedly so that rarely all individuals in a fission-fusion society are found together within a small area (Aureli et al. 2008). Fission-fusion societies are found in, for example, spotted hyenas, African elephants, dolphins, spider monkeys (*Ateles* spp.), and chimpanzees (*Pan troglodytes*). However, some degree of fission-fusion dynamics is found in virtually every group living species and particularly in species living in multilevel societies. Fission-fusion societies evolved as an adaptive strategy to the unpredictable distribution of resources, their patchiness, and the fact that food sources could not accommodate all animals within the society; parties reduce food competition between members of a society. In African elephants, kinship and resource availability affect

fission-fusion dynamics and individuals form different parties but the mother-calf pair remains a stable core unit. Fission-fusion dynamics are also affected by demographic factors. In communities of chimpanzees, for example, when the size of the community decreases, individuals form larger parties that are more frequently composed of both males and females than in large communities (where females often travel alone or with their dependent infant). Such a change in fission-fusion dynamics is explained by male reproductive strategies: in small communities, males are less likely to encounter and mate with females so they spend more time travelling and in association with females.

### Dominance

When resources such as food, shelter, or mating partners can be monopolized, animals living in group are expected to form a dominance hierarchy and compete to attain a dominant position. A dominance hierarchy is established and maintained through a series of aggressive/submissive interactions between group members, and animals that win most of the conflicts are dominant and those who lose are subordinates. Dominance networks can be described by three basic forms of hierarchy: linear, circular, and radial. A hierarchy is described as linear when group members can be assigned a dominance rank position that follows a linear order. For example, animal A is dominant over all the other group members, B is dominant over all the other group members but A, and so on. Linear hierarchies are common in insects, crustaceans, most birds, fish, and mammals (Wilson 2000). A circular hierarchy can be observed when, for example, A is dominant over B, B over C, and C over A. Finally, a radial hierarchy is observed when, for example, A is dominant over B and C, but B and C have no resolved dominance relationships and can equally win conflicts with one another. Dominance relationships are also described as steep or shallow along a continuous gradient. In a steep hierarchy, a dominant animal always (or most of the time) wins fights with a subordinate individual, provided no other individual is involved (i.e., the conflict is dyadic). In a shallow hierarchy, the

outcome of a dyadic conflict is context and temporally dependent, meaning that A may win some conflicts with B and lose some other depending on when, where, and over what resource they fight. The establishment of dominance hierarchy is an important factor that helps keeping a group stable and limits the risk of escalated aggression: subordinate group members tend to avoid dominant animals and so incur in a lower risk of aggression and injuries. Clearly, this is not the case if an animal is challenging the dominant position of another group member, and rank reversals often result in severe injuries and even the death of one of the contestants. Finally, dominance hierarchy can be very stable over time or change frequently over a short period of time, especially if group composition changes rapidly due, for example, to immigration, emigration, or deaths. What dominance position an animal can attain has a pronounced impact on access to resources: dominant animals typically gain more benefit (e.g., access to food) than subordinates that can result in fitness advantages (greater reproductive success). For example, dominant female spotted hyenas have a greater access to food in a competitive feeding situation than subordinates. In primates, high-ranking males have greater fecundity and mating success than low-ranking males (Majolo et al. 2012). However, counter-strategies from subordinates, such as sneaky copulations, can significantly reduce the differences in reproductive success between dominant and subordinate animals. For example, low-ranking male baboons may form alliances to try and outcompete dominant males and/or establish social bonds with females to increase their mating opportunities.

### Dispersal

In mammals, the spatial distribution and grouping patterns of females are considered key elements affecting male intrasexual competition, and females are the main ecological force driving social evolution (Wilson 2000; Emlen and Oring 1977; Lindenfors et al. 2004). Species living in groups may have sex-biased dispersal, whereby either males or females leave their natal group when they are about to reach sexual maturity and try to emigrate into other groups. In some species,

however, both males and females are equally likely to disperse. Dispersal and emigration from the natal group reduce the risk of inbreeding and affect the degree of genetic diversity within and between groups in the same population. In species with a sex-biased dispersal, members of the nondispersing sex often have several kin members in their group. For example, in primate species with a male-biased dispersal, like macaques, females form matriline composed of genetically related individuals and different matrilines compete to attain the dominant positions. This often results in the fact that all members of a matriline occupy adjacent rank positions and daughters attain the dominant position immediately below that of their mother. Moreover, in species with a male-biased dispersal, emigrating males may temporarily join bachelor groups and attempt to challenge males who have access to females.

### Social Bonds

One of the key features of group living is that animals can form social bonds with other group members. Social bonds can last for the whole life of an animal, especially between individuals of the nondispersing sex. The strength of these social bonds is affected by a number of factors: on average social bonds are often established between kin, familiar individuals, or individuals of similar sex, age, or rank. Social bonds are described by three dimensions: value, compatibility, and security. Value describes the benefits that individuals gain from the social bond. Compatibility describes the general tenor of the social bond and security measures the likelihood that a social bond would change over time. Social bonds can be established and maintained by a large range of species-specific behaviors, including allopreening, proximity, allogrooming, agonistic support, and embraces and physical contact. Animals sharing strong social bonds are more likely to support each other in conflicts with other group members, to tolerate each other near food source, to provide alloparental care, to gain mating opportunities or protection from predators. Ultimately, social bonds give fitness benefits to animals (including humans): individuals who have a larger or stronger network of social bonds survive

longer, have more offspring, a lower risk of stillbirths, more resilience to stress, and/or greater emotional stability (Dunbar 1998).

### Intraspecies Variation in Grouping Patterns, Mating Strategies, and Social Structure

With the growing amount of research on different populations, evidence is building that extensive differences in social dynamics exists within species. These within-species differences may be observed within a group, for example, in response to seasonal changes (e.g., rainy vs. dry season) or to unexpected events that change the habitat (e.g., a tornado). Moreover, within-species differences can also occur between populations of the same species and be more persistent over time. In guppies (*Poecilia reticulata*), populations living in areas where predation risk is high tend to form larger size shoals than populations where predators are scarce. Guppies appear to be flexible in their group dynamics and can rapidly adjust to new ecological conditions. For example, moving guppies from areas with high predation risk to predator-free streams rapidly decreases their tendency to shoal but they increase their shoaling behavior if moved back to areas with many predators. Similarly, in years when the population density of leopards is high, chacma baboons (*P. ursinus*) tend to forage in larger subgroups, and interindividual distances between group members during foraging are small. The same flexible responses may be observed for food competition. In a cyprinodontid species, the Japanese medaka (*Oryzias latipes*), when food resources are abundant individuals show high level of social tolerance and avoid consuming energy on conflicts with other group members; conversely, they increase conflicts over food when resources are scarce.

More permanent differences within species may be observed. A classic example is represented by the group dynamics of the chacma baboons. In some groups and populations baboons form one-male units whereas in other populations they form multimale-multifemale groups. These differences



in grouping patterns also change the behavior of baboons. Males living in one-male units are more vigilant and intervene in conflicts between their group females more frequently than males in multimale-multifemale groups. Differences within species in their grouping patterns may have fitness consequences. Red howler monkeys (*A. seniculus*) can live in both one-male units and in multimale-multifemale groups. Juvenile females have a higher mortality in multimale-multifemale groups than in one-male units, probably because they receive more aggression from unrelated males in multimale-multifemale groups. This difference in aggression received results in the fact that female survival is greater in one-male units than in multimale-multifemale groups.

## Conclusion

A clear distinction of taxa in terms of their grouping patterns is complicated by the flexibility of the social dynamics of taxa across seasons or populations. Under some ecological conditions (e.g., during the mating season or in the presence of a rich food source), individuals from a solitary species can be found in large aggregations in a small area. At the same time, animals usually living in groups can spend significant amount of time far away from the rest of their group, for example, when feeding or giving birth. Group living can be described by a series of “layers,” interconnected with one another, describing the mating and ranging patterns: type, strength, and size of the kin and social relationships; and the dispersal patterns and dominance style of the individuals in a group. The occurrence of these layers significantly varies across species as well as between populations or within the same social group across the seasons. Clearly, the flexibility and complexity of social dynamics is not uniquely human but is observed in many, distantly related taxa. Such flexibility and complexity represent a challenge for scientists, because it requires a stronger effort to study a large number of taxa instead of concentrating on just a few model taxa. At the same time, such flexibility and complexity of social dynamics represent an

opportunity to investigate the complex patterns and history of social evolution in the animal kingdom.

## Cross-References

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- ▶ [Costs of Group Living](#)
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## Group Nesting

- ▶ [Huddling](#)

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## Group Singing

- ▶ [Chorus](#)

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## Grouping

- ▶ [Chunking](#)
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## Growth

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## Guesser-Knower Paradigm

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## Definition

Experimental procedure designed to investigate organisms' understanding of others' mental states, particularly discrimination of knowledgeable vs ignorant informants, in a cooperative-communicative context.

## Introduction

Humans are highly skilled mind readers; that is, we have the ability to think about others' internal mental states, such as desires and beliefs. This skill is known as theory of mind or mind reading. Theory of mind informs our attempts to interpret, predict, and even manipulate others' behavior and thus is central to much of our social interaction, including our strategies for communication, cooperation and competition, empathy, and deception. For several decades – since Premack and Woodruff (1978) asked the seminal question, “Does the chimpanzee have a theory of mind?” – researchers have been attempting to determine whether this critical human skill is unique to our species. Over the years, a variety of elegant paradigms have been developed in the service of this effort. Early among them was the guesser-knower paradigm.

## Guesser-Knower Paradigm

Povinelli et al. (1990) designed the guesser-knower paradigm to test whether humans' closest relatives, chimpanzees (*Pan troglodytes*), were capable of modeling others' perspectives. Specifically, the authors wondered whether chimpanzees could correctly infer whether human experimenters were knowledgeable or ignorant of the location of hidden food based on whether the experimenters had witnessed the food being hidden.

In the original study, the chimpanzees watched as one experimenter, the knower, hid food behind a barrier, in one of four cups. Thus, although the apes could not see where the food was hidden, they were aware that it had been hidden and that the knower had performed this act. A second experimenter, the guesser, waited outside of the room until the baiting was complete. Once the guesser had entered the room and both experimenters were positioned behind the four cups, each pointed to a different cup. The knower always pointed to the correct cup, and the guesser

always pointed to one of the empty cups. The chimpanzee was then allowed to choose one of the cups. If she chose the knower's cup, the knower gave her the food beneath. If she chose any other cup, the knower revealed the food under his cup and the subject received nothing.

The logic behind the guesser-knower paradigm is that if chimpanzees (or other species) recognize that the knower, but not the guesser, has knowledge of the food's location, they should selectively follow the knower's points to find the hidden food. Importantly, the roles of the two experimenters were alternated across trials so that the subjects couldn't solve the task by simply learning which of the two experimenters reliably indicated the correct food location. Moreover, in a subsequent transfer phase, the procedure was modified in several key ways in order to control for some low-level explanations. Both the guesser and the knower remained in the room behind the apparatus, the baiting was performed by a third experimenter, and the guesser wore a paper bag over his head during baiting so that he remained ignorant of the food's location.

All four chimpanzees in the study quickly learned to choose the cup indicated by the knower, and three continued to do so in the transfer phase. Povinelli et al. (1990) interpreted their results to indicate that chimpanzees may have correctly attributed knowledge of the hidden food's location to the knower and that they may understand generally that knowledge is acquired through seeing. However, the researchers also acknowledged that the subjects may have learned, at least in part, to identify the reliable pointer based on salient cues like whether he was present/absent or wore a paper bag during baiting.

## Other Species

The guesser-knower paradigm has been used to study the social cognitive abilities of several species besides chimpanzees. Povinelli himself tested human children (*Homo sapiens*) as well as rhesus macaques (*Macaca mulatta*), finding that 4-year-

old human children, but not 3-year-olds or macaques, could selectively use the communicative cues of the knowledgeable informant in order to find the hidden food (Povinelli and deBlois 1992; Povinelli et al. 1991). Notably, Flombaum and Santos (2005) later provided positive evidence for rhesus macaques' sensitivity to others' perspectives as well, by adapting Povinelli's paradigms for a competitive setting (similar to work with chimpanzees: Hare et al. 2000, 2001, 2006). Other researchers have also shown positive evidence of guesser-knower differentiation in domestic dogs (*Canis familiaris*) as well as common ravens (*Corvus corax*) (Bugnyar 2011; Catala et al. 2017; Maginnity and Grace 2014).

## Interpretation and Criticism

Findings from the guesser-knower paradigm have been interpreted in several ways. In line with the alternative raised by Povinelli et al. (1990), Heyes (1998) argued that chimpanzees in the original study simply learned to discriminate present vs absent and bagged vs unbagged experimenters based on consistent differential rewarding; that is, they were reading behavior, not minds. Following negative evidence of chimpanzee perspective-taking from several related studies and analysis of other works on animal theory of mind, Povinelli and colleagues also concluded that existing paradigms provided little evidence of mental-state attribution in chimpanzees (Penn and Povinelli 2007; Povinelli and Eddy 1996; Povinelli et al. 1994; Povinelli and Vonk 2003). More recent adaptations of the guesser-knower paradigm have included additional controls aimed at constraining the applicability of behavior reading explanations and strengthening the case for mind reading (e.g., Catala et al. 2017); however, the debate about whether any nonhuman animals can attribute mental states to others rages on.

Povinelli and Heyes have suggested that tasks like the guesser-knower paradigm fall short of demonstrating theory of mind because they cannot completely control for the possibility that animals are able to succeed solely by identifying statistical regularities in others' behaviors (i.e.,

behavior reading, e.g., distilling regularities into behavior rules like "agents orienting toward food during its baiting typically indicate the correct location of the food"), without needing to make any additional inferences about actors' mental states (Heyes 1998; Penn and Povinelli 2007; Povinelli and Vonk 2003). In contrast, others have postulated that, although individual behavior rules can be developed to explain animals' success in specific tasks, it is more parsimonious to assume that correct performance across diverse tasks is explained by a single unified theory of mind mechanism than by a suite of individually learned behavior rules (Call and Tomasello 2008; Hare 2011). These authors have also attempted to control for behavior reading in task designs by restricting behavioral cues that are available at the time of test (Hare 2011). Although consensus remains elusive, recent advances have contributed new methodologies that may help to tease apart competing explanations for the social cognitive skills of nonhuman animals (e.g., Buttelmann et al. 2017; Karg et al. 2015; Krupenye et al. 2016; Schmelz et al. 2011).

## Ecological Validity

Mechanisms aside, the guesser-knower paradigm and others like it – which test social cognitive skills in cooperative-communicative contexts – have also been at the center of discussions over which methods are most suitable for investigating the cognitive abilities of a given species. Although chimpanzees were successful in the original guesser-knower task, they performed more poorly in a number of subsequent tests that required them to communicate or interpret communication in cooperative contexts. Tomasello et al. (2003) argued that chimpanzees' failure may reflect a lack of ecological validity rather than a lack of theory of mind. That is, chimpanzees may respond inconsistently to pointing not because they cannot infer the knowledge state of the pointer but because they rarely communicate in such cooperative ways and thus do not understand the intentions behind the pointing. In contrast to cooperative-communicative settings, Hare

(2001) suggested, apes may be more skillful in competitive contexts, since it is likely in these contexts that apes most commonly employ the cognition under study. Indeed, experiments involving competitive contexts have provided much of the evidence for primates' most sophisticated social cognitive skills (e.g., Flombaum and Santos 2005; Hare et al. 2000, 2001, 2006; Kaminski et al. 2008; Karg et al. 2015; Krupenye et al. 2016; Schmelz et al. 2011). Interestingly, dogs excel in cooperative-communicative interactions with humans and, fittingly, have performed much better than primates in paradigms that rely on such contexts, like the guesser-knower paradigm (e.g., Catala et al. 2017; Maginnity and Grace 2014).

Although experimental contexts that are based on the challenges that animals naturally face in the wild may be best for capturing apparently sophisticated behavior, Povinelli and Vonk (2003) have also noted that these are the contexts in which animals may have had the most opportunity to learn behavior rules or for which they may have evolved innate mechanisms. A nuanced appreciation of ecological validity is thus necessary to design experiments for which animals are sufficiently motivated but which may be able to control for competing explanations.

## Conclusion

In conclusion, the guesser-knower paradigm is an experimental method developed by Povinelli et al. (1990) to test for theory of mind in nonhuman animals. Subjects face a pair of experimenters, one knowledgeable and one ignorant, who are indicating, correctly and incorrectly, respectively, which of several cups contains hidden food. Subjects could solve the task (i.e., choose the cup containing the food) by inferring the different mental states of the pointers (i.e., by mind reading) or by applying learned rules based on superficial cues to determine which actor is most likely to indicate the correct location (i.e., by behavior reading). Variants of the paradigm have been used to study social cognition in several species, including chimpanzees, rhesus monkeys, dogs, and common ravens.

Given that the paradigm relies on a cooperative-communicative context – one that is highly relevant for humans but not for all other species – the guesser-knower paradigm has been the topic of considerable discussion about ecological validity in experimental design. Apes may generally perform poorly in paradigms where they must interpret cooperative pointing because they rarely engage in such communication naturally, whereas human children and domestic dogs may have evolved specialized sensitivity to such cooperative-communicative cues. Thus, while the guesser-knower paradigm continues to be used to investigate social cognition in additional species, variation in performance across species must be interpreted with consideration of the ecological validity of the task to the individual species under study as well as the skills besides behavior or mind reading that may be foundational to success on the task. Combining this task with other existing tasks and novel ones aimed at addressing persistent alternative explanations (e.g., Heyes 1998; Penn and Povinelli 2007) will help researchers to determine the extent to which theory of mind is distributed among species other than humans and how it evolved.

## Cross-References

- Cecilia Heyes
- Deception
- Experience Projection
- Goggles Experiment
- Intentionality
- Josep Call
- Michael Tomasello
- Pointing
- Theory of Mind

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## Gustation

- [Hominoidea Sensory Systems](#)
  - [Primate Sensory Systems](#)
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## Gustatory

- [Chemoreception](#)
- 

## Gustatory Signals

- [Chemical Signals](#)
- 

## Gyrus Dentatus

- [Dentate Gyrus](#)

# H

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## Habituation

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### Synonyms

[Desensitization](#); [Nonassociative learning](#)

### Definition

Habituation refers to a decrease in behavioral responding as a result of repeated exposure to a stimulus that is not attributed to sensory adaptation or motor neuron fatigue.

### Introduction

Have you ever been stuck on a noisy train car? When you first got on the train, you were probably annoyed by the conductor's loud voice over the speaker, the screeching sounds of the train as it stops and starts, or the person next to you yelling into her phone. However, as the ride went along, you probably stopped paying attention to the loud noises and may have forgotten about how annoying these noises were when you first boarded the train. This is an example of habituation. Habituation is the basic learning mechanism involving a decrease in responding with repeated

presentations of a stimulus (Domjan 2015). Habituation typically helps an organism ignore stimuli within their environment after learning a stimulus is not biologically relevant. From the example above, you might learn to ignore the train sounds or the person on the phone because they do not have a direct impact on you. You might even forget what the conductor said over the loud speaker or what the person was yelling about on the phone.

### Characteristics

A number of characteristics have been identified to explain how various factors impact the process and strength of the habituation process. Habituation can occur for varying amounts of time. Short-term habituation generally occurs when a response-eliciting stimulus is presented repeatedly within short intervals, while long-term habituation occurs with delayed but continuous presentations of a stimulus. Long-term habituation persists for longer periods of time and is generally attributed to enduring changes in learning compared to short-term habituation, which can dishabituate\* relatively quickly (Domjan 2015). Long-term and short-term habituation rely on different neural mechanisms, which can be attributed to the differences in the strength of habituation for each process (Squire 1987). Habituation can also be affected by time through spontaneous recovery\* (this is the identifying

characteristic of short-term habituation). If an organism is habituated to a stimulus and shows a decrease in responding, the response can at least partially recover with the passage of time (Thompson and Spencer 1966). Habituation can occur more quickly after the presentation of multiple stimulus-response presentations followed by spontaneous recoveries. Spontaneous recovery occurs faster for habituation resulting from high stimulation frequencies than habituation resulting from the presentation of low frequencies of stimulation (Rankin et al. 2009). The stronger the stimulus, the less likely habituation will occur, while weaker stimuli allow habituation to occur more quickly, showing a stronger decrease in the response. Habituation training that continues to occur after the response to a stimulus has disappeared or remained constant will result in slower recovery of the behavioral response (Thompson and Spencer 1966). Habituation for one response to a stimulus can also generalize toward other, similar stimuli. When presented with a separate (and usually stronger) stimulus, the stimulus will elicit the recovery of habituation (or decreased responding) to the original stimulus, also known as the process of dishabituation (Rankin et al. 2009). When the dishabituating stimulus is repeatedly presented to the organism, this can lead to a reduction in dishabituation, allowing the organism to habituate to the stimulus once again.

Habituation is not the only type of learning involving decreased responses to a stimulus.

A decrease in responding to a stimulus is considered habituation if it cannot be attributed to sensory adaptation or motor neuron fatigue. Sensory adaptation\* occurs when the sensory organs temporarily fail to respond to a stimulus. Sensory adaptation can occur when you enter a dark room and have trouble seeing because your eyes have not adjusted to the change in light. Motor neuron fatigue occurs when the muscles are temporarily unable to make the response to a given stimulus. Motor fatigue can occur if you are touching a vibrating object and you stop feeling the vibration because your motor neurons have weakened. Both of these concepts are not considered habituation, in part because they occur outside of the nervous

system. During habituation, the organism no longer responds but is still fully capable of sensing the stimulus and making the muscle movements required for the response (Domjan 2015).

Habituation can also be distinguished from motor neuron fatigue because habituation is *stimulus* specific. To rule out motor neuron fatigue, we look at different stimuli. If the organism does not produce a response to a stimulus, but can produce the same response to a different stimulus, the decline of the target response cannot be explained as response fatigue (Domjan 2015). A study by Epstein et al. (1992) illustrates this point. During this study, female participants were exposed to a repeated stimulus (tasting lemon or lime juice) for 10 trials. As the trials progressed, responding (amount of salivation) decreased over the course of 10 trials. At test, participants were exposed to a novel stimulus (the flavor they did not receive during the initial trials). After exposure to a novel stimulus, participants showed a significant recovery in responding (i.e., salivation). Results from this study showed that participants habituated to the repeated stimulus (i.e., the familiar flavor), and the salivation response could be restored with the presentation of a novel flavor.

Habituation can be distinguished from sensory adaptation because habituation is *response* specific. To rule out sensory adaptation, we look at different responses elicited by the same stimulus: If the organism does not produce a certain response to a stimulus, but still produces other responses to the same stimulus, the decline of the target response cannot be explained as sensory adaptation (Domjan 2015). For example, in the study by Epstein et al. (1992), repeated exposure to a flavor (either lemon or lime juice) resulted in a decrease in not only salivation but also a second response, namely, hedonic ratings. Had the authors observed a decline in only one of these responses (e.g., decrease in salivation, but not in hedonic ratings), their experiments would have also ruled out sensory adaptation.

Neuroscience research shows evidence supporting the role of neural mechanisms in the habituation process (see Kandel 2000; Thompson and Spencer 1966). While sensory adaptation occurs in the

sensory organs and motor neuron fatigue occurs in the effector muscles, habituation occurs within the nervous system\*. An organism fails to respond when habituation occurs due to changes in the nervous system, which prevent sensory neural impulses from reaching the motor neurons to perform a response (Domjan 2015). For example, Kupfermann and Kandel (1969) examined how behavior is modified by neuron activity by observing behavior in *Aplysia*, a species of sea snail. Their focus was on the process of sensitization\* – a fear response that emerges when an animal learns to produce strong responses to a neutral stimulus. Specifically, they examined the defense reflex, which involves gill withdrawal in response to aversive stimuli. *Aplysia* will withdraw their gills when they encounter a tactile stimulus to a specific part of the body known as the siphon. When an aversive shock was applied to the tail, *Aplysia* identified this as dangerous and evoked the defense reflex. However, when a neutral stimulus was applied to the *Aplysia*, the animal still produced a strong response to the stimulus. Results from this study suggest that *Aplysia* did not habituate to the stimuli but evoked strong defense reactions toward aversive (and nonaversive) stimuli. Kandel (2000) also showed that the process of long-term and short-term memory for sensitization differs. Long-term memory requires new proteins to be synthesized and is determined by the number of repeated exposures to the aversive stimulus. Repeated exposure to aversive stimuli with the implementation of a short delay between each presentation led to longer duration of memory for the aversive stimulus, lasting for days. In contrast, a single exposure to an aversive stimulus generated short-term memory of the stimulus, lasting only a few minutes. While research finds evidence linking habituation, learning, and neuroscience, more research is needed to fully understand *how* these mechanisms contribute to the learning process.

## Theoretical Support

The dominant theory for the underlying causes of habituation is known as the *dual-process*

*theory*. Proposed by Groves and Thompson (1970), the dual-process theory states that both increases and decreases in responding to a stimulus are guided by specific neurological processes. The theory suggests that habituation is guided by a process that decreases responding to a stimulus, while sensitization leads to increases in responding to a stimulus. Groves and Thompson suggested that each process occurs in distinct parts of the nervous system. While sensitization occurs in the state system, to determine the readiness of an organism to respond to a stimulus, habituation occurs in the S-R system, which allows an organism to make a specific response to a stimulus. The S-R system is activated for each stimulus eliciting a response while the state system is only activated in the presence of arousing stimuli. According to this theory, habituation and sensitization each attempt to control behavior, and the specific behavior elicited is determined by the net result of both processes (Domjan 2015). If a decrease in behavior emerges, this suggests that the strength of the habituation process is stronger than the strength of the sensitization process, leading to decreases in responding.

## Cross-References

- ▶ [Acclimatization](#)
- ▶ [Dishabituation](#)
- ▶ [Nervous System](#)
- ▶ [Plantae](#)
- ▶ [Sensitization](#)
- ▶ [Spontaneous Recovery](#)

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## Habituation Effect

- [Sensitization](#)

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## Hamilton's Paradigm

- [Inclusive Fitness](#)

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## Hamilton's Rule

- [Inclusive Fitness](#)

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## Hand

- [Opposable Thumb](#)

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## Hand Preference

- [Laterality \(Handedness\)](#)

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## Handicap Hypothesis

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## Synonyms

[Costly signaling](#); [Handicap principle](#)

## Definition

The hypothesis that in order to be honest, animal signals must be costly.

## The Handicap Hypothesis

The handicap hypothesis is an idea proposed in 1975 by Amotz Zahavi as a mechanism to explain how honesty is maintained in animal communication. The hypothesis proposes that in order to be honest, signals must have costs that are borne by signalers. Under this hypothesis, only high-quality individuals can afford to bear the costs of a high-quality signal, leading to honesty in communication. The hypothesis was critiqued by a number of authors through the 1970s and 1980s, including one of the preeminent theoretical evolutionary biologists of the era, John Maynard Smith. The handicap hypothesis remained largely discredited within the field until a game theoretic model was produced by Alan Grafen in 1990. In this model, a separating equilibrium was found in which the optimal strategy for signalers of different quality was to give a different signal type that reflected that quality. To achieve this outcome, Grafen associated cost functions with signals, with the costs experienced by signalers differentiating by signaler quality. This means that lower-quality signalers pay a higher cost than higher-quality signalers do to give a high-quality signal. Grafen (1990) added differentiating signal costs as a second condition to Zahavi's (1975) original concept of high costs to signalers, such that the handicap hypothesis is often now associated with



two conditions together: (1) that individuals pay a high cost to give their signal to maintain honesty (Zahavi's 1975 hypothesis) and (2) that lower-quality individuals pay a higher cost than higher-quality individuals do to give a higher-quality signal (Grafen 1990). Following this modeling, Grafen (1990) concluded that "Zahavi's major claims for the handicap principle are thus vindicated." In the years that followed, the handicap hypothesis became one of the best known and most commonly investigated hypotheses in the whole of evolutionary biology.

Interestingly, throughout the discussion of handicaps and the costs of signaling in the biological literature, there was a parallel literature in economics, which began with Spence (1973). Spence's model aimed to determine the mechanisms by which two graduating PhD students, one of whom is of low productivity and the other of high productivity, would honestly signal their respective productivities on the academic job market. Spence's model was later expanded to a more general condition, with continuous quality types, usually known as the Spence-Mirrlees condition. This series of work drew similar conclusions to the later model of Grafen (1990). However, this theoretical literature did not conclude that costs paid by signalers to give their own signal, i.e., condition #1 outlined above, proposed by Zahavi (1975), were necessary without applying further constraints. Since then, a range of models in the biological literature have drawn similar conclusions. As such, although Grafen (1990) concluded from his model that the finding of a separating equilibrium when differential signal costs are present supports the handicap hypothesis, other authors have concluded that this very same finding does in fact *not* support it. Under this latter interpretation, costly signaling models do not make any predictions about the costs that signalers must pay to give their own signals. They predict only that individuals give a signal that reflects their quality and that the costs associated with increasing signal expression beyond this are not worth the benefits of doing so. Individuals of high quality that give high-quality signals do not need to bear a cost to do so. The only cost required to enable this system to be honest is a potential

cost that low-quality signalers would pay to give a high-quality signal, should they choose to do so (to cheat). The conclusion from this is that signal costs experienced by signalers are not a *necessary condition* for honest signaling (i.e., condition #1, Zahavi 1975) above is unnecessary.

In addition, a second point to come out of these theoretical models is that signal costs experienced by signalers are also not a *sufficient condition* for honest signaling. Without condition #2, differential signal costs, a separating equilibrium cannot be found (Grafen 1990). Regardless of how costly it is for a high-quality individual to give a high-quality signal, a low-quality individual should also give that high-quality signal too, unless it experiences an additional cost for doing so. What makes individuals of all quality types give a signal that reliably reflects their condition is the differential signal cost. Thus Zahavi's (1975) hypothesis (condition #1 above) is not only unnecessary for honest signaling but is also not sufficient for honest signaling. Nonetheless, based on considerable confusion in the theoretical literature, and the subtleties of the above distinctions, it remains the most widely cited and considered explanation for honest signaling. Condition #2 above, introduced by Grafen (1990), is, in contrast, both necessary and sufficient for honest signaling.

A number of other types of models for honest signaling have been proposed in the evolutionary biology literature. One form is where there is alignment of interest between signalers and receivers, such that the optimal outcome for both individuals is the same. Under this scenario, theoretical models have shown that cheap honest signaling can evolve easily, given that there is no conflict between the signaler and receiver over the outcome of the interaction. Both individuals are selected to signal and respond honestly with no signaling costs required, beyond the efficacy costs associated with stimulating the receiver's sensory system. Another proposed mechanism is that of an index, in which individual signalers cannot cheat because signal expression is too tightly linked to anatomical or physiological condition. Under the index hypothesis, signals need not be costly to be honest. However, it is not clear that such a mechanism is distinct from that of a differential signal

cost scenario, as most interpretations of those models also do not predict that individuals must pay costs to give their own signal. Consistent with this, recent theoretical work on the evolution of index signals has supported the fact that indices can support cheap honest signals, essentially, by deriving a similar model and set of conditions (differential potential signal costs) to that seen in the costly signaling models (Biernaskie et al. 2014). Other proposed and commonly cited honest signaling mechanisms include punishment of cheaters, and reputation, whereby low-quality individuals who give high-quality signals are punished for it, and/or suffer a cost to their reputation. Because these are mechanisms by which lower-quality individuals experience higher costs for exhibiting high-quality signals than high-quality individuals do, they might be best seen as mechanisms for fulfilling the requirement of differential signal costs (condition #2 above).

Given the complex theoretical literature that has emerged on the topic of honest signaling, it has been difficult for empiricists to derive clear testable predictions from theory. Dozens, if not hundreds, of papers in animal behavior and evolutionary biology have tried to address the question of signal honesty by asking whether the signals that individuals exhibit are costly (i.e., testing condition #1 above). Typically, such studies have measured the signals that individuals express, while measuring physiological correlates of these signals, to ask if there might be “costs” associated with signal expression that might be involved in keeping signals honest. Results have been mixed. While some studies have found apparent costs associated with signal expression, others have not. Part of the reason for this might be that, as outlined above, it is not clear that costs should be expected in most cases given that they are not a *necessary condition* for honest signaling. Further, even if these costs are found, they do not necessarily indicate honesty because they are also not a *sufficient condition* for honest signaling.

A much smaller number of manuscripts have taken a different approach, testing condition #2 above – that of differential signal costs for higher- vs lower-quality individuals. Such studies have asked whether individuals pay additional costs to

give higher levels of signal expression than they actually exhibit, relative to individuals of higher quality. These studies have indeed often found success. For example, Madden (2002) found that when low-quality bowerbird males had their bowers artificially enhanced to resemble those of a high-quality male, they attracted more females, but provoked costly aggression from high-quality males. This cost is a differential signal cost – high-quality males do not experience such aggression for exhibiting a high-quality bower.

While there continues to be controversy and disputes around the nature of honest signaling, there seems to be broad theoretical agreement that differential signal costs are required for honest signaling when there is a conflict of interest between the signaler and the receiver. This means that high-quality signals must have costs for lower-quality individuals that are not present for higher-quality individuals. Because lower-quality individuals do not usually give high-quality signals in an honest system, such costs may be seen only when lower-quality individuals cheat, and give a high-quality signal. Empiricists are therefore on safest ground when undertaking experiments in which individuals are forced experimentally to exhibit increased levels of signal expression beyond those normally exhibited. Renewed interest in the theoretical basis for honest signaling in recent years will hopefully lead to broader agreement about the requirements for honest signaling, and also on more broadly agreed guidelines for empiricists as to what questions might most usefully be asked to address questions of signal honesty in animal systems.

## Cross-References

- [Cheating](#)
- [Communication](#)
- [Signaling](#)

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## Handicap Principle

- [Handicap Hypothesis](#)

## Haplorhine

- [Haplorhini](#)
- [Primate Sensory Systems](#)

## Haplorhini

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## Synonyms

[Anthropoid](#); [Ape](#); [Catarrhine](#); [Great ape](#);  
[Haplorhine](#); [Hominoid](#); [Human](#); [Lesser ape](#);  
[Mammal](#); [Monkey](#); [New World monkey](#); [Old  
World monkey](#); [Platyrrhine](#); [Prosimian](#);  
[Strepsirhine](#); [Strepsirhini](#); [Tarsier](#)

## Definition

*Haplorhini* is one of two suborders in the order *Primates* and a type of eutherian mammal. Haplorhine (*Haplorhini*) primates consist of tarsiers, monkeys, apes, and humans.

## Haplorhini Taxonomy and Range

*Primates* are an order of eutherian (placental with advanced development before birth) mammal. Within the primate order, there are two suborders: *Haplorhini* (the haplorhines) and *Strepsirhini* (the strepsirhines). Haplorhines consist of tarsiers, monkeys, apes, and humans. *Haplorhini* can be further divided into two infraorders: *Tarsiiformes* (tarsiers) and *Simiiformes* (monkeys, apes, and humans). The *Simiiformes* can be further divided into two parvorders: *Platyrrhini* (platyrrhines or New World monkeys) and *Catarrhini* (catarrhines or Old World monkeys, apes, and humans).

Haplorhines live in most tropical and some temperate regions across the globe, in habitats ranging from tropical forest to woodland to savanna to temperate forest environments. While tarsiers live in tropical forests on islands off the coast of southeastern Asia, New World monkeys live in tropical forests in Central and South America (i.e., the “New World”). Old World monkeys live in a range of habitat types in Africa and Asia (i.e., the “Old World”), including the savanna (e.g., baboons, *Papio* spp.), tropical forest (e.g., mangabeys, *Cercocebus* spp.), cloud forest (e.g., colobus monkey, *Colobus* spp.), and Asian temperate forest (e.g., Japanese macaque, *Macaca fuscata*). Nonhuman apes live in tropical regions in Africa (e.g., gorilla and chimpanzee; *Gorilla* spp. and *Pan* spp.), southeastern Asia (e.g., gibbon and siamang; family *Hylobatidae*), and some islands of Indonesia (e.g., orangutan, *Pongo* spp.) (Estrada et al. 2017).

## Haplorhini Characteristics

In contrast to most strepsirhine species, which are solitary, nearly all haplorhines live in social groups consisting of two or more individuals of the same species (Dunbar 2010). The one exception is a catarrhine genus, the orangutan (*Pongo* spp.), which is semi-solitary. The gregarious social lives of haplorhines have influenced their cognitive adaptations. While all primates show a high level of ecological intelligence relative to other mammals, haplorhines perform better

on tasks associated with social intelligence compared to strepsirhines (Byrne 1995). Within the haplorhines, Great apes (family *Hominidae*: gorillas, orangutans, chimpanzees, and humans) show even greater social intelligence than monkeys (Byrne 1995).

Haplorhines are also characterized by increased reliance on vision and decreased reliance on sense of smell compared to strepsirhines. Catarrhines and platyrrhines have different nose shapes, with catarrhines having narrow nostrils that are close together and platyrrhines having wider nostrils that are further apart. Most haplorhines are diurnal (active during the day), although tarsiers and one genus of platyrrhine (owl monkey, *Aotus* spp.) are nocturnal (active at night). To reflect this tendency for diurnal activity, haplorhine eyes lack *tapetum lucidum* (a reflective layer causing eye shine at night) and have retinal fovea (pits in the retina which improve central vision in daylight) (Ollivier et al. 2004). Haplorhines such as catarrhines and one genus of platyrrhine (howler monkey, *Alouatta* spp.) also have full color vision, allowing them to better perceive habitat features in daylight (Liman 2006). In contrast, most other platyrrhines can see some color but cannot differentiate between red and green, while one genus (owl monkey, *Aotus* spp.) can only perceive shades of gray (Liman 2006).

Haplorhines live in both arboreal (tree-based) and terrestrial (ground-based) environments (Larson 2018). They travel through their habitats using a broad range of locomotory methods, including vertical clinging and leaping (clinging to tree trunks before leaping to other trees; e.g., tarsiers, family *Tarsiidae*), arboreal quadrupedal (walking along the tops of branches on four limbs; e.g., platyrrhines like howler monkeys, *Alouatta* spp.), terrestrial quadrupedal (walking along the ground using four limbs; e.g., catarrhines like baboons, *Papio* spp.), suspensory (using elongated arms to swing from branch to branch in trees; e.g., catarrhines like gibbons, *Hylobates* spp.), knuckle walking (walking along the ground using four limbs with weight put on the knuckles of the forelimbs; e.g., catarrhines like chimpanzees and gorillas, *Pan* spp. and *Gorilla* spp.), and bipedal locomotion (walking upright on two

limbs; e.g., catarrhines like humans, *Homo sapiens*; Larson 2018). While all living primates have strong grips and some degree of manual dexterity, platyrrhines and catarrhines are best at using their hands and feet to manipulate objects with control and accuracy (Liman 2006). Many platyrrhines have additionally evolved prehensile tails, which act as extra limbs to support body weight during travel and feeding in arboreal environments.

Haplorhines show a range of dietary adaptations, with the smallest (e.g., tarsiers and platyrrhines such as marmosets and tamarins, family *Callitrichidae*) being insectivores (showing preference for insects) or gummivores (showing preference for tree sap and gum), and larger haplorhines (e.g., larger platyrrhines and catarrhines) being frugivores (showing preference for fruit) or folivores (showing preference for leaves; Hohmann 2009). Some folivorous Old World monkeys (leaf monkeys, subfamily *Colobinae*) have specialized morphological adaptations for better digestion of cellulose, including sacculated stomachs and elongated intestines. In order to process a wide range of food items, primates have generalized dentition with different types of teeth adapted to perform different functions. These consist of incisors (used to cut food), canines (used to grip and tear food), premolars (used to tear and crush food), and molars (used to crush and grind food). Different groups of haplorhines have evolved different dentition. Tarsiers have a dental formula of 2.1.3.3/1.1.3.3 (i.e., 2 incisors, 1 canine, 3 premolars, 3 molars in each quarter of the upper jaw, and 1 incisor, 1 canine, 3 premolars, and 3 molars in each quarter of the lower jaw), most platyrrhines have a dental formula of 2.1.3.3. (i.e., 2 incisors, 1 canine, 3 premolars, and 3 molars in each quarter of the mouth), and catarrhines have a dental formula of 2.1.2.3 (i.e., 2 incisors, 1 canine, 2 premolars, and 3 molars in each quarter of the mouth).

## Conclusions

Haplorhines show greater reliance on vision and less reliance on sense of smell compared to other primates. Most are diurnal and group-living, with

greater social intelligence than other primates. They live in a range of arboreal and terrestrial environments worldwide and have a broad range of diverse locomotory and dietary adaptations.

## Cross-References

- [Catarrhine Cognition](#)
- [Catarrhine Communication](#)
- [Catarrhine Diet](#)
- [Catarrhine Life History](#)
- [Catarrhine Locomotion](#)
- [Catarrhine Morphology](#)
- [Catarrhine Navigation](#)
- [Catarrhine Sensory Systems](#)
- [Hominid](#)
- [Hominoid](#)
- [Platyrrhine Cognition](#)
- [Platyrrhine Diet](#)
- [Platyrrhine Locomotion](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Communication](#)
- [Primate Diet](#)
- [Primate Sensory Systems](#)
- [Primate Social Structure](#)
- [Primate Suspensory Behavior](#)
- [Primates](#)
- [Prosimian Cognition](#)
- [Prosimian Communication](#)
- [Prosimian Diets](#)
- [Prosimian Life History](#)
- [Prosimian Locomotion](#)
- [Prosimian Morphology](#)
- [Prosimian Navigation](#)
- [Prosimian Sensory Systems](#)

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## Haplotype

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## Definition

*Haplotype* is a region or segment of chromosome comprising a group of genes in an organism that is inherited together from a parent. Haplotype is a contraction of the two words “haploid” meaning a single set of chromosomes and “genotype” meaning the genetic constitution of an organism.

## Main Text

The term haplotype can be variously defined pertaining to the genetic context. *First*, haplotype can signify an evolutionarily linked group of genes on a chromosome that has been transmitted as a single entity over thousands of years such as the mitochondrial or the Y-chromosome DNA. The human mitochondrial and Y-chromosome DNA are comprised of several evolutionary conserved *haplogroups*. A haplogroup arises from a distinct new single nucleotide polymorphism (SNP which are single base mutations) known as a unique-event polymorphism (UEP) that is carried by all the descendants. The new inherited mutation defines a particular haplogroup. Several



new SNPs do not make their way through the several thousands of years and those that do, form these haplogroups. To simplify, a new SNP arising now if gets descended over thousands of years will eventually form a new haplogroup. The same haplotype shared by several organisms can be used to trace the origin of the haplogroup to a specific individual or a specific clan of people. *Second*, haplotype can also mean a collection of a group of genes that gets inherited as a cluster over several generations of reproduction. *Third*, a specific meaning for haplotype can refer to a set of SNPs that always occur together. Haplotype can refer to a single SNP or a group of SNPs. *Fourth*, haplotypes can be identified as genetic signatures formed by a set of short repeat stretches of polymorphic DNA (regions of the DNA that are susceptible to genetic variability) known as *microsatellite markers* that get inherited as a linked region.

## Haplotype and Ancestry

Haplotypes get inherited from ancestors across the generations. Over several generations, only some haplotypes from a few ancestors tend to be inherited. These genealogical ancestors are also the genetic ancestors whose part of the genome is carried down to the future generations. More than 99% of our genealogical ancestors do not make it to being our genetic ancestors as the genetic information gets lost or modified by chance events during meiosis and processes of natural selection (Barton 2010). The genetic haplotypes also tend to get shortened over generations by random recombination. The exceptions to this rule of “loss of genetic information” are the mitochondrial and the Y-chromosome DNA, which are always inherited intact across their specific lineages. They have been routinely used for ancestry studies. The mitochondrial DNA is passed down exclusively by maternal inheritance, from the mother to the offspring. Only the female offspring passes this on to its next generation. The Y-chromosome DNA on the other hand is inherited by the son from the father and passed only to the male offsprings of subsequent

generations. These two are the exclusive cases unlike the autosomes that are a patchwork of genetic information from some ancestors. One question to consider is, if these ancestral haplotypes accumulate mutations over several generations would their ancestry still be recognizable? The simple answer to this is yes. The amount of mutation accumulated in the DNA over thousands of generations is very less due to it being a slow process. This would not hamper in detecting the ancestral haplotypes (Smolenyak and Ann 2004).

$$\begin{aligned} \text{Mutations accumulated} &= \text{Mutation rate} \\ ? & \quad \text{*number of generations} \\ & \quad \text{*length of base pairs} \end{aligned}$$

The human mutation rate is equivalent to one mutation in every 30 million base pairs per generation (Xue et al. 2009). These mutations assimilated over time in the genome contribute to its *genetic diversity*.

## Haplotypes and Genetic Disorders

Haplotypes are informative in the study of genetic disorders. Haplotype of any organism can be inferred from its genotype. *Genome-wide linkage analysis* is often used in the study of many Mendelian disorders (disorders caused by mutation in a single gene). Microsatellite markers present on all the chromosomes are typed to study *genetic linkage*. Linked DNA sequences that lie close together have lesser chance of recombination (a process that exchanges genetic material between homologous chromosomes) between them and tend to get inherited together. Genetic linkage analysis can be parametric (where the genotype and phenotype relation is known) or nonparametric. Logarithm of odds (LOD) score is frequently used in determining genetic linkage. It is a statistical test that examines the probability of obtaining a haplotype because of linkage or as a matter of chance. As a common rule, LOD score ( $Z$ )  $\geq 3$  means a higher probability of genetic linkage and lower values diminish the linkage probability. A LOD score of +3 indicates 1000 to 1 odds that the linkage does not occur by

chance. Although depending on the genetic complexity of inheritance of certain disorders, lower LOD scores can still be meaningful in the process of genetic linkage analysis. This approach is used in several genetic studies to identify the locus or the haplotype that segregates with the disorder in a family of several affected individuals. It can be used to determine the causative gene and mutation for the disorder in a family. This approach has been used as a powerful diagnostic tool to identify genes in many families with known and unknown genetic defects.

Haplotypes are useful in the study of complex diseases with genetic heterogeneity using another approach called the genome-wide association studies (GWAS). GWAS is used to study a large number of genome-wide variants in different individuals with a common trait to identify variants that associate with the phenotype. This kind of an association study is helpful in identifying new genes through variant association for complex disorders. One consideration in GWAS is phase resolution also known as haplotype estimation, to identify which chromosomes the mutations belong to. For example, in a two-phased heterozygote (A:G and T:C) 4 Mb apart, the appearance of A (position 1) and T (position 2) together all times does not assure that they are on the same haplotype. There could be several mutations within the 4 Mb region that could break up the haplotype. Finer the genotyping better the haplotype resolution. The GWAS technique has identified new candidate genes for bipolar disorder, rheumatoid arthritis, and coronary heart disease to name a few. Advances in the identification of new genes for rare genetic disorders are useful to advance the diagnosis and development of drugs and therapy for such disorders.

The International HapMap Project initiated in the year 2002 has developed a haplotype map of the human genome that catalogues the genetic variations associated with health, disease, drug and environment response (The International HapMap Consortium 2003). Although different populations do share haplotypes, their frequencies vary extensively. HapMap contains population-specific genetic profiling of variants to aid population-specific GWAS studies.

Studying shared haplotypes is useful to determine evolutionary patterns and specifically important in the study of genetic disorders. It can hence be used as a flexible tool in the context of studying the specific genetic question at hand.

## Cross-References

- Autosome
- DNA Marker
- Genotype
- Heredity
- Microsatellite Marker
- Mitochondrial DNA
- Recessive

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## Haptic

- Platyrrhine Sensory Systems

## Haptic Perception

- Depth Perception

## Haptic Sense

- Hominoidea Sensory Systems

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## Hare

- ▶ [Lagomorpha Life History](#)
  - ▶ [Lagomorpha Navigation](#)
- 

## Harem Defense Polygyny

- ▶ [Female Defense Polygyny](#)
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## Harry Harlow

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### Introduction

Harry Frederick Harlow was born on October 31, 1905, in Fairfield, IA, as Harry Israel. He attended Stanford University as a psychology major, working under Lewis Terman, along with Calvin Perry Stone, an animal behaviorist, and Walter Richard Miles, a vision expert. He received his Ph.D. in 1930 and became a professor at the University of Wisconsin-Madison, where he established his Primate Laboratory and did most of his work. In 1970, he moved to the University of Arizona. He was prolific, publishing 325 articles and chapters (Suomi and LeRoy 1982). He is considered highly controversial due to his treatment of the monkeys in his lab, but at the same time as one of the most important psychologists to contribute to the field. His most well-known and similarly controversial doctoral student was Stephen S. Suomi. He died December 6, 1981, in Tucson, AZ, at 76 years of age.

### Scientific Interests

In the beginning of Harlow's career, Behaviorism was the main school of thought in the animal psychology field (see "▶ [Behaviorism](#)").

Behaviorism maintained that one could scientifically study overt behaviors, but nothing else (no cognitive function, no emotions). This was done through the use of conditioning (see "▶ [Classical Conditioning](#)"), as was made famous by Pavlov (see "▶ [Ivan Pavlov](#)"). The belief was that animals were not capable of other functions (such as emotions or cognition), or, if they were, those things were immeasurable. The behaviors that were measured were those that were conditioned to occur – clearly a significant limitation in understanding animals. Harlow broke with this practice and studied learning in rhesus macaques (*Macaca mulatta*) in a different way. He started working with monkeys by accident – the rats that psychologists typically studied had gone from the University of Wisconsin, and he needed to find a different subject. Starting at the zoo, he eventually created a macaque primate lab at the university. Harlow was not interested in the rats or the monkeys for their own sake, but for what they could tell him about humans.

Harlow used the Wisconsin General Testing Apparatus (WGTA), created in his lab by Drs. Paul Settlage and Walter Grether, for macaques (Harlow 1949), in order to understand intellectual organization and personality structure. Harlow showed that monkeys could think abstractly and problem solve. He utilized the object-quality discrimination learning problem, which required the monkey to choose a rewarded object over a neutral object based on varying characteristics and shifting positions in a balanced order; he also compared the results to human children, showing the similarity of the learning curves (Harlow 1949). This was the impetus for many later studies looking at monkey intelligence and learning capacity. This type of experiment also allowed animal psychology to move beyond Behaviorism, and encouraged the comparison of ability in monkeys and human children (Suomi and Leroy 1982). It is thought by some that Harlow's work was heavily influenced by John Bowlby, a founder of attachment theory in humans, and vice versa, both cited one another, and Harlow was able to show what Bowlby had theorized about in terms of the effects of attachment and separation (van der Horst et al. 2008) but could not test

because of the ethics standards of testing on humans that are absent for monkeys.

To understand what parts of the brain corresponded with different learning and memory tasks, Harlow also carried out lesion studies to assess the macaque brain and to see which parts were associated with learning (e.g., Harlow and Dagnon 1943; Harlow 1949, 1952). This was widely accepted at the time (and currently), because it was/is not allowed to experiment on human subjects. Experimenting on animals, then, was considered the next best thing to advance science. These studies showed, for example, that animals with bilateral frontal lesions were not affected in visual discrimination tests, but those with posterior lesions were. The opposite results were found for tests of delayed response (although without complete loss of function). Neither group performed as well as unoperated monkeys in a complex learning test (Harlow 1950; Harlow et al. 1952). These results were considered important in that they outlined that different parts of the brain are responsible for different functions, although not with exclusivity.

## Theory of Affection

In order to study development and motivation, Harlow established a breeding colony of macaques in the 1950s. As was typically the practice at the time, Harlow kept the macaques in isolation, in what was thought to be best to protect from the spread of such diseases as tuberculosis (van der Horst et al. 2008). In doing so, he noticed that the macaques were not behaving “normally” – that is, they displayed non-nutritional sucking behaviors, stereotypies, hostility, and inability to form social relationships (Harlow et al. 1965). Harlow hypothesized that basic needs were not the only motivation for monkeys – that affection, or love, was a necessary component for bonding. He showed this with his infamous cloth mother experiments (Harlow and Zimmermann 1959), where baby monkeys were observed to prefer a cloth “surrogate” mother (a contraption made with wire and covered with cloth) without food to a wire surrogate with food (variations on this

were carried out in which the cloth surrogate was considered preferable to other stimuli than food – to a heating pad, for example). He came to the conclusion that bonding was a result of contact rather than being fed (Harlow 1958), which he called “contact comfort” (Harlow and Zimmermann 1959). This is considered one of Harlow’s breakthroughs, as the theory at the time supposed that human babies need only nutrition to survive normally. Harlow’s experiments changed the thinking in that area. In addition, Harlow subjected the infants to fright-inducing stimuli, to assess their response to the surrogate mothers (Harlow and Zimmermann 1959). When the infants were subjected to the frightening stimulus, they would run to the cloth surrogate – after rubbing their bodies on hers, they would then lose their fear of the stimulus, visually exploring it, and some actually approaching it. Harlow hypothesized that nursing, then, was not only a nutritional resource but meant to increase contact between mother and infant, so that the infant could easily obtain contact comfort (Harlow and Zimmermann 1959).

Following these experiments, Harlow’s interest in attachment and separation grew, especially as it pertained to development. To understand these mechanisms, he conducted increasingly extreme experiments. In what many would consider one of his most egregious experiments, he subjected infants to 2-year long isolation periods in small cages in order to record how it would affect their behavior (Harlow et al. 1965). He found, unsurprisingly, that it did, in very adverse ways, with the monkeys showing extreme abnormal behaviors, including severely impairing social, sexual, maternal, and aggressive behaviors. He claimed that 6-month total isolation was “so devastating and debilitating” (Harlow et al. 1965), and expected that a longer period of isolation could not possibly be worse. Unfortunately, he tested that theory, and proved himself wrong. While some consider all of Harlow’s work unacceptable, even those who support his strict adherence to the scientific method and the information he uncovered might at this point wonder exactly what useful information these extreme experiments revealed, and at what cost.

Next, Harlow tried to reverse the effects of the social isolation to which he subjected the monkeys, with varying results (Harlow and Suomi 1971). Some mothers showed appropriate maternal behavior with prolonged exposure to an infant, but nothing more, while infants exposed to untested peers had limited recovery. Infants exposed only to surrogate mothers were able to interact at a low level among themselves, but not with others. When Harlow exposed 6-month old isolated monkeys to 3-month old untested infants, however, the 6-month olds were able to recover normal behavior completely, at least as tested by the experiments available in Harlow's lab (Harlow and Suomi 1971).

What Harlow found changed how psychologists thought about motivation and development not only in monkeys but in humans as well (Suomi and Leroy 1982; although see Mason 1968, for another opinion). They revealed how important social interaction is for social species, especially at the developmental level, but also for learning (Harlow et al. 1965) and maternal behavior (Seay et al. 1964). Notably, Harlow used the term "love," which was considered unorthodox in referring to animals' feelings both at that time and currently.

In later years, Harlow tried to assess depression in macaques that was instigated by the social isolation that he imposed on them. His aim was to find a parallel with human depression (Harlow and Suomi 1971). In order to do so, he aimed to meet three conditions set by McKinney and Bunney (1969): external expressions and behaviors of depressed humans and depressed monkeys must be parallel; etiological conditions must be similar, such as heredity, anxiety, or social loss; and that any therapeutic interventions that work successfully for humans should also, therefore, work for the monkeys. Harlow concluded that he could induce depression similar to that found in humans in monkeys via separation. He also attempted to reverse it, with varying results (Harlow and Suomi 1971; Suomi et al. 1976). Harlow claimed he had both acted as a sadist in trying to create abnormal behavior, and as a psychiatrist in trying to rehabilitate the depressed monkeys (Harlow et al. 1971).

## Awards and Honors

Harlow was awarded the Howard Crosby Warren Medal in 1956, the Distinguished Psychologist Award from the American Psychological Association in 1960, the National Medal of Science in 1967, the Gold Medal from the American Psychological Foundation in 1973, the Von Gieson Award from the New York State Psychiatric Institute, and the International Award from the Kittay Scientific Foundation. He held many positions of honor, including as Carnegie Fellow of Anthropology at Columbia from 1939 to 1940, the George Cary Comstock Research Professor of Psychology from 1944 to 1974, President of the Midwestern Psychological Association from 1947 to 1948, President of Division of Experimental Psychology at the American Psychological Association from 1950 to 1951, Head of Human Resources Research branch of the Department of the Army from 1950 to 1952, Head of the Division of Anthropology and Psychology of the National Research Council from 1952 to 1955, Consultant to the Army Scientific Advisory Panel, President of the American Psychological Association from 1958 to 1959, Director of the Regional Primate Research Center from 1961 to 1971, and President of the Division of Comparative & Physiological Psychology at the American Psychological Association from 1964 to 1965.

## Controversy

Harlow is considered a controversial figure in psychology today – many admire him and believe he advanced the field of animal psychology in a way no one else did, while others consider him to be needlessly cruel and capricious in his social isolation experiments (Blum 2002). He has been credited with igniting the animal rights movement (Blum 2002). In addition, his blatantly sexist commentary (e.g., Tavis 1973) is viewed by some to be a sign of the times or as his intentionally mocking personality, and by others as indicative of his sexism.



## Cross-References

- [Behaviorism](#)
- [Classical Conditioning](#)
- [Ivan Pavlov](#)

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## Hatching

- [Eclosion](#)

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## Hawk

- [Accipiters](#)

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## Healthy Mate Hypothesis

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## Synonyms

[Good genes hypothesis](#)

## Definition

The healthy mate hypothesis states that mate choice is based on secondary sexual characteristics that act as a proxy for assessing the potential mate’s overall health and parasite resistance.

## Introduction

Sexual selection works on the premise that, out of a pool of potential mates, only few succeed to mate. Usually, the member of the sex that invests more into reproduction undergoes some form of assessment of the potential mate in order to maximize their reproductive success, which in turn

creates a selection pressure. Maybe one of the most famous examples of sexual selection is that of the peacock and the peahen. The long, elaborate tail of the peacock has played a role in Darwin's development of sexual selection theory (Darwin 1859, 1871). Darwin could not explain this attribute with natural selection, as the extravagant tails of peacocks do not appear to be a form of adaptation for survival. Sexual selection, however, provides an explanation to the persistence of such an extravagant male morphological trait (Darwin 1871). Although the trait has a negative impact on the peacocks, due to the increased risk of predation and decreased agility, they remain in the population due to the increased reproductive success of those males due to female choice (Andersson and Simmons 2006). This type of selection arises from mate choice and mate assessment. When an individual's reproductive output is limited or costly, assessing potential mates and basing the choice on that assessment results in many benefits (Breed and Moore 2015). Although sexual selection is widely accepted as the selection force on traits that cannot be explained by natural selection, the mate choice that drives sexual selection can be explained by various hypotheses and models, including the healthy mate hypothesis. The healthy mate hypothesis suggests that females choose healthy mates for the direct benefit of avoiding disease transmission or for indirect benefit of passing on their "good genes" for parasite resistance.

### **Mate Choice and the Benefits of Mate Assessment**

Animals can base their choice of a mate on several criteria, which can be divided into two main categories: those that provide direct benefit (such as good territory, parental investment, or nutritional gifts received during courtship) and indirect benefits such as the genetic quality of the potential mate. However, it is important to note that these are not mutually exclusive and a mate choice can be made based on several of these in the same population (Breed and Moore 2015).

### **Direct Benefits**

Many animals choose their mate on the direct benefits they gain from the mating. These are in the form of nongenetic benefits that have a positive impact on the offspring production or survivorship. These include females choosing mates based on the quality of their paternal care (Davies 1992), the quality of nuptial gifts presented during courtship (Thornhill and Alcock 1983), or access to better territories (Alatalo et al. 1986; Candolin 2003).

### **Indirect Benefits**

Female choice based on indirect benefits is harder to detect as the benefits are experienced by the next generation as either increased survivorship ("good genes") or higher mating success ("sexy sons") (Andersson 1994).

### **Sexy Sons**

The "sexy sons" model suggests that the only benefit of the female's choice of a mate is the increased reproductive success of her sons (Lande 1981). This model explains the exaggeration of secondary sexual characteristics, such as those of the peacock tails discussed earlier, through a consistent preference for a certain trait which, over generations, produces an extreme form. For example, if females persistently choose to mate with males that are brightly colored, then brightly colored males will produce more offspring. Subsequently the male offspring will be more brightly colored and therefore sexually attractive, and the female offspring will inherit the preference for the bright colors (Fisher 1930). Although the characteristic can be regulated to a certain point by natural selection, this form of selection can easily result in an exaggeration of the trait that is being selected (Fisher 1930). This form of selection is referred to as runaway sexual selection and explains how deleterious characteristics could arise and persist in a population. The consistent selection for a specific trait will then decrease the genetic variation in the next population, as sexy sons have higher reproductive success, and this results in

the trait quickly becoming fixed in the population (Rowe and Houle 1996).

## Good Genes

The “good genes” model, on the other hand, suggests that females use proxies, such as secondary sexual characteristics or bright plumage, to assess the quality of the genes of the potential mate. In order to demonstrate the benefits of females choosing a mate based on their “good genes,” there are several criteria that need to be met. These include:

1. The male survivorship needs to genetically vary in a given population.
2. The behavior or ornaments the females use to assess the quality of their mates should provide accurate information on the survival ability.
3. Females must base their choice on these attributes.
4. There is a direct benefit to the offspring survival or reproductive success based on their mother’s choice (Andersson 1994).

## Healthy Mate Hypothesis

The healthy mate hypothesis is a subcategory of the “good genes” model. It states that mate choice is based on secondary sexual characteristics, which act as a proxy for assessing the potential mate’s overall health and parasite resistance. The healthy mate hypothesis can be further subdivided into two categories based on the type of benefits: indirect benefits (Hamilton-Zuk hypothesis) and direct benefits (parasite avoidance hypothesis) gained by mate choice (Borgia 1986; Hamilton and Zuk 1982).

### Hamilton-Zuk Hypothesis

The Hamilton-Zuk hypothesis suggests that genetic variation in the population can be maintained by the interaction of mate choice and the negative impact of parasitic load on secondary sexual traits (Hamilton and Zuk 1982). Hamilton and Zuk suggested that females make their choice

based on the perceived health of the potential mate and suggest that males that have higher parasite resistance will have more exaggerated secondary sexual characters, which in turn facilitates female choice (Hamilton and Zuk 1982). This means that the male trait and female preference never reaches an equilibrium due to the evolutionary arms race between the parasite and their hosts (Møller and Saino 1994). Genes for the parasite resistance change in response to the parasites’ adaptations, and, therefore, the fittest genotype changes from generation to generation. This explains the variation in male traits associated with resistance. Similarly, to the “good genes” model, in order for the Hamilton-Zuk hypothesis to work, there are several assumptions that need to be met. These include:

1. Host fitness need to decrease with increased parasitic infection.
2. Ornament condition needs to decrease with increased parasite burden.
3. Female choice must favor the most ornamented males.
4. Female choice must favor the least parasitized males.

### Parasite Avoidance Hypothesis

An alternative to the Hamilton-Zuk hypothesis is the parasite avoidance hypothesis which suggests that females preferentially choose males that are healthy due to the direct benefit of avoiding disease and parasite transmission (Borgia 1986; Hamilton and Zuk 1982). This hypothesis is especially relevant in species with directly transmittable diseases and parasites, and, unlike the Hamilton-Zuk hypothesis, it does not require all the assumptions to be met. The parasite avoidance hypothesis does not predict a negative impact of parasites on traits nor that females assess the health of a potential mate based on those traits (Møller 1990; Zuk 1992). Few studies, including a study on satin bowerbirds, show that females avoid mating with parasite-infected males and they hypothesize that this can help them avoid novel pathogens that could be transmitted by those parasites (Borgia and Collis 1989).

## Conclusion

Mate choice is the basis of sexual selection. Although there are numerous models and hypotheses described in the literature on mate choice and the benefits of assessing a potential mate, they are not inherently exclusive. Mate choice does not have to strictly be about direct or indirect benefits as mate choice is often based on several criteria. Even within indirect benefits, whether a choice has been based on “sexy sons” or “good genes” model is often hard to distinguish. There appears to be a dichotomy between these two models in the literature, but they are not mutually exclusive, and both should be carefully considered (Kirkpatrick and Ryan 1991). The healthy mate hypothesis has been of great interest since Hamilton and Zuk proposed it in 1982 and remains so to this day. However, there is still more to investigate as the issue of mate choice is far more complex than a single hypothesis can encapsulate.

## Cross-References

- [Charles Darwin](#)
- [Evolution](#)
- [Female Choice](#)
- [Fisher](#)
- [Fitness](#)
- [Handicap Hypothesis](#)
- [Mating](#)
- [Nuptial Gift](#)
- [Red Queen Effect, The](#)
- [Runaway Selection](#)
- [Sexual Dimorphism](#)
- [Sexual Selection](#)

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## Hearing

- [Accipitriformes Sensory Systems](#)
- [Cetacean Sensory Systems](#)
- [Falconiformes Sensory Systems](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Sensory Systems](#)

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## Heart

### ► Circulatory System

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## Heat Regulation

### ► Thermoregulation

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## Helper

### ► Alloparental Care

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## Helping Behavior

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*Helping behavior* is any action performed by an individual that benefits other individual/s. Helping does not imply a pro-social motivation or unselfish intent to alleviate others' needs or increase their welfare as an end in itself. In fact, there might be difficulties to identify and evaluate those motivations, especially in nonhuman animals, in which even the mere existence of them is being discussed.

Explanations of helping behavior can be organized in terms of proximate and ultimate causes. Proximate causes point to how helping behavior was acquired and occurs in a specific context. They are the mechanisms directly implicated in the development and display of helping, such as the learning history and the cognitive, emotional, and physiological reactions in a specific situation.

Ultimate causes are explanations of why helping behavior has been selected throughout evolutionary history. They refer to the functional utility of helping behaviors for the survival of the helper and the reproduction of his/her genes. This entry is focused on those ultimate causes.

## Types of Helping Behavior

It is possible to distinguish types of helping behavior depending on the costs and benefits to the helper.

### Altruism

Altruistic helping is defined as the aid to another individual with a cost for the helper. At first glance, it may be hard to understand how a costly behavior such as this may have persisted through evolution, since natural selection tends to eliminate any trait that reduces the individual relative fitness (i.e., one's reproductive success relative to that of other members of the population). Thus, for altruism to remain across generations, it should increase the propagation of the helpers' genes. Charles Darwin realized that this is the case when altruistic helping is directed toward an individual genetically related to the helper (Darwin 1859). This idea is at the core of William D. Hamilton's *kin selection theory*.

Hamilton (1964), observing the behavior of insect colonies (bees, ants and wasps), proposed that kin selection involves indirect fitness (i.e., copies of one's genes in other bodies). He created an equation that predicts altruistic behaviors are more likely to be favored by natural selection when the reproduction benefits for the recipient, weighted by the degree of relatedness between helper and recipient, are greater than the reproduction costs for the helper.

Kin selection can explain helping behavior toward genetically related individuals, but why is helping sometimes oriented toward nonkin as well? One answer to this question was offered by the concept of *reciprocal altruism* (Trivers 1971). In reciprocal altruism an individual aids other individuals because chances are they will respond



in kind, benefiting the helper at some point in the future, thereby increasing the likelihood of the helper's survival and hence the selection of this altruistic trait. Reciprocal altruism requires conditions that increase the frequency of interactions between the helper and the recipient: (a) long life span of both individuals (which provides more opportunities for them to interact with each other over time), (b) low dispersal rate (an individual interacts more often with the same others), and (c) interdependence of members (they need each other so they tend to stay closer to one another, increasing their interactions). Reciprocal altruism has been documented in humans and nonhuman individuals, in laboratory and field studies in the former case, and mainly in field studies in the latter. Although reciprocal altruism has been usually used to account for altruistic behavior toward unrelated individuals, it can also explain providing help to relatives (Trivers 1971). For instance, in species with parental care, helping offspring could be selected by evolution because they tend to reciprocate the help to the parents. In sum, kin selection and reciprocal altruism could both explain altruistic behavior toward relatives.

In humans, reciprocal altruism is seen in several different situations, as in the helping exchanges between members of the same neighborhood, and the games about sharing and allocating resources to others which are played in controlled, experimental contexts. Reciprocal altruism is facilitated in humans due to their cognitive ability to remember past interactions with the recipient and to project who is likely to return the help in the future.

For nonhumans species, reciprocal altruism has been observed in fishes and shrimps cleaning other species (Feder 1966). They get ectoparasites from the gills or mouth of host individuals and ingest them. The reciprocity of the hosts involves refraining themselves from eating the cleaners, along with protecting them from other predators.

Fishes and shrimps would meet the three conditions for reciprocal altruism reviewed. However, Trivers (1971) additionally discussed the relevance of detecting "cheaters" (individuals who do not return the favors), who act against the development of reciprocal altruism. This detection mechanism can be found in humans,

but it is hard to prove in nonhuman species. Detecting cheaters requires the capacity of individual recognition, which can be observed in mammals (e.g., dogs), and birds, such as the *Wilsonia citrina* or the *King penguins* (Tibbetts and Dale 2007). Nevertheless, there is not consistent evidence about cheater detection in nonhumans. Thus, this is one of the main challenges for future studies.

An extreme case of altruism is rescue behavior: rescuers risk their lives when helping others. Evidence for this type of altruistic behavior has been found in field studies conducted on dolphins, monkeys, ants, and humans (e.g., Taylor et al. 2013). Ants rescue conspecifics only, while humans extend this behavior toward members of other species as well. Monkeys and dolphins rescue conspecifics, but there is not yet evidence that they do so with members of other species. The rescue behavior toward conspecifics could be explained by kin selection (considering the shared genes between helper and recipients) or reciprocal altruism (depending on the conditions reviewed above).

## Cooperation

Cooperation occurs when two or more animals act together in the same activity, which benefits them. In this case each helper is also a recipient. Although some individuals in the group may benefit less than others (e.g., getting a smaller piece of the prey they were all hunting down together), they would still get rewarded by obtaining something they could hardly achieve by working individually. Thus, this type of helping behavior promotes the survival of all the helpers and therefore the transmission of their cooperative genes to the next generation. Cooperation has been observed in numerous species in laboratory and field research, mainly in contexts where there is a common threat (a predator, for example) or when individuals can benefit by acting together: ants work in groups to transport pieces of food, lions make the same to protect their group, birds have cooperative breeding systems, and humans coordinate their actions to create economic goods (see Rubenstein and Abbot 2017).

In nonhuman species cooperation is mainly seen among individuals who have lived together

for a long time. An interesting exception is the thorn-tailed Rayadito (*Aphrastura spinicauda*; Furnariidae), a nontropical suboscine species that lives in the south of Chile and Argentina. Although they maintain short-time ties between them, they show coordination to defend their territory (Ippi et al. 2017).

In humans, cooperation is frequently observed between acquainted and unacquainted individuals, who work together to obtain material resources (e.g., food or money) as well as more abstract resources (e.g., social status), which requires more cognitive development.

In sum, according to ultimate causes of helping behavior, altruistic and cooperative traits have been naturally selected for the reasons reviewed. An alternative evolutionary explanation for altruism postulates its selection at a group level.

## Altruism and Group Level Selection

*Multilevel selection theory* claims that traits can be selected at different levels, from genes to groups (Wilson and Sober 1994). According to this theory, altruism is not selected at the within-group level because altruistic individuals have a relative fitness disadvantage because they increase the fitness of selfish members at a cost to themselves and without receiving help in return. On the other hand, altruistic groups do beat selfish groups. Groups with a higher proportion of altruistic individuals have stronger functional organizations than those composed mainly of selfish individuals, resulting, for instance, in their more solid system of feeding and defense against external threats which, in turn, allows them to have more offspring. Therefore, altruistic traits are selected at the between-groups level because they give altruistic groups a reproductive advantage over the selfish groups. In sum, according to this theory, altruism evolves whenever between-group selection prevails over within-group selection.

An extreme example of selection between groups is eusocial species such as some types of ants, wasps, termites, and bees. They are composed of sterile and nonsterile members. The former cannot reproduce themselves but benefit the

colony, for example, by taking care of the young ones, which is an essential function to maintain the colony survival (Wilson and Hölldobler 2005).

## Conclusion

According to ultimate causes of helping, it is possible to differentiate between altruistic and cooperative types depending on the costs and benefits to the helper. Altruism toward a related individual could be explained by either kin selection or reciprocal altruism, while helping toward nonkin by the latter theory only. Additionally, it is necessary more research in nonhumans species about the “cheater” detection system required for reciprocal altruism. Likewise, more studies are needed on cooperation in short-time relationships.

According to multilevel selection theory, there are different levels of natural selection of traits, from genes to groups. In terms of survival and reproduction rates, groups composed of many altruistic individuals have an advantage over those integrated by few altruistic individuals; therefore, those traits will evolve if between-group selection is stronger than within-group selection.

It is debated whether kin and multilevel selection theories are different approaches or the former is a special case of the latter: altruistic behaviors toward members in a group with high genetic similarity benefit both the kin (i.e., kin selection) and the group over others (i.e., group selection). Another debate is whether there is genuine altruism in evolutionary theories or it is only selfishness in disguise. For multilevel selection theory, altruistic behavior involves a cost for the helper and a benefit for the group, but according to kin selection and reciprocal altruism theories, altruism would be just apparent because it is driven by indirect fitness and a returned help in the future, respectively, so it is self-beneficial.

## Cross-References

- [Altruism](#)
- [Cooperation](#)
- [Karen Hollis](#)

- ▶ Kin Selection
- ▶ Pro-social Behavior
- ▶ Reciprocity

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## Hematophagy

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### Definition

Feeding on blood of another living organism.

## What Is Hematophagy?

Hematophagy (also known as sanguinivory) is the practice by some animals of feeding on the blood of other vertebrate animals (or in some cases the hemolymph of invertebrate animals). The first known hematophages (blood feeders) were the protomosquitoes, of which there is fossil evidence from 220 million years ago (Schutt 2008). Today there are thousands of species that feed on the blood of other animals (their hosts), both obligately and facultatively. Obligate hematophagy has evolved multiple times in the invertebrates, including the insects and arachnids (15,000 blood-feeding species representing at least six evolutionary events; Mans et al. 2002; Lehane 2005), leeches (Hirudinea; Schutt 2008), and nematode worms (Munn and Munn 2002). Hematophagy is also seen in some vertebrates, including the infamous vampire bats (three species in the *Desmodontinae*; Schutt 2008) and fish (such as the lampreys and candiru; Schutt 2008). Obligate blood feeding is not known in other classes of vertebrates, but some bird species feed on blood facultatively. This includes one of Darwin's finches, *Geospiza septentrionalis*, the vampire finch, a subspecies of the sharp-beaked ground finch that supplements its diet of seeds and nectar with the blood of the blue-footed booby (Grant et al. 2000).

## Adaptations for Hematophagy

There are several constraints that hematophagous organisms need to overcome to survive on a diet of blood. Blood feeders need to (i) find a host on which to feed, (ii) attach to the host in order to feed, (iii) access the blood of their host, and (iv) digest the blood meal. There are only a certain number of ways that hematophages can achieve these tasks, which has led to some striking examples of convergent evolution across distantly related taxa.

### Locating a Host

Finding a host can be a complex challenge for hematophages. Some species have overcome this

issue by forming permanent associations with their hosts as ecto- or endoparasites. This includes lice, parasitic polychaete bugs, and nematodes (Lehane 2005; Schutt 2008). The bat flies (Diptera: Nycteribiidae and Streblidae) have developed an obligate association with specific species of bats, feeding exclusively on the blood of their host, some even embedding into the skin and existing as endoparasites (ter Hofstede et al. 2004; Dick and Patterson 2006; McAlister 2017). Many bat fly species, particularly the Nycteribiidae, no longer have functional wings as they rely entirely on their bat hosts for dispersal (phoresy) to find new hosts in communal roosts (Lehane 2005; McAlister 2017). Another group of blood-feeding insects, the bed bugs (Hemiptera: Cimicidae), have also lost functional wings after they came to rely on their mobile hosts for dispersal (Cummings 1949; Lehane 2005).

There are many species that are not permanently attached to their hosts, however, and thus these species must find hosts on which to feed. The complex nature of host-finding behavior is apparent when we look at the diversity of antennal receptors across the insects. Species with more constant associations with their hosts (such as the lice) have far fewer antennal receptor types than those needing to seek out hosts on which to feed (Lehane 2005). The function of these receptors relates to the complexity and diversity of the cues these organisms use to find their hosts. Most species use a combination of visual, olfactory, and temperature cues to find their hosts, and the range at which species are searching influences which cue combinations are the most informative. Visual and volatile olfactory cues provide information to hematophages that are engaged in appetitive searching at longer distances, but after becoming attracted to these cues, many species use heat, humidity, and olfactory cues at a closer range (Lehane 2005; Hinkle et al. 1991). CO<sub>2</sub> emitted from a respiring host is perhaps the most commonly used cue across hematophagous species, but it is typically used in combination with other host kairomones that permit the expression of more specific host preferences, the evolution of host specificity (Lehane 2005), and even the speciation through host-race formation (Balvin et al. 2012).

## Attaching to a Host

In order to feed on blood, hematophagous species must attach to their hosts unnoticed for long enough to attain a sufficient volume of blood to survive and reproduce. There are a range of physiological adaptations displayed by hematophages to attack and evade their hosts, and many of these show striking convergence.

For instance, the use of analgesic components in the saliva, ctenidia (or combs), hooks, suckers, and denticles that allow attachment to the pelage and skin of the host and flattening of the body (anteriorly and dorsoventrally) to avoid being groomed off the host and to permit easy movement in feathers and fur (Lehane 2005; Schutt 2008). The behavior of hematophages is also critical to avoiding host detection, for instance, many species congregate on areas of the body that their hosts cannot access, such as in the nostrils (like some leeches; Lehane 2005). The vampire bats appear to have developed a particularly novel solution to pacify their hosts and allow them to feed – when feeding on domestic hens, they snuggle into the brood patch or jump on the female's back. These behaviors are thought to mimic the action of brooding chicks or mating cockerels, pacifying the hen, and allowing the vampire bat to feed on female hosts undisturbed (these strategies do not work on male hosts; Schutt 2008).

## Accessing Blood

Once a host has been located and latched on to, a hematophage must get access to the blood in the body of its host. In some cases blood feeders (usually facultative hematophages) take advantage of open wounds or lesions on their hosts (Schutt 2008). More commonly, however, the hematophage possesses adaptations that allow it to pierce the host integument to access a blood meal.

There are several ways to access the blood, most of which have involved modification of the mouthparts; these can be broadly categorized as piercing/sucking or ripping/tearing, which allow for either true bloodsucking or pool feeding,

respectively. Bloodsuckers such as the nematoceran Diptera (mosquitoes and midges), the Hemiptera, and the vampire moth use proboscis-like structures to pierce the skin and strong pharyngeal muscles to create a negative pressure gradient that moves the blood from its host into the digestive system (Lehane 2005). Pool feeders include most species of blood-feeding brachyceran flies and vampire bats; they cut through the skin of the host and lap or suck up the blood from the resulting wound (Schutt 2008; Lehane 2005). The structure and function of the adaptations a species possesses to obtain a blood meal can provide information about how hematophagy has evolved. For instance, the strong lancetlike proboscis of the vampire moth (*Calyptra eustrigata*, Lepidoptera: Noctuidae) has most likely evolved from an ancestor with mouthparts adapted to piercing fruits (Lehane 2005) and the high-pressure feeding strategy of the hemipteran blood feeders likely evolved from a sapsucking ancestral state. The cutting/scraping mouthparts of the blood-feeding muscid flies may have evolved from a more generalist ancestor that fed opportunistically on scabs and open wounds (Lehane 2005). Regardless of how blood is accessed, one feature common to the majority of blood-feeding species is the presence of anticoagulant components in the saliva. These components are applied to the host wound to prevent clotting and allow uninterrupted feeding for long periods of time (Lehane 2005; Schutt 2008).

## Digesting Blood

The challenges associated with a hematophagous lifestyle extend past obtaining a blood meal, particularly for species that rely solely on blood for nutrition. Although blood is a high-value protein resource that often represents an unoccupied niche, there are a number of challenges inherent in digesting and sequestering it. Blood is comprised of protein and water, which means that the energy it contains cannot always be easily stored in the long term. This means that blood meals need to be large, but the high water content results in many blood feeders becoming engorged

after feeding, with leeches and ticks being obvious examples (Schutt 2008). The weight and size gain associated with blood feeding is risky, and recently fed hematophages are vulnerable to predation after feeding. The costs of digestion and processing of the blood shape the behavioral ecology of obligate hematophages. This is perhaps most apparent in the vampire bat, which has novel adaptations to deal with both digestion (blood moves into the intestine before the stomach, which allows water to be excreted more rapidly; Wimsatt and Geurriere 1962) and locomotion (crawling along the ground and “catapult” jumps to initiate flight after a large blood meal; Altenbach 1979). The constraints on energy storage also mean that vampire bats cannot survive for long without a blood meal. This, combined with their social habits, is thought to have contributed to their altruistic behavior, which is a key example of how altruism can be beneficial through reciprocity, not only kin selection (Wilkinson 1984; Schutt 2008).

In large amounts blood can be poisonous due to iron toxicity, and excess protein can be damaging, and so hematophagous species need to neutralize these risks. In addition to potential toxicity, blood also lacks many key nutrients, for instance, vitamin B (Kikuchi 2009). Because of the low nutritional content of blood, most hematophagous species have associated endosymbiont bacteria that act mutualistically to provide the lacking dietary components (Kikuchi 2009). In the many obligate hematophagous insects, these bacteria are housed in the mycetome, which is an intestinal organ that contains symbionts that aid digestion and nutrition (Lehane 2005).

## Significance and Summary

Hematophagy is found in a wide phylogenetic range of taxa and demonstrates the power of natural selection in overcoming seemingly overwhelming issues in terms of locating, attaching to, feeding on, and digesting the blood of their hosts. There is much to be learned from hematophagous species in terms of their behavioral and physiological adaptations, but many of these species are also



important from an applied perspective. When hematophagous species feed on the blood of humans, and the domestic animals associated with them, they can threaten human health and economy by transmitting a range of diseases. Many hematophagous species vector some of the world's deadliest and most debilitating diseases, such as rabies (the vampire bat), typhus (mites and fleas), plague (fleas), and Lyme disease (deer ticks). The female *Anopheles* mosquito is perhaps the most deadly example, responsible for transmitting all four species of malarial plasmodia that affect humans, and causing millions of deaths per year (Lehane 2005). Other insects, such as the tsetse fly and various assassin bug species, spread trypanosomes, the pathogenic protozoa that cause sleeping sickness and Chagas disease in humans and nagana in cattle (Lehane 2005).

Despite the considerable damage to human and animal health that hematophages can impose, they have also contributed significantly to the improvement of human health. Anticoagulants and analgesics found in the saliva of hematophagous species such as the leech and the vampire bat have led to enormously important medical developments, such as in the treatment of strokes and chronic pain. Leeches are still used in the medical sciences today; treatment with leeches prior to tissue reattachment prevents venous congestion and increases the success of the procedure (Conforti et al. 2002). Much remains to be discovered about the hematophages (particularly those that have not shown to be of medical or economic importance), and the adaptations that allow these species to find and subsist on blood will no doubt continue to contribute to our understanding of evolution as well as lead to many more critical medical advances.

## Cross-References

- [Altruism](#)
- [Chemical Cues](#)
- [Convergent Evolution](#)
- [Endoparasite](#)
- [Facultative Trait](#)
- [Foraging](#)

- [Obligate Trait](#)
- [Symbiotic Relationship](#)

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## Hemispheric Dominance

### ► Hemispheric Specialization

## Hemispheric Specialization

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## Synonyms

[Behavioral lateralization](#); [Brain/cerebral/hemispheric asymmetry](#); [Hemispheric dominance](#)

## Definition

Hemispheric specialization refers to the differential role of the left or right brain side in processing a specific neuronal task or behavior. One hemisphere might be predisposed to adopt a function because of specific structural and/or computational characteristics. This dominance can be expressed in enhanced sensory performances, decision-making, and/or superior motor skills.

## Introduction

Bilaterian animals are characterized by a basically symmetrical body plan including a nervous

system typically ending with brain-like structures at the front. Each half of the brain processes information from one environmental half field and controls one body side. In several cases, however, one hemisphere dominates a specific function (hemispheric specialization). Consequently, this hemisphere takes control in organizing and controlling motor responses that become visible as asymmetrical behavior. Humans, for instance, preferentially use one hand (typically the right one) for writing or tool use reflecting dominance of the contralateral (left) hemisphere for fine-tuned motor control (handedness). Humans also have a preferred leg for kicking a ball and a favored eye for looking through a camera lens and open their mouth asymmetrically while speaking. The right side opens more widely due to left-hemispheric control of articulation. This asymmetry is related to a general left-hemispheric dominance for speech processing. Consequently, left-hemispheric strokes entail loss of speech since the right brain side cannot efficiently compensate deficits. The careful description of patients with left-hemispheric language impairments by Paul Broca (1865) was actually the dawn of asymmetry research (Ocklenburg and Güntürkün 2017). In contrast to what this example indicates, hemispheric specialization does not necessarily mean that the other hemisphere is not able to conduct a function at all or that it does not participate in task performance. Concerning speech processing, the right hemisphere, for instance, is specialized to analyze rhythm and word melody (prosody), which are necessary to understand the emotional content or irony of a speech (Ocklenburg and Güntürkün 2017).

Hemispheric asymmetries have been originally regarded as an exclusively human trait evolved within the scope of tool use abilities, upright body posture, or generally higher cognitive skills. The scientific community therefore assumed that brain lateralization is based on an asymmetrical cortical forebrain organization (Ocklenburg and Güntürkün 2017). Recent research, however, provides more and more examples of lateralized brain processes in other vertebrates and even in invertebrate species (Concha et al. 2012; Frasnelli

2013; Rogers et al. 2013; Rogers and Vallortigara 2017; Vallortigara and Rogers 2005). Preferential limb use for object manipulation is shown for primates, monkeys, lemurs, mice, bats, wallabies, parrots, or toads (Fig. 1a), and even invertebrates preferentially use one of their limbs including locusts, spiders, or octopuses (Frasnelli 2013; Niven and Frasnelli 2018). Motor asymmetries can also be expressed as positional or turning biases. Individuals may show consistent side preference when avoiding an obstacle, exploring the natural or laboratory test (maze) environment, or display a consistent turning bias during escape responses (as shown, e.g., ants, bumblebees, chicks, cuttlefish, fish, octopuses, or rodents).

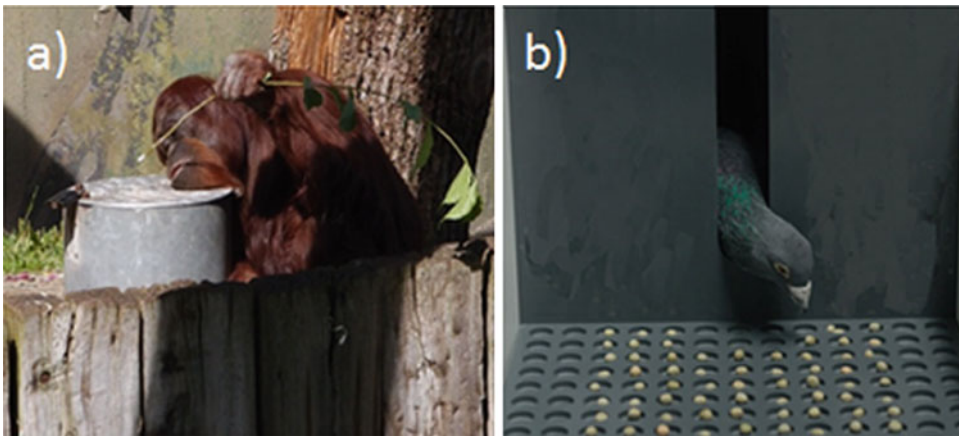
Apart from motor asymmetries, individuals can display perceptual asymmetries. This means they preferentially use one of their eyes, ears, or olfactory organs when exploring the environment. Perceptual dominances are, however, rarely based on peculiarities of the sense organs themselves. They mostly reflect specializations of the correspondent hemisphere. In this sense, turning bias or positional asymmetries can be indicative for hemispheric specialization since this behavior brings the side in focus, which is specialized to analyze the currently

relevant stimuli. In a variety of mammalian species, for instance, the right hemisphere controls social interactions. Accordingly, these species display a preference to keep a social partner on the left side (Giljov et al. 2018).

These first examples indicate the widespread distribution of cerebral lateralization in the animal kingdom. Accordingly, the term hemispheric specialization does not only comprise asymmetries of (cortical) forebrain structures but refers in the following to the functional dominance of one brain side independent from the specific neuronal organization of a species.

## Hemispheric Specialization Pattern

In vertebrates, several aspects of lateralization can be traced back to a complementarily organized behavioral pattern. The left hemisphere plays a dominant role in routine (especially feeding) behaviors including foraging, discrimination of food objects, or prey catching. In contrast, the right hemisphere controls emergency responses and is therefore in charge of novelty or predator detection and avoidance behavior (Fig. 2; Vallortigara and Rogers 2005). This



**Hemispheric Specialization, Fig. 1** Examples of lateralized behavior: (a) orangutan fishing for food with the left hand using a bow indicating that this individual is a left-hander; in contrast to chimpanzees and bonobos, which display population-level right-handedness, orangutans as well as gorillas display individual-level handedness

(Hopkins 2006). (b) A pigeon pecking for symmetrically scattered peas thereby preferentially orienting to the left hemifield. This so-called cancellation task indicates functional dominance of the right hemisphere controlling visuospatial attention (Diekamp et al. 2005)

|                                                       | left brain side                                                                                                                                                                                                                                   | right brain side                                                                                                                                                                             |
|-------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| processing strategy                                   | <ul style="list-style-type: none"><li>▪ serial processing style</li><li>▪ high frequency analysis</li><li>▪ local stimulus analysis</li></ul>                                                                                                     | <ul style="list-style-type: none"><li>▪ parallel processing style</li><li>▪ low frequency analysis</li><li>▪ global stimulus analysis</li></ul>                                              |
| general dichotomy                                     | <ul style="list-style-type: none"><li>▪ approach</li><li>▪ routine behavior</li></ul>                                                                                                                                                             | <ul style="list-style-type: none"><li>▪ avoidance</li><li>▪ emergency response</li></ul>                                                                                                     |
| specific tasks                                        | <ul style="list-style-type: none"><li>▪ detailed object analysis (discrimination, categorization of food objects)</li><li>▪ landmark orientation</li><li>▪ fine-tuned sensorimotor control</li><li>▪ conspecific vocalization (mammals)</li></ul> | <ul style="list-style-type: none"><li>▪ novelty detection</li><li>▪ predator detection</li><li>▪ geometric orientation</li><li>▪ visuospatial attention</li><li>▪ face recognition</li></ul> |
| functions with left- and right-hemispheric components | <ul style="list-style-type: none"><li>▪ emotional processing</li><li>▪ spatial cognition</li><li>▪ social cognition, communication</li></ul>                                                                                                      |                                                                                                                                                                                              |

**Hemispheric Specialization, Fig. 2** Overview of typical lateralization pattern in vertebrates

dichotomous lateralization pattern might be related to an ancient pattern of lateralization that is eventually linked to approach and avoidance behavior (Lippolis et al. 2009). Even invertebrates like the cuttlefish are more likely to favor the left visual field to scan for potential predators (avoidance) and the right visual field for prey attack (approach; Schnell et al. 2016).

Apart from these general patterns, specific functions are lateralized in vertebrates. Different mammalian species including chimpanzees, sea lions, or dogs show dominance of the left hemisphere for conspecific vocalization, while the right hemisphere controls visuospatial attention (Fig. 1b) or face recognition. The direction of limb preferences varies on the other hand profoundly between different species (Ocklenburg and Güntürkün 2017).

Dominances for specific functions are related to hemispheric-specific differences in preferential processing styles (Fig. 2). Different models suggest that the left hemisphere prefers a serial processing style relying on local or high-frequency

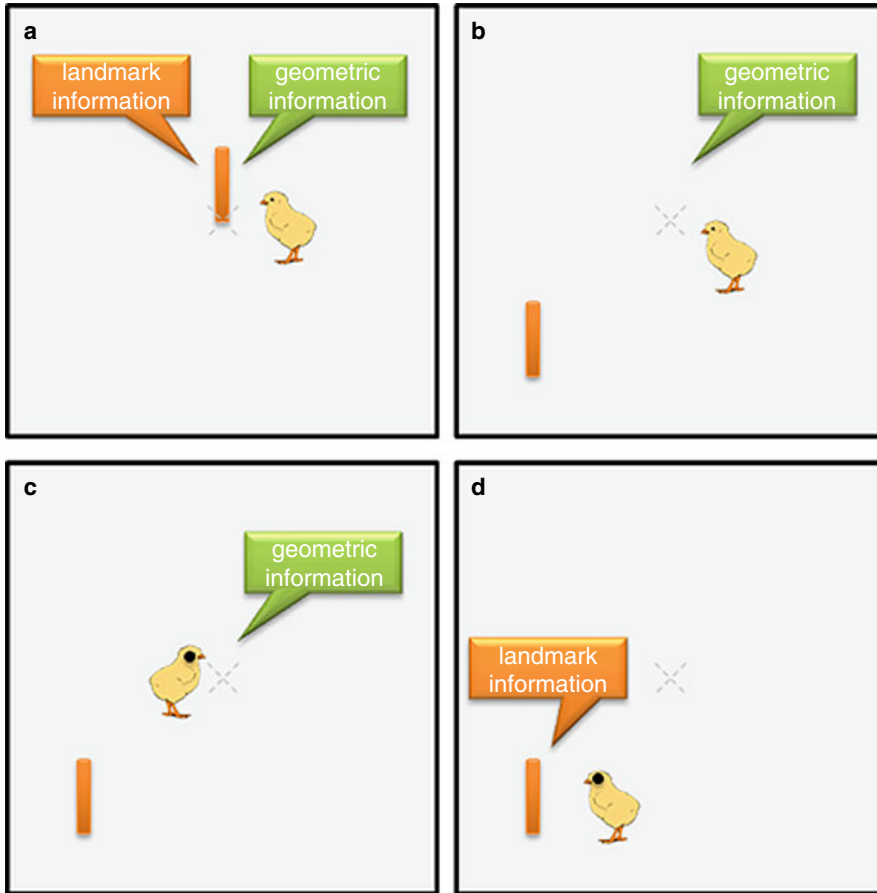
aspects of stimuli, while the right hemisphere favors parallel or configural processing, encoding global or low-frequency information. These preferences might predispose one hemisphere to adopt a specific function. The left-hemispheric dominance of conspecific vocalization might be related to its specialization in high-frequency analysis (Ocklenburg and Güntürkün 2017). This means that one hemisphere might dominate a function because of structural and/or physiological advantages, which enable quicker computational processes. In addition, the dominant hemisphere may actively inhibit parallel processing tendencies within the contralateral brain side via commissural systems. In this regard, the action of the corpus callosum in the mammalian brain is deeply discussed (Ocklenburg and Güntürkün 2017).

Allocation of dichotomous analysis strategies enables efficient use of different environmental information depending on the environmental conditions. In the case of spatial orientation, for instance, landmarks provide local feature cues,

while distances represent geometric, global information. Individual can use both types of information whereby the left hemisphere preferentially relies on local cues, while the right hemisphere orients on the basis of geometric cues (Fig. 3).

Hemispheric dominance may vary depending on the environmental context, available cues,

or age, sex, and experience of an individual. Accordingly, many cognitive modules like social or spatial cognition include left- as well as right-hemispheric components, which display differential lateralization pattern in a species-typical manner (Manns and Ströckens 2014; Ocklenburg and Güntürkün 2017).



**Hemispheric Specialization, Fig. 3** How individuals use differential environmental cues for spatial orientation is exemplified in chicks searching for food hidden under sawdust in the center of a square arena. Distances from the wall provide geometric information (indicated by the cross, which is not visible in the real experiment). The orange bar serves as a landmark providing an additional local cue (a). After binocular training, the chicks are confronted with conflict information under different seeing conditions. Since the landmark is shifted to one corner, local and geometric information provide conflicting cues about the localization of food. When seeing with both eyes, chicks search in the center indicating that they rely on geometric

information (b). When using only the left eye (since the right eye is occluded), chicks also concentrate search to the center indicating that the right hemisphere uses geometric information (c). Right-eye-seeing chicks on the contrary search near the landmark indicating that the left hemisphere considers local information (d). A comparison of all results suggests that the right-hemispheric geometric strategy dominates visuospatial orientation (according to Tommasi and Vallortigara 2001). Similar results indicating that the left hemisphere favors a local and the right hemisphere a geometric strategy are reported for food-storing birds (Clayton and Krebs 1994) or pigeons (Bingman and Gagliardo 2006)



## Evolutionary Aspects of Hemispheric Specialization

Cerebral asymmetries seem to be an ancient characteristic of functional brain organization existing since more than 500 million years. Signs of behavioral or morphological asymmetries are reported from fossils of so different extinct and living phyla like Arthropoda, Annelida, Mollusca, Chordata, Conodonts, or Trilobites (Ocklenburg and Güntürkün 2017). A beautiful example are fossilized trilobites, which display 3x more bite marks at their right compared to their left rear. This implicates that their predators tended to attack from the right side or that the trilobites took a skewed position when being attacked (Babcock 1993).

The widespread distribution of cerebral asymmetries suggests profound phylogenetic advantages of a lateralized brain. It is conceivable that the different specialization of the left and right brain hemispheres increases brain efficiency since neuronal division of labor avoids needless double computations and interhemispheric conflicts. A couple of studies support that an increase in lateralization enhances task performances. Chimpanzees with stronger individual handedness are more successful when fishing for termites; in pigeons, enhanced visual asymmetry is correlated with success in discriminating food grains from pebbles (Güntürkün et al. 2000); lateralization enhances numerical skills in the guppy (Dadda et al. 2015); lateralized cuttlefish individuals show faster prey attacking than non-lateralized conspecific (Schnell et al. 2016), and lateralized fruit flies and antlion larvae display enhanced learning or memory abilities (Pascual et al. 2004; Frasnelli 2013; Miler et al. 2017). Moreover, lateralization saves neuronal capacities since an individual can simultaneously process two different tasks. In chickens, for instance, allocation of function with a left-hemispheric dominance for food discrimination and right-hemispheric superiority for predator vigilance enables the birds to efficiently search for food while scanning the environment for potential danger. Similar results were reported for the tropical fish *Girardinus falcatus* or marmoset monkeys (Rogers 2018).

Despite potential advantages, degree and direction of hemispheric asymmetries might vary between individuals of a population. Apart from the absence of any asymmetry, lateralization can be observed at the individual or at the population level (Fig. 3). Lateralization pattern can change during ontogeny and may vary in direction and degree between males and females of a population. Female cats, for instance, are most likely to show right-paw preferences, while male cats more often use their right paws.

In principle, evolutionary advantages of hemispheric specializations should be independent from their direction. Accordingly, some studies prove that strength of lateralization is a predictor of high performance, while direction is not (Ocklenburg and Güntürkün 2017; Rogers 2018). Presence of population-level asymmetries therefore requires specific explanations. Vallortigara and Rogers (2005) suggested that an alignment of behavioral asymmetries in a population arises when individually asymmetrical organisms must coordinate their behavior with that of their conspecifics. Thus, the appearance of asymmetries at population level may have evolved under social selection pressures as an example of an “evolutionary stable strategy.” Thus, population-level asymmetry is more likely when lateralized behavior involves social interactions. This idea is especially proved in insects with social species displaying more lateralized behavior than closely related unsocial ones (Niven and Frasnelli 2018).

## Structural Foundations of Cerebral Asymmetries

Functional lateralizations rely on variances in the organization of the left and right brain side and establish a neuroanatomical basis for any processing advantages. Anatomical asymmetries can be detectable as macroscopic left-right differences, e.g., in the size of gyri and sulci in the mammalian neocortex, or as microscopic differences in intra- and interhemispheric connectivity pattern. In some cases, unique neuronal elements are present on only one side of

the nervous system; in other cases, elements are present on both sides but display left-right differences in number, size, axodendritic complexity, or synaptic organization (Concha et al. 2012).

Depending on the complexity of the nervous system, different kinds of anatomical asymmetries can be present in one species. The fruit fly *Drosophila melanogaster*, for example, possesses an unpaired brain structure (the so-called asymmetrical body (AB)), which is typically present only within the right hemisphere. Mutants with symmetrical organization of AB display impaired retrieval of long-term memory and therefore exemplify the functional relevance of a lateralized brain organization (Pascual et al. 2004). Another example of neurons, which are present on only one brain side, are chemosensory neurons of the nematode *Caenorhabditis elegans*. This worm possesses a limited number of neurons whereby four. The head ganglion of this worm contains a specific cell pair with neuron ASEL located on the left and neuron ASER on the right side. Although anatomically quite similar, the cells differentially respond to different concentrations of the same salt and promote different behavioral reactions. ASEL controls length of forward locomotion, whereas ASER promotes changes in direction (Concha et al. 2012).

In the vertebrate brain, the diencephalic epithalamus, comprising pineal organ and habenulae (Hb), combines different anatomical types of asymmetry. The pineal complex, which includes photoreceptive cells controlling circadian rhythm, is, for instance, confined to the left brain side in zebra fishes. Left- and right-hemispheric Hb on the other hand display prominent differences in size, connectivity pattern, and subcellular organization. Only the left Hb receives input from the pineal complex, while the right one receives input from specific olfactory bulb fibers (Concha et al. 2012). Accordingly, most neurons that respond to odors are located on the right Hb, while left Hb neurons preferentially respond to light stimuli. Loss of typical brain lateralization leads to impaired sensory processing (Dreosti et al. 2014) and results in enhanced fear behavior (Facchin et al. 2015).

The functional impact of projection asymmetries is exemplified in the lateralized visual system of birds like chicks and pigeons. In both species, a neuroanatomical element of lateralized visual processing is represented by a difference in projection strength between the two hemispheres. In pigeons, higher bilateral input to the left brain side is related to a more complete representation of information from both visual hemifields (Güntürkün and Ocklenburg 2017; Manns and Ströckens 2014).

Synaptic asymmetries are reported for the mouse hippocampus. Synapses between CA3 and CA1 neurons display left-right differences in spine morphology, NMDA receptor density, and synaptic plasticity depending on whether afferents originate in the left or right CA3. Disruption of these structural differences is correlated with impaired spatial learning and working memory (Shipton et al. 2014).

## Ontogeny of Hemispheric Specialization

Structural and functional neuronal asymmetries emerge by complex gene-environmental interaction during ontogeny. Genetic factors provide signals, which establish a basic framework for asymmetrical processing. Environmental cues modulate the inherent pattern by influencing final differentiation of neuronal networks. Thereby activity-dependent processes modify the number and structure of synapses or change local and long-range connectivity pattern. Long-lasting effects might be mediated by epigenetic mechanisms, which constantly modify gene expression pattern (Güntürkün and Ocklenburg 2017).

Neuronal asymmetry formation starts very early during development when body axes of the embryo are determined under the control of complex gene signalling cascades, which are highly conserved in bilateral animals. Already during this phase, the described asymmetries of *C. elegans* neurons are determined. In vertebrates, these genes determine asymmetry of inner organs with the heart on the left or the gallbladder on the right side but also induce asymmetrical bending of the spine resulting in an asymmetrical

body position of the embryo. A central component is the nodal signalling pathways, which plays a second critical role in inducing neuronal left-right differences in the brain by determining, for instance, epithalamic asymmetries (Concha et al. 2012; Signore et al. 2016). These left-right differences can be, however, modified by visual stimulation (Andrew et al. 2009).

The critical impact of sensory experience is exemplified in the visual system of chicks and pigeons, which develops anatomical as well as functional asymmetries in response to asymmetric light stimulation (Güntürkün and Ocklenburg 2017; Manns and Ströckens 2014). Due to the genetically controlled bending of the spine, embryos turn their head so that the right eye is close to the light-translucent eggshell, while the left eye is covered by the body. As a consequence, the right eye and, hence, the left hemisphere are more strongly activated and induce the development of anatomical left-right differences, which are related to the functional dominance of the left hemisphere for visuomotor control and which enable efficient interhemispheric cooperation (Manns and Römling 2012).

Apart from sensory stimulation, hormones (like corticosteroids and sex hormones), social experiences, cultural influences, or stress level can affect asymmetry formation and, hence, functional lateralization pattern. Sex hormones impact the organization of lateralized brain structures and modulate hemispheric-specific processing mode as well as degree of interhemispheric communication. Consequently, males and females often display differential functional lateralization pattern (Ocklenburg and Güntürkün 2017).

## Testing Hemispheric Specializations in the Lab

There are many ways to investigate hemispheric specialization pattern in different species (for a detailed overview, see Rogers and Vallortigara 2017):

### 1. Behavioral Observation

The easiest way to detect hemispheric specialization is behavioral observation since

asymmetrical behavior indicates a lateralized motor strategy, which is controlled by the dominant brain hemisphere. Preferential limb use, turning of the head or tail, or complete body or asymmetrical interactions with objects or conspecifics can be easily recorded and quantified. True dominance for motor control, however, is only proved when a preference is constant across time and consistent between different tasks.

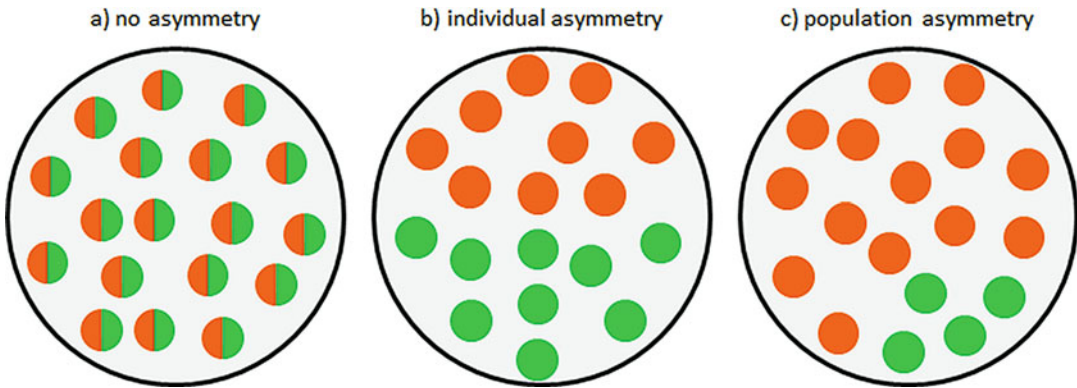
One may analyze lateralized behavior of individuals while conducting a specific task under controlled conditions in the lab. These are, however, eventually artificial situations, which may not occur within the natural environment of a species. Accordingly, more and more studies report asymmetrical behavior obtained from observations in the wild or zoo.

### 2. Sensory Input Restriction

For a deeper understanding how behavioral asymmetries are related to hemispheric specialization, it is often helpful to direct sensory input to one hemisphere. When paired sense organs project to only one brain side (fibers of retinal ganglion cells, for instance, cross completely in many vertebrate species; while in bees, input from one antenna projects to ipsilateral antennal lobe), separate testing of the hemispheres can be easily conducted by temporarily occluding one eye, ear, nostril, or antenna. Honey bees, for instance, display better olfactory conditioning when trained with the right antenna (Frasnelli 2013). It is also possible to investigate if an individual displays performance differences depending on the brain side in use (Fig. 4). The better hemisphere is then the dominant, specialized one, which may also dominate under bihemispheric test conditions (Fig. 3).

### 3. Unihemispheric Lesions

Comparing left- and right-sided performances indicates hemispheric specializations but does not unravel the underlying structural organization. Lesion studies are suitable tools to unravel asymmetrical participation of specific brain areas. When an individual does not show a behavior anymore after damage of a particular neuronal structure, then this target area must be critically involved in the



**Hemispheric Specialization, Fig. 4** Differential types of lateralization pattern (orange circles indicate left-hemispheric dominance; green circles right-hemispheric dominance): (a) when individuals of a population do not possess a preferential hemisphere controlling a task, no asymmetry is present; (b) individual-level asymmetry

means that the left hemisphere is consistently dominant for one half of the population and the right one for the other half; (c) population-level asymmetry means that a majority of animals display consistent dominance of one hemisphere for a specific task (e.g., the left one) (based on Ocklenburg and Güntürkün 2017)

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generation of this behavior. Permanent lesions or transient silencing of left- and right-sided structures shed therefore light on left- and right-hemispheric contributions on cognitive task performances. Hemispheric-specific deficits point to the functional dominance of the lesioned brain side. The pioneering work of Fernando Nottebohm (1971), for instance, demonstrated a left bias for song production in chaffinches (*Fringilla coelebs*) by cutting the left or right tracheosyringalis nerves, which innervate the syrinx as the vocal organ in songbirds. Only cutting the left nerve led to impairment of song production.

#### 4. Neurophysiological Measures

Knowledge about the participating brain regions does not explain the neuronal mechanisms underlying hemispheric specialization. Electrophysiological recordings allow investigating differential computation modes of left- and right-hemispheric circuits. Comparing the response pattern of visual neurons of pigeons, for instance, indicates a more elaborated processing of visual information within the left visual forebrain, which is related to the functional dominance of the left hemisphere for visuomotor control (Freund et al. 2016).

Additionally, brain imaging techniques provide noninvasive methods to investigate processing differences of left- and right-

hemispheric areas. This method is the major technique in human asymmetry research, but first studies used these techniques to investigate hemispheric differences in animal species, too (e.g., Jonckers et al. 2015).

## Cross-References

- ▶ [Approach/Withdrawal Theory](#)
- ▶ [Avoidance](#)
- ▶ [Behavioral Genetics](#)
- ▶ [Behavioral Variation](#)
- ▶ [Bird Migrations](#)
- ▶ [Brain Asymmetry](#)
- ▶ [Cognition](#)
- ▶ [Coping Style](#)
- ▶ [Corticosterone](#)
- ▶ [Embryo](#)
- ▶ [Encoding](#)
- ▶ [Equine Sensory Systems](#)
- ▶ [Escape Response](#)
- ▶ [Evolutionarily Stable Strategies](#)
- ▶ [Face-Selective Neurons: Comparative Perspectives](#)
- ▶ [Genetic Variation](#)
- ▶ [Geometric Encoding](#)
- ▶ [Heredity](#)

- ▶ Heritability of Behavior
- ▶ Hippocampus
- ▶ Hormones and Behavior
- ▶ Landmark
- ▶ Language
- ▶ Laterality (Handedness)
- ▶ Memory
- ▶ Natural Selection
- ▶ Navigation
- ▶ Neocortex
- ▶ Nervous System of Invertebrates
- ▶ Neural Control of Behavior
- ▶ Neuroanatomical Plasticity
- ▶ Nicola Clayton
- ▶ Observational Methods
- ▶ Ontogeny
- ▶ Passerine Vocal Communication
- ▶ Personality in Animals
- ▶ Spatial Orientation
- ▶ Species-Specific Behavior
- ▶ Testosterone
- ▶ Vertebrates (Chordata)
- ▶ Vigilance
- ▶ Visual Search

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## Herbert Spencer

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### Definition

Herbert Spencer (1820–1903) was a Victorian natural and social scientist polymath whose most notable contributions were as a theorist of biology and psychology, although he wrote many other works in various disparate fields. He published articles on the theory of evolution as a general process before

Darwin's *On the Origin of Species*, but he did not specify any concrete or verifiable mechanisms by which it took place, instead being content to define evolution simply in terms of an ongoing differential complexity in biological forms, homogeneity being transformed into heterogeneity (Spencer 1852a, 1857; Hull 2002, E-12).

### Introduction

Spencer's two most representative works *The Principles of Biology* (1864) and *The Principles of Psychology* (1855) went through numerous revised editions across the second half of the nineteenth century, including some large-scale expansions from single to multiple volumes, and if book sales are an important measure of scientific achievement then Spencer was a first-year success. His first book was entitled *Social Statics* (1851) and a year later he published an account of population and animal fertility (Spencer 1852b), indicating an early interest in the natural world. Other significant works by Spencer included book-length accounts of sociology, ethics, and the state, in which he promoted a liberal conception of freedom defined by him through a law of equal freedom allocated to each individual person in a given society.

However, as there are numerous general accounts of Spencer's work taken as a whole for readers to consult (for example, see Francis 2007), this relatively short entry on Spencer will concentrate mainly on those aspects of his work that are relevant to evolutionary psychology and to an understanding of animal cognition, as these are the focus of this particular encyclopedia, but before this, his wider scientific importance requires brief consideration.

### Spencer's Scientific Importance

By far Spencer's single greatest and most enduring claim to intellectual fame is that he coined the term "survival of the fittest" in 1864, which was then keenly adopted by Charles Darwin, firstly in his book *The Variation of Animals and Plants*

under *Domestication* in 1868 and then in the fifth edition of *On the Origin of Species* published in 1869 (Bowler 2008, p. 115, 120). This phrase has been criticized by some as the most famous tautology in the scientific world, as (by definition) those that survive are seen also as the very fittest.

However, although Spencer was almost as well-known as a biological theorist as Darwin was in his own time, Spencer's current reputation has been entirely eclipsed by that of Darwin, to the point that the phrase "who now reads Spencer" is currently as ubiquitous as his term "survival of the fittest." Spencer is also often blamed for the distortion of the Darwinian approach that was promoted as Social Darwinism, and which crassly and erroneously aimed to apply the "survival of the fittest" idea as a form of social policy within contemporary human societies.

Darwin judged that Spencer's theoretical works were usually too abstract to be of any use to him in his own work on understanding evolution, dismissing one of Spencer hypothesized general laws with the rather unflatteringly evaluation: "speculation on the subject is almost useless" (Darwin 1872 [1859], p. 100), and the scientific status of Spencer's law-like speculations were questioned even in his own time (Hull 2008, p. 19). Spencer's works were nevertheless of some importance in promoting the idea to the wider public that the natural world had undergone a process of continuous evolution over a geological timescale.

For example, it is evident from his writings that – for Spencer – evolution was the central originating process across the whole natural world, declaring that: "Life under all its forms has arisen by a progressive, unbroken evolution" (Spencer 1855, p. 578). He explained: "For myself, finding that there is *some* positive evidence of evolution in the modifications undergone by all organisms under changed conditions, in the development of every living creature – I adopt the hypothesis until better instructed" (Spencer 1855, p. 578). Elsewhere, Spencer defined life as the "continuous adjustment of internal relations to external relations," his formulation of the process of organisms adapting to their environments (Spencer 1855, p. 374).

## Spencer on Cognition

In addition to promoting the general concept of evolution, Spencer was a nineteenth-century advocate of cognitive science. He defined cognition as a "group of inner relations" that corresponded to external or outer relations, with a false cognition occurring when the internal relations do not match the external relations accurately (Spencer 1855, p. 471, 470). He explained further on cognitive processes that:

The cognitions of exact science are distinguished from interior cognitions in this; that the mental process involves a symbol answering to every constituent of the phenomenon. For this infallible guidance to be had, however, requires that *all* the elements of the relation be cognized. Whenever a group of inner relations, a cognition, is completely conformed to a group of outer relations, a phenomenon, by a rational process – whenever there is what we call an understanding of the phenomenon; it is that the genesis of the phenomenon is, in a sense, paralleled by the genesis of the cognition. (Spencer 1855, p. 471: italics in the original)

Spencer clearly distinguished between the cognitive and the emotive faculties of perception as a strongly marked contrast, but he then confirmed that all mental phenomena (both reason and emotion) were the evolutionary result of "correspondence between the organism and its environment" (Spencer 1855, p. 584).

In addition to focusing attention on cognitive function, Spencer recognized in outline the "localization of function in the cerebrum" and other parts of the brain, declaring that different parts of the cerebrum served different kinds of specialized mental process: "every bundle of nerve-fibres and every ganglion, has a special duty" (Spencer 1855, pp. 607–608). He even anticipated (in vague terms) the idea of a psychological mechanism, defining a mental faculty as an "internal plexus of nervous relations" with a specific focus (Spencer 1855, p. 609; Fodor 1983, p. 1983). Spencer also wrote explicitly on "Mental Evolution in Animals" (Spencer 1884), reviewing George Romanes's book on the subject (Romanes 1883), and it has been suggested that Romanes's discussion of mental activity in this book "depended largely on Spencer's

psycho-evolutionary theory” (Richards 1987, p. 348), to which attention is now turned.

## Spencer as the First Evolutionary Psychologist

It is customary for some scholars to declare that Darwin is the true originator of the evolutionary approach to understanding psychology. However, Darwin himself said something quite different on the topic, declaring in the sixth edition of *The Origin of Species* as follows: “In the future I see open fields for far more important researches. Psychology will be securely based on the foundation already well laid by Mr. Herbert Spencer, that of the necessary acquirement of each mental power and capacity by gradation” (Darwin 1872 [1859], p. 428). Thus, according to Darwin in 1872, it was Spencer who was the true originator of the then futuristic subject of evolutionary psychology.

It could be argued that Darwin was just playing lip service to a possible Spencer claim for priority, either out of politeness or to avoid any potential conflict, but the subject certainly merits further investigation. Darwin specified directly which Spencer book he had in mind in his “Historical Sketch” from the *Origin*: “The author (1855) has also treated Psychology on the principle of the necessary acquirement of each mental power and capacity by gradation” (Darwin 1872 [1859], p. xix), this being a clear reference to the first edition of *The Principles of Psychology* (Spencer 1855). This book contained a substantial chapter on “Instinct” and was published sometime before the first edition of Darwin’s *Origin*. Does this work, as Darwin suggested, in fact provide the first foundations of the subject of evolutionary psychology? The next section will attempt to answer this question directly.

## Spencer on Instinct

In the preface to *The Principles of Psychology*, Spencer explained that his aim in the book was to describe both “the evolution of Life in general”

and “the nature and genesis of the different modes of Intelligence, in terms of the relation which obtains between inner and outer phenomenon” (Spencer 1855, p. iv), this later aim involving the comprehension of the evolution of mind and of the instincts contained within it.

Spencer defined instinct – or what he called the mentally generated actions of the nervomuscular apparatus – as a compound reflex action that, in its initiation, combined a number of separate stimuli in a complex sequence, which was then realized through the functioning of automatic connections of nervous actions. The higher the instinct in operation, the more complex were both the directive and executive coordinations involved in its execution (Spencer 1855, pp. 539–540, 542, 548). He then explained that, by the evolution of accumulated experiences, these compound reflex actions developed out of the simple reflex ones, this particular evolution being what Spencer called the experience hypothesis.

One key passage from *The Principles of Psychology* on the experience hypothesis linked the evolution of intelligence by the multiplication of experiences, to inner relations corresponding with outer relations resulting from a continued registration of these experiences (Spencer 1855, p. 551). The passage was as follows:

we see that the conclusions deducible from the experience-hypothesis, are in harmony with such facts as we possess. We see that the evolution of instincts, as resulting from experience, is quite comprehensible. We see that, if produced by experience, this evolution must proceed from the simple to the complex; which is the indication of positive evidence so far as it is attainable. And we see that by a progression thus wrought out, instinct must in the end insensibly pass into a higher order of psychical action; which is just what we find it to do in the higher animals. (Spencer 1855, p. 553)

This passage fairly obviously contains the germ of the idea that instincts originate by evolutionary processes, although the Darwinian concept of evolution by natural selection had (in 1855) yet to be publicly outlined.

The following key passage from Spencer’s *The Principles of Psychology* contains an even clearer formulation of the idea of the natural evolution of instincts as psychological phenomena. He

declared that he formulated “the law that habitual psychical successions entail some hereditary tendency to such successions, which, under persistent conditions, will become cumulative in generation after generation, to supply an explanation of all psychological phenomena” (Spencer 1855, pp. 578–579). Although it is certainly true that Darwin was pursuing an evolutionary approach to understanding instincts well before 1855, as his notebooks clearly illustrate – “new instincts can originate” (Darwin 1974 [1838], p. 284) – Spencer was first to actually publish a book on this topic, 4 years before the publication of the first edition of *On the Origin of Species* in 1859 (Spencer 1855). Darwin’s modification of the passage in the *Origin* on “the necessary acquirement of each mental power and capacity by gradation” to include Spencer’s claim to priority thus makes sense in historical terms.

In addition, in *The Principles of Psychology*, Spencer began to attempt to plot the relation between instinct and other mental processes such as reason. He stated on this relationship that:

How then can any particular phase of complexity or infrequency be fixed upon as that at which Instinct ends and Reason begins? Will any one be so absurd as to say, that so long as the external phenomenon responded to does not involve more than twenty elements, the response is instinctive; but that if it involves twenty-one the response is rational? (Spencer 1855, p. 565)

Spencer suggested that what he called the progressive complication of instincts involved a diminution of their automatic character and a greater involvement of reason and memory, although this complication process was asserted by him on purely speculative grounds. Overall, Spencer’s attempt to ground an understanding of mental processes and the subject of psychology in purely natural science terms was innovative in its day.

## Conclusion

As has already been previously outlined and as has been further argued in this entry, Spencer was the first published author to attempt to provide

(in outline at least) an evolutionary account of the origin of mind, mental processes, and instincts that is consistent with the precepts of contemporary evolutionary psychology (Carneiro 2012, p. 518; Rylance 2000). Of course Spencer’s account was very basic and general in nature, and Darwin soon provided a much more sophisticated account of instincts and mental evolution in the *Origin* (and also in *The Decent of Man*), but the fact that Spencer’s work reinforced Darwin’s naturalistic approach to understanding cognition rather than countered it was of some significance in historical terms at least in the mid-1850s. Arguably, apart from his invention of the phrase “survival of the fittest,” Spencer’s pioneering work on the evolutionary understanding of mental processes was his most enduring scientific achievement.

## Cross-References

- [Instinct](#)
- [Origin of Species](#)
- [Social Darwinism](#)

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## Herbert Terrace

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**Herbert S. Terrace** is a professor of psychology at Columbia University. He is best known for his experimental work in comparative and animal cognition, particularly on the topics of errorless learning, serial learning, and metacognition, as well as for attempting to train a chimpanzee to use sign language, and for his analysis of the evolution of language.

## Early Life and Education

Terrace was born November 29, 1936. He received an undergraduate degree in psychology from Cornell University in 1957 and a PhD from Harvard University in 1961, advised by B. F. Skinner. Among his early influences, Terrace credits Skinner's approach to operant conditioning as influencing him substantially. However, two other figures (S. S. Stevens and

H. M. Jenkins) also shaped his early views (Terrace 2010b), motivating his initial research interest in dissecting the role of psychophysical discriminations in operant behaviors. Work in this domain gradually revealed the limitations of a purely behavioral approach and demonstrated the effectiveness of combining cognitive theories with rigorous experimental design.

## Stimulus Discrimination in Operant Research

Terrace's first major interest was the role of errors (formally, responses to S-) in discrimination learning. Contrary to the principles of operant learning (as well as current assumptions of prediction-error-driven learning), Terrace's early work showed that subjects (mainly pigeons) could learn relatively difficult stimulus discriminations between two similar wavelengths of light while making almost no errors during training (Terrace 1964). Errorless learning was accomplished by initially presenting highly discriminable stimuli, such that learning could occur within a trial or two, and then gradually reducing the difference between S+ and S-.

Systematic study of discrimination learning (reviewed in Terrace 1972) helped to resolve a crucial question of the time: Under what circumstances is S- aversive? In classic Skinnerian procedures, pigeons presented with S- routinely produced behaviors collectively described as "frustration," such as general agitation and, occasionally, aggression toward the stimulus, suggesting that S- was intrinsically aversive. However, frustration was not observed during errorless learning. Through a series of careful experiments, Terrace showed that the aversiveness of S- was contingent on a history of unrewarded responses to S-. It was not aversive if subjects learned to discriminate without errors.

Using a similar gradual training approach, Terrace showed that other aspects of discrimination learning were also contingent on a subject's learning history. For example, it was well established that if an animal was trained to respond to a specific wavelength of light (S+), there was less



responding to wavelengths greater than or less than S+. Following discrimination learning with errors, the peak shifted to an untrained wavelength, away from S-. However, peak-shifts did not occur following discrimination learning without errors.

Terrace also collaborated on several projects to investigate the phenomenon of autoshaping, whereby the presentation of S+, followed by non-contingent reward, caused subjects to respond to it, a circumstance in which the subject shaped its own behavior. These efforts yielded two important conclusions. One was that the logarithm of trials to acquisition was a linear function of the log duration of the intertrial interval. This meant that the ratio between stimulus duration and the intertrial interval was constant (Gibbon et al. 1977). A more unsettling conclusion was that the basic stimulus-response relation at the heart of Skinner's operant conditioning paradigm was incomplete because it failed to take biological constraints into account.

## Project Nim

In December 1973, Terrace acquired an infant chimpanzee named Nim Chimpsky and started "Project Nim," an intensive effort to teach sign language to a nonhuman animal (Terrace 1979). Project Nim asked if a chimpanzee who was immersed in an environment that used American sign language (ASL) could not only learn individual words, but also learn to construct grammatical sentences. Although several primate language studies had been underway since the late 1960s, most had an informal structure and no consistent framework for data acquisition (Terrace and Bever 1976). Project Nim was different. In addition to continuous social interaction with a large team of volunteers, Nim also received extensive training in a controlled classroom setting, during which he was videotaped. This provided Terrace and colleagues with a representative corpus of the signs Nim and his teachers exchanged.

This video archive was essential to understanding the nature of Nim's utterances. At the project's conclusion in 1977, Terrace and colleagues set

about analyzing the data, and seemed to have enough evidence to argue that Nim had a rudimentary grammar. However, during subsequent slow motion analyses of the same videotapes, it became clear that Nim's multisign utterances were prompted by his teachers. In virtually every instance, the videotapes showed that Nim's teachers unwittingly produced the relevant signs a fraction of a second before Nim did. Furthermore, all of the thousands of utterances they recorded were imperative. None were declarative. Thus, to the question, "Can an ape create a sentence?" Terrace and colleagues concluded that the answer was "No" (Terrace et al. 1979).

## Animal Cognition and Serial Learning

In the wake of Nim's failure to acquire grammar, it was nevertheless clear that nonhuman animals were able to solve sophisticated discrimination problems in ways that could not be satisfactorily explained by operant or Pavlovian means. Consequently, Terrace subsequently asked, what can an animal learn *without* linguistic competence?

Terrace's extensive study of the nuts and bolts of operant conditioning revealed that many features of learning, which were taken to be intrinsic by behaviorists, were contingent on a subject's learning history (Terrace 1984a). It also became increasingly difficult to account for much learned behavior without reference to the then-emerging cognitive terminology of memory, attention, and representation. During the early 1980s, Terrace played an instrumental role in creating the subfield of animal cognition, a new area of comparative psychology (Roitblat et al. 1984).

Of particular interest was the topic of sequence learning. Terrace showed that Skinner's attempts to account for human language acquisition in terms of operant chains failed because a stimulus-driven account could not explain how humans and other animals processed simultaneously presented stimuli. That insight inspired the development of the simultaneous chaining procedure (SCP), an experimental paradigm in which subjects learned to respond, in a particular order, to arrays of simultaneously visible stimuli

(Terrace 1984b). In contrast to Skinner's successive chaining paradigm, in which performance could be explained by reference to external stimuli, the execution of a simultaneous chain required subjects to represent the ordering of the stimuli during the execution of a sequence. In that sense, an animal's execution of a simultaneous chain provided an intermediate step between association and linguistic models of behavior (Terrace 1987).

The study of serial learning in nonhuman animals presented a major opportunity for comparative psychology. Although it isn't possible to study the evolution of human language directly, because of a lack of natural counterexamples, serial learning in nonhuman primates might provide insight into evolutionary precursors (reviewed in Terrace 2010a). With that goal in mind, Terrace's early SCP work transitioned from pigeons to rhesus macaques in the early 1990s. With a series of collaborators, Terrace investigated the flexibility of serial representations (Chen et al. 1997), evolutionary precursors to numerical reasoning (Brannon and Terrace 1998), the emergence of serial expertise (Terrace et al. 2003), imitation of sequences (Subiaul et al. 2007), and task switching (Avdagic et al. 2014).

More recently, Terrace sought to systematically relate SCP to the transitive inference (TI) paradigms. TI is another paradigm for studying serial order, in which subjects are presented with only two stimuli at a time and must choose which one comes earlier in an implied list (Merritt and Terrace 2011). Unlike the SCP, in which the full list is visible on each trial, and in which subjects must explicitly respond to all of the items in the correct order, TI requires that subjects learn lists implicitly. Terrace and colleagues demonstrated that despite such different task demands, knowledge of a list's serial order is transferred both ways between SCP and a TI task (Jensen et al. 2013), such that each task can be used to train a list order that can then be exploited within the other paradigm. Terrace's current work on serial order uses the SCP and TI paradigms to probe their common underlying cognitive mechanisms with tools of computational and experimental neuroscience (Jensen et al. 2015; Tanner et al. 2017).

## Metacognition

In the early 2000s, Terrace began to study comparative metacognition (Terrace and Metcalfe 2005; Metcalfe and Terrace 2013). As with his earlier work on primate language, Terrace was concerned that many published studies that made dramatic claims about nonhuman abilities lacked enough experimental rigor to rule out simpler explanations (Terrace and Son 2009). For example, in order to distinguish metacognition from unrelated skills, Terrace and colleagues demonstrated that nonhuman subjects could readily transfer a hint-seeking ability on which they were trained to novel tasks (Kornell et al. 2007).

Of particular importance was the introduction of new paradigms in which nonhuman subjects could be trained to strategically express confidence about risky behavior. There were two variations. An animal could make use of metacognitive information prospectively (prior to making a choice) or retrospectively (after making a choice, but before receiving feedback). Terrace and colleagues investigated both possibilities in a delayed match-to-sample task using a token economy (Morgan et al. 2014). Tokens were visible on a touch screen throughout the task. When a sufficient number of tokens had been obtained, they automatically produced a food pellet. Subjects were differentially rewarded for high- and low-risk confidence judgments following correct or incorrect responses on a discrimination problem. On each trial, they could make a high-stakes bet (+3 tokens if correct, -3 tokens if incorrect) or a low-stakes bet (+1/-1 tokens). In the retrospective condition, subjects were first shown a target. Following a short delay, they had to choose that target from a set of distractors. They were then required to place a bet and were immediately given the appropriate reward or punishment. Consistent with the metacognitive hypothesis, monkeys preferred low-stakes bets on trials on which they were less likely to be accurate. In the prospective condition, subjects were shown the target, then made their wager after a brief delay, and finally ended the trial with the memory test. In both the prospective and the retrospective conditions, subjects placed their bets strategically.

## The Evolution of Language

The negative results of Project Nim prompted Terrace to ask two related questions (Terrace 1985). First, why couldn't chimpanzees learn to make declarative statements? Second, how did words evolve? His recent analyses of hominid ancestry and of the development of linguistic skills of human infants led him to conclude that chimpanzees weren't able to learn to name objects because they lacked the ability to engage in two foundational precursors: intersubjectivity and joint attention (Terrace 2011). Further, language requires the capacity of an individual to have a theory of mind that recognizes the capacity of another individual to understand verbal utterances (Studdert-Kennedy and Terrace 2017; Terrace forthcoming).

## Cross-References

- [Autoshaping](#)
- [B.F. Skinner](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Discrimination Learning](#)
- [Joint Attention](#)
- [Language Research: Great Apes](#)
- [Operant Conditioning](#)
- [Serial List Learning](#)
- [Theory of Mind](#)

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## Herbivore

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## Introduction

The sun is the ultimate source of energy, and plants are capable to trap the visible spectrum of sun's radiation. Therefore, plants are known as photosynthesizers, which have the ability to

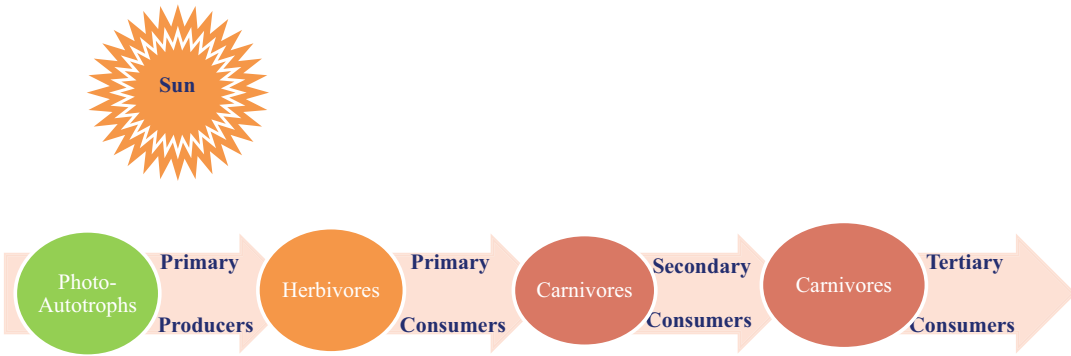
synthesize food in the presence of sunlight. The entire living world relies directly or indirectly on this photosynthetic produce and gets energy for their various life processes; therefore the plants are considered as producers or photoautotrophs (Raven 2019). The energy obtained by the plants gets transferred to a heterotrophic organism that eats plants, subsequently to another organism relying only on animals for their feed. Thus, the animals are heterotrophic and known as consumers (Raven 2019). Therefore, there is a successive relationship among the organisms where one organism relies on other for its food (Fig. 1). Each living organism is connected with each other in a straight chain for food and occupies its specific position, known as trophic level in this linear series (Fig. 1). This succession of living organisms, known as food chain, is connected as producers–primary consumers–secondary consumers–tertiary consumers at first trophic level, second trophic level, and third trophic level or even higher (Figs. 1 and 2). Subsequently, this establishes a natural consumption link, the food webs via interconnected food chains in an ecosystem (Raven 2019).

## Herbivores and Herbivory

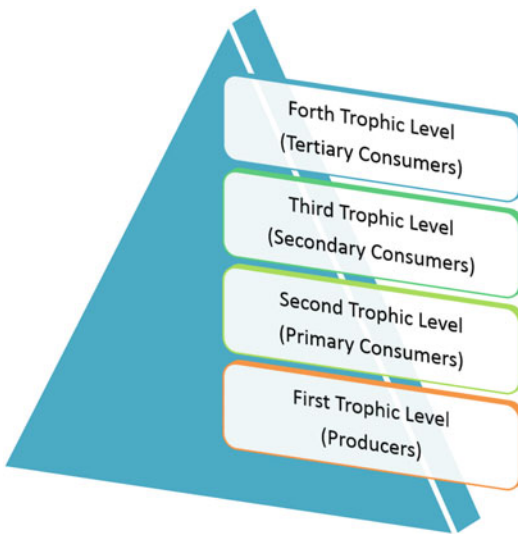
An herbivore is simply an exclusive plant eater. A heterotrophic animal that feeds only on different types of plants (i.e., algae, bryophytes, herbs, shrubs, and trees) or plant parts such as leaf, stem, root, fruits, seeds, etc., is known as herbivore, and the feeding strategy of herbivores is known as herbivory. Herbivores are integral key elements of food chains/webs that transfer photosynthetic produce, being a link between the primary producers and secondary consumers (Pape and Löffler 2012; Figs. 1 and 2). Herbivores, therefore, play a pivotal role in maintaining equilibrium in an ecosystem by being the first one to eat photoautotrophs and transfer the energy ahead in the living world (Figs. 1 and 2).

## Diversity of Herbivores

There is a great diversity of plant species in the living world, which is largely responsible for the



**Herbivore, Fig. 1** Flow of energy and food in an ecosystem: a food chain



**Herbivore, Fig. 2** Feeding strategies of the organisms in an ecosystem

diversity of the herbivores, i.e., animals that feed on them. Subsequently, there is a great diversity of herbivores that include insects, mollusks, and mammals and may range from small aphids (an insect) to snails and large elephants, rhinoceros, gorillas, and also the endangered red panda (Fig. 3).

Among all, insect herbivores are the most common. It has been expected that around half of the insects are herbivores that includes millipedes, mites, worms, and some other species of insects. Several large insect groups are totally plant feeders that include butterflies, gall wasps, leaf beetles, leaf-mining flies, moths, plant bugs,

weevils (e.g., a common cotton boll weevil), etc., and exert a great threat to agricultural crop.

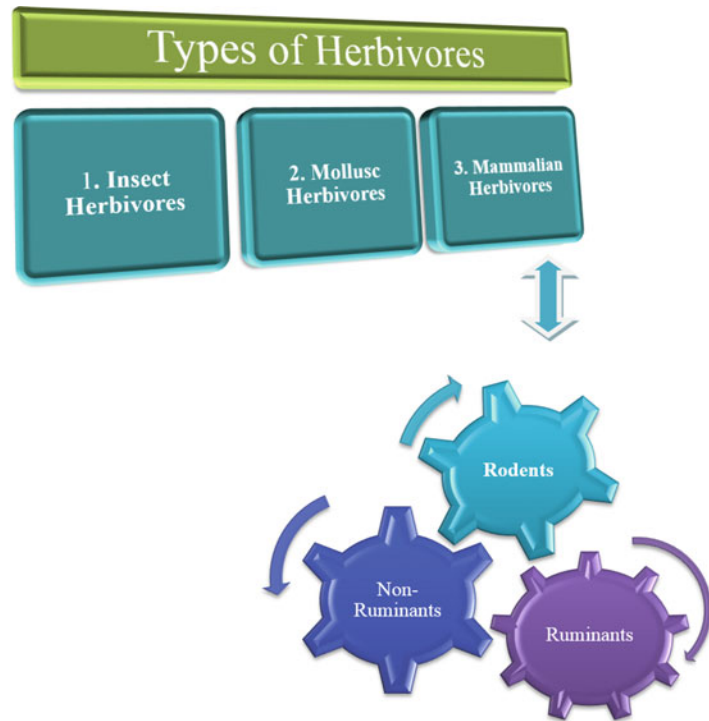
Among mollusks, most of the Chitons, calcareous marine animals and some gastropods are grazing herbivores, e.g., snails, etc. Besides, crabs, ducks, krill, sea slugs, sea snails, sea urchins, parrot fish, surgeonfish, etc., are some other aquatic herbivores.

Mammals include small- and large-size organisms that may be further categorized as rodents, ruminants, and non-ruminant animals (Fig. 3). Rodents are mammals of the order Rodentia, which are characterized by a single pair of continually growing incisors in both of the upper and lower jaws (Single et al. 2001). Rodents include mice, rats, prairie dogs, squirrels, chipmunks, chinchillas, guinea pigs, porcupines, gerbils, beavers, hamsters, capybaras, hares, rabbits, and pikas. Most rodents are herbivorous which feed exclusively on plant materials such as seeds, leaves, stems, flowers, and roots.

Plants have many complex structures such as leaves, stems, rhizomes, tubers, roots, flower parts, fruits, seeds, etc., that animals have to overcome in order to use plants as a source of food. Besides, the plant cells are encased by a tough cell wall, made of complex polysaccharides such as cellulose, lignin, pectin, etc., that makes a plant tough to digest. Among all ruminant and non-ruminant mammalian herbivores, cellulose, a complex polysaccharide molecule of linear chain of thousands of glucose molecules, is the major source of food component, and mammals do not have enzymes to digest this complex molecule.



**Herbivore, Fig. 3** A generalized cataloging of terrestrial herbivores



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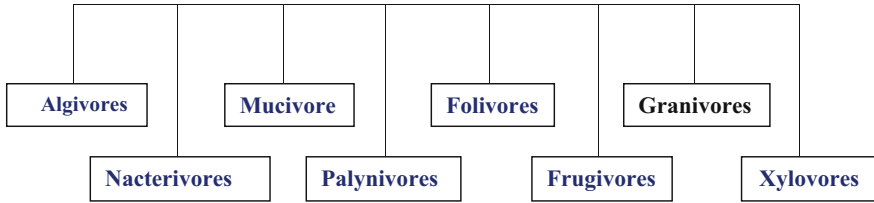
Ruminating mammals having specialized multi-chambered stomach include antelopes, buffaloes, cows, deer, gazelles, giraffes, goats, sheep, etc. (Fowler 2010). They rely on certain symbiotic microorganisms for breakdown of the complex molecule, cellulose, into simple monosaccharide molecules, glucose, to obtain energy by fermenting principally through microbial actions. Ruminant mammals have this cellulose digesting microorganism living in symbiotic relationship in one of the chamber, probably the largest one, rumen. The largest chamber, rumen, also allows rumination in such mammals where the partially digested food to regurgitate back in the large cheek pouches to rechew the cud. The food is further digested in other chambers of their huge multi-chambered stomach.

Non-ruminant mammals having single chambered and relatively small stomach including donkey, elephants, hares, horse, kangaroos, mules, rabbits, zebras, etc., also depend on plants exclusively for their feed. These mammals and even rodents also have some different way of digesting this complex molecule, cellulose. The cellulose-

digesting microorganisms live in a large pouch known as cecum that lies at the posterior side of the small intestine in such non-ruminant mammals. Such organisms do not regurgitate the food back to cheek pouches. However, some of the non-ruminating mammals, like hares and rabbits, show coprophagy, a habit of eating their feces back thereby allowing them another way to digest cellulose. Such animals are known as coecophagus.

Besides, various complex plant structures may vary from species to species and thus provide wide range of feeding opportunities to herbivores, eventually reflecting the wide diversity of herbivores and plants too (Fig. 4). Therefore, herbivores can also be categorized as:

- **Algivores:** Algivores herbivore gets food from Algae. Algivores include Crab, Sea urchin, Krill, Sea snail, flamingo, Parrotfish and Surgeonfish
- **Nacterivores:** They feed on Nectar, ex. Honey possum
- **Mucivores:** They feed on plant fluids, i.e. Sap. It includes Aphids



**Herbivore, Fig. 4** A specialized cataloging of herbivores based on feeding habit

- **Palynivores:** Their food materials are pollen grains, ex. Bees
- **Folivores:** They feed on leaves of plants it include Koalas
- **Frugivores:** It includes those herbivores which gets food from fruits, ex. Ruffed Lemurs
- **Granivores:** Their food materials are seeds, ex. Hawaiian Honey creepers
- **Xylovores:** They feed on woods, eg. Termites

### Herbivory: Relationship Between Plants and Herbivores

The “battle” between plants and herbivores is likened to an arms race and has led to strong relationships between many herbivores and plants. Such relationship ranges from animals feeding only on particular plant groups or species; this kind of specialization where an animal relies on a certain plant or plant group to grow is referred to as “plant-host specificity.” Herbivores are often smaller than the plants on which they rely for their food; thus, they may damage a single plant or crop over days or weeks however without killing it but causing serious economic losses. Besides, an elimination of a particular plant species or group may result in the loss of several animals from an ecosystem. To understand the relationship between plants and animals is really important for the survival of an ecosystem in a better way.

### Herbivory: Adaptations and Modifications Among Herbivores

The herbivorous animals have developed specialized physical features and feeding strategies to utilize fibrous plants as a source of food. Many

special features and adaptations are exhibited by the herbivores that allow them to access the complex structures among autotrophs such as:

- Grazing and browsing herbivores have a heterodont pattern; they have evolved grinding teeth to break up tough plant tissues and use their six lower incisors to crop off grass and leaves and make use of the flat and wider pre-molars and molars for stripping leaves and grasses and as grinding surfaces to break up the cellulose of the vegetation they eat.
- Cheek pouches to store the engulfed food material (e.g., mammals).
- Specialized digestive system with multi-chambered stomach where microorganisms are accommodated to help to digest the food through fermentation. Ruminants (sheep, goats, deer, giraffes, camels, and cattles such as cow, buffalos, etc.) can regurgitate its partially digested food, known as cud, and chew it again.
- They have long small intestine generally that is specialized for absorbing proteins, which are in short supply in their diet.
- The trunk, a flexible, gripping nose of the elephant.
- Long tongue and long neck to get to leaves on long trees (e.g., giraffe).
- Continuously growing upper and lower incisors in cecotrophs. They can ingest their partially digested feces back to digest it again and get nutrients (e.g., hare and rabbit).
- Modified legs for digging and to access rhizomes, tubers and roots, etc.
- Modified mouthparts and legs especially among insects, cutting and chewing mouthparts (e.g., beetles) or piercing mouthparts (e.g., wasp ovipositor), sawlike mouthparts

- (e.g., sawfly ovipositor), and several other appendages like claws, spines, or suckers that allow some herbivores to cling the surface and giving them to access to internal structures that allow them to feed on plants.
- Wings that help them to reach at the top of the highest plant (e.g., insects).

## Herbivory: Defense Systems Among Plants and Herbivores

Plants have evolved several morphological and phytochemical defense systems to deter the herbivores. Plants have different developmental stages of growth such as new leaves are growing and roots are extending, while elsewhere on the same plant, leaves are aging and roots are decaying. Thus, during growth and development, plants change their morphology and phytochemical structures. Therefore herbivores and plants develop some resistance against each other by developing:

### Defense Systems Among Plants

#### Morphological Defense Systems in Plants

- Development of trichomes – Numerous hair-like appendages, i.e., trichomes, develop on the surface of stems, leaves, and roots that repel some of the small-sized herbivores, chiefly the insects. Interestingly, some are glandular trichomes which secrete certain chemicals that are lethal to small-sized herbivores.
- Plants also use thorns, spines, prickles, and sticky plant parts that play an important role to deter some of the herbivores.
- Even in some plants, after grazing leaf meristems may grow out and replace the lost part.

#### Deposition of Complex Chemical Structures in Plant Cell Walls

- To maintain their physical structure and support, plants use complex compounds such as cellulose, pectin, and lignin. These compounds are tough, water insoluble, and also difficult to digest.

- Some plants deposit silica, sticky resins, and other compounds in leaves and stems that make their surface abrasive to avoid themselves eaten by the herbivores.

### Phytochemical Defense System in Plants

Plants produce many active compounds or chemicals for defense against herbivores that may deter herbivores from feeding or kill them (Fraenkel 1959). These phytochemicals, commonly known as secondary metabolites (alkaloids, essential oils, terpenes, phenolics, tannins, etc.), are differentially synthesized in small or large quantities in different plants or plant parts in response to initial plant damage by the herbivores and thus herbivores avoid eating such plants or plant parts further (Bennett and Wallsgrove 1994; Maffei et al. 2012).

Plants produce ethylene, jasmonates, and salicylates on grazing or eating that act as phytohormones and signaling agents to induce several other defense mechanisms in plants (Maffei et al. 2012).

Even in some plants, the nectar and other secretory glands secrete sweet nectar, oils, waxes, latex, essential oils, some scented and aromatic substances, etc. to lure and repel the bees, flies, moths, and some other insects, birds, and some animals too, thus maintaining the prey–predator ratio, keeping themselves protected and away from some herbivores (Bennett and Wallsgrove 1994; Maffei et al. 2012).

### Defense Systems Among Herbivores

Herbivores too have a number of feeding strategies to overcome these complex plant tissues and chemical structures such as:

- Eating tough or complex plant tissue by using chewing mouthparts.
- Avoiding complex plant tissue by eating soft internal tissues.
- Eating complex plant tissue by forming alliances with other organisms.
- Avoiding complex plant tissue by eating plant fluids.

- Some herbivores either evolve resistance against some secondary metabolites of the plant or get shift to some other resource to avoid inter- or intraspecific competition.

## Significance of Herbivory

- Herbivory plays foremost and an important role in maintaining food chain of an ecosystem.
- Herbivores are important ecosystem engineers having ability to make changes in grazing plant communities, modifying habitat structures, and altering nutrient flows (Asner et al. 2009; Olf and Ritchie 1998; McNaughton et al. 1997; Jones et al. 1994).
- Herbivory can have significant impacts on the composition, structure, and diversity of plant communities on earth, their habitat, and health.
- It avoids the overcrowding of the plants with each other and influences plant communities in terms of individual plant's growth and development.
- It may increase the chances of successful seedling growth.
- It improves conditions for plant growth by pruning plants and allow light to reach the surrounding area.
- It increases and maintains soil fertility contributing to the plant litter and the nutrient pool in soil by nutrient recycling from plants.
- Increases in nutrient uptake and productivity of plants.
- Plant can be detoxified by herbivores (Dearing et al. 2000).
- It also improves plant defense mechanism after initial plant damage from herbivory.
- Herbivores also have cultural, social, and economic importance for the people (Zachrisson 2008).

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## Herding

► [Artiodactyla Navigation](#)

## Hereditary Carrier

► [Carrier](#)

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## Heredity

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## Synonyms

### Genetics

## Definition

The transmission of traits encoded in genes from parent to offspring.

## Introduction

Until the 1830s, heredity remained poorly understood. In 1858, one of the most significant developments in the study of hereditary processes was represented when the theory of natural selection was proposed by Charles Darwin and Alfred Wallace. However, our knowledge of heredity and modern understanding of inheritance of traits originates from the principles proposed by Gregor Mendel in 1865 who provided particular laws of inheritance for the passing of distinct traits from one generation to the next (Cobb 2006; Miko 2008a).

Heredity is biological processes in which particular characteristics are passed from parents to their offspring through the genes. The subject concerned with the study of heredity is known as genetics.

## Basis of Heredity

Genes are the building blocks of heredity which are composed of DNA and determine specific characteristics, such as height or hair color. DNA is a long polymer molecule that integrates four types of interchangeable bases (adenine, thymine, cytosine, and guanine) and encodes genetic information. In fact, the sequence of bases alongside a

certain DNA molecule specifies the genetic information. Mutations can modify DNA structures and genes which yield new alleles. Therefore, the new allele may affect the trait that is controlled by affected gene leading to change of the phenotype of the organism. In the nucleus, DNA molecule is packed many times around proteins called histones and forms nucleosomes. Then nucleosomes tightly coil up and create chromatin loops. The chromatin loops are then wrapped around each other and make thread-like structures called chromosome. Chromosomes are condensed structures within cells carrying genetic information in the form of genes. Human cells have 23 pairs of chromosomes; of these, 22 contain the non-sex chromosomes (autosomes) and the 23rd pair is the sex chromosome which determines gender. Females have two X chromosomes and males have one X and one Y chromosome. Therefore, females have two copies of every gene.

Genetic material is inherited from parents in the form of homologous chromosomes. Homologous chromosomes are chromosome pairs, each derived from one parent, having the same length, gene sequences, and centromere location.

Traits are observable characteristics that are passed down from parent to offspring. Some traits are inherited and others result from interactions with the environment. Traits are autosomal or sex-linked which are determined by the location of the alleles in the genome. Sex-linked traits are controlled by an allele which is found on the sex chromosomes, while autosomal traits are depended on the presence or absence of certain alleles located on non-sex chromosomes. Several traits are influenced by heredity including physical characteristic, intellectual capabilities, and emotional characteristics.

Simple creatures duplicate their genetic information and then splitting to form the same creature. More complex creatures produce gametes that carry half of the genetic information and then combine these to form new creatures. Therefore, the second generation will have diversity that they inherit from the first generation. Most of traits are influenced and controlled by multiple interacting genes and the environment (Berkowitz 1996).



## Gene Transmission in Mitosis

Mitosis and meiosis cell division transmit genetic material in very different ways. Mitosis division is the procedure of nuclear division that produces two identical cells (daughter cells) from a single cell and takes place in all types of somatic cells. The DNA is copied before cell mitosis resulting in two new cells each inheriting the DNA sequence in the nucleus. Therefore, each cell will receive the same number of chromosomes and identical genetic content as its original cell.

## Gene Transmission in Meiosis

Meiosis is a process that one diploid cell undergoes two cycles of cell division to produce four sex cells (gametes) with half the number of chromosomes as the parent cell. The resulting gametes have 23 new chromosomes (haploid) that represent distinct mixtures of the original maternal and paternal copies. During sexual reproduction, when the sperm and egg fuse by the process of fertilization, the number of chromosomes in the offspring is restored.

Crossing over or genetic recombination is a significant process that happens during meiosis resulting in new combinations of genes and increase genetic variability within a species and helps them to survive. Siblings with the same parents have some traits over others because they inherit a few genes from each parent instead of inherit identical DNA from one parent. In somatic reproduction, variation arises mainly from mutation in a DNA sequence. However, in sexual reproduction, variation arises from both mutation and recombination. Mutation creates the different versions of the same gene. Then during meiosis parental alleles are recombined. Owing to recombination, sexual reproduction yields more variation than somatic does (Miko 2008b).

## Mutation

Mutations, main cause of diversity among organisms, are changes that affect genetic sequence.

These changes can occur at many different levels, and based on their context or location they can be neutral, useful, or harmful. Mutations usually result in the development of new traits that are heritable or capable of being inherited. Since many mutations happen during the growth and development process, all cells in the body do not have identical genomes.

Mutagens are chemical or physical factors that increase the rate of mutation. Mutations are resulted from insertion or deletion errors during DNA replication or other types of damage to DNA. Generally, gene mutations are classified in two major types: germline mutations and somatic (acquired) mutations. Germline mutations are present in the germ cells and passed on offspring from a parent. On the other hand, somatic mutations are present only in somatic cells and usually caused by environmental factors, including UV radiation, chemicals, and viruses. However, these mutations cannot be passed on to the offspring. Most hereditary diseases are related to a mutation such as cystic fibrosis, sickle cell anemia, phenylketonuria, and color blindness (Loewe 2008).

## Genotype and Phenotype Relationship

Wilhelm Johannsen categorized the difference of genotype and phenotype in 1912. Genotype and phenotype are related concepts but have different meanings. The genotype is the set of genes in our DNA and inheritable genetic identity carried by all living organisms, which is responsible for a specific characteristic. Genotypes are either homozygous (two identical alleles) or heterozygous (different alleles). The phenotype is the visible expression of the gene information, combined with the environmental influence on an organism's appearance or behavior. In fact, genotype codes for the phenotype. Most phenotypes are influenced by both genotype and circumstances. Although the genotype is a major influencing factor in the development of phenotype, the phenotype arises from the complex interactions between genes and environment (Miko 2008a).

Genes are functional units of heritable material that are found within all living cells. Meanwhile

human cells carry two copies of each chromosome; they have two versions of each gene. Alleles are different versions of a gene and defined as either dominant or recessive.

The terms dominant and recessive are related to the inheritance patterns of particular characteristic and define how it is likely a particular phenotype pass from parent to offspring. The study of heritable traits helps scientists to determine which traits are dominant and are likely to be transferred from one parent to the next generation. These terms are useful in prediction of the probability of genetic disorders. Dominant alleles show their effect though individuals have one copy of the allele, which can come from just one parent. Therefore, for dominant trait you only need one copy of the alleles. For example, for having brown eyes you only need one copy of the “brown eye” allele. On the other hand, recessive trait only will be passed on if both parents possess it. An example of recessive trait is blue eyes, which can manifest in the offspring only if the individual has two copies of recessive alleles, one from each parent. Furthermore, once both alleles are dominant and expressed equally in offspring it is called codominance. The resulting trait is caused by both alleles. Indeed, an allele (from both parents) combines in the descendants and the offspring shows both phenotypes. For example, blood group AB is the result of codominance of the A and B dominant alleles (Peirson 2013).

## Natural Selection

The theory of natural selection, first developed by Charles Darwin, is regarded as one of the basic mechanisms of evolution. Natural selection is referred to a process in nature in which organisms possess certain genotypic characteristics that make them better adapted to their environment. Indeed, favored heritable traits increase an organism's chances of survival and reproduction and make them able to transmit and preserve their crucial genotypic potentials to their consequent generations (Endler 1986; Millstein 2002).

## Conclusion

Heredity is the biological process responsible for the transmission of heritable traits from parents to offspring via DNA. Heredity is a central component of evolutionary alteration, and variant characters highlight the complexity of understanding genetic impacts on phenotypes. Through heredity, differences within or between species can accumulate and increase the ability of individuals to survive by natural selection. Environmental elements can also interact with genetic information and resulting in even more genetic diversity.

## Cross-References

- ▶ Alleles
- ▶ Autosome
- ▶ Centromere
- ▶ DNA
- ▶ Genes
- ▶ Gene Pool
- ▶ Genotype
- ▶ Homozygosity
- ▶ Mendel's Laws
- ▶ Nucleus
- ▶ Recessive

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## Heritability

### ► Heritability Estimate

## Heritability Estimate

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## Synonyms

### Heritability

## Definition

Heritability is defined as a statistical study of genetics that provides an estimation of the amount of variation in a phenotype of individuals within a population that is due to genetic variation (Wray and Visscher 2008). Thus, heritability estimates tell us what percentage or ratio of variation in a given trait or a disorder is due to genes versus the environment.

## Introduction

Varying phenotypes between individuals of a population are due to both environmental and genetic factors, along with the several interactions between the two. Heritability is a concept that describes how much of the variation in a trait is due to variation in genetic factors. This term is most often used in reference to the similarity between parents and their offspring. In this context, high heritability suggests a strong

resemblance between parents and offspring with regard to a specific trait, while low heritability indicates a low level of resemblance. There are many common misconceptions on the exact meaning and interpretation of heritability. Heritability is not the ratio or percentage of a phenotype that is genetic, but rather, the ratio or percentage of phenotypic variance that is due to genetic factors.

The value of the heritability estimate lies between 0.0 and 1.0, where 0.0 indicates that genetics are not a contributing factor at all and 1.0 indicates that genetics are the only contributing factor for the trait in question. For example, the heritability estimate for any particular disorder is 0.5, which means that half of the variation seen in that disorder across a population is due to genes (biologically inherited) and half is due to the environment (school, work, home life, etc.). In other words, it can be said that genes and environment both are contributing equally to this disorder.

## Heritability Types: Broad-Sense Heritability and Narrow-Sense Heritability

Broad-sense heritability ( $H^2$ ) reflects all possible phenotypic variance due to the genotype, i.e.,  $H^2 = V_G$  (Genotypic Variance) /  $V_P$  (Phenotypic Variance). Phenotypic Variance ( $V_P$ ) is due to the sum of three components: environmental variance ( $V_E$ ), genotypic variance ( $V_G$ ), and variance resulting from the interaction of environment and genotype ( $V_{GE}$ ), i.e.,  $V_P = V_E + V_G + V_{GE}$ . However, Genotypic Variance ( $V_G$ ) can be further divided into additive, dominance, and epistatic variances. An  $H^2$  value that approaches 1.0 indicates that the environmental conditions have had little impact on phenotypic variance. An  $H^2$  value close to 0.0 indicates that environment has been almost solely responsible for the observed phenotypic variations.

Narrow-sense heritability ( $h^2$ ) includes only that proportion of genetic variation that is due to additive genetic values ( $V_A$ ), i.e.,  $h^2 = V_A/V_P$ . Additive genetic variation ( $V_A$ ) refers to genetic effects where each allele at each of the many genes that codes for a trait has a small effect on

the phenotype and the phenotype depends on the sum of the effects of all of these alleles with each allele contributing equally.

## Methods for Estimating Heritability

Genetic gain or selection response (R) can be calculated by the product of heritability ( $h^2$ ) and the selection differential (S). Heritability estimates generally depend on the assumptions of large random mating populations in the absence of mutation, migration, selection, and genetic drift. Most methods for estimating heritability are available for diploids with normal meiosis. Sex-specific differences in recombination should also be taken into account while estimating heritability (Sakamoto et al. 2000).

Generally, there are two types of methods used for heritability estimation. The first method makes use of regression and correlation to estimate heritability whereas the second method involves use of analysis of variance (ANOVA) and estimation of variance components to estimate heritability. The different methods for estimating heritability can be explained in the following ways (Friars and Smith 2010):

### (i) Regression Between Parents and Offspring

This method estimates the amount of the transmission of any particular trait from parent to offspring and uses the following formula:

$$y = a + bx$$

where x, y = mean values of the trait for the parents and offspring, respectively,

a = intercept, and

b = regression coefficient.

The heritability will be equal to the regression coefficient, i.e.,  $h^2 = b$ , when the mean values of a trait from both parents will be used; however, when the offspring will be compared with just one parent, then the heritability will be  $h^2 = 2b$ .

### (ii) Hierarchical Matings

This is also known as North Carolina mating design I. This method estimates the source of variation in the population and uses the following formula:

$$Y_{ijk} = \mu + S_i + D_{ij} + e_{ijk};$$

where  $Y_{ijk}$  = trait measurement on the  $k^{\text{th}}$  progeny of the  $j^{\text{th}}$  dam (female parent) mated to the  $i^{\text{th}}$  sire (male parent),

$\mu$  = overall mean of the population,

$S_i$  = effect of the  $i^{\text{th}}$  sire,

$D_{ij}$  = effect of the  $j^{\text{th}}$  dam mated to the  $i^{\text{th}}$  sire, and

$e_{ijk}$  = environmental plus genetic segregation effect on the  $k^{\text{th}}$  progeny of the  $j^{\text{th}}$  dam mated to the  $i^{\text{th}}$  sire.

The heritability in this case can be calculated from the sire component ( $h^2_S$ ), the dam component ( $h^2_D$ ), and the sire and dam component ( $h^2_{S+D}$ ), whose formulas are as follows:

$$h^2_S = 4 \sigma^2_S / \sigma^2_S + \sigma^2_D + \sigma^2_e$$

$$h^2_D = 4 \sigma^2_D / \sigma^2_S + \sigma^2_D + \sigma^2_e$$

$$h^2_{S+D} = 2(\sigma^2_S + \sigma^2_D) / \sigma^2_S + \sigma^2_D + \sigma^2_e$$

where

$\sigma^2_S$  is the sire component of variance,

$\sigma^2_D$  is the dam component of variance, and

$\sigma^2_e$  is the environmental plus genetic segregation component of variance.

### (iii) Factorial Matings

This is also known as North Carolina mating design II. In this method, sets of matings (in which sires and dams of each strain are mated to each other) are used for partitions of variance components, where the theoretical expectations of

| Variance component | $\sigma^2_A$ | $\sigma^2_D$ | $\sigma^2_{AA}$ | $\sigma^2_{AD}$ | $\sigma^2_{DD}$ | $\sigma^2_{Ec}$ | $\sigma^2_{EG}$ | $\sigma^2_M$ |
|--------------------|--------------|--------------|-----------------|-----------------|-----------------|-----------------|-----------------|--------------|
| Between families   | 1/2          | 1/4          | 1/4             | 1/8             | 1/16            | 1               | 0               | 1            |
| Within families    | 1/2          | 3/4          | 3/4             | 7/8             | 15/16           | 0               | 1               | 0            |

additive and nonadditive effects are as follows (McKay et al. 1986):

- $\sigma^2_A$  = variance due to additive genetic effects
- $\sigma^2_D$  = variance due to dominance
- $\sigma^2_{AA}, \sigma^2_{AD}, \sigma^2_{DD}$  = variance due to epistatic interactions of additive-additive, additive-dominance, and dominance-dominance types, respectively
- $\sigma^2_{Ec}$  = variance due to environmental effects between tanks
- $\sigma^2_{EG}$  = other environmental effects not due to tank effects
- $\sigma^2_M$  = variance due to maternal effects

(iv) **Breeding Values**

In this method, the selection criteria for the prediction of breeding values in large data sets are based on best linear unbiased prediction (BLUP) of additive genetic effects. Another most commonly used method for the estimation of variance components of mixed linear models in animal breeding is restricted maximum likelihood (REML) method (Hofer 1998).

(v) **Inbred Lines**

In this method, the use of variance between and within inbred lines can be used to estimate genetic variance and heritability using the following formula:

$$h^2_t = h^2_o (1 - F_t) / (1 - h^2_o F_t);$$

where

$h^2_o$  is the heritability in the base population, and  $h^2_t$  and  $F_t$  are the heritability and inbreeding coefficients at time represented by generations  $t$ .

(vi) **Linear Heritability Estimates**

This method is based on selection of potential parents for which estimates of average genotypic and phenotypic values are obtained from a pedigree population (Abplanalp 1961). In this method, a regression of genotypic on phenotypic values is estimated from a straight line joined through the points representing the mean genotype and phenotype of selected parents on one axis and the population mean genotype and phenotype on the other.

(vii) **Clonal Lines**

In this method, firstly mitotic gynogenetic diploids were produced and reared in a common environment, and then the lines were identified using DNA fingerprinting and after that human twin model were employed to observe the separated genetic and environmental variances (Taniguchi et al. 1996).

(viii) **Discrete Traits**

In this method, heritability can be estimated from an underlying continuous scale using techniques, which provide a quantification of multiple gene effects (Robertson and Lerner 1949).

(ix) **Animal Model**

In this method, an animal model is used for heritability estimate by estimating its breeding value through the information of animal's records, its parents, and its progeny details. This method is based on the condition that provided pedigree information of the animal is accurate and complete.

**Conclusion**

The heritability plays an important role in the phenotypic individual differences. Statistical definition of heritability can be given as the ratio of



phenotypic variance derivable to the genetic variance. This ratio always ranges from 0 to 1 depending upon whether genes don't contribute at all or contribute fully for individual phenotypic differences. For example, nearly all heritability estimates lie in the moderate range of .30–.60 for human behavior. Knowledge of this statistical parameter helps breeders in choosing if it is more effective to enhance qualities through management or through selection of a particular livestock/crop/species.

## Cross-References

- [Behavioral Genetics](#)
- [DNA](#)
- [Genes](#)
- [Heredity](#)

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## Heritability Fallacy (in Behavioral Genetics)

- [Genetic Fallacy](#)

## Heritability of Behavior

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## Definition

Heritability of behavior is a quantitative estimate of how much proportion of a variation in an observed behavioral trait can be attributed to the genetic factors. A variation in an observed behavioral trait is assessed using population statistics.

## Introduction

The postulate that animal behavior has a genetic basis is now well supported by scientific literature, and the determination of heritability has been an important measure in current quantitative behavioral genetics. Nature versus nurture (or gene versus environment) contribution in expression of a trait (i.e., phenotype) has been a longtime conflict, leaving scholars either denying contributions by one of

these or claiming dominance over each other. Environment refers to anything other than genotype, to which an individual is exposed and which may influence expression of a trait. Psychologist Eric Turkheimer proposed three laws of heritability which got wide acceptance among the scholars of behavioral studies. The first law says all human behavioral traits are heritable. The second law says the effect of shared family environment is less than genes. The third law states that a substantial proportion of variation in complex behavioral traits is not explained either by environment or genes (Turkheimer 2000). These laws are in stark contrast to the primitive views regarding biological basis of behavior which had given sole importance to the environment. Although now enough literature is available which provides scientific basis for the heritability estimation in behavior, the evidence also supports inclusion of the counter view (Flynn 2001). Conceptually, heritability doesn't ensure that any percentage of the said behavioral trait will be solely decided by genes. Current view is that although genes may have an essential role, animal behavior is decided by the intricately multifaceted interplay of the contributing factors and not by any single factor in isolation (Johnson 2007).

For individuals sharing the similar environment, genes may have a greater say in deciding observed variance in a trait; in turn, for the individuals who share a common genotype, any variance may be attributed to the environment. Also, a genetic influence on behavior can be amplified or buffered by environmental conditioning, and the environments which are not shared by others and are unique to the individuals may have specific impacts on the behavior of exposed individuals.

### **Heritability: Concepts, Mechanisms, and Misconceptions**

Heritability is nearly a century-old concept introduced by Sewall Wright and Ronald Fisher which provides estimate for the contribution of the nature (i.e., genes) for phenotype variations in nature versus nurture (i.e., environment) conflict and can be expressed in proportions (between the variation in a phenotype due to genes and total

variations). Although in literary sense heritability signifies resemblance of traits between parents and offspring, in scientific use, it is a statistical parameter. Conventionally heritability is symbolized as " $h^2$ " (explained by Sewall Wright's path coefficient model, he used " $h$ " for heredity and square of this presented correlation or regression between phenotype and genotype variances) (Visscher et al. 2008). The numerical value of heritability ranges from 0 to 1 (or can be expressed in percentage 0–100), signifying no role to absolute role of genes for a phenotype/trait. Heritability is specific to the population and environment and a selective parameter to measure genetic influence on the variance for a trait at population level rather than in single individuals. Heritability can be described as narrow-sense heritability ( $h^2$ , what we conventionally call as heritability), which accounts specifically additive effects of the contributory genes, and broad-sense heritability ( $H^2$ ) which includes all genetic factors.

Genetic factors other than additive gene effects may be gene-gene interactions (epistasis) and gene-environment interaction. Epistasis implies that when more than one genes are influencing the same trait, their combined effects may not be additive but follow complex interactions resulting in phenotypic outcomes. The epistatic mechanism involves inter-allelic interactions between loci for more than one gene and this way may mask or modify the expression of some genes manifesting invariant phenotypes. Inter-allelic interaction within loci for the individual genes may result in dominant and recessive phenotypes for a particular trait (Phillips 2008).

Mechanisms operating in gene-environment interactions are not comprehensively known yet, but gene expression changes mediated by transcription factors, micro-RNA-mediated gene silencing (Geeleher et al. 2012), and epigenetics are some known mechanism mediating gene-environment interactions. Epigenetics registers environmental influences on the base or chromatin structure of a chromosome by specific mechanisms without bringing any change in the base-pair sequence, by this influencing the expression of genes (Zhang and Meaney 2010). Trans-generational epigenetics (Jensen 2013) has been

considered as a plausible explanation for missing heritability (for the traits for which no genetic markers could be found in genome-wide association studies (GWAS) to support its estimated heritability) (Marian 2012). Although most of the epigenetic changes are routinely erased from the genes by epigenetic reprogramming during gametogenesis, challenging its significant contribution to the heritability of traits, a recent research evidence suggests some epigenetic changes implicated in specific behavioral aspects may escape the erasure and may be inherited to the offspring, which may be crucial for expression of specific behavioral traits, indicating a probable role of epigenetic mechanisms in heritability of behavior (Hackett et al. 2013).

Heritability is traditionally estimated as the correlation of phenotype variance between offspring and parents, between full and half siblings, or difference in correlation of monozygotic and dizygotic twin pairs. Broad-sense heritability which includes all genetic factors can be defined as the proportion of genotypic value ( $V_G$ , combined effect of all inter-allelic interactions including dominance and epistasis) to phenotypic variance ( $V_P$ ),  $H^2 = V_G/V_P$ . Narrow-sense heritability only includes the additive effect of genes ( $V_A$ ) and presented as  $h^2 = V_A/V_P$ .

In artificial selection experiments (selective breeding of the organisms to get desirable traits), heritability can be estimated from the ratio of the observed selection response ( $R$ ) to the observed selection differential ( $S$ ) which is also known as breeder's equation heritability ( $H^2 = R/S$ ). Observed selection response ( $R$ ) has been a post-selection change in the population mean for a trait, and observed selection differential ( $S$ ) is the difference between the mean of the parents and that of the original population under observation for a trait.

A novel method of heritability estimation has been suggested by comparing the percentage of genetic similarity between siblings (derived from the genome-wide expression of genetic markers) with phenotypic variance (Visscher et al. 2006). Another novel method for heritability estimation implied DNA fingerprint markers and maximum likelihood calculation without using any prior

information on the relatedness of the subjects (Mousseau et al. 1998).

An interesting observation about heritability is that it may change with time and age caused by changes in genetic variations in a population. Genetic variations are known to change with time and age in response to new environmental conditions which may alter allelic frequencies or may induce new mutations in the genome (Visscher et al. 2008).

## Misconceptions

Heritability may be misunderstood as the inheritance of a trait (which is definitely an exclusive function of genes) a common misconception among beginners in population genetics. Contrary, heritability is a statistical estimate which doesn't give any information about the genetic structure of the individual. It rather gives an indication that genes may be attributed for certain fraction of a variation in a trait at the level of population. Heritability estimate is also specific to each population, and nontransferable, but surprisingly it has been almost conserved across populations and species.

Another common misconception regarding the definition of heritability to take care is it is not the proportion of phenotype but that of phenotype variation explained by genetic factors which constitute heritability (Visscher et al. 2008).

## Study Designs for Estimating Heritability of Behavior

### Twin Studies

Classical twin studies have been employed mostly for estimating heritability. The monozygotic twins (identical twins who share hundred percent of genes) when compared with dizygotic twins (who share, on average, only 50% of genes) if have been exposed to same kind of environments, a deviation of behavior can be attributed to the genes (because environment has been the same for both comparing groups).

### Adoption Studies

This study design gives an indication of the role of the environment. When siblings of the similar genetic background (especially, monozygotic or identical twins) are reared up in a different family environment, as genes are similar, any deviation in a behavioral trait may be attributed more to the environment. This study design can be also used for the siblings who will have a certain level of genetic similarity which can be assessed by using DNA markers (Visscher et al. 2006); if raised in a different family environment, the heritability of a behavioral trait can be estimated from phenotype variation versus shared genes plot.

### Children of Twins

Children of the twins can be followed for the continuation of the deviant behavior in changing rearing-up environment which can be attributed to the genes, and appearance of a new deviant behavior which parents didn't bear can be attributed to the environment.

### Molecular Genetic Designs

**Genome-wide association studies (GWAS):** Searching for SNPs (single-nucleotide polymorphs) in the whole genome can be attributed for the noted variance in the behavior. Nowadays, this study design is commonly used for estimating heritability, but an overly emphasized use of statistics complicates the whole issue, and slight variation of statistical parameter yields magnificent changes in GWAS results. This is the reason that GWAS studies are seen with skepticism.

**Candidate genes:** Several candidate genes have been tagged with various behavioral aspects (e.g., MAOA gene to antisocial behavior, dopamine receptors DRD2 and DRD4 to aggression and antisocial behavior, serotonin transporter 5HTTLPR for depression, SLC6-a noradrenalin polymorph to attention deficit hyperactivity disorder (ADHD), and GABRA2-a GABA polymorph to childhood conduct disorder and substance abuse

in adults (Kretschmer and Delisi 2016)). Many other candidate genes have also been reported which may influence animal behavior, but never a major causal relationship has been proved for any such gene. For the details on candidate genes implicated in behavior, interested readers may consult referred source (Flint and Munafò 2013).

### Developmental Models

Developmental models are based on the concept that heritability changes over age course of individuals as they grow. If a child is followed over the course of life for continuity of a particular behavioral trait, a change may be attributed to the changing environment or to the experience the child has gained while growing up, but a gene-environment interaction or influence of the genes in selection or rejection of the environmental conditions or adjustment of the individual to the faced environment may not be denied.

### Empirical Evidence for Heritability of Behavior

Heritability estimation through scientifically designed studies has been done for almost each aspect of the behavior; majority of the studies focused on personality traits (Bouchard 2004), intelligence (Devlin et al. 1997), attitude (Olson et al. 2001), and cooperative (Cesarini et al. 2008) and antisocial behavior (Grove et al. 1990). Heritability of cognitive traits such as memory, learning, and fear has been also studied (Croston et al. 2015). Advancement in genetic research has established the imperative role of the cascade of genes in behavioral complexity (Plomin et al. 1994), providing an empirical basis to the heritability of behavior. Heritability estimate ranges between 30% and 60% for various aspects of animal behavior (see "Heritability: Introduction"/Colorado University-Psychology). Heritability of personality traits alone in average has been estimated as 40% (Vukasović and Bratko 2015).

Certainly, classical twin studies have been most commonly used for this purpose as this study design provides unique opportunity to deduce conclusion on gene-environment conflict, as we discussed above. Although there have been conflicting views on the heritability of behavioral traits, taking the example of intelligence for which determinative role of nature (Plomin and Deary 2015) or nurture (Kendler et al. 2015) has never been resolved and research evidence appear in favor of both. If we consider intelligence that is measured by the intelligence tests and represented by IQ, sufficient evidence regarding heritability for this trait is now available (Snickers et al. 2017). Uniquely, heritability estimates for intelligence have been shown to be also influenced by assortative mating (a tendency of individuals to mate with a person of similar traits) and cultural transmission (transmission of environmental factors that are related to a trait and passed from the parents to offspring and are shared between siblings) further perplexing the nature versus nurture debate (Vinkhuyzen et al. 2012).

### Gene-Environment Interplay for Behavioral Traits

**Gene-environment interaction:** Not separately genes or environment but the interactions of both may be the guiding element for variance in behavior.

**Gene-environment correlation:** Genes may be deciding the coming environment an individual will face, for example, an anxious child may prefer to keep away from the challenging environment.

### Fallacy of Classical Twin-Based Studies Estimating Heritability of Behavior

The twin-based study designs for estimating heritability had been in question for relying on the assumption regarding the environment (Moore and Shenk 2017). In the classical twin-based studies, monozygotic and dizygotic twins are assumed

to have been exposed to similar environments, and heritability estimates are based on that, but what scholars suggest is, unknowingly, parents might provide monozygotic twins an environment more similar than that given to dizygotic twins due to the inherent behavioral similarities and close preferences for the things and surroundings in the siblings of monozygotic twins induced by identical genes (Moore and Shenk 2017). A breach in the assumed similarity of the environments for the monozygotic and dizygotic twins will definitely influence the heritability estimates to some extent, although it doesn't nullify the contribution of genes for the induced variation in a trait. An assumption-free method of heritability estimation in full siblings is based on the percentage of gene sharing between them as a function of variation in a trait, reported by Visscher et al. (2006), but its application in behavior quantitative genetics is still not confirmed.

### Applied Implications

Heritability estimation can be used for predicting the risk of the parent to offspring continuance of the behavioral traits or disorders. Heritability estimation of behavioral traits has been often used to provide justification for the logics regarding an indispensable role of genes in deciding the behavior of an individual, which may be a deciding factor in formulating policies for punishments or rehabilitation for a deviant behavior in adult or children (Joseph 2001). A behavioral trait which depends more on the environment than genes would suggest environmental modification may improve a deviant behavior and a higher heritability vice versa may indicate stubbornness for any improvement. But alternative view has been given for this, even in a case of high heritability; environmental modifications may improve individual's behavior through gene-environment interplay (Kendler et al. 2015).

Heritability also explains why individuals (even in a close community or family or twins) are so different in behavior (due to their unique genetic makeup) and helps understand a necessary social



value for the diverse behavioral attributes among individuals which has to care while drafting social policies (Manski 2011). It also reminds us that everything wanted can't be inserted or vice versa everything unwanted can't be erased in the society through modification of the environment only, and stubbornness of genes for a radical change and their complex interplay with the environment have not to be ignored. Heritability estimate may also be used for predicting continuance of behavioral or related disease traits in offspring in case of the selective mating of the parents.

## Cross-References

- Additive Genetic Variance
- Assortment
- Behavioral Variation
- Candidate Gene
- Epistasis
- Gene Expression
- Genetic Fallacy
- Genotype
- Heritability Estimate

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## Heritable Factors

### ► Polygeny

## Hermann von Helmholtz

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Hermann von Helmholtz 1821–1894

## Preface

This entry is based extensively on three biographies of Helmholtz, Cahan (2018), Koenigsberger (1902/1965), and Muelders (2001/2010), and on Boring (1950) for his emphasis on Helmholtz's relevance for Psychology. These four references overlap considerably on the facts of Helmholtz's life and many accomplishments relevant to physics, physiology, and psychology. Therefore, source citations for each and every fact presented here from these four sources will be limited generally to quotations or matters unique to a source. Other references are cited as needed to document particular points of interest.

## Pre-University Years

Hermann Ludwig Ferdinand Helmholtz was born on August 31, 1821, in Potsdam, Germany. His father August Ferdinand Helmholtz was a teacher at the Potsdam Gymnasium (high school) and his mother (née Caroline Penne) was a remote descendent of William Penn, Founder of Pennsylvania (1681).

Helmholtz grew up in an upper-middle class home but enjoyed cultural advantages above his family's station, as his father was a teacher and a military veteran and his mother was the daughter of a military officer. Helmholtz learned and enjoyed playing piano. He took his piano with him to college and said later that it was beneficial when he wrote a treatise on the psychology of music.

In high school, Helmholtz followed a classical curriculum that included physics, mathematics, Latin, Greek, French, English, Italian, Hebrew, and rudiments of Arabic. He was said to be a good but not exceptional student.

## University Education and Service as Physician-Surgeon in Prussian Army

Helmholtz's preference for advanced study in physics and mathematics was deemed impractical financially, so in autumn of 1838, he passed the entrance exam and enrolled in the Prussian Army's medical school, the Friedrich-Wilhelm Medicosurgical Institute in Berlin. The Medicosurgical Institute was affiliated with the University of Berlin's Medical Faculty. Room and instruction were free to all students, but Helmholtz had additional financial needs that compelled him to commit to 8 years' service upon graduation as a physician-surgeon in the Prussian Army.

Helmholtz was most impressed by Johannes Müller's lectures in physiology at the University of Berlin. Müller was Germany's most renowned physiologist based upon (among other accomplishments) having completed his 8-volume *Handbuch der Physiologie des Menschen* in 1840 (see Boring 1950, pp. 34–35 for brief summaries of each of the eight volumes or see “Müller, Johannes Peter” in this Encyclopedia).

Müller supervised Helmholtz's doctoral thesis. Helmholtz received his diploma on November 2, 1842.

Helmholtz became friends with some of Müller's students and assistants, including Emil du Bois-Reymond, Ernst Wilhelm von Brücke, and Carl Ludwig. du Bois-Reymond became well known at the University of Berlin for his research in muscle electrophysiology. Brücke became an eminent physiologist at the University of Vienna where Sigmund Freud was his student for 5 years; Freud described Brücke as his greatest teacher. Carl Ludwig would become Chair of Physiology at the University of Leipzig where he influenced Wilhelm Wundt, founder of Experimental Psychology, and Ivan Pavlov, discoverer of the conditioned reflex.

Müller believed in vitalism (i.e., a “life force” in biology that could not be reduced to chemistry and physics). du Bois-Reymond, Brücke, Ludwig, and Helmholtz strongly opposed vitalism. du Bois-Reymond and Brücke pledged to compel the truth that “No other forces than common physical chemical ones are active within the organism” (Boring 1950, p. 708). Surely Ludwig and Helmholtz shared this view, but perhaps they were absent when the pledge was made. Below we shall see that two achievements by Helmholtz essentially demolished vitalism, although some biologists persisted in believing in vitalism decades later (see Guyer 1931, pp. 22–23).

After completing his dissertation in 1842, Helmholtz began to intern at the Charité Hospital, a teaching hospital in Berlin, and subsequently qualified to become a physician-surgeon. In October 1843, Helmholtz began his service as a Prussian Army physician. During his military service years, Helmholtz made two of his most important contributions, both of which refuted vitalism.

In 1847 (age 28), and based upon many experiments in physiology, especially, metabolism, Helmholtz formulated the law of conservation of energy which he published as *Ueber die Erhaltung der Kraft* (On the Conservation of Force). Cahan (2018, p. 151) summarized the law as follows:

Nature as a whole contained a store of force . . . that could be neither Increased nor decreased; its total quantity was “eternal and unchangeable like the quantity of matter.”

A passage from its philosophical introduction (approximately 1 3/4 pages) may be seen in English translation in Fulton and Wilson (1966, pp. 22–24).

## Determining the Speed of Neural Conduction

On September 30, 1848, Helmholtz was released from his last 3 years of military service. He also abandoned the practice of medicine. On May 19, 1849, he was appointed Extraordinary Professor of Physiology at the University of Königsberg.

Johannes Müller believed that the speed of neural conduction was on the order of the speed of light and that it would never be measured. In his *Handbuch*, Müller cited sources for three possible speeds, the highest being 60 times the speed of light (Boring 1950, p. 41). This, presumably, supernatural speed for neural transmission and Müller’s belief that it could never be measured importantly influenced his belief in a “life force” (i.e., vitalism). On January 15, 1850, approximately 6 years after Müller’s prediction that the speed of nerve conduction was immeasurable, Helmholtz sent to du Bois-Reymond a short report: “On the Rate of Transmission of Excitation in Nerve.” Helmholtz also sent the report to Müller. Using a frog nerve-muscle preparation, Helmholtz had determined the speed of neural transmission to be on the order of 90 ft/s. Later, Helmholtz would find comparable results using sensory nerves.

## Vitalism’s Parallel in Psychology

In psychological science, most researchers show no hesitation in attributing “emergent properties” to phenomena being studied; such activity is now referred to as “emergentism.” The readiest example of emergentism is the reification of fictional concepts, for example, “stress caused her illness.” “Stress” can be neither a cause nor an effect (e.g., his impending final examination in calculus cause him “stress”) because “stress” is fictional in the

sense of having no material (i.e., chemical-physical) reference, a concept that merely names the condition it is purported to cause. It is far too common to reify such concepts in psychological research, and many examples could be cited easily. See related discussion of emergentism in animal cognition and the reification of concepts in the “► [Morgan’s Canon](#)” and “Müller, Johannes Peter” entries in this *Encyclopedia*.

## Helmholtz’s Other Academic Positions

After his years at the University of Königsberg, 1849–1855, Helmholtz relocated to the University of Bonn, 1855–1858, where he was Professor of Physiology and Anatomy. From 1858–1871, Helmholtz was Professor of Physiology at the University of Heidelberg, and from 1871 to 1888 he was Professor of Physics at the University of Berlin. At the time he was appointed to them, the Professorships in Physiology at Heidelberg and in Physics at Berlin were Germany’s most prestigious positions in those respective fields. Finally, Helmholtz served as Rector (President) of the Imperial Physico-Technical Institute in Charlottenburg from 1888 until his death in 1894.

## Additional Accomplishments by Helmholtz

Helmholtz had so many scientific accomplishments that only a few can be included here. It is reasonable to suggest that, had the Nobel prize existed before Helmholtz died in 1894 (the first Nobel Prizes were awarded in 1901), he likely would have qualified for at least two, one for having developed the law of conservation of energy and one for measuring the speed of neural transmission, both of which were supported by numerous experiments in his laboratory. Two other areas of accomplishment will be discussed here, namely, Helmholtz’s theoretical and experimental work in vision and audition, two fields to which his important contributions might also have qualified him for Nobel prizes.

### Helmholtz's Research in Vision

Perhaps, the first accomplishment to be mentioned is his 3-volume, *Handbuch der Physiologischen Optik: Vol. 1* (1856), *Vol. 2*, (1860), *Vol. 3* (1866) about which Boring in 1950 wrote, "It remains today a gospel in its field" (p. 302). The three volumes spanned physics, physiology, and psychology.

**Invention of the ophthalmoscope.** Helmholtz is recognized for inventing the ophthalmoscope, an instrument that enabled critical advancement in the study of visual optics. Helmholtz noted that Ernst Brücke had come within "a hair's breadth of the invention of the ophthalmoscope" (Helmholtz quoted in Cahan 2018, p. 96). Cahan (2018, p. 96) added:

It was only Brücke's failure to inquire about the return path followed by the light sent to the observed eye and how an optical image is formed in the observer's receiving eye that prevented him (in principle) from becoming the ophthalmoscope's inventor.

Helmholtz commented further that there were five to ten other German scientists:

... who doubtless would have performed in a completely logical way exactly the same as I if they had been put before the same tasks and under the same conditions. (Helmholtz quoted in Cahan 2018, p. 96)

It may be of interest to note that one of Helmholtz's primary motivations for inventing the ophthalmoscope was that he wanted a way to demonstrate the anatomy of the retina to his students.

Helmholtz formally published his invention of the ophthalmoscope in 1851. It was a handheld instrument designed to enable a physician or researcher to view the retina with focused illumination from the instrument and, in Helmholtz's time, with 20 times magnification. It remains an important instrument in the ophthalmologist's armamentarium, although many improvements have been made since Helmholtz's was introduced.

Next, Helmholtz turned his interest to the study of the accommodation of the lens of the eye and that led to his invention of the ophthalmometer

(1852) to calculate the curvatures of the cornea and lens from measurements of the sizes of images reflected on their surfaces.

### Color Vision

In 1801, British physicist Thomas Young lectured before the Royal Society of London "On the Theory of Light and Colours." The lecture was published as Young (1802). Drawing heavily on Isaac Newton and others, Young argued that sensitive points in the retina consisted of particles that undulate (Young preferred "undulate" to Newton's "vibrate") to provide the different sensations of color. For Young, red, yellow, and blue were primary, and other colors resulted from resonant undulations with the primaries.

Helmholtz rejected most of Young's theoretical foundations, but he embraced the general concept of Young's trichromatic theory of color vision. Helmholtz's contributions to the theory of color vision led others to label it the "Young-Helmholtz trichromatic theory of color vision." Young had not known of the cells of the retina, but Helmholtz (*Handbook of Physiological Optics Vol. 1*, 1856) distinguished among nerve fibers, ganglion cells, and rods and cones in the retina. However, the functional difference between rods and cones was determined later (1866) by Max Schultz who was Helmholtz's successor at the University of Bonn.

Through his psychophysical research, Helmholtz decided that cones reacted differently to different wavelengths of light, and he proposed three types of cones: (a) short-wavelength-preferring cones, blue; (b) middle-wavelength-preferring cones, green; and (c) long-wavelength-preferring cones, red. Technology was not yet sufficient to determine how the cones reacted differently to wavelength of light as measured with a diffraction grating. That would come nearly a century later with the identification of three types of cones containing chemicals within that varied in the range and peak wavelengths of light to which they best reacted, namely, cyanolabe (cyanopsin) for sensitivity to blue, chlorolabe (chloropsin) for sensitivity to green, and erythrolabe (erythopsin) for



sensitivity to red. It was a century later that George Wald was awarded the Nobel Prize in 1966 for his research on the absorption spectra of the photopigments in the rods and cones of the retina.

Helmholtz and others studying color vision relied almost exclusively on human experimentation with psychophysical data (biochemical and electrophysiological data were still far into the future). Ewald Hering reported results that the Young-Helmholtz trichromatic theory could not explain, and Hering proposed an opponent-process theory of color vision that could account for his psychophysical research findings.

**Christine Ladd-Franklin (1847–1930) and Helmholtz.** Ladd-Franklin's name does not appear in the three Helmholtz biographies used here, but she may have been the only American (certainly the only American woman) to spend time in Helmholtz's laboratory and in Ewald Hering's laboratory to study color vision. This occurred when she accompanied her husband, Fabian Franklin, a mathematician, on his sabbatical from Johns Hopkins University to Germany in 1891–1892. Ladd-Franklin had earned a PhD in mathematics and logic at Johns Hopkins in 1882. However, women were not recognized formally, and she did not receive her doctorate until 1926. After her research experiences in both Helmholtz's and Hering's laboratories, Ladd-Franklin became a self-identified psychologist.

Ladd-Franklin developed a theory of color vision intended to account for both Helmholtz's trichromatic and Hering's opponent-process theories and to supersede them (Kargon 2014). Ladd-Franklin's theory was first presented at the International Congress of Psychology in London (1892) in a session on color vision. That evening, Helmholtz was part of a private discussion where he spoke disparagingly of one of the contributions (not Ladd-Franklin's). Someone asked Helmholtz what he thought of Dr. Ladd-Franklin's color theory. Helmholtz replied, "Ach, Fran Franklin, die versteht die Sache" (*Oh, Fran Franklin, she understands the matter*, quoted by an unidentified writer in Ladd-Franklin 1929, p. 148). This author

has been unable to find a definition for "Fran" in German. There may have been a typographical error, and "Frau," "Mrs." in German, may have been intended.

### Helmholtz's Research in Audition

Helmholtz's research on phenomena associated with sound and hearing overlapped his research on light and vision. His single volume about hearing, *Die Lehre von den Toneempfindungen als physiologische Grundlage für die Theorie der Musik* (*On the Sensations of Tone as a Physiological Basis for the Theory of Music*), was published in 1863. It presented a "resonance-place theory" for how the ear processes sound; that is, he assumed that places along the basilar membrane of the cochlea resonated differently to frequencies of sound somewhat like the strings of a piano. Helmholtz's knowledge of the anatomy and physiology of the function of the cochlea did not have the benefit of more advanced technology later used by Georg von Békésy who received the Nobel Prize in 1961 for his research showing the vital role of the basilar and tectorial membranes and the hair cells of the cochlea in auditory processing of different sound frequencies. However, in von Békésy's Nobel address, he stated:

For me the most stimulating book on hearing was Helmholtz's *Die Lehre von den Toneempfindungen* . . . Helmholtz's method of viewing physiology and psychology in physical terms is today just as fresh as the day it was written. (von Békésy quoted in Muelders 2010, p. 154)

### Three of Helmholtz's Most Notable Protégés

Helmholtz had many notable protégés in physics, physiology, and psychology, but the three considered here were clearly among the most outstanding.

#### Physics

**Heinrich Rudolph Hertz (1857–1894).** Hertz was a devoted student perceived apparently by

Helmholtz to be a rising star, and Helmholtz was a devoted mentor. Hertz provided some insight regarding social interactions with Helmholtz. On one occasion Helmholtz and his wife Anna invited Hertz to tea. Anna was the easier conversationalist. Hertz described Helmholtz as:

... very charming ... but he speaks in such a slow and measured manner that, for me at least, it's impossible to keep one's attention on him, except when it's a matter of things in which every word must be weighed. Then, however, the conversation stops, since I don't want to put my opinion up against him. (Hertz quoted in Cahan 2018, p. 605)

Hertz was often invited to social events at the Helmholtz's, and, as time passed, such events became much more relaxed for Hertz.

As a mentor, Helmholtz supported Hertz's research fully, offering suggestions and guidance when useful but allowing Hertz the freedom to work as he preferred. Helmholtz saw to it that Hertz's research was well published and promoted. Related to Hertz's future accomplishments, Helmholtz was the most energetic German scientist in bringing James Clerk Maxwell's theoretical work on electromagnetism from Scotland to the Continent. Helmholtz arranged to have Maxwell's *Treatise on Electricity and Magnetism* (1873) translated into German, and Helmholtz encouraged Hertz to bring experimental proof to Maxwell's theory. After some strong but preliminary work on proving Maxwell's theory, in 1888 Hertz hesitantly asked Helmholtz's assistance in publishing his latest work in *Sitzungsberichte*, which was the publication for the proceedings of the Prussian Academy of Sciences:

Yet the work in question was Hertz's epochal experimental proof of the identity of electromagnetic and light waves, a work that Helmholtz called "absolutely genius." Helmholtz asked du Bois-Reymond to rush Hertz's manuscript into print in the academy's *Sitzungsberichte*; it appeared soon thereafter. (Cahan 2018, p. 609)

Hertz died relatively young at age 36, a result of surgeries associated with severe migraines that led to infection.

In 1930, in honor of Heinrich Hertz, the unit *hertz* (Hz) was established by the International

Electrotechnical Commission as the standard unit for *frequency*, that is, the number of times that a cyclical event occurs per unit of time, i.e., cycles per second (cps). In 1960, the unit, Hz, was adopted by the General Conference on Weights and Measures, and although acceptance of Hz to replace cps was slow initially, by 1970 Hz had essentially replaced cps.

### Neurobiology and Biophysics

**Julius Bernstein (1839–1917).** Bernstein earned his medical degree under Emil du Bois-Reymond's supervision at the University of Berlin in 1862 (Seyfarth 2006). Bernstein had succeeded Wilhelm Wundt (see below) as Helmholtz's assistant at the University of Heidelberg in 1864 and succeeded Helmholtz as Interim Head of Physiology when Helmholtz left the Chair in Physiology at Heidelberg in 1871 to become the Chair in Physics at the University of Berlin. This writer has seen relatively little about Helmholtz's and Bernstein's personal relationship, but from what is available, it is clear that Bernstein was appreciative of Helmholtz.

It was during his time as Helmholtz's assistant that Bernstein accomplished that for which he is best remembered, namely, being the first to record the action potential of neurons (1866). He was able to do so using a special instrument (the *differential rheotome*) that he designed and constructed. Much later (1902) Bernstein published his membrane theory (see Seyfarth 2006, pp. 5–7), which enabled an understanding of the electrochemical basis for the action potential. In 1912, Bernstein published a treatise titled *Elektrobiologie*, which Seyfarth (2006, p. 7) summarized as follows:

His treatise amounts to the first quantitative theory of nerve- and muscle action based on solid experiments, exact measurements, and biophysical models that finally led to a paradigm shift in the understanding and further investigation of bioelectrical processes.

Bernstein was the first Jewish Rector (President) of a German university (the University of Halle).

Although antisemitism was widespread, Seyfarth (2006) found no evidence to indicate any discrimination against Bernstein. Such was not the case for Bernstein's sons. In 1933 when the Nazis came into power, Bernstein's two sons who held university faculty positions, respectively, at the University of Halle and at the University of Göttingen, were dismissed from their positions, and they and their families were forced into exile.

## Psychology

**Wilhelm Wundt 1832–1920.** Wundt is well remembered as the founder of Experimental Psychology at the University of Leipzig in 1879, that being the year he was assigned half a building for his research laboratory. Educated as a physiologist, it was as Professor of Philosophy that Wundt went to Leipzig. As “Wilhelm Wundt” is the subject of another entry in this Encyclopedia, information about Wundt here will be limited mostly to his association with Hermann von Helmholtz.

While earning his doctorate in medicine at the University of Heidelberg in 1856, Wundt also spent a semester studying with Johannes Müller in Berlin. After receiving his doctorate, Wundt remained at Heidelberg as a Dozent (lecturer). In 1858 Helmholtz arrived at Heidelberg as the Chair in Physiology. Wundt became Helmholtz's assistant. Regarding Helmholtz's and Wundt's relationship, Boring (1950, p. 319) wrote:

Altogether there seems to have been respect and mutual admiration between Helmholtz, 11 years senior, and Wundt, the junior, but no great personal intimacy.

Helmholtz and Wundt overlapped at Heidelberg for 14 years, but when it involved their research, each preferred to work independently. Nevertheless, Cahan (2018, p. 253) wrote:

They had a good working relationship, though, and Wundt greatly admired Helmholtz. [Paragraph Break] Helmholtz for his part, had a quite positive view of Wundt both as a teacher and as a researcher . . . . [Paragraph Break] Helmholtz also tried to help Wundt get Heidelberg to name him Extraordinary Professor of anthropology and medical psychology in the Medical Faculty . . . . Wundt received the Extraordinary Professorship the following year.

Wundt hoped to succeed Helmholtz in Heidelberg's Chair in Physiology, but as noted above, that appointment went to Julius Bernstein. Wundt stayed on at Heidelberg until he accepted a position in Philosophy at the University of Zurich in 1874. By then, part 1 (1873) and part 2 (1874) of Wundt's *Grundzüge der physiologischen Psychologie* (*Textbook of Physiological Psychology*) were published, and Wundt was leading the effort to have Psychology recognized as an independent discipline.

Regarding Psychology as a discipline, Helmholtz's research over his career has been described as physics, physiology, and psychology, but he believed firmly that the scientific aspects of psychology belonged in physiology, and the rest of psychology belonged in philosophy. Interestingly, in 1868, Helmholtz had written to du Bois-Reymond that “Philosophy is, incidentally, a dreadful wasp's nest, which one should never touch” (Cahan 2018, p. 533).

## Closing Remarks

### Helmholtz's Wives

It would be remiss to fail to mention Helmholtz's wives, both of whom Helmholtz clearly loved and respected. He married Olga von Velton in 1849 and with her had two children. However, after several years of failing health, she died in December 1859. About a year later, Helmholtz met Anna von Mohl. Despite their age difference (Anna, 26; Helmholtz, 39), they quickly realized they would be a good match. They were married in May 1861, approximately 18 months after Olga's death. Some saw it as an insult to Olga's memory, but most friends and family saw it as a good marriage, in part, because Anna was happy to assume the care of Helmholtz's children. Helmholtz and Anna were also a close match intellectually, and he named her to be his Literary Executor following his death. That duty included finalizing some of his unpublished manuscripts.

### Helmholtz's Ill Fated Voyage to the United States

In 1892, the Reich government asked Helmholtz to represent Germany at the International Electrical Congress in August in Chicago, USA. Being in less than optimal health, Helmholtz resisted initially but eventually agreed. Also being much concerned about Helmholtz, Anna requested and received funds from Germany's Chancellor to accompany him. The trip lasted from early August to early October. They visited many of the famous tourist sites (e.g., the Rockies and Niagara Falls) and were hosted and honored at several major universities, especially Columbia University where one of Helmholtz's students was an influential ophthalmologist. On the voyage home, while Anna was resting in their cabin, Helmholtz fell down a long set of stairs. He retained consciousness but was conveyed to the more comfortable captain's cabin where, according to Anna, he was ably attended by the ship's doctor. Helmholtz resumed his duties in November as Rector at the Imperial Physico-Technical Institute in Charlottenburg, but he never fully recovered. He died on September 8, 1894. Anna died in 1899 at age 66.

### Honors and Awards

It is fitting to end this brief biography of Helmholtz by listing a few of his major awards and honors.

- 1873. He received The Order of Merit for the Arts and Sciences. The award was established by Frederick Wilhelm IV (King of Prussia from 1840 to 1861) in 1842 to honor extraordinarily distinguished persons, and it was intended to be Germany's highest civilian award.
- 1883. Helmholtz attained nobility (viz., the title "von") at the instigation of the Crown Prince and Princess. Hereafter, he would be Hermann von Helmholtz. Such a title placed Helmholtz above most of his fellow scientists which caused him some concern, but he realized he could not deny the benefits of nobility to his family and descendants.
- 1889, June 6. Helmholtz's statue in front of the main building at University of Humboldt was dedicated (see below).

- In Charlottenburg, Berlin, the street *Helmholtzstraße* is named after von Helmholtz.



Statue of Hermann von Helmholtz at the University of Humboldt

### Cross-References

- ▶ [Action Potentials](#)
- ▶ [Auditory Processing and Perception](#)
- ▶ [Auditory Signals](#)
- ▶ [Color Change](#)
- ▶ [Electromagnetic Fields](#)
- ▶ [Energy](#)
- ▶ [Neural Impulse](#)
- ▶ [Sensory Receptors](#)
- ▶ [Wilhelm Wundt](#)

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## Hermaphrodite

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## Synonyms

Alternative mating tactics; Dual sexuality; Sex changer

## Introduction

A hermaphrodite is an organism that possesses the reproductive organs of both sexes and can reproduce as either male (by producing sperm or pollen) or female (by producing ova). The term “hermaphrodite” has sometimes been used to refer to humans whose biological sex is ambiguous. This usage has fallen out of favor and in any case was technically incorrect. The essential characteristic of hermaphrodites is the ability to *reproduce* as both male and female. No such case has been identified in any human (Puts 2009).

## Types of Hermaphroditism

Hermaphrodites are divided into two categories: *simultaneous* and *sequential*. Simultaneous hermaphrodites are both male and female from the time of sexual maturity, whereas sequential hermaphrodites switch sexes one or more times during the lifespan. Sequential hermaphroditism is further divided into *protandry*, in which individuals mature as males and later change into females, and *protogyny*, in which females become males. In species with *bi-directional sex change*, individuals may begin as either male or female and subsequently switch to the opposite sex. *Serial sex changers* can change sexes more than once (Avisé 2011). In contrast to hermaphrodites, *gonochorous* organisms, such as most mammals, possess the reproductive organs of only one sex throughout the lifetime.

The overwhelming majority of animal mating systems are either *dioecious* (in which all individuals are gonochorous) or hermaphroditic (all individuals are hermaphrodites). *Androdioecy*, by contrast, is a rare mating system in which males and simultaneous hermaphrodites of the same species coexist. Cases of gynodioecy, in which breeding groups are made up of females and simultaneous hermaphrodites, are even less common but are found in some angiosperm plant species (Bawa 1980). Among simultaneous hermaphrodites, *self-fertilization* is possible and is common in some (mostly plant) species, whereas it is totally absent in others, such as several simultaneously hermaphroditic fish.

## Examples of Hermaphroditism

Examples of simultaneous hermaphrodites include most (80%) angiosperm flowering plants (Willmer 2011), approximately 25 fish species (Avisé 2011), and all oligochaetes (a class of animals that includes earthworms; Purves 2004). Approximately 250 (1%) of the world's teleost (bony) fish species are hermaphroditic. The vast majority of these are sequential and protogynous hermaphrodites, although there are also cases of protandry, bi-directional sex change, and simultaneous hermaphroditism. Among hermaphroditic invertebrates, most species are simultaneous hermaphrodites, but at least 15 classes, including the limpets (class Gastropoda), are primarily



protandrous. Several species of corral-dwelling gobies (fish in family Gobiidae) express serial, bi-directional hermaphroditism, starting as either males or females and switching sexes one or more times throughout life (Avisé 2011).

### Evolution of Hermaphroditism

Several potential explanations for the evolution (via natural selection) of hermaphroditism have been advanced. Because sequential and simultaneous hermaphroditism each comes with its own set of reproductive and energetic costs and benefits, no single adaptive explanation will suffice, but all such explanations have one thing in common: Sex change is adaptive if it increases individual reproductive success.

The *size-advantage hypothesis* posits that sequential hermaphrodites begin as members of the sex with higher reproductive potential at small sizes and switch to the opposite sex when they have attained a body size at which the that sex's potential reproductive success is higher (Munday et al. 2006). The *risk-of-movement hypothesis* has been proposed to account for the evolution of serial bi-directional sex change in several species of fish. It posits that in sparsely distributed species with high predation risk, individuals change sex in order to avoid risky mate searching when mates of the same, but not the opposite, sex are available in the immediate home range (Avisé 2011). Finally, a prominent explanation for the evolution of simultaneous hermaphroditism is the *low-density model*. This model suggests that when organisms live at low population densities, encounters with members of the opposite sex may be extremely infrequent but can be doubled if each individual possesses the reproductive organs of both sexes (Ghiselin 1969).

### Cross-References

- [Alternative Reproductive Tactics](#)
- [Gametes](#)
- [Mating](#)
- [Ova](#)
- [Sex ratio](#)
- [Sex Role Reversal](#)

- [Sexual Selection](#)
- [Sperm Competition](#)

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## Heterogametic

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### Synonyms

[Heterozygous chromosomes](#)

### Definition

Heterogametic means nonuniform distribution of sex-chromosomes in an organism.

## Heterogametic

Heterogametic describes presence of different types of sex chromosomes in an organism. Heterozygosity is mostly associated with sex

chromosomes than autosomes and plays a key role in sex-determination among organisms. For example, in case of human beings, XY chromosomes define a male sex while XX chromosome represents a female sex. Sex chromosomes are present as single copy in an organism and complement the gene product quantity through dosage compensation or the meiotic silencing (Forsdyke 2000; Johnson and Lachance 2012). Sex chromosomes show strong impact of evolutionary processes (mutation, selection, genetic drift, and meiotic drive) and play an important role in natural phenomena like hybrid incompatibility and speciation. Besides animals and birds, heterogametic chromosomes are occasionally observed in plants also (Johnson and Lachance 2012).

Sex chromosome systems vary considerably. In some organisms, as in mammals and many insects, the males are heterogametic (have two different sex chromosomes) and females are homogametic (have two of the same sex chromosome) (Ellegren 2011). In others, such as birds and butterflies, females are heterogametic and males are homogametic.

Because of varied chromosomes, the modes for sex determination are also different in all organisms. The method used for determination of sex helps to understand the evolution of heterogametic nature in different sexes. Like in the Protenor mode of sex determination as XO and the Lygaeus mode of sex determination as XY. In some species like chickens and in moths, the heterogametic sex chromosomes exist in the female. The distribution of chromosomes does affect the fertility of these organisms; like in case of birds and Lepidopterans, females (also known to be heterogametic) are more often inviable or sterile, while in the mammals the heterogametic males are more often affected (Vicoso and Charlesworth 2006; Turner 2007).

It is suggested that presence of heterogametic sex chromosomes could be due to inviability or sexual transformation. Haldane's rule also supports heterogametic nature of chromosomes.

As said above female heterogamety is also prevalent in many organisms including birds, reptiles, amphibians, fishes, crustaceans, and moths and butterflies. Among these also, birds, moths,

and butterflies are known to consistently follow heterogamety through many generations while in case of moths and butterflies only a small minority works this way.

Other than male and female, heterogametic nature of sex chromosomes is also dependent on environment factors – environmental sex determination. For example, in case of birds, Z and W chromosomes are largely homologous in all species. In Lepidoptera, data from a limited number of species suggest that the Z chromosome has retained conserved synteny across the whole group. Moreover, female heterogamety is also found in caddis flies (Trichoptera), the sister group to moths and butterflies, suggesting that their sex chromosomes had already started to evolve in a common ancestor of Lepidoptera and Trichoptera more than 190 million years ago (Malcom and Wyckoff 2003; Ellegren 2011; Forsdyke 2000). Various factors involved in causing heterogametic nature of sex chromosomes are:

### Mutation

The mutation rate is usually much higher in males than in females because developing male gametes usually undergo many more rounds of replication than do female gametes.

### Random Genetic Drift

Sex chromosomes and autosomes also experience differential effects from random genetic drift.

### Selection

Various forms of selection such as sexual antagonism influence the differential evolution of sex chromosomes and autosomes.

### Female Heterogametic Systems

Birds and snakes are the two major vertebrate groups with ZZ/ZW sex chromosomes (i.e., females are heterogametic).

### Cross-References

- [Alleles](#)
- [Chromatid](#)

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## Heterogamy

- [Assortative Mating](#)

## *Heterohyrax brucei*

- [Hyracoidea](#)

## Heterosis

- [Hybrid Vigor](#)
- [Inversion Effects](#)

## Heterospecific Group

- [Polyspecific Associations](#)

## Heterothermy

- [Hibernation](#)

## Heterotroph

- [Omnivore](#)

## Heterozygote Advantage

- [Heterozygote Superiority](#)

## Heterozygote Superiority

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## Synonyms

[Heterozygote advantage](#); [overdominance](#)

## Definition

Heterozygote superiority (heterozygous advantage) is the case or state in which the heterozygous genotype has a higher relative fitness due to the overdominance in contrast to homozygous dominant or homozygous recessive genotype.

## Introduction

The term heterozygote superiority was first proposed by Fisher in 1923. The phrase heterozygote advantage is often used as a synonym for heterozygote superiority. Heterozygote superiority (heterozygous advantage) describes the case in which the heterozygous genotype has a higher relative fitness than either the homozygous dominant or homozygous recessive genotype.

In population studies, mean fitness of heterozygotes is higher than the mean fitness of all homozygotes, but in laboratory studies and evolutionary models, heterozygotes are superior to both parental homozygotes. Heterozygote superiority is fascinating because it is mysterious that why seemingly harmful mutations like those causing fatal diseases still exist in populations today which should be eliminated by natural selection. It might be possible that some form of balancing and diversifying selection is operating consistently over long periods of evolutionary time. Genetic variations in natural populations as well as heterosis or hybrid vigor are the ultimate results of heterozygote superiority because heterozygote superiority, or heterozygote advantage, play very important role in maintenance of variations in population by selection.t

Gillespie Model

Before Gillespie model, it was believed that reason behind the heterozygote superiority was complementation (or dominance) or the masking of deleterious recessive alleles by wild-type alleles, but Gillespie model in the year 1974 revealed that the main cause behind heterozygote superiority is overdominance. Population geneticist John H. Gillespie established the following model:

|                   |      |      |      |
|-------------------|------|------|------|
| Genotype:         | A1A1 | A1A2 | A2A2 |
| Relative fitness: | 1    | 1-hs | 1-s  |

where h is the heterozygote effect and s is the recessive allele effect. Thus, given a value for s (i.e.,  $0 < s < 1$ ), h can yield the following information:

- h = 0: A1 dominant, A2 recessive
- h = 1: A2 dominant, A1 recessive
- $0 < h < 1$ : incomplete dominance
- h < 0: overdominance
- h > 1: underdominance

The case  $h < 0$  in the Gillespie model is the possible explanation for the case of heterozygote superiority.

Elemental Force Behind the Heterozygote Superiority

Heterozygote superiority necessarily involves some combination of the major evolutionary processes: mutation, genetic drift, and natural selection. We will consider each of these in turn.

Mutation

One possible explanation for a high frequency of deleterious alleles at a particular locus is that the gene in question has a particularly high mutation rate (Valles 2010). However, some mutations that are associated with disease have been found only rarely, and the known pattern of allelic variation across the gene was not suggestive of a particularly high mutation rate. Additionally, if the mutation rate of the gene was extraordinarily high, it would be difficult to explain why the frequency of disease is high only in specific area.

Genetic Drift

Wright and Morton (1968) argued that while it was very unlikely for a recessive lethal allele to drift to as high frequency, there are thousands of potential lethal mutations across the genome. Most researchers have a rejected the possibility of genetic drift as responsible for the observed incidence of heterozygote superiority because in most of the cases of disease, population has been too large or too long for drift to be a plausible explanation.

Natural Selection

Natural selection has historically acted very strongly against mutations in homozygotes. Role of selection in developing and maintaining the high frequency of mutated alleles must therefore be through some advantage to heterozygotes with one mutated allele and one fully-functional allele. Thus, this is clear that the natural selection plays very important role in heterozygote superiority.

All the factors which have been discussed above might contribute synergistically for the heterozygote superiority.

## Evidences in Favor of Heterozygote Superiority

Numerous cases of heterozygote superiority have been demonstrated in several organisms, including humans. The first experimental confirmation of heterozygote superiority was with *Drosophila melanogaster*, a fruit fly that has been a model organism for genetic research. However, most of the examples of heterozygote superiority are associated with disease resistance and are maintained only in the presence of disease or other gene–environment interaction.

### Sickle-Cell Anemia

Sickle-cell anemia (SCA) is a genetic disorder caused by the presence of two incompletely recessive alleles. When a sufferer's red blood cells are exposed to low-oxygen conditions, the cells lose their healthy round shape and become sickle-shaped. This deformation of the cells can cause them to become lodged in capillaries, depriving other parts of the body of sufficient oxygen. The genetic disorder is incompletely recessive; a person with only one SCA allele and one unaffected allele will have a “mixed” phenotype: The sufferer will not experience the ill effects of the disease, yet will still possess a sickle cell trait, whereby some of the red blood cells undergo benign effects of SCA, but nothing severe enough to be harmful. However, convincing evidence indicates, in areas with persistent malaria outbreaks, individuals with the heterozygous state have a distinct advantage (and this is why individuals with heterozygous alleles are far more common in these areas). There were selective advantages because if there were no selective advantage to the recessive allele, we would expect it to slowly be removed from the gene pool, and the frequency of individuals with sickle cell disease should approximate the mutation rate of the normal A allele to the S allele, which is extremely rare. Heterozygote AS is resistant to the malarial parasite *Plasmodium falciparum*, so copies of the S allele are lost from the gene pool when they occur in individuals affected with sickle cell disease since they do not reproduce, but more copies are created in the offspring of AS individuals. The heterozygote

advantage of the sickle-cell gene is context-dependent and depends on the frequency of the protozoan parasite in the population, outside malaria-infested areas. In this instance, the state of the organism's environment will provide selection, with a net effect either favoring or working in opposition to the gene, until an environmentally determined equilibrium is reached. Thus, heterozygote superiority in case of sickle cell anemia is a perfect example of GxE.

### Cystic Fibrosis

Cystic fibrosis (CF) is an autosomal recessive hereditary monogenic disease of the lungs, sweat glands, and digestive system. The disorder is caused by the malfunction of the CFTR protein, which controls transport of chloride ions, which is vital to maintaining equilibrium of water in the body. The malfunctioning protein causes formation of viscous mucus in the lungs and intestinal tract. Earlier, children born with CF would have a life expectancy of only a few years.

The presence of a single CF mutation may influence survival of people affected by diseases involving loss of body fluid, typically due to diarrhea because the heterozygote had less secretory diarrhea than normal, homozygote. Thus, it appeared that resistance to cholera explained the selective advantage or heterozygote superiority to being a carrier for CF.

Another theory for the prevalence of the CF mutation is that it provides resistance to tuberculosis. Thus, CF heterozygotes affected the survival of typhoid fever, secretory diarrhea (including cholera), and tuberculosis (Valles, 2010).

### Triose Phosphate Isomerase

Triose phosphate isomerase (TPI) is a central enzyme of glycolysis, the main pathway for cells to obtain energy by metabolizing sugars. In humans, certain mutations within this enzyme, which affect the dimerization of this protein, are causal for a rare disease, triose phosphate isomerase deficiency. Other mutations, which inactivate the enzyme (= null alleles), are lethal when inherited homozygously (two defective copies of the TPI gene), but have no obvious effect in



heterozygotes (one defective and one normal copy). However, the frequency of heterozygous null alleles is much higher than expected, indicating a heterozygous advantage for TPI null alleles.

### Resistance to Hepatitis C Virus Infection

There is evidence that genetic heterozygosity in humans provides increased resistance to certain viral infections. A significantly lower proportion of HLA-DRB1 heterozygosity exists among HCV-infected cases than uninfected cases. These statements constitute evidence that heterozygosity provides an advantage among carriers of different supertype HLA-DRB1 alleles against HCV infection progression to end-stage liver disease in a large-scale, long-term study population (Hraber et al. 2007).

### MHC Heterozygosity and Human Scent Preferences

Females prefer the scent of males who are heterozygous at all three MHC loci. However, it has been argued that heterozygosity at MHC loci results in more alleles to fight against a wider variety of diseases; possibly increasing survival rates against a wider range of infectious diseases because heterozygosity enhanced their health and survival rates against multiple-strain infections. Heterozygote individuals can have higher fitness (heterozygote superiority) due to higher resistance to multiple parasites (Hedrick, 2012). MHC heterozygotes are expected to be superior to both homozygotes because they can present a wider variety of peptide antigens to T lymphocytes, the triggering event of the adaptive immune response. Heterozygote superiority is expected to emerge after serial or simultaneous coinfections when resistance is dominant and the susceptibility profiles of two pathogens are opposite or reciprocal (Potts and Slev 1995). We will refer to this as the dual infection heterozygote superiority (DIHS) hypothesis because when animals are infected with two pathogens that show opposite susceptibility profiles, heterozygotes are found to be superior, whereas when animals are infected with two pathogens that show similar susceptibility profiles, heterozygotes are predicted to be intermediate.

### BAFF and Autoimmune Disease

B-cell activating factor (BAFF) is a cytokine encoded by the TNFSF13B gene. A variant of the gene containing a deletion (GCTGT→A) renders a shorter mRNA transcript that escapes degradation by microRNA, thus increasing expression of BAFF, which consequently upregulates the humoral immune response. This variant is associated with systemic lupus erythematosus and multiple sclerosis, but heterozygote individuals have decreased susceptibility to malaria infection (Steri et al. 2017).

### Livestock and Pets

There are a number of mutants in livestock and pets that have heterozygote superiority because of artificial selection for these mutants in heterozygotes and strong detrimental effects from natural selection in homozygotes. In livestock, these mutants include ones that influence milk yield in dairy cattle, fecundity in sheep, litter size in pigs, muscling in beef cattle, color in horses, lean meat content in pigs, and comb morphology in chickens. In pets, these mutants include ones that influence tail length in cats and hairlessness, muscling, color, or ridgeback hair in dogs.

### Other Examples

The allelic trichromacy of long-to-middle wave sensitive (L/M) opsins in New World monkeys is a good example of heterozygote superiority (Hiwatashi et al. 2010). As trichromatic females in a population of wild white-faced capuchins (*Cebus capucinus*) are more accurate in selecting ripe, reddish fruits than are males or dichromatic females. Females heterozygous for the L/M opsin are capable of trichromatic vision, whereas the remaining homozygous females and all males are dichromatic.

The fertility polymorphisms documented in BMP15 and GDF9 also represent one of the best examples of heterozygote superiority yet described, with the genetic basis, fitness differentials, and the mechanism of selection well understood (Hanrahan et al. 2004).

21-hydroxylase deficiency is an autosomal recessive disorder due to mutations in the 21-hydroxylase gene (CYP21) located on the

short arm of chromosome 6 where it lies in close proximity to a nonfunctional pseudogene (CYP21P). In affected homozygotes, decreased adrenal 21-hydroxylase activity interferes with cortisol and aldosterone biosynthesis, adrenal androgen biosynthetic pathway intact, but there is a survival advantage to 21-hydroxylase heterozygotes as adrenal gland of heterozygotic carriers would be upregulated or primed to secrete cortisol, because the clinically imperceptible decrease in cortisol secretion had led to increased ACTH secretion.

## Conclusion

Even after many decades, it is hard to portray about heterozygote superiority as it is an important and very diplomatic phenomenon in biology because as a coin has positive and negative both, heterozygous superiority is also the case of the negative positive genetics as heterozygote superiority is the case where the heterozygote carries both advantages and disadvantages, while both homozygotes carry a disadvantage. For example, heterozygotes of flowering plants will provide high yield and may show high vigor with pest resistance to disease tolerant, but on negative sides, if heterozygosity increases in case of plants, it will increase infection rate, host invasion, lethality, and drug resistance, even these heterozygotes show high survival rate and eco-climatically adapted.

## Cross-References

- [Balancing Selection](#)
- [Heterosis](#)
- [Inbreeding Depression](#)
- [Overdominance](#)

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## Heterozygous Chromosomes

- [Heterogametic](#)

## Hibernation

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## Synonyms

[Endotherms](#); [Heterothermy](#); [Hypometabolism](#); [Multiday torpor](#); [Physiology](#)

## Definition

Hibernation is a physiological mechanism used by heterothermic animals to conserve energy. It is a process classically categorized by lowering one's metabolic rate or heart rate, reducing body temperature, and regulating oxygen consumption. The intensity of these processes varies between taxa and can fluctuate from daily to multiday torpor (hibernation).

## Introduction

Endotherms have high energy requirements and maintain their core body temperature ( $T_b$ ) by means of heat production. Maintaining  $T_b$  in itself is energetically costly but is required for proper cell function, reproduction, and behavioral efficiency (Geiser 2013; Martin 2001). Endothermic animals regularly exhibit what is called hypometabolism during periods of inactivity, where an individual lowers their normal metabolic rate by an average of 20% and most often in conjunction with lowering  $T_b$  by  $\sim 2^\circ\text{C}$  (Heldmaier et al. 2004). Heterothermic animals are endotherms with the capacity to adjust their body temperature to their environment, well below this threshold.

Endothermy is understood to have evolved independently twice, once in birds and once in mammals. Birds and mammals originate from distinct reptilian lineages, with bird endothermy having evolved much later than in mammals. Heterothermy is a primitive trait of pre-mammals, with an original purpose to cope with low metabolism. Now, scientists suggest hibernators use heterothermy as a method of conserving energy. Thus, an increased metabolic rate in extant mammals would be an adaptation for conserving energy (Rial et al. 2010).

Due to a larger surface area (relative to body size), smaller animals experience more heat loss and are more affected by seasonal and climatic changes in their environment. These animals are more likely to be heterothermic, in order to cope with such energetic challenges. In environments with extreme climates or seasonal stressors (i.e.,

when resources are scarce), heterothermic animals can conserve energy by using a prolonged period of hypometabolism, such as torpor (Geiser 2004; Ruf and Geiser 2015). Torpor is a state of lethargy where an organism notably lowers its metabolic rate, core  $T_b$ , heart rate, and oxygen. Animals that use this mechanism vary from levels of daily torpor (often referred to as daily heterothermy) to multiday torpor (hibernation). In regard to endothermic animals, torpor and hibernation are the most effective methods for conserving energy in demanding environments (Geiser 2013).

Daily heterotherms will enter a torpid state for a few hours during a part of the day and at a lesser degree – most frequently defined as animals lowering their body temperatures below  $\sim 30^\circ\text{C}$ , but not lower than  $15^\circ\text{C}$ . Hibernators, on the other hand, will remain torpid for multiple days or an entire season and are characteristic of lowering their  $T_b$  well below  $15^\circ\text{C}$ , closer to  $5^\circ\text{C}$  (deep or “true” hibernation).

## The Process of Hibernation

During the process of hibernation, an individual reduces their metabolic rate to a fraction of their basal metabolic rate, while lowering their body temperature well below normothermia. Normothermia is the condition where an individual is within their normal body temperature range, which for birds and mammal is around  $37^\circ\text{C}$  (Heldmaier et al. 2004). Hibernators rely heavily on metabolic inhibitions in addition to  $T_b$  adjustments to reduce their metabolic rate, whereas daily heterotherms can rely more on  $T_b$  to lower their metabolic rate (Geiser 2004).

Hibernators often adjust into a specific body posture when they become torpid, similar to the posture they enter for natural sleep (Lyman et al. 1982). In this posture, the animal will position the back to an insulating material or structure, such as a nest, tree hole, or burrow. Tucking the head under the chest keeps the heart warmer than the body when an animal lowers its  $T_b$ . This posture helps to maintain optimal thermal comfort while minimizing any sudden changes in ambient

temperatures during hibernation that might disrupt the process. To further decrease exposure of body surface, some species hibernate in groups or huddled together – this is often referred to as “social thermoregulation” (Bright and Morris 1991; Lyman et al. 1982; Masing and Lutsar 2007; Mueller 1999).

Throughout the process of hibernation, an animal will go through periodic arousals where they self-generate heat, a process called euthermy, to increase their body temperature gradually toward normothermy. Sporadic arousal within torpor (inter-bout arousal) is the greatest energy expenditure of the entire hibernation process (Thomas et al. 1990).

As arousal is an energetically costly process, some animals save energy by the use of behavioral thermoregulation, such as sun-basking, or the use of postural and locomotion adjustments that help to conserve and generate heat (Whittow 2013). Basking behavior is frequently used by species with a low metabolic rate, such as marsupials. In addition to being an energy-saving method, basking also saves time, decreasing the amount of time spent in arousal (Geiser 2004).

After complete arousal at the end of a hibernation bout, an animal will begin semi-passive behavior, exploring and assessing its surrounding environment. This behavior is known as risk assessment behavior (RAB), where the animal assesses the safety of their surroundings (e.g., predators, competitors, resource availability) with vigilance and scanning. After RAB, an animal will begin what is called goal-directed behavior. Goal-directed behavior can range from foraging to searching for mates to locating a safe place of rest (Cooper et al. 2003).

## Hibernators

As technology improves, physiological research in the field has expanded our abilities to understand better the processes of torpor and hibernation in wild animals. Species that were previously unknown to be heterothermic were studied extensively in captivity. Expanding research in the field has brought us to learn that some species use

torpor regularly in the wild or only in response to extreme environmental changes (Geiser 2013). Animals that are capable of daily torpor include birds, bats, and various species of mammal. Less species are known to use the extreme process of hibernation, including only one known species of bird, insectivorous bats, and a handful of mammals, discussed below.

### Birds

Birds display a greater level of hypometabolism in their inactivity phase, where they are capable of regularly decreasing their metabolic rate by 30% and lower their  $T_b$  by 4 °C (Heldmaier et al. 2004). The common poorwill *Phalaenoptilus nuttallii* is the only bird species known to hibernate (Woods and Brigham 2004). Other birds (i.e., hummingbirds and the tawny frogmouth *Podargus strigoides*) are known to be daily heterotherms but do not enter a torpid state long or deep enough to be considered hibernators (Geiser 2013).

### Chiroptera

Only the insectivorous (insect eating) bats are known to use hibernation, whereas the frugivorous (fruit eating) bats have only been found to use daily heterothermy. Insectivorous bats fall within the genus *Chiroptera* with known hibernating species being *Barbastella barbastellus*, *Eptesicus fuscus*, *Myotis lucifugus*, *M. myotis*, *Nyctalus noctula*, *Nyctophilus geoffroyi*, *N. gouldi*, *Pipistrellus pipistrellus*, and *Tadarida brasiliensis*.

### Mammalia

#### Monotremata

The short-beaked echidna, *Tachyglossus aculeatus*, is the only monotreme species known to hibernate (Lyman et al. 1982). This species maintains a normothermic average of 32.2 °C, with the lowest recorded  $T_b$  of 4 °C, and will most often arouse from hibernation for mating (Geiser 2004).

#### Marsupialia

Marsupials are unique among the hibernators. Marsupials began as poikilotherms, which later evolved into homeothermy followed by

heterothermy. This means the physiological ability to withstand cold temperatures is plesiomorphic (Rial et al. 2010). There are currently four known hibernating marsupials, belonging to the genera *Acrobates*, *Burramys*, *Cercartetus*, and *Eudromicia*. *Acrobates pygmaeus*, the feathertail glider, is a species that uses both torpor and hibernation, depending on the environmental stressors, namely, ambient temperatures. They are true hibernators based on the degree to which they lower their body temperature and metabolic rate; however, they do not perform pre-hibernation fattening as many species do (Geiser 1994). The marsupial mountain pygmy possum, *Burramys parvus*, is a seasonal hibernator, ranging in high altitude mountains. The eastern pygmy possum *Cercartetus nanus* can enter hibernation for up to five weeks during any time of the year, with a body temperature as low as 1–6 °C (Geiser 1994). The little pygmy possum *Eudromicia lepidia* has been observed to enter multiday torpor for a total of 12 days (Bartholomew and Hudson 1962).

#### Placentalia

The state of hibernation in placental mammals is entered through a process of sleep called slow-wave sleep (SWS). Of the mammalian subgroups, placentals have the most hibernators. Rodents have been studied, arguably, most thoroughly of all the placental hibernators. This is largely due to the convenience of studying them in captivity, their small body size, and the variations discovered between species of Rodentia. There are many species of rodent that use hibernation and so have been a large focus for understanding the mechanisms and interpretation of thermoregulation by animals (Whittow 2013).

The Arctic ground squirrel *Spermophilus parryii* is especially unique, as it can lower its body temperature below freezing, to –2.9 °C (Barnes 1989). The golden-mantled ground squirrel (*Callospermophilus lateralis*) has been recorded to enter hibernation for as long as 16 consecutive days (Pengelley and Fisher 1961). Due to the large quantity of hibernating rodents, here we note a few of the most notable: *Eliomys quercinus*, *Glis glis*, *Marmota flaviventris*, *M. marmota*,

*M. monax*, *Mesocricetus auratus*, *Spermophilus lateralis*, *S. tereticaudus*, *S. mexicanus*, *S. citellus*, *S. saturatus*, *S. mohavensis*, *S. richardsonii*, *S. parryii*, *Tamias amoenus*, *T. striatus*, *Zapus hudsonicus*, and *Z. princeps*.

Aside from rodents, placental hibernators range very diversely in body mass from the small insectivores, such as shrews, to as large carnivores, such as bears. A handful of elephant shrews are known to be short-term hibernators, including Cape rock elephant shrew *Elephantulus edwardii*, *E. rozeti*, and *E. myurus*. The common tenrec *Tenrec ecaudatus* is an insectivore endemic to the island of Madagascar. This species can hibernate for up to 9 months of the year (most commonly during the austral winter) and is unique among mammalian hibernators in their lack of displayed inter-bout arousal (Lovegrove et al. 2014). Hibernating hedgehogs including the European hedgehog *Erinaceus europaeus* can lower their body temperature to as low as 2 °C. There is one species of armadillo that is known to hibernate, the pichis *Zaedyus pichi*. This species uses both hibernations during the cold winter season and daily heterothermy during the non-hibernating season (McNab 1980).

Of the Primates, only two species are so far known to be hibernators, the Western fat-tailed dwarf lemur *Cheirogaleus medius* and the pygmy slow loris *Nycticebus pygmaeus*. Other species are known to use daily torpor, including *Microcebus murinus* and *Galago moholi* (Nowack et al. 2013).

Bears (black bear *Ursus americanus*, grizzly bear *Ursus arctos horribilis*) and badgers (e.g., Japanese badger *Meles anakuma*) are not true hibernators, but rather experience shallow hibernation. While bears display all of the characteristics of a true hibernator, such as seasonal hibernation and storing fat pre-hibernation, they only lower their body temperature by a few degrees.

## Sleep and Hibernation

The state of hibernation is entered and exited through slow-wave sleep (SWS), which is also



known as non-rapid eye movement or NREM (Rial et al. 2010). Because of this transition, hibernation and sleep were considered to be related physiological states, with hibernating individuals achieving both energy conservation and sleep benefits simultaneously (Walker and Berger 1980). Recently, however, neuroscientists have discovered that hibernation and sleep may be distinct physiological states, with hibernation preventing the entering of REM (rapid eye movement) or complete restorative sleep.

Most often, an arousing hibernator will locate a safe resting place to return to slow-wave sleep, where they display sleep rebounds. Sleep rebound has been observed to be more intense with a greater drop in  $T_b$  during hibernation, suggesting hibernating individuals are experiencing sleep deprivation (Rial et al. 2010). While sleep rebound is not displayed in all hibernating species, it is most prominently observed in mammals, unsurprisingly, as they require adequate sleep for physiological and cognitive functions. While inter-bout arousal throughout the hibernation process is still largely unknown, some researchers suggest this too may be correlated to sleep rebound, and animals are regularly exiting hibernation to experience brief sleep rebounds.

Furthermore, only birds and mammals are known as true sleepers, while reptiles and other animals only experience rest. This is largely due to their distinct physiological changes, as well as presence of different sleep stages. However, animals considered to only rest have displayed a rest rebound, similarly to sleep rebound in birds and mammals (Rial et al. 2010).

## Cross-References

- Arousal
- Biological Rhythms
- Energy
- Environmental Influences
- Huddling
- Thermoregulation
- Torpor

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## Hidden Humans

### ► Turing Test

## Hippocampus

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### Definition

The hippocampus (from the Greek “seahorse”) is a brain structure located in the medial temporal

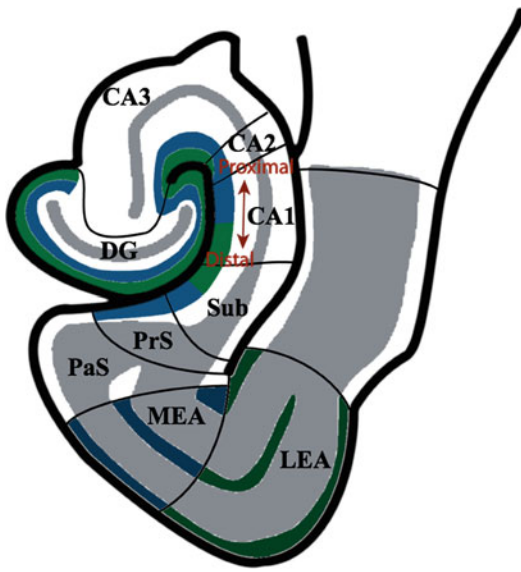
lobe that is primarily responsible for mapping spatial relations, temporal sequence information, and the formation of episodic memories.

### Introduction

The hippocampus (from the Greek “seahorse”) is a brain structure located in the medial temporal lobe that is primarily responsible for mapping spatial relations and the formation of episodic memories. The hippocampus is commonly described as being made up of the cornu ammonis (divided into sub regions CA1, CA2, CA3) and dentate gyrus. The “hippocampal formation” may also include the subiculum, parasubiculum, pre-subiculum, and entorhinal cortex (See Fig. 1). The hippocampus’ main computational functions are thought to involve pattern separation, pattern completion, and distributing new memories to cortex via memory consolidation (McNaughton and Morris 1987). Spatial theories of hippocampal function argue that its neurons form an allocentric spatial map that tracks an animal’s position and movement through space, allowing for the computation of online spatial relations like shortcuts. Theories of hippocampus suggest that it is central to relational or episodic memory that link together temporal, perceptual, spatial, and contextual information into unique events and common elements (Ergorul and Eichenbaum 2004).

### Historical Developments

In 1547, the hippocampus was first described by Julius Caesar Aranzi, a Venetian anatomist who compared the shape of the structure to both a silk worm and a sea horse. Vicq d’Azyr made a distinction between the hippocampus major and minor (now identified as the calcar avis). In 1742, De Garengeot chose the term cornu ammonis (CA) to describe the region, which invoked the ancient Greek God Ammon (related to the Egyptian God Amun), who is often represented as possessing the horns of a ram (Falougy and Benuska 2006).



**Hippocampus, Fig. 1** The hippocampal formation including the cornu ammonis subregion (CA1, CA2, CA3), dentate gyrus (DG), subiculum (Sub), presubiculum (PrS), parasubiculum (PaS), and lateral (LEA) and medial (MEA) entorhinal area (Permission granted by Lara Rangel and Jon Rueckemann)

In the early days of evolutionary theory, surrounding the publication of Darwin's *On the Origin of Species*, there was a public debacle known as the Great Hippocampus Question. In 1857, Richard Owen suggested that the hippocampus minor (now classified as the calcar avis) was unique to humans, and that it was not present in monkeys. In 1858, Thomas Henry Huxley (affectionately known as Darwin's Bulldog) grew irritated and systematically dissected multiple monkeys to collect evidence against Owen's case. Huxley and Owen's debate became public in 1860 at a debate on evolution at Oxford University, culminating in a heated series of lectures and publications between Owen and Huxley, eventually leading to Owen's more systematic refutation by William Henry Flower in 1862. The "Great Hippopotamus Test" was immortalized in Victorian culture in 1862 by Charles Kingsley who published a children's book *The Water-Babies, A Fairy Tale for a Land Baby* satirizing the incident. By 1866, Owen had retracted his previous statements about monkeys lacking this structure

and admitted his mistaken view in his book *On The Anatomy of Vertebrates* (Gross 1993).

In 1873, Golgi developed a new method of using silver staining techniques to uncover the structure of the axons, cell bodies, and dendrites of neurons. Ramon y Cajal (1911) perfected Golgi's method and used this method to study the connectivity of individual neurons in hippocampus. In 1934, Cajal's student Lorente de No provided the anatomical descriptions of the CA regions that are widely accepted today (Falougy and Benuska 2006). In 1937, Papez proposed that emotional experience was rooted in connectivity between the hypothalamus and medial temporal areas. Building on Papez's theory, (MacLean 1949) suggested that the hippocampus along with the amygdala, septum, and hypothalamus was part of the "visceral brain" or "limbic system" which was primarily recruited for the generation of emotional experiences.

In the 1950s, the Montreal Neurology Group lead by Wilder Penfield searched for the mechanistic origins of temporal lobe epilepsy (Penfield et al. 1952). A significant advance in identifying the functional role of hippocampus came from the famous case study of patient H. M. (after his death identified as Henry Molaison). H. M. suffered from major temporal lobe seizures and lapses of consciousness multiple times daily, and Dr. William Beecher Scoville decided to remove the hippocampus bilaterally with hopes of relieving the symptoms. After the removal of his hippocampus (along with surrounding tissue) bilaterally, H. M. was unable to form new episodic memories, having a condition known as anterograde amnesia. Brenda Milner gave H. M. a battery of psychological tests to empirically determine the memory deficits of bilateral hippocampal lesions in humans and demonstrated that other lesions to related medial temporal areas like the amygdala did not have the same types of memory deficits (Scoville and Milner 1957).

While the hippocampus was established as playing an important role in emotion and memory formation, by the early 1970s, the discovery of spatially selective cells, known as "place cells" in the rodent hippocampus, led the field to focus primarily on its role in navigation (O'Keefe and

Dostrovsky 1971). This fascinating one to one mapping between cellular function and the external environment was conducive to extensive empirical investigation. Consideration of the hippocampus' role in temporal processing and context have served a unifying role between the navigation literature on hippocampal function in rodents to that of the formation of episodic memory.

### **Hippocampal Neuroanatomy: Gross Anatomy and Microcircuitry**

The hippocampus is a three layered brain structure described as being made up of the cornu ammonis (CA1, CA2, CA3) and dentate gyrus. The first layer is known as the stratum oriens, which has a mixture of afferent and efferent projections and interneurons. The second layer is called the stratum pyramidale. The third layer is known as the stratum moleculare, which in CA3 is further divided into the stratum lucidum, stratum radiatum, and the stratum lacunosum-moleculare. The CA regions and DG regions are present throughout the dorsal, intermediary, and ventral portions of hippocampus (Amaral and Witter 1989; van Strien et al. 2009).

The trisynaptic loop is the canonical circuit described by Ramon y Cajal and De No (1911) which reciprocally connects cortex and hippocampus completing what is known as the cortico-hippocampal loop (Andersen 1975). The first synapse of the trisynaptic circuit is made by pyramidal cells in lateral entorhinal cortex (IEC) layer II, whose axons perforate through the subiculum, synapsing onto the granule cells of the dentate gyrus. These bundles are known as the perforant pathway (Amaral and Witter 1989). The mossy fiber pathway is a set of axons which project from the granule cells of the dentate gyrus to the pyramidal cells of CA3 forming the second synapse of the trisynaptic circuit (Van Strien et al. 2009). Pyramidal cells from CA3 project axons, known as the Schaffer collaterals, up to CA1 where they converge on CA1 pyramidal cells' apical dendrites. This is where CA1 pyramidal cells project back to deep layers of the entorhinal

cortex, completing the hippocampal-cortical loop (Amaral and Witter 1989; Van Strien et al. 2009). The trisynaptic pathway is a robust pathway present in all mammals and is a general organizing principle for understanding hippocampal processing.

The trisynaptic circuit describes a robust set of connections, but there is additional connectivity which was not included in the canonical circuit. There are also projections from medial and lateral entorhinal cortex onto CA1, with lateral entorhinal inputs converging onto the dendrites of CA1 cells located closer to subiculum, and the medial entorhinal inputs converging onto the cells closer to CA3 (Steward 1976). Interestingly, area CA2 has been historically left out of the circuit altogether. CA2 pyramidal cells project onto CA1 dendrites, and have been shown to drive CA1 activity when stimulated. It has been found that the granule cells in the dentate gyrus also converge onto CA1 cells and also project axons to area CA2. CA2 pyramidal cells receive input from the supramammillary nucleus and vasopressinergic cells from the paraventricular nucleus of the hypothalamus (Dudek et al. 2016).

In regards to extrahippocampal connections, the parahippocampal region is a six layered cortical region highly integrated with the hippocampal formation and includes the presubiculum, parasubiculum, entorhinal cortex (medial and lateral), perirhinal cortex, and postrhinal cortex. The hippocampus has major output pathways to the subiculum, retrosplenial cortex, parietal cortex, and lateral septal nucleus. The hippocampus also has connectivity with the medial prefrontal cortex, which supports temporal sequence processing (Van Strein et al. 2009).

### **Computational Roles of Hippocampal Subregions**

The dentate gyrus has many more neurons than the inputs it receives from entorhinal cortex, which then project back down to a smaller number of neurons in CA3. This structural property suggests that the dentate gyrus may have an ability to perform a computational process known as

pattern separation. This separation process involves taking highly similar inputs, projecting those input patterns onto a larger population of cells, allowing for the generation of more differentiated output pathways than the initial inputs (Deng et al. 2010). The perforant pathway between the EC and the DG was the site of the discovery of long-term potentiation (LTP) (Bliss and Lomo 1973). Long-term potentiation is believed to be a primary mechanism that governs neural plasticity, which suggests that synapses between neurons become strengthened when neurons have action potentials close together in time. The dentate gyrus is the only site of neurogenesis in the hippocampus, allowing for new cells to be born throughout an organism's life (Gage 2002). Theories and computational models of dentate gyrus suggest that these newborn neurons allow for the temporal separation of similar events that take place in similar contexts (Rangel et al. 2014).

CA3 has two types of reciprocal connectivity to allow its theorized function of pattern completion. CA3 excitatory pyramidal cells project heavily onto themselves forming what is known as the "longitudinal association pathway." These excitatory connections are believed to allow for heteroassociation, which is the ability to recall a complete representation or sequence only given a partial subset of the original (McNaughton and Morris 1987). CA3 pyramidal cells also project onto inhibitory basket cells which allow for recurrent inhibition.

## Place Cells and the Cognitive Map

O'Keefe and Dostrovsky discovered "place cells" in the hippocampus and published the results in 1971. They reported that about 10% of the cells they recorded from in the CA1 region responded to an animal's spatial position while facing a certain direction. This led O'Keefe and Nadel (1978) to develop a spatial theory of hippocampus building on the work of Tolman, suggesting that these neurons represented an allocentric "cognitive map" of the environment. Tolman developed a cognitivist account of purposive and goal-oriented behavior and suggested that motion through an environment could be represented

topologically allowing for the identification of "cognitive" maps. CA1 place cells have receptive field known as place fields, which correspond to an increased firing rate while the animal is in a certain position in the environment (O'Keefe and Nadel 1978). Neurons in the dorsal region respond more robustly to spatial relationships, while the ventral regions coded more for emotional and social stimuli. Head-direction cells, which respond to different positions of the head relative to the body of the animal, have been discovered in the septal presubiculum, entorhinal cortex, retrosplenial cortex, thalamus and mammillary nucleus (van Strien et al. 2009). McNaughton and colleagues suggest that the hippocampus is part of a system for path integration. This system involves the integration of place cells with head-direction cells in the presubiculum, cortex, and thalamus (McNaughton et al. 1996). The cognitive map also involves other more complex abstract spatial representations supported by circuits between hippocampus, parietal cortex, and retrosplenial cortex (Alexander and Nitz 2015).

The Morris water maze is a popular experimental paradigm used to test hippocampal dependent memory. In this task, a rat is placed in a large circular pool of milky or opaque water where there is a hidden platform that allows the rat to escape from the water. The rat initially explores the environment randomly until finding the platform, and after the rat climbs on top of the platform the rat is removed from the maze. When placed back in the water maze, given that there are no local cues indicating the location of the platform, the animal depends on its memory of the platform's location relative to the global environment (Morris 1984). It has been shown that animals with hippocampal lesions have significantly impaired performance on this spatial memory task.

## Hippocampal Rhythms: Theta and Sharp Wave Ripples

In rats and other animals, including rabbits, cats, and monkeys, the local field potential in the hippocampus is dominated by the hippocampal theta



rhythm, which is an oscillation that occurs at approximately 5–10 Hz. The local field potential is an electrical potential that is measured by embedding wires in the extracellular matrix of a group of neurons (Buzsaki et al. 2012). The theta oscillation increases in amplitude when the animal is moving throughout the environment and reduces when the animal is still. Hippocampal theta has been determined to be a dynamic wave that travels along the septotemporal axis of the hippocampal region (Lubenov and Siapas 2009). The origins of the theta oscillation are still unclear, but there is evidence to suggest that cholinergic cells in the medial septum might act as “pacemakers” for the hippocampal theta rhythm. The supramammillary nucleus of the thalamus with heavy connectivity to the septum is also a candidate for acting as a theta pacemaker (Buzsaki 2006). It is also possible that hippocampal interneurons play a role in regulating theta, as they are the only cell types that receive projections from medial septum, and also project from hippocampus to medial septum (Freund and Antal 1988).

CA1 place cells have been demonstrated to organize their action potentials to particular phases of the theta oscillation according to their temporal relationships. Phase precession is the phenomena where place cells coordinate their action potentials to different phases of the hippocampal theta oscillation representing where the animal currently is, where it is going, and where it has been (Buzsaki 2006). Models of hippocampal memory function suggest that this phase-dependent coding scheme might be a method for organizing memory encoding and retrieval (Hasselmo and Stern 2014).

Another rhythmic pattern in the hippocampal local field potential is the sharp wave ripple, which is a 140–200 Hz transient burst that occurs during wake and sleep (Buzsaki 2006). Hippocampal ripples have been observed in mice, rats, rabbits, monkeys, and humans (Logothetis et al. 2012). In awake animals, after running through a sequence of places tracked by place cell activity, when they stop running, sharp wave ripples occur. During those stop times, place cells fire in coordinated phase with the oscillatory ripples, in fact it was found that it was the same sequence of place cells rapidly firing in reverse temporal order

(Foster and Wilson 2006). It is believed that this sequential replay is a functional process which allows for memory consolidation.

## Temporal Coding

The hippocampus not only has a part in computing the animal's position in space but also information related to time. Lesions of the hippocampus can result in deficits in the recall of temporal order. In one task testing temporal order recognition, rats were trained to run through random sequences on an 8-arm radial maze. In the test phase, rats were presented with two arms simultaneously and were tasked with running through the arm which appeared earlier in the training sequence. Rats with lesions of the hippocampus performed poorly as compared to control rats on arms that were in close temporal proximity to each other (Chiba et al. 1994). CA1 place cells have also been observed to selectively fire to odors presented in a sequence. Similarly to the radial maze, the two temporally related odors were presented simultaneously and the rat was given a reward if it chose the odor that was presented earlier in the training sequence. This suggests that there are additional temporal dimensions that are coded along with the spatial mapping functions of CA1 place cells (Eichenbaum 2014).

## Conclusion

The hippocampus is a complex brain structure that carries out functions that are central to an organism's sense of spatial relations and memory formation. Future studies will be tasked with integrating the functional processes related to spatial maps and episodic events. Multiple studies have also been conducted where rats navigate a virtual reality environment, and it has been found that place cell activity is diminished to a significant degree (Aghajanian et al. 2015). Additionally, CA1 place cells have recently been shown to map onto more than just allocentric space. A recent study showed then when a rat was given a joystick to control an auditory signal, that CA1 place cells

mapped onto auditory dimensions suggesting that it might be necessary to broaden the definition of “place” with regard to “place cell” activity (Aronov et al. 2017). There are many questions to be answered about the relation between hippocampal function and structure, and will likely be the central focus of analyses for years to come with hopes to understand the representation of events, space, and time in the brain.

## Cross-References

- ▶ Action Potentials
- ▶ Axon
- ▶ Entorhinal Cortex
- ▶ Hypothalamus
- ▶ Medial Entorhinal Area (MEA)
- ▶ Neuron
- ▶ Parahippocampal Cortex (PHC)
- ▶ Susan D Healy

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## Holding On

### ► Grasping Reflex

## Home Base

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A conspicuous spatial regularity in the exploratory behavior of many organisms is the existence of a home site or home base. In the wild, animals have such a site to which they return regularly after exploring their home range or territory, be

they, e.g., ants, bumble bees, millipedes, small mammals, or wolves. In behavioral neuroscience experiments, the animal’s “home base” refers to its most preferred place, from which it performs excursions or forays into the environment (Eilam and Golani 1989). Upon being introduced into a novel laboratory arena, rats establish one or two places that stand out in terms of the time spent in them, the number of visits paid to them, and the incidence of grooming, and other behaviors that are typically performed in them, like crouching, turning in place around the forequarters, and the high frequency of rearing episodes performed in them. An accumulation of time through a high number of visits also characterizes the home base of, e.g., mice (Fonio et al. 2009; Benjamini et al. 2011), infant rats, and zebra fish (Stewart et al. 2010).

The conspicuousness of the home-base phenomenon begs an examination of its significance in spatial cognition. One common way of studying spatial cognition involves the study of maplike representations of physical space in the brain and the computational and neural analysis of navigational strategies involving different ways of information processing like piloting, dead reckoning, and the use of cognitive maps. The cognitive significance of the home base has been studied by using a complementary, ethological strategy, of obtaining a view on the organization of spatial cognition by studying the growth and differentiation of moment-to-moment spatial behavior (Gomez-Marin et al. 2016).

On a large platform placed away from walls, devoid of objects or markers, each individual rat will establish its own home base in a specific place, often at a corner but sometimes in the center area, in a location that is idiosyncratic to it. The selection of a location and the establishment of a home base in it thus reflect an endogenous constraint, characterizing the organization of exploratory behavior, independent, at least partly, of proximal features located in the environment. Home base location constrains cognitive spatial behavior.

The home base exerts its influence on the rodent’s behavior across the entire explored area. Visits to the home-base partition the path into

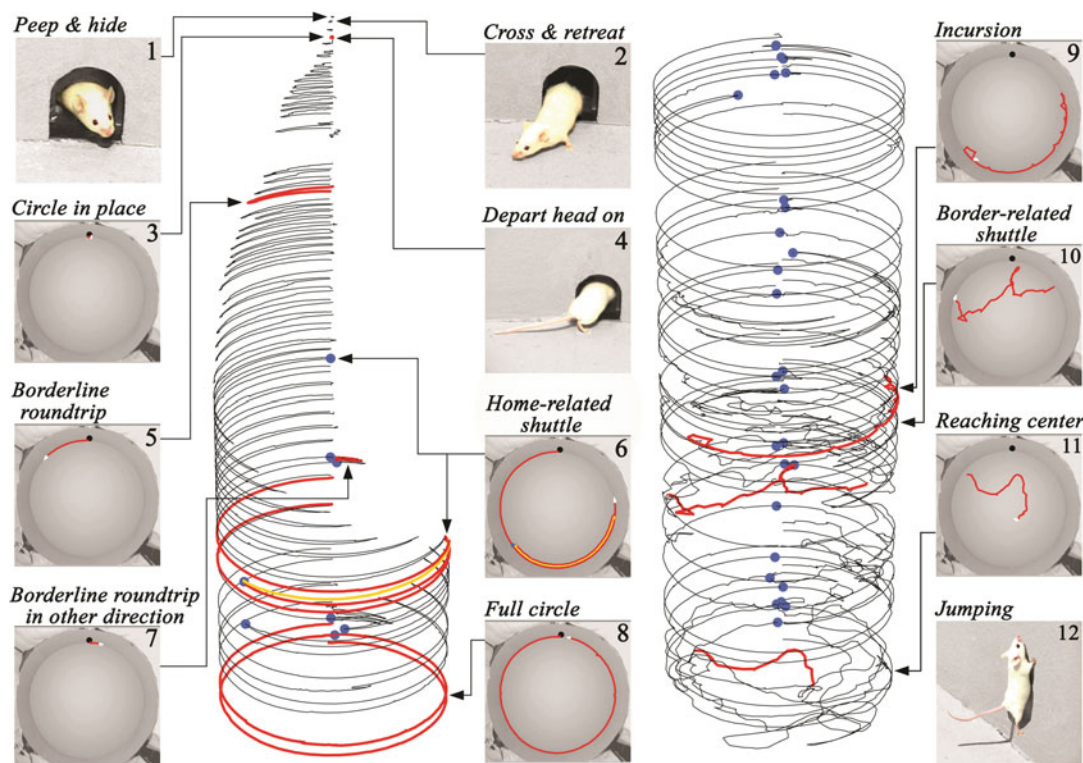
excursions in the environment. The latter are further partitioned into progression segments and lingering (staying-in-place episodes) (Drai et al. 2000). In rats, excursions initially consist in slow outbound and fast inbound portions, the outbound one comprising intermittent progression involving multiple lingering episodes (Tchernichovski et al. 1998). With repeated performance the velocity profile is reversed, as the outbound portion becomes fast and the inbound one slow and intermittent. The speed of progression has been shown to correlate in rats with how well-trodden (familiar) the path is, exhibiting faster progression on well-trodden paths. It has been claimed that the rodents maximize novelty signal-to-noise ratio during each excursion, where novelty is defined as the accumulated information gain. In this view, the rodents maximize novelty during outbound exploration and use novelty-triggered withdrawal-like retreat behavior, exploring the environment in a novelty-descending sequence. The piecemeal occupancy of a novel environment involving multiple repetitions of excursions characterized by incremental growth highlights how constrained behavior is during its morphogenesis. This contrasts with the view projected by mainstream studies of navigation, which study the maplike representations of physical space in the brain. These studies dispense with moment-to-moment morphogenesis and focus on full-blown behavior, at a stage when navigation appears to be relatively unconstrained. To become relatively free, spatial cognition requires, however, growth and differentiation.

The observation that the homeward trajectory of the excursion in rats is relatively straight and ballistic led to a series of studies, performed by Whishaw and colleagues, of lesioned animals, demonstrating a loss of that type of trajectory in the lesioned animals. This loss has been interpreted to indicate the use, in intact animals, of the dead-reckoning strategy during the inbound portion. It has been suggested that the lesioned part has been involved, when intact, in the computation of the inbound trajectory both in light and dark conditions. The brain structures claimed to be involved in computing the ballistic inbound trajectory included the hippocampus, the posterior cingulate

region, the fimbria-fornix, the posterior cingulate cortex, Ammon's horn and dentate gyrus, and the vestibular system (e.g., Wallace et al. 2006).

While growth and differentiation of the exploratory repertoire in intact rats imply more freedom, dopaminergic drug stimulation induces a cognitive shutdown of freedom: amphetamine (0.5–5 mg/kg Sc; Eilam and Golani 1994) and more so chronic treatment with the dopamine D2–3 stimulant quinpirole consolidate an increasingly smaller number of well-trodden routes along which increasingly shorter excursions are performed, and apomorphine (1.25 mg/kg Sc) disconnects behavior from locale space (Szechtman et al. 1985). The excessive, repetitive returns to the home base and the associated compulsive checking with quinpirole have been considered an animal model for obsessive-compulsive disorder (OCD; Szechtman and Woody 2004).

In intact mice, the growth in complexity of excursions is modular (Fig. 1), first enacting in an arena surrounded by a smooth wall of the terrain around the doorway (so-called garden); (zero-dimension space; <https://www.youtube.com/watch?v=Oc-JEn-j1xM>); then the borderline surrounding the arena consisting of monotonical outbound and monotonical inbound movement (one-dimensional space; [https://www.youtube.com/watch?v=rOHZC\\_qWkY](https://www.youtube.com/watch?v=rOHZC_qWkY)); then the inbound portion that becomes non-monotonical, incorporating the so-called shuttles on the inbound direction (<https://www.youtube.com/watch?v=ykGq3jNNiBw>); and then the radial dimension, away from the borderline and toward the center (two-dimension space; <https://www.youtube.com/watch?v=OqhHRCDD5nU>) and only then jumping up on the wall (three-dimensional space). A main feature of this process is the modularity of growth: the mice engage in building up one dimension at a time for extended bouts of behavior (Fonio et al. 2009). The fact that they enact space on a dimension by dimension basis suggests that space is composed of locally integrated “physiological dimensions,” which amalgamate into a functional unity. Modularity is thus a major built-in constraint on attention and cognition.



**Home Base, Fig. 1** The moment-to-moment actual genesis of deliberate exploration performed from a mouse's home cage that serves as a home base. The home cage is connected by a doorway to a large circular arena surrounded by a smooth wall. The developmental landmarks were exhibited in a specific BALB/c mouse – session performed across a 3-h period. The spiral proceeding from top to bottom, first in the left and then in the right column, presents the time series of 2-D locations on the path traced by the mouse. The enumerated figure inserts

show the 12 landmark motions that characterize the behavior, traced in red within the arena and on the spiral. Blue dots indicate instances in which the mouse approached the cage doorway and did not enter the cage (cage skips) or stopped short of returning all of the way home during a return (home-related shuttle). Absence of a blue dot implies departure into the home cage. Yellow path stands for the return portion within a home-related shuttle (Courtesy of Fonio et al. 2009)

Another major constraint, exhibited in rats but not in mice, is the initially slow and then fast increase in home-base attraction with every additional stopping episode, also expressed as the existence of an intrinsic upper bound on the number of stops. Once the upper bound is reached, the rat concludes the excursion and returns to the base without stopping, even when far away from the home base. In a large arena, rats extended inter-stop distances rather than crossing the upper bound on the number of stops per excursion (Golani et al. 1993). The same phenomenon has been observed by David Eilam in voles. This constraint implies some form of measurement performed by the animal in reference to the home base.

The connectedness (Saint-Hilaire 1822) exhibited between the home base, the excursions, the progression segments, and lingering episodes, and the outbound versus inbound portions, suggests that origin-related exploration might be homologous in vertebrates and perhaps also in arthropods (Cohen et al. 2015), sharing the same architectural plan of movement in allocentric space. The connectedness that unfolds at the kinematic level calls for a search for a corresponding connectedness at the neural level. If the measures are indeed homologous, then the likelihood of discovering a corresponding neural plan sharing a parallel connectedness will be increased. Such correspondence, however, has been investigated



to date mostly with regard to the inbound-outbound parts of excursions, suggesting the involvement of the hippocampus in mediating the structure of the inbound part of excursions (Wallace et al. 2006).

Understanding the organization of a living anatomical structure by studying its morphogenesis is standard in comparative anatomy (von Baer 1828). Since behavior, navigation included, is an extension of anatomy (Lorenz 2013), this also applies to navigational behavior. Measuring the morphogenesis of behavior in reference to the origin(s) used by the animal can thus reasonably be expected (Golani 2012). The home base is one such reference, shared by vertebrates and arthropods, and it is used during navigation. It would thus be expected that the home-base kinematic variables and their connectivity would be used as a search image in the pursuit of the key neurophysiological measures that support them. It would also be expected that these neurophysiological variables would be measured in reference to the animal's home base. In summary, home-base-related exploration constitutes a constrained process of origin-related growth and differentiation involving the emergence of freedom of movement along specified, modulated dimensions, reflecting a gradual emancipation of the animal's exploratory path from both endogenous and environmental constraints.

## Cross-References

- [Cognitive Map](#)
- [Dead Reckoning](#)
- [Navigation](#)

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## Home Range

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### Definition

A home range is an emergent space use pattern that results from animals restricting their movements within a certain area over a specific time period, while attempting to meet their needs for growth, survival, and reproduction. Home ranges are measured in units of area, or volume if altitude is taken into account, and time, and can be defined at different spatial scales, determined by the selected isopleth value of the utilization distribution.

### Introduction

All animals move, at least during some life-history stages, to obtain the resources for growth and survival, to reproduce, to escape from predators, etc. It is a common observation that most mobile animals repeatedly use the same area over time, instead of roaming over the entire available landscape, a behavior called site fidelity. Site fidelity leads over time to the emergence of home range patterns – a relatively small area (compared to the movement capacity of animals) repeatedly used by an animal over a specific period of time (Burt 1943; Börger et al. 2008). This type of behavior has fundamental consequences on evolutionary, ecological and behavioral processes, as individuals in a population do not mix but interact locally with a restricted set of individuals, which affects social interactions, habitat use, population density, population and meta-population dynamics, meta-community structure, spatial predator-prey dynamics, disease dynamics, etc. (Horne et al. 2020). Thus animal home ranges are an important focus of ecological and behavioral studies, yet at the same time the field has been

characterized by frequent and protracted methodological debates about how to estimate animal home ranges from animal location data (Fieberg and Börger 2012).

### Home Range Structure and Dynamics

Site fidelity is the defining characteristic of home range space use – if animals do not restrict their movements to a confined area over the time interval considered, one cannot speak of a home range. Consequently, if an animal moves within a home range, there should be temporal stability in the area used, with repeated visits to certain areas within the home range. Home ranges are emergent space use pattern and thus are not something directly selected for by animals (“today I will use 150 ha”); instead, they are a useful index or probe for quantifying and investigating animal movement and space use behavior. Home ranges and territories are strongly linked but determined by fundamentally different processes – home ranges are defined and estimated without reference to defense or advertisement or reaction to intrusion by neighboring individuals, only the presence of the individual is required; territoriality instead arises when individuals exhibit spatially oriented aggressive behavior, i.e., aggressive defense of a space containing limiting resources, thus a territory is estimated by delineating the location of defense events and the location of competing neighbors is needed to define the area of exclusive use (Burt 1943). A territory is always part of a home range – often smaller in size, or of equal size to the home range, as, for example, for some large carnivores (Börger et al. 2008). The movements of animals within a home range are typically not uniform and the structure of home ranges is often multi-nuclear, with one or more frequently used areas and centers of activity. The area of more frequent (or intense or concentrated) use is called the core area, and the area of the home range external to the core area is called the home range “periphery” (Fieberg and Börger 2012; Horne et al. 2020). Home ranges are dynamic spatial patterns, driven by temporal, spatial, and individual-level behavioral and

environmental processes affecting the movements of animals, and the size and structure of home ranges can change by several orders of magnitude within and between individuals across time and space (Börger et al., 2006b). Importantly, home ranges may not cover always the same area during the life of the individual, with animals moving between areas and hence leaving the old home range and setting up a new one (Burt 1943). Home ranges are also closely connected and often part of other space use behaviors, especially dispersal and migration. Migratory animals often stay in stable home ranges before and after migration; similarly, dispersal is a three-stage process, with dispersing individuals staying in a home range before and after the transient dispersal event.

### Estimating and Modeling Home Ranges

A home range is estimated from a regular sample of animal movements (Börger et al., 2006a), collected over a defined time interval (which is important to address issues such as autocorrelation, see Fieberg and Börger 2012), typically using GPS or VHF tags attached to animals. Before modeling or analyzing home ranges, it is important to verify that the animal was moving within a home range; this can be done using net squared displacement or variogram methods (Horne et al. 2020). Much debate in the field has centered about differences between different home range estimation methods, but these concerns can be comprehensively addressed by closely selecting the most suitable methods to address specific biological questions (Fieberg and Börger 2012), evaluating if the sampling regime used to collect animal movement data is adequate to answer the biological questions of interest and if differences between methods have actually a relevant impact on the inferences obtained or not (Börger et al., 2006a). It is also important to consider the broad range of approaches available to estimate and model animal home ranges, which goes well beyond diatribes about specific methods. Overall there are

three different approaches to model animal home ranges (reviewed in Börger et al. 2008) – mathematical modeling approaches, or mechanistic home range analysis; individual-based modeling approaches based on optimal foraging theory; and statistical modeling approaches – with a more unitary view of home range behavior emerging in the past decades across these once rather separate fields of enquiry. A central question addressed by mechanistic home range analysis is understanding the behavioral processes which lead to the emergence of stable home ranges from otherwise unbounded movements. Early models uniquely focused on the role of scent-marking behavior of territorial species, whereas more recent models have started to develop more generally applicable models, especially including the role of memory (Ellison et al. 2020). Optimal foraging-based home range and territory models focus on the role of resource distribution and movement costs within a cost-benefit approach (Sells and Mitchell 2020), with strong links to cognition and sensory ecology. Statistical modeling approaches focus on identifying and quantifying the dynamic scale-dependent processes which determine the size, structure, and variation of home ranges across space and time (Börger et al., 2006a), the overlap between home ranges (Winner et al. 2018), etc. To do so, modern approaches use location data to estimate the most likely probability density function of the home range and use this likelihood function to evaluate the contribution of different hypothesized drivers affecting the size and structure of the home range. Thus, instead of methods which provide only an outline of the home range boundary, modern approaches use statistical methods such as kernel density estimation (Fieberg and Börger 2012), as they provide an estimate of the relative frequency distribution within the home range area of an animal's location over time – this is called the utilization distribution function (UD) and can be thought of as a measure of the probability to encounter an animal in a certain area. UD values range between 0% and 100%, and the area enclosed by a line of constant UD value, called an isopleth line, provides measures

of home range and core area size – typically, 95% or 90% isopleths are used to delineate the home range (Fieberg and Börger 2012). Using multiple UD isopleth measures, closely linked to clear ecological questions, can markedly increase the biological inferences obtained Börger et al. (2006b). A more recent group of kernel density estimation methods, the autocorrelated Kernel density estimation (AKDE) home range estimators (see Horne et al. 2020 and references therein), includes the autocorrelation information in movement data and allows to correct for small effective sample size, irregular sampling in time of animal locations, and deriving robust home range overlap estimates (Winner et al. 2018). It is important however, when using these latter methods, to verify that the strong underlying assumptions of the AKDE approach are adequate for the data used and the questions addressed. If sufficiently frequently sampled movement data are available, further understanding can then be obtained by using newer methods which go beyond the utilization distribution and link home range analysis to methods used in movement path analysis, for example, directly allow to identify home range areas that are intensively exploited or repeatedly visited (Benhamou and Riotte-Lambert 2012), as well as using multi-sensor biologging methods (e.g., accelerometers, magnetometers, temperature and dive depth recorders, etc.) which allow to include further metrics, such as the type of behavior displayed at specific locations or the state of individuals.

## Conclusion

Animal home ranges are a central focus of research in ecology, animal behavior, and cognition, especially concerning the role of memory and sensory information. A very large set of methods and approaches can be used, and methodological advancements in the field are continuous. To make the most of this potential, it is important to focus on the biological questions and select the most appropriate set of methods and approaches. A new frontier in the field lies

also in including behavioral information into home range analysis, especially by using multi-sensor biologging methods.

## Cross-References

- [Artiodactyla Navigation](#)
- [Core Area](#)
- [Territoriality](#)
- [Territory Defense](#)

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## Homeobox Gene

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### Definition

Homeobox genes are a group of similar genes having a common DNA sequence (a homeobox) responsible for coding a homeodomain. They play a vital role in governing the formation of bodily segmentation and cell differentiation during embryonic development.

### Introduction

A homeobox is comprised of a DNA sequence, around 180 base pairs long, and resides inside the genes governing the patterns of anatomical development (morphogenesis) in various organisms like plants, fungi, and animals (Gehring 1992). These genes were initially described in *Drosophila melanogaster* where they function as the master regulators of the various bodily segmentation and structures during the embryonic development process (Schofield 1987). They code for a string of 60 amino acids termed as homeodomain. An important feature of the homeobox genes is that they are present on every human chromosome, often appearing in clusters (Boncinelli 1997).

### The Homeodomain

Homeodomain is the part of the protein that attaches (binds) to specific regulatory regions of the target genes. This region is highly conserved, and the 60 amino acids are arranged in a

helix-turn-helix configuration. Interestingly, most homeodomain-containing proteins function as transcription factors, which means that they bind to and control the activity of other genes (Bürglin and Affolter 2016; Gehring 1992, 1993).

### Structure of the Homeodomain

The 60-amino-acid long chain of the homeodomain comprises of three alpha helices. Helix 1 and Helix 2 are joined together by a short loop, thus forming the HTH (helix-turn-helix) structure, whereas the third one is responsible for the direct interaction with DNA involving a number of hydrogen bonds, hydrophobic interactions, as well as indirect interactions via water molecules, occurring between the particular side chains and exposed bases of the DNA in the major groove (Schofield 1987).

### Sequence Specificity

Homeodomain proteins show a proclivity toward the DNA sequence 5'-TAAT-3'. However, non-specific binding has also been reported but it takes place with lower affinity. It binds with the B DNA with the aid of its C-terminal recognition helix, rich in lysine and arginine, which aligns with the DNA's major groove, while the N-terminus aligns in the minor groove (Carton et al. 1993).

### Classes of Homeobox Genes

Homeobox genes can be divided into a number of classes that have been shown along with their few examples in Table 1 below (Bürglin 2001; <https://www.genenames.org/>).

Among these, Hox genes are of high importance and have been explained in detail in the following section.

### Hox Genes

Human Hox genes are present in the four homeotic clusters, namely, A, B, C, and D



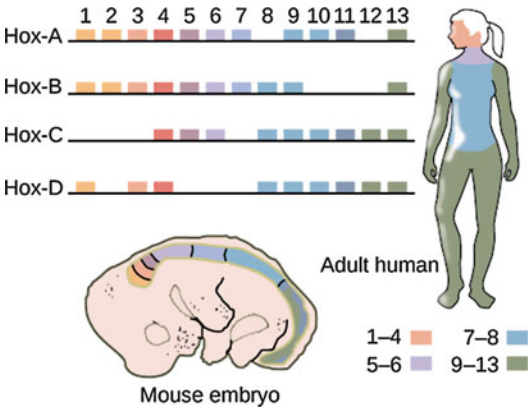
**Homeobox Gene, Table 1** Different classes of homeo-box genes with a few examples

| Classes of homeobox genes | Examples               |
|---------------------------|------------------------|
| Hox cluster genes         | Antp, ubx, ftz         |
| Dispersed Hox-like genes  | Ems, cad               |
| POU class                 | Unc-86                 |
| Prd class                 | Drosophila gene paired |
| Prd-like class            | Gene family Alx, Argfx |
| LIM class                 | ISL1, ISL2             |
| ZF class                  | ADNP, ADNP2            |
| Cut class                 | CUX1, CUX2             |
| HD zip class              | AIRE, ASH1L            |
| TALE class                | IRX1, IRX2             |
| Pros class                | PROX1, PROX2           |

located on different chromosomes. It is known that the genes of the different clusters work in cooperation in order to establish the identity of body segments along the head-tail axis. Each homeotic cluster further comprises of 13 genes as shown in Fig. 1. Hox genes are homologous in the entire animal kingdom implying that the nucleotide and the protein sequence along with their positions have a lot of similarity among most animals. This is because they were present in a common ancestor of flies, mice, and humans (Fig. 1). It is peculiar to observe that the genes located in the beginning are responsible for the development of the structures near the head region of the organism, whereas the genes located at the end are responsible for the development of the lower (or tail) end of the organism.

Biological Function

In the case of humans, the homeobox gene family comprises approximately 235 functional genes and 65 pseudogenes (Holland et al. 2007). In humans, they are known to be associated with a number of vital activities like the genesis of the different organs and limbs along the anterior-posterior axis, nucleocytoplasmic trafficking of Hox transcription factors, and cell differentiation. Homeoprotein transcription factors are responsible for switching on the



**Homeobox Gene, Fig. 1** Homology between mice and human Hox genes. A similarity is seen between the Hox gene expression in the body segments of both the mouse and the human as depicted by orange, pink, blue, and green shading. Provided by OpenStax CNX. (<http://cnx.org/contents/185cbf87-c72e-48f5-b51e-f14f21b5eabd@10.8>)

cascades of other genes. Some members of the Hox gene family are also known to be involved in vascular remodeling and angiogenesis by governing the changes in matrix degradation, integrins, and components of the extracellular matrix.

Additionally, some homeobox genes are also known to act as tumor suppressor genes, controlling the division of the cells in an uncontrolled way. As evident, Hox genes have diverse functions, and therefore, any mutation in these genes can cause serious manifestations and developmental disorders in the body. For instance, a mutation occurring in the HOX group of homeobox genes renders malformed limbs; in PAX group, it results in eye disorders, and in MSX group, it causes multiple abnormalities related to the head, face, and tooth. Further, as these genes also function as tumor suppressor genes, their mutation or changed expression can also lead to cancer (Zhao and Westphal 2002).

Conclusion

Homeobox genes code for a 60-amino-acid long homeodomain and are of utmost importance in the normal morphogenesis in animals including humans. The homeodomain region is highly

conserved across organisms indicating the important role played by them. They mostly function as transcription factors that act on the promoter region of their target gene. Mutation studies linked with the homeobox genes have demonstrated that any mutation in these genes can lead to serious abnormalities in different parts of the body. Studies based on the genetic engineering linked to the homeobox genes have shown great potential in the field of development of new organs from our own tissues. Henceforth, studies on these genes would unlock many embryonic development-related mysteries and aid in better treatment of the malformations and abnormalities occurring due to mutations in these genes.

## Cross-References

- [DNA](#)
- [Gene Expression](#)
- [Genes](#)
- [Mutations](#)

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## Homeostasis

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## Introduction

**Homeostasis** refers to a relatively constant internal body state achieved by negative feedback mechanisms. French physiologist Claude Bernard (1813–1878) was the first scientist to propose that animals maintained a relatively constant internal state, regardless of external conditions. Bernard observed that animals have an ability to maintain a stable internal environment – *milieu intérieur* – even in stressful and harsh environments. He discovered that animals subjected to cold weather respond with vasoconstriction (narrowing) of superficial blood vessels, which diverts blood to deeper tissues of the body in order to conserve heat. It took approximately 50 years for Bernard’s visionary concept to be studied further. The term “homeostasis” was coined by physiologist Walter Cannon (1871–1945) in 1926. In his book, *The Wisdom of the Body* (1932), Cannon postulated that the interior of the body is at “equilibria,” but the equilibria is maintained within a range rather than a discrete value. He proposed that deviations from equilibria are automatically met with a commensurate response that counteracts the change. Cannon further proposed that there are discrete mechanisms acting simultaneously or consecutively to achieve homeostasis; he noted that homeostasis does not occur by chance and is a part of organized, self-government (Cannon 1932; Davies 2016).

Another prominent scientist involved in the early study of homeostasis was Curt Richter, a psychobiologist at Johns Hopkins University. In his early work, Richter removed the adrenal glands from rats, disrupting sodium and potassium homeostasis. Richter noted that rats compensated for sodium loss by consuming hypertonic saline (Richter 1936a, b). He published similar studies regarding calcium homeostasis. Richter et al. observed that removing the parathyroid glands

from rats lead to the rats consuming more calcium in their diets (Richter and Eckert 1937). Richter’s contributions to the field of homeostasis were unique from Bernard’s and Cannon’s. Richter demonstrated that animals could compensate for shifts in a biological set point with behavioral changes. However, Richter only considered one element of the homeostatic regulatory mechanism: the ability to respond to a deviation. However, homeostatic regulatory mechanisms involve several different elements to achieve a steady state or equilibrium. Homeostatic control systems require the establishment of biological set points, detection of deviations from the set point that compare “input value” (or stimulus) to the established set point, activation of mechanisms to counteract deviations, and restoration of the biological set point.

Maintaining Homeostasis

Most biological variables are controlled within a range, not a specific value. For instance, the set point for normal body temperature is 98.6° F in humans. However, it is well-established that healthy humans oscillate around this set point, with temperature being slightly higher or lower at any given time. Because of the variability in biological set points, it is appropriate to consider the body in a state of **dynamic constancy** (VanPutte et al. 2014). Dynamic constancy means that most variables are controlled within a range, and some biological variables deviate from normal in the short term but are stable in the long term (e.g., blood glucose is high post-meal but returns to pre-meal levels over time). Additionally, an individual may be out of homeostasis for one biological parameter but not another. Therefore, a normal set point applies to *each* biological variable. Many biological variables, including ion concentrations, have different intracellular (inside of a cell) and extracellular (outside of a cell) set points (Table 1). Osmolality, pH, blood plasma glucose levels, plasma oxygen levels, and others (Table 2) are also maintained around a set point, but the “normal” levels may vary depending on body compartment or other state-dependent factors (fasting vs. non-fasting). Loss of homeostatic

**Homeostasis, Table 1** Homeostatic levels of biologically important ions in humans

| Ion   | Extracellular concentration (in millimolar) | Intracellular concentration (in millimolar) |
|-------|---------------------------------------------|---------------------------------------------|
| Na+   | 145                                         | 15                                          |
| Ca2+  | 1.2                                         | 10 <sup>-7</sup>                            |
| K+    | 4.5                                         | 120                                         |
| Cl–   | 116                                         | 20                                          |
| HCO3– | 25                                          | 16                                          |

**Homeostasis, Table 2** Fasting blood levels of important biological variables in humans (Fox 2016; Padilla 2018)

| Biological variables | Normal range        |
|----------------------|---------------------|
| Arterial pH          | 7.35–7.45           |
| Oxygen               | 17.2–22.0 ml/100 ml |
| Proteins             | 6.5–8.0 g/100 ml    |
| Glucose              | 75–110 mg/100 ml    |
| Free amino acids     | 3.3–5.1 mg/100 ml   |
| Triglycerides        | < 250 mg/dL         |
| Hemoglobin           | Females: 12–16 g/Dl |
|                      | Males: 14–17 g/dL   |
| Osmolality           | 290 mOsm            |

control can result in death or disease of an organism. Many clinical biomarkers detect deviation from the normal set point and are used in the diagnosis of infection and disease.

Biological homeostasis is largely achieved by the use of negative feedback loops. The concept of negative feedback was first proposed by engineer and mathematician Norbert Weiner (Weiner 1948). Negative feedback loops are those in which a change (deviation from set point) is detected and an action is taken that opposes the change. Homeostatic regulatory systems utilizing negative feedback are comprised of several different components. First, a change (stimulus) must be detected by a **sensor** that measures the biological parameter. The information about the change must be compared to a set point by an **error detection** system. The error detection step compares the measured stimulus (an “input value”) to an established set point. By comparing the stimulus and set point, the **control center** of the regulatory system evaluates if action needs to be taken. In the event that the input value and set point are

not within an acceptable range of similarity, **effectors** are directed by the control center to evoke a response that opposes the action of the stimulus (Modell et al. 2015). In the case of human thermoregulation, thermoreceptors in the skin act as sensors to detect changes in temperature. Thermoreceptors convey temperature information to the hypothalamus by way of afferent pathways. The hypothalamus is actively involved in thermoregulation; it establishes the set point for body temperature. The hypothalamus acts as both the error detector and control center in this example. In instances of low body temperature (97.6° F or lower), the anterior hypothalamus stimulates contraction of piloerector muscles, increasing energy expenditure and heat production. The hypothalamus, which also serves as an autonomic regulator, stimulates the sympathetic nervous system to vasoconstrict cutaneous blood vessels. Peripheral vasoconstriction diverts blood to deeper body tissues, preventing heat loss (Hall 2016; VanPutte et al. 2014). In this example, the sympathetic nerves, because they provide motor output from the CNS and mediate the effects, act as effectors. It is important to note that the set point in a homeostatic control system can change depending on the body's biological priorities. In instances of infection, the hypothalamus can change the body temperature set point to a higher value, thus eliciting fever (Saladin 2017). An elevation in body temperature can slow microbial growth and allow the immune system to better combat the infectious agent (Willey et al. 2017).

## Homeostasis and Adaptation

Although homeostasis is a phenomenon that is universal in living organisms (even unicellular organisms), the organismal strategies used to maintain steady state are remarkably diverse. Many organisms have adapted to their environments through generations of natural selection in order to survive and thrive within their niche. For example, modern day Tibetans, who live in high altitude/low oxygen environments, are resistant to hypoxic (low oxygen) conditions that would harm humans living at sea level (Petousi and Robbins 2014). Such resistance to hypoxic conditions is

likely the result of natural selection. However, many organisms possess the ability to rapidly change homeostatic set points in a changing environment or regulate in some other way. Humans (even non-Tibetans) will very rapidly compensate for low oxygen levels by increasing rate of ventilation (Grover 1965); this is a classic example of negative feedback.

Not every animal maintains homeostasis the same way in a changing environment. Animals may be placed into one of the two categories: *regulators* or *conformers*. Conformers, such as starfish, match their internal body conditions to that of the external environment. Conformers can change the homeostatic set point in the presence of variable environmental conditions. For example, when *Asterias* (starfish) are placed in a high salinity water solution, they will increase body fluid salinity until they reach equilibrium with the external environment (Randall et al. 2002). For this reason, they are called *osmoconformers*. Osmoconformity is a useful strategy for many marine creatures that negates the need for them to absorb or expel water as they navigate waters of varying salt levels. Regulators use physiological or behavioral means to regulate internal body systems but do not change the internal set point in variable environmental conditions. If placed in a high salinity fluid, an osmoregulator's body fluid will stay below the concentration of fluid in the external environment. If an osmoregulator is placed in a low-salinity fluid, its body fluid will remain more concentrated than the external environment. Although many exceptions exist, most vertebrates are regulators and most invertebrates are conformers. Decapod crustaceans and some insects and mollusks are regulators (Randall et al. 2002). Thus, some organisms (including humans) actively work to maintain internal constancy, while others (such as starfish) change the biological set point to match external conditions, thus achieving equilibrium.

## Redundancy of Homeostatic Regulatory Mechanisms

If a particular biological variable is essential to survival, there are likely multiple feedback loops

involved in its regulation. For instance, blood pressure regulation in humans is achieved by multiple feedback loops and regulatory mechanisms. The heart is a circulatory system structure that pumps blood to and drains blood from the cells and tissues of the mammalian body. The heart is comprised of cardiac muscle tissue. In a state of systole (contraction), the heart pumps blood into arteries with a great deal of force. Blood pressure (BP) is a measure of the force blood exerts against blood vessels walls. Arterial blood pressure is a function of cardiac output (i.e., how much blood the heart pumps in 1 min), blood vessel elasticity (i.e., blood vessels with high elasticity distend and absorb force better than those with low elasticity), blood vessel diameter (i.e., dilated vessels have lower pressure while constricted vessels have higher pressure), and blood volume (i.e., volume and pressure are directly proportional). Normal adult blood pressure is approximately 120/80 mmHg, where 120 mmHg is the systolic (contraction) pressure and 80 mmHg is the diastolic (relaxation) pressure. Low blood pressure (hypotension) can lead to decreased blood perfusion to important organs, while high blood pressure (hypertension) puts small blood vessels at risk of aneurysm and the kidneys at risk of damage to the filtration membrane of the glomerulus. The circulatory system is responsible for nutrient delivery, waste removal, and gas transport to body cells; thus, significant deviations in blood pressure can be dangerous for multiple organ systems. Maintaining blood pressure homeostasis requires a multiorgan/system approach.

Blood pressure is detected by stretch **sensors**, called **baroreceptors**, located in the walls of two large arteries carrying blood away from the heart: the aorta and common carotid (Fox 2016). The baroreceptors respond to stretch signals and act as **sensors** of the blood pressure homeostatic control system. In instances of low blood pressure and low arterial stretch, the baroreceptors respond by firing action potentials at a lower-than-normal frequency. In instances of high blood pressure and high arterial stretch, the baroreceptors respond by firing action potentials at a higher-than-normal frequency. The electrical signals from the baroreceptors are conducted to the central nervous system by way of the glossopharyngeal and vagus nerves. The

glossopharyngeal and vagus nerves project to the nucleus tractus solitarius (NTS) located in the medulla oblongata. The medulla oblongata is part of the central autonomic network (see “► [Vasal-Vagal Stimulation](#)” entry) involved in regulation of the parasympathetic and sympathetic nervous systems. In this instance, the medulla oblongata acts as **error detector** and **control center** of the blood pressure control system. The medulla will interpret the signals sent by the baroreceptors. *If the deviation is low blood pressure*, autonomic centers of the medulla activate the sympathetic nervous system (aka “fight-or-flight” division of the peripheral nervous system); thus, the sympathetic nervous system serves as an **effector**; parasympathetic activity is reduced in instances of hypotension. The sympathetic nervous system innervates the heart pacemaker and myocardium, arterioles (small arteries), and veins. The sympathetic nervous system releases norepinephrine onto the heart to increase heart rate and force of heart muscle contraction. These effects raise cardiac output and blood pressure. Additionally, the sympathetic nervous system triggers vasoconstriction of arterioles (increasing peripheral resistance) and veins (increasing cardiac output) via the actions of epinephrine and norepinephrine. Thus, the net effect of sympathetic stimulation is an elevation in blood pressure which counteracts the original stimulus (low BP). *If the deviation is high blood pressure*, autonomic centers of the medulla activate the parasympathetic nervous system (aka “rest-and-digest” division of peripheral nervous system); thus, the parasympathetic nervous system serves as an **effector**. The parasympathetic nervous system innervates the pacemaker of the heart by way of the vagus nerve. The vagus nerve releases acetylcholine onto the SA and AV nodes, decreasing heart rate and cardiac output. A reduction in cardiac output decreases blood pressure (Chopra et al. 2011). Stimulation of the neurally mediated blood pressure regulation system will cease when the baroreceptor firing pattern reflects that of normal pressure conditions for that individual. Control systems regulating important biological variables such as blood pressure often contain multiple sensors, error detectors, control centers, and/or effectors.

The endocrine system produces several hormones that target the kidneys to help eliminate



excess fluid or retain fluid; some of the endocrine system's hormones regulate ionic (electrolyte) homeostasis, as well. Because of their roles in fluid balance, the endocrine and urinary systems are important in blood pressure regulation. Aldosterone is the “salt-retaining” hormone produced by the adrenal cortex. Aldosterone is released from the adrenal cortex when blood pressure drops, blood  $\text{Na}^+$  levels fall, or blood  $\text{K}^+$  levels rise. Aldosterone acts in the kidneys to reabsorb  $\text{Na}^+$  into the blood for retention and secrete  $\text{K}^+$  into the urine for elimination. As  $\text{Na}^+$  moves into the blood, chloride and water follow and are retained by the blood. As water moves into the blood, blood volume and blood pressure rise. Aldosterone secretion ceases when blood pressure and electrolyte levels return to the homeostatic set point (Saladin 2017). Angiotensin is a hormone whose production is triggered by a decrease in blood pressure (Saladin 2017). The active form of angiotensin, called angiotensin II, acts at both central and peripheral sites to restore blood pressure. Angiotensin II triggers widespread vasoconstriction, raising blood pressure. It also acts in the hypothalamus to stimulate a thirst sensation which encourages fluid intake. Fluids consumed will be absorbed from the gastrointestinal tract into the bloodstream, raising blood volume and pressure. Antidiuretic hormone (ADH), or vasopressin, is produced in the hypothalamus and stored in the posterior pituitary gland. During dehydration-induced (low blood volume; high blood osmolarity) hypotension, ADH is released from the posterior pituitary into the blood stream. ADH acts in the collecting duct of the kidney, stimulating the production and installation of aquaporins (water channels) (Boron and Boulpaep 2012). As aquaporins are installed, more water is reabsorbed back into the blood, restoring normal blood volume and blood pressure. Atrial natriuretic peptide (ANP) is produced by the atrial myocardium of the heart. ANP is released into the bloodstream when systemic blood pressure is high. It uses two main strategies to lower blood pressure. First, ANP increases urine production in the kidneys (increases blood flow to kidneys and attenuates reabsorption of  $\text{NaCl}$  and water); more water is eliminated via

the urine. Second, ANP inhibits the secretion of aldosterone, angiotensin, and antidiuretic hormone (all of which raise blood pressure). By inhibiting hormones that raise blood pressure, systemic blood pressure will fall (Hall 2016). Paracrine (local) mechanisms for blood pressure control also exist; cells within the walls of blood vessel can secrete chemicals which regulate blood pressure (Hickey et al. 1985). The blood pressure homeostatic control mechanisms outlined in this entry illustrate the truly complex nature of maintaining internal biological constancy. Other important biological variables, such as acid-base balance, have equally elaborate control mechanisms. Like blood pressure homeostasis, acid-base homeostasis involves multiple organ systems, including the urinary, respiratory, and skeletal systems.

## Cross-References

- [Angiotensin](#)
- [Circulatory System](#)
- [Endocrine System](#)
- [Excretory System](#)
- [Hypothalamus](#)
- [Nervous System](#)
- [Neurotransmitters](#)
- [Thermoregulation](#)
- [Vasal-Vagal Stimulation](#)

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## Homicide

- [Martin Daly and Margo Wilson](#)

## Homing

- [Bear Navigation](#)

## Hominid

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## Introduction

Hominids are the group of primates known as the great apes, which includes orangutans (Tapanuli, *Pongo tapanuliensis*, Sumatran, *Pongo abelii* and Bornean, *Pongo pygmaeus*), gorillas (Western gorilla, *Gorilla gorilla*, and Eastern gorilla, *Gorilla beringei*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and humans (*Homo sapiens*). The following chapter will address some of the most prominent cognitive abilities assessed among nonhuman hominids, addressing both physical and social cognition and where the two domains intersect. This will be followed by a discussion of how cognition is linked to behavior, particularly with regard to social behavior. The covariation between cognitive abilities and behavioral traits will then be addressed, considering indications that both share the same underlying mechanisms.

## Hominid Cognition: What Is Known So Far

Among nonhuman apes, two broad cognitive categories have been defined – physical cognition and social cognition. Physical cognition is defined as the ability to deal with the physical environment, through locating, selecting, and extracting food (Herrmann et al. 2007). To forage successfully, individuals must be able to deal with space, quantity, and causal reasoning, the latter referring to the relationship between, for example, a tool

(the cause) and the retrieving of food (the outcome). Social cognition on the other hand deals not with inanimate objects but with the social environment. Social skills are imperative to group living, enabling an individual to form bonds which are crucial to receiving social support during disputes. Social cognition allows individuals to balance competition and cooperation in a group, through learning from, manipulating, and predicting behavior of others (Herrmann et al. 2007). To achieve these goals, social learning, communication, and perception are key.

The Primate Cognition Test Battery (PCTB) is a series of tests that encompass both physical and social cognitive ability in great apes (Herrmann et al. 2007). These tests range from assessing spatial memory, quantity discrimination, and tool use to tasks which require problem-solving by observation, following cues to find a hidden reward, and understanding intentions. The extent to which different species perform on these tasks varies. Chimpanzees perform better than orangutans, but similar to human children, on tasks assessing physical cognition. Contrastingly, chimpanzees and orangutans perform about the same on social cognition tasks, which is significantly lower than the performance of children (Herrmann et al. 2007). When chimpanzees are compared with their closer cousins, bonobos, there is overall little difference in performance in either domain; however notably, chimpanzees outperform bonobos on tool use tasks, whereas bonobos are more successful than chimpanzees on tasks assessing Theory of Mind (Herrmann et al. 2010), that is, the ability to understand the perspective, intentions, or feelings of another. Such differences likely derive from the immediate environmental demands of each species. Chimpanzees experience higher resource competition than bonobos, which could make extractive foraging skills advantageous in an environment where food is harder to come by. Bonobos on the other hand experience a more socially tolerant society, which is likely to provide selection pressure for empathetic and perspective-taking behaviors.

While it appears that there are cognitive similarities throughout the great apes, species variation in cognition could be attributed to differences in social systems. Species that exhibit fission-fusion dynamics, where group composition

changes continuously, have been found to perform better on tasks testing inhibition, such as through foregoing a smaller reward to wait for a bigger one (Amici et al. 2008). In these tasks, chimpanzees, bonobos, and orangutans outperformed gorillas. This supports the theory that living in a socially unstable environment is associated with more behavioral flexibility and, importantly, highlights that social structure rather than taxonomy should be considered when understanding species differences in cognition. An additional point to consider is that, while tests such as the PCTB treat physical and social cognition as distinct entities, group living often requires that these two domains be employed simultaneously. Indeed, data from 62 primate species (including chimpanzees, bonobos, the Bornean orangutan, and the Western gorilla) found that traits of both physical and social cognition are highly correlated, suggesting coevolution of different intelligence domains (Reader et al. 2011). To better understand how social and physical cognition intersect one another and to understand the behavioral and ecological relevance of these cognitive domains, it is necessary to consider their application in not only a captive but also a wild context.

## Hominid Behavior: Links to Cognition

In terms of physical cognition, behavior is important in understanding how individuals deal with their environment. For example, without observing tool use in wild chimpanzees, there is no way to understand the ecological relevance of observing spontaneous tool use in a captive population. The way in which a tool is chosen, manipulated, and applied can provide insight into the underlying cognitive processes. If an individual is observed cutting or stripping a stick to make it shorter or sharper for a particular purpose, it could be said that they understand the causal relation between a particular tool type and a given food source. An understanding of cognitive abilities is thus very dependent on observational studies and, furthermore, measuring behavioral responses.

Captive studies now indicate that chimpanzees, bonobos, and orangutans do seem to have a concept of false belief, which has long been considered

to be a uniquely human aspect of Theory of Mind. Buttleman and colleagues (2017) found that the apes behaved similarly to 16- and 18-month-old human children in a helping task that required them to understand that the experimenter had a false belief about the location of an object. The apes were more likely to correctly locate the object for their human counterparts in the false belief trials compared with trials when the experimenter knew where the object was or was generally ignorant about the location of the object. While such studies are pivotal in understanding and defining ape cognition, especially in comparison to humans, an understanding of concepts such as Theory of Mind is not complete without studies from wild populations. For example, chimpanzees have been found to warn naïve group members of potential danger (a planted model snake) when they are aware that the group member is unaware of the danger (Schel et al. 2013). The fact that alarm calls were directed to the arrival of friends, and only stopped when new arrivals observed the snake, suggests that wild chimpanzees can understand what conspecifics do and do not know and that they can use communication intentionally to alter the behavior of conspecifics. Such a finding suggests that perspective-taking is evident in wild chimpanzees and is not simply an artifact of captivity. This is also a key example of how physical cognition (knowledge of potential danger) and social cognition (communication about the potential danger) are integrated into group activity and individual behavior.

One problem with studying the relation of behavior to cognition is that the overlap between the two is sometimes hard to define. For example, empathy can be a part of cognition in the form of perspective-taking, such as “putting oneself in someone else’s shoes”; but it can also be as basic as a physiological response, as in the form of emotional contagion, a response that completely bypasses the need for cognitive input (de Waal 2008). Helping behavior is also considered a form of empathy, another example of where cognition and behavior intersect. Chimpanzees will give a tool to a requesting conspecific, if they do not need the tool themselves (Yamamoto et al. 2009), thereby understanding the request of the conspecific (social cognition) and the purpose for

which the tool is required (physical cognition) and choosing whether or not to act on that understanding (behavior).

In addition to aiding an understanding of cognitive abilities observed in captivity, studies from the wild highlight the importance of studying behavior and cognition in parallel. Like different cognitive domains, the two do not operate independently. The current understanding of ape cognition is based very much on evidence from captivity, where controlled experiments such as Theory of Mind tests and test batteries are easier to conduct. Yet the continued study of wild behaviors, such as localized differences in tool use, social learning, helping behavior, and social knowledge, is informative in understanding the origins of cognitive abilities.

## Underlying Mechanisms of Cognition and Behavior

In general, observing behaviors informs two diverging questions: (1) with regard to species differences and (2) with regard to individual differences. The consideration of species differences has already been highlighted above. This section will therefore focus on individual differences.

Since the days of Darwin, observers of behavior have noted that the behavior of any given population may be variable. Where some individuals are shy, others are bold. Where some are aggressive, others may be fearful. The question thus is not whether behavioral variation exists, but why it exists. Behavioral ecologists have argued that variation in the population is required for natural selection to act, and is the basis for, rather than a product of, natural selection. It is now becoming clear that in a socially complex group, there is not one optimal strategy and that individuals produce consistent patterns of behavior across time and context which can differ from other group members. In recent years, a stronger focus has fallen on understanding individual differences in behavioral variation, which is now often framed in terms of “personality.”

Assessing personality is informative in cognitive terms to understand why some individuals succeed at tasks where others fail or why some

individuals are motivated toward a given task where others lack interest. Assessment of individual differences is also informative to understanding the links between cognition and behavior. While the study of behavior is of particular relevance to the understanding of cognition, behavioral traits may also covary with attention to or performance on particular tasks. Captive chimpanzees rated by keeper questionnaires as being high on openness, a component comprising traits such *inquisitive* and *inventive*, were found to be more consistently engaged in a series of touch screen tasks that assessed aspects of physical cognition (Altschul et al. 2017). Individuals with higher conscientiousness scores (not *reckless*, not *distractible*) also participated in these tasks more often and were less likely to drop out than low-conscientiousness counterparts. These and similar findings are indicative of underlying shared mechanisms that contribute to variation in cognition and behavior. Assessing not only the links between cognition and behavior but also the possible mechanisms that contribute to their covariation – be it genetic, environmental, or epigenetic – is an important step in understanding intraspecific variation in cognitive abilities.

Interspecific comparisons of personality also allow an understanding of how species differ in behavioral variation and provide consideration of what differences in selection pressures could have resulted in these trait differences. For example, it is hypothesized that the complexity of fission-fusion societies, as found in chimpanzees, bonobos, orangutans, and humans, has led to separate dimensions of agreeable and extraverted traits, compared with gorillas, who live in tight family units and exhibit a single dimension of sociable traits (Eckardt et al. 2014).

These studies highlight the role that personality assessment can play in understanding not only intraspecific variation in cognition but also a comparative understanding of cognition and behavior among the great apes. Combined with observations in the wild and cognitive tasks implemented in captivity, personality assessment provides a third dimension to the understanding of great ape cognition.

## Conclusion

This chapter highlights the different aspects of hominid physical and social cognition, their overlap and links to behavior, and finally the importance of considering individual differences when studying behavior and cognition. It is important to note that this is in no way a thorough assessment of the literature and provides simply an overview which should allow readers direction should they wish to learn more on these topics. It is also noteworthy to add that, while the study and knowledge of hominids is growing, much of this research is biased toward chimpanzees, likely due to their larger group sizes which are more suited to research. The comparative perspective would certainly benefit from more cognitive research in gorillas.

## Cross-References

- [Catarrhine Cognition](#)
- [Comparative Cognition](#)
- [Hominoid](#)
- [Primate Cognition](#)
- [Primate Communication](#)
- [Primate Social Structure](#)
- [Prosimian Cognition](#)

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## Hominid Phylogeny

### ► Last Common Ancestor

## Hominoid

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## Introduction

This chapter will be similar in structure to the chapter on hominids, with the exception that it will focus on the similarities and differences in

physical cognition, social cognition, and behavior between the great apes (hominids) and all apes (hominoids) which includes the addition of the lesser apes, gibbons (Hylobatidae). Current phylogenetic understanding of the gibbons proposes that there are 4 distinct genera, *Hoolock*, *Symphalangus*, *Nomascus*, and *Hylobates*, and up to 20 distinct species (Fan et al. 2017). Despite such diversity, comparative assessment of cognition has focused primarily on the great apes, and there is much still to understand about hominoid cognition as a whole. Yet the behavioral differences between gibbons and their great ape cousins could provide a better basis for the phylogenetic understanding of the variation in cognitive ability. This chapter will touch on the need to understand environmental influences that may have provided selection pressures for particular cognitive abilities, such as habitat, group size, and social structure. Such an understanding could be influential in addressing differences in ability across the primate phylogeny.

## Gibbon Cognition: Are Lesser Apes Lesser?

As the taxonomic link between hominids and Old World monkeys, the study of gibbon cognition is key to understanding the evolution of both physical and social cognitive abilities among primates. Comparisons on the Primate Cognition Test Battery between apes (chimpanzees and orangutans) and Old World monkeys (long-tailed macaques and olive baboons) reveal that cognitive differences between the two clades are perhaps not as vast as has been suggested (Schmitt et al. 2012). Comparisons revealed parallels in performance across species in tasks assessing physical and social cognition, the primary difference being in the monkeys' lower performance than apes on causal reasoning tasks, such as using a tool to obtain a reward (for more details see chapter "► Hominid"). Given this indication of domain-level similarities in monkey and great ape cognition, it is interesting to consider where the gibbons or "lesser" apes fit into this picture.

The following section will consider this picture in more detail.

Assessed on a task that examined their ability to demonstrate flexible learning, gibbons (*Hylobates*, *Symphalangus*, and *Hoolock*) failed to transfer knowledge from one learned association to another, something that has been demonstrated in rhesus macaques and chimpanzees (D'Agostino and Cunningham 2015). Such an ability should simplify learning on a new but similar task to one learned previously. Despite not making the knowledge transfer quickly, gibbons from four different species were able to learn individual food color associations, with notable differences in learning rate between species. This latter finding may point to different environmental pressures in learning rate. For example, *Hoolock* gibbons, who live in a highly variable environment, learned faster than their *Hylobates* counterparts, whose access to food resources is more stable (D'Agostino and Cunningham 2015). While strong conclusions cannot be drawn regarding the relationship between learning in a captive group and its relation to natural selection pressures, these findings raise the question whether differences in environment, and not just phylogenetic similarities, should be considered when addressing comparative cognition.

A key aspect of physical cognition is the ability to use and manipulate tools to access food. On a task assessing tool use, captive housed hoolock gibbons (*Bunopithecus hoolock*) were able to use a rake to access a food reward, showing similar if not slightly better performance to a similar task done with chimpanzees and capuchins (Cunningham et al. 2006). While this finding suggests that the gibbons may have had a causal understanding of the spatial relationship between the tool and the reward, the fact that some individuals performed below chance to start with and then improved their performance with time could also indicate associative learning. Observations of gibbons' use of tools are somewhat limited (Geissmann 2009), suggesting that either they do not commonly use tools in the wild or that observations and reports of gibbon tool use

are simply lacking. In one observation, it was suggested that a female white-handed gibbon (*Hylobates lar*) frequently used an enclosure door as a tool by incorporating the sound of a door slam into her "great call," a phase of a call sequence where the male and female form a duet (Geissmann 2009). Renowned for their call repertoires, it is perhaps key to understanding gibbon cognition to explore the role of communication in relation to their knowledge and understanding of both the social and physical environment.

Assessment of gibbon social cognition reveals, similar to the limited findings for physical cognition, that gibbons do not consistently compare with their great ape cousins. In an assessment of gaze following – an important prerequisite to perspective-taking behavior – gibbons of four different species (genera *Hylobates* and *Symphalangus*) did demonstrate gaze following in response to a human glancing upward, in a manner comparable to great apes (Liebal and Kaminski 2012). However, this finding did not hold when only initial looks were considered, that is, in first response to the experimenter, gibbons were generally more vigilant but did not necessarily follow their gaze directly. Unlike adult chimpanzees, the gibbons also did not habituate, i.e., change their response, as they became accustomed to the looking behavior of the experimenter. This suggests that their response was reflexive, rather than representing a more developed cognitive process, such as perspective-taking.

As discussed in the "► Hominid" chapter, perspective-taking has been demonstrated in a variety of ways in great apes. Given that an understanding of perspective-taking in other primate species could redefine the general definition of what it means to be human, it is a topic of heated discussion among primatologists. A topic of similar debate is that of self-recognition. Is a sense of self uniquely human, or do other primates possess a similar self-awareness that distinguishes them in their mind from others? There is strong evidence that chimpanzees, bonobos, and orangutans exhibit mirror self-recognition through the use of spontaneous self-exploratory behaviors in front of

a mirror. The evidence from gibbons, however, indicates otherwise. When faced with a mirror, members of three different gibbon species (*Hylobates*, *Symphalangus*, *Nomascus*) did demonstrate some self-directed behavior; however all failed to pass the mark test, i.e., to exhibit any behavior directed toward a mark made on the forehead, as has been observed in great apes (Suddendorf and Collier-Baker 2009).

These studies of social cognition indicate that there do appear to be differences in the perceptions of self and other between gibbons and great apes. In general, the limited evidence available on physical and social cognition in gibbons suggests that they do not compare with great apes' ability to perceive and manipulate their world. Whether this is a matter of phylogeny or of differences in selection pressures relating to social complexity remains to be seen: this shall be explored in the following section.

### Gibbon Behavior: Links to Cognition

To understand the selection pressures behind gibbon cognition, one should draw not only on the phylogenetic distance of Hylobatidae from humans and other apes but also on the environment in which they live. In addition to the variation in experience of environmental fluctuations among the Hylobatidae family, the social environment experienced by gibbons is contrastingly different to the fission-fusion groups of *Pan* and *Homo*, the multi-female harems of *Gorilla*, or the semi-solitary lifestyle of *Pongo*. Gibbons typically form pair bonds and live in family units with immature offspring, although these pair bonds are not necessarily lifelong, and extra-pair copulations have been known to occur (Palombit 1994). The gibbon duet is considered to be an indicator of pair bond strength: in captive siamangs, duetting activity positively relates to grooming frequency and behavior synchronization between mates, and negatively to distance between mates, which supports the notion that duetting may act to strengthen pair bonds (Geissmann and Orgeldinger 2000). Although

gibbon units experience emigration of offspring, and may also experience immigration of a new bond partner, the fluctuation in their social group is relatively less than experienced by the majority of their great ape cousins. With the exception of orangutans, group size of gibbons is typically smaller too. According to the social complexity hypothesis, group social complexity provides selection for higher cognitive ability, in order to keep up with the cognitive demand for maintaining an increasingly large social knowledge. The lack of such social complexity in gibbons could explain the apparent differences in cognition between the small and great apes.

There are however also behavioral similarities between these two clades. For example, a broad and variable repertoire of tactile and visual gestures has been observed in captive siamangs (*Symphalangus syndactylus*) (Liebal et al. 2004). While the context of these gestures often appeared flexible, some were used in similar ways to chimpanzees, such as the *wrist offer*, a submissive gesture, which was used by a subadult female siamang in response to aggression from her mother. The gestures observed also bore some similarities to those noted in monkeys, in that the siamangs used more tactile rather than visual gestures in social interactions (Liebal et al. 2004). By this evidence, the Hylobatidae seem to share aspects of both monkey and great ape communication. From here, a useful approach would be to draw links between social cognition and species-specific behavioral repertoires of gibbons, which would be informative to understanding the role of both social and environmental factors in cognitive ability.

An additional area of behavioral research that has been little addressed in gibbons is the assessment of individual differences. Like their great ape cousins, individual gibbons have been observed to vary in their interest in, boldness toward, and performance on cognitive tasks (D'Agostino and Cunningham 2015; Suddendorf and Collier-Baker 2009). There is, however, no apparent assessment of how these responses to test stimuli covary in some way with particular behavioral traits. Furthermore, a comparative

assessment of intraspecific behavioral variation between gibbons and great apes could help to establish patterns of trait commonalities across the hominoid family.

## Conclusion

The evidence presented in this chapter suggests that there is considerable variation in cognitive ability among the hominoids, with gibbons generally showing performance on physical and social cognition tasks that are not comparable with performance observed in great apes. While it is easy to hypothesize that these differences could be related to a reduced social complexity in gibbons, it is important to remember that cognitive and even behavioral studies conducted on gibbons are far fewer than for great apes. Furthermore, sample sizes are often too small to draw any definitive conclusions about species-wide ability (Liebal and Kaminski 2012). More urgent in the gibbon literature is the need to establish a clear phylogeny and to implement effective conservation measures for threatened species. Second to that comes the understanding of behavior or cognition. Yet a more detailed assessment of gibbon cognition, as well as its behavioral correlates, particularly in direct comparison to both great apes and Old World monkeys, would be greatly beneficial to a comparative understanding of primate cognition, and to what extent this is related to differences in environmental and social demands, or phylogeny.

## Cross-References

- Catarrhine Cognition
- Catarrhine Locomotion
- Comparative Cognition
- Haplorhini
- Hominid
- Primate Cognition
- Primate Communication
- Primate Social Structure

- Primate Sensory Systems
- Prosimian Cognition

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## Hominoidea Gaits

- Hominoidea Locomotion

## Hominoidea Locomotion

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## Synonyms

[Ape gaits](#); [Ape locomotion](#); [Hominoidea gaits](#)

## Definition

Patterns of movement observed in members of the Hominoidea superfamily.

The ape superfamily, Hominoidea, is a clade of Old World anthropoids (Catarrhini) (Fig. 1) that are native to Africa and Southeast Asia. In contrast to other primates, apes are tailless, wide bodied, and possess a wider range of motion at the shoulder joint. This greater degree of shoulder range of motion likely evolved as a result of arm-swinging (i.e., brachiation), which is the ability of animals to suspend and swing from tree to tree only using the forelimbs (Haviland et al. 2013). The Hominoidea superfamily consists of two families: Hominidae (great apes) and Hylobatidae (gibbons).

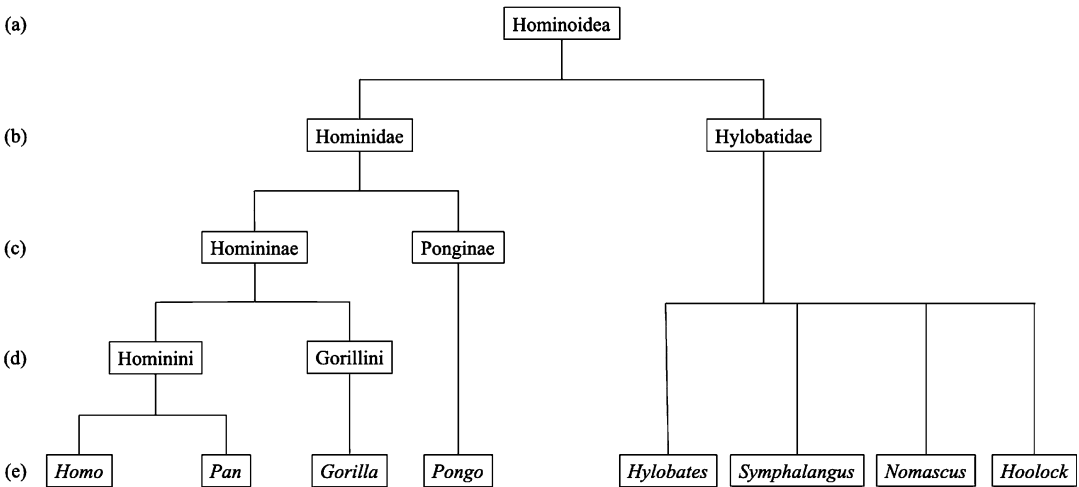
Gibbons, also known as “lesser apes” or “smaller apes,” are the most diverse extant taxa of Hominoidea. They are further classified into four genera: *Hylobates*, *Symphalangus*, *Nomascus*, and *Hoolock*. Unlike the Hominidae, gibbons are smaller in size and show minimal sexual dimorphism. They live in the subtropical and tropical rainforests of Southeast Asia, South China, Bangladesh, and Northeast India (Cunningham and Mootnick 2009). Gibbons are highly arboreal apes that are masters of brachiation. They are often

referred to as “acrobats of the forest” due to their ability to leap up to 8 m between branches with speeds reaching approximately 56 km/h (Cunningham and Mootnick 2009). Their alternate mode of locomotion on tree branches is bipedal, holding their extraordinarily long arms aloft for balance as they walk (Cunningham and Mootnick 2009). Additionally, gibbons are capable of quadrupedal climbing (Feldhamer et al. 2007).

Hominidae are the largest primates and exhibit strong sexual dimorphism, with males being larger than females (Feldhamer et al. 2007). The Hominidae family is composed of two subfamilies: Homininae and Ponginae. The Ponginae subfamily has one extant genus, *Pongo* (orangutans), with three extant species, all of which the International Union for Conservation of Nature (IUCN) currently lists as critically endangered (Ancorenaz et al. 2016; Nowak et al. 2017; Singleton et al. 2017). These Ponginae species are the Sumatran orangutans (*Pongo abelii*), Tapanuli orangutans (*Pongo tapanuliensis*), and Bornean orangutans (*Pongo pygmaeus*). Orangutans are large apes usually found living in lowland and hilly tropical rainforests. They spend most of their time in trees and their main mode of locomotion is brachiation and inverted quadrupedalism. Using their long arms, orangutans move slowly and travel great distances through the lower tree branches (Haviland et al. 2013).

Homininae, also called “African apes,” are further divided into two taxonomic tribes: Hominini and Gorillini. Homininae walk quadrupedally on their knuckles and are also capable of standing erect to walk bipedally (Haviland et al. 2013). The Gorillini tribe contains one extant genus: *Gorilla*. The gorillas are the largest in the Hominoidea species and are mostly found in the tropical rainforests of East and West Africa (Feldhamer et al. 2007). They are herbivores and spend most of their day eating plants (Haviland et al. 2013). Though primarily terrestrial, gorillas are capable of climbing trees and may even nest in them at night (Feldhamer et al. 2007; Haviland et al. 2013). In addition, male gorillas will also stand bipedally to perform their chest-beating displays (Feldhamer et al. 2007).





**Hominoidea Locomotion, Fig. 1** Cladogram of the extant Hominoidea: (a) Hominoidea superfamily; (b) Hominidae and Hylobatidae families; (c) Homininae and

Ponginae subfamilies; (d) Hominini and Gorillini tribes; (e) *Homo*, *Pan*, *Gorilla*, *Pongo*, *Hylobates*, *Symphalangus*, *Nomascus*, and *Hoolock* genera

Hominini has two extant genera: *Homo* and *Pan*. The genus *Pan* consists of two extant species: *Pan troglodytes* (chimpanzees) and *Pan paniscus* (bonobos). Both chimpanzees and bonobos are currently listed as endangered species by the IUCN. Moreover, in 2017 the Convention on Migratory Species selected the chimpanzees for special protection (Redmond 2017). Chimpanzees, also called “common chimpanzees,” “robust chimpanzees,” or “chimps,” are adapted for both arboreal and terrestrial locomotion. Their diet is composed of fruits, leaves, seeds, flowers, and meat (Feldhamer et al. 2007; Goodall 1986). Chimpanzees are widely distributed in sub-Saharan African forests and the savannah, with a tendency to build their nests over a wide area (Haviland et al. 2013). Bonobos, also called “pygmy chimpanzees,” are slightly smaller than common chimpanzees (Feldhamer et al. 2007). Bonobos are found exclusively in the rainforests of the Democratic Republic of Congo. In contrast to chimpanzees, they prefer to build their nests close to one another (Haviland et al. 2013). The bonobo’s diet is herbivorous, primarily consisting of fruits, leaves, seeds, flowers, and other plant matter (Feldhamer et al. 2007). Both chimpanzees and bonobos forage quadrupedally by knuckle-walking on the ground during the day and then return to the trees at sunset (Haviland et al. 2013).

Chimpanzees and bonobos are also capable of bipedalism, but this locomotor mode is less frequently used because the “bent-hip bent-knee” bipedal posture of these species is expensive energetically (Aiello and Dean 2002; Alexander 2004).

The genus *Homo* contains only one extant species, *Homo sapiens*, referred to as hominins or humans. The ability to stand upright and accommodate bipedal locomotion is a distinct feature of hominins, relying on the positioning of their body’s center of gravity directly over the area of the feet in standing position. Moreover, horizontal displacement of the center of gravity during bipedal locomotion is minimized by the structure and positioning of the femur, which results in a shorter lateral distance movement above the alternating stance legs (Aiello and Dean 2002).

## Major Locomotor Modes

The various modes of *Hominoidea locomotion* are specially adapted to navigate both the arboreal and terrestrial environments in which they live. During arboreal locomotion, one of the most common locomotor modes employed is climbing, most often on vertical supports. Vertical climbing is of vital importance to apes, as it is essential for

travel, escape, foraging, and seeking safe locations to rest (Cartmill 1985; Granatosky et al. 2019; Hanna et al. 2017). In primates, symmetrical gaits are mainly used to climb vertically if the diameter of the substrate (the tree) is smaller than the diameter of the body (Granatosky et al. 2019). These gaits utilize a lateral-sequence gait pattern (hindlimb followed by ipsilateral forelimb), during which the hindlimb serves as the primary support for the body weight and functions to propel the ape vertically throughout climbing (Hanna et al. 2017). Furthermore, while vertically climbing with symmetrical gaits, apes tend to move slowly with long intervals of grasping the substrate to maximize both their stability and security (Granatosky et al. 2019). However, asymmetrical gaits are most often used for vertical climbing when the diameter of the substrate is substantially larger than the diameter of the body, as the ape is forced to wrap itself around the substrate to ascend. In these gaits, each pair of feet (fore and hind) function more or less together and move at the same time or in couplets (Cartmill 1985; Hildebrand 1989).

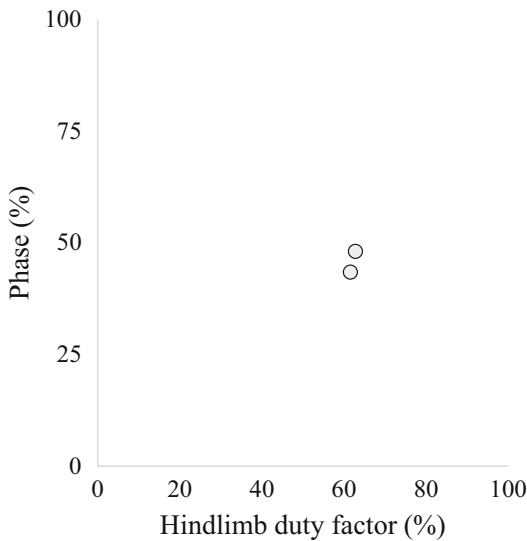
Suspensory locomotion is perhaps the most common form of locomotion associated with the apes, despite the fact that such behaviors are rarely observed in African great apes beyond the juvenile stage (Granatosky 2016). Below-branch quadrupedal locomotion, also known as inverted quadrupedal locomotion, is common for the orangutans. During below-branch quadrupedal locomotion, the torso is pronograde (parallel to the ground) with both the forelimbs and hindlimbs used to hang beneath the substrate (the tree branch) and bear the body weight, loading the limbs in tension (Granatosky and Schmitt 2019; Stern 1975). Diagonal-sequence gait patterns (hindlimb followed by contralateral forelimb) are utilized and the forelimbs are the dominant weight bearing limbs, suggesting that this locomotor form may be a mechanical intermediate transition to another suspensory locomotor mode known as arm-swinging (Byron et al. 2017; Granatosky and Schmitt 2019).

Arm-swinging (also referred to as brachiation) is a form of forward movement where an ape hangs beneath the substrate and then advances

forward only using the forelimbs. This fluid motion appears to operate on the principle of the pendulum, in which energy is saved by switching between kinetic energy (movement of the body) and potential energy (height of the body) throughout the swing (Byron et al. 2017). However, these natural pendular motions only function as a way to reduce energy use (muscular involvement) in continuous-contact locomotion and very slow speeds. The complex three-dimensional arboreal environments in which arm-swinging occurs makes this simple pendular motion difficult to maintain for any appreciable distance. Instead the ability to maintain flexible locomotor cycling takes precedence over energy conservation (Byron et al. 2017; Fleagle 2013).

During both arboreal and terrestrial locomotion, apes utilize quadrupedalism as their most common locomotor mode (Granatosky 2018; Hunt et al. 1996). However, it is important to recognize that the primate quadrupedal gait is unique compared to the quadrupedal gaits of other mammals. Most other quadrupedal mammals tend to use lateral-sequence footfall patterns with a retracted humerus at forelimb touchdown and higher peak vertical forces on the forelimbs relative to the hindlimbs. Conversely, primate quadrupedal locomotion employs a diagonal-sequence footfall pattern with a protracted humerus at forelimb touchdown and higher peak vertical forces on the hindlimbs relative to the forelimbs (Granatosky et al. 2019; Granatosky and Schmitt 2019; Schmitt and Lemelin 2002). Apes, especially the gorilla and chimpanzee, often violate the diagonal-sequence diagonal-couplet pattern when walking on the ground and instead adopt lateral-sequence diagonal couplet gaits (Fig. 2).

African apes are unique in that they display a further specialization of quadrupedal locomotion known as knuckle-walking (Fleagle 2013; Schmitt et al. 2016). This form of quadrupedalism is favored as it is thought to reduce the finger bending loads of palmigrade and digitigrade postures (Schmitt et al. 2016). Knuckle-walking is differentiated from the other forms of quadrupedalism via the elevation of the palm and proximal phalanges above the substrate. The



**Hominoidea Locomotion, Fig. 2** “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in *Gorilla* and *Pan troglodytes* ( $n = 2$  species)

hand may be pronated or partially supinated with flexed intermediate phalangeal joints and neutral or slightly hyperextended metacarpophalangeal joints (Fleagle 2013; Schmitt et al. 2016). This places most of the body weight on the dorsal aspect of the middle phalanges, which are contacting the substrate. In a similar vain to reduce loads on the long digits, the orangutans have adopted their own unique form of quadrupedalism known as fist-walking. While fist-walking, the interphalangeal and metacarpophalangeal joints are flexed (making a fist) with the hand pronated or partially supinated and the thumb either touching the ground or not. This places the weight on the proximal phalanges as opposed to the middle phalanges as in knuckle-walking. If an orangutan is fist-walking either adducted or abducted (wrist deviated either radially or ulnarly), then the weight can be borne on the medial or lateral edge of the manus, on the thumb and medial edge of ray two, or on the lateral edge of ray five (Schmitt et al. 2016).

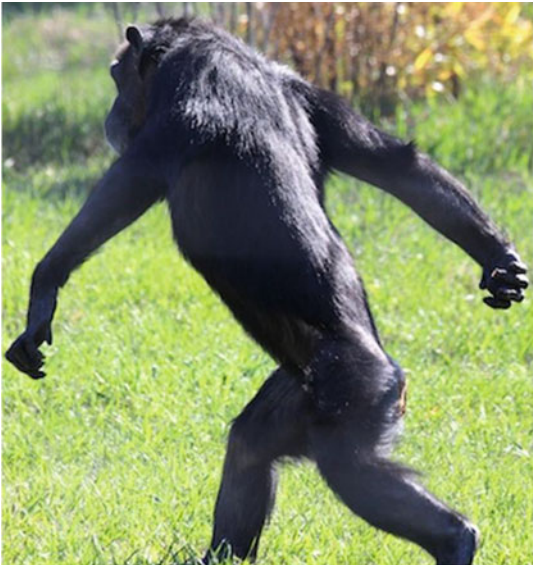
Although apes usually travel quadrupedally terrestrially and arboreally, almost all demonstrate some manner of bipedal tendencies (Alexander 2004; Hunt et al. 1996). Similar to arm-swinging,

walking bipedal gaits are dependent on the principle of the pendulum, or in the case of bipedalism, an inverted pendulum. Although this type of motion is able to conserve energy when walking, it does not do so during running. Nevertheless, elastic mechanisms are able to preserve energy during running because the kinetic and potential energy lost in the first half of a step is stored as elastic strain energy in stretched tendons and ligaments then released through elastic recoil in the second half of the step (Alexander 2004). The use of bipedalism in apes is rare, often demonstrated in the context of display or food acquisition (Alexander 2004; Richmond et al. 2001). In fact, 80% of chimpanzee bipedalism, most of which is postural, occurs during feeding. Bipedalism is favored over quadrupedal locomotion in this situation as it permits a higher reach into short trees and the ability to continuously gather fruit with both hands (Richmond et al. 2001).

The bipedal gait of apes, commonly described as bent-hip bent-knee walking, positions the trunk sloping forward and the knees strongly bent at mid-stance, placing the body’s center of mass in front of the hips. In this posture, the trunk is more erect than in quadrupedal walking and the knees must be kept anterior to the hips throughout the stance phase to ensure the force on the foot is vertical and in line with the center of mass. Furthermore, the longitudinal components of force on the ground allow the forward velocity of the center of mass to pass through a minimum while moving over the supporting foot, which keeps the resultant force on the foot in line with the center of mass. This is achieved by the foot pushing both forward and down while in front of the body to decelerate as well as support it and then pushing backward and down when behind the body to accelerate it. When moving bipedally, apes often take shorter strides than in quadrupedal locomotion and tend to utilize plantigrade locomotive postures (placing the entire foot on the ground) with the heel and lateral midfoot striking the ground at the same time (Alexander 2004) (Figs. 3 and 4).

In contrast, the human bipedal gait is often referred to as “striding.” This is largely attributable to the smooth means of traveling during

**Hominoidea Locomotion, Fig. 3** Differences in where the body weight passes during bipedal locomotion in (a) *Pan* and (b) *Homo*. Medial portion of both feet are on the left



(a)



(b)

**Hominoidea Locomotion, Fig. 4** Differences in the bipedal postures of chimpanzees and humans: (a) bent-hip bent-knee walking; (b) striding

which the energy output of the body is reduced to a physiological minimum (Sockol et al. 2007). While striding, humans weakly bend the knees at mid-stance, hold their trunk vertically and place the heel on the ground before any other part of the foot (Alexander 2004). The normal human walking cycle is separated into the stance phase when the foot is on the ground (further divided into heel strike, foot flat, mid-stance, and push or toe-off) and the swing phase when the foot is moving forward (further divided into acceleration, mid-swing, and deceleration). Although these phases operate simultaneously by alternating sides with the completion of each cycle, the human gait spends 60% of the time in stance phase. The center of gravity begins the cycle midway between the feet and anterior to the ankle joint, then moves in a posteroanterior direction toward the swing limb and before toe-off shifts it to the stance side where the weight is balanced to allow for forward propulsion of the swing limb. Moreover, during this cycle the body weight passes from the heel to the head of the fifth metatarsal and across the remaining metatarsal heads to the hallux (Fig. 3). This cycle is also accompanied by the regular motions of the shoulders, arms, and head, with the opposite arms and legs swinging in tandem. Arm movement in the anteroposterior plane reduces shoulder rotation keeping the head forward and balances pelvic rotation keeping the trunk straight (Schiowitz et al. 2005).

### Technological Innovation and the Evolution of Human Bipedalism

*Hominoidea locomotion* has long been an area of scientific interest, perhaps due to the wide range of locomotive modalities observed within the group and because of the common lineage shared between human and ape ancestors. Furthermore, understanding *Hominoidea locomotion* offers insight into the origin and evolution of human bipedalism, which can facilitate various technological advancements. One recent area of interest is the potential use of innate neuromotor circuits conserved across ape ancestors to treat human patients with locomotor impairments (Zehr et al. 2009).

Habitual bipedal locomotion is the defining characteristic of the earliest hominins and represents a critical divergence of humans from other ape lineages (Sockol et al. 2007). It was once believed that the inverted pendulum model observed in human bipedal walking was the result of a simple transition from quadrupedalism in a terrestrial ancestor. However, more recent experimental studies on human and nonhuman primate locomotion suggests that bipedalism evolved through multiple complex transitions that likely originated from a climbing, arboreal fore-runner (Schmitt 2003). Nevertheless, much uncertainty still surrounds the evolution of human bipedalism. One particular area that remains ambiguous is the mode of locomotion that the most recent human ancestors utilized (Fleagle 2013; Richmond et al. 2001; Stern 1975). Theories regarding the nature of locomotion of our most recent ancestor can be described using three main models: a terrestrial knuckle-walking model, a brachiation model from a small bodied suspensory ancestor, and a model based on a vertical climbing ancestor. Molecular data supporting the close phylogenetic relationship between chimpanzees and humans provides strong evidence for the terrestrial knuckle-walking model. However, there is still debate over whether or not bipedal locomotion offers a significant advantage in terms of energy conservation over quadrupedalism for the earliest hominids (Schmitt 2003; Sockol et al. 2007). To the contrary, recent experimental studies utilizing biomechanical models of climbing hominin ancestors suggest that, in terms of mechanical requirements, human bipedalism is more similar to arboreal climbing than terrestrial quadrupedalism. Nonetheless, it is likely that the earliest hominins displayed diverse locomotive modalities and that there is no single model that encompasses the gradual ten million year evolution of human bipedalism (Schmitt 2003). Scientific understanding of the hominin evolutionary timeline will continue to change as new fossil discoveries and technological advancements improve the ability to determine the species that are ancestral to humans (D'Août et al. 2014).

A crucial evolutionary model, in respect to treatment of patients with locomotor impairments,



suggests that bipedalism evolved as a result of arboreal foraging behaviors similar to those displayed by chimpanzees and orangutans (Fleagle 2013; Richmond et al. 2001; Stern 1975). More specifically, when these primates climb on branches seeking fruit, they simultaneously stand up, grasp a branch for support with one arm, and gather food with the other arm. While this may seem foreign, observing children on the playground “monkey bars” or watching infants pull themselves up when first learning to walk suggests otherwise. Recent research supports the idea that despite the different use of forelimbs during bipedal and quadrupedal locomotion, innate neuronal circuits coding for interlimb coordination and movement are preserved from our distant quadrupedal ancestors. Evidence from reflex studies in humans shows arm and leg coordination during the walking cycle that suggests the conservation of neuronal linkages for forelimb and hindlimb movements. With the help of novel technology, these innate reflexes can be used to facilitate the recovery of locomotor impairment in patients with motor deficits (e.g., after a stroke or spinal cord injury). Previous strategies used to treat neurotrauma patients focused on compensating for deficits and reconstructing damaged nerve fibers. However, emergent therapies are based on the concept that this innate neuronal network operates as the motor output for locomotion and can be exploited in rehabilitation post-neurotrauma. By activating the underlying neural circuitry linking the upper and lower extremities, the neural commands involved in rhythmic arm movement could facilitate locomotor retraining in the lower extremities (Zehr et al. 2009). Therefore, innovative rehabilitation technologies have the ability to advance towards using the intrinsic nervous system to assist in motor reprogramming.

One such innovation showing great promise in restoring mobility for severely paralyzed patients is the use of brain machine interfaces. These devices transmit neural inputs into commands that can be used to control artificial limbs, robotic wheelchairs, and similar external apparatuses. Brain machine interface technology relies on the premise that brain cortex function is preserved in a

spinal cord injury. This approach uses an artificial device to bypass the damaged spinal cord activity and enact voluntary motor intentions (Carmena et al. 2003). Experiments have shown promising results in nonhuman primates, including the ability of macaque monkeys to reach and grasp for virtual objects using a robotic arm as well as the ability to learn and navigate robotic wheelchairs with cortical activity as the primary control signal (Carmena et al. 2003; Rajangam et al. 2016). Thus, studying neuronal firing and locomotion patterns in both human and nonhuman ancestors is of critical importance for the future of neuroprosthesis.

## Conclusion

This chapter introduces the taxonomy of the Hominoidea superfamily and describes the major locomotor modes they utilize, which are vertical climbing, suspensory locomotion, quadrupedalism, and bipedalism. Suspensory locomotion and vertical climbing are important locomotor modes used by Hominoidea to navigate the arboreal landscape in which they live. The quadrupedalism of Hominoidea exhibits the distinctive features of primate locomotion and can be further specialized through the knuckle-walking of African apes or the fist-walking of orangutans. Hominoid bipedalism varies from the bent-hip bent-knee bipedal postures of chimpanzees to the habitual bipedal striding of humans. Careful observation and studying of these primary modes of *Hominoidea locomotion* has led to many hypotheses about the evolution of human bipedalism. The more recent data suggests that hominin bipedalism evolved through multiple complex transitions that likely originated from a climbing, arboreal forerunner. Furthermore, new research indicates that the innate neuronal circuits coding for interlimb coordination and movement are preserved from our distant quadrupedal ancestors, which may have important implications for the future of neuroprosthesis. Brain machine interfaces are one such ramification of this knowledge and may have the potential to restore body mobility

to paralyzed patients in the not too distant future. The future of Hominoidea locomotor research has much potential and deserves more attention, as it may one day produce lifesaving technologies that were once thought to be impossible.

## Cross-References

- Activity Budget
- Adaptation
- Adaptedness of Behavior
- Adaptive Radiation
- Arboreality
- Basal Metabolic Rate (BMR)
- Brachiation
- Canopy
- Captivity
- Catarrhine Cognition
- Catarrhine Communication
- Catarrhine Diet
- Catarrhine Life History
- Catarrhine Locomotion
- Catarrhine Morphology
- Catarrhine Navigation
- Catarrhine Sensory Systems
- Common Ancestor
- Dispersal Ability
- Dispersal Patterns
- Diurnality
- Ecology
- Evolution
- Extinction in Learning
- Gait
- Herbivore
- Home Range
- Hominid
- Hominoid
- Hominoidea Morphology
- Hominoidea Navigation
- Hominoidea Sensory Systems
- Homology
- Homoplasia
- Knuckle-walking
- Locomotion
- Morphology
- Muscular System
- Natural Selection
- Navigation
- Paleontology
- Phylogeny
- Primate Locomotion
- Prosimian Locomotion
- Quadrumanous
- Quadrupedal
- Species
- Taxa
- Terrestrial
- Vertebrate Nervous System
- Zoo
- Zoology

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## Hominoidea Morphology

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## Synonyms

Anatomy; Ape; Evolution; Primate; Taxonomy

## Definition

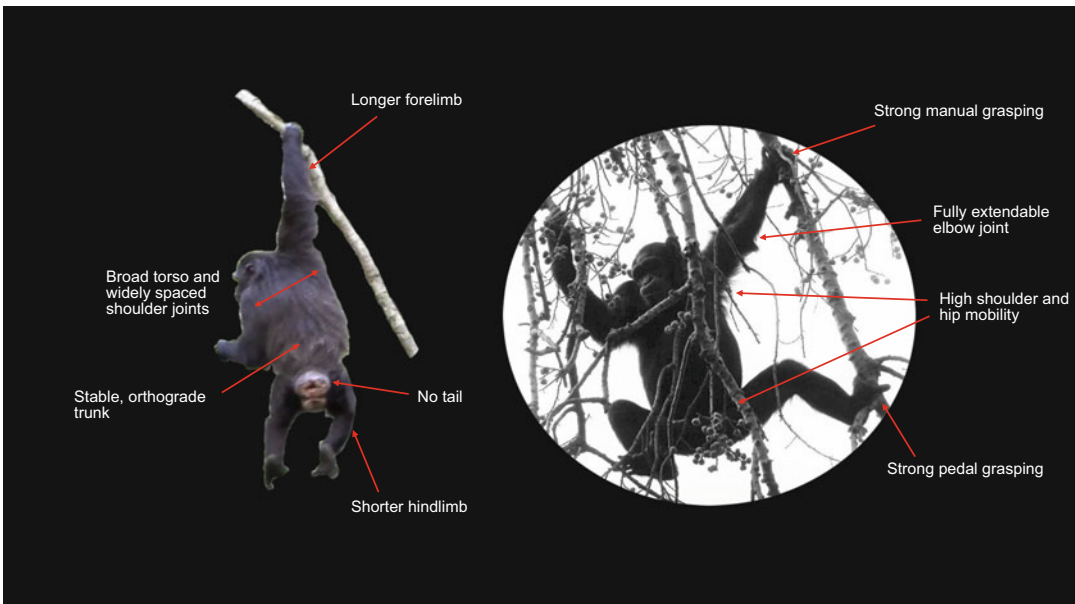
Hominoidea is the taxonomic superfamily name for all living and fossil apes and humans. Hominoidea and Cercopithecoidea (the superfamily name for Old World Monkeys) together comprise the Infraorder Catarrhini.

## Introduction

The hominoids are a group of primates comprised of the smaller-bodied hylobatids (siamangs and gibbons, body sizes range from 5 to 12 kg) and the much larger hominids (great apes and humans, body sizes range from 33 to 175 kg) (Smith and Jungers 1997). The hylobatids are taxonomically diverse, with ~20 recognized species, but are restricted to the mainland and islands of southeast Asia and are generally similar to one another in terms of overall body plan, ecology, and behavior. For example, the hylobatids are all territorial and highly arboreal, form monogamous pair bonds, have high intermembral indices (much longer forelimbs than hindlimbs), locomote using brachiation (sequential manual suspension), and feed on fruit and leaves. The hominids are less diverse in terms of living representatives, with only four genera (*Pongo*, *Gorilla*, *Pan*, and *Homo*). However, each genus has distinctive patterns of social behavior, sexual dimorphism, substrate use, locomotion, and diet (discussed below). In terms of

geographic distribution, the hominids (with the obvious exception of *Homo*) are found in tropical forests of equatorial Africa (*Gorilla* and *Pan*) and southeast Asia (*Pongo*).

All nonhuman hominoids are united by a suite of functionally significant morphological features that distinguish them from other primates and other mammals. Many of the postcranial features are thought to be related to the challenges of engaging in arboreal travel and feeding at a large body size. For example, nonhuman hominoids lack a tail and combine a stable, orthograde (upright) trunk, broad torso, and widely spaced shoulders with relatively long forelimbs, high joint mobility, and strong pedal and manual grasping (Fig. 1). These traits allow them to engage in versatile locomotion in which their fore and hindlimbs can be differentially employed, such as during suspension and acrobatic and/or vertical climbing, permitting them to distribute their body weight across multiple supports as needed. But while the hominoid niche ancestrally includes the arboreal realm, the stable lower back and differential use of the fore and hindlimbs



**Hominoidea Morphology, Fig. 1** Posterior view of a chimpanzee suspending unimanually from a single branch (left) and anterior view of a chimpanzee climbing on multiple small supports (right). The arrows indicate distinctive hominoid features, including: no tail, orthograde trunk,

broad torso, widely spaced shoulders, long forelimbs, shorter hindlimbs, high hip and shoulder mobility, fully extendable elbow, and strong pedal and manual grasping. The chimpanzees are both wild *Pan troglodytes schweinfurthii* from Kibale forest, Uganda

have led some taxa (*Pan*, *Gorilla*, *Homo*) to also successfully exploit terrestrial habitats (e.g., through knuckle-walking and bipedality). Such locomotor versatility underlies the evolutionary “success” of all crown hominoids and was present to some degree in early fossil hominoids (MacLatchy et al. 2015).

In addition to having the largest bodies among the primates, hominoids also have the largest brains, both of which are implicated in their slow life history.

While humans are hominoids, and share many of these traits, this entry principally focuses on nonhuman members of the group.

## Morphology Overview

### Cranium

The cranium is responsible for housing the brain and sensory organs as well as for mastication and aspects of social communication. Its morphology represents a compromise of physiological function, phylogenetic history, and allometric scaling that together give rise to variation in the relative size and shape of different cranial structures (Bilsborough and Rae 2015).

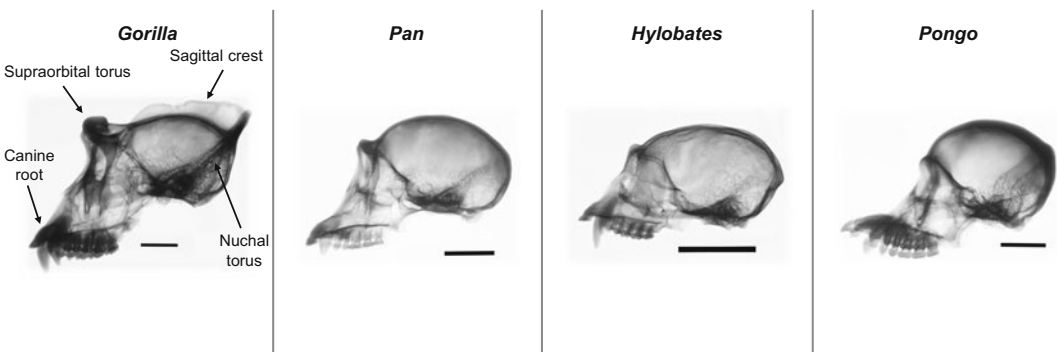
The great apes possess prominent nuchal tori, and the African apes possess prominent supraorbital tori, serving to buttress and accommodate substantial muscular attachments (ibid.; Fig. 2). The great apes are also characterized by higher

cranial capacities compared to monkeys, reflecting their absolutely large brain size.

The African and Asian apes differ in several cranial attributes, including paranasal sinus morphology and the relative orientation of the orbits, palate, and basicranium. *Pongo* and the hylobatids lack ethmofrontal sinuses, which African apes and humans possess (ibid.). Additionally, *Pongo* and the hylobatids, although to a lesser extent, exhibit crania characterized by airohynchy, or an upward orientation of the palate and face relative to the basicranium (Fig. 2). By contrast, *Pan*, *Gorilla*, and *Homo* exhibit klinorhynch, or a downward orientation of the palate and face relative to the basicranium (ibid.).

Hominoids share in having a widened anterior palate, and hypertrophied incisor and canine roots (ibid.). Hominoids are also less prognathic than many other catarrhines, having a subnasal region that is flatter and less projecting; however, males in all large-bodied apes exhibit more subnasal prognathism than do females (ibid.).

The masticatory demands of hominoids vary, leading to differences in the relative size of chewing muscles and their points of attachment. *Gorilla* and *Pongo* have particularly robust attachments for the temporalis and masseter muscles on the lateral aspect of the vault (parietal and temporal bones), the zygomatic arch, and the vertical ramus of the mandible (Aiello and Dean 1990). Such traits are sexually dimorphic and will be described further below.



**Hominoidea Morphology, Fig. 2** Left lateral radiographs of *Gorilla*, *Pan*, *Hylobates*, and *Pongo* crania. Compare the deflection of the palate relative to the

basicranium in the African apes (klinorhynch) versus the Asian apes (airohynch). Scale bars are 5 cm



## Dentition

Hominoids generally retain primitive tooth morphology compared to other catarrhines (Fleagle 2013). Relative to monkeys, hominoids have broader incisors (*ibid.*), with frugivores (fruit eaters) having wider incisors than do folivores (leaf eaters). The canines in hominoids are wider, shorter, and relatively blunted compared to those of cercopithecoids. However, this pattern is less apparent in the hylobatids who possess relatively longer and thinner canines than those of the large-bodied apes. Humans have reduced canines with the upper canine having the same crown height as the upper incisors (Aiello and Dean 1990). Overall, compared to cercopithecoids, there is more variation in hominoid canine size, shape, and degree of sexual dimorphism (Fleagle 2013).

The premolars and molars of hominoids are relatively simple and unspecialized. The lower molars have an expanded talonid basin and the upper molars are quadrate in shape (*ibid.*). Hominoids differ in molar morphology according to diet, with folivores exhibiting longer shearing crests running between taller cusps, than do frugivores, as the crests facilitate breaking down leaves. Hominoids additionally have variable enamel thickness relative to their body size. *Pan*, *Gorilla*, and hylobatids have thinner molar enamel, *Pongo* has thicker enamel, and humans have varyingly thick enamel (Shellis et al. 1998; Smith et al. 2005).

## Postcranium

### The Vertebral Column, Thorax, and Pelvis

Like most mammals, apes have 7 cervical (neck) vertebrae; however, the thoracic region (chest) is typically comprised of 13–14 vertebral segments, an increase of 1–2 segments over most primates. The rest of the vertebral column of hominoids also differs from that of most other primates in terms of the number of vertebral segments in each region. The lumbar region (lower back between the chest and pelvis) is comprised of fewer segments (3–5), the sacral region (fused segments adjoining the pelvis) is comprised of more segments (4–6),

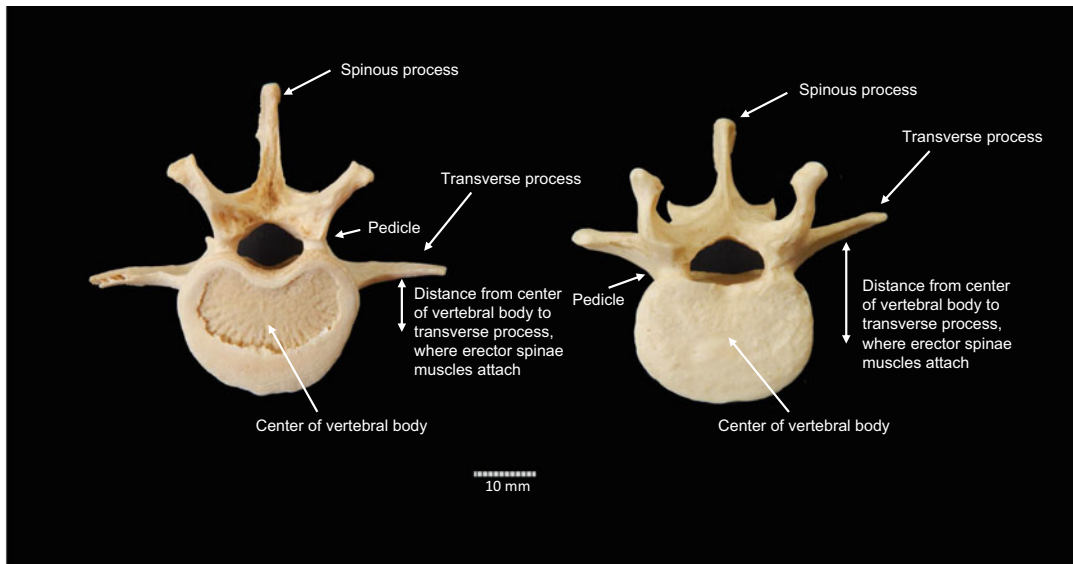
while the caudal (tail) vertebrae consist of a few, internalized segments (Pilbeam 2004). In contrast, other anthropoid primates, with the exception of a few New World monkeys, have longer lumbar regions (~7 vertebrae), shorter sacral regions (~3), and a series of caudal vertebrae that constitute the tail (*ibid.*).

The shortening of the lumbar region is a particularly salient trait, as it reduces the range of flexion and extension of the lower back, serving to stiffen this region and facilitate orthogrady of the trunk (Shapiro 1993). In the great apes, the ilia (upper pelvic bones) are also high and flare laterally, entrapping the lumbar vertebrae and stiffening the spine further. Hylobatids typically have slightly longer lumbar regions and the ilia are not as flared as in the great apes. Individual lumbar vertebrae are relatively compressed craniocaudally in apes, further shortening this region.

The spinous and transverse processes of each vertebrae serve as attachment points for the muscles of the back. In apes, the lumbar transverse processes emerge from the pedicle rather than from the vertebral body as in monkeys and most other primates (Fig. 3). This more dorsal position of origin serves to move the erector spinae muscles, extensor muscles of the back, further from the intervertebral joints, increasing their leverage and thus the efficiency of the muscles in keeping the torso upright (Shapiro 1993).

The thoracic vertebrae articulate with the ribs dorsally, and the vertebrae are slightly invaginated into the ribcage. In cross section, the ribcage is elliptical in shape, broad mediolaterally but shallow dorsoventrally. This broad chest is significant anatomically as it serves to increase the spacing between the scapula, which are situated on the dorsum (back) of the ribcage rather than the sides, as in most primates. This also has important implications for shoulder mobility (see below).

The lack of a tail in hominoids has been argued to be related to ancestral reliance on cautious arboreal climbing, which makes the tail, as a balancing organ, less necessary (Cartmill and Milton 1977). In hominoids, the tail musculature is reorganized to support the abdominal viscera, a correlate of orthogrady.



**Hominoidea Morphology, Fig. 3** Inferior view of a monkey (*Papio*) (left) and an ape (*Pan*) (right) lumbar vertebra. Note the greater distance between the center of the vertebral body to the transverse process. This greater

distance is thought to improve the mechanical advantage of the erector spinae muscles of the back in keeping the back from bending forward

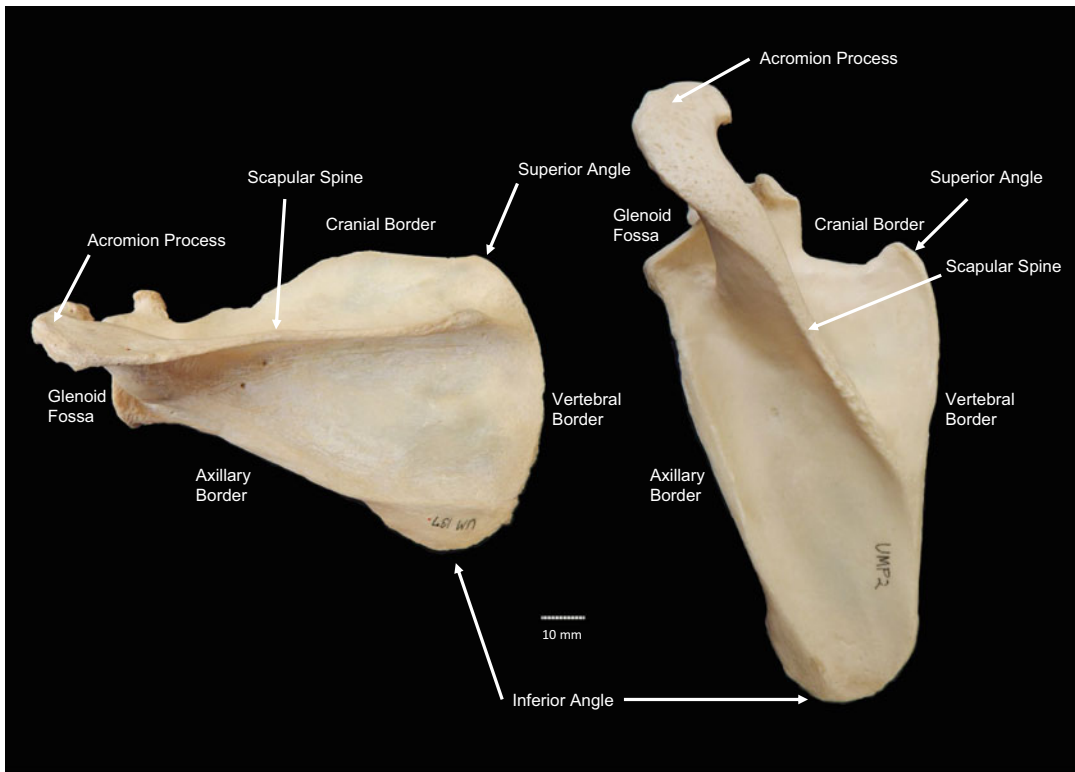
Although pelvic anatomy is fairly conservative across primates, the great apes have laterally broad iliac blades as noted above. The width and orientation of the iliac blades likely reflects both the broad shape of the thorax and locomotor adaptation. The dorsal surface of the ilium gives rise to the gluteal muscles, which act as extensors of the hip. The relatively large surface area for attachment of the gluteal muscles may be necessary during arboreal behaviors such as vertical climbing, especially at large body sizes.

### Forelimb

The hominoid forelimb is distinctive in being relatively long with highly flexible joints (Young 2003). The shoulder joint is capable of circumduction, or 360° of movement (Larson 1993). As noted above, some of this capacity is afforded by the dorsal position of the scapula, which results in a laterally directed glenoid fossa (shoulder socket). The glenoid fossa is also broad and shallow and gently curved in all directions to serve in this dynamic use of the shoulder (MacLatchy et al. 2000). The overall shape of the hominoid scapula facilitates overhead movement of the forelimb, being relatively short in the

distance from the vertebral border to the glenoid fossa and broad in the distance between the superior and inferior angles compared to other primates (Larson 1993; Fig. 4). This morphology enhances the action of two rotators of the scapula: the serratus anterior muscle, which attaches to the inferior angle, and the trapezius muscle, which attaches to the acromion process and scapular spine (Aiello and Dean 1990; Larson 1993). The acromion process is more laterally projecting and cranially oriented in apes compared to other primates, yielding further mechanical advantage to the deltoid in arm-raising behaviors (Aiello and Dean 1990).

There are several key features of the proximal humerus that distinguish hominoids from other primates. First, the shape of the humeral head is relatively spherical compared to the condition in quadrupedal monkeys, reflecting multiplanar movement of the shoulder (Larson 1993). Second, the deltoid muscle inserts more distally in hominoids, approaching the humeral midshaft. This lengthening of the deltoid increases its moment arm and adds to the lever advantage of the muscle for humeral abduction (i.e., movement away from the midline of the body) (Aiello and Dean 1990;



**Hominoidea Morphology, Fig. 4** Dorsal view of a monkey (*Papio*) (left) and an ape (*Pan*) scapula. In the monkey, the length of the vertebral border (the distance from the superior angle to the inferior angle) is shorter than the length of cranial border (the distance from the glenoid

fossa to the superior angle). In the ape, the vertebral border is much longer than the cranial border. See text for details. Note also that the glenoid fossa is tilted cranially in the ape scapula compared to the monkey scapula

Larson 1993). Third, the projection of the greater tubercle is reduced in hominoids relative to other primates, never extending above the height of the humeral head. This serves to avoid interference with abduction of the forelimb, contributing to the flexibility of this joint (Larson 1993).

Hominoids overlap in much of their forelimb morphology despite their wide ranging and differing locomotor behaviors (Young 2003). However, hylobatids and *Pongo*, who rely more on suspension, have relatively longer forelimbs, more globular humeral heads, further reduced greater tubercles, and more distally inserting deltoids. *Gorilla* and *Pan*, as terrestrial quadrupedal knuckle-walkers, have forelimbs that are closer in length to their hindlimbs, and their humeral heads have relatively less surface area with more robust greater tubercles, fostering more stable glenohumeral joints (ibid.).

The elbow involves the meeting of three bones: the humerus, the ulna, and the radius. The hominoid humeroulnar joint is capable of 180° of flexion and extension. This range is possible because the olecranon process, a proximal extension of the ulna, is greatly reduced in hominoids and so does not interfere with full extension (Aiello and Dean 1990). The elbow is also capable of 180° of supination and pronation, that is, the entire forearm can rotate along its long axis at the humeroradial joint. This is facilitated by a round humeral capitulum (the distal articular surface on which the radial head rotates) and an adjacent, stabilizing buttress (ibid.).

Pronation and supination of the forearm is further enabled by wrist morphology. A fibrocartilaginous disc, or meniscus, intervenes between the reduced styloid process of the ulna and the carpal (wrist) bones. In addition to permitting

greater supination, the meniscus also allows greater adduction at the wrist (deflection toward the fifth digit) than is possible for other primates that have a direct bony articulation between the ulna and the carpals (Aiello and Dean 1990).

The African apes have proportionally larger, broader wrists for compressive weight bearing during knuckle-walking. By contrast, the Asian apes have short and narrow wrists to facilitate greater mobility (Zihlman and Underwood 2019; Fleagle 2013).

Hand morphology similarly varies across hominoids according to their locomotor repertoires, although hominoid hands share in being strong, flexible, and close to equal size with the feet, unlike the hands of monkeys which tend to be smaller than the feet (Zihlman and Underwood 2019). *Pongo* and the hylobatids possess longer, more curved metacarpals and proximal phalanges compared to the knuckle-walking African apes. *Pan* and *Gorilla* additionally exhibit a distinctive dorsal ridge on their distal metacarpals that is correlated with knuckle-walking.

Unlike humans, apes have relatively short, non-opposable thumbs and so must use the side of their index fingers, combined with the thumb, to manipulate objects (Aiello and Dean 1990). The hylobatids are particularly distinct in their thumb morphology, possessing a cleft between metacarpals I and II.

### Hindlimb

The hominoid hindlimb is shorter than the forelimb, except in humans, whose long hindlimbs reflect habitual bipedalism. Hominoid hips are more mobile compared to those of most monkeys, which is important to facilitate climbing and suspensory locomotion (Fleagle 2013). The distribution of the articular surface in the hip socket (acetabulum) is related to movement patterns at the joint. In contrast to the condition in pronograde quadrupedal monkeys, who have a near uniform distribution of articular surface, in hominoids the cranial aspect of the articular surface is expanded, likely reflecting the increased cranial loading of the hip during orthograde.

The spherical femoral head in hominoids has more extensive articular surface than in most other

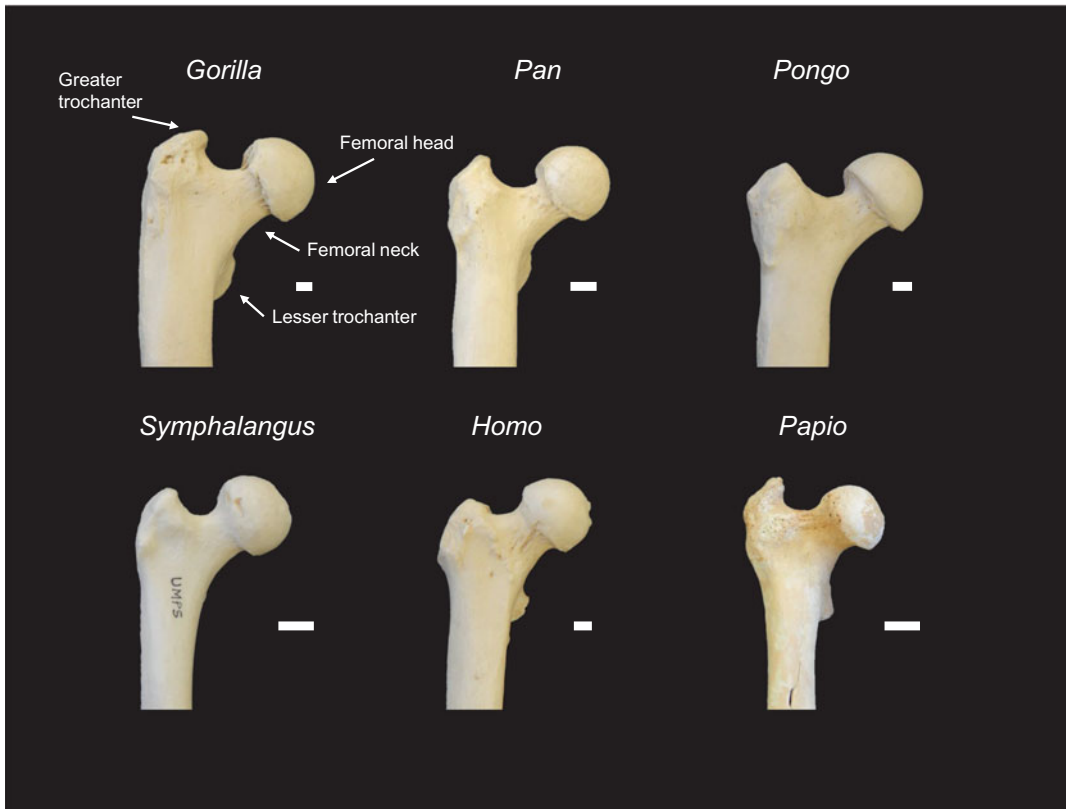
primates. Apes also tend to have long femoral necks (Fig. 5), elevating the femoral head and increasing mobility. The greater trochanter height in *Pongo* is reduced, facilitating abduction and reflecting the increased variety of hindlimb positions utilized by *Pongo* during arboreal locomotion. African apes have relatively smaller femoral heads and taller greater trochanters compared to *Pongo* and *Homo* (Fig. 5).

The nonhuman hominoid knee is broader than that of monkeys, with a larger medial condyle compared to the lateral condyle (Aiello and Dean 1990). Most explanations for condylar asymmetry invoke enhanced knee rotation and the use of an abducted hindlimb, particularly during climbing (MacLatchy et al. 2000). The femur also has a more bowlegged orientation in some nonhuman apes, such as in *Gorilla*, with more weight being borne on the medial side (ibid.).

The hominoid ankle is more mobile and flexible than that of monkeys. Hominoids have a trapezoidal-shaped distal tibial articular surface, whereas that of monkeys is squarer in shape (DeSilva 2009). This shape may enhance dorsiflexion, the movement that brings the top of the foot close to the tibia, and which occurs during vertical climbing (DeSilva 2009).

The talus is perhaps the best studied of the seven tarsal (ankle) bones. All tarsals have facets that allow each to articulate with one another. In the talus of nonhuman hominoids, these facets tend to be more curved, which allows for increased mobility in the joints. Humans are unique among hominoids, having a shortened talus with facets that have minimal curvature (Parr et al. 2014). This allows for a more stable foot during terrestrial bipedalism (ibid.). The degree of articular facet curvature varies, with *Symphalangus* and *Pongo* having increased curvature, and *Hylobates* and *Homo* having reduced curvature (ibid.). *Gorilla* and *Pan* are intermediate in terms of curvature, reflecting their use of propulsion during quadrupedalism and their need for mobility during arboreal locomotion (ibid.).

The ape foot is capable of substantial inversion, or inward rotation at the ankle, and all apes have long, curved grasping toes with an opposable hallux (big toe). The metatarsals and phalanges of



**Hominoidea Morphology, Fig. 5** Anterior view of hominoid (*Gorilla*, *Pan*, *Pongo*, *Symphalangus*, and *Homo*) and cercopithecoid (*Papio*) femora. Note the roundness of the femoral head in the hominoids. The

height of the greater trochanter is variable. In general, a shorter greater trochanter relative to femoral head height facilitates hip mobility in the hip, particularly abduction and rotation. Scale bars are 10 mm

hylobatids, *Pongo* and *Pan* are relatively longer than those of *Gorilla*. *Pongo* has especially mobile feet, with highly elongated lateral digits and a relatively reduced hallux (Fleagle 2013).

## Soft Tissue Features

### Brain

Although there is considerable overlap between apes and monkeys in the size of the brain relative to body size, the great apes possess the largest brains in absolute size, a parameter that has been closely linked to enhanced cognitive abilities (Deaner et al. 2007). Apart from size, great apes also share several critical neuroanatomical features tied to their complex behavior and sociality, with humans representing the extreme in all

features. For example, great apes possess an expanded prefrontal cortex, a region of the brain associated with working memory and executive function, or goal-directed behavior (Smaers et al. 2017). Hominoids have also been found to exhibit enlarged cerebella relative to the size of the neocortex, although this pattern is only slight in the lesser apes. As the cerebellum is associated with voluntary sensory-motor control, this augmentation serves in fine coordination of motor movements and has been linked to technical intelligence (Barton and Venditti 2014). Great apes also exhibit an expanded anterior cingulate cortex (ACC), a region of the neocortex associated with the interface between emotion and cognition (Allman et al. 2001). This area is involved in social cognition and attention control, allowing for the shifting of focus when confronted with



novel or unexpected information. Within the ACC, the great apes also possess specialized spindle-shaped neurons that facilitate the integration of the prefrontal cortex with other regions of the brain, such as the amygdala. This increased interconnectivity allows for more complex problem-solving and more profound processing of emotional and social information. The largest concentration of these neurons is found in humans, with a decreasing concentration in apes with increasing phylogenetic distance from humans (*ibid.*).

### Gut

Despite some variation in diet, mostly in proportions of fruit versus leaves, hominoid gastrointestinal tracts are similar in overall structure, with a single-chambered, smooth-walled stomach, a small intestine, a cecum terminating in a vermiform appendix, and a large, sacculated colon (Chivers and Hladik 1980).

### Reproductive Anatomy: Relative Testes Size, Sexual Swellings, and Secondary Sex Characteristics

As in other mammals, there is a correlation between relative testicular size and sperm competition among hominoids. Larger testes produce more sperm, so for taxa in which females mate with multiple males during a reproductive cycle, larger testes are favored. Among hominoids, relative testes size and sperm competition are low in both gorillas and gibbons. Paternity data have corroborated these patterns: for pairbonding hylobatids, the male in the pairbond is usually the father; and for gorillas, although they may live in either multimale/multifemale or single male/multifemale groups, the dominant male tends to be the father (Baker and Shackelford 2017). For *Pongo*, where both males and females are solitary compared to other hominoids, the dominant male in a territory has a modest advantage over other males and has somewhat larger testes, higher sperm competition, and lower conception success than in *Gorilla* or hylobatids (*ibid.*).

Both species of *Pan*, the chimpanzee and the bonobo, live in multimale/multifemale groups, where sperm competition is intense, hence relative testes size is the largest among the hominoids. *Pan* is also notable because females have conspicuous sexual swellings in which the genital and perineal skin experience pronounced edema over the course of the menstrual cycle, with maximal tumescence during periovulation. The swelling occurs in some Old World Monkeys, and in most cases, such primates also live in multimale/multifemale societies.

Other notable morphological features associated with sex include the silver hair that marks the back of a dominant male gorilla and the facial flanges that develop in a dominant male *Pongo*. Male *Pongo* also develop laryngeal pouches, allowing them to produce a characteristic “long call.”

### Hair and Sweat Glands

There is a negative correlation between body size and hair follicle density in primates, resulting in large-bodied hominoids having less hair than smaller bodied hominoids (Sandel 2013). Both *Pan* and *Homo* have the same number of hair follicles as other apes of their size but have more vellus (small, unpigmented) hair follicles (Sandel 2013). Nonhuman hominoids have increased eccrine (sweat) gland density relative to Old World Monkeys, and *Homo* has increased eccrine density compared to other apes (Kamberov et al. 2018). Increased sweating and hair loss are both associated with thermoregulatory stress, but more work is necessary to assess distribution and density of eccrine glands across primates.

### Implications of Morphology for Behavior and Evolution

#### Hominoid Morphology and the Terminal Branch Forest Frugivory Hypothesis

As noted, living hominoids are distinguished from almost all other primates by postcranial features related to orthograde and differential use of the fore and hindlimbs such as during suspension or during acrobatic climbing with abducted limbs. The central tenet of hypotheses advanced to

explain the adaptive significance of the acquisition of these positional behavioral adaptations is that they contribute to foraging fitness, by enabling medium- and large-bodied primates to access high quality items like fruit in areas such as terminal branches or the upper canopy where flexible, small supports abound (e.g., Avis 1962; Cartmill and Milton 1977; Temerin and Cant 1983). Suspension may also increase speed and decrease the path length of arboreal travel in these habitats (Temerin and Cant 1983), as well as allow an increase in body size. Suspension has been emphasized in most scenarios of hominoid evolution, but quadrumanous climbing has also been highlighted, as have vertical climbing and orthograde (Fig. 1).

A synthesis by Hunt (2016) of paleontological and neontological lines of evidence led him to suggest that apes evolved their postcranial specializations to feed in the terminal branches on ripe fruit, through coevolution with cercopithecoids whose dental (e.g., bilophodonty) and digestive (e.g., tolerance for tannins, alkaloids, etc.) adaptations, coupled with smaller body size, allowed them to outcompete hominoids for access to unripe fruit, ripe fruit in small patches, and leaves.

A focus on arboreal ripe fruit may have played a role in hominoid cognitive evolution. Arboreal fruit is less abundant and more seasonally variable than both arboreal and terrestrial herbaceous vegetation (leaves, piths, roots, etc.); thus, more frugivorous hominoids are subjected to greater foraging challenges, including greater feeding competition, than are more folivorous hominoids. It has been noted that the large-bodied apes that are more frugivorous, namely chimpanzees and orangutans, show greater use of tools and extractive foraging in the wild than do the more folivorous bonobos and gorillas (Rosati 2017). The more frugivorous great apes also exhibit cognitive predispositions including enhanced spatial memory and greater risk tolerance during foraging (ibid.).

### Hominoid Sexual Dimorphism and Behavior

Sexually dimorphic features in hominoids include body size and musculature, canine size, pelage color and pattern, and a few other anatomical

features (Leutenegger and Kelly 1977). Higher degrees of sexual dimorphism are associated with polygynous mating systems in which males compete for access to multiple females. Increased sexual dimorphism in apes is also associated with their large body sizes and may be related to the long interbirth intervals in apes, which decreases reproductive opportunities for males and therefore increases competition. In contrast, more monogamous species tend to have lower sexual dimorphism as males have higher paternal certainty, incentivizing energy investment in offspring rather than mate competition (Leutenegger and Kelly 1977).

*Gorilla* is highly sexually dimorphic, with an average adult body mass of 162.5 kg for males and 97.5 kg for females in mountain gorillas and 175.2 kg for males and 71.0 kg for females in lowland gorillas (Smith and Jungers 1997; Plavcan and van Schaik 1997) (Fig. 6). Male gorillas possess numerous cranial features that distinguish them from females, including a sagittal crest along the midline of the neurocranium where the temporal bones meet (Fig. 2). Males also possess an enhanced nuchal crest for attachment of the neck muscles that support the head. Male gorillas exhibit deeper upper and lower jaws, necessitated by the significantly larger canines in males compared to females. The male to female canine length ratio is 1.73 (Plavcan and van Schaik 1997).

*Pongo* is also highly sexually dimorphic; males have an average adult body mass of 86.3 kg while it is 38.7 kg for females (Plavcan and van Schaik 1997). Due to the extremely long interbirth intervals (>7 years), reproductively receptive females are rare and thus highly competed for (Leutenegger and Kelly 1977). Adult male orangutans possess several features that are distinct from females, including more well-developed cranial crests, cheek flanges and laryngeal pouches, and considerably larger canines, with a male to female canine length ratio of 1.69 (Plavcan and van Schaik 1997).

Both species of *Pan* (*P. troglodytes* and *P. paniscus*) live in multimale-multifemale mating systems and show moderate levels of sexual dimorphism, with bonobos slightly less



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**Hominoidea Morphology, Fig. 6** Two examples of sexual dimorphism in apes. Above: male (left) and female (right) orangutans (*Pongo tapanuliensis*); photo credit Tim

Laman. Below: male (left) and female (right) gibbons (*Hylobates lar*); photo credit Matthias Kabel

dimorphic than chimpanzees. In chimpanzees, average adult body mass is 39.6 kg for males and 29.8 kg for females; in bonobos, body mass is 39.8 kg for males and 32.9 kg for females (Plavcan and van Schaik 1997). The canine length ratio is 1.42 for *P. troglodytes* and 1.38 for *P. paniscus* (Plavcan and van Schaik 1997).

Hylobatids are monogamous in their mating system and show a low degree of sexual dimorphism with body size ratios ranging from 0.9 to 1.1 and canine length ratios ranging from 1.03 to 1.18 across the Hylobatidae family (Plavcan and van Schaik 1997). Some species display pelage dichromatism between the sexes (Fig. 6).



### Hominoid Brain Size, Body Size, and Life History

As noted, hominoids have absolutely large brains. The large brain and associated factors including the cognitive demands of foraging and sociality, as well as the reduced predation associated with possessing both large body size and being arboreal, have all been implicated in contributing to the hominoid life history slow-down. This slow-down is associated with a suite of distinctive features, including single births, long interbirth intervals, a long period of maternal dependence, delayed sexual maturation, and a long life.

While size and evolutionary history are important contributors to the slower life history of hominoids, diet may contribute as well. “The Ecological Risk Aversion” (ERA) hypothesis (Janson and van Schaik 1993) attempts to explain variation that occurs in life history among the hominoids. According to the ERA hypothesis, slow growth in juvenile-aged primates is a response to ecological risks, including predation and starvation. Those who have a lower risk of starvation, or are more folivorous (i.e., because leaves are relatively plentiful), will grow more quickly than those that have a higher risk of starvation, or are more frugivorous (i.e., because fruit is less plentiful). Hominoids generally follow this pattern. For example, folivorous gorillas exhibit *faster* growth rates, given their body size, relative to more frugivorous chimpanzees and orangutans.

### Parallel Evolution and Hominoid Morphology

An enduring question about hominoid morphological evolution concerns which aspects of the postcranial similarities found in all living apes (and that underlie an arboreal niche that involves torso-orthograde suspension and climbing) are due to shared ancestry (homology) versus parallel evolution (homoplasy). Despite a rich fossil record in the Miocene, and dozens of recognized fossil hominoid species, no fossil taxon is unambiguously linked to an extant ape lineage. So, it is not possible to reconstruct the evolution of individual ape genera, in contrast to the human lineage, which has a rich fossil record starting ~4 million years ago. Moreover, there is no simple story of primitive apes gradually evolving into more derived forms.

Some lineages show derived features very early in the evolutionary history of apes, while primitive features persist in younger taxa. For example, one of the oldest stem apes, *Morotopithecus* (known from Uganda and dated at >21 Ma), possessed a stiff lumbar column (MacLatchy et al. 2015), while younger taxa, such as *Sivapithecus*, a genus from Pakistan linked by some to *Pongo* (and dated to ~12.7–8.5 Ma), is reconstructed to have had a more monkey-like, rather than an ape-like, torso (Morgan et al. 2015).

Inferred primitive, monkey-like features of fossils from the upper limb of a possible early human ancestor, *Ardipithecus*, have been used to argue that it, and all other extant hominoid lineages, independently evolved their distinctive broad torso, stiff lower back, and dorsal placement of the scapula (Lovejoy et al. 2009). This line of interpretation reasons that if a recent (~4.4 Ma) taxon like *Ardipithecus* evolved from a lineage with a monkey-like body plan, then all ape lineages, which branched phylogenetically prior to humans, would have had to independently undergo a similar process. Such a scenario raises many questions. If invagination of the vertebral column, widening of the torso, and a dorsal shift in the placement of the scapula evolved multiple times, then what were the selection pressures? Could enhanced arm circumduction alone, in the absence of orthograde arboreality, as some have suggested (White et al. 2015), be sufficient? Or, are shoulder mobility, orthograde, and lumbar stiffness, which seem crucial in order to use fore and hindlimbs differentially and are found in all extant hominoids, critically and functionally linked to arboreality? Furthermore, if all orthograde/suspensory adaptations evolved in parallel, why are modern hominoids so similar for multiple anatomical suites of characters, yet so variable in positional behavior (Young 2003)?

An interesting interpretation of hominoid similarity proposes that developmental constraints may be relaxed in taxa such as apes that have undergone selection for the limbs to be used differentially, as in suspension (Young et al. 2010). Hominoid postcranial evolvability may thus result from selection pressures that decreased fore- and hindlimb genetic integration and allowed the

limbs to evolve more freely (ibid.). Inferred differential limb use in *Morotopithecus* and younger Miocene taxa (MacLatchy et al. 2015) provisionally supports Young et al.'s (2010) supposition that limb “evolvability” may at least be a widespread, if not an ancestral hominoid trait. This emphasis on development mechanisms, rather than the sequence and frequency of postcranial adaptive evolutionary events, is compelling and is having a profound effect on the study of hominoid morphology.

- [Phylogeny](#)
- [Primate Locomotion](#)
- [Primate Suspensory Behavior](#)
- [Primates](#)
- [Quadrumanous](#)
- [Quadrupedal](#)
- [Secondary Sex Characteristics](#)
- [Sexual Dimorphism](#)
- [Sexual Selection](#)
- [Skeletal System](#)
- [Taxa](#)
- [Terrestrial](#)

## Cross-References

- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Radiation](#)
- [Arboreality](#)
- [Bipedalism](#)
- [Brachiation](#)
- [Canopy](#)
- [Catarrhine Cognition](#)
- [Catarrhine Communication](#)
- [Catarrhine Diet](#)
- [Catarrhine Life History](#)
- [Catarrhine Locomotion](#)
- [Catarrhine Morphology](#)
- [Catarrhine Navigation](#)
- [Catarrhine Sensory Systems](#)
- [Common Ancestor](#)
- [Ecology](#)
- [Evolution](#)
- [Extinction in Learning](#)
- [Hominid](#)
- [Hominoid](#)
- [Hominoidea Navigation](#)
- [Hominoidea Sensory Systems](#)
- [Homology](#)
- [Homoplasy](#)
- [Intersexual Selection](#)
- [Knuckle-Walking](#)
- [Life History](#)
- [Locomotion](#)
- [Morphology](#)
- [Muscular System](#)
- [Opposable Thumb](#)
- [Paleontology](#)

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## Hominoidea Navigation

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## Synonyms

Chimpanzee; Cognition; Nature; Navigation; Primate

## Definition

Navigation, Cognition, Complex cognition, Conditional cognition.

## Introduction

In the wild, animals need to travel to find their food, sleeping places, and other resources within their home range. Food is naturally dispersed in the environment and comes very often in clumped patches requiring from the animals to move between patches if they want to obtain enough food to survive and reproduce. In addition, fruit availability in the environment is seasonal and ephemeral requiring some additional knowledge to find them efficiently at the right moment. Depending on the environment, the density of food sources can vary dramatically with some food sources being very abundant and others much rarer. The rarer they are, the more important it is to find them in time when facing food competitors. Thus, some navigation skills will be a selective advantage to the individuals.

Navigation has been studied in the laboratory, where by definition the environment complexity is very low and the distances to reach the goal for the subject are extremely small compared to the natural situations. Therefore, early on, experiments were proposed to wild animals in nature to understand the decision process of primates as they look for food. If such experiments were an important improvement over lab studies in terms of ecological validity, they represented still a simplified version of the challenges that primates have to resolve to obtain a balanced diet. Luckily, thanks to constant progress in the statistical analyzing tools, recently it has become possible to study the navigation of individuals when looking for food in the highly complex tropical rainforest situation. This has allowed to understand unexpected and complex cognitive skills in wild primate navigation skills.

## About Navigation

Depending on the diet specialization of the species, the challenge to find patchy food sources may require sophisticated navigation skills. Folivores, for example, will be able to find food more easily, as leaves are overabundant and constantly present in the tropical forests. Obviously,

folivores are also selective, in the sense that they do not eat leaves indistinctively, but select leaves from some species only, and often as well prefer young leaves over older ones (Clutton-Brock, 1975; Struhsaker, 1975). A large number of primate species are omnivores, eating vegetable and animal food types with relatively few examples of dietary specialization, like some small nocturnal species, such as galago, dwarf lemur, aye-aye and the loris that are substantially insectivorous, or some marmoset species that specialized in eating gums (Garber, 1987). Insectivores face a rather similar situation, as insects are quite abundant in the forest, but require from the hunter swift reactions, as insects will avoid being captured. Therefore, insectivores tend to be small-bodied primates (Garber, 1987). Generally, primates eat at least some species of fruits, and great apes, except for the gorillas, eat mainly fruits and preferably ripe fruits. Frugivorous, on the other side, have to navigate more precisely, as large fruiting trees that can abundantly provide food to a group of individuals are rare and often dispersed throughout the forest. Since fruits are ephemeral and seasonal, we should expect different selective pressures on the cognition of the individuals depending on their diet to forage efficiently in the habitat.

Fruit-eaters face the challenge not only to find the specific trees, but find them timely when they are ripe. Even an unspecialized fruit eater, like the baboon, will eat them only once they start being consumable, while the chimpanzees will wait until they are fully ripe and tasty. This means that not all fruit-bearing trees are a food source, and when they become edible will be species-specific. In all cases, fruits are very seasonal and can be eaten only over a limited period of time, requiring flexibility from the primates looking for different fruiting tree species at different times of the year. At this point, tree species distribution, abundance, and fruit production become essential factors for detection by the fruit eaters, and the rarer and more widely dispersed fruiting trees are, the more demanding it will be to find them. In other words, navigation complexity to find food will be a function of diet as well as of distribution of available food sources.

### Navigation in the Laboratory

Research on navigation have often been done in the laboratory where for reasons of better control of the different possible confounding variables, the ecological contexts presented are abnormally simple preventing a deeper understanding of the cognition needed in nature. In the sense that the spatial challenges that can be studied in such a simple space will limit the expression of a more complex cognitive performance. For example, many studies of navigation require the subject to find its way in two-dimensional maze, constituted of two to three lateral branches (like the Morris Water Maze, Tan et al., 2017), or alternatively to place objects in a simple model with other objects rotated in different ways (like the Three Mountains Test, Newcombe, 2019). Rarely do the subjects have to actively move to perform the test, and when needed, it will be over very short distances.

Such well-controlled laboratory experiments, exploring animal spatial cognition, address often questions that have very little ecological validity, as they differ significantly from the challenges encountered in nature, and as such it is very difficult to see how they can contribute to an understanding of natural navigation skills in primates. Discrepancies in results from captive studies with such ones done on wild living animals have often puzzled scholars, as they are very hard to understand and put in perspectives. On one side, captive animals may appear to outperform wild counterparts. Janson and Byrne 2007 discussing on Cramer and Gallistel's (1997) results about captive vervet monkeys appearing to use for the first time a "traveling salesman"-type of foraging said: *"The difference between results could be due to several factors: (1) the species may differ intrinsically in cognitive use of spatial knowledge, (2) the wild monkeys have to deal with much larger spaces across which they cannot see their foraging goals and thus cannot precisely estimate the distances to each goal, let alone the distances between them, (3) the wild monkeys are hungrier and discount more distant resources so heavily that they do not include them in their decisions, (4) the wild monkeys may benefit from foraging in*

*nearby areas they already know to be free from competitors—and the list could go on. Although both results are intriguing, the captive result may tell us little about how a cognitive potential is used in the wild"* (Janson & Byrne, 2007, pp. 358–359).

On the other side, captive animal studies may underestimate the abilities of wild counterparts to navigate. For instance, work on captive capuchin monkeys that needed to find food in boxes rotated when they could not see the rotation suggests that they learn only simple associations between a goal and a local landmark (Poti 2000). Nevertheless, wild capuchin groups appear to use information about the location of at least two resources relative to each other to decide on a foraging route. Janson and Byrne (2007) concluded: *"Thus, their apparent limitations in captive tests either do not apply to the wild or they use some other mechanism to circumvent this cognitive limitation. This caution applies particularly in the case of captive-reared primates, which may not have had the experience to develop or practice navigation abilities in large-scale space* (Menzel & Beck, 2000)" (p. 359).

Similarly, spatial skills in chimpanzees have been studied extensively in the laboratory by proposing an environment drastically less challenging than the wild one, with the aim to understand their ability to conserve length and distance, to rotate objects in landscape, or to plan in the future and remember object locations (e.g., Beran & Minahan, 2000; Rooijakkers et al., 2009; Poti, 2000; Poti & Langer, 2001; Premack, 2007; Premack & Premack, 1983). Such experiments generally required from the captive chimpanzees sitting to follow invisible displacements of grapes or sweets hidden under cups that are moved or not, pile wooden blocks on one another, or place miniature houses or cars in landscape oriented differently in space. The scientists tend to agree in finding limitations in chimpanzees both in the vertical and horizontal displacements. This could have been expected, considering that the bare environment experienced by captive chimpanzees for years do not select for much spatial skills when looking for food or a sleeping place.

### Navigation in the Natural World

Contrary to individual animals kept in captivity, finding food requires from the wild individuals an important time investment to forage over extended spatial areas where the distances covered prevent a direct visible comparison of the different food sources. Just to take a few example, white-faced capuchin (*Cebus capucinus*) adults devote between 50% and 65% of the day to foraging and traveling and cover a day range of approximately 3000 m (Garber & Brown, 2005). Wedge-capped capuchins (*Cebus olivaceus*) spend almost 70% of their active hours searching and processing food, while traveling 2141 m per day. Spider monkeys (*Ateles spp.*) forage in small fission-fusion parties within a home range of many hundreds of hectares and travel up to 3000–5000 m per day. Mantled howler monkeys (*Alouatta palliata*) travel in a line within a home range of 2–40 ha, with a day range of 100–450 m (Garber & Jelinek, 2005). Chimpanzees in the Tai forest range within a territory of 10–40 km<sup>2</sup>, looking for food for about 40% of the day time, with a day journey length of 5000–10,000 m (Boesch & Boesch-Achermann, 2000).

### Monkey Navigation with Field Experiments

Therefore, studying the cognition of navigation is equally challenging to the researchers, as we need to know the availability of food and the location of the trees with fruits at the time the individual is looking for food. As this needs to be known for ephemeral and seasonal food sources, this requires an unusual investment. To circumvent such challenges, some researchers skillfully developed an experimental paradigm whereby they presented food on a small number of platforms (Janson, 1998; Janson & Byrne, 2007; Garber, 1988; Garber & Jelinek, 2005). Such experiments allowed the researchers to know constantly the position and the amount of food available to the monkeys. However, they could not control for the other food types that might have been available at the same time in the forest, which could have interfered with the foraging route adopted by the monkeys. Inasmuch as possible, some studies tried to present the

experiments during periods of the year when food availability was very low, and the individuals were seen to almost exclusively feed on the food provided by the researchers.

In monkeys, the studies concur to show the importance of landmarks and memory that seem the main elements for the individuals or groups to find the food sources and be able to revisit them by applying an energy-optimizing strategy. In addition, they confirmed some of the negative effects of captivity on the development of cognitive capacities when it comes to find food (Janson & Byrne, 2007). In addition, since food is naturally only temporally available for a short period of time, capuchin monkeys were found to possess and use integrated memories of prior food-patch use, including those where the patch is relative to their current location, productivity of the patch, and how long it has been since they last visited the patch (Janson, 2016).

Orientation in the tropical rainforest remains a constant challenge to find food sources that are seasonal and often hardly predictable. The tropical rainforest is constituted by an impressive richness of a multitude of tree species, ranging from the smallest ones to the tree giants emerging at some 50 m of height. As the tropical rainforest is home of the largest biodiversity of primates, this is a challenge that most of them have to resolve. Whenever a monkey or an ape moves in the forest searching for food in the trees or on the ground, the very limited visibility within the forest makes finding ripe food quite challenging.

### Chimpanzee Navigation in the Tropical Rainforest

If the challenges of finding food in chimpanzees sounds at a first look very similar to what monkeys face, the challenges are exacerbated: Chimpanzees' home range is much larger than the monkey ones, being between 10 and 40 km<sup>2</sup> wide. In addition, they are specialized ripe fruits eaters (over 75% of their diet). Finally, they have a very diverse diet eating up to 150 different food items and daily up to 8 different fruit species. These three aspects of the chimpanzee life increase the demands on navigation in the forest.

Therefore, the selection of the fruiting trees carrying ripe fruits will be specially demanding, as the time window when trees are carrying the fruits of the appropriate state of ripeness requires precise temporal memories to find the appropriate trees.

Thus, cognitive complexity should be expected in spatial skills, as the dense African rainforest strongly limits visibility on the ground, which represents a distinct challenge for an animal species ranging daily over 10 km (Janmaat et al., 2013a, 2013b; Normand et al., 2009). The challenge of finding trees full of ripe fruits should not be underestimated, as the likelihood to find a fruiting tree during a walk in straight line has been estimated to be one for every 10–21 km walked (Janmaat et al., 2016; Pontzer & Wrangham, 2004). Knowing that a chimpanzee eats fruits daily from about eight different species of fruits and travels daily a minimum of 2–4 km, the selective pressure to improve spatial skills in the forest is massive. This is further complicated by the fact that fruit production is not only seasonal, but very irregular: trees bear ripe fruits at most for a month, and, within a same species, fruit production can vary extensively among individual trees, across season, and across years (Janmaat et al., 2016). Thus, in wild chimpanzees, detailed spatial knowledge to select and reach trees from all possible directions needs to be combined with long-term memory, botanical knowledge, and long-term planning of movements (see Normand & Boesch, 2009; Normand et al., 2009; Janmaat et al., 2013a, 2013b, 2014, 2016).

Thanks to the progress of statistics, we were not only able to explore the complexity of the spatial knowledge, by including a large number of factors into the model (between 4 and 6), but as well to control for the contextual dimension, by including a number of control variables (up to 7) (Janmaat et al., 2014). It is only with such a complex model that we could identify the level of complexity of the chimpanzees' spatial skills when searching for ripe fruits in such high diversity and low-visibility forest. Detecting such level of cognitive complexity is presently out of reach from captive studies and has only become possible thanks to the recent progresses of our statistical tools. In a review of the challenge to find fruits in the African tropical

forest, the authors concluded: *“In short, ecological intelligence involves much more than solely remembering the spatial location of a number of food trees within a large home range. We conjecture that successful foraging depends on a combination of cognitive skills, especially an ability to obtain, store and retrieve knowledge on temporal availability of food in individual trees. Here, we hypothesized on the existence of a suite of cognitive strategies that chimpanzees can employ to maximize food finding efficiency in periods of scarcity by using individual and species-specific information on the predictability of their food in individual trees”* (Janmaat et al., 2016, p. 15).

Navigation in wild chimpanzees can be further complicated by their ability to not only include a suite of information about the fruit trees but by their ability to include material information about objects. For example, Tai chimpanzees are famous for cracking hard nuts with the help of heavy and hard natural-occurring hammers. These stone hammers can be rare in the forest and some of the tree producing nuts are equally rare: Chimpanzees are therefore required to make long transports of the hammers, if they want to crack the very hard *Panda* nuts (Boesch & Boesch, 1983, 1984; Sirianni et al., 2015). However, to do so, chimpanzees do not only consider the distance of the transport needed to carry the stone hammer from its original location to the nut-producing tree, they also consider the hardness and the weight of the hammer. Indeed, for hard nuts a hard and heavy hammer is mandatory to crack open the nut, and decide where the nuts will be cracked, on the ground or directly on a branch in the tree.

Thus, navigation in the forest for chimpanzees does not only mean having a notion of direction and distance, but also be able to combine these with additional information that allows them to anticipate the location of a food source, its quality, by memorizing its previous production, and its likelihood of the state of production. Such type of navigation in nature is not only about spatial knowledge but it combines in the mental map contextual and past information about the environment that allows to make predictions about the decisions to take, such as to find high-quality food or which type of hammer to select.



## Conclusion

Navigation for forest living primates requires the ability to remember the locations of tree out of sight, to be able to reach them from different directions as they forage in the forest, and to re-orient themselves flexibly with regard to different food sources and different directions. If this needs still to be demonstrated for different primate species, the evidence is already strong for species, like capuchin monkeys and chimpanzees. Such abilities are developing progressively in humans between the ages of 6 and 12 years with important individual differences (Newcombe, 2019). As in humans, primates with harder challenges develop more elaborate navigation abilities.

A decisive complexity in navigation is seen in chimpanzees, as spatial information is combined with many contextual information making the decision process conditional on different factors. These observations stress the need to consider the interactions of the individuals with its environment and within their specific population biology of the population. Navigation in nature is survival important, and therefore, we should expect very high selection pressure to resolve the ecological challenges efficiently.

## Cross-References

- [Catarrhine Cognition](#)
- [Catarrhine Navigation](#)
- [Cognitive Map](#)
- [Embodied Cognition](#)
- [Episodic Memory](#)
- [Platyrrhine Cognition](#)
- [Prosimian Navigation](#)
- [Spatial Orientation](#)
- [Tai Chimpanzees](#)
- [Technical Intelligence Hypothesis](#)

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## Hominoidea Sensory Systems

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## Synonyms

Apes; Eyesight; Gustation; Haptic sense; Humans; Olfaction; Sensation; Smell; Taste; Touch; Vision

## Definition

Apes and humans comprise the superfamily Hominoidea. Together with their sister superfamily, the monkeys of Africa and Asia (Cercopithecoidea), they form the parvorder Catarrhini. While humans are now exceptionally widespread, other members of the Hominoidea are restricted to a few tropical regions of Africa and Southeast Asia, and are among some of the most imperilled primates globally. Sensory systems form the interface between animals and the external world and are also used to sense and respond to their internal environment. In performing these roles, sensory systems play a key role in shaping the behavior, ecology, and morphology of species, as well as their molecular underpinnings. Like other primates, humans and apes use their sense of touch, smell, vision, taste, and hearing to find and select foods, avoid predators, and communicate with members of their own and other species. In this section, the sensory systems of hominoids are discussed, with a focus on similarities to and differences from other primates.

## Introduction

Five systems are traditionally discussed in the context of primate sensory ecology (reviewed in Kawamura and Melin 2017): vision, olfaction, hearing, touch, and taste. I cover each of these here, beginning with those used in perception over long distances (hearing, olfaction, vision), and ending with senses engaged at close proximity (taste and touch). It is important to note, however, that hearing, olfaction, and vision often also play important roles in close-distance evaluation (Melin and Veilleux in press). While research on primate sensory systems has historically been heavily biased toward the visual system, more attention has recently been given to olfaction, taste, and audition, with the sense of touch still relatively understudied (Dominy et al. 2001; Heymann 2006; Melin and Veilleux in press). For each sense, the main morphology, genetic underpinnings, and behavioral uses are summarized, with a focus on similarities and differences

with other primates and mammals. It is also worthwhile to mention that hominoids also possess other sensors, such as thermal sensors and proprioceptors, that are used to monitor both the internal and external environment. These senses play essential survival roles but are not considered further here.

## Audition

Hearing is a mechanical sense and often the farthest-reaching sense due to propagation and perpetuation of sound waves over long distances but is also involved in the perception of quiet sounds heard over short distances (Dominy et al. 2001). Unlike other primates, including the tarsier and strepsirrhines, hominoids – along with other anthropoid primates – have lost highly mobile ears, and their pinnae (external ear morphology) are relatively small (Coleman and Ross 2004). Approximately 70 genes have been linked to the auditory sense in humans (Frenzel et al. 2012), but a comparative study of the genetic basis and evolution of this sense across Hominoidea is almost nonexistent. Despite the reductions in morphology and concomitant changes in sensory abilities relative to other mammals, including tarsiers, lemurs, and lorises, the sense of hearing remains critical to humans and apes, and much research has investigated audition in the context of social communication (e.g., Hashiya and Kojima 2008).

Audition plays an essential role in hominoid communication as it allows the vocal cues and signals produced by conspecifics and heterospecifics to be heard and evoke behavioral responses. For example, pant hoots produced by chimpanzees vary among social contexts and receivers may respond in context-specific ways (Clark and Wrangham 1993). The spectral frequencies to which hominoid auditory systems are tuned are shaped by natural selection and by physiological and phylogenetic constraints. Species-specific audiograms – which present the audible thresholds for different frequencies – have been generated for several species (e.g., Heffner 2004). Comparative behavioral, anatomical, and computational studies have related aspects of the audiogram to the size and shape of

the inner ear bones (auditory ossicles) that transmit sound waves to the eardrum through vibrations generated in the external world, which are eventually sensed as audible noise. These studies have enabled fascinating research into the sensory ability of extinct hominoids, such as *Paranthropus robustus*, whose auditory ossicles in part resemble *Homo* and in part resemble those found in African and Asian Great Apes (Quam et al. 2013).

In foraging contexts, the sense of hearing can be used to locate food sources. For example, fruiting trees are identified by the food-associated vocalizations of conspecifics or other foragers or by the sounds of dropping fruit (Dominy et al. 2001). Some hominoids, including chimpanzees and humans, also tap fruits, and hollow sounds may be used as a sign of ripeness (Melin and Veilleux *in press*). Hunting for vertebrate as well as invertebrate prey also can involve active acoustic foraging (tap scanning), as exemplified by the specialist aye-ayes (Ramsier and Dominy 2012), or passive listening. For example, chimpanzees have been noted to change activities to hunting in response to prey-derived sounds (Boesch and Boesch 1989). In addition to being hunters, apes and humans can also be prey, and auditory detection of both alarm calls from other animals as well as detection of predator-generated noises may have shaped hominoid sensory ecology and evolution in complex ways. Finally, hearing often works in conjunction with other senses. For example, primates will automatically turn their heads to fixate their gaze upon hearing a sound of interest, known as the “visual orienting reflex.” Intentional multisensory investigations of stimuli are also common during foraging (Melin and Veilleux *in press*), and multiple senses are also simultaneously involved during communication. Visual cues such as lip movements appear to reinforce and improve (or confuse or interfere with, if mismatches are presented) auditory communication in humans and other primates (Sugihara et al. 2006).

## Olfaction

The sense of smell is a versatile and complicated chemosense. The nasal epithelium houses

olfactory receptors that can bind with multiple volatile compounds. Uptake of odors can take place long distances from their source; however, the sense of smell also plays an important role in assessment at very close distances, such as during active sniffing of a food item or a conspecific (Melin and Veilleux [in press](#)). Scents can persist in the environment for long periods, such that the sense of olfaction can be informative about past events, such as another group of animals being present in a location through scent marks. Evidence that primates make use of odors from conspecifics can be found in behavioral studies. For example, chimpanzees actively investigate urine odors, especially urine from nongroup members (Henkel and Setchell [2018](#)).

Odorants of biological relevance to apes, humans, and other primates potentially include predator-related odors, scents from foods that can either stimulate ingestive behaviors or cause rejection of foods, and body odors of conspecifics that can seemingly lead to attraction or detraction (Shepherd [2004](#); Dominy et al. [2016](#)). However, olfaction remains a poorly understood sense, and the types of odors that primates, including hominoids, can detect (along with their sensitivity thresholds and functional roles) are poorly resolved.

A common dialogue in the story of primate evolution is that the sense of smell became increasingly unimportant and markedly lower in the ancestors of hominoids. However, this view is slowly and consistently dissipating, and it is now acknowledged that primates are more sensitive to some odors – such as those common in ripening fruits – than are other mammals renowned for their sense of smell, including dogs (Laska et al. [2000](#)). Furthermore, while it was previously believed that apes have fewer functional genes responsible for coding olfactory receptors (OR) than monkeys have, this incorrect idea has been recently overturned, although the loss of OR genes may be more common in species with folivorous diets (Niimura et al. [2018](#)). Humans and apes seem to have several hundred, perhaps as many as 400, functional olfactory receptor genes. While more seemingly functional OR

genes have been reported for the wet-nosed (strepsirrhine) primates, especially the nocturnal species such as mouse lemurs, the number for hominoids is similar to those reported for other haplorrhine primates (Niimura et al. [2018](#)). A consistent trend in primate evolution is for highly species-specific loss and gain of OR genes, and extensive heterozygosity in OR genes, leading to individualized sensory experiences (Hoover [2010](#)). Anosmic humans report difficulties with both social and food-related behaviors, and as methodologies advance, future research will continue to reveal the breadth and depth of roles our sense of smell plays (Hoover [2010](#)).

## Vision

Vision, the perception of electromagnetic energy as visible light, is a key sense to humans and apes. Like other primarily diurnal anthropoids, hominoids have forward-facing eyes and acute spatial vision due to high densities of cone photoreceptors in the retina. Unlike many mammals, hominoids and other primates have round pupils and relatively large eyes (Banks et al [2015](#)). Vision is involved in many aspects of daily life, including finding and selecting both conspicuously colored and cryptic foods and predators, as well as communicating over short-to-mid distances with conspecifics. While their visual acuity and color vision fall short of the abilities of some birds, hominoid primates are outstanding among mammals in their capacity to resolve fine detail and to see a wide gamut of colorful hues (Kremers [2005](#)).

All species of apes, including humans, have routine trichromatic color vision, meaning all individuals have three types of cone cells: short wavelength (blue) sensitive, middle wavelength (green) sensitive, and long wavelength (red) sensitive. This system of color vision allows individuals to distinguish greenish from reddish hues, as well as bluish from yellowish hues (Kawamura and Melin [2017](#)). Hominoids share this uniform trichromacy with other catarrhine primates

(African and Asian monkeys), but the color vision of platyrrhines and strepsirrhines is more variable and is typically either characterized by uniform or sex-linked dichromacy (red-green colorblindness; Kawamura and Melin 2017).

The roles of color vision have been explored at some length in humans and among some monkeys and lemurs. While some of the benefits of trichromacy for food detection and selection, likely extend to members of the hominoidea, little has been asked about the role of color in intraspecific communication outside of humans (reviewed in Moreira et al. 2019). Human color vision is surprisingly different from apes and other catarrhine primates. Available studies suggest that humans have a far greater number of opsin gene mutations than other hominoids, and as a result, a much higher number of individuals with color vision anomalies (Kawamura and Melin 2017). Whether this reflects relaxed selective pressures or potentially selection favoring low frequencies of dichromatic and anomalous trichromatic phenotypes in populations remains debated, as dichromacy may confer adaptive benefits for breaking camouflage.

## Taste

Like olfaction, gustation – our sense of taste – is chemosensory and works closely with our sense of smell to perceive chemicals in the environment. Taste receptors are expressed on the surface of the tongue, and ligand binding stimulates downstream responses. Perception of tastants can stimulate acceptance/preference behaviors or rejection/avoidance behaviors. For example, chimpanzees and humans show behavioral preferences for solutions containing sucrose over those comprised of water, and frugivorous hominoids and other primates can detect sugar in low concentrations, an adaptation for the frugivorous components of hominoid diets (Remis 2006). The bitter taste receptors, on the other hand, are more diverse and are involved in the avoidance of bitter – and potentially toxic – compounds (Wooding et al. 2006).

The genetic basis of taste perception in hominoids is simpler than that of olfaction and, in part as a consequence, is better understood. Humans possess around 25 taste receptor genes coding for bitter sensors and 3 genes coding for taste receptors that are responsible for sweet and umami sensations. Evolutionary diversification coinciding with adaptive radiation can be seen in bitter taste receptor (TR) genes of apes and other primates (Fischer et al. 2005; Imai et al. 2012). Available research using comparative genomic approaches, and heterologous cell expression assays that allow TR genes to be expressed and investigated in the lab, have led to numerous advances in our understanding of functional adaptive variation between species. However, these types of studies remain in their infancy, and much work remains to be done.

## Touch

The haptic sense, or sense of touch, is perhaps the least understood of the five senses discussed here. Like audition, it is a mechanical sense, and the stimulation of cutaneous mechanoreceptors, that is, the touch receptors sensitive to vibrations and indentations of the skin (Merkel's disks, Meissner's corpuscles, Ruffini's corpuscles, and Pacinian corpuscles) generate electrical impulses perceived by the brain through the somatosensory system. Touch is used during foraging to assess (e.g., by squeezing) and to manipulate foods prior to and during ingestion, most commonly in the hands, feet, and mouth (Dominy et al. 2016; Melin and Veilleux *in press*). Some apes and humans are also adept at fashioning tools to aid foraging, a task that requires manual dexterity and extensive abilities for fine discriminative touch for detailed manipulation of objects (Russon et al. 2015; Lamon et al. 2018). Given the capacity for fine manual motor control possessed by tool-making hominoids, it is likely their sense of touch is derived relative to other catarrhines and primates, but few comparative studies of the morphology or genetic basis of touch have addressed this interesting question. Turning to the social realm, touch plays a key role



in bonding and wellbeing through direct contact, grooming, and other social activities involving touching (Nummenmaa et al. 2016).

Perhaps unsurprisingly, the mechanosenses – hearing and touch – may share a common genetic underpinning. This hypothesis was brought about by observations that people with hearing impairment can also suffer from poor haptic acuity. Although the molecular basis of touch is still relatively unknown compared to other senses, several candidate genes have recently been identified (Frenzel et al. 2012). Comparative analysis of the haptic sense across primate species with varying manual and buccal morphologies and behaviors would be a fascinating area for future work.

## Conclusion and Future Directions

Sensory systems play crucial roles in hominoid life by facilitating interactions with the physical and social environments. Research on the sensory ecology of apes and humans has shown how sensory systems contribute to adaptation and evolution, but much remains unknown, including large gaps in our understanding of genotype-phenotype interactions of nonvisual senses, use of the chemosenses during social interactions and foraging, and dynamics of multimodal sensory integration across contexts. Future research in these areas will continue to shed light on the adaptive origins of hominoids and other primates.

## Cross-References

- [Catarrhine Communication](#)
- [Catarrhine Sensory Systems](#)
- [Haplorhini](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Communication](#)
- [Primates](#)
- [Primate Sensory Systems](#)
- [Prosimian Communication](#)
- [Prosimian Sensory Systems](#)
- [Sensory Receptors](#)

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## Homo erectus

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## Definition

*Homo erectus* (upright man) is an extinct species of human that occupies a fascinating spot within the human evolutionary lineage. These prehistoric hunter-gatherers were highly successful in adapting to extremely different habitats across the Old World, as fossils connected with this species have been found ranging from Africa all the way to Southeast Asia (Brauer et al., 1992). With the earliest remains appearing around 1.9 million years ago (MYA), and continuing into the Middle Pleistocene, *Homo erectus* spanned an extraordinarily large time frame. However, the amount of variation between different fossils from different times and places has raised questions regarding the actual classification of the species, and its accurate role in the evolutionary story.

## Who Were They?

In the 1890s, fossils found at the site of Trinil by Eugene Dubois on Java, Indonesia, became the first to be classified as *Pithecanthropus erectus* (Dubois 1926). After this discovery, more *Homo erectus* fossils were found in Indonesia, then China, and finally in Africa from the 1960s. This species most likely originated in East Africa or perhaps Eurasia from an earlier species of *Homo* (most generally thought to be *Homo habilis*) (Grine et al., 1996). They may have given rise to *Homo heidelbergensis*, which is seen as a direct precursor of *Homo sapiens*.

The difficulty is, however, that the fossils that have been designated as *Homo erectus* span an almost preposterous amount of both time and geographical distance and show huge variations when they are examined together. The question is whether they can really be classified as one species, or whether these fossils comprise a number of related species.

On the one hand, there are those who contend for a broad, single-species model (*Homo erectus sensu lato*), surrounding all or almost all fossils from Southeast Asia to Africa that have been classified so far (Grine et al., 1996). In this vision, the distinction falls within the range of an otherwise cohesive species and might be due to the adventurous, globe-trotting nature of this species, with time and space impacting on their physiques. This broad definition is so convenient, though, that it becomes tempting to toss every new fossil find that seems to somewhat match the characteristics of *erectus* in with this group.

On the other hand, a narrower definition of *Homo erectus* has been recommended that excludes all of the African fossils, or at least the part found at Koobi Fora, suggesting that these constitute a different species, named *Homo ergaster* instead (Klein 1999). *Ergaster* is then seen as the species that is linked with the lineage leading to *Homo sapiens*, whereas *Homo erectus sensu stricto* (in the strict sense, so only the Asian part) may have been a dead end.

This discussion will no doubt continue until more fossils are obtained to address this issue. At the moment, the prevailing view is that the characteristics of the fossils support the single-species hypothesis – so *Homo erectus* in the broad sense is the current preferred nomenclature.

## Geographical Extend

Fossils assigned to the broad definition of *Homo erectus* are found all the way from Africa to Southeast Asia (Johanson et al., 1996). Areas and sites include Trinil on Java, Indonesia, China, Eurasia (including Georgia, where finds at Dmanisi are so puzzling they seem to blur the lines between *Homo habilis*, *Homo rudolfensis*,

and *Homo erectus* and might even end up qualifying as a separate species (*Homo georgicus*)), East Africa (sites at for instance Olduvai Gorge), and South and North Africa. Some finds in Western Europe have also at some points been characterized as *Homo erectus*, but there is now fairly broad agreement that most of these forms are better matches with *Homo heidelbergensis*.

*Homo erectus* was an early species of adventurers, thought to have started their lengthy migration out of Africa, through the Middle East, the Caucasus, and ultimately East Asia around 1.9–1.8 MYA, reaching China and Indonesia by ca. 1.7–ca. 1.6 MYA. But what spurred them on? In 2016 (East Africa) proposed a model suggesting that *Homo erectus* followed the large herbivores during their migrations, while also keeping an eye on flint deposits, and avoiding areas populated by carnivores, at least early on in their association. (We can ignore this as this is not required).

## What Did They Look Like?

*Homo erectus* was both bigger and smarter than previous *Homo* species (Van Arsdale, A. P., 2013). Their skeletons were basically similar to modern humans although they were heavier). They were the first humans to have limb and torso proportions similar to modern humans, which allowed them to walk upright on 2 ft and literally travel the world.

A few of these humans were relatively tall, with the African-based segment reaching a standard height of a lofty 170 cm, much like with our present-day population. *Homo erectus* across dissimilar regions demonstrates a wide variety of sizes, ranging between approximately 145 cm and 185 cm in height and weighing between 40 kg and 68 kg. *Homo erectus* was without a doubt a lot taller relative to previous human species.

Similarly, compared to *Homo habilis*, *Homo erectus* not only was significantly bigger but it also grew larger across evolutionary time. Early members of this species have cranial capacities between 600 cm<sup>3</sup> and 800 cm<sup>3</sup>, but later *Homo erectus* go beyond 1000 cm<sup>3</sup>, which falls within the range seen in *Homo sapiens*. They had heavy

brow ridges and a low cranial vault, and their teeth were smaller (*Homo erectus* 2018) and more slender than those of earlier humans.

## Mode of Life

*Homo erectus* relatively large brains and bodies required a lot of energy to sustain them. They ate a diverse and broad diet, perhaps including tubers, and definitely a substantial amount of meat (Groeneveld 2017). Animal leftovers with well-defined marks left by butchery have been found near *Homo erectus* skeletons, which suggests that they frequently utilized animal carcasses – most likely through both hunting and scavenging – at least 1.75 MYA (Groeneveld 2017).

There is evidence that *Homo erectus* knew and used fire. The earliest proof for the use of hominin fire dates back to around 1.8 MYA (Brown et al., 1985), and from at least 500,000 years ago, cooking became widespread. From 400,000 years ago, well within *Homo erectus*' time span, human species were noticeably and purposefully using fire. Hearths lit up the living spaces of these societies and provided not just a means for cooking food but also provided heat, protection from predators, and were good hubs for social communication, often in caves or overhanging cliffs.

*Homo erectus* was also a toolmaker, related to the Oldowan, but more generally with Acheulean stone tool manufacturing, and was often linked with the formation of the first hand-axes, which represent the first major modernization in stone tool technology. A broader set of tools would have helped *Homo erectus* stay alive across a broad range of environments, which may explain the wide geographic range in which *Homo erectus* fossils have been found.

When it comes to picturing *Homo erectus* around a hearth inside a cave, feasting on a butchered bison steak, we cannot tell whether they would have had proper conversations or not. Several social elements must have been present, but verbal communication is a tough one to determine. Anatomical clues cannot confirm or deny the capability for verbal communication or a small kind of human-like proto-language in

*Homo erectus*, and since no DNA exists, scientists cannot look for the FOXP2 gene, which is connected with verbal communication in humans and is seen in both the later Neanderthals and Denisovans (Groeneveld 2017).

On the whole, *Homo erectus* may well have been the most primitive species within this lineage to show so many human-like characteristics.

## Other Remarkable Fossils

The first *H. erectus* fossil found was a one-million-year-old skull discovered by Dutch surgeon Eugene Dubois in Indonesia in 1891. Other remarkable fossils include the 1.77-million-year-old skull of an aged man, exposed in Dmanisi, Georgia (Lordkipanidze et al., 2013). According to the Smithsonian Institution, the man had missing most of his teeth long before he passed away, causing much of his jaw to degrade (Smithsonian). This leads researchers to consider that other members of the man's social group must have cared for him, one of the first examples of such sympathetic social performance in a human ancestor.

## Relationship to *Homo sapiens*

### The Question of Origin

A small number of researchers have opposed the view that *H. erectus* was the direct ancestor of later species, including *Homo sapiens* (Jelinek 1978). Louis Leakey (1960) argued that *H. erectus* populations, particularly in Africa, overlapped in time with *Homo sapiens* and therefore could not be ancestral. Some support for Leakey's point of view has come from analysis of anatomic characteristics exhibited by the fossils. By emphasizing a difference between "primitive" and "derived" character in the renovation of associations between species, some paleontologists have attempted to demonstrate that *H. erectus* does not make an appropriate morphological ancestor for *Homo sapiens*. Because the braincase is long, low, and thick-walled and presents a strong brow ridge, they claim that

*H. erectus* shows derived (or specialized) features not shared with more modern humans. At the same time, *Homo sapiens* does share several characteristics, including a rounded cranium, with earlier hominins such as *H. habilis*. For these reasons, a number of paleontologists (including Leakey) think that the more slender, or “gracile,” *H. habilis* and *H. rudolfensis* are more closely related to *Homo sapiens* than is *H. erectus*. These findings are not broadly accepted, however. Instead, studies of size in human progress point out those representatives of *Homo* can be grouped into a sensible ancestor-to-descendant sequence showing increases in body size (Franciscus et al., 1988, Tobias and Rightmire 2006). Despite having a heavier, more flattened braincase, *H. erectus* and the African representatives of the species sometimes called *H. ergaster* fit nicely in this sequence.

Even if *Homo erectus* was ancestral to modern humans, there is still uncertainty as to how and where *H. erectus* ultimately gave increase to *Homo sapiens*. In the study of human evolution, this is a most important question. Some hypotheses have been proposed, but there is still no firm consensus supporting models of gradual change as opposed to scenarios of hasty evolution in which change in one state is followed by movement of the new populations into other areas.

### Theories of Gradual Change

A conventional paleontological view is that a species may be transformed gradually into a succeeding species (Tobias and Rightmire 2006). In the evolutionary series, successive species are called chronospecies. Because these changes are small and seen over a long time period, the borders between chronospecies are almost impossible to determine by means of any objective anatomic or functional criteria. Such a chronological boundary may have to be drawn arbitrarily between the last survivors of *H. erectus* and the earliest members of a succeeding species. The problem of defining the end point of chronospecies is not unique to *H. erectus*; it is one of the most vexing questions in paleontology. A steady transformation with stability between successive forms has been postulated especially

for North Africa, where *H. erectus* at Tighenif is seen as ancestral to later populations at Rabat, Temara, Jebel Irhoud, and elsewhere. For Southeast Asia, gradualism has also been hypothesized, where *H. erectus* at Sangiran may have given rise to populations such as those at Ngandong (Solo) and at Kow Swamp in Australia. Similar developments could have occurred in other parts of the world (Tobias and Rightmire 2006).

The presumed interrelation of cultural accomplishment and the shape and size of teeth, brain, and jaws is purely theoretical, and not all paleoanthropologists support this connection (Tobias and Rightmire 2006). Throughout the human fossil evidence, there are examples of disconnection between size and shape of skull on the one hand and cultural accomplishment on the other. For example, a smaller-brained *H. erectus* may have been among the first humans to domesticate fire, but a lot bigger-brained humans in other regions of the world living later in time have left no evidence that they used fire. Gradualism is at the core of the so-called “multiregional” hypothesis, in which it is theorized that *H. erectus* evolved into *Homo sapiens* not once but sometimes as each subspecies of *H. erectus*, living in its own region, passed some postulated crucial gateway.

### Theories of Punctuated Change

An ongoing transition from *H. erectus* to *Homo sapiens* is one explanation of the fossil evidence, but the evidence also can be read differently. Some researchers propose what can be termed an accentuated view of human evolution (Tobias and Rightmire 2006). This view suggests that species such as *H. erectus* may have demonstrated little or no morphological alteration over long periods of time (evolutionary stasis) and that the shift from one species to a descendant form may have occurred comparatively quickly and in a restricted geographic region rather than on a universal foundation. Whether any *Homo* species, including our own, evolved slowly or rapidly has not been definitively determined; this underlines the need for many more fossils to establish the assortment of physical variation of *H. erectus* and to allow more exact dating.



## Conclusion

In the study of modern human origins, *Homo erectus* is tremendously important. The Middle Pleistocene was where the modern human post-crania developed, the modern cranial features began to develop, and substantial enhancement in brain size occurred. It is also significant because many behavioral changes took place in this time era, for example, tool use, the controlled use of fire, meat-eating, hunting, etc. This is where the things people consider “human” started to develop to the point where most people would recognize these patterns of anatomy and behavior as similar to our own species.

## Cross-References

► [Homo sapiens](#)

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## Homo ergaster

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## Definition

An early species within the genus *Homo*.

## Introduction

*Homo ergaster* (“work man,” reflecting the presumed associated stone tools) is the nomen applied by Colin Groves and Vaclav Mazak to the pair of associated hominin hemimandibles catalogued in the Kenya National Museums as KNM-ER 992 (Groves and Mazak 1975). Found at Ileret in the East Turkana region of northern Kenya, and dated to about 1.5 Ma, ER 992 had initially been discovered by Richard Leakey in 1971; and when Leakey described the fossils, he allocated them simply to *Homo* sp. (Leakey 1971). At the time, ER 992 was notable among East Turkana hominin finds for its narrow, gracile mandibular corpuses and the modest proportions of its cheek teeth. And its recovery, early in the spectacular sequence of East Turkana discoveries that was made in the decade following 1968,

marked the first in a series of findings that many paleoanthropologists at the time saw fit to compare with the (much younger) *Homo erectus* from Java and eastern China. At the time, however, official policy at East Turkana was to remain vague, and to refer to any clearly non-australopith hominids simply as *Homo*, species unspecified. “Australopiths,” by the way, is the informal name given to the archaically proportioned hominin group from which it is believed our genus *Homo* emerged.

## Systematics

The discovery of the gracile ER 992 mandible slightly preceded the nearby recovery of the cranium ER 3733 and the calotte ER 3883, the somewhat older fossils that caused many to conclude that here was something much closer to later species of *Homo* than anything else known from East Turkana. The main influencing factor seems to have been brain size: at 848 and 804 ml, respectively, endocranial volumes were not far below that of classic Javan *Homo erectus* (the Trinil type specimen comes in at about 950 ml). For reference, australopith brain volumes center around 450 ml, and modern *Homo sapiens* centers on 1330 ml: Holloway et al. 2004). Eventually, Richard Leakey and Alan Walker formally capitulated and allocated all these East Turkana specimens to *Homo erectus* (Leakey and Walker 1976), despite the fact that the specimens (<1.6 Ma) were not only about a million years older than the Javan type material, but did not share any notable cranial morphologies with them.

The argument for “early African *Homo erectus*” seemed to be triumphantly substantiated by the 1984 discovery at Nariokotome, in West Turkana, of KNM-WT 15000, the “Nariokotome Boy.” WT 15000 is a remarkably well preserved ~1.6 myr-old skeleton of an adolescent individual whose brain volume was already 880 ml (headed for an estimated 909 ml had he survived to adulthood), and whose overall body proportions, revealed for the first time, were clearly much closer to those of *Homo sapiens* than to anything else of comparable age (Walker and Leakey 1978, 1993). Whatever one’s view of the proper

identification of these various Turkana specimens (which may in the end prove to represent more than one species), there can be little doubt that these fossils form a coherent grouping, and that they are the earliest hominins that can be included within a morphologically coherent genus *Homo*. In contrast, the inclusion within our genus of anything that has been allocated to the poorly defined “*Homo habilis*” group (and indeed, anything earlier) is questionable.

Ever since *Homo* (then *Pithecanthropus*) *erectus* was described from Trinil by Eugene Dubois during the 1890s, the boundaries of Dubois’s species have been steadily expanded by the inclusion of new specimens. Within the limits of eastern Asia, this expansion seems to be reasonable; but nothing outside this geographical region, either in Europe or in Africa, shares the peculiar features of cranial morphology (long, flat, low braincase with sharp angulation at the back, and shelf-like supraorbital region at the front) that characterize the type material (Schwartz and Tattersall 2000). On the other hand, while one can undoubtedly draw morphological distinctions among the east African materials (ER 992, 3733, 3883, WT 15000, and so forth) that have been included in “early African *Homo erectus*,” it seems at least heuristically useful for the moment to be able to refer to them all by Groves and Mazak’s name *Homo ergaster*. In this view, *Homo ergaster* is the stem species of our genus *Homo*, best documented in East Africa but very possibly also represented in the fossil record elsewhere in the continent; and it gave rise to later species of our genus both in Africa, and widely across the Old World.

Those ancient species would have included *Homo erectus*, which is most plausibly a local and terminal development in eastern Asia. Back in the late nineteenth and early twentieth centuries, with only a few Neanderthal fossils otherwise known to document human evolution, it might have seemed entirely reasonable to view *Homo erectus* as a “stage” within a linear human evolutionary framework: a stage that would almost by definition have embraced precursors in Africa and Europe as well as Asia; but by now, it is clear that the evolutionary history of our subfamily has not been the simple story of gradual refinement of a central lineage over the eons that this scenario

envisions. Instead, the evolutionary pattern we see within the hominins (and within the genus *Homo*) has been pretty typical for any successful mammal group. It clearly involved vigorous experimentation with the hominid potential via the generation of multiple species, each of which had to do battle for ecological space on a Pleistocene stage that was marked by notably fluctuating environments.

Sadly, the paleoanthropological mindset remains linear enough that one still hears a lot about “African *Homo erectus*.” So be sure you know to what fossils the author is referring whenever you see the species mentioned in the literature. Nonetheless, Groves and Mazak’s naming of *Homo ergaster* does offer significant possibilities for freeing human phylogeny from the linear grip in which it has existed for well over half a century; and the auguries are reasonably good for having a more realistic taxonomic framework for the genus *Homo* in the foreseeable future.

## Archaeology and Behavior

Meanwhile, if we take *Homo ergaster* as the initial species of the genus *Homo*, or something close to it, we can begin to come up with a coherent account of how our unusual lineage emerged. Most significantly, *Homo ergaster* lies early in the trend toward increasing brain size that characterized the genus *Homo* throughout the Pleistocene (small-brained and relatively recent forms such as *floresiensis* and *naledi* should probably be excluded from our genus). Two other key things are also clear from the body build of WT 15000. First, *Homo ergaster* had finally abandoned the partly arboreal australopith way of life, and as an obligate biped it had committed itself to life in more open savanna environments. Second, the relatively slender trunk structure of *Homo ergaster* indicates a reduction in the size of the gut. Putting these two observations together, Wrangham (2009) has argued that hunting and the use of fire would have been necessary to support the radically new lifestyle.

Brains are energy-hungry organs; and although animal fats and proteins were (hazardously) available on the savanna in the form of animal carcasses, along with small vertebrates that could be

hunted, the energy they contain remains physiologically relatively unavailable to a creature without a specialized predatory gut – until they are cooked. Cooking with fire would have increased the energy yields from animal and plant products alike, as well as detoxifying them; and the control of fire would additionally have helped early hominins to protect themselves from the numerous predators and scavengers with which they competed. This is a circumstantial argument for the early use of fire by *Homo ergaster*; but it is quite a persuasive one, at least until one considers that the earliest evidence of the control of fire in hearths comes from only around one million years ago – almost a million years after the initial hominin occupation of the savanna. It is possible that the lack of early physical evidence for fire use is due to the fragility of that evidence; but at present, the jury must remain out on this one.

Still, it remains true that members of *Homo ergaster* had significantly larger brains than those of the australopiths; and this fact must have been reflected in some aspects of both cognition and behavior. By the time that *Homo ergaster* appeared, at ~1.8 Ma, the physically archaic australopiths had been making simple “Oldowan” stone tools – mainly simple sharp cutting flakes and crude “pounding” implements – for the best part of a million years, and possibly a good bit longer. Yet, despite all of its physical novelties, *Homo ergaster* continued to make stone tools in the exact same tradition. With a single outlier at 1.78 Ma, we do not commonly find the more complex “Acheulean” handaxes in the East African archaeological record until about 1.6 Ma. This is not actually surprising – *Homo* evidently emerged among the australopiths, and new species and new technologies have never appeared hand-in-hand in the hominid record – but it does mean that we have no material record of any cognitive and behavioral innovations that may have accompanied the new anatomy, and probably more importantly, the new environment. It seems intuitively reasonable to believe that “intelligence” as somehow defined scaled positively with brain size, and that it played a leading role in the time-trend toward larger brains in the genus *Homo*; but it is impossible to specify exactly what “intelligence” implies in this context.

Still, the handaxe clearly represented a major leap in technological complexity and concept. The Oldowan tools of the australopiths (which continued to be made) were mainly sharp flakes, whose main attribute was a cutting edge. It did not matter what they actually looked like, although their manufacture often involved forward planning, stones with the necessary material qualities often being carried several kilometers before being knapped into tools as needed. But the larger handaxe, invented within the tenure of *Homo ergaster*, was conceptually entirely different, involving the elaborate shaping of a stone “core” with multiple blows to both sides until a desired shape – usually that of a teardrop – was obtained. Clearly, tools were now being made to a “mental template” that existed in the mind of the tool-maker before knapping began. The world was beginning to be perceived in a new way.

## Cognition: A Caveat

It is important to understand that the kind of “intelligence” we are looking at in *Homo ergaster* was not a crude variant of modern human symbolic cognition, something that we see emerging only *after* our own species *Homo sapiens* had originated at around 200 Ka. Modern human cognition involves an entirely unprecedented way of manipulating information in the mind; and its acquisition was actually followed by a *reduction* in brain size (Tattersall 2018). What *Homo ergaster* does give us is a glimpse of the very early stages of the evolution of the intuitive, non-declarative, mode of hominin intelligence that preceded the adoption of the symbolic algorithm. It is this type of intelligence that may well have scaled with brain volume, driving the parallel increases in brain size that we see over the Pleistocene in several different lineages within the genus *Homo*.

## Cross-References

- [Bipedalism](#)
- [Homo erectus](#)
- [Homo sapiens](#)
- [Stone Tools](#)

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## Homo floresiensis

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*Homo floresiensis* is an extinct hominin species that survived on the Indonesian island of Flores during the Pleistocene Epoch. Skeletal remains of *Homo floresiensis* were first discovered during archaeological excavations in the early 2000s at Liang Bua, a large limestone cave located on the western part of the island (Morwood et al. 2004). This species is characterized by small body and

brain size, as well as a combination of primitive and derived traits not seen in other hominin taxa (Brown et al. 2004; Morwood et al. 2005).

## Holotype

The holotype of this species is known as Liang Bua 1 (LB1) and consists of the partial skeleton of an adult. Its official repository in the National Research Center for Archaeology is in Jakarta, Indonesia. Preserved elements include a cranium, mandible, atlas and other vertebral fragments, ribs, right clavicle, right humerus, left and right ulna, left and right hip bones, left and right femora, left and right patella, left and right tibiae, left and right fibula, and a number of hand and foot bones. During life, this individual would have stood ~106 cm tall and weighed ~27.5 kg (Grabowski et al. 2015). The cranium is strikingly small in comparison to other species in the genus *Homo*, and its brain size is estimated at ~420 cm<sup>3</sup>, roughly one-third the size of the brain in modern humans (*Homo sapiens*). The endocast is similar in overall shape to that of Asian *Homo erectus*, but also displays some uniquely derived features (e.g., extremely wide temporal lobes, expansions in the frontal polar region, and position of the lunate sulcus) that are suggestive of higher cognitive processing capabilities (Falk et al. 2005). The anatomy of the hip and lower limb bones, as well as that of the vertebrae and the position of the foramen magnum on the cranium, indicate terrestrial bipedality as the principal mode of locomotion. However, the length proportions of the upper to lower limbs, and a foot that is long relative to the leg, suggest that this species would have been more proficient in climbing, rather than running, in comparison to modern humans (Jungers et al. 2009).

## Other Individuals

Skeletal remains of several other *Homo floresiensis* individuals have also been recovered from Liang Bua. These include: a right ulna and mandibular third premolar (LB2); a left radius (LB3); a juvenile left radius and right tibia

(LB4); an atlas (LB5); a mandible, right scapula, right radius, left ulna, and multiple hand and foot bones (LB6); a right tibia (LB8); a pollical proximal phalanx (LB10); and a right mandibular fourth premolar and left maxillary central incisor (LB15).

## Age

All skeletal elements and stone artifacts attributed to *Homo floresiensis* are stratigraphically overlain by volcanic tephra T1 and T3, respectively. Based on a combination of dating methods that includes infrared stimulated luminescence, thermoluminescence, uranium series (<sup>234</sup>U/<sup>230</sup>Th), and <sup>40</sup>Ar/<sup>39</sup>Ar, T1, and T3 are estimated to be ~60 and 50 thousand years (ka) old, respectively. In addition, direct <sup>234</sup>U/<sup>230</sup>Th dating of ulnae from three *Homo floresiensis* individuals gave modeled ages ( $\pm 2\sigma$ ) ranging from  $86.9 \pm 7.9$  to  $71.5 \pm 4.3$  ka (LB1),  $71.4 \pm 1.1$  to  $66.7 \pm 0.8$  ka (LB2), and  $66.0 \pm 4.3$  to  $54.6 \pm 2.1$  ka (LB6), all of which reflect minimum ages of deposition. Thus, the current chronological evidence suggests that the skeletal remains of *Homo floresiensis* are likely between ~100 and 60 ka old, and stone artifacts reasonably attributable to this species range in age from ~190 to 50 ka (Sutikna et al. 2016).

## Stone Artifacts

Tens of thousands of stone artifacts made by *Homo floresiensis* have been recovered at Liang Bua. These artifacts are mostly the result of free-hand hard-hammer percussion, where a hammer stone held in one hand is forcefully struck against a stone held by the other hand, although burination, truncation, and bipolar techniques were also used. Various studies of this artifact assemblage have shown that it shares broad similarities in both morphology and technology with Oldowan assemblages in eastern Africa (Oldowan artifacts are the simplest form of stone tools produced by freehand hard-hammer percussion), as well as with Early and Middle Pleistocene assemblages elsewhere on Flores (Moore et al. 2009).



## Ecology

*Homo floresiensis* lived alongside Komodo dragons (*Varanus komodoensis*), a proboscidean (*Stegodon florensis insularis*), and two large carnivorous birds, giant marabou stork (*Leptoptilos robustus*) and vulture (*Trigonoceps* sp.), along with a variety of smaller animals (mostly rats and bats) with body masses less than ~3 kg (Sutikna et al. 2018).

## Phylogeny

*Homo floresiensis* is almost certainly a descendant species of an ancient hominin lineage that was present in Asia before the estimated time of divergence (~765–550 ka ago) of the lineages that ultimately led to the evolution of Neanderthals and Denisovans in Eurasia, as well as modern humans in Africa. This ancient ancestral lineage is probably the result of an earlier hominin dispersal from Africa more than ~1.5 million years ago. The ancestor of *Homo floresiensis* (or the species itself) likely arrived on Flores by at least one million years ago, based on the presence of stone artifacts at sites in central Flores and ~700 ka old *Homo floresiensis*-like teeth and lower jaw fragments discovered in this area (Brumm et al. 2016). Hypotheses explaining the origin and evolution of *Homo floresiensis* often take the form of one of two possibilities: (1) this taxon is a descendant species of Asian *Homo erectus*, and the smaller body and brain size of *Homo floresiensis* probably evolved in isolation on Flores; or (2) *Homo floresiensis* is a descendant species of another premodern taxon of *Homo* that was smaller bodied and smaller brained when it first reached Flores. Each of these hypotheses is supported by a different combination of the available evidence, and further discoveries are needed to resolve which, if either, is correct.

## Cross-References

- [Homo erectus](#)
- [Homo sapiens](#)

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## Homo heidelbergensis

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### Definition

A controversial Middle Pleistocene (~780–130 ka) hominin species, part of the same genus (*Homo*) as extant humans.

### Introduction

The taxonomy and phylogeny of *Homo heidelbergensis* is much debated (for a review see Stringer 2012), so much so that this period in human evolution has been dubbed the “muddle in the Middle [Pleistocene].” There is little agreement on which specimens should be included in *H. heidelbergensis* (that is to say, the group of specimens which constitute what is known as its “hypodigm”), nor even whether it constitutes a valid species at all. Many Middle Pleistocene hominins (taxa more closely related to *H. sapiens* than to chimpanzees) share primitive features with earlier species, such as *H. erectus*, but also share derived traits with later Pleistocene specimens such as *H. sapiens* and Neanderthals (e.g., Rightmire 2013). This mosaic morphology has led researchers to group them together as a single Afro-European species designation: *H. heidelbergensis*. Some have also suggested that additional Asian Middle Pleistocene fossils may extend the range of *H. heidelbergensis* (e.g., Stringer 2012). One reason for the great interest in *H. heidelbergensis* is that the Middle Pleistocene is the epoch during which the *H. sapiens* lineage split from our sister taxa, the Neanderthals and Denisovans, and *H. heidelbergensis* has long been considered a possible last common ancestor (LCA) for these two lineages (Buck and Stringer 2014; Mounier et al. 2009; Rightmire 2008; Stringer 2012). Knowing the identity of the LCA

would allow us to see which differences between our own species and Neanderthals are derived in which lineage, enabling us to better understand our own evolution and that of our closest relatives.

### What Is *H. heidelbergensis*?

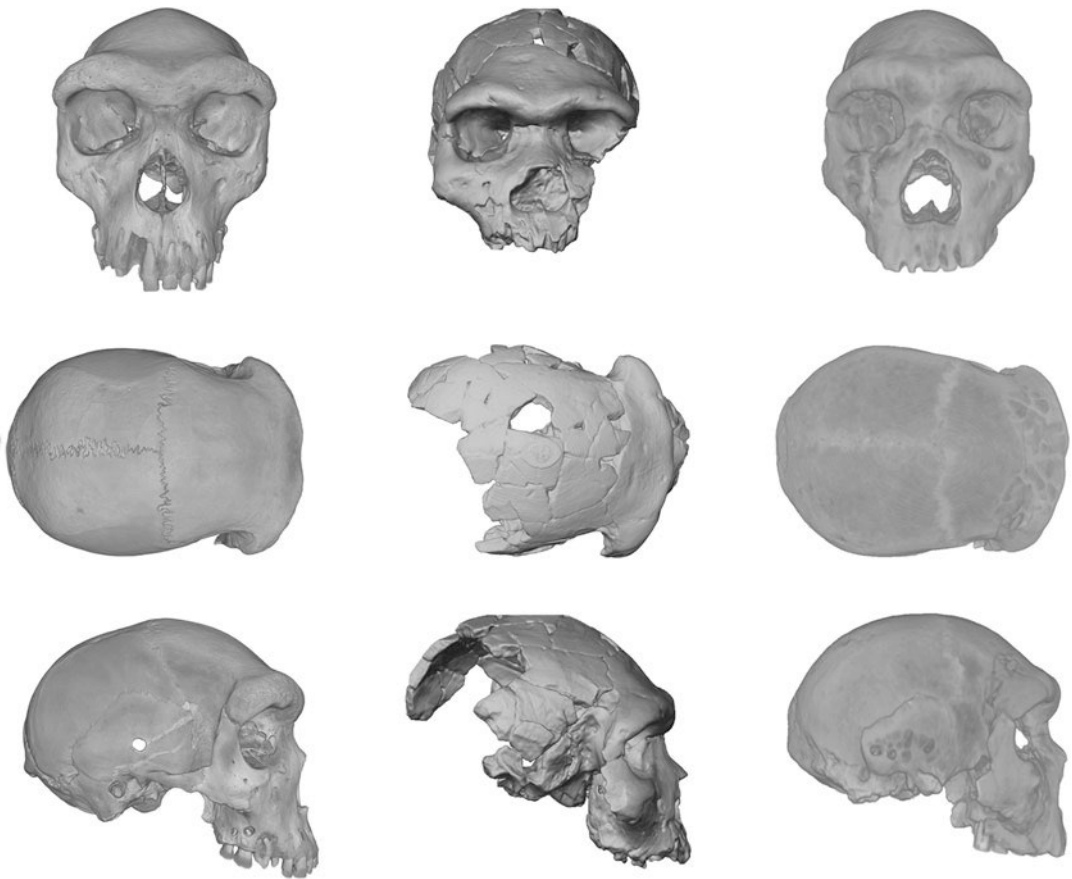
The name *H. heidelbergensis* comes from the Mauer mandible, a ~600 ka (1000 year old) fossil found near Heidelberg, Germany, in 1907. This remarkably robust mandible is the type specimen for *H. heidelbergensis*, the specimen against which all potential members of the species must be compared. This means that no hypodigm can be called *H. heidelbergensis* without the inclusion of the Mauer mandible. The size and robusticity of the Mauer mandible are reminiscent of *H. erectus*, yet it is much younger than any European *H. erectus* and also displays characteristics linking it to later taxa, such as smaller teeth (Stringer 2012). There are similarities between the Mauer mandible and a mandible from Arago (France, ~400 ka) and a partial cranium from Arago shows affinities with Middle Pleistocene fossils from elsewhere in Europe and Africa, allowing the entire hypodigm to be designated *H. heidelbergensis* (Mounier et al. 2009; Rightmire 2008).

The use of a mandible for the important role of type specimen has complicated our understanding of *H. heidelbergensis* (Stringer 2012). Few mandibular fossils are known from the Middle Pleistocene, making it hard to link specimens from different sites with the Mauer mandible and thus with the species designation *H. heidelbergensis*. Furthermore, there are fewer diagnostic traits on the hominin mandible than the cranium, making it a less reliable region for dividing taxa. Comparative shape analysis of Mauer and other Middle Pleistocene mandibles supports an Afro-European species diagnosis of *H. heidelbergensis* (Mounier et al. 2009), but this depends on the hypodigm. If Spanish material from the site of Sima de los Huesos is excluded, based on recent reinterpretations of these fossils as early Neanderthals, there is less evidence for linking the Mauer mandible to the rest of the

hypodigm (Stringer 2012). It has been suggested that the Mauer mandible should be discarded as the type specimen for *H. heidelbergensis* (Hublin 2009), in which case the name *H. rhodesiensis* (taken from the fossil Kabwe from Zambia, previously Rhodesia) would probably be applied to an Afro-European taxon combining Middle Pleistocene material such as Bodo, Kabwe, and Petralona (Fig. 1) (Buck and Stringer 2014; Stringer 2012; Thackeray et al. 2020). For clarity, the designation *H. heidelbergensis* will be used here throughout to describe this general hypodigm.

### What Are the Characteristics of *H. heidelbergensis*?

Middle Pleistocene fossils diagnosed as *H. heidelbergensis* (Fig. 1) exhibit a combination of primitive, *H. erectus*-like, features with those that are derived compared to *H. erectus* and are found in chronologically younger taxa. Primitive characteristics of this group include the occipital morphology, wide interorbital breadth, and large browridges, while more derived features include greater brain volumes, the basicranial morphology, and reduced facial projection (Rightmire



**Homo heidelbergensis, Fig. 1** *H. heidelbergensis* fossils. Three of the most iconic potential *H. heidelbergensis* specimens (left to right): Kabwe (Broken Hill) from Zambia dated to ~300 ka, Bodo from Ethiopia dated to ~600 ka, and Petralona from Greece dated to ~400 ka. From top to bottom, images are of front, top, and side views of crania. (Images are of virtual

models created using CT data, courtesy of the Natural History Museum (London), University of Vienna and University of Thessaloniki, respectively). The side view of Kabwe has been mirrored horizontally for consistency as the right side of the fossil is better preserved. Images have been approximately scaled to equal size for better comparison

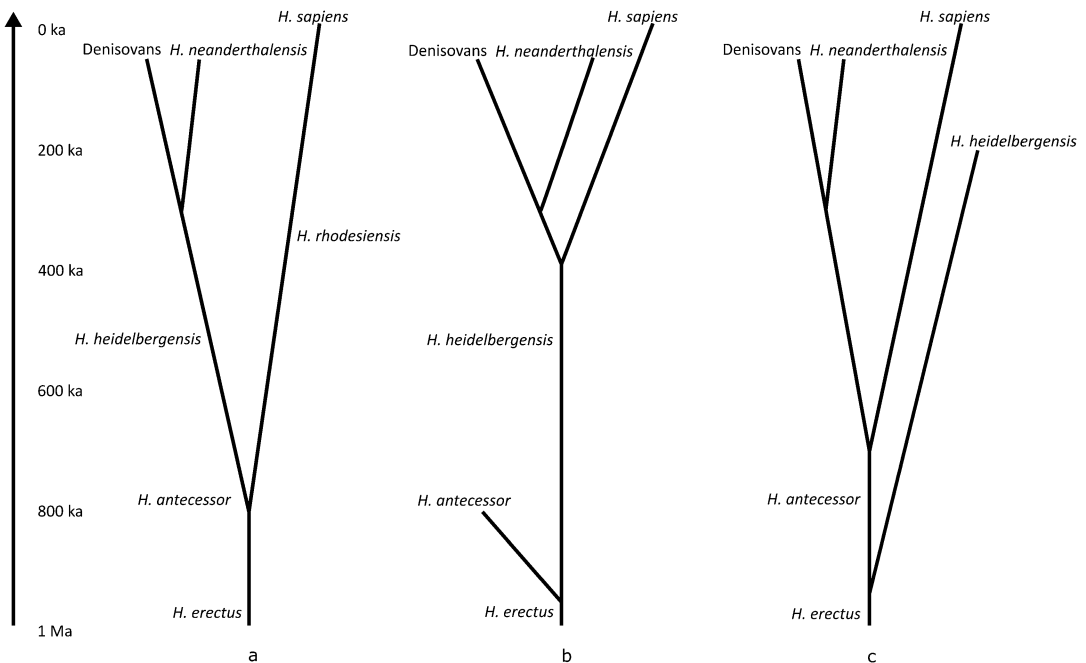
2008, 2013). There is, however, much variation within the group, even within geographical regions. Many species show considerable variation due to factors such as sexual dimorphism, adaptation to local environments, and population history and opinions differ as to whether the levels of variation within the *H. heidelbergensis* hypodigm exceed those plausible for a single species (Lacruz et al. 2019; Mounier et al. 2009; Rightmire 2008; Stringer 2012).

Archaeological sites attributed to *H. heidelbergensis*, such as Boxgrove (UK, ~500 ka), have yielded rich lithic assemblages including beautiful Acheulian handaxes (Roberts et al. 1999). Organic remains of this ancient are rarely preserved, but extraordinary wooden artifacts, possible spears, from the sties of Clacton (UK, ~400 ka (Allington-Jones 2015)) and Schöningen (Germany, ~300 ka (Conard et al. 2015)) hint at considerable technological and hunting sophistication during this epoch. The Middle Pleistocene

also sees the first good evidence for control of fire, with the remains of clear hearths at sites such as Beeches Pit (UK, ~400 ka) (Roebroeks and Villa 2011). This archaeology provides insights into how these hominins were able to colonize high latitude regions of Europe during the Middle Pleistocene.

## The Role of *H. heidelbergensis* in Human Evolution

For some time, *H. heidelbergensis* has been widely thought of as the possible LCA of *H. sapiens* and Neanderthals (Fig. 2). *H. heidelbergensis* is a suitable candidate for this role as the *H. sapiens* and Neanderthal/Denisovan lineages diverged in the Middle Pleistocene and potential *H. heidelbergensis* fossils are found in both Africa, the birthplace of *H. sapiens*, and Europe, the birthplace of Neanderthals. Depending on the



**Homo heidelbergensis, Fig. 2** Possible position for *H. heidelbergensis* in the phylogeny of mid-late genus *Homo*. Three main hypotheses for the taxonomic position of *H. heidelbergensis*. Time is on the left-hand axis, Ma: millions of years ago, ka: thousands of years ago. (a) European *H. heidelbergensis* as ancestral to

Neanderthals (*H. neanderthalensis*) and the related Denisovans, while African Middle Pleistocene specimens are placed in *H. rhodesiensis*; (b) *H. heidelbergensis* is the last common ancestor of *H. sapiens*, Neanderthals and the related Denisovans; (c) *H. heidelbergensis* as not directly ancestral to either *H. sapiens* or Neanderthals

hypodigm favored, *H. heidelbergensis* also shows cranial expansion and facial characteristics that can be argued to foreshadow the morphology of both *H. sapiens* and Neanderthals (Buck and Stringer 2014; Mounier et al. 2009; Rightmire 2008; Stringer 2012; Thackeray et al. 2020).

An alternative viewpoint for many years has been that *H. heidelbergensis* was limited to Europe, where it was ancestral to the Neanderthals alone (e.g., Dean et al. 1998) (Fig. 2). In this scenario, Middle Pleistocene African fossils formed part of another taxon, most likely *H. rhodesiensis*. This hypothesis relied heavily on the inclusion in *H. heidelbergensis* of fossils from the Spanish site of Sima de los Huesos, since these specimens show many Neanderthal characteristics, placing them firmly on the Neanderthal lineage. The redating of the Sima de los Huesos fossils from ~600 to ~430 ka (Arsuaga et al. 2014) has convinced many that they are best interpreted as early Neanderthals, rather than *H. heidelbergensis*, reducing support for exclusively European *H. heidelbergensis* (Buck and Stringer 2014; Stringer 2012). The presence of some Middle Pleistocene European fossils lacking Neanderthal characteristics, such as Ceprano (Italy, ~430 ka), and no clear chronological sequence in the development of Neanderthal morphology, may instead indicate taxonomic complexity and the coexistence of multiple lineages (Martín-Torres et al. 2012; Bermúdez-de-Castro et al. 2016).

## Changing Places: Recent Developments

The iconic cranium from Kabwe (Broken Hill) has been pivotal to discussions of *H. heidelbergensis*, in part due to its similarities with Petralona from Greece, which support the taxon's Afro-European distribution (e.g., Harvati et al. 2010; Stringer 2012). Recent work has, however, begun to undermine the status of this fossil as a representative of the LCA of *H. sapiens* and Neanderthals. Since its discovery in 1921, Kabwe has been difficult to date precisely and it was given an indirect approximation of ~700–300 ka, which made it a reasonable

candidate for a member of the LCA (Klein 1973). After years of reanalysis, Kabwe has now been directly dated to about 300 ka ( $299 \pm 25$  ka) (Grün et al. 2020). Recent work shows that some characteristically *H. sapiens* features are already present at ~300 ka at sites such as Jebel Irhoud in Morocco (Richter et al. 2017) and the same is true of Neanderthal features in European fossils from ~400 ka onwards (e.g., Sima de los Huesos from Spain, Swanscombe from the UK, and Steinheim from Germany (Dean et al. 1998)). This being the case, Kabwe, which displays no clear Neanderthal or *H. sapiens*-derived morphology, is less convincing as a representative of the LCA. Earlier potential *H. heidelbergensis*, such as Bodo (~600 ka), are chronologically possible representatives of the LCA, but with split times for *H. sapiens* and Neanderthal lineages based on aDNA modeling at ~600 ka (Meyer et al. 2016), an older taxon is also plausible.

An alternative LCA is *H. antecessor*, a species known only from the Early Pleistocene (~860 ka) site of Gran Dolina, Spain (Bermúdez-de-Castro et al. 2017; Stringer 2016). *H. sapiens* is peculiar amongst hominins in its small, vertically orientated face (Lacruz et al. 2019; Stringer and Buck 2014). A fairly complete juvenile face from Gran Dolina appears to have distinctively *H. sapiens*-like morphology, suggesting it could be part of our lineage, while in other characteristics *H. antecessor* fossils resemble Neanderthals (Bermúdez-de-Castro et al. 2017). An *H. sapiens*-like face in *H. antecessor* suggests the facial morphology of the LCA was preserved in the human lineage, while Neanderthal morphology diverged (Lacruz et al. 2019). The young developmental age of the crucial *H. antecessor* fossil was initially a concern, but computer modeling, which virtually aged the fossil along different potential growth trajectories, supported the assertion that its diagnostic morphology would have been retained into adulthood (Freidline et al. 2013). Microscopic examination of juvenile fossil bone surfaces is also suggestive. These analyses reveal patterns of areas where bone is either laid down or sculpted away, producing characteristic adult shape over the course of development. Of all the hominin taxa currently



investigated, only *H. antecessor* seems to have a *H. sapiens*-like facial growth pattern (Lacruz et al. 2013, 2019). The facial evidence thus supports the hypothesis that *H. sapiens*-like morphology was already present in *H. antecessor*, the potential LCA, during the Early Pleistocene (~1800–780 ka) and was preserved in its descendent, *H. sapiens*. Those who take this viewpoint do not necessarily discount the validity of *H. heidelbergensis* as a species, but suggest it is tangential to the evolution of *H. sapiens* and Neanderthals (Lacruz et al. 2019).

## Conclusion

Recent years have to some extent clarified the “muddle in the Middle” and evidence is building that *H. heidelbergensis* may not be the LCA of *H. sapiens* and Neanderthals. Whether it is a valid species and what constitutes its hypodigm if so, however, is still an open question. Indeed, there is growing recognition in Paleoanthropology that strict species designations are human constructs that only approximate biological reality and can be particularly problematic when applied to the fossil record e.g., (Thackeray et al. 2020).

There is strong morphological evidence that at least some African and European Middle Pleistocene fossils can be combined in a hypodigm, which in the absence of mandibular evidence for the key specimens is probably best referred to as *H. rhodesiensis* (Stringer 2012). Asian Middle Pleistocene fossil material has been to some extent overlooked during this discussion and the addition of Asian fossils to this hypodigm is also still possible. One key example is the newly announced cranium from Harbin, China. This specimen appears to have similarities to the Afro-European hypodigm, but it has yet to be formally described (Lacruz et al. 2019). A number of other new discoveries, or new dates, of crania from sites such as Harbin, Auerira (Portugal; Daura et al. 2017), and Apidima (Greece; Harvati et al. 2019) show increasing evidence of taxonomic complexity in the genus *Homo* during the Middle Pleistocene and multiple taxa seem likely in several regions (Martín-

Torres et al. 2012; Rak et al. 2011). Advances in aDNA research may help to unpick the relationships between Middle Pleistocene taxa. Genetic material has been sequenced from the ~430 ka Sima de los Huesos fossils, supporting their close relationship with Neanderthals and showing that Middle Pleistocene DNA can be successfully retrieved and analyzed (Meyer et al. 2016). Recent work shows the introgression of DNA from “ghost” taxa (hominins of unknown taxonomic designation, perhaps those for which there is no known fossil evidence as yet) into both *H. sapiens* and extinct species, such as the Denisovans (Wolf and Akey 2018). Perhaps better understanding of these ghosts, as well as additional aDNA recovery from fossils, will illuminate the true nature of *H. heidelbergensis*.

## Cross-References

- [Homo erectus](#)
- [Homo ergaster](#)
- [Phylogeny](#)

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## Homo sapiens

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## Synonyms

Anatomically modern humans (AMH); Human  
being; Modern human

Definition

The binomen *Homo sapiens* is composed of the genus name *Homo* (“human being” in Latin) and the species name *sapiens* (“wise”), and it designates all living humans (and their extinct direct relatives). According to the fossil record, the origin of *Homo sapiens* is around 200,000 to 300,000 years ago in Africa. Today, it is the only existing species of the genus *Homo*, which in the past included numerous species now extinct (e.g., *Homo habilis*, *H. erectus*, *H. neanderthalensis*, etc.).

Introduction

The species name *Homo sapiens* was invented by C. Linnaeus in 1758, in the 10th edition of his *Systema Naturae*, to accommodate all living humans. In the late eighteenth and early nineteenth century, fossil representatives and extinct species of the genus *Homo* were not known, and in a fixist (i.e., non-evolutionist) context, *Homo sapiens* was thought to be the only human species that ever existed. Accordingly, its original description by Linnaeus was minimalist, consisting only in the famous – but not very informative – “*Nosce Te Ipsum*” (“Know Thyself”). For obvious reasons, no type specimen (or “holotype,” the reference specimen of the species) has ever been designated for *Homo sapiens*, and it is today the only valid species with no holotype. Indeed, we all know that all of us actually belong to the same species. But, together with the absence of a clear morphological definition of the species, it contributes to make the attribution of fossil specimens more complicated.

Among mammals, *Homo sapiens* belongs to the order primates. It is one of the c. 300 known living species of primates, and our closest living relatives are the two chimpanzee species: the common chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*). One of the most frequently used taxonomies (Table 1) places *Homo sapiens* in the tribe Hominini, a subdivision of the family Hominidae. The family Hominidae includes all extant great apes (orangutans,

**Homo sapiens, Table 1** Taxonomy of the family Hominidae at the genus level, including extinct hominins (indicated by †). This is one option among the various currently accepted taxonomies for Hominidae. This taxonomy does not include fossil genera for tribes other than hominins, nor of the extinct tribe of Eurasian apes Dryopithecini, in the subfamily Homininae

|                                 |
|---------------------------------|
| Family Hominidae (hominids)     |
| Subfamily Ponginae (pongines)   |
| Genus <i>Pongo</i>              |
| Subfamily Homininae (hominines) |
| Tribe Gorillini (gorillins)     |
| Genus <i>Gorilla</i>            |
| Tribe Hominini (hominins)       |
| Genus † <i>Ardipithecus</i>     |
| Genus † <i>Australopithecus</i> |
| Genus † <i>Kenyanthropus</i>    |
| Genus † <i>Orrorin</i>          |
| Genus † <i>Paranthropus</i>     |
| Genus † <i>Sahelanthropus</i>   |
| Genus <i>Homo</i>               |
| Genus <i>Pan</i>                |

gorillas, chimpanzees, and humans) and their extinct relatives. The tribe Hominini (“hominins”) includes humans and chimpanzees, although chimpanzees are sometimes placed in a separate tribe called Panini. Hominini also includes all extinct relatives of humans and chimpanzees since their Last Common Ancestor (“LCA”), which according to fossil and genetic evidence lived between c. 10 and 6 million years ago.

Since the mid-nineteenth century, discoveries made in the fields of palaeoanthropology and prehistory document a very rich and long evolutionary history for the hominins. This is especially true for the branches of the evolutionary tree where the genera *Australopithecus* and *Homo* are found. Abundant fossils corresponding to several distinct extinct species have been recognized in those two genera, indicating that *Australopithecus* lived from about 4.4 to 1.9 million years ago and *Homo* from 2.8 million years ago until today. The manufacture of stone tools had for a longtime been directly and exclusively linked in the definition of the genus *Homo*. However, in recent years, several discoveries broke this certainty, like the discovery of animal bones with cutmarks or percussion points (and thus

indirectly showing the use of stone tools) close to remains of *Australopithecus* (*A. afarensis*, *A. garhi*), before the recent finding of 3.3 million-year-old large stone tools (anvils, nucleus, flakes at Lomekwi, Kenya; Harmand et al. 2015). These discoveries indicate that the production and use of stone tools appeared several hundred thousand years before the emergence of *Homo* and are thus probably linked/associated to *Australopithecus*-like hominins. To the contrary, the evolutionary history of the chimpanzees since the LCA is still poorly documented in the fossil record, and the very early stages of the evolution of the hominins remain to be understood. At the end of the 1990s and early 2000s, fossils dated to between c. 7 and 4 million years ago have been discovered. They correspond to three genera (*Sahelanthropus*, *Orrorin*, and *Ardipithecus*) which show indices of upright posture and bipedal locomotor behavior, i.e., one of the main “human” features. No archaeological evidence of any technical behavior (i.e., tools) is associated to these three genera. However, some authors argue that the use and/or production of stone tools by nonhuman great apes like chimpanzees could indicate that this cultural (material culture) trait may have been shared by very ancient hominins.

Most of the evolutionary history of the hominins took place in Africa, until some human groups went out of Africa for the first time, probably at around two million years ago or even earlier. The origin of *H. sapiens* is also African, as indicated by genetic and fossil evidence. The oldest fossils currently described as “fully *H. sapiens*” have been found in Ethiopia and are dated to c. 200,000 years ago (McDougall et al. 2005). Recent studies of fossils found at Jebel Irhoud (Morocco) indicate that “*Homo sapiens*-like” hominins were present in Northern Africa by at least 300,000 years ago (Hublin et al. 2017). Those fossils lack very few anatomical features to be considered as anatomically modern humans (AMH) and revive the debate on the exact list of anatomical features defining *H. sapiens*. If we have a fairly good knowledge of the variation of the morphological traits of present-day *H. sapiens*, several fossils found in Africa and Asia, for instance, show that the

morphological and genetic diversity of our species was larger in the Upper Pleistocene than it is today. This is also true for cultural or behavioral features. For years, *H. sapiens* was archaeologically defined by a set of elements constituting the so-called modern behavior (e.g., complex hunting weapons, symbolic behaviors). However, new discoveries and new studies show that, in the past, it is quite difficult to identify clear differences between *H. sapiens* and other closely related and/or contemporaneous species such as *H. neanderthalensis*. It is also challenging because extant humans, who stand as the reference point for comparisons, appear to be extremely diverse in their biological, cultural, and behavioral attributes.

## **Homo sapiens Today**

### **We Are All Homo sapiens**

Whatever the region of the world in which we live today, we all belong to one and the same species, *Homo sapiens*. However, compared to other animal species – including our closest living relatives in the primate order – *H. sapiens* has a huge geographical range, it occupies a very wide range of habitats, and it is an extremely diverse species. Observing human groups living today in various places of the world, there is a considerable amount of biological, cultural, and behavioral variation. Accordingly, if there is no doubt about the fact that we all belong to the same species, to give a consensual definition of this species is a complicated task.

### **How to Recognize a Living Homo sapiens**

*H. sapiens* is often defined as a primate with a bipedal gait and erect posture, endowed with culture, making and using tools, and capable of empathy and emotions. Although, taken one by one, none of these features are actually exclusive to *H. sapiens*, their combination is probably unique. Anatomically, *H. sapiens* is also distinguished from its closest living relatives by a large brain relative to body mass, a face that is reduced in size and not projected forward, a modified vocal tract (involved in spoken language), body

proportions (e.g., long legs relative to arms), hands with opposable thumb and abilities of precision grip and manipulation, reduced hairiness, and pigmented skin. Several of these physical attributes (e.g., body proportions, skin pigmentation) can show a large range of variation in the species under the influence of environmental factors such as altitude and sun exposure. Sexual dimorphism, i.e., the difference in size and shape between males and females, is reduced in *H. sapiens*. This characteristic is linked to the fact that human social groups are based on cooperation rather than on competition between males for access to females, differing from many other primate species in which males are much larger than females. In an evolutionary perspective, it is often considered that the combination of all those anatomical features defines “anatomically modern humans” (AMH), although the use of “modernity” in a biological sense is questionable and is a frequent source of confusion with socio-cultural considerations.

Extended childhood – the period of time during which an offspring is not able to care for itself – is also an important characteristic of *H. sapiens*, although its time of appearance in the evolutionary history of hominins is debated. It is linked to a hypothesis called the “obstetrical dilemma” by Washburn in 1960, who argues that “adaptation to bipedal locomotion decreased the size of the bony birth-canal at the same time that the exigencies of tool use selected for larger brains. This obstetrical dilemma was solved by the delivery of the fetus at a much earlier stage of development” (Washburn 1960: 74). The evolutionary answer to this dilemma is to give birth to “highly immature children.” This implies prolonged growth and learning period, which have important consequences on human social structures (unavailability of the mother for reproduction, cooperation among adults to take care of the children, etc.).

### ***Homo sapiens*: A (Hyper)social Species?**

In the behavioral and cognitive fields, *H. sapiens* is also characterized by a large variability, even if a large part of human social traits are shared with other mammals, particularly primates. After all, we share 98% of our genetic pool with other

primates like chimpanzees. And as recent studies highlight, genetic and cultures are intimately linked, or, more exactly, genetic structure proceeds partially from cultural choices and social selection (Richerson et al. 2010). Such examples include stature differences between males and females within human populations, or the different frequencies of genes related to lactase persistency (i.e., highest frequencies in regions where people consume animal milk, linked to the transmission through time of animal domestication and dairying practices).

Generally speaking, extant modern humans belong to very diverse (hyper)social communities, living and evolving in groups which are cohesive in terms of spoken language, material cultures *sensu lato*, or social structure (residence rules, patri- or matrilinear, monandry, polygamy, etc.). From birth, *H. sapiens* is (pre)configured for sociability, which facilitates brain maturation, particularly during childhood, and development of the learning capacities and the social transfer of knowledge mechanisms. Our species is stimulated by its life in community, within territories whose management and exploitation are in themselves factors of morphological and cultural evolution. Some researchers point out, for example, that the *H. sapiens*' success story throughout its tens of thousands of years of dispersal and expansions is largely grounded on its abilities of empathy behaviors, facilitated by the development of a brain sensitive to its social environment. This development of the senses of organization, cooperation, and mutual aid among a social group might have been a major element during times of demographic or environmental crisis.

Together with other brain structural enhancements, resulting, for example, in language and memory skills, these social traits appear as driving forces in the evolution of *H. sapiens*, compared to other primates. The aptitude of early modern humans to adapt to very diverse and contrasted situations in terms of climate and landscape (and more generally in terms of natural and cultural environments) might also have been in itself a factor of innovations. These innovations defined the so-called modern behavioral package of *H. sapiens*, even though the concept of



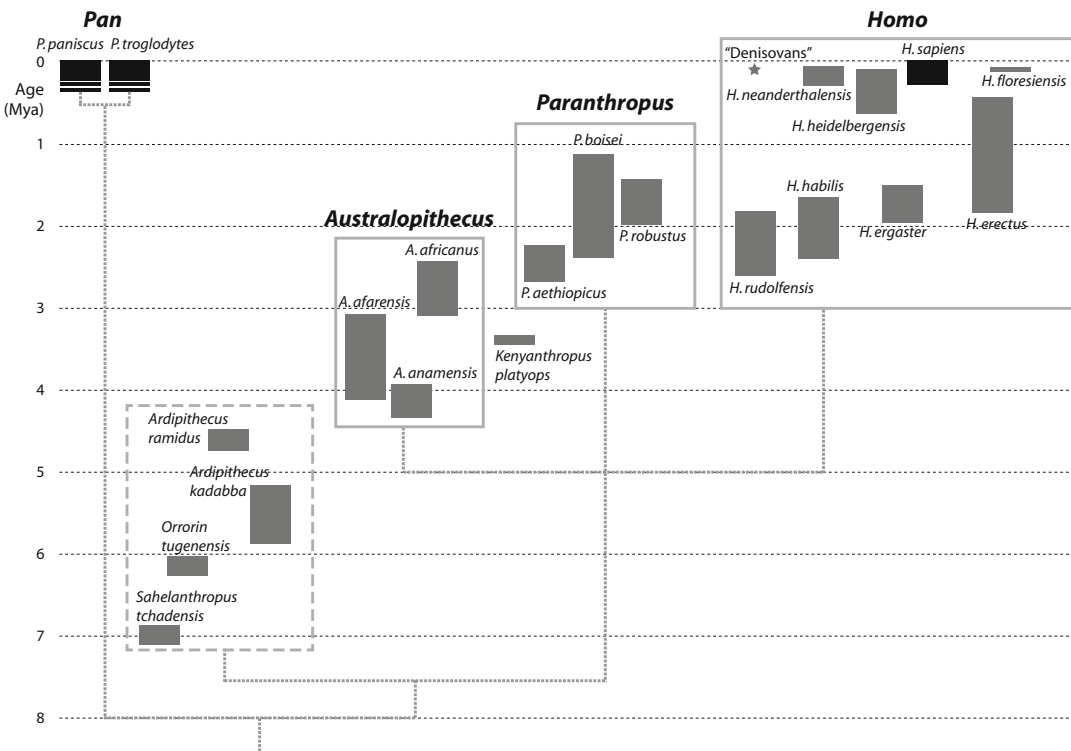
“modernity” is also questionable here. Nevertheless, this capacity to overcome complex situations by the development of new strategies probably helped AMH to “conquer the whole world” in few tens of thousands of years.

**Homo sapiens in the Past: Origin and Evolutionary History**

**Early Hominins and the Origin of the “Human Lineage”**

The phylogeny of extant hominids (living great apes, including *H. sapiens*) is now resolved, but

it is far from being the case of the whole family Hominidae, with all extinct hominins known today (Fig. 1). Most of the nodes (i.e., “hypothetical ancestors” of two diverging branches), tempo of evolutionary changes of key anatomical features, and detailed phylogenetic relationships remain debated in our family tree. The earliest recognized hominins (the genera *Sahelanthropus*, *Orrorin*, and *Ardipithecus*) have reduced canines and anatomical traits that are generally interpreted as pointing to some degree of terrestrial bipedalism. Those features align them preferentially with *Australopithecus*, *Paranthropus*, and *Homo*, forming the “human



**Homo sapiens, Fig. 1** Chronological extension of the key genera and species of the tribe Hominini, with a simplified tentative phylogeny (chronology is in millions of years ago: Mya; extinct species: gray boxes, extant species: black boxes; divergence times in the phylogeny are purely indicative; adapted and modified from Wood and Boyle 2016). “Denisovans” are indicated by a single star, because they are still known from a very limited number of fossils and no new species name has been formally published for them yet. *Kenyanthropus* is not included in the simplified phylogenetic hypothesis. It is

still a poorly known genus, with a single species (*K. platyops*), but it is possibly the manufacturer of the earliest stone tools known to date (Lomekwi in Kenya, at c. 3.3 Mya, Harmand et al. 2015). Several fossil species are omitted for clarity purposes, or because they are still debated/known from few fossil specimens: *Australopithecus sediba* at c. 2 Mya, *A. deyiremeda* at c. 3.5–3.3 Mya, *A. garhi* at c. 2.5 Mya, *A. bahrelghazali* at c. 3.6 Mya, *Homo georgicus* at c. 1.8 Mya, *H. antecessor* at c. 1.2–0.7 Mya, *H. rhodesiensis* at c. 0.6–0.3 Mya, and *H. naledi* at c. 0.3–0.2 Mya

lineage” characterized by facultative or obligate terrestrial bipedalism, rather than with the chimpanzees which are arboreal and terrestrial knuckle-walkers (knuckle-walking is a specialized type of quadrupedal walking, with ground support of the upper body on flexed manual phalanges). However, the posture and locomotor behaviors of the LCA (between *Pan* and the “human lineage”) remains largely unknown, and the fossil record for *Pan* and its direct ancestors is excessively poor (mainly known from few teeth recovered in Kenya and dated to c. 500,000 years ago). This situation might explain why at the moment *Sahelanthropus*, *Orrorin*, and *Ardipithecus* tend to align more closely to the human lineage which is documented by thousands of fossil remains rather than with the virtually undocumented *Pan* lineage. The genus *Australopithecus* is known from a great number of fossils discovered since the 1920s in Africa. Several distinct species have been recognized based on fossil assemblages recovered from Eastern Africa (e.g., *A. anamensis*, *A. afarensis*, *A. garhi*), Southern Africa (*A. africanus*, *A. sediba*), as well as from Central Africa, in present-day Chad (*A. bahrelghazali*). Among those different species of *Australopithecus*, there is a great deal of interspecific and intraspecific anatomical variation documented in most skeletal parts, including those involved in locomotion. If it points to diversified locomotor behaviors with generally dominant terrestrial bipedalism, it also contributes to complicate the understanding of the exact phylogenetical relationships and evolutionary history of the genus *Australopithecus*, which is most probably paraphyletic (i.e., a composite group of species which share a common ancestor, but not all of its descendants).

Similarly complex and unresolved is the phylogeny of the three commonly recognized species of *Paranthropus*: *P. aethiopicus* and *P. boisei* in Eastern Africa and *A. robustus* in Southern Africa. They are characterized by very large post-canine teeth (i.e., premolars and molars) and a massive masticatory apparatus, and they were previously assigned to the genus *Australopithecus* (the so-called robust *Australopithecines*). For many years now, there are doubts whether those

three species form an actual monophyletic group (i.e., all the descendants of a common ancestor) or if they instead descended independently from different ancestors – different *Australopithecus* species – in Eastern Africa on the one hand and in Southern Africa on the other hand. The actual evolutionary relationships of *Paranthropus* species with the earliest members of the genus *Homo* (*H. habilis* and *H. rudolfensis*), which were living in the same regions of Africa at the same time, also remain poorly understood.

### The Genus *Homo*: A Single Living Species, Numerous Extinct Species

Historically, early members of the genus *Homo*, to which *H. sapiens* belongs, were first discovered by Louis and Mary Leakey in the site of Olduvai, present-day Tanzania, in geological layers dated to c. 1.8 million years ago which also yielded stone tools. In a seminal paper published in 1964, Louis Leakey, Phillip Tobias, and John Napier described the morphology and context of discovery of the fossils and decided to assign them to a new species of the genus *Homo*: *Homo habilis*. But to do so, in the same article, they first had to revise and modify the definition of the genus *Homo* which was generally accepted at the time, but which was too restrictive to accommodate the fossils found in Olduvai. In fact, this definition has been frequently modified and its limits enlarged since the mid-nineteenth century – and especially during the twentieth century – so that the genus *Homo* may include new fossil discoveries assigned to new extinct hominin species. This was the case, for instance, for *H. neanderthalensis* in 1856, for *H. heidelbergensis* in 1908, for *Pithecanthropus erectus* published in 1894 but regarded as *H. erectus* since the 1950s, and for *H. habilis* in 1964, where few pieces of evidence except for their association with stone tools were actually arguing for the attribution of the Olduvai fossils to the genus *Homo* rather than to the genus *Australopithecus*. Until today, the definition of the genus *Homo* is a rather easy task when dealing with living Hominidae only, but remains a much discussed topic in prehistory and palaeoanthropology on which no actual consensus has been reached yet.

Throughout the years, however, the most commonly accepted definition of the genus *Homo* remains based on four criteria: (1) a large absolute brain size (greater than 600 cm<sup>3</sup>), (2) the possession of spoken language, (3) hands with an opposable thumb and precision grip capabilities, and (4) the ability to manufacture stone tools.

This list has been and is still debated for two main reasons. On the one hand, some of those features are obviously difficult to assess from fossil remains, such as the possession of spoken language which is extremely difficult to ascertain only from the study of fossil endocasts. On the other hand, taken one by one, none of these features is actually restricted to members of the genus *Homo*, complicating the task of assigning most – if not all – hominin fossil assemblages to the genus *Homo*. Alternative approaches to this complex issue of the definition of the genus *Homo* have been proposed. In the early 2000s, some palaeoanthropologists considered long-distance (or endurance) running and associated anatomical and physiological traits as being unique to the genus *Homo* (Bramble and Lieberman 2004). At the same time, using only objectively verifiable criteria to test several phylogenetic hypotheses about hominin evolution, other researchers proposed that the genus *Homo* should be restricted and exclude *H. habilis* and *H. rudolfensis* to be an actual monophyletic group (Wood and Collard 1999).

Shortly after two million years ago, hominins expanded out of Africa for the first time and settled in various regions of Eurasia. At c. 1.8 million years ago, some groups were present in the Caucasus (site of Dmanisi, in present-day Georgia) and at about the same time period in East Asia (China). Fossil assemblages indicate that, starting at around 1.6 million years ago, hominins were occupying Southeast Asia (site of Sangiran, Indonesia) and at c. 1.2 million years ago Occidental Europe (site of Sima del Elefante in Atapuerca, Spain). There is no real agreement on how many different species should be recognized for these hominin groups, which were widely dispersed in space and chronology: few different species (or even only one, *H. erectus*) or several.

Although environments and climates can vary dramatically inside the African continent, the vast majority – if not the whole – of the early fossil record for the genus *Homo* known to date in Africa is derived from “Savannah-like” past environments. There are possible biases (e.g., preservation and fossilization conditions, preferentially targeted areas for researches in the field) which could explain this situation, but it seems quite obvious that, after some of them ventured out of Africa and settled in various regions of the Old World, hominins had to cope with very different and very diverse living conditions. Hominins were then occupying territories dispersed on various areas in Africa and Eurasia, implying increased distances between groups and very diverse environmental conditions (temperatures, precipitations, natural resources such as mineral resources for stone tools, animals and plants for consumption, etc.) acting on the natural selection of biological features at a microevolutionary scale. Those factors probably played a major role in driving these groups (or species) along diverging biological and cultural evolutionary paths, resulting in the appearance of various adaptive strategies. A whole area of modern researches in prehistory consists in understanding if the adaptive strategies adopted by those many different species of the genus *Homo* which occupied the Old World in the past were the same as those of *Homo sapiens*, and if not, how and how much they differ from them. Anatomically speaking, comparisons based on the fossil record show that the morphological variation documented between those groups was considerably larger than that of present-day *H. sapiens*.

### **From Cro-Magnon to Omo Kibish: The Earliest Fossil Evidences for *Homo sapiens***

Fossils and genetics indicate that the origin of *H. sapiens* is undoubtedly African. With few hundreds of thousands of years of existence, it is a young species in view of the long – several million years old – evolutionary history of our family Hominidae, and it is obviously the species for which we have the richest fossil record.

Although it was actually not the first time ancient *Homo sapiens* were found, the discovery of fossil human bones in Abri Cro-Magnon in Les Eyzies-de-Tayac (Dordogne, France; Lartet 1868) was a major milestone in the history of two emerging disciplines at the time: prehistory and palaeoanthropology. Indeed, the human skeletal remains from Cro-Magnon corresponding to at least four adult individuals were described as belonging to *Homo sapiens*, but with marked differences in morphology and size with people living in this region of Europe in recent times. Few years after the publication of *On the Origin of Species* by Darwin in 1859, the Cro-Magnon findings pointed for the first time at a possibly very long (pre)history of our species *Homo sapiens*. Since then, several fossils recognized as belonging to early *H. sapiens* have been discovered, at considerably older dates than the c. 30,000-year-old Cro-Magnon individuals. The oldest fossils currently described as “fully *H. sapiens*” correspond to two individuals (Omo 1 and Omo 2) recovered from geological layers dated to c. 200,000 years ago at the Omo Kibish site, near the Omo River in Ethiopia (McDougall et al. 2005). Interestingly, the morphologies of those two individuals show great differences, documenting a variation that is larger than what is found inside a single population of present-day *H. sapiens*. While Omo 1 presents a very derived, “anatomically modern,” cranial and postcranial skeleton, the skull of Omo 2 retains much more “primitive-looking” features. More recently, new discoveries and new studies of fossils from the site of Jebel Irhoud (present-day Morocco) indicate that “*Homo sapiens*-like” hominins were present in Northern Africa by at least 300,000 years ago (Hublin et al. 2017). Although the Jebel Irhoud fossils present few cranial and endocranial primitive-looking features, their facial, mandibular, and dental morphology align them with AMH, at a time period that is more than 100,000 years earlier than that of the Omo Kibish fossils. Despite a fossil record for African hominins that is still very scanty between c. 500,000 and 200,000 years ago, the Jebel Irhoud findings indicate that the origin of *H. sapiens* might have been more

gradual than what was thought before. It possibly involved various human groups present on the whole African continent and mosaic evolutionary processes with the appearance of *H. sapiens* skeletal features at different times, during a rather long period of time.

### How to Recognize a Fossil *Homo sapiens*?

These early African fossils illustrate perfectly the difficulties related to the definition of *H. sapiens* in an evolutionary perspective, i.e., including fossil specimens and thus based on features which are preserved and observable on fossil assemblages. If there are a large number of skeletal features which distinguish *H. sapiens* from other living great apes, it is much more difficult to pinpoint the features which are actually differentiating *H. sapiens* from other penecontemporaneous species of the genus *Homo*. *H. neanderthalensis* is obviously the best-known extinct hominin since it is documented by numerous fossil assemblages, representing dozens of different individuals and absolutely all skeletal elements. For many years, palaeoanthropologists were able to list series of features which are different between *H. neanderthalensis* and *H. sapiens*, often considering that this list was de facto defining the latter species. However, this was considerably revised, especially after the discovery near Lake Turkana in Kenya of the c. 1.6 million-year-old Nariokotome skeleton (the “Turkana boy”) in 1984. This skeleton of an adolescent assigned to *H. ergaster* (or *H. erectus* for some authors) presents most of the skeletal features which were listed as characteristic of *H. sapiens*, indicating that it is in fact the skeletal anatomy of *H. neanderthalensis* which is highly derived, and not necessarily that of *H. sapiens*. Taking into account its present-day variation and the most recent fossil discoveries, *H. sapiens* can be defined from the following skeletal features: a *mentum osseum* (i.e., a “true bony chin”), a large and globular braincase, a short face, a flexed basicranium, small teeth with a simplified (external and internal) morphology, and few postcranial features related to the shape of the pelvis and femur (e.g., Stringer 2016). The main

problem with those features is that, once they are quantified and analyzed for the genus *Homo*, most of them show a large intra- and inter-specific variation, which makes the recognition of a “threshold” for *H. sapiens* very difficult (or arbitrary). The qualification of “*Homo sapiens*-like” hominins for the Jebel Irhoud fossils is a good illustration of this conundrum. Because the shape of their braincase is less globular than what is documented in living and fossil *H. sapiens*, some scholars consider that it is not possible to assign them to *H. sapiens s.s.*, but others consider they present “enough” derived features of *H. sapiens* to be actually considered as such.

### Hypotheses on the Origin of *Homo sapiens*

The question of the origin (place and time) of our species has always been a major topic of interest, and it was the subject of a particularly vivid debate for more than 50 years (from the 1940s to the 1990s). Based on fossil and archaeological evidence, two main evolutionary hypotheses were proposed. The first one, developed after the pioneer work of F. Weidenreich in the 1930s and 1940s, is traditionally known as the “multi-regional model.” According to this hypothesis, hominin evolution was marked by a single major Out of Africa event, corresponding to the dispersal of *Homo erectus* into various regions of the Old World (e.g., East and Southeast Asia, Europe). This major dispersal event was followed by continuous processes of regional evolution and frequent episodes of interbreeding between populations living in neighboring regions. Combined together throughout time, those processes led to the gradual emergence of *H. sapiens* more or less simultaneously in different regions of the Old World. This hypothesis was challenged by an alternative model called the “Out of Africa” hypothesis. According to this hypothesis, the origin of the species *H. sapiens* is quite recent and African only, that is, *H. sapiens* went out of Africa from where the species originates and dispersed into Eurasia, replacing other species of the genus *Homo* which were still possibly present in those regions (like *H. neanderthalensis* in Europe, late *H. erectus* in Indonesia, etc.). In the 1990s and

early 2000s, discoveries of fossils in Africa and genetics of living human populations brought an almost unanimous support to the “Out of Africa” hypothesis. Analysis of present-day human mitochondrial DNA (“mtDNA”), Y chromosome, and nuclear DNA allowed us to trace back the origin of all living *H. sapiens* to regions situated in Eastern or Southern Africa and a major Out of Africa event dated to c. 60,000–80,000 years ago (e.g., Quintana-Murci et al. 1999; Underhill et al. 2000).

### The Onset of a Specific *Homo sapiens* “Modern Behavior”?

Archaeologically, the behavioral traits, cultural diversity, and cognitive changes which accompanied the appearance and evolution of *H. sapiens* are also difficult to assess. Nevertheless, for the last three decades, besides the results of paleoanthropological and genetic studies, the many discoveries of cultural assemblages (material remains) allowed us to better characterize the emergence of our species from a cultural point of view, defining new theoretical approaches (together with new methodological developments). These studies resulted in the recognition of a “modern behavioral package,” which would characterize the uniqueness of AMH. Several models have been proposed to contextualize this (r)evolution.

One of the first models was arguing for a relatively late development of modern behavior during the Late Upper Pleistocene. Thus, even if “modern morphological features” were already present in the Early Upper Pleistocene, “modern behaviors” would have developed later, between 50,000 and 40,000 years ago, in relation with cognitive changes in the human brain, which allowed the expansion of the Upper Paleolithic in Europe (Klein 1995).

Pointing out the eurocentrism approach of this paradigm and the push back in time of the AMH roots (i.e., new ages of Omo or Jebel Irhoud fossils) as well as those of some important technical shifts in Africa (e.g., blades, retouched point, Levallois debitage methods) from ~300,000 years ago – and thus predating the first AMH – fostered new models. One of it argues for a gradual



and mosaic emergence of new major technical and socioeconomical features, appearing and disappearing at different times and places, from the end of the Middle Pleistocene (Foley and Lahr 1997; McBrearty and Brooks 2000). Technical evolution toward a more elaborated and diverse toolkit than before and hafting technology is linked to the development of complex hunting strategies. The invention of projectile weaponries with retouched point manufacture, recurrent blade production, diminution size of the weapons, and hafting proceeds appears thus to have not only been a technical evolution but also a major behavioral and social shift, facilitating territory management and population movement/mobility and demography and forcing new structured social organization. These societal organization enhancement would then have been accelerated during Later Stone Age in Africa from mid-Upper Pleistocene (i.e., from c. 70,000 to 50,000 years ago; Villa et al. 2012) and a trend to an important weaponry diminution in size and the microlithization of tools (bladelet production, backed pieces, and geometrics).

Besides these major developments, other structuring traits of *Homo sapiens* highlighting a complex social organization are correlated to the diversification and intensification of symbolic behaviors. Complex behaviors linked to non-direct utilitarian production and related to the expression of singular and conceptual relationship with environment, such as rock paintings, personal ornamentation, or even mortuary practices, are not born with modern humans. Many references show that this kind of practices predates the emergence of AMH, including Neanderthals' expansion. Nevertheless, during the last 100,000 years ago, new symbolic practices are directly related to the development of *Homo sapiens*. These new activities can be seen as a kind of "modern signature," whose Upper Paleolithic from c. 40,000 years ago and its artistic expression explosion are the most representative. Nevertheless, even before, they appear and develop more or less sporadically in Africa and can be attested by the production of engravings on pigment pieces and ostrich eggshell or the manufacture of eggshell personal ornaments. Finally,

as other innovations, those related to symbolic behavior of *H. sapiens* took their singularity in their diversity and intensification through time.

In this sense, the way members of our species take care of their dead is symptomatic, even if mortuary practices are not a modern humans' apnage, nor a "specific" innovation. Indeed, examples of special attention to the deceased predate *H. sapiens*, as shown by human remains recovered from the sites of Bodo (African *H. heidelbergensis* or *H. rhodesiensis*) or Sima de los Huesos (*H. heidelbergensis*), for instance. More recently in the chronology, Neanderthals had similar primary burial practices with *H. sapiens*, whether they had independent or inherited origins. Nevertheless, *H. sapiens*' prehistoric societies also show highly diverse and variable mortuary/funerary practices, resulting in many different practices that can be seen nowadays.

In fine, more than a specific and linear "modern" behavioral drift, all these gradual modifications provide a mosaic image of the sociocultural characteristics of *H. sapiens*. The variety and variability of these traits may thus be one of the trace elements of our species roots (Shea 2011).

All the more so as because large part of these major changes (technical innovations, complex social structuration, or symbolic behavioral traits), which question the emergence of a specific modern cognition, are challenged by the presence of similar cultural advancements among penecontemporaneous Neanderthal populations. These common features shared by different human species at the same time highlight the difficulty that we, present-day *H. sapiens*, encounter to define, identify, and conceptualize our specific (or not) and original (or not) cultural mechanisms, which drove the success of the "conquest" of the all world by our species.

## ***Homo sapiens* at the "Conquest" of Planet Earth**

### **Leave (and Not Leave) Africa: *H. sapiens*' Dispersals Throughout Africa**

The history of the Out of Africa and dispersals of *H. sapiens* can sometimes seem misleading. One

must not imagine that, as soon as the species was born in Africa, all of its members left it completely. Since the time of its origin until today, the history of *H. sapiens* is largely African. Our cradle is African, although its precise location remains the object of debates. In the present state of our knowledge, the earliest fossils of *H. sapiens* have been found in Eastern and Northern Africa, and they are dated to around 200,000 years ago and 300,000 years ago, respectively (see section “[From Cro-Magnon to Omo Kibish: The Earliest Fossil Evidences for Homo sapiens](#)”). Genetics of living populations alternatively pinpoint Eastern Africa or Southern Africa as the possible regions of origin for all living humans. Surprisingly, the processes involved in and the timing of the early dispersals of *H. sapiens* inside Africa are still rather poorly documented and understood. Between 120,000 and 100,000 years ago, *H. sapiens* was present in Southern Africa, as shown by discoveries made in several sites, such as Klasies River Cave, Border Cave, and Blombos Cave, for instance. The earliest *H. sapiens* fossils known to date from Central Africa were found in the site of Ishango (Democratic Republic of Congo), and they are dated to only 20,000–25,000 years ago (Crevecoeur et al. 2016). However, as for early hominins, the fossil record of Western and Central Africa for ancient *H. sapiens* is very poor, possibly due to unsuitable conditions for conservation and fossilization of skeletal remains.

### A Series of Aborted Out of Africa Events?

The first Out of Africa events of *H. sapiens* are documented by data and results derived from palaeoanthropology and genetics which are a priori contradictory. For years, the oldest fossil *H. sapiens* known outside Africa were those discovered in the 1920s–1930s in the Levantine sites of Skhul and Qafzeh (present-day Israel) and dated to between 120,000 and 90,000 years ago. More recently, two series of important discoveries related to earlier dispersals of *H. sapiens* out of Africa were announced. Fossil teeth of *H. sapiens*’ morphology and dated to between 80,000 and 120,000 years ago have been discovered in 2011–2013 in Fuyan Cave (present-day China), indicating an early presence of *H. sapiens*

far away from the African cradle (Liu et al. 2015). And a fragmentary maxilla with teeth discovered in Misliya Cave (Israel) and dated to at least 177,000 years ago may suggest that *H. sapiens* was already present outside Africa long time before the time period documented in Skhul and Qafzeh (Hershkovitz et al. 2018). All these fossils present morphological attributes that leave few doubts about the fact that they belong to the species *H. sapiens*, but genetics indicate that the Out of Africa event which is at the origin of all humans currently living on the Eurasian, Australian, and American continents occurred later, between 60,000 and 80,000 years ago (see section “[Hypotheses on the Origin of Homo sapiens](#)”). The most parsimonious explanation for those apparently discordant results is that these early dates may correspond to one or several “aborted” Out of Africa events. Human groups involved in those early dispersals may have disappeared without leaving any descendants in present-day human populations.

### New Territories, Encounters, and Interbreeding

During the chronological windows during which *H. sapiens* expanded out of Africa, it was not the only species of the genus *Homo* living on the planet. To date, at least two – probably three – other different human species have been recognized in the fossils recovered from Eurasia. The most famous and best documented of these species is *H. neanderthalensis*, whose first fossil remains were discovered as early as 1829 (Engis 2 child, though its actual recognition as a Neanderthal occurred several years later). There is a very rich fossil record for *H. neanderthalensis*, which indicates that the species lived between more than 350,000 years ago and c. 40,000 years ago. Neanderthals occupied a geographical area covering Europe, the Levant, and Central Asia, with its easternmost extension known to date in the Altai Mountains (Siberia, present-day Russia). A long-standing question in prehistory and palaeoanthropology is as follows: “Did *H. sapiens* meet with *H. neanderthalensis* after its Out of Africa? And if so, what happened?” While there is still very little solid archaeological

and fossil data to address those two questions, ancient DNA (i.e., extracted from hominin fossils) gave major results. The first successful sequencing of ancient hominin DNA was obtained from the mtDNA of *H. neanderthalensis* skeletal remains in the 1990s, then rapidly increasing in numbers during the 2000s (see Nielsen et al. 2017). The results of the first studies showed that *H. sapiens* and Neanderthals differ significantly in their mtDNA. However, their nuclear DNA, which was first successfully sequenced in 2010 (Green et al. 2010), gave quite different results. Nuclear DNA indicates that *H. sapiens* and *H. neanderthalensis* had a long shared evolutionary history with a rather recent date of divergence (various estimations between c. 800,000 and 400,000 years ago), which is coherent with what is known from the fossil records. But these studies show that several independent events of interbreeding between the two groups occurred in Eurasia, well after their initial divergence. Because all present-day “non-African” humans carry a very small percentage (1.8–2.6%) of “Neanderthal DNA” and not Africans, it seems that those interbreeding events occurred in Eurasia only, after the main *H. sapiens*’ Out of Africa. In 2010, while attempting to sequence the DNA of a fragmentary hand phalanx from Denisova Cave (Altai Mountains, present-day Russia) which was supposed to be that of a Neanderthal, Krause and colleagues (2010) obtained a mtDNA sequence which was close to but significantly different from both *H. sapiens* and *H. neanderthalensis*. Several other DNA sequences have been obtained from additional fossils (teeth) since 2010, confirming that a previously unknown hominin was indeed living in Denisova Cave between c. 50,000 and 30,000 years ago. Because the fossil evidence is still too scarce for a proper morphological description of this new hominin, no new species name has been published for them yet (it is not allowed to publish a new species based on DNA sequences only), and they are still called “Denisovans.” Surprising also with the sequencing of those still rather “mysterious” hominins is the indication that they also interbred with *H. sapiens*. Small percentages of “Denisovan DNA” are found in

some present-day human populations, mainly from East Asia and Oceania, but the exact timing and geographical location of those interbreeding events between *H. sapiens* and “Denisovans” are still largely unknown.

### Asia, Australia, Europe, America, and the Pacific

The hypothesis which is currently the most widely accepted for the earliest dispersal of *H. sapiens* into Eurasia is that, after going out of Africa c. 80,000–60,000 years ago, they first went east, following a southern coastal route along the Indian Ocean. The archaeological evidence is still relatively scarce (and palaeoanthropological evidence virtually absent) to understand the details of their expansion in South Asia, but they probably reached Southeast Asia and Australia quite quickly, where they settled at least 60,000 years ago (Clarkson et al. 2017). The settlement of Australia is considered as an important milestone in the prehistory of *H. sapiens*’ dispersal because it implied sea-crossings, thus some sort of early navigation. However, *H. sapiens* was not the first hominin to cross the sea in island Southeast Asia. Indeed, the discovery of fossils assigned to the species *Homo floresiensis* in 2004 (Brown et al. 2004) indicates the presence in the cave of Liang Bua on Flores Island (present-day Eastern Indonesia) of these very small-bodied hominins from c. 100,000 to c. 60,000 years ago. Additional hominin fossils discovered in another site of Flores Island (open air site of Mata Menge) in layers dated c. 700,000 years ago demonstrate that hominins possibly related to *H. erectus* were able to cross the sea long time before *H. sapiens* and that these hominins subsequently experienced the effects of insular endemism (“insular dwarfing”). It is currently not known if *H. sapiens* and *H. floresiensis* actually met, but the chronologies of their presence in the region potentially overlap, and suggestions have even been made of a possible correlation between the extinction of *H. floresiensis* with the arrival of *H. sapiens*. Up to now, it is not possible to know if interbreeding events occurred because sequencing of *H. floresiensis* DNA has been unsuccessful so far.

The chronology of the earliest presences of *H. sapiens* in Asia indicates its populations extended to the north, probably from Southeast Asia to Eastern and Central Asia. However, this hypothesis might need to be revised if the early dates for *H. sapiens* in China are confirmed and if they are related to the same global dispersal events (and not one of the possible aborted Out of Africa events; see section “[A Series of Aborted Out of Africa Events?](#)”).

Europe, which was occupied by *H. neanderthalensis* until c. 30,000 years ago, was one of the last large areas of Eurasia to be settled by *H. sapiens*. The timing and process of the Neanderthal demise, and their replacement by AMH between c. 45,000 and 30,000 years ago is still debated. The early phases of Upper Paleolithic, assumed to highlight the very first arrival of AMH groups in Europe, are diagnosed from the assessment of technical features, particularly based on blade, bladelet, and bone tool production. They have been viewed as transitional and regional facies representing AMH migration from Central Asia and Levant. Nevertheless, human fossils are rare, and therefore pinpointing the authorship of these productions is sometimes challenging and the focus of extensive discussion. Two fragmentary fossils from Western Europe (Kent’s Cavern in the UK and Grotta del Cavallo in Italy) gave dates at c. 40,000 years ago, but their exact age and/or attribution to *H. sapiens* remains to be discussed. The earliest and best documented individuals securely attributed to *H. sapiens* are from Eastern Europe, like the individuals from Peștera cu Oase dated to 37,000–42,000 years ago. It roughly corresponds to the timing of the onset of Upper Paleolithic features in Europe, which frames the progressive replacement of the Neanderthal Middle Paleolithic populations. Interestingly, DNA analysis of one of the individuals from Oase showed that 6–9% of its genome is derived from Neanderthal (Fu et al. 2015; and see section “[New Territories, Encounters, and Interbreeding](#)”).

The timing of the first arrivals and the processes of dispersal of *H. sapiens* in America have been debated for a very long time. While

archaeological findings attributed to *H. sapiens* dated to c. 30,000 years ago have been reported from South America, it is currently accepted that *H. sapiens* arrived at least 15,000 years ago (Goebel et al. 2008). By that time, *H. sapiens* was present on most of the planet, with the exception of the northernmost latitudes and of the hundreds of islands of remote Oceania Pacific, which were settled later on by skilled long-distance navigators (Kirch 2017).

## Conclusion

At around 60,000 years ago, *Homo sapiens* was only one of the at least three and possibly four different species of the genus *Homo* which were living on earth. It is the only one which survived until today. *Homo sapiens* has a long evolutionary history, which started several hundred thousand years ago, somewhere in Africa. Its abilities led our species to inhabit all regions of the world, including some of the harshest ones, surpassing cyclic global environmental changes. Such challenges allowed our species to achieve exceptional levels of technological skills development, resulting today in a large cultural and biological diversity.

Marked by a complex link between biological and cultural adaptations, the evolution of *H. sapiens* is singular. This link seems to have strengthened since the onset of the Neolithic c. 12,000 years ago, which appears to be a “revolution” in terms of relationships between humans and nature. From this period, the impact of human activities on the environment changed the balance of natural selection. This new tendency toward an increased *anthropization* of landscapes finally resulted in a new situation where one species – *H. sapiens* – can influence and deeply affect climate changes and biodiversity (“sixth extinction” issues). *H. sapiens* can also, at least to some extent, guide its own evolution, modifying its biology through cultural choices. In this sense, *H. sapiens* is becoming the first biocultural group in the history of life to endorse major responsibilities in global future, including its own.

## Cross-References

- [Cultural Transmission](#)
- [Culture](#)
- [Hominid](#)
- [Hominoid](#)
- [Primates](#)
- [Stone Tools](#)
- [Tool Use](#)

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## Homogametic

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## Synonyms

### Homogamety

## Definition

“Organisms or individuals producing one kind of gametes.”

## Introduction

The term **homogametic** is often used to define an organism or individual producing all the gametes of same type. The homogametic individuals possess matching pair of sex chromosomes in contrast to **heterogametic** individuals which carry sex chromosomes of different types. Because of the presence of identical sex chromosomes, the homogametic individuals produce one type of gametes carrying identical sex chromosome whereas heterogametic organisms produce two different types of gamete with distinct sex chromosomes (Graves 2006; Namekawa and Lee 2009). For example, in human, females carrying two “X” chromosomes (i.e., sex chromosomes in female) produce only one type of gametes (X-bearing) and are homogametic while males possessing both “X” and “Y” chromosomes (i.e., sex chromosome in male) are heterogametic producing half of the gametes having X- chromosome while the other half are Y- bearing (Graves 2006; Namekawa and Lee 2009).

Homogamety or heterogamety is not restricted to one specific sex. Both the phenomena could be seen in both the sexes. Although in most cases males are heterogametic and females are homogametic, in certain other species males are homogametic while females are heterogametic. Some examples of homogametic male and homogametic females are given below.

## Homogametic Male

Examples of homogametic males are represented by most of the avian species, moths, and few species of fishes. Here, males retain two identical sex chromosomes that are designated as “ZZ” while female hold either two different sex chromosomes (ZW) or only one sex chromosome (Z0). This can be further divided into two types:

- (a) **Z0-ZZ Type:** In this case, the male individual possesses two identical sex chromosomes

“ZZ” and therefore, produces all the gametes of same type with “Z” sex chromosome. However, females are heterogametic and produce 50% gametes with “Z” chromosome while other 50% gametes without “Z” chromosome. This is called as **Z0-ZZ** type of sex determination. The sex of organism is determined by the gametes produced by female organism. If male gamete bearing “Z” chromosome fuses with female gamete carrying “Z” chromosome, the progeny will be a male while fusion of male gamete (Z) to female gamete carrying “0” sex chromosome resulted in a female organism, e.g., butterflies and moths (Kaiser and Bachtrog 2010)

- (b) **ZW-ZZ Type:** Here, the male organism produces all the gametes with “Z” sex chromosome. However, unlike “Z0-ZZ” mechanism, female organism of “ZW-ZZ” arrangement produces half of the gametes with “Z” chromosome while second half of the gametes with “W” chromosome. Like “Z0-ZZ” system, determination of sex is decided by the gametes derived from female germ cells (Schartl 2004; Graves 2009). The ZZ-ZW system of sex determination has been reported in several reptiles and birds.

### Homogametic Female

Here, female organism possesses two identical sex chromosomes and therefore, produces all the gametes of same type. This can also be divided into two types.

- (a) **XX-XY Type:** This type of sex determination is present in mammals including humans, plants, and many insect species like *Drosophila*, etc. The homogametic females produce only one type of gamete all having “X” chromosome. However, heterogametic males produce 50% gametes with “X” chromosome while the rest 50% with “Y” chromosome. Mostly, sex is decided by the male gametes, although in some species like *Drosophila*, it is the ratio of autosomes and sex chromosome which determine the sex of an individual (Waters et al. 2007; Ellegren 2011).
- (b) **XX-X0 Type:** Here, female individual is homogametic and produces only one type of

gamete. The male individual produces half of gametes with “X” chromosome and rest half gametes without “X” sex chromosome, i.e., (0). The sex is decided by the gametes generated by the heterogametic individual, for example, grasshopper, cockroach and cricket (Kaiser and Bachtrog 2010).

Like animals, homogamety as well as heterogamety has also been reported in plants. In plants also, homogametic sex produces only one type of gametes while heterogametic sex produces two type of gametes, i.e., male determining gametes and female determining gametes in equal proportions. Several species of angiosperms, gymnosperms, and bryophytes carry heteromorphic sex chromosomes in one sex and identical sex chromosomes in another sex, similar to XY/male and XX/female system. Identification of homogamety or heterogamety in plants is very complex and can be determined by different ways including identification of heteromorphic sex chromosomes, crossing between dioecious (male and female flowers occur on different individuals) and bisexual, i.e., male and female flowers occur on the same plants species, self-fertilization (or intercrossing) of bisexual individuals from normally dioecious or sub-dioecious species, etc. *Melandrium* and *Fragaria* represent the male and female heterogamety, respectively. The complexity of determination of homogamety and heterogamety in plants occur due to presence of dioecious, monoecious (i.e., stamens and pistils are restricted to separate flowers on the same plant), and hermaphroditic (male and female are found in the same flower) sexes in plants as well as absence of morphologically distinct sex chromosomes among two sexes (Westergaard 1958; Charlesworth 2016).

### Evolution of Sex Chromosomes: Homogamety and Heterogamety

Since, homogamety or heterogamety of an organism is dependent upon the presence or absence of distinct sex chromosomes, the evolution of sex chromosomes is very important to understand these two phenomena. Sex chromosomes evolved independently from the autosomes under certain

evolutionary forces which ceased the recombination and eventually led to the formation of discrete chromosome types. The evolution of two distinct sex chromosomes such as “X” and “Y” chromosomes leads to heterogamety. Further, partial or complete inhibition of recombination or genetic exchange between sex chromosomes is associated with the lack of genetic homology between the relevant regions of “X” and “Y” chromosomes which eventually help to retain the heteromorphic nature of sex chromosomes (Charlesworth 1991; Ellegren 2011).

Evolution of sex chromosomes in plant has evolved recently and independently in different taxonomical groups. Some plants may be in the early stage of evolving separate sexes, and therefore these plants lack sex chromosome. Some plants seem to have small nonrecombining regions, i.e., proto-sex chromosomes; however, a few species possess cytologically detectable heteromorphic sex chromosomes with large non-recombining regions (Charlesworth 2016).

## Cross-References

- ▶ [Autosome](#)
- ▶ [Heterogametic](#)

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## Homogamety

- ▶ [Homogametic](#)

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## Homogamy

- ▶ [Assortative Mating](#)

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## Homological

- ▶ [Homology](#)

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## Homologous

- ▶ [Homology](#)

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## Homologous Recombination

- ▶ [Targeted Mutation](#)

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## Homology

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## Synonyms

[Homological](#); [Homologous](#)

## Definition

Homology is the concept of physiological, morphological, or behavioral features in an organism that arise from common evolutionary ancestry.

## Introduction

When organisms diverge from each other in evolution, the resulting specialized traits can appear (and function) vastly different. However, upon closer inspection, evolutionary links often remain in the related species. A well-studied example of this can be observed in Fig. 1. The figure shows the similarities in structure development between a human hand and that of a bat wing. While the general bone positions and number are comparable, their functions are very different. Through time, the originally similar bat and human bones have evolved to serve unique purposes. Although it is probably most well-known for relating the physical characteristics of animals together, homology has been an important concept in exploring fields like genetics, learning, and behavior. By observing traits in different



**Homology, Fig. 1** A comparative image showing the homologous bone structure of two mammals, a bat and human, each serving very different functions

organisms with common ancestors, conclusions can be made about the evolution, function, and interaction of those traits in their homologous counterparts. Homology is not to be confused with the similar term analogy; homologous features are of the same origin and may have modified purposes, while analogous features come from different origins but serve the same purpose.

## Homology in Physical Features

### Homology and Evolution

Natural selection acts on populations over time to optimize physiological function and morphological characteristics necessary for survival and reproduction in their environment. This process can be observed in the physical structure of animal bodies, such as the musculoskeletal system. Because bones can be preserved through time, they can be used to identify the history of evolutionary pathways in an organism. Even with changes to embryonic developmental mechanisms, homologous features in skeletons can still remain (Hirasawa and Kuratani 2015).

### Neurological Homology

Homology is also useful in understanding the structure of an organism's nervous system and can lead to inferences about neural function, sensory systems, learning and memory, and cognitive ability. In mammals, stimulating homologous regions of the brain has been shown to create similar emotional responses across species. More than seven types of homologous expressive reactions have been identified this way (Panksepp 2011).

### Homologous Genes

Advances in genome mapping have now allowed researchers to quantify the genetic makeup of animals and identify homologous genes. This ability is useful in modeling common genetic ancestry across multiple species, such as fruit flies (*Drosophila melanogaster*). Different behaviors or symptoms due to genetic expression of homologs in *Drosophila* can be compared directly to genetic expressions in humans, but with

much faster time scales and controlled settings (Chakraborty et al. 2011).

## Homology in Cognition/Learning and Behavior

### Human-Animal Behavioral Homology

Aspects of homology can also be found in learning and behavioral characteristics. Because animals can have homologous nervous systems, the behavioral responses and learning abilities of those systems can also be homologous. In humans, these cognitive similarities are present during the start of development (Platt and Spelke 2009). The similarities in biological evolution allow for research into human cognitive disorders by observing animal models with homologous conditions (Geyer and Markou 2000). Dogs, in particular, have been presented as effective models for assessing psychiatric conditions in people. If the disorders found in canines have a homologous counterpart in humans, research concerning treatment for one species can further that of the other (Overall 2000).

### Uniform Homologous Behavior

All mammals have identifiable behavioral homologies that represent uniform cognitive traits which aid in survival and fitness (Kiley-Worthington 2017). The presence of social learning (learning influenced by other individuals) has been found in a wide range of animals, including insects (e.g., *Drosophila*) and is argued to stem from homology and homologous characters. The evolutionary value of such similar behavior systems should not be overlooked (Collet 2012).

## Conclusion

When employed properly, studying homology gives valuable insight to many aspects of animal biology and behavior. By studying the evolutionary history of these shared characteristics, researchers are coming to new and exciting

conclusions about connections that might have been impossible to discover previously. Between the similarities in body design to the corresponding cognitive and behavioral traits, homology is a vital part of understanding animal biology and behavior.

## Cross-References

- [Animal Models](#)
- [Common Ancestor](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Divergent Evolution](#)
- [Last Common Ancestor](#)

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## Homology Directed Repair

### ► Targeted Mutation

## Homoplasy

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### Definition

Homoplasy can be defined as the similarity between taxa which is due to independent evolutionary change. In simple terms, similarity in sequence or structure that cannot be derived from common descent.

### Homoplasy

Homoplasy is an interesting and infrequent incidence of evolution. This term was given by Lankester in 1870. Homoplasy and homology are very confusing terms and a thin line difference lies between these terminologies. Homology is the similarity of a trait due to shared ancestry and offers valid phylogenetic signal (Hall 2007). However, homoplasy is the similarity of a trait that can be due to evolutionary convergence, parallelism, or character-state reversals and adds an evolutionary noise. If not properly accommodated, it jeopardizes the phylogenetic tree (Wake et al. 2011; Robinson et al. 2008).

For example, the wings of birds and bats are an example of both homology and homoplasy. The bones within the wings are an example of

homology because internal structure of bones such as breast bone, large upper arm bone, two forearm bones, and hand bone share common ancestry group. However, the wings themselves are an example of homoplasy because bats and birds evolved their wings to fill a niche and survive in their respective environments.

Homoplastic traits are derived from three evolutionary mechanisms (Wake et al. 2011, Wake 2015, Campbell and Hodos 1970):

- (a) **Convergence:** The homoplastic trait is not present in the common ancestor. The structures originated by convergence are called analogy. This kind of homoplastic traits has evolved independently through different development pathways. An example is the wings of insects and birds.
- (b) **Parallelism:** Ancestral condition of a variable trait is present in common ancestor but derived trait has evolved independently through similar development pathways, e.g., development of four chambered heart in birds and mammals (Abouheif 2008).
- (c) **Reversals:** Reversals are instances of homoplasy in which a character appears, subsequently disappears, and later reappears along the descendants in one lineage.

Statistically, amount of homoplastic trait present in a cladistic tree can be measured by three methods:

- (a) **Consistency index:** It is introduced by Kluge and Farris (1969) as a measure of a homoplastic character, which has been widely known. It is calculated as the minimum number of changes in the cladogram divided by the actual number of changes needed for the cladogram. It occupies a range from 0 to 1. A low consistency index (less than 0.5) indicates that much homoplastic trait and high consistency index ( $\geq 1$ ) indicates no homoplastic trait present in the cladogram.
- (b) **Retention index:** It can be measured as the proportion of taxa whose states are not homoplastic (i.e., do not evolve more than once). It also measures synapomorphies character of a clade (Archie 1996; Farris 1989).

- (c) **Homoplasy excess ratio:** It is the best way to measure homoplastic traits and widely utilized. It is calculated as the amount of homoplasy observed on a tree relative to the maximum amount of homoplasy (Archie 1989).

## Cross-References

- [Convergent Evolution](#)
- [Evolution](#)
- [Homology](#)
- [Phylogeny](#)
- [Taxa](#)

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## Homosexual

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## Synonyms

[Homosexual ideology](#); [Homosexuality](#); [Homosexuals](#)

## Definitions

Homosexual *orientation* refers to a set of traits and preferences whereby an organism is exclusively sexually attracted to and interested in same-sex individuals. Homosexual *behaviors* refer to sexual behaviors with same-sex individuals.

## Introduction

Homosexual *behaviors* occur in most sexually reproducing species, whereas homosexual *orientation* (exclusive sexual interest in and preference for same-sex individuals) may be unique to humans (Baker and Bellis 2014/1995; Kirkpatrick 2000). Individuals of many species display homosexual behaviors to gain acceptance, solidify a social bond, or experience pleasure. Males that display homosexual behaviors may participate in anal sex, oral sex, or mutual masturbation with males, and females that display homosexual behaviors may participate in mounting, oral sex, and mutual masturbation with females (Baker and Bellis 2014/1995; Sommer and Vasey 2006; Vasey 2004). In many species, males do not engage in homosexual behaviors after reaching reproductive age. Homosexual behaviors may be displayed by heterosexually, bisexually, and homosexually oriented individuals.

## How Homosexual Orientation Persists in the Population

There is evidence that homosexual orientation is heritable such that homosexual males and females carry genes that contribute to the development of homosexual orientation (Apostolou 2013; Baker and Bellis 2014/1995; Blanchard and Bogaert 1996; Iemmola and Ciani 2009; Kirkpatrick 2000). Bisexual individuals also may carry genes that contribute to the development of homosexual orientation. Thus, individuals that copulate with a homosexual or bisexual individual may transmit genes to offspring that contribute to the development of homosexual orientation.

Birth order accounts for some of the variation in male homosexuality in humans. Men with a greater number of older brothers are more likely to be homosexual (Apostolou 2013; Blanchard and Bogaert 1996; Ellis and Blachard 2001; Iemmola and Ciani 2009; Kirkpatrick 2000). The maternal immune hypothesis suggests that mothers produce higher rates of antibodies to testosterone during each subsequent male pregnancy. Later-born sons are more likely to become homosexual when the mother passes antibodies to testosterone to the fetus during pregnancy, which reduces the hormone's biological activity of the fetus (Ellis and Blachard 2001; Iemmola and Ciani 2009).

## Homosexual Evolved Psychology

Homosexual and heterosexual humans share an evolved psychology for sexual preferences, although they differ in the target of these preferences. Like heterosexual men, homosexual men prefer sexual variety, physical attractiveness, and youth (Ha et al. 2012; Valentova et al. 2017). Male preference for physical attractiveness evolved because attractive females are more likely to produce healthy offspring (Apostolou 2013; Ha et al. 2012). Male preference for youth evolved because younger women have greater reproductive value – they are able to birth more children in their remaining reproductive lifespan (Apostolou 2013; Ha et al. 2012). The preference for sexual variety

motivates heterosexual men to pursue copulation with multiple partners. Although homosexual men do not produce offspring by copulating with other men, homosexual men value traits in the target of their sexual desire that indicate higher reproductive value when displayed in women. Homosexual men likely have similar mate preferences to heterosexual men because they have sex-typical evolved psychology.

Homosexual women also have sex-typical preferences including the desire for higher status, resources, and investment (Ha et al. 2012; Valentova et al. 2017). These preferences evolved because women and their offspring benefit by securing resources and investment from a long-term partner. Higher status is associated with access to resources (Valentova et al. 2017). The similarities between heterosexual and homosexual mate preferences may reflect an evolutionary mismatch – the mate preferences that are advantageous for heterosexuals do not solve the same adaptive problems for homosexuals.

In humans, a long-term partner's real or suspected infidelity is the primary cause of jealousy. Men are more upset by a partner's sexual infidelity because paternity is threatened when his partner copulates with another man. Women are more upset by a partner's emotional infidelity because her partner may invest time, attention, and resources into another woman and her children. Jealousy among homosexual individuals is less clearly sex differentiated (Ha et al. 2012; Valentova et al. 2017).

## Costs and Benefits of Homosexual Behaviors

Homosexual behaviors are not uncommon in many species; they occur with greater prevalence compared to exclusive homosexual orientations and may be associated with social and reproductive benefits. Individuals of many species engage in homosexual behaviors to secure social acceptance and to achieve higher ranking within a group. For instance, female bonobos display mounting, genital licking, and mutual masturbation with higher-status females (Sommer and Vasey 2006; Vasey

2004). Females of several primate species may provide sexual favors to higher-status females as displays of kindness or cooperation and thereby secure social support and acceptance from female troop members.

Some mammals, vertebrates, reptiles, and birds may engage in pre-reproductive homosexual behaviors to gain experience in courtship (Baker and Bellis 2014/1995; Sommer and Vasey 2006; Vasey 2004). Males that engage in anal intercourse with other males may improve their mounting skills and learn how to interact sexually with a partner, including practicing submissive and dominant roles. Such practice may improve a male's mating success with females. Males that are accommodating to the female during copulation are more likely to stimulate female orgasms, which may facilitate sperm retention (Baker and Bellis 2014/1995). Females that engage in pre-reproductive homosexual behaviors benefit by improving their sexual skills, practicing sexual receptivity, and experiencing orgasms. In humans, females may experience orgasms more frequently or more reliably during sex with females than with males. Thus, females may learn to control and achieve orgasm with males as a consequence of practicing sexual acts with females (Baker and Bellis 2014/1995).

Exclusive homosexuality may be associated with benefits to genetically related individuals, in the form of kin care. One theory suggests that homosexual individuals can invest resources in kin members, given that they do not incur the costs of rearing their own children (Apostolou 2013; Kirkpatrick 2000). Investing resources in kin may contribute to inclusive fitness. However, the siblings of last-born homosexual sons may have attained more resources from their parents, thereby increasing their reproductive success without the help from the youngest brother. Also, homosexual individuals may allocate resources to same-sex partners, which decreases the amount of resources distributed to kin.

## Conclusion

Homosexual behaviors are more common than is exclusive homosexual orientation. The persistence

of homosexual orientation in populations is influenced by genes and birth order. Pre-reproductive homosexual interactions may prepare both sexes for copulation with individuals of the opposite sex and may improve mating success. Homosexual humans have sex-typical preferences. In humans and other primates, homosexual behaviors may facilitate social acceptance and bonding with same-sex group members.

## Cross-References

- [Affiliative Bond](#)
- [Bisexual](#)
- [Fraternal Birth Order Effect](#)
- [Overdominance Hypothesis for Male Homosexuality](#)
- [Pair Bond](#)
- [Reproductive Fitness](#)
- [Sex Differences](#)
- [Sexual Identification](#)
- [Sexual Selection](#)
- [Sociosexual Behavior](#)

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## Homosexual Ideology

► [Homosexual](#)

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## Homosexuality

► [Homosexual](#)

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## Homosexuals

► [Homosexual](#)

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## Homozygosity

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## Synonyms

[Autozygosity](#)

## Definition

Homozygosity is the state of having two identical alleles or chromosomal segments of DNA in diploid organisms.

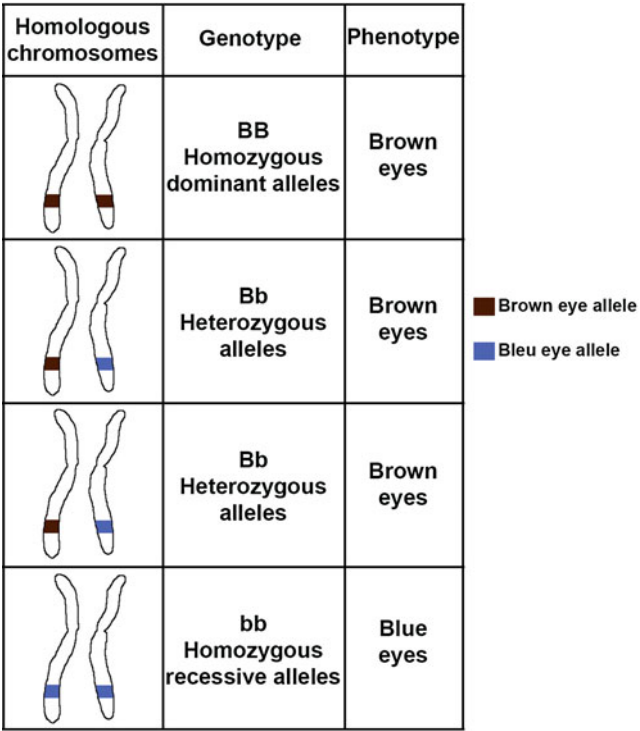
## Introduction

Living organisms use molecules of deoxyribonucleic acid (DNA), organized into colloid structures called chromosomes, to store the genetic material that they inherit from their parents. The way in which genetic traits are passed on between generations was first described by Gregor Mendel (1865), before anyone knew that DNA existed. Organisms that reproduce sexually have a defined number of chromosome pairs, with each pair member received from each parent. Throughout the length of each chromosome distinct units appear called genes, which carry the genetic instructions to make the main elements of any biological activity: the proteins. The somatic cells of diploid organisms, such as human, have two copies, or alleles, of every gene that are located in the same locus, or position, on homologous chromosomes. Although the locus of an individual gene on homologous chromosomes is the same and may code for a specific physical trait, or phenotype, that gene can exist in different forms, or alleles. When both parents deliver the same allele of a defined gene, the offspring is called homozygous for that gene. Gene alleles produce phenotypes that are either dominant or recessive. When an organism carries one dominant and one recessive allele for a given gene, the dominant allele expresses itself at the expense of the recessive allele, which is only expressed in homozygous background. The genetic governing the expression of most traits is very complex, because one trait might utilize more than one gene to make a defined character. For example, eye color is influenced by more than one gene, but it is well known that the alleles that give rise to blue (b) eye color are recessives, while the alleles for brown (B) eye color are dominants (Sturm and Frudakis 2004) (Fig. 1).



**Homozygosity,**

**Fig. 1** *Brown versus blue* eye color determination. Allele for *blue* eyes (b) is recessive. Allele for *brown* eyes (B) is dominant. An individual with *brown* eye color will have one of the following genotypes, BB or Bb. An individual with *blue* eye color will be homozygous for the *blue* allele (bb)

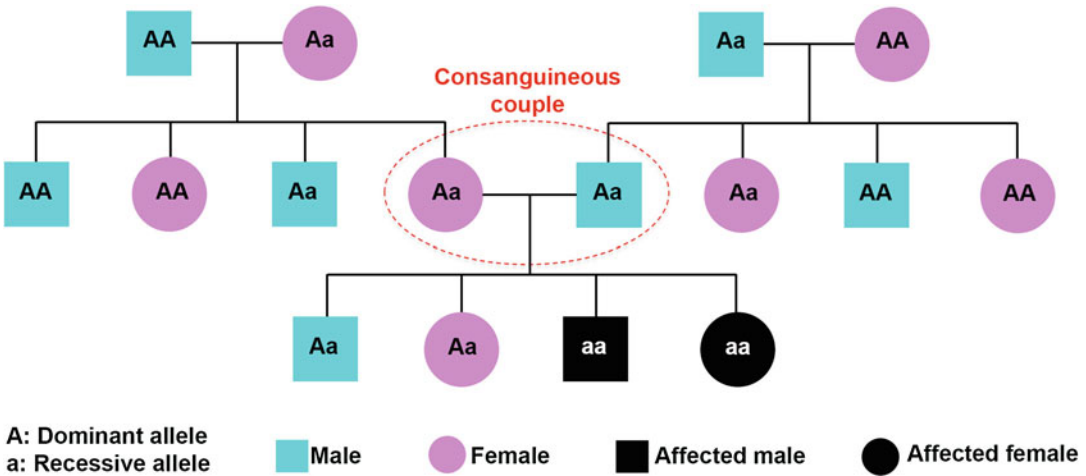


**Definition of Homozygosity**

Homozygosity is used to describe a state of holding identical alleles at one or more gene loci on homologous chromosomes segments. When these alleles are different, we talk about heterozygosity (Fig. 1). One of the major mechanisms that are linked to homozygosity is inbreeding, or mating between relatives, a phenomenon that occurs in many animal and plant species, including human. As a result, inbred individuals inherit the same chromosomal segments from both parents, who inherited them from a common ancestor, recently in the case of a cousin marriage. By this mechanism, the quantity of homozygosity increases, while the amount of heterozygosity decreases. Therefore, the recessive alleles that are hidden by the dominant alleles will be expressed by inbreeding (Alvarez et al. 2011) (Fig. 2). The excess of homozygosity is distinguished by calling it autozygosity to reflect the recent common origin of the alleles.

The identical genomic segments that are present in the human genome because of identical

alleles that are transmitted from parents to their offspring are called “run of homozygosity” (ROH) (Purfield et al. 2012). ROH might also concern multiple adjacent single nucleotide polymorphisms (SNPs) in the genome (Nothnagel et al. 2010). An abundance of ROHs was first demonstrated in European populations using short tandem repeat (DNA regions with short repeat units) markers (Broman and Weber 1999). With the increasing availability of high-density genome scan data, attention has intensified to discover whether a more reliable and accurate estimate of homozygosity might be derived on the basis of genomic marker data. Currently, ROH might be statistically measured up to 1.5 Mega-base or more (McQuillan et al. 2008). The identification and characterization of ROH is important to ascertain inbreeding levels and the genetic relationship between individuals and populations (Ferencakovic et al. 2013). It is also critical to understand the occurrence of recessive disorders, mainly in human (Lencz et al. 2007) (See also the next paragraph).



**Homozygosity, Fig. 2** Typical pedigree of an autosomal-recessive disorder

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## Consequences of Homozygosity

The genetic material of an individual is the target of many alterations, including SNPs, and deletions, insertions, or translocations of genomic material. The majority of genetic disorders are harmful if the two copies of a gene are affected, meaning that both gene alleles produce defective proteins that fail to operate correctly. In heterozygous genotypes, one copy of the gene is not affected and generates a functional protein; thus, these individuals are not affected and are considered just carriers, or might suffer from a milder form of the disease (Fig. 2). Because the genetic material is passed from parents to offspring, the consequence of genetic alterations in inbred individuals is an increase in the levels of homozygosity for deleterious recessive alleles, leading to a reduction in individual health. Charles Darwin was the first to report that inbreeding could lead to reduced fitness in plants (Darwin 1876). In human, the majority of cases of the rarest recessive genetic diseases occur as a result of consanguineous marriages due to homozygous expression of recessive genes inherited from their common ancestors. Recessive gene variants cause many deleterious genetic diseases such as cystic fibrosis, phenylketonuria, and Tay-Sachs disease.

A continuing goal of the human genome project is to determine the function of all human genes. Of particular interest is the identification of human phenotypes associated with the mutation of each gene. Although considerable progress has been made, the majority of genes causing complex and Mendelian disorders have yet to be identified.

## Cross-References

- Alleles
- Heredity
- Hybrid Vigor
- Mendel's Laws

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## Homunculus

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## Synonyms

Cortex man; Cortical somatotopic map

## Definition

The primary sensory and motor cortical map representing the human body according to the area it covers for each body part.

## Introduction

In Latin, “homunculus” means the “little man” (Bear et al. 2007; Purves et al. 2014). It is the disfigured neural representation of the body in the primary somatosensory (post-central gyrus) and primary motor cerebral cortex (pre-central gyrus) (Barker et al. 2017; Snell 2010). It is a result of numerous trials and efforts made to localize the brain functions by mapping it, with the help of various electrical stimulation studies and neuroimaging techniques (Penfield and Boldrey 1937; Purves et al. 2014).

In the 1930s, Marshall observed that touching a specific part of an animal’s body results in an evoked potential in the contralateral cortex (Hudspeth et al. 2013). Evoked potentials are electric signals recorded from cells which represent their summed activity. This method was later used by others to map the brain (Hudspeth et al. 2013). In 1937, the mapping work of Wilder Penfield, Edwin Boldrey, and Theodore Rasmussen figured out two separate sensory and motor homunculi (Penfield and Boldrey 1937; Penfield and Rasmussen 1950).

In the late 1940s, Penfield stimulated the somatosensory cortex of patients and found that it produced sensations of touch in the contralateral hand or leg (Hudspeth et al. 2013; Nicholls et al. 2001). Thus, he concluded that sensation from the lower limbs is mediated by neurons located near the midline, whereas sensations from the upper body, hands and fingers, the face, and lips are mediated by neurons located laterally, on the post-central gyri (Barrett et al. 2009; Hudspeth et al. 2013; Snell 2010). This organization helps differentiate the types of epilepsy based on origin. Seizures originating in the primary motor cortex manifest in the form of the Jacksonian march, whereas those originating in the supplementary motor area (SMA) manifest as repetitive and complex movements (Barker et al. 2017). In 1950, Penfield and Rasmussen contrived a sensory and a motor homunculus, which differed in very few aspects (Penfield and Rasmussen 1950).

## Evidence

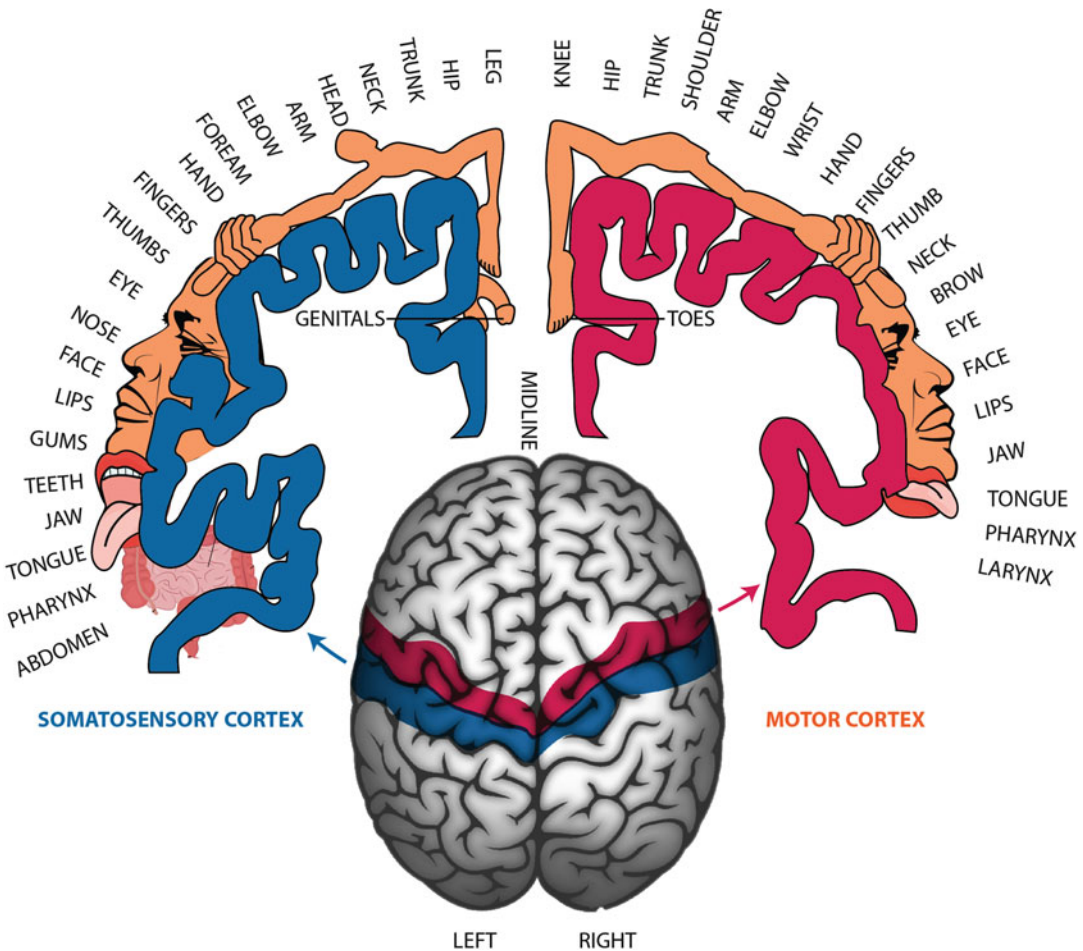
The sensory and motor pathways are topographically arranged in the cortex (Hudspeth et al. 2013;

Nicholls et al. 2001; Purves et al. 2014). Even though all parts of the body are represented somatotopically (Fig. 1), the area of cortex dedicated to a body part is not proportional to its mass. Rather, it correlates to the fineness of sensory discrimination (which consequently corresponds to a higher density of sensory receptors) and degree of motor control (Bear et al. 2007; Hudspeth et al. 2013). In other words, usage of the body part determines the size of cortical area devoted to it (Barrett et al. 2009). Therefore, homunculus is considered as an altered representation of the body (Fig. 1), having size of its body parts proportional to its concerned cortical area (Snell 2010). Therefore, the human homunculus

has an excessively enlarged face, tongue, hands, and fingers. In contrast, the trunk, proximal arms, and legs are shrunk (Purves et al. 2014).

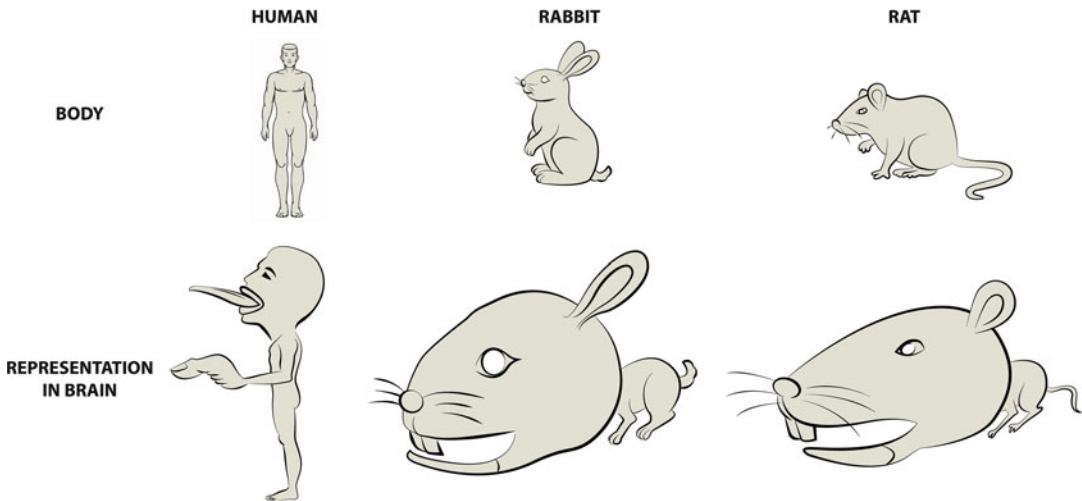
In the somatosensory cortex, large areas are concerned with hands, lips, and tongue, as opposed to the elbow, upper legs, arms, and torso (Hudspeth et al. 2013; Purves et al. 2014). The output from the motor cortex is also arranged similarly with much more area devoted to muscles of fingers and those pertaining to speech (Hudspeth et al. 2013). These aspects translate into anomalies observed in the homunculi. This demonstrates that speaking, dexterity, and facial expression are critical and therefore require central circuitry to govern them (Purves et al. 2014).

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**Homunculus, Fig. 1** The human homunculus is a distorted, neural, cortical representation of the body. All parts of the body are topographically arranged. Area of

cortex concerned with a particular body part is correlated with fineness of sensory input or control of motor output



**Homunculus, Fig. 2** Comparative cortical representation of the body in human, rabbit, and rat. The cortical representations of different parts of the body with respect to its actual physical size complement its importance to the species

The arrangement of components in the primary somatosensory and primary motor cortex follows a general rule of representation (Fig. 1), with few modifications. The sensation of eye movement is solely represented in the pre-central gyrus. Conjugate eye movements are represented further in front. Salivation is often a somatosensory response rather than a motor one (Penfield and Rasmussen 1950).

Functionally, the cerebral cortex is organized into cellular columns spanning the white and gray matter. The cells in each column comprise a computational module which has a specific function. The number of these computational columns is proportional to the area of cortex devoted to a body part (Barker et al. 2017; Hudspeth et al. 2013). Similarly, distorted depictions can be observed in other species (Fig. 2). In rats, whiskers are represented as disproportionately big because of its paramount role in sensing the environment (Bear et al. 2007). Raccoons have exaggerated paws, and the platypus overrepresents its bill (Purves et al. 2014). In rabbits, the face and snout have the largest representations because they are crucial in sensing the environment. Cortical representations of the parts of the body (Fig. 2) complement its importance to the species (Hudspeth et al. 2013; Purves et al. 2014).

## Conclusion

The sensorimotor homunculi represent functionality of different body parts on the contralateral side. A salient feature of the homunculi is its weird body proportions (Purves et al. 2014). The hands, fingers, mouth, and lips are disproportionately large when compared to the torso, arms, and legs. This indicates that a larger area of the cortex is dedicated to sensory input or motor output of organs which are exaggerated. Similar representations are seen in other species.

The “little man” has gained popularity since its inception because it is easy to assimilate in memory. It is a powerful tool that portrays the neural maps of the cortex at first glance. The homunculus, however, is an oversimplification (Nicholls et al. 2001). Many nuances of the neural maps, the intricate neural networks, and their projections are not described. How these projections process sensory information or conduct motor activity aren’t depicted in the homunculi (Nicholls et al. 2001).

## Cross-References

- [Embryo](#)
- [Evolution](#)



- [Neural Control of Behavior](#)
- [Neural Network](#)
- [Sensory Receptors](#)

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## Honest Mimetic Signal

- [Müllerian Mimicry](#)

## Honest Signaling

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### Definition

Honest signaling conveys information that is a true indicator of the underlying quality of the sender and it is useful to the receiver.

## Introduction

In animal communication, information is transmitted from a sender (signaler) to a receiver, and the receiver acts upon the signal (McFarland 2006). Signals can be “honest” when giving reliable information or “dishonest” when the sender is sending out false information to a receiver (Laidre and Johnstone 2013).

## Evolution of Honest Signaling

According to signaling theory for a signal to be preserved in the population, the interaction should be beneficial for the sender and receiver. Furthermore, the honest signal should convey information that the receiver cannot obtain in another way. Honest signaling does not need to be perfectly informative, but it needs to be useful, so that certain behavioral responses to the signal are advantageous, in comparison with the behavior that would occur in absence of the signal. Therefore, honest signals in communication are given when both the sender and receiver benefit from the result (Laidre and Johnstone 2013).

Dishonest signaling doesn't have to suggest conscious deception, rather it has functional meanings in animal communication (Shettleworth 2010). Deceit takes place when the signaler can exploit the receiver in order to improve its fitness, and it is common in communication between species. Similarly, manipulation is when the receiver acquires information from the signaler contrary to his interests (McFarland 2006), and this may arise when sender and receiver have opposite interests (Laidre and Johnstone 2013). In evolutionary terms, dishonest signaling may persist if it doesn't harm recipient fitness or when it has a low frequency of occurrence (Laidre and Johnstone 2013).

Although animal communication is open to cheating, the receiver can choose whether or not to respond to a signal and therefore can impose honesty. Signals must be truthful indicators of underlying quality because the value of the signaled information rests on the degree to which it

enables the receiver to increase its fitness. If signals become unreliable, then the recipient will no longer respond to them (Laidre and Johnstone 2013).

Signals favored by natural selection are those that enhance an animal's probability of reproduction. Therefore, the honesty of a signaler's messages is guaranteed by their cost and that makes them evolutionarily stable. According to the Zahavi (1975) in mate choice and parental care, honest signaling develops because some signals are too costly for signalers to cheat, and that is termed "the handicap principle" (Laidre and Johnstone 2013) or "costly signaling" (Higham 2014). An individual without handicapping marker does not advertise its quality, so a potential mate cannot perceive it. That is to say, when the receiver answers only to costly signals, the sender's ability to pay the cost to define the evolution of communicative signals. Zahavi (1975) considered that signals such as loud calls or rich displays that require a lot of energy are reducing the fitness of the sender and so it can show its quality by its capability to survive in spite of the costs, i.e., handicap caused by signaling.

The handicap principle is generally acknowledged (Shettleworth 2010), but is still discussed (Higham 2014). However, the handicap principle is only one of several mechanisms that give possible explanations for the honesty in animal signaling, and honesty is possible without significant costs. For example, if signalers and recipients are related to each other or when they have negligible conflicting interest, then signals may be free of charge. Moreover, even when signalers and recipients have strong conflicts of interest, honesty is guaranteed if it requires lower cost than lying (Higham 2014; Laidre and Johnstone 2013).

In conclusion, signaling strategies may vary from cost-free cues to costly handicapping signals. Where any benefit for evolutionary fitness occurs, a cue may progress into to signal with a certain amount of exaggeration. Signals become exaggerated only when they start as weak cues of individual quality, but not when

they start as strong cues of quality (Biernaskie et al. 2018).

## Examples

The classic example of a costly honest signal that can't be explained by natural selection is the peacock feather tail. The tail has large feathers that require a lot of energy to grow, it is heavy, and it makes hard for peacocks to move around and to hide from predators. This signal is so costly that the signaler can hardly lie about its quality. However, this investment is effective because it improves the ability of females to choose mates of good quality (Shettleworth 2010; Zahavi 1975).

It is believed that Thompson's gazelles "stot" is an honest signal because it demonstrates gazelle's good body condition, stamina, and strength. Indeed, higher rate stotters appear to be better at running and escaping. This discourages the predators from attacking, and therefore the signal provides an advantage to both parties. The gazelle is less likely to be attacked, and the predator avoids a long, unproductive pursuit (Krebs and Davies 2006; Dawkins 2007).

Leal (1999) studied push-up display in lizard *Anolis cristatellus*, which is common in anoline social interactions. In the research, lizards were faced with a model of a natural predator, snake *Alsophis portoricensis*. The research confirmed that the number of push-ups that lizard performed toward the predator was positively correlated with lizard's endurance capacity, i.e., by push-ups the lizard was communicating to the snake its alertness and that is able to escape an attack. However, endurance was not correlated with lizard's body size, so the snake was not able to evaluate the ability of the lizard to escape based on its visual bodily qualities. Therefore, the author concluded that: "predation pressure and sexual selection may simultaneously favor the evolution of honest communication to allow both the predator and the potential mate or male rival to assess individual quality using the same signal" (Leal 1999).

Animals with conspicuous colors and specific body structures, such as some amphibians and insects, are honestly signaling that they are unpalatable. Their appearance is selected by evolution because predators learn to avoid animals with such prominent warning signals (Shettleworth 2010).

## Conclusion

In the animal kingdom, honest signaling is shaped by evolution but is liable to change by environmental conditions. Finally, plants may also use signals that can be honest or dishonest, when communicating with animals.

## Cross-References

- [Communication](#)
- [Handicap Hypothesis](#)
- [Signal](#)
- [Signaling](#)

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## Hood's Gravity Rules

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## Synonyms

[Gravity bias](#); [Gravity error](#); [Naïve physics](#); [Tubes task](#)

## Definition

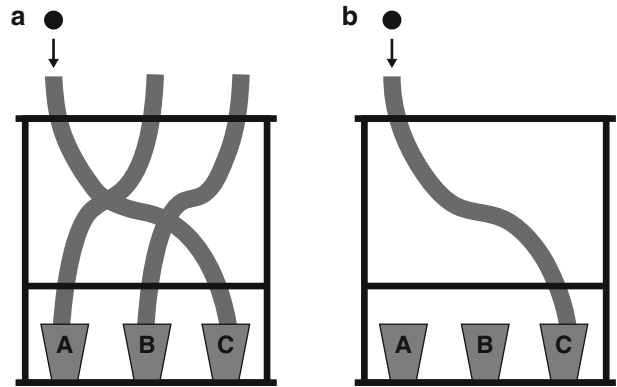
The gravity bias or gravity error is the naïve expectation that an unsupported object will fall straight down, regardless of any obstacles that impede, constrain, or divert its trajectory. This bias is typically revealed by participants making “straight down” search errors in action-based tasks, most strikingly in the tubes task (Hood 1995). Specifically, when an object is dropped down an opaque diagonal tube, an individual exhibiting a gravity bias makes a predictable error: they search the location directly beneath the top of the tube that the object is dropped into (“A” in Fig. 1a, b), rather than searching the correct location that is connected to the bottom of the tube (“C” in Fig. 1a, b). According to Hood’s (1995, 1998) account, an important feature of a naïve gravity bias is that the error is challenging to overcome and persists in spite of counter-evidence. In the tubes task, this is exemplified by repeated searching of the gravity location across trials, despite seeing the actual end location of the object each time.

## Hood's Discovery of the Gravity Bias in Young Children

The gravity bias was first discovered by Bruce Hood (1995), who set out to investigate the development of spatial reasoning abilities in young human children (2- to 4.5-year-olds) using the

**Hood's Gravity Rules,**

**Fig. 1** Versions of the tubes task typically used with (a) human children (three intertwined tubes) and (b) non-human animals (single diagonal tube).  
*A* = gravity location,  
*B* = middle location,  
*C* = correct location



tubes task. In the original version of the task, children were presented with a frame containing between one and three opaque, intertwined tubes, each connected to a cup at the base of the apparatus (Fig. 1). The apparatus was designed so that the top of each tube had a cup directly beneath it (aligned), but the bottom of that tube was always connected to an alternative cup (nonaligned). Children watched an experimenter drop a ball down one of the tubes and were then encouraged to search for the ball. The experimenter then switched the position of the tube(s), dropped the ball down one of them again, and the child searched again (Hood 1995, Exp. 1). This was repeated across multiple trials for one-, two-, and three-tube versions of the task. To an adult, it seems obvious that the ball will end up in the cup connected to the end of the tube that it was dropped down – you simply have to follow the path of that tube from top to bottom. However, while 4-year-olds generally succeeded at all versions of the task regardless of the number of tubes, children up to around 3.5 years of age struggled to locate the ball when multiple tubes were intertwined, and most 2-year-olds could not even pass the simplest one-tube version (Fig. 1b; Hood 1995).

In examining children's search errors, Hood observed something intriguing: when children searched incorrectly, regardless of their age and the number of tubes, their errors were not randomly distributed; rather, they tended to search the cup aligned directly beneath the top of the tube that the ball was dropped into, or the "gravity location" ("A" in Fig. 1a, b). We will refer to searching the gravity location as the "gravity

error." Furthermore, even though children were allowed to continue searching until they found the ball on each trial, which meant they received visual feedback regarding the actual end location of the ball, children did not make this mistake only once and then succeed on their next trial; this erroneous searching of the gravity location persisted across multiple presentations of the task.

To see whether it might be the case that switching the configuration of the tube(s) between trials was confusing for the youngest children, causing them to default to searching the gravity location, Hood presented ten 2-year-olds with a simplified version that we will call the "diagonal tube task" (Hood 1995, Exp. 4; Fig. 1b). This version involved a single diagonal opaque tube that was configured top-left to bottom-right of the frame and remained in a fixed position across trials. However, even in this relatively straightforward version of the task, the majority of 2-year-olds persisted in searching the gravity location (bottom left) across trials (trial 1: 9/10, trial 2: 8/10, trial 3: 9/10; overall gravity searches: 62%; Table 1).

This demonstrates that even when the task is visually less confusing and children are given the opportunity to learn where the item ends up (because it ends up in the same place on every trial), 2-year-olds show a persistent gravity bias according to their search behavior (Hood 1995). Nine out of the ten children tested eventually learned to solve this task (based on a criterion of five consecutive correct searches), after which the configuration of the tube was switched so it was positioned top-middle to bottom-left of the frame, and a single trial presented. Five of the nine

**Hood’s Gravity Rules, Table 1** Performance of different species in the diagonal tube task

| Species                                                                                                             | Trial 1 gravity searches | Trial 2 gravity searches | Overall gravity searches <sup>a</sup> (%) | Reference                                          |
|---------------------------------------------------------------------------------------------------------------------|--------------------------|--------------------------|-------------------------------------------|----------------------------------------------------|
| <b>2-year-old children</b> ( <i>Homo sapiens</i> )                                                                  | 9/10                     | 8/10                     | 62                                        | Hood (1995), Exp. 4 pre-test                       |
| <b>Great apes</b> ( <i>Pan troglodytes</i> , <i>Pan paniscus</i> , <i>Gorilla gorilla</i> , <i>Pongo pygmaeus</i> ) | 8/22                     | +                        | ~20                                       | Cacchione and Call (2010), Exp. 2 silent condition |
| <b>Cotton-top tamarins</b> ( <i>Sanguinus oedipus oedipus</i> )                                                     | 7/9                      | 2/9                      | 39                                        | Hood et al. (1999)                                 |
| <b>Common marmoset</b> ( <i>Callithrix jacchus</i> )                                                                | 4/7                      | +                        | ~30                                       | Cacchione and Burkart (2012)                       |
| <b>Domestic dog</b> ( <i>Canis familiaris</i> )                                                                     | 8/16                     | 6/16                     | 19                                        | Osthaus et al. (2003), Exp. 1 diagonal condition   |
| <b>Domestic dog</b> ( <i>Canis familiaris</i> )                                                                     | 5/16                     | 3/16                     | 16                                        | Tecwyn and Buchsbaum (accepted), Exp. 1a           |

<sup>a</sup>For studies involving multiple test sessions, performance in session 1 is reported  
+ indicates data unavailable

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children reverted to a gravity bias and searched the new gravity location (the bottom middle location), suggesting that they had previously learned to succeed based on reinforcement (i.e., learning the correct location to search across trials), rather than coming to understand the tube’s physical-causal mechanism. The gravity bias is described as “theory-like” on the basis that, like formal theories, it produces behavior that is initially challenging to overcome (Hood et al. 2006), even in the face of contradictory evidence, as exemplified by perseverative search of the gravity location despite receiving visual feedback regarding the correct end location of the ball.

Subsequent Developmental Studies

Since Hood’s (1995) seminal study, the gravity bias seen in young children has been shown to be a robust effect that has been replicated across several different studies and research groups (e.g., Bascandziev and Harris 2010; Baker et al. 2011; Freeman et al. 2004; Hood et al. 2006; Jaswal 2010; Joh and Spivey 2012). In the following section, we discuss studies that have attempted to uncover the mechanisms underpinning young children’s gravity bias, as well as how children are ultimately able to overcome

searching on the basis of this bias. These studies suggest that (1) understanding the causal mechanism of the tube and (2) inhibitory control both have a role to play.

Understanding the Causal Mechanism of the Tube

Although at first glance solving the tubes task appears fairly simple, knowing how the hollow tube affects where the dropped object will end up requires several pieces of knowledge about the physical world. Necessary prerequisites for searching correctly in the tubes task include knowledge of object permanence, invisible displacement, object solidity, containment, gravity, and how these factors interact to constrain the path of the object through the tube. It is therefore possible that young children fail to locate the reward because they do not understand the tube’s causal mechanism; i.e., that it is hollow and constrains the reward’s path as it travels through it.

Indeed, there is evidence that acquiring knowledge about the physical-causal mechanism of the tube is important for success in the tubes task and results from other tasks suggest that physical reasoning skills do improve between 2- and 3.5-years (Seed and Call 2014). Several studies have shown that manipulations to the tubes task that highlight



the causal role of the tube in some way can improve performance and reduce searching of the gravity location. Modifications that have enabled children to perform better include: making the openings at the top of the tubes more visible (Bascandziev and Harris 2011); verbal testimony about the causal role of the tube in constraining the object's movement (Bascandziev and Harris 2010); instructing children to imagine the ball rolling down the tube (Joh et al. 2011; Palmquist et al. 2018); and making the tubes different colors to accentuate their separate trajectories (Joh and Spivey 2012). Thus, better understanding of the tube's causal mechanism likely contributes to children's ability to overcome their gravity bias by around 4 years of age. However, as another series of studies suggests, poor understanding of the tubes' causal mechanism does not fully explain younger children's gravity-biased search.

### Gravity-Specific Bias

If a general inability to understand the causal mechanism of the tube was the sole factor leading children to make a gravity error, then they would be expected to make a comparable error in other tasks involving the invisible displacement of objects through tubes. For instance, it is possible that searching the "gravity location" could reflect a more general incorrect causal belief that moving objects travel in a straight line, or a default strategy of searching the location closest to where the object was dropped from.

However, this does not appear to be the case. In one study, when children were shown video footage of the tubes task that involved upwards motion (where the ball was "sucked up" a tube), they were more likely to correctly identify the end location of the ball compared with when the task involved downwards (i.e., gravity-based) motion (Hood 1998). A horizontal version of the tubes task revealed a similar pattern of results (Hood et al. 2000) – 2-year-olds who were presented with both vertical and horizontal trials with the tubes apparatus were more successful at locating a ball when it moved horizontally through a tube compared with when it fell vertically. Children's better performance in versions of the task involving upward and horizontal motion demonstrates

that children who exhibit a gravity error in the original version of the tubes task are better able to understand the tube's physical mechanism under other conditions. These findings provide evidence that the nature of young children's search error in the tubes task is specific to falling/gravity-based displacement events, as opposed to being explained by a more general straight-trajectory bias or a proximity bias.

Taken together, these studies suggest that the gravity error in children reflects a naïve theory that all dropped objects fall straight down, even if their path is constrained or redirected. Why might a gravity specific bias exist? It seems likely that the gravity error is based on experience of the ubiquitous influence of gravity on objects in the world, specifically, experience of observing falling objects and seeing where they land (Hood et al. 1999, 2000). Indeed, in most cases objects *do* in fact land straight below the location they fell from, so this is usually a sensible heuristic to follow. Data from humans infants seem to support this idea: 4-month-old humans are not sensitive to the influence of gravity on falling objects according to a looking-time measure (Spelke et al. 1992), and even at 10-months infants do not seem to expect an object travelling in a straight line to continue to do so (Spelke et al. 1994). However, with the development of motor skills, experience of dropping objects increases in frequency which could lead to the development of a gravity bias.

### Inhibitory Control

Inhibitory control – specifically, the ability to inhibit responding on the basis of a naïve theory of gravity – is also thought to play a central role in the ability to correctly search for the object in the tubes task. Children's performance in the horizontal and upwards tubes tasks suggests that their naïve gravity bias may be competing with their emerging understanding of the tubes' causal mechanism, leading to poorer performance when the two are in conflict, and the gravity bias must be inhibited. Evidence for the role of inhibitory control in successful performance in the tubes task comes from a study showing that 4-year-old children who pass the standard 3-tube version of the

task revert to searching the gravity location if two balls are dropped simultaneously, thus increasing the task's attentional demands and cognitive load (Hood et al. 2006). Additionally, 3-year-olds' ability to search correctly in the standard version of the task was significantly correlated with their performance in an unrelated task where it was necessary to inhibit a prepotent response (Baker et al. 2011), suggesting that an ability to inhibit an underlying gravity bias might be playing a role in their performance.

Thus, it seems that in the case of the original version of the tubes task, children's tendency to search the vertically aligned container is best explained by a bias that is specific to gravity-based invisible displacement. At 2 years of age, children may lack complete understanding of the tube mechanism and also have relatively weak inhibitory control skills, and so are unable to inhibit searching on the basis of their gravity bias. Older children (i.e., 4-year-olds) who have developed sufficient inhibitory skills and an understanding of the tube's causal mechanism typically search correctly, but revert to gravity-based search when their cognitive skills are taxed, thus suggesting that the bias continues to exist, but is usually "dormant."

### Explicit Versus Implicit Measures of the Gravity Bias

All of the tubes task studies discussed so far have used search behavior as a measure of understanding; i.e., they have all used action-based ("explicit") measures. However, in addition to possessing the prerequisite knowledge about the physical world to be able to infer where the object will end up, and being able to inhibit responding on the basis of a gravity bias, asking participants to search for the object also necessitates holding a representation of the object in mind and generating an appropriate search response. It is possible that the additional demands posed by requiring participants to search for the item tax young children's limited cognitive resources and thus contribute to gravity-biased search. To investigate whether this is the case, different measures based

on, e.g., looking-time or gaze direction ("implicit" measures), which eliminate the additional task demands, can be used.

Only one study (Lee and Kuhlmeier 2013) has explored how children perform in the tubes task according to an implicit measure. Two-year-olds were presented with one-tube and two-tube versions of the task. However, rather than allowing participants to search for the ball, Lee and Kuhlmeier (2013) measured their eye gaze patterns (implicit measure) and pointing behavior (explicit measure). In the one-tube version, all children directed their gaze to the correct location, but only some also pointed to this location. In the two-tube version, neither looking nor pointing was directed to the correct location. When children made pointing errors, they tended to be directed at the gravity location, corroborating the findings of previous studies where children had to actively search for the object (Hood 1995). However, some children who incorrectly pointed at the gravity location in the one-tube version directed their gaze to the correct location at the end of the tube (when there were two tubes, which increased the complexity of the task, 2-year-olds both looked and pointed at the gravity location). Thus, according to their spontaneous eye movements, some 2-year-olds were implicitly aware of the end location of the ball in the one-tube version of the task, even though they were not able to elicit a correspondingly correct pointing response. This provides evidence for a potential dissociation between implicit and explicit measures in the diagonal tube task: some children's eye-gaze was directed towards the correct location, whereas their pointing behavior appeared to be guided by a gravity bias (Lee and Kuhlmeier 2013). Based on current evidence, it is not clear what might explain this dissociation between the two behavioral measures; differences in processing load (with pointing demanding more processing resources than spontaneous looking), or the nature of the underlying representation required to support the different behaviors (a stronger representation is required to guide pointing than gaze), are both plausible.

The studies discussed so far provide evidence that 2-year-old children show a clear gravity bias

in the tubes task, especially according to the search-based measure typically used. This bias is resistant to counterevidence – it persists across repeated trials, even if there is only one tube and the apparatus remains configured in the same way – and is evident until a later age if more tubes are intertwined. Eventual success in the task at around 4 years of age seems to depend on (a) being able to understand how the tube constrains a falling object's movement and (b) possessing sufficient inhibitory control skills to suppress inappropriate responding on the basis of a naïve gravity bias.

In the next section, we present comparative work with nonhuman animals that has aimed to investigate whether a gravity bias might be shared across species, or conversely, could be unique to human children. Do other species also exhibit a comparable error when searching for objects invisibly displaced by gravity?

## Nonhuman Animal Studies

Might a naïve theory about the trajectory of falling objects be unique to humans, or do other species also exhibit a gravity error when searching for invisibly displaced dropped objects? The ability to track and locate objects that have moved out of sight is an ecologically relevant problem for many species (Hauser et al. 2001). Terrestrial and arboreal species in particular – especially those that forage for food that falls to the ground – frequently experience the effects of gravity on unsupported objects. It is therefore reasonable to expect that they, like children, might have a naïve gravity bias, and indeed it has been claimed that nonhuman species including monkeys (Hood et al. 1999) and dogs (Osthaus et al. 2003) do have a gravity bias.

The tubes task was designed for use with preverbal children, and its simplicity makes it suitable for conducting comparative studies with diverse nonhuman species. It is possible to implement the task without using verbal instructions, with relatively little pretraining, and the motor demands are minimal. Several studies have adapted the tubes task – mainly using the single

diagonal tube task of Hood's (1995), Exp. 4 (Fig. 1b) – to examine performance in nonhuman animals and how it compares to that of human children. The aim of these studies has been to shed light on the mechanisms underpinning the gravity bias and enhance our knowledge of the nature and origins of theory-like physical reasoning and cognitive mechanisms more generally. We discuss these studies in the following sections.

## Nonhuman Primate Studies

The majority of nonhuman studies using the tubes task have focused on our closest relatives – the nonhuman primates. In the first nonhuman study, nine cotton-top tamarins (*Sanguinus oedipus oedipus*) were presented with the diagonal tube task (Hood et al. 1999). Seven out of nine individuals searched the gravity location in their first trial, providing evidence for an initial gravity bias in this species (Table 1).

However, in their second trial only 2/9 monkeys searched the gravity location, and across all trials only 39% of searches were directed at the gravity location. Therefore, while this study provides the most compelling evidence to date that a nonhuman species' search behavior might initially be guided by gravity, this pattern of dramatically reduced searching of the gravity location in trial 2 does not fit the "challenging to overcome" criterion proposed by Hood (1998) when describing the gravity bias he observed in young children.

Additionally, tamarins that had previously participated in a horizontal version of the diagonal tube task did not exhibit a gravity bias when subsequently presented with the vertical version, even in their first trial (Hauser et al. 2001). This suggests that any gravity bias may not be very robust in this species and can be overcome with experience of food moving through tubes in a nongravity-based context. In contrast, 2-year-old children who participated in a transparent version of the vertical tubes task (and were able to solve it) still exhibited a gravity bias when they were tested with the opaque version immediately afterwards (Hood 1995).

Findings from subsequent studies with monkeys and apes further suggest that the gravity bias might in fact not be a phylogenetically widespread

phenomenon, even within primates. Only 4/7 common marmosets (*Callithrix jacchus*) searched the gravity location in their first trial of the diagonal tube task, and only 39% of all trials in session 1 of the study were directed to the gravity location (Cacchione and Burkart 2012; Table 1). A looking-time version of the task showed that, similarly to young children directing their gaze towards the correct end location (Lee and Kuhlmeier 2013), marmosets looked longer when the object was revealed to have ended up in the impossible gravity location, compared with when it ended up in the correct location (Cacchione and Burkart 2012), demonstrating a lack of a gravity bias according to this implicit measure.

Two studies have used versions of the tubes task to investigate whether nonhuman great apes have a gravity bias. A study by Cacchione and Call (2010) presented all four nonhuman great ape species with the standard diagonal tube task. Apes searched randomly in trial 1, but more individuals searched the correct location than the gravity location, and the overall number of gravity searches in session 1 of the experiment was low at around 20% (Cacchione and Call 2010; Table 1). However, when apes did make an error, they were significantly more likely to search the gravity location than the middle location, suggesting that apes may indeed hold naïve beliefs about gravity, but they are usually able to suppress acting on the basis of this belief when it is inappropriate. On the basis of these results, it has been suggested that great apes might be less susceptible than monkeys and 2-year-old children to making gravity errors because of their superior inhibitory skills – it is not necessarily the case that apes do not have naïve beliefs about the influence of gravity on unsupported objects; it could just be that they are better able to suppress acting on the basis of this bias (Cacchione and Call 2010).

In addition, several of the apes in this study had previously completed an “acoustic” version of the task, in which they were able to hear the reward rolling down the tube, thus providing information regarding the causal mechanism of the tube. Since causal mechanism information improves children's performance, it is difficult to know how this experience might have influenced apes'

subsequent performance in the traditional “silent” version of the diagonal tube task, rendering direct comparisons of the ape data with data from other species problematic.

The findings of an earlier study by Tomonaga et al. (2007) supports the possibility that great apes might have a gravity bias that they are able to inhibit. Tomonaga and colleagues presented immature and adult chimpanzees (*Pan troglodytes*) with a task involving two crossed tubes, but rather than searching for the object after it had been dropped down the tube, chimpanzees had to predict where the object would appear by putting their hand at the bottom of one of the tubes before it was released. The authors reported that chimpanzees in both age groups consistently selected the gravity location directly beneath where the reward was held, providing some evidence that chimpanzees' reasoning about the trajectory of falling objects might be influenced by gravity. Based on the results of these two studies, it is possible that apes are able to solve the single diagonal tube task, but reveal a gravity bias when the task is more complex because more tubes are intertwined, which is known to increase children's preference for the gravity location (Hood 1995; Lee and Kuhlmeier 2013). However, given that there were other differences between tasks in addition to the number of tubes – two versus three search locations; prediction – versus search-based measure – it is difficult to compare these findings directly with the other nonhuman studies discussed in this section.

Overall, there appears to be mixed evidence for gravity biases in nonhuman primates. While there is evidence that the search behavior of all of the species tested to date is influenced by gravity to some extent – tamarins searched the gravity location in trial 1 (Hood et al. 1999), marmosets were more likely to search the gravity than the middle location when they erred (Cacchione and Burkart 2012), as were apes with a single tube (Cacchione and Call 2010), and chimps with two crossed tubes showed the most compelling gravity bias (Tomonaga et al. 2007) – whether the performance of any of these species is indicative of a naïve theory of gravity comparable to young children's is less clear.

### Domestic Dog Studies

To date, the only nonprimate species to have been presented with the diagonal tube task is the domestic dog (*Canis familiaris*; Osthaus et al. 2003; Tecwyn and Buchsbaum [accepted](#)). Osthaus et al. (2003) found that 8/16 dogs searched the gravity location in trial 1 and this proportion decreased steadily across repeated trials (Table 1). Despite this weak evidence for an initial gravity bias in dogs, this paper has often been interpreted in the literature as demonstrating that dogs have a robust gravity bias – at least initially – in the diagonal tube task (e.g., Bascandziev and Harris 2011; Cacchione and Call 2010; Joh et al. 2011; Tomonaga et al. 2007). A recent study that replicated and extended the diagonal tube task with dogs also found no evidence that this species searches on the basis of a naïve gravity bias, either in their very first trial (5/16 gravity searches), or across all trials (16% of searches directed to the gravity location; Tecwyn and Buchsbaum [accepted](#); Table 1). Dogs in this study also did not search correctly immediately, and in some modified versions of the task, they failed to learn to search correctly even across multiple trials, which suggests that they may be particularly poor at understanding the tube's causal mechanism.

### Conclusion

Two-year-old children show a compelling gravity bias in even simple versions of the tubes task, and this bias is also seen in children up to around 3.5 years of age when multiple tubes are intertwined. This finding is robust and has been replicated across multiple studies. The evidence that any nonhuman animals possess a gravity bias – at least to a comparable extent to young children – is less conclusive. Despite being widely described as having a gravity bias across the literature, there is currently little evidence for a gravity bias in dogs. It is possible that the search behavior of some monkey species is initially guided by gravity (e.g., cotton-top tamarins; Hood et al. 1999), but there is little evidence that this gravity-biased search persists across

multiple trials, and thus an important criterion of a naïve gravity bias according to Hood (1995, 1998) – resistance to counterevidence – is not met. The most suggestive evidence of a gravity bias was found in the great apes, who may show a gravity bias when multiple tubes are intertwined, similar to 3-year-old children. At present, whether and to what extent any nonhuman species share young children's persistent gravity bias remains an open question that warrants further investigation.

### Current Limitations and Future Directions

Several factors limit the extent to which it is possible to make valid comparisons between different species. Given that there is evidence that the number of tubes influences children's performance in the task and the extent to which they exhibit a gravity bias (Hood et al. 1995; Lee and Kuhlmeier 2013; Palmquist et al. 2018), this makes meaningful comparisons between existing child and nonhuman animal studies challenging. It is possible that if the apparatus was more complex (i.e., more tubes were intertwined, as in the majority of developmental studies), nonhuman animals would also be more susceptible to a gravity bias – and indeed there is some evidence from chimpanzees to suggest that this is the case (Tomonaga et al. 2007). Several other methodological inconsistencies between studies with children and nonhuman animals (and indeed between different nonhuman animal studies) render valid cross-species comparisons tricky, including: whether the tube configuration is variable or fixed between trials; differences in pretraining procedures; differences in the number of test trials presented; variation with regards to prior experience with related tasks; and a lack of availability of trial-by-trial data.

Future work should address these issues by replicating the existing nonhuman studies with larger samples and also by systematically manipulating the number of tubes in the apparatus to see if/whether this influences the strength of the gravity bias. Extending the paradigm to additional species that are known to differ with respect to their causal reasoning abilities, inhibitory skills, and ecology in terms of the extent to which they



have experience of the effect of gravity on unsupported objects could be particularly valuable for improving our understanding of the mechanisms underpinning gravity-biased versus successful performance in the tubes task. A developmental comparative approach that examines performance in both immature and mature individuals across species would enable us to better understand the evolutionary origins of naïve beliefs about gravity.

## Cross-References

- [Comparative Cognition](#)
- [Folk Physics](#)
- [Invisible Displacement](#)

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## Horizontal Gene Transfer

- [Conjugation](#)

## Hormones and Behavior

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## Introduction

Hormones are secretions from the ductless glands (known as endocrine glands) and specialized cells in the specific animal organs, which circulate through blood to reach target destinations in specific parts of the body (including the brain) for action.

Modern view for the hormones is that a hormone is any substance that acts at the cellular level to initiate, stop, or modulate a cellular process, and they include all chemical messengers synthesized by the body that act by binding with high affinity to target cells within the same individual. Some scientists also consider pheromones as hormones. Pheromones are those molecules which act in a

similar way as hormones – leave the body of one individual to act on another individual. The site of action can be nearby or at a distant target.

Hormones can act via paracrine, autocrine, or intracrine mechanisms. A hormone may act both locally and at distant target sites traveling through the bloodstream. To enter the brain, hormones have to cross the blood-brain barrier (BBB) which has differential regulation for specific hormones and also come in direct contact with the neurons in certain brain regions lacking a natural BBB. Conversely, some hormones which are synthesized inside the brain have to cross the BBB to reach to the target sites present in the periphery. In the brain, hormones alter neural transmission at synapses and induce other neuroplastic changes, which, with their concomitant action on the peripherally present neuromuscular effectors, influence neurophysiological functions pertinent to a behavior.

“Hormone” comes from the Greek word *hormon* which literally meant “to set in motion,” providing a clue for its inductive influence on the behavior. Relation of the hormone with behavior is a complex phenomenon that cannot be explained in the terms of direct causality. Both show a kind of mutual dependence and certain important to note intricacies. A hormone itself doesn’t generate a behavior but creates a homeostatic conditioning conducive for its occurrence, i.e., it increases the chance that the organism will show a particular behavior when physiological and environmental conditions are optimum.

Empirical studies have shown that almost all the aspects of behavior are influenced by hormones – including survival, sovereignty, circadian functions, feeding, reproduction, and proliferation of the organisms. The specific branch of the behavioral science devoted to study hormonal influences on animal behavior is known as “behavioral endocrinology.”

New advances and research updates in the field have given “behavioral endocrinology” an edge in explaining humoral bases of animal behavior. An emerging concept “epigenetics” has revolutionized this field providing the mechanisms for how the hormonal influences on the behavior get tagged to the genetic structure of the organism which not only may persist for the life time but may also presumably pass into the next

generations. This chapter is aimed to provide a summarized account of the basic concepts and mechanisms, applied implications, and research updates in “hormones and behavior.”

## Hormones: Basic Handcuff

(Types and structure, sources, mechanisms of action, physiological effects)

### Types and Structure

The prototype chemical structure of the hormones is that of a protein, but some are also peptides, amines, or steroids. The protein, peptide, or amine hormones are water soluble and hence cannot enter into the cell directly; in contrast, steroid hormones are lipid soluble and hence can enter inside the cell directly. Lipid soluble hormones act slow but their effects last longer than water-soluble hormones.

### Sources

Hormones are synthesized and secreted chiefly by the endocrine organs – which are either components of the brain or situated peripherally in the body – and also by the specific tissue components of the other organs such as the heart and kidney (Table 1).

The endocrine organs and specific hormone-secreting cells (inside the other organs) in response to the neural stimuli (or humoral cues released from specific hypothalamic nuclei) release their secretions in the venous blood draining those organs. In their further course, from the venous tributaries, hormones reach to the central blood channels from where through the arterial branches they get distributed to the target organs (including the brain).

### Local Synthesis by Cortical Neurons

Certain hormones (including sex hormones) are synthesized locally by cortical neurons in specific brain regions (in addition to their prime secretion from endocrine organs) and get delivered through their axons to the targeted brain regions which contain receptors for specific hormones (Table 2). Hippocampus neurons are known to secrete sex hormones and express their receptors (Ish et al. 2007).

### Mechanisms of Action

Biologically effective amounts of hormones are very minute which get usually measured in micrograms ( $\mu\text{g}$ ,  $10^{-6}$  g), nanograms (ng,  $10^{-9}$  g), or picograms (pg,  $10^{-12}$  g).

A hormone other than steroid (except thyroid hormones) attach to the receptors present on the surface of target cells creating the hormone-receptor complex, which in turn engages a G protein-dependent secondary messenger pathway (like cAMP, cGMP, diacylglycerol,  $\text{Ca}^{++}$ , etc.) to induce protein kinases/phosphorylases related to specific biological events. Steroid hormones, being lipid soluble, may additionally enter into the cell to reach nucleus tagged with transporters or binding protein present in the cell cytoplasm, where they set free from the carrier molecule and attach to the nuclear receptors (binding sites) at DNA promoter regions for the genes assigned for forming specific proteins (Fig. 1).

Although thyroid hormones are chemically amine, their three-dimensional structure resemble that of the steroid hormones and hence can enter the cell and reach to the specific nuclear receptors with the help of specific transporters present at the cell membrane (facilitated diffusion) and in the cell cytoplasm.

Hormones coordinate an animal's physiology and behavior by managing its bodily functions. Hormones are functionally similar to the chemical mediators including neurotransmitters and cytokines and also interact with them in influencing a behavior. They often function locally as the neurotransmitters.

Hormones may synergize or antagonize with each other in influencing a behavior. For example, various sex hormones released during ovulation in a female add up their effects inducing a reproductive behavior; in contrast, the estrogen which is followed by the progesterone in the menstrual cycle induces opposite behavioral effects.

### Endocrine System and Physiological Effects of Hormones

Classically, the endocrine system of the body has three main components: a brain part, pituitary (anterior part), and target endocrine organ. Neurosecretory cells in the brain (as in hypothalamus) synthesize releasing/inhibitory neurohormones, which reach to the pituitary gland via

**Hormones and Behavior, Table 1** Salient animal hormones, sources, and major functions

| Glands/hormone                                                   | Cell/tissue source                                                                  | Major functions                                                                                                | Glands/hormone   | Cell/tissue source                                | Major functions                                                                                                                                         |
|------------------------------------------------------------------|-------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------|------------------|---------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Hypothalamus</b>                                              |                                                                                     |                                                                                                                |                  |                                                   |                                                                                                                                                         |
| Corticotropin-releasing hormone (CRH) <sup>a,b,c</sup>           | Paraventricular nuclei (PVN)                                                        | Stimulates release of ACTH and B-endorphin from anterior pituitary                                             | <b>Pituitary</b> | Anterior pituitary                                | Stimulates synthesis and release of glucocorticoids                                                                                                     |
| Gonadotropin-releasing hormone (GNRH) <sup>a,b,c</sup>           | Preoptic area; anterior hypothalamus                                                | Stimulates release of FSH and LH from anterior pituitary                                                       |                  | Posterior pituitary                               | Increases water reabsorption in kidney                                                                                                                  |
| Luteinizing hormone-releasing hormone (LHRH) <sup>a</sup>        | Nuclei; medial basal hypothalamus (rodents and primates); arcuate nuclei (primates) | Stimulates release of LH from anterior pituitary                                                               |                  | Intermediate lobe of pituitary and throughout CNS | Analgesic actions                                                                                                                                       |
| Somatostatin (growth hormone-inhibiting hormone) <sup>a</sup>    | Anterior periventricular nuclei                                                     | Inhibits release of GH and TSH from anterior pituitary; inhibits release of insulin and glucagon from pancreas |                  | Anterior pituitary                                | Stimulates development of ovarian follicles and secretion of estrogens; stimulates spermatogenesis                                                      |
| Melanotropin-release inhibitory factor (Dopamine) <sup>a,c</sup> | Arcuate nuclei                                                                      | Inhibits the release of MSH (no evidence of this peptide in humans)                                            |                  | Anterior pituitary                                | Mediates somatic cell growth                                                                                                                            |
| Neuropeptide Y (NPY) <sup>a,c</sup>                              | Arcuate nuclei                                                                      | Regulation of energy balance                                                                                   |                  | Anterior pituitary                                | Stimulates Leydig cell development and testosterone production in males; stimulates corpora lutea development and production of progesterone in females |
| Neurotensin <sup>a,c</sup>                                       | Arcuate nuclei                                                                      | Regulation of energy balance                                                                                   |                  | Anterior pituitary                                | Affects memory; affects skin color in amphibians                                                                                                        |
| Orexin A and B <sup>a,c</sup>                                    | Lateral hypothalamic area                                                           | Regulation of energy balance/food intake                                                                       |                  | Posterior pituitary                               | Stimulates milk letdown and uterine contractions during birth                                                                                           |
| Thyrotropin-releasing hormone <sup>a,c</sup>                     | Paraventricular nuclei (PVN)                                                        | Stimulates release of TSH and PRL from anterior pituitary                                                      |                  | Anterior pituitary                                | Many actions relating to reproduction, water balance, etc.                                                                                              |
| Histamine <sup>a,c</sup>                                         | Tuberomammillary nucleus (also from mast cells)                                     | Increases wakefulness, prevent sleep                                                                           |                  | Anterior pituitary                                | Stimulates thyroid hormone secretion                                                                                                                    |

| <b>Adrenal gland</b>                                                        |                                                                                               | <b>Thyroid/parathyroid</b>                                                                  |                                       |                                                                                             |
|-----------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------|---------------------------------------|---------------------------------------------------------------------------------------------|
| Mineralocorticoids                                                          |                                                                                               | Calcitonin (CT)                                                                             | C-cells of thyroid                    | Lowers serum Ca2+ levels                                                                    |
| Aldosterone                                                                 | Zona glomerulosa of adrenal cortex                                                            |                                                                                             |                                       |                                                                                             |
| 11-Deoxycorticosterone (DOC)                                                | Zona glomerulosa of adrenal cortex                                                            | Parathyroid hormone (PTH)                                                                   | Parathyroid gland                     | Stimulates bone resorption; increases serum Ca2+ levels                                     |
| Glucocorticoids                                                             |                                                                                               | Thyroxine or tetraiodothyronine (T4) <sup>b,c</sup><br>Triiodothyronine (T3) <sup>b,c</sup> | Follicular cells                      | Regulate oxidation and basic metabolic rates in tissue; learning associated neuroplasticity |
|                                                                             |                                                                                               | <b>Placenta</b>                                                                             |                                       |                                                                                             |
| Cortisol (hydrocortisone) <sup>b,c</sup> /<br>corticosterone <sup>b,c</sup> | Zona fasciculata and z. reticularis of adrenal cortex                                         |                                                                                             |                                       |                                                                                             |
|                                                                             |                                                                                               | Increases carbohydrate metabolism; antistress hormone                                       |                                       |                                                                                             |
|                                                                             |                                                                                               | Increased carbohydrate metabolism; antistress hormone                                       | Placenta                              | LH-like functions; maintains progesterone production during pregnancy                       |
| Dehydroepiandrosterone DHEA                                                 | Zona reticularis of adrenal cortex                                                            | Chorionic gonadotropin (CG)                                                                 |                                       | Acts like PRL and GH                                                                        |
|                                                                             |                                                                                               | Weak androgen; primary secretory product of fetal adrenal cortex                            | Placenta                              |                                                                                             |
|                                                                             |                                                                                               | Chorionic somatomammotropin or placental lactogen (CS)                                      |                                       |                                                                                             |
| Epinephrine or adrenaline (EP) <sup>b</sup>                                 | Adrenal medulla                                                                               | <b>Pancreas</b>                                                                             |                                       |                                                                                             |
| Norepinephrine or noradrenaline (NE) <sup>b</sup>                           | Adrenal medulla                                                                               | Glucagon <sup>b,c</sup>                                                                     | a-cells                               | Glycogenolysis in liver                                                                     |
| <b>Ovary</b>                                                                |                                                                                               | Insulin <sup>b,c</sup>                                                                      | b-cells                               | Glucose uptake from blood; glycogen storage in liver                                        |
|                                                                             |                                                                                               | Increases blood pressure                                                                    | d-cells                               | Inhibits insulin and glucagon secretion                                                     |
| Estrogen <sup>c</sup>                                                       | Follicles (also in brain regions like hippocampus, hypothalamus, prefrontal cortex, amygdala) | Somatostatin                                                                                |                                       | Effects on gut in pharmacological doses                                                     |
|                                                                             |                                                                                               | Pancreatic polypeptide (PP)                                                                 | Peripheral cells of pancreatic islets |                                                                                             |
|                                                                             |                                                                                               | <b>Gut</b>                                                                                  |                                       |                                                                                             |
| Progesterone <sup>c</sup>                                                   | Corpora lutea, placenta                                                                       | Bombesin <sup>a</sup>                                                                       | Neurons and endocrine cells of gut    | Hypothermic hormone; increases gastrin secretion                                            |

(continued)



**Hormones and Behavior, Table 1** (continued)

| Glands/hormone                                               |  | Cell/tissue source                   | Major functions                                             | Glands/hormone                                        | Cell/tissue source                                                                | Major functions                                                                                                                            |
|--------------------------------------------------------------|--|--------------------------------------|-------------------------------------------------------------|-------------------------------------------------------|-----------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Testes</b>                                                |  |                                      |                                                             |                                                       |                                                                                   |                                                                                                                                            |
| Androstenedione <sup>c</sup>                                 |  | Leydig cells                         | Male sex characters                                         | Gastric inhibitory polypeptide (GIP)<br>Gastrin       | Duodenum<br>G-cells of midpyloric glands in stomach antrum                        | Inhibits gastric acid secretion<br>Increases secretion of gastric acid and pepsin                                                          |
| Dihydrotestosterone (DHT) <sup>c</sup>                       |  | Seminiferous tubules and prostate    | Male secondary sex characters                               | Gastrin-releasing peptide (GRP)                       | GI tract                                                                          | Stimulates gastrin secretion                                                                                                               |
| Testosterone <sup>c</sup>                                    |  | Leydig cells                         | Spermatogenesis; male secondary sex characters              | Vasoactive intestinal peptide (VIP) <sup>a,c</sup>    | Small intestine (also in central and enteric nervous system, and nerve terminals) | Inhibits gastric acid secretion and increases intestinal secretion of water and electrolytes; a neurotransmitter/neuromodulator in CNS/ENS |
|                                                              |  |                                      |                                                             | Serotonin <sup>a,c</sup>                              | GI tract and blood platelets (also a neurotransmitter in brain)                   | Maintain mood, sleep, appetite, and digestion. Regulate bowel function and movements                                                       |
| <b>CNS</b>                                                   |  |                                      |                                                             |                                                       |                                                                                   |                                                                                                                                            |
| Dopamine (DA) <sup>a,c</sup>                                 |  | Arculate nuclei of hypothalamus      | Inhibits prolactin release (and other actions)              | Melatonin <sup>a,c</sup>                              | Pineal gland                                                                      | Affects reproductive and circadian control of bodily functions                                                                             |
| Serotonin (5-HT) <sup>a,c</sup><br>(also a neurotransmitter) |  | Multisites in CNS (including pineal) | Stimulates release of GH, TSH, ACTH; inhibits release of LH | Norepinephrine or noradrenaline (NE) <sup>a,b,c</sup> | Hypothalamus (PVN) (also as a neurotransmitter from locus ceruleus)               | Regulates HPA axis (and other actions)                                                                                                     |

| Miscellaneous                 |                                                                |                                              |                                                                                                     |                                                                                                                        |                                                                                                                                                    |
|-------------------------------|----------------------------------------------------------------|----------------------------------------------|-----------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------|
| Leukotrienes (LT)             | Lung                                                           | Long-acting bronchoconstrictors              | Prostaglandins E1 and E2 PGE1 and PGE2                                                              | Multiple type of cells                                                                                                 | Contraction/relaxation of smooth muscle cells in vessels, aggregation/disaggregation of platelets, sensitization to pain (and other actions)       |
| Atrial naturetic factor (ANF) | Atrial myocytes (heart)                                        | Regulation of urinary sodium excretion       | Klotho <sup>c</sup>                                                                                 | Multiple organs                                                                                                        | Enhances cognition, protects against aging                                                                                                         |
|                               | Arcuate nucleus (hypothalamus)<br>Regulation of energy balance | Regulation of energy balance                 | Acetylcholine (also a neurotransmitter in brain)<br>Insulin-like growth factor (IGF-1) <sup>c</sup> | Bronchial epithelial cells<br>Hepatocytes. Also by neuronal and nonneuronal tissue in brain. Cross blood brain barrier | Regulates bronchoconstriction and mucus secretion<br>Supports cell growth and differentiation, vascular remodeling. Neurotrophic function in brain |
| Thymosin<br>Thymostatin       | Thymocytes (thymus)                                            | Proliferation/differentiation of lymphocytes |                                                                                                     |                                                                                                                        |                                                                                                                                                    |

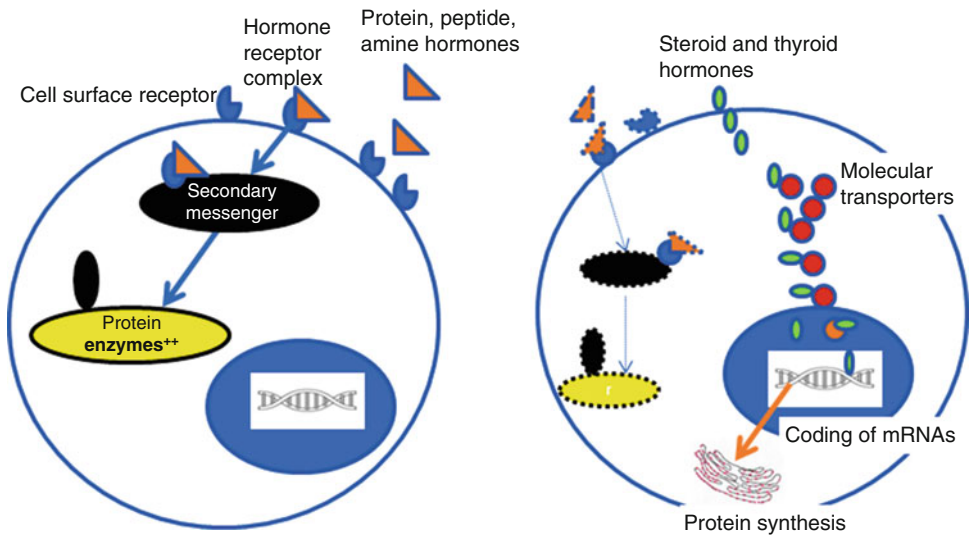
<sup>a</sup>neurohormone

<sup>b</sup>stress hormone

<sup>c</sup>implicated in behavioral functions

**Hormones and Behavior, Table 2** Hormone synthesis by cortical neurons

| Brain region              | Hormone                | Receptor             |
|---------------------------|------------------------|----------------------|
| Hippocampus               | Estrogen progesterone  | Estrogen             |
|                           |                        | Progesterone         |
|                           | Testosterone           | Testosterone         |
|                           |                        | Oxytocin             |
|                           |                        | Vasopressin          |
| Prefrontal cortex         | Estrogen, progesterone | B-endorphin          |
|                           |                        | Estrogen             |
|                           |                        | Progesterone         |
|                           |                        | Testosterone         |
|                           |                        | Oxytocin             |
| Amygdala (quasi-cortex)   | Estrogen               | Vasopressin          |
|                           |                        | B-endorphin          |
|                           |                        | Estrogen,            |
|                           |                        | Progesterone         |
|                           |                        | Testosterone         |
| Anterior cingulate cortex | Estrogen               | Oxytocin             |
|                           |                        | Vasopressin          |
|                           |                        | B-endorphin          |
|                           |                        | Estrogen,            |
|                           |                        | Progesterone         |
|                           |                        | Testosterone         |
|                           |                        | Oxytocin vasopressin |
|                           |                        | B-endorphin          |



**Hormones and Behavior, Fig. 1** Mechanisms of action a. Protein, peptide, and amine hormones b. Steroid and thyroid hormones

hypothalamic-hypophyseal portal system and stimulate the pituitary gland to secrete its products into the general blood supply of the body. Pituitary hormones stimulate target cells in the endocrine organ to secrete specific hormones. In the brain, the output hormone has a negative feedback loop, regulating the brain's secretion of neurohormones. This three-tier system of control operates for all endocrine organs in the body such as the gonads and adrenal and thyroid glands, though all hormones don't follow the three-tier system as those secreted from posterior pituitary (posterior part of the pituitary is considered as extension of the brain and secretes oxytocin and vasopressin which have important physiological and behavioral effects) and from specific cells of the brain (other than the hypothalamus) or other bodily organs (Table 1).

Hormones are involved in the maintenance of physiological functions not only involved in day-to-day activities like sleep, feeding, drinking, etc. but also that with prolonged course of effects like reproduction, growth, aging, immunity, etc. (Table 1). Hormonal regulations of the physiological processes have been co-opted with the behavior linked to these processes in the evolutionary course to ensure better survival of the organism.

## Behavioral Endocrinology As a Discipline

### History

George Montagu in 1802 had noted that songbirds sing more at the times of the year when their testes are larger. The first study of behavioral endocrinology as per records was done by Arnold Adolph Berthold in 1846. Berthold showed that male typical behavior could be restored by reimplanting the testes in the cockerel birds (what they had lost following the castration). He thought it is caused by certain substances – androgens – secreted from the testes (Fusani 2017).

Further founding works in this field were done by Frank et al., using domestic or laboratory animals. In 1960, the advent of radioimmunoassay

(RIA) had allowed to measure hormones in small blood samples. RIA had revolutionized behavior endocrinology research because it made easy to study in living animals and to keep them alive for further observations and follow-ups or involve human subjects (Fusani 2017).

## Commonly Used Investigations and Experimental Methods

The concentration of hormones in the blood or serum in the living animal can be investigated with the immunoassays (radioimmunoassay, enzyme immunoassay, and fluorescence immunoassay) and more recently high-performance liquid chromatography (HPLC) and mass spectrometry combined with gas chromatography (MS-GC). The general investigations used for in vitro determination of hormones or their receptors are immunocytochemistry (ICC), autoradiography, in situ hybridization, and blotting. Brain imaging techniques (like PET scan and f-MRI) which reveal brain activation during certain behaviors, paired with endocrine manipulations or monitoring, can provide important information about hormone-behavior interactions (Fusani 2017).

Standard scientific approaches to experimentally manipulate the hormonal production and observe the resultant change of behavior are mentioned below:

**Ablation:** A hormone-dependent behavior disappears when the source of the hormone is removed or the hormone actions are blocked – it is done by surgery (an endocrine organ is removed), antagonist or blocker (hormone receptor is blocked), or gene knockouts.

**Replacement:** Restoration of the missing hormonal source or its hormone restores the absent behavior – it is done by hormone implants (planted under skin), agonists or mimics (induce signaling cascade acting on the hormone receptor), and natural or engineered gene mutation.

**Hormone-behavior correlation:** Behavior is studied for the covariation with the changing concentrations of the hormone.

## Hormonal Homeostasis and Its Linking to Behavior

Major hormonal centers in the body work in unison in attempt to maintain a state of functional equilibrium with each other and put an accumulative influence on the neurocognitive functions, which is reflected in the behavioral performance of the animal. The hypothalamus in association with the anterior pituitary and adrenal gland constitutes HPA axis – the central axis in the body maintaining neuroendocrine homeostasis. HPA axis is extremely important for the development of adaptive behavior – which is necessary to deal with the stress. A parallel axis connecting the hypothalamus and anterior pituitary to gonads (testis in male and ovary in female) constitutes HPG axis. In HPG axis, release/inhibitory hormones are secreted from specific hypothalamic nuclei which induce synthesis/release of stimulating/luteinizing hormones from anterior pituitary which in turn induce synthesis/release of sex hormones from the gonads (Table 1) which makes basis of sexual and reproductive behavior in both sexes.

Extensive connections of the hypothalamic nuclei to the key brain regions especially that dealing with the emotion, learning, and memory make HPA axis crucial in behavioral endocrinology.

Uniquely, HPA axis components don't connect to each other through neural pathways, but regulatory instructions and feedbacks between the axis components reach through the blood. A venous portal system from the hypothalamus carries corticotrophin-releasing hormone (CRH), released from the paraventricular nuclei (PVN) to the anterior part of the pituitary (adenohypophysis) where they stimulate/inhibit release of adrenocorticotrophic hormone (ACTH). ACTH in the blood stimulates release of cortisol/corticosterone (a glucocorticoid) from the adrenal gland cortex, which is directly released in the veins draining this organ and through the blood reaching to the target destinations, which express glucocorticoid receptors (GR) for action.

HPA axis mediated neuroendocrine homeostasis, and consequent neural stabilization of

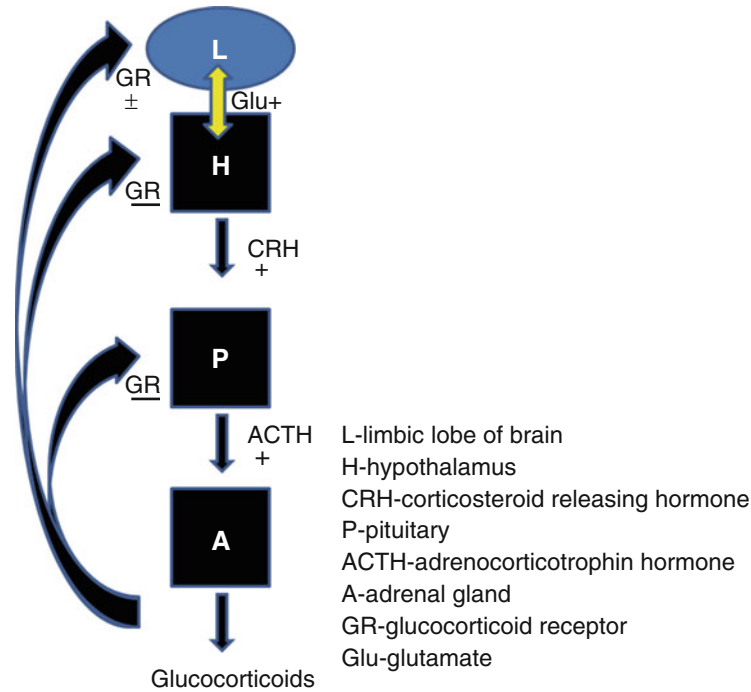
cognitive domains of the brain is largely involved in maintenance of healthy behavior. HPA axis responses to the stimuli are controlled by negative and positive feedback loops running between the HPA centers and target destinations. A positive feedback should increase the hormonal secretion, and vice versa a negative feedback should in turn decrease the hormonal secretion. Though, a positive feedback loop is less common in practice than the negative feedback loop in HPA axis regulation. Final command for the feedback loops comes from the hypothalamic nuclei (through releasing or inhibitory hormones). Functionally, HPA axis extends to the limbic cortex of the brain (HPA-L axis – the limbic cortex deals with the emotion and affective behavior and contains amygdala, hippocampus, medial prefrontal, insular, and cingulate cortices as chief constituents. Different limbic system components may have varying influence on HPA axis as has been noted between the hippocampus and amygdala (Fig. 2) (Kumar et al. 2017a). A dysregulation of extended HPA axis has been extensively implicated in the genesis of stress-induced behavioral pathologies (Phillips et al. 2006; Kumar et al. 2017a).

## Circadian Control of Hormone-Regulated Behavior

Specific nuclei in the hypothalamus, namely, suprachiasmatic (SCN) and paraventricular nucleus (PVN), regulate timed release of hormones. The pineal gland is also known to maintain timed release of melatonin which depends on exposure of the organism to the light (Tsang et al. 2014). The circadian releases of the hormones from the hypothalamic and pineal nuclei are affected by the duration and intensity of the light the organism is exposed to. The information of the light exposure reaches to the SCN and other hypothalamic nuclei through bidirectional retinohypothalamic connections (Tsang et al. 2014). Pineal gland nuclei are also connected (Tsang et al. 2014). Control of circadian rhythm through SCN and PVN nuclei is a complex biological process which is conserved among species and genetically determined (Andreani et al. 2015).



**Hormones and Behavior,**  
**Fig. 2** Feedback  
regulations at extended  
HPA-L axis



The molecular repertoire of the SCN has been presented in brief in Table 3.

The molecular repertoire maintaining circadian rhythms were found present in many bodily organs and tissues, which together create a complex molecular network system which gets its central command from SCN (Hughey and Butte 2016).

Cortisol, the HPA axis output hormone, also follows circadian rhythm, with its peak secretion in the morning with lesser serum values along the day. A dysregulation of circadian synthesis/release of cortisol was found implicated in stress-induced psychiatric disorders (Kumar et al. 2017a, b).

**Blood-Brain Barrier (BBB): A Body-Brain Interface in Hormonal Action**

**Crossing Blood-Brain Barrier (BBB)**

A hormone would pass through the BBB or not depending on its chemical structure. Steroid hormones are lipid soluble and hence can easily pass to-and-fro through the BBB (the peripherally synthesized hormones enter the brain and those

**Hormones and Behavior, Table 3** Molecular repertoire of SCN

|                                                |
|------------------------------------------------|
| Brain and muscle ARNT like protein-1 (Bmal1)   |
| Clock (or Npas2 in neuronal tissue)            |
| Cryptochrome (cry) 1,2                         |
| Period (per)1,2,3                              |
| E-box                                          |
| Retinoid-related orphan receptor (Ror) α, β, λ |
| Rev-Erb α, β                                   |
| Chrono                                         |
| Casein kinase 1 (ck1) δ, ε                     |

synthesized inside the brain reach to periphery), but protein, peptide, amine, and other non-lipid hormones can do it with help of the transporters/ binding proteins only. Availability of the transporters/binding proteins in the blood makes passage of lipid-insoluble hormones a saturable/ rate-limited process.

**No BBB in Selective Brain Regions**

Selective sites of the hormone synthesizing brain regions called circumventricular organs are devoid of a blood-brain barrier (BBB) which

**Hormones and Behavior, Table 4** BBB free regions in brain

|                                            |
|--------------------------------------------|
| Circumventricular organs                   |
| 1. Organum vasculosum of lamina terminalis |
| 2. Subformical organ                       |
| 3. Subcommissural organ                    |
| 4. Median eminence (hypothalamus)          |
| 5. Intermediate lobe of pituitary gland    |
| 6. Posterior pituitary                     |
| 7. Pineal gland                            |
| 8. Area postrema (4th ventricle)           |

facilitates the release of the stored hormones in the blood (Table 4).

These BBB-free regions are also the site for receiving peripherally released hormones and contain receptors for such hormones – presenting a unique opportunity for neuron-hormone interactions.

**Neuron-Hormone Interactions Inside the Brain**

**Hormone-Induced Neuroplasticity**

Hormonal exposure induces adaptive plastic changes at the neural synapses – basic unit of the information processing in the nervous system. The key brain regions involved in the neuroendocrine regulation (like amygdala, hippocampus, hypothalamus, prefrontal and limbic cortex) densely express receptors for the hormones implicated in cognitive and emotional development (like sex and thyroid hormones, oxytocin, and vasopressin).

Any change in the physiological levels of a hormone reaching the brain centers involved in a behavior-induced structural and functional changes at the synapses – alter membrane excitability, induce synaptic protein formation and activate membrane signaling cascade, and alter presynaptic release of neurotransmitters and/or response at postsynaptic membrane – in turn influences synaptic transmission. Hormonal influence is also evidenced in the formation of the new synapses, neurite outgrowth and spine density, dendritic arborization, myelination, neural

connectivity, and other parameters of the neuroplasticity. Additionally hormonal stimulation induces release of neurotrophins, mainly brain-derived neurotrophic factor (BDNF), which shows neural activity-dependent secretion in the cognitive domains of the brain and can induce the analogous neuroplastic changes (Kumar et al. 2017b).

Estrogen has a significant role in both sexes in improving learning and memory acting at hippocampal neurons which are known to synthesize estrogen locally and also densely express receptors for it. These synaptic and other neuroplastic changes are remodeled with further hormonal level changes to reinforce or weaken a behavior. Hormone-induced neuroplastic changes supposedly create a basis for such more changes in future – a neuroscience concept known as “meta-neuroplasticity” (Salma 2014). Behavior-specific neural networks get hormonal modulation when challenged with specific stimuli. Release of a hormone in response of a stimulus is orchestrated by specific hypothalamic nuclei – which is the command center for the synthesis/release of all hormones. Hormones specifically induce synthesis/release of various neurotransmitters/modulators in different parts of the brain. Unique of the steroid receptors present in the brain is that they may be activated by the neurotransmitters and intracellular signaling systems other than the cognate hormone by a process known as ligand-independent activation (Blaustein 2004). Together these molecules differentially modulate the components of the synaptic transmission and neural network properties. A hormone-induced neuroplasticity is specific and unique to the individuals which brings diversity in their behavior, i.e., two individuals may behave differently even in the similar environmental contexts.

**Cortical and Subcortical Control**

Hormones show region-specific influence on the cerebral cortex. The reflex-based, primitive and instinctual, emotional, and survival behaviors (fright, flight, fight!) which are common to all animals depend more on the control of the hormones and involve cortical regions which are older in evolution like the hippocampus and

dentate gyrus, olfactory cortex, and medial prefrontal/orbital and cingulate cortex. In contrast, executive behaviors like thinking, strategizing or planning, and decision making – which are salient characteristics of human – show less hormonal influence and involve newly evolved cortical brain regions like lateral prefrontal and associative regions of the neocortex.

The amygdala – a quasi-cortical structure which is the nodal brain center for the primitive behaviors like fear, rage, and anger and densely expresses receptors for many hormones like steroid (especially sex hormones and cortisol) and amine hormones, and also for oxytocin and vasopressin – shows high influences of the hormones.

Hippocampal neurons (including dentate gyrus) not only densely express receptors for the above named hormones but are also known to synthesize some sex hormones *de novo* (Table 3), especially estrogen (Ish et al. 2007). Synthesis of sex hormones in the hippocampus and expression of their receptors in this and other cortical brain regions are considered important for the sex-specific differentiation of the brain during embryonic development. Hormonal influence in the hippocampus is believed to contribute more than any other brain region owing to wider impact of the hippocampal functions in behavior. The hippocampus is the nodal region for learning and memory and also maintains functional connectivity with other brain regions. Estrogen is neuroprotective and contributes substantially to the hippocampal functions, particularly by inducing structural plasticity at synapses. Testosterone, oxytocin, and vasopressin also improve the hippocampal functions (in contrast, cortisol improves the hippocampal functions in acute exposure but diminishes in chronic exposure). Oxytocin receptor signaling in hippocampal neural circuits is thought to mediate discrimination of social stimuli and affiliation or avoidance behavior guiding social recognition (Raam et al. 2017).

Hormones also influence hippocampal neurogenesis – which has been evidenced to keep going lifelong (in dentate gyrus) and said to facilitate inclusion of new information – and hence bear an important role in learning and

memory, and a dysregulation of this has been implicated in genesis of psychiatric disorders (Kumar et al. 2017a, b). Hormonal influences on parahippocampal brain regions, especially of testosterone, are known to improve spatial performances.

Specific hypothalamic nuclei secrete hormones which reach to various target centers inside the brain and periphery through blood streams and induce release of a distinct set of hormones/neurotransmitters/modulators. Hypothalamic nuclei are also intricately connected to the cortical, sub-cortical, brain stem nuclei and spinal autonomic centers through the nerve fibers. Thus at specific hypothalamic nuclei, neural feedbacks integrate and balance with that derived from the hormones running in the circulatory system which helps the organism to respond to the internal cues like food, sex, or body temperature. For illustration, in hunger or satiety, specific hormones are released from the endocrine glands in the digestive system into the draining veins which are further carried to the parts of hypothalamus through the blood. In the hypothalamus, specific nuclei groups further transmit the impulses to the cortical neurons to create a conscious awareness of feeding status of the organism.

A miniature reign like neural structure located at the posterior limit of the hypothalamus – the habenula – which connects subcortical gray matter structures to the brainstem centers containing aminergic nuclei is known to implicate in the learning of the adaptive behavior (Kumar et al. 2017c). Habenular pathways get also influenced by the HPA axis hormonal changes which is said to be instrumental in the pathological development of submissive behaviors like social defeat (Kumar et al. 2017c).

### **Aminergic Release from the Brain Stem and Hypothalamic Nuclei: A Closer Function as Hormones**

The specific nuclear groups in the brain stem secrete aminergic/cholinergic molecules which are released at target sites in different brain regions through axonal endings (Table 5).

These molecules have the similar influences on the synaptic processing as blood-running

hormones and are referred to as neurohormones, though some of them can work like neurotransmitters (or neuromodulators) – as dopamine, serotonin, noradrenaline/norepinephrine, and acetylcholine (Tables 5 and 6). Some of these molecules are also synthesized in the hypothalamic nuclei – as dopamine, serotonin, and histamine. These aminergic centers have widespread reciprocal connections in the brain and have crucial involvement in controlling neural networks involved in emotional, survival, and adaptive behavior of the animal. The brain stem aminergic molecules in association with that released from hypothalamic nuclei help in maintaining consciousness and keeping the organism alert and also influence circadian control of feeding and sleep behavior.

**Hormones and Behavior, Table 5** Aminergic/cholinergic secretion by brain stem neurons

|                                                                                                                 |
|-----------------------------------------------------------------------------------------------------------------|
| Amines                                                                                                          |
| Norepinephrine – locus ceruleus, ventral tegmental area (VTA)                                                   |
| Epinephrine – reticular formation (along motor nuclei in the floor of 4th ventricle) and in periaqueductal gray |
| Serotonin – raphe nuclei                                                                                        |
| Dopamine – substantia nigra, ventral tegmental area (VTA)                                                       |
| Choline                                                                                                         |
| Pedunculopontine nucleus (PPN) – acetylcholine                                                                  |

**Hormones and Behavior, Table 6** Types of neuronal secretions in brain

|                                                                                                       |
|-------------------------------------------------------------------------------------------------------|
| A neurotransmitter                                                                                    |
| Is released at synapses                                                                               |
| Passes through synaptic cleft to affect postsynaptic neurons, a muscle cell, or another effector cell |
| A neuromodulator                                                                                      |
| Affects groups of neurons or effector cells with appropriate receptors                                |
| Often acts through second messengers and can produce long-lasting effects                             |
| A neurohormone                                                                                        |
| Is released into the blood and therefore may exert its effects on distant peripheral targets          |

**Setting of Moods, Emotions, and Impulses**

Hormones influence information transmission speed at the synapses which provide a neural substrate for the mood, emotions, and impulses in the organism. The synthesis and release of the hormones are stimulated or suppressed by the environmental cues, i.e., a prolonged exposure of the organism to a favorable environment induces synthesis/release of the particular hormones necessary to promote a behavior suitable to the context. For example, when an animal is kept in contact with a potential mate, synthesis and release of the sex hormones will show an upsurge. Similarly, exposure to a rival will upsurge release of testosterone and stress hormones – which are implicated in combating behavior.

Both male and female sex hormones by influencing release of neurotransmitters/modulators like dopamine and serotonin make an impact on mood and emotion driving an individual into reproductive behavior. A cyclical change of sex hormones during menstruation in female is associated with the mood changes/swings; women report enhanced mood in part of menstrual cycle when estrogen will have higher secretion and vice versa (Dreher et al. 2007). Some mood disorders like premenstrual or postnatal depression and perimenopausal depression (or psychosis) signify influence of estrogen in maintenance of mood in female. In male, high serum testosterone has been associated with increased concentration, visual acuity and geo-spatial abilities, positive mood, and also with the rage and impulsive behavior. Endogenous opioids, which are physiologically secreted during heavy exercise or the habitual strenuous physical activities, increase threshold for the pain and create a euphoric feeling. Internally secreted hormone-like molecules in the brain – neurohormones – which work like neuromodulators and some as also neurotransmitters (dopamine, serotonin, noradrenaline) have a critical role in setting and maintenance of the mood (Table 7).

An intricately regulated cocktail of neurohormones is said to control the rate, rhythm, coupling, and synchronization of the cortical oscillatory waves in the neurocognitive networks

**Hormones and Behavior, Table 7** Neurohormones

|                                                  |                               |
|--------------------------------------------------|-------------------------------|
| Corticotropin releasing                          | Thyrotropin releasing         |
| Hormone (CRH)                                    | Hormone                       |
| Gonadotropin releasing                           | Histamine                     |
| Hormone (GNRH)                                   | Vasopressin or antidiuretic   |
| Luteinizing hormone releasing                    | Hormone)                      |
| Hormone (LHRH)                                   | ADH or AVP                    |
| Somatostatin (growth hormone-inhibiting hormone) | Oxytocin                      |
|                                                  | Norepinephrine                |
|                                                  | Dopamine                      |
| Melanotropin release                             | Serotonin                     |
| Inhibitory factor (dopamine)                     | Melatonin                     |
| Neuropeptide Y (NPY)                             | B-endorphin                   |
| Neurotensin                                      | Agouti-related protein (AGRP) |
| Orexin A and B                                   | Estrogen                      |

of the brain – which is crucial for setting and maintenance of the mood.

Oxytocin and vasopressin which are secreted from posterior pituitary during labor and breastfeeding in female, and during sexual intercourse and intimate behavior in both the sexes, are known to have positive effect on mood and emotion. Oxytocin has a higher secretion in female and vice versa, vasopressin witnesses higher secretion in male, and their effects have been known to match to estrogen and testosterone, respectively.

**Autonomic Nervous System (ANS)-Hormone Cross Regulation**

ANS comprises of sympathetic and parasympathetic limbs that are involved in the antagonistic components of the behavior – crucial for the development of sexual and adaptive behavior in the organisms. ANS plays a central role in the genesis of psychological and pathophysiological stress and control of animal behavior, by being intricately involved in the regulation of neuroendocrine balance, neuroeffector communication, and behavioral response of the individual. Sympathetic and parasympathetic activations are associated with release of specific hormones inside the brain and also from the peripheral endocrine

organs. Sympathetic nerves release adrenaline/epinephrine which has an activational role in fight-flight behavior and also increase heart rate acting at sinoatrial (SA) node; in contrast, parasympathetic nerves release acetylcholine which has calming effect and also decrease the heart rate.

Adrenaline/epinephrine is secreted from the adrenal medulla (which contains developmentally migrated sympathetic ganglions) in response to the neural stimulus reaching to it through sympathetic nerves. Both components of the ANS engage distinct sets of the hormones, neurotransmitters, and modulators to execute their effect. Hypothalamus is the master regulator of the ANS integrating the influences of all the contributory components and mechanisms.

**Gut Hormones: Influence on Behavior**

The hormones secreted in the gut (Table 1) not only have regulatory roles in feeding behavior, i.e., control hunger and appetite, but are also involved in maintaining mood and emotion, which has given rise to the concept of gut-brain axis. The gut-brain axis gets influenced by the common hormones (or hormone-like molecules) which are secreted in the gut as well as inside the brain – like peptide hormones (especially neuropeptide Y) and serotonin. The gut-brain axis is also influenced by the enteric nervous system (ENS) – which is predominantly autonomic in function. ENS in concert with the gut hormones helps to maintain the mood and emotion which will have a direct impact on the behavior of the organism – a dysregulation of gut hormone-ENS found implicated in many behavioral pathologies (Zhou and Foster 2015). Interestingly, human studies support influence of gut microbiota on behavior involving gut hormone-ENS (Skibicka and Dickson 2013).

**Hormonal Induction of Behavior: Underlying Mechanisms**

Animal behaviors range from simple reflexive actions like withdrawal of the limb when touched



with a prick or hot stick to a complex action like responding to the advances of a potential mate, the human-specific behaviors like playing a musical note, or responding to the offers of a business partner. Hormones have an influence on almost all aspects of animal behavior with the greater impact on that related to the species survival and proliferation like feeding and reproductive behavior and dealing with the threats to life and self-respect. (In Table 1 hormones implicated in various aspects of the animal behavior are indicated in superscript “c.”)

A hormonal influence on behavior depends on multiple factors, viz., age, sex, built, genetic makeup, developmental history, and early-life experience of the individual, also on the environmental context, duration of exposure to the stimuli, and associated rewards or threats. Hormone-driven behaviors such as sexual arousal and mate seeking, aggression to sexual opponent, response for food when hungry, etc. are conserved in animal kingdom and can be reproduced in the matching environmental and personal context (in contrast to the intellectually driven behaviors, which are specific to human and contain less hormonal influence and show more inter-individual variation).

A single hormone bears impact on many types of behaviors, or more appropriately a set of hormones together determine a particular behavior. A hormone’s final influence on behavior depends on the type and expression of the cognate receptors present on the target structures in the central and peripheral nervous system, which in turn depends on the encoding genes and their isoforms (Pfaff 1997; Maney 2017).

Hormones have two kinds of effect on the institution of behavior – “organizational” and “activational.” “Organizational” effect of the hormones is set during the development of the brain, and it determines the future response of the individual to the stimulus. In contrast, “activational” effect depends on the current status of the hormone in the body and determines immediate response.

Most of the hormones which are implicated in behavioral functions are either produced by neuronal tissue or by the components of central neuroendocrine axis regulating behavior – HPA/HPG

axis. In exception, some hormones – such as growth hormone (GH) secreted from anterior pituitary, thyroid hormones, and a newly known hormone Klotho, which is secreted from multiple animal organs (chiefly kidney, liver, skin) (Dubal et al. 2014), which are chiefly meant for somatic functions – have also been implicated in behavioral functions improving cognition (Table 1).

Hormone-behavior interaction is bidirectional, i.e., both can induce each other. The mutual dependency of the hormone and behavior provides conceptual basis for the behavioral corrections with therapeutic hormone manipulations and vice versa and hence constitutes a fundamental concept in the “behavioral endocrinology.”

### Genetic and Epigenetic Mechanisms

Hormone-driven behavior is hardwired in the genes and is seen grossly conserved across the animal kingdom. Any interindividual variation is attributed to the different gene isoforms for the hormones and their cognate receptors existing in the species population. Though, it is known to vary with the developmental history, early and current life experiences of the individual, which are not explained with any genetic theory. In recent years, a new concept “epigenetics” has been put forward to explain such lifetime variations in the hormone-driven behavior, which is defined as “a change in the DNA structure of an organism without introducing any change in its code sequence.” Such epigenetic changes in the DNA are environment induced and brought about by the chemical tagging of the DNA bases by methylation, or there can be changes in the DNA packaging material like histone proteins (methylation/acetylation) or in the methyl-binding proteins or through noncoding RNAs (micro-RNAs and long ncRNAs) (Cao 2014). Hormone-induced sexual differentiation of the developing brain and its impact on adult sexual behavior and also infant-mother interactions and other early-life experiences which may have grave impact on the future behavior as an adult are mediated through epigenetics. Though epigenetic mechanisms introduce environment-induced adaptive changes in the genomic structure of the organism, by a default mechanism, most of the epigenetic changes (gathered by an individual

either during embryonic development or through personal life experiences) do not carry forward in the offspring and get erased during gametogenesis (Hackett et al. 2013). Pertinent here is to mention that certain epigenetic changes as that created from severe chronic stress (involving HPA axis) may pass into next generations bypassing the default erasure – the phenomenon is called “trans-generational epigenetics” (Hackett et al. 2013; Jensen 2013). Epigenetics is considered to be instrumental in stress-induced alterations in HPA axis settings and their consequent effects on neurocognitive functions.

### **Institution of Social Behavior in a Newborn**

How social behavior is instituted in a newborn is not well understood. Supposedly, a newborn learns how to behave interacting with the environmental cues (although some of the newborn behaviors are innate and conserved – like crying just after birth, frequent startling, and exploratory behavior such as putting things in mouth). Empirical studies suggest that mother’s hormones in the breast milk bear impact on a newborn’s learning of the behavior (Grey et al. 2013). This observation has applied importance that any exogenous intake of hormones – like anabolic steroids – by the mother may be a hindrance to this learning. Excess glucocorticoids (mainly cortisol) released during stress in pregnant mother were found to have pathological impact on programming of HPA axis and consequent learning of behavior in fetus (Kinsella and Monk 2009).

### **Hormonal Disruption in Developing Fetus: Residual Effect on Adult Behavior**

Many chemicals released from artificial sources – industrial effluents and pesticides, heavy metals and plastics, and natural sources – derived from plant products, phytochemicals, when entered into the body as contamination, act as decoy ligands which hijack some components of the biological actions of the original hormones. Such chemicals are called hormone disruptors or endocrine-disrupting chemicals (EDCs) (Barrett and Patisaul 2017). Environmental estrogens and phytoestrogens are the prime hormone disruptors, known to affect neurocognitive domains in developing fetus, disrupting HPA/HPG (gonadal) axis,

in turn affecting institution of behavior. Loss of behavior will be noted not only for sexual and reproductive domain in affected fetus as adult, but normal intelligence and memory and social behavior may also get compromised.

### **Hormonal Correlates of Homosexual Behavior**

Homosexual behavior is known in human from archaic times and can be seen in many animals also. A scientific theory supporting the biological basis of homosexuality suggests that it has an in utero origin linked to prenatal overexposure of the fetus to an opposite sex hormone (Rice et al. 2012). Developing fetus faces a contrasting situation in utero, and maternal and fetal hormone levels adjust for the better survival of the fetus (Rice et al. 2012). Although both sex fetuses get exposed to both kinds of sex hormones normally, in certain cases, a sex hormone may dominate on others helping the survival, which may or may not be matched to the sex of the fetus. A contrasting exposure of a developing fetus to a sex hormone is proposed to influence its sexual behavior afterward as an adult, i.e., in utero exposure of a male fetus to estrogen-predominating environment may influence its sexual orientation in adult, and vice versa may be true for the testosterone exposure to a female fetus (Rice et al. 2012).

In an alternative view, a same sex hormonal predominance in the uterus for a pregnancy (necessitated for the survival of a particular sex fetus) may get tagged in the genome of the mother to get reactivated in subsequent pregnancies (through a phenomenon called epigenetics) and may influence in utero development of next opposite sex fetuses (Rice et al. 2012). A reversed 2D/4D ratio also was found predictive of homosexual behavior in the men (Xu and Zheng 2016).

### **Hormone-Induced Behaviors: A Brief Overview**

#### **Survival and Adaptive Behavior**

HPA axis hormones like CRH, ACTH, and cortisol and other hormones like arginine vasopressin – from posterior pituitary – and adrenalin/noradrenaline from adrenal gland are secreted in response to the acute and chronic stress (Table 8).

**Hormones and Behavior, Table 8** Hormones of stress

|                                                     |                    |
|-----------------------------------------------------|--------------------|
| CRH ↑                                               | Glucagon- ↑        |
| AVP ↑                                               | Insulin ↓          |
| ACTH ↑ glucocorticoids ↑ (cortisol, corticosterone) | Angiotensin- ↑     |
|                                                     | GnRH ↓             |
| Epinephrine ↑                                       | GH ↑               |
| Norepinephrine ↑                                    | Prolactin ↑↓       |
| Endorphin ↑                                         | Thyroid hormones ↓ |

HPA axis hormones are implicated in the mechanism of avoidance learning and escape – an adaptive behavior. Release of the stress hormones is associated with concomitant activation of the sympathetic system which adds up into the effect. Release of stress hormones in acute stress helps the organism to prepare for the flight or fight behavior (both of these bear survival values for the organism and constitute adaptive behavior). Conversely, the chronic exposure to the stress leads to abnormal forms of the behavior – like anxiety, panic, and depression – mediated by key molecular cascades like immediate early genes at synapses induced by persistently raised levels of the stress hormones (Senba and Ueyama 1997; Kozlovsky et al. 2008).

### Sexual and Reproductive Behavior

Sex hormones bear an exclusive influence on sexual orientation and drive of the animals including human. Both testosterone and estrogen are secreted in each sex, former being dominating in male and latter in female. Testosterone is convertible into secondary male hormones and also estrogen with the action of aromatic enzyme alpha-reductase in the brain and in periphery. Secondary male sex hormones are essential for the development of secondary sexual characters during puberty, and conversion of testosterone to estrogen by aromatization in medial preoptic nuclei of hypothalamus is obligatory for sexual motivation in males (Balthazart 2017). Different brain regions bear the receptors for sex hormones, especially that involved in maintaining neurocognition – the prefrontal and limbic cortex (including the hippocampus), hypothalamus, and amygdala (Blaustein 2004). Dimorphic sexual

behavior is regulated by sex hormones-directed modular gene expression in these brain regions. Various components of sexually dimorphic behaviors are governed by separable genetic programs, i.e., single genes control the specific components of the male/female sexual behavior (Xu et al. 2012).

Sex hormones induce an immediate sexual drive – while effects of testosterone are more robust and may induce aggression, the effects of estrogen are comparatively modest. Both hormones induce sex-specific behavioral and physical characteristics, as evidenced in diseases with sex hormone dysfunction and experimental studies in the animals. Male teens with androgen insensitivity syndrome in which dysfunction lies at the testosterone receptor have been shown to bear female-like physical and psychological characteristics, including sexual orientations and preferences. In contrast, in cases of in utero early testosterone exposure of a female fetus in a twin pregnancy (when another fetus is a male) or in case congenital adrenal hyperplasia (CAH) which may bring some masculine features in the female child and may also reflect in the behavior – showing characteristics of a male typical behavior. A sex-specific change of behavior also got noted in empirical studies involving animal models where either testis or ovary was castrated; conversely, the change of behavior got undone with reimplant of the removed gonad.

Sex hormones bear wider impact on interpersonal relationship involving opposite sexes. Cyclical change of the sex hormones in female are said to influence sexual behavior which might be reflected in interpersonal relationships. However, studies are lacking to support if same phenomenon is also occurring in the male. Though diurnal and periodic variations of the testosterone have been noted, corresponding changes in sexual behavior is not much defined in male animals, with exception of rabbits (in which a cyclical variation has been noted) (Degerman and Kihlström 1961). In male animals, alterations in sex hormone levels and accompanied sexual drive are limited by exposure to the female, freedom to intimacy, and engagement or abstinence from the sexual activities. Seasonal or annual surge of sex hormones is common in animals with exception

of the highest rank primates including human – in whom there is no such fixed pattern. The cyclic or periodic changes of sex hormones may be associated with sexual urge and fantasies and self-stimulating/gratifying practices. A periodic, seasonal, or annual surge in secretion of sex hormones is controlled by the releasing and stimulating hormones from hypothalamic and pituitary centers, respectively (Table 1).

Other than the sex hormones, posterior pituitary oxytocin and vasopressin are also noted to involve in sexual and reproductive behavior (discussed elsewhere in this chapter). Uniquely, an anterior pituitary hormone prolactin which is generally known to be associated with infant-parent bonding has also been found to be associated with the heterosexual pair bonding and its variation in secretion found to correlate with the amount of sexual behavior and contact affiliation in both sexes (Snowdon and Ziegler 2015).

### **Aggressive and Violent Behavior**

Empirical studies present evidence for causal association of testosterone in aggressive and violent behavior though a causal association has been challenged putting forward counter argument that aggressive/violent behavior is a by-product of testosterone's impact on individual's concern for gaining higher social status (Eisenegger et al. 2010). Sex violence by males has been almost exclusive and also correlated positively with serum testosterone levels (Studer et al. 2005). Testosterone is also found linked to incidences of aggressive behavior and violence by gun owners (Klinesmith et al. 2006).

### **Unethical Behavior**

Empirical studies have supported that a combination of the testosterone and cortisol may drive the subject into unethical behavior (Lee et al. 2015). Testosterone is said to influence a person's drive to acquire status-bearing resources (money, power, leadership, etc.) which gets further intensified by cortisol. Cortisol is released essentially in reaction to a stress and may be raised in a moral conflict leading to the mental strain, and it was found to associate with the reward-seeking and fear-reducing influence of the testosterone in studies (Lee et al. 2015). Individuals were found to

have lower serum levels of cortisol after committing unethical behavior as the commission of the act perhaps had given them a sense of relief from the mental strain (Lee et al. 2015).

### **Oxytocin: A Molecular Mediator of Positive Behavior and Bonding**

(Maternal behavior, sexual intimacy, romantic love, generosity, trust, ethical and spiritual behavior)

Oxytocin is the hormone in which most of the behavioral endocrinologists show particular interest. The physiological functions of oxytocin in breast milk ejection during child feeding, and its copious release during sexual intercourse and childbirth, are known since long. Oxytocin's role in maternal behavior is outstanding. A study noted induction of maternal behavior in virgin rats after intracerebroventricular injection of oxytocin (Pedersen et al. 1979).

Contemporary research has established its substantial role in intimate and positive aspects of behavior (Kosfeld et al. 2005; Insel 2010). In consecutive studies along the years, oxytocin has been strongly implicated in the peer bonding, romantic, and intimate relationship (Insel 2010), and many positive aspects of behavior such as trust, ethics, spirituality, and generosity (Kosfeld et al. 2005; Van Cappellen et al. 2016). A study implicated it in inducing an altruistic behavior in social groups against the ethnic backdrops (Marsh et al. 2017). Studies also implicated its determining role in the economic behaviors – such as in building the trust of the customers in the investors (Kosfeld et al. 2005).

Though having a substantial role in social behavior, all is not fascinating about this molecule. A study implicated it in some negative aspects of behavior as well, like doing a bias in favor of a social group to which individual belongs (Shalvi and De Dreu 2014). Further, an oxytocin-mediated behavior was found to be dose dependent and inducing at optimum serum/CSF concentrations only – violation of which may show contrasting behavioral effects, making its pharmacological exploitation for behavioral corrections difficult (Zhong et al. 2012; Bales et al. 2013). Furthermore, oxytocin is a biological mediator and facilitator of a positive behavior but cannot generate itself, which limits its

pharmacological use for this purpose. After all, expanded understanding of the oxytocin-mediated biological mechanisms has now brought the opportunity for the behavioral interventions aimed at inducing the positive behavior and bonding in various applied conditions.

### Personality Trait Association

Personality hormone association has not been a defined one, though unconfirmed descriptions of high testosterone and thyroid hormone association to certain personality traits being competitive, focused, and aggressive can be found in the literature. Plasma oxytocin level was found positively correlating with extravert behavior in studies (Bendix et al. 2015). Uniquely, an anthropological measurement comparing the length of the 2nd and 4th digits of the hands (2D/4D ratio), which is believed to reflect the prenatal testosterone/androgen exposure of the fetus, was found associated with sex-specific behavior as the adults (Galis et al. 2010; Xu and Zheng 2016). A lower 2D/4D ratio was found correlating with a more male typical behavior and vice versa was found true for a more female typical behavior. A mismatched prenatal exposure of the sex hormones have been associated with the borderline personality disorders.

### Pathological Behavior

Studies implicated hormones in the genesis of pathological behavior like gambling, drug addiction, and obsessive-compulsive disorders (OCD) such as compulsive stealing, binge eating, etc. HPA axis hormones are implicated in chronic stress-induced genesis of psychiatric disorders such as major depressive illness, bipolar disorder, schizophrenia, and PTSD (Kumar et al. 2017b). Chronic stress permanently alters the HPA axis regulation resulting in a persistently increased level of cortisol, creating basis for the pathogenesis of such psychiatric disorders by inducing the structure/function changes at synapses altering neural transmission and blunting the growth of the neuronal processes making connections in key brain regions involved in learning and memory – like hippocampus and prefrontal cortex. Behavioral effects of stress-induced cortisol are mediated by epigenetic changes at GR and involve MAPK signaling

pathway and Egr-1 (Revest et al. 2005). Another hormone, melatonin – which is known for maintaining circadian rhythm – was also found implicated in genesis of psychiatric disorders by various studies. Melatonin dysregulation perhaps plays by disrupting molecular clock in SCN of the hypothalamus and also the normal sleep pattern leading to detrimental changes in structure/function of hippocampus neurons, primarily suppressing continued neurogenesis which is crucial for learning and memory.

A persistently low serum level and diminished cortisol release response in acute stress challenge links with anhedonia – feeling no pleasure in normally pleasurable activities, depression, and suicidal behavior. A cortisol release response against presented acute stress challenge indicates how fervent or disheartened individual would respond to an eminent challenging situation. An optimum cortisol challenge response seems necessary for maintaining the healthy behavior.

Neuroplasticity induced by the hormones set the basis for the further neuroplasticity in future, a concept known as meta-neuroplasticity (Salma 2014). A dysregulation of the meta-neuroplasticity has been implicated in the progression of neurocognitive dysfunctions and also in the genesis of many neuropsychiatric diseases in adult where etiology has been developmental or early-life stress (Lai and Huang 2011).

### Cross-References

- [Hormones and Cognition](#)
- [Hypothalamus](#)
- [Passive Avoidance Learning](#)
- [Rescue Behavior](#)
- [Social Behavior](#)

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## Hormones and Cognition

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## Introduction

Definitions of cognition generally refer to the ability of an organism to acquire, retain, process, and use information when required (Niemelä et al. 2013). Although these definitions are correct, they rarely capture the complexity involved in the

cognitive process or the role the endocrine system plays in driving cognition (Erlanger et al. 1999). The endocrine system is responsible for a plethora of functions from reproduction and growth to metabolism and stress but also has an effect on behavior, psychology, and cognition (Burdick 1938; Selye 1936, 1976). Of the more than 50 basic hormones produced by the 18 endocrine glands and specialized tissues, only a handful of these are responsible for exerting a direct or indirect effect on cognitive processes. Here, we discuss four of the most recognizable hormone groups that influence cognition: stress, reproductive, thyroid, and nonapeptide hormones. It should be noted that these are not the only, nor the most important, hormone groups that are able to influence cognition but they are easily recognized among the general public and researchers.

### Stress Hormones and Cognition

When faced with a possible homeostasis-altering stressor (natural/anthropogenic), the stress response of an organism is activated. Here, the sympathetic nervous system, the hypothalamic-pituitary-adrenal (HPA) axis, and the central neurotransmitter system are activated, all of which have effector mechanisms within the brain that play a role in information processing (Joëls and Baram 2009). The HPA axis, including the many affiliated endocrine glands and feedback loops, is responsible for the production and synthesis of corticosteroids (Sapolsky et al. 2000; Selye 1936). The secretion of these corticosteroids occurs in a pulsating and rhythmic fashion (Young et al. 2004). However, at any given time, the perception of a possible threatening situation, be it physical or physiological in nature, can result in a rapid increase of corticosteroid concentrations above the observed rhythmic peak (Groeneweg et al. 2012; Joëls and Baram 2009).

In this regard, the adrenal gland is responsible for the production and secretion of two important corticosteroids: glucocorticoids (GCs) and mineralocorticoids (MCs). In mammals, aldosterone is an important MC responsible for the control of extracellular fluid volume and blood pressure

(Joëls 2006). Cortisol and corticosterone, which are secreted in considerably higher amounts than aldosterone (~100 times), are GCs responsible for diverting energy supplies to the necessary organs while regulating cardiovascular and metabolic parameters (Reeder and Kramer 2005; Romero 2002). Despite the importance of both MCs and GCs in maintaining homeostasis, the role of corticosteroids in determining behavior and cognitive function (perception, attention, learning, and remembering; Wirth 2015) is often disregarded. The engagement of any cognitive process requires considerable amounts of energy, which is facilitated by the glucose metabolism function of GC (Erickson et al. 2003). And yet, GCs play a major role in both the consolidation and retrieval of information during the memory process. *Memory consolidation* refers to newly acquired information being converted from an unstable state (short-term memory) into a stable, long-term memory system (McGaugh 2000). *Memory retrieval* refers to the retrieval/remembering of already consolidated information (Souza-Talarico et al. 2011). This, however, is driven by the corticosteroid receptors present within the brain.

### Corticosteroid Receptors and Cognition

Both corticosteroid classes are produced by the adrenal cortex and secreted into the bloodstream before reaching the brain. Here their lipophilic nature results in the rapid movement of MC and GC across the blood-brain barrier (Sandi 2013). Despite their ability to enter the brain, the hormones are either (i) irreversibly degraded in the cytosol (Sandi 2004) or (ii) retained in cells where nuclear mineralocorticoid (MR) and glucocorticoid receptors (GRs) are present (Lu et al. 2006; Van Eekelen et al. 1988). In this regard, MRs are located primarily in the limbic system, with a preferential distribution in the hippocampus, amygdala, and motor cortex (Gass et al. 2000; Karst et al. 2010; Munier et al. 2012), while GRs are distributed in high densities throughout the prefrontal cortex and subcortical structures, including the hippocampus, amygdala, and hypothalamic paraventricular nucleus (Lupien et al. 2007). These regions of the brain have been shown to play an important role in cognitive,

emotional, and neuroendocrine control during the stress response (Joëls and Baram 2009; McGaugh 2004; Sánchez et al. 2000). Because MRs have a high affinity for corticosteroids, they are largely occupied even when stress hormone levels are low (de Kloet et al. 2005). In contrast to this, GRs have a tenfold lower affinity such that the receptors are only partially occupied at basal GC concentrations; and an increase in GC following a stressful event leads to an increase in occupation (Joëls and Baram 2009; Joëls et al. 2008). This allows for a mechanism whereby circulating GC can have different and/or opposing effects upon the hippocampus, depending on the concentrations present (basal vs. stressed; McEwen and Sapolsky 1995).

Both receptor types have been shown to exert slow, genomic actions, as well as rapid, non-genomic actions when binding to GC and MC. In terms of the former, GR activation following a stressful event ensures a delayed suppression of neuronal excitement and synaptic plasticity; this could assist in protecting information that is consolidated following a stress event (Joëls et al. 2007; Kim and Diamond 2002). Additionally, hormone-bound receptors translocate to the nucleus where they are responsible for regulating gene transcription, resulting in the generation of multiple isoforms of GR proteins via alternative RNA slicing (see Zhou and Cidlowski (2005) for a detailed review on GR). Each of these isoforms, and the possible receptor variances, accounts for a

range of unique biological responses such as development, growth, metabolism, and behavior (Sapolsky et al. 2000). During this process, it is the activation of MRs within the hippocampus that enables ongoing information processing.

In contrast to the receptors found within the brain, a number of localities outside of the brain also contain GRs and MRs, specifically the plasma membranes (Groeneweg et al. 2012). These receptors generally exert a rapid, non-genomic action by acting on steroid recognition sites at the plasma membrane (Groeneweg et al. 2012; Sandi 2004). When an imminent threat is perceived by an organism, the secretion of corticosteroids works to inhibit the HPA axis while promoting a rapid adaptive response. This response is largely behavior-based (“fight or flight”) but can also affect a number of cognitive processes (Roozendaal et al. 2010).

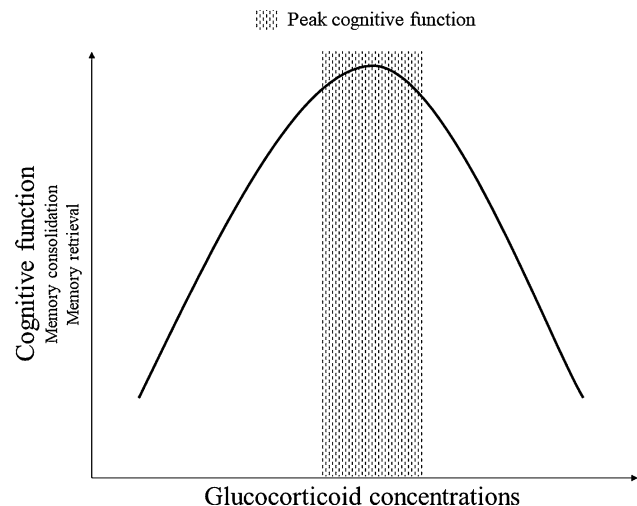
## Dose-Dependency

### Moderate GC Dose

The effect of GC on memory and information processing has been shown to be dose-dependent; this dependency has been defined as an *inverted U-shaped* relationship (Fig. 1) (Calabrese and Baldwin 2003; Joëls 2006). This dose-response relationship is primarily determined by the relative number and affinities of GR and MR within the brain (Wirth 2015). In order to achieve

## Hormones and

**Cognition, Fig. 1** The inverted U-shaped dose-dependent relationship between glucocorticoids and cognitive function, with moderate glucocorticoid concentrations showing optimal cognitive functioning



maximum long-term potentiation, and thus optimal memory consolidation, GC levels should be elevated enough to ensure that the majority of higher-affinity MRs are occupied by GC molecules, while an intermediate proportion of the lower-affinity GRs present within the brain are occupied (Joëls 2006; Wirth 2015). Thus, as MR-GC bindings reach optimal levels, MR-mediated effects such as hippocampal neurogenesis, neural excitability, and synaptic plasticity promote memory formation while maintaining integrity and plasticity in specific brain regions (Vogel et al. 2016). Furthermore, moderate GC concentrations have been shown to result in optimal receptor binding, translation, and electrophysiological functioning within the hippocampus which leads to long-term potentiation and primed burst potentiation (Schilling et al. 2013). The optimal MR/GR binding point is highlighted in the *GC Receptor Balance Hypothesis*; when the MR/GR ratio is high, i.e., GC concentrations are moderate with high occupation of MR but low GR occupation, memory performance is enhanced (Souza-Talarico et al. 2011). Specifically, moderate corticosteroid concentrations within the basal lateral amygdala, basal ganglia, and hippocampus facilitate memory processes (de Kloet et al. 1999; Erickson et al. 2003). An increase in GC and corticotropin-releasing hormone, a precursor of corticosteroids, in the hippocampus and amygdala promotes an increase in norepinephrine cell activity within the brain; this mechanism is known to enhance memory, especially when relating to fearful events (Butler et al. 1990).

#### Low and High GC Dose

In terms of the *inverted U-shaped* relationship between GC and cognitive function, considerably low or high GC concentrations are responsible for impaired cognitive capacities. The release of GC via the HPA axis is modulated according to the stress intensity experienced by an individual. Stress intensity is a term often used when describing the “strength” of the stress response to a perceived threat, as well as the time period over which the response is activated. As such, the intensity of the stress response experienced

by an organism is an important determinant of cognitive function (Sandi 2004, 2013).

If a perceived threat offers minimal danger to an individual (low-intensity stimuli), the production and secretion of GC into the bloodstream is limited, resulting in fewer binding events and, by extension, limited neuronal activation. This can lead to impaired information consolidation of both neutral and emotional information, as well as being detrimental to delayed memory consolidation (Lupien et al. 2002; Maheu et al. 2004). For example, Lupien et al. (2002) demonstrated that a reduction in circulating GC, which prevents the activation of the cortisol response in humans, resulted in a number of deleterious effects on delayed memory, specifically the retrieval of previously learned information.

Research over the last three decades has confirmed that chronically elevated GC can have a negative, deleterious effect on cognitive function. The activation of the stress response, and subsequent elevation in GC production over a prolonged period, will result in a high concentration of GC entering the brain. According to the *GC Receptor Balance Hypothesis*, during such periods of elevated GC, the MR/GR ratio is low and the occupation of MR and GR high; this level of occupation will result in cognitive impairment (de Kloet et al. 2000). This impairment has been observed in a number of different stages and types of memory processes, most notably *memory consolidation*, *retrieval of long-term memory*, *emotional memory consolidation*, and *working memory* (Wirth 2015). Such deleterious effects occur as a result of the atrophy in the apical dendrites of CA3 pyramidal neurons (Watanabe et al. 1992; Woolley et al. 1990), as well as increased apoptosis of newly generated neurons in the hippocampus, leading to a reduction in hippocampus plasticity and neurogenesis (McEwen 2000; Simon et al. 2005; Souza-Talarico et al. 2011).

The effect of low, moderate, and even high GC concentrations on cognitive function can be individual specific. Additionally, receptor densities within the brain not only differ between individuals (Champagne et al. 2008; McGowan et al. 2009) but can also fluctuate within an individual



over time (Pariante 2004). The receptor densities are largely determined by previous life experiences which determine GR gene expression, via methylation of DNA, over the long term (Wirth 2015). Interestingly, life experiences can influence GR gene expression, which determines receptor abundance within various regions of the brain, by modulating methylation of DNA over the long term. For example, higher infancy care in rodents results in less DNA methylation and greater receptor expression as adults, which impairs cognitive function at lower GC concentrations compared to adults that received less infant care and, thus, exhibit lower receptor expression (Champagne et al. 2008; Wirth 2015).

## Thyroid Hormones and Cognition

Thyroid hormones (THs), which include both triiodothyronine (T<sub>3</sub>) and tetraiodothyronine (T<sub>4</sub>), are important hormones that predominantly regulate metabolic pathways, through oxygen consumption, resulting in alterations in protein, lipid, carbohydrate, and vitamin metabolism (Smith et al. 2002). Though THs are also crucial for brain development, deficits of such hormones can result in permanent, deleterious, and profound effects on adult neurological function (see Zoeller et al. (2002) for a list of references (1–22)). The production of THs is driven by the hypothalamic-pituitary-thyroidal (HPT) axis in response to an energy-driven stimulus; the biologically inactive T<sub>4</sub> and to a lesser extent biologically active T<sub>3</sub> are produced by the thyroid follicular cells. However, the majority of T<sub>3</sub> is formed in peripheral tissues, such as the kidneys and liver, following deiodination of T<sub>4</sub> by the enzyme 5'-iodothyronine deiodinases type 1 and 2 (Bianco et al. 2002; Rivas and Naranjo 2007; Smith et al. 2002). However, when an individual's energy demands exceed its energy intake, T<sub>4</sub> conversion to T<sub>3</sub> is considerably decreased, thus lowering the concentration of available T<sub>3</sub> (Chatzitomaritis et al. 2017). Where food availability is not limited, T<sub>3</sub> concentrations are upregulated to meet energy demands during important periods such as molting, gonadal development,

pregnancy, somatic growth, and reproductive behaviors (Behringer et al. 2014; Gesquiere et al. 2018; Gobush et al. 2014).

## Thyroid Hormone Receptors and Cognition

Following their production and secretion into the bloodstream, both T<sub>3</sub> and T<sub>4</sub> bind to a variety of plasma proteins, with only a small percentage of T<sub>3</sub> and T<sub>4</sub> found in free form (Smith et al. 2002). Once THs reach their target organs (e.g., the brain), they enter the target cells through passive diffusion or a transport mechanism where further protein binding for intracellular transport occurs (Lazar 1993; Morte et al. 2010). Similar to GR and MR, thyroid hormone receptors (TR) are found throughout the central nervous system and brain, especially within the hippocampal area responsible for cognitive function (Bernal 2002). Here, TR are encoded by two genes, namely, TR $\alpha$  and TR $\beta$ , each of which has a number of isoforms (Lazar 1993; Rivas and Naranjo 2007). Following the binding of T<sub>3</sub> to TR within the brain, the expression of target genes by co-activators is activated. Both the TR and co-activators are responsible for a range of transcription modifications; as a result of this functionality, TH effects can be cell, tissue, and organ specific (see Cheng et al. 2010 for a review). Here, the TH are then responsible for accelerating the myelinating process while influencing cell migration, differentiation, and maturation. Additionally, TH control over the expression and transcription of various genes can regulate various forms of synaptic plasticity and memory formation (Rivas and Naranjo 2007). Although many of the TH actions are genomic in nature, they can also exert non-genomic, TR-independent activities by acting at the plasma membrane level; this includes the regulation of the ion channels and the activation of numerous signalling cascades (Davis et al. 2005).

## Dose-Dependency

Thyroid dysfunction, whether through trauma, disease, neoplasm, or hypo-/hyperthyroidism, and the resulting alterations in cell structure, function, and behavior, *have* shown the importance of THs in the development and maintenance of

neuronal systems and cognition (Erlanger et al. 1999; Smith et al. 2002). It is especially the alteration in hippocampal structure that is responsible for cognitive and behavioral deficits (Akaike et al. 1991; Alzoubi et al. 2009). In individuals with hypothyroidism, a decrease in T3 levels leads to a lower expression of certain genes, specifically positively regulated genes, while the expression of negatively regulated genes increases. The mechanisms involved in these effects of hypothyroidism include (i) the potential loss of T3 signaling and TR transactivations, as well as (ii) the intrinsic activity of unliganded TR, which are responsible for the repression of positive genes and the enhancement of negative genes (Gil-Ibañez et al. 2013) that lead to a reduction in neurite growth, synaptogenesis, and dendritic elaborations (Thompson and Potter 2000). As a result, deficits in attention, visual perception, executive function, memory, and emotions have been recorded (Grigorova and Sherwin 2012; Wahlin et al. 1998). However, the degree of deleterious effects of low T3 concentrations on cognitive function depends on the magnitude, duration, and timing of such a decrease. This has been highlighted in a number of studies which show contrasting results on the effect of low T3 concentration on cognition (Ritchie and Yeap 2015). Although hyperthyroidism can lead to a number of cognitive function deficits, this is usually to a lesser extent than observed in hypothyroidism. Similar to the latter, chronically elevated T3 levels will lead to impaired attention, memory, visuospatial abilities, and motor speed (see Bégin et al. 2008 – Table 5). In healthy humans, however, an increase in T3 levels led to no significant impairment of cognitive function and could even lead to improved verbal and visual processing (Kathmann et al. 1994; Münte et al. 2001).

## Reproductive Hormones

### Estrogen

Estrogens, a group of neuroactive steroid hormones, are primarily known as female reproductive hormones responsible for the development

of primary sexual characteristics and the induction of secondary sexual characteristics and eliciting pituitary response during pregnancy; while in males these hormones modulate libido, erectile functions, and spermatogenesis (Giese 2003; Schulster et al. 2016). Three endogenous forms of E are produced during various life stages; estrone (E1) primarily synthesized during menopause, the most prevalent and highly lipophilic form 17- $\beta$ -estradiol (E2), and estriol (E3) synthesized during pregnancy. Two types of E receptors (ER), ER $_{\alpha}$  and ER $_{\beta}$ , have been found in regions of the brain, particularly the hippocampus and amygdala, associated with memory, learning, and cognition (Gasbarri et al. 2012; Genazzani et al. 2000; Gundlah et al. 2000; Shughrue and Merchenthaler 2000). The abundance, tissue localization, and expression of ER demonstrate species-, intra-, and sex-specific differences (McEwen and Alves 1999; Muramatsu and Inoue 2000). Due to the general association of these regions with learning- and memory-related processes, E are believed to have modulatory effects on several neurotransmitter systems; in this regard the decrease in estrogen concentrations could increase the vulnerability of brain cells, particularly dendritic spine densities, to damage and degeneration (McEwen and Alves 1999; Woolley and McEwen 1994). Further studies found that, indeed, E can regulate neuroplasticity and neuronal excitability by both genomic and non-genomic pathways (Acconcia and Kumar 2006), in a time- and dose-dependent manner for a variety of mammalian models (Barha and Galea 2010). Additionally, E was found to have neuroprotective effects on the brain through transcriptional mechanisms that limit cell death (Hilton et al. 2004), as well as other receptor-mediated and non-receptor-mediated pathways (McCarthy 2008). A number of studies investigating gonadal hormone therapy, with particular applications in aging or memory-impaired individuals, found that E2 improves nonspatial memory of rats (Frick et al. 2002), initiated spatial learning and memory consolidation of meadow voles (Galea et al. 1995), and enhanced cognitive performance of *Rhesus Macaques* (*Macaca mulatta*, Hao et al. 2007). Though recent reviews

by Korol (2004) and Chisholm and Juraska (2013) suggest that several factors must be considered in determining the exact effect E has on cognition, some studies demonstrated that E impairs rather than improves cognitive performance (Fernandez and Frick 2004; Holmes et al. 2002), while another study found no significant effect during specific tasks (Galea et al. 2001).

### Testosterone

Testosterone (T), a steroid hormone from the androstane class, is secreted primarily by the Leydig cells of testicles in males. Testosterone is also secreted, though to a lesser extent, in the ovaries of females and the adrenal glands of both males and females (Appelgren 1969; Baird et al. 1969). Testosterone is predominantly responsible for the development of primary and secondary sexual characteristics, as well as a multitude of other peripheral functions (Bain 2007; Lee et al. 2009; Mooradian et al. 1987; Tuck and Francis 2009). Testosterone and its metabolites are also the primary determinants of both sexual and social behavior in male and female individuals, due to the interaction between peripheral and central actions of the hormones (Baucom et al. 1985; Pinna et al. 2005). Androgen receptors are not only found in brain regions crucial for learning and memory but may also modify the physiology and function of these regions by altering the synaptic density of the neurons (Janowsky 2006). However, there are multiple T mechanisms, such as T aromatization or neuronal biosynthesis from endogenous cholesterol, that make it difficult to discern the mechanism of action that leads to the enhancement of neural tissue and, by extension, the improvement of cognitive performance (Mukai et al. 2006; Naghdi et al. 2001; Roselli et al. 2009) (Davey and Grossmann 2016; Frye et al. 2001; Sak and Everaus 2004). Testosterone-related enhancement of cognitive functioning appears to be age-specific, sexually dimorphic, and dose-dependent (Goudsmit et al. 1990; Roof 1992; Spritzer et al. 2011), though androgen administration to specific regions of the brain also determines whether learning and memory performance is enhanced or impaired (Edinger and Frye 2004).

### Progesterone

Progesterone (P) and its neurosteroid derivative, allopregnanolone (AP), are primarily secreted by the ovaries and the placenta during pregnancy and synthesized in smaller amounts by the adrenal glands in both males and females (Barros et al. 2015). There are also mechanisms that exist within the central nervous system, neurons and glia, with the ability to biosynthesize AP and a neurotransmitter-type derivative, neuroprogesterone (Chabbert-Buffet et al. 2000; Schumacher et al. 2001, 2014; Sripada et al. 2013). Two isoforms of P receptors, P<sub>A</sub> and P<sub>B</sub>, are co-expressed in most tissues and widely distributed in various regions of the brain responsible for memory consolidation and learning, though some are exclusively estrogen-inducible (Alves et al. 2000; Schumacher et al. 2014). The majority of studies that investigated the neuroprotective effects of administered P or synthesized derivatives on cognitive performance to date have used animal models that are aged, have undergone gonadectomy, or mimic certain cognitive dysfunctions or age-related neurodegeneration diseases (Singh and Su 2013). Though P has generally preserved cognitive performance in such compromised cases (Cutler et al. 2007), a few studies have shown no effect (Chesler and Juraska 2000), or even a negative effect on cognitive performance/processes, such as long-term potentiation (Foy et al. 2008). Although the general consensus varies, many studies concur that P and AP differentially enhance cognition depending on age (Lewis et al. 2008), the timing of the treatment (Harburger et al. 2008), and the type of progestin and dosage administered (Djebaili et al. 2004). In addition, combined administration of both estrogen and progesterone may improve cognitive performance differentially in aged females (Gibbs 2000), which has shown to be dependent on menstrual cycling in females (Kromrey et al. 2015).

### Nonapeptide Hormones

Two related nonapeptide hormones with unrelated functions, oxytocin (OT) and vasopressin (VP), may influence cognitive function, memory

formation, and even protection against age-related impairments in rodents and nonhuman primates (NHPs). Oxytocin and arginine vasopressin (AVP), the common mammalian form with the exception of *Suinae*, are synthesized predominantly in magnocellular neurons of the paraventricular and supraoptic nuclei of the hypothalamus, respectively, and extend to the posterior pituitary gland or to sites within the central nervous system (Buijs 1990; Insel 1992; Lee et al. 2009; Swaab et al. 1975). The general peripheral functions of OT include reproductive effects such as uterine contractions, penile erections, and other facilitative effects on sexual behavior, as well as effects on social behaviors such as grooming, maternal care, pair-bonding, and others (Argiolas and Gessa 1991; Burbach et al. 2006; Insel and Shapiro 1992; Jarcho et al. 2011).

### Oxytocin

Oxytocin has been previously described as a neurotransmitter within the brain that has the potential to influence neuronal excitability (Buijs 1983; Kovacs and Telegdy 1982), with priming abilities that rewire neural networks to influence behavior (Ludwig and Leng 2006). Early evidence of this was determined by the presence of an OT receptor and OT receptor mRNA expression within various regions of mammalian brains involved with memory consolidation, learning, and social cognition (Baribeau and Anagnostou 2015; Chang et al. 2013; Gimpl and Fahrenholz 2001; Yoshimura et al. 1993). The localization of OT receptors, and by extension the levels of OT, throughout the brain shows species-, intra-, and sex-specific differences in distribution and concentrations; this can be influenced by species-specific social organization or structure (Beery et al. 2008; Insel and Shapiro 1992; Rosenblum 2002) and is susceptible to change throughout development and aging (Arsenijevic et al. 1995; Tribollet et al. 1992; Yoshimura et al. 1993). A plethora of studies have investigated the effects of OT within the brain of primates and humans, and these studies demonstrated that OT is important for the acquisition of social memory and maternal memory consolidation (D'cunha et al.

2011; Ferguson et al. 2002) especially in cases where OT levels were significantly low, resulting in social memory deficits (Ferguson et al. 2000). However, some results seem to indicate that OT may selectively facilitate social cognition rather than act universally (Bartz et al. 2010; Heinrichs and Domes 2008).

### Vasopressin

Though VP principally acts as an antidiuretic hormone within the kidneys, AVP is also responsible for vasoconstriction and blood pressure regulation in peripheral tissues and acts synergistically with corticotropin-releasing hormone to regulate pituitary adrenocorticotrophic hormone secretion during stress (de Bree and Burbach 1998; Ma and Lightman 1998; Robertson 2001; Strupp 1984). Arginine vasopressin receptors are separated into three groups according to the intracellular mechanisms employed: V1a and V1b and V2 (Egashira et al. 2009; Hammock et al. 2005). The type, distribution, and abundance of AVP receptors within various regions of mammalian brains differ between species, within species and individuals, and are often sexually dimorphic (Hammock et al. 2005; Young et al. 1999). Prefatory studies in the 1970s and early 1980s tested AVP's effects on memory consolidation and retrieval; the results suggested that AVP and its analogs may have the ability to prevent or reverse amnesia (van Wimersma Greidanus et al. 1983). With particular interest in aging or aged individuals, AVP, its analogs, and to a lesser extent lysine vasopressin have been found to improve cognitive performance, enhance learning and memory behavior, and prevent memory function deficits caused by neurotoxic peptide-induced loss of memory (Bartus et al. 1982; Buresova and Skopkova 1982; Jing et al. 2009; Pan et al. 2010).

### Cross-References

- [Cognition](#)
- [Comparative Cognition](#)
- [Corticosterone](#)
- [Endocrine System](#)

- ▶ [Estrogen](#)
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- ▶ [Hippocampus](#)
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- ▶ [Short-term Memory](#)
- ▶ [Stress](#)
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## Hormones and Face Preferences

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### Introduction

Preferences for a particular face are unique and personal; however, there are overall trends in what men and women find attractive in a face and their preference for any given face to look more masculine or feminine. Face shape, facial coloration, brow ridge, cheekbone placement, and jaw line all contribute to the overall look of a face and whether that face is perceived as masculine, feminine, and attractive in general. A masculine face is typically characterized by a more prominent nose and brow ridge, as well as a wider and more angular chin or jaw line. Conversely, a feminine face has a softer brow ridge and more rounded jaw line. Changes to these aspects of the face effect whether the face is perceived as masculine or feminine. While these preferences are personal, both men and women exhibit changes in facial preferences associated with changes in hormone levels. These preferences change for women during the natural menstrual cycle and for men with fluctuations in testosterone as well as with the woman's changing hormonal profile.

### Theoretical Background

The face preferences of women and men change during the menstrual cycle and with fluctuating hormone levels (e.g., Jones et al. 2008; Penton-Voak et al. 1999; Penton-Voak and Perrett 2000; Puts et al. 2013; Roberts et al. 2004; Welling et al. 2007). These preferences may shift towards more masculine or feminine facial characteristics or be exhibited as more attraction during a particular phase. While it is known that these face preferences change across the menstrual cycle, the exact mechanisms and reasons for these shifts are

unknown. However, several theories predict possible preference shifts. For women, one such theory predicts that during ovulation, when fertility and likelihood of conception is highest, women may show increased attraction to male faces that exhibit cues to heritable immunity to disease (Folstad and Karter 1992). The theory suggests that women should show a preference for male features that signal her offspring could inherit the benefits of immunocompetence. However, these benefits can only be gained if conception occurs following copulation. Therefore it is expected that women should show a preference for immunological competence when conception is most likely, during the follicular phase. (Gangestad and Simpson 2000; Gangestad et al. 2004; Thornhill and Gangestad 2008). This theory would then predict an increased attraction to masculine facial features during the follicular phase of the menstrual cycle. Indeed, masculine traits and ratings of men's facial masculinity are positively associated with estimates of good health and signal indirect benefits to the woman of heritable immunological competence for her offspring (e.g., Gangestad et al. 2004; Johnston et al. 2001; Penton-Voak et al. 1999; Penton-Voak and Perrett 2000). However, the masculine features associated with immunocompetence are also associated with increased testosterone levels and dominance. While a preference for a masculine face might confer indirect benefits during high fertility, it may also be costly due to decreased paternal investment. Less masculine faces confer direct benefits of paternal investment and familial support. Therefore, there exists a tradeoff between good genes conferred through masculine facial preferences and high parental investment for more feminine faces (Gangestad and Simpson 2000). Due to this tradeoff, it would benefit women most to modulate their mate facial preferences depending on likelihood of conception (Fink and Penton-Voak 2002; Gangestad and Simpson 2000). When conception is not likely and the body is preparing for pregnancy, such as during the luteal phase of the menstrual cycle, women may then exhibit a stronger preference for more feminized faces that characterize benefits such as material support and parental investment.

Consequently, the theory suggests that changes in facial preferences across the menstrual cycle might be due to a mixed mating strategy whereby a female might choose a primary partner with low facial masculinity for direct benefits of paternal care, but then may also copulate with males with high facial masculinity when most fertile for indirect benefits of immunocompetence (Folstad and Karter 1992). For males, changes in facial preferences across the female menstrual cycle more likely have to do with gaining a competitive advantage. Unlike other mammals, ovulation in human females is not readily obvious. Cues to fertility and ovulation are largely hidden, which creates an adaptive issue for males (Thornhill and Gangestad 2008). Therefore, the males that are able to detect subtle cues to ovulation would have a significant advantage in being able to mate with the fertile females (Puts et al. 2013). It would be beneficial, then, for males to exhibit a preference for female faces when they are in the fertile phase or near ovulation so that they can focus their mating efforts. These theories may help to explain the current findings on why men and women experience facial preference shifts.

### Female Face Preferences and Hormones

During a woman's menstrual cycle, there are fluctuations in hormones that dictate fertility. Across the normal menstrual cycle (i.e., no hormonal contraceptives), a woman's preferences for a masculine or feminine faces change. The cycle can be split into the follicular, luteal, and menstrual phases. During the follicular or fertile phase, estradiol levels begin low and steadily increase, peaking just prior to ovulation. Progesterone levels are low in this phase and remain steady until ovulation has occurred. When ovulation occurs, estradiol levels temporarily decrease. During the luteal phase, the corpus luteum forms at the site of ovulation and causes estradiol and progesterone to increase and peak mid-phase before sharply decreasing just prior to menstruation if pregnancy has not occurred. If fertilization and implantation do not occur, the uterus sheds its lining and menstruation occurs.

During the follicular or fertile phase of their menstrual cycle, women are more likely to prefer and choose a face with more masculine features compared to other phases of the cycle (e.g., Johnston et al. 2001; Jones et al. 2008; Penton-Voak et al. 1999; Penton-Voak and Perrett 2000; Welling et al. 2007). This finding is in line with the theory that predicts women should prefer more masculine faces when conception is most likely. The exaggerated masculine features indicate higher testosterone and are associated with characteristics that signal immunological benefit to offspring when conception is most likely (e.g., Folstad and Karter 1992; Gangestad and Simpson 2000). However, when conception is not likely, this effect is not seen. During the luteal phase or menstrual phase when fertility is low, women prefer more feminized male faces (Johnston et al. 2001; Jones et al. 2008; Perrett et al. 1998). The feminized male faces are positively associated with personality attributions such as being perceived as more cooperative and a good parent, and these attributions correlate with actual behaviors (Berry and Wero 1993). Additionally, face preferences can change when the face is being judged as attractive for a long-term versus short-term relationship. When conception risk is high (i.e., follicular phase or near ovulation), masculine faces are preferred for short-term relationships. However, when women judge attractiveness for long-term relationships, preferences remained constant preferring more feminized faces. These cyclic changes in preferences are absent in hormonal contraceptive users, whose fertility is not changed with the menstrual cycle (Folstad and Karter 1992). Yet conception risk cannot be the mechanism for the change in facial preferences. There must be a hormonal mechanism driving the change in behavior and preferences across the menstrual cycle. Indeed, lower progesterone levels, such as during the follicular phase of the menstrual cycle, are associated with preferences for more masculine faces (Jones et al. 2005a, b). Conversely, estrogen levels alone are not associated with preference changes across the menstrual cycle (Puts 2006; Jones et al. 2005a, b). The change in progesterone level seems to be an important mechanism for the change in face

preferences, yet it is not the only hormonal mechanism at work. Like progesterone levels, testosterone levels fluctuate during the menstrual cycle. Testosterone levels start off relatively low following menstruation then slowly increase and peak near ovulation before steadily declining again. When women's testosterone levels are highest around ovulation, they show the strongest preference for masculine faces (Welling et al. 2007). Importantly, this behavior change associated with testosterone level is independent of progesterone or estrogen levels. This suggests that both progesterone and testosterone are involved in the mechanism for preference changes across the menstrual cycle.

It is not just changes in preferences for attraction that fluctuate during the menstrual cycle. Preferences for facial resemblance to self also vary across the menstrual cycle. Facial resemblance or other facial cues of kinship can signal direct benefits such as support from family when raising children. However, these same cues can signal decreased indirect benefits such as inbreeding and less genetic variability for the offspring (DeBruine et al. 2008). These may be some of the reasons contributing to the preference changes for facial resemblance seen in women during the menstrual cycle. Women show a greater preference for self-resembling faces when they are in the luteal phase, when fertility and conception risk are low. This preference for self-resembling faces is not present during the fertile follicular phase (DeBruine et al. 2005). The preference for self-resemblance is positively associated with progesterone levels, which suggests that women may increase their preference for kinship cues when the body is preparing for pregnancy and they might need familial support the most.

Similarly, facial cues to health can vary across the menstrual cycle. Women show a greater aversion to faces that signal poor health and illness (e.g., pallor) during the luteal phase when progesterone level is high and the body is preparing for pregnancy (Jones et al. 2005a, b). This effect is particularly pronounced when women are judging male faces on attractiveness for short-term relationships. The change in attraction to faces with cues to high or low health is associated with the

change in progesterone level. This again suggests that women may have a preference for faces with cues to good health when the body is preparing for pregnancy and the cost of becoming ill is high.

## Male Face Preferences for Females

Women are not the only ones who experience facial preference shifts during the menstrual cycle. Men too show preference shifts during the female menstrual cycle and with their own fluctuating hormone levels (e.g., Probst et al. 2016; Puts et al. 2013; Roberts et al. 2004; Welling et al. 2008). While women experience those shifts due to their own changing hormone profiles, men do not have a monthly cyclic change in hormone levels. Therefore, the mechanism by which men's facial preferences change is both indirect through the female's changing hormones and direct through their own. In many nonhuman mammals, when the female is fertile near ovulation, she will show changes in appearance, smell, and behavior (Gangestad and Thornhill 2008). These changes signal to the male that the female is most fertile and receptive, and in turn the male makes behavioral changes to increase mating efforts. If ovulation was readily apparent in humans, this could explain the male shift in facial preferences. However, in humans, cues of ovulation are not so obvious or able to be consciously perceived. Yet, subtle changes in facial shape or color may be detectable subconsciously. Indeed, when men view photographs of women's faces in the fertile window versus the luteal phase, they judge the women in the fertile phase as more attractive (Puts et al. 2013; Roberts et al. 2004; Welling et al. 2007). Additionally, when the face shape characteristics of different cycle phases are isolated and made into average composites for either the follicular or the luteal phase, men again rate women's faces associated with follicular phase as more attractive (Bobst and Lobmaier 2012). The subtle face shape changes are theorized to be due to changes in progesterone. Indeed, the changes in progesterone are negatively associated with facial attractiveness ratings (e.g., Puts et al. 2013; Roberts et al. 2004).

In other words, men rate women's faces as more attractive when progesterone is low, such as during the follicular phase. Estradiol alone does not show these same effects, likely because it does not differ significantly between the late follicular and luteal phases. However, the ratio of women's testosterone-to-estradiol ratio does play a role. Men rate women with a low testosterone-to-estradiol ratio and low testosterone as having more attractive faces (Probst et al. 2016). These indirect mechanisms of preference shifts are dependent upon the female's changing hormones. However, men's own testosterone levels can affect their facial preferences as well. Much like women, testosterone also plays a role in changing face preferences. When men's salivary testosterone is relatively high, they judge attractiveness of women's faces that have been feminized as more attractive. In other words, they are more attracted to femininity when their testosterone levels are high compared to when they are low (Welling et al. 2008).

## Conclusions

Both women and men experience shifts in their facial preferences. For women, the mechanism by which these shifts happen is more direct and linked to her changing hormones during the menstrual cycle. For men, these shifting preferences can be both direct through their own changing hormone levels, or indirect and dependent on the woman's hormonal shifts. Overall, women show a preference for more masculine faces when they are in the fertile phase and near ovulation compared to other phases of the menstrual cycle. During the fertile phase, progesterone levels are low and testosterone levels are at their peak. Conversely, in their non-fertile phases, when progesterone levels are high and testosterone levels are low, women exhibit preferences for faces that are more feminized. The exact reason for these preference shifts across the menstrual cycle is not known; however, several theories support these findings. One possible theory is that women show increased attraction to masculine faces near ovulation because masculine faces signal heritable

immunity to disease. This preference may happen during ovulation because it is when conception risk is highest. When conception is not likely, such as during non-fertile phases, women should show a preference for more feminized faces which are associated with greater parental investment. This type of dual mating strategy would allow the woman to choose a primary partner with a more feminized face associated with good parental investment, but occasionally choose to mate with more masculine faced men during times when conception is likely to confer indirect benefits of good genes and health to her offspring. Men show a preference for women who are in the fertile phase of the menstrual cycle over those who are in non-fertile phases. This corresponds to a preference for low levels of progesterone and a low testosterone-to-estradiol ratio. Additionally, men are most attracted to femininity of faces when their own testosterone levels are highest. These preference shifts are likely due to an adaptive advantage for men to pick up on subtle cues of fertility. Males who are able to detect fertile females then have the advantage of focusing their mating efforts towards only females likely to conceive and thus pass along the male's genetic information.

## Cross-References

- ▶ [Estrogen](#)
- ▶ [Estrous](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Extra-Pair Copulation](#)
- ▶ [Family Resemblance](#)
- ▶ [Female Choice](#)
- ▶ [Fertility](#)
- ▶ [Healthy Mate Hypothesis](#)
- ▶ [Hormones and Behavior](#)
- ▶ [Inbreeding Depression](#)
- ▶ [Intersexual Selection](#)
- ▶ [Mating](#)
- ▶ [Mating Effort](#)
- ▶ [Parental Investment](#)
- ▶ [Paternal Behavior](#)
- ▶ [Peak Fertility](#)
- ▶ [Progesterone](#)

- [Psychopharmacology of Sex Steroids](#)
- [Reproductive Fitness](#)
- [Sexual Dimorphism](#)
- [Sexual Selection](#)
- [Testosterone](#)

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## Horse

- [Equine Communication](#)

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## Horse Gait

- [Perissodactyla Locomotion](#)



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## Horse Gaits

► [Equine Locomotion](#)

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## Horse Locomotion

► [Equine Locomotion](#)

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## Horseback Riding

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### Synonyms

[Competition](#); [Equestrianism](#); [Racing](#); [Recreation](#); [Riding](#); [Skills](#); [Techniques](#); [Trail riding](#); [Training](#)

### Definition

The sport, recreation, or activities in riding horses.

### Introduction

Horses have been an integral part of human history and progress in diverse ways throughout history. A popular pastime between humans and horses is horseback riding. A variety of activities and lifestyles are used in horseback riding, and riders are trained in various disciplines and styles of riding. Each type of horseback riding incorporates unique skills and equipment for pleasure, sport, and recreation. The two main styles of horseback riding are English and Western. Each style of riding includes diverse activities for riders, which are used for competitions and pleasure. In addition to English and Western style, horseback riding also includes racing, rodeo, trail riding, vaulting, and therapeutic riding.

## English Style

English horseback riding has endured throughout history and includes several diverse activities and competitions. Although most English style riding activities consist of the use of a flat saddle and reins are controlled by both hands, each English riding activity has a unique style, purpose, and trained skills. Horseback riding consisting of English style activities includes dressage, show jumping, hunter jumping, eventing, and polo, as well as flat class competitions (Driscoll 2019; Extension Campus 2019).

Dressage, which is noted as a classical form of training and horseback riding, can be traced back to the ancient Greeks of the fourth century BC, although its French name was not coined until the eighteenth century (Crossley 1987). The word *dressage* is derived from the French verb *dresser*, which means to train or adjust (Crossley 1987). The purpose of modern dressage competitions is to evaluate the horse's training, which increases in difficulty with the progression of training (Extension Campus 2019). The areas of evaluation in dressage competitions include the horse's obedience and harmony with the rider, transitions between movements, precision, and smoothness while completing a prescribed pattern of movements (Extension Campus 2019). Dressage is also a popular event in the Olympics and is compared to ballet as the horse is performing to a series of movements choreographed to music (Driscoll 2019).

Show jumping is a popular competitive equestrian sport. The earliest historical descriptions of show jumping can be traced back to the eighteenth-century French cavalry (Smith 1987), which influenced international popularity and competition. In show jumping events, the horses are specifically trained to jump large jumps within a specific time limit without knocking down the jumps or refusing to make the jumps (Extension Campus 2019). If all of the horses in the competition successfully complete all of the jumps, the horse with the fastest time will be declared the winner (Extension Campus 2019). Show jumping is also a popular event in the Olympics.

Hunter jumping is one of the earliest forms of horseback riding, which has a rich history in England as part of fox hunting, and it is considered a tradition in British culture (Clayton 1987). The role of the horse in early hunter jumper competitions was to be able to gallop and jump fences and ditches without hesitation in pursuit of the fox (Clayton 1987). Hunter jumping has also been combined with racing activities in which racecourses are designed like riding in a country setting and includes streams, fallen logs, and other natural elements which the horses are required to jump (Driscoll 2019). In most hunter jumper competitions, hunters are judged on manners, quality and ease of gaits, and safety over fences (Extension Campus 2019).

Eventing is an equestrian triathlon competition, which can trace its development to the training of military horses (Extension Campus 2019). This type of horseback riding competition includes elements of dressage, show jumping, and the speed and endurance of hunter jumping (Pontifex 1987). Eventing is a rigorous form of horseback riding and competition that tests the abilities and athleticism of the horse and rider, and it is also a popular event in the Olympics.

Polo is a horseback riding activity that originated in China more than 2000 years ago (Macgregor-Morris 1987). Polo gained in popularity in India and England before becoming an international sport and competition (Macgregor-Morris 1987). In the game of polo, four-person teams of horses and riders use a stick called a mallet to hit a ball through goal posts for a period of 7 min known as a chukker (Extension Campus 2019). Polo is a fast moving sport, and most polo players ride different horses for each chukker played in a competition (Extension Campus 2019).

Flat class horseback riding is an English activity that does not include jumping. Flat class competitions include walking and trotting, and horses are evaluated on their manners and responsiveness to the rider, as well as the quality of their gaits (Extension Campus 2019). This type of horseback riding is popular because it includes many different types of riders and horses of diverse breeds, skills, and abilities.

## Racing

Racing horses was also a part of the rich history of Ancient Greece, and it was included as an Olympic event (Driscoll 2019). Although most cultures engaged their horses in racing, it was England who introduced Thoroughbreds to the sport, and it became a popular pastime for the aristocracy (Driscoll 2019). The Thoroughbred was developed through selective breeding in seventeenth-century England, but modern Thoroughbred breeding and racing is an international industry (Condry 1987).

The first official Thoroughbred race in the United States took place in 1873 in Saratoga Springs, New York, but racing became more popular in Kentucky, host of the famous Kentucky Derby at Churchill Downs, which was established in 1883 (Driscoll 2019).

The equipment used in horse racing is similar to other English riding activities. Racing saddles are very lightweight, and the riders, known as jockeys, must also maintain a certain weight so that the horse's speed is not inhibited by excess weight.

## Western Style

Western style riding is commonly thought of as the "cowboy" way, but this type of horseback riding also includes many diverse activities. Unlike English riding saddles, Western saddles are larger and heavier, and many saddles also have a horn on the front for various riding activities. Unlike English style in which riders use reins in both hands, Western style riders typically use reins in one hand to accomplish skills and tasks (Driscoll 2019). Western horseback riding includes western pleasure, reining, and team penning (Extension Campus 2019). Other Western horseback riding activities may also include steer or calf roping, as well as other rodeo activities, such as barrel racing or pole racing (Driscoll 2019).

Western pleasure horseback riding is judged on the horse's ability to perform required gaits of riding, such as a walk or a jog, in a quiet and enjoyable manner (Extension Campus 2019).

Reining and team penning are popular Western horseback riding activities that can also be included in rodeo activities. Reining competitions evaluate the horse's response as controlled by the rider while performing a set pattern that includes various skills such as spinning turns and sliding stops (Extension Campus 2019). Team penning is a timed competition in which a team of horseback riders must separate specific cattle from a herd and hold them in a penned area (Extension Campus 2019).

Roping events, such as steer or calf roping, exhibits the horse's ability to track a running calf or steer, allowing the rider to lasso the animal and temporarily restrain it (Extension Campus 2019). In competitions, the team that most quickly ropes the animal, dismounts, and ties three of the animal's legs together, wins the event (Extension Campus 2019).

## Rodeo

Rodeo is a competitive type of Western horseback riding that includes several events and activities, which is based on skills that cowboys need to perform their jobs on the range and large ranches. Popular rodeo activities, such as bareback or saddle bronc riding in which the rider tries to stay on a bull for 8 s and calf roping to catch animals for branding, are often included in rodeos (Extension Campus 2019). Barrel racing demonstrates the speed and quickness of horses as they race around barrels placed at opposite ends of the arena in a cloverleaf pattern (Extension Campus 2019). Pole bending is a horseback riding competition in which the rider must weave the horse in and out of six tightly spaced poles. Although it was originally known as a "cowboy" style of riding, the rodeo is a popular international event, and it officially became part of the Olympics in 2002 (Driscoll 2019).

## Trail Riding

Trail riding is one of the most popular disciplines in horseback riding, which is open to all riders and breeds of horses, as well as a way to connect with

nature and other horse enthusiasts (Extension Campus 2019). Additionally, trail riding is a non-competitive, recreational activity that can include English or Western equipment and styles of riding (Driscoll 2019). In trail riding competitions, the test includes the horse's ability to safely, calmly, and willingly negotiate obstacles normally encountered on a trail, which may include walking over a bridge or opening and closing a gate (Extension Campus 2019).

## Vaulting

Vaulting is an activity in which riders perform movements on and around the horse (PATH Intl 2019). The activities included in this type of horseback riding are similar to movements in gymnastics and dance and are performed in harmony with the horse (Extension Campus 2019). Interactive vaulting can also be a part of therapeutic riding, as it fosters teamwork, independence, and confidence, as well as introducing all gaits of riding in a short period of time (PATH Intl 2019).

## Therapeutic Riding

Historical sources also suggest that horses were viewed as healing or therapeutic for humans since the time of the early Greeks (Hallberg 2018; Battestella-Williams 2019). References to the healing and recovery processes using horses can be found in writings from ancient Greco-Roman times (Bachi et al. 2011; Battestella-Williams 2019), including Hippocrates, who believed that horseback riding provided a healing rhythm (Hallberg 2018) because it moves the body in a similar manner to a human gait, which helps improvement in balance, flexibility, and muscle strength (PATH Intl 2019). Lis Hartel, who was paralyzed from the knees down after contracting polio, is often considered the pioneer of therapeutic horseback riding (Hallberg 2018; Battestella-Williams 2019). Hartel won the silver medal for Denmark in the 1952 Helsinki Olympics (Bachi et al. 2011; Hallberg 2018; Battestella-Williams 2019). Shortly afterward, Hartel formed the first

therapeutic riding center in Europe for people with disabilities (Hallberg 2018; Battestella-Williams 2019). During the 1950s and 1960s, other rehabilitative riding programs were formed throughout the United Kingdom, the Netherlands, and Belgium (Hallberg 2018). Today, therapeutic horseback riding is used for diverse physical, physiological, and neurological symptoms. This type of horseback riding is typically known as *adaptive riding*, which refers to a nontherapy type of equine-assisted activity that includes horseback riding and horsemanship skills to students with disabilities or special needs and is sometimes used synonymously with the term “therapeutic riding,” (Hallberg 2018; Battestella-Williams 2019). Therapeutic riding is an activity working with horses with the purpose of contributing positively to the cognitive, physical, emotional, and social needs of individuals with special needs (PATH Intl 2019).

## Conclusion

Horseback riding is a very diverse recreational activity that many different levels and types of riders can enjoy. Additionally, there are many other types of activities that include horseback riding, such as vacations at dude ranches and various types of shows and attractions that feature horses.

## Cross-References

- Equestrianism
- Horseback Riding

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## Horses

- Equine Cognition
- Equine Sensory Systems

## Hospitalism

- Anaclitic Depression

## Hostile Behavior

- Aggression

## Hostility

- Benefits for Aggression in Humans

## Host-Parasite Interactions

### ► Cuckoo Brood Parasitism

## Hotshot

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## Definition

An attractive potential mate that garners both male and female attention which received a disproportionate percentage of copulations in a mating season.

## Description

While many species engage in mating rituals that advertise territory quality, parental care, or other tangible resources, several species engage in lek polygyny, whereby male animals aggregate on an arena or “stage” to engage in competitive displays (i.e., lekking) with the ultimate goal of securing female mates (Fiske et al. 1998). Most lekking species are birds (e.g., grouse, ruff, manakins, birds-of-paradise), although some mammals (e.g., waterbuck, some pinnipeds, and the topi), amphibians (e.g., bullfrogs), reptiles (e.g., marine iguanas), fish (e.g., cichlids), and insects (e.g., midge, ghost moth) also engage in lekking (Fiske et al. 1998).

Lekking represents a paradox because in lekking species, typically only one or a few males are successful at garnering a mate. Thus, if persistent female mate choice for particular traits exists, how can genetic diversity in lekking species be maintained, and how can choice of mates persists (Miller and Moore 2007)? In other words, how could lekking have evolved?

One hypothesis is the hotshot hypothesis (Beehler and Foster 1988). Unlike the female preference model (Bradbury 1981) or the hotspot model (Bradbury and Gibson 1983), the hotshot model is the only hypothesis attributing males as the driving force behind lekking behavior. According to this hypothesis, attractive males (hotshots) attract females via behavioral or morphological attributes. Other, less successful males cluster near the hotshots and are able to obtain more matings than they otherwise would had they displayed alone (Beehler and Foster 1988). According to the hotshot hypothesis, four factors can promote the development of a lek mating system: (1) male-male competition for dominance, (2) an initial inequality of mating success among males, (3) simple and conservative female mating patterns, and (4) secondary male reproductive strategies. Thus, the hotshot hypothesis downplays the importance of female mate choice based on male traits (contrary to the female preference model by Bradbury et al. 1985), and emphasizes the importance of male social dominance.

Experimental evidence supports the hotshot hypothesis. Jiguet and Bretagnolle (2006) manipulated little bustard leks using decoys to alter sex ratio and male phenotype. They found that hotshot males exist in this species (the decoys attracted both wild females and males) though they also found evidence for the female preference hypothesis (females preferred a particular lek size). Thus, hypotheses for the evolution of the lek mating system may not be mutually exclusive.

## Cross-References

- Female Choice
- Polygyny

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## Hotspot

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## Synonyms

Biodiversity hotspot

## Definition

A hotspot is a region which has at least 1,500 endemic vascular plants (>0.5% of the world's total) and has 30% or less of its historical habitat remaining.

## Introduction

The combination of anthropogenic activity and climate change threatens biodiversity (da Fonseca et al. 2007). Conservation of biodiversity is necessary to supply ecosystem services and to support their health and resilience (Millennium Ecosystem Assessment

2005). Despite being a global concern to sustain and protect biodiversity, biodiversity loss is increasing (Isbell 2010). The major causes of biodiversity loss include habitat fragmentation and destruction, overexploitation of selected species, hunting, introduction of exotic/invasive species, pollution, control of pests and predators and climate change (Barnosky et al. 2012).

Given the importance of biodiversity, conservation strategies are currently focused on maintaining and increasing it around the world (Wanjui 2013). Mayer (1988) introduced the term “hotspot” for the ten tropical forest areas with extraordinary number of endemic plant species and a high level of habitat loss. Identifying these hotspots highlight biodiversity rich areas under the acute threat and can focus research priorities for conservation (Myers 1988). A habitat is considered a hotspot if it meets two strict quantitative criteria. First, the region has to contain at least 1,500 vascular plants as endemics (>0.5% of the world's total) and second, it has to have 30% or less of its original vegetation (extent of historical habitat cover) remaining. A total of 35 regions across the globe now meet the hotspot criteria with each region holding at least 1,500 endemic plant species and each having lost 70% or more of its original habitat extent. These regions collectively hold not less than 50% of vascular plants and 42% of terrestrial vertebrates (amphibians, mammals, birds and reptiles) as endemics (Mittermeier et al. 2004). Combined, the 35 hotspots (listed in Table 1) once covered a land area of 23.7 million km<sup>2</sup>, or 15.9% of Earth's land surface, approximately the size of Russia and Australia together. However, as a result of habitat destruction in these areas over the past century, what remains of the natural vegetation in these areas is now just 2.3% of the world's land area (~3.4 million km<sup>2</sup>), slightly more than the land area of India.

In contrast with the terrestrial biome, data on the distribution and status of aquatic species are just beginning to be synthesized at a global scale. Roberts et al. (2002) have provided the first comprehensive global assessment of conservation priorities for coral reefs, an aquatic ecosystem, and brought much-needed attention to

**Hotspot, Table 1** List of global biodiversity hotspots

|                                            |                                               |
|--------------------------------------------|-----------------------------------------------|
| <b>A. Africa</b>                           | 20. Sundaland                                 |
| 1. Cape Floristic Region                   | 21. Wallacea                                  |
| 2. Coastal Forests of Eastern Africa       | 22. Western Ghats and Sri Lanka               |
| 3. Eastern Afromontane                     | <b>C. Europe and Central Asia</b>             |
| 4. Guinean Forests of West Africa          | 23. Caucasus                                  |
| 5. Horn of Africa                          | 24. Irano-Anatolian                           |
| 6. Madagascar and the Indian Ocean Islands | 25. Mediterranean Basin                       |
| 7. Maputaland-Pondoland-Albany             | 26. Mountains of Central Asia                 |
| 8. Succulent Karoo                         | <b>D. North and Central America</b>           |
| <b>B. Asia-Pacific</b>                     | 27. California Floristic Province             |
| 9. East Melanesian Islands                 | 28. Caribbean Islands                         |
| 10. Himalaya                               | 29. Madrean Pine-Oak Woodlands                |
| 11. Indo-Burma                             | 30. Mesoamerica                               |
| 12. Japan                                  | <b>E. South America</b>                       |
| 13. Mountains of Southwest China           | 31. Atlantic Forest                           |
| 14. New Caledonia                          | 32. Cerrado                                   |
| 15. New Zealand                            | 33. Chilean Winter Rainfall-Valdivian Forests |
| 16. Philippines                            | 34. Tumbes-Chocó-Magdalena                    |
| 17. Polynesia-Micronesia                   | 35. Tropical Andes                            |
| 18. Southwest Australia                    |                                               |
| 19. Forests of Eastern Australia (new)     |                                               |

marine hotspots. Coral reefs represent the highest point of marine diversity (Reaka-Kudla 1997) but are seriously threatened by human activities such as ocean warming and acidification (Hoegh-Guldberg et al. 2007). Data on marine habitats remain scarce compared to information on terrestrial ecosystems (Sala and Knowlton 2006), and the lack of knowledge about freshwater systems is even more pronounced. However, significant advancements are being made on aquatic biodiversity such as the Global Freshwater Biodiversity Assessment (Darwall et al. 2005) and the Global Marine Species Assessment, which includes comprehensive status assessments completed for reef-

forming corals (Carpenter et al. 2008). Although not entirely free from criticism (Marchese 2015), the hotspot approach has played an important role in conservation prioritization. Since it is not possible to conserve all biodiversity due to lack of resources, international conservation agencies have used it as the most effective approach to minimize species extinctions on a global scale. However, focusing all the conservation attention on biodiversity hotspots could create a disproportionate impact on the maintenance of biodiversity in other biomes. For instance, although desert ecosystems cover 17% of the world’s landmass and harbor surprisingly high biodiversity, they have not received substantial financial support for conservation actions (Durant et al. 2014). More integrative strategies, which enable the conservation of biodiversity from all habitats, can better identify areas of high conservation priority.

Conclusions

The impacts of biodiversity hotspots on conservation have been diverse and profound. For instance, several project prioritizing conservation strategies were well supported by the funding agencies across the globe after the introduction of the hotspot concept. Identifying hotspot regions will help provide primary data on marine, fungal, invertebrate, and microbial diversity to ensure the conservation of biodiversity in holistic way.

Cross-References

- [Birds](#)
- [Conservation](#)
- [Endemism](#)
- [Pollution](#)

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## Huddling

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## Synonyms

Aggregation; Clustering; Clumping; Crèching; Grouping; Group nesting; Nest sharing

## Definition

Huddling is defined as mutualistic social thermoregulation where two or more animals are in body contact, increasing body temperature (ectotherms), or decreasing costs of thermoregulation (endotherms). Typically, huddling occurs in resting (including sleeping) individuals, but

in penguins it can also occur in moving individuals (moving huddles of breeding emperor penguins and crèches of juvenile emperor and king penguins; *Aptenodytes forsteri* and *A. patagonicus*).

## Introduction

Individuals can save costs of thermoregulation by using torpor and hibernation and/or by huddling, i.e., two or more individuals are in body contact and share in the metabolic thermogenesis of each other (Gilbert et al. 2010). As all individuals benefit at the same time when huddling, this represents a form of mutualistic cooperation. Huddling permits individuals to minimize heat loss and thereby lower their energy expenditure (Ancel et al. 1997) and possibly allows them to reallocate the saved energy to other functions such as growth or reproduction (Gilbert et al. 2007a). Huddling is especially important when animals face high heat loss, such as small animals with a high surface-to-volume ratio, individuals living in cold environments, or individuals experiencing poor insulation during molt. Huddling conserves energy and allows individuals to reduce their metabolic rate, lower their food intake, decrease their body mass loss, reduce their water use, increase their growth rate, and maintain a more constant body temperature. Thus, huddling is adaptive, probably increasing survival probability and reproductive success.

## Where Does Huddling Occur?

Huddling occurs in both invertebrates and vertebrates. Examples for huddling insects are monarch butterflies (*Danaus plexippus*) forming large aggregations in their overwintering trees in Mexico (Brower et al. 2008). Here, thousands of butterflies huddle closely together, covering entire trees. Honey bees (*Apis mellifera*) are another example: here the entire colony huddles together at night and from autumn to spring, when it is too cold for them to go out and forage. Clusters of hundreds to thousands of overwintering spiders in

close body contact have also been observed, and the same phenomenon is known from ladybirds.

Huddling also occurs in ectotherm vertebrates. Many amphibians and reptiles including lizards and snakes share overwintering refuges, where they rest close to each other in body contact.

Among birds, huddling has been observed in at least 23 species (including partridges, quails, swallows, pelicans, cormorants, and penguins) (Gilbert et al. 2010). Juvenile emperor and king penguins and breeding emperor penguins form huddles from hundreds to thousands of individuals. In contrast to most other species, individuals in these huddles are not resting but moving, creating metabolic heat, moving the egg on their feet (emperor penguins) such that they get evenly warmed, and potentially competing for the warmest spots in the huddle. Huddling is also common in mousebirds (family Coliidae, living in southern Africa), which form groups of up to 20 individuals. Mousebirds huddle closely together when resting at night or during cold winter days (frost being possible in South Africa).

Huddling is very common in small mammals such as bats, shrews, and rodents (Canals et al. 1989). Many bat colonies are characterized by individuals huddling together. Many species of rodents huddle together during their resting period. Many species of shrews and rodents that are solitary during the breeding season become sociable afterward and then form huddling groups. Other small mammals such as social mongooses, for example, meerkats (*Suricata suricatta*), also huddle closely together in their den during their resting period. But huddling also occurs in large and very large mammals, such as resting wild boar (*Sus scrofa*), and southern elephant seals (*Mirounga leonina*) during their 1-month lasting molt when they renew their hair and their cornified epidermis, making them vulnerable to loss of body heat (Chaise et al. 2018). Last but not least, huddling is also very common in humans, for example, pairs sharing their bed, a huddle which will very quickly attract their children too. In humans, huddling is even recommended officially as a safety measure in emergency situations, such as evacuating a boat in lifeboats, or during alpine disasters.

## Benefits of Huddling

The function of huddling is to improve thermoregulation. Monarch butterflies create a beneficial microclimate by huddling closely together in trees (Brower et al. 2008). Inside the huddle, it is significantly warmer during the night and significantly cooler during the day, with higher relative humidity throughout the day. Thus, butterflies in the huddle get some protection from freezing, might reduce their rate of lipid burning, and lower their rate of water loss (Brower et al. 2008). In colonies of bees, the effects on the microclimate are even stronger, as they do actively increase the temperature by shivering, keeping the temperature between 27 °C and 34 °C. The workers rotate through the huddle from the outside (approx. 9 °C) into the warmer center.

In birds and mammals, huddling is regarded as a form of social thermoregulation to minimize heat loss and thereby lower energy expenditure (Gilbert et al. 2010; Scantlebury et al. 2006). Through huddling, birds can reduce their energy expenditure by 6 to 50% and mammals by 8 to 53%, depending on the efficiency of huddling (Gilbert et al. 2010), varying according to group size, ambient temperature, intensity of huddling, and species (Fig. 1).

Emperor penguins are well insulated, but huddling is the key energy-saving mechanism for males to endure their 4 months incubation fast during the Antarctic winter, when their energy expenditure is decreased by 16% (Ancel et al. 1997). The birds huddle at nighttime, and the maximum ambient temperature recorded inside a huddle was 37.5 °C (ambient temperature was −19 °C), which is close to the birds' deep body temperature (Gilbert et al. 2006). Without the possibility to huddle, reproductive success decreases significantly, as the period males can fast (incubate the egg without feeding) decreases and as such the percentage of males that desert their egg increases (Gilbert et al. 2007a).

Huddling permits newborn altricial mammals such as mice and rabbits to decrease their metabolic rate, to increase their growth rate, and to acquire faster their thermoregulatory capacities

(Gilbert et al. 2007b). In African striped mice (*Rhabdomys pumilio*), solitary sleeping individuals spend up to 50% more energy than individuals sleeping in huddling groups, and reduced costs of thermoregulation by huddling are believed to be the main reason for group-living in this species (Scantlebury et al. 2006). Theoretical models and empirical studies indicate that the optimal size for huddling groups is 4–6 individuals. Energetic benefits due to huddling are more prone in small animals, which are facing a higher heat loss due to a higher surface-to-volume ratio than in large animals. This can explain why huddling is more common in small than in large mammals. However, huddling can also occur in large species. Female southern elephant seals huddle in mud pools, allowing them to molt faster and with this to reduce the time spent fasting on land (Chaise et al. 2018). Huddling in sleeping groups at night might even have been an important adaptation allowing a naked species of apes, humans, to colonize areas outside of the tropics.

Small body size, poor insulation, and living in cold environments are factors increasing the benefits of huddling, thus favoring its evolution. Increased benefits in cold environments can also explain why many species of small mammals form huddling groups especially in winter. In sum, huddling allows ectotherms to increase body temperature and endotherms to reduce energetic costs of thermoregulation, possibly allowing them to reallocate the saved energy to other functions such as growth, survival, and reproduction.

## Costs of Huddling

Being in close proximity with conspecifics can be very costly in terms of the risk of getting infected by ecto- and endoparasites as well as by other pathogens. Bird nests, where chicks are huddling together, are often heavily infected by mites and fleas. Huddling rodents such as striped mice regularly change nesting sites, possibly to avoid the spread of ectoparasites. However, studies testing in how far huddling leads to an increased risk of getting infected by parasites and other pathogens are mainly missing.



**Huddling,**

**Fig. 1** Examples of endotherm species saving energy by huddling. Top: Huddle of thousands male emperor penguins during the incubation period at Dumont d'Urville. Inside the huddle, the temperature can reach  $37^{\circ}\text{C}$  despite the ambient temperature is  $-19^{\circ}\text{C}$ , reducing costs of thermoregulation, leading to a decrease of energy expenditure by 16%. (credit: CNRS/IPEV/DEPE). Bottom, infrared-recording from striped mice huddling together at night in a natural nest. Even in summer, night temperatures in the habitat of that species, the Succulent Karoo semidesert of South Africa, can go down to  $5^{\circ}\text{C}$ . Striped mice sleeping alone spend up to 50% more energy at night than striped mice sleeping in huddling groups. (credit: C. Schradin)



H

**Proximate Mechanisms of Huddling**

Individuals often aggressively defend territories and resources and keep a distance from each other, especially during the breeding season. However, to come into very close proximity to huddle, individuals must be nonaggressive toward each other and be attracted by each other. In many species that are solitary and aggressive during the breeding season, such as shrews and some species of voles, the behavior changes in the non-breeding

season: they become less aggressive and instead show amicable behavior toward conspecifics to which they are attracted. Thus, the cessations of aggression and instalment of amicable behavior together with being attracted either by each other or to the same resting place are essential mechanisms allowing huddling. Endocrine mechanisms associated with this include a decrease of reproductive hormones after the breeding season, especially of testosterone and progesterone. In species that are gregarious and form huddling groups also

during the breeding season (these groups typically consist of close kin such as family groups), neuronal networks in the brain allow for such a form of social organization. One mechanism that has been discussed here is the expression of the estrogen receptor  $\alpha$  in male rodents.

## Conclusion

Animals huddle together either to increase their body temperature above ambient (ectotherms) or to reduce the energetic costs of thermoregulation (endotherms). Huddling thus evolved when the benefits of improved thermoregulation were higher than the costs of reduced aggression (to enable proximity) and increased risk of infection. This depends on the body size, life history, and ecology of the species, explaining why huddling is more common in small species and during the cold non-breeding season.

## Cross-References

- [Adaptation](#)
- [Group Living](#)
- [Homeostasis](#)
- [Social Behavior](#)
- [Thermoregulation](#)

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## Human

- [Haplorhini](#)

## Human Approach Test

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## Synonyms

[Approach test](#); [Avoidance test](#); [Voluntary animal approach](#); [Voluntary approach test](#)

Animal's perception and response to humans are associated with the animal's species, experience with humans, nature of the interaction, motivational state, temperament, age, genetics, and can even be influenced by rearing environment conditions and prenatal stress levels (Claxton 2011; Sherwen and Hemsworth 2019; Slaney et al. 2018; Waiblinger et al. 2006). These key

components are determinants in establishing a human–animal relationship, which can be classified in three ways: negative, where the animal exhibits fear to humans and avoids its proximity or contact; neutral, where the animal manifest low levels of fear, but still avoids human contact; and positive, when there are no fear manifestations and the animal is confident with people (Claxton 2011).

In this context, the Human Approach Test is a task used to assess human–animal relationships and to monitor animal welfare. In laboratory animals, this test is also used to evaluate motivated behavior or anticipation towards rewards (Arhant and Troxler 2017; Augustsson et al. 2002; Dalla Costa et al. 2016; Ishiyama et al. 2019). Briefly, by recording the animal's reaction to a standing or approaching human, this test evaluates the latency, distance, and behavior of the animal towards a human. This test has variations depending on the experimental procedure and measures of interest, where we find: Voluntary Animal Approach: in which the animal approaches a stationary human, and Avoidance/Approaching Test: where the human approaches the animal, and the distance and manner in which the animal reacts is determined. Also, depending on the experimental procedure, this test can measure the impact of human–animal interaction on the animal's emotional state, its affiliative, aggressive, ambivalence, or fearful behavior towards humans, and correlate them with physiological or productive parameters. This test has also been complemented with reports, questionnaires, or evaluation of the stock person, zoo-keeper, shelter staff, or owner's opinion or behaviors towards the animal. The measurements selected for evaluation in this test should ideally be determined considering their validity (i.e., measure's scientific validation, specificity, and accuracy) and reliability (i.e., precision, sensitivity, consistency, and resolution). Also, this test usually requires observers or experimenters training, as well the assessment of interobservers evaluation, determining the degree of correlations and consistency of their reports (Arhant and Troxler 2017; Bergamasco et al. 2010; Breuer et al. 2000; Carlstead 2009; De Meester et al. 2011; Gourkow

et al. 2014). Due to the nature of the human–animal relationship and the context of their interaction, this test presents some variations when being assessed in domestic, zoo, and laboratory animals.

## Use in Domestic Animals

This test is used in pets and farmed animals (including pigs, poultry, horses, small and large ruminants, and fur animals, such as foxes and mink) to evaluate the human–animal relationship and as an indicator of animal welfare. In pets, the Human Approach Test has an important part of behavioral testing and evaluation of a pet's temperament, allowing the identification of behavioral problems. This is also relevant in rescue shelter animals and useful for predicting the animal's best “pet-owner match.” Also in these animals, Human Approach Test is used to evaluate and monitor the animal's emotional state before and after changes in human animal-interaction, examining their affiliative, aggressive, anxious, content, or frustrated behaviors (De Meester et al. 2011; Gourkow et al. 2014; Hewison et al. 2014; Martínez-Byer et al. 2020; Waiblinger et al. 2006; van der Borg et al. 1991). Emotional reactivity has also been evaluated in a productive context and used to assess animal welfare, wherein pigs and silver fox, Human Approach Test has been correlated to the animal's vocalization responses or heart rate as a measurement of emotional state (Gogoleva et al. 2010; Leliveld et al. 2017). Due to the tight relationship of pets with humans, the Human Approach Test is frequently implemented using familiar or unfamiliar humans in different behavioral contexts, for example, standing, walking, talking, looking directly at the eyes of the animal, or attempting to touch. This capacity to recognize and increase an approach towards a familiar person is not restricted to pets, but it is also present in farm animals like calves (Hewison et al. 2014; Kerepesi et al. 2015; Rousing et al. 2005; van der Borg et al. 1991).

Particularly in domestic animals, the tight-contact between these animals and humans

makes human posture relevant, so this test can be accompanied by aggressive or submissive signals from the human. This approach has been used in rescue shelter dogs, where in order to assess and monitor animal welfare and to evaluate the impact of a human–animal interaction program, authors used the Human Approach Test including the use of a friendly or threatening human, in addition to other behavioral tasks, while they also evaluated the dog’s heart rate and salivary cortisol as physiological parameters (Bergamasco et al. 2010). Other variations of this test include the use of neutral, threatening, or friendly approaches from humans associated to different stimuli (e.g., an artificial hand, flapping blanket, sound stimuli, doll, and dogs), with or without the presence of the owner, in order to assess a dog’s temperament and social behavior (De Meester et al. 2011). This has also been evaluated in horses, establishing that these animals prefer to approach to an unfamiliar human with a submissive posture (i.e., closed body posture: slouching, hands in front of the body, feet close to each other, relaxed knees, and hunched shoulders) over one with a dominant one (i.e., open body posture: standing tall, puffed chest, hands placed on the side, shoulders squared, and feet hip-width apart) (Smith et al. 2018). In respect to the uses of the Human Approach Test in farm animals, these measures are mostly assessed: Avoidance Test, referred to as the minimal distance that the animal tolerates for a human to approach; Voluntary Animal Approach, which measures the voluntary approach behavior of an animal towards a stationary human; and the measurement of the animal’s reaction to handling. Considering the agriculture and productive context of farm animals, the effect of human–animal interaction is relevant to evaluate in these animals, due fear of humans can be a detrimental factor that impacts its well-being, animal profitability, productivity, and affects the quality of the final product. This has been observed in cows, where it was determined that less approach to a stationary human was correlated with low milk production. Also in hens, where fear of humans was correlated with low egg production. Fear of humans also has metabolic costs, affects reproductive success, induces acute and chronic stress, and an animal’s

escape attempts from humans can predispose them to injuries and even death (Barnett et al. 1992; Breuer et al. 2000; Dalla Costa et al. 2016; Rousing et al. 2005; Waiblinger et al. 2006). These findings make assessing human–animal relationships not only a welfare issue but also an economical one.

## Use in Zoo Animals

Approach Test has been implemented using zookeepers, visitors, conspecifics, novel objects, and obstacles; however, due to bioethical conflicts and potential safety hazard for humans and animals, direct Human Approach Test is more difficult to assess in this context (Carlstead 2009; Hardie and Buchanan-Smith 2000). To overcome this problem, Carlstead (2009) used a test called “Keeper Calling Animal,” in which both the animal’s looking, approaching, ambivalence, or aggressive reactions to its zookeeper’s call (outside of the enclosure), as well as the zookeeper behavior, evaluating verbal, locomotor, gestures, non-verbal noise intensity, and body posture are recorded. Another variation of this test includes the determination of an animal’s “visitor effect,” observing the animal’s approach or avoiding behavior towards visitors (Sherwen and Hemsworth 2019). Since it has been established that developing a good human–animal relationship is also a potential tool of environmental enrichment, which must maintain the goal to ensure a positive experience for both human and captive animals, while it also satisfies the zoo’s mission (Claxton 2011), it is relevant to develop experimental procedures to evaluate the welfare impact of this relationship and develop a Human Approach Test both safe for both humans and animals.

## Use in Laboratory Animals

In laboratory animals, the Human Approach Test has been used in social animals, like rats, to assess the animal’s motivation for human contact (Augustsson et al. 2002). In these species, the



use of heterospecific play allows to not only measure the rewarding value of “tickling” and of “rough-and-tumble play,” but it also allows the assessment of a Human Approach Test using the experimenter’s hand, which is used to determine the latency and velocity to approach the hand to be tickled, or to identify signs of anxiety and fear (Burgdorf and Panksepp 2001; LaFollette et al. 2018b). This test can be performed in the home cage or a “test cage,” where it can also evaluate the time near an experimenter’s stationary hand, the interaction and direct contact to the hand, the location of the rat in the cage, and burrowing behavior. Also, the Human Approach Test has the advantage that it can be determined in one or multiple rats at the same time (Cloutier et al. 2018; LaFollette et al. 2017).

Using the “tickle” task, the Human Approach Test can be evaluated before, immediately, or even days after tickling, observing a decrease in the latency to approach the hand immediately after tickling and having mixed results when it is determined days later (LaFollette et al. 2017). In rats, it was determined that social isolation decreased the latency in the Human Approach Test (Burgdorf and Panksepp 2001). Also as an indicator of motivation, it was observed that a slowly approaching human hand, in anticipation of the act of tickling, evoked hedonic vocalizations at a frequency of 50 kHz (Ishiyama et al. 2019). The Human Approach Test has also been used in a Pavlovian conditioning study (Cloutier and Newberry 2008), in which the act of tickling was paired with an intraperitoneal injection of saline solution, in order to determine the rewarding aspect of tickling and the reduction of stress in routinary laboratory procedures. In this experiment, after conditioning and using a Y-maze, the rat was allowed to choose between the hand of an unfamiliar experimenter placed in one arm of the maze or a mock-hand located on the other. The latency, the number of visits, entries, and time spent in each arm were evaluated. Since laboratory animal welfare is not only a bioethical issue but fear and anxiety in routinary procedures can also interfere with experimental conclusions, it is relevant to evaluate human–animal relationships in a

laboratory context. These tests can even be determined in less social animals, like mice, observing a decrease in the latency of approaching after non-aversive handling. This determination is also important in pet stores, where due to an increase conception of rodents as pets, the relevance of assessing human–animal interaction using the Human Approach Test, particularly using unfamiliar humans, acquires more relevance due to the animal’s welfare (Augustsson et al. 2002; Hurst and West 2010; LaFollette et al. 2018a).

## Conclusions

In the evaluation of the human–animal relationship, it is also relevant to determine animal welfare, where Human Approach Tests are part of the behavioral battery test used to assess their impact. Depending on the animal species and measures of interest, different experimental procedures can be applied, such as approach or avoidance to a standing or moving human (associated or not to different visual stimuli), or determination of an animal’s reaction to handling, allowing to assess: animal welfare, fear to humans, identify behavioral problems, evaluate an animal’s temperament or personality, social motivation, or monitor the impacts of human–animal interaction. These determinations can also be correlated with physiological or productive indicators of the animal, and ideally, the selected measurements evaluated should be determined by their reliability and validity. Also, this test is usually complemented by the assessment of the behavior or opinion of the human about the animal, as well by the degree of confidence and correlation of interobservers records. These tests are frequently used in domestic and laboratory animals, and less frequently in zoo animals, due to bioethical issues and human–animal safety hazard. The Human Approach Test is a useful tool for determining the impact of the human–animal relationship in a domestic, productive, and scientific context, having, in this matter, a social (in the case of pets), economic (farmed animals), and scientific (zoo and laboratory animals) relevance.



## Cross-References

- [Affiliative Behaviors](#)
- [Agonistic Behavior](#)
- [Animal Welfare](#)
- [Appetitive Response](#)
- [Arousal](#)
- [Avoidance](#)
- [Caretaker Effect](#)
- [Classical Conditioning](#)
- [Familiarity](#)
- [Human-Animal Interaction](#)
- [Instrumental Learning](#)
- [Motivation](#)
- [Pain and Ethics of Animal Care and Use](#)
- [Pets](#)
- [Temperament](#)
- [Zoo](#)

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## Human Being

### ► *Homo sapiens*

## Human Cooperation

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## Definition

Cooperation refers fundamentally to the exchange of ideas, material goods, or labor in pursuit of common interests held by two or more individuals. Whereas classical perspectives consider cooperation to be the opposite of competition, current evolutionary approaches hold that cooperative behaviors are often essential during competitive exchanges, especially as the size of competing groups increases.

## Introduction

The study of cooperation in human societies holds substantial import for several disciplines, ranging from economics and political science to mathematical biology and evolutionary psychology. This entry focuses on four key theoretical developments in approaching cooperation in human evolutionary biology and psychology. In particular, this entry covers the early formative theories of reciprocal altruism and kin selection as well as more recent developments in cultural group selection and multilevel selection theory.

## Reciprocal Altruism

Early evolutionary theories of cooperation sometimes found explanations of cooperative behaviors to be challenging to reconcile theoretically. One key difficulty for such theories was the advantages derived by so-called free riders of a social group (Dawkins 2006). In free-riding situations, individuals take advantage of a social group by exploiting their collected resources and labor without personally incurring any costs. The greater individual success of free riders over cooperators caused some theorists to assume that selection for cooperation should be lessened in groups with increased numbers of free riders in the population. Reciprocal altruism provided one of the first definitive solutions to these problems by demonstrating the situations when and reasons why individuals would concede some personal benefit to help an individual who is unrelated to them. Today, the explanatory breadth of reciprocal altruism appears limited in comparison to when it was first introduced; however, it still holds foundational importance to theories on the evolution of altruistic cooperative behaviors.

Trivers (1971) specified three initial preconditions for reciprocal altruism to continuously arise in social interactions among group members: personal recognition, frequent interaction, and memory of past actions. In the first case, individuals must be able to recognize those they interact with in order to differentiate individuals who have helped themselves or others in the past from those who have not and therefore may be acting as free riders. Secondly, if these individuals do not interact frequently, they will be less likely to build a mutual rapport to provide incentives for further cooperation. Lastly, individuals who do not remember the relative benefits received and costs incurred during prior cooperative acts cannot be expected to effectively reciprocate, given the time delay that is often present in reciprocal interactions.

As identified by Patton (2000), altruistic behaviors such as sharing, mutualistic labor, and coalitional combat appear to be evolutionarily linked to reciprocity. Further, reciprocal behavior reduces the individual and collective risk of

pursuing certain aims, such as multi-day hunts or violent combat. This does not, however, eliminate certain risks, such as accidental cooperation with free riders. Nowak and Sigmund (2003) discuss responses to similar risks in describing indirect reciprocity, where the reputation of an individual correlates with the relative payoff they are expected to receive in a cooperative arrangement. Individuals who choose to free-ride are more likely to develop a negative reputation and be socially excluded from cooperative endeavors, thus limiting the benefits they are capable of accumulating and incentivizing cooperation.

## Kin Selection

The theory of kin selection is originally traceable to J.B.S. Haldane. It describes the differential pathways by which individuals can achieve reproductive success without, or in addition to, personal reproduction. In models of kin selection, this concept is primarily understood through an understanding of the distribution of an individual's genes throughout their close and distant kin. Closer relatives possess greater genetic similarity with each other, thus hypothetically impacting their behavior when interacting. More distant relatives are less likely to cooperate as consistently and closely as near relatives but are still more related than non-kin and thus may behave differently in certain contexts.

Kin selection is represented in various forms throughout the literature. In Maynard Smith's conception (Smith 1964), a trait is increasingly likely to be favored as the degree of genetic relatedness between two individuals increases. In Hamilton's conception (Hamilton 1970), a trait's indirect-fitness consequences are the most influential in determining whether or not it is selected for. Lastly, in Frank's (1998) view, kin selection distinguishes between direct and indirect selection in all natural selective processes. As a result of these variations, kin selection has often been used to describe substantially different phenomena and scientific theory; however, the core ideas of Hamilton appear to underpin most conceptions both historically and today.

Kin selection was first formalized mathematically by Hamilton (1970) in his work on the likelihood of altruism between close and distant kin. Hamilton formulaically depicted this with a simple inequality:

$$rB > C$$

Here,  $r$  provides the coefficient of relatedness between two individuals,  $B$  represents the benefits derived by an act of altruism, and  $C$  represents the costs incurred by an act of altruism. Though formative in the early days of kin selection theory and still influential today, the wide use of this formulation, known as Hamilton's rule, has been critiqued by Nowak et al. (2017), who claim that its derivation is not actually testable empirically.

Madsen and colleagues (2010) attempted to test kin-selected behavior according to Hamilton's rule with two experimental models in South Africa and the United Kingdom. The authors found that individuals were more likely to act altruistically and willingly incur a cost as relatedness to the person benefitting from their action increased. However, they noted that reciprocity and age of the recipient of the altruistic act maybe confounds of the study. Kin selection has also been studied in various field studies, but many of these attempts have been critiqued for not including the often temporally distant costs and benefits, relative to population structure, of altruistic actions (Nowak et al. 2017). As a result, beyond some experimental and observational paradigms in humans, the most persuasive evidence for kin selection is still derived from nonhuman literature.

## Multilevel Selection and Cultural Group Selection

Beyond reciprocal altruism and kin selection, in the 1960s, it was proposed that between-group competition could also lead to the evolution of within-group cooperation (i.e., *group selection theory*). Although group selection theory was initially well received, several researchers criticized the perspective on the basis that genes, rather than

individuals or groups, featured the necessary characteristics for replication (Dawkins 2006). Critics also argued that groups' homogenization due to individual dispersal reduces the likelihood of natural selection operating at the group level (Dawkins 2006). Moreover, mathematical models identified that in the absence of kin selection and reciprocity, groups of altruists were susceptible to the invasion of free riders leading to the extinction of this prosocial strategy (Dawkins 2006).

Even though some evolutionary biologists continue to insist that group selection is not supported on both theoretical and empirical grounds, several researchers have reexamined the ongoing debate and reached an epistemological compromise. For instance, Damuth and Heisler (1988) identified that most of the criticisms directed toward group selection stemmed partly from the obfuscation of two types of multi-level selection: MLS1 and MLS2. Per the authors, in MLS1, group selection concerns the effects of group membership upon individuals' fitness, wherein both phenotypes and fitness are individual-level properties. Consequently, a hierarchical structure emerges with individuals nested within groups and groups contained within populations. Evolutionary inferences are limited to changes in the frequency of individual phenotypes within a population. Conversely, in MLS2, group selection describes a change in the frequency of different types of groups, with groups varying in their phenotypes and fitness. Evolutionary extrapolations are restricted to the estimated change in the frequencies of groups within a population. Okasha (2009) further distinguished MLS1 and MLS2 according to how the unit of selection, either individuals or groups, reproduces. Whereas under MLS1 only individuals reproduce, in MLS2, groups have the ability to sire other groups. Hence, most of the criticisms directed toward MLS, in general, are limited to MLS2 dynamics.

In recent years, several researchers have adopted an MLS (mostly concordant MLS1) perspective for understanding human cooperation in an array of social contexts, including lethal coalitional aggression. For instance, Walker and Bailey (2013) interpreted the number of war

casualties in lowland Amazonian societies through an MLS lens. Per the authors, these societies' levels of intense and frequent conflict could be attributable in part to the high between-group genetic variance observed. According to their review, isolation, small population sizes, and genetic drift allowed Amazonian communities to attain high autosomal  $F_{ST}$  scores, an indicator of genetic differentiation, compared to other human societies around the globe (~15%). Similarly, current estimations suggest that relative to other sociopolitical systems, Amazonian communities exhibit lower intragroup genetic heterozygosity, increasing their likelihood of within-group cooperation. Although several authors have argued that warriors attain a direct fitness benefit from raiding rival communities (e.g., the Yanomamo in Venezuela), recent studies have found that this pattern does not generalize well to other small-scale societies characterized for their high frequency and intensity of between-group conflict (e.g., in the Waorani, belligerent individuals have fewer offspring; Walker and Bailey 2013). Moreover, for the authors, mechanisms of cooperation, such as direct reciprocity and mutualism, do not provide a satisfactory explanation for the evolution of blood feuds and revenge cycles among these societies, wherein individuals do not necessarily attain any direct benefit. Consequently, MLS could explain the persistence of lethal coalitional formation even in situations where individuals do not obtain a direct fitness benefit.

Even though kin selection and reciprocal altruism are often considered to be adequate evolutionary forces involved in the emergence of cooperation within small-scale societies, in larger communities, anonymity and one-time interactions increase the risk of defection and the collapse of large-scale cooperation. In response to these theoretical limitations, Richerson and Boyd (2008) proposed that sizable societies could maintain considerable levels of cooperation by evolving punitive institutions to limit the spread of free-riding behavior. Likewise, Bowles and Gintis (2013) suggested that intragroup cooperation in large groups emerges in part due to the effects of strong reciprocity. According to this framework, individuals are willing to punish

defectors, even if this behavior entails a cost to the punisher and benefits the group. Bowles and Gintis also argued that within-group cooperation and intense between-group competition covary across human societies. The authors' mathematical models and empirical evidence indicated that societies featuring high in-group prosocial biases and out-group antagonism (i.e., parochial altruism) outcompeted rival groups displaying higher levels of within-group competition.

Although critics have claimed that genetic differentiation among human groups is not sufficient to sustain within-group cooperation, Richerson et al. (2016) proposed that cultural differentiation (i.e., as reflected by cultural  $F_{ST}$  scores) could provide enough behavioral intergroup variation for selection to operate. The authors collected information on individuals' beliefs and behaviors from various online surveys (e.g., World Values Survey, Scottish Health Survey, and Afrobarometer, among others) and estimated cultural  $F_{ST}$  values for numerous human groups. Above and beyond differences in group size, the authors determined that most cultural  $F_{ST}$  scores were greater than 0.01, with several traits surpassing a 0.05 threshold and consequently generating the necessary conditions for cultural group selection to take place. The analyses also revealed that cultural  $F_{ST}$  was considerably larger than genetic  $F_{ST}$ , indicating a greater probability of group selection acting directly upon cultural variation, rather than on genetic differences between groups. It is worth noting, however, that these examinations did not discriminate between MLS1 and MLS2.

## Discussion

This entry provides a description of some of the key theoretical approaches to the study of cooperation in humans. The bases of contemporary work on the topic are described using reciprocal altruism and kin selection theory. Problems with both of these early evolutionary theories have led contemporary researchers to different solutions that either supplant or subsume those early approaches within other frameworks. A couple



of those approaches seen commonly today are the theories of cultural group selection and multilevel selection, both depicted here.

## Cross-References

- [Altruism](#)
- [Coalition Enforcement](#)
- [Cooperation](#)
- [Hamilton's Rule](#)
- [Kin Selection](#)
- [Pro-social Behavior](#)

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## Human Infancy and Childhood

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H

## Synonyms

[Attachment](#); [Cross-cultural](#); [Early learning](#); [Gestures](#); [Language](#); [Parenting](#)

## Definitions

*Social Learning:*

learning and information transmission occur through social interaction by means of observation, imitation, and teaching.

*Attachment Theory:*

a developmental theory first put forth by John Bowlby to explain how the parent-child relationship emerges and influences child development the method and practice of teaching information or skills to another

*Pedagogy:*

systematic descriptive study of a particular human society or cultures

*IDS:*

infant-directed speech, a speech characterized by simpler sentences, a slower speech rate, and a more variable prosody

|                            |                                                                                                                                                             |
|----------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Triadic engagement:</i> | infants coordinate attention between a social partner and an object of mutual interest.                                                                     |
| <i>Joint attention:</i>    | a form of social cognition; a cluster of behavior that shares the common goal of communicating with another person about a third entity in a nonverbal way. |
| <i>Prosody:</i>            | the rhythm of language and the way a speaker's voice rises and falls.                                                                                       |
| <i>Imitation:</i>          | the reproduction or performance of an act that is stimulated by the perception of a similar act by another person.                                          |
| <i>Social Referencing:</i> | the process wherein infants use the affective displays of an adult to regulate their behaviors toward the environment.                                      |

**Extended period of dependency.** Humans are unique in that they are born highly dependent on others for survival, and this dependency lasts several years, often the first decade of a child's life. This is often referred to as the extended period of dependency. There are various theories regarding the function or purpose of this extended time. There is, however, a general consensus that this period of time serves a particular function or purpose in the human species. It has been speculated that this extended period of dependency allows for the infant to begin the process of social learning and forming an attachment with a caregiver (Bowlby 2005; Gergely 2006). It may, in fact, allow for human cultural learning – a kind of social learning or transmission of information through a social process that, while it exists, is unmatched in other species. During this extended period, human infants not only have time to bond exclusively to those who are caring for them, but also there is time to learn information from those caregivers. It is thought that this extended time for learning from others is the key element that allows humans to develop and transmit information that enables complex cultures to form, transmit, and maintain information.

One theory regarding the specificity of human cultural learning is that humans are born premature and thus dependent on others for survival for an extended period of time. During this time, human caregivers have the opportunity to bond emotionally with the infant and begin the process of this teaching-learning system that will eventually allow them to learn the relevant information to ensure survival. The infant and caregiver develop their nonverbal communication system, which allows them to bond and share information. This emotional bond allows for infants to develop within a teaching-learning or pedagogical system with the primary caregiver.

Cultural learning is critical to human survival (Boyd et al. 2011). Consider that humans (one single species) have spread all over the globe, surviving in extremely diverse ecological contexts. It is argued that cultural learning enables such survival (Boyd et al. 2011). If one were to suddenly arrive in the arctic or the savannah without other humans to learn the key elements of survival, it would be impossible. The ability for humans to transmit culturally relevant information to one another is thought to allow human learning and therefore survival in different contexts. Each cultural context allows infants to be born into an opportunity for learning, as the learning system transcends diverse cultural contexts. Human infant minds are adaptive and flexible (also seen in patterns of brain development) allowing them to mold to the particular cultural context and focus and learn the relevant information needed within that context.

**Attachment facilitates learning.** Infants are born highly dependent on the protection and provisioning of primary caregivers for survival (Ainsworth 1979; Bowlby 2005). But that is not all. Nearly a century of research tells us that infants need affection and bonding to survive and thrive (Ainsworth 1979; Bowlby 2005). Without such love and care, human infants and young children do not develop in ways that are typical for most children, with deficits in cognitive abilities, intelligence, and even language development (Chisholm et al. 1995). However, with care, infants and caregivers form an intense bond. The infant learns that the caregiver is their secure

base – someone from whom they can depend upon (Bowlby 2005). It is thought that this attachment is the foundation for all other relationships later in life. From this early emotional bond, infants learn that other relationships are dependable – a safe and secure base from which they can explore the world (Bowlby 2005; Waters et al. 2002). The idea is that they develop and later form a mental model based on this first relationship (Stern 2018). At the core of Attachment Theory is the idea that the infant must develop an emotional bond to one primary caregiver, and this primary caregiver is typically the mother (Broesch et al. 2021). However, there is also evidence in the field of anthropology – typically extrapolated from qualitative ethnographic methodology, but also some quantitative observations of infants and young children across diverse societies, indicating that infants may be cared for by multiple caregivers (Tronick et al. 1987; Keller 2013). This evidence suggests that infants may be capable of attaching to multiple caregivers with no primacy of the mother.

**Sensitive parenting enables attachment.** Achieving a secure attachment requires sensitive caregiving. Attachment research has found that caregivers who respond in a sensitive, timely, and appropriate manner to their infants have children who demonstrate a secure attachment to their caregiver in the first few years of life. Sensitive responding is a vague and fuzzy concept that, until recently, was investigated primarily with mother-infant dyads in Western societies (Broesch et al. 2016; Keller 2013). We now know that responding to infants in a consistent manner appears to shape their developing social expectations and aid in forming a secure relationship with the caregiver. In fact, infants show a preference for other adults with the same responsive signature as their primary caregiver (Bigelow and Rochat 2006). This suggests that they are forming expectations and preferences for social behaviors even in the first few months of life, which is quite remarkable. Research examining parental responsiveness indicates that infants as young as a few months of age are sensitive to the timing of the caregiver's response – typically responding within 1 s of the onset of an infant's behavior.

Accordingly, infants also show distress to a break in the social interaction – referred to experimentally as the “still face” paradigm (Rochat 2001). Around 5 months of age, when there is a sudden break in a dyadic social interaction between an infant and another individual, the infant responds with distress and negative emotional expressions. This research suggests that infants are not only forming an emotional bond, but they are developing expectations regarding the pattern of interaction. Sensitive parenting is correlated with secure attachment, but what are the critical elements of sensitive parenting?

**Mutual joy as a critical aspect of sensitivity.**

Although infants are communicative and responsive from the outset, it is not until sometime between the 5th and 8th week of life that they begin to produce a social smile. A social smile is a smile in response to social interaction – typically gazing into the others' eyes and responding to an interaction – verbal or facial (Wörmann et al. 2012; Messinger and Fogel 2007). At this point, we see infants show the first signs of delight at enjoying the social company of another. They gaze into the eyes of a smiling caregiver and smile in response. These moments of “mutual joy” (Broesch and Carpendale 2021) set the stage for early communication. What is often overlooked is the emotional element to early communication; yet, it is present and clear from very early in life. While research suggests that the caregiver plays a vital role in helping infants and children regulate their affect (Rochat 2001; Stern 2018), very little research has examined the precise role of experiencing mutually shared positive emotions. Some have argued that this shared experience of positive emotions is also critical for attachment and well-being (Broesch and Carpendale 2021).

**Early forms of communication allow early learning:** Even newborn infants are drawn to the unique features of a human face (Rochat 2001). Very early in life, infants show a preference for human face configurations, their mother's voice, and dynamic and high contrast features such as the eyes and mouth of a human face. This early preference springboards social interaction with the caregiver and others as the infant experiences

the caregivers' gaze from birth and soon after, the infant gazes back. This early dyadic interactive behavioral system leads to other more complex forms of communication later on as the infant and caregiver learn to anticipate and respond to one another. Adults also aid in language learning even in the first moments of life. Adults speak to infants in a modified manner – adjusting the acoustic and prosodic qualities of their speech (Snow and Ferguson 1977). Adults and older children speak to infants more slowly than to other adults, using a higher and more variable pitch (Broesch and Bryant 2018). It is thought that this may aid in language learning or draw the attention to the caregiver and facilitate and support this affective human bond. There is also cross-cultural evidence indicating that parents across diverse cultures engage in modifying their speech to address infants, compared to addressing adults. This is referred to as infant directed speech (IDS) or motherese. Infants are born into a communicative system in which they produce signals and caregivers respond to them. One idea that has been proposed is that this system facilitates efficient and rapid transfer of cultural information, knowledge, and skills. This is referred to as the theory of natural pedagogy (Csibra and Gergely 2009). Evidence for this theory lies in infants' ability to receive subtle pedagogical cues from others as well as caregivers' tendency to produce these cues. These subtle behaviors such as pointing, eye gaze, and infant directed speech highlight relevant information to infants and draw their attention to specific moments or features in a learning situation. They allow efficient and high-fidelity transfer of cultural information.

**Learning through locomotion:** The continuing development of locomotion helps children acquire the ability to adapt to the physical and social environment. The explosion of motor skills in the first year of life helps infants gain new opportunities for interacting with the environment in increasingly complex ways (Adolph and Robinson 2015). As infants develop the ability to sit, crawl, and walk, these changes provide infants with new learning opportunities to interact with objects and their caregivers. Research suggests that achievement of new motor milestones may

facilitate the development of language, later cognitive ability, and concept formation (Gonzalez et al. 2019). Despite the existence of motor milestones, these stages are not fixed and are influenced by the interplay between the child and their environment. In the process of adapting different social and cultural environment, children promote adaptive action responding by their social partners, during their daily routines. The widespread variability in the timing and sequence of motor milestones between cultural groups suggests that motor development is a complex interaction process of biological aspects with environmental influences and experiences. The process of motor development during infancy involves patterned neural activity, perception, cognition, and social interaction. The development of locomotion, therefore, presents infants with new opportunities to discover and practice general principles and mechanisms that are essential to relevant developmental changes.

**Triadic engagement allows referential communication (joint attention):** Human forms of communication are unmatched in other species (Tomasello and Rakoczy 2003). Although other species communicate in complex ways, the recursive nature of human communication is unique. Humans communicate about the unseen, the imagined, the past, and the future. To allow for this, one must be able to represent the ideas of another in the mind. There are several theories existing for human communication and most of them rest on humans' remarkable and unmatched ability for triadic communication and joint attention. Infants begin communicating through crying and, only a few weeks later, they are able to smile in response to a social interaction by producing the first social smile. By the 12th month of life, they have started pointing and uttering their first words. By 18 months, they are amidst a vocabulary spurt. Joint attention occurs when the child and the caregiver are mutually attending to the same thing and they are aware of each other's attention. They demonstrate this through gazing back and forth between the social interactive partner and an object of interest (Tomasello and Farrar 1986). This kind of communication indicates a recognition and a desire to attend to and enjoy

the same thing. This kind of communication is thought to facilitate or even springboard language development.

**Learning from others: Imitation and social referencing.** From early in life, infants imitate others (Meltzoff and Moore 1999). Humans are unique in the extent to which they imitate others (Nielsen and Blank 2011). Not only do infants imitate the emotional expressions of others, but they are also sensitive to the sequence of behavior. What is interesting, however, is that around 18 months of age, infants will start to imitate the intent behind a behavior and not just the behavior itself (Gergely et al. 2002a). This indicates that they have begun to move beyond the observable behavior of their social interactive partners and instead identify the intention underlying the observable behavior, and act on that accordingly. Interestingly, around this age (15–18 months), infants also begin to use others as a social reference, meaning that when an infant encounters an uncertain situation, they refer to the caregiver and modify their response depending on the emotional response of the caregiver (Cohn and Tronick 1989; Carver and Vaccaro 2007). Not only are they using the emotional cues of others to alter their behavior, they are learning critical information about the safety and function of the world. All of this suggests that they are learning important communicative skills and culturally relevant information for survival and success, as early as the first year and a half of life.

**Cultural variation in parental responsiveness:** Although we see striking similarities in the kinds of behaviors parents produce with infants (Broesch et al. 2016), there are significant differences in the selectivity of the response as well as how parents respond to and subsequently shape children (Kärtner et al. 2008). One research group examining cultural variation in caregiving responses to infants proposed a model of development that takes into account cultural variation and results in diverse developmental pathways (Greenfield et al. 2003). Under this model, parenting goals (as a result of societal pressures and the ecology) which parents are not always aware of – shape parenting behaviors – both subtle behaviors in interactions with infants and more overt or

explicit choices parenting older children. These different parenting styles can be considered or referred to as collective or individualistic – interdependent or independent cultural lifestyles. Although each society and family has elements of both, the position of the self in relation to others is what determines behaviors in either direction or pathway. We see differences emerge as early as the first few months of life with mothers engaging with their infants and interacting in different ways. Mothers in more independent societies typically engage with infants with face-to-face interactions but with a little touch. In more interdependent societies, mothers engage with more holding and touch and are in close proximity to infants. Responsiveness (which is deemed critical for attachment, but also for shaping social expectations of behavior) is also different depending on parenting goals within and between societies. Mothers respond using touch or face-to-face stimulation. We also see differences in object exploration and communication – suggesting that early forms of triadic interaction vary across cultures (Little et al. 2016). All of this is to suggest that indeed there are foundational elements of the human experience that are critical for healthy, typical development; yet, there are rich social differences that depend upon a milieu of factors, and these differences shape the developing child. Culture acts as a filter, shaping the output of parental behavior and hence a child's early social experiences.

**Referential communication: Gestures and Language.** In the second half of an infant's first year of life, they begin producing and responding to gestures and other nonverbal cues such as pointing (Kettner and Carpendale 2018). These gestures are typically learned through social interactions and daily routines with caregivers (Kettner and Carpendale 2018). Eventually, once mastered, they allow the infant to communicate with others by referring to objects and engaging in triadic communication using symbolic gestures and referents. This ability allows humans to communicate about forms that are not in the present or directly in view. For example, these forms that human can communicate about are things such as the mind – internal feelings, thoughts, and



perspectives. Keep in mind that these feelings, thoughts, and perspectives often require communication to be symbolic. This unique ability for symbolic communication, in combination with the pedagogical system, allows humans to learn culturally relevant information from other individuals.

## Cross-References

- ▶ Attachment
- ▶ John Bowlby
- ▶ Language
- ▶ Learning
- ▶ Parenting

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## Human Leukocyte Antigen (in Humans) and H-2 (in Mice)

### ► Major Histocompatibility Complex

## Human Motor Control

### ► Perception-Action Theory

## Human-Animal Interaction

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### Definition

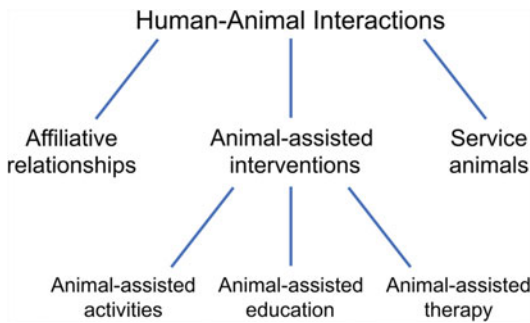
Human-animal interaction captures the mutual and dynamic exchanges between humans and other animals and their psychophysiological effects on humans (Griffin et al. 2011). Types of human-animal interaction include affiliative interactions (e.g., pet ownership), animal-assisted interventions, and service animals.

### Introduction

Contact between humans and other animals – human-animal interaction (HAI) – involves the mutual and dynamic exchanges between people and animals and their psychophysiological impact on individuals (Griffin et al. 2011). Though originally focusing on cardiovascular benefits of companion animals, researchers from a host of scientific fields – ranging from clinical and experimental psychology to public health and veterinary medicine – have demonstrated a wide range of positive effects of HAI on human health and well-being. A taxonomy of HAI categorizes it into the affiliative relationships between humans and animals, animal-assisted interventions, and use of service animals for clinical populations (Fig. 1).

### Types of Human-Animal Interactions

The ever-present reciprocal relationships between humans and animals in societies throughout history translate today into both traditional social interactions as well as those catered to the evolving needs of the present day. In ancestral times, humans shared affiliative bonds with animals



**Human-Animal Interaction, Fig. 1** Types of human-animal interactions

through cooperative hunting and companionship. Today, we have integrated animals into human society in novel ways, including bringing them into classrooms and therapy rooms. Although the bulk of HAIs involve dogs, these interactions can involve many other species as well. A number of clinical therapies incorporate horses into treatment plans, for example, and interventions catering to elderly populations employ small birds and fish (Beetz et al. 2012). The nature of HAIs, including the goals and degree of structure and training involved, leads to three classifications: affiliative relationships, animal-assisted interventions, and service animal interactions (Fig. 1).

### Affiliative Relationships

Affiliative relationships between humans and their companion animals, or ► [Pets](#), entail a strong emotional attachment that facilitates the exchange of physical and psychological benefits. Pet ownership correlates with a number of health benefits, such as increased physical activity and lower baseline blood pressure (McCune et al. 2014). Because ownership is a choice, however, it is difficult to establish whether affiliative relationships cause health benefits or people likely to benefit choose to own pets.

### Animal-Assisted Interventions

Animal-assisted interventions (AAI) involve trained practitioners (e.g., handlers, researchers, teachers, therapists) bringing animals into an environment to interact with people for the

purpose of providing psychophysiological benefits. AAIs cover a wide range of interactions, from improving students' reading ability in classrooms to helping stroke victims recover social and functional abilities. As such, the American Veterinary Medical Foundation (AVMA) partitions interventions into animal-assisted activities, education, and therapy (AVMA 2019).

#### Animal-Assisted Education

Structured and goal-oriented interventions aiming to improve educational outcomes are referred to as animal-assisted education (AAE; AVMA 2019). AAEs in primary schools incorporate dogs and small animals (e.g., guinea pigs, rabbits) in programs tailored to typically developing students as well as those with special needs. Reading programs are the most common, empirically supported interventions for typically developing students (Brelsford et al. 2017), but classrooms also house animals to promote students' general concentration, motivation, and relaxation (Beetz et al. 2012). Interventions for students with emotional or behavioral needs use dogs for the same purposes, as well as to improve social and emotional outcomes in the classroom (Brelsford et al. 2017).

#### Animal-Assisted Therapy

Animal-assisted therapy (AAT) requires specific goals for enhancing an individual's cognitive, emotional, physical, or social functions (AVMA 2019). AATs are structured, short-term interactions delivered in therapeutic contexts by professionals in the field. Animals have been used in therapies for children with autism, adults with spinal cord dysfunction, older adults with dementia, and prison inmates (Beetz et al. 2012; Muñoz Lasa et al. 2015).

#### Animal-Assisted Activities

Unlike animal-assisted education and therapy, animal-assisted activities (AAAs) are not exclusive to structured and goal-oriented programs, leading to rich variety in these interactions. AAAs enhance individuals' quality of life and center the animal as a motivational or social tool in an interaction with the aid of a trained

volunteer, paraprofessional, or professional (AVMA 2019). For example, AAAs include having animals interact with college students in de-stressing events (Crossman and Kazdin 2015), elderly populations in geriatric facilities (Souter and Miller 2007), and children during doctor's visits (Beetz et al. 2012).

### Service Animals

Service animals are individually trained to help disabled persons overcome specific disabilities. They promote a more independent livelihood, facilitating, for example, mobility for the visually impaired, low blood sugar detection for diabetics, or support for veterans with post-traumatic stress disorder (PTSD; McCune et al. 2014; Rodriguez et al. 2018a). In the United States, the Americans with Disabilities Act and other federal legislation regulates service animals as those explicitly trained to perform tasks for individuals with disabilities. Animals that also live with individuals and are prescribed by medical professionals to improve health and well-being, such as emotional support animals and comfort animals, are not recognized as service animals because they have not been trained to perform explicit tasks. The Americans with Disabilities Act limits service animals to ► [Service Dogs](#) and small horses (AVMA 2019).

## Effects of Human-Animal Interactions

The variety of possible types of interactions that occur between humans and animals results in an equally rich variety of effects on human health and well-being, including behavioral, educational, physiological, and/or psychological effects.

### Behavioral

HAIs seem to strongly influence social behavior, perhaps due to the social nature of the interactions. All HAI types promote social interaction. Affiliative interactions resulting from child pet ownership, for example, promote positive social interactions, autonomy, and responsibility and decrease aggression (Purewal et al. 2017). The explicit goal of many AAIs is to facilitate social

interactions, such as therapies for autism spectrum disorders, dementia, or intellectual disability (Muñoz Lasa et al. 2015). Service animals facilitate social interactions as well, demonstrated by disabled persons experiencing more positive social interactions when their service dog is present than without (Beetz et al. 2012).

### Educational

HAIs, most commonly AAIs, provide motivational, social, and emotional benefits to students across all levels of education. Primary education classrooms use dogs to promote a range of behaviors to improve their experience and performance (e.g., concentration, motivation, relaxation) in classrooms generally as well as through reading and behavioral programs (Brelsford et al. 2017). AAIs on college campuses, on the other hand, cater explicitly to relieving exam-related stress (Crossman and Kazdin 2015). These stress-relief sessions, where students interact with animals for short periods of time at their will, occur outside classrooms on campuses to reach a large number of students.

### Physiological

The physiological effects of HAIs relate to stress, bonding, and physical activity. The physiological benefits of HAI can be direct, such as decreased blood pressure, or indirect, such as with increased levels of the hormone oxytocin in bonding.

### Stress

Long-term affiliative interactions can influence cardiovascular measures associated with physical health (e.g., blood pressure, heart rate, heart rate variability). In individuals with cardiovascular disease, for example, pet owners have lower mortality than nonowners (Schreiner 2016). In healthy populations, pet ownership correlates with lower heart rate, lower blood pressure, and faster stress recovery (Schreiner 2016). AAIs also elicit cardiovascular effects, where the intervention mediates cardiovascular responses to short-term stressors. These shorter-term interventions aim to reduce stress in doctor's offices, before dental procedures, and in laboratory settings (Beetz et al. 2012).

HAI influences skin conductivity, or electrodermal activity (EDA), a measure associated with emotional arousal (Rodriguez et al. 2018b). Fiocco and Hunse (2017) introduced a dog following a stressful event, for example, and individuals with the AAI showed lower electrodermal activity than those without, suggesting the intervention reduced their stress response.

HAI also affects cortisol, a hormone shown to increase in response to short-term stress, such as cognitive challenges, and long-term stress, such as depression (Schreiner 2016). Studies with both pets and AAIs show decreased levels of cortisol in the saliva following brief interactions, whether under stressful or normal conditions (Beetz et al. 2012). Service animals also affect cortisol levels, such as in veterans with PTSD who have service dogs (Rodriguez et al. 2018a).

#### Bonding

HAI influences other hormones related to social behavior. Oxytocin, a hormone and neurotransmitter that promotes social bonding, responds to interactions in both humans and the animals involved. When pet owners physically contact or look into the eyes of their dogs, oxytocin levels in their blood/urine increase in both owner and dog, an effect observed in AAIs between humans and unfamiliar dogs (Beetz 2017).

#### Physical Activity

Physical activity is a critical component of human health linked to decreased cardiovascular disease, diabetes, and other illnesses. Dog owners are more likely to meet national guidelines for physical activity (McCune et al. 2014). The physical activity that dog ownership requires (e.g., dog walking) is mutually beneficial, ensuring active lifestyles for both the owner and the animal. There are also animal-assisted interventions that facilitate physical activity, namely, for disabled individuals. For example, there are AATs for those with nervous system impairments to improve balance, limb-control, and walking (Muñoz Lasa et al. 2015).

#### Psychological

Human-animal interactions of all types elicit positive psychological effects in clinical and

nonclinical populations across the lifespan. Pet owners are less lonely, depressed, and anxious, though the risk of extreme grief due to pet loss should not be overlooked (Schreiner 2016). AAIs can not only improve general mood (Beetz et al. 2012), but they can reduce symptoms of emotional disorders such as depression (Souter and Miller 2007) and anxiety (Beetz et al. 2012) and behavioral disorders such as attention deficit-hyperactivity disorder and autism spectrum disorders (Busch et al. 2016; Muñoz Lasa et al. 2015). Medical professionals prescribe individuals emotional support animals to mitigate these symptoms as well.

## Conclusion

Humans have interacted with animals for millennia, and these interactions are becoming more common in our daily lives. Because of the rise in the frequency of these interactions, a broad research effort exists to investigate how these interactions improve human and animal health and well-being. More collaborative scientific research is vital to grow and establish a theoretical understanding of the reciprocal relationship between humans and animals observed across the lifespan.

## Cross-References

- [Animal-Assisted Intervention](#)
- [Pets](#)
- [Service Dogs](#)
- [Swine Cognition](#)

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## Human-Horse Interaction

### ► Perissodactyla Cognition

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## Human-Horse Interaction

### ► Equine Cognition

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## Humans

### ► Hominoidea Sensory Systems

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## Humiliation

### ► Shame and Guilt

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## Hummingbirds

### ► Susan D Healy

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## Hunt

### ► Safari

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## Hunting

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### Synonyms

Trapping; Sporting

### Definition

Hunting can be defined as the pursuit of wild animals with the intent of killing or trapping them.

### Introduction

Up until the mid-twentieth century, it was widely accepted that the earliest of hominids actively hunted wild animals for sustenance and that these animals made up a significant proportion of their diets. This widespread view was questioned by Richard B. Lee who played a major role in theorizing that this was not necessarily the case for all hominids, particularly those existing in more temperate latitudes. Following 15 months of fieldwork in 1968, Lee demonstrated the reality of a largely plant-based diet in the !Kung Bushmen, a marginalized group which inhabits the semiarid Kalahari deserts of Botswana. Lee suggested that it was reasonable to consider the possibility that the prehistoric “hunter” diet was reflected in that of the !Kung Bushmen’s, which was made up of between 30% and 40% meat.

In the late 1980s, Lee’s hypotheses were confirmed through the development of more sophisticated archeological and taphonomic techniques (Speth 1989). These developments lead to re-examinations of some of the most principal sites on which some of the earliest hunting hypotheses were based on. These analyses challenged the widespread consensus that hominids existing in the Pleistocene period were the fierce, large-game hunters that they were traditionally

believed to be. More likely, they were opportunistic omnivorous scavengers who acquired meat in the form of game abandoned by other predators (Binford 1986; Speth 1989).

In 1976 Robert Andrey, an American paleoanthropologist, proposed the “hunting hypothesis,” a fundamental theory which prioritized the role of hunting in the evolution of the genus *Homo*. Andrey’s hunting hypothesis suggests that the act of hunting leads to bipedalism, the production of tools made from stone or bone, and, eventually, the use of fire. *Homo erectus*’ active hunts are believed to have been the catalyst for language acquisition and the formation of religion and various cultures (Hewes et al. 1973; Narr 2008). Following the innovation of hunting tools, active hunting of wild animals persisted as the sole means to a source of a protein-rich meat until approximately 11,000 years ago when animals were first domesticated (Zeder 2012). Despite the domestication of livestock, hunting wild animals has remained a significant and reliable resource in many areas of the world where they are relied upon for their pelts, furs, hides, and leather for clothing and bones and sinew for tool making and as a source of protein.

Historically, overhunting has played a major role in the changes of the Earth’s ecosystems by disrupting the balance of biological interactions. The Holocene epoch is currently experiencing the “sixth extinction,” which has been ongoing for at least the last 11,700 years, since the most recent Ice Age. Overhunting has been a prominent driving force of this mass extinction, particularly for megafauna existing outside of Africa who quickly succumb to these pressures (Lyons et al. 2004). In many marginal climates or impoverished regions, hunting wild animals is still deemed essential for food security, yet the current rates of extraction may threaten ecosystems and human communities (Ripple et al. 2016). Coupling this with global exponential population growth has led to an exacerbation in the reliance that humans place upon wild fauna and the frequency of human-wildlife interactions (Ripple et al. 2016).

Modern-day hunting has evolved due to the prospect of monetary gain and has been further

enabled by the ease of access to firearms. Money can be gained through sport hunting and from the trade of animals destined to be pets and derivatives for consumption or traditional medicine and for use in cultural and religious ceremonies (Bersacola et al. 2014; Ripple et al. 2016). Poverty is a primary incentive for supplying wild animals for such uses. Together, these factors pose serious threats to vast quantities of biodiversity on both a global and location-specific scale (Ripple et al. 2016).

Legal hunting is at the forefront of many international governing bodies' discussions. Sport hunting and trophy hunting are terms which refer to the business linked to hunting wild game for pleasure. It is in particular a widely debated topic, largely because of the inflammatory nature of killing one animal in the efforts of conserving a population of others. Unfortunately, sport hunting is often subject to corruption and improper management (Lindsey 2008). Such ineffectiveness has led to quotas being exceeded, which threatens species population numbers. To add, poorly managed hunting practices have likely weakened the gene pool for future generations since the individuals with the most desirable characteristics, whether it be the biggest tusk in the case of elephants or the most impressive mane in the case of lions, are likely the carriers of the highest-quality and evolutionary fit genes (Knell and Martinez-Ruiz 2017). Moreover, a lack of reinvestment in conservation and local development has been recognized and has stunted the potential success of these conservation tactics (Crosmar et al. 2015; Ripple et al. 2016). Despite this, properly managed tourism and trophy hunting has been recognized as a potentially suitable method of conserving wildlife in national parks where alternate efforts have in the past been unsuccessful (Crosmar et al. 2015). Furthermore, trophy hunting has proven to be a useful tool in local development by providing jobs and in enhancing the value placed upon wildlife at a local level, thereby decreasing poverty levels and increasing a willingness to conserve wild fauna (Nelson et al. 2013).

Illegal hunting, referring to any hunting or extraction of wildlife unauthorized or prohibited

by state, is widely practiced as deterrents to such activities are inherently weak. Prosecuting, levying suitable fines, seizing goods, recouping proceeds obtained as a result of criminal activity, and issuing prison sentences against lawbreakers not only punish the offender but can also serve as an effective deterrent to other members of the society who may consider offending (Nijman 2017). This too should be the scenario when taking action against criminals who inhibit the success of species conservation – effective law enforcement has the potential to benefit species conservation tremendously (Du Saussay 1984). For example, Sierra Leone, a nation recognized as one of the world's most important biological hotspots most affected by poverty (Fisher and Christopher 2007), still prosecutes offenders based on an outdated Wildlife Conservation Act from 1972. The Act, for example, states that the hunting of prohibited animals, such as elephants (genus: *Loxodonta*) with tusks of a combined weight of less than 5 kg, is punishable by nothing more than a fine of up to Le100 (<\$0.01), up to 6 months in prison, or a combination of both a fine and imprisonment, for the first conviction. These repercussions are too lax to serve as a sufficient deterrent for hunters.

The IUCN (2019) recognizes hunting or trapping as a threat to 3673 of the 27,000 plus species that have been surveyed. Hunting, coupled with the other copious levels of anthropogenic pressure placed upon animals, poses severe consequences to a number of species and subspecies. For example, 2018 saw the northern white rhinoceros (*Ceratotherium simum cottoni*) reclassified as functionally extinct, with the passing of the last known male of the species as a result of exploitation for wildlife trade (Smith 2018). A number of initiatives need to be put in place to combat both illegal overhunting and poorly managed or corrupt legal hunting, as well as other factors that inhibit species success and conservation efforts. Poverty alleviation and food security, education, and inherent value placed upon wildlife are three crucial sectors that need to be combated to alleviate the pressures exerted upon wild fauna (Reynolds and Bettinger 2008).

## Hunting for Bushmeat

Bushmeat refers to wild, undomesticated game that is hunted and later consumed by humans. Due to growing human populations, the dependence placed upon bushmeat has amplified tremendously over the past few decades, exerting increased pressure on wild animal populations, with terrestrial mammals in particular suffering significantly (Ripple et al. 2016). Hunting wild animals for food consumption is one of, if not, the most prominent reasons that people resort to hunting (Ripple et al. 2016). Bushmeat hunting is a contributing factor to the epidemic of species population decline with an estimated 301 terrestrial mammal species being recognized as being vulnerable to extinction (Ripple et al. 2016). Despite being a global issue, populations of wild animals existing throughout areas of South Asia, Africa, and South America are declining at an unprecedented rate (Ripple et al. 2016).

Ease of acquisition is a contributing factor in the popularity of bushmeat. In Central and Western Africa, bushmeat is sold at the side of the road or is often taken to vast markets in cities where it has the potential of yielding a more profits (Bersacola et al. 2014). In Cameroon, for example, Wilcox and Nambu (2007) highlight that bushmeat can be found in rural areas, to be significantly low-cost compared to the alternative sources of protein available in the adjacent town. Although hunting for household consumption may in some cases be locally sustainable, the level of extralocal demand associated with the commercial trade of bushmeat is typically far greater than the forests can support (Bennett et al. 2006). The global bushmeat hunting crisis is particularly alarming since it is intimately linked to local development challenges such as famine and malnutrition and emergent zoonotic disease risks.

Not only is bushmeat hunted in areas unregulated by local authorities, zones designated specifically for the protection of wildlife suffer also. Illegal hunting in protected areas is a major issue afflicting national park's wildlife populations. For instance, migratory herbivores in the Serengeti National Park, Tanzania, have

fallen victim to hunters, resulting in drastic population declines (Loibooki et al. 2002). Following agriculture, bushmeat is considered to be the most important means of generating cash flow in the Serengeti National Park, with estimates of anywhere between 52,000 and 60,000 individuals participating in illegal hunting within protected areas each year (Loibooki et al. 2002). The income generated by the sale of wildlife in these areas has been recognized as not only vital for sustenance but also for paying government taxes and local development levies (Loibooki et al. 2002).

The dynamics of bushmeat hunting and trade can in some areas be dictated by local political influences. For example, the availability of different species at bushmeat markets and the quantities in which they are sold can differ greatly dependent on political tension (De Merode and Cowlshaw 2006). During peacetime in the Democratic Republic of the Congo, endangered and protected species represent more than half of all bushmeat sales in the urban market, and this number only increases during war time (De Merode and Cowlshaw 2006). During times of political stability, the commodity chain is governed by the local army who, despite allowing the illegal hunting of protected species, do regulate the number of citizens allowed to hunt (De Merode and Cowlshaw 2006). In contrast, during times of political instability when the army is transferred out of the local area, lower ranking soldiers take control of the commodity chain and loosen hunting restrictions resulting in an additional influx of protected species entering markets for trade (De Merode and Cowlshaw 2006). In more rural markets however, which are supervised by the local authorities, political instability seems to be an unrelated factor to the species which appear at the market as these authorities impose stricter guidelines (De Merode and Cowlshaw 2006). In both times of political stability and instability, protected species constitute an insignificant proportion of bushmeat traded in rural markets.

In order to reduce the unsustainable bushmeat hunting and therefore increase wildlife conservation, consumers must be educated and be given access to adequate and affordable alternatives

(Reynolds and Bettinger 2008). Reducing the price of livestock and increasing the availability of domestic meat for local consumption would likely reduce the demand of bushmeat (Milner-Gulland and Bennett 2003).

## Hunting and Wildlife Trade

Wildlife trade can be defined as any sale or exchange of wild animals or their derivatives between humans (Wright et al. 2016). Illegal wildlife trade in wild species and products can include different biological resources including rhino horn, elephant ivory, medicinal plants, timber, shark fins, and pangolins scales, to name a few. Poaching and illegal wildlife trafficking has now reached an unrivaled stage. This deprives local communities of conservation- and tourism-based employment opportunities that are dependent on the presence of wildlife as a result of dwindling biodiversity in some areas (Wright et al. 2016). As of 2011, the value of global trade of illegal and prohibited goods was calculated to be worth between \$7.8 billion and \$10 billion per year, ranked just behind the illegal drug trade (Wright et al. 2016).

The lack of ownership and value assigned to wildlife by local communities, coupled with ineffective land use, poverty, food insecurity, and corruption, drives the illegal trade. To illustrate, poaching of the African elephant (*Loxodonta africana*) has risen to a level that threatens the long-term viability of the species (Gao and Clark 2014). Poaching and the associated illegal ivory trade is currently considered to be the most significant threat to the species, requiring urgent, collective, and cooperative action (Gao and Clark 2014). Data shows that poaching has increased from 2006 onwards and rose to an unsustainable level with illegal killing rates estimated to average approximately 6.8% between 2010 and 2012, amounting to approximately 33,630 elephants killed per year (Witemyer et al. 2014). International non-governmental organizations (NGOs) and media often attribute the basic problem to China's domestic ivory market (Gao and Clark 2014). Given the substantial

evidence that is now available, it is undeniable that the current Chinese domestic ivory market is an important driver of poaching and trafficking problem (Gao and Clark 2014). In China, the possession of ivory is a sign of wealth, affluence, or importance. Chinese craftsmen use ivory to create smoking pipes, daggers, chopsticks, jewelry, ornaments, souvenirs, and hair accessories. Some Asian nations also highly value elephant tusks for their apparent medicinal properties. If the price of ivory in China remains high, and effective measures are not taken in a timely manner, poaching will continue unabated to the detriment of the species. Any solution requires concerted action and collaboration from all countries concerned. It is vital to regain control of the ivory trade in all markets, especially in China, through effective multi-agency cooperation, regulation, policing, and monitoring. Efforts from NGOs and authorities have greatly improved public awareness of the problem.

Pangolins (genera: *Manis*) are widely recognized as the world's most illegally trafficked mammal. Pangolins inhabit Africa and most of Southeast Asia and are seriously threatened by illegal hunting to supply international trade (Pantel and Chin 2009). The greatest threat to pangolins is illegal hunting for both national and international trade. A large proportion of the pangolins hunted are to supply the extensive demand for their meat and scales used in tonics and traditional medicine, particularly in China (Pantel and Chin 2009). Surveys in China have found that live pangolins and/or their scales are commonly available in open markets. Pangolins are particularly vulnerable to overexploitation, as they are easily hunted, have a very slow reproduction rate, and do not easily breed in captivity (Pantel and Chin 2009). While subsistence hunting of pangolins has likely been prevalent for centuries, large-scale commercial harvesting has boomed in the last few decades, drastically influencing the decline observed in population numbers in the genera.

Primates have been recorded to be among the most frequently hunted group of animals to supply a demand for bushmeat, traditional medicine, and the desire for them as pets (Nijman and Healy



2016; Ripple et al. 2016; Svensson and Friant 2014). The illegal primate trade is known to be a major impediment to primate conservation, especially in Africa (Nijman and Healy 2016; Svensson and Friant 2014). The use of primates in traditional medicinal practices (including *mujji*, more commonly referred to as witchcraft) has been recorded to be on the rise, both in Africa and in Asia. Svensson and Friant (2014) report that 59% of the primate species in Asia and 32% of primate species in Africa are used for these practices. The different uses of primates also seem to differ between regions. For example, hunters in Nigerian local communities report hunting African Lorises for food and medicine and rarely keep them as pets. However, as a result of recent viral media depicting slow lorises (genera: *Nycticebus*) as pets, Western demand for these newly perceived charismatic species has increased dramatically (Nekaris et al. 2013).

Measures to combat illegal trade are advancing, especially in the countries most affected by poaching activities. Law enforcement and conservation education in local communities to enhance sustainable livelihoods are the most promoted actions (Cooney et al. 2017). Cooney et al. (2017) made the reasonable assumption that for wildlife conservation to prevail over poaching activities, one of the essential conditions is that local communities benefit from being involved in wildlife conservation and that this engagement should provide greater benefits than those gained from illegal trade activities. Positively shifting the perception of conservation engagement by the concerned local communities serves to ensure their commitment and empowerment (Cooney et al. 2017), which in turn reduces the allure of illegal hunting. For example, conservation education such as workshops with communities, including targeted interventions, motivates the members of the communities to see the value in wildlife and start protecting the animals around them on their own accord while still obtaining benefits from wildlife resources (Cooney et al. 2017). Furthermore, adequate and powerful forms of enforcement can focus on motivated community members to feel included to protect wildlife and therefore become active partners in combating

illegal wildlife trade (Cooney et al. 2017). In this model enforcement plays a critical role as it upholds and protects the rights of individual community members, rather than potentially undermining them (Cooney et al. 2017).

## Hunting for Sport

Many national parks are currently under funded by governments, resulting in inadequate protection of native wildlife, enabling both illegal and poorly managed legal sport hunts to perpetuate. Some conservationists do, however, suggest that sustainable and well-managed trophy hunts can be a viable option to acquire necessary funding to protect endangered wildlife within those national parks. The premise of trophy hunting is that a permit is obtained that allows the participant, often a wealthy ecotourist, to track, hunt, and eventually kill charismatic fauna, whereby some of the monetary profits acquired from the lucrative sale of the permit is supposedly returned to conservation programs and local community development efforts. In some scenarios the sale of hunting permits is seen to be essential to the conservation of a whole community of wildlife within a protected range. However, mismanagement can jeopardize the feasibility of trophy hunting as a conservation tool and therefore exacerbate the hunting pressure exerted on highly sought-after species. This mediocre handling can be the result of a poor reinvestment of the trophy hunting proceeds into conservation and local community development.

Another issue regarding the sustainability of trophy hunting is the lack of long-term monitoring indicating whether or not hunted populations are still stable and therefore whether or not current management of the trophy hunting is appropriate. The resilience of wildlife populations to trophy hunting is considered to be species-specific. Wide-ranging species with low reproductive rates and sophisticated social structures are generally those most appealing to trophy hunters and are often keystone species to their respective ecosystems (Crosmary et al. 2015). Unfortunately, many species with the aforementioned

characteristics are classified as endangered on the IUCN Red List, and populations could quickly decline to an irreparable number if hunting is improperly managed. This status however has an intrinsic appeal to many hunters who are keen on hunting a “rare” and “alluring” species, which results in an inflated price to acquire a hunting permit for the species (Crosmarý et al. 2015). Contrastingly, hunting pressures can favor the survival of “less-desirable” species, or individuals within a species with less-appealing characteristics than another member of its group. For instance, Crosmarý et al. (2013) investigated the influence of trophy hunting on horn size for antelope in Africa. Longer horned individuals were preferred by hunters resulting in a relatively high hunting pressure expended on sable antelopes (*Hippotragus niger*) along with a higher valued price tag, compared to a relatively low hunting pressure in impalas (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*). Over time the hunting and killing of large-horned sable antelopes has resulted in an evolutionary response, with horn length having been found to have decreased.

One of the most dramatic downsides of the high market demand for rare and endangered animals is that these species are usually the least capable of withstanding any additional anthropogenic pressures. For example, the management of wild lion (*Panthera leo*) trophy hunting differs depending on country legislation, and therefore its conservation outcome also varies. Lion populations and their ranges in Africa have decreased considerably in the past 30 years. Nelson et al. (2013) estimate that 30% of lion populations have perished since 1970. Lions are among one of the most economically valuable species in Africa’s trophy hunting market mainly due to its charismatic perception by the general public. Recent debates regarding the lion trophy hunting industry focused on restricting trophy hunting as a measure to address concerns about excessive offtakes of lions which threaten its conservation status.

Tanzania, Southern Africa (including Zimbabwe, South Africa, and Namibia), and Kenya all boast an important lion population, and trophy

hunting occurs in all three regions. Tanzania hosts the second largest trophy hunting industry in Africa and holds four of the six remaining wild lion populations, with over 1000 breeding individuals recorded. Lions are particularly important to Tanzania’s hunting industry because, in contrast to nearly all neighboring countries, lions are legally included in the quotas assigned for the majority of hunting permits. Income generated by lion hunting is particularly lucrative as individual lions can bring in around \$70,000 (Nelson et al. 2013).

Furthermore, in Southern Africa trophy hunting accounts for 84% of annual revenue, by far dominating other regions in Africa. It also has a unique shared regional experience of adopting a number of important wildlife management and policy reforms that have led to wildlife recoveries across large areas of both private and communal land. Economically, trophy hunting can be significant. It makes up around 14% of the whole tourism industry in Namibia, which represents 2.3% of the total Namibian economy. The offer of hunting experiences for upper-income recreational hunters, mostly from Europe, is an important part of the Namibian tourism industry. Trophy hunting in Namibia is controlled both by government and private agents and is allowed on both private and public land (Humavindu and Barnes 2003). In 2000, an estimate of 13,310 game animals were shot by an estimated 3640 hunters, of which 84% were European tourists (Humavindu and Barnes 2003).

Finally, in Kenya hunting has been illegal since 1977; therefore it is the only African country with a population of over 1000 lions that does not presently allow any licensed trophy hunting. Despite the ban on trophy hunting, wildlife conservation efforts in Kenya have been recorded to be prominently unsuccessful (Nelson et al. 2013). Lion populations have declined by 60% to 70% since the 1970s in state protected areas and on communal lands. Lions in Kenya, although not subjected to any legal hunting, are rapidly declining because of human-wildlife conflict interaction and with consequence of killing through poisoning or other means, loss of habitat, and depletion of prey (Nelson et al. 2013). In these cases, it can

be interpreted that trophy hunting can provide conservation benefits for lions when well managed or alternatively constitute a significant threat when governance of the industry is poor (Nelson et al. 2013). The hunting of elderly, ostracized male lions who have already met their biological purpose of passing on their genes could still yield huge profits to benefit conservation and local development, without restricting the gene pool at all.

## Human-Wildlife Interactions

The margin separating the proximity of which humans and wild animals exist is shrinking on a daily basis. Humans are persistently encroaching on vast quantities of land once populated solely by wild flora and fauna as a result of global population growth. As a result, deforestation is occurring at an unprecedented rate in order to secure resources for the human species. Logging, mining, land tenure, and land degradation for livestock purposes are a few of the major activities that continuously disrupt wildlife ranges and the ways in which humans and wildlife interact. As a result of deforestation, natural habitats are destroyed, and areas that were once inaccessible to illegal hunters have opened up, allowing them to pursue wild game in areas in which this was previously unachievable (Chivian and Bernstein 2008).

One of the greatest threats toward humans in a world with an increased reliance placed upon wildlife and a greater likelihood of human-wildlife interactions occurring is the substantial risk for cross-species transmission. The risk of zoonotic disease transmission associated with hunting wild animals for bushmeat and traditional medicine is a topic of increasing interest to public health officials. One of the biggest issues with associated with zoonotic disease is that the animals react very differently to humans and may at first appear asymptomatic. It is well documented that wildlife can act as a reservoir for pathogens to multiply and later be passed on to humans who come into contact with contaminated bodily fluids. For instance, HIV-AIDS was first

transmitted to humans as a result of exposure to the bodily fluids of chimpanzees (*Pan troglodytes*) in West Africa, most likely during the preparation of their bushmeat (Chivian and Bernstein 2008). Those who ready the animal for consumption are at a disproportionately higher risk of transmitting disease due to the fact that they more frequently cut themselves during preparation. This event was likely the impetus for the global pandemic that is recognized today as HIV-AIDS. More recently, on December 6, 2013, the world's most prolific Ebola outbreak began. It was initiated by a 2-year-old in Meliandou, a small village that lies in the upper Guinean forest region, who became infected with a strain of the Ebola virus after eating contaminated bushmeat (Baize et al. 2014). The disease soon spread to more populous cities with international roads crossing to Sierra Leone and Liberia. The World Health Organization (WHO) was not notified of the outbreak until March 23, 2014, who then on August 8, 2014, proclaimed the epidemic to be a "public health emergency of international concern" (WHO Ebola Response Team 2014). By September 14, 2014, cases of the Ebola virus had been recorded in Guinea, Liberia, Nigeria, Senegal, and Sierra Leone (WHO Ebola Response Team 2014). The outbreak resulted in 28,616 cases and 11,310 deaths being recorded across the 3 most prominently affected countries (Guinea, Liberia, and Sierra Leone) (CDC 2016).

## Conclusion

The need to resolve the issue of global defaunation cannot be emphasized enough. Humans place a great deal of reliance upon wildlife and their resources. Thus, hunting plays a critical role in various cultural and economic pursuits for humans in both undeveloped and developed regions around the globe. The practice of hunting has become deeply rooted in many families' traditions and even extends to culture and religion. While remaining sensitive toward these traditions, and the facts that hunting can play a major role in food security, revenue generation, and local development, unsustainable hunting

practices will inevitably result in the loss of species, and a disjointed ecosystem will follow. Governance of hunting is weak and/or inadequate in many countries. The promise of community-based, devolved wildlife management models remains in most cases tantalizingly unrealized, while “top-down” models of centralized command and control often offer little promise of long-term sustainability and/or ignore or override indigenous or local rights and livelihood needs. Despite the necessity that we as humans place upon these animals, the need for collaborative, multifaceted, and environmentally stable models is pertinent.

While sustainable hunting, particularly for bushmeat, alleviates the atmosphere of greenhouse gases produced by the most common alternative, farm-bred animals, the future of some wild species victim to persistent overhunting is bleak. Most notably, species with long-life histories are those most susceptible to unsustainable hunting practices such as orangutans (genera: *Pongo*), chimpanzees, and elephants (genera: *Loxodonta*).

It is unrealistic to expect hunting of all wild animals to one day be completely abolished. However, the continued offtake of game can only be sustained for as long as hunting-induced mortality of any subjected species is exceeded by production (Fa and Peres 2001). Therefore, strict regulation and management is crucial to the survival of our most cherished species. Furthermore, outreach is needed to educate the public on the implications of speciation loss and the zoonotic threats that wildlife poses to humans. In order to be as effective as possible, efforts must incorporate culturally accepted practices (Reynolds and Bettinger 2008).

## Cross-References

### ► Bushmeat Trade

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## Husbandry

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## Synonyms

Animal care; Animal management

## Definition

Historically, animal husbandry was a term used to define the agricultural practice of raising



livestock. Its modern usage has evolved to incorporate all animals in human care, including exotic animals and companion animals. Husbandry can be described as the proper management and care of animals, including the regulation of water, food, environment, and breeding.

## Introduction

Although the term “husbandry” did not appear in the English language until the early fourteenth century, the discipline of animal management has been in practice for roughly 11,000 years (Vigne 2011). The domestication of livestock and development of a stock keeping system marked a monumental transition point in the evolution of the human lifestyle. The invention of this type of agricultural operation allowed for a more sedentary existence and eventual abandonment of the hunter-gatherer system, leading to the development of modern society. Over the centuries, the degree of human involvement and intensity of these management systems have gradually increased, with occasional spikes in activity as new species are domesticated or new technologies invented. Today’s animal husbandry methods are some of the most intensive to date, taking into consideration every aspect of an animal’s signalment, diet, environment, health, and breeding.

Good husbandry practices are a critical component of animal ownership. Despite the monumental strides taken to raise standards of care in the last 50 years alone, there is still much to be learned. Poor husbandry is still one of the leading causes of illness in certain species (Tully et al. 2012). Not only is husbandry one of the largest factors related to health and quality of life, but it also plays a role in several other controversial subjects. In agriculture, for example, the quality of animal husbandry is positively correlated with the efficiency of resource conversion. Therefore, management improvement leads not only to a higher production value, but also makes modern farming and ranching more environmentally sustainable. In fact, from 1994 to 2007, advances in technology and husbandry techniques resulted in a 59% increase of milk production in US dairy

farms while using 64% fewer cows (United States Department of Agriculture and National Agricultural Statistics Service 2010). In a time where excessive meat consumption has been accused as a source of significant greenhouse gas emissions (IPCC 2014), the importance of this effect cannot be overlooked. Good management also reduces the cost of agricultural products to consumers and improves food security and food safety. Another example of husbandry’s role in society relates to the controversy of using animals for research purposes. While the validity of the animal model continues to be hotly debated, it has been demonstrated that animals that are better cared for produce more accurate and reliable research findings (Prescott 2017). Regardless of one’s involvement in the animal care industry, the effects of animal husbandry continue to be pervasive in our everyday lives.

Of course, the major issue pertaining to husbandry still revolves around the ethics of animal use for human gain. Due to changing ideals and a greater respect for nonhuman life, there is a sweeping trend in today’s society to question the morality of animal exploitation (Fraser 2001). This is true for all animals in human care, whether they are being raised for meat and goods, in captivity for educational or conservation purposes, or being used for research. Some animal rights activists even go so far as to say that pet ownership is a form of captivity, as it restricts the free will of the animal. This scrutiny has necessitated the strict examination and improvement of common husbandry practices and in many cases, improved publicity of these practices.

## The Basics

The first aspect of animal care that should be addressed in a good management system is water. Water is the most critical nutrient in any diet and can be withheld for the least amount of time. In well-developed countries with quick access to running water, this necessity is easily oversimplified. Good management systems, however, take into account many considerations regarding the presentation and quality of the

water being delivered. Regular inspection of water sources should be conducted, ensuring that the water is free of pollutants and debris. In climates where standing water basins may freeze, thermoregulatory systems such as heated buckets should be employed. It is also necessary to regularly check the amount of water consumption that is occurring. For a single animal or a small group of animals, increased or decreased water consumption may be an early warning sign of disease. In larger herds or colonies where it may be more difficult to detect these subtle changes, monitoring is still an important component for detecting larger problems with the water delivery system. Some species may require extra considerations regarding the presentation of water. A good management system will ask questions such as, "Does this species or individual prefer flowing or running water?" and "Where is the best location for the animal(s) to be able to access water easily and comfortably?" An example of a specialized water delivery system is the pressurized spigot/water nipple system commonly employed when raising sows and piglets, which allows them to get clean water at an appropriate rate. In instances where an animal is not drinking sufficient amounts of water without any evidence of disease, it may be indicated to supplement the water with veterinary-approved flavorings, a practice commonly employed with horses. Although water may seem like one of the simpler aspects of animal management, the importance of this nutrient requires that it is never overlooked.

Another fundamental component of animal care is diet. Unfortunately, this aspect is far more complicated than a supply of fresh, clean water. Proper nutrition means something different for each species, life stage, and health status. Each diet should be formulated based on the specific needs of the animal, oftentimes requiring evaluation by a professional. In general, a good diet will consider the natural history and physiology of that species, the known requirements for each of the major nutrients, and research supporting the use of that diet. These considerations vary widely between species (and sometimes individuals within a species) and must be evaluated on a case-by-case basis. For example, despite the

relative similarity of cats and dogs in the grand scheme of the animal kingdom, feeding a diet that is intended for dogs to a cat could cause numerous detrimental health impacts because of cats' significantly higher requirement for protein (Zoran 2002). Adequate nourishment plays a significant role in animal health, resulting in lower instances of disease, a longer lifespan, and higher rates of production and fertility (Shepherd 2014). In some agricultural practices, low fertility rates are a common reason for a cow to be culled from the herd (Hersom et al. 2015), meaning that a good diet could actually be the difference between life and death. Nutritional intervention is also a commonly used medical management technique in certain diseases, such as the breakdown of struvite uroliths, a type of urinary stone, in canines (Lulich et al. 2016). Outward signs of a good diet may include softer coats, less dandruff, or neater feathers. In agriculture, this equates to a higher quality, and therefore value, of products such as wool or meat. When formulating a diet, the amount and frequency of feedings is an important factor. While some animals, like certain types of snakes, may only eat a meal once every few weeks, natural grazers such as horses do better on smaller feedings several times per day. Young animals also need to be fed much more frequently, and neonates may need their meals as often as every few hours. The feedings should be proportioned based on the metabolic demands of that animal or herd, as feeding too many or too few calories can lead to obesity or malnutrition, respectively, each of which comes with its own set of secondary health concerns. It is important to reevaluate a diet whenever changes occur to ensure that the most current information is being used and that the health of the animal(s) is maintained.

Environment makes up another important facet of animal husbandry. At its minimum, good housing will provide relief from extreme heat or cold, shelter from harsh elements, and space for most natural behaviors. Better management systems will also take into account disease mitigation, quality of life, and species-specific requirements. An excellent example of this is the revolution of modern animal habitats by zoos and aquariums.

Where concrete and metal cages used to be the standard, there are now intricate and precisely designed enclosures. Ideally, these enclosures are constructed in a way that allows for the safety of the animals and keepers, the ease of husbandry or medical procedures, and the encouragement of natural behaviors. The best husbandry systems will take a wide variety of factors into account, including the temperature and humidity, ideal type of soil or bedding, the right amount of sun versus shade, the number of trees available to climb or nest in, the types of structures to hide behind or dig under, etc. Again, the necessities for each species vary widely and should be evaluated by someone with extensive knowledge of their specific needs. Disease mitigation is another important factor of enclosure design. It requires consideration of animal density, the types of species that are interacting with each other, and even the air flow and housing materials. In general, a less densely populated environment with fewer cross-species interactions has a lesser risk of disease outbreaks. Air should flow in a way that prevents aerosolized infectious agents from settling in the environment, and materials in the environment should be easily cleaned or replaced. New or ill animals that have the potential to shed infectious organisms should be quarantined from the rest of the group, typically for 28 days. While a well-managed environment may not have the obvious or immediate health implications as that of water or nutrition, it can have enormous impacts on quality of life and psychological state (Wolfensohn and Honess 2005).

In most instances, breeding management is also an important part of animal husbandry. Selective breeding has been used since the domestication of the wolf centuries ago (Vigne 2011), leading to the many different dog breeds we have today. It plays a particularly large role in livestock, where certain qualities are far more valuable than others. Selective breeding can improve the quality and marbling of meat cuts, the rate of gain or size of an animal, the value of products such as hide or wool, and the hardiness of the animal. This prevents undesirable traits such as susceptibility to disease from being passed down to new generations and contributes to the

increased productivity of modern agriculture. Today, breeding management is also an important part of exotic animal conservation. In 1981, the Association of Zoos and Aquariums (AZA) created the Species Survival Plan Program, which allows for the population management of certain species that are of critical status in the wild (Association of Zoos and Aquariums 2017). This process involves the coordination of hundreds of facilities and often involves the temporary transfer of certain individuals to be with their genetically ideal mates (colloquially known as being on “breeding loan”). Careful planning of known family lines and the development of new biotechnologies make it possible to foster offspring that can help maintain the biodiversity of a given exotic population the same way that it can improve the productivity of the modern livestock industry (Renaville and Burny 2002).

## Additional Considerations

Given the overwhelming diversity of the animal kingdom, there is no comprehensive list of the factors a husbandry system must consider to be complete. Each species has additional considerations that must be evaluated. Sometimes even individual animals within a species require special deliberation. It is important to consult the current literature as well as experienced personnel in order to assure that all potential issues have been addressed. In instances where there is limited information available, it is not uncommon to extrapolate data from closely related species, but this method should be used with caution. Additional items to consider may include nail, hoof, or beak trimmings; the harmoniousness of social groupings; the ability to perform natural behaviors; and mental stimulation with enrichment activities (Wolfensohn and Honess 2005).

Zoos, in particular, tend to employ the use of environmental enrichment devices (EEDs), which are toy-like items commonly used to stimulate animals and prevent stereotypic behaviors related to boredom. If EEDs are going to be used, they should first be evaluated for safety (not containing toxic materials, not able to be broken apart or

ingested, etc.) and also for their relevance to the natural behaviors of that species. Other forms of enrichment include the presentation of unusual food items, the deliberate positioning of food in locations that encourage hunting or foraging behaviors, and even music. Training behaviors can also be used to add mental stimulation, help forge a human-animal bond, and also facilitate animal health while maximizing human safety. This method is most commonly performed in zoological environments, where most animals' first training exercises are approximations towards behaviors that facilitate medical procedures, such as taking medications or blood collection. Regardless of the type of animal, good management systems will consider these additional needs and meet them with methods appropriate for that species.

It should be evident at this point that the development and implementation of good husbandry practices is not a one-man job. "It takes a village," as it were, and there are several other sources that should be consulted when establishing an animal management system. As discussed previously, proper nutrition is of vital importance to overall health. In instances where thoroughly researched diets (e.g., well-known commercial pet foods) do not already exist, it would be prudent to hire a nutritionist who has experience working with the given species. Another resource of information that must not be forgotten is the veterinarian. Veterinarians possess additional knowledge that permits them to make clinical judgments regarding the health of an animal and detect illnesses that may have been overlooked by others. They will be able to recommend when treatment is indicated and what precisely that treatment should include. Preventative care is also an important aspect of husbandry, and a veterinarian can advise when certain therapies are necessary, such as vaccinations or parasiticides. Some veterinarians have gone through additional training to become board-certified in various areas of medicine; their expertise may be required when dealing with more complex cases. Note that good record keeping is also an important part of animal health, and thorough documentation should be made of any treatments or therapies administered.

A final resource that should not be overlooked is the body of current literature. Peer-reviewed articles or manuals can provide more in-depth instruction for the specific requirements of the species at hand, the value of which cannot be underestimated. In order to ensure the best quality of care, it is essential that the husbandry team, veterinarian, and any other parties involved work together to develop a comprehensive action plan for animal care.

## Relationship to Welfare

A good state of animal welfare is the direct result of proper husbandry. Just as with humans, good animal care takes into account physical, mental, emotional, and social wellbeing. In recent years, public concerns have drawn particular attention to the welfare of animals, regardless of whether they live on a farm or in a zoo. Unfortunately, there is no formal consensus as to what measurements should be used to evaluate welfare. One of the earlier and certainly most notable attempts to create a systematic assessment is from the 1979 publication of the Farm Animal Welfare Council. It introduced a list that is commonly referred to as the "five freedoms" and includes freedom from hunger or thirst; freedom from discomfort; freedom from pain, injury, or disease; freedom to express (most) normal behaviors; and freedom from fear or distress. Yet even this modest list is not without its complications, particularly when one or more "freedoms" do not coincide. One example of this is the housing of hens in battery cages. While this housing style restricts movement and can induce abnormal behavior (Duncan 2001), it is also associated with fewer instances of diseases (Fossum et al. 2009). Still, others cite physiologic evidence (growth rate, health, and behavior) or subjective experiences (ability to access desired stimuli and absence of avoided stimuli) as a way to measure welfare (Mendl 2001). Despite the many attempts that have been made to determine whether an animal's husbandry is adequate, our evaluations are at best close approximations to what we think they may be experiencing and never the precise reality. For

example, if an employer were asked to judge the welfare of their employees, they might evaluate a number of factors including punctuality, physical appearance, and attitude; however, as we all know, the ability to show up to work looking moderately presentable and exchange pleasantries does not always equate to the pinnacle of welfare. Given that we are by no means experts at assessing the welfare of members of our own species, it is no surprise that we struggle to do the same for our animal charges.

However, definitive standards of care are in place to ensure a minimum level of wellness and in many cases will define “best of care” practices. These husbandry requirements are set by many different groups at various levels of enforcement. Towards the lower end of this spectrum are group bylaws or codes of conduct. Many organizations, including the AZA and the Pet Industry Joint Advisory Council (PIJAC 2017), provide their own set of standards that must be followed in order to be a part of their association. In some cases, governmental entities can also recommend a certain set of standards within their jurisdiction. An example of this would be the counsel and regulation of facilities that house marine mammals at the national (Canadian Council on Animal Care 2014) or local (Ontario Ministry of Community Safety and Correctional Services 2014) levels. In contrast, the Animal Welfare Act (1966) is the only federally enforced law that regulates the treatment of animals in the United States. It is undeniable that without thorough knowledge and implementation of good animal husbandry practices, good welfare would be unattainable.

## Conclusion

Animal husbandry is ubiquitous in modern society. It has a significant role in numerous aspects of everyday life, from pet ownership, to animal welfare, to consumerism. While the debate regarding the utilization of animals for human purposes will likely never end, it is generally agreed upon that adhering to the best known standards of care is hugely beneficial for both animals and humans

alike. With due consideration of proper water, nutrition, shelter, and breeding practices, we are better able to ensure the optimal health and wellbeing of the animals in our care.

## Cross-References

- ▶ Animal Society
- ▶ Animal Welfare
- ▶ Captivity
- ▶ Conservation
- ▶ Corticosterone
- ▶ Diurnality
- ▶ Domestication
- ▶ Ethogram
- ▶ Farrowing Crate
- ▶ Feed Industry
- ▶ Feeding
- ▶ Fertility
- ▶ Foraging
- ▶ Group Living
- ▶ Herbivore
- ▶ Human-Animal Interaction
- ▶ Nest Construction
- ▶ Nutrients
- ▶ Omnivore
- ▶ Pets
- ▶ Play Behavior
- ▶ Reinforcement
- ▶ Sleep
- ▶ Social Behavior
- ▶ Sociosexual Behavior
- ▶ Species-Specific Behavior
- ▶ Stress
- ▶ Zoo
- ▶ Zoology

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## Hybrid

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## Definition

The progeny of a mating couple from two distinct genetic populations.

## Description

The resulting offspring of two genetically non-identical species is deemed a hybrid. The genetic and/or phenotypic characteristics of a hybrid can be anywhere from a duplication of one parental genus to an even mixture of the two parental species. The hybrid may also be a novel entity without physical similarities to either parent (Evin et al. 2015). Subsequent generations of hybrid breeding can lead to increased genetic and phenotypic diversification and eventual speciation, or the development of a new species (Buerkle et al. 2003).

Some examples of hybrid species include the mule (the F1 progeny of a male donkey and female horse) and the hinny (the F1 progeny of a male horse and a female donkey). Both of these hybrid species are almost always sterile, although there is record of a female mule giving birth after mating with a donkey. The owners of the unlikely foal say it has horse, donkey, and mule-like physical characteristics (Rong et al. 1985).

## Fertility and Viability

Continued hybrid breeding can have varying effects on a species based on fertility and the viability of the hybrids formed. Fertile hybrids can be backcrossed to one parental species to introduce genetically favorable traits and potentially increase the adaptability of the parental species. Hybrids may also interbreed to eventually form a new species. If the genetics of the novel species are more evolutionarily favorable than those of the parental species, one or both of the parental species may become extinct. The novel species, in essence, may replace the parental species as a more evolutionarily robust alternative.

In contrast, hybrid progeny may be infertile or even inviable. Continued unsuccessful mating or production of such offspring can lead to a population decrease of the parental species and threaten extinction if not properly balanced with successful reproduction (Goulet et al. 2017).

## Natural and Artificial Hybridization

Natural hybridization occurs when two unique species successfully mate in the wild without human intervention. At present, natural hybridization is relatively rare; however, genetic testing has shown evidence that hybridization occurred at least once during the evolution of myriad plant and animal species in existence today. It can be beneficial to study some of these occurrences to more-intricately analyze changes in the flow of genes during evolutionary selection (Abbott et al. 2016). Additionally, comparing the genetic similarities and differences between species can help to reveal their relative divergence time (Goulet et al. 2017). Thus, natural hybridization can help to decipher the path of complex phylogenetic trees and allow humans to gain insight into not only how current species have evolved into being but also how they may continue to evolve over time.

Artificial hybridization involves human interference with the mating practices of two species, often by selecting the mating pair that will form the hybrid progeny. The development of hybrid

species through human-controlled hybridization allows for the creation of unique systems that can be considered more biologically advantageous. Humans can use hybridization data to increase the amount of genetic variability and experimentally select for traits most beneficial for a specific purpose. Examples for selected traits include size, disease resistance, diet, and physical appearance (Zhang et al. 2014).

Artificial hybridization, although beneficial, still has its limitations. It can take many generations to observe a distinct difference in phenotypic and/or genotypic characteristics in a hybrid line. The length of time to attain multiple generations can vary from days to decades depending on the organism. Sexual compatibility and hybrid fertility are other obstacles commonly encountered when trying to create a hybrid line. To break through some of these barriers, scientists have developed ways to genetically modify crops using methods such as radiation treatment as well as cellular and molecular techniques (Raybould and Gray 1993). While the use of these techniques is controversial, they allow for new types of hybridization once never thought possible.

## Cross-References

- ▶ [Artificial Selection](#)
- ▶ [Divergent Evolution](#)
- ▶ [Domestication](#)
- ▶ [Gene Targeting](#)
- ▶ [Speciation](#)

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## Hybrid Vigor

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## Synonyms

[Heterosis](#)

## Definition

Hybrid vigor or heterosis can be defined as the superiority of F1 hybrid over both the parents in terms of productivity and robustness.

## Introduction

Heterosis can be defined as increase in the vigor that is observed in progeny after mating of diverse individuals belonging to different species or population. It is of immense economic value in the field of agriculture. Heterosis has been harnessed for increased productivity and better livestock that results in crop improvement. Although it is a well-known phenomenon, underlying mechanism still needs to be explored.

## Origin and History of Hybrid Vigor

The phenomenon of heterosis is known for its superior or improved agronomic performance via heterozygous F1 hybrids in comparison to two genetically different homozygous parents. This superiority can be in terms of product yield, biomass, size, fertility, development, and resistance to environmental calamity of any kind when compared to their homozygous parental inbred lines (Hochholdinger and Hoecker 2007). Hybrid vigor is used as a synonym of heterosis. Koelreuter (1763) first reported heterosis in the hybrids of tobacco, *Datura*, etc. Mendel later on (1866) observed this in pea crosses. A long-lasting mystery of hybrid vigor was first described by Charles Darwin (1876) after observing the progeny of cross-pollinated maize (*Zea mays*) which were 25% taller than progeny of inbred maize. Heterosis has been exploited since decades in the field of horticulture and agriculture. It has been a matter of debate, whether it's the genes at multiple loci or the molecular complex inherited pattern behind the underlying cause of heterosis.

A number of enthralling hypotheses are converging toward a consensus explanation incorporating differential gene expression pattern as well as one or more metabolic pathways affecting yield of the crop behind the manifestation of heterosis. With recent advancements in functional genomics, transcriptomics, proteomics, and metabolomics, we end up having clues from genetic, transcriptomic, as well as epigenetic studies (Baranwal et al. 2012).

- (i) **Genetic hypothesis:** According to the genetic model of heterosis, both “dominance” and “overdominance” nonadditively explains phenotypic behavior as a consequence of differences in the genetic component of individual homozygous parents and the hybrid generated. The dominance hypothesis explains the increased vigor of hybrid progeny results due to complementation of superior dominant allele from both the parents at multiple loci over unfavorable allele (Bruce 1910) The “overdominance” hypothesis explains heterosis on the basis

of allelic interaction at multiple loci in hybrids resulting in much superior traits when compared to their homozygous inbred parental lines (Hochholdinger and Hoecker 2007). Recent literature along with genetics reflects the involvement of epigenetics in heterosis.

- (ii) **Molecular hypothesis:** To establish a causative link between heterotic phenotype and the molecular mechanism involved is the greatest challenge faced by many researchers. They proposed a “phenomics” platform where they focused on high-resolution quantitative trait locus (QTL) mapping for measuring multiple traits with the thought of dissecting the fundamental components of heterosis (Lippman and Zamir 2007). It is well known that environment plays an important role in the manifestation of heterosis, so QTLs may respond differently in greenhouse when compared to field conditions. Although various molecular studies showed the involvement of various loci in heterosis, no QTLs associated with heterosis have yet been cloned.
- (iii) **Epigenetic hypothesis:** As heterosis is a genome-wide phenomenon, global genetic and protein expression alterations are not new to discuss. It is very clear that heterosis results from complex interaction occurring inside the nucleus of a hybrid. Besides the interaction of genes from homozygous inbred lines, DNA methylation machinery and its regulatory components would also interact in supporting epigenetic status of heterosis. In the past 3–4 years, global methylation, siRNA distribution, and miRNA expression pattern have been analyzed (Ha et al. 2009). Altered methylation levels were correlated with the transcriptional status of the genes in hybrids. Increasing knowledge of epigenetic signatures provide new prospects to understand the reason for non-inheritance of F1 heterosis traits in subsequent generations (Groszmann et al. 2011).

Still after various heterosis-related studies, one can say genome sequencing of several

genotypes can help in understanding the importance of genomic organization. Differential expression profiling and microarray data of different genotypes and at different developmental stages might help us in explicating inbred lines with the hybrids generated. Data available so far showed no correlation between genetic component and molecular hypothesis related to heterosis. Heterosis is a result of gene diversity, pathways known and yet to be discovered. Not a singular, unifying mechanism can explain the process of heterosis. We should focus on recent and advanced genomic resources to dig out the Mendelian factors involved behind the process of hybrid vigor. It might solve an issue of evolutionary relationship of heterosis and help in crop improvement.

## Cross-References

- [Heterozygote Superiority](#)
- [Hybrid](#)

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## Hydroregulation

### ► Water Balance

## Hymenopteran Eusociality

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### Introduction: The Paradox

Eusocial insects posed early difficulties for the theory of evolution by natural selection, so much so that Darwin (1859) himself described the dilemma as follows:

...first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind. (p. 269)

In response to this perceived challenge to his theory, Darwin would go on to provide an explanation for selection occurring at the unit of the *family*, stating that the reproducing morph (e.g., the “queen”) within any given family (the “colony”) serves as the indirect route through which all of the highly specialized, but sterile, morphs (such as the “workers” and the “soldiers”) propagate. Although Darwin evidently believed that this provided an adequate description of the situation, certain theoretical quandaries persisted. Most notably, Darwin’s eusocial insect *family* happens to simultaneously constitute the whole insect *society*, as the entire colony is typically (but not always) of one lineage. Thus, how shall we today construe the action of natural selection on these systems? Can a clear distinction between *kin selection* and *group selection* be drawn?

## Hamilton’s Solution

These issues, among many others, caught the eye of a young W.D. Hamilton, who published his approach to understanding the evolution of eusociality in 1964, called *inclusive fitness theory*. To illustrate his theoretical framework, Hamilton referenced the *Hymenoptera*, a large order of insects in which all of the stinging insects, meaning the *Aculeata* (ants, bees, and wasps), are found, which includes approximately 14,000 eusocial species. Specifically, he discussed their unusual form of sexual reproduction, known as *haplodiploidy*, a process that results in a female wasp having higher genetic relatedness with her full sisters ( $r = 0.75$ ) than with her very own daughters ( $r = 0.50$ ). The proportions of shared genes between her and her full sisters and her and her daughters are represented here by  $r$ , otherwise known as the coefficient of relatedness between two individuals. The female wasp may then, if driven to pass on the maximal number of copies of her genes, aid the efforts of her mother in producing more full sisters, rather than have daughters of her own. Such decisions are what have been presumed to have led to the “sterile” worker caste found across many of these species. In these cases, sterility applies only to the production of diploid daughters, which cannot be done by the worker female, because these individuals do not possess a *spermatheca* for the storage of sperm, and daughters are only able to hatch out of fertilized eggs. On the other hand, haploid sons can sometimes be produced by workers, as they are able to hatch out of unfertilized eggs through parthenogenesis. Asexual reproduction of this sort is not common, however, as most attempts by worker females to do so are thwarted by either other workers or the queen, who simply consume the eggs upon discovery.

Thus, the altruistic behavior of eusociality, which previously appeared to hold more costs than benefits, could now be seen potentially beneficial in terms of reproductive fitness due to the action of this principle, which has been termed *Hamilton’s rule*. However, his theory of inclusive fitness does not apply only to the Hymenoptera. The logic of Hamilton’s Rule is generalizable to



any situation in which the relative coefficients of relatedness support the *inclusive* fitness benefits outweighing the costs. Quantitatively, this inequality can be expressed as follows:

$$rB > C$$

As discussed above,  $r$  represents the coefficient of relatedness between two individuals,  $B$  is the cumulative representation of benefits resulting from altruism, and  $C$  is the cumulative representation of costs resulting from altruism.  $B$  and  $C$  are considered in the context of reproductive fitness.

J.B.S Haldane is known for the quip that he would “lay down his life for eight cousins or two brothers.” This provided an early description of the later-named process of *kin selection*. This mechanism provides individuals with the ability to succeed reproductively by investing bioenergetic and material resources in the propagation of those genes they share with others, rather than solely in those that they share with their own offspring. Hamilton (1964) equated this notion of Haldane with his inclusive fitness theory. Twenty years later, it was used by Brandon and Burian (1984) in an attempt to better articulate the opposition between supporters of individual and group selection. Since both kin selection and inclusive fitness theory involve the directing of altruism towards whoever shares the most genes with a given individual, Hamilton (1964) considered them to be identical and did not attempt to draw any theoretical distinctions between the two. To simplify this concept, both ideas were taken to be grounded in the notion that recent genetic descent from a common family member provided the shared genes.

## A Continuing Conundrum

Though that story began answering key questions about the Hymenoptera, it was far from conclusive. One main issue is the fact that approximately 136,000 Hymenopteran species are solitary, not eusocial, yet continue to reproduce by means of haplodiploidy.

Additionally, Hymenoptera is not the only order where eusocial insects are found. In fact,

three other orders contain eusocial species: the *Isoptera* (containing all eusocial termites), the *Homoptera* (with some eusocial aphids), and the *Thysanoptera* (with some eusocial thrips). Yet, only the Thysanoptera are haplodiploid like the Hymenoptera. Some Homopteran species are eusocial, but all are diplodiploid like humans. And all Isopteran termite species are both eusocial and diplodiploid.

Despite their not being haplodiploid, many have still attempted to place termite eusociality within the purview of inclusive fitness theory and kin selection, contending that “If relatedness between helpers and reproductives produced averages of 50%, as is the case in monogamous families, only slight ecological benefits are required to favor helping alleles” (Howard et al. 2013, p. 1). In this theory, it is understood that the surrounding ecology can alter fitness tradeoffs enough for the promotion of altruism without large differences in relatedness, like those of the Hymenoptera, ever being necessary. Despite these observations, other researchers have continued searching termites for analogous cases of haplodiploidy. Lacy (1980) hypothesized that the translocation complexes of sex-linked chromosomes should generate higher intrasex coefficients of relatedness than intersex. Others predicted that some form of extensive inbreeding would be the culprit. And finally, some researchers even argued that inbreeding-outbreeding cycles, occurring both intra- and intercolonially, would yield greater intragenerational relatedness than intergenerational, bolstering  $r$  to levels like those of some Hymenoptera. All of these hypotheses would eventually be put to the test with multilocus DNA fingerprinting (Husseneder et al. 1998, 1999), with none proving conclusive. Instead, Husseneder and colleagues concluded that “ecological factors and constraints must be considered a major selective force.”

In summary, these findings demonstrate that standard parent-offspring and full sibling-sibling diplodiploid relatedness of 0.5 (or one even lower) can still lead to the development of eusociality, as long as the local ecology ends up favoring more selective benefits than costs.

Thus, the extreme case of a sister’s relatedness outnumbering that of a daughter by a full quarter is

not required for eusocial behavior. Incidentally, Hamilton's rule always expressed this principle quantitatively; however, solid empirical proof at the molecular-genetic level was absent until Husseneder and others' analyses. In the Hymenoptera, we can see how their haplodiploidy-induced coefficients of relatedness could facilitate the evolution of eusociality, without being either necessary or sufficient. Such an outcome can occur from a multitude of permutations of contributing factors, as long as they result in fitness benefits.

## The Evolutionary Natural History of Eusociality

This theory finds itself further supported by evidence from the natural history of some primitively social wasps. The traditional haplodiploid story of bonds formed intergenerationally among mother and daughter in newly founded colonies was determined, by West Eberhard (1967), not to apply very well to the least evolutionarily developed societies of wasps. Instead, these colonies formed intragenerational *foundress associations* among networks of females who varied in genetic relatedness to one another but were all fully fertile. The many challenges faced by such associations among group members, especially for the most urgent cooperative activities (such as nest defense and raising offspring), result in the pressures of kin selection being extended all the way to "quite distant relatives" (West Eberhard 1975, p. 1). In the further evolved societies of eusocial wasps, along with comparably advanced eusocial ant and bee societies, the *monogynous* process of "worker" females becoming full-time "nest attendants" for the singular foundress queen becomes quite uniform. However, this likely did not occur *ancestrally* in their early evolutionary history and is instead *derived* subsequently, in the case of the social wasps.

Such findings are not intended to imply that imbalances of genetic relatedness are wholly irrelevant to eusociality, rather that they are one of several variables working in concert as it evolves (e.g., Bourke 2014; Kapheim et al. 2015; Waibel et al. 2011). Additionally, one must not ignore Tinbergen's (1963) *Four Questions* and the key

role of *phylogeny* in this narrative. Along these lines, Evans and West Eberhard (1970) provided the following evolutionary history when discussing the evolution of sociality in wasps:

A brief summary of the apparent major steps in the evolution of nesting behavior of solitary wasps may assist in an understanding of the origin of sociality. These steps are progressive in the sense that they must occur in approximately this order and that they lead from simple to more complex behavior. They may be thought of as "rungs in the social ladder" in the sense that the social wasps must once have "climbed" them (Fig. 75); but of course each rung must have its own adaptive value, since many wasps inhabit each rung successfully and the evolution of sociality was by no means preordained. (pp. 114–115)

This inquiry was continued exhaustively, with several subtypes nested within seven overarching steps of social wasp evolution from solitary origins. The resultant list of Hymenopteran milestones on the road to eusociality concludes their findings:

We considered four developments to be preadaptations to sociality: (a) the possession of a nest to which the female returns repeatedly; (b) placement of numerous cells at one site; (c) provisioning more than one cell at a time; and (d) increased longevity of females. All of these would contribute to the likelihood of nesting in groups and, in particular, in groups of close relatives. . . (p. 203)

Herein we find a more thorough explanation for the Hymenopteran universal of haplodiploidy, but relative rarity of eusociality. Those species which are today eusocial succeeded in climbing this social ladder, resulting in the adaptation of behaviors embodying such sociality. This now makes haplodiploidy just one factor among many aiding in the evolution of eusociality. It is not a requirement for such evolution to take place, nor is it a sufficient cause alone when present. Further, and surprisingly for some, Wilson and Holldobler (2005) revealed that the correlation between haplodiploidy and eusociality across species is not even statistically significant.

## The Comparative Method

To get a better picture of the many contributing factors that might be involved, we may step back

and productively apply the *comparative method* to determine which of many permutations of these putatively causal influences might yield eusociality in other taxa. Looking beyond the Hymenoptera, we see that the eusocial termites also possess preadaptations of sociality. One common example takes place when they periodically moult out of their exoskeletons, along with their internal gut lining. Lost with the gut lining are the symbiotic gut protozoa, which allow termites to digest wood and are thus required for survival. To replenish these essential microbiota, the recently moulted termite must consume the anal secretions of nearby conspecifics. This process tilts termites in the direction of increased sociability, which likely contributes to their many other expressions of social behavior, like the construction and defense of nests, protection of offspring, and gathering of vital nutrients. A distinction between wasps and termites, however, is the complete lack of solitary species of termite. Eusociality appears to be universal in that order. Thus, our phylogeny above cannot be as illustrative in explaining their case.

Further complicating matters is the story of the eusocial aphids (Homoptera). They are typically found producing and inhabiting *galls*, insect-induced tumors that spread on their plant hosts. Female aphids are produced parthenogenetically, and a subsection of species have even developed sterile “soldiers” who will reliably sacrifice themselves in battle against any parasites and predators. Inside of these clonal aphid colonies, we find a coefficient of relatedness of 1.0, greater than those full sisters of the Hymenoptera. Presumably, this would lead them to develop even stronger altruistic tendencies through kin selection. However, many aphid colonies have been found with equal relatedness and *without* any signs of eusociality. The preadaptive variables relevant to aphid eusociality are still to be discovered (Abbot 2009).

Lastly, comparable to these aphids, the galls of some thrip (Thysanoptera) species are known to have evolved self-sacrificial “soldier” castes, but the thrips are haplodiploid, and instead of approaching the aphids’ complete clonality, mirror the Hymenoptera with their variable coefficients of relatedness. And similar again to the

Hymenoptera, all Thysanoptera are haplodiploid, while these thrips have only evolved a select number of eusocial species (Gadagkar 1993). Due to greater inbreeding coefficients, the original eusocial thrips are found to possess higher intragroup relatedness, fitting better within kin-selected explanations of altruism (Chapman et al. 2000). Similar hypotheses were levied for the eusocial termites but still lack empirical grounding.

## Multilevel Selection

These examples assist in bringing us back to the dilemma of kin selection versus group selection in explaining insect eusociality. As it now can be shown, neither need be selected over the other. The battle, which some still fight today, was created by early supporters of kin selection (Bahar 2017). These theoreticians viewed group selection as distinct, and occasionally, as completely false. Meanwhile, some group selectionists looked upon kin selection as a subtype of their broader theory, bolstered in its descriptive capacity by relatedness. And though some group selectionists spoke positively upon kin selection, the sentiment was not returned. This is further stated by D.S. Wilson as follows (<https://evolution-institute.org/blog/the-tide-of-opinion-on-group-selection-has-turned/>):

An important development in the history of thinking on kin and group selection is called equivalence – the possibility that the two theories do not invoke different causal processes and are inter-translatable, thereby deserving to co-exist rather than one replacing the other.

Even W.D. Hamilton altered his original stance. This was documented by Sober and Wilson (1998), who discussed Hamilton’s autobiographical essays, where conversations with George Price are shown to have catalyzed the shift. Price, a chemist turned evolutionary biologist, created the famous *Price Equation*, which took Hamilton’s kin selection and mathematically placed it within the theoretical purview of multilevel selection. Instead of adding formulae on relatedness between two individuals, Price

quantitatively addressed the relations between intra- and intergroup gene frequencies.

In so doing, Price (1970, 1972) placed both multilevel selection theory and inclusive fitness theory under one quantitative umbrella, greatly eliminating theoretical distinctions which had previously seemed irreconcilable mathematically (e.g., Frank 1995; Gardner et al. 2011; Hamilton 1975; Korb and Heinze 2004; Kramer and Muenier 2016; Leigh 2010; Lion et al. 2011; Marshall 2011). With this, the *Price Equation* yields the first-ever mathematical model of multilevel selection, through combination of the factors underlying both intra- and intergroup covariance. Wilson and Wilson (2007) have described its impact:

Hamilton's key insight about the importance of genetic relatedness remained valid, but his previous interpretation of inclusive fitness theory as an alternative to group selection was wrong, as he freely acknowledged. (p. 335)

The conversation between Hamilton and Price resulted in this paper: *Innate Social Aptitudes in Man: An Approach from Evolutionary Genetics* (1975). Sober and Wilson (1998, p. 75) summarized it by writing that "...Hamilton re-described inclusive fitness theory as representing a multilevel selection process." The authors believe that Hamilton moved closer than ever before to agreement with Darwin, commenting more extensively that:

Hamilton now saw the multi-group nature of social interactions, regardless of when and where breeding occurs. Social interactions among genetic relatives correspond to the nonrandom formation of groups. The significance of relatedness for the evolution of altruism is that it increases genetic variation among groups, thereby increasing the importance of group selection. Furthermore, any process that increases variation among groups will accomplish the same job... Genetic relatedness loses its status as the exclusive factor responsible for the evolution of altruism and becomes one of many factors that can promote group selection. Hamilton (1975) left no doubt that the difference between inclusive fitness theory and group selection theory is a matter of perspective, not process. Earlier (1963) he had said that group selection should be treated with reserve so long as it remains unsupported by theoretical models. Now those models were available and the major so-called competing theory had vanished. The only process to explain the evolution of altruism was the one that Darwin identified long ago. (pp. 76–77)

Both Price's late-career discovery in a new field and Hamilton's agreeable compliance with its implications for his theory are inherently uncommon, and commented on as such in Price's biography, written by Frank (1995). Instead of defending his views to the grave, Hamilton appeared to be quite pleased with the *post-Price synthesis* of inclusive fitness theory. However, as noted by Sober and Wilson, the rest of his field did not behave so openly. Hamilton's later publications received far fewer citations and general approval from those who had previously embraced him. Most, instead of supporting Hamilton, chose to hold course and maintain a segregated view of kin and group selection. Hamilton (1996) discussed this reception, noting that his 1975 paper was not only cited infrequently but also found itself prone to mischaracterization when cited. Dawkins, for example, cited Hamilton's work in order to claim victory over group selection. The thought of Hamilton remaining fixed in his pre-1975 state seemed bizarre to Sober and Wilson, who marvel at the selective treatment of his work after connection with Price's.

In his 1975 work, Hamilton carefully articulated the separation between kin selection and inclusive fitness theory as being predicated on whether or not recent common descent explained the spread of genes within a group. He went on to demonstrate that this notion of transferring genes through recent common descent was solely used to clarify his quantitative model, not to hold fixed status as a required theoretical facet in understanding altruistic and eusocial evolution. The difference between the two theories was therefore based on this simplification. Kin selection theory held the clarification to be true and necessary, since relatedness among kin was a required part of the term, and inclusive fitness theory was said to be operable without proof of sharing genes through recent common descent.

## The Controversy

Regardless of all this theoretical progress, Dawkins (1976) and others of his same persuasion

continued writing on the belief that sharing genes through recent common descent was required for the evolution of altruistic behavior by kin selection. Others, however, found different solutions to this theoretical problem. With his *genetic similarity theory*, Rushton (1989) claimed that individuals could reliably perceive genetic variance, whether directly related or not, as well as whether consciously or not. This, in his view, forms the basis of human relationships and enduring partnerships. Genetic similarity theory differs here from kin selection in its lack of requirement for shared genes wherever sociality and altruistic behaviors are expressed. Thus, genetic similarity theory diverges from kin selection at the very assumption as does Hamilton's (1975) inclusive fitness theory. In fact, the two theories appear nearly identical when viewed alongside each other. Nevertheless, Dawkins and others failed to acknowledge the potential validity of either, levying the same critique based on an insistence upon the simplifying assumption of shared common descent.

Today, an increasing number of *neo-group selectionists* (Okasha 2006) have written on the theoretical and quantitative accuracy of group selection. With Wilson and Sober's determination that group selection reaches grounds for both plausibility and strong explanatory power (Okasha 2006, p. 177 *et seq.*), kin selection now finds itself again placed within the broader group selection. As Nowak et al. (2010) claim, it is kin selection, not group selection, which "requires stringent assumptions, which are unlikely to be fulfilled by any given empirical system." Found here is the exclusion of processes requiring synergism or the interaction between more than two individuals, as it is assumed that such behaviors are additive and pairwise. Additionally, inclusive fitness theory can only be applied to a limited range of population types (Bahar 2017, p. 277). This places Nowak, Tarnita, and Wilson in solidarity with one another, observing that inclusive fitness theory describes nothing that is unexplainable by group selection.

When observing cooperative group behavior and underlying structure, these present neo-group selectionists place more weight on

ecological variables than relatedness. This is primarily so because of the findings on eusocial insects. In one striking case, researchers both discovered natural super-colonies of unrelated termites and successfully caused the creation of artificial super-colonies in a lab environment by experimentally placing ecological pressures on colonies of genetically unrelated termites (Howard et al. 2013). Combined with the literature above, we continue to find that eusociality and relatedness correlate weakly.

Whereas high levels of relatedness had always been seen as contributory to eusociality, with contention on whether or not it was invariably required, Nowak and colleagues posited that *ecology* should instead hold primacy of causal position. Yet, most still see genetic relatedness as a catalyst for eusociality. Though Hamilton and Wilson agree on its necessity, Wilson has more consistently modeled-in potential nongenetic ecological factors, implicitly lowering his weighting of relatedness. With these distinctions drawn, we are now able to describe, far more lucidly, the true impact of relatedness on cooperative structures where several potential drivers coexist. Relatedness remains necessary, but now within a wider contextual footprint so that its proportion and connection with other variables can take theoretical precedence over its previously perceived supremacy.

Moving to other areas of the solely theoretical literature, we find that intra- and intergroup relatedness receives varied perception. In certain mathematical circles, higher population *viscosity*, born out of the gradual displacement of social group members from their birthplace (also known as *philopatry*), seems to encourage a greater likelihood of cooperative exchange in genetic relatives. However, the core principle driving such altruism appears to simultaneously encourage greater competitiveness among those very same relatives. And in the net, both cooperation and competition cancel, yielding a nearly equilibrated state (Mitteldorf and Wilson 2000; Taylor 1992; Wilson et al. 1992). Yet, other mathematicians (Schonmann et al. 2013) attempted to model comparable scenarios and found the opposite to be true, stating that:



We conclude that contingent forms of strong altruism that benefits equally all group members, regardless of kinship and without greenbeard effects, can spread when rare under realistic group sizes and levels of migration, due to the assortment of genes resulting only from population viscosity. (p. 1)

When actually observing the social insects, as opposed to modeling them mathematically, we find less extreme variation in conclusions. For instance, in the case of the primitive social wasps, far less of today's literature is occupied by models like those of Hamilton's (1964) kin selection theory, with haplodiploidy-inflated coefficients of relatedness stemming from the shared genes of recent common descent. This alteration is primarily due to the documented existence of *foundress associations*, which find fully fertile females cooperating in nest construction and other crucial tasks. Hamilton's theory was seemingly developed in ignorance of these associations, instead operating under the assumption that colonies were created by mother-daughter bonds. The foundress associations have been studied using molecular genetic methods, and though results have not uncovered a full genealogical progression, they were shown to conform qualitatively but not quantitatively to Hamilton's previously determined levels of relatedness requisite for the evolution of kin-selected altruism, in that foundress associations do express higher intragroup than intergroup genetic relation, when genetically contrasted with the broader outside wasp population (e.g., Bluher 2018; Wehren et al. 2007). This appears to be at least partially mediated by behavior, since foundresses have been recorded migrating between nests, presumably optimizing inclusive fitness: "A clear motivation for moving to new nests was high genetic relatedness; by the end of the foundress period all females were on nests with full sisters" (Seppa et al. 2012, p. 1). Researchers have also claimed that relatedness could influence the overall differential dominance seen with nestmates (e.g., Bolton et al. 2006; Sumner et al. 2002). These instances are assumed to begin the evolutionary progression towards eusociality, including towards the evolution of the so-called *sterile* "workers."

## Conclusions

We now come full circle back to the case of the eusocial Hymenoptera. Genetic relatedness is herein established as relevant but not required for the evolution of eusociality in Hymenoptera and beyond. We further realize that *kin selection theory*, as extended in *genetic similarity theory* (Rushton 1989), can be viewed together within Hamilton's most recent version of *inclusive fitness theory* (1975), which (as far as we know) was its final form. Altruism among kin may hence evolve regardless of the degree of relatedness between each relative, given suitable ecological conditions. Nevertheless, in the case of many Hymenopteran species, increasingly shared genetic variance within a group can result in the promotion of gregariousness, and eventually, lead to eusociality.

We therefore conclude that the evolution of Hymenopteran eusociality is best seen through the lens of multilevel selection theory (see Hertler et al. 2020), in which multiple causal influences are recognized to be at work, and that the primacy previously ascribed to haplodiploidy, although highly influential in the history of evolutionary science, was ultimately a very incomplete account of a much more complex phenomenon.

## Cross-References

- [Cooperation](#)
- [E.O. Wilson](#)
- [Ecology](#)
- [Evolution](#)
- [Inclusive Fitness](#)
- [Insect Life History](#)
- [Kin Selection](#)
- [Natural Selection](#)
- [Sociobiology](#)
- [William Donald Hamilton](#)

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## Hyoid Bone, The

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### Synonyms

Lingual bone; Tongue bone

### Definition

Unpaired, irregular, horseshoe-shaped bone that forms the attachment for the tongue suspends the larynx and assists in respiration, swallowing, and posture.

### Introduction

The hyoid bone is an irregular bone due to its unique quality of not articulating with any bones, rather connecting to other adjacent bones

via muscles and tendons. It forms the attachment for the tongue and suspends the larynx, although not considered to be a part of the larynx itself. This unpaired bone provides attachment for numerous muscles, which function to either elevate or depress the hyoid bone, as well as assist the body in swallowing. In addition, these muscles also help to support the hyoid itself, so that it is able to maintain its position. However, its exact position differs due to individual differences and situational circumstances within these individuals (Gray and Carter 2013; Ferrand 2013; Seikel et al. 2005).

### Anatomical Location and Structure

The hyoid bone is found superior to the larynx, inferior to the mandible, and anterior to the upper cervical vertebrae. The specific level of cervical vertebrae (i.e., C1–7) in which it is anterior to is contingent upon the individual's age and changes throughout the lifespan. It is located at the level of C2 or C3 from birth to age two and then moves slightly from the lower half of C3 and the upper half of C4 in older children and adults. From a sagittal viewpoint, the distance between the hyoid and cervical vertebrae remains the same until around puberty, when the hyoid moves slightly anteriorly (Hudgins et al. 1997). Figure 1 below depicts the position of the hyoid bone in relation to the larynx and mandible.

The hyoid is open posteriorly, thus giving it a horseshoe-like shape. It is comprised of three major components: the body, pair of greater cornu, and pair of lesser cornu. The body, also called the corpus, is convex anteriorly and concave posteriorly. It is also the point of origin or insertion for several muscles. These three components can be found in Fig. 2.

The greater cornu, or horn, articulates with the body laterally and extends itself posteriorly toward the cervical vertebrae. The hyoglossus, a muscle of the tongue, attaches to its outer surface, and the thyrohyoid, an infrahyoid muscle (i.e., below the level of the hyoid), attaches to its lower border.

The lesser cornu, or horn, is a small, cone-shaped projection that sits on the junction of the greater cornu and body. The stylohyoid, a suprahyoid muscle, is attached to its apex (Gray and Carter 2013). Figure 2 below depicts the point of attachment for these muscles.

## Function

The hyoid functions as the necessary attachment of the muscles responsible for respiration, swallowing, and preventing regurgitation. Apart from this role as of anchoring muscles, the hyoid itself is responsible for balancing the head by moving synchronously along with it. That is, if the head moves posteriorly or anteriorly, the hyoid will move posteriorly or anteriorly, respectively. Additionally, when the head moves dorsally, the hyoid

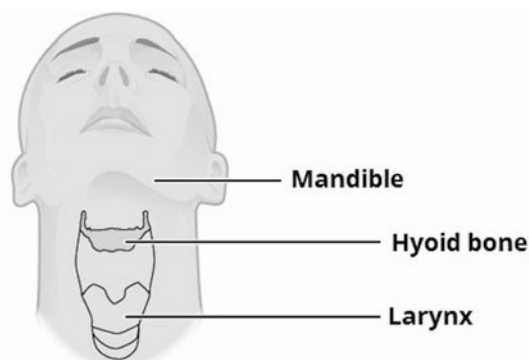
bone rises, and when the head moves ventrally, the hyoid bone lowers (Bibby and Preston 1981).

## Muscle Articulations

There are several muscles anchored by the hyoid that serve several respective functions. These muscles can be divided into two general groups: suprahyoid (i.e., above the level of the hyoid) and infrahyoid (i.e., below the level of the hyoid). The suprahyoid and infrahyoid muscles can be identified in Fig. 3.

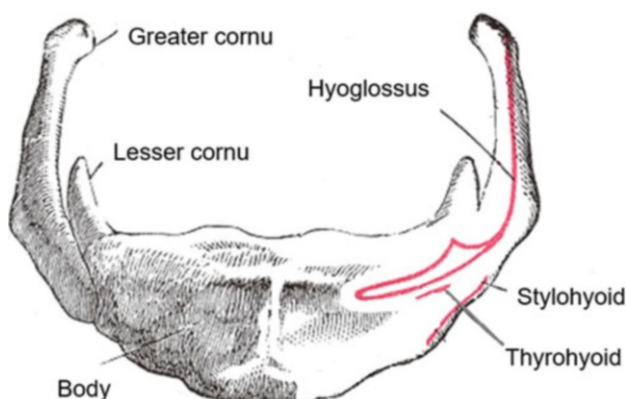
The suprahyoid muscles consist of the digastric, stylohyoid, mylohyoid, and geniohyoid. Their primary function is to raise the hyoid bone and larynx. These muscles also play an intricate role in swallowing by helping to raise the tongue and depress the mandible during this process. Swallowing consists of two major parts. The first part is comprised of the food being shifted from the mouth into the pharynx, via the hyoid bone and tongue moving superiorly and anteriorly. This is made possible by the digastric, mylohyoid, and geniohyoid muscles. The second part is comprised of the food passing through the pharynx and the hyoid bone rising back to its original position. The digastric and stylohyoid complete the process of this elevation of the hyoid bone. In addition, these muscles also prevent food from coming back up into the mouth.

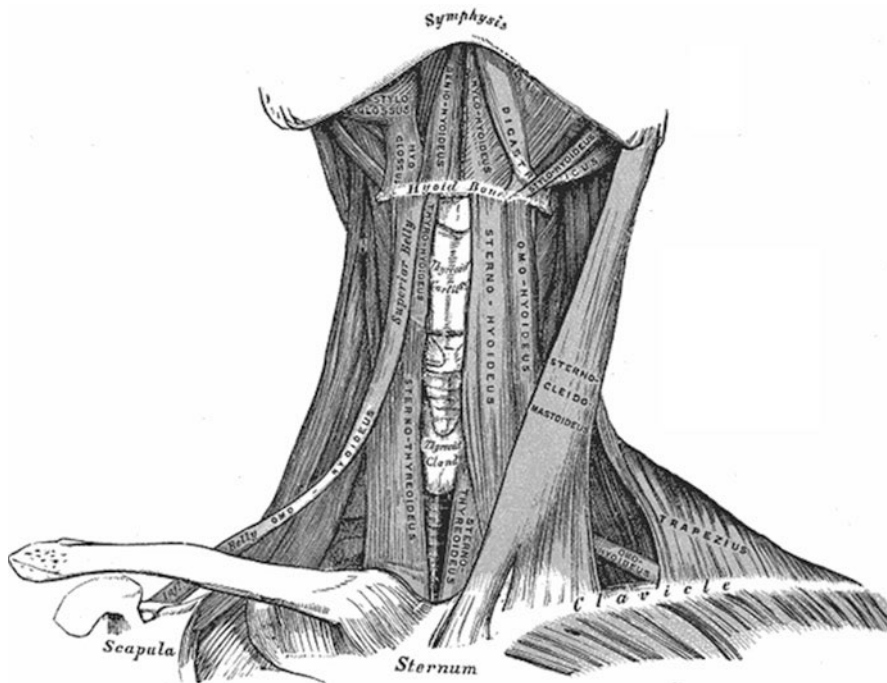
The infrahyoid muscles consist of the sternohyoid, thyrohyoid, and omohyoid. Their primary function is to depress the larynx and



**Hyoid Bone, The, Fig. 1** Hyoid bone in relation to the larynx and mandible (Young et al. 2013)

**Hyoid Bone, The, Fig. 2** Superior view of the hyoid bone featuring the three main components (corpus, greater cornu, lesser cornu) and the place in which several muscles attach to it (Adapted from Gray and Carter 2013)





**Hyoid Bone, The, Fig. 3** Suprahyoid and infrahyoid musculature (Gray and Carter 2013)

hyoid bone after they have been drawn up in the process of swallowing. Furthermore, the omohyoid is specifically useful for drawn-out inhales.

In addition to the suprahyoid and infrahyoid muscles, the muscles of the tongue also have attachments to the hyoid bone. These muscles consist of the geniohyoglossus, hyoglossus, chondroglossus, and styloglossus. The hyoid provides support for the tongue and attachment for these muscles (Gray and Carter 2013; Seikel et al. 2005).

## Ossification

The hyoid undergoes a lengthy process of ossification (i.e., the process by which a cartilaginous structure becomes hard bone). While it eventually becomes fully ossified in adults, it appears as soft tissue in pediatrics. Although not considered part of the larynx, the hyoid is identified as the earliest laryngeal calcification. In fact, it is the only laryngeal structure that undergoes ossification before

the age of 20 (Turkmen et al. 2012). When ossified, it consists of a bony matrix, osteoid, and osteoblasts.

The hyoid, in both males and females, becomes ossified over general ages in specific anatomical parts. The greater horns become ossified toward the end of pregnancy, and the body becomes ossified following right after the pregnancy. Furthermore, the lesser horns ossify leading up to and during puberty, with the ends of these horns ossifying by age 30. Thus, the hyoid appears as a single bone by age 30, while appearing as two separate structures, the corpus and posterior cornus, in earlier ages (Turkmen et al. 2012, 2014).

## Abnormalities

Abnormalities in the hyoid bone itself are often found together with cleft lip, cleft palate, or Pierre Robin syndrome (Turkmen et al. 2012, 2014). In addition, abnormalities associated with muscle articulations to the hyoid bone can also cause



pathologies. Ossification of the stylohyoid ligament, part of the stylohyoid muscle apparatus, causes Eagle's syndrome. This is marked by chronic throat pain and is due to tissue structures applying excess pressure to the stylohyoid (Baig et al. 2012). Additionally, abnormal positioning of the hyoid can lead to obstructive sleep apnea (OSA). OSA is due to a blockage of the pharynx by the tongue during sleep and leads to snoring or insufficient inhalation of oxygen (Gent et al. 2014).

## Fracturing

The hyoid is rarely fractured naturally or as a result of sport injury, due to its location inferior to the mandible, which conveniently provides the hyoid protection. However, if the hyoid is fractured, it is generally a result of strangulation. A fractured hyoid leads to great pain in speaking and swallowing, due to the tongue having several muscle attachments at the hyoid.

## Cross-References

- [Feline Communication](#)
- [Fetus](#)
- [Morphology](#)

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## Hypertensin

- [Angiotensin](#)

## Hypometabolism

- [Hibernation](#)

## Hypophysis

- [Pituitary Gland](#)

## Hypothalamic Pituitary Axis

- [Psychopharmacology of Sex Steroids](#)

## Hypothalamus

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## Definition

A structure of the brain responsible for maintaining a stable internal environment in the body.

## Introduction

The hypothalamus is located in the brain underneath the thalamus and above the pituitary gland. It is responsible for maintaining stable internal conditions, known as homeostasis, in the body. The hypothalamus, which is part of the limbic system, receives sensory information from the environment and either sends signals to the autonomic nervous system or releases hormones to the endocrine system in order to correct bodily imbalances. Hypothalamic hormones interact with the endocrine system via the pituitary gland by controlling the production of pituitary hormones. Some processes regulated by the hypothalamus are heart rate, blood pressure, body temperature, thirst, water excretion, childbirth, sleep, hunger, sex drive, rage, and fear (Beaton 2013).

## Interaction with the Autonomic Nervous System

The autonomic nervous system, which is split into the sympathetic and parasympathetic pathways, works with the hypothalamus to regulate autonomic functions and reflexes. Neurons in the hypothalamus are connected to various receptors in the body and receive a wide array of environmental and internal sensory signals such as pain, change in blood levels, and changes in light, temperature, and smell. After receiving these signals, the hypothalamus makes direct and indirect connections with sympathetic and parasympathetic neurons in the brain stem and spinal cord which cause the body to react and return to homeostasis. The hypothalamus, via the autonomic nervous system, is in control of processes such as blood pressure, heart rate, breathing, digestion, sweating, salivation, and bladder emptying (Beaton 2013; Dampney 2011; Hall and Guyton 2006).

## Interaction with the Endocrine System

The hypothalamus is linked with the endocrine system by the interaction its hormones have

with the anterior and posterior pituitary glands. Hormones produced by the hypothalamus are:

- **Thyrotropin-releasing hormone (TRH)** – triggers the release of thyroid-stimulating hormone (TSH) and prolactin which in turn regulate metabolism, brain development, muscular control, and energy.
- **Gonadotropin-releasing hormone (GnRH)** – triggers the release of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) that are connected to puberty and reproductive function.
- **Growth hormone-releasing hormone (GHRH)** – triggers the release of growth hormone (GH) that controls physical development in children and metabolism in adults.
- **Corticotropin-releasing hormone (CRH)** – triggers the release of corticosteroids that help regulate physical and emotional stress, metabolism, and immune response.
- **Dopamine (DA)** – when acting as a hormone and not a neurotransmitter, DA inhibits the release of prolactin which, in turn, stops the production of milk.
- **Somatostatin (SS)** – inhibits the release of growth hormone (GH) and thyroid-stimulating hormone (TSH).
- **Oxytocin (OXY)** – stimulates uterine contraction during childbirth and the lactation reflex during breastfeeding.
- **Vasopressin/antidiuretic hormone (ADH)** – increases water absorption in the kidneys and constricts blood vessels.

After hormones are produced in the hypothalamus, they are transported to either the anterior pituitary or the posterior pituitary. Oxytocin and vasopressin are released into the bloodstream via the posterior pituitary and act on distant target organs. TRH, GnRH, GHRH, CRH, dopamine, and somatostatin all travel to the anterior pituitary where they control the release of pituitary hormones (Beaton 2013; Hall and Guyton 2006; Jones 2010).

## Behavioral Functions

Stimulation or lesioning of the hypothalamus can have extreme emotional and behavioral effects on animals and humans alike. Some emotional reactions caused by stimulation are fear and punishment behaviors as well as changes in sexual drive. Stimulation of the lateral hypothalamus causes extreme thirst, increases in feeding and energy, as well as rage and fighting behavior (Berthoud and Münzberg 2011). Lesioning that same area causes an opposite reaction in the form of a decrease in drinking and eating to a point of starvation, as well as extreme passiveness. Stimulation of the ventromedial nucleus of the hypothalamus causes effects such as satiety and peaceful behaviors. Lesioning that same area has the effect of increases in eating and drinking as well as extreme rage (Hall and Guyton 2006).

## Cross-References

► [Oxytocin](#)

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## Hypothesis-Driven

► [Top-Down Processing](#)

## Hyracoidea

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## Synonyms

[Bush hyrax](#); [Dassie](#); [Dendrohyrax arboreus](#); [Dendrohyrax dorsalis](#); [Dendrohyrax validus](#); [Heterohyrax brucei](#); [Procavia capensis](#); [Rock hyrax](#); [Rock rabbit](#); [Tree hyrax](#); [Yellow-spotted rock hyrax](#)

## Introduction

Hyracoidea are an order with only one extant family, Procaviidae. Though the Procaviidae family mostly resemble medium-sized rodents, around 2–3 kg in size, they are more closely related to elephant and sengi and sit in the super-order Afrotherian. Five species now form this family that can be found throughout Africa and the Middle East; the rock hyrax (*Procavia capensis*, Fig. 1), yellow-spotted rock hyrax or bush hyrax (*Heterohyrax brucei*), western tree hyrax (*Dendrohyrax dorsalis*), southern tree hyrax (*Dendrohyrax arboreus*), and the eastern tree hyrax (*Dendrohyrax validus*). All species, with the exception of the eastern tree hyrax which is threatened across its range, are currently relatively common across their wide-ranging distribution.

Rock hyrax, the most studied of all hyraxes, live in arid savanna, rocky outcrops across sub-Saharan Africa, and the North-East Africa through to the Middle East. Some populations

**Hyracoidea, Fig. 1** Rock hyrax (*Procavia capensis*) at RZSS Edinburgh Zoo. (Photo by Declan Duffy)



have also moved into urban areas taking advantage of man-made holes and crevices (McPherson et al. 2016).

Bush hyrax can be found across the east of Africa with an isolated population in Angola, living, often in close association with rock hyrax, around rocky outcrops and boulders that are surrounded by bush or woodland (Barry and Shoshani 2000).

Dendrohyrax research had been limited to captive studies in the late 1970s and 1980s but with technological advances there has been an increase in wild studies on these species. Southern Tree hyrax are found from East Africa to South Africa and as with all tree hyrax they are arboreal, spending most of their time high in the canopy or in tree holes making them difficult to observe (Milner and Harris 1999a). Eastern tree hyrax distribution is severely fragmented across Tanzania and into south eastern Kenya (Roberts et al. 2013). High population densities were recorded in undisturbed forests and canopy structure (important for arboreal pathways) and is deemed to be a limiting feature of eastern tree hyrax populations (Topp-Jørgensen et al. 2008).

Other than being a food source for humans (Fa et al. 2000), very little has been published about the western tree hyrax. They are found in the western area of Africa from Sierra Leon to western Uganda (Shultz and Roberts 2013). Prey for leopards, raptors, pythons, golden cats, servals, chimpanzees, and bush meat for humans, they have also been noted in instances of play by chimpanzees in Bossou, Guinea (Hirata et al.

2001). This chapter summarizes what is known so far of the hyrax behavior and cognition.

## Nutrition and Feeding Behavior

All hyrax are hind gut fermenters, a category that also includes the lagomorphs, rodents, and callitrichid primates. They have an unusual two chamber stomach with a glandular and non-glandular section. They have a very well-developed and efficient digestive system with fermentation taking place in the caecum of the large intestine. A long transit time allows microbial fermentation to aid digestion and these microbes produce volatile fatty acids which are likely to serve as an energy source for the hyrax (Leon 1980). All hyrax defecate in a single spot, often communally, known as a midden or latrine.

Rock hyrax are grazers, feeding mainly on grasses in the wet season but moving to browse later in the dry season (Hoeck 1975). Species from the Dendrohyrax and Heterohyrax genus are considered to be more browsers than their grazing cousins. Tree and shrub leaves make up the bulk of bush hyrax diet though they will also consume tree bark as well as flowers, fruits, and grass, particularly in the wet season (Hoeck 1975 and Girmay et al. 2016).

All dietary information on the tree hyrax has been taken from studies on the southern tree hyrax species. Southern tree hyrax predominately consumes tree leaves but also shrubs, flowering plants,

and ground forbs (Gaylard and Kerley 1997; Milner and Harris 1999b).

Hyrax dentition reflects the diet with the grazing rock hyrax possessing hypsodont molars (high crowned teeth that are good for fibrous food) and the other species having brachydont molars (low crowned/short teeth). The length of the upper premolar series also varies; in bush hyrax they are equal to the length of molar series. Rock hyrax have much shorter upper premolars than molars, and in the genus *Dendrohyrax*, the upper premolars are longer than molars (Jones 1978). They possess well-developed upper incisors shaped into sharp tusks and lower incisors that are unsuitable for biting but used for grooming fur. The molars are used for biting and chewing food quickly, allowing the ability to ingest food quickly (Sale 1966). The rock hyrax basal metabolic rate is low and as such they have low energy requirements (Leon 1980). Milner and Harris (1999b) found that southern tree hyrax also show behaviors typical of the low metabolism strategy shared with the rock hyrax. Other arboreal folivores, such as arboreal marsupials and sloths, also share this strategy, driven by a diet with low nutritional value. However, short feeding bouts from quick consumption and low intake combined with low activity levels has benefits, through better predator avoidance strategies (Sale 1966).

## Behavior

### Sociality

Rock hyrax and bush hyrax are gregarious, diurnal species, both forming similar social structures. Their grouping consisting of a harem with one dominant male and females with their offspring (Fourie and Perrin 1987). Group sizes are usually between 10 and 20 individuals, though bush hyrax group sizes have been recorded as large as 34 individuals (Barry and Shoshani 2000) and there have been reports of rock hyrax group sizes reaching up to 80 individuals (Olds and Shoshani 1982). They forage socially, individuals often forming sentries and can also form heterospecific groups (Hoeck 1975).

Grooming has been recorded in most hyrax species. The lower incisors are rubbed through the fur, a behavior which has been observed socially in captivity with the bush hyrax and western tree hyrax (Jones 1978). All hyrax also possess a long nail on the inner toe of the hind foot, which is used for scratching.

Basking is an important behavior as hyrax have a poor ability to thermoregulate. The two social species' will also huddle in groups for warmth and tree hyrax can insulate against cooler nights in tree hollows. Indeed, whilst studying the southern tree hyrax, Milner and Harris (1999b) recorded lower activity levels when the ambient temperature was cooler.

Tree hyraxes are solitary, nocturnal, and arboreal animals, though the extent of these characteristics varies geographically. They are active at night but captive studies found that they will feed during the day (Rudnai 1984). Milner and Harris (1999b) observed feeding at dusk and dawn and regular diurnal movement as well.

Predators strongly shape the behavior and activity patterns of all hyrax populations (Druce et al. 2006). Out from under the safety of cover, the hyrax are more susceptible to predation and so large group sizes and sentinels, as well as staying close to refuge sites, are all coping strategies. Where large avian predators are present, their activity pattern shifts to a more nocturnal one (Milner and Harris 1999b). Druce et al. (2006) modelled the foraging behavior of hyrax against other factors and found interactions between season and foraging distance, suggesting that during dry period rock hyrax risk greater chance of predation as they seek food farther from their dens. Equally human disturbance also has an effect, where there is an increase in hunting by snares, the tree hyrax become more arboreal (Topp-Jørgensen et al. 2008).

### Locomotion

Hyrax are quadrupedal plantigrade mammals, but each species in the Procaviidae family have become adapted to their specific niche. Tree hyrax prefer to travel across upper tree zone and several studies have found evidence that they spend a higher amount of time on the ground



than was understood previously (Rovero et al. 2014; Milner and Harris 1999b). Despite footpads with hoof-like nails, they are excellent climbers ascending and descending quickly (Richard 1964). Jones (1978) noted that the feet of the tree hyrax may be rotated inward to aid tree climbing and captive individuals have been observed holding vines in their teeth to help ascend the tree.

Rock hyraxes are also good climbers, and Serruya and Eilam (1996) observed the rock hyrax to climb onto low branches and bask in the sun. They have a special adaptation for squeezing into crevices or small holes where they spend the night, with early morning and evening making up the core activity periods (Olds and Shoshani 1982). They use the presence of whisker like hairs that cover their body to help navigate around their rock crevice surroundings (Sarko et al. 2015). Their locomotion behavior is made up of very rigid and conserved movements reminiscent of stereotypical behavior (Serruya and Eilam 1996). They move in short bursts or chunks and this chunking process is also seen in the learning process as a way of managing an increasing load of information (Serruya and Eilam 1996). This behavioral conservation strategy may require less cognitive effort to allow them to spend more energy on predator vigilance.

As the wet season ends and the dry season begins, male aggression increases in the rock hyrax, who will chase and bite other males and wounds are frequently observed during this period (Serruya and Eilam 1996). Aggressive interactions include snarling and chasing, though rarely does physical contact occur with tree hyrax (Milner and Harris 1999b).

## Reproduction

Sexual maturity is reached around 28 months in males and 16 months in females, with seasonal mating being triggered by the photoperiod (Fourie and Perrin 1987). Males may reach puberty earlier than this (+16 months) but are often prevented from mating by other older males (Sale 1970). There is evidence of precocial puberty being reached by females from 4/5 months old, though this is limited to certain geographical areas

(Fourie and Perrin 1987). Rock hyrax litter size is around three individuals and older or younger individuals tend to produce smaller litter sizes (Fourie and Perrin 1987).

At around 17–24 months, adolescent male rock hyraxes will be forced to disperse from the natal group and find their own group or join a bachelor group on the periphery of the natal group (Sale 1970). Adult male rock hyraxes may only be with a group for around 2 years before being challenged and evicted by a bachelor (Fourie and Perrin 1987).

A clear reproductive season is apparent in the bush hyrax corresponding with the wet season. Bush hyrax population sizes will fluctuate with rainfall (Barry et al. 2015). Thus, reproductive season is likely driven by resource availability and that this corresponds to rainfall in the equator region and photoperiod outside of this zone (Barry et al. 2015). This is particularly apparent in areas that experience two rainy seasons and bush hyrax correspondingly experience two peaks in reproduction (Hoeck 1975). No specific birth period has been noted in some southern tree hyrax populations (Milner and Harris 1999b), but there was a clear calling season, indicating a reproductive season exists.

Hyrax has a particularly long gestation (6–8 months) and growth phase for their size and lifespan (living up to 12 years). Both these features are likely to be residual features from their larger ancestors (Olds and Shoshani 1982).

In addition to the advantage of larger group sizes, the heterospecific groups of rock and bush hyrax also offer the benefit of nursery care for their precocial calves (Barry and Shoshani 2000). Generally, the lactation period is less than 6 months in rock and bush hyrax (Fourie and Perrin 1987; Barry and Shoshani 2000). Infant rock hyrax develops the majority of vocalizations between the ages of 2 and 15 months (Fourie 1977).

## Communication

All five hyrax species are very vocal, with particular vocalizations specific to each species. Rock hyraxes are known to make up to 21 vocalizations (Koren and Geffen 2009). Male and female rock hyraxes produce a loud alarm call but male rock

hyraxes also have a much more complex vocal communication advertising a variety of attributes about the communicator to others; from attracting a mate, display the singers' identity (Koren and Geffen 2011), age, social status, and body mass as well as signaling distress (Koren and Geffen 2009). Only males sing and counter-sing and singers are usually older, more dominant, and have higher cortisol levels (Koren and Geffen 2009). The function of singing is not clear but as the frequency of singing reduces after the mating season, it is likely that this is a form of sexual advertising (Koren and Geffen 2011).

Rock hyrax calls are made up of wails, chucks and snorts. The chucks are emitted in one single breath leading Koren and Geffen (2009) to deduce that this implied the size of the singer as larger lungs are needed for to hold the sound.

In addition to vocal communication, chemical communication in the hyraxes is likely. They possess a distinct vomeronasal system (Olds and Shoshani 1982), and tree hyrax have been observed to scent mark by rubbing their glands on branches, and at least in the western tree hyrax, producing a scent that smells of cinnamon (Richard 1964).

Both male and female southern tree hyrax make deep croaks followed by loud screaming vocalization, which is more prevalent in the end of the dry season (Milner and Harris 1999b). There may be some link between call season and reproduction, despite little evidence of birth seasonality, as only single females will call, though the purpose of the call may be to defend a territory rather than to attract a mate (Milner and Harris 1999b). Western tree hyrax, as with the southern tree hyrax, emit a series of long screams that gradually get louder, culminating in a crescendo and abrupt climax (Shultz and Roberts 2013). This type of ending also seen in other hyrax is considered important for the communication, and in rock hyrax more males respond to songs with climatic endings (Demartsev et al. 2017).

There may be up to 50 species or subspecies in the family Procaviidae which is continuously being disputed. At present, there are at least 24 subspecies of *Heterohyrax brucei* alone (Barry and Shoshani 2000). There is some debate

as to whether the eastern tree hyrax is a separate tree hyrax species or if it is a subspecies of the southern tree hyrax; however, its distinct call characteristics have kept it apart from the southern species at present (Roberts et al. 2013). Current studies are investigating whether different calls can help to shed further light onto hyrax species identity (Koren pers. comm.). One example of a recently suggested new species is the geographically isolated Benin tree hyrax, which has a distinct vocalization from other western tree hyrax (Bearder et al. 2015). Research by Kershenbaum et al. (2012) suggests cultural drift explains the formation of distinct dialects, where hyrax songs diffused over short distances. As no genetic correlation in male vocal song has been found (Koren and Geffen 2011), the ability of song learning in hyrax needs further consideration (Kershenbaum et al. 2012).

## Cognition

Very little has been published on the cognition of Hyracoidea species. However, as suggested by Limacher-Burrell et al. (2016), the extensive social nature of the rock hyraxes and their large vocal range and repertoire indicate that their cognitive make-up is likely to be as complex as in other mammals. Other Afrotherian species show high level cognitive abilities (Plotnik et al. 2010). Depending on the evolution of this cognitive process, hyrax may possess their own cognitive specialties (Limacher-Burrell et al. 2016).

A small number of studies investigating the rock hyrax neuronal systems have been published aiming to enhance the understanding of the evolutionary processes associated with the brain's nuclear organization (Limacher-Burrell et al. 2016; Gravett et al. 2009). Studying the amygdala (an area in the brain, thought to be important in behavioral activities), Limacher-Burrell et al. (2016) found that the hyrax amygdala seems quite conserved, making this good baseline for studying other more specialized mammals.

Gravett et al. (2009) observed two distinct neuronal types in one area of the rock hyrax brain that differ from previous studies of this

area in other mammals. Leading the authors to suggest there may be usual effect on the rapid eye movement (REM) sleep patterns of this species and possibly other species within the Afrotherian superorder. Gravett et al. (2012) analyzed the sleep patterns of wild caught hyrax in a lab setting and found the REM stage of sleep was extremely short, at only around 6 min out of a 15.89-h sleep. Whereby, in other mammals, REM sleep is normally around 17% of total sleep time. A novel type of sleep state was also observed, whereby the brain activity appeared to be in the waking stage and the muscles activity, as seen in the EMG, were reduced in amplitude (similar to slow wave sleep) but not as reduced as REM (Gravett et al. 2012).

## Conclusions

There is a dearth of information on Dendrohyrax species in comparison to the other species, especially the rock hyrax, which has received the most attention. Detailed behavioral studies are needed in these other species, in particular investigating their thermoregulation behavior and reproductive drivers. The unusual neuronal patterns, found in the rock hyrax brain, and their novel sleep states is a noteworthy finding and its existence in other similar taxa would be of further evolutionary interest. Overall, despite the small number of extant species currently recognized in the Hyracoidea there is much more to be understood about these unusual animals. The relatively long gestation and growth period suggests a high level of learning, particularly in terms of vocal communications. Rock hyrax show complex, repeated vocalizations (or songs) that is rarely documented in mammals beyond animals such as cetaceans and primates, considered to have a high cognitive ability. Geographical variations in these songs as well as the function of the song pattern and information transfer have been investigated. Extended exploration of these vocalizations to determine the learning mechanisms, dispersal pathways, and complexity across the Hyracoidea would help to further our understanding in the field of communication.

## Cross-References

- ▶ [Amygdala](#)
- ▶ [Communication](#)
- ▶ [Contact Calls](#)
- ▶ [Sleep](#)
- ▶ [Thermoregulation](#)

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## IACUC

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### Introduction

An institutional animal care and use committee (IACUC) is a requirement at most institutions that have animal research or teaching programs in the United States. Similar committees exist at research and teaching institutions in other countries (Varga 2013). These may go by names other than the IACUC, such as animal research ethics committee, but they have similar functions in complying with national or regional mandates. This chapter describes IACUCs in the United States.

An IACUC is charged with self-regulation over animal care and use in compliance with all US federal laws, regulations, policies, and guidelines that govern animal welfare in research, testing, or teaching (National Research Council 2011). Self-regulation allows an institution the flexibility to determine how it will conduct its IACUC procedures in ways that are most efficient and productive for its own research program. Although self-regulating, an IACUC must meet

certain requirements – its members must be appointed to fill specific roles for which they must be qualified, and the committee must carry out its specific responsibilities. The committee is appointed by a chief institutional official, such as a dean of research or a president or vice president. The committee members must include scientists, a member unaffiliated with the institution, and, in some cases, a nonscientist. Unaffiliated members are intended to represent public attitudes about animal research. An attending veterinarian with appropriate qualifications in laboratory animals must be appointed as an ex officio member to consult on veterinary matters in protocol review and other committee activities. Researchers interact with their IACUC in four ways: submission of their animal protocols for review, identification of occupational health and safety issues related to an animal protocol, participation in training mandated by the IACUC, and inspection of their laboratory areas where animals are housed or studied.

### Ethics of Animal Research

In the United States, federal regulations, policies, and guidelines provide the framework for humanely conducting animal research. The Federal Animal Welfare Act (AWA) covers the use of animals in research, teaching, and exhibition, and it is enforced by the Animal Welfare Regulations and Standards (AWR) (United States



Department of Agriculture 2017a). The AWA and AWR first date from 1966. Since then, there have been many amendments to the law and changes in the regulations. Animals covered by the law and regulations are limited to warm-blooded animals with the exclusion of laboratory strains of mice, rats, and birds, as well as agricultural animals that are used for teaching or research in food and fiber production. Therefore, covered animals include nonhuman primates, dogs, cats, rabbits, guinea pigs, hamsters, gerbils, wild species of rats and mice, and so on. Farm animals are covered when used for biomedical research. Cold-blooded species – amphibians, reptiles, fish, and invertebrates – are excluded. Any institution conducting research or teaching with covered species must be registered with the United States Department of Agriculture (USDA) via the Animal Care Program. The registered institution must have an IACUC, see to the training or qualifications of personnel in key areas of animal care and use, conduct semiannual inspections of its program and facilities, maintain required documentation, file annual reports with the USDA, and submit to unannounced inspections. The USDA's Animal Care Policy Manual provides detailed interpretations of the AWR (United States Department of Agriculture 2017b). It specifies compliance with two nonfederal guidelines: The AVMA Guidelines for the Euthanasia of Animals (American Veterinary Medical Association, AVMA) and the Guide for the Care and Use of Agricultural Animals in Research and Teaching (Federated Animal Science Societies, FASS) (American Veterinary Medical Association 2013; Federated Animal Science Societies 2010).

Additional oversight is provided under the Public Health Service Policy for the Humane Care and Use of Laboratory Animals (referred to as the PHS Policy herewith). It is a federal mandate that enforces the US Health Research Extension Act of 1985 (United States Department of Health and Human Services 2015). It covers a larger range of species: all vertebrates. Therefore, many species excluded by the AWA and AWR are covered by the PHS Policy – in particular, laboratory strains of mice, rats, and birds; reptiles; and amphibians and fish as well as their larval forms

posthatching. The PHS Policy requires compliance with the *Guide for the Care and Use of Laboratory Animals* (National Research Council 2011) as well as the AVMA and FASS guidelines mentioned above. Compliance with the PHS Policy is required when an institution's funding source for animal research and teaching is the US Federal Government. An institution must file an Assurance with the Office of Laboratory Animal Welfare (OLAW) at the National Institutes of Health (NIH) (National Institutes of Health Office of Laboratory Animal Welfare 2017a). The assured institution must have an IACUC, see to the training or qualifications of personnel in key areas of animal care and use, maintain required documentation, conduct semiannual inspections of its program and facilities, file annual reports with OLAW, and submit to scheduled inspections. Many research institutions must comply with both the AWA/AWR and the PHS Policy because of the dual conditions of using USDA-covered species and having research supported by federal funding.

Besides those described above, other laws, regulations, and guidelines may apply to animal activities. For example, anesthesia and analgesic medications in the treatment of laboratory animals often involve the use of controlled substances, falling under both state statutes and federal law and regulations. Because of the complexity of the regulatory landscape, researchers need to rely on their institution's compliance staff for ensuring that all relevant mandates are followed in the conduct of their animal studies. Compliance personnel are typically affiliated with the IACUC office, the animal facility, or the environmental and safety office.

Many institutions exceed minimum compliance with regulations governing the use of animals in research by attaining accreditation for excellence in laboratory animal care. Accreditation distinguishes an institution for providing quality in animal welfare and good science in animal research. AAALAC International is a private, nonprofit organization that is the only worldwide accrediting body for animal care and use programs. Accredited institutions undergo an extensive self-evaluation by preparing a Program Description according to a template. The Program Description is used to assess the institution in a

site visit. Institutions maintain accreditation by submitting annual reports and repeating the assessment process every 3 years. AAALAC International is well recognized among scientists, research institutions, grant agencies, and professional associations. Accreditation is a critical factor in funding decisions by some grant agencies and is a requirement by others (e.g., the American Heart Association and the American Stroke Association) (American Heart Association, American Stroke Association 2017). AAALAC accreditation requires compliance with three primary standards: the *Guide for the Care and Use of Laboratory Animals*, the *Guide for the Care and Use of Agricultural Animals in Research and Teaching*, and (in Europe) the European Convention for the Protection of Vertebrate Animals Used for Experimental and Other Scientific Purposes – Council of Europe (ETS 123) (AAALAC International 2017). In addition, other standards may be required if relevant to the accredited program.

Other than those mentioned above, guidelines, codes of ethics, and position statements have been developed by scientific professional or membership organizations to express commitment to ethics in animal research and to support the highest standards in the care and use of animals in research and teaching. For example, the National Research Council's *Guidelines for the Care and Use of Mammals in Neuroscience and Behavioral Research* focus on general animal care and use principles and considerations in this area of research (National Research Council 2003). The American Psychological Association's code of ethics, *Guidelines for Ethical Conduct in the Care and Use of Nonhuman Animals in Research*, exhorts psychology researchers to consider the costs and benefits of procedures involving animals (American Psychological Association 2012). This document lays out principles for research justification, personnel, care and housing of laboratory animals, experimental procedures, field research, and educational use of animals. The American Association for Laboratory Animal Science has position statements on many issues, including *Alleviating Pain and Distress in Laboratory Animals* and *Animal Use in Precollege Education* (American Association for Laboratory Animal

Science 2017). The American College of Laboratory Animal Veterinarians has many position statements, including reproducibility of animal studies; and medical records for animals used in research, testing, and teaching (American College of Laboratory Animal Medicine 2017).

A central theme in the ethics of animal research is the consideration of alternatives to the use of animals in experimental studies and teaching. The AWA and AWR stipulate that principal investigators consider "alternatives to any procedure likely to produce pain to or distress in an experimental animal. . ." (United States Department of Agriculture 2017a). These alternatives are interpreted as the three R's – principles first published by Russell and Burch and known as Replacement, Reduction, and Refinement (Russell and Burch 1992). These principles aim to minimize the use of animals and their pain or distress, while still achieving critical scientific objectives for advances in health and medicine. Replacement means that, where possible, animals should be replaced by nonanimal methods. Reduction means that the number of animals should be reduced to the minimum needed to obtain statistically significant data. Refinement means that methods used with animals should be modified to lessen the potential for pain or distress in those animals that must be used.

To responsibly conduct animal research, investigators must be qualified and therefore trained in areas of: relevant institutional policies, biological requirements of the species they will work with, safe and humane handling and restraint of the animals, humane conduct of animal procedures, and avoidance or alleviation of animal pain and distress. Animal use protocols (see next section) should identify personnel who will perform the animal procedures. These individuals should be verified as suitably trained or they must receive such training before the protocol is approved. For example, to conduct a surgical procedure on animals, researchers must be qualified on the following as applied to animals: aseptic technique; principles of surgery and the particular surgical technique to be used; anesthesia principles and technique for induction, maintenance, monitoring and recovery; and postoperative monitoring and

care. The IACUC must have evidence that these individuals know what clinical signs to look for in a given species so they can recognize pain or distress arising from their procedures. Otherwise, signs of pain in animals may go unrecognized. For example, in mild to moderate pain, dogs may not whine, limp, cringe, or even reduce their food intake. Evidence of pain may be more subtle, such as turning the head toward the painful area, occasional lip licking, licking or sniffing the painful area, or even just a reduction in overall activity level. Researchers must be competent to recognize signs of pain in the species and to administer pain medications and other treatments as specified in their protocols. In addition, the AWA/AWR stipulates that all personnel be trained on the reporting of deficiencies in animal care and treatment by any employee of the facility (United States Department of Agriculture 2017a).

Each institution has a training program to assure that researchers and other personnel learn how to work humanely and safely with the animals. Often these programs combine training modalities. Online courses convey in-depth information on ethics, policies, and species information. Hands-on instruction develops skills in animal procedures. Facility tours orient researchers to important rules and operations. Face-to-face training builds rapport between researchers and facility personnel, and researchers learn whom they can contact for assistance. Although facility staff provides training services for common techniques used in conventional species, specialized techniques or handling of unusual species may be best taught by the researchers themselves. For example, in field studies, personnel may need training in dart-tranquilizing and tracking systems implantation, and experienced researchers may be the best qualified to train on these techniques (Gannon and Sykes 2011). Therefore, IACUCs and investigators should collaborate on how to meet the training requirements for a protocol.

## Animal Use Protocol

Every use of animals, whether for a scientific or an educational purpose, must be reviewed in an

animal use protocol submitted to the IACUC (United States Department of Health and Human Services 2015; United States Department of Agriculture 2017a). No study or instruction with animals can be initiated prior to IACUC approval. Animal use protocols must fully describe a research project to enable the IACUC to adequately review the proposed care and use of the animals, in alignment with legal requirements and institutional policies. Prior to IACUC review, a veterinary consult helps address important elements in the protocol related to animal welfare and minimizing animal pain and distress. Per PHS Policy, a protocol may be approved for a maximum of 3 years. For ongoing studies, a new review is required at least every 3 years.

A protocol must be carefully planned as all study personnel will be expected to adhere to it. The protocol is like a contract for the privilege of using research animals, and its terms must be strictly upheld. Nevertheless, a protocol can be written with flexibility to allow handling of uncertainties, give reasonable options, and avoid overly restrictive parameters. For example, multiple acceptable options for anesthetic and analgesic regimens may be included by referencing a standard operating procedure (SOP) of the institution. This would allow changes in the study's drug regimens according to the current SOP and its future amendments. Incorporating flexibility in the protocol can reduce the chances of noncompliance and avoid administrative delays due to future protocol amendments. Investigators should confer with the attending veterinarian or the IACUC office on how to prepare a protocol with the flexibility needed to accomplish scientific goals.

The USDA requires that investigators consider alternatives to procedures that may cause more than momentary or slight pain or distress to the animals. The USDA also requires that studies are not duplicated unnecessarily. Most often, a literature search is conducted on alternatives to the use of animals related to the three R's principles of replacement, reduction, and refinement. The protocol should describe the search strategies used. If no alternatives can be found, investigators are asked to write a narrative description of the methods and sources used to determine that alternatives were not available.

Animal cognition studies frequently include invasive procedures such as brain surgery, implantation of electronic devices in the brain or body, lesioning practices, chemical manipulations, and other invasive techniques. If animals will undergo painful and/or distressful procedures or conditions, humane endpoint criteria should be included for ending a study prematurely, relieving pain or distress, or euthanizing the animals. Determining the level of pain and discomfort is critical for animal welfare. The description of the experimental design, animal procedures, and humane endpoints should allow the IACUC to understand the care and use of animals from start to finish. Thereby, the IACUC can assess the likelihood of and the intensity of pain or distress the animals may experience in the proposed study. The IACUC considers whether the methodology is appropriate for the intended use of animals and whether less invasive or less painful procedures would be suitable alternatives to the proposed methods.

Although protocol forms vary by institution, they typically cover the same type of information. Animal use is specified by species, age, weight or size, sex, genetic make-up, microbiological status, source, housing location and type, animal identification methods, number of animals to be used, and method of transportation. Study objectives should explain the aim of the study and why the study is important to human or animal health or to the advancement of knowledge or education. A rationale for the use of animals should include justifications for the appropriateness of the species and the number of animals to be used and, if possible, refer to a power analysis for the animal group size. A protocol should answer questions such as the following: Will animals be physically or chemically restrained? If so, how will the animals be monitored while restrained? If the restraint method is physical, how will the animals be adapted to the restraint device? What limits, e.g., duration, will be applied to the restraint? If animals will be trained to cooperate with procedures, how will the training program be conducted? Will animals be submitted to restrictions in food or water? If so, the restrictions must be scientifically justified and limited to acceptable standards to prevent distress. If drugs will be used,

whether for chemical restraint, anesthesia, analgesia, or testing, what will be the dose, frequency and route of administration, and duration of treatment? If a paralytic drug will be used, how will adequate analgesia be assured? How will animal pain or distress be assessed during all the procedures? How will aseptic technique be applied for catheterizations and surgeries? In a surgery, how will the animal be monitored for physiological parameters and for effectiveness of analgesia during the operation? How will the animals be monitored for recovery from anesthesia and surgery? How will these observations during anesthesia and surgical recovery be documented and at what frequency? What care will the animals receive postoperatively or for chronic catheterizations and implants? If biological samples will be collected, what will be the anatomical sites, frequency of collection, and sample volumes? Will anesthesia or sedation be used for sample collection? What adverse events might be anticipated in the animal procedures, and how might these events be managed? How will animals be disposed of at the end of the study – by adoption, transfer to another protocol, or euthanasia? If animals will be euthanized, what methods will be used?

The protocol must be thorough, accurate, and clear. Approval of a study may be delayed if the IACUC needs clarification or additional information. It is important to write in language a nonscientist would understand. Each specialty has its own jargon, and animal cognition and behavior are no exception. Consider that most IACUC reviewers are not experts in all scientific disciplines, so common words should be used. Furthermore, it is possible that a protocol may be read by regulatory and accreditation authorities, if the study is inspected at a future time.

## **Animal Housing and Enrichment**

Housing and living conditions can greatly affect how animals respond as research subjects in behavior and cognition studies, as well as in many other disciplines (Zelevnikow-Johnston et al. 2017). Laboratory animal facilities provide standardized care and a uniform environment in

caging, temperature, humidity, lighting, and sanitation. Manufactured diets and other feedstuffs are nutritious and scientifically determined to meet species requirements. The AWA and AWR require psychological enrichment for nonhuman species and an exercise plan for dogs. The AWA and AWR permit exemptions to these requirements for scientific purposes if sufficiently justified in the protocol and approved by the IACUC. Coleman and Novak (2017) discuss objectives, challenges, and benefits in developing an environmental enrichment plan for nonhuman primates.

The *Guide for the Care and Use of Laboratory Animals* discusses the use of environmental enrichment to enhance the welfare of all species (National Research Council 2011). Enrichment can be categorized as animate (human, conspecific) or inanimate (toys, feeding-interactives, housing, interactive-structures) (Ellis 2009). Most animal cognition studies routinely use enriched housing because sterile environments are known to inhibit normal brain function and development, whereas enrichment enhances normal brain function and development. Animals become better research models if allowed to develop normal cognitive function through enrichment (Morris et al. 2011). One concern with enrichment is neophobia, which is a negative response to novelty. Neophobia can affect both behavioral and immunological responses. For example, circulating cortisol levels are frequently used in animal cognition studies. Cortisol levels are particularly sensitive to changes in environment, circadian rhythm, and social interaction. Care must be taken to minimize the effects of stressors, including those caused by neophobia, on research outcomes. One technique of reducing neophobia is to apply positive reinforcement training to acclimatize the animals to enrichment materials.

Social species are often pair or group housed to encourage positive species-typical behaviors. Gilbert and Baker (2011) found that social contact among rhesus macaques decreased stress and adverse physiological effects and thus may improve research outcomes. However, Tardif et al. (2013) suggest that social housing may create problems in research due to frequent separation and reintroduction during research projects.

Hawkins (2014) reviewed the issues and effects of social and single housing on animals used in biotelemetry studies. This author presented the pros for social housing (lower stress, lower negative behaviors) and the cons (risk of radio interference, injury, or equipment damage).

Fillman-Holliday and Landi (2002) and Weed and Raber (2005) reviewed the often contradictory findings of the effects of enrichment on research results. They pointed out that environmental variability across experimental and control groups can influence physiological responses within experiments and create more noise in the data. A protocol should be planned carefully to meet species-specific social needs, and it should take into account a cost-benefit analysis weighing best housing, enrichment, and scientific goals. Part of the role of the attending veterinarian is to evaluate these elements and, where possible, offer assistance through suggested alternatives.

In some types of studies, research subjects are not housed in the laboratory but instead live in homes, animal shelters, and zoos (Horowitz 2014; Plotnik et al. 2014; Dale 2010). There is some risk of producing noise in the data due to variability in environment, although evidence suggests that this is much less of a problem than previously thought (Horowitz 2014). Certainly, it is more complex for the IACUC to evaluate such living circumstances for standards of care. Animals maintained outside the research environment are subject to considerable differences in nutrition, exercise, socialization, activities, etc. To accommodate these studies, creative thinking is necessary by both the researcher and the IACUC. For example, pets have been volunteered by owners for a number of veterinary and neuroscience procedures, including blood analyses and functional magnetic resonance imaging (fMRI). Pet dogs have been successfully trained to lie still during fMRI procedures without sedation (Andics et al. 2014). In another example, a study on spatial cognition and diet was conducted on dogs recruited from local shelters (Craig et al. 2012). Dogs meeting specific size, sex, and age criteria were removed from the shelters and kept in professional boarding facilities (not laboratories) for the duration of the study. All dogs were maintained on specific diets, were



exercised twice daily, socialized in groups in environmentally enriched yards, and tested in a radial arm maze. As part of the socialization experience, dogs were given basic obedience training in preparation for their adoption at the study's end. This study was evaluated and approved by the IACUCs of the collaborating organizations – the university's and the pet food company's.

## **Occupational Health and Safety in Animal Activities**

The PHS Policy and the *Guide for the Care and Use of Laboratory Animals* require that institutions offer an occupational health and safety program for personnel working with animals (United States Department of Health and Human Services 2015). The IACUC therefore has the responsibility to consider how human, animal, and community safety can be maintained in the conduct of animal activities. Prior to protocol review, risk assessments by safety personnel identify the hazards related to the kinds of animal activities proposed. Such hazards include injuries inflicted by animals (e.g., bites and scratches), infectious agents (zoonotic or experimental), chemical substances, ionizing radiation, temperature extremes, equipment, and poor ergonomic practices. Research in the field enlarges the range of safety issues, as personnel could become injured or ill due to, for example, falls and sprains, contact with poisonous plants, bites by venomous snakes, zoonotic diseases from biting insects, and so on. Safety equipment and practices may be recommended for each type of activity, and study personnel may be referred to the occupational health program for medical prophylaxis, such as immunizations. Personnel are not required to participate in their institution's occupational health and safety program, but those who decline may be not permitted to take part in the animal activities.

## **Protocol Review Outcomes**

The IACUC has two methods by which it may review an animal use protocol: full committee

review or designated member review. Full committee review takes place by a convened quorum and may result in approval, requirement for modifications (to secure approval), or withholding of approval. Designated member review is performed by one or more members selected by the committee Chair, provided that no members called for full committee review. Designated member review may result in approval, requirement for modifications (to secure approval), or referral to the full committee for review (in lieu of withholding approval). Regardless of the method for review, provisional or conditional approval of a protocol is never allowed. Furthermore, the investigator is not permitted to begin animal work before receiving IACUC approval.

## **Ongoing Oversight of Approved Protocols**

The IACUC has the responsibility for ongoing oversight of animal activities, which may include continuing protocol review, laboratory inspections, and observations of animal care and research procedures. To ensure optimal compliance, many institutions undertake a higher-level process known as post-approval monitoring, in which compliance staff inspects study procedures to verify that animal use is conducted according to the approved protocols and that animal-related records are thorough and accurate. This process helps investigators ensure their research meets regulatory requirements. Often, post-approval monitoring is focused on high-risk studies, for example, those involving surgery or causing unalleviated pain or distress in animals.

## **Changes to Approved Protocols**

When significant changes are needed in an approved protocol, an amendment must be submitted to the IACUC for review and approval. Significant changes are those that may have a negative impact on animal welfare. Examples include: a new principal investigator; a procedure resulting in greater pain/distress and invasiveness;

changing a surgery from nonsurvival to survival; a housing location that is not IACUC approved; different animal species; new study objectives; and heightened risk to personnel safety.

Some significant changes to approved procedures in a protocol may be handled administratively without an amendment (and therefore without further IACUC review) provided that specific requirements are met (National Institutes of Health Office of Laboratory Animal Welfare 2017b). A critical requirement is the IACUC's approval of guidance, such as a policy or SOP, describing the significant changes allowed and their scope. Without preexisting IACUC-approved guidance, a protocol amendment would be required. One change permitted administratively is increasing animal numbers above what was specified in the approved protocol, so long as the increase is in alignment with the IACUC guidance. In a process known as veterinary verification and consultation (VVC), the IACUC can authorize a veterinarian to allow specific types of changes in: anesthesia, analgesia, sedation, or experimental substances; euthanasia by any method approved in the AVMA Guidelines for the Euthanasia of Animals; and duration, frequency, type, or number of procedures performed on animals. The veterinarian verifies that the proposed changes comply with the IACUC guidance and are appropriate for the specific situations and animals. VVC does not permit the addition of new procedures to the protocol, as these would require an amendment.

## Noncompliance

Any deviation from an animal uses protocol is handled as a noncompliance and can potentially result in suspension of the study. The institution is required to notify the USDA, when the IACUC suspends an animal activity (United States Department of Agriculture 2017a). The institution is also required to report to OLAW any suspension of an animal activity as well as any serious or continuing noncompliance with the PHS Policy or the *Guide for the Care and Use of Laboratory Animals* (United States Department of Health and

Human Services 2015; National Research Council 2011). Moreover, OLAW reports to the USDA incidents it perceives as possible violations of the AWA and AWR. Violations will be investigated by the USDA, can be prosecuted in a court of law, and may incur large financial penalties and the suspension of registration as a research institution. Collectively known as enforcement actions, these may damage the institution's reputation because they are made public via the USDA website. They can also jeopardize the investigator's privilege of conducting research at that institution if funding support is terminated as a result of the violation or if the institution bars the investigator from using animals in order to minimize research risks.

## Conclusion

Supporting animal welfare and minimizing pain and distress are major considerations through every phase of an animal's care and use in science – procurement, housing and feeding, study procedures, and euthanasia. All personnel, including researchers, the IACUC, and animal facility staff, must collaborate to best support animal welfare while meeting scientific goals.

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## Ideational Behavior

### ► Insight

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## Identity by Descent (IBD)

### ► Allele Sharing

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## Illusion

### ► Top-Down Processing

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## Image Score

### ► Reputation

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## Imagination

### ► Top-Down Processing

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## Imitation

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## Synonyms

Copying; Social learning

## History of Defining Imitation

Historically there has been little agreement on which behavioral or cognitive phenomena constitute imitation in animals. For example, because the term imitation is frequently used colloquially, some scientists have used the word in a loose sense when referring generally to social learning mechanisms. On the other end of the spectrum, some consider imitation to be a complex ability that is likely rare or nonexistent in nonhuman animals. Indeed, this problem of operationalizing imitation has roots in the work of early proponents of evolutionary approaches to behavior and is still frequently discussed in contemporary writings.

When Charles Darwin's protégé, George Romanes, published his famous collection of anecdotes on animal behavior in 1882, descriptions of imitation-like feats abounded. However, no definition of imitation was provided. Instead, Romanes reported a panoply of seemingly imitative behaviors, ranging from specific case-studies (for example, the cat that adopted the food-begging habits of a cohabiting terrier), to more general observations (for example, how some species of birds model their vocalizations on environmental noises). Romanes' anecdotal approach to animal behavior sparked general interest in the topic of the animal mind, but also encouraged others to consider more conservative

interpretations of seemingly intelligent behavior in animals; for example, Lloyd Morgan proposed his famous canon, where he emphasized that animal behavior should not be interpreted as the outcome of "a higher psychological faculty," if it can instead be explained by "lower" processes (1894, p. 53). And indeed later, Morgan (1900) made an effort to categorize various imitative-like phenomena, highlighting the distinction between instinctive and deliberate forms. Instinctive imitation was said to occur in cases where an observed behavior acts as a releasing stimulus for that same behavior in a conspecific (describing what is generally referred to as behavioral contagion today; Hoppitt and Laland 2013), while for deliberate imitation to occur an animal was required to possess an intention to imitate a behavior. Interestingly, Morgan compared deliberate imitation in nonhuman animals to the type of imitative ability demonstrated by human children (*Homo sapiens*), framing imitative behavior in an anthropocentric manner.

Another pioneer in the field of animal behavior, Edward Thorndike, provided further guidance on how imitation in animals should be approached, supplying the first definition of imitation. He described imitation as "learning to do an act from seeing it done" (Thorndike 1911). To this day, many scientists use this broad definition as the basis for discussing imitation, before applying a number of operational caveats, a trend that Thorndike himself instigated. Thorndike was clear about a number of behaviors that did not qualify as imitation. For example, bird song was considered a special case, as vocal imitators did not seem to possess more general imitative capacities, and because, in the auditory domain, the perceptual overlap that is available to vocal imitators, between performance by self and other, is considerably greater than the overlap in the visual domain afforded to imitators of action. While today our understanding of both vocal and physical imitation is significantly enriched, these areas of research are still largely independent of one another.

To be confident that an animal has demonstrated imitative ability, Thorndike suggested one must also rule out a number of so-called

pseudo-imitative processes (what we now know as non-imitative mechanisms of social learning). Following Morgan, Thorndike (1911) stressed that instinctive forms of action imitation are categorically different from true imitation and that some “simple acts” triggered upon observing a behavior (e.g., yawning) should also not be considered truly imitative (however, the distinction between “simple” and “complex” behaviors was not made explicit by Thorndike).

Distinguishing imitation from other social learning mechanisms, or this “definition-by-exclusion” approach, has been hugely influential in the field of imitation research both theoretically and methodologically. This approach, when complemented by the explanatory parsimony central to the school of comparative psychology spearheaded by Morgan and Thorndike, drove imitation research throughout the last century and largely still stands today. Influential writings on primate behavior published throughout the early and mid-twentieth century, for example, would often begin with descriptions of non-imitative phenomena. Yerkes and Yerkes (1929) explicitly highlighted mechanisms that did not constitute imitation (e.g., local enhancement) before discussing their observations of imitation-like behavior in chimpanzees (*Pan troglodytes*). The care in describing imitation in animals can also be found in the writings of Hayes and Hayes (1952). The Hayeses intentionally described the imitative-like behavior they observed in their home-raised chimpanzee Viki without formal classification or definition of imitation, allowing readers to draw their own conclusions about whether their observational and experimental findings justified an imitative description.

Work on non-imitative social learning mechanisms seems to be driven largely by the need to isolate imitation, and so discussion of imitation cannot proceed without some allusion to other social learning mechanisms (described extensively elsewhere in this Encyclopedia). Consider the following observation from the perspective of a researcher interested in imitation: “Shortly after observing a conspecific cracking nuts with a rock, a monkey approaches the same rock, now idle, and uses it to crack a nut.” A human observer

recording this event might conclude that a monkey learned to imitate this nut-cracking behavior, that is, the monkey learned to perform a behavior from seeing it done. But it could also be argued that the mechanism leading to the performance of the behavior was local enhancement; the monkey was merely attracted to the nut-cracking site through the presence of the individual, and the nut-cracking behavior was acquired through trial-and-error learning. Other mechanisms that could facilitate this nut-cracking behavior and confound the study of imitative ability include stimulus enhancement (the monkey was attracted to the rock and the nut), affordance learning (the monkey learned about the physical properties of the rock and/or nut), goal emulation (the monkey learned that a nut could be extracted from a shell), and response facilitation or contagion (the nut-cracking behavior was already in the monkey’s behavioral repertoire and was merely primed by observing the same behavior; note the distinction between response facilitation and contagion largely depends on whether priming is learned or innate; Hoppitt and Laland 2013). The thoroughness of the “definition-by-exclusion” approach has generated both a useful taxonomy of social learning mechanisms (e.g., Whiten and Ham 1992) and inspired ingenious methodologies. However, the definition of imitation is not limited to a description of what imitation is not. Once Morgan’s canon has been applied to the observation of an imitative-like behavior, there remains a number of possible explanations for what exactly has taken place cognitively. This extra level of analysis applied to imitation has traditionally tended to focus on how powerful imitation might be as a social learning mechanism.

## The Complexity of Imitation

Thorndike did not necessarily consider imitation an intelligent process, writing that “an imitative act could be performed quite unthinkingly” (1911, p. 79). However, he discussed imitation as a phenomenon that requires “reason,” and also explicitly made a distinction between complex and simple imitative phenomena. Today, cognitive



complexity is often considered central to imitation. At its most complex, imitation is defined as the ability of an animal to learn how to perform an action previously not present in its behavioral repertoire after seeing the action performed by another individual (Byrne 2002). The novelty criterion frames imitation as a significant means of learning new behaviors, but novelty is also difficult to operationalize. To know if an animal's behavior is novel, a researcher must compile a comprehensive list of all the previous behaviors an animal has performed, a logistically improbable feat in most cases. Also, upon reaching maturity an animal is likely to have already executed the vast majority, if not all, potential physical movements, rendering novel action, and therefore imitation, impossible. Thorpe (1963) applied a more liberal novelty criterion, describing imitation occurring when the copied act is either novel or *improbable*. However, while the improbability caveat bypasses the problem of identifying novelty, Thorpe did not clarify how exactly one should operationalize "improbable."

To overcome these empirical and theoretical limitations while maintaining a powerful role for imitation in learning new skills and abilities, a weaker novelty criterion has been proposed. Imitation could still facilitate novel behavior but not at the level of physical action. Instead, contextual imitation occurs when an animal learns how to perform actions already in their behavioral repertoire in novel contexts (Byrne 2002). Under this interpretation, imitation is still a powerful learning tool, allowing animals to exploit resources in new settings. It has also been suggested that novelty could be demonstrated when an animal learns how to combine familiar actions into a novel action-string, again emphasizing the role of imitation in learning (see production imitation, Byrne 2002).

But novelty is not the only way in which imitation has become cognitively loaded. Some have suggested that understanding the intentions or goals of the individual being imitated is central to "true imitation" (Tomasello et al. 2005). However, while this may be a sensible distinction to make theoretically, it also leads to empirical problems, since identifying intention reading in an animal is far from trivial. Indeed, other

mechanisms of social learning have been defined to specifically describe when an animal learns about the goals or outcomes of an action (e.g., emulation), rather than the action itself, so it may not be useful for researchers of imitation to consider these phenomena as one, at least not in an operational sense.

For others, imitation is more simply the matching of topographical features of behavior (van de Waal and Whiten 2012; Voelkl and Huber 2000). This approach captures the spirit of Thorndike's definition, as long as "act" is interpreted specifically to mean an animal's physical behavior, rather than the psychological processes that lead to the behavior or the effects this behavior may have on the environment. While other phenomena of social influence (for example, contagion) also require the matching of topographical features, as contagious acts are limited in number and stereotyped in form, they can be readily documented and ruled out when distinguishing a "truly" imitative act.

Action imitation, without novelty or intention-reading, is still thought to require considerable cognitive effort because of the "correspondence problem." The correspondence problem was described by Nehaniv and Dautenhahn (2002) as the difficulty faced by an observer in recreating an action that perceptually, cognitively, or motivationally corresponds to the actions of the model. Consider the difficulty faced by a dog attempting to imitate its human owner's action, say, opening a door. As paws and hands differ in many morphological features (e.g., arrangement of the phalanges), the dog is required to perform an action that perceptually corresponds little to what they have observed. A lack of perceptual correspondence is also problematic within species. When an animal observes the actions of another, the perceptual input rarely maps directly to the perceptual experience of observing oneself. Indeed, in cases where an action is completely unobservable, or opaque, to the animal performing the act (e.g., a facial expression), an imitator must recognize that the perceptual qualities observable in an action (e.g., a conspecific's frown) correspond to some specific muscle movements (e.g., constriction of the corrugator supercilii). This example represents

an extreme case in relation to perceptual correspondence; however, low levels of perceptual overlap occur across most cases of action copying. While it is unknown how imitators may solve this problem, some have suggested that the mirror neuron system, a subset of neurons that have been found to map sensory information about an action onto neurons linked to that action's performance, might help bridge the correspondence gap (Gallese et al. 1996). However, the link between imitation and mirror neurons is far from clear, and there is still no consensus on the cognitive processes that enable animals, humans included, to convert an observed action into a corresponding motor response.

Overall, while some may argue that the study of imitation has been muddled by conceptual discrepancies, the vigorous debates over the classification of imitation have ensured researchers are careful when interpreting and categorizing imitative-like behavior. Furthermore, this discussion has led to the development of a number of innovative methodologies that allow researchers to distinguish between varied social learning phenomena.

## Methods of Studying Imitation

As well as providing the first definition of imitation, Thorndike (1911) also pioneered the use of controlled experimental methods to explore imitative behavior. His studies of chicks, cats, dogs, and monkeys largely involved allowing a naïve individual to observe an experienced conspecific escape from a cage. The naïve animal would observe from either the same cage as the escapee or through some wire mesh, always able, if attentive, to observe the behavior of their neighbor. Thorndike noted the attentiveness of the observer, recording the number of instances that the naïve individual was orientated towards the experienced animal, and subsequently measured how long it took the animal to escape following repeated observations of the conspecific's performance (e.g., pulling a string to open a cage-door). Although his studies found little evidence that social demonstration led to quicker escape times

in comparison to individuals that had not received social information, one could also fairly criticize whether these methods even allow discrimination of imitation from other social learning mechanisms. As imitation is considered more cognitively demanding than other social learning mechanisms, conclusive identification of imitative learning in an experimental paradigm must rule out the possibilities of other mechanisms giving rise to the observed effect.

When housing animals within the same or adjacent enclosures, it is difficult to distinguish which exact mechanisms might lead to learning. However, while ineffective in distinguishing true imitation, this method has been used extensively to examine social learning abilities of animals more broadly. To more reliably evaluate the learning mechanisms at play in social arenas, the highly influential two-action method was introduced (Dawson and Foss 1965). The two-action method requires an apparatus that can be manipulated in two different ways; for example, a lever may be pressed to either the left or the right to receive a reward. If, upon observing an animal interact with this apparatus using one of the two methods (e.g., observing an animal move a lever to the right rather than the left), the observer is more likely to perform that same action when compared to an individual who had not experienced a social demonstration, it can be concluded that some form of social learning has taken place. However, again, the use of this method in many cases does not explain whether the animal has learned specifically about the actions used upon the apparatus, or rather the affordances of that apparatus. Nonetheless, the two-action method has been successful in identifying more general social learning phenomena in a range of species. To control for some of the limitations of the two-action method, automated apparatuses, or "ghost apparatuses," have been used in some studies of social learning. These ghost apparatuses allow an experimenter to reveal the affordances of an object (for example, the movement of a lever) without a social agent acting upon the manipulanda. If animals can learn the actions necessary to operate the apparatus in only the cases where a social demonstrator is present, it is

argued that action imitation is likely to have driven this behavior, rather than other phenomena.

A variation of the two-action method has been used to specifically examine imitation of actions performed by different body parts. Under this method, researchers train model animals to interact with an apparatus using one of two different body parts. For example, one model might be trained to open a canister with its mouth, while another would be rewarded for using its hand or paw to achieve the same goal. The model then demonstrates the trained actions in the presence of naïve conspecific observers before the observers themselves are given the opportunity to interact with the apparatus. Following the social demonstration, if the observer uses the same observed action more often than the alternative, then body-part imitation can be said to have taken place. Studies using this method have identified evidence of body-part imitation in primates (e.g., *Chlorocebus pygerythrus*, van de Waal and Whiten 2012; *Callithrix jacchus*, Voelkl and Huber 2000), as well as some species of birds (e.g., *Coturnix japonica*, Akins and Zentall 1996), and those who favor the definition of imitation as action matching have described these findings as evidence of true imitation.

Another method of identifying imitation of actions is the “do-as-I-do” paradigm. This procedure requires an experimenter to first train an animal to perform a number of actions on command. Subsequently, the trainer performs one of the trained actions, introduces a cue or command signal (e.g., “do this”), and rewards an animal only if it performs the same action. This training procedure of action shaping and positively reinforced copying is repeated for a number of actions, and finally some novel untrained actions are introduced. The question is whether animals are able to generalize their training such that they respond as if they recognize the cue as an instruction to imitate. It has been argued that this is the most reliable method of identifying intention to imitate, of the sort proposed by Morgan, as to succeed on this task it is thought that the animal must have conceptualized what it means to imitate. This method has successfully identified

imitative capacity in enculturated apes and dogs (e.g., *Pongo pygmaeus*, Call 2001; *Canis lupus familiaris* Topál et al. 2006), but not monkeys (*Cebus apella*, Frigaszy et al. 2011). More recently this method has been adapted to test if beluga whales (*Delphinapterus leucas*) can learn to imitate conspecifics, through the use of a “do-as-they-do” task with promising preliminary results (Abramson et al. 2017). The controlled use of the “Do-as-I-do” paradigm and two-action method have added empirical validity to less systematic bodies of evidence of imitative behavior.

Experimental research is clearly the most valid and reliable way of understanding the abilities of animals, but it is worth highlighting that some of the most compelling evidence of complex imitative ability is anecdotal in nature. Viki, a chimpanzee raised as a human child by Catherine and Keith Hayes, for example, seemed to imitate a number of human-like behaviors. One of the most compelling examples involved Viki taking a tube of lipstick, applying the color to her lips in front of a mirror, then, pressing her lips together before rubbing the color with her fingers (Hayes and Hayes 1952). According to the Hayeses, this behavior was untrained, unrewarded, but nonetheless resembled closely the sequence of behaviors Viki would have observed performed by a human. Russon and Galdikas (1993) reported a number of instances of orangutans (*Pongo pygmaeus*) imitating human activities including fire-preparation behavior, the building of a bridge across a river, and painting. Again, each behavior was unrewarded and was performed unprompted. These cases of human-like behavior performed in novel contexts and the novel combination of behaviors certainly seem to meet many of the more restrictive novelty or improbability criteria proposed to set imitative behavior apart from other forms of social learning. Anecdotes of interspecies imitation of this sort, where the model is not human, is rare, but one convincing case involves a dolphin (*Tursiops aduncus*) imitating the swimming technique of a Cape fur seal (*Arctocephalus pusillus*) that was housed in the same pool; the dolphin was observed to propel itself through the water using flipper movements

rather than dolphin-typical fluke movements (Taylor and Saayman 1973).

These anecdotal accounts paint a richer picture of the possibility of complex imitative abilities of large-brained mammals; however, they also lack the rigor of the experimental methods described above, making it difficult to assess specifically which mechanisms might allow these behaviors to arise. Nonetheless, these accounts provide fascinating examples of the complex social abilities of some animals when allowed to interact without limits placed on their behavioral repertoire, as is often the case in experimental settings. Importantly, these observations can also enrich and inspire experimental work. For example, Hayes and Hayes (1952) developed the “Do-as-I-do” method, in an effort to more carefully study the imitative behaviors that they already observed Viki perform. It is worth noting that the majority of these anecdotal reports involve primates that have had extensive interactions with humans, in some cases raised by humans. While spontaneous imitation of complex behavior is less common in non-enculturated animals, it is unclear whether this is because human interaction drives the development of imitative behavior or merely facilitates the collection of anecdotes. A chimpanzee performing a typically human behavior (e.g., applying lipstick) will offer more compelling evidence of imitation than would anything involving common species-typical behaviors (e.g., a specific foraging behavior like nut-cracking). The experience potentially necessary for imitative behavior to develop is well worth exploring, and we have a lot to learn about how imitative phenomena may be facilitated by human interaction.

While great steps have been made in understanding imitation and other social learning mechanisms through the use of varied methodologies, it is worth remembering that no one method will be able to paint a complete picture of this phenomenon across all taxa. Anecdotal claims will continue to inspire more careful observation of behavior as well as insightful experimental designs, and together, these methods will continue to help researchers better understand a range of imitative phenomena.

## Mirror Neurons and Imitation

To understand the mechanism of imitation, researchers have spent considerable effort exploring neural substrates that have been linked to imitative behavior in primates. Mirror neurons, first discovered in the F5 region of a pigtailed macaque’s (*Macaca nemestrina*) parietal lobe by researchers in Parma (Gallese et al. 1996), may provide the neural foundation that allows an animal to solve the “correspondence problem.” Neurons sampled in the premotor area have been found to fire when macaques perform an action (i.e., grasping a peanut), and also when the monkey observed the researcher perform the same action. These initial studies described neurons with both visual and motor properties, single cells that could represent information about another’s actions in egocentric terms. A thorough exploration of this neural subset was published in 1996, outlining multiple properties of these cells (Gallese et al. 1996). For example, these neurons fired when monkeys observed an experimenter acting upon an object but did not fire when the object or the action were presented in isolation, suggesting some functional role in goal directed behavior. Furthermore, while most neurons were active for specific motor actions (e.g., a power grip or precision grip), some neurons were more sensitive to the goal of the action, firing irrespective of effector (i.e., three sampled neurons fired when the experimenter picked up an item using either the hand or mouth). Subsequent studies of single neurons have explored a range of properties of these macaque mirror neurons (for a review see Kilner and Lemon 2013), and while it is likely that a similar system is present in other primates, currently, the only other evidence of a homologous system has been reported in humans (Iacoboni et al. 1999; although there is some preliminary evidence that a similar system may be present in the common marmoset, Suzuki et al. 2015). Although the function of mirror neurons has been disputed, a parsimonious interpretation suggests mirror neurons play a role in recognizing the actions of others, and so while the primary function of mirror neurons may not be directly

related to imitation, by facilitating action recognition these neurons could still contribute to resolution of the correspondence problem by recruiting additional brain regions.

## The Origins of Imitation

Considering imitation from the comprehensive ethological perspective championed by Nikolaas Tinbergen (1963) requires consideration of a number of different factors. However, it seems that empirical work on imitation has been disproportionately concerned with understanding the distribution, or phylogeny, of imitative ability throughout animals, with a particular focus on the primate clade. The mechanism of imitation has also been studied extensively, specifically when it comes to understanding which social and nonsocial stimuli are necessary for imitation and other social learning phenomena to be observed (see the discussion of methods above). Furthermore, much effort has also been expended to explore potential neural mechanisms of imitation. On the other hand, the remaining Tinbergian questions of ontogeny and adaptive function are currently not well understood in relation to imitation.

While it makes logical sense that the ability to imitate actions would be adaptive in facilitating the learning of new skills more quickly when compared to trial-and-error learning, it is difficult to find empirical support for this assumption (as is the case for many hypotheses concerning adaptation). However, while difficult to empirically demonstrate adaptive benefits, computer-based models of foraging strategies conclude that an ability to exploit social information is highly adaptive (e.g., Rendell et al. 2010). Theoretically, then, it is likely that there has been some selective pressure on social learning mechanisms like imitation. Indeed, some theories of brain evolution propose that sociocultural pressures may have driven encephalization in primates and other large-brained species. This cultural intelligence hypothesis proposes that social learning mechanisms may lead to more complex traditions and culture, which in turn place greater selective

pressure on these mechanisms (Whiten and van Schaik 2007). This theory complements other perspectives on social drivers of intelligence in animal societies but places a stronger emphasis on the domain of social learning. While theoretical and correlational work provide at least some insights into the potential adaptive value of imitative behavior (see Whiten and van Schaik 2007), in contrast, the ontogenetic roots of imitative behavior remain underexplored from any angle. Indeed, it is possible that misunderstandings about the complementary roles of adaptive and ontogenetic processes may have unintentionally stymied research on development. That is, if researchers assume that imitation is an evolved adaptive capacity, it might also be assumed that this entails hardwired processes largely independent of individual variation in experience or learning opportunities. As a consequence, developmental processes may be overlooked.

One of the most debated areas in imitative research is the question of whether an ability to imitate actions is present at birth in some species. Much of the discussion concerning both mirror neurons and imitative ability seem to implicitly suggest that imitation is an evolved capacity, with observations of imitative ability in infant primates presented as evidence of this fact. Imitative ability has been identified in the infants of a number of primate species including rhesus macaques (*Macaca mulatta*), chimpanzees, and humans (for a review see Oostenbroek et al. 2013). However, it is unlikely that these phenomena are responsible for all imitative behavior in primates, especially given that many of these early imitative behaviors are only present for a restricted range of actions (e.g., in one case only two of four actions tested were imitated by infant macaques; Ferrari et al. 2006), and are only present during very specific time-windows (e.g., imitation of actions by infant macaques only occurred on their third day of infancy; Ferrari et al. 2006). One mechanistic model proposed to explain this phenomenon is the intermodal mapping model of imitation (AIM) which describes an innate process that matches the representation of observed motor actions with proprioceptive feedback from the performance of the same action (Meltzoff and



Moore 1997). It is conceivable that the mirror neuron system is the neural mechanism that supports this intermodal matching system; however, there is currently no empirical evidence in support of an innate mirror neuron system.

Even if an innate action-matching capacity exists in animals, it is likely that later experience also shapes imitative ability. One developmental view of imitation, the Associative Sequence Learning (ASL) hypothesis, proposes that through repeated experience of observing and performing actions in social contexts, an animal begins to associate sensory representations of specific actions with the motor representations of the same actions (Heyes and Ray 2000). Consider a flock of birds that upon reaching a foraging site begin manipulating the soil with their beaks to extract insects or grains. According to the ASL view, if this experience is repeated, an individual will learn to associate their own pecking behavior with the sensory experience of their group mates performing the same behavior. Building up specific associations between observed and performed actions may then in the future facilitate action imitation. These sensory-motor associations could be formed when environmental factors (like foraging opportunities) synchronize behavior but also when observing one's own actions, and in some species, they may be created when being imitated by parents or conspecifics. This approach posits that the correspondence problem can be overcome through associative process that are widespread among animals and questions the level of cognitive complexity necessary for an animal to match the behavior of a conspecific. Support for this approach is found in studies where imitation biases are reduced or eliminated by providing animals with sensory-motor experience that would disrupt previously formed associations. For example, in one case, dogs (*Canis lupus familiaris*) were rewarded for opening a door with their mouth after seeing a human open the door with their hand, and vice versa. These dogs were later found to struggle to learn an imitative stimulus-response association, when being trained to open a door with the same effector, compared with dogs that had not received the prior incompatible training (Range

et al. 2011). These effects have been also shown in humans, and capuchin monkeys (*Sapajus sp.*), demonstrating that imitative effects are indeed malleable in response to sensory-motor experience in some species (O'Sullivan et al. 2017), but overall, much more work is needed to understand how these experiential accounts can explain imitation of complex actions in animals.

It is important to remember that evolved and developed capacities interact and overlap, and that there is likely no purely innate or learned explanation for imitation, as is the case for most behaviors. An open-minded approach is essential to fully understand the origins of imitative behavior, and this should also extend beyond a primate-centric view of imitation. Evidence of imitation has largely emerged from work with primates, but it may be that by labelling imitation, a complex mechanism, research efforts have focused too extensively on animals considered to possess a cognitive toolkit similar to our human one. A truly comprehensive evolutionary approach to imitation, on the other hand, would stress how environmental and social pressures acting upon imitative capacities should function across animal species and that much of the experience posited to facilitate action imitation is potentially available to members of a range of social species throughout development. With this in mind, future efforts to explore imitative ability, defined as morphological matching, can avail of a wide range of species and methods to develop a more complete picture of this ability.

## Imitation in Humans

The phylogenetic distribution of imitative ability is an open empirical question, but humans are certainly imitative, regardless of how the term is operationalized. Studies of neonatal imitation suggest humans may have some innate disposition to imitate action from birth (see Oostenbroek et al. 2013). However, evidence of neonatal imitation in nonhuman primate species that are poor imitators when tested in later development (Ferrari et al. 2006), and indeed, uncertainty over the generalizability of imitative ability in human

infancy (Oostenbroek et al. 2013), makes it difficult to draw concrete conclusions about how neonatal imitation may facilitate imitation in later life. Focusing on the ontogeny of imitative behaviors in human children, developmental psychologists have described how progressively more complex abilities develop throughout the first years. For example, children imitate actions that make sounds before they can produce opaque actions (Jones 2007), and by three years, the propensity for imitation in any guise (whether intentional, improbable, etc.) is highly developed in humans (Horner and Whiten 2005; Jones 2007). Recent studies show that the motivation to imitate in adults and children even leads to the copying of causally irrelevant behaviors in cases where it seems obvious that the completion of a task (e.g., opening a box) does not require the additional actions (e.g., unnecessary tapping on the box-lid; Horner and Whiten 2005). Furthermore, it seems that this “over-imitation” is also uniquely human. Studies that have directly examined the imitation of actions unnecessary for a task’s completion across both human children and apes have to-date found that apes will perform actions relevant to the task’s completion, ignoring additional demonstrated behaviors, while children will imitate more comprehensively all actions whether relevant to the task’s completion or not (e.g., Horner and Whiten 2005). Indeed, it has been suggested that the human species’ ability to accumulate suites of progressively more complex socially learned behaviors over time might be attributed to these tendencies for high-fidelity social learning (Acerbi and Tennie 2016).

Imitation is largely defined in the context of learning; however, in humans, imitation is also linked to other social variables. In both adults and children, the matching of specific behaviors (e.g., body postures, behavioral movements, etc.) has been linked to other aspects of sociality (e.g., affiliation). For example, in one study, adults who were imitated by an experimenter’s confederate reported liking the person more than if not imitated (Chartrand and Bargh 1999). Further, there is evidence that this link between sociality and imitations is present early in development, as 18-month-old children were found to be more

likely to help individuals who had previously mimicked them (Carpenter et al. 2013). One study in nonhuman primates demonstrated that capuchin monkeys preferred to interact and attend to humans who had imitated them (Paukner et al. 2009), but it is unclear how generalizable this relationship is in either capuchins or other primate species. Indeed, the link between instrumental and socially motivated imitation has yet to be fully understood in humans. Nonetheless, whether driven by learning, affiliation, or other factors, the imitative phenotype is obvious in humans from an early age. On the other hand, and as discussed above, the identification of imitation in nonhuman animals depends on its operationalization, and some of the most conservative definitions rule-out its presence in most species. It is difficult to conclude, however, whether this difference is one of degree or kind; the disparity is great, but this empirical question is yet to be answered.

## Summary and Conclusions

Work in the late nineteenth century by early proponents of evolutionary approaches to cognition began a tradition of exploring imitation, a term whose meaning still defies consensus. However, the existence of a rich literature concerned with understanding the meaning of animal imitation ensures that researchers today are careful in their use of the term, thoroughly and explicitly highlighting what imitation means to them. To some, imitation occurs with an entirely novel behavior is learned through observation; to others, an old behavior learned to be performed in a new context qualifies. Imitation might be described as a chain of old behaviors produced in a novel order, or true imitation might be most simply, the matching of morphological topography.

If imitation is considered to require novelty or intention, then currently it may only be evidenced through the Do-as-I-do task in a few species. However, if imitation is defined more liberally as the matching of actions, this phenomenon is observed across a range of social species including dogs, apes, monkeys, and birds. The best

efforts taken to methodologically isolate imitative ability are commendable in offering great insight into the eliciting stimuli and contexts in which social learning takes place, but these methods are also limited by the constraints of experimental control, which often entails the removal of the full range of potential social and nonsocial inputs. Imitative behaviors are likely to occur in conjunction with enhancement effects, emulation, affordance learning, and other phenomena; a tapestry of mechanisms scaffolding each other and facilitating adaptive behavior in complex social environments. Learning the affordances of an object is likely to canalize specific actions, while the capacity to match behavior likely facilitates learning about object affordances. How imitation works in conjunction with other mechanisms has yet to be properly understood, and this is a noble goal for the future field of imitative research. Many years have passed since Romanes and Thorndike first considered the questions of animal imitation, reaching very different conclusions informed by their respective methodological paths. Today, there are lessons to be learned from both pioneers. Both empirical rigor and careful observation continue to perform critical and complementary roles in elucidating animal abilities for learning to do, from seeing done.

## Cross-References

- [Andrew Whiten](#)
- [C. Lloyd Morgan](#)
- [Cecilia Heyes](#)
- [Cognitive Imitation](#)
- [Contagion](#)
- [Copying](#)
- [Edward Thorndike](#)
- [Emulation](#)
- [George Romanes](#)
- [Ghost Control](#)
- [Morgan's Canon](#)
- [Primate Cognition](#)
- [Rational Imitation](#)
- [Social Learning](#)
- [Stimulus and Local Enhancement](#)
- [Tom Zentall](#)

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## Imitation Game

### ► Turing Test

## Immanuel Kant

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**Kant, Immanuel** (1724–1804). German philosopher, leading mind of the Enlightenment, and one of the most influential thinkers of civilization. He contributed to epistemology, ethics, and political theory, as well as to natural philosophy (the partly speculative precursor of the natural sciences). Kant remarked on animals in ethics, metaphysics, and natural philosophy. In ethics, he formulated human-centered arguments against animal cruelty; in metaphysics, he determined the ontological status of animals; and in natural philosophy, he was the first Western thinker to give a systematic account of material self-organization that implies a human descent from animals. A problem, which affects several of his positions, is that Kant lived at a place and in a time that imposed theological constraints on animal studies.

### Anthropocentric Animal Ethic

Kant's most influential contributions are in the field of practical philosophy. Well-known are his arguments for decolonization and his case for a United Nations in political theory, and a principle of action to assert human rights, the Categorical Imperative in ethics. In *Groundwork to the Metaphysics of Morals* (1785), Kant gives several formulations of the Categorical Imperative; by the second formula, one should treat humanity, whether in one's own person or in that of another, always as an end and never as a mere means only (cf. Kant, *Gesammelte Schriften*, 4:429). Humans are autonomous beings because of their potential for independent rationality. This capacity to act according to judgment reveals humans as self-governed organisms, and in this sense they are ends in themselves. The Categorical Imperative is a demand for human rights. It is not a demand

for animal rights; however, for animals, in Kant's understanding, cannot act on judgment and are therefore heteronomous, governed not by reason but by other drives, such as instincts and inclinations.

According to a student transcript, *Moral Philosophy: Collins's Lecture Notes* (1784–1785), Kant taught that since humans but not animals are capable of judgment, only the former have moral standing, and all our duties are duties to humanity. To animals, we have no obligations, at least not directly (27:459). Nonetheless, Kant acknowledges that there are clear constraints on how to treat animals. Animal cruelty is wrong; first, because animals are sentient, since we see “how greatly they care for their young,” and second, because a person who mistreats animals “is also no less hardened towards men” (27:459). Animal cruelty is a wrong against humanity, for such misconduct creates liabilities for other humans. Following Thomas Aquinas, Kant concludes that the duty not to mistreat animals is a duty *about* animals but not owed *toward* them; duties to animals are indirect duties to humanity (27:460).

### Animals Have Souls

In his metaphysics class, according to student notes, *Metaphysics L<sub>I</sub>* (ca. 1775), Kant distinguishes the structure of reality into types. One distinction obtains between material and immaterial beings; that is, between nonlife and life, or “inanimate” and “animate” nature (28:274). Matter as such is inanimate, but there are also immaterial beings, and these are minds. That animals have material bodies does not make them “mere machines or matter; rather, they have souls” (28:274). “Soul,” for Kant, is an immaterial being that interacts with the body, is constituted by such interaction, and ceases to be when the body dies (28:273–274). “Spirit,” by contrast, would be a speculative immaterial being able to cognize in disembodied form. Empirically, we distinguish nonlife from life through



movement – if something moves by itself, it is alive and thus endowed with a soul. “To the extent matter is animated,” Kant notes, “it is *ensouled*: a principle of life underlies animals, and that is the soul.” (28:275). A question he wrestles with is how to distinguish animal minds from human minds. In the metaphysics-lectures, his answer remains ambiguous. On the one hand, animals possess cognition in that they are “beings that have mere sensibility and power of representation” (28:274). On the other hand, it is unclear how animal cognition compares to human cognition; this issue highlights “the limits of reason” and makes us “acquainted here with our ignorance” (*ibid.*).

In his *Lectures on Philosophical Encyclopedia* (1775–1782), he believes to have isolated a qualitative difference between animal and human souls. While both types of souls are sentient (‘sensibility and power of representation’), human souls are endowed with “consciousness,” which is “the main and nearly the only difference . . . but this is also so large that it cannot be replaced by anything” (29:44). However, strictly speaking, this qualitative difference is only a difference in time, for what makes these remarks interesting is that Kant also argued for the gradual emergence of qualitatively new properties in the course of nature’s self-organization.

## Evolutionary Descent and Material Emergence

In *Critique of the Power of Judgment* (1790), Kant suggests that humans have descended from animals; that animals evolved from primitive life; and that primitive life has self-organized from interplay of matter and energy (5:419). The evidence for a “system” or “principle of generation” lies in “the agreement of so many genera of animals in a certain common schema” or in “an analogy of forms.” (5:418). While he concedes that this sought-for principle of generation has not been found yet and that settling this issue must await further scientific progress, the evidence is sufficiently suggestive to “strengthen the suspicion of a real kinship among [animals]

in their generation from a common proto-mother [*Urmutter*], . . . from human beings down to polyps, and from this even further to mosses and lichens, and finally to the lowest level of nature that we can observe, that of raw matter: from which . . . the entire technique of nature . . . seems to derive” (5:419).

In the early, pre-critical treatises, *True Estimation of Living Forces* (1747), *Universal Natural History* (1755), and *Physical Monadology* (1756), Kant gives a speculative account of nature’s self-organization. Self-organization begins dynamically with energy (1:17) and structurally with polarity. For the logic of being, polarity means there is no simple first principle of ontology. Instead, Kant argues in *New Elucidation* (1755), the first principle is complex: a binary schema of negative and positive combined as contradiction (1:388–390). In *Living Forces*, he explains how energy stretches out as space, and how space weaves a web of power points (1:22–24). In *Physical Monadology*, he theorizes how spatial power points are dynamic sources of matter: polarized in attraction and repulsion, any point source radiation expands a tiny dimensional manifold, an impenetrable, repellent “activity sphere,” which accretes with other such energy bubbles into elementary form that constitutes material particles (1:481–484). In *Universal Natural History*, he reasons how a cosmic fog of scattered particles contracts into clouds that evolves into galaxies, star systems, and planets (1:254–256, 263–269). Planets, once formed and cooled (1:199–200), spawn biospheres with plants, animals, and humans (1:352–353). How life unfolds to higher levels of self-organization, Kant surmises, is due to the varying density of matter; the less dense the material substratum is, the more highly evolved organisms will be, up to a step ladder of conscious beings (1:358). Consciousness, he speculates, would have to be ubiquitous in the cosmos, and humans, far from being the pinnacle of creation, occupy only the middle rung on the ladder of beings (1:359).

Instead of self-organization or emergence, Kant uses the phrase *Auswicklung der Natur*, literally “out-wrapping” or “unfurling” of nature (*cf.* 1:201, 1:226). This is Kant’s Germanized

form of the Latin *evolutio* (cf. also 16:324). The Latin term denotes the opening of book scrolls. The image is that the book of nature is like a gradually unfolding scroll, disclosing steadily more lines of information. (Kant's term for complexity is *zusammengesetzte Richtigkeit*; "compound soundness," cf. 1:226). The emergence of complexity – from matter to life, from life to animals, and from animals to consciousness – is driven by "a general world-spirit, an intangible, pervasively efficacious principle, which is the secret engine of nature" (1:203). Although Darwin was the first to put the hypothesis of human evolution in scientific form, Kant was the first to put it in systematic conceptual form. But since Kant conceived of evolution as the self-organization of order from chaos and of complexity from simplicity, he is less a predecessor of Darwin and more a precursor of Prigogine's work on dissipative structures.

### Censorship and Politicization of Evolution

The historical context of Kant's reflections on animals was generally repressive. There was little freedom of speech on such issues before the division between church and state was complete, although by the 1780s, one could be more open than in the 1750s. In early modern Europe, ethical and metaphysical questions on animals – their moral standing, and their relation to humans – had been decided by the churches. Deviation from Biblical doctrine was branded as heresy, and dissent was a punishable offense. As the Enlightenment (1680s to 1780s) proceeded, punishments grew more lenient but oppression remained. Notions such as animal rights, animal cognition, and human evolution were rated as blasphemous. Although witch-hunts had ceased in Prussia before Kant was born in 1724 (executions stopped in 1701; trials ended in 1714), persecutions elsewhere in German lands lasted well into the 1770s. The enforcement of religious orthodoxy had chilling effects. Academics in support of animal cognition had to do so secretly to avoid unemployment or deportation.

In Kant's day, thinkers known for dissent from doctrine were referred to as free-thinkers, or Spinozists.

A further complication concerns the status of evolutionary ideas in natural philosophy. The evolutionary hypothesis had been brought to Europe from China by Jesuits in reports of East Asian belief-systems such as Daoism. Evolution of life from nonlife, and emergence of complexity through polarity (*yinyang*) are key ideas in Daoist metaphysics (cf. *Daodejing* c. 42 and *Zhuangzi* c. 18). The missionary reports were studied by Kant's philosophical predecessors such as G. W. Leibniz. In 1721, China shut down the mission and banned Christianity. After the expulsion of the priests, evolutionary ideas were associated with pagan defiance, and its proponents were ruthlessly silenced. That a non-Christian nation defied Christian nations had also political ramifications, which made support for Chinese ideas dangerous, as the pioneer of the German Enlightenment, Leibniz's student C. Wolff, learned when fleeing into exile in 1723.

When Kant published on the evolutionary hypothesis, he did so either obliquely, in a technical context in the 1740s, or anonymously to avoid censure. Even so, he could not avoid problems. *Living Forces* was rejected as a magisterial dissertation and Kant left school without a degree in 1748, only to return after the passing of the Pietist professor who had barred his advancement. *Universal Natural History* was published anonymously, but in 1756, the book was traced to him, which damaged his career, forced him to retract his views, and delayed his appointment to a professorship until 1770. At the same time, and despite this recanting, he did not refrain from dropping the odd remark either in class or in his publications.

### Appraisal

The anthropocentrism of Kant's animal ethics has drawn criticism by environmental ethicists and animal rights theorists alike. Both sentience (the capacity for experiencing pain) and subjectivity (the fact that animals are experiencing subjects of life) are reasonable grounds for according animals

moral standing and thus to conclude that direct duties are owed towards them. As philosophically deserved, these objections are, they are also historically misguided, because Kant had little choice to argue differently, since anthropocentrism was the politically enforced doctrine.

The evolutionary hypothesis, developed in Kant's pre-critical philosophy of nature, has not yet received the attention it deserves, largely because its context is metaphysics, which Kant in his mature critical thought subjects to skepticist deconstruction. But considering that his early speculations were prescient anticipations of eventual advances in cosmology, chemistry, and biology, they deserve another look.

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## Immobilization

### ► Restraint

## Immune

### ► Immunology

## Immune System

### ► Immunology

## Immunity

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## Definition

Immunity is the homeostatic balance of adequate biological defenses to fight infection, disease, or other unwanted biological invasion while having sufficient tolerance to avoid allergy and autoimmune diseases. In multicellular organisms immunity can be generally defined by the ability of a cell to react immunologically in the presence of an antigen, which provides protection to a particular disease by either a natural or acquired resistance.

## Introduction

Organisms (mammalian) are constantly exposed to pathogens that enter through either external surface (i.e., the skin) through wounds or the internal surfaces (i.e., epithelia) lining the respiratory and gastrointestinal (GI) tracts. The response to infectious challenge occurs in a coordinated two-step immune response. The first line of defense is called the innate immunity, which exists from birth before exposed to any pathogen or disease occurs. The innate response is a non-specific immediate and rapid response that is

activated by any pathogen it encounters. The innate immune response is also a critical step in the activation and regulation of the second line of the immune response, which is termed adaptive or acquired immunity. Acquired immunity is specific to one particular pathogen/disease, which creates an “immune memory” that allows the body to respond even faster and more effectively if a second infection with the same pathogen occurs. Normal innate and adaptive immune responses rely on a plethora of signals ranging from specific types of immune cells to numerous immunoregulatory molecules. Thus, both types of immunity are mediated partly by the actions of specific immune cells and partly by the actions of molecules secreted by various immune cells.

## The Innate Immune Response

The innate immune response comprises five main elements: (1) physical barriers, (2) pathogen recognition systems, (3) innate immune cells, (4) immunoregulatory molecules (as known as humoral innate immunity), and (5) the coordinated recruitment of other immune cells (i.e., adaptive immune cells). For a comprehensive review of innate immunity in vertebrates, see Riera Romo et al. (2016).

Innate immune responses usually begin with the physical barriers that prevent pathogens from entering the body. However, additional immune response mechanisms destroy pathogens after they enter or flush them out before they can establish infection. Barrier defenses do not respond to infectious insult, like other innate immune responses, but continuously work to protect against infectious insult. Barrier defenses are associated with the external surfaces of the body, where pathogens may enter the host. The primary barrier to the entrance of microorganisms into the body is the skin. The skin is covered with a layer of dead, keratinized epithelium that prevents or reduces bacterial growth; in addition these cells are continuously sloughed off from the skin; thus, bacteria and other pathogens are carried away from the body. The skin also produces sweat and

other skin secretions, which lower pH, contain toxic lipids, and physically wash microbes away. Salivary secretions in the mouth, as well as the acidic environment of the stomach, also act as a physical barrier for prevention of infection. Saliva is rich in an enzyme termed lysozyme, which destroys bacteria by digesting their cell walls, while the acid of the stomach is fatal to many pathogens. The mucus layer of the gastrointestinal tract, respiratory tract, reproductive tract, eyes, ears, and nose traps both microbes and debris and facilitates their removal. In the case of the upper respiratory tract, ciliated epithelial cells move contaminated mucus upward to the mouth, where it is then swallowed into the digestive tract, ending up in the acidic environment of the stomach.

Pattern recognition receptors (PRRs) are critical for the detection of invading pathogens and subsequent activation of the innate immune response. PRRs are primarily expressed by antigen-presenting cells such as macrophages and dendritic (see below for more information on macrophages and dendritic cells) but can also be expressed by the mucosal-associated epithelium. These cells express a variety of PRRs, such as the membrane-associated Toll-like receptors (TLRs) and cytoplasmic Nod-like receptors (NLRs) as well as retinoic acid-inducible gene like helicase receptors (RLRs). These PRRs recognize the conserved pathogen-associated molecular patterns (PAMPs) that are present on microbial proteins (i.e., nucleic acids, lipids, and carbohydrates). PAMP-containing molecules act as ligands that trigger PRR-dependent intracellular signaling pathways that ultimately induce the expression of pro-inflammatory and antimicrobial cytokines. Secretion of these cytokines at the site of an infection promotes the recruitment of neutrophils and natural killer (NK) cells (see below), which eliminate pathogenic microbes and infected cells.

Immunoregulatory molecules, such as antimicrobial peptides, reactive oxygen species, as well as the pH and lipid composition of the internal and external surfaces, prevent microbial growth and invasion. While all of the immunoregulatory molecules are necessary for a normal innate

immune response, several key immunoregulatory components of the innate immune response are cytokines, chemokines, interferons, complement, and acute-phase proteins. Cytokines are proteins made and released by innate immune cells, which have the ability to affect the behavior of other cells (e.g., activate other cells) and promote or stimulate cell–cell interactions. Cytokines released by immune cells serve several functions: (1) regulation of the production of new immune cells from precursor cells, (2) activation of lymphocytes and phagocytes, (3) coordinate the cell-mediated and adaptive immune responses, (4) promote and control the process of inflammation, and (5) direct killing of infected and/or diseased cells (Banyer et al. 2000). Important families of cytokines include the tumor necrosis factor family (e.g., TNF- $\alpha$ ) and the interleukins family (e.g., IL-8). Chemokines are produced and released in a very similar fashion to cytokines; however, their main function is to attract additional cells (e.g., monocytes and neutrophils) to the site of an infection. Interferons (IFNs) are proteins that are primarily involved in the immune response to viral infection. IFNs enhance resistance to viral replication and upregulate the cell-mediated immune response to viral infection. The complement system is comprised of a large number of plasma proteins, which results in a stepwise chain reaction that ultimately cover the surface of a pathogen in proteins when activated, a process termed *opsonization*, facilitation the recognized and ingested by professional phagocytes. Phagocytes are immune cells that engulf, ingest, and destroy pathogens in a process called phagocytosis. The complement system can be activated through three different biochemical pathways (i.e., the classical pathway, the alternative pathway, and the lectin pathway); see Walport (2001a, b) for a review of the complement system. Finally, acute-phase proteins (e.g., C-reactive protein, mannan-binding lectin, and pulmonary surfactants A and D) are produced early during the inflammatory response to infection. These proteins are important for the opsonization of pathogens, the clearance of monocytes that have ingested pathogens, and the initial activation of the complement cascade.

The cell-mediated arm of the innate immunity is orchestrated primarily by granulocytes, monocytes/macrophages, dendritic cells, and natural killer (NK) cells. Granulocytes (as known as polymorphonuclear leukocytes [PMNs]) are a type of white blood cells (i.e., leukocytes) that are characterized by large granules and oddly shaped nuclei with multiple lobes. PMNs represent approximately 60% of all circulating leukocytes (Yaseen et al. 2017), with neutrophils being the most abundant. Neutrophils not only serve as primary phagocytes; they excrete toxic substances from their granules, which can readily kill invading pathogens. Neutrophils produce a host of bacteria-killing molecules, such as myeloperoxidase, defensins, azurophil-derived bactericidal factors, bactericidal permeability-increasing protein, cationic proteins, gelatinase, and lactoferrin. Furthermore, neutrophils participate in the regulation of the local defense response by releasing cytokines and chemokines, which help to recruit and activate additional PMNs, as well as macrophages to the site of an injury or infection. Monocytes and macrophages are leukocytes with a single-lobed nucleus that also act as phagocytes, as opposed to the multilobed nucleus of the PMNs. Monocytes circulate in the blood until they are recruited to the site of pathogen incursion into the body. Once they are at the site of infection, they swell in size and develop into the mature cells (i.e., macrophages), which then enter the tissues to combat infection. Macrophages, as well as monocytes, eliminate pathogens by phagocytosis, following ingestion and destruction macrophages and monocytes exhibit pathogen-derived proteins and other molecules (i.e., antigens) on the cell surface. Display of pathogen-derived antigens is critical step for the activation of the adaptive immune response. Finally, monocytes and macrophages also produce certain cytokines that help regulate immune system activity. Dendritic cells also are mononuclear phagocytes derived from monocytes. Their main role is to capture, ingest, and process antigens in order to present them on their surface to cells of the adaptive immune response (i.e., to the T-lymphocytes, see below). Thus, dendritic cells play a crucial role in linking innate and adaptive



immune responses. Lastly, NK cells recognize cells that have low levels of a protein called class I major histocompatibility complex (MHC) on their surface and eliminate these cells. This reduced class I MHC expression can result from infection with certain types of viruses or cancer. The innate immune response provides the first line of defense against invading pathogens and plays a key role in the activation and regulation of the adaptive immunity.

## The Adaptive Immune Response

The innate immune response to a pathogen is followed by an adaptive or acquired immune response. The adaptive immune response is specific to one particular pathogen and is formed following the first exposure to one particular pathogen. Following exposure an immune memory is created; this allows the body to respond even faster and more effectively if a second infection with the same pathogen occurs. The activation of the adaptive immune response depends on the display of antigens from the invading pathogen on the surface of antigen-presenting cells (e.g., monocytes or dendritic cells) in a way that can be recognized by the cells of the adaptive immune response (i.e., T-lymphocytes [T-cells] and B-lymphocytes [B-cells]). For a review of the adaptive immune response, see Bonilla and Oettgen (2010).

T-cells are responsible for the cell-mediated arm of the adaptive immune response. T-cells are formed in the bone marrow and mature in the thymus, hence the name T-cells. T-cells circulate in the body in an inactive (naïve) state until they encounter a specific antigen. This encounter activates the T-cells, which then further differentiate into different subtypes. While our knowledge of the number and function of T-cell subtypes is continually expanding, two important subtypes of T-cells are helper T-cells and cytotoxic T-cells. Helper T-cells produce cytokines to stimulate the activity of other immune cells. Helper T-cells are further categorized into multiple subsets, with Th1, Th2, and Th17 helper T-cells being recognized as key T-helper cell subsets. For

further information on T-cell subsets, please see Raphael et al. (2015). Th1 cells produce IFN- $\gamma$  and mediate immunity against intracellular pathogens, while Th2 cells produce IL-4, IL-5, and IL-13 and promote humoral immunity and participate in the allergic response. Finally, Th17 cells produce IL-17, IL-21, and IL-22 and are implicated in host defense against fungal and bacterial pathogens, as well as autoimmunity. Helper T-cells are characterized by the presence of a molecule called CD4 on their surface. Cytotoxic T-cells recognize antigens on the surface of virus-infected or transplanted cells and destroy these cells; each cytotoxic T-cell recognizes only one specific antigen. Cytotoxic T-cells are characterized by the presence of a molecule called CD8 on their surface.

B-cells are responsible for the humoral arm of the adaptive immune response. They produce immune molecules called antibodies or immunoglobulins, which can either be display on the cell surface or secrete. Antibodies recognize and interact with antigens, and each B-cell produces antibodies that recognize only one specific antigen. The antigen–antibody interaction either through soluble antigen encounter or by antigen presentation through APCs leads to the activation of the B-cell. Activated B-cells multiply and mature fully in a series of developmental processes that are accompanied by changes in the class of immunoglobulin that the cell produces (i.e., immunoglobulin class switching). For further information on the different immunoglobulin classes and immunoglobulin class switching, please see Methot and Di Noia (2017). Immunoglobulins produced by each specific B-cell, and its daughter cells specifically recognize the same antigen. In most cases, the resulting B-cells develop into plasma cells, which secrete large amounts of the specific antibody into the blood or fluid between cells. These antibodies then will bind to any matching antigen molecules (i.e., those on an invading pathogen) in the blood or on other cells, thereby marking them for destruction. Other B-cells following antigen exposure develop into memory B-cells that will remain dormant in the body for years and can be activated rapidly if a second infection with the same pathogen occurs.

The activities of T-cells and B-cells are intricately intertwined through the actions of various cytokines for an effective immune response to any pathogen. The innate and the adaptive immune responses are critical for effective host defense to infectious challenges.

## Cross-References

- [Bacteria](#)
- [Cell Membrane](#)
- [Circulatory System](#)
- [Endoparasite](#)
- [Fungi](#)
- [Immunology](#)
- [Posttranslational Modification](#)

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## Immunologically

- [Immunology](#)

## Immunology

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## Synonyms

[Immune](#); [Immune system](#); [Immunity](#); [Immunologic](#); [Immunologically](#); [Immunopathology](#)

## Definition

The branch of biology that focuses on the immune system, as a whole or in part, to study their development, structure, and function, in particular how they recognize the self or non-self and provide defense responses for the animal body (Cooper and Alder 2006; Kindt et al. 2006). There are many branches of immunology, for example, neuroimmunology and psychoneuroimmunology are two subdisciplines that study the interaction between nervous and immune systems, which specifically targets the neurological health essential to normal animal cognition and behavior (Sattler 2017; Schaller et al. 2015).

## Introduction

Like humans, animals can be afflicted with infections when foreign agents enter their bodies or when their body parts malfunction. Animal immunology aims to improve the health and wellbeing of companion, production, and wild animals by studying structure and function of all the different molecules, cells, tissues, and organs that comprise an animal immune system (Cooper and Alder 2006; Kindt et al. 2006; Yuan et al. 2014). As a defense system, the two core functions of the

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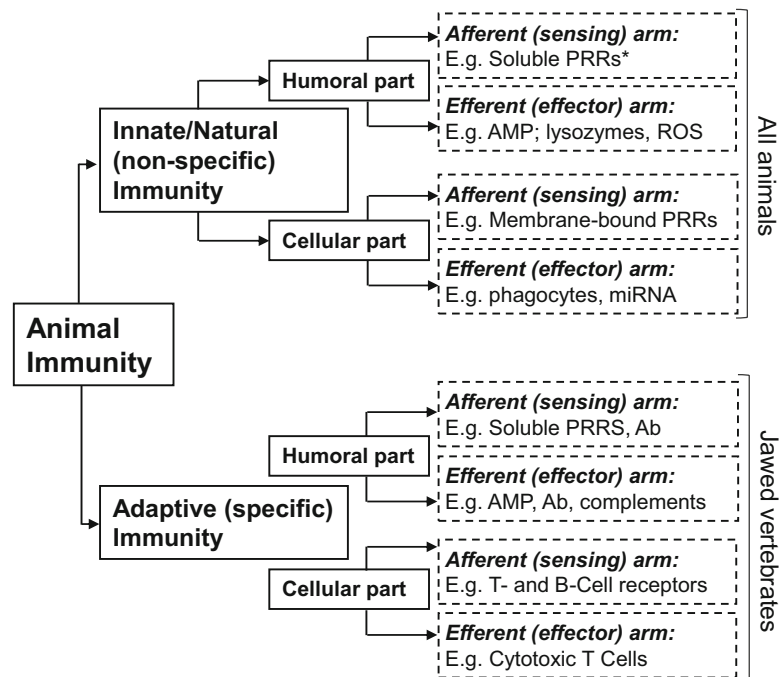
immune system are recognizing and repelling foreign invaders such as microbes or eliminating malfunctioning cells and tissues such as cancer cells and tumors. All animals, essentially all organisms, have at least one form of defense known as innate or natural immunity. Higher vertebrates beginning with jawed fish and spanning to humans have evolved a complete immune system which includes adaptive immunity atop the innate immunity and has more specific immune organs (e.g., bone marrow, spleen, thymus, and lymph nodes), cells (e.g., T- and B-cells), and proteins (e.g., antibodies). Both innate and adaptive immunity are composed of humoral and cellular portions, in which each part consists of: (1) afferent arms for determining the self and non-self to recognize invaders and (2) efferent arms for inactivating and repelling invaders (Fig. 1) (Cooper and Alder 2006; Sang et al. 2011). Both innate and adaptive immunities work together and interact with other systems of the body to provide protection for both mental and physical health, which is essential for animal physiology underlying normal cognition and behavior (Sattler 2017; Schaller et al. 2015).

## Innate Immunity

Innate immunity is an in-born immune system and the first line of defense for the animal. Innate immunity responds immediately to an infection. Distinguishing features of innate immunity are that it is nonspecific and antigen-independent. Major components of innate immunity include: (1) physical barriers such as the skin and mucosa, (2) proteins and other immune mediators in the blood that cause immediate immune responses including inflammation and complement reaction, and (3) innate immune phagocytes including macrophages and neutrophils that are always ready to engage the antigens or whole microbes. Although less specific for recognizing individual antigens, the humoral and cellular arms of animal innate immunity do contain afferent components, namely pattern recognition receptors that detect the conserved features of pathogens that are not present in the uninfected host. This pattern-based detection provides an efficient and broad discrimination, thereby to sum up a variety of innate immune arsenal (efferent arms) to repel and kill the invaders. Innate immunity provides protection for all animal species and is the only immune

### Immunology,

**Fig. 1** Animal immune system. Schematic of animal immune system and its major parts in humoral and cellular formats. The afferent and efferent arms of each immune part are illustrated to highlight the immune function for determining and repelling foreign invaders. See text for detail. Abbreviation: *Ab* antibodies, *AMP* antimicrobial peptides, *miRNA* regulatory microRNA, *PRR* pattern recognition proteins, *ROS* reactive oxygen species



mechanism in animals other than jawed vertebrates. In addition to providing general protection to initially keep infection under control, innate immune responses also save time by activating adaptive immunity through the process of antigen presentation. Presenting antigenic peptides is a mechanism the cell uses to signal that it is infected and requires activation of adaptive immunity for antigen-specific defense (Cooper and Alder 2006; Kindt et al. 2006).

## Adaptive Immunity

Innate immunity provides a foundation for the adaptive immune system, which stands as a more complex and specific apex of animal immunity in higher vertebrates (Cooper and Alder 2006). Functionally, it serves as the final line of defense that will step in when innate immunity has failed to stop a pathogen from causing a disease and an infection has been established in the animal body. Adaptive immunity is the antigen-specific and antigen-dependent immune response that relies on recognition and processing of an antigen to activate a pathogen-targeting immunological response. After recognition of a specific antigen, the adaptive immune system adapts a clone selection process to propagate a plethora of antigen-targeting proteins (immunoglobulins) and immune cells (B- and T-cells). In addition to creating a directed response to the specific antigen, the adaptive immunity possesses the ability to create memory of every type of antigen it encounters which will allow for a faster, stronger, and more efficient response if the same antigen is encountered in the future (Cooper and Alder 2006; Kindt et al. 2006; Yuan et al. 2014).

To accomplish the above functions, adaptive immunity utilizes T and B cells. T and B cells originate from hematopoietic stem cells that are primarily located in the bone marrow. From the bone marrow, each of the two cell types has a unique path: T cells leave the bone marrow and mature in the thymus, after maturation B cells leave the bone marrow already expressing an antigen-binding receptor on the outside of the cytoplasmic membrane. T cells require antigen-presenting cells

(APC) to activate, while B cells are able to identify antigens directly for activation to become antibody-producing plasma cells (Kindt et al. 2006).

After activation, T cells will differentiate into two major groups: T helper cells and cytotoxic T cells. As the name suggests, the cytotoxic T cells are responsible for attacking and destroying cells that have been infected by a pathogen. Unlike the cytotoxic T cells, the T helper cells play an important role in directing the nature and intensity of immune responses such as to help B cells to secrete antibodies and cytotoxic cells to destroy ingested pathogens. Different subsets of T helper cells accomplish this task by directing other immune cells to function quickly and properly through production of a series of immune mediators (termed cytokines). As previously stated, the adaptive immunity is capable of creating memory. The host body will retain some of antigenically specific T cells and store them after an immune response so that these cells are available to differentiate quickly and mount a rapid response if the body is exposed to the same pathogen again.

In contrast to T cells, B cells serve the immune system by producing antibodies to neutralize antigens. After activation, B cells will either differentiate into antibody secreting plasma cells or memory cells. Again the memory cells will be stored and used if there is an antigenic re-exposure, while plasma B cells will die after the specific immune response has ended. Like the coordinative role between the innate and adaptive immunities in protection of animal body, the T cell B cell responses in adaptive immunity also work together; however, T cell responses are more effective for intracellular pathogens and cancers, whereas antibody response in humoral branch reacts more to extracellular antigens and microbes (Kindt et al., 2006).

## Conclusion

Innate immunity represents the rapid and first response by the immune system that occurs within hours of the detected presence of foreign agents. It is an in-born and nonspecific response used to fight against infections. This response is mediated by humoral mediators and immune cells. In

addition to general innate immunity existing in all animals, adaptive immunity in high vertebrates develops a specific response to target and eliminate pathogenic threats escaping from innate immune protection. Adaptive immunity depends on the communication between APCs, T cells, and B cells to not only mount an immunological response but also to develop memory. Development of memory provides the system with the ability to absorb and record involvements with previously encountered pathogens, which allows for a more rapid response in the event of future exposures. It is the combination of the specific adaptive immunity and the broad but immediate innate immunity that offers a complete defense for the animal when functioning properly. Remarkably, current views state the role of physiological regulation of immune system in maintenance of animal homeostasis even in healthy animals, which integrates into the wholesomeness of animal health physically and mentally (Sattler 2017).

## Cross-References

- [Parkinson's Disease](#)
- [Pathogen](#)
- [Proteome](#)

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## Immunopathology

- [Immunology](#)

## Imperceptibles

- [Unobservables](#)

## Implicit Memories

- [Cognition](#)

## Impossible Task Paradigm

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## Synonyms

[Unsolvable task paradigm](#)

## Definition

Experimental procedure eliciting an immediate and unanticipated *expectancy violation*.

## Introduction

Research in comparative cognition and ethology has grown exponentially in the last few decades, and with this growth, we have seen a diversity of paradigms for studying the cognitive abilities of animals. The impossible task paradigm is one of these developments, and its use provides insight



into the decision-making processes of animals, particularly in the realm of expectancy violation.

## Methods and aims of the impossible task paradigm

The impossible task paradigm consists of a number of solvable trials in which the experimental subject solves an easy task to obtain a reward (e.g., food or toy) by manipulating an apparatus, followed by an unsolvable trial in which the reward becomes unreachable. This paradigm is a useful tool for assessing capacities for requesting help and the decision-making process in different species. In fact, it is a widely used procedure used by behavioral scientists who study canine cognition, and particularly how canines communicate with humans while attempting to solve problems.

The impossible task resembles the problem-solving paradigm. However, in the latter the animal tries to solve a task not knowing if it is solvable or not, whereas in the impossible task, the experimental subject initially learns that the task is easy to solve, but afterward the same task becomes unsolvable. The problem-solving task could also become impossible when the animal is not able to solve the task, but the focal element (i.e., violation of expectation) is missing.

The impossible task paradigm can be applied using different devices. Miklósi et al. (2003) used bin-opening and rope-pulling tests in which animals learn to obtain food by opening a bin or pulling on a rope from a cage during training trials. Afterward the animals are exposed to the impossible trial, in which the bin was closed mechanically or a hidden end of the rope was fastened to the cage, making the task unsolvable. A different device was employed by Marshall-Pescini et al. (2009): for the solvable trials, the apparatus comprised a wooden platform upon which food was placed and covered with an upside down plastic container that could be either moved off the platform or overturned to obtain the food. During the unsolvable trial, the container was screwed to the wooden platform and

food became inaccessible. Horn et al. (2012) constructed an impossible task with an apparatus consisting of two wooden discs attached in two-tiered fashion. The lower disc held six round food containers that could be accessed by rotating the upper disc to align it with a hole that allowed the subject to retrieve the food. The apparatus also included a locking mechanism that, when activated, prevented rotation of the upper disc. In Persson et al. (2015), the apparatus consisted of three plates on a solid foundation covered by three transparent lids. The subjects could reach the food inside the plate by sliding a lid to the side. In their experimental setup, one of the three lids was secured, making it impossible to open. In all cited studies, at least one person is present during the test phase (an experimenter or a person who is familiar to the animal), whom remains inactive, leaving the subject free to choose whether to interact with him or her.

Research using the impossible task paradigm with canids focuses on various behaviors that indicate expectancy violation. Generally the most commonly observed behaviors during the unsolvable phase of the tests could be grouped into two broad categories: apparatus-directed behaviors and human-directed behaviors. The former category includes all types of interaction or manipulation of the apparatus (e.g., rubbing, smelling, touching) and head and eye gaze orientation toward it. The human-directed behaviors are categorized as either active (e.g., jumping on the person, pawing to call attention) or passive (e.g., proximity, maintaining close physical contact). Human-directed behaviors might also include gaze or looking back behaviors (e.g., from a stationary position, the subject turns/lifts its head toward human faces, without approaching). In order to clarify whether the animal's orientation toward a human may be a request for help, Smith and Litchfield (2013) stressed the importance of using precise terminology and to minimize ambiguous definitions. For example, the behavior of gaze and looking back may be interpreted differently: the first behavior refers to those experimental contexts in which it is possible to observe the direction of the animal's

eyes, while in the second case, it is possible only to deduce the orientation of animal's head without seeing its eyes. The gaze alternation between human and apparatus is considered a communication tool and is often used in the analysis of the behavior during the unsolvable task. Other behaviors that can be observed during an unsolvable task are vocalizations (e.g., bark, howl) and stress behaviors (e.g., shaking, yawning, panting, lip-licking).

Results from studies using the impossible task paradigm have demonstrated that specific behaviors, such as physical contact or gaze toward the human, can depend on genetic factors (Persson et al. 2015), likely due to the process of domestication (Miklósi et al. 2003). On the other hand, some investigators have emphasized the role of ontogenesis, showing that the tendency to gaze at humans was positively correlated with age (Passalacqua et al. 2011) and can depend on the type of training that dog received (D'Aniello et al. 2015, Scandurra et al. 2015) or by the living conditions, with kennel dogs gazing less to humans than pet dogs (D'Aniello and Scandurra 2016). Comparative studies suggest that in toddlers and dogs gaze alternation is both an intentional and referential communicative act (Marshall-Pescini et al. 2013).

## Cross-References

- [Canine Cognition](#)
- [Decision-Making](#)
- [Problem-Solving](#)
- [Stress](#)

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## Imprinting

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Imprinting (or, Praegung, in German) has been defined as the development of a stable preference for an object or pattern as a consequence of a relatively brief exposure to said object during a limited and specific developmental stage, referred to as the critical period. It is also distinguished by the absence of extrinsic reinforcement (Klopfer). In the early part of the twentieth century, it was described by the German ornithologist, Heinroth,

who noted that newly hatched waterfowl, who normally follow their parent when they first leave their nest, would instead follow him if he had substituted himself at the time the young were ready to leave and would thereafter ignore their parent, preferring to follow him. Some years later, in the 1930s, Lorenz popularized the topic with films showing goslings that he had hatched following him around his lawn or while swimming in his pond, rather than adult geese. As the animals reached maturity, their sexual behavior was also preferentially directed towards him. Following the end of the war, in the early 1950s, Lorenz and his students focused much of the early work at his field station in Seewiesen, Bavaria, on imprinting and its consequences, and it was they who were largely responsible for bringing it to the attention of students of behavior and psychology in other countries.

Allusions to the process of attachments being established as a result of brief exposures early in life date back much further than the work of Heinroth and Lorenz, however. The first explicit references appear in a paper by a young tutor in England, Spalding, who, in 1872 reported experiments with newly hatched chickens that were comparable to those performed decades later by Lorenz and his students. That study, however, did not attract much attention until rediscovered in the 1950s by Spurway. And, in 1880, William James alluded to the phenomenon in his *Principles of Psychology*. Studies of imprinting, however, did not truly blossom outside of Seewiesen and the Lorenz lab, until the early 1950s, when the topic was highlighted by Thorpe in his, at the time monumental, treatise, *Learning and Instinct in Animals*.

As imprinting became an increasingly interesting topic for students of behavior, a variety of different questions emerged:

1. How universal a process is it? The “following response,” which leads to imprinting in geese, obviously cannot occur in altricial birds, so is imprinting limited to precocial species? Do similar processes occur in animals other than birds? In mammals? In insects? In Heinroth

and Lorenz’s examples, the imprinting is onto a parent figure, which subsequently becomes the object of sexual attachment. However, entomologists had long known that the plant species on which some butterflies deposit their eggs determines the preference for the oviposition site of the next generation. Is this a comparable process? In goats, Collias had shown that a newly born kid would only be accepted by its mother if she had been permitted contact with it during the first few minutes or so directly after its birth. Was this also an instance of imprinting?

2. What sensory modalities are involved? In the case of ducks and geese, it is obviously vision, but what happens when the species nests inside tree hollows or underground, where the “following response” is limited and the parent may not be visible? Gottlieb and his associates found the calls of the female duck to be significant and that imprinting to auditory signals could occur. In the case of butterflies, and insects in general, olfactory imprinting seems to be involved, as well as in mother-infant bonding in mammals.
3. There is a critical period during which and only during which imprinting can occur. What factors determine its onset and end? In the case of newly hatched goslings, it is obvious that they are unable to locomote freely until they are about 18–20 or so hours out of the shell and their down has dried. Thus, that is the earliest age at which imprinting can occur. By about 30 h post-hatching, it is difficult to elicit the “following response” and imprinting. Why is that? In the case of the goats studied by Collias, it appears that hormonal influences, specifically the breakdown of oxytocin, ends the mother’s interest in her offspring. What other factors could be involved?
4. The existence of the so-called critical period, the restricted time during which and only during which imprinting can occur, has led to a metaphoric comparison to sealing wax which can receive the imprint of a seal only during the brief period that it is still soft. How malleable is that interval? Sealing wax, if kept warm, can

retain the ability to accept an imprint. Can the critical period be extended?

5. What are the later consequences of imprinting? Lorenz claimed that in his ducks and geese the sexual partners at maturity were determined at the time the “following response” was first elicited. His geese would continue to follow their imprinted “parent,” which could be Lorenz himself, until they were fully fledged, by which time the “following response” would have waned. But, later, once sexual maturity was attained, it would be that imprinted object that would be the preferred target of attention. If imprinting was onto oviposition sites, as in insects, or, in mammals, to particular foods whose odors were present in the amniotic fluids of their mothers, what consequences might follow?
6. Is imprinting an ancient, conserved trait or an adaptation that has appeared independently in different lineages? Genomic studies related to imprinting have yet to be conducted but would do much to clarify many of the questions surrounding this unusual form of learning.
7. Imprinting is said to differ from other forms of learning due to both the existence of a critical period and the absence of extrinsic reinforcers. Are there not intermediate conditions, or is imprinting truly a unique form of learning?

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## Impulse Control

- [Inhibition](#)

## Impulsivity

- [Benefits for Aggression in Humans](#)

## Inattention Blindness

- [Cognition](#)

## Inborn Reflex

- [Rooting Reflex](#)
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## Inbreeding Depression

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### Definition

In a heterozygote, the inbreeding raises the possibility of homozygosity of injurious recessive alleles in an innate population. In another hand, one of the consequences of inbreeding is a loss in vigor (i.e., not as much of productive vegetatively and reproductively) which usually accompanies a huge swell in homozygosity known as inbreeding depression.

### Introduction

Inbreeding depression would possibly or may not be caused by inbreeding because it is the reduction within the fitness of the offspring created through sexual reproduction either through the breeding or mating system of individuals which are strongly connected genetically. This method ends up in homozygosity. The inbreeding depression is especially caused by inbreeding that may be a universal development that depends on selection, past mutation, and genetic drift.

This development happens altogether in wild animals, in humans, and in addition in plant populations, representing those genetic variations in fitness traits exist each inside and among the normal populations. Inbreeding depression plays a significant role within the crop breeding and within the evolution of outcrossing coupling systems.

For a long time, man has accepted inbreeding depression. In several species marriage between

closely connected ancestries is prohibited. Hindu society may present an acute example, where marriage between individuals connected by ancestry is prohibited.

### Inbreeding Depression in Plants

Onion, carrot, maize, sunflower, etc. are few examples of plants created by inbreeding depression either by the self-pollination or cross-pollination method. This development is discovered in many different plant species that are a unit any sorted supported the subsequent four classes.

- **High inbreeding depression:** An oversized proportion of plants created by the self-pollination ends up in severe depression and exhibits a lethal result. It's terribly laborious to keep up the line once, after three to four generations due to the loss of vigor and fertility. These are principally seen within the alfalfa of a family *Leguminosae* and in carrots.
- **Moderate inbreeding depression:** At the side of the lethal effects, sublethal effects are seen in the offspring's made by the self-pollination. There's a substantial decrease in the fertility, as some lines formed are very poor and are lost. *Maize*, *Pennisetum americanum*, and *Sorghum* could be a few samples of plants showing moderate inbreeding depression.
- **Low inbreeding depression:** A minor proportion of the plants exhibit lethal characteristics. The loss of vigor and fertility is lesser, and due to the poor fertility, a line can't be maintained which ends in a reduction in yield due to inbreeding being low or absent. Onion, squash, pumpkin, and sunflower are a few examples of plants showing low inbreeding depression.
- **No inbreeding depression:** This development is especially seen within the self-pollinated species as they do not show any inbreeding depression, although they are doing to show heterosis. It's as a result of they reproduce each by self-pollination with developed homozygous balance and cross-pollination by heterozygous balance.



## Inbreeding Depression in Animal Breeding (*Vipera berus*)

*Vipera berus* is frequently referred to as European adder or European viper. It is a venomous snake that's very widespread in Western Europe and East Asia.

A set of 40 *Vipera berus* experienced inbreeding depression, and a bigger range of distorted and stillborn offspring were made within the isolated population than within the larger population. Once when introducing the *Vipera berus* from different inhabitants into the isolated population, they manufacture by recovering a developed segment of viable offspring.

The reason behind the recovery is that a species of *Vipera berus* with a one recessive harmful allele will be healthier and can reduce the carrier's fitness. Therefore, less copy finishes up in the next generation.

At last, the inbreeding depression is generally seen only in the minor population rather than the larger population. For the reason that is in the minor population, when the families buddy, there are possibilities that a progeny inheriting two copies of the equal recessive harmful allele will undergo the significances of expressing the harmful allele.

In humans, this development is incredibly rare. It's especially found in the case where the marriages between closely connected ancestries are performed.

## Mode of Action

Ayroles et al. (2009) also assessed the mode of gene action associated with inbreeding depression. They generated a collection of three "outbred" lines by crossing the three homozygous high inbreeding depression lines every alternative and contrasting gene expression between these parental inbred lines and their F1 hybrid offspring showing heterosis for the third chromosome. Results indicated that the expression of roughly 75% of all differentially expressed genes related to inbreeding depression were additive or dominant and concerning 25% of all of those genes

expressed patterns of overdominance. This was surprising, on condition that overdominance for expression is assumed to be rare (Gibson et al. 2004). Through an experiment, comparable studies by Gibson et al. (2004) and Hughes et al. (2006) found fewer genes showing vital patterns of overdominance (>5% of genes) in *Drosophila melanogaster*. Moreover, it's necessary to denote that only a miniscule fraction of the genome has been sampled in the majority of studies on inbreeding depression, thus far creating any general mechanistic interpretation premature (Ayroles et al. 2009).

## Genetic Origin of Inbreeding Depression

Following the find of Mendelian genetics, two main hypotheses were developed to account for the existence of inbreeding depression and heterosis (gains in fitness following outbreeding; reviewed in Wright 1977; Charlesworth and Charlesworth 1999). The overdominance hypothesis (East 1908) argues that state confers properties that are superior to either homozygote. The loss of heterozygosity through inbreeding can so decrease the mean of traits related to fitness and lead to inbreeding depression (Lynch and Walsh 1998). The dominance hypothesis (Davenport 1908), on the opposite hand, argues that the majority mutations are neutral or injurious and usually recessive (MacKay 2001). Increasing the proportion of homozygotes through inbreeding will raise the probability of unmasking these deleterious alleles (Charlesworth and Charlesworth 1999), leading to inbreeding depression (Keller and Waller 2002). Which of the two hypotheses explains most of the decline in fitness related to inbreeding remains being debated (Ritland 1996; Käärkkäinen et al. 1999; Roff 2002). Though proof exists to support each models (Hughes 1995, Li et al. 2001, Carr and Dudash 2003), the dominance hypothesis seems to be favored on the idea of obtainable empirical knowledge and on theoretical grounds (Charlesworth and Charlesworth 1999). Others have suggested that inbreeding depression can also be explained, a minimum of partially, by synergistic or epistatic

interactions among genes (Templeton and Read 1994; Charlesworth 1998).

## Molecular Approaches to Inbreeding Depression

Although inbreeding depression has been a central theme in biological research for quite a century, very little is understood regarding its underlying molecular basis. For example, we've got no plan what the number of loci is also concerned in inflicting inbreeding depression of fitness and its parts. The amount may be tens, hundreds, or even thousands (Frankham et al. 2002). The genes or gene pathways related to inbreeding depression are also unknown.

For some decades, molecular genetics approaches to inbreeding depression have relied predominantly on the use of neutral markers (i.e., RFLPs or microsatellite markers) for assessing levels of genetic variation. Using RFLPs, one can detect genetic variation among individuals by cutting every individual's DNA with a selected restriction enzyme, subjecting those DNAs to electrophoresis in agarose gels, and transferring them to charged nylon membranes by use of Southern blots. Nylon membranes are then hybridized to radioactively or biotin-labeled clones (i.e., specific pieces of DNA). Useful clones will be those showing polymorphism between two or more individuals. Once identified, microsatellites are amplified using the polymerase chain reaction and sized using gel electrophoresis or an automated sequencer. Microsatellites owe their variability to associate redoubled rate of mutation compared with other neutral regions of the DNA. High rates of mutation are often explained predominantly by slippage throughout DNA replication. Each of these techniques allows the detection of homozygous and heterozygous loci for each DNA sample. For example, from a conservation perspective, populations of varying size could be compared for levels of genetic variability. Small populations with low levels of variation very likely have the highest risk of inbreeding depression and have a high risk of experiencing continuing losses of genetic

variation resulting from perennial bottlenecks and genetic drift (Wayne and Morin 2004).

More recently, neutral markers are used for mapping quantitative trait loci in an attempt to know the molecular basis of inbreeding depression (Carr and Dudash 2003).

With the generation of huge amounts of DNA sequence data and therefore the advent of DNA (cDNA) microarrays (Schena et al. 1995), in the case of inbreeding depression, changes in the multigene patterns of expression will give clues regarding the amount of genes concerned, their modes of action, and the biochemical pathways leading to such effects. This newly based study of gene-expression patterns is often named as "functional genomics" (Amundson 2008).

## Conclusion

It is apprehensible that inbreeding depression is related to a large number of gene transcripts, primarily genes related to metabolism, stress, and defense. Genetic drift alone is an unlikely clarification for these patterns given the moderately large amount of replicates within and across many studies that have repeatedly uncovered identical genes and gene pathways. Whether there are a large number of genes of small effect or a few key genes that have an effect on the expression of many different genes (i.e., epistatic effects) is unclear. However, when the proportion of genes differentially expressed across inbred lines by chromosomal location were assessed, roughly simple fraction of the differentially expressed genes were on the third chromosome, and roughly common fraction of the differentially expressed genes were on the second, fourth, and X chromosomes. Since these lines were variable just for the third chromosome, variation found on the second, fourth, and X chromosomes had to originate from genes located on the third chromosome.

## Cross-References

► [Evolution](#)

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## Incentive Relativity

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## Introduction: From Folk Psychology to Experimental Research

Helen saw a picture of an attractive man in an online dating page and is happy that he accepted to meet her in a coffee house. As he arrives, Helen feels disappointed because the picture posted online does not reflect the current looks of the person. Is Helen's disappointment caused by his current looks or by the expectation she developed after seeing his picture? Tom used to like sweets, but after being treated for surgery-related pain, he developed an opioid addiction. Now, whenever he is having ice cream all he can think of is going home and taking a few pills. Has Tom lost his sweet tooth or does anticipating an opioid high make him lose his appetite for that ice cream he used to like so much? These two examples illustrate the fact that in addition to its absolute value, an incentive's value may depend on how it compares to other incentives that were expected to occur (as it happened to Helen) or are expected to occur in the near future (as in Tom's situation). *Incentive relativity* refers to a distortion in the absolute value of an incentive when the

incentive occurs in the presence of expectancies of different value.

Incentive relativity is connected to a variety of psychological processes, including expectancy, motivation, emotion, and memory. To illustrate its relevance, imagine living surrounded by people who can only evaluate incentives by their absolute value. In such a society, the same outcome would have the same emotional impact regardless of prior experience. Two people losing a thousand dollars in a Las Vegas casino would have a similar emotional response whether one of them is a successful lawyer in a Manhattan firm and the other an unemployed worker. Incentive relativity may allow the lawyer to remember the casino experience as exciting, while the jobless worker would feel emotionally devastated. Similarly, a wave of public protest against government decisions can be described in terms of “relative deprivation,” that is, the experience of being deprived of something a person feels entitled to receive. Incentive relativity can also interfere with our ability to empathize with friends when we see their problem from our perspective, rather than theirs, or lead us to underestimate or overestimate our resources and abilities because we have inaccurate expectations of what we can achieve. The pervasive influence of incentive relativity in daily life makes it relevant to understand the conditions, mechanisms, and neural machinery that make such comparisons possible.

## Brief Historical and Terminological Background

The role of incentives in animal learning has been a major topic of interest since the early twentieth century (Flaherty 1996). Initially, the interest was in comparing the effectiveness of rewards that differed either qualitatively or quantitatively in their capacity to change behavior. Incentives were conceptualized as the goal that aroused, directed, and brought to a conclusion the behavior of an animal. A major breakthrough came when Tolman (1932) demonstrated that animals form expectations of future events, rather than responding via stimulus-response associations,

as proposed by Thorndike (1911). Some years earlier, O. L. Tinklepaugh, a graduate student in Tolman’s lab, reported that monkeys accepted a piece of lettuce under a cup after seeing the experimenter depositing the lettuce there, but they refused to eat the lettuce after seeing the experimenter placing a piece of banana, their favorite incentive, under the cup and even displayed aggressive responses directed at the experimenter. Similar results were reported in analogous experiments with rats exposed to a downshift from a more preferred food to a less preferred, but acceptable food, or from a larger amount of food to a smaller amount of food. In these experiments, the instrumental performance of downshifted animals rapidly deteriorated in comparison to that of animals always receiving sunflower seeds – the unshifted control. *Incentive relativity* refers to the fact that the value of an available reward is in some cases weighed against the value of expected rewards.

Incentive relativity effects were not compatible with then dominant learning theories (e.g., Thorndike 1911). As a result, this research had a long-lasting influence on the development of learning theory that reaches to our day, about a hundred years later. There are several procedures designed to study incentive relativity and the terminology requires clarification (see Table 1). The term *contrast* refers to an apparent exaggeration of reward differences brought about in animals experiencing two rewards in a particular situation (Flaherty 1996). Contrast implies a comparison of incentives in which one is always present and the other may be present, remembered, or anticipated. In successive contrast effects, the organism is exposed to a transition in incentive value from higher to lower (*successive negative contrast*, SNC) or from lower to higher (*successive positive contrast*, SPC). *Incentive* has been used traditionally to refer to a reward expectancy, but here it is used simply as a synonym of reward and appetitive reinforcer. *Expectancy*, in turn, refers to a prediction of the impending presentation of an incentive with specific properties. Typical incentives include sucrose, saccharin, food pellets, natural foods, drugs, and brain stimulation. The term *successive* refers to the fact that there is usually a

**Incentive Relativity, Table 1** Incentive relativity procedures mentioned in this entry as typically studied in rats

| Task and description                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Consummatory successive negative contrast (cSNC)</b><br><i>Downshift condition:</i> Exposure to a large reward followed after a few sessions by exposure to a small reward<br><i>Control:</i> Always exposed to the small reward<br><i>Dependent variable:</i> Reward consumption (fluid intake, lick frequency)<br><i>Effect:</i> Downshifted animals consume less of the small reward than unshifted controls                                                                                                                                                      |
| <b>Instrumental successive negative contrast (iSNC)</b><br><i>Downshift condition:</i> Exposure to a large reward followed after a few sessions by exposure to a small reward<br><i>Control:</i> Always exposed to the small reward<br><i>Dependent variable:</i> Anticipatory behavior (running, lever pressing)<br><i>Effect:</i> Downshifted animals respond less for the small reward than unshifted controls                                                                                                                                                       |
| <b>Anticipatory negative contrast (ANC)</b><br><i>Experimental condition:</i> Exposure to a small reward followed every day after a short interval by exposure to a large reward (small→large)<br><i>Control:</i> Exposure to the small reward followed every day after a short interval by exposure to a small reward (small→small)<br><i>Dependent variable:</i> Consummatory behavior (fluid intake, lick frequency)<br><i>Effect:</i> Animals respond less to the small reward when it is followed by the large reward than when it is followed by the small reward |
| <b>Consummatory successive positive contrast (cSPC)</b><br><i>Unshift condition:</i> Exposure to a small reward followed after a few sessions by exposure to a large reward<br><i>Control:</i> Always exposed to the large reward<br><i>Dependent variable:</i> Reward consumption (fluid intake, lick frequency)<br><i>Effect:</i> Upshifted animals consume more of the large reward than unshifted controls                                                                                                                                                          |
| <b>Instrumental successive positive contrast (iSPC)</b><br><i>Upshift condition:</i> Exposure to a small reward followed after a few sessions by exposure to a large reward<br><i>Control:</i> Always exposed to the large reward<br><i>Dependent variable:</i> Anticipatory behavior (running, lever pressing)<br><i>Effect:</i> Downshifted animals respond more for the large reward than unshifted controls                                                                                                                                                         |
| <b>Simultaneous negative or positive contrast</b>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |

(continued)

**Incentive Relativity, Table 1** (continued)

| Task and description                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Experimental condition:</i> Responding for a small reward in one stimulus condition and for a large reward in a different stimulus condition<br><i>Controls:</i> Exposure to the small reward or to the large reward in both stimulus conditions in different control groups<br><i>Dependent variable:</i> Anticipatory behavior (running, lever pressing)<br><i>Effects:</i> Experimental animals respond less for the small reward than small-reward controls (negative), but more for the large reward than large-reward controls (positive)                                                                                                                                                                                                                              |
| <b>Behavioral contrast</b><br><i>Conditions:</i> Receiving a large reward magnitude or high reward frequency under one stimulus and a small magnitude or low frequency under another stimulus, within a session (multiple schedules of reinforcement)<br><i>Dependent variable:</i> Response rate<br><i>Effect:</i> Low responding for a small reward when the previous or following component involves a large reward relative to responding for a low reward when the previous or following component also involves a small reward (negative). High responding for a large reward when the previous or following component involves a small reward relative to responding for a large reward when the previous or following component also involves a large reward (positive) |

single transition in reward that occurs across sessions. Successive contrasts have been studied in instrumental (iSNC, iSPC) and consummatory (cSNC, cSPC) situations. *Instrumental responses* are assessed before the animal comes into direct contact with the incentive and are thus anticipatory. Typical measures involve errors, latency, speed, and response frequency. *Consummatory responses* involve interaction with the incentive, usually in terms of consumption. Typical measures include licking frequency, cumulative time in contact with the reward, and fluid intake. In a cSNC experiment, the effects of reward downshifts are assessed in terms of consummatory behavior, typically after a downshift in sucrose concentration (e.g., a downshift from 32% to 4% sucrose). Such a downshift leads to a transient suppression of consummatory behavior relative to that of an unshifted 4% sucrose control. This model is playing a key role in our understanding



of incentive relativity processes and is covered below in detail.

In addition to successive contrast, reward relativity has also been studied in simultaneous and anticipatory contrast procedures (Flaherty 1996). In *simultaneous contrast* situations, trials with small or large rewards, each signaled by a discriminative stimulus, are mixed randomly within a session and the performance in either of these trials is compared to unshifted small and unshifted large controls, respectively. The key outcome in simultaneous contrast experiments is that animals receiving both reward magnitudes exhibit lower performance for the small reward than animals that only receive the small reward (i.e., an instrumental simultaneous negative contrast effect). Negative simultaneous contrast is also obtained in consummatory procedures. For example, animals exposed to repeated access to two sucrose solutions (32% and 4%) within the same session consumed more of the 32% and less of the 4% than unshifted controls exposed just to 32% sucrose or just to 4% sucrose, respectively.

In a similar procedure, often termed *behavioral contrast*, two or three reward schedules differing in reward magnitude or frequency alternate within a session, each with its own discriminative stimulus. Performing an operant response (lever press, nose poke) in each component is usually the key response measure. In this case, the rate of responding maintained by a constant schedule during one stimulus is increased by reductions in the reinforcement rate during an alternative component of the schedule (Flaherty 1996).

Incentive relativity may also influence behavior in an anticipatory manner (see below). Rats exposed to two palatable solutions in sequence may suppress intake of the first solution (e.g., 0.15% saccharin, 4% sucrose) if the second solution is preferred (e.g., 32% sucrose).

In the rest of this entry, we will focus on two incentive relativity paradigms extensively analyzed from a psychobiological perspective: successive and anticipatory contrast, especially as they are studied in consummatory situations involving reward downshifts. References to other procedures may be brought to bear on specific issues. This concentration reflects contemporary interests in

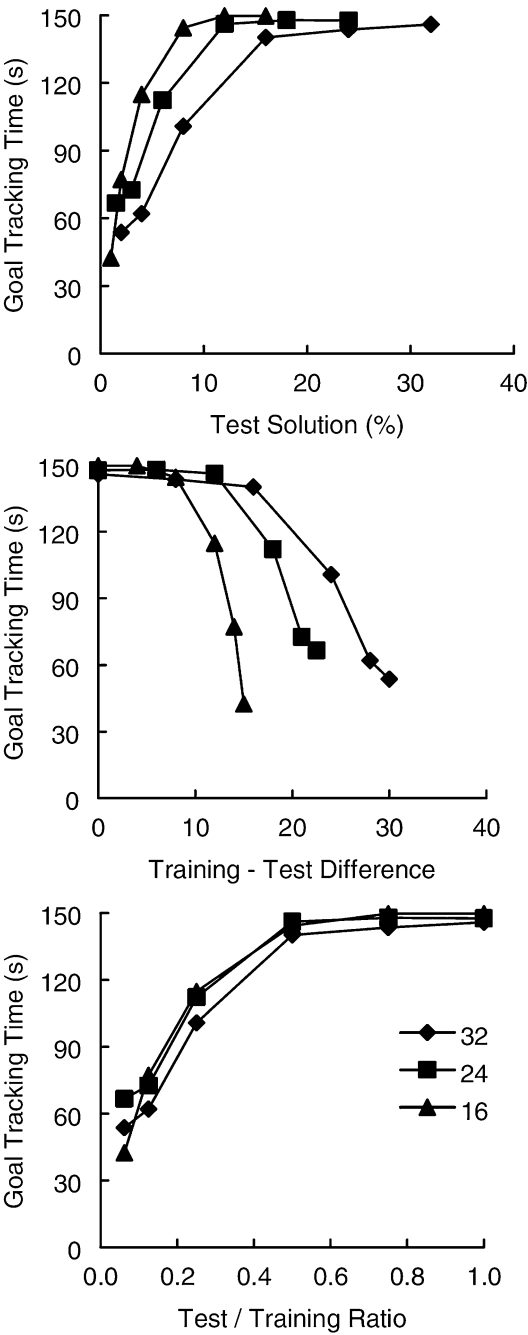
these forms of contrast, in their similarities and differences, and in their usefulness as models for the study of psychological pain, conflict, and addictive behavior.

## Consummatory Successive Negative Contrast (cSNC)

Basic behavioral phenomena associated to cSNC have been extensively reviewed in readily available articles (Flaherty 1996; Ortega et al. 2017; Papini et al. 2015; Torres and Papini 2016). Here we will center on four factors: detection, motivation, emotion, and memory.

### Detection

Rats trained in a runway to collect various numbers of food pellets and then downshifted to one pellet exhibit an iSNC effect directly proportional to the size of the disparity between pre- and postshift magnitudes. What is the rule regulating the detection of such reward disparity? To uncover the detection rule, Papini and Pellegrini (2006) gave three groups of rats access to either 16%, 24%, or 32% sucrose in four trials per day. Every other day, the second or third trial in the session involved an occasional downshift. For each group, six concentrations were used in downshift trials chosen so as to generate the same postshift/preshift ratios (8-to-1). When the cumulative time in contact with the sipper tube for each group was plotted against the absolute postshift concentration or against the difference between the preshift minus postshift concentrations, the functions for these three groups diverged significantly. However, when consummatory behavior was plotted against the ratio of postshift/preshift concentrations, the three functions overlapped and all differences disappeared (see Fig. 1). Therefore, consummatory behavior during a downshift episode was determined by a *ratio invariance rule* akin to Weber's law for sensory comparisons. A second experiment using the conventional cSNC preparation confirmed these results, except when the postshift solutions were either too high (above 16% sucrose) or too low (below 2% sucrose). This ratio invariance rule also



**Incentive Relativity, Fig. 1** Groups exposed to 32%, 24%, or 16% sucrose (called “training solutions”) were occasionally downshifted to a series of sucrose concentrations between 1.5% and 24% sucrose (called “test solutions”). When the results were plotted as a function of the test solution *top*) or the training minus test difference (*middle*), there were significant differences between groups receiving reward downshifts from different training solution to the same test solution (e.g., 16-to-8% vs. 32-to-

8% sucrose). However, when the same results were plotted as a function of the test/training ratio, the functions overlapped and differences were not observed. Such overlap suggests that the degree of consummatory suppression during a downshift depends on the proportion between the two solutions, rather than their absolute values or their difference. Results from Papini and Pellegrini (*Learning and Motivation*, 2006, Fig. 2, reproduced with permission from Elsevier)

applies iSNC (Pellegrini and Papini 2007). Rats reinforced for running with either 32 or 16 pellets exhibited overlapping postshift performance after a downshift to four or two pellets, respectively. Interestingly, ratio invariance was strong far from the goal, but it was less clearly observed close to the goal compartment of the runway. Using a rat autoshaping preparation with sucrose solutions as the reward, Pellegrini and Papini (2007) replicated the absence of iSNC when sucrose solutions are used as the reinforcer (see Flaherty 1996), but still observed ratio invariance after reward downshifts.

Little is known about the neural basis of ratio invariance in the SNC situation, but the hypothesis that opioid receptors are involved has received some support (Ortega et al. 2017). In one experiment, independent groups were exposed to the following downshifts: 32-to-6% and 16-to-3% sucrose (ratio: 0.19), and 32-to-12% and 16-to-6% sucrose (ratio: 0.38). Treatment with naloxone, a nonselective opioid receptor antagonist, before the first downshift session shifted the behavioral response from a ratio-based to a difference-based rule: the suppression was maximal for animals exposed to the 32-to-6% sucrose downshift, which experienced a 26% drop in sucrose concentration, and minimal for animals exposed to the 16-to-6% sucrose downshift, which were subject to a 10% reduction in sucrose concentration. Antagonist drugs, like naloxone, do not generate action potentials; rather, they prevent endogenous opioids to act on the receptor. Therefore, this naloxone effect on cSNC implies that endogenous opioids must be released during an experience of reward devaluation. Although the brain site of this effect is not known, one prime candidate is the amygdala (see below).

### Motivation

Behavior in a situation involving reward shifts also depends on internal factors. A major internal factor in situations involving access to food is the extent of food deprivation (Flaherty 1996). In the cSNC situation, for example, nondeprived animals usually drink less 32% sucrose than 4% sucrose, a fact that complicates the analysis of postshift performance. Nondeprived animals also

respond differently to reward downshift relative to deprived animals, showing an extended cSNC effect. This extended cSNC effect may be related to a reduced need for calories in nondeprived rats, provided that a downshift from 32% sucrose to 0.15% saccharin, which lacks caloric content, also leads to an extended cSNC effect. Similarly, inducing a need for sugar with exogenous insulin eliminates the cSNC effect based on sucrose intake.

The value of a reward also seems to depend on the internal state of the animal at the time the reward is consumed. Cuenya et al. (2015) fed animals with food pellets either before or after a session involving access to sucrose solutions during ten preshift sessions in a cSNC situation. Presession feeding should have devalued the sucrose solution, whereas postsession feeding should have had at best a modest effect on sucrose consumption. All animals experienced presession feeding before each postshift session, when the concentration of the sucrose solution was devalued from 32% to 4%. Whereas animals that had experienced postsession feeding during preshift sessions exhibited a cSNC effect, those that had experienced presession feeding failed to show evidence of a cSNC effect. The implication is that presession feeding had devalued the 32% sucrose such that a downshift to 4% sucrose was not experienced as particularly significant. Overall, these data suggest that the value of the 32% sucrose reward depends not only on its absolute properties but also on the internal state of the animal at the time of its consumption.

### Emotion

Since the early demonstrations of incentive relativity, interpretations have favored either emotional or cognitive mechanisms to account for the response to reward downshift. There is no question that reward downshift provokes an increase in search behaviors that seem appropriate to either find the missing resource or switch to another source of reward (Flaherty 1996). For example, when trained in a small conditioning box, rats subjected to a 32-to-4% sucrose downshift exhibit increased activity and rearing behavior and when trained in a radial arm maze,

exploratory behavior in nonbaited arms increases during postshift trials. While emotional and cognitive changes are not necessarily incompatible, there is evidence that search behavior is not necessary for a cSNC effect to occur. Lopez Seal et al. (2013) trained rats to voluntarily enter a tube to collect sucrose solutions. Once inside, animals were unable to turn around but could either lick or not at the sipper tube dispensing the solution. Under conditions that prevented full-blown search behavior, rats still exhibited a cSNC effect. The implication is that incentive relativity is accompanied by a negative emotional response that inhibits or redirects approach to the site previously associated with a highly valuable reward.

In fact, unexpected reward omissions and devaluations are known to induce changes associated with negative emotion, including distress vocalizations, odor emissions, stress hormones, and aggressive behaviors, among others (see Papini and Dudley 1997). An additional aspect that evokes a clear connection with emotion is the extensive overlapping between incentive relativity and physical pain, leading to the notion that reward loss and devaluation can be conceptualized as psychological pain (Papini et al. 2015). In accordance with this view, opioid and cannabinoid agonists reduce the cSNC effect, whereas opioid antagonists enhance it (Ortega et al. 2017). Another source of evidence involves the bidirectional interacting relationships between reward relativity and sensitivity to peripheral pain. Animals exposed to a 32-to-4% sucrose devaluation exhibit reduced sensitivity to physical pain in a variety of situations. By contrast, exposure to peripheral pain and restraint stress enhance the size of the cSNC effect (Papini et al. 2015).

The attenuating effect on cSNC of anxiolytics provides a third source of evidence that reward relativity is accompanied by negative emotion. Flaherty (1996) reviews extensive evidence that benzodiazepine anxiolytics (e.g., chlordiazepoxide, midazolam) and ethanol reduce the cSNC effect during the second downshift session but have no measurable effect during the first downshift session. If the typical 5-min session is substantially lengthened or several cycles of reward devaluation are administered, then the cSNC

effect is reduced by anxiolytics during the initial downshift session. Thus, some experience with reward devaluation is needed before anxiolytics can act, a fact that prompted Flaherty (1996) to propose a multistage model of cSNC. According to this model, negative emotion arises when the animal enters into an approach-avoidance conflict stage, with the anxiolytics then reducing avoidance and ameliorating the cSNC effect.

Compelling evidence that reward relativity induces negative emotion comes from a phenomenon traditionally known as escape from frustration. In this situation, rats are confined to a location where they have access to a large reward for several sessions. On one session, they encounter no reward (extinction) and then, after a few seconds, a door that had been closed is opened. These animals exit the extinction location faster than controls that had never received a reward in that box. This effect is eliminated by opioid blockade with naloxone (Papini et al. 2015).

Extensive research with inbred Roman high- (RHA-I) and low- (RLA-I) avoidance strains also provides evidence consistent with a relationship between reward downshift and negative emotion (Torres and Sabariego 2014). RLA-I rats, which exhibit high anxiety levels in a variety of situations, also show a longer cSNC, a greater iSNC, and a faster extinction after reward omission. Interestingly, RLA-I increased ethanol consumption and preference immediately after experiencing appetitive extinction, a result interpreted in terms of emotional self-medication. Outbred Wistar rats also showed increased consumption and preference for ethanol and the anxiolytic chlordiazepoxide immediately after experiencing a 32-to-4% sucrose devaluation (Torres and Papini 2016).

Finally, evidence suggesting a link between reward relativity and negative emotion comes from the effects of neural manipulations on cSNC. For example, transient lidocaine inactivation of the centromedial amygdala impairs the cSNC effect, increased activity in the open field, and had no effect on ANC (Kawasaki et al. 2015). Several studies further show that corticomedial amygdala lesions, diazepam infusions into the central amygdala, lesions of the insular cortex,

lesions of the ventrolateral orbital cortex, and lesions of the anterior cingulate cortex modulate the cSNC effect (Ortega et al. 2017; Papini et al. 2015).

### Memory

Adjustment to the cSNC situation implicates several memory processes (Papini 2003). First, the animal learns to expect access to 32% sucrose during the initial ten sessions. This *expectancy memory* is required to account for the rejection of the 4% sucrose on session 11, once the animal has detected the negative discrepancy between obtained and expected rewards. Second, if the initial downshift event is sufficiently aversive, an emotional memory may be encoded. Because this memory includes aspects of the animal's own emotional reaction to the downshift, it is called *egocentric memory*. Third, every time the animal tastes the downshifted solution a process of memory update would adjust the expectancy learned during pre-shift sessions (32%) to the new value (4%). Because this memory encodes information of the new reward, it could be called *allocentric memory*—a memory of the environmental change. Allocentric memory would reduce and eventually eliminate the negative discrepancy. Fourth, during downshift sessions, there is the inevitable pairing between negative emotion and 4% sucrose, which, although less than expected, it is still rewarding, especially for a food-deprived animal. Such pairings would result in a *counterconditioned memory* of negative emotion, a process that would attenuate rejection and promote approach to the downshifted solution (Amsel 1992). Therefore, allocentric memory and counterconditioning should both contribute to the recovery of consummatory behavior to the level of unshifted controls.

Research has attempted to provide evidence for these memory processes in experiments with a variety of designs, for example, by varying the retention interval between the last pre-shift session and the first postshift session. Flaherty (1996, pp. 40–42) summarized several studies with retention intervals ranging between 1 and 32 days, suggesting that between 10 and 17 days, the cSNC effect is attenuated by the interval. He suggested that long retention intervals weaken

the memory of the pre-shift solution, thus attenuating contrast.

Theoretically egocentric and allocentric memories are formed somewhat simultaneously during the initial downshift session. Whereas the former encourages behavioral suppression, the latter prompts the animal to consume the downshifted reward. Therefore, the cSNC effect should be prolonged either by enhancing egocentric memory or by interfering with allocentric memory, whereas the cSNC effect should be reduced either by interfering with egocentric memory or by enhancing allocentric memory. Following this rationale, memory enhancers such as corticosterone (a stress hormone) and D-cycloserine (an NMDA-receptor partial agonist) administered immediately after the first downshift session prolong the cSNC effect in subsequent sessions (see Papini et al. 2015). It is hypothesized that corticosterone and D-cycloserine enhanced the reactivation of the egocentric memory of the reward devaluation. Posttraining administration of benzodiazepine anxiolytic chlordiazepoxide also extends cSNC. Because chlordiazepoxide has a memory-interfering effect, these results were interpreted in terms of disruption of allocentric memory.

Counterconditioned memory can be studied by assessing transsituational transfer effects. Amsel (1992) argued that partial reinforcement training counterconditions a frustration response that increases persistence during extinction. Furthermore, the reactivation of frustration in other situations would induce persistence even in the absence of partial reinforcement training. Consistent with this view, partial reinforcement training during pre-shift trials (random mixture of 32% sucrose and water sessions) attenuates the cSNC effect after a 32-to-4% sucrose downshift. In addition, anxiety-prone rats (RLA-I) trained in the cSNC situation later exhibit a reduced iSNC effect and, vice versa, first trained in iSNC later reduced the cSNC effect. Interestingly, such transfer effects were not observed in the RHA-I strain (Cuenya et al. 2015). Thus, it appears that recovery from one situation involving incentive relativity and negative emotion may attenuate the impact of an analogous manipulation under different conditions.



## Anticipatory Negative Contrast (ANC)

ANC was first observed in the course of a study investigating whether conditioning could affect the glucoregulatory system. Animals were exposed to pairings of saccharin as the conditioned stimulus (CS) and sucrose as the unconditioned stimulus (US). As a consequence of such pairings, the intake of saccharin was reduced when it served as a predictor of sucrose, suggesting that incentives can influence behavior in an anticipatory manner (Flaherty 1996). The occurrence of ANC is paradoxical with respect to a simple application of the law of effect and from a reinforcement perspective: following a behavior with a preferred substance should increase, not decrease, the initial behavior. In fact, if one alters slightly the procedure to produce ANC, the opposite result (referred to as positive induction) may occur. For example, if rats are trained to press a lever to obtain a low-valued food reward, the rate of responding for this reward increases if a high-valued food reward is available within the session. For example, animals decrease their consumption of a 1% sucrose when the solution is followed by access to a 32% sucrose, but the same animals increase their rate of operant lever pressing for a 1% sucrose if a 32% sucrose or food pellet is upcoming (King et al. 2002).

When ANC is obtained, the most common interpretation assumes that it represents Pavlovian conditioning in which the initial substance functions as a CS and the second one as a US. After several pairings, the CS would enter into an association with the US, enabling the animals to learn predictive relationships and reducing the hedonic value of the first solution (Flaherty 1996). However, alternative explanations based on the insensitivity of ANC to devaluation of the preferred substance have also been proposed. For example, Onishi and Xavier (2011) argued that ANC depends on two memory processes: (1) the memory of the relative value of the first solution (which is daily updated on the basis of gustatory and/or post-ingestive comparison of the first and second solutions) and (2) the memory of past pairings.

## Detection

Many studies focusing on the factors influencing the detection of disparities between rewards suggest that the ANC effect depends on the absolute and relative incentive value of the first and second rewards, their hedonic/nutritional properties, and the temporal interval between reward presentations. The first evidence of this phenomenon involved the use of a 0.15% saccharin solution available for 3 min and followed after an inter-solution interval of 5 min by a 32% sucrose solution for 5 min. Control groups received either 2% sucrose as the second solution or only the 0.15% saccharin. After 12 sessions, groups receiving saccharin only or saccharin followed by 2% sucrose showed a more accelerated lick function as compared with animals receiving 0.15%–32% pairings. This result was interpreted on the basis of the greater hedonic value of 32% sucrose solution compared to the 0.15% saccharin (see Flaherty 1996). However, the question remained whether this phenomenon was anticipatory (i.e., based on the anticipation of the impending sucrose) or successive (triggered by the comparison between the current 0.15% saccharin and the 32% sucrose presented as the second reward on the previous day). Several experiments discarded the latter interpretation. First, increasing the inter-solution interval from 5 to 30 min significantly reduced the suppressive effect of 32% sucrose on saccharin intake. Additional support for a within-day anterograde process was reported by Flaherty and Rowan (1985), who conducted a within-subjects study in which both the contrast (0.15%–32%) and the control (0.15%–0.15%) conditions were presented to the same subject in alternation across days. The rationale behind this experimental design was as follows. If contrast is based on the 32% sucrose presented on the previous day, then lick rates for the initial 0.15% saccharin solution should be lower on days when the animals received the 0.15%–0.15%, provided that these days always follow a 32% sucrose trial. By contrast, if a within-day anticipation is involved in ANC, then the lick rate for the 0.15% solution should be lower when the 0.15% saccharin predicts 32% sucrose. The results indicated that rats licked less for the 0.15% saccharin on

0.15%–32% days than on 0.15%–0.15% days. The differences between trials appeared regardless of the inter-solution interval (15 s vs. 1 min) and even after reversing the cue-solution pairings.

Once it was demonstrated that ANC depends on anterograde mechanisms, subsequent experiments showed that variations in either the first or the second reward influence the size of the effect (see Flaherty 1996). For example, when the initial substance has low hedonic value relative to the second one (e.g., water or an empty tube followed by 32% sucrose), positive induction is observed. Increasing the hedonic value of the first solution resulted in ANC, rather than positive induction. The greater the hedonic value of the first solution, the sooner and the larger the ANC. However, when other reward combinations are used the results are far from conclusive.

In addition to their gustatory/hedonic properties, differences in nutritional load between rewards may also influence the ANC effect in a complex manner. Moss et al. (2002) systematically studied the relative contributions of hedonic/gustatory properties and nutritional loads to the ANC, by replacing the first 0.15% saccharin solution with soy milk. Soy milk has a greater hedonic value than sucrose (16%), but similar nutritive properties. According to the hedonic disparity hypothesis, ANC should have been found when using sucrose-soy milk pairings, but not soy milk-sucrose pairings. Contrary to what was expected, the sucrose-soy milk sequence failed to produce ANC, whereas the soy milk-sucrose sequence did yield a reliable suppression of soy milk intake, showing a direct function of the sucrose concentration. Taken together, these results reveal the complexity of the factors taking part in the detection of reward disparity in the ANC paradigm.

### Motivation

Apart from the hedonic properties, the rewards, their caloric value, and the temporal presentation pattern, ANC is also modulated by motivational factors (see Flaherty 1996). Some studies have explored how food deprivation influences animal's behavior in anticipatory situations. In food-deprived animals, ANC was obtained when 2% or 4% sucrose preceded by 15 s, but not by

5 min, access to 32% sucrose. In nondeprived animals, the reduced intake of either 2% or 4% sucrose appeared whenever these rewards were presented 5 min before 32% sucrose. Interestingly, the influence of the deprivation condition was not observed when saccharin-sucrose pairings were used, suggesting that the caloric value becomes important with long inter-solution intervals under conditions of food deprivation.

The level of deprivation has also been investigated by Weatherly et al. (2005), who found that deprivation promoted positive induction, rather than ANC. Induction was observed when subjects were food deprived and exposed twice a day to 1% sucrose (3 min) followed (after 0, 15, or 60 s) by a 3 min access to 32% sucrose. However, nondeprived animals did not show either a reliable positive induction or an ANC effect. The authors concluded that although induction was never observed when subjects were not food deprived, eliminating food deprivation was not sufficient to produce contrast.

A different approach to address the issue of how motivation impacts ANC involves using rewards with high incentive value, such as abuse drugs. The model was initially based on the frequent observation that rats avoid the intake of a gustatory CS such as saccharin after it has been paired with an aversive US (e.g., the toxin lithium chloride). Drugs of abuse (e.g., cocaine, morphine, heroine) also suppress saccharin intake following repeated pairings. Based on its similarity with conditioned taste aversion procedures, this effect was initially interpreted as indicative that abuse drugs have both reinforcing and aversive properties. However, the suppressive effects of drugs of abuse differ in many ways from those of aversive stimuli, leading to an interpretation of this phenomenon based on reward comparison: Rats would decrease saccharin because its value is outweighed by that of a highly reinforcing psychoactive drug (Grigson 1997).

As opposed to ANC tests, in which free access to both rewards is the standard procedure, drug-induced suppression of CS intake usually involves forced administration of the US. Despite such differences, the suppressive effects of abuse drugs and sucrose on CS intake share a number of similarities: (a) both depend on

the nature of the gustatory CS; (b) both are attenuated by food deprivation; (c) both are greater in selected rats highly reactive to abuse drugs (Lewis rats); (d) both are increased in rats exposed to chronic morphine; and (e) both are disrupted by lesions of the gustatory cortex and gustatory thalamus (Grigson 2008). Overall, the data suggest that both behavioral phenomena are related to mechanisms of anticipated reward comparison and devaluation. Supporting this contention, recent results showed that a reduction in CS intake induced by a single saccharin-morphine pairing is accompanied by a marked blunting of the nucleus accumbens dopamine response to the saccharin reward cue (Grigson and Hajnal 2007).

### Emotion

While hedonic devaluation provides a parsimonious explanation of ANC, alternative mechanisms have also been proposed. One possibility is that the presentation of a low reward after being paired with a high reward triggers negative emotion (Flaherty 1996). While there is evidence for such a mechanism in other forms of contrast (as in SNC, see above), three sources speak against this possibility in the case of ANC (Flaherty 1996; Papini et al. 2015). First, anxiolytics (such as chlordiazepoxide, cyproheptadine, buspirone, and testosterone) fail to affect ANC. Similarly, the administration of drugs known to enhance aversive memories of reward downshift events (such as corticosterone), do not influence ANC. The pharmacological manipulation of opioid receptors (known to be involved in psychological pain) also shows negative results when applied to the ANC effect (Katsuura and Taha 2014).

Second, lesion studies involving brain regions known to regulate negative emotions fail to alter ANC. Unlike cSNC, neither electrolytic lesions of the central nucleus of the amygdala (see Flaherty 1996), nor the transient inactivation of the centromedial region of the amygdala induced by lidocaine microinfusions affected ANC (Kawasaki et al. 2015).

Third, studies based on comparisons between strains of rats that differ in emotional reactivity are not conclusive with respect to

ANC. Maudsley reactive (MR) and Maudsley nonreactive (MNRA) rats showed little difference in ANC when licking frequency was used as dependent variable. However, whereas MNRA rats exhibited longer latencies to lick 0.15% saccharin when this solution was followed by 32% sucrose, a positive induction effect was found in the MR strain (Flaherty 1996). Regarding the extensively phenotyped RHA-I and RLA-I rats in anxiety tasks, no differences in ANC were found (Torres and Sabariego 2014).

Taken together, these data suggest that ANC situations may not involve negative emotion. However, this conclusion should be taken with caution. For example, Gómez et al. (2000) explored whether individual differences in saccharin intake suppression induced by morphine correlated with circulating corticosterone levels. Greater suppression of CS intake was associated with higher corticosterone levels. In the same vein, McFalls et al. (2016) found that those animals exhibiting greater levels of saccharin intake suppression showed increased mRNA expression for elements of the stress/CRF signaling pathway within the hippocampus, medial prefrontal cortex, and ventral tegmental area.

### Memory

Since its discovery, the ANC effect was thought to be due to Pavlovian associations and anterograde memory processes, both involving the anticipation of the highly preferred sucrose reward when the less preferred saccharin solution is presented. A few studies have addressed the neurobiological basis of the memory processes that support ANC. Electrolytic lesions of the gustatory thalamus impaired ANC but had no influence on simultaneous contrast (Reilly et al. 2004). These results suggest a role of the gustatory thalamus in the comparison between the value of an available reward and the memory of a preferred reward that is anticipated in the near future.

The gustatory insular cortex has also been involved in reward anticipation. Kesner and Gilbert (2007) found that quinolinic acid lesions of the agranular insular cortex disrupted ANC in rats receiving 2%–32% sucrose pairings in their home cages. The fact that animals did not show any deficit in the discrimination between both

solutions (as shown by preference testing) suggests that the gustatory insular cortex may be involved in memory and reward anticipation. Finally, ANC has been proposed not to depend on anticipation of the second reward since it is insensitive to the devaluation of the second reward (Onishi and Xavier 2011). According to this view, the relative incentive value of the first solution would be estimated on the basis of the memory of past pairings, as well as on daily updating based on both gustatory and/or post-ingestive comparisons between solutions.

## Conclusions

The scenarios proposed at the start of this entry on incentive relativity illustrated daily life situations that are simulated in the lab with animal models. Thus, Helen's disappointment when her date did not resemble what she had seen in a picture is an example of SNC. High expectations based on prior experience led to negative emotion, just as expecting 32% sucrose induces frustration when a rat encounters 4% sucrose instead. Tom's problem was akin to ANC. His taste for sweets was reduced when they were paired with opioids, much like anticipating 32% sucrose reduces intake of the lesser-valued 0.15% saccharin. The study of incentive relativity offers an inroad to understand these distortions of reward value.

The study of incentive relativity is providing some insights into several issues of basic and translational importance. Something these effects have in common is their connection to a wide range of psychological processes, despite being produced by seemingly simple situations. Three areas are highlighted here.

First, SNC effects, both instrumental and consummatory, have been studied more extensively from comparative and developmental perspectives. The SNC effect is not a general phenomenon among vertebrates. It has been reported in several species of mammals (e.g., rats, mice, monkeys, dogs, and opossums), but it has failed to occur in studies with pigeons, reptiles, amphibians, and fish (Papini 2003). Similarly, the iSNC effect emerges around 24 days of age in rats, in

correlation with the maturation of the hippocampal formation (Amsel 1992). There are no similar comparative data on the ANC effect.

Second, the SNC has become a model to study the consequences of negative emotions. The main idea is that the reduction of an incentive is analogous to an experience involving loss. Experiments show that such experiences may distort sensitivity to peripheral pain, are influenced by manipulations of pain-related systems in the brain (e.g., opioid and cannabinoid receptors), are modulated by tranquilizers, and are affected by lesions in brain sites known to be connected to emotional responses (Papini et al. 2015). These studies have implications for an understanding of how an experience of loss may affect both the emotional and health spheres of human functioning.

Finally, both SNC and ANC provide useful paradigms to model the connection between incentive relativity and addictive behavior. SNC promotes the voluntary oral consumption of anxiolytics capable of reducing negative emotions – an emotional self-medication effect (Ortega et al. 2017; Torres and Papini 2016). Since anxiolytics such as ethanol and benzodiazepines have addictive potential, this effect offers a possible view of the initial stages of addictive behavior. ANC offers insights into how drugs devalue natural rewards and also how natural rewards may help protect individuals against drug misuse and abuse (Grigson 2008).

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Disgust](#)
- ▶ [Fear Response](#)
- ▶ [Instrumental Learning](#)
- ▶ [Operant Conditioning](#)
- ▶ [Partial Reinforcement Extinction Effect](#)

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## Inclusive Fitness

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## Synonyms

[Altruism](#); [Darwinian fitness](#); [Hamilton's paradigm](#); [Hamilton's rule](#); [Kin selection](#)

## Definition

Inclusive fitness is a method of measuring evolutionary success. It is the ability of an individual to



transmit genes to the next generation, including genes shared with relatives. In accordance with this rule, an individual's inclusive fitness can depend, in part, on altruistic behavior and cooperation. The term *inclusive fitness* was introduced in 1964 by William Donald Hamilton, an English evolutionary biologist. Hamilton distinguishes two types of fitness: (a) direct fitness, defined as the number of offspring produced directly by an individual, regardless of who rears, supports, or rescues the offspring; and (b) indirect fitness, defined as the number of related individuals produced, multiplied by the degree of relatedness of those individuals (Hamilton 1964a, b). Inclusive fitness is defined as an individual's direct fitness plus an individual's indirect fitness.

In the above-mentioned definition, one offspring is defined as an individual's own child, which shares 50% the individual's genes, in sexually reproducing species. Following this logic, a sibling's child, which shares 25% of the individual's genes, is half an offspring equivalent, and a cousin's child, which shares 6% of the individual's genes, is an eighth of an offspring. From a gene-centered perspective, evolutionary success is achieved when a gene has a relatively high number of copies in the population. It can be achieved by producing one's own direct offspring, and/or by helping kin produce offspring.

## Introduction

Hamilton's calculations showed that passing a gene to one's offspring is not the only way of successfully transmitting it to the population. Another way of transmitting copies of a gene is by promoting survival and reproduction of those sharing copies of the gene by descent. The latter process is called *kin selection theory*, or *inclusive fitness theory*, and it is a key mechanism affecting the evolution of social behavior. For example, yellow-bellied marmots put themselves in danger and attract a predator's attention by producing loud calls warning their social group (usually consisting of related individuals) about danger (Blumstein et al. 1997). This seemingly

counterproductive behavior has evolved because ensuring the survival of kin will increase an individual's overall, inclusive fitness.

## Hamilton's Rule

The introduction of the concept of inclusive fitness helped to explain the prevalence of behaviors often perceived as altruistic. Hamilton argued that supporting kin increases one's evolutionary success by the mechanism of inclusive fitness, not direct fitness. For example, in ground squirrels, calls warning others about approaching predators occur most frequently if relatives of the calling individual were around (Milius 1998); in red squirrels, females adopt orphans only when they are related to them; adoptions were never observed for non-kin (Gorrell et al. 2010); and in humans, when declaring willingness to help children, close relatives are preferred over distant relatives, and distant relatives are preferred over unrelated children (Antfolk et al. 2017). That means that natural selection favors organisms behaving in a way that leads to increases in inclusive fitness, and also ensures that the helper's "altruistic" gene (or complex of genes) is more widely present in the next generation. Hamilton developed a simple formula ( $c < rb$ ) for calculating whether a gene "for" altruistic behavior will become more widespread in the population. The formula calculates whether the actor's reproductive costs incurred by displaying altruism are lower than the degree of relatedness times the reproductive benefit to the recipient. If it is, then it will be beneficial for the actor and, therefore, help in spreading the relevant gene(s) in a population.

Another concept important for understanding inclusive fitness is the *green-beard effect*, a thought experiment explaining selective altruism, a way of recognizing behaviors considered altruistic, expressed by unrelated individuals willing to provide support. The idea of the green-beard effect is that a gene or genes (i.e., those coding the hypothetical green beard) must produce a recognizable phenotype that is preferentially treated by individuals with the same gene.

## Cross-References

- [Altruism](#)
- [Fitness](#)
- [Genes](#)
- [Green Beard](#)
- [Kin Selection](#)
- [Phenotype](#)
- [Population](#)
- [Predator](#)
- [Reproduction](#)
- [Social Behavior](#)
- [William Donald Hamilton](#)

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## Incomplete Penetrance

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## Synonyms

[Reduced penetrance](#); [Variable expressivity](#)

## Definition

Incomplete penetrance occurs when individuals with a certain genotype in a population do not necessarily express the associated phenotype.

## Introduction

Incomplete penetrance is a phenomenon of interest to many geneticists, with particular emphasis on disease expression. It occurs in genes of many animals, including humans, and is common with autosomal dominant diseases. However, it can also be found in recessive patterns of inheritance, though this is rare. Expression of a phenotype is most likely a result from many factors, including: genetic, environmental, and lifestyle. With a wide variety of factors influencing incomplete penetrance, current research focuses on individual expression of disease phenotypes, as well as carrier genotypes where phenotypic expression may not occur until the next generation of offspring. Incomplete penetrance of genes also renders prediction of disease expression among members of a population or family difficult (Field 1970).

## Case Study: Inbred Mice Study with Mutated Collagen Gene (COL1A1)

Pereira et al. (1994) conducted experiments to assess the risk of Osteogenesis imperfecta by examining the severity of spontaneous bone fractures in inbred mice as a result of incomplete penetrance caused by a mutated collagen gene. They hypothesized that uterine position may be a factor in explaining the variability in phenotypic expression but found there was only a slight effect of uterine position. Severe and minimally affected individuals were equally distributed in the uterine horns of female mice, and the “normal” individuals (i.e., those lacking bone fractures) were positioned primarily at the base and lower regions of the uterus. The researchers also found that incomplete penetrance of spontaneous fractures was not explained by levels of gene

expression or variations in genetic background, but instead caused by an “inherent feature of expression of a mutated collagen gene” (Pereira et al. 1994).

### Case Study: Management of the Blindness of Wolves Bred in Captivity

Many captive-bred wolves in Scandinavian zoos were born blind in the 1960s and 1970s. The first blind wolf from the population was found in 1967, but the breeders continued using the animal's siblings in the breeding program. In the early 1990s, Laikre et al. (1993) found the primary issue was a lack of pedigree management, which may have caused a reduction of genetic variability and increased prevalence of founder alleles for blindness in the captive population. Laikre et al. (1993) found that removing high-risk carriers for the founder allele for blindness and decreasing inbreeding is a good management approach to decrease phenotypic expression of blindness without severely affecting other founder allele survival (loss of genetic variation) in the wolf population.

### Conclusion

Lack of consistency in incomplete penetrance makes it difficult to predict future mutations or disease expression in some species, including humans. Animals bred in captivity may be especially prone to problems with incomplete penetrance due to inbreeding of genetic lineages. In cases with incomplete penetrance, predicting members of a population that will express a disease, or which individuals are at risk for passing the disease onto their offspring can be difficult. Animals carrying alleles for a mutation or disease but who have not expressed the phenotype may be at risk for passing on those alleles to offspring if they are bred with another animal with the same alleles at the target loci. For autosomal dominant diseases, only one parent needs to have the genotype for the disease (AA, Aa), while homozygous recessive genes (aa) requires both parents to carry a portion of the recessive disease.

### Cross-References

- ▶ [Alleles](#)
- ▶ [Carrier](#)
- ▶ [Chromosomes](#)
- ▶ [DNA](#)
- ▶ [Fetus](#)
- ▶ [Gene Expression](#)
- ▶ [Genes](#)
- ▶ [Genetic Code](#)
- ▶ [Heredity](#)
- ▶ [Recessive](#)

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### Incubating

- ▶ [Brooding](#)

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### Incubation

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### Synonyms

[Egg brooding](#)

## Definition

Incubation behavior is the active transmission of heat from parent to embryo to foster development.

## Introduction

Oviparity, in which a large component of development occurs in an egg outside the female body, is commonly accepted as the mode of reproduction ancestral to all animals. Although the occurrence of embryonic development outside the female body offers enhanced adult mobility and predator avoidance, the laying of eggs in a discrete location leaves embryos exposed to predators and potentially harsh environmental conditions. Thus, tending to eggs in some way, so as to enhance offspring survival, may arguably be the most widespread form of post-fertilization parental care in the tree of life (Smiseth et al. 2012). During this time, eggs must be kept at optimal environmental conditions to facilitate embryonic development. These conditions include temperature, humidity, and egg positioning and, generally, are maintained by a range of behavioral adaptations, which vary across taxa and environmental conditions.

Like any series of chemical reactions, growth occurs most rapidly at an optimal temperature, and its speed declines at either extreme. Behaviorally, incubation in terrestrial vertebrates typically refers to a form of egg attendance in which developing embryos experience an amount of heat and humidity that are under parental control and generally much less variable than expected under prevailing environmental conditions. In many groups, the environmental conditions to which embryos are exposed can be held relatively constant by burying eggs underground. With few exceptions, eggs of ectotherms do not require as much energy and maintenance of optimal conditions as do the eggs of endotherms. For example, many reptilian species abandon their eggs after laying, but females might nevertheless control the temperature at which embryos develop indirectly through choice of an oviposition site, which, in turn, can shape offspring sex ratios (i.e., temperature-dependent sex determination). In other reptiles, the incubation period entails

protection from one or both parents, with temperature control being a co-evolved benefit.

Generally, species that incubate their eggs fall into two main categories: (i) external incubators in which embryos develop within eggs laid outside the body and (ii) internal incubators in which development occurs in eggs that remain inside the body (i.e., ovoviviparity). Internal incubators include mouth-brooding fish and a host of invertebrates (where “brooding” is usually used synonymously with “incubating”) and prototherian mammals (development within the duck-billed platypus begins with internal, followed by external, incubation) and may even occur briefly in a few species of modern bird (Birkhead et al. 2010).

For most birds, little embryonic development within the egg occurs during egg production, until the onset of incubation. Incubation denotes the period of time when parents warm their eggs directly by sitting atop them. During the breeding season, the sex that incubates has a brood patch on the abdomen – an area that lacks feathers to allow for direct skin contact with the eggs. The brood patch facilitates more efficient heat transfer from parent to eggs. There are some exceptions to this type of incubation; for example, many megapode species bury their eggs in a pile of leafy vegetation, and incubation is accomplished via the warmth produced by decomposition of the vegetation. Additionally, species in hotter climates must shade their eggs during incubation to ensure they do not overheat. The optimal temperature for developing embryos varies widely across species, with some having a larger range of tolerable temperatures. Despite this variability, all species show increased sensitivity to hyperthermia compared to hypothermia.

Incubation also requires maintenance of humidity since relative humidity can influence embryo temperature, with the optimal relative humidity to ensure hatching between 40% and 70%. While desiccation would be detrimental, some water evaporation from the egg during incubation is essential; an air pocket within the egg increases in size during incubation to allow direct oxygen exchange between embryo and environment and facilitate successful hatching.

Avian incubation also requires the periodic turning of eggs within the nest, especially early

in the incubation period. Egg turning prevents adhesion of the embryo to the shell membrane, aids in fluid transport and embryonic growth, and increases the hatchability of eggs. Rates of egg turning differ between species, with the eggs of precocial species requiring less turning than altricial species due to the albumen content within the eggs. Egg turning allows the embryo to successfully utilize the fluids and proteins within the albumen. The eggs of altricial species tend to have a higher albumen content than those of precocial species, which explains why they must be turned more frequently (Deeming, 2009). Contrary to avian eggs, reptilian eggs do not require turning during incubation, and egg turning can be detrimental to embryos in some cases.

Incubation duration ranges from as short as 10 days in brood-parasitic passerines to up to 84 days in larger species. Duration of the incubation period depends on environmental conditions but also on parental behavior. Incubation constancy, or the amount of time the eggs are tended to versus left exposed, can be an effective method of maintaining embryonic temperature. In warmer conditions, parents tend to reduce the number of on-off bouts, remaining away from the nest for longer periods of time (Mueller et al. 2019). Properties of the clutch can also impact incubation duration. Due to the physics of heat loss, larger clutches and smaller eggs typically require a longer incubation period than smaller clutches and larger eggs (Williams 1996).

## Incubation as a Conceptual Framework

Like all of animal behavior, the study of incubation in itself is valuable to advancing human knowledge, whereas, perhaps more importantly, understanding the natural history of incubation also provides a useful context in which to explore more general questions in animal physiology, ecology, and evolution. For example, by controlling incubation behavior, parents in many bird species may exert fine control over offspring development depending on the onset of incubation relative to clutch completion. The mechanisms behind avian ovulation and egg laying

dictate that clutch completion cannot occur instantaneously; at least a day, or more in many species, elapses between the laying of subsequent eggs. Consequently, initiating incubation behavior prior to clutch completion causes some embryos to begin development earlier than their slightly younger siblings, thereby creating a size hierarchy early in life that has consequences for offspring fitness (Mock and Parker 1997).

The role of prolactin and other hormones, including glucocorticoids, in regulating the onset of incubation, also provides a useful context in which to understand parental investment and physiology, the costs of reproduction, and intersexual selection (Williams 2012). Most forms of parental care are usually assumed to be costly, and these costs may affect the fitness of males and females in different ways. Although both male and female parents incubate eggs in some species, the sexes differ considerably in incubation behavior, even in species with biparental incubation; in others, only one parent (usually the female) is responsible for all incubation effort (Skutch 1957).

It has been debated whether the incubation period is costly for parents in terms of the amount of investment required. There is a necessary trade-off between the amount of time a parent is able to spend incubating versus foraging and an increase in metabolic rate to raise body heat to warm the eggs (Reid et al. 2002). Despite this, recent studies have shown that the incubation period may serve as a beneficial period of recuperation for parents before the extremely costly period of young rearing (Sakaluk et al. 2018). Ultimately, the costliness of incubation depends on the life history of the species, including nutritional and health requirements, the mating system, and environmental conditions.

Incubation behavior represents a relatively simple behavioral modification applied to an ancestral mode of post-hatching parental care. External incubation is especially adaptive in birds through reduction of flight costs associated with carrying a brood of developing embryos within the body, and results of experimental studies indicating uncertainty associated with costs of incubation further suggest an advantage associated with external incubation in flying endotherms. Future research utilizing incubation as a context



for investigating general problems will shed further light on our understanding of animal behavior and evolution.

## Cross-References

- ▶ [Altricial](#)
- ▶ [Biparental Care](#)
- ▶ [Brooding](#)
- ▶ [Environmental Influences](#)
- ▶ [Intersexual Selection](#)
- ▶ [Life History](#)
- ▶ [Parental Investment](#)
- ▶ [Passerine Life History](#)
- ▶ [Precocial](#)
- ▶ [Prolactin](#)
- ▶ [Reproductive Fitness](#)
- ▶ [Thermoregulation](#)

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## Incubation Behavior

- ▶ [Cuckoo Brood Parasitism](#)

## Indicator Species

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## Synonyms

Bioindicator; Biomonitor; Ecological index; Environmental index; Proxy species; Sentinel species; Surrogate species

## Definition

Indicator species are one or more taxa whose relative absence, presence, or abundance serves as measure of the health of a given ecosystem.

## Species as Indicators

Species can serve as biological indicators of ecological health and have a number of distinct uses. In recent years, the use of the term “indicator species” has been widely adopted by researchers, and the concept has been adapted and applied to a range of scientific assessments. Researchers use indicator species’ relative absence, presence, or abundance as a representation of an environmental trait or condition. Their status is used as both an ecosystem monitoring and management tool by ecologists and biologists alike.

Using a single species, or group of species, as a proxy of environmental health provides a reliable, cost-effective, and efficient method for studying a complex system. Ecosystems are generally comprised on innumerable species and each of these species has a complex network of interactions. More than 1.5 million species have been

described, and many more are described each year (Roskov et al. 2017). Attempting to qualify and quantify every species and its corresponding web of interactions would be a lofty, if not impossible, task.

Species designated as “indicators” are selected to describe or monitor environmental events, the current environmental state, or its changes over time. Primarily, researchers use indicator species to monitor overall ecosystem health and environmental integrity (Siddig et al. 2016). This can include reflecting both biotic and abiotic components of ecosystem states or representing the biodiversity of other taxa within the area. Indicator species are also used to reflect both positive and negative environmental change and microclimates. Changes in the status of an indicator species may be a result of environmental degradation, climate change, pollution/contamination, another species distribution, or habitat restoration. Finally, indicator species are occasionally studied as a preventative measure to monitor for early warnings of environmental change.

## Species Selection

The term indicator species can refer to a single species, multiple species within a taxon, or several species across taxa. Most often, researchers use groups of species within and across taxa as ecological indicators rather than a single species (Siddig et al. 2016). Using species groups is advantageous because they cover a larger range of ecological properties. This robust range provides redundancy to even out potential normal variation or fluctuations in the measurement of choice. Larger data sets also open up the possibility to utilize a suite of statistical analysis tools and allow for comparisons across data sets. Multi-species indicator studies are also a precaution in the event of the local extinction of one species as the other species can continue to be assessed.

While there are many advantages to using species groups as indicators, there are situations in which using a single species is beneficial. More detailed information can be collected if only one

species is being studied. Detailed data on the developmental stages or reproduction rates could result in discoveries that would otherwise be overlooked. Another benefit of using a single species is that they require fewer resources to monitor. Studies on a smaller scale are more feasible and cost-efficient than large-scale investigations. Information about single species is also more easily related to and accepted by the public, especially when the chosen species is well-known and charismatic.

Species are selected by researchers based on their ecosystem and topic of interest. There are several common selection criteria to be considered when choosing an indicator species. The species must first be readily present in the area of interest and easy to locate. The ecological data obtained from these species must be available and reliable. Often they are stenecious or live only within a certain habitat range. Indicator species must also be able to be assessed in a standardized manner. Selected species must be moderately tolerant by being both sensitive and hardy. To represent an ecosystem, they must be sensitive to unusual environmental changes but not strongly influenced by normal fluctuations (Dale and Beyeler 2001). Environmental conditions must be reflected in the species’ behavior and physiology, ultimately affecting their health and reproduction. Some species are poor candidates because they are too adaptable and are therefore not representative of other species.

Historically, the justification for selecting a specific species or species group to be a surrogate include basing selection on previous research, ecological importance, local abundance, conservation status, or a combination of two or more of these reasons (Andelman and Fagan 2000; Siddig et al. 2016).

Not all selection criteria for indicator species are based solely on scientific merit. While indicator species are a cost-effective solution to large-scale, detailed assessments of entire ecosystems, the cost of the assessment is still of concern. Establishing efficient methods for studying ecosystems that require monitoring for extended periods of time is critical. Researchers also

consider public perception and the potential relatability of the species, specifically when indicator species are used to represent negative environmental change or to inspire habitat restoration and protection. Charismatic animals tend to garner public support as rallying points for change. Considerations can also include prior public knowledge about the species.

## Valuable Taxa

Most researchers use groups of species within or across taxa as signifiers of the ecosystem health. Plant, microorganism, invertebrate, and vertebrate taxa have all been selected as indicators (Siddig et al. 2016). Among animal taxa, reptiles, amphibians, and mammals are utilized the least, and invertebrates are selected the most as indicators. Invertebrates are often chosen to represent aquatic and wetland health. Fish tend to be selected for assessing the effects of organic pollution because most fish species are heavily reliant on dissolved oxygen in the water (Bechtel and Copeland 1970). Fish populations decline rapidly when dissolved oxygen levels decrease due to organic pollutants.

## Indicator Habitats

Indicator species are selected based on their presence in a specific ecosystem. These habitats can be chosen for many reasons including having been rarely studied, currently threatened by anthropogenic disturbances, or impacted by zoonotic diseases. Aquatic and wetland ecosystems are most commonly assessed followed by terrestrial habitats (Siddig et al. 2016). Indicator species are only occasionally used when studying atmospheric conditions. Although using indicator species as a proxy for environmental health is effective, it is important to recognize the limitations of using a single species' population trends to represent a dynamic system. Ideally, a suite of contextual data along with data from indicator species is considered before drawing conclusions.

## Indicator or Keystone Species

Keystone species and indicator species are easily confused terms. However, they represent different ecological concepts. Indicator species reflect the health of an ecosystem when researchers observe the population. In contrast, a keystone species is a species with a large influence on their environment relative to their population size. Removing a keystone species from an ecosystem would cause the ecosystem to collapse. For example, Duggins (1980) described sea otters as a keystone species in kelp forests. Sea otters are one of the few natural predators of sea urchins. Sea urchins consume the kelp forest that many species of fish use for shelter and spawning. If their population is not preyed by sea otters, they destroy kelp forests and the fish population along with them. When sea otters were almost hunted to extinction, the sea urchin population exploded and consumed vast amounts of kelp causing the fish population to decline rapidly (Duggins 1980).

## Cross-References

- ▶ [Ecology](#)
- ▶ [Endemism](#)
- ▶ [Pollution](#)
- ▶ [Species](#)

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## Indirect Association

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### Definition

Indirect association studies refer to discovery-based approach that does not require prior information about potential disease risk loci (Roper 2004).

### Association Studies

Genetic factors play a crucial role in affecting the susceptibility of an individual toward disease pathology. However, it becomes really challenging, to identify the relevant gene, as each causal gene contributes a little to the overall heritability of a particular disease.

Genetic or candidate gene association studies offer a potentially affective platform in identifying and mapping the disease-associated genes. However, this approach can only be used to study small number of genes at a time. Genome-wide association studies on the other hand provide a large platform to study multiple genes at a time. It is used to rapidly screen markers distributed across the whole genome to identify genetic variations associated with the particular disease phenotype. Once the variants are identified, it can be used to develop various strategies which will help in detection, treatment, and prevention of the disease. Candidate gene studies utilize either association or resequencing

approaches; however, genome-wide studies include both linkage mapping and genome-wide association approach.

## Linkage Disequilibrium

Linkage disequilibrium or LD defines a non-random association of alleles located at two or more loci. This term was first used by Lewontin and Kojima in 1960 (Lewontin and Kojima 1960; Slatkin 2008). It is the property of SNPs (single nucleotide polymorphisms) that defines the degree of association of allele of one SNP with the allele of another SNP in a population. It is used to study the genetic variation in a population over time.

### Indirect Association

The presence of LD can be used to generate two possible outcomes from a genetic association study. For the first outcome, if we have a strong hypothesis regarding the association of a particular allele with disease condition, then that allele can be directly genotype. This type of approach is often referred to as **direct association**, and the genotyped SNP is called as functional SNP. However, the second possibility is that the risk SNP is not directly typed, but in its place, a tag SNP which is in high LD with the risk SNP is genotyped. This is called as **indirect association**. Tag SNPs are specifically selected to capture the variation at neighboring sites in the genome, as the alleles for these SNPs tag the nearby stretch of LD (Bush and Moore 2012). International HapMap project (Tam and International HapMap Consortium. 2003; International HapMap Consortium. 2005) and various other potential databases (Sachidanandam et al. 2001; Hinds et al. 2005) have now facilitated young researchers across the globe to select useful sets of tagged SNPs that can be used as a marker for indirect association studies.

Thus, for a case-control study of measured genotype, based on the type of exposure examined, the study can be divided into two groups,

i.e., direct association and indirect association. Direct association study on one hand relies on genetic polymorphism studies of risk SNPs of a candidate gene; indirect association studies rely on polymorphic markers of genomic region.

## Cross-References

- [Allelic Association](#)
- [Linkage Analysis](#)
- [Single Nucleotide Polymorphism \(SNP\)](#)

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## Indirect Perception

- [Top-Down Processing](#)

## Indispensability Reduction: Decrease

- [Need Reduction](#)

## Individual

- [Population](#)

## Individual Differences

- [Personality in Animals](#)

## Individual Genotype Growth

- [Fitness](#)

## Individual Recognition

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## Definition

Animal social behavior depends on recognition. There are many types of recognition, including self, kin, mate, gender, friend, offspring, predator, and prey. All recognition involves (i) cue production by the signaler, (ii) cue perception and template matching by the receiver, and (iii) a behavioral response by the receiver (Sherman et al. 1997).

Multiple definitions of individual recognition have been proposed that differ slightly in their specificity and complexity. The most common definition of individual recognition proposes that



receivers discriminate a signaler from others based on the signaler's unique characteristics and associate the unique characteristics with individual-specific information about the signaler (Tibbetts and Dale 2007) (Fig. 1). For example, king penguins (*Aptenodytes patagonicus*) exhibit individual recognition because each chick has individual-specific calls (signaler's cue). Parents learn their chick's unique calls and respond in a unique way; they treat their own chick differently than other chicks (Aubin and Jouventin 1998).

Steiger and Müller (2008) proposed a less restrictive definition of individual recognition: receivers need only discriminate a signaler from others based on the signaler's unique characteristics. As long as receivers have a unique phenotype, the behavior is considered individual recognition, even if receivers associate the unique characteristics with class-specific information about the signaler. For example, if a bird has multiple chicks and learns to discriminate their own chicks from among unrelated chicks using the chicks' unique calls, this behavior would be termed individual recognition. Others would consider this offspring recognition, a type of class-level recognition, rather than individual recognition because the parents treat all their chicks similarly.

A challenge associated with Steiger and Müller's definition is that it can be difficult to assess whether or not receivers perceive cues as unique if receivers don't have unique behavioral responses. Cues that appear unique to researchers might not be perceived as unique by the receiver's sensory system. For example, computer-based

acoustic analysis suggests that the alarm calls of meerkats are individually distinctive yet receivers do not respond differently to alarm calls based on the identity of callers (Schibler and Manser 2007). How can we test if meerkats perceive the alarm calls from different individuals as unique without a unique behavioral response?

Others argue for a more restrictive definition of individual recognition that requires receivers to learn and recall multiple, unique individuals (e.g., Thom and Hurst 2004). Under this restrictive definition, king penguins would not have individual recognition because parents only learn and identify one chick at a time.

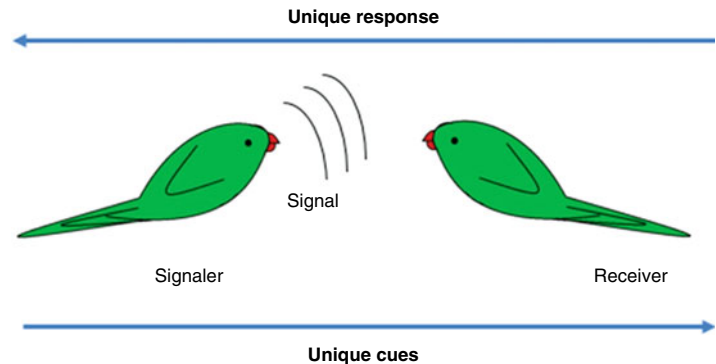
## Introduction

Individual recognition is interesting from a cognitive perspective because it is considered a relatively specific and complex form of recognition. During individual recognition, receivers must learn the unique features of conspecifics, associate the features with individual-specific information, and recall the feature/information link during subsequent interactions. Individual recognition is also interesting from a cognitive perspective because it allows the formation of individually differentiated social relationships. The potential for individually differentiated social relationships influences the type and sophistication of social interactions possible within a society (Platt et al. 2016).

In this entry, individual recognition will be addressed from both the receiver and signaler

### Individual Recognition,

**Fig. 1** The criteria for individual recognition. Signalers have unique cues and receivers behave in a unique way toward the signaler



perspectives. Receivers assess, perceive, and respond to signals. In some cases, receivers have perceptual and cognitive adaptations to facilitate accurate individual recognition. On the other side, signalers have unique phenotypes that are used for recognition. This entry will discuss the contexts in which individual recognition is used, how individual recognition varies across contexts, receiver cognitive and sensory adaptations for individual recognition, and how selection acts on the signaler to facilitate individual recognition.

## Social Contexts in which Individual Recognition is Used

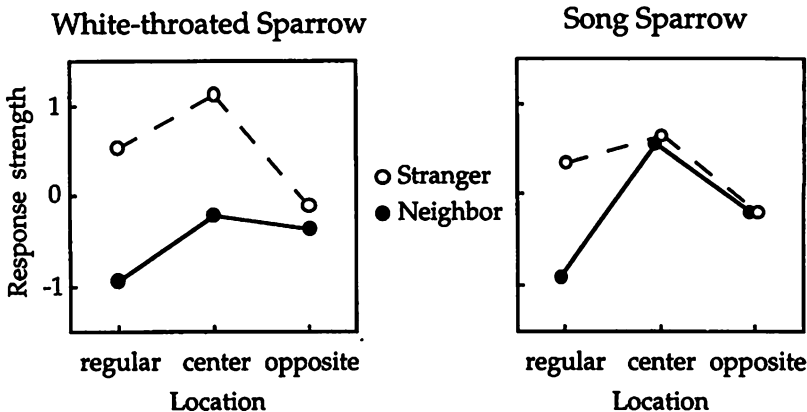
### Interspecific Variation in Individual Recognition across Contexts

Individual recognition is common in social contexts when there are repeated interactions between the same target individuals and also nontarget individuals. Such situations include territoriality, dominance interactions, cooperation, providing parental care, and pair bonding (Tibbetts and Dale 2007).

Much of the earliest research on individual recognition examined recognition of territorial neighbors (originally termed “dear enemy”

recognition). For example, many birds use song to identify the identity and position of their neighbors. Birds largely ignore playbacks of neighbor songs positioned on the correct territorial boundary but responded aggressively to playbacks of neighbor songs positioned on the incorrect territorial boundary and to playbacks of stranger songs (Stoddard 1996). Individual recognition is thought to reduce the energetic costs of territorial defense by enabling territory holders to focus their aggressive efforts on non-territorial floaters instead of their less threatening neighbors (Fig. 2).

Individual recognition is also important during aggressive competition because it can reduce the costs associated with competition and stabilize dominance hierarchies (Barnard and Burk 1979). Individual recognition is likely to be beneficial when there are repeated aggressive interactions between small numbers of individuals. In this situation, learning the individual identity and competitive ability of conspecifics will provide a precise way to assess rivals without multiple fights. For example, some species of fish, including brook trout (*Salvelinus fontinalis*), individually identify rivals via scent. Trout assess relative dominance ranks based on the outcome of their own aggressive interactions as well as observations of others via transitive inference. If a fish



**Individual Recognition, Fig. 2** The dear enemy approach to testing individual recognition. White-throated sparrow (*Zonotrichia albicollis*) is less aggressive to neighbor songs on the correct territorial boundary than neighbor songs on the incorrect territorial boundary, indicating that white-throated sparrow recalls the individual identity and position of neighbors. Speakers played back

neighbor and stranger songs from the boundary shared with the neighbor (*regular*), the center of the territory (*center*), and the boundary shared with a different neighbor (*opposite*). The behavioral data are normalized composite scores for the number of flights and the closest approach to the playback speaker (Taken from Stoddard 1996)

beats rival A in a fight and then observes A win in a contest with B, the fish will correctly infer that it is more dominant than individual B (White and Gowan 2013). Transitive inference was once thought to be a cognitively complex task restricted to few taxa but has now been found in many vertebrate species with individual recognition that form dominance hierarchies (Paz-y-Miño et al. 2004). Individual recognition associated with aggressive competition is widespread in nature, as many species use individual recognition to minimize the costs of conflict (Barnard and Burk 1979).

Although cooperation can occur without individual recognition, there is much evidence that cooperative behaviors such as reciprocity, alliances, social prestige, punishment of non-cooperators, and image scoring are facilitated by individual recognition. As a result, many taxa with complex social interactions rely on individual recognition. Individual recognition of group members is ubiquitous in primates and also occurs in many species that live in cooperative groups, including mammals, fish, and birds (Sharpe et al. 2013). Although social insects have complex social behavior, individual recognition is relatively rare in social insects. Instead, most social insect societies rely on class-level recognition and self-organization to produce apparently complex behavior with little individual cognitive investment.

Individual recognition is involved in multiple aspects of reproduction, including parent-offspring interactions and monogamous pair bonding. Individual recognition during parental care is particularly likely to occur when there is potential for confusion among offspring, such as among organisms that breed in high-density groups with synchronous reproduction and reduced recognition potential based on positional information. For example, the Australian sea lion *Neophoca cinerea* reproduces in large colonies. Both mothers and pups use individual-specific calls to find each other after the mother's foraging trips (Charrier et al. 2009). Monogamous species with biparental care use individual recognition to maintain pair bonds and mate guard and defend territories. For example, *Chaetodon multicinctus*

butterfly fish uses visual and olfactory cues to discriminate their mate from non-mates (Boyle and Tricas 2014).

Individual recognition during monogamous pairing and parent-offspring recognition is sometimes considered simple forms of individual recognition because receivers need only learn and recall one individual. Some argue "true" individual recognition requires receivers who can individually discriminate many individuals (Thom and Hurst 2004). As a result, future work that tests whether multiple mates, parents, or offspring can be individually identified will be useful. For example, in taxa with multiple offspring, do parents treat different offspring uniquely? For instance, there is evidence that parents of the songbird black redstart (*Phoenicurus ochruros*) respond more to the calls of the fledglings that they preferentially fed, suggesting that parents can discriminate between offspring (Draganoiu et al. 2006).

While most examples of individual recognition occur within species, individual recognition is not restricted to conspecifics. Some animals recognize individuals of other species. For example, mockingbirds learn to assess the level of threat posed by different humans. When the same human approaches a mockingbird's nest for 4 successive days, mockingbirds begin flushing from the nest when the human is a great distance from the nest and also increase alarm calling and attack flights. Mockingbird response to humans who have not threatened the nest does not change (Levey et al. 2009).

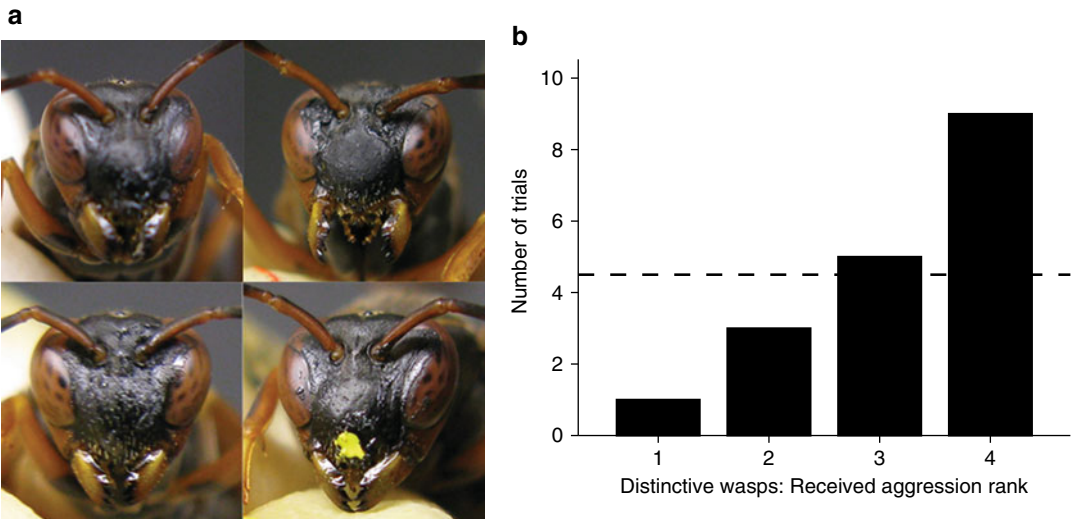
### Intraspecific Variation in Individual Recognition across Contexts

A large body of research has examined the types of social behavior associated with interspecific variation in individual recognition, but less is known about intraspecific variation in individual recognition. Examining intraspecific variation is important because responses to individual identity signals may vary across the biotic and abiotic environment. For example, a species may use individual recognition during aggressive encounters in certain social or environmental circumstances, but not in other circumstances.

Previous work has shown that there is some intraspecific variation in receiver responses to signals. For example, receiver responses to quality signals often vary with traits like sex, maturity, season, habitat, and social context. Many studies have shown that the biotic and abiotic environment influences whether females choose male partners based on sexual signals or ignore sexual signals during partner choice (Searcy and Nowicki 2005). Such variation occurs because assessing and responding to signals can be costly, so receivers will only pay attention to signals when signal response is sufficiently beneficial. Therefore, intraspecific variation in recognition may occur whenever the benefits of recognition differ across contexts.

A few studies have found intraspecific variation in individual recognition. Notably, pair-bonded male prairie voles learn to recognize individual females, while single males do not learn to recognize females. The authors found no difference in male motivation to contact females across paired and unpaired males, so they speculate that recognition differs because the social relevance of information about females varies across contexts (Blocker and Ophir 2015).

In the paper wasp *Polistes fuscatus*, the social benefits of individual recognition and receiver capacity for individual recognition vary across castes. Specifically, workers are less able to learn and remember individual conspecifics than foundresses (Tibbetts et al. [in press](#)). During social interactions, workers are unable to remember unique individuals following a 6-day separation, though foundresses remember other foundresses for 6 days. The differences in individual recognition across castes are initially surprising because *Polistes* lack discrete queen/worker castes. Workers and queens are morphologically similar, and workers can take over nests as queens. Differences in recognition may occur because the social benefits of individual recognition differ across foundresses and workers. Workers do not benefit by being individually recognizable on stable queenright nests because worker-worker aggression on queenright nests is low and workers do not reproduce or have unique roles in the colony. In contrast, foundresses benefit by being individually recognizable, as it reduces aggression and stabilizes social interactions among cooperating foundresses (Fig. 3). Individual recognition also allows foundresses to



**Individual Recognition, Fig. 3** Being individually distinctive is beneficial. Faces of *Polistes fuscatus* foundresses were manipulated so three wasps had a common, indistinguishable appearance while one wasp had a unique appearance (a, lower-right image). Distinctive

wasps received the least aggression (1, most; 4, least) in a disproportionate number of trials, indicating that a unique appearance that allows individual recognition is beneficial. Dotted line represents the expected aggression received by chance (b) (Taken from Sheehan and Tibbetts 2009)

keep track of individual social relationships, including division of aggression, food, and work (Sheehan and Tibbetts 2009).

## Complexity of Individual Recognition

There is enormous variation in the cognitive demands of individual recognition. Learning and remembering a few individuals for a short time may be relatively simple compared with learning many individuals, maintaining memories for long periods, or associating multiple types of information with individual identity. In this section, cognitively challenging aspects of individual recognition are described.

Most early individual recognition research examined how animals recognize others using a single cue in a single sensory modality. However, more recent work has shown that many animals integrate multiple cues from the same or different sensory modalities during individual recognition. For example, golden hamsters (*Mesocricetus auratus*) have multiple odor glands, and hamsters generalize between different scents from the same individual. The authors suggest that males form integrated representations of conspecifics that incorporate multiple odors (Johnston and Bullock 2001). Other species form cross-modal representations of known individuals by combining unique auditory and visual cues. For example, ring-tailed lemurs (*Lemur catta*) can produce multisensory representations by matching olfactory and visual signals to individually recognize conspecifics, though the specific proximate mechanisms that are used for sensory integration are not yet clear (Kulahci et al. 2014).

Many animals can remember individual conspecifics after a lengthy separation. For example, fur seal pups (*Callorhinus ursinus*) remember their mother's unique calls for at least 4 years (Insley 2000). Dolphins (*Tursiops truncatus*) may be able to remember unique conspecifics for decades (Bruck 2013). Male hooded warbler birds (*Wilsonia citrina*) use song to recognize their neighbors individually and are able to retain the memory after being separated for 8 months. During the

separation, birds do not sing and migrate to Central America (Godard 1991). Ravens (*Corvus corax*) remember previous individual calls after up to a 3-year separation (Boeckle and Bugnyar 2012).

Long-term individual memory may be particularly important in societies with fission-fusion dynamics, where individuals meet after unpredictably long periods of separation. Memory is also affected by the context in which the recognition is effective. For example, the mantis shrimp *Neogonodactylus bredini* can remember conspecifics for 4 weeks, perhaps because this amount of time correlates with their reproductive periodicity because female's receptivity and male-female pairing is timed with the full moon (Vetter and Caldwell 2015).

The cognitive challenges of individual recognition are also influenced by the number of individuals that are learned. African elephants (*Loxodonta africana*) have large recognition networks, as adult females can recognize up to 100 other females (McComb et al. 2000). Elephant females can recognize their own family, as well as approximately 14 other families they regularly encounter. Such impressive networks of vocal recognition may be typical of long-lived species that have fission-fusion social systems and long-distance vocal communication.

Some species learn to identify surprisingly few individuals despite apparently high levels of social complexity. For example, gelada baboons (*Theropithecus gelada*) use vocalizations for individual recognition only within the small social group known as a "unit." They do not vocally recognize other males, even males from their own band with whom they have extensive social overlap (Bergman 2010).

It is often difficult to assess whether memory constrains individual recognition. Does reduced recognition in geladas occur because males have poor memories, reduced motivation, or little social need for individual recognition? In a creative experiment, Stoddard tested whether memory constrained the ability of song sparrows (*Melospiza melodia*) to learn neighbor's songs. Song sparrows can memorize the full song repertoire of new neighbors without a decline in overall



learning performance and without forgetting the old songs, even when the number of songs learned approached the number of songs a song sparrow would have to know to make accurate discriminations across neighbors (Stoddard et al. 1992).

Another factor that influences the complexity of individual recognition is the types of information associated with individual identity cues. For example, baboons (*Papio hamadryas ursinus*) simultaneously classify other females according to dominance rank and matrilineal kinship. Associating both rank and kinship information with the unique calls of conspecifics increases the challenge of individual recognition as well as the functional complexity of social interactions (Bergman et al. 2003). To our knowledge, there is no evidence for this type of two-dimensional classification outside primates, so research in additional taxa will be important.

Some nonhuman primates use individual recognition to keep track of others' relationships. For example, baboons are more likely to approach and tolerate an opponent if they hear a "reconciliatory" grunt of a close relative of the opponent. However, "reconciliatory" grunts from individuals unrelated to the opponent have no effect on behavior. This behavior means baboons keep track of relatedness between other individuals rather than merely remembering their own relatives. Recognition of others' relationships will dramatically increase the amount of information individuals need to remember. For example, in a group of 80 individuals, a baboon who keeps track of their own relationship with each group member may only recall two pieces of information about the 79 other group members: are they related or unrelated to the focal individual and are they dominant or subordinate to the focal individual? In that same group of 80 individuals, there are 3160 possible dyad and 82,160 triad combinations (Platt et al. 2016). Current data suggests baboons can identify the relatedness and relative rank in all those potential groupings, a truly outstanding feat. In the future, additional work will be important to understand how well nonhuman species keep track of other's relationships.

## Cognitive and Sensory Adaptations in Receivers to Facilitate Accurate Recognition

Learning and remembering many unique individuals are thought to be cognitively challenging. As a result, some species have cognitive adaptations to facilitate accurate individual recognition. These adaptations fall into three categories: (1) general increase in cognitive capacity in species with individual recognition, (2) specialized increase in cognition related to individual recognition, and (3) sensory adaptations to facilitate assessment of individual identity signals.

First, individual recognition may produce generalized increase in cognitive capacity. The social intelligence hypothesis proposes that the benefits of being able to learn and remember multiple individuals and social relationships have selected for increased cognitive capacity in many social taxa (Dunbar 1998). Between species comparisons have provided consistent support for the social intelligence hypotheses. Across many taxa, species with more complex social behavior have larger brains or brain regions than species with less complex social behavior (e.g., primates, hyenas, lemurs, ungulates, carnivores, cetaceans, birds). For example, a comparative analysis in nonhuman primate species found that relative neocortical volume is linked with social group size, but not ecology, suggesting that individual social relationships are a key factor that shapes brain size evolution (Dunbar 1992).

Other analyses have found no relationship between brain size and social complexity. For example, a comparative study on brain size and social complexity in 29 species of vespids (including solitary and social wasps) showed that brain size does not correlate with colony size, social structure (hierarchies), and type of nest foundation (solitary vs. social) (O'Donnell et al. 2015). The authors hypothesized that insects can perform relatively complex tasks with minor adjustments of neural circuitry. Further, many highly social insects have been selected to have more specialized brains rather than larger brains. More generally, there is a growing appreciation

that understanding the relationship between social behavior and cognition requires nuanced assessment of social complexity that is relevant to the taxa of interest (Platt et al. 2016).

Second, some species have specific cognitive adaptations that facilitate individual recognition. *Polistes fuscatus* paper wasps use individual face recognition and are specialized for face learning; wasps learn to identify conspecific faces more quickly and accurately than other visual information. In contrast, paper wasp species without individual recognition perform poorly at face learning. A closely related wasp species that lacks individual face recognition, *P. metricus*, lacks face specialization and has trouble learning conspecific faces. The divergence in face learning between closely related wasp species suggests that face specialization in *P. fuscatus* is an adaptation to facilitate individual recognition (Sheehan and Tibbetts 2011). Face specialization in paper wasps may be associated with some neural changes in the antennal lobe and the mushroom body sub-compartments. However, there appears to be no major optic lobe specialization in species with visual individual recognition, suggesting that the visual processing capabilities of paper wasps might be preadapted to discriminate complex visual features, such that the ability to discriminate facial markings could require relatively small changes in their neuronal substrate (Gronenberg et al. 2007).

Neural specialization for individual recognition has been best studied in primates. Humans are experts at using facial features for individual recognition. Humans can learn and remember many individuals over their lifetime and only require short exposure to form individual memories. Humans also use configural processing to learn faces, as the spatial arrangement of facial features is integrated into a single “face image” rather than recognition being based on the component parts of a face. Finally, humans have neural specialization for face learning; there is a network of distributed neural regions that respond specifically to faces, not other visual stimuli. Damage in specialized area can produce individuals who are unable to recognize individual faces (Tsao and Livingstone 2008). Nonhuman primates also use faces for individual recognition

and have some specialization for face learning, including face-selective neural responses in certain regions of the brain. Some primates also use configural processing to discriminate between individual faces, though most primates rely less on configural face processing than do humans (Leopold and Rhodes 2010).

Finally, some animals have sensory adaptations to optimize assessment of individual identity signals. Paper wasps with visual recognition have larger facets in the eye’s acute zone than species without visual recognition. Larger facets improve resolution of small images, such as wasp facial signals. Therefore, the wasps’ sensory systems may evolve to optimize signal assessment (Fig. 4) (Sheehan et al. 2014). In mice, odors (major urinary protein) signal individuality. The neurons in the vomeronasal system (olfactory system) are activated selectively by odors that signal individuality and gender, suggesting an olfactory adaptation for individually recognition of conspecifics (Cheetham et al. 2007).

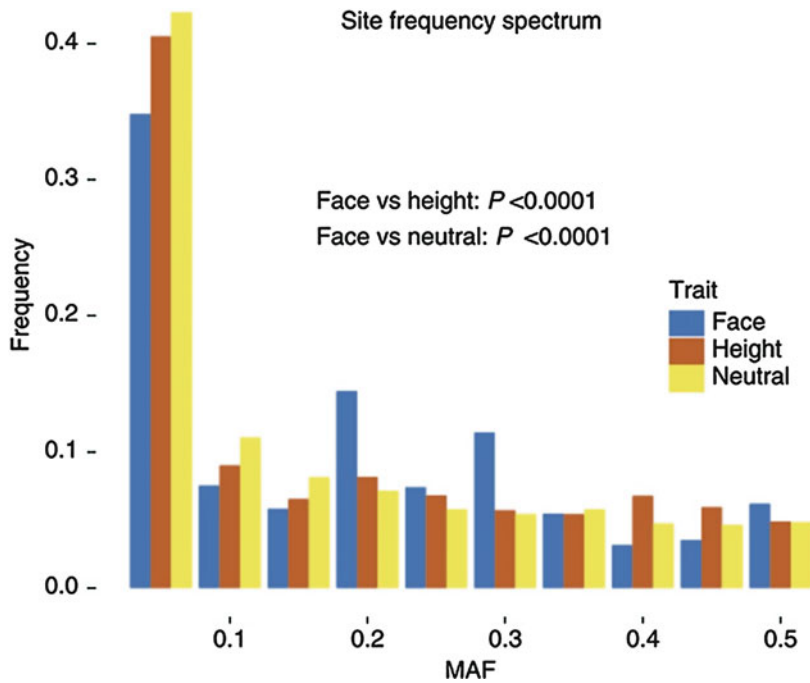
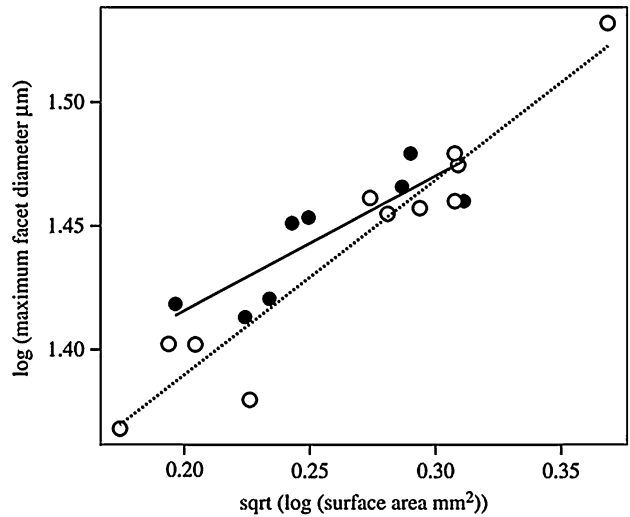
## Individual Recognition from the Signaler’s Perspective (Individual Identity Signals)

### Signals Versus Cues

Individual recognition can occur via signals or cues. Signals and cues are similar in that both modify the behavior of receivers. The key difference between signals and cues is that signals benefit the signaler, while cues do not (Searcy and Nowicki 2005). For example, human faces are signals that convey information about individual identity to receivers. Humans likely benefit by having unique, easily recognizable faces. As a result, human facial variation has been selected to optimize receiver recognition, and this selection has shaped human facial variation as well as the genetic regions that code for human facial variation (Fig. 5; Sheehan and Nachman 2014). In contrast, human fingerprints are a cue of individual identity. While it is possible to discriminate among individual humans based on fingerprints, variation in fingerprints is a by-product of development. Fingerprints have not been selected to

Individual Recognition,

**Fig. 4** *Polistes* wasp species that exhibit visual signal also exhibit larger facets than expected in the eye acute zone. *Filled circles*, visual signaling species; *open circles*, nonvisual signaling species. Having larger facets is considered an adaptation to facilitate recognition via visual signals (Taken from Sheehan et al. 2014)



**Individual Recognition, Fig. 5** Genomic regions associated with facial morphology show evidence of selection for individual identity signaling. Bars represent the proportion of SNPs within each minor allele frequency (MAF). Genomic regions associated with facial morphology have elevated levels of intermediate-frequency alleles when

compared with neutral regions or genomic regions associated with variation in height. The higher genetic diversity in face-associated SNPs is consistent with negative frequency-dependent selection acting on human facial features (Taken from Sheehan and Nachman 2014)

convey information about individual identity, so fingerprints and the regions that code for fingerprint variation will not have signatures of selection to optimize distinctiveness.

The distinction between signals and cues is important because signals show signatures of adaptive evolution to facilitate receiver responses, while cues do not. The following sections

describe the predicted characteristics of individual identity signals.

### Negative Frequency-Dependent Selection Acts on Signalers

Individual identity signals are expected to evolve via negative frequency-dependent selection (Dale et al. 2001). Individuals with rare phenotypes are favored by selection because they are less likely to be confused with other individuals than those with common phenotypes. There is experimental evidence in both *Polistes* paper wasps and guppies, *Poecilia reticulata*, showing that individuals with a rare appearance are favored relative to individuals with a more common appearance. For example, *Polistes fuscatus* paper wasps have highly variable facial patterns that are used for individual recognition (Tibbetts 2002). Wasps with unique faces that are easy to discriminate receive less aggression than wasps with common, less distinguishable faces. Receiving aggression is costly, so these results indicate that individuals with unique phenotypes benefit by revealing their identity (Sheehan and Tibbetts 2009; Fig. 3). Field studies have shown that guppies with rare body coloration benefit by receiving more mates than guppies with a common appearance (Hughes et al. 2013). Guppies use body coloration for individual recognition, so the mating benefit may arise through identity signaling if rare guppies are easier to learn and remember than common guppies.

Comparative work provides further evidence that individual recognition selects for increased phenotypic diversity. In paper wasps, mammals, swallows, and bird eggs, individual identity signaling is linked with increased phenotypic diversity (Tibbetts et al. 2017). This relationship is consistent with the hypothesis that social benefits of being individually recognizable favor increased phenotypic diversity in certain social contexts. For example, computer-based model has shown that egg signatures by hosts of the common cuckoo evolve surprisingly fast in the presence of brood parasites. The simulation suggests many hosts evolve unique, highly recognizable egg pattern signatures as a defense against cuckoo egg mimicry (Stoddard et al. 2014).

### Effects of Individual Identity Signaling on Phenotypes and Genotypes

Because identity signals evolve under negatively frequency-dependent selection, identity signals are expected to be highly variable and multimodal and have low intercorrelation among identity signaling traits. These predictions are developed in detail in the model by Dale and colleagues (2001). Further, in the taxa that have been tested, there is low intercorrelation among identity signaling traits (Dale 2000; Tibbetts 2002). Finally, reliable identity signals are predicted to be stable over time rather than plastic.

Theoretical and empirical work suggests that individual identity signals will be highly heritable and have low condition dependence. The few individual identity signals studied have high heritability (Dale 2000). Identity signals are also expected to have low costs associated with signal production and maintenance because phenotypes that are not costly will spread to a higher equilibrium frequency than costly phenotypes. For example, the birds ruff sandpipers (*Philomachus pugnax*) and red-billed queleas (*Quelea quelea*) live in dense aggregations in which individual recognition is key for territory defense. In both species, plumage coloration is highly heritable and has low production costs (Dale et al. 2001). Similarly, rock hyrax (*Procavia capensis*) uses the same highly variable calls for individual recognition across multiple years, and these calls are not linked to geographic locations or relatedness (Lee and Eli 2011). Paper wasps use facial patterns for individual recognition. Facial patterns are fixed during adulthood, and facial pattern development is not condition dependent, as larval diet quality has no effect on facial pattern development (Tibbetts and Curtis 2007).

Because individual identity signals are highly heritable traits under negatively frequency-dependent selection, selection for identity signaling may increase genetic diversity. Positive selection for signaling individual identity may have more widespread genetic effects than other cases of negative frequency-dependent selection because identity signaling favors high levels of variation in multiple, uncorrelated traits (Tibbetts et al. 2017). In contrast, other examples of negative frequency-dependent selection typically

maintain a limited number of morphs at stable ratios in the population.

The precise effects of individual identity signaling on the genome will differ based on the genetic architecture of identity signals (Tibbetts et al. 2017). For example, negative frequency-dependent selection acting on individual identity signals will have broader genomic consequences if signal development is influenced by many, independently segregating loci than if signal development is influenced by epistatic interactions in a small cluster of genes. Population genetic evidence indicates that negative frequency-dependent selection acting on loci that encode human facial features influences genomic diversity in humans. Specifically, loci that encode human facial features have higher nucleotide diversity than loci associated with variation in height or neutral, intergenic variation, consistent with human facial features experiencing negative frequency-dependent selection (Fig. 5; Sheehan and Nachman 2014). Further, the genomic regions surrounding areas that code for face variation also have increased nucleotide diversity, indicating that selection on human identity signals has broader effects on genomic diversity. In contrast, selection for identity signaling in mice has limited genomic consequences. Mice use major urinary proteins (MUPs) as chemical signals of individual identity. Although variation in MUPs is maintained by negative frequency-dependent selection, identity signaling in mice has little overall effect on the genome because a small number of clustered loci produce the overall MUP signature (Sheehan et al. 2016).

## Conclusions

In this entry, we consider the evolution of individual recognition from the perspective of the receiver and signaler. Studies of individual recognition from the receiver's perspective are very common and have demonstrated that individual recognition is an important aspect of social behavior in a wide range of taxa, including birds, mammals, reptiles, insects, and aquatic invertebrates. Individual recognition is also used in diverse

contexts, including territoriality, dominance interactions, cooperation, providing parental care, and pair bonding.

Individual recognition can be cognitively demanding for signal receivers, especially when receivers learn many individuals, maintain those memories for long periods, or associate multiple types of information with individual identity. Complex behaviors involving individual recognition that were once thought to be rare (e.g., transitive inference) have recently been found to be surprisingly common. Further, many taxa have surprisingly sophisticated individual recognition, including long individual memories and the ability to recall many individuals and associate diverse information with individual identities. Future research will likely continue to uncover the diversity and sophistication of individual recognition across taxa.

Individual recognition also has important selective consequences for signalers. In particular, there is growing evidence that signalers are selected to reveal their individual identity by having phenotypes that are memorably different. Individuals with rare phenotypes are favored by selection because they are less likely to be confused with other individuals than those with common phenotypes. Selection on signalers to reveal their individual identity may be an underappreciated mechanism for the origin and maintenance of phenotypic and genetic diversity. Given the growth of genomic data in non-model organisms, future work examining the genetic architecture of individual identity signals as well as the consequences of individual identity signals on animal phenotypes and genotypes will be important.

## Cross-References

- ▶ [Agonistic Behavior](#)
- ▶ [Alarm Calls](#)
- ▶ [Auditory Signals](#)
- ▶ [Chemical Signals](#)
- ▶ [Dear Enemy Effect](#)
- ▶ [Dominance Hierarchy](#)
- ▶ [Frequency-Dependent Selection](#)
- ▶ [Heritability of Behavior](#)



- ▶ Individual Recognition
- ▶ Insect Communication
- ▶ Insect Sensory System
- ▶ Learning
- ▶ Long-Term Memory
- ▶ Olfactory Discrimination
- ▶ Perception
- ▶ Polymorphic
- ▶ Primate Cognition
- ▶ Primate Communication
- ▶ Receiver
- ▶ Sensory Receptors
- ▶ Single Nucleotide Polymorphism (SNP)
- ▶ Social Intelligence Hypothesis
- ▶ Territory Defense
- ▶ Visual Recognition in Birds

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## Individual Sow Accommodation

► [Gestation Stall](#)

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## Individual-Based Modelling

► [Agent-Based Modelling](#)

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## Individual-Orientated Modelling

► [Agent-Based Modelling](#)

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## Inductive Reasoning

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### Definition

**Inductive reasoning** is a logical process in which multiple premises, all believed true or found true most of the time, are combined to obtain a specific conclusion or to supply evidence for the truth of a conclusion. **Inductive reasoning** is often used to generate predictions or to make forecasts. Inductive reasoning differs from deductive reasoning in that while the conclusion of a deductive inference is certain, the truth of the conclusion of an

inductive inference is only probable, where the degree of certainty is based upon the strength (or consistency) of the evidence. In other words, the conclusion of an inductive inference is not a logical certainty (such as when a meteorologist predicts snow). Inductive reasoning also encompasses most cases of where a general principle is derived or where categories are formed based on specific observations (provided that they are probabilistic in nature).

In practice, inductive reasoning is the logical foundation of science, and all fields (from physics to sociology) share the inductive method at their core. (In this regard, it is worth noting that, unlike mathematicians and logicians, scientists can never be 100% certain about their “truths” and can only make approximations based on accumulated empirical evidence.) But the application of inductive reasoning goes much beyond science and is critical for a multitude of more commonplace and prosaic activities in humans and other animals. Many cognitive activities, ranging from problem solving to social interaction to motor control, can be seen as containing an element of inductive reasoning.

## Introduction

Inductive reasoning is one of the most important and ubiquitous of all problem-solving activities, and its use by nonhuman animals is of great interest within fields of psychology and biology such as cognitive psychology, ethology, evolutionary biology, learning, and neuroscience. In its most elementary form, it seems that most animals exhibit some capacity for inductive reasoning. For instance, sea slugs respond to a stimulus inductively based on past experiences with it (e.g., by “concluding” that the stimulus can be ignored; a case of habituation). Similarly, the fear response of a rodent to a stimulus that was repeatedly and predictably presented in conjunction with a harmful outcome is to some extent the result of an inferential prediction (i.e., the rodent “concludes” by induction that a bright light always precedes a foot shock). And Pavlov’s dogs salivated in response to the ring of a bell

that always came before meal time (the dogs “concluded” by induction that bells are a signal for lunch.)

There exists, however, an old divide on the interpretation of the relevant data on inductive reasoning: Associationism holds that the data can be mostly explained by simple associative processes whereby *reflexes* are modified through experience, while rationalism holds that more complex mechanisms are involved, and the existence of inductive reasoning is required to better explain the data (see Rescorla (1988) for a more complete analysis of these contrasting views).

Traditional associationist models posit that an organism’s learned response to a stimulus is represented by the strength of the relevant associations between stimuli. In this view, the animal adapts to its environment through the process of reflex modification, and that the animal need not make predictions or choose between potential responses. In this sense, reasoning would be unnecessary to explain the examples provided above. Typically, associationists have argued that abstract, rule-governed representations do not really exist and that animals’ (and humans’) behavior can be just as well explained in terms of more specific learned associations between task inputs and outputs. Hence (according to this view), the only thing researchers should be concerned with is the specification of what gets associated with what (easier said than done, but still a relatively straightforward goal). Due in part to the predominance of associationism in psychology during the last century, it was until recently a commonplace assertion that inductive reasoning was beyond the capacity of nonhuman animals. In the past few decades, however, there has been an accumulation of evidence for animal inductive reasoning.

While traditional associationist models assume that an animal’s interaction with the environment is passive (the animal behaves by the automatic adjustment of strengths of association only in reaction to stimuli), rationalist models assume that the interaction is active – the animal actively probes the environment to make determinations about optimizing behavior (Gallistel 2003). In that framework, “figuring things out in nature” is

guided by how useful a stimulus is in reducing the animal’s uncertainty about the time of occurrence of some relevant event. This knowledge comes in part from a distribution of graded degrees of belief over a range of candidate hypotheses, or in other words, it depends on inductive reasoning. Rationalists believe that there are problem-specific computational mechanisms that evolved to inform animals’ behavior (Gallistel 2000). In this light, inductive reasoning is seen as a set of algorithms devoted to particular cognitive processes, such as causal inferences, probabilistic inferences, optimization of strategies from sampling, and categorization/concept formation (Nisbett et al. 1983). Here we will focus on these complex rational solutions that are (mostly) agreed upon to be cases of inductive reasoning.

It should be noted that the higher-order cognition proposed by rationalists and the associative rules proposed by associationists are not necessarily mutually exclusive. De Houwer et al. (2016) propose that associative learning is best thought of as an effect (i.e., the impact of paired events on behavior) rather than a specific mental process (e.g., the formation of associations). In other words, learning and behavior are mediated by higher-order mental processes akin to problem-solving processes such as inductive reasoning. (For more on that topic, see De Houwer et al. 2016).

## Causal and Probabilistic Inferences

Causal inference is the process of reasoning about a causal connection between events based on the co-occurrence of those events. As noted in the Introduction, there are many parallels between instrumental and classical conditioning phenomena in animals on the one hand and contingency assessment and causal judgments by humans on the other (see Shanks (2007) for a recent review). The scientific framework for thinking about causal inference emerged from the associationists’ work on instrumental conditioning. Nevertheless, despite the extensive evidence that bottom-up processes such as instrumental and Pavlovian learning play a fundamental role in the acquisition of causal knowledge, there is also accumulating

evidence for the involvement of top-down processes of causal induction in animals. In this light, the co-occurrence of events is not simply stimuli for an automatic association but in fact evidence for the animal's rational mechanisms to make inferences about the world.

Some interesting examples help illustrate the case that animals have the capacity for complex causal inference. Takagi et al. (2016) used an expectancy violation procedure in cats similar to what is used with human infants to probe their understanding of causal relations and physical laws. The study asked whether cats can use a causal rule to infer the presence of an unseen object on hearing the noise it made inside a container (Takagi et al. 2016). Cats were presented with either an object dropping out of an opaque container or no object dropping out after hearing either a rattling sound (by shaking the container with the object inside) or no sound (by shaking the empty container). The relation between the sound and the object matched with physical laws in half of the trials (congruent condition) and mismatched in the other half (incongruent condition). Inferring the presence of an unseen object from the noise was predicted to result in longer looking time in the incongruent condition (indicating "surprise," i.e., that the cats' expectancy had been violated). In addition, the cats were also able to predict and reach for an object appearance when the container was turned over. These results all suggest that cats have a causal understanding of auditory stimuli, which is indicative of their capacity for inductive reasoning.

In another example, Cheney et al. (1995) examined if baboons can understand cause-effect relations in the context of social interactions by using a playback experiment. Under natural conditions, dominant female baboons grunt repeatedly to subordinate mothers when attempting to interact with those mothers' infants. The subordinate mothers occasionally respond to these grunts by uttering submissive fear barks. So, in their study, Cheney et al. played causally inconsistent scenarios to the baboons in which a lower-ranking female apparently grunted to a higher-ranking female and the higher-ranking female apparently responded with fear barks. As an important control to rule out simple associative processes, baboons heard a

sequence made causally consistent by the inclusion of grunts from a third female that was dominant to both of the others. The researchers found that baboons responded very differently to each scenario: in the causally consistent scenario, they either ignored the calls or looked briefly in the direction of the speaker, while in the causally inconsistent scenario, the baboons stared (seemingly surprised) for a long time. That suggests that baboons recognize by inductive reasoning the factors that cause one individual to give submissive vocalizations to another.

Even rats also seem capable of some degree of causal reasoning. In one study, Blaisdell et al. (2006) concluded rats are able to derive predictions of the outcomes of interventions after passive observational learning of different kinds of causal models. Those outcomes, according to the study, cannot be explained by associationist models but are instead consistent with inductive reasoning models. As a last example, it is important to note that causal reasoning is also critical for the ability to adapt an object for use as a tool, a skill that has been demonstrated by many animals.

The ability to infer causation also depends on the ability to estimate probabilities, as actions (causes) do not always lead to the outcome (expected effects). Animals often face circumstances in which the best choice of action is not certain. Because of this, the ability to reason about probabilities has ecological relevance for many species. Environmental cues may be ambiguous, and choices may be risky (for a review on the theoretical side of decision-making under uncertainty, see Trimmer et al. 2011). The use of inductive reasoning to estimate probabilities requires sampling, and for that an individual must be able to estimate proportions.

Multiple species of animals seem to be able to successfully make judgments on proportions. For example, when foraging, animals go to where more will be available by considering the amount of food in alternative locations and the number of other individuals feeding at these different locations (Rugani et al. 2015). Or in a social context, some primates show inequity aversion; they are able to judge their own effort and payoff *relative* to another individual's (Brosnan and de Waal 2003).



Probabilistic inference goes one step beyond the ability to compare proportions, because the subject also needs to understand the sampling part of the procedure; that is, they need to make inferences about the probable identity of items drawn from populations, based on the distribution of items in those populations. In fact, a study on capuchin monkeys shows that some individuals could make judgments about proportions but could not reason about probabilities (Tecwyn et al. 2017). Capuchins had to select between hidden single-item samples randomly drawn from two jars. In their first experiment, Tecwyn et al. familiarized subjects with the single-item sampling procedure and determined their baseline performance in this task with two populations of items, where each jar contained only preferred or non-preferred items (100% preferred vs. 100% non-preferred), a task that does not involve any probabilistic judgment. In the other experiments, the researchers investigated the ability of the subjects to make inferences about random samples drawn from mixed pools of items in the two jars. Their results revealed that capuchins' performance suffered when the jars had mixed pools, because it required the individuals to reason probabilistically. Some individuals were still able to infer correctly, but not all did so. As the authors later discuss, this suggests that probabilistic inference might also require other complex mental processes such as inhibitory control and working memory.

Probabilistic inferences are not only restricted to apes. Even mice, for example, possess at least a simpler form of that capability (Berkay et al. 2016) and can adaptively modulate their decisions based on their experienced probability of outcomes. Probabilistic inference also seems to play a critical role in animals' social behavior, including decisions made according to game theory (Crowley 2003).

### Optimization of Strategies from Sampling

The capacity of sampling for probabilistic inference is also related to an inductive inference of integrating information together, such as when an

animal navigates home by triangulating spatial cues or develops optimal foraging strategies by combining different food densities in each area. In other words, this inductive reasoning optimizes strategies and decision-making by deriving the "whole" from samples of the component parts.

Wass et al. (2012) studied a form of inductive reasoning for foraging in mice using a Binary Tree Maze, inspired by procedures developed in human decision analysis for identifying the most efficient strategies to reach a goal. The Binary Tree Maze is a decision tree that bifurcates (at decision points) into branches. Each decision point is a potential goal location, and the end of each branch terminates in two "leaves," each of which also contains potential goal locations, providing (in this example) a total of 14 potential goals (although only a random selection of goals were baited on any particular trial). In Wass' study, the mice's task was to navigate the maze so as to inspect every potential goal for a piece of food. While there are many possible search strategies (or paths) to visit every node in a decision tree, the vast majority of these paths would be inefficient due to unnecessary node crossings (in other words, they would involve unnecessary retracing of a path or crosses of a location that had already been explored). What distinguishes the Binary Tree Maze from a standard maze learning task is that no single path is "best"; many routes are equally efficient, and a mouse might perform errorlessly across trials yet not follow the same route on successive trials. The degree to which a mouse could comprehend the structure of the maze from successive experiences in it and implement that information from its current location is a reflection of inductive reasoning. In the study, Wass et al. found that in their initial exposures to the decision tree maze, the mice's pattern of behavior suggested a disorganized random search. However, within six trials, the patterns of individual animals stabilized and remained stable. At the end of several days of testing, many mice were performing at optimal foraging efficiency, suggesting that the mice quickly came to appreciate the underlying structure of the maze and fix on a strategy for its solution. (However, some mice still performed poorly, which is indicative of wide variability in those mice's inductive reasoning.)

Furthermore, Wass et al. (2012) also determined if mice were relying on rote paths through the maze or whether they were engaging in an active search of the maze (a requisite for inductive reasoning). To make this determination, each mouse was allowed to begin its exploration of the maze, and upon making its first entry into a second level branch, the adjacent branch was blocked by lowering a black guillotine door. Had a mouse been following a rote (but nominally efficient) path through the maze, this manipulation would have disrupted the utilization of that rote path. Even after this, mice were still able to perform at a high level of efficiency.

This process of optimization of search is also seen in animals as evolutionarily distant from mammals as honey bees. Naug and Arathi (2007) investigated possible sampling and decision rules that the foragers use to choose one option over another by presenting foragers with choice tests in a foraging arena. They showed that a large part of the sampling and decision-making process of a foraging honey bee can be explained by decomposing the choice behavior into dichotomous decision points and incorporating the cost of sampling. The results suggest that a honey bee forager, by using a few simple rules as part of a probabilistic inference process, is able to effectively deal with the complex task of successfully exploiting foraging patches that consist of dynamic and multiple options (Naug and Arathi 2007).

## Categorization

When encountering a new object in one's surroundings, the ability to recognize the item as a member of a known category, such as a potential food item or predator, can be crucial for survival. This process involves inductive reasoning given that it requires derivation of general principles from specific, sample observations (extracting the relevant rule out of limited samples and multiple options). Categorization has been well documented empirically, and many animals possess that ability.

In the 1960s, Herrnstein and Loveland (1964) showed that pigeons could learn to peck for

reinforcement whenever pictures of people appeared on a screen and not to peck whenever pictures without people were presented. Many similar demonstrations followed, where birds and mammals were trained to categorize diverse classes of natural items, from trees and water to other animal species (examples in D'Amato and Van Sant 1988; Roberts and Mazmanian 1988). In addition to natural categories, animals have also successfully classified objects that would have no evolutionary significance to them, such as "cars" and "chairs" (Bhatt et al. 1988), ruling out the possibility that categorization is only based on innate concepts.

Some interesting examples help illustrate the case that animals are able to form categories from sampling the environment. A study with chimpanzees tested the animals' abilities to categorize photographs of natural objects (Tanaka 2001). Chimpanzees were initially trained to match different color photographs of familiar objects from four possible categories. In training, all the comparison stimuli were from the same category in one condition and from different categories in another condition. For all subjects, training performance was consistently better for the "different category" than for the "same category" trials. In probe trials after training, the sample and positive comparison stimuli were different items from the same category, and the foils were selected from among the three other test categories. Remarkably, individual performance was above chance in probe trials, suggesting that categorization by chimpanzees may transcend perceptual resemblance. Furthermore, the researchers replicated these same results later using novel stimulus items from the same four categories. This study demonstrates that chimpanzees can group perceptually different exemplars within the same category and suggests that these animals formed conceptual representations of the categories.

In an analogous study, Range et al. (2008) presented dogs with a touch-screen testing procedure, which allowed them to test visual discrimination without the presence of social cueing (social cues from humans are a known to be a big confounding factor in cognitive/behavioral studies with dogs, as they coevolved to be very

sensitive to our cues). They first trained dogs to differentiate between a set of dog pictures and an equally large set of landscape pictures. All subjects learned to discriminate between the two sets and showed successful transfer to novel pictures. Interestingly, presentation of pictures providing contradictory information (novel dog pictures mounted on familiar landscape pictures) did not disrupt performance, which suggests that the dogs made use of a category-based response rule with classification being coupled to category-relevant features (of the dog) rather than to item-specific features (of the background).

Categorization is not only restricted to visual patterns; of course, it is just that those stimuli are easier for humans to study. In an investigation of categorization of song notes in great tits (Weary 1990), the birds were trained first to discriminate between two synthetic song notes. These sounds were models of naturally occurring song notes and differed from one another in five acoustic parameters. Once the birds learnt to discriminate between the two training notes, they were tested with notes that presented all combinations of the five parameters. Responses to these sounds showed that great tits relied almost exclusively on note frequency to form categories; other parameters such as amplitude modulation, frequency modulation, and the interaction between frequency and amplitude were all used to a much lesser extent.

In light of the abovementioned studies, one might wonder: How is inductive reasoning employed during the formation of categories? There are two main theories on how categorization is formed: exemplar theory and prototype theory. For decades, the exemplar theory was dominant in the categorization literature, and it assumes that there is one representational/processing system that serves all needs of categorization. According to the theory, organisms store exemplars as separate, individuated memory traces, refer new items to these stored exemplars, and include them in the category if they are similar enough. However, new research has shown that animals have prior expectations of prototypes (or family resemblance or natural kinds) and exclude exceptional cases (such as a weird looking

predator exemplar from their list of that predator). In other words, inductive reasoning does not do the work from scratch in forming categories as expected by the exemplar theory. Instead, animals use inductive reasoning (among other processes) to infer coherent family resemblance based on prototypical categories already in place. In a review piece, Smith et al. (2016) argue that, based on converging evidence from multiple species, exemplar processing is insufficient to account for the available data on categorization. They claim that prototype averaging might be less effective and create errors of categorization in lab experiments (since in hypothetical situations, you can always imagine weird exemplars) but that in nature prototyping is good enough for a world with so many similarities within categories (most eagles look like eagles, most fruit trees look like fruit trees, etc.), and so being attuned to prototypes would be more advantageous for faster decisions. Or as Smith et al. (2016) writes: “family-resemblance categories dominate. Animals are adept at what they experience and what they need. Their adeptness is neither a coincidence nor a disability” (p. 273).

## Conclusion

Inductive reasoning is present in many different animals, and the multiple ways in which it is expressed show continuities in nature: to different degrees and levels of competence, animals seem to be able to perform causal inference, probabilistic inference, optimizations of strategies based on observation, categorization, etc. Thus, animals are crucial behavioral ambassadors to the study of inductive reasoning in humans.

It is also important to keep in mind that although ubiquitous and important, inductive reasoning in practice can be riddled with problems, even in humans. We are far from the perfect, ideal case from which animals should be compared to, as we, in our daily/ecological (out of the armchair) lives, commit many mistakes in categorization and probabilistic inference (as shown by multiple studies that followed the seminal work of Kahneman and Tversky on how people overlook

statistical variables such as sample size, correlation, and base rate when they solve inductive reasoning problems (Tversky and Kahneman 1974).

## Cross-References

- Analogical Reasoning
- Categorization
- Intelligence
- IQ
- Learning
- Working Memory

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## Inequity Aversion

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## Synonyms

[Equality](#), [Equity](#), [Fairness](#), [Justice](#)

## Definition

Inequity aversion in animals is a response to outcomes that are less than, or more than, what a social partner receives.

## Introduction

Humans are an exceptionally cooperative species, regularly engaging in cooperative acts with both related and unrelated individuals. Cooperation in humans has played a fundamental role in the success of our species, yielding unprecedented collective action and a capacity to transmit information through vast social networks, which has provided humans with a key selective advantage that has enabled population growth into even boreal climates (Boyd et al. 2011). In particular, such cooperative tendencies have been vital to our cultural development, facilitating our ability to accumulate complex traits and knowledge over time (cumulative culture), a process that is widely believed to underpin humanity’s extraordinary biological success. Given the selective advantage wide-scale cooperation has conferred to our species, it is important to address why this capability may have evolved and the processes that may underpin it. In this entry, we consider one mechanism that may be essential to maintaining the success of cooperation, inequity aversion.

When considering behaviors, evolutionary scientists typically focus on two features: its function, or why it evolved, and the mechanism(s) by which it operates. Regarding the first of these, the evolutionary pathway that leads to cooperation is relatively well understood. It is typically accounted for by one of the three theories: kin selection, reciprocity, or mutualism. The kin selection account of cooperation is that cooperation can evolve when cooperative acts provide a fitness advantage to related individuals, despite a cost to helper organisms. The account of cooperation that involves direct reciprocity indicates that cooperation can arise when the short-term net losses are outweighed by the long-term benefits of cooperative interactions, often with specific partners. Finally, mutualism describes cooperation that can result in greater immediate payoffs resulting from working together as compared to working alone, without necessarily requiring future interaction. Central to all theories of cooperation is the cost-benefit ratio resulting from collaboration; cooperation requires average individual inclusive fitness to be increased, directly or



indirectly, when cooperating with genetically similar individuals. Herein lies the challenge; for cooperation to evolve, it must provide more benefit than the actor pays in costs.

One way in which this might be done is through a sense of “fairness,” or more precisely, an ability to recognize inequitable outcomes (see Brosnan 2011, for further discussion of the link between inequity aversion and fairness). Specifically, sensitivity to inequity allows organisms to identify when a partner unduly benefits from collaborative interactions versus when partners mutually and fairly benefit. Recognizing when payoffs are equitable or inequitable can inform actors whether it is beneficial to engage in future collaboration or whether it is time to find a new cooperative partner. Indeed, one advantage of having a sense of inequity is that it might allow individuals, in some cooperative contexts, to recognize when they are being cheated by receiving less than they should (rather than receiving nothing at all; Brosnan and Bshary 2016).

In the past few decades, there has been increasing empirical and theoretical attention on whether species recognize inequitable outcomes and how this is (or is not) related to species’ cooperative tendencies. Empirically, researchers have established that many species are averse to inequitable payoffs in at least some contexts. This is described by the term “inequity aversion,” a negative response to an unequal payoff to oneself, relative to others that can take the form of disadvantageous inequity aversion – a response to receiving less than others – or advantageous inequity, a response to receiving more than others (Brosnan 2006). Theoretically, inequity aversion has been hypothesized to constitute one of the mechanisms by which cooperation can be maintained because it allows individuals to judge the value of their partners. Specifically, individuals can judge when they should (i) discontinue interactions with partners that take more than their share of the benefits of cooperation, (ii) replace such unfair partners with more equitable partners, (iii) encourage future interactions with valuable partners by distributing rewards in an equitable manner, and/or (iv) manage their reputation as a fair partner

(e.g., by rejecting unequal but beneficial gains). Such strategies may play an important role in long-term cooperative actions (Brosnan 2011), particularly when unrelated individuals stand to benefit from reciprocity and mutualism. Of course, not all of these benefits will appear in every species, and such behavior could evolve without individuals understanding the function; all that is needed is an evolved negative response to inequitable outcomes that causes individuals to seek out other partners.

In this entry, we take an explicitly evolutionary approach to explore how inequity aversion evolved as an adaption to meet particular environmental and social challenges. We first provide background on the study of inequity aversion in humans, following which we discuss the empirical evidence for inequity aversion in nonhuman species and, in particular, nonhuman primates. We then consider what this tells us about the phylogenetic trajectory of the inequity response. These results indicate that inequity aversion and cooperation coevolved, supporting the argument that inequity aversion is a mechanism to promote successful cooperation. Following this evolutionary view, we look at the degree to which inequity may impact cooperation between individual organisms. Inequity does lead to a breakdown in cooperation, again indicating the degree to which inequity responses are important in cooperation. We end with a consideration of how inequity is related to the human sense of fairness and to what degree studying responses to inequity in nonhuman species can help us understand the evolution of our sense of fairness.

## **The Study of Inequity Aversion in Humans**

One challenge to an evolutionary approach to fairness is that fairness is a social ideal, and it is impossible to study ideals in nonverbal species. Therefore, in order to study this empirically, researchers have operationalized the sense of fairness as an ability to recognize disadvantageous and advantageous outcomes relative to those of a partner. One way researchers have empirically

approached this question has been to examine the choices participants make when they are faced with allocating resources between themselves and a partner. Various scenarios, or “games,” borrowed from the field of economics have been used to investigate the contexts in which humans care about equity. In one such game, called the “dictator game,” a resource (i.e., money) is provisioned to an individual (the proposer) who decides how to divide it between themselves and a “recipient.” In the dictator game, the recipient plays a passive role and has no option to influence the proposer’s offer. Thus, the proposer can share resources at a cost (reduce advantageous inequity or even create disadvantageous inequity) or monopolize resources (maximize advantageous inequity). As the partner does not have a say in the distribution, a situation is created in which selfish behavior pays. This setup has been informative for establishing whether humans make “fair” offers when there is no opportunity for a partner to encourage fairness by reciprocity or recourse.

Dictator games have been played with children and adults of different societies, yielding some interesting developmental and cultural differences. In children, younger individuals act selfishly, keeping all, or the majority, of rewards (e.g., Gummerum et al. 2010). This picture begins to change at around the age of 5, with a developmental shift toward acting more fairly, and children will often begin to distribute the rewards equally. This, and similar research, supports the proposition that children begin life acting in a rather self-centered manner before more egalitarian tendencies begin to set in at around 5–7 years of age. Turning to adults, the typical amount allotted to a partner in dictator games averages around 20% (Forsythe et al. 1994) suggesting that, when a cost is involved and repercussions are absent, humans do not maximize their absolute gains but they are also not perfectly fair, either; instead, they make non-zero but nonetheless inequitable offers that favor themselves.

Comparing the dictator game to the “ultimatum” game shows that contextual features can influence how fairly humans act toward others. The ultimatum game mirrors the dictator game,

with the exception that the recipient can reject the proposed reward allocation, in which case both players receive nothing. This is both a form of punishment and an inequity response (although rejecting means that the recipient now ends up with absolutely less than they could have had, the outcome is relatively equal). In this context, average offers made in Western adults increase to approximately 30–40% (Camerer and Thaler 1995). This indicates that when proposers can lose resources, proposals become more equitable, albeit typically still not equal. The ultimatum game mimics situations in which individuals, at a cost, can defect from partners that cheat or unduly benefit, a situation that encourages equity. That human fairness judgments are linked to contextual and social factors is further highlighted by cross-cultural studies. Interestingly, economic games, such as the dictator and ultimatum games, played with different societies, reveal large between-group variations in the proposals humans make (Henrich et al. 2004). Such findings suggest that the human notion of fairness is very sensitive to differences in social and ecological environment as well. In particular, as is expected if the hypothesized link between fairness and cooperation is correct, more generous offers are proposed in societies that rely heavily on cooperation and trade (Henrich et al. 2004).

Researchers have also made use of the “inequity game” to explore humans’ reactions to inequitable outcomes. In this game, two participants take the role of the “actor” and “recipient” and the experimenter provisions either equitable or inequitable rewards. The actor then makes a decision of whether to accept or reject the reward distribution, the latter of which results in both participants receiving nothing. By including rewards that benefit and disadvantage actors relative to the partner, investigators can establish whether subjects may be averse to advantageous, disadvantageous, or both forms of inequity. The inequity game was recently employed in a large-scale study encompassing seven different societies and over 800 pairs of children, finding that children in all populations tested rejected disadvantageous rewards. Disadvantageous inequity aversion appeared around the age of 4 but with variation in

the age of onset across the populations (Blake et al. 2015). Rejection of advantageous rewards, in contrast, occurred only in some societies and at a later age. Importantly, such findings have helped to disentangle advantageous from disadvantageous inequity and emphasize that a self-serving bias to avoid disadvantageous outcomes appears to be a universal human trait, whereas aversion to advantageous outcomes appears to be influenced by society and culture.

Researchers have hypothesized that inequity responses evolved in tandem with cooperation (Brosnan 2006, 2011; Fehr and Schmidt 1999). In particular, inequity is purported to act as a mechanism to compare one's own outcome to those of others following collaborative effort. Experimental support for this has been emerging in the nonhuman literature (discussed below) but several lines of evidence link fairness decisions to cooperation in the human literature as well, often indicting that cooperation strengthens subjects' motivations for fair payoffs.

Investigators have exposed children to experimental cooperation tasks very similar to those run with nonhuman primates, allowing some direct comparisons to be made. In one such example, Warneken et al. (2011) set 3-year-old children the task of working together to gain otherwise unavailable rewards that were either separated into two distributed piles, and thus could not be easily monopolized by one child, or were clumped into a single pile that could be easily monopolized. Importantly, children as young as 3 years of age mostly split the resources evenly in the clumped resource condition, suggesting children knew what was "fair." This result contrasts with contexts that do not require children to engage in joint action, which reveal more selfish intentions in children of this age (e.g., in the dictator game: Gummerum et al. 2010). If we compare this to cooperative studies with chimpanzees (*Pan troglodytes*), we find high levels of resource monopolization and a break down in collaboration in chimpanzees, but not children (Hare et al. 2007). Bonobos (*Pan paniscus*), argued to be more socially tolerant than chimpanzees, tested on this paradigm behaved more similarly to humans, outperforming chimpanzees in the clumped

resource condition. That being said, more recently, chimpanzees have been shown to share food more often and show greater tolerance in this context than bonobos, leaving open the question of how our closest evolutionary ancestors shared food (Jaeggi et al. 2010). Nevertheless, such findings linking tolerance and cooperation have led researchers to hypothesize that social tolerance over resources plays an important role in mediating cooperation and that the low-tolerance levels observed in some species is a major constraint on their cooperative tendencies. Thus, ensuring equity, either actively by sharing or through high social tolerance for co-feeding, may be a key factor in sustaining collaboration, whereas disadvantageous inequity aversion, coupled with competitive tendencies, may limit such opportunities. This supports the prediction that cooperation may be maintained over the long term by distributing rewards in an equitable manner or choosing to work with partners who do so.

Similar cooperation studies show that by the age of 3, children will correct resource inequity after working together, sharing resources to a greater extent after such collaboration than when working in parallel or when simply gifted with resources (Hamann et al. 2011). Children are also more likely to share rewards evenly with those who collaborate than with free riders (Melis et al. 2013). These findings suggest that children engage in equitable reward distribution based on collaboration and work effort (equity) rather than simply ensuring equality irrespective of collaboration. Comparative work with chimpanzees shows no such flexible sharing according to whether others collaborate or not, indicating a potentially important species difference (Hamann et al. 2011). In addition to correcting resource inequities following cooperation, humans also anticipate who may serve as good collaborators. For example, at 15 months of age, children already select partners that are fair over unfair ones (Burns and Sommerville 2014). By adulthood, cooperative partners are selected according to how generous they are, they will act more generously when observed and will even compete to be more generous than each other when future cooperation can lead to

personal gain (Barclay and Willer 2007). Of course, individuals need not always be aware of the future benefit of selecting fair over unfair partners (e.g., 15 month olds almost certainly do not understand this) nor need they understand how such strategies work. Instead, attraction to or a preference for fair or generous partners (in combination with a preference to end unfair cooperative relationships) could maintain selectivity for partners that are likely to provide equal or beneficial gains in future collaborations.

The study of inequity aversion in humans has taken many forms, using tasks, joint activities, games, and vignettes, with various dependent measures ranging from self-reports or emotional reactions to active resource allocations and the rejection of absolute gains if they lead to relative inequality. Key findings have emerged that provide insight into which facets of fairness children may be biologically predisposed to pay attention to and which may require some social experience and culture. Concerning the former, that children from an early age (around 3–4 years old), and from various cultures, respond to disadvantageous inequity across multiple experimental contexts, suggests that disadvantageous inequity aversion is a robust response; humans, it seems, do not like to receive less than partners and are willing to pay a price to avoid such circumstances. On the other hand, an aversion to receiving more than partners – advantageous inequity – follows a different developmental trajectory, appearing later in development (around the age of 8 in Western populations) and is subject to strong cultural influence (Blake et al. 2015). Equity choices also depend upon contextual factors, suggesting that fair behavior is not employed indiscriminately. Rather, sharing depends upon factors such as who the partner is and how much effort they devoted to a task (cooperation) and whether the partner can influence payoffs (e.g., ultimatum games) or not (e.g., dictator games). Such selectivity begins with choosing with whom we prefer to interact or cooperate. This indicates that our treatment by others (e.g., fair or unfair) influences whether we choose to engage with them or select someone else with whom to work.

## The Study of Inequity Aversion in Nonhumans

Humans show strong responses to inequity, but what about other species? Evidence accumulated over the past few decades shows that some other species react negatively to receiving a less desirable outcome than their partners. In a typical test of inequity aversion in nonhuman species, two partnered individuals each complete a task to receive a reward. The task is completed sequentially – with each individual taking turns – and the rewards provisioned to each partner are either the same (equity condition) or different (inequity condition). If subjects are inequity averse, a pronounced reaction should occur in the inequity condition relative to the equity condition. While different tasks have been used to study inequity aversion (and in some cases, no task at all), the majority of studies have employed an exchange paradigm in which subjects take, and then return, an object (“token”) to the experimenter for a food reward, essentially bartering it. This method was originally conceived by Brosnan and de Waal (2003) and applied to brown capuchin monkeys (*Cebus [Sapajus] apella*). The authors documented higher levels of rejection (unwillingness to exchange a token or consume a reward) in individuals that were offered cucumber (a less preferred food reward) following their partner’s receipt of grape (a favored food) as compared to their rejection rate in the baseline equity condition, in which both exchanged for cucumbers. The authors interpreted this result as reflecting a response to inequitable outcomes based on social comparison, that is, “inequity” based on the reward disparity between oneself and others, rather than a reaction to personally observed or experienced reward differences.

This interpretation did not go unchallenged. Two alternative explanations to the authors’ conclusion were based on nonsocial responses to unequal “pay.” First was “food frustration effects” in which the mere presence of a better reward could enhance rejections if the favored food was present in the inequity, but not in the equity, condition. The second challenge was the potential

frustration brought on by a violation of an expectation to receive a favored, and previously experienced, food when the subject instead receives a less preferred food (i.e., an expectation based on past reward history). More recent studies of inequity, however, have controlled for these alternative explanations by ensuring that both favored and non-preferred foods are visible in all study conditions and by the inclusion of controls for potential frustration, typically with a condition in which subjects are shown a favored food before offering a less preferred food, and by randomizing the order in which conditions are presented. Even with these controls, social comparison, or inequity aversion, still occurs. This suggests that refusals are not simply (or only) due to seeing better rewards or any potential frustration caused by expecting a better reward than is received.

Brosnan and de Waal's initial study of inequity aversion in capuchin monkeys paved the way for new research exploring such capabilities across the primate order and, in a recently emerging trend, non-primate species. At least 30 studies have now been published, and these find substantial variation across species and contexts (see Brosnan and de Waal (2014) for a table including all studies published to that date). Here we briefly summarize this research, focusing on what species show a response to social inequity and, where possible, the influence of procedural and contextual variables on the manifestation of the inequity response.

## The Phylogeny of Inequity Aversion

Among the great apes, chimpanzees are the most studied species. Chimpanzees generally show some degree of inequity aversion, much like the brown capuchin monkeys (see Brosnan and de Waal 2014; Price and Brosnan 2012). However, they are notable because their responses are subject to high levels of group and individual variation that has been linked to various social and personal factors, not always in consistent ways. Investigations using very similar protocols have shown that dominance, social affiliation, and gender can all influence inequity responses in

some, but not all, situations. Brosnan and colleagues, for example, have documented a stronger response in dominant individuals when they were undercompensated relative to a lower-ranking partner, but this dominance effect was not found in other studies (see Price and Brosnan 2012 for a review of these data). Similarly, there have been cases of chimpanzees with close social ties (i.e., housed together for long periods) being less responsive to a partner being overcompensated as compared to chimpanzees that were housed together for much shorter periods, although again, there have also been studies in which no such variation was seen. Such inconsistencies have encouraged researchers to search for individual differences that may account for some of this variation. Personality, for example, was recently found to correlate with social inequity responses, although it seems likely that relationship quality, which influences which individuals will voluntarily pair together for the tasks themselves, affects their responses as well (Brosnan et al. 2015).

Other factors not yet considered likely also underpin this variation. For example, the social configuration and tolerance of partnered animals may influence responses to inequity (reviewed in Price and Brosnan 2012), as could variation in subjects' daily food intake and any social change that may occur in the group at the time of testing. There may also be interactions between factors. For example, dominant individuals may show strong inequity responses simply because they are more satiated at the time of testing, through prior resource monopolization, relative to less dominant individuals. Satiation likely increases the likelihood of the costly behavior of forgoing an immediate, less preferred food in inequity conditions. Furthermore, dominants may be used to receiving the best foods from humans, strengthening potential inequity responses. Depending upon one's group, and indeed housing facility, dominant individuals' propensity to monopolize food could vary, with implications for the food refusal rates. One open question, then, is whether inequity aversion in the context of food rewards is an artifact of captivity, as forgoing an immediate reward incurs little cost where there is reliable, and sufficient, food provisioning. This question



requires investigation in natural populations and could be examined by documenting participation levels in coordinated activities following equitable and inequitable gains, for instance, looking at whether coordinated hunt participation lowers following disadvantageous inequitable food returns and exploring how participation may interact with food scarcity. It will also be important to determine in which other contexts inequity may influence behavior in natural conditions, particularly outside of the context of food.

Turning to the other great apes, comparatively less work has been conducted on inequity aversion. We know nothing of gorillas' (*Gorilla spp.*) capabilities, except that they do not respond to inequity when rewards are "gifted" by the experimenter (i.e., in the absence of a task; see Brosnan and de Waal 2014). However, no response in a free-feeding context is common across species. In every primate species in which inequity has been documented, subjects only respond negatively when the food rewards are received subsequent to completing some sort of task; when rewards are handed out "for free," the same subjects do not respond negatively even when they are unequal. We know little more about the other great apes, with only one published exchange study focusing on bonobos and two on orangutans (Bräuer et al. 2009; Brosnan et al. 2011). For bonobos, evidence points toward some presence of inequity aversion; however, as only five subjects have been tested, the results are inconclusive (Bräuer et al. 2009). The two studies that have examined whether orangutans respond to disadvantageous inequity document no such trend in socially housed orangutans (Bräuer et al. 2009; Brosnan et al. 2011). This is interesting, should it hold, as orangutans are among the least social primates, particularly in comparison to other great apes, and rarely cooperate in the wild. However, given this paucity of data in bonobos and gorillas, it is difficult to determine how inequity responses may have evolved among the apes.

Experimental studies of inequity have also focused on monkeys, including macaques (*Macaca spp.*), capuchins (*Cebus spp.*), squirrel monkeys (*Saimiri spp.*), owl monkeys (*Aotus spp.*), marmosets (*Callithrix spp.*), and tamarins

(*Saguinus oedipus*; see Brosnan and de Waal 2014 for a review of this literature, including citations for studies on each species). Capuchin monkeys, like chimpanzees, have been highly studied, and also like chimpanzees, show variation in their responses, with some studies finding evidence of inequity aversion while others have not. Interestingly, among the other New World monkeys that have been tested (common marmosets, owl monkeys, squirrel monkeys, and tamarins), no species has been shown to respond to disadvantageous inequity. However, much like in the great apes, the focus primarily on one species – capuchins – with very little data available concerning other New World monkeys makes it premature to conclude that other New World species lack a response to inequity, particularly given the variation in individuals' responses in the best studied species. The situation is even less clear in Old World monkeys, for which only macaques have been tested. Both species tested thus far (rhesus and long-tailed macaques) do respond negatively to social contrast. More recently, researchers have studied non-primate species, and initial data indicate that domestic dogs, rats, and corvids respond to the presence of, or the potential for, inequity (reviewed in Brosnan and de Waal 2014).

Considering variability within species, one factor proposed to explain such discrepancies, at least in part, is the experimental procedures employed. The combination of work effort provided by a task and subject's proximity to their partner appear to be important for the expression of inequity aversion, with studies that have distant partners and/or no task generally reporting a lack of a response to inequity, even in species and groups that show inequity in other contexts (Brosnan and de Waal 2014). Other factors, such as the relative value of the rewards may also impact inequity aversion; for instance, the preference discrepancy between some food pairings (e.g., pine nuts versus sunflower seeds) may differ to those used in other studies (e.g., cucumber versus grape). While the relative value of foods is always established *within* studies, these values still differ *between* studies, and recent research in capuchins shows that relative food values strongly impact inequity responses (Talbot et al. 2017).

Finally, social and individual differences impact inequity aversion in chimpanzees, which may also play a role in other species' unfairness judgments. For example, the relatedness of subjects and partners are rarely reported but could have a profound effect on whether animals are inequity averse or not. Individuals' propensity to use social over personal information may also determine responses to inequity. Many animals collect both kinds of information but are reported to prioritize personal over social information (Rieucan and Giraldeau 2011), meaning that animals may not always attend to social contrasts.

Considering the variability across species, what does this phylogenetic dispersal of inequity aversion tell us about the evolution of disadvantageous inequity aversion? Most apparent is the inconsistent distribution of disadvantageous inequity aversion across the primate order and its presence in diverse taxa both within the primates and beyond (e.g., corvids and rats). From this, it is evident that convergent evolution is at play (Brosnan 2011); disadvantageous inequity has evolved independently in various organisms, likely in response to similar ecological and/or social niches. Such pressures have been hypothesized to include species' sociality and degree of cooperation with non-kin. Sociality alone does not appear critical here as some gregarious species, living in large social groups, are nonetheless insensitive to inequity (e.g., squirrel monkeys). Instead, recent theory has favored a link between inequity aversion and cooperation with non-kin; of course, regular exposure to non-kin relates to species sociality/social structure, but the cooperation component seems to be important. Wild chimpanzees engage in coordinated hunts, territory defense, and coalitions, suggesting cooperation or at least behavioral coordination between group members. Likewise, the social behavior of capuchins and macaques hints at cooperation with non-kin. A number of experimental studies also show a degree of cooperation in these species, and even that inequitable outcomes will disrupt cooperation, providing further evidence for this link.

In considering the relationship between inequity aversion and cooperation, factors that complicate the picture should be noted. First,

cooperation between non-kin alone does not appear sufficient for the emergence of inequity aversion. Cooperative breeders (marmosets and tamarins), species in which both parents and, sometimes, older offspring work together to raise infants, show no reaction to inequity. This may be due to the high level of interdependence between males and females that renders a negative response to inequitable outcomes more costly than beneficial (i.e., the cost of finding a new mate, and risking losing one's current reproductive investment, is higher than the cost of inequity in most contexts; Brosnan 2011). One caveat here is whether cooperative breeders may be socially tolerant in some, but not other, situations. Cooperative breeders, for example, may be sensitive to inequitable contributions in work effort but tolerant of inequitable food returns. Second, as many studies have been conducted in highly controlled laboratory contexts, the extent to which the apparent sensitivity to inequitable outcomes generalizes to the natural environment remains unknown. Third, given the large variation in the inequity response documented within those species most studied (chimpanzees and capuchins), caution must be used when assuming an absence of inequity aversion in species based on just one or two studies. Finally, it is important to keep in mind that ecologically valid measurements of cooperation in natural populations could have more relevance to interpreting the possible relationship between inequity aversion and cooperation than those derived from captive studies, which may be more artificial. This is highlighted by orangutans, a semi-solitary species, that in two independent studies did not respond to inequity nor do they show high cooperative tendencies in the wild, yet they will work together to gain a reward in a captive setting, cooperating much like chimpanzees and capuchins (Chalmeau et al. 1997).

Overall, while it is currently the best-supported hypothesis, additional data are required to test the hypothesis that inequity aversion and cooperation coevolved. In particular, contrasts between closely related species known to cooperate with non-kin in the wild and those that do not, and social versus solitary species, would be useful in this regard. Another means to examine the link

between cooperation and inequity aversion has been to establish whether inequitable outcomes directly influence the success of cooperation. To do so requires studies in which resource distributions can be manipulated or controlled; thus, while ecological valid measurements in the wild are important, the available evidence derived from controlled experimental tests of cooperation must also be considered.

### The Influence of Inequity on Cooperation in Nonhumans

As discussed above, inequity aversion is hypothesized to help maintain cooperation by enabling organisms to do one or more of the following: (i) disengage from collaborating with those from whom they receive unfair returns, (ii) encourage more equitable future gains by choosing equitable partners, (iii) encourage future cooperation by distributing rewards in an equitable manner, and (iv) manage their reputation as a fair partner by rejecting unequal but beneficial gains. We have previously described how humans readily distribute rewards equitably following collaboration, select fair or generous partners, and will sometimes reject advantageous inequitable rewards. In this section, we consider whether inequity aversion constitutes a key mechanism supporting long-term cooperation in nonhumans by focusing on each of these predictions.

Studies of inequity aversion show that some individuals are less likely to participate in tasks when they receive unfavorable outcomes relative to a social partner. Inequity tasks, however, do not require cooperation between partners, which is a key component of this hypothesis. As a result, additional work has been done focusing explicitly on cooperation and reciprocity. In one such study, Brosnan et al. (2006) designed methods to directly test the assumption that unequal rewards influence levels of cooperation. Pairs of capuchins could perform a joint action (pull in a counterweighted tray) to gain rewards that were either equitable or inequitable. Key to this study was that participants, who were co-housed in the same enclosure, had to decide who worked for each reward. Thus,

conflict could arise over the unequal resources. The authors found that when a dominant partner “unfairly” benefited by monopolizing the better reward, cooperation tended to break down. Indeed, cooperation rates when partners took turns in gaining the better reward were two to three times higher than when dominants monopolized the better outcomes, and cooperation with unfair partners broke down even in control tests in which rewards were equal. What this research suggests is that capuchins will cooperate over long periods even when short-term rewards are unequal as long as each partner is willing to “play fair” over the long term, yielding (roughly) equitable gains to both partners overall.

Similar findings have been documented in chimpanzees; they select partners based on their previous history of tolerant sharing (Melis et al. 2006), reduce their cooperation when rewards can be monopolized by dominant individuals (Hare et al. 2007), and, when not cooperating with kin, prefer to work with partners of similar rank, who are presumably more socially tolerant partners (Suchak et al. 2014). These findings indicate that some primates remedy inequity through partner selectivity, that is, by not working collaboratively when resources are or can be monopolized and/or by taking turns gaining the beneficial but inequitable outcome of collaboration. Thus, there is some support for the predictions that inequity aversion may result in (i) leaving collaborators that take more than their share, (ii) using partner choice to manage future gains, and possibly even (iii) distributing rewards in an equitable manner to promote cooperation between individuals (i.e., capuchins taking turns to gain the best reward).

The last prediction indicates that inequity aversion may aid cooperation when individuals reject inequitable, but beneficial, outcomes (i.e., advantageous inequity aversion), perhaps encouraging future reciprocity or gaining a good reputation to attract future partners by establishing oneself as a fair partner. Interestingly, while in no study to date have monkeys minded options that reward themselves more than a partner, one study documented chimpanzees rejecting a preferred food when a partner received a non-preferred food (i.e., advantageous inequity aversion), albeit at a *much* lower

rate than they rejected a less preferred food when a partner received a more preferred food (reviewed in Brosnan and de Waal 2014).

Researchers have also tested nonhuman primates on the ultimatum game. As in the human ultimatum game described above, two individuals are assigned the “proposer” and “responder” roles. The proposer offers some of the resources to the responder, who can accept the offer, in which case each receives the rewards set out by the proposer, or reject the offer, in which case neither receives anything. Interestingly, as would be predicted by game theory, chimpanzees appear to accept any non-zero reward offers, suggesting they are rational maximizers (Jensen et al. 2007; Proctor et al. 2013). This is unlike humans, who will reject offers below around 20% of the endowment. Chimpanzee proposers, on the other hand, make both fair (Proctor et al. 2013) and selfish offers (Jensen et al. 2007). In one study, proposers did not make the fair offer to their partners (Jensen et al. 2007); however, these chimpanzees also showed the costly behavior of delivering zero rewards to their partner, which had high rejection rates (44%), despite the availability of a second self-serving option that was only rejected by their partners 14% of the time. This, coupled with responders’ rejection of zero offers on only 44% of trials, suggests that the chimpanzees only had a limited understanding of this task. In a more recent version, chimpanzees did prefer fair offers in the ultimatum game more so than in a preference test that was similar to a dictator game (Proctor et al. 2013). Key to this study was that fair reward options were favored only when partner chimpanzees had recourse to reject offers (i.e., the ultimatum condition), whereas selfish offers were favored when partners had no such ability (i.e., the dictator analogue), suggesting that the chimpanzees understood the procedure. Indeed, the lack of refusals by the responder may be logical in a repeated game with a known partner; rather than rejecting and ending the relationship, chimpanzees could protest and encourage the proposers to choose the more equal outcome. Therefore, even though the recipient will receive less on a few occasions, overall it is worth their while to continue the interaction (Proctor et al. 2013).

Further indication that chimpanzees may be sensitive to gaining more than conspecifics is a finding that chimpanzees, in a group situation, counterintuitively opt to follow the low-paying behavior of a dominant chimpanzee, despite the presence of a better-paying alternative (Hopper et al. 2011). The authors interpreted this as chimpanzees “conformity” to the low-paying behavior of the dominant chimpanzee (Hopper et al. 2011). An alternative explanation is that the selection of the low-paying behavior could be due to an aversion to advantageous inequity: perhaps the costs of receiving more than the model were too high to make it worthwhile to use the better option.

Research over the past two decades highlights the link between cooperation and inequity aversion. Further research is required to tease apart in which situations primates are indifferent versus being sensitive to others’ payoffs and how this is mediated by opportunities to cooperate, reciprocate rewards, and, in some cases, punish others or manage one’s reputation. Nonetheless, several studies now support the hypotheses that primates manage cooperation by leaving unfair collaborations and by being selective about which partners they choose. Less clear is whether nonhuman primates actively distribute rewards fairly (as could be the case of capuchins taking turns to gain the best reward) and, related to this, the degree to which any nonhuman species routinely shows refusal of unfair but beneficial personal gains. These qualities might constitute notable species differences between humans and other primates, as may other cognitive abilities (i.e., inhibiting one’s desire to accept the better reward or planning for future interactions).

## The Evolution of Fairness

Inequity aversion has been found in diverse species, including rats, dogs and wolves, some birds, and primates. The comparative literature has provided important insights into the evolution of the human sense of fairness. Knowing that inequity aversion has evolved in these diverse taxa

indicates that convergence, rather than evolution through common descent, has been at play. Researchers have also now established that a sense of fairness can take different forms, and while disadvantageous inequity appears more widespread across taxa, advantageous inequity aversion is extremely rare. Indeed, even among humans, disadvantageous inequity aversion appears to be both more widespread and to develop at an earlier age, indicating a strong biological influence. Species found to have both forms of inequity aversion come close to having the “complete” sense of fairness seen in humans. Of course, humans’ sense of fairness entails other aspects that are likely not present in other species, such as explicit group norms of behavior. How humans’ advanced sense of fairness, which requires advanced cognition and emotional control, arose during the course of our evolution remains a significant question for science. Nonetheless, one explanation consistent with the current evidence is that fairness coevolved with cooperation with non-kin, and functions to help individuals maintain beneficial cooperative relationships. It is clear that individuals benefit from leaving partnerships in which they routinely get less than the partner, but they may also benefit from declining an unfair advantage. By paying the short-term costs of rejecting an unfairly advantageous outcome, individuals signal to their partner (and potentially to others) that they value the partner. If they can ameliorate their partner’s frustration, the long-term relationship can continue (see Brosnan and de Waal 2014). Humans, with our exceptional abilities at delay of gratification and planning for the future, inhibition, and understanding of others’ thoughts and feelings (i.e., theory of mind), were able to take these roots and develop the full-blow sense of fairness seen in humans today.

## Cross-References

- [Cooperation](#)
- [Dictator Game](#)
- [Game Theory](#)
- [Ultimatum Game](#)

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## Infant Depression

### ► Anaclitic Depression

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## Infanticide

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## Definition

The act of killing a young offspring who is usually dependent and vulnerable.

## Introduction

Across the animal kingdom, there are cases of infants being targeted for murder by parents or unrelated individuals. Although the killing of a young seems counterintuitive since it puts an end to the genetic lineage, there might be an evolutionary explanation for this behavior in animals. Infanticide is costly, particularly for the parent that has invested greatly into rearing and taking care of their offspring, and of course, it is fatal for the infant. This article will go over the main hypotheses for why infanticide occurs among animals and highlight some counterstrategies that have evolved to prevent infanticide.

## Hypotheses for the Role of Infanticide

One explanation for infanticide is that it is non-adaptive, meaning it is not providing any benefits to the perpetrator (Ebensperger 1998). Infanticide could occur when group members are being overly aggressive and since infants are less able to defend themselves; they are more likely to be injured or killed. For example, during intense male-male competition for mating access, infants might accidentally get caught in harm's way and die. In other words, perpetrators are not purposefully killing infants for fitness gains; therefore, infanticide is nonadaptive. Although there are always cases of accidental deaths in the wild, the prevalence and pattern of infanticide suggest that it is not simply a "one-off" phenomenon but serves an evolutionary purpose. Therefore, the next three hypotheses offer adaptive explanations for infanticide.

The predation hypothesis states that infants are killed to provide nutritional gains; infants are killed and then consumed as a food source (Hrdy 1979). This hypothesis could be used to explain cases of interspecific and nonparental infanticide where predators choose infants as easy targets to capture and feed on. It has been found that the frequency of infanticide and cannibalism increase when food is scarce, thus further supporting the predation hypothesis. If the perpetrators are the parents, then the benefits gained from consuming the infant should outweigh the costs of losing an offspring for this behavior to persist.

The resource competition hypothesis states that infants are killed to eliminate a competitor for access to physical resources such as food and space (Hrdy 1979). By killing an infant, the perpetrator can then have more of these resources for themselves and/or their own offspring. Parental infanticide can be a strategy by the parent to downsize their litter so there is less competition for limited resources and a greater investment per infant – quality over quantity. There is more support for the resource competition hypothesis in cases of nonparental infanticide. For example, in a coterie of black-tailed prairie dogs (*Cynomys ludovicianus*), lactating females were the most common perpetrators of infanticide and their

victims were the offspring of close kin (Hoogland 1985). Infanticide was not always followed by cannibalism, so this does not satisfy the predation hypothesis, but the resource competition hypothesis offers a compelling explanation. Lactating females are getting rid of future competitors so that both her and her offspring will have more access to resources. The most common examples of infanticide in mammalian species are when invading males kill unrelated infants in the group. Invading males are removing competitors from the group so that they will not compete for resources or challenge their dominance in the future.

Hrdy (1979) proposed the sexual selection hypothesis to justify the sex-biased occurrences of infanticide since the majority of observed cases were male-inflicted. This hypothesis states that infanticide is a male adaptive strategy. Males kill unrelated infants to eliminate other males' progeny and potential mating competitors and by doing so, increase their own chances of reproductive success. Indeed, most cases of infanticide are nonparental; the perpetrator is targeting infants that are not likely to be related to them. In addition, the interbirth interval of females often gets shortened if she loses her offspring, which makes her sexually receptive to mate again. In Hanuman langurs (*Presbytis entellus*), infanticide was most common after the resident alpha male had been ousted by a new male (Borries and Koenig 2000). In addition, females that just lost their infants had shorter interbirth intervals and the perpetrator subsequently sired their next infants (Borries and Koenig 2000). This example demonstrates that there is a reproductive advantage for the males to kill unrelated infants, thus, adding support for the sexual selection hypothesis. Phylogenetic analyses of mammalian species have shown that infanticide is more likely to occur in species where females are able to breed throughout the year (Lukas and Huchard 2014). Selection pressure favors infanticide only when the mother is able to be sexually receptive following the infant's death, therefore, the male perpetrator is gaining reproductive advantage.

In mammals especially, the female has invested tremendous time and energy into rearing and

caring for her offspring, which makes infanticide extremely costly. Therefore, a sexual conflict arises whereby males want to increase their reproductive fitness by killing unrelated infants while females want to increase their reproductive fitness by keeping their infants alive. This conflict of interest creates an evolutionary arms race between the sexes which result in the development of counterstrategies.

## Counterstrategies to Infanticide

One female counterstrategy to prevent infanticide is to actively defend her infants from male aggressors. Oftentimes, the male that sired the infant will also defend against the attacker since it is in his best interest to protect his young. Females will sometimes join together to attack infanticidal males, and this has proven to be successful in lions (*Panthera leo*) (Packer and Pusey 1983). There is strength in numbers and one benefit of forming social bonds in a group is that members can come to each other's defense during times of need. A second counterstrategy is to avoid infanticidal males. As discussed above, infanticide is common following the takeover of a group by a new male. During these takeovers, mothers can leave the group with their offspring, either temporarily or permanently. Once her infants have become independent, then the mother may choose to return to the group where risk of death for her offspring has decreased. Another female counterstrategy is sexual promiscuity, where a female will mate with multiple males to confuse paternity and lower the chances of her infant being targeted (Hrdy 1979). Since any one of the males she mated with could have sired the offspring, they should not risk killing their own infant. Females sometimes display "pseudo-estrous" where they continue to mate even after conception. This behavior has no obvious benefits to the female other than to confuse paternity. Finally, the last counterstrategy is actually an effort on the infant's part to prevent infanticide, and that is accelerated infant development. Ursine colobus infants (*Colobus vellerosus*) have a distinct white natal coat that makes them extremely

susceptible targets by infanticidal males. Male infants, who are targeted more often since they pose a greater threat as future competitors, transitioned from white to grey earlier than female infants (Bădescu et al. 2016). Accelerated infant development may have evolved as a counterstrategy to infanticide.

## Conclusion

Infanticide could be a nonadaptive behavior with no benefits for the individuals involved. However, there is strong support for adaptive explanations of infanticide, such as for nutritional gains, less resource competition, and increased male reproductive success. Counterstrategies have also evolved to prevent infanticide, such as parental defence, avoidance of infanticidal males, female sexual promiscuity, and accelerated infant development. There is evidence to support and refute each of the hypotheses presented; nevertheless, it is imperative to continue to investigate why this behavior has persisted in a variety of animal taxa.

## Cross-References

- ▶ [Aggression](#)
- ▶ [Avoidance](#)
- ▶ [Cannibalism](#)
- ▶ [Competition](#)
- ▶ [Parental Investment](#)
- ▶ [Promiscuity](#)
- ▶ [Reproductive Fitness](#)
- ▶ [Sexual Selection](#)

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## Infectious Agent

- [Pathogen](#)

## Infectious Particle

- [Pathogen](#)

## Inference by Exclusion

- [Reasoning by Exclusion](#)

## Inferior Temporal Cortex

- [Delay Neurons: Comparative Overview](#)

## Infidelity

- [Extra-Pair Copulation](#)

## Information Processing

- [Plantae](#)
- [Top-Down Processing](#)

## Information Theory

- [Insect Communication](#)

## Information Transmission

- [Insect Communication](#)

## Informational RNA

- [Messenger RNA](#)

## Information-Based Approach

- [Perception-Action Theory](#)
- [Social Affordance](#)

## In-Group

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## Synonyms

[Intragroup](#); [Within-group](#)

## Definition

An in-group is a social category or group with which one strongly identifies with (Kurylo 2013, p. 141).

## Introduction

A well-studied area within animal cognition is that of in-group biases, or as it is sometimes called,

favoritism. These biases can be described as within-group members cooperating more strongly together than with outgroup members (Masuda and Fu 2015). This affects behavior in several species of animals, including birds, chimpanzees, and fish (Campbell and de Waal 2011; Gallup et al. 2017; Palagi et al. 2009). Three of the most common in-group behaviors are affiliation, aggression, and cooperation. These behaviors are often affected by other behaviors and situations that occur both inside and outside of the group (Asensio et al. 2008; Boesch 1994; Brintjes et al. 2016; Heinsohn and Packer 1995; Radford 2011; Risenhoover and Bailey 1985; Southwick 1967).

Affiliative behaviors altered by cognitive biases include grooming, stretching, and yawning (Campbell and de Waal 2011; Gallup et al. 2017; Palagi et al. 2009). Chimpanzees, baboons, and birds will often increase these behaviors when exposed to members of their own in-group through videos or in physical proximity. For example, birds exhibit increased stretching when around other group members. In chimpanzees, contagious yawns are more frequent when they see a member from their own group. For baboons, contagious yawning and grooming increase when the animals are socially near their own group. Grooming is also considered an affiliative behavior among species of birds when an outgroup threat is present (Brintjes et al. 2016; Radford 2011). In both cases, whether the outgroup threat is a physical altercation or just a threat, affiliation will increase. In birds, grooming of another in-group member increases after an out-group threat. The grooming will also occur for longer periods of time if the out-group threat is located within close proximity. In fish, affiliative behaviors also occur, but not grooming. Instead, soft touching and parallel swimming occur more frequently after a physical altercation with an outgroup member.

Aggression is frequently seen among group members, as well. The size of the group can determine whether the aggressive behavior increases or decreases. Studies examining the relationship between group size and aggression all agree the two variables are related, but how they are related differs (Asensio et al. 2008; Risenhoover and

Bailey 1985). In mountain goats, aggression tends to decrease when the animal group increases in size. However, in spider monkeys, aggressive behavior will increase as the group becomes larger. Aggression is also more frequent when there are new members introduced into the group. This behavior can be exhibited in both rhesus monkeys and spider monkeys. These new members will initiate aggressive behavior in members because of their group status (Asensio et al. 2008; Southwick 1967).

Finally, group members participate in situation-specific cooperative behaviors with their group members. Specifically, cooperation affects tolerance to group members with regard to hunting and territorial defense (Boesch 1994; Heinsohn and Packer 1995). Lions and chimpanzees surprisingly tolerate members who do not cooperate with others in the group. In lions, those who do not take part in the cooperation of defending territory are not always punished by those who do. The same behavior can be exhibited in chimpanzees when certain members do not participate in hunting for food. Group members do not always receive consequences from others when they eat the food without hunting. Specifically, chimpanzees who participate in the hunting will tolerate these “cheaters” more if they are related to them. This shows how kinship also has an effect on these cooperative behaviors.

## Future Directions and Conclusions

These findings illustrate how in-group biases affect affiliative, aggressive, and cooperative behaviors in the animal kingdom. Future research ought to investigate the relevant functions and mechanisms of these biases to better understand the underpinnings of social evolution. As a whole, this research shows how and when in-group bias and various in-group behaviors are exhibited among different animal groups, as they are in humans. Together, these behaviors show the favoritism and benefits extended toward members of one's group; continued exploration will help researchers better understand the effects of these biases and behaviors.



## Cross-References

- [Affiliative Behaviors](#)
- [Agonistic Behavior](#)
- [Contagious Yawning](#)
- [Cooperation](#)
- [Grooming](#)
- [Social Grooming](#)

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## Inhibition

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## Synonyms

[Behavioral control](#); [Impulse control](#); [Self-control](#); [Suppression](#)

## Definition

Inhibition refers to an individual's ability to halt their behavior and control an urge to do something that is tempting; ultimately, suppressing this behavior allows individuals to try a new behavior or response that may be more effective.

## Introduction

Inhibitory mechanisms lie within the frontal lobe of the brain. Impulses can be overridden by higher order control processes when an individual has inhibitory control. Inhibitory control involves an active process in which subjects execute cognitive control over responses, stimuli, and tasks by inhibiting them (Aron 2007).

Inhibitory control has evolved in a variety of species for adaptive responses in different contexts. In humans, inhibition control is defined as an ability to stop an immediate but disadvantageous behavior in exchange for a more favorable one. Human research has focused on two types of inhibition: cognitive and motor. Cognitive inhibition is the ability to regulate actions that are irrelevant to the task at hand. Motor inhibition is the regulation of physical responses or behaviors. Research on motor control has measured inhibition with tasks and questionnaires. Inhibitory control in humans is heritable (Bezdjian et al. 2011) and has been associated with wealth, health, and public safety (Moffitt et al. 2011), addictions (Fillmore and Vogel-Sprott 1999), anxiety and stress (Falconer et al. 2008;

Hardin et al. 2009), obesity (Hofmann et al. 2009), and eating disorders (Jasinska et al. 2012).

Animals have also evolved inhibitory control, but species differences are dependent upon the context. Animals exhibit inhibition towards novelty, food, aggressive behaviors, sexual behaviors, and displays. For example, wolf packs show restraint in pouncing behavior, and in their mating behaviors; the pack works cohesively and at length to hunt together, while also supporting only the alphas in sexual reproduction and offspring rearing. Similarly, frugivorous species must wait until the fruit ripens before eating, while juvenile males in many species must refrain from mating with females with the ominous threat of dominant alphas. In animals, cognitive inhibition is associated with general intelligence (Beran and Hopkins 2018), problem-solving (Müller et al. 2016), behavioral flexibility (Amici et al. 2008), reproductive success (Boogert et al. 2011), cooperation (Burkart and Van Schaik 2010), inequity aversion (Brucks et al. 2017b), persistency, compulsivity, and decision speed (Brucks et al. 2017a).

Overall, the driving forces behind the evolution of cognitive abilities are a mystery. However, previous research has sought to measure cognitive skills in closely related species in an attempt to pin the underlying drivers. Variation in the ecology and sociality between species are separate and predominant theories in cognitive evolution. As such, researchers have found that inhibitory control is more pronounced in social groups (Amici et al. 2008), and has a high prevalence in fission-fusion groups, as opposed to cohesive groups (Aureli et al. 2008). In addition, across species, absolute brain size and dietary breadth predict cognitive performance on inhibitory tasks (MacLean et al. 2014). These studies support both theories; ecology and sociality place pressure on the evolution of cognitive skills, specifically inhibition.

## Examples

Different approaches have sought to measure inhibitory control abilities in a variety of species.

The following tasks have been used in different species to assess inhibition.

**Detour Task.** This task presents an individual with an object that houses a reward. The direct route to the reward is blocked and a longer detour is necessary in order to obtain the reward. There are two types of detour tasks: continuously visible and initially visible. Continuously visible are those in which the reward is always in sight. Initially visible detour tasks are those in which the reward disappears from sight after the initial start. Success at this task exemplifies inhibition; individuals are using their cognitive toolbox to take the less obvious route to retrieve the reward. For example, two groups of sheep were tested on a cylinder task (Knolle et al. 2019). The opaque cylinder is open at the end, and a reward is placed inside. Success occurs when the sheep retrieved the reward at the open end of the cylinder. Failure occurred when the sheep physically touched the clear exterior of the cylinder before retrieving the reward. Sheep performed significantly better than chance, with younger sheep performing the best. This suggests that sheep were able to inhibit their desire to approach the clear barrier, and instead move further to retrieve the reward from the opening (Knolle et al. 2019).

**Delay of Gratification/Impulse Control.** Subjects are presented with a small, immediate food reward. If they take the food reward, the trial is over. If they wait a certain amount of time, they are presented a larger and more enticing food reward. The time delay grows throughout trials to encourage animals to inhibit the urge to take the immediate food reward. This task mimics foraging decision for animals in the wild. Most famously, researchers provided children with a delayed reward task. Children were given the option of taking a smaller, less preferred reward, or waiting for a larger, more valuable reward. When given the opportunity to wait out of sight from the smaller reward, children were able to control their impulse and receive a larger reward (Mischel and Ebbsen 1970).

**Object Displacement.** This test consisted of a presentation of multiple containers. Initially, the containers are empty and visually available to the subjects. Then, the containers are baited in

full view of subjects and closed. Subjects are allowed to select all containers with food, unless they choose an empty container on their first try. Food reward can be moved into different containers, containers can be shifted around after food placement, and containers can vary in physical proximity to subject. Inhibitory control encourages subjects to select only those containers with food, regardless of proximity, or prior trial placement. In a 2001 study by Josep Call, orangutans, chimpanzees, and human children received visible and invisible displacements with species-specific rewards. Across species, subjects were able to correctly select visible displacements, but more likely to select the empty container when it was physically closer, suggesting poor inhibition (Call 2001).

**Object Permanence/A-not-B Task.** This task is based on work by Jean Piaget (1954). A reward is hidden under box “A” for several consecutive trials. The subject forms an association between box “A” and the reward. After several rounds of success, the reward is moved under box “B” in sight of the subject. Inhibitory control encourages the subject to move past the previous association and select box “B” for the reward. Selection of box “A” demonstrates a lack of object permanence. Bray, MacLean, and Hare measured inhibitory control using an A-not-B task in dogs. After observing the food reward moving from “A” to “B,” the dogs were encouraged to inhibit searching in “A” in favor of “B” (Bray et al. 2014). A majority of the dogs were successful in choosing the “B” location, suggesting that they were able to inhibit their urge to attend to “A” (Bray et al. 2014).

**Multiaccess Box.** This box presents multiple solutions to a central reward. Each solution requires a different behavioral repertoire. Initially, the subject is permitted to choose any of the options. Upon success, that solution is then locked. The locking of different solutions encourages innovation and requires inhibition of previously solved, now locked solutions. Auersperg and colleagues developed the multiaccess box, or MAB, to test kea and New Caledonian crows (Auersperg et al. 2011). Both species were able to solve more than one solution,

suggesting the cognitive ability to inhibit extinguished responses (Auersperg et al. 2011).

**Serial-Reversal-Learning.** Subjects are taught to respond to multiple stimuli. When success in response is achieved, the reward contingencies are reversed. So, the reward associated with the first stimuli is now associated with the second stimuli, and vice versa. This alternation can be repeated, and changed from 2-choice discriminations, to multichoice discriminations. In a serial-reversal-learning task of dogs, researchers found that dogs were able to inhibit their learned behavior of the previously rewarded object, and choose the previously unpaired stimuli (Brucks et al. 2017). This suggests that inhibitory control is present and provides an evolutionary advantage in food association and learning (Brucks et al. 2017).

**Social Inhibition.** In a social inhibition task, subjects are taught to differentiate between a generous and a stingy experimenter or conspecific. The generous experimenter always shared the food or reward, whereas the stingy experimenter never shared the food or reward. This experiment could potentially reverse the roles of the stingy and generous experiments. Researchers presented evidence that dogs were able to exhibit inhibitory control as they avoided the stingy experimenter, even when the experimenter held a higher value food (Bray et al. 2014). This presents evidence that inhibitory control is important in social contexts when discriminating between conspecifics, or heterospecifics.

**Stop-Signal Task.** This task was developed in 1984 by Logan and Cowan. It asks the participants to inhibit prepotent responses. The participant initially responds quickly to a predetermined, pretrained stimulus. However, they are also required to stop responding when a stop signal stimulus is displayed. For example, a participant may respond to the stimulus until they observe the stop signal; at this point, all further responding should stop. If they are presented with the stop signal first, they should not respond to the subsequent stimuli. Success is inhibiting the desire to attend to the stimulus after the stop signal display. Honeybees naturally produce stop signals (Nieh 1993). When the

colony's food stores are full of nectar, foraging bees will spend a long time searching for an open storage spot (Nieh 1993). They then begin to tremble dance which signals a stoppage of dancing, reduced recruitment to feeding sites, and increased the colony's nectar intake rate by stimulating bees to function as food-storage bees (Nieh 1993).

**Stroop Task.** This task was first presented in 1935 and measures interference, inhibition, and processing speed (Stroop). This task for humans asks subjects to name the color of the word presented to them. For example, the word green will be printed. In a congruent trial, the word green is the color green, and as such, the subject selects green. In an incongruent trial, the word blue is the color red. To be correct, the subject should select red; failure would be selecting blue. The Stroop effect is the increase in time it takes to inhibit the urge to select blue when the correct answer is red. Response inhibition on this task has been associated with alcohol consumption. More than 500 participants were tested on a Stroop task (Peeters et al. 2015). Their ability to successfully inhibit incorrect responses predicted the initiating of the first drink (Peeters et al. 2015). These results suggest that inhibitory control in humans may predict alcohol use (Peeters et al. 2015).

**Reversed Contingency.** In this task, subjects are given a choice between a smaller quantity, lesser valued food, and a larger quantity, higher valued food. The subjects received the opposite food reward of the one they chose. For example, most subjects would choose the larger quantity, but receive the smaller quantity. In a reversed-contingency task, rhesus macaques were given the option between one and four pieces of food (Murray et al. 2005). All subjects initially selected the larger quantity and received the smaller amount (Murray et al. 2005). However, the monkeys learned to choose the smaller amount, exhibiting inhibitory control and learning of the reversed-contingency task (Murray et al. 2005).

## Conclusion

Challenges in each species' environment encourage the evolution of cognitive mechanisms.

Inhibition is a behavioral skill that is crucial for behavioral flexibility and appropriate decision making. Inhibitory control suggests a high level of cognitive awareness in various species as demonstrated by different tasks. As such, inhibitory control may be context-specific and even vary in individual performances.

## Cross-References

- ▶ [A-Not-B Problem](#)
- ▶ [Behavioral Variation](#)
- ▶ [Cognition](#)
- ▶ [Conditioned Inhibition](#)
- ▶ [Inhibition of Delay](#)
- ▶ [Innovation](#)
- ▶ [Problem-Solving](#)
- ▶ [Reversal Learning](#)

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## Inhibition of Delay

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## Synonyms

Long-delay conditioning

## Definition

A delay in the peak of a conditioned response (CR) across the duration of a (usually) long conditioned stimulus (CS).

## Introduction

In the classical conditioning paradigm, presentation of a stimulus (e.g., a tone) is paired with presentation of an unconditioned stimulus (US, e.g., food). These pairings usually result in the stimulus coming to elicit a response (e.g., salivation); that is, the previously neutral stimulus becomes a conditioned stimulus (CS) which can elicit a conditioned response (CR). In the most common arrangement, known as *delay conditioning*, the CS onset occurs shortly before US delivery, and the CR develops as

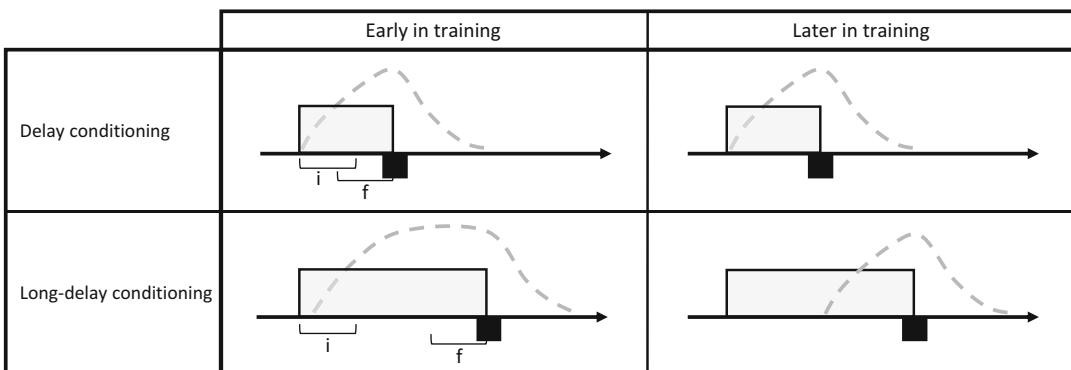


an anticipatory response triggered by the CS in preparation for the US. In general, one may assume that subjects come to respond to the CS as a unitary event; however, if the CS has a long duration, the CR onset may be delayed, peaking during the temporal segments of the CS presentation that are most contiguous with the US. Thus, rather than eliciting a response through its entire duration, the CS elicits little to no responding during its initial segments and robust responding during its final segments (a “segment” is any portion or subunit of the stimulus unit, defined by its temporal characteristics; see Fig. 1). Because this procedure is a variation of the commonly used delay conditioning procedure, with exception of the longer duration CS, inhibition of delay is also known as *long-delay conditioning*.

Pavlov (1927) described several studies in which a long CS produced a pattern of response with the CR developing progressively, being unobservable during the initial presentation of the CS and gradually increasing as time of US delivery approached. Figure 1 presents a graphic representation of the inhibition of delay (long-delay conditioning) procedure and some of its primary characteristics, which will be discussed in subsequent sections.

Characteristics and Parameters

Inhibition of delay has three primary characteristics: (1) a progressive reduction in the CR elicited by the early portion of the CS, (2) a CR that is progressively confined to the later portion of the CS, and (3) the capacity of the early segment of the CS to attenuate the CR that another stimulus would otherwise elicit (Rescorla 1967). Inhibition of delay has been reported in a variety of species including cats (e.g., Oleson et al. 1973), dogs (e.g., Pavlov 1927; Rescorla 1967), rabbits (e.g., Vogel 2012), and rats (e.g., Brush and Gendron 1998; Escobar et al. 2015; Schachtman et al. 1987), using a variety of stimuli, including auditory, visual, and tactile with a variety of durations (see Pavlov 1927, for a review). Late peaks of CR occur when the US is an appetitive event such as food (e.g., Pavlov 1927) or sugar (e.g., Escobar et al. 2015) or when the US is an aversive event such as a shock (e.g., Rescorla 1967; Vogel 2012). Finally, inhibition of delay can be observed in multiple response systems, including the salivation reflex (Pavlov 1927), goal-tracking responses (Escobar et al. 2015), avoidance responses (Rescorla 1967), the pupillary reflex (Oleson et al. 1973), conditioned freezing (Schachtman et al. 1987), and the blinking reflex (Vogel 2012).



**Inhibition of Delay, Fig. 1** Comparison of the typical delay and long-delay conditioning procedures. *Arrows* represent the time line, *gray boxes* above the time line represent CS presentation, and *black marks* under the time line represent US delivery. Early in training, both short and long CSs produce CRs (*dotted gray line*) that are elicited through the duration of the CS and for a time period following CS termination. Later in training,

however, CR elicitation in the long CS is no longer evident in its initial segment (*i*), starting late and peaking during its final segment (*f*). Likely because of the close proximity and overlap of the initial and final segments of the short CS, the peak of the CR changes little throughout training. The shift of the peak of the CR toward the final segment of the long-delay CS reflects the occurrence of inhibition of delay

## What Is Learned During Inhibition of Delay?

Pavlov (1927) described conditioning through the duration of a long-delay CS as having two phases. During the initial phase, the *inactivity phase*, little responding should be observed; in contrast, during the final *activity phase*, robust responding should be observed. The transition between the inactivity and activity phases was not abrupt; the CR would increase in strength gradually until peaking during the final, activity, phase. Based on these observations, Pavlov suggested two possible explanations for the observed lack of responding during the inactivity phase. First, during the initial phase, the strength of the CR could be accumulating or summing, such that when it reaches enough strength, it is finally elicited. He rejected this possibility because if the same stimulus is used, but with a shorter duration, the CR is robust and occurs almost simultaneously with the presentation of the CS (it would be unlikely that simply by extending the CS duration, a different summation rule would need to apply to elicit a CR). Second, an antagonistic (i.e., opposite) process could be operating during the initial phase, such that any CR that could be potentially elicited by the CS is overcome by it. The candidate process would be *inhibition*, a type of learning in which the presence of the CS comes to predict the absence of an otherwise expected US. Pavlov's observations led to the conclusion that the long delay resulted in *internal inhibition* processes that mask the CR. He supported this view with multiple observations. First, presentation of an irrelevant stimulus disrupted the inactivity phase and "unmasked" the CR. This is known as *external disinhibition*, the observation that a stimulus external to the situation can disrupt the inhibitory process that masks the response. Second, if a short CS that elicited a strong CR was presented during the initial phase of the long-delay CS, responding to the short CS was attenuated. This is known as *negative summation* and reflects the observation that a stimulus that has acquired inhibitory properties can transfer those properties to other stimuli that elicit CRs (known as *excitatory stimuli*).

Rescorla (1967) trained dogs to perform an avoidance task, in which presentation of a long CS was followed by delivery of a foot shock (US) to one of the compartments of a shuttle box. The dogs could escape the US by jumping over a barrier that separated the shock compartment from a "safe" compartment. The dogs could avoid the shock by jumping over the barrier immediately following the CS onset. Rescorla observed that the dogs produced the avoidance response late in the CS presentation, and the initial phase of the CS attenuated the fear responses otherwise exhibited by the dogs when placed in the shuttle box (i.e., negative summation). Thus, Rescorla's studies supported Pavlov's view that long-delay conditioning resulted in a form of inhibitory learning, *inhibition of delay*. A problem with this interpretation is that *inhibitory conditioning* is a process that cannot be easily measured directly (e.g., if a dog does not salivate when presented with a sound, is it because conditioning has not occurred or because an inhibitory process has developed?).

The standard assessment of conditioned inhibition involves the concurrent use of two indirect tests: the *negative summation test* which, as described above, involves determining whether the inhibitor can prevent the response otherwise produced by an excitor, and the *retardation test* which assesses the rate of acquisition of the CR to a potential inhibitor. A potential problem with the summation test is that decreased CR to the excitor could be explained in terms of the inhibitor capturing the animal's attention. A potential problem with the retardation test is that slow rates of acquisition could be explained in terms of the inhibitor being ignored by the subject. Rescorla (1969) suggested that each test could be used to control for the other's alternative explanation if used in conjunction: A stimulus that commands increased attention cannot be ignored. Because animals cannot attend and ignore a stimulus at the same time, the use of both tests (the *two-test strategy*) has become the standard procedure to assess whether a stimulus is inhibitory. Escobar et al. (2015) used the two-test strategy in a study in which rats experienced a long CS that predicted sugar pellet delivery. When the peak of the CR was firmly

established in the final portion of the CS, either a second CS that predicted sugar delivery in its initial portion was presented together with the long-delay CS (summation test) or pellets were delivered during the initial portion of the long-delay CS to assess the development of an excitatory response (retardation test). The initial portion of the CS was slow in becoming excitatory (i.e., retardation), but it failed to attenuate the CR produced by the second CS (i.e., no summation). Thus, long-delay CSs can exhibit inhibitory properties during their initial segment as assessed with either a summation or a retardation test but, to date, no study has demonstrated such inhibitory properties within a single preparation.

Despite these seemingly conflicting results, Pavlov's (cf. 1927) explanation continues to be the most accepted view of inhibition of delay: Excitation (response production) develops early to the entire CS duration, but inhibition (response suppression) develops over training to the portion of the CS that is more distal from the US, eventually overcoming excitation (see Fig. 1). Vogel (2012) assessed this possibility by training rabbits in a preparation in which a long-delay CS signaled the presentation of a mild shock US delivered to the subjects' eyelid. As training progressed, rabbits began to blink in anticipation of the US, and this blinking became confined to the later portion of the CS (i.e., inhibition of delay). Presentation of a novel stimulus immediately prior to CS onset changed the peak of the CR to an earlier portion of the CS, suggesting some "hidden" excitation in the early portion of the CS, which was unmasked by the novel stimulus.

## Theoretical Explanations of Inhibition of Delay

The main challenge to providing a theoretical explanation of inhibition of delay is that CSs are typically regarded as unitary entities that acquire a value as predictors of the US. However, although parsimonious, this perspective ignores the fact that organisms learn not only about the physical properties of a stimulus but also about the temporal characteristics that define that stimulus

(e.g., Arcediano and Miller 2002). Indeed, different portions of a stimulus have different characteristics. For example, the onset of a stimulus is accompanied by a state change in which the absent stimulus is now present, whereas the termination of a stimulus is accompanied by a state change in which the present stimulus becomes absent. The duration of a stimulus also has temporal characteristics (e.g., each instant occurs a given time after onset and a given time before termination). So-called *real-time theories* assume that learning is a continuous event in which each instant of an experience is a stimulus element that develops associations to other elements of the same stimulus and to elements of other stimuli experienced in close proximity; the pattern of activation resulting from all components of that experience is what determines the response. For example, Vogel et al. (2003) suggested that elements sampled during the final portion of the stimulus are very likely to be sampled together with elements of the US, whereas elements sampled during the initial portion of the stimulus are less likely to be sampled together with elements of the US. Thus, elements from the final portion of the stimulus will develop strong excitatory associations with the US. In contrast, elements from the initial portion of the stimulus will eventually develop inhibitory associations to the US because they are more often sampled apart than together. By viewing each stimulus as a collection of elements rather than a unitary event, componential models can easily accommodate the temporal displacement of the CR that is the hallmark of inhibition of delay.

## Conclusion

Inhibition of delay (long-delay conditioning) is a robust phenomenon that has been reported with a variety of species, stimuli, stimulus durations, and response systems. The behavioral characteristics of the phenomenon (a CR that progressively decreases in the initial segment of a long CS and peaks in the later segments of the CS) are well defined, but exactly why this pattern of behavior emerges is not clear. The most accepted view is

that the CS is initially excitatory but, with progressive training, the distal (initial) segment of the CS becomes inhibitory and this inhibitory process eventually overcomes the previously acquired excitation. Whether this inhibitory process is of the same nature as other forms of conditioned inhibition is still debated. However, it is clear that the phenomenon is consistent with the view that CSs are not unitary events and that the temporal characteristics of a CS can be as powerful determinants of the response it elicits as are its physical characteristics.

## Cross-References

- [Classical Conditioning](#)
- [Conditioned Inhibition](#)
- [Timing](#)

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## Inhibitory Avoidance

- [Passive Avoidance Learning](#)

## Injury-Feigning Behavior

- [Broken Wing Display](#)

## Innate Behaviors

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## Synonyms

[Instinct](#); [Kinesis](#); [Modal action patterns](#); [Reflexes](#); [Taxis](#)

## Definition

Innate behaviors are those behaviors that are genetically hardwired in an organism's behavioral repertoire. They are performed in response to very specific, environmental stimulation. They include reflexes, fixed or modal action patterns, taxis, and kinesis.

Behavior is classified into two broad, mutually exclusive categories: innate behaviors and instrumental (aka voluntary) behaviors. Innate behaviors are genetically determined and linked to a specific releaser stimulus in the environment. Most have apparent survival value and may even appear in neonates or the very young, while others may not appear until sexual maturity.

## Reflexes

Reflexes are observed in both human and non-human animals. They are involuntary, nearly

instantaneous responses to specific environmental stimuli called releaser stimuli. There are dozens of reflexes across species. In humans (and many other vertebrates), common examples include shivering, sneezing, coughing, and the startle response. Newborn humans have several primitive reflexes, such as rooting, sucking, and the palmar grasping reflex; some of these primitive reflexes disappear as the infant matures.

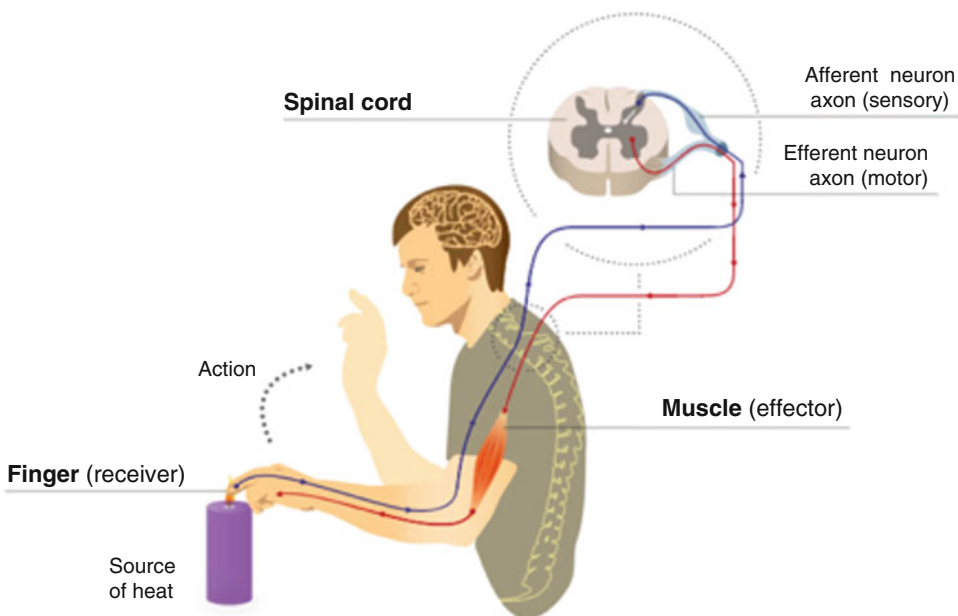
**Releaser stimuli.** All reflexes (and other innate behaviors) are elicited by very specific stimuli called releaser stimuli or sign stimuli. A releaser stimulus is defined as a feature of a more complex stimulus array that will provoke the reflex. For example, food caught in your throat that irritates the trachea elicits coughing; a tap on the patellar tendon causes a knee jerk, and light shined in the eye causes pupil constriction. There tends to be a direct, hard-wired relationship between a releaser stimulus and its corresponding reflex that is often mediated via the reflex arc.

The reflex arc is a neural pathway that controls reflexes (see Fig. 1). There are two types of reflex

arcs. The *autonomic reflex arc* is a chemically mediated process that regulates organ systems by maintaining homeostasis between the sympathetic and parasympathetic nervous system. It regulates systems like the heart, the lungs, and the digestive tract using smooth muscles. The *somatic reflex arc* controls bodily responses like the patellar reflex, or knee jerk, and the heat/pain withdrawal reflex. For a detailed biological explanation of autonomic and somatic reflex arcs, see Biga et al. (2018).

In most vertebrates, the *somatic reflex* does not require cerebral control of the circuit. Reflexive synapses occur in the peripheral nervous system (PNS), although additional signals to the brain via the central nervous system (CNS) do make us aware of the stimulus and the response. However, bypassing cerebral involvement allows for very fast responding. The speed of the reflex arc causes the analysis and awareness of the reflexive behavior to occur after the response has already occurred.

**The Somatic Reflex Arc.** Environmental stimulation is detected in the skin by sensory neurons,



**Innate Behaviors, Fig. 1** The reflex is mediated by the reflex arc. Environmental stimulation is detected by sensory neurons, called afferent neurons, which propagate a neural signal to the spinal cord. Inside the spinal cord, the afferent neuron the motor neuron, called the efferent

neuron. The motor neuron sends a signal to the muscles which contract and cause movement. Note that there is no required cerebral involvement. (Source: Wikimedia Commons. Reflex arc, Wikimedia commons. [https://commons.wikimedia.org/wiki/File:Img\\_arc\\_reflex\\_muda.svg](https://commons.wikimedia.org/wiki/File:Img_arc_reflex_muda.svg))



called *afferent neurons* that propagate neural signals to the *posterior horn* of the spinal cord (or to the brain stem). Inside the spinal cord, the afferent neuron stimulates an *interneuron* that in turn stimulates the motor neuron, called the *efferent neuron*. The motor neuron sends a signal from the *anterior horn* to the muscles that, in turn, cause the reflexive movement.

**Reflexes and Invertebrates.** Reflexes that are mitigated by the reflex arc, by definition, occur in most vertebrate animals, including mammals, birds, reptiles, bony and cartilaginous fishes, and amphibians. But some simple reflexes, such as limb or gill retraction in response to touch, or electrical stimulation have been shown to occur in certain invertebrates such as stickbugs (Bassler 1992), locusts (Seigler and Burrows 1986), aplysia (Cleary et al. 1995), and crayfish (Skorupski 1992). Watanabe and Mizunami (2007) demonstrated conditioning of the salivation reflex in cockroaches, using a procedure that mimicked Ivan Pavlov's early classical conditioning work with dogs. However, in the recent study, the dependent variable was the reflexive neural firing rate of the salivary neuron instead of a direct assessment of salivation. This was the first study to demonstrate conditioned salivation in insects.

## History of the Reflex

René Descartes, a French philosopher, scientist, and mathematician in the seventeenth century (see Fig. 2), first described *reflexes* as responses that reflected the stimuli that produced them. In his, *Discourse on the Method* (1637), Descartes suggested that the behavior of animals was purely mechanical. He was the first to propose the mechanisms that govern reflexes.

According to Descartes, some responses were initiated by stimuli in the physical world while others were initiated in the mind. He argued that animals and humans shared the involuntary, stimulus-based behaviors that he called *reflexes*. His explanation of the underlying mechanism of these responses was based on a simple sensory input/motor output system controlled by the environment, nerves, the brain, and the mind. *Animal*



**Innate Behaviors, Fig. 2** René Descartes (1596–1650). Philosopher, scientist, and mathematician. (Source: Wikimedia Commons. Rene Descartes, Frans Hals, Artist. Public Domain, Wikimedia Commons. [https://en.wikipedia.org/wiki/File:Frans\\_Hals\\_-\\_Portret\\_van\\_Ren%C3%A9\\_Descartes.jpg](https://en.wikipedia.org/wiki/File:Frans_Hals_-_Portret_van_Ren%C3%A9_Descartes.jpg))

*spirits* would then travel up tube-like nerves to the brain where the spirits would be reversed. The same spirits would eventually travel back down the same nerves and manifest as a motor response. Descartes argued that the same mechanism could be used to explain human reflexive behavior (see Fig. 3).

Descartes believed that animals were limited to involuntary, reflexive behavior; only humans exhibited willful, voluntary behaviors believed to have their origins in the mind – a nonphysical entity where consciousness was thought to reside. Via its connection to the pineal gland, the mind sent willful responses to the body using the same neural tubes. In this way, Descartes was able to employ the same mechanical system for humans while maintaining his mind-body, dualistic philosophy of man as being made in the image of God and separate from the animal kingdom.

Following in Descartes' footsteps, a number of physiologists, anatomists, and psychologists



**Innate Behaviors, Fig. 3** The Withdrawal Reflex. *For example, if the fire (A) is close to the foot (B), the small particles of fire, which as you know move very swiftly, are able to move as well the part of the skin which they touch on the foot. In this way, by pulling at the little thread (CC), which you see attached there, they at the same instant open e, which is the entry for the pore (d), which is where this small thread terminates; just as, by pulling one end of a cord, you ring a bell which hangs at the other end.... Now when the entry of the pore, or the little tube, (de), has thus been opened, the animal spirits flow into it from the cavity (F), and through it they are carried partly into the muscles which serve to pull the foot back from the fire, partly into those which serve to turn the eyes and the head to look at it, and partly into those which serve to move the hands forward and to turn the whole body for its defense.* (From Descartes' *Treatise of Man* (1662). Image Source: Wikimedia Commons. The Withdrawal Reflex. Rene Descartes, Artist. Public Domain, Wikimedia Commons. <https://af.m.wikipedia.org/wiki/L%C3%AAer:Descartes-reflex.JPG>)

began to unravel the true nature of the reflex. Table 1 outlines the major discoveries that occurred over the next two centuries.

Over the next century and a half, the reflex would be integrated into the wider understanding of the nervous system. In psychology, Pavlov's notion of the stimulus-response nature of conditional reflexes would dominate the understanding of all behavior for nearly 50 years (For a detailed summary, see Domjan 2015). In the early part of the twentieth century, John B. Watson (one of the leading behaviorists in America) embraced S-R

learning and would promote the idea that emotional behavior responded to conditioning in a manner similar to other conditional responses, like salivation. His study of Little Albert in which a toddler acquired conditioned fear responses through Pavlovian conditioning techniques would go on to become one of the most famous studies in psychology and learning theory (Watson and Raynor 1920). Not until the work of B. F. Skinner (1938) would the view of voluntary behavior (aka instrumental behavior) truly diverge from the original idea that all behavior was reflexive, as put forth by Descartes.

## Other Innate Behaviors

Three other forms of innate behavior classically described in most textbooks on learning and animal behavior are fixed- and modal-action patterns, taxis, and kinesis.

### Fixed and Modal Action Patterns

Fixed and modal action patterns refer to complex behavioral sequences that require more cerebral involvement than simple reflexes. They occur only in certain nonhuman animal species. Like the reflexes, action patterns are hardwired and involuntary and require releaser stimuli, called *sign stimuli*. Unlike reflexes that tend to occur broadly across the taxonomic rank, action patterns are species-specific behaviors. They are usually associated with courtship, reproduction, territoriality, aggression, foraging/caching, and predator evasion. They tend to occur uniformly in a fixed manner, or in modal ways with limited variability across all members of a single species (although they can be restricted to one sex or the other). All fixed and modal action patterns are genetically determined; many appear at sexual maturity and are often linked to hormonal states. Those action patterns associated with territoriality and courtship may appear only during the breeding season. Familiar examples include elaborate courtship displays in many bird species ranging from familiar backyard birds like wrens, robins and doves to more exotic birds like the grebes, sand hill cranes, grouse, and the classic peacock (Fig. 4).

**Innate Behaviors, Table 1** Over two hundred years of research on the reflex after Descartes

| Scientist        | Year (s) | Nationality and field of study | Discovery                                                                                                                          |
|------------------|----------|--------------------------------|------------------------------------------------------------------------------------------------------------------------------------|
| Swammerdam       | 1664     | Danish biologist               | Demonstrated that the reflex was caused by the external “irritation” of the nerve.                                                 |
| Von Leeuwenhoek  | 1717     | Dutch biologist                | Describes nerve fibers in cross section                                                                                            |
| Galvani          | 1791     | Italian biologist              | Discovered that external stimulation using electricity caused movement in dissected frog leg muscles                               |
| Bell & Magendie  | 1811     | English physiologist           | Demonstrated that separate sets of nerves transmitted information from the sense organs to the CNS and from the CNS to the muscles |
| Magendie         | 1821     | French physiologist            | Differentiates dorsal and ventral roots of the spinal column                                                                       |
| Hall             | 1837     | English physiologist           | Discovered that a decerebrate newt moved when the skin was pricked                                                                 |
| von Helmholtz    | 1849     | German physiologist            | Discovers the speed of neural impulses in frogs                                                                                    |
| Du-Boise-Reymond | 1850     | German physiologist            | Invents the nerve galvanometer                                                                                                     |
| Von Kolliker     | 1852     | Swiss anatomist                | Describes the origin of motor neurons in the anterior horn of the spinal cord                                                      |
| Sechanov         | 1863     | Russian physiologist           | Publishes <i>Reflexes of the Brain</i>                                                                                             |
| Erb & Westphal   | 1875     | German neurologists            | Describe the knee jerk reflex                                                                                                      |
| Pavlov           | 1903     | Russian physiologist           | Cons the term <i>conditional reflex</i>                                                                                            |
| Sherrington      | 1906     | English physiologist           | Coins the term <i>synapse</i> ; publishes <i>The Integrative Action of the Nervous System</i> (1906)                               |
| Langley          | 1907     | English physiologist           | Coins the terms <i>autonomic nervous system</i> and <i>parasympathetic nervous system</i>                                          |
| Pavlov           | 1904     | Russian physiologist           | Wins the Nobel prize for physiology in 1904                                                                                        |

After Chudler (n.d.). *Milestones in Neuroscience Research*



a) Clark's Grebes\*



b) Sandhill Cranes†



c) Greater Sage Grouse\*

**Innate Behaviors, Fig. 4** Examples of modal action pattern courtship displays in several avian species. (Image Source: \*Wikimedia Commons & †Public Domain Files. (a) Clark's Grebes, Wikimedia Commons [https://commons.wikimedia.org/wiki/File:Clark%27s\\_Grebes\\_%22Rushing%22\\_Courtship\\_Display\\_\(34470939122\).jpg](https://commons.wikimedia.org/wiki/File:Clark%27s_Grebes_%22Rushing%22_Courtship_Display_(34470939122).jpg). (b) Sandhill

Cranes, Public Domain Files. [http://www.publicdomainfiles.com/show\\_file.php?id=13958723412914](http://www.publicdomainfiles.com/show_file.php?id=13958723412914). (c) Greater Sage Grouse. Public Domain, Wikimedia Commons [https://en.wikipedia.org/wiki/Greater\\_sage-grouse#/media/File:Greater\\_sage-grouse\\_\(Centrocercus\\_urophasianus\).jpg](https://en.wikipedia.org/wiki/Greater_sage-grouse#/media/File:Greater_sage-grouse_(Centrocercus_urophasianus).jpg))

The classic example of modal action patterns occurs in the three-spined stickleback fish (*Gasterosteus aculeatus*). The tiny fish is found in waters north of 30°N. They are anadromous, living at sea except during the breeding season when they nest in brackish or freshwater. The male stickleback establishes and defends a breeding territory; he will build a tube-like nest in the substrate with sand, algae, and a silk-like substance secreted from the kidneys called *spiggin*. When the nest is complete, the male stickleback then begins to exhibit various aggressive and defensive territorial behaviors and ritualistic courtships behaviors in response to specific sign stimuli (Fig. 5).

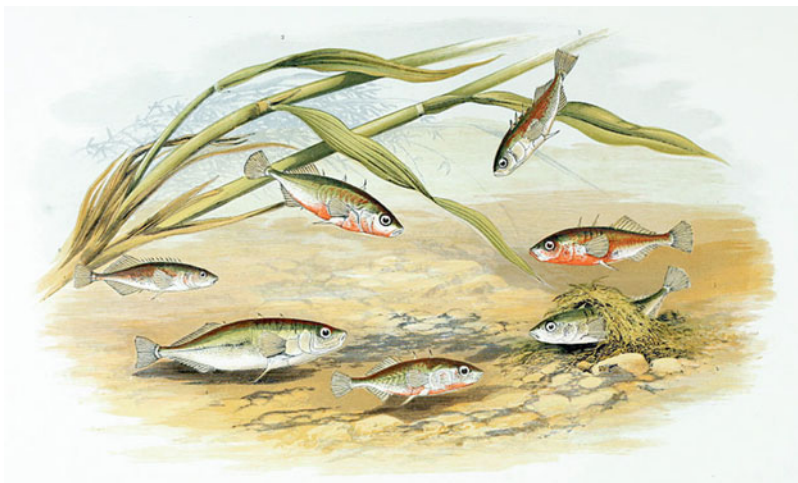
During the breeding season (late March to early August), adult sticklebacks migrate into freshwater. As a result of hormonal changes, breeding males' bellies flush red, and they begin to set up territories and build their tube-like nests. Any other breeding male conspecific that enters a resident male's territory is met with the erection of the three spines on the dorsal side of the fish (a reflex), and modal action patterns that include aggressive rushing and biting that will continue until the intruder male leaves the territory.

In a classical study of these aggressive modal action patterns in the stickleback, Tinbergen

employed the use of clay models to determine the nature of the specific releaser, or sign stimulus. He found that almost any shape of clay would suffice to elicit aggressive behavior as long as the ventral side of the clay was painted red (Fig. 6).

Once a male stickleback has successfully repelled conspecific competitors, his reproductive success is the result of elaborate combination of reflexes and model action patterned interactions with the female. The presence of a gravid female into the breeding male's territory elicits modal fanning and swimming in a zigzag direction toward the female and then toward the nest. Once the female approaches the nest, the male will swim through the nest repeatedly until the female enters the nest, or leaves the area. Pressure on her lateral line serves as a releaser stimulus for the reflex of egg-laying. The male will follow her into the nest and fertilize the eggs as she is forced out. The presence of the female serves as the necessary sign stimulus for the initial release of these courtship behaviors in the male (Candolin 1997).

Early in the field of ethology, action patterns were believed to be somewhat fixed and inflexible. Once elicited, the behavior would run its course almost automatically despite potential



**Innate Behaviors, Fig. 5** Juvenile and adult three-spined stickleback fish (*Gasterosteus aculeatus*). The red belly of the breeding male serves as sign stimuli for territorial aggression and courtship. Note: the female in the nest.

(Image Source: Wikimedia Commons. *Gasterosteus aculeatus*, Alexander Francis Lydon, Artist. Public Domain, Wikimedia Commons [https://commons.wikimedia.org/wiki/File:Gasterosteus\\_aculeatus\\_1879.jpg](https://commons.wikimedia.org/wiki/File:Gasterosteus_aculeatus_1879.jpg))



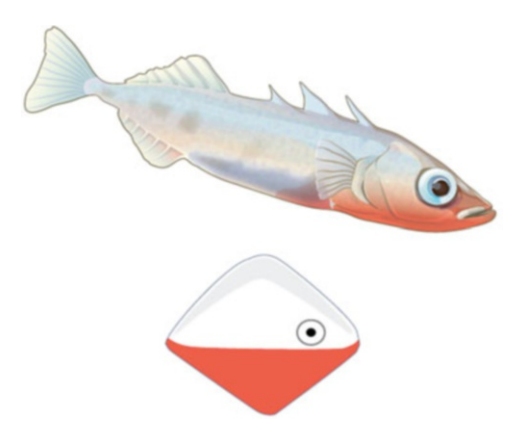
interruptions. Eibesfeldt (1974) described persistent egg-case spinning in banana spiders (*Cuppiennius salei*) despite his attempts to interrupt the behavioral sequence by removing the baseplate of the cocoon, or by removing her silk organ. The female spider failed to make adjustments to the sequence of behaviors to accommodate these interruptions. However, more recently, it has been shown that modal action patterns can be somewhat flexible in some ways. Although

the sequence of behaviors appears to be relatively consistent across individuals, Candolin (2017) showed that the rate and duration of modal courtship behaviors in three-spined stickleback fish diminished in the presence of a predator. As a result, female choice declines and individual reproductive success can be reduced.

Taxis

Taxis is the term for innate locomotor responses to specific environmental/releaser stimuli. Taxes involve directed movement toward (positive taxis) or away (negative taxis) from the specific stimulus. Taxes, like action patterns, may appear willful in that they involve directed movement that is responsive to the environment. However, taxes, like action patterns, are innate and consistent across all members of a species. Taxes are present across a wide variety of species including vertebrates and invertebrates. Table 2 outlines examples of various forms of taxes.

*Synthesis of Action Patterns and Taxes.* Lorenz and Tinbergen (1938) had shown that, in some species, action patterns may evolve into even more elaborate behavioral sequences through the superimposition of orienting motions onto fixed- or modal-action patterns. These orienting motions result from minor shifts or changes in the sign stimulus that elicit accommodating adjustments to the otherwise, stereotyped action pattern.



**Innate Behaviors, Fig. 6** A male three-spined stickleback fish during the breeding season and an example of the clay models used by Tinbergen (1951) to elicit territorial aggression. (Image Source: Stickleback and Clay Model, Open Stax, Creative Commons, [https://cnx.org/contents/GFy\\_h8cu@10.53:mNyatk93@4/Behavioral-Biology-Proximate-and-Ultimate-Causes-of-Behavior](https://cnx.org/contents/GFy_h8cu@10.53:mNyatk93@4/Behavioral-Biology-Proximate-and-Ultimate-Causes-of-Behavior))

**Innate Behaviors, Table 2** Examples of taxes across a variety of species

| Type of Taxes | Releaser stimulus       | Species                       | Description                                                                    |
|---------------|-------------------------|-------------------------------|--------------------------------------------------------------------------------|
| Anemotaxis    | Wind                    | Flying insects like locusts   | Flight corrections using hair sensilla on the head                             |
| Galvanotaxis  | Electrical current      | Electric fishes               | Two-way electrocommunication                                                   |
| Gravitaxis    | Gravity                 | King crab larvae; fruit flies | Moving toward or away from gravitation pull, aka geotaxis.                     |
| Magnetotaxis  | Earth’s magnetic fields | Motile, aquatic bacteria      | Orient and swim along magnetic field lines.                                    |
| Phonotaxis    | Sound                   | Crickets                      | Females are attracted by the male’s song                                       |
| Phototaxis    | Light                   | Dung beetle larvae            | Burrow into dung and away from the light                                       |
| Rheotaxis     | A current in water      |                               | Hold position in a current.                                                    |
| Thermotaxis   | Temperature             | Mammals                       | Seek warmth to maintain body temperature                                       |
| Thigmotaxis   | Physical contact        | Rats and mice                 | Will gravitate toward a wall or object and maintain contact with that surface. |



The classic example is the grey-lag goose. The graylag goose is a ground-nesting bird. If an egg becomes displaced from the nest, the parent goose will attempt to roll the egg back into the nest. The egg itself is the releaser stimulus for the FAP of reaching out and pulling on the egg with the beak. Unfortunately, eggs are not perfectly round and as such tend not to roll in a straight line. The egg will wobble slightly to the left or right. The unpredictable behavior of the egg serves as a releaser stimulus to make slight head tilts on the part of the goose to realign the egg's path toward the nest. This is a form of taxis: directional adjustment of the head to accommodate the movement of the egg. Together, the FAP of egg-pulling combined with the taxis of head and beak adjustments will successfully return the egg to its proper place in the nest (Fig. 7).

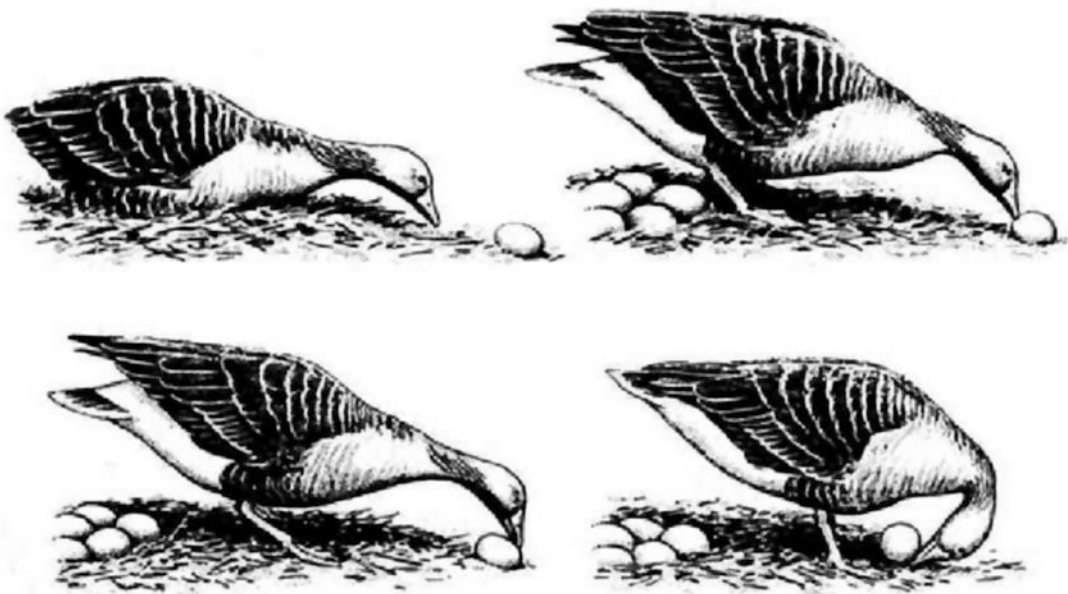
### Kinesis

Kinesis, like taxis, refers to movement of an organism (or cell) in response to an external stimulus. Kinetic movement, however, is non-directional; it usually involves the speeding or

slowing of locomotion, a shift from rest to movement, or the frequency or rate of turning. The animal does not move toward or away from the stimulus. Instead, the environmental stimulus, which is often associated with a suboptimal environmental condition, results in a change in general movement patterns. In a nutshell, organisms in optimal environments tend to stay put; organisms in suboptimal environments tend to move around until they stumble onto something better.

Many of us have witnessed the “flopping-about” behavior of a fish in the bottom of a boat. The behavior is clearly nondirectional. The absence of water and oxygen causes the kinetic movement that will continue as long as the fish has sufficient energy and resources to move, or until the environment dramatically improves. But with enough wriggling and a bit of luck, the fish may flop out of the boat and become “the one that got away.”

Kinesis is seen from single-celled organisms to complex animals. The classic example of kinesis (Gunn 1937) can be found in the wood louse (*Porcellio scaber*). In an optimal environment that



**Innate Behaviors, Fig. 7** Greylag goose fixed action pattern (FAP) of egg pulling is one part of a synthesis of FAP and taxes (head and beak adjustments) needed to return the egg to the nest. (After K. Z. Lorenz and

N. Tinbergen (1939). Greylag Goose and Egg rolling. K. Z. Lorenz and N. Tinbergen (1939) *Zeitschrift für Tierpsychologie*, 2, 1–29)

provides sufficient humidity, the wood louse is quiescent. However, as humidity declines, the louse begins to move rapidly about its environment. If the louse should stumble upon a more humid, more ideal environment, it will gradually become still. Failure to encounter a sufficiently humid location, the louse will become dehydrated and die. This sensitivity to humidity is called *hygrokinesis*.

There are two types of stimulus-driven kinesis; often they work in tandem, altering speed and direction as a single kinetic movement.

*Orthokinesis* refers to changes in locomotor speed that depends on stimulus intensity. Increasing locomotor speed is called *positive orthokinesis*; a decrease in speed is referred to as *negative orthokinesis*. Unlike taxes in which positive and negative describe directional movement in relation to the releaser stimulus, the same terms imply no such directionality with orthokinesis. Rather they refer to the acceleration or deceleration of the movement only. Examples of orthokinesis include woodlice, lamprey larvae (*Lampetra planeri*) that are more active in high intensity light environments, and cockroaches (*Periplaneta americana*) that are more active in the dark. Think of the cockroaches that shun the kitchen floor in the daytime, only to congregate there late at night.

*Klinokinesis* is a form of kinesis wherein the frequency or rate of directional change (or turning) is proportional to the intensity of the stimulus. Frequent changes in direction in response to increases in light (*photokinesis*) have been classically described in the flatworm (*Dendrocoelum lacteum*) by Ulliyott 1936, and in planeria (Reynierse et al. 1969). In large animals, an example of kinesis can be observed in dogs that circle repeatedly prior to laying down. If the bed does not provide ideal stimulation, the dog will continue to circle until the substrate is more suited to the dog's comfort. The dog is not moving closer to the bed, rather the dog circles and each turn slightly changes the substrate. Only when the bed is acceptable/optimal, does the dog actual lie down to sleep. Whether you are talking about the dog bed from your local pet store or grass for ancient wild dogs, the concept is the same. The suboptimal substrate serves as the stimulus that

initiates kinetic circling that continues until the substrate is more optimal. One might even draw similarities between the dog circling behavior and human "tossing and turning" behavior before we falling asleep.

## Cross-References

### ► Pavlovian Conditioning

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## Innate Reflex

- ▶ [Rooting Reflex](#)
- ▶ [Step Reflex](#)

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## Innate Releasing Mechanism

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## Synonyms

[Releaser stimulus](#); [Sign stimulus](#); [Supernormal stimulus](#)

## Definition

Releaser mechanisms describe the relationship between a releaser stimulus (aka sign stimulus) and an innate behavioral response; these stimulus-response relationships exist within reflexes, fixed and modal action patterns, taxis, and kinesis.

## Releaser Mechanisms

The term *releaser mechanism* refers to an innate, biological relationship between an external sensory stimulus and a specific innate behavior. This relationship tends to remain invariant within a species, although it may be limited by maturity, sex, or hormonal status. For example, many innate behaviors are limited to only males, or only infants, or only occur during the breeding season.

All innate behaviors (including reflexes, fixed and modal action patterns, taxis, and kinesis) are elicited by these very specific stimuli called releaser stimuli or sign stimuli. Those releasers associated with reflexes, taxis, and kinesis are typically simple environmental stimuli that produce a similarly simple response. For example, a light shone into the eye results in reflexive pupil constriction, bees will innately fly toward a light source, and a fish out of water will flop about wildly until they accidentally flop out of the boat. These releaser mechanisms (e.g., the light, the lack of oxygen, etc.) are relatively simple and involve involuntary responses to the environmental stimulation.

Fixed or modal action patterns also rely on releaser stimuli and are equally involuntary. Although they may appear more complex, the relationship between releaser and behavior is similarly fixed. Familiar action patterns include vocalization exchanges, courtship rituals, or food caching. Releasers may be the presence of potential competitors, mates, nesting materials, or food items.

The terms *releaser stimulus* and *releaser* may be used interchangeably. A releaser stimulus is defined as a single feature of a complex stimulus array that will initiate an innate response. The term *sign stimulus* refers primarily to stimuli that are associated with fixed and modal action patterns. The relationship between the releaser or sign stimulus and the innate response is believed to be the result of evolutionary processes; the behaviors are often closely aligned with survival or reproduction. Responding to the releaser requires little or no cognitive engagement; the stimulus is presented and the response or response sequence follows – often all the way through to

completion in the case of action patterns. In the case of reflexes, the stimulus-response relationship may occur at the level of the peripheral nervous system long before awareness of the response is registered, such as with the patellar or knee jerk reflex. But even more complex behaviors, such as fixed and modal action patterns, are equally fixed and rigid, so much so that, in some cases, interruptions that should render the behavior completely ineffective may not be sufficient to disrupt the behavioral sequence (Eibl-Eibesfeldt 1970). An example of the rigidity of the stimulus-response relation in a model action pattern is egg case spinning in spiders.

Eibl-Eibesfeldt (1970) described the rigidity of egg case spinning in the tiger wandering spider (*Cupiennius salei*). After creating a base plate with a rim, the female spider lays her eggs and then closes the egg case. If the process is interrupted and the base plate is removed, the female will begin another attempt but without respinning the base plate beyond a few threads. The bottom of the new egg sac remains open, and the eggs laid will either fall through or not be protected. Eibl-Einsfeldt also observed that when the silk gland dried up (under hot filming lights) and no silk was available, the female spider

continued the behavioral sequence (as if spinning the base plate) and then laid her eggs in mid-air. For the spider, the urgent need to lay her eggs provides the necessary stimulation to proceed with her egg sac weaving behaviors, despite being completely unaffected by the failure of her efforts.

Table 1 lists a few examples of releasers and their corresponding innate responses across reflexes, taxis, kinesis, and action patterns.

Some sign stimuli are explained in terms of communication in that they transmit important information between individuals and which may elicit behaviors that directly affect survival and/or reproductive fitness. Tinbergen (1951) coined the term “social releaser” to describe such stimuli that influence the behavior of other animals.

Intraspecific Sign Stimuli

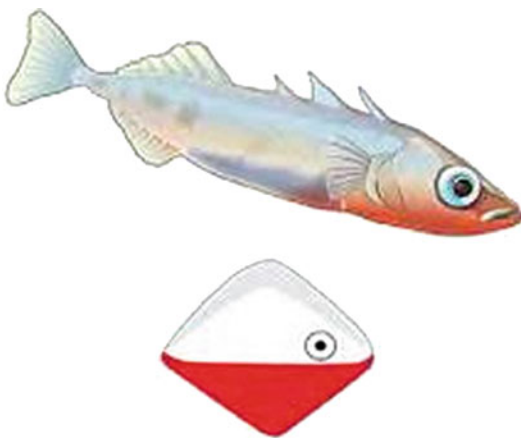
Releaser mechanisms can be important between members of the same species, especially where courtship and reproduction are concerned. Innate responses to specific morphologic features or stereotyped behavior patterns can greatly influence whether or not an individual finds a mate and successfully raises their offspring.

**Innate Releasing Mechanism, Table 1** Releasers associated with various innate behaviors. Examples include reflexes, taxis, kinesis, and fixed or modal action patterns

| Type of behavior     | Releaser stimulus                                        | Behavior                                                             | Species                       |
|----------------------|----------------------------------------------------------|----------------------------------------------------------------------|-------------------------------|
| Nursing reflex       | Nipple in the mouth                                      | Suckling                                                             | Most mammals                  |
| Patellar reflex      | Tap on patellar tendon                                   | Knee jerk                                                            | Most mammals                  |
| Coughing reflex      | Irritation of the trachea                                | Coughing                                                             | Mammals, birds                |
| Phototaxis           | Light                                                    | Approach or avoidance of light                                       | Jellyfishes, insects          |
| Rheotaxis            | A stream’s current stimulates the lateral line           | Facing into or moving away from the current                          | Fishes                        |
| Thigmotaxis          | Open field                                               | Maintain close physical contact with a physical object (like a wall) | Rodents                       |
| Orthokinesis         | Increased humidity                                       | Increase locomotor speed                                             | Woodlice                      |
| Klinokinesis         | Increased light                                          | Increased turning                                                    | Flatworms                     |
| Modal action pattern | Red belly of competitor males during the breeding season | Aggression in the resident, breeding male                            | Three-spined stickleback fish |
| Modal action pattern | Presence of a female during the breeding season          | Male courtship dances                                                | Insects, birds, fishes        |

**Red belly of the three-spined stickleback fish.** Perhaps the most familiar example of a sign stimulus occurs in the three-spined stickleback fish (*Gasterosteus aculeatus*). The male stickleback establishes and defends a breeding territory. During the breeding season, the male builds a nest in the river substrate. When the nest is complete, the male stickleback then begins to exhibit various aggressive and defensive territorial behaviors and ritualistic courtship behaviors in response to specific sign stimuli: the presence of other breeding males or receptive females.

From late March to early August, breeding males' bellies turn red as they set up territories and build their nests. When intruder male with a red belly enters a resident male's territory, he is met with the erection of the three spines on the dorsal side of the resident fish (a reflex), and modal action patterns include aggressive rushing and biting that will continue until the intruder male leaves the territory. In a classic study looking at the stimuli that produce these aggressive behaviors, Tinbergen (1951) used clay models of various shapes to determine the nature of the sign stimulus (see Fig. 1). He found that almost any shape of clay would suffice to elicit aggressive behavior as long as the ventral side of the clay was painted red.



**Innate Releasing Mechanism, Fig. 1** A breeding three-spined stickleback male, and a clay model (aka sign stimulus) similar to those used by Tinbergen to elicit aggression from competing males during the breeding season. Males responded to various clay shapes as long as they had a “red belly.” (Image taken from Behavioral biology: Figure 1 by OpenStax College, Biology, CC BY 4.0)

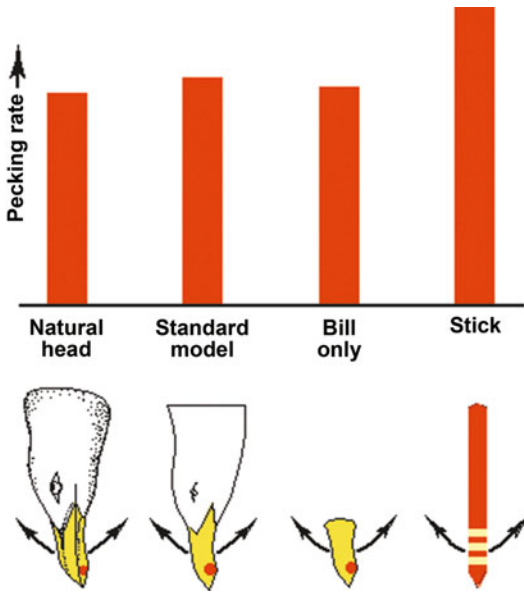
**Red spot on the herring gull's beak.** In another study using models, Tinbergen and Perdeck (1950) investigated the stimulus associated with feeding responses between herring gulls and their chicks. In the wild, herring gull chicks peck at a red spot on the parent bird's bill as food solicitation. When the chick does so, it stimulates food regurgitation in the parent. Tinbergen manipulated the appearance of the red spot using realistic models of herring gulls with a red spot, as well as artificial models, some reduced to a simple pencil-like shape with alternating red and white bars on the tip. Tinbergen found that although the realistic model did elicit pecking by herring gull chicks, those models did not produce the most vigorous responses. The pencil-like stimuli with greater than normal length and more red than normal produced the most robust responses (see Fig. 2).

## Interspecific Sign Stimuli

Sign stimuli can influence interactions between species as well. Morphological releasers may alter the behavior of a predator or competitor through mimicry.

**False eyespots in moths and butterflies.** Some members of the genus *Lepidoptera* (butterflies and moths) have evolved false eyespots on their wings that are similar to owl eyes (see Fig. 3). When threatened by predatory birds and mammals, the moth will spread its wings and expose the spots. The innate response by certain insectivorous predators is to flee from anything resembling the eyes of their own predators, such as an owl. Similar evidence exists for fishes (Karplus and Algom 1981). Often used an example of the “escalating arms race” between predatory and prey, the evolution of false eyespots in moths and butterflies demonstrates the importance of interspecific sign stimuli. Recently, a study of over 70 species of moths and butterflies (*Lepidoptera*) have shown that the level of detail in these false eyes spots includes a white highlight called a “sparkle” which appears to enhance the deterrent effect of the spot (Blut et al. 2012).





**Innate Releasing Mechanism, Fig. 2** Different herring gull beak models used by Tinbergen and Perdeck (1950) to demonstrate the key features of sign stimulus control on pecking in young chicks. (Taken from [http://www.flyfishingdevon.co.uk/salmon/year1/psy128ethology\\_experiments/ethexpt.htm](http://www.flyfishingdevon.co.uk/salmon/year1/psy128ethology_experiments/ethexpt.htm))



**Innate Releasing Mechanism, Fig. 3** False eyespots in the moth *Automeris*. Note the sparkle of white in the fake eyes. This increases the false eye's deterrent value. (Photograph taken by Patrick Coin, CC BY-SA 2.5, <https://commons.wikimedia.org/w/index.php?curid=768361> Wikimedia Commons)

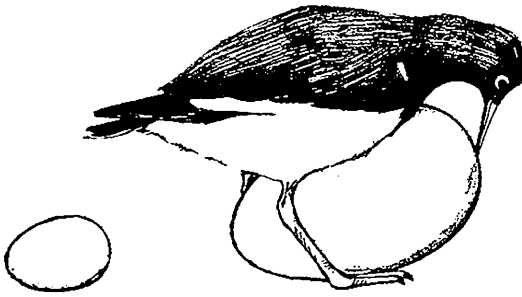
## Supernormal Stimuli

Unlike experiments that reduce the characteristics of a sign stimulus to their minimally essential features (e.g., the clay models of the three-spined stickleback fish), a supernormal stimulus is an artificially altered sign stimulus – often made

larger, brighter, or more salient to test response strength or bias. By exaggerating certain characteristics of a sign stimulus, innate responses are similarly exaggerated and, often, nonadaptive. Birds, for example, may show a strong preference for an unusually large egg – one that they could not physically lay. How could this odd, non-adaptive bias evolve?

One explanation is that natural selection has favored naturally larger eggs. Larger eggs produce larger, more robust offspring, and so those avian parents who invest care in the larger egg are more likely to produce offspring that are more likely to survive. Favoring the larger egg increases one's reproductive fitness when it results in more offspring who live long enough to reproduce themselves. But viable body size of the parent is determined by resource availability and leads to an upper limit in bird body size. Since birds can only get so big, eggs' size too is limited – but not by behavioral choice. If eggs become too large, the parent simply may not survive, and her genes are removed from the gene pool. If the environment restricts the upper limit of bird size, then it is advantageous for the female to choose the largest eggs she can possibly lay. Natural selection favors the “choose large” strategy because there is no selection mechanism that could favor choose a “large but not too large” strategy. The result is a strong, positive behavioral bias that can be tested by presenting the female with an unnaturally large egg. Because the species has never faced selection pressures for “don't choose too large,” that component has never become part of the equation. Not all bird species exhibit the “choose large” strategy. Evolutionary stable strategies depend on various factors. But for some bird species, like warblers and oystercatchers (see Fig. 4), choosing the large egg is a strong bias. In the case of the warbler, it is so strong that it puts them at risk for brood parasitism.

The cuckoo bird (*Cuculidae*) is the classic example of a brood parasite; they have evolved a nesting strategy that takes advantage of the “choose larger eggs” bias in other birds. Cuckoos, and other brood parasites like the cowbird, lay their own large eggs in the nests of other smaller bird species, including warblers, vireos, and



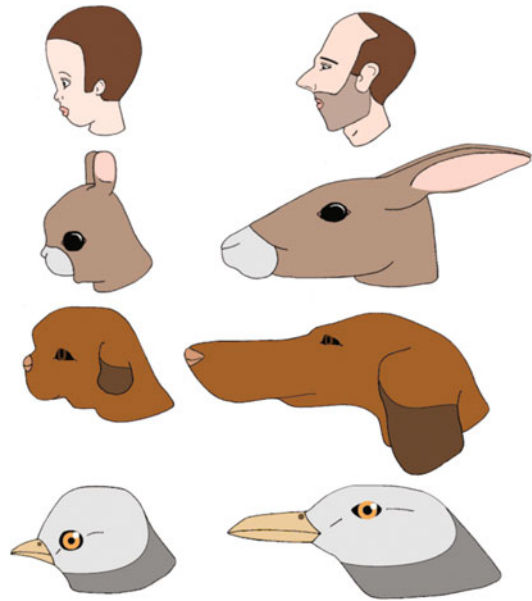
**Innate Releasing Mechanism, Fig. 4** An oystercatcher choosing to sit on an unnaturally large, supernormal egg over a normal egg. (Adapted from Tinbergen 1951)

buntings (King 1954). The cuckoo's eggs are often similar in appearance to the host bird's eggs but larger. Host parents typically do not object to the unusually large egg in their nest and will continue to brood it along with its own eggs. The exaggerated size of the egg elicits parental care that favors both the large egg and the resulting chick; often resulting is the loss of their own offspring. Other brood parasitic birds include indigobirds, whydahs, honey guides in Africa, and North American cowbirds. For more information, see "Brood Parasitism."

## Sign Stimuli in Humans

There is mixed opinion on whether sign stimuli exist for humans. Conrad Lorenz suggested that baby animals of many species share a "babyishness" with human babies – large eyes, bulging foreheads, and small chins (see Fig. 5). He suggested that this baby-like appearance tends to elicit certain parenting or nurturing behaviors like affection toward baby animals as well as human babies.

Contagious yawning has also been suggested as an example of a social sign stimulus in humans. The observed yawn serves as the releaser stimulus for the elicited yawn in the observer. Contagious yawning has been confirmed experimentally by Provine (1986), who found that 55% of subjects yawned after viewing a 5-min series of 30 yawns. However, the conventional definition of a sign stimulus typically states that all members of the species respond to the stimulus in a similar way. Most human examples do not fit this definition.



**Innate Releasing Mechanism, Fig. 5** "Humans feel affection for animals with juvenile features: large eyes, bulging craniums, retreating chins (left column). Small-eyed, long-snouted animals (right column) do not elicit the same response" (Lorenz 1971). (Animal human growth skull neoteny cuteness maturation.png taken from <https://creativecommons.org/licenses/by-sa/4.0/>)

## Limiting Factors

Finally, it is important to note that some releaser stimuli do not exert their influence independent of context. The effect of a releaser may depend on the context in which it appears. A male stickleback fish will aggress on another male if the intruder enters the resident fish's breeding territory. But the same competitor may cause other males to flee if encountered outside their own territories (Fantino and Logan 1979). The context is key in determining the response elicited by the sign stimulus. Similarly, seasonality may also play a role in determining the effect of a releaser stimulus. The European robin, harbinger of spring, will sit at the top of a tree and sing repeatedly in response to the songs of other robins. The rest of the year, robins are not known for such robust singing.

## Cross-References

► [Innate Behaviors](#)

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## Innovation

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## Synonyms

Animal innovation; Behavioral innovation;  
Invention

## Introduction: History and Definitions

A Barbados bullfinch, *Loxigilla barbadensis*, lands on a table at a coffee shop, flips over a sugar packet, and, after piercing it with its beak, feeds on the sugar. A bottle-nose dolphin (*Tursiops* sp.) in the Shark Bay, Australia, removes a marine sponge from the substrate and wears it over its rostra as it probes the rough seafloor. A New Zealand kea (*Nestor notabilis*) skillfully topples over a trash bin lid, gaining access to the food scraps within. The apparent ability of nonhuman animals to develop novel solutions to the challenges of everyday life is a constant source of delight for the broader public and one of the constant scientific enquiries for scholars. Behavioral innovations, defined as novel behaviors or preexisting ones used in novel contexts, are now recognized as a key source of behavioral plasticity and, as such, have become central to our thinking of how animals adjust to novel and changing environments.

While one can reasonably expect behavioral innovations to arise in a variety of functional domains, most of what is known about innovation in nonhumans relates to the foraging domain. In the late 1990s, Louis Lefebvre and his colleagues from the University of McGill, Canada, published a series of keystone contributions that led to an explosion of research on the topic. Using a readily available large body of low-impact ornithological publications, Lefebvre and his co-workers counted for each avian species the number of anecdotal reports of novel and unusual feeding behaviors in the wild (Lefebvre et al. 1997, 1998). Over the last decade, these taxon-level, field-based “innovation counts,” or “innovation rates,” when corrected for brain-body allometric relationships, have been related to a large number of morphological (e.g., brain size), ecological (e.g., migratory status), and evolutionary parameters (e.g., taxonomic radiation) and have been used to investigate the adaptive value of animal innovations and their evolutionary consequences (reviewed by Lefebvre (2011)). Therefore, it is now relatively well established that foraging innovations facilitate invasion of novel habitats (Sol et al. 2002, 2005), enhance survival in harsh (Sol et al. 2005) and variable environments (Sayol

et al. 2016), and accelerate taxonomic radiation (Nicolakakis et al. 2003). More recently, experimental research has explored the attributes of innovative individuals, the contextual factors that facilitate innovation, and the psychological mechanisms that underlie the expression of innovative behavior (Griffin and Guez 2015; Griffin et al. 2013; Morand-Ferron et al. 2011). For this, researchers have developed a paradigm known as “innovative problem solving” or just “problem solving.”

### Problem Solving: The Paradigm

In stark contrast to methodologies established in the ecological approach to the study of animal cognition, which has emphasized the need to test animals in ecologically meaningful contexts, causal analyses of animal innovations have drawn upon the experimental principle of presenting animals with novel problems they are unlikely to have encountered in their natural environment. Usually, novel problems involve some kind of extractive foraging task with which subjects need to interact to gain access to food. Innovation propensity is then gaged by measuring their ability (latency, success) to solve it. Recently attempts have been made to find an alternative motivator than food and used problems that animals need to solve to gain access to their nest (Cauchard et al. 2013) or to improve their sexual displays (Keagy et al. 2011). Interindividual variation in performance is then related to individual attributes (e.g., sex, age); alternatively, the effects of manipulating context on performance are examined (e.g., group size). Also of interest has been whether specific problem-solving techniques spread through groups and even through free-ranging populations seeded experimentally with trained problem solvers (Aplin et al. 2015). Tasks generally involve a one-stage solution, but the use of multistage tasks has become more common within the context of quantifying to what extent animals reason about the consequences of their actions on the problem at hand and the causes of their success and failure (Huber and Gajdon 2006; Taylor et al. 2009).

One can reasonably wonder to what extent anecdotal reports of innovations in the wild and experimental measures of innovative problem solving quantify the same behavioural trait. Demonstrating the convergent validity of behavioral tests is by no means an easy task, but several studies in free-ranging birds have found that the taxonomic distribution of innovation counts overlaps with the taxonomic distribution of problem-solving performance (Diquelou et al. 2016; Webster and Lefebvre 2001). Species that belong to the Corvidae family (e.g., crows) have high innovation counts and perform well on problem-solving tasks, whereas species belonging to the Columbiformes (e.g., doves) have few innovation counts and tend to perform poorly, with Passerines (e.g., starlings) occupying the middle ground on both measures. Recently, Griffin and Guez (2014) attempted to evaluate the convergent validity of problem solving and innovation counts by examining whether factors predicted and demonstrated to cause and influence innovation counts also cause and influence problem solving. They concluded that in most respects, problem solving is determined by the same underpinning mechanisms and is influenced by the same factors as those predicted to underpin and influence innovation, providing additional evidence of convergent validity.

### Problem Solving: Who Are the Innovators?

Spurred along by a strong history of relating field-based innovation counts to taxon variation in relative brain size and finding that avian and primate taxa with higher innovation counts had larger brains relative to their body size, much of the initial work on problem solving argued for a strong relationship between problem solving and cognitive performance. Since then, a variety of other potential individual attributes has been considered with a particular focus on factors that alter the likelihood that an animal will make contact with a novel situation in the first place. Following the natural sequence in which behavior occurs (i.e., approach must occur prior to deployment of

any cognitive ability), this section will first introduce the factors that determine contact, followed by what is understood about the role of cognition. Finally, focus will be put on the results from recent work that has explored the role of motor flexibility in problem solving.

### Are Innovators Particularly Motivated or Exploratory?

One possibility is that individuals that innovate tend to be particularly motivated to solve the problem at hand. Motivation has been evaluated by quantifying the persistence with which an individual engages with the (typically foraging) problem (e.g., beak-to-task contacts) (reviewed by Griffin and Guez 2014) or by using proxies collected outside the problem-solving context (body weight, body fat, body condition) (Griffin et al. 2014). Perhaps unsurprisingly, individuals that engage more with the problem at hand are more likely to solve it and solve it more quickly than individuals that engage less with the task. For example, both great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) are more likely to solve an extractive foraging task the more time they spend it its proximity and the more they have tried (Morand-Ferron et al. 2011). Experimental manipulations of motivation, such as food deprivation, also enhance problem-solving performance (Griffin et al. 2014). There is little evidence, however, that assumed proxies of motivation collected outside the task moderate problem-solving performance. For instance, Cauchard and co-workers (Cauchard et al. 2013) found that the time taken by great tit parents to remove an obstacle to access their nest had no bearing upon how frequently they fed their nestlings. Morphological proxies for motivation (e.g., body condition) are also unrelated to problem solving.

Another option is that innovators are those individuals that are more willing to approach and interact with novel situations. They are more innovative simply because they come into contact more frequently with novel situations in which they can invent a novel behavior or to which they can apply a preexisting behavior. Innovators are then simply individuals that are less wary of

novelty, perhaps even more attracted to novelty, and in that sense more exploratory. So far, evidence for this hypothesis is mixed. In some studies, innovators are less fearful of novelty and more exploratory, supporting the hypothesis, while in others, there is no relationship between innovation performance and these behaviors (reviewed by Griffin and Guez (2014)). Differences in the way these responses are measured might be the reason behind inconsistent results.

### Are Innovators More Intelligent?

The finding that avian and primate taxa with larger relative brain sizes have higher innovation counts has been taken to mean that innovations represent the behavioral expression of greater cognitive endowment (but see Healy and Rowe 2007). Given that interindividual variation in a given trait provides the raw material upon which selection acts to drive the evolution of variation at higher levels, researchers set out to find interindividual variation in innovation propensity with the expectation that these should correlate with interindividual variation in cognition. Most often, individual performance ranks on innovation tasks (most often solving latencies) have been correlated with individual performance ranks on learning tasks (typically acquisition speed or errors) to investigate whether more innovative individuals are also those that learn faster or more accurately (reviewed by Griffin and Guez 2014). Given the view that innovations are linked to general cognition, learning has been quantified in the context of tasks assumed to measure “general” learning abilities, including operant and classical conditioning, rather than learning abilities considered to be more modular, such as song learning and spatial learning.

To date, five of six studies using operant learning as a measure of cognition have found that innovation propensity and learning covary. For example, in European starlings (*Sturnus vulgaris*), pigeons (*Columbus livia*), and Carib grackles (*Quiscalus lugubris*), birds that solve an innovative problem-solving task in a shorter amount of time acquire a novel foraging technique faster (e.g., flipping a lid on a container) (Boogert et al. 2008; Overington et al. 2011). Although



these studies provide tentative support for the idea that innovative behavior is linked to at least one facet of cognition (operant learning), they are not designed to exclude the possibility that associations between innovation and learning might be the result of associations between the rates at which novel information is encountered (via activity/exploration) rather than correlations in the capacity to process and store environmental information per se (i.e., cognition).

Pavlovian learning and reversal learning tasks, which assess more accurately how fast an individual acquires environmental information over and above how often it encounters opportunities to learn, have yielded much more mixed results than those using operant learning. Common mynas (*Acridotheres tristis*) that take longer to discover the solution to an extractive foraging task learn a Pavlovian association more quickly; however, these individuals also learn more slowly the new state of the world when that association is altered (i.e., reversal learning; Griffin et al. 2013). In another mixed set of findings, Carib grackles (*Quiscalus lugubris*) that discover the solution to one extractive foraging task more quickly learn a Pavlovian association more slowly, whereas how fast the birds find the solution to an alternative task bears no relation with their Pavlovian learning speed (Ducatez et al. 2014).

Perhaps the most robust approach to evaluating the relationships between innovation propensity and cognition at the interindividual level has involved testing animals on batteries of learning tasks and then using a principle component analysis to extract a “general learning factor” whose correlation with innovation performance can be examined. Most promisingly, spotted bowerbirds’ (*Ptilonorhynchus maculatus*) problem-solving performance loads positively, albeit weakly, on to the same principle component as a general learning factor (Isden et al. 2013).

Up to now, consideration has been given to whether cognitive abilities correlate with innovation propensity. For cognitive processes to be a *causal* determinant of innovation (i.e., solution discovery in a problem-solving task), animals must have (1) the capacity to select specific motor actions before using them based on prior

knowledge and/or (2) the capacity to “hone in” on the solution until solving occurs for the first time. New Caledonian crows (*Corvus moneduloides*) are capable of goal-directed solving in that they have been shown to extract and store functional properties of objects and apply them to other problem-solving opportunities (Taylor et al. 2009). Establishing these capacities generally involves training test subjects extensively prior to establishing whether they carry over acquired knowledge to solving yet other novel problems. When suitably designed, these tests disentangle the roles of causal reasoning from those attributable to associative learning processes. Given their complexity and the extensive training often involved prior to spontaneous problem solving, less clear is the extent to which such tasks reproduce a suitable context to the study the mechanisms of avian innovations more generally. This is particularly so when these include seemingly simple novel foraging patterns such as removing caps from milk bottles, catching insects on the wing, foraging for prey by artificial light, or digging for prey in sand (Lefebvre et al. 1997, 1998).

Rather than causal reasoning, perceptual rules offer an alternative mechanism by which animals can appear to select a motor action prior to using it. Perceptual rules, such as making preferential contact with object edges, with areas of high visual contrast, or protruding surfaces, could guide animals’ interactions with objects. Such rules might be acquired as a consequence of experience of past pairings with rewards (e.g., pecking the edge of an object is more likely to break/move it than pecking its center) or might have become genetically assimilated in those species that routinely interact with objects. Such rules would remain tightly bound to the perceptual attributes of objects but would nevertheless assist animals in solving innovation tasks without assuming that they have any understanding of how solutions work.

Gradual honing in on a solution occurs when an animal learns that a particular motor action is associated with a secondary cue indirectly paired with reward delivery. For example, Carib grackles discover the solution to an extractive foraging task faster when parts of the device are made to move

in response to actions by the bird than when these movements are blocked (Overington et al. 2011). This finding suggests that movement stimuli might act to increase the likelihood that the “successful” motor action is repeated. This is a learning process that is most often referred to as “shaping.” Another possibility is that secondary cues increase the likelihood of the animal perseverating, that is, of attempting again to solve, independently of which motor action is used. This is not a learning process because no association is formed between a particular motor action and a secondary cue. The hallmark of a learning process is a gradual narrowing in motor frequencies with motor actions that produce secondary cues that are increasing and those that are not decreasing; changes in perseverance will be characterized by increases in the number of attempts without changes in the frequencies of which motor actions are expressed.

## Motor Flexibility

Many instances of innovation involve the expression of a behavioral variant, namely, a behavior that deviates from the individual’s or population’s behavioral norm. These might be completely novel or small variations of existing motor actions. With this in mind, it seems reasonable to assume that an individual or species with a larger, more diverse, motor repertoire is likely to express more motor innovations. In most published data sets, motor diversity is conceptualized as a greater number of distinct motor actions or number of areas contacted (e.g., Benson-Amram and Holekamp 2012; Griffin et al. 2014; Overington et al. 2011). More recently however, researchers have developed an index that takes into account both the number of different motor actions and the relative frequency with which they are expressed (Diquelou et al. 2016; Griffin and Diquelou 2015). Both a higher number of actions expressed, and even probabilities of each one occurring, serve to raise motor flexibility. Several studies have now shown that motor flexibility explains a significant proportion of interindividual and interspecies variation in innovative problem solving

(Benson-Amram and Holekamp 2012; Diquelou et al. 2016; Griffin et al. 2014; Overington et al. 2011).

To simulate the effects of motor flexibility on problem solving, Guez and Griffin (2016) recently developed a computational model to examine the combined effects of motor flexibility, learning, and persistence on problem-solving performance by a hypothetical agent. First, an agent was assigned four possible motor actions, with only three leading to task solving. The probability of expression of each motor action was either skewed toward one motor action to simulate low motor flexibility or evenly distributed between the four motor actions to simulate the effects of high motor flexibility. Guez and Griffin (2016) then integrated the effects of learning by allowing expression probabilities to change each time a secondary cue occurred, whereas changes in persistence in response to secondary cues were simulated by making another attempt more likely. The simulations revealed a positive effect of learning on problem-solving performances in cases where secondary cues were very common and the change in motor frequencies each time a movement cue occurred were very large. In most other modeled scenarios, increases in persistence improved problem solving more than learning. These simulations suggest that problem solving might often be caused by a combination of motor flexibility combined with changes in perseverance induced by secondary cues, placing variation in innovativeness at the individual level firmly within the realm of random motor variation rather than any variation in information processing capacity.

## Conclusions

Avian innovation counts are thought to provide a direct measure of cognition. Some researchers have gone a step further to assert that interindividual variation in innovation propensity is a measure of cognitive ability. A small body of evidence suggests that innovation propensity is a repeatable individual attribute. However, this interindividual variation appears not to be reliably

associated with interindividual variation in learning in either empirical work or simulations. In contrast, task-directed motivation and motor flexibility are more reliably associated with innovative problem solving. Interindividual variation provides the raw material for the evolution of cross-taxon differences. How then can the consistently positive associations between cognition and innovation found in the cross-taxon comparisons be reconciled with the mixed patterns of associations between innovative problem solving and learning performance at the within-species level? It has been argued that cognition and innovation might share a correlational rather than causal relationship (Griffin and Guez 2016). In other words, these phenotypes might covary at the cross-taxon level, not because cognition causes innovation but rather because, as suggested by theories of brain and cognitive evolution and environmental models of diet generalism, both cognition and diet diversity undergo evolutionary selection under conditions of environmental variability. However, it is diet diversity, via its effects on motor diversity, that drives innovativeness and not enhanced cognition. Only future research will tell.

## Cross-References

- [Adaptation](#)
- [Associative Learning](#)
- [Behavioral Variation](#)
- [Classical Conditioning](#)
- [Cognition](#)
- [Coping Style](#)
- [Culture](#)
- [Ecology](#)
- [Environmental Influences](#)
- [Ethogram](#)
- [Evolution](#)
- [Fitness](#)
- [Foraging](#)
- [Intelligence](#)
- [Learning](#)
- [Motivation](#)
- [Neophobia](#)
- [Operant Conditioning](#)

- [Problem-Solving](#)
- [Shaping](#)
- [Technical Intelligence Hypothesis](#)
- [Tool Use](#)

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## Insect Communication

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## Synonyms

[Animal communication](#); [Information theory](#);  
[Information transmission](#); [Signaling](#)

## Definition

Exchange of information between a sender and receiver in insects

## Introduction

Broadly, communication refers to any exchange of information between individuals. The individual transmitting the information is the “sender,” while the individual to whom the information is transmitted is the “receiver.” The sender can be a single individual or a group of individuals, just as the receiver may be an individual or a group of individuals. Often, the information transmitted is meant to influence the current or future behavior of the receiver. This information is referred to as a “signal”; the sender is the “signaler.” Theory predicts that for a signal to evolve, both the sender(s) and receiver(s) should benefit from their interaction (Bradbury and Vehrencamp 1998). Thus, there should be tight coevolution between signal production and subsequent perception and response.

Insects communicate in various contexts, both between and within species. These contexts include but are not limited to mate choice, competition with conspecifics for access to mates, avoiding predators, locating resources, and kin recognition.

**Mate choice:** Individuals (typically males) attempt to attract potential mates with conspicuous visual displays, sounds, and smells. The

responsive sex (typically females) can respond to mating advances with similar displays of their own.

**Competition:** Individuals signal to others in agonistic interactions to secure mates, territories, or other resources.

**Predator avoidance:** Insects send alarm signals to warn others against nearby predators or warning signals to deter predators themselves.

**Resource localization:** Members of the same species or colony share information about accessing food and other resources.

**Kin recognition:** Some signals are species- or kin-specific and allow insects to identify intruders, avoid inbreeding, and prioritize the safety of close kin.

## Modalities of Insect Communication

**Visual signaling** involves the display of distinct body parts, typically referred to as the signal. Of all insects, butterflies, flies, dragonflies, and damselflies use visual signals most often.

**Mate choice:** Many insects use visual signals, especially colorful wings, to attract mates. The red admiral butterfly, *Vanessa atalanta*, uses bright coloration on the dorsal wing surface that gains the attention of potential mates.

**Predator avoidance:** The ventral side of the aforementioned red admiral butterfly is drab, camouflaging the species from predators (Opler and Krizek 1984). Some insects have bright advertisement signals, called *aposematic signals*, that warn predators of their unpalatability (Mappes et al. 2005). Lady beetles, tiger moths, and blister beetles all broadcast long wavelength colors like red and orange colors that advertise the bitter-tasting chemicals in their bodies. Many butterfly and moth species have large round eyespots on their wings. In some cases, these spots mimic the eyes of another, potentially more dangerous animal. For example, *Hemeroplanes triptolemus* larvae expand the front segments of their bodies, mimicking a snake and scaring off predators. Otherwise, the spots encourage a predator to attack a part of the insect's body that is less vital to its survival. When a predator attacks, it will go for the

eyespot located on the wings, avoiding the thorax or abdomen.

**Resource localization:** One of the biggest discoveries in animal communication is that honeybees, *Apis mellifera*, use visual communication to share information about nearby resources. These bees use two forms of dance behavior, the waggle dance and the round dance, that share information with other members of the colony about the direction and distance to patches of flowers yielding nectar and pollen, water sources, or new nest-site locations (Riley et al. 2005). As the distance between the resource and the hive increases, the round dance transforms into variations of a transitional dance, which, when communicating resources at even greater distances, becomes the waggle dance (Seeley et al. 2006).

**Kin recognition:** Visual signals can be used to identify individuals living among a group. Paper wasps, *Polistes fuscatus*, have highly variable yellow facial and abdominal markings that are signals of individual identity. Queens and workers form a linear dominance hierarchy that determines how food, work, and reproduction are divided within the colony. This stable hierarchy is facilitated by individual recognition between the different ranks (Tibbets 2002).

There are many advantages to visual signals. This form of communication is long range and effective in all directions, regardless of wind speed. Since visual signals travel at the speed of light, they are the fastest of all signaling types. If the signal is passive, like many aposematic signals, they require little to no energy to broadcast. There are some disadvantages to visual signaling, such as the requirement for the receiver to have a clear view of the signaler. Since visual signals are only effective when they are visible to the receiver, many insects display only when the sun is out. *Bioluminescence* is an exception to this rule, where some insects such as adult *Photuris* fireflies, glowing click beetles and cockroaches, and railroad worm larvae produce their own light and signal at night. Lastly, active signals, like sexual signals, can be metabolically expensive to produce, and visual signals can be broadcast to unintended receivers like predators who can more easily spot prey adorned with these elaborate signals.



**Acoustic signaling** involves the production and propagation of sound toward a receiver. In the absence of the vocal structures reserved to vertebrates, insects have evolved diverse mechanisms for sound production. Crickets and katydids sing by stridulating or rubbing together specialized wing structures to generate pulses of sound (Alexander 1961). Similarly, grasshoppers rub their hind legs against hardened forewings, creating sound like a bow on a violin. Cicadas have specialized organs called tymbals that generate sound when flexed back and forth (Young and Bennet-Clark 1995). Several beetle species make sounds by rubbing body parts together or on an external source. For example, deathwatch beetles bang their heads repeatedly on hard surfaces to generate a ticking noise (White et al. 1993). Other insects, such as Madagascar hissing roaches, produce hissing sounds by expelling air through spiracles (Nelson 1979). Like other terrestrial animals, most insects use a thin membrane known as the tympanum to process sounds. Insect tympana can be located anywhere on the body, including the legs (crickets and katydids), wings (butterflies), mouthparts (sphingid moths), abdomen (cicadas), and thorax (tachinid flies, praying mantis) (Greenfield 2016).

*Mate choice and competition:* Male crickets, katydids, grasshoppers, and cicadas produce songs that attract females in mate choice. In some families (such as katydids), females may respond to mating attempts with songs of their own (Villarreal and Gilbert 2013). Males of these species can also employ sound in competition to establish dominance or warn other males not to approach (Alexander 1961).

*Predator-prey dynamics:* Sounds also play a role in predator avoidance and prey localization. For example, cicadas emit a distress call when disturbed, warning others of a potential predator (Young and Bennet-Clark 1995). Some moth species emit sounds that jam a predatory bat's echolocation sense (Corcoran et al. 2009). Predators and parasites such as tachinid flies use their exceptional hearing to find prey (Lehmann 2003).

Acoustic signaling provides several advantages for insects. Since sound is easily

manipulated, slight changes in sound characteristics (amplitude, frequency, periodicity) can produce a wide range of signals conveying different kinds of information. Sound waves also move relatively quickly to receivers. However, sound can be metabolically expensive to produce, and acoustic signals can often reach deadly targets such as predators and parasites. Sound also attenuates (reduces in intensity), and the strength of the signal is lost over long distances. In noisy environments, receivers may have trouble perceiving an acoustic signal.

**Chemical signaling** is one of the oldest and most common forms of insect communication. Insects regularly signal with **pheromones** (within species) and **allelochemicals** or **allomones** (between species) (Regnier and Law 1968; Ali and Morgan 1990). Many also use non-volatile, short-range hydrocarbons as chemical signals (Singer 1998). Individuals generally sense long-range chemical signals with olfactory reception and short range with forms of contact reception, such as taste. Chemical communication is most famously studied in group-living and social insects such as hymenopterans (ants, bees, wasps), aphids, and termites.

*Resource localization:* As picnic-goers often notice, ants use pheromone trails that lead nest mates toward food sources in a behavior known as *tandem running*. This behavior is also commonly found in termites, which lay chemical trails that facilitate group foraging (Kaib 2013). Solitary insects also use chemicals in resource communication; bark beetles use pheromones that convey the location of a new host tree to their conspecifics.

*Predator avoidance:* Termites, alongside social bees and wasps, also use alarm pheromones that recruit their kin into attacking predators (Kaib 2013). More defensively, several ant and aphid species employ chemical alarm signals that warn nest mates to scatter as a predator approaches (Yamaoka et al. 2006). Many solitary insects either exude unappealing scents or directly chemically incapacitate a predator. The aptly named brown marmorated stinkbug produces foul smells that deter its predators. Several beetles, flies, and moths use chemical repellants

in areas where they lay eggs to divert potential predators or competitors. Cockroaches secrete chemicals onto their dorsal side that harden like glue in a predator's mouth, allowing the roach time to escape (Farine et al. 2002). Bombardier beetles famously expel fatal chemical steam from their abdomens when threatened (Eisner 2003).

**Kin recognition:** The ability to recognize kin often facilitates an extreme division of physical and reproductive labor in social insects. Ants, social bees, and social wasps use colony-level chemical "profiles" to identify relatives and expel intruders without the same cues, avoiding exploitation by outsiders. Pheromones can also directly mediate the reproductive division of labor. Queen honeybees produce pheromones that both limit the development of ovaries in workers and attract drones (males) to mate (Hoover et al. 2003). These chemicals ensure that only queens reproduce in a colony.

**Mate choice:** In social insects, mating behavior is generally limited to the queen (ants and social bees), king (termites), and reproductive workers (semisocial wasps). There are few such limitations in solitary insects, where males and females alike use pheromones to attract and locate mates. When the chemical causes searching behavior, it is referred to as a *sex attractant*; when it induces mating behavior, it is called an *aphrodisiac*. Moth sex attractants are particularly well studied, as females release long-distance pheromones (30+ miles in some silkworm families) that signal availability to receptive males. In tiger moths, females select males based on pheromone production, which acts as an honest indicator of male fitness (Lofstedt 1993). In species with multiply-mating females, males use chemicals to ensure paternity. For example, tsetse fly sperm contains chemicals that act as an anti-aphrodisiac, discouraging other males from mating with a female (Carlson and Schlein 1991).

There are several advantages to chemical communication in insects. Most chemicals are highly effective in low doses, meaning that small quantities can provoke behavioral responses. Chemical signaling is therefore less metabolically expensive

than many other forms of communication. Chemicals do not degrade quickly or become harder to sense in different visual conditions; they are effective across long distances and many environments. However, since long-distance signals depend on air transmission, chemical communication may not be as effective if a receiver is upwind of a signaler. Chemical signals are also not as variable as acoustic signals, and thus do not carry as much information about the signaler. While less conspicuous than visual and acoustic signals, predators can still exploit chemical cues. For example, parasitoid wasps can mimic the scent of their prey to infiltrate habitats and lay parasitic eggs and larvae.

**Vibratory signaling** involves the use of low-frequency, substrate-borne (rather than air-borne) vibrations to communicate. Insects produce vibrations in diverse combinations of percussive drumming, tremulation or abdominal and body jerking, tymbal clicking, and stridulation.

**Predator avoidance:** Many termite species produce vibrational signals to warn nest mates of predator disturbances or pathogenic fungal spores in the nest (Kirchner 1997; Rosengaus et al. 1999).

**Resource localization:** Interestingly, vibrational communication plays a large role in the evolution of some *mutualisms* between different insect species. Larvae and pupae of ant-associated butterflies produce substrate-borne signals that attract high numbers of ants, thereby increasing their protection against predators (Travassos and Pierce 2000). Perhaps the best example of vibratory insect communication is in group-living treehoppers, which communicate almost exclusively using vibratory signals. Vibratory signals are associated with defense and parental care (Cocroft 1999) and are used to locate feeding sites (Cocroft 2001). Similarly, gregariously living sawfly larvae use vibrational signals that maintain colony cohesion and locate fresh food sources (Cocroft 2001).

**Mate choice:** Male treehoppers send vibrations that attract females, and responsive females will signal in return. Before mating, males and females will engage in vibrational duetting, with the male and female signaling back and forth. Some

crickets and katydids also use vibrations to attract mates.

Vibrations are an essential form of communication for many small insects. In order to effectively communicate with air-borne acoustic signals, smaller insects need to produce very high-frequency signals, which are prone to greater degradation (Bennet-Clark 1998). Thus, smaller insects use vibrational signals because they are far-reaching and relatively low cost. Propagation of vibrational signals is also less diffuse, and the signal is confined to the substrate through which it is being sent. Therefore, it is easier to locate, but less likely to attract aerial predators. As long as the continuity of the substrate is maintained, the transmission of a vibratory signal is not greatly affected by obstacles in its path. Substrate-borne communication has some disadvantages. Primarily, vibratory signals are distorted in time and frequency, and vibrations become more degraded with increasing distance between the signaler and the receiver.

**Multimodal communication**, or the use of signals in two or more modalities, is ubiquitous in insects. In fact, unimodal signaling may be the exception rather than the norm. These signals can either convey different messages about the signaler or redundant information to reinforce the impact of one message (Hebets and Papaj 2005).

*Resource localization:* Honeybees use visuals, vibrations, and chemicals in different parts of the waggle dance to elicit foraging behavior from their hive mates (Hölldobler 1999).

*Predator avoidance:* Wood tiger moths use both aposematic coloration and chemical signals to warn blue tits against eating them; the combination of signals is a more effective deterrent than either in isolation (Rojas et al. 2019). Similarly, some species of ants use a combination of vibrational tapping and alarm pheromones to warn hive mates of danger (Hölldobler 1999). Alarm chemicals are more effective than vibrations, but the combination has the most impact.

*Mate choice:* Male field crickets use both courtship songs and contact chemicals to attract mates, conveying different information about male fitness in each one (Simmons et al. 2013).

Similarly, some katydids use air-borne sounds and substrate vibrations during courtship to improve the localization of a stridulating male (Kalmring et al. 1997). In some chorusing insects, like those in the family Gryllotalpidae, the vibrational component of the male advertisement call determines how far apart calling males are from each other in the wild (Hill and Shadley 2001). Male *Drosophila* also use vibrational tapping and chemical aphrodisiacs to attract mates (Butlin et al. 2011).

## Conclusion

The world around us is full of insect signals – the electric iridescence of the emerald green ash borer, the soothing song of a serenading cricket, the marching ants directing each other with chemicals, and the vibrational duetting of tree-hoppers. Insects have evolved incredible means of communicating in many contexts. In addition to representing the spectacular diversity of signal evolution, the study of insect communication has many implications for the overall study of animal behavior. Like most animals, insects can communicate information about identity, status, future actions, environmental discoveries, etc. to multiple receivers (Bradbury and Vehrencamp 1998). Studying how such signals evolve across insect taxa can help elucidate general evolutionary principles. The many modalities that insects use to communicate also inform the creation of human biomimetic devices. For example, the incredible sound localizing abilities of the tachinid fly *Ormia ochracea* prompted the development of a new line of hearing aids (Kuntzman and Hall 2014). Studying insect communication also has various practical implications. The field of forensic entomology relies on understanding how insect localize and communicate resources to glean important information at crime scenes. Studying the signals requisite to mate attraction and other biologically relevant function can inform conservation practices for endangered insect species. Lastly, researchers have used mating and resource localization

signals to develop reproductive suppression and biological control plans in pest management.

## Cross-References

- ▶ [Aposematism](#)
- ▶ [Arthropod Cognition](#)
- ▶ [Bear Sensory Systems](#)
- ▶ [Chemical Signals](#)
- ▶ [Chemoreception](#)
- ▶ [Communication](#)
- ▶ [Insect Sensory System](#)
- ▶ [Modality](#)
- ▶ [Olfactory Perception](#)
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- ▶ [Predator Defense](#)
- ▶ [Predator Detection](#)
- ▶ [Secondary Sex Characteristics](#)
- ▶ [Sensory Receptors](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Sexual Selection](#)
- ▶ [Visual Recognition of Prey and Predators](#)

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## Insect Diet

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## Definition

Insect diet refers to the food usually eaten by an insect for growth, tissue maintenance, and reproduction, as well as the energy necessary to maintain these functions.

## Introduction

Most insects have qualitatively similar nutritional requirements in proteins, carbohydrates, lipids, vitamins, minerals, trace elements, and water (Table 1). These chemical compounds can either be synthesized by the insects themselves, provided by beneficial symbionts or acquired in food (Chapman 2012). Insect diets, and thus the fraction of nutrients acquired in food, can considerably vary among species and developmental stages of the same species, resulting from adaptations to particular environments in which access to nutrients is restricted by the types and diversity of foods available. Herbivores, which make up the majority of insects, eat plants and are typically trophic specialists, which means that they consume only one or a few plant species. By contrast, entomophagous, carnivorous, zoophagous, detritivorous, xylophagous, graminivorous, and omnivorous insects tend to be more generalists.

While the domestication of insects started somewhere around 5000 years ago, with the cultivation of silkworms and honey bees, research on insect nutrition only developed at the beginning of the twentieth century. Key discoveries were made



possible through the multiplication of attempts for designing artificial diets, whose composition can be only partly (meridic diet) or fully (holidic diet) defined. In 1908, Bogdanov was the first to rear an insect (blowflies) entirely on an artificial diet made of peptone, meat extract, starch, and minerals. Since then, famous entomologists, such as Painter, Fraenkel, Dadd, Waldbauer, Dethier, Scriber, and Slansky and Bernays and Chapman, among others, have developed methods and concepts that set a revolution for research on animal nutrition (for a brief thematic history, see (Raubenheimer et al. 2009)). These experiments demonstrate that insects actively attempt to achieve of nutritional balance by carefully regulating their intake of several nutrients simultaneously either from artificial diets or natural foods. Beyond advancing fundamental knowledge on insect nutrition, this research also provided a framework for a series of pioneering nutritional ecology studies that helped establish major concepts of biology and ecology, such as, for instance, ecological niches.

## Nutrients

Foods are complex mixtures of nutritional and non-nutritional (sometimes toxic) compounds. For insects, these compounds typically involve

macronutrients (proteins, carbohydrates, and lipids), micronutrients (vitamins and minerals), and water, which all directly participate to physiological functions (Cohen 2015). Some of these nutrients are essential, which means that insects lack the ability to synthesize them on their own and must acquire them in food or from beneficial symbionts (Table 1). Others, such as food additives (stabilizers, preservatives, bulking agents) and token stimuli (plant secondary compounds) have no direct nutritional function.

## Proteins

Proteins are made of amino acids (organic compounds containing an amino (-NH<sub>2</sub>), carboxyl (-COOH) groups, and a specific chain) and are the principal source of nitrogen for insects. While free amino acids can be present in foods, most often they are linked together by peptide bounds to form proteins. Once assimilated, proteins are broken down into their amino acid components and turned into different proteins that can be used for a wide range of biological functions, such as cell structure, enzymes, transport and storage, or receptor molecules. Insects require nine to ten essential amino acids (Table 1). The others, non-essential, amino acids are generally synthesized in the fat body provided that precursors are available in the food, although other tissues can also be

**Insect Diet, Table 1** Minimal (irreducible) nutrients shown to be useful or essential to insects. Depending on species, some of these nutrients can be nonessential or even toxic (e.g., cellulose). (Modified from (Cohen 2015))

| Proteins              | Lipids                | Carbohydrates   | Vitamins               | Minerals   |
|-----------------------|-----------------------|-----------------|------------------------|------------|
| Polypeptides          | Sterols               | Hexose          | Water-soluble vitamins | Calcium    |
| Glycoprotein          | Cholesterols          | Glucose         | Ascorbic acid          | Chlorine   |
| Lipoprotein           | β-Sitosterol          | Fructose        | Thiamine               | Copper     |
| Essential amino acids | Stigmasterol          | Disaccharides   | Riboflavin             | Iron       |
| Arginine              | Campesterol           | Sucrose         | Pyridoxine             | Magnesium  |
| Histidine             | 24-methyl-cholesterol | Polysaccharides | Nicotinic acid         | Manganese  |
| Isoleucine            | Phospholipids         | Starch          | Pantothenic acid       | Phosphorus |
| Leucine               | Fatty acids           | Glycogen        | Biotin                 | Potassium  |
| Lysine                | Linoleic acid         | Cellulose       | Folic acid             | Sodium     |
| Methionine            | Linolenic acid        |                 | Choline                | Sulfur     |
| Phenylalanine         |                       |                 | Cyanocobalamin         | Zinc       |
| Threonine             |                       |                 | Inositol               |            |
| Tryptophan            |                       |                 | Lipid-soluble vitamins |            |
| Valine                |                       |                 | Tocopherol             |            |
|                       |                       |                 | Vitamin A              |            |

important (e.g., proline and glutamine are synthesized in the mosquito midgut). Most proteins contain approximately half essential and half non-essential amino acids.

### Lipids

Lipids consist of fatty acids, phospholipids, and sterols. Lipids are an important source of energy, essential components of cell membranes, nutrient transporters, and defensive compounds, serve as pheromones, and are involved in hormone synthesis (e.g., sterols are involved in ecdysteroid or molting hormones and fatty acids in juvenile hormone). Insects can synthesize most fatty acids and phospholipids. However, to do so, polyunsaturated fatty acids are required in the diet. Sterols can serve for energy and the production of hormones and carbohydrates. The major essential sterol, the cholesterol, is abundant in animal tissues but only present in low quantities (if not present at all) in plants and fungal food. Therefore, most phytophagous insects must synthesize cholesterol via dealkylation of plant sterols (e.g.,  $\beta$ -sitosterol and campesterol) (Behmer and Nes 2003).

### Carbohydrates

Carbohydrates include simple sugars (e.g., the monosaccharides sucrose, fructose, glucose, maltose), starch, and other polysaccharides (e.g., cellulose). They serve as respiratory fuel, provide the carbon basis in molecular synthesis, and constitute building materials for the insect cuticle (e.g., polysaccharide chitin). Insects can synthesize glucose by gluconeogenesis from lipids or amino acids (Miyamoto and Amrein 2017) in such a way that some species can live without any sugar intake at all (e.g., wax moth and screw-worm). By contrast, other insects require considerable amounts of carbohydrates in their diet (e.g., honey bee or locust). Not all sugars are usable by all insects (e.g., melibiose is digested by many flies but not by honey bees), and some monosaccharides can be toxic because they compete with other essential sugars (e.g., mannose blocks glucose pathway in bees). The digestive capability for carbohydrates also varies among insect species. For instance, flour beetles can hydrolyze a

broad range of polysaccharides, whereas the grasshopper *Melanoplus* only accepts simple sugars. Digestibility of carbohydrates also varies between developmental stages of the same species (e.g., mosquito larvae use starch and glycogen while adults cannot). Cellulose cannot be digested by most insects and thus has no nutritional value.

### Vitamins

Vitamins are organic compounds required in trace amounts for growth. Vitamins are classified in two groups depending on their solubility in water or lipid. Water-soluble vitamins have a relatively short half-life (excreted and lost from the insect's metabolic pool), while lipid-soluble vitamins remain compartmentalized in lipid stores. The main water-soluble vitamins include vitamin C (ascorbic acid) and the B vitamins. Vitamin C serves as phagostimulant and antioxidant and promotes the synthesis of collagen and the extracellular matrix in insects. The B vitamins are involved in many metabolic pathways, including ATP production (thiamine, riboflavin, niacin), acyl group transfer (pantothenate), and growth factor (biotin and folic acids). Some insects also require small quantities of other water-soluble vitamins such as choline (for the production of cell membrane), carnitine (for lipid metabolism), cyanocobalamin, and lipoic acid. Lipid-soluble vitamins essential to insects are the vitamin A complex ( $\beta$ -carotene and related carotenoids relatives) and vitamin E (tocopherols). Vitamin A is required for visual pigments function and formation. Vitamin E serves as fertility factor, including spermatogenesis and egg maturation.

### Minerals

Calcium, chloride, copper, iron, magnesium, manganese, phosphorus, potassium, sodium, and zinc are vital in small quantities to many insects. These compounds are involved in the synthesis of coenzymes and metalloenzymes. Potassium, chloride, calcium, and sodium are essential for the excitability of tissues (e.g., muscle cell and neurons). Potassium and magnesium are major actors of the bioenergetics activity, respectively, via the ATP and glycolysis pathway. Pollutant minerals, present in the environment and passively ingested

by insects, can replace dietary minerals and act as toxins.

### Water

Water is essential to all insects. It provides the medium in which all metabolic processes proceed. As such it is necessary for the absorption of macronutrients. Water often contains naturally occurring micronutrients such as mineral salts. Insects actively ingest free water, have physiological mechanisms controlling thirst, and suffer fitness consequences if water is excessive or deficient in the diet. Meal size and inter-meal duration are both influenced by free water availability.

## Consequences of Diet on Behavior and Physiology

Insects have evolved behavioral and physiological strategies to acquire appropriate amounts and balances of the required nutrients from complex food mixtures. In most environments, no single food provides an optimally balanced diet for the insects. In such case, individuals must adjust their dietary choices and nutrient assimilation rates to reach and maintain a balanced diet (Simpson and Raubenheimer 2012).

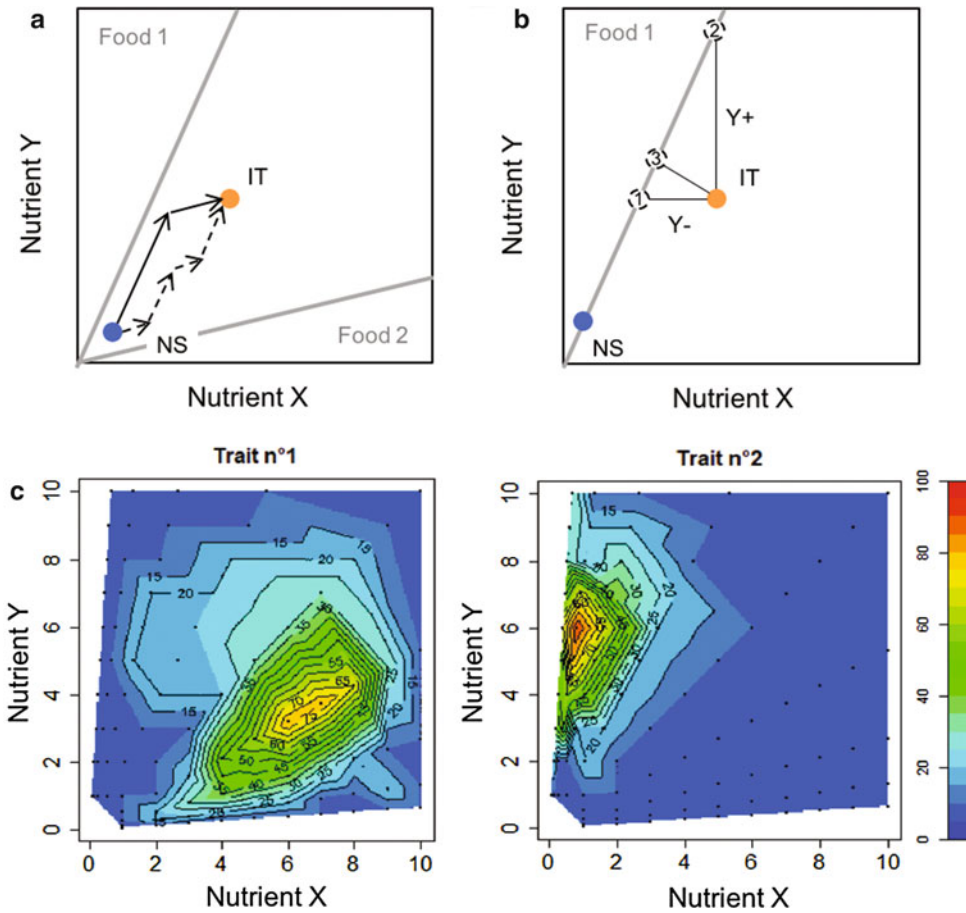
### Studying Nutrient Regulation: Nutritional Geometry

The study of nutrient regulation by insects took a significant step forward at the end of the twentieth century when Raubenheimer and Simpson (1993) introduced a unifying theoretical framework for nutrition studies known as “nutritional geometry.” This framework employs a state-space modeling approach taking into account the multiple interactions among mechanisms regulating the intake of different classes of nutrients. Individual insects, foods, and their interactions are represented graphically in a geometric space (a nutrient space) defined by two or more food components, typically carbohydrates and proteins (see examples Fig. 1). Foods are radials through the nutrient space at angles determined by the balance of nutrients they contain (nutritional rails). The insect’s state (nutritional state) is a

point or region that changes over time. As the insect eats, its nutritional state changes along the rail for the chosen food. The functional aim for the insect is to eat foods in appropriate amounts and ratio to direct it to an optimal nutritional state (intake target). This intake target moves over time as the quantity and mix of nutrients change with activity, growth, development, reproduction, and senescence. For instance, in larval insects, early stages typically have diets richer in nitrogen than later stages. The intake target also shifts over evolutionary times as insects adapt to different diets. Insects that feed on other animals have high amino acid and fat requirements relative to carbohydrates, reflecting the relatively high protein and low carbohydrate content of animal tissues. Plant-feeding insects, however, generally require approximately equal amounts of amino acids and carbohydrates. Over the past decades, nutritional geometry has proved a powerful tool to understand how insects and other animals balance their diet across a wide diversity of taxa, feeding guilds and ecological of environments both behaviorally and physiologically (for a recent review, see (Raubenheimer and Simpson 2018)).

### Behavioral Regulation

An insect can respond to a dietary imbalance in one of three ways. First, it can move from eating one food to another with a different nutrient balance. Hence, when given a choice between complementary foods (foods defining a nutrient space containing the intake target of the animal), most insects have been shown to self-compose a nutritionally balanced diet (Fig. 1a). This is possible because insects have separate appetites for different nutrients. Grasshoppers, caterpillars, aphids, flies, and cockroaches regulate their intake of protein and carbohydrates to a single intake target. Predatory ground beetles (Carabidae) have separate protein and lipid appetites. In locusts, levels of water are also regulated together with protein and carbohydrates (Clissold et al. 2014). This ability to adjust food intake to nutritional requirements implies some feedback of nutritional status on food selection and feeding behavior. In locusts, blood-borne nutrient feedback from eating a diet rich in amino acids depresses the sensitivity of peripheral contact



**Insect Diet, Fig. 1** Examples of nutritional geometry models for hypothetical insects. (Modified from (Lihoreau et al. 2018)). (a) Nutritional rails (gray lines) represent the ratio of nutrients X and Y in foods. The blue dot is the nutritional state (NS) of the individual, and the red dot is its intake target (IT). Foods 1 and 2 are individually imbalanced but complementary (fall on opposite sides of the IT). The individual can reach its IT by combining its intake from the two foods (arrows). (b) The

individual is restricted to a single imbalanced food and can (1) satisfy its needs for Y but suffer a shortfall of X; (2) satisfy its needs for X but over-ingest Y; and (3) suffer a moderate shortage of X and excess of Y. (c) Nutritional performance landscapes showing the effects of nutrients X and Y on fitness traits 1 and 2. In this example, trait 1 is maximized for a high X to Y ratio, whereas trait 2 is maximized for a low X to Y ratio

chemoreceptors to amino acids in the diet but has no effect on the sensitivity of chemoreceptors to sucrose. Conversely, if the insect feeds on a diet with high levels of carbohydrates, the sensitivity of its receptors to sucrose is depressed. In species that heavily rely on learning and memory for foraging, such as bees, cognitive capacities are crucial for nutrient balancing by enabling insets to associate the quality of the food with feedback on their own nutrient status based on the visual, olfactory, and tactile characteristics of foods. In drosophila,

protein appetite in mated females results of a sex peptide that is introduced with male's seminal fluid during mating, which stimulates special sensory neurons in the female's reproductive tract. An additional mechanism responding to the protein demands of egg development then controls how much yeast is eaten, involving TOR/S6 kinase and serotonin signaling pathways in the central nervous system (Vargas et al. 2010).

Second, insects feeding on imbalanced foods can also adjust the total amount ingested to

acquire enough of the most limiting nutrients. Grasshoppers, caterpillars, cockroaches, aphids, and ants have been shown to increase the amount eaten if the entire nutrient composition of a diet is diluted with some inert non-nutritional substance. Insects can also selectively compensate for deficiencies in a class of nutrients by increasing the total amount eaten. When confined to a single, nutritionally imbalanced food (that does not allow the intake target to be reached), insects can compromise between overconsuming excess nutrients and eating too little of the nutrients in deficit. The form of this compromise in a nutrient space varies according to the nutrients involved and the ecology of species (Fig. 1b). For instance, when forced to ingest diets containing an unbalanced ratio of proteins and carbohydrates, specialist migratory locusts (*Locusta migratoria*) do not substantially overconsume the excess nutrient to decrease its deficit of the other nutrient. In contrast, in the generalist desert locust (*Schistocerca gregaria*), individuals ingest a greater amount of either protein or carbohydrate to gain more of the more limiting nutrient. This pattern of host-plant generalists being more willing to tolerate nutrient excesses than host plant specialists is widespread across grasshoppers and caterpillars and is accompanied by a greater tendency by generalists to store excesses in body reserves (Behmer 2009).

### Physiological Regulation

A third mechanism to face food nutritional imbalance is to adjust the efficiency with which the insect uses the ingested nutrients. The importance of such post-ingestive regulation has been best studied in locusts. These insects maintain a relatively constant increase in body nitrogen despite a threefold increase in the amount of nitrogen ingested. Most of the excess of protein is excreted as uric acid or some other unknown nitrogenous end product of catabolism. Other means of post-ingestive regulation include differential secretion of digestive enzymes to lower the efficiency of digestion excess carbohydrate or protein in the diet, the adjustment of the timing of gut emptying to alter the ratio of protein and carbohydrate absorbed from the gut, the increase of metabolic

rate to burn off excess ingested carbohydrate, or the selection of environmental temperatures that favor the utilization of either proteins or carbohydrates.

### Consequences of Diet on Fitness

Although some growth occurs on foods containing widely differing levels of nutrients, optimal performance requires the nutrient levels to be appropriately balanced. Ingesting and processing excessive quantities of food in order to obtain enough of a particular component that is present only in low concentration in the diet can prove costly in various ways. Firstly, some nutrient excess can be toxic or have deleterious effects (e.g., excess of carbohydrates can result in obesity-like syndromes in many insects). Secondly, interconversions from one compound to another can be metabolically costly and the rates at which they occur limited. These effects can affect a wide range of fitness traits such as growth, development, reproduction, immune responses, cognition, and life span. The interacting effects of nutrients on fitness traits are evident when mapping insect performances into nutrient spaces of nutritional geometry (Fig. 1c). Different traits often have different nutritional optima, which means that insects must make feeding decisions to trade-off between optimizing multiple traits simultaneously. The ability of insects to resolve these nutritional trade-offs has been first demonstrated in the fruit fly *Drosophila melanogaster* (Lee et al. 2008). When confined to 1 of 28 artificial diets varying in protein and carbohydrate content, female flies achieve a maximum life span on a diet containing a 1:16 ratio of protein to carbohydrate, while maximum egg laying rate is reached on a 1:2 protein to carbohydrate ratio. When allowed to self-select complementary foods, flies mix a diet comprising a 1:4 protein to carbohydrate ratio which maximizes lifetime egg production, a measure of global fitness. Similar trade-offs have been observed in many other insect species for life span and reproduction, immunity and reproduction, or even traits related to different stages of reproduction that cannot be attained simultaneously.



## Consequences of Diet on Biotic Interactions

Upon its influence on the physiology, behavior, and fitness of individual insects, the diet can affect social behaviors and interspecific interactions (e.g., with symbionts, competitors, predators) and ultimately influence species assemblages and communities.

### Social Behavior

In gregarious and social insects, diet influences collective behaviors and social structures (Lihoreau et al. 2018). At the most basic level, a deficit in key nutrients in the environment can generate mass movements. In the Mormon cricket, *Anabrus* the lack of proteins and mineral salts due to intense competition and food depletion during population outbreaks triggers intense cannibalistic interactions. By attempting to eat each other, crickets engage in mass migrations, whereby millions of individuals form marching bands extending over several kilometers (Simpson et al. 2006). In social caterpillars that forage in trails, differences in the nutritional states among trail members determine the identity of leaders (hungry) that guide the group and followers (well-fed) that follow behind. In more integrated insect societies, differences in early food experience can also mediate reproductive division of labor. This is the case in cooperative breeding burying beetles that feed on shared carcasses, where dominant females that access food in priority ingest more proteins and become breeders, whereas subordinate individuals that acquire relatively less proteins become sterile helpers. In eusocial insects, such as honey bees, differential nutrition of the larvae influences caste determination, so that female larvae fed a diet rich in royal jelly become reproductive queens, whereas female larvae fed lower levels of jelly become sterile workers.

### Ecological Interactions

#### Symbionts

An estimated 10% of all insects utilize diets that are nutritionally so poor or unbalanced that they

depend on beneficial symbiotic organisms for sustained growth and reproduction. These associations provide them with metabolic capabilities or additional nutrients (e.g., essential amino acids in insects feeding on plant sap, vitamins in insects feeding on blood, and sterols in insects utilizing wood). In some insects, resident microorganisms degrade complex dietary components to a form that can be assimilated by the insect. This is the case of termites that rely on a rich gut microbiota community to degrade cellulose or soil matter (Bignell et al. 2010). In plant-sap feeding hemipterans that eat phloem and xylem low in essential amino acids, the microorganisms have a biosynthetic function. In *Drosophila*, where gut symbionts are acquired from the environment, variations in microbe communities can trigger different foraging strategies in the hosts that need to compensate for different nutrients (Wong et al. 2017). Other insect species have evolved ectosymbiotic associations. This is the case of fungus-farming termites and leaf-cutter ants that cultivate their own crop in well-protected gardens. In these social insects, foragers collect plant materials not digestible by the insects to feed a fungus that provides accessible key nutrients to the insects. In ants, workers regulate food intake to nourish the fungus with nutrient balances that maximize the production of edibles for the colony, at the expense of fungus reproduction (Shik et al. 2016).

#### Parasites and Pathogens

The diet can also affect the immunological responses of insects and their interactions with parasites and pathogens. For instance, caterpillars of the African cotton leafworm (*Spodoptera littoralis*) infected with either a bacterial or viral pathogen survive better as the ratio of protein to carbohydrate in the diet is increased despite the toxic effect of protein on life span. By contrast, uninfected larvae perform best on an intermediate nutrient ratio. When given a choice between multiple artificial diets, infected caterpillars tend to increase their consumption of protein, which has the consequence of enhancing the immune response, a nutritional behavior akin to self-medication (Lee et al. 2006).

### Dietary Breath and Niche Partitioning

At a broader observation scale, variation in insect diet can determine the coexistence of species and shape local development of biodiversity. For instance, closely related species of generalist-feeding herbivores (grasshopper species in the genus *Melanoplus*) eat protein and carbohydrates in different absolute amounts and ratios even if they eat the same plant taxa (Behmer and Joern 2008). The existence of species-specific nutritional niches, such as this one, provides a cryptic mechanism that helps explain how generalist herbivores with broadly overlapping diets coexist.

### Conclusions

There is a long history of developing artificial diets to culture insects for the food industry and academic research. This approach has showed that most insects have qualitatively similar requirements for macro- and micronutrients as other animals. Over the past decades, new concepts of nutritional ecology have moved the focus from the identification of essential and nonessential nutrients in insect diet to the study of interactions between food components and their consequences on fitness. Insects have evolved sophisticated behavioral and physiological strategies to reach and maintain nutrient balances and concentrations maximizing multiple fitness traits, and this is flexible throughout development. These consequences of diet can be observed at the individual level and beyond, across levels of biological organization. Integrative approaches of modern insect nutrition research offer a means for addressing more general problems in ecology, including the structuring of food webs, the regulation of food chain length, the flow of nutrients through ecosystems, and the dynamics of communities and ecosystems (Simpson et al. 2015).

### Cross-References

- ▶ [Amino Acid](#)
- ▶ [Arthropod Diet](#)
- ▶ [Digestive System](#)
- ▶ [Division of Labor](#)

- ▶ [Energy](#)
- ▶ [Feeding](#)
- ▶ [Fitness](#)
- ▶ [Foraging](#)
- ▶ [Herbivore](#)
- ▶ [Lipid](#)
- ▶ [Nutrients](#)
- ▶ [Optimal Foraging Theory](#)
- ▶ [Protein](#)

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high reproductive capacity. At the broadest level, they are organized to produce the greatest number of successful, mature offspring. Almost all of them are born from eggs, with larvae and adults encased in an exoskeleton which is periodically shed to allow for an increase in body size.

Although some common groups can live for two or more years, most of them live for a short period of time. Some insects in the temperate region adopt strategies to remain active during the winter, while others migrate to a warmer climate or enter a state of torpor. There are species in which the number of generations is constant, with few occurrences during the year, and others that can complete their life cycle in a few weeks, with many generations per year.

These are just some of the ways in which insects adapt to life in the world around us. In this chapter, we point out the main patterns in the life history of insects, including interesting and often unique characteristics of types of reproduction, mating behavior, reproductive system, egg structure, embryogenesis, growth, and development.

## Insect Life History

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## Introduction

Insects are one of the most abundant and diverse groups of animals on Earth, inhabiting almost every conceivable terrestrial and freshwater environment and, less commonly, the marine habitat. Their morphological diversity and characteristics of life history are highly adaptable to live in various conditions, including extremes of heat and cold, wet and dry, and unpredictable climates. The success of the Insecta is largely related to their

## Types of Reproduction

The usual reproductive mode of insects is sexual reproduction. It consists in the fusion of male and female gametes to form the zygote. Except for Apterygota, where males deposit the spermatophore on the substrate for females to collect, the common way for insects to copulate is to transfer sperm directly to the female during copulation. In general, copulation occurs when the male introduces its copulatory organ into the female genital capsule. Less commonly, male use the aedeagus to pierce the abdomen of the female and inject sperm into the abdominal cavity. This unusual mode of copulation, known as traumatic insemination, occurs in fruit flies (Diptera), Stylopodia (Strepsiptera), and it is prevalent and best investigated in bed bugs (Cimicidae, Hemiptera) (Peinert et al. 2016).

Many insects reproduce asexually. The phenomenon of parthenogenesis, in which eggs do not need to be fertilized to develop embryos, is present in several groups. Parthenogenesis can be mandatory, but not as common as sexually

reproducing, or facultative. The latter may occur as a response to fluctuations in environmental conditions, or even when females fail to find a mate. An unfertilized egg can generate only female individuals (thelytokous parthenogenesis, e.g., aphids), only male individuals (arrhenotokous parthenogenesis, e.g., bees and ants), or individuals of both sexes (deuterotoky parthenogenesis, e.g., cynipid wasps and micro-malthid beetles).

Another way of asexual reproduction in insects is the polyembryony; it occurs when a single egg undergoes fission giving rise to two or more embryos. This sort of reproduction is restricted predominantly to Hymenoptera and few Strepsiptera, and seems to have evolved independently among different groups of animals. In the parasitic wasps, the number of embryos produced can be influenced by the size of the host, varying from 10 to several hundred embryos arising from one egg. Characteristically, the eggs of polyembryonic species are devoid of yolk, and its nutrition is acquired from the host's hemolymph through a specialized enveloping membrane called the trophamnion, a modification of the serosa layer (see [Embryogenesis](#) section).

## Mating Behavior

### Mate Location and Recognition

The reproductive success of the insect species depends on the synchronicity of gonadal maturation and the location of the mating place. It can be facilitated by several species-specific signals produced by each individual to find and attract a sexual partner of the same species. These signals can be visual, like the flashing lights of fireflies; acoustic, such as the song of cicadas and crickets; or chemical, where individuals release olfactory substances (sex pheromones) to be recognized by the opposite sex.

Another fundamental behavior of insects for bringing the sexes together is swarming. It is observed in several groups of insects such as dragonflies, mayflies, butterflies, and many dipterans. The individuals in the swarm are usually all males, although swarms of females also occur

in some species. The process of swarm formation is more evident when many individuals are involved, but a single male insect taking over a spot is also possible. In both cases, females use visual cues to identify the site. During group swarming, males commonly do not perform intrasexual aggression in the absence of females, and when they arrive, females are immediately grabbed and the copulation takes place without courtship. In some groups, such as drosophilid and tethritid fruit flies, aggressive males form substrate-based aggregations in order to defend a territory against conspecific males and court of arriving females.

### Courtship

Courtships rituals are intraspecific and intersexual behaviors that stimulate the receptivity of a potential partner before mating, especially in species where females are normally aggressive. These rituals have great influence on the choice of a partner by the female, being an important role in sexual selection. In general, the courtship includes visual displays of adorned parts of the body and specific movements, including sound production. Male of some drosophilid fruit flies, per example, vibrate their wings producing a sound that has a function both as a sexual stimulant and in sexual isolation (Costa and Sene 2002). In many groups of insects, tactile stimulation using the antennae, palps, and legs occurs with the proximity of individuals before mating, and may continue during copulation. An interesting example of courtship can be seen in the hanging flies (Bittacidae) and dagger flies (Empididae), where males offer to the females a prey as a nuptial gift to be consumed during copulation. If the courtship is successful, and the movements are performed correctly, mating occurs (Vahed 2007).

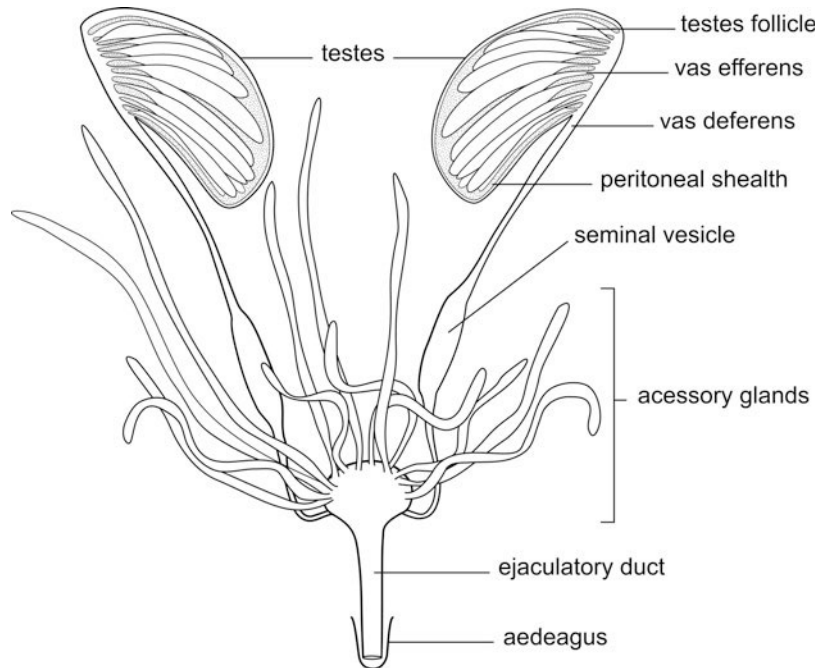
## Reproductive System: Male

### Internal Reproductive Organs

The reproductive system of male insects is typically formed by paired testes, vas deferens and vas efferens, seminal vesicle, a median ejaculatory duct, and several accessory glands (Fig. 1). The

**Insect Life History,**

**Fig. 1** Schematic drawing of an internal reproductive organ of a male insect showing its basic parts



paired testes may be located above or below the gut, connected or not with each other. They are responsible for the spermatozoa production after successive stages of maturation within a series of sperm tubes. While in some lepidopterans the testes can be fused to form a single structure, more primitive insects may have only a single testis. Individual vas efferens connect the sperm tubes to the vas deferens of each testis. The transport of sperm from the testes is made by peristaltic contractions of the muscular wall of the vas deferens which leads the sperm to the seminal vesicles. This structure is an enlarged area of the vas deferens and is frequently glandular, which may indicate a possible nutritive function. The terminal portion of the vas deferens is connected to the anterior tip of the ejaculatory duct, that is composed by a cuticular lining with walls entirely sclerotized. Posteriorly, the ejaculatory duct may run through an evagination of the body wall, which thus forms an intromittent organ, the aedeagus. In insects that form a complex spermatophore, subdivision of the ejaculatory duct into specialized regions may occur. The accessory glands may be attached with the vas deferens or the ejaculatory duct. They consist of a single layer

of cells that may be coated with a muscular tissue, and their number and forms are variable among insects. Male accessory glands become active and increase greatly in size as a result of the synthesis and accumulation of materials used in spermatophore and/or seminal fluid. They are also responsible for producing substances that affect the behavior and physiology of the female. During insemination, peptides produced by the accessory glands are frequently involved in triggering her reproductive processes, including oogenesis and oviposition, or terminating subsequent female mating behavior to prevent her from acquiring the sperm of another male. Since insects have a diversity of mating systems, the specific functions of accessory gland secretions are likely to reflect this variation.

### Sperm Production

The sperm tubes, or testicular follicles, are bound together by connective tissue or peritoneal sheath each one containing the gametes development areas. The follicle number varies considerably, with only 1 follicle in some coleopterans up to more than 100 in certain orthopterans. Within each follicle, several zones of development can



be readily distinguished. At the anterior portion is the germarium in which spermatogonia are produced from germ cells. As the spermatogonium moves posteriorly into the zone of growth, each one becomes enclosed by a layer of somatic cells to form cysts. Within the cysts, each spermatogonium undergoes mitotic divisions and then moves down to the zone of maturation. In this portion, the spermatocytes become haploid spermatids after multiple meiotic divisions and complete a developmental transformation into flagellated spermatozoa. At this point, the cyst wall breaks and the spermatozoa migrate to the seminal vesicles where they remain as a reservoir of sperm until the insect copulates with a female.

### Transfer of Sperm to the Female

The sperm and the seminal fluid are transferred from male to female during copulation into a process known as insemination. It may occur in distinct ways (indirect or direct insemination) and depends on a variety of circumstances such as male investment, female selection of mates, sperm competition, and structure of genitalia. In some cases, spermatophore (sperm packet) is produced by the male before copulation or, more often, as copulation proceeds. In the most primitive insects, the male deposits a spermatophore onto the substrate for the female to take it up to the reproductive tract; in springtails it occurs quite independently of the presence of a female, which preferably selects spermatophores of males that were exposed to a competitor (Zizzari et al. 2013). In more advanced insects, the sperm are transferred directly in seminal fluid and the spermatophore is no longer produced. In such instances, copulation involves the physical apposition of male and female genitalia and the transfer of seminal fluid via the insertion of part of the aedeagus into the reproductive tract of the female. The aedeagus is thin-walled and erected by hydrostatic pressure, either of the hemolymph or fluid contained within a special reservoir of the ejaculatory duct. It extends far into the genital tract of the female and ends adjacent to the spermatheca. Alternatively, the aedeagus may be rigid and erection achieved using muscles, penetrating only a short distance into the female's genital tract.

## Reproductive System: Female

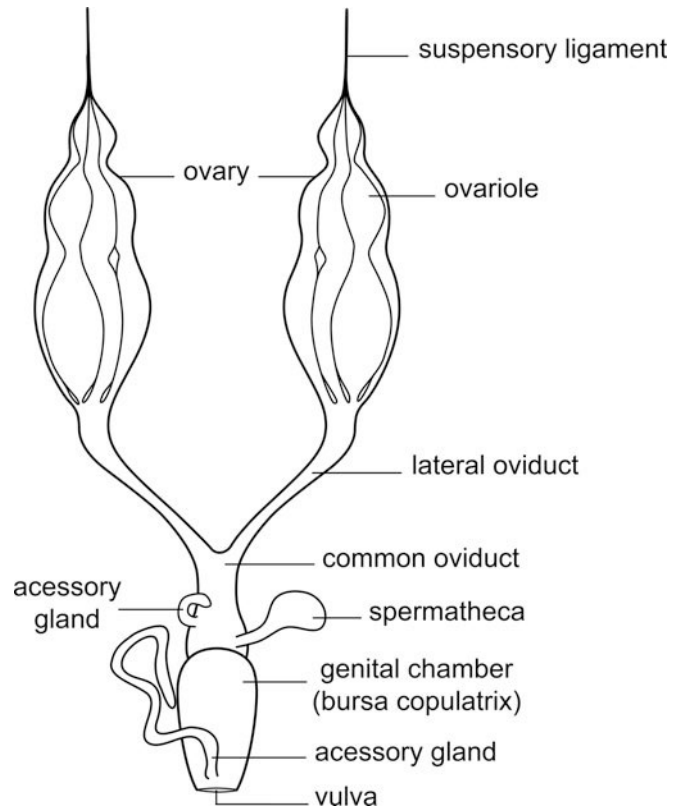
### Internal Reproductive Organs

The basic components of the female system are paired ovaries connected at their posterior ends by a pair of lateral oviducts that converge to a common oviduct (Fig. 2). Posteriorly, the common oviduct is confluent with the vagina. The ovaries are usually dorsolateral to the gut and are composed of a series of tapering units, called ovarioles. The number of ovarioles varies among species and its particular life history, being from 4 to 10 per ovary in most insects up to 1000 or even more per ovary in queen termites. At the anterior end of each ovary, all ovarioles are united by a suspensory ligament that anchors the ovary to the body wall. The essential parts of the ovarioles consist of a terminal filament, germarium, vitellarium, and pedicel. When fused, the terminal filaments form the suspensory ligament. The pedicel connects each ovariole to a lateral oviduct. This structure is characterized by a thin-occluded tube formed by epithelial tissue, which is lost during ovulation.

The common oviduct can be associated with multiple specialized structures as a spermatheca, genital chamber, bursa copulatrix, fertilization chamber, and accessory glands (Fig. 2). After insemination, the sperm are stored in the spermathecae and then released into the common oviduct through spermathecal ducts. The genital chamber is the result of a modification to the common oviduct capable of incubating eggs internally. Within the chamber is an additional pouch into which sperm are first deposited after mating, the bursa copulatrix. In some species, the bursa forms a diverticulum externally to the oviduct. In nearly all lepidopterans the bursa is physically distinct from the oviduct and opens to the outside via the vulva. A narrow sperm duct connects the bursa with the oviduct and forms the route along which the sperm migrate to the spermatheca where they are stored more permanently. Another additional sperm storage organ present in some acalyptate flies is the fertilization chamber, formed by a cuticular extension of the ventral wall of the bursa copulatrix. The sperm initially stored in the chamber is transferred to the

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**Fig. 2** Schematic drawing of an internal reproductive organ of a female insect showing its basic parts



spermathecae for long-term storage while a smaller number is retained in the chamber for the fertilization of eggs. It is believed that the presence of multiple sperm storage organs is driven by sexual selection making females able to manipulate the ejaculations, in addition, to reduce wastage of sperm prolonging their refractory period (Twig and Yuval 2005). Accessory glands may be present and usually open into the bursa, but in some groups, they are associated with the lateral oviducts. Among a variety of functions, the accessory glands are responsible for the production of substances for sperm maintenance, transport, and fertilization, as well as for the protection of eggs.

### Oogenesis

Within ovarioles, just beneath each terminal filament is the germarium, where the oocytes begin to grow from the oogonia. As oocytes mature, they pass back down the ovariole and are clothed by a follicular epithelium, which is derived from mesodermal prefollicular tissue located at the junction

of the germarium and vitellarium. Oocyte growth continues apace by cell division. In the vitellarium, the yolk is deposited in the oocytes in a process called vitellogenesis. At this stage, follicle cells no longer divide becoming stretched over the oocyte as a flattened squamous epithelium. As yolk accumulation nears its end, the function of the follicle cells changes and they produce the vitelline envelope and the ligands responsible for determination of the terminals of the embryo and its dorsal-ventral axis. In the last stage, they produce the chorion (eggshell).

### Ovulation and Fertilization of the Egg

The passage of an egg from the ovariole into the oviduct is known as ovulation. Muscular contractions of the oviduct walls are coordinated by hormones that are secreted by neurosecretory cells when the central nervous system receives a confirmation that mating has occurred and that eggs are indeed mature. In a first moment, the anterior portion of the spermathecae contracts, sperm are

forced down the spermathecal duct where they are held until sensory cells indicate that the egg has achieved the proper position in the genital chamber. Many female insects store the sperm that they receive from one or more males in their spermatheca. Sometimes, sperm may remain viable in the spermatheca for a considerable time, being maintained by secretions from the female's spermathecal gland; honey bees can store sperm for more than three years (Collins et al. 2006).

Eggs are fertilized as they pass down the median oviduct and vagina. At that point, the sperm enters the egg via one or more micropyles, a modification of the normally impermeable chorion. The micropyle or micropylar area is orientated towards the opening of the spermatheca during egg passage, facilitating sperm entry.

### Oviposition

Once fertilized, the eggs pass from the external genital opening or vulva to the outside of the female body through an ovipositor. This process is controlled by peristaltic waves of muscle contractions. In most insects, the ovipositor consists of two to three pairs of slender valves, the valvulae, arising from basal plates, or valvifers, on the eighth and ninth abdominal segments. The third pair of valves originates from the posterior region of the second valvifers. Accessory glands of the common oviduct may produce cement that allows the deposited eggs to be glued together or attached to the substrate. Alternatively, in some insects, the eggs may be retained for variable periods until the eggs hatch or the larvae mature.

Oviposition is often associated with behaviors such as digging or probing into an egg-laying site. The eggs may be deposited on or near the food required by the offspring upon hatching, but often they are simply dropped to the ground or into water.

## Egg and Embryology

### Egg Structure

Insect eggs are extraordinarily diverse in forms, mostly varying between spherical, oval, elongate,

conical, barrel-, or disk-shaped. The eggshell may also be sculptured with ridges, spines, or other processes, and some are brightly colored. However, their appearance may be affected by factors like adult body size, feeding habits, ecological and life history, and mainly by the ecology of oviposition (Church et al. 2019; Hinton 1946). Shifts to aquatic and internal parasitic oviposition, per example, were significantly associated with the evolution of different structures like respiratory horns in aquatic hemipterans, and smaller eggs in parasitoid wasps, allowing flexibility during passage down the narrow ovipositor.

Insect centrolecithal egg cells (oocytes) have a great amount of lipids and yolk, which serves as the source of nutrients for the development of the embryo. The cytoplasm is distributed in diffuse strands throughout the yolk (reticulum) and in peripheral bounding layer (periplasm). Nucleus usually occupies a posterior position, lying within the yolk. Enclosing all these components is the eggshell protecting the developing embryo from external elements, predators, and parasites.

The innermost layer of the eggshell is the vitelline membrane. It may vary in thickness in distinct insects and in different parts of the egg. In insects that lay eggs in dry places, a wax layer occurs adjacent to the vitelline envelope, assuring resistance to desiccation. Above the wax layer is a complex multilamellar chorion formed by two main layers: a proteinaceous endochorion and an exochorion rich in carbohydrate. The thickness and presence of both layers, however, is variable among many groups. Openings in chorion are restricted, limiting water loss. However, to allow gas exchange between the egg and environment, the chorion is perforated by microscopic pores (aeropyles). During fertilization, sperm entry to the oocyte is facilitated by the tiny openings of the egg called micropyles. Finally, the chorion of some species has a line of weakness along which it splits, allowing the larva to more easily escape during hatching.

Many insects are capable to produce extra egg coverings by secretions of female colleterial glands. Some insect lineages enclose their thin-shelled eggs in protective tanned or foamy outer covering (ootheca), notably orthopterans,

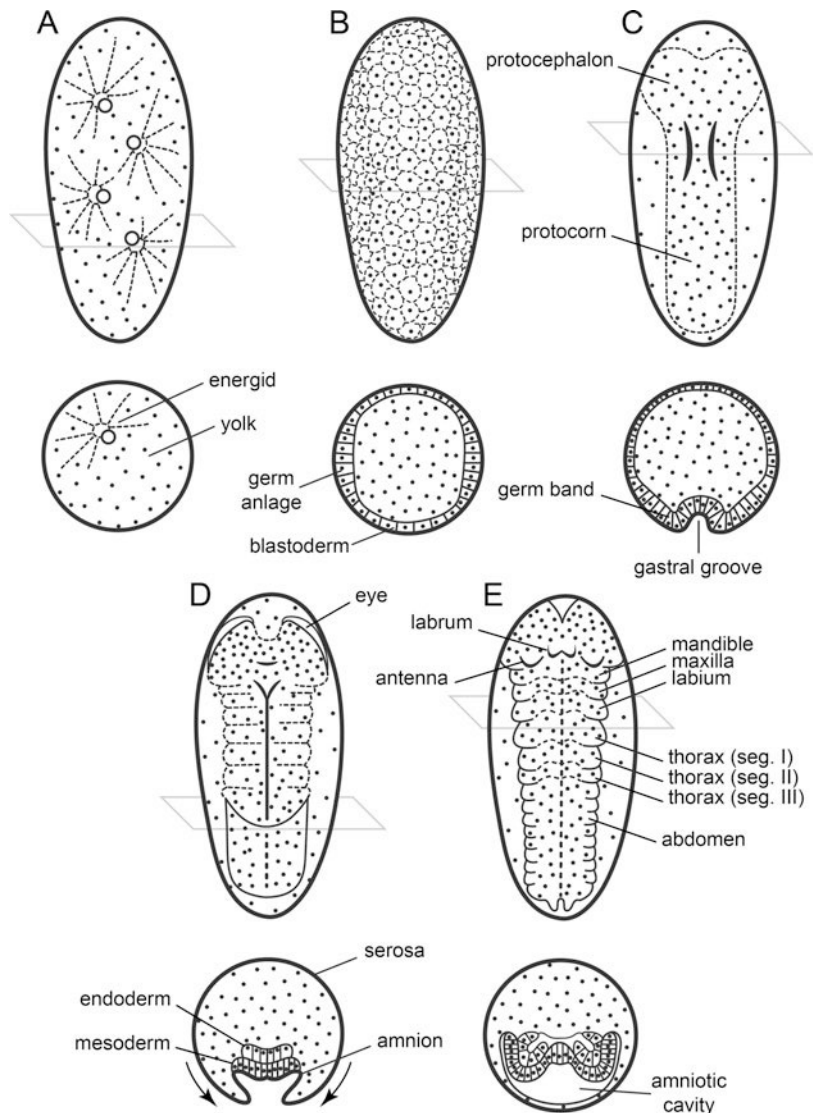
mantids, and cockroaches, or cover the eggs with some sort of protective material, like a proteinaceous secretion or cement.

## Embryogenesis

Embryogenesis begins once the egg has been fertilized. It involves multiplication of cells by mitosis, resulting growth, movement, and differentiation into all the tissues and organs. Due to a large amount of yolk, insect eggs undergo an unusual type of superficial cleavage.

In an earlier moment, there are no cell divisions and only the zygote nucleus divides. The daughter nuclei together with their surrounding cytoplasm (energids) migrate to the egg periphery to form a syncytium (Fig. 3a). After energids settle in the periplasm, nuclear division proceeds followed by subsequent cellularization, resulting in the blastoderm, a single sheet of cells that surrounds the yolk (periblastula stage) (Fig. 3b). Energid cells that drift to the posterior pole of the egg become the germ cells. They migrate later to the developing gonads and turn primary sperm and eggs. Insects with yolkless eggs may have complete

**Insect Life History, Fig. 3** Early stages of insect development. Figures below show cross-section of the eggs immediately above the following: (a) syncytial cleavage; (b) blastoderm and the thickened germ anlage; (c) gastrulation and formation of the gastral groove; (d) germ band after gastrulation, with segment borders and amniotic folds forming (arrows indicate the movement of the serosal cells to enclose the germ band); and (e) advanced germ band stage, with appendage buds, and transient coelomic sacs formed by the mesoderm



cleavage (with complete earlier division of cells), like parasitic wasps, aphids, and springtails.

Blastoderm cells of the ventral region differentiate into the germ anlage, a disc of cuboidal cells that will develop in the future embryo. The remaining blastoderm becomes the extraembryonic membranes (serosa and amnion). The serosa forms the yolk sac and later adjacent cells of germ anlage grow around it, enclosing the embryo in an amniotic cavity bounded by protective amnion membrane (Fig. 3) – serosa and amnion may remain connected or become completely separated. In many holometabolous insects (e.g., lacewings, dipterans, lepidopterans, and hymenopterans) the germ anlage develops from almost the entire blastoderm surface.

Gastrulation begins when the germ anlage thickens and becomes the germ band which corresponds to the ventral portion of the embryo. At this time, the formation of the three germ layers takes place. The mid-ventral cells of the germ band move upward into a space between the embryo and the yolk, thus forming a two-layered embryo with the outermost cells in contact with the amniotic cavity becoming the ectoderm, while cells bordering the yolk resulting the mesoderm (Fig. 3c). At this moment, the dorsal closure occurs, forming the lateral and dorsal parts of the embryo by growth and posteriorly mid-dorsal fusion of the edges of the germ band over the remaining yolk (Fig. 3d). The mesoderm proliferates inward as a longitudinal gastral groove, absorbing the yolk mass and paired coelomic spaces appear (Fig. 3e), while ectoderm ingrowths at the front and rear of the embryo’s body to form the mouth, anus, and fore and hindgut. Endoderm is formed later and results in the future midgut, which establishes contact with the fore and hindgut. It can be formed in three different ways: by the formation of a mid-ventral furrow that subsequently closes over (most orders), by the lateral

overgrowth of a mid-ventral plate (many hymenopterans), or by ingression of individual ventral midline cells (lepidopterans) (Heming 2003).

Segmentation and appendages formation take place nearly simultaneously with the gastrulation (Fig. 3d, e). These processes are controlled by a complex genetic regulatory cascade that specifies the insect body plan along the anterior–posterior axis (Peel et al. 2005). In most orders, the germ band is differentiated into a broad anterior region (protocephalon) and a narrow posterior portion (protocorm) (Fig. 3c).

During the remainder of development, both the mesodermal and ectodermal layers undergo differentiation into tissue-specific cell types and cell rearrangements required to form the final organ structures. Paired coelomic cavities develop as clefts in each segment of the protocorm and in association with the pre-mandibular and antennal segments in the protocephalon. At the same time, the primary body cavity (epineural sinus) develops as a space between the upper surface of the embryo and the yolk. During mesoderm differentiation the coelomic sacs collapse and their lumina fuse with the primary body cavity, thus forming a hemocoel (mixocoel). In Diptera, no coelom cavities are formed (Chapman et al. 2013). In metamorphic insects a cluster of cells invaginates below the ectoderm, forming imaginal discs that do not undergo any differentiation until later larval stages. The fate of germ layers during organogenesis is summarized in Table 1.

Polyembryony occurs in some insect taxa, particularly in parasitic Hymenoptera and few Strepsiptera. In this form of development, the early embryo splits clonally to give rise to two to thousands of embryos. The earlier embryo is referred to as primary morula and later enters the proliferation stage of embryogenesis. It results in the formation of an increasing number of secondary morulae, which consist of nondifferentiated

**Insect Life History, Table 1** Developmental fate of insects’ germ layers in organogenesis

| Germ layers | Organs and structures of adult insects                                                                                                                                  |
|-------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Ectoderm    | Epidermis, exocrine glands, brain and nervous system, sense organs, fore and hindgut, respiratory tracheal system, Malpighian excretory tubules, and external genitalia |
| Mesoderm    | Heart, blood, circulatory system, endocrine glands, muscles, gonads, and fat body                                                                                       |
| Endoderm    | Midgut                                                                                                                                                                  |



cells surrounded by extraembryonic membranes (Strand 2009).

## Viviparity and Ovoviviparity

In viviparity, the eggs are retained within the parental body after fertilization and the embryos receive nourishment directly from the mother. Due mainly to the lower number of functional ovarioles, viviparous species usually have fewer offspring. Three main types of viviparity frequently occur in different insect groups.

Pseudoplacental viviparity occurs when yolk-deficient or yolkless dechorionated eggs develop within the female genital tract and are nourished by a maternal placenta-like tissue (pseudoplacenta) through which nutrients are transferred to developing embryos. The oocyte is retained in the ovariole, being enclosed by the thickened follicle epithelium that forms a primary maternal pseudoplacenta. Later, it is replaced by an embryonic (fetal) pseudoplacenta formed by serosa and amnion. Nourishment may occur by a communication opening with another extraembryonic cavity (cephalic vesicle), by the ovariole sheath or directly by the serosa membrane, which turns into a trophic organ. Viviparous development continues up to the time of hatching. It is common among many aphids, earwigs, psocids, and polyctenid true bugs.

In adenotrophic viviparity, fully chorionated eggs normally develop in the uterus and larva hatches within it, being nourished by special secretions of maternal accessory milk glands. The larvae remain in the female until mature when they are laid and immediately pupate. A single chorionated oocyte is produced at a time, with another oocyte starting its development just before larviposition. It occurs only in a few blood-sucking dipterans, like tsetse flies (*Glossinidae*) and louse flies (*Hippoboscidae*).

In hemocoelous viviparity fertilization, development occurs in the hemocoel with nutrients taken up by osmosis directly from the hemolymph. Ovaries lack oviducts and larvae emerge from yolkless oocytes and go outside through female genital canals. It is common throughout strepsipterans and gall midges (*Cecidomyiidae*), in the latter case pedogenic larvae feed initially on

parental tissues before escape through a rupture in the female wall.

Ovoviviparous insects provide a safe internal brooding chamber to their developing egg-shelled oocytes but do not supply directly oxygen and nourishment. The embryos are nourished only by the egg yolk. The eggs are retained in genital tract until the offspring are ready to hatch or larvae are deposited just after hatch. Ovoviviparity occurs sporadically or obligatorily in many species of different orders, like mayflies, cockroaches, thrips, aphids and true bugs, moths, a few beetles, and several dipterans (e.g., *Muscidae*, *Sarcophagidae*, and *Tachinidae*).

## Postembryonic Development

### Hatching

The stimuli that give start to the hatching process are mostly unknown and the timing for insects to hatch seems to be intimately close to the development stage. It is known, however, that some factors like temperature, light, and oxygen may influence or even stop hatching from occurring. Insects use a variety of strategies to burst out of their eggs. Most of them simply force their way out by the increase of their body volume (ingestion of extraembryonic fluid and air) and by waves of muscular contraction that bumps the hemolymph to the head and thorax, applying pressure in the interior of the shell. In groups with a thick serosal endocuticle in the egg, hatching is aided by the production of an enzyme that digests this cuticle prior to the hatching process. Some cuticle structures, known as egg busters, also help in the hatching process and are found in a great number of insects, such as dragonflies, grasshoppers and crickets, true bugs, neuropterans, caddisflies, dipterans, beetles, and fleas (Richards and Davies 1997). They may possess many different sizes and shapes, from a central tooth to a pair or a row of spines. Their position in the body also varies, being present in the head, thorax, or abdomen.

The position of the egg rupture usually depends on where the insect puts pressure to hatch. This rupture can occur longitudinally or transversely, and also be guided by one or more

lines of weakness where the chorion splits (hatching line, explained in the [Egg Structure](#) section). After hatching, lepidopteran caterpillars eat the eggshell to their base, and sometimes may even eat the top of the adjacent unhatched eggs. Some insects may possess an embryonic cuticle that is shed during or soon after hatching, in a process called intermediate mould (Chapman et al. 2013).

### Immature Development

Postembryonic development is discontinuous and characterized by a series of stages, separated from each other by a moult and posterior ecdysis. They occur until the insect is an adult and no further (except in Apterygota groups). The moult is controlled by the prothoracicotropic hormone (PTTH), which is produced in the brain and stored at the corpora cardiaca positioned near the aorta wall. The PTTH is latterly released in great amount to initiate each moulting process. The series of stages (usually referred to as instars) mark a period of growth, but usually without a great change in body form. This is only different when the individual moults from the last larval instar to the adult stage. This last change, called metamorphosis, bears a variable amount of modifications usually related to the loss of larval adaptative features and the gain of adult ones, besides the development of the reproductive system. The extent of these modifications is related to the degree of ecological modifications between the last larva instar and the adult.

### Metamorphosis

The difference between the metamorphosis and the initial moulting process is the low level of the juvenile hormone (JH). This hormone, produced by the corpora allata, is responsible for inhibiting the development of adult traces throughout nymphal and larval life during the moulting process. During the last juvenile instar, the corpora allata becomes atrophied and stops producing JH. In adult insects, brain neurosecretions reactivate the corpora allata and JH is secreted again. It is essential in stimulation of the yolk production, spermatophore, and secretions of the accessory glands in males.

Insects can be classified into three categories regarding the changes during metamorphosis: ametabolous, hemimetabolous, and holometabolous. Ametabolous insects bear no differences between adults and juveniles, except that adults stop increasing in size and reach the reproduction maturity. In hemimetabolous groups, the larvae are morphologically similar to the adult, except for the absence of mature reproductive system and wings, and the presence of some larval features such as tracheal gills for aquatic groups. In the holometabolous, however, the larval morphology is completely dissimilar from that of the adult. Between the larval and adult phases, the pupal stadium grants the complete transformation in morphology to the adult form.

Larvae of hemimetabolous basically resemble adults and are commonly referred to as nymphs to distinguish them from the holometabolous, radically different larvae. In nymphs, the wings develop as external pods that become bigger at each moult, finally enlarging during metamorphosis. In holometabolous, the wings develop as invaginations of the epidermis and are only visible when everted during the pupal stadium. The larvae of holometabolous have a huge variety of forms, but they basically fit into three main patterns: the oligopod, with thoracic legs and usually well-developed head capsule and mouthparts; the polypod, which possess abdominal prolegs in addition to the thoracic ones; and the apod, with no legs and poorly sclerotized body. Polypods larvae are found on lepidopteran caterpillars, scorpionflies, some beetles, and hymenopterans sawflies. Oligopod and apod larvae are vastly spread throughout the holometabolous insect orders. An interesting feature, usually common but not restricted to parasite insects, is called hypermetamorphosis. It consists in the presence of two or more types of larvae in the life cycle of the same species and is common throughout microcaddisflies (Hydroptilidae), strepsipterans, and some beetles (Meloidae and Ripiphoridae).

As stated before, the degree of change between the larval and adult phases varies a lot when comparing different insect groups. In hemimetabolous insects, metamorphosis is responsible for the growth of the wing pads into fully formed

wings, besides the development of a membranous basal region and accessory sclerites. The genitalia are progressively developed by the modification of the terminal abdominal segments, but more remarkable changes occur during metamorphosis (Chapman et al. 2013). In holometabolous insects, the development of the adult's features is related to the degree of differentiation between the larvae and adult. In neuropterans and beetles, where the larvae are more similar to the adult, little reconstruction occurs. But in dipterans, per example, the larvae tissues are solved and digested and the adult tissues are almost completely restored (Jindra 2019).

There are two different types of pupae present during holometabolous metamorphosis: the exarate pupa, which has the appendages freely extended from the body, and the obtect pupa, which has the appendages glued to the body. A further differentiation regarding the mandibles is also possible. When articulated mandibles are present in the pupae, the condition is called decticous. The alternative condition, with immobile mandibles, is called adecticous (Hinton 1946). Most insect pupae are immobile and therefore vulnerable, requiring some protection. Many will pupate in a cell, chamber, or cocoon, or will bear protective structures (Gross 1993; Hinton 1946).

### Polymorphism

Polymorphism usually indicates variation in phenotype within a species based on variations in its genome. Polyphenism is the phenomenon where two or more phenotypes are produced by the same genotype and are one of the major reasons for adaptive insects' success. It allows them to partition life-history stages, to adopt different seasonal phenotypes, to cope with temporally heterogeneous environments, and to partition labor within social groups (Simpson et al. 2011).

One of the most interesting cases of polyphenism is the castes in social insects. Among social hymenopterans, for instance, queens and workers are all females. While sex is determined genetically, caste is determined by conditions experienced during larval life. The same occurs between ant workers and soldiers. Aphids also

share a variety of forms, from parthenogenetic females to sexual generations, wingless and winged forms (the latter to disperse to other hosts). All this complexity is guided by environmental factors, like temperature and photoperiod. Besides these examples, many other groups may possess variation in color, form and behavior in response to the habitat conditions.

### Cross-References

- ▶ [Adaptive Radiation](#)
- ▶ [Arthropod Cognition](#)
- ▶ [Arthropod Morphology](#)
- ▶ [Asexual Reproduction](#)
- ▶ [Communication](#)
- ▶ [Courtship Rituals](#)
- ▶ [External Fertilization](#)
- ▶ [Insect Communication](#)
- ▶ [Insect Morphology](#)
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- ▶ [Reproductive Synchrony](#)
- ▶ [Reproductive system](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Sexual Selection](#)

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## Insect Locomotion

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## Synonyms

Adolescence; Adulthood; Juvenescence; Pubescence; Sexual maturity; Youth

## Alternative Words

Insect mobility; Insect mobileness; Insect motion; Insect progression

## Definition

Insects are truly a unique creation of nature. The astonishing success of insects in enduring the changes throughout the course of evolution is marveled by scientists the world over. There are over 900 species of insects reported so far and it has been assumed that there are even more left the discovered yet! The significance of this assumption cannot be stressed enough. It highlights the fact that insects have had a phenomenal success in surviving through the years where most of the other species have struggled. They have thrived in every environment and seem ready to endure even the harshest climatic condition. Insects are found almost all over the world and exhibit various levels of adaptability.

One such adaptability is observed in insect locomotion. Locomotion is an essential component of the insect lifestyle. It helps insect to commute from one place to another. Insects residing in different regions and habitats across the world exhibit different forms of locomotion. These forms include walking, running, crawling jumping, swimming, and flight. Insects are armed by appendages which allows them to move free and without hindrance. The thorax and its associated appendages are primarily responsible for movement in insects. We shall thus delve into the structural details of the locomotary appendages, modifications associated with these appendages, as well as the different types of locomotions found in insects. Insect flight and wing structure has not been included in this chapter as it requires a separated chapter dedicated to itself. The other forms of locomotions have been discussed in details. We shall commence our discussion on insect locomotion by first looking into the structural aspects of insect legs before proceeding to the different mechanisms of locomotion.

## Insect Legs

### General Structure

In most adult and nymphal insects, legs can be segmented into fore, mid, and hind legs. The legs occur on the prothorax, mesothorax, and metathorax, respectively. Each leg can be divided into six segments typically from proximal to distal regions articulating with each other by mono- or di-condylic articulations set in a membrane, the corium.

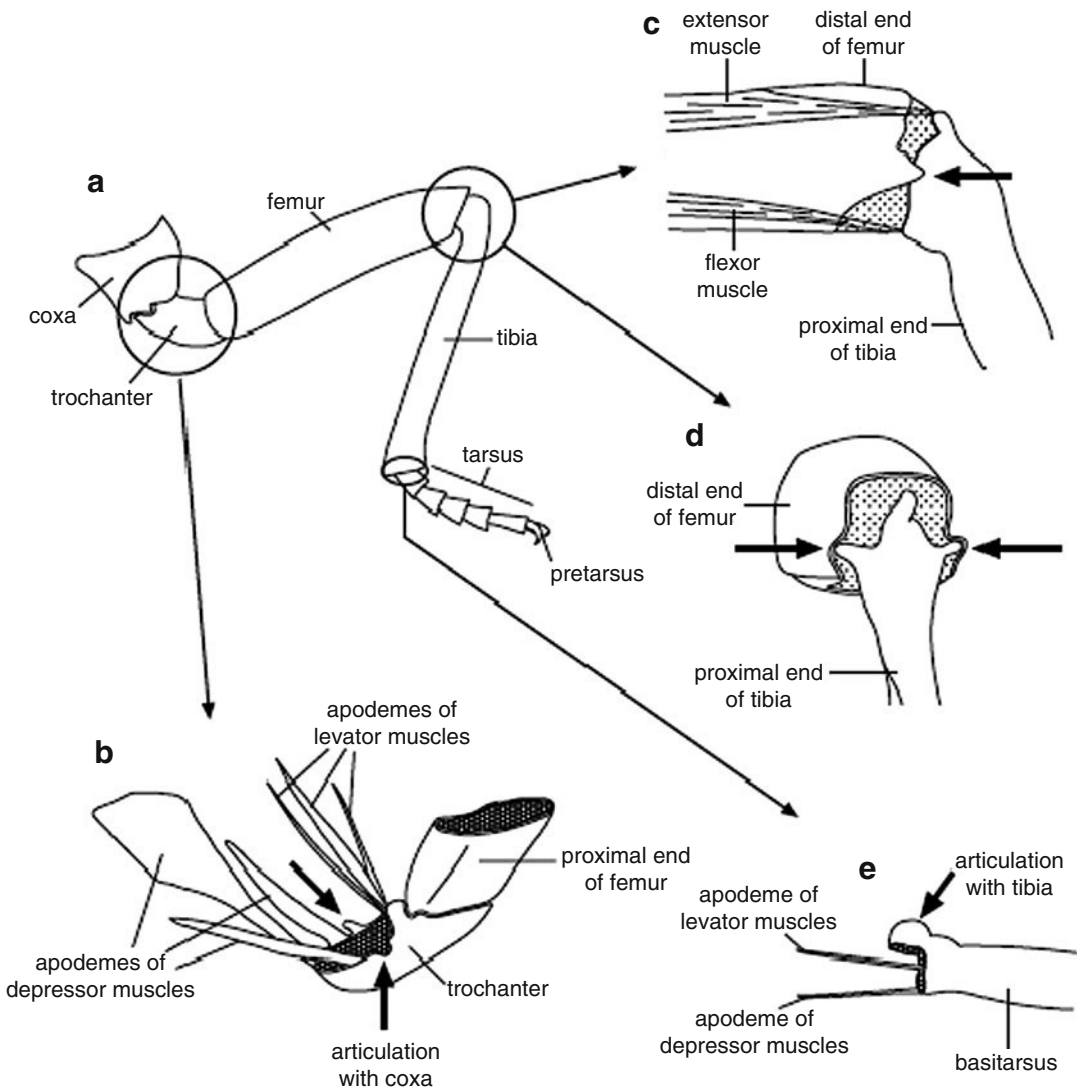
They are: coxa, trochanter, femur, tibia, tarsus, and pretarsus with claws. Additional segments the prefemur, patella, and basitarsus can also be recognized in some fossil insects and other arthropods, such as arachnids, and one or more of these segments are evident in some Ephemeroptera and Odonata. Primitively, two more segments called the epicoxa, associated with the wing articulation (tergum), and the subcoxa, articulated with the pleuron, were also found. The coxa is often in the form of a truncated cone and articulates basally with the wall of the thorax. There may be only a single articulation with the pleuron in which case movement of the coxa is very free, but frequently there is a second articulation with the trochantin. The part of the coxa bearing the articulations is often strengthened by a ridge indicated externally by the basicostal sulcus which marks off the basal part of the coxa as the basicoxite. The trochanter is a small segment with a dicondylic articulation with the coxa such that it can only move in the vertical plane. In Odonata there are two trochanters and this also appears to be the case in Hymenoptera, but here the apparent second trochanter is, in fact, a part of the femur. The development and size of femur and tibia are intrinsically related to their role in different modes of locomotion, although usually they are considered to be the longest leg segments. For example, walking (grasshopper) and running (cursorial) insects usually have well-developed femora and tibiae on all legs, whereas jumping (saltatorial) insects such as grasshoppers have disproportionately developed hind femora and tibiae. In aquatic beetles (Coleoptera) and bugs (Hemiptera), the tibiae and/or tarsi of one or more pairs of legs usually are modified for swimming (natatorial) with fringes of long, slender

hairs. Many ground-dwelling insects, such as mole crickets (Orthoptera: Gryllotalpidae), nymphal cicadas (Hemiptera: Cicadidae), and scarab beetles (Scarabaeidae), have the tibiae of the fore legs enlarged and modified for digging (fossorial), whereas the fore legs of some predatory insects, such as mantispid lacewings (Neuroptera) and mantids (Mantodea), are specialized for seizing prey (raptorial).

The tarsus is subdivided into five or fewer components, called tarsomeres. This is so called as there is only one tarsal muscle, giving the impression of a segment, but in reality it is only a single segment. Hence, it is also referred to as a pseudosegment. The first tarsomere sometimes is called the basitarsus. The underside of the tarsomeres may have ventral pads, pulvilli, or euplantulae, which assist in adhesion to surfaces. The surface of each pad is either setose or smooth. The pretarsus, which lies at the distal end, bears a pair of lateral claws (also called ungues) and usually a median lobe, the arolium which may be membranous or partly sclerotized. Dipterans possess a central spine-like or pad-like structure empodium (plural: empodia) and a pair of lateral pulvilli. It is because of these structures that flies are allowed to walk on walls and ceilings. The pretarsus of Hemiptera may bear a variety of structures, some of which appear to be pulvilli, whereas others have been called empodia or arolia, but the homologies are uncertain. In some beetles, such as Coccinellidae, Chrysomelidae, and Curculionidae, the ventral surface of some tarsomeres is clothed with adhesive setae that facilitate climbing. The tibia and basal tarsomere of each hind leg of honey bees are modified for the collection and carriage of pollen (Fig. 1).

Although the thoracic legs have been observed in every adult insect form, the abdominal legs are more or less confined to the larval stages of the insect. The term proleg is used for the larval leg. Prolegs on the abdomen, especially on caterpillars, usually are lobelike and each bears an apical circle or band of small sclerotized hooks, or crochets. The thoracic prolegs may possess the same number of segments as the adult leg, but the number is more often reduced, apparently through fusion. In other cases, the thoracic prolegs, like





**Insect Locomotion, Fig. 1** Leg and articulations. Points of articulation shown by bold arrows (mainly after Snodgrass 1935, 1952). (a) Typical insect leg. (b) Dicondylic articulation of trochanter with coxa and the apodemes of muscles moving the trochanter. Notice that

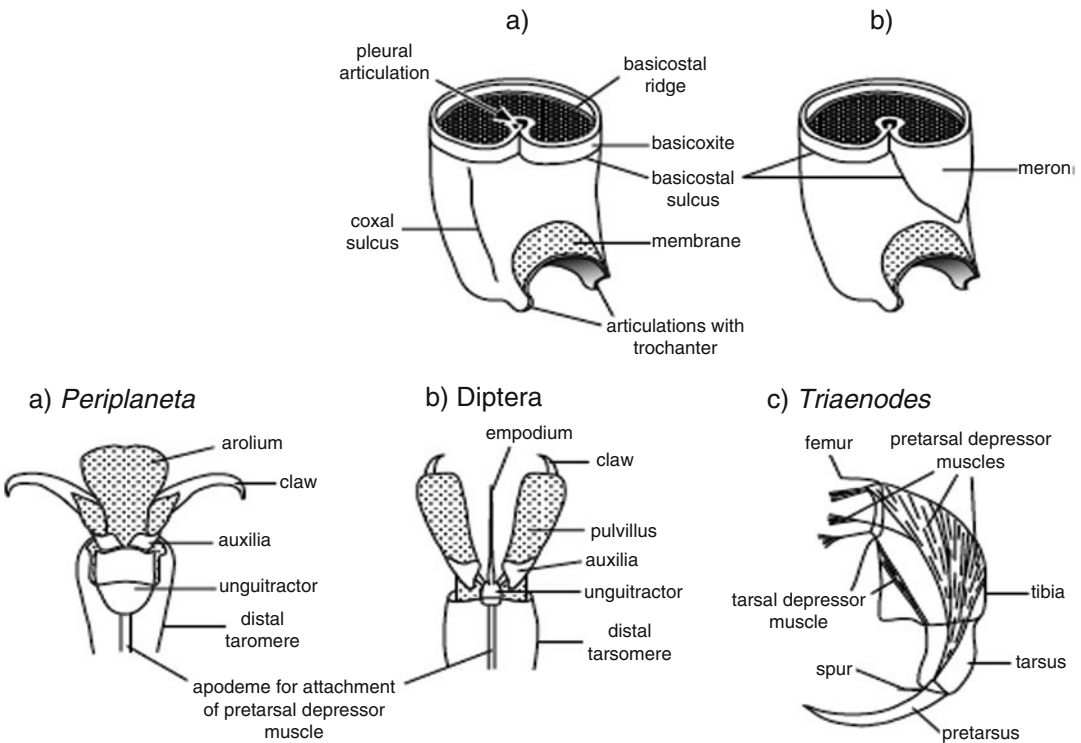
the femur is united with the trochanter; there is no moving joint. (c), (d) dicondylic articulation of tibia and femur, (c) side view, (d) end view. (e) Monocondylic, ball articulation of tarsus with tibia. (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)

those of the abdomen, are unsegmented out-growths of the body wall, often bearing apical hooks (Fig. 2).

## Muscles

The muscles of insect legs can be classified into two main categories based on their location. The

intrinsic muscle which lies inside the legs and extrinsic muscles which lie outside the legs. The intrinsic muscles ran wholly from one segment to the other. The extrinsic muscles have a wide range of roles that it conducts. The movement of coxa is seen to be regulated by the extrinsic muscles attached to the thorax. This is illustrated by the promotor and remotor muscles arising on the tergum, abductor and adductor muscles from the



**Insect Locomotion, Fig. 2** Pretarsus. (a) Pretarsus of *Periplaneta*, ventral view (after Snodgrass 1935). (b) Pretarsus of a dipteran, ventral view (after Snodgrass 1935). (c) Distal part of prothoracic leg of larval *Triaenodes*

(Trichoptera) showing a simple pretarsal segment (after Tindall 1964). (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)

pleuron and sternum, and rotator muscles also from the sternum. The roles of various muscles vary in part due to its nature of articulation as well as roles of other muscles. For example, In *Apis* (Hymenoptera), which has rigid pleural and sternal articulations, promotor and remotor muscles from the tergum are absent. In the pterothoracic segments (thoracic segments related to the attachment of wings), muscles run from the coxae to the basalar and subalar sclerites. They are concerned with movements of the wings as well as the legs.

The intrinsic musculature includes of pairs of antagonistic muscles in each segment. In *Periplaneta*, there are three levator muscles of the trochanter arising in the coxa and three depressor muscles, two again with origins in the coxa and a third arising on the pleural ridge and the tergum. The attachment of femur to the trochanter is such that it is usually immovable, but the tibia is moved by extensor and flexor muscles arising in the femur

and inserted into apodemes from the membrane at the base of the tibia. Levator and depressor muscles of the tarsus arise in the tibia and are inserted into the proximal end of the basitarsus, but there are no muscles within the tarsus moving the tarsomeres. The pretarsus has a depressor muscle but no levator muscle. Levation of the pretarsus results from the elasticity of its basal parts.

Insects have only striated muscles, so-called because of overlapping thicker myosin and thinner actin filaments giving a microscopic appearance of cross-banding. The typical striated muscle fiber has many cells, with a common plasma membrane and sarcolemma, or outer sheath with tracheolar invagination for oxygen supply. Contractile myofibrils run the length of the fiber, arranged in sheets or cylinders. When viewed under high magnification, a myofibril comprises a thin actin filament sandwiched between a pair of thicker myosin filaments. The muscles contract

the same way as they do in higher organisms. This includes sliding of actin filaments over myosin. Innervation comes from one to three motor axons per bundle of fibers, each separately tracheated and referred to as one muscle unit, with several units grouped in a functional muscle. There are several different muscle types. The most important division is between those that respond synchronously, with a contraction cycle once per impulse, and fibrillar muscles that contract asynchronously, with multiple contractions per impulse. Examples of the latter include some flight muscles and the tymbal muscle of cicadas. There is no inherent difference in action between muscles of insects and vertebrates, although insects can produce prodigious muscular feats, such as the leap of a flea or the repetitive stridulation of the cicada tympanum. Reduced body size benefits insects because of the relationship between (a) power, which is proportional to muscle cross-section and decreases with reduction in size by the square root, and (b) the body mass, which decreases with reduction in size by the cube root. Thus, the power/mass ratio increases as body size decreases.

### Muscle Attachments

Insects have an external skeleton. Hence, there are stark differences in the attachment of muscles to these skeletons. As musculature is mesodermal and the exoskeleton is of ectodermal origin, fusion must take place. The fusion occurs by the growth of tonofibrillae, fine connecting fibrils that link the epidermal end of the muscle to the epidermal layer. At each molt, the tonofibrillae are discarded along with the cuticle and therefore must be regrown. At the site of tonofibrillar attachment, the inner cuticle often is strengthened through ridges or apodemes, which, when elongated into arms, are termed apophyses. The presence of resilin renders elasticity at the muscle-attachment sites of the cuticle that resembles the vertebrate tendons. Some insects, including soft-bodied larvae, have mainly thin, flexible cuticle without the rigidity to anchor muscles unless given additional strength. The body contents form a hydrostatic skeleton, with turgidity maintained by criss-crossed body wall "turgor" muscles that continuously contract against the

incompressible fluid of the hemocoel, giving a strengthened foundation for other muscles. If the larval body wall is perforated, the fluid leaks, the hemocoel becomes compressible and the turgor muscles cause the larva to become flaccid.

On the basis of location, insect muscles can be classified into intrinsic and extrinsic muscles. Intrinsic muscles can be found completely within the leg, running from one segment to another, whereas extrinsic muscles arise outside the leg. The movement of different parts of the legs is governed by the movements of these muscles. The coxa, for example, is moved by the extrinsic muscles arising in the with promotor and remotor muscles arising on the tergum, abductor and adductor muscles from the pleuron and sternum, and rotator muscles also from the sternum. The intrinsic musculature involves a pair of antagonistic muscles in each segment. In *Periplaneta*, for example, three levator muscles of the trochanter arise in the coxa, whereas there are three depressor muscles, two arising in the coxa and a third arising on the pleural ridge and the tergum. The tibia is moved by the flexor and extensor muscles of the femur and inserted into apodemes from the membrane at the base of the tibia, but the femur itself is immovably attached to the trochanter. Levator and depressor muscles of the tarsus arise in the tibia and are inserted into the proximal end of the basitarsus, but there are no muscles within the tarsus moving the tarsomeres.

The legs of insects are also well equipped with sensory systems. Proprioceptors include hair plates and campaniform sensilla and chordotonal organs. It is well observed in *Periplaneta* and *Carausius*. Exteroreceptors include mechanosensitive trichoid sensilla which is prominently observed in the final larval stages of grasshopper *Schistocerca americana*. Many insects are able climb and hold onto the smooth surfaces due to the presence of adhesive setae. *Rhodnius* and some other Reduviidae have adhesive pads at the distal ends of the tibiae of the front and middle legs. *Epilachna*, there are two pads on the underside of each tarsus. The flexibility of the setae enables them to make contact with irregular surfaces much more efficiently as well as greatly increases the power of adhesion.

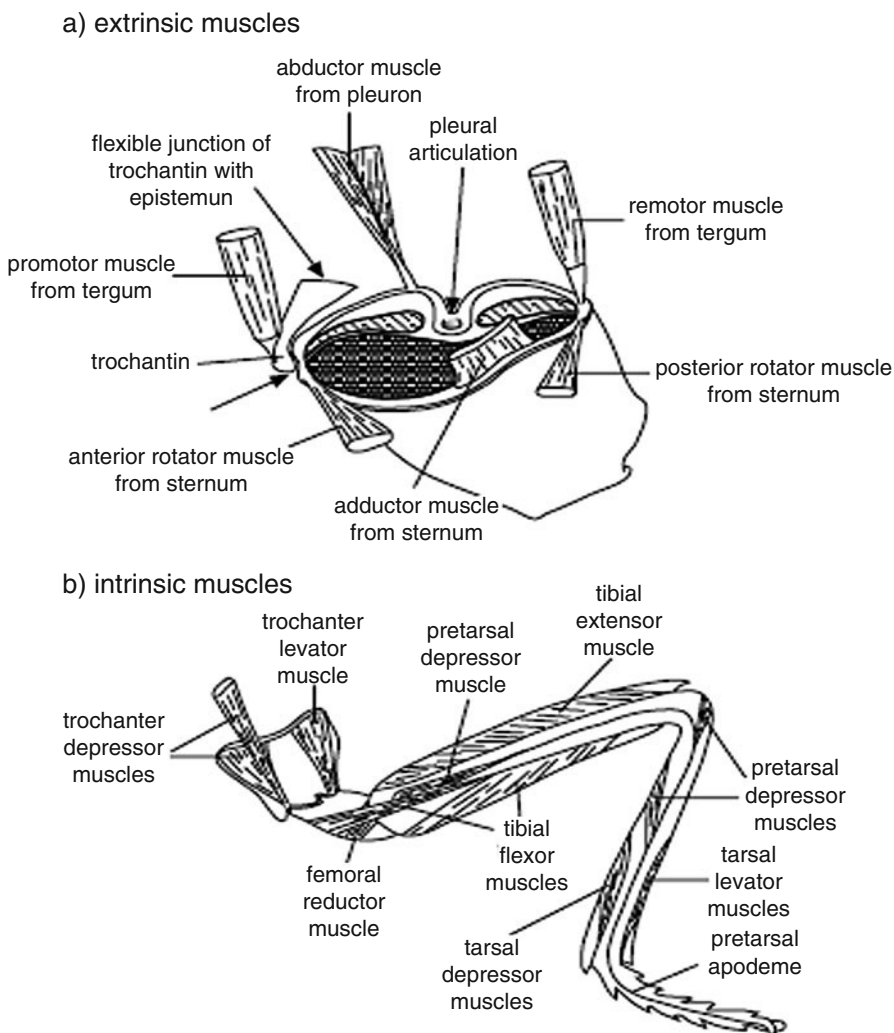
Insect legs have been modified for various forms of locomotion. These include jumping,

swimming, digging, grasping, grooming, and stridulation. Digging is best observed in *Gryllotalpa* wherein a very short and broad forelimb is found. The tibia and tarsomeres have stout lobes which are used for excavation. Larval cicadas always have legs for digging or burrowing. They have large, toothed fore femora, the principal digging organs, and strong tibiae which may serve to loosen the soil. Predatory insects have a well-developed leg for grasping. This includes the occurrence of pincers formed by the apposition of tibia on the femur. This feature of grasping is very

prominent in ectoparasites where well-developed claws can be seen. The legs and mandibles are the most widely used for grooming (Fig. 3).

## Locomotion in Insects

The insects move in different modes. The different forms of locomotion are walking, running, jumping, crawling in terrestrial forms, whereas aquatic insects also exhibit unique mechanisms in mechanisms. In order to properly understand



**Insect Locomotion, Fig. 3** Leg muscles. (a) Extrinsic muscles of coxa as seen from the midline of the insect. Muscles arising from the areas marked with diagonal hatching are omitted (from Snodgrass 1935). (b) Intrinsic

muscles. Note that one trochanter depressor muscle is extrinsic (after Snodgrass 1927). (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)

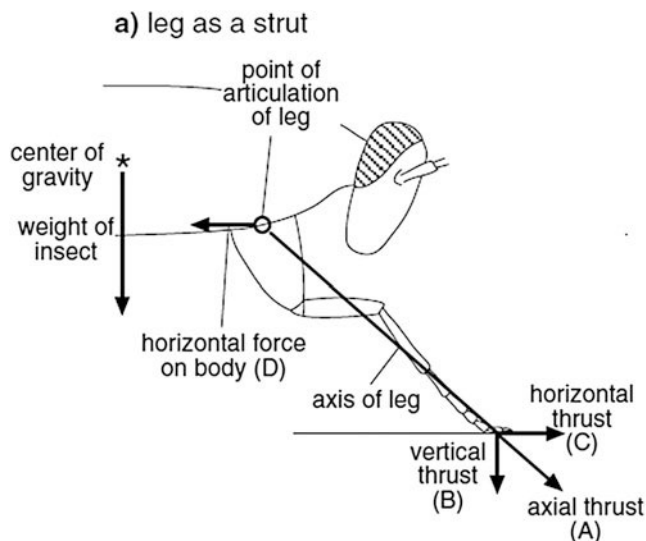
the locomotion mechanisms, it is important to be acquainted with certain terminologies associated with locomotion. They are as follows (Hughes 1952)-

- (A) Protraction: complete movement forwards of the whole limb relative to its articulation with the body.
- (B) Promotion: the movement of the coxa resulting in protraction.
- (C) Retraction: the backward movement of the leg relative to its articulation between the time the foot is placed on the ground and the time it is raised.
- (D) Remotion – the corresponding movement of the coxa.
- (E) Adduction – the movement of the coxa towards the body.
- (F) Abduction – the movement of the coxa away from the body.
- (G) Levation – the raising of the leg or a part of the leg, part of protraction.
- (H) Depression – lowering the leg, or a part of the leg.

- (I) Extension – an increase in the angle between two segments of the leg.
- (J) Flexion – a decrease in the angle between two segments of the leg.

### Walking and Running

A leg can act as a strut, a lever, it can also be used to propel the body forward or backward. When the body needs to stay static, the leg can act as a strut. From the point of attachment of the insect leg to the substratum, an axial thrust is generated. This axial thrust can be resolved into a horizontal and vertical component which provides to forces for the forward motion. But as the insect feet are in contact with the surface of the substratum, it is not allowed to move. But an opposing force at the point of articulation of the leg develops which is equal in magnitude but opposite in direction to the horizontal component of the axial thrust. Since the opposing forces are equal in magnitude, they balance each other out and the insect remains static (Fig. 4).

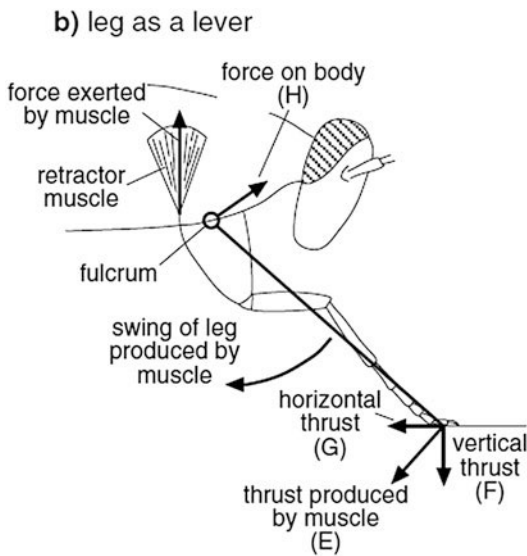


**Insect Locomotion, Fig. 4** A leg acting as a strut. The axial thrust (a) is exerted down the length of the leg by virtue of the weight of the insect. The size of the axial thrust depends, among other things, on how much of the weight is borne by the other legs. It can be resolved into vertical and horizontal components (b and c), but because the foot is

held by friction with the substratum it does not move. Instead, a horizontal force (d), equal and opposite to force (c) acts on the body and, in this case, tends to push it back unless balanced by other forces. (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)

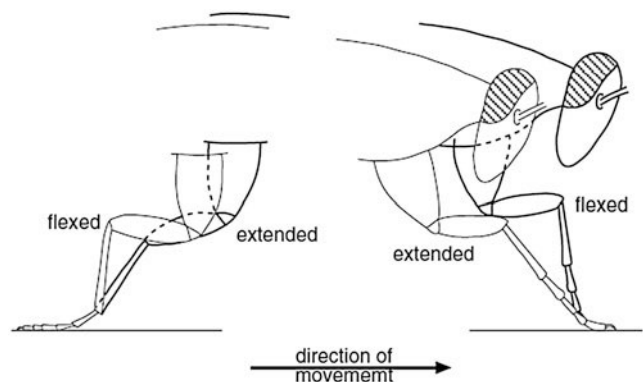


Insect legs are used as levers to rotate about a fulcrum. Contraction of retractor muscles tends to swing the legs back which generate a force on the ground. This force can be resolved into a vertical and a horizontal component. But due to friction, the feet is held still thus creating a forward force in the body of the insect. The direction of the forward force is such that it pushes the body forwards and upwards (Fig. 5).



**Insect Locomotion, Fig. 5** A leg acting as a lever. Contraction of the retractor muscle tends to swing the leg back so that the foot exerts a thrust (E) on the ground. This can be resolved into vertical and horizontal components (F and G), but since the foot is held still by friction an equal and opposite force (H) acts on the body pushing it forwards and upwards. (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)

**Insect Locomotion, Fig. 6** Extension of the coxotrochanteral and femoro-tibial joints of the hind leg pushes the body forwards. Flexion of the coxotrochanteral and femoro-tibial joints of the foreleg pulls the body forwards. (Illustration taken from *Insects-Structure and Function*, R.F. Chapman; 4th edition)



The forward movement of insects is facilitated by intrinsic muscles which can also exert forces on the body by flexing or extending the legs. If the leg is extended anteriorly, the flexion of the joints will pull the body forwards, whereas if the legs are directed backwards extension of the coxotrochanteral and femoro-tibial joints of the hind leg will push body forwards (Fig. 6).

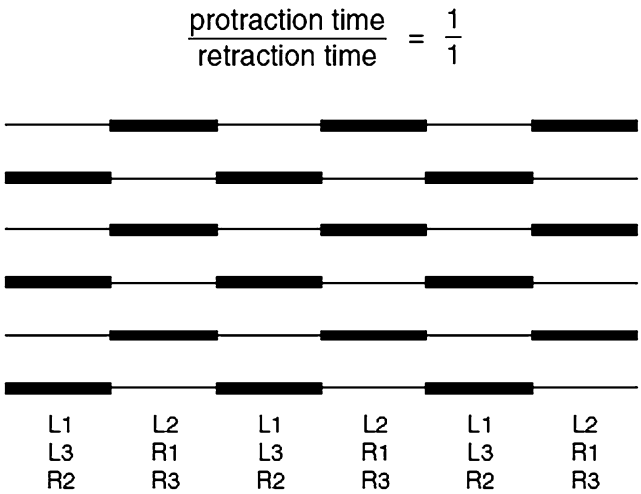
## Patterns of Leg Movement

The stepping patterns of the insect leg are illustrated by coordinated movement between the left and right forelegs and hind limbs. During slow movements, the legs are protracted singly illustrating the pattern R3 R2 R1 L3 L2 L1 R3, etc. (where R and L indicate right and left, and 1, 2 and 3 the fore, middle, and hind legs, respectively). As the speed of steps increases, a more synchronous pattern wherein three legs, the fore and hind legs of one side and the middle leg of the other, lift together so that the insect can be supported by the other three legs. The three supporting legs form a tripod which allows the insect to maintain balance during the high speed movements (Fig. 7).

Some insects are quadrupedal, which means they can protract the feet of both sides at the same time. At high speed, *Tripidopola* moves by the sequence L1/R1 L2/R2 L1/R1. They maintain stability using their abdomen. Mantids also exhibit this property such that they move in the sequence L3 L2 R3 R2 L3 or L3/R2 L2/R3 L3/R2.

**Insect Locomotion,**

**Fig. 7** Showing the synchrony between the legs on either side of the body forming a tripod. The simultaneous movement implies that protraction and retraction time is same. Thick lines indicate retraction with the foot on the ground, thin lines protraction with the foot in the air. (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)



**Neural Coordination of Leg Movements**

The three neurons (fast, slow, and inhibitory) are active during walking. The example of *Schistocerca* best illustrates this statement. *Schistocerca* lifts its fore foot off the ground at the beginning of protraction, the fast and the slow neurons are activated. This has the effect of extending the tibia as the leg swings forwards. The activity of the slow neuron keeps firing at a moderately high rate through the first half of retraction but the fast neurons are silenced quickly. The activity of the inhibitory neuron peaks during the second half of retraction, when the slow axon is silent (Burns and Usherwood 1979; Wolf 1990).

The alternating movements of protraction and retraction are the result of regular patterns of activity of antagonistic muscles in the different segments of the leg. In *Periplaneta*, for example, the levator muscle of the trochanter is active during protraction, lifting the foot off the ground; the trochanter depressor muscle is inactive but it starts to contract before the foot is placed on the ground while the levator muscle is still active. At the same time, the contralateral depressor muscle is continuously active as this foot is on the ground. Similar patterns of activity have been recorded for other pairs of antagonistic muscles and for other insects (Fig. 8).

**Jumping**

Jumping is observed in the orders Orthoptera, Siphonaptera, Homoptera, and some beetles,

where legs are used for jumping. However, there are orders which do not use legs to jump. These include the orders Collembola, Elateridae, and *Piophil*a (Diptera). The enormous energy required by the legs to jump is generated in the muscles and is stored in the muscle itself as well as the cuticle. Muscular contraction enables the release of the stored energy producing the requisite power.

Jumping in insect is exhibited both in the presence and absence of legs in specific orders. In orders which jump in presence of legs, the example of grasshopper is very prominent. The femoro-tibial joint of the hind leg is adapted in such a way that it allows development of maximum force by the extensor tibiae muscle. The rapid release of energy as a result of this force leads to the sudden extension of the tibia. The extensor tibiae muscle consists of a series of short fibers inserted obliquely into a long, flat apodeme. In *Schistocerca*, many of the fibers of this muscle are innervated only by a fast axon. As a result of their oblique arrangement, a force up to 16 N can be developed as opposed to only 0.7 N by the flexor tibiae muscle. Just above the articulation with the tibia, the cuticle of the femur is heavily sclerotized forming a dark area known as the semilunar process. Beneath the articulation, the cuticle of the femur is thickened internally to form a process, known as Heitler's lump, over which the apodeme of the flexor tibiae slides (Fig. 9).

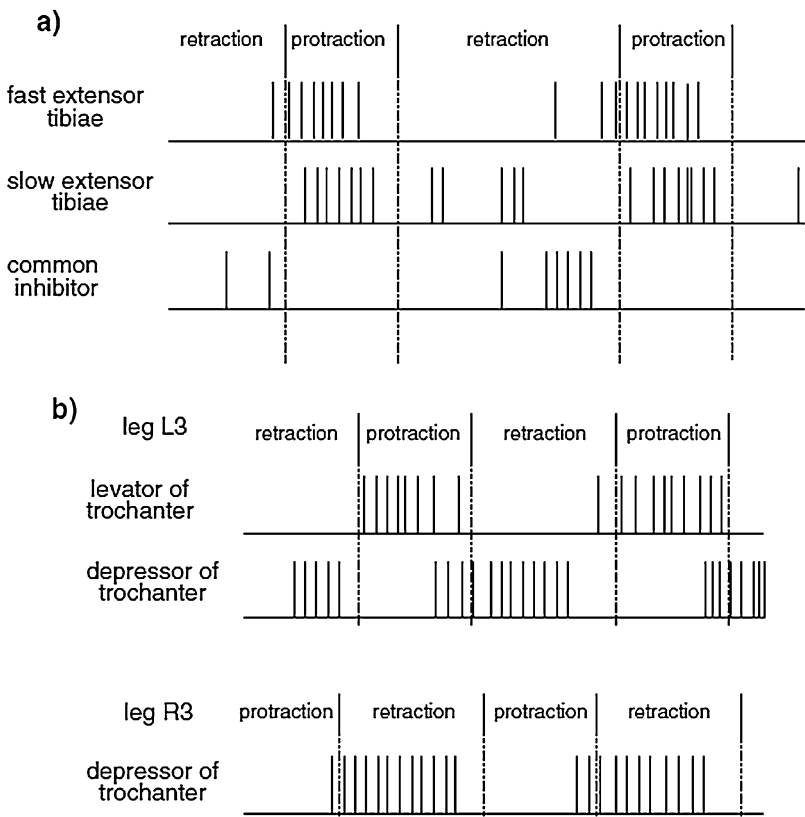
Insects without the presence of legs are also able to jump. A prominent example is that of

**Insect Locomotion,**

**Fig. 8** Neuromuscular

activity during walking. (a) Activity of the fast, slow, and inhibitory axons to the extensor tibiae muscle of the prothoracic leg of *Schistocerca* (data from Burns and Usherwood 1979). (b) Activity of muscles moving the trochanters of the hind legs of *Periplaneta*.

Antagonistic muscles in L3 are in antiphase, and the depressor of L3 is in antiphase with the depressor of R3. (Data from Delcomyn and Usherwood 1973). (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)



Collembola which can jump using modified abdominal appendages. Arising from the posterior end of the fourth abdominal segment is a structure called the furca, which consists of a basal manubrium bearing a pair of rami, each divided into a proximal dens and a distal mucron. The furca can be turned forwards and held flexed beneath the abdomen by a retinaculum on the posterior border of segment three. The jump is produced by the furca swinging back rapidly to the extended position so that it strikes the substratum and throws the animal into the air. Movement of the furca is produced by powerful longitudinal muscles in the abdomen coupled, in at least some species, with distortion of the cuticle so that it acts like a spring (Christian 1978, 1979) (Fig. 10).

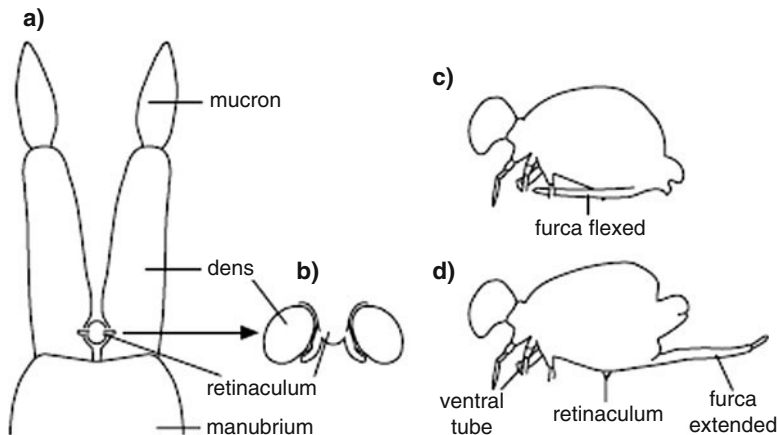
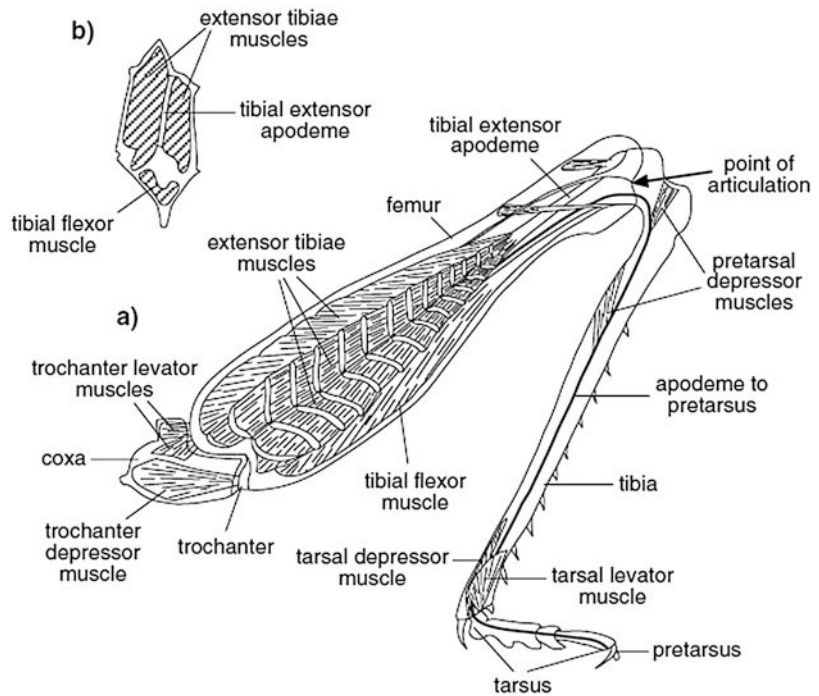
**Crawling**

This form of locomotion exhibits movement by changing the shape of the body rather than movement by legs. It is characterized by the presence of

a soft and flexible cuticle, a hydrostatic exoskeleton, and a turgid body. Most holometabolous insect larvae exhibit such locomotion. Caterpillars provide an excellent example in this regard. Hollow cylindrical outgrowths called prolegs are found in the abdomen of these larvae. The lumen of the proleg is continuous with the hemocoel. An apical area, less rigid than the sides, is known as the planta and it bears one or more rows or circles of outwardly curved hooks, or crochets, with which the proleg obtains a grip. Retractor muscles from the body wall are inserted into the center of the planta so that when they contract it is drawn inwards and the crochets are disengaged. The leg is evaginated by turgor pressure when the muscles relax. On a smooth surface the prolegs can function as suckers. The crochets are turned up and the planta surface is first pressed down on to the substratum and then the center is slightly drawn up so as to create a vacuum (Hinton 1955). Caterpillars move by serial contractions of the

**Insect Locomotion,**

**Fig. 9** Jumping. Hind leg of a grasshopper (after Snodgrass 1935). (a) Leg seen in transparency to show the musculature (b) transverse section of the femur. (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)



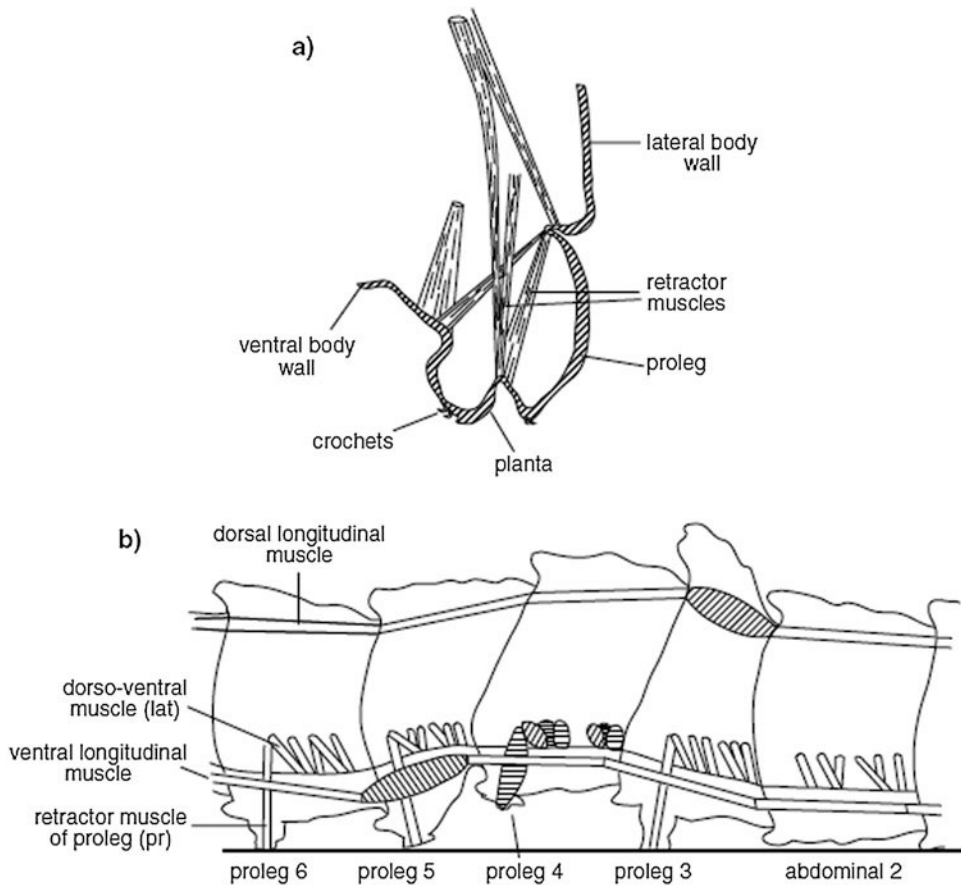
**Insect Locomotion, Fig. 10** Jumping in Collembola (partly after Denis 1949). (a) Furca and retinaculum seen from below. (b) Diagram showing the retinaculum holding the dentes. (c), (d) Diagrams of a collembolan with the

furca in the flexed and extended positions. Jumping is produced by the swing from the flexed to the extended position. (Illustration taken from *Insects: Structure and Function*, R.F. Chapman; 4th edition)

longitudinal muscles which forms a wave from the posterior to the anterior end of the body. Each segment is lifted by contraction of the dorsal longitudinal muscles of the segment in front and its own dorso-ventral muscles, while at the same time the prolegs are retracted (Johnston and Levine 1996a, b; Weevers 1965) (Fig. 11).

## Locomotion in Aquatic Insects

Aquatic insects show a large variety of movement patterns depending upon their structure as well as niche within the aquatic environment. A prominent distinction in locomotion can be observed between insect residing in the



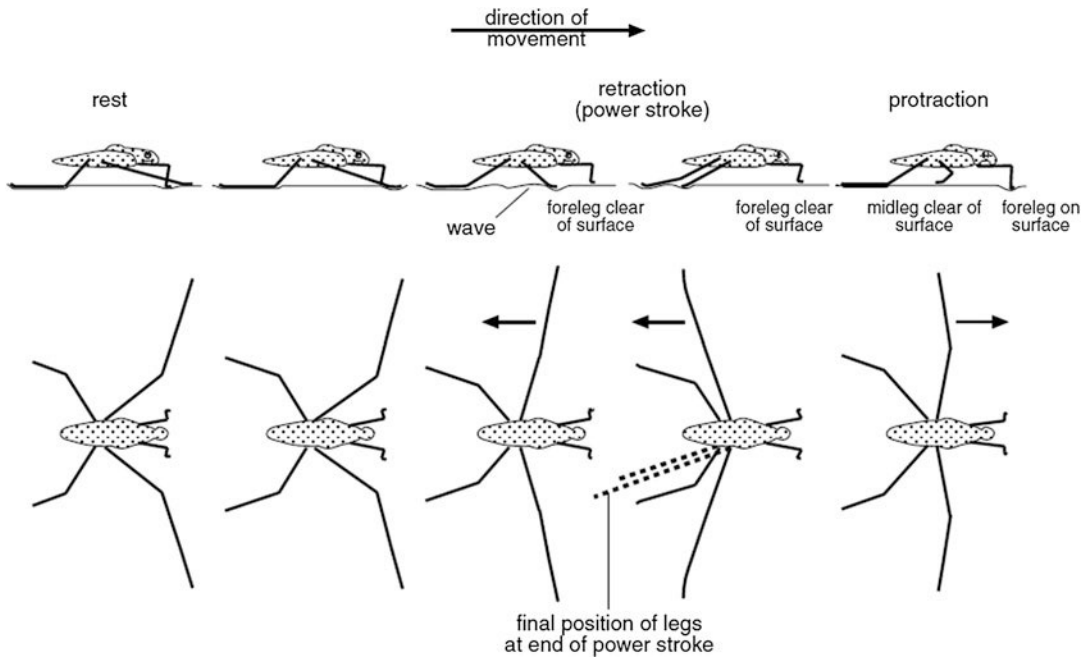
**Insect Locomotion, Fig. 11** Caterpillar crawling. (a) Transverse section through part of an abdominal segment of a caterpillar showing a proleg (Hinton 1955). (b) Longitudinal section through the abdomen of a caterpillar showing a wave of contraction which passes along the

body from behind forwards (left to right) and produces forward movement. Contracted muscles are shown hatched. There are no prolegs on abdominal segment 2 (based on Hughes 1965) (Fig. 12)

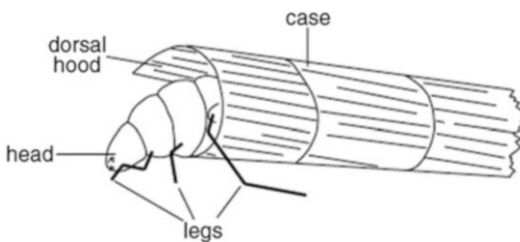
substratum compared to insect residing as bottom dwellers and free swimmers. Among the surface dwellers, aquatic Collembolan such as *Podura aquatica* can spring from the water surface using a caudal furca. The Heteropteran *Gerris* can stand over the water surface and row over it using legs which possesses hydrofuge properties (Bowdan 1978). The Coleopteran *Stenus* live in grass stems in mountain streams where it tends to fall frequently. They can walk on the surface of water slowly, however later secretion of five chemicals, most notably “stenusin,” from the pygidial glands, rapid locomotion is also observed. Among the bottom dwellers, larval Anisoptera are quite

prominent. These larvae can walk on the substratum of the water body. These larva however are also capable of escaping through forceful ejection of water by their branchial chambers. The larval case of *Triaenodes* larva (Trichoptera) provides an interesting read. The larval case of the caddis fly, *Triaenodes*, is built of plant material arranged in a spiral, the most anterior whorl of which extends dorsally beyond the rest of the case above the thorax. This dorsal whorl provides a certain amount of lift, helping to carry the case off the bottom. This lift is controlled by the movements of the legs, which tend to produce a downward thrust (Fig. 13).





**Insect Locomotion, Fig. 12** Movement on the water surface. Positions of the legs of *Gerris*. Arrows show the directions of movement of the legs relative to the body; insect moving from left to right (after Nachtigall 1974)



**Insect Locomotion, Fig. 13** Diagram of *Triaenodes* larva (Trichoptera) in its case (after Tindall 1964)

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## Insect Morphology

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## Introduction

Morphology is the branch of biology dedicated to the study of form and composition of body parts. It is the foundation of various fields in biology, such as taxonomy and evolutionary studies. There is a deep connection between form and function, considering that the *bauplan* of a species has been shaped for millions of years as a result of physical adaptations to different types of environments and tasks to be executed.

Lineages have a unique history, which is reflected by modifications to existing structures. Terrestrial arthropods, for instance, possess a series of adaptations to live in a dry environment. Total disconnection from the ancestral aquatic environment required a set of evolutionary steps, which include developing stronger and more efficient support and locomotor appendages and physiological and structural adaptations to withstand osmotic stress and allow aerial gas exchange.

The extreme diversity of external form found in insects blatantly portrays a group that has surpassed countless adaptive obstacles. Parallel to this diversity, there is a massive glossary of morphological terms. Knowing all the names for all types of structures and forms can be an arduous task, not only for students but also for experienced entomologists. Hence, a brief description of the most important structures and their variations within Insecta is both necessary and expedient.

## General Body Plan

The insect body is segmented in a series of tandem units, as a result of their metameric teloblastic development. Primitively, these units (metameres) were very similar, each bearing a pair of appendages. However, over the course of evolution, the arthropod *bauplan* underwent significant modifications in which groups of segments clustered and specialized in different functions. Each of these groups of segments is named tagma, and the evolutionary process that originated the tagmata is known as tagmosis. This process likely played a decisive role in the evolution of insects, paving the way for further adaptive radiation.

Metameres in insect bodies are clustered in three tagmata: head, thorax, and abdomen, typically with 5, 3, and 11 segments, respectively. Although segments are usually distinguishable by clear boundaries, traces of their original outlines have largely disappeared in the head. Appendages are present in the head and thorax segments, and in the posterior segments of the abdomen. However, signs of the presence of appendages in an ancestral state can be seen in almost all segments during the embryonic development. Typically, each tagma can be attributed to a specific function: the head receives sensory input, concentrates neural integration, and is

responsible for processing and ingesting food; the thorax is involved in locomotion; and the abdomen is involved in excretion, mating and various sensory functions.

Insect species body sizes range from about 0.25–330 mm in length. However, certain Palaeozoic species grew more than twice that size. Color patterns may vary from drab to vibrant and iridescent. The astonishing diversity of morphological features in Insecta allow different species to run, jump, swim, burrow, and, perhaps most notably, fly—an exclusive feature among all invertebrates.

### Body Wall

An insect's exoskeleton is a hardened case that provides support and protection for soft tissues and organs. Externally, it is composed by a series of plates (sclerites) formed in a process known as sclerotization, jointed by sutures and membranes. Internally, protruding ridges extend from these plates to act as a surface for the attachment of muscles. These heavily sclerotized sclerites work as a protective armor, making it difficult for predators and parasites to pierce through, while also granting protection against adverse environmental conditions.

The body wall, or integument, of an insect is composed of three main layers: basal membrane, epidermis, and cuticle (Fig. 1). The basal membrane is a thin noncellular membrane underlying epidermal cells, which forms the inner lining of the body wall. The epidermis consists of a single layer of ectodermal cells responsible for producing the cuticle. All epidermal cells are glandular and may be involved in a variety of functions,

such as producing silk, defensive and adhesive substances, wax, glandular hairs, milk in viviparous flies and composing various head glands (Chapman 2013).

The cuticle is the outermost layer, made of chitin—a long-chain polymer of N-acetylglucosamine—embedded in a protein matrix. The combination of these molecules is what grants an exoskeleton its rigidity. Variations in the protein matrix composition and molecular architecture explain the diversity of cuticles found between different body parts and across species (Andersen 2010).

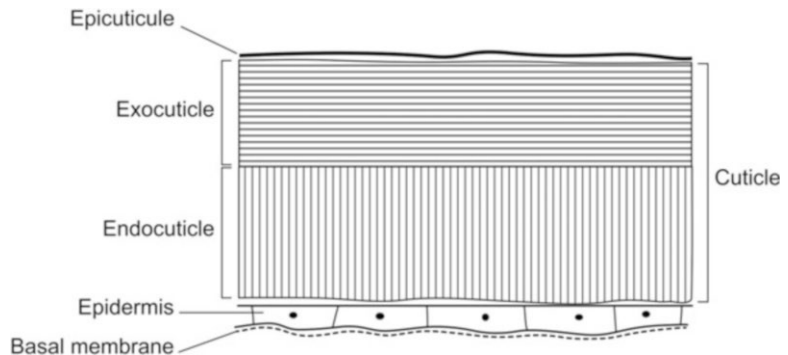
Cuticles can have up to three different layers, depending on their position in an insect's body. The sclerotized layer of a cuticle is known as exocuticle, beneath which a non-sclerotized layer called endocuticle is often present. This flexible endocuticle forms the membranes that connect sclerites. External to the exocuticle is the epicuticle: waterproof layers of wax and cuticulin, and a cement layer that protects the wax against abrasion. This cover is essential for terrestrial insects, since it is the primary mechanism that prevents water loss.

Specific parts of the cuticle can be modified to form organs involved in communication. These can produce chemical signals, like the pheromones released in the environment, or visual signals, either composing specialized structures, like the surface of a firefly's lantern, or exhibiting pigmentation and physical colors.

Another important feature of the integument is the externally visible lines that subdivide the sclerites. A sulcus is a groove formed when the cuticle infolds, and an internal ridge (costa)

### Insect Morphology,

**Fig. 1** Schematic drawing of the integument layer of an insect



or rod-like invagination (apodemes) is formed to act as surface for muscle attachment. Carina or crest is a ridge formed by integumental evagination. Whenever two formerly distinct sclerites are fused, the grooves that mark their previous boundaries are called sutures.

## Head

The head of insects is the anterior-most tagma (Fig. 2a). It articulates with the thorax through a flexible membranous neck and bears appendages involved in feeding (i.e., mouthparts) and sensorial (compound eyes, ocelli, and antennae) functions. The ocelli and compound eyes may be secondarily lost in some groups. For many groups, morphology of antennae and mouthparts is an important diagnostic feature.

Historically, the origin of each head segment has been debated among morphologists, though many believe that the current head *bauplan* of insects is the result of the fusion of several segments that were present in an ancestral condition (Headrick and Gordh 2009). Basically, the archetypal segments of an insect's head include seven segments: ocular, antennal, second antennal, mandibular, superlingual, maxillary, and second maxillary (labial). Each is individually innervated by the central nervous system, which is commonly known as the brain. This brain is divided in three main ganglia: the protocerebrum (innervates the eyes), deutocerebrum (innervates the antennae), and the tritocerebrum (innervates the postantennal appendages). Sutures and grooves mark the external surface of the head, and may reflect the original segmental divisions, ecdysial lines or internal inflections. Inflections may extend deep into the head, merging with one another to form an internal skeleton, which strengthens and protects the head, while providing spots for muscle insertion (Chapman 2013). These merged cuticle invaginations are collectively known as tentorium.

## Orientation

Head orientation is determined by the position of mouthparts relative to the rest of the body. Mainly there are three types of orientation: prognathous,

hypognathous, and opisthognathous. The prognathous condition, in which mouthparts are forward-oriented, is commonly found in predatory species (e.g., tiger beetle, Carabidae; antlion larvae, Myrmeleontidae). In the hypognathous condition, mouthparts are perpendicular to the anteroposterior axis, forming a continuous parallel series with the legs (e.g., grasshopper, Orthoptera; praying-mantis, Mantodea), and it is widely considered to be the most likely primitive condition for insects (Chapman 2013). Lastly, in the opisthognathous condition, mouthparts tilt back toward the posterior end, extending between the forelegs (e.g., assassin bugs and cicadas, Hemiptera).

## Compound Eyes, Ocelli, and Stemmata

Typically, insects have ocelli (simple eyes) during larval stages, though they are often present in juveniles and adults. In adults, ocelli usually form a triad or a dyad on the head's anterodorsal surface. Holometabolous insect larvae have stemmata or larval eyes, single-lensed visual organs positioned bilaterally on the larval head. These structures are the precursors of compound eyes during development (Murphy and Moiseff 2019).

Compound eyes are typically present in adult insects. Numerous similar units are called ommatidia, whose number may vary from one to several thousand, aggregate to form these eyes (Chapman 2013). Compound eyes are always paired, though some may be extremely modified and split into two—lower and upper portions—making it seem that there are four eyes (Ephemeroptera, Gyrinidae). They are typically located laterally in the head, with a pair of antennae inserted between them.

Eye size varies greatly between different groups. Occasionally, some species have such large eyes that they even touch each other medially. This condition is called holoptic and generally occurs in Diptera (Acroceridae, Bombyliidae, Pipunculidae, and Tabanidae), but can also occur in males of other orders that swarm and engage in aerial copulation (e.g., some Ephemeroptera). There are cases in which eyes may be completely absent or strongly reduced. Although this is a derived condition, it may occur as an adaptation

to specific environments (e.g., cave-dwelling and subterranean) or lifestyle (e.g., parasitism).

### Antennae

All insects have a pair of antennae, the anterior-most appendages in the head (Fig. 2b). There are many different types of antennae (Fig. 3) and terminology may vary depending on the group. Their function is almost exclusively sensorial, but in some cases, they can bear secondary sexual characters. In soldier beetles, for instance, males possess relatively large antennae, then the larger an individual's antennae are, the higher are the chances of locating suitable females for mating (Mason 1980). The antenna is subdivided into three regions (from base to apex): scape (first antennomere), pedicel (second antennomere), and flagellum. The scape attaches to the head via a membranous socket and articulates via the

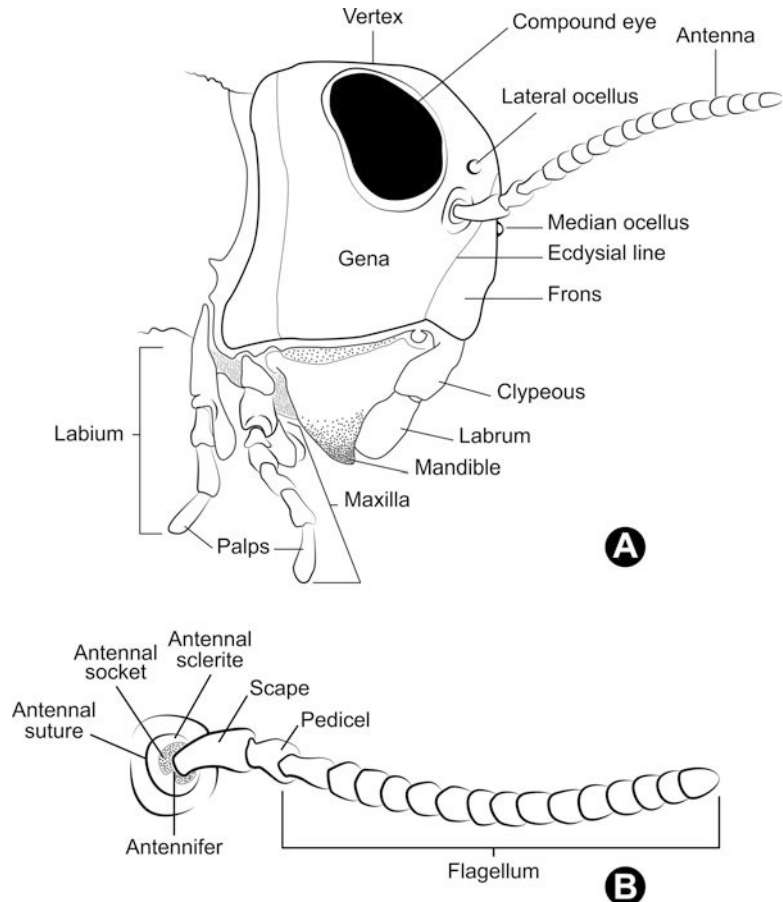
antennifer, which is a small sclerotic process. The flagellum is often divided into several flagellomeres interconnected by membranes, and can vary greatly in shape and number depending on the insect group. Using the term segments to refer to flagellomeres is incorrect, since, by definition, the term refers to parts of the body that possess insertion of musculature—such as abdominal and leg parts, except for the tarsomeres (Chapman 2013). In non-insect Hexapoda, intrinsic muscles are present in the scape, pedicel, and flagellum of antennae. These muscles, with the exception of the ones attached to the scape, were lost at the base of the Insecta lineage (Brusca et al. 2016).

### Mouthparts

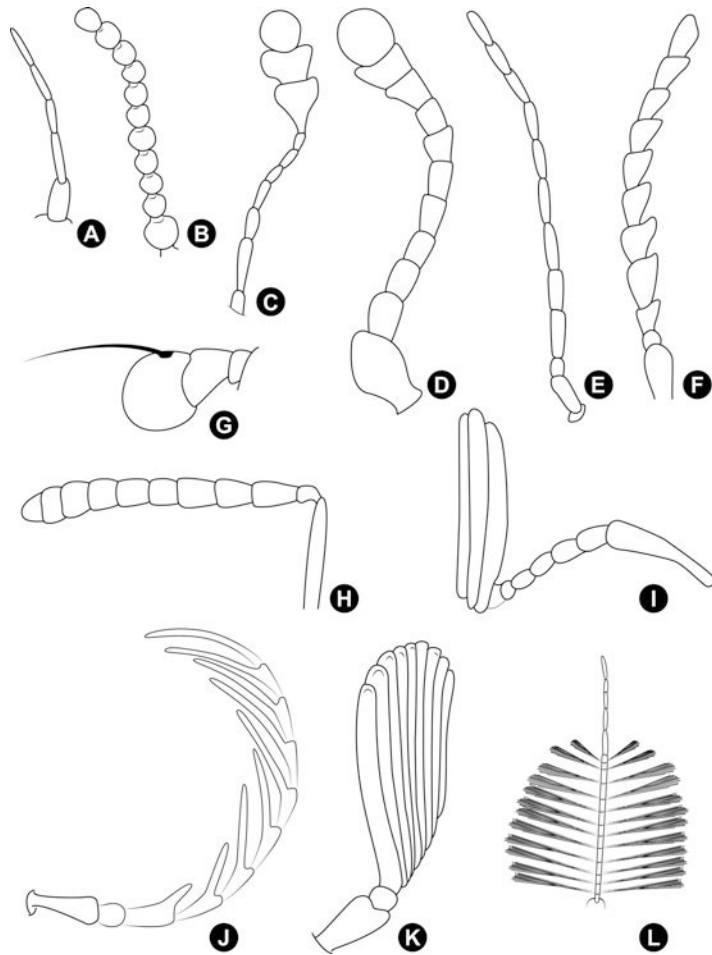
Insect mouthparts are exposed (ectognathous) (Fig. 2a). The labrum is a movable plate attached to a projected frontal head piece, the clypeous, and

### Insect Morphology,

**Fig. 2** Common structures on the insect head (a) lateral view; (b) detailed morphology of the antenna







**Insect Morphology, Fig. 3** Some types of antenna in insects: (a) setaceous (e.g., bristle-like shape; e.g., dragonflies and damselflies, Odonata); (b) moniliform (e.g., bead shaped; e.g., termites, Blattodea); (c) capitate (flagellum abruptly clubbed at the end, found in butterflies, Lepidoptera); (d) clavate (flagellum is gradually clubbed toward the end; e.g., carrion beetles, Silphidae; pleasing fungus beetles, Erotylidae); (e) filiform (thread-like flagellum; e.g., ground beetles, Coleoptera; grasshoppers, locusts and crickets, Orthoptera); (f) serrate (flagellum saw shaped;

e.g., click beetles, Elateridae); (g) aristate (found in flies, Brachycera); (h) geniculate (antenna is hinged or bent like an elbow; ants and bees, Hymenoptera); (i) lamellate (flagellum ending in nested plates; e.g., scarab beetles, Scarabaeidae); (j) pectinate (flagellum shaped like a comb; e.g., can be unipectinate as some fireflies, Lampyridae; or bipectinate as some moths, Lepidoptera); (k) flabellate (flagellomeres fan-shaped; e.g., some fireflies such as *Amydetes* spp.); (l) plumose (antenna have a feather-like shape; mosquito male *Culex* spp., Diptera)

together they form the clypeolabrum. Mandibles are strongly sclerotized, typically toothed. Maxillae are generally multiarticulate and bear a palp, which may be absent in some species. The labium comprises the fused second maxillae and typically bears two palps. The hypopharynx is a mostly membranous, unpaired lobe. The salivary duct opening is usually located between the hypopharynx and the labium.

The morphology of each mouthpart appendage is related to a species diet, and variation is often used to delimit major insect groups. There are two basic types of mouthparts with several modifications for each appendage: one is adapted for biting and chewing solid food; and the other is adapted for sucking up fluid. In sucking insects, both mandibles and maxillae are transformed into stylets used in perforation of the substrate, or the

mandibles may be entirely lost. In Ephemeroptera and Trichoptera, for instance, adult mouthparts are reduced so these insects do not feed in their adult stage. In Brachyceran flies, the labium is modified into a pair of porous lobes called labellae. Similarly, in Lepidoptera, the maxillae form an elongated suction tube, known as spirignath or spiritrompe.

## Neck and Thorax

The neck or cervix of insects is a membranous region that connects the head to the thorax, providing certain flexibility and freedom of movement to the head. The thorax is divided into three segments (from anterior to posterior): prothorax, mesothorax, and metathorax. Their tergites have the same prefixes: pronotum, mesonotum, and metanotum. When present, the wings originate from the mesothorax and metathorax, articulating with processes on the tergite (notum; dorsal sclerite), and pleura of the somites (body segment). Each of the three thoracic segments bears a pair of legs.

## Thoracic Appendages

### Wings

The wings are specialized organs for flight, found in a variety of shapes, forms, and types. Most winged insect species have two pairs of wings, one on the mesothorax and one on the metathorax. Wings are appendages derived from the insect's integument, and they are most commonly composed of a translucent membrane with veins that contain circulating hemolymph. Some groups may have modifications on either the anterior or posterior wings. Examples of anterior wing modifications include the tegminized wings found in Orthoptera and Dermaptera, which is a sclerotized wing used for purposes other than flight, like defense or stridulation; the elytra in Coleoptera, is a drastic modification in which the anterior wings form a rigid carapace that encases and protects the posterior pair of membranous wings. In Diptera, the second pair of wings is reduced, forming club-like halteres, used as a balance organ during flight. In many lineages, wings

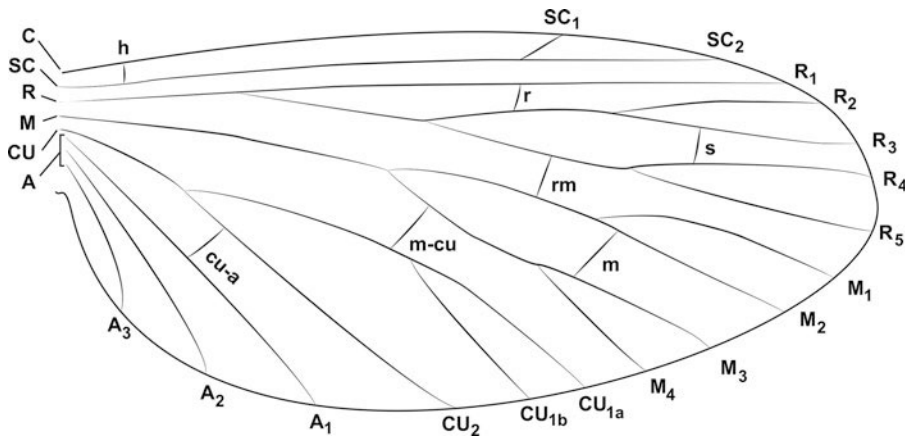
were either shortened, to the point of losing their use for flight (brachypterous), or totally lost (apterous). Furthermore, some lineages may lack the second pair of wings, while the first pair is maintained (e.g., some Ephemeroptera). In Amphiesmenoptera (Trichoptera and Lepidoptera) both pairs of wings are entirely covered in hairs (modified into scales in Lepidoptera).

In fossils, wings are often the only preserved remnants of extinct insects. Wing morphology, especially the study of veins, has been widely used to classify insects. In many groups there were fusions or losses of some veins, with a clear reduction in the ancestral wing venation pattern (Diptera, Thysanoptera). The arrangement of wing veins may be very useful as diagnostic characters, yet the origin and homology of vein distribution is still intensely debated. We can generally recognize six main longitudinal veins: costa (C), subcosta (SC), radius (R), media (M), cubitus (CU), and anal (A); and seven main cross veins: humeral (h), radial (r), sectorial (s), radiomedial (rm), medial (m), mediocubital (m-cu), and cubitoanal (cu-a) (Fig. 4). The areas formed by longitudinal and cross veins are called cells. Some of these cells may have pigmentation and can also receive specific nomenclature depending on the group.

In some insects, both pairs of wings can work together as a single unit. This is possible thanks to hook-like structures between the posterior border of the anterior wings and the anterior border of the posterior wings, such as the hamuli of the Hymenoptera and the frenula of the Lepidoptera, which couples the wings on each side together.

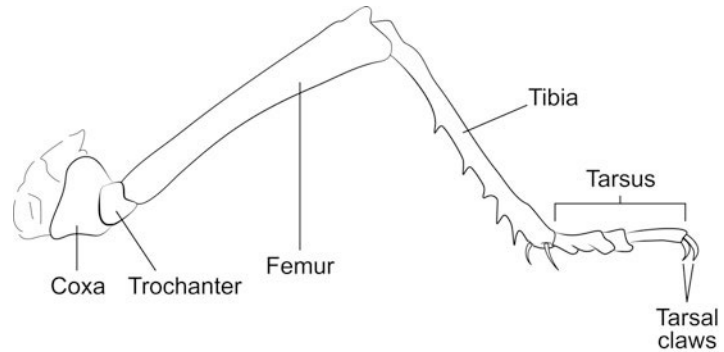
### Legs

All adults of Pterygota have three pairs of thoracic legs, each inserted in a segment: anterior (prothoracic or proleg), medium (mesothoracic or mesoleg), and posterior (metathoracic or metaleg). The legs may be absent in nymphs of Sternorrhyncha (Hemiptera) and in some Holometabola larvae, a condition known as apodous. Insect legs are composed of two parts (Fig. 5): a proximal protopodite (or coxopodite) and a distal telopodite. The protopodite is formed by two elements, a coxa and trochanter, while the



**Insect Morphology, Fig. 4** Hypothetical wing of an insect with the basic vein nomenclature. Longitudinal veins are coded with capital letters, while cross veins are in lowercase letter. See text for abbreviations

**Insect Morphology, Fig. 5** Example of a leg of an insect with the nomenclature of its parts



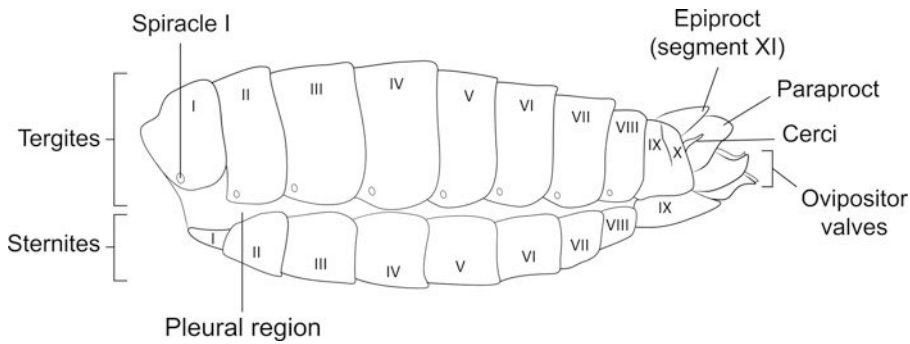
telopodite consists of four segments, a femur, tibia, tarsus, and pretarsus. The tarsus is commonly subdivided into additional articles known as tarsomeres. There is no intrinsic musculature in the tarsal elements, so they are considered subdivisions of a single original segment. Some adult pterigotes and Holometabola larvae have a single lateral claw on the pretarsi, though the vast majority of hexapods have a pair of lateral claws. Many also have a median arolium, a cushion-like adhesive structure for climbing on smooth surfaces, an unguitrator plate or a medium claw (Brusca et al. 2016).

## Abdomen

The abdomen is the posterior-most tagma in the insect body and, in contrast with the head and

thorax, it is relatively simple in structure and less sclerotized. In many holometabolous larvae, for example, there is no sclerotization and the abdomen is entirely membranous (Diptera, Hymenoptera, Trichoptera, Coleoptera, and Lepidoptera). In the basic *bauplan* of Hexapoda, the abdomen is composed of 11 segments, and can be sorted into three groups: pregenital, genital, and postgenital segments (Gillott 2005) (Fig. 6). The pregenital segments usually lack appendages, and the genital and postgenital segments can be modified for mating and oviposition, with additional sensorial structures.

Each abdominal segment consists of a sclerotized tergum and sternum joined by membranous pleural regions. This membrane increases the flexibility and dilation capacity of the segments, and allows the tergite and sternite to overlap. Tergum, sternum, and pleural elements of some



**Insect Morphology, Fig. 6** Schematic drawing of an abdomen of an insect showing its parts

segments, usually the terminal ones, may fuse to form a complete sclerotized ring (Odonata, Ephemeroptera, Dermaptera, and Machilidae). The sclerotized tergum and sternum may be subdivided, resulting in a series of small sclerites (larvae of *Calosoma* and Trichoptera). An intersegmental membrane connects each segment, allowing longitudinal extension of the abdomen. Segments may also be fused together, wholly or partially (Acrididae and Coleoptera).

Most insects have 10 or 11 abdominal segments; nevertheless, this number is variable among insects with typically reduced postgenital segments. The segment I is also frequently reduced or absent, or even fused with the thorax, as seen in many Hymenoptera. The apical non metameric segment XII, or telson, is found today only in Protura (Chapman 2013).

### Abdominal Appendages

The abdominal appendages are either derived from typical appendages (Lepidoptera and Collembola), or independent secondary structures. In Apterygota and some non-insect hexapods, abdominal appendages are present in all stages of development. Pregenital abdominal appendages are present in Pterygota only in immature stages, and the only appendages seen on adults are those on the genital segments and the cerci (with the exception of male Odonata). Apart from the abdominal appendages related with male and female genitalia, the abdominal appendages in Apterygota and non-insect hexapods may appear as styliform structures, often associated with eversible vesicles.

In addition to water absorption, gas exchange and other functions, abdominal appendages are primarily related with attachment and locomotion, and exhibit a variety of forms and functions, mainly in holometabolous larvae. Prolegs are leg-like outgrowths of the body wall (Symphyta), armed with hook-shaped structures (crochets, Lepidoptera) or digitate in form (Mecoptera). Prolegs count may vary, and when absent, a raised pad armed with spines, called creeping welt, can be found in the same position. In many Diptera larvae, both prolegs and creeping welt are present and are equal in function. The larvae of a number of Diptera families have abdominal suckers, which may be derived from prolegs (Psychodidae, Blepharoceridae). In the larvae of *Maruina* (Psychodidae), these are responsible for anchoring the body in waterfalls. In larval Trichoptera, anal prolegs on segment X are present, and, when fully developed, exhibit two basal segments and a terminal claw; these appendages enable the larva to hold onto its case. Other abdominal structures associated with gas exchange (spiracles), osmoregulation, sensory system, as well as defensive functions, may be present in several groups of insects.

### External Genitalia

The genital segments VIII–XI, together with other terminal structures, are referred to as terminalia. Postgenital segments are typically reduced in insects, and the only indications of an 11th segment are a dorsal lobe, the epiproct, and two latero-ventral lobes, the paraprocts. When the segment XI is present, it forms a conical end piece

that bears the anus at the apex, flanked laterally by articulated cerci (Fig. 6). When the segment is absent, cerci originate in a membranous area between the epiproct and the paraproct.

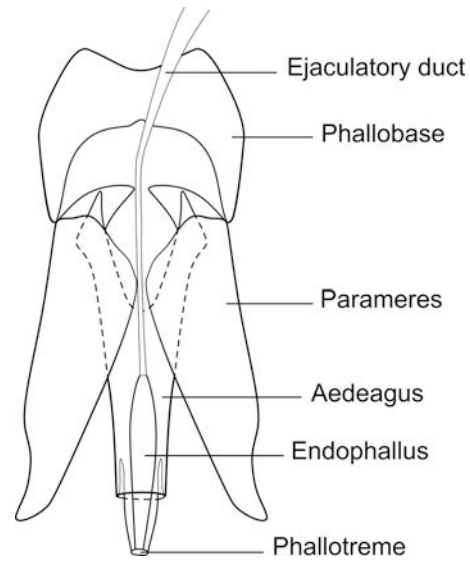
Cerci are present in Apterygota and hemimetabolous orders, with the exception of hemipteroids. In holometabolous insects, they are found in adults of Mecoptera and some Diptera, but are absent in the larval stage. The shape and size of the cerci may differ between males and females and its morphological variation in male may play an important role in copulation. Contact chemoreceptors and olfactory receptors may be present (Diptera), or even play a role in gas exchange (Zygotera) (Gillott 2005).

The collective of organs specifically related with copulation and egg oviposition is called genitalia. Segments containing the reproductive opening system are usually highly modified. In males, these modifications result in a copulatory apparatus, while in females, they form an ovipositor. The genital opening (gonopore) is located, in the majority of Pterygota, on or behind the sternum VIII or IX in females, and behind the sternum IX in males.

### Male

External elements of male genitalia are very diverse and have considerable taxonomic importance since it is extensively used for distinguishing species. On the other hand, such diversity makes it difficult to understand homologies among some structures and creates a vast variety of names for the many genitalia elements. In general terms, it consists of articulated clasping organs (parameres) arising from a common base (gonobase), and a median intromittent organ (aedeagus), which is often weakly sclerotized. Invaginated within the aedeagus is typically an endophallus, into which the ejaculatory duct enters. During copulation, the endophallus may be everted so that the gonopore is extruded. Phallotreme is the opening of the endophallus through which the semen flows (Fig. 7).

Upon this ground plan morphology, tremendous variation and complexity has evolved in the male genitalia, perhaps driven by sexual selection (Hosken and Stockley 2004). In addition,



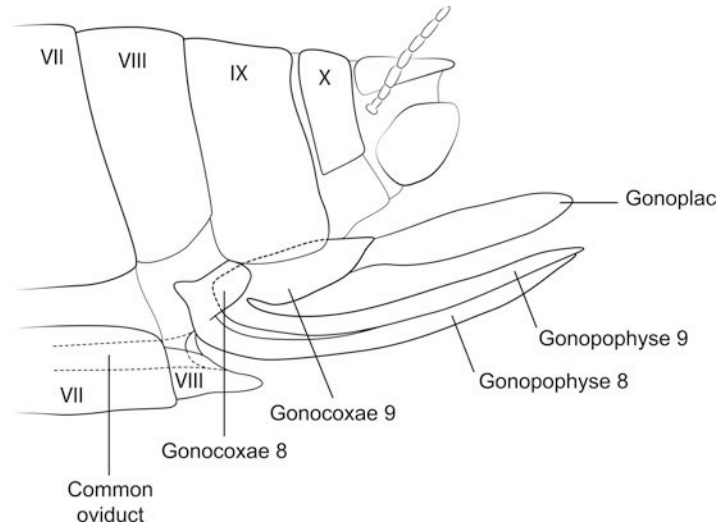
**Insect Morphology, Fig. 7** Schematic drawing of a general male genitalia of an insect

modifications such as appendages and spines can operate in coercing unreceptive females to copulate, prolonging copulations, or defending females from takeover attempts by other males (Simmons 2001). Several structures work in protecting the phallus. In many insect groups, for example, the sternum of the last abdominal segment extends to form a subgenital plate. This structure is seen in many groups, but they are not necessarily homologous. In many Plecoptera, there are no claspers, the sexes being held together by the fit of the intromittent organ into the female bursa. Male Archaeognatha, Thysanura, and some non-insect hexapods have no aedeagus, or terminal segments similar to those in females, or exhibit a median phallus, which is bilobed in Thysanura (Chapman 2013).

### Female

As with male external genitalia, there has been considerable variation in the terminology used to describe female external genitalia. When derived from abdominal appendages of segments VIII and IX, it is called appendicular ovipositor and is composed of articulated appendages. These consist of two pairs of gonocoxae (valvifers), each one with a distal



**Insect Morphology,****Fig. 8** Schematic drawing of a general female genitalia of an insect

gonostyli. Where eversible vesicles occur, the genital segments have long, narrow, annulated structures called gonapophyses, or valvulae. The first and the second pair of gonapophyses form the ovipositor axis (Fig. 8). Additional processes may be present in the second gonocoxa; the gonoplace and the gonangulum. In most insects, the gonoplace (or third valvula) has protective and sensory function, but in Orthoptera it is involved in penetrating the substrate in order to oviposit. The gonangulum is a small sclerite that interconnects movements of the first and second gonapophyses, improving mechanical efficiency of the ovipositor (Grimaldi and Engel 2005).

The general condition described above is present in some Archaeognatha, many Odonata and Orthoptera, some Hemiptera (Auchenorrhyncha), and Hymenoptera. However, subsequent modifications also occur in the ovipositor of Pterygota. In Ephemeroptera and Dermaptera, the female has lost the ovipositor and each ovary opens externally via its own oviduct. In some Hymenoptera, the ovipositor can be modified into a poison injector stinger.

In most Holometabola insects, the same elements present in the appendicular ovipositor structure are smaller, and not involved in oviposition. Instead, the terminalia is telescopic in shape, and retraction and extension movements are controlled by muscles of the tergum. It is a substitutive ovipositor called as oviscapit.

**Cross-References**

- Adaptive Radiation
- Arthropod Cognition
- Arthropod Morphology
- Bear Sensory Systems
- Communication
- Insect Communication
- Insect Diet
- Insect Life History
- Insect Locomotion
- Insect Sensory System
- Locomotion
- Nomenclature
- Reproduction
- Reproductive Fitness
- Reproductive System
- Sexual Dimorphism
- Sexual Selection
- Skeletal System

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## Insect Movement

### ► Arthropod Navigation

## Insect Navigation

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## Definition

Insect navigation refers to the ability of many insects to find their way accurately to goals.

## Introduction

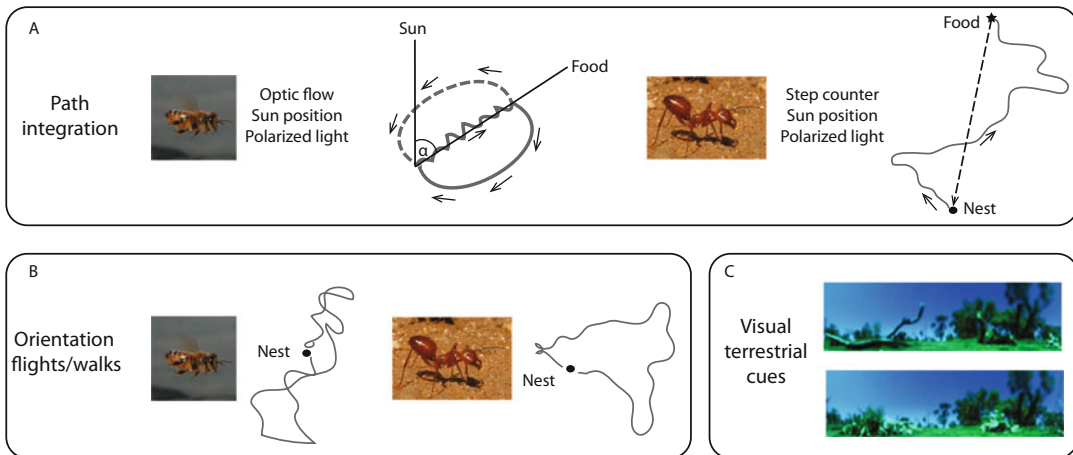
Insects, just like many other moving animals, have evolved navigational abilities in order to

accurately move in their environment and exploit the available resources. The spatial abilities of insects have engaged the curiosity of naturalists since at least the nineteenth century. It was found early on that insects could return home from long distances after displacements. Fabre (1882), for instance, marked bees and wasps caught near their nests and displaced them to locations up to several kilometers away. Many of these insects returned home, and they did so even when carried along extensive detours, shaken or rotated in dark containers, or deprived of their antennae. More recently, von Frisch (1965) demonstrated that honey bees that have discovered a rich food source return to the nest and communicate the location of the food source to their nestmates using a waggle dance frequently described as a “symbolic language” (Fig. 1a).

Since then, the development of increasingly sophisticated technologies to track, analyze, and model the spatial movements of insects has provided insights into the mechanisms underpinning these impressive behaviors. A large proportion of behavioral studies has focused on a very few species of social Hymenoptera (ants, bees, and wasps), primarily because of the relative ease of handling, training, and obtaining good quality data sets. These insects show the particularity of rearing young in communal nests from which foragers often take learnt visual routes between productive foraging areas and their nest. The experimental manipulation of foragers at different phases of route formation in the field and in the lab has revealed much of the diversity and complementarity of the guidance systems sustaining insect navigation, also known as the “navigational toolkit” (Wehner 2009). Hence, this entry focuses predominantly on small-scale-foraging navigation by central place foraging Hymenoptera.

## Basic Orientation to Cues

Many if not all mobile organisms have evolved strategies to find favorable environmental conditions within their local environment. Perhaps the first to do so were unicellular organisms climbing gradients of attractants. Similar mechanisms are found in insects in response to olfactory, visual,



**Insect Navigation, Fig. 1** Navigational strategies in insects. **(a)** Path integration information in the waggle dance of the honey bee (*Apis mellifera*) and the homing paths of the Australian desert ant (*Melophorus bagoti*). Both insects use the sun and the polarized light as compass cues. However, honey bees gain distance information through optic flow whereas ants through a step counter.

**(b)** Example of orientation flight around the hive (left) and orientation walk around the nest (right). **(c)** Panoramic images of the habitat of *M. bagoti*. Orientation flights/walks serve to familiarize oneself with the visual surroundings and to learn the corresponding visual cues along a foraging route. (Picture credits: S. Schwarz, honey bee and desert ant, A. Wystrach, panoramic images)

temperature, and humidity stimuli. An insect adopting such a strategy navigates by alternating periods of relatively straight movements with random turns and reorientation. When the insect perceives an increase in the attractant stimulus, the turning rate decreases and vice versa. As a result, periods of straight movements are biased toward the stimulus source. With this strategy, called “kinesis”, the orientation is indirect as the stimulus only yields a change in turning rate or amplitude. Changes can also involve an increase or decrease of speed, which ensures that the insect stays around when conditions are favorable or leaves when they are not.

Also widespread in insects is the production of rhythmic lateral oscillations during locomotion. Interestingly, when coupled with the production of lateral oscillations, kinesis strategies become remarkably efficient at producing a variety of oriented responses (Wystrach et al. 2016). The stimulus perceived still modulates speed or turn amplitude, but the direction of the turn is determined by the state of the oscillator. This simple strategy is enough to climb visual or odor gradients, to track pheromone plumes, and even to follow learnt routes, using visual familiarity to modulate turn amplitude.

Having a bilateral body offers an additional advantage to insects. Signal intensity can be directly compared between the left and the right sensors, and the resulting difference can be used to steer toward or away from the stimulus producing a directly oriented response called “tropotaxis”. Flies, bees, ants, and cockroaches exploit this strategy by turning toward the side where the antenna is exposed to the strongest olfactory intensities, enabling them to climb odor gradients or follow chemical trails. Perhaps surprisingly, cutting an antenna, which in theory should result in constant turns toward one side, has only a moderate effect on trail-following. Single-antenna insects typically manage to maintain a correct overall direction of movement suggesting the existence of other means to maintain a bearing. Indeed, insects can maintain a bearing using global reference cues from the sky. Sky information typically involves multiple cues such as the pattern of light polarization, the gradient of light colors and intensity, the Milky Way, the sun, or the moon itself (Wehner 2009). This ability to maintain an arbitrary orientation relative to a celestial cue is called “menotaxis”.

Whether in humble navigators such as *Drosophila* flies, long-distance migrators such as

locusts and monarch butterflies, or central place foragers such as ants and bees, this ability to maintain a bearing appears to involve a highly conserved brain area called the central complex. The central complex consists of several neuropils forming an elaborate neural network in the middle of the brain. This brain area combines multiple sensory inputs, notably celestial cues, into a unique signal (“bump”) of neural activity. Remarkably, this bump of neural activity tracks the insect orientation by moving along the central complex neuropils as the insect rotates. This bump of activity can be interpreted as a representation of the insect’s current heading. Crucially, the central complex can influence turning behavior by comparing the current heading to a memorized internal directional goal, thus enabling the insect to maintain a straight course relative to external cues. In the absence of celestial cues, the central complex can still track the insect’s current heading using terrestrial cues or even self-motion cues (Seelig and Jayaraman 2015). Other modalities such as wind are also likely to influence the insect’s current heading representation. Such a convergence of multiple directional dictates into one, unique representation of heading direction explains the robustness of insects’ sense of direction.

## Searching Behavior

Sometimes insects may not be able to use any directed navigational routine. This happens when cues are not available, become unreliable, or the animal is inexperienced. It may also happen that the insect fails to find the target or simply gets lost. In these cases, insects can resort to searching behavior.

### Exploratory Search

In their simplest form, searching strategies are based on innate preferences. Mating aggregations of some butterflies, beetles, flies, wasps, bees, and ants occur above prominent objects such as hills or large trees, a behavior known as “hilltopping”. Innate attraction to such prominent locations is sufficient to find them, even in unknown

environments. However, if an unknown area needs to be investigated, insects engage in an exploratory search (Bell 1991). Individuals move along meandering paths which often contain elements of a random walk strategy, such that the choice of step lengths, turning angles or waiting times follows a random process. The path can nonetheless be optimized to whatever resource the insect is looking for. A general characteristic of such searches is that a maximum area is covered with the least effort. This means that the path should cross itself as little as possible and that the unexplored gaps between paths are kept small. The exact spacing and layout of the movement path depends on the sense that is used and how far it reaches, and on the cost/benefit balance of searching an area exhaustively. Even in environments that offer no cues for navigation, the searching insect might know something about the locations it is looking for. For example, it may have learned that some food sources such as flowers occur in patches: if one flower is found by chance, the next flower is likely not far away. One available strategy is to intersperse bursts of short movements to move within a patch, with very long movements to reach the next patch. The movement patterns of some searching insects (honey bees, bumblebees) are now known to have properties of “Lévy walks”, i.e., random walks with a high incidence of long movement steps (Schultheiss et al. 2015). However, it remains unclear whether Lévy walks stem from internal mechanisms or external environmental drivers.

### Systematic Search

An insect that has just navigated to a location but fails to find the target also engages in searching behavior as a kind of backup. In this case, however, the animal has previous knowledge, as it was guided to this location by navigational cues. The point where this guidance ended is therefore the most likely place to find the target or further cues. Bees and ants engage in systematic searching behavior, in which the path is structured in loops around the starting point, to which it repeatedly returns. This looping search expands over time to avoid searching the same area over and again

(Schultheiss et al. 2015). The area covered by this systematic search is also adapted to how precise the insect navigated before getting lost or how “certain” the insect is about its location. The systematic search is restricted to a small area if navigation was precise and covers a larger area if less precise. It thus matches the probability distribution for the target location. The systematic structure of these searches relies on the continued use of navigational routines. To return to the point of origin, the insect needs to track its location in space, e.g., through visual cues or path integration. Some ants and ladybird beetles show indications of a spiral structure in their systematic search paths, which maximizes the area that is covered.

## Path Integration

Bees, wasps, and ants routinely venture out of their nest or hive and search for food and water which they subsequently deliver back to the nest. Those foraging trips are often not straight but winding, and distances can be several 1000 times the insect’s body length (Wehner and Srinivasan 2003). Yet the foragers manage to return to their starting point, i.e., their nest, in a relatively straight line. In other words, they are able to transform information from the meandering outbound trip into a straight inbound trip. This phenomenon is called “path integration”. In order to return in a direct line to a starting point, a continuous update of the direction and distance of the movement trajectory has to be recorded. Insects use a celestial compass system for directional cues and optic flow and stride information as an odometer system. Together, both systems are capable of integrating a homing vector that guides the animal toward the starting point.

Arguably the two most impressive examples of path integration in insects are the waggle dance of honey bees (von Frisch 1965) and the homing behavior of *Cataglyphis* desert ants (Wehner 2009) (Fig. 1a). If a successful foraging bee returns to the hive and wants to promote a worthy food source, it can transfer its path integration information of its last foraging trip to others in the hive. The bee performs a dance consisting of

repeated movements along a shape reminiscent of an eight. The bee follows the shape of the eight and does a waggle run after finishing each loop by rapidly shaking its abdomen from side to side. The angle between the vertical axis of the eight and the waggle run indicates the direction of the food source in accordance to the angle between the sun’s azimuth and the direction the bee should fly once out of the hive. The duration of the waggle run indicates proportionally the distance to the food source from the hive. In terms of ground dwellers, *Cataglyphis* desert ants impressively show that they can efficiently navigate through barren salt-pan habitats with seemingly none or few visual terrestrial cues around them (Wehner and Srinivasan 2003). In both cases path integration helps the insects to either convey navigational information to other foragers or guarantee a “lifeline” for homing in hostile environments. Both behaviors have been exploited by researchers to investigate how insects extract direction and distance information for the path integrator.

## Directional Information: Celestial Compass

For diurnal insects, the obvious celestial cue is the sun and its azimuthal position. Ants, bees, and other insects rely on the sun’s position to determine a heading direction. More than 100 years ago, Santschi (1911) blocked out the real sun and mirrored it to the opposite side of the sky above homing ants, which lead to a 180-degree U-turn in the path of the foragers, showing unambiguously the importance of the sun’s position for navigating ants. Bees are even capable of considering the azimuthal movement of the sun during long and extensive (marathon) waggle dances in which they adjust their directional waggle run axis over time in accordance to the changed position of the sun. For nocturnal insects, the moon, and even the entire Milky Way, can serve as a heading scaffold (Dacke et al. 2003).

The polarized light can also provide insects with directional information. Polarized light creates a distinct pattern that is visible for many insects and can be used for guidance toward a goal location even if the sun is occluded by clouds or the animal is moving through shady areas.



Specific ommatidia (facets) usually located at the dorsal part of the insect compound eye show cellular specializations and sensitivity to polarized light. This “dorsal rim” area helps the insect to decipher the information of the polarized skylight pattern. Ocelli (or simple eyes) between the compound eyes also have polarization processing capabilities in many navigating insects and add to the celestial compass system. Von Frisch (1965) was the first to demonstrate that honey bees are able to use the polarized skylight by showing that after manipulating the visible part of the sky with a polarization foil, bees adjusted their waggle dance direction accordingly.

These celestial compass cues are complemented by a spectral light gradient. The ratio between short and long wavelengths in the sky varies, especially around the sun where the sky shows no polarization but a high amount of long wavelength radiation. While this compass system is less accurate than the sun position or the polarization pattern in the sky, navigating insects can acquire robust directional information for path integration through the combination of several celestial cues.

### Distance Information: Odometer

Directional information from celestial cues is not sufficient for successful homing. Insects also need distance information – an odometer to estimate the correct length of their homing path. Flying insects were first believed to estimate the traveled distance by assessing their energy loss during the outbound trip. Experiments on honey bees loaded with an extra weight of a small ball of steel indicated a greater distance to the food source during their waggle dance than bees without the ball. Later, however, it was found that this response was in fact triggered by the visual input during the foraging flight, as loaded bees probably flew closer to the ground. Bees and other insects rely on optic flow for odometry during path integration. This is well illustrated by experiments testing honey bees in tunnels with either horizontal or vertical stripes on the walls. Individuals trained in tunnels with horizontal stripes on the walls experience less optic flow and indicate shorter distances during their waggle dance than conspecifics trained in tunnels with vertical stripes (Heinze et al. 2018).

Although optic flow is also used for distance estimation by walking insects, it only plays a minor role. Ants primarily rely on a stride counter to measure distances during their foraging trips (Wittlinger et al. 2006). In a series of nifty experiments, foraging *Cataglyphis fortis* ants were shown to overshoot their homing distance when provided with leg extensions, i.e., pig bristles glued to the legs of the foragers serving as stilts. By contrast, ants with truncated legs had a shorter stride length and undershot the distance to the nest in test conditions. Interestingly, walking bumblebees are also able to locate a feeder in total darkness suggesting that they can use nonvisual cues to estimate travel distance.

### Integration of Direction and Distance Information

Neurobiological advances have enabled the characterization of certain areas in the insect brain and their potential functions. The mushroom bodies and the central complex play a pivotal role in path integration in insects. Computational models that incorporate recent new findings of compass and speed neurons are able to explain which brain area may contribute what and when to provide functional path integration in bees (Stone et al. 2017). Compass information and odometric information are integrated in the central complex to gain a heading direction for the foraging insect. After accumulating vector information during the outbound trip, the system can be offloaded to lead the forager back to the starting point or nest, respectively.

### Learning Terrestrial Visual Cues

Many insects learn important locations, such as a profitable food site or their nest, using visual memories of the goal and its surrounding environment, combined with the sensory input or internal state when it is at or near its future goal. The use of visual cues for learning locations was first evidenced by Tinbergen (1932) who showed that the beewolf *Philanthus triangulum* uses objects (e.g., a ring of pinecones) to relocate its nest hole in the sand. If these landmarks are artificially

displaced, the wasp searches at the location of the landmarks.

### Learning Walks and Learning Flights

Besides using single landmarks, insects also perform multiple maneuvers at multiple spatial scales to extract the information from a set of views that allows for visual guidance. Upon leaving its nest for the first few times, a bee, wasp, or ant typically engages in a series of convoluted movements made of arcs or loops covering increasing areas as it moves outward, during which it acquires visual memories of the nest location (Fig. 1b). The insect regularly turns back to face the direction of the nest or prominent nearby landmarks. During these turns, an individual could potentially be acquiring panoramic snapshot views of the goal location (Zeil and Fleischmann 2019). At the end of these maneuvers, bees change their flight altitude by gradually gaining height until they fly above surrounding objects, possibly increasing the reach of their visual memories to include the more distant panorama. Once the insect has learnt views of the nest surroundings, it can later engage in successful homing. These panoramic views are used for long-distance navigation toward the location of the hive (Fig. 1c). Bumblebees often approach the goal in a type of zigzag flight so that the visual patterns during the turns match those of the turns in the learning flight. This putative “parallax-matching” means that the insect searches for the nest (or goal) at the correct metric distance from the surrounding visual cues.

### Route Following

To get from one particular place to another, insects often develop routes. The majority of ants are simply able to follow a pheromone trail deposited on the surface by a conspecific. Such behavior is entirely based on tropotaxis and requires no previous experience. However, thermophilic desert ants do not lay pheromones and develop visually guided routes that allow fast, reliable, and safe passage to and from profitable feeding sites. Essentially, such a route is a series of navigational instructions. With experience visual cues can override the home vector

information established by path integration, as seen in the desert ant *Melophorus bagoti* (Kohler and Wehner 2005). Individual foragers learn and maintain idiosyncratic routes leading them from the nest to a feeder and back again. The outward route of an ant can be distinct from the returning inbound route back to the nest. Ants displaced along their route or encountering their route during search behavior seem to be able to follow it starting from any point along it. In the European desert ant *C. velox*, individual foragers learn multiple inward and outward routes through their habitat (Mangan and Webb 2012). These routes are learned rapidly, stored in long-term memory, and recalled for guidance as appropriate given the correct visual cues are presented to the ant. Learning multiple paths through the habitat over successive journeys provides a mechanism by which ants memorize a series of interlaced courses and thus perform complex navigation.

During the process of route formation, insects tend to gradually adjust their path in order to reduce travel distances. This optimization is evident in bees that exploit multiple small but regularly replenishing patches of flowers over large territories. Orchid bees, bumblebees, and honey bees were all found to develop multi-destination routes linking multiple feeding locations using a stable visitation sequence called “traplines”. When allowed to forage on a stable array of ever replenishing feeders for several consecutive hours, individual bees attempt to take the shortest possible route to visit all locations once, a spatial optimization task akin to the traveling salesman problem (Lihoreau et al. 2012). Unlike mathematicians, bees cannot compute and compare the absolute distances of all the possible routes to solve this task (there are over three million possible routes for visiting ten feeders). Rather, it has been proposed that insects assess overall travel distances between all flight legs between feeding sites, using path integration and visual memories, and refine their routes through trial and error. This iterative improvement approach replicates the behavior of naïve bees displaying many revisits to feeders and that of more experienced bees following near-optimal routes.

## Integration of Multiple Navigational Cues

Information can be transferred between different navigational strategies. This is the case when insects are following patchily distributed orienting cues and need to decouple their body orientation from their travel direction. Wasps and hoverflies fly forward toward a goal by matching their currently perceived view with their memorized views. To pinpoint the exact location of the goal, insects intersperse transverse sweeps to search for further cues. Another example is backward-walking ants that are pulling large prey items to the nest. Ants regularly drop the prey briefly and turn around to get a nestward view. In both cases (flying wasps/flies and walking ants), the insects orient themselves by aligning views and then transferring the derived travel direction to a compass system that works independently of body orientation (Schwarz et al. 2017).

Depending on context, navigating insects can also switch flexibly between different guidance strategies. Path integration, for instance, is prone to accumulating errors, especially with increasing travel distances. For many insects, this strategy may provide a sound scaffold for long-distance travel and direction, complemented by systematic searches and panoramic landmark guidance to pinpoint a location such as a small nest entrance or a blossoming flower at finer scales. However, in the real world, different navigational tools rarely operate in isolation. Multiple cues are often available at the same time, or currently perceived cues need to be reconciled with previously stored memories. Many insects are therefore able to integrate different navigational dictates, which is especially evident when they are set into conflict experimentally. This is, for example, easily achieved in navigating ants by displacing terrestrial visual cues or displacing the ants, as this puts the visual route guidance strategy in conflict with the ants' path integrator. Integration of navigational dictates usually leads to intermediate directions, with separate cues being weighted optimally according to their salience or reliability. One prominent strategy may therefore dominate the integrated output, as was the case in Tinbergen's experiments with

beewolves (Tinbergen 1932). Based on our current understanding of how navigational strategies operate and interact, recent models suggest that such an integrating navigational toolbox has a decentralized architecture (Hoinville and Wehner 2018).

## Conclusions

The majority of experiments on insect navigation have been performed on a very few species of social Hymenoptera, chosen because of the relative ease of handling, training, and obtaining good quality data sets. These experiments suggest that impressive navigational behavior can be explained by a relatively simple navigation toolkit comprising a series of interconnected navigational units in a modular architecture (Wehner 2009). Future investigations of the neural mechanisms underpinning navigation, using modern techniques for genetic engineering, brain recording, and controlled behavioral experiments in virtual reality setups, should help identify this modular organization and how it controls behavior. These approaches, available in model organisms (e.g., *Drosophila*), will indicate to what extent principles of navigation identified in Hymenoptera are common across insects.

## Cross-References

- ▶ [Arthropod Navigation](#)
- ▶ [Dead Reckoning](#)
- ▶ [Homing](#)
- ▶ [Landmark](#)
- ▶ [Learning](#)
- ▶ [Long-Term Memory](#)
- ▶ [Memory](#)
- ▶ [Navigation](#)
- ▶ [View-Based Homing](#)

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## Insect Sensory System

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## Introduction

Insects are the richest organisms on earth in terms of species, biomass, and distribution (Goulson 2019). Such richness is highly associated with morphological, ecological, and behavioral diversity, along with lineages diversifications that have been driven by coevolution with angiosperms (Hunt et al. 2007), which make insects the main pollinators and great dispersers. To play that role, along with many others, insects evolved simple, connected sensory organs, which receive and filter

the information around and process it differently according to the context. These organs are involved in the insects' evolutionary success and promote a perception of the environment through their stiff exoskeleton. As such, and due to their thick physical barrier, insects rely upon a range of mechano- and chemosensory structures, both spread throughout the major axis of their body.

The insect's sensory systems have been extensively investigated, mainly from model organisms, such as *Drosophila melanogaster* Meigen, 1830. Research has uncovered several structures and genes, leading to characterization of several sensory-motor pathways, as well as a better understanding of their roles (Schnaitmann et al. 2020; Mohapatra & Menz 2019). Noteworthy, these canonical studies paved the way for recent surveys on sensory systems in a variety of extant taxa, a soaring effort that has been shedding light on the role of evolution in different systems (e.g., visual) and typical genes involved (e.g., *Opsin*). Likewise, other model organisms also fill important gaps (e.g., *Tribolium castaneum* [Herbst, 1797], *Cloeon dipterum* [Linnaeus, 1761]) on how multiplexity in sensory systems and structures, and also evolutionary novelties, arise in insects as a whole (Altincicek et al. 2008; Almudi et al. 2019). These kinds of studies were, and still are, mostly focused on insects, especially because they dwell in a diversity of environments and habitats, and most of them undergo metamorphosis in different environments from which they emerge. For example, larvae usually are physiologically, morphologically, and ecologically unique from adults, especially in cases when each larval stage develops in different environments, requiring other resources for that. Therefore, a variety of mechanisms, structures, and consequently mechano- and chemoreceptors are required for sensing environments.

Insects display a range of organs and structures known to play a role in perception, from the external surface of their body to internal organs, which can fall into two major sets of receptors: mechano- and chemoreceptors. Mechanoreceptors usually are hair-like projections from the cuticle which arise from a socket that permits

movement. In this regard, movement triggers neural stimulation resulting in perception. Chemoreceptors deal with the environment from olfaction and contact chemoreception (gustation or taste). An array of chemoreceptors is spread over the cuticle and is sensitive to different scents and chemicals. These receptors are usually used in contexts other than feeding, being able to detect chemicals in solutions and dry surfaces, important to gathering information from the surroundings. However, processing this information is rather different within the central nervous system. Differently, visual systems, communication, and temperature perception rely on other structures, such as visual organs, antennae, and legs.

Visual or chemical communication can be driven by the context, warning predators or attracting partners. Therefore, itemizing which components play a role in sensory organs, and how it occurs can be a challenging task even for experts. The extreme diversity of forms and functions in insects portrays the countless, and extremely complex, structures involved in the sensory system. Therefore, the main goal of this chapter is to characterize the principal components involved in the insect's sensory system, how each element is triggered according to the context, and their respective role in a variety of taxa.

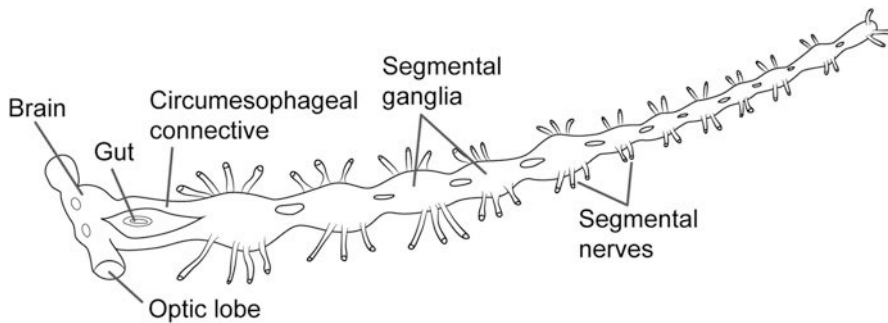
## Nervous System

### Basic Elements

A complex nervous system, such as those of the insects, are characterized by a variety of specialized cells responsible for processing information, driving impulses, promoting the functional integration of organs and systems, and generating specific behavior in appropriate response to the environment (Oland & Tolbert, 2003). The insect's nervous system consists of a brain located in the head, and a nerve cord located ventrally, with ganglia in each segment (Fig. 1). Nerve cells communicate through synapses with the action of neurotransmitters, such as acetylcholine.

The first basic element is the nerve cell, or **neuron**. The neuron consists of a cell body called





**Insect Sensory System, Fig. 1** Central nervous system of a hypothetical insect. (Adapted from Brusca et al. (2016))

**soma** or **perikaryon** containing mitochondria, a rough endoplasmic reticulum, and Golgi complexes. From the soma one or more cytoplasmic projections extend to make contact with other neurons or with effector organs, mainly muscles. These projections can be **dendrites**, responsible for the reception of incoming signals, or a long process called an **axon**, which conducts signals over long distances and is responsible for passing on signals to other neurons or effector organs. Neurons can be monopolar, bipolar, or multipolar and the type of neuron varies according to the region and its function. For example, most neurons from the central nervous system are monopolar, the peripheral sense cells are bipolar, and multipolar neurons occur in the ganglia of the nervous system (Chapman et al. 2013).

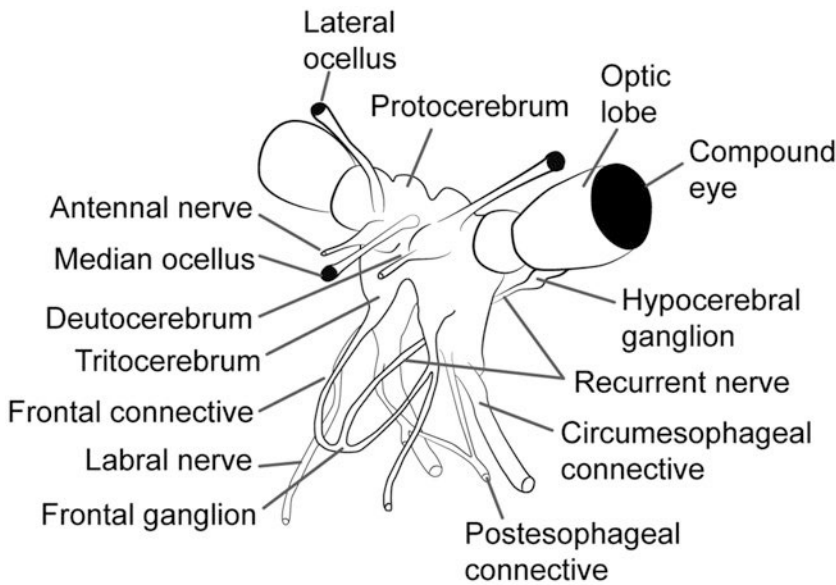
In addition to neurons, the nervous system also includes a variety of **glial cells**. Glial cells surround neurons with one or more folds, sometimes as several cells folded over themselves. Some neurons do not have glial cells surrounding them. As in vertebrates, the insect glial cells are normally outnumbering neurons in the central nervous system (Saint Marie et al. 1984). However, when compared to mammals, for example, the nervous system of insects has far fewer glial cells, about 10% of the cells of the central nervous system in an adult fruit fly (*Drosophila melanogaster* Meigen, 1830) (Edwards & Meinertzhagen, 2010) and 90% of brain cells in mammals (Blinkov & Glezer, 1968). In addition to the nursemaid role long been assumed (Hoyle, 1986), the functions of glial cells go beyond the protective role for neurons, such as: (i) assisting

neuronal development by providing trophic support; (ii) reference points for axonal location; (iii) maintenance of cells; (iv) neuronal isolation; and (v) regulation of extracellular space around mature neurons by acting in neurotransmitter clearance and recycling as well as in ionic regulation (Edwards & Meinertzhagen, 2010). In this context, changes in glial function can affect different behaviors in relation to locomotion, sleep cycles, and mate choice, for example.

### Brain

The insect brain is characterized by an anterior area with ganglion fusion. Like the general plan for arthropods, the insect nervous system is divided into three regions, each of which originates from a pair of coalesced ganglia: the **protocerebrum**, the **deutocerebrum**, and the **tritocerebrum** (Fig. 2). Each of these regions is responsible for innervating certain head appendages. The protocerebrum is the most anterior region, comprising most of the brain mass and innervates the eyes. It is bilobed and extends laterally to the **optic lobes**, which in turn extend to compound eyes. The deutocerebrum contains the antennal lobes – which receive olfactory stimuli, the antennal mechanosensory, and motor center. The tritocerebrum is the smallest part of the brain, consisting of two lobes located beneath the deutocerebrum. From it, the periesophageal connectors bypass the esophagus and connect to the lateral regions of the subesophageal ganglion.

In addition, insects have a hypocerebral ganglion between the cerebral ganglion and the foregut, which is associated with two pairs of



**Insect Sensory System, Fig. 2** Frontolateral view of the brain of a locust (Orthoptera), showing the three regions of the brain (protocerebrum, deutocerebrum, and

tritocerebrum) and the most important connectors, ganglia and nerves. (Adapted from Brusca et al. (2016))

glandular bodies of important endocrine function: **corpora cardiaca** and **corpora allata**. Together with the prothoracic glands and neurosecretory cells of the protocerebrum, they form an important endocrine center that regulates growth, metamorphosis, and other functions (Brusca et al. 2016). The corpora cardiaca stores and releases neurohormones, such as prothoracicotropic hormone, which stimulates the secretory activity of the prothoracic glands. Corpora allata, on the other hand, is responsible for the secretion of “**juvenile hormone**,” the main hormone involved in the insects’ moulting and metamorphosis, which opposes or prevents the metamorphosis of immature insects (Williams, 1956). However, the biological action of the juvenile hormone is observed only in the presence of active prothoracic glands or its secretory product, ecdysone (hormone responsible for inducing moulting in insects) (Williams, 1959).

### Peripheral Nervous System

The peripheral nervous system is formed by nerves that leave or reach the central nervous system to innervate muscles or sense organs. That is, it is responsible for receiving all external stimuli and sensations and establishing an

immediate communication with the brain. The nerves can be of two types according to their function: (i) **afferent**, or sensory, when they arrive at the central nervous system, bringing information about the stimulus received by the sense organs, and (ii) **efferent**, when they leave the central nervous system and give instructions to muscles and appendages.

### Stomodaeal Nervous System

The stomodaeal (or stomatogastric) nervous system (SNS) is the anterior portion of the insect nervous system, characterized by innervating the visceral organs through a peripheral complex of ganglia and nerve fibers, being closely linked to the brain and the endocrine system (Ayali, 2009). In general, the SNS innervates the muscles of the mouth cavity, foregut, and midgut, and regulates food uptake and food transport (Hartenstein, 1997). Within this context, the behavior related to food, that is, the different variations of the motor pattern appropriate to the various types of food and food particle consistencies, is the primary physiological role of the SNS. Because it is considered a plesiomorphic character, being present in all higher invertebrates (starting with

Annelida), the SNS is of interest from an evolutionary perspective for comparative studies on the nervous system (Ayali, 2009).

The main ganglion of this system is the **frontal ganglion**, located in front of the brain (Fig. 2), playing a key role in the control of foregut movements (Ayali, 2004). Studies examining the effect of frontal ganglion ablation on the behavior and development of the insect have shown its fundamental function in the passage of food through the anterior intestine and in crop (i.e., area of the foregut where food is temporarily stored for enzymatic digestion) emptying (Ayali, 2004). However, in addition to its function in feeding, the frontal ganglion is fundamental in another important behavior of insects, namely moulting and ecdysis. In this regard, the SNS has also a role in moulting, by increasing the internal air pressure in the digestive tract, acquired by swallowing air during ecdysis in aerial arthropods (e.g., allows the external cuticle to detach from the new). Likewise, aquatic arthropods swallow water for subsequent cuticle division (Ayali, 2009).

Interestingly, the formation of the SNS has many parallels with the development of the vertebrate peripheral nervous system. In addition to having functions comparable to the vertebrate autonomic nervous system, the development of SNS in insects has similarities with the neural development in vertebrates, in particular the neural crest and sensory placodes (for more detailed information, see Hartenstein, 1997).

## Perception and Sense Organs

Insect perception is mainly driven by neural and glandular reactions in response to stimuli from the environment. All insects have sense organs that make it possible to detect scents, sounds, produce images, etc. The signals generated by the receptors of the sensory system travel to the brain where an appropriate behavioral response is generated according to the necessity, such as avoiding danger, foraging (i.e., search for prey/food), finding a mate, and reacting to environmental changes, among many others.

Receptors of the sensory system can be divided into two categories: (i) **exteroceptors**, which detect external stimuli, and (ii) **interoceptors**, which detect signals from the body itself. Proprioceptors, which detect changes in the position of the body or body parts, are a type of interoceptor. Receptors are also classified in terms of functionality and direction of impulse (**mechanoreceptors**, **chemoreceptors**, and **photoreceptors**).

### Mechanoreception

Mechanical stimulation is caused mainly by pressure and air displacement to detect sound, deformations of body regions, movements, vibrations, or other mechanical disturbances, which can either be caused by external forces or by self-produced movements (Keil, 1997). In arthropods in general, stimuli are processed by the distortion or flexion of bristles and membranes arranged along the body. Mechanical stimuli serve several different purposes, such as: (i) sound receptors can be involved both in intraspecific communication (for example, the song crickets and cicadas), as well as in the avoidance of predators (e.g., moths avoiding bats) or certain parasitoids (e.g., caterpillars avoiding wasps); (ii) air current receptors may be involved in alarm behavior (e.g., by filiform hair on the cerci of crickets and cockroaches) as well as prey detection (e.g., trichobothria of spiders); and (iii) touch receptors (bristles) report direct mechanical contact, but are also involved in regulating body position (e.g., hair plates around the neck of bees and flies) (Keil, 1997).

### Sensors

Sensors are basic functional units composed of receptors. They usually have a cuticular portion, with one or several neurons, and peripheral cells. The most common types of mechanoreceptors according to cellular, subcellular, and cuticular organization are: (i) **tactile hair** or **bristle**; (ii) **hair plate**; (iii) **campaniform sensillum**; and (iv) **chordotonal organ** (for reviews and pictures see Keil, 1997 and Tuthill & Wilson, 2016).

Trichoid sensors, usually referred to as bristles or tactile hairs, are the most common

exteroceptive organs on the body surface. These are elongated structures, with the base wider than the tip. They have two pores, a terminal and a basal one, in which the latter is in direct contact with the nerve cell. Just below the bristle, there is a cavity filled with lymph, which reinforces the signal captured by the cuticular structure from the movement of the bristle (Chapman et al. 2013). As the most common and abundant mechanoreceptor in the body of insects, the bristles are associated with a wide range of behaviors in insects. The movement of tactile hair can serve as an alert to the presence of foreign objects, such as dirt and parasites, on the body surface (Tuthill & Wilson, 2016). The stimulation of the bristles can be involved in detection of strong air currents in locusts (Camhi, 1969a, 1969b) and can detect wind, courtship song, and the wingbeats of a predator in crickets and cockroaches (Tuthill & Wilson, 2016). The bristles modified on the cerci of crickets and cockroaches are also called **trichobothria**. They are long relative to the diameter and, unlike the usual trichoid sensors, do not taper (Chapman et al. 2013).

In addition to individualized bristles, they can occur in small groups of short, stiff, and parallel hairs, each of which is innervated by a single sensory neuron, in which they are called hair plates. They are often positioned at folds in the cuticle, being deflected during joint movement (Tuthill & Wilson, 2016). In *Drosophila* it functions as a proprioceptor found in the joints of the legs (Pringle, 1838), while in cockroaches it can function as an exteroceptor at the base of the antennae (Okada & Toh, 2000).

Campaniform sensillum do not have elongated cuticular structures like the bristles. Instead, they have a malleable cuticle, called **dome**, which is composed of three layers: a thin outer layer, a porous middle layer, and a more fibrous internal layer. An articular membrane surrounds the dome. These small domes detect tension and compression in the surrounding cuticle and they are often found grouped in areas where disturbances in the cuticle are likely to be high, such as in the proximal regions of the leg and antennae, which are regions subject to torsion (Tuthill & Wilson, 2016). The nerve cell binds to the three cuticular

layers through the dendrite, which is responsible for transmitting the signals received (Chapman et al. 2013). Studies have shown that campaniform sensilla plays an important role in coordinating joint movement both within a leg and across legs, and that natural tripod gaits are shaped mainly by sensory feedback to motor circuits (Tuthill & Wilson, 2016), and not by sensory neurons present in the legs (e.g., *Drosophila melanogaster* is not affected in tripod gait and left-right coordination when its neurons are deprived in the legs [Mendes et al. 2013]).

Chordotonal, or scolopophorous, organs are structurally complex mechanoreceptors distributed throughout the insect's body, working to detect a wide range of mechanical stimuli, from gross motor movements to airborne sounds (Yack, 2004). Chordotonal organs include several types of mechanoreceptors in which one or more bipolar neurons establish a connection between two internal surfaces of the exoskeleton. Along with each bipolar neuron there are two other cells forming a sheath (the **escolopale** cell) and an attachment point (the **cap cell**). Together, these three cells create a unit called **scolopidia**, which can occur individually or, most commonly, in groups of similar units. The scolopale cell contains the scolopale, a ring or a series of rods made of fibrous material. The neuron is triggered by the movements of the scolopidium's apex. Common types of these organs are: Johnston's organ, tympanal organ, and subgenual organ.

The **Johnston's organ** is the largest chordotonal organ found in insects and is located at the base of the antenna, between the pedicel and the first flagellum of most species, although they are particularly prominent in individuals of the order Diptera – flies and mosquitoes. The structure is formed by one or several masses of scolopidia, which respond to movements of the flagellum relative to the pedicel and the number of scolopidia in one Johnston's organ in different insects' groups can vary from 30 to 5000 (Schmidt, 1972 *apud*. Jeram & Pabst, 1996b). In many insects, Johnston's organ functions as a proprioceptor, monitoring the position and movements of the flagellum according to the active or passive movements of the antennae and body (Jeram & Cokl, 1996a) and to detect air particle

vibrations from near-field sound sources (Sane & McHenry 2009). In male mosquitoes (order Diptera, family Culicidae) and chironomid midges (order Diptera, family Chironomidae) it functions as auditory organ to detect flight sounds of conspecific females in mating behavior (Burkhardt & Gewecke, 1965; Yack, 2004). In flies (order Diptera, family Calliphoridae) and locusts (order Orthoptera), the Johnston's organ is involved in controlling the speed and direction of flight. Interestingly enough, in dancing honeybees (*Apis mellifera* Linnaeus, 1758) Johnston's organs are responsible for detecting the airborne sound close to the field generated by the wings during the waggle dance and used to transmit information to other bees about the sources of nectar in the environment (Dreller & Kirchner, 1993). Finally, it can act as a gravity receptor, controlling the position of the body in water, in water bugs (order Hemiptera, family Belostomatidae), and as a detector of water currents in other aquatic insects (Jeram & Pabst, 1996a).

Groups of insects such as crickets, bees, grasshoppers, and some flies have independently evolved auditory **tympanal organs**. The tympanic organs are chordotonal organs specialized in detecting pressure waves from distant sources of sound (Sane & McHenry, 2009). They consist of a thin cuticular membrane stretched through a sac filled with air. Chordotonal organs attached to the tympanic membrane detect high-frequency mechanical vibrations (2–100 kHz), acting in a similar manner to a vertebrate's eardrum. Insects that do not have tympanic organs depend on Johnston's organ for detecting sound, limiting their hearing to lower frequencies (<1 kHz) (Tuthill & Wilson, 2016).

The number of scolopidia present in tympanic organs varies widely within insects, from a single scolopidium found in *Plea* Leach (order Hemiptera, suborder Heteroptera) to more than a thousand in some cicadas (order Hemiptera, suborder Homoptera) (Marques, 2012). In addition, tympanic membrane can be found in different parts of the body, as in the legs of crickets and bush-crickets, in the abdomen of grasshoppers and cicadas, and in the thorax of moths (Snodgrass, 1926; Sane & McHenry, 2009).

Finally, another specialized chordotonal organ found in most insects is the **subgenual organ**, which is a fan-shaped array of scolopidia located in the proximal part of the tibia (Tuthill & Wilson, 2016). This organ is sensitive to vibrations of the substrate upon the animal stands. In cockroaches and ants, the subgenual organ is extremely sensitive, playing an important role in perceiving vibrations emitted by possible predators, and in some cases, intraspecific substrate-borne sound communication, as in the green lacewing, *Chrysoperla carnea* (Stephens, 1836) (order Neuroptera, family Chrysopidae), (Devetak & Pabst, 1994) and in stink bugs (order Hemiptera, family Pentatomidae) (Čokl, 1983).

### Chemoreception

It is the detection of chemical stimuli, either through **olfaction** (chemical compounds commonly carried by air) or **contact chemoreception** (gustation or taste) which is transmitted by solutions or dry surfaces. The functional distinction between olfaction and contact chemoreception is usually clear, based on the characteristics of the stimuli (volatility), the means of transport (water versus air), and the morphology of the sensillum (Stadler, 1984). In addition, processing within the central nervous system is quite different for olfaction and contact chemoreception. However, olfactory receptors can respond to substances in solution and contact chemoreceptors can respond to high concentrations of some odors (Chapman et al. 2013).

### Olfaction

Olfaction is the ability to detect compounds in the gaseous state, and insects have a wide range of receptors sensitive to odors. Insects can detect odor through the antennae and the maxillary and/or labial palp. The importance of olfaction for insects is very evident mainly through the existence of different forms of antennae. Basically, the distal segment of the antennae and the palpi is covered with olfactory sensilla of different shapes and structures. Insect antennae probably evolved from structures that were predominantly mechanosensory. While the antennae of primitive terrestrial arthropods have intrinsic musculature,



responsible for the great flexibility of movement, they have a low number of sensilla, presenting a very ineffective chemoreception capacity. On the other hand, the insect's antennae are rich in sensillum, but lack intrinsic musculature, being in most lineages specialized structures for the detection of odor molecules (Schneider, 1964; Hansson & Stensmyr, 2011). However, there are exceptions such as the water scavenger beetles (family Hydrophilidae, order Coleoptera), whose antennae do not actually have an olfactory function but functions as an auxiliary breathing apparatus, which are used as oxygen replenishment reservoir located in a cavity between the elytra and the abdomen, where the respiratory spiracles are located (Hrbáček, 1949). In some groups, the sound detection function by the antennae is evident, along with the olfactory function. Mosquitoes are a good example in which the evolution of antennal morphology was most likely driven by an olfactory and hearing demands (Wheelwright et al. 2021).

There are several types of olfactory sensillum, the most common of which are the **trichoids**: long, thin-walled (0.5 micrometers or more) hair-like structures without a socket at base. Other shapes have also been described as follows: **basiconic**, which are shorter projections than the trichoids, digitiform, and with thinner wall (0.3 micrometers or less); **placoid**, continuous plates arranged in the internal integument; and **celloconic**, which are projections arranged within small cuticle invaginations (Chapman et al. 2013).

Cuticles are multiporous. These pores allow the detection of odorous substances. The main difference between mechanoreceptors and chemoreceptors is the number of pores, which help in the capture of olfactory substances, along with the dendrites inside the sensor, reaching the pores.

#### Contact Chemoreception

A strong feature of contact chemoreceptors is that they are internally hollow and, unlike the olfactory sensilla, they have only one pore at the tip. It is through this large apical pore that stimulating chemicals reach dendrites of the gustatory receptor neuron. A clear example is during feeding. The

sensilla of the insect's mouthparts is usually bathed in the fluid released by the food during feeding, which generates a response by neurons to chemical substances in solution, being comparable to the taste receptors in the mouth of vertebrates (Chapman et al. 2013).

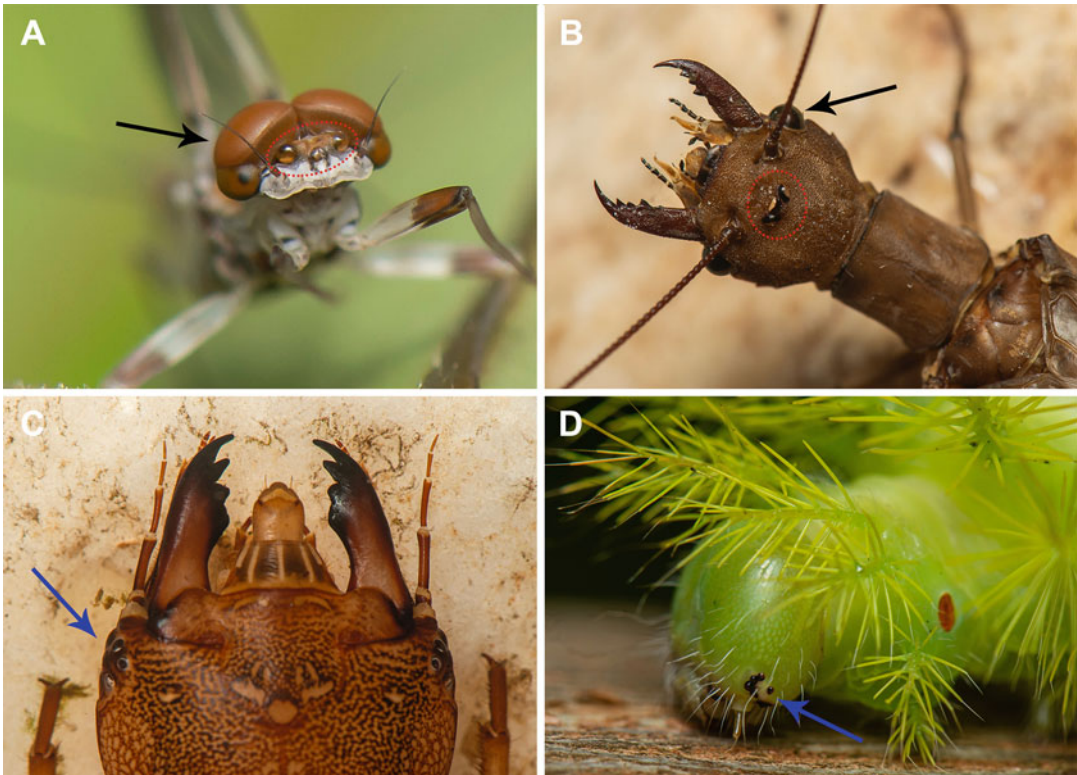
Although they may have very different external shapes, the most common contact chemoreceptor is a trichoid bristle. Normally, bristle sensilla have sockets similar to those of mechanoreceptor hairs that provide some motility. More rarely, contact chemoreceptors can also be basiconic, in this case not having a socket and being continuously surrounded by the insect's cuticle.

Chemoreceptive contact sensilla are found in the main parts of the body, but most are located in the mouthparts and tarsi (more distal segments of the legs, anterior to the claw when present). However, chemoreceptive contact sensilla have already been identified in the wings, ovipositor, and antennae (see Stadler, 1984). Basiconic sensilla are most commonly found in the feeding channel, that is, inside the mouthparts (Chapman et al. 2013).

The gustatory organs of blood-feeding mosquitoes, for example, include the tarsal segments of the legs, the labellum and labrum of mouth parts, and the cibarium, an internal organ of the head responsible for sucking. The sensilla found in the tarsi of the legs are responsible for the first detection with a potential source of blood or oviposition site. Once the food source has been found, the needle-shaped labrum pierces the prey and then the contact of blood chemicals will be made through the sensilla of the labellum and the cibarium (Baik & Carlson, 2020).

#### Photoreception

Insects can perceive light from different optical and dermal structures. The most common structure is the **compound eye** (Fig. 3a, b). However, other structures, such as the **ocelli** (Fig. 3a, b) and **stemmata** (Fig. 3c, d) are also found in insects. Stemmata are found only in the larval phase of holometabolous insects (i.e., type of development where larval morphology is completely dissimilar from that of the adult, having a pupal stage between the larval and the adult phases).



**Insect Sensory System, Fig. 3** Photoreceptive organs in insects: compound eye (black arrow), ocelli (red dashed line), and stemmata (blue arrow). (a) male subimago of mayfly of the genus *Thraulodes* showing its surprising compound eyes divided into two portions (an upper portion and a lower portion) and triad ocelli. (b) adult female

of dobsonfly of the genus *Corydalus* with emphasis on compound eyes and ocelli in triad. (c) aquatic dobsonfly larvae of the genus *Corydalus* showing the stemmata. (d) saturniid caterpillar showing the stemmata (Family Saturniidae). (Pictures were kindly provided by Frederico F. Salles (Universidade Federal de Viçosa, Brazil))

All eyes originate from embryonic ectoderm and they have similar basic structures. Eyes are composed of an optical portion and a nervous portion. The optical portion specializes in capturing light and the nervous portion specializes in transducing and translating the light signal.

#### Compound Eye

The compound eye is the main and most developed photosensitive structure in insects. Most adult insects have a pair of compound eyes, which can be greatly reduced or absent in parasitic groups and in many cavedwelling forms (Brusca et al. 2016). Compound eyes are composed of smaller units, called **ommatidium** (Fig. 4a). The number of ommatidia per eye can vary from 800 in drosophilids to 20 thousand in some dragonflies, and the number of ommatidia determines

the visual acuity of the compound eyes (Marques, 2012). A single ommatidium consists of two elements: an external optical part composed of a **lens** and a **crystalline cone**, and an internal sensory part composed of a **rhabdom** and **sensory cells** (Brusca et al. 2016; Chapman et al. 2013).

Below the lens is the crystalline cone, formed by four **Semper cells** and surrounded by two **pigmented corneagenous cells** (Triplehorn & Johnson, 2005). The retina is the eye's innermost part, and it is a junction of seven to nine elongated neurons called **retinular cells** (or **sensory nerve cells**), the photoreceptors cells. The peripheral part of each retinular cell is a set of tightly packed microvilli called **rhabdom**, a light collection area that converts light energy into nerve impulses. The retinular cells are surrounded by several (12–18) secondary pigment cells, which isolate

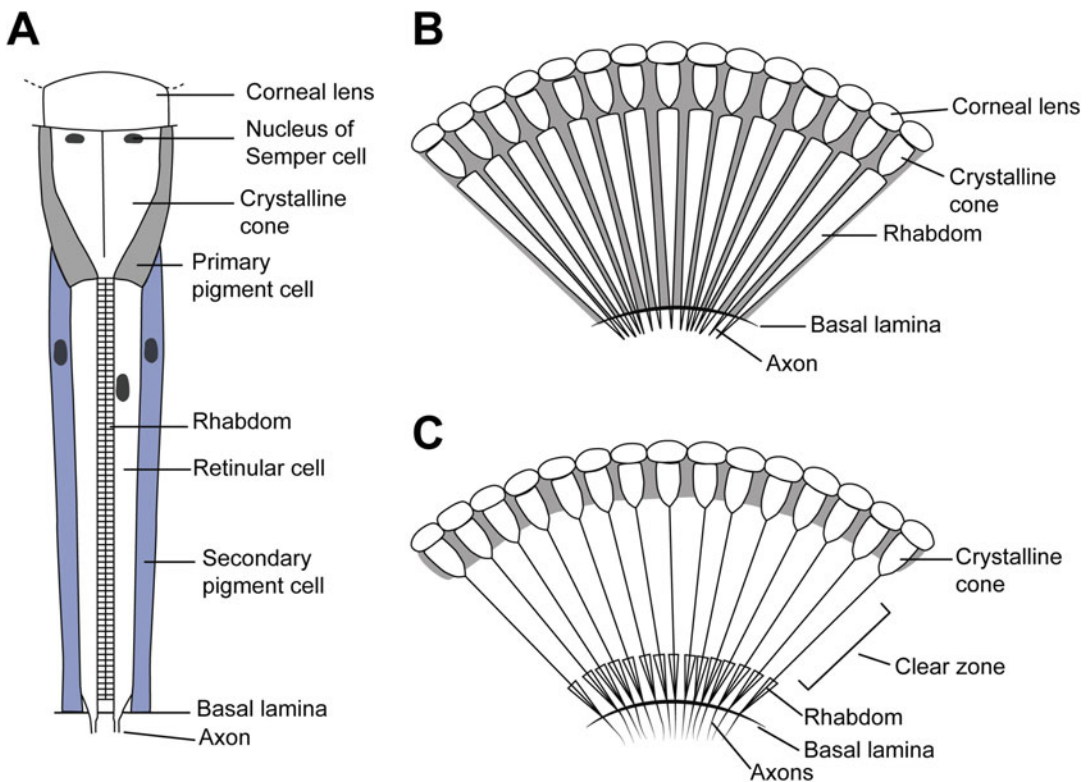
each ommatidium from its neighbors (Brusca et al. 2016).

Insects have two types of eyes: **apposition eyes** or **superposition eyes**. These differ in relation to the distance between the sensory cells and the lens, which vary according to the insect's habitat. Most diurnal insects have the sensory receptor cells ending close to the lens (Fig. 4b). In this case, the pigment surrounding one ommatidium extends along its entire length, then the light reaching a rhabdom comes through only this one ommatidium. As a consequence, the image formed is in mosaic, in which each ommatidium forms an equal image. In contrast, most nocturnal insects have eyes with a clear zone between the lenses and the sensory receptor cells (Fig. 4c), forming a much brighter image than the apposition eye (Chapman et al. 2013). When light enters an ommatidium, it can pass to the adjacent ones through the wall

of the unit, optimizing the luminous perception and helping in the formation of the image (Fig. 4c).

#### Ocelli

Ocellus ("little eye" in Latin) is a second visual system in addition to the insect's compound eye. It is often found dorsally in a triad (Fig. 3a, b) (but can be from 1 to 3) in different locations on the heads of flying adults of most orders and in immatures of most nonholometabolous orders. While compound eyes are sophisticated visual organs responsible for functions that require good spatial resolution (e.g., motion detection, pattern recognition, and color vision), ocelli are able to detect only changes in light intensity over a wide visual field for having high aperture diopter. Although compound eyes are much more complex organs, precisely because they are simpler, ocelli are superior in terms of photic sensitivity and speed of



**Insect Sensory System, Fig. 4** Compound eye of a hypothetical insect. (a) a single ommatidium of an apposition eye. (b) apposition eye. (c) superposition eye. (Adapted from Chapman et al. (2013))

signal transmission, thus complementing the functions of compound eyes (Mizunami, 1995).

Ocelli consist of a single lens, and beneath, the ocellar receptor cells are arranged differently than in a compound eye. In the compound eye, the receptor cells are arranged in an ordered array with its rhabdoms presented as a mosaic of guides for the passage of light. Whereas in the ocellum, the rhabdoms are arranged as irregularly packed cells forming a network of baffles (Wilson, 1978), probably maximizing their ability to capture light scattered diffusely across the retina (Mizunami, 1995).

### Stemmata

Stemmata are the visual structures of holometabolous larvae, occurring laterally on the head and can vary in number from one (most typically) to six on each side (Chapman et al. 2013) (Fig. 3c, d). Stemmata have been wrongly called lateral ocelli, but they differ in morphology and origin. Studies based on morphology and DNA revealed that stemmata evolved from compound eye ommatidia of hemimetabolous (i.e., type of development where the larvae are morphologically similar to the adult, except for the absence of wings and being sexually immature, in addition to the presence of some larval characteristics such as tracheal gills for aquatic groups) ancestors (Paulus, 1986; Liu & Friedrich, 2004).

These structures are composed of a cuticular lens in the outermost portion, above the lens. Below the lens are retinular cells, which can vary in number and shape. From the arrangement of these cells, a single rhabdom or many rhabdoms can be found, conditions that vary from group to group (for a comprehensive review of stemmata see Gilbert, 1994).

### Dermal Light Sense

Some insects are also able to sense luminosity from photosensitive epidermal cells, or extra-ocular photoreceptor cells. These cells are usually small receptors with a transparent cuticle diffusely distributed in the body surface. Unfortunately, we still know relatively little about this way of sensing light, but Ramirez et al. (2011) made a review about the knowledge about dermal light sense in

animals. Although studies in the area are scarce, it is already known, for example, that some butterflies use a small set of photoreceptors located at the end of their abdomens to control copulation in males and oviposition in females (Arikawa et al. 1997).

## Temperature and Humidity

Sensory cells that respond to temperature and humidity are usually present together in a single sensillum called **thermo-hygroreceptor**. The mechanisms responsible for the ability of insects to respond to humidity and temperature gradients are still poorly understood, but all species that have been studied have sense cells responsive to temperature and humidity on the antenna (Chapman et al. 2013). Sensor cell consists of a short peg bristle without pore and an immovable socket.

While one of the hygroreceptors responds to an increase in humidity (**moist receptor**), the other responds to a decrease in humidity (**dry receptor**). The thermoreceptor responds to a drop in temperature, called the cold receptor. The response rate of these receptors varies according to the insect, but in *Periplaneta* Burmeister, 1838 (order Blattodea), for example, the dry receptor has a higher tonic firing at low humidities than the moist one, being more quickly affected in drier environments. Also, the same receptor is sensitive to temperature, with a higher firing rate at higher temperatures than in lower ones (Chapman et al. 2013).

## Cross-References

- [Arthropod Cognition](#)
- [Arthropod Life History](#)
- [Arthropod Morphology](#)
- [Insect Communication](#)
- [Insect Diet](#)
- [Insect Life History](#)
- [Insect Locomotion](#)
- [Insect Morphology](#)



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## Insectivora or Eulipotyphla Locomotion

### ► Insectivore Locomotion

## Insectivore Diet

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## Introduction

In 1960, insects were estimated to have a worldwide biomass of 1000 billion metric tons (Williams 1960), but current estimates have lowered that estimate to half that amount – only 500 billion metric tons (Koerth-Baker 2017). This is still an order of magnitude greater than humans (60 billion metric tons) and an quarter of all animal biomass on earth (2000 billion metric tons) (Bar-On et al. 2018).

The diversity of insect species is staggering – over a million species have been identified to date, likely only a small fraction of the total. Insects are found in every ecosystem on earth and in nearly every niche, with every type of life history imaginable – short-lived, long-lived, seasonal, year-round, flying, burrowing, parasitic, social, and more.

*Insectivores*, insect-eating animals, exploit this resource, turning this abundant biomass into their own fuel. (Colloquially, the term “insectivore” is often applied to animals that consume insects as well as other arthropods such as arachnids (spiders and scorpions) and myriapods (centipedes and millipedes.) Insectivorous animals include nearly all amphibians, numerous bird, fish, and rodent species as well as anteaters, armadillos, pangolins, the aardvark, and many insects themselves. Nearly every taxa of animals, though, consumes insects as some part of their diet.

## Being an Insectivore

Insects vary in abundance across both space and time. Many insects have strong seasonal or even multiannual cycles of abundance (e.g., 17-year cicadas). Insectivores must therefore acquire sufficient food to meet their energetic and nutrient needs throughout the year from an ever-rotating set of different insect populations. Specialization in a singular insect species is therefore rare – most insectivores are generalists within a particular niche. For example, pangolins, armadillos, anteaters, and sloth bears are all termite-eaters. However, they may eat from dozens of different species of termites, as well as ants, bees, wasps, and moths living in many different nest types – arboreal nests, dead trees, or elaborate concrete-like mounds. Aerial feeders often fly above bodies of water, consuming whichever insects are hatching at that time of year. Such a diverse diet likely helps balance deficiencies and smooth over temporal differences in insect species' abundance. Many vertebrate species are only seasonally insectivorous, taking advantage of the large booms in insect populations during some seasons, even if they are primarily frugivorous or granivorous the rest of the year. For example, many otherwise herbivorous birds will consume large amounts of insect prey when they are feeding nestlings. Insects form an important part of the reproductive cycle for these species. Still other insectivores may eat insects only occasionally, such as chimpanzees and gorillas, who feed on insects as a small part of their diverse diets. A hallmark of insectivory is flexibility – both evolutionarily in terms of different methods to catch insect prey and behaviorally in terms of different techniques and search patterns.

### Detecting Insects

Insectivores must first find insects. Some use a sit-and-wait strategy, such as a spider waiting in its carefully spun web or the African bullfrog, which waits for its prey to come near before ambushing. Other species may search a general area to locate patches of insects, such as an anteater inspecting a field of termite mounds or a swift circling a lake looking for swarms of midges. Still others actively

search across an area looking for individual insects (such as a frogmouth taking short flights to look for large moths, or chickens pecking in a field) or spend considerable energy breaking into fortified and defended hives (bee-predators such as honey badgers, bears, and giant armadillos) or termite mounds (anteaters, giant armadillos, armadillo, sloth bear).

Depending on the species and the hunting method, all senses may be involved. Aerial predators typically use sight, although some, such as bats, use echolocation to detect their prey. Termite eaters use smell as well as audio and visual cues to find nests. Trout can detect insects visually above the water or use their tactile senses via their “whiskers” to detect an insect or worm in the water. Shrews locate insects using their senses of smell and hearing as their eyesight is poor. Insect insectivores may use all of the above to detect insects.

### Capturing Insects

The methods by which insectivores capture insects are nearly as diverse as the predators or prey themselves. Amphibians capture prey with a projectile thrust of their tongue, calculating their prey's trajectory and timing their movements to coincide with its movement. Anteaters also use their tongue, but instead of a projectile, their tongue acts as a sticky tool able to feel its way around inside the tunnels of a termite nest, extracting the insects within (and often a fair amount of mound material and soil). Praying mantids capture their prey with lightning fast leg movements and use spikes on their legs to hold their prey firmly. Web-building spiders use perhaps the most famous mechanism, spinning an elaborate web of nearly invisible silk and waiting for their prey to become stuck. Spiders may feed immediately or will wrap the prey in silk for a later meal. Aerial insectivores, such as swifts and bats, catch insects in flight, particularly at dawn and dusk when the prey are most abundant.

### Energetics of Insectivory

Successful insectivory requires balancing the nutrients and energy gained from insects with

the costs and risks of acquiring and digesting insects. Several strategies are common among insectivores. Many insectivores have low basal metabolic rates compared to noninsectivorous species (McNab 1986, 2002, 2009). Insectivorous marsupials, bushbabies, lorises, tarsiers, and xenarthrans (anteaters and armadillos) have characteristically low metabolic rates (McNab 1978; Elgar and Harvey 1987; Nagy 2005). Among birds, many insectivorous species exhibit torpor, and even short periods of no consumption can cause drops in core body temperature (McNab 1966; Weathers et al. 1984, 1990). Birds that exhibit torpor are highly likely to be either frugivorous, nectivorous, or insectivorous – in other words, they rely on foods that vary in availability (Hainsworth et al. 1977; Barclay et al. 2001; Schleucher 2004). These low energy adaptations likely help animals survive periods of low insect abundance.

## Insects as Food

### Insect Lifestage

Insects develop through several distinct lifestages, and their nutrient composition changes with their changing body forms. Larval stages tend to be higher in fat while adult insects are typically higher in protein. For example, mealworm larvae contain 49% and 35% protein and fat, respectively, on a dry matter basis, while the adult beetle form contains 65% and 15% protein and fat, respectively (Finke 2002). The more sedentary or nonfeeding a lifestage is, the more likely it is to be high in fat because it must store energy for its next transformation. Waxworm larvae, which do not feed at all, contain only 34% protein but are over 60% fat, while cricket nymphs, which resemble miniature adults, contain nearly double that level of protein (67%), and have only a quarter of the fat (14%; dry matter basis, (Finke 2002)). The amino acid profile of insects is generally very good, often on par with that of vertebrate prey (Bosch et al. 2013, 2014).

### Insect Diet

The insect's diet can also impact its macronutrient composition. For example, cockroaches, black

soldier flies, and mealworms reared on a high protein diet were higher in protein than those reared on low protein diets (cockroaches: 61% vs. 38%, black soldier fly: 46% vs. 39%, mealworms: 51% vs. 44% (Oonincx et al. 2015)). These nutrient changes may be due to direct changes in body composition or simply via the availability of nutrients found in the undigested food in the gut.

Insects also vary in their content of calcium and phosphorus depending on the mineral concentrations in their own diet. Many insects, both wild and commercially raised, are either deficient in calcium or the ratio of calcium: phosphorus is too low to meet vertebrate mineral requirements (Finke 2002, 2012, 2015; Oonincx and van der Poel 2011; Oonincx and Dierenfeld 2012). Vertebrate insectivores likely have mechanisms to cope with this, such as selecting insect types with higher calcium levels or feeding on calcium-rich items such as eggshells, bones, limestone, or clay. They may also have metabolic mechanisms to increase absorption or retention of dietary calcium. For example, tissue calcification has been observed in many tamanduas consuming diets containing amounts of calcium that would be normal for most other mammals (Woc Colburn 2015), indicating that they may retain more calcium than many other species.

### Chitin

The chitinous exoskeleton of insects can function in ways similar to fiber in the diet of herbivores. Many animals, including insectivores, produce endogenous chitinase enzymes, which can break down chitin, releasing energy. For others, chitin may provide necessary substrate for intestinal microflora and thereby support gut health. Giant anteaters, for example, have improved fecal condition on diets supplemented with either commercial chitin supplements or other fibrous compounds such as ground peat (Wyss et al. 2013; Leuchner et al. 2014; Gull et al. 2015).

### Other Nutrients

Outside of the macronutrients, insects cannot be categorized easily as generally “high” or “low” in particular vitamins, fatty acids, or other chemical compounds. Most insectivores will consume a

variety of different insect types to amass the nutrients they need.

Carotenoids (red and orange pigments found in many plants) are consumed by insects, primarily from plants or blue-green algae. Frogs consuming carotenoid-rich prey show improved coloration (Brenes-Soto and Dierenfeld 2014), immunity, and reproductive health (Ogilvy et al. 2012).

The diet can also impact the nutritional value of an insect in a different way – through the gut contents. For captive animals, a common technique used to increase the content of certain nutrients such as calcium, vitamins, or carotenoids is to *gut-load* insect prey by feeding the insects foods high in the target nutrient. Insectivores thereby receive these nutrients when they consume the prey along with its gut contents. Gut contents likely provide key nutrients to wild insectivores as well.

## The Future of Insectivory

Worldwide, insect populations are in decline (Vogel 2017). In Germany, flying insects declined by over 75% over a 10-year period (Hallmann et al. 2017). In England, over 2/3 of the moth species showed reductions over a 35-year period (Conrad et al. 2006). Bees face many threats (NRC Committee on the Status of Pollinators in North America 2007; Fisher et al. 2012; Vanbergen and Initiative 2013), putting large sectors of human agriculture at risk. Population data for other insect species and locations is largely unknown, but anecdotal evidence is that nearly all insects are in steep decline.

Another risk to insectivores is mismatched timing due to the effects of climate change. Insects may hatch out of sync with the foods they eat or the blooming of the flowers they pollinate, risking the populations of both the insect and floral species. Birds may hatch out of sync with insect populations, meaning parents have less food available to offer their growing brood (Roy and Sparks 2000; Schweiger et al. 2008; DeLucia et al. 2012; Renner and Zohner 2018) and may risk malnutrition (Burgess et al. 2018).

On the other hand, insects have high feed:gain ratios, meaning that more edible product

is produced from fewer inputs (DeFoliart 1989; Bernard et al. 1997; Huis et al. 2013; Anankware et al. 2015). This makes them one of the most efficient ways to begin to feed the world's growing human and animal populations.

## Cross-References

- ▶ [Aardvark](#)
- ▶ [Basal Metabolic Rate \(BMR\)](#)
- ▶ [Echolocation](#)
- ▶ [Nutrients](#)
- ▶ [Pangolin](#)
- ▶ [Torpor](#)

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## Insectivore Locomotion

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## Synonyms

Insectivora or Eulipotyphla locomotion; Mole, hedgehog, or shrew locomotion

## Definition

Movement used by solenodons, moles, shrews, and hedgehogs to traverse their environment.

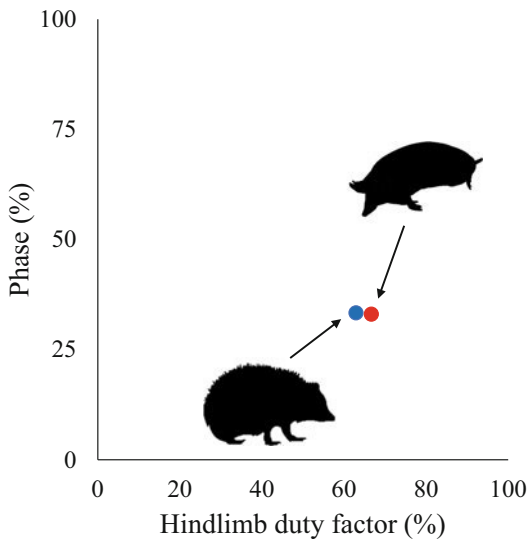
Insectivores are fossorial, terrestrial, and/or semiaquatic mammals. They are generally found worldwide except in Australia, Antarctica, and South America. For years, “*Insectivores*” has been treated as somewhat of a wastebasket taxon and there has been considerable disagreement on the exact composition of the group until genetic analyses established the order Eulipotyphla (D’Agostino 2015). Within Eulipotyphla, the families are *Soricidae* (shrews), *Solenodontidae* (solenodons), *Talpidae* (moles), and *Erinaceidae* (hedgehogs and gymnures). Insectivores comprise nearly 10% of all mammalian species and are quite small in size ( $\leq 1$  kg). Generally, they have soft and dense fur, but some species such as hedgehogs have altered their fur into stiff,

protective spines. Insectivores are useful in aerating soil and controlling vermin as well as insects that damage crops. Most are terrestrial or fossorial, with a few species displaying semi-aquatic behavior or arboreal adaptations. They occupy a wide range of habitats such as sand dunes, tropical rainforests, deserts, and high elevation mountains (Kurta 1995).

## Shrew Locomotion

Shrews (family *Soricidae*) generally have a long cylindrical body with short legs and simple feet (i.e., they have five toes on their forefeet and hind feet). Shrews display a variety of locomotor behaviors including burrowing, climbing, and swimming (Woodman and Wilken 2019). The gait repertoire of a shrew includes walks, trots, and bounds (Moskowitz 2010) (Fig. 1). Walks and trots are classified as symmetrical gaits (i.e., footfalls of forelimbs and hindlimbs are evenly spaced in time), whereas, a bound is an asymmetrical gait (i.e., actions of forelimbs and hindlimbs are unevenly spaced in time). The American water shrew (*Sorex palustris*) is semi-aquatic and exhibits “water-walking” behavior due to its large webbed hind feet with stiff hairs on the sides of each of the toes. Air bubbles become trapped in the fur, allowing the shrew to remain on the surface (Grosvenor 1979).

Shrews often utilize a crouching posture, allowing them to maintain close contact with the ground. However, crouching behaviors come at increased costs during locomotion. Riskin et al. (2016) explored the mechanical cost of crouching in shrews compared to more upright, but similarly sized, voles. Compared with crouching shrews, more upright voles used less positive power to increase the kinetic energy of the body during locomotion, making the total requirement of mechanical power per kg for locomotion smaller. This suggests that the metabolic cost of locomotion is reduced by an upright gait compared with a crouching one. The persistence of crouching in shrews, despite the mechanical advantages of a more upright gait over a crouching one, suggests that some other selective benefits to crouching



**Insectivore Locomotion, Fig. 1** Hildebrand plot showing the relationship between hindlimb duty factor (%) and Phase (%) for two species of insectivores [Blue = European hedgehog (*Erinaceus europaeus*); red = European mole (*Talpa europaea*)]

must exist. Ease of movement through tight burrows and reduced conspicuousness to predators are two obvious ones. Another would be readiness to accelerate quickly, without the need for a pre-jump crouch that would be necessary for an animal standing on outstretched limbs. Furthermore, Fischer (1994) has argued that advantages of crouching include an improved ability to maneuver around unexpected obstructions.

Due to high surface-area to volume ratios and metabolic rates, energy requirements play a major role in the selection of a suitable territory for shrews. Smaller shrews tend to occupy larger and less productive territories than larger individuals (Hanski and Kaikusalo 1989; Saarikko 1989). This may be a result of interference competition, in which larger shrews are able to outcompete smaller individuals in highly productive habitats with a greater variability in food availability. When there is a significant reduction in food availability, larger shrews decrease their activity. In contrast, smaller shrews must compensate by increasing their foraging activity. According to Saarikko (1989), shrews physiologically adapt to colder conditions or a decrease in

food resources by reducing the size of their body and skull to minimize energy use. This is achieved through the breakdown of cartilage and bone near the spine as well as the bones at the joints of the skull.

## Mole Locomotion

Fossorial insectivore species, such as moles (family *Talpidae*) have short forearms that are specialized for digging, and practice a sprawling, rather than upright, stance. The palms of moles contain a falciform bone (“sixth digit”), increasing the surface area of the palm. Enlarged claws on each toe break apart compact soil and larger, paddle-shaped forefeet act as shovels (Kurta 1995). In the forelimb, the trochlea of the humerus limited most pronation or supination, and olecranon process of the ulna is quite large for the attachment of triceps musculature. Together, this enhances its utility for lateral thrust digging, which causes dirt to be pushed away laterally from the body (Barnosky 1982). The humerus is also short, broad, and compact with prominent muscular attachments. This forelimb anatomy assists moles in traveling long distances to search for and transport food. Its clavicle is short and is directly connected to the humerus instead of the acromion, absorbing the stress from lateral thrust digging.

Moles use a symmetrical gait, in which the contralateral hindlimb and forelimb move synchronously with minimal lateral body-roll. Throughout stance phase, the sixth digit remains in front of the shoulder and elbow joints and it is used to move the body forward (Lin et al. 2019). This pattern is similar to a human using a cane or walker. The sixth digit is the only point of contact during locomotion. This suggests that the sixth digit supports the entirety of the mole’s bodyweight.

As burrowers, it is necessary for moles to be able to move and transport various types of soil. Lin et al. (2019) studied a fundamental difference in how moles use their forelimbs to burrow versus other mammalian diggers. Moles move substrates upward or outward from the body midline to

compress it into the side of the tunnel. This contrasts with the traditional method utilized by burrowers that displace substrates directly rearward. While moving through tunnels, their humerus is retracted and protracted in the parasagittal plane above, rather than in or below the horizontal plane. This pattern allows moles to traverse through underground tunnels with their arms sprawled out in front of them, preventing the destruction of their self-built tunnels.

The locomotor mechanics of underground animals, such as moles, can be useful in the development of search and rescue robots in areas that are not readily accessible. Lee et al. (2020) used information gleaned from the locomotor behavior of moles to develop a directional drilling robot. With a linear actuator simulating the mole's scapula, and an excavator mimicking that of the mole's forefoot, the robot would be capable of efficient excavation. Lee et al. (2020) stresses the importance of a device which could drill, clear any associated debris, and traverse within it.

## Hedgehog Locomotion

Hedgehogs (family *Erinaceidae*) have a slow, waddling gait, with the ability to accelerate to high speeds for brief periods of time (Quesenberry and Carpenter 2011). They have a distally fused tibia and fibula, as well as five digits on their forefeet and four digits on their hind feet. Their back is covered by spines, composed of keratin and modified hairs, which serve as a protective mechanism from predators. Hedgehogs utilize a lateral-sequence diagonal-couplet walking gait (i.e., each hindlimb footfall occurs before that of ipsilateral forelimb, with simultaneous movement of contralateral forelimb and hindlimb) (Granatosky 2019; Villanova et al. 2000). This gait provides enhanced stability for walking when the body is supported by two or three legs and prevents a lateral-body roll. At moderate speeds, hedgehogs are also capable of a trotting gait (i.e., symmetrical running) in which contralateral forelimbs and hindlimbs move together simultaneously. When moving at higher speeds, the limbs are extended to raise the body above the

ground (Rondinini and Doncaster 2002). Its fossorial ability is indicated by the brachial fossa being positioned in front of the greater tubercle on the anterior portion of the humerus and a clavicle that attaches to the acromion process of the scapula and to the manubrium. These features of the forelimb limit the motion of the shoulder in the anteroposterior plane (Goodarzi 2018; Hashemi et al. 2009).

Hedgehogs have done remarkably well in urban areas. In fact, many urban areas in Britain have higher hedgehog populations than the surrounding countryside. Likely, this is attributable to a greater abundance of food resources and lower incidence of predators. Pettett et al. (2017) demonstrated that as European hedgehogs (*Erinaceus europaeus*) move further away from buildings daily energy expenditure increases, possibly as they ranged larger distances on arable land. This suggests that hedgehogs select villages owing to the lower energy demands in comparison to arable farmland. Additionally, the presence of predators (i.e., badgers) also influences daily energy expenditure (hedgehogs show approximately 30% lower daily energy expenditure on sites with badgers). Pettett et al. (2017) speculate that on badger-occupied sites, hedgehogs may restrict movement and foraging in response to a threat from predation and thus have reduced daily energy expenditure. Therefore, hedgehogs may also seek refuge in villages where the perceived threat of predation is lower, and foraging is unrestricted. However, Patrick et al. (2008) demonstrated that within urban areas hedgehogs are attracted to linear features (i.e., roads). In such settings, hedgehogs are often involved in motor vehicle collisions, rendering roads as a barrier to movement.

## Conclusion

This chapter discusses the wide range of locomotor behaviors displayed by insectivores. Largely plantigrade, insectivores utilize symmetrical walking gaits. Exceptions to this include the American water shrew (*S. palustris*) that displays a "water-walking" behavior. Shrews also are able

to climb, burrow, and swim, with a wide gait repertoire that includes walks, trots, and bounds. The unique limb morphology of moles enhances the utility of lateral thrust digging, while allowing them to traverse through tight spaces without collapsing their self-built tunnels. Hedgehogs, identified by the coarse spines overlying their backs and sides, exhibit a slow waddling gait with the propensity to trot in short bursts. Insectivores also display unique behaviors and adaptations in response to environmental changes. Shrews, for example, are able to shrink their body and skull size through remodeling of cartilage. Hedgehogs, on the other hand, are often found in urban areas and are attracted to linear features, such as roads, which may predispose them to accidental road deaths. Future applications of insectivore locomotion include the creation of a directional drilling robot model, based on mole locomotion, which can potentially navigate difficult terrains and diffuse land mines.

## Cross-References

- Activity Budget
- Adaptation
- Adaptedness of Behavior
- Adaptive Radiation
- Basal Metabolic Rate (BMR)
- Dispersal Ability
- Dispersal Patterns
- Ecology
- Evolution
- Extinction in Learning
- Gait
- Home range
- Homology
- Homoplasy
- Insectivore Diet
- Locomotion
- Natural Selection
- Navigation
- Phylogeny
- Quadrupedal
- Species
- Taxa
- Terrestrial
- Territoriality
- Vertebrate Nervous System
- Zoo
- Zoology

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## Insects

### ► Arthropod Cognition

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## Insight

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## Synonyms

“a-ha moment”; Apprehension of relations;  
Eureka effect; Ideational behavior

## Definition

Insight refers to a family of phenomena related to problem-solving and understanding. In humans these typically involve the sudden realization of how to solve a problem that previously resisted resolution and, in animals, the sudden execution of a solution where previously there was failure, with discontinuity between the inappropriate and the correct behavior. There are considerable ambiguity and variation in the use of the term by different authors, sometimes referring to a type of behavior – sudden innovative solutions – other times to the subjective experience of understanding the problem and its solution, and other times to the hypothetical cognitive mechanisms underlying the observable behaviors and subjective experiences. This variety in definition (which, to complicate things, frequently is not made explicit) may explain some of the unresolved debates around the notion of insight within comparative psychology, both historical and contemporary. Although initially described in primates, insight has been attributed to a variety of avian and mammal species.

## Origins of the Notion of Insight: Köhler on Chimpanzee Problem-Solving

The Gestalt psychologist Wolfgang Köhler (1917/1921) formally introduced and popularized the term “insight” in psychology when reporting the results of his pioneering experiments on chimpanzee problem-solving. The apes – he claimed – acted not with blind trial and error but with “insight” [*Einsicht*]. In this original use, Köhler did not intend to coin a new technical term, but to use it as a synonym of “intelligence” or “understanding” in the common sense of these words (indeed the original title of the book known in English as *The Mentality of Apes* was *Tests of Intelligence on Anthropoid Apes*). His key finding was that chimpanzees confronted with problems (an obstacle preventing them from achieving a goal) responded with behaviors resembling what we call “intelligent” in ordinary language – finding an indirect way to overcome the obstacle. For



example, the apes used sticks to get food that they could not reach directly with their hands or moved boxes under a hanging fruit that they could not grasp from the floor.

The term “insight” came to identify the opposite of trial and error. E.L. Thorndike’s (1898/1910) earlier influential work on animal intelligence reported that cats trying to get out of a puzzle box learned the solution (pushing a lever) only through slow, prolonged trial and error learning – “a gradual elimination of unsuccessful movements, and a gradual reinforcement of the successful one” – which came to be known as the “law of effect.” Köhler argued that Thorndike’s tests had a key flaw – the mechanisms of the puzzle boxes were not visible to the cats, and therefore, they were in no position to demonstrate any understanding of them. For his chimpanzees, Köhler chose tests whose conditions (target, obstacles, and any relevant elements) were fully visible, and he used a wide variety of tasks ranging from easy (e.g., approaching the goal through a roundabout or using one stick) to very difficult (e.g., combining sticks or moving the goal in a projected roundabout; see later).

Under these conditions, the apes produced sudden solutions preadapted to the structure of the problem without having to go through blind trial and error. Although in a given problem the chimpanzees might at first engage in unsuccessful attempts (e.g., trying to directly reach the goal with their arms), they abruptly changed their approach executing correct solutions in a smooth, continuous way. Köhler concluded that the chimps showed “intelligence or insight of the human type.” Even when failing problems, they frequently made “good errors” reflecting a “partial insight” of the situation, for example, trying to lift a door over a stone blocking its path, instead of removing the stone, or piling boxes to build a higher tower, but without attending to the visual statistics to optimize box balancing.

In his first use of the term “insight,” therefore, Köhler intended it to be synonymous with “intelligence” or “understanding.” He did not initially propose a specific theory of intelligence or insight, although he suggested this would come from within the nascent school of Gestalt psychology.

In later elaborations, Gestalt psychologists used insight in a more general, potentially explanatory sense – the ability to “apprehend the relations” between the elements of a situation, which in problem situations would require a restructuring to lead to a solution. This apprehension of relations included not only the perceptual field but also the subjects’ actions and previous experiences, which were part of the field of relations that needed restructuring to solve the problem.

Other Gestalt psychologists (e.g., Duncker 1935) adopted the term insight to investigate problem-solving in humans. In this area, the term is associated not only to the production of sudden innovative solutions but also to the subjective “a-ha experience” – the feeling of clearly and suddenly “seeing” and understanding the solution to the problem. Insightful problem-solving has continued to be the object of intensive research in human cognitive psychology and neuroscience (Bowden et al. 2005) with some conceptual and methodological issues overlapping with comparative psychology.

One recurrent problem in animal psychology is to what extent and in what sense animals experience a representational “understanding” of the problem and its solution before executing the latter and how this could be investigated.

## Definitions of Insight

In comparative psychology, definitions of insight make reference to the novel and sudden nature of the behavior that resolves a problem. One of the most widely used definitions is W. H. Thorpe’s (1956), who distinguished between “insight” as the “apprehension of relations” in perception and “insight learning” as “the sudden production of a new adaptive response not arrived at by trial behavior, or the solution of a problem by the sudden adaptive reorganisation of experience” (Thorpe 1956, p. 100). Although a definition in terms of suddenness and novelty of behavior could appear to be objective, in fact it is difficult to specify precisely what counts as “sudden” and “novel.” How different from previous experience and existing behaviors should an insightful

solution be? How discontinuous its emergence? Is it necessary that there is a previous impasse with unsuccessful attempts?

The definition of insight is further complicated when reference is made to specific mechanisms or unobservable experiences, as Thorpe does in the second part of his definition. How can we tell if there has been a “reorganization of experience,” other than by the production of the novel behaviors mentioned in the first part of the definition?

Other authors propose that insight requires that the novel behaviors are based upon a causal understanding of the structure of the problem and how the solution works, while others emphasize the need for “mental planning,” where the steps of the solution are mentally represented before their execution. What counts as causal understanding? How much causal understanding is necessary – should every component of the solution be causally represented? Should all steps be represented in advance, and in how much detail? We will discuss examples of these later.

Thus, although insight seems to be an intuitive concept, in practice from its inception, it has remained difficult to define and operationalize with precise criteria (Hartmann 1933; Shettleworth 2012). One recurrent debate is if insight is an expression of general cognitive mechanisms or it involves unique, specific mechanisms that set it apart from other manifestations of intelligence. Within learning theory, the question is if insight is a special type of learning or a manifestation of general learning principles.

## Insight and Behaviorism

In the years following Köhler’s publications, insight became a challenge for the increasingly dominant (not only in comparative but also in psychology in general) paradigm of behaviorism. In America the notion had been further popularized through the work of Yerkes (1916), who had reported insightful behaviors in an orangutan at the same time as Köhler. Although he initially referred to this as “ideational behavior,” he eventually adopted Köhler’s term. Behaviorist

psychologists attempted to provide accounts of insight from inside behaviorist theory.

For example, Harlow (1949) proposed that it was a manifestation of “learning set,” the progressive facilitation in the acquisition of new responses based on previous experience with similar situations (“learning to learn”). In Harlow’s arbitrary discrimination tests, initially monkeys needed many repeated trials to acquire by trial and error the correct discrimination. As the number of discrimination tasks learned by the monkeys increased, the time to discover the correct option progressively diminished until, after 200 problems, they could discover the correct option of new problems by the second trial (the first trial always remained 50%, as the correct choice was arbitrary). Harlow argued that this transition from chance to perfect performance in just one trial was a case of insight, but one that was clearly dependent upon a previous, extended and progressive sequence of associative learning. He suggested that, in standard insight problems, animals must produce their sudden solutions relying on some unrecorded previous experience of this type. It is, however, contentious that Harlow’s discrimination problems, where the correct choice is always arbitrary, are equivalent to traditional insight problems, where the structure of the situation is transparent and the correct solution is in principle achievable from trial one. The relevance of the notion of learning set for understanding insight remains, therefore, doubtful.

Schiller (1952) proposed that the tool using patterns exhibited by chimpanzees (e.g., stick use and box displacement) were in fact “instinctive” action patterns that may have become associated with the appropriate situations by trial and error. He observed that, when provided with sticks and boxes outside a problem-solving situation, chimpanzees playfully produce the behaviors needed to solve Köhler’s problems. For example, they drag the boxes around, climb on them, and jump from them with outstretched arms. He suggested that when placed in a problem-solving context (e.g., a banana hanging from the ceiling), it would be a matter of time until by chance they produced the “appropriate” behavior, either already in their repertoire or highly likely to emerge “by instinct.”

Within behaviorism, therefore, some authors resolutely sought to demonstrate that insightful behaviors were fully explainable from the general principles of associative learning. Other authors tried to account for insight through more sophisticated versions of behaviorism with more complex notions than basic stimulus-response associations (e.g., Tolman's (1932) purposive behaviorism and his studies of insight in rats learning mazes). Hebb (1949) argued that an important effect of the notion of insight in America was to discard "naïve" associative theories of trial and error learning, forcing behavior theorists to develop more sophisticated accounts of learning to try to accommodate insightful behaviors.

### Insight as Practical Intelligence

Many developmental psychologists adapted Köhler's tasks as tests of practical intelligence for infants and children. The most important contribution came from the Swiss psychologist Jean Piaget (1936), who incorporated insight into his theory of practical or sensorimotor intelligence, arguing that, in human infants, innovative solutions without overt groping are first produced during the final stage of sensorimotor intelligence (18–24 months) through "mental groping" with interiorized actions or "the invention of new means through mental combinations." For Piaget, insightful solutions were in strict continuity with prior stages in the development of practical intelligence (means-ends coordinations of known schemas at 8–12 months; creation of new adapted schemas through overt directed groping at 12–18 months). Groping here is not *blind* trial and error (if anything, this occurs during stage 3 of sensorimotor intelligence, at 4–8 months of age, when infants repeat actions that provoke interesting effects without attending to their causal connections) but active or goal-directed experimentation. In insight, this experimentation occurs internally in the mind of the child.

Piaget saw insight as one more manifestation of the constructive development of the sensorimotor

system of intelligence and criticized Gestalt psychology for implying that such reorganizations could be the result of innate laws of form ingrained in the nervous system.

### Blind Versus Insightful Trial and Error

Insight is traditionally contrasted with trial and error (T&E) learning. However, both may not be mutually exclusive. As pointed out by Piaget, T&E can be "intelligent" or goal-directed. Moreover, even in blind T&E (with actions randomly generated), errors may become a source of insight, helping the animal understand what is the correct approach. This would amount to having a retrospective insight. A common phenomenon in human experience is indeed to discover an effect by chance and then realize why it works by examining the structure of the situation. For example, I might discover by chance, after several blind trials, how to unfold a chair and realize why this particular pulling movement works and from then on keep the movement, not just because it worked once but because I now know how it works.

Something similar might happen in animals. One of the more difficult problems faced by Köhler's chimpanzees was the "projected roundabouts" task, where the by then well-practiced schema of dragging objects to oneself with a stick no longer works because an elevated U-shaped screen prevents the animals from reaching the raked in target. The solution is to push the target away from themselves until it can be moved sideways out of the U-trap and raked as usual to themselves. Most apes struggled with this problem. They raked the object to themselves, sometimes trying to lift it with the stick against the screen. One of the chimpanzees benefitted from a chance solution – he pushed the target so forcibly against the screen that it rebounded in the correct direction away from the trap. This happy accident prompted him to produce the correct solution for the first time (pushing away instead of pulling). He still needed a few more such happy accidents to start with the correct pushing movement in subsequent trials. This example suggests

the possibility of insightful T&A where a chance occurrence helps lead to a correct solution (pushing away), which fundamentally differs from the action that led to the happy accident (pulling). Insightful T&A in animals needs systematic investigation.

## Insight and Experience

A common misconception of insight is that sudden innovative solutions must not depend upon any previous experience and that any demonstration of an effect of experience would discount them as insight.

However, in the original conception by Köhler and later elaborations like Piaget's, experience plays a key role in insight. What matters is that this experience (existing behaviors) is not by pure trial and error, and its reorganization is not reduced to a mere generalization of previous responses. There must be a generation of new solutions, but these inevitably build upon previous experience with the relevant materials and situations. An excellent example, both of the misunderstanding and how experience may operate in problem-solving, comes from Birch (1945), who in a carefully controlled experiment demonstrated that, with no previous experience with sticklike objects, chimpanzees were unable to produce the behavior of raking in out-of-reach targets. After only 2–3 days of experience with natural sticks, the chimps were able to produce the raking solutions. However, during their free exploration of the sticks, they produced only poking and stabbing behaviors, no dragging actions. It was only when confronted again with out-of-reach targets and rakes that they immediately produced for the first time correct raking actions. Thus, on the one hand, *some* experience with the relevant material was necessary, but this did not provide the movements required for the solution – these emerged only when confronted with the problem situation. Although sometimes this study is quoted as evidence against insight, it in fact may fit well the original accounts of insight as restructuring of existing experience and schemas.

## Training Insight: A Behavior Analysis Recipe

Behavior analysis studies conducted in the 1970s showed that, if pigeons are painstakingly pre-trained in the separate components of a solution, ensuring that the necessary actions and responses are firmly established in their repertoire, they may spontaneously produce a novel combination without any specific training for this. Epstein et al. (1984) trained pigeons to step upon a box fixed under a hanging target to peck the target and win a reward. Separately, the pigeons were trained to move a box to particular floor locations marked with green circles to receive rewards. Both actions were separately trained through a prolonged process of gradual shaping. Once these responses were solidly established, the birds were placed in a novel test situation, where the box was away from the hanging target. Initially the pigeons acted “confused,” moving to and fro under the target and looking at the box. Then they started to “rather suddenly” push the box toward the hanging target, adjusting its position until they could climb on it, peck the target, and receive the reward. Interestingly, pigeons trained to push boxes randomly, not to a target, were not able to produce the solution. The “insight” effect happened only if the two components had been firmly pre-established, and the box pushing behavior was target-directed.

Epstein explained the pigeons' behavior strictly with behavior analysis concepts, such as conflict between controlling stimuli, functional generalization, and spontaneous chaining. He suggested that similar learning processes may explain the insightful behaviors observed in chimpanzees and humans, who – he assumed – acquire on their own the behavior components that had to be so painstakingly trained in the pigeons. Epstein's analysis, therefore, did not aim to explain away animal insight, but rather to provide a behavior analysis framework to explain creative and generative behaviors in both animals and humans, including insight.

This approach has some problems. For one thing, insight here is narrowly defined as a novel

combination of fully existing behaviors, rather than the generation of new behaviors. In Piagetian theory, the production of new combinations of existing schemas corresponds to a less complex level of practical intelligence (appearing at 8–12 months), whereas more sophisticated explorative groping and insight develop later (second year of life) and are characterized by the creation of new behavior patterns adapted to novel situations. For example, in Birch's (1945) chimpanzee studies, the key innovation consisted of the creation of the dragging movement with a rake, not just a new combination of existing patterns. A second problem with Epstein's analysis is the assumption that apes' exploratory play would be equivalent to strict goal-directed training. The apes' spontaneous playful behaviors with boxes or sticks may in fact be more comparable to the pigeons that just got rewarded for moving objects around and who failed to show "insight."

### **Spontaneous Avian Insight: The Mentality of Corvids**

In recent years, several studies have reported spontaneous insightful behavior in birds without the need of programmed training and shaping. For example, Bird and Emery (2009) reported that captive rooks – a corvid species that does not use tools in the wild – show insightful problem-solving with a variety of tools and situations. Among other achievements, they selected stones of appropriate sizes to insert through an aperture to make a platform collapse and access rewards. They correctly chose stones even when out of sight of the apparatus, which suggests representational and planning ability. They flexibly used sticks instead of stones, when these were not available, and they modified nonfunctional tools to make them functional, such as bending a wire to create a hook, an ability also found in New Caledonian crows.

Ravens, crows, and keas insightfully solve string-pulling problems to gain access to the food attached to a hanging rope (Heinrich and Bugnyar 2005). From the beginning, they systematically pull the rope up while holding with their

foot the loop after each pull, so that it does not fall back while preparing to perform another pull. If the rope is hanging above them in a pulley disposition, they change at once the pulling direction. This is interpreted as evidence of insight and causal understanding in several Avian species.

As in the 1940s to 1950s with nonhuman primates, these claims have attracted criticism and alternative explanations. For example, Taylor et al. (2012) suggested that string-pulling birds may just apply a familiar food catching pattern – peak pulling combined with foot holding – which is immediately reinforced by the sight of the approaching food. The birds repeat the rewarded movement until they get the food itself, without understanding the causal connection between rope and food. They found that, if the rope was placed in a horizontal position and not fully stretched, when the first pulls failed to produce the rewarding view of the approaching food, the crows stopped pulling without anticipating how the strategy would eventually lead to success. They concluded that the birds lacked the ability to mentally plan the solution with a causal representation of the task. Rather than displaying insight, the birds must have learned this behavior by operant conditioning – the view of the food moving closer acting as an "internal mental reinforcement" that makes them repeat the pull-step sequence until getting the food.

This, however, may fail to explain why the birds applied the pull-step actions to ropes, instead of food, in the first place. Moreover, reliance upon perceptual feedback in the execution of a solution need not be inconsistent with insight, if the solution is pre-adjusted to the perceived conditions. For example, using a stick to retrieve an out-of-reach object without feedback (not seeing the stick, the target, and its reaction to contact) may be difficult for reasons other than understanding their causal connection. In rope pulling, the birds may see the rope as connected to the food and anticipate that pulling should move the food to them, but they may not understand the details of the connection (e.g., the need for the rope to be tight and continuous, providing an uninterrupted connection to the food). That the lack of effect of the first pulls makes them abandon the strategy



could indicate limited causal understanding, but not necessarily a dependence on blind associative reactions.

## Insight Mechanisms: Causality and Planning

The Avian string-pulling debate further exemplifies a definitional issue affecting insight from its inception – should insight be defined by reference to specific mechanisms responsible for the solution (in this case, appropriate causal understanding and representational planning)? The insight debate in recent comparative psychology has indeed merged with the wider, closely related problem of whether animals understand the causal structure of the world. Povinelli (2000) revisited and extended Köhler's classical studies concluding that the amount and nature of failures displayed by chimpanzees should be interpreted as indicative of lack of true causal understanding in apes. This, for him, requires explicit representations of unobservables, such as abstract notions of force or gravity dissociable from the perception of superficial contact or weight. This claim has been contested by other authors reporting evidence that nonhuman primates do not confuse superficial illusions of continuity but correctly use actual functional connections when solving string or support problems. This is consistent with findings that apes are in general not good at learning responses from arbitrary cues in physical tasks (Albiach-Serrano et al. 2015; Mayer et al. 2014).

A “hyper-representational” approach to causality creates the problem of how to probe experimentally the representation of unobservables as distinct from their perceptual cues (e.g., perceptual continuity from causal connection; weight from gravity). For example, Neilands et al. (2016) found that crows did not choose stones of the correct weight to drop on a collapsible platform to obtain rewards, concluding that they lack a causal conception of “force” as separate from “contact.” However, had the crows passed this test choosing heavy enough stones, it could still be argued that they are using the perception of weight

as a concrete correlate of force, and therefore, the test would always fail to demonstrate the alleged representation of unobservables.

A second cognitive mechanism proposed to underlie insight is mental planning or anticipatory representation of the response to be executed. Taylor et al. (2012) argued that the interruption of rope pulling by crows when they could not see the effect of the action showed lack of mental planning. If their behavior was guided by a mental representation of the solution, they should keep pulling without immediate perceptual feedback. However, from this “hyper-mental-planning” perspective, it remains unclear how complete and detailed plans must be to count as insightful. Rather than complete detailed plans, animals (and humans) may produce mental “sketches” of the type “use the stick to contact and drag the food”, leaving open to negotiate with the target the exact type of contact and movement needed in response to perceptual/action feedback. The need for feedback in particular segments of the solution should not make solutions less insightful in the classical sense. A more useful definition of planning could be based upon a notion of mental “sketch” with degrees of freedom to be determined during the execution of the solution itself.

Stipulations of deep causal understanding and full mental planning may depart from the original conception of insight as an expression of practical intelligence linked to dynamic perceptual and action systems and manifest not only in complete, successful solutions but also in “good errors.” A way of integrating these approaches may be through the distinction between implicit and explicit knowledge, with abstract notions of unobservables linked to the latter and schemas of perceptual-motor integration to the former. Importantly, these schemas may embody practical or implicit notions of object, space, or causality. It must be noted, however, that the notions of implicit knowledge and understanding, although widely invoked in psychology and cognitive science, remain themselves poorly defined (Gómez et al. 2017).

Insight may offer a unique opportunity to explore the nature and interplay of explicit and implicit systems of knowledge, as it appears to

occupy a curious position in this characterization. On the one hand, in humans, the process that leads to an insightful solution is opaque to consciousness – the solution just appears to us. On the other, we have a distinct and clear awareness of the solution and why it is going to work, which is very different to a solution found by trial and error, where we know that it works only after seeing the result.

## Conclusion

In sum, insight is a seminal notion that has generated a wealth of research in comparative psychology and other disciplines. It is polysemic, in that the term is used to refer to related, but not entirely equivalent, phenomena (e.g., innovative solutions at the objective behavioral level, the subjective experience of finding a solution at the phenomenological level, or the causal understanding and planning mediating the solution at the level of mechanisms). It is conceptually provocative but also confusing. It is related to key theoretical issues such as notions of implicit knowledge and practical intelligence, but has never been conceptually clarified in its different meanings. More than 60 years after Thorpe's (1956) thoughtful and influential reflections on insight, we can still conclude with him that, although "substantial progress" continues to be made, we still lack a "generally agreed conclusion" about what insight is. However, the notion is still used because it seems to fill a conceptual gap – pointing to something fundamental about the nature of intelligence and understanding that other notions seem to miss.

## Cross-References

- Means-End Reasoning
- Problem-Solving
- Representation
- Robert Mearns Yerkes
- Serendipity
- Tool Use
- Wolfgang Köhler (1887–1967)

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## Insight in Pigeons

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## Synonyms

Aha moment; Eureka effect; Intuition; Understanding

## Definition

Insight is a spontaneous, continuous, and direct way of solving a problem, also known as the eureka effect or Aha moment. In pigeons, Epstein et al. (1984) defined insight as the spontaneous interconnection of repertoires of behavior.

## Introduction

Sultan, one of the chimpanzees (*Pan troglodytes troglodytes*) of the experiments carried out by Köhler in 1914, was the first ape to solve some of the problems he tested. One of them consisted of reaching a banana after stacking up boxes,

without any specific training. Sultan solved it in a spontaneous, continuous, and direct way. Köhler came up with the German word “Einsicht” to define this way of solving problems; it was translated in English as insight in his book *The Mentality of Apes* (Köhler 1925).

According to Hartmann (1935), the term insight was already used in English colloquially, as a synonym for understanding and, occasionally, intuition. In psychiatry and social psychology, the term is understood as a personality trait that included awareness of the condition of oneself or one’s state (Marková 2005). The Berlin school of Gestalt defined insight as “an understanding of the innermost nature of the field, the stresses not merely apprehended but comprehended” (Hartmann 1935, p. 189), and the explanation of insight given by Köhler was a perceptual restructuring of the field that it was seen as a goal-directed jump in learning, as opposed to gradual learning (Köhler 1925). Nevertheless, the term used to refer to the phenomenon of insight as originally reported by Köhler was changing during the past century, as it was also associated with processes related to intelligent behavior, such as reasoning (Maier 1931) or means-end understanding (Cook and Fowler 2014). Currently, in the Cambridge Dictionary (2019), its definition is “a clear, deep, and sometimes sudden understanding of a complicated problem or situation.”

The insight perspective of learning generated a great debate in the last century, both in experimental and comparative psychology that still has not been solved. The discussion is about the causal explanation of the appearance of new behaviors to solve a problem, due to the conception of the influence of planning-mental learning as a factor in the problem solution as opposed to trial-and-error learning (Hanus 2016). The problem is that the nature of the planning in which nonhuman animals engage is far from clear, so it could be challenging to distinguish from a trial-and-error solution.

Planning should include means-end behavior to represent the insight phenomena because it is said to involve the deliberate, planned execution of a sequence of steps to achieve a goal in

situations where an obstacle must be removed to reach it (Piaget 1954), but sometimes it can also be driven by physical knowledge. This knowledge is not based on abstract and unobservable object properties but on first-order perceptual information like visual feedback. Seed et al. (2011) explained that, in this case, “abstract means that the information is not equivalent or reducible to concrete, analogue sensory input, but rather has undergone further processing in which meaning is extracted” (p. 2). For example, in different problem tasks where the reward is out of reach, the approximation of the reward to the subject can have a reinforcement effect that finally leads to the solution of the problem. Thus, associative mechanisms and trial and error appear to explain the solution to the problem (Jacobs and Osvath 2015; Taylor et al. 2012).

The importance of perceptual feedback as well as other possible variables in the emergence of insight is very much debated currently (see Krasheninnikova 2018), so there is a need for additional research. In this way, we could assess the factors that affect the acquisition of problem-solving and planning skills, the flexibility and complexity of such abilities, and the manner in which these skills are limited (Kuczaj and Walker 2012).

Nevertheless, findings of insight have been reported in humans (Wertheimer 1982), non-human primates (Herrmann et al. 2008; Neves-Filho et al. 2014), corvids (Taylor et al. 2010; von Bayern et al. 2009), elephants (Foerder et al. 2011), pigeons (Cook and Fowler 2014; Epstein et al. 1984; Epstein 1985, 1987; Luciano 1991), and rats (Neves-Filho et al. 2015).

In primates and corvids, the spontaneous problem-solving has been explained as a mental trial-and-error process, in which the animals could plan the solution before the behavioral execution (Taylor et al. 2012; Tomasello and Call 1997). The study of insight in pigeons began in 1979 when Skinner, Epstein, and Lanza worked on a series of experiments called the Columban Simulation Project. The objective of the project was to demonstrate the effect of experience on the emergence of complex behaviors generally attributed to cognitive processes in humans, so they explained

the insight emphasizing behavioral phenomena, rather than mental processes (Epstein et al. 1984).

## The Generativity Theory

Epstein et al. (1984) reproduced in the laboratory, with pigeons as subjects, the sudden performance of Sultan in Köhler’s task of reaching the banana. This problem was named the single-box displacement test (Cook and Fowler 2014) and consisted of reaching a plastic banana fixed on the roof of the experimental chamber, without jumping or flying. To solve the problem, the pigeons had to push a box in the direction of the banana, to climb the box, and to peck the banana. The main objective was to establish the effect of specific previous learning in the emergence of a spontaneous solution to a problem.

In the 1984 experiment, Epstein et al. used 11 male pigeons at 80% of their ad libitum weight. They used a feeder located on the floor of the chamber to train two prerequisite behaviors. The responses required to solve the problem, also called prerequisite behaviors, were trained independently. One behavior was trained until the subject achieved an acquisition criterion, and then the second one was trained. One prerequisite behavior was directed pushing that required pushing a box toward a green dot, of 4 cm in diameter, in a position assigned randomly along the wall of the experimental chamber. Pushing responses were extinguished in the absence of the green dot. The plastic banana was not present in these training sessions. Another behavior was to climb the box and peck the plastic banana; other responses that could reach the banana like flying and jumping were extinguished. The box remained fixed on the floor of the chamber, below the banana. Pushing the box had no consequences during the training of this response. The position of the box and the banana was randomized for each training session. Nevertheless, the conditions and amount of training were different among groups.

The experimental group was trained in both behaviors. Four other control groups were trained differently: one group was trained to climb, to

peck the banana, and to push the box but without the green dot; the second group was trained only to peck the banana, the third group was trained only to climb the box; and the fourth group was trained to do both behaviors, but without extinction of other ways to reach the banana, like flying or jumping.

After training, the pigeons were tested for 10 min. The test was carried out in the same experimental chambers of the training sessions of the prerequisite behaviors. In the test, the plastic banana was suspended at a random position in the chamber edge and the box placed in the opposite side. At the beginning of the test, the pigeons of the experimental group directed their behavior to the banana and the box, stretching their necks toward the banana and climbing into the box. After this initial moment, or state of confusion, they began to push the box toward the banana and stopped pushing the box as soon as it was near the banana when, immediately, they climbed into the box and pecked the banana. This performance was named by Epstein et al. (1984) insight or spontaneous interconnection of behavior repertoires. The pigeons with training in one behavior, or without training to push the box toward a goal, did not solve the problem. Thus, pigeons interconnected different behaviors devising a new sequence to solve the problem when they were competent in each response.

Epstein identified some principles about how, under new circumstances, behavior is generated. He described the spontaneous solutions found in pigeons moment by moment in his Generativity Theory (Epstein 1990) dividing the process into four phases: (1) apparent confusion, caused by *stimulus matching* because the test situation had two stimuli, box and banana, that control two different behaviors; (2) first push to the box, in the competition between the two behaviors, the actions directed to the box should win the competition because jumping and flying to the banana were extinguished; (3) to push the box toward the banana is due to *functional generalization* (Bruner et al. 1956), the transference of the function of the green dot to the banana; and (4) cessation of pushing right under the banana, through an *automatic chaining*, because pigeon's own behavior of

pushing produces the stimulus (to be under the banana) that was controlling the other prerequisite behavior, to climb and peck.

In another study, Epstein (1985) investigated whether solving the problem would be more difficult if the number of prerequisites trained was increased. One male pigeon deprived of food and maintained at 90% of the weight ad libitum was the subject. The equipment employed was similar to that of Epstein et al. (1984). The pigeon was trained in three behaviors: (a) to climb a box, (b) to push the box toward a green spot, and (c) to peck a banana. So, the main difference between this experiment and the previous one was the division of the behavior of climbing the box and pecking the banana into two behaviors. In the test, the overall performance was similar to successful performances reported in Epstein et al. (1984) as the period of confusion and the appearance of the solution in the same time interval (1 min approximately), but the performance did not seem to be especially insightful, that is, in a spontaneous, smooth, and directed way. In this performance, there was little evidence of sighting to the banana while pushing the box or even when the box was under the banana. In addition, the pigeon did not climb as soon as the box reached the banana just as it did not peck as soon as it climbed on the box, but nearly 10 s elapsed between both. Notwithstanding, Epstein claims that neither was a trial-and-error performance, because the pigeon kept the box close to the banana before climbing and pecking so the banana would have acquired some control.

Finally, Epstein (1987) expanded the prerequisites trained to four independent repertoires necessary to the solution of a still more complicated problem: (a) to open a door 18 cm high, (b) to push a box toward a green spot, (c) to climb onto a box, and (d) to peck a banana. He used one adult male maintained at 80% of the ad libitum weight. The pigeon had to open the door to access the box, push and climb on it, and peck the banana. In the test, it was also presented a period of confusion but it solved the problem in approximately 4 min. In this case, the solution was not smooth, but Epstein (1987) did not discuss whether he found insight; instead, he argued that multiple



controlling stimuli were interacting in the pigeon's performance creating a more complex situation. He explained the importance of the disposition of the stimuli during the test, because they had never before been combined in this way, only independently during the training of each behavior. So, when multiple stimuli were presented at the same time in the test, it can generate an increase in the competition between behaviors because of all of them are discriminative due to reinforcement history and are controlling the behavior. The subject must decide what behavior to do first and what later. Epstein (1991) concluded that operant behavior is generative and that mechanisms of variation should be investigated more thoroughly along with the elaboration of the principles that predict the transformation of previously established behavior under new circumstances.

Luciano (1991) replicated the single-box displacement test in pigeons doing variations in the type of training of prerequisite behaviors with the objective to identify the stimulus that would control directional pushing behavior in the test. She divided four pigeons into two groups and exposed them to the test. In this case, three behaviors were trained, rather than two, dividing the task of climbing and pecking in two parts. Both groups were equally trained in climbing and pecking tasks. In the pushing task, however, while one group learned the task pushing toward the green spot, the other group learned to push in the opposite direction of the spot. So, this second group, or opposite group, learned the behavior with a different goal, to push the box away of the green spot. In the test, a pigeon from the opposite group, pushed the box in the opposite direction of the banana, and the other one did not push the box at all. Both pigeons trained to push toward the spot suddenly solved the problem, showing insight. Luciano's observations suggest that specific training modified the performance in the final test, even if this training was not functional for solving the problem presented, the directional pushing behavior was influenced in the same direction as was the training. Luciano highlighted the relevance of training for the emergence of insight because it could provide

the functional properties to the stimuli that acquired control over the behavior.

## Means-End Reasoning in Pigeons

Cook and Fowler (2014) tested a two-box displacement procedure to investigate the pigeon's understanding of the means-end properties, or affordances, of the stimuli toward reaching the target. Two male pigeons maintained at 80–85% of their free-feeding weight were trained to move two boxes toward a goal within the arena. Pigeon 1 replicated Epstein's single-box displacement test. It was trained to push a wooden box and tested in the single-box displacement. Then, after three training sessions with a red box, it was tested in the novel box displacement that consisted in standing on a novel box of the same dimensions and weight, but painted red, to peck at the banana. It was successful, yet slower when tested with the novel red box. The authors explained that this behavior emerged from the generalization of goal-directed behavior established with the similar wooden box and its history of appearing in different locations but also can be considered in a means-end account as the pigeon had a concept of "box" and its potential functional application or affordance for solving the displacement problem.

The two-box displacement test consisted of the introduction of two new boxes in the training and testing. Both boxes were blue and with identical dimensions. The first box was functional, as its design allowed standing in order to reach the banana. The second box was nonfunctional in design as it could not be stood upon. Thus, it could be moved but was not appropriate for solving the problem of reaching the banana. The pushing box training of the Pigeon 1 was with three boxes (the red box and the two new blue boxes) presented randomly, but the training of standing and pecking was done with the red box, the functional one. Pigeon 2 was experimentally naïve, and its training was conducted using the red box for the standing and pecking behavior and the two blue boxes for the pushing. Both pigeons learned to move the two boxes to a black target dot during training. There was no difference in their

ability to move either box to the target dot, and pigeons were tested in the displacement problem for the first time with both boxes. Then, Pigeon 1 participated in two baseline training sessions, and Pigeon 2 received seven baseline training sessions, and both were tested for a second time in the two-box displacement test.

In the first two-box displacement test, Pigeon 1 exhibited no differential behavior toward the functional box, and it did not solve the test. Pigeon 2 exhibited differential behavior to the boxes pushing the functional box and solved the problem, but it displaced the box around the arena for more than 180 s, so the authors did not consider an insight resolution as the pushing was undirected toward the banana goal. In the second two-box displacement test, Pigeon 1 had a similar performance as in the first test and did not solve the problem. Pigeon 2 showed no differential behavior between the two boxes this time, although after 262 s, it pecked the banana and solved the problem. Finally, only with Pigeon 2, the authors did a single-box displacement test with the functional box present without the nonfunctional box, and the pigeon solved the test in 24 s, enough to consider it as an insight resolution.

The conclusion of Cook and Fowler (2014) is that pigeons solved the single-box displacement test due to the temporal and spatial relations of the physical elements in the task and their prior trained behaviors, although without a means-end understanding of the elements of the problem. Nevertheless, we should consider these results with caution because the sample size is small ( $n = 2$ ) and one of the pigeons actually showed a preference for the functional box in the first test, even though it solved the second two-box displacement test. To show two boxes at the same time could interfere with the solution of the test by adding difficulty and confusion to the problem situation, maybe as a result of a competition between stimuli reinforced previously and overshadowing of the emergence of standing behavior. Also, it is not clear if pigeons can distinguish visually between boxes and if they can predict their functionality because, at the moment of the test, they have not yet climbed on them. So, more research is necessary to prove the lack of pigeons'

means-end understanding, perhaps exposing pigeons to stimuli with different functions and testing if they choose the most useful in a simpler task would provide such evidence.

## Conclusions

The insight studies on pigeons have demonstrated the relevance of the subject's learning history for the insight and how the topography of the response during the test is dependent on it. As Luciano (1991) maintained, the responses necessary to perform the solution to the problem should be learned in some way before the problem exposition in order for each stimulus under the test conditions to become a functional stimulus for response chaining to occur. However, there are some factors that can interfere in the emergence of insight, as the arrangement of the problem situation, number of stimuli present, type and quantity of behaviors required to solve it, and type and structure of training.

Epstein (1985, 1987) demonstrated that the number of behavior repertoires trained and the number of stimuli present in the test are important variables. Just like in the arrangement of Cook and Fowler (2014), the more stimuli are controlling pigeons' behavior, the more complex will be the problem situation for them. It generates a greater competition between the behaviors controlled, and, therefore, the solution would probably be less fluid. The same happens with the number of behaviors trained, considering that only the most probable behavior is performed and the pigeon can only perform one at a time, but other behaviors can also be highly probable to occur at the same time. Luciano (1991) showed that the responses that have been previously acquired in relation to the stimuli also present in the test will be more likely to appear in as they were previously carried out.

On the other hand, the question still remains unsolved about the relation between higher cognitive capacities such as reasoning, associative learning (Andrews 2015), and insight. In animals like pigeons, this question is still more complex because they have generally been considered

cognitively simpler than mammals and even other birds such as corvids and parrots (Emery and Clayton 2005). Some authors consider that the specific training invalidates the emergence of insight because spontaneous problem-solving is caused only by specific cognitive processes that came from a specific phylogeny without previous learning (Taylor et al. 2010). Other authors support the idea that means-end understanding could be only a human characteristic (Povinelli 2000).

We should focus here on how the specific training is different from other previous experiences as free exploration or indirect learning in order to define means-end reasoning as opposed to it because previous learning of some behavioral repertoires that are required in a specific problem situation can be a determinant to solve. The specific training of prerequisite behaviors to solve a problem does not necessarily involve learning a rigid sequence of behaviors, but it can lead to a recombination of them in a flexible way to perform the sequence that best suit the problem situation (Voronin and Firsov 1967, cited in Reznikova 2007). To a certain degree, this is similar to some investigations on problem-solving where subjects are exposed to different types of problems throughout their research; as was the case in the Köhler studies, although they did not learn directly how to solve a specific problem, they have a greater repertoire of behaviors, so more interconnections can occur in a future problem situation (Neves-Filho et al. 2016). So the point is that the relevance of the phenomenon of insight would be not only to investigate the emergence of it but also to focus on the process that leads to its emergence.

## Cross-References

- [Goal-Directed Behavior](#)
- [Insight](#)
- [Insight in Rats](#)
- [Means-End Reasoning](#)
- [Problem-Solving](#)
- [Wolfgang Köhler \(1887–1967\)](#)

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## Insight in Rats

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## Synonyms

Aha moment; Deep understanding; Eureka effect; Reasoning

## Definition

Insight is a spontaneous, continuous, and direct way of solving a problem, also called Eureka effect or Aha moment. In rats, it is defined as spontaneous interconnection of behaviors to reach a goal and has also been related to the concept of causal reasoning.

## Introduction

Köhler was one of the first authors who proposed the spontaneous way of solving problems as opposite to a gradual or trial-and-error solution. He tested in apes the use of roundabout methods to achieve a goal in different tasks, also called “Umweg” or “detour” problems, and he came up with the German word “Einsicht” to define the process of spontaneously solving them. The

word was translated in English as insight in *The Mentality of Apes* (Köhler 1925).

At the beginning of the twentieth century, investigations were carried out on the spontaneous resolution of problems in rats, called insight. However, the definition of insight has been controversial since the word *Einsicht* was translated; the most cited and standard definition until now (Foerder et al. 2011) is Thorpe's (1956) "sudden production of new adaptive responses not arrived at by trial [error] behavior. . . or the solution of a problem by the sudden adaptive reorganization of experience" (p. 100).

Helson (1927) was the first publication in rats with the term "insight in the white rat." The principal objective of his study was to measure rats' visual perception learning and to determine if the rat's response was conditioned to the element connected with the goal or if there was a structural and functional learning of the specific problem situation, so the elements in the situation could change while the response was maintained. Helson related this experiment in rats with Köhler's experiments of insight in apes defining insight as an "ability to respond to a part in the light of the whole, a modification of activities to meet the exigencies of a situation in a manner we may call sensible, or the transposition of the general properties from one situation to another" (p. 380).

In Helson (1927), four rats were exposed to different intensity stimuli: gray color scheme and degrees of illumination. Rats were placed in a room with two compartments both with food, each light intensity was randomly assigned. In the first five series, Rat 1 and Rat 2 received food in the brighter gray color or light (60-watt vs. 15-watt) compartment, and Rat 3 and Rat 4 received food in the darker one (60-watt vs. 15-watt light). If the rat entered the wrong side, the plate with food was removed out of its reach. In the last four series, the values of intensity of the stimuli changed; for example, for Rat 1 and Rat 2, the brighter light was of 150-watt, and for Rat 3 and Rat 4, the darker light was of 1-candle-power (cp) light.

Helson (1927) concluded that there was insight in the rats' behavior because they followed structure-function principles and not connections

between identical elements. "Rats responded to and retained the structure, neglecting the absolute element as such; for example, although Rat 1 and Rat 2 had been choosing the 60-watt light in the first five series of experiments, when presented with the 15-watt light, they chose the brighter and neglected the 60-watt light as they had previously been neglecting the 2-cp light" (pp. 383). Rats learned to follow the brighter light in opposition to the specific stimuli conditioned, the 60-watt light. This learning rule imply that rats adapted better to dynamic but consistent environments, through a cognitive-like reasoning approach.

## Testing Rats' Insight in Mazes

Tolman and Honzik (1930) published the second article of insight in rats in which they conducted three experiments with different mazes. They defined insight as "a material, inner relation of two things to each other" that can be seen in the response as sudden changes in response. The authors hypothesize that some learning occurs in the absence of observable changes in performance, and it does not manifest until the reward is introduced, when the response appears in an insightful way.

The first experiment consisted of a replica of Hsiao's (1929) experiment, but this time with more subjects. They used the same labyrinth to test rats' insight. Rats had to infer that, if a common section was closed, none of the paths led to food access, so the only alternative was to take a third path to get the food. They trained rats to run through the paths and develop a strong preference for Path 1, a less strong preference for Path 2, and a weak or no preference for Path 3. They found that 4 of the 10 rats tested avoided Path 2 after returning out of Path 1 in the first group and 1 of 11 rats in the second group. Therefore, they concluded that the results were not sufficient to prove insight in rats, and they conducted a second experiment in which the maze was modified to require a larger movement between Paths 2 and 3. It was found that 5 of 11 rats avoided Path 2 on the first run, but they argue that these results were not clear to conclude that subjects chose pathways based on



the most efficient way to reach the goal and not on the strength of the pathway's habit.

In the third experiment, Tolman and Honzik (1930) built an elevated maze with similar characteristics: three different paths to reach the final box. They scored the number of dead-end arms rats entered, considered as errors, during each trip from start to goal box. They created three groups: reinforcement, not reinforcement, and delayed reinforcement. The reinforcement group was always rewarded with food when rats reached the end of the maze, and the number of errors decreased dramatically as a function of the number of trips they made. Rats in the not reinforcement group were just taken out of the maze when they reached the end of it, committing more mistakes, and rats in the delayed reinforcement group were taken out of the maze for the first 10 days, but rewarded at the end of it on the eleventh and subsequent trials. In this group, the number of errors made dramatically decreased on the twelfth and subsequent trials, even more than the reinforced group. The authors explained that rats in the delayed reinforcement group developed a "cognitive map" of the maze during exploration and that such mental representation guided the behavior in the rewarded sessions – evidence that learning can occur without performance. The insight run was given on the fourteenth day, and they found that, in the first run, 14 of 15 rats in Group A and 7 of 10 in Group B avoided Path 2, taking Path 3 immediately, in spite of the strong preference and habit for Path 2 acquired during the training period. They concluded that rats can show insight behavior when they can see the situation as a whole in an elevated maze.

Replications of Tolman and Honzik's third study with rats (Caldwell and Jones 1954; Gilhousen 1931) obtained similar results. Notwithstanding, the authors questioned the term insight as an explanation of the data, due to the lack of operationalization of the concept, so the interpretation of the solutions is ambiguous. For example, Caldwell and Jones (1954) explained that if insight is defined as one-trial learning which is subsequently maintained, then this definition was not applicable in their replication, because the subjects did change their performance in subsequent trials. They suggested a redefinition

of the concept that encompasses this non-maintained performance; otherwise, it could be explained in terms of associative learning.

Gilhousen (1931) highlighted factors to account for the emergence of insight. He tested insight in rats with an elevated open maze, a solution to the problem required suddenly to oppose previous habit and preference. Rats were trained to go through a jumping path to avoid going through a running block path to a food box. The hypothesis was that the more jumps rats must do, the harder that path will be, so they will choose the running path instead of the jumping-habitual path. In the test, Gilhousen moved the paths closer, so the rat had the opportunity to avoid most of the jumps, running to where it was blocked through the running path and then taking a single jump to get to the food through the jumping path. However, all rats continued choosing the jumping path in the test.

Gilhousen suggested that factors such as the type of behaviors requested to solve the problem, the dimensions of the maze, or the amount of previous training affect the emergence of insight. Running and jumping constitute separate abilities, which hinders the sudden change from one behavior to another. An unbiased test would require more similar behaviors. It would be relevant to study the effects of varying the dimensions of the maze, as it would require different abilities to jump. It could be expected that the longer the rats were required to jump, the more effort would be involved, so the rat would prefer the other path. In addition, the amount of previous training given can be important because the more training is given, the stronger the habit will be, and therefore, the appearance of a sudden change of behavior will be reduced.

### **Fortuitous Observations of Insight in Rats**

Hamilton and Ballachey (1934), in an experiment on social behavior in rats, observed one of the rats solving their task in a different and insightful way. Rats had to climb over a barrier to access a tin of food in an open area. They usually did not eat it there but took a piece of food from the tin and

returned across the barrier to eat it in a smaller enclosed space. One of them seized the tin and dragged it to the barrier and jumped to the top of the barrier, so the food tin was temporarily out of her visual field, and then “slowly leaned forward and down, grasped the tin again with her teeth, pulled the tin to the top of the barrier and dropped it on the inside” (p. 260). The authors considered this behavior an example of insight because the rat did it in a spontaneous and goal-directed way.

Another example is Ewer (1971), who conducted different tests in free-living rats to investigate performance when food was placed out of their reach. A task consisted of vertically pulling a string with a nut attached, and the rats took no more than two trials to find out how to pull the string up and reach the nut. Ewer concluded that, although the rats did not solve the tests on the first attempt, they did not show learning by trial and error, but by trial and success, because “once a success was achieved, even if this was more or less by chance, they were extremely quick to learn what to do” (p. 164).

The definition of insight proposed by Ewer (1971) created confusion in the area and is one of the problems that still persist. The behavior described by Ewer (1971) may not be strictly insight because the solution, the first response, appeared after several attempts; however, maintenance was sudden and quickly obtained, so this may be an example of faster learning but not truly insight. Nonetheless, the description may fit what most people think of as insight. The problem becomes then of interpretation; how fast should the response be to be considered as insight? Could the solution in the second attempt be considered as insight, or is the experience with the first trial sufficient to consider the solution as a result of trial-error learning? These questions are still in need of resolution.

## Hebb's Theory of Insight

Hebb proposed one of the earliest theoretical analyses of insight in *The Organization of Behavior* (1949). Hebb manipulated rats' experience before exposing them to novel problems. He found that

faster learning abilities and insightful solutions were more common in laboratory rats that freely explored his home and were manipulated as pets than in rats housed in standard laboratory conditions. Also, he explained that there is a permanent effect of early experience on problem-solving, so animals exposed to specific environments can have the requisite experiences, which can be interconnected to solve new problems presented in adulthood.

In Hebb's theory, the insight is an organized set of responses to a new situation that arises from the reorganization and integration of experiences that have been learned given specific consequences, but such new organization has not been learned. Hebb emphasized the necessity of experience in the emergence of insight, just as Maier (1935) pointed out in rats.

Hebb (1949) considered that insight continually affects learning, because it complements it, and, thus, the distinction between learning and insight must be a matter of degree. He concluded that insight is not a separate phenomenon from learning because it is part of the same processes. He claimed that Köhler's chimpanzees could have been using both associative learning and causal reasoning to solve problems. There is no need to limit insight to situations when there is a fast solution of the problem, but also delayed solutions can be conformed in a similar way, for example, after a confusion period that could take a time or even several trials. This approach is consistent with Ewer's (1971) definition of insight.

## Insight: Is It a Synonym of Reasoning in Rats?

Extensive research with *detour* or *Umweg* problems was conducted by Maier (1935) with rats. The problems were situations where the subjects have to overcome an obstacle, so they had to use a roundabout method to achieve a goal. He postulated that, when solving a problem, two distinct abilities interact: (1) to integrate contiguous experiences as described by the laws of association, which he identified as learning, and (2) to bring together spontaneously elements of past

experience without having them previously associated by contiguity, which he designated as reasoning. Therefore, for Maier, the phenomenon described by Köhler as insight was termed “reasoning.” He was the first to claim that spontaneous integration of different experiences was insight learning.

One of the mazes that Maier built to assess reasoning in rats (1929) consisted of placing rats on a table with a ladder that gave access to the ground. The table was divided by a grating that prevented rats from entering the other part of the table. Experience I involved the rats walking freely through the place. In Experience II, a second table was positioned with an elevated pathway connecting the inaccessible location of the first table. The second table had three ring stand ladders that connected it to the ground. At this stage, the animals climbed from the ground to the new table and crossed the bridge from the new table to the inaccessible area of the first table. The test consisted of placing the animals at the first table and presenting food in the inaccessible area of the first table. Animals should recombine Experiences I and II to solve the problem. Maier analyzed the number of correct responses, time scores, and the directness of the run and concluded that experienced rats were able to recombine them, but rats without Experience I or II failed to solve this task.

In contrast, Wolfe and Spragg (1934) did not replicate Maier’s results (1929) using three adaptations of Maier’s apparatus with both elevated and enclosed pathways. They found that rats’ performance was not superior to chance, so rats were apparently unable to combine two segments of behavior successfully. In a fourth variation, the behavior of Maier’s rats was replicated, but Wolfe and Spragg criticized the amount of training that rats needed to get it. They concluded that success in the task cannot be called reasoning because the training procedure would have introduced learning (i.e., association by contiguity) and solutions were achieved in “a manner entirely consistent with ordinary learning principles” (p. 469). Maier (1935) argued that the amount of training does not mean that they learn to recombine more easily because the route to food cannot be learned,

since it is different each day. They increased their exploration but not their ability to find which path leads to food, because the training does not determine which path leads to food on a test.

Other possible methodological variables that Maier emphasized as important when recombining experiences are the training procedure and the differences in the apparatus. Wolfe and Spragg did not carry out a general exploration period on the days of the tests and changed the position of the food box and starting point in the maze. If the pathways to be selected were near the starting point, rats easily chose a pathway without a possible appearance of a confusion period, committing mistakes. Instead, when the starting point was next to the food, which was behind a wire obstruction, rats attempted to reach it first without success, and during this confusion period, they can “reason” which path to take to reach the food.

Shepard (1933) also used the term reason in rats and defined it as adaptive reactions that are “a combination, in advance of the reaction, of factors from separate experiences, and where such separate experiences involve essential contradictory or differing elements that must be functionally recognized” (p. 149). He exposed rats to enclosed mazes with food boxes with different start points, alleys, sections, and shortcuts. One maze consisted of long *cul-de-sacs* and a subsequent correct path to food. After letting the rats thoroughly explore it, a shortcut was opened in one of the dead ends. In the first trial, it passed the blind as usual but paused when it came to the new opening, explored the area, and went through it to the food box. Then, the rats were removed and placed at the start point again. Most of the rats turned at the appropriate junction and took this former blind alley to go directly to the food. Shepard suggests that rats reasoned because they spontaneously took the shortest path to the food.

More recently, comparative psychologists have been interested in causal reasoning and other cognitive processes mediating problem-solving behavior. Some studies with rats found evidence of causal reasoning using instrumental and Pavlovian procedures (Blaisdell et al. 2006; Polack et al. 2013). However, in these cases, causal reasoning is not defined as a spontaneous

combination of experiences but as rats' inferences about their actions and other events in the future, a trait that is implicit in the insight phenomena (Shettleworth 2012). Some other researchers prefer to just describe the behavior as "spontaneous or innovative problem-solving," because the insight concept may have hypothetical cognitive mechanisms underlying further implications, as planning actions (Taylor et al. 2012).

### Insight as Spontaneous Interconnection of Behaviors in Rats

A classic test to study insight in animals was developed by Epstein et al. (1984): the box-displacement task. This test is an adaptation of Kohler's experiment with chimpanzees in which a banana was suspended in the ceiling and the subject had to stack boxes to reach it. In Epstein et al.'s (1984) experiment with pigeons, the banana was replaced by a plastic banana, and every time it was pecked by the pigeon, food was given. In the test, the pigeon had to move a box under the plastic banana to reach it. Pigeons were able to solve the task in a direct, smooth, and continuous way, after specific training of three prerequisite behaviors: to push a box, to climb onto a box, and to peck a banana. Epstein et al. considered these solutions evidence of insight in pigeons and proposed the "generativity theory" (Epstein 1990) to better characterize the phenomena as "spontaneous interconnection of separate repertoires of behavior" (p. 117). For more information, see *Insight in Pigeons* (► "Insight in Pigeons" by Longán and Buriticá, this volume).

Leonardi et al. (2011), based on Epstein's theory, reported four experiments using the box-displacement task to obtain evidence of insight in rats. In rats, the displacement-box task is like Epstein et al.'s (1984), but instead of pecking the banana plastic, rats had to pull a chain with a ring attached to a bar that activated a water dispenser. Rats were trained to do three prerequisite behaviors: to push a cube directionally toward a point of light that was changing position, to climb onto the cube, and to pull the chain (Leonardi et al. 2011). Nevertheless, rats did not show insight in this task,

except one, which solved the task in a sudden, direct, and continuous way, but required more than one test and additional training of prerequisite behaviors.

Leonardi et al. (2011) suggested that rats' negative results could be due to the importance of visual cues to solve this task. The albino rat appears to have consistently impaired visual acuity, and this high-effort visual task is demanding for rats. So, in comparison with chimpanzees and pigeons, this task could be more difficult for this specie and strain. Likewise, the authors noted other procedural variables that could be affecting the ability to spontaneously solve problems: if the learning criteria of the prerequisite behaviors are strict, as well as if rats are trained in the same order in which the resolutions are expected, insight resolutions are more probable to appear during test.

Based on Maier's study, Neves-Filho et al. (2015) showed insight in rats in a new problem situation called "the dig and climb test." The task was to place a rat in a cage where food was visible but unreachable. The cage was divided into two parts by a transparent acrylic barrier. On the left side, the ground was full of sawdust. On the right side, there were ladders that gave access to the platform with food. The transparent barrier had a hole, covered by sawdust, connecting both sides of the cage. So, the rats in the right side had to dig in the sawdust until they found the hole, cross it to get to the other side of the cage, and to climb the ladders to access the food. The behaviors that expected to be spontaneously recombined were (1) to dig in the sawdust and (2) to climb a ladder.

All rats had a pretest session to establish if they were able to solve the task just by exploration, without any training of the prerequisite behaviors, but none of the six rats tested solved the problem in the pretest. Then, Neves-Filho et al. created three groups of two rats each. The full group learned the two prerequisite repertoires, while the other two groups lacked training of one of the two repertoires; one was called digging group, and the other one climbing group. Once all rats reached a learning criterion of the behaviors, they exposed them to the problem. In the test, only the full group solved the task in an "insightful" way. They described the resolution as "the

two subjects crossed the hole as soon as they found it, and immediately climbed the two ladders" (p. 8), one in 83 s and the another in 135 s. The performance was like Epstein et al. (1984) behavior in pigeons, that is, in a continuous, fluid, and direct way, although Neves-Filho et al. recognized that "insight is not a clear operational term to describe problem-solving behaviors" (p. 11). For example, there are no specific time criteria to define a solution as insight or trial and error.

Neves-Filho et al. (2015) also did a post-training of the lacking behavior to the climbing and digging groups and a post-test in the same task. In this case, one out of the four subjects solved the task but with pauses between crossing to the other side of the chamber and climbing the ladder. To explain this difference, Neves-Filho et al. suggested that the type of training affected the sudden solution of the problem. In the case of the full group, the training was concurrent; that is, one behavior was trained just after the other; while in the case of the climbing and digging groups, the behaviors were trained at different times, independently or sequentially. As just concurrent training showed spontaneous solving of the task, the authors point out that it facilitates insight rather than an independent training of the behaviors.

Further, Neves-Filho et al. (2016) examined the differences in rats' insight in the dig-climb task using different types of training and orders in the sequence trained. Surprisingly, subjects of all experimental conditions solved the final task ( $n = 5$ ), and two did it by insight. One subject of the group with both behaviors trained at the same time (concurrent), and another trained first with one and then the other (sequential). Therefore, they conclude that order of training did not increase the emergence of insight. However, they did find that the rats trained concurrently solved the problem in a shorter time than the sequentially trained ones – data that provides some evidence that the type of training can affect the spontaneity in resolution. They argue that the use of a less strict behavior learning criteria than Neves-Filho et al. (2015) could have negatively affected the emergency of insight, so more research is needed to confirm these hypotheses.

Using "the dig and climb test," Longán and Buriticá ("Effects of Environmental Enrichment in the Insight in Rats", in preparation) studied the effects of environmental enrichment in the insight and problem-solving in rats in different types of training and order of behaviors. The experimental group ( $n = 8$ ) were reared under enriched housing conditions in trios; in such conditions, the animals could develop an ample repertoire of behaviors (to move in different surfaces, social interactions, etc.) through interaction with conspecifics and different objects like an activity wheel and various materials such as wood and fabrics. A control group ( $n = 9$ ) lived in trios in common housing: acrylic box with sawdust.

Longán and Buriticá established that an insight resolution must be as Epstein et al. described: continuous, fluid, and direct. The link between the two prerequisite behaviors should take a short time to be considered as insight, and other behaviors should not be performed between them. In the first exposure to the problem without any training, called pretest, one rat of the social group and three rats of the enriched group solved "the dig and climb test," one of the enriched group by insight (37 s between the two prerequisite behaviors). Then, a training of one prerequisite behavior was done, and after rats reached the same behavior learning criteria as Neves-Filho et al. rats were exposed to Test 1. One rat of the enriched group solved the task by insight (19 s) in Test 1, after the climbing behavior training. Then, rats learned both prerequisite behaviors in a sequential training, and a second test was done (Test 2). One more rat of the enriched group solved it by insight (22 s), and none of the social group subjects solved the task in Test 2. As in Neves-Filho et al. (2016), no significant differences were found in the order or type of behavior training. Instead, the enriched group was faster in reaching the climbing learning criteria than the social group. These results provide evidence that environmental enrichment facilitates insight, problem-solving, and response acquisition, supporting the hypothesis proposed by Hebb.

Finally, Dicezare (2017) designed a new insight task in rats based on Köhler (1925) in chimpanzees. It consisted of pushing a cube



toward a platform and climbing on it and then onto the platform to get food. A concurrent training was carried out of two prerequisite behaviors: to push the cube toward a lit partition and to climb on the cube and on a platform. Other ways to climb on the platform were extinguished. Rats ( $n = 2$ ) solved the problem in a spontaneous, direct, and continuous way. They performed the second behavior (to climb) right after finishing the first behavior (to push), with 1 second of difference. It was concluded that the procedure adopted made possible the emergence of insight in rats in a methodologically similar way to that used by Epstein et al. (1984) in pigeons.

## Conclusions

The recent insight research with rats suggest that its study may not require such elaborate problems or specific species. Spontaneous problem-solving in rats has been demonstrated in several studies for a century, and it is still studied nowadays. Despite great efforts, the term “insight” remains confusing in relation to the processes that underlie it. More elaboration and specificity of the phenomenon through behavioral and time criterion are needed to provide a solid measure to evidence it and identify its mechanisms.

The literature established the importance of experience like specific training or environmental enrichment to the emergence of insight in rats. Training of prerequisite abilities may be enough for the interconnection of behaviors to occur, but there are also variables that can hinder the appearance of insight, for example, the specific difficulty of the problem task to the specie or the amount of experience related to the task (i.e., low learning criteria), while environmental enrichment can favor the acquisition of new behaviors and the emergence of insight in rats.

The theoretically contentious question is whether insightful behavior is the product of a special mechanism or process, as opposed to processes used in routine problem-solving like trial and error. The relation between higher cognitive processes such as reasoning, insight, and associative learning still remains unsolved, due to the lack

of observational data to evidence it. Rather, attempts at showing such cognitive processes must first demonstrate that insight study cannot be accounted for in terms of associative learning. Some pioneering studies are already solving this question demonstrating neural correlation with the phenomenon in rats to explain sudden responses in problem-solving (Durstewitz et al. 2010).

## Cross-References

- [Goal-Directed Behavior](#)
- [Insight](#)
- [Insight in Pigeons](#)
- [Means-End Reasoning](#)
- [Problem-Solving](#)
- [Wolfgang Köhler \(1887–1967\)](#)

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## Instinct

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In the *Origin of Species*, Darwin (1809–1882) endorsed what he took to be the common notion of instinct: "An action, which we ourselves should require experience to enable us to perform, when performed by an animal, more especially by a very young one, without any experience, and when performed by many individuals in the same way, without their knowing for what purpose it is performed, is usually said to be instinctive" (Darwin 1859, p. 207). He then proposed that instinctive behavior in animals could be explained using the resources of his theory, such behavior essentially being no different than other adaptations. Darwin's characterization of instinct would have been recognized by many naturalists writing long before the nineteenth century and long thereafter.

## Theories of Instinct Prior to the Nineteenth Century

In the second century of the common era, Claudius Galen (130–210) performed what became known much later as the deprivation experiment. He took a young goat from its mother by cesarean section, thus preventing any opportunity for learning. He and his colleagues then placed before the young kid several bowls of food stuff – wine, oil, milk, honey, etc. After sniffing at each of the bowls, it started lapping

up the milk. He and his assistants gave a yell, seeing realized what Hippocrates had said: “the natures of animals are untutored” (Galen 1824). Galen’s procedure, while not without problems, yet meets the general requirements of the “deprivation experiment,” which Konrad Lorenz (1903–1989), in the twentieth century, specified as the empirical foundation for his own conception of instinct: deprive an animal of any opportunity to learn and if it yet exhibits a species-specific pattern of behavior, then that behavior is innate and can be called “instinctive” (Lorenz 1965, pp. 83–100).

In the Medieval Period, Avicenna (980–1037) developed a theory of instinct based on Aristotle’s notion of incidental perceptibles – e.g., the white milk being incidentally perceived as sweet. The distinctive and skillful behaviors of animals convinced him that their souls had an estimative faculty, an internal sense that detected meanings (*intentiones*) not available in the immediate data of the external senses. This awareness resulted from a divine inspiration that the Latin translator variously rendered as *cautela naturalis* and *instinctus insitus* (Avicenna 1968–1972, vol. 2, pp. 37 and 73). Thomas Aquinas (1225–1274), in his own commentary on Aristotle, described this faculty of the animal soul as a “natural estimative power (*aestimativa naturalis*) given to animals through which they are directed, in their actions and passions, to seek or avoid things appropriate to their nature” (Aquinas, lec. 13).

In the seventeenth century, René Descartes (1596–1650) rejected the notion of the medieval Aristotelians that animals had a particular kind of soul with capacities of sensory cognition. Descartes regarded animal behavior as explicable according to mechanistic laws. Yet both Descartes and the Aristotelians agreed that complex animal behavior (e.g., birds’ building their nests or bees’ their cells) had to be explained by instincts, which they understood as fixed patterns of behavior determined by the Creator for the welfare of his creatures.

A reaction set in against the very idea of animal instinct during the eighteenth century. The Abbé de Condillac (1715–1780) argued for a continuity between animal and human intelligence, holding

that intelligence arose simply from the association of ideas, which were only less vivid images derived from sensation. So that what was taken as innately determined behavior could better be understood as originally intelligent behavior that had become habitual (Condillac 1798, vol. 3, pp. 435–439). Jean-Antoine Guer (1713–1764) also adopted this sensationalist epistemology. He asserted that the ascription of instinct to animals confounded any attempt at reasonable explanation, for “nothing is easier to say about whatever animals do than they do it from instinct” (Guer 1749, vol. 2, pp. 191–192). The sensationalist position ultimately derived from the rejection by Locke and other empiricists of innate ideas, whether in humans or animals (Richards 1979).

Those researchers that studied animal behavior with care had strong evidence on their side. Hermann Samuel Reimarus (1694–1768), for instance, pressed the kind of experimental observations undertaken by Galen, namely, that animals exhibited arrays of fully formed, complex behaviors before they had any opportunity to learn them: chicks shortly after emerging from the egg could peck at grain with coordinated movement and caterpillars that had never seen a cocoon skillfully wove one in the same design as their ancestors. Automatic behavior that characterized most members of a species seemed hardly different from anatomical traits and was so regarded by early evolutionists (Richards 1987).

## Early Evolutionary Conceptions of Animal Instinct

Erasmus Darwin (1731–1802), grandfather of Charles, trained as a physician at Edinburgh medical school, whose faculty had, during Darwin’s student years, received their own education at Leyden, where the mechanistic ideas of Herman Boerhaave (1668–1738) largely prevailed. In his medical treatise *Zoonomia* (1794), Darwin joined a mechanistic materialism with a sensationalist physiology. He proposed that a subtle fluid – the so-called *spirit of animation* – coursed through the brain and nerves causing contractions of muscle fibers. This fluid reacted to both internal and

external stimuli and operated according to principles of association, so that “all animal motions which have occurred at the same time, or in immediate succession, become so connected, that when one of the them is reproduced, the other has a tendency to accompany or succeed it” (Darwin 1796, vol. 1, p. 320). The nervous fluid formed ideas within the brains both of animals and humans, ideas that were only faint copies of sensations (pp. 105–107). Darwin’s sensationalist psychology thus allowed him to assume continuity between animal intelligence and human intelligence. It also allowed him to assume that those patterns of behavior usually assumed as instinctive actually arose from intelligence and habit. For instance, he regarded nest-building in birds as the result of observation and “their knowledge of those things, that are most agreeable to their touch in respect to warmth, cleanliness, and stability” (pp. 171–173). It took a bit more ingenuity, however, to explain those patterns of behavior that some animals expressed just after birth, without obvious opportunity to learn, for example, the coordinated pecking and swallowing by newly hatched chicks. But Darwin was not without imaginative resources. He supposed that the chick, while still ensconced in the egg, would be continually gaping and gulping embryonic fluid, thus induced to practice and learn the very behaviors it would exhibit after hatching (pp. 138–139). (In the 1920s, the radical behaviorist Z. Y. Kuo made similar objections to the isolation experiment. Using examples comparable to those of Darwin, Kuo argued that conditioned learning could occur even while the chick was still in the egg. See Kuo 1929).

Despite his sensationalist biological assumptions, Darwin advanced a powerful evolutionary conception. His theory allowed for traits acquired by ancestors to be passed to offspring; like Lamarck, he was convinced of the inheritance of acquired characteristics. Anatomical traits acquired by parents through exercise – e.g., the blacksmith’s strong arms – could be passed to offspring, with the tendency to vigorous arm movement, for instance, already begun in the womb. Embryology allowed Darwin to project the processes of learning back to the very beginning:

All warm-blooded animals have arisen from one living filament, which THE GREAT FIRST CAUSE endued with animality, with the power of acquiring new parts, attended with new propensities, directed by irritations, sensations, volitions, and associations; and thus possessing the faculty of continuing to improve by its own inherent activity, and of delivering down those improvements by generation to its posterity, world without end! (Darwin 1796, vol. 1, p. 509)

While Darwin’s evolutionary account did not mesh well with his sensationalist psychology when trying to explain stereotyped patterns of behavior, another early evolutionist, also of sensationalist inclinations, was much more successful in giving an evolutionary account of instinctive behavior.

Jean-Baptiste de Lamarck’s (1744–1829) three-volume *Flore française* (1778) helped advance him to membership in the French Academy. His systematic survey of French plants brought him to the attention of Georges Leclerc, Comte de Buffon (1707–1788) at the Jardin des Plantes, where Lamarck was later appointed to the chair of botany in 1788. After the Revolution he was made professor of zoology in the *Muséum national d’Histoire naturelle*, where he was put in charge of insects and invertebrates. His extensive study and classification of mollusks brought him international celebrity among his peers. In 1800, this conventional, if highly technically competent, zoologist gave a talk at the *Muséum* that set him on a radical path. In his “Discours de ouverture,” Lamarck proposed that animals adjusted their behaviors to changing environmental circumstances and that the resultant modifications of organs would be heritable, producing new alterations in species (Lamarck 1801). Shortly thereafter he added another principle to account for the slow change in species over time. In his *Recherches sur l’organisation des corps vivans* (1802), he maintained that the imponderable fluids of caloric and electricity, acting on mucilaginous materials in the earth, could generate small, living monads and that the continued activity of these fluids would produce gradually more complex organisms. These two principles became the anchors of his *Philosophie zoologique* (1809), where his evolutionary theory came to completion (Lamarck 1809). The imponderable fluids would

continuously bubble up new organisms and push them to greater complexity, while habit becoming instinct would alter organs keying them into environmental niches.

In his *Discours d'ouverture* of 1814, Lamarck defined instinct as “that singular power which operates without premeditation and from the consequences of felt emotion” (Lamarck 1972, pp. 179–185). He distinguished it from both intelligent acts, which do not always attain their desired end, and mere habits that were not driven by a felt need. Moreover, specific instincts characterized a whole species of animal; they were not idiosyncratic expressions.

Lamarck's evolutionism found some allies in his native country – e.g., Etienne Geoffroy Saint-Hilaire (1772–1844) – and several early adherents in Germany, such as Friedrich Tiedemann (1781–1861) and Gottfried Reinhold Treviranus (1776–1837). In Britain, Charles Darwin's early tutor Robert Grant (1793–1874) thought his own study of sponges supported Lamarck's transmutation hypothesis. But Lamarck's theory met crushing opposition from the doyen of French Naturalists, Baron Georges Cuvier (1769–1832). In the introductory volume of his *Recherches sur les ossements fossiles* (1812), Cuvier mounted three objections that would be reiterated against Darwin's theory: (1) no transitional species are found in fossil deposits; (2) experience shows that species only vary in nonessential traits; and (3) mummified animals from ancient Egypt are recognizably the same as those found in modern Egypt (Cuvier 1834, vol. 1, pp. 198–218). In his *éloge* for Lamarck, his recently deceased colleague, after citing a few respectable achievements, Cuvier came to the infamous theory and reduced it to rubble. In his caricature: “It is the power of the desire to swim that produces the membranes between the toes of aquatic birds; it is by reason of going in the water but wishing not to get wet that river birds have their legs lengthened; it is the power of desiring to fly that has changed their arms into wings and has developed their hair and scales into feathers” (Cuvier 1835, p. xix). Lamarck's theory later fell on ears more receptive, those of the young Charles Darwin.

## Darwin's Evolutionary Construction of Animal Instinct

Though fully aware of his grandfather's views and Lamarck's theory, Charles Darwin remained orthodox in his biology while on the Beagle Voyage (1831–1836). It was only when he returned to England and started cataloguing his materials that he began to speculate on species change. He had sent back to the British Museum large samplings of organisms, among which were three varieties of mocking bird, taken from different islands of the Galapagos. Since the islands were volcanic and relatively young, Darwin assumed the birds had gotten blown over from the mainland and that their morphological alterations were merely varietal, induced by the different environments of the islands. When John Gould (1804–1881), the chief ornithologist at the Museum, contended that the birds represented three different species, he tripped a mind at the ready (Sulloway 1982). Darwin began immediately speculating on species change in spring 1837, and in various early notebooks (March 1837–June 1838), he considered what might be the causal factors that produced species change. He immediately considered Lamarck's imponderable fluids but quickly concluded: “all structures either direct effect of habit, or hereditary effect of habit” (Darwin 1987, p. 175). He argued to himself that new habits, if practiced by a population over long periods of time, would turn into instincts and that these latter would eventually modify anatomical structures and so would alter species. From Darwin's perspective, the intermediary of instinct would preclude any conscious, intentional activity on the part of animals, and so his nascent theory would not be subjected to the common charge brought against his predecessor that animals supposedly willed themselves new parts. Darwin, undoubtedly, was engaged in a bit of self-defensive scholarship. His own device of species change in this early period hardly differed from that of Lamarck; his modification of the essentially Lamarckian device could shield only a naïve researcher. Darwin's confidence grew after he formulated his chief principle of natural selection. Yet, Darwin never abandoned the idea



that the environment could directly induce heritable changes and that habit could ultimately give rise to instincts and alterations of species. These assumptions are feathered throughout the *Origin of Species*, but they became secondary causes to his new discovery of natural selection in fall of 1838 (Richards 1987).

In early fall of that year, Darwin, as he recalled in his *Autobiography*, picked up “for amusement” Thomas Malthus’s *An Essay on the Principle of Population* (Darwin 1969, pp. 119–120). With the reading of Malthus’s *Essay*, he had the beginnings of the idea that would blossom into natural selection. Malthus provided him the idea of population pressure under scarce resources, which might produce a struggle for existence. All of this “wedging,” as he called it, had the “final cause” of filtering out all but the most fit organisms and thus adapting them (actually, leaving them preadapted) to their circumstance. Thus, the more fit organisms would live to reproduce and pass their advantages on to their progeny and consequently slowly alter the species (Darwin 1987, pp. 374–375). Through the next several years, Darwin would develop his principle of natural selection; he found it exquisitely useful in accounting for highly complex anatomical adaptations, especially ones that would not easily yield to Lamarck’s device of use and disuse. However, instincts still seemed more easily explicable by inherited habit.

Problems arose for the habit-instinct conception. Several natural theologians, in the late 1830s and 1840s, insisted that animals exhibited instincts without any knowledge of the purpose of their actions. The caterpillar spun its web without foreknowledge that the purpose was to provide shelter for metamorphosis. Examples such as the caterpillar’s production of a cocoon precluded any intentionally developed habit as source for the instinct. As a result of considering such examples, Darwin began to apply natural selection theory to account for those instincts that habit could not explain. But when he read William Kirby and William Spence’s theologically driven *Introduction to Entomology* in 1843, he was stumped (Kirby and Spence 1818). They described the “wonderful instincts” of different

species of social insect. Soldier bees, for instance, instinctively guarded the nest and sacrificed themselves to protect it; worker bees had the instinct of constructing perfect hexagonal cells to store honey. These kinds of instinct, the authors maintained, could be explained only by divine providence. When Darwin attempted to account for these “wonderful instincts,” he quickly ran into trouble. Natural selection operates to preserve individuals who manifest advantageous traits. But self-sacrifice seems to offer the individual soldier bee no advantage – quite the contrary. Moreover, as Darwin came to appreciate, worker bees and ants were sterile; they did not breed in the first place. In June 1848, after he considered these difficulties, he lamented: “I must get up this subject – it is the greatest *special* difficulty I have met with” (Darwin 1848). In chapter 7 of the *Origin*, Darwin reiterated: the difficulty “at first appeared to me insuperable, and actually fatal to my whole theory” (Darwin 1859, p. 236). In working on that chapter, he hit upon the solution in the nick of time, one that we now more or less have adopted: natural selection works on the whole hive or nest. Those hives that had, by chance, more aggressive individuals were selected over those with fewer. And so the instinct of defensive action by bees, even at the cost of their lives, would gradually evolve over time. Darwin not only had a resolution to the almost “insuperable” difficulty, he offered it also as potent objection to his rival Lamarck (Richards 1987).

Darwin’s solution to the problem of instincts in the social insects had another dividend, a very large one. In the *Descent of Man* (1871), he considered what was distinctive about the human animal. It wasn’t reason, since even his hunting dogs exhibited a modicum of reason. It was moral conscience. If he could not give an account of morality, a wedge would be opened for the return of the deity. Darwin began a construction of a theory of moral behavior, and here his work on the social insects proved crucial. He argued that if advanced animals developed reason sufficient to become reflective, language to communicate needs, and habits to solidify social relationships, then if such proto-human groups also instinctively engaged in cooperation, self-

sacrifice, and mutual care, they would have the advantage over groups that had fewer such altruists. As he wrote in the *Descent of Man*:

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. (Darwin 1871, vol. 1, p. 166)

Darwinian morality is frequently caricatured as selfish and individually self-aggrandizing. Only the unaware and blinkered critic would so regard it. Darwin himself thought his theory removed “the reproach of laying the foundation of the most noble part of our nature in the base principles of selfishness” (p. 98). The essential grounds for his theory of morality were the social instincts of cooperation, mutual care, and altruism (Richards 1987).

## Instincts After Darwin

As a youth, William James (1842–1910) was enamored of Herbert Spencer’s (1820–1903) evolutionary ideas. He became wary of Spencer, however, through the animadversions of his friend Charles Sanders Peirce (1839–1914). Peirce skewered Spencer’s vagueness and lack of evidentiary foundations for his particular evolutionary considerations, especially in contrast to those of Darwin. James had been introduced to Darwinian theory in medical school through the courses offered by Jeffries Wyman (1814–1874), an early champion of the new theory. That introduction would be reinforced by Peirce and another friend Chauncey Wright (1830–1875). When James himself became a lecturer in the Anatomy Department at Harvard in 1873, he gradually deployed Darwinian theory in his courses. And during this early period in his career, he formulated an evolutionary argument for the

independence of human mind; he debuted the argument in a series of lectures given at Johns Hopkins in 1878.

James’s point of departure in his argument was Thomas Henry Huxley’s (1825–1895) essay “On the Hypothesis that Animals are Automata” (Huxley 1874). Huxley held that mental events were purely epiphenomenal. That is, the brain might be stimulated by sensory impulses that had two effects: (1) a causal train confined to the brain that would produce motor activity and (2) a conscious awareness of phenomena caused by that brain activity. The phenomenal experience might simply be that of, for instance, a black cat and the action to avoid it. But the motor activity of avoiding the cat would be the immediate result only of that causal sequence of brain activity, yielding the motor movement. Consciousness would merely be the passive observer, produced by brain activity but impotent on its own to effect anything. To this epiphenomenal theory of mind, James made a potent objection, which he more carefully spun out in his article “Are We Automata?” (James 1879). James maintained that if consciousness were an evolved trait, then over the course of our gradual descent from ape-like ancestors, that consciousness would become more sophisticated and more finely articulated through natural selection. But natural selection only operates on traits that make a difference to the organism that give it an advantage. If consciousness was naturally selected, it would have to have a use. But if it had a use, then it had to be causally effective in the environment. If the brain were doing all the work, consciousness would be superfluous, and certainly not an evolved trait. Thus, on the premise of the evolution of consciousness, mind had to be effective and had to be independent of the brain (James 1890).

James’s psychology was thoroughly Darwinian, most especially in his theory of emotion, a theory that deployed as a fundamental ground the assumption of human instincts. James proposed a definition of instinct conformable to Darwin’s: “the faculty of acting in such a way as to produce certain ends, without foresight of the ends, and without previous education in the performance.” Though it was usually assumed that

human beings had fewer instincts than brutes, James argued that they were, on the contrary, “more richly endowed in this respect than any other mammal” (James 1887, p. 666). He counted over 30 classes of human instinct (a list large enough to choke the behaviorist John Watson). James wove his conception of instinct into his theory of the emotions. That theory, independently arrived at by the Danish physiologist Carl Lange (hence, the James-Lange theory of emotion), asserted that cognition did not cause emotion, rather that emotion was a direct response to the instinctive wisdom of the body. The bear comes charging after you, instinctively your eyes widen, your body trembles, your heart races, and you start to run. These behaviors, in James’s view, were protective instincts that resulted from millennia of natural selection. Our feeling of this bodily reaction was the emotion. In James’s conception, then, we don’t feel fear and then run, rather we run and as a result become afraid.

### The Behaviorist Reaction to Theories of Instinct

L. L. Bernard (1881–1951), a social psychologist who trained at University of Chicago, surveyed the writings on instinct of over 300 authors publishing between 1900 and 1924. With some amazement, he cataloged 1594 different classes of instinct that had been attributed to men and animals. His study appeared in 1924, the same year as John B. Watson (1878–1958) published a declaration of war against such vague and experimentally recalcitrant subjects as instinct. In his book *Behaviorism*, Watson exclaimed: “Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in and I’ll guarantee to take any one at random and train him to become any type of specialist I might select – doctor, lawyer, artist, merchant-chief and, yes, even beggar-man and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and race of his ancestors” (Watson 1930, p. 104).

Watson’s attack on innate traits represented an about-face. In his first book, *Behavior: An Introduction to Comparative Psychology* (1914), he

framed his study of sensation, instincts, and learning in terms of Darwinian evolutionary theory. His own earlier field research had been on the instincts of the noddy and sooty terns in the Tortugas (Watson 1908). A scant 10 years later, the only inborn responses Watson recognized were three emotional reactions: love, rage, and fear. Out of these elements, very complex edifices of character and behavior could be constructed without recourse to instinct or even conscious mind. Watsonian behaviorism and its reincarnation in Skinnerian conditioning procedures swamped all lingering concerns with instinct in psychology departments in anglophone countries during the first half of the twentieth century. The coffin was nailed shut with the reaction to the eugenic movements in America and Europe, especially the version cultivated by the Nazis in the 1930s and 1940s.

### The Rebirth of Instinct Theory in Ethology

Behaviorists assumed animal and human mind to be void of any preprinted messages, blank slates to be inscribed only by modes of conditioning. This was a doctrine that seemed well-tuned to the American ethos of frontier possibilities, where any little boy might grow up to be president if he had enough gumption and opportunity. In a more hierarchical society, the same presumption would not likely obtain (Richards 2008). In Germany and Austria, evolutionary theory took rather firm root, especially as the result of the impact of Darwinian champions like Ernst Haeckel (1834–1919) and August Weismann (1834–1914). The individual who did the most, however, to adopt and further develop the Darwinian conception of instinct was the Austrian Konrad Lorenz (1903–1989), who, along with the Dutchman Nikolaas Tinbergen (1907–1988), established the discipline of ethology.

Lorenz followed the path of his father to medical school, yet became more occupied by studies of the geese, ducks, and jackdaws that populated his father’s estate just outside of Vienna. His friend and mentor Oskar Heinroth

(1871–1945), a fellow ornithologist, encouraged him to cast his interests within a Darwinian framework. In a paper published in 1932, Lorenz began to refine Heinroth's theory of "drive activities" (*Triebhandlungen*) or what he later would call "instinctive activities" (*Instinkthandlungen*) – using the older, Latinate name to distinguish his conception from psychoanalytic and behaviorist views of drive. In his 1937 paper, "The Establishment of the Instinct Concept," Lorenz discriminated five criteria that would stabilize the concept: (1) fixed behavior would characterize most members of a species; (2) such behavior would be exhibited even by animals raised in isolation from learning; (3) the behavior would usually be more complex than the learning ability of the animal; (4) the actions would sometimes be performed incompletely (*Intentionsbewegungen*) or in inappropriate circumstances (*Leerlaufreaktionen*) – e.g., a kitten stalking a ball of yarn; and (5) the behavior would be rigid and exhibited as fixed reflex chains, not idiosyncratic and flexible actions (Lorenz 1971).

Though Lorenz originally conceived instincts as a chain of reflexes wrought by natural selection, he began to suspect that instinct was more than reflex, rather a drive that sought release, often in inappropriate circumstances. Erich von Holst (1908–1962), a Baltic German and neurophysiologist, in conversations with Lorenz, suggested just the mechanism to explain the behavioral phenomena that his friend observed. Von Holst had discovered endogenous neural centers of rhythmic discharge and coordination, which led Lorenz to hypothesize that animals had reservoirs of response-specific energy gradually accumulating and motivating animals to seek release (Lorenz 1937). It was a theory not unlike that of Freud's notion of libidinal energy that also builds up and seeks release, even in relation to inappropriate objects.

Before the Second World War, Lorenz had begun a collaboration with the comparative psychologist Nikolaas Tinbergen, with whom he would share the Nobel Prize for physiology in 1973, along with Karl von Frisch (1886–1982), for their collective work in the founding of the discipline of ethology. Both spent part of

the war-years in concentration camps, Tinbergen under the Nazis (1942–1944) and Lorenz under the Russians (1944–1948). After the war, they renewed their joint efforts, though they had to work through their political differences first, since, like many German physicians, Lorenz had formally joined the NSDAP (*Nationalsozialistische Demokratische Arbeiter Partei*) (Burkhardt 2005). Typical of the kind of experiments done on animal instinct were those demonstrating what they took to be an "innate releasing mechanism." The three-spine stickleback fish, when confronted with another male with a red belly, or even a crude model with a red underside, would assume the stereotypical threat posture; but when confronting a female with a non-red, swollen belly, it would dance the fixed steps of the mating ritual. A red belly released one kind of instinctive pattern in the male stickleback, while a swollen belly released a very different pattern of behavior (Tinbergen 1951, 1952).

Lorenz's theory of instinct met a hostile reaction from several prominent American psychologists in the 1950s, during the period when behaviorism dominated the profession. Undoubtedly Lorenz's membership in the NSDAP partly accounts for the animus, but the objections caused Lorenz to rethink his conception of instinct. Daniel Lehrman (1919–1972) complained that Lorenz's dichotomous categorization of behavior into learned and innate ignored the genetics of the situation, namely, that any genetic disposition requires internal and external environmental conditions for expression (Lehrman 1953). To make his objection explicit, Lehrman cited the studies of Z. Y. Kuo (1898–1970), who argued against the notion of the perfect isolation experiment. The chick that emerged from the egg and immediately pecked at grain with coordinated movement might well have undergone a kind of conditioning while still sealed in the egg: the head of the embryonic chick, which would be bent over the thorax, would bob up and down with its heartbeat, so the chick might "learn" while still isolated in the egg (Kuo 1929).

In a later monograph, Lorenz met Lehrman's objection in a twofold way. First, he maintained that the concepts of the innate and the learned

were not necessarily antithetical; from an evolutionary point of view, the ability to learn was itself an adaptation naturally selected for, thus part of the phylogenetic program of the species. Second, in the specific case of the chick being condition in the egg to peck at grain, several other species of bird – pigeons, for example – though their heads may have undergone the same bobbing movement in the egg, yet when hatched they didn't peck at grain but shoved their beaks into their parents' mouths. The instincts to peck at grain or to act on the parent were adaptations specific to the kind of animal and thus naturally selected as opposed to having been learned. Lorenz yet conceded that the final shape of behavior was also a function of environmental circumstances but that only the genes carried the specifying information (Lorenz 1965, p. 1).

## The Contemporary Resolution

Three basic positions have been taken on animal instinct. From Descartes through the early work of Lorenz, instincts were understood to be constituted by chains of reflexes that respond to certain environmental releasers. James Watson, B. F. Skinner, Z. Y. Kuo, and other behaviorists in the first part of the twentieth century rather attempted to account for apparently fixed patterns of behavior by appeals to subtle modes of conditioning. The later Lorenz and evolutionary biologists like Ernst Mayr (1904–2005) established the third and most recent conception of instinct, one that recognized the role of genetically determined, species-specific information as well as the environmental conditions required for the implementation of the information. Mayr epitomized this recognition in his proposal that two kinds of programs governed animal behavior, a more closed program and a more open program (Mayr 1974). Closed programs were those in which the releasing mechanisms were controlled by the genome of the species, such as mate recognition and display in many animals. For instance, fertile female *Drosophila* of one species, if reared in isolation and placed among males of several species that displayed to her, would unerringly receive only

the male of her own species. However, freshly hatched graylag goose chicks would follow any object of the right size, if exposed to the moving object (e.g., Lorenz's head while swimming) during a critical period in the young gosling's life. The chicks rapidly learned the stimulus that released the fixed behavior of following. In some species of bird, a chick raised with chicks of a different species would imprint on the foster species and attempt to mate with its members. These cases of imprinting represent a more open program. The mechanisms of instinct, therefore, differ depending on the species of animal and the relative open or closed character of the program. Most behavior biologists today recognize these different instances of instinctual modes of behavior and have thus revitalized the instinct concept.

## Cross-References

- Behaviorism
- Charles Darwin
- Fixed Action Patterns
- Innate Behaviors
- Jean Baptiste Lamarck
- John B. Watson
- Konrad Lorenz
- Nikolaas Tinbergen

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## Instinctive Reflex

- [Rooting Reflex](#)
- [Step Reflex](#)

## Instruction

- [Learning](#)

## Instrumental Behavior

- [Free Operant Response](#)

## Instrumental Blocking

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## Definition

Instrumental blocking refers to the ability of a previously trained discriminative stimulus to block the acquisition of a new discriminative stimulus in establishing stimulus control.

## Introduction

Classical conditioning involves the pairing of a neutral stimulus (e.g., a light) with an unconditioned stimulus (e.g., food) that naturally elicits

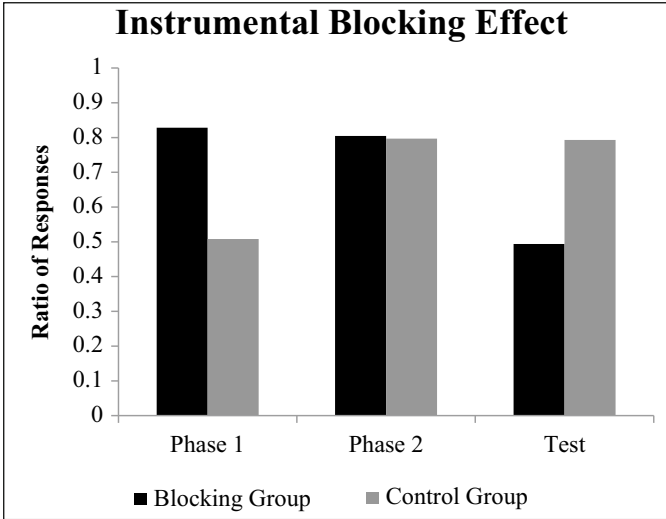
an unconditioned response (e.g., salivating), such that with repeated pairings the neutral stimulus becomes a conditioned stimulus that can alone elicit a conditioned response. Within the structure of CS-US pairings, different types of learning effects can be observed, one of which is called blocking. Blocking occurs when a previously trained CS-US pairing (e.g., light and food) prevents later acquisition of another CS-US (e.g., tone and food) pairing in eliciting the conditioned response when presented in compound (Kamin 1968). While blocking was first demonstrated within classical conditioning paradigms, it was latter demonstrated to occur within instrumental learning contexts (von Saal and Jenkins 1970).

Instrumental blocking functions much the same manner as blocking phenomena within classical conditioning with some important differences. Firstly, within the instrumental context stimuli are viewed within the framework of available response reinforcer contingencies. Put simply while in a classical conditioning experiment a tone may be learned to signal the arrival of food, in the instrumental context the tone signals the availability of a particular response-reward pairing, for example,

bar-pressing for food. As such, the stimuli are designated as discriminative stimuli that establish stimulus control over the behavior of the organism. For example, if a light signals the availability of food after bar pressing, presentation of the light will cause the animal to engage in greater amounts of bar pressing than in its absence. Similar to classical conditioning, instrumental blocking occurs when one discriminative stimulus is trained and then presented in compound with a new discriminative stimulus (Fig. 1).

Instrumental blocking has been demonstrated to impact both external discriminative stimuli as well as internal stimuli. For example, internal cues such as memory of reward delivery have been used to block acquisition of an external flashing light in establishing discriminative control of maze running (Haggbloom 1981). Likewise, shifts in the reward contingencies prior to compound stimulus training have been demonstrated to prevent blocking acquisition of a new discriminative stimulus in controlling responding. Additionally, both the amount of prior training and saliency of stimuli have been demonstrated to influence the strength of blocking.

**Instrumental Blocking,**  
**Fig. 1** How Instrumental  
Blocking is Tested



|                |                  |             |      |
|----------------|------------------|-------------|------|
|                | Phase 1          | Phase 2     | Test |
| Blocking Group | Light Correlated | Tone+ Light | Tone |
| Control Group  | Light Unrelated  | Tone+ Light | Tone |

In particular, greater prior training with a discriminative stimulus and subsequent reward delivery on the contingent schedule will increase blocking of stimulus control for stimuli paired in compound with the already learned discriminative stimulus. Furthermore, the greater the saliency of the blocking stimulus, the stronger the blocking effect will be on subsequent stimuli presented in compound. Related to saliency, the “surprisingness” or contiguity of the stimuli in signaling the response contingency influences the degree of blocking, with highly contiguous stimuli producing the greatest blocking effect (Haggbloom 1985).

Research into instrumental blocking has resulted in a wealth of theories that describe associative learning as resulting from variations in attention processes to differing associative memory strengths. It has also led to a reconsideration of the once held dichotomy between classical and instrumental approaches in associative learning. In particular, within both contexts the degree to which the previously trained stimulus is at asymptote for controlling behavior directly determines the amount of blocking observed. This has led to theories that specify an upper limit on the degree to which any stimulus can control behavior (Rescorla and Wagner 1972), as well as supported hierarchical accounts of associative learning (Williams 1995).

## How Instrumental Blocking Is Tested

Subjects are placed into an experimental (blocking) and control group and trained to engage in a response and reward contingency, such as lever pressing for food. In phase 1, the first discriminative stimulus (a light) is introduced to both the experimental and control groups. In the experimental condition, the stimulus signals when lever pressing will deliver food, while in the control condition the stimulus is uncorrelated with reward delivery. Thus, when examining the ratio of lever pressing between trials when the stimulus is present vs. absent, there will be greater lever pressing in the experimental group when the light is present than when absent. In phase 2, both

control and experimental groups receive a compound presentation of the trained stimulus and the stimulus to be blocked (a light-tone pairing) that signals reward delivery for lever pressing in its presence. Under this condition, both groups will exhibit greater amounts of lever pressing in the presence of the compound cue than in its absence. After training on the compound stimulus, blocking can be observed by measuring the stimulus control of the second discriminative stimulus when presented in isolation between the control and experimental groups. Within this setup, blocking manifests as a lessened effect of the second discriminative stimulus in controlling responding on the reinforced contingency for the experimental group. That is to say, in the example above blocking of the second discriminative stimulus by the first would result in equal amounts of lever pressing occurring during both the absence or presence of the second discriminative stimulus.

## Cross-References

- [Blocking](#)
- [Classical Conditioning](#)
- [Instrumental Learning](#)

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## Instrumental Conditioning

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## Instrumental Learning

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### Synonyms

[Instrumental conditioning](#); [Operant conditioning](#)

### Definition

Instrumental learning is a type of learning in which behaviors are strengthened or weakened by their consequences. It refers to nonreflexive behaviors that are *instrumental* in producing changes to the environment. Instrumental learning differs from Pavlovian (aka respondent or reflexive) conditioning in that it involves voluntary behaviors or actions, both overt and covert. Consequences are typically classified as either reinforcing (which have a strengthening effect on the response) or punishing (which have a weakening effect).

### Introduction

Instrumental learning is a naturally occurring, general process that dictates the conditions under which

behaviors are modified by their consequences. This process differs from Pavlovian conditioning because it involves voluntary behavior rather than reflexes. It was first described by B. F. Skinner (1938) who believed that behavior itself could serve as the object of study and promoted the idea that the best way to understand behavior was to approach it from an experimental and analytical perspective. Skinner referred to these responses as *operants* because they directly operate on the environment. He believed that instrumental learning consists of a three-component system called the *three-term contingency* that includes an antecedent stimulus, the target response, and the consequence (for a detailed review, see Domjan 2015).

## The Three-Term Contingency

### The Antecedent

Antecedent stimuli (aka *discriminative stimuli* or *SD*) consist of salient environmental stimuli that are reliably present when the target response produces a consequence. Over time, the SD comes to signal the specific relationship between the response and the consequence. In other words, the antecedent signals the probability of a specific consequence, given the target behavior. For example, in the presence of a green key light, a pigeon's key peck is highly likely to be reinforced with food. Over time, the SD (or green light) may come to prompt pecking. Common SD stimuli for people include things like streetlights and stop signs that gradually gain control over our driving and braking behavior.

### The Response

Instrumental behaviors are voluntary behaviors, not reflexes. They are defined in terms of the action of an individual. According to Johnston and Pennypacker (1980, p. 48),

*The behavior of an organism is that portion of the organism's interaction with its environment . . . that results in a measurable change in at least one aspect of the environment.*

Put simply, behavior affects the environment, which in turn affects the behavior. It is a reciprocal process that leads to continued adaptation to one's environment. An instrumental behavior can be

described or measured along several dimensions, including count, frequency (count/time), duration, magnitude, latency, and probability. In the laboratory, common responses include lever pressing for rats and key pecking for pigeons, whereas common everyday responses for people include nearly any voluntary behavior that can produce an outcome. They can be as simple as turning on a light switch (the consequence is the light coming on) or as complex as dancing the tango (the consequence may be “not stepping on your partner’s toes”).

**The Consequence**

The consequence of a behavior is the specific change in the environment that is produced by the instrumental response itself. It is the direct outcome of the behavior. Consequences can be described as either reinforcing or punishing and can have a strengthening or weakening effect on the future probability of the behavior. They alter the likelihood that a given response will be repeated in the future under similar circumstances.

Consequences vary along several dimensions such as the type of contingency (or correlation). A positive contingency involves adding a stimulus to the environment following the target behavior. Conversely, a negative contingency involves preventing or removing a stimulus. Another dimension is the type of stimulus involved. Appetitive stimuli are those stimuli or activities that the organism will work to earn. Aversive stimuli or activities are things the organism will work to avoid.

When combined, these dimensional qualities of the consequence produce four basic behavior change procedures (Table 1). Two of these procedures strengthen or increase behavior; two weaken or decrease behavior.

Consequences can be as simple as food or unpleasant noise or as socially complex as attention or criticism. They can also be counterintuitive in that some individuals may work to earn a consequence that another would find aversive (e.g., negative attention or even pain). The important thing to note is that consequences must be defined with respect to the individual recipient. From an evolutionary perspective, one might say that we repeat those behaviors that increase our fitness or improve our immediate situation while forgoing those

**Instrumental Learning, Table 1** Schedules of reinforcement. Four possible outcomes of operant conditioning based on the type of contingency and the type of stimulus involved

|                     | Positive contingency   | Negative contingency   |
|---------------------|------------------------|------------------------|
| Appetitive stimulus | Positive reinforcement | Negative punishment    |
| Aversive stimulus   | True punishment        | Negative reinforcement |

responses that have proven less than beneficial or that led to unpleasant consequences, in the past.

Together, the three terms (Antecedent→Behavior→Consequence) form a functional triadic process that allows antecedent stimuli (*discriminative stimuli or SDs*) to develop control over behavior by signaling a specific response-reinforcer relationship. When a behavior reliably occurs in the presence of an SD, the behavior is said to be under *stimulus control*. In the presence of established SDs, we are more likely to engage in those behaviors that have previously produced reinforcers and less likely to engage in those behaviors with a punishing past.

**Strengthening Behavior**

**Positive Reinforcement**

Positive reinforcement is defined as the contingent occurrence of an appetitive stimulus following the target behavior, such that the future probability of that response is increased. Put simply, when a behavior produces a reinforcer, that response is likely to recur in the future. If an employee invests extra time and effort on a particular project at work and is given a salary bonus for her efforts, we would predict that she would be highly likely to offer similar efforts on future projects.

**Negative Reinforcement**

Negative reinforcement is defined as the contingent prevention or removal of an aversive stimulus following the target behavior such that the future probability of that behavior is strengthened. This process relates to *escape* and *avoidance*



behaviors. Example, many people wear sunglasses in the summer to reduce glare as a result of negative reinforcement. However, some of us wait to put on our sunglasses until we are outside in the sun. If you put your sunglasses on to remove or terminate the glare, you are responding to an *escape contingency*. On the other hand, a few wise individuals will put the sunglasses on before stepping into the sun. For these individuals, an *avoidance contingency* is controlling their behavior.

## Weakening Behavior

### Positive Punishment

Positive punishment is defined as the contingent occurrence of an aversive stimulus following the target behavior such that the future probability of that behavior decreases. If you follow a behavior with a punisher, the likelihood that the behavior will recur in the future is reduced. Although this decrease in behavior may occur slowly over repeated experiences with punishment, behavior typically declines. Of course, long-standing behaviors with a history of reinforcement will respond to punishment more slowly than a behavior that is punished the first time it occurs. If you have a long history of biting your nails, the use of punishment to reduce that behavior may take some time. But the first time you put your hand on a hot stove is likely to be the last time.

### Negative Punishment

Negative punishment is defined as the contingent removal or termination of an appetitive stimulus following the target behavior such that the future probability of that behavior declines. If you follow a behavior with the removal of a valued reinforcer, the likelihood that the behavior will recur in the future will be reduced. There are numerous negative punishment techniques including time-out and response costs. *Time-out* consists of the contingent suspension of the ability to earn reinforcers and is a popular form of punishment among parents. However, time-out is most effective when the time-out location does not offer alternative sources of reinforcement. *Response*

*costs*, on the other hand, involve the loss or removal of a tangible reinforcer. Many teenagers are familiar with the use of response cost contingencies, like having the car keys taken away, following some egregious misbehavior like staying out beyond curfew.

## The History of Instrumental Learning

B. F. Skinner is universally regarded as the father of instrumental learning. His theory of operant conditioning was shaped, in part, by the works of Darwin, Thorndike, and Watson. In his classic paper, *Selection by Consequences* (1981), Skinner describes the analogy between Darwin's (1859) natural selection and the evolution of species and the role of selection through behavioral consequences on the adaptation of the behavior of individuals:

*What we call behavior evolved as a set of functions furthering the interchange between organism and environment. . . Since a species which quickly acquires behavior appropriate to a given environment has less need for an innate repertoire, operant conditioning could not only supplement the natural selection of behavior; it could replace it. (Skinner 1981, p. 501)*

Skinner viewed behavioral adaptation as complementary to the evolution of morphology and structure. To his view, behavioral adaptation could do, for the individual, what Darwinian natural selection could not. His translation of natural selection into selection by consequences through operant conditioning enabled him to argue that the processes relevant to instrumental learning are equally vital to the survival of life on earth. Needless to say, the concepts of operant conditioning and instrumental learning were (and continue to be) shaped by the influences of Darwin's most fundamental concepts.

Skinner was also influenced by E. L. Thorndike who stated that

*. . . Of several responses . . . those which are accompanied or closely followed by satisfaction to the animal will . . . be more firmly connected with the situation, so that when it recurs, they will be more likely to recur; those which are accompanied . . . by discomfort . . . (will) have their connections with that situation weakened, so that when it recurs, they will*

*be less likely to occur. The greater the satisfaction or discomfort, the greater the strengthening or weakening of the bond.* (Thorndike 1911, p. 244)

Eventually, the terms “satisfying” and “discomforting” would be replaced with Skinner’s “reinforcement” and “punishment.” But Thorndike’s law of effect resonated with Skinner and fit with his selectionist view. The law of effect states that a stimulus-response (S-R) association develops between the contextual stimuli and the instrumental response when reinforced. This highlighted the importance of environmental stimuli and their ability to develop control over behavior. Here Skinner found the foundation for the discriminative stimulus, and the three-term contingency was born.

Finally, Skinner was also influenced by Watson’s desire for psychology to abandon the introspective methods of Wundt and structuralism of James and to embrace an empirical science of behavior (Watson 1913). But he disagreed with Watson’s efforts to extend Pavlovian conditioning beyond their original limited scope. Skinner embraced the new American psychology of behavior but perceived Pavlovian conditioning as far too simplistic to explain the complexities of instrumental learning.

The final result was a solid foundation for Skinner’s instrumental learning that would carry behavioral psychology forward. Over the past eight decades, important advances beyond Skinner’s initial laboratory work have shaped the study of instrumental learning.

## Schedules of Reinforcement

As far back as the work of Ferster and Skinner (1957), schedules of reinforcement have been central to the study of instrumental learning. How and when reinforcement is delivered can have profound effects on the strength, rate, and pattern of instrumental behavior. A schedule of reinforcement is basically a rule that describes the specific conditions under which a behavior will be reinforced. The effect on behavior will vary depending on how reinforcers are arranged with respect to timing and effort.

### Continuous Reinforcement

When a single response produces a reinforcer every time, it is referred to as *continuous reinforcement or CRF*. Many examples of CRF schedules are evident in our everyday lives. For example, light switches require only one flip of a switch and the lights go on; the relationship between your steering wheel and the tires on a moving car makes learning to steer easy; pressing the keys on your keyboard produces one letter for every press. Although we can think of examples of CRF, most of our behavior is not reinforced in this manner. Most reinforcers are earned only after repeated instances of behavior, on an intermittent schedule of reinforcement.

### Intermittent Reinforcement

*Intermittent reinforcement* tends to produce more robust behavior because it strengthens both the behavior and its persistence in the absence of reinforcement. CRF, on the other hand, is less likely to produce persistent behavior, and responses will extinguish more rapidly in the absence of reinforcement. Think of that light switch; if we flip the switch and no light goes on, we rarely persist in trying the switch over and over. But if a slot machine in Las Vegas fails to return a big win, we are more than happy to insert more coins. The strength of the occasional payoff keeps us playing as long as we still have coins in our pocket.

Intermittent reinforcement can be arranged in many ways (i.e., different schedules) that can have distinct effects on instrumental behavior. The most common schedules are derived based on two major characteristics:

1. Whether the reinforcers are based on the number of responses (i.e., ratio schedules) or whether there is a delay component prior to an effective response (i.e., interval schedules)
2. Whether the response requirement is fixed or variable

**Fixed-Ratio Schedules.** The fixed-ratio (FR) schedule results when reinforcement depends on a specific number of responses. Whenever this schedule is in effect, the same

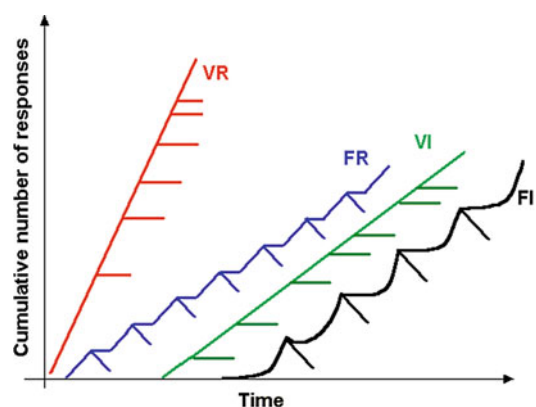
number of responses is required to produce the reinforcer. For example, a local phone call usually requires you to press seven buttons to place the call. Whenever you place that same local call, you press the same number of buttons before you get to speak with your friend (or his voicemail). Interestingly, responses that are repeatedly reinforced on an FR schedule become somewhat stereotyped (see Fig. 1), consisting a rapid sequence of responses (called a *ratio run*) followed by a pause after each reinforcer (called a *post-reinforcement pause*). In the laboratory, rats will respond at very high rates on FR schedules, alternating between rapid runs and pauses. The length of the pause is highly correlated with the response requirement: the greater the FR value, the longer the pause. If you watch middle school kids climb flights of stairs, you will often see this break and run pattern with them racing up each flight followed by a brief pause between flights.

**Fixed-Interval Schedules.** A fixed-interval (FI) schedule results when reinforcers are contingent on the first response following a set interval of time; this interval never changes from episode to episode. For example, washing machine cycles are set on FI schedules. The same wash cycle requires a set period of time, followed by a response – opening the washer to remove the clothes. Responding too soon results in clothes that are not yet clean (or spun). FI schedules, like FR schedules, are predictable and, as such, produce a unique response pattern called an *FI scallop*. This pattern is characterized by extremely low (or even zero) responding early in the interval followed by a slow but gradually increasing rate of responding as the end of the interval grows nearer (see Fig. 1). It is believed that the positively accelerating nature of the FI scallop is the result of differential reinforcement of shorter and shorter inter-response times (IRTs). This pattern of behavior is common among college students studying for exams scheduled at regular intervals. Studying behavior is generally low during the early part of the interval, but picks up as the exam draws closer – often ending with a cramming session the night before the exam.

**Variable-Ratio Schedule.** Variable-ratio (VR) schedules are similar to FR schedules, but

they have specific ratio requirements that change from instance to instance, trial to trial. Typically, the VR has a specific value (e.g., VR 30), but this value describes the average number of responses required over the long run. Thus each individual instance of reinforcement may require slightly more or slightly fewer responses than the average. For example, the number of steps from your front door to the closest corner may be an average of 80 paces. However, it could be slightly more or less depending on weather, style of shoe, or any other factor that might influence stride length. But over the long run, there would be an average number of paces (for each person).

How much variability exists within a VR schedule depends on the specific behavior or on the explicit schedule set by the programmer (e.g., slot machines often run on predetermined VR schedules). Variable ratios tend to be very unpredictable from trial to trial and as such produce a relatively high, but steady rate of responding (see Fig. 1). Remember, the absence of any time constraints in a ratio-based schedule allows the individual to respond as rapidly as they wish. Rapid responding brings each reinforcer faster. So it is to the advantage of the individual to respond quickly and efficiently in order to maximize reinforcement. It is this rapid response



**Instrumental Learning, Fig. 1** Idealized patterns of cumulative responses based on the four major schedules of reinforcement. Tick marks signify the delivery of a reinforcer. (Image reprinted with permission from “Operant conditioning: Schedules of Reinforcement,” by Lumen Learning (2017), CC BY-SA 4.0)

rate produced by the VR that allows the gambling house to maximize its profits, at our expense.

**Variable-Interval Schedules.** The variable-interval (VI) schedule occurs when reinforcement is contingent on the first response after an average amount of time elapses. Here too, the interval requirement is specified for each trial, but its duration can vary across occurrences of the behavior. Thus, an FI 30-s schedule will have a delay that is approximately 30-s long before a response is effective. But that interval can be longer or shorter from one instance of the behavior to the next. Again, the range of interval values will vary depending on the specific behavior, but VI schedules typically produce moderate, steady response rates without stereotyped patterns (see Fig. 1). Examples include how often your boss checks your work. If she checks reliably but unpredictably, you are likely to keep the rate and quality of your work at a reasonably high level in order to earn her praise (or avoid her criticism).

### Extinction

Extinction is a unique schedule in which previously reinforced instrumental behavior no longer produces reinforcers. When an instrumental response is no longer effective in producing reinforcement, there can be an initial increase in response rate, called an *extinction burst*, followed by a gradual decline until the response no longer occurs. It can also increase response variability whereby the individual may try variations of the behavior before giving up. How much or how long a behavior persists under extinction before finally being extinguished depends on a variety of factors. Extinction occurs more rapidly after continuous reinforcement (CRF) and more slowly after intermittent reinforcement, known as the *partial reinforcement extinction effect (PREE)*. A number of interesting theories regarding the mechanism(s) of this phenomenon have been suggested over the years (Amsel 1992; Capaldi et al. 1996; Jenkins 1962; Grace and Nevin 2000), but the final answer remains unclear (Domjan 2015).

### Other Schedules

There are many other schedules of reinforcement (such as the differential schedules, compound

schedules, concurrent schedules, mixed and multiple schedules, chain and tandem schedules). Schedules can operate in sequence or in tandem to simulate the most complex of reinforcer arrangements. Such variations are useful in investigating the factors responsible for distinctive patterns of complex instrumental behavior. In 1957, Ferster and Skinner produced the most in-depth compendium of complex schedules to date; it is considered to be the classic seminal work on complex schedules of reinforcement.

**Choice Behavior.** One such area involving complex schedules of reinforcement involves the study of choice-related behavior. Choice can be described simply as the opportunity to select from more than one concurrently available alternative or schedule. Typically, choice behavior is measured by calculating the percent of behavior that we allocate to each alternative, called the *relative rate of responding*.

In 1961, Richard Herrnstein proposed a simple idea: that the relative rate of responding on two alternatives tended to match the relative rate of reinforcement across the two alternatives. It was called *the matching law*, and it simply meant that we allocate our responses in manner consistent with the rates of reinforcement available. A schedule that produces 75% of our reinforcers will receive 75% of our effort. The matching law has been a robust theory and guiding principle for over a half century, and it has produced many procedural derivatives and theoretical extensions and has been employed across a wide range of instrumental behaviors. It has been a source of continued experimentation for decades, and the mechanisms that produce matching have been the focus of prolonged debate (for a review, see Davison and McCarthy 2016).

### Response-Reinforcer Relations

The relationship between the response and the reinforcer is important to the understanding of instrumental learning. Specifically, there are several key aspects of the response-reinforcer (R-R) relation that determine whether learning will be facilitated or inhibited, including (a) timing, aka

temporal contiguity, (b) the nature of the R-R contingency, and (c) the biological relevance between response and reinforcer.

### Temporal Contiguity

The timing of reinforcement is critical to effective instrumental learning. Long delays between a response and its outcome can slow or even inhibit learning altogether. It is thought that the difficulty lies in the ease with which the association between the response and reinforcer is formed. When presented immediately, it is fairly easy to form an association between behavior and its consequence. But with long delays, other events or behaviors may intervene, making an association between the correct response and the reinforcer more difficult.

For many species, bridging stimuli (*aka conditioned reinforcers*) can mitigate R-R delays if they are presented immediately after the required response. This is a well-known method used by animal trainers who rely on clickers or whistles to immediately mark a behavior well done and later provide the reinforcer. Of course, conditioned reinforcers must be trained first by repeatedly pairing the neutral clicker or whistle with food until a Pavlovian association is formed. Then the conditioned reinforcer can be used effectively to bridge a long delay between response and reinforcer. However, immediacy of reinforcement still applies. A bridging stimulus presented at the beginning of a delay can facilitate learning; but if presented at the end of the delay, the same stimulus can block learning (Williams 1999).

### Response-Reinforcer Contingency

Contingency refers to the dependent, causal relationship between the response and the reinforcer. When a behavior directly produces the consequence, the likelihood of instrumental learning is maximal. However, there are exceptions. In cases of accident reinforcement (i.e., the accidental occurrence of an appetitive stimulus immediately after a specific behavior), it is possible for a behavior to change superstitiously. This is common among athletes: we are all familiar with the odd, superstitious behaviors of the baseball pitcher before throwing a pitch or of the golfer

before making a putt. These responses were often accidentally reinforced the first time with a base hit, or a hole-in-one!

**Learned Helplessness.** Another phenomenon related to contingency is our ability to learn about the absence of a contingency. Learned helplessness (Maier et al. 1969) occurs following repeated exposure to inescapable aversive experiences. Later, when presented with impending aversive events, those individuals, who have previously learned that any attempt at escape is useless, fail to learn the new escape behavior. In such cases, learned helplessness may result from incompatible behaviors like freezing, inattention due to a focus on the impending event, or they simply have learned there is no R-R contingency – making the acquisition of escape behaviors even harder. Modern clinicians are aware of the learned helplessness effect among veterans of combat, and among abuse and rape victims, and have investigated neurobiological correlates of both (Hammack et al. 2012).

**Biological Relevance.** In the first half of the twentieth century, proponents of instrumental learning tacitly accepted the notion that any reinforcer could strengthen any behavior. By the 1960s, this *equipotentiality hypothesis* was displaced in favor of a more ethological interpretation that acknowledged biological constraints on the learning processes. This approach, known as the *behavior systems approach*, focused heavily on the biological relevance of the response-reinforcer relation. According to this approach, certain behaviors and reinforcers belong together as part of each behavior system (e.g., foraging and feeding systems, courtship and mating systems, escape/avoidance behaviors and predator evasion systems, etc.). When a behavior and reinforcer belong to the same behavior system, instrumental learning is facilitated. However, when a reinforcer from one system is used to reinforce a behavior from an incompatible system, learning is inhibited. For example, Fantino et al. (1966) demonstrated that lever pressing alone was not easily learned as an avoidance responses in rats; however adding an ethologically appropriate response like running (an escape-relevant behavior) toward the lever allowed lever pressing to be



acquired rapidly. But when the running requirement was removed, even after lever pressing had been acquired, the lever press behavior was lost. The influence of response-reinforcer relevance is key to a thorough understanding of instrumental behavior (for a detailed review, see Timberlake 2001).

## Instrumental Learning and Behavioral Neuroscience

Traditionally, the focus of instrumental conditioning has been between environmental stimuli and behavior. Brain involvement was seen as merely the circuitry of connection for input to become output. Little attention was paid to any direct neural contribution to behavior. As our technology has grown in sophistication, the accessibility of neural contributions to behavior has become more viable as a valid line of investigation. McIlvane and Dube (1997) suggest that seeing neural pathways as important links in a sophisticated behavior chain might lead to insights into the integrated synthesis of the environmental and the behavioral determinants of instrumental behavior.

### Early Brain Stimulation

In 1954, Olds and Milner established reliable responding in rats by delivering electrical stimulation in the limbic septal area of the brain. This finding began the search for the neural pathways and structures associated with both Pavlovian and instrumental learning. Since then, half a century of research supports the idea that neural events (both central and peripheral) are important to behavioral contingencies (for a review, see Guerra and Silva 2010) including the nature of reinforcement and what makes a reinforcer reinforcing.

A more recent example of the effect of peripheral nervous system stimulation on instrumental learning was conducted on the *Aplysia*, a marine snail (Brembs et al. 2002). *Aplysia* feed on seaweed. When they forage, they bite randomly, but only swallow when they obtain seaweed. When a snail swallows seaweed, the esophageal nerve fires. To test whether the esophageal nerve serves as a reinforcer for biting and swallowing, external stimulation of the esophageal nerve was used

following random bites that did not naturally produce swallowing. Results showed that esophageal stimulation increased biting above the rates observed in control snails. Hence, the firing of the nerves associated with swallowing effectively function as a reinforcer for biting.

### Dopamine and Reinforcement

It was long accepted that dopamine, a basic neurotransmitter, is released in the presence of SDs and reinforcers during instrumental learning. Moreover, direct manipulation of the dopamine system can have direct effects of the value of reinforcers: extra dopamine and the value of food and water increase. Dopamine depletion simulates satiation and can impede learning (see Guerra and Silva 2010). Most recently, an investigation of the mechanisms of dopamine mitigation and incentive motivation would change the traditional stimulus-response (S-R) view of the brain-behavior interaction.

**Wanting and Liking.** Berridge and Robinson (2016) discuss the notion that “wanting” and “liking” a reinforcer may not be synonymous. While easily construed as the same concept, the incentive motivation (or “wanting”), that sets behavior in motion, waxes and wanes in step with dopamine increases and decreases. But “hedonic orofacial expressions elicited by sweetness” do not. In other words, even when dopamine is depleted and our motivation to earn a sweet treat is extinguished, we still respond facially to the taste of sweet. Our face says we like it, but our behavior says we don’t want it.

According to Berridge and Robinson (2016), the incentive nature of “wanting” is mediated by midbrain dopamine projections to the forebrain. The strength of the signal depends on dopamine levels and on the strength of the association between the cue and the reward. Dopamine creates a state-dependent increase in “wanting.”

“Liking,” on the other hand, is related the experience of pleasure: all kinds of pleasure including foods, drugs, and even social pleasures. The neural structures for liking are, according to Berridge and Robinson (2016), tiny, neurochemically limited “hotspots” dispersed across the larger limbic system that appear to be independent of the dopamine-based “wanting”

system. For example, the hotspot in the nucleus accumbens represents less than 10% of the entire structure. In humans, these hotspots also occur in the limbic prefrontal cortex and in deep subcortical regions of the brain. The critical issue here is that the two systems appear to be independent, each controlling different aspects of the nature of reinforcement. As their data suggest, neural structures and the role of dopamine are critical to our understanding of what makes a reinforcer effective or not. These results will undoubtedly have profound clinical implications for behavioral interventions in mental health and addiction.

## Instrumental Learning and Comparative Cognition

Within psychological theory and research, the cognitive tree and the behavioral tree have been slowly growing together for over a half a century. Interest in the behavioral correlates of cognition has grown exponentially and extends to memory, categorization, timing, decision-making, problem solving, tool use, and even language. After decades of hostile competition and mutual criticism, cognitive psychologists and behavioral psychologists, along with cognitive ethologists, are now engaging one another and working together to better understand nonhuman animal behavior (for a review, see Wynne and Udell 2013). Two examples illustrate the role of instrumental learning in comparative cognition: the study of behavioral timing and memory.

### Temporal Regulation of Behavior

One great constant in instrumental learning is the influence of time. Temporal regulation of behavior is well established across nonassociative learning, Pavlovian conditioning, and instrumental learning. The degree to which time alone can alter behavior is noteworthy. As such, it begs the question: Can animals keep track of time? And if so, what factors are implicated in the ability to keep track of time? While a complete account has yet to emerge, a host of interesting comparative data has accumulated in the last several decades.

According to Meck and Church (1983), an animal is considered to be timing if the duration

of an event can serve as an SD for them. In fact, sensitivity to duration has been established across a variety of vertebrates (Buhusi et al. 2005; Stubbs 1968; Talton et al. 1999). An illustrative example comes from Fetterman (1995) who demonstrated that pigeons could easily learn to discriminate and respond differently to two key light durations (2 and 10-s). Similarly, Roberts (1981) showed that rats could use different stimulus durations to modulate responding around two distinct schedules (FI 20-s or FI 40-s) with the peak in their responding centered on the point in time when the reinforcers on each schedule would be delivered. Although a resolution regarding the underlying mechanism of timing remains under investigation, there is no doubt that sensitivity to time and temporal regulation of behavior are evident across many species (Lejeune and Weardon 1991).

### Memory

The study of memory has been a shared interest for behavioral psychology and comparative cognition for over a century. The pioneering work on memory and forgetting by Ebbinghaus (1885) fostered a curiosity that extends deep into the modern fields of comparative-cognitive psychology and traditional instrumental learning. Within instrumental learning, the delayed matching-to-sample procedure (Blough 1959) has become the most commonly used and productive method of investigating factors important to short-term memory and forgetting (White 2013).

**DMTS.** In the delayed matching-to-sample (DMTS) procedure, a sample stimulus is presented, and following a delay, a choice must be made between two alternatives. The goal is to match the choice to the sample. Correct matches are reinforced; errors are not. By means of this elegant method, the effects of various factors have emerged by studying the behavior of rats (Cohen et al. 1986), pigeons (Grant 1976), dolphins (Roitblat et al. 1990), primates (D'Amato and Worsham 1974), and humans (Paule et al. 1998).

According to Grant (1976), the longer the delay between sample and choice, the poorer the matching accuracy. Additionally, longer samples facilitate matching performance. These factors may seem obvious, but other influences are less so. For example, extended training with moderate

delays between sample and choice leads to markedly improved accuracy with even longer delays at a later time (Sargisson and White 2001). Other productive memory procedures that have focused on spatial memory as a naturally selected strategy include the Morris water maze (Morris 1984), the radial arm maze, and complex, three-dimensional foraging rooms.

**Morris Water Maze.** Morris (1981) showed that rats could successfully navigate through a tank of opaque water to an invisible platform as long as the distal (room-based) cues remained fixed and could adjust their path when starting from various locations in the tank. He went on, with others, to study the neural correlates of spatial learning (de Hoz et al. 2003; Vorhees and Williams 2006) as well as sex and species differences (Jonasson 2005) and relevant clinical applications (Bromley-Brits et al. 2011) for spatial water maze performance.

**Radial-Arm Maze.** In 1976, Olton and Samuelson designed the first radial arm maze (RAM) to assess memory for places visited. The first radial-arm maze consisted of eight arms (4 ft in length) that radiated out from a central hub. The end of each arm could be primed with small pieces of food, and rats could be evaluated in terms of whether they revisited “empty” arms after having already retrieved the food. Exploration of new arms results in reinforcement; old arms produce extinction. From an evolutionary (optimal foraging) perspective, revisiting an arm wastes valuable energy to the detriment of the animal. The point is that the animal must recall which arms have already been emptied so as to visit only the remaining “loaded” arms. This procedure is a more ecologically valid laboratory simulation of actual foraging than the Morris water maze for many species.

Typical findings show that rats (and other species) learn the maze quickly, in as few as five to ten trials (Olton 1978). Various mechanisms of this high performance have been tested and rejected including olfactory cues like scent marking (Olton and Samuelson 1976) or intra-maze cues like the use of fixed spatial algorithmic strategies (e.g., always go to the arm on the left, Zoldek and Roberts 1978). More recently, Cole

and Shapell-Stevenson (2003) using a 48-arm maze estimated that spatial memory in rats appears to be limited to between 16 and 24 locations. Similar to the Morris water maze, evidence positively suggests reliance on distal cues such as windows or picture frames on the wall; movement of distal landmarks increases errors (Suzuki et al. 1980). But O’Keefe and Nadel (1979) cautioned against the rejection of spatially separated intra-maze cues. Reliance on intra- and extra-maze cues need not be mutually exclusive. Their warning was later supported by Wages (1987) who found no differences in performance between extra-maze and intra-maze stimuli.

The use of radial arm maze studies has led to extensive and broad research in comparative psychology related to spatial orientation, cognitive maps, and the evolutionary mechanisms of maze-related choice behavior (Jonasson 2005). More recently, the influence of neuroanatomical variation effects on radial arm maze performance has been studied in rodents (Crusio and Swegler 2005) and even in humans using virtual reality technology (Goodrich-Hunsaker and Hopkins 2010). The evidence suggests that hippocampal damage increases response latencies and errors in both human and nonhuman subjects, further implicating neural structures as important mediators of spatial navigation and memory.

**Food Caching in Corvids.** Spatial navigation and memory are also critically important to food caching – the storage of food by certain highly adapted species of birds (e.g., corvids like jays and nutcrackers) and rodents (e.g., squirrels). The ability to survive the winter for seed-caching birds like pinyon jays and nutcrackers hinges heavily on their ability to recall the locations of their caches long after they have stored the seeds. Pinyon pine seeds constitute 70–90% of the pinyon jay diet, even in winter when seeds are no longer available (Ligon 1978). Thus, seed retrieval from caches is critical to winter survival (Balda and Kamil 2006). In years with high pinecone production, individual pinyon jays may store up to 26,000 seeds in as many as 20,000 caches (Marzluff and Balda 1992). Given the seasonal changes in landscape topography from cache (in the fall) to recovery (in winter), sufficient retrieval requires specially

adapted or evolved strategies. Many broad mechanisms have been suggested including the use of olfaction, a biological compass, or the use of landmarks or beacons. None of these are mutually exclusive and require independent testing using instrumental procedures.

For example, the classic laboratory study of spatial memory in corvid birds requires special equipment. Kamil and Balda (1985) devised a room that had 180 sand cups ( $12 \times 15$ ), available for caching seeds, mounted flush within the floor. Where the birds stored seeds during three caching sessions in the 18 cups that were available (the other cups were capped) was observed. After storage, the birds were not allowed into the room for 10 days. Following this mandatory retention interval, the birds were then allowed to forage in the room with all 180 cups available. Across several tests, the birds performed above chance levels by relying only spatial memory and not other mechanisms such as olfaction.

More recently, the study of caching behavior has focused on the neural substrates involved in spatial memory and analyses of phylogenetic relatedness between corvid species. Based on comparative brain studies and behavioral differences, de Kort and Clayton (2006) suggest that specific caching adaptations across related avian species may well be the result of convergent evolution, despite a caching common ancestor. Furthermore, these adaptations may have extended beyond simple spatial memory to specialized episodic memory since the content of a caching memory appears to be sensitive to relative degradation risk of individual caches in some species (Clayton and Dickinson 1998). The modern integration and collaboration across behavioral, structural, and evolutionary approaches provides a more thorough understanding of the nature of spatial memory and the adaptations that make each species successful.

## Conclusion

Of course, the aforementioned topics and examples only scratch the surface of the questions being studied by proponents of instrumental

learning and their colleagues. Today, the field of behavioral psychology is more interdisciplinary than ever, with crossovers in comparative cognition, neuroscience, psychopharmacology, and animal behavior. The study of instrumental behavior (both public and private) is benefitting from this multidisciplinary triangulation and collaboration. Furthermore, the experimental analysis of behavior has provided an empirical foundation of principles and laws that are applied to more human endeavors including education, mental health, medicine, and particularly in the treatment of people with intellectual disabilities like autism and Down syndrome.

## Cross-References

- ▶ B.F. Skinner
- ▶ Behavior Systems
- ▶ Behavioral Neuroscience
- ▶ Behaviorism
- ▶ Charles Darwin
- ▶ Comparative Cognition
- ▶ Contingency
- ▶ John B. Watson
- ▶ Law of Effect
- ▶ Learning
- ▶ Positive Reinforcement
- ▶ Schedules of Reinforcement
- ▶ Short-Term Memory
- ▶ Stimulus Control
- ▶ Timing

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## Instrumental Object Manipulation

### ► Tool Use

## Insuck

### ► Upsuck Hypothesis

## Integumental System

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## Synonyms

Cutis and its derivative; Derma and its derivative;  
Skin and its derivative

## Definition

The integumentary system is the largest organ system of human body consisting of the skin and its derivatives.

## Introduction

The integumentary system is a complex organ that forms the external covering of the entire body surface, including the external acoustic meatus, the lateral side of tympanic membrane, and the vestibule of the nose. It consists of the skin, hair, nails, and exocrine glands which is protective against infection, mechanical abrasion, and chemical and radiation injuries. It is the largest organ of the human body, constituting 15–20% of its total body mass. In an average 70 kg person, total weight of skin is about 13 kg and its total surface area is around 2 m<sup>2</sup> (Strandring 2016). It varies in thickness from 1.5 mm to 5.0 mm and the thickness depends on location.

The skin consists of a superficial layer of avascular, stratified squamous epithelium, the epidermis, and a deeper, vascular, dense fibrous tissue, the dermis (Romanes 2015). The skin is separated from muscles and bones by superficial and deep fasciae. The intervening tissue between the dermis and deep fascia is called hypodermis which contains fibro-areolar and adipose tissue.

## Functions of Skin

1. It provides an effective barrier against microbial organisms and forms first line of defense. After antigen interaction, Langerhans' cells of the epidermis provides immunological information to the lymphatic system (Datta 2010).
2. It protects against mechanical abrasion, chemical assault, thermal injury, and ultraviolet radiation damage.
3. It is water-proof due to presence of the stratum corneum. So it prevents loss of body fluid (Datta 2010).
4. It is helpful in Dermatoglyphics.
5. Skin helps in the synthesis of vitamin D under the influence of ultraviolet B (UVB) radiation and also has an important role in synthesis of cytokines, hormones, and growth factors.
6. It controls body temperature mainly by regulating heat loss from the cutaneous circulation and sweating.
7. It relays the sensory information like touch, temperature, pain, and other stimuli from the exterior to the nervous system.
8. It also helps in excretion by excreting secretion from sweat, sebaceous, and apocrine glands (Pawlina 2016).
9. Sexual signaling: Apocrine sweat glands and other skin glands secrete sex pheromones which are important for sexual attraction (Mescher 2013).

## Types of Skin

1. Thin hairy skin: It is present over most of the body surface. It has much thinner epidermis which contains hair follicles.
2. Thick (glabrous, hairless) skin: It is present over palms, soles, and flexor surfaces of the digits.

## Microscopic Structure of Skin

### Epidermis

The epidermis is derived from the surface ectoderm. It is composed of keratinized stratified squamous epithelium in which four layers is found. But in case of thick skin, a fifth layer is also found. From deeper to superficial, these layers are as follow:

- (a) Stratum basale (stratum germinativum): It consists of a single layer of cuboidal to low columnar cells that rest on the basal lamina. It contains the stem cells which give rise to new cells by mitosis which are called keratinocytes. The stem cells undergo mitotic division 2–3 times, after that they move to deeper surface of stratum spinosum, where they lose their mitotic activity (Datta 2010).

These basal cells are connected to each other with the help of desmosome while basal cells are linked to the basal lamina by hemidesmosome (Standring 2016). Melanocytes interspersed in this layer which transferred melanin pigment in the cytoplasm of basal cells (Pawlina 2016).

- (b) **Stratum spinosum (prickle cell layer):** It consists of several layers of large, polyhedral, and closely packed keratinocytes. On light microscopic examination, there are numerous cytoplasmic processes or spines emerge from each keratinocytes, which joined to similar processes of adjacent keratinocyte with the help of desmosomes. Melanosomes either singly or aggregated within membrane-bound organelles are also present in the cytoplasm of keratinocytes.
- (c) **Stratum granulosum:** It consists of 3–4 layers of flattened cells with pyknotic nuclei which is a hallmark of degeneration. Keratinocytes contain numerous keratohyalin granules. These granules are composed of protein profilaggrin which has abundant histidine and trace amount of sulfur. The profilaggrin is the precursors of the protein filaggrin in stratum corneum. Profilaggrin helps in aggregation of the keratin filaments of the stratum corneum. The Golgi-derived lamellar granules are responsible for the release of hydrophobic glycopospholipid material into the intercellular space. This glycopospholipid provides permeability barrier to the epidermis (Standring 2016).
- (d) **Stratum lucidum (clear Layer):** It is present only in thick skin. Some researchers assumed that the stratum lucidum is a part of the stratum corneum. It consists of a thin, translucent layer of flattened eosinophilic keratinocytes held together by desmosomes. Later on, the keratin filaments gradually get deposited in the cell and nucleus and cytoplasmic organelles start disrupting and finally get vanished.
- (e) **Stratum corneum:** It consists of most differentiated cells (corneocytes) of the epidermal layer. The nucleus and cytoplasmic organelles disappear and cytoplasmic matrix is completely filled with keratin filaments.

Under normal conditions, there is a balance between the production of keratinocytes in the stratum basale and the loss of corneocytes from the stratum corneum. But when there is excessive desquamation of corneocytes, leads to dandruff formation on the scalp. In excessive amounts of friction at any sites, this cornified layer becomes thicker which leads to calluses formation.

Normally total epidermal turn-over time is about 52–75 days. In psoriasis, the turnover rates and transit times are significantly shortened around 8 days.

### Cells of Epidermis

1. **Keratinocytes:** Epidermis predominately consists of keratinocytes. These cells take origin from the stratum basale of the epidermis. They convert from polygonal living cells to dead flattened cells which form mature keratin. This process is called as cornification. They also form a component of epidermal water barrier.
2. **Melanocytes:** Melanocytes represent 8% of the epidermis cells (Maranduca et al. 2019). Melanocytes are derived from neural crest cells and during third month of the gestation they migrate as melanoblast at the junction of the epidermis and dermis. They are scattered among the basal cells of stratum basale and produce and distribute melanin into keratinocytes. Each melanocyte supplies melanin to approximately 35–40 neighboring basal keratinocytes. The ratio of melanocytes to keratinocyte is 1:4 to 1:10. In humans, melanin exists into two forms, the brown-black eumelanin and the red-yellow pheomelanin (Del Bino et al. 2018). Normally natural melanin are combination of both eumelanin and pheomelanin. The skin color is decided by the ratio of eumelanin to pheomelanin. The skin color is not related with the number of melanocytes, because it is relatively constant in all skin types (Davis et al. 2019). In black-skin people, the melanocytes are larger, more dendritic as well as contains more late staged melanosomes. In black-skin people,

melanosomes are present throughout the epidermis, including the stratum corneum, and melanin is degraded more slowly due to less lysosomal activity of keratinocytes (Maranduca et al. 2019). Melanin has a protective role against the harmful effects of UV radiations on the nuclear DNA of Stratum basale. It also eliminates harmful free radicals by scavenging processes.

#### Clinical Implication

- (a) **Albinism:** It is an autosomal recessive disorder due to the complete absence or decrease biosynthesis of melanin pigments in melanocytes. They are not able to oxidize tyrosine into DOPA due to agenesis of enzyme tyrosinase (Marçon and Maia 2019).
- (b) **Vitiligo:** It is characterized by localized depigmentation of skin due to loss of ability of melanocytes to produce melanin. It is an autoimmune response to a trigger (sunburn, mechanical trauma, chemical exposures, etc.), which eventually targets melanocytes. It is an autoimmune disorder which manifests as white macules on the skin, especially eyelids, mouth, and hands (Manga et al. 2016).
3. **Langerhans' Cells:** These are dendritic and antigen presenting cells scattered throughout the epidermis. They are derived from common lymphoid progenitor cells in bone marrow and ultimately reach the epidermis via blood stream. When any antigen enters through the skin, the Langerhans' Cells captured and processed the antigen. After that they reach the regional lymph node where the antigen interacts with T-lymphocytes. Langerhans' cell is responsible for delayed (type IV) hypersensitivity reaction in contact dermatitis. Histiocytosis X (Langerhans' cell histiocytosis) is a malignant tumor of Langerhans' cells in which abnormal Langerhans' cells spread in various parts of body and affect them (Pawlina 2016).
4. **Merkel's Cells:** These are embryologically developed from epidermis. These are clear oval dendritic cells which are located in the stratum basale. These cells are bounded to nearby basal keratinocytes with the help of

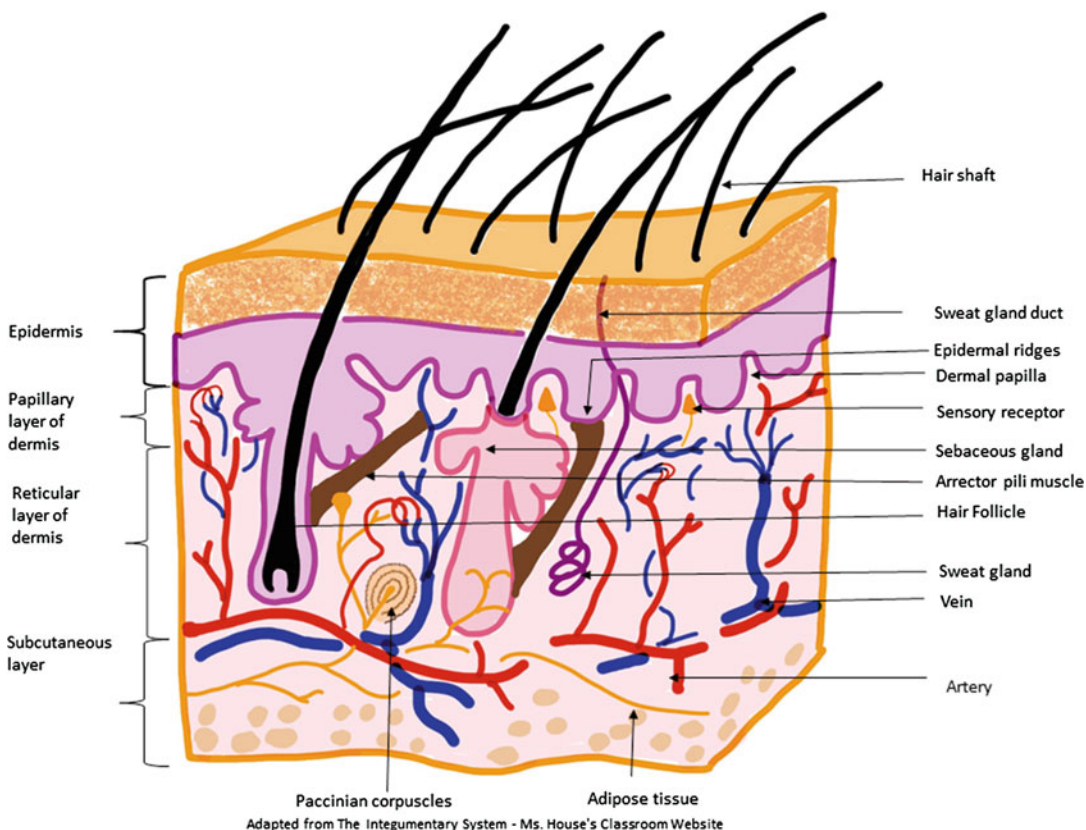
desmosomes. The cytoplasm contains small intermediate filaments and 80-nm dense-cored neurosecretory granules. They are slowly adapting mechanoreceptors which is activated by hair movement. Merkel cells carcinoma is a very rare and highly aggressive tumor, may be triggered by the Merkel cell polyomavirus. It effects most commonly sun exposed area and spread quickly via lymphatic route.

#### Dermis

The dermis lies beneath the epidermis which has an irregular, fairly dense connective tissue. It is derived from the mesoderm. It is composed of collagen, elastic, and reticular fibers in an amorphous-ground substances which is rich in glycosaminoglycans. The fibroblast is main component of dermis which is a primary source of collagen, elastin, and other proteins. It is composed of two layers: a narrow, outer papillary layer and an inner reticular layer (Fig. 1).

The papillary layer consists of loose connective tissue lies beneath the epidermis with a higher density of cells, a higher content of proteoglycan, and a weaker alignment of collagen fibers (Rippa et al. 2019). It has numerous finger-like connective tissue protrusions, dermal papillae that project into the undersurface of the epidermis which interdigitate with the corresponding recesses of the epidermis, epidermal ridges, or rete ridges (Fig. 1). The dermal papillae contain Meissner's corpuscles which acts as touch receptor. The dermal papillae are rich in the blood vessels and sensory nerve endings.

The reticular layer lies deep to the papillary layer and separated from the papillary by the vascular plexus, rete subpapillare (Rippa et al. 2019). It is thicker and less cellular than the papillary layer. It is composed of the mostly parallel bundles of collagen and elastic fibers which is responsible for the formation of regular lines of tension in the skin called Langer's lines. Surgical skin incision should be given parallel to Langer's lines to achieve best healing with minimal scarring (Pawlina 2016).



**Integumental System, Fig. 1** The diagram showing the organization of skin and skin appendages

## Surface Irregularities of Skin

1. Tension lines/Cleavage lines/Langer's lines: They run longitudinally in the limbs and circumferentially in the neck and the trunk.
2. Flexor lines: These are acquired permanent lines which are found in the vicinity of synovial joints. Along these lines, the skin is thin and attached strongly to underlying deep fascia. These are more prominent on the flexor surfaces of palms, soles, and digits.
3. Papillary (friction) ridges: These are present on the fingers and toes, the palm of the hand, or the sole of the foot. They form ridges which is separated by parallel curved grooves. The apertures of sweat ducts open at regular intervals along the summit of each ridge. A fingerprint is an impression which is formed by the friction ridges of a human finger. This is

unique and not identical in any two individuals and used for medicolegal purposes. The study of these ridge patterns is known as Dermatoglyphics.

## Hypodermis (Tela Subcutanea; Subcutaneous Tissue)

It is layer of loose connective tissue which consists of varied thickness of adipose tissue (Fig. 1). This layer acts like thermal insulator, shock absorber, and storehouse of metabolic energy. It gives passage to nerves, vessels, and lymphatics and also contains striated muscles, such as platysma. The subcutaneous tissue has a very rich vascular supply, so insulin or other drugs is preferably injected into this tissue to promote absorption of drug (Mescher 2013).



## Epidermal Skin Appendages

These are derivative of epidermal epithelium. These include hairs with hair follicles, sebaceous glands, sweat glands (eccrine and apocrine), and nails.

**Pilosebaceous unit:** It consists of the hair, hair follicle, arrector pili muscle, sebaceous gland, and sometimes an apocrine gland.

## Hair and Hair Follicles

Hairs are elongated keratinized structures that develop from the hair follicles. They present over almost the entire body surface except the thick skin of the palms, soles, the flexor surfaces of the digits, lips, nipples, glans penis, prepuce, clitoris, the labia minora, and the inner aspects of the labia majora. The hair density of the face is about 600 per cm<sup>2</sup>, whereas rest of the body has 60 hairs per cm<sup>2</sup> (Strandring 2016). The hair helps in thermoregulation, in case of scalp they protect from external injuries and solar radiations.

**Part of hairs:** Each hair is composed of a shaft, root, and bulb. Shaft projects above the skin which is dead part of hair. The root lying within the hair follicles. The bulb is the enlarged base of the root of hair. The shaft consists of three layers: medulla, cortex, and cuticle.

The medulla is innermost part of the shaft which contains vacuolated (air) cells and melanosomes. The medulla is present only in thick hairs. The cortex is located superficial to the medulla and contains closely packed cuboidal cells. These cells are filled with heavily keratinized cells and melanosomes. The cuticle is composed of keratinized squamous cells which forms the outermost layer of the hair shaft.

**Hair follicle:** The hair follicle is an epidermal invagination either deep (3 mm) into hypodermis or superficial (1 mm) within the dermis which contains hairs. The apical part of the follicle receives the sebaceous gland duct (Fig. 1). The hair follicles are divided into three zones: Infundibulum, isthmus, and inferior segment. The infundibulum is a part between the opening of sebaceous gland duct and opening of hair follicle

at skin surface. The isthmus lies between openings of sebaceous gland duct to the insertion of the arrector pili muscle. The inferior segment is a deeper part which expands to form bulb. The base of hair bulb encloses a bunch of vascularized loose connective tissue which is called dermal papilla.

**Alopecia areata:** It is an autoimmune disease in which there is a non-scarring hair loss without any structural damage of the hair follicle. Hair loss ranges from well-defined patches to diffuse hair loss. The scalp is mostly involved in patchy type hair loss. It affects approximately 2% of the general population. On examination of skin biopsies of the affected skin, it shows a lymphocytic infiltration in and around the hair bulb (Pratt et al. 2017).

## Arrector Pili Muscles

The arrector pili muscles are small bundles of smooth muscle cells. They lie between isthmus of hair follicles and the papillary layer of the dermis (Fig. 1). The sebaceous gland is located between the muscle and the hair follicle (Fig. 1). Therefore, contraction of muscles helps in secretion of the sebaceous gland contents. When these muscles contract, there is erection of the hair shaft to upright position and depression of skin at the site of attachment of muscle to the dermis. This leads to formation of gooseflesh appearance of skin. Arrector pili are absent in some places like facial and axillary hairs, eye brow and eye lashes, nostril hairs, and external acoustic meatuses.

## Sebaceous Glands

These are holocrine glands found in the dermis which secrete oily secretion (Fig. 1). They develop as lateral outgrowths of the outer root sheath of the hair follicle. They are part of pilosebaceous unit because they are associated with hair follicles and the arrector pili muscle. They are located over the whole body except the palms, soles, and flexor surfaces of digits. The meibomian glands at the margins of the eyelids

and ceruminous glands in the external auditory meatus are modification of this gland. In most part of the body, they release their secretory product through the hair follicles. But in some area of hairless thin skin, their ducts open directly on to the skin surface and release sebum, e.g., on the lips, nipples (Montgomery's glands), areolae of the female breast, glans penis, inner surface of the prepuce, clitoris, and labia minora. The number of sebaceous gland is an average of about 100/cm<sup>2</sup> of skin to 400–900/cm<sup>2</sup> in the face and scalp. The total time duration for sebum production from the time of basal cell mitosis to the secretion of the sebum is around 8 days (Pawlina 2016). Sebum acts as the epidermal barrier and pheromone, as well as also helps in the skin's immune system.

At birth, sebaceous glands are quite large, but further during development it regresses, and again, at puberty, its growth and secretory activity increases due to hormonal influence of androgens. At puberty due to androgen influence, there is excessive production of sebum. This disproportionate amount of sebum may become obstructed within the duct and leads to comedone formation. This may get infected and inflamed and leads to acne formation (Standring 2016).

Acne vulgaris: It involves the pilosebaceous unit. It may be either noninflammatory lesions (open and closed comedones) or inflammatory lesions (papules, pustules, and nodules). *Propionibacterium* acne is an important causative agent for acne. Other factor which may be related to acne are family history of severe acne, diet (chocolate and dairy consumption), smoking, occlusive cosmetics, and occupational exposures (Tan et al. 2017).

## Sweat Glands

There are two types of sweat glands in the body:

1. Eccrine sweat glands:-These are widely distributed over most of body surface especially on the forehead, palms, and soles. They are absent from the lips, tympanic membrane, nail bed, nipple, and part of the external

genitalia. Eccrine sweat glands are simple coiled glands which consists of two segments: A secretory segment located deep in the dermis and a long and less coiled duct segment that extends from the secretory segment to the epidermal surface (Fig. 1). It helps in temperature regulation of body by sweating under the influence of cholinergic system. It also acts as excretory organ because it excretes hypotonic watery solution which contains low amount of protein, sodium chloride, urea, uric acid, and ammonia. Eccrine sweat glands may also be activated in emotional condition under control of sympathetic nervous system.

2. Apocrine sweat glands: These are located in few places like the axilla, areola and nipple of the mammary gland, skin around the anus, the external genitalia, the ceruminous glands of the external acoustic meatus canal and the apocrine glands of eyelashes (glands of Moll). They take origin from the same downgrowths of epidermis from which hair follicles arise. Their ducts open in the hair follicle just above the entry of the sebaceous duct. Like eccrine sweat glands, apocrine glands are also coiled tubular glands, but the secretory portion of apocrine glands consists of wider lumen. Apocrine glands become functional at puberty due to development of axillary and pubic hairs. Apocrine glands secrete protein rich and milky fluid which contain pheromones. When secreted, the fluid is odorless, but later on due to bacterial action, it develops an acrid odor. Apocrine glands can be activated by emotional and sensory stimuli only under influence of sympathetic control.

## Nails

Nails are plates of keratinized epithelial cells of stratum corneum on the dorsal surface of distal phalanx which is composed of hard keratin. Each Nail consists of root, body, and free distal border. The nail root is implanted in a fold of epidermis and covers the cells of the germinative zone, or matrix. The matrix consists of stem cells which give rise to new cells at root and after

keratinization these cells are responsible for nail growth. The matrix extends beneath the body of nail as an opaque crescent-shaped white area called as the lunula. The edge of skin fold (stratum corneum) covering the root of the nail is called eponychium, or cuticle. The distal free border of nail is connected to underlying epidermis by hyponychium. The body of nail rest on a nail bed which consists of epithelial cells that are continuous with the stratum basale and stratum spinosum.

The nail apparatus consists of the nail plate, proximal and lateral nail folds, nail matrix, nail bed, and hyponychium (Standring 2016). The perionychium comprises the three nail folds (two lateral and one proximal) and the nearby nail bed.

Nail growth depends on the proliferating capacity of the matrix cells which is different in different digit, age, environmental condition, nutritional status, trauma, and various diseases. Generally, the rate of growth is directly proportional to the length of the digit, therefore it is fastest (approximately 0.1 mm per day) in the middle finger of the hand and slowest in the little finger.

### Clinical Correlation of Nail

1. Clubbing: In clubbing, both anteroposterior and lateral diameter of the nails are increased due to proliferation of connective tissue between nail matrix and the distal phalanx. In normal nail, the angle between the nail bed and the proximal nail fold is approximately  $160^\circ$ , but in the clubbing, there is increase in the normal angle  $\geq 180^\circ$  which leads to increase in convexity of the nail plate. It is an important clinical sign in some disease like bronchiectasis, lung abscess, lung carcinoma, cirrhosis of liver, cyanotic congenital heart disease, etc. (Sarkar et al. 2012).
2. Paronychia: It is an inflammation of the fingers or toes in one or more nail folds (Leggit 2017).
3. Koilonychia: In this condition, nails become spoon-shaped with concave curvature, i.e., central depression of nail with lateral elevation of nail plate. In iron deficiency, 5.4% of the patients shows koilonychia (Razmi et al. 2018).

## Embryology

The skin develops from the surface ectoderm and its underlying mesenchyme. The epidermis and its appendages are developed from the surface ectoderm. The dermis is derivative of mesenchyme and takes origin from three sources: (a) lateral plate mesoderm forms dermis of limbs and body wall, (b) paraxial mesoderm give rise to somites which forms dermis of the back, (c) dermis of the head is derived mostly from neural crest cells (-Sadler 2015). The mesoderm also forms the Langerhans' cells. Neural crest cells form melanocyte which imparts the skin its color, which migrate into the epidermis during epidermal development. Neural crest cells also form specialized sensory nerve endings (Hall 2018). Sebaceous glands, sweat glands, and mammary glands are developed due to epidermal proliferations.

## Vascular Supply of Skin

Cutaneous blood flow is about 5% of the total cardiac output (Standring 2016). It mainly helps in thermoregulation. The epidermis is avascular structure. Mainly blood vessels present in dermis which supply stratum basale of the epidermis and structure present within the dermis. The direct cutaneous, musculocutaneous, and fasciocutaneous systems give blood supply to the skin (Standring 2016). Numerous arteriovenous anastomoses are present in dermis which regulate blood flow through capillary bed and help in thermoregulation.

## Nerve Supply of Skin

1. Motor nerves: These are autonomic nerve fibers which supply blood vessels, arrector pili muscles, and sweat glands.
2. Sensory nerves: These are somatic nerve fibers which carry sensations from the skin by forming various types of sensory nerve endings. These are following:
  - (a) Free nerve endings in the epidermis terminate in the stratum granulosum and carry fine touch, heat, and cold sensations.

- (b) Pacinian corpuscles: They are present in deep dermis and detect pressure changes and vibrations applied on the skin surface (Fig. 1).
- (c) Meissner's corpuscles: They are present in dermal papillae and detect light touch sensation.
- (d) Ruffini's corpuscles: They are present in deep dermis and sensitive to skin stretch and torque.
- (e) Root hair plexuses: They are present around roots of hair follicles and detect movement by tactile receptors.

## Clinical Significance

1. **Atopic dermatitis (Atopic eczema):** It is chronic, pruritic, and inflammatory skin disorder that mostly effects children (Lee et al. 2016). It may relapse.
2. **Seborrheic dermatitis:** It most commonly involves the scalp as well as other seborrheic areas like face, retro-auricular area, and the upper chest. It commonly presents as itchy and flaking or scaling skin. Sebaceous secretions and fungal colonization may be associated with the disease (Borda and Wikramanayake 2015).
3. **Psoriasis:** It is an autoimmune disorder with genetic predisposition. Among the various skin manifestation, plaque-type psoriasis is the most common type (Rendon and Schäkel 2019). The classic clinical presentations of plaque psoriasis is well-demarcated, symmetric, and erythematous plaques with overlying silvery scale which mainly involve the scalp, trunk, buttocks, and extremities (Di Meglio et al. 2014).
4. **Pemphigus vulgaris:** It is an autoimmune disease in which autoantibody targets the intercellular proteins, desmosomes, which is responsible for binding of keratinocytes to each other. The desmosome destruction leads to the disruption of epidermal adhesion, resulting in flaccid blisters (Izumi et al. 2019).
5. **Bullous Pemphigoid:** It is another blistering disease in which linear deposition of autoantibodies along the dermal-epidermal junction

- that target the hemidesmosomes resulting in subepidermal tense blisters (Izumi et al. 2019).
6. **Skin Cancer:** There are three major types of skin cancer: (1) basal cell carcinoma (BCC), (2) squamous cell carcinoma (SCC), and (3) malignant melanoma. The BCC and SCC together are also known as nonmelanocytic skin cancers (NMSC). In general, skin cancers are related with long-standing unprotected exposure to the sun's ultraviolet radiation (UVR). Ultraviolet radiation causes DNA damage and genetic mutations, which result in skin cancer (Narayanan et al. 2010).

BCC is the most common skin cancer type that effects 80–85% of all NMSC. Basal cell carcinoma grows very slowly having good prognosis after surgical removal of the tumor. Superficial BCC mainly effects the most exposed area to sun's UVR and usually presents as a red, pearly translucent, scaly, little wrinkled and ulcerative lesion (Orthaber et al. 2017).

The second most common type of NMSC is SCC and effects 15–20% of all NMSC. People with SCC present a small red, painless nodule, scaling, and thickened patch on UVR exposed skin. Metastasis can occur after disruption of the basement membrane. It is more aggressive than BCC and causes death more frequently than BCC (Orthaber et al. 2017).

Malignant melanoma is the most serious and very rare form of skin cancer which developed in skin melanocytes. The characteristic features of malignant melanoma are (a) asymmetrical shape of skin lesion with irregular border, (b) color variations or multiple colors, and (c) diameter of skin lesion >6 mm (Pawlina 2016). Early stages, melanoma can be managed with surgery alone with good prognosis, but after metastasis, the prognosis is very bad (Davis et al. 2019).

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## Intellectual Abilities

### ► Platyrrhine Cognition

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## Intellectual Capacities

### ► Platyrrhine Cognition

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## Intellectual Functions

### ► Platyrrhine Cognition

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## Intellectual Processes

### ► Platyrrhine Cognition

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## Intelligence

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## Introduction

The question of animal intelligence has long been of human interest dating back to Plato, Aristotle, and Plotinus's notion of *scala naturae*, the natural order of organisms. Later, Romanes, a colleague



of Darwin's, published *Animal Intelligence* (1882) in which he reported collected anecdotes of animal behavior from pet owners and naturalists which suggested that many animals show intelligent behaviors. Romanes's approach tends to ask which human abilities are shared by other animals, but it suffers from the flawed logic exemplified by the cartoon depicted in Fig. 1. Given this bias, it is not surprising that animals that are more similar to us in their sensory, motor, and motivation systems are often judged by us to be more intelligent.

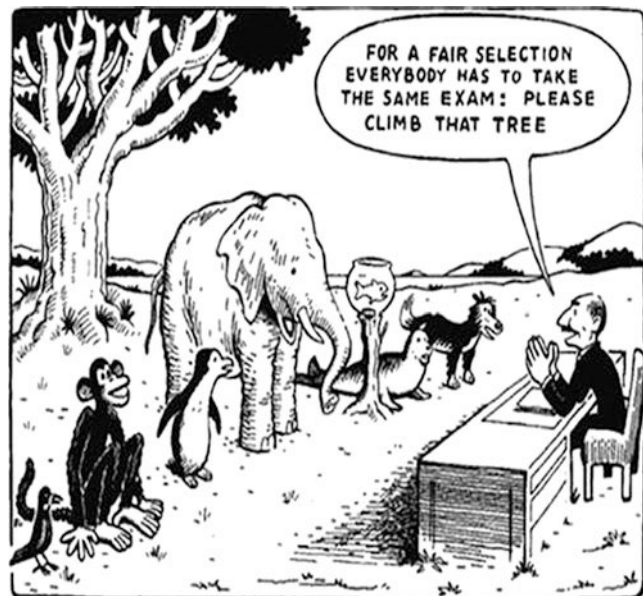
Alternatively, we could take a more evolutionary perspective like that proposed by Desmond Morris (1967) that intelligence is only one means of adapting to rapid environmental change. Other highly successful species such as bacteria and viruses have managed to survive without intelligence, as we know it, by very rapid asexual reproduction, relying on mutations to provide the variability needed to adapt to rapidly changing environments. Furthermore, it can be argued that intelligence per se is not correlated with a high rate of survivability. Consider the relatively small numbers of our ape and, even more broadly, primate relatives. Still more relevant, consider the number of hominid species that have gone extinct.

In general, surprisingly, there is a negative correlation between species intelligence and biological success (as measured by the number of surviving members of a species; Morris 1967).

With the above sobering recognition in mind and because of our interest in our species-centric comparisons, it would be informative to ask about the relative intelligence of other species. The easiest objective potential measure of intelligence would be the volume of the brain of various species. However, brain size is highly correlated with body size so relative brain to body mass or cephalization index would be a better measure of intelligence. Yet even that measure does not take into account the fact that what we consider to be intelligent behavior is regulated by activity in the neocortex (Lui et al. 2011) nor does it consider the fact that species such as birds need to minimize the weight of their brain as they must counteract the effects of gravity. Animals that live in water, however, can afford to have larger brains because the water tends to compensate for the effect of gravity. Thus, a better measure of intellectual potential might be number of neurons in the neocortex. This would appear to be a better correlate of intelligence, were it not for the fact that only mammals have a neocortex. To further

### Intelligence,

**Fig. 1** A visual illustration of the problem of presenting the same test to species with morphological differences



complicate matters, current theory suggests that what we consider to be human intelligence (e.g., the ability to reason) may be an epiphenomenon (Dunbar 1993). Instead, among primates at least, the high correlation between brain size and size of the social group suggests that the neocortex, from which we derive intelligence, evolved to keep track of the social interactions among members of our social group (e.g., those who cooperated with us and those who are freeloaders).

But what about species that do not live in well-integrated groups? One could argue that each species has evolved a brain best suited for its needs within the ecological niche in which it lives. That would mean that it makes little sense to compare the intelligent behavior of other species to our own. And yet, as psychologists we have been doing so for at least the last 150 years because we would like to know how intellectually similar other species are to us.

### Learning to Learn

One measure of intelligence is the degree to which learning is flexible, but we must be careful to assess the learning flexibility of other animals without biasing them by using sensory, motor, and motivational conditions that are most suitable to our own species. Bitterman (1975) has suggested that one can obtain a less biased assessment of the comparative cognitive abilities of species by assessing those abilities relative to the species' own baseline. That is, it may not be appropriate to assess differences in the rate of learning because that will depend on differences in sensory, motor, and motivational abilities. Instead, we might look at differences in an animal's ability to learn *from the experience of learning*. In other words, to what extent can learning facilitate new learning (*learning to learn*)? Then, using the rate of original learning as a baseline, one can determine the degree to which later learning, presumably involving the same processes, is facilitated. That is, how much faster the animal is at learning reversals as the number of reversals increase (i.e., to what extent can they learn to learn?). By this measure there is evidence that rats show more improvement than pigeons, and pigeons show more improvement than goldfish (Bitterman and Mackintosh 1969).

A different approach to learning to learn is to look for improvement in the rate at which discriminations involving *new* stimuli are learned. This phenomenon, known as learning set (Harlow 1949), has been studied primarily using visual discriminations with monkeys, but good evidence for such effects has also been found with olfactory discriminations with rats (Slotnick and Katz 1974). In the limit, learning of a new discrimination, or of a reversal, can occur in a single trial. When it does, it is referred to as a win-stay-lose-shift strategy because stimulus choice is completely controlled by the consequences of choice on the preceding trial. One means of developing such a strategy is to *learn to forget* the consequences of trials prior to the immediately preceding trial. In fact, research has shown that memory for the specific characteristics of the stimuli from prior discriminations does decline as the number of discriminations learned increases (Meyer 1971). Thus, animals approach optimal learning by learning to ignore the effects of all but the most recent experience.

### Relational Learning

According to Mackintosh (1965) animals learn not only which stimulus is associated with reward but also the relation between that response and others, such that with sufficient experience animals can learn about the underlying dimension along which the stimuli vary (e.g., brightness, color, auditory frequency, etc.). Mackintosh's theory provided an account of the paradoxical overtraining reversal effect. If rats are trained, for example, on a brightness discrimination, and are given additional training beyond the acquisition criterion, they are able to reverse the discrimination faster than controls that are trained merely to the acquisition criterion. This finding is of interest because according to more traditional theories of learning (e.g., Hull 1943), the buildup of habit strength should be monotonic with training. According to Mackintosh, however, those animals that were overtrained also learned to attend to the brightness dimension, such that when the discrimination was reversed and the formerly negative stimulus became positive, attention to the brightness dimension allowed the stimulus reversal to be acquired faster for animals that were

overtrained than for those that were trained to criterion.

In the sections that follow, I will examine the evidence that nonhuman animals have the capacity to develop cognitive abilities traditionally viewed as uniquely human. The list of phenomena covered is not meant to be exhaustive, but they are presented to demonstrate the large number of abilities that are not uniquely human. I will start with the ability to categorize stimuli, abilities that represent what humans often consider intelligent behavior.

### **Categorization or Stimulus Class Formation**

Can nonhuman animals learn to classify or group stimuli according to the category to which they belong?

#### **Perceptual Classes**

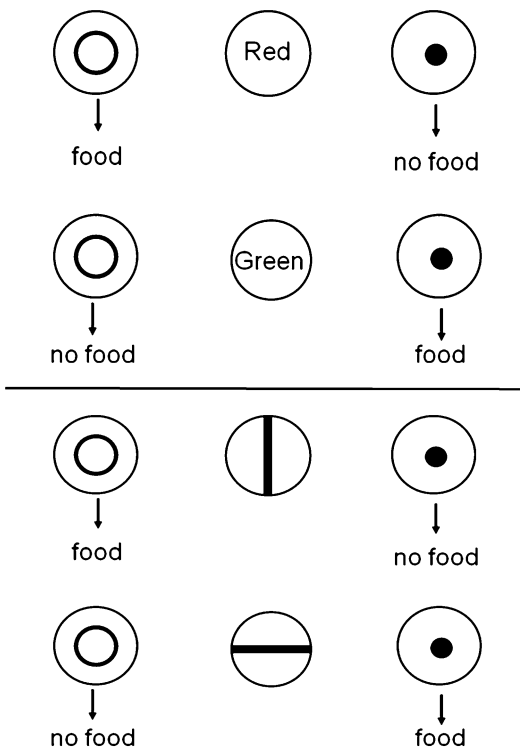
Pigeons are remarkably adept at responding selectively to photographs of natural scenes, depending on whether the scene involves a human form (Herrnstein and Loveland 1964) or trees or water (Herrnstein et al. 1976), and those objects need not be anything that they might have actually encountered in their past (e.g., underwater pictures of fish, Herrnstein and deVilliers 1980; cars and chairs, Bhatt et al. 1988; paintings by Monet and Picasso, Watanabe et al. 1995). To show that the pigeons did not simply memorize the set of stimuli, Herrnstein et al. presented the pigeon with novel instances of the category and found that they responded to them appropriately.

Although perceptual classes are sorted according to characteristics that they have in common versus those that are absent (consider the class of pictures that contain a human form), there is generally no specific set of characteristics that exemplify all of the members of the class. Even humans who can easily sort members of the class from nonmembers are hard pressed to specify the basis for the discrimination other than the name of the concept itself (person present versus absent). This suggests that the principle underlying this kind of stimulus class formation is complex and difficult to identify.

#### **Equivalence Classes**

A different kind of stimulus class formation involves the arbitrary association of stimuli that have a unique characteristic; what is learned about one or more members of the class transfers to the other members of the class. That is the ability to symbolically represent objects and events. The best example of human equivalence classes is the role that semantics plays in human language. When a word comes to mean the same as the objects that it represents, there is an equivalence relation between them such that what is learned about one member of the class automatically transfers to other members of the class. For example, if experience with dogs and the word dog form an equivalence class, new experiences with dogs will transfer to the word dog, and what one is told about dogs will transfer to the way one interacts with dogs. This powerful aspect of human language allows us to learn about the characteristics of objects without having to experience them ourselves or even observe others experiencing them. That is, one can learn about objects in their absence. Although generally, other animals are not known to communicate about the characteristics of objects not present, there is evidence that animals can form functional equivalence relations (see, e.g., Zentall and Smeets 1996). For example, given that pigeons acquire conditional discriminations (symbolic matching-to-sample) in which a red light and a vertical line are both associated with reinforced choice of a large circle and a green light and a horizontal line are both associated with reinforced choice of a small circle (see Figure 2), it can be shown that the red light and the vertical line form one equivalence relation and the green light and the horizontal line form another. The key to a functional equivalence relation is what is learned about one member of the class transfers without further training to other members of the class. Thus, if one is then trained to choose a white light when presented with the red light and to choose a blue light when presented with a green light, the equivalence relations can be demonstrated by asking if, without further training, the pigeons will choose the white light when presented with the vertical line and will choose the blue light when presented with the horizontal line. Clear evidence for such transfer of training has

### Matching-to-Sample



**Intelligence, Fig. 2** Many-to-one matching training used to show that pigeons will learn that *red* and *vertical* (as well as *green* and *horizontal*) “mean the same thing.” If *red* and *green* samples are now associated with new comparison stimuli, *blue* and *white*, respectively, there is evidence that *vertical* and *horizontal* line are also associated with the *blue* and *white* stimuli, respectively

been found by Urcuioli et al. (1989) (see also Wasserman et al. 1992). Thus, equivalence relations (or symbolic representation), the building blocks of semantics (a critical component of human language), is a form of intelligence for which even pigeons are capable.

### Same/Different Learning

A special case of stimulus class formation is the abstract concept of same/different learning. Given that animals have learned to “match” one set of stimuli (e.g., to select the circle not the cross when presented with a circle and to select the cross not the circle when presented with a cross), will they then be better able to match completely different stimuli (e.g., the colors red and green)? Although

early research suggested that pigeons are not able to show such generalized same/different learning (Cumming and Berryman 1961), later research showed that they have some ability to do so (Zentall et al. 1981; Zentall and Hogan 1976; see also Wasserman et al. 1995; Wright and Katz 2006).

### Memory Strategies

The task most often used to study working or short-term memory in animals is delayed matching-to-sample in which animals such as pigeons are trained to choose the red comparison not the green after seeing a red sample and the green comparison not the red after seeing a green sample. To assess working memory, following acquisition, a delay is inserted between the offset of the sample and the onset of the comparison stimuli, and matching accuracy is assessed as a function of the delay. This procedure generally underestimates the animals’ working memory capacity because not only is the delay a novel unexpected event that results in a generalization decrement, but often the delay is similar in appearance to the intertrial interval which may lead to an “instructional ambiguity” (see Sherburne et al. 1998). If pigeons are given sufficient training with delays, considerably better accuracy has been found (Dorrance et al. 2000).

Of more interest in the study of animal intelligence than the assessment of memory per se is the extent to which animals demonstrate strategies that maintain memory.

### Directed (Intentional) Forgetting

In human memory research, the role of the active maintenance of items in memory has been studied by telling human subjects that they should remember certain items but that they can forget others. When the subjects are later asked to recall all of the items, they typically are able to retrieve more of the items that they were instructed to remember than those that they were told they could forget. The finding has been taken as evidence that memory is an active rather than a passive (automatic) process. But what about other animals? Early

research with pigeons using a cued delayed matching-to-sample task suggested that they too actively retain sample memory (Grant 1981). Specifically, on some trials, a cue to remember was presented during the delay which was followed by presentation of comparison stimuli and reinforcement for a correct response. On other trials, a cue to forget was presented during the delay, and the trial ended following the delay. The problem with this design is there is differential incentive motivation on remember and forget trials because food can be obtained only on remember trials. In a more complex design that controls for motivational effects and that better approximates the human-directed forgetting procedure by allowing the animal to reallocate its memory from the sample to an alternative memory on forget trials in training, better evidence for directed forgetting in pigeons has been demonstrated (Roper et al. 1995). Thus, there is also evidence in nonhuman animals that memory is an active process.

### Episodic Memory

Human memory can be separated into categories according to the degree to which cognitive processes are involved. At the most automatic and least cognitive level is procedural memory, the memory for actions. Perhaps the best example of a human procedural memory that is different from other kinds of memory is learning how to ride a bicycle. It is procedural because although one learns how to do it, it is very difficult to describe how to do it. It is a kind of motor memory that requires trial and error, but even once it has been mastered, it typically defies description.

Declarative memories all involve memories that can be described. In human memory they are referred to as semantic memories because they describe learned facts or rules. When driving one should stop at a red light. The capital of France is Paris. Of course not all memories are purely procedural or semantic. For example, one may be told the posture one should take to hit a tennis ball, but over time it should become procedural, as one becomes proficient at the action.

Episodic memory is a kind of declarative memory that involves personal experience. In principle, to retrieve an episodic memory, one must

“mentally travel back in time.” If one is asked, what did you have for dinner last night, one would think back to the episode to retrieve the answer to the question. It has been argued by some (e.g., Tulving 2005) that humans are the only species that have episodic memory. Furthermore, there is some controversy as to what one should accept as evidence for episodic memory in a nonverbal organism. For example, Tulving (1972) originally proposed that an episodic memory should include the *what*, *where*, and *when* of an experience. Using this criterion, Clayton and Dickinson (1999) showed that western scrub jays that cached peanuts and wax worms (what) on one side or the other of an ice cube tray (where) learned that their preferred wax worms would be edible after 1 day but after 4 days only the peanut would be edible (when; see also Babb and Crystal 2006, for a similar finding with rats).

Alternatively, it has been argued that the *what*, *where*, and *when* of an experience are not sufficient because certain rule-based memories (e.g., historical facts) can satisfy those criteria. Instead, it has been argued that better evidence for an episodic memory would be the retrieval of a memory for a past event when, at the time of the episode, there would have been no expectation that a request to remember the event would be made (Zentall et al. 2001). For example, in the classic example, what one had for dinner last night typically would not be something that would have been encoded in memory for later retrieval. Instead, to retrieve that information, typically, one would have to “mentally travel back in time.” Stated otherwise, episodic memory involves the retrieval of events that have been incidentally encoded. According to this definition, evidence for episodic memory might be demonstrated if after being trained on a conditional discrimination (e.g., to choose the vertical line when the sample was yellow but choose the horizontal line when the sample was blue) animals were unexpectedly asked to recall the location of the comparison line last pecked (Singer and Zentall 2007; see also Zhou et al. 2012). The results of such research suggest that pigeons and rats have some ability to retrieve memory of episodes unlikely to be encoded as rules.



### Prospective Memory Processes

Traditionally animal memory has been viewed as a rather passive process. According to this view, sensory events can leave a trace that may control responding even when the event is no longer present (Roberts and Grant 1976). However, there is evidence that animals can also actively translate or code the representation of a presented stimulus into an expectation of a yet-to-be-presented event (Honig and Thompson 1982).

To get a feeling for what a prospective memory process might be like, imagine a pigeon trained on a delayed matching task with vertical and horizontal line sample stimuli and red and green comparison stimuli. One can then ask what is it that the pigeon remembers during the delay prior to the presentation of the comparison stimuli. The most obvious memory would be of the line that was presented as the sample stimulus, but it is also possible that the pigeon has translated the sample into a response intention (e.g., to choose the red comparison stimulus at the end of the delay). A response intention would be an example of a prospective memory. The ability to use expectations, or prospective coding processes, has important implications for the cognitive capacities of animals. If the expectation of a stimulus, response, or outcome can serve as an effective cue for comparison choice, it suggests that animals may be capable of exerting active control over memory, and, in particular, it may suggest they have the capacity for active planning. Although most research has found that pigeons remember the sample that was presented prior to the delay (Urcuioli and Zentall 1986), there is some evidence that under the right conditions pigeons can be induced to code memories prospectively (e.g., Jackson-Smith et al. 1993).

- i. *The differential outcome effect.* Strong evidence for a prospective memory process in animals is the differential outcome effect. This effect can be shown most simply in the acquisition of a conditional discrimination. If, for example, a correct response following one sample is followed by one kind of outcome (e.g., food) and a correct response following the other sample is followed by a different

outcome (e.g., water), acquisition of the conditional discrimination by rats is faster than if both correct responses are followed by food or by water (Trapold 1970). Furthermore, if one inserts a delay between the offset of the sample and the onset of the comparison stimuli, pigeons that have been trained with differential outcomes show less of a decrement in accuracy with increasing delays than if the outcomes are nondifferential (Peterson et al. 1980). Finally, and most convincingly, there is evidence from transfer-of-training experiments that in the absence of other cues, such as an appropriate sample stimulus, outcome anticipations can serve as sufficient cues for comparison choice. That is, if the original samples are replaced by other stimuli associated with the same differential outcomes, positive transfer has been found (Edwards et al. 1982; Peterson 1984). What is important about these experiments is that pigeons are making their choice based not only on their memory of the sample presented on the current trial but also (and in the case of the transfer of training experiments, exclusively) based on their expectation of the outcome that they anticipate will follow.

- ii. *Future planning.* One of the hallmarks of human cognitive behavior is our ability to consciously plan for the future. Although other animals appear to show similar behavior (they build nests and cache food for the winter), this behavior is clearly under genetic control. That is, if we had some way to ask a nest-building bird why it is building a nest, it would likely reply that it just has an urge to do so with little expectation of later use. Trial and error learning would not be reliable enough for such an important behavior. But even if learning was involved in a behavior that appeared to prepare the animal for the future and an animal could articulate why it was engaged in the behavior that will lead to a future reward, how would one distinguish between future planning and a long delay of reinforcement?

Suddendorf and Corballis (1997) have suggested that the behavior indicative of future planning must occur in the absence of the relevant

motivation. For example, will a sated animal work for food that it does not currently need but it has learned that it will likely need at a later time? In a review of the future planning literature, Roberts (2002) has suggested that monkeys do not appear to plan for the future. He cites several examples, including the anecdote that when monkeys in a zoo are fed once a day, after they have eaten, they often throw away the remaining food rather than keep it in anticipation of hunger later in the day.

However, evidence for future planning has been suggested by research with western scrub jays by Raby et al. (2007). These birds, which cache food for future use, learned that unpredictably, they would either spend the night in a side compartment in which in the morning they would find one kind of food (peanuts) or in a side compartment in which they would find a different kind of food (kibble). On test trials, the night before, they were allowed to first eat the provided food in a central compartment and then cache some of the remaining food in either side compartment. When they were given peanuts in the central compartment, they tended to cache the remaining food more in the kibble compartment, and when they were given kibble, they tended to cache the remaining food more in the peanut compartment. That is, in the absence of a current motivation for food, they cached the remaining food in the compartment in which they would not find that particular food in the morning. Thus, they showed the ability to anticipate where the current food would not be present and cache the current food there.

Although some animals appear to have the ability to plan for the future and also show evidence of episodic memory, it is clear that we humans engage in such activity to a much greater extent. In fact, it can be argued that we humans spend more time occupied in recovering past memories and in planning the future than we spend engaged in the present (Farb et al. 2007). One of the goals of meditation is to encourage humans to focus on the present, but in the absence of current task-related activities, it is not always easy to do (Chan and Woollacott 2007).

## Navigation

We humans are not known for our navigational skills, which explains our use of external supports such as compasses, maps, and global positioning devices. Other species, however, are able to navigate seasonally over hundreds, even thousands, of miles using a variety of mechanisms including magnetic fields, chemical gradients, and star patterns. Homing pigeons, unlike other species, are central place foragers, and they sometimes travel great distances in search of food and find their way back. Research suggests that the navigational tools that they use are complex including where the sun is in the sky, magnetic fields, and possibly odors (Wiltschko and Wiltschko 2003). They also use both natural and man-made landmarks (Lipp et al. 2004).

From a cognitive perspective, an interesting human ability is the use of cognitive mapping, the ability to imagine the pathway one should follow to get to a destination. With humans, one can study cognitive mapping by asking subjects to describe the route that they would follow to get to a goal. Alternatively, a nonverbal indirect means of assessing the ability to form a cognitive map can be obtained by asking if a subject can get to a familiar destination by means of a novel path when the familiar path is blocked. The ability to form a cognitive map suggests the knitting together of landmarks one has experienced, such that the relation among those landmarks can serve as the basis for understanding the direction one should take to arrive at the destination along a path that has never been taken. The idea is landmarks are needed to *form* a cognitive map, but they should not be needed to *use* a cognitive map.

Some animals have the remarkable ability to navigate in the absence of landmarks or other external cues. For example, desert ants use path integration or dead reckoning which involves the representation of direction and distance one has traveled from a starting point to food such that one can take a more direct path back to the nest than the often circuitous route taken on the way out. This ability can be demonstrated by displacing the ant after it has found food and is ready to return to its nest. When it is released, it sets off along a path

parallel to the appropriate path. Then it begins searching at an appropriate distance, had it started out from the location from which it had been displaced (Collette and Graham 2004). The distinction between path integration and cognitive mapping has been a point of controversy. However, under conditions that cannot be accounted for with either landmark use or path integration, there is evidence for the development of a simple cognitive map in dogs (Chapuis and Varlet 1987) and rats (Singer et al. 2007). That is, Singer et al. found that under conditions that would be unfavorable for the formation of a cognitive map but should be satisfactory for path integration, rats do not systematically choose the appropriate novel path, whereas when conditions are more favorable for the formation of a cognitive map, rats are more likely to choose the appropriate path.

## Counting

The term counting is used to describe what humans do when they assign numerical symbols to objects in a set. To qualify as counting, the order of the symbols is fixed (i.e., 1, 2, 3, . . .), but the symbol given to each object is not fixed, and the last symbol is also similar to the name of the whole set (e.g., the fifth object and five objects). There is evidence that chimpanzees can be trained to assign Arabic numerals to quantities of objects and even combine Arabic numerals demonstrating simple addition (Boysen and Berntsen 1989; see also Pepperberg 1987); however, most research with animals has involved numerical competence, a simpler process that might be differentiated from human-like counting by the ability to respond appropriately to the presence of a specified number of objects presented either simultaneously or successively (Boysen and Capaldi 1993).

An excellent review of the animal counting literature was provided by Davis and Memmott (1982), who concluded that “although counting is obtainable in infra humans, its occurrence requires considerable environmental support” (Davis and Memmott, p. 566). In contrast, Capaldi (1993) concluded that under the right conditions,

animals count routinely. In simple but elegant experiments, Capaldi and Miller (1988) demonstrated that following training, rats can anticipate whether they will get fed or not for running down an alley depending solely on the number of successive times they have run down that alley and found food or the absence of food on successive earlier trials (see also Rayburn-Reeves et al. 2010). That is, numerical competence is easier to demonstrate in animals if the events have importance to the animals (e.g., the number of times it has obtained food).

The difference in the conclusions reached by Davis and Memmott (1982) and by Capaldi and Miller (1988) has general implications for the study of intelligence in animals (including humans). As it turns out, the context in which one looks for a particular capacity may determine whether one will find evidence for it. Because we, as human experimenters, devise the tasks that serve as the basis for the assessment of intelligence, we must be sensitive to the possibility that these tasks may not be optimal for eliciting the behavior we are assessing. That is, much of our view of the evolutionary scale of intelligence may be biased in this way by species differences in sensory, response, and motivational factors.

## Reasoning

Reasoning can be thought of as a class of cognitive behavior for which correct responding on test trials requires an inference based on incomplete experience. One example of human reasoning is the transitive inference task (Piaget 1928). In its simplest form, transitive inference can be described as: if A is greater than B ( $A > B$ ), and B is greater than C ( $B > C$ ), then it can be inferred that A is greater than C ( $A > C$ ), (where the letters A, B, and C represent arbitrary stimuli). It is assumed that a correct response requires that an inference be made about the relation between A and C based on their common relation to B. With this version of the task, there is the possibility of a non-relational solution based on the fact that although A is greater than something, and B is greater than something, C is not greater than

anything. Thus, A must be the correct response. To avoid this non-relational solution, sometimes referred to as an end-point effect, experimental researchers typically use a task that involves four propositions:  $A > B$ ,  $B > C$ ,  $C > D$ , and  $D > E$ , and the test involves the choice between B and D, each of which is sometimes greater and sometimes lesser.

When the transitive inference task is used with animals, there is another problem. With humans, the task is presented verbally as relationships (e.g., Alice is taller than Betty, and Betty is taller than Carol – who is taller Alice or Carol?). That is, the stimuli are all presented relationally and do not have any absolute characteristics, such as size. Thus, the height of the stimuli (children?) is not specified, whereas with animals the stimuli must have absolute value (e.g., they must be presented visually). But if the stimuli differ in observable value, a correct response can be made without the need to make an inference because clearly B would be greater than D.

McGonigle and Chalmers (1977) suggested that a nonverbal relational form of the task could be represented by simple simultaneous discriminations in which one stimulus is associated with reinforcement (+) and the other is not (–).  $A > B$  can be represented as  $A+B-$ ,  $B > C$  as  $B+C-$ , and so on. With four propositions an animal would be exposed to  $A+B-$ ,  $B+C-$ ,  $C+D-$ , and  $D+E-$ . A is always positive, and E is always negative, but B and D, stimuli that were never paired during training, would share similar reinforcement histories. If animals order the stimuli from A is best to E is worst, then B should be preferred over D.

Findings consistent with transitive inference have been reported in research with species as diverse as chimpanzees (Gillan 1981), monkeys McGonigle and Chalmers (1977), rats (Davis 1992), and pigeons (Fersen et al. 1991). Before concluding that all of these species are capable of transitive inferences, one needs to ensure that there is not a simpler account of these findings. For example, Couvillon and Bitterman (1992) have suggested that the particular sequence of reinforced and nonreinforced responses to the target stimuli B and D may account for the preference for B. In training it may be that there were

more reinforced responses to B or more non-reinforced responses to D. To control for this possibility, Lazareva and Wasserman (2012) provided pigeons with a large amount of additional training with the  $D+E-$  pair and still found a preference for B. A second, non-inferential account was proposed by Fersen et al. (1991) who suggested that in a simultaneous discrimination, some of the value of the positive stimulus ( $S+$ ) will transfer to the negative stimulus ( $S-$ ) with which it is paired. Then because the always positive A stimulus in the  $A+B-$  pair has more value to give to B than the sometimes positive C stimulus (in the  $C+D-$  pair but sometimes negative C stimulus (in the  $B+C-$  pair has to give to D, B will be preferred over D (see also, Steirn et al. 1995). Weaver et al. (1997) tested this hypothesis with pigeons by using a procedure in training that equated the values of the A, C, and E stimuli. When they tested the BD pair, they still found a preference for B over D. Thus, pigeons have shown transitive inference results that to date are not easily accounted for by simpler mechanisms (but see Vasconcelos 2008).

## Perspective Taking

Sometimes called theory of mind, taking the perspective of others means one understands what others do and do not know. In the three mountain problem, for example, a child is placed on one side of a three-dimensional display with a doll on the other side, and the child is asked what the doll sees. Young children respond that the doll sees whatever they themselves see, but older children report what one would see from the other side of the display. To demonstrate perspective taking in animals is more complicated because in the absence of language, perspective taking must be inferred from other behavior.

Hare et al. (2001) attempted to study perspective taking by exposing chimpanzees to a food competition task in which a subordinate chimpanzee could see where food was placed and could also see either that a dominant chimpanzee did or did not see where the food was placed. They reported that the subordinate chimpanzee was

more likely to get to the food first if it could see that the dominant chimpanzee did not see where the food was placed. The presumption was that the subordinate got to the food because it knew that the dominant did not know where the food was placed. It is possible, however, that if the dominant chimpanzee knew where the food was placed, it would be staring at the food, and the subordinate chimpanzee would tend to avoid the location where the dominant chimpanzee was staring. That is, the dominant chimpanzee provided a cue at the time the subordinate chimpanzee was released.

## Self-Recognition

Recognizing the image of oneself in a mirror is an ability that was traditionally viewed as a human quality until in a carefully controlled experiment Gallup (1970) demonstrated that chimpanzees also have that ability. Gallup developed what has been referred to as the mark test for self-recognition. After considerable exposure to a mirror, a mark is placed on the face of the chimpanzee, and when the mirror is reintroduced, the chimpanzee passes the mark test by making contact with the mark that can only be seen in the mirror. Mirror-directed mark exploration appears to occur generally in the great apes (orangutans and perhaps also in gorillas) but not in monkeys even with extensive mirror experience (Gallup and Suarez 1991). However, more recently evidence has been found for self-recognition in dolphins (Reiss and Marino 2001), elephants (Plotnik et al. 2006), and magpies (Prior et al. 2008). Thus, self-recognition appears to occur in several non-primate species also thought to show other kinds of cognitive skills.

## Imitation

According to Piaget (1951) perspective taking has been implicated in the ability to imitate the behavior of another. But imitation can refer to a broad range behavior much of which would not necessarily involve perspective taking. For example, the finding that a sated animal will begin eating

again if placed in the context of another animal that is eating would more parsimoniously be considered an example of behavioral contagion (Zentall 1996). And it is possible that the mere presence of another animal may increase the arousal or motivation of a focal animal leading to the more rapid acquisition of a target response such as pressing a lever (social facilitation, Zajonc 1965). Furthermore, in some cases observation of a conspecific performing a response may demonstrate the affordances of the environment (e.g., the downward movement of a lever is followed by the arrival of a reward, learned affordances (Klein and Zentall 2003).

The two-action procedure was developed to provide a control for these alternative forms of copied behavior (Zentall et al. 1996). In the two-action procedure, observers are exposed to a demonstrator performing a response in one of two topographically different ways (e.g., a bird stepping on a treadle or pecking at the treadle). Imitation is said to occur if the observer performs the response in the same way that it has seen it performed (Akens and Zentall 1996). There is even evidence that pigeons can imitate a sequence of two responses, operating a treadle (by stepping or pecking) and pushing a screen (to the left or to the right; Nguyen et al. 2005), an example of what Byrne and Russon (1998) refer to as program-level imitation.

Can one conclude from this evidence for imitation that these observer birds can take the perspective of their demonstrators? Although logically one could argue that perspective taking is likely involved, children do not develop the ability to take the perspective of another until they are 5–7 years old, yet they are able to imitate others at a much earlier age. Thus, although cognitively interesting, imitation may not provide evidence for the kind of cognitive behavior implied by perspective taking.

## Tool Use

When we consider tool use, we tend to think of it anthropocentrically, and examples that come to mind involve primates that have opposable thumbs. Thus, there is evidence that chimpanzees



use tools when they collect a flat rock and use a second rock that can be held in the hand to break the shell of a nut by hitting it as it rests on the flat rock (Boesch and Boesch 1990). Similarly, when a chimpanzee fashions a flexible stem from a plant and chews on the end to spread it out before sticking it into the hole in a termite hill, it is using a tool to collect termites to eat (Fay and Carroll 1994). Similarly, when a sea otter swims to the bottom to collect a rock and a sea urchin, and at the surface hits the sea urchin against the rock placed on its chest, it also qualifies as tool use. Less obvious is the sea gull flying with a clam to drop it onto rocks to break open the clam (Cadée 1989). Although the tool (the rock) is not actually manipulated, some would argue that it functions as a tool because it consists of an external object used to help the animal gain a desired end (Beck 1980). More compatible with what we consider to be similar to human tool use is the use of twigs by New Caledonian crows to pry grubs free from holes in dead logs (Hunt 1996).

However, when considering intelligent behavior, we try to distinguish between tool use that might be genetically predisposed or species typical and tool use that has been arrived at through problem-solving or reasoning. Weir et al. (2002) found that New Caledonian crows can learn to use a bent piece of wire to hook the handle on a small food bucket that has been placed at the bottom of a tall cylinder. Such a task would not have been encountered in nature nor would bendable wire hooks have been available with which to retrieve the bucket. Even more remarkable, when the bent wire was not available, one crow managed to bend the wire into a hook that could then be used to retrieve the bucket.

## Language

Many species communicate naturally. They give calls to warn others of the presence of predators (Charnov and Krebs 1975), to attract a mate (Ballentine et al. 2004), and to defend their territory (de Kort et al. 2008). Honeybees are even able to communicate about the location and amount of resources that they have found (Gould 1974), and vervet monkeys are able to

communicate about the *kind* of predator that they have seen, an ability that indicates what kind of evasive action their troop-mates should take: climb high in a tree if the predator is a large cat, hide in the bushes if the predator is a bird of prey, or rear on their hind legs to locate the danger if the predator is a snake (Seyfarth et al. 1980). But humans are the only species that naturally acquire a complex form of communication known as language.

What makes a language different from communication is it can refer to objects and events not currently present, and it combines symbols in complex ways that makes the order of the symbols important (the quality of syntax or grammar) and production (the ability to communicate about things for which one does not already have a symbol, e.g., a chimpanzee named Washoe signing “water-bird” upon seeing a swan).

Although humans are the only species that has naturally developed what we refer to as language, several projects have trained chimpanzees in various forms of symbol use that approximate language. The earliest of these was using American Sign Language with Washoe (Gardner and Gardner 1998), and that project demonstrated that she was able to learn a large vocabulary. A different approach using plastic symbols for words focused on objects, their properties, and object categories (e.g., same/different) was developed by Premack and Premack (1983). A third project introduced syntax, a quality thought to be missing from the other two projects (Savage-Rumbaugh et al. 1998; see also Herman et al. 1984, using dolphin subjects). Interpretation of the results of these projects as examples of language acquisition remains somewhat controversial (see e.g., Terrace 1979). At the very least, however, those projects have forced us to better define what it is that makes language unique.

## What Animals Can Tell Us About Suboptimal Human Behavior?

Certain behaviors may not qualify as intelligent or rational but because they are prevalent in humans and have been attributed to the unique experiences of humans, if they can be found in other species,

they have implications for the understanding of human biases and heuristic behavior.

### Cognitive Dissonance

One of these biases has to do with a phenomenon widely studied in humans known as cognitive dissonance. Cognitive dissonance is the discomfort that comes when there is a discrepancy between one's beliefs and one's behavior. For example, if one believes that one should tell the truth, one is likely to feel dissonance on occasions when one fails to do so and one can resolve that dissonance by finding reasons to justify lying. Cognitive dissonance can be attributed to the need humans have to be considered consistent. Cognitive dissonance has been considered to be a form of social intelligence (Festinger 1957), and it is difficult to imagine how one would go about studying it in animals.

One approach would be to examine a form of cognitive dissonance called *justification of effort* (Aronson and Mills 1959). Justification of effort is the added value that one often gives to rewards depending on the effort required to obtain the reward. For example, rewards that are difficult to obtain are often valued more than the same rewards that are easy to obtain. One way to study this effect in animals is to require an animal to work hard for Signal A for a reward and not so hard for Signal B for the same reward and then ask the animal which signal it would prefer A or B. Clement et al. (2000) found evidence for such an effect in pigeons which showed a preference for stimuli that they had to work harder to obtain (see also Kacelnik and Marsh 2002). But is there a simpler explanation?

Zentall and Singer (2007) suggested that this choice behavior may result from the contrast between the relatively negative emotional state of the organism at the end of the greater effort and presentation of the reinforcer (or upon presentation of the signal for reinforcement). Thus, contrast may provide a more parsimonious account of the pigeons' choice behavior. There is also evidence that contrast plays a role in the justification of effort effect found in humans (Alessandri et al. 2008; Klein et al. 2005; Lord 1992). Could contrast also play a role in the more

general cognitive dissonance phenomenon found with humans?

### Suboptimal (Gambling-Like) Behavior

When humans buy lottery tickets or operate slot machines, they are engaging in suboptimal behavior because the return on the bet is typically less than the bet. Humans justify their decision to gamble by describing it as a source of entertainment, and although it is difficult to show that gambling is not entertaining, if one were to remove the monetary aspects of the gamble, it is not as likely that those people would be willing to engage in the activity.

An alternative approach to the question of whether entertainment is the basis of human gambling behavior would be to ask if other animals are as likely to engage in suboptimal gambling as humans. According to optimal foraging theory (MacArthur and Pianka 1966) generally, animals have been selected by evolution to make optimal choices (so they would be more likely not to engage in gambling behavior).

This hypothesis has been tested in a number of experiments, and results quite similar to those with humans have been found. For example, pigeons were given a choice between two alternatives: the gambling alternative in which there was a 20% chance of receiving a green light that predicted they would receive ten pellets of food (the "jackpot") and an 80% chance of receiving a red light that predict they would receive no food (the loss) and the nongambling alternative in which they received a signal that they would always receive three pellets of food (Zentall and Stagner 2011). The results indicated that the pigeons showed a strong preference for the gambling alternative even though they would have received 50% more food for choosing not to gamble.

The mechanism responsible for this suboptimal behavior appears to be the fact that the signal for nonreinforcement fails to gain the inhibitory value that one would expect (Stagner et al. 2012). Thus, the ten-pellet signal for reinforcement is judged to be better than the three-pellet signal for reinforcement, irrespective of the lower frequency of its occurrence. A more direct test of this hypothesis was conducted by Smith and

Zentall (2016) who had pigeons choose between a 50% chance of receiving a signal for 100% reinforcement and a 100% chance of receiving a signal for 100% reinforcement. Once again intuition would predict that the alternative that provided reinforcement 100% of the time should be preferred but given that the two signals for reinforcement, once they occurred, predicted reinforcement equally, the pigeons were indifferent between them. This account appears to be consistent with research with humans that has found that gamblers overvalue wins in spite of their low probability of occurrence, and they give too little negative value to their losses, in spite of their high probability of occurrence (Blanco et al. 2000). These results suggest that gambling behavior is likely to have a simple biological basis and although social and cognitive factors may contribute to human gambling behavior, the underlying mechanism is likely to be simpler and characteristic of other animals as well.

### Sunk Cost

The sunk cost effect occurs when one allows an amount of money, time, or other resources already invested in an activity to affect one's decision to invest more resources. For example, one may sit through a film that one does not like because to leave would be to waste one's investment of the price of the ticket. But there is no way to recoup that already expended cost of the ticket, and by continuing to sit through the film, one is spending additional resources and time that could be better spent in other activities. Similarly, although economists generally warn against it, one may choose to continue with a failing business because of the past investment one has made in it.

This phenomenon comes under the general rubric of prospect theory (Kahneman and Tversky 1979) which suggests that humans will take greater risks to avoid a loss than to obtain a gain. The question is to what extent does this behavior stem from the cultural tenet to avoid wasting resources and to complete what one has started. If one could show that animals, such as pigeons, show the same behavior, it would suggest that sunk cost is a general phenomenon that has basic behavioral origins.

In fact, evidence for sunk cost has been found in pigeons (Navarro and Fantino 2005; Pattison et al. 2012). For example, pigeons learn that pecking a green light requires 30 pecks, whereas pecking a red light requires only 10 pecks. They then learn that after pecking the green light a number of times (that varied from trial to trial), they would be able to choose to continue with the green light (to complete the 30 pecks) or switch to the red light for which 10 pecks were required. Results indicated that the pigeons often chose to return to the green light even when 20 more pecks are required. Thus, pigeons show a sunk cost effect that is very similar to that shown by humans. Why pigeons show the sunk cost effect is not clear. One can speculate that it arises from the fact that in nature switching to a different *patch* often involves uncertainty, some travel time, and possible danger. In any event, one can conclude that culture and language are not necessary components.

### When Less Is More

When humans are asked to judge the value of a set of objects of excellent quality, they often give it higher value than those same objects with the addition of some objects of lesser quality (Hsee 1998). It has been found when humans are asked to judge the value of sets of dishes or sets of baseball cards (Hsee 1998), and it also has been found when academics are asked to judge the quality of a curriculum vita (Hayes 1983). For example, a vita with three publications in excellent journals is judged better than one with the same three publications in excellent journals plus six more in lesser-quality journals. This bias is an example of the affect heuristic in which humans appear to judge the average quality of a set of objects to determine the value of the set rather than the total number of objects in the set. The phenomenon has become known as a less is more effect.

Recent evidence suggests that even pigeons are susceptible to this bias. For example, pigeons will work for dried peas and dried milo seeds, but when given a choice between the two, they prefer the peas. However, when they are given a choice between a pea and a pea together with a milo

seed, they prefer the pea alone (Zentall et al. 2013). Apparently, the pigeons, too, are averaging the high-quality pea with the lower-quality milo seed and value the pair less than the pea by itself. Similar results have been found with monkeys (Kralik et al. 2012) and dogs (Pattison and Zentall 2014). The basis of this bias may originate in the need to make rapid decisions, presumably because of intense competition from conspecifics and the possibility of predation, and they use this heuristic in the laboratory even when speed is not a factor. Once again, the fact that other animals show this sub-optimal choice indicates that the bias is probably not dependent on human cultural influence.

## Conclusions

The broad range of positive research findings that have come from investigating the cognitive abilities of animals suggests that many of the “special capacities” attributed to humans may be more quantitative than qualitative. In the case of many cognitive learning tasks, once we learn how to ask the question appropriately (i.e., in a way that is accommodating to the animal), we may often be surprised with the capacity of animals to use complex relations.

In evaluating the animal (and human) intelligence literature, we should be sensitive to both the overestimation of capacity (what appears to be higher level functioning in animals that can be accounted for more parsimoniously at a lower level; see Zentall 1993) and the underestimation of capacity (our bias to present animals with tasks convenient to our human sensory, response, and motivational systems). Underestimation can also come from the difficulty in providing animals with task instructions, an aspect of the assessment of intelligence that is often underappreciated (see Zentall 1997). The accurate assessment of animal intelligence will require vigilance, on the one hand, to evaluate cognitive functioning against simpler accounts and, on the other hand, to determine the conditions that will maximally elicit the animal’s cognitive capacity.

The study of human biases by examining animals for the presence of similar phenomena in

animals can also help us to determine if simpler mechanisms are involved. Thus, the study of animal intelligence not only can inform us of the cognitive abilities of animals but also can suggest the bases of certain human phenomena thought to have complex social origins.

## Cross-references

- ▶ [Arthropod Cognition](#)
- ▶ [Bovine Cognition](#)
- ▶ [Conservation](#)
- ▶ [Discrimination Learning](#)
- ▶ [Divided Attention](#)
- ▶ [Episodic Memory](#)
- ▶ [Imitation](#)
- ▶ [Meta-Cognition](#)
- ▶ [Platyrrhine Cognition](#)
- ▶ [Problem-Solving](#)
- ▶ [Problem-Solving](#)
- ▶ [Reasoning by Exclusion](#)
- ▶ [Relational Concepts and Symbolic Logic](#)
- ▶ [Same/different Learning](#)
- ▶ [Stuck-in-time Hypothesis](#)
- ▶ [Theory of Mind](#)
- ▶ [Timing](#)
- ▶ [Tool Use](#)
- ▶ [Transfer of Learning](#)
- ▶ [Transposition](#)

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## Intentionality

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## Definitions

The term “intentionality” has two related but different meanings. One, normally associated with psychology, refers to the ability to act

purposefully or deliberately, guided by intentions in the sense of mental representations of goals. The second, associated with philosophy, refers to the property of mental states to be about an object or be directed to a content – we do not simply perceive or think: we see something, think about something, or desire something.

The psychological meaning is more restricted: it applies only to particular types of mental states with a goal or purpose. The philosophical sense includes the psychological one (all purposeful intentions are about something) but extends to all other mental states. For example, we may accidentally hear or see something. This is unintentional in the psychological sense, but intentional in the philosophical one, since our accidental perception has a content, is *about* something.

## Intentionality as Aboutness

The philosophical sense was proposed by the philosopher Franz Brentano to capture the fundamental property of mental phenomena that distinguishes them from physical phenomena. For Brentano, mental phenomena cannot exist on their own but are always “directed at” something and have a content different from themselves. This content needs not be a real object – it can be an imaginary or nonexistent one, like thinking of a unicorn or of an event that has not yet happened (e.g., an impending trip). The objects of mental states therefore may exist only “intentionally,” i.e., in the mind of the thinker (Crane 1998).

Dennett (1983) introduced this sense of the term to comparative psychologists and ethologists with a proposal to adopt the “intentional stance” in animal psychology, i.e., to describe animal behavior in mentalistic (intentional) terms: animals as agents that desire, believe, know things, etc.

He proposed a schema with different levels of potentially recursive intentionality to think about animal behavior. A zero-level intentionality account would correspond to reflex-like or conditioned reactions where animals have no anticipation or representation of the world but just act as some sort of automata responding to stimuli. For instance, to use Dennett’s own example about vervet monkeys’ alarm calls, at *zero-level*

intentionality, a monkey responding to the presence of a leopard with the leopard alarm call, or a monkey reacting to the call with the appropriate escape response, would be merely engaging in reflex reactions devoid of understanding or representation. With *level 1 intentionality*, monkeys would call because they *perceive* a predator and thereby give the alarm, maybe with the purpose (intentional in the psychological sense) that the other monkeys escape. With *level 2 intentionality*, monkeys would in addition represent others' knowledge or desires, for example, they could "intend" that the other monkeys "notice" the predator and run away. This level ascribes to animals a "theory of mind" ability – the ability to entertain mental states about mental states (see below). With *level 3* of intentionality, they would, for example, *intend* to make another animal *know* that they *want* them to go away or that they have *seen* a predator and so on. For some this latter level 3 would be the minimum required for communicative intentionality (see later).

Although Dennett's schema was proposed from the wider philosophical meaning of the term (intentionality as aboutness), it is frequently used by psychologists with the more specific meaning of intention as goal-directedness, especially in discussions of animal communication.

Dennett offered his "intentional stance" approach not as an "a priori" explanation of animal behavior but as a tool to help frame empirical questions, for example, designing experiments to probe at what level of intentionality vervet monkeys produce their alarm calls. Some expressed concern that such liberality in cognitive terminology may lead to unsubstantiated mentalistic claims about animal behavior if based on purely observational evidence, defending experimental evidence as the sole reliable empirical source to probe animal intentionality (Heyes and Dickinson 1990).

### Intentionality as Purpose

In psychology the more frequent sense of intentionality is as purpose, i.e., the ability to mentally represent goals and the means to achieve them through goal-directed, deliberate behaviors. In comparative psychology intentionality in this

sense has always been at the heart of disputes between reductionist, mechanistic stimulus-response models and cognitive interpretations of animal behavior based on teleological models of causation (Dickinson 2011).

Early comparative psychology (e.g., Romanes and his followers) was liberal in uncritically attributing to animals intentions and purposes among other mental states. However, the advent of behaviorism at the beginning of the twentieth century, both in its American (e.g., Thorndike, Watson) and Russian (Pavlov) strands, questioned the use of such mentalistic, folk-psychological notions in the scientific study of animals and even humans (Boakes 1984).

The behaviorist account was that purposeful behaviors could be explained as caused by acquired stimulus-response (S-R) associations. For example, a rat in a Skinner box pressing the lever could be folk-psychologically described as "acting with the intention to get food from the feeder." However, the behavioristic explanation is that rats are caused to press the lever by their past learned associations between the physiological state of hunger, objective discriminative stimuli, and the appearance of food. Rats press the lever not *in order to* get food but *because* they got food in the past. Operant conditioning works analogously to natural selection – through "selection by consequences," the former in the lifetime of individual organisms, the latter in phylogenetic time. In the same way that animal morphological features may appear to be designed with a purpose, when in fact they are the result of blind natural selection, acquired behaviors that appear to be purposeful may be the result of selection by contingencies of reinforcement (Skinner 1981).

The underlying epistemological concern is that purposeful or teleological explanations proceed from the future to the past, instead of explaining the future from past and current causes. This would be a logical impossibility, as the future has not yet occurred. Against this concern, one could argue that it is not the future itself that causes behavior but a representation of (possible) future events, i.e., a current state of the nervous system that is itself caused by past and current events.

Early challenges to behaviorism's dismissal of intentionality came from Gestalt psychologists studying animal problem solving (Köhler 1921). They proposed the notion of insight to describe the way in which chimpanzees solve problems. This notion assumes that behavior is intentional and goal-directed, as animals select and organize their responses to problem situations through an intention to reach the target which dominates the perceptual and behavioral field. Intentionality of action is a cornerstone of notions of insight and practical intelligence.

From within behaviorism itself, there were also attempts at accommodating notions of purposeful behavior. The most important was Tolman's "purposeful behaviorism," which was partly an attempt to reconcile behaviorism with aspects of Gestalt psychology (Tolman 1932). Tolman proposed that behavior should not be analyzed at the S-R level but at a more molar level, one where the key organizational component of behavior is the goal or purpose of the action, which controls the behaviors selected by organisms in different situations. His aim was to provide objective, scientific, non-mentalistic definitions of purpose and other cognitive notions. Tolman's approach has influenced modern behaviorist approaches in which notions of goal-directedness and intention are accepted and operationalized, but in the 1940s and 1950s, they were not the mainstream behaviorist approach to animal behavior.

## Intentionality and Goal-Directedness

With the advent of the cognitive revolution in psychology and related disciplines in the 1960s, notions of purpose and intentional action returned to the forefront in the study of human and animal behavior (Miller et al. 1960). In the 1940s–1950s, the new discipline of cybernetics (Wiener 1948/1961) had showed that notions of goal-directedness and purpose were necessary to explain the behavior of mechanical devices with negative feedback loops that allow for self-correction until a goal state is achieved (e.g., a self-guiding missile). It seemed unsustainable to keep avoiding in psychology notions that were

useful in explaining the behavior of mechanical devices. Cybernetics provided objective models of intentional action that could be applied to human and animal behavior. Stimuli not simply trigger responses but activate mechanisms controlled by feedback loops, one of whose key components is some internal instantiation of goal states and an ability to evaluate provisional outcomes against set goals and change behavior accordingly.

Animals started to be seen as "goal-seeking agents that acquire, store, retrieve and internally process information at many levels of cognitive complexity" (Menzel and Fischer 2011, p. 2). Accounts of natural and captive animal behavior started to use again notions of purpose, as part of a broader "intentional stance" (Dennett 1983; see above). There was, however, concern that the attribution of intentionality should not become an uncritical default assumption for animal behavior without appropriate experimental scrutiny. For example, Dickinson proposed that intentional goal-directedness exists only when behavior is controlled by "knowledge of the instrumental relation" between actions and their associated consequences, in contrast with mechanical stimulus-response associations that, once learned, are automatically triggered by the presence of stimuli (Dickinson 2011). He argued that goal-directed behavior in rats is empirically demonstrated by the finding that, after learning to press a lever to get food through ordinary operant conditioning, they become less likely to respond if an aversion to that type of food is separately established. When placed again in the original training room, rats do not automatically react to the stimuli by pressing the lever. Their knowledge of the instrumental relation between lever pressing and food delivery modulates their response in view of the now aversive value of the goal.

## Criteria of Intentional Action in Nonverbal Organisms

Defining intentionality as goal-directed behavior has the potential advantage of objectivity – it is possible to appeal to observable features of behavior and use mechanical devices as objective models of intentionality, which may in principle



be investigated independently of the question of consciousness (Burghardt 1991).

Like animal psychologists, developmental psychologists studying preverbal infants face a similar challenge in defining and identifying intentionality. Piaget (1936) made the ability to coordinate schemas of action in increasingly complex means-ends structures a pillar of infant sensorimotor intelligence during the first 2 years of life – from simply holding an action (grasping an object) until another act (pushing aside an obstacle) makes it viable to the innovative use of tools as intermediaries to reach goals. Piaget defined intentionality behaviorally as “the differentiation between means and ends,” but he also emphasized that cognitively this differentiation resulted in an “awareness of desire or the direction of actions, with this awareness itself being a function of the number of intermediary actions needed for the main act” (Piaget 1936).

Bruner (1973), building on cybernetics-inspired notions of goal-directedness, proposed a set of behavioral criteria to identify intentional action in preverbal infants. These included anticipation of outcomes, cessation of means deployment when the end state is achieved, and continuation with selection of alternative means when the goal is not achieved. Some of these criteria may themselves require further specification and operationalization. Developmental and comparative psychologists typically use variants of these criteria to identify intentional action in nonverbal organisms.

### Is Intentionality the Same as Goal-Directedness?

Some authors have proposed more nuanced distinctions. For example, McFarland (1989) distinguishes between goal-achieving, goal-seeking, and goal-directedness. Goal-achieving and goal-seeking systems behave in such a way that an end state is reached by virtue of the physical forces at work in a given system, but there is no representation of the goals. For example, a ball thrown spinning into a bowl will always reach the minimum down point, as if “seeking” it, but there is no representation of the end point guiding the ball, just an inevitable end outcome given the mechanics of the ball and the physical situation.

Genuine goal-directedness, for McFarland, requires an explicit representation of the goal, and when this representation is mental, then we have intentional behavior. McFarland warns that most instances of apparent goal-directed and intentional behavior in animals may in fact be explained as goal-achieving or goal-seeking and that this might be the case also for humans, even if through introspection we may believe ourselves that a given action is intentional.

For many a hallmark of intentionality is still the awareness and mental representation of the goal (and the means) that may precede and guide the execution of goal-directed actions. The intentionality displayed by living organisms may be different to mechanical goal-directedness. Intentionality with explicit representations of goals and means may allow for more flexible adaptive responses, as in the above example of the rats refraining from pressing the lever when they separately learn that the food is now aversive. However, defining what counts as explicit versus implicit representations of goals may prove to be challenging, as part of the more general problem of characterizing implicit vs. explicit knowledge (Gómez et al. 2017).

One advantage of intentionality is behavioral flexibility – the same goal can be pursued with alternative means adjusted to different circumstances. The particular means displayed by any given organism may depend upon their understanding of the causal structure of the situation (e.g., a chimpanzee or a corvid confronted with an out-of-reach reward may display tool use, whereas other animals may just try to find alternative routes to approach it). Definitions of intentionality tend to emphasize the representation and awareness of the goal; however, awareness and representation of the means and their causal relation to the goals are an equally important component. This might be a criterion to distinguish mere goal-directedness or goal-seeking from intentionality. The essence of intentionality as purpose lies in the representation and coordination of both means and ends.

### Planning

Mentally representing goals and means may allow to *think* about how to reach goals when they are

not immediately available and to keep them in mind while performing the indirect behaviors required to get them. Planning – thinking of means to a goal before being in a position to execute them – is a complex example of intentionality. It is contentious how much advanced planning animals are capable of and in how much detail they can represent goals and means before executing goal-directed actions.

In insight tasks it is frequently discussed to what extent the steps of a solution are planned in advance. For example, crows pulling a string to get food attached at its end may proceed through a loop of perceptual-motor feedback where the act of pulling is reinforced and maintained by the sight of the approaching reward. This perceptual-motor feedback explanation assumes goal-directedness but denies planning – a mental representation of the solution guiding the behavior of pulling – because crows without access to immediate visual feedback of the approaching reward stop pulling without realizing that perseverating will eventually get them the reward (Taylor et al. 2012).

Experiments on episodic memory and prospective planning show that apes may secure tools well in advance of being in the situation where they can use them (Osvath and Osvath 2008). For example, apes can take with them a tool that they will not be able to use to get food until much later and in a different room. They can even do this overnight, which suggests a robust ability to plan goal-directed actions in the future irrespective of their direct execution and without immediate direct feedback.

There is probably no sharp divide between pure goal-directedness in sensorimotor systems (which, one could argue, may not require explicitly represented intentions to guide behavior) and pure offline representational planning separated from active implementation but a continuum of possibilities where both may be combined to different degrees.

## Intentions About Intentions: Theory of Mind

Intentionality, both in the philosophical and psychological senses, is related to the problem of

whether animals are capable of attributing mental states to others. In Dennett's schema (1983), this involves having intentions about intentions – second-order intentionality. Intentionality as purpose featured in Premack and Woodruff's (1978) pioneering paper that introduced the notion of theory of mind. They asked if a chimpanzee watching a human stretching his arms toward a bunch of inaccessible bananas would just code the physical characteristics of the movements or also the underlying intention giving sense to the behavior – the goal of obtaining the bananas. They concluded that chimpanzees attribute intentions because, after watching videos of a human trying to solve problems like this, their subject was able to select photographs depicting correct solutions (e.g., the human stepping onto a chair).

Apes understand goal-directed action in other agents, visually anticipating where agents will search for their goals (Kano and Call 2014). Whether this is done through the attribution of intentions as unobservable mental states or through some alternative mechanism relying on observable properties of behavior is subject to debate as part of the more general problem of theory of mind in nonhumans.

One alternative approach to animal mentalism, building upon Brentano's notion of intentionality as aboutness, proposes that animals code intentionality through the perception and representation of "directedness" as a Gestalt quality of behavior, not as a derived property of inferred mental states. For example, gaze following may not require attributing subjective experiences of seeing or attending but perceiving the behavior of looking as being *about* or *directed at* particular objects. Such coded intentional relations may in turn be kept in memory as information concerning the "intentional availability" of objects to agents. Evolution may have selected adaptations to behaviorally express and detect relations of intentionality between agents and objects (including other agents). In this way organisms may adapt to a variety of intentional states based on perceived properties of aboutness, rather than inferred unobservable representations (Gómez 2008).

## Communicative Intentionality

Animal communication can be studied without any reference to intentionality, and indeed some scientists prefer an approach to communication that is agnostic about animal intentions. Communicative signals can be described and classified and their functions analyzed in terms of antecedents, consequences, context, and functions without addressing the problem of intentionality (Slater 1983).

However, many comparative and evolutionary psychologists are interested in whether animals can produce communicative signals intentionally. The debate about intentional communication in animals is more complex than the debate about individual intentionality because it has been proposed that communicative intentions may be different to individual intentions. The issue is complicated by disparate definitions and (often implicit) assumptions and criteria across different authors and approaches, which in part reflects wider-spread unresolved debates in psychology and cognitive science about the nature of intentional communication in humans.

There is extensive evidence that many animal species produce signals with the goal of affecting others' behaviour (level 1 intentionality in Dennett's intentionality schema; see above), but there is disagreement about whether they understand how signals work by affecting others' mental states. Accounts of intentional communication in humans usually consider that, to be communicative, the intention behind a signal must refer to the mental states of the receiver, which in Dennett's terms would imply higher orders of intentionality.

### Communicative Intent and the Notion of Ostension

In humans communicative intentions have been proposed to be special, more complex than ordinary intentions. An influential line of analysis (Grice 1957; Sperber and Wilson 1986) proposes that in communication humans combine two types of intentions – *informative* (e.g., conveying the information that I want water) and *communicative* or *ostensive* (conveying the information that

I want to convey the information that I want water). Sometimes we just act with an informative intention (e.g., by covertly pretending that I am trying to drink from an empty glass I can try to make my host understand that I want water, without asking for it openly). However, when we openly ask for water, we *want* not only that our host *understands* that we *want* water but also that we *want* her to *understand* that we *want* water, which adds up to at least five orders of intentionality, with an ostensive “loop” of mutually embedded intentions that appears to be cognitively very demanding.

There are two important things in relation to this analysis. First, this implied cognitive complexity is counterintuitive, in that it does not appear to correspond to our subjective experience in everyday communication. Second, ostensive communication does not require language because we could simply show our host the empty glass of water and smile while looking at her to convey our message. It is therefore in principle possible that nonlinguistic organisms engage in ostensive communication.

Indeed human infants are credited with ostensive-like communication from as early as 9 months of age when they start addressing pointing gestures to others to request and show things of interest. Showing gestures, sometimes dubbed “protodeclaratives,” have been hailed as an important proof of communicative intent, because the infants seem to try to influence the mental states of others in an open, intentional way. In contrast, apes mainly engage in “imperative” gesturing to request actions from others, but rarely, if at all, produce declarative gestures. This could indicate that they only act pursuing individual goals of the type “give me X” but without ostensive communication that would require more complex mentalistic intentionality (Scott-Phillips 2015).

However, although apes' ultimate goal might be affecting others' behavior, they may still show mentalistic intentionality, because in their requests they display joint attention behaviors. For example, they address their gestures to the recipients seeking eye contact with them (an acknowledged marker of ostension in

humans) and even call the attention of recipients that are distracted (Leavens and Hopkins 1998).

This may indicate that, within their imperative motives, apes may use forms of ostensive communication. However, these may not require recursive, mutually embedded intentionality, as ostensive functions can be achieved through joint attentional behaviors, such as eye contact, where any recursive intentionality would remain implicit. Ostension without recursive intentions may help understand how humans engage in ostensive communication without explicitly going through the steps suggested by Gricean analyses (Gómez 1996).

An alternative approach is to avoid the Gricean intentionality issue in animal research and concentrate on simple goal-directed intentionality avoiding the notion of ostensive intentions, so difficult to test objectively. The challenge of a fully empirical approach is to find objective markers of goal-directed communication. Building on the efforts of students of prelinguistic communication in human infants, several authors have proposed behavioral criteria of intentional communication, such as persistence until reaching the goal, orientation to the receiver, or variation in means displayed as a function of the outcome (Townsend et al. 2017). However, the fact that criteria like these may be met by very distantly related species, such as fish (Vail et al. 2013), creates the doubt of whether existing objective criteria are fine-grained enough to capture any peculiarities of communicative intentionality. In addition, any attempt at defining in empirical detail the criterion of “orientation to the receiver” may need to eventually address the problem of ostensive intentions.

### Shared Intentionality

Closely related to the problem of communicative intentionality is the issue of shared intentionality. It has been proposed that a distinctive human ability is to form and pursue joint or shared intentions in cooperative contexts, when we need to engage in complementary activities without which a goal would be unattainable (e.g., moving together a piece of furniture). This “we” intentionality allows the coordination of collective action

and is assumed to require not only an understanding of each other’s intentions and knowledge but to overtly share this. Tomasello and Carpenter (2007) suggest that this might be a distinctive human ability, with apes remaining at a level of individual intentionality, pursuing individual goals, where they can attribute intentions to others, but not “share” them with others to coordinate their actions and achieve goals jointly. For example, although in competitive contexts chimpanzees interpret *reaching to* a box as a signal of their rival’s intention to get food there, they find it difficult to interpret *pointing to* the box as a cooperative signal intended to tell them where the food is (Hare and Tomasello 2004). Shared intentionality would require special forms of cognition and cooperative motives and would be at the root of human culture.

Other authors argue that, although humans indeed excel at shared intentionality, this is already present in nonhuman primates, because they are capable of engaging in cooperative activities in the wild (e.g., hunting) and in captivity (solving problems that require joint coordinated action). The debate is about whether it is possible to explain this cooperative action as a result of coordinating individual intentions without “sharing” them, which poses a difficult problem of definition of what should count as “shared” versus “coordinated.” It has been suggested that the evolutionary roots of shared intentionality may be deeper and could be found in the elaborate social play displayed by mammals, especially primates (Heesen et al. 2017).

### Conclusion

Notions of intentionality – both in the sense of aboutness and purpose – have been applied or rejected in the study of animal behavior in different ways and at different times. They have always been at the center of debates between behaviorist and cognitive approaches to animal behavior. In some formulations (intentionality as individual goal-directedness), they are currently accepted as relevant and empirically grounded even by modern learning theorists and used in the study of a

variety of aspects of animal behavior and cognition, although problems of definition and scope still persist. Notions of communicative intentionality remain more controversial and subject to polarized debate, due to lack of conceptual agreement and the difficulty of finding reliable behavioral indicators of the cognitive and motivational components of communicative intent. Intentionality touches upon some central epistemological problems about the nature of explanation in animal behavior and the methodological challenge of going beyond observable behavior and finding objective behavioral criteria of cognitive processes.

## Cross-References

- ▶ Alarm calls
- ▶ Behaviorism
- ▶ Comparative Psychology
- ▶ Edward C. Tolman
- ▶ Goal
- ▶ Insight
- ▶ Primate Communication
- ▶ Theory of Mind

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## Intentionality Test

### ► [Accidental/Intentional Experiment](#)

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## Interactionist Theory

### ► [Cognition](#)

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## Interbirth Interval

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### Definition

An interbirth interval (IBI) is the period in between two consecutive births. The interval often takes into account only viable births, ignoring miscarriages, still births, or premature deaths. IBI is only meaningful for iteroparous species, which reproduce in multiple bouts over the course of a reproductive lifespan. Most available data on IBI tend to focus on the clade Placentalia and

particularly on large-bodied taxa with low reproductive output per bout, such as carnivores, elephants, primates, ungulates, and whales. In humans, where conception date can often be identified, IBI may be replaced by “inter-pregnancy interval,” defined as the period in between delivery of a live-born child and the estimated conception of the next pregnancy. In egg-laying taxa, such as amphibians or birds, the concept of IBI may be expanded to the time interval between consecutive clutches or the number of clutches produced per breeding season.

### IBI in Life history theory

IBI is a key life history variable used to characterize the pace of reproduction of a species. Across mammals, IBI is positively correlated with weaning age, age at sexual maturity, and gestation length (marsupials only), independently of body size variation (Promislow and Harvey 1990). Within species, the IBI is a major determinant of female reproductive success, together with the total reproductive lifespan, and offspring mortality (Clutton-Brock 1988). Lifetime reproductive success would be maximized by frequent reproduction, i.e., shorter IBIs, only if reproductive lifespan and offspring mortality exert their effects on reproductive success independently of the IBI. However, too short an IBI is not optimal because IBI co-varies in particular with offspring quality, such as survival, birth weight, small for gestational age, or reproductive success later in life. For example, in humans, the risk of adverse birth outcomes increases as inter-pregnancy intervals decrease (Blurton Jones 1986; Conde-Agudelo et al. 2006; Wendt et al. 2012). Similarly, in Great Tits, the offspring of parents whose following clutches had been experimentally removed were tended for a longer period and enjoyed higher survival rate in their first year of breeding (Verhulst et al. 1997). The negative correlation between IBI and offspring quality has been explained using life history theory, which posits that investment in offspring number utilizes finite resources that would be otherwise available for

investment in offspring quality (Stearns 1989). Following this view of life history trade-offs, a shorter IBI means insufficient restoration of resources depleted from investment in the previous reproductive event, consequently limiting the resources available for current reproduction. As a result, short IBIs would undermine the quality of current offspring, in the form of negative birth outcomes or lower reproductive success for the current offspring later in life.

### IBI as a proxy of parental investment

Due to the trade-off relationship between IBI and offspring quality, the IBI is seen as an index of parental investment, which is any investment in one offspring at the cost of a parent's ability to invest in future offspring. It is adaptive for a parent to keep an IBI short so that it does not compromise the parent's chance of producing future offspring. It is therefore likely that mechanisms for regulating IBI have evolved to maximize parental fitness depending on the context. For example, a study on a British human birth cohort has shown that IBIs are shorter when previous offspring are in severe but not fatal medical condition. This finding suggests that parental investment would be reduced for offspring displaying low expected fitness. Increased resource availability is another context in which IBIs can become shorter. Compared to great apes (>5 years), human IBI lengths in natural fertility populations (in the absence of controlled fertility) are in general shorter in their median length (3.5–4 years). The shortening of human IBI lengths may suggest that the costs involved in short IBI – notably, the deprivation of maternal resources and its consequence for the following infant – have been effectively alleviated through co-evolved strategies, such as cooperative breeding and earlier food supplementation for weaning.

### IBI in mammals

The mammalian IBI is comprised of three main phases: (i) postpartum anovulation (PPA);

(ii) cycling; and (iii) gestation. Variation in the length of gestation is small relative to the length of the first 2 periods that constitute time to maternal re-conception. In particular, PPA has gained most attention for its contribution to the variation of IBI. In most mammals, suckling during lactation and the presence of and physical interaction with offspring suppress maternal reproductive function. Thus, some maternal behavior (e.g., rejection of an offspring's nipple contact attempt) and some offspring behavior (e.g., tantrums, begging) may influence the duration of PPA. Food resources and energy balance might have particularly strong influences on the lengths of both PPA and cycling. In seasonally breeding mammals, the length of cycling may be additionally influenced by environmental cues linked to seasonality, such as photoperiod, precipitation, and temperature. For example, among rodents, there is a general trend for an increased length of breeding season with increased interval between successive litters.

### Cross-References

- Fertility
- Parental Investment
- Reproductive Fitness

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## Interbrood Conflict

- [Discriminative Parental Solicitude](#)

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## Interchange

- [Exchange Behavior](#)

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## Intercommunity Aggression

- [Chimpanzee Raiding](#)

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## Interconnected Structure

- [Neural Network](#)

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## Interconnected System

- [Neural Network](#)

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## Interference

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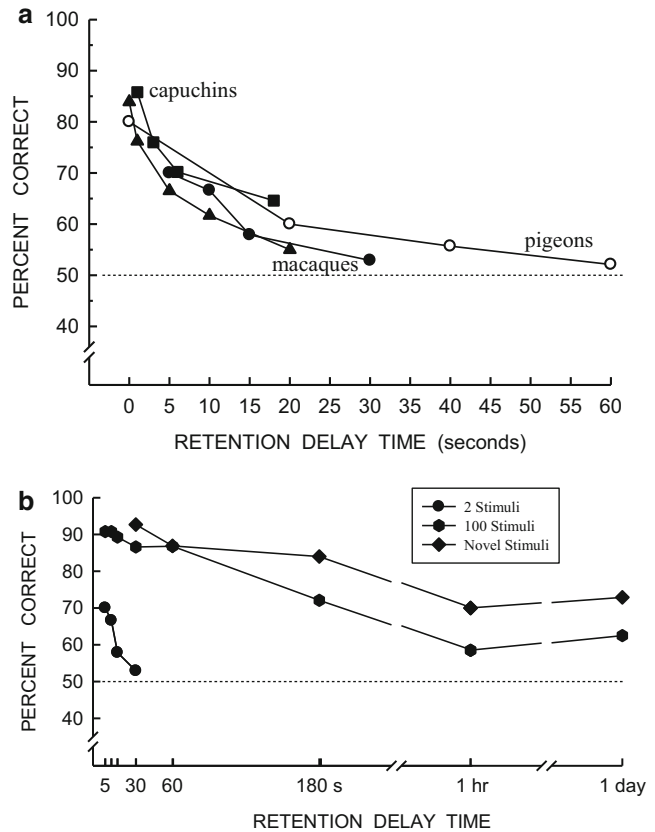
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Investigations of animal memory have traditionally been studied in terms of how long animals can remember single items, often in delayed matching-to-sample tasks. Results from some delayed matching-to-sample tasks can be seen in Fig. 1a for capuchin monkeys (filled squares), macaque monkeys (filled circles, diamonds), and pigeons (unfilled circles). These studies all used just two stimuli (See Wright, 2007 for references of these studies and further discussion). The sample presented on each trial was one of the two stimuli, followed by a delay and then a choice between these two stimuli for which stimulus matched the sample. With no delay (0s), performance accuracy was more than 80% correct. But performance rapidly declined, reaching 50% correct (chance performance) in 1 min or less. At issue is what do such results tell us about animal memory? Such results are unlikely to convey limits of the animal's memory because the animals would not be able to survive (e.g., remember food source locations, nesting sites, mates, filial relationships, dominant individuals, and predator locations). But for one study included in Fig. 1a (filled circles), the 2 stimuli were increased to 100 stimuli and then further increased to all novel stimuli (Fig. 1b). These stimulus increases resulted in progressive and dramatic increases in memory performance (Overman and Doty 1980). Indeed, even after a 24-h delay, performance was better than after 30s in the two-stimulus condition!

Consider what an animal faces when making a choice in the two-stimulus condition. The animal is presented with the same two stimuli on every trial and must decide which stimulus matches the sample stimulus. Even after a brief delay,

**Interference, Fig. 1 (a)**

Four single-item memory functions from different laboratories using only two stimuli in delayed matching-to-sample experiments: macaque monkeys (filled circles and filled triangles), capuchin monkeys (filled squares), and pigeons (unfilled circles). (b) Three delay functions with rhesus monkeys (Overman and Doty 1980). The two-stimulus function is the rescaled filled circle function from (a) above. In the 100-stimulus condition, repetitions of the stimuli were separated by many trials. In the novel stimuli condition, all stimuli were novel and trial-unique. Dotted lines represent chance performance



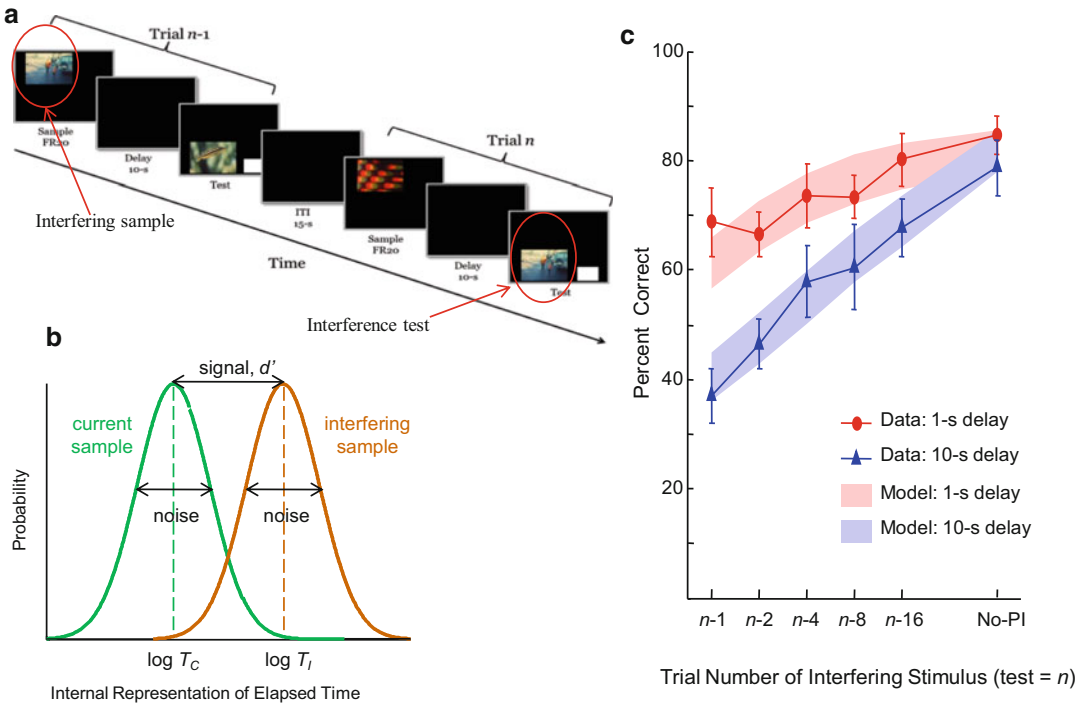
confusion can occur as to which trial the test stimulus had been seen and processed. This issue of proactive interference adversely affecting later memory performance can be present in virtually any memory task as Keppel and Underwood showed in 1962 for the buildup of proactive interference (and increase in errors) as humans experienced an accumulation of stimulus repetitions over the testing session.

### Proactive Interference in Pigeon and Monkey Same/Different Tasks

#### Pigeons: Time-Based Proactive Interference

Proactive interference similar to that which occurs in delayed matching-to-sample tasks also occurs in same/different tasks. In same/different tasks, one (sample) stimulus is presented (to be remembered), and after a delay, a second (test) stimulus

is presented in a location below the previous sample stimulus (Fig. 2a). If the test stimulus matches the sample stimulus, then a response to the test stimulus is correct. If the test stimulus does not match the sample stimulus, then a response to the white rectangle to the right of the test stimulus is correct. In same/different tasks, proactive interference (PI) occurs when a previously seen sample is re-presented as a test picture on later *different* trial. Having seen that test picture before, possibly as a sample stimulus in the immediately previous trial, tends to create confusion and increases the likelihood that a *same* response (incorrect response) will be made (Fig. 2a). Since stimulus repetitions in general produce cumulative proactive interference, to evaluate PI, the vast majority of trials in a session would need to involve trial-unique stimuli (i.e., without proactive interference). With such a background of low or no-PI, only then can occasional test trials of proactive interference be



**Interference, Fig. 2** (a) Example of two trials from proactive interference tests with pigeons where the interfering stimulus was presented on the preceding trial ( $n-1$ ) and repeated as the test stimulus on trial  $n$  with 10-s delay between offset of sample stimulus and onset of test stimulus. (b) Signal detection theory model of elapsed time: log

time to the sample on the current (test) trial ( $\log T_C$ ) and log time to the interfering sample ( $\log T_I$ ). (c) Percentage correct performance for 1- and 10-s delays, with model fits (1-sigma bands) based on the ratio of log times ( $T_C/T_I$ ) – see Wright et al. (2012) for further details

inserted within a session to test how far back in time PI can affect memory accuracy.

One such PI test was conducted with four pigeons (*Columba livia*) for interfering stimuli that were presented 1–16 trials previous to the test (Wright et al. 2012). A large stimulus set of 1024 images (pictures of objects, natural scenes, animals, etc.) was used so that stimuli would be trial-unique and not repeated for more than 2 weeks of testing. PI was tested by placing potentially interfering stimuli either 1, 2, 4, 8, and 16 trials prior to test trials. Pigeons pecked the sample stimulus 20 times, followed by a delay (1 s or 10 s, in a block design), a test stimulus and white rectangle, a choice response, and a 15-s intertrial interval. Each daily session consisted of 64 trials with 5 interference tests (1 test each at the 1-, 2-, 4-, 8-, and 16-trial separations). Trials other than those of the interference tests (*no-PI*, or baseline, trials) contained randomly selected (without

replacement) pictures from the 1,024 picture set. There were 32 *same* and 32 *different* trials per session, 24 sessions per block, and 4 blocks alternating between 1-s and 10-s delays.

Even with the shorter 1-s delay, there was considerable PI, and this PI dissipated as a function of increased trial separation (Fig. 2c). With the longer 10-s delay, there was a considerably larger 47% PI effect with the interfering stimulus in the preceding trial which dissipated with increasing trial separation, but there was still a residual interference effect of 11% for stimuli presented 16 trials prior (more than 6.5 min prior), considerably greater than that with the 1-s delay.

Greater interference at the longer 10-s delay than at the shorter 1-s delay is counterintuitive. Interfering stimuli encountered more distantly in the past (144 s at  $n-16$  for 10 s vs. 1 s) should, according to models of decay or limited capacity,



translate to more forgetting and therefore less interference. But just the opposite occurred. This counterintuitive finding was shown to obey a Weber-Fechner time ratio of time discriminations (Fig. 2b) from the test to the current-trial sample stimulus divided by time to the interfering stimulus (see Wright et al. 2012). Longer testing delays allow for greater opportunities for noise to come between the current sample and test and increase chances that the interfering stimulus will adversely affect the correct *different* response and enhance the chances of making an incorrect *same* response. This model based on the Weber-Fechner time ratio of time discriminations was fit simultaneously to both PI functions using the same parameters (bias and maximum accuracy) accounting for 95% of the variance, including the no-PI condition (Fig. 2c).

#### Monkeys: Event-Based Proactive Interference

Three rhesus monkeys (*Macaca mulatta*) were tested in same/different memory tasks for proactive interference (PI) from prior trials (Devkar and Wright 2016). Most of the conditions including trial-unique pictures selected from the same 1024 picture set without replacement on baseline trials; interference tests separated by 1, 2, 4, 8, or 16 trials prior; 15-s intertrial intervals; numbers of trials per sessions; sessions per block; and repetitions of blocks were the same for monkeys as they were for pigeons (described above). One difference was that monkeys were tested with three delays (1-s, 10-s, and 20-s delays). The 20-s delay was used to explore better the limits on time-based proactive interference. Nevertheless, there was no evidence of time-based proactive interference in monkeys (i.e., no statistical significant differences or interactions for the three PI functions of Fig. 3a).

As a follow-up test to further explore the possibility of any time-based proactive interference in monkeys, a shorter intertrial interval of 5 s was tested to increase interactions among stimuli from different trials and possibly enhance any time-based proactive interference. In this study, the 20-s delay was used which also should enhance any time-based proactive interference across trials. The longer 15-s intertrial interval was retested for comparison and alternating block testing

design. Decreasing the intertrial interval by this amount (66.6%) decreased time to the interfering stimulus by 10s per trial (i.e., 160 s for 16 trials), and any time-based proactive interference like that shown for pigeons should be increased proportionately.

Even with these shorter 5-s intertrial intervals and longer 20-s delays, there were no statistical differences between the PI functions for 5-s versus 15-s ITIs (Fig. 3b). Despite a lack of any time-based PI, all PI functions showed pronounced PI effects. Moreover, these PI functions covered a very large performance range, as much as a 50% accuracy range (e.g., 40–90% accuracy). Such large proactive interference effects along with a total lack of time-based proactive interference converge on the conclusion that these primates' proactive interference is *event* based. Event-based versus time-based PI conjures up well-known processing distinctions of remember versus know judgments, explicit versus implicit memory, and episodic versus familiarity memory.

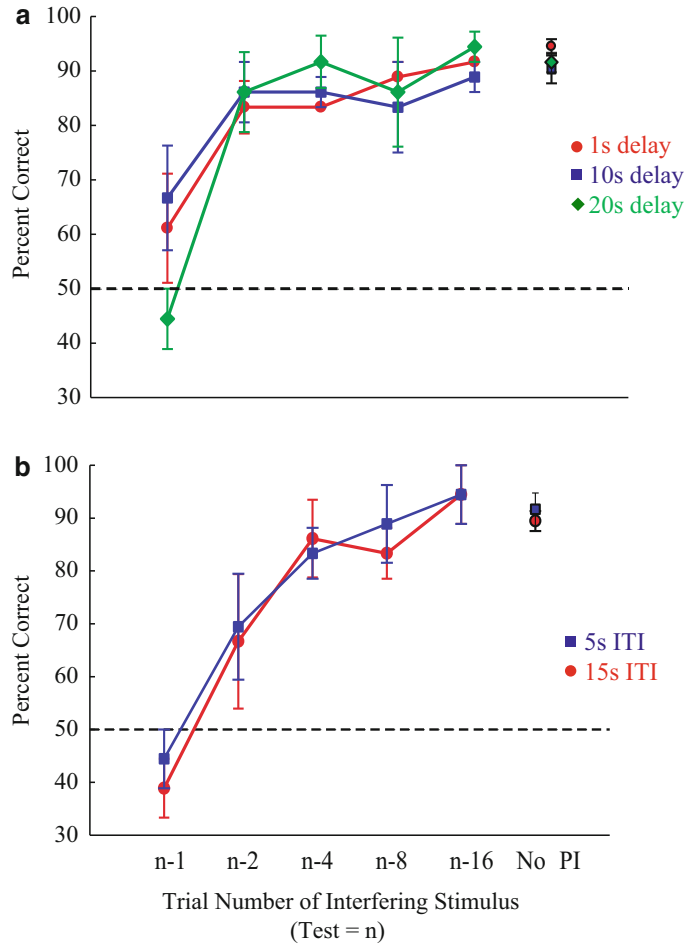
#### Interference in List Memory Tasks

List memory tasks are closely related to same/different tasks which should make them susceptible to the same buildup of proactive interference when small sets of testing stimuli are used and other manipulations to produce proactive interference functions. Many animals trained in list memory tasks are first trained in same/different tasks, followed by gradually expanding the number of sample stimuli. List items are presented in the sample location (e.g., 1-s presentations and 1-s between items), followed by a delay, and then a test item appearing below the sample/list location. A response to the test item is correct when it matches one of the list items; a response to the white rectangle is correct when the test item does not match any list item.

In one study, monkeys and humans were tested for proactive interference with three-item lists (Fig. 4). Tests with a large set of 211-item picture set resulted in high accuracies of 93% and 96% correct for monkeys and humans, respectively. But when they were tested with a small six-item

**Interference,**

**Fig. 3** Mean performance for three monkeys with five different separations between an interfering stimulus and a test stimulus compared to no-interference (no-PI) baseline trials. **(a)** Three delays, 1-s, 10-s, and 20-s delays, with 15-s intertrial intervals. **(b)** 5-s and 15-s intertrial intervals with 20-s delays



picture set, accuracy fell to 70% and 89% correct for monkeys and humans, respectively (Sands and Wright 1980). In a related study, monkeys were tested with 4-item lists selected from a 420-item picture to be trial-unique each session. Over 3 months of testing, their overall accuracy of 75% correct declined to 60% correct. This gradual decline in accuracy was similar to that shown by Keppel and Underwood (1962) but over a longer time scale; novel stimuli tests resulted in an accuracy increase to 82% correct (Jitsumori et al. 1988).

Another study showed buildup and release from proactive interference by testing monkeys with four-item lists composed of examples from one of two categories (flower or primate face pictures). Over 40 trials of testing with one of the categories, accuracy dropped from 86% to

71% but returned to 86% when the switch to the other category was made and then dropped again over the next 40 trials with that category. This is an example of category-specific proactive interference, resulting in what has been termed “release from proactive interference” upon the category switch (Jitsumori et al. 1989).

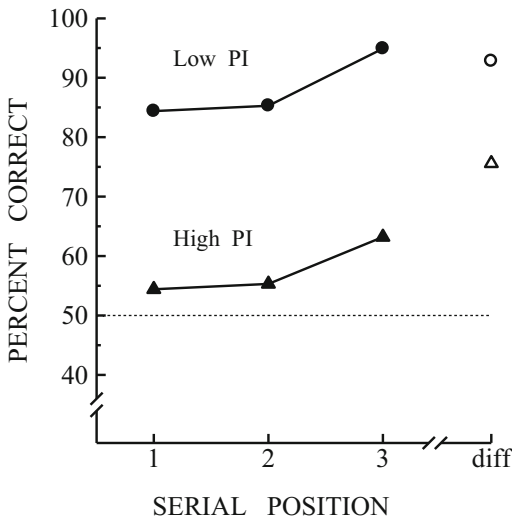
PI function tests can be conducted with list memory tasks much like with the same/different task by test items that match a list item from a previous trial but not a list item from the current trial. Such PI tests were conducted with a rhesus monkey well trained in a ten-item list memory task. On occasional interference trials, interfering stimuli were placed one, two, three, four, five, or six trials prior to the test (Fig. 5). When the interfering items were in the immediately preceding trial, performance was 64% (with

50% being chance performance). As trial separation grew (to as many as 60 items prior), performance increased to 83% but was still less than the no-PI baseline performance of 93% correct (Wright et al. 1986). These findings show that

proactive interference can extend to as much as 60 items prior.

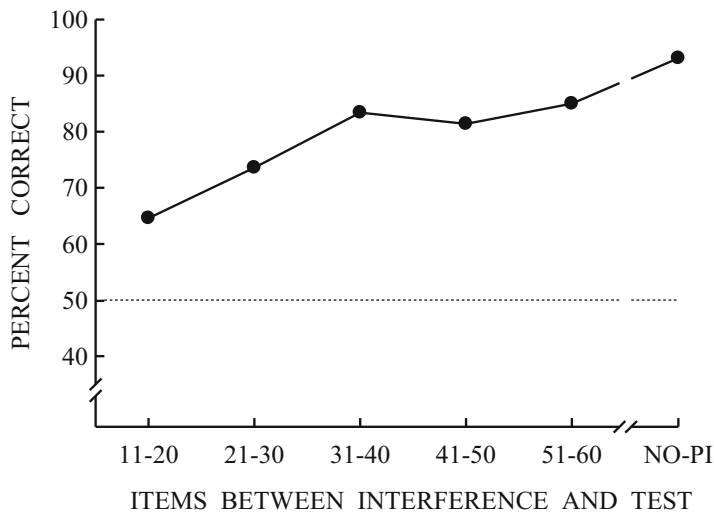
In conclusion, proactive interference is endemic to virtually all experimental studies of memory where stimuli and events are repeated. For some primates, certainly rhesus monkeys (and possibly humans), proactive interference is event based and varies inversely with the number of intervening events. For some bird/avian species, certainly pigeons, proactive interference is time based and varies inversely with the passage of time since the interfering event and directly with delay to the processing of the test stimulus (as ratio of log time). Of course, time is the interval between events, and events have to be distinctive to be remembered. Therefore, avian (pigeon) time-based proactive interference must at some level be event based as well. But as shown with primates (rhesus monkeys), proactive interference can be event based, exclusive of time-based proactive interference.

Because proactive interference is such an important component of learning and memory, it will be of considerable importance to determine the generality of the division of time-based proactive interference for avians versus event-based proactive interference for primates as described here. For example, an avian species with outstanding memory for events like the Clark's nutcracker (a corvid species) might provide a good test of event-based proactive interference because these



**Interference, Fig. 4** Repeated-item interference of a rhesus monkey's three-item list memory results with memory items selected from a low interference condition (low-PI) using a set size of 211 distinctly different items compared to high proactive interference condition (high-PI) with items selected from a small six-item set. Serial position 1 was the first list item. Unfilled symbols (diff) show performance on trials (*different*) where the test did not match any list item. The dotted line represents chance performance

**Interference, Fig. 5** Interference tests of a rhesus monkey's ten-item list memory performance as a function of the number of items occurring between a test item on a *different* trial and its previous presentation. The no-PI condition is a no-interference condition. The dotted line represents chance performance



birds depend on remembering the many locations (Where) of pine seed caches (What), which change yearly (When), and are recovered in the dead of winter when the forest is covered with snow. Perhaps the critical component for pure event-based proactive interference will turn out to be well-developed episodic or episodic-like memory (What, Where, and When).

(Note: there are retroactive as well as proactive effects among the items that make up lists, particularly auditory lists, but discussion of those within-list effects can be found in Wright (1999) and the *Encyclopedia* entry ► “List Memory Effects (Primacy and Recency).”

## Cross-References

- Cognition
- Corvids
- Decision-Making
- Declarative Memory
- Delayed Match-to-Sample
- Episodic Memory
- Interference
- Memory
- Oddity
- Pigeon (*Columbidae*)
- Primate Cognition
- Primates
- Proactive Interference
- Same/Different Learning
- Working Memory

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## Intergenic

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## Synonyms

Junk DNA; Spacer DNA

## Definition

“Stretch of DNA sequence located between the two successive genes.”

## Introduction

The human genome is an enormous, cryptic store of information with approximately three billion bases that encode, either directly or

indirectly, the instructions for synthesizing nearly all the molecules essential for the formation and function of each human cell, tissue, and organ. The genome of most of the eukaryotes comprises several protein-coding genes, nonprotein-coding genes, and transcription regulatory elements such as enhancers, suppressors, promoters, etc. In addition, there are sequences that are responsible for regulation of chromosomal structure and dynamics (Dunham et al. 2012). However, all these regions contribute to a very little fraction of whole genome and essentiality of much of genomic regions is yet to be defined. To understand the term “intergenic,” first, one must have knowledge of genes and the extent of genic region in the genome. To define the structure of **gene** precisely is very difficult; however, it can be defined as the entire DNA sequence including regulatory regions that can synthesize a functional protein or RNA molecule. **Intergenic regions**, also known as **spacer DNA** or sometimes **junk DNA**, are the long stretch of DNA sequences located between protein-coding regions of two successive genes (Shabalina et al. 2001). However, this definition is incomplete because there are many genes including genes encoding the t-RNA and r-RNA that are nonprotein coding and therefore, according to this definition can be considered as intergenic.

### Genic Versus Intergenic Region

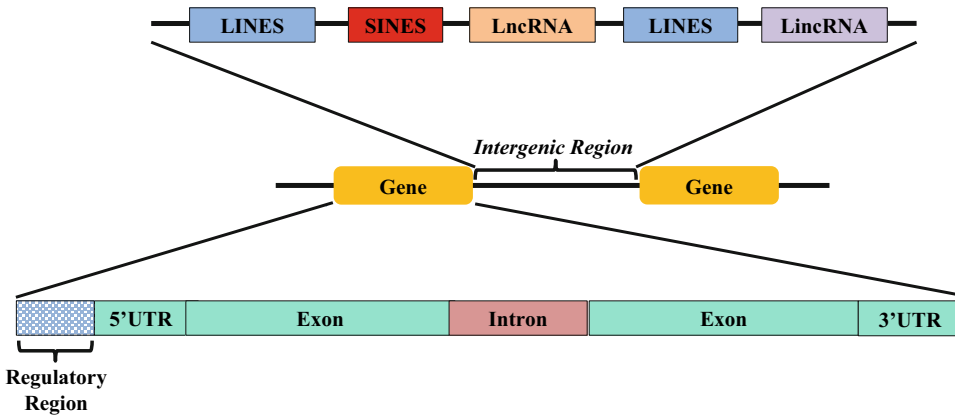
In general, eukaryotic genes consist of multiple protein-coding regions, the exons, separated by non-coding regions, the introns, and 5' and 3' untranslated regions. In addition, they also include the regulatory regions such as promoters, enhancers, etc. The introns are stretch of noncoding DNA sequence between two successive exons. On the other hand, the genome of prokaryotes lacks introns in their genes. The untranslated regions of a gene are also noncoding but play essential role in regulating the stability and localization of transcripts. In contrast, intergenic regions do not encode protein and are poorly conserved in the genome. The length of intergenic regions varies in eukaryotic and prokaryotic genomes. For example, eukaryotic

genes are usually separated from each other by long stretch of noncoding DNA sequences, i.e., intergenic sequences, while intergenic regions of bacterial and yeast genomes and mitochondrial genome are comparatively very short or completely absent (Wolstenholme 1992). These regions are poorly defined and might have regulatory elements such as binding sites for transcriptions factors, enhancer, promoters, operators, etc. Intergenic regions differ from intragenic non-coding regions because introns are comparatively shorter in length and are highly conserved at their ends.

### Genome Architecture and Intergenic Region

Intergenic regions are very abundant and cover more than half of the entire genome in many eukaryotes. For example, in human, approximately 1% of the entire genome is comprised of the protein-coding exons and the remaining 99% of the genome are covered by introns (24%) and intergenic DNA (75%) (Venter et al. 2001). Of the intergenic DNA, nearly 44% is derived from transposable elements including long interspersed nuclear elements (LINEs), short interspersed nuclear elements (SINEs), long terminal repeats (LTRs), and cut-and-paste type elements (Fig. 1). LINEs are ~6 kb long repeat sequences that are present in hundreds-thousands in numbers either in transpositionally active (e.g., *L1* elements) or inactive form (e.g., *L2* and *L3* elements). In contrary, SINEs are 100–400 bp long repeat sequences and the second most abundant transposable elements in human genome. Most of the SINEs are transpositionally inactive (*MIR*, *MIR3*), except *Alu* elements which are the only active SINEs. LTRs are hundreds of thousands of identical or nearly identical DNA sequences of approximately 300 bp that are flanked at opposite ends of an integrated retrovirus or a retrovirus-like element. These transposable elements are repetitive sequences that are interspersed throughout the genome. Nearly 70% of entire human genome is comprised of repetitive and repetitive-derived DNA elements such as microsatellites and minisatellites which are dispersed





**Intergenic, Fig. 1** Diagrammatic presentation of components of a typical eukaryotic genic and intergenic region

in the intergenic regions also (Snustad and Simmons 2012).

Recent studies have shown that approximately 60–70% of the entire human genome is transcribed as either processed or primary transcripts (Djebali et al. 2012); however, only 2% of all transcriptional output encodes the proteins (Mattick 2001). The remaining 98% transcriptional products are nonprotein coding and include housekeeping noncoding RNA (r-RNA, t-RNA, and small nucleolar RNA (snoRNAs)), introns, plentitude of antisense transcripts, intergenic transcripts, and a large number of predicted transcriptional units (Mattick 2001). These noncoding RNAs can be categorized into small noncoding RNA, including microRNAs (miRNA) and small interfering RNAs (siRNA, etc.), and long intronic noncoding RNA and long intergenic noncoding RNA (lincRNA) that are dispersed throughout the genome. Both miRNA (or small temporal RNA) and siRNA are about 21–25-nucleotide long RNA molecules that are derived from the processing of approximately 70-nucleotide long double-stranded precursor hairpins by Dicer ribonuclease III. The genes encoding these small regulatory RNAs are dispersed throughout the intergenic and intragenic regions and occasionally in exons. Long intergenic noncoding RNAs (lincRNAs), also known as **dark matter** are a subset of long noncoding RNA that is transcribed by RNA polymerase II from the DNA sequences

between two successive genes. LincRNA undergoes processing by both 5' capping and 3' poly (A) additions and spliced (usually with alternative isoforms, but with fewer exons than coding mRNAs) and have an average length of 1 kb. In human genome, more than 8000 putative lincRNA transcripts have been identified so far; however, the number may be even more. These lincRNAs show a similar expression level and expression pattern to those of protein-coding genes, although they lack the protein-coding capacity. Additionally, these transcripts show significant evolutionary conservation compared to neutral sequences (Cabali et al. 2011). Moreover, these RNAs may also bind with chromatin regulatory proteins. Unlike to eukaryotic genome, prokaryotic genomes are much shorter and lack the intronic regions in their genes. Most of the regions of prokaryotic genomes are transcribed and translated to protein products; however, they do possess intergenic DNA sequences that transcribe noncoding RNAs, untranslated regulatory regions, and repetitive elements (Sorek and Cossart 2010).

## Functions of Intergenic Regions

Since intergenic regions are noncoding, they were often believed as **junk DNA** suggesting that they had no defined function in the organism. However, several studies in last three

decades have shown that these regions do encompass functionally essential regulatory elements such as enhancers and suppressors. Approximately, 99% of human and mice protein-coding genes have conserved sequence homology, suggesting that variations in the phenotypes of both the species are possibly due to differences in the nonprotein-coding sequences. In addition, the genome of higher organisms such as mammals is comparatively much bigger than the lower organism, e.g., *Caenorhabditis elegans*. However, numbers of proteins in mammals are only two- to threefold higher than in simple nematode *C. elegans* (Venter et al. 2001). Further, along with increase in the complexity of organism, there is a concomitant increase in the noncoding intergenic and intronic sequences (Mattick 2001). This suggests that intergenic regions of mammals are at least as functionally important as their genes, because the intergenic regions might hold the key to the complexity of mammals (Shabalina et al. 2001). Emerging evidences from several recent studies demonstrated that lincRNAs are implicated in various biological processes including cell-cycle regulation, immune surveillance, embryonic stem cell pluripotency, embryonic development, etc. For example, lincRNA-ST8SIA3 or lincRNA-RoR (regulator of reprogramming) modulate the cellular reprogramming and helps in the establishment and maintenance of pluripotency. However, exact molecular mechanism of lincRNA-RoR functioning is not known till date (Loewer et al. 2010). LincRNAs, for example, HOTAIR, which is highly abundant in breast cancer, may also regulate the cancer metastasis by targeting the chromatin-remodeling complex PRC2 (polycomb repressive complex 2) which eventually alters the H3K27 methylation and gene expression (Gupta et al. 2009). Studies in zebra fish have shown that two highly conserved lincRNA, i.e., linc-oip5 (cyrano) and linc-birc6 (megamind), play important role in brain morphogenesis and eye development, and these functions are retained in their mammalian orthologues (Ulitsky et al. 2011). These regions also regulate the endocrine differentiation of pancreatic tissues by acting as a transcriptional

enhancer and as a polycomb response element. In addition, intergenic spacer regions are useful in distinguishing the pathogenic and nonpathogenic strains of bacteria, fungus, and other organisms (Tokajian et al. 2016). Synthetic intergenic regions can also be used to attenuate the pathological activity of certain virus, e.g., hemorrhagic fever arenaviruses (HFAs), and thus might be helpful in preventing the high rate of morbidity and mortality across the world (Iwasaki et al. 2016). In plants, functions of lincRNA are relatively less studied; however, large-scale RNAseq and tiling microarray studies have revealed the presence of many lincRNA in the plants also. These lincRNAs regulate the gene expression by recruiting proteins regulating the chromosome modification, alternative splicing by binding and sequestering the proteins required for alternative splicing, and inhibiting the interaction between miRNA and their targets mRNA (Yamada 2017). Roles of miRNA and siRNA are well defined in the regulation of various morphological events including embryonic development. These small regulatory RNA bind to their target mRNA and regulate the expression of protein-coding genes in plants and animals.

## Conclusion

Studies in last few years have shown that lincRNA are not “junk” as described earlier and may have certain role in biological processes; however, our knowledge about the exact biological functions of these transcripts is limited and very few such transcripts have been defined, yet. Increasing knowledge about the role of lincRNA may be useful in developing diagnostic markers and treatment of several pathological conditions. Further studies may explore many more of these transcripts and would be helpful to solve the puzzle of huge volume of nonprotein-coding portions of the genome.

## Cross-References

- [Exon](#)
- [Genes](#)

- [Intron](#)
- [Messenger RNA](#)
- [microRNA](#)
- [Mitochondrial DNA](#)
- [Noncoding RNA](#)

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## Intergenic Complementation

- [Complementary Genes Hypothesis](#)

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## Intergroup Violence

- [Raiding](#)

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## Intermediate Phenotype

- [Endophenotype](#)

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## Intermittent Reinforcement

- [Partial Reinforcement Extinction Effect](#)

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## Internal Clocks

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## Definitions

Internal, biological clocks can be found in all organisms and regulate a variety of functions, including: learning and memory, reproduction, growth, and aging. Biological clocks, like our mechanical versions, are valuable because they synchronize the timing of events, coordinating

internal events with each other, and with the external environment.

Biological clocks can be classified in a number of ways. For example, clocks can be classified according to their mechanism into hourglass or interval timers and oscillatory clocks. Hourglass clocks, or “countdown” clocks, determine intervals and are found in processes that describe development, aging, and learning. Oscillatory clocks keep time, spontaneously regenerating with a fixed period and are found in processes that coordinate internal processes with naturally occurring cycles in the environment such as reproduction and feeding. Clocks can also be characterized by their period length. Those with periods less than a day are ultradian, periods longer than a day are infradian, and those with periods close to an hour are circadian. There are also complex clocks that combine mechanisms and period length as in sleep (Harfmann et al. 2015).

### Hourglass Clocks

Development, puberty and ageing have species dependent, predictable durations. These clocks play important roles in coordinating cell division and differentiation related to growth and senescence. Once triggered, hourglass clocks run out their cycle and do not reset. Many mechanisms are currently under investigation including telomere length. Telomeres are repeating sequences at the end of DNA strands that do not code for protein and protect the sticky ends of DNA from joining. Telomeres are long in young animals and, as they are incompletely replicated during cell division, become shorter with age correlating with gestation and ageing. Elongation of telomeres increases the life span of transgenic animals supporting a role for telomeres as count down/hourglass clocks in animals (Rensing et al. 2001). The role of telomeres in development and ageing of plants is less clear (Watson and Riha 2011).

### Embryogenesis and the Developmental Clock

Embryogenesis – the progression from egg to organism is a complex series of events many of which occur at predictable times suggesting orchestration by a developmental clock. The creation of somites – precursors for bones muscles

and tissues in segmented organisms – is the best described. Somite formation occurs in waves – with species-specific periodicity that is determined by oscillating genes within presomite tissue. Perturbation of the oscillations disrupts development and results in the loss and fusion of vertebrae and ribs. Cells within a group must be synchronized for proper development of the somite. Neuronal cells differentiate in response to the rhythmic release of HES-1 – a transcriptional repressor that promotes neuronal proliferation. HES-1 is regulated by a molecular feedback loop. As it is not clear, if the period can be adjusted or synchronized more work must be done to determine if this process is driven by a clock (Webb and Oates 2016).

### Epigenetic Clock and Aging Correlation

Age is defined by the decrease in homeostatic mechanisms that negatively alter gene expression and molecular pathways, causing tissues to age. Though aging is largely affected by genetic influences, DNA sequences and telomere length, epigenetic influences carry a significant amount of weight. Epigenetic mechanisms can alter DNA methylation, posttranslational histone modifications and non-coding RNA. First, DNA methylation is necessary for development because of its role in cell fate determination; there is an overall decrease in DNA methylation as individuals age. DNA methylation also shows involvement in genomic imprinting, female X-chromosome inactivation, and gene silencing. Second, posttranslational histone modifications involve eight histone marks (acetylation, methylation, phosphorylation, etc) that regulate gene function. Modifying these histones consequently remodels chromatin and, ultimately, gene expression. These posttranslational histone modifications are also found to alter the aging process in worms and *Drosophila*. Third, non-coding RNA are also known to be involved in aging and have been found to be altered throughout the aging process. For example, microRNAs (miRNAs), short non-coding RNAs, are involved in the repression of gene translation. Because they are necessary for growth and development, the malfunctioning of miRNAs can lead to disease. Overall, the accumulation of

these epigenetic mechanisms significantly impacts the aging process (Huidobro et al. 2013).

### Seasonal Hourglass Clocks

Many species respond to the seasons with changes in reproduction, coat color, and hibernation (Paul et al. 2008). Vertebrates with relatively short life spans (i.e., a year or so) seem to use interval timer triggered by day length to initiate and reset their cycles. For example: syrian hamsters maintained on photoperiods with less than 10 h of light per 24 h experience testicular regression over 10–12 weeks. Prolonged exposure (i.e., more than 14–16 weeks) renders the animals insensitive or refractory to the daylength and the testis return to their original size and function. Exposure to long days resets the clock so that reexposure to short days once again induces regression. In vertebrates, this version of infradian clock requires an intact circadian system and melatonin.

Several mechanisms have been proposed including: an internal coincidence model in which seasonal changes are induced by light induced, changes in the relationships of internal circadian oscillators, and an external coincidence model in which seasonal changes are induced by light falling on photo inducible phases of the underlying circadian rhythm.

## Oscillatory Clocks

True biological clocks are characterized by: their persistence in the absence of time cues, their ability to be synchronized by periodic external cues and their resistance to changes in temperature. The best known clock is the circadian clock which directs rhythms with periods of about 24 h. There are also clocks with longer periods (infradian) that regulate monthly and seasonal rhythms and those with shorter periods (uniradian) that regulate hourly burst of activity. Interestingly, the circadian system is involved in these clocks as well.

### The Circadian Clock

Circadian rhythms are found in every cell and every species, waxing and waning with the

minutes and hours of the day. These rhythms underlie our ability to tell time, to coordinate our activity with the sunrise and sunset and the changing seasons. Deficits in the circadian system may influence susceptibility to disease, productivity at work, and attention (Turek 2016).

In vertebrates cellular clocks are synchronized and coordinated by neural elements. For example, the Suprachiasmatic Nucleus (SCN) houses the biological clock that synchronizes rhythms in homeostatic mechanisms and behavior (Sollars and Pickard 2015). The SCN receives input from specialized cells in the retina that synchronize its rhythms to external light cues and maintains connections with the hypothalamus and pineal gland to regulate a variety of functions. Transplantation of the SCN into the hypothalamus synchronizes rhythms – restoring behavioral rhythms (wheel running) without direct innervation suggesting that chemical messengers – neurotransmitters and hormones – must be involved (Brain Research Reviews 33 (2000) 34–77 [www.elsevier.com/locate/bres](http://www.elsevier.com/locate/bres) Full-length review The suprachiasmatic nucleus and the circadian time-keeping system revisited a b a, Lisette (K.) E. van Esseveldt, Michael N. Lehman, Gerard J. Boer\*). The pineal plays a critical role in birds and reptiles – transplantation of the pineal can restore rhythms in arrhythmic sparrows (Zimmerman and Menaker 1979).

The circadian clock is regulated by a negative feedback loop that is maintained by the oscillation of the core clock genes, transcriptional factors that govern negative and positive feedback loops (van Esseveldt et al. 2000). Genes that govern this 24-h internal clock are referred to as clock genes: *Bmal1*, *Clock*, *Per1/2* and *Cry1/2*. A significant example of the internal clock at work can be noted in skeletal muscles, which make up about 45% of the body's total mass (Harfmann et al. 2015). 2300 genes in skeletal muscle are involved in the expression of circadian rhythms, which drive the functioning of this clock. Skeletal muscles are directly stimulated through feeding and activity but also indirectly through light entry into the SCN. This mechanism is synchronized with the rhythms of the environment and other issues of the body. When circadian rhythms of skeletal tissues



are disrupted, the structure of the sarcomere is changed; there is a decreased mitochondrial respiration rate and, ultimately, the muscle function is altered.

### Infradian/Lunar, Semilunar and Tidal Clocks

As noted by fishers, throughout the centuries many marine organisms utilize the cycles of the moon to regulate reproduction and growth. The nature of these clocks varies by species. For example, reproductive maturation of the marine worm *Platynereis dumerilii* is regulated by a circalunar clock that is synchronized by a circadian clock (Zantke et al. 2013), while the lunar rhythm of spawning in the Goldlined spinefoot fish is set by an hourglass clock (Takeuchi et al. 2018). Interestingly, the foraging behavior in the intertidal isopod, *Scyphax ornatus*, is regulated by the “beat frequency” created by the intersection of circadian and tidal rhythms (Cheeseman et al. 2017).

### Infradian/Seasonal Clocks

Species that live for many years in temperate climates show changes in physiology and reproduction that persist in constant conditions with periods close to a year. These rhythms can be synchronized to the external seasons with daylength and maintain different periods depending on the length of day they are exposed to indicating the existence of a circannual clock. A putative circannual clock has been identified within the pars tuberalis of seasonal vertebrates. This area of the pituitary contains thyrotrophs that lack receptors for thyrotropin releasing hormone. These PD-specific TSH cells show seasonal changes related to the production of the clock-regulated transcription regulator (EYA3). EYA3 induces TSH expression triggering long-day responses in birds and mammals (Wood and Loudon 2018). The PD-TSH cells contain melatonin receptors and are driven by melatonin which, in turn, is driven by the circadian system.

### Ultradian Clocks

Very short oscillations (2–4 h) in feeding and activity bouts have been identified in a number of species including, hamsters, voles, mice, and

deer. While the function of these rhythms is not clear – researchers have speculated that ultradian rhythms function to coordinate bouts of feeding in the wild providing safety in numbers. Ultradian rhythms correlate with circadian rhythms but are not dependent on them. Manipulations that alter circadian periods also lengthen ultradian periods. Nonetheless, ultradian rhythms persist under conditions that abolish circadian rhythmicity. For example, ablation of the SCN enhances ultradian rhythmicity indicating that the oscillations are not driven by the SCN. Ablation of the arcuate and the retrochiasmatic area abolishes ultradian rhythmicity suggesting a critical role for this area.

Several lines of evidence suggest that Dopamine may also play a role. Dopamine is released into the striatum (a key component in locomotor activity) in bouts that correlate with ultradian rhythmicity and manipulations that lengthen or shorten these bouts create parallel changes in ultradian periods suggesting that the VTA/SN may also be involved. Finally, it should be noted that a number of hormones are released in bursts. Ultradian rhythms are also present in a number of hormones including those that regulate reproduction, growth, and stress. Changes in the frequency of gonadotropin releasing hormones drives reproductive activity; changes in the pulsatile delivery of glucocorticoids is correlated with a number of diseases including: Alzheimers, anxiety depression, and PTSD (Prendergast and Zucker 2016).

## Sleep and Interval Timing

The regulation of sleep has been intensely studied and is still largely a mystery! The onset of sleep is determined by the circadian clock – we are sleepy at times readily predicted by the rhythms of alertness and our core body temperature. How long and how deeply we sleep appears to be dictated by an hourglass clock that is phase-locked with the 24-h biological clock but varies depending on the previous night's length of sleep. Sleep and interval timing are significantly connected mechanisms. One of the main functions of sleep is thought to be synaptic plasticity. Sleep acts as a mechanism for memory consolidation. This can

occur after a few minutes, hours or full night's sleep (Tucci 2012).

The connection between circadian rhythms and interval timing is not well-known. Some studies show that interval timing is dependent upon oscillatory mechanisms, noting a close relationship between these two entities. For example, studies have shown that circadian rhythms, which are longer, can alter shorter intervals, which can be seconds or minutes in length. On the other hand, other studies suggest that interval timing and circadian rhythms are separate entities, through SCN lesion studies and studies of interval timing in mice with arrhythmic circadian rhythms (Tucci 2012).

## Clocks and Disease

Several disorders can result from disruptions to the circadian clock. (Disruptions in circadian rhythmicity induced by shift work and jet lag have been linked to disorders of metabolism and the immunity that predispose diabetes and cancer.) Mental health disorders such as major depressive disorder and seasonal affective disorder appear to result from endogenous factors that misalign the circadian system with the external environment. More recently studies suggest that alzhiemers may desynchronize the circadian system, rendering it more susceptible to other disorders. Far less is known about how hourglass clocks contribute to our health and as hourglass timers regulate development and ageing – more attention should be paid to these systems (Bass and Lazar 2016).

## Cross-References

### ► Day/Night Cycle

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## Internal Fertilization

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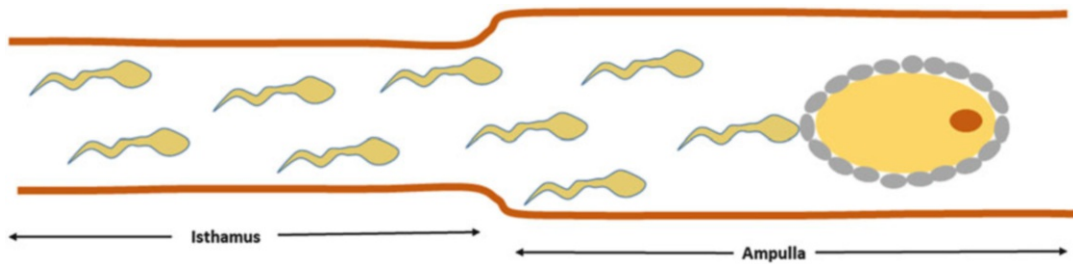
Internal fertilization is the process in which fusion of male and female gametes occur inside the body of females. Internal fertilization is most common in land-based terrestrial animals, but few aquatic animals also employ this mode of fertilization. Fertilization refers to the amalgamation of haploid male and female gametes (sperm and oocyte) in a series of well-coordinated molecular events, which eventually leads to the formation of diploid zygote. Fertilization leads to the merging of genetic material within the species, which results in genetic variation in the organisms. In sexual reproduction, two modes of fertilization have been noted in animals – internal fertilization and external fertilization. In internal fertilization, the amphimixis (fusion of male and female gametes) process occurs within the body of females, and the zygote starts developing inside the mother's body. Under external fertilization, the union of eggs and spermatozoa occurs outside the female body in a medium like water where the concerned animals reside. In this entry, we will be discussing internal fertilization in more detail. Internal fertilization which is often seen in land animals has three types:

1. Oviparity: The fertilized eggs are laid outside the female's body and develop there; yolk part of the egg serves as the source of nourishment.
2. Ovoviviparity: The fertilized eggs are retained in the female, and the embryo fulfills its nourishment requirement from the egg yolk.

3. Viviparity: The embryo formed develops within the female and receives its nourishment from the mother's blood through a placenta.

The significant events which take place during the process of fertilization include copulation and insemination, transport of sperms, binding of the spermatozoon to the egg, induction of acrosomal reaction by spermatozoa, and fusion of spermatozoon and egg which ultimately results in a diploid zygote. All these events require excellent coordination between all the key molecules involved in this intriguing process.

Millions of spermatozoa travel through the cervix, until some of them successfully reach oocyte, and in this course of the journey, many of them die due to the acidic environment, innate immune responses by the female reproductive tract. Spermatozoa undergo the process of capacitation by which they attain functional maturation in the fallopian tube (Ickowicz et al. 2012). Once spermatozoa attain capacitation, they become hypermotile and move toward the oocyte. Capacitation involves alterations in the phosphorylation state of proteins, a rise in intracellular pH and calcium levels and hyperpolarization of membrane potential. An exocytotic event occurring after capacitation is acrosomal reaction, which is another prerequisite for fertilization to occur. It makes a spermatozoon capable of penetrating the zona pellucida layer of the oocyte (Crozet 1994). Izumo, a kind of protein, specifically present on sperm, plays a pivotal role in binding and fusion of sperm and egg plasma membrane. A member of the folate receptor family, Juno, recognizes IZUMO, which is followed by fertilization taking place. The fusion between oocyte and spermatozoon causes the cessation of the beating of the tail by the spermatozoon. Sperm is drawn into the oocyte by the elongation and fusion of the microvilli of the egg, and this leads to the incorporation of sperm nucleus and other organelles into the oocyte cytoplasm (Georgadaki et al. 2016). The membrane of oocyte undergoes depolarization massively after fertilization. This depolarization is achieved by the influx of plethora of  $\text{Na}^+$  ions depolarization of the egg is followed by repolarization via  $\text{K}^+$



**Internal Fertilization, Fig. 1** Schematic illustration of spermatozoa traveling through the fallopian tube, from isthmus making its way toward ovum, which lies in the ampulla region of the fallopian tube. Spermatozoon

interacts with the zona pellucida, and this interaction leads to changes in the zona pellucida as a result of which other spermatozoa are not able to interact with the ovum, thus inhibiting polyspermy

leakage, which induces fast block polyspermy and the sperm is not able to fuse membrane that is not  $-70$  mV. A permanent barrier is established for sperm entry by cortical reaction which propagates over the egg surface (Gilbert 2000).

Internal fertilization has certain advantages over external fertilization as a mode for reproduction in animals, which includes the protection of young one against predators, thus increasing the chances of survival; the probability of successful fertilization is much higher in case of internal fertilization versus external fertilization, and the dehydration of gametes is also prevented in case of internal fertilization. Moreover, internal fertilization is less demanding in terms of resource expenditure along with greater survival chances of young ones. However, in internal fertilization male and female has to be in intimate contact for game transfer and under this process limited number of offspring are produced as compared to external fertilization. Additionally, in internal fertilization chances of sexually transmitted diseases pose a risk to copulating individuals in all animal species, which is not the case in external fertilization (Fig. 1).

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## Interpretation Bias

### ► Judgment Bias

## Intersexual Differences

### ► Sexual Dimorphism

## Intersexual Selection

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## Introduction

Reproductive traits are those parameters that are most influenced by evolutionary change. There are several evolutionary forces like genetic drift, mutation, and natural selection that become threat

to the survival of any species. Males and females both change their mating behavior in accordance to the prevailing environment so as to adapt and increase their survival and fitness. Males and females have varying strategy for achieving reproductive fitness. According to Bateman's principle (1948), female produces very less number of gametes that constitute enormous proteins and other biomolecules as compared to the male gametes that are smaller, numerous, and not so nutrient enriched either. Female gametes are therefore more costly than of males and consequently females becomes a limiting sex. So there is a tendency in males to compete for maximum number of females for mating and inherit maximum number of progenies to increase their fitness, while females choose the best male which will bore them the fit progeny. Females have more parental care roles besides reproduction, and as a result females throughout all species are very selective for choosing mating partners. This creates an antagonistic coevolution and causes high competition among males to possess maximum elaborative features. Choosing mates on the basis of sexual and other reproductive traits in one sex by the other causes intersexual competition, and its permanence during the course of evolution leads to intersexual selection.

Females ascribe their fitness to certain parameters present in males such as territorial quality, food, or decorative phenotypes. There are enormous examples of mating behavior displayed by males displaying such attributes to attract females. Charles Darwin and Alfred Russel Wallace first gave the concept of attracting mating partners by males through specific behavior, e.g., mating calls in frogs by croaking at the water's edge, and then the female chooses the male with the deepest croaking sound and territorial quality so that it would pass to her progeny and by that she can have maximum grandchildren. According to Richard Dawkins (1976), females that prefer long and attractive tailed males tend to have mothers that have the same trait of choosing such males, and therefore female progeny carry two traits, one the preference for long tail and other to bear such trait so that it will pass to her son. So in nature these two traits are linked with

each other and both have positive correlation with each other. According to Bateman's principle, female when searching for mate keeps rejecting males that she considers unsuitable for her, and then such males are unable to pass their genes in nature, while for female the risk of dropping such "unfit" males is lower than investing time and resources in searching for the attractive and fit male. So according to Bateman, the sex whose main objective is to produce the most fit progeny and choose mates accordingly becomes the limited sex for which other one competes. Males reside in intense competition in possessing these parameters better than others and strive for access to maximum number of females. This can be a very strong reason for why modification brought in secondary sexual characteristics is predominantly in males.

So it drives species through adaptation responses toward mate choice (Darwin and Wallace 1858). This sort of mate choice is called as sexual selection, and it leads to sexual dimorphism in secondary sexual characteristics in both males and females. The presence of elaborate and colorful tail feathers in male peacock manes in lions, antlers in deer and songs in birds during breeding seasons, difference in body color between males and females in birds, larger body size of males in Cichlid fish *Neolamprologus callipterus*, black-throated blue warblers and Guianan cock-of-the-rocks that also differ radically in their plumage between the sex are the various examples of this observable fact. Sexual selection is also found in plants and fungi (Moore et al. 2011).

Intersexual selection creates genetic variation and thus more fit generations are produced. It is mainly caused by presence of intrasexual competition among males. Factors influencing male intrasexual competition are cases where food, habitat, and mates become a limiting factor which leads to aggression among males. In male-biased sex ratios, even small males take the risk of fighting with larger male in the presence of female for mating opportunities. These sorts of conditions put pressure on males to modulate their mating behavior and on secondary sexual characteristics, i.e., phenotypic traits to increase their fitness.



**Intersexual Fitness:** This is defined as achieving fitness by male or female at the cost of the others' lifespan. Usually males perform more matings than females, and it decreases longevity of the former, while females are found to be adaptive toward increased matings. Male harm females either physically like traumatic insemination, forced copulation, love darts, etc. or physiologically like transfer of accessory proteins, e.g., in *Drosophila* that would decrease female's longevity. Females too evolve counter-adaptations in order to protect themselves from frequent matings. In some species females respond by various means like sexual cannibalism and increased aggression to males (e.g., praying mantis).

## Sexual Conflict

Sexual conflict is a specific type of evolutionary conflict that occurs when males and females have evolved different reproductive behavioral strategies to gain fitness (Parker 2006). This conflict leads to evolutionary arms race due to the mode of reproduction in each sex that harms the other one to achieve fitness (Lessels 2006). There are cases of sexual conflict, for example, where male dominance is found as in wolves, rabbits, and crocodiles and female dominance like spiders, ants, and orcas. In species which are male dominated, males are usually polygamous and larger in size, possess high reproductive success, and have less or no parental care, while in female-dominant populations, females are larger in size with high fitness and prefer mates only on the basis of territorial, habitat, or food offered to her by the male before mating. Therefore sexual conflict is a factor that makes evolutionary changes in both the sexes. In *Drosophila*, e.g., males displace the previous mated male's sperm and transfer biochemical metabolites that enable the female to remate for some time interval. Males also show aggressive behavior toward other males in the form of male-male combat and toward female in the form of mate guarding or forced copulation. They behave in these manners in order to assure their paternity success. Morphological adaptations in males toward competition include development

of male claspers, altered genitalia (e.g., spiky genitals), and copulatory plugs (*Lacerta monticola*). The level of intrasexual competition for mates also affects the anatomy of reproductive glands, seminal vesicles, and interior prostates. Sexual conflict before and during mating comprises following aspects:

**Infanticide:** Some animals also perform infanticide. In this case mostly males used to cause damage to their eggs or kill their young ones to increase its fitness. The advantage gained by this is that the parent, who is providing care to the eggs, after the destruction of eggs or death of the offspring, will be available for mating with the destroyer male or female individual. Examples of such cases are found in big cats, *Jacana jacana*, and mice.

**Traumatic insemination:** In this type of mating behavior, male used to penetrate his genitalia inside females reproductive tract, forcefully in order to ensure paternity success. This is called traumatic insemination. In some cases it leads to death of the female, e.g., bed bugs and spiders.

**Physiological barriers:** In *Drosophila melanogaster*, males used to transfer toxic semen that contains accessory proteins to the mating female that hinder her lifespan. In *Drosophila hibisci*, males used to create mating plugs in female to provide nourishment to her besides preventing the sperm of rival male to fertilize the female.

**Aggression:** Males in many species commit force copulation with female in which they do harassment and grasping. In harassment, male chases female and annoys her from distance. In the case of Malabar ricefish, when the male observes that female is ready to copulate, it attacks her from distance and releases his club-shaped organ inside the female which causes harm to the female. Males perform grasping in order to avoid the female to be mated by rival male and ensure his paternity success. The resistant female is able to remove the male from her side, but the female which is not so strong becomes unable to move due to the weight of the male attached to her.

*Sexual cannibalism*: It includes the consumption of the mating male by the female partner in order to increase the quality of her offspring by receiving nutrients from the consumed male. Males sometimes manipulate females and use their strong appetite to their advantage by giving them edible gift of another males to protect themselves from being eaten, e.g., funnel-web spider (*Hololena curta*).

*Antiaphrodisiac*: In this behavior males transfer certain chemicals to females that are only produced in males and which let other males to identify individuals as males. So when these chemicals will be transferred to females, other males will consider them as males and will avoid any mating. This will help the male that had first mated with the female to reduce competition for mating and secure its paternity.

## Theories on Evolution

Evolution of male secondary sexual characters and other ornamental features can be attributed to choosiness of female in selecting elaborative males who pretend to be more fit and capable of raising “superior sons” and increase fitness in females. Males too evolve by deceiving females of their fitness traits and attracting maximum of them and then causing harm to them.

*Good Genes Theory*: This theory is termed as the sexy son hypothesis and was first proposed by Weatherhead and Robertson (1979). According to this hypothesis, females prefer to mate with those males that mostly produce male offspring and that too of high reproductive success. Ronald Fisher (1930) gave the term “sexy son hypothesis” which means that females tend to mate with those males that possess attractive phenotypic features and will produce alike sons with elaborative traits. It may be a reason why only such peacocks are observed today that have elaborative feathers because this trait had been selected in nature due to the preference of such males over others that lack such traits. Females in all subsequent generations that had inherited these qualities of preferring such males and continued reproducing sons and daughters from such mating allow selection of

these traits in nature creating “Fisherian runaway sexy son process” (Mead and Arnold 2004). This creates a condition of assortative mating or homogamy in which individuals who are alike prefer to mate with each other and lead to the survival of individuals which have similar genotypes and phenotypes.

*Zahavi's Principle*: This theory was first postulated by Zahavi, 1975. According to this theory, males in certain species show traits that negatively affect their fitness, and therefore they signal that in spite of possessing elaborative and costly features that hinder their fitness and other life history traits, they are carrying it with ease. So it signals that males that carry such traits are more fit, females chooses these males because they consider them to be strong and hence prefer them over other males to produce such sons which will have such traits.

In 1984, W. D. Hamilton and Marlene Zuk proposed a theory of “Bright Male” according to which females consider males with exaggerated features as they consider them to be resistant toward diseases and deficiency and therefore fit to mate.

## Sex-Biased Gene Expression

Sexual dimorphism is due to selective expression of certain genes in different environmental conditions in both males and females. The role of natural selection on the sex that expressed maximum of the characters required to achieve fitness or subjected to sexual selection amidst of intrasexual competition and mate choice can be attributed to difference in gene expression (Ellegren et al. 2007). Sexual antagonism is another concept that creates sex-specific gene expression due to the occurrence of sexual conflict that leads to evolutionary arms race, i.e., when certain competing set of genes coevolve. This gives rise to selection of these genes in males and females differentially at single or multiple locus and eventually selection of those locus that are antagonistic in one sex to the other. These loci carry genes that enhance certain traits in one sex and suppress the same in the other one. This helps in retaining all alleles in

both sexes and thus evolves interlocus sexual conflict (Partridge et al. 1998). There are genes in X chromosomes and autosomes that represent traits that are antagonistic to the opposite sex in the animals worldwide. They can be present on autosomes, and their expression can be either sex limited or absent but harmful for the other sex. In *D. melanogaster*, there are antagonistic genes present on X, second, and third chromosomes.

## Sexual Dimorphism

It occurs in different forms like size, weight, color, markings, and behavioral and cognitive differences. These differences are selected in nature when they are beneficial for the species during the course of evolution. There are following attributes of sexual dimorphism:

*Ornamentation and coloration:* Ornamentation and coloration are a form of sexual dimorphic trait which is found in birds and reptiles. When animals carry these traits in which mostly are males, they have to compensate its costs while carrying and maintaining it while increasing its fitness at the same time, e.g., peafowl, birds of paradise, and argus pheasants. In the case of nestling blue tits, males develop violet-tinted plumage because they feed on lepidopteran larvae, which contain large amounts of the carotenoids, lutein and zeaxanthin. Females prefer such males because blue-colored plumage is an indicator of male parental abilities and that it is capable of obtaining carotenoid and thus has strong immune function.

Females prefer males which possess brightly colored features against males that appear pale and dull, and one example is male guppies which possess colorful spots and ornamentations, while females are generally gray in color. Males with colorful spots are preferred over males that don't possess such.

*Physiological differences:* In redlip blennies, male fish develops an organ at the anal-urogenital that produces antimicrobial substances and protects egg from microbial infections.

*Spiders and sexual cannibalism:* In spiders and insects like praying mantis, there is selection for large body size in females for mating by males because such females avoid eating the male before copulation and males therefore prefer to mate with females that are feeding at the time of courtship or they modify the female's web or provide a nuptial gift to them in the form of a dead insect so they are escaped from death.

*Fish:* In fishes, mostly females are larger in size than males, but wherever males have more parental care role, they are found to be larger, e.g., *Lamprologus callipterus*. In this females choose larger males because they will be able to collect maximum empty shells and females need these shells to lay their eggs and if female are larger than a limit, it will not fit in the shell and will be unable to breed. Choosing larger males allows female to join its brood and allow itself to increase its size because that male can collect large shells. Male-male aggression and combats are also responsible for male's large size to increase the access to maximum number of females. Another example is dragonet, in which males are larger than females and possess longer fins.

*Amphibians and reptiles:* In reptiles there is a wide range of sexual dimorphism observed across taxa. It differs in various traits in anatomy like relative length of tail, relative size of head, overall size (e.g., vipers, lizards), coloration (e.g., amphibians, snakes, and lizards), ornamental features (e.g., newts and lizards), and morphological and physiological differences (e.g., frogs). Male coloration in dragon lizards *Ctenophorus pictus* is an indicator of innate anti-oxidation capacity to females that protects against oxidative DNA damage (Olsson et al. 2012).

*Birds:* Sexual dimorphism in birds can be observed in size and plumage differences. Generally males are larger than females except in some cases like birds of prey, hummingbird, and some species of flightless birds (Andersson 1994). Plumage dimorphism varies among the birds which depend upon

the role of males in raising the younger one. If the male contribution is only limited to mating and copulation, then these males' plumage is more vibrant than those who take care of their young ones by defending and feeding them. Birds acquiring vibrant features have to pay its cost by becoming more conspicuous to predators and putting their life in danger. So long as the benefit of these attractive features in increasing their fitness is more than the cost of losing life, these features are selected in nature and propagated by enormous number of young ones produced by attractive males.

**Mammals:** In mammals males are always larger in size than females, and it is due to the effect of reproductive hormones that play a role at early stages of embryonic development. This difference in size is due to presence of more male aggression, defending the mate and involvement in parental care.

**Reproductive advantage:** In maximum number of cases, females are larger than males because during the course of evolution, female has this load of producing maximum young ones and male must search for females while females tend to be sedentary. This also led to selection of distinct morphometric and physiological traits in both the sexes.

Intersexual selection is thus driven by intersexual conflict that persists in almost each taxon of animal kingdom. It involves modification in mating, phenotype, and physiological aspects in both the sexes but predominantly in males because they should display all such characters to increase their fitness, while for females they are the costlier and choosier sex. In all groups where males are involved in less parental care, they either are more attractive or show distinctive mating calls and territorial ability, aggression, and manipulation. In species where the mating pair is monogamous in nature, there is very less difference between sexual dimorphism between male and female, e.g., sandhill crane, seahorse, gray wolf, barn owl, gibbons, black vultures, and beavers. So it clearly indicates that occurrence of gender roles

creates various types of sexual conflict and leads to intersexual selection.

## Cross-References

- [Female Choice](#)
- [Reproductive Fitness](#)

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## Interspecific Brood Parasitism

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### Definition

A breeding strategy in which one species is able to manipulate a different host species into forfeiting some or all of their parental investment into rearing the parasite's offspring. This often coevolutionary relationship is a potential source of evolutionary arms races as species develop increased measures to defend reproductive investment in the case of hosts, or for parasites, to more successfully ensure host compliance.

### Introduction

For many species, the process of reproduction is a period of high-energy investment with profound consequences for organismal fitness, and in ideal mitigation of these costs, an unusual breeding strategy has emerged. Interspecific brood parasitism (IBP) is a breeding strategy in which a parasitic species seeks to exploit the reproductive investment or parental care of another host species for their own offspring's benefit. This breeding strategy often elicits vivid relationships among parasites and hosts: a Superb Fairywren (*Malurus cyaneus*) feeding what it believes to be its offspring; a begging Bronze Cuckoo (*Cacomantis variolosus*) chick multiple times its size (Langmore 2012); a Large Blue butterfly (*Maculinea rebeli*) caterpillar receiving royal treatment and from an *Myrmica* ant colony after mimicking the ant queens' movements and scent (Akino et al. 1999); a mouthbrooding African lake cichlid providing food and shelter for Cuckoo Catfish (*Synodontis multipunctatus*) offspring from the inside of its own mouth (Sato 1986).

Parental care is widely known to be highly impactful in improving offspring survival, but this is not without cost (Clutton-Brock 1991). Behaviors such as offspring defense, nest

building, and food provisioning are activities that are highly time- and energy-consuming and may often imply an increase in predation risk for the parental individual (Trivers 1972; Roldán and Soler 2011). Considering these costs, the ability for a parasite to bestow costly parental duties onto another, unrelated species can be a high reward to the parasitic individual allowing for more time and energy to gather resources, avoid predators, and even, theoretically, to have more offspring (Payne 1977; Rothstein 1990). By engaging in this form reproductive behavior, these brood parasites can gain a variety of benefits for them and their offspring including nest usurpation, theft of stored resources, exploitation of eusocial worker labor, or even gaining complete care and provisioning by the host species (Soler 2019). Consequently, a host that plays into supporting or raising a completely different species than its own is a major detriment to the host's fitness usually through the diversion of resources away from the host's own young. However, if the care of parasitic offspring imposes such a great burden to the host or if the parasite eliminates the host's own offspring completely, the breeding success of the host diminishes to zero (Kilner and Langmore 2011; Feeney et al. 2014; Soler 2019). These drastic costs to host fitness are what often leads to the evolution of reciprocal host defenses to avoid being parasitized and these may include such strategies as parasite egg rejection, increased vigilance, nest site selection defense, and even nest abandonment (Soler 2019). This basic framework of parasite and host species evolving to select for adaptations that better appropriate or defend valuable reproductive investment is responsible for the well-documented and studied, coevolutionary "arms race" that may develop (Feeney et al. 2012).

In spite of the seemingly contrived nature of IBP, the breeding system itself is rather widespread phylogenetically, occurring across multiple lineages in birds, insects, and fish. Given this widespread and often visible nature, IBP has, and continued to be, a topic of persistent research across a multiple biological subfields. To that end, the abundant and diverse literature on IBP has become filled with systematics, models, and



theories to best explain the taxonomy of interspecific brood parasites, how IBP arose evolutionarily, and the diverse adaptations of parasites and hosts that have come to characterize this breeding strategy.

## Taxonomy of IBP

Across the animal kingdom, forms of brood parasitism are presumed to be rather common in species that exhibit parental care (Soler 2019). Although interspecific brood parasitism in particular is also widespread, it is more restrictive, with the only known species engaging in IBP being insects, birds, and fish.

The most widely known and studied cases of interspecific brood parasitism occur in birds. Within this group, IBP is found within 4 orders of the 40 orders of birds worldwide—Anseriformes (Family Anatidae), Cuculiformes (Family Cuculidae), Piciformes (Family Indicatoridae), and Passeriformes (Families Viduidae and Icteridae) (Mann 2017). Among insects, interspecific brood parasites are most common in social hymenopterans such as wasps, bees, bumblebees, and especially ants. Although concrete numbers for interspecific insect brood parasites are more difficult to estimate due to the volume of potential candidate species, there are more than 200 described species in eusocial ants, the best studied of this group (Soler 2019). The only other known cases of interspecific brood parasitism are found within the cichlid fish family: the Cuckoo Catfish (*Synodontis multipunctatus*) and the Sapuwa (*Bathyclarias nyasensis*) (Sato 1986; Stauffer and Loftus, 2010).

## IBP Evolution and Coevolution

In spite of its known and presumed abundance within many insect clades, the evolution of IBP in insects has been largely neglected (Buschinger 2009). However, given that many parasitic species and their hosts are close phylogenetic relatives, some have speculated that IBP in insects has evolved many times independently (Buschinger

2009; Soler 2019). However, given that some insects engage in IBP across of orders, such as in the caterpillar of the butterfly's (*Maculinea rebeli*) parasitism of *Myrmica* ants, there must be even more profound changes to the parasites' life history, physiology, and ecology (Akino et al. 1999). The complexities between these kinds of changes has made the prospect of gaining a clear consensus on IBP's evolution in insects an intriguing challenge for further studies.

Generally speaking, avian brood parasites have received the most attention and through examination over the years, and while a clear consensus on the evolution of IBP within this group has not emerged, the plethora of studies on avian IBP has lent itself to multiple perspectives on the origins and maintenance of this breeding strategy. Most theories regarding the evolutionary origins of IBP have suggested that IBP emerged later in species that had already been engaging in conspecific brood parasitism (CBP) (Lyon and Eadie 2017). This had been reasoned through the idea that due to CBP also alleviating parental care costs, parasitic species engaging in CBP may have been more likely to use this strategy without significant negative effects. Particularly in populations with many individuals partaking in CBP, parasitizing other similar species' nests could have developed as another option to retain the benefits of parasitism while not being constrained to find conspecific hosts (Lyon and Eadie 2017). However, other studies have used phylogenetics to conclude that CBP and IBP are not necessarily as closely linked, suggesting that the state of parental ancestral care can lead to brood parasitism without explicitly requiring CBP to act as a precursor (Krüger and Pauli 2017). Multiple other factors, such as cooperative breeding, increased nest predation, and nest site competition, have been suggested as potentially favoring the evolution of avian IBP, but unanimous support for any of these factors, among others, has not been achieved (Feeney et al. 2012; Soler 2019).

When examining the evolution of IBP, it is imperative to also take into account the coevolution of host defenses as these crucial, reciprocal adaptations play an equally important role in the

commonly associated evolutionary arms race between parasites and hosts. This basic arms-race framework has been dissected and expanded upon in recent years to better explain how these interactions may have further developed into the brood parasitic relationships observed (Feeney 2017). One of the most successful modalities of understanding this coevolution is through the division of the coevolutionary arms race into a complex sequence of coevolutionary stages in which no stage of defense is independent of each other, and, in which the arms race between parasites and hosts functions on each level (Soler 2019). To that end, a successful adaptive defense at any stages of the breeding cycle would prevent the evolution of later lines of defense, and successful resistance by a host can be achieved with one or more successful defenses at any stage of the breeding cycle. These stages in which the coevolutionary arms race functions on parasite and host adaptations are: the pre-laying stage, the egg stage, the nestling stage, and the fledgling stage.

## Adaptations and Counter-Adaptations Through Coevolutionary Stages

### The Pre-laying Stage

The first opportunity parasites and hosts to develop strategies and defenses is before the egg is even laid, and the interactions in the pre-laying stage have become known as “frontline” defenses (Feeney et al. 2012). During this stage, hosts can utilize a variety of different tactics to avoid being parasitized that include asynchronous breeding phenology (Medina and Langmore 2016), nest concealment or placement (Hauber and Russo 2000), attacking or mobbing known parasites (Feeney et al. 2012), among others. At this stage, parasites have also evolved certain strategies in order to combat these frontline host defenses. Many studies have focused on the cognitive adaptations that have been seen in certain avian brood parasites that have allowed them to circumvent some of the pre-laying defenses of hosts. These include increased spatial memory in females, assessment of host readiness, and the modification

of nest searching strategies in relation to host availability (Guigueno et al. 2014; Jelinek et al. 2014). Parasites may also use deceptive camouflage as well as to cryptic behavioral and movement patterns to spy on susceptible hosts and lay eggs quickly and discreetly in unguarded nests (Feeney et al. 2012; Langmore 2012). Lastly, it has been shown that one commonly studied brood parasite, the Brown-headed Cowbird (*Molothrus ater*), may tactically destroy hosts found too far into the breeding cycle. This “farming” behavior forces hosts to renest, potentially increasing available nest sites in the future (Swan et al. 2015).

### The Egg Stage

If the hosts’ defenses fail at the pre-laying stage and the brood parasite is able to lay an egg in the host’s nest, another arms race can be said to occur at this stage, also known as the egg stage, of the breeding cycle. Over the years, many studies have examined what is perhaps the most widespread and effective host defense against brood parasitism: the rejection of parasitic eggs (Soler 2019). Although egg rejection is known to have a genetic basis (Martín-Gálvez et al. 2006), factors such as egg-recognition ability, physical capabilities of the host species, and particular characteristics of the parasitic egg are all known to influence the actions of the host. Additionally, egg rejection is not without potential costs as incorrectly rejecting one of the host species’ own eggs or accidentally breaking the hosts’ own eggs during rejection has negative impacts on fitness (Soler 2019).

The rejection of parasitic eggs, especially of those between different species, is a complex cognitive process that has been, and remains, a topic of continued research (Bán et al. 2013). Two different cognitive mechanisms have been identified being key in this behavior: rejection by discordance, in which rejection is based off of the parasitic egg being a minority among the clutch of more similar eggs, and true rejection, in which the parasitic egg differs from the host’s own internal picture on what its eggs resemble (Bán et al. 2013). Once the host has discriminated and then chosen to reject an egg from its nest, there are four known ways in which it may do so: by burying the parasitic egg within the nest material, by

constructing a new nest on top of the clutch containing the parasitic egg, by deserting the parasitized nest, or by ejecting the parasitic egg (Soler 2019). Ejection of the parasitic egg is the most widely observed and effective defense among hosts with more than 60% of potential avian host species, even many not currently known to be parasitized, being able to eject a dissimilar parasitic egg (Soler 2019). Birds are physically able to eject the parasitic egg by grasping the entire egg with their bill or puncturing the eggshell and grasping the shell through the resulting hole (Soler 2019).

To avoid egg rejection or ejection, interspecific parasites have evolved a variety of counter-adaptations to better ensure that the host accepts the parasitic egg. Most of these counter-adaptations revolve around the evolution and production of eggs that are either difficult to distinguish in the nest, more attractive to potential hosts, or, are harder to eject or destroy (Davies 2011). Perhaps the most common evolutionary strategy that parasites use against egg rejection is egg mimicry: laying eggs that seek to ape the appearance of host eggs. A multitude of studies have demonstrated that host species tend to reject dissimilar eggs leading to parasites developing eggs that mimic the size, shape, color, pattern, and weight of their average hosts' eggs (Soler 2019; Davies 2011). Increases in egg mimicry elicits a strong evolutionary push for hosts to develop better egg discrimination abilities, which in turn, pushes parasites to select for more deceptive egg attributes (Davies 2011).

In addition to developing more similar egg attributes, interspecific parasites have used other tactics to enforce host acceptance of parasitic eggs. Certain avian parasites have been known to depredate the nests of noncompliant hosts that have rejected the parasites' eggs. This "mafia-like" behavior induces renesting in hosts, and upon subsequent parasitism, a higher potential for these hosts accepting the parasitic egg (Hoover and Robinson 2007). This is largely because, in this system, rejection may incur an increased cost for hosts when compared to accepting the parasitic egg. Due to the parasites' behavior, egg rejection will result in complete

clutch and nest destruction while acceptance provides at least the potential to retain some of the hosts offspring. Thus, the fitness costs imposed through these parasites' retaliatory behavior interestingly encourages selection for host acceptance of parasitism (Hoover and Robinson 2007).

### The Nestling Stage

While host defenses against parasitism at the pre-laying and egg stages of the breeding have been much more intensively studied, there has been considerably less research undertaken for potential adaptations at the nestling stage. This is because chick discrimination has largely been thought of to be a nonexistent or a weak defensive tactic against parasitism due to the high cost of incorrectly rejecting one's own chick, and relatively low concrete fitness benefits of rejection at this stage (Soler 2019). Furthermore, Lotem (1993) provided a strong model reasoning that nestling recognition tactics are less likely to evolve as the cognitive behavior of "mis-imprinting," or learning to recognize the parasite's offspring as the parents' own, exceeds the benefit of correct learning. In spite of these ideas, recent studies have found evidence for nestling rejection being a more viable possibility among host species. Studies on Australia's Superb Fairywren (*Malurus cyaneus*) have shown that these frequent hosts of various brood parasitic cuckoo species were able to reject cuckoo offspring by not provisioning the nestling or by abandoning the nest altogether (Langmore et al. 2003). As per the course of organisms involved in coevolutionary arms races, this adaptation has selected for parasites to develop counter-adaptations to prevent nestling discrimination. These adaptations have included parasitic offsprings' mimicking the appearance of host-nestlings, among other known adaptations (Davies 2011; Soler 2019). In fact, multiple mechanisms have been described as ways for parasitic nestlings to ensure compliance and procure increased parental care from their host parents. Some of these parasitic adaptations include the mimicry of host offspring's begging calls, more pronounced or conspicuous begging calls than the host's offspring, and integrating visual nestling displays (Soler 2019). All of

these adaptations are likely to select for more counter-adaptations that increase the competitive ability of host nestlings (Feeney et al. 2014).

### The Fledgling Stage

There is little information on the coevolutionary adaptations of hosts and parasites during the post-fledgling period of the breeding cycle. In spite of this, a few recent studies have determined that the coevolutionary arms race may indeed persist through this period. In Grayish Baywings (*Agelaioides badius*), potential host defenses at the fledgling stage can be observed in the provisioning behavior of parents; parasitic fledglings of one cowbird species – the Screaming Cowbird (*Molothrus rufoaxillaris*) – that mimics the begging behavior of the graywing offspring received provisioning while the fledglings of another parasite that does not mimic host offspring begging behavior – The Shiny Cowbird (*Molothrus bonariensis*) – did not receive much parental care (De Mársico et al. 2012). Another example of a potential host defense at the fledgling stage has been observed in Magpies (*Pica pica*). Magpies, the main host of the Great Spotted Cuckoo (*Clamator glandarius*), will feed parasitic fledglings only when the parasite is reared along in the nest; when a parasite is raised among the host magpie's own brood, the parent refuses to feed the fledgling (Soler 2019). Although evidence for parasitic counter-adaptations to these host defenses still remains scant, one study within the same magpie-cuckoo system determined that cuckoo fledglings from mixed-brood parents that were receiving less frequent parental care would abandon their magpie "parents" and join with other cuckoo fledglings that had been raised in non-mixed broods where they could be provisioned until independence (Roldán and Soler 2011). In this situation, the cuckoo fledgling's new magpie hosts would indeed "adopt" the fledgling, suggesting that the presence of the hosts' own fledglings may serve as an indicator for the host to identify parasitic fledglings (Roldán and Soler 2011; Soler 2019). Through these examples, among some others, it is known that the coevolutionary arms race does continue to encourage different adaptations at the fledgling of the breeding cycle.

### Conclusion

From its origins to the diverse adaptations associated with maintaining it, our understanding of interspecific brood parasitism, along with the coevolutionary arms race between parasites and hosts that it elicits, is a complex and continually changing affair. While the majority of research on this topic has overwhelmingly focused on avian IBP, new discoveries in insects and fish are providing the framework for deeper experimental dives onto the more discrete adaptations and counter-adaptations within these taxa. And as more research into the specifics of IBP in insects and fish continue, the genetic tools and perspectives that have bolstered our research in avian IBP will hopefully be applied here, helping to answer questions on the taxonomy and distribution of IBP in these understudied taxa. In addition, developmental, genetic, and neuroendocrine approaches to IBP research across taxa are continuing to refine and expand our understanding of different aspects of the breeding system such as the cognition of egg rejection, transgenerational effects of parasitism, and so much more. As these approaches answer questions regarding aspects of IBP in which our knowledge is already established, they will likely create new methods, ideas, and questions that can only seek to better explain the complexities of this extraordinary breeding strategy among species.

### Cross-References

- [Coevolution](#)
- [Mimicry](#)
- [Parental Investment](#)

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## Interspecific Group

### ► Polyspecific Associations

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## Interstimulus Interval (ISI)

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In Pavlovian conditioning, the interstimulus interval (ISI) is defined as the time between the onset of a conditioned stimulus (CS) and the onset



of an unconditioned stimulus (UCS or US). It is therefore often referred to as the CS-US interval. Traditionally, investigators have viewed the ISI as determining whether or not learning will occur. The focus has been on identifying the interval that provides the best evidence of learning and identifying the limits of the ISI that will permit learning. The typical finding is that the shorter the ISI, the greater the likelihood of conditioned responding and/or the greater the conditioned response. For example, Schneiderman and Gormezano (1964) found that for conditioning of the nictitating membrane (secondary eyelid) of rabbits, a 250-ms ISI resulted in nearly 100% conditioned responding in 350 trials. In contrast, with a 4,000-ms ISI, conditioned responding did not increase much beyond 25% in 560 trials. Subsequently, the optimal ISI for nictitating membrane conditioning was found to be between 200 and 400 ms (Smith et al. 1969; but see also Levinthal et al. 1985).

There are two types of Pavlovian conditioning procedures that may influence the timing between the CS and the US (Domjan 2015): (1) delayed conditioning which occurs when the CS starts before the US and continues during the US or ends when the US begins and (2) trace conditioning which is similar to delayed conditioning in that the CS starts before the US but the US is not presented until some time after the CS has ended. Therefore, the latter has a gap in time between the CS and US. In general, though with some exceptions, stronger conditioning occurs with delayed rather than trace conditioning.

Substantial levels of conditioned responding have been observed with relatively long delays between the onset of the CS and the onset of the US in other conditioning preparations, such as taste aversion learning (e.g., Garcia et al. 1966). Taste learning occurs when a novel-flavored food or liquid (CS) is ingested and results in some form of illness and/or aversive outcome, the US (Reilly and Schachtman 2009). If the illness is delayed for several hours (a long ISI), a taste aversion may still occur (Garcia et al. 1966). However, even in this preparation, the general finding has been that acquisition is inversely related to the length of the ISI.

More recently, evidence has indicated that the length of the ISI also determines *what* subjects learn

rather than whether or not they learn. For example, Holland (1980) tested the effects of the interval between the onset of visual and auditory CSs and a food US in rats. The results showed that short-duration (1, 5, and 10 s) auditory CSs evoked high frequencies of startle and head jerk responses, while long-interval (30 and 60 s) auditory CSs evoked less startle and head jerk movements and more magazine-directed conditioned responses. Thus, auditory and visual CSs paired with food evoked considerably different topographies of conditioned behavior, and the nature of these differences depended on the length of the ISI.

More recent research with Japanese quail and the sexual behavior system has provided additional evidence for changes in the response topography as a function of the ISI. Male Japanese quail served as subjects, and access to a sexually receptive female served as the US. Previous studies have shown that with a spatially localized CS (i.e., a wooden block), subjects learn to approach and increase their time near the CS as sexual conditioning proceeds (Domjan and Hall 1986). Initial studies using traditional measures of approach to the CS (time spent close to the CS) suggested that learning was inversely related to the length of the ISI and occurred only if the US was presented within 10 min of the start of the CS. However, more extensive observations indicated that increases in the length of the ISI changed the nature of the conditioned response. Approach behavior was evident with intervals as short as 1 min, but increased locomotor activity (pacing behavior over a wide spatial area) occurred when the interval was as long as 20 min. (Akins et al. 1994) Therefore, using different behavioral measures, learning was obtained with ISIs as long as 20 min. In this study, both approach and locomotor activity were conditioned responses because they were not evident in any of the control groups.

These findings are consistent with the behavioral systems view of learning proposed by Timberlake and Lucas (1989). According to this model, presentations of a US in a conditioning procedure activate the behavior system relevant to that US. Behavior systems are assumed to consist of a series of modules organized in a temporal-

spatial sequence. Thus, for example, presentations of small portions of food to hungry animals are assumed to activate the feeding system. The feeding system is organized in a temporal-spatial sequence, starting with general search behavior (controlled by contextual cues). Once a potential source of food has been located, a focal search module is activated, which results in behavior limited to a smaller area in which the food is presumably located. Once the food has been located, food handling and consummatory response modules are activated. According to this behavior systems view, Pavlovian conditioning results in integration of the CS into the behavior system activated by the US. The conditioned behavior that comes to be elicited by the CS depends on which module is activated at the time of the CS presentation and that in turn depends to a large extent on when the CS is presented relative to the presentation of food, the interstimulus interval. Long ISIs are assumed to result in the conditioning of general and localized search responses. By contrast, short ISIs are assumed to result in the conditioning of food handling and consummatory responses. Thus, the nature of the conditioned behavior is assumed to vary as a function of the ISI.

## Cross-References

- ▶ [Appetitive Response](#)
- ▶ [Behavior Systems](#)
- ▶ [Contingency](#)
- ▶ [Delay of Reinforcement](#)
- ▶ [Interval Timing](#)
- ▶ [Learning](#)
- ▶ [Michael Domjan](#)
- ▶ [Schedules of Reinforcement](#)
- ▶ [Taste Aversions](#)
- ▶ [Unconditioned Response](#)
- ▶ [Unconditioned Stimulus](#)

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## Interval Timing

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## Synonyms

[Time perception](#)

## Definition

Interval timing refers to perception and behavioral control with respect to time in the seconds to minutes range.

## Introduction

Adapting behavior to the temporal relationships that occur in the environment is critical for survival and requires both perception and behavioral control with respect to time. The perception of time without an external aid, such as a clock, is a capacity that is so inherent that it is often overlooked. We can easily conclude that a stoplight is broken because we sense that we have been sitting at the light for longer than is typical. But how is this temporal sense and behavioral control manifest? Modalities such as vision, audition, and olfaction are processed through dedicated sensory structures that are impacted by different forms of energy, in the form of light, sound waves, or volatile particles to influence perception. In contrast, time perception does not result from measuring change in one specific form of external energy, but instead appears to result from one or more neural systems processing their own dynamics (at least under conditions in which other sensory signals are not changing). Indeed, one can imagine being blind, deaf, or anosmic as a result of disruption of specialized sensory receptors, but it is nearly impossible to imagine existing without sensitivity to the passage of time.

## Temporal Ranges

Sensitivity to time is commonly broken down into three primary categories as a function of their duration, and these systems have different neural underpinnings: circadian, interval, and millisecond timing. In descending order of duration, circadian timing evolved with respect to the 24-h solar period. Circadian rhythms primarily regulate sleep and motor activity, although a range of physiological functions demonstrate a 24-h periodicity. The circadian system, heavily dependent

on the suprachiasmatic nucleus of the hypothalamus, is very precise (e.g., the standard deviation in wheel running activity in rodents is less than 2% of the 24-h period – Herzog et al. 2004), but pays for this precision with inflexibility. It is limited to timing intervals close to 24 h, and it is slow to reset when the light cycle abruptly shifts (e.g., we get jet lag). Interval timing allows temporal perception and control in the seconds to minutes range, although sensitivity to durations that are several hours long has also been deemed to utilize interval timing processes. Besides allowing temporally specific expectations, interval timing contributes to optimal foraging (Kacelnik and Brunner 2002) and associative learning (Balsam et al. 2006). Perception of intervals in the seconds to minutes range lacks the precision of the circadian system, with variability in temporal production in rodents on the order of 25% of the interval being timed (Church et al. 1994). However, the interval timing system appears to be equally sensitive to all durations in its range and is able to begin timing a new interval without waiting for a previous interval to elapse. Multiple durations can even be timed concurrently. While the neural structures underlying interval timing remain highly debated, this capacity does not require the suprachiasmatic nucleus (Lewis et al. 2003). Lastly millisecond timing systems allow detection and control of behavior of very short intervals. For example, fine motor control, such as used for speaking and its corresponding auditory perception, relies on millisecond timing mechanisms. Such fine temporal processing appears to depend on computational processes directly tied to anatomical features or synaptic dynamics (Buonomano and Merzenich 1995). For example, delay lines, allowing the speed of action potential transmission to mediate the interval, are a basic mechanism in the detection of location of an auditory signal by computing the difference in a sound's arrival time at the ears.

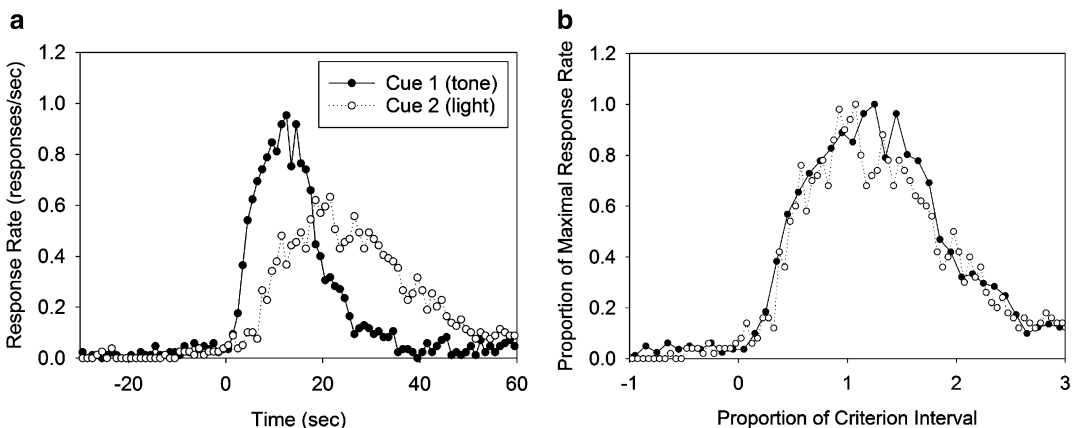
## Timing Tasks and Properties

Interval timing has been demonstrated across a wide range of species. While verbal estimation

and production procedures have been used in human research (e.g., “How long did that interval last?”; “Please indicate when 15s has elapsed.”), the potential for between-subject variability in mapping verbal labels to intervals may result in difficulties in interpreting results from these approaches. As such, the use of reproduction and discrimination procedures, which can be used similarly for both verbal and nonverbal animals, is preferred to assay the degree to which an organism is perceiving and utilizing temporally specific information. A commonly used reproduction task is the peak-interval procedure. In this task, subjects are trained on a discrete trial, fixed-interval schedule, in which the first operant response (e.g., a lever press), following the passage of a criterion duration from the onset of a signal, is reinforced. For example, a hungry rat might receive a food pellet for making a lever press after 10 s has elapsed since onset of a tone. Upon reinforcement, the signal terminates and an intertrial interval presents an opportunity for the food to be consumed. Lever presses prior to the criterion interval, and lever presses emitted in the absence of the signal are recorded, but there is no programmed consequence to their occurrence. After sufficient training, subjects respond selectively during the signal and differentially as a function of time since signal

onset. Plotting the average rate of lever pressing as a function of time since signal onset reveals that responding occurs at a low rate early in the interval and then increases in a nonlinear manner (i.e., a scallop pattern), reaching a maximal rate around the time of the fixed-interval duration. As an increasing response rate function might result from a nontemporal rule, “increase rate if prior response wasn’t reinforced,” non-reinforced probe trials lasting several times the fixed interval are presented on a subset of trials (e.g., 25% of trials) to ascertain the temporal specificity of responding. On these probe trials, average responding first increases as in a fixed-interval trial, but then following the criterion duration, response rate decreases, resulting in a roughly normal-shaped response function centered around the fixed-interval duration. The time of maximal responding, the peak time, is treated as the subject’s estimate of the time of reinforcement. A representative example of the average peak function from a single rat trained on this procedure is shown in Fig. 1.

As mentioned above, the interval timing system has considerable flexibility, enabling timing of multiple intervals. The data shown in the left panel of Fig. 1 came from a rat that was trained that one cue (i.e., a tone) indicated that food might



**Interval Timing, Fig. 1** Average response rate functions from a single rat trained in the peak-interval procedure. In this procedure, a food pellet could be earned for the first response made 10 s after onset of a tone or 20 s after onset of a light. Responses prior to these intervals had no programmed consequence. Data displayed are from non-

reinforced probe trials that lasted at least 60 s. The left panel shows the raw response rate in real time, while the right panel plots these same functions as a proportion of elapsed time and normalized by maximal rate, thereby showing the scalar property (Unpublished data by McGovern and Matell)

be available after 10 s, whereas a different cue (i.e., a light) indicated that food might be available after 20 s. As can be seen, the peak time of responding for each cue matches the fixed interval associated with the cue, a property referred to as mean accuracy (Wearden and McShane 1988). Several other important properties of interval timing behavior can be seen in this figure. Peak spread (i.e., the standard deviation of the response function or the width at half maximal responding) is used as a measure of the precision or confidence of an organism's temporal estimates. Importantly, peak spread is directly proportional to the duration being timed, a relation known as the scalar property (Gibbon 1977). In other words, the entire response function scales or stretches to the interval being timed. The scalar property is frequently demonstrated by normalizing each response function by its maximal rate (i.e., its peak rate) and then plotting them as a function of the proportion of the fixed interval being timed. When this is done, the response functions for the two durations superimpose (shown in the right panel of Fig. 1). This relation can also be seen by computing the coefficient of variation (i.e., the peak spread/peak time), which will be constant for different durations if the scalar property holds. The scalar property is Weber's law for perceptual change applied to time. The third commonly seen property is that the peak rate is higher for shorter durations than for longer durations when trained with equivalent probabilities and amounts of reinforcement. As peak rate is viewed as an indicator of motivation related to expected reward value, the lower peak rate for the longer duration indicates that organisms discount the value of signaled reward as a function of the wait time. The steepness of this delay discounting function has been linked to impulsivity, and it is typically measured by identifying the duration at which subjects are equivalently likely to choose between an immediate small reward and a delayed larger reward.

Finally, it should be noted that the smooth peak functions shown in Fig. 1 are an artifact of averaging across trials. On an individual trial, responding is well characterized by a two-state, step-shaped pattern of responding in which the animal abruptly switches from responding at a

low rate to responding at a high rate prior to the fixed interval (i.e., the start time) and then abruptly switches back to a low rate after the interval has passed (i.e., the stop time) (Church et al. 1994). Because the time at which these abrupt response rate transitions vary from trial to trial, the step function is smeared, resulting in the smooth peak function. Single-trial analyses that identify the start time, stop time, spread, and midpoint of responding on individual trials allow for a more complete assessment of the processes generating temporal control. For example, the decision to initiate responding appears to be independent of the decision to terminate responding (Balci et al. 2009).

The peak-interval procedure measures prospective timing, which means that the animal is actively withholding responding until it deems sufficient time has elapsed that responding will be reinforced. This differs from retrospective timing, which occurs after the stimulus to be timed has been presented and the animal has to make a judgment concerning how much time elapsed before the termination of the stimulus. The temporal bisection task is used to demonstrate these posttrial temporal judgments. In this task, a stimulus is presented for either a short (e.g., 2 s) or a long (e.g., 8 s) duration, after which an option to respond on two different response manipulanda is provided (e.g., left and right levers are extended). The subject is reinforced when they respond on the manipulandum corresponding to the presented duration (e.g., if the stimulus was presented for 2 s, a left lever response is correct, and vice-versa). After duration discrimination reaches high levels of accuracy, intermediate durations are then presented, and the subject classifies each duration as "short-like" or "long-like" by responding on the corresponding lever. Plotting the probability of a long response as a function of presented duration is well described by a sigmoidal, or s-shaped, function. The point of subjective equality (PSE), the duration at which subjects are equally likely to classify an interval as short-like versus long-like, typically falls around the geometric mean of the anchor durations (e.g., 4 s for durations of 2 s and 8 s), although it sometimes falls closer to the arithmetic mean (i.e., 5 s for



durations of 2 s and 8 s). Bisection at the geometric mean has been interpreted as indicating that responding in this task is based on ratio, rather than absolute, similarity (i.e., ratio:  $2/4 = 4/8$ ; absolute  $5-2 = 8-5$ ). However, bisection at the geometric mean would occur with an absolute rule if temporal perception were based on a logarithmically growing percept, rather than a linear percept. Besides the PSE, one half of the difference in the durations for which the subject classifies an interval as long-like 25% of the time, versus 75% of the time, is referred to as the difference limen and, like peak spread in the peak procedure, reflects temporal precision. The scalar property is, of course, evident in this procedure as well, as computation of the Weber fraction (i.e., the difference limen/PSE) will be constant for different anchor durations. Some caution should be used when interpreting results from this task as indicating retrospective temporal assessment. When the response manipulanda are spatially oriented, rats and pigeons will show prospective-like timing behaviors, such that they will position themselves around the location of the short-associated manipulandum early in the trial and then move and position themselves around the long-associated manipulandum late in the trial. To minimize such mediating behavioral strategies, researchers have used different visual signals to indicate the short and long response and randomly varied their spatial position across trials (Machado and Keen 1999).

## Psychological Processes

While they differ in their mechanisms, all timing models can be conceived of in terms of an information processing structure that incorporates a clock process, a memory process, and a decision process. The clock process is instantiated by the generation of physiological signals that vary as a function of time, thereby creating a presumably isochronic relationship (i.e., a one-to-one mapping of brain states to elapsed time). The memory process stores a representation of the brain state associated with a particular biologically relevant interval (e.g., at the time of reinforcement) in

either short-term or long-term memory. The decision process compares the current percept (i.e., the evolving brain state) with the temporal memory or memories, and a response or choice is based on the similarity between the two.

To probe the mechanisms of timing, a common approach is to perturb the organism in some manner (either behaviorally or physiologically) and examine how temporal control is impacted. For example, the systemic administration of psychostimulants, such as methamphetamine, prior to a testing session in the peak procedure will cause the entire response function to immediately shift earlier in time (Meck 1996). These shifts are proportional to the duration being timed and, with continued training under the influence of the drug, will disappear (i.e., peak time will again be veridical). If drug administration is then discontinued, the response function will immediately shift right (i.e., later in time), again in a proportional manner, and will renormalize with continued training off the drug. Together, these immediate, proportional, and normalizing shifts are consistent with a change in the speed of an internal clock process and indicate that dopaminergic transmission plays a central role in modulating temporal perception and control. Besides altering the clock process, temporal accuracy (i.e., peak time) can be impacted by alterations of temporal memory processes, for example, through the administration of cholinergic drugs (Meck 1996) or through forced ambiguity of the appropriate temporal expectation (Swanton et al. 2009). Altering the latency to activate timing processes can also impact peak time. This effect, often attributed to attention, would result in an absolute, rather than a proportional, shift. Other manipulations, such as providing alternative targets for behavior, can alter temporal precision (i.e., peak spread), suggesting an impact on decision processes. However, an increase or decrease in variability in any of the central processes (clock, memory, or decision) will lead to changes in peak spread. The use of single-trial analyses can help dissociate the process alteration that gave rise to the change in peak spread. For example, if the spread of the high response state becomes broader, without an increase in variability of the start and stop times,

one can infer that the required similarity in the decision stage between the current percept and temporal memory has been relaxed.

## Interval Timing Models

Models of timing can be placed into three classes based on their mechanisms for the clock process: a pacemaker-accumulator mechanism, an array of temporal elements, and network state changes. Pacemaker-accumulator models consist of a pacemaker, which runs continuously, typically emitting pulses with Poisson variability (i.e., the time between pulses is exponentially distributed, with no relationship between one inter-pulse interval and the next). Upon onset of a signal to be timed, these emitted pulses are accumulated, thereby providing a signal that grows in a monotonic manner as a function of time. Within this class of models, scalar expectancy theory (Gibbon 1977) proposes that the pacemaker runs at a constant rate irrespective of duration being timed, and the value of the accumulator grows linearly as time elapses. One critical weakness of this model is the issue of instantiating such an unbounded accumulation process with neural architectures. In contrast, the behavioral theory of timing, its learning to time variant, and a drift diffusion-based model of timing (Simen et al. 2013) all propose that the rate of the pacemaker is inversely proportional to the delay to reinforcement. As a result, accumulation always occurs to a fixed bound, irrespective of the interval. As a model in the behaviorist tradition, the behavioral theory of timing does not utilize a cognitively accessible accumulation process per se, but instead deems the sequence of the animal's behavioral states to reflect elapsed time. Models that utilize temporal elements propose that different neurons or neural circuits operate with different time courses spanning the interval timing range, and by selectively strengthening and weakening the influence of these different elements, behavioral expression can be matched to the interval to be timed. Examples of models that utilize this approach are the spectral timing model (Grossberg and Schmajuk 1989) and the multiple oscillator connectionist model

(Church and Broadbent 1991). Finally, network state models propose short-time scale neural processes continuously interact, resulting in the evolution of a network state that varies with time (Buonomano and Merzenich 1995; Matell and Meck 2004). In contrast to the other classes of models, it is not clear that different network states can be viewed as evolving in a monotonic manner (e.g., activity becoming more/less complex or spreading/shrinking across the brain as durations increase), and thus it is difficult to evaluate whether the corresponding temporal memories (i.e., network states) can be acted upon via arithmetic operations. Such arithmetic operations are evidenced by findings that animals can combine the durations of independently trained cues to form a temporal map of events (Arcediano et al. 2003), that the number of trials to conditioned responding relates to the ratio of intervals between conditioned and unconditioned stimuli (Gibbon and Balsam 1981), and that rats respond in a scalar manner at an intermediate duration when presented with a compound of different modality cues that have been associated with different durations (Swanton et al. 2009).

## Neural Mechanisms

Given the multitude of models of timing, it should come as no surprise that the neural processes subserving the perception and behavioral control with respect to time remain unclear. Indeed, a long-standing, central question in the field (Roberts 1982) is whether time is processed by a network of dedicated neural structures or whether temporal processing is distributed, such that most or all neural structures process time as a central aspect of their activity. Support for the dedicated processing notion comes from findings that lesions to certain brain structures like the striatum (Meck 2006) severely disrupt the temporal control of behavior and from electrophysiological (Emmons et al. 2017; Mello et al. 2015) and functional imaging studies (Coull and Nobre 1998; Rao et al. 1997; Wiener et al. 2010) showing activation of specific neural structures within the frontal and parietal cortices and the basal

ganglia and cerebellum. Furthermore, temporal interactions across modalities (Roberts 1982; Swanton et al. 2009) and behavioral systems (Delamater and Holland 2008) suggest a common site at which such interactions could occur. On the other hand, to identify causal relations between the innumerable environmental events that come and go in time, one must keep track of the temporal relations between these events, which, given the multiplicative combination in possible relations, results in a computational explosion. Dealing with such a vast number of possible temporal relations may not be feasible by a dedicated neural framework (Ivry and Schlerf 2008). Indeed, temporally specific signals have been seen in areas such as the primary visual cortex (Shuler and Bear 2006) and the amygdala (Dallérac et al. 2017), and even in organotypic cultures (Johnson et al. 2010) suggesting that temporal information may be represented throughout the brain. Similarly, the fact that interval timing behavior has been seen across species, ranging from humans to rodents, birds to fish, and even invertebrates, suggests that timing does not rely on specific neuronal structures or cell populations.

## Conclusion

In summary, the perception of time in the range of seconds to minutes is a critical facility allowing a broad range of species the ability to organize their behavior with regard to the dynamics of the world. While there is agreement regarding many of the psychophysical features of interval timing, identifying the psychological and neural mechanisms of this capacity requires on going work.

## Cross-References

- [Associative Learning](#)
- [Behaviorism](#)
- [Classical Conditioning](#)
- [Discrete Trials](#)
- [Discrimination Learning](#)
- [Dopamine Receptor](#)

- [Inhibition of Delay](#)
- [Operant Conditioning](#)
- [Optimal Foraging Theory](#)
- [Reinforcement](#)
- [Schedules of Reinforcement](#)
- [Timing](#)

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## Intervening Variables

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## Definition

An *intervening variable* is an abstract scientific concept that scientists invoke to label or summarize relationships between independent and dependent variables across a variety of circumstances. Commonly cited examples of intervening variables include gravity, thirst, learning, and intelligence.

## Introduction

During his presidential address to the American Psychological Association in 1937, Edward C. Tolman used the term *intervening variable* in his comments regarding theories and facts:

But what is a theory? According to Professor Hull, a theory is a set of definitions and postulates proposed by the theorist (on the basis presumably of some

already found facts) from which other empirically testable facts, or as he calls them, theorems, can be logically deduced. These deduced theorems will be new empirical relationships which the theorist—or more often, his research assistants—can, then and there, be set to look for.

For my own nefarious purposes, however, I wish to phrase this matter of the relationship of a theory to the empirical facts out of which it arises and to which it leads in somewhat other terms. A theory, as I shall conceive it, is a set of “intervening variables.” These to-be-inserted intervening variables are “constructs” which we, the theorists, evolve as a useful way of breaking down into more manageable form the original complete  $f_1$  function.

Tolman’s  $f_1$  function referred to the causal relationship or the description of the dependence of the behavior (i.e., dependent variable) on the preceding stimulus (i.e., independent variable). To illustrate, consider Tolman’s hypothetical learning experiment involving the intervening variable of “hunger” (Tolman used the term “demand”). In this experiment, the researcher manipulates the hours since rats last ate (12-, 24-, 36-, 48-, 60-, 72-h prior) and measures the tendency of the rats to turn down the alley with the food. The independent variable of time since last meal corresponds to level of hunger. The more time that passes since an organism last ate, the hungrier the organism becomes. Presumably rats who last ate 72 h before entering the maze would be hungrier than rats who had eaten 24 h before entering. Resulting differences between groups of rats in the dependent variable of turning down the alley with the food would by definition directly mirror the variations in level of hunger. Rats who quickly learned to find the food would be the hungrier rats. The concept of hunger describes the causal relationship between time since last meal and speed of learning to find food.

Around the time, Tolman gave this address, Hull was using terms including “hypothetical construct,” “symbolic construct,” and “intervening variable” more or less interchangeably. Tolman’s 1937 address and 1938 paper sparked extensive discussion and debate among psychologists, particularly among learning theorists, about the extent to which the concepts differed, and to what extent it even mattered. MacCorquodale and Meehl (1948) are among those who

contributed to disentangling *hypothetical constructs*, which presume the existence of a tangible entity, process, or event, from *intervening variables*, which make no such presumption. Clearly distinguishing between these two concepts is crucial to understanding intervening variables.

## Distinguishing Intervening Variables from Other Unobservable Concepts

Hypothetical constructs are salient in a number of settings. Scientists postulate hypothetical constructs at a point in time when tangible entities are as yet undiscovered and unobservable. Gregor Mendel, for example, deduced from his records that pea plants must produce different variations of egg and pollen cells. Though Mendel himself was unable to measure differences in these cells, his hypothesized *Erbfaktoren* (heritable factors) were later confirmed by direct measurement with advanced technology. Of course, now *DNA* and *genes* commonly appear in science curricula as tangible things, but at the time Mendel was conducting his research, Mendel’s heritable factor was a hypothetical construct.

Researchers must address hypothetical constructs when designing and drawing conclusions from studies. In an experiment, for example, a researcher manipulates an independent variable, measures a dependent variable, and controls as many extraneous variables as is practical in an effort to rule out the effects of other likely causal variables. The researcher must also randomly assign subjects to experimental conditions in order to control for variables that may influence the outcome, but which may be impractical or impossible to control or which may indeed be unknown. These variables are presumably very real and as such are hypothetical constructs. Similarly, when drawing conclusions from correlational and quasi-experimental designs, researchers should be careful to avoid inferring cause because of possible “third variables.” While a study may show that a relationship exists between variables, a researcher cannot conclude a causal relationship between the two variables because of the many other variables, known or



otherwise, that could account for the observed relationship. As in experiments, these variables are presumably real, but unknown.

In MacCorquodale and Meehl's analysis, an *intervening variable* differs from a hypothetical construct in that an intervening variable involves no hypothesis of a tangible entity, process, or event. Intervening variables are unobservable concepts that are inferred from the manner in which the independent and dependent variables are operationally defined and are employed as logical links between independent and dependent variables (Bugelski 1956; Goodwin 2015). Though *intervening variables* are inferred to be causal, they are in fact labels for relationships between measurable variables rather than tangible entities in their own right. Gardner and Gardner (1998) offer a hypothetical experiment in classical conditioning to illustrate this point. Suppose that on each trial the experimenter flashed a light, then gave the dog some food. The experimenter measured the number of drops of saliva collected in a test tube on each trial after flashing the light, but before presenting the food. A graph would then show the learning curve, that is, how the number of drops of saliva increased from trial to trial.

Where is the learning in this curve? Obviously, there is no learning in the saliva in the test tube. Equally obviously, there is no learning in the light or in the food. A single trial can never yield any evidence of learning. The only evidence of learning is in the relationship between trials. We can see and measure the saliva, and we can see and measure the light and the food and the time between them, but we can only infer the relationship from trial to trial by looking at the record and making inferences. (Gardner and Gardner 1998, p. 6)

Intervening variables include mathematical constants, such as the acceleration of a falling body, as well as the myriad internal states or processes within organisms that fall under the umbrella of *psychological constructs* or *cognition*, such as learning, hunger, fear, intelligence, motivation, self-esteem, attachment, memory, consciousness, introversion, perception, and attention.

In order to advance an intervening variable as a causal factor, a researcher must rule out

competing hypotheses. Halliday (1983) illustrates this point with the example of forgetting:

We may say a person has forgotten a behavior if the behavior doesn't occur as often. Forgetting would be an intervening variable. We can't measure it directly, but it affects behavioral output. In order to say that "forgetting" has occurred, we have to rule out other possible explanations for why the behavior may not be exhibited. We would have to rule out maturation, for example. If the behavior disappeared because of normal biological development, we couldn't say that the behavior had been forgotten. If a response to a stimulus declines over time after repeated exposure, we might say that we forgot the response, but habituation would account for that. We would have to rule out fatigue as well. (p. 105)

A researcher would also have to rule out the use of drugs or intoxicants, level of sleep deprivation, state of health, etc. The fact that learned behavior fails when the person is intoxicated, tired or sick does not mean that forgetting has occurred. When the person returns to a normal state, performance may return to normal levels even without additional training (Hilgard and Bower 1966).

## Conclusion

MacCorquodale and Meehl (1948) suggest that intervening variables are useful for their convenience. Their summarizing nature allows scientists to develop more coherent and parsimonious theories (Hilgard 1956). Though intervening variables have no tangible substance, researchers can accurately compare findings across studies when intervening variables have unequivocal and measurable operational definitions. And intervening variables allow for ease of discussion. It is easier to say, "This child has an IQ of 100," than it is to say, "This child behaves as intelligently on this sample of test problems as the average child of his age" (Chaplin and Krawiec 1960). As Halliday (1983) cautions, however, "when an intervening variable is invoked, we should not believe that anything has been explained; all that has been done is that some phenomenon that requires explanation has been identified" (p. 105).

Despite MacCorquodale and Meehl's efforts to illustrate the difference between intervening

variables and hypothetical constructs, the term *intervening variable* continues to appear in contexts where using *hypothetical construct* would be more precise.

## Cross-References

- Acquisition
- Behaviorism
- Cognition
- Cognitive Bias
- Correlation
- Extinction in Learning

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## Intimate Partner Violence

- Martin Daly and Margo Wilson

## Intolerance

- Xenophobia

## Intrabrood Conflict

- Discriminative Parental Solicitude

## Intragenic Complementation

- Complementary Genes Hypothesis

## Intragroup

- In-Group

## Intraparietal Sulcus

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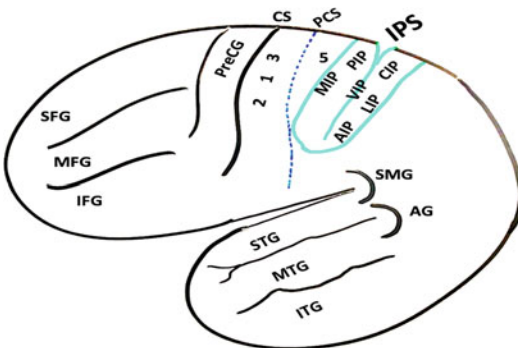
## Introduction

The ability of an organism to integrate sensorimotor functions and visuospatial processing confers major survivability advantages, because they allow organisms to adjust their behavior in response to the environment. The intraparietal sulcus is the location for many of these functions in humans. The primary somatosensory area is located posterior to the central sulcus and is guarded more posteriorly by a postcentral sulcus. Dorsal to postcentral sulcus, the intraparietal sulcus (IPS) divides the parietal lobe into superior and inferior parietal lobules consisting of areas 5 and 7, which are considered to be the sensory

association areas (Fig. 1). Turner in 1866 described the intraparietal sulcus to be located within the parietal lobe and having an ascending and horizontal course. He also mentioned that IPS could be recognized from the 6th month of intra-uterine life (Turner 1866). Cunningham in 1892 studied the configuration of intraparietal sulcus and its relation to that of the postcentral sulcus and classified it into five types. There is also a short sulcus called the anterior intermediate parietal sulcus of Jensen described on the inferior bank of the IPS which descends across the inferior parietal lobule and separates the supramarginal gyrus from the angular gyrus (Cunningham 1892). The type where intraparietal sulcus was fused with the superior segment and the inferior segment of the central sulcus was found to be the most common variety (Ono et al. 1990).

Toward the end of the twentieth century, many researchers extensively studied the cortical area within the depth of intraparietal sulcus and divided it into different areas (Choi et al. 2006). These areas of the cortex of the IPS are implicated in various functions and sensorimotor integration, saccadic eye movements, visuospatial information processing, and hand movements including grasping (Shikata et al. 2008).

But the consensus about the precise role of these areas responsible for such functions is lacking.



**Intraparietal Sulcus, Fig. 1** Schematic diagram showing the location of various areas related to the intraparietal sulcus (IPS). CS, central sulcus; PCS, postcentral sulcus; SFG, superior frontal gyrus; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; SMG, supramarginal gyrus; AG, angular gyrus

## Intraparietal Sulcus in Macaques

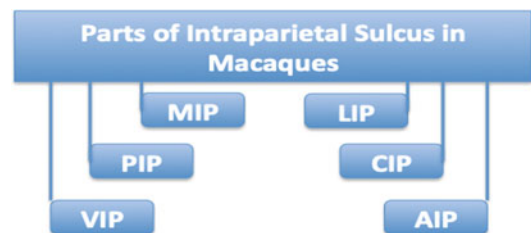
The cortical gray matter in the region of IPS in macaques has been divided into a number of smaller functional areas such as anterior intraparietal area (AIP) and is concerned with planning and organizing grasping movement of the hands. The lateral intraparietal area (LIP) is associated with the planning of eye movement (Andersen and Buneo 2002) and also supplies the visual information about shape and position of objects to the AIP (Janssen et al. 2008).

The ventral intraparietal area (VIP) situated in the depth of the IPS is related to the response to the visual stimuli or light touch (Duhamel et al. 1998). The medial intraparietal (MIP) area and posterior intraparietal (PIP) area act altogether and function in the planning of reaching movements and also guide the course of movement to avoid errors and perform the smooth reach of the intended objects (Mulliken et al. 2008).

Finally, the caudal interparietal (CIP) area, on the caudal part of the lateral bank of the intraparietal sulcus, is involved mainly in the higher-order visual processing but not in the somatosensory processing, being a part of the parietal cortex (Fig. 2).

## Neurological Connection of Intraparietal Sulcus

The human intraparietal sulcus is divided into three areas, HIP1, HIP2, and HIP3, which resembles areas AIP, VIP, and MIP, respectively, in



**Intraparietal Sulcus, Fig. 2** Schematic representation of the different areas in the intraparietal sulcus. MIP, medial intraparietal area; PIP, posterior intraparietal area; VIP, ventral intraparietal area; LIP, lateral intraparietal area; AIP, anterior intraparietal area; CIP, caudal interparietal area

macaque monkeys (Scheperjans et al. 2008). hIP 1 and hIP 2 are situated in the anterior part of the intraparietal sulcus. hIP 1 is situated at the bottom of the intraparietal sulcus, and hIP 2 is situated alongside the lateral wall (Choi et al. 2006). These anterior regions of the IPS are chiefly connected by association fibers with the ventral premotor cortex and the middle frontal gyrus. hIP 1 is also connected to the insular region. hIP 1 region is involved in the grasping of the objects, manipulating of the objects, and processing of the three-dimensional object features, which are relevant for grasping (Fig. 3).

The hIP 2 region by virtue of its connectivity with the frontoparietal networks is important for transforming visuospatial information from hIP3. hIP 1 and hIP 2 together are involved in supporting more complex aspects of numerical and mathematical information processing. The hIP 3 is located in the medial wall of the IPS and connected with the extrastriate areas. It has a large number of fibers along the fronto-occipital fasciculus connecting to the fronto-occipital cortex. Because of this networking, hIP3 has a great role in modulating the visual information from the occipital cortex for further processing, i.e., visuo-spatial transformation. The combined action of these areas is essential for integration of the visual information with the spatial, motor, and somato-sensory information for graceful hand-eye coordination and movement through the environment (Schall et al. 1995).

## Functional Imaging for Intraparietal Sulcus

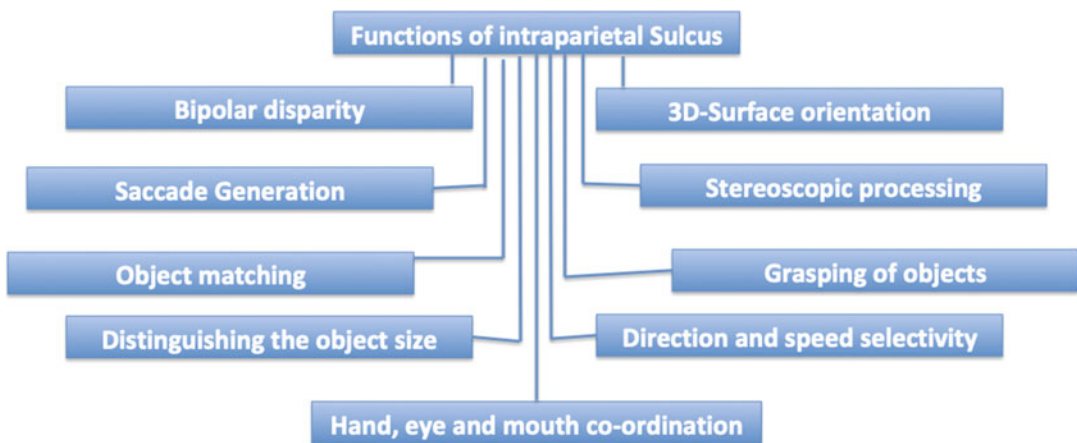
Functional neurophysiological studies done using the fMRI revealed the complexity of the areas in the intraparietal sulcus in macaques as well as in humans (Murata et al. 2000). Studies conducted on humans showed grasping areas in the depth of intraparietal sulcus. One of the studies illustrated that any vascular or traumatic lesion to the anterior part of the IPS results in impaired grasping behaviors, while similar lesions in the posterior part of the IPS have no effects on the grasp pattern of the subjects (Binkofski et al. 1999).

Observation showed that grasping abnormalities were present in the form of slower hand opening while reaching the objects, formation of larger gaps, or apertures between the thumb and other fingers as compared to the non-affected side of the same patient and also with age-matched controls.

Effects of grasping and manipulation of rectangular blocks showed the areas of activation in the lateral part of the IPS. Subsequently, studies were carried out to confirm the activation of the anterior part of the IPS during grasping and manipulation of objects (Frey et al. 2005).

## Clinical Correlates for Sulcus

Various neurological and visual disorders were correlated with the involvement of the



**Intraparietal Sulcus, Fig. 3** Briefing of functions of the various areas in the intraparietal sulcus

areas of intraparietal sulcus. The particular area in the intraparietal sulcus is concerned with the saccade generation but, due to the vascular or traumatic lesion to the area, may result into the increased saccadic latencies and reduced amplitude of contralateral directed reflexive saccades (Pierrot-Deseilligny et al. 1987) and memory-guided saccades (Muri et al. 2000).

Some authors also correlate the involvement of intraparietal sulcus in developmental difficulties in mathematics, also called as developmental dyscalculia (DD) (Molko et al. 2003). He carried out analysis of Turner syndrome (TS) patients with mathematical deficits and revealed abnormal structural organization of the right IPS. In a second study, Molko et al. (2004) supported this finding with voxel-based morphometry (VBM) evidence that TS subjects showed decreased gray matter volume in the left superior temporal sulcus and right IPS. A more recent VBM study revealed reduced gray matter volume in the right IPS in DD children relative to controls (Rotzer et al. 2008).

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## Intra-sexual Competition

- [Intra-sexual Selection](#)
- [Mating Effort](#)

## Intra-sexual Selection

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## Synonyms

[Intra-sexual competition](#); [Male-male competition/ combat](#); [Sexual selection](#)

## Definition

Intra-sexual selection is part of sexual selection where members of the same sex (males) compete with each other to gain access to mate with females.

## Introduction

It is the rule of nature when multiple individuals eye on the same resource whether it is food, shelter, or mate; consequently, competition arises among them. In sexually reproducing animals, sexual selection operates in a similar manner like natural selection. If sexual selection results in direct combat between members of the same sex of a species, concerning the propagation of species, it is referred to as intra-sexual selection. The intra-sexual selection reflects the competition between members of the same species (specifically males) in order to gain opportunities to mate with the opposite sex. For example, the

males compete with each other for mating with females. Intra-sexual selection mainly occurs in a group of animal species where the female mainly involves in parental care and male likely to compete with each other for success in mating (Hall and Strickberger 2008). As a result of frequent competition, the individual with better adaption in combat strategies/traits has more chances to attract females. It is opposite of intersexual selection which is also known as a female choice, where female chooses the male based on certain characters/ornaments, e.g., a peacock's tail. Although the term inter/intra is rather capricious because competition for a mate must be within the members of the same species, the term inter/intra is mostly used for within two groups and between the same group, respectively.

Since the intra-sexual selection involves a rivalry between members of same species, the conflict can result into direct interactions causing severe fight, thus individual of a species are well adapted for intra-sexual competition mostly have developed better armaments or intra-sexually selected weapons (ISW) than their competitor.

The origin of intra-sexual selection concept came to existence in 1871 when Darwin described the sexual selection theory and how the evolution of many beautiful and sophisticated traits occurred in nature. According to Darwin, "Success of certain individuals of a species over others in relation to the propagation of species is the result of sexual selection."

In nature, the intra-sexual selection is more prominent, where males being polygynous mate with many females (Hall and Strickberger 2008). In such species, males generally have well-developed masculine traits or armaments in order to gain a mate. Due to selection pressure, these characters become inherited and lead to distinct sexual dimorphism (Weir 2013; Singh et al. 2019). For example, males are generally found to be larger in body size with respect to female body size (male elephant seals; *Mirounga leonina*), male dung beetles (*Onthophagus taurus*) have longer horns, similarly in melon flies (*Bactrocera cucurbitae*) the males and female show several dimorphic features, where male being shorter than female and structural variation

in wing morphology also present (Singh et al. 2019). The sexually dimorphic traits are generally under hormonal control.

**Armaments:** It has been found that intra-sexually selected weapons (ISW) are mostly found in the animals with bilateral symmetry. In a report by Rico-Guevara and Hurme (2019), they have reported that most of the ISW comes in pairs, located mostly near the head region, and are part of modified endo- or exoskeleton. These structures may excessively develop over generations due to selection pressure. In the terrestrial system, most of the modifications are observed in feeding parts and locomotory appendages. Some examples of ISW are longer horn in male dung beetles (*Onthophagus taurus*) which is modified chitinous exoskeleton. The development of a longer horn in dung beetle is dependent on the nutritional regime on which the insect has fed during development. Male bighorn sheep (*Ovis canadensis*), native to North America, have huge horn over their head which they use in headbutt during combat with other males, to gain excess to female. Intra-sexual conflict in Alaskan bull-moose males (*Alces alces gigas*) is so intense that sometimes both males die due to tangling of their horns. The male gorilla has well-developed musculature, fist, and canine which he uses in combat.

## Competition

Since competition is the main driving force for intra-sexual selection, it can be categorized into two groups. The first one is a case where the male, who reaches the female first, will be able to mate (scramble). The second is where two or more males compete over female and the winner will mate (contest). The first in the list of competition, i.e., scramble, which refers to race for getting female first. For example, in damselflies (order Odonata), the male with the help of its claspers grasps the head of the female as soon as she arrives. There is variation in the structure of the claspers from species to species. In fact, it is species characteristics to prevent interspecific mating. Scramble competition is also cited in the case of dung beetles and elephant seal (Moya-

Laraño et al. 2007). Here the small-sized males succeed over large males in getting female due to their fast and active movement, whereas large-sized elephant seal tends to win in contest, i.e., combat.

It must be considered that males with larger size are more successful over smaller sized but have reduced daily reproductive ability, whereas the smaller animals have high agility and more daily reproductive capability. Being intermediate in size is beneficial for animals to be reproductively more successful.

## Alternative Mating Strategies

From the above discussion, it could seem like smaller-sized male or males with inferior combat strategies or ISW would be at a disadvantage during contest competitions for mating. But it is not always true; in some species the inferior male has developed some alternative mating tactics for ensured reproductive success (Pagel 2002).

**Sneaking Strategy:** sometimes the smaller male waits for the opportunity when the dominant male gets engaged in combat with some other males or mating with another female; the smaller male sneaks in and copulates with the female. For example, in red deer (*Cervus elaphus*), the smaller males with inferior antlers instead being indulged in direct combat with superior males wait near a female deer until the large male gets engaged in a contest with another competitor; the inferior male then sneaks in and copulates with the female. This kind of strategies is also used by inferior males of elephant seals and cichlid (*Herichthys minckleyi*) (Cherfas 1977; Frankenhuis and Fraley 2017).

**Tunnel digging** by males of horned beetles (*Onthophagus acuminatus*). In horned beetles, the dominant males with long horn guard the female nest/tunnel and combat with other males trying to enter the tunnel. The subordinate male instead of direct encountering dominant male at the tunnel entrance digs a secondary tunnel to intercept the female tunnel (Pagel 2002).

**Early maturation** in coho salmon (*Oncorhynchus kisutch*) – coho salmon is an

anadromous fish of Salmonidae family. After embryonic development, the male and female spent 3 years in seawater before they return to freshwater for spawning. Some of the males leave the seawater at 2 years of age and are called as Jacks (smaller in size); other males who spent 3 years in seawater are larger and are known as Hooknoses (Oldfield et al. 2014).

## Sperm Competition

When a female has mated with one male, it is possible that another male can also fertilize her releasing its sperm in the female genital tract (Wigby and Chapman 2004). In hymenopterans, especially in honeybee (*Apis*) and many coleopterans, the queen female has the capability to mate with two or more drones and even store their sperms. Later the female on its will uses the sperm to fertilize her eggs. This process of sperm selection is often known as sperm discrimination. When virgin queen goes for a mating flight, she mates with up to seven to ten males. The male drone inserts its endophallus and releases sperm. After completion of mating, the drone pulls away, but a part of endophallus get ripped off and remain attached to the female's body. When another male mates with the same female, it has to first remove the existing endophallus of the previous male. This type of behavior in several insects leads to the basis of sperm competition, where the sperm of one male competes with the sperm of another male inside the female reproductive tract. To prevent this sperm competition, some species have developed certain strategies. The fundamental way is copulation guarding. The male guards the female prior to copulation until she gains sexual maturity and till the female laid her eggs or produce progeny (Wigby and Chapman 2004).

There are two specialized methods, which have been evolutionary curretted for sperm competition:

**Scrapers** – In some species, the males have modified body structure to remove the sperm of other males from the female reproductive tract, for example, dragonfly males (Langley 2016).

**Mating Plugs** – In some species, the males release certain chemicals or protein which makes the female incapable to receive sperm from other males. This method is also known as the copulation plug. Mating plug is generally gelatinous secretion released by males in the female reproductive tract. For example, mating plug in a female Richardson's ground squirrel (*Spermophilus richardsonii*) and *Bombus terrestris* (Baer et al. 2000; Wigby and Chapman 2004).

A third category which is reported in *Drosophila* is **sperm fertilization power**, where the males increase the fertilization capacity of their sperm resulting in more chance that their sperm will fertilize the female eggs. The content of male seminal fluids also contributes to dominating female fertility and sexual behavior.

## Consequences on Female Fitness

Intra-sexual competition between males can have both negative and positive effects on female fitness. As we have discussed above, the success of superior males in mating leads to the inheritance of its gene. But it is not always correct. In a population with a high density of males over female, a large number of males try to mate with female resulting in a negative impact on female reproductive organs. Even a higher rate of male-male competition could lead to the loss of superior male after some combat. High level of intra-sexual competition leads to a decrease in female investment toward mating and parental care (Weir 2013; Cayuela et al. 2016).

## Consequences on Male Fitness

Intra-sexual selection in the course of evolution leads to deposition of certain traits which result in prominent sexual dimorphism, and such traits become inheritable. Some of the examples are traits which are useful in mate search and dispersal of male (e.g., male wing morphology in dragonflies and damselflies); traits involved as ISW/armaments; and traits that enhance copulation capability and sperm competition which would have fair chance to be favored. Improvement of endurance is also an important

aspect which increases superior male mating ability (Rico-Guevara and Hurme 2019).

## Sexual Selection in Human Perspective

Scheyd (2018) described a lot about sexual selection in human perspective. In the human's case, sexual selection operates merely more or less in the same way as in the case of the whole animal kingdom. Huge reports are available on the psychology of human about sexual and romantic jealousy and partner selection. In humans, males are more prone to sexual infidelity, whereas females are prone to emotional infidelity. In simple words, males are suspicious, whereas females are emotional. Intra-sexual rivalry in the human case also results in a sort of aggressive remedy (Brase et al. 2004). Typically male-male rivalry relies on sort of physical violence mostly covert, whereas female-female rivalry mostly overt relies upon verbal aggression damaging reputation of rival (Hyde 1984; Werner and Crick 1999).

Sexual selection (both intra- and inter-sexual) plays a key role in our system too. Sexual dimorphism is key to sexual attraction in every dioecious system. Human males don't get involved in direct combat with another male to attract women; rather, they spent valuable time and resource in the gym for developing body musculature and make their physical appearance more prominent (Scheyd 2018). The same muscle system can be involved in combat tactics. Here the intra- and inter-sexual selection operates at the same time. Spending time in parlor and salon for their look is part of inter-sexual criteria. In nature, the strong musculature and smart look are related to sexual wellness, productivity, and superior future generation.

Human females, similar to human males, are also prone to sexual selection conflict at the same level. Fisher (2013) studied this aspect with a catalogue of behavioral characteristic, including some sort of aggression, like breaking confidences, criticizing others, clothing, appearance, personality, gossiping, and so on. In the case of same-sex rivalry, females are found to be superior to males (De Backer et al. 2007). All these

behavioral phenomena are intra-sexual competition for desirable mates. In simple words, all sorts of behavior correspond to female-female competition, with the sole purpose to be superior over others. In addition to this intra-sexual aggression, they also go for self-promotion and mate manipulation (Fisher and Cox 2010). In a study by Hill and Durante (2011), it has been found that when women were shown images of other beautiful women, they showed and increased behavior to enhance their own attractiveness.

## Conclusion

In the course of evolution, natural selection has governed the selection of certain individuals over others with respect to fitness. Sexual selection, on the other hand, shaped the sexual dimorphism and inheritance of those traits which results in better adaptability of future progeny, although exception does exist. Reproductive success is the primary way by which nature judges an organism's success over others. In either intra- or inter-sexual selection, the sole purpose is the selection of superior mate over others. Although the superior mate may have certain undesired genetic endowment, however, due to its selection as a potential mate, it is capable to inherit such traits to ensuing generations.

## Cross-References

### ► Intersexual Selection

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## Intromission

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## Synonyms

Coitus; Copulation; Sexual intercourse

## Definition

Intromission is a step of sexual reproduction that involves the insertion of a male intromittent organ into the cavity of a female reproductive organ to facilitate insemination and internal fertilization.

## Fertilization through Intromission

Because sexual reproduction necessitates the combination of gametes from two different individuals, a variety of modalities have evolved across taxa to achieve fertilization. Within the kingdom Animalia, sexual reproduction can be divided into categories according to where fertilization occurs: internal or external to the body. Among internal fertilizers, males of many taxa have evolved intromittent organs that are designed to deposit spermatozoa inside the female reproductive tract, although never directly on ova (see Eberhard 1985, 2010). There are notable exceptions of internal fertilization occurring without the use of intromission, most prominently among many avian and reptilian taxa, in which insemination occurs through transfer of male gametes to female reproductive tract across the cloacae in a process commonly called a “cloacal



kiss” (e.g., Morrison et al. 2018), which may mimic copulation. The majority of taxa of the order Urodela reproduce via indirect insemination, during which a male drops a spermatophore on an external surface and females may select to insert it through a cloacal opening (e.g., Houck and Arnold 2003). However, intromission is the most common means of fertilization among terrestrial animals (Austin 1984). Intromission is ubiquitous throughout the class Mammalia, although in at least one species (*Homo sapiens*) fertilization has been documented to occur unaided (i.e., without artificial intervention) without intromission (e.g., Achour et al. 2019), although such cases are rare. Intromission is typically reproductive in purpose, although non-reproductive sexual behaviors in general (to include intromission) are common especially among social taxa (e.g., Furuichi et al. 2014).

Males and females occupy distinct reproductive niches that result in sex-related differences in reproductive traits (see Eberhard 1985, 1996; Trivers 1972). Many of these adaptations are the result of sexually antagonistic selection or sexual conflict (Parker 2006; see Dougherty 2017). In short, sexual adaptations in one sex often facilitate the reproductive interests of individuals of that sex at the expense of the reproductive or survival interests of the individuals of the other sex (Lessells 2006; cf. Eberhard 2010). Thus, the behaviors and circumstances surrounding intromission vary widely across taxa, as do the morphologies of sexual organs (see Austin 1984; Eberhard 1985, 2010). For example, the hectocotylus of the class Cephalopoda is a limb that stores and delivers spermatophores to females by means of insertion (Laptikhovsky and Salman 2003). Similarly, Arachnida males use an appendage called a pedipalp, on which a spermatophore is typically deposited, stored, and eventually inserted into female reproductive organs (Michalik and Ramírez 2014). Pedipalps are not genitalia, but rather an intermediate organ for reproduction with other functions, such as sensation (Talarico et al. 2008). Female reproductive organs have likely evolved to alter the reproductive process, thus driving the evolution of

intromittent organs, although more research is needed on the morphological variability of female genital organs in order to better understand this copulatory coevolution (Brennan 2016).

## Cross-References

- External Fertilization
- Gametes
- Internal Fertilization
- Mating
- Reproduction
- Sex Role Reversal
- Sex-Linked
- Sexual Antagonism Hypothesis
- Sexual Dimorphism
- Sperm Competition
- Zygote

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## Intron

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## Synonyms

### Noncoding DNA

## Definition

Introns are noncoding regions of an RNA transcript, or the DNA encoding it, which are eliminated by splicing before translation.

## Introduction

In 1977, using the adenovirus model system, Philip A. Sharp and Richard J. Roberts independently discovered that genes could be discontinuous (Berget et al. 1977; Chow et al. 1977). Subsequent research in four different laboratories revealed that intervening noncoding sequences were also present in genes encoding different proteins in vertebrates such as the rabbit  $\beta$ -globin gene, the mouse  $\beta$ -globin gene, and the chicken ovalbumin gene. These noncoding intervening sequences were given the term introns by Walter Gilbert.

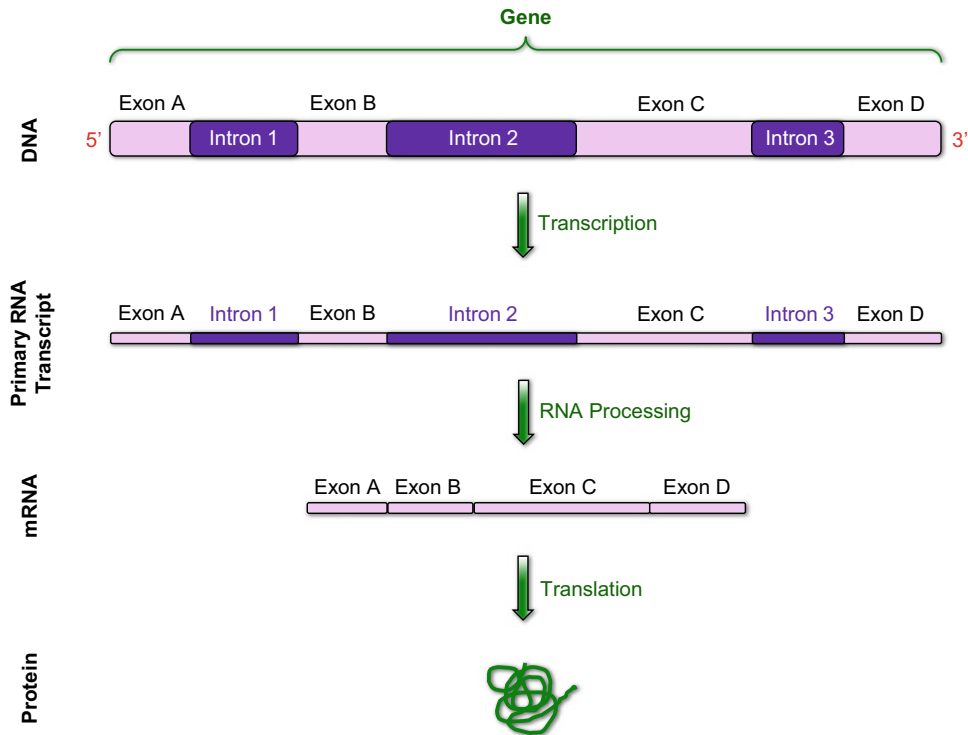
## Size of Introns

Noncoding intervening sequences are part of most eukaryotic genes. The frequency and size of introns vary largely. For example, the *Xenopus laevis* (African clawed frog) gene that encodes vitellogenin A2 is known to have 33 introns. The Ultrabithorax gene of *Drosophila* has an intron that is about 70,000 nucleotide pairs in length. The gene encoding for the  $\beta$  chain of hemoglobin has two introns – a long intervening sequence of 550 base pairs and a short one of 120 base pairs that split the  $\beta$ -globin gene into three coding sequences. Intron sequences constitute approximately 25% of the human genome, of which <0.01% of the introns are <20 bp in length and <10% of introns are more than 11,000 bp in length (Sakharkar et al. 2004) (Fig. 1).

## Types of Introns

Four classes of introns have been identified and studied in detail:

- (i) Introns of tRNA precursors – These introns are excised in two steps by endonucleolytic cleavage and ligation reactions catalyzed by splicing endonuclease and ligase. Studies on tRNA precursor splicing have been carried out in detail in the yeast *Saccharomyces*



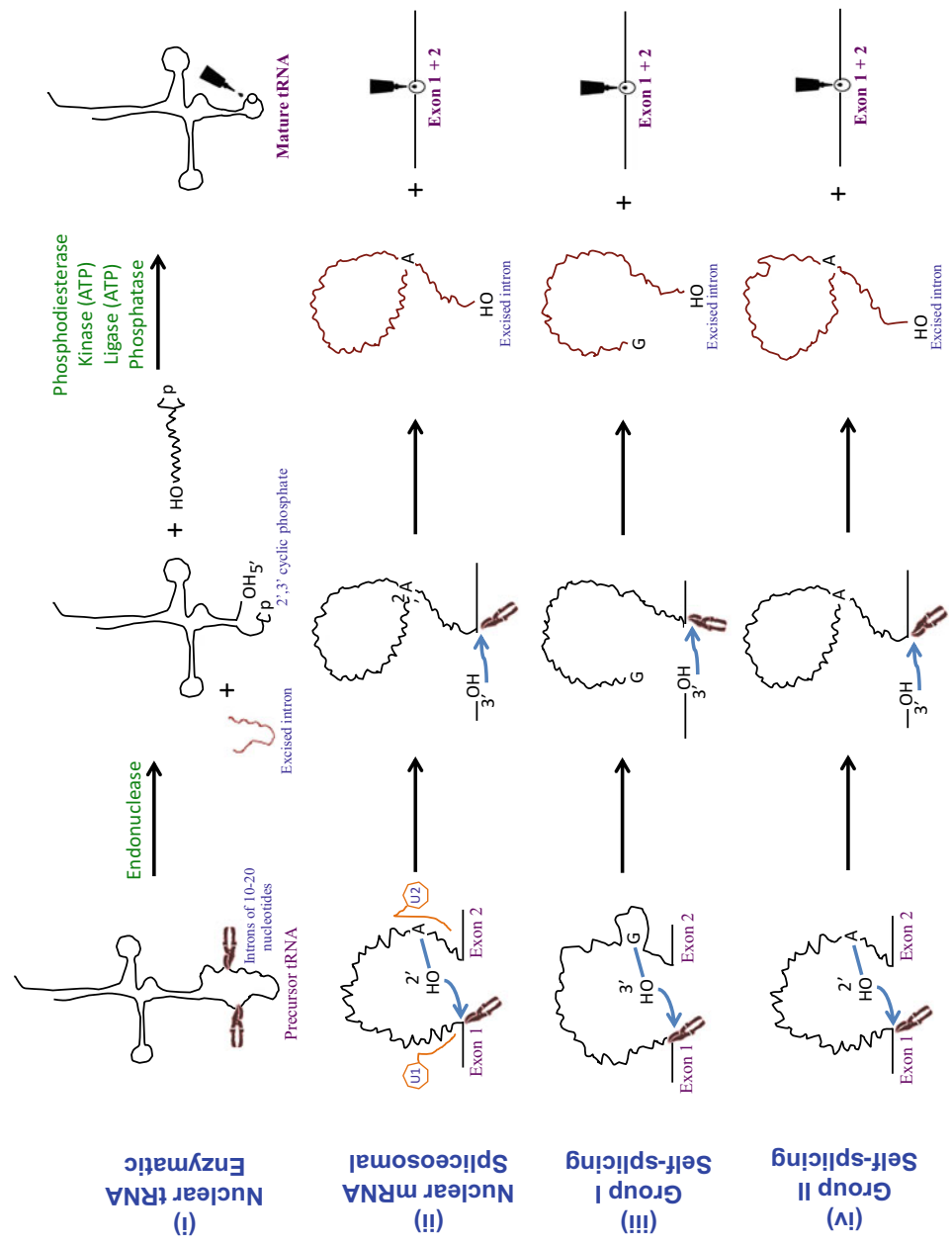
**Intron, Fig. 1** Introns are noncoding sequences of nucleic acids that interrupt the coding sequences (i.e., exons) in a gene. An intron is excised from the primary RNA transcript by splicing and is a common feature of eukaryotic genes

*cerevisiae* model. In the first step, a nuclear membrane-bound splicing endonuclease makes two precise cuts at the ends of the intron. In the next step, a splicing ligase joins the two halves of tRNA to form the mature form of the tRNA molecule (Greer et al. 1983).

- (ii) Introns of nuclear pre-mRNA transcripts – Nuclear pre-mRNA introns, also known as spliceosomal introns, are characterized by specific intron sequences located at the boundaries between introns and exons (GU at 5' end of the intron and AG at 3' end of the intron). These introns also have a branch point site close to the 3' end of the intron with a highly conserved A residue followed by a polypyrimidine tract. These introns are excised by complex transesterification reactions in two steps by RNA/protein structures called spliceosomes. Spliceosomes are dynamic structures made

up of uridine-rich small nuclear RNAs (snRNAs) and protein complexes called small nuclear ribonucleoproteins (snRNPs). Through complex RNA-RNA, RNA-protein, and protein-protein interactions, the snRNPs mediate the splicing of introns in nuclear pre-mRNA (Watson et al. 2003).

- (iii) Group I introns – Group I introns share common folding pattern and are self-splicing introns, i.e., they catalyze their own excision from mRNA, rRNA, and tRNA precursors. In these introns the splicing reaction is initiated by guanosine or one of its 5'-phosphorylated forms (GMP, GDP, or GTP), which attacks the phosphorus atom at the 5' end of intron and forms a 3', 5'phosphodiester bond to the first nucleotide of the intron. The 5' exon, now having a free 3' hydroxyl group, then attacks the phosphorus atom at the 3' end of the intron resulting in ligation of the exons and excision of the intron (Cech



**Intron, Fig. 2** (continued)

1990). These introns are found in mRNA, tRNA, and rRNA in the mitochondria and chloroplasts. They are also present in bacteriophages, eubacterial genomes, and nuclear genomes of non-vertebrates.

- (iv) Group II introns – Group II introns are also self-splicing and catalyze their own excision from mRNA, rRNA, and tRNA precursors. The splicing of these introns involves two transesterification reactions similar to that of nuclear pre-mRNA introns. These introns are present in the mitochondria and chloroplasts. They are also found in cyanobacteria and proteobacteria (Fig. 2).

## Conclusion

Regarding the origin of introns, there are two opposing views. According to the “introns early model,” protein-coding genes were interrupted by numerous introns even in the early stages of evolution. The absence of spliceosomal introns in prokaryotes is considered to be a result of “genome streamlining.” According to the “introns late” hypothesis, spliceosomal introns emerged late in evolution in eukaryotes and got inserted into protein-coding genes continuously throughout the evolution of eukaryotes. Irrespective of which view is correct, presence of introns and the need to remove them allows for alternative splicing. Alternative splicing is the molecular mechanism that can generate multiple protein products from a single

gene in a eukaryotic cell, thereby enhancing the protein repertoire and genetic diversity.

## Cross-References

- ▶ [Alternative Splicing](#)
- ▶ [Exon](#)
- ▶ [Genes](#)
- ▶ [Protein](#)
- ▶ [RNA](#)
- ▶ [Transcription](#)

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**Intron, Fig. 2** Steps in the splicing mechanisms of the four classes of introns. (i) **Splicing of tRNA precursors:** many precursor tRNAs contain introns of 10–20 nucleotides in length. These introns are removed by a series of enzymatic reactions (which uses endonuclease, kinase, and ligase). The endonuclease generates a 2',3' cyclic phosphodiester which is opened by a phosphodiesterase to provide a 3'-OH for the ligase reaction. Every splicing episode uses 2 ATP molecules. (ii) **Splicing of introns in pre-mRNAs:** Splicing is initiated at the “branch” point where 2'-OH of an A forms a phosphoester with the first G of the intron. Splicing occurs through transesterifications. The 3'-OH of the upstream exon reacts

with first nucleotide of the downstream exon, so that the two exons join through phosphoester transfer mechanism. snRNPs (U1, U2, etc.) form functional spliceosome on pre-mRNA and catalyze the splicing reaction. (iii) **Group I introns splicing:** the 5' phosphate of the first intronic nucleotide get connected to the 3'-OH of the G nucleotide with the 3'-OH of the last nucleotide of the upstream exon available and join the 5' phosphate of the first nucleotide of the next exon. This excises the intron and the two exons join by phosphoester transfers. (iv) **Group II introns splicing:** The mechanism of group II introns splicing is similar to that of nuclear pre-mRNA splicing. These splicings can also be reversible like in the group I introns.



## Introspection

► [Self-Awareness](#)

## Intuition

► [Insight in Pigeons](#)

## Intuitive Physics

► [Folk Physics](#)

## Invention

► [Innovation](#)

## Inversion Effects

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## Synonyms

[Adaptive superiority](#); [Heterosis](#)

## Definition

Inversions are the chromosome structural aberrations brought about when a segment of a gene on chromosome breaks, and turned 180 degrees and rejoin to the remaining chromosome.

## Introduction

Figure 1 is showing a heterozygous para-centric inversion in the third chromosome of



**Inversion Effects, Fig. 1** Photomicrograph of para-centric heterozygous inversion present in third chromosome of *D. bipectinata*

*D. bipectinata* observed in a natural population. Structural changes in chromosome, like deletion, duplication, inversions, and translocation, are known to occur in humans as well as plant and animal species. Inversions are the most common structural changes in chromosome. As a result of inversion, the order of the segment gene is inverted. Chromosomal inversions were the first type of genetic variations to be studied in *Drosophila* due to the involvement of an inversion. The occurrence of inversions in the polytene chromosome of *Drosophila* can be clearly observed and has been extensively studied from time to time in its different species of this group.

Generally, inversions are generated by the non-allelic homologous between inverted repeats, but in some other species like human, DNA repair mechanisms also involve originated inversions i.e., double-strand repair mechanisms like non-homologous end joining and replication-based repair mechanism. However, in most of the cases, there is no effect on gain and loss of DNA (Puig et al. 2015).

Chromosomal inversions aberration can be observed as inversion heterozygotes (ST/In) always manifested in the form of a loop in the polytene chromosome, and inversion homozygote (In/In) observed as the polytene chromosome is in a permanently paired state.

There can be two types on inversions based on the presence of centromere, the inverted segment includes the centromere, then such inversion is referred to as pericentric inversion, and

paracentric inversions are those which do not include centromere. Pericentric inversions were observed in plant, grasshopper, and crickets and have been extensively studied in grasshopper from Australia and have been discussed from an evolutionary point of view. Paracentric inversions are very common and occur at a high frequency in a number of species due to their adaptive significance for them and have been widely studied in genus *Drosophila* (Singh and Singh 2018; Singh 2019). However, translocation and pericentric inversions are very rarely reported in *Drosophila* (Singh and Singh 2015).

Inversions which occur frequently in a species are described as cosmopolitan, and their frequency always remains higher than other inversions in every population. The inversions remaining at very low frequency, i.e., less than 5% but present in most of the populations, are called rare cosmopolitan. Some inversions are occurring in some individuals of a population, described as rarely occurring inversions.

A number of species of the genus *Drosophila* have been investigated for their chromosomal polymorphism like *D. melanogaster*, *D. ananassae*, *D. bipectinata* species complex, *D. pseudoobscura*, *D. willistoni*, *D. subobscura*, *D. nasuta*, etc.

Fixation or elimination, distribution, and frequency of an inversion in a population depend on their phenotype consequences and mostly on the evolutionary forces such as natural selection and genetic drift.

## Role of Inversion

On the basis of recent theory and data that are observed by some population, geneticists addressed the potential role of inversion in speciation and evolution. Basic population genetics marker to check the genetic variations between different species of a group or genus is chromosome inversion, and it has significantly affected the rate of adaptation, survival, mating success, rate of development, competitive ability, fecundity, longevity, fertility, etc. (Sperlich and Pfriem 1986). Inversions have been involved affecting the phenotype in multiple species: in *Drosophila* inversions can affect the size

and development time: flowering in plants or adaptation to freshwater in stickleback.

Based on the inversion polymorphism, recently some studies have been conducted to understand the impact of inversions on evolution because an inversion present in a natural population, after several generations in laboratory, may be lost or present in a polymorphic state.

In many nondrosophilids species like black flies and seaweed flies, inversion polymorphisms may influence development time, size, and viability; however, effects on these traits also vary with environmental conditions (Butlin and Day 1989). Blyth and Gilburn (2005) also observed the role of chromosome inversion on sperm displacement in seaweed flies and concluded that when female mates rapidly, sperm carrying opposite karyotypes are favored and increase the higher number of heterokaryotypic offspring. Colombo (2002) and Pensel and Remis (2007) studied the role of pericentric inversions at body size and lifespan of the male of New World grasshopper. The body size is similar in higher latitude and altitude individuals, but the frequencies of inversion polymorphism changed between beginning and end of the adult lifespan, and the survival is more in the highly polymorphic males.

*Anopheles gambiae* complex have some insecticide resistance influencing genes that present on the two paracentric inversions, i.e., 2La and 2Rb, associated with dieldrin and DDT resistance, respectively (White et al. 2007a, b). Hardikar and Nath (2001) suggested that inverted heterozygotes tropical midge, *Chironomus ramosus*, have lower chances of infection with nematodes than homozygotes, and heterozygosity is also associated with the larval size in midge.

## Inversions and *Drosophila*

Genetic marker and inversion both were used as marker in cytological studies. Inversion polymorphism has been used in many species of *Drosophila* to test suppressive effect on recombination, heterosis, size, and time of development (Yadav and Singh 2006). The suppressive effects of inversion on recombination have been first time

observed in *D. melanogaster*. The effect of heterozygous superiority of inversion in different species of *Drosophila* was observed. For example, in *D. pseudoobscura* heterozygosity of inversion prevents the recombination in the chromosome (Dobzhansky and Epling 1948), in *D. melanogaster* heterozygous inversion of X chromosome shows same situation, and Grell (1962) also observed heterozygous inversion in *D. melanogaster* that increases the frequency of crossing over in X chromosome. Some other observations in different species of *Drosophila* show that X-chromosome heterozygous inversions enhance the effect of recombination in the autosome. Inversion polymorphism is a most important traditional marker in population genetics to discuss the phylogenetic relationship between the different members of a species complex (Tomimura et al. 2005; Banerjee and Singh 2016). Singh and Singh (1987) suggested that recombination is also influenced by the heterozygosity of inversion in *D. ananassae*. It has also been observed that the larger size of heterozygous inversion increases the frequency of crossing over in chromosome. Inversion polymorphism plays a crucial role in some adaptive traits. Mating propensity is one of them that is associated with inversions, and it has been demonstrated in many species of *Drosophila*. Singh and Chatterjee (1986) observed mating ability of different inversion karyotypes in *D. ananassae*, and they concluded that heterosis was associated with male mating ability, and inversion occurring in high frequency in a population was associated with higher mating ability.

## Inversions and Human

The existence of inversions in humans has been long known during the time of primate evolution and speciation. After a long time, still we have not much information about the presence of polymorphic inversions in the human chromosome and the significant association of inversions with gene expression, adaption, disease, or recombination (Feuk et al. 2005).

It's very difficult to detect and identify inversions in the human genome; some cytogenetic techniques and molecular tools like G-banded karyotypes, fluorescence in situ hybridization,

Southern blot hybridization, or pulsed-field gel electrophoresis help us to observed human inversion. In the human genome, many identified inversions do not have association with any phenotypic effect, but some of them significantly have been related to several diseases.

Some paracentric inversions in human directly affect the frequencies in different human populations. For example, pericentric inversion in chromosome 9 (mainly heterochromatic sequences inverted) shows the variation in frequencies in different populations from 0.26% to 3.57% in Asian and African origin, respectively (Thomas et al. 2008). Besides this, some other few inversions have been responsible for some diseases, such as hemophilia A and Hunter syndrome. Two types of inversions presented on the X chromosome have been involved in familial hemophilia A in which mutation is inherited in offspring by a male patient from an unaffected mother (Antonarakis et al. 1995). The common cause of Hunter syndrome in human is the alteration in the X-chromosome-linked IDS-related sequences by an inversion of the IDS gene, which encodes the iduronate-2-sulfatase enzyme (Bondeson et al. 1995).

Based on the cytogenetic and traditional molecular approaches and evidence in multiple species including human indicated that inversion can directly influence, alter, and affect the gene and their expression by regulating different levels. However, most of the inversions have not been observed for their effect on the human genome. Based on the mating propensity, it is concluded that the inversions may assist the evolution of sex chromosome by influencing recombination between sex chromosome and alleles which have sex-specific effects.

## Cross-References

- [Chromosomes](#)
- [Crossover](#)
- [Genetic Variation](#)
- [Heterozygote Superiority](#)
- [Homozygosity](#)
- [Polymorphic](#)

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## Invertebrate Cognition

### ► Cephalopod Cognition

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## Invertebrate Food Habits

### ► Arthropod Diet

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## Invertebrate Forage

### ► Arthropod Diet

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## Invertebrates

### ► Arthropod Cognition

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## Invisible Displacement

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### Synonyms

[Object permanence](#)

### Definition

Invisible displacement is the ability to track the movement of a hidden object after seeing that object placed in, under, or behind an occluder and moved into or behind a second occluder.

### Introduction

Invisible displacement is the sixth, and final, stage of object permanence ability. Object permanence is the understanding that objects exist even when they cannot be directly perceived. Piaget (1954) proposed that human children develop object permanence during the sensorimotor period of development and that this skill developed slowly over six stages. In the first stage, human infants show no response to the disappearance of an object. Infants in stage 2 will track an object of interest that is visible, but will not follow the object once it is out of sight. Further, they show no anticipation of where the object would logically be once it moves out of sight. By stage 3, children can locate partially hidden objects such as a toy that is sticking out from under a blanket. Children will successfully retrieve fully hidden objects in stage 4. This is visible displacement. By the fifth stage, children are capable of finding an object where it was the most recently hidden without making a typical error called the A-not-B error. This is when children will look at in a familiar hiding location even when they witness an object hidden in a new container. The sixth stage of object permanence development involves seeing an object hidden under a displacement device and

then moved to a new hiding location. The object is surreptitiously placed in the new location and the empty displacement device is shown to the child. This is invisible displacement. Children who have mastered stage 6 object permanence are able to track the movement of the hidden object and correctly locate it in the new location.

### Testing Methodology

Invisible displacement ability is tested through one of three basic tasks. These include a containment task, a rotation task, and a transposition task.

#### Standard Piagetian Task

The standard test for invisible displacement involves hiding an object inside a displacement device. This can be any opaque container. Next, the displacement device is placed inside one of several opaque containers. The object is surreptitiously removed from the displacement device and the device is removed. Subjects see the empty displacement device. Successful completion of this task involves indicating which opaque container contains the hidden object. An example of this would be to show a child a piece of candy and then wrap it inside a fist. The hand is then placed into a pocket and the candy is released. Upon seeing an empty hand, a child would indicate that the candy was in the pocket.

#### Rotation

Rotation tasks can also be used to assess whether an individual can track the movement of a hidden object. In this type of task, an object is hidden inside one of two opaque containers. The two containers are then moved with a rotating mechanism such that containers 1 and 2 switch places (a 180° switch). Other rotations tasks involve only a 90° rotation of the containers (e.g., Miller et al. 2009). The goal is to identify where the hidden object is after the containers stop moving.

#### Transposition

Transposition involves hiding an object inside one of several opaque containers. Then the container itself is moved to a new location. Subjects



must indicate where the hidden object is in the new location.

## Invisible Displacement in Animals

The literature is mixed on the question of whether animals other than nonhuman primates are capable of solving invisible displacement tasks. Several species of birds, dogs, cats, dolphins, prosimians, lesser apes, and great apes have all been tested using one or more of the methodologies described above (see Jaakkola 2014 for a thorough review). The evidence suggests that many primate species demonstrate invisible displacement capacity (e.g., Call 2003). Some studies suggest that adult dogs are capable of invisible displacement (e.g., Zentall and Pattison 2016). However, there are also numerous studies that suggest the dogs' success was merely the result of simpler, associative rules (e.g., Collier-Baker et al. 2004). For example, animals may be able to use a rule such as "*Pick the last container touched,*" "*Pick the container the experimenter is near,*" or "*Go to the container closest to the displacement device.*" Further, animals that attend to social cues may solve invisible displacement tasks by using eye gaze or body orientation of the experimenter. One solution to this problem would be to "blind" the experimenter by having them look away from the apparatus, shield their eyes, or hide completely out of sight of the research subject. A final concern is that the tasks designed to test invisible displacement to date have not been ecologically relevant. It has been suggested that if animals were given a task that was more natural, they may be more likely to pass the invisible displacement task. For example, Jaakkola et al. (2010) reported failure of their dolphins to pass invisible displacement using a traditional containment procedure. However, Johnson et al. (2015) used an occlusion task rather than a containment procedure and their results indicate that indeed, dolphins were capable of solving invisible displacement. The occlusion task was more natural for a dolphin than a containment task.

## Conclusion

Invisible displacement is the most complex stage of object permanence. While many animals are capable of the earlier stages of object permanence such as visible displacement, very few are able to solve invisible displacement tasks when appropriate controls are used to prevent the use of social or sensory cues and associative rule learning. Thus far, the great apes, and perhaps dolphins, appear to be the only species, other than humans, that consistently pass.

## Cross-References

- [A-Not-B Problem](#)
- [Visible Displacement](#)

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## **IQ**

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### **Introduction**

Intelligence is the ability to think rationally, learn effectively, understand complex ideas, and adapt to the environment. Accordingly, intelligence is best seen as a general ability that can influence performance on a wide range of cognitive tasks. IQ (the intelligence quotient) is the quantification of an individual's intelligence relative to peers of a similar age. IQ is one of the most heritable psychological traits, and an individual's score on a modern IQ test is a good predictor of many life outcomes, including educational and career success, health, longevity, and even happiness (Gottfredson 1998). Like humans, several species of animals express a "general cognitive ability" that influences performance on broad and diverse cognitive tasks, and moreover, animals exhibit a wide range of individual variations in this ability.

### **Intelligence and Intelligence Testing (IQ) in Humans**

It has long been recognized that intelligence varies across individuals. Colloquially, we refer to someone as "brilliant" or comment that our dog is a "little dull." While it is easy (and common) to make these kind of characterizations, it has historically been difficult to formulate a definition of this trait. In 1995, a committee of the American Psychological Association stated that "Individuals differ from one another in their ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, to engage in various forms of reasoning, to overcome obstacles by taking thought. Concepts of 'intelligence' are attempts to clarify and organize this complex set of phenomena" (Neisser et al. 1996). In an article in the Wall Street Journal

(December 13, 1994) signed by 52 intelligence researchers, it was asserted that intelligence was "a very general mental capability that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience. It reflects a broader and deeper capability for comprehending our surroundings."

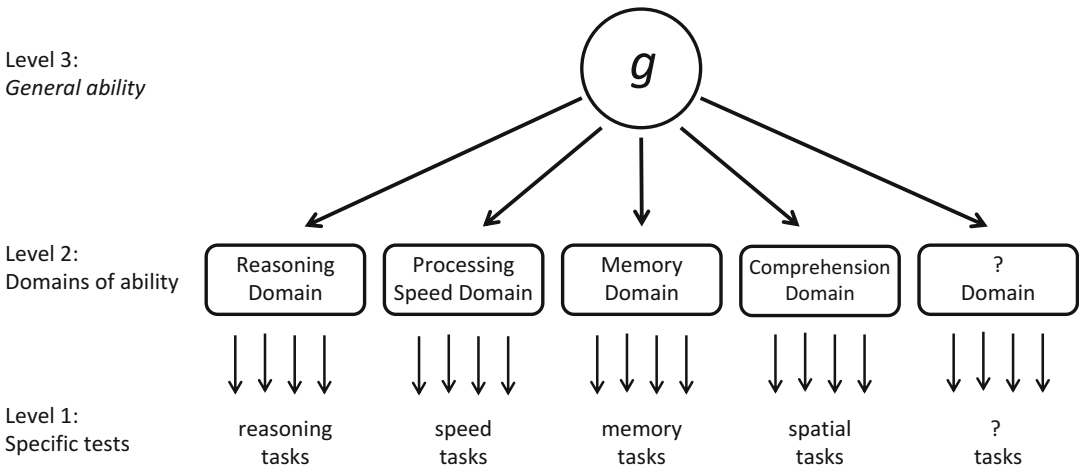
The above definitions are simultaneously vague and broad. Although provided by experts on intelligence, they differ little (if only in form) from colloquial descriptions of the trait that one might hear from a random sample of college undergraduates. While it has been more than 100 years since Spearman (1904) formally described the concept of "general intelligence" (also called "g"), we still struggle with its definition, but nevertheless, we recognize it and we make inferences about its consequences. In this regard, the *quantification* of intelligence is best relegated to performance on psychometric tests. The rationale for most psychometric tests is roughly based on Spearman's early observation that performance on a wide range of cognitive tasks is positively correlated (i.e., if you perform well on one, you tend to perform well on others) and, as such, can be reduced to a single index of aggregate performance across a battery of diverse tests. In fact, psychometric tests (e.g., the Stanford-Binet, the Wechsler or WAIS, and the Raven's Progressive Matrixes or RPM) do differ in their content and structure. For instance, the Stanford-Binet includes questions that are culturally relevant and thus is best suited to predict performance in a particular culture's school system. The WAIS is less culturally biased but, like the Stanford-Binet, includes categories of questions that are presumed to reflect domains of abilities (verbal comprehension, working memory, perceptual reasoning, processing speed). An individual's performance on tests within a particular domain (e.g., reasoning) tends to be highly correlated, while performance on tests across domains (e.g., a reasoning task and a spatial task) is usually less correlated. Nevertheless, positive correlations are observed between performance on *all* tests in

the battery. This is in line with the conclusion that *all* cognitive abilities are regulated (to varying degrees) by one general factor, or Spearman’s “g,” while other specific abilities might influence performance within a particular domain. These kinds of observations have led to the development of hierarchical models regarding the structure of intelligence, where *g* influences domains of specific abilities, which influence tasks within those domains. An illustration of a hierarchical model is provided in Fig. 1.

Since many studies on intelligence use factors analyses, a brief explanation of this technique is warranted. Briefly, a factor analysis is a statistical method which reduces a large number of correlations into as few explanatory factors as possible. If, for example, all of the correlations across several tests of cognitive ability are strongly positive, the factor analysis recognizes that a common source of variance contributed to performance on all tasks, and this would be described as a general factor. In reality, the outcome of such an analysis can be much more complicated, and of course we might be interested in large numbers of cognitive tasks, some of which represent clusters of what are

presumed to be specialized abilities. In these cases, the factor analysis might extract a general factor, as well as secondary factors, which explain relationships between only subsets of the tasks being considered. Of course, if no single source of variance was common to all tasks, a factor analysis might reveal no common factor at all. When factor analyses are performed on human intelligence test data (such as from the WAIS), it is typical to find a general factor (i.e., general intelligence) as well as secondary factors that describe specific cognitive domains (e.g., spatial abilities; see Fig. 1).

Remember that the Stanford-Binet and the WAIS include tests of many different abilities, and an individual’s aggregate performance across all of these tests is used to estimate that individual’s intelligence. In contrast, the RPM is an intelligence test that is based exclusively on only *one* ability and, accordingly, includes only progressively difficult tests of perceptual (analogical) reasoning. This test structure is based on an assumption that reasoning is representative of *the* core ability that regulates all intelligence (Raven et al. 1998). Because of its



**IQ, Fig. 1 The hierarchical model of intelligence.** *Level 1* represents specific tests that are emblematic of various domains of cognitive ability. Some potential domains are illustrated in *Level 2*. The number and content of these domains is a matter of some debate, although there is wide agreement on the existence of the four domains that are illustrated. The fifth domain (?) acknowledges that other domains may exist. People who perform well on tasks from

one domain tend to perform well on tasks from other domains. This suggests the existence of a general influence on cognitive abilities, represented in *Level 3*. This general influence is commonly referred to as general intelligence or simply “intelligence.” This model does not require only *one* type of intelligence. Rather, it assumes that a general ability influence other more domain-specific abilities.

format, the RPM requires no knowledge of culture or language.

Unlike a qualitative description of intelligence, the IQ *score* is a *quotient*, that is, it is an individual's score on a standardized test *relative* to that individual's age-matched peers. It is true that an individual's IQ score will tend to remain stable across the lifespan, i.e., the IQ scores of a group of 8-year-olds will be highly correlated with their scores at 90 years of age ( $r = \sim .80$ ). This does *not* mean that individual's raw cognitive ability is the same across the lifespan. For example, were we to administer an RPM to one individual at 8, 25, 50, and 90 years of age, the number of correct answers would be about the same at 8 and 90 years of age, while at 25, the individual would answer at least twice as many questions correctly (with the 50-year-old somewhere in between). So why do we say that an individual's IQ remains constant across the lifespan? Because IQ is approximately unchanging *relative* to persons of a similar age, i.e., a person who is smarter than most of his/her peers at 8 years of age will be smarter than his/her peers at 50 and 90 years of age (Deary 2014), despite the inevitable truth that our cognitive abilities decline with age.

Regarding the nature of intelligence or IQ, many persons will incorrectly assume that high intelligence is necessarily reflected in a high level of *knowledge*. In fact, high intelligence promotes the ease with which we acquire knowledge, but intelligence itself is independent of knowledge. Why then do some IQ tests (such as the Stanford-Binet) have components that test knowledge? Simply because all other things being equal, a smarter individual is likely to acquire more knowledge. Learning is *easier* for that individual than it might be to someone of lesser intelligence. In this regard, scholastic aptitude tests such as the SAT are often a good approximation of intelligence as measured on a knowledge-free test such as the RPM ( $r = .5-.6$ ). However, knowledge and intelligence need not always be related. For instance, an individual with innately high intelligence might (through some act of fate) live in an impoverished environment where the opportunities to acquire knowledge are severely limited. This is exactly why an IQ test such as the

RPM has no measures of knowledge (only perceptual reasoning) and is considered by many to be a more pure measure of innate ability.

Given the different content and structure of psychometric intelligence tests, it might be surprising to find that individuals' scores on these tests are strongly correlated ( $r$ s will typically range from 0.8 to 0.9). Even more surprising is the popular assertion (sometimes even by some with advanced degrees in psychology) that "IQ tests measure nothing of functional significance." Standardized intelligence tests first received widespread recognition owing to the US government's use of a modified version of the early Stanford-Binet to determine assignments of new recruits in World War I. These assignments were highly effective (relative to the previous practice of assignments based on patronage or chance) and are widely regarded as having contributed to the USA's success in WWI. Since that time, we have collected a wide array of data regarding the predictive capacity of IQ tests. For instance, a child's IQ score is highly predictive of obvious outcomes such as educational and career success, as well as lifetime income. But IQ test performance predicts many less obvious outcomes such as the distance one will travel from his/her place of birth, the likelihood of incarceration, the likelihood of drug addiction, the age of death, incidence of type II diabetes, ratings of happiness, and even your *spouse's* income and IQ (for a comprehensive review of the predictive capacity of the IQ test, see Gottfredson 1998). IQ scores are even inversely related to the likelihood that an individual will murder their spouse! To quote Gottfredson (1998, page 24), "No matter their form or content, tests of mental skills invariably point to the existence of a global factor that permeates all aspects of cognition. This factor seems to have considerable influence on a person's practical quality of life. Intelligence as measured by IQ tests is the single most effective predictor known of individual performance at school and on the job" as well as many other aspects of well-being. Thus, far from being a "social construct" with no functional significance, the modern IQ test is a highly effective (and widely used) diagnostic and predictive tool.

### Intelligence in Nonhuman Animals

Although studies of individual differences in animal intelligence had been frequent early in the twentieth century (Thorndike 1911, 1935; Tolman 1924; Tryon 1940), the emergent focus on experimental (rather than correlational) studies tended to limit the interest in this topic in the later part of that century. However, during the past two decades, interest in individual differences in animal intelligence has seen a dramatic reemergence. As discussed above, contemporary definitions of intelligence tend to be vague, broad, and, to some degree, a matter of debate (Sternberg 1985). Nevertheless, psychometric tests of intelligence do appear to characterize a trait captured in both colloquial and empirical definitions of intelligence, i.e., the ability to understand, learn, and reason. To explore a trait analogous to intelligence in nonhuman animals, researchers have developed tests to characterize a similar set of skills, most notably in mice and monkeys.

Genetically heterogeneous mice (i.e., mice with genetic variability that translates into measurable individual differences) have been tested on large batteries of cognitive tasks to determine the existence of a general cognitive ability in mice analogous to IQ. In one such study (Kolata et al. 2008), 241 mice were tested on seven cognitive tasks, which included tests of working memory capacity, associative learning, operant learning, and spatial learning abilities. Using factor analysis, it was observed that a general factor influenced performance in these mice and this factor accounted for 38% of the variance across tasks. This is comparable to what is known from tests of humans' abilities, where it is believed that general intelligence accounts for 40–50% of the variance in performance across a broad array of cognitive tests. In addition, a domain-specific factor was found to account for the performance of mice on a subset of tasks that shared a dependence on spatial processing. These results provide evidence for a general learning/cognitive factor in genetically heterogeneous mice. Furthermore (and similar to human cognitive performance), these results suggest a hierarchical structure (see Fig. 1) of cognitive abilities in mice, where a general factor influences performance on sub-

domains of abilities. Importantly, mice also exhibited considerable variability in their general cognitive performance. In fact, the general abilities of mice were normally distributed, such that most mice expressed average abilities, while some were “bright” (performing well on all tasks), while some were “dull” (performing poorly on all tasks).

As described above, reasoning is considered to be a hallmark of intelligence and is considered by some to be *the* general factor that underlies variations in intelligence. It has previously been established that humans are capable of “fast mapping” (Carey and Bartlett 1978), a process whereby a new concept can be acquired based on a logical inference, corresponding with Aristotle's description of deductive reasoning. Fast mapping is believed to play a critical role in the extraordinarily rapid acquisition of information during early human development and explains (in part) the prodigious rate at which children gain vocabulary. For example, when faced with a group of familiar items described by familiar words, an infant will quickly associate an unfamiliar word with a novel item added to the set of familiar items, and this association requires no overt “pairing” of the novel word and its corresponding novel item.

Fast mapping based on responses to human language has also been demonstrated in dogs (Tomasello and Kaminski 2004; Pilley and Reid 2011), where border collies can successfully find a novel object when commanded (with a novel word) to retrieve that novel object from within a large set of familiar objects. Using a similar strategy, fast mapping has been assessed in mice, although the task was not based on responses to language. Mice were first trained to associate pairs of objects, where, upon exposure to a sample object, the correct choice of a target object earned the mouse a food reward. Following training, the mice could successfully use the sample object to guide its choice of a target object out of a set of familiar objects. (This type of performance is emblematic of “paired associate learning.”) To test “fast mapping,” the animal was then presented with a novel sample object and allowed to choose a target object from a set containing several familiar objects and one novel object. If the mice were



capable of fast mapping (inference by exclusion), they should choose the novel target object (in response to the novel sample) since all other objects in the set had a previously established meaning. Mice perform quite well in this task, choosing the novel object at an average rate far better than chance. However, not all mice perform similarly, and while some exhibit perfect performance, some consistently make incorrect choices. The likelihood of a mouse's success in this fast mapping task is correlated with their performance on other more elemental cognitive tasks (e.g., associative learning, spatial learning, operant learning), suggesting that as in humans, this form of reasoning ability is related to more general cognitive abilities (Wass et al. 2012).

General cognitive abilities of mice have also been described by Galsworthy et al. (2002), who compared the performance of 40 genetically heterogeneous mice across a battery of cognitive tests distinct from those reported in the studies described above. All measures of cognitive performance loaded positively on a principal component that accounted for 31% of the variance across mice, again suggesting the presence of a common influence on performance on all tasks. In addition, Galsworthy et al. calculated the heritability of this general cognitive ability in mice. (This was accomplished through a classic sibling analysis, which assesses the degree of relatedness between siblings on some variable of interest, in this case general cognitive ability.) The heritability of the general cognitive ability of mice was estimated at approximately 0.4 (on a scale of 0–1), suggesting a moderate genetic contribution to the expression of this trait. These results of Galsworthy et al. are quite informative. They indicate that the “intelligence” of mice is moderately heritable, at a level that is comparable to what is observed among teenage humans. Note that the heritability of human intelligence actually *increases* across the lifespan, reaching a plateau of approximately .80 at 50 years of age. This increase in heritability is presumed to reflect the interactions of genes with the environment, where persons of similar IQ become even *more* similar as they gravitate to similar cognitive challenges. Unlike typical humans, laboratory mice are maintained in a

behaviorally sterile and homogeneous environment. Consequently, these mice cannot select the environments or challenges that might maximize cognitive differences, thus constraining the gene-environment interaction.

In addition to rodents, individual differences in a general cognitive ability have been observed in several species of nonhuman primates. While most studies of nonhuman primates have been designed to compare differences in intelligence between species (leading to a popular hypothesis that brain size is related to intelligence; Burkart et al. 2016), at least one study was designed explicitly to assess individual differences in the expression of a general cognitive influence within a single species. Banerjee et al. (2009) administered a large and diverse battery of cognitive tests to 22 tamarin monkeys (*Saguinus oedipus*). The cognitive tasks covered a wide range of cognitive skills and domains, including occluded reach, targeted reach (reward retrieval from a moving pendulum), adaptation to an observed change in reward location (a measure of executive control), reversal learning, novel object recognition, numerical discrimination, acoustic habituation, object tracking (an index of attention), social tracking (gaze at a conspecific), hidden reward retrieval after various delays, and a food retrieval puzzle (which was asserted to tax reasoning). Banerjee et al. observed positive correlations in the monkeys' performance across all tasks. Using a type of factor analysis, all tasks loaded positively on a common factor. The weight of these loadings (an index of the degree to which a variable is impacted by that factor) could be described as “weak” to “moderate.” Expectedly, the tasks with the least obvious cognitive demands (targeted reach and social tracking) loaded most weakly. In total, these results provide evidence for individual differences in the expression of a general cognitive ability among tamarins, and moreover, that the general factor's influence is directly related to the level of the cognitive demand.

### What is the Latent Factor that Regulates Intelligence?

Many factors, such as speed of processing or brain size, have been suggested to underlie variations in

intelligence. However, correlational analyses have typically found only weak relationships between these factors and intelligence. Two clear exceptions should be noted. Both reasoning ability and working memory capacity are strongly predictive of IQ (and as noted previously, the RPM intelligence test is based solely on performance on analogical reasoning tasks). Although it was once commonly asserted that reasoning ability was *the* latent factor which regulated individual differences in intelligence, it has been more recently hypothesized that working memory may serve such a function. In his classic textbook on intelligence, Mackintosh describes the full rationale for this hypothesis and points out that it is easy to surmise the way that working memory could influence reasoning, as will be seen below, while it is more difficult to imagine the opposite being true (Mackintosh 1998).

Since their inception, intelligence test batteries commonly included tests of simple memory span (e.g., the number of items from a briefly studied list that an individual can correctly recall). Somewhat surprisingly though, this seemingly elemental ability has only a weak relationship to general intelligence. In 1980, an important observation by Daneman and Carpenter (1980) shed light on the relationship between memory and intelligence. Daneman and Carpenter found that simply remembering a list of words was only weakly related to general intelligence (in this case, estimated through reading comprehension). In contrast, if the same words appeared at the end of sentences, the ability to remember those words was strongly correlated with general intelligence. This led to the hypothesis that simple retention had only a small (if any) role in the regulation of intelligence, while “working memory capacity” had a more central role.

While short-term memory simply holds information, the working memory system is one which stores information while manipulating and utilizing that information (often during conditions of high interference) for a particular goal. Working memory is employed for most cognitive tasks. For instance, your ability to read and comprehend this paragraph requires that you remember words, synthesize the meaning of strings of words, and

try to extract the overall message embedded in those strings of words. Obviously, your memory and manipulation of words and thoughts can become confused depending on the content of the paragraph. A similar rationale for the implementation of working memory can be applied to virtually any task; imagine doing a mental math problem or solving a spatial puzzle. In this regard, an analogical reasoning problem (such as might appear on the RPM test of intelligence) requires the individual to hold potential solutions in memory, compare the utility of those solutions, revise the solutions, and store the revised solutions in temporary memory. But while analogical reasoning depends on the efficient application of working memory, it is not clear that the application of working memory has any dependence on reasoning abilities. It is this ubiquitous demand for working memory that has led to the assertion that working memory may be the basis for the overall performance on an intelligence test. Since the original report of Daneman and Carpenter, many studies have found evidence for the relationship of working memory capacity to general intelligence (for a brief review, see Engle 2002).

Unlike human research, only limited work has been done to assess the relationship between working memory and intelligence in nonhuman animals. Some studies have found a relationship between working memory and intelligence in mice, but such correlations cannot be assumed to reflect a cause-and-effect relationship. The direction of cause between working memory and intelligence cannot be determined, and moreover, both traits might be influenced by a third, hidden variable. It should be noted that the same difficulties exist when interpreting this relationship in humans. However, in both humans and mice, a causal relationship between working memory and intelligence has been explored. For instance, Jaeggi et al. (2008) exposed humans to intensive working memory training by having them perform a “dual n-back” task for several weeks. The dual n-back task requires the subject to simultaneously monitor a stream of visual and auditory cues (a sequence of visual locations and a sequence of auditory letters). The subject’s task

is to identify matches that occur in each stream of information (e.g., auditory “B” matches auditory “B,” or upper right grid location matches upper right grid location) that occur a specific number of places back in the stream of information, e.g., 2-back, 3-back, and 4-back. Humans typically find this task to be extremely difficult (and even stressful), and the larger the n-back requirement (e.g., 4-back rather than 2-back), the more difficult the task becomes. This task is considered to tax working memory capacity, and humans will typically improve across days of training; they may initially find 2-back to be *very* difficult but might eventually master 6-back. Jaeggi et al. observed that several weeks of such training improved working memory and had positive (although small) effects on intelligence test performance. This suggests that working memory has a direct *causal* influence on an individual’s intelligence.

The work by Jaeggi et al. (2008) is by no means conclusive. While it has been replicated several times, others have failed to replicate these results, often after extensive attempts to do so (Redick et al. 2012; Shipstead et al. 2012). Relatedly, commercial “brain training” devices based on working memory training have been widely criticized as ineffective (Simons et al. 2016). Although this controversy has not been resolved, it is clear that training working memory in humans is complicated by the fact that humans *regularly* engage in the use of working memory outside of the laboratory (e.g., your comprehension of this paragraph), and so any working memory training that occurs in the laboratory is small in comparison. To this end, it might be useful to consider the effects of working memory training on laboratory animals that live in sterile cognitive environments. Light et al. (2010) developed a task to train working memory in mice. In this task, the mice were required to perform simultaneously in two mazes, and each maze required the animals to keep track of eight locations. Since the locations were marked by a common set of visual cues, the mice become very confused (presumably owing to an overload of working memory). Like n-back training, mice get better at these mazes over a period of weeks and, when later tested, exhibit

improvements in working memory. Likewise, they exhibit improvements in general cognitive performance, suggesting that the efficacy of working memory can under certain circumstances have a direct causal impact on a mouse’s intelligence. In the case of both humans and mice, these studies of the impact of working memory training on intelligence provide further evidence that intelligence is *malleable*. That is, although intelligence is heritable, genes interact with environmental experience to regulate an individual’s IQ.

Space does not permit a detailed explanation of the neuroanatomical systems that contribute to the expression of intelligence or working memory. However, these kinds of analyses also suggest that these abilities are strongly related. Brain areas that are active during tests of general intelligence overlap considerably with brain areas active during performance of a working memory task (Jung and Haier 2007), and the same brain areas have been implicated in the processing of working memory in both monkeys (Konecky et al. 2017; Riley and Constantinidis 2015) and rodents (Wass et al. 2013). In total, and although this issue is far from resolved, our current state of understanding suggests that variations in working memory capacity contribute directly (at least in part) to variations in intelligence.

## Conclusion

Humans and nonhuman animals exhibit individual differences in their ability to “reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience” (Neisser et al. 1996). This complex of abilities is referred to as intelligence. In both humans and animals, this trait can be assessed through batteries of cognitive tests, and in humans, these tests give rise to an intelligence quotient (an “IQ score”) which quantifies an individual’s performance *relative* to those of a similar age. Studies in nonhuman animals, most remarkably in primates and mice, have utilized diverse batteries of cognitive tests to measure something analogous to IQ. The intelligence in these animals varies among individuals and seems to be

correlated with processes such as reasoning and working memory. Recent research in both humans and mice suggest that working memory training might make causal contributions to the improvement of IQ. Those findings have not only theoretical implications concerning the structure and neurobiological insatiation of intelligence, but it also opens up opportunities for future practical applications.

## Cross-References

- [Analogical Reasoning](#)
- [Behavioral Genetics](#)
- [Behavioral Variation](#)
- [Genetic Variation](#)
- [Heredity](#)
- [Heritability of Behavior](#)
- [Inductive Reasoning](#)
- [Intelligence](#)
- [Learning](#)
- [Working Memory](#)

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## Irene M. Pepperberg, PhD

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### Research Interests

Pepperberg was the first to demonstrate that Grey parrots learn best through social interaction and that their abilities with respect to various concepts (e.g., number, relative size, same/different, inferential reasoning by exclusion) are equivalent to those of nonhuman primates, cetaceans, and ~5–6-year-old children. To teach her parrots referential use of English speech, she departed from the standard operant methods in use at the time and adapted Todt's (1975) two-person “model/rival” training technique, by alternating the roles of the person who modeled what the parrot was to learn with that of the person acting as respondent and using referential rewards – a 1:1 correspondence between the label to be trained and the object presented to the parrot for its use of that label. Via this technique, a Grey parrot, Alex,

learned to label more than 50 different objects, seven colors, and seven different shapes (“one-”, “two-”, “three-”, “four-”, “five-”, “six-”, or “eight-corner”). He learned to use English number labels (“one” through “eight”) to distinguish quantities of objects, including collections made up of novel objects, heterogeneous sets of objects, and sets in which objects were placed in random arrays. He could perform addition on small sets and with Arabic numerals. He induced the ordinality of his known numbers from their value and the cardinality of new number labels from their position on the number line. He combined his vocal labels to identify proficiently, request, refuse, categorize, and quantify over 100 different objects, including those that varied somewhat from his training exemplars. He had functional use of “no” and of phrases such as “come here,” “want X,” and “wanna go Y” (X, Y being appropriate object or location labels). He fully understood the concept of same/different: not merely identity versus nonidentity but that two objects could simultaneously be the same with respect to some attributes and different with respect to others. He and another Grey, Griffin, demonstrated, by vocally stating what they saw, the ability to interpret optical illusions (Müller-Lyer, Kanizsa figures, occluded figures) as do humans. Grey parrots have also used English speech in ways that allowed an examination of other advanced cognitive abilities, such as probabilistic inference. Pepperberg has shown that Grey parrots have executive functioning equivalent to that of young children (e.g., by passing the “marshmallow test”).

### Early Life, Educational Background

Dr. Pepperberg was born on April 1, 1949, in Brooklyn, NY, and raised in Laurelton (Queens), NY. An early interest in science was fostered by teachers at Andrew Jackson High School. She received a Bachelor of Science in Chemistry from MIT (1969) and a PhD in Chemical Physics at Harvard from the soon-to-be Nobel Laureate, William N. Lipscomb (1976). During her graduate career, she published several papers on molecular



orbital theory and boron hydrides. While at Harvard, she realized that her long-standing interest in animal behavior was stronger than her interest in theoretical chemistry. She began attending seminars and auditing courses on the communicative behavior of animals in nature, avian biology, interspecies communication, and on language acquisition in humans, working up to 80 h per week so as not to neglect her doctoral studies. After completing her doctorate, she switched fields completely.

## Professional Career

Moving with her then-husband, Dr. Pepperberg began her career in 1977 at Purdue University, as a research associate in biology and part-time instructor in psychology. With space borrowed from members of the biology department and the purchase of a Grey parrot, she began conducting experiments on interspecies communication and conceptual behavior in an avian subject. Despite the absence of a faculty appointment, she received the first of many NSF grants in 1979 and later a Harry Frank Guggenheim Foundation Fellowship. In 1984, she became a visiting assistant professor in the Anthropology Department at Northwestern University and a member of their Program on Language and Cognition. She remained at Northwestern until January 1991. At that time, she assumed an associate professorship in the Department of Ecology and Evolutionary Biology at the University of Arizona, receiving tenure in May 1994. She concurrently had a faculty appointment in the Department of Psychology and was an affiliate in the Program in Neuroscience. While at Arizona, she took a leave of absence (1999–2001) to work at the MIT Media Lab to design human-animal-computer and animal-computer interfaces and to explore the use of her research in building intelligent learning systems. Her visit developed into a research position that ended because of budgetary cutbacks at the Lab. To compensate for breaking her contract, MIT created a short-term research situation to enable her to continue her work; the parrot lab moved to Brandeis University,

where she was a research associate professor and later an adjunct associate professor until 2013. After a Radcliffe Fellowship (2004–2005), she was invited to join the Vision Lab at Harvard as an unpaid research associate. She began teaching at Harvard in various capacities soon thereafter. Her research since MIT has been supported by two NSF grants and *The Alex Foundation*, a 501(c)(3) nonprofit of which she is the president. In 2013, she moved the parrot laboratory to Harvard's Department of Psychology.

While at the University of Arizona, Dr. Pepperberg was the recipient of numerous awards for teaching and student mentoring and received a John Simon Guggenheim Fellowship. She was made a fellow of the American Psychological Association, the American Psychological Society (now the Association for Psychological Science), the Animal Behavior Society, and the American Ornithologists' Union, was an alternate for the Cattell Award for Psychology, and was nominated for the Weizmann Woman and Science Award.

While at MIT, Dr. Pepperberg received the 2000 Selby Fellowship from the Australian Academy of Sciences, was made a fellow of the American Association for the Advancement of Science (AAAS), and was nominated for the Grawemeyer Award in Psychology, the L'Oreal Women in Science Award, and the Quest Award from the Animal Behavior Society.

Since arriving at Harvard, she has won the 2005 Frank A. Beach Award, given by Division 6 of the American Psychological Association for best paper in the *Journal of Comparative Psychology*; the Christopher Award for her *New York Times* best-selling book, *Alex & Me*; and the Christopher Clavius S.J. (Sigma Xi) Award from St. Joseph's University. She was a consultant for ITALK (2007–2012), a program for robotics research. She became a fellow of the Eastern and Midwestern Psychological Associations, was renominated for the L'Oreal and Grawemeyer Awards, and was nominated for the Hebb Award (Division 6, APA) and the Exemplar Award (Animal Behavior Society). She served as associate editor of the *Journal of Comparative*

*Psychology* (2011–2016). She has also received numerous teaching awards.

Dr. Pepperberg has served on the editorial boards of seven different journals, on the National Science Foundation Animal Behavior grant review panel, on the board of directors for the Eastern Psychological Association and *Thinking Animals*, on the Science Advisory Board for the Austrian Science Fund, the review panel for the biannual conference on The Evolution of Language (*Evolang*) five times, the executive council for the American Ornithologists' Union (AOU), and as representative to the Ornithological Council for both the AOU and the Cooper Society. She has chaired the Public Affairs Committee and ran a legislative email alert system for the Animal Behavior Society. She is a foreign affiliate of the British Psychological Society.

Dr. Pepperberg has authored or coauthored over 60 peer-reviewed publications and over 80 book chapters, commentaries, and reviews and has given over 60 keynote or plenary addresses, over 370 invited professional presentations, and almost 80 contributed talks and posters. She also speaks several times each year at non-academic outreach events. She is the author of *The Alex Studies* (Harvard University Press) and *Alex & Me* (HarperCollins), co-edited *Animal Cognition in Nature* (Academic Press), and is an associate editor for the *APA Handbook of Comparative Psychology* (2017). She is a yearly contributor to *The Edge* annual question. With respect to the popular press, her research has been featured in articles in venues as diverse as the *New York Times*, *Die Welt*, *National Geographic*, the *Wall Street Journal*, *Audubon Magazine*, and the *New Yorker*; in television programs such as *Scientific American Frontiers*, *Discovery*, *BBC Nature*, and *Nova Science Now*; and in various outlets in Europe and Japan. After the parrot Alex died in 2007, his obituary was published worldwide, including in *The Economist*, the *New York Times*, *Der Spiegel*, and *Time* magazine.

## Cross-References

► [Alex the Parrot](#)

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## Isocortex

### ► Neocortex

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## Ivan Pavlov

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## Definition

Ivan Pavlov (1849–1936) was a Russian physiologist, Nobel Prize winner, and well known in the field of psychology for his research on classical conditioning.

## Introduction

Ivan Petrovich Pavlov, a Russian physiologist, is well known in the field of psychology for his research on classical conditioning. Pavlov began his career by becoming a skilled surgeon, which permitted him to perform many experiments on the digestive system of animals without severely

inhibiting normal functioning. These experiments allowed him to understand the process of classical conditioning, as well as contribute to the fields of abnormal and personality psychology. Today, several ongoing areas of research have their roots in Pavlov's research, and Pavlov has become immortalized in textbooks from a variety of fields in psychology.

## Early Life and Career

Ivan Petrovich Pavlov (1849–1936) was born in Ryazan, Russia, on September 26, 1849. His father, Peter (1823–1899), was an orthodox priest and his mother, Varvara (1826–1890), stayed at home with Ivan and his ten siblings. Although he was born into a religious family, attended religious instruction, and enrolled in the seminary, Ivan Pavlov soon redirected his attention to studying chemistry and physiology at the University of St. Petersburg (Furedy 2003). Even though his father withdrew financial support when Pavlov decided to pursue studies in the natural sciences, Pavlov continued and completed his degree in animal physiology. Under the mentorship of Elias de Cyon, a skilled surgeon, Pavlov became an expert in surgical procedures and skilled with the scalpel. During this time, Pavlov focused his research on the heart and digestive systems (Fields 2006).

After graduating with honors, he went on to the Imperial Academy of Medical Surgery in 1875 (Fields 2006). Controversy related to Cyon led Pavlov to leave the Academy and enroll in the Veterinary Institute of St. Petersburg where his focus remained on the digestive system.

Pavlov soon traveled to Germany to begin his work with an expert in digestion, Rudolf Heidenhain. While in Germany, he continued to improve his surgical skills and developed his theory of nervism while working on his dissertation (Palmer 2000). This theory posits that nerves control the majority of bodily functions.

Pavlov married a friend of author Fyodor Dostoyevsky, Seraphima Vasilievna Karchevskaya (1855–1947) in May of 1881. They went on to have four sons and a daughter, though they lost one son during childhood (Fields 2006).

Pavlov earned his medical doctoral degree in 1883 from the University of St. Petersburg. In 1884, Pavlov returned to Germany to begin his work with Karl Ludwig who was a cardiovascular physiologist (Fields 2006). With Ludwig and Heidenhand as collaborators, Pavlov created his own laboratory where he continued his studies on nervism (Palmes 2000). It was under Heidenhand's tutelage and having studied Nikolai Eck's shunt creation that Pavlov implemented the use of pouches and the creation of gastric and pancreatic fistulas in animals that enabled him to study organs without worrying about environmental or surgical procedures interfering with normal functioning (Palmes 2000).

Pavlov believed that stress influenced physiological reactions of animals and that this led to interference with his results. He disagreed with the practice of vivisection or surgery on live animals and instead championed the policy of surgically altering animals under anesthesia before conducting research so the animal would experience less stress and behave more typically than if in distress. He continued to train young scientists to perform procedures to limit the stress and pain animals experienced so that neither influenced the outcomes of their research (Kopaladze 2000).

In 1891, he was invited to be the director of the physiology department at the Institute of Experimental Medicine. In 1895, he simultaneously held this position and a professor of physiology appointment at the Imperial Military-Medical Academy in St. Petersburg (Asratyan 1953). It was at the Institute of Experimental Medicine that Pavlov conducted his research on the digestive system that eventually led to his Nobel Prize award (Marks 2004). In 1935, he presided over the XV International Congress of Physiological Sciences in Moscow. Six months later, in February of 1936, Pavlov died of pneumonia. To honor him, his research laboratory was preserved as a museum (Cambiaghi and Sacchetti 2015).

## Pavlov's Contributions to Psychology

Though Pavlov was awarded a Nobel Prize for research on the digestive system, he is most well known in the psychology field for his research on

classical conditioning. Pavlov studied the digestive system in dogs by conducting surgical procedures, which allowed him and his colleagues to measure saliva and other digestive secretions in healthy, awake animals. It was during these experiments that Pavlov realized the dogs would start salivating in response to other stimuli besides their food. After careful experimentation, Pavlov concluded that the salivating to a non-food stimulus was a conditioned reflex, which is a reflex that occurs in response to a particular stimulus only after that stimulus has been paired with another stimulus which has previously elicited the same reflex without conditioning. In Pavlov's lab, the unconditioned stimulus was the dogs' food, which naturally caused salivation (unconditioned reflex). The conditioning process happened when research assistants brought the dogs their food, as both assistants and food repeatedly appeared at the same time. Eventually, the dogs would salivate upon seeing the research assistants (conditioned stimulus), even when no food was present (conditioned response) (Fields 2006). This is the process of classical conditioning, as it commonly referred to in psychology, also known as the conditioned reflex.

In many accounts of how Pavlov discovered or studied classical conditioning, a bell is repeatedly paired with food and eventually becomes a conditioned stimulus so that the bell alone would cause the dogs to salivate. The accuracy of the accounts where Pavlov used a bell has sometimes been questioned as false; however, other historians have found that Pavlov used many different stimuli, including lights, sounds, and objects, including a bell (Jarius and Wildemann 2015).

Prior to Pavlov's experiments on conditioning, it was not well understood why a dog would salivate even before food was placed in its mouth. As Pavlov began to manipulate the type of food and conditions in which food was presented to his research subjects, he termed this response "psychic secretion" because it was the dogs' brains and nervous systems that caused the salivation response (Todes 1997). These experiments demonstrated that the dogs anticipated being able to eat the food and were even able to generalize different stimuli and environmental conditions as indicating that food would soon be

given to them, a very adaptive trait. Adaptability to changing environmental conditions allows for a better chance of survival and Pavlov recognized that his subjects' rapid habituation and dishabituation to environmental stimuli allowed for such adaptability (Marks 2004).

Though Pavlov's early research was strictly physiological, Pavlov had an increasing interest in mental phenomena which he felt could not be dealt with scientifically unless they were measured in terms of physiological quantities. Pavlov was interested in the mind's subjective nature and was not a strict behaviorist as he has often been labeled. The study of associative learning, one of the major research fields in psychology today, began with Pavlov's systematic experiments on dogs' salivation in 1901 (Gray 1999). Pavlov was strict in his direction of the laboratory's experimental methods, ensuring that all research assistants and colleagues followed rigid methodical protocols in order to reduce error and confounding variables.

After many years of careful experimentation and hundreds of publications on the topic, Pavlov published *Conditioned Reflexes* in 1926. The now world-famous term "conditioned reflex" likely resulted from an error in translation. The Russian term that Pavlov used is argued by some to be more accurately translated as "conditional reflex" and has a slightly different meaning (Todes 2014). The term "conditional" implies that the resulting action or reflex is not an innate response to a stimulus in the traditional sense of the word "reflex." One criticism of Pavlov's work is that he attributed all associative learning to cortical areas of the brain, despite this being false because some animals without a cortex are capable of associative learning (Todes 2014).

Pavlov is most commonly associated with classical conditioning, but he also made several other contributions to the field of psychology. The many experiments Pavlov conducted with the dogs over an extended period of time allowed Pavlov to see that there was a wide range of individual differences among the dogs, which he emphasized as needing to be considered when designing experiments. Pavlov even noted that the results of

experiments were influenced by the temperament or personality of each dog, demonstrating the biological basis of personality (Dewsbury 1997). Additionally, the area of abnormal psychology became of interest to Pavlov after several of his dogs developed neurotic behavior. In one circumstance, extensive flooding of Pavlov's laboratory left several dogs traumatized and behaving abnormally (Fields 2006), while in another circumstance, a sensory experiment caused abnormal behavior (Windholz 1997). Pavlov attributed the dogs' abnormal behavior to the sensory overload that was experienced in both events and attempted to apply his observations to the field of human psychoses and psychotherapy. The Russian method of psychiatric patients being treated in unstimulating, quiet rooms was developed based on Pavlov's view that excessive inhibition and abnormal behavior was a protective mechanism and due to overstimulation (Horsley 2012). Under trained psychiatrists, Pavlov studied human psychoses, specifically schizophrenia, through interviews and observation (Windholz 1997). Other psychology topics that Pavlov addressed were aging, language, and problem solving (Horsley 2012; Windholz 1997).

## **Pavlov's Legacy: Scientific Contributions, Contemporary Research, and Political Influence**

### **Scientific Contributions**

Pavlov's legacy includes his contributions to the development of medicine, physiology, and pathology of higher nervous system activity. His research on digestive functions and diseases forms the foundation for modern scientific medicine (Pivovarov and Shok 2016). He was a pioneer on work with vascular surgery and the use of portocaval shunts. His work on digestion made him a household name in Russia. He was also among the first scientists to reach recognition outside of the Russian scientific community, and he became highly regarded worldwide (Palmer 2000). For example, in the 1950s the term "Pavlovian response" was commonly used to describe



the automatic, reflex-like reactions of the Chinese soldiers (Furedy 2003). In addition to his research contributions, he also was ahead of his time by describing ethical guidelines when working with live animal subjects (Kopaladze 2000).

Pavlov is remembered today for his numerous achievements and awards during his outstanding scientific career. In 1901, he was elected a corresponding member of the Russia Academy of Science. In 1904, he won the Nobel Prize in medicine for his research on digestion. Numerous honorary memberships in scientific societies were bestowed to him, notably at Cambridge University in 1912. In addition, he was awarded the Order of Legion of Honor by the Medical Academy in Paris in 1915 (Palmes 2000).

### Contemporary Research

Classical conditioning is the foundation of the modern science of learning. Pavlov's most important conceptual contribution to science was in the field of experimental psychology. The "dog-and-bell scenario" is described in all major textbooks and has become "common knowledge" (Jarius and Wildemann 2015). Even today, classical conditioning is referred to as Pavlovian Conditioning and a Pavlovian Society advocates for guiding principles related to understanding behavior derived from Pavlov's work (Furedy 2003).

Many psychological researchers over the years have utilized Pavlov's work on learning and conditioning in their own scientific studies. Pavlovian concepts such as reinforcement, extinction, and generalization have become critical components of modern psychology (Windholz 1997). There have been a wide variety of topics studied utilizing classical conditioning including conditioning sexual responses in humans (Rachman and Hodgson 1968), contextual fear conditioning in animals (Rudy et al. 2004), and using fear conditioning and extinction to understanding anxiety disorders and PTSD (VanElzakker et al. 2014). Understanding the development and treatment of phobias (and later anxiety) have been extensively studied using Pavlovian techniques since initially proposed by Watson and Rayner (1920). In anxiety disorders, such as PTSD, the

symptoms fail to extinguish after repeated exposure, or reminders of past events, even decades later. Fear conditioning and extinction research paradigms have proven extremely relevant to understanding and possibly preventing anxiety disorders and PTSD (VanElzakker et al. 2014).

Recently Pavlov's ideas on the causal and functional approaches to behavior (Pavlov 1927) have expanded to include ecological and cognitive perspectives.

Ecological perspective – This perspective explores the ways in which conditioning is important for an animal to survive and reproduce. Researchers are concerned with how Pavlovian signaling of biologically important events allows animals to respond adaptively (Hollis 1997). An example of this line of research in the blue gourami fish is a demonstrated competitive advantage during male-male competition, including a phenomenon where winners keep winning and losers keep losing in competition. Classically conditioned males tended to win both the first and second fights, whereas losers lost again (Hollis et al. 1995). Similarly, anti-predator defense research in the ecological perspective has produced many well-known studies such as species specific defense reactions (SSDR) (Bolles 1970) elicited in rats (freezing in defense of danger) and the behavior systems theory, which organizes behavior into categories such as feeding, mating, and avoiding predators (Timberlake 1994). Research on courtship and reproduction in birds has found that classically conditioned mating cues increase reproductive success (Hollis et al. 1997). Other areas in the Ecological Perspective that Pavlov has influenced include research on food recognition, psychoneuroimmunology, and drug tolerance and addiction (Hollis 1997). For example, Siegel (2005) built upon earlier findings linking classical conditioning to drug (i.e., heroin) overdose, symptoms of withdrawal, and environmental cues related to addiction. Overall, this research perspective supports the theory that classical conditioning can influence behaviors crucial for survival, such as knowing what to eat. It also provides an understanding of how classical conditioning can help with behavior change

problems, such as breaking addiction, in everyday life (Hollis 1997).

**Cognitive perspective** – Starting in the latter half of the twentieth century, a paradigm shift in psychology led researchers to focus on cognitive processes including exploring the mental mechanisms that occur during classical conditioning (Hollis 1997). This transition was not widely accepted by behavioral researchers. Even today, the Modern Pavlovian Society does not condone the shift to a cognitive paradigm due to limitations of the concept of representation and the computer metaphor often employed in cognitive theory (Furedy 2003).

Other researchers have used Pavlov's work on classical conditioning as a starting point from which to explore topics such as how the mind organizes the relationship between the conditioned stimulus and the unconditioned stimulus and the different kinds of responses that occur following the stimuli (Hollis 1997). In a summary of this work, Hollis (1997) describes studies ranging from the description of cellular neural mechanisms responsible for classical conditioning to examining differences in conditioning across taxa. One well-known theory to be proposed based on Pavlov's work by Rescorla and Wagner (1972) explained the effect of conditioning which appears to be based on the strength of the association between the stimuli.

All of the above examples demonstrate that Pavlov's work has been influential in many areas of psychology.

### Political Influence

Well-known for his discoveries in the laboratory, Pavlov used his position as a respected Russian scientist to openly and publicly advocate for human rights (Pivovarov and Shok 2016; Windholz 1997). He became a national hero for criticizing the Russian government for their oppression and infringement on academic and religious freedom (Todes 2014). Due to his worldwide notoriety, he was one of the few public and independent voices in the Soviet political system. Pavlov's frustration with limited research resources and funding led him to deliver incendiary speeches and write numerous letters to

Russian officials criticizing the regime. Government officials tolerated his vocal dissent due to his prominence. They eventually supported Pavlov's research requests and his efforts to enhance the reputation of the Russian contributions to the scientific community while maintaining a level of disdain for Pavlov himself (Pivovarov and Shok 2016). Pavlov was a voice for science, even when it was potentially costly for his livelihood and freedom.

### Summary

A Nobel Prize-winning physiologist and prominent researcher, Ivan Petrovich Pavlov is a figure central to the history of psychology and the conception of classical conditioning. Though his experiments with the iconic dogs salivating at a ringing bell were not as simple or serendipitous as many textbook portrayals, Pavlov's contributions to the understanding of behavior shaped by classical conditioning are essential to modern psychology research and practice. Pavlov's surgical skills, experimental practices, and interest in behavior all shaped the research for which Pavlov became famous. Pavlov's legacy continues to live on through his immortalization in the historical narrative of psychology and through the numerous areas of contemporary research that he inspired.

### Cross-References

- ▶ [Associative Learning](#)
- ▶ [B.F. Skinner](#)
- ▶ [Behaviorism](#)
- ▶ [Canine Cognition](#)
- ▶ [Classical Conditioning](#)
- ▶ [Fixed Action Patterns](#)
- ▶ [Operant Conditioning](#)
- ▶ [Personality in Animals](#)
- ▶ [Reflex](#)
- ▶ [Temperament](#)
- ▶ [Unconditioned Response](#)
- ▶ [Unconditioned Stimulus](#)

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## J Bruce Overmier

J. Bruce Overmier

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J(ames) Bruce Overmier, born in New York and trained as a chemist at Kenyon College (1960), stumbled into psychology in 1960 based on hearing lectures at Denison University by Joseph Brady on the “Executive Monkey” (1958) and by William Mayer (Mayer 1959) on the Korean POWs and their “giving up” under random stresses and rewards. These had significant impact and the themes re-emerge in his research career. He was educated in psychology at Bowling Green State University (Ohio, MA 1962) under mentor John R Schuck and at University of Pennsylvania for PhD (1965) under mentor Richard L. Solomon. He also did postdoctoral work in England in zoology and comparative physiology. Overmier taught at the University of Minnesota for 49 years publishing some 200 papers, chapters, books, and reference CDs over that career. The underlying research was funded virtually continuously by NSF, NIMH, and NICHD and involved fish, rats, pigeons, dogs, and humans. Overmier’s research is surveyed briefly in two general domains: basic behavioral and behavioral neuroscience, each roughly broken into several contributing bodies of work in comparative psychology each with a dozen or more publications. The cited publications below were often co-authored by

Overmier with his PhD students and postdoctoral fellows who have gone on to distinguished careers and to whom he is genuinely indebted.

Overmier’s basic behavioral research involves three interrelated lines. The first line of research associated with Overmier is that of “Learned Helplessness” that grew out of his interests in the POW experiences. This work began with a paper that discovered the proactive interfering effects of moderate trauma experience on subsequent learning to escape aversive events (Overmier and Seligman 1967). In that paper, the authors describe the empirical phenomenon of learned helplessness and its dimensions, and they introduced the theory of learned helplessness as a cognitive state of expectations of the uselessness of trying to cope. Overmier (1968) also showed that it impaired future avoidance as well as escape, and began an experiment with Seligman and Maier (1967, see their footnote) that identified the uncontrollability of the initial trauma as a critical causal feature. Few doubted the empirical phenomenon (but see Lawry et al. 1978); but the cognitive construct was savaged by strict behaviorists (e.g., Levis 1976). Learned helplessness gained recognition as a proposed model for depression and for PTSD. Over the years, the construct and its causal features were modified (Abramson et al. 1978), and the unitary dimensionality of learned helplessness came to be seen as at least bi-dimensional (Overmier and Wielkiewicz 1983) involving separately the loss of control (general learned helplessness) and the

absence of prediction (general learned irrelevance) (Dess and Overmier 1989). Eventually, Overmier came to argue that the “learned helplessness” construct was an artifact of the early design and selected normal reference condition (Overmier 1998), and that failure of coping was the default condition of trauma and that opportunities to predict or control aversive events reduced the experienced trauma allowing for more effective future coping. This stimulated new research by Maier (Maier and Watkins 2010) that yielded new insights and physiological mechanisms of stress and trauma (see overview, LoLordo and Overmier 2011).

A second line of related research involved questions of the nature of avoidance learning and how pure Pavlovian conditioning (i.e., involving no instrumental motor contingencies) could come to convey to CS the power to evoke separately learned responses. This does not sound very novel – even then – because M. May (1948) had reported an experiment that claimed to show this phenomenon of CSs evoking escape responses. But Overmier observed a procedural flaw in the May experiment that had transformed the supposed escape trained response into actual avoidance responses, and an experiment (Ehrman and Overmier 1976) confirmed that the May report erred. This was important because the May experiment was the foundation for the explanation of avoidance learning promulgated by Kimble in his textbook (1961) and widely accepted. In fact, fear CSs could only evoke previously trained avoidance responses. Overmier and associates then widely explored the properties of both aversive and appetitive CSs in controlling instrumental responses learned under appetitive or aversive conditions (e.g., Overmier and Lawry 1979). This line of research goes under different rubrics – “transfer of control,” “Pavlovian-instrumental transfer” (PiT) – but continues today in many laboratories because of the importance of these phenomena in understanding so-called cognitive capacities (Holden and Overmier 2010; Overmier 2010).

A third line sprang from the second line in the form of a question about what features of evoked central states functioned to control the responses

in the transfer of control experiments. The “obvious” and common initial answer taken from O.H. Mowrer was that a conditioned motivational state had properties in common with the motivational state – fear – controlling the learned avoidance response, and this commonality led to a generalized response. But then, one might ask, are fears of different aversive events different (Overmier et al. 1971)? And the answer is “yes,” and this difference can come to selectively evoke different instrumental responses (Trapold and Overmier 1972); they interpreted this as revealing that, in addition to any motivational properties, the discriminative stimulus or CS evoked central states also had cues that acted to guide responses. This led to a line of research infelicitously called the “differential outcomes effect” in which it was demonstrated that the learning discriminated choice responses is speeded, better remembered, and resistant to disruption – say by some drug or distractor (Overmier et al. 1999) – if each response is followed by a distinctive or “differential” outcome. This finding, so simple, has had many applied outcomes in teaching children, learning disabled, and senile patient populations things that they could not otherwise even learn (Hochhalter et al. 2000; Maki-Kahn et al. 1995). Other experiments have demonstrated the neural correlates of these differential outcomes and the evocation of the different choice responses (Browning et al. 2011; Mok et al. 2009). One of the more surprising results of using the differential outcomes procedure is that, while making the choice, it seems that the chooser does not even remember the discriminative cue but only the expected outcome (Holden and Overmier 2015).

Overmier’s behavioral neuroscience domain research is basically divisible into two lines. In each of these, the research also harked back to issues and/or methods used in the basic behavioral work, but the focus was on the neuroscience mechanisms. The first of these behavioral neuroscience lines involved analysis of the role of the telencephalon (forebrain) of the teleost. Early experiments in the 1930s had lesioned or even extirpated the telencephalon in fish and reported virtually no effects! Such reports are stunning given the importance of the forebrain in “higher”



vertebrates. Because he had been working on avoidance and limbic structures were critical for avoidance learning in mammals, he and fellow students simply assumed this to be true for fish as well, and they demonstrated exactly that (Hainsworth et al. 1967). Overmier followed up on this finding with a series of other researches seeking to identify just what element or form of learning was disrupted by the forebrain ablation (escape: no; classical conditioning: no, integration of the two: yes, etc., Flood et al. 1976) and other assessments of forebrain function (Overmier and Gross 1974; Overmier and Papini 1985).

A second line of behavioral neuroscience research harks back to those Executive Monkeys who he learned died of gastric ulcers as a result of their avoidance challenge. But the research on this did not begin until the 1980s (Murison et al. 1986), wherein he and Norwegian colleagues began to take up this old problem. Using a model ulcer induction procedure, they identified many experiential stress factors that influenced the precipitation, induction, and persistence of gastric ulcers and linked them to underlying physiological factors (e.g., Murison and Overmier 1993). Of course, “causes” of ulcers became an unpopular topic with the discovery of *helicobacter pylori* and the claim that it accounted for the epidemiology of ulcers. But a recent review (Overmier and Murison 2013) concluded that the *helicobacter* emphasis was much overdone and that psychological factors as demonstrated in Overmier and Murison’s research program are significant factors in the ulcer profile of individuals.

Beyond these lines of research, he has coauthored papers that contributed basic data foundational to things like the Opponent Process theory (Church et al. 1966), understanding somatic disability (Overmier 2002), the surprising importance of assumedly trivial methodological factors (Lyte et al. 2005; Meyers-Manor and Overmier 2015), and international reference works (Overmier and Overmier 2004).

Overmier has won many awards for his research (e.g., D. O. Hebb Distinguished Scientific Contribution Award in Behavioral Neuroscience and Comparative Psychology, 2015), for his

contribution to psychological societies (American Psychological Association Award for Distinguished Service to Psychological Science, 2005), and for his teaching (e.g., American Psychological Association BEA Outstanding Graduate Teaching of Psychology as a Core STEM Discipline Award, 2014). He has received three honorary doctorates. He has served as president of five national psychology organizations and of the International Union of Psychological Science, and as an officer or board member of several other national and international psychology organizations (e.g., International Council of Science, Paris).

Throughout his career, Overmier has argued for basic animal researches as models that can give fundamental insights into the health status – mental and physical – of humans (e.g., Overmier and Patterson 1988). His research career has reflected this with his basic researches building towards accounts of the human condition and challenges.

## Cross-References

- [Associative Learning](#)
- [Avoidance](#)
- [Classical Conditioning](#)
- [Cognitive Bias](#)
- [Corticosterone](#)
- [Executive Monkey Study](#)
- [Fear Response](#)
- [Instrumental Learning](#)
- [Learned Helplessness](#)
- [Motivational State](#)
- [Proactive Interference](#)
- [Transfer of Learning](#)

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## J.E.R. Staddon

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## Personal History

John Eric Rayner Staddon was born on March 19, 1937, in Grayshott, Hampshire, England, a village about 74 km (46 miles) southwest of London. He was the first child of Leonard John (Jack) Staddon and Dulce Norine Rayner

Staddon. The parents had met when Jack Staddon was serving in the military in Rangoon. The Staddons, including his grandmother, Irene Florence Rayner, moved to London a year later and settled finally in Cricklewood, an area of north-west London. Staddon’s earliest memories center around World War II and the bombing of London. His father was on active duty and his mother was working outside of the home. Staddon was raised during this time by his grandmother.

Staddon attended Burgess Hill, a progressive school that permitted much student freedom. Staddon remembered he was able to avoid math and that every boy had a knife. The 2 fun years of Burgess Hill did not prepare Staddon well for the *eleven plus* exams that determined the next educational step. Staddon did well enough to be accepted at St. Marylebone Grammar School, although he was to need additional tutoring in math. About this time, Staddon began to develop a serious interest in biology. He had several aquaria and had purchased a used microscope. Staddon’s record of *A-level* passes did not guarantee acceptance at a top-level research university. He matriculated at Battersea Polytechnic, which was accredited to grant degrees from the University of London. The school was not a good match, and Staddon discovered that he could transfer into the psychology track at University College London (UCL) if he did well enough on a standardized test. Staddon enjoyed UCL; he skipped a lot of lectures and tutorials and became involved with the student newspaper as a movie and art reviewer.

Staddon’s father had moved to Northern Rhodesia for work. The family joined him there, including John Staddon in the middle of his UCL career. Staddon found a job working for a program to study disease (e.g., malaria and bilharzia) and nutrition in the region. Staddon worked as a lab and physician’s assistant on the project. Staddon lived there from 1957 to 1959 and then returned to England to finish his final year at UCL.

Staddon passed his exams at UCL, but not at the level to be accepted for postgraduate work at a research university. Nor did he have research lab experience that might have led to a stronger personal recommendation. Staddon decided to try his

luck in North America. He found ads at the UCL Psychology Department for research assistantships at Kansas State University, McMaster University in Hamilton, Ontario, Canada, and Hollins College in Roanoke, VA. He received a similar offer from all three schools. He chose Hollins because it would be warmer and less flat.

Staddon arrived at Hollins in 1960 to discover that it comprised only women students at the undergraduate level. Another shock was the American educational system, which required regular class attendance and featured frequent testing. Staddon was to meet Robert Bolles, who introduced Staddon to Murray Sidman's (1960) *Tactics of Scientific Research*. Sidman was a student of B. F. Skinner. The book explained Skinner's methodology, which was focused on the performance of individual subjects. This approach was to be used by Staddon throughout his career. A second memorable event of Staddon's time at Hollins was that he met his first wife, Nada Ballator. Hollins did not offer a Ph.D. degree, and Staddon applied to three programs, receiving an acceptance at Harvard University.

The Harvard Psychology Department was located in the enormous basement of Memorial Hall. At one end were the pigeon labs and the office of B. F. Skinner. The other end contained the office of S. S. "Smitty" Stevens, famous psychophysicist and methodologist. The combined location of faculty, graduate students, and labs on the same floor led to extensive interactions among the labs. Staddon took several courses at the Massachusetts Institute of Technology where he learned to think about feedback systems from a computational viewpoint.

Richard Herrnstein was the supervisor of Staddon's dissertation, B. F. Skinner having retired from active laboratory work. Research activity in the operant conditioning lab was focused on Herrnstein's *matching law*, the principle that relative (or proportional) response rate would match relative reinforcement rate in a two-choice conditioning task. Staddon, however, was interested in a different topic, the influence of timing on responding. Pigeons can adapt to a *Fixed-interval 30-s* schedule, in which food is

available only after a period of 30 s and will not respond for a period of 10 to 15 s from the beginning of the interval. However, if the task is to pause 10 s before making the next response, then pigeons find this to be a very difficult task. Staddon investigated whether providing feedback signals of too early or late responses would improve performance. The results were mixed and showed that pigeons did not use feedback in a human-like manner.

Staddon's first job was at the University of Toronto in Canada, and it did not proceed as anticipated. The winters were interminable, and the intellectual temperature in the department was cool, too. The major animal learning theorist in the department was a neo-Hullian, Abram Amsel, famous for his *frustration theory*. Frustration was a drive-like condition that was supposed to be elicited by the nonoccurrence of an expected reward. Staddon developed a more parsimonious explanation of the effect and presented it to the Amsel group. Predictably, it did not produce a welcome reaction. (See Staddon and Innis 1969, for the analysis.)

Staddon began to look about for a new position and saw an ad for a position at Duke University. His interview was in January and it was sunny and balmy in Durham, NC. The animal learning atmosphere was warmer, too. The senior learning person was Norman Guttman, a former student of Skinner. Staddon took the job and remained at Duke for the rest of his career. He retired in 2007 as a James B. Duke Professor of Psychology and Neuroscience but has remained intellectually active since then.

Interested readers should consult Innis (2008) and Staddon's autobiography (Staddon 2016) for additional details of his career.

## Brief Overview of Staddon's Work

Staddon's most cited paper is the replication of Skinner's (1948) superstition experiment (Staddon and Simmelhag 1971). Skinner reported when food was presented to a hungry pigeon on a periodic basis independent of the pigeon's behavior, then an operant conditioning effect was

produced. Whatever behavior occurred closest in time to presentation of the food was repeated such that it was likely to reoccur close in time to the next food presentation. The effects were interpreted to indicate the power of temporal contiguity of a reinforcer to stamp in a response even when there was no causal connection between the two events. It is important to note that almost no data is presented in the article. Instead, Skinner presents verbal descriptions and his conclusions.

Staddon and Simmelhag (1971) replicated the basic procedure of Skinner (1948) of presenting response-independent food, with important additions. They developed a coding system to record the different activities by the pigeons and the temporal location of the activities during the interfood interval. Their results showed that the behavior closest in time to food in the initial sessions (e.g., head in the feeder) was often displaced abruptly by another activity (e.g., pecking the wall near the feeder) in later sessions. The result was a direct contradiction of the account that temporal contiguity of response and reinforcer alone can explain the emergence or persistence of behavior.

Staddon and Simmelhag noted that the other activities (dubbed *interim activities*) occurred also in a reliable sequence. The observation led to the question of the cause of the regular occurrence of those activities since they are both unnecessary for and temporally distant from food reinforcement. Their insight was that a hungry animal was not in search of food alone. Instead, it had several requirements (food, water, avoidance of predators) that had to be met. The problem for the animal was *allocation of behaviors*, when is the best time to do what activity. A period of low food probability is a good time to engage in other activities. This issue of the problem of behavior allocation was to occupy Staddon for several years.

Staddon (1979) pursued the issue formally (mathematically) by recasting operant conditioning as a behavior allocation issue. Reinforcement schedules restrict an organism's access to one activity by requiring it to engage in a second activity. The problem for the animal is how to balance the preferred levels of both activities (the *free behavior point*) given the

constraints imposed by the contingency. Staddon used both geometrical and algebraic analyses in his *minimum distance* model to suggest that the final performance is one that brings the mix of behaviors closest to the mix of the free behavior point. Staddon (1980) edited a volume of contributions that showed the allocation issue ranged from plants to human behavior in the suburbs.

### A Simple Example of Staddon's Modeling Approach: Habituation

Staddon's (2001) current method of investigation is to create formal models of the manner in which behavior changes in time. These models are black box models. No attempt is made to justify these models by appealing to current views of the nervous system or cognitive metaphors, such as *expectancy*. The approach follows the Turing test argument. You have an adequate model of thinking when a reasonable questioner cannot discriminate between a machine and a human being. The goal of development of these models is *parsimony*. The more simple the mechanism then, the more widely it may be used in nature.

An example of Staddon's approach can be seen in a simplified description of his analysis of habituation (Staddon 1993). *Habituation* is the waning of the strength of a response with repeated elicitation by a specific stimulus. The speed of habituation increases when the frequency of presentation of stimulus is increased. There is recovery from habituation when the stimulus is not presented for some time period. Habituation represents a dynamic case of behavior change in time.

Figure 1 shows a diagram of a basic habituation unit (Staddon 1993). The relevant equations are

$$V(t+1) = aV(t) + (1-a)X(t), 0 < a < 1 \quad (1)$$

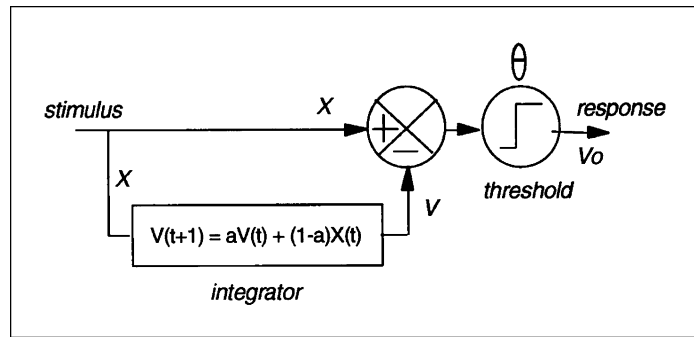
$$V_0 = X - V, \text{ if } V_0 > \theta \quad (2)$$

The model operates like a digital clock, with each increment in  $t$  the equivalent of a tick of the clock. The figure indicates two effects



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**Fig. 1** Diagram of habituation unit adapted from Staddon (1993). See text for details



induced by the stimulus (“ $X$ ”): an excitatory component where stimulus strength directly increases response strength and an inhibitory component (“ $V$ ”) that suppresses responding. Equation 1 describes the effect of the current trial on  $V$  for the next tick of the clock. When  $X > 0$ , then inhibition will increase and  $aV(t)$  is described as a *leaky integrator*. The leaky integrator sums (integrates) prior experience with the stimulus, but the inhibitory effect ( $V$ ) will wane (leak) with time according to the value of the constant,  $a$ , with smaller values producing greater leakage in  $V$ . The occurrence and strength of the response are predicted in Eq. 2 by the mathematical difference between current excitatory and inhibitory values (i.e.,  $X - V$ ) if it exceeds a threshold ( $\theta$ ). If the stimulus is absent ( $X = 0$ ), then  $V(t + 1)$  will decrease according to the size of  $aV(t)$ .

The question of interest to Staddon is whether this mathematical equation will reproduce the basic dynamic effects of habituation, as described above. If the model does so, then it has passed a kind of Turing test, an equivalency of the behavior of the model and an animal. The advantage of the model is that the behavior has been described without a commitment to a specific theoretical account. The basic unit may then be combined with other habituation units in series or parallel to describe more complex behaviors (Staddon 1993, 2005; Staddon and Higa 1996, 1999).

Current learning theories tend to fall into a small number of approaches, using mainly cognitive or neuroscience metaphors. Staddon’s emphasis on the descriptive powers of mathematical models offers a third, distinctive approach.

## Cross-References

- [Habituation](#)
- [Mathematical Modeling](#)
- [Schedules of Reinforcement](#)
- [Superstition Experiment](#) (Staddon and Simmelhag 1971)

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## Jane Goodall

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### Definition

Conservation leader and humanitarian who made several ground breaking discoveries on chimpanzee behavior in Tanzania and is a current advocate for animal welfare around the world.

### Introduction

In a time when humans were the only species in the world to make tools, naming conventions of study subjects were restricted to numbers, and women in science were few and far between, Jane Goodall stepped onto African soil and changed the way we thought about animals, the environment, and ourselves. Goodall spent over 20 years researching the chimpanzees in Gombe to discover groundbreaking facts about their previously elusive behavior, and, perhaps even more alluring to the public, their social relationships, individual personalities, and emotions. Rich with experience and full of courage and compassion, Goodall's life has become the topic of numerous articles, novels, children's books, movies, television shows, and conversations. To this day, Goodall is absorbed in her conservation work, traveling most of the year in order to spread a message of conservation and peace to all citizens of the world (Jane Goodall Institute 2016). Goodall has become a legend in the study of chimpanzee behavior and a symbol of conservation because she has dedicated her life, professional and personal, to these causes.

### Personal Life

On April 3, 1934, Valerie Jane Morris-Goodall was born in London. Her mother, Vanne Morris-Goodall, was a novelist and her father, Mortimer

Herbert Morris-Goodall, was a businessman (Jane Goodall Institute 2016). When Mortimer enlisted in the military during WWII and no longer lived at home, Vanne served as a strong, independent female role model for Jane and her younger sister Judy. When Jane was 12, her parents divorced and Jane continued to live with her mother's family in the countryside, where they had moved during the war (Goodall and Berman 1999).

Living in the countryside allowed Jane to be immersed in nature from a young age. There are many anecdotes of Jane exploring the outdoors and observing animals, such as chickens and the family dog. Jane showed an interest in animal welfare from a young age: she took care of earthworms and did not want to hurt dragonflies. Goodall's favorite toy as a child was a stuffed chimpanzee that was given to her by her father (Jane Goodall Institute 2016). Other early influences in Jane's life included her grandmother who was another strong female role model, and a number of books, especially the story of Dr. Doolittle and Tarzan (Jane Goodall Institute 2016). These books sparked an interest in studying the wildlife of Africa, one of her long-term goals.

Throughout her childhood, Jane continued to demonstrate her love of wildlife by starting "The Alligator Club," in which Jane, Judy, and their two friends learned about wildlife together and held small events. Goodall was a good student, but preferred to be outdoors with animals rather than inside a classroom. However, she did complete her secondary education and went on to train as a secretary. Throughout her childhood and young adult life, Goodall reflected on the nature of humans, often wondering how they could sometimes be so intelligent and yet be responsible for atrocities such as the Holocaust (Goodall and Berman 1999). Goodall's curiosity with the nature of aggression and human self-awareness would later be reflected in her reports on violent and peaceful aspects of chimpanzee societies and her work as a United Nations Messenger of Peace (Jane Goodall Institute 2016).

After Jane trained as a secretary, she went to work at the University of Oxford Registrar's Office and then a film studio in London, but these jobs were not particularly fulfilling. When one of her friends from school invited Jane to visit

her father's farm in Kenya, she was ecstatic, as it was her dream to visit Africa. She moved back home to work as a waitress in order to save money and boarded a Kenya-bound ship in 1957. Jane loved being in the very place she read about in her favorite stories as a child, and sought employment to extend her stay (Goodall and Berman 1999).

Jane was hired as a secretary for the paleoanthropologist, Louis Leakey, who was the curator of the Coryndon Museum in Nairobi. Jane accompanied Leakey and his family on fossil digs in the Olduvai Gorge. There, Jane was able to be a part of the search for the missing links in the evolution of *Homo sapiens*. Leakey spoke of his desire to research the behavior of wild chimpanzees because ancient human behavior was not fossilized, and the closest option for looking at prehistoric human behavior was to observe the closely related chimpanzees. Eventually Jane vocalized her desire to observe chimpanzees, which led Leakey to make logistical arrangements and secure funding from the Wilkie Foundation and National Geographic Society for Jane's expedition (Lindsey 1999).

Vanne Morris-Goodall accompanied Jane to what is now the field station at Gombe National Park, Tanzania. The mother-daughter pair proved to be resilient in the foreign environment and persevered through a period of sickness and fever. Vanne set up a medical clinic at their research camp, which helped to establish a rapport with the locals and demonstrate that Jane and her mother were there to help. After several years of fieldwork and a few new discoveries, Jane secured continued funding for the project. In 1962, her sponsor (the National Geographic Society) sent Hugo van Lawick to photograph and film Jane and the chimpanzees in Gombe. By 1965, she was married to van Lawick and had earned her PhD from the University of Cambridge with Robert Hinde as her advisor. Goodall is one of just a handful of people who had been granted a PhD without first earning a bachelor's degree (Jane Goodall Institute 2016).

By 1967, Goodall gave birth to a son (Hugo Eric Louis van Lawick, aka Grub) and had created the Gombe Stream Research Centre with funding from the National Geographic Society. Graduate

and undergraduate students from the United States, Europe, and Tanzania flocked to the new center to conduct field research on chimpanzees. As the new center's Scientific Director, Goodall encouraged a cooperative, tight-knit community, where researchers shared data, exchanged information, and presented their findings in open, casual settings. As the number of researchers in the center expanded, so did their species of interest; some began studying other primate species' behavior as well (Greene 2008). The additional man-power enabled Goodall to spend most of her time writing research findings, proposals, advising students, attending to administrative duties of the center, and raising Grub. As a new mother, Goodall spent as much time as possible with her son in Gombe. Many of Goodall's mothering techniques were actually learned from observing the chimpanzee Flo raise her own children. Goodall followed Flo's affectionate example of child rearing, even though it was considered unorthodox at the time (Pratt 1997). At the age of nine, Grub returned to England for schooling and lived with his extended family there.

As the findings of the Gombe Stream Research Centre were disseminated and the number of researchers grew, Goodall began to give more lectures and talks overseas. She traveled as a visiting professor of Psychiatry and Human Behavior at Stanford University from 1970 to 1975 and published her first book, *In The Shadow of Man* (1971). Goodall divorced Hugo in 1974 and later remarried Derek Bryceson, director of Tanzania's national parks, in 1975 (Goodall and Berman 1999). The same year, four foreign students in the research center were abducted by armed revolutionary soldiers, and as a precaution, no foreign students were allowed back until 1989. In the intermediary, day-to-day operations of the research center relied almost entirely on the African researchers and staff. Goodall created the Jane Goodall Institute for Wildlife Research Education and Conservation to financially sustain research in Gombe and returned from her position in Stanford, enjoying her life with the small, all-African research group once more. However, even the duration of her own visits to Gombe were restricted. Goodall and Derek lived happily

together until he succumbed to cancer in 1980, which Goodall has described as an extremely painful time in her life (Goodall and Berman 1999).

Goodall returned to Gombe to heal and experienced a moment of clarity after a thunderstorm in the forest (Goodall and Berman 1999). She set out to compile her findings of many years in Gombe into a single book that would both contribute to the field scientifically and be easily understood by the public. After 6 years she published *The Chimpanzees of Gombe* (1986), which distinguished Goodall as a leader in the field of primatology and chimpanzee behavior. To celebrate, Drs. Goodall and Heltne (Chicago Academy of Sciences) organized a conference on the topic of chimpanzees that would subsequently change the direction of Goodall's career, and begin her voyage as one of the modern era's most famous advocates of animal welfare and conservation.

## Research

When Goodall began her research in Gombe Stream Chimpanzee Reserve on Lake Tanganyika in 1960, very little was known about wild chimpanzee behavior. Goodall's mentor and advocate for the study, Louis Leakey, was a paleoanthropologist who believed that studying such a close relative of the human species would provide insight into the evolutionary origins of human behavior (Lindsey 1999).

Research in the forests of Tanzania was not an easy task. Upon Goodall's arrival at Gombe, the chimpanzees were elusive and avoided close proximity to her. Everyday Goodall would climb trees, travel through the thorny undergrowth, carefully avoid other wild animals, and endure long spans of time without food and water in order to search for, and observe the resident chimpanzees of Gombe. Sometimes Goodall would even sleep near the chimpanzees' nest site so that she could wake up with them the next morning (Goodall 1963). After several months, a chimpanzee Goodall previously named David Greybeard allowed Goodall to approach him. This was an

invaluable step of progress for Goodall's research, as it enabled closer observation of the rest of the chimps and their gradual desensitization to Goodall's presence.

Goodall visually identified all 89 chimpanzees who inhabited the territory at Gombe (Goodall 1986). Unlike most other scientists at the time, Goodall gave each research subject a name, acknowledged that they had unique personalities, and immersed herself in their environment (Jane Goodall Institute 2016). Leakey saw Goodall's lack of formal training as an advantage because it meant that she did not bring some of the preconceptions and biases someone with a formal education would possess (Jane Goodall Institute 2016). However, her education level, anthropomorphic tendencies, and gender caused Goodall's observations, interpretations, and abilities as a researcher to be the target of doubt and criticism by many others in the research community. Regardless, Goodall made many remarkable discoveries concerning chimpanzee communication, social structure, relationships, ranging patterns, foraging tendencies, hunting, aggression, affiliative behavior, dominance, sexual behavior, territoriality, tool use, and social awareness, among other cognitive abilities (Goodall 1986).

Chimpanzee relationships provided Goodall with context for their social interactions. She categorized relationships as friendly, unfriendly, or sexual and found that the social bond between mother and offspring was the strongest in her population (Goodall 1986). Goodall learned that young chimpanzees stayed with their mothers for up to 7 years after birth, helped to care for siblings, and formed long-lasting bonds with members of their social group. Although the chimpanzees had a larger social unit that was relatively stable over time, individuals or smaller family units were often found apart from the larger group, which constituted a "fission-fusion" society (Goodall 1963). The males of each social group had their own dominance hierarchy, and while there was also a dominant individual among female chimps, she did not maintain her dominance in the male hierarchy (Goodall 1963).

As Gombe's chimpanzee social unit began to fragment, Goodall was able to document the

aggressive nature of chimpanzees. The two new communities established territorial boundaries within the larger territory they had previously shared. The males of a group patrolled the boundaries of their territory together. Goodall reported on how several members of one group would isolate and attack a member of the neighboring group, killing the individual or inflicting fatal wounds in a sort of primitive warfare (Goodall and Berman 1999). Goodall also witnessed several cases of infanticide, where a mother-daughter pair killed newborns of other mothers within the same social group. These observations contributed to the discussion on whether aggressive tendencies of humans and chimpanzees are learned or inherited.

However, Goodall assured that the vivid displays of chimpanzee violence did not occur more frequently than peaceful interactions, and continued to report on the chimpanzees' caring and cooperative nature (Goodall 1986). The chimpanzees engaged in close physical contact upon greeting one another with gestures that resembled human hugs, holding hands, and kisses. Goodall learned that chimpanzee mothers had different mothering styles, just like humans. Some chimpanzee mothers were very protective, while others allowed their young more freedom, sometimes ignoring them altogether (Goodall 1963). The chimps spent long periods of time grooming one another, tickling each other, and laughing. Goodall described how chimpanzees would engage in seemingly selfless acts to help fellow group members, including one instance when an adult male adopted a young orphaned chimp, which was a very atypical social arrangement (Goodall and Berman 1999).

In her descriptions of chimpanzee foraging and hunting behavior, Goodall revealed that chimpanzees were not primarily vegetarians and fruit eaters as previously thought (Goodall 1986). Chimpanzees ate mammals, including bushpigs, rats, and mice and often shared their kills with their group mates. They also ate birds, termites, and a variety of vegetation such as leaves, blossoms, stems, seeds, and fruit (Jane Goodall Institute 2016). Even more remarkable than the finding that chimpanzees ate meat were Goodall's

observations of the chimpanzees making and using tools to extract termites from mounds. Goodall was the first to document their process of modifying a twig, dipping it into the insects' underground tunnels, and extracting the twig covered in termites to eat, which was termed "termite-fishing" (Goodall 1970). At first, many scientists did not believe that Goodall had actually witnessed tool use and tool modification in another species. However, later photo documentation of the process verified to the world that humans were no longer defined solely by their ability to use tools. The most famous quote on this matter came from Louis Leakey himself when he said, "Now we must redefine man, redefine tool, or accept chimpanzees as humans!" (Jane Goodall Institute 2016). Over time, Goodall witnessed the chimpanzees using leaves as tools for other tasks, such as soaking up water, cleaning themselves, and wiping wounds (Lindsey 1999).

In addition, Goodall discovered that chimpanzees had a rich vocal and nonvocal system of communication. Although the vocalizations of the chimpanzees did not form a complete language, Goodall documented approximately 30 distinct calls (Goodall and Berman 1999). After spending considerable time with each chimpanzee, she was able to identify individuals based on their vocal characteristics and learned the meaning of several vocalizations from context. She believed that these signals could also be used while conveying psychological and emotional state and never doubted the chimp's ability to feel emotions that other scientists reserved for humans (Goodall 1986; Goodall and Bekoff 2002). She witnessed the chimpanzees building the nests they slept in at night, playing in the rain, and watched them mourn the death of a family member.

Goodall began to publish her novel findings and was featured in a National Geographic television program, which resulted in her international celebrity status (Lindsey 1999). This positively affected the Jane Goodall Institute and ultimately the Gombe Stream Research team. Continued funding permits the Tanzanian researchers, accompanied by students from all over the world, to continue Goodall's work by studying narrow



research topics in great depth (Jane Goodall Institute 2016). Today, the Gombe Stream Research Centre hosts many researchers whose study topics include health, genetics, mother-infant relationships, maternal stress, personality, social networks, cooperation, aggression, aging, menopause, and conservation using spatial mapping technology (de Donno et al. 2015). This research center has over 55 years of continuous data on over 300 chimpanzees from three populations and has been part of over 400 publications. Goodall has especially inspired many women to pursue primatology, conservation, and wildlife research. Additional research is conducted at Jane Goodall Institute's Tchimpounga Chimpanzee Rehabilitation Center to better understand many aspects of chimpanzee health and behavior and ultimately to provide tools to better protect them.

## Conservation Work

The 1986 "Understanding Chimpanzees" conference in Chicago was a transformative experience for Goodall (Goodall et al. 2009). Chimpanzee experts from around the world presented their research, but underlying the entire conference were conversations on the increasingly threatened state of chimpanzees in the wild (Goodall 2001). A session on conservation reviewed the unsustainable deforestation occurring across the chimpanzees' range, the increased consumption of bushmeat, the sale of infant chimps into captivity, and their poor living conditions once there (Goodall 2001; Goodall et al. 2009). After the conference, Goodall felt she could no longer prioritize fieldwork while her voice and celebrity status could help the chimpanzees' many dire plights (Goodall et al. 2009; Peterson 2006). The end of the conference marked the founding of the Committee for the Conservation and Care of Chimpanzees (CCCC) by 30 conference attendees at the top of their field, and Goodall reborn as an animal welfare advocate (Goodall 2001).

Goodall began actively traveling as a lecturer and activist an average of 300 days a year (Jane Goodall Institute 2016). She gave presentations to

schools and corporations, attended conferences, fundraisers and meetings, solicited funds, met with politicians, and attempted to convince environmental group leaders to take a more active role in conservation efforts (Goodall 2001). Although the Jane Goodall Institute was still being used to support wild chimpanzee research in Gombe, its mission began to expand with the creation of the CCCC, and it gradually became recognized as a leader in the conservation nonprofit sector (Goodall 2001; Pratt 1997). Today the institute supports programs in conservation science, research, advocacy, protecting chimpanzees and other great apes, public awareness, environmental education, healthy habitats, and has initiated two successful community-based outreach programs: Roots & Shoots and TACARE.

Roots & Shoots is a grassroots service program that aims to foster respect, compassion, and understanding in young people, as they work to increase the wellbeing of the human community, animal welfare, and the local environment (Goodall 2002). The program's name was symbolic in that it described the strong, foundational aspect of roots that were everywhere, and the indomitable nature of a young tree that seems weak at first but is capable of growing up to break through brick in order to reach the sun (Goodall 2002; Peterson 2006). The grassroots program that began with 12 children in Dar es Salaam now has Roots & Shoots clubs in nearly 100 countries with over 5,800 reported conservation and service projects (Jane Goodall Institute 2017). The program seeks to empower youth and build strong, introspective, purposeful, empathetic, adaptable, optimistic, inspirational leaders who think critically and work well as a team, and maintains that every individual can make a difference. While initially designed and implemented for students from elementary school to university, there are now Roots & Shoots members of all ages, all around the world (Goodall 2002; Jane Goodall Institute 2017).

The Lake Tanganyika Catchment Reforestation and Education (TACARE) Program was specifically targeted towards individuals who lived in the same areas as wild chimpanzees (Lindsey 1999). By offering courses in

sustainable natural resource management, TACARE empowers locals to protect the land, plant nurseries, and become financially independent. In this way, TACARE addresses the socioeconomic needs of people in the local community, as well as chimpanzees' need to have accessible habitat, and the environment's need to recover. The program addresses humanitarian concerns such as community development, encourages forestry initiatives such as tree planting, teaches sustainable agricultural practices, initiates health projects such as family planning and reproductive education, and introduces the Roots & Shoots program to local youth (Lindsey 1999).

Goodall has improved the lives of many human and animal communities around the world. Most notably, she has created multiple sanctuaries for chimpanzees orphaned due to the bushmeat trade (Goodall and Berman 1999; Lindsey 1999). In addition, the Jane Goodall Institute has helped improve the quality of care for animals in low-income zoos, particularly in developing countries. The ChimpanZoo Project called for much-needed behavioral analysis of captive chimpanzee populations. With this, Goodall aimed to compare wild chimpanzee behaviors with behavioral reports from their captive counterparts. By discovering the needs of captive chimps, such as larger enclosures, social interaction, and environmental enrichment, ChimpanZoo continues to help improve chimpanzee exhibits all over the world (Lindsey 1999).

After touring a medical research laboratory in 1987, Goodall created a list of minimum requirements needed for the wellbeing of research chimpanzees. While these requests were initially dismissed, Goodall's basic requirements (i.e., larger cages and social interaction) were slowly incorporated into the industry (Goodall 2001; Peterson 2006). Goodall continued to persist, and as of 2015, the National Institute of Health (NIH) announced the retirement of all biomedical research chimps. Today, all chimpanzee medical experimentation has ended, and any remaining chimps in labs are being transported to chimp sanctuaries or retirement centers (Golden 2017). While Goodall is especially passionate about improving the treatment of chimpanzees (and

other animals) in captivity, she does not condone extremist activist groups, as she feels that polar opposition does not facilitate a conversation for a sustainable future. While violence may have evolved as part of our nature, Goodall believes we can (and should) choose to solve problems peacefully (Goodall and Berman 1999). Instead of pointing blame, Goodall focuses on hope.

Goodall has authored books conveying a more humane view of wildlife for children (*The Chimpanzee Family Book*) and argues for a deeper connection between people and the natural world (*The Ten Trusts*). She believes that understanding more about nature enables us to care, and it is that caring that ultimately enables us to take action (Goodall and Bekoff 2002). *The Ten Trusts* (2002) calls for a more compassionate attitude towards animals from scientists and the general public. The "trusts" ask us to acknowledge that (1) we are part of the animal world (and that we are not the only animals with emotions such as fear, joy, embarrassment, anger, love, sadness, or grief), (2) there is a value in every being (animal or plant) which deserves our respect, (3) that we can learn from many species and (4) should teach a love and respect for nature at a young age, (5) aim for a smaller carbon footprint, (6) work towards reversing extinction by reducing pollution and man-made noise, (7) refrain from using harmful methods to study animals, (8) take action, (9) help conservationists, and (10) remember to have hope.

In other novels, Goodall explores the idea of hope in the modern world. She details the capacity of humans to rescue many endangered species from near extinction (*Hope for the Animals and Their World, Reason for Hope*). Although Goodall was initially skeptical of captivity, she now embraces the immense benefits that captive facilities, their associated breeding programs, and teams of researchers can have on animals, especially those who are critically endangered or extinct in the wild. Goodall lists her reasons for hope as "(1) the human brain; (2) the resilience of nature; (3) the energy and enthusiasm that is found or can be kindled among young people worldwide; and (4) the indomitable human spirit" (Goodall and Berman 1999, p. 233).

During her lectures and invited talks, Goodall is known for presenting her “symbols of hope,” such as a California condor feather, which she carries with a permit (Goodall et al. 2009). She also travels with a leaf from a very resilient old tree, another feather from a peregrine falcon thought to be locally extinct for 100 years, and a paw print cast of one of the last wild black-footed ferrets believed to exist in 1986. These items not only carry symbolic importance for Goodall, but are used in her speeches to convey that many species can come off the endangered, and even extinct, species lists. She believes that too often we are told about species dying, but we do not celebrate the successful ventures of breeding programs and recovery efforts with the same vigor (Goodall et al. 2009). Currently, Goodall offers a class about conservation through an online education platform (MasterClass 2017). Her syllabus includes lessons on animal behavior and intelligence, anthropogenic effects on the environment, conservation biology, tips on presentations, how to advocate without hostility, and Goodall’s reasons for hope in the next generation of conservationists.

## Conclusion

The research that Goodall began in 1960 has snowballed into a global research effort to understand and protect primates and their environment. With discoveries including meat-eating, tool-making, termite-fishing, child-rearing, aggression, and affiliative behavior, Goodall began a legacy of research that continues today, and has taught the world about our closest evolutionary cousins. She has authored several books, from scientific to autobiographical, such as the best-seller, *In the Shadow of Man* (1971). Much like her career, her book titles have shifted focus to encourage readers to stay hopeful and active in the face of animal extinctions and the changing world. As she calls out to the public to rise in action, she also calls out to scientists: Goodall believes that there is still a great deal of work to do towards implementing compassionate research methods and improving the welfare of animals in

captivity, as well as the habitats of their wild counterparts (Goodall and Bekoff 2002).

Goodall’s continued efforts to improve the quality of life for all animals, communities, and environments have earned her more than 60 awards and recognitions (Doak 2015). Among them are the San Diego Zoological Society’s Gold Medal of Conservation, the J. Paul Getty Wildlife Conservation Prize, the Animal Welfare Institute Schweitzer medal, the National Geographic Society Centennial Award, and the Kyoto Prize for Basic Sciences, which is the Japanese equivalent to the Swedish Nobel Prize. In 2002, she was recognized as a United Nations Messenger of Peace and was granted the title of Dame of the British Empire by Queen Elizabeth II in 2003 (Welty 2011).

Although her conservation work has taken her far away from her beloved chimps, and Gombe, Goodall’s peaceful-yet-powerful actions, rational outspoken mentality, and ethical integrity are an inspiration for so many around the world. The Jane Goodall Institute has blossomed in recent years with programs to monitor and protect habitats that are critical to the chimpanzees, educate local communities, raise awareness, promote sustainable consciousness, and encourage grassroots efforts among youth. Through her lectures, classes, advocacy, and institution, she has impacted the environment and future generations of conservationists to come.

## Cross-References

- ▶ [Affiliative Bond](#)
- ▶ [Allogrooming](#)
- ▶ [Animal Welfare](#)
- ▶ [Bushmeat Trade](#)
- ▶ [Conservation](#)
- ▶ [Culture](#)
- ▶ [Dominance Hierarchy](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Fission-fusion](#)
- ▶ [Louis Leakey](#)
- ▶ [Maternal Behavior](#)
- ▶ [Observational Methods](#)
- ▶ [Primate Cognition](#)

- ▶ Primate Communication
- ▶ Primate Research Centers
- ▶ Primate Social Structure
- ▶ Primates
- ▶ Pro-social Behavior
- ▶ Robert Hinde
- ▶ Roots and Shoots
- ▶ Social Grooming
- ▶ Territoriality
- ▶ Tool Use

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## Jealousy

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## Synonyms

Envy; Possessiveness

## Definition

A desire for attention, affection, or resources given to competitors/rivals within the context of close social relationships.

## Introduction

Jealousy is one of the secondary emotions along with shame, embarrassment, guilt, and pride (Miller and Leary 1992). It is sometimes confused with envy, but envy is generally defined as the desire for an object, whereas jealousy can be defined as the desire for affection or attention directed at another (Cohen-Charash 2009). Unlike the other secondary emotions, jealousy and envy do not involve the evaluative component that involves reflection on how one is perceived by others (Morris et al. 2008). For example, embarrassment stems from the feeling

that one has done something to encourage derision from others. The secondary emotions are tied to the emergence of self-awareness in humans and are expressed for the first time within the last half of the second year of life in typically developed humans (Lewis et al. 1989). This is the same age at which mirror self-recognition is evidenced and personal pronouns are used. For this reason, and because of the absence of strong evidence for self-awareness in nonhuman animals, it has been of interest to determine whether animals may experience secondary emotions, such as jealousy (Bekoff 2002).

Jealousy may emerge earlier in humans – as early as 9 months (Hart 2016) – making it more likely that it might be shared more widely within the animal kingdom compared to late-emerging emotions such as embarrassment and pride. However, it is extremely difficult to test the experience of emotions in nonverbal species. For that reason, researchers must rely on observations of behavioral manifestations that may be linked to human experiences of jealousy. In addition, there is recent neurophysiological evidence that supports the claim that some species may experience something akin to human jealousy.

## Adaptive Value

Emotions such as jealousy may serve an adaptive function in motivating individuals to compete for resources such as mates. Jealousy may motivate others to prevent rivals from monopolizing or interfering with important social relationships – with mates, siblings, and potential allies (Chung and Harris 2018; Harris and Prouvost 2014). It might be presumed that jealousy is more likely to be experienced in highly social species; however, it may be adaptive for any species that compete with siblings for a parent's attention, or with rivals for mates. Thus far, jealousy has not been explored in relatively less social species, and in fact, its study has been restricted to animals in human care such as animal companions (primarily domestic dogs) and species closely related to humans, such as nonhuman primates.

## Pet Owner Surveys

Researchers have asked pet owners to report on emotions that they believe they have observed in their animal companions. Although people frequently describe their pets as behaving jealously anecdotally (Hötzel et al. 2019; Mathes and Deuger 1982; Mitchell and Hamm 1997; Morris et al. 2008), those reports generally follow an immediate precipitating event rather than being indicative of a longstanding abstract emotional response to existing relationships. Morris et al. (2008) found that owners reported jealousy at higher rates compared to the other secondary emotions. Among dog owners, jealousy was most commonly attributed to dogs when the owner was affectionate toward another human, in particular, their romantic partner. The more attached people were to their animal companions, the more they attributed emotions to them. Jealousy was attributed to dogs and cats at high levels in another study as well (Su et al. 2018). A drawback of the survey report method is that it cannot speak to the underlying emotional experience of the animal and results may reveal more about the circumstances in which humans are likely to ascribe a familiar human emotion to animals. That is, animal caregiver reports may reflect little more than the human tendency for anthropomorphism. Nonetheless, the species that jealousy has been most commonly ascribed to and the contexts in which it is presumed to occur may inform viable directions for further research.

It is possible that behaviors appearing to reflect underlying feelings of jealousy are instead responses to the perceived loss of a resource. In some dog breeds, guarding behavior, which may mimic jealous reactions, may have been selected for over generations and may not reflect the same underlying emotional motivation. Dogs may also be reacting to the loss of reinforcement for positive behaviors. Dogs that behave aggressively to a stranger that is receiving attention from their owner may be experiencing fear or anger rather than jealousy. The owners might preferentially interpret the behavior as motivated by jealousy because such emotions reflect the bond between human and companion animal.



## Experimental Work

Experimental work could tease apart dogs' responses to attention that is redirected to another from their owners compared to other humans with whom they have no attachment or weak attachment. Prato-Previde et al. (2018a, b) did not find that dogs in their studies differentiated between caregiver and stranger interactions with identical objects. These findings might cast some doubt on the likelihood that the dogs' response could be conceptualized as human-like jealousy. To further understand the motivations underlying behaviors appearing to reflect jealousy, researchers have also investigated the response of dogs when their caregiver directs attention to different objects. For example, Abdai et al. (2018) demonstrated that dogs exhibited more jealous-like behaviors when caregivers attended to other social partners rather than to inanimate objects. Harris and Prouvost (2014) found that dogs engaged in more aggressive and attention-seeking behavior when their caregiver was paying attention to a toy dog that moved and barked compared to when they paid attention to a book or other inanimate object. Furthermore, researchers compared these apparent jealous reactions in cases where attention was simply withdrawn but not directed to another recipient, and failed to find an increase in ostensive jealous behaviors in such cases. Cook et al. (2018) additionally found greater amygdala activation (indicating emotional reactivity) when dogs observed their owners providing food to fake dogs compared to when they simply placed dog in a bucket. Unfortunately, the availability of food for the dog subjects was not carefully matched and the dogs may have been responding to the food rather than their owner's attention in this study. In addition, there was no control condition where the fake dog did not receive food from the subject dog's owner (Vonk 2018).

Moreover, some researchers have questioned whether dogs really perceive fake toy dogs are being animate, and therefore as legitimate rivals for affection (Prato-Previde et al. 2018a, b). Fake dogs may elicit more attention from the subject dogs because they are strange and unfamiliar objects that fail to behave as expected.

Furthermore, dogs in Prato-Previde and colleagues' studies did not try to interfere with the caregivers' interactions with the fake dogs or to redirect the caregivers' attention to themselves. These results cast further doubt on the legitimacy of the general paradigm.

## Neurobiology of Emotion

Despite its shortcomings, Cook et al.' (2018) study was notable for investigating amygdala activation in addition to observing the behavioral response of the dogs. Jealousy has been linked to activation in the amygdala in humans (Harmon-Jones et al. 2009), making the finding of activation in dogs while observing their owners interacting with fake dogs intriguing. Rilling et al. (2004) observed similar activation in the amygdala and related brain areas of male rhesus macaques that observed their mates interacting with other males. Rilling et al.'s study is also one of a few examining animal's reactions in the context of relationships with conspecifics rather than humans. Thus far, such studies have been conducted only with nonhuman primates. For example, Maninger et al. (2017) observed monogamous male coppery Titi monkeys using functional imaging to examine cerebral glucose metabolism. They also measured hormones involved in mate guarding, such as testosterone, cortisol, oxytocin, and vasopressin. They allowed the male titi monkeys to observe their own mates and unfamiliar females positioned next to unfamiliar males. The males looked longer when their mates versus the unfamiliar females were paired with the stranger males. Potentially more compelling was the finding that neurological and hormonal changes in the expected direction coincided with these behavioral differences leading Maninger and colleagues to speculate that these physiological changes could be identified as markers of jealousy in nonhuman primates. These changes might be adaptive in maintaining reproductive units.

Jealousy may be experienced outside of the reproductive context in nonhuman primates as well. For example, Webb et al. (2020) observed

a group of captive chimpanzees when new members were introduced into their social group. Male chimpanzees were more likely than females to intervene when close male associates interacted with novel group members of the same sex. The negative reactions were the most pronounced for relationships that were described as especially close. These strong reactions to male-male dyads clearly do not serve to maintain reproductive bonds, but may serve to protect and enhance coalitionary relationships, which enhance fitness in a different way. The sex differences are interesting as it is male chimpanzees that hunt and patrol together and form alliances to defend their own group and attack males of rival groups (Mitani and Watts 2005).

In conclusion, jealousy may be adaptive in a range of competitive contexts, primarily within close social relationships and therefore is assumed to be widespread among social animals. However, it is unlikely to be restricted to group-living animals as it may allow the young of any mother-reared animals to compete for resources. Thus far, studies have been conducted only with some domestic companion animals and primates and few paradigms have been used leaving this a rich topic for further study.

## Cross-References

- [Affiliative Bond](#)
- [Attachment](#)
- [Discrimination of Emotion](#)
- [Emotional Contagion](#)
- [Empathy](#)
- [Human-Animal interaction](#)
- [Pair Bond](#)
- [Shame and Guilt](#)

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## Jean Baptiste Lamarck

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## Synonyms

Charles Darwin; Lamarkism; Traits

## Definition

Evolution is the phenomenon of informative hidden potentialities. It is the improvement within the genetic characteristics of biological populations over additional generations. This is the method of evolution that has given rise

to diverseness at each level of biological establishment, as well as the amount of species, individual organisms, and molecules.

## Introduction

Lamarck a French naturalist, biologist, and an early pitch of the thought that evolution (ancestry with moderation) occurred and began in accordance with natural laws. Lamarck, however, is remembered today mainly in relatedness with his now displaced theory of heredity, the “inheritance of acquired traits.”

In a broad surrounding, Lamarckism remains of use when examining the evolution of cultures and ideas. It is generally held in terms of some religious views on “karma” and inheritance of sin, and remains relevant to some scale for bacteria and microorganisms. Lamarck was also one of the first to use the term *biology* in its recent perception, and he coined the term invertebrates.

## Biography

Lamarck was born in Bazentin-le-Petit, Picardie, into an impoverished family (hence the title of *chevalier*, knight).

Lamarck served in the army before fetching interested in natural antiquity and writing a multi-volume flora of France. This caught the attention of Georges-Louis Leclerc, Comte de Buffon who arranged for him to be appointed to the Museum National d'Histoire Naturelle in Paris, France. After years working on plants, Lamarck was scheduled curator of invertebrates. He also began a series of public lectures.

Earlier 1800, Lamarck was an essentialist who whispered species were rigid; however, after working on the mollusks of the Paris Basin, he build up assured that transmutation of species, or change in the construction of species, appeared over time. He set out to develop a description, which he outlined in his 1809 work, “*Philosophie Zoologique*.” Lamarck urbanized two laws to describe evolution: the “*law of use and disuse*”

and the “*law of inheritance of acquired characteristics*.”

Lamarck saw spontaneous generation as being ongoing, with the simple organisms thus created being transmuted over time becoming more complex and closer to some notional idea of perfection. He thus believed in a teleological process where organisms became more perfect as they evolved.

Lamarck founded a school of French *Transformationism* which included Etienne Geoffroy Saint-Hilaire, and which corresponded with a radical British school of comparative anatomy based at the University of Edinburgh, which embraced the surgeon Robert Knox and the explorer Robert Edmund Grant. Professor Robert Jameson wrote an anonymous paper in 1826 approving “Mr. Lamarck” for justification how the superior animals had “evolved” from the “easiest worms,” this was the first utilize of the word “evolved” in a current wisdom. As a young student, Charles Darwin was trained by Grant and worked on marine creatures with him.

During his life span, Lamarck became controversial; his disapproval of the paleontologist Georges Cuvier’s anti-evolutionary stance won him no friends.

Lamarck married three, perhaps four, times. His first wedding was to his courtesan from 1777, Marie Delaporte, the mother of his first six children, whom he married in 1792 on her death-bed. He remarried in 1795 to Charlotte, but she died in 1797. Lamarck wedded his third wife, Julie Mallet, in 1798. She died in 1819. Rumor exists of a fourth wife and widow but no written proof exists of her. Lamarck slowly turned blind.

On 28 December 1829, Lamarck passed away in Paris.

## Lamarckism

Lamarckian progression is a theory put additional based on the heritability of acquired features by Lamarck, the once widely received design that an organism can pass on characteristics that it acquired all the way through its life span to its offspring.

Lamarck suggested that individual efforts during the lifetime of the organisms were the main mechanism operating species to adaptation, as they supposedly would acquire adaptive changes and pass them on to offspring. While extremely admire during the near the beginning nineteenth century as an account for the complication observed in living systems, after publication of Charles Darwin’s theory of natural selection, the importance of separate efforts in the generation of adaptation was significantly reduced. Later, Mendelian genetics replaced the concept of inheritance of acquired traits, ultimately leading to the progress of the modern evolutionary synthesis, and the general deportation of the Lamarckian theory of evolution in biology.

## Lamarck’s Theory

The evolution of giraffe necks is frequently used as the example in simplification of Lamarckism.

Erasmus Darwin wrote *Zoonomia* suggesting “that all warm-blooded animals have arisen from one living filament,” and “with the power of acquiring new parts” between 1794 and 1796 in response to stimuli, with each round of “improvements” being inherited by consecutive generations. Subsequently Lamarck proposed in his “*Philosophie Zoologique*” of 1809 the theory that characteristics that were “needed” were diminished during the lifetime of an organism were then passed on to the offspring. He saw this resulting in the evolution of species in a continuous chain of development towards higher forms.

Lamarck based his theory on two inspections, in his day examined to be generally true:

1. Individuals lose characteristics they do not necessary and develop characteristics that are useful.
2. Individuals inherit the traits of their ancestors.

With this in mind, Lamarck evolved two laws:

1. **Law of use and disuse.** *In each animal which has not proceed the limit of its development, a more frequent and continual use of any organ gradually strengthens, develops, and enlarges*

*that organ, and gives it a power proportional to the span of time it has been so used; while the durable disuse of any organ imperceptibly weakens and deteriorates it, and progressively diminishes its functional capacity, until it finally disappears.*

2. **Inheritance of acquired traits.** *All the acquisitions or depletion wrought by nature on individuals, through the impact of the environment in which their race has long been placed, and hence through the consequences of the major use or permanent disuse of any organ; all these are preserved by reproduction to the new individuals which arise, provided that the acquired modifications are common to both sexes, or at least to the discrete which produce the young.*

Examples of Lamarckism included:

- Giraffes stretching their necks to get to leaves high in trees strengthen and slowly lengthen their necks. These giraffes have offspring with moderately longer necks (also known as “soft inheritance”).
- A blacksmith, during his work, strengthens the muscles in his arms. His sons will have analogous muscular growth when they adult.

In essence, a change in the environment brings about change in “needs,” resulting in change in behavior, bringing change in organ usage and development, bringing change in form over time – and thus the gradual transmutation of the species.

Although such a theory strength describe the notable diversity of species and the first law is generally true, the major argue against Lamarckism is that experiments basically do not hold up the second law – simply “acquired traits” do not appear in any significant logic to be inherited. For example, a human child must learn how to propel a ball even though his or her parents learned the same feat when they were children.

The dissension that instinct in animals is confirmation for hereditary knowledge is generally regarded within science as false. Such behaviors are more possibly passed on through a mechanism

called the Baldwin effect. Lamarck’s theories acquired preliminary acceptance because the mechanisms of Mendelian inheritance were not explained after Lamarck’s death, until later in the nineteenth century.

## Proponent

The “*Vestiges of the Natural History of Creation*,” written by Robert Chambers and published certainly in 1844 in England, suggested a theory modeled after Lamarckism, causing political debate for its radicalism and unorthodoxy, but exciting popular interest and paving the way for Darwin.

In the 1920s, experiments by Paul Kammerer on amphibians, certainly the midwife toad, emerged to find attestation supporting Lamarckism but were disgraced as having been falsified. In *The Case of the Midwife toad*, Arthur Koestler suspected that the specimens had been faked by a Nazi sympathizer to disgrace capacities Kammerer for his political views.

In the 1920s, Harvard University researcher William McDougall studied the potentialities of rats to correctly solve mazes. He claimed that offspring of rats that had learned the maze were able to race it faster. The first rats would get it wrong an average of 165 times before being able to run it perfectly each time, but after a few generations, it was down to 20. McDougall credited this to several variety of Lamarckian evolutionary method.

When Trofim Lysenko assisted Lysenkoism, a shape of Lamarckism was released in the Soviet Union of the 1930s, which complemented the ideological opposition of Joseph Stalin to genetics. This unscientific agricultural policy was extinct blamed for crop failures and famine.

Steele et al. (1998) produced some indirect corroboration for somatic transfer of antibody genes into sex cells via reverse transcription.

Homologous DNA sequences from VDJ – regions of parent mice – were created in germ cells and then their offspring. However, there has been no definitive experiment.



Neo-Lamarckism is a theory of inheritance based on an alleviation and addition of Lamarckism, necessary to prolonging the principle that genetic changes can be modulated and absorbed by ecological factors.

## Lamarckism and Single-Celled Organisms

While there is no confirmation with respect to higher organisms for Lamarckism – that is, there is no proof that acquired changes are genetically transmitted – a number of scientists quarrel that it can be perceived among microorganisms, with influenced changes inherited in the middle of bacteria and protozoans (Cairns 1998).

John Cairns, Stefan Miller, and Julie Overbaugh suggested in a publication in *Nature* in 1988 that some *E.coli* mutations could extend in a Lamarckian approach (Cairns et al. 1988). The class took a mutated strain of *E. coli* that was impotent to consume the sugar lactose and placed it in an environment where lactose was the only food source. They detected over time that mutations occurred within the colony at a rate that recommended the bacteria were overcoming their handicap by modifying their own genes. Cairns, among others, dubbed the process adaptive mutagenesis.

If bacteria that had overcome their individual incapability to get through lactose passed on this “learned” trait to future generations, it could be disagreed as a form of Lamarckism, though Cairns later select to distance himself from such a situation. More ordinarily, it might be observed as a form of ontogenic evolution.

There have been a few researches into Lamarckism and prions. A category of researchers, for example, discovered that in yeast cells containing a particular prion protein Sup35, the yeast were able to acquire new genetic material, some of which gave them new capabilities such as resistance to a particular herbicide. When the researchers mated the yeast cells with cells not containing the prion, the trait reappeared in some of the resulting offspring, indicating that some information indeed was

passed throughout, though whether or not the information is genetic is debatable: trace prion amounts in the cells may be passed to their offspring, giving the appearance of a new genetic trait where there is none (Cohen 2004).

Finally, there is growing evidence that cells can activate low-fidelity DNA polymerases in times of stress to induce mutations. While this does not directly converse advantage to the organism on the organismal level, it makes sensation at the gene-evolution level. While the succession of novel genetic traits is unsystematic, and assortment residues Darwinian, the dynamic process of identifying the necessary to mutate is considered to be Lamarckian.

## Lamarckism and Inheritance of Acquired Artistic and Spiritual Characteristics

Jean Molino (2000) has suggested that Lamarckian evolution may be accurately appealed to cultural evolution. This was also formerly suggested by Peter Medawar (1959) and Conrad Waddington (1961).

Likewise, religions generally cohere to the view of the inheritance of acquired spiritual traits. That is, there is an observation that manners in one’s life concern one’s spirit and that such passes down to one’s lineage in the form of religious merit or demerit. This is the outlook that the “sins of the fathers, when they have not been properly expiated, are passed on and lead to evil consequences for subsequent generation” (Wilson 1991). The set of guidelines of karma, common to many Eastern religions, as well as the inheritance of sin in several Western religions, reflects this point of view.

## Conclusion

The process and development of organic evolution is slow and gradual. The second part of Lamarck’s machinery involved the inheritance of acquired traits for evolution. He trusted that traits changed or acquired over an individual’s life span could be permitted to its offspring.

Darwin's theory has been assisted by a lot of confirmation. Lamarck's "Theory of Inheritance of Acquired Characteristics" (second law) has been not proved. The other way that Lamarck's theory has been confirmed incorrect is the study of genetics. Darwin knew that traits are approved, but he never understood how they are accomplishing. Lamarck is most excellent notorious for his theory of "Inheritance of Acquired Characteristics," first presented in 1801 (Darwin's first book dealing with natural selection was published in 1859): If an organism changes during life in order to adapt to its environment, those changes are passed on to its progeny. Lamarck's contribution to evolutionary theory consisted of the first truly cohesive theory of biological evolution, in which an alchemical complexifying force drove organisms up a ladder of complexity, and a second environmental force converted them to local environments through use and disuse of characteristics. Lamarck and Darwin's theories were extremely different but they were also much related. They both thought that organisms changed. They thought these changes could be very helpful and could help them endure. Lamarck and Darwin's theories are both the same and dissimilar in several ways.

## Cross-References

- Evolution
- Vestigial Organ

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## Jeff Bitterman

► [Morton Edward Bitterman](#)

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## Johannes Müller

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## Introduction



Johannes Peter Müller, 1801–1858

Johannes Peter Müller was born on July 14, 1801 in Coblenz, Germany, an ancient city in middle Germany. Some well-respected historians spell his surname “Mueller” (Young 1990). Müller died on April 28, 1858 in Berlin. Among numerous outstanding achievements during his career, he published several books including the eight books between 1833 and 1840 that comprised his *Handbuch der Physiologie des Menschen*. The *Handbuch* established Müller as the most renowned physiologist of his time. He made important discoveries in physiology, improved upon the discoveries of others, and mentored some of the most important physiologists/physicists of the nineteenth century. In his later years, he devoted most of his effort to the study of single-celled marine animals.

Born the son of a shoemaker, Müller was initially destined to have a career in leather work, but his success in the gymnasium (high school) resulted in his father being persuaded to allow him to enroll in the University of Bonn in 1819. In 1822, Müller earned a medical degree based on a study of animal movement, especially arthropods. Müller then spent a year and a half at the University of Berlin where his principal mentor was Carl Rudolphi, Germany's most eminent anatomist. Müller returned to Bonn initially as a lecturer but eventually as professor. Rudolphi died in 1832. In 1833 Müller was invited to succeed him at the University of Berlin. Müller remained at the University of Berlin until his death from cause unknown; some suggested suicide. Müller spent much of his adult life suffering from depression largely attributed to overwork and to constant financial problems. His financial problems were usually caused by spending too much of his personal income on equipment, etc., needed in his research.

This introduction is based mainly on Steudel (2008), but bits here and there were gathered from Fulton and Wilson (1966) and Wight (2000). Because Müller was so eclectic in his research and information about him is so scattered, most of the entry will be written without citing specific references for each fact or set of facts, but all can be verified among the References at the end of this entry.

## Handbuch der Physiologie des Menschen

Among Müller's most memorable achievements was his *Handbook of the Physiology of Men* which was published in eight volumes from 1833 to 1840. Boring (1950) summarized each book's emphases as follows. Book 1 (288 pages) considered the circulation of blood and lymph. Book 2 (308 pages) considered chemical correlates of respiration, nutrition, growth, reproduction, secretion, digestion, excretion, and chylification (formation of chyle, which has complex functions in the intestines). Book 3 (270 pages) considered physiology of the nerves. Book 4 (248 pages) considered general muscular movement with special attention to voice and speech. Book 5 (256 pages) began with the formulation of the "doctrine" (Boring 1950, p. 35) or "law" (Finger 1994, p. 135) of specific nerve energies (more on this below) before considering the five senses. Book 6 (82 pages) was titled "Of the Mind" and considered association, memory, imagination, thought, feeling, passion, the mind-body relationship problem, phantasms, action, temperament, and sleep. Boring did not differentiate books 7 and 8 (179 pages for both) but noted that they considered reproduction and development, embryonic and postnatal. Boring considered books 3–6 most important for psychology.

### The Law of Specific Nerve Energies

Reduced to its essence, specific nerve energies (SNE) mean that each sensory nerve can only convey information to the brain that arises from the specific activation of the associated sensory receptors or nerves. There are corollary SNE associated with muscle activity, but the emphasis here is on the senses. To explain what SNE meant, Anonymous (1911) wrote:

... the kind of sensation following stimulation of a sensory nerve does not depend on the mode of stimulation but upon the nature of the sense-organ. Thus light, pressure, or mechanical stimulation acting on the retina and optic nerve invariably produces [only] luminous impressions (p. 962).

Boring gave less credit than most authors do to Müller for "discovering" SNE, but Boring did recognize Müller for its clearer formulation. Boring considered that the prior work by the

Scotsman, Charles Bell (1774–1842) and the Frenchman, François Magendie (1783–1855) in differentiating sensory and motor spinal nerves laid the groundwork for Müller's formulation of the concept of SNE (see Boring 1950, pp. 31–33).

## Other Accomplishments by Müller

Müller's research was so prolific that only a small sampling of his accomplishments can be mentioned here,

### Physiology

As noted earlier, Müller's dissertation dealt with locomotion in animals. He began with arthropods but eventually addressed locomotion in other classes of animals. In 1820, the Bonn Faculty of Medicine offered a prize to whoever could prove that a fetus can breathe in the womb. Müller confirmed that a prenatal lamb did breathe in its mother's womb. Using self-experiments and self-observation, Müller determined that optical perceptions can arise without an adequate stimulus, such as mystical visions including ghosts. It is unclear whether Müller realized that memories acquired via first- or second-hand reports might be the basis for such visions.

### Embryology

Many of Müller's contributions to embryology were methodological. He published on the development and structure of glands. He discovered the embryonic duct that formed the fallopian tubes, uterus, and vagina.

### Neurophysiology and Neurology

Controversy had arisen involving Charles Bell and François Magendie regarding priority for the discovery of the distinction between spinal sensory and motor nerves, and after Magendie retracted some of his findings as his methods had been questioned, Müller entered the fray. First, he tried to do research using rabbits that yielded ambiguous results. Müller then began to use frogs, which offered the advantage that the spinal cord is easier to remove with its functions well preserved, and the relationships between the nerves were more apparent. Müller's results using

frogs were unambiguous and reproducible; thus, was the validity of Bell's and Magendie's findings established. Müller went on to study cranial nerves. He showed that two branches of the trigeminal nerve were sensory and the third branch was predominantly motor but with sensory fibers that provided feedback from the muscles. Any student of neuroanatomy should be familiar with the intricate sensory-motor feedback loops that prevent muscles from over-contracting, thus detaching from the bones, yet sufficient to maintain muscle tonus. Müller also studied the glossopharyngeal, vagus, and hypoglossal nerves.

### Müller's Students and the Issue of Vitalism

Brazier (1959, p. 20) described Müller as the "greatest physiologist of his time" and a "gifted teacher." Müller had many more students than the few mentioned here: (a) Emil du Bois-Reymond was a pioneer in electrophysiology of muscle, (b) Theodore Schwann developed cell theory, (c) Rudolf Virchow was well recognized for his research on anatomical pathologies, (d) Ernst Brücke became a distinguished physiologist at the University of Vienna and was described by Sigmund Freud who studied with him for 5 years as his most highly respected teacher, (e) Carl Ludwig was the most distinguished physiologist at the University of Leipzig in his time where he significantly influenced Wilhelm Wundt. Ivan Pavlov studied with both Müller and Ludwig, and (f) Hermann von Helmholtz. Had the Nobel Prize existed in Helmholtz's time, likely he would have qualified for four: one for his research in vision, one for his research in audition, one for his formalization of the Law of Conservation of Energy, and one for being the first to measure the speed of nerve conduction.

#### "Vitalism: The Best and the Worst"

This heading is the title to chapter 4 in Meulder's (2010) biography of Helmholtz. It followed chapter 3, "Johannes Müller "Man of Iron." Most authorities agree that Müller was a vitalist throughout his career. Muelder raised some doubt about whether Müller was a vitalist at the end, but acknowledged

that his students, Helmholtz, du Bois-Reymond, Brücke, and Ludwig successfully branded Müller as a "vitalist."

Vitalism is the belief that living matter is sustained by a vital or "life force" that cannot be reduced to chemistry and physics. Biologists today believe that it was necessary to reject vitalism to enable biological science to progress. Between them, du Bois-Reymond and Ernst Brücke made a pact to compel and establish the truth that "No other forces than common physical chemical ones are active in the organism" (Boring 1950, p. 708). Helmholtz and Ludwig must not have been present for the pact, as they surely would have joined in.

Two of Helmholtz's greatest accomplishments served directly to refute vitalism. First was his determination that the speed of nerve conduction was approximately 150–180 ft/s (Cahan 2018, p. 93). Müller speculated that nerves conduct at the speed of light and that "We shall probably never attain the power of measuring the velocity of nervous action" (Boring 1950, p. 41). Such speculation and belief imply that nerve conduction was in the realm of the supernatural. Second was Helmholtz's formalization of the Law of Conservation of Energy. Cahan (2018, p. 151) summarized the Law as follows:

Nature as a whole contained a store of force . . . that could be neither Increased nor decreased; its total quantity was "eternal and unchangeable like the quantity of matter."

There is an emerging parallel to vitalism that is plaguing animal cognition research today, namely, an advocacy for emergent properties. Here such advocacy will be termed "emergentism." Duane Rumbaugh and his colleagues have been at the forefront of such advocacy. Anonymous (2009) wrote:

Throughout his professional life, Rumbaugh has sought ways to test and understand intelligence that does not depend on the human capacity for complex language. In addition, he has sought to go beyond the two traditional methodologies: "respondents," innate, involuntary reactions to stimuli based on conditioning; and "operants," limited, voluntary actions that are designed to gain an award through operating on a particular environment. Rumbaugh has added a new methodology: "emergents," which are unusual problem-solving behaviors that are not based on repetition or



associative learning, but instead seem to emerge from a kind of integrative process based on genetics, instinct, and cognitive reasoning.

See also Rumbaugh (2002) Rumbaugh et al. (2003) and Rumbaugh et al. (1996). Belief in emergentism accepts that behavioral scientists may investigate phenomena that are not in principle reducible to physics and chemistry.

Emergentism has its roots in the nineteenth century theory of “mental chemistry” advocated by the philosopher, John Stuart Mill. Interestingly, John Stuart Mill’s view was in opposition to his father’s advocacy of “mental mechanics.” In brief, John Mill believed that “the whole is equal to the sum of its parts” versus John Stuart Mill’s belief that “the whole is greater than the sum of its parts.” As “proof” of mental chemistry, J. S. Mill used water to argue that water has properties that cannot be predicted from its elemental constituents’ oxygen and hydrogen. The “mental mechanist” would counter that when we know all the properties of hydrogen and oxygen, we will be able to account for all the properties of water.

In other words, to be a vitalist or emergentist promotes giving up and avoiding the hard work necessary to establish the physicochemical foundations of biological and psychological phenomena. For a more detailed account of the hazards of and parallels between vitalism and emergentism, please see Thomas’s entry, “Morgan’s canon” in this *Encyclopedia*.

## Cross-References

- [Afferent and Efferent Impulses](#)
- [Energy](#)
- [Hermann von Helmholtz](#)
- [Laboratory Research](#)
- [Respiratory System](#)
- [Sensory Receptors](#)
- [Vertebrate Nervous System](#)

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## John B. Watson

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More than other intellectual pioneers, John B. Watson’s views have been so simplified and distorted by successive generations of authors that it is difficult to discern his actual message. Watson founded behaviorism in 1913; the difficulty lies in

the fact that this doctrine directly contradicts the ancient folk psychology that forms the basis for our languages and for our strongly ingrained beliefs. Most readers, including almost all psychologists, have escaped the difficulties by adopting a simplified and false interpretation of his doctrines and leaving it at that. In fact, most handbooks and textbooks corroborate that falsely caricatured version.

Todd (1994) surveyed textbook treatments of Watson over the decades and found that they became “standardized” after 1960. According to that portrayal, Watson “appeared suddenly in 1913” and promoted a narrow brand of psychology that assumed that all behavior was learned and that led to an unethical “baby-frightening experiment.” Given the mass of work Watson produced studying instinct in animals in the laboratory and the field and the countless infants he worked with in Baltimore, he would have been exasperated, but probably not surprised, to read such a summary.

The purpose of this essay is to correct the record by concentrating on a few major aspects of his work. Many complete accounts appear elsewhere (Buckley 1989; Malone 1990/2004, 2009; Malone and Garcia 2014).

## Introduction

John Broadus Watson was born in 1878 on a farm near Greenville, South Carolina. He earned a master’s degree in 1899 at Furman University in Greenville and went on to the prestigious University of Chicago, where he became the youngest recipient of a PhD and remained as an instructor. He soon established a reputation as a researcher of animal behavior, and in 1908 the opportunity of a lifetime arose when he was offered a professorship and department chairmanship at the Johns Hopkins University in Baltimore. Watson also became editor of the *Psychological Review*, affording him tremendous influence over the development of psychology. Malone (2014) noted that he was “. . . attractive, strong, scientifically accomplished, and forceful” at a time when other psychologists and zoologists “. . . seemed weak, tentative, mealy mouthed, and ineffectual.”

Watson was combative and articulate, a real fighter who dismissed the psychology that existed at the time. And he was a full professor at Johns Hopkins at the age of 29! He was universally respected as both a researcher and scholar and came with a plan for action, rather than traditional quiet discussion and polite debate.

Watson had begun his career in the study of animal behavior (Malone 2017), both in the laboratory and in the field, including physically demanding research on noddy and sooty terns in the Dry Tortugas. He clearly considered himself a comparative psychologist and 80 years later so did comparative psychologist Donald Dewsbury (1994). But after 1915 his interest centered on child development. His academic career was cut short in 1920, partly due to a scandalous divorce (Buckley 1989; Malone 1990/2004). Isolated from academics, he began a very successful second career in advertising, first with J. Walter Thompson agency and later with William Esty. He continued to lecture occasionally and published frequently, but usually in popular magazines. His influence on modern psychology was evidenced in 2014, when the centennial of his 1913 seminal lectures announcing the founding of behaviorism was celebrated by the Association for Behavior Analysis International (ABAI) and the publication of many testimonial articles. It is commonly known that he established behaviorism, a movement that fractured (or blossomed) into many disparate parts over the years.

## Behaviorism

This is a way of treating the entire subject matter of psychology as activity, or behavior. That seems a simple thing to say, but its implications are difficult for many people to grasp and easy to misunderstand. Imagine that common psychological terms like “memory” and “visual images” are replaced by “remembering” and “seeing.” Instead of things like memories and images that are somehow stored in the brain and perceived by an inner ghost, we treat the psyche only as activities and dismiss our childish notions of bodies with computer brains controlled by magic spirits. When Watson proposed that we can study psychology

in an objective way, just as we study the rest of the physical world by concentrating on behavior, some listeners and readers were enthralled, but most were shocked. They believed in 1913, as they believe now, that Watson had forbidden the study of the mind!

Watson was not limiting psychology; Hilgard (1987) argued that he was expanding its field of study. Psychology had been obsessed with the analysis of consciousness, restricted to humans able to understand and use language and who were more or less sane. They were trained to “introspect” and describe their conscious experience using labels that they were taught, like “sensation,” “feeling,” and “image.” Behaviorism, on the other hand, applied to children and other non-verbal individuals, as well as subhuman animals and the insane.

## Consciousness?

Watson argued that the concept of consciousness derives from the invention of the soul by lazy but clever ancients who discovered that they could manipulate people through fear of the supernatural (1924). In both the 1924 and 1930 editions of *Behaviorism*, it was “The Advent of the Behaviorists” that first began to set things straight by banishing the soul, consciousness, and other fictional subjective terms and so providing a psychology that is “as objective as baseball.”

The assumption that we have minds that operate our body machines is pure folk psychology. Watson never argued that minds exist but are not objective, so cannot be studied. This misunderstanding has persisted for a century. He actually said that there is no “mind!” There are activities like seeing, hearing, listening, remembering, and imagining, but do they constitute a “mind” that is separate from the body?

Watson emphasized repeatedly that the mind/body distinction is a false one, writing that “Surely no one could ever be bold enough or rash enough to question that there is such a thing as mind or that it is made up of conscious units. And yet this is just what the Behaviorist did” (1926). We do not study the Easter Bunny

(or the mind) because there is no profit in studying things that exist only as words. The mind/body distinction was invented by savages and, though incoherent, was passed on as folk wisdom that is believable only because it is drilled into us in our language. The cultural belief in mind and body does not make minds exist.

Similarly, does the word sensation mean anything? If not, why try to analyze our experience into sensations? Or, as Watson urged, should we study the conditions that produce reports of “red” and the range of stimuli to which we are sensitive and the conditions that cause red/green confusions, as he did with a variety of animal subjects (Malone 2017)? Do we really want to hear your description of the feeling of “redness” or my description of the feeling of the chime of a bell? But that was psychology in 1913.

## Reactions to Watson’s Behaviorism

No one enjoys watching their life’s work dismissed, especially when the movement responsible gains traction and acclaim as revolutionary. Woodworth (1931) referred to “the outbreak of behaviorism” as if the movement was a disease. Behaviorism was a “youth movement,” and Woodworth disapproved of the fact that Watson “had won the public ear” (1931). He was unhappy with reviews of *Behaviorism*, Watson’s (1924 1930) flagship book: “The *New York Times* said of the book, ‘It marks an epoch in the intellectual history of man.’ The *Tribune* was more effusive: ‘Perhaps this is the most important book ever written. One stands for an instant blinded with a great hope’ (Woodworth 1931). And Woodworth was neither the only critic nor the harshest. Jastrow (1929) was furious, referring to Watson’s “extravagant and irresponsible claims... superman-ic disdain for one’s fellow scientists,” coming from someone whose “standing is unchallenged, his ability exceptional, his contribution notable.” That made Watson’s hostility toward conventional psychology even more egregious, as if a “modern Machiavelli” was seeking to confound the world. Watson was using the prestige and authority he had earned to “throw

the labors of everyone else into the discard. . .” (Jastrow 1929).

More recently, Harzem (1993) provided a detailed account of the harsh treatment Watson received from the psychological establishment, the press, and powerful enemies after his sensational divorce in 1920 and his departure from a pinnacle of academic success at Johns Hopkins. Harzem wrote that Watson had “dismissed at one stroke the entire body of literature on experimental psychology. . . painstakingly built over many decades. . . the academic reaction to this action was strong.”

Even today, it is difficult to find a textbook or handbook or encyclopedia entry that presents a fair rendition of Watson’s views. The leading biography of Watson is generally well done, but Kerry Buckley (1989) mistitled it *Mechanical Man*, implying a robotic/erector set orientation. Watson’s behaviorism holds that explanations must deal with our activity (behavior), not with supposed underlying, usually hypothetical machinery. But like the cat attracted to the laser pointer spot, the public is fascinated by colorful brain scans, believing that they somehow explain the workings of the mind. Watson was expert in biology, yet included no illustrations of brain mechanisms, since he knew that a nervous system was not necessary for intelligent behavior and that attributing behavior to the brain was only a distraction. No reader of his books could conclude that Watson denied private experience and treated us as complicated machinery; ironically, that better describes many cognitive theories! Yet, long after his death in 1958, his famous descendent B. F. Skinner showed no hesitation in throwing Watson under the bus while damning him with faint praise (e.g., 1974) and implying that Watson was guilty of the list of such sins (like portraying us as automatons) that are often still attributed to all behaviorists.

## Mary Calkins Understood

Mary Calkins (1930) had studied under the great William James in the 1890s, and she correctly understood Watson’s behaviorism. In 1930 she

distinguished between “moderate” and “extreme” behaviorism, which roughly corresponds to what Skinner (1945) would call “methodological” and “radical” behaviorism. The former holds that the mind cannot be treated by science because it is subjective, a position never held by Watson or by Skinner, but which is often attributed to both. The latter, radical behaviorism, promoted by Watson and named by Skinner, holds that mental terms are fictional products of folk psychology and that the mind/body distinction is a false one. Calkins was more perceptive than most psychologists who followed, since she recognized that Watson’s behaviorism was the radical kind and she wrote, “Rather, no theory is rightly called behaviorism which does not effectively ‘scrap’ mind and consciousness alike,” published the year she died (1930).

Though Watson claimed in 1936 that he never understood John Dewey’s lectures when a student at Chicago, the professor and the graduate student shared some important beliefs. According to Dewey (1930), modern justification for mind/body dualism comes in part from physics, of all sources, and he probably was thinking of Galileo when he wrote, “Qualities ejected from physics found a home in mind, or consciousness.” This is because Galileo viewed reality solely as physics and dismissed sensations, like “warm” or “bright,” as unreal, since they are subjective. Dewey pointed to “. . . the authority of physics for taking them to be mental and psychic in nature.” The separation of physics and sensation “. . . created. . . the beginnings of modern psychology and impregnated its terminology. Behaviorism is a reaction against the confusion created by this mixture” (Dewey 1930).

So “mind,” “consciousness,” “sensation,” “image,” and other terms are jargon, fictions that have no referent, but they “impregnated” our terminology. If Watson asked you to define those mental terms, he claimed that you would soon be “tongue-tied” since “you don’t know what you mean by them” (1924). Bergmann (1956) famously displayed a complete misunderstanding of Watson’s behaviorism writing, “His premise, that there are no minds, is false and sheer nonsense. . . when. . . I speak of minds, these are

so-called mental contents, or awarenesses, or phenomenal givennesses. . .” (Bergmann 1956).

Bergmann confused Watson’s denial of mental causes, like mind, sensation, and the rest, with denial of seeing, imagining, thinking, and other aspects of private experience that were never denied by Watson or by anyone, *ever*. This is always a contentious subject, because most of us feel that we experience imagery and it’s easy to recoil when someone tells us that there are no “images,” as Watson did and as Skinner later agreed. But even cognitivists agree that there are no “pictures in the head, so there is no argument among most psychologists today (see Malone 2009). There are better descriptors than “phenomenal givennesses,” such as “qualia,” but whatever they’re called, pieces of private experience are not “mental content,” and they’re not causes of observable behavior or speech; they are also behaviors/activities that are part of the fabric of all behavior. How experience “feels” is best left to the humanities to describe.

Nonetheless, the astute Mary Calkins (1930) also had her doubts that behaviorism could replace the study of consciousness wondering, “Is thinking merely a kind of doing?” We wonder (with Watson) what else it could be. Consider first Watson’s bare-bones “theory of learning;” once understood, his views on thinking, emotion, child development, and psychopathology become clear.

## Pattern Reactions

In 1919 Watson wrote that we are “what we come with and what we have been through,” and the latter is by far the most important. We come with a set of innate reactions called out by specific stimuli, so touch produces movement, an air puff causes a blink, food in the gut produces peristaltic movements, an object crossing the visual field causes orienting and following, and a sudden noise causes fear reactions. In the womb the infant reacts incessantly, adjusting to constantly changing stimulation, and adjustment continues until death, the final adjustment.

Through life, we adjust, constantly, with the whole body. These *pattern reactions* comprise three general categories: manual (M), “laryngeal (L),” and visceral (V), corresponding to motor, communicative, and emotional behaviors. Whether calm or agitated, reading or walking, asleep or awake, these three classes of behavior simultaneously are active, though in different degrees. For example, quiet reading may show low levels of manual and visceral behaviors and higher levels of laryngeal activity, as could be symbolized mLv. That could change in a moment if we react to the sound of a scream, becoming MLV.

This principle applies easily to learning, say a baby learning to grasp a bottle, which it does “by the sweat of its brow” (Watson 1919). The shiny object calls out its whole set of reactions – arms, legs, vocal cords, salivation, and stomach secretion – the MLV set. Eventually, the bottle is pushed away or grasped and adjustment is achieved. The evoking stimulus has changed and whatever behavior accomplished that will be likelier to occur when such a stimulus recurs. That behavior will also occur when similar stimuli appear, and this acquisition of old responses to new stimuli forms the basis for all learning and the formation of one’s personality.

## Embodiment

Watson repeated often that we adjust with the whole body – “Let me emphasize again – *whole*” (1924). And we place “. . . no more emphasis on the brain and spinal cord than upon the striped muscles of the body, the plain muscles of the stomach, the glands, etc. . .” (1924). In fact, a nervous system merely “speeds up the message,” but the message still gets through in the absence of a nervous system, just more slowly (1924). As a biologist, he also realized that the whole body is *alive*, therefore not really “mechanical,” in the sense that we usually refer to nonorganic devices such as erector set robots.



Watson's *Behaviorism* presents psychology as the activity of the whole body. In current cognitive jargon, that is "the embodiment of mind," described well by Killeen and Glenberg (2010), who trace the history of the "situating" of mind from Descartes to the present. Watson would be pleased to see that the old "information processing" model is now becoming passé, as we realize that digital computers are awful models for organic intelligence. Louise Barrett (e.g., 2011) showed how powers that were previously ascribed to the brain are actually explained by body structure and the environment, just as Watson and many modern writers argue. As Watson pointed out, there are "...many animals and free swimming plants without nervous systems" (1924, p. 43). This is not to say that a central nervous system is superfluous, but many writers have joined Barrett (2011) in condemning the brain reverence of the past century (e.g., Tennenhouse 2017).

## Thinking

Watson wrote that "...man both talks and thinks with his whole body – just as he does everything else with his whole body" (1930). But earlier he had *suggested* that laryngeal movement was an important physical embodiment of thinking, as well as talking (e.g., 1913), and this was seized by critics eager to show that a functioning larynx was not essential for thought. But even his contemporary critics recognized that interpreting thinking as "behavior" did not necessarily mean activity of the laryngeal vocal apparatus.

Watson dealt with this specific issue in both editions of *Behaviorism* (e.g., 1924) and earlier when he issued "A Correction of Statement" in 1920 at the Congress of Philosophy that met at Oxford. He wrote, "In advance of any argument I think we can say that he (the behaviorist) has never really held the view that thinking is merely the action of the language mechanisms... Like everything that we do thinking is done with the whole body." Further, if the body is damaged so

that limbs or organs are missing, "he thinks with the remaining parts... thinking, whatever its type, is an integrated bodily process."

## Silent Problem Solving

When problem solving, our behavior is no different from that of a rat learning a maze. Suppose a man is given a gold cigarette case with a secret release mechanism and told that he can have the case if he can figure out how to open it (Watson 1920). We watch as he spends several minutes manipulating it but fails to find the release mechanism. Now we send him away to a room by himself and tell him to come out when he has figured it out. After a few minutes, he comes out and proudly shows that he has figured out the trick to open it. But how did he do it? We didn't see what he did when he was sent to that room. But we saw him at work for several minutes before entering the room – why would we suppose that he did anything different once we couldn't observe him? The parallel with observable behavior and thinking is obvious; just because we can't see or hear the process doesn't mean that it is different in kind from the problem-solving behavior that we do see.

## Other Thinkers

To *really* understand another's "thinking," the behaviorist, "as well as the psychoanalyst... (require) a minute search into the subject's biography as far back as infancy" (1920). Watson went on to criticize the study of moment-by-moment private experience since that requires introspective training, with the subject repeating the labels for "conscious experience" that were just taught – what else could they be? He continued, "The report by the subject throws very little light." The same applies when the behaviorist considers his own thinking, which yields little via introspection and really requires examination of one's own life history. However, we find that most of our past experiences were not verbalized, and the body of

that wordless “memory” constitutes the unconscious. Watson suggested that “The theory of the unverbalized in human behavior gives us a natural science way of explaining many things that the Freudians now call “unconscious complexes,” “suppressed wishes” and the like” (1930). This explains Watson’s respect in his early work for the methods of psychoanalysis.

## Psychoanalysis

Watson criticized psychoanalysis in his last works, just as he criticized all “subjective psychology.” But for decades he approvingly cited Freud and even published a detailed endorsement of Freudian psychoanalysis in 1916, when Freud had not yet become a household word. This was a scholarly piece, published in *The Scientific Monthly*, which Watson concluded by arguing that everyone who dares should undergo psychoanalysis. This applies especially to those occupying stressful high-level government or business positions, so that their pressures are not augmented by the stresses of unresolved conflicts arising in childhood and youth that they are incapable of verbalizing! Years before and after that article, Watson referred repeatedly to Freudian psychology, criticizing some of its language, but endorsing it in general. Perhaps surprising, Watson was a conspicuously vocal defender of Freudian psychology, though Freud never realized this (Bergmann 1956).

## Psychopathology

The adjustments we make through life produce sets of reactions to the innumerable situations we have encountered, and those reactions are organized so that we can also adjust to new situations. Though “new” unfamiliar circumstances resemble familiar situations to some degree and the more they resemble the familiar, the easier the adjustment. So a person familiar with high school can adjust to college easily, but the adjustment to military life may be more difficult, since it includes stimuli that demand responses we lack.

Our learned adjustments total to become our personality, and a well-adjusted personality can deal with new situations that are encountered. But what if the new situation is so novel that it leaves us unable to adjust?

As Watson wrote, “Almost any event or happening might start a change; a flood might do it, a death in the family, an earthquake, a conversion to the church, a breakdown in health, a fist fight – anything that would break up your present habit patterns. . .” (1930). Recovery from such trauma may be difficult and lengthy, since it requires a rebuilding of personality. We do not learn chemistry or become a piano virtuoso in a day, and reshaping a personality may be more difficult than either, but Watson was sure that it could be done.

## Advertising and More

In 1920 Watson was 42 years old and left Baltimore for New York City, banished from academics and embittered; the publicity produced by his divorce and the viciousness of his former wife’s influential family was too much (Buckley 1989). He was introduced to people associated with J. Walter Thompson Advertising Agency and provisionally hired. By 1924 he was a vice president and became a wealthy man, living first on Fifth Avenue and later on a 40-acre “farm” in Westport, Connecticut.

Watson could have dedicated *Behaviorism* to Pavlov, or Darwin, or Bertrand Russell, but both editions were dedicated to Stanley Resor, who led the J. Walter Thompson Advertising Agency from 1916 to 1955. With his wife’s creative genius behind ad campaigns, Resor built JWT into a worldwide power, eventually setting records in billings. The dedication to Resor owed to that man’s “unfailing interest in both industry and science,” an interest shared by Watson, clearly evidenced in his 1913 manifesto. According to the archives of JWT, “To foster a scientific approach to advertising the company established a Research Department in 1915 and hired eminent academics such as John B. Watson, the founder of behavioral psychology. These professionals

added a new dimension to marketing research as J. Walter Thompson applied motivational studies to advertising, initiated the use of scientific and medical findings as a basis for copy, and established the Consumer Panel. . .” (J. Walter Thompson Archives).

The behavioral approach to advertising was simple and effective. His research with infants suggested that there are three innate emotional (visceral) reactions – fear, rage, and love. The cues related to each of those, plus food, sex, and shelter, can form 720 combinations and should be used in advertising displays as often as possible to attract the viewer’s attention. So Johnson’s baby powder came to signify love, by pairing its image with that of a loving mother patting a healthy, happy baby. Scott’s toilet tissue was paired with imagery of a bowel surgery and the warning that harsh toilet paper can lead to scary results. Further examples appear elsewhere (Malone 1990/2004). Walter Dill Scott had already changed advertising from informative to persuasive. But Watson carried that strategy further than it had been applied, and he is credited for it in advertising circles (*Advertising Age* 1999).

It appears that Watson’s legacy to business was more than just his work with advertising copy. He also produced innovations in personnel selection and management, as noted by DiClemente and Hantula (2000), who scoured the Library of Congress for documents providing a more complete picture of Watson’s business life and legacy. They wrote, “Indeed, the terms ‘behavioral’ and ‘experimental’ are often used to describe Watson and his work, and they have overshadowed his contributions to I-O psychology. . .many of his ideas endure today. . .He pioneered much of the work in selecting successful sales people and argued for personality testing in personnel selection before ‘The Big Five’ were introduced to contemporary research. . .This may be perhaps his lasting legacy. . .”

## Remembered by His Son

Watson’s son James was interviewed by Hannush (1987), providing an account of memories of life

with his father, with “no promises about objective observation.”

James remembered his father as having a sense of humor, as charming, and “a delightful person to be around.” He was bright, sociable (yet shy), fastidious, and *masculine*. James said that “Dad was very concerned with manly activities. . .courage and personal capabilities. . ., bravery and manliness, manual work, farm work, carpentry, and all of the manly arts including boxing.”

He showed more affection for animals than for people, and the only times he expressed much anger was when he saw “cruelty or abuse of other people or animals. . .cruelty to animals and children. . .That’s something he couldn’t stand.” He always had a huge garden and he was a skilled carpenter, who built bridges, barns, greenhouses, workshops, corrals, riding rings, dams, and stone walls.”

Watson’s so-called “behavioral” method of child raising was totally idiosyncratic and forbade any displays of warmth or emotion; James attributed his difficulties in life and his brother’s suicide to that upbringing, which he thought left them without the self-esteem necessary for a healthy life. He wrote, “Tragically, that’s the antithesis of what Dad expected from practicing those behavioral child raising philosophies.”

Following Rosalie’s death in 1936, Watson was devastated and seemed “confused” and depressed for several years. James was barely a teenager when she died, and his recollections of his father, then in his late fifties, show a less combative man. James could only say that he had “heard about” his father’s competitiveness and aggressiveness in his earlier career, but it evidently diminished after Rosalie’s death.

## Cross-References

- ▶ [Animal Psychopathology](#)
- ▶ [Anthropomorphism](#)
- ▶ [Behaviorism](#)
- ▶ [Cartesian Dualism](#)
- ▶ [Embodied Cognition](#)
- ▶ [Learning](#)
- ▶ [Thinking](#)

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## John Bowlby

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## Introduction

John Bowlby is best known as the father of attachment theory. First developed in the 1950s, attachment theory was both shaped by and significantly influential on the study of animal behavior. This entry will describe Bowlby's biography as it relates to the development of attachment theory, the major principles of and significant influences on his theory, and its applications to animal research.

## Early Life

Edward (John) Mostyn Bowlby (1907–1990) was born in London, England, to an upper-middle class family. As was characteristic of the time, he and his five siblings were raised primarily by a series of nannies and nursemaids. Bowlby only visited with his mother for an hour each day and with his father considerably less. His first nursemaid, Minnie, served as a mother substitute for him, and when she left the family when Bowlby was four-years-old, it served as a devastating loss. This would prove to be profoundly influential on his later research interests (Van Dijken 1998).

## Education and Clinical Experience

At the age of 11, Bowlby was sent to boarding school and at 14 entered the Royal Naval College, Dartmouth. In 1924, after spending less than a year training on a naval ship, Bowlby decided to leave the navy and pursue the study of medicine (Van Dijken 1998). He received his undergraduate degree from Trinity College at the University of Cambridge in 1928. While there, Bowlby recalled focusing a considerable amount of his time on evolutionary biology, which would prove influential on his development of attachment theory (Van Dijken 1998). He was also introduced to the field now known as developmental psychology, then in its nascence (Bretherton 1992). This persuaded him to leave his studies in medicine for psychology for the remainder of his undergraduate years. He would, however, return to the field to medicine, earning his degree from London's University College Hospital, in order to pursue a career in psychiatry. This was partially influenced by his work at a school for maladjusted children where he encountered children whose psychological problems appeared to be closely linked to their early childhood experiences of parental deprivation. Witnessing this association between early familial relationships and later development solidified Bowlby's interests in child psychiatry (Bretherton 1992).

As Bowlby pursued his studies in medicine and psychiatry, he also began training in psychoanalysis at the British Psychoanalytic Institute. His supervisor, Melanie Klein, shared his interests in early relationships and the damaging effects of early loss. However, as was characteristic of the field at the time, Klein's focus was almost exclusively on unconscious processes, to the exclusion of examining the actual experiences of children. Bowlby rejected this premise and sought out to prove that real-world experiences of trauma and loss have the most powerful influence on personality development (Bretherton 1992). This was supported by his first empirical paper which traced the development of 44 juvenile thieves back to their history of early separation from their mothers and other adverse childhood experiences (Van Dijken 1998).

Following the completion of his psychiatric and psychoanalytic training, Bowlby was appointed head of the Children's Department at Tavistock Clinic, an organization focused on social and preventative psychiatry. It was here that attachment theory was first developed.

## Development of Attachment Theory

### Core Tenants of Attachment Theory

At its core, attachment theory argues that the parent-child relationship is critical for both the child's immediate survival and their long-term psychological well-being. In Bowlby's writings, this is traditionally described as the mother-child relationship although he acknowledged the role of "mother substitute" figures, perhaps harkening back to his own childhood experiences with his nursemaid. Bowlby's theory is based in both developmental psychology and ethology. He argued that the attachment relationship is built upon a series of instinctual behaviors designed to bond infants and mothers together in order to ensure that the vulnerable infant receives the care they need. This need for protection, and the depth of the bond formed, helps to explain why infants demonstrate such significant separation



anxiety when apart from their mothers and why long-term separation can have such devastating psychological consequences, as Bowlby observed in his studies of maladjusted children and juvenile thieves (Bowlby 1982; Bretherton 1992).

Bowlby defined attachment as a behavioral system, similar to but separate from mating or feeding, which has evolved to promote the survival and reproductive success of the individual. In the case of the attachment system, the infant is drawn to maintain proximity to their attachment figure (the person who is most responsive to the infant's needs for care). As the child develops, so does the attachment relationship, becoming what Bowlby described as "goal-corrected partnership" as the child becomes more attuned to their caregiver's psychological perspective. Bowlby also argued that children's experiences with their attachment figures become mentally represented via what are known as "internal working models" (IWMs) which are then used as a way to predict future interactions with relationship partners and the world in general (Bowlby 1982).

### **Collaboration with Mary Ainsworth and the Assessment of Attachment**

Several years after Bowlby's arrival at the Tavistock Clinic, a scientist by the name of Mary Ainsworth joined his research unit. It was Ainsworth who completed the first empirical study of attachment, observing 26 families with infants living in Uganda over a period of 9 months. It was here that Ainsworth first noted three distinct patterns of attachment-related behavior: babies who seemed content in the presence of their mothers and explored comfortably under her supervision (now classified as securely attached), those who cried frequently in her presence and explored little (insecure ambivalent), and those who showed little regard for whether or not their mother was present (insecure avoidant). Upon returning from Uganda, Ainsworth began a second observational study of 26 families in Baltimore where again Ainsworth was struck by the individual differences in how both infants and mothers responded to each other (Bretherton 1992). From this work, Ainsworth developed a

standardized laboratory procedure, the Strange Situation, which was designed to capture the quality of the infant-parent attachment relationship over the course of a 20-min observation (Ainsworth et al. 1978). The Strange Situation is still considered the gold standard for attachment assessments, and Ainsworth's empirical work helped to provide evidence in support of Bowlby's theory.

### **Ethological and Comparative Psychology Influences on Bowlby's Work**

Bowlby's theory of attachment was born out of his education and training in both developmental psychology (which, at the time, was heavily steeped in psychoanalytic theory) and evolutionary psychology. In taking an evolutionary approach to explain the origins of the attachment relationship among human parents and children, Bowlby recognized that this type of relationship was also likely to exist in our closest evolutionary kin. He was also interested in attachment-related behaviors, such as imprinting, which are present in other species. For example, Bowlby was drawn to Konrad Lorenz's research on imprinting in goslings, which demonstrated the critical role that the parent-child connection plays in promoting the survival of vulnerable young. Bowlby was also drawn to Lorenz and others' ethological approach, which requires the observation of animals in their natural environment, and was similar to Ainsworth's work in Uganda and Baltimore and other research being conducted at Tavistock (Bretherton 1992).

Although Bowlby favored an ethological approach to animal research, he was also deeply influenced by the work of Harry Harlow who used experimental methods to study affectional bonds in rhesus monkeys. Harlow was particularly interested in the effect of parental deprivation on infant monkeys. In 1957 Bowlby and Harlow began a written correspondence which eventually led Bowlby to visit Harlow's monkey laboratory at the University of Wisconsin. Bowlby often cited his observations at Harlow's lab in explaining the behavior of human infants, for example, linking pathological thumb sucking in children to the nonnutritive sucking behavior demonstrated by

monkeys who had been raised in isolation (van der Horst et al. 2008).

## Contributions to the Study of Animal Behavior

As Bowlby recognized, the attachment bond is not unique to the human species. This fact has long been supported by research with nonhuman primates, including chimpanzees and rhesus monkeys. It is worth noting, however, that attachment relationships are not universal across primates. Research on New World monkeys, such as capuchins, and prosimian species has demonstrated that they imprint on their mothers but do not form the complexity of an attachment bond (Suomi 2016).

The study of rhesus monkey attachment dates all the way back to the 1950s with Harry Harlow. Just as Harlow's work was influential on Bowlby as he developed attachment theory, so was Bowlby's new theory influential on Harlow's subsequent research. For example, in a series of experiments, Harlow tested Bowlby's theory of separation syndrome (the stages of protest, then despair, that Bowlby argued human children demonstrate when separated from their caregivers) by separating infant rhesus monkeys from their mothers (van der Horst et al. 2008).

An extension of Bowlby's theory has been the physiological mechanisms of attachment. This research has its origins in the study of stress responses in rat pups and thus represents a feedback loop between the study of human and animal behavior. Bowlby had already proposed that, in humans, separation from an attachment figure represents a signal of danger. The precise physiological responses of rats separated from their mothers have been meticulously tracked through a series of experiments that would be impossible in human children (Polan and Hofer 2016).

The tools to assess individual differences in attachment have also been extended to the study of nonhuman species. For example, Mary Ainsworth's Strange Situation Procedure has been adapted to assess the owner-dog relationship (Rhen et al. 2013; Topál et al. 1998). Results from

these studies generally support the idea that dogs do form attachment bonds with their owners, which can be assessed along the same dimensions of security and insecurity as the parent-child attachment relationship. The same research has been extended to the study of the cat-owner relationship although there is little evidence of an attachment bond with owners within the feline species (Potter and Mills 2015).

## Conclusion

John Bowlby was a pioneer in the field of human psychology, but his work has long-reaching influences on the study of animal behavior as well. This is fitting given how steeped in ethology and animal research the development and application of attachment theory has been. Nearly 60 years after it was first developed, Bowlby's attachment theory continues to generate new research in both human and nonhuman species. Indeed, the lasting generativity of attachment theory is relatively unique in the field and sets John Bowlby apart as one of the most influential psychologists of the twentieth century.

## Cross-References

- ▶ [Attachment](#)
- ▶ [Canine Cognition](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Feline Cognition](#)
- ▶ [Harry Harlow](#)
- ▶ [Human-Animal Interaction](#)
- ▶ [Imprinting](#)
- ▶ [Konrad Lorenz](#)
- ▶ [Observational Methods](#)
- ▶ [Parenting](#)

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## John David Smith

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J. David Smith received his B.A. in Anthropology from Yale in 1975. His background and course training in music, music theory, composition, and counterpoint led to an honor's thesis on the cultural shaping forces that produced the music and the music-theoretic structure of Indonesia's Gamelan. At this point, David aimed toward graduate study in ethnomusicology. In his early career, David made significant contributions to the study of music, cognition, and aesthetics (e.g., Smith 1987; Smith and Melara 1990). He has

also taught courses in these topics for many years at the graduate and undergraduate level.

Seeking a contribution through public service, David entered the Teacher Corps from Yale. He worked for two years as a classroom teacher at schools in Spanish Harlem. Concurrently, he completed coursework and requirements at the Bank Street College of Education, receiving in 1977 an M.S. Ed. in Early Childhood Education. These experiences, and his thesis on cultural differences in cognitive styles and their impact on educational success, led David toward graduate study in cognitive psychology and cognitive development. He has taught many courses in development, education, testing, intelligence, and socioeconomic influences in these areas.

David received his Masters and Ph.D. in Psychology (Cognitive) from the University of Pennsylvania in 1982, advised by Deborah G. Kemler Nelson and Jonathan Baron, with important influences in cognitive-developmental psychology by Rochel Gelman. Equally important, David was taught at Penn by an extraordinary group of behavioral and comparative psychologists, including Richard "Dick" Solomon, Robert Rescorla, Randy Gallistel, Paul Rozin, and David Premack. At that time, Penn may have had no equal for training in behavioral and comparative psychology. David still remembers with awe his riveting first seminar with Solomon. He was well prepared to extend his scholarship into the field of comparative cognition when the time came.

In fact, David has always approached his studies in animal cognition from a perspective shaped by human cognitive psychology. For example, David realized, after teaching, and teacher training, and two masters theses on cognitive-developmental issues, that scholars were misunderstanding humans' high-level cognitive capacities in important ways. Considering metacognition, in particular, they interpreted that capacity as highly verbal, declarative, and explanatory. So they also tested the capacity in children in that way. They made this interpretation to the point that even children at age 6 or 7 often seemed not to be metacognitive, because they would fail some of the existing assessments. David was

struck by the conflation with language and with introspection that needed to be explicitly declared. Surely metacognition in its essence might be language quiet while still introspectively lively, undeclared but still available for behavioral use by the organism.

Many comparative psychologists will know where this train of thought led. It produced an influential new area of research exploring animals' metacognitive capacities (e.g., Smith 2009; Smith et al. 2003, 2012b). David's initial studies with rats were not published because those rats, in the method adopted, did not express any metacognition. The verdict is probably still out on rats, considering the multiple studies completed since. But then a dolphin clearly showed a data pattern that might be construed as metacognitive (Smith et al. 1995), prompting a long and sharp debate in comparative psychology about theoretical interpretation and about the appropriate methods for tapping metacognition (Carruthers 2008; Crystal 2014; Hampton 2009; Kornell 2014; Smith et al. 2008a, 2009). The dam burst, with many ensuing studies on various species of vertebrates (e.g., Beran et al. 2012). David explored the case of the New World and Old World monkeys principally (e.g., Beran 2014; Smith et al. 1998, 2006, 2010b, 2013; Zakrzewski et al. 2014), creating new paradigms and building the case that some nonhuman primates have a form of metacognitive monitoring that is on the spectrum toward humans' full-fledged metacognitive capacity. After a long debate, this interpretation is now the majority interpretation in the field.

Given his educational background and developmental training, David also has a lifelong interest in concepts and category learning, together with their underlying neuroscience. His work in this area helped produce a sharp rebalancing of theory in the human categorization literature. In this rebalancing, the dominant exemplar theory was sharply delimited to its proper, small domain of application, while prototype theory's importance was appropriately expanded (e.g., Smith and Minda 1998, 2000, 2002). This research was important in resolving a 30-year-long difficult debate in cognitive psychology.

Remarkably, David's animal studies were instrumental to this resolution. His experiments on pigeons, capuchins, and macaques, as much as his results from humans, showed clearly that many vertebrate species do not memorize all of the specific exemplars they encounter, which is the central tenet of exemplar theory (Smith et al. 2008b). Rather, they inherently abstract and average their exemplar experience, forming central-tendency category representations or prototypes (Smith et al. 2010a, 2012a, c). In this area, there was an extraordinary synergy between David's cognitive and comparative research, as the animals helped establish the roots of humans' categorization, and helped reveal the essential truth about vertebrates' categorization processes that probably run tens of millions of years deep.

In collaboration with the Federal Aviation Administration and the Transportation Security Administration, David applied his expertise on concepts and categories to the problem of Homeland Security. He studied the difficult threat-recognition problem that airport X-ray screeners face and explored ways to improve the level of threat detection within the security system. This research showed that the visual search for threat targets elicits highly-specific recognition processes that generalize poorly to novel tokens of target/threat categories (e.g., Smith et al. 2005). Thus, though screeners may become excellent at detecting in baggage the specific knives they have been trained to detect, this will not mean that they will detect novel knives that have not been part of their training. The security concern raised by this finding is that actual threats will generally be novel tokens from outside the training set that has been used to prepare screeners, and so these actual threats may tend to be less well detected by screeners. This research illuminates the fundamental nature and problem of threat detection, and it has profound and sobering implications for applied security domains.

David's sharpest interest remains comparative-cognition research, as he seeks the earliest roots of human cognitive capacities like metacognition and prototype formation. In this search, given his training, he takes a distinctive theoretical perspective on comparative psychology that is an

intrinsically important part of his biography. He has seen that cognitive psychology has served itself generously in growth and insight for 40 years by taking: (1) a systems perspective that differentiates different levels and characters of cognition in mind, and (2) a neuroscience perspective that grounds these different learning processes in distributed brain processes. David believes that comparative psychology will also reward itself generously if it begins to adopt related approaches more broadly and systematically (Smith and Church 2017).

At present, David is exploring ways to unplug and disable humans' and animals' associative-learning processes, so that their parallel explicit learning processes – when and if these exist – can be studied clearly in isolation for the first time. David and others have clearly demonstrated qualitative dissociations of this kind with human participants using a variety of methodologies. In David's view, these approaches are good examples of the systems approach that should naturally be applied across species as well. They have the potential to open new empirical approaches to many areas of comparative research.

David's research has been supported by funding from the National Science Foundation, the National Institutes of Health, the European Science Foundation, and the Federal Aviation Administration and Transportation Security Administration. His research has been featured in numerous places, including *NPR*, *New Scientist*, the *Washington Post*, *Huffington Post*, the *Wall Street Journal*, and *US News and World Report*. He was elected President of the Southern Society for Philosophy and Psychology (2012). During more than two decades on the faculty of the Psychology Department at the University at Buffalo, SUNY, he collaborated with Language Research Center scientists to advance his studies of human and monkey cognition. In 2014, he joined those colleagues as part of the Department of Psychology at Georgia State University.

Throughout his career, David's primary pastime has been mountains and mountain climbing. One high point of many came when David summited Denali, the highest peak in North America, with just his one partner. A low point

came when David – with his young children – was caught by a freak hail and lightning storm above tree line on a difficult climbing path in the Alps. A point when time stood still came when David lost his way climbing down from 22,800 feet in the Andes. With his partner, he settled down at 21,000 feet enveloped by ice fog to wait through an endless night. But morning came, and the route down was revealed when saffron-robed monks appeared climbing toward them. David has climbed the Matterhorn, the Eiger, the Jungfrau, the Dent Blanche, Mt. Blanc, the North Face of the Tour Ronde, Denali, Aconcagua by its Polish Glacier route, and other peaks as well. His children sometimes will still go to the mountains with him.

## Cross-References

- [Categorization](#)
- [Meta-cognition](#)
- [Metamemory](#)
- [Uncertainty Paradigm](#)

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## John James Audubon

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## Introduction

**John J. Audubon** was an ornithologist, painter, and conservationist most recognized for his contributions to the field of ornithology with North American species. He performed the first known American project with bird banding to study nesting behavior in birds. However, he is most remembered for his life-size magnum opus collections of drawings and paintings, *The Birds of America*, which included over 700 hand-colored, engraved copper plates depicting species in their natural habitat. Furthermore, his collection and its sequels, *The Ornithological Biographies*, have been considered some of the most noteworthy works completed in the field.

## Early Life and Background

Audubon was born on April 26, 1785, as Jean Rabin in the French colony of Saint Domingue (now Haiti). His mother, a chambermaid and mistress of his maritime father, died during his infancy from tropical disease (Rhodes 2004). Civil unrest regarding slavery in the Caribbean persuaded his father to return to France, after which he arranged for Jean and his half-sister to accompany him (Rhodes 2004). In order to naturalize the children as French citizens, they were legally adopted by their father and his French wife from prior to Saint Domingue. Additionally, they received name changes, with Jean's becoming Jean-Jacques Fougère Audubon (Rhodes 2004).

In his youth, Audubon excelled in many skills including music, dance, fencing, riding, and hunting. Among his other pastimes, his father fostered his love and curiosity for nature, most notably with birds (Burroughs 1902). At the age of 12 Audubon was enrolled in military school to eventually join the navy at the urging of his father (Rhodes 2004). This maritime path was averted, as his naval career was short lived due to his seasickness, distaste of naval studies, and failing his qualifications tests (Audubon et al. 1868).

He immigrated to the United States in 1803 at the age of 18, and anglicized his name to the familiar John James Audubon (Rhodes 2004). He took over a farm his father had previously purchased in PA called Mill Grove which held lead mines and the potential to be profitable (Audubon et al. 1899). It was at Mill Grove where his ornithological career began regarding his depicting birds in their natural habitats and recording their behavior, where he improved his taxidermy skills, and where he met his future wife (Audubon et al. 1899). However, after determining that the mines were too great of a pecuniary risk, Audubon sold part of Mill Grove and journeyed to NY to study new business trades in order to support his marriage (Audubon et al. 1899).

After moving to Louisville, KY, in 1808, Audubon married Lucy Bakewell and began a family including two sons and two daughters. Unfortunately, both girls died before the age of

two (Audubon et al. 1899). Audubon's newfound trade business in Kentucky struggled following President Jefferson's embargo placed on British trade (Rhodes 2004). This hardship prompted his moves to Henderson, KY, and then later to Ste. Genevieve, MO, before deciding to eventually terminate his business partnership in 1811 in pursuit of his ornithological and artistic career (Audubon 1826).

In 1812 he returned to KY from a trip to discover his collection of over 200 works of art had been eaten by rats. This left Audubon wracked with depression for weeks before resolving to recreate his entire lost collection at a higher standard (Rhodes 2004). Still struggling to provide for his family, he became business partners with his wife's brother. Their stability improved until the Panic of 1819 which left Audubon bankrupt and temporarily jailed for his debt, with his main income coming primarily from death-bed portraits and other sketches (Rhodes 2004).

## Bird Banding

In 1804 while at Mill Grove, Audubon performed the first recorded experiment with bird banding in America by testing if phoebes returned to the same nesting locations annually (Rhodes 2004). He secured light threads to the legs of nestlings just prior to them leaving the nest. These bands were loose enough not to cause the birds harm, but were fastened so that the birds could not remove the threads themselves. He then noted when the birds departed and recorded when some of the phoebes returned with the thread still attached the following spring. His continued study of the phoebes in this particular location ended after one of the farm's workers killed several of the birds to use as fish bait (Rhodes 2004).

## Vulture Study

Audubon studied feeding behavior in both black and turkey vultures in 1826 through a set of experiments in which he tested to see if vultures

scavenged with their sense of sight, smell, or both (Audubon 1835). He first began by hiding rotten meat behind pieces of paper with caged vultures nearby, only to have it go unnoticed by the birds. His experiment then entailed leaving a foam stuffed deer decoy in an open, visible area which was investigated by uncaged birds. In his final trial, he hid a fragrant deer carcass out of sight, and no birds were able to find it (Strycker 2014). After this experiment, despite poor experimental methods and flawed results, he published a paper on his work stating that vultures discovered food by sight rather than smell, nor a combination of the two (Audubon 1835). The paper, "Account of the Habits of the Turkey Buzzard, Particularly with the View of Exploding the Opinion Generally Entertained by Its Extraordinary Power of Smelling," was ridiculed by the public and fellow scientists. His findings elicited additional studies and opinions regarding the buzzards, including work from his colleague and friend Rev. John Bachman and the young Charles Darwin (Strycker 2014).

## Professional Career

Following a brief job as a taxidermist at a Cincinnati museum, he set out in 1820 to create a portfolio containing all of the birds in North America (Burroughs 1902). He hoped his prospective publication could surpass the level of artistic renderings done by fellow American ornithologist, Alexander Wilson. Beginning by traveling south, Audubon picked up side jobs including giving drawing lessons, selling or trading drawings for goods, and doing charcoal portraits upon request (Burroughs 1902). However, being away from his family for months at a time left his wife as the primary breadwinner with her job as a teacher (Rhodes 2004).

The content of Audubon's work was based on considerable field research and detailed note-taking while observing birds and other species (Audubon 1831). His typical process included extensive observation before killing a species, particularly if it was a newfound one, which was

quickly followed by hanging the creature from wires and threads to pose them for his art (Rhodes 2004). Once the specimens were taken down, they were occasionally dissected for study before being cooked and eaten by the end of the evening (Riely 2011). Audubon strived to create works of art that displayed species in their most authentic natural habitat; he went at lengths to ensure the accuracy of his work with both artistic technique and scientific accuracy (Riely 2011). Details he aimed to demonstrate include nest structure or materials, contents such as eggs or juveniles, and background details like flora typical of their diet or what they used as resources. Natural predators of the subject in his work were also occasionally featured (Audubon 1826). Some of his work contained different subspecies, for example different kinds of woodpeckers, to illustrate minute differences in appearance. Audubon chose to pose and draw his subjects before doing any taxidermy work so the animals still held more of their natural posture, rather than being rigid (Rhodes 2004). Similarly, he would feature the same species repeatedly within a composition to display different angles and anatomical views of the subject he was illustrating.

With the increase in his established works, Audubon ventured to Philadelphia in 1824 seeking publication for his drawings, only to be rejected (Audubon et al. 1899). He did, however, receive recommendations to pursue support from European investors, and with his wife's encouragement went to England in 1826 with his portfolio featuring hundreds of drawings (Burroughs 1902). Funding from advance subscriptions, exhibitions, oil painting commissions, and selling animal hides raised enough money to begin publishing Audubon's first volume of *Birds of America* throughout Europe in the form of hand-colored, engraved copper plates (Audubon 1826). Upon his return to America in 1829, he was reunited with his family and continued growing his drawing collection (Audubon et al. 1899). In 1830 he was elected a Fellow of the American Academy of Arts and Sciences while working on his sequel, *Ornithological Biographies*, a collection of life histories of each species included

within his first work (Audubon 1831). Both compilations were published between 1827 and 1841 in five volumes. Audubon was able to make significant contributions regarding bird anatomy, distribution, and our understanding of their habitual behavior based on his field notes and journals. In addition to these records, he also detailed how palatable each species was (Riely 2011).

Between 1840 and 1844 Audubon published an octavo edition of his *Birds of America* featuring more than 65 new plates in the collection (Audubon 1826). In 1846, he released the first volume of the *Viviparous Quadrupeds in North America* in collaboration with his colleague Rev. John Bachman regarding scientific text and his sons with drawings (Audubon and Bachman 1846). Although still working on continuing his collection of drawings of mammals, Audubon's health began to deteriorate in 1848 after he suffered from a stroke while starting to display signs of dementia. In 1851 he passed away peacefully in NY at his family home (Rhodes 2004). Following his death, the second volume of the *Viviparous Quadrupeds of North America* was published with the majority of the drawing contributions included done by Audubon's son, John Woodhouse Audubon, and the scientific information contributed by Bachman (Rhodes 2004).

Audubon's collective work at the end of his life included five volumes of *The Birds of America* and five volumes of *Ornithological Biography*. He became a member of several prestigious scientific groups such as the American Academy of Arts and Sciences, the Royal Society of Edinburgh, the Linnaean Society, and the Royal Society of London (Rhodes 2004). He was one of the first American conservationists in response to his observations regarding declining populations of native species from human interference, and expressed his concern over this decline within his writing (Riely 2011). Throughout his lifetime he discovered 25 new species, as well as 12 subspecies (Rhodes 2004).

## Cross-References

### ► Bird Migrations

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## Joint Attention

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### Synonyms

Coordinated joint engagement; Coordinated  
person-object orientation; Joint visual attention

### Introduction

*Joint attention* is the state of shared attention by two or more parties to an entity or event. Bakeman and Adamson (1984) defined “coordinated joint engagement” as a state in which the “infant is actively involved with and coordinates his or her attention to both another person and the object that person is involved with” (p. 1281). Thus, the core developmental milestone is the ability to simultaneously engage with both social partners and objects or entities in the world – this coordination develops in Western populations in the latter half of the first year of life and continues into the second year; while often taken as representative of all humans, it remains an open question whether these developmental patterns are culture-specific or universal. There is considerable contemporary debate over the kinds of activities that should be subsumed under the rubric of “joint attention.” In developmental psychology, joint attention has been studied with respect to three classes of behavior: *initiating behavior regulation* (IBR), *initiating joint attention* (IJA), *responding to joint attention* (RJA). Acts of IBR involve requests for object delivery – for example, pointing towards or reaching for an out-of-reach bottle, while alternating gaze between the bottle and a caregiver. Babies display RJA when they are able to follow a social partner’s gaze or pointing gestures to particular locations. When babies point to entities for reasons other than to request that a social partner deliver the indicated object to them, then they are said to display IJA. A majority

of contemporary researchers in developmental psychology include only RJA and IJA as examples of joint attention, arguing that these states of engagement differ from IBR in better predicting language development, in their apparent social orientation (often taken to contrast with the instrumental nature of IBR), and in their electrophysiological correlates (e.g., Vaughan Van Hecke et al. 2007). More inclusive definitions of joint attention include IBR as a facet of joint attention, based on the common behavioral constituents that characterize all three kinds of triadic engagement: an identifiable “topic” (the entity that forms the joint focus of attention), a directive gesture or cue (gaze or pointing), successive visual fixation of the entity and a social partner – these define a referential triangle, irrespective of whether the babies are apparently requesting an action on an entity or requesting an adult to share in emotional exchange about the entity (Bates et al. 1975). Even more inclusive definitions take IBR, IJA, and RJA as manifestations of joint attention and also such phenomena as *social referencing*, where babies use a parent’s emotional cues to regulate their own approach to novel objects, and *imitation*, which is often predicated on mutually attentive social partners jointly engaged on an activity in a coordinated manner (Leavens and Racine 2009). For many philosophers and developmental psychologists, joint attention implies the mutual awareness that two people are engaged in this state of shared attention; however, even proponents of this approach note that “knowing together” is difficult, if not impossible to objectively measure in any species, including humans (e.g., Carpenter and Call 2013). Here, we will review the evidence for various aspects of joint attention in humans and animals, with special reference to our nearest living relatives, the great apes (Hominidae).

### Joint Attention and Language Development

In developmental psychology, joint attention is considered a key mechanism for language acquisition in humans (Butterworth 2003). If a child



points to a dog and her caregiver turns to look at the dog, uttering the label, “doggie!” and turns back to face the child with a huge smile, this encourages the formation of an association between dogs (referents) and the verbal labels (symbols) for those dogs. Similarly, if a child can follow a caregiver’s point to an entity while the caregiver utters its label, this could also serve as a mechanism for grounding symbols in real-world entities. In longitudinal studies, many researchers have found predictive relationships between IJA and RJA and both concurrent and later language abilities (reviewed by Colonnese et al. 2010).

### Joint Attention Across Species

These triadic competencies that define joint attention in our species are not displayed by human children until well towards the end of their first year of life. The fact that joint attention is not displayed early in human development has fostered considerable debate over the species-specificity of joint attention, with vigorous contemporary debate over theoretical positions that range from (a) claims that joint attention implicates uniquely human social cognitive capacities to (b) arguments that it is a product of the effect of uniquely human environmental circumstances on generalized mammalian social orientations to (c) claims that the state of joint attention is a widely distributed mammalian characteristic.

### Initiating Behavior Regulation (IBR)

Human babies begin making requests with gestures long before they can speak (Butterworth 2003). Pointing-to-request is often the earliest-developing use of referential gestures. It is widely believed that IBR is cognitively or motivationally distinct from IJA. Unlike IJA, IBR is not a reliable predictor of language development, and is not clearly tied to frontal regions of the brain associated with executive control (Vaughan Van Hecke et al. 2007). However, in the first study to discriminate IBR from IJA by Bates et al. (1975), the

authors characterized both IBR and IJA as requests (albeit with a different terminology). In their characterization, IBR constituted the use of a social agent to obtain an object, whereas IJA was the use of an object to obtain attention from the social agent; thus, both IBR and IJA were seen to be examples of a common cognitive ability for means-ends reasoning.

In later years, it became clear that children with autism spectrum disorder displayed a specific deficit in IJA, whereas their IBR behavior was not affected (Baron-Cohen 1989). This widely replicated finding is a central pillar of the contemporary view that IJA reflects a capacity for reasoning about others’ minds or a motivation for social engagement that does not exist in other species. At present, it is unclear whether the relative lack of IJA in people with autism is a core cognitive concern or a motivational matter. If autism spectrum disorder is characterized by a lack of motivation for social engagement, then the apparent lack of appreciation of others as mental beings could simply be a secondary consequence of a primary difference in motivation – if people do not find social engagement rewarding, then they will not display IJA to seek such social attention (i.e., they will not display the communicative means to elicit the social ends). There is, however, wide agreement that IBR reflects means-ends reasoning and no compelling evidence that IBR is restricted to the human species.

It is now well-demonstrated that great apes in captivity, with no special training, will capture the attention of a human observer and point to entities (usually, but not always, desirable food) in apparent requests for delivery of the indicated entity (reviewed by Leavens and Racine 2009). They do not point to unreachable food in the absence of an observer, therefore, these deictic (directive) gestures are communicative in function – this is determined by filming the apes in the presence and absence of a human observer. Great apes wait to point or otherwise gesture when somebody is looking at them, demonstrating that they discriminate visual attention in others (Bodamer and Gardner 2002; Krause and Fouts 1997). Thus, IBR as it was first defined in human populations, by requestive pointing, is often displayed by apes

in captivity. Reports of IBR in wild populations are more controversial – begging behavior is very commonplace in feral populations of great apes, and involves a characteristic begging gesture being interposed by the begging individual into the line of sight of another individual who possesses desirable food, and this is a quintessential pattern of IBR (Bard 1992). To date, requestive pointing, however, has only been reported once in wild chimpanzees (Hobaiter et al. 2014).

## Responding to Joint Attention (RJA)

The ability to follow gaze and pointing cues develops gradually in humans. In the second half of the first year of life, babies will follow pointing cues and gaze cues to nearby objects that are already in their field of view. By about 18 months of age, babies are able to follow gaze and pointing gestures to specific targets located behind them (Butterworth 2003). Among nonhuman primates, it is well-demonstrated that monkeys and apes follow the gaze of their conspecifics. Despite this evidence, there is a widespread contemporary belief that apes have difficulty with RJA.

**The Object Choice Task.** One experimental paradigm that measures an individual's capacity with regard to RJA is the Object Choice Task (OCT). The OCT involves an experimenter baiting one of (usually) two or three opaque containers out of view of the subject, and then presenting a deictic cue, typically a gaze or pointing cue, to indicate to the subject in which of the containers the bait is located. Human infants are successful at following pointing cues from around 12 months of age (Behne et al. 2012) and gaze cues from around 14 months of age (Behne et al. 2005). OCT studies with nonhuman subjects have demonstrated that individuals from a number of species demonstrate an ability to follow pointing cues, including domestic pigs, African elephants, domestic goats, and bottle-nosed dolphins, although animals' sensitivity to gaze cues is, at present, far more variable, both within and between species. Many studies have shown domestic dogs to be adept at passing the OCT, and this has led some authors to propose a theory

of convergent evolution between humans and dogs that has equipped the latter with specialized socio-cognitive skills in comprehending human communicative cues (Hare and Tomasello 2004). In contrast, nonhuman primates' frequent poor performance on the task has led to the propagation of theories of a human-unique ability to comprehend deictic cues within the primates that led to the emergence of verbal communication in our species (Herrmann et al. 2007), which appears to conflict with findings of some nonhuman primates successfully passing the OCT under some conditions (Mulcahy and Call 2009; Lyn 2010).

Miklósi and Soproni (2006) highlighted the variation in procedural aspects of the OCT, for example, the range of different pointing cues that are presented across species, and demonstrate that such differences can elicit differing levels of performance from individuals of the same species. Specifically, their review demonstrated that the distance and temporal properties of pointing cues appear to either facilitate or constrain comprehension in a number of species. For example, great apes tested with a *static* point, where the experimenter is in the pointing position prior to the subject entering the test room and remains so until the subject has chosen one of the containers, performed at almost ceiling level when the distance between the experimenter's fingertip and the baited container was minimal, with a majority of below-chance performances when this distance was greater than 50 cm. It has further been suggested that disparities in the literature with regard to the performance of nonhuman primates could be better explained by methodological and procedural inconsistencies than by species-level ability. Lyn (2010) suggested that the apparent failure of nonhuman primates to comprehend human declarative cues on the OCT is not due to their evolutionary history, but may in fact be attributed to the tendency in the current literature to disregard environmental factors, specifically rearing history, in the experimental samples. Considering that RJA capacity is a developmental process in human infants that emerges following an intensive period of interaction and engagement with human adults, with frequent exposure to deictic cues, it is important to consider nonhuman

subjects' experiential history with humans before drawing species-wide conclusions about ability based on evolutionarily adaptive explanations. Illustration of this point comes from Lyn et al. (2010) findings that apes raised in an environment rich in human interaction with intensive exposure to sociolinguistic engagement (so-called enculturated apes) significantly outperformed on the OCT apes raised in a more impoverished, institutional environment where interaction with humans was limited to daily husbandry tasks.

Mulcahy and Hedge (2012) highlighted further procedural inconsistencies in the OCT literature, noting that apes are typically tested with a *central* version of the task, in which the containers are in the direct line of vision of the subject, compared with a number of other species, including domestic dogs, who tend to be tested with a *peripheral* version, in which the containers are placed widely apart. They argued that in the *central* version, the salience of the containers, in which the subject is aware that a food reward is hidden, may override the salience of the cue presented, and this, combined with an increased implied effort in retrieving the reward in the *peripheral* version may inadvertently disadvantage the apes. In fact, the authors report that in the minority of studies in which apes are tested with a *peripheral* version, their performance levels are greatly increased. It is thus important to take into account these incommensurate sampling and testing protocols when discussing species' relative abilities with regard to RJA. As Leavens and Racine (2009) noted, "[b]ecause so many apes . . . clearly do follow pointing gestures, *given adequate experience*, failures to follow pointing are not diagnostic of any cognitive implication beyond a lack of either motivation or sufficient task-relevant experience to use the gesture" (pp. 254–255, fn. 5, emphasis in original). Table 1 lists 43 individual great apes who have passed the OCT.

## Initiating Joint Attention (IJA)

IJA is defined as pointing to "comment" or to "inform" another about the state of the world. In the original formulation of IJA in human children,

Bates and her colleagues (1975) described a developmental sequence of exhibition of self, offering objects to another, giving objects to another, and, finally, pointing to objects in apparent attempts to elicit infant-directed emotional engagement. Viewed in this way, exhibition of self is a commonplace behavior in both captive and wild great apes. For example, chimpanzees will overtly offer part of their body to another seeking tickles or grooming at that site (Bard et al. 2014). Wild chimpanzees have been reported to scratch at the site on their own bodies at which they seek to have another chimpanzee concentrate its grooming activities (Pika and Mitani 2006). Great apes exhibit frequent "displays" that seem to function to draw attention to the self; from the standpoint of the exhibition of self, it seems clear that this aspect of IJA, presentation of oneself to others, is widely shared among great apes (reviewed by Leavens and Racine 2009).

However, the use of pointing to direct attention to a distal event or entity of interest is less frequently observed in humans' nearest living relatives, the great apes. Notably, however, the two existing reports of pointing by wild apes (a bonobo, Veà and Sabater-Pi 1998, and a chimpanzee, Hobaiter et al. 2014) described pointing as part of a sequence of IJA. In the report by Veà & Sabater-Pi, a bonobo noticed the observers behind some foliage and pointed twice at the humans, while looking back and forth between the observers and the rest of his troop. Hobaiter et al. reported that a juvenile chimpanzee seemed startled by something after peering into Hobaiter's camera lens, then retreated rapidly towards her mother, pointing towards the camera while turning to look at her mother. In captivity, IJA has been reported in "enculturated" apes by Carpenter et al. (1995); Pedersen et al. (2009); and Lyn et al. (2011). More generally, virtually all of the ape language training projects involve tests of language comprehension in which the animals must choose a correct response by pointing to or otherwise selecting the correct referent ("X") when challenged with a question of the form, "Where is X?" (reviewed by Leavens and Bard 2011). These kinds of informative gestures are usually

**Joint Attention, Table 1** Great apes who have been reported to pass Object Choice Tasks<sup>a</sup>, demonstrating the capacity for Responding to Joint Attention (RJA)

| Species                                       |                               |
|-----------------------------------------------|-------------------------------|
| Name                                          | Source                        |
| <b>Chimpanzees (<i>Pan troglodytes</i>)</b>   |                               |
| Darrell, Sheba, Kermit, and Sarah             | Povinelli et al. (1990, 1992) |
| Pendesa and Pana                              | Itakura and Tanaka (1998)     |
| Travis, Erika, and Peony                      | Itakura et al. (1999)         |
| Candy, Brandy, Megan, Apollo,                 |                               |
| Kara, Jadine, and Mindy                       | Povinelli et al. (1999)       |
| Annette, Fifi, Sandra, Alex,                  |                               |
| Alexandra, Jahaga, Dorien, and                |                               |
| Frodo                                         | Mulcahy and Call (2009)       |
| David, Lana, Mercury, Sherman,                |                               |
| and Panzee                                    | Lyn et al. (2010)             |
| <b>Bonobos (<i>Pan paniscus</i>)</b>          |                               |
| Limbuko, Kuno, and Joey                       | Mulcahy and Call (2009)       |
| Elikya, Panbanisha, Kanzi,                    |                               |
| Matata, and Nyota                             | Lyn et al. (2010)             |
| <b>Gorillas (<i>Gorilla gorilla</i> spp.)</b> |                               |
| Cola, Caroline, Zoe, and Dian                 | Peignot and Anderson (1999)   |
| <b>Orangutans (<i>Pongo</i> sp.)</b>          |                               |
| Chantek                                       | Tomasello et al. (1997)       |
| Sakura                                        | Itakura and Tanaka (1998)     |

<sup>a</sup>Note that considerable variation occurs between studies in procedures administered (Lyn 2010; Mulcahy and Hedge 2012) and often multiple cue conditions are administered within a given study; individuals named have passed some version of an OCT, but not necessarily discriminated all cue types provided to them

classified as examples of IJA when human children display them, but apparently not when animals perform informative actions (e.g., Carpenter and Call 2013). This double-standard of interpretation may contribute towards biased perceptions of the distribution of IJA among humans and their nearest living relatives, although few would

dispute that most humans, barring psychopathology, engage in joint attention at frequencies not matched in other great ape species. Thus, while humans may not uniquely display joint attention, they may display joint attention relatively more frequently than even language-trained or home-raised apes.

Conclusions

With respect to IBR, there is widespread agreement that great apes and other animals display this component of joint attention (Leavens and Racine 2009). Surprisingly, despite the high performances on the OCT by the dozens of apes listed in Table 1, there are numerous contemporary claims to the effect that great apes have difficulty with RJA (e.g., MacLean 2016); in fact, this is not consistent with the evidence, which suggests that apes have no particular difficulty in understanding communicative cues when they are given adequate experience with these signals (Leavens 2014, and see Table 1). Evidence for IJA in animals remains somewhat controversial; when such actions as exhibition of self are included in the definition of IJA, then there is substantial evidence that great apes display IJA in this sense, both in captivity and in the wild. Evidence for the use of pointing or other deictic gestures to draw attention to some distal entity, without also requesting it, is substantially more limited, but not nonexistent. Hence, every one of the components of joint attention typically studied in human children (IBR, RJA, IJA) has been displayed by great apes and other animals.

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## Joint Visual Attention

### ► Joint Attention

## Jonathon Crystal

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## Introduction

The objective of work in the laboratory of Jonathon Crystal is to develop animal models of memory, focusing on the types of memory that are impaired in human diseases. This work involves development of a range of models to evaluate elements of human memory in animals. For example, a number of techniques for evaluating cognition in rats have been developed, including binding of episodic memories (Crystal and Smith 2014), prospective memory (Wilson et al. 2013), what-where-when memory (Babb and Crystal 2006; Zhou and Crystal 2009), source memory (Crystal et al. 2013a), and retrieval

practice (Crystal et al. 2013b). These models can be applied to translational models of human diseases of memory, such as Alzheimer's disease.

## Biographical Information and Career History

Crystal was born and raised in Toronto, Ontario. He was an undergraduate at the University of Toronto, where he was fortunate to have two outstanding mentors, Ken Cheng and Sara J. Shettleworth. He spent almost 3 years in Ken's lab and a year in Sara's lab. He was also fortunate to publish articles with Ken (in 1993 in the *Journal of Experimental Psychology: Animal Behavior Processes*) and Sara (in 1994 in *Animal Learning & Behavior*), based on research he conducted as an undergraduate (including an honor's thesis conducted in Sara's lab). The Natural Sciences and Engineering Research Council of Canada (NSERC) provided Undergraduate Research Awards, which allowed him to spend three summers in the lab at "1 Spadina" (where Ken and Sara had their labs). The environment at 1 Spadina was outstanding for animal behavior and cognition (in addition to Ken and Sara, others included Jerry Hogan, David Sherry, and their grad students). Dave Brodbeck and Rob Hampton (grad students at 1 Spadina) were particularly influential for Crystal. Crystal received a Bachelor of Science degree from Toronto in 1992.

Crystal became interested in time perception from immersion in Ken's lab and courses offered by Sara and Ken. This interest led Crystal to attend Brown University for grad school and to work in the laboratory of Russell M. Church beginning in 1992. Crystal was fortunate to have Russ as an outstanding mentor in science, academics, and life. At Brown, Crystal focused on testing the hypothesis that timing is based on multiple endogenous oscillators. Crystal received 4 years of support from NSERC as a 1967 Science and Engineering Scholar at Brown. At Brown, he met his future wife, Andrea Hohmann, who was also a grad student in psychology. They were married in Providence RI in 1997. Crystal

received from Brown a Master's of Science in 1994 and a PhD in 1997. Part of Crystal's dissertation research was recognized by the New Investigator Research Award in Experimental Psychology (in 2000, from the American Psychological Association, Division 3).

In 1997, Crystal became an assistant professor of psychology at the College of William & Mary. In 1999, Crystal moved to the University of Georgia, where he and Andrea both took positions as assistant professors of psychology. In 2004, Crystal was promoted to associate professor, and in 2009 he was promoted to full professor. In 2010, Crystal and Hohmann moved to Indiana University, Department of Psychological & Brain Sciences. Other affiliations at Indiana University include the Program in Neuroscience, the Cognitive Science Program, and the Center for the Integrative Study of Animal Behavior. In 2013, Crystal became the Director of the Program in Neuroscience, a position that ends in 2018.

Crystal has served in a number of editorial roles. In 2016, Crystal became the Editor-in-Chief of *Learning & Behavior*, a position that ends in 2019. Earlier, he served as an Associate Editor of *Learning & Behavior* (2007–2015) and an Associate Editor of *Behavioural Processes* (2003–2007). Service on editorial boards include *Animal Cognition*, *Journal of Experimental Psychology: Animal Learning and Cognition*, *International Journal of Comparative Psychology*, *Comparative Cognition & Behavior Reviews*, and *Behavioural Processes*. Crystal was fortunate to serve as the Guest Editor of special issues of *Behavioral Processes* in honor of Russ Church (in 2007) and Tony Wright (in 2010, co-edited with Jeff Katz).

Crystal has also served in a number of leadership positions. In 2017, he serves as the President of the Society for Experimental Psychology and Cognitive Science (Division 3 of the American Psychological Association, a position that ends in 2018). He has a long-standing connection to the Comparative Cognition Society (President: 2010–2012. Secretary: 2006–2010. Executive committee member: since 2006. A founding member in 1999).

Crystal is a Fellow of the American Psychological Association (Division 3 in 2006 and Division 6 in 2011), the Association of Psychological Science (2007), the Psychonomic Society (2014), and the Eastern Psychological Association (2013).

## Contributions to Science

Crystal has made a number of contributions to science, as outlined below. A complete list of publications can be found at the National Library of Medicine:

<http://www.ncbi.nlm.nih.gov/sites/myncbi/jonathon.crystal.1/bibliography/40423670/public/?sort=date&direction=ascending>

## Animal Model of What-Where-when Memory

The Crystal lab developed and validated a rodent model of what-where-when memory. The field of research into episodic memory in nonhumans began with a prominent paper in *Nature* by Nicky Clayton and Tony Dickinson (using food-storing scrub jays) in 1998. Although a number of labs were initially unable to develop an analogue using other species (papers in 2002–2005), the Crystal lab developed a working model in rats (Babb and Crystal 2005, 2006). A major alternative to episodic memory (focusing on judgments of relative familiarity) was published in *Science* by Bill Roberts in 2008. The Crystal lab developed an approach to eliminate the relative familiarity alternative explanation, which was published in *PNAS* (Zhou and Crystal 2009). Subsequent work has used this later approach to the problem of familiarity. Although the question of episodic memory in nonhumans was initially controversial, this body of work is now widely accepted. The approach taken by the Crystal lab focuses on the content of episodic memory, not on any subjective experiences that are thought to accompany episodic memory in people.

## Animal Model of Source Memory

The Crystal lab developed the first evidence of source memory in a nonhuman (Crystal et al. 2013a). Source memory refers to memories about the conditions under which information was acquired. Episodic memory typically involves source memory because those memories focus on the origin of representations. Importantly, source memory allows us to differentiate one episodic memory from another because source memory includes features that were present when the memory was formed. This model has been validated and used to demonstrate that episodic memories are bound by the source features encoded with the episode (Crystal and Smith 2014).

## Animal Model of Prospective Memory

The Crystal lab developed the first evidence for prospective memory in a nonhuman (Wilson and Crystal 2012; Wilson et al. 2013). Prospective memory is the ability to remember to take some action in the future. Failure of prospective memory is a common feature of aging and negatively impacts both health and independence. Currently, the only other working model of prospective memory in nonhumans comes from research with nonhuman primates.

## Other Models of Memory

The Crystal lab developed a number of other animal models of memory. These models are integrative as research seeks to identify the elements of human memory that can be modeled in nonhumans. Compelling evidence for episodic memory in nonhumans comes from the demonstration that rats can answer an unexpected question after incidentally encoding information, an ability that requires a functioning hippocampus (Zhou et al. 2012). The Crystal lab showed that rats use episodic memory to remember multiple events (at least 30 items in context; Panoz-Brown et al.

2016). The Crystal lab also developed the first evidence for retrieval practice in a nonhuman (Crystal et al. 2013b) and independent working memory buffers (Bratch et al. 2016). Previously, the Crystal lab developed methods to assess meta-cognition in rats (Foote and Crystal 2007).

## Contributions to Timing Literature

Crystal's early work focused on testing the hypothesis that timing is based on multiple endogenous oscillators. This work integrated approaches from chronobiology with techniques from interval timing. This research program provided evidence that short-interval timing is based on endogenous oscillators with short periods (extending the reach of chronobiology) and that long intervals (below the limited range of circadian entrainment) can be timed (extending the reach of scalar timing into the range of hours, e.g., 3–16 h) (Crystal 2012).

## Collaborators

In addition to the influence of mentors (Cheng, Shettleworth, and Church), Crystal has been fortunate to have a range of other collaborators. He has benefited from talented graduate students (Matt Pizzo, Stephanie Babb, Allison Foote, Wenyi Zhou, George Wilson, Xan Smith, and Danielle Panoz-Brown) and undergrads (Aaron Ketzenberger, Xan Smith, Stefan Dalecki, and Alex Bratch). His lab has benefited from a small army of undergrads who have enabled the lab to explore memory using olfactory stimuli, many of whom are coauthors on papers from the lab (Bratch et al. 2016; Panoz-Brown et al. 2016). Collaborators at the University of Georgia include Ruth Furukawa, Marcus Fechheimer, and John Wagner, who provided opportunities to explore cognition in transgenic mouse models of Alzheimer's disease. Frequent collaborations with the Hohmann lab have opened outstanding new opportunities too numerous to list.

## Cross-References

- [Biological Rhythms](#)
- [Circadian Rhythms](#)
- [Comparative Cognition](#)
- [Endogenous Oscillations](#)
- [Episodic Memory](#)
- [Interval Timing](#)
- [Memory](#)
- [Meta-Cognition](#)
- [Prospective Memory](#)
- [Sara Shettleworth](#)
- [Timing](#)
- [Working Memory](#)

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## Josep Call

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## Synonyms

[Cognition](#); [Comparative psychology](#); [Great apes](#);  
[Max Planck Institute for Evolutionary Anthropology](#);  
[Nonhuman primates](#); [University of St. Andrews](#);  
[Wolfgang Köhler Primate Research Center](#)

## Curriculum Vitae

Josep Call was born in Barcelona, Spain, and started to study psychology in 1986, with the aim to become a comparative psychologist and primatologist. After receiving his bachelor's degree in 1990 from the Universitat Autònoma de Barcelona, he moved to Emory University, Atlanta, USA, where he received a master's degree in psychology in 1995. Only 2 years later, in 1997, he finished his PhD on "The understanding of intentions and knowledge in orangutans, chimpanzees, and human children.

A comparative and developmental perspective” under the supervision of Prof. Michael Tomasello. He then started a lecturer position at the School of Biological Sciences at the University of Liverpool. In 1999, he moved to Leipzig, Germany, to work as a scientist at the newly founded Max Planck Institute for Evolutionary Anthropology in the Department of Developmental and Comparative Psychology. Together with Michael Tomasello, he established the associated Wolfgang Köhler Primate Research Center at the Zoo Leipzig and shortly after became the director of this center. In this unique research facility, which Josep Call and his colleagues designed especially for noninvasive behavioral studies with four species of nonhuman great apes (western lowland gorillas, Sumatran orangutans, bonobos, chimpanzees), he played a significant role in planning, conducting, and coordinating a range of research activities with nonhuman great apes. Since 2013, he is a professor in Evolutionary Origins of Mind at the School of Psychology and Neuroscience at the University of St Andrews, UK, where he is involved in establishing the Budongo Research Unit for chimpanzees at the Edinburgh Zoo.

Josep Call was the editor of the *Journal of Comparative Psychology* (2011-2017) and is member of numerous editorial boards of journals such as *Frontiers in Comparative Psychology*, *Primates*, *International Journal of Comparative Psychology*, *Learning and Behavior*, *Cognition*, and *Open Mind*. Furthermore, he is a member of the scientific committee of the Fyssen Foundation.

## Scientific Achievements

Josep Call is a comparative psychologist dedicated to exploring the cognitive skills and cultural processes of humans and other great apes to disentangle which of those are unique to the human species and which are shared with the other primates. His theoretical, empirical, and methodological contributions, groundbreaking findings, and numerous frequently cited publications have shaped the field of comparative psychology and our knowledge about the cognitive skills of other

primates. While he initially focused on nonhuman primates, he got increasingly less taxonomically centered and, in addition to great apes and human children, became interested in studying other non-primate species. With his enthusiasm for comparative psychology, he has nurtured a new generation of young scientists who continue to distribute his spirit and share the fascination for the cognitive skills of human and other animals.

His research has influenced different fields within psychology and the cognitive sciences, but also receives attention from the natural (e.g., biology) and social sciences (e.g., economics), as well as from engineering (robotics, artificial intelligence). According to Google Scholar January 2018, his work was cited almost 33,000 times, with approximately 2500–3000 annual citations, resulting in the h-index of 87 and the i10-index of 259. He has published almost 300 peer-reviewed articles, more than 40 book chapters, and several books (e.g., Call and Tomasello 2007; Call et al. 2017), including the seminal book *Primate Cognition* (Tomasello and Call 1997), which represents a milestone in the field of comparative cognition research and is still used as introductory literature and textbook for interested students and researchers.

From a theoretical perspective, Josep Call has enormously influenced the field of comparative cognition by proposing a new theory of primate cognition questioning the role of associative learning (Tomasello and Call 1997) and developing a revised view of theory of mind abilities in nonhuman primates (Call and Tomasello 2008). In addition he contributed to the development of the cultural intelligence hypothesis (Tomasello et al. 2005). Josep Call further invented new methods and tests to investigate, for example, metacognition, inferential reasoning, and inhibitory control in nonhuman animals, which were often applied for large-scale taxonomic comparisons (Call 2006; Amici et al. 2008). His signature papers report discoveries that have shaped the field of comparative cognition and inspired new lines of investigation. Among many others, his key findings are that dogs can learn verbal labels for objects by fast mapping (Kaminski et al. 2004) and that apes save tools for future use (Mulcahy



and Call 2006) and have robust long-term memories (Martin-Ordas et al. 2013). Only more recently, he achieved another breakthrough by demonstrating that nonhuman great apes can predict others' actions based on their goals and beliefs (Krupenye et al. 2016).

Josep Call has received several awards and acknowledgments for his research activities. Between 2005 and 2006, he was Fellow at the Zentrum für interdisziplinäre Forschung, Universität Bielefeld in Germany. Currently, he is Fellow of the American Psychological Association, USA (since 2013), and of the Cognitive Science Society (since 2015). In 2016, he has been elected Corresponding Fellow at the Royal Society of Edinburgh, which singled him out as being “one of the top scientists in the world in the field”, “involved in the highest calibre of scientific enquiry.”

## Cross-References

- [Catarrhine Cognition](#)
- [Catarrhine Communication](#)
- [Cognition](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Episodic Memory](#)
- [Evolution](#)
- [Intelligence](#)
- [Long-Term Memory](#)
- [Meta-cognition](#)
- [Michael Tomasello](#)
- [Object-Choice Test](#)
- [Ontogeny](#)
- [Phylogeny](#)
- [Primate Cognition](#)
- [Primate Communication](#)
- [Primates](#)
- [Theory of Mind](#)

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## Journey

- [Migration](#)
- [Safari](#)

## Joystick

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A joystick is any manner of computer hardware peripheral in which spatial deflections of a narrow cylinder cause accompanying, preprogrammed manipulations to stimuli on a connected

computer. Using a joystick, an experimentally savvy animal can navigate through [virtual] space, categorize stimuli, make decisions, and otherwise participate in any number of computerized cognitive-behavioral research tasks (Washburn et al. 1989).

By the 1980s in the United States, the relative availability and utility of home computers and gaming systems had made feasible psychological testing apparatus more complex than the operant levers and button boxes of experimental psychology's earlier history. However, although the experimental rigor afforded by home computers was equivalently useful to researchers of both human and animal psychologies, the mouse and keyboard apparatus that became standardized for use with the new technology was hyper-specified for human hands and brains. Adaptation of joystick technologies from the computer game industry for trained nonhuman animals allowed them to interface with the new technology and any software a creative psychologist could program. Some joystick-based apparatus, like the Language Research Center – Computerized Testing System that innovated the use of such technologies in comparative psychology, have seen use in hundreds of unique experimental designs (Richardson et al. 1990).

Joystick apparatus are most fruitfully used by animals with dexterous wrists and fingers and forward-facing eyes. Common species in the history of laboratory-based primate research, like chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo pygmaeus*), rhesus macaques (*Macaca mulatta*), and capuchin monkeys (genus *Sapajus*), have each proven prolific users of joysticks, as have some unexpected species such as rats and elephants (Hyatt 2013; Washburn et al. 2004). And, the use of joysticks fundamentally changed how primate cognition was viewed as the adaptation of computer testing was as profound a change as had been development of other apparatus such as the Wisconsin General Test Apparatus (Washburn et al. 2013).

In the past 10 years, touchscreens and tablets have become available to consumers to such degree that they now occupy much the same comparative testing niche that joysticks historically

have. Joysticks are less expensive, if only because the computer display and core components can be protected separately from the response apparatus. Joysticks also offer flexibility of response that is more easily attained by some animals (via the array of quick or sustained deflections that can be tracked at an arbitrary degree of precision) than the more motorically demanding taps, pinches, and swipes that touchscreens require. These advantages come at the cost of a steeper learning curve for both animal and psychologist, because the animal must first be trained with the joysticks and some programming skill will invariably be required of the psychologist for even the simplest of joystick/computer interactions. Joysticks also perhaps require an additional representational feat: an animal presented with a touchscreen need not understand the spatially discontinuous relationship between a floating stick in the hand and a set of pixels shaped like an insect on a nearby computer monitor, it just has to tap the bug! Joysticks, however, require overcoming the stimulus-response discontinuity problem that was a major limitation in early behavioral research using manual apparatus (McClearn and Harlow 1954; Murphy and Miller 1958; Stollnitz and Schrier 1962). However, with time and experience, numerous species learn to handle this discontinuity using joystick technology (e.g., Beran et al. 2007; Rumbaugh et al. 1989).

Just as operant chambers continue to exist alongside their would-be replacements, joysticks will likely continue to be used on their own merit and alongside touchscreens and other emerging apparatus into the future. Joysticks remain the superior response apparatus for tasks in which a high degree of response sensitivity is at a premium, like some mazes. In designs in which the entire suite of behaviors an animal produces during a trial can offer unique psychological insights, like mazes or metacognitive uncertainty tasks, joysticks are uniquely valuable in that hesitations and suboptimal responses are captured continuously. Even several decades after their initial adoption in comparative psychology, joysticks retain some unique strengths and untapped potential for furthering the study of animal cognition.

## Cross-References

- [Computerized Testing Paradigm in Primates](#)
- [David Washburn](#)
- [Duane Rumbaugh](#)
- [Harry Harlow](#)
- [Wisconsin General Test Apparatus](#)

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## Judgment Bias

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## Synonyms

[Active choice judgment](#); [Ambiguous cue interpretation](#); [Interpretation bias](#); [Operant cognitive bias](#); [Response bias](#)

All in combination with the terms task, test, or paradigm.

## Definition

There are numerous operational definitions of judgment bias. Combining definitions of Boleij et al. (2012) and Bateson and Nettle (2015), judgment bias is defined as follows (Roelofs et al. 2016, p. 2): A judgment bias is a relative reaction to an ambiguous stimulus, expressing an “interpretation” of this stimulus and an “expectation” of the consequences of the reaction (Boleij et al. 2012). In judgment bias tasks, “(...) animals that respond to the ambiguous stimuli similarly to the positive stimulus are interpreted as displaying a high expectation of reward in the presence of ambiguous information, and hence an ‘optimistic’ cognitive style indicative of a positive affective state. In contrast, animals that respond to the ambiguous stimuli similarly to the negative stimulus are interpreted as displaying a higher expectation of punishment or lower expectation of reward, and hence a more ‘pessimistic’ cognitive style

indicative of a more negative affective state” (Bateson and Nettle 2015, p. 3).

## Introduction

In its simplest explanation, judgment bias describes optimistic and pessimistic decisions made under ambiguity. It is a bias in the judgment of ambiguous information, influenced by emotional state. Thereby, ambiguous stimuli, which are not inherently positive or negative (i.e., which are affectively neutral), are interpreted in light of a current emotional state or mood. A negative emotional state, such as anxiety or depression, increases the likelihood of making a negative or pessimistic judgment of an ambiguous stimulus. A positive emotional state increases the likelihood of making a positive or optimistic judgment of an ambiguous stimulus.

Judgment bias is a form of cognitive bias, where emotional state influences cognitive processes (Mendl et al. 2009; Paul et al. 2005). Multiple cognitive processes are required for judgment bias to occur: a stimulus has to be registered by a sensory system, it has to be evaluated, and a response to the stimulus has to be decided on (Bateson 2016). It is as of yet unknown which of these components of decision-making under ambiguity are influenced by emotional state. That the process of decision-making under ambiguity as a whole is indeed influenced by emotional state has been shown by the many accounts of judgment bias following experimental manipulation of emotional state in both humans and animals.

## Measuring Judgment Bias in Animals

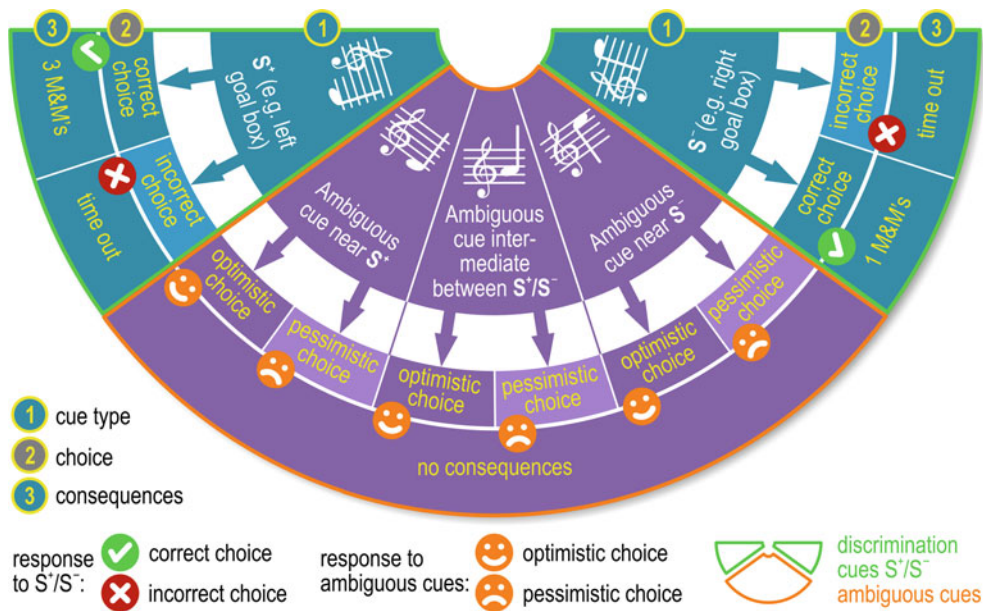
To measure judgment bias in an animal, it has to display a measurable expectation of either a relatively positive or a relatively negative outcome in response to an ambiguous stimulus. To achieve this, judgment bias paradigms for animals all contain several key elements (see Fig. 1). Animals are trained to discriminate between two reference stimuli, predicting either a positive or a negative outcome. The animal is trained to perform a

distinct behavior in response to each stimulus. After discrimination training, the animal is presented with ambiguous stimuli. Its responses to these stimuli can be interpreted as a measure of judgment bias. Harding et al. (2004) were the first to successfully apply such a paradigm to animals, using it to measure judgment bias in rats.

## Discrimination Training

During operant discrimination training, the animal learns to discriminate between a positive and a negative reference cue/stimulus. The animal will learn to associate the positive reference cue with a specific behavioral response and a positive outcome. The same goes for an association between a negative reference cue, a negative outcome, and another behavioral response. Reference cues used can be spatial (e.g., access to left or right arm of a radial arm maze), visual (e.g., different levels of color saturation), auditory (e.g., high- and low-frequency tones), olfactory (e.g., different odors), or tactile (e.g., coarse and fine sandpaper).

When training an animal to respond to these reference cues, either a go/no-go task or an active choice task can be used. In a go/no-go task, the animal has to perform a behavioral response when presented with the positive reference cue. When presented with the negative reference cue, this behavioral response has to be suppressed. For example, when the animal is presented with the positive cue, it has to approach a goal box to collect a food reward. When it is presented with the negative cue, approaching the goal box will result in a punishment. The distinction between a “go” response and a “no-go” response can be made by using a cut-off point, i.e., if an animal does not respond to the cue within a predetermined time period that starts with presenting the cue, a “no-go” response is scored. If it does respond within that period, a “go” response is scored. Alternatively, “no-go” responses can be distinguished from “go” responses when analysis of response latencies shows that the animal takes significantly longer to respond to the negative cue than to the positive cue. In an active choice task, an active behavioral response is required after both the positive and the negative reference cue. For example, when the animal is presented with



**Judgment Bias, Fig. 1** Example of a judgment bias test paradigm. The animal is trained to associate a positive reference stimulus/cue ( $S^+$ ) with a positive outcome and a specific behavioral response, and a negative reference stimulus/cue ( $S^-$ ) with a negative outcome and another specific behavioral response. During judgment bias testing, the animal's response to ambiguous stimuli is assessed. Here, reference stimuli used are auditory (1). A low-frequency tone predicts a large food reward (three chocolate candies) in a designated location (e.g., the left of two goal boxes). A high-frequency tone predicts a small food reward (one candy) in another designated location (e.g., the right of two goal boxes). During discrimination training, a correct response to a reference cue (approaching the appropriate goal box) is rewarded, while failing to show the correct response is punished by giving the animal a time

out and no food reward (2). After discrimination training, ambiguous stimuli that are intermediate between the reference cues are presented (here, tones of intermediate frequencies between  $S^+$  and  $S^-$ ). When the animal performs the behavioral response it associates with a positive outcome (approaching the left goal box), this is scored as an optimistic choice (2). When the animal performs the behavioral response it associates with a negative outcome (approaching the right goal box), this is scored as a pessimistic choice. Abbreviations:  $S^+$ , positive reference stimulus used in operant discrimination training preceding judgment bias testing, predicting a positive consequence;  $S^-$ , negative reference stimulus used in operant discrimination training preceding judgment bias testing, predicting a negative consequence

the positive cue, it has to push one of two available levers to gain access to a food reward. When it is presented with the negative cue, it has to press the other lever to avoid punishment. In contrast to go/no-go tasks, active choice paradigms allow the animal to refrain from choosing if it is unmotivated to do so. In go/no-go tasks, decreased motivation is always confounded with pessimistic choosing. When the animal does not respond, this is scored as a “no-go” instead of an omission.

To produce positive and negative associations with the reference cues, two possible reinforcement designs can be used:

1. Correct responses to the positive reference cue are rewarded, while incorrect responses to the negative reference cue are punished. The animal is trained to obtain a reward during positive trials and to avoid receiving punishment during negative trials. For example, in a go/no-go design, approaching the goal location is rewarded during positive trials, while negative trials should consist of a no-go response. Should the animal erroneously approach during a negative trial, it will be punished by exposure to a frightening stimulus (e.g., a loud noise).
2. Correct responses to the positive reference cue are rewarded with a highly preferred reward



(e.g., a large food reward in Fig. 1), while correct responses to the negative reference cue are rewarded with a less preferred reward (e.g., a smaller food reward in Fig. 1). The animal is trained to obtain rewards of different value during positive and negative trials. Incorrect performance leads to losing a chance of being rewarded. For example, in an active choice design, pressing one lever is required to obtain a reward during positive trials, while pressing another lever during negative trials will result in a less favorable reward (e.g., a smaller amount of food or a delayed reward).

Both reinforcement designs can be applied to either go/no-go or active choice paradigms. Over the course of multiple trials, animals are trained on the operant discrimination task. A predefined learning criterion is used to determine when discrimination training has been successful. For example, an animal can only proceed to judgment bias testing when it responds correctly to both the positive and the negative reference cue in 80% of its daily training trials.

### Judgment Bias Testing

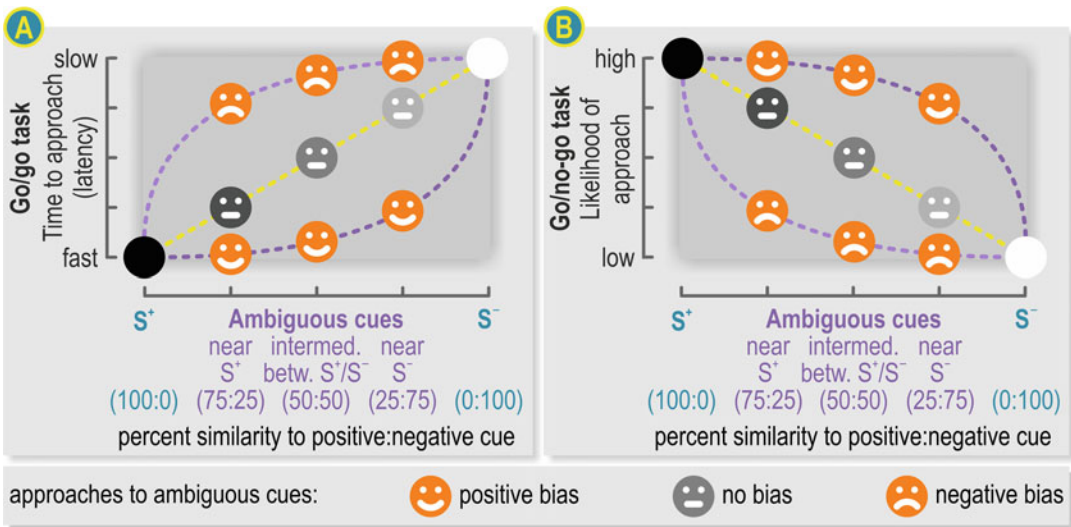
Judgment bias testing can commence when an animal has successfully completed discrimination training. During judgment bias testing, ambiguous stimuli are introduced which are intermediate between the reference cues used during discrimination training. For example, when using a high- and low-frequency tone as reference cues, tones of intermediate frequencies can be used as ambiguous stimuli (Fig. 1). Often, multiple ambiguous stimuli are used, with varying levels of ambiguity. In addition to one ambiguous stimulus which is truly intermediate between the reference cues, “near-positive” and “near-negative” ambiguous stimuli can be presented, which have an increased similarity to the positive/negative reference cue. When presented with an ambiguous stimulus, the animal has to decide whether it considers this cue to be a predictor of the learned positive or negative outcome. Judgment bias can then be measured by recording the animal’s behavioral responses to the ambiguous cues. An animal can make an optimistic choice by performing the learned

response to the positive reference cue. A pessimistic choice can be made by performing the learned response to the negative reference cue (see Fig. 2 for examples of interpretation of go/no-go and active choice paradigms).

When an animal makes relatively more optimistic or pessimistic choices, this is taken as an indication of a more positive or negative emotional state, respectively. This is how judgment bias tasks can be used to compare (groups of) animals with assumed differences in emotional state. Similarly, the same animal(s) can be tested before and after experimental manipulation of emotional state. Judgment bias can be assessed in response to any of the ambiguous cues. In general, animals display a generalization gradient in response to the ambiguous cues, with the rate of optimistic choosing increasing as a cue’s similarity to the positive reference cue increases (Fig. 2). The shape of this response curve can differ for animals in a positive versus a negative emotional state, but also for animals experiencing different forms of negative emotions (Salmeto et al. 2011). For example, a negatively biased interpretation of the near-positive ambiguous cue indicates an animal has a decreased expectation of the positive outcome (i.e., decreased optimism). A negatively biased interpretation of the near-negative ambiguous cue indicates an animal as an increased expectation of the negative outcome (i.e., increased pessimism).

### Advantages of Judgment Bias Tasks for Animals

Judgment bias tasks for animals provide a cognitive measure of emotional state. As such, these tasks are useful in studies of animal welfare (Baciadonna and McElligott 2015; Bethell 2015) and studies using animal models of mood disorders. Measuring judgment bias can be a useful tool in assessing the effects of experimental manipulation of emotional state. For an animal welfare study, such manipulation could consist of barren versus enriched housing conditions. A biomedical study might assess the effects of mood enhancing drugs on judgment bias. An important advantage of judgment bias over other measures of animal emotion is that it provides a measure of the valence of emotional



**Judgment Bias, Fig. 2** Interpretation of judgment bias task results. Panel A: Time to approach plotted against cue type for an active choice task. Time to approach decreases as cues increase in similarity to the positive reference cue. When there is a positive judgment bias, approach times after ambiguous cue presentation will be faster compared to approach times for a negative judgment bias. Panel B: Likelihood of approach plotted against cue type for a go/no-go task. Likelihood of approach increases as cues

increase in similarity to the positive reference cue. When there is a positive judgment bias, the likelihood of approach after ambiguous cue presentation is higher than the likelihood of approach for a negative judgment bias. Note that measures of response latency and likelihood of responding can both be used in either an active choice or a go/no-go task. Abbreviations: Go/Go, active choice; S<sup>+</sup>, positive reference cue; S<sup>-</sup>, negative reference cue; intermed. betw., intermediate between

state. Other frequently used measures, such as heart rate or cortisol secretion, only provide a measure of emotional arousal. This distinction between positive and negative emotional state allows judgment bias studies to formulate clear hypotheses. Additionally, judgment bias tasks can provide a measurable indication of a positive emotional state. Such measures have been lacking in studies of animal emotion, where measures of negative emotion are much more numerous.

Another advantage of judgment bias tasks for animals is their applicability to a wide range of species. The different components of judgment bias paradigms (cues, reinforcers, and behavioral responses) can all be adjusted to suit the species to be tested. Reference and ambiguous cues can be chosen which are ecologically relevant and easily detectable. For example, a range of visual stimuli can be unsuitable for a species lacking a dependence on visual information in their everyday life. Reinforcers can be chosen which are distinguishable as positive and negative/less positive, while

having properties that are actually rewarding or aversive to the tested species. By applying such adjustments, judgment bias has now been successfully measured in species ranging from carpenter ants (d’Etorre et al. 2016) to bottlenose dolphins (Clegg et al. 2017).

### Limitations to Judgment Bias Tasks for Animals

Despite the potential of judgment bias tasks as a widely applicable test of animal emotional state, there are some limitations which have to be taken into account when designing judgment bias tasks and interpreting their results. The operant discrimination training that is required for judgment bias testing generally takes a considerable amount of time. Such extensive training can act as a form of cognitive enrichment and thereby be a confounding factor on test results. For example, the enjoyment of working for food rewards can offset any detrimental effects of experimental treatment on the animals’ emotional state.

Therefore, the training period prior to judgment bias testing can lead to a more positive emotional state than would be assumed based on experimental manipulation alone. This could lead to overestimation of effects of mood enhancing treatment, and detrimental effects of experimental treatment on emotional state could be underestimated or entirely absent from judgment bias results. To avoid a confounding influence of cognitive enrichment, the training schedule prior to judgment bias testing should be as short as possible. This can be facilitated by choosing appropriate reference cues which are easily distinguishable by the animal and requiring behavioral responses which are in the animal's natural behavioral repertoire.

During judgment bias testing, ambiguous trials are often not rewarded (Fig. 1). This can lead to animals learning to associate ambiguous cues with no reward over the course of the testing period. When this happens, ambiguous cues effectively lose their ambiguity, as they are now considered predictors of a specific (negative) outcome. Such loss of ambiguity during judgment bias testing can be another confounding factor. An association between ambiguous cues and a negative outcome (i.e., lack of reward) can lead to an increase in pessimistic choosing as judgment bias testing progresses (Doyle et al. 2010). This can lead to incorrect conclusions of a more negative emotional state. Therefore, it is important to prevent loss of ambiguity when designing a judgment bias paradigm. Most importantly, a lack of reward during judgment bias testing must not stand out as a negative outcome for the animals. This can be achieved by using a partial reinforcement schedule during discrimination training, allowing animals to become accustomed to occasional unrewarded trials (Düpján et al. 2017). To maintain responsiveness in spite of a lack of reward, secondary reinforcers can be used during training and testing.

A final common limitation inherent to judgment bias tasks for animals is the use of a learning criterion for discrimination training. Because only those animals are tested which reach the pre-defined learning criterion, results of judgment bias tasks can be biased towards animals capable of completing discrimination training.

Conclusions and recommendations based on such a subset of the studied population may not be generalizable to animals which could not reach the learning criterion. The more difficult the required operant discrimination task, the more animals will be excluded and the more biased the results of the judgment bias test will be. Therefore, it is important to ensure that the operant discrimination task is suitable for the species/group which is studied and that most, if not all, animals are able to master it.

## Conclusion

Judgment bias tasks for animals provide a cognitive measure of the valence of emotional state. A positive emotional state results in an optimistic interpretation of ambiguous stimuli, while a negative emotional state results in a pessimistic interpretation of ambiguous stimuli. Although there are some limitations to judgment bias measurements in animals that need to be taken into account, judgment bias can be successfully measured in a wide range of species.

## Cross-References

- [Associative Learning](#)
- [Cognitive Bias](#)
- [Decision-Making](#)
- [Discrimination Learning](#)
- [Operant Conditioning](#)

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## Junk DNA

- Intergenic

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## Junk RNA

- Noncoding RNA

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## Justice

- Inequity Aversion

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## Juvenescence

- Insect Locomotion
- Puberty

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## Juvenile Period

- Adolescence

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## Juvenilization

- Neoteny

# K

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## Kainozoic Era

► [Cenozoic Era](#)

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## Kangaroo Method

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## Introduction

Kangaroo method of care or kangaroo mother care (KMC) is a special way of nurturing preterm and low birthweight babies (LBW) (Charpak et al. 2017). KMC was developed by a Columbian pediatrician, *Dr Edgar Ray* (Ruiz-Peláez et al. 2004).

## Components of KMC

KMC involves three components – kangaroo position (skin-to-skin contact), kangaroo nutrition (exclusive breastfeeding), and kangaroo discharge policies (early discharge in kangaroo position

regardless of weight or gestational age) (Charpak et al. 1996).

## The Need for KMC

Humans are endothermic/homeothermic animals. Temperature-regulating mechanism of human neonates, especially the premature and low birthweight ones is underdeveloped. So, these babies were usually kept in incubators to maintain their body temperature. This leads to separation of mother and baby-inducing stress in both mother and neonate leading to poor survival of the neonates and depression in mother which may later cause poor milk ejection reflex. Moreover, there is a shortage of incubators in developing countries, and KMC is a better alternative in this scenario.

## Administration of KMC

KMC can be started at birth and can be given continuously or in small sittings of not less than an hour. KMC can be given not only by the mother but also by the father or the grandparents. It should be started as earlier as possible to ensure maximum benefit for the baby.

While giving KMC the baby must be placed directly in contact with the chest, and the baby's head must be placed in between the two breasts in a frog position. The baby is held in position by a



soft fabric, and it should cover the baby until the shoulders. KMC is a skin-to-skin contact therapy; therefore there should not be any barrier between the caregiver and the child to ensure that there is a better therapeutic effect. There should be minimum or no discomfort while giving KMC. This therapy helps in enjoying the gift of motherhood for new mothers.

## Precautions During KMC

The person giving KMC must be seated in a quiet and calm environment. Parents must be preferably seated in a rocking chair wearing comfortable clothing. The parents must reduce their activity when the infant shows signs of distress, overstimulation. The caregiver must give enough time for the baby to feed and sleep without disturbance.

## Advantages of KMC

Due to constant skin-to-skin contact, KMC helps in constant thermal regulation and prevents the neonates from hypothermia. In low birthweight infants, there is better recovery and decreased chance of infection. So, KMC reduces mortality and morbidity in low birthweight infants (Conde-Agudelo et al. 2003).

Keeping mother and newborn in constant close contact makes the initiation of breastfeeding easier. Close contact with child establishes oxytocin and prolactin release in mother leading to formation and secretion of milk. When the child is given KMC, it helps the suckling reflex of the newborn, thus establishing a positive feedback cycle ensuring enough milk production for the baby.

The mother and the baby are under constant stress when they are separated. KMC reduces the stress and ensures better development and bonding with the mother (Charpak et al. 1996). The constant skin-to-skin contact facilitates the release of oxytocin in mother, which has a calming effect on the mother, and promotes bonding and affection with the newborn. This effect is further enhanced by prolactin release in mother; it makes her sleepy and relaxed. Thus, KMC

relieves the mother of postpartum stress (Cooijmans et al. 2017).

## Cross-References

- [Feeding](#)
- [Oxytocin](#)
- [Prolactin](#)

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## Kanzi

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Kanzi is a bonobo (*Pan paniscus*) that fundamentally changed our understanding of nonhumans' capability to learn human language. The presence of language in humans and its presumed lack in all other animals had been one of the enduring assumptions of comparative psychology. The broad appeal of the presumption of the uniqueness

in human language is illustrated by centuries-old folklore from across the world about how people were given language, animals that had language, and/or people that could “talk” to animals. The assumption that language is unique to humanity was not even tested scientifically until the late 1800s (Furness 1916), but is definitely challenged by findings from Kanzi, and later participants in the studies at the Language Research Center of Georgia State University in Atlanta, Georgia.

Only since the 1960s have we successfully studied the language abilities of apes, our closest evolutionary relatives. This success was founded on the work of the Gardners (Gardner and Gardner 1969) who recognized that other efforts to teach apes to speak had failed because the focus was on verbal speech. In contrast, they trained their chimpanzee, Washoe, to use a form of American Sign Language. Later research detailed similar results with several other chimpanzees (Gardner et al. 1989) and even potential evidence of generational transmission of signing among the apes (Fouts et al. 1982). These paradigm-shifting results resulted in a wave of publications and sign language research projects with gorillas (Patterson 1978), Orangutans (Miles 1999), and other chimpanzees (Terrace 1979). Additional language projects with apes were inspired by the Gardners and included chimpanzee work with computer keyboards (Rumbaugh 1977; Savage-Rumbaugh 1986) and plastic symbols (Premack 1985). The field, however, was the focus of vicious criticism that alleged that much of the findings across all studies were founded on anthropomorphic over-interpretation and direct imitation of human caregivers by the apes (Sebeok and Rosenthal 1981; Terrace et al. 1979). The criticisms particularly focus on the idea that the apes had been trained to associate food with random “arm waving” (Pinker 1994) and that the strings of symbols produced by the apes in no way resembled syntactical sentences (Terrace et al. 1980).

## Early Findings

The bonobo language project began in the midst of this backdrop. Bonobos are very closely related to chimpanzees (in fact, they were previously

called pygmy chimpanzees), but these species have extremely different ecology and behaviors. Bonobos were considered to be potentially more intelligent, and certainly less aggressive, having a matriarchal social structure and a tendency to diffuse conflict with sexual interactions (de Waal 1989). Importantly, their physical structure was said to more closely resemble humans, leading to the hypothesis that their cognitive and communicative abilities were more human-like as well (Savage-Rumbaugh et al. 1985). In the early 1980s, the researchers at the Language Research Center borrowed Matata, an older female bonobo, from the Yerkes National Primate Research Center to take part in a language project in early 1981. Matata brought with her an adopted son, Kanzi, who was 6 months old when Matata began her training on the use of a computerized keyboard with abstract symbols (lexigrams) that represented objects, actions, and ideas (see Fig. 1). During this time, Matata was being conditioned to use the keyboard to obtain rewards, similar to the training that had taken place in previous language projects. Matata was guided to press a key on the keyboard, the English word was spoken, and the symbol lit up on a panel above the keys. Matata was then rewarded with the item she had chosen; however, Matata never consistently utilized any of the keys she was trained on (Savage-Rumbaugh 1986).

Kanzi was present for all of Matata’s training sessions, but was never the focus of the conditioning. If Kanzi used the keyboard, the caregivers would respond as they would to a human child – by speaking a response in English as well as using the keyboard. Kanzi would sometimes receive the items he requested, and other times would not. When Kanzi was 2 years old, Matata was sent back to Yerkes for breeding. The researchers prepared to begin training Kanzi. Instead, Kanzi began to use the keyboard on his own – even following up on his requests with gestures and body posturing toward the referents of the symbols he selected. He had learned the meanings of many of the keys before the first day of his training. Kanzi’s abilities were first reported in the book *Ape Language from Conditioned Response to Symbol* in which Savage-Rumbaugh et al. detailed his early learning and the novel testing



**Kanzi, Fig. 1** First page of the lexigram keyboard. The final keyboard comprised three panels of 128 symbols each. The third panel was added in the last few years of the Language Research Center study and was mostly syntactical and linking words (were, on, that, etc.). Early

versions were computerized and a key press would trigger a display of the lexigram and a repetition of the English word. Later versions were laminated paper that could be easily carried throughout the study area

paradigms that were created in order to establish his abilities scientifically (Savage-Rumbaugh 1986). His findings and those of his sister, Mulika, were then more thoroughly documented in 1986 (Savage-Rumbaugh et al. 1986). He was the first nonhuman primate to learn any aspect of human language in an observational and spontaneous manner (Hixon 1998; Sundberg 1996).

After this revelation, the researchers decided to re-think and re-invent Kanzi’s learning environment. Instead of providing incentives to Kanzi, his caretakers would simply talk to him and React to his attempts at communication as one would to a young child. When speaking to Kanzi in English, they would also activate the lexigrams that corresponded with their words, but gave no direct reinforcement. Kanzi’s language environment was expanded to the nearby 50-acre woods, in which specific foods had been placed in 17 different locations, all labeled by lexigrams (see Fig. 2). He was encouraged to use the keyboard to indicate the location he wanted to reach following demonstrations by experimenters. When the researchers would allow him, he would frequently

lead them to the location he had chosen. Kanzi also was engaged in many daily activities such as doing the laundry and preparing food – playing with toys and other bonobos, as well as games that were invented for him (a costumed bunny and gorilla that would sometimes be found in different areas of the property). While engaged all of these activities, Kanzi continued to learn and use the symbols on the keyboard appropriately.

One final surprise was in store for the researchers. As Savage-Rumbaugh et al. (1986) explain, one day a researcher mentioned that Kanzi seemed to be responding not just to the lexigrams, but to the English words that the experimenters used. Initially skeptical, Savage-Rumbaugh dismissed the accounts until one day when she mentioned the lights in the room (in English), and Kanzi immediately ran to the switch and began flicking the switch on and off (1986). Later tests confirmed that Kanzi could and did associate both the English word and the lexigram with the referent. This was the first time that nonhumans were shown to understand spoken English and the first time that nonhumans



K

**Kanzi, Fig. 2** Map of the woods locations at the LRC

had been shown to attach referential meaning to symbols without specific training. As such, Kanzi fundamentally changed the direction of the field.

### Reference

A subject frequently broached in the studies of animal language was whether they understand that symbols *refer to* external objects/actions/

locations or whether they have simply associated those symbols with getting those objects/actions/locations. To test external reference, researchers devised a double-blind testing procedure in which the symbols would be divorced from the rewards. In this procedure, Kanzi was presented a testing “booklet” – basically two boards that were hinged at the back. Testing items were arrayed on the bottom board, and the top was closed over the bottom – sandwiching the test array between the

boards. The boards were then handed to the experimenter (who did not know which items were in the test array). The experimenter would then ask Kanzi to indicate a specific item and open the booklet facing Kanzi, so he could respond by pointing to the corresponding picture or lexigram. The experimenter could ask in English – e.g., “Show me the apple” – or could show Kanzi a lexigram (or picture) above the test booklet. Kanzi, and later his sisters Mulika and Panbanisha as well as Panpanzee (a chimpanzee), scored well above average on these tests (Kanzi scored 178/185 on his first symbolic tests: 96.2% correct), indicating that they did associate the various symbols with the external objects (Savage-Rumbaugh 1986).

Further studies supported the idea that Kanzi (and the other apes who later came to the Language Research Center) had complicated knowledge of the symbols rather than the interpretation that had previously been argued – that the apes’ behavior was based on learning simple one-to-one associations between a symbol (button press, arm-wave) and an object (see Pinker 1994 for an example). An examination of the errors that the apes made on their vocabulary tests showed the same kinds of errors that humans make when speaking (Lyn 2007). Predominately categorical in nature, errors were also based on the sound of the English word, the physical representation of an object, and items that were frequently associated with each other (e.g., cereal and milk). This “web of associations” belies the idea that the symbols were nonmeaningful to the apes.

## Semantic Combinations

As there was continuing criticism regarding the syntactical abilities of apes, Savage-Rumbaugh and Lewin (1994) defined a few properties that a body of rules must meet in order to be designated as a “grammar.” The first several of these criterion are not specifically syntactic; rather they describe the semantic requirements underlying the organization of sequences. One such criterion is that each component must function independently. In

order to demonstrate this criterion, Greenfield and Savage-Rumbaugh (1993) tested whether Kanzi understood each individual word that he produced as part of a combination. Their analysis required that a word could only be considered a distinct element if it occurred spontaneously on 9 out of 10 occasions and if he responded with a corresponding behavior in 9 out of 10 subsequent occasions. As an example, if Kanzi requested a banana, he would be presented with an array of his favorite foods. Only if he then selected the banana from that array would “banana” be considered a communicative element. Eighty percent of Kanzi’s corpus met this criterion. Additionally, in other sessions, Kanzi would be asked to choose an appropriate lexigram (after hearing the English word) from an array. In these trials, the researcher was not aware of where the object was located. He successfully chose the correct lexigram in 73% percent of trials. In addition, Kanzi rarely repeated himself or produced semantically unrelated phrases, which suggests that the grammatical rules he used passed the second criterion for grammar which states that the combinations of words must be semantically related (Savage-Rumbaugh and Lewin 1994).

Another criterion for syntax is that there is a rule of relationships between two categories (Savage-Rumbaugh and Lewin 1994). In English, these rules are generally marked through word order. For example, usually the first word in a sentence is the agent of the action and the action follows as the second word – e.g., “Jim ran.” There are additional markers such as articles, prepositions, and cases, but the main syntactical rules in English are of word order. Therefore, “dog bites man” means something different than “man bites dog.” In several studies, Greenfield, Savage-Rumbaugh, and Lyn showed preferential word ordering in Kanzi and two other apes (Greenfield and Savage-Rumbaugh 1990; Lyn et al. 2011a).

In these studies, the apes’ utterances were coded into a number of semantic (as opposed to syntactic) categories: for example, agent, action, recipient, possessor. In early language learning, children’s two-word utterances most commonly fall into the categories of eight semantic combinations: agent-action, action-object, agent-object,



action-location, entity-location, possessor-possession, entity-attribute, and demonstrative-entity (Brown 1973). Seven of these relations were included in Kanzi's corpora, and 76% of his expressed relations fell into one of these categories. Other combinations included low-frequency semantic functions that did not fall into Brown's top eight semantic categories such as attribute of action. However, both still have semantic functions, they are just rarely combined. Panpanzee's (chimpanzee) and Panbanisha's (bonobo) utterances were also predominantly made up of the same semantic relation categories, with additions that were not found in Kanzi's corpora. For example, Panpanzee and Panbanisha would put an affirmative first and a goal, entity, or action second. This combination was also not copied from their caregivers, suggesting that the symbol ordering preference was created by the apes (Lyn et al. 2011a).

In those requests where both a lexigram and a gesture were included, semantic patterns were also observed. In these lexigram-gesture combinations, all three apes had a tendency to put the gesture last across a large range of semantic relations. Humans, on the other hand, most frequently put the gesture first in such combinations. Therefore, the development of this word-order strategy was independent of what had been demonstrated by their human caregivers. Word orders also varied depending on whether the phrase was produced using two gestures, as opposed to combinations of a lexigram with a gesture. For example, in action-goal combinations when only lexigrams were used, Panbanisha and Panpanzee would most frequently place the action word first (following the humans' preference), while in the lexigram-gesture combinations they would place the goal first (following Kanzi's preference). These changing preferences were characterized by Lyn et al. (2011a), as a potential proto-transformation – similar to the syntactical rules that switch word order preference depending on the sentence function (e.g., verb last, except in questions, in which case, verb first).

Both bonobos and chimpanzees combine semantic elements, but much less frequently than children. In addition, there is little evidence for

combinations based on syntactic categories (Noun vs. Verb).

## Syntactic Comprehension: Ape and Child

In a landmark study in 1993 designed to test whether apes could comprehend syntax, Kanzi's comprehension of English sentences was compared to that of a 2½ year old child, Alia (Savage-Rumbaugh et al. 1993). Alia was exposed to a very similar indoor environment to Kanzi – being raised half time at the Language Research Center, exploring the same wooded environment and using the lexigram keyboard with her mother and other experimenters. In the study, Kanzi and Alia were each presented (separately and with a double blind methodology) with several hundred English sentences and their responses to those sentences were recorded. Thirteen different request types and subtypes were presented to both (see Table 1). Each tested different semantic and syntactic capabilities.

Kanzi and Alia's success rates were similar (Kanzi was correct on 74% of blind trials, Alia on 65%). This was the first time an ape had shown language abilities that approached those of a human child. There were interesting differences in the errors made, however.

## Error Types: Alia and Kanzi

Both subjects rarely responded incorrectly to all sections of a phrase. For example, they would try to carry out an object with what they believed was the appropriate action, and in the case of those phrases with two objects, they rarely chose an incorrect object for both. The indication here is that they understood the overall structure of the sentence but not necessarily all the words. Alia exhibited more of a tendency to retrieve a variety of objects, only one of which would be the requested item. When Kanzi retrieved multiple items, it was most frequently under the circumstance where more than one of the requested object was present. When given the "announce information" sentence type, Alia would often

**Kanzi, Table 1** Sentence types for Kanzi and Alia. (Adapted from Savage-Rumbaugh and Lewin 1994)

| Type | Sentence form                                   | Example                                       |
|------|-------------------------------------------------|-----------------------------------------------|
| 1a   | Put object X in/on transportable object Y       | Put the ball on the pine needles              |
| 1b   | Put object X in nontransportable object Y       | Put the ice water in the potty                |
| 2a   | Give (or show) object X to animate A            | Give the lighter to rose                      |
| 2b   | Give object X and object Y to animate A         | Give the peas and the sweet potatoes to Kelly |
| 2c   | (Do) action A on animate A                      | Give rose a hug                               |
| 2d   | (Do) action A on animate A with object X        | Get rose with the snake                       |
| 3    | (Do) action A on object X (with object Y)       | Knife the sweet potato                        |
| 4    | Announce information                            | The surprise is hiding in the dishwasher      |
| 5a   | Take object X to location Y                     | Take the snake outdoors                       |
| 5b   | Go to location Y and get object X               | Go to the refrigerator and get a banana       |
| 5c   | Go get object X that's in location Y            | Go get the carrot that's in the microwave     |
| 6    | Make pretend animate A do action A on recipient | Make the doggie bite the snake                |
| 7    | All other sentence types                        |                                               |

state her own intent regardless of the request, which may indicate that she understood this form of phrase had a different function as the others. The most difficult types for both Alia and Kanzi were type 6 where they were requested to make a pretend animate A do an action A on a recipient Y (Savage-Rumbaugh et al. 1993).

One syntactical concept that some researchers believed was uniquely human is the ability to understand embedded sentences. To understand those phrases involves a comprehension of the fact that one word references a word previously presented in a sentence and that the second word changes the meaning of the first (Chomsky 1963). In the example “Go get the ball that’s outdoors,”

“Go get the ball” does not indicate the location in which the ball is located. When “That’s outdoors” is added, the meaning of the phrase changes to indicate the ball is located outdoors. Interestingly, however, Kanzi actually had more success in understanding these phrases, showing a success rate of 77% as opposed to Alia’s 52% (Lloyd 2004).

One argument surrounding the apes’ syntactical abilities as revealed by this study is the relative contribution of syntactical versus semantic knowledge. Researchers (e.g., Wynne 2008) argue that in many sentences, Kanzi (and Alia) could reliably complete the task with no syntactical knowledge at all. They argue that given reference (which was an earlier criticism, recall) and the words “PUT,” “KEY,” and “TABLE,” it would take no syntactical knowledge to correctly place the key on the table. There were a couple of reversible sentences in the study, on the order of “man bites dog” (e.g., “make the doggie bite the snake” (both toys) and “make the snake bite the doggie”), but these were a small proportion of the sentences tested (Wynne 2008). Evidence also does not suggest they understand embedded sentences, relative clauses, or subordinating constructions (Lyn et al. 2011a). However, a full exploration of these abilities has not been undertaken to date.

## Biology and Language

Kanzi’s abilities – and those of the other apes in the language program, have continued to re-shape the scientific understanding of what is unique about human language. For example, one of the first arguments to take shape after Kanzi spontaneously used the keyboard was that this was an ability humans shared only with bonobos. The second phase of the language project reared a bonobo (Panbanisha) and a chimpanzee (Panpanzee) together to specifically test this theory (Savage-Rumbaugh 1986). When the chimpanzee performed at a similar level to the bonobo, that myth was dismissed.

One concept that has been upheld is the concept of the critical period (early childhood) in which language is most easily learned. Two

bonobos that differed in age by only a year were compared. One (Panbanisha) was exposed to human language from the age of 7 weeks, the other (Tamuli) from the age of 3.5 years. For her infancy, Tamuli was mother-reared and only allowed contact with Panbanisha, Kanzi, and human caretakers sporadically. At 3.5 years, she was introduced to the same rearing methods as Panbanisha and Kanzi with the full range of lexigram exposure, English use, and activities. While Panbanisha and Kanzi were able to understand and use lexigrams very young in life, Tamuli did not successfully pass tests of lexigram comprehension even after her integration into the linguistically enriched environment. It seems as though, like humans, there is a critical exposure period related to the development of production and comprehension of language (Williams et al. 1997).

## Declarative Communication

Another concept put forward as the marker of human communicative uniqueness is declarative communication. It has been argued that apes only use imperative (request-based) communication, based on research studies in chimpanzees in which they failed to comprehend declarative pointing (Tomasello 2006).

One hypothesis that attempts to explain this deficit states that because chimpanzees tend to live in competitive, as opposed to cooperative, social groups, they do not respond or use declarative communication, which relies on cooperative motives. This hypothesis was tested by using an object choice task: a human would point towards one of two objects; the one that had the reward hidden inside. This object choice task was modified to compare competitive and cooperative gestures, and the chimpanzees performed better when the gesture was competitive (Hare and Tomasello 2004).

While declarative utterances were less frequent than requests, all three apes in the language program made thousands of declarative utterances (Lyn et al. 2011b). These utterances were compared directly to those of two children in the one-

word stage, and similar type of functional declaratives were found in children and apes. Apes also named objects that were already in their possession, indicating that they were not merely attempting to acquire the object (Lyn et al. 2011b).

More importantly, apes that were reared in the language environment outperformed typical research apes in the same object choice task that was used to spark the competition hypothesis (Lyn et al. 2010). It seems as if the key difference is not a biological capacity capability, but of a quantitative difference triggered by early environment – most specifically interaction with humans (Leavens and Bard 2011; Lyn 2010; Lyn et al. 2010).

## Other Skills/Studies

Kanzi has also been tested in his ability to make and use tools by anthropologists Kathy Schick and Nick Toth (e.g., Schick et al. 1999). The initial study showed that Kanzi could use a human-flaked stone knife to cut through a rope holding closed a puzzle box, with only one demonstration of a human using a similar knife. By the end of the first day, Kanzi consistently used a human-made flake of stone to cut the rope and was later able to differentiate between sharp stones and regular stones. Finally, Kanzi was given only nonshaped stones. After 25 exposures however, Kanzi was able to break apart the rock, detach a flake, and cut the cord that held the box closed. Following his first successful tool production, Kanzi formed his own tool on 15 occasions across a 75-day period. He had used both his own methods and those of his demonstrators to create the most productive method of opening the device, suggesting that bonobos were biologically capable of producing and using stone tools (Schick et al. 1999; Savage-Rumbaugh and Lewin 1994).

In 2004, Kanzi was re-located to Des Moines, Iowa, to the Great Ape Trust (also sometimes called the Iowa Primate Learning Sanctuary). He continues to be an active participant in research at the facility, since 2015 operating under the name of The Ape Cognition and Conservation Initiative (ACCI).

## Cross-References

- [Ape Cognition and Conservation Initiative \(ACCI\)](#)
- [Sue Savage-Rumbaugh](#)

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## Karen Hollis

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**Karen L. Hollis** was born on January 21, 1948, in Pittsburgh, Pennsylvania, to Norman E. Hollis, a partially self-taught industrial engineer with Screw and Bolt Corporation of America (now Ampco-Pittsburgh Corporation) and Clara Kammermeier Hollis, whose parents had immigrated to Pittsburgh from Germany. Hollis was educated in local parish schools and, inspired by a gifted mathematics teacher while in High School, a Franciscan nun, decided to enter

Slippery Rock State College (now Slippery Rock University of Pennsylvania) as a mathematics major. Although Hollis' father had taken several mathematics college courses in Pittsburgh, neither of her parents had college degrees. Indeed, her mother was the first in her family to graduate from high school. While at Slippery Rock, Hollis became greatly interested in a fledgling experimental psychology program chaired by a recent Ph.D. student of Herbert Kimmel, namely, William E. (Bill) Kirk, who mentored Hollis, convincing her to apply to graduate programs in experimental psychology. Hollis graduated with a B.A. from Slippery Rock State College in 1969 and entered the University of Minnesota the following year. Hollis' undergraduate participation in Kirk's classical conditioning research led her to University of Minnesota researcher J. Bruce Overmier, who became her Ph.D. advisor. Overmier was deeply committed to his students, and his mentorship was critical to her subsequent success as a researcher and professional academic. As she wrote in the acknowledgements of her Ph.D. thesis, a study of the role of the telencephalon in both classically conditioned and instrumentally conditioned species-specific behavior of *Betta splendens* fish, Overmier "expended more effort taking care of [his students'] careers than, frequently, they did themselves." Overmier never stopped doing so and continued his mentorship for the remainder of her career. He steered Hollis toward a 2-year research and teaching internship at the University of Toronto, where Hollis worked in the laboratory of Sara Shettleworth and taught one of the many sections of Toronto's introductory psychology course. Although that internship initially was planned to follow her graduation from the University of Minnesota, Hollis finished analyzing her thesis data while in Toronto, obtaining the Ph.D. in 1979 and the Richard M. Elliott Most Outstanding Dissertation, 1975–1979, from the Department of Psychology. Continuing to follow her interest in species-specific behavior, Hollis joined the Animal Behavior Research Group at the University of Oxford, under the direction of David McFarland.

While at Oxford, where the relatively new field of behavioral ecology was having a profound



influence on all aspects of the study of animal behavior, Hollis began working on two related projects, a theoretical review revealing the ubiquity of classically conditioned responses serving animals' reproductive success (Hollis 1982) and an experimental study demonstrating the biological function of classical conditioning that she began to formulate in graduate school (Hollis 1984). As she described many years later in an interview published in Lee Alan Dugatkin's text, "Principles of Animal Behavior, 2nd, 3rd and 4th ed." (2004, 2009, 2017), Hollis' thesis work afforded her a serendipitous observation of aggressive behavior, one that provided the raw material for years of subsequent research and shaped the rest of her career:

My project required me to transport each *Betta* male in its home tank to another room where it would have the opportunity to display to a rival. After a few days of this procedure, I noticed that when I approached the shelf on which the males were located and reached for a particular male's tank, it became quite agitated. After a few more days, each male that I selected began to display – at me! And, at eye level that display looked pretty ferocious! I recognized that some features of my appearance obviously had become a learned cue for the subsequent interaction with a territorial rival. At that time, associative learning in *B. splendens* already was well established (even if the experimenter-as-signal was a little unconventional). However, what was even more interesting to me was the realization that this kind of learning [i.e., classical conditioning] could be a wonderfully adaptive mechanism, providing a territory owner with a definitive competitive edge: Confronting a potential usurper with a full-blown aggressive display could be a very effective aggressive strategy for a territory owner. A few years later, as a postdoctoral student at Oxford, I had the opportunity to conduct those experiments with blue gouramis, *Trichogaster trichopterus*; and, as the data showed rather convincingly, the best defense is, indeed, a good offense.

Following her postdoctoral work at Oxford, Hollis returned to University of Toronto to accept a 1-year Visiting Assistant Professor position continuing her research and teaching the introductory psychology course. In 1982, she accepted a permanent position at Mount Holyoke College, a small liberal arts undergraduate institution in South Hadley, Massachusetts. Hollis remained at Mount Holyoke for the remainder of her career,

continuing her research on the adaptive value of classically conditioned behavior in blue gourami fish (and several other species), in both aggressive and reproductive contexts. For example, Hollis and her students showed how aggression in gouramis could be shaped by learned inhibition; how classically conditioned responses could have both short-term and long-term effects, the latter contributing to the phenomenon in which "winners become winners and losers stay losers" (Hollis et al. 1995); and how the ability to anticipate a rival enables subordinate fish to secure food using sneaky strategies (Hollis et al. 2004). A 1997 paper with her students, demonstrating how classically conditioned courtship displays provided male fish with paternity advantages (Hollis et al. 1997), was awarded Frank A. Beach Comparative Psychology Award "for the best paper published in *Journal of Comparative Psychology*, 1997."

Hollis was able to expand her research focus as a result of sabbaticals at the University of Cambridge and the National Institute of Biology in Ljubljana, Slovenia, the latter stay enabling her to switch species to insects. In 2007 she began a research collaboration with Elise Nowbahari, Ph.D., focusing on the predator-prey relationship between ants and larval antlions. Among their findings, Nowbahari and Hollis demonstrated the important role of rescue behavior in ants' ability to escape capture by antlions (Nowbahari et al. 2009; Hollis and Nowbahari 2013), as well as ants' ability to learn to avoid antlion pits (Hollis et al. 2017). On the other side of this predator-prey relationship, they demonstrated the role of learning in antlions' ability to obtain and process food efficiently (Hollis et al. 2011).

Hollis served as the head of the American Psychological Association's sixth division (Behavioral Neuroscience and Comparative Psychology) from 2006 to 2007 and the third division (Experimental Psychology) from 2010 to 2011. Hollis was the first woman to head both the third and sixth divisions. She has served on the editorial boards of several journals, including *Journal of Comparative Psychology*, *Animal Learning and Behavior*, *Psychonomic Bulletin*, and *Review and Behavioral Processes*, as well as Associate Editor of *Learning & Behavior* from 2002 to 2015. In

2016 Hollis was honored by the Comparative Cognition Society for her contributions to the study of animal cognition.

## Cross-References

- Adaptation
- Adaptedness of Behavior
- Aggression
- Arthropod Cognition
- Associative Learning
- Classical Conditioning
- Conditioned Inhibition
- Dominance Hierarchy
- Ecology
- Evolution
- Fitness
- Frank Ambrose Beach
- Inhibition
- Ivan Pavlov
- Learned Helplessness
- Learning
- Operant Conditioning
- Predator
- Predator Defense
- Prey
- Resource Defense Polygyny
- Sara Shettleworth
- Stand and Wait Feeding Behavior
- Territoriality
- Territory Defense
- Ultimate Causation
- Unconditioned Response
- Unconditioned Stimulus

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## Karyotype

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## Synonyms

Constitution; Make-up; Physical composition

## Definition

A karyotype is the visual representation of the number and appearance of the complete set of

chromosomes in a species or in an individual organism.

## Introduction

Every other organism is characterized by a set of chromosomes to carry their genetic information. Karyotypes assess the chromosome count/ploidy of an organism and how they are visualized under a light microscope. It refers to a laboratory technique that depicts the image/photograph called as karyogram, in which the chromosomes have been arranged and sorted by size and position of centromere for chromosomes of the same size. Specific significance is given to their length, the position of their centromeres, any distinction between the sex chromosomes, and any other physical uniqueness. The significance of karyotype can be utilized for many purposes, to examine taxonomic relationship and past evolutionary events, to study chromosomal aberrations and cellular function. Nowadays, medical genetics has become increasingly integrated with clinical medicine leading karyotype to become a source of diagnostic information for certain birth defects, genetic disorders, and even cancers (O'Connor 2008).

## Understanding Karyotype

Humans have a total of 46 chromosomes, 23 from each parent which we can visualize in a karyogram. In a karyogram, homologous chromosomes or pairs of chromosomes that are of same size and shape are arranged together. Humans have 22 of these pairs called autosomes. Autosomes are chromosomes that have genes for everything but the determination of the sex. In humans, autosomes are numbered 1 through 22, having two for each. Chromosome 1 is the largest and chromosome 22 is the smallest. The remaining two chromosomes are the sex chromosome which determines a person's gender, male or female. They are placed after autosomes in a karyogram. The sex chromosomes are not numbered, but instead given letters X and Y. If someone has two X chromosomes, then they are

female. If someone has an X and a Y chromosome, then they are male (Swafford 2015).

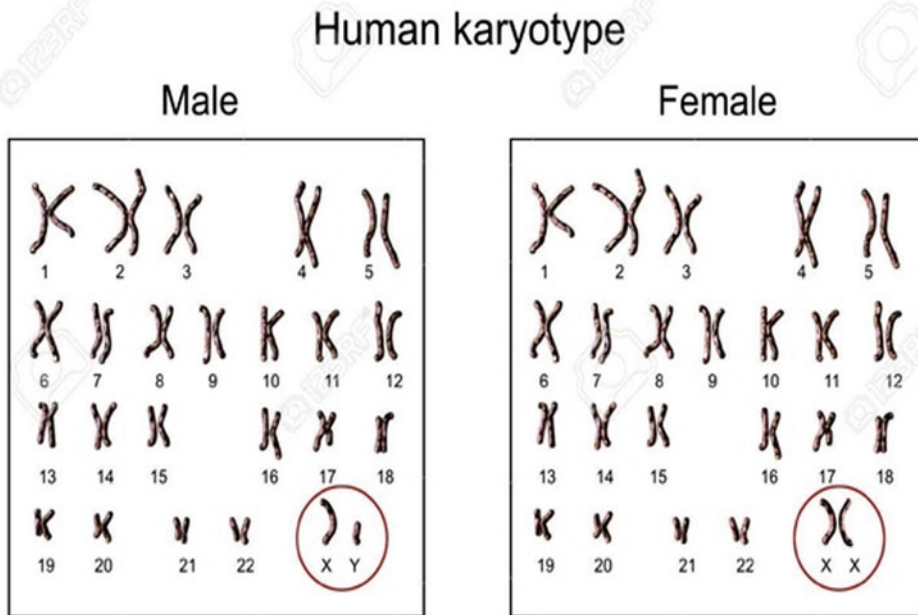
## Preparing a Karyotype

A variety of tissue types can be used as a source of mitotic cells that have been arrested in their metaphase or prometaphase portion of the cell cycle to be used for karyotype analysis. For prenatal diagnosis, amniotic fluid is used as the source of cells. For cancer diagnosis, specific specimens include bone marrow samples or tumor biopsies and for other diagnoses, use of skin biopsies or peripheral blood samples is prompted. The process of generating a karyotype begins with the interim culture of cells isolated from a specimen. After the cells grow and multiply, dividing cells are detained in metaphase by addition of colchicine, which are spindle inhibitors. In metaphase stage of mitosis, chromosomes assume their most condensed conformations hence become visible under a light microscope. Therefore, almost all cytogenic work is done under metaphase stage. The cells are then treated with a hypotonic solution, which causes the cell to burst open and osmotic swelling of nuclei resulting in spreading of the chromosomes. The nuclei are then treated with a chemical fixative, and then slide is prepared by placing a drop of cell suspension followed by staining which reveals structural features of chromosomes (Fig. 1).

## Chromosome Staining-Banding Techniques

It is crucial to distinguish chromosomes from one another and group them accordingly to their size and the placement of their centromeres. Therefore, to make analysis more effective and proficient, cytologists have developed staining techniques that generate characteristic banding patterns for different chromosomes.

(a) **General techniques:** According to the study (Veerabhadrapa et al. 2016), certain human



**Karyotype, Fig. 1** Photographic representation of human chromosomes: male and female karyotype (<https://www.dreamstime.com/stock-illustration-male-female-karyotype-human-chromosomes-d-illustration-image98510413>)

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chromosomes are distinguished on morphological grounds alone, for example, position of primary and secondary constrictions and length of chromosome arms. Autoradiography and aceto-orcin staining method can be used for studying morphology of chromosomes. Due to shortcomings, both are now replaced by banding techniques.

- (b) **Banding techniques:** In 1970, Torbjorn Caspersson and his colleagues described the first banding technique, known as Q-banding which involves the use of fluorescent dye quinacrine (O'Connor 2008). It was the first banding technique to stain all the human 46 chromosomes with quinacrine and visualize them under ultraviolet light. Q-banding is crucial for chromosomal translocations, especially ones including the Y chromosome. Others include, G (Giemsa) banding, R (Reverse) banding, C (centromeric heterochromatin) banding, T (telomeric) banding, and high resolution (fine) banding. Today, most karyotypes are stained with Giemsa dye in clinical cytogenetics, which though

produces same characteristic banding patterns as quinacrine but with more stable preparation and greater resolution and accuracy.

The base composition of DNA and local differences in chromatin structure are usually the molecular causes for staining differences along the length of a chromosome. In G-banding, prior to staining with Giemsa, metaphase chromosomes are initially treated briefly with a proteolytic enzyme, like trypsin (Veerabhadrapa et al. 2016). Trypsin denatures chromosomal proteins, hence relaxing chromatin configuration and allowing Giemsa dye access to the DNA. When the chromosomes are stained with Giemsa, G-bands appear on the light microscope. The G-bands constitute alternate light and dark bands, which reflect differential chromosome condensation. Heterochromatin regions (more condensed chromatin), with adenine and thymine-rich base pair region and few active genes, stain more darkly in contrast to euchromatin (less condensed chromatin), with guanine and cytosine-rich and higher active genes, giving light bands in G-banding.

G-banding generates reproducible patterns for each chromosome giving 400–800 bands distributed among 23 pairs of human chromosomes. Photographic presentation of the entire metaphase spread is taken and both homologs of each chromosome pair are arranged alongside in numerical order for precise analysis, which allows identification of delicate changes in banding patterns due to chromosomal abnormalities.

Other banding techniques, like R-banding, are also commonly used which generates the reverse pattern from G-banding. The chromosomes are subjected to heat treatment before Giemsa stain is applied. The heat treatment preferentially melts the DNA helix in the AT- rich regions that bind Giemsa stain most strongly, leaving the gene active GC-rich regions to take up the stain. This enhances analysis of small structural rearrangements in various parts of the genome which usually lead to phenotypic abnormalities. Another method is C-banding which specifically stains chromosomes at the centromeres rich in repetitive DNA sequences as well as constitutive heterochromatin. T-banding involves staining the telomeric (end) regions of the chromosomes and CT-banding which stains both the heterochromatin as well as the telomere of chromosomes to produce the CT- bands.

## Classification of Chromosomes for Karyotyping

As already mentioned, diagnostic information obtained from a chromosome preparation involving individual chromosomes is set in a standardized format known as a karyotype, or more precisely, a karyogram. Following international parameters, human autosomes or nonsex chromosomes are numbered 1 to 22, in descending order by size, exceptions are chromosome 21 and 22, followed by sex chromosomes.

Chromosomes are arranged into seven groups, based on size and centromere location (Veerabhadrapa et al. 2016). They can be categorized based on the position of centeromere; Metacentric chromosomes (center): chromosomes 1, 3, 16, acrocentric chromosomes (near one end):

chromosomes 13, 14, 15, 21, 22 and submetacentric chromosomes (slightly displaced from center): chromosomes 2, 6, 10. Chromosomes are aligned along a horizontal axis shared by their centromeres. According to the study (O'Connor 2008), individuals ones are depicted with their long q arms- q for “queue”- at the bottom and short p arms- p for “petite”- at the bottom.

Group A: Chromosomes 1–3 are the largest with median centromere.

Group B: Chromosomes 4–5 are large with submedian centromere.

Group C: Chromosomes 6–12 are medium-sized with submedian centromere.

Group D: Chromosomes 13–15 are medium-sized with acrocentric centromere.

Group E: Chromosomes 16–18 are short with median or submedian centromere.

Group F: Chromosomes 19–20 are short with median centromere.

Group G: Chromosomes 21–22 are very short with acrocentric centromere.

Chromosome X is similar to group C.

Chromosome Y is similar to group G.

## Application of Karyotype

In humans, majority of the genetic abnormalities are directly related to the chromosomal aberrations. Hence, karyotyping is extensively performed in the field of cytogenetics: (1) amniocentesis, to determine the sex of the child by observing the XX (female) or XY (male) chromosome pair and (2) aneuploidy, to check any deviation from the usual diploid or  $2n$  condition of chromosomes and translocations of tiny parts of chromosomes to one another. Since such procedures allow each pair of chromosomes to be notable individually, it has facilitated our understanding of the chromosomal basis of crucial genetic disorders. Researchers have utilized karyotyping procedure in prenatal diagnosis as well as neonatally discovered congenital abnormality and treatment of male infertility and screening in sperm donors to reduce birth defects (Xiao-bo et al. 2012).



## Cross-References

- [Diploid](#)
- [Mitosis](#)
- [Translocation](#)

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refinements to Clark Hull's mathematical framework for understanding behavior. Although the two published together only once, the comprehensive perspective that they complementarily advocated is generally known as the Hull-Spence theory of learning. Hull himself acknowledged Spence's tremendous influence in numerous publications, including in his seminal text, *Principles of Behavior* (Hull 1943; see also Hilgard 1967; Kendler 1967). At the time of his death, Spence was one of the most highly cited and influential psychologists in the world. Kenneth Spence is also remembered as a prolific professor, responsible for directing 75 Ph.D. dissertations, primarily at the University of Iowa, where he served as head of the psychology department for 22 of the 26 years he was on faculty. At that time, it has been said that nearly every major psychology department in the United States included at least one former Spence student on its faculty (Wagner 2008). Consequently, Professor Spence's influence continues today through this academic legacy as well as through the scholarship he contributed to the literature.

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## Kendall's Compound B

- [Corticosterone](#)

## Kenneth Spence

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Kenneth Wartinbee Spence (May 6, 1907 – January 12, 1967) was an American experimental psychologist and influential learning theorist, widely recognized for his systematic research on motivation. His research on conditioning and discrimination learning with rats, chimpanzees, and humans was reported in more than 100 journal articles and several books and guided his

## Personal History

Kenneth Spence was born in Chicago, Illinois to Mary E. (Wartinbee) and William James Spence. Kenneth would spend his childhood, adolescent, and early-adult years in Montreal, Canada, after his father, an electrical engineer, was transferred there in 1911 by Western Electric. Young Spence attended West Hill High School, where he excelled in basketball, tennis, bowling, and track. He subsequently enrolled at McGill University in Montreal, where he remained active in sports. However, a back injury sustained during a track meet would change the course of Kenneth Spence's career, to the considerable benefit of psychology. To recover from his injury, Spence moved to LaCrosse, Wisconsin to live with his grandmother. There, he attended the LaCrosse Teacher's College as a physical education major. It is not clear what sparked Spence's interest in psychology during this period – perhaps it was another serious sports injury he received

while there, which resulted in 6 weeks of hospitalization – but when he returned to McGill, he did so as a psychology student, although he continued to work as a YMCA basketball coach (Hilgard 1967). Spence earned Bachelor of Arts (1929) and Master of Arts (1930) degrees in psychology from McGill. In 1930, he coauthored the first of what would become many empirical papers (Spence and Townsend 1930), a so-called comparative study of the relation between intelligence and learning of a finger maze by 20 psychology undergraduates. The modest article – the authors themselves acknowledged, “The study was undertaken primarily with the view of gaining some knowledge of the technique and problems of experimental psychology, and not with the hope of being able to make any great contribution to psychology” (p. 113) – serves nevertheless to introduce the kind of meticulous attention to methodology and careful and detailed analysis of behavior that would characterize Spence’s subsequent and more impactful publications. A coauthored statistical publication (Kellogg and Spence 1931) would also result from his McGill research.

For graduate study, Spence attended Yale University, where he was clearly influenced by psychology professor Clark Hull. For example, Spence’s 1932 publication on maze-learning by rats was developed from a paper presented in a seminar taught by Professor Hull, in which Spence reanalyzed data from Tolman and Honzik (1930) from a Hullian perspective (Spence 1932). This article would be followed by other Hull-inspired studies of learning, as with the Spence and Shipley (1934) study of blind-alley maze-learning. Rats were tested on a maze with paths occluded by black curtains and demonstrated a strong orientation toward goal-pointing alleys instead of the nongoal-pointing alleys. Further analysis into individual alley error rates supported a Hullian goal-gradient hypothesis of maze learning.

However, Spence was not a “Hull student” in the formal sense. Rather, Spence worked as an assistant to Robert M. Yerkes while completing his graduate degree. His dissertation, completed

in 1933 under the direction of Yerkes, concluded that the visual acuity of a chimpanzee was comparable to that of adult and adolescent human subjects (Spence 1934). After earning his doctorate, Spence spent four postdoctoral years as a National Research Council Fellow at the Yerkes Laboratories of Primate Biology, in Orange Park, Florida. (Dr. Spence had applied for postdoctoral training in mathematics, reflecting his belief that psychological science must be expressed computationally; however, his fellowship application was denied because it was felt that a psychologist would not benefit from such training; Kimble 1998.) Many of Dr. Spence’s other early publications were studies of chimpanzee vision and discrimination learning, including some of his earliest attempts to investigate transposition, insight, and other Gestalt notions within an associative framework (e.g., Spence 1938, 1941).

In 1937, Spence moved to the University of Virginia for a 1-year replacement position, and subsequently accepted faculty appointment at the State University of Iowa, where he would spend the majority of his career. Already one of the most important psychology departments in the country, the University of Iowa (as it is now known) became a fountainhead of theoretical and neo-behaviorist psychology with Spence’s assistance and leadership.

Professor Spence also garnered individual accolades during this period. He was elected to the National Academy of Sciences and the Society for Experimental Psychologists and received the Howard Crosby Warren Medal from the Experimentalists in 1953. He was the first psychologist selected for the prestigious Silliman Memorial Lectures (1954), an honor awarded since 1901 generally to scholars from astronomy, chemistry, geology, anatomy, and other natural sciences. In 1956, Kenneth Spence was one of the three inaugural recipients (with Wolfgang Köhler and Carl Rogers) of the American Psychological Association Award for Distinguished Scientific Contributions to Psychology.

In his personal life, Spence married twice. While in LaCrosse, he met and married Isabel

Temte, with whom he had two children. After their divorce, Spence married Janet Taylor in 1960. In 1964, Kenneth and Janet Taylor Spence (who would emerge as one of the most important and influential psychologists in her own right) moved to Austin, Texas, where he joined the faculty at the University of Texas. Three years later, Professor Spence died from cancer at the age of 59.

## Contributions

Across his too-short career, Kenneth Spence combined rigorous methodological behaviorism with a neobehaviorist search for the mathematical relation between intervening variables, each carefully operationalized, that might describe, predict, and ultimately explain behavior in a comprehensive way. Through investigations of maze solving, discrimination learning, and eye-blink conditioning, Spence sought general principles regarding motivation and the effects on habit strength, or learning, of responses that serve to reduce these drives. His theoretical-experimental research not only refined his own version of the Hull-Spence framework but also provided significant empirical foundation for Hull's writings, often challenging the elder scholar to revise his theory so as to accommodate Spence's findings. It is said Hull added the intervening variable "incentive-motivation" to his hypothetico-deductive theory in response to his former student's arguments, and labeled the variable "K" in honor of Kenneth Spence.

A significant example of Spence's theoretical model was published just 3 years after he completed his Ph.D., in a formative review of discrimination learning in nonhuman animals (Spence 1936). Building on previous work by Lashley (1929) and Krechevsky (e.g., 1932), Spence attempted to account for systematic response biases that were demonstrated by nonhuman animals prior to learning. Arguing that discrimination learning involves changes in the excitatory and inhibitory tendencies of both task relevant and irrelevant stimulus characteristics, Spence

suggested that the prelearning behavior of a subject was not due to spontaneous hypothesis testing or insight, but offered instead a continuous learning, associative account – that an animal's pre-acquisition response pattern reflects the early stages of learning.

Twenty years later, Spence's theoretical model, and the decades of research behind it, was fully explained in *Behavior Theory and Conditioning* (1956), the volume that resulted from his Silliman lectures at Yale. In those essays, Spence summarized how his computational framework, derived to explain simple conditioning phenomena, can also explain more complex forms of behavior. Bruner (1957) praised the book as "at once modest in its scope and passionately grand in its aspirations" (p. 155).

In the final years of his life, Spence's research focus shifted from studies of nonhuman animals to conditioned eye-blink research with humans. For example, he examined the effects of anxiety on eyelid conditioning. Many of these studies were conducted in collaboration with Janet Taylor Spence, who is widely recognized as a leader in the study of anxiety. Kenneth and Janet Taylor Spence also worked together to edit *The Psychology of Learning and Motivation* series. These contributions to the understanding of human behavior are important, but it is also important to remember that these developments were richly informed by his earlier research with nonhuman animals.

Three years after Kenneth Spence died, Myers (1970) analyzed citation rates in the 14 most prestigious journals in psychology, together with other measures to produce a ranking of the most eminent psychologists. For the period of the review, Spence ranked #1 in citations and #8 in overall importance of all contemporary psychologists.

Additional evidence of Spence's eminence is found in his academic legacy. Supported by prolific publication of clever, systematic research and critical, integrative literature reviews discussed above, Spence trained a generation of disciples under his passionate and intimidating direction. In addition to supervising the doctoral projects of

75 students (four times the number supervised at Yale by Hull; Wagner 2008), Spence annually taught multiple graduate seminars on learning, courses were as rigorous and meticulous as were his published works (Amsel 1995; Wagner 2008). In contrast to the atheoretical Skinnerian behaviorism and the phenomenon-driven cognitive psychology that would follow, Spence's students were instructed and inspired to make contributions to psychology that advanced both data and theory. This was the lofty standard to which Spence held his mentees. This was the standard to which Kenneth Spence held himself.

## Cross-References

- B.F. Skinner
- Clark L. Hull
- Classical conditioning
- Comparative cognition
- Comparative psychology
- Discrimination Learning
- Insight
- Motivation
- Robert Mearns Yerkes
- Sue Savage-Rumbaugh
- Transposition
- Wolfgang Köhler (1887–1967)
- Yerkes Primate Research Center

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## Ketone

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### Definition

A ketone ( $\text{RC}(=\text{O})\text{R}'$ ) is a molecular compound composed of a carbonyl group bonded to two carbon-containing substituents. The symbols R and R' represent any alkyl group (Solomons 1978).

### Introduction

In chemistry, a functional group contains chemical elements that are bonded in a specific arrangement, which leads to specific chemical and physical properties. Important functional groups in physiological chemistry include alcohols, aldehydes, ketones, carboxylic acids, and amines (Harper et al. 1979). This entry will focus on the ketone, which has a role in animal physiology and pathophysiology.

### Naming Ketones

Ketones typically end in the suffix *-one*, and the ketone chain is numbered in which the carbonyl carbon receives the lowest number in the scheme. Ketones can also have common names, which are often derived by naming the two groups on either side of the carbonyl group and ending with the word ketone. Examples of ketones with their common names in parentheses include propanone (acetone), butanone (methyl ethyl ketone), and 2-pentanone (methyl propyl ketone) (Solomons 1978).

## Physical Properties

Although the carbonyl group of ketones gives rise to polarization and the formation of strong bonds to water between the carbonyl oxygen and the water hydrogen, ketones cannot form strong hydrogen bonds between one another (Solomons 1978). Also, the oxidation of ketones does not readily occur because oxidation would require an alkyl C–C bond to break in order for the ketone to lose a hydrogen atom. In contrast, ketones can undergo a reduction reaction, which results in the formation of a secondary alcohol. Ketones can also go through a condensation reaction to create  $\beta$ -hydroxyl acids, which demonstrate a role in fatty acid metabolism (Harper et al. 1979).

### Ketosis

When carbohydrates are depleted in the body and free fatty acids are mobilized, the liver oxidizes these fatty acids to produce ketone bodies as an energy source. This process is termed ketosis, and it can occur with many states, including during starvation, diabetes mellitus, pregnancy, and lactation (Harper et al. 1979). As pathological disorders occur, chemical changes also occur in the blood, urine, or milk of the affected animal. This is of great importance to the dairy cattle industry because as ketone bodies increase in a dairy cow, their milk production decreases. The ketone bodies of acetone, acetoacetate, and  $\beta$ -hydroxybutyrate can be measured in the blood and urine. For the dairy cattle industry,  $\beta$ -hydroxybutyrate in the blood is typically evaluated to determine if a dairy cow is in a ketotic state, which may be the cause for a decreased milk yield or other production or health-related problems (Overton et al. 2017).

### Conclusion

A ketone is a functional group in chemistry that contains a carbonyl group and two alkyl groups.



Ketones are an important chemical structure for the animal body to survive. Ketone bodies are created during fatty acid metabolism during times when the primary source of energy in the body, carbohydrates, is depleted. Ketone bodies can be measured in an animal to determine if ketosis is occurring and should subsequently be treated.

## Cross-References

- [Basal Metabolic Rate \(BMR\)](#)
- [Methylation](#)

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## Kin Selection

- [Fitness](#)
- [Inclusive Fitness](#)

## Kinesis

- [Innate Behaviors](#)

## Kinship

- [Coefficient of Relatedness](#)

## Knockout Genes

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Gene knockout (KO) is a genetic engineering method by which both the alleles of certain gene/genes are made inoperative/nonfunctional or deleted from the organism's genome. Knocking out a particular gene provides valuable information about functional role played by that gene and has proved as an effective method to study genetic basis of various diseases including cancer, diabetes, neurodegeneration, as well as aging. Gene knockout could be a “whole body knockout” if the particular gene is deleted from every cell of a multicellular organism or it could be a “conditional knockout” if the gene is deleted only in specific group of cells/tissues or from a particular organ. Gene knockout is one of the essential components of functional genomics whereby using homologous recombination or more recently clustered regularly interspaced short palindromic repeats (CRISPR), a mutated version of wild gene achieved by in vitro mutagenesis is exchanged with original gene to render it nonfunctional. More than 11,000 genes have been knocked out so far in mice accounting for half of the total genome in this most common laboratory animal (Vogel 2007). For the first time in 1989, Mario Capecchi, Martin Evans, and Oliver Smithies successfully created the world's first knockout mice and were jointly awarded Nobel Prize in Physiology and Medicine in 2007.

Gene targeting techniques including gene knockout by CRISPR/Cas9 systems are used to change the genomes of any living organisms. When a mutation is deliberately induced in a gene of interest for rendering it functionally inactive, it is called gene knockout (KO). Scientists use KO techniques to draw various inferences by observing the differences between normal individuals and KO models from the same species. Gene knockout approaches are used to classify a

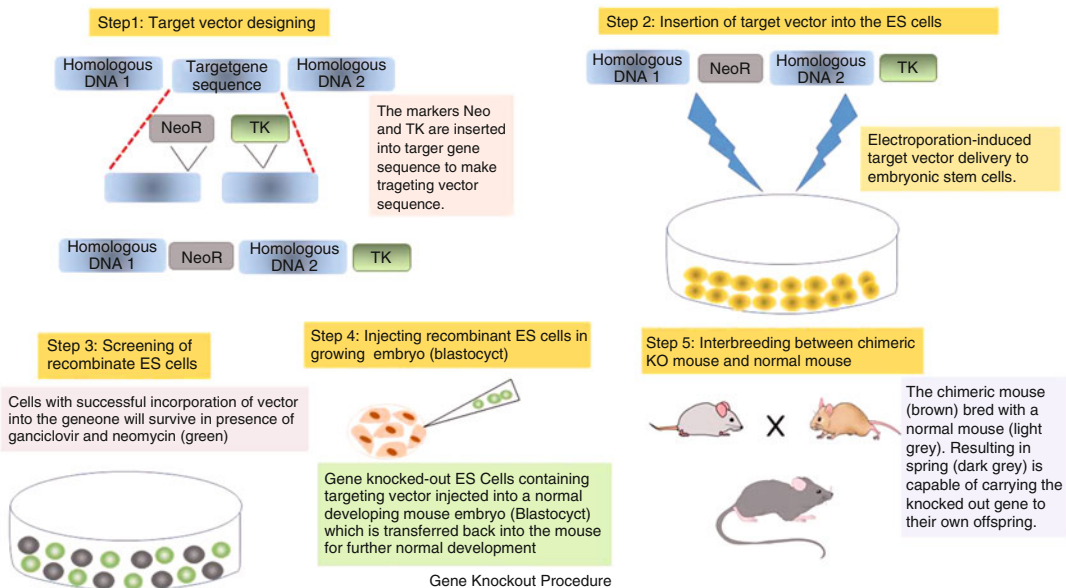
particular gene function by inhibiting the gene of interest. Gene knockout is found both in classical genetics and in modern techniques such as functional genomics (Lin et al. 1984). The gene knockout was carried out during the initial time scale by transposon mutagenesis, but the major drawback of that approach was that it was laborious to screen out the knocked out gene. In vitro techniques are used to change genes on plasmids or bacterial artificial chromosomes (BACs), and then the cell culture techniques pass these modified constructs to the organism of interest. The best approach for creating a gene knockout is homologous recombination, and a single gene is deleted/inactivated by gene knockout techniques at a time, without affecting all the other genes in an organism. With the aid of such genetic engineering techniques for gene knockout, the resultant organism is known as “knockout” organism, where the gene of interest is inoperative unlike “gene knockdown” approach where the expression of an original gene of interest is inhibited by RNA interference technology without deleting the original gene. When more than one gene is knocked out in an organism then depending on the

number of genes, it is called double knockout or DKO, triple knockout or TKO, and quadruple knockouts or QKO, respectively. However, it is noteworthy to mention that when both the alleles of a gene are knocked out, it is called “homozygous KO,” but when only one of the alleles is deleted from the two alleles of a gene, it is called “heterozygous KO,” respectively.

## Strategies for Generating Gene-Knockout

Various basic and advanced genetic engineering strategies based on homologous recombination as well as site-specific recombination and engineering embryonic stem cells have been utilized to generate gene knockout organisms such as knockout mouse (Hall et al. 2009) (Fig. 1). Recently, some advanced methods like CRISPR/Cas9 as well as TALENs have also been used for the same purpose with more accuracy and maneuverability. Below are the most common and recent techniques used to achieve gene knockout organisms.

K



**Knockout Genes, Fig. 1** Site specific recombination for generation of gene-knockout mouse employing embryonic stem cells

### Site-Directed Mutagenesis and Gene Targeting in Embryonic Stem Cells (Homologous Recombination)

This method was pioneered during the late 1980s and one of the first techniques used in construction of whole-body gene knockout mice (Thomas and Capecchi 1987). This method is based on the principle of homologous recombination where a synthetic DNA sequence similar to the gene to be knocked out is altered in such a way that when it gets inserted at the place of original gene due to homologous recombination, this gene is rendered inactive. Additionally, this newly inserted and base sequence-altered DNA also contains a marker gene, usually an antibiotic resistance gene like neomycin resistance marker (NeoR) for killing nonrecombinant cells and only allowing recombinant ones to survive because of the ability conferred by marker gene. The vector DNA also contains a negative selection marker gene such as thymidine kinase (TK) which is derived from herpes simplex virus and is located outside the right arm of targeting vector. Normally, mouse cells are able to grow in the presence of an antiviral drug called ganciclovir. The TK gene is also called a “cell suicide gene,” but cells having the TK gene can convert ganciclovir to a potent toxin thereby killing the animal cell. This gene is used to screen the recombinant cells where the targeting vector has been properly inserted at the loci of “gene of interest” and not anywhere else non-specifically. In case of non-specific insertion of vector, the cells will be containing both the genes NeoR and TK which will kill cells when grown in the presence of ganciclovir drug. This site-directed mutagenesis and consequent integration of altered DNA in place of wild gene are achieved by the help of cre recombinase enzyme usually called as “Cre-Lox recombination” (Hall et al. 2009; Marth 1996). After designing the vector, the next step in the creation of gene knockout is delivering this targeting vector to embryonic stem cells of animal models such as mouse. Microinjection and electroporation are the most widely recognized strategies which are applied to transfer this DNA construct into the embryonic stem cells under in vitro culture conditions. The joining of vector

develop into target site relies upon the DNA repair mechanism of the organism’s cells or can be achieved by Cre-Lox recombination machinery. When incorporated, the vector component will bring about shift of wild-type gene and in the long run creation of nonfunctional protein and also inserting the markers in place of original gene. After this, the screened recombinant/knockout ES cells are injected into a developing embryo (blastocyst) so that these knockout ES cells will be a part of the growing embryo and may contribute to the formation of many organs in the fetus resulting in chimeric animal. This chimeric animal is interbred with normal animal of the same strain to produce offspring among which some will be homozygous for this gene knockout thereby completely lacking the concerned gene. However, the productivity of homologous recombination accounts just up to  $10^{-2}$  to  $10^{-3}$  mix of DNA (Gaj et al. 2013). In diploid organisms, which contain two alleles for most genes, and may as well contain several related genes that collaborate in the same role, additional rounds of transformation and selection are performed until every targeted gene is knocked out. Selective breeding may be required to produce homozygous knockout animals.

### Site-Specific Nucleases as Tools for Gene Knockout

Apart from homologous recombination between native gene and insert vector, genome editing can also be rather rapidly achieved by the use of highly specific and precisely programmable nucleases (enzymes that cut DNA), which produce sequence changes in regions of our interest by creating double-strand breaks (DSBs). These DSBs are later repaired by various cellular mechanisms naturally present in the cells. However these repair mechanisms including non-homologous end joining (NHEJ) is highly prone to error. Thus these repairs would cause several gene insertions, deletions, or substitutions in the target area (Cox et al. 2015; Gaj et al. 2013; Sander and Joung 2014). These insertion/deletion-based mutations may interrupt or eliminate or render the gene inoperational thus creating

gene knockout. These “programmable” nucleases include mainly meganucleases, transcription activator-like effector nucleases, zinc finger nucleases, as well as CRISPR/Cas9 system (Epinat et al. 2003; Jinek et al. 2012; Miller et al. 2011; Urmov et al. 2010). Among these, the last three systems, zinc fingers, TALENs, and CRISPR are currently exploited for the purpose of gene knockout research.

#### Zinc Finger Nucleases

Zinc finger nucleases (ZFNs) are restriction enzymes broadly utilized in genome building for starting double-strand breaks. They are referred to go about as site explicit endonuclease which can tie to DNA at a particular site (Gaj et al. 2013). Zinc finger nucleases (ZFNs) contain two sections, a zinc finger DNA restricting area and a DNA cleavage part. The DNA holding area is comprised of 3–6 zinc finger rehashes which can additionally perceive and tie 9–18 base combines in a particular DNA grouping (Gaj et al. 2013). On the other hand, the cleavage domain includes a type II restriction endonuclease FokI. At the point when both the domains are assembled together, the zinc finger endonuclease protein goes about as a profoundly compelling genomic scissors. When conveyed in a cell, zinc finger nucleases (ZFNs) deliver site explicit DNA double-strand break followed by homologous recombination. As ZFN plasmids can communicate ZFN and successfully focus on a double-strand break, they give a great chance to predesign a set up to insert or delete a specific area in the genome. ZFNs give a few advantages in focusing on genome altering such as:

- The ZFNs can easily incorporate or interrupt any genome location.
- Mutations produced by ZFNs are permanent and can be hereditary.
- Genome editing is possible using a single transfection round.
- They can be used for a wide range of mammalian cell lines, and positive clone selection requires no antibiotic selection.
- Knockout/knockin results are seen to occur almost within 2 months. Additionally, zinc

finger nucleases (ZFNs) are used in many cell lines to produce full knockout.

- In cell-based screening methods, they can be used to produce knockin cell lines where endogenous target genes can be tagged with promoter, reporter, or fusion tag proteins.
- They are also useful for generating higher amounts of specific proteins or antibodies in cell lines.
- Another important aspect of the ZFN technology is that it does not need selectable markers to identify the targeted events or cells. This has a huge practical importance especially in industrial applications where recombinant protein is manufactured, and continuous expression of exogenous and undesirable marker genes is undesirable.

Although zinc finger nucleases (ZFNs) show several promising effects, there are also chance of having potential side effects. When the ZFN constructs do not target specifically and remain off target, cleavage takes place at random creating many DSBs in the genome beyond the ability of repair mechanisms causing cellular apoptosis. Off-target cleavage also generates random integration in the host genome increasing the risk of immunological response developed by cells in response to therapeutic agents.

#### TALENs (Transcription Activator-Like Effector Nucleases)

TALENs are enzymes which are genetically engineered to edit several genes. These enzymes are basically isolated from the bacteria of *Xanthomonas* species, and in the bacteria, they participate in binding and activating the host promoter. Similar to ZFNs, TALENs also contain two groups fusing transcription activator-like (TAL) proteins with FokI nuclease (Joung and Sander 2013). TAL protein consisting of repeating motifs composed of 33–34 amino acids which can strongly recognize nucleotides of interest (Gaj et al. 2013). They are also known as repeat variable di-residue (RVD) due to their variable nature. As in TALENs, there exists a direct relation within DNA and amino acid recognition; it is possible to engineer a specific domain to bind DNA by

changing the combination of repeating motif with specific RVD. By fusing TAL with FokI, it can effectively cut the genome. In the presence of two domains of TALENs, FokI create a double-strand break. After constructing TALENs, they are transfected to host cell with the help of plasmid vector. Inside the host cell, the construct gets expressed and has access to the genome by entering into the nucleus. Additionally, in cells, TALENs could also be transferred as mRNA which does not require genomic integration process. In comparison with zinc finger nucleases (ZFNs), TALENs offer several advantages, such as:

- The design of TALEN is much easy in comparison with ZFNs. Many TAL repeats can be created with RVD code which will bind strongly with the genomic DNA with high affinity.
- The amount of TALEN repeats can be extended based on the desired length.
- TALENs are used widely for plant genome modification.
- They are useful for the production of biofuels.
- They have been used to generate knockout in organisms such as zebrafish, rat, mice, or *C.elegans*.

#### CRISPR/Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats Associated Nuclease Cas9)

Genome editing technology re-emerged in 2012 with the development of CRISPR/Cas9 system, which is an important genetic manipulation tool derived from the defense systems of several bacteria offering protection against viruses and plasmids. This method is easy to apply and has been used in diverse experimental animal models apart from cell lines, plants, and even in human clinical trials.

CRISPR/Cas9 is a rapid genome editing method which is used to delete or modify specific sequences of DNA which contains a guide RNA complexed with a Cas9 protein (Gaj et al. 2013). CRISPR can be found naturally in certain types of bacteria. When invaded by a bacteriophage, the bacteria use CRISPR/Cas9 method to cut and disintegrate the viral DNA. The guide RNA

(gRNA) can be engineered to match a desired DNA sequence (gene of interest to be knocked out) through simple complementary base pairing, as opposed to the time-consuming assembly of constructs required by zinc fingers or TALENs (Ni et al. 2014). In bacteria, there exist three types of CRISPR-associated systems; among them, type II endonucleases are most widely studied for genome editing associated with Cas9 endonuclease of *Streptococcus pyogenes*. At this method, once cut into small parts, the invading DNA gets incorporated into CRISPR locus. Once transcribed in the cell, small short repeats of RNA or crRNA/CRISPR RNAs are generated within the cell. crRNA next gets joined by another non-coding RNA known as trans-activating CRISPR RNA or tracrRNA and activates the endonuclease Cas9 to target the invading viral DNA. crRNA together with tracrRNA forms a single guide RNA or sgRNA. CRISPR/Cas9 generates DNA double-strand breaks which can be repaired by two mechanism: (i) non-homologous end joining or NHEJ, where homologous double strands are absent and (ii) homology-directed repair which occurs in the presence of synthetic DNA repair template. Following the discovery of CRISPR/Cas9 system, it has been extensively used in several organisms for gene targeting such as plants, humans, *C.elegans*, zebra fish, yeast, drosophila, or mouse. They are now days used to produce single-point mutations in the presence of single gRNA. In comparison with TALENs and ZNFs, CRISPR/Cas9 is easy to use as here only crRNA required redesigning to target any gene specifically. Additionally, this method also enables genome-wide analysis of gene function by producing libraries of large gRNA.

#### Applications of Gene Knockout Technology

Using engineered or bacteria-derived nucleases, the advancements in genome editing technologies have provided diverse possibilities of targeting and manipulating genomic sequences of almost all eukaryotic as well as prokaryotic systems. Gene targeting or knockout has incredibly



extended our ability to investigate the contribution of genetics to various diseases by employing the creation of more accurate animal and cell-based models of pathological processes. KO technologies have displayed extraordinary potential in a variety of fields including human diseases, pharmacy, drug designing, basic research, and applied biotechnology as well as in biomedical research benefiting mankind tremendously (Li et al. 2020). Below are the major applications of gene knockout and associated genetic engineering technologies in diverse fields.

## Gene Editing and Human Health

Targeted gene modification via chimeric genome editing tools is a powerful method to assess gene function and precisely manipulate cellular behavior and function (Li et al. 2020). Gene KO technology has made it easier to understand the etiology behind various diseases and to clarify molecular mechanisms. It has extended to a border field of cancer research, for example, engineering of hematopoietic stem cells (HSCs) and tumor-targeted T cells. Genome editing tools like zinc finger nucleases (ZFNs), TALENs, and CRISPR/Cas9 have revolutionized the domain of cancer research (Sánchez-Rivera and Jacks 2015). Similarly, studies have shown that the use of HER2-positive cell-penetrating peptide (CPP) conjugated to mammalian mTOR-specific ZFN made the mTOR locus nonfunctional and inhibited relevant cancer signaling pathways (Li et al. 2020), providing insight into the design of novel molecular-targeted therapeutics for breast cancer (in particular) and other types of cancers in general. Recently, TALEN gene editing technology has been used to knockout genes in cancer cells (including cells from prostate cancer, breast cancer, and hepatocellular carcinoma (HCC)) and is a very powerful and broadly applicable platform to explore gene mutations at the molecular level (Ho et al. 2018). The CRISPR/Cas9 system has attracted considerable attention, and scientists gradually consider it to be a powerful therapeutic tool for treating diseases associated with genome mutations (Ramanan et al. 2015). The ultimate

goal of cancer therapy with CRISPR/Cas9 is to remove malignant mutations and replace them with normal DNA sequences. The CRISPR/Cas9 platform also provides a new tool to manipulate noncoding regions of the cancer genome, accelerating the functional exploration of aspects that are hitherto poorly characterized (Sánchez-Rivera and Jacks 2015).

The first report in the world describing the treatment of genetic diseases through in vivo gene editing was provided by Benioff Children's Hospital at the University of California, San Francisco. There, an American man with Hunter's syndrome, was treated with the delivery of ZFNs via an AAV for in vivo genetic editing to treat his disease (Li et al. 2020). Such reports further demonstrate that gene editing has extremely important clinical applications and huge potential for the treatment of genetic diseases. Genome editing technology has also been combined with tumor immunotherapy to provide more updated options for human disease treatment. As one of the most innovative and successful approaches in tumor immunotherapy, CAR T-cell therapy was officially approved for use in the clinic in 2017 as a "breakthrough therapy" and approved its treatment for leukemia and lymphoma (Chavez et al. 2019).

CRISPR/CAS9 is showing tremendous potential in its applications with regard to the field of allograft bioengineering, including the refinement of heart transplant (Ho et al. 2018). Knocking out specific genes as cardiovascular disease prevention (CVD) approaches has also received widespread attention especially in diseases like cancer, neurodegeneration, and diabetes (Chai et al. 2018; Fan et al. 2018). Gene editing technology has applications in treatment of metabolic diseases where different knockout models have been generated to study their impact in the pathology (O'Rahilly 2009). As an important "experimental tool," the animal models of diabetes disease can be used for pathological observation, preclinical experiments, and drug screening. This technology finds its applications in neurodegenerative diseases, viral diseases, hereditary eye diseases, and hematological diseases where loss of function (gene knockout) studies are carried out to study the

onset and pathological outcomes of the defected gene. Moreover, the important and most recently observed application of gene knockout and CRISPR/Cas9-based technologies have been seen in transplantation immunology where xenografts from pigs or other animals are used to replace organs in humans by knocking out genes from human cells which play an active role in xenograft rejection (Cowan et al. 2019). Ultimately, researchers aim to use gene knockout technologies like CRISPR/Cas9 to rapidly develop genetically modified pigs which will be rightly poised to provide compatible xenografts to human patients.

### Use of Gene Knockout in Biomedical Research

Apart from its potential use in treating human diseases and improving human health, gene editing technologies have a vital role to play in biomedical research including development of refined cell imaging techniques, studying the epigenetic modification as well as regulation of gene expression under various pathophysiological conditions, and therapeutic drug designing as well as genetic diagnosis of hereditary diseases in advance of symptoms (Hongbao et al. 2013, Li et al. 2020). Although the off-target effect in the implementation of gene editing technology still needs further optimization, innovative genome editing complexes and more specific nanostructured vehicles have improved efficiency and reduced toxicity during the delivery process, bringing genome editing technology closer to the clinic. With deeper exploration into this technology and the cooperation of the world scientific community, it is reasonable to believe that genome editing technology has the potential to ultimately elucidate biological mechanisms behind several dreadful diseases as well as their treatment, thus providing novel therapies and finally promoting the development of the life sciences.

In summary, knockout animal models such as knockout mice are exceptional tools to study the function and regulation of certain important genes in biomedical research investigations. Despite several ethical and moral concerns and limitations in applying this technology, gene knockout techniques provide useful insights into understanding

the progression of several diseases. The creation of a gene knockout mouse is a watershed landmark and a massive advance in the pharmaceutical as well as biomedical fields. Such genome editing methods will allow scientists with ample opportunities and powerful tools for investigating gene function during disease and development. With more advancement in genetic engineering and molecular biotechnology, future gene knockout technology will revolutionize the field of medicine and disease management.

### Cross-References

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## Knowing

### ► Learning

## Knuckle-Walking

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## Definition

Knuckle-walking is a form of quadrupedal locomotion in which forelimb weight is born on the dorsa of the middle phalanges of the hand (not actually on the “knuckles” as its name implies). The hand is held in a position in which the interphalangeal joints are flexed and the metacarpophalangeal joints are extended or in a neutral position (Fig. 1). This is in contrast to the palmigrade or digitigrade hand positions used by most mammals in which the palmar surfaces of the hand and/or digits, respectively, make contact with the substrate.

## Distribution

Knuckle-walking is primarily performed by the African great apes, *Pan troglodytes* (chimpanzees), *Pan paniscus* (bonobos), *Gorilla gorilla* (western gorillas), and *Gorilla beringei*



**Knuckle-Walking, Fig. 1** Image of a gorilla using knuckle-walking. Note the weight is borne on the middle phalanges, the wrist is in a neutral position, the elbow is extended, and the shoulder is internally rotated. (Photo credit: Dr. Angel Zeininger)

(eastern gorillas); however, it has also been documented in the giant anteater (*Myrmecophaga tridactyla*) in the order Xenarthra. In general, knuckle-walking is adopted during terrestrial, and frequently arboreal, quadrupedal locomotion by large-bodied arboreal animals possessing long, curved digits. Knuckle-walking allows these animals to retain these long, curved digits, useful for arboreal locomotion such as climbing and suspension while protecting them from increased bending loads during the compressive loading of terrestrial quadrupedalism. The evolution of knuckle-walking in the African apes has received considerable attention because of the implications of a common versus independent ancestry for models of the evolution of human locomotion (see below).

## Mechanics and Functional Variation

The manner and extent to which animals knuckle-walk vary among its practitioners, although all knuckle-walkers bear weight on their middle phalanges and tend to use wrist postures in which extension is limited. All adult African apes knuckle-walk consistently when walking quadrupedally on the ground; however, considerable interspecific and intraspecific variation has been observed in the extent to which *Pan* uses knuckle-walking in the trees. While *P. paniscus*

tends to be more arboreal in general, traveling using arboreal pathways (Doran 1993; Doran and Hunt 1994), *P. paniscus* as well as *P. troglodytes schweinfurthii* (eastern chimpanzees) at Mahale, Tanzania, tend to use palmigrade quadrupedalism in the trees (83–87% for *P. paniscus* and 77–94% for *P. troglodytes schweinfurthii*), while *P. troglodytes verus* (western chimpanzees) in the Tai National Park, Ivory Coast, tend to use knuckle-walking quadrupedalism in the trees most (57–72%) of the time (Doran and Hunt 1994).

Variation in the manner in which African apes knuckle-walk has been used in support of hypotheses of parallel ancestries for *Pan* and *Gorilla* knuckle-walking. Variation has been documented in forelimb position, hand position, force distribution across the digits, and the extent to which members of each species use knuckle-walking during ontogeny (growth). Gorillas tend to use more pronated forelimb positions than chimpanzees, and gorillas tend to use more neutral distal forelimb positions in which the hand and wrist are stacked on top of one another compared to more extended positions in chimpanzees (Tuttle 1969; Inouye 1992, 1994; Kivell and Schmitt 2009). Gorillas and bonobos use hand positions in which the palm faces backward (posteriorly), while chimpanzees use a combination of palm-in and palm-back positions (Wunderlich and Jungers 2009; Matarazzo 2013). Plantar pressure distribution has been used to measure the manner in which force is distributed across the hand during knuckle-walking. During terrestrial knuckle-walking, gorillas tend to distribute pressure evenly across digits 2–5 and consistently touch off and have the highest pressure on the second digit (the index finger in humans). During arboreal knuckle-walking, bonobos also distribute force across digits 2–5, but they touch down and off on digit 3 (Samuel et al. 2018). Chimpanzee pressure distribution is more variable than gorillas or bonobos on both terrestrial and arboreal substrates, likely because of their variation in hand posture. The highest pressure and touch off can be on digits 2, 3, or 4, and this is dependent on their hand posture (Wunderlich and Jungers

2009; Matarazzo 2013). Matarazzo (2013) found the third digit experienced the highest load and was the last to be loaded in chimpanzees in terrestrial palm-back positions and attributed this to the longer third digit in chimpanzees compared to gorillas. However, all of these pressure studies have been, by necessity, conducted only in captive settings and on a limited number of individuals. African apes in the wild must knuckle-walk on a variety of terrestrial and arboreal substrates and thus likely show much more variation in their hand postures (knuckle-walking and otherwise) and digit loading than captive studies can quantify. Indeed, a study of wild mountain gorillas' (*Gorilla beringei beringei*) terrestrial hand postures showed that only 60% of the individuals used exclusively knuckle-walking on the ground, while others sometimes loaded the dorsa of their proximal phalanges (fist-walking) or metacarpals (Thompson et al. 2018).

Use of knuckle-walking varies during development in African apes. While both gorillas and chimpanzees (*P. troglodytes*) begin palmigrade quadrupedalism at 4.5–5.5 months, gorillas begin using knuckle-walking postures much earlier than chimpanzees. By 10–15 months gorillas use knuckle-walking 61% of the time, and by 2 years 97% of their quadrupedalism is knuckle-walking. Chimpanzees engage in very little quadrupedalism at young ages (6–23 months), and when they do, it is predominantly (72%) palmigrade. It is not until 29 months that knuckle-walking comprises over 50% of their quadrupedal bouts. When body size is considered (e.g., a 2-year-old chimpanzee compared with 10–11-month-old gorilla), locomotor patterns are more similar between chimpanzees and gorillas (Doran 1997).

## Morphological Correlates

Because of the implications for human evolution (see below), extensive attention has been given to morphological features associated with knuckle-walking, their variation among knuckle-walking apes, and their presence in the fossil record.

Although not useful for examining the fossil record, all extant knuckle-walking apes exhibit skin callous, dermatoglyphs, and depilation on the dorsum of the middle phalanges. Most features discussed with respect to knuckle-walking adaptations of the upper limb are musculoskeletal features. African apes have more robust phalanges than the Asian apes who are more highly arboreal and do not knuckle-walk (orangutans use a hand position called “fist-walking” that seems to serve the same purpose of protecting their long, curved fingers). Knuckle-walking has also been associated with a unique yet controversial suite of musculoskeletal features of the wrist. These include the fusion of two wrist bones, the scaphoid and os centrale (also present in humans), a dorsal ridge on the capitate and hamate, a deep groove and dorsal ridges on the metacarpal heads, wide articular surfaces on metacarpal heads 3 and 4, and a distally extended and medially projecting dorsal ridge on the distal radius. Most of these features are believed to be functionally associated with prevention of excessive extension of the wrist and hand.

Considerable variation has also been noted in these and other morphological features associated with knuckle-walking. Like the functional variation, morphological variation and ontogenetic variation have been cited as evidence for independent evolution of knuckle-walking in African apes. Gorillas have shorter and less variable ray lengths than chimpanzees (Inouye 1992). Gorillas have relatively longer and more robust fifth metacarpals, while chimpanzees have third digits substantially longer than the other digits such that they are positioned anterior to the other digits during knuckle-walking (Matarazzo 2013). While *Pan* consistently exhibits capitate waisting, extension-limiting ridges and concavities on the hamate and capitate, and a dorsal concavity and ridge on the scaphoid, these features are less pronounced and present with considerably less frequency in *Gorilla* (Kivell and Schmitt 2009). Similarly, while *Gorilla* engages in more frequent knuckle-walking at much earlier ages than *Pan* (Doran 1997), many of these “knuckle-walking” features of the wrist do not develop earlier as would be expected if these morphologies are



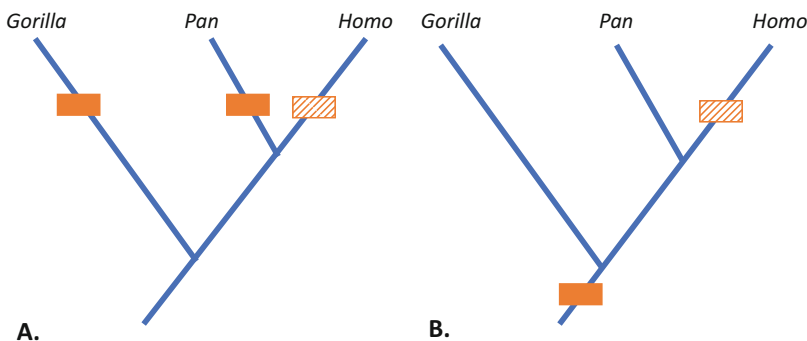
either necessary for or a result of knuckle-walking behaviors (Kivell and Schmitt 2009). Furthermore, dorsal ridges on the wrist bones and metacarpal heads are argued to be the result of cartilage remodeling during ontogeny rather than osteological features that limit extension within the wrist and hand during knuckle-walking (Simpson et al. 2018).

## Implications for Human Evolution

Acceptance of the molecular evidence that *Pan* and *Homo* share a more recent common ancestor than either does with *Gorilla* brought knuckle-walking and its associated morphological features to the forefront of a debate regarding the nature of locomotion in the last common ancestor (LCA) of *Pan* and humans. While morphologically based phylogenies allowed for the evolution of knuckle-walking in a *Gorilla*-*Pan* clade, the monophyly of *Pan*-*Homo* requires that either the LCA of *Gorilla*, *Pan*, or *Homo* was a knuckle-walking quadruped (a scenario usually considered to be combined with a partially arboreal lifestyle as in modern African apes) or knuckle-walking has evolved more than once in parallel within the Hominae (the group including *Gorilla*, *Pan*, *Homo*; Fig. 2).

In light of the molecular evidence supporting a close relationship between African apes and humans, Washburn (1967) first explicitly suggested that human evolution included a knuckle-walking stage prior to bipedalism. Since then, various researchers (e.g., Corruccini 1978; Shea and Inouye 1993; Begun 1993, 1994; Richmond and Strait 2000; Richmond et al. 2001) have supported a knuckle-walking ancestor based on (1) suggested homology of knuckle-walking features in African apes, meaning these features would have to have evolved before the *Gorilla*-*Pan*/*Homo* split, and (2) evidence in early hominins and/or modern humans of morphological features associated with knuckle-walking such as the distal projection of the dorsal radius, fused scaphoid-os centrale, waisted capitate neck, and long middle phalanges (see Richmond et al. (2001), Table 3, for complete list and explanation).

Support for parallel evolution of knuckle-walking in *Pan* and *Gorilla* (and usually a more arboreal common ancestor of *Pan* and humans) has been based on demonstrations of (1) morphological variation across African apes in most of the features traditionally associated with knuckle-walking (detailed in Kivell and Schmitt 2009); (2) variation in the ontogenetic trajectory of knuckle-walking morphological features



**Knuckle-Walking, Fig. 2** Alternative scenarios for the evolution of knuckle-walking. Knuckle-walking as a behavioral trait or suite of morphological features is indicated by the solid rectangle, and bipedalism is indicated by the hashed rectangle. (a) Knuckle-walking evolves independently in *Pan* and *Gorilla*, and terrestrial bipedalism

evolves in humans. This scenario implies an arboreal last common ancestor of African ape and humans. (b) Knuckle-walking is homologous in *Pan* and *Gorilla* and present in the last common ancestor. Knuckle-walking is retained in *Pan* and *Gorilla* and is lost upon the acquisition of bipedalism in the hominin lineage

(Dainton and Macho 1999; Kivell and Schmitt 2009) suggesting the same adult morphology may not reflect the same developmental pathway; (3) functional variation in knuckle-walking across African apes (e.g., Tuttle 1967; Inouye 1992, 1994; Shea and Inouye 1993; Matarazzo 2013) that suggests knuckle-walking itself is a different phenomenon in different animals; (4) functional or biomechanical similarities between climbing and bipedalism (e.g., Prost 1980; Fleagle et al. 1981; Stern and Susman 1981; Ishida et al. 1985); (5) use of bipedalism by great apes frequently in the trees (e.g., Hunt 1994; Thorpe et al. 2007; Crompton et al. 2010); and (6) the retention of arboreal features in early hominins (e.g., Tuttle 1981; Jungers, 1982; Stern and Susman 1983; Duncan et al. 1994) that implies bipedalism evolved in an animal adapted primarily for an arboreal environment and that used bipedalism when it came to the ground.

Reconstruction of the morphology and behavior of the last common ancestors of *Pan* and humans is fundamental to our understanding of the selective pressures and mechanisms by which our hominin ancestors diverged from other apes, and clarifying the evolution of knuckle-walking, a mode of locomotion shared almost uniquely within the animal kingdom by *Pan* and *Gorilla*, is essential to this process. Disentangling the morphological correlates of knuckle-walking, furthering our understanding of the ontogeny and biomechanics of knuckle-walking, and improving the representation of apes and the earliest hominins in the fossil record will all be critical to resolving debates regarding the morphology and behavior of African apes and our ancestors.

## Cross-References

- [Catarrhine Locomotion](#)
- [Convergent Evolution](#)
- [Hominid](#)
- [Hominoid](#)
- [Hominoidea Morphology](#)
- [Primate Locomotion](#)
- [Quadrupedal](#)

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## Konrad Lorenz

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## Definitions

Action Pattern,  
Fixed (FAP)

Synonymous to  
“Erbkoordination.”  
“Innate” behaviors similar to reflexes, the basic, species-specific elements of behavior, generated by neuronal “pattern generators” in the motor column of the spinal cord and being disinhibited either via short sensory-motor reflex loops or via the long associative loops activating the pallial motor neurons. The evolutionary prefabricated responses for the standard challenges of life. Their intensity varies with the quality of an external stimulus (see sign stimulus) and with motivation.

Behaviorism

Late nineteenth and twentieth century proponents were Edward Thorndike, John B. Watson, Burrhus F. Skinner. Although at least partially acknowledging the role of inheritance (e.g., reflexes), behaviorists held that behavior was mainly learned. Skinner denied heritable, species-specific

|                           |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |                    |                                                                                                                                                                                                                                                                                                                                                                                                        |
|---------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Evolutionary Epistemology | elements of behavior and “private” factors, such as emotions.<br>EE is a naturalistic approach, emphasizing the importance of natural selection in two primary roles: (1) In selection as the generator of our senses and cognitive mechanisms, explaining the “fit” between them and the world; (2) Trial and error learning and the evolution of scientific theories are construed as selection processes (Stanford Encyclopedia of Philosophy <a href="https://plato.stanford.edu/entries/epistemology-evolutionary/">https://plato.stanford.edu/entries/epistemology-evolutionary/</a> ). Main proponents were Donald T. Campbell, Karl Popper, Rupert Riedl, and Gerhard Vollmer. KL contributed significantly to EE (1941a, 1973b, 1977, 1992). | Innate Schoolmarm  | KL’s main argument against the stance of behaviorists (above), that most, if not all behavior would be learned (1978, 1980): To be adaptive, learning needs a (species-specific) innate template to direct individual attention towards the relevant contexts, thereby filtering the wealth of contexts and stimuli an individual may be exposed to.                                                   |
|                           |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       | Ethological Theory | On the mechanistic and also, functional causation of behavior (Tinbergen 1963), essentially a theory of instincts (Tinbergen 1951; Lorenz 1978). Behavior is adapted and behaviors (action patterns) are innate elements, triggered by external (key) stimuli and internal motivation. Learning makes for flexibility; what will and can be learned is constrained by an “innate schoolmarm” (above).  |
| Imprinting (Social)       | How altricial birds such as Greylag geese quickly learn who their parents are; time pattern different in precocial birds. Unclear whether this also applies to mammalian pups. In coherence with other elements of the Lorenz-Tinbergian theory, an “innate schoolmarm” provides a template in naïve hatchlings/pups in which fitting “sign stimuli” (shape, movement, sound) trigger a quick, lasting learning process. Further investigated by E. Hess.                                                                                                                                                                                                                                                                                             | Kindchenschema     | Earned KL and Niko Tinbergen the Nobel Prize in medicine 1973, together with Karl von Frisch.<br>Example of a syndrome of “sign stimuli” (“Schlüsselreize,” below), facilitating caregiving motivation on side of the receiver. This syndrome includes stimuli such as big, roundish heads, large eyes, short ears, and noses. Met in toddlers, in mammalian puppies or in precocious bird hatchlings. |

|                                                |                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
|------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Psychohydraulic Model of Motivation            | Cybernetic model of thought, holding that the specific motivation for each action pattern would accumulate (the “action specific potentiality”) and finally “spill over” if not acted out. Hence, the intensity of a behavioral response would be caused by the strength of an external triggering stimulus in combination with the intrinsic motivation. Today considered outdated as a general theory of motivation.                                                    | Sign Stimulus | all three modalities are active at the same time. “Schlüsselreiz-Konzept”: Perception coevolved with relevant stimuli in a way, that they specifically fit each other like lock and key, for example, red belly of opponent triggering territorial aggression in sticklebacks (Tinbergen 1951) or the stimulus features of the “Kindchenschema” (Lorenz 1973b, 1978).                                                                                                                                                                                                                                                         |
| Reflex Chain Theory                            | Pavlovian theory that behavior consists of chains of reflexes, as every action changes the stimulus context/propriosensory feedback and thereby, triggers the next action. Flexibility by learning, for example, conditioned reflexes. Refuted by E. v. Holst and KL, based on their results that behaviors can occur “spontaneously” and that via “appetitive behavior” individuals may actively seek for certain stimuli. Base for developing the “ethological theory.” | Vitalism      | Conceptual system leaving metaphysic loopholes in science. Proponents are early twentieth century biologists and psychologist, such as Gavin Rylands de Beer (1899–1972) and Jakob von Uexküll (1864–1944). They insist on a metaphysical (nonmaterial) element in instinct (“could neither be explained scientifically, nor would they be in need of such an explanation”). In contrast, KL always held that all behavior needs to be explained solely on the base of the “physicochemical mechanisms” in the brain. Thereby, he formulated the materialistic-reductionistic principles all science is obliged to adhere to. |
| Reizsummenregel (Alfred Seitz’s Summation Law) | Different external stimulus modalities trigger the same behavior and reinforce each other. For example, following behavior in precocious bird hatchlings towards an subject/object they are imprinted, is triggered by the shape, the movement and the vocalization of a “parental” subject/object; strongest if                                                                                                                                                          |               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |

### The Genesis of a Genius Observer: A Commented Chronology

Based on earlier biographies and contributions (e.g., Bischof 1991; Evans 1975; Festetics 1983; Föger and Taschwer 2001; Koenig 1988; Kotrschal et al. 2001; Lorenz 1985, Lorenz et al.



1998; Nisbett 1976; Schleidt 1988; [http://klha.at/kl\\_cv\\_cv.html](http://klha.at/kl_cv_cv.html)).

Konrad Zacharias Lorenz (KL) was born in Vienna/Austria and raised in Altenberg, a village at the river Danube NW of the capital Vienna, November 7, 1903. He was the last of the two children (his brother Albert was 18 years older, see A. Lorenz 1952) of Emma and Adolf Lorenz. Extremely talented and ambitious father Adolf (1854–1946) was of working class origin (Adolf's father was a saddler). He became professor for orthopedics at the Medical branch of the University of Vienna and a world leader in the innovative treatment of innate hip dysplasia and other skeletal conditions. He earned and – for different reasons – lost a fortune three times over his lifetime. For his scientific achievements, Adolf was himself nominated for the Nobel Prize eight times but never received it. In 1903, when KL was born, the representative and spacious historicistic Lorenz family villa in Altenberg was just completed. In this house and its park-like garden, KL kept and raised a wealth of different animals from early childhood on and thereby, acquired his mental library of systematic observations of animal behavior which became the substrate for developing his general basic theory of behavior and psychology, essentially a theory of instincts.

KL's mother Emma Lorenz (prev. Lecher, 1862–1936) was a Vienna Belle Époque lady, working hard in her husband Adolf's praxis. She was born as one of six children of the leftish journalist Zacharias Lecher, for some time director of the liberal Austrian newspaper *Die Presse* (still existing today). Emma was related and befriended with a range of leading Vienna entrepreneurs and artists, among them writer Richard Engländer, alias Peter Altenberg (1859–1919). Hence, KL grew up in a wealthy, cultural, and intellectual fin de siècle upper-class environment. But he also grew up embedded in nature and in intense touch with animals, his great passion and keen interest from early childhood on. KL was co-raised by his nurse Resi Führinger, a farmer's daughter, who kept being an essential assistant in animal keeping, even as the boy grew into a young man. At the same time, KL shared with his father a faible for the newest technology, notably, posh

cars and motorcycles. Within this frame the gifted child developed into a genius observer and biologist, able to express himself in perfect German, English, and French, both in speaking and writing. Like Sigmund Freud, his writings were not only cheered for contents but also for their literary quality. Hence, the quality of KL as a biologist was rivalled only by his skills as an incredibly charismatic communicator. This was certainly a blessing for the new discipline of ethology/behavioral biology to become rapidly acknowledged and popular among scientists and laypersons as well. On the downside, particularly in the second half of the twentieth century, KL's assertive style and also, his skeptical stance towards hypothesis testing were not in favor for the development of the science of behavioral biology.

KL was born into the early twentieth century, which saw a dynamic and diverse development of psychology and behavioral sciences. In 1904, the University of St. Petersburg-based Physiologist Ivan Pavlov (1849–1936) was awarded the Nobel Prize for his research on the conditioned reflex and the development of the “reflex theory” of behavior. This theory was refuted 30 years later by KL and Erich von Holst and developed into the “ethological theory,” based on the simple, but revealing experiments by von Holst, showing that motor behavior can be generated even at the absence of external stimuli or sensory feedback. At the beginning of the twentieth century Sigmund Freud (1856–1939) published some of his most well received concepts, including on “drives.” Interestingly, KL never explicitly related to, or quoted Freud, except for ridiculing some of Sigmund Freud's “drives,” for example, “Thanatos” (the death drive). Still, their instinct theories were relatively similar to each other, supporting the assumption that KL was influenced by Freud. This is more likely, as KL learned most of his basic psychology at University of Vienna-based psychologists Karl Bühler (1879–1963; “Gestalt psychology”) and Charlotte Bühler (1893–1974; “Viennese Child Psychology School”).

Niko Tinbergen, KL's lifelong colleague and lifelong close personal friend, was born April 15, 1907, in Den Haag (died 1988 in Oxford/UK), The Netherlands. At that time, 4-year-old

KL started keeping animals in aquaria, such as spotted newts, assisted by his nurse, he raised a first duckling which imprinted on him and was disappointed by the lack of loyalty of his first dog, a dachshund. The little boy first wanted to become an owl, but then changed his mind in favor of being a duck, when he learned that owls cannot swim, or a goose, motivated by Selma Lagerlof's "Niels Holgerson." KL entered elementary school in 1909 and soon engaged in first systematic studies on crustaceans.

In 1910 Oskar Heinroth, Berlin zoo-based biologist and one of the founders of the "Vergleichende Verhaltensforschung" (comparative ethology) published his classical paper on the behavior of ducks. He was later "adopted" by young KL as a scientific father figure and mentor (Koenig 1988). KL's own father Adolf was tolerant towards the animal passion of his son, turning scientific already early on; but he did not see his son's future in zoology. Instead, he would later urge KL to study medicine, which would turn out to benefit the scientific development of KL.

In 1915, KL entered the Vienna elite high school "Schottengymnasium," where he remained until 1921. During this period, post-World War I Austria degenerated into an intellectually dull catholic "Ständestaat" dictatorship, terminated 1938 by the Nazi occupation. Under the Ständestaat regime teaching evolution at schools was discouraged, which only changed with the Nazi regime. Therefore, it is remarkable that KL was inspiringly taught about Darwin and evolution in high school by Philip Heberdey, a Benedictine monk. Basically, he had already discovered evolution by himself by observing nature and reading Wilhelm Bölsche at the age of 10. During high school, KL started keeping and breeding many songbirds.

In 1918 Wallace Craig (1876–1954), University of Maine-based, US experimental psychologist and behavior scientist published "The comparative ethology of Columbidae" (pigeons), a classic of late US zoologist Charles O. Whitman (1842–1910). This influenced KL to a significant extent, as did his regular exchange of letters with Oskar Heinroth (Koenig 1988). Later, during his

time of assistantship at F. Hochstetter (below), KL was in contact with W. Craig and he, as well as O. Whitman and O. Heinroth laid the ground for classical ethology, established later by KL and N. Tinbergen. Actually, W. Craig first criticized first KL's adherence to the Sherrington/Pavlovian reflexology, on the basis of the existence of "appetitive behavior" (i.e., the active search for favorable contexts or stimuli), long before E. v. Holst (below) convinced him of the flaws of this theory. All of them may be considered the founders of ethology, which was always fully acknowledged by KL.

In 1921, KL excelled in his final high school exams. Together with his friend Bernhard Hellmann he conducted observational and experimental work on crustacean development and also, on aggression in a *Geophagus* cichlid. This crucial experience inspired KL's concept on drives and motivation, which is generally referred to as the KL "psychohydraulic model of motivation" and was a base for his most widely perceived and controversial book *On aggression* (1963, 1966). His Jewish companion and friend Bernhard Hellman would later be killed in a Dutch Nazi concentration camp.

In 1922, his father Adolf urged KL to study medicine instead of Biology or Paleontology, as preferred by KL; he sent his son off to take two semesters of medicine courses at the New York Columbia University. The main intention behind this was to interrupt KL's relationship with his long-term girlfriend Margarethe "Gretl" Gebhardt (1900–1986), his later wife. Gretl was KL's close partner and companion from early childhood on but was lower class in origin and therefore, not considered an adequate match. However, the paternal attempt to influence KL's mate choice failed. They finally married (below), Gretl became an engaged medical doctor and contributed much of the income of the growing young family before till and after World War II. In the USA, KL spent more time studying marine organisms on his own in the field than with his official university duties. He also met the eminent, California Institute of Technology-based US biologist and geneticist Thomas Hunt Morgan (1866–1945, Nobel Prize

1933), but it remains unclear how influential this was for KL's further development.

KL successfully engaged in motorcycle racing from 1924 to 1930, when he broke his lower jaws in an accident and ever since wore his characteristic chin beard. On intervention of Gretl, he had to stop racing. Still, Gretl herself was an enthusiastic and successful motorcycle racer. She only stopped racing after she had two children.

In 1926 KL hand raised his first jackdaw "Tschok," an experience which contributed much to his theory on imprinting. From 1927 till the mid of the 1930s he published a series of papers (e.g., 1927, 1933), initially mentored by eminent Berlin ornithologist Erwin Stresemann (1889–1972). These papers on innate behavior and instinct laid the ground for his early international reputation as a leading behavioral biologist, particularly with birds.

KL and Margarethe Gebhardt, both students of medicine, married on June 24, 1927. Their first son Thomas was born on October 31, 1928 (–1982). He became an acknowledged researcher in physics at the University of Munich. KL finished his medical PhD and thereupon, accepted an assistant professorship at the University of Vienna II. Anatomical Institute, headed by eminent comparative anatomist and embryologist Ferdinand Hochstetter (1861–1954). KL learned much about ontogenetic development, which influenced his thinking quite a bit. In parallel, KL started studying zoology, mainly at the University of Vienna Zoological Institute of Jan Versluys. He accidentally cross-bred his male German shepherd with his wife's female Chow Chow, resulting in a behaviorally most fascinating dog ("Stasi"). Stasi also became the star in one of KLs most popular books (*Man Meets Dog*; 1950, 1954). Inspired by this book, a new FCI dog breed was established in the 1960s, the "Eurasier." In 1930 their daughter Agnes (married "von Cranach" – 2009) was born.

In 1931 KL met Oskar Heinroth for the first time, followed by 10 years of intense correspondence between the two, mainly on bird behavior. These letters were edited (i.e., cleansed of political and private content) and published 1988 by Otto Koenig (1914–1992), a Vienna-based

naturalist and ethologist and scholar of KL, who established the Vienna "Biologische Station Wilheminingenberg," which still exists as "Konrad Lorenz Institute of Comparative Ethology," presently part of the Veterinary University of Vienna.

In 1932, KL saw "fly catching" behavior at the absence of an aerial insect in a captive starling. He concluded, that behavior can be "spontaneous" (i.e., triggered by intrinsic factors). The same year, the German Ornithological Society convened her annual meeting in Vienna. Participants, among them the King of Bulgaria, visited the "Ornithologische Versuchsanstalt," KL's private research institute, in Altenberg. Father Adolf was amused about all this fuzz about birds, but at the same time he was deeply impressed by the international and high-level attention his son received. Gretl Lorenz finished her PhD in medicine. In 1933, KL finished his zoological PhD on the topic of bird flight (see also Lorenz 1935) and met Julian Huxley (1887–1975) in 1934, at an ornithological Conference in Oxford.

When Ferdinand Hochstetter retired from his professorship in 1935, KL was longer employed by his successor at the anatomical institute, Eduard Pernkopf. KL frequently attended the seminars of the University of Vienna psychologist Karl Bühler and his assistant Egon Brunswick, who pointed KLs attention to the fact that his comparative results contradicted the vitalistic or "instinctivistic" school of W. MacDougall and the behavioristic school of J.B. Watson et al. KL was struck by the ignorance of behavioral mechanisms by these eminent experimental psychologists, as expressed in one of his letters to O. Heinroth (Koenig 1988). He felt overwhelmed by, and took responsibility for, the huge mission ahead: to produce a unified, evolutionary theory of animal and human behavior and psychology.

In 1936, KL hand raised his first Greylag goose (*Anser anser*) "Martina." This started a lifelong scientific and emotional passion, later continued at his Max Planck Institutes at Buldern and Seewiesen, and after his retirement, at the Konrad Lorenz Forschungsstelle in Grünau (below). KL met Niko Tinbergen (1907–1988; Dutch behavioral biologist, later University of Oxford-based founder of ecoethology), for the first time at a

symposium at Leiden University. A lifelong close collaboration and tight personal friendship began, manifest in hundreds of long letters (unpublished) exchanged between the two over the decades, till NT died. Their friendship outlasted all serious topical and political challenges. Ivan Pavlov died in Leningrad. The same year KL met Erich von Holst (1908–1962), in Berlin February 12, on the occasion of a lecture KL gave in Berlin. This started a lifelong cooperation. Von Holst was a German neuro-ethologist and later, codirector with KL, of the Max Planck Institute of Behavioral Physiology in Buldern and in Bavarian Seewiesen thereafter. Von Holst quickly changed the mind of KL regarding the Pavlovian “reflex chain theory” KL had adhered to till then, albeit with little enthusiasm. Both men independently reached the conclusion that “spontaneous” behavior is not just triggered by external sensory stimuli or sensory feedback. Thereby, they falsified the Pavlovian theory. This was key in establishing the new ethological theory.

In early summer 1937 Niko Tinbergen and KL cooperatively conducted experiments on the “Instinkt- Dressur-Verschränkung” (i.e., the interdigitation of instinct and learning) and investigated some of the features of innate behaviors (i.e., “Instinct and Taxis” in these behaviors, later called “Fixed Action Patterns,” one of the core concepts of classical ethology) in the garden of the Altenberg Lorenz villa. Their example was the egg-retrieval behavior (“Eirollbewegung”) in Greylag geese (Lorenz and Tinbergen 1938). The geese they worked with were F1 hybrids between greylag and domestic geese. KL recognized somewhat changed instinctive behavior in these hybrids as compared to greylags. This sparked his lifelong concern regarding the genetically caused “degeneration of instincts” in domesticated animals or in “self-domesticated” man (1974). Together with Otto Koehler (1889–1974), German ethologist, KL became editor of the “Zeitschrift für Tierpsychologie” (from 1985 continued as “Ethology”). First translations of KL papers were published in the USA, he wrote major contributions on instinct (Lorenz 1937) and became “Privatdozent” (“Habilitation,” an

academic procedure following the PhD till today in the German-speaking countries) at the University of Vienna with the *Venia legendi* for anatomy and animal psychology, because behavioral biology as a discipline was not yet established.

The Nazis occupied Austria in 1938. KL at first sympathized with the regime and even applied for NSDAP membership that year (Föger and Taschwer 2001). KL was taken by the modernistic, progress- and science-oriented appearance of the new regime, which swept out the dull catholic Austrian dictatorship. Like his father and many other biologists, he was in favor of the Nazi’s emphasis on eugenics and produced contributions in outright Nazi jargon (1940). But all evidence indicates that KL was neither racist nor anti-Semitic. Almost certainly, KL hoped that his adaptive conformism with the Nazi regime would earn him a Kaiser-Wilhelm Research Institute (the forerunner of German Max Planck Institutes) in Altenberg. However, this did not work out; KL was sent to the Russian front as an ordinary soldier in 1944, underlining his minor role in the Nazi system.

In 1938, Karl Bühler had to give up his professorship at the University of Vienna, because he rejected to divorce his Jewish wife Charlotte. The Böhlers fled to the UK and Norway and finally, to the USA. Mentored by Erich von Holst and Eduard Baumgarten, German philosopher and sociologist (1898–1982), KL became full professor for Psychology at the University of Königsberg in 1939, as one of the successors of Immanuel Kant. KL described the “Kindchenschema” (schema of childlike characteristics) and his PhD student Alfred Seitz worked out the “Reizsummenregel.”

Daughter Dagmar was born in Vienna, January 11, 1941, and the family moved to Königsberg in June. On October 10, KL was drafted into the German army. A major publication of KL on Kant’s theory of the *a priori* in the view of Darwinian biology appeared and another one on the taxonomic value of innate behaviors in anate birds (ducks, swans, and geese). From 1942 KL worked as an army psychiatrist in a military hospital in Posen/Poland, for some months, where, as

a medical doctor, he had the opportunity to get some firsthand knowledge about neurosis, particularly hysteria, and about psychosis, particularly schizophrenia. KL also assisted in the interviewing of “mixed-race” German-Polish people and in racist phenotypic measurements, which, however, left no trace in his writings. During this time he could still continue his scientific exchange, for example, with Max Planck. He once more refuted the teleological thinking of Dutch animal psychologist Bierens de Haan (1883–1958) and of other “vitalists.”

In 1942 KL was sent to the Russian front near Vitebsk, where he was captured only months later. From 1942 to 1948, KL was POW in various camps in Russia and Armenia till 1948. For example, he first worked in a hospital at Chalturin, mainly with traumatized soldiers. As a camp doctor and psychologist, KL cared for fellow prisoners at Oritshi and later, in a number of POW camps in Armenia. In friendly contact with fellow Russian doctors he saw the parallels between Nazi ideology and Marxist indoctrination, which immunized him against ideological appropriation for the rest of his life. He wrote a manuscript on general and human ethology (“The Russian manuscript”) with potassium permanganate ink on concrete sack-ing paper. At home, KL was officially declared dead. Father Adolf Lorenz died at the age of 92 in Altenberg, February 16, 1946.

On February 18, 1948, KL returned to Altenberg, together with his hand-raised Armenian starling “Friederich” in a self-knit wire cage and with the “Russian manuscript” in his backpack. This manuscript remained unpublished at first, was even lost in the 1960s, and was found in the attic of the Altenberg home of KL after his death. It was finally published by daughter Agnes von Cranach (1992).

After returning home, KL had no job. He and his family received some support by academic colleagues and friends, such as Wolfgang Schleidt, Otto Storch, Otto König, and Wilhelm Marinelli. Soon, the Austrian Academy of Sciences financed the KL research station in Altenberg with the money donated for that purpose by the English poet and writer J. B. Priestley.

KL just had money to support animal keeping. To feed the family and KL’s research team, Gretl Lorenz had given up her medical practice to run the farm of her parents near the city of Tulln. Wolfgang Schleidt (1927–), by that time associated Garden University/USA, Ilse and Heinz Prechtl (1927–2014), later professor at Groningen University, as well as Eleonore and Irenäus Eibl-Eibesfeldt (1928–), later a founder of human ethology, joined KL’s initial research team.

In autumn 1948, William H. Thorpe of Cambridge University/UK visited KL to offer him a lectureship in England. But KL was confident to receive a call from an Austrian university, which indeed happened, as Karl v. Frisch left his chair in Graz for Munich. However, Felix Hurdes, the Christian-conservative Austrian minister of education vetoed against KL, the “Darwinist.” Now, KL was ready to accept a University of Bristol lectureship position, with the additional task of ethological research at the Severn Wildfowl Trust at Slimbridge. Seemingly, Sir Peter Scott (1909–1989), British ornithologist, conservationist, painter, naval officer, broadcaster, and sportsman, was another driving force behind this.

To keep KL in Altenberg, the German Max Planck Society paid KL a moderate salary, as there were already plans to establish a Max Planck Institute for him. Hence, KL remained in a waiting position at home over 1949. His wife Gretl persuaded KL to use his talents for earning money. Hence, KL wrote two popular books, best sellers at first and long-sellers till today, one featuring autobiographic animal stories (1949, 1953: *King Solomon’s Ring*) and another one on dogs (1950, 1954: *Man Meets Dog*).

On May 5, 1950, the first ethologists meeting after the war was convened in Wilhelmshaven/Germany, reuniting KL with his friend Niko Tinbergen, who spent part of the war in a Nazi concentration camp. The Max Planck Society established the first “Max-Planck-Institut für Verhaltensphysiologie” for KL in codirectorship with E. von Holst in Buldern/Westfalia, Germany, where he moved on October 25 together with his family, joined by assistants Irenäus Eibl-Eibesfeldt, Wolfgang Schleidt, and Heinz Prechtl. KL was elected honorary member of the British



Association for the Study of Animal Behavior (ASAB).

In 1951 KL became honorary member of the German Ornithological Union as well as of the American Ornithologists Union. This started of a long series of awards, medals, honorary memberships and a total of 11 honorary degrees from universities worldwide, including Yale 1967. The University of Salzburg was the only one to withdraw KL's honorary degree in 2016, out of presentistic morality related to KL's Nazi involvement. Niko Tinbergen published his "Theory of Instincts" (1951).

In 1953, Daniel S. Lehrmann (1919–1972), US naturalist and comparative psychologist launched a vigorous critique of the ethological concept of the innate in the top-journal "Science." Discussions followed in a series of meetings, starting in Paris 1954, convened by Pierre-Paul Grassé. The conflict between nature-orientated European ethologists, notably KL and nurture-orientated US experimental psychologists, resulted in fertile discussions, prompting Niko Tinbergen (1963) to include ontogeny into his "four levels" (below). This debate dissolved the false dichotomy between "innate" and "learned" (Lorenz 1961), thereby anticipating modern epigenetics.

In 1954 the Max Planck Society decided to create a new institute for KL and Erich von Holst in Bavaria ("Seewiesen," a name coined by Wolfgang Schleidt (above), later professor for ethology at the University of Maryland. This new MPI for Behavioral Physiology was opened September 16, 1958, by Otto Hahn (1879–1968), German chemist, Nobel Prize winner 1944 and president of the Max Planck Society.

In 1960, for the first time in his life, KL SCUBA-dived coral reefs in Florida, guided by US behavioral biologist Art Myhrberg. This sparked KL's ideas on the functions of poster coloration and was a major inspiration towards his book on aggression (1963).

In 1962, Erich von Holst, his long-term colleague, friend, and mentor died.

In 1963 KL published his hotly debated and probably most influential book *Das sogenannte Böse* ("On Aggression"), where he described aggression as an adaptive system (contradicting

mainstream psychological "frustration theory"). This book triggered a wave of biopsychological research on aggression. The same year Niko Tinbergen published his programmatic paper: "On Aims and Methods of Ethology," which was dedicated to KL at the occasion of his 60th birthday. The so-called four levels of Tinbergen describe the major levels features and characters of evolutionary origin can be investigated, evolutionary and proximate function, ontogeny and evolutionary history. Tinbergen formalized the Lorentzian approach, which till today remains the fundamental research not only in ethology but in entire organismic biology. This basic theory frame was based on concepts by Greek philosopher Aristotle (384–322 BC) and by Scottish Philosopher and Economist David Hume (1711–1776), among others.

In 1970, KL's older brother Albert Lorenz (1885–1970), medical orthopedist doctor and assistant of father Adolf (see A. Lorenz 1952) and mentor of KL died.

In 1971 KL first published a popular book, which was among his most recognized texts: *Civilised Man's Eight Deadly Sins* (1973a), a discussion of human social problems from an (outdated and biologicistic) evolutionary perspective. The book has a strong culture-pessimistic tone, inspired by late German Idealism and by Philosophical Anthropology in the tradition of Arnold Gehlen (1904–1976), German philosopher, anthropologist, and sociologist. This book shows that KL faithfully adhered to his ideas on the "self domestication" of man even after World War II.

In 1973 KL retired from his directorships at the MPI in Seewiesen and returned to Austria. He transferred a free-flying flock of >100 Greylag geese into the Upper Austrian Almtal, near Grünau and the same year established the local Konrad Lorenz Research Station (KLF), hosted by the Duke of Cumberland Foundation. Essentially, he would spend the summers there till his death, in the company of his Greylag geese and collaborators. KL was elected head of the Behavioral Biology section of the Austrian Academy of Sciences which also started moderate funding of the KLF. KL published the foundations of his

“Evolutionary Epistemology,” inspired by a combination of evolutionary theory and Kantian concepts, in his book *Behind the Mirror* (1973b, 1977). On December 10, KL, Niko Tinbergen, and Karl von Frisch were awarded the Nobel Prize for Physiology and Medicine “for their discoveries concerning organization and elicitation of individual and social behaviour patterns”: [https://www.nobelprize.org/nobel\\_prizes/medicine/laureates/1973/lorenz-facts.html](https://www.nobelprize.org/nobel_prizes/medicine/laureates/1973/lorenz-facts.html)).

In 1974 KL built his huge, 34,000 l reef tank in Altenberg with the Nobel Prize money in a building owned by chemist and former Seewiesen assistant Guido Hückstedt. Old KL basically spent his winters writing and observing reef fishes in Altenberg, his summers observing geese in Grünau. Most of his fish work remained unpublished, only parts were published after his death (1998, see below). The aquarium was destroyed after KL had died.

In 1978, KL published his textbook *Vergleichende Verhaltensforschung* (“Comparative Behavioral Biology”), dedicated it to Niko Tinbergen.

In 1979 KL reluctantly accepted his role as a spearhead environmentalist at the forefront of establishing a Green party in Austria. After his bad World War II experiences with the ideological abuse of science he tried to stay off politics, but still took increasing interest in, and responsibility for environmental issues. He had an important role in preventing yet another big hydroelectric power plant at the river Danube, which would have destroyed much wetland and as part of a movement of citizens he had an important role in keeping Austria free of atomic power plants.

In 1981, the Konrad Lorenz Institute of the Austrian Academy of Sciences, with branches in Altenberg and Grünau was established.

KL's wife Margarethe Lorenz died January 16, 1986. Lifelong she was his best friend, his manager, his main partner, critically discussing his manuscripts and not the least, his moral custodian. As a medical doctor she earned the living for her growing family before 1940, when KL was unemployed and concentrated on behavioral research and she was the social backbone of virtually every institute where KL was leading

director. In 1988 KL's last book, a semiscientific monography on Greylag goose behavior was published (Lorenz 1988). However, KL was unable to finish his last project, a monography on the behavior of perciform fishes, intended to integrate his lifetime experience, collected virtually from his cichlid experiments in the 1920s to Moorish idol social ontogeny research in the 1980s.

On February 27, 1989, Konrad Lorenz died at the age of 86 in his Altenberg home.

The Austrian Academy of Sciences stopped funding of the Konrad Lorenz Forschungsstelle in Grünau. Still, this research station survived till today, since 1990 headed by the author of this contribution; it first existed as a cooperation between the local landowner (Duke of Cumberland), the State of Upper Austria, and the University of Vienna. In 2011, the KLF reached University of Vienna Department status. The two other “Konrad Lorenz Institutes” are the “KLI for Comparative Behavioral Biology” at the Vienna Wilheminenberg, founded by Otto Koenig after World War II, later an Institute of the Austrian Academy of Sciences, today part of the University of Veterinary Medicine, Vienna. Finally, there is the privately funded “KLI for evolution and cognition research,” residing first in the Lorenz-Villa in Altenberg, now in an institute building in Klosterneuburg, near Vienna. The Grünau and the Wilheminenberg institutes are dedicated to empirical/experimental behavioral biology till today, the Klosterneuburg Institute remains theoretically orientated.

In all three cases, there is indirect continuity between Konrad Lorenz and his successors. In contrast to Niko Tinbergen, KL initiated no vital and continuous “school” of behavior results, but influenced present day research more indirectly than Tinbergen did. Also, the original intention of the Max Planck society was not fully successful, to establish a group of geniuses around Konrad Lorenz in Seewiesen, and thereby, catalyze an explosion of novel high-class interactive research. This was certainly a highly fertile Institution, but the kind of close cooperation between ingenious researchers and disciplines the MPG had in mind did not fully materialize.

## Achievements: What Remained and What Did Not

KL built his oeuvre on years of systematic observations and experiments. Actually, he frequently advocated “unbiased observation” as a major approach to detect novelty (e.g., 1992) and tended to be skeptical of “testing hypotheses.” He also reacted to the speculative, vitalistic, and behaviorist concepts on behavior of many experimental psychologists and behaviorists in the first half of the twentieth century. Basically valid till today remained the centerpieces of “ethological theory”: As O. Whitman and O. Heinroth before him, KL found that basically innate, stereotyped behavioral elements (“Erbkoordinationen,” i.e., “Fixed Action Patterns”; FAPs) are the core elements in animal behavior, including humans. They are species-specific, hence varying less within than between species. The species-specific shape of the FAPs renders them useful for taxonomic classification (Lorenz 1941b) the same way as anatomical characters in classical taxonomy. Another element of classical ethology is that perception and behavior coevolved like a lock and its fitting key; this “key stimulus” concept holds that many of the FAPs are triggered by specific but generally simple stimuli.

KL together with Erich von Holst found that animals including humans, are not only behaving in response to external stimuli or sensory feedback, but that they may be “spontaneously” active, meaning they respond to internal stimuli, which in sum are called “motivation.” Together with Niko Tinbergen, KL elaborated on the fixed and “taxis” (i.e., orientation) components of FAPs (Lorenz and Tinbergen 1938). In response to, and in development of, Ivan Pavlov’s “reflex chain theory.” KL and others refuted, that individuals are born with “*tabula rasa*” minds and that all behavior(s) would be learned, as, for example, the behaviorist, notably, Frederic B. Skinner (1904–1990) advocated. KL knew that learning would adapt species and individuals to cope with environmental variability, but held that they would be born with innate perception/attention structures. Actually, KL acknowledged that the discussions with D. Lehrman

inspired his “innate schoolmarm” concept (1980), later called “instinct to learn” by Peter Marler. This “innate schoolmarm” orchestrates what is learned and what not. KL described “social imprinting,” notably in Jackdaws and in Greylag goose hatchlings, and he conducted some experiments on the stimuli involved. Still, at the focus of KL’s work were innate, instinctive behaviors (Lorenz 1937), not so much the mechanisms of learning. To this day, the Lorenz-Tinbergian principles remain basic to behavioral biology and biopsychology.

Based on his broad and systematic knowledge of animal behavior in integration with some concepts of Immanuel Kant, KL too laid the theoretical foundations for human ethology. In particular, he made clear, that the human perception and brain and thus, cognitive abilities, must have been selected for their survival value. Thereby, he also contributed to “Gestalt Psychology” and “Evolutionary Epistemology” (“Evolutionäre Erkenntnistheorie”; 1973b, 1992; with University of Vienna-based biologist and philosopher Rupert Riedl 1925–2005 as a major proponent). It also remains a lasting contribution of KL not to see aggression simply as a “social pathology” but as a potentially adaptive motivational/emotional system (1963, 1966). But some of the Lorentzian ideas did not stand the test of time, for example, his concept on the proximate mechanisms of motivation: KL suggested that each behavior (FAP) would have its own, independent drive system. And if a certain action pattern would not be used for a while, “action-specific energy” would build up (KL’s “psychohydraulic model of motivation”) and finally, “spill over.” This may adequately describe the aggressive behavior of a territorial cichlid fish, but it is unsuitable as a general model of motivation of aggression or of other domains of behavior. The general rule of today tends to become the special case of tomorrow, as KL himself frequently put it.

KL tended to overstretch the societal relevance of his behavioral concepts and of the (crude) genetics of his time. This is particularly evident in the context of his lifelong preoccupation with the “self-domestication of man” (e.g., 1971, 1974). KL advocated eugenics in the 1940s, as

many biologists worldwide did at that time. But he publicly regretted this mistake after the war and particularly apologized for his 1940 papers when being awarded the Nobel Prize in 1973. Still, he seemed to remain convinced, that civilization would change selection pressures in a way causing the “genetic degeneration” of mankind. This would lead to a general deterioration of human social behavior. This misled genetic determinism and cultural pessimism in the tradition of Arnold Gehlen remains a problematic part of KL’s legacy, which, however, is not directly connected to his major ethological concepts.

After World War II, KL turned towards the mechanisms of social organization he observed in the animals he had previously employed for establishing the general principles of individual behavior, geese and perciform fishes. Even at the boom times of individual selection, in the late twentieth century, KL remained a convinced group selectionist, opposing, for example, the writings of E.O. Wilson. In contrast to his work before World War II, only little of his late results and thinking were adequately published (see Lorenz 1973b, 1978, 1998). Instead, KL increasingly commented on those developments in society, he was deeply concerned about (e.g., Lorenz 1973a). This made him a “guru”-like figure (he was not really happy with such a role) for generations of environmentalists.

KL was an eminent scientist and a splendid communicator. He made behavioral biology a “real” science (e.g., in contrast to the early twentieth century vitalistic approaches). From early on, KL was convinced that all behavior needs to be explained via the “physicochemical processes in the brain.” Based on the Darwinian principles he made clear, that animal and human psychology are inseparably the same discipline. This kind of synthesis is in fact, reflected in contemporary academia. KL popularized behavioral biology worldwide, particularly, in German-speaking countries.

For an autobiographical sketch highlighting also KLs scientific milestones see [https://www.nobelprize.org/nobel\\_prizes/medicine/laureates/1973/lorenz-bio.html](https://www.nobelprize.org/nobel_prizes/medicine/laureates/1973/lorenz-bio.html)

## Cross-References

- Adaptedness of Behavior
- Aggression
- Aristotle
- B.F. Skinner
- Behaviorism
- Birds
- Comparative Psychology
- David Hume
- Domestication
- E.O. Wilson
- Edward Thorndike
- Epigenesis
- Ethogram
- Fixed Action Patterns
- Gestalt
- Immanuel Kant
- Imprinting
- Instinct
- Ivan Pavlov
- John B. Watson
- Learning
- Motivation
- Nature Versus Nurture
- Nikolaas Tinbergen
- Ontogeny
- Patrick Bateson
- Taxis
- Ultimate Causation
- Wolfgang Köhler (1887–1967)

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- Relatively complete Bibliographies of KL can be found in some biographies below, at [https://de.wikipedia.org/wiki/Konrad\\_Lorenz#Schriften](https://de.wikipedia.org/wiki/Konrad_Lorenz#Schriften) or at <http://klf.univie.ac.at/de/das-institut/konrad-lorenz/publikationen-von-konrad-lorenz/>.
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## K-Reproductive Strategy

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## Definition

A K-reproductive strategy is a set of life history traits that would be selected for when a population reaches highest density. The terminology is taken from a parameter in population growth models, where carrying capacity ( $K$ ) is the maximum population size that can be supported by an environment. The opposite strategy is an  $r$  reproductive strategy, after the parameter for the maximum intrinsic rate of natural increase ( $r_{max}$ ) at theoretically zero density.

## Origin of the Concept

The terms  $r$ - and  $K$ -strategy originated from “ $r$ -selection” and “ $K$ -selection,” which were first coined by MacArthur and Wilson (1967). On a



hypothetical island with a starting point of abundant resources, these resources would become limited as the island is fully occupied. Using this example, the authors proposed that different selection regimes would operate as resource limitation experienced by a population changes between two opposing ends of density dependence – low to high density. Under this scenario, high density and thus high level of competition over resources would favor traits that maximize carrying capacity, hence the K-selection.

Pianka (1970) expanded the concept of *r*- and *K*-selection to develop a theory of life history strategies. He considered that the life history of an organism is a position on a continuum between a quantitative extreme (the *r*-endpoint) and a qualitative extreme (the *K*-endpoint). Importantly, Pianka developed a set of predictions for the life history correlates expected under *K*- and *r*-selection. In a high-density environment, *K*-selection would favor traits that allow for organisms to persist in the face of scarce resources such as high competitive ability, delayed maturation, longer lifespan, larger body size, and iteroparity. A suite of opposite traits would be expected under a low-density environment through *r*-selection. These alternative sets of life history traits became known as “*K*-strategies” and “*r*-strategies.”

The idea of *r*- and *K*-selection, and Pianka’s broadening of the idea into life history strategies, have been influential to the study of life history evolution. Most of all, it appealed to the desire to enumerate a simple yet generalizable explanation for life history diversity. Here the degree of density dependence was used as a major axis to explain the covariation of certain life history traits across species. For example, based on an inverse correlation between  $r_{max}$  and body size, Pianka compared insects and vertebrates for their non-overlapping distribution of body size to suggest bimodality in life history traits among relatively *r*- and *K*-selected organisms. Similarly, later studies incorporated the comparative approach for different species or different populations of the same species. But differences in the density experienced by organisms were often only assumed or inferred but not directly tested for its causal contribution to life history differences.

## Current Developments

Numerous empirical and theoretical studies have pointed out the limited applicability of *r*- and *K*-selection theory. First, in experimental evolution studies, fruit flies (Mueller 1988) or pitcher plant mosquitoes (Bradshaw and Holzapfel 1989) bred under high or low densities evolved differences in competitive ability, consistent with MacArthur and Wilson’s predictions. However, their life history traits did not differ by breeding lines as Pianka would predict. Second, mathematical models of selection have shown limitations of the *r*- and *K*-selection theory. For example, the theory assumes that *r* and *K* approximate fitness, but this assumption would be valid only when population growth rates follow the logistic equation and not when we take into account of factors such as population dynamics or age structure. Current theories, including those put forward by Charlesworth (1980) and Stearns (1992), further incorporate age-specific mortality or density-independent factors such as environmental stability to understand the causal link between the environment and an optimal life history. Theoretical consideration has also provided no support for the idea that density-dependent selection will explain the evolution of semelparity vs. iteroparity.

Due to these problems, the theory of *r*- and *K*-selection was gradually replaced by models that describe specific conditions of population density dependence and the magnitude of environmental effects. As accurate measures of these factors are hard to evaluate in natural populations, challenges remain for current paradigms of life history evolution.

## Cross-References

- [Competition](#)
- [Fertility](#)

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## Kyoto

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## Introduction

KYOTO is a prefecture in Japan, located in West-Central Honshu (Kansai region). Previously the capital city of Japan, it has over 2000 temples and shrines and attracts many tourists from all over the world. There are many universities and colleges in Kyoto, including Kyoto University. Kyoto University occupies an important position in the field of animal cognition and evolution in Japan as it established the Primate Research Institute, leaders in Japanese primatology. This entry describes the development of the Primate Research Institute, with a special focus on one of its founders, Dr. Kinji Imanishi.

## Kinji Imanishi (1902–1992)

Kinji Imanishi is considered one of the key founders of Japanese primatology. He began his research studying aquatic insects as a graduate student and received a Ph.D. from Kyoto University in 1939. His thesis, entitled “Mayflies from Japanese torrents,” proposed his original theory of

evolution, based on his studies of Ephemeroptera in the Kamo River in Kyoto (Imanishi 2002). His theory emphasized the society of species and divided organisms into three layers, namely, individual, species, and holospecies. Imanishi considered individuals living in the same niche to have similar characteristics and comprise a species (Matsuzawa and McGrew 2008).

During World War II, Imanishi went to Mongolia and began to study mammalian society in wild horses and nomadic people. After the war, he returned to Japan and continued to study horse society in Misaki-uma, a breed of semi-wild horse, in Cape Toi, Miyazaki Prefecture. During this project, Imanishi and his colleagues met a group of wild monkeys and decided to study the society of monkeys, beginning with wild Japanese monkeys on Koshima Island, Miyazaki Prefecture, in 1948. Imanishi went on to study wild monkeys at 19 sites in Japan, including Yakushima and Takasakyama, over the next 7 years. He emphasized that the social systems in human society may just be an institutionalization of a primate-like ancestor’s social systems and proposed a primatological approach to analyzing human social systems (Nishida 1984).

Imanishi also developed a novel method for observing animal society: individual identification, habituation to humans (including provisioning), and long-term observation. These methods are now commonplace and often used without reference to Imanishi, so that de Waal (2003) called his achievement a “silent invasion.” Using these methods, Imanishi and his colleagues revealed several interesting aspects of Japanese monkey society, including the culture-like transmission of sweet potato washing behavior (Kawai 1965).

In 1956, researchers from Kyoto University and the University of Tokyo (including Imanishi) established the Japan Monkey Center (JMC) at Inuyama, Aichi Prefecture, with the cooperation of the Nagoya Railroad Co., Ltd. The JMC aimed to promote primate research, education, conservation, welfare, and public education regarding non-human primates. Initially it comprised a research department, a zoo, and an amusement park. The JMC also launched the international scientific

journal *Primates* in 1957, which is the oldest journal in primatology and one of the most popular.

In 1958, the research department dispatched Kinji Imanishi and Junichiro Itani to Africa, where they conducted research in Kenya, Uganda, Congo, and Cameroon, among other locations. The Japanese team started to study wild chimpanzees at Mahale in 1965, in parallel with Jane Goodall's study at Gombe.

The JMC research department was abolished in 1976, affected by the establishment of the Primate Research Institute next to the JMC. The amusement park was detached when it became unprofitable, and the JMC became a Public Interest Incorporated Foundation in 2014. Tetsuro Matsuzawa, a former director of the Primate Research Institute at Kyoto University, described Imanishi's achievements as follows: (1) providing an equitable and harmonious "holistic" viewpoint for understanding the world of organisms, (2) supporting this viewpoint by conducting field research in nonhuman primates, and (3), as a result of establishing "primatology," enhancing the development of a range of related research fields including morphology, genetics, psychology, and physiology (Matsuzawa and McGrew 2008).

## The Primate Research Institute at Kyoto University

In tandem with the development of primatology led by Imanishi and his colleagues, in 1964 the Science Council of Japan recommended the establishment of a national primate research institute to the Cabinet of Japan. In response to the recommendation, Kyoto University established the Primate Research Institute (PRI) adjacent to the JMC at Inuyama, Aichi Prefecture, in 1967. In 1975, the PRI completed the nine sections proposed in the original plan. Initially most of the researchers, aside from those in the morphology, society, and life history sections, were from outside primatology; their backgrounds were diverse, including agricultural science, veterinary medicine, human medicine, and literature. Through intense

discussion, they shared the central proposition of the PRI to develop an overall picture of primates and better understand human origin (Sugiyama 1985).

## Ai Project

"Ai," a wild-born 1-year-old female chimpanzee from the Guinean Forest in West Africa, arrived at the PRI in 1977. Soon after that, "Akira," a 1.5-year-old male, and "Mari," a 1.5-year-old female, also arrived at the Institute (Matsuzawa 2003). Following on from the success of other researchers' studies with chimpanzees such as Washoe (Gardner and Gardner 1975), Sarah (Premack 1971), and Lana (Rambaugh et al. 1973), the Ai project investigated artificial language acquisition in chimpanzees. The Ai project used the KU (Kyoto University) lexigram presented on a computer-controlled apparatus. Importantly, the study was conducted not as an "acquisition of language" study but as a "symbolic matching to sample" task, allowing researchers to analyze its acquisition and generalization in a descriptive and objective manner (Matsuzawa 2003). Three chimpanzees including Ai successfully learned naming of objects and colors. They could use combinations of corresponding lexigrams to answer a presented object and its color (Asano et al. 1982). Researchers also found that chimpanzees had difficulty generalizing a learned relationship in the opposite direction without appropriate training (Kojima 1984; e.g., they could learn to choose B when A was presented, but had difficulty generalizing to choose A when B was presented). Ai also learned to discriminate 26 letters of the alphabet as a test of shape perception and visual acuity and Japanese Kanji characters expressing different colors for classification of colors (Matsuzawa 2003). The Ai project started to focus on recognition of number concepts in chimpanzees when Ai was 5 years old (Matsuzawa 2009). First, Ai mastered numerical naming of items in a display ranging from one to six (Matsuzawa 1985). Then, she mastered ordering numerals from zero to nine (Biro and Matsuzawa 1999). Even when all

numbers were masked after touching the first number, Ai demonstrated an impressive ability to touch the masked numbers in the correct sequence, indicating a capacity to remember the sequence of numbers comparable to that of humans (Kawai and Matsuzawa 2000; Inoue and Matsuzawa 2007).

In 2000, three chimpanzees (Ai, Chloe, and Pan) produced offspring via natural copulation. The PRI researchers began to study cognitive development in chimpanzees. To investigate infant chimpanzees' natural social/cognitive development, infants were reared not by humans, but by their mothers in a community with other chimpanzees. Studies investigated a range of developmental indicators, including recognition of the mother's face, mutual gaze between mother and infant, gaze following, and triadic interactions, and compared the chimpanzee infants' results with human infants (Tomonaga et al. 2004). Chimpanzee infants showed comparable responses to human infants except for triadic interactions between mother-infant-object. At 1 to 2 years old, chimpanzee infants often watched the mother manipulate a novel object and then tried to manipulate it themselves. This triadic interaction differs from that of humans, because the chimpanzee infant seldom looked back at, showed the object to, or gave the object to the mother. Furthermore, the chimpanzee mothers did not show or give the object to the infants (Tomonaga et al. 2004).

### Activities for Chimpanzee Conservation

Researchers at the PRI also put their heart into chimpanzee conservation. Since 1997, they have been working in cooperation with the Institute for Environmental Research at Bossou and local villagers, and with the support of the Japanese Embassy in Guinea, the Guinean government, and various international organizations, to establish a green corridor. The green corridor consists of trees planted along a 300-m-wide and 4-km-long stretch of savanna running between Bossou and the Nimba Mountains, to

re-establish migration of chimpanzees between the Bossou and Nimba populations (Matsuzawa et al. 2011; Green Corridor Project website: <https://www.greencorridor.info/en/green-corridor/>).

In 1998, researchers mainly at the PRI founded "SAGA" (Support for African/Asian Great Apes) to (1) conserve the natural habitat of wild great apes, (2) enrich the lives of those in captivity, and (3) bring an end to the use of great apes as subjects in invasive studies (SAGA website: <https://www.saga-jp.org/indexe.html>). At that time, there were 388 chimpanzees in Japan, including 138 individuals used for invasive biomedical research by pharmaceutical companies. In 2006, all invasive biomedical research on chimpanzees in Japan was stopped completely. All chimpanzees formerly involved in biomedical research have been retired and are comfortably housed at Kumamoto Sanctuary, run by Kyoto University (SAGA website). SAGA also emphasizes the importance of maternal rearing, not human rearing, to give normal social experiences for chimpanzee infants. Experience of maternal rearing in infancy is very important for normal social development and expression of appropriate parental behavior toward offspring in adulthood. Human rearing should be avoided, except temporary separation for medical reasons (Matsuzawa 2016). SAGA has repeatedly issued statements against the inappropriate rearing and exhibition of chimpanzees (SAGA website).

### Wildlife Research Center at Kyoto University

In 2008, Kyoto University established the Wildlife Research Center, to promote scientific research and education on wild animals. Its missions are (1) to conduct basic research on endangered and threatened species of wild animals, (2) to integrate different areas of science to create new disciplines applicable to field settings, and (3) to collaborate with zoos, sanctuaries, aquariums, and museums to promote youth environmental education (the Wildlife Research Center website: <https://www.wrc.kyoto-u.ac.jp/en/index.html>). Administration of the Koshima and

Yakushima field stations was transferred from the PRI to the Wildlife Research Center. The Center also includes the Kumamoto sanctuary for chimpanzees. In addition to primates, the Center also conducts studies on other species including elephants, dolphins, and seals, in cooperation with zoos and aquariums in Japan. Today, both the concepts and methodology of primatology founded by Kinji Imanishi and his colleagues in Kyoto are engrained in the field and utilized globally.

## Cross-References

- ▶ [AI \(chimpanzee\)](#)
- ▶ [Language Research: Great Apes](#)
- ▶ [Lexigrams](#)
- ▶ [Primate Cognition](#)
- ▶ [Primates](#)
- ▶ [Washoe](#)

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## Laboratory Research

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Knowledge about animals can be gained through research conducted in naturalistic settings as well in captive settings such as zoos, sanctuaries, and laboratories. The type of knowledge that can be gained in these different settings also varies because of the limitations inherent to each setting. For example, observational research conducted in naturalistic settings provides information about the species' behavior in its natural habitat, while similar research in zoos, sanctuaries, and laboratories contributes to our understanding of the core cognitive or learning processes that give rise to the same behavior, although it may be differently manifested in captive settings. Gaining a deeper scientific understanding of a species' behavioral and cognitive abilities including their underlying biological bases, developmental processes, and social influences often requires a controlled environment – an environment that allows for a systematic assessment of different factors on specific behaviors. Such control can be achieved neither in the animals' natural habitats nor in captive settings such as zoos and sanctuaries. Rather, it requires the study of animals, most of which are specifically bred for research in a laboratory setting, where scientists can control genetic, dietary,

social, and other environmental factors that affect behavior and cognition. Methodologies used in laboratory-based studies range from simple observations of animals' behaviors to more complex designs that include manipulating the animal's environment and measuring behavioral outcomes as well as effects on physiological factors such as blood sugar, hormones, and other neurochemicals.

Reliability of research findings depends not only on sound scientific methodology but also on appropriately maintained research animals. A formal system of regulatory oversight of animal research, in the USA, is just over 50 years old. Long prior to the federal system, the research community recognized the value of knowledge that can be gained through laboratory-based animal research and the importance of standards for animal treatment, as is evidenced by the long history of various professional societies addressing the well-being of laboratory animals through the adoption of standards and codes of conduct (see Table 1).

## Federal Oversight

In the USA today, laboratory animal research is a highly regulated activity and involves oversight at multiple levels by different entities. At the federal level, the US Department of Agriculture (USDA) is charged with enforcement of the Animal Welfare Act (AWA), which Congress passed in

**Laboratory Research, Table 1** Historical Developments in Professional and Governmental Attention to Laboratory Animal Wellbeing (Adapted from Dewsbury, D. (unpublished, personal communication); Gordon 1999; Schwindaman 1999; Smith et al. 1988)

|      |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1904 | Director's log at the Hygienic Laboratory, which was the precursor to NIH – <i>Animals are to be used in the proper work of the lab, but anything that inflicts pain upon them will not under any circumstances be allowed</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| 1908 | American Medical Association (AMA) issues first set of guidelines for the humane care of animals in laboratory research                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| 1925 | <i>APA Committee on Animal Research and Experimentation (CARE)</i> established and APA adopts the <i>AMA Guidelines for Laboratory Animal Care</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| 1949 | APA adopts its own set of rules for research with animals, developed by CARE. Most recent revision of the <i>CARE Guidelines</i> was in 2012                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| 1950 | NIH Director issues <i>Rules Regarding Animals</i> :<br>Source of animals only from dealers, with stray dogs to be turned over immediately to . . . authorities<br>Comfort and sanitation, with animals on long experiments to be maintained under veterinary supervision<br>Operations to be performed only under the supervision of the director of the institute concerned<br>Anesthesia requirements<br>Treatment of an animal at the close of the experiment, with exception to euthanasia<br>A group of veterinary scientists interested in exchanging information about laboratory animal care establish the Animal Care Panel (ACP), which was the precursor to the American Association for Laboratory Animal Science<br>Institute for Laboratory Animal Resources, ILAR (now called the Institute for Laboratory Animal Research) is established at the National Academies. ILAR is now responsible for the periodic update of <i>The Guide</i> |
| 1963 | ACP published the first edition of <i>The Guide</i> . The most recent revision of <i>The Guide</i> was in 2011                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| 1964 | ACP tests a pilot program for inspecting and accrediting animal research facilities                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| 1965 | American Association for Assessment and Accreditation of Laboratory Animal Care, AAALAC (now called AAALAC International) established                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| 1966 | Laboratory Animal Welfare Act (AWA) enacted. It has been amended eight times, with the most recent amendment in 2013                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| 1971 | First NIH Policy on Care and Treatment of Laboratory Animals applicable to institutions that receive NIH funding for research with warm-blooded animals                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| 1973 | First Public Health Service (PHS) Policy is issued – <i>Principles for Use of Laboratory Animals</i> – it applied to all vertebrate animals                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| 1985 | Health Research Extension Act is enacted and provides statutory basis for the PHS Policy<br>AWA amendments pertaining to research passed by Congress – requiring institutions to (1) provide training for all personnel involved in the care and use of animals in research, (2) conduct semiannual inspections of animal research facilities, (3) attend to the psychological well-being of nonhuman primates in research, and (4) provide exercise for research dogs<br>An Interagency Research Animal Committee promulgates the <i>US Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training</i>                                                                                                                                                                                                                                                                                             |
| 1986 | Final version of the <i>PHS Policy on Humane Care and Use of Laboratory Animals</i> went into effect, incorporating provisions mandated by the Health Research Extension Act of 1985                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |

1966 (Animal Welfare Act of 1966, 2013). The AWA regulates the care and treatment of certain animals that have been bred for sale, for research, or for public exhibition, thus covering animals in a range of settings that include not only dedicated research facilities but also zoos, sanctuaries, entertainment, breeders, and dealers. AWA includes requirements for animal husbandry, handling, housing, nutrition, sanitation, ventilation, and veterinary care.

Within the USDA, the Animal and Plant Health Inspection Service (APHIS) Animal Care Unit is responsible for the oversight of laboratory animal research. All research facilities that support research with animals covered by the AWA are required to register with APHIS. APHIS fulfills its oversight responsibilities through annual inspections of registered research facilities. The AWA and ensuing regulations cover research conducted with live or dead dogs, cats, nonhuman

primates, guinea pigs, hamsters, rabbits, or other warm-blooded animal except rats of the genus *Rattus*, mice of the genus *Mus*, and birds specifically bred for research.

While research with rats, mice, and birds is not regulated by the USDA under the AWA, the enforcement of standards for the humane care and treatment of these species in research falls within the purview of other federal agencies, including the National Institutes of Health (NIH) Office of Laboratory Animal Welfare (OLAW). OLAW implements the Public Health Service (PHS) Policy on Humane Care and Use of Laboratory Animals (PHS Policy) (Public Health Service Policy on Humane Care and Use of Laboratory Animals 1986). The PHS Policy applies to all live vertebrates used or intended for use in PHS-funded research as well as research funded by the National Science Foundation (NSF).

The Health Research Extension Act of 1985 (Health Research Extension Act 1985) provides the statutory basis for the enforcement of the PHS Policy for PHS-funded research with animals. The PHS Policy requires institutions to use the standards described in *The Guide for the Care and Use of Laboratory Animals (The Guide)* (National Research Council 2011) as the basis for developing and implementing their animal care and use programs. That same year, Congress also amended the AWA to specifically address issues related to improving standards for the humane care and treatment of laboratory animals. In addition, the 1985 AWA amendments included a provision mandating the Secretary of the Department of Agriculture to coordinate with the Secretary of the Department of Health and Human Services on the promulgation of specific requirements under the AWA. Finally, also in 1985, a federal Interagency Research Animal Committee promulgated the US Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training (US Government Principles) (Office of Science and Technology Policy 1985), which was adopted by all US federal agencies that conduct or support research with vertebrate animals. The US Government Principles provide a framework for conducting research that complies with both the AWA regulations and the PHS Policy.

OLAW meets its regulatory mandate by requiring institutions that receive PHS funding for research to have an OLAW-approved Animal Welfare Assurance before conducting any research involving vertebrate animals. In the Assurance, the institution attests to compliance with all relevant regulations, the US Government Principles and the PHS Policy. The Assurance also provides detailed information about the institution's animal care and use program, its Institutional Animal Care and Use Committee (IACUC), and an inventory of the species housed at the institution. Similar to the APHIS, OLAW delegates oversight responsibility at the local level to the IACUC, which reviews and approves proposals for research with animals, and submits an annual report to OLAW certifying that semiannual inspections were completed and report serious noncompliance, if any. OLAW evaluates all allegations of noncompliance and conducts approximately ten not-for-cause site visits of assured institutions. The Office also offers education programs focused on sustaining research animal well-being.

## Public Transparency

Federal laws, such the Freedom of Information Act (FOIA) as well as state sunshine laws, provide the general public with access to information regarding research regulated by the USDA and OLAW. Public transparency of the oversight process includes access to USDA and OLAW records, including annual facility reports of the number of animals housed and number involved in research, semiannual inspection reports, and reports of noncompliance, if any.

## Nongovernmental Oversight

In addition to oversight by federal bodies such as APHIS and OLAW, institutions that support animal research programs can choose to be accredited by a private entity, AAALAC International (formerly known as the Association for Assessment and Accreditation of Laboratory

Animal Care International). AAALAC International assesses the institution's animal research program not only to ensure compliance with all relevant federal, state, and local regulations and policies but also the extent to which the animal care and use program meet or exceed the standards set forth in *The Guide*. Institutions that obtain AAALAC International accreditation are required to submit an annual report that provides AAALAC International with up-to-date information on the institution's animal care and use program. AAALAC International conducts site inspections every 3 years to determine whether the institution can maintain its accreditation status. As a private entity, AAALAC is not subject to public records requirements.

### Local Oversight

Both the AWA regulations and PHS Policy assign primary accountability for research animal well-being to the institution through the establishment of an Institutional Animal Care and Use Committee (IACUC). Per the AWA regulations, an IACUC at a USDA-registered facility should consist of, at minimum, three members and include a chairperson, a laboratory animal veterinarian, and a community representative who is unaffiliated with the institution. IACUC functions include a semiannual review of the institutions' program for the humane care and use of animals and a semiannual inspection of the institution's animal facilities. The IACUC is responsible for reporting the findings of its reviews and inspections to the responsible institutional official, noting both minor and significant deficiencies in the program, if any. In the case of significant shortcomings, the IACUC should provide a time line for addressing the identified deficiencies. If the deficiencies are not addressed within the specified time frame, then the IACUC is required to report it to APHIS within 15 days of the lapsed deadline.

The IACUC at an OLAW-assured institution is mandated by PHS Policy to have a minimum of five members – a chairperson, a laboratory animal veterinarian, an affiliated community representative, a scientist with animal research experience,

and a nonscientist. The IACUC must submit an annual report to OLAW detailing any changes to the animal care and use program at the institution, the institution's AAALAC accreditation status, IACUC membership, and dates of its semiannual reviews of the institution's animal care and use program and its animal facilities. The IACUC is responsible for promptly reporting to OLAW any serious or continuing noncompliance with the PHS Policy, serious deviations from *The Guide*, and the suspension of any activity by the IACUC. OLAW provides IACUC with detailed guidance on fulfilling its duties.

### IACUC Protocol Review Criteria

In addition to the semiannual reviews and inspections of the institution's animal research program, a major function of the IACUC is to review and approve proposals for the conduct of research studies involving animals. The IACUC is responsible for implementing federal policies as well as state and institutional policies that might be more stringent than federal requirements.

Before approving proposals, the IACUC reviews and documents that the proposed study is not duplicative and that the researcher has considered alternatives to the use of animals for the proposed study. Thus, the protocol must contain a written narrative that describes the research literature as well as the outcome of searches for alternatives on specific databases. The IACUC also ensures that the researcher has described steps that will be taken to minimize any pain and distress, if any, to the animals and how research procedures that involve more than momentary pain and severe or chronic pain or distress will be handled. In addition, the proposal must provide evidence that all research procedures will be conducted by appropriately trained and qualified personnel. The IACUC must ensure that clearly specified requirements for procedures involving surgery are met and that no animal is used in more than one major operative procedure, unless scientifically justified. The IACUC also must evaluate the appropriateness of species for the proposed study and the number of animals required to

obtain scientifically valid results. And lastly, the IACUC ascertains that the animals' living conditions are appropriate. Although assessing the scientific merit (peer review) of proposed research is not within the purview of the IACUC, it is responsible for judging the scientific relevance of the proposed research including its potential to contribute to the health of humans or other animals, to the advancement of knowledge, and/or to the good of the environment or society in general.

In conclusion, laboratory-based research with animals is subject to much more stringent and rigorous oversight than any other activity involving animals, including similar research conducted in other settings such as zoos, sanctuaries, and the wild.

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## Lactogen

- [Prolactin](#)

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## Lactogenic Hormone

- [Prolactin](#)

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## Ladder of Being

- [Scala Naturae](#)

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## Lagomorpha Diet

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## Introduction

Within the order *Lagomorpha* there are two living families, the *Leporidae* which include hares and rabbits and *Ochotonidae* which are the pika. There are 63 species in the *Leporidae* family, while in the *Ochotonidae* family there are 28 species. Rabbits and hares are often thought of as one group of animals – yet they are actually quite different. Both are considered mid-sized herbivorous mammals and hind gut fermenters – but their general habitat and natural food selection differs (Mišta et al. 2015). Rabbits are generally smaller than hares, the pygmy rabbit is the smallest rabbit weighing only 300 g while the European hare is the largest hare and can weigh as much as 5 kg. There are 30 species of hares and they all belong to the same genus *Lepus*; whereas, there are 10 different genus of rabbits (Caravaggi 2018).



## Digestive Morphology

### Teeth

Lagomorphs possess long-crowned (hypsodont), continuously growing (elodont), and open-rooted (aradicular) teeth. This continuous growth is not constant but compensates for the wear of the respective tooth and is an evident adaptation to compensate for tooth wear (Vella and Donnelly 2012). The rates of wear and growth must match in ever growing teeth in order to maintain proper occlusion (Muller et al. 2014). Lagomorph dentition is heterodont or functionally different types of teeth. Lagomorphs have what is known as diphyodont dentition, which means they have deciduous (primary) and secondary (adult) teeth. Rabbits have 16 deciduous teeth and 28 permanent (secondary) teeth (Rabbit Teeth – Problems & Anatomy of Rabbit Teeth – Veterinary Dentist Wisconsin, Minnesota n.d.). Rabbits and hares have 28 teeth, pika have 26. The dental formula for rabbits and hares is  $2.0.3.3/1.0.2.3 = 28$  (Van Caelenberg 2008). The dental formula for pika is  $2.0.3.2/1.0.2.3 = 26$  (Smith et al. 2018). Tooth growth is strongly related to tooth wear. Rabbit's tooth wear is very dependent on the diet and the tooth position (Muller et al. 2014). While lagomorphs and rodents each have large diastemas (the gap between the incisors and the molar teeth), the lagomorph small peg-like incisors, without a cutting edge, lie immediately behind the larger first incisors – this characteristic distinguishes them from rodents (Smith et al. 2018).

Lagomorphs are generalized herbivores and possess a very large gut that houses bacteria to aid in the digestion of cellulose (Smith et al. 2018). The digestive tract of *Lagomorpha* is comprised of a single-chamber glandular stomach with a well-developed fornix, a long cecum with lymphoid formations and a deep spiral fold, and a colon forming a number of muscular pockets. The large intestine of pikas is more complicated and differentiated than that of hares and rabbits (Naumovaa et al. 2014).

Both families *Leporidae* and *Ochotonidae* have a colonic separation mechanism. When the separation mechanism diverts fine particles into

the caecum, only large food particles are passed and the animal produces hard faeces. When the mechanism is not functioning, fermented caecal materials are excreted as soft faeces. These soft faeces are rich in vitamins and microbial proteins and are reingested. During the daytime, both soft and hard faeces are defecated and all of the faeces are reingested. At night, the animals only excrete hard faeces – which tend not to be reingested unless the animal is starving. Hard faeces are basically a refuse, when daytime hard faeces are reingested the animal will thoroughly masticate the large particles to fine ones that are then good for fermentation. The regular reingestion of daytime hard faeces thus improves food digestibility and nutrient utilization (Hirakawa 2001).

### Diet

All of the lagomorphs are herbivores; the breadth of the diet varies between species and depends on local environmental conditions and relative availability of food item (Caravaggi 2018).

Pikas are very small mammals only weighing 120–300 g (Ge et al. 2013). Pikas live in mountainous regions in the northern hemisphere (Matthee 2009). Only three species of pika live outside of Asia, two species in Europe, and one species in the United States. Pikas are generalized herbivores; they forage on nearly all vegetation found within their habitat. Berries, seeds, shrubs, buds, grasses, mushrooms, lichens, leaves, and shoots are consumed when they are available, with green parts of available vegetation constant in their diet year-round (Smith et al. 2018). A study of wild plateau pika (*Ochotona curzoniae*) showed a relationship between altitude and diet as well as the diversity of plants included in the diet at different altitudes. The dominant plants in the wild diet of plateau pika is locoweed (*Oxytropis kansuensis*) (Li et al. 2016) which is interesting because this weed contains swainsonine which is known to be toxic to livestock and is believed to cause apoptosis in brain cells (Lu et al. 2013). A general review of the common plants found in the diet of different species of pika can be found in

*Lagomorphs – Pika, Rabbits and Hares of the World* (Smith et al. 2018).

An important distinction between the rabbits and the hares is their reproductive mode. Rabbit kittens are born naked (altricial) following a relatively short period of gestation. Their eyes open about 4–10 days following birth. In contrast, hare leverets are generally well developed (precocial) at birth. Gestation in hares is longer, and leverets are born fully furred with their eyes open. It is also important to note that the common names for some species within the Leporidae are deceptive. For example, the hispid hare (*Caprolagus hispidus*) is a rabbit, and jackrabbits are hares (genus *Lepus*) (Smith et al. 2018).

Rabbits tend to live in forest or shrub areas and dig burrows in the ground for their nests. The herbivorous diets of rabbits reflect their environment. The 2010 publication *Nutrition of Rabbits* (de Blas and Wiseman 2010) provides an excellent and thorough review on the digestion, nutrition, and feeding behaviors of domestic rabbits. This book also includes a chapter on the feeding and nutrition of pet rabbits. A general review of the common plants found in the diet of different species of wild rabbit can be found in *Lagomorphs – Pika, Rabbits and Hares of the World* (Smith et al. 2018).

Hares tend to live in open areas and have simple ground nests, they can be found in a variety of habitats, from dry, hot deserts to the Arctic tundra (Caravaggi 2018). The herbivorous diet of hares also reflects their environment. A general review of the common plants found in the diet of different species of hares can be found in *Lagomorphs – Pika, Rabbits and Hares of the World* (Smith et al. 2018). An interesting study published in the journal *Folia Zoologica* on European hares revealed that individual animals appear to have dietary preferences (Katona and Altbäcker 2002).

Although we have studied and know a great deal about the nutrient and dietary needs of many lagomorph species, there is still a great deal we need to learn. An example is the endangered volcano rabbit (*Romerolagus diazi*) from south Mexico. This animal has a very limited and fragmented range (Caravaggi 2018). Volcano rabbits depend on three species of native grasses:

*Festuca amplissima*, *Muhlenbergia macroura*, and *Stipa ichu*, feeding on the young leaves of grasses and some spiny herbs. Nutrient analysis of these grasses show, at the typical intake of the rabbit, they are inadequate to provide the nutrition necessary to maintain the stable body condition observed in most wild populations. Other plant species, that we are yet unaware of, must complement the diet (Smith et al. 2018). This is only one example of the work needed to more fully understand the nutritional needs and forage selectivity of endangered lagomorphs in order to ensure their habitat can support them.

## Conclusion

There are around 91 living species of lagomorph, many are classified as threatened (vulnerable, endangered, and critically endangered) by the International Union for Conservation of Nature (2017) and/or are Evolutionary Distinct and Globally Endangered (EDGE) species (Fontanesi et al. 2016). Lagomorphs have a global distribution; representative species can be found on every continent with the exception of Antarctica. The habitat requirements for each species vary considerably and some species have very specific environmental needs.

## Cross-References

- [Hare](#)
- [Herbivore](#)
- [Pika](#)
- [Rabbit](#)

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## Lagomorpha Life History

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## Synonyms

Growth; Hare; Leporid; Longevity; Pika; Rabbit; Reproduction

## Definition

Mammalian life history traits include length of gestation, size and number of offspring, growth patterns, weaning age, timing of sexual maturity, adult body mass, reproductive lifespans, individual longevity, population density, and group composition and size (Jones et al. 2009).

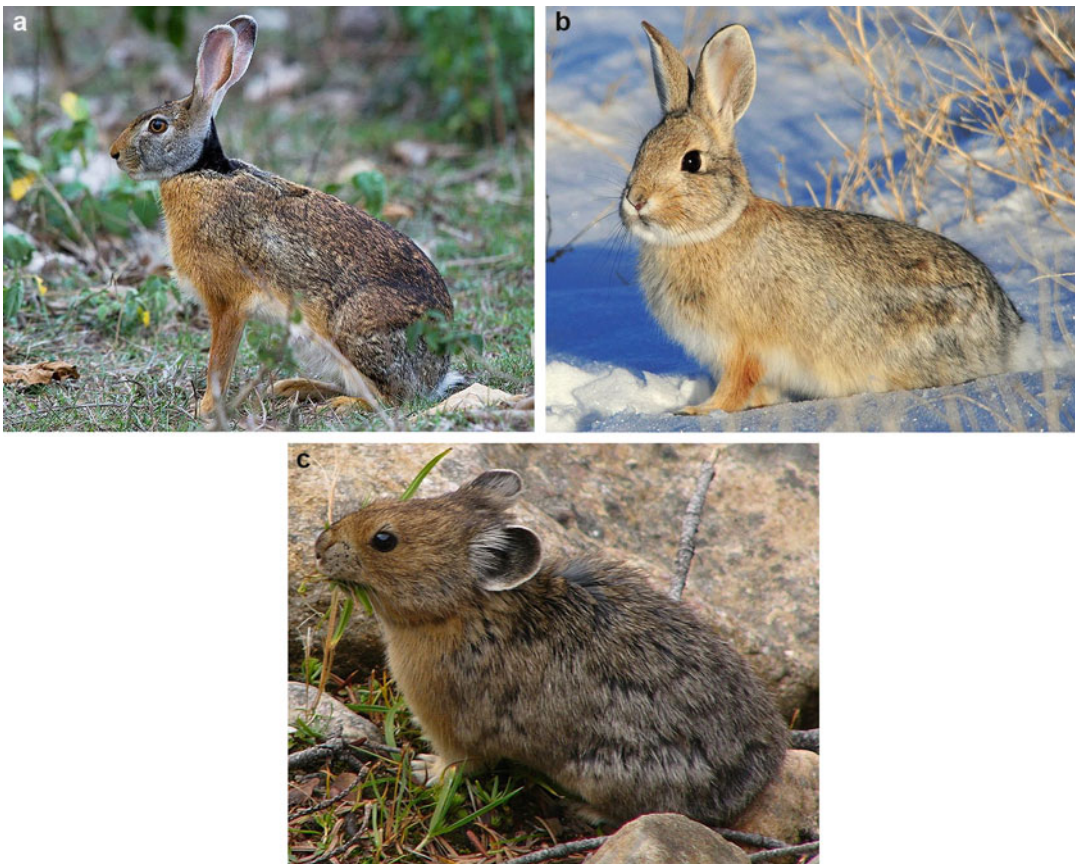
## Introduction

The term “lagomorph” describes species of the mammalian order Lagomorpha (lit: “hare-form”), which is made up of two families, the hares and rabbits (Leporidae; also known as leporids) and the pikas (Ochotonidae). These two groups are united by shared morphological traits which are unique among extant mammals, including several aspects of cranial anatomy and a circulatory channel running through the heel bone (Fostowicz-Frelik and Meng 2013). The evolutionary history of lagomorphs is not clear, though

ongoing research continues to shed light on the origins of the order. Leporids and pikas diverged in the Eocene, around 40 million years ago (mya), a split which may have been facilitated by abrupt changes in climate. Lagomorphs were certainly more diverse than they are in the present, with over 230 species from over 75 genera represented in the fossil record. Pikas initially diversified much more rapidly than leporids, but, over time, this situation was reversed and there are now fewer species of pika, which occupy a far smaller overall area, than there are of hares and rabbits. In addition to genetic differences, the families are easily distinguished visually by comparative morphology (Fig. 1 and subsections herein).

There are around 91 living species of lagomorph, many of which are classified as threatened

(vulnerable, endangered, and critically endangered) by the International Union for Conservation of Nature (2017) and/or are Evolutionary Distinct and Globally Endangered (EDGE) species (Fontanesi et al. 2016). The order has a global distribution, with representative species being found on every continent with the exception of Antarctica, from between the equator and 80°N and between 0 and 5000 m above sea level (Fontanesi et al. 2016). Habitat requirements can vary considerably, with some species being more specific in their requirements and, hence, having a more limited distribution than others. For example, volcano rabbits (*Romerolagus diazi*) are an endangered species found in four volcanoes in southern Mexico which, even within their limited, fragmented range, have a strong preferences for



**Lagomorpha Life History, Fig. 1** Photographic examples of (a) hare, Indian hare (*Lepus nigricollis*; photo by N. A. Nazeer); (b) rabbit, mountain cottontail (*Sylvilagus*

*nuttallii*; photo by USFWS Mountain-Prairie; (c) pika, American pika (*Ochotona princeps*)



subalpine habitats, particularly pine forests (Velazquez and Heil 1996). In contrast, the European hare (*Lepus europaeus*) can utilize a wide range of habitats; it has a broad distribution in its natural range and has been successfully introduced to a number of countries and islands, worldwide (Flux and Angermann 1990).

Lagomorphs have considerable ecological, scientific, and economic importance as they are human food sources, agricultural pets, quarry for field sports, model laboratory animals, and significant components of ecological systems and processes (Chapman and Flux 2008; Fontanesi et al. 2016). These mammals feature prominently in the diets of many predators, with annual mortality rates of up to 80–90% in some species. Fortunately, all lagomorphs have short gestation periods, newborns grow rapidly, and there is little maternal investment in the young after weaning. This means that they are often highly fecund, producing multiple litters of several young, per year (Table 1).

All of the lagomorphs are herbivores; the breadth of the diet varies between species and depends on local environmental conditions and relative availability of food items. With a diet rich in tough cellulose, these mammals have solved the problem of cellulose digestion by utilizing hindgut fermentation and reingestion of first-feces (coprophagy), soft black pellets known as caecotrophs. The secondary digestion allows lagomorphs to further digest the plant matter and maximize nutrient extraction.

Here I give an overview of differences in life history traits between the leporids (subdivided into hares, and rabbits) and pikas, illustrating the variation in the order. While this text details a number of species, there are many for which we have few life history data (Jones et al. 2009).

## Hares

Hares are the most diverse of all the lagomorphs, comprising 32 species, all of which occur within a single genus, *Lepus* (ITIS 2017). The genus contains several species which are commonly known as jackrabbits, e.g., the Tehuantepec jackrabbit

(*L. flavigularis*). They are all, however, true hares. Hares are generally the largest of the lagomorphs, weighing between 2 and 5 kg and are readily distinguished from rabbits by their long ears and hind legs. Their long legs allow them to run at extremely high speeds to escape predators; both the antelope jackrabbit (*L. alleni*) and the European hare have been recorded at 72 kmh (Garland 2009), and it is likely that other large hares can attain similar speeds. The cost of high-speed flight can be substantial, however, and hares will often remain in their forms until a predator is almost within striking distance before fleeing.

Hares can be found in a variety of habitats, from dry, hot deserts to the Arctic tundra. Across their range, they display an array of physiological and behavioral adaptations which have allowed them to thrive. For example, the ears of the antelope jackrabbit, which is found in arid regions of Arizona and Mexico, are extremely large and have an abundance of blood vessels, helping the animals to dissipate heat while minimizing water loss (Dawson and Schmidt-Nielsen 1966). In contrast, those of the mountain hare (*L. timidus*), an arcto-alpine species complex with a circumpolar distribution which inhabits uplands and northern latitudes, are much smaller and heavily furred to reduce heat loss. Hares also molt their coats, from a relatively thin summer coat to thicker, insulating winter pelage and vice versa. In some species such as the European hare in which the summer coat is a light brown compared to the reddish-brown winter coat, there are few obvious differences between seasons. Others, such as mountain hares, go from brown in the summer to white in the winter. This seasonal change confers additional protection from predators via camouflage with snowpack, though the trait has limited plasticity, meaning that white animals at the southern edge of the species range will become increasingly vulnerable as snow cover recedes under climate change (Zimova et al. 2014).

The majority of hare species are largely solitary, only coming together during the breeding season. However, some species such as the Arctic hare (*L. arcticus*) can be highly social, resting and feeding in groups which may number dozens of individuals. The mating behavior of hares is,



**Lagomorpha Life History, Table 1** Selected life history information for 30 of the 90 extant species of lagomorphs. The data describe ranging behavior (home range), breeding ecology (gestation length, litter size, and litters per year),

and growth (neonate body mass, adult body mass). Species are sorted alphabetically according to their Latin names (Data were derived from Ernest 2003, IUCN 2017, and Jones et al. 2009)

|                         |                                  | Average                       |                         |             |                  |                       |                     |
|-------------------------|----------------------------------|-------------------------------|-------------------------|-------------|------------------|-----------------------|---------------------|
| Common name             | Latin name                       | Home range (km <sup>2</sup> ) | Gestation length (days) | Litter size | Litters per year | Neonate body mass (g) | Adult body mass (g) |
| Rabbits                 |                                  |                               |                         |             |                  |                       |                     |
| Pygmy rabbit            | <i>Brachylagus idahoensis</i>    | 0.004                         | 39                      | 5.81        | 2.00             | 16.40                 | 431                 |
| Riverine rabbit         | <i>Bunolagus monticularis</i>    | 0.140                         | 35                      | 1.22        | DD               | 42.42                 | 1750                |
| Assam rabbit            | <i>Caprolagus hispidus</i>       | 0.004                         | 40                      | 3.46        | 2.81             | DD                    | 2497                |
| Swamp rabbit            | <i>Sylvilagus aquaticus</i>      | 0.010                         | 37                      | 3.00        | 2.94             | 55.70                 | 2133                |
| Desert cottontail       | <i>Sylvilagus audubonii</i>      | 0.030                         | 28                      | 3.00        | 5.00             | 34.36                 | 881                 |
| Brush rabbit            | <i>Sylvilagus bachmani</i>       | 0.002                         | 27                      | 3.35        | 4.50             | 27.25                 | 715                 |
| Eastern cottontail      | <i>Sylvilagus floridanus</i>     | 0.010                         | 27                      | 4.62        | 4.81             | 34.15                 | 1207                |
| Marsh rabbit            | <i>Sylvilagus palustris</i>      | 0.030                         | 33                      | 2.96        | 6.00             | DD                    | 1355                |
| New England cottontail  | <i>Sylvilagus transitionalis</i> | 0.004                         | 28                      | 4.41        | 2.50             | 30.00                 | 814                 |
| European rabbit         | <i>Oryctolagus cuniculus</i>     | 0.040                         | 30                      | 5.24        | 4.50             | 39.11                 | 1591                |
| Hares                   |                                  |                               |                         |             |                  |                       |                     |
| Antelope jackrabbit     | <i>Lepus alleni</i>              | 4.530                         | 42                      | 1.96        | 3.50             | 182.00                | 3930                |
| Snowshoe hare           | <i>Lepus americanus</i>          | 0.040                         | 37                      | 3.54        | 2.50             | 67.84                 | 1568                |
| Arctic hare             | <i>Lepus arcticus</i>            | 2.260                         | 52                      | 5.62        | 1.50             | 105.00                | 4413                |
| Black-tailed jackrabbit | <i>Lepus californicus</i>        | 0.560                         | 42                      | 2.68        | 4.05             | 84.93                 | 2422                |
| Cape hare               | <i>Lepus capensis</i>            | 0.410                         | 42                      | 2.44        | 3.00             | 114.09                | 2047                |
| European hare           | <i>Lepus europaeus</i>           | 0.310                         | 42                      | 2.14        | 4.40             | 123.00                | 3816                |
| Indian hare             | <i>Lepus nigricollis</i>         | 0.010                         | 36                      | 1.76        | 7.15             | DD                    | 2294                |
| Alaskan hare            | <i>Lepus othus</i>               | DD                            | 46                      | 6.15        | 1.00             | 102.46                | 4837                |
| Scrub hare              | <i>Lepus saxatilis</i>           | DD                            | 38                      | 1.52        | 5.35             | 98.00                 | 2594                |
| Mountain hare           | <i>Lepus timidus</i>             | 0.860                         | 50                      | 3.16        | 3.00             | 113.49                | 3105                |
| White-tailed jackrabbit | <i>Lepus townsendii</i>          | DD                            | 41                      | 4.49        | 3.29             | 89.99                 | 3372                |

(continued)

**Lagomorpha Life History, Table 1** (continued)

|               |                            | Average                       |                         |             |                  |                       |                     |
|---------------|----------------------------|-------------------------------|-------------------------|-------------|------------------|-----------------------|---------------------|
| Common name   | Latin name                 | Home range (km <sup>2</sup> ) | Gestation length (days) | Litter size | Litters per year | Neonate body mass (g) | Adult body mass (g) |
| Pikas         |                            |                               |                         |             |                  |                       |                     |
| Alpine pika   | <i>Ochotona alpina</i>     | 0.009                         | 29                      | 3.07        | 2.00             | 8.19                  | 150                 |
| Gansu pika    | <i>Ochotona cansus</i>     | 0.001                         | 24                      | 3.65        | 2.25             | DD                    | 69                  |
| Collared pika | <i>Ochotona collaris</i>   | 0.001                         | 30                      | 3.35        | 2.00             | DD                    | 129                 |
| Plateau pika  | <i>Ochotona curzoniae</i>  | 0.001                         | 23                      | 4.39        | 3.50             | 11.20                 | 159                 |
| Northern pika | <i>Ochotona hyperborea</i> | 0.002                         | 28                      | 3.02        | DD               | 9.59                  | 120                 |
| Pallas' pika  | <i>Ochotona pallasi</i>    | 0.002                         | 25                      | 7.45        | 2.50             | 7.00                  | 180                 |
| American pika | <i>Ochotona princeps</i>   | 0.001                         | 30                      | 2.88        | 2.00             | 11.00                 | 158                 |
| Steppe pika   | <i>Ochotona pusilla</i>    | DD                            | 22                      | 8.59        | 3.50             | 6.74                  | 143                 |
| Afghan pika   | <i>Ochotona rufescens</i>  | DD                            | 26                      | 6.05        | 4.00             | 11.40                 | 250                 |

DD data deficient

broadly speaking, very similar across the genus. Males aggregate around receptive females, which they will regularly chase at high speeds, and actively compete to establish a dominance hierarchy. Direct competition occurs in the form of “boxing,” the hares rearing up on their hind legs and striking with forepaws, as well as striking with the hind legs while on all fours. Females, which are dominant, also use boxing, as well as grunts and aggressive body language to fend off amorous males (Chapman and Flux 1990).

Most hare species favor an open landscape featuring sufficient cover for rest and offering protection from predators. There are a number of exceptions, including the Manchurian hare (*L. mandshuricus*) which inhabits forests in north-eastern China and Russia (Loukashkin 1943), and the snowshoe hare (*L. americanus*), which inhabits successional boreal forests, swamps, and transitional habitats (Flux and Angermann 1990). The snowshoe hare also demonstrates the importance of many lagomorphs to trophic food

webs as the abundances of avian and mammalian predators and secondary prey species fluctuate in accordance with the snowshoe hare’s 10-year population cycle (Krebs et al. 2001). Hares are largely nocturnal and/or crepuscular, feeding at night and during hours of twilight and resting during the day. These patterns often show seasonal variation, however, with activity commencing before sunset and ceasing after sunrise (i.e., during hours of daylight) when days are longer (Schai-Braun et al. 2012). Hares have among the largest home ranges of the lagomorphs; home ranges for antelope jackrabbits average 4.5 km<sup>2</sup>, and most hares have ranges in excess of the largest found among rabbits (Table 1).

The length of the breeding season varies according to a number of factors including day length and ambient temperature; some species have breeding seasons which last for over 250 days of the year. Reproductive patterns vary by latitude, with larger litters occurring during the shorter breeding seasons in the north. Hares

generally have litters of two to four young (Table 1), although litters as small as one and as large as six have been recorded in some species, and several litters may be produced each season (Rioja et al. 2011). They do not dig burrows or holes in which to give birth, instead creating a depression in the ground, known as a “form,” which is sometimes covered with grass or other vegetation. Young hares, or leverets, are born precocial; their eyes are open, they are fully furred, and they are capable of independent movement soon after birth. This is in contrast to rabbits, which are born much earlier in development (see *Rabbits*). Females place leverets under vegetation such as trees and shrubs (Arctic hare) or grass (Cape hare, *L. capensis*) to hide them from predators. Leverets are nursed once per day with highly concentrated milk. Early offspring survival (i.e., survives the first 3 weeks) is usually between 40% and 50% (Rioja et al. 2011). The average lifespan of a wild hare is between 4 and 7 years.

## Rabbits

The rabbits comprise 29 species across ten genera (*Brachylagus*, *Bunolagus*, *Capolagus*, *Nesolagus*, *Oryctolagus*, *Pentalagus*, *Poelagus*, *Pronolagus*, *Romerolagus*, *Sylvilagus*). Some species are referred to as “hares,” for example, the Natal red rock hare (*Pronolagus crassicaudatus*), though all of the aforementioned species are true rabbits. The most speciose of these are the New World cottontails (*Sylvilagus* sp.), with 17 extant species (ITIS 2017). Rabbits are a diverse group, ranging from species of uplands like the Appalachian cottontail (*S. obscurus*), to dense tropical forest like the Sumatran striped rabbit (*N. netscheri*), to swamps like the semiaquatic swamp rabbit (*S. aquaticus*). Their ranges vary considerably, for example, the European rabbit (*O. cuniculus*), historically restricted to the Iberian Peninsula, has been introduced to a large number of countries and islands and so is one of the most widely distributed mammalian species. In contrast, many other species, including members of more primitive genera such as *Caprolagus*, *Pentalagus*, and *Nesolagus*, many

of which are endangered, are restricted to small habitat patches and/or islands (Alves et al. 2008).

Rabbits are generally smaller than hares, weighing 0.5–2 kg (Table 1). Like hares, they also have large eyes and long ears and back legs, though both are shorter in rabbits. Unlike hares which rely on speed and endurance to evade predators, rabbits generally move in swift, darting movements, relying on burrows and/or vegetation for protection. However, most species are far from ponderous; cottontails (*Sylvilagus* spp.) can attain speeds of 40 kmh, while the European rabbit has been recorded at 56 kmh (Garland 2009). Home range sizes vary between species, from 0.002 km<sup>2</sup> in the brush rabbit (*S. bachmani*) to 0.140 km<sup>2</sup> in the riverine rabbit (*Bunolagus monticularis*; Table 1). Home range sizes also vary according to sex, habitat quality, and population density. In cottontails, for example, males range further than females – the territory of a single male overlaps those of several females – and home ranges are smaller when population densities are higher as there is increased competition for resources (Chapman and Flux 1990).

Rabbits are generally thought of as being much more gregarious than hares, often occurring in groups and at high densities (e.g., the European rabbit). This is not the rule, however, and population densities can vary considerably showing marked differences within and between species and depending on a wide variety of factors including local climate, habitat, and predator guild composition and relative abundance. The riverine rabbit, one of South Africa’s most endangered mammals with a restricted distribution following widespread habitat destruction, is a largely solitary species which produces very few litters, annually (Table 1). Riverine rabbits also occur at low densities of around 11 individuals per square kilometer (Duthie et al. 1989).

Rabbit social behavior is highly variable, with some species like the European rabbit and the swamp rabbit being highly territorial, while others like the eastern cottontail (*S. floridanus*) are non-territorial. With the exception of the volcano rabbit which emits high-pitched sounds, they are largely nonvocal, alerting others of potential threats by thumping their feet on the ground.

The breeding behavior of rabbits is broadly similar to that of the hares, with males competing for access to receptive females. Both the European rabbit and swamp rabbit display synchronized mating, where matings across the population occur around the same time, resulting in multiple conceptions and an abundance of similarly aged young.

All rabbits give birth to altricial young (kits), which are born naked and with their eyes closed after a gestation period of between 25 and 40 days (e.g., Table 1). However, there is a trade-off between the length of gestation and litter size. Longer gestation results in larger, more developed young which can more ably fend for themselves. However, larger young generally means smaller litters. For example, swamp rabbit kits weigh 56 g when born, after a gestation of 37 days, compared to those of the desert cottontail (*S. audubonii*) which weigh 34 g after a gestation period lasting 28 days. The average litter size of both species is comparable at three kits per litter, but the desert cottontail has more litters per breeding season (five, compared to three for the swamp rabbit; Table 1). Moreover, as with hares and other non-hibernating mammals, the reproductive patterns of rabbits have been observed to vary according to latitude. For example, new world rabbits have shorter gestation periods and produce larger litters in the northern parts of their range when compared to individuals of the same species in the south (Conaway et al. 1974). Such adaptations are a response to latitudinal variations in environmental conditions; breeding seasons are shorter in the north than in the south, and the rabbits maximize their reproductive output, while conditions are favorable (Chapman and Flux 2008).

Old World rabbits actively excavate holes and burrows within which they create a nest of grasses and fur; these offer the vulnerable kits protection from predation and the elements. New world rabbits do not dig, instead utilizing burrows dug by other species, but do create nest holes which are depressions similarly lined with soft vegetation and fur and hidden by a covering of vegetation (e.g., Chapman and Willner 1981). The kits of all species require intensive parental care by the mother (doe) for 2–3 weeks after which they are

fully weaned. Young rabbits attain sexual maturity at around 3 months. Mortality can be extremely high, with as few as 8% of young surviving past their 1st year, depending on several factors including population densities, predator abundance, and disease.

## Pikas

Pikas are a complex of 30 species within a single genus, *Ochotona*, which is itself split into three subgenera: *O. (Pika)*, which is comprised of 8 species; *O. (Ochotona)*, which is comprised of 9 species; and *O. (Conothoa)*, which is comprised of 13 species (ITIS, 2017). Most species of pika occupy cold, remote, mountainous habitats in Asia, Eastern Europe, and North America, though several inhabit open steppe or forest and shrubland. Two species are found in North America, with the remainder found in Asia, particularly China (24 species).

Pikas are smaller than hares and rabbits (70–300 g; Fig. 1; Table 1) and have rounded bodies, rounded ears, and no visible tail. They also differ in skull morphology and dentition (Smith 2008). Adult individuals of the largest species, which include the Chinese red pika (*O. erythrotis*), weigh over 250 g and can reach 30 cm in length. Unlike hares and most rabbits, they are very vocal, communicating via high-pitched calls and whistling barks. They move swiftly in response to a potential threat, taking cover among rocks and/or vegetation, though their hind legs are proportionally shorter than those of other leporids and their gait is very different, being more of a bounce than a hop. Most pikas are diurnal, and they do not hibernate. The average home range of most pika species is small at around 200 m (Table 1). Most species of pika collect caches of vegetation, known as “haypiles,” during the summer which they use as sustenance throughout the winter (Smith 2008). They defend their haypiles vigorously, attempting to ward off potential thieves.

The pikas are split into two major groups: (1) long-lived, territorial species with low reproductive rates which live in rocks or talus, which

includes all North American and half of Asian species and (2) species which generally have short lifespans, high reproductive rates and live in grassland or steppe habitat and are very social (Fontanesi et al. 2016; Smith 2008). There are a few intermediate species which utilize both habitats, adopting the life history traits of the relevant group. Intermediate species include the Afghan pika (*O. rufescens*) and Pallas's pika (*O. pallasii*) (Smith 2008). Pikas are cold-temperature specialists, with high body temperatures; they are sensitive to high ambient temperatures (MacArthur and Wang 1974) and changes in climate (Leach et al. 2015), making them superb indicators of localized warming. This sensitivity means that their distribution is directly associated with climate. While recent studies on American pika (*O. princeps*) have found that they are able to adapt to variations in climate by utilizing favorable microclimates and adjusting their foraging and thermoregulatory behaviors (Beever et al. 2017), pikas are nevertheless generally highly susceptible and likely to experience range contraction to the extent that some species, such as Kozlov's pika (*O. koslowi*), may be driven to extinction (Leach et al. 2015).

There are several differences between the two pika groups. For example, burrowing species such as the steppe pika (*O. pusilla*) have larger litters (around 9 young) and more litters per year (3.5) than rock-dwelling species like the collared pika (*O. collaris*) which gives birth to 2 litters of around 3 young, annually (Table 1). Rock-dwelling species utilize a monogamous mating system, largely due to the dispersal of females across the landscape. Burrowing species also employ monogamy but will also use polygynous, polyandrous, or polygynandrous systems. Both groups are similar – as indeed are all lagomorphs – in that the young are cared for by the absentee mothers; females visit and nurse the young infrequently and for short periods of time. Burrowing pikas are capable of breeding during the summer in which they were born, giving them a higher reproductive capacity than rock-dwelling species which breed in the following year (Smith 1988). There are also differences in population dynamics with rock-dwelling pikas that are largely asocial, occurring at low densities that are generally

stable, year-on-year. Adults vigorously defend territories, though they may be less aggressive toward potential mating partners than other members of the population (Smith and Ivins 1984). In contrast, burrowing pikas are often highly social, utilizing familial burrows; they can occur at high densities (300/ha in plateau pikas, *O. curzoniae*) and their populations exhibit temporal fluctuations. Annual mortality is low in most rock-dwelling species which live for an average of 3–4 years when compared to mammals of comparable size, while mortality is high in burrowing pikas, which also have shorter lifespans (around 2 years) and whose populations have a large yearling cohort (Smith 1988, 2008).

## Cross-References

- [Conservation](#)
- [Home Range](#)
- [Lagomorpha Diet](#)
- [Lagomorpha Navigation](#)
- [Social Behavior](#)

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## Lagomorpha Locomotion

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## Synonyms

[Pika locomotion](#); [Rabbit and hare locomotion](#)

## Definition

Movement of pikas, rabbits, and hares that enable them to move about their environment.

The order Lagomorpha is composed of two extant families: Leporidae (rabbits and hares) and Ochotonidae (pikas). Leporidae consists of 29 rabbit species and 32 hare species. Leporidae typically live in tropical forests, temperate steppes, plateaus, deserts, and Arctic areas (Ge et al. 2013). They are found on all continents except Antarctica and are native to all continents except for Australia and Antarctica (Chapman and Flux 2008; Delaney et al. 2018). Ochotonidae, of which there are 30 species, can be found in North America, Eastern Europe, and Asia. They typically prefer a cold, semiarid, high-altitude environment, and often live in plateau steppe and talus habitats (Chapman and Flux 2008; Delaney et al. 2018).

While lagomorphs can be found in a variety of diverse regions, some species have a narrow habitat tolerance (Chapman and Flux 2008). For instance, the pygmy rabbit requires dense sagebrush, the riverine rabbit is restricted to floodplain vegetation, and the volcano rabbit to zacate grassland (Chapman and Flux 2008). Despite the differences in such habitats, the locomotion in lagomorph species has been adapted for quick movement to escape from predators. Rabbits and pikas generally sprint for cover towards bushes and burrows, while hares are equipped to maintain long distances to outlast predators (Chapman and Flux 2008).

## Gait Sequences

Lagomorphs utilize an asymmetrical gait pattern (Hildebrand 1989). In asymmetrical gaits, the forelimb and hind limb activities are not evenly spaced in time (Granatosky 2018a). The asymmetrical gait occurs close to running speeds which results in decreased contact time between the ground and feet (50% lower than the period of a stride); for a jackrabbit, the contact time between the ground and feet can be as low as 16–18% of the stride. The hind limbs have a longer duration of contact to the ground than forelimbs. This difference in ground contact is also exhibited between the right and left sides (Hildebrand 1989). For instance, the right hind limb may contact the ground for longer than

the left hind limb and vice versa. Within the lagomorph taxa, the pika is the least cursorial followed by the rabbit, with the jackrabbit having the greatest specialization for running (Young et al. 2014).

The preferred mode of asymmetrical gait used by lagomorphs is the half-bound. This gait is seen in animals that use multiple leaps and suspensions with powerful hind legs (Hildebrand 1989). A bound occurs when both hind limbs touch the ground simultaneously followed by both forelimbs. A half-bound occurs if both hind limbs touch the ground simultaneously while the forelimbs are clearly the lead. Both gaits are more conducive for small-to-medium travel spans (Hildebrand 1989). The half-bounding gait of the hare is also useful for “observation leaps,” which aid the animal in avoiding predation by allowing it to better visualize the predator and surrounding area (Bramble 1989). Furthermore, hares are remarkably flexible and can make sudden directional changes as well as rapidly alter their acceleration to flee from predators. Additionally, they can jump to evade predators and can occasionally utilize bipedal locomotion (Williams et al. 2007).

Generally, hares do not exhibit steady-state locomotion. At low speeds, hares saltate (leap); at high speeds, they gallop (Williams et al. 2007). A gallop occurs when there is a lead in both fore and hind pairs of feet. The gallop can either be transverse or rotary. A transverse gallop occurs when both fore and hind leads are on the same side while a rotary gallop occurs when both fore and hind leads are on opposite sides (Hildebrand 1989). Jackrabbits exhibit a rotary gallop. The black-tailed jackrabbit (*L. californicus*) gallop consists of four stages. In the first two stages, the front support on both forelimbs is followed by a suspension stage in which all four limbs are off the ground and are gathered together. In the second gathered suspension stage, the forelimbs are pointed posteriorly while the hind limbs are pointed anteriorly. The third stage is the hind support in which both hind limbs are contacting the ground and are used to thrust into the fourth stage. In the fourth stage, there is an extended suspension with all four limbs off the ground again (Bramble 1989).

## Limb Loading

The hind limbs of lagomorphs work simultaneously to convey a powerful force, allowing the body to move into suspension. The forelimbs are then capable of taking the brunt of the force when they touch the ground from a long leap (Hildebrand 1989). As such, lagomorphs are exposed to frequent abrupt loading on the forelimbs due to their bounding gait (Bramble 1989). As with most terrestrial tetrapods (Granatosky et al. 2018b), the hind limbs function to provide thrust while the forelimbs serve a stabilizing and deceleration role (Williams et al. 2007).

Robust musculature within the proximal hind limb of the hare allows for increased power production and acceleration, which may additionally support the saltation of the hare (Williams et al. 2007). Distal limb muscles of the hare have been shown to produce high force compared to those in the proximal limb. Particularly, the *m. flexor digitorum superficialis* (involved in digital flexion) and the medial and lateral *m. gastrocnemii* (involved in ankle extension) generate the highest force (Williams et al. 2007). The longer fascicles of the proximal limb musculature compared to the shorter fascicles of the distal limb musculature illustrate this difference in specialization. The distal limb muscles also have longer tendons, which reduce the mass of the distal limb and provide a supply of elastic strain energy. Furthermore, abduction/adduction musculature provides stability in the event of sudden turns or change in directionality (Williams et al. 2007).

The forelimbs function as brakes when coming down from a vertical plunge (Bramble 1989). The duration of forelimb-assisted braking is approximately 48–56% of the duration devoted to reacceleration back up into suspension (Bramble 1989). Wild antelope jackrabbits (*L. alleni*) observation leaps have been recorded to produce loads on the body greater than 15 gravitational force equivalent (G) (Bramble 1989). *Lepus californicus* maintains a peak load of 3.5G when its forelimbs contact the terrain in a fast gallop and loads of 9–12G after observation leaps (Bramble 1989). However, the gravitational force is likely greater as these numbers do not consider rough

grounds or spontaneous turns used in natural environments (Bramble 1989).

## Locomotor Kinematics

The kinematic movement of lagomorphs, specifically pikas, is divided into three parts: forelimb movement, spine movement, and hind limb movement. Forelimb protraction and retraction are executed mainly by scapular displacement. Retraction of the scapula begins from the most flexed position at 35–40° in the late swing phase. The mean touchdown angle of the scapula is 46° and mean scapular lift-off angle is 80°. The humerus is almost horizontal at a mean angle of –1° and is held there until the first quarter of the swing phase. The motion of the forearm is mostly parallel to the movement of the scapula especially during the stance phase. The mean touchdown angle of the pika is 33° for the forearm. Forearm retraction continues through the end of stance phase and ends after the start (10%) of swing phase. The mean lift-off angle in the forearm of pikas is 96°. Mean hand touchdown angle is 14°. Hand retraction starts in the second half of the stance phase and ends in the first third of the swing phase. Scapular retraction accounts for 66% of step length in pikas predominating forelimb movement.

For knee and ankle joints, one flexion and extension, a biphasic angular movement per each stance and swing phase is observed. However, in hip joints, a monophasic behavior is shown at asymmetrical gaits. This means that extension enters a plateau during the beginning of stance in pikas. Maximum extension of the hip is reached before lift-off of the trailing limb. Maximum angular extension of the hip joint ends at lift-off in leading limbs. The knee joint flexes before touchdown and reaches maximum flexion at mid-stance when the foot passes underneath the hip joint. Flexion of the knee joint starts earlier in trailing limbs compared to leading limbs (Fischer et al. 2002).

Numerous studies have shown that sagittal bending movements have a major impact on mammalian locomotion and that asymmetrical

gaits are the most efficient mode of locomotion (Schilling and Hackert 2006). Velocity is increased with increased step length via the integration of a long aerial phase and extended stance and swing phases. Cineradiography has been used to assess the intervertebral joint movement in pikas, showing movement from the level of T14/15 to the pelvis. Due to the lack of a tail extending past the contour of the pika's body, individuals show a nearly vertical touchdown ( $100\text{--}111^\circ$ ) and more protracted lift-off position of the pelvis ( $131\text{--}151^\circ$ ). This results in a relatively higher contribution to step length compared to other small therian species with tails that display a horizontal touchdown and retracted pelvis during lift-off (Schilling and Hackert 2006).

### Locomotor and Respiratory Coupling

Lagomorph locomotion has served as the model system to understand the relationship between ventilation and locomotion. Currently, there are three hypotheses on the relationship between ventilation and locomotion. The visceral piston (VP) hypothesis, proposed by Bramble and Carrier (1983) and Bramble (1989), states that during galloping the relative motion of the visceral mass may influence the respiratory cycle. It is thought that upon landing, the cranial motion of the visceral mass, especially the liver, which is attached to the diaphragm, facilitates expiration by decreasing the thoracic volume. Likewise, during the forelimb flight phase, caudal motion of the visceral mass facilitates inspiration by expanding the thoracic volume (Simons 1999). Hence, with each stride, inertial movements of the visceral mass drive cranial and caudal movements of the diaphragm, ultimately inducing expiratory and inspiratory airflows. This concept was further modeled and analyzed by Alexander (1989) in wallabies. In the wallaby, with the deceleration of landing, the viscera moved forward, enhancing expiration. Likewise, with forward and upward acceleration, the viscera moved caudally, enhancing inspiration (Boggs 2002).

According to Young et al. (1992), the vibration mechanics during galloping suggest otherwise.

The vibration mechanics (VM) hypothesis proposes that displacement of the liver is unlikely to drive ventilation. It states that the liver should oscillate nearly  $180^\circ$  out of phase if inertial forces alone were responsible for the motion of the liver. This hypothesis supports the idea of a simultaneous rearward motion of the liver during expiration (Simons 1999).

Simons (1996) argues that the timing of respiration and locomotion is best explained by a pneumatic stabilization (PS) hypothesis, which states that the lungs serve as an important role in the stabilization of the thorax during locomotion. The simultaneous exhalation and forelimb support results in positive pressure in the pleural cavity, which ultimately drives the visceral mass caudally, providing mechanical stability for the heart and other organs (Simons 1999). Boggs (2002) describes this idea as inflated lungs acting like "air-bags," protecting the heart from the full impact of force exerted from the ground.

Analyses of cineradiographic and pneumotachographic data obtained from *Oryctolagus* support the PS model. Since the lungs are intimately associated with the chest walls and are positively pressurized during landing, they may provide mechanical support to the viscera during running (Simons 1996). The results of another study by Simons (1999) confirms that the motion of the liver moves caudally during expiration and cranially during inspiration, supporting the pneumatic stabilization and vibration mechanic hypotheses (Simons 1999).

Running and breathing in mammals report consistent 1:1 locomotor-respiratory coupling (LRC) during galloping (Bramble and Carrier 1983). Since rabbits utilize an asymmetrical gait, the half-bound, they are expected to have a LRC ratio of 1:1. According to Simons (1999), the occurrence of 1:1 LRC increases at higher speeds and stride frequencies, despite the fact that rabbits exhibit a variability in LRC (Simons 1999).

Among most mammals, increased consistency of 1:1 LRC is observed in more cursorial species. Additionally, there are shared anatomical features of cursorial species that noncursorial species lack (Simons 1999). For instance, Ochotonidae is considered to be a more primitive family that is

composed of noncursorial species (Gambaryan 1974), whereas hares (*Lepus*) consist of specialized runners, combining speed, endurance, and agility (Howell 1965; Gambaryan 1974; Bramble 1989). Hares are shown to have unique anatomical variances such as a relatively large heart and lung mass, well-defined grooves in the lung tissue, tissue of the right cranial pulmonary lobe between the heart and sternum, and strong pericardial attachment to the sternum. The *Oryctolagus* and *Ochotona*, both noncursorial species, lack most of these features entirely (Simons 1996). This supports the idea that various anatomical parts within the thorax work in unison during locomotion.

## Opportunity for Bioinspiration

Learning more about Lagomorpha locomotion potentially has a wide range of applications. For example, gaining a better understanding of the biomechanics of the Lagomorpha knee joint may further elucidate the effects of mechanical loading on bone, which can ultimately lead to osteoarthritis (OA) or fractures (Gushue et al. 2005). Specifically, understanding the tibiofemoral joint contact load distribution may be used in theoretical and experimental studies of the rabbit hind limb to draw comparisons to the human knee and further the advancements of OA or fracture treatment (Gushue et al. 2005). Furthermore, studying the gaits of the Lagomorpha may spur advancements in robotics. Pikas, for instance, exhibit the Raibert “self-stabilizing mechanics” with nominal use of neuronal or computational effort while retaining energy (Hackert et al. 2006). Further studies of this phenomena can result in novel applications of Lagomorpha locomotion to robotics.

## Conclusion

Lagomorpha species are terrestrial animals, with considerable variation in their habitat preferences. Ochotonidae (pikas) live in plateau steppe and talus habitats, whereas Leporidae (rabbits and

hares) live in forest, temperate steppe, plateau, desert, and Arctic areas (Ge et al. 2013). The lagomorphs are united by their use asymmetrical, half-bounding gait with interspersed observation leaps. These cursorial and saltatorial adaptations have evolved to promote quick escape from predators. This either involves increased speed in rabbits and pikas or endurance as seen in the hares. Moreover, the hind limbs of the Lagomorpha provide a powerful support to thrust into suspension while the forelimbs absorb the brunt of the force when landing. Lagomorph locomotion has also been used as the model system for understanding how locomotion and respiration are coupled. Finally, studying the Lagomorph locomotion has a plethora of applications. Precise knowledge about their biomechanics may spur robotic innovation as well as medical innovation.

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Radiation](#)
- [Basal Metabolic Rate \(BMR\)](#)
- [Captivity](#)
- [Dispersal Ability](#)
- [Dispersal Patterns](#)
- [Diurnality](#)
- [Domestication](#)
- [Ecology](#)
- [Evolution](#)
- [Extinction in Learning](#)
- [Gait](#)
- [Greyhound Racing](#)
- [Herbivore](#)
- [Home Range](#)
- [Homology](#)
- [Homoplasy](#)
- [Husbandry](#)
- [Lagomorpha Diet](#)
- [Lagomorpha Life History](#)
- [Lagomorpha Navigation](#)
- [Locomotion](#)
- [Morphology](#)
- [Muscular System](#)



- ▶ [Natural Selection](#)
- ▶ [Navigation](#)
- ▶ [Paleontology](#)
- ▶ [Pets](#)
- ▶ [Phylogeny](#)
- ▶ [Quadrupedal](#)
- ▶ [Species](#)
- ▶ [Taxa](#)
- ▶ [Terrestrial](#)
- ▶ [Territoriality](#)
- ▶ [Vertebrate Nervous System](#)
- ▶ [Zoo](#)
- ▶ [Zoology](#)

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## Lagomorpha Navigation

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## Synonyms

[Behavior](#); [Hare](#); [Movement](#); [Pika](#); [Rabbit](#)

## Definition

Navigation – the theory and practice of charting a course to a remote goal (Schöne 1984).

## Introduction

The daily movements of animals are governed by many factors including the need to find food, water, conspecifics, and favorable environmental conditions while trying to avoid predators, dominant ecological competitors, and unfavorable habitats and conditions. Animals use external cues such as odor (Gagliardo 2013), landmarks (Baader 1996), day length (Baoping et al. 2009), the position of the stars (Dacke et al. 2013), and the Earth's magnetic field (Chernetsov et al. 2017) to guide their movements in the landscape and the timing thereof.

The order Lagomorpha is comprised of two families, the hares and rabbits (Leporidae or leporids) and the pikas (Ochotonidae). The navigational capabilities of lagomorphs are poorly understood, with the few movement studies to have been conducted focusing on dispersal, home range behavior, foraging, and habitat use. Indeed, movement behavior has been entirely unstudied in most lagomorph species. Studying the navigational capabilities of small-to-medium-sized mammals can be challenging as the equipment required for fine-scale data collection (e.g., GPS collars) are often too heavy and/or have limited battery life. For example, the maximum weight for GPS collars is defined by the size of the subject. This is known as the “5% rule” (Cochran 1980); the weight of the collar should not exceed 5% of the focal animal's mass. For a very large hare weighing 5 kg, that would equate to a GPS collar weighing 250 g. The typical battery life for such a collar is around 500 days, though that is based on the recording of only a handful of “fixes” (i.e., records of the individual's location) per day – not enough for nuanced analysis of movement behavior such as navigational strategies (Handcock et al. 2009). The frequency of fixes required for such studies would exhaust the battery in only a few days. However, technological

advances such as the use of micro-GPS and snapshot receivers (McMahon et al. 2017), as well as increasingly lightweight collars and improved batteries, mean that many obstacles are slowly being overcome. It is likely that future technological improvements and dedicated research will lead to a greater understanding of movement behavior and navigational strategies, particularly in larger lagomorphs.

Given the lack of navigation-specific literature, here I broadly summarize research on movement behavior, particularly in the context of home ranges, habitat use, and dispersal, in each group of lagomorphs.

## Hares

Hares (genus *Lepus*; 32 species) are crepuscular/nocturnal open-habitat specialists with long hind legs which allow them to flee from potential predators at high speeds. They are poorly adapted for a digging and rest during that day in above ground depressions, known as forms. As they are not reliant on burrows for shelter and protection, hares generally range over much wider areas than most rabbits and certainly all pikas (see ► “[Lagomorpha Life History](#),” Table 1). However, all hares and their offspring (“leverets”) make use of emergent vegetation for concealment. For example, the Irish hare (*L. timidus hibernicus*), a subspecies of the mountain hare (*L. timidus*), favors open-field habitats (Dingerkus and Montgomery 2002) but is also associated with rough grassland which offers potential cover in the form of stands of rushes (*Juncus* sp.; Caravaggi et al. 2015). Similarly, woolly hares (*L. oiostolus*) favor montane grasslands for foraging but require intermediate shrub habitats for cover (Lu 2011). Researchers studying movements of translocated European hares (*L. europaeus*) found that, rather than establishing home ranges at release sites, the translocated individuals moved to find better habitats which were more similar to those from which they had been removed (Ferretti et al. 2010). Hares will also recurrently use a network of paths between foraging and/or resting sites (Caravaggi et al. 2016).

Dispersal, i.e., the movement of young out of the natal range (natal dispersal) or the movement

of adults to another breeding area (breeding dispersal), is an important process with a key role in population dynamics. The benefits conferred by individuals moving within and between populations and into previously uncolonized habitats are such that dispersal is considered to underpin the persistence of many species (Avril et al. 2011). The causes of dispersal are poorly understood, though it is likely that inbreeding avoidance, mate competition, resource availability, and the density of conspecifics all play a role. The availability of cover vegetation may be a particularly important factor in determining the eventual settlement locations of dispersing females (Avril et al. 2011). Dispersal is ubiquitous and common among hares, though breeding dispersal occurs at lower frequencies than natal dispersal. Moreover, the proportion of young which disperse from the natal range, and the distances travelled, varies between and within species. However, movement behavior during dispersal can give clues to navigational capabilities. For example, dispersing leverets have been observed to use direct long-distance exploratory movements over 1 km before returning to the same resting location, over several days (Reid and Harrison 2010). This return behavior suggests a capacity for accurate navigation on a landscape scale.

The locomotor activity of hares often varies seasonally, with an increase in activity particularly around the start of the breeding season. During this time, individuals will move from their home ranges in search of mating opportunities. It is possible, perhaps even likely, that olfaction plays a role in the location of mates, though olfactory communication in hares is currently not a research priority. Locomotion may also be affected by perceived predation risk (i.e., lunar illumination) and local predator density and abundance (Rogowitz 1997); hares spend more time moving between habitat patches, reducing stationary foraging time in each patch.

## Rabbits

There are ten genera of rabbits (*Brachylagus*, *Bunolagus*, *Capolagus*, *Nesolagus*, *Oryctolagus*, *Pentalagus*, *Poelagus*, *Pronolagus*, *Romerolagus*, *Sylvilagus*), with a total of 29 species. Rabbits differ

physically from hares in that they have comparatively shorter hind legs and shorter ears and are physically smaller (► [Lagomorpha Life History](#), Table 1). Old World rabbits (all genera except for *Sylvilagus*) are diggers, creating underground holes, burrows, and communal warrens in which to rest, avoid threats (e.g., predation, poor weather), and raise their young (known as kits or kittens). In contrast, new world rabbits (*Sylvilagus* sp.) will either utilize holes or burrows dug by other species or raise their young in aboveground forms. The movement behavior of rabbits is poorly understood, with substantial knowledge gaps in all aspects.

Rabbits choose their home ranges with reference to the vegetative composition of the landscape, preferring areas with an abundance of vegetation which could be used for cover. For example, researchers in Spain found that the warrens of European rabbits (*O. cuniculus*) were strongly associated with the *Retama monosperma*, a dense flowering bush (Dellafiore et al. 2008). Rabbits make use of cover vegetation to provide shelter and concealment, often using the same paths through ostensibly safe habitats to reach foraging areas in their home ranges. European rabbits also live in underground warrens which may span a considerable area and have multiple entrances. Within their home range, therefore, European rabbits have a number of options which offer safety from potential threats. Flight to places of concealment is usually direct, suggesting that the animal is aware of its position relative to relevant landscape features.

The proportion of dispersing juveniles is often high, particularly in low-density populations, and, as with many mammal species, dispersing cohorts are often male-biased. However, levels of dispersal may be similar between the sexes when populations occur at high densities (Richardson et al. 2002). In many species, dispersing subadults barely venture beyond their natal home range; males are often more likely than females to make long-distance movements. For example, one male marsh rabbit (*S. palustris*) was recorded as having dispersed over 2 km from its place of birth, compared to most females which did not leave their natal ranges (Forys and Humphrey 1996). In contrast, a study of pygmy rabbits (*Brachylagus*

*idahoensis*) found that females dispersed up to three times further than males (Estes-Zumpf and Rachlow 2009). Dispersal distance may be related to population density (e.g., European rabbit) (Richardson et al. 2002), with long-distance movements being more common in low-density populations.

### Pikas

There are 30 species of pika, all of which are classified within a single genus, *Ochotona*. Pikas are the smallest of the lagomorphs (► [Lagomorpha Life History](#), Table 1), with rounded bodies and ears and no visible tail. Pikas are broadly split into two groups: (i) rock- or talus-dwelling species and (ii) species of grassland or steppe habitats. The two groups have different social behaviors, though they do not differ in life history or ecology. As with other leporids, there is little information available on their movement behavior and navigational capabilities.

Steppe and grassland pikas are social, living in often high-density groups. In contrast, talus pikas are largely solitary and highly territorial. Nevertheless, the dispersal behavior of the two groups is similar. For example, both breeding and natal dispersal distances of plateau pika (*O. curzoniae*; a steppe species) and American pika (*O. princeps*; a talus-dwelling species) are often extremely short, rarely extending beyond two family ranges (Dobson et al. 1998). However, genetic analyses suggested that American pikas may occasionally disperse up to 2 km from their natal range and that intermediate movements may be common (Peacock 1997). Juvenile males are often the primary dispersers in plateau pikas, a pattern not observed in American pika.

The (re)colonization potential of pikas has been shown to be strongly influenced by the degree of habitat patch connectivity, as well as patch quality (Franken and Hik 2004). However, while juveniles are more likely colonize neighboring patches in fragmented habitats, dispersal rates are not necessarily compromised, with a mixture of short- and long-distance dispersal events resulting in a genetically contiguous metapopulation (Peacock and Smith 1997). Thus, dispersing pikas likely use similar exploratory

behaviors to those found in other lagomorphs, facilitated by emergent vegetation and landscape features (e.g., rocks). Researchers investigating the social behavior of the northern pika (*O. hyperborean*) have shown that the species exhibits spatial awareness and recall, with individuals recurrently returning to the same shelter and breeding pairs using multiple collective food caches (Gilwicz et al. 2005).

### Conclusion

Navigational abilities are common features among animals. All lagomorphs exhibit behaviors which can be interpreted in terms of navigational skills, including foraging behavior and the utilization of burrows and/or vegetation for cover. Therefore, it is reasonable to assume that lagomorphs have long-term awareness and understanding of the composition of the habitats and microenvironments found within their home ranges. These cognitive maps (i.e., representations of an animal's environment which are used in decision-making; Tolman 1948) allow them to effectively navigate between foraging and resting areas within their home ranges and beyond such as when making exploratory forays beyond the natal range. However, navigation and movement behavior are understudied in lagomorphs, and, hence, data are scarce. There is scope to expand research in spatial cognition, e.g., mental mapping, into lagomorphs, thus giving researchers greater insight into population dynamics and habitat utilization and requirements, as well as potentially benefitting conservation and management processes.

### Cross-References

- [Home Range](#)
- [Lagomorpha Life History](#)

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## Lamarckism

- [Jean Baptiste Lamarck](#)
- [Social Darwinism](#)

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## Land Animals

- [Terrestrial](#)



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## Land Fowl Gait

### ► Galliformes Locomotion

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## Landmark

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### Definition

The term “landmark” has numerous meanings even within the spatial domain: it can refer to a prominent object that allows one to determine where they are or which direction they are facing (a mountain that is west of a home range), an object used as a beacon (a tree that bears fruit within), or an object that aids in finding another place in a process referred to as piloting (“40 m south of the statue”). These meanings are functional definitions, referring to ways in which an object can guide spatial behavior, rather than properties of the object itself: a landmark can be large like the skyline of a city or small like a rock on the ground. These various functions of spatial landmarks have been studied in numerous species ranging from invertebrates to humans.

### Introduction

Whether an animal uses a cue or which cue an animal uses to guide spatial behavior cannot be determined by observation alone. For example, an ant that suddenly veers to the left may be navigating with the help of visual cues, turning based on motor memory or pheromone trails, or avoiding an obstacle or danger on the right. Identifying whether a particular cue is used as a landmark requires experimental manipulation; typically, the presumed cue is changed in some way to see if it alters behavior, referred to as the transformational approach (Cheng and Spetch 1998).

Most of the research summarized here will concern how landmarks are used to guide search toward a specific location (i.e., piloting). Piloting is generally considered to be a complex process because it cannot be accomplished by a simple approach mechanism but instead involves learning spatial information about the direction and/or the distance between landmark(s) and the goal.

### Classic Studies of Landmark Use

#### Tinbergen’s Wasps

Tinbergen (1972) performed a classic test of landmark use in the field in solitary digger wasps. These insects lay their eggs in nests dug into the ground. During foraging flights, they exit and enter through an inconspicuous hole. To determine whether the wasps use nearby visual cues to find their nest upon returning with food, Tinbergen placed a ring of pinecones around the nest, while the wasp was inside. He then displaced the ring of pinecones to one side of the nest, while the wasp was away foraging. Upon returning, the wasp searched for the nest entrance within the ring of pinecones rather than at the actual nest, clearly indicating the use of the visual cues to guide search to the nest entrance.

#### Rats in a Water Maze

A classic laboratory study of landmark use was conducted in rats using the now-famous water maze task (Morris 1981). The task involves placing rats in a tub of milky water containing a hidden platform that the rat can climb on to escape from the water. Visual cues are provided to help the rat learn where the platform is. If the cues are located at the platform, they can be used as beacons to head toward. If they are located outside of the maze or at a location in the maze but distant from the platform, they can be used to guide search to the platform by learning the direction and/or distance from the cues (i.e., piloting). Studies have shown that these functions are distinct, with piloting by proximal or distal landmarks relying on different brain regions than beaconing to a cue at the goal (e.g., Save and Poucet 2000).

## Piloting by Landmarks

Piloting by visual landmarks has now been experimentally demonstrated in a wide variety of animals, ranging from invertebrates to humans. In an example of experimental research on landmark-based piloting, Cheng (e.g., 1988; see Cheng and Spetch 1998 for review) gave pigeons the task of finding a goal (bit of food hidden under sawdust) in a rectangular search arena. A visual landmark, consisting of a stripe on the wall or an object in the tray, was located at a fixed distance and direction from the hidden food. Over trials, the pigeon learned to accurately find the food, and tests in which the location of the landmark was shifted indicated that the birds used the landmark. Use of this cue was more subtle, however, than simply following exactly the distance and direction specified by the landmark. For example, if the goal was located near one of the edges of the enclosure, the pigeons shifted their search in the direction parallel to the edge in response to landmark shifts, but not in the direction perpendicular to the edge. In addition, shifts of searching were rarely the full distance of the landmark shift, indicating that information from the landmark was used in conjunction with other cues, resulting in a compromise. These general results were replicated in a study with chickadees (*Poecile atricapillus*; Cheng and Sherry 1992) and were also found in a study conducted on a touch-screen computer monitor with pigeons (Spetch et al. 1992). These touch-screen tasks differed from the navigational tasks in numerous ways (e.g., smaller scale of space, graphic landmarks instead of objects, top-down view, pecking instead of moving through space); the similar use of landmarks in these very different tasks suggests that these studies tapped central processes underlying how landmarks guide spatial behavior, rather than task-specific behaviors. Moreover, the partial shifts of searching in the direction of the shifted landmark indicate that multiple cues guided search behavior.

### When and Which Landmarks to Use

Although piloting by visual landmarks is prevalent in a wide range of organisms, there are species differences in the extent to which spatial behavior

is guided by landmarks and the type of landmarks that are used. These differences can reflect many factors, most notably differences in sensory mechanisms and in environmental or ecological adaptations. Studies with ants illustrate both of these factors. Ants have a number of mechanisms for finding their way back to their nest after a bout of foraging; these can include chemical signals from pheromone trails, path integration mechanisms for keeping track of distance and direction traveled, learning of familiar routes, or guidance by landmarks (e.g., Cheng et al. 2009). Habitat seems to influence the relative extent to which ants rely on path integration or guidance by visual cues, with more reliance on path integration for ants living in barren habitats that have few salient landmarks than for ants living in cluttered environments with many visual cues that could guide search (Cheng et al. 2009). The importance of sensory mechanisms was suggested by a study on ants in which the researchers attempted to train the ants to use a large colored cue as a landmark to guide their exit from an enclosure (Legge et al. 2010). The ants ignored this seemingly obvious landmark (to the human eye) but can use skyline panorama, which fits well with the nature of the ant's visual system (Graham and Cheng 2009).

### Using Multiple Landmarks

Using multiple cues to find a goal makes adaptive sense for many reasons. First, redundancy allows for a backup in case one of the cues becomes unavailable (e.g., because of weather-related changes in visibility). Second, use of multiple cues may provide more precise localization of a goal (Kamil et al. 2001) because the bearings from each landmark are subject to error that increases with distance and each additional bearing can be of help to reduce the error. This "multiple-bearing hypothesis" has been supported in studies with Clark's nutcrackers (*Nucifraga columbiana*; Kamil et al. 2001) and humans (Forloines et al. 2015). Third, using multiple landmarks can increase the certainty or confidence that the location is correct. Studies have indicated that humans (e.g., Du et al. 2017) and nonhumans (e.g., Legge et al. 2016) integrate information from landmarks

by weighting the cues according to their reliability or the certainty with which they indicate the goal location. This is consistent with evidence that organisms will integrate information from different types of cues, such as path integration and visual memory (Wystrach et al. 2015) or celestial and terrestrial cues (Legge et al. 2015), often in a Bayesian fashion (see Cheng et al. 2007).

### Competition Between Landmarks

Although information from multiple landmarks is often combined, there are also cases in which the presence of one landmark competes, or interferes, with learning of another landmark. Failure to learn about a new cue when it occurs together with already learned cues is referred to as “blocking,” a well-established finding in the domain of associative learning. Such blocking sometimes also occurs between discrete landmarks in spatial learning tasks (honeybees *Apis mellifera*, Cheng and Spetch 2001; rats, Stahlman and Blaisdell 2009). Even when learning about the location of a goal for the first time, competition can also occur because of differences in the salience or usefulness of cues. This kind of competition, which also occurs frequently in associative learning, is called “overshadowing.” Several studies have found that landmarks nearer to a goal can overshadow learning of landmarks farther from the goal (e.g., pigeons, Leising et al. 2011; Spetch 1995; Clark’s nutcrackers, Goodyear and Kamil 2004).

### Landmark Arrays: Absolute Versus Relational Learning

Consider a situation in which you encounter a patch of wild strawberries when you are out walking, and you want to remember where it is so that you can return to it later. The patch is approximately equal distance in different directions from four nearby spruce trees. You might encode these trees as an array of landmarks and remember that the strawberries are in the middle of the landmark array – an example of relational learning. Or instead you could encode the trees as individual landmarks and encode the direction and absolute distance from one or more of these landmarks. To test whether relational or absolute information is used, experimentally provided landmarks can be

shifted after the learning phase, for example, by expanding the distance between them, to see whether search occurs at the relational location (e.g., in the middle of an expanded array) or at an absolute location (e.g., the learned vector from individual landmarks).

Which type of encoding animals display seems to depend on several factors. One factor is whether the animal needs to use the landmarks to figure out which direction is which. If the animal is already oriented within the search space (as would be the case if you knew your heading direction when you were walking or if a pigeon searches in a space containing salient directional cues such as a door on one side of the room), then the landmarks may be used for goal localization but are not needed to get bearings. In this case, many species seem most likely to use absolute information, learning the distance and direction from one or more of the individual landmarks, rather than searching at the relational location (e.g., Collett et al. 1986; Mac Donald et al. 2004; see Kelly and Spetch 2012 for a review). Pigeons do this both with arrays of graphic stimuli on a touch-screen monitor and with real objects in an open space, suggesting that this absolute spatial encoding is not task-specific (Spetch et al. 1997). This result contrasts strongly with adult humans, who almost always respond based on the relational rule (Spetch et al. 1997). On the other hand, if distal directional cues are blocked, animals show relational encoding of the landmark array (Sturz and Katz 2009). Moreover, birds can use landmark configuration to distinguish between different landmark arrays (Sutton 2002), and they can encode relational information from an array of landmarks if training precludes the use of absolute information (e.g., by varying the distance between the landmarks in training; Kamil and Jones 1997; compare to Kelly et al. 2008). These results suggest that animals show considerable flexibility in how landmarks are used and they illustrate the distinction between what animals typically encode from a landmark array and what they can encode. The effects of training also suggest a possible reason why adult humans typically show relational learning of landmark arrays: our extensive experience with scale transformations

of space from pictures and maps may predispose us to prioritize relational information. Interestingly, honeybees also seem to respond to relational information from arrays of landmarks, searching farther from an array of landmarks when the distance between them is experimentally increased (Cartwright and Collett 1983). In this case, the reason appears to be because the bees use a view-matching process in which they search at a location that best matches the remembered image of the landmarks from the goal. Finally, rats in water mazes appear to learn the confirmation of landmarks to find the platform (Benhamou and Poucet 1998), perhaps because they use these cues for orientation as well as goal localization.

### How Landmarks Are Used to Guide Search

There is ample evidence that many animals can extract both distance and direction information about a goal location from discrete landmarks. It is less clear exactly how the information is extracted. Some studies have suggested that bees (Cheng 1998) and birds (Cheng 1994; Pritchard et al. 2015) independently encode distance and direction information, whereas at least one study with rats suggested that whole vectors from landmarks were encoded (Gibson and McGowan 2014).

### Conclusions

Using visual landmarks to pilot to a goal is widespread among animals and is one of several navigational mechanisms that allow animals to find their way around and return to important places such as home or sources of food. Accurate and efficient navigation is often crucial to survival, so it is unsurprising that animals show flexible and often sophisticated mechanism for selecting among or integrating information from cues to guide spatial behavior.

### Cross-References

- [Associative Learning](#)
- [Blocking](#)

- [Cognitive Map](#)
- [Morris Water Maze](#)
- [Navigation](#)
- [Nikolaas Tinbergen](#)
- [Orientation](#)
- [Overshadowing](#)
- [Pigeon \(\*Columbidae\*\)](#)
- [Spatial Orientation](#)

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## Landmarks

### ► Mustelidae Navigation

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## Language

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## What Is Communication?

Communication is the process through which one individual transmits information to another. This



process involves some form of behavior, such as the production of a signal that is generated by one individual that acts as a sender and is transmitted to another individual that acts as a receiver. When a receiver is present to perceive the sender's signal and process the associated information, communication is said to have occurred. Others have clarified this distinction as, "Communication does not begin when someone makes a sign, but when someone interprets another's behavior as a sign" (Knight et al. 2000). In many forms of communication, the sender can then transmit another signal in response, and thus both individuals take on both roles in the course of communicating. The information from a sender can be transmitted in many different ways. For example, the information can be as simple as one organism being seen by another and thus revealing its location. That same information can also be conveyed through other modalities, such as listening to the sounds that a distant organism produces and determining its location in that way. These are very simple examples of information being transmitted, but exchanged information can also be much more complex, as is the case of the detailed information contained in a recipe for chocolate cake or the nuanced information conveyed in a friend's warm smile and cheerful tone of voice.

One of the most familiar forms of communication that humans use is language. Language is an especially efficient means of communicating complicated ideas quickly and effectively, and it is a powerful tool to help people describe their ideas, express their emotions, and understand the thoughts and feelings of others. Language involves the use of sounds or written symbols, and these constitute a lexicon through which a sender imparts information to a receiver. This is often done by taking turns, such as alternation of speaking during a conversation or an exchange of texts or emails, and individuals who are fluent in a given language use those sounds and symbols equally well as either sender or receiver. The ability to use those relatively few sounds and symbols in specific arrangements to convey an amazing diversity of complex ideas is thought to be a defining characteristic of human cognition (Prather et al. 2017). In the following sections, we will discuss spoken and written language as a means of communication, the influence that

language has had in humans' emergence as the dominant species on our planet, the cells and circuits through which the nervous system enables communication through language, and the ways in which those insights relate to our understanding of how humans communicate in ways other than spoken or written language.

## What Is a Language?

Despite being such a prominent feature of our everyday experience, language can be challenging to define. Some researchers have defined it as "a system of arbitrary vocal symbols by means of which a social group cooperates" (reviewed in Cyelan 2017). This definition captures language as an entity that is communicated through speech, but it leaves unaddressed the ways that we communicate using written language, as in the case of this text, or manual gestures, as in the case of signed languages. Others have described language as the ability to communicate, as both sender and receiver, using a specific and shared set of symbols such as sounds or written letters (reviewed in Cyelan 2017). This much broader definition is consistent with what many people mean when they use the term language, but it also leaves open questions about how different a set of symbols must be in order to identify them as different from those of another language. For example, even among people who are fluent in the same language, no two people speak in exactly the same way. These individual idiosyncrasies do not impede the process of communication, so those two people would be described as each speaking the same language. If we look beyond individual speakers, we can sometimes encounter much greater differences in pronunciation or terminology, and these are often distributed across different geographical regions. These localized differences are called dialects of the language, as their differences are clearly detectable, but they do not hinder an individual's performance as either sender or receiver, and therefore they do not impede the process of communication. These examples highlight that there can be variation in how the symbols that comprise a language are produced by different individuals. There is no

single definition of how much variation is required to establish a boundary between different languages, but it is clear that successful communication is the primary requirement in considering whether symbols constitute different languages. In that light, a useful functional definition of language is a set of symbols through which senders and receivers can exchange information, express ideas and emotions, and influence the thoughts and activities of others who share the same set of symbols.

In communication through the use of language, information can be transmitted through vocal gestures, as occurs in spoken conversations, or through written symbols or other forms of manual gestures, as occurs when we write or type letters such as those you are reading now. These types of complex vocal and manual gestures are inherent to how we communicate using language, but complex behaviors alone are not sufficient to say that language is being used. For example, many animals use vocalization as an important form of communication, such as the roar of a lion or the songs and calls of a bird. Those vocalizations are key elements of how those species communicate, but they are typically used to communicate relatively simple information such as territoriality or aggressive intent (Catchpole and Slater 2008). In other species such as chimpanzees, individuals modify their use of vocalizations in different social contexts such as different calls in association with food sources of different sizes (reviewed in Cheney and Seyfarth 2018), but even those vocalizations are lacking a key feature that defines communication through use of human language. That feature is the rules-based organization of symbols into combinations through which complex information can be transmitted. These have been referred to as the “design features of language” and more recently as the “faculty of language,” and they include things like the ability to structure words in such a way that they refer to abstract ideas or objects that are not physically present, or they clarify that the sender is describing the past or the future, or they provide the sender with the ability to use language to talk about language just as we are doing here (Hauser et al. 2002; Pinker and Jackendoff 2005;

Wacewicz and Zywickzynski 2015). Through the symbols and organizational rules of language such as recursion, fluent speakers can assemble a finite set of symbols into different combinations to reliably communicate an infinite set of facts, thoughts, and emotions. Thus, a central aspect of the beauty and importance of language lives in the ability to create the infinite from the finite. By applying the rules of linguistic structure, future plans can be made, and the consequences of possible actions can be considered. Objects can be referenced and described even if they are unfamiliar because they existed far away or long ago or even if they may have never existed at all.

No set of behaviors with as much complexity and communicative power as human language has ever been described in other species. Some aspects of those communicative advantages are present in the behaviors of other species, such as a bird’s identity being detectable from the traits of the songs that it sings or a bird’s ability to produce strings of sounds with patterning that has led some to speculate that it constitutes a form of syntax (Catchpole and Slater 2008; Gentner et al. 2006). However, none of those vocalizations appears to have anything approximating the descriptive and referential power of the sounds that we use in language, and no set of animal behaviors incorporates all of the traits that define human language. Interestingly, bees appear to be able to use their complex “waggle dance” behaviors to communicate about the location and quality of food sources (Price and Gruter 2015). This has led to speculation about the intellectual capacity of bees and whether their movements related to food may meet some of the criteria to call those behaviors a rudimentary form of language. Although elaborate and useful to communicate specific information, those behaviors appear to be restricted such that they are used only to refer to food sources and relevant navigational information to find those sources. In contrast, humans are unrestricted in what we can describe using language. In some cases, training or other forms of relevant experience may be necessary to communicate about abstract ideas or new discoveries, but that can be readily achieved by fluent speakers, and the ability to learn and achieve such expansion highlights

the power of language as a tool to link current status to almost unlimited future possibilities.

A key feature of communication through language is that both the sender and the receiver must use the same set of symbols. This highlights the role that learning plays in acquiring those symbols and developing fluency in a language. As detailed in a later section, the ability to communicate using language is an imitative form of learning. Factual content appears to be learned intentionally, such as the fact that a canine pet is called a “dog” in English, but the fact that we learn language at all appears to emerge from a natural predisposition to interpret the noises made by others as meaningful signals (Pinker and Jackendoff 2005). Language is typically acquired during very early life, with nascent speakers learning the sounds that comprise their native tongue by listening to the sounds produced by others around them (reviewed in Prather et al. 2017). Humans are extraordinarily skilled in our ability to hear the detailed features of sounds used in language, as evident in the features of different regional accents often shared by children and the parents from whom those children learned their language. This link between sounds that are heard and sounds that are produced relies heavily on the sense of hearing, with a healthy sense of hearing being essential for young speakers to learn those sounds and refine their imitation of those model behaviors (reviewed in Prather et al. 2017). This is most clearly evident in people who are deaf or experience other forms of hearing impairment. People who are deaf from birth have great difficulty acquiring and refining the sounds used in spoken language. Even among people who achieve complete fluency prior to any hearing impairment, their clarity of spoken language is typically reduced if their hearing impairment is severe or prolonged. Other animals such as parrots and songbirds are also very skilled at imitating the sounds they hear produced by others, and these species are even capable of expressing regionally distinct features that are sometimes described as dialects. Yet despite the complexity of their songs and their skill in imitative learning, there is no evidence that birds are capable of using their vocalizations to refer to a range of different ideas

or otherwise communicate with the complexity and productivity of human language. Together, these examples from the animal kingdom serve to highlight the extraordinary utility of human language. In fact, the ability to communicate so broadly and so effectively through language appears to be uniquely human.

## Written Language and Its Role in Human History

Writing enables thoughts and emotions that are expressed in language to persist through time, and it enables the accumulation of information far beyond the knowledge of any single individual. Through translating thoughts into a system of symbols, thoughts can last far longer than a single utterance or even a single lifetime. Those symbols can represent entire words, as in the characters used in Chinese, Japanese, Korean, and Vietnamese writing, or they can represent consonant and vowel sounds arranged in a specific sequence, as in the letters of the English language that are used here. This latter form of written representation constitutes an alphabet, and the individual letters represent the basic sounds of language (Bright and Daniels 1996). The first use of an alphabet to represent linguistic sounds is thought to have occurred among the Phoenicians, and those written symbols were used as a tool for communication in trade throughout the Mediterranean area (Bright and Daniels 1996). That system is thought to have influenced the development of the Greek alphabet, as the Greeks adapted the Phoenician writing system to represent the sounds they used in their own language (Bright and Daniels 1996). The Greeks built on the Phoenician writing system to create a system with individual symbols that represented both consonants and vowels and that could be arranged in a linear sequence to communicate information. For this reason, some people consider the Greek writing system to be the first true alphabet (Bright and Daniels 1996). Others further adapted the Greek system for their own needs, such as the Latin script that was an ancestor of the 26 letters that compose the English alphabet (Bright and Daniels 1996).

Alphabets were transformative because they enabled people to archive their thoughts. Prior to that, the ideas and traditions that compose a people's culture were passed from one generation to the next orally. Writing enabled those stories to be collected and placed into reservoirs that could be preserved and consulted anew by members of subsequent generations. These reservoirs, which we call "books" in English, were originally made from thin bits of material taken from the bark of trees. The Latin word for that material (*librum*) gave rise to the terms *liber* to refer to what we would call a book and *librarium* to refer to a place where books were collected and stored. In its earliest days, creating books was a very laborious task, with scripts written by hand onto sheets of fragile material that were very challenging to store and preserve. It could take a very long time to create even a single book, and it was even more challenging to create multiple copies. Thus, books were a means of archiving information if they were stored very carefully and protected from catastrophic events such as the fire that engulfed the Library at Alexandria in 48 BCE, but books were still not practical as a means of disseminating that archived information.

A key advance in our collective ability to archive and share information broadly came in the year 1493 when German inventor Johannes Gutenberg invented the printing press. Modeled on the wine and olive presses of that time, Gutenberg's means of pressing paper onto movable type could produce finished sheets much more quickly than the speed at which texts could be copied by hand. This was vastly more efficient, and it enabled more rapid production of texts that could be shared among many readers. Advances in the ability to communicate have continued to emerge, and they now enable nearly instantaneous communication through electronic tools such as phones, texts, and emails. These advances have increased the speed and breadth of dissemination, but in their essence they all rely on language as the means through which communication is possible.

Language has given humans an amazing ability to describe and disseminate our ideas. With the assemblage of those ideas into culture and technological advances, language has been a key

feature in driving our collective history. Through spoken and written language, humans have communicated across space and time. That accumulated knowledge allows us to benefit from intellectual masterpieces produced by earlier thinkers, such as Plato's *Republic* and Newton's *Philosophiae Naturalis Principia Mathematica*. It allows us to revel in gripping stories, such as the *Epic of Gilgamesh* and the works of Shakespeare. It allows us to learn from the insights of others, such as Aesop's *Fables* and China's *Shangshu*. It allows us to share sacred texts, such as the *Torah* and the *Koran*, and it has allowed us to learn from historical documents, such as the *Sumerian Code* and the *Magna Carta*, as we continue to refine the policies that shape our governments and social structure. Through these examples and countless others in our collective history, communication through language has shaped our conceptualization of technological and cultural wonders and our advancement as a species.

## Acquisition of Spoken Language

Ideas can be communicated and archived through written communication, but they can be brought alive through forms of behavioral emphasis such as changes in vocal pitch and emphasis that are expressed through intonation. Many concepts can be equally well conveyed through written or spoken language, but in some cases additional aspects of meaning can be communicated in speech that are difficult or impossible to express in written language. Just as punctuation plays a key role in written communication, intonation can play a key role in illustrating a person's meaning in speech, such as the rising intonation that occurs during the final words of a person asking a question in English. These prosodic elements can also clarify a person's complete meaning in words that might otherwise be easily misunderstood, such as occurs in emphasis, contrast, irony, or sarcasm (Purves et al. 2001).

The properties of speech can be described using parameters such as rhythm, articulation, and voice. Rhythm refers to the temporal organization and the sense of movement in speech,

evident in the timing and stressed nature of some syllables, as well as the number of syllables in each word (Gleason and Ratner 2016). For example, in the English language, unstressed syllables are spoken more quickly than stressed syllables, acting as an indicator of the focus of a message. Also inherent to rhythm are brief epochs of silence, with very short pauses used to separate words, slightly longer pauses used to separate phrases much as commas do in text, and longer pauses used to provide emphasis or to illustrate breaks between complete thoughts, acting in the same way that periods or paragraphs break written language into meaningful chunks. Articulation refers to the precise movements of the structures involved in actually producing the sounds used in speech, such as the lips and tongue (Gleason and Ratner 2016). Strictly speaking, these are elements of vocal production and therefore speech rather than aspects of the conceptualization that characterizes language. However, articulation is an integral part of producing spoken language, and disorders of that ability can complicate a person's ability to communicate. Voice (sometimes called "vocalization") refers to how we use our vocal folds and breath to create the sounds used in speech (Gleason and Ratner 2016). Voice is also used in ways other than speech. For example, voice serves as an auditory identifier such that we can recognize different individuals by hearing their voice even if other identifiers such as their face are not visible. Voice can also indicate emotional state, and these features can be detected even by newborn babies (Missana et al. 2017). Together, these features of vocal production and behavioral emphasis give rise to the rich and complex signal that is spoken language.

Spoken and written languages share the feature that symbols are used to represent specific thoughts. For example, either reading the word "dog" or hearing it spoken by your friend could equally well produce a mental image of a cute furry pet. As we noted earlier, information is communicated in written languages through symbols such as characters or letters. Those symbols can be combined to represent thoughts, and those thoughts can be communicated in their full rich entirety. In spoken language, the relevant building

block of meaning is called a phoneme. Phonemes are perceptually distinct units of sounds that distinguish one word from another (Gleason and Ratner 2016). As you listen carefully to spoken words, phonemes are the smallest unit of each word that provides specific meaning. For example, "cat" and "bat" are very similar in the middle and final portion of those words, but they are very different in their first sounds. The difference between those sounds is typically very easy for listeners to distinguish, and that facilitates a listener's easy identification of those words and rapid realization of their meaning. Phonemes are produced with specific temporal patterns that allow the speaker to be understood by the listener. These rules that govern the structure of sentences in a language are collectively called syntax (Gleason and Ratner 2016). When a speaker fails to adhere to the syntax of a language, the listener may misinterpret or be unable to interpret the message being conveyed. When the many traits of a language such as rhythm, voice, and syntax, come together to enable rapid and efficient communication, a person has achieved fluency in that language (Gleason and Ratner 2016).

Fluency in a language is a learned behavior that we acquire by imitating other speakers of that language. Typically, language develops at a very young age, beginning at around 6–9 months of age (Gleason and Ratner 2016). Those first steps toward linguistic ability are often characterized by vocalizations that are difficult to recognize and consist of a series of sounds that is devoid of linguistic meaning. That stage of development is called babbling, and it is thought to be associated with young speakers developing their vocal control, preparing them to be able to repeat common words they hear and recognize the associations with those words (Gleason and Ratner 2016). This process of gradually learning to produce the phonemes that define meaning in spoken language and to bind informational content to specific sounds is the beginning of vocabulary and semantics (Gleason and Ratner 2016). As the young speaker continues to develop, they typically make grammatical or other errors of syntax, and these are usually corrected through experience or instruction from others. When these



vocal, semantic, and syntactical features of spoken language improve in concert, the young speaker is on their way to fluency of spoken language. That skill in spoken language then becomes the basis for subsequent acquisition of written language. Fluency emerges as the young person becomes progressively more skilled at communicating in both realms.

When the process of language development is successful, the individual acquires fluency as both sender and receiver, and communication can occur easily and reliably. However, difficulties in communication can emerge if either sender or receiver experiences challenges such as difficulty perceiving sounds, trouble producing sounds, difficulty with rhythm and continuity such as stuttering, challenges with voice control such as dysphonia, or other challenges that impair production or comprehension. These difficulties can cause communication to be slowed or complicated or to fail completely. Creating solutions to those challenges through the development of mechanistically targeted therapies will require an understanding of the neural mechanisms that are affected in each type of disorder. That desire to improve the lives of the many people impacted by those conditions has been the driving force behind over a century of research into how we learn, perceive, and perform the sounds we use in spoken language.

## Language and the Brain

The link between language and specific areas of the brain first emerged through studies that investigated speech deficits and corresponding injuries to specific regions of the brain. In 1840, a French patient named Louis Victor Leborgne was admitted to a Paris hospital with symptoms that included being able to utter only one syllable (Domanski 2013). That syllable was “tan,” and even though Mr. Leborgne could inflect his voice and he often accompanied that syllable with various expressive gestures, he could not speak any additional content. Whatever had happened to induce this state had left him with an impaired ability to communicate that was far from the

fluency that he had previously enjoyed. Dr. Pierre Paul Broca had an opportunity to treat Mr. Leborgne. Dr. Broca specialized in the study of language, and he found it very curious that a patient could suffer such a loss in one realm but be apparently unaffected in other faculties. Dr. Broca carefully documented this loss of the ability to speak in Mr. Leborgne and other patients, and in papers published in the 1860s he described a condition that we now call expressive aphasia or Broca’s aphasia. When Mr. Leborgne died, it was discovered that he had a large lesion in a specific area of his brain. That area, the posterior inferior frontal gyrus in the left hemisphere of the brain (specifically the pars opercularis and pars triangularis, also described as Brodmann’s areas 44 and 45), is now commonly referred to as Broca’s area (Dronkers et al. 2007). This link between the sudden emergence of nonfluent speech and a corresponding brain injury was the first hint that a specific brain site could play such an important role in language.

In the years following Broca’s discoveries, others also became interested in the possibility that injuries in other sites could also be related to the emergence of other types of language difficulties. In 1874, Dr. Carl Wernicke described another type of aphasia in which patients had fluent speech in which they could produce many different words, but those words were disordered to such a degree that it was difficult or impossible to understand the patient’s meaning (Purves et al. 2001). His patients also commonly had difficulty understanding speech, and this was evident as impairment of their ability to follow directions or to repeat a sentence that they had just heard. This form of impairment is now called receptive aphasia or Wernicke’s aphasia. After the patients expressing receptive aphasia died, it was discovered that their linguistic deficits were also associated with injury to a specific brain site, but in these cases the injuries were at a different site than reported for Broca’s patients. These patients with receptive aphasia had damage in a region near the interface of the temporal and parietal lobes in the left hemisphere of the brain, in a region including the posterior portion of the superior temporal gyrus and other sites that are collectively called

Wernicke's area (Mesulam et al. 2015). This led Wernicke and others to propose that specific regions of the brain may be specialized to shape different aspects of behavior and that the full range of behaviors emerged through the interaction of those and other sites. Additional studies have also found other areas of the brain that are closely associated with other aspects of behavior, such as other areas near the classically defined Wernicke's area that also influence speech comprehension, and visual regions that contribute to how we recognize faces (Binder 2017; Cohen et al. 2019), but these early studies by Wernicke and Broca provided the first insights into the neural sites and pathways that play key roles in language (Hagoort 2019; Scott 2019; Tremblay and Dick 2016).

The fact that Broca's and Wernicke's areas both resided in the left hemisphere of the brain suggested that linguistic function could be lateralized such that it resides primarily or exclusively in the left hemisphere. Subsequent studies confirmed that there can be differences between functions associated with corresponding areas of the left versus the right hemisphere, but they have also revealed that language is affected to at least some degree by both hemispheres (reviewed in Taylor and Regard 2003). This is called hemispheric dominance, and in most people the left hemisphere is dominant for language (reviewed in Prather et al. 2017). The left hemisphere appears to play the dominant role in articulatory ability, such as being able to form meaningful sequences to respond to questions, but areas of the right hemisphere corresponding to Broca's and Wernicke's areas in the left hemisphere also contribute to subtle features of understanding that accompany linguistic ability. For example, patients with injury to those regions of the right hemisphere can lose the prosodic elements of language, such as intonation, stress on certain syllables, and the rhythm of speech production. Patients with injury to the right hemisphere can also have difficulty with word-association tasks, suggesting that the right hemisphere may help us to bind meaning to specific words, even if it is not directly driving articulation of those words. These patients can also have difficulty categorizing

things or understanding metaphors, drawing inferences, or grasping the non-literal meaning of idioms used in speech (e.g., "it's raining cats and dogs," Taylor and Regard 2003). Thus, the left hemisphere plays a dominant role in the production and comprehension of language in most people, but both hemispheres contribute to the full richness of communication.

The quest to continue expanding our understanding of the neural basis of language drives much current research. Central to that effort are studies of learning, as learning to imitate the sounds we hear perform by others is a central component in our acquisition of language. In its essence, that learning process consists of auditory perception instructing motor performance. When that process proceeds to accurate completion, imitation emerges. That is especially evident in the regional accents that humans express, such as the gentle lilt of accents from certain regions of the American South. If parents and others in the region speak with such an accent and their children model their vocal development on the sounds that they hear throughout development, then the children are very likely to imitate with sufficient precision that they also speak with that accent. Accents and other examples make it clear that the human brain is capable of very precise imitation in the acquisition and performance of language, but it remains unknown how the brain enables perception to inform motor performance.

Specialized brain regions in other species offer us a chance to gain high-resolution insight into mechanisms of imitative vocal learning. For example, songbirds acquire their songs by imitating the sounds they hear performed around them during their juvenile development (reviewed in Catchpole and Slater 2008). Although those songs are not used in the same way that we employ our language, they are learned, rehearsed, and performed in a way that is strikingly similar to how we acquire speech (Catchpole and Slater 2008). Songbirds also have specialized neural circuits that underlie that process, and those circuits are analogous to circuits in the human brain (reviewed in Prather et al. 2017). Therefore, studies of the cells and mechanisms through which songbirds learn to perform their songs may also

inform our understanding of the imitative process through which we acquire the sounds we use in speech.

A study performed using sparrows revealed cells in which activity is closely related to auditory perception. Those cells are very selective in their auditory responses, with robust responses to one song in the bird's vocal repertoire (Prather et al. 2008, 2009). Those cells are thus among the most selectively responsive sensory neurons ever described. Different cells are responsive to different song types such that the entire vocal repertoire is represented in the population of these cortical neurons (Prather et al. 2008, 2009). Closer examination of the song that is capable of driving a response in each cell reveals that there are highly detailed song features, such as a combination of two notes produced rapidly in a sequence, that are the salient features in driving the auditory response of the cells that are tuned to that song type (Prather et al. 2008). Behavioral studies combined with experimental alteration of the parameters of that salient feature revealed that the cells are not active in association with the specific parameters such as note duration. Instead, the cells are active in association with the bird's perception of the note (Prather et al. 2009). Those highly selective cells are typically unresponsive to the songs of other birds, but if that salient feature is present in the song of another bird, then they respond (Prather et al. 2008). Thus, each of these cells is selectively responsive to an element of the sounds these birds use in communication.

A breakthrough in our understanding of the possible link between perception and production came when researchers recorded from the same cells described above as the bird performed the salient song feature. They discovered that those cells were as selective in the motor domain as they were in the auditory domain, with each cell being active in association with one song type in the bird's vocal repertoire (Prather et al. 2008). The key finding was that these cells were active in association with the same song type in each domain, so that each cell was active in association with both perception and production of one and the same vocal behavior (Prather et al. 2008). Each of these cells was active in association with

one learned vocal behavior, regardless of whether that behavior was perceived through the ears or performed through the voice. This colocalized representation of both perception and performance in these cells earned them the name "mirror neurons" (reviewed in Prather et al. 2008, 2017). Because each of these cells is a site where there is a link between perception and performance, they are ideally suited to serve as a mechanism linking those behaviors in imitative learning. Many authors have speculated that this sort of link between perception and performance also underlies human acquisition of language (Lieberman et al. 1967). The discovery of such a mechanism in songbirds provides researchers a context in which to explore the properties of one such link. Discoveries that continue to emerge from studies of neural mechanisms in songbirds will help guide exploration and understanding of corresponding mechanisms in humans, opening the door to development of new mechanistically targeted therapies to ameliorate the challenges of impaired human communication.

### **Communication in Ways Other than Spoken or Written Language**

For some people, such as those who are deaf or otherwise hearing impaired, communication through spoken or written language can be very challenging. In those cases, other forms of linguistic communication are necessary. Languages that incorporate visual-manual communication to convey meaning are known as signed languages. These are complete, natural languages, possessing their own lexicon and grammatical systems in addition to other aspects that are also present in other forms of language (Sandler and Lillo-Marton 2006). Signed languages use a combination of manual articulations to produce the content of a sentence, and they use non-manual elements to convey grammatical function. The patterns of vocal stress and intonation that are used to enhance meaning in a language may not be possible in these contexts, but those forms of prosody are preserved in signed languages through non-manual elements, such as body posture or the

movement of the head, eyebrows, eyes, and mouth. Through the use of non-manual elements such as facial expressions, the speaker can indicate emotional content, such as whether they're making a statement, asking a question, adding emphasis, or being sarcastic (Liddell 2003).

Signed languages are distinctly separate from other visual-manual communication systems such as “baby sign language” and signs learned by non-human primates. In baby sign language, parents teach hearing babies a small set of signs to facilitate clear and effective communication between parent and baby. This type of signed communication is a form of symbolic support for the development of spoken language rather than the development of a language itself (Fitzpatrick et al. 2014). Humans sometimes teach non-human primates signs to allow them to facilitate communication between those primates and their human caretakers. These cases indicate that non-human primates are capable of forging links between symbols and meaning and thus communicating through signs, but their development of that skill fails to progress into the full grammatical complexity that is characteristic of a complete signed language (Wallman 1992). Thus, although babies and non-human primates can learn to express themselves through signs, they have not been shown to develop their knowledge of a human language as a complete system.

Signed languages should not be confused with body language, though they may appear similar. Body language is a form of non-verbal communication that uses physical behaviors, such as facial expressions, posture, eye contact, and gestures to express emotion or convey information (Pease and Pease 2004). Unlike signed languages, body language lacks a grammar system and can be broadly interpreted, rather than have specific meanings that correspond with specific movements or gestures. As a result, body language is not considered a language in the lexical and grammatical sense, but is central to how we communicate emotional content, and we colloquially refer to it as a language because of its prevalence and its importance in social communication (Waciewicz and Żywiecziński 2010). Culture has a strong influence on how body language is perceived.

For example, greeting someone with a firm handshake can have a different connotation in one culture compared to another. A firm handshake in Western culture is perceived as confident, whereas, in Eastern culture, it is perceived as aggressive (Black 2010). Other gestures can mean the difference between praise and insult, such as giving a thumbs up. In American and European cultures, a thumbs up is a sign of a job well done or understanding; however, in some Middle Eastern cultures, that same gesture would be interpreted as dismissive and a form of insult (Black 2010). Depending on the cultural context in which they are expressed, a range of different behaviors including eye contact, sitting position, and silence can hold an entirely different meaning (Pease and Pease 2004). In contrast, the semantic properties of individual words in a language are much more constant across a similarly wide range of contexts.

Another means through which humans communicate, especially about our emotional status, is music. Similar to language, music has a hierarchical structure that can be broken down into the smallest relevant units of sound, with those units being phonemes in language and individual notes in music (McMullen and Saffran 2004). As in the case of languages, music has “rules,” or a sort of “grammar,” to govern the logic of how individual notes can be used (Mehr et al. 2019; Patel 2008). Notes can be combined into sequences or chords that coalesce to create melodic and harmonic lines of a song. In music, the melody is the main focus of a song, and it serves as a means of communication between composer and audience. A rich variety of information, such as emotional context, can be implied through various aspects of the melody, and harmonies can serve as an additional supporting framework for the melody. In that way, the emotional content and story inherent in the melody can be made richer and fuller by the addition of harmonies into a piece that might otherwise sound hollow and fail to achieve its emotional impact. Through this rich acoustic content, music possesses affect and is thus capable of stirring emotion and conveying meaning.

Because of the prevalence and ability of music to convey emotion across human cultures that

speak many different languages, some authors have referred to music as a “universal language” (Longfellow 1835). Studies seeking to investigate that possibility have revealed that certain features of music, such as pitch or tempo, can be used by listeners of many different cultures to accurately interpret whether a song is about a specific emotion such as love or sadness (Mehr et al. 2019). Those studies also revealed that tonality, referring to the organization of musical pieces around a central note and the relationships between notes and chords that can be used to build or resolve tension, is also widespread (Mehr et al. 2019). These findings point to music as ubiquitous and influential across a range of diverse cultures and musical types, consistent with the idea that it might play some role as a universal form of communication. Experts, however, caution against the colloquial usage of the term “language” to describe music as compared to how it is used to describe spoken and written communication (Jackendoff 2009). For example, the quality and beauty of a piece of music can be quite different for members of different cultures, especially for those that reside in cultures where the tonal content of their local musical style is quite different from that of the piece of music that is played for them (Patel 2008). In that light, the role of music as an artistic means of conveying emotion appears to be broadly conserved across humans, but its role as a means of providing enjoyment appears to be more culturally based rather than holding a universal status.

### **Language as a Dynamic Entity Central to Culture**

Language is central to human culture, providing a means through which humans are able to express ideas, emotions, and needs. The development and use of language is ubiquitous in human history, as evident in the fact that much of history itself is archived through the use of language. A review of our collective history makes it clear that languages have changed as they have evolved over time, as different cultures have come into contact with one

another, and as we have adapted to new needs and opportunities in communication. For example, humans have developed tools to encode languages in ways that help to increase inclusivity and overcome distances that separate people. One such tool is Braille, which is a tactile writing system of raised dots that can be read with the fingers by those who are visually impaired (Sadato 2005). Braille itself is not a language, but rather a code for language to be written and read. It transforms a previously established alphabet into representative shapes and bumps, with no new grammar or vocabulary. Thus, Braille conveys information through a new representation of already-established letters and words, and therefore it is considered a tool of communication rather than a language all to itself. Similarly, Morse code is a method that encodes text characters as a sequence of dots and dashes (Coe 2003). Codes are transmitted as electrical pulses of varying lengths, often detected as pulses of sound or visual cues such as light flashes. Morse code provided a means of communication that can cross vast distances, eventually giving way to other tools such as the radio, telephone, and television that are so familiar today. As is the case with Braille, Morse code is a change in representation, facilitating communication through already-established languages rather than the emergence of a new language.

History also reveals changes in the prevalence and properties of languages as different cultures have come into contact with one another (Lee 2020). For example, a pidgin is a grammatically simplified means of communication that develops between groups who encounter one another but do not have a shared common language (Lee 2020). The pidgin that emerges from that interaction can serve as a bridge for communication among native speakers of different languages. In some cases, pidgins are then passed onto the next generation of speakers and become a formalized native language with fully developed grammatical and syntactical systems. When a pidgin language has been transformed from a communication bridge to a full-fledged language, it is known as a creole language (Lee 2020). In contrast to pidgins,



creoles have a consistent system of grammar, large stable vocabularies, and are learned by children as their native language, distinguishing them as languages rather than just blends of other languages.

In other instances of interaction between speakers of different languages, their languages have changed more drastically, sometimes becoming either endangered or extinct. Today, there are approximately 7,000 languages in use (Anderson 2012). Some of those languages are experiencing challenges to their prevalence because of younger generations not acquiring them, or because they are spoken by small and dwindling numbers of people, or because they are being used in only certain circumstances, such as family use, but not others, such as commercial use (Lee 2018). These languages are considered to be endangered (Lee 2018). Among these endangered languages are Irish Gaelic, Hawaiian, Louisiana Creole, Zenaga, Bih, many Native American languages, and many other languages spoken in various regions around the world (Eberhard et al. 2020). Their endangered status means that they are vulnerable to loss as a tool of communication and a central element of their associated cultures. In addition to having relatively few current speakers, some of these languages are especially vulnerable to loss because they are primarily or exclusively spoken languages that are not written down and thus have no dictionary, literature, or historical record.

Outside influences such as globalization can contribute to the loss of local languages, as global influence and the demands of commerce can lead members of those cultures to adopt languages that are spoken more broadly. Some languages are spoken so broadly as either a native or a second language that they are considered “world languages.” These include languages that are commonly used in trade and international relations, such as English and French (Eberhard et al. 2020). If speakers of local languages transition to speaking primarily or exclusively those world languages, that can result in local languages being further threatened or perhaps even going extinct, with other languages taking over the role of that

lost language in the local culture. If those languages fade away in their usage, cultures can lose an important facet of their identity. In response to such concerns, groups seeking to preserve cultural history have collected recordings of those speakers and examples of their literature to help preserve the cultural identity of the associated group. Through those efforts, it is hoped that cultural treasures can be preserved that would otherwise be lost as the language in which they are composed becomes increasingly more threatened.

Languages are ever-evolving, living entities that are still changing today. With the emergence of new social trends, language can grow through the introduction and wide incorporation of new slang words. As these words become integrated into wide use, they can eventually be added as formal additions to the dictionaries that define that language. Thus, the vibrant social trends that a language enables are also the engine that can drive its change. This is especially evident in some of the words that have moved from slang to inclusion in canonical dictionaries. For example, the English word “ain’t” is a contraction with many possible usages and meanings, including “am not,” “are not,” “is not,” “have not,” or “has not.” For many years, use of the word “ain’t” was considered incorrect and was discouraged for use beyond casual conversation. This was despite the fact that “ain’t” first appeared in dictionaries in the 1830s. More recently, words like “hangry,” which is a portmanteau of “hungry” and “angry” that describes the feeling of irritability due to hunger, and “vacay,” meaning a form of vacation holiday, have also been added to the dictionary. These examples and many others make it clear that languages are living entities that will continue to grow and adapt as they both drive and respond to changes in human cultures.

## Cross-References

- [Cetacean Communication](#)
- [Cognition](#)

- Communication
- Critical Period for Song Learning
- Georgia State University's Language Research Center
- Human Infancy and Childhood
- Insect Communication
- Language Research: Dolphins
- Language Research: Great Apes
- Language Research: Parrots
- Passerine Vocal Communication
- Primate Communication
- Protolanguage
- Referential Communication

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## Language Acquisition Device

### ► Cognition

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## Language Research Center Computerized Test System (LRC-CTS)

### ► Computerized Testing Paradigm in Primates

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## Language Research: Dolphins

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## Introduction

Historically, one of the cognitive hallmarks ascribed to humans has been the ability to communicate using language. Language is a multifaceted and complex ability that allows us to assign arbitrary symbols meaning and to use and understand these symbols in referential exchanges with others that draw joint attention to agents, objects, and events both present and displaced in space and time (Nelson 1977; Savage-Rumbaugh 1986). Language also allows us to employ rules called syntax to generate different combinations of symbols that extend meaning beyond the individual symbol, and allows the same symbols in different combinations to create completely different meanings (Bronowski and Beluggi 1970; Savage-Rumbaugh et al. 1993). Neurobiology, cognition, and the acoustic and social environments to which we are exposed at an early age all have a profound influence on the initial language or languages we acquire (Hoff 2014). Yet even as adults our linguistic abilities are cognitively pliable allowing us to learn new languages involving symbols and syntax that are different from our so-called mother tongue. While the requisites for language development are still debated, there is no disagreement that language is a powerful tool that allows humans to negotiate interactions within large, complex long-term social networks. Yet we are not a unique species in having large social networks of this type, and it is this shared feature with humans along with a relatively large brain, cognitive abilities including imitation that rival many nonhuman primates, a protracted period of maternal care giving, and naturally learned vocal labels associated with individuals (Marino et al. 2007), that has inspired

researchers to investigate language abilities in bottlenose dolphins (*Tursiops truncatus*). Below, I review this research focusing first on studies exploring the referential function of naturally developed signature whistles, and then on studies using artificial systems to investigate the dolphin's ability to acquire two key aspects of language, semantics and syntax.

### **Research on the Referring Function of Dolphin Signature Whistles**

Bottlenose dolphins develop novel individually unique whistle contours termed "signature whistles" (Sayigh et al. 2007). These specialized whistles become part of a dolphin's vocal repertoire and can function to announce personal identity. Although signature whistles have been studied since the 1960s (Caldwell and Caldwell 1965), several findings over the last 20 years have provided evidence that these whistles can be used in referential communication. Individual signature whistles are developed when dolphins are young through vocal learning in which calls heard in their environment are modified to create a frequency modulated pattern that is used instead of voicing characteristics to acoustically encode a dolphin's identity (Janik et al. 2006). The production of signature whistles in captivity when one dolphin from a group voluntarily isolates itself, or the exchange of signature whistles between individuals in the wild before joining other groups, suggests that these whistles can be used to maintain cohesion between group members (Janik and Slater 1998). In addition to the majority of a dolphin's whistle repertoire being its own signature whistle, it may also imitate the signature whistles of close associates (Tyack 1986), and distinguish the whistles of family members from other familiar individuals (Sayigh et al. 1999). The question of whether signature whistles for dolphins, like names for humans, can have a referring function in addition to broadcasting a dolphin's own identity has intrigued researchers for decades. Janik (2000), using a hydrophone array to localize vocalizing wild dolphins in the Moray Firth, Scotland, found that a dolphin after hearing

the signature whistle of another dolphin out of visual range vocally matched this dolphin's signature whistle within less than a second. Based on these findings, Janik (2000) suggested that bottlenose dolphins might use signature whistles to address each other. More recently, King and Janik (2013) provided compelling evidence that the production of a facsimile of a dolphin's signature whistle can be used to address that individual. During focal follows of dolphins off Scotland, the researchers first recorded a dolphin's signature whistle, then created a synthetic version of that whistle with voice characteristics removed (i.e., in order to model the production of that dolphin's signature whistle by another dolphin), and finally either played back this facsimile or control whistles of either a familiar dolphin from the same population or an unfamiliar dolphin from a different population. Within one minute of the playback, dolphins hearing the facsimile of their own signature whistle responded most often by producing their own version of their signature whistle, a response that rarely occurred with the familiar controls and was absent with the unfamiliar controls. The findings supported the hypothesis that signature whistles can be used and understood in referential exchanges between dolphins. However, thus far there is no evidence of the use of signature whistles in different syntactic forms, and no evidence beyond signature whistles of the natural vocalizations in a dolphin's repertoire being used to refer to objects, locations, or events.

### **Research on the Comprehension of Sentences Within an Artificial Language System**

In the late 1970s Dr. Louis M. Herman, founder and director of the University of Hawaii's Kewalo Basin Marine Mammal Laboratory, launched a series of groundbreaking studies to investigate the ability of bottlenose dolphins to respond accurately to imperative and interrogative sentences given within artificial languages that required processing of both semantic and syntactic components (Herman et al. 1984, 1993a; Herman and

Forestell 1985). Herman chose to focus on sentence comprehension rather than production because of problems encountered by early ape language studies that focused on sentence production. These problems included procedural flaws allowing for nonlinguistic cueing of apes, the often erroneous assumption that an ape's production of a symbol to acquire something implied that it understood this symbol referentially, and that ape productions of strings of signs were often highly redundant, generally failed to extend meaning, and lacked the essential feature of sentences that changes in word order can change meaning (Terrace et al. 1979; Seidenberg and Petitto 1979; Savage-Rumbaugh et al. 1980; Ristau and Robbins 1982). Herman also took into account the finding that in humans, language comprehension tends to precede and exceed production (Bates 1993). Two young female dolphins, Phoenix and Akeakamai (Ake), were trained respectively in an acoustic-based language and a visually based language in which either brief computer-generated sounds projected into the dolphins' pool or individual gestures of a trainer's arms and hands were associated with different agents, objects, actions, modifiers, relationships, and function words. Phoenix's initial vocabulary consisted of 32 symbols and Ake's 30 symbols (Herman 1986). The goal of the study was not to determine how large a vocabulary the dolphins could master, but rather to explore whether object symbols were understood referentially and the extent to which the dolphins could spontaneously understand the different meanings conveyed by many unique combinations of vocabulary items. The set of grammatical rules that governed how symbols could be combined into different orders in each language allowed for the creation of over 2700 sentences up to five words in length.

### The Dolphin's Understanding of Imperative Sentences

Imperative sentences consisted of nonrelational instructions requesting that a named action (A) be performed to a named Direct Object (DO), and relational instructions requesting that a

relationship (R) be created between a DO and an Indirect Object (IO). The dolphins were also taught contrasting symbols that could serve to modify named objects. Phoenix was taught the modifiers SURFACE and BOTTOM (of her pool). Ake was taught the modifiers RIGHT and LEFT (from her perspective when being signed to). During trials, several different pairs of surface and bottom objects or left and right objects were present so that the occurrence of the modifier alone did not by default designate a particular object.

The syntactic rules in each language were identical for nonrelational sentences. Two-word nonrelational sentences took the form DO+A and indicated that the named action should be performed to the named object. For example, BALL+TOSS instructed the dolphin to find a ball from a variety of objects in its pool and toss it with its rostrum. Three-word nonrelational sentences took the form Modifier (M) + DO+A and indicated that the named action should be performed to the modified named object. For example for Phoenix, BOTTOM+PIPE+TAIL-TOUCH instructed her to touch her tail flukes to the pipe lying on the pool floor. For Ake, LEFT+-HOOP+UNDER instructed her to swim under the hoop to her left.

For relational sentences, the syntactic rules were different for each dolphin, but in both cases specified that a DO should be either transported to the side of an IO if R was FETCH or placed in or on top of an IO if R was IN. For Phoenix, the sequence of symbols matched the order in which the sentence was to be carried out, with three-word relational sentences taking the form DO+R + IO. For example, FRISBEE+FETCH +BASKET instructed Phoenix to bring the Frisbee to the basket. For Ake, an inverse syntactic rule was used to construct relational sentences such that the sequence of symbols was not directly correlated with the order in which the sentence was to be carried out. Here, three-word relational sentences took the form IO+DO+R. Thus, to ask Ake to create the same relationship as required of Phoenix above, the trainer would sign BASKET+FRISBEE+FETCH. For both dolphins, relational imperative sentences of four and five words could be created from their respective



three-word relational sentence syntactic forms by adding a modifier prior to one or both object names. Thus, the two four-word sentence forms for Phoenix were M + DO+R + IO and DO+R + M + IO, and for Ake they were M + IO+DO+R and IO+M + DO+R. Likewise, the five-word sentence form for Phoenix was M + DO+R + M + IO and for Ake it was M + IO+M + DO+R. The use of the inverse syntactic rule for relational sentences of three, four, and five words in Ake's language not only tested for dolphin mental flexibility in understanding different syntactic structures, but also examined sentence parsing in which the question of how to treat the initial object symbol of a sentence was conditional on the remaining elements. Thus, when Ake sees the gestural sign BASKET, she must wait for the next gestural sign to know whether basket is to be treated as a DO as in BASKET+SPIT (meaning *spit water at the basket*), or as an IO as in BASKET+BALL+IN meaning *put the ball in the basket*. Regardless of structural differences between Phoenix and Ake's languages, both contained identical conceptual features essential for examining sentence comprehension. First, each semantic element within a sentence whether M, DO, IO, or R could be fulfilled by multiple exemplars within a category. Thus, every word used in a sentence was functional and meaningful. Second, the structure of the relational sentences allowed for the construction of semantically reversible sentences (i.e., sentences in which the same words appeared but in different orders creating changes in sentence meaning). For example, for Ake the same three words appear in the sentences PERSON+SURFBOARD+FETCH and SURFBOARD+PERSON+FETCH. However, the former sentence instructs Ake to transport the surfboard to the person while the latter instructs her to transport the person to the surfboard. For Phoenix, the semantically reversible sentences connoting parallel meanings to those expressed above would be SURFBOARD+FETCH+PERSON and PERSON+FETCH+SURFBOARD.

After the dolphins were taught the sounds or gestures for each of a small set of objects, actions,

and the relationship fetch, as well as how to respond to two-word nonrelational sentences and three-word relational sentences using these symbols, they were tested for comprehension of two types of novel sentences, lexically novel sentences in which new words were placed in one or more syntactic slots of a familiar syntactic form creating semantic propositions the dolphin had never experienced previously, and structurally novel sentences involving the creation of a new syntactic form on which the dolphin had not been trained. Language sessions occurred regularly and employed a variety of controls, including opaque goggles being worn by trainers, to prevent cueing.

### The Dolphins' Responses to Lexically Novel Sentences

Herman (1986) reported that Phoenix and Ake performed wholly correctly, meaning that they interpreted accurately each of the words in a sentence as well as its structure on 67.5% of 191 lexically novel sentences and on 65.4% of 214 lexically novel sentences, respectively. Both performances were well above what would be expected by chance (calculated at 4% or less depending on the sentence type). Furthermore, during tests of the dolphins' responses to all of the various types of nonrelational and relational sentences (both familiar and novel) in the languages, Phoenix responded wholly correctly to 81% of 234 relational sentences and Ake responded wholly correctly to 66% of 128 relational sentences. On those sentences that were semantically reversible Phoenix was correct on 77% of 128 sentences and committed only one error in which she reversed object order and function (i.e., taking the IO to the DO), and Ake was correct on 59% of 69 sentences and never committed a reversal error. Collectively, the dolphins' responses to lexically novel sentences provide compelling evidence that both the meaning of the words (the semantic component) and their arrangement (the syntactic component) were processed accurately. Furthermore, the dolphins

immediately transferred their understanding of symbols to novel exemplars and to novel situations (Herman 1986, 1987). For example, the gesture for hoop was initially taught to Ake using a specific large octagonal hoop. Subsequently, she immediately transferred this gesture to hoops of varying shapes and sizes. Both dolphins also regularly rearranged their environment to make requested actions possible to perform. When given HOOP+THROUGH *meaning swim through the hoop*, and encountering for the first time a hoop lying flat on the bottom, Ake lifted one end of the hoop with her rostrum and darted through. Thus, Ake (as well as Phoenix) understood that object symbols referred to classes of objects rather than to specific exemplars and also understood action symbols conceptually.

### The Dolphin's Responses to Structurally Novel Sentences

Several types of structurally novel sentences were presented to each dolphin including for the first time for Ake, four-word sentences. Although Ake had previously experienced M + DO+A and IO+DO+R sentences, she had never experienced a Modifier within a relational sentence. Nonetheless, the first time she was signed sentences following the syntax M + IO+DO+R and IO+M + DO+R she responded accurately. Phoenix had experienced a modified DO within a relational sentence previously, but not a modified IO. Nonetheless, she responded accurately on the first occasion she experienced a DO+R + M + IO sentence. In addition, Phoenix adapted her responses meaningfully to structurally novel sentences that either linked two action words within a relational sentence or conjoined two non-relational sentences into a single sentence. In the first case, Phoenix was given sentences in which the word FETCH was followed by either the word THROUGH or UNDER or OVER. Prior to this time, she had only experienced FETCH singly in a relational sentence and the words THROUGH (*meaning swim through*), UNDER (*meaning swim under*), and OVER (*meaning jump over*) in non-relational sentences. The first time Phoenix

experienced FRISBEE+FETCH+UNDER+HOOP, she responded accurately by transporting the Frisbee under the hoop. Subsequently, she was wholly correct on 53% of 436 trials of the three types of linked actions within relational sentences. Phoenix was also given 15 trials conjoining two non-relational sentences, for example, PIPE+OVER+PIPE+TOSS to which she first jumped over the pipe and then tossed it with her rostrum. She carried out both named actions to the named object correctly on 11 of the 15 trials including the first time she experienced a sentence conjoining two nonrelational sentences.

### The Dolphin's Responses to Anomalous Sentences

Among the strategies used to investigate what children understand about the grammar they employ is to examine their responses to so-called anomalous sentences (i.e., sentences that either violate a grammatical rule or a semantic relation or substitute "nonsense" words for real words) (e.g., de Villiers and de Villiers 1972; Carr 1979). The assumption is that a child's interpretation of such sentences reflects its understanding of the syntactic rules in its language, the semantic characteristics of words, and the semantic relations between words. Herman et al. (1993a) investigated Ake's responses to both syntactic and semantic novel anomalous sentences. Syntactic anomalous sentences were those containing extended strings of gestures that violated Ake's familiar syntactic language structure. For example, as noted earlier nonmodified relational sentences for Ake took the form IO+DO+R with those objects that she could transport serving as possible DOs and both transportable objects (T) and nontransportable typically stationary objects (S) serving as IOs. Thus, using the terminology of transportable objects and stationary objects, Ake's nonmodified relational sentence form IO+DO+R could be rewritten as (either T or S) + T + R. One syntactic construct that violated this familiar relational form was the sequence S + S + T + R because there is no

syntactic rule that uses a string of three object words followed by a relationship word. Nonetheless, when Ake was presented with such syntactic violations she commonly extracted subsets of words that comprised a “legitimate” grammatical rule. For example, when given the anomalous sentence SPEAKER+WATER+PIPE+IN for the first time, Ake extracted the legitimate sequence SPEAKER+PIPE+IN and placed the pipe on top of the speaker. Ake’s extraction not only conformed to the familiar syntactic rule  $S + T + R$ , but also revealed her composing a meaningful sentence from two nonadjacent object words. This type of solution when faced with a syntactic anomaly occurred not only for the form  $S + S + T + R$  but also for  $S + T + S + R$  and  $S + T + T + R$ . In total, out of 19 four-word anomalous sentences, Ake extracted legitimate sequences of two object words on 14 occasions and was wholly correct, meaning she also performed the correct relational term in 12 cases.

Semantic anomalous sentences were those in which a legitimate syntactic form was followed in constructing a sentence but a semantic rule was violated. For instance, the form  $(T \text{ or } S) + S + R$  is legitimate syntactically (i.e., it contains two object names followed by a relationship term), but asks Ake to transport a nontransportable object (S). For instance, WATER+SPEAKER+IN instructs Ake to put the stationary speaker on top of the stream of water coming from a hose attached to the pool railing. Ake was given 12 novel semantic anomalous sentences of the type  $(T \text{ or } S) + S + R$ . In the majority of cases, Ake rejected the sentence (simply remaining at her station), and in several instances she substituted a transportable object for the designated nontransportable DO, thus composing a sentence that could be performed. Overall, Ake’s responses to anomalous sentences that violated both syntactic and semantic rules revealed that she understood the functional relationship of various grammatical frames to each other, the functional relationship of word positions within these frames, and the functional relationship of different categories of words (i.e., which named objects were transportable and could be substituted legitimately for designated nontransportable objects).

## **The Dolphin’s Responses to Sentences Referring to Objects Displaced in Space and Time**

A key feature of language is the ability to understand linguistic references to arbitrary objects (i.e., those that are not biologically or ecologically meaningful) that are displaced in space and time (Hockett 1960). Such comprehension demonstrates both that the symbols and their referents are represented mentally and that the symbols can act as surrogates for the objects they represent (i.e., the symbols are understood as referencing the objects even in their absence). Herman et al. (1984) carried out studies with both Phoenix and Ake exploring their ability to accurately carry out two-word nonrelational sentences to objects that were displaced in space and time. With their pool empty of objects, a sentence was either signed to Ake or projected to Phoenix. Once the sentence was completed, seven different objects were introduced into the pool from arbitrary locations. The dolphins performed equally well, each correctly carrying out 81% of 43 different two-word sentences. Following this, Ake was tested on the same type of displacement procedure with delays between sentence completion and the introduction of objects into the pool up to 30 seconds. Although there was some degree of memory loss with increasing delay, Ake performed accurately on 53 (88%) of 60 two-word sentences. In other tests in which when the sentence was given the objects were located out of sight in a remote pool that Ake could only access through a narrow channel, she was correct on over 95% of the trials. Collectively, these findings demonstrate that both dolphins could understand references to objects displaced in space and time.

## **The Dolphin’s Responses to Interrogative Sentences About the Presence of Objects in Her Pool**

Herman and Forestell (1985) developed a specific interrogative sentence form to further investigate Ake’s ability to understand semantic references to objects displaced in space and time.

The interrogative sentence form OBJECT NAME+QUESTION asked Ake to report symbolically on whether the named object was currently present in or absent from her pool. To respond to such queries, Ake was provided with a paddle to her right, designated as the “Yes” (i.e., object present) paddle and one to her left, designated as the “No” (i.e., object absent) paddle. Thus, if the trainer signed HOOP+QUESTION and there was hoop in her pool, Ake would press the Yes paddle indicating that the named object was present. Alternatively, with no hoop in her pool, Ake would press the No paddle indicating that the named object was absent. Ake was trained to report presence and absence in response to the OBJECT NAME+QUESTION interrogative sentence with a single named object, the hoop, and then she was tested for transfer of the concept with five named transportable objects from her language (frisbee, pipe, basket, net and ball) all of which she had responded to previously in imperative sentences but which she had never been asked about using the OBJECT NAME+QUESTION interrogative. The five transfer objects allowed 10 novel trials to be conducted, 5 in which the object referred to in the query was present and 5 in which it was absent. During testing sessions, between 1 and 3 objects were shown to Ake and tossed into the pool behind her. The trainer donned opaque goggles and then signed either OBJECT NAME+QUESTION or DO+A. If when given the latter sentence the named object was present, she was correct if she carried it out in her normal fashion. If it was absent, Ake was correct if she pressed the No paddle. Overall, Ake responded correctly on 82% of 324 imperative and interrogative sentences including correctly reporting object presence on 80% of 108 trials and object absence on 77% of 108 trials. She also carried out the correct DO+A sentence on 88% of 108 trials in which the named object was present. A key finding was that Ake reported presence or absence correctly on 9 of the 10 novel transfer trials described earlier. Combined, Ake’s ability to accurately report presence and absence strongly supports the idea that she understood the referring function of gestural symbols for objects in her

language, and that these symbols could act as surrogates for the objects they represented.

### **The Dolphin’s Understanding of References to an Individual Whose Behavior It Should Copy**

Important to any demonstration of referential understanding is that symbols can be understood in different contexts and functions. As shown above, Ake understood the gestural signs for objects in her language in multiple contexts and functions including as direct or indirect objects in imperative sentences and as the subjects of interrogative sentences. The latter strongly demonstrated that Ake understood the referring function of these symbols in that no response to an object was required, only a symbolic report on its state of existence in the pool. This suggests that when the trainer signed an object name, it evoked within Ake a mental representation of that object. A further context within which Ake’s gestural symbols were understood referentially requested her to imitate the motor behaviors of either a person in the pool or the dolphin Phoenix (Herman et al. 1993b). During a 24-trial test with Phoenix and a person simultaneously performing different motor behaviors, Ake responded accurately to the sentences PERSON+-IMITATE and PHOENIX+IMITATE by attending to the behavior performed by the referenced individual (79% correct) and creating either a close approximation or an exact facsimile of that behavior (84%). These high performance levels not only showed that the object symbols were understood in a radically different context from those previously employed but also that they served to manage joint attention, a key feature of referential communication (Savage-Rumbaugh 1986).

### **Research on Artificial Symbol Production**

The success of Herman’s work as described above reveals the importance and fruitfulness of examining receptive language competencies in

dolphins as well as in other animal species (Herman 1987). Nonetheless, given the success of language studies focusing on both comprehension and production in bonobo chimpanzees (*Pan paniscus*) using objects that are functionally different and meaningful (Savage-Rumbaugh 1986; Savage-Rumbaugh et al. 1993), some recent studies with dolphins have attempted to examine symbol production beyond signature whistles. Earlier and prior to the behavioral imitation work with Ake, she was trained to vocally imitate arbitrary computer-generated underwater sounds in response to the sequence AKE + IMITATE+ MODEL SOUND (Richards et al. 1984). Ake was highly proficient in mimicking a variety of model sounds including those sounds novel to her experience. She was also able to mimic some of the sounds used in Phoenix's language to represent objects. Following this, she showed that she could produce facsimiles of these sounds when the physical object associated with the sounds was shown to her. However, there was no evidence of her producing these sounds out of this context to request or comment on the associated object, possibly because most of the language objects were specifically designed to be arbitrary and not functionally meaningful in different ways to the dolphins.

In other work at Marine World Africa in California, Reiss and McCowan (1993) examined the interactions of two young male dolphins with a keyboard on which different visual symbols (keys) appeared in different configurations. When a key was pressed, it resulted in the underwater projection of a computer-generated whistle associated with that key followed by a human either offering the dolphin an object (ball or ring) or an action (rub) associated with that particular key and sound. The dolphins were not trained through operant procedures to press a key to obtain a sound or its associated object or action, but instead were allowed to explore the contingencies of the keyboard on their own. As the dolphins began pressing keys, they also began both mimicking the sounds and producing facsimiles of these sounds. The production of four facsimiles, two for ball and two for ring, on four separate occasions occurred just prior to one of

the males hitting the appropriate associated key. A much larger set of appropriate facsimile productions of whistles for ball, ring, rub and a combination of the separate whistles for ball and ring into a single continuous whistle were recorded in the context of a dolphin being in contact with the object or objects associated with that whistle or whistle combination. This occurred in 80% of 92 ball productions, 73% of 64 ring productions, 100% of 5 rub productions, and 82% of 28 ring-ball combination productions. Although intriguing, these data on symbol production were not sufficient to consider the communication referential.

A later underwater keyboard project conducted with two male dolphins at EPCOT's Living Seas in Walt Disney World, Florida, used humans to demonstrate the contingencies of activating keys on the keyboard in addition to the dolphin's own explorations (Xitco Jr. et al. 2001). The activation of a symbol on the keyboard simultaneously resulted in the projection underwater of the English word associated with the particular food, toy, tool, or location represented by the symbol. During sessions, one or two human SCUBA divers were paired with a dolphin and together searched the habitat for named goal objects in named locations. The goal objects consisted of food, toys, and tools that were typically hidden randomly in the habitat in transparent containers that, for a dolphin, required human assistance to open. Following 6 months of exposure, each dolphin after attending to a human activating a symbol on the keyboard was observed to swim ahead of the human, rather than waiting for him or her, to the correct object or location represented by that symbol and point to the object with its rostrum and aligned body while gazing back and forth between the object or location and the human. Each dolphin also began spontaneously activating the symbols themselves. However, while details were provided on the dolphin's spontaneous pointing behavior, suggesting that it was referential in character (Xitco Jr et al. 2001), not enough detail was provided of the dolphin's symbol production and comprehension to evaluate whether the symbols themselves were understood referentially.



## Conclusions

Our understanding of dolphin language abilities has increased dramatically since the initial descriptions of dolphin signature whistles in the early 1960s (Caldwell and Caldwell 1965). Recent findings on signature whistles of bottlenose dolphins are consistent with the interpretation that these natural learned whistles reflect individual dolphin identity and are used and understood in symbolic referential exchanges between individual dolphins (Sayigh et al. 2007; King and Janik 2013). Laboratory studies by Herman and colleagues have revealed that dolphins can be successfully tutored in artificial languages that contain various linguistic features (Herman and Uyeyama 1999). These studies demonstrate not only that dolphins can understand the referring function of arbitrary sounds or gestures towards objects, even in their absence, but also that they can immediately respond accurately to imperative and interrogative novel sentences that require an accounting of both word meaning and word order (Herman et al. 1984, 1993a, 1993b; Herman 1986, 1987). Other laboratory studies using keyboards in which dolphins are not explicitly taught the meaning of keys but discover this either on their own and/or through observational social learning have provided evidence of the vocal production of different learned whistles associated with desirables in appropriate contexts (Reiss and McCowan 1993), and have led to spontaneous referential pointing by dolphins to direct the attention of human companions towards items they desire (Xitco Jr et al. 2001). Fruitful directions for future studies of dolphin language abilities might examine whether dolphins can understand declarative sentences, can respond to interrogatives beyond questions about object presence, and can produce symbols in multiple contexts that demonstrate an understanding of their referring function.

## Cross-References

- Cetacean Cognition
- Cetacean Communication

- Cognition
- Displacement
- Imitation
- Joint Attention
- Language
- Language Research: Great Apes
- Learning
- Louis M. Herman
- Mimicry
- Pointing
- Referential Communication
- Representation
- Semantics
- Syntax

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## Language Research: Great Apes

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## Definition

Great ape language research explores how and when mechanisms for language may have evolved and explores the range and dynamics of linguistic capabilities in great apes. This research is concentrated around the mid- to late 1900s and turn of the century and includes a wide variety of studies focused on the induced development of language ability across a variety of modalities, spoken, signed, and visual, in several species of Hominidae: Pongo (orangutan), Gorilla (eastern and western gorilla), and Pan (the common chimpanzee and the bonobo).

## Introduction

Language research is inextricably tied to questions of human uniqueness. For all the different ways in which animals communicate – auditorily, visually, chemically, even electrically – language has evolved only one time. Modern language research is a culmination of the efforts of researchers from diverse fields including linguistics, evolutionary biology, and cognitive, developmental, and comparative psychology. The practice of cross-fostering apes or rearing them in the home environments similar to that of the foster parents' (human) own children, has fallen out of practice, and the ethical and practical considerations coupled with changing interests has led to the conclusion of the bulk of language research with great apes. Subsequently, research has largely diverged into study of primate cognitive ability more generally but consisting of a greater variety of capabilities (working memory, problem solving, metacognition, etc.).

While a thread of criticism and question to the validity of experimental findings (Terrace 2019) runs through much of the research conducted with apes as language users, there is a consistent focus for future researchers on improving language studies of the past. The first nonhuman primate linguistic studies consisted of attempts to teach spoken English, which gave way to signed languages and an emergent visuo-symbolic language using graphic representations. A wide variety of methodology for instruction in language and tests of accurate and effective production have been used in many different ape species, and these primates' abilities have led to studies of other cognitive abilities beyond the development of linguistic ability.

## Spoken Language

### Unnamed Orangutan

There is a longstanding tradition of cross-rearing in the great ape subjects of language research. In one of the earliest investigations into the linguistic

capabilities of nonhuman primates, Furness (1916) reared two orangutans and two chimpanzees largely in his Pennsylvania home. With slow and gradual coaching, one successful orangutan (*Pongo* spp.) was able to produce the word "Papa" appropriately as a proper noun referring to her caretaker, Furness. With manual training and manipulation of the nose and mouth, the unnamed orangutan was able to produce the word "cup," and eventually the "th" sound as a precursor to intended future study of words such as "this," "that," and so forth. When the orangutan died, Furness (1916) employed a similar method in an attempt to teach one of his chimpanzees to produce English nouns as well, but was unsuccessful, coming to the conclusion that orangutans held more promise as conversationalists.

### Gua

Interested in both language and questions of nature versus nurture, Kellogg and Kellogg (1933) co-reared the common chimpanzee (*Pan troglodytes*) Gua, acquired from the Anthropoid Experiment Station of Yale University (which would become the Yerkes Primate Center before its move to Atlanta, Georgia) alongside their infant son, Donald beginning at 7.5 and 9 months, respectively. Aiming to provide an upbringing to both that was as similar as possible, the Kelloggs provided comparative reports on the skill and behavioral development of both Gua and Donald. At 16 months, Gua's testing indicated a comprehension of 58 English words and phrases; at 18.5 months, Donald comprehended 68. Vocalizations were produced by Gua; however, these were affective in nature and never amounted to a spoken word. Several gestures were used by Gua, however, which corresponded with desires such as eating or sleeping. This behavior led Kellogg and Kellogg (1933) to speculate that signed languages may be an avenue for achieving language in apes.

### Viki

Perhaps the most successful verbal English-using ape, at just a few days of age, Viki, a common chimpanzee, was adopted into the home of

Florida-based Yerkes Primate Center researchers Hayes and Hayes (1951, 1952). As some success had been seen in cases of great apes raised in a manner similar to a human child, Viki was also bottle fed, wore diapers, and high importance was placed on a typical infant upbringing, though with a key difference in language tutoring. Viki participated in extensive and rigorous “speech therapy” and vocabulary training. Viki would be one of the last great apes to participate in research focused on production of spoken language, but she achieved production of four words: “Mama,” “Papa,” “up,” and “cup,” as well as other sounds, and demonstrated comprehension of spoken words and phrases directed at her (Hayes and Hayes 1951, 1952).

Teaching Viki to speak was a challenge, and in reflection, Hayes and Nissen (1971) considered the cognitive ability and practical physical limitations of a chimpanzee. Drawing comparisons to American Sign Language (ASL), evidence from Viki’s successes and shortcomings indicated future studies may benefit from using signs or gestures as opposed to spoken words.

## Signed Language

### Washoe

At their home in Reno, Nevada, RA Gardner and Gardner (1969) were already using ASL with Washoe, a common chimpanzee who arrived for study at 10 months old in 1966, named for the home of the University of Nevada, the first of Washoe’s affiliations. A cross-fostering design under human conditions yet utilizing laboratory guidelines for speech exposure and ASL instruction differentiates Project Washoe from other great ape communication studies. Looking at how chimpanzees used gestures in the wild, coupled with knowledge from past spoken English studies, Project Washoe was devised to teach language entirely free from speech, and great pains were taken to ensure Washoe experienced as little spoken language as possible, with all interactions directed at her or between researchers conducted entirely in ASL (Gardner and Gardner 1985).

One year of work with Washoe found her capable of appropriately producing over 30 ASL signs. She demonstrated the ability to use these signs spontaneously, stringing two or more together to make requests, answer questions, name objects, and communicate more effectively than any spoken English ape research had yet found (Gardner and Gardner 1971). Work continued with Washoe under a new research team as she moved in 1970 to University of Oklahoma’s Institute of Primate Studies (IPS) in Norman, Oklahoma, and finally, the Central Washington University’s Chimpanzee and Human Communication Institute (CHCI) in 1993. After several years of study, Washoe’s vocabulary comprehension was extensive and she was capable of producing at least 133 individual signs (Gardner et al. 1989).

### Pili, Moja, Dar, Tatu; Loulis

A project with two-fold intention was initiated in 1972 by Gardner and Gardner. Retaining the same scaffolding of strict ASL training, exposure, and testing, the two aims of the project were to replicate and validate findings from studying Washoe and to observe the effects of co-rearing multiple chimpanzees on ASL production and comprehension. Pili died before study completion, but at 60 months into the project, Moja, Dar, and Tatu produced between 120 and 150 signs each, and were able to use semantic categories in a similar manner to Washoe (Gardner and Gardner 1998).

Another chimpanzee, Loulis, was adopted by Washoe in 1979 at 10 months old. Born at Yerkes Primate Research Center in Atlanta, Georgia, Loulis was not cross fostered. Instead, growing up among signing chimpanzees at IPS and later CHCI, Loulis became the first nonhuman to learn language from other nonhumans, two of whom were Washoe and Moja (Cianelli and Fouts 1998).

### Nim

Inspired by signing ape projects but in a sharp departure from the then typical practices of rearing, including cross-fostering from infancy, Neam Chimpsky (Nim), a common chimpanzee, was acquired from a breeding facility days after birth by Herbert Terrace’s team in 1973. Nim’s environment consisted of a variety of language

tutors in several different settings, with training sessions at Columbia University campus classrooms in intensive daily 2-h bursts. Terrace et al. (1979) describes these classrooms as cold and oppressive even from the perspective of humans. Nevertheless, after 4 years, Nim had acquired 125 ASL signs across a range of semantic categories that he used in different combinations.

Later analysis by Terrace, Petitto, Sanders, and Bever (1979) led to the researchers' conclusion that Nim's use of sign did not amount to any true grasp of language. Examining videotape of Nim's interactions that initially looked promising was instead decided to indicate response to cueing from his teachers or purely reward-seeking imitations of ASL. Linguistic analysis by Bever aided in Terrace's conclusion that Nim was incapable of producing any language on his own. Project Nim was quickly disbanded following increasing incidents of aggression from the growing chimpanzee and disillusionment of Terrace, the primary investigator. Terrace remains a staunch critic of all great ape language research and maintains that Nim was never able to produce meaningful ASL (Terrace 2019).

### Koko, Michael

Francine "Penny" Patterson at Stanford University in Stanford, California began work in 1972 with Koko, a western lowland gorilla (*Gorilla gorilla gorilla*). Born in the previous year at San Francisco Zoo on the fourth of July, Koko (Hanaki-Ko, which translated from Japanese to "Fireworks Child") was the first gorilla to be involved in linguistic study. Exposed to both English and a modified ASL dubbed GSL or "Gorilla Sign Language," Koko eventually came to hold over 1000 signs in her vocabulary, sign at least six in combination, and recognize over 2000 English words (Patterson and Cohn 1990).

The Gorilla Foundation in Woodland, California became home of both Koko and Michael, an orphaned western lowland gorilla from Cameroon in 1976–77. Michael was introduced to Koko as a potential mating partner, but he and Koko developed a relationship of kin instead. Michael received signing training and acquired hundreds of signs and English words. He and Koko signed

to themselves and one another. Koko and Michael were able to use sign to ask and answer questions, create new meanings in sign and generalize known signs, use displacement, deceive, and understand abstract concepts (Patterson 1986; Patterson and Cohn 1990).

### Chantek

Born in 1977, the Sumatran (*abelii*)/Bornean (*pygmaeus*) orangutan (*Pongo*) hybrid, Chantek, was part of a University of Tennessee at Chattanooga (UTC) ASL program. Chantek was initially raised without spoken language much in the same way as Washoe and kin and taught signs by modeling. Later, a methodological shift took place wherein most signs were learned by imitation and spoken English was permissible. The ASL used consisted of proper signs but were presented largely in English word order, amounting to a pidgin sign. Nevertheless, Chantek learned at least 140 signs, which he could combine into two- and three-word strings, often used displacement, and evidence suggests he had mental representations of signed concepts (Miles 1990).

## Visuo-Symbolic Language

### Sarah

Brought to the United States and adopted in 1964 at less than 1 year of age for cross-fostering, the common chimpanzee Sarah participated in a new type of nonverbal, nonsigned language development program. In their laboratory at the University of California at Santa Barbara, Premack and Premack (1972) devised a system of symbolically representing English words and concepts as plastic tokens. Gradually, Sarah was taught more complex relational words and instructed in how to combine these plastic chip "words" using real world objects they represented as referents. By using this gentle increase in complexity to the system over time, Sarah was introduced to and eventually able to produce about 130 words, using the chips successfully and appropriately and demonstrated understanding of relational concepts. Questions have been raised



about research design and as to whether Sarah merely participated in associative-naming exercises between objects and chips, which Premack recognized as a possible explanation of Sarah's performance (Savage-Rumbaugh et al. 1980).

### Lana

With the success of plastic tokens as symbolic markers of English words, the Language ANAlog (LANA) project was developed to expand on logographic language for use with primates. Lexigrams, abstract and semantically and syntactically unambiguous, were created to serve as translations for English words. Arranged on a keyboard and "spoken" by selecting keys on a computer with a built-in correlational grammar, the artificial language "Yerkish" was born (Rumbaugh et al. 1973).

The first to use Yerkish and lexigrams was Lana, a common chimpanzee born in 1970 at Yerkes Primate Research Center. Initially trained to string together lexigrams from compatible semantic categories under the rules of Yerkish grammar, Lana was eventually able to use the keyboard to make requests, answer questions, name objects, and comment on her surroundings. She learned at least 140 lexigrams and produced chains at greater than 90% accuracy. She even developed her own way to self-monitor her performance with the board, pressing the ending or final key repeatedly to abort a sentence with incorrectly ordered or mistakenly pressed lexigrams (Rumbaugh and Gill 1977).

### Ai

Across the Pacific, lexigram work was being conducted at the Primate Research Institute of Kyoto University. Ai, a western chimpanzee (*Pan troglodytes verus*) was born in 1976 and imported to Japan where she participated in cognition research by way of language use. Past studies with lexigrams raised questions about the way chimpanzees perceived the world and the types of mental processes great apes were capable of engaging in. Language held promise as one way to examine these questions. Initially, Ai was able to learn eight lexigrams for nouns and mastered a symbolic match-to-sample task. Along with two

other chimpanzees (Akira and Mari) who participated in the project, Ai later mastered color lexigrams, labels, numbers and Arabic numerals, letters of the alphabet, and even developed spontaneous word order preferences (Asano et al. 1982).

### Sherman and Austin

Where many past studies involving lexigram use focused on communication with human researchers, Savage-Rumbaugh et al. (1986) proposed a primary focus on language use between conspecifics. Sherman and Austin, common chimpanzees, were co-reared and began training with lexigrams at 2.5 years and just under 1 year of age, respectively. Problem solving requiring use of the keyboard was used to look at comprehension of lexigrams and appropriate use. Sherman and Austin were able to learn and use lexigrams in this new way and generalize new items into existing semantic categories, providing the strongest evidence up until that point of symbolic representation as opposed to paired associate learning.

### Kanzi

Born in 1980, Kanzi, a bonobo (*Pan paniscus*), was 6 months old when his adoptive mother Matata began training to use lexigrams. She was an adult when she began her training with lexigrams and largely did not meet the goals of the language projects taking place at the Language Research Center (LRC) in Atlanta, Georgia, only learning a few lexigrams reproducible in limited situations. Present during all of his mother's formal training, Kanzi was never formally instructed with lexigrams as an infant. Then, while Matata was temporarily off site for a breeding program, a young Kanzi without his mother to attend to or occupy him began spontaneously using the lexigram keyboard (Savage-Rumbaugh et al. 1986).

After just 1 week of observation, Kanzi was found to effectively use eight different lexigrams. His performance and the naturalistic way through observation that Kanzi learned to use the lexigram keyboard resulted in a shift in the LRC's research protocol. Formal and explicit training was

replaced by an immersive, language-rich methodology. Researchers would go about tasks, keyboard in hand, to continuously model both spoken English and lexigram use, be it to the apes or other researchers. Over the next 17 months, Kanzi acquired a total of 44 lexigrams and used them in 764 unique combinations (Savage-Rumbaugh et al. 1986). Kanzi is estimated to have learned hundreds of symbols, identifying 348 with 89–95% accuracy (Williams et al. 1997) and several signs in GSL, learned from watching videos of Koko. His comprehension of English is in the range of thousands of words, and he has been shown to respond to new sentences that have a multitude of possible meanings depending on the relationship between noun and verb as well as word order. (Savage-Rumbaugh et al. 1993).

### Panbanisha and Panzee

Matata's offspring, Panbanisha, as well as the common chimpanzee, Panzee, participated in an immersive language project involving co-rearing. Born at the LRC in 1985, Panbanisha was raised by Matata for 7 weeks before joining the project. Panzee was born a short time later at Yerkes Primate Research Center and joined Panbanisha at 8 days old. At the LRC, as was developed shortly after the promise of Kanzi's naturalistic learning, this environment was one of English and lexigrams used concurrently and at every opportunity by researchers. Both Panbanisha and Panzee came to comprehend English words upward of 100 and produce over 100 lexigrams as measured by rigorous standards (Brakke and Savage-Rumbaugh 1996).

### Criticism

As great ape language progressed, so did criticism of it. Future studies often were developed to address concerns of the past, the most obvious example of this being that the premise of teaching apes to speak English was abandoned when it was suggested that there may be modalities (signed language, visual symbols) better suited to the inclinations and anatomy of apes. Criticism of

the whole of ape language research as not failing to capture any true ability and as being wishful thinking of overly invested researchers has been a continuous concern (Savage-Rumbaugh et al. 1980). Staunch objectors such as Herbert Terrace continue to reiterate past criticisms of apes' ability to use words outside of repeating back facsimiles of what humans have produced. Terrace (2019) expresses beliefs that language use is not meaningfully understood by apes and all signing and lexigram use is repetition of human behaviors motivated by reward.

Terrace (2019) initially believed Nim was able to produce meaningful signs using ASL, but, upon later examination of recorded videotapes, decided Nim was merely reproducing what he saw his teachers signing at him, induced by cueing behaviors. He argues that Nim's interruption of signers demonstrates that the behavior was merely imitation, intended to evoke a reward or directly ask the caretaker for something (imperative communication). Terrace goes on to claim that, not in any known study, is any ape producing meaningful words when speaking, signing, or using lexigrams. Not the first to be concerned with the implications of Nim's recorded interruptions as evidence of this, many studies specifically state the rate of interruption as compared to Nim's performance (Miles 1990). Rigorous testing has also been used to demonstrate that cueing does not explain language performance, such as Gardner and Gardner (1984), using a double-blind test specifically to ensure there was no cueing behavior from experimenters that may explain the vocabulary of the four chimpanzees studied.

Repeatedly researchers report the "babbling" of cross-fostered apes, (e.g., Hayes and Hayes 1951, 1952; Savage-Rumbaugh 1986) as evidence of practicing signs for improvement in later use. Michael and Koko (Patterson 1986) signed both to themselves and one another in the absence of the research team. In fact, it is reported in many cases, particularly among co-reared apes, that talk between one another occurs in the modality of instruction under non-testing conditions and largely outside of researcher observation, be it ASL (Cianelli and Fouts 1998) or lexigrams (Brakke and Savage-Rumbaugh 1996).

Savage-Rumbaugh et al. (1986) specifically designed the learning paradigm for Sherman and Austin as one that would control for this supposed false vocabulary set and found nonhuman-dependent spontaneity of lexigram usage.

Imitation as the only process by which great apes can produce something that appears to humans as language use would be an indication that apes possess no understanding of the words they are using, as Terrace (2019) implies. Terrace has stated he felt Nim was only acting on an imitative basis to his teachers, another explanation for the interruptions he engaged in (Terrace et al. 1979). Concerns of ape productions as mere association has also been expressed by earlier critiques (Savage-Rumbaugh et al. 1980). Nonimitative behavior is then any that occurs without an example to imitate, as in the case of ape-initiated language use or any instance of waiting until a human's attention is fixed on an ape before using language. Washoe, Moja, Dar, and Tatu, for instance, have been reported as performing attention-getting behaviors such as producing loud noises, then waiting for a researcher to direct gaze toward the loud sound, and finally producing signs (Gardner and Gardner 1998).

In an episodic memory study, several different objects were hidden, one at a time, in different outdoor locations with Panzee's knowledge but out of her reach and hidden from sight (Menzel 1999). Later, after an imposed delay of up to 16 h, Panzee approached human caretakers indoors who were often naïve to the experiment, invoked attention with noises and gestures before further engagement, and then used lexigrams and gestures to refer both to the object's identity and location outdoors. No prompting occurred from human caretakers and no behavior to imitate had been provided. In this case and that of Gardner and Gardner (1998), apes intentionally invoked the attention of humans and then produced signs without first observing a human performing signs or using lexigrams that could be imitated.

Reward-seeking behavior alone is another of Terrace's (2019) explanations for apes as non-language users. The issue could present itself in an extremely skewed ratio of greater imperative than declarative statements. His position is that

human children produce declarative statements at greater frequency, so if an ape is producing imperative statements instead, the explanation is that imperatives get the ape access to things or provide rewards, so this is the production they are most likely to recreate. In contrast to this supposition are cases in which detailed notes of production content were recorded and revealed to produce speech data that is largely declarative, as in the cases of Kanzi, Panbanisha, and Panzee (Lyn et al. 2011).

Food rewards are a specific concern of Terrace, and he states food motivation and constant treat-providing may assist in the formation of word development and be a primary factor in why apes produce signs. The concern about ever-present food is not indicated in the literature. With few exceptions (Premack and Premack 1972), and perhaps Terrace's own Nim (Terrace et al. 1979), food is not an explicit motivator provided to communicative apes. While other rewards may exist in the form of experimenter praise or attention as known agents that held control of resources that may explain the motivation for engaging in language use, to generalize to such a degree does not grasp the whole of the picture in a long-term study. The literature does not indicate food reward was given in response to correct behaviors with the degree of frequency Terrace (2019) implies; these other types of reward have not been established as definitively undermining performance results.

## Conclusion

Great ape language research reached a pinnacle of scope and scale around the turn of the century that is unlikely to ever be matched, at least in comparable form. For apes in the wild, the average lifespan may be 50 years, and this is often extended in captivity. The practical aspects of housing and finances alone stand in the way. Additionally, the ethical and political landscape is changed, as are the questions surrounding cognition, linguistics, and human uniqueness. Still, these studies and those like them will likely continue to be an influence on future cognitive research.

The bulk of great ape language research comes with critique. At the foundational level, many of the most successful ape projects involved cross-fostering, which aimed to promote an environment of development as similar to that of a human child as possible. This allowed natural language learning in early stages of development and also bonded not only the ape to the researchers but the researchers to their apes as well. Rooted in the earliest studies is a built-in attachment, for example, Furness' (1916) orangutan learned to say "Papa" before anything else, and he provides an anecdote about bringing the orangutan into his pool in his arms until she pleaded with her word "Papa" over and over again.

As the research progressed, researchers attempted to create new methods and testing procedures to address the concerns of critics. Varying across the work of different researchers and over time, broadly this can be split into two different categories of instruction and two categories of testing. The first instructional type involves a more traditional or explicit training with object introduction, modeling of the word that refers to the object, and then invocation of the word from the ape student. The second instructional type, such as the shift in paradigm at the LRC, involves a more naturalistic and immersive environment where teaching is imparted in the way many cultures teach human children, primarily based on modeling. Testing or the drawing of conclusions follows a similar dichotomous pattern, with studies like those conducted with Washoe and kin (Gardner et al. 1989) imposing strict and rigid requirements for sign use before classifying a sign as learned, producing a result of an exact quantifiable language achievement. Later researchers such as Miles (1990) being more focused on capabilities and due to the changing nature of the questions being asked – "What are the cognitive capabilities?" – taking the place of "How many signs can be used?" – naturally, more varied dimensions of ability analysis occurred.

Criticisms from researchers such as Terrace have remained relatively consistent, believing apes to have no concept of language or ability to use it outside of imitative contexts and those motivated by food reward. Evidence refuting those claims including double-blind studies of the

Gardners (Gardner and Gardner 1984), self-initiated behaviors as demonstrated by Panzee (Menzel 1999), and word usage directed at self and fellow apes (Patterson 1986) indicates these criticisms have grounds for contest. Great ape language research may not exist in similar form as the future studies of wide-ranging cognitive capabilities progress, but the impact of these 1900s and turn-of-the-century studies is apparent in modern primatology and psychology.

## Cross-References

- ▶ [Ai \(Chimpanzee\)](#)
- ▶ [Categorization](#)
- ▶ [Charles R. Menzel](#)
- ▶ [Communication](#)
- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)
- ▶ [Computerized Testing Paradigm in Primates](#)
- ▶ [Counting](#)
- ▶ [Cross-Fostering Studies](#)
- ▶ [David Premack](#)
- ▶ [Duane Rumbaugh](#)
- ▶ [Episodic Memory](#)
- ▶ [Georgia State University's Language Research Center](#)
- ▶ [Herbert Terrace](#)
- ▶ [Kanzi](#)
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- ▶ [Primate Cognition](#)
- ▶ [Primate Communication](#)
- ▶ [Primate Research Centers](#)
- ▶ [Sue Savage-Rumbaugh](#)
- ▶ [Washoe](#)
- ▶ [Yerkes Primate Research Center](#)

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## Language Research: Parrots

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### Synonyms

[African grey parrot](#); [Birds](#); [Communication](#); [Cognition](#); [Ornithology](#); [Psittacus erithacus](#)

### Definition

A review of language-centered studies on parrots and implications for understanding parrot cognition.

### Introduction

Language-based animal studies have previously focused on teaching language to nonhuman primates in an attempt to understand how language evolved in humans. However, they eventually branched out, using language as a tool to understand cognition in other animals such as dolphins and birds (e.g., Hayes and Nissen 1971; Herman 1980; Pepperberg 1981). Several bird species have demonstrated an ability to imitate human speech, including corvids, songbirds, and, notably, parrots. Parrots (*Psittacidae* sp.) are a family composed of approximately 390 species. Language research on parrots has focused on African grey parrots (*Psittacus erithacus*), particularly the work of Dr. Irene Pepperberg, which used their ability to interface with humans to explore their cognitive ability. This work paved the way for

other researchers to continue examining parrots and their cognition through language. These studies have allowed for an understanding of how parrots learn and how this ability compares to other species, including humans.

### Why Parrots?

Parrots are a suitable study species for language-based research for several reasons. The main reason is parrot's ability to imitate human speech, allowing for limited communication between researcher and subject. This ability has been observed in various parrot species, all of which were found to learn quickly (e.g., Lashley 1913). Additionally, parrots are social animals and display nonsexual affiliative vocalizations with other group members, making them more willing to engage with researchers and build relationships with them (Colbert-White et al. 2014). There is also evidence that parrots learn through social interactions with others, as seen with orange-chinned parakeets (Power 1966). Several neurological features also make them suitable for language research. Despite having small brains compared to other animals used in language studies, parrots have a larger relative sized brain than expected for their body size (Péron 2012). Similar to humans, they also show brain asymmetry and a bias for communication related structures (e.g., Bottjer and Arnold 1985). Together these features make parrot species ideal for examining cognition through language ability.

### Irene Pepperberg's Studies with Alex the Parrot

The most notable subject in language research using parrots was Alex the African grey parrot, who was trained and studied by psychologist Dr. Irene Pepperberg, from 1977 until his death in 2007. Unlike early language studies on apes, these studies with Alex attempted to develop an understanding of animal cognition rather than human language development. Pepperberg's work focused on testing cognitive ability using language as a tool

and teaching Alex to communicate by training him to use English speech.

This training was accomplished by using a Model/Rival technique, which used social interactions with his trainers to demonstrate desired behaviors (Pepperberg 1981). For example, Alex would view one researcher asking another researcher questions about an object of interest, discussing the object name, size, shape, or color. When these questions were answered, the other researcher would be praised or scolded appropriately. Additionally, these roles would be reversed in order to show that either participant in an interaction may ask questions, encouraging Alex to do so himself. When being tested, if Alex correctly identified an item, he was rewarded with either the item itself (helping to intrinsically reinforce the name with the object) or a desirable treat that was requested (e.g., a piece of banana after saying “I want banana”) (Pepperberg 1988).

To ensure accuracy while testing Alex’s understanding of language, several precautions and controls were employed during testing procedures. To avoid Alex forming an association between certain trainers and certain types of questions, trainers would not repeat the same question topic during their trials (Pepperberg 1981). Additionally, objects and questions used in training were randomly ordered by a researcher who would subsequently not administer the training to avoid cuing from trainers and to prevent Alex from preempting certain questions for a topic (e.g., Pepperberg 1990). Questions of the same type were also never repeated within a session, unless answered incorrectly (e.g., several “how many” questions). Randomized order and no repetition of question types also helped to maintain consistency across sessions in terms of Alex’s attention, avoiding behaviors such as preening, interruptions, or discontinuing engagement (Pepperberg 1999). In the case of the trainer mistakenly judging a response as incorrect, Alex was trained to repeat his response, allowing for a second confirming judgment (Pepperberg 1999). Additionally, accuracy is further ensured by another trainer repeating any answer given by Alex, reducing the chance that a similar to correct response is accepted (Pepperberg 1981). A control was also implemented to dissuade Alex from

asking repeatedly for an item rather than correctly identifying the one he is presented with. In these situations, he was allowed four attempts at a correct identification, before moving on, and with no rewards being given for incorrect answers (Pepperberg 1981).

Model/Rival training allowed researchers to test Alex’s ability to label and request items, understand categories, comprehend similarities and differences, as well as understand absence, numbers, and size of objects relative to each other. For example, Alex could successfully identify 100 objects, as well as 7 colors and 5 shapes in approximately 80% of trials (Pepperberg 1999). Additionally, Alex also performed well in recursive tasks in which he was tested on several categories at once (e.g., “which object is shape-b?”) and even when a conjunctive condition was added (e.g., “what object is color-a and shape-b?”) (Pepperberg 1990). Alex also used the term “none” to indicate the absence of an item, despite not being taught this label (Pepperberg and Gordon 2005). Outside of his training sessions, Alex was observed engaging in sound play, often related to labels that he was being taught in training (Pepperberg et al. 1991). Overall, these studies and observations allowed for the examination of African grey parrot’s cognitive abilities in detail.

## Other Subjects

Alongside research on Alex, additional studies were carried out on three other African grey parrots, named Griffin, Kyaaro, and Alo, all previously untrained and varying in age. The aim of studying these individuals was to determine how using a Model/Rival technique was effective for training Alex in order to gain insight into how he learned. This was achieved by breaking the technique down into its major components and then removing one or more to examine their importance (Pepperberg 1994). The components were defined as referencing (e.g., labelling objects and rewards for successful use of labels), context and function (e.g., motivating use of a label through tasks such as requests), and social interaction (e.g., interaction with the subject, which guides

the learning experience) (Pepperberg 1994). Removal of all three components or removal of social interaction, context, or referencing resulted in no learning being observed in experiments with the three subjects, with successful learning only resulting from the presence of all three components (Pepperberg 1994).

Further studies by Pepperberg and colleagues examined the parrots' understanding of labels and, if they assume mutual exclusivity, the belief that a label defines an entire object rather than a specific feature such as color or shape. To investigate this, comparisons were made between how Alex and Griffin were taught labels for objects. While Alex was told features of objects alongside the object names themselves (e.g., ball, red ball), Griffin was taught these labels separately (e.g., ball, red) (Pepperberg 1981; Pepperberg and Wilcox 2000). Consequently, Alex showed no mutual exclusivity when using labels, and Griffin did, responding to questions only with the first label he learned for items.

Another study examined the categorization abilities of two African grey parrots, Shango and Zoe (Giret et al. 2009). They were taught words that either belonged to food (e.g., chickpea), object (e.g., fork), or neutral (e.g., "hello") categories, and then the parrots recorded during and after training sessions to examine their spontaneous vocalizations. Researchers found that Zoe used spontaneous food labels more when faced with food items, and Shango did so for food and object items, suggesting that they grouped items based on edibility.

Giret et al. (2010) next examined how effective different training methods would be when learning labels across ten parrots. Initially, three parrots were trained with the Model/Rival method used in Pepperberg's studies and the other seven used variants upon this. They were also exposed to an Intuitive training method in which items were handled by a trainer while saying their label, a Repetition/Association method, in which items were produced when the subject says a label they've been exposed to, and a Diffusion/Association method, where recordings of labels were played to the parrots (Savage-Rumbaugh and Lewin 1994). They found that the Repetition/

Association method was most effective for learning, while Diffusion/Association failed. However, the researchers noted that Model/Rival was likely less effective due to differing housing conditions and individual circumstances with the subjects compared to Pepperberg's studies.

Other studies have described how African grey parrots are capable of substituting words with similar meanings and uses within contexts, such as "street" and "road" (Kaufman et al. 2013). Vocalizations of an untrained subject, Cosmo the pet African grey parrot, were found to display such substitution in sentences such as "Cosmo wanna," in which she used words such as "talk," "go," and "cuddle." In this situation, Cosmo understood that "Cosmo wanna" symbolizes a request and the words following represent the requested action. Another study on Cosmo found that she used vocalizations depending on context (Colbert-White et al. 2011). For example, when she was separated from her owner, Cosmo would emit vocalizations discussing where she or her owner where (e.g., "where are you"). Outside of studies focusing on Alex, several other researchers have conducted investigations on parrots and language.

## Implications and Similarities to Other Species

The findings of these studies offer insight into the cognitive capabilities of African grey parrots. For example, the ability to understand and switch between categories of labels such as colors and shapes demonstrates a higher-order class concept and an understanding of abstract concepts (Hayes and Nissen 1971). An understanding of how items can be the same or different from each other may suggest a simple understanding of language, as labels must be understood in order to describe relationships between items (Premack 1978). In addition to this, an understanding of absence suggests advanced cognitive development (Brown 1973). This is supported by the ability to compare items relative to each other (e.g., "which color bigger?") in which information about two features are attended to simultaneously. Kaufman et al. (2013) suggest that Cosmo's use of substitution may also suggest

complex cognition. Studies removing elements of Model/Rival training highlight the essential aspects of learning for African grey parrots: referentiality, contextual use, and social interaction. Colbert-White et al. (2011) also demonstrate the importance of social interaction for learning. However, further studies demonstrated that mutual exclusivity occurs when subjects learn labels purely in a context-dependent manner, similar to that of young children (Liittschwager and Markman 1994). Similarly, the use of perceptual features to categorize objects seen in Shango and Zoe resembles the categorization ability of children under 1 year (Madole et al. 1993). Another parallel with language development in children can be seen in Alex's use of sound play outside of training sessions (Pepperberg 1991). As well as similarities to language development in humans, African grey parrots also display cognitive similarities with other species. Nonhuman primate, cetacean, and pinniped species have also demonstrated an ability to comprehend recursive and conjunctive tasks and the relationships between items, as well as use labels and make requests (e.g., Herman 1987). Pepperberg (1999) proposes that parrot cognitive ability is similar to that of primates, cetaceans, and pinnipeds due to their shared long-life history and complex social system.

### Controversy and Limitations of Parrot Language Studies

While language studies on parrots have uncovered much about their cognition, they also have limitations and have been criticized. For example, Hebert Terrace, who previously conducted studies on chimpanzees and language, proposed that Alex the parrot's responses were simply based on external guidance from trainers rather than a real understanding of the task (Smith 1999). However, there were measures taken during the experiments with Alex to avoid such cuing from trainers (e.g., Pepperberg 1990). One frequent limitation of these studies is a low sample number, often only with one subject (e.g., Kaufman et al. 2011). While this is true for studies that aim to compare between groups, researchers have argued that if one individual can perform a task, this suggests

that the species is generally also capable of doing so (Triana and Pasnak 1981). However, repeated experiments and additional subjects can be useful for highlighting issues with methodology, such as in Giret et al. (2010) in which the Model/Rival method failed in one lab involved, but not the other. Other issues may occur due to individual features such as personality, motivation, age, or sex (Cussen 2017).

### Conclusion

Despite limitations and criticisms, language-based studies of parrots have uncovered much about African grey parrot cognition, showing that, contrary to previous beliefs, they demonstrate complex cognition. Examples of their capabilities include referential labelling, making requests, categorization, word substitution, and an understanding of context, many of which are comparable to those of human children. While language studies on nonhuman primates decreased over time, studies of parrot cognition using language are still being conducted today.

### Cross-References

- ▶ [Alex the Parrot](#)
- ▶ [Irene M. Pepperberg, PhD](#)
- ▶ [Language Research: Great Apes](#)
- ▶ [Psittacine Cognition](#)
- ▶ [Psittacine Cognition](#)
- ▶ [Referential Communication](#)

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## Last Common Ancestor

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## Synonyms

[Closest living relative](#); [Common descent](#); [Hominid phylogeny](#); [Shared ancestor](#)

"Last common ancestor" (LCA) refers to the most recent species from which two or more species share a common descent. The term is most commonly used to refer to the last ancestor that is shared by both modern humans (*Homo*) and our extant great ape cousins, the chimpanzees and the



bonobos (genus *Pan*). Chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) are humans' closest living relatives, sharing approximately 98.6% of their genetic material with us. It is estimated that the *Homo* lineage diverged from the *Pan* lineage only around 5 to 7 million years ago but possibly as early as 8 million years ago (Langergraber et al. 2012; Prüfer et al. 2012). Chimpanzees and bonobos are themselves highly related, and recent research has shown that they even share genetic similarities with modern humans that they do not share with each other (Prüfer et al. 2012). Given their close genetic relationship to humans, both chimpanzees and bonobos represent crucial living models for enabling us to reconstruct our last common ancestor and, moreover, for identifying uniquely human features.

Despite being closely related and showing many similarities, bonobos and chimpanzees also show some striking differences spanning behavior, cognition, physiology, development, morphology, and neural-anatomy (Hare and Yamamoto 2017). Comparing the similarities and differences of the two *Pan* species is important for constructing balanced models of human evolution (Gruber and Clay 2016). Moreover, recent research has highlighted striking diversity and behavioral flexibility among both chimpanzee and bonobo populations (Boesch et al. 2002). Thus, as well as comparing between the two species, it is also crucial to consider behavioral flexibility within subspecies and subpopulations of both species. Taking into account this variation, both within and between species can provide a much more nuanced view of the behavioral flexibility of our great ape relatives, who can be considered to sit along a continuum shaped by various ecological factors within their surrounding environments. This approach can enable a more valid reconstruction of the LCA between *Pan* and *Homo*.

Although a paucity of data has historically prevented models of the hominin LCA incorporating insights from both *Pan* species, numerous attempts have been made to construct models of early hominins using findings from nonhuman primates. Among the first were Washburn and Avis (1958). Most models have traditionally

focused on chimpanzees as the referential model for early hominins (Tanner and Zihlman 1976), although a recent surge of interest in bonobos is now addressing that imbalance (Gruber and Clay 2016). One recent phylogenetic analysis revealed notable stasis on *Panin* evolution and that bonobos have undergone fewer changes in their musculoskeletal anatomy as compared to chimpanzees and, thus, may be a more appropriate model, at least anatomically, for the last common ancestor (Diogo et al. 2017).

Based on similarities between chimpanzees and bonobo social systems, it is estimated that the LCA likely lived in a fission-fusion hierarchical social system, where both males and females competed for available mates and food resources (Boesch et al. 2002). Shared presence of complex tool use in both bonobos and chimpanzees indicates our LCA was likely to have been a competent tool-user (Gruber et al. 2010). Regarding reproductive behavior, modern humans do not display the conspicuous sexual swellings seen in *Pan* species. Whether this has led to more pronounced concealed ovulation in humans is under debate, particularly because this trait is present to some extent in the prolonged swelling stages of both *Pan* species, especially bonobos. Although the pressures that led to concealed ovulation remain uncertain, it seems reasonable to assume that our LCA lived in a complex social system in which sexual selection highly influenced social interactions and both sexes developed strategies to prevail in this competition. Species differences in intersexual and intra-sexual social bonding suggest that behavioral flexibility probably was present in our LCA. Interpopulation and intersex variability in our LCA probably enabled them to adapt patterns in sociality in response to prevalent social and ecological conditions, further enhancing their success in radiating on the planet.

## Cross-References

- [Common Ancestor](#)
- [Evolution](#)
- [Evolutionary Psychology](#)
- [Phylogeny](#)

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## Latent Inhibition

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Latent inhibition (LI), a phenomenon discovered in Pavlovian conditioning, refers to “the detrimental effect of passive, nonreinforced preexposure of

a stimulus on the subsequent ability of an organism to form new associations to that stimulus” (Lubow 1989). Behaviorally, repeated non-reinforced preexposure of the to-be-conditioned stimulus (CS) produces a decrement in learning performance (Lubow and Moore 1959; Lubow 1989; Lubow et al. 1981). The phenomenon is also known as the CS-preexposure effect.

LI has been evaluated in different experimental preparations such as conditioned suppression, conditioned avoidance, and conditioned taste aversion, among many others. This phenomenon has been widely seen in nature, principally (but not exclusively) in mammals, suggesting an evolutionary behavioral mechanism in order to grasp relevant stimuli or events and avoid irrelevant ones in ecological niches (Lubow and Weiner 2010). LI is biologically significant and a relevant psychological phenomenon because it allows the organism to generate faster responses to new rather than familiar stimuli. In a changing environment, organisms must learn to respond properly to new stimuli, which may signal danger, food, safety, etc.

## Background

The CS-preexposure effect was first reported by Lubow and Moore in 1959, who labeled it latent inhibition. It comes from a study designed to evaluate “latent learning” in an animal model. The goal was to explore if learning would happen without reinforcement and whether reinforcement itself was necessary for it, as well as to establish potential differences between learning and performance. Lubow and Moore reported a series of experiments in which subjects (i.e., goats and sheep) received nonreinforced preexposure to a single stimulus (i.e., a flashing light or a moving rotor, counterbalanced), expecting to see an increment in subsequent learning (i.e., conditional leg flexion to a mild shock) involving the preexposed stimulus. This was already observed in other learning situations, such as maze solving and problem-solving tasks, among others. Nevertheless, they observed the opposite results: Subjects reached the response criteria slower when they were previously preexposed to the stimulus. The authors

proposed that the lower rate of subsequent conditioning of the preexposed stimulus compared to the novel stimulus was a function of the learning that occurred during the nonreinforced presentation of the stimulus by itself (Lubow and Moore 1959). In short, LI comes from early experiments of latent learning, in which the term latent was used to designate the learning that “appears” later when an adequate test is performed, and the term inhibition was used to describe the subsequent learning decrement.

### Conditions for Latent Inhibition

In LI experiments, stimuli (pre) exposures are not followed by a significant event, which is common to other learning phenomena, such as habituation, learned irrelevance (preexposure of both unconditioned stimulus [US] and CS), extinction, and perceptual learning, among others. Three features differentiate LI from those other learning phenomena: the conditions for producing it, the conditions for measuring it, and the direction of the differences between groups (Lubow and Weiner 2010). Thus, to demonstrate LI, it is needed to preexpose (either) a target stimulus in one of two groups of subjects or participants, with the other group working as a nonpreexposed control group (a between-subjects experiment); or b) a target (i.e., preexposed) and a control stimulus in a single group (a within-subject experiment). Then, both groups learn an association between the target stimulus and the US (i.e., acquisition). Hence, when the conditioned responses to the target stimulus are compared in both conditions, subjects or participants in the CS-preexposed group respond less or slower than subjects or participants in the control group, showing evidence of LI.

### Theories of Latent Inhibition

The most traditional psychological learning theories can account for the general CS-preexposure effect, and their explanations can be clustered in two families depending on whether the phenomenon represents a failure to learn an association (acquisition-

focused perspective) or a failure to manifest an association (retrieval-focused perspective).

From an acquisition-focused perspective, LI represents an acquisition deficit in which the organism learns to reduce CS processing due to its preexposure during the acquisition or training phase. During the preexposure and conditioning phase, some mechanisms affect the succeeding associability of the preexposed stimulus, due to a loss of salience from an attentional process. All these different models are focused on the attention of the organism to explain LI. Some theories highlight the reduction of attention (e.g., Mackintosh 1975), the loss of associability (e.g., Pearce and Hall 1980), the conditioning of inattention (Lubow 1989), and habituation (e.g., Wagner 1978), to explain LI. Wagners approach puts the focus on the attention to the US, while Pearce and Halls and Mackintoshs theories focus on the attention to the CS. Lubow assumes that the change in attention to a stimulus is continuous and has no separate processes and that the absence of reinforcement reduces the attention to the repeatedly presented stimulus.

From a retrieval-focused perspective, response reduction in LI is due to an interference effect that affects performance at the moment of retrieval rather than during acquisition. That is, organisms learn from both the nonreinforced (CS) and the reinforced trials (CS-US), and reduced conditioned responding is determined by what happens at the moment of testing. At test, both acquired associations concerning the CS (CS and CS-US) are retrieved and compete for expression, interfering with each other (Bouton 1993; Miguez et al. 2018; Miller et al. 2015). The retrieval-focused perspective is supported by two complementary types of evidence, one supporting the idea that LI is affected by changes of context between the preexposure and the acquisition phases, and another supporting the idea that LI is affected by changes in time intervals (i.e., delay or no delay) between the acquisition and test phases (e.g., Miller et al. 2015).

In brief, the acquisition- and retrieval-focused perspectives lie on the premise that something is learned during the preexposure phase but differ on how what was learned is expressed as behavior later (i.e., conditioned response).

## Relevance

LI as a conditioning phenomenon has been important for the development of modern learning theories. Moreover, this phenomenon has been useful to understand some mental disorders such as schizophrenia, and consequently, explain the positive symptoms of this disorder. It is assumed that the process underlying LI is dysfunctional in patients with schizophrenia, that is, they exhibit an inability to avoid irrelevant stimulus (i.e., to show LI; Lubow and Weiner 2010).

Last, LI can be relevant as a preventive technique to avoid the acquisition of fears and phobias (e.g., dental phobia, school fear, veteran post-traumatic stress disorder, etc.). Preexposure of stimuli and situations that are expected to be associated with aversive experiences in the future (e.g., dentists office, school, war zone) could reduce later fear acquisition to those stimuli and situations (Lubow and Weiner 2010).

## Cross-References

- [Associative Learning](#)
- [Conditioned Inhibition](#)
- [Contingency](#)
- [Counterconditioning](#)
- [Ivan Pavlov](#)
- [Learning](#)
- [Perceptual Learning](#)
- [Reflex](#)
- [Spontaneous Recovery](#)
- [Taste Aversions](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Latent Learning

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## Synonyms

[Blodgett effect](#)

*Latent learning* refers to changes in potential for behavior that remain hidden or unmanifest until some later test. Although latent learning is best illustrated by the effects of classroom instruction or similar situations in which individuals acquire knowledge or skills that are not demonstrated until later, when they are tested, the concept is

rooted in maze-learning studies with rats, almost 100 years ago. The phenomenon was important in the emergence of neobehaviorist and cognitive frameworks.

## Background

The term “latent learning” was coined by Blodgett (1929) to describe the sudden improvement in rats’ maze performance that accompanied the introduction of a previously withheld reward. Blodgett ran three groups of rats through a maze and measured the number of blind-alley entrances that occurred each day. The first group, a control, received a reward for each successful run of the maze. The second group was not provided a reward until the third day of maze exposure, and the final group was not rewarded until the sixth day. The control group demonstrated the typical pattern of maze-learning errors: high error rates on the first several trials, followed by a steady decline in errors. The other groups showed little evidence of learning prior to the introduction of food rewards; however, both experimental groups showed an immediate and steep decrease in errors once successful runs were rewarded. Within 2 days of reward introduction, each groups’ performance was indistinguishable from that of the control group, meaning that the rate of improvement was greatest for the experimental groups. Blodgett used the word *latent*, meaning hidden or concealed, to describe the learning that must have occurred on earlier nonrewarded trials but that was not manifest in performance until the delivery of food.

This was a result (also called the Blodgett effect) that was difficult to accommodate into the dominant learning frameworks of the period. The prologue to contemporaneous attitudes about learning included Pavlov’s seminal classical conditioning studies, and though Pavlov himself generally dismissed psychology, his method had found favor with psychologists like John B. Watson who were dissatisfied with earlier introspective and mentalistic approaches (Brennan 1994). Many studies demonstrated the learning of stimulus and response events that occurred together and described the effects of

frequency, intensity, and timing on the learning of the stimulus-response relation. In opposition to this, contiguity perspective on learning was Thorndike’s catalog of learning principles in general and his famous Law of Effect in particular (Thorndike 1911, 1927). Thorndike postulated that stimulus-response connections were differentially reinforced by the consequences of a response: behaviors that resulted in annoying outcomes were not as strongly connected to stimulus conditions as were responses that produced more satisfying outcomes. A great deal of evidence was generated in support of differential reinforcement as the primary predictor of trial-and-error learning, which some interpreted as indication that learning could not occur in the absence of positive or aversive consequences of behaviors. The most cogent and influential summary of these perspectives on learning was provided by Skinner (1938), who described the stimulus-stimulus associative learning as Type S (Pavlovian, respondent, or classical conditioning) and the stimulus-response learning as Type R (or operant conditioning).

Some contemporaries of Skinner willingly embraced behaviorism’s basic tenet, namely, that observable behavior constituted the primary datum for the science of psychology but were willing also to allow a role for inferred variables in explaining how associations between stimuli and/or responses are formed and altered. These theorists, sometimes referred to as neo-behaviorists, embraced “logical constructs, intervening variables, or symbols” (Hull 1943, p. 21) such as habit strength, frustration, hypothesis, and goal in describing the mechanisms of behavior change. Clark Hull and Kenneth Spence, for example, described learning in terms of reaction potentials, which could be mathematically expressed as a function of factors like stimulus intensity, motivation, drive strength, and habit strength (Hull 1952; Spence 1944). Their framework struggled to accommodate findings of latent learning like those reported by Blodgett, as Hullian learning was incremental rather than sudden and depended on reinforcement by way of need-reduction (or drive-reduction). Proponents of the Hullian view scrambled to explain latent learning, appealing to needs like curiosity or an



animal's desire to return to its home cage as potential drives to be reduced. They postulated Hullian constructs like fractional anticipatory goal responses, surrogate responses, momentary effective reaction potentials, goal gradients, and shifts in incentive to explain the rapid learning shown by rats in Blodgett's latent learning paradigm (e.g., Le Ny et al. 1970; Seward 1947, 1949). However, other researchers found these theoretical accounts to be unsatisfying, logically inconsistent, and inadequate to account for the phenomenon (e.g., Buel 1938; Deutsch 1956a, b; Wolpe 1953).

Alternatively, Edward Tolman (in whose laboratory Blodgett made his discovery of latent learning), emphasized the acquisition of expectations, cognitive in nature, that were reinforced via confirmation rather than reward (Tolman 1932). Tolman, who is typically called a neobehaviorist but who preferred the label of the "molar behaviorist," explained latent learning by postulating that the rats learned about the spatial arrangement of the maze in the absence of food reinforcement. Rats that had acquired this latent cognitive map of the maze were thus advantaged over naïve animals when the time came to learn the path to the baited goal box. In contrast to the reinforcement-dependent learning of Thorndike, Skinner, and Hull, Tolman and other proponents of cognitive explanations of latent learning emphasized the importance of internal representations and expectations rather than overt reinforcement for learning. In the words of Wolpe (1953, p. 340), the Hullian view "loses sight of the fact that the events that intervene between stimulus and response take place inside the organism, and that consequently behavioral antecedents may have intraorganismal consequents without behavioral consequents." For Tolman and similar theorists, these explanations and others stimulated intense, decades-long debates and inspired an entire body of research dedicated to the latent learning phenomenon. A comprehensive review of this work was conducted by Thistlethwaite (1951) who argued that latent learning experiments took on four distinct forms. One type of latent learning experiment was collectively termed "the Blodgett variety," as they were iterations of Blodgett's

landmark study (Thistlethwaite 1951, p. 99). The first of these was conducted by Tolman and Hoznik, in which they employed a 14-unit T-maze, a larger sample of animals, and two control groups instead of one (Tolman 1948). The first control group received food throughout the experiment, and the second control group never received it. The experimental group, which received food beginning Day 11, demonstrated the same pattern of responses as Blodgett's rats. That is, they did not appear to learn much of anything the first 11 days of the experiment, but on Day 12, their performance improved dramatically. Several additional experiments were carried out using this procedure, and these produced similar findings.

A second theme in latent learning experiments involved the use of satiated animals for training and the subsequent food or water deprivation of these animals for testing. For instance, Spence and Lippett (as reported in Tolman 1948) conducted an experiment in which water and food were kept in separate alleys of a simple Y-maze. During the training period, satiated rats ran the maze four times a day (two trips down each alley) for a week. At test, one group of rats was deprived of food and the other of water. Within a single trial, hungry rats immediately traversed the maze to the food alley, while the thirsty rats moved directly to the water alley. As in earlier experiments, it would seem that, unreinforced, the rats learned the location of food and water within the maze, and once suitable motivation presented itself, they navigated directly to the item in need as though they were using a cognitive map. Similar experiments yielded a mixture of positive evidence for latent learning and more ambiguous findings that, for one reason or another, remained open to interpretation.

In a related design, some experimenters baited mazes with food and/or water, goals which were either relevant or irrelevant to food- or water-deprived rats. After a time, the rats' need states were alternated (i.e., a previously hungry rat was now kept thirsty, and vice versa), and they were tested in the same maze to determine whether, in the course of learning the location of a previously desired reward, the rats had learned the location of

the irrelevant goal. Some success with this approach was reported, but other attempts did not produce evidence for latent learning.

A fourth type of design commonly used in latent learning experiments was deployed by Haney (1931). Haney allowed an experimental group of rats to occupy a maze for 18 h daily for four consecutive days and found that they made significantly fewer errors at test than did controls. Variations of this experiment included the use of both longer (Buxton 1940) and shorter exploratory periods, doors to prevent route retracing (Daub 1933), or manipulation of cues within the maze (e.g., Buxton; Seward 1949). Familiarity with the maze under conditions of non-reward seemed to result in latent learning with a fair degree of consistency (Thistlethwaite 1951).

Interest in latent learning eventually waned. However, researchers are still asking questions about latent learning today, though it would seem that the interest stems from slightly different orientations. Some psychologists and neuroscientists use latent learning procedures for the purposes of evaluating cognitive impairments that occur as a result of aging (Smith and Stouffer 2014; Stouffer and Helsey 2013) or of particular pathologies like renal failure (Jones et al. 2015). In a similar vein, the effects of particular substances on latent learning performance have also been evaluated (e.g., Luchiani et al. 2015; Malin et al. 2015). Others have explored latent learning in understudied species, including ants (Franks et al. 2007) and zebrafish (Gomez-Laplaza and Gerlai 2010), or in understudied domains like auditory perception (Molloy et al. 2012). Still others have induced lesions to elucidate neuroanatomical structures underlying latent learning in spatial tasks (Kimble and Greene 1968; Kimble et al. 1982). Despite the fact that these recent experiments used latent learning procedures for purposes other than revision of learning theory, the family of experiments dealing with latent learning for learning's sake has not gone entirely extinct. Rather, it seems to have found a permanent home in the domain of spatial learning, where experimenters have combined technologies old and new to evaluate constructs derivative of Tolman's cognitive map. Jensen (2006) reviewed

some of this research, but beyond these studies, cognitive maps have recently been invoked to describe hippocampal processing (Dabaghian 2016), to clarify spatial learning in visually impaired populations (Papadopoulos et al. 2017) and discussed for use in artificial intelligence (Villacorta-Atienze et al. 2015). Some still deal directly with the rat and the maze (Grieves and Dudchenko 2013). For those looking for a comprehensive treatment of the topic, Kitchin and Freundschuh's (2000) book might prove useful.

In terms of critical reception, the primary goal of researchers interested in the topic was to outline the conditions that facilitated latent learning in hopes of refining learning theory (Chaplin and Kraweic 1960; for a review of these conditions, see Thistlethwaite 1951) and there is some lingering question as to whether or not that goal was accomplished. Of course, the substantial investment of research effort into latent learning experiments did not pass without criticism. Jensen (2006) suggested a few reasons latent learning research might have been largely abandoned in the mid-1960s, including the idea that the debate itself had reached an impasse and the notion that preferences in experimental apparatus had shifted away from the maze toward other, more sophisticated methods. Further, there is some indication that more recent conceptualizations of latent learning and its place in the broader zeitgeist has been widely misrepresented (Jensen 2006), perhaps due to its close ties to behaviorism, a school of thought that, some argue, has also been commonly misunderstood (Abramson 2013).

Criticism aside, it is fair to say that latent learning spawned a generation of inventive experimental and theoretical approaches to learning. Rumbaugh (2002) cited latent learning as a key example of emergents – in contrast to the respondents and operants that Skinner described – and thus a cornerstone of what he called “rational behaviorism.” It also sparked a debate that has recently been reignited, and that is the theoretical justification for the learning-performance distinction. A full review of the learning-performance distinction is beyond the purview of the current undertaking, but a brief description is warranted, as it appears in Tolman's (1932) own description

of latent learning (which, in a footnote, he credited to both M.H. Elliot and Karl Lashley; see, for example, Elliot 1929): “Differential effects are, that is, necessary for *selective performance* but they are not necessary, or at the most in only a very minor degree, for the mere learning *qua* learning which underlies such performance.” This argument has been adopted in the decades since to explain how experimental manipulations can improve performance but not learning (or vice versa; for a review, see Soderstrom and Bjork 2015).

## Cross-References

- ▶ [Behaviorism](#)
- ▶ [Classical Conditioning](#)
- ▶ [Cognitive Map](#)
- ▶ [Operant Conditioning](#)

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## Lateral Intraparietal Region (LIP)

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## Synonyms

Lateral intraparietal area

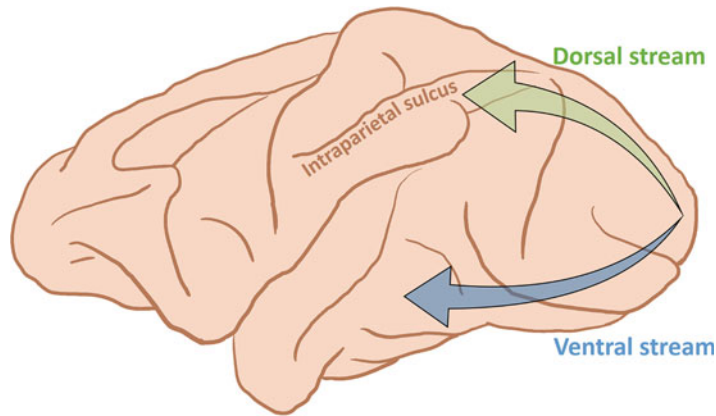
## LIP: A Dorsal Stream Region

An influential idea in cognitive neuroscience is that primates have at least two cortical visual processing streams that differ in both anatomy and function (e.g., Milner and Goodale 1995). Information on the patterns of light that hits the eyes is sent to the primary visual cortex in the occipital lobe at the back of the brain. Some of this information is then further processed in the ventral stream, going ventrally from the primary visual cortex to the temporal lobe. The ventral stream is important for object identification and has thus been dubbed the “what” stream. The dorsal stream, also originating in the primary visual cortex but ending in the parietal lobe, plays a role in representing spatial information and has therefore often been called the “where” stream, but has more recently been called the “how” stream because of its importance in action guidance (Fig. 1).

Spatial distortions from parietal damage have long been known. Holmes (1919), about a hundred years ago, described the symptoms of patients who suffered from gunshot wounds to the posterior and upper parts of the parietal lobe. These patients seemed unable to construct spatial representations from visual information; their eyes would randomly drift instead of purposefully scanning the scene, they would reach for an object in the completely wrong direction, and they would even directly walk into walls as if they had no idea of their position in space.

## Lateral Intraparietal Area

### ► Lateral Intraparietal Region (LIP)



**Lateral Intraparietal Region (LIP), Fig. 1** The primate visual system processes visual information along two processing streams. Both streams originate in the primary visual cortex. The ventral stream reaches the temporal

cortex, while the dorsal stream goes toward the parietal cortex. The lateral intraparietal region (*LIP*), a brain region near the endpoint of the dorsal stream, lies on the lateral bank of the intraparietal sulcus

Initially it was thought that an all-purpose spatial representation resided in the posterior parietal lobe. However, primates are capable of complex interactions with their environment. Complex action capabilities might require not just a single representation of space, but many specialized ways of representing where things are and how to potentially react to them. A monkey swinging from branch to branch presumably needs to have a neural system capable of calculating the direction and distance of the next branch relative to where she is looking, relative to where her hand is with which she intends to grasp the branch, and so on. Since the visual information is originally only available in a retinotopic frame of reference, where nearby neurons tend to respond to light falling on locations close to each other on the retina of the eye, these new spatial representations require the transformation of the original retinotopic space into so-called egocentric coordinate frames, where spatial locations of important things in the world are coded with reference to a part of the animal's own body, such as the eyes, head, hand, trunk, or mouth (Milner and Goodale 1995).

The main function of the parietal cortex in primates is often thought to be to carry out such transformations from sensory signals to a format more directly useful for motor output or action guidance (Cohen and Andersen 2002; Milner and

Goodale 1995; Rizzolatti et al. 1997). Within the intraparietal sulcus, several regions can be found, each of which might mainly encode locations in a reference frame centered on a particular part of the body, such as the head or eye (Cohen and Andersen 2002; Colby and Goldberg 1999). An eye-centered reference frame is obviously of use when deciding where to look next, and the lateral intraparietal region (*LIP*), a region high up in the dorsal visual stream, has been implicated in such eye movement guidance; several other roles of this region have also been proposed, including “higher” cognitive functions such as visual attention.

## Anatomy

As the name implies, the lateral intraparietal region lies on the lateral bank of the intraparietal sulcus (Andersen et al. 1985). The region has been heavily studied in the macaque monkey, but homologous regions are thought to exist in the human brain; human intraparietal regions IPS1 and IPS2 are likely candidates as these regions show various functional similarities with area *LIP* in monkeys (Silver and Kastner 2009).

*LIP* has sometimes been further subdivided into a ventral (*LIPv*) and a dorsal zone (*LIPd*) based on differences in architecture, connectivity,



and function (e.g., Chen et al. 2016; Lewis and Van Essen 2000; Webster et al. 1994). For example, LIPv has strong reciprocal connections to brain regions involved in visual motion processing, including area MT, while LIPd might be relatively more connected to particular regions of the ventral stream (Lewis and Van Essen 2000; Webster et al. 1994). Anatomical differences as well as potential different functional roles could indicate that LIPv and LIPd are two separable brain regions.

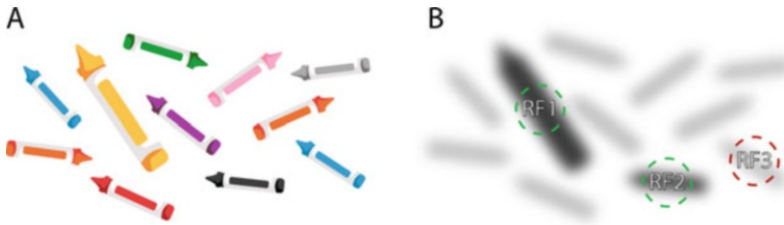
## Visual Orienting

Orienting was originally considered to be a non-specific reflex that involved turning the eyes, head, and ears (for animals whose ears prick up) to the direction of stimulation (Sokolov 1963). Orienting in primates might mainly rely on shifts in eye position, although orienting can more broadly be thought of as engaging with an outside source through coordinated overt bodily movements and covert attentional deployment for the purpose of information gathering. LIP is generally thought to play an important role in visual orienting, in particular visuospatial attention and saccadic eye movements (jerky eye movements that rapidly change the location of gaze), although the precise function of this brain region is still widely debated (see Bisley and Goldberg 2003, 2010; Colby and Goldberg 1999; Gottlieb et al. 1998).

LIP is well situated to guide orienting based on visual information. It has structural connections with several visual areas such as V2, V3, V4, and MT (Lewis and Van Essen 2000). It is also connected to areas implicated in oculomotor behavior such as the superior colliculus (SC; Ferraina et al. 2002; Field et al. 2008), the frontal eye fields (FEF; Lewis and Van Essen 2000; Ferraina et al. 2002), and the cerebellar oculomotor domains (Prevosto et al. 2010). LIP appears to mainly represent space in an eye-centered coordinate frame, useful for calculating where important things worth attending to and looking at are relative to the center of gaze (Cohen and Andersen 2002).

An LIP neuron might show light-sensitive, memory-related, and/or saccade-related activity, responding vigorously when a visual stimulus is shown in a particular location relative to the center of gaze, when no stimulus is currently shown in a particular location, but this location has to be memorized, or before, during, or after a monkey makes a saccadic eye movement to a particular location (Barash et al. 1991). A preferred spatial location of an LIP neuron can be referred to as the neuron's receptive field (more emphasis on visually evoked responses) or response field (less emphasis on visually evoked responses) or just simply the neuron's RF. Neurons in LIP can however transiently shift their spatial representations immediately preceding an intended saccadic eye movement, where a neuron might briefly code for a location not relative to the current center of gaze, but relative to the immediate future center of gaze were the saccadic eye movement is to be executed, a process known as remapping (Duhamel et al. 1992). LIP might thus be said to have the available machinery to represent space not just relative to current eye position, but also relative to the center of a "virtual eye." This predictive remapping might help with the integration of visual information across eye movements and contribute to the apparent stability of the visual world even when the eyes jump around a visual scene.

Although LIP neurons tend to be light-sensitive, in the sense that their activity generally increases when a visual stimulus appears in their RF, there is some indication that visually related activity might not primarily represent the visual properties of a viewed object. Instead, it might mainly indicate the priority assigned to a location and/or the object occupying that location; the activity of neurons within LIP as a whole could thus serve as a priority map (Balan and Gottlieb 2006; Bisley and Goldberg 2010), where visual stimuli in different locations are assigned different weights based on their salience, current task demands, as well as other factors such as long-term experience (Fig. 2). High priority might thus be assigned to an object in a particular location if it is visually striking (such as when viewing something bright among dark things or dark among



**Lateral Intraparietal Region (LIP), Fig. 2** Prioritizing visual information. Panel (a): In this hypothetical example, the task is to find the *black* crayon among several other crayons. Panel (b): A schematic depiction of a hypothetical priority map, where darker colors signify greater priority. As *black* is a behaviorally relevant feature in the visual search task shown in panel A, anything *black* in the original scene is assigned a high priority value. However, one crayon is noticeably different from all of the rest due to its larger size. As this object is visually salient even though it is not the searched-for object, it could also be assigned a relatively high priority; all things equal, something that stands out from the rest of the environment is worth exploring. If this object would fall within the RF of a particular LIP neuron (RF1), one might expect this neuron

to increase its activity, signifying high priority; the same is to be expected from a second LIP neuron whose RF lies in the location of the searched-for target color (RF2). However, a third LIP neuron – whose RF encompasses an inconspicuous object not directly relevant to the current task – might not become particularly active, signifying the low priority assigned to the object in this location (RF3). An object within a location assigned the highest priority, as represented by the activity of a population of LIP neurons, might then be selected to become the focus of attention as well as the target of an animal's saccadic eye movement. The original crayon images were designed by [Vexels.com](http://Vexels.com) and are used in the current images with the consent of [Vexels.com](http://Vexels.com)

bright things) or behaviorally relevant (such as when an object's visual features match those of a searched-for target). If LIP mainly serves the role of a priority map, LIP activity might neither primarily represent visual attention nor the intention to move the eyes, a subject of some debate. Instead, it could provide information on where important things might be found, information which can then be utilized to orient the eyes and attention to the most active location of this priority map (e.g., Bisley and Goldberg 2010).

Visual attention and eye movements are highly related, so that when something catches attention, it generally also catches the eye. It might therefore make sense to use a single common priority map both for attentional and oculomotor guidance. However, overt (eye movements) and covert (visual attention) visual orienting can be separated, such as when you refrain from rudely staring at a weird-looking person that you nonetheless watch from the corner of your eye. The two subdivisions of LIP, LIPd and LIPv, have been proposed to play different roles in attentional and oculomotor guidance, with LIPd activity being primarily related to the planning of saccadic eye movements to particular locations (overt visual orienting), while LIPv might take part in overt as

well as covert visual orienting (Liu et al. 2010). It has however also been proposed that LIPd is more dedicated to visual processing, while LIPv is more important for saccadic eye movements (Chen et al. 2016). The functional differences of LIPd and LIPv are still not well understood.

## Other Functions

Several studies on LIP muddy the waters when it comes to the precise function of this brain region, as LIP activity appears to be affected by several nonspatial factors that either modulate spatial representations of LIP neurons or are even independent of them (Gottlieb and Snyder 2010). For example, LIP neurons have been reported to be involved in numerical processing, as the activity of several LIP neurons systematically changes with the number of visual elements (Roitman et al. 2007). The activity of LIP neurons can also be affected by learned category membership, such as when a monkey is taught to treat several motion directions as members of two distinct motion categories with an arbitrary category boundary (Freedman and Assad 2009). Some LIP neurons can respond selectively to the shape of

visually presented objects (Serenio and Maunsell 1998; Sigurdardottir and Sheinberg 2015). They can become selective for color arbitrarily associated with a particular behavior (e.g., red means look left; green means look right), and this color selectivity can be separated from a neuron's preferences for saccadic eye movement direction (Toth and Assad 2002). There has also been a body of work looking at the role of LIP in decision-making (Gold and Shadlen 2007). Several other nonspatial factors also appear to affect LIP responses (for further discussion, see Gottlieb and Snyder 2010).

However, it is somewhat unclear to which extent LIP is actively involved in nonspatial tasks and to which extent nonspatial signals in LIP mainly support the region's role in visual orienting (Gottlieb and Snyder 2010). For example, it has been suggested that shape selectivity in LIP might support overt and covert visual orienting, where the shape of an object biases the eyes and attention in a particular direction either due to learning or because of inherent biases (Sigurdardottir and Sheinberg 2015). Surgically removing area LIP also does not prohibit the relearning of a task that requires monkeys to arbitrarily associate colors with actions, suggesting that at least some such arbitrary associations are not dependent on this region (Rushworth et al. 1997). Similarly, Katz et al. (2016) recently showed that while decision-related signals in LIP were strong, they apparently did not play a causal role in decision-making as inactivation of this region did not impair decision-making performance. Instead, silencing LIP neurons affected spatial selection and oculomotor behavior, consistent with this region's primary role in visual orienting.

## Conclusion

LIP is a high-level brain region somewhat far removed from purely sensory- and purely motor-related areas. It is therefore perhaps not surprising that LIP neurons show complex activity related to various aspects of sensation, cognition, and action. However, while LIP might well partake

in other functions, this region's importance for the guidance of overt and covert visual orienting is especially well established. LIP might serve the role of a priority map, where various bottom-up and top-down signals directly influence weights given to objects in different spatial locations, thus biasing where one looks and pays attention.

## Cross-References

- [Attention](#)
- [Decision-Making](#)
- [Dorsal Pathway](#)
- [Parietal Lobe](#)
- [Primates](#)
- [Saccadic Eye Movement](#)

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## Laterality (Handedness)

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## Synonyms

[Behavioral lateralization](#); [Cerebral asymmetry](#); [Hand preference](#)

## Definitions

*Laterality* is where one hemisphere exerts dominance over the other in the control of a particular behavior or function.

*Handedness* may be defined as the tendency to use one forelimb preferentially for a specific task.

## Introduction

In 1861, Paul Broca published the first paper that tied a cerebral asymmetry to a specific behavioral function and localized that function to a particular hemisphere of the human brain. By finding that “Broca’s area” in the left hemisphere controlled the ability to speak, a new area of research was initiated. Laterality is the condition wherein a function is controlled by a specific hemisphere of the brain. In Broca’s treatise, language is

“lateralized” to the left hemisphere. Human primates (*Homo sapiens*) have an unusually high population-level right-hand preference that is displayed across cultures (Hecaen and Ajuriaguerra 1964). This right-hand preference is highly correlated among fine manipulative tasks and tasks associated with hand/eye coordination (Seltzer et al. 1990). Many have hypothesized that speech and manipulative ability involve similar types of motor control whereby individual systems of muscles must be timed to excite and inhibit in a sequential manner (Kimura 1976). Understanding the progression of the relationship between motor control systems that serve manipulation and speech may best be achieved through the study of nonhuman primates. This is because they have more specialized neuroanatomy for motor control of the forelimb (Nudo and Masterton 1990; Nudo et al. 1995) and a morphological forelimb structure that permits greater mobility of the fingers (Napier 1980).

The primate hand and brain have undergone changes in structure that allow for enhanced neuromuscular control of the fingers. The progression from prehensile grasping to individuated finger movements is exhibited to varying degrees among primate species and offers an opportunity to examine how the hand may have led the brain in evolution (Preuschoft and Chivers 1993). A related aspect of hand/brain function is related to manual specialization wherein a particular hand is favored over the other for a particular task. *Handedness* may be defined as the tendency to use one forelimb preferentially for a specific task. The way in which the tendency is determined has involved using statistics to evaluate whether left- or right-hand usage has occurred significantly more than chance. The statistical procedures have generally utilized either standard scores (z-scores) or a handedness index (HI) (for a review of these approaches, see Hopkins 1999).

Handedness is generally seen to reflect an underlying cerebral lateralization or hemispheric specialization wherein the right hemisphere controls functions on the left side and the left hemisphere controls the right (Hopkins 2007). The lateralization or specialization of each hemisphere may represent evolutionary trends as hypothesized by MacNeilage (2007). This progression

mirrors the evolution of forelimb manipulative abilities and may also be related to the species feeding niche specializations. MacNeilage et al. (1987) believe that the rudimentary form of lateralization that is still evident in Prosimians and specifically in insectivorous vertical clingers and leapers involved a right hemisphere (left-hand) specialization for insect capture and a left hemisphere (right-hand) specialization for postural support. With speciation and pressure to expand the insectivore niche to include fruit or foods that require increased manipulative skill to remove the edible portions from the matrix in which they are embedded, a change in manual specialization was required. This change involved the left hemisphere (right hand) changing its specialization from postural support to manipulative skill and associated refinement in individuated finger movements and a precision type of grip. MacNeilage et al. (1987) proposed that this progression may be seen in the way in which anthropoid primates and especially old-world primates use their hands to forage for embedded food resources where the left hand retains its prehensile grasp on the food item and the right hand manipulates the husk or peel to reach the edible portions. Although there is good amount of evidence to support these ideas in the prosimian literature (for reviews see Ward et al. 1993; Watson and Hanbury 2007), the progression toward a right-hand manual specialization hypothesized among anthropoids is less consistent but becomes somewhat more consistent when hand preferences are interpreted in light of the behavioral task and when body posture is also taken into account (MacNeilage 2007).

Although many researchers support an evolutionary approach to the study of lateralization that predicts a continuity in behaviors tied to cerebral asymmetries within the order Primates, there are those who believe the human language represents a unique ability that differentiates *Homo sapiens* from the rest of the animal kingdom (Corballis 1991). It is proposed that the lateralization of speech seen in human language helps to magnify the associated right-handedness seen in the human population. Because a similar *population-level* trend is not seen in other primate species, this is taken as evidence against the gradual evolution of



primate handedness. McGrew and Marchant (1997) performed a meta-analysis on 241 published primate laterality studies and found that only captive chimpanzees displayed some degree of right-handedness that would begin to approximate the human condition. They also did not find any appreciable phyletic progression toward this right preference and argued against the validity of handedness data derived from captive populations.

Many of the inconsistencies noted in the old-world monkey literature are due to differences in the tasks used to evaluate handedness and whether postures were accounted for. For example, measures of hand preference have generally enlisted a simple food-reaching task that involved the primate reaching for food and then eating it. While this may provide a measure of lateralization related to simple food reaching, it may be the case that a different hand is used to hold the food while it is being consumed or perhaps the feeding task is bimanual with one hand holding food and the other extracting edible portions from the peel. In this sense it is sometimes difficult to assess handedness because the hands are perhaps being used for different elements of the feeding task. It has been demonstrated that factors such as reach posture (bipedal vs. quadrupedal), substrate (arboreal vs. terrestrial), type of grasp (prehensile vs. precision, bimanual vs. unimanual), food type, and size do influence the direction and strength of handedness (Meguerditchian et al. 2013). It is only through careful analyses utilizing multiple measures of hand use that we may reveal factors that may have promoted early forms of lateral preference. It could be the case that the gradualist approach hypothesized in the postural origin theory may be too general with respect to the transition to right-handedness in Anthropoid primates and that several species-specific factors may converge and result in a population-level trend.

## Cerebral Asymmetry

The search for anatomical asymmetries that are indicative of cerebral lateralization has focused on morphological or electrophysiological differences between the hemispheres. The finding that great

apes and humans share a larger area 44 (homologue to Broca's area) in the left hemisphere when compared with the right indicates that at least in chimpanzees and gorillas, a structural lateralization similar to the human condition exists (Cantalupo and Hopkins 2001). Like humans, chimpanzees and gorillas have demonstrated characteristics of symbolic language (Savage-Rumbaugh et al. 1986; Patterson and Linden 1981). Similar asymmetries have not been found in the brains of old-world monkeys, but other interesting facets related to communication have been identified. In a study of rhesus monkeys, metabolic activity was compared between the left and right hemisphere when either control sounds or species-specific monkey calls were played (Poremba et al. 2004). It was revealed that significantly greater metabolic activity occurred in the left superior temporal gyrus but only in response to the monkey calls rather than the control sounds. Rhesus monkeys do not have a similar structure to Broca's area, but these results indicate that there was perhaps a hemispheric specialization for interpreting sounds used in communication that could have preceded the vocal complexities associated with language.

Electrophysiological asymmetries in the hand representation of primary motor cortex (area 4) were correlated with hand preference in squirrel monkeys and involved larger surface area for hand movement and greater spatial complexity of the motor movement representations in the dominant hemisphere (Nudo et al. 1992). Squirrel monkeys do not have a population-level hand preference but the neural control asymmetries were consistent with the preferred hand of each animal tested.

Potential factors that could have preceded motor lateralization may be seen in non-primate species and generally involve lateralized differences in perceptual abilities or social behavior (for review see Rogers and Andrew 2002; Vallortigara 2006). Many studies in rodent, bird, reptile, and amphibian species have found population-level tendencies for pawedness, prey capture, social behaviors related to courtship, and aggression. After more than 150 years of study, much has been written about cerebral lateralized structures and functions, but few phyletic

comparisons reveal a simple evolutionary progression from sensory to motoric lateralization. What is apparent is that lateralized functions and associated cerebral asymmetries do exist and must confer an advantage to the animal in order to be selected for. It may be the case that these selection pressures function differently not only between species but also within individuals of the same species. How the human species became so rigidly lateralized for speech functions remains a valid question for research, but it is also important to understand the factors that influence lateralization in other species as well.

## Cross-References

- [Behavioral Lateralization](#)
- [Cerebral asymmetry](#)
- [Feeding Behavior](#)
- [Hand Preference](#)
- [Hemispheric Specialization](#)
- [Language](#)

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## Laterality Effect (Face Perception)

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Face recognition is an essential skill that in many species is associated with apparently specialized neurological and cognitive mechanisms. This chapter summarizes some of the behavioral and neuroscientific research on laterality effects in face perception, with a focus on face identity processing in humans and animals.

### Laterality Effects: Humans

Certain regions of the human ventral visual pathway, which plays a crucial role in visual recognition, tend to respond vigorously to particular types of visually presented objects, such as buildings, words (in literates), and faces. The most famous face-selective region is no doubt the fusiform face area (FFA) that tends to selectively respond to faces relative to other visual objects. The FFA might however act as a hub in a whole network of face-responsive areas. Two other well-known face-selective regions are the occipital face area (OFA) and the superior temporal sulcus (STS). As can be seen in Fig. 1, all three show a laterality effect with more pronounced face selectivity in the right hemisphere.

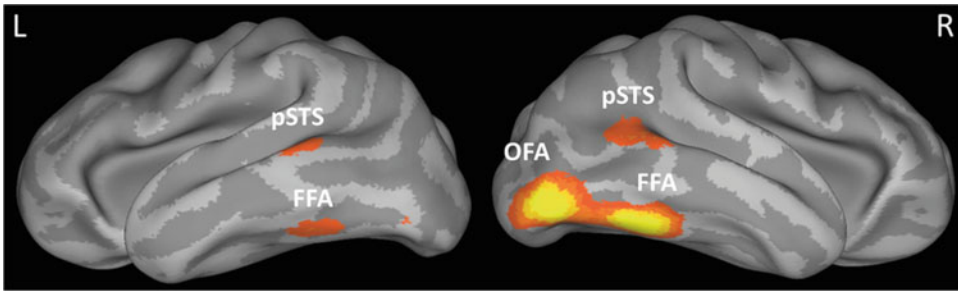
### Right-Hemisphere Dominance of Human Face Processing

Neuroimaging, electrophysiology, and behavioral studies all support the general advantage of the right hemisphere in face processing. The face-sensitive N170 event-related potential component is right-lateralized. People also tend to be faster at processing faces presented to the left visual field – which projects to the right hemisphere – compared to the right visual field. Similarly, when

shown chimeric human faces (Fig. 2) composed of either the left or right side of a picture of an original whole face, people are likely to perceive the left chimera rather than the right chimera as resembling the original. Interestingly, this might not extend to the perception of monkey faces, at least not for observers with limited exposure to monkeys, indicating that the laterality effect could be experience-dependent or, perhaps less likely, species-dependent (for the role of experience in visual object recognition, see, e.g., Sigurdardottir and Gauthier 2015). Tachistoscopic presentation of faces in split-brain patients has also confirmed the dominance of the right hemisphere for face recognition. Electrical stimulation of the right fusiform gyrus has been found to induce the conscious perception of faces, while stimulation of face-related regions in the left fusiform gyrus caused a nonface visual change, although this could be dependent on hemispheric dominance for language processing and/or handedness. Research has also shown that unilateral right damage can lead to prosopagnosia (facial recognition disorder), at least in right-handed individuals. There are a few reports of left-handed people with prosopagnosia with unilateral left damage, suggesting the possible role of handedness in face lateralization. However, face-selective regions in left-handed individuals still appear to be right-lateralized, with the exception of FFA that seems to be less lateralized or even left-lateralized in most left-handers.

### Origins of Hemispheric Differences

There is a debate on whether the general right hemisphere dominance for face processing is due to prespecified properties of the neural network (nature) or if it is experience-related and the network becomes specialized after repeated exposure or training (nurture). Unlike selectivity for some other object classes, face selectivity has a delayed developmental trajectory, where lateralized face-selective areas such as FFA, OFA, and STS are not consistently found in young children. It is possible that such a trajectory is predefined, but it could also be due to increased visual expertise with faces, in particular



**Laterality Effect (Face Perception), Fig. 1** Laterality of neural face processing in the human brain. The fusiform face area (FFA), occipital face area (OFA), and the posterior part of the superior temporal sulcus (pSTS) of the left (L) and right (R) hemispheres are shown. The yellow/

orange shows face selectivity, here defined as the contrast of faces vs. nonface objects. (The image is originally from Huang et al. (2014). The image is used according to a Creative Commons (CC BY) license. Copyright © 2014 Huang, Song, Li, Zhen, Yang and Liu)

Original face

Left chimera

Right chimera



**Laterality Effect (Face Perception), Fig. 2** Laterality effects in face perception have been measured by face chimeras. Here, the left and right parts of an original face (author HMS) were used to make two chimeric faces, one

from the left half-face image and one from the right. Humans and some animals tend to choose a left rather than a right chimera as being similar to an original full face

increased reliance on so-called configural processing (perceiving relations among features, such as where the eyes are relative to the nose, although the term might refer to a few distinct processes, see, e.g., Maurer et al. 2002) in which the right hemisphere might excel. The right lateralization of neural face processing has also been suggested to be influenced by competition during reading acquisition between neural representations of visually presented faces and words in the left hemisphere (language processing is generally left-lateralized). Consistent with this hypothesis, some research has indicated that the degree of face lateralization varies with literacy

(see, e.g., Dundas et al. 2013). The lateralization shift of the FFA in left-handers has also been suggested to be a result of reduced left hemisphere neural competition between faces and words. On the other hand, seemingly consistent with prespecified face perception mechanisms, right-lateralized face-selective neural responses have been reported in young infants well before reading acquisition. Nonetheless, depriving the right – but not the left – hemisphere of visual input during infancy selectively impairs later ability for configural processing of faces (specifically, sensitivity to spacing of facial features). Thus, laterality effects in face processing might be

driven by a mixture of predefined hemispheric biases and visual experience.

### Hemispheric Specialization

Although various studies have shown the dominance of the right hemisphere in face processing, the right and left hemispheres are likely both involved in face recognition but in different ways. The right hemisphere is superior at processing low spatial frequency information from faces, while the left hemisphere appears to be more specialized for processing high spatial frequencies. Related, while the right hemisphere is more involved in configural processing of faces, the left hemisphere might show superiority for featural or analytic processing of faces. When faces are inverted, judging their configuration becomes difficult, and this eliminates or reduces the right hemisphere advantage. These findings are in line with neuropsychological evidence, indicating that prosopagnosic patients, who tend to have right hemisphere lesions, might perform equally well when matching upright and inverted faces (no face inversion effect). Divided visual field methodology studies have also shown the superiority of the left hemisphere when feature-by-feature processing of faces was induced by task manipulation. For more information on laterality effects in human face perception, see, e.g., Gainotti (2013) and Júnior et al. (2014).

### Laterality Effects: Animals

The visual system of nonhuman primates shows many similarities with that of humans. The Rhesus macaque system is best documented, but visual face processing in other primates, other mammals such as sheep, and even other non-mammalian species, has been studied. For reviews on face processing in animals, see, e.g., Kendrick (2006), Leopold and Rhodes (2010), Parr (2011), and Tate et al. (2006).

#### Primates

Chimpanzees, like humans, can quickly identify individual conspecifics by their faces. Chimpanzee face recognition is impaired by distortion of the configuration of faces. Like

humans, chimpanzees find it more difficult to recognize inverted compared to upright conspecific and human faces (face inversion effect), often thought to be due to disruption of configural processing which in humans is right-lateralized. Accordingly, some evidence supports that face processing in chimpanzees is right-lateralized. For example, when chimeric chimpanzee or human faces were made by vertically flipping a half-face around the midline (see example in Fig. 2), chimpanzees showed a tendency to choose a left rather than right face-half chimera as being more similar to an original centrally presented whole face. This probable right hemisphere advantage might increase with age and/or experience with faces. Accordingly, configural face processing in chimps might be experience-dependent, as no reliable face inversion effect in chimps was found for the faces of an unfamiliar species (brown capuchins), and their configural processing also appears to be greater for chimpanzee faces than human faces. It should be noted that chimpanzees tend to be right-handed, and handedness could possibly be related to brain asymmetries in face processing. There are however some apparently conflicting results, where chimps were equally likely to match a left and right chimera to an original whole face.

Rhesus macaques can also distinguish between conspecifics based on their faces, and a whole network of interconnected face-responsive regions has been mapped in the macaque brain. Some behavioral studies have reported a lack of lateralization of face processing in macaques. For example, a study using chimeric faces (Fig. 2) revealed that macaques failed to show asymmetry for face matching with either monkey or human faces. Possibly related, a face inversion effect in macaques has not consistently been found (although some studies do report such an effect), which has been interpreted in favor of less reliance on configural – and presumably right-lateralized – processing as opposed to featural processing. Consistent with this, even infant macaques with no previous exposure to faces can discriminate between faces based on both facial features and their spacing or configuration. Early work on split-brain Rhesus



macaques also found no lateralization for learning to discriminate photographs of monkeys. fMRI studies have also reported bilateral face-selective activity in the monkey temporal cortex, although some do report more extensive right-hemispheric activation for faces. There are also some split-brain studies that support right-hemisphere superiority in macaques, particularly for upright as opposed to inverted faces. To complicate matters even further, early single-cell recordings in macaques reported a more abundant population of face-selective neurons in the left compared to right temporal cortex, hinting that monkeys and humans might use a qualitatively similar mechanism for face processing with a different direction of cerebral asymmetry. Left hemisphere lateralization for learning to discriminate monkey faces has also been reported specifically for female macaques. The lateralization of face processing in other monkey species has not been extensively studied, although stronger activation in the right temporal cortex in vervets has been reported for the passive viewing of faces in comparison to nonface objects.

### Nonprimates

Some nonprimate species are reported to have right-lateralized visual face processing. Domestic dogs can identify the face of their owner, and many dogs discriminate between the face or head of their owner and that of another familiar person. Dogs show greater activation in a putative dog face area of the right temporal cortex when observing faces of dogs or humans as compared to nonface objects. Sheep also show greater activity in the right compared to left inferior temporal cortex when viewing upright faces but not inverted faces. Sheep also recognize conspecific faces more by the left visual field (right hemisphere advantage), and this effect is stronger for familiar faces. Interestingly, while sheep can discriminate between human faces, they show a smaller inversion effect for human faces than seen with sheep faces and in general show little indication of configurally processing human faces. Sheep also have no left visual field advantage or even a slight right field advantage for human faces. This might suggest a role of expertise for developing a right brain hemisphere advantage

for the configural processing of faces but could also be consistent with an innate species-specific mechanism. Laterality effects in face processing have rarely been studied in nonmammals, but there are some studies that provide support. For example, the right hemisphere of chicks appears to be better equipped for visually processing information relevant to the recognition of other chicks, and several species of teleost fish are reported to mainly use right-side brain structures when viewing conspecifics.

### Summary

To summarize, while the lateralization of face processing in nonhuman primates is somewhat controversial, humans appear to share right hemisphere lateralization for face processing with animals as diverse as dogs and sheep and possibly even some birds and fish. Although by no means conclusive, these results could indicate that some face processing capabilities might be shared among mammals, and some researchers have even suggested that lateralization of the visual analysis of stimuli provided by conspecifics is shared by all vertebrates (Sovrano et al. 1999).

### Cross-References

- ▶ [Canine Cognition](#)
- ▶ [Domain Specificity](#)
- ▶ [Face Processing in Different Brain Areas and Face Recognition](#)
- ▶ [Face-Selective Neurons: Comparative Perspectives](#)
- ▶ [Filial Imprinting](#)
- ▶ [Hemispheric Specialization](#)
- ▶ [Hormones and Face Preferences](#)
- ▶ [Imprinting](#)
- ▶ [Inversion Effects](#)
- ▶ [Laterality \(Handedness\)](#)
- ▶ [Mirror Self-Recognition](#)
- ▶ [Nature versus Nurture](#)
- ▶ [Primate Cognition](#)
- ▶ [Primates](#)

- Prosopagnosia
- Temporal Lobe
- Visual Perception
- Visual Recognition in Birds
- Visual Self-Recognition

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## Lateralization

- Equine Sensory Systems

## Latrine

- Mustelidae Navigation

## Laurie Santos

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Laurie Santos is a cognitive psychologist who studies the origins of human cognition. Specifically, Dr. Santos compares human cognitive capacities with those of nonhuman primates and domesticated dogs. She is broadly interested in the question of what makes human cognition unique.

Dr. Santos began studying human psychology from a comparative perspective as an undergraduate student at Harvard. She joined the lab of then Harvard professor Dr. Marc Hauser, where she began studying two species of nonhuman primates: cotton-top tamarins (*Saguinus oedipus*) at Harvard and rhesus monkeys (*Macaca mulatta*) living at the Cayo Santiago Field Station in Puerto Rico. After graduating from Harvard in 1997, Dr. Santos continued studying at Harvard with Dr. Hauser as a graduate student. Her PhD work explored how monkeys represent different kinds of objects. Many developmental psychologists have argued that human learners have mechanisms that allow them to focus their attention on conceptually relevant perceptual inputs during early learning (see reviews in Santos and Caramazza 2002). Dr. Santos's PhD work tested whether nonhuman primates share these domain-specific categorization biases. To do so, she systematically contrasted primates' knowledge of

two different domains of objects – foods (Santos et al. 2001) and tools (Santos et al. 2005). Her work on this topic revealed important similarities in the way that human children and primates reason about different kinds of objects, suggesting that similar (possibly evolutionarily ancient) domain-specific learning mechanisms might be at work across these different populations.

After completing her Ph.D. in 2002, Dr. Santos began a faculty position at Yale University. She set up a laboratory of captive brown capuchin monkeys (*Cebus apella*) and also continued the work she began as an undergraduate working with rhesus macaques at Cayo Santiago. While at Yale University, she began a set of studies testing the nature of primate object cognition and whether primates share human-like representations of object. Over the past few decades, developmental psychologists have learned a great deal about the “core knowledge” abilities that human infants use to represent objects and their motions (see review in Santos 2004). Dr. Santos and her students began testing whether primates shared human infants’ core object reasoning capacities, exploring whether nonhuman primates, like human infants, make accurate predictions about objects and the way they behave. Her early work revealed that primates seem to represent objects in much the same way as human infants. She and her students have shown that adult primates recognize that objects continue to exist when occluded and trace continuous paths in space and time (see Santos 2004 for a review). Her work suggests that nonhuman primate may reason about physical objects in much the same way as human infants; specifically, primates may also represent objects in terms of Dr. Elizabeth Spelke’s principles of continuity, cohesion, and solidity (see Santos 2004).

In addition to making discoveries about primates’ understanding of the physical world, Dr. Santos’s research has also provided important insight into what primates know about the social world. One of the hallmarks of human cognition is our species’ ability to reason about the minds of other individuals, a capacity commonly referred to as a theory of mind (ToM). Although developmental studies have revealed much about the

ontogeny of our ToM abilities, there is still much controversy about the evolution of ToM capacities and the question of whether primates share human-like mechanisms for understanding other minds (see review in Drayton and Santos 2016). Dr. Santos and her students have discovered that primates represent some – but not all – of the psychological states of others (see reviews in Drayton and Santos 2016; Martin and Santos 2016). Specifically, she and her students have found that monkeys recognize what others see, hear, know, and intend but fail to represent others’ beliefs. Dr. Santos’s current work is now focused on better understanding these limitations on primates’ social-cognitive capacities (see review in Martin and Santos 2016).

Dr. Santos is also known for her work on what some have referred to as “monkeynomics” – studying the origins of human economic biases in non-human primates. Specifically, she and her colleagues have gained important insight into the evolutionary origins of some of our species’ irrationalities and economic biases. Dr. Santos’s work discovered that primates share an impressive number of human-like irrational biases. She and her students discovered that monkeys share a human tendency to “rationalize” choices (Egan et al. 2007). She has also discovered that monkeys exhibit many of the same economic biases as humans (see reviews in Lakshminaryanan and Santos 2012). After developing a “token economy” method for testing monkeys’ economic decisions, she and her students found that capuchins frame their decisions in terms of gains and losses and tend to show loss aversion (e.g., Lakshminaryanan et al. 2011). Overall, Dr. Santos’s work has shown that nonhumans show many of the same cognitive biases as humans.

There is one domain, however, in which Dr. Santos has begun to discover that humans may be uniquely irrational – the domain of *social irrationalities*. Classic work in social psychology has shown that humans have the tendency to automatically copy the actions, preferences, and ideas of others. This tendency is useful when others’ ideas and actions are effective but leads us astray when others behave inefficiently or have incorrect ideas. Dr. Santos’s ongoing work is beginning to

show that primates may not have this same tendency to copy others' mistaken actions and beliefs. She has found that rhesus monkeys are not affected by others' mistaken beliefs in the same way as humans (see Martin and Santos 2016). She has also discovered that capuchin monkeys do not fail prey to "pricing biases," the tendency to think that higher priced goods – ones that others like – are more valuable (Catapano et al. 2014). These new results suggest that humans may be unique among primates in our tendency to irrationally copy the unwise ideas and preferences of others.

To better test the origins of our human "social irrationalities," Dr. Santos and her students have recently begun testing a different nonhuman species that may be more attuned to others' social information than primates: *domesticated dogs*. During domestication, dogs were required to learn from humans in some of the same ways as human children learn from their elders. Dr. Santos has thus begun using dogs as an important model for studying the role that social learning plays in the development of both the smart and less smart aspects of human cognition. In December of 2013, Dr. Santos launched the Canine Cognition Center at Yale, a new facility aimed at testing how dogs learn from other social agents, as well as other questions in canine cognition. Using this new canine cognition approach, her lab is currently pursuing new studies aimed at providing insight into the origins of human pedagogy and cultural learning more broadly.

Dr. Santos and her work have been featured in numerous media outlets, such as *The New York Times*, *The Wall Street Journal*, *The Economist*, and *The New Yorker*. She has won numerous awards for science, teaching, and mentorship. She was awarded the Stanton Prize from the Society for Philosophy and Psychology for outstanding contributions to interdisciplinary research. She was named one of Popular Science Magazine's "Brilliant 10," and a TIME magazine "Leading Campus Celebrity." Her TED Talk has well over a million views. In 2016, Dr. Santos was named Head of Silliman College at Yale.

## Cross-References

- Canine Cognition
- Categorization
- Cognition
- Cognitive Bias
- Comparative Cognition
- Comparative Psychology
- Learning
- Primate Cognition
- Primates
- Social Learning
- Theory of Mind
- Tool Use

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## Law of Effect

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### Synonyms

Associative learning; Operant conditioning; Reinforcement

### Definition

The Law of Effect is one of the basic laws of learning formulated by Thorndike. It states that a behavior followed by appetitive consequences will tend to be repeated in the future.

### Introduction

Edward Lee Thorndike published an experimental work in 1898 that not much later was explicitly defined as the Law of Effect, as Thorndike stated in his book *Animal Intelligence* (Thorndike 1898, 1911). In this work, Thorndike addressed three relevant topics in learning: the comparative role of learning between humans and other animals, the experimental methods employed to investigate similitudes and differences in behavior between species, and, finally, the Law of Effect (Lattal 1998). All these topics were focused outside the anecdotic method for animal reasoning, as Thorndike effusively defended.

The formulation of the explicit Law of Effect could be seen as a legacy from Darwin's evolution theory (Postman 1947). Thorndike was also influenced by Spencer-Bain's theory, in terms

that the incoming pleasure benefits the animals and they are going to try to achieve it constantly. *The Principles of Psychology* by William James were also relevant for Thorndike's work.

At first, Thorndike understood the Law of Effect in a double view: appetitive outcomes enhance behavior, and aversive ones decrease the frequency of the contingent conduct. But from the data of his experiments with different species, results led to think that the effect of reward and punishment were not exactly equivalent, thus having a different nature (Postman 1947).

### The Origin: The Puzzle Boxes

Thorndike modeled the Law of Effect with his famous experimental series about how several cats escaped from boxes designed to keep the animals inside. This apparatus had different mechanisms that the cats had to trigger if they wanted to escape. In his studies, Thorndike measured how fast the animals escaped and how the reaction time to scape decreased if an appetitive reinforcement was waiting out the box. Puzzle boxes were handmade by Thorndike, and each had a different way to scape. Pulling or pressing one or several mechanisms had the release of the animal from the box as a result. Cats seemed to find the way to scape, following a trial-and-error process. Thorndike could draw different patterns of reaction time to escape, trial by trial and for each subject.

The Law of Effect appeared when all the empirical data from the puzzle boxes were combined. At the same time, Thorndike formulated the Law of Exercise: as more connections are established between the behavior and the pleasant outcome, the stronger the behavior gets. However, after his experiments, the Law of Exercise was discarded, and Thorndike made the Law of Effect protagonist (Postman 1947). The empirical evidence, mainly with cats, dogs, and chicks, led Thorndike to think that the simple practice of a habit was not enough to establish an association. His experimental subjects showed that certain effects or consequences were required to strengthen a behavior (Lattal 1998).



## Implications

The Law of Effect is considered the prelude and the basis of operant conditioning and the subsequent reinforcement theory. Reinforcement is the formal term to designate the consequences of a specific behavior with the aim to strengthen or diminish its frequency. With this law, Thorndike opened a formal discussion about how motivational drives could encourage certain behaviors in animals. At this respect, subsequent theories have discussed the role of concepts such as instinct, hedonistic variables, or purposes in the path to understand the Law of Effect as a motor of behavior.

In the applied fields, educational and clinical matters have widely used the reinforcement theory and the Law of Effect. Additionally, the Law of Effect is also the central issue in animal training. It should be pointed that reward and punishment have been fundamental in educational disciplines, being the central issue for behaviorism and preluding Watson and Skinner's subsequent work (Skinner 1969).

## Cross-References

- [Associative Learning](#)
- [Behaviorism](#)
- [Operant Conditioning](#)

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## Law of Independent Assortment

- [Assortment](#)

## Law of the First Wave Front

- [Precedence Effect](#)

## Learned Affordances

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Psychologist James J. Gibson introduced the term affordance in his 1977 chapter “The theory of affordances” and defined it as all action possibilities latent in the environment (Gibson, 1977). Based on Gestalt theories, affordance theory states that the world is perceived not only in terms of object shapes and spatial relationships but also in terms of the possibilities of objects for action.

Objects generally have affordability. The affordance of an object is what one can do with it. The affordance of a static door knob is something that one can hang things on. But the affordance of the door knob changes, if one sees a person turning the door knob. Now the affordance of the door knob is that it is something that turns. Seeing the person pull the door knob after turning it changes its affordances and that of the door. The closed door has limited affordance but once the door knob is pulled and the door is opened the door now provides a new kind of affordance. The door knob now allows the door to be moved in an arc along one vertical edge towards the observer and that movement provides a space through which one can walk. The new affordances allow one to learn that the

door knob turns to the right, that it can then be pulled, that pulling it causes the door to pivot along the right edge exposing an opening through which one can pass. And all of that occurred with minimal reference to the demonstrator. Thus, one does not need to refer to the observer's behavior or to use the term imitation (see section on imitation) to explain how, after observing a demonstration, the observer knows to turn the door knob and pull the door open to pass through to the other side.

In a similar way the observation of a demonstrator rat, for example, pressing a lever can change the affordance of the environment seen by an observer. Observing a lever on an operant panel is likely to provide limited affordance but if one can see another animal pressing the lever, it changes the environmental affordance of the lever from a stationary object to an object that can be pressed downward and that returns by itself. Thus seeing another animal press the lever changes the affordance of the lever. That change in the affordance of the lever may change the probability that the observer will press the lever. Thus, affordance learning is related to stimulus enhancement (see entry on local/stimulus enhancement) in the sense that with stimulus enhancement, the movement of the lever draws the observer's attention to the lever. But affordance learning also implies that the observer can learn about the action of the lever. Thus, the action of the demonstrator changes the affordance of the lever and that change may lead to an increase in the probability that the observer would press the lever but it would not be considered imitation in the sense that the observer had learned about the behavior of the demonstrator through observation.

Affordance learning is related to emulation (see the section of emulation) in the sense that the observation of a demonstrator acting on an object may change the affordance of that object. In the case of emulation, the change in affordance is associated with the outcome obtained by the demonstrator, and if it acts to motivate the observer to obtain the outcome, it may cause the observer to emulate an action that leads to the same result. Once again, although the observer's behavior leads to the same result as

that of the demonstrator, it would not be considered imitation (see Zentall 2012).

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## Learned Helplessness

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The phrase “Learned Helplessness” refers sometimes to a trauma-based empirical phenomenon, sometimes to a cognitive theory about the mechanisms underlying the empirical phenomenon, and sometimes to both at the same time. The empirical phenomenon and the elements of the proposed cognitive mechanism were first introduced by Overmier and Seligman (1967). The basic phenomenon seen in their dogs was a dramatic proactive interference with making and learning coping behaviors, primarily escape behavior, observed a day after having been exposed to 60 unpredictable and uncontrollable 5-sec electric footshocks distributed over an hour. The Learned Helplessness had three features: behavioral, the lack of behavioral coping efforts noted above; associative, a failure to learn the escape response even if they made an escape; and emotional, an apparent passivity to the shocks. Seligman and Maier (1967), in an experiment begun with Overmier (see authors' footnote), showed that the uncontrollability of the shocks was a critical causal feature for the induction of the Learned Helplessness by using the

so-called “triadic design” paradigm that compared three groups: one group (the Master group) received 60 trials with electric footshocks but was able to escape from or avoid any of the footshocks; a second group (the Yoked group) that was exposed to the same number, duration, and intensity of electric footshocks as experienced by the Master group; and a third group (Normal) that was exposed to the shock apparatus for the same session length but received no shocks. When tested in a second phase 24 h later for their ability to escape in a new apparatus, the Master and Normal groups reliably performed well, while the Yoked group that had experienced the uncontrollable footshocks generally failed to escape at all – they seemed helpless. The degree and duration of this interference is related to the number, duration, and spacing of the trauma experience(s) and can last up to months (Seligman and Groves 1970), and the individual aversive events that make up the trauma cannot be too short (e.g., not less than 1–2 sec) no matter how numerous if one is to produce the Learned Helplessness effect (Overmier and Seligman 1967).

Most are familiar with “Learned Helplessness” which has been cited or invoked in texts more than 3000 times since its introduction and more than 50 times in 2016 according to PsycINFO. Some whole journal issues have been devoted to it. So why has Learned Helplessness remained in the research spotlight? We offer four reasons.

First, the observed phenomenon in the initial experiments was quite dramatic. Induced “helpless” animals would in phase 2 passively endure a series of minute-long continuous intense footshocks instead of trying to escape. This led to many of follow-up experiments (see review by Overmier and Lolordo 1998) using a number of vertebrate species including humans, fish, mice, and rats and other non-rodent species such as birds and even insects in variety of induction and assessment environments with surprisingly consistent proactive interference results. That is, it was a pretty reliable general phenomenon. Second, “Learned Helplessness” consisted of a syndrome of effects from the first three reported in the initial report of behavioral deficit, a cognitive/learning deficit, and an emotional deficit

(anhedonia) to several other less discussed features of the syndrome such as depletions of CNS neurotransmitters (e.g., Anisman et al. 1980), immunosuppression (Laudenslager et al. 1983), enhanced susceptibility to cancer tumor growth (Sklar and Anisman 1979), pain analgesia (Drugan and Maier 1983), anorexia and hypersensitive taste finickiness (Dess et al. 1988), and gastric ulcer (Overmier and Murison 2000). Third, Learned Helplessness became an animal model for testing for antidepressant drugs (e.g., Katz and Sibel 1982). Fourth and most importantly, Seligman (1974) hypothesized that Learned Helplessness in animals closely paralleled reactive depression in humans and that the further study of Learned Helplessness in animals and humans would yield insights into the behavioral, cognitive, and physiological mechanisms of depression. Shortly thereafter, Seligman (1975), in a popular book, extended the application of the presumed cognitive construct underlying Learned Helplessness to a wide variety of other dysphoric psychological phenomena affecting children, adults, and the aged. As Learned Helplessness theory was applied to human dysfunctions, it needed to be enriched with reference to human cognitions and attributions that could be studied (Abramson et al. 1978), but in doing so, it eliminated any *direct* causal chain between specific experiences and the resultant state of Learned Helplessness (see Overmier 1988).

Several reviews of the parallels between Learned Helplessness syndrome and human depressive psychopathology appeared (e.g., Overmier and Hellhammer 1988), but another by Foa et al. (1992) focused on parallels between Learned Helplessness and post-traumatic stress disorder (PTSD) and argued that Learned Helplessness was better as a model of PTSD. Indeed, some parallels to PTSD do seem more appropriate. A result has been new papers exploring Learned Helplessness as an animal model of PTSD (e.g., Koba et al. 2001). Why didn't Seligman initially link it to PTSD? For starters, PTSD was not a recognized diagnostic entity at the time. Further, of course, PTSD has diagnostic features overlapping with depression. But we note that many of the diagnostic features for PTSD are simply not

accessible in animals (e.g., reexperiencing the trauma via flashbacks and reportable nightmares, impaired concentration).

Many of the important proactive effects of Learned Helplessness inducing trauma have been linked to the uncontrollability of the trauma elements. Indeed, as noted, this became part of the definitional nexus for Learned Helplessness. It was certainly what Overmier and Seligman hypothesized in their 1967 paper, and it was what Seligman and Maier tested in their paper.

Mineka and Kihlstrom (1978) argued that dimensions of uncontrollability and unpredictability of events were separate contributory features that induce experimental neuroses. In that line, Overmier and Wielkiewicz (1983) argued that unpredictability of traumatic events is also an important feature for Learned Helplessness induction and has separable – albeit less dramatic – effects from uncontrollability and more specifically that the uncontrollability as one dimension contributed to the behavioral deficit, while unpredictability as an independent dimension contributed to the cognitive/associative/learning deficit of the Learned Helplessness syndrome. Dess et al. (1983) did an interesting confirmatory experiment that showed different temporal loci of effects of unpredictability and uncontrollability on the stressfulness of trauma experiences, both immediate and future ones.

Concurrent with the basic behavioral studies on Learned Helplessness, there was a parallel line of neuroscience analyses of the brain mechanisms that might underlie Learned Helplessness. Already briefly mentioned above were efforts to find parallels between the behavior and CNS neurotransmitter states and efforts to link findings to psychopharmacological treatments. A promising line of research from the Maier-Watkins laboratory on the neural basis of Learned Helplessness focused much research on the pain perception and the involved neural pathways after experiencing uncontrollable shocks. Special attention was given to the resulting activation of the dorsal raphe nucleus, and this culminated in recent work on the moderating role of the medial prefrontal cortex on the dorsal raphe after experiencing escapable – but not inescapable – shocks

(Maier 2015). This new neuroscience work suggests that the *original theory* of Learned Helplessness was wrong in hypothesizing that when events are uncontrollable and unpredictable that organisms learn that their actions are useless and thus they become helpless. Rather, the neuroscience data as reviewed suggest that helplessness is the direct primary result of an activated dorsal raphe and that experiencing controllable and predictable events and learning to control and to predict them are encoded in the medial prefrontal area and suppress the dorsal raphe output. This neuroscience data is exactly congruent with an earlier behavioral hypothesis (Minor et al. 1991) challenging the original Learned Helplessness concept and recharacterizing the nature of the empirical syndrome.

Preventing and overcoming Learned Helplessness is a topic that flows naturally from discovery and elaboration of the syndrome because of its likely important implications for human dysfunction and psychopathology. An understanding of Learned Helplessness should lead investigators to potential new approaches to therapy, prevention, and resilience.

First in this line of investigation, Seligman and Maier (1967) provided evidence that interference of Learned Helplessness was preventable by pretraining the dogs to learn that shock termination was contingent upon responding. Second, Seligman et al. (1968) highlighted the critical role of “taking back control in the face of adversity” by having the dogs guided (forced) to make a few escape response to terminate shock in the test after being previously exposed to inescapable and uncontrollable traumatic shock. This “putting through therapy” was successful in overcoming the otherwise manifested Learned Helplessness. Third, “therapeutic” action of electroconvulsive shocks was demonstrated in dogs (Dorworth and Overmier 1977) exposed to Learned Helplessness. Fourth, using rats as subjects, cessation conditioning (i.e., signaling the end of inescapable shocks) in the induction phase prevented the development of the interference effect of Learned Helplessness (Minor et al. 1990). Fifth, long-term physical activity prevented one the debilitating neurochemical depletion effects of Learned

Helplessness in rats as measured by an attenuation of 5-HT neural activity in the DRN that is thought to play a key role in the expression of Learned Helplessness (Greenwood et al. 2003). Sixth, group housing of mice in an enriched environment wherein the rats had opportunities for play and were spontaneously more active also minimized the negative impact of induced Learned Helplessness in comparison to mice group-housed in an impoverished environment (Chourbaji et al. 2005); the presumed mechanism for this was by supposedly improving physiological moderators of stress such as corticosterone levels among myriad others. Seventh, young rats handled during a 3-week period exhibited fewer negative consequences of Learned Helplessness when tested in adulthood, although no specific mechanism was identified (Costela et al. 1995). This could well be of practical value in child-rearing, although the effects of early handling/maternal separation are complex. Eighth, the efficacy of different pharmacological treatments has been established in many studies and continues to be of great interest (e.g., Takamori et al. 2001). Some of these findings likely have practical value, and all have heuristic value for further researches on Learned Helplessness.

Of course, no line of research is without at least some potential shortcomings. Learned Helplessness has been widely employed as an animal model for understanding mechanisms of depression. However, it is noteworthy that sex differences in animal models of psychopathology may lead us to question the applicability to men and women. Notably, Dalla et al. (2008) suggested that Learned Helplessness involves sex-specific behavioral effects in rats. The authors observed that the female rats initially exposed to uncontrollable electrical shocks did not show impairment in learning to escape on a subsequent escape task in comparison to male rats that were markedly impaired and did not learn to escape on this novel task. On the other hand, other researchers have found that Learned Helplessness can be induced in both males and females, although estrous state modulates its severity (Jenkins et al. 2001). Although this question of sex differences has not been a major focus of interest so far, it

clearly calls for more replications and investigations before drawing any firm conclusions; we believe that it deserves some attention in the future to confirm that Learned Helplessness is a valid animal model of depression, PTSD, and dysphoria relevant for both men and women.

The case of Learned Helplessness is an intriguing one. It emerged from early animal basic science experiments seeking to test aspects of Mowrer's theory of avoidance learning and led to possible applications to humans and therapeutic treatments or immunizations that increase the resilience and coping by humans. It illustrates well how at the outset, one cannot know where basic researches will lead nor their likely future values. In the course of experiments on Learned Helplessness, the field discovered more about behavior, learning, stress, ulcers, pain mechanisms, steroids, opioids, neurotransmitters, and regional processing interactions in the brain and probably about depression, PTSD, and dysphoria. It is still an ongoing story to which new researchers will continue to contribute and more new discoveries will emerge.

## Cross-References

- [Avoidance](#)
- [Classical Conditioning](#)
- [Escape Response](#)
- [J Bruce Overmier](#)

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## Learning

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## Synonyms

Discovery; Enlightenment; Finding; Finding out;  
Instruction; Knowing; Mastering; Schooling;  
Searching; Studying; Training; Understanding

Let us begin humbly: It is very hard, perhaps even impossible, to define learning *strictly*, in a conclusive, perfectly clear and precise way that specifies *all* the necessary and sufficient conditions (constitutive properties or essential attributes) for something to truly or really *be* learning and pleases most psychologists. As Bolles (1979) put it:

The big question—What is the fundamental nature of the learning process?—is as unsettled today as it has ever been. There is, however, less concern today than there used to be about this ultimate question. One reason for this loss of concern may be a growing skepticism about whether the question can ever be answered. A second and perhaps more important reason is that, even though there is little agreement about the basic *processes* of learning, a good agreement has grown about the *procedures* that produce learning. The procedures are relatively clear and useful, whereas the processes remain uncertain and rather conjectural. (p. 137)

This “big question” remains unsettled today, as others have admitted. Catania (2013) put it thus: “From the start, we must face the fact that we won’t be able to define learning. There are no satisfactory definitions” (p. 2). Haselgrove (2016) expressed a similar sentiment: “... it turns out to be relatively difficult to pin down an entirely satisfactory definition of the phenomenon” (p. 1). Mazur (2017) was no less humble: “... even specialists have difficulty defining the term *learning* precisely” (p. 2).

I will be equally humble and not try to give a strict definition either, but seek something far less hubristic, but this does not mean any less concern

over the nature of learning, despite reasonable skepticism about ever settling it. I read Catania’s reassuring defiance in the above quotation, “we won’t let that stop us,” as an advice not to let such skepticism intimidate us into lessening our concern over the nature of learning. We can still *do our best* to understand it as much as possible, even if only in an ever-closer but never final asymptotic approach of sorts. Who knows? We could find valuable clues along the way. Besides, there have been advances since Bolles’ book, a few of which I will mention later, which might illuminate the search.

It is common to speak of “the definition of learning,” but all proposals in this regard are too rough, preliminary, and tentative to deserve the name of “definitions,” as this term traditionally connotes all-too-lofty ideals of definiteness, clarity, and precision. At best, they are *working ideas* or *notions* of learning, as I will call them here. As such, it is wiser to take them all as open-ended and revisable.

In sum, instead of giving a definition of learning as such, I will engage in a standard philosophical and scientific task known as *historical-conceptual analysis*, but it will just be the very beginning of only a possible analysis. Many others are possible. Mine will be very far from being exhaustive, conclusive, perfectly clear and precise, or even simple. It will only take a few steps into one possible path or, rather, multiple thorny, convoluted paths crisscrossing in myriad dimensions. This entry, then, will only continue the search of the nature of learning, leaving it unfinished. If I could add a subtitle, the full title of this entry would be “Learning: Continuing the Search for Its Nature.” The search is likely endless, but, as is often the case, what matters is the adventure itself, more than its ending. Let us thus press onward into what may well be a fool’s errand, but undaunted by this possibility, inspired by Captain Kirk’s reaction in this dialogue from the *Star Trek* movie *Generations*:

**Kirk:** I take it the odds are against us and the situation is grim.

**Picard:** You could say that.

**Kirk:** ... Sounds like fun!

I will first summarize ordinary-English meanings of the term **learning**, beginning with its etymology and then fading in into modern meanings, ordinary and more technical in psychology. The second section presents how I view the current situation in discussions about the learning notion in psychology. The last section is the bulk of the entry, where I discuss the family of learning notions I see as the dominant one in the psychology of learning, giving possible reasons why that is the case but ending with a preference for notions that are more encompassing.

### Ordinary-English Meanings

The term's etymology gives some clues about the nature of learning, even if too vaguely. According to Skeat (1910, p. 334), for instance, the word "learning" is a derivation of "learn," which appeared in Middle English (roughly between 1200 and 1460) as "lernen," from the Anglo-Saxon "leornian" (between about 400 and 1150) and the Old German "linōn" (between about 700 and 1100), both meaning "to learn." Its Teutonic type "leisan," or "to trace out," the principal part of which, "leis," occurs in Gothic with the meaning "I know" in the sense of "I have found out." The Online Etymology Dictionary ([https://www.etymonline.com/word/learn#etymonline\\_v\\_6626](https://www.etymonline.com/word/learn#etymonline_v_6626)) provides a similar account but adds "to hear of, ascertain" and "to get knowledge, be cultivated; study, read, think about." According to this dictionary, the noun "learning" appeared in ordinary English around the fourteenth century AD as "leornung," with the base sense "study, action of acquiring knowledge."

These origins remain in current meanings. The entry for **learning** in a current ordinary-English dictionary (<https://en.oxforddictionaries.com/definition/learning>) includes this meaning: "The acquisition of knowledge or skills through study, experience, or being taught. Knowledge acquired through study, experience, or being taught." This meaning remains current in educational psychology, where the focus is on human learning in the classroom or school, but it is not my focus in this entry. Another dictionary (<https://www.merriam->

[webster.com/dictionary/learning](https://www.webster.com/dictionary/learning)) gives similar meanings but includes a more modern one closer to my focus: "1: the act or experience of one that learns. 2: knowledge or skill acquired by instruction or study people of good education and considerable learning. 3: modification of a behavioral tendency by experience (such as exposure to conditioning)."

Meaning (2) repeats the educational psychology one. Meaning (3) is more modern and closer to my focus here, applicable to creatures other than humans. It also echoes a notion widely cited in the field: "... learning refers to a more or less permanent change in behavior which occurs as a result of practice" (Kimble 1961, p. 2). Colman (2015) submitted a similar notion: "Any lasting change in behaviour resulting from experience, especially conditioning" (p. 416); he also included the more traditional notion: "The act or process of acquiring knowledge or skill, or knowledge gained by study" (ibid.).

I do not mean to reject the traditional idea of learning as knowledge acquisition by education in humans, but it is not my area of expertise, as important as it is. I am more familiar with the more general notions discussed in the experimental psychology of learning, my focus in this entry. The mention of conditioning in the preceding notion refers to a family of learning phenomena widely studied in experimental psychology, under the name of "associative learning." It includes Pavlovian (after Pavlov 1928; also known "classical" or "respondent") conditioning and operant (or instrumental) conditioning.

The other family, nonassociative learning, includes habituation and sensitization. These terms have their own entries in this encyclopedia, so I shall not discuss them at length, to avoid excessive overlap. I will focus on Pavlovian conditioning as a paradigmatic example of learning, only to make some general points about the nature of learning. I do not intend this focus to reduce all learning to Pavlovian conditioning, or even associative learning. I would like what follows to be applicable to as many phenomena as possible that have been called "learning," but I will not be able to fulfill this wish completely in this entry (perhaps in my lifetime). A proper assessment of

this generality will require extensive further discussion well beyond this entry.

## Two Families of Learning Notions in Psychology

Perhaps the most general disagreement among learning scientists over the nature of learning processes is whether it is behavioral or nonbehavioral (Burgos 2018). This disagreement has led to two seemingly irreconcilable families of notions of learning. According to behavioral notions, some kind of behavior or performance change (functionally related to certain external environmental conditions) is *constitutive* of, essential or fundamental to (at least *necessary* for something to *be*), learning (I shall use all those expressions equivalently). An example is Kimble's (1961) classical notion cited above. As usually cited, it seems to be purely behavioral in that it appears to view learning *only* as a kind of performance change functionally related to certain kind of external environmental conditions (but see below).

A behavioral notion need not be *purely* behavioral. Some are *impurely* behavioral by including nonbehavioral entities as *equally* constitutive of learning. For example, Corsini (1999) submitted this notion: "**learning** the process of acquiring new and relatively enduring information, behavior patterns, or abilities; modification of behavior as a result of practice, study, or experience" (p. 541). This notion is behavioral in that it includes a certain kind of behavior change as constitutive of learning, but impurely so, as it also postulates certain nonbehavioral features (information acquisition; more on this later) as equally constitutive of learning.

The other family consists of *purely* nonbehavioral notions, according to which no behavior change is essential to learning. They thus view learning *only* as an inferred, supposedly internal, process, *if* expressed in behavior. They thus view the term **learning** as *theoretical*, in the traditional sense of referring to publicly unobservable processes. The emphasized "if" means that learning can (in fact, quite often does) occur without any change in the *relevant* behavior or performance of

*interest*, the *behavior measured for the dependent variable*. Consequently, *this* performance is inessential to learning. (I mean all these emphases to anticipate a key clarification: the behavior to which these notions refer is not necessarily *any* behavior.)

Kimble's (1961) notion seems to be purely behavioral, but to conclude this would be hasty. Quotations of this notion, as abundant as they are, fail to mention that he referred to it as "factual" in viewing learning as "observable events in the physical world" (p. 2). Such notions, he clarified, "make no effort to describe underlying mechanisms or to identify the 'true nature' of learning" (p. 8). Kimble also referred to notions of learning that "attempt to accomplish such objectives" (p. 9) as "theoretical." He thus appears to have viewed the true nature of learning as given by underlying mechanisms, not behavior change.

## Purely Nonbehavioral Notions

Most psychologists find purely behavioral notions inadequate and prefer purely nonbehavioral notions. For example, Bolles (1976) submitted this notion: "... learning may be defined as the process of associating ordered events. Note that there is no evidence of learning at the time learning occurs; evidence of learning consists of a subsequent change in behavior" (p. 21). This notion echoes *associationism* (but see later), the most widely held view about the nature of learning. He elaborated as follows:

If an experimental situation provides an ordering of events such that one event follows another in a lawful manner, and if an animal's behavior changes as a result of this arbitrary ordering, then we may say learning has occurred. The learning itself is difficult to identify because it is not an observable thing or relationship but a hypothetical process, which has been variously conceived as forming a neural connection, building a habit, establishing an association, or acquiring an expectancy. But however the process is conceived, the change in behavior merely constitutes evidence of learning (ibid.).

Domjan (2015) proposed this notion: "Learning is an enduring change in the mechanisms of behavior involving specific stimuli and/or responses that results from prior experience with those of

similar stimuli and responses” (p. 13). He clarified that “... the preceding definition attributes learning to a change in the *mechanisms of behavior*, not to a change in behavior directly ... Learning is defined in terms of a change in the mechanisms of behavior to emphasize the distinction between learning and performance” (p. 13).

In making the learning-performance distinction, a common practice among most learning scientists, Domjan implies that learning is *not* behavior change. The purely nonbehavioral character of this notion seems clear: Behavior change is not constitutive, only evidence of learning. It is key not to confuse the two. *How* we know whether learning has occurred (evidence of learning) hinges on *what* is learning (the nature of learning). In order to know whether learning has occurred, we must *first* have *some* idea, however rough, of what is learning.

Olson and Hergenhahn (2016) provided a similar notion in a chapter entitled “What is learning?.” After paying lip service to a modified version of Kimble’s (1961) factual notion, they settled for the following:

... whatever we study in psychology, must be expressed through overt or covert behavior, but this does not mean that the behavior we study *is* learning. We study behavior so that we can make *inferences* concerning the process believed to be the cause of the behavioral changes we observe. In this case, that process is learning. Most learning theorists discussed in this book agree that the learning process cannot be studied directly; instead, its nature can only be inferred from changes in behavior ... most learning psychologists look on learning as a process that mediates behavior. For them, learning occurs as the result of certain experiences and precedes changes in behavior. In such a definition, learning is given the status of an **intervening variable** ... a theoretical process that is assumed to take place between the observed stimuli and responses ... Independent variables cause a change in the intervening variable (learning), which in turn causes a change in the dependent variable (behavior). (pp. 2–3)

## Why Prefer Purely Nonbehavioral Notions?

One answer to this question is the lack of compelling reasons against nonbehavioral notions. The

usual Skinnerian attacks of dualism, public unobservability, and impracticality leave such notions unscathed (Burgos and Killeen 2019). These attacks also apply to impurely behavioral notions. The attacks, then, seek to leave purely behavioral notions as the last ones standing.

Another answer has to do with the so-called “behavioural silence” argument (I will keep using the American form “behavioral”), formulated by Dickinson (1980) as follows:

... we cannot assume that nothing is learned in the absence of a behavioral change. ... the main reason for rejecting simple behaviourism was that learning could occur in the absence of any overt change in behaviour, or in other words that learning could be behaviourally silent. (p. 15)

This argument favors purely nonbehavioral notions of learning, but not just in theory. It also has some empirical support in laboratory observations of certain conditioning phenomena. Dickinson (1980) summarized one, but there are more. The support is indirect, but this does not make it any less convincing. The Skinnerian ideal (e.g., Skinner 1950) of definite (direct, hard, abundant) empirical support is too strict (Burgos and Killeen 2019).

A key clarification here (anticipated in Note 2), not explicit in defenses of the argument and purely nonbehavioral notions, is that “behavioral silence” here does not necessarily mean that animals are behaviorless throughout the training phase. I seriously doubt supporters of the argument believe this. Instead, following the principle of charitable interpretation (which I strive to do, with moderation), I interpret the argument (and the purely nonbehavioral notions it supports) as referring only to the behavior measured for the dependent variable.

**Conditioned suppression of barpressing in rats.** Rats are first trained to press a bar through operant contingencies (response-dependent reinforcement) and then receive pairings of a cue (the conditioned stimulus or CS, e.g., a light or a tone) with an electric shock applied to the paws (the unconditioned stimulus or US), in Pavlovian fashion. Afterwards, rats receive trials of the cue, which significantly reduce barpressing frequency.

Only studies of this phenomenon where the bar is *absent* during the Pavlovian training support the



behavioral-silence argument. In many, perhaps most studies, the bar remains present during this training, and some (e.g., Testa 1975) report a change in the behavior of interest (barpressing). These studies do not allow exclusion of the necessity of such change. However, the Pavlovian training in other studies (e.g., Ayres, Axelrod, Mercker, Muchnick, & Vigorito, 1985, Experiment 3) has occurred offline, without the bar. In these studies, no barpressing can occur during the training, which implies, according to purely behavioral notions, that no learning occurred. Yet, test trials of the cue with the bar reinstated result in a significant response suppression. This result implies, according to the behavioral-silence argument, that some learning occurred during the Pavlovian training phase, despite the non-occurrence of any change in the response.

**Pavlovian-instrumental transfer.** A related family of phenomena comprises Pavlovian-instrumental transfer (PIT), where Pavlovian conditioning facilitates operant conditioning. It is commonly studied with appetitive US and rewards. In specific PIT, the CS facilitates a response trained in operant conditioning with a reward used as the US initially paired with the CS. In general PIT, the CS facilitates a response trained in operant conditioning with a reward different from the US that was initially paired with the CS.

As in conditioned suppression, these phenomena provide a clearer support to the behavioral-silence argument if the operandum is absent during Pavlovian training, which is often the case in these studies. No change in the response of interest can occur without the operandum during Pavlovian training, which implies the absence of learning, according to behavioral notions. Despite this, as the behavioral-silence argument predicts and against behavioral notions, the facilitation of the operant response by the cue later on strongly suggests that some learning occurred during the Pavlovian training.

**Sensory preconditioning.** Subjects first receive trials of a target cue X (e.g., a light) paired (presented in some optimal temporal and probabilistic relation) with trials of another cue A (e.g., a tone). The US does not occur during this phase;

hence, nor does the UR, the response of interest. The kind of behavior change that according to behavioral notions constitutes Pavlovian conditioning (i.e., acquisition of the conditioned response or CR) cannot occur in this first phase.

Subjects then receive A-US pairings according to a standard Pavlovian procedure, followed by test trials of X alone. The result is a substantial CR to X (compared to a control group that did not receive the X-A pretraining), despite the fact that X was never paired with the US. According to the behavioral-silence argument, some learning must have occurred during the X-A pretraining, but whatever it is (many believe it is at least an X-A association), it does not require the occurrence of the unconditioned reflex of interest. This result is yet another challenge to behavioral notions.

**Latent inhibition (CS-preexposure effect).**

Subjects first receive a number of trials of a cue X without the US (cue preexposure), followed by X+ trials. Latent inhibition is a significant retardation in the acquisition of the CR during X+. Because the relevant change in the behavior of interest does not occur during the CS-preexposure phase, behavioral notions imply that no learning occurred during that phase. The results, once again, contradict this implication and support the behavioral-silence argument that some learning must have occurred during that phase, despite the absence of the relevant change in the behavior of interest.

It is common to distinguish between attentional and learning processes, even if the latter depend on the former. Most explanations of this phenomenon appeal only to *attentional* processes and, hence, postulate no associative learning during the CS-preexposure phase. This distinction, coupled with those explanations, would weaken the empirical support this phenomenon might lend to the behavioral-silence argument *if* this argument were restricted to associative learning, but there is no good reason to do this.

**US-preexposure effect.** In a related phenomenon, first reported by Randich (1981), subjects first receive preexposure to the US without any scheduled discrete cue as the CS, followed by Pavlovian CS-US training. Like latent inhibition, the effect is a significant retardation of the

acquisition of the CR, although the evidence is more complicated to explain. The dominant explanation of the associative effect is that the US is conditioned to the context during the pre-exposure phase, where the context is viewed as just another CS. Because the same context is present during the CS-US training, the context functions like a previously conditioned CS (A), which blocks conditioning to the new CS (X).

In short, according to this explanation, the effect is just another case of blocking a widely studied phenomenon in associative learning. Still, I do not view most other cases as evidence that supports the behavioral-silence argument. The reason is that such cases use the standard blocking procedure, which involves A as a *discrete* CS (in contrast to the continuous presence of contextual cues). Some of these cases also involve measuring responding to A during the A-US training, and this measuring shows a relevant behavior change. This change goes unreported in some studies that use the standard blocking procedure. Despite this, the explanation of the US-preexposure effect as a case of blocking assumes that such change occurs, rendering it largely unnecessary.

**Second-order conditioning in autoshaping.** Rescorla (1980, pp. 18–24) reported further evidence that empirically supports the behavioral-silence argument and crucially involves the phenomenon of autoshaping. This phenomenon is the acquisition of a skeletal, prototypical operant response (e.g., keypecking in pigeons) not unconditionally elicited by the primary reinforcer, at least not in the same way food unconditionally elicits salivation. This acquisition occurs under a Pavlovian cue-reinforcer contingency that operationally requires no responding, more reliably when the cue is visually localized where the animal is expected to respond (e.g., a light projected directly on a key, if the response of interest is the pigeons' keypecking).

In Rescorla's (1980, pp. 18–24) experiments, however, pigeons first received tone-food pairings. No keypecking occurred during this training, presumably because a tone is a diffuse cue that is not as precisely spatially localized as a key light. The implication of a purely behavioral

notion of learning as just some kind of performance change is that there was no learning during this phase, because there was no performance change *in the relevant response* (keypecking). However, in a second phase, the same pigeons received key light-tone pairings, according to a second-order conditioning procedure. Lo and behold, pigeons pecked the key at significant levels, compared to control pigeons that also received the light-tone but not the tone-food pairings. The implication is that the pigeons in the experimental condition must have learned something during the tone-food training, which seems more plausible than the implication from behavioral notions that the pigeons learned nothing during that training.

**Learning with impaired responding.** Other evidence that supports the behavioral-silence argument and, to this extent, purely nonbehavioral notions comes from reports of learning with impaired responses. The classical example is impairment of skeletal responses with curare. In the first report of this attempt, Harlow and Stagner (1933) reported that curarized cats and dogs failed *avoidance* conditioning of certain skeletal (striated muscle) responses (e.g., flexing a leg, leaping from a potentially painful place), but not pupil dilation (mydriasis), an autonomic response. The authors concluded that the "peripheral" or "motor view," akin to purely behavioral notions of learning, was correct.

This conclusion applied only to the skeletal responses the authors measured, insofar as they reported no impairment of the unconditioned mydriasis to an electric shock and successful Pavlovian conditioning of this response to a bell in the curarized dogs. This result would seem to support purely behavioral notions of learning with this response. However, Girden (1942) reported absence of a conditioned mydriasis response to a bell in dogs with elimination of sympathetic innervation to the right eye, although he did not report the effect of this elimination on the unconditioned mydriasis to the shock.

Not even Harlow and Stagner's (1933) limited conclusion held in the light of further evidence showing that other methods of skeletal response impairment (e.g., crushing spinal motor limb

innervations during training; e.g., Light and Gantt (1936) did not prevent a conditioned skeletal response after recovery from the impairment (regeneration of the innervations). Other evidence suggested that the impairing effects of curare were not restricted to muscle contraction, but also extend to the brain (more on this later). Harlow (1940) eventually retracted: "... the data from the curare experiments cannot be used to support the motor theory of learning" (p. 281).

**Conditioned inhibition.** Another phenomenon that could provide further empirical support of the behavioral-silence argument and, to this extent, purely nonbehavioral notions is conditioned inhibition, first reported by Pavlov (1928). In his early studies, he designed what is presently a standard procedure to obtain this phenomenon experimentally. The basic procedure (omitting all the necessary controls) consists in presenting compound AX- trials randomly intermixed with A+ trials, where A and X denote two different cues (e.g., a light and a tone) and "-" denotes the absence of the US and "+" a pairing with the US. The evidence shows that X becomes a conditioned inhibitor.

A major issue is that inhibition, contrary to excitation, lacks any overt behavioral expression, at least in the response system of interest, unconditionally elicited by the US. Therefore, no direct overt behavioral indicator allows for a reliable distinction between the absence of responding in conditioned inhibition and such absence in extinction or even to a *neutral* CS. The behavioral indicators of X as a conditioned inhibitor must then indirect. This issue led some to question the validity of the idea of inhibition in the psychology of learning.

For decades, there was little agreement on how solve this problem, until Rescorla's (1969) widely influential proposal: Determining whether X is a conditioned inhibitor requires an acquisition test and a summation test. X must "pass" *both* tests to consider it as a conditioned inhibitor. X passes an acquisition test if acquisition of the CR under X+ is significantly slower after a conditioned-inhibition procedure, compared to control groups that did not receive such training (or received different trainings). X passes the summation test

if responding to a BX compound is significantly lower in the experimental group, where B is yet another excitatory CS (sometimes called "transfer excitor").

Cole et al. (1997) reported the most compelling demonstration thus far of conditioned inhibition using both tests, but they admitted it might still be insufficient to warrant postulation of a construct of conditioned inhibition as a single fundamental learning process. To this extent, conditioned inhibition may be a weaker empirical support for the behavioral-silence argument than the other phenomena.

## In Sum

Overall, the preceding very brief account empirically favors purely nonbehavioral notions. Not only have the usual attacks against these notions failed. These notions also have some empirical support, even if indirect and limited to Pavlovian conditioning, although this limitation does not imply that all learning is Pavlovian conditioning. The thesis that some kind of behavior change is essential (at least necessary) to learning still lacks compelling empirical support, especially for operant conditioning, where any support is operationally impossible to obtain, even for purely nonbehavioral notions. This situation may change in the future. In the meantime, at the risk of being mistaken, I will follow the zeitgeist and dedicate the rest of this entry to a more detailed discussion of purely nonbehavioral notions.

## Subfamilies

The preceding discussion is not the end of the matter by any means. I have discussed purely nonbehavioral notions too sketchily. The behavioral-silence argument is valid and has some evidential support, but does not give an *unequivocal specific* answer to the key issue of what learning is. To put it more precisely, what do all learning processes have in common? What kind of process is learning? The features nonbehavioral notions postulate (nonbehavioral,

inferred from and mediating behavior, publicly unobservable) are too general. Many animal processes have such features but are not learning processes (e.g., protein synthesis, metabolism, renal filtration, oxygen transport by erythrocytes, phagocytosis by leukocytes, viral and bacterial infections, muscle fatigue, neurotransmitter synthesis, etc.), or so it would seem.

None of the evidence summarized above supports unequivocally a more precise account of what learning processes have in common that distinguishes from other kinds of processes. This situation is clear from the presence of numerous accounts in the literature, all of which are equally compatible with that evidence. I will dedicate this section to discuss some of them, in their two varieties: neurobiological and cognitive.

**Neurobiological notions.** Kimble (1961) believed that many psychologists of his time preferred these notions: “[m]any of the theoretical definitions of learning are physiological” (p. 9). Some quotations, however, use the more precise “neural.” Kimble (1961), for instance, quoted this assertion: “Learning is the process of the formation of relatively permanent neural circuits” (p. 9). This belief is not new by any means. Thorndike (1913) submitted the following notion: “Learning is connecting. . . There are millions” of connections, including “connections leading to actual conduction in neurones” (p. 54); “The process of learning is one of simple making and keeping connections and readinesses to conduct” (p. 56), hence the term **connectionism**, often used to label his position. Reminiscent of this connectionism is Hull’s (1943) notion in a section entitled “The Problem and General Nature of Learning”: “The essential nature of the learning process may . . . be stated quite simply. . . the process of learning consists in the strengthening of certain . . . connections as contrasted with others, or in the setting up of quite new connections” (pp. 68–69).

**Connections as synapses: the synaptacist notion.** Whether by “connections” Hull (1943) meant “synapses” is unclear, as he did not use the latter or its singular, despite having been coined decades earlier and his use of the term “neurones” a few times in his seminal book. The term **connection** is often used as equivalent to

“synapse,” but the two terms are not synonyms. The term **connection** is much broader and less technical, as it can refer to relations between myriad entities other than neurons (e.g., people, electrical circuits, murder cases, events, literary works, stimulus-response, etc.). The term **synapse** is more precise and technical, referring only to a connection between neurons. The expression **synaptic connection**, then, is not redundant. Nor does talk of “connection” necessarily refer to this expression, unless **connection** is used as synonymous with **synapse**, in which case, the latter is preferable.

Thorndike (1913) used “synapses” several times throughout his works, but only once in the book dedicated to the psychology of learning: “Ultimately degrees of strength of a connection in behavior will be defined as degrees of some anatomical or physiological fact whereby synapses between neurones differ in intimacy” (p. 3). This quotation, coupled with his above-cited notion of learning, suggests that he might have been the first to identify learning with *synaptic change*. (It is more customary in neuroscience to speak of “synaptic plasticity,” but I prefer to speak of synaptic change, as **plasticity** is a *dispositional* term that denotes a *propensity* to change, without necessarily any change actually taking place. The term **change**, in contrast, focuses on actual, not potential, learning as synaptic change.) although he used “connection” far more often and seemingly not always as synonymous with “synapse.” Such identification, if Thorndike indeed intended it, may well be the first expression of what could be called, for want to a better name, the *synaptacist* notion of learning, according to which learning is *just* synaptic change. More precisely, all learning processes are just synaptic-change processes.

This formulation is extreme, and no author has formulated it quite like this. Strictly, only assertions like “learning is essentially *only* synaptic change,” “*only* synaptic change is constitutive of learning,” or “learning is fundamentally *nothing more* than synaptic change” express the notion in such an extreme way. As far as I know, no author has put it exactly like this. Consequently, I will not attribute it to any particular author. However, I will keep discussing it as a clear, coherent, and precise conceptual possibility.

As formulated above, the notion would seem to suffice as a statement of the nature of learning. Unfortunately, it does not, because it is too superficial and general to be acceptable as a valid account of the nature of learning. To deserve such honor, the notion requires empirical support, the predominant way to evaluate and validate concepts in science. In the following sections, I summarize a few advances in that regard, leaving out most of the technical details.

As a brief reminder about the synapse concept today, most synapses studied in neuroscience are chemical and consist of a presynaptic process, a synaptic cleft, and a postsynaptic process. The presynaptic process is an axon terminal or button of a neuron, and the postsynaptic process can be a dendritic spine, shaft, soma, or even axon terminal of *another* neuron. The key feature of a synapse for the synapticist notion is its strength, neuroscientifically characterized in various ways. One is in terms of the degree of spatiotemporal coincidence between a presynaptic active zone and a postsynaptic density. The former varies directly with the amount of neuroactive substance (typically a neurotransmitter) released by the presynaptic process. The postsynaptic density is the proportion of receptors on a region of the postsynaptic process. In this characterization, stronger synapses are relatively stable, higher spatiotemporal coincidences between more highly active presynaptic zones and higher postsynaptic densities.

***Some evidence of synaptic changes during learning.*** There has been abundant research on this in behavioral neuroscience, but I cannot possibly do it justice in this short entry. I will only give one of the most representative examples: the groundbreaking, Nobel prize-winning research of Eric R. Kandel and colleagues with the marine snail *Aplysia californica*'s gill-withdrawal response. This response is unconditionally elicited by tactile stimulation to the animal's siphon, and its magnitude is given by its duration. This evidence has shown that all such forms of learning, at least in this species, involve relatively persistent, long-term changes in certain synapses.

In habituation, the decrease in the duration of the response by repeated stimulation of the siphon is highly correlated with a reduction in calcium influx to the axon terminals of the siphon sensory

neurons, which reduces ACh release. Sensitization, Pavlovian, and operant conditioning, in contrast, are highly correlated with serotonergic *facilitation* (via axo-axonic synapses) of ACh release, mediated by a second messenger (cAMP) that opens various ion channel species (calcium, potassium), induces the docking of synaptic vesicles to release sites, and even alters DNA in the nucleus.

A primary aim of this kind of research has been to make detailed measurements of behavioral, neuronal activation, and synaptic changes, to determine how they correlate across these levels of organization. Thus far, numerous studies suggest that such interlevel correlations are strong, although it is not immediately apparent exactly what this means for the synapticist notion of learning as just synaptic changes.

*What does it mean?* Such a strong correlation suggests a role of synaptic change in learning. Does it conclusively support a strict synapticist notion of learning as *only* synaptic change? Not quite, because changes in neuronal activations and behaviors still occur in those studies, and this precludes excluding them as possibly constitutive of learning. Takeuchi et al. (2014) have proposed that a convincing exclusion must meet four conditions, three of which involve experimental synaptic manipulations that raise enormous technical challenges. I will abbreviate them as the *DRAM* conditions, after the initial of the terms these authors used to name them (enclosed in double quotes in parentheses).

One (*D* for "detectability"), training in a learning task should bring about demonstrable changes in identified synapses of some brain region. Two (*R* for "retrograde alteration"), comparable modifications *after* training should alter performance during test. Three (*A* for "anterograde alteration"), experimental modifications of those synapses *before* training should alter performance during training. Four (*M* for "mimicry"), direct experimental production of comparable synaptic changes *without* any training should bring about performance comparable to that observed during test after training without such production. The absence of training in *M* implies the non-occurrence of neuronal activations and behaviors specifically caused by the training and, hence,



possibly constitutive of learning the task. Meeting these conditions is a matter of degree, not an all-or-none affair.

This very simplified outline does little justice to the formidable technical challenges this kind of research presents, but overall there has been great progress in approximating those conditions, although no single study has yet met them fully. Unsurprisingly, progress in approximating  $D$  has been greater with invertebrates, due to the relative simplicity of their nervous systems. *Aplysia californica*, discussed above, is the most widely known example. Knowledge of specific changes in identified synapses (e.g., from siphon and tail sensory neurons to gill motor neurons) critical for various forms of learning in this species has approximated  $D$  quite closely. The same can be said of other invertebrate species used in experimental learning research.

There has also been much progress in approximating the *DRAM* conditions in vertebrates, particularly rodents and birds, the most widely used animals in experimental learning research. Their nervous systems, however, are far more complex, which makes closer approximation to  $D$  and  $M$  that much more technically challenging. This research has approximated more closely  $A$ , mainly surgically, through certain brain lesions (e.g., the amygdala, which weakens various components of fear conditioning in rats).

Overall, the evidence lends reasonably good empirical support to the synapticist notion of learning. However, the support remains quite incomplete. The *DRAM* conditions remain to be tested with many other learning tasks, their underlying brain circuits, and species. Replicability of all these tests also needs to be assessed. Tests across different species, in particular, might encourage comparative research that could promote the kind of evolutionary thinking about learning that gives much importance to biological constraints on learning. All this research will be key to test the limits, generalities, specificities, and evolutionary relevance of the synapticist notion and, in this way, inform in detail about its validity as an account of the nature of learning. Because of all this, at present, it seems wiser to view the notion as a promising but still working hypothesis.

***The necessity to theorize.*** So far, I have spoken only about empirical support of the synapticistic notion and have hinted at the extraordinary growth of the experimental database on this, although more research is needed. Whether such undeniable empirical progress necessarily means a better *understanding* of the nature of learning is far less clear, as much hinges on exactly what understanding is. Empirical data are at least necessary for understanding. Some say it is sufficient, others disagree. I will side with the latter, following the venerable and widespread view in science that understanding requires *explanations* of observations, which in turn requires *theorizing*.

A major reason for theorizing is the *complexity* of the phenomena of interest. Theorizing, then, is simplification in the form of abstraction of a few elements or factors hypothesized to be essential to the phenomenon of interest. This divide-and-conquer strategy is common in all science, and neuroscience is not the exception. The search for the nature of learning, then, is at least as strongly theoretical as it is empirical, and the two ways feed on one another. The aims of theoretical work are explanatory and predictive, more easily achieved with simplified models. The more complex a model, the harder it will be to use it for these aims.

Such simplification is even more vital in relation to brains, which can be quite complex, even those of nonhuman species used in learning research, far simpler than human brains. This complexity is directly relevant to neurobiological notions of learning. A major lesson learning psychologists have learned (no pun intended) is that a brain need not be as complex as a human, or even a cat or dog, or even a rat or pigeon, or even an insect, brain to make the nature of learning very hard to discover. The complexity of such far simpler brains seems to be far more than enough for that.

There were early efforts, during the mid-twentieth century, to theorize about chemical transmission in single synapses and action potentials in single axons, through computational models that included only a few hypothesized essential features as quantitative factors. These models were foundational and set most of the tone of theoretical research in the following

decades, in what has come to be *computational neuroscience*. This research is a sort of very (perhaps too) strictly played imitation game that seeks to emulate as closely as possible specific features of neuronal and synaptic structure and functioning in specific circuits, as known from hard cellular and synaptic data. The effort is so strong that I cannot but wonder whether it has lost the main purpose of theorizing, which is, precisely, to simplify.

In any case, much of it has sought to improve, elaborate upon, and combine the early models, guided by the hypothesis that synaptic transmission in brain circuits depends crucially on neuronal activations (action potentials reaching axon terminals). Such combinations have been used to simulate the dynamics of various brain circuits functionally dependent on neuronal activations and synaptic transmission, as observed in vitro. In these simulations, synapses are often simulated as fixed, which is unrealistic for those who seek to play the imitation game (emulate brain structure and functioning) as strictly as possible. If computational-neuroscience models are to be applicable to learning in animals (more on this limitation later), theorizing about synaptic change is also needed.

*Enter Donald O. Hebb.* In the first effort to do this, Hebb (1949) continued the connectionist view initiated by Thorndike and Hull. For example, he proposed these notions:

Connections rigidly determine what animal or human being does, and their acquisition constitutes learning. (p. xvii)

Learning according to the present ideas consists of a lasting change of facilitations between the activities of specific neural structures. The change results when two structures (single pathways or assemblies) that have sufficient anatomical connections are active at the same time. (p. 180)

... one can conceive of conditioning as the establishment of relations between cerebral neurons (in the first place) and between systems of neurons (in the second). (ibid.)

Based on those notions, Hebb (1949) proposed his widely influential “neurophysiological principle”:

When an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it,

some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased. (p. 62).

This principle was the first hypothesis of synaptic change and remains quite influential today, especially in modeling, the kind of synaptic change believed to constitute hippocampal LTP. The evidence strongly suggests that this change follows the Hebbian principle, for which the latter has inspired models of the former, so much so that many view LTP as Hebbian in nature.

*Models of synaptic change in computational neuroscience.* Hebb's principle led to modeling synaptic change as a major research area in computational neuroscience. Most models of synaptic change come in two varieties, but both include some Hebbian component (refined to solve certain problems, e.g., prevent unlimited synaptic strengthening; to take into account long-term depression, a lasting synaptic weakening by extended low-frequency firing stimulation). Biophysical models, on the one hand, are more in line with most computational neuroscience modeling and seek to emulate the details of the biochemical and physiological processes thus far known to result in changes in synaptic transmission (a few of which I summarized above).

Phenomenological models, in contrast, treat synapses as *input-output black boxes*, leaving aside their molecular, physiological, or cellular details. Hence, these models are more abstract. Some view the pre- and postsynaptic firing rates as the key input, where higher (above-threshold) rates result in stronger, longer lasting excitatory synapses. Other phenomenological models view relative *timing* between pre- and postsynaptic pairs as the primary determinant of synaptic change (briefer times tend to promote more lasting synaptic strengthening).

*Neo-connectionist notions.* Still, his proposals anticipated many of the intuitions behind later theoretical developments. Far from fading, a connectionist view of learning reached critical momentum during the resurgence of connectionism in cognitive psychology and artificial intelligence during the mid-1980s. This new form of connectionism, for want of a better term, can be named “neo-connectionism,” to distinguish it

from the early forms of connectionism. After a period dominated by traditional, Turing-machine, symbolic artificial intelligence, neo-connectionism became strongly guided by the synaptocist notion of learning, where the use of neural network models has been the preferred mode of theorizing. Nowadays, learning in neural-network modeling is viewed as changes in the *connection weights* or “free parameters” of a neural network (see **neural network** in this encyclopedia). However, in contrast to computational neuroscience, computational modeling in neo-connectionism is far more abstract, as it seeks to play the imitation game much less strictly. New-connectionist models are not as closely guided by hard data about action potentials and synaptic plasticity as models in computational neuroscience. Consequently, the former tend to be much more abstract and simplified.

Here is an example of a neo-connectionist notion: “Setting the connection strengths correctly is what network learning is about” (Anderson, 1995, p. 55). In similar spirit and letter, Enquist and Ghirlanda (2005) assert that:

... a better definition of learning is “changes in memory caused by experience,” whether or not such changes are immediately reflected at the level of behavior. ... In neural network models, memory and learning can be given precise interpretations reflecting this definition. Memory is equal to connection weights, the analog of synapses in nervous systems. ... learning amounts to changes in the weights. (p. 130)

What makes the second definition better than the first? The authors give the behavioral-silence rationale mentioned above for nonbehavioral notions of learning: “An experience, however, may change later behavior without this being immediately apparent” (p. 130). In any case, these authors’ notion of learning seems to be very close to the synaptocist notion, albeit still far more abstract than its development in computational neuroscience. Connections in artificial neural networks are interpreted as very abstract synapses, whereas connection weights are interpreted as very abstract synaptic strengths.

The part of a connectionist neural network model that describes changes in connection weights is the learning rule. There are several

learning rules, usually separated into two families: supervised and unsupervised. In supervised learning, changes in the connection weights of a neural network are overseen by an imaginary teacher of sorts that tells the network when it has made a mistake in performing a certain task of interest. These networks only learn when they make mistakes: no mistakes, no learning. Literally, it is *just* learning by error. In unsupervised learning, networks learn on their own, without any teacher (for more details, see **neural networks** in this encyclopedia).

An early example of supervised learning in neural-network modeling is Rosenblatt’s (1958) perceptron, which the author presented in the title of his paper as “a probabilistic model for information storage and organization storage in the brain” (p. 386). The term “probabilistic” indicates that, contrary to most learning models in psychology, the perceptron is consistent with the general implication of early models of synaptic transmission at single synapses stochastic in nature. The term “information” in that title has wider ramifications that I will discuss later. But in current mathematical renditions of the model, the learning rule critically involves the computation of an error signal, defined as the arithmetic difference between the network’s actual output activation and a desired or expected output activation (dictated by the task of interest).

The Hebbian principle provided an early notion of unsupervised learning and has been mathematized in various ways in neural network modeling. All of them assume that the mathematical relation between the co-activations of connected neurons is *multiplicative*. The simplest version of this assumption is that the weight  $w$  of a connection between units  $i$  and  $j$  ( $w_{i,j}$ ) with activations  $a_i$  and  $a_j$  at time  $t$  equals the weight at  $t - 1$  (at the immediately preceding moment) plus the product of  $a_i$  and  $a_j$  at  $t$ . More succinctly:  $w_{i,j,t} = a_{i,t}a_{j,t}$ . This mathematical rendition of the Hebbian principle has been found inadequate for various reasons, but I need not get into further technical details here. Suffice it to say that connectionist notions like the ones illustrated here restrict learning to changes in synaptic strengths relevant to a certain task: Learning is nothing more than these

changes. The synapticist notion of learning thus seems to be held in connectionism.

Connectionist notions of learning flourished and became more mathematically oriented with the publication of the *Parallel Distributed Processing* (PDP) volumes (McClelland, Rumelhart, and The PDP Research Group 1986). However, the adoption of this approach in computational modeling of learning as studied experimentally in animals has been scarce. Most connectionist models have focused on Pavlovian conditioning and been inspired by the Rescorla and Wagner (1972) model. Perhaps, this situation is due to the preference most learning psychologists have for cognitive notions, which I will discuss later. Connectionist modeling of operant conditioning has been even less common, likely due to the Skinnerian view (e.g., Skinner 1950) that still dominates operant-conditioning research, which eschews any nonbehavioral theorizing as unnecessary, neurobiological theorizing included.

**Non-synapticist neurobiological notions.** Not all neurobiological notions restrict learning to synaptic change. In fact, an implication of synapticist notions seems like a conceptual stretch: If learning is *just* synaptic change, an *in vitro* neuronal circuit where only synaptic strengths change (e.g., in a strict test of the mimicry condition) can be said to learn. This implication does not obtain in neurobiological notions that are more inclusive by viewing other brain processes as equally constitutive of learning and, hence, get closer to impurely behavioral notions. An example is the beginning of the section entitled “What is learning?” of Dudai’s (1989) book:

It is generally accepted that learning is an experience-dependent modification in behaviour, or in potential to behave . . . . This definition may satisfy psychologists or ethologists, but possibly not neurobiologists. A neurobiological definition should take into account the level of analysis with which neurobiology is concerned, namely, neurones, neuronal circuits and nervous systems. . . . I suggest that learning be defined in terms of a fundamental property of nervous systems, which is their ability to encode internal representations.” (p. 100)

Dudai might be surprised to know that most psychologists of learning repudiate purely behavioral

notions, although they prefer cognitive notions, discussed in the next section. Another feature of this quotation, more directly relevant here, is the absence of the term **synapse**. Synapses are tacitly included in neuronal circuits and nervous systems.

By “internal representations” Dudai (1989) meant

“... structured bodies of information possessed by the organism about the world and about appropriate reactions to the world. Representations are, thus, neurally encoded stylized versions of the world, capable of guiding behaviour. Internal representations are expected to vary tremendously in their complexity. (ibid., p. 101)

Dudai might also be surprised to know that most cognitive notions of learning adopt the information processing/storage view, but without reference to any neurobiological processes. This absence implies that information processing/storage is not unique to nervous systems. Dudai also clarified that “Specific representations are encoded by the activity *and* connectivity of circuits” (ibid., p. 101, emphasis added) and that “Learning is a multilevel phenomenon, and its analysis can be performed at levels ranging from the molecular to the behavioral” (ibid., p. 102). In contrast to the synapticist notion, this neurobiological notion does not identify learning with synaptic change: Changes in neuronal *activation* processes and patterns constitute learning as well. Moreover, the notion includes the behavioral level, suggesting that the notion might be behavioral, after all, but impurely so.

Similarly, in his notion of learning as a “change in the mechanisms of behavior,” quoted above, Domjan (2015, p. 16, Figure 1.5) suggested nervous-system mechanisms as primary candidates for the nature of learning, viewing neural systems, circuits, cells, and synapses as “levels of analysis of learning.” This suggestion makes for a neurobiological notion that does not restrict the nature of learning to synaptic changes, but includes other brain processes. Domjan, though, in contrast to Dudai, clarifies that behavior is not constitutive, only indicative of learning. It is unclear whether Dudai believes the same.

Although the synapticist notion has good evidence in its favor, overall most of the research in the neuroscience of learning still seeks to determine correlations across different levels of organization (molecular, synaptic, cellular, and behavioral) in phenomena called “learning.” These correlations provide a key empirical basis for postulating causal relations between learning (nonbehaviorally viewed) and behavior (always keeping in mind that correlation is not causation). Consequently, the evidence in this research provides stronger support for neurobiological notions that are more inclusive than the synapticist notion.

**Cognitive notions.** Neurobiological notions are readily applicable to learning in animals that have nervous systems, even if so severely lesioned that might be said to be incomplete, as in spinal (decerebrated) vertebrates (e.g., Grau and Joynes 2005). (This research has prompted a debate that is yet another example of my claim in Notes 1 and 3 that conceptual discussions about learning are ontological in character. In this debate, Grau and Joynes (2005) expressed frustration at years of being questioned about whether they “were examining *true* learning,” where some reviewers gave “demerits for falling outside traditional categories” (p. 46). Such questioning is symptomatic of an ontological stance on the real nature of learning that certain behavioral changes in spinal vertebrates allegedly do not satisfy. Grau and Joynes (2005) put it thus: “Frustrated by this continued assault, we have turned the question around and asked why learning should be so narrowly defined?” (p. 46). Why, indeed. Presumably, they believe that a wider notion inclusive of spinal vertebrates could be a closer approximation to the real nature of learning.) These notions also apply to insects (e.g., Dukas 2018) and very simple invertebrates that do not seem to have much of a brain as we know it in vertebrates or even insects, but still have a nervous system.

The view, however, is inapplicable to learning in *aneural* organisms, which lack anything even close to a nervous system as traditionally conceived in neuroscience (system of interconnected *neurons*). Aneural organisms that have been attributed a learning ability are paramecia

(Armus et al. 2006), bacteria (e.g., Yi et al. 2000), and plants (e.g., Gagliano et al. 2016).

One way is to seek out a more inclusive notion that includes learning in neural and aneural organisms, perhaps even inorganic systems. Cognitive notions can fulfill this role, even if this might not be the main reason why most psychologists of learning prefer such notions. Their generality makes them applicable to any organism, even inorganic machines (see Burgos 2018), regardless of their physical constitution. Such generality can be quite alluring, reminiscent of the still elusive “theory of everything in physics.” Generality supposedly is one of highest if not *the* highest ideal of science. It can lead to major advances if pursued wisely, in particular, not at the cost of specificity.

**Learning as information processing.** Many if not most of these notions add the following idea: Whatever neurobiological processes constitute learning, they carry out *information processing*. This idea is present in some of the notions cited earlier, but there are many others. For example, Dukas (2018) proposed the following notion: “Learning is the acquisition and retention of neuronal representations of new information” (p. 257).

In these notions, information processing and storage are properties of brains. Therefore, information processing/storage is entirely compatible with brain processes. Unfortunately, others see a fundamental incompatibility. After his earlier associationist notion, Bolles (1979) proposed this one: “. . . learning consists *not* in the acquisition of S-R associations but in the assimilation and storage of information about the environment” (p. iii, emphasis added). Gallistel and King (2010) have also proposed such incompatibility, in what may be the most zealous view of learning as information processing with Turing-machine architecture, a combination known as “algorithmic information theory” or AIT.

Such extreme cognitive notions are against the more inclusive kind of notion I seek here. They preclude the possibility that instances of learning as a kind of brain process constitute a proper subset of learning processes as involving information processing/storage. Fortunately, these extreme notions are very debatable. Bolles



(1979) offers no rationale whatsoever for his above notion. Gallistel and King (2010) justify AIT by this claim: “the behavioral data *imply* that brains are powerful organs of computation” (p. viii, emphasis added). This claim is fallacious, if by “imply” they mean *deductive* or *formal* implication qua *logical entailment* from certain premises to a conclusion via the application of deductive inference rules (a reasonable interpretation, given their uncritical commitment to AIT). However, as logicians and philosophers of science clarified over a century ago, there is no rule to *deduce* theory from data, strictly speaking. The fact that certain behavioral data (e.g., dead reckoning) can be explained computationally does not mean they imply AIT.

Happily, most learning theorists, like the neuroscientists cited above, see information processing/storage as entirely compatible with certain brain processes. This compatibility is clear in most computational models of Pavlovian conditioning, which come in two varieties. In the cue-competition variety (e.g., Rescorla and Wagner 1972), different cues “compete” for a limited amount of association supported by the US. In the comparator variety (e.g., Stout and Miller 2007), associations change independently of one another, and their expression in performance depends on comparisons among them. An emphasis of how this expression obtains, known as a response rule, is a hallmark of these models. On this view, all Pavlovian conditioning phenomena differ primarily in how the expression of learning in performance occurs.

Both kinds of models, just like neurobiological notions, allow for talk of associations combined with talk of information processing/storage, without the fear of contradiction lurking in the more extreme notions discussed above. In those models, then, it is entirely valid to state, for example, that a CS reliably paired with the US is “more informative” of the occurrence of the US than a CS that is unreliably paired with the US. Such talk implies that learning as association formation relates closely to, perhaps is identical to, information processing, although not necessarily viewed as having Turing-machine architecture. It is also quite common in these models to speak of the CS

and US “representations,” although not necessarily viewed as symbolic in nature.

**Encompassing neurobiological notions.** Cognitive notions that allow for compatibility between associative processes and information processing/storage have been characteristically formulated without any reference to any brain processes. This feature makes these notions suitable for capturing learning in aneural organisms, perhaps even inorganic machines (see Burgos, 2018). Can they encompass learning according to neurobiological notions, as a kind of brain process? I think they can, based on viewing these cognitive notions as *abstractions* of neurobiological notions. It is crucial to this view that such notions allow for said compatibility, as associations are more easily interpreted as synapses and associative strengths as synaptic strengths. Less clear is how to interpret neuronal activations in these notions. One possibility is to view them as stimulus *representations* or attention to stimuli. This interpretation can accommodate the two kinds of brain processes postulated by neurobiological notions (changes in neuronal activations and synaptic strengths) into cognitive notions, at least in principle.

More precisely, these brain processes are *physical implementations or realizations* of the more abstract learning processes postulated in cognitive notions. The notion of a physical implementation is central to the widely influential functionalism about the mind (not to be confused with the Chicago psychological school). According to this philosophy, brain processes are just *one* physical implementation of mental (cognitive, perceptual) processes. Brain processes are not the only *possible* physical implementations of mental processes. The latter can *also* be implemented in other, non-neural kinds of physical systems, such as those found in aneural organisms and even inorganic machines. That is to say, the nature of mental processes, according to this philosophy, is not given by their physical implementation, but their functional features. Mental processes, then, can occur in physically very different systems.

Extending this philosophy to learning, cognitive notions could in principle encompass learning processes in aneural organisms as nonneural

physical realizations of the *same kinds* of processes postulated by these notions. If these processes are cognitive in nature, an implication is that aneural organisms have cognition, which seems like a conceptual stretch. Exactly how this counterintuitive implication could be handled remains an open issue. Still, this interpretation implies that learning processes could occur in physically very different systems, like humans as plants. It remains to be seen whether this interpretation leads to a more unified notion of learning. In particular, an issue is the extent to which the biological details of learning in aneural organisms satisfy the notion of information processing/storage.

## Cross-References

- Action Potentials
- Arthropod Cognition
- Associative Learning
- Autoshaping
- B.F. Skinner
- Behaviorism
- Biological Preparedness
- Clark L. Hull
- Classical Conditioning
- Cognition
- Conditioned Inhibition
- Donald O. Hebb
- Edward Thorndike
- Functionalism
- Goal
- Habituation
- Hippocampus
- Information Processing
- Intervening Variables
- Ivan Pavlov
- Latent Inhibition
- Long-Term Potentiation
- Motivation
- Need Reduction
- Neural Network
- Neuron
- Operant Conditioning
- Positive Reinforcement
- Satiation
- Sensitization
- Turing Test

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## Learning Set Formation

### ► Learning to Learn

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## Learning Theory

### ► Cognition

## Learning to Learn

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### Synonyms

Deutero-learning; Learning set formation;  
Transfer of learning

### Definition

Learning to learn refers to the observation that prior learning often facilitates subsequent learning.

### Introduction

... in the late 1940s he [Harlow] achieved a major conceptual and methodological breakthrough with his discovery of learning sets. (Suomi and LeRoy 1982, p. 321)

Harlow's 1949 article, clearly describing for the first time, the concept of learning set formation, is one of the most widely cited articles in the animal behavior literature. (Schrier and Thompson 1984, p. 109)

Harry F. Harlow (1905–1981) is known for discovering the learning set (e.g., learning how to learn) phenomenon .... (Rumbaugh 1997, p. 197)

Despite Harlow's students' (e.g., Schrier and Suomi) and colleagues' enthusiasm for attributing the "discovery" of "learning to learn" to Harlow, it had been known in various guises, such as "formal discipline" or "transfer of training," at least, since the 1890s (Hall 1966, pp. 477–479). Nevertheless, an important event in the study of learning to learn, especially with nonhuman animals, was the publication of Harry Harlow's concept of "learning set formation" and, more importantly, his developing methods to investigate it and providing insightful measures to assess it. This was first presented in his presidential address on May 7, 1948, at the meeting of the

Midwestern Psychological Association and then published in the *Psychological Review* (Harlow 1949).

Generally unrecognized, 7 years prior to Harlow (1949), Gregory Bateson (1942), using the term *deutero-learning*, published a highly similar conceptualization to Harlow's (1949) learning set formation. Originally, Bateson's was a 16-page commentary on a presentation by his wife, the renowned anthropologist, Margaret Mead. It was reprinted with the publisher's permission in Bateson's more accessible *Steps to an Ecology of Mind* (Bateson 1972a) where he added a significant, related essay (Bateson 1972b).

Although Bateson did not have empirical data as Harlow did, Bateson presented two hypothetical data graphs (Bateson 1972a; please consult Bateson for "Fig. 1" and "Fig. 2") that projected results that remarkably anticipated Harlow's (1949) first two experimental results graphs ("Fig. 2" and "Fig. 3"); Harlow's "Fig. 1" (please consult Harlow for "Figs. 1, 2, and 3") was the well-known Wisconsin General Testing Apparatus (WGTA) developed by Harlow at the University of Wisconsin. The WGTA's most important function was to prevent an experimenter from inadvertently giving animals cues to make correct responses. Additionally, both Bateson (1942) and Harlow (1949) used the phrase "learning to learn" referring to the processes each was writing about.

Perhaps for understandable reasons, Harlow did not cite Bateson's prior work, as it was in a relatively obscure source for animal learning investigators. However, priority per se is not an issue here, as neither Bateson nor Harlow claimed originality regarding "learning to learn." Because Bateson published his contribution first, it will be addressed first. However, Harlow's contribution had a greater impact on comparative cognition, and it will be addressed more extensively.

### Gregory Bateson (1904–1980) and Deutero-Learning

Bateson (1972a) coined the terms "proto-learning" and "deutero-learning" to make the following distinction.

Let us say that there are two sorts of gradient discernible in all continued learning. The gradient at any point on a simple learning curve (e.g., a curve of rote learning) we shall say chiefly represents rate of proto-learning. If, however, we inflict a series of *similar learning experiments* on the same subject, we shall find that in each successive experiment the subject has a somewhat steeper proto-learning gradient, that he learns somewhat more rapidly. This progressive change in rate of proto-learning, we will call deutero-learning. (p. 167)

Later, Bateson (1972b) renamed proto-learning and deutero-learning as Learning I and Learning II, and he anticipated an even higher order or learning, Learning III, which is mind-boggling in its implications. If someone can determine how to investigate it scientifically, it has the potential to have a far greater impact than deutero-learning or learning set formation. However, further consideration of that is not appropriate here, and this entry will continue using the term “deutero-learning.”

Bateson (1942) did not consider his concept of deutero-learning to be original. Before coining the terms proto-learning and deutero-learning, he had written:

Now it so happens that in the psychological laboratories there is a common phenomenon of a somewhat higher degree of abstraction or generality than those which the experiments are planned to elucidate. It is a commonplace that the experimental subject – whether animal or man, becomes a better subject after repeated experiments. He not only learns to salivate at the appropriate moments, or to recite the appropriate nonsense syllables; he also, in some way, *learns to learn*. He not only solves the problem set him by the experimenter, where each solving is a piece of simple learning; but, more than this, he becomes more and more skilled in the solving of problems. (Bateson 1972a, p. 166; emphasis added)

As Bateson expressed it, he had merely coined the term “deutero-learning,” “. . . to avoid the labor of defining operationally all the other terms in the field (transfer of learning, generalization etc.)” (Bateson 1972a, p. 167).

Among his predecessors Bateson cited Maier (1940). Bateson wrote “. . . the concept of deutero-learning can be seen as almost synonymous with Professor Maier’s concept of “direction” (Bateson 1972a, p. 167). Bateson was too generous.

Maier’s concept of “direction” differed from Bateson’s “deutero-learning” and Harlow’s “learning set formation,” because Maier referred vaguely to improvement over unrelated tasks and Maier did not show how “direction” might be quantified.

### Harry Harlow (1905–1981) “The Formation of Learning Sets”

As mentioned above, Harlow’s (1949) article was his presidential address at the meeting of the Midwestern Psychological Association in May, 1948. In terms of the chronological development of the learning set formation concept, a footnote to the 1949 article shows that it was based on research that was “. . . supported in part by grants from the Special Research Fund of the University of Wisconsin for 1944–1948” (Harlow 1949, p. 51). The origin of Harlow’s learning set formation may be traced to an article published in 1944 (Harlow 1944) whose manuscript was received on June 18, 1942. Thus, although Harlow did not use the phrase “learning set formation” until 1949, he may have been developing it empirically and contemporaneously with Bateson (1942). Meanwhile, it is the 1948 presidential address and the resulting 1949 article that are typically cited as the beginning of Harlow’s learning set formation, and they will be considered first.

In Harlow’s 1948 presidential address, he began to discuss the broader role that learning plays in human and nonhuman animals’ lives. He asserted that “Our emotional, personal, and intellectual characteristics are not the mere algebraic summation of a near infinity of stimulus-response bonds” (Harlow 1949, p. 51). He continued,

The learning of primary importance to primates, at least, is the formation of learning sets; it is the *learning how to learn efficiently* in the situations the animal frequently encounters. (p. 51)

Harlow then described some of his empirical research, including an illustration of the WGTA and several graphs of illustrative data. As noted earlier, Harlow’s empirically based Figs. 2 and



3 were remarkably well-predicted by Bateson's (1942/1972a) hypothetical data graphs, Figs. 1 and 2.

Perhaps because the article was the text for an oral presentation, Harlow cited no references. However, Suomi and Leroy (1982) listed Harlow's 323 publications in chronological order beginning in 1932 and ending in 1978. Near the end of Harlow's (1948) presidential address, he identified what he believed to be his unique contribution.

The emphasis throughout this paper has been on the role of the historical or experience variable in learning behavior- the forgotten variable in current learning theory and research. Hull's Neo-behaviorists have constantly emphasized the necessity for an historical approach in learning, yet they have not exploited it fully. Their experimental manipulation of the experience variable has been largely limited to the development of isolated habits and their generalization . . . . Psychologists working with human subjects have long believed in the phenomenon of learning sets and have even used sets as explanatory principles . . . . These psychologists have not, however, investigated the nature of these learning sets . . . we have carried out studies that outline the development and operation of specific learning sets . . . it is our hope that our limited data will be extended by those brave souls who study real men and real women. (pp. 64–65)

## The "Evolution" for Harlow of the Concept of Learning Set Formation

Harlow (1944) was his first experimental research article related to "learning set formation" (hereafter LSF). However, he did not use the phrase LSF; rather, he considered the interpretation that the discrimination learning was occurring *insightfully* based on the use of "hypotheses" (Harlow 1944, p. 7).

Later, in the Discussion section, Harlow described the LSF process, although, as already noted, he did not use the phrase "learning set formation."

Indeed, once a monkey has solved a preliminary series of discriminations and has formed habits of responding to stimulus objects regardless of their position in space, later discriminations will be solved in a single trial or less, in a majority of

cases. Thus, if the first response is by chance correct, no additional errors will be made. If the first response is by chance incorrect, the error will be corrected on the succeeding trial and no additional errors will be made. In gestalt terminology the discrimination learning is occurring 'insightfully'. (Harlow 1944, p. 10)

[Five paragraphs later]

. . . once appropriate *reaction sets* have been formed in monkeys these sets may be transferred from one pair of discrimination objects to another making it possible for the subjects to meet a strict criterion for formation of a discrimination with a minimum amount of specific training. (p. 11)

Zable's and Harlow's (1946) interpretational emphasis was on forming "hypotheses," but their use of "hypotheses" was not that developed later by Harlow's student, Marvin Levine, whose "win-stay, lose-shift" hypotheses became so well associated with LSF (Levine 1959). Levine meant, if the animal chooses correctly on trial 1, that is a "win" and to obtain maximum reinforcement on succeeding trials, it should "stay" with its original choice. If the animal chooses incorrectly in trial 1, that is to "lose" and it should "shift" to the other discriminandum to obtain maximum reinforcement. As tests of LSF developed, new problems might be introduced for varying numbers of trials. However, the common practice that eventually emerged was to introduce a new problem every six trials. Discriminanda have typically been objects, and Harlow often described the task as "object quality learning set."

Learning to learn can be investigated in other ways as Harlow (1959) did with reversal learning. Harlow's emphasis here was on the development of learning, and he used rhesus monkeys ranging from neonates to adults. One example was to use a Y maze to train an infant monkey to learn to first go to the left arm of the Y for reinforcement until it met a predetermined number of trials-to-criterion (e.g., 90% correct responses in 20 trials). Then, the investigator reverses location of the reinforcers to the right arm of the Y maze. Typically, there is a persistence in going to the left arm but eventually, the monkey learns that reinforcement is now received with responses to the right arm. After a number of reversals and if the animal is

learning to learn, it will detect the reversal more quickly. Often, one nonreinforced trial is sufficient to inform the animal that a reversal has occurred. Of course, reversal learning can be done in many ways. For example, rather than left versus right in a Y maze, the animal might learn reversals between, say, black versus white alleys with position of the alleys changed on 50% of the trials. Generally, Harlow's young monkeys also performed the alley reversal task well.

As noted, Harlow changed the left-right position of the "correct" alley in the black-white alley reversal task on 50% of the trials, and it is widely realized that with most tasks (including LSF), the positions of the discriminanda must be changed over trials randomly or quasi-randomly. Quasi-random changes have advantages as described by Fellows (1967) whose article includes quasi-random series that many investigators have used in their research.

The 6-trial, object quality LSF task has been used with many species, so it will be the remaining focus here. The experimenter determines which discriminandum will be reinforced (typically but not always with food) for the six trials. The animal can choose only by chance on trial 1, but if learns to learn, it will learn to use information about trial 1 to choose correctly (e.g., "win-stay, lose-shift") for the remaining five trials. Trial 2 performances have been the most used measure of LSF.

## A Failed Application of LSF

Warren (1965) suggested that LSF formation might be a good way to compare species' learning abilities, and he published a graph where the ordinate was PER CENT CORRECT ON TRIAL 2 and the abscissa was PROBLEMS. Warren reported data from six species. The best performer was a rhesus monkey with 85% correct on trial 2 after 400 problems. A rat and a squirrel tied for worst performance with 60% correct after 1800 problems.

This application of LSF reached its zenith with a graph presented by Hodos (1970) on which he plotted data from 16 species including two children. The best performer was a child (age

unspecified but  $IQ = 136$ ) who had 100% correct on Trial 2 after 100 problems. The tree shrew was the worst performer at 50% correct on trial 2 in 1000 problems.

However, Warren (1974), who had initiated the use of LSF as a way to compare learning abilities of various species, also brought it to its end when he wrote:

Primates differ from other mammals in their extraordinary development of the visual system. They surpass most other mammalian species in respect to their capacity for color vision, stereopsis, and visual acuity. . . it is apparent that we have no basis for guessing the degree to which the inferior performances of non-Primate species in visual learning set problems reflect an inferiority in visual sensitivity and perception instead of a defective capacity for learning. (Warren 1974), p. 448.

Warren and others (e.g., Thomas 1980) discussed other contextual variables that might provide some species with advantages and other species with disadvantages in performing learning tasks. Optimally, in species' learning or intelligence test comparisons, such contextual variables will be adapted to be most suitable for each species.

Warren (1974) cited a study by Slotnick and Katz (1974) who used olfactory learning set discriminanda (floral scents) to study LSF by rats. The scents could only be delivered one at a time via a complicated, expensive, and tedious-to-use apparatus. The authors did not report percentages correct on trial 2, but they did report a number errorless or one-error problems, and they "... suggested that a "win-stay, lose shift" hypothesis was in effect" (Slotnick and Katz 1974, p. 798).

Not cited by Warren (1974), Langworthy and Jennings (1972) used a much simpler and less expensive way to present olfactory discriminanda to study oddity concept learning by rats which can also reveal LSF as shown below. They used ping pong balls saturated with the odors of one of eight food flavorings. As a given odor might be odd on some problems and nonodd on other problems, no odor could be exclusively associated with either odd or nonodd.

Three balls, two of the same odors and the third of a different odor, were presented side by side on a platform holding an open-air chute in which the balls were inserted. Marks on the chute showed

how far the rat had to nudge the odd ball aside to access the food cup beneath it. Langworthy and Jennings (1972) reported good results, but it was unclear whether the food reinforcer was only beneath the odd ball. If so, it is possible that the rats detected the correct ball by smelling the food beneath it.

Thomas and Noble (1988) and Bailey and Thomas (1998) followed Langworthy and Jennings in using odoriferous ping pong balls as discriminanda, but among other differences, they used 16 (Thomas and Noble) or 18 (Bailey and Thomas) food flavorings and 5-trial problems. As with Langworthy and Jennings, no odor was associated exclusively with odd or nonodd. They also baited all food wells, so food odor could not be a cue to the odd ball.

Bailey and Thomas (1998) made other changes, and for present purposes their study might be considered the more useful than the other. Both studies were designed to determine whether rats might learn the oddity concept, but the problems were presented in a learning set paradigm. Neither Thomas and Noble (1988) nor Bailey and Thomas (1998) found evidence of oddity concept learning, as performances on the first trials of new problems were at chance, but Bailey and Thomas who administered 60 problems found that their three rats averaged 87% correct on trial 2, on problems 16–30 and 81% correct on trial 2 on problems 16–60.

## LSF's Place Among Other Learning Processes

Harlow (1958) identified some problems' association with the study of' the evolution of learning including:

Another difficulty lies in existing limitations to a precise classification of the forms of learning and learning problems into levels of difficulty... the problem is far from solved; and no one has even attempted to scale the various learning problems or classes of problems . . . (p. 269).

Before we can return to the topic of this section, it is necessary first to show the progress made since Harlow's observation just quoted.

Gagné (e.g., 1970), who focused on human learning, proposed a hierarchy of eight types of learning, which he asserted to encompass any and all types of human learning. They were, generally deemed to be hierarchical on the assumption that lower levels, usually, were prerequisites for higher levels. From lowest to highest in Gagné's hierarchy were signal learning (i.e., classical or Pavlovian conditioning), stimulus-response learning (i.e., operant conditioning), chaining, verbal association, discrimination learning, concept learning, rule learning, and problem solving. Gagné's examples for verbal association and for his top three levels were taken from human learning literature, and most would not be feasible with non-human animals.

Thomas (1980) sought to develop a comprehensive hierarchy of learning types that could be used with all animals including humans. Thomas discovered that Bourne's (1970) approach to concept learning, which was to base it on tasks constructed to comply with formal logic (explained below), could replace Gagné's highest three levels and still account fully for any and all types of learning at Gagné's three highest levels. Additionally, this approach could be used with humans and nonhuman animals.

Gagné (1970) regarded verbal association to be parallel to chaining, so verbal association being less amenable to testing among most animals could be eliminated from Thomas's hierarchy (Thomas 1980). Thomas noted that Gagné had overlooked a lower form of learning than signal learning, namely, habituation and its complementary process, sensitization. Gagné clearly described discrimination learning as learning multiple discrimination problems concurrently, so Thomas renamed it concurrent discrimination learning.

Bourne (1970) based concept learning on tasks that were constructed to comply with the truth-function tables in formal logic. Bourne's lowest level involved only the logical operations affirmation and negation, which Thomas considered to be the foundations for class concepts. For Thomas (1980), this became level 6, class concepts. Bourne's middle level of concepts were based on the logical operations, conjunction, disjunction, or conditional and their complementary processes,

all of which Bourne considered to be parallel processes. Agreeing with Bourne that they were parallel processes and assuming that class concepts were prerequisites for concepts based on them, Thomas's level 7 became relational concepts involving conjunction, disjunction, or conditional operations and their complementary processes. Finally, Bourne regarded the logical operation for the biconditional and its complementary process to be above the three at his middle level, because the conditional is a prerequisite to the biconditional. In Thomas's hierarchy, level 8 became relational concepts based on the biconditional and its complementary process. Most research has focused on the primary as opposed to the complementary processes, so the complementary processes will be ignored here henceforth. However, one must always assume they can be present and tasks may be constructed based on them. Thomas equated learning ability with intelligence, and he considers his hierarchy to be a learning-intelligence hierarchy.

### Thomas's Learning-Intelligence Hierarchy

8. Relational Concepts based on the Biconditional
7. Relational Concepts based on the Conditional, Conjunctive, or Disjunctive
6. Absolute and Relative Class Concepts based on Affirmation and Negation
5. Concurrent Discrimination Learning
4. Chaining (Chains of S-R Learning Units)
3. Stimulus-Response (S-R) Learning or Operant Conditioning
2. Classical or Pavlovian Conditioning
1. Habituation and Sensitization

Note that both Gagné's (1972) and Thomas's (1980) hierarchies are on an *ordinal scale*. Thomas followed Gagné's order generally; however, Thomas considers that levels 2 and 3 (Classical and Operant Conditioning, respectively) might be parallel. Also, as it has been shown that representative species from all vertebrate classes (except amphibians appear not to have been tested) can succeed to some extent at level 5, Thomas believes that most mammalian and avian differentiations in learning abilities are

likely to be found among Levels 6–8, class and relational concepts.

To show class concept learning at level 6, one must use trial-unique discriminanda, or if the same discriminanda are presented more than one time, evidence for concept learning must be limited to the data from the first trials of presentations of new discriminanda. Otherwise, the animal might have learned the task by rote based on trial and error. *With absolute class concepts, it is not necessary to compare discriminanda.* For example, if the concept being investigated is "tree" and the animal is shown trial-unique examples of trees, and if the animal knows or has acquired the concept of "tree," it will respond directly to the discriminandum of a tree to show that it recognizes new exemplars as being trees. Some exemplars may be a fuzzy fit, and those may cause errors (e.g., shrubs vs. trees).

With relative class concepts *it is necessary to compare discriminanda to affirm which discriminandum represents the concept.* Perhaps the most studied relative class concept with animals has been the "oddity concept." Typically, the animal is shown trial-unique examples of three discriminanda, two of which are identical and the other is different or "odd"; and to recognize which one is odd it must compare the discriminanda.

Since Thomas's first publication of the learning-intelligence hierarchy 1980, he has had occasion to make minor emendations (e.g., Bailey et al. 2007). In Bailey et al., Thomas addressed a matter that had puzzled him for decades, namely, where in the hierarchy of learning types does LSF fit. He decided it best fit as a parallel process subsumed under concurrent discrimination learning. For Gagné, concurrent discrimination learning referred to multiple discrimination problems learned in parallel. LSF refers to multiple discrimination problems learned serially. Thomas (2012) explained further why LSF should not be considered to be an instance of concept learning.

### Concluding Remarks

"Learning to learn" has a long history under a variety of labels. However, it was Gregory

Bateson and Harry Harlow who gave it a more substantial theoretical foundation, and Harlow provided clear means to investigate and measure it. Ironically, Bateson (1942, 1972a) had expressed doubt that it could ever be studied in the laboratory, although later (Bateson 1972b) acknowledged Harlow (1949).

Thomas (2012), who concluded that LSF is not at the level of concept learning, also wrote:

Nevertheless, some may consider it to be an open question whether to agree with Thomas and colleagues, and many who study concept learning in animals regarding (a) what “conceptualization” means or (b) that the necessary evidence for conceptualization requires that the subject respond correctly to trial-unique [exemplars] or first trials with new exemplars of the concept. For example, one might argue that learning a strategy or “rule” such as that which humans might verbalize as “win-stay, lose-shift” involves conceptualization. However, it must also be recognized that with animals it is unlikely that they learn anything akin to such verbalizations of a rule or strategy, not to overlook that it is unlikely that an experimenter could provide unequivocal evidence that they did. (p. 1968.

Finally, there may be room to advance the status of LSF, and that may be a challenge for future investigators.

## Cross-References

- [Comparative Cognition](#)
- [Harry Harlow](#)
- [Intelligence](#)
- [Learning](#)
- [Olfactory Discrimination](#)
- [Primate Sensory Systems](#)
- [Reversal Learning](#)
- [Transfer of Learning](#)
- [Wisconsin General Test Apparatus](#)

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## Learning-Set Paradigm

- [Two-Alternative Forced-Choice Paradigm, The](#)

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## Lemur

- [Prosimian Cognition](#)
- [Prosimian Communication](#)
- [Prosimian Life History](#)

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## Lemur, Tarsier, New World and Old World Monkey, and Ape Locomotion

- [Primate Locomotion](#)

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## Leporid

- [Lagomorpha Life History](#)

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## Lesley J. Rogers

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### Early Life and Educational Background of Professor Lesley J. Rogers BSc (Hons), DPhil, DSc, FAA

Lesley J. Rogers was born in Brisbane, Australia, in 1943 and grew up in the outskirts of Adelaide, South Australia. From very early, she was fascinated by animals, both pets and wild animals then abundant in the bushland and creeks where she lived.

On completion of her schooling, she won a Bursary and Commonwealth Scholarship to the University of Adelaide. Initially, she planned to major in physics, but after experiencing the constant displays of overtly negative and sexist behaviour of male staff and predominantly male students in that field, she shifted her attention to the study of animal biology, published her first scientific paper (Rogers 1966) and graduated with first-class honours in Zoology (1964). Her outstanding results won her a scholarship and teaching fellowship to continue her studies at postgraduate level at Harvard University, USA, which she took up the following year. That was at the height of the protests against the Vietnam War in the mid-1960s. She had already been involved in anti-war activities in Adelaide and continuing them in Boston led to her being forced to leave Harvard University after 18 months of study. Although her stay in the USA was under threat, she managed to stay on for a further year working as a research assistant to Professor Marshall M. Kaplan on the isoenzymes of alkaline phosphatase, finding a method to separate plasma isoenzymes generated by the liver versus bone and hence to an easy and accurate diagnosis of liver and bone disorders (Kaplan and Rogers 1969).

In 1968, she moved to London, where she taught science to secondary school students before commencing study for a Doctor of

Philosophy at Sussex University and simultaneously tutoring physics and chemistry to students at the newly established Open University. Under the tutelage of Professor Richard Andrew at Sussex University, she followed her life-long interest in animal behaviour (ethology) and was awarded a Doctor of Philosophy degree in 1971 for research on attentional effects of testosterone on domestic chicks (Andrew and Rogers 1972).

## Professional Career

In 1972, Lesley returned to Australia to take up an academic position in the physiology department at Monash University in Melbourne. There, she conducted research in the laboratory of Richard Mark on the biological correlates of learning and memory. When Richard Mark moved to take up a professorial position at the Australian National University, Canberra, she joined him at the ANU as a senior research fellow in behavioural biology to complete a number of projects.

It was during this time that she made the breakthrough discovery of asymmetry of visual processing in the avian brain; viz., the left hemisphere dominates the ability of the animal to learn a visual discrimination task, whereas the right hemisphere controls aggressive and sexual behaviour (Rogers and Anson 1979).

On returning to Monash University, in the pharmacology department, she continued investigation of lateralized brain function and made her second landmark discovery that development of lateralization in the chicken depends on light exposure of the embryo before hatching: visual stimulation during a critical stage of ontogenesis establishes asymmetry of visual processing. Rogers thus became a leading scholar who discovered asymmetry in the non-human brain and overturned the previously held view that brain asymmetry is determined entirely by genetic processes (as acknowledged and discussed by Güntürkün et al. 2020).

Appointed in 1985 as a lecturer in the physiology department at the University of New England, Armidale, NSW, and following the award of a Doctor of Science from Sussex University in

1987, she rose through the ranks to a personal chair in 1993.

In 2000, she became an elected fellow of the Australian Academy of Science as one of the internationally significant figures in Australian science. On retirement in 2007, she was the first woman at her university to be appointed as emeritus professor.

Her main research collaborators have been professors Richard Andrew at Sussex University, the United Kingdom; Giorgio Vallortigara at the University of Trento, Italy; and Gisela Kaplan at the University of New England, Australia. As of 2020, she has published 233 peer-reviewed papers, 52 book chapters, 12 authored or co-authored books, 7 edited books and 6 special volumes of journals. She continues to conduct research and publish her findings.

## Research Contributions

On returning to Australia in the 1970s and joining the research group of Professor Richard Mark at Monash University, Rogers conducted research on the biological correlates of learning and memory. Using different inhibitors of neural function, it was shown that short- and long-term memory depend on separate cellular processes. One part of this research discovered that long-lasting effects on learning could be caused by brief inhibition of brain protein synthesis in young chicks (Rogers and Drennen 1978). This emerged as a tool for investigating functional differences of the left and right sides of the chick brain.

At that time, asymmetry, or lateralization, of the brain was thought to be a unique characteristic of the human species, a specialization separating us from all other species. Rogers made a breakthrough discovery of asymmetry of visual processing in the avian brain. Disruption of the chick's ability to learn to find grains of food scattered amongst pebbles was caused by treatment of the left hemisphere with cycloheximide, but it did not occur after the same treatment of the right hemisphere (Rogers and Anson 1979). Treatment of the left hemisphere, she found, intercepted biological processes of development

in the first week of life after hatching, and it was followed by short period of susceptibility of the right hemisphere. Thus, it was found that each hemisphere develops at a different rate and each assumes a different way of processing visual information. This asymmetry can be revealed simply by testing a bird with a patch over one eye and then comparing the effect on behaviour with that occurring when the patch is on the other eye.

The next significant step in Rogers' research was the discovery that asymmetry of visual behaviour develops only if the embryo in the egg is exposed to light during a critical period just before hatching. No visual asymmetry develops if the eggs are incubated in the dark (Rogers 1982). The reason for this is that the embryo is oriented inside the egg so that only its right eye can be stimulated by light. Rogers was able to reverse the direction of asymmetry by opening the egg just before hatching, occluding the embryo's right eye and allowing only the left eye to be stimulated by light (Rogers 1990). The behavioural differences between chicks using their left versus right eye were traced to asymmetry of one of the visual pathways in the brain (Rogers and Sink 1988). Hence, brain and behavioural asymmetry, she showed, can be generated and modulated by sensory stimulation in early life. This discovery overthrew another belief about brain lateralization, viz. that it is fixed by expression of the genes alone.

The discovery of asymmetry in the avian brain led to research on lateralization in other species, and in Rogers' laboratory at the University of New England, this included amphibians, marsupials and mammals (summarized by Rogers et al. 2013b). The latter also included research on hand preferences in orangutans conducted with Gisela Kaplan (Rogers and Kaplan 1996) and a series of studies on lateralization in common marmosets (e.g. Cameron and Rogers 1999; Hook and Rogers 2000). In collaboration with Kaplan and students, lateralized visual behaviour was also shown in other avian species, especially the Australian magpie (e.g. Koboroff et al. 2008).

In collaboration with Giorgio Vallortigara at the University of Trento, Italy, Rogers has considered the advantages and disadvantages of having a

lateralized brain (Vallortigara and Rogers 2005). Together with their students, they showed empirically that lateralized chicks have a clear advantage over non-lateralized chicks when they have to use each hemisphere simultaneously to process different information, viz. the left hemisphere to search for food and the right to detect a predator (Rogers et al. 2004). Furthermore, by comparing lateralized behaviour of social and solitary species of bee, they showed that a bias for lateralization to be aligned in a population depends on whether a particular behaviour involves social interaction (Rogers et al. 2013a, 2016).

In both dogs and primates, Rogers and students demonstrated that hand/forepaw preference, as a reflection of which hemisphere is in control, is associated with cognitive bias, exploration behaviour and stress responses (e.g. Gordon and Rogers 2015). Recognition of this led to considering the interface between lateralization, cognition and welfare of animals (e.g. Rogers 2010; Rogers and Kaplan 2019).

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## Leslie Matrix

### ► Fitness

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## Lessening

### ► Need Reduction

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## Lesser Ape

### ► Haplorhini

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## Levallois Technique

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The term “Levallois technique” refers to a strategy of stone tool production, specifically a means of taking a block of stone (core) and producing sharp-edged flake tools through percussive application of a stone hammer. This particular strategy is based around the production and organization of a specific “prepared-core” form (sometimes referred to as “tortoise” or “turtle-backed” cores). This strategic approach to core organization and flake production contrasts with simpler (migrating platform) reduction techniques, which involve simply rotating the core and selecting suitable striking positions on a more ad hoc basis. Stone-tool industries manufactured by these strategies begin to appear broadly simultaneously in both East Africa and Europe around 300,000 years ago (Tryon and Faith 2013), suggestive of convergent technological developments in these different regions (Adler et al. 2014). As with much of the terminology surrounding description of Palaeolithic stone tools, the term “Levallois” is derived from France and refers to the suburb of Paris where such industries were discovered in the late 1800s (Bar-Yosef and Dibble 1995). Following their initial appearance, stone-tool assemblages that include a Levallois component are known from sites across Africa, Europe, and Asia, although they appear to have been less commonly used in East Asia compared with other regions.

The appearance of Levallois industries during the latter half of the Middle Pleistocene has

contributed to an enduring interest in these industries among archaeologists. Based on their chronology and their geographic distribution, the use of the Levallois technique has an association with both Neanderthal populations (*Homo neanderthalensis*) and early modern humans (*Homo sapiens*). This associates the emergence of Levallois industries with a key phase in human evolution, when relative brain sizes were approaching the modern human range, and the point at which our own species was emerging (Hublin 2009). These factors – as well as the implication that these industries represent an organized and strategic approach to predetermined stone flake production – has contributed to the role these artifacts have also played in discussions surrounding the evolution of cognitive abilities, planning strategies, learning strategies, and linguistic capabilities during the latest phases of human evolution (Schlanger 1996; Lycett and Eren 2013). By no means is there agreement among archaeologists on several of these matters, and a diversity of opinions can be seen in the literature surrounding these industries.

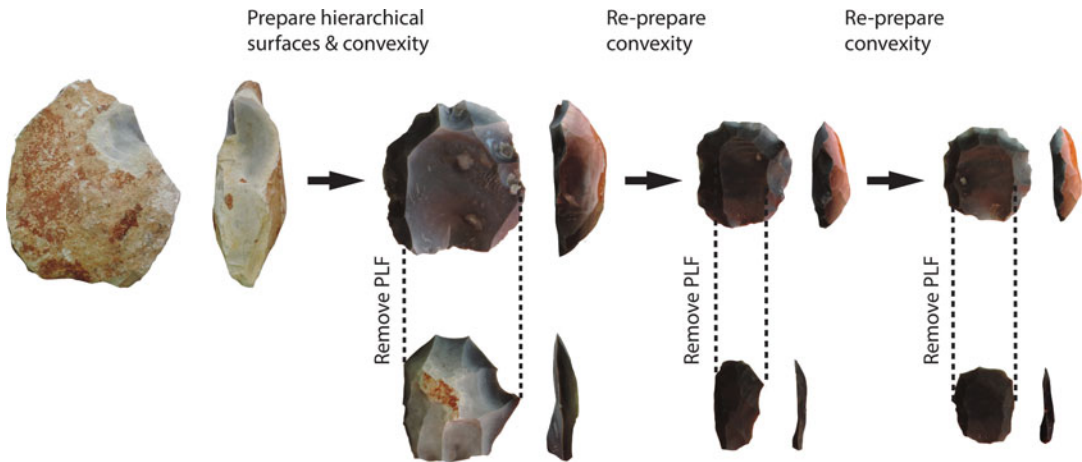
Levallois-style industries began to draw academic attention during the late 1800s (for historical reviews see Bar-Yosef and Dibble 1995; Lycett and Eren 2013). Spurrell, an archaeologist who described a series of sites in southeast England in 1884, for example, referred to the geometric configuration of domed cores he was observing, the specific use of “prepared” surfaces, and the production of large “knife-like” and “turtle-backed” flakes from these specially prepared cores (see Lycett and Eren 2013 for discussion and further references relating to this history). This emphasized the idea that specific core forms were being produced in order to procure flakes that removed a large portion of the core’s specially prepared surface. During the early part of the nineteenth century, scholars in France and the United Kingdom repeated many of these sentiments, setting much of the tone of discussion relating to Levallois industries over the subsequent years. In the 1950s, the famous French archaeologist François Bordes lay down what may be the quintessential definition of Levallois as a means of producing large flake(s) “predetermined

by special preparation prior to its detachment from the core” (translation from Schlanger 1996: 231). Paraphrases of this definition can be seen in archaeological and human evolution textbooks to the present day.

Of particular note in discussions of Levallois has been reference to the “Levallois flakes,” or the flakes that are removed from the specially prepared and domed surfaces of the Levallois core. The influence of Bordes in particular led to Levallois industries often being defined and classified on the presence and frequency of these “Levallois” flakes. In some respects, however, this emphasis on flakes resulted in Levallois industries being thought of in archaeological terms, less as a technique or process, but more as an end product or result. By the 1980s, however, disquiet concerning the reliability by which so-called Levallois flakes could be reliably identified was increasingly being stated. These difficulties surrounding the definition and conceptualization of Levallois industries have been referred to as the “Levallois problem” (see Van Peer 1992 for review).

Recognition of the Levallois problem led some to return the issue of technique and process of manufacture as a central concern (Schlanger 1996). Most notably, Boëda (1995) outlined an influential description and definition of Levallois manufacture based around what he referred to as the “volumetric concept.” Boëda’s conceptualization of Levallois production emphasized several points. Among these was the bifacial configuration of the core, consisting of two flaked surfaces that intersected (Fig. 1). One of these surfaces was steeper than the other and may retain remnants of the original rock surface. The other face was extensively flaked, being domed in form. It is from this latter surface that the Levallois flakes were removed through removal of a flake or flakes by means of a blow at an angle broadly parallel to the plane of intersection (i.e., margin) demarcating the core’s two surfaces. Upon removal of these flakes, the core’s domed surface can be reinstated by removing a series of short flakes from around the core’s margin. Thereafter, further Levallois flakes can be removed. It has been shown that several series of these flaking episodes on a single





**Levallois Technique, Fig. 1** Classic sequence of Levallois reduction, showing the removal of a “preferential Levallois flake” (PLF) at the close of each sequence. In the initial phase (left), a nodule is taken and the bifacial configuration of the core is established, consisting of two flaked surfaces that intersect. These surfaces are

hierarchically organized: one being for the preparation of striking platforms, the other being the surface from which PLFs are removed. This latter surface is domed, exhibiting convexity across its surface. Following initial removal of the first PLF, the convexity of the primary surface can be reprepared and further PLFs may be removed

core may have been undertaken by prehistoric peoples (Van Peer 1992; Schlanger 1996).

In recent years, increased attention has been given to the motivating factors potentially underlying the widespread production of Levallois industries. This has included recognition that Levallois reduction may have statistical dimensions of variability that distinguish it from more ad hoc (migrating platform) strategies of production. This includes a demonstration that Levallois cores configured according to Boëda’s (1995) volumetric concepts, can result in an economic means of core reduction while simultaneously maximizing the length of cutting edge removed from the primary flaking surface of the core (Brantingham and Kuhn 2001; Lycett and Eren 2013). Recent discussions have also emphasized that, at a statistical level, the Levallois technique provided prehistoric peoples with a means of producing flakes with strong edge angles and greater potential to be resharpened repeatedly (Eren and Lycett 2016). Current discussions are, therefore, emphasizing a range nonmutually exclusive features that, in combination, may explain why assemblages made through application of the Levallois technique were so widespread during the latter part of the Pleistocene.

## Cross-References

► [Stone Tools](#)

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## Lexigrams

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## Synonyms

[Lexigraph](#)

## Definition

A lexigram is a single symbol that graphically represents a single word or concept. A collection of lexigrams makes up a lexigraphy, a logographic writing system in which English words are represented by pictures or symbols. Lexigrams are designed to be unequivocal, with meanings semantically and syntactically unambiguous.

## Introduction

The lexigram as a word-symbol was developed in tandem with artificial language consisting of the first set of lexigrams, named “Yerkish” in honor of Dr. Robert M. Yerkes and Yerkes National Primate Research Center (“Yerkes”) at Emory University in Atlanta, Georgia, where lexigrams were first used (Rumbaugh et al. 1973; von Glasersfeld 1974).

Lexigrams were developed for the purposes of exploring the capacity for language in great apes and have been used extensively in chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) communication research, notably including Kanzi, arguably the most proficient nonhuman primate language user (Lloyd 2004). Since the inception of lexigrams as analogues for English, use has expanded beyond great ape language research to include communication research in other animals such as the domestic dog (*Canis familiaris*, Rossi and Ades 2007). Work with human children indicates arbitrary lexigrams, such as those used in nonhuman communication research, are comparably learnable to iconic images that display visual similarity to referents (Barton et al. 2006). Communication aids using pictures, lexigrams, and other symbols are also used as an instrument to facilitate communication for children and adults with developmental delays and language disabilities. This practice has largely been found to be effective in improving vocabulary comprehension and production (Allen et al. 2017; Lancioni et al. 2007). Lexigrams are an important tool in the work of animal communication researchers, developmental researchers, and language disorder specialists.

## Development

The development of lexigrams was a response to great ape language research. The work of Gardner and Gardner (1969) demonstrated vocabulary acquisition in the chimpanzee, Washoe, and the subsequent work of Gardner and Gardner (1971) and Premack (1971) in visual signs and symbols as a means of communication led Rumbaugh et al. (1973) to question the limits of ape language behaviors and in turn develop a technology primarily for the purposes of objective and efficient investigation into language acquisition and ability.

The first 125 lexigrams were developed at Yerkes as a part of the Language ANAlog (LANA) project, Lana being the first chimpanzee to be trained in the use of lexigrams. The design of these lexigrams, their computerization, and

Yerkish grammar was carried out by von Glasersfeld and Pier Paolo Pisani with three guidelines in mind that can be summarized from von Glasersfeld (1974) as:

1. Design constraint: Visual, single-word symbols able to be represented on single keys and combined to form a keyboard.
2. Unequivocal meaning: Discrete semantic and syntactic meaning with no ambiguity.
3. English Translation: Similar enough to English for word-for-word translations to be understood by English speakers.

### Design Constraint

Rumbaugh et al.'s (1973) design for the original lexigrams adhered to a design code characterized by the presentation of specific design elements that could be superimposed atop one another. Nine single design elements, including lines and shapes, were combined in unique ways to yield 255 symbols (Fig. 1). These symbols were differentiated by eight basic colors. Red, for example, corresponds with ingestible items, such as the lexigram for "food" and "drink," while green indicates parts of the body (Fig. 2). With shared design elements and color-coded features, a simple semantic code was achieved, wherein conceptual categories are indicated by shared symbolic features (von Glasersfeld 1974).

### Unequivocal Meaning

Discussed by Rumbaugh et al. (1973), these initial lexigrams were based upon spoken English language, with specific care taken to eliminate the natural syntactic and semantic ambiguity of words. Each lexigram corresponds to a single meaning of a single English word, and are therefore semantically unambiguous. For example, the lexigram for "stick" always refers to a long, thin, solid, rounded object, such as a small piece of wood from a tree, and never to one object adhered to another, to a "stick" of butter, or any other use of the word.

Strict one-for-one relationships between concepts and lexigrams address semantic ambiguity. Syntactic ambiguity refers to a sentence in which the receiver cannot discern the meaning due to ambiguity regarding role assignment. The

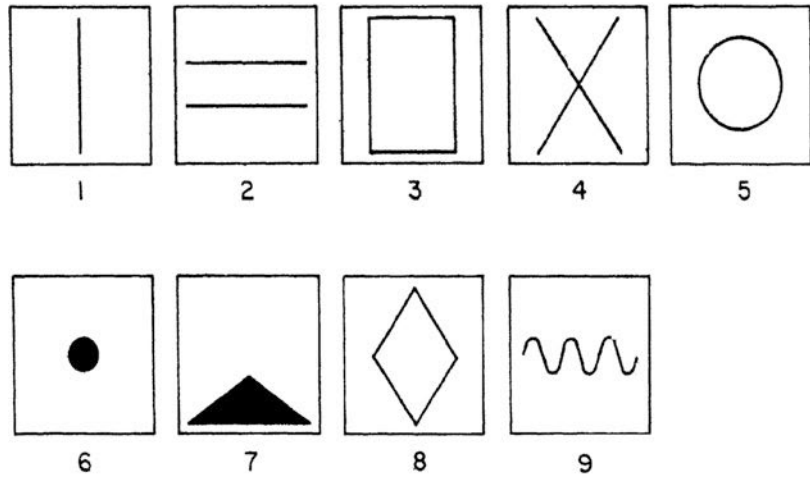
sentence "He put the ketchup on himself" consists of words that are semantically unambiguous, yet syntactic ambiguity results in a listener unsure whether he put the ketchup in his lap or on an appropriate food item all by himself. Eliminating syntactic ambiguity for lexigrams was achieved by using a correlational grammar structure developed previously by von Glasersfeld (1974) in his work with machine translation and automatic language analysis.

The grammar structure of lexigram phrases is correlational due to the way in which lexigrams are linked. Adjacent lexigrams can be thought of as a left-hand (LH) and a right-hand (RH) piece, linked by an implied correlator between them. The initial vocabulary of lexigrams consisted of 35 conceptual classes, with possible RH lexigrams for each LH determined by the characteristics of its class and each class differing from each other. Where English grammar allows the separation of semantics and syntax, lexigram phrases do not. The order of lexigrams defines the grammatical structure, as Rumbaugh et al. (1973) explain regarding the phrase "Lana eats juice." While the use of the English word "eats" is semantically incorrect in referring to "juice," the syntactic validity of the statement remains. This is a phrase that conforms to English grammar. The phrase "Lana eats juice" constructed with lexigrams, however, is neither semantically nor syntactically valid. "Juice" does not belong to a conceptual class that allows the subject to "eat" it, and therefore, the phrase violates the rules of correlational grammar.

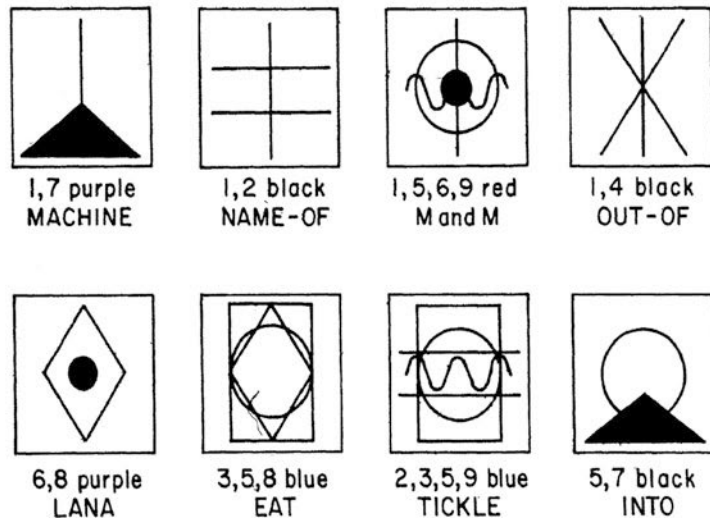
The number of lexigrams and grammatical correlators was limited during initial inception, but Rumbaugh et al. (1973) point out the system is open-ended, with no inherent constraints on the possible number of lexigrams that could be incorporated into a language system and no limit to the number of conceptual classes or resulting correlators. With strict adherence to a unitary one-lexigram one-meaning system, a system of lexigrams can be composed of many semantically distinct words, and as a vocabulary that utilizes correlational grammar grows, so too does the number of conceptual classes and correlators that connect these words, without violating the principals of unequivocal semantic and syntactic meaning.

**Lexigrams, Fig. 1** Design Elements and Examples of Lexigrams, attributed to von Glasersfeld 1974 ((c) ACL.) (Licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 International License. Presented unaltered)

# DESIGN ELEMENTS



# EXAMPLES OF LEXIGRAMS



## English Translation

As lexigrams were developed primarily for use by researchers in exploring communication, the translations between lexigram phrases and their word-for-word English translations are intended to be understood by English speakers. Word meanings have a direct relationship between lexigram and English, but as von Glasersfeld (1974) confers, the grammar employed is

specifically designed to be simple, consistent for the learner, and structurally similar to English in order to aid understanding by the receiver, as evident in the phrase “stick which-is blue dirty.” The phrase in lexigrams does not require adverbs such as “the,” nor linking verbs such as “is.” Despite using different rules of grammar, the direct translation “[the] stick which is blue [is] dirty” is salient for English speakers.

## Semantic Colour-Coding of Lexigrams

| Colour     | General Type                            | Lexigram Classes                               |
|------------|-----------------------------------------|------------------------------------------------|
| violet     | Autonomous Actor                        | AP, AV, AO, AM.                                |
| orange     | Spatial Objects,<br>Spatial Concepts    | FA, FP, TF, CT, WR.                            |
| red        | Ingestibles                             | EU, EM, ED.                                    |
| green      | Parts of Body                           | PB.                                            |
| blue-grey  | States and Conditions                   | ST, LS, CD.                                    |
| blue       | Activities                              | VA, VB, VC, VD, VE, VG,<br>VL, VM, VP, VS, VW. |
| black      | Prepositions, Determiners,<br>particles | DC, DD, DQ, DP, LP, ID,<br>NF, PP.             |
| white (+)  | Affirmation                             | "YES"                                          |
| yellow (+) | Sentential Modifiers                    | Query, Please, Negation,<br>Period.            |

(+) White and yellow are available in the first feedback projector (left) only, where the sentential modifiers appear.

**Lexigrams, Fig. 2** Semantic Color-Coding of Lexigrams, attributed to von Glasersfeld 1974 ((c) ACL.) (Licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 International License. Presented unaltered)

## Animal Language Research

### Kanzi

Born at Yerkes in October 1980, Kanzi, a bonobo, was assigned to the Language Research Center (LRC), at Georgia State University in Atlanta, Georgia, alongside his mother at 6 months old. Lexigram keyboards were typically used at the LRC in accordance with language training

procedures established in part by Rumbaugh et al. (1973), though the lexigram communication system itself differed considerably. Lexigrams used at the LRC did not feature color codes for class or adherence to a correlational grammar (Savage-Rumbaugh et al. 1986).

Kanzi, while present during his mother's training exercises, was never a participant himself. Despite this, Sue Savage-Rumbaugh's team



reportedly observed Kanzi, in his mother's absence, spontaneously use the lexigram keyboard. This use of lexigrams without explicit training and instruction changed the way LRC research with chimpanzees and bonobos was carried out, instead shifting to a language learning model involving more naturalistic methodology. As Savage-Rumbaugh et al. (1986) report, this language-rich environment would consist of both lexigrams and spoken English, with researchers modeling lexigram use concurrently with typical spoken conversation between one another as well as when communicating directly to subjects.

Within the first week of following Kanzi after his mother temporarily left the LRC, he was found to proficiently use eight lexigrams, and over the next 17 months, effectively used 44 different lexigrams in 764 unique combinations (Savage-Rumbaugh et al. 1985). Kanzi's vocabulary has continued to grow, with reportedly high success both using lexigrams and understanding spoken English (Savage-Rumbaugh et al. 1993).

### Sofia

A noteworthy case of lexigram use in non-primate animal research is that of Sofia, a dog born in São Paulo and raised in Rossi's home as a pet (Rossi and Ades 2007). The lexigram keyboard used includes configurations closely resembling the original eight design elements of Rumbaugh et al. (1973), consisting of six distinct configurations of lines and shapes, plus a blank key, and sheet of newsprint. These lexigrams include the English meanings: walk, petting, toy, water, food, crate, and lastly urine, corresponding with the sheet of newsprint. Arranged into a three-dimensional lexigram keyboard, these symbols were used to investigate the production of communicative behavior (Rossi and Ades 2007).

Sofia was able to use these lexigrams in Rossi and Ades' (2007) trials with a significant success rate, with gaze-direction and nondirected action patterns such as nose-licking suggesting both intention and motivation. Lexigrams were shown to be generalizable, with Sofia using a single lexigram to refer to many items within the same category: Toy, for example, was induced by stuffed toys, balls, and a laser pointer. Spontaneously,

Sofia was also able to use lexigrams directed at strangers naïve to the experiment. The study of Sofia's use of lexigrams by Rossi and Ades (2007) was the first of its kind to be conducted with dogs, and speaks to the enduring value of lexigrams in animal communication research.

## Human Augmentative and Alternative Modes of Communication

Systems for aiding communication with children and adults with developmental delays and language disabilities can broadly be referred to as Augmentative and alternative modes of communication (AAC) and include tools such as the Picture Exchange Communication System (PECS) or comparable pictorial systems, and voice output communication aids (VOCAs). PECSs include lexigrams as well as iconographic imagery, and these combined form sets of graphics that are used to facilitate communication as an alternative or augmentation to spoken language. VOCAs are electronic devices that produce verbal messages in response to manual selection of images such as those found in PECSs (Lancioni et al. 2007).

AAC devices, both PECSs and VOCAs, have been studied to determine efficacy in use with persons with developmental disabilities such as autism, clinically severe to profound mental retardation, childhood apraxia of speech, and other complex communication needs. These systems have been found to be successful for the introduction of request-making, vocabulary skill improvement of single words, and improvement in production of multi-symbol expressions (Allen et al. 2017; Lancioni et al. 2007).

## Conclusion

Rooted in the initial designs of the LANA project, lexigrams have changed since their creation as a system of the artificial Yerkish language. Whereas color-coded conceptual classes and correlational grammar were not used by the LRC, the group was instrumental in popularizing use of lexigrams

with headline-making chimpanzees and bonobos. Great ape use of lexigrams persists, as does use in communication research with other animals, including domestic dogs. Lexigrams are also used as a tool to facilitate communication with children and adults with developmental delays and language disabilities.

## Cross-References

- Canine Communication
- Communication
- Comparative Psychology
- Computerized Testing Paradigm in Primates
- Duane Rumbaugh
- Georgia State University's Language Research Center
- Kanzi
- Language
- Language Research: Great Apes
- Primate Communication
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- Robert Mearns Yerkes
- Sue Savage-Rumbaugh
- Washoe
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## Lexigraph

- Lexigrams

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## Libido

- Psychopharmacology of Sex Steroids

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## Life Cycle

- Lifetime Expectancy
- Microchiroptera Life History

## Life Expectancy

### ► Lifetime Expectancy

## Life History

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## Introduction

All living organisms, ranging from archaea and bacteria to fungi, plants, and animals, can be described through their life cycle, which is how and when they grow, mature, reproduce, and die. The description of the life cycle is what we define as the life history of a species. The study of the diversity of life histories allows us to understand the causes and consequences of the variation in life cycles that range from a few hours for some bacteria to a few centuries for some plant species. When it comes to understanding the tremendous diversity of life histories found in nature, two traits become particularly important: survival and fecundity. Indeed, the probability that an organism survives long enough to reproduce (juvenile survival), the probability that it survives long enough to do so repeatedly (adult survival), and the number of offspring produced at each reproductive event (fecundity) add up to determine the total number of offspring produced throughout the lifetime of an organism. Lifetime number of offspring provides an estimate of Darwinian fitness (the genetic contribution of an individual to the next generation's gene pool) and is what natural selection ultimately acts on. Hence, variations in life history, and by extension variations in survival and fecundity, are molded by natural selection and expected to mirror adaptation of populations and species to their environment (Roff 1992; Stearns 1992).

Variations in life history and adaptation to the environment can be classified along a fast–slow

continuum, with high reproductive rate and low survival at one end versus slow reproductive rate and high survival at the other end. Organisms with fast life histories thrive in unpredictable or unstable environments that cause large fluctuations in population growth rates ( $r$ ) and population sizes. Organisms with slow life histories, however, prosper in more stable environments thereby allowing their population sizes to be close to the maximum sustainable size in the given environment or carrying capacity ( $K$ ) (Oli 2004; Saether and Bakke 2000; Salguero-Gómez et al. 2016). In population ecology, fast and slow life histories are thus referred to as  $r$ - and  $K$ -strategies, respectively (MacArthur and Wilson 1967). Organisms with fast life histories include, among others, bacteria, annual plants (grasses), and small mammals (mouse), whereas organisms with slow life histories are well represented by perennial plants (trees) and large mammals (elephants and humans). Yet, most organisms' life history falls somewhere in-between a fast and a slow pace of life.

## Fitness and Life History Trade-Offs

Following the theory of evolution by natural selection, an organism should maximize its Darwinian fitness at any given time. Thus, an organism with highest Darwinian fitness would start reproducing directly after being born, reproduce continuously, produce an infinite number of offspring at each reproductive event, and live indefinitely. The existence of such an organism, the so-called *Darwinian demon*, presumes the absence of any constraints at all. However, all living organisms need energy and time to grow, maintain their bodies, and reproduce. In nature, resources are usually in limited supply, and there is often competition to access them (e.g., food patches for animals, access to sunlight and minerals for plants). When food is unlimited, such as during large migrations of prey species, in mast years of seed production, or under artificial conditions, there are still limitations on how much food an organism can ingest and in how efficiently it transforms energy enclosed in food into cellular

energy, used to fuel its life cycle. Therefore, each organism is expected to have access to limited (non-infinite) resources that must be divided among life history traits such as growth, body maintenance, and reproduction. In addition, all biological, chemical, and physical processes take time to complete and have a specific order in which they need to be realized. Thus, each organism is also expected to be constrained in terms of when and how it should allocate its limited resources among different life history traits. How much energy and time is allocated to one life history trait at the expense of others is what defines a life history trade-off (Stearns 1992). As mentioned above, from an evolutionary perspective, the optimal solution to a life history trade-off is one that maximizes Darwinian fitness. There is, however, rarely a single solution to a given life history trade-off, and multiple solutions, depending on environmental conditions, are possible. As a consequence, solutions to a trade-off can greatly differ among species but also among populations within a species and among individuals within a population (McNamara and Houston 1996). Alternative solutions to a given life history trade-off are defined as alternative life history strategies.

There are a large number of trade-offs that can be defined in the context of energy and time allocation to reproduction and survival. Some of the most important trade-offs that organisms face through their life cycle are (i) how fast and how long to grow before starting to reproduce, (ii) how often to reproduce and how much time and energy to invest in each reproductive attempt, and (iii) how to divide resources between offspring number and size.

### The Trade-Off Between Growth and Reproduction

The trade-off between growth and reproduction determines an organism's size and age at first reproduction. Some stages of the life cycle of organisms, specifically the early stages, are particularly vulnerable to predation. As the probability of dying from predation greatly declines when an organism increases in size, selection should favor individuals with a fast growth during the

life stages most susceptible to predation. Furthermore, when predation remains important throughout the life cycle, selection is also expected to favor individuals that reach sexual maturity quickly and have an early onset of reproduction. Examples of the trade-off between growth and reproduction are found across fish species, where small species like guppies (*Poecilia reticulata*), which mainly feed on invertebrates, use their energy to grow fast and reproduce rapidly, but never attain the size that would give them defense against predators. Larger fish, like the Atlantic bluefin tuna (*Thunnus thynnus*) or the great white shark (*Carcharodon carcharias*), which are opportunistic predators, reach a large size but have a much delayed reproduction. In species that grow continuously throughout their life, selection will select for an optimal size at first reproduction following two conditions: first, fecundity needs to increase with size (e.g., female fish produce more eggs as they grow larger, and trees produce more seeds as they grow bigger); and second, growth rate needs to decrease after reproduction started, due to energy being allocated to both reproduction and growth rather than to growth alone. Age at first reproduction in Atlantic cod (*Gadus morhua*) is a good example of the growth versus reproduction trade-off. A reduction in age at first reproduction of Atlantic cod has been observed with an increase in fishing pressure on larger-sized animals, which removed some of the benefits of growing large before reproducing for the first time (de Roos et al. 2006; Rowell 1993). Similarly, an optimal size at first reproduction is also expected in species that do not grow continuously but where individuals could start to reproduce before completing body growth. In bighorn sheep (*Ovis canadensis*), where females could start to reproduce at 2 years old and grow until 6 years old, age at first reproduction is strongly affected by body size suggesting an optimal size for first reproduction (e.g., Martin and Festa-Bianchet 2012).

### The Trade-Off Between Current Reproduction and Survival

The trade-off between current reproduction and survival posits that the amount of resources

allocated to immediate reproduction at the cost of survival will be justified by the probability of reproductive success. It is therefore expected that the frequency and amount of reproduction are negatively correlated with the longevity of a species. It is easy to think of circumstances under which reproduction could lead to decreases in survival. Reproductive individuals might be more visible (e.g., birds' plumage colors during reproduction, mating displays and calls that attract both mates and predators), more active, slower, or less agile than nonreproductive individuals and thus may suffer higher risk of predation. Higher risk of predation due to reproductive behavior can arise in four different ways. First, predators or parasites may detect mating calls or mating displays such as opossums locating mate calling frogs (Ryan et al. 1981). Second, instead of detecting mating calls, predators might attract prey by mimicking their mating calls. In fireflies, females of the species *Photuris versicolor* attract and predate male of other firefly species by mimicking the mating flashes of other female species (Lloyd 1975; Lloyd and Wing 1983). Third, the increase in activity linked to reproduction might increase an animal's predation risk by either making it more visible or by simply increasing its probability to encounter predators. In tick-tock cicadas (*Cicadetta quadricincta*), mate-seeking males are more frequently captured by web-building spiders than females are (Gwynne 1987). Fourth, defense of young by parents might place a reproductive individuals at higher risk of predation when the predator can prey upon both parents and the offspring. In sticklebacks, males guard and defend the brood against fish predation (Pressley 1981). In addition to an increase in predation-related mortality, reproductive individuals might be exposed to a higher risk of death by disease, if the energy invested in reproduction is diverted from the immune system and physiological maintenance of the organism. Thus, trade-offs between current reproduction and survival are linked to trade-offs between reproduction and body condition, since most of the time a decrease in survival probability after reproduction is due to a decrease in overall body condition. Furthermore, the trade-off between reproduction

and survival is strongly linked to the trade-off between current and future reproduction since an individual must survive in order to reproduce in the future.

### The Trade-Off Between Offspring Quantity and Quality

Once an individual commits to reproducing, given the set amount of energy it can allocate to reproduction, a major trade-off is the trade-off between offspring quantity and quality. This concept considers that offspring survival is dependent on their "quality," e.g., body size. Thus, in order to maximize Darwinian fitness, the limited amount of resources invested in reproduction should be maximized as a function of number of offspring and offspring quality. Should the majority of energy be invested in producing only one sizeable offspring or multiple smaller offspring? When offspring survival is low, two main strategies could arise to maximize the probability of offspring reaching maturity. First, if increasing the size of an offspring increases its survival, then producing fewer, larger offspring would be adequate. However, this is also a risky strategy since only a few offspring are produced. The second strategy to counterbalance low juvenile survival is not to try to increase juvenile survival but simply to produce an extremely large number of offspring, thus leading to a high probability of having some offspring reaching maturity. Orchids are a good example for the strategy of producing large numbers of offspring with minimum energy invested per individual offspring, given that orchids have the smallest seeds of all flowering plants and produce millions of them. An orchid seed has virtually no reserves and relies on symbiotic interactions with a fungus to develop (Kull et al. 2009). On the other hand, flowering plants such as the coco de mer (*Lodoicea maldivica*) produce only a few seeds, but each seed weighs between 15 and 30 kg, allowing them to germinate and grow on really poor-quality soil. The trade-off between number and size of offspring could also be observed within species. A classic model for this trade-off is Lack's clutch size in birds (Lack 1954), which illustrates that there are an optimal number of offspring to produce. The model



stipulates that if the survival probability of an offspring decreases as the number of offspring produced increases, then there are an optimal number of offspring that maximize the number of offspring surviving. The decrease in offspring survival probability with larger clutch size could be due to a decrease in egg size or an increase competition between offspring for parental care.

### **Life History Trade-Offs and the Evolution of Viviparity and Parental Care**

Increasing the size of the egg or the offspring is not the only strategy to maximize the number of surviving offspring. The probability of an offspring surviving until adulthood is an important parameter linked to a number of different trade-offs. Since juvenile survival has a direct impact on Darwinian fitness, strategies to increase early survival are under strong selection. The evolution of different modes of reproduction, from oviparity to ovoviviparity and viviparity, was driven also by life history strategies that allow reducing early juvenile mortality and favoring the production of fewer offspring but of higher quality. Oviparous animal species lay eggs that contain high amount of nutriment and that develop outside the body cavity of their mother. In ovoviviparous species, the embryo is still relying on resources enclosed in the egg for its development, but the eggs are retained inside the female's body cavity until they are ready to hatch. It allows reducing exposure to predation and pathogens during the egg stage. Finally, viviparous species produce very small eggs that have few or no nutrients, the embryo must feed on resources passed on from the mother during development, and thus mothers give birth to live offspring. It allows the production of larger and more mature offspring, further reducing the costs of predation and pathogen exposures. Generally, the same is true for the evolution of any form of parental care that reduces juvenile mortality and permits greater investment in fewer, larger offspring (Clutton-Brock 1991; Royle et al. 2012).

### **Life History Trade-Offs in Semelparous and Iteroparous Reproductive Strategies**

Life history traits, such as fecundity, timing of reproduction, size and number of offspring, and parental care, can be grouped together into general reproductive strategies that are used by multiple species. Semelparity occurs when a species reproduces only once during its lifetime, produces a large number of offspring, and then dies. Semelparity is thus also known as "big bang" reproduction. Semelparous species accumulate resources and use them during a single reproductive event, detrimental to their own condition, to the point that they do not survive. Semelparity is seen in annual plants, in long-lived plants such as agaves, in many species of fish such as salmon, in insects, and in mollusks, but rarely in large vertebrates. Iteroparity describes species that reproduce repeatedly during their lifetime. Some animals are able to mate only once per year but survive through multiple mating seasons. Most perennial plants are iteroparous, as are most mollusks, insects, and vertebrates, including most reptiles as well as virtually all mammals, birds, and most fish. Semelparous and iteroparous strategies are the result of alternative prioritization of life history trade-offs. In semelparous organisms the main trade-off is how much an organism should grow before reproducing, given that size and fecundity are related, whereas in iteroparous organisms, the main trade-off is how much to invest in each reproductive event versus maintenance and survival.

### **Acquisition and Allocation of Resources in Life History Trade-Offs**

While studies of life history trade-offs have been highly successful at illustrating trade-offs comparing multiple species and using a phylogenetic approach, studies of trade-offs within species are often more problematic. Life history trade-offs are, by definition, a compromise in resource allocation. However, not all individuals acquire the

same amount of resources, a notion known as individual heterogeneity in resource acquisition. When among-individual variation in resource acquisition is small relative to the variation in resource allocation to reproduction and survival, then a trade-off between survival and reproduction could be observed (van Noordwijk and de Jong 1986). On the other hand, when variation in energy acquisition is large relative to the variation in energy allocation, a positive correlation between survival and reproduction is observed instead of a trade-off. As an example, when testing for trade-offs between growth and reproduction, there may be no apparent trade-offs if size and resource acquisition covary, and thus larger individuals have more resources than smaller individuals to invest in both growth and reproduction (Reznick et al. 2000). However, once the variation in size or resource acquisition is controlled for, either experimentally or statistically, trade-offs should become apparent (Reznick et al. 2000). Thus, when studying life history trade-offs, it is important to understand and consider the existence of individual heterogeneity (Tettamanti et al. 2015).

The amount of available resources for organisms to acquire and allocate to life history traits frequently varies with environmental conditions in either a predictable or an unpredictable manner. In a variable and predictable environment, being able to adjust resource allocation according to environmental conditions and thus to resource acquisition is key to maximizing Darwinian fitness. The capacity to respond differently to different environmental conditions is referred to as phenotypic plasticity. Phenotypic plasticity in life history traits is observed in a wide range of species. For example, spring temperature is a good predictor of timing of food availability in insectivorous great tits (*Parus major*), and the date on which adults lay their eggs varies as a function of spring temperature. This allows synchronization of the hatching date of individuals' clutches with the date of peak caterpillar abundance, thus optimizing resource availability for offspring growth and fitness (Charmanier et al. 2008).

## Mechanisms of Life History Evolution

For life history traits to evolve, they must have a genetic basis. Hence, our understanding of the evolution of life history trajectories also requires an understanding of the genetic, molecular, and physiological pathways that link the genotype to the phenotype. A main assumption of life history theory is that trade-offs are generated by competitive allocation of resources, with the allocation of limiting resources to one trait having negative consequences for other traits requiring the same resources (Flatt and Heyland 2011; Zera and Harshman 2001). As a consequence, the diversification of life histories is closely linked to all the molecular and physiological activities that regulate the flow of energy through the body of organisms – that is to say their metabolism. Variation in the secretion of hormones with strong effects on the metabolism and on life history trade-offs is thus one of the mechanisms underlying the integration of life history traits. In animals, this includes steroid hormones such as the male hormone testosterone and the stress hormone corticosterone, which both regulate the trade-off between reproduction and survival, and metabolic peptides such as the insulin-like growth hormone that regulates the trade-off between growth and somatic maintenance (Flatt and Heyland 2011; Zera and Harshman 2001). Remarkably, genes encoding for such hormones and their receptors, which match growth and reproduction to nutrient supply, have been found to be evolutionarily conserved in the animal kingdom, ranging from organisms such as the budding yeast (*Saccharomyces cerevisiae*), the nematode worm (*Caenorhabditis elegans*), and the fruit fly (*Drosophila melanogaster*) to humans (Flatt and Heyland 2011). Mechanistic explanations of life history trade-offs do not rely uniquely on competitive resource allocation, and systems such as metabolic waste management can also generate non-resource-based trade-offs. For example, in aerobic organisms, the transduction of energy from food to cellular energy during mitochondrial respiration has, as an inevitable side effect, the production of reactive oxygen species that can

damage the soma as well as reduce organism reproduction and survival (Monaghan et al. 2009). Indeed, when the production of reactive oxygen species outweighs the cellular antioxidant defenses, organisms are exposed to oxidative stress. This stress can mediate life history trade-offs, such as that between reproduction and survival, if the processing of resources allocated to reproduction creates an oxidative debt on survival (Monaghan et al. 2009; Stier et al. 2014).

## Life History and Behaviors

For a long time, animal behaviors have been poorly considered when studying life history and natural selection. However, the emergence of research on animal personalities has led to both the development of new theories and the accumulation of evidence about the importance of behaviors in shaping species' life histories (Réale et al. 2009; Martin et al. 2014). In particular, the existence of feedback loops between behaviors and life histories or morphological traits has been shown to provide an adaptive explanation for the evolution of animal personality and for the development of life histories (Wolf et al. 2007). For example, individuals with high expectations of future reproduction, that have much to lose, should be more risk-averse than individuals with low expectations. In addition, being more risk-averse increases survival probability and thus by definition increases expectations of future reproduction. This creates a positive feedback loop where the behavior and life history strategy are reinforcing each other.

Studies on sexual selection also illustrate important correlation between life history and behaviors with the existence of alternative mating strategies (Réale et al. 2009). Alternative mating strategies are usually defined by alternative mating behaviors, allowing the emergence of alternative reproductive and life history strategies. A good example is the difference between different mating strategies in the Atlantic salmon (*Salmo salar*). Dominant males grow rapidly, migrate to sea, delay maturation, and mate guard females whose eggs they can easily fertilize.

Sneaker males do not migrate to sea, have limited growth, have early maturation, cannot mate guard females, and have to avoid mate-guarding males to try and fertilize females' eggs. However, they can outcompete dominant males in sperm competition for fertilization by producing higher-quality sperm (Vladić and Petersson 2015).

## Conclusion

Life history theories state that organisms maximize their Darwinian fitness through optimization of their life history traits as a function of multiple trade-offs. The study of life history trade-offs and of the diversity of life histories helps to understand the main selection pressures that organisms are facing in addition to why and how they are adapted to their environment. To gain insights on the diversity of life histories, it is important to not only understand the ultimate consequences of trade-offs but to also understand the proximate mechanisms underlying them. Finally, life history traits are not limited to morphological and reproductive traits but include physiological and behavioral traits. The pace-of-life syndrome hypothesis specifies that a suite of metabolic, hormonal, immunity, and behavioral traits have coevolved with life history particularities related to different ecological conditions (Réale et al. 2010). This hypothesis therefore provides an integrative framework to study both proximate mechanisms of behaviors and their ultimate consequences for life history evolution.

## Cross-References

- [Acquisition](#)
- [Additive Genetic Variance](#)
- [Arthropod Life History](#)
- [Artiodactyla Life History](#)
- [Bear Life History](#)
- [Bovine Life History](#)
- [Canine Life History](#)
- [Cephalopod Life History](#)
- [Cetacean Life History](#)
- [Feline Life History](#)

- Genetic Variation
- Insect Life History
- Lagomorpha Life History
- Lifetime Expectancy
- Marsupial Life History
- Microchiroptera Life History
- Mustelidae Life History
- Passerine Life History
- Personality in Animals
- Phenotype
- Pinniped Life History
- Prosimian Life History
- Rodentia Life History
- Salientia Life History
- Squamate Life History
- Swine Life History
- Testudines Life History

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## Life History Strategies

- [Bear Life History](#)

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## Life History Trade-Offs

- [Semi-aquatic](#)

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## Life History Traits

- [Bear Life History](#)

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## Life Table

- [Bear Life History](#)

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## Lifespan

- [Lifetime Expectancy](#)

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## Lifestyle

- [Catarrhine Life History](#)

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## Lifetime Expectancy

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## Synonyms

[Aging rate](#); [Biological time](#); [Life cycle](#); [Life expectancy](#); [Life history](#); [Lifespan](#) [Longevity](#); [Maximal longevity](#)

## Definition

Lifetime expectancy can be defined as either the average or the maximal duration of the lifetime (lifespan) of individuals of an animal species after birth or eclosion. The average or typical (modal) duration of individual lifespan is dependent on a variety of factors, including habitat, habits, extrinsic mortality rates, and environmental variables, but still varies within the maximal known lifespan of the species.

## Introduction

How long an animal lives is not a freely variable amount of time that depends simply on extrinsic, environmental factors. Fruit flies and lab worms live not much more than 3 weeks in the best of conditions; mice hardly ever reach 2 years of life even if kept fed, sheltered, and safe from all predators in controlled animal housing facilities; the healthiest humans are still not expected to live much more than one century. The fact that different animal species have characteristic maximal lifetime expectancies, and that these vary across species from under 1 day to over one century, strongly indicates that there are innate, biological determinants of longevity. This entry explores some of the current knowledge and theories about what factors determine lifespan, and therefore lifetime expectancy.



## Life History, Biological Time, and the Pace of Life

How much of life goes by for different species within a similar period of time? Only 4 days separate the day when an individual *Caenorhabditis elegans* worm ecdyses and when it is biologically capable of laying eggs and reproducing, and only under very rare circumstances and conditions will that worm individual still be alive 1 month later. In contrast, humans are still just about as helpless at 1 month as they were at 4 days of age, and it will take over a decade until they become biologically competent to reproduce. Although the biological bases of animal life are universal, life runs at a different *pace* for different species: *biological time* is not directly comparable across animals. The combined, absolute, and relative duration of time spent in each stage of life – embryonic development, infancy/postnatal growth, adolescence, sexually competent adult life, old age – is referred to as the *life history* of a species. How come biological time and therefore life history varies by four orders of magnitude across species remains one of the main fundamental unanswered questions in biology – although important insights have occurred recently.

The temperature at which the body functions and therefore at which all chemical reactions occur is of course a major variable across the enormous diversity of non-vertebrate animals, and also among fishes, amphibians, and non-avian reptiles. Broadly speaking, the warmer the temperature at which the body of an animal works, the faster its metabolic rate (as expected from simple thermodynamics), the faster the pace of life, and the shorter the lifespan of the animal. Similarly, metabolic rate per gram of body also decreases as animals become larger, and along with it the pace of life seems to slow down, and life expectancy increases. However, this relationship breaks down upon closer inspection. For instance, birds function at systematically higher body temperatures and have predictably higher metabolic rates than mammals of similar size, yet birds have a lifetime expectancy that is as much as 20 times that of rodents. Indeed, as explored further below, even when body temperature is removed from the equation by nature, life

history remains enormously variable. Across endotherm, homeotherm animal species (birds and mammals), songbirds live systematically longer lives than primates, which in turn live systematically longer lives than non-primate mammals of similar body mass.

Despite the apparent regularities across the entire animal phylum as a whole, it is obvious already at the most superficial level of observation that different animal species live at different rates. There is enormous diversity in life, and not one single way or pace of living. What determines biological time for different animal species?

## Extrinsic Factors

For decades, one favored explanation for the different life histories spanning four orders of magnitude across animal species, from one day to one century, was extrinsic mortality rates: the higher the likelihood of being predated upon on an average day, the stronger is the selective pressure for a species to develop quickly and reach sexual maturity earlier rather than later, which over generations would lead to lifetime acceleration as an adaptive feature driven by natural selection (Charnov 1993). As a consequence, longevity should increase as the probability of death caused by extrinsic factors decreases (Austad and Fischer 1991). In support of that proposition, there are known instances in which documented changes in predation risk have indeed been accompanied by changes in lifetime expectancy in the predicted direction within particular species. In the case of birds, flight has been evoked as a factor that significantly lowers predation risk and thus might account for the slower life history and longer life expectancy (Munshi-South and Wilkinson 2010) – although in that case *all* bats would be expected to be longer-lived than other mammals of similar size, which is not the case. Besides the scant experimental support, one major difficulty with this line of reasoning is that it presupposes that biological life histories are highly plastic, which is not compatible with available evidence. Most importantly, pinning the determination of lifetime expectancy down on extrinsic factors runs inevitably into a mathematical tautology (since increased longevity *is defined* as lower

probability of death at any age) and circular reasoning that do not account for *how* diversity in biological lifetimes would arise in the first place, before any selection occurs. Another strong argument against extrinsically determined life histories is that there are striking regularities in lifetime expectancy across species, explored below, that make it far more likely that there are intrinsically, biologically determined mechanisms that set the pace of growth, maturation, and aging.

### **Intrinsic Factors: Rate-of-Living and Rate-of-Aging**

One highly influential theory for an endogenous mechanism of setting the pace of life is the appropriately named Rate-Of-Living theory (Pearl 1928), according to which the duration of life of an organism is curtailed upon the exhaustion of a fixed quantity of something vital at a rate proportional to the metabolic rate. The value of this fixed quantity would depend on an intrinsically, genetically determined “metabolic potential,” and also on the rate of metabolism, which may be determined extrinsically (by environmental temperature, e.g., in the case of heterotherm animals) or intrinsically (in the case of endotherm animals).

As mentioned above, body temperature does affect all chemical reactions in an organism, including proteostasis (the balance between rates of protein synthesis, folding, damage, and disposal), and impact life history in *C. elegans* as expected, shrinking life history and shortening lifetime expectancy as populations are raised in warmer environments (Stroustrup et al. 2016). Shorter life histories as a whole, and lifetime expectancies, in particular, are predicted by models that presume progressive accumulation of damages to both proteins (Santra et al. 2019) and DNA (Hoeijmakers 2009), depending both on temperature and metabolic rate (West 2018). The process of accumulation of damages to proteins, DNA, lipids, and other vital molecules and structures is now widely considered as an underlying feature of aging. Thus, variation in lifetime expectancy across animal species and individuals is currently largely presumed to originate from variations in the rate of aging. At this point, however, variations in the rate of aging across species

remain mostly an intuition not yet backed by strong experimental support. For example, while the rate of telomere shortening and presumably DNA repair ability is an excellent predictor of maximum longevity across a small sample of nine warm-blooded species (Whittemore et al. 2019), it is possible that it is the larger accumulation of DNA damages with a longer life that makes DNA repair ability appear higher in longer-lived species. It is difficult to tease apart cause and consequence in the generation of lifetime diversity from simple correlations.

### **Resilience to Aging**

Recently, however, a novel variable brought into play did make simple correlations highly revealing by showing that body size and metabolic rate are not required to explain the wide range of variation in lifetime expectancy across warm-blooded animals, or the clade-specific differences (Herculano-Houzel 2019). The combination of a large dataset on life history with a novel dataset on the numbers of neurons that compose the brains of different species showed that across birds and mammals alike (not including bats, which were not available for analysis), variations in the estimated number of neurons in the pallium (cerebral cortex) account for as much as 74% of the variation in lifetime expectancy (measured as maximal longevity) across a sample of 750 species. Most importantly, clade-specific differences across birds, primates, and other mammals disappear; and after accounting for the number of pallial neurons in each species, residual analysis shows that body size and specific metabolic rate are mathematically irrelevant. Thus, the more the cortical neurons found in the adult brain of a warm-blooded species, the longer its life history, with sexual maturity reached only at older ages and expanded maximal longevity after reaching maturity – and humans are no exception (Herculano-Houzel 2019). It is too early to tell what lies underneath that correlation, and even if numbers of cortical neurons do have a determining role in life history and longevity or are simply a proxy for the true determinant factor, although it has been proposed that the correlation *is* causal through increased resilience to aging incurred with more

postmitotic, cortical neurons in the brain (Herculano-Houzel 2019). Importantly, this proposition is well in agreement with the large body of evidence showing that in a wide range of animal species, and also across individuals, caloric restriction and exercise, the two manipulations that undisputedly extend longevity, also protect neurons in the cerebral cortex in a variety of ways.

## Conclusion

Biological time differs across species, as evidenced by the fact that there is enormous diversity in lifetime expectancies across animal species, and that this diversity in turn originates from similarly enormous diversity in life histories. The pace of life does have some dependence on factors that affect metabolic rate, like body size and temperature, especially across heterotherm animals. However, a new possibility to be investigated is that in homeotherms, the damages that define aging accumulate at similar rates, regardless of metabolic rate, and a new factor comes into play: the number of cortical neurons in the network that maintains the physiological integration of the body, in such a way that the larger that population of neurons is, the more resilient is the network, and so longer the body remains viable.

## Cross-References

- Allometry
- Life History
- Senescence

## References

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## Lifetime Reproductive Success

- Fitness

## Light/Dark Cycle

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## Definition

Light/dark cycle refers to the periodic alternation between different levels of illumination in an environment.

## Concept, Implications and Applications

Light/dark cycles are oscillations in the light level in a given natural or artificial environment, with a regular periodicity. The natural light/dark cycle of our planet has a period of 24 h. Most natural and artificial light/dark cycles have a state of complete darkness (dark phase), alternated with a state of

bright light (light phase). However, the dark phase may consist of dim light, in some ecological contexts or in artificial light/dark cycles built for specific purposes, as explained below.

The natural daily light/dark cycle experienced at a point on Earth results from the rotation of the planet around itself, which promotes the periodic oscillation between bright days and dark nights every 24 h, due to alternate exposure to the Sun. No natural light is expected to reach environments at depths below 10 cm in land or 1000 m in the oceans; thus, these places are devoid of light/dark cycles (Beale et al. 2016). What we recognize as light is only a portion of the compound electromagnetic radiation that comes from the Sun during the light phase (Spitschan et al. 2016). The total Sun radiation is composed of different wavelengths, and “light” consists of the wavelengths that stimulate the human eye (400–700 nm). In the dark phase, extra illumination may come from the Moon, depending on the lunar phase. A clear sky on a cloudless day may be as bright as 100,000 lux, while the illuminance of a full moon night sky is less than 1 lux (Spitschan et al. 2016).

In natural environments, there are smooth transitions between the light and the dark phases, the twilights (Roenneberg and Foster 1997). Twilights are formally defined as the times of the day when the Sun is below the horizon, at angles between 0° and –18° (Daan and Aschoff 1975; Spitschan et al. 2016). Besides the change in light level, a daily variation in light color is also found within the light phase, mostly during the twilights. This implies that, at different times of the day, there is a change in the relative proportions of the wavelengths that reach the Earth’s surface (Spitschan et al. 2016). Such changes result from the different angles with which the Sun radiation passes through the atmosphere.

Due to the Earth’s round shape and its inclined axis of rotation at 23°, the proportion between light and dark hours (photoperiod) is not the same throughout the year and along the latitudes (Bradshaw and Holzapfel 2007). At low latitudes close to the equator, the yearly variation in photoperiod is smaller. At extreme latitudes close to the poles, profound photoperiod variations occur, with constant nights in the winter and constant

days during summer, although there are still daily oscillations in light composition (Krüll 1985).

Along with the light/dark cycle, daily changes in abiotic and biotic variables constitute the day/night cycle experienced by organisms within the 24 h, in diverse natural environments. Different from most of the other variables, the light/dark cycle is precisely stable from year to year at the same location, so that today’s light/dark cycle will be repeated precisely, on the same day in the next year or 10,000 years from now (Bradshaw and Holzapfel 2007). However, changes in weather, vegetation cover, and terrain may impact the daily light oscillation perceived in specific microenvironments (DeCoursey 1989).

The predictability of the natural light/dark cycle rendered it as a pervasive environmental cue that is used as a time reference for living organisms to adjust themselves to the day/night cycle. The existence of daily changes in light, since ancient geological times, was an evolutionary pressure that promoted the selection and consolidation of endogenous daily variations in physiology of most organisms, the circadian rhythms. These rhythms are the expression of circadian clocks, self-sustained physiological pacemakers that are synchronized daily by the light/dark cycle (Roenneberg and Foster 1997). Thus, the role of the light/dark cycle is not only an acute signal of day and night but also a dynamic signal that sets the phase and period of endogenous circadian clocks. Since photoperiod also changes in a precise fashion along the year, it is a trustworthy cue to the seasons. Therefore, similarly to its role in the daily timing of circadian rhythms, the light information is also used as a cue to the time of year (Bradshaw and Holzapfel 2007). Photoperiod adjusts the timing of annual rhythms in reproduction, migration, and other biological phenomena in many species.

Given its importance in signaling time to living organisms, artificial light/dark cycles have been widely used in experimental research on circadian rhythms and photoperiodic responses. Most experimental protocols apply rectangular light/dark cycles, built from abrupt transitions between the light and dark phases (DeCoursey 1989),

although some studies attempt to model natural twilights and the changes in light color. Depending on the purpose of the study, experimental research may use light/dark cycles with different periods, different proportions between the light and dark hours, and with variable average and amplitude in light level oscillation.

The behavior and habitat use of an animal, in the temporal and spatial dimensions, contribute to how it experiences the daily light/dark cycle (DeCoursey 1989; Roenneberg and Foster 1997). For instance, migrating organisms that travel through varying latitudes and longitudes experience unique light/dark information. Dendwelling, fossorial, and subterranean animals only expose to light while outside of their burrows in the light phase. Likewise, human beings in urban locations stay within low-light environments during most of the day and only experience full natural light while in transit between home and work.

Human societies have yet another source of variation in the light/dark cycles. Urban cities are illuminated pervasively by electrical light, which imposes exposure to light at times when the natural environment should be in the dark (Spitschan et al. 2016). Light exposure at night is even greater for individuals that work night shifts. This light information at unexpected hours has been associated to disturbances in human sleep and circadian rhythms and has been correlated to health issues, such as obesity and cancer (Navara and Nelson 2007). Experimental light/dark cycles that mimic artificial light at night have also found concerning effects on the health of model laboratory organisms (Navara and Nelson 2007). Moreover, the disruption of natural light/dark cycles by light at night has impacts on the physiology and ecology of nonhuman organisms within and close to urban centers (Irwin 2018).

## Cross-References

- Biological Clocks
- Biological Rhythms
- Cathemeral

- Circadian Rhythms
- Crepuscular
- Day/Night Cycle
- Diurnality
- Internal Clocks
- Photoperiod

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## Limb Phase

- Gait

## Linear Egocentric Spatial Information

- Egocentric Frame



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## Linear Perspective

### ► Ponzo Illusion

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## Lingual Bone

### ► Hyoid Bone, The

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## Linkage Analysis

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### Introduction

Linkage analysis is a well-established statistical method in the field of reverse genetics, where in the predisposing gene(s) causing a heritable trait is/are identified.

### Description

#### Basic Concepts

Linkage analysis being a statistical method requires understanding of some basic terms such as recombination fraction, likelihood functions, maximum likelihood estimation, and odds ratios.

#### Genetic Recombination, Linked Genes, Genetic Distance, and Physical Distance

Genetic recombination is a biological phenomenon occurring in the parental gametes during the process of meiosis before eggs and sperms are formed. This phenomenon leads to exchange of chromosome material between homologous chromosomes via a crossover event with the crossover location thought to be determined by chance. Thus, each child inherits a unique set of recombinant chromosomes of their grandparents.

Genes located close enough to each other on a chromosome and whose expected crossover rate within the genetic material separating them at meiosis is less than 50% are said to be linked genes.

The distance between two or more linked loci can be expressed in two ways, i.e., by genetic distance or physical distance. Physical distance is the number of nucleotide base pairs present between them and is determined by DNA sequence analysis, whereas genetic distance is the frequency of recombination between two loci and is determined by observing recombination in a set of families. Thus, genetic distance is relative and is dependent on the distribution of crossing-over with recombination along each chromosome. Genetic distance may not reflect the physical distance because crossing-over is not evenly distributed along all chromosomes resulting in blocks of nonrecombinant stretches of DNA existence in between (Nussbaum et al. 2007).

#### Recombination Frequency as a Consequence of Genetic Distance Between Two Loci

Linkage occurs when two gene loci are physically close enough on the same homologous chromosome that they tend to be transmitted together. Estimating the genetic distance between any two gene loci relates to how often the genetic recombination does or does not occur between those loci. The recombination fraction, often represented as  $\theta$ , is calculated by counting the number of recombinant offspring for a given pair of loci divided by the total number of offspring (recombinants plus nonrecombinants). It measures the proportion of recombinations observed between two loci in a group of offspring. If  $\theta=0$ , it means the two loci are very much close to each other and have very high chance of getting inherited together. If  $\theta=0.5$ , it means that the two loci are far apart and assort independently. All the values of linkage lie between 0 and 0.5 indicating the varied degrees of linkage. A recombination rate of 1 (100%) is considered to be a Morgan (M) unit. A recombination frequency of 0.01 (1%) corresponds to one centiMorgan (cM). The centiMorgan is used as a typical unit of genetic linkage. This unit is defined on the basis of relative chance of separation of

different traits per meiotic division. A distance of 1 cM between the two markers that are coding for different traits is separated to different chromosomes on average once per 100 meiotic product, thus once per 50 meioses (Griffith et al. 2000).

#### Determination of the Relative Distance of Three Gene Loci Using Recombinant Frequency

The genetic distances and the order of three loci can be determined by a testcross of parental genotypes. For example, there are three gene loci A, B, and C of unknown distance from each other, and their observed recombination frequencies using test cross of parental genotypes are as follows: The distance from locus A to locus C is 0.06 (6%); the distance between locus B and locus C is 0.29 (29%); and the distance between A and B is 0.31 (31%). Thus, the three genes are located in the order A–C–B (Vogel et al. 1997).

#### LOD Scores Method Analysis

This method was designed by Newton Morton in 1955. LOD score represents the logarithm in base 10 of the odds of linkage of a trait at a recombination fraction  $r$  with a particular marker locus compared to a recombination fraction ( $\theta$ ) of 0.5 between the marker and the trait. It provides a different way of assessing the significance of a linkage signal, other than a  $p$ -value. This method is an efficient and economical method for studying families because once a decision is reached, it is not necessary to study additional families.

$$LOD = Z$$

$$= \log_{10} \frac{\text{probability of birth sequence with a given linkage value}}{\text{probability of birth sequence with no linkage}}$$

$$= \log_{10} \frac{(1 - \theta)^{NR} \times \theta^R}{0.5^{(NR+R)}}$$

LOD score greater than 3.0 is an evidence for linkage, whereas score less than -2.0 is considered evidence to exclude linkage (Morton et al. 1955).

#### Linkage Analysis Testing Procedures and Software Programs

Linkage analysis utilizes data on family structures, trait values, and genome-wide markers and involves tagging segments of a person's genome with markers that allow identification of segments

that have been inherited through the family along with disease and detects the degree of recombination between those genetic markers and traits in that particular family pedigrees. The genetic markers used in this method are typically **microsatellites** or SNPs that are genotyped and tested in a study sample of pedigrees, and those showing the strongest statistical evidence of linkage exceeding a predetermined threshold localize the trait gene to the chromosome segment where the markers reside. Parametric linkage (model based) analysis is used for Mendelian traits that follow a specific pattern of inheritance consistent with a single gene, i.e., X-linked, autosomal recessive, or autosomal dominant. For genetically complex traits (due to incomplete penetrance and/or genetic heterogeneity), nonparametric linkage analysis is used where the initial approach is similar to the one used for Mendelian traits, but the mode of inheritance is not known and not specified. Various computer programs have been included to make linkage analyses more precise and powerful which are briefly listed in the following table.

The following are the web pages for various linkage analysis software listed above:

1. GENEHUNTER. <http://www.broad.mit.edu/ftp/distribution/software/genehunter/>
2. LINKAGE. <ftp://linkage.rockefeller.edu/software/linkage>
3. LOKI. <http://www.stat.washington.edu/thompson/Genepi/Loki.shtml>
4. MENDEL. <http://www.genetics.ucla.edu/software/>
5. MERLIN. <http://www.sph.umich.edu/csg/abecasis/Merlin>
6. OSA. <http://wwwchg.duhs.duke.edu/research/aplosa.html>
7. SAGE. <http://darwin.cwru.edu/sage/>
8. SIMWALK. <http://www.genetics.ucla.edu/software/simwalk>
9. SOLAR. [http://www.sfbr.org/Departments/genetics\\_detail.aspx?p=37](http://www.sfbr.org/Departments/genetics_detail.aspx?p=37)

#### Applications

Linkage analysis studies have been used in routine OPDs to do positional cloning of genes in disorders such as cystic fibrosis (autosomal recessive),

**Linkage Analysis, Table 1** showing the list of various softwares for linkage analysis that can be used for binary traits and quantitative traits in large pedigree families and nuclear families (Cantor et al. 2013)

| Linkage analysis software |                 |                     |                                                |          |
|---------------------------|-----------------|---------------------|------------------------------------------------|----------|
| Binary traits             | Large pedigrees |                     | Nuclear families                               |          |
|                           | Program name    | Model               | Program name                                   | Model    |
|                           | LINKAGE         | Par                 | GENEHUNTER/ESTIMATE                            | NP       |
|                           | MENDEL Option 2 | Par                 | SAGE/LODPAL                                    | NP       |
|                           | SAGE/LODLINK    | Par                 | SAGE/SIBPAL                                    | NP       |
|                           | SAGE/LOD        | Par                 | MERLIN                                         | Par      |
|                           | SIMWALK         | Par / NP            |                                                |          |
| Quantitative traits       | Program name    | Model               | Program name                                   | Model    |
|                           | LOKI            | MCMC algorithm      | GENEHUNTER / MAPMAKERSIBS, NPL, HASEMAN ELSTON | Par / NP |
|                           | SOLAR           | Variance components | MERLIN/REGRESS                                 | NP       |
|                           |                 |                     | SAGE/ SIGPAL                                   | NP       |

*Par* = Parametric model; *NP* = Nonparametric model; *Both* = parametric and/or nonparametric

neurofibromatosis type-1 (autosomal dominant) using parametric models as well as for complex disease gene position cloning such as Crohn's disease using nonparametric models. See Table 1 for software for analyses.

### Advantages and Drawbacks

Linkage methods are particularly useful for the detection of rare variants with a large effect size in the population. These methods, however, have shown inconsistent results for common diseases. Factors such as heterogeneity, pleiotropy, reduced penetrance, and variable expressivity, in addition to variability in environmental exposures, weaken the power of linkage studies in complex traits. Although, linkage methods are able to identify candidate regions, the identified regions are much larger, sometimes spanning up to 40 Mb. Due to the availability of "next-generation" DNA sequencing and its promise to allow identification of the rare variants, interest in linkage analysis methods is undergoing a renaissance.

### Conclusion

Since the time it is developed, several methods and computer programs have been included to

make linkage analyses more precise and powerful. Linkage studies were used in the past only to isolate genes that cause rare genetic syndromes. Coupled with whole genome sequencing, this method has been successfully used to identify the association of rare variants to phenotypic traits such as hearing impairment, familial goiters, and familial hypertension. Thus, linkage analysis is again emerging as an extremely useful method in genomic analysis.

### Cross-References

- [Candidate Gene](#)
- [CentiMorgan \(cM\)](#)
- [Gene Map](#)
- [LOD Score](#)
- [Microsatellite Marker](#)
- [QTL Linkage Analysis](#)

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## Linkage Maps

### ► Gene Map

## Lipid

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## Synonyms

Fats; Membrane lipid

## Definition

Lipids are large nonpolar water-insoluble biomolecules that provide ample amount of energy in less volume and stored inside the body in different form to perform different physiological functions.

## Introduction

Biological lipids are chemically diverse group of organic compounds which are insoluble or only poorly or partially soluble in water. They are readily soluble in nonpolar solvents such as either chloroform or benzene. The water or

polar insolubility of lipids is due to the hydrophobicity of the predominant hydrocarbon chains (-CH<sub>2</sub>-CH<sub>2</sub>-CH<sub>2</sub>-) in their structures. Lipids are not polymers like the other biological molecules like proteins, nucleic acids, and polysaccharides. Lipid molecules are considered as the most crucial building block of cell membrane and cell signalling mediators. It is also an energy-providing molecule and stored as fat in the body. Although it is potentially beneficial, deregulation of lipid can become toxic and pathogenic for the cell causing cell death. The surplus-stored lipids are mobilized during starvation to provide energy or available for phospholipid synthesis. The lipids in the droplet form are also protective against lipotoxicity and oxidative stress.

## Classification of Lipids

Lipid can be classified based on its structural modification such as:

- (a) Fatty acid
- (b) Triacylglycerols (lipid droplet)
- (c) Glycerophospholipids/phosphoglycerides
- (d) Sphingolipids
- (e) Steroids
- (f) Others such as waxes, terpenes, eicosanoids

## Fatty Acids

Fatty acid is one of the simplest forms of lipids that helps to build the complex form. They are long-chain hydrocarbons (4 to 36 carbons long) with one carboxyl group. In biological system, usually it contains an even number of carbon atoms. The 16 and 18 carbon fatty acids are most common. The acyl chain may be saturated or unsaturated. Unsaturated fatty acids may contain one or more double bonds. Being amphipathic by nature they have both nonpolar and polar ends. From the numbering of carbon, the first carbon attached with the carboxyl group (-COOH) is considered as  $\alpha$  carbon followed by  $\beta$ ,  $\gamma$ ,  $\delta$ ,  $\theta$ , etc., and the last carbon is the omega  $\omega$ .

## Saturated Fatty Acid

See Table 1.

## Unsaturated Fatty Acid

The predominant fatty acid residues are those of  $C_{16}$  and  $C_{18}$  species palmitic, oleic, linoleic, and stearic acids in higher plants and animals where over half of them are unsaturated and are often polyunsaturated. Fatty acids with  $<14$  or  $>20$  carbon atoms are unlikely to be in nature. Most fatty acids have an even number of carbon atoms concatenation of  $C_2$  unit. Bacterial fatty acids are commonly branched and hydroxylated or contain cyclopropane ring but rarely polyunsaturated.

## Essential Fatty Acids

Due to the paucity of enzyme to introduce double bonds in carbon atoms beyond  $C-9$  in the fatty acid chain, mammals cannot synthesize linoleate and linolenate. The two essential fatty acids are linoleate and linolenate. The term essential means that they must be obtained from the diet because they are required by an organism and cannot be endogenously synthesized. Endogenously synthesized fatty acids are termed as nonessential.

## Melting Point of Fatty Acids

Chain length and degree of unsaturation are the two parameters which denotes the melting point of fatty acids. Melting point is proportional with the chain length and inversely proportional to the

unsaturation or number of double bonds. Unsaturated fatty acids are rigid due to the presence of double bonds. Consequently, unsaturated chains cannot pack themselves in crystals efficiently and densely as saturated chain, so they have lower melting point as compared to saturated fatty acids. Similarly the unsaturated fatty acids with cis unsaturated fatty acids have lower melting points than the trans unsaturated fatty acids.

## Triacylglycerol (Lipid Droplets)

The fats and oils that occur in plants and animals consist largely of mixtures of triacylglycerol (triglycerides and neutral fats). These nonpolar, water-insoluble substances are fatty acid triesters of glycerol. It acts as energy reservoirs in animals and is therefore most abundant class of lipids even though they are not components of biological membrane. Lipid droplets are emerged from the ER and are phospholipid monolayer unlike bilayer membrane.

According to the identity and placement of their three fatty acid residues, they differ in structure. The so-called simple triacylglycerol contain one type of fatty acid residue. For example, tristearoylglycerol or tristearin contains three stearic acid residue. Mixed triacylglycerols contain two or three different types of fatty acid residues and named according to their placement on the glycerol moiety. Fats (solid at room temperature) and oils (liquid at room temperature) are complex mixtures of simple and mixed triacylglycerols whose fatty acid composition vary with the organism that produced them. In respect to storing metabolic energy, fats are a highly efficient because they are less oxidized than are carbohydrates or proteins and can yield more energy

**Lipid, Table 1** List of saturated fatty acid (Voet et al. 2008)

| Symbol | Common name    | Systematic name | Structure             | Carbon no. | No. of double bond |
|--------|----------------|-----------------|-----------------------|------------|--------------------|
| 12:0   | Lauric acid    | Dodecanoic      | $CH_3(CH_2)_{10}COOH$ | 12         | 0                  |
| 14:0   | Myristic acid  | Tetradecanoic   | $CH_3(CH_2)_{12}COOH$ | 14         | 0                  |
| 16:0   | Palmitic       | Hexadecanoic    | $CH_3(CH_2)_{14}COOH$ | 16         | 0                  |
| 18:0   | Stearic acid   | Octadecanoic    | $CH_3(CH_2)_{16}COOH$ | 18         | 0                  |
| 20:0   | Arachidic acid | Eicosanoic acid | $CH_3(CH_2)_{18}COOH$ | 20         | 0                  |



on oxidation. Furthermore, fats being nonpolar substance, it can be stored in anhydrous form requiring less energy as compared to glycogen in physiological condition.

Some of the key lipid molecules are chylomicron (formed in the intestine, carry dietary lipid to the circulation after a meal, and degraded in the liver), very-low-density lipid (VLDL, triglyceride-rich lipoprotein made in the liver and converted to lower density form), low-density lipid (LDL, cholesterol-rich lipoprotein produced from VLDL), and high-density lipid (HDL, produced in both the intestine and liver and carries cholesterol from the liver to periphery, considered as healthy lipid molecules in the body).

According to the lipid molecule shape, it forms different structure, such as cone-shaped monoacyl lipid forms micelle and diacyl lipid forms lipid bilayer (compact) or liposome (cavity inside).

## Phosphoglycerides

Phosphoglycerides or glycerophospholipids (GPL) are the major lipid components of biological membrane. Phospholipid is an amphipathic molecules constructed from four components: a platform of glycerol or sphingosine backbone to which the fatty acids are attached, the fatty acyl chain, a phosphate the head group, and head group substituent attached to the phosphate. GPL are amphiphilic molecules with nonpolar aliphatic

“tails” and polar phosphoryl-x “heads.” The fatty acids at the sn-1 position (C-1) tend to be saturated (no double bond) or monounsaturated (one double bond), whereas the sn-2 (C-2) fatty acids are mostly monounsaturated or polyunsaturated (multiple double bond) (Table 2). The c-3 hydroxyl group of the glycerol backbone is esterified to phosphoric acid (the head group) where the head group substituents are attached. The simplest phosphoglyceride is phosphatidic acids where no further head substituents present are found in small amount in most natural system. The common alcohol moieties of phosphoglycerides are serine, ethanolamine, choline, glycerol, and inositol. If the alcohol is choline, the phosphoglycerides molecule is called phosphatidylcholine (lecithin), and if serine, then it is called phosphatidylserine, etc. Some GPL have common names, e.g., phosphatidylcholine are known as lecithins, and diphosphatidylglycerol the double glycerol phospholipids are known as cardiolipins (first isolated from the heart muscle). Plasmogens are GPL in which the c1 substituent to the glycerol moiety is bonded to it via an  $\alpha$ ,  $\beta$  unsaturated ether linkage in the cis configuring rather than through an ester linkage. Ethanolamine, choline, and serine form the most common plasmogen head groups (Fig. 1 and Table 3).

**Sphingolipids:** Nonglycerol but sphingosine (long-chain c-18 amino alcohol)-derived phospholipids are called sphingophospholipids or sphingolipids. They are also varied depending on their composition.

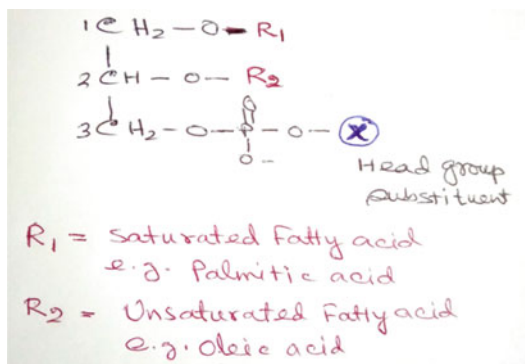
**Lipid, Table 2** List of Unsaturated fatty acid (Voet et al. 2008)

| Symbol  | Common Name    | Systematic name                                                                     | Structure                                                                         | Carbon no. | No. of double bond |
|---------|----------------|-------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------|------------|--------------------|
| 16:1n-7 | Palmitoleic    | Cis- $\Delta^9$ -hexadecenoic/9 hexadecenoic acid                                   | $\text{CH}_3(\text{CH}_2)_5\text{CH}=\text{CH}(\text{CH}_2)_7\text{COOH}$         | 16         | 1                  |
| 18:1n-9 | Oleic acid     | Cis- $\Delta^9$ -octadecenoic/9 octadecenoic acid                                   | $\text{CH}_3(\text{CH}_2)_7\text{CH}=\text{CH}(\text{CH}_2)_7\text{COOH}$         | 18         | 1                  |
| 18:2n-6 | Linoleic acid  | Cis- $\Delta^9, \Delta^{12}$ octadecadienoic/9,12 octadecadienoic acid              | $\text{CH}_3(\text{CH}_2)_4(\text{CH}=\text{CHCH}_2)_2(\text{CH}_2)_6\text{COOH}$ | 18         | 2                  |
| 18:3n-3 | Linolenic acid | Cis- $\Delta^9, \Delta^{12}, \Delta^{15}$ octadecatrienoic/9,12,15 octadecatrienoic | $\text{CH}_3(\text{CH}_2)(\text{CH}=\text{CHCH}_2)_3(\text{CH}_2)_6\text{COOH}$   | 18         | 3                  |

**Sphingomyelin:** A fatty acid is joined to a sphingosine via an amide linkage to form ceramide (sphingomyelin) as a common structure of all sphingophospholipids. J.L.W. Thudichum in 1884 first coined the term “sphingo-” which means the riddles of the sphinx. Herbert Carter and colleagues in 1947 introduced the term “sphingolipide.” Sphingolipids are extremely versatile molecules which contribute to gather knowledge in animal and plant tissue in their healthy and abnormal disease state. *Sphingomonas* and *Sphingobacterium* are the few bacterial genera containing sphingolipids.

**Glycosphingolipid (glycolipid):** Lipid-containing carbohydrate groups are called glycolipids where glycosphingolipid is the important one and also third important component of membrane. Carbohydrate chains are connected at –OH group of C-1 of ceramide.

**Cerebroside:** Ceramides with monosaccharide chain.

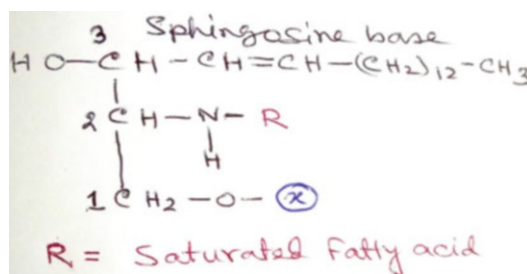


**Lipid, Fig. 1** Phosphoglyceride

**Globoside:** Ceramides with oligosaccharide chain.

**Ganglioside:** Globoside with complex oligosaccharide containing N-acetylneuraminic acid, sialic acid, etc. Ganglioside moiety (GM), GM1 (M) where 1 sialic acid attached, GD (D) 2, and so on. In vertebrates alone depending on the variation in the carbohydrate chain, there are 188 of the complex as ganglioside. One of the important lipid of the CNS is the sphingolipids (Fig. 2 and Table 4).

**Steroid:** Complex derivative of triterpenes with four fused rings (cyclopentanoperhydrophenanthrene) is the steroids nucleus. The only polar component is the C-3 OH. One of the best examples is cholesterol, an essential component in animal cell membranes, which acts as a precursor for the biosynthesis of all steroid hormones and bile salts. In the cells cholesterol is as a fatty acid ester. In plants and fungi, it is absent (ergosterol an exception in fungi). Stigmasterol, sitosterol, and campesterol are some of the examples of plant cholesterol.



**Lipid, Fig. 2** Sphingolipid general structure

**Lipid, Table 3** Phospholipids and its different head group substituents

| Phosphoglyceride         | Head group substituents (x) |
|--------------------------|-----------------------------|
| Phosphatidic acid        | None                        |
| Phosphatidylcholine      | Choline                     |
| Phosphatidylethanolamine | Ethanolamine                |
| Phosphatidylserine       | Serine                      |
| Phosphatidylinositol     | Inositol                    |
| Phosphatidylglycerol     | Glycerol                    |
| Cardiolipin              | Phosphatidylglycerol        |
| Phosphatidylglucose      | Glucose                     |

**Lipid, Table 4** Sphingolipid and its different head groups

| Sphingolipid              | Head group (x)      |
|---------------------------|---------------------|
| Ceramide                  | Hydroxyl            |
| Sphingomyelin             | Phosphocholine      |
| Ceramide                  | Phosphoethanolamine |
| Glucose ceramide          | Glucose             |
| Galactose ceramide        | Galactose           |
| Complex glycosphingolipid | Oligosaccharide     |
| Ceramide-1-phosphate      | Phosphate           |

## Eicosanoid

The potent biological signaling molecules originated from 20 carbons, polyunsaturated fatty acids, and eicosanoic acids, particularly arachidonic acid. Prostanoids and leukotrienes are two examples. It also acts as local hormones.

Prostaglandins derived from prostanoid (C8-C12 form the cyclopentene ring) were first identified in human serum. Apart from RBC, all mammalian cells produce prostaglandin. Prostaglandin is designated as PG followed by A-I, which represent the nature of substitute and then numerical number for individuals.

## Metabolism of Lipids

### Biosynthesis of Lipids

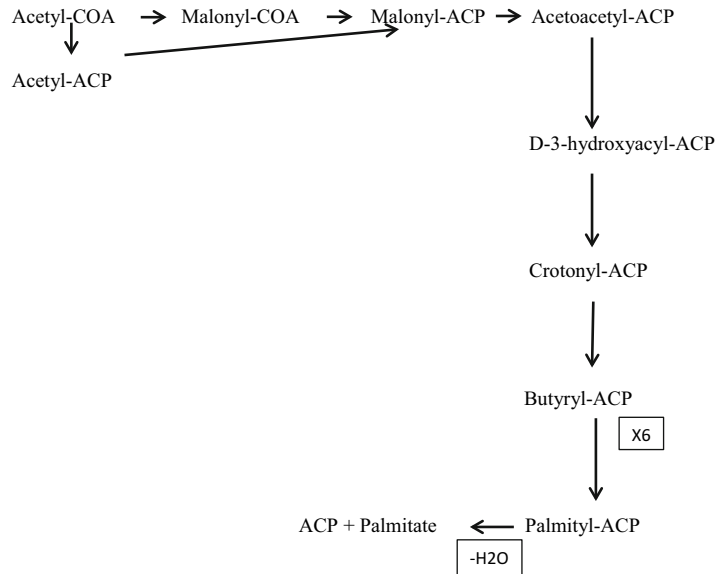
#### A. Fatty acid biosynthesis

Each step 2 carbon number increases and even number fatty acids are produced.

**B. Lipid droplet biosynthesis:** In ER and other organelle, lipid droplets are biosynthesized and modified in a multistep process (Fig. 3).

1. Triacylglycerol synthesis (Fig. 4): Neutral lipid triacylglycerol and sterol ester synthesis is the first step in lipid droplet biogenesis. This form a lens-like structure of lipid.
  - (a) Glycerol-3-phosphate acyltransferase/ Acyl-CoA, b) acylglycerolphosphate acyltransferase/ Acyl-CoA, c) phosphatidic acid phosphate, d) diacylglycerol acyl transferase
2. Emergence and nascent lipid droplet formation: Nascent lipid droplets are formed by recruiting seipin and other lipids to the lens. Difference in surface tension of the two faces (luminal and cytoplasmic) of ER membrane causes release of lipid droplet.
3. Budding and growth of lipid droplet: Budding and fusion of lipid droplet define the

**Lipid, Fig. 3** Biosynthesis of lipid droplets (Voet et al. 2008)



Glyceroldehyde-3-phosphate  $\rightarrow$  Lysophosphatidic acid (LPA)  $\rightarrow$  Phosphatidic acid (PA)  $\rightarrow$  Diacylglycerol (DAG)  $\rightarrow$  Triacylglycerol (TAG)

**Lipid, Fig. 4** Biosynthesis of Triacylglycerol (TAG) (Voet et al. 2008)

end of the process (Olzmann and Carvalho 2019).

### C. Sphingolipid synthesis: Figs. 5 and 6.

## Catabolism of Lipids

Lipids are digested by lipase enzyme into fatty acid and glycerol. For example, phospholipase A1 acts in the C1 ester linkage of fatty acyl with glycerol backbone, phospholipase C in the phosphoester bond attached with glycerol backbone at C3. The fatty acids undergo beta oxidation.

### A. Fatty Acid Beta Oxidation

It follows four steps.

- Activation of fatty acids: Acyl-CoA attached at the terminal end of fatty acid and form fatty acyl-CoA in an energy-dependent manner.
- Formation of ketone at the beta position: At the beta carbon it is oxidized to form ketone ( $-C=O$ ) from  $CH_2$  by three reactions.
- In the final step, thiolysis form the acetyl-CoA and 2C less fatty acyl chain with the help of  $\beta$ -ketothiolase and add another CoA to the remaining acyl chain.
- The cycle continues to form half the number of acyl-CoA ( $N/2$ ), if it is even

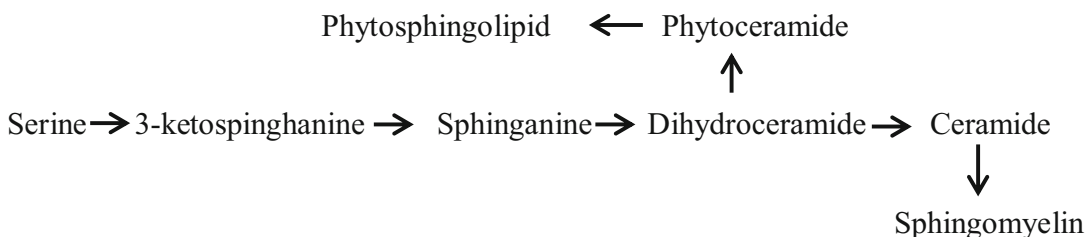
number of fatty acid, whereas 1 propionyl CoA and  $(N/2-1)$  number of acyl-CoA is formed. Here  $N$  = carbon number of fatty acyl chain. The NADH and FADH<sub>2</sub> produced as a reaction intermediate are utilized to form ATP via electron transport chain complex.

- Similarly alpha and omega oxidation happens in alpha and omega carbon of fatty acyl chain. Refsum disease is one example of lack of alpha oxidation. For unsaturated fatty acid, the unsaturation shift to form ketone at beta position of carbon and the same steps are followed as described in beta oxidation.

### B. Degradation of Sphingolipid

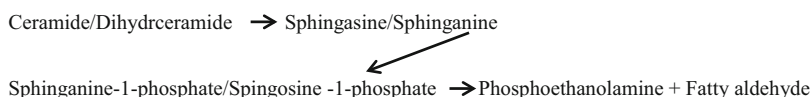
## Functions of Lipid

- Fat serves as a food reserve for both plants and animals. It also helpful to provide energy supply for the hibernating and aestivating animals.
- In migratory birds, fat deposition (Zugdisposition) is an indication and helpful for migration.
- They provide more energy 9.3 Kcal/gm than carbohydrate (4.5Kcal/gm) in less volume.
- Due to capability of conversion of fat to carbohydrate, fat can be stored in the oil seeds.



**Lipid, Fig. 5** Biosynthesis of Sphingolipids (Voet et al. 2008)

**Lipid, Fig. 6** Ceramide synthesis (Voet et al. 2008)



- (e) Presence of polyunsaturated form, it provides thermal insulation to many animals living into the cold temperature. Blubber, a thick fatty layer in whale, and polar bear are two examples.
- (f) It also helps in protecting from UV radiation and loss of water.
- (g) Brown fat in infant also helps in thermogenesis.
- (h) Acts as a shock-absorbing cushion for different vital organ like eye balls, gonads, kidneys, etc. in the human body.
- (i) Edible oils are used as cooking. Animal milk fats are also used for the production of butter, ghee, etc.
- (j) Soap is prepared from animal and plant lipid.
- (k) In paint industry dry oil is useful.
- (l) Wax helps to form a protective layer in animal fur to avoid evaporation.
- (m) Myelin sheath of the neurons is also made up of lipid.
- (n) Cell membranes are formed from phospholipid molecule.
- (o) Terpene which is a plant product is used as terpene oil, is a fatty substance.
- (p) Acts as a lubricant for many animals.
- (q) Fat as a source of metabolic water in extreme desert conditions.

## Diseases

### A. Relationship Between Lipid Composition and Disease

The different diseases related to lipid composition and alteration are categorized mainly due to genetic or by lipid itself or lipidomic changes. The tables here listed different form

of disease and its reasons, substance accumulation, and dysfunctions (Haryama and Riezman 2018) (Table 5).

### B. Dysregulation of Lipid Droplet-Related Disease

In the formation and degradation of lipid droplets, different disease pathologies are found in the human. The following tables listed the details (Olzman and Carvalho 2019) (Table 6).

### C. Dysfunction of Sphingolipid Metabolism-Associated Disorders

The following table characterized the different diseases related with deficiency in the enzymes involved in the sphingolipid metabolism causing impairment and toxic substance accumulation (The table is taken from the medical biochemistry page by Michael W king, <https://themedicalbiochemistrypage.org/sphingolipids.php>) (Table 7).

## Conclusions

In brief lipids are one of the most important biomolecules which provides more energy in less volume compare to other important biomolecules like carbohydrate. Simultaneously it has different physiological function and also helps in the construction of neuron forming myelin sheath. It acts as insulator, protector, and storage of foods in animals. Basically it is in the most common TAG form. The membrane lipids are phospholipid. It is present in the form of sphingolipid, cholesterol, prostaglandin, eicosanoid, wax, oil, etc. Lipids are degraded by different lipases and also undergo oxidation. Dysfunction of lipids or dysregulation of lipid metabolism in the body causes different diseases.

**Lipid, Table 5** Categorizing of disease related to lipid dysfunction

| Diseases                    | Reasons                                                   | Substance accumulation                 | Dysfunction               |
|-----------------------------|-----------------------------------------------------------|----------------------------------------|---------------------------|
| Genetic disease             | Mutation or single nucleotide polymorphism-related enzyme | Aberrant lipid composition             | Biological dysfunction    |
| Disease caused by lipids    | Upstream cause                                            | Aberrant lipid composition             | Biological dysfunction    |
| Noncausal lipidomic changes | Biological dysfunction<br>Changes in cellular composition | Secondary changes in enzyme expression | Aberrant lipid metabolism |



**Lipid, Table 6** Disease due to mutation of different genes related with lipid metabolism

| Disease                                  | Substance accumulation                                                                  | Pathomechanism                                                                                                                                                           | Mutation                                                                                                                                                                                                                                                                                                                                                                                                                                               | Dysfunction/outcome                                                                                                                                   |
|------------------------------------------|-----------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------|
| Obesity                                  | Accumulation of excess lipid droplets in the liver, skeletal muscle, and heart          | Lipid droplet-associated proteins                                                                                                                                        | Patients with mutation in cell death inducing DFFA-like effector C (CIDEc)                                                                                                                                                                                                                                                                                                                                                                             |                                                                                                                                                       |
| Nonalcoholic fatty liver disease         | Aberrant accumulation of lipid droplet in hepatocyte                                    | Failure to sequester lipids<br>Impaired secretion of very-low-density lipoproteins (VLDL)<br>Impaired stabilization of lipid droplets during hepatitis c viral infection | Mutation in lipid droplet lipase PNPAL3 and TM6SF2 (involved in VLDL lipidation)                                                                                                                                                                                                                                                                                                                                                                       | Simple steatosis<br>Nonalcoholic steatohepatitis<br>Liver cirrhosis and cancer                                                                        |
| Cardiovascular disease (atherosclerosis) | Accumulation of cholesterol and cholesterol ester in arteries                           | Protective reverse transport of cholesterol esters from peripheral tissue to liver is impaired. Free cholesterol accumulate and forms atherosclerotic plaque             |                                                                                                                                                                                                                                                                                                                                                                                                                                                        | Thrombosis and infraction in artery                                                                                                                   |
| Neutral lipid storage disease            | Deposition of TAG in multiple tissues                                                   |                                                                                                                                                                          | Autosomal recessive mutation adipose triglyceride lipase (ATGL), 1-acylglycerol-3-phosphate O-acyltransferase (ABHD5)                                                                                                                                                                                                                                                                                                                                  |                                                                                                                                                       |
| Lipodystrophy                            | Variable loss of fat tissue of whole (generalized) or some region of the body (partial) |                                                                                                                                                                          | Mutation in the gene involved in lipid metabolism and lipid droplet function<br><b>Congenital generalized lipodystrophy</b><br>Autosomal recessive mutation in acylglycerol-3-phosphate acyltransferase 2 (AGPAT2), seipin (BSCL2), caveolin1 (CAV1), cavin1 (PTRF)<br><b>Familial partial lipodystrophy</b><br>Heterozygous mutations in PLIN1, PPARG, AKT2, and homozygous autosomal recessive mutation in CIDEc and LIPE (hormone-sensitive lipase) | Metabolic abnormalities, insulin resistance, and associated metabolic phenotype (diabetes and hypertriglyceridemia)                                   |
| Hereditary spastic paraplegia            | Dysregulation in lipid droplet biogenesis and function                                  |                                                                                                                                                                          | Mutation in seipin, atlastin, spartin, spastin, and REEP1                                                                                                                                                                                                                                                                                                                                                                                              | Inherited neurological disorder, progressive weakness, and spasticity of the legs<br>Ataxia, cognitive impairment, peripheral neuropathy and epilepsy |

**Lipid, Table 7** Different diseases due to deficiency of enzyme related to lipid metabolism

| Disease                      | Deficiency of enzyme                           | Accumulating substance                              | Symptoms                                                                                                                    |
|------------------------------|------------------------------------------------|-----------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------|
| Tay-Sachs disease            | Hexosaminidase (hex)                           | GM2 ganglioside                                     | Mental retardation, blindness, early mortality                                                                              |
| Sandhoff disease             | (HEXA & B)                                     | Globoside, GM2 ganglioside                          | More rapid Tay-Sachs symptoms                                                                                               |
| Tay-Sachs AB variant         | GM2 activator                                  | GM2 ganglioside                                     | Same as Tay-Sachs                                                                                                           |
| Gaucher disease              | Acid $\beta$ -glucosidase (glucocerebrosidase) | Glucocerebroside                                    | Hepatosplenomegaly, mental retardation in infantile form, long bone degeneration                                            |
| Fabry disease                | $\alpha$ -Galactosidase A                      | Globotriaosylceramide<br>Ceramide trihexoside (CTH) | Kidney failure, skin rashes                                                                                                 |
| Niemann-pick disease         | Sphingomyelinase<br>NPC1 protein               | Sphingomyelins LDL-derived cholesterol              | Hepatosplenomegaly in type A with severity, neurological severity leads to early death, only visceral involvement in type B |
| Krabbe disease               | Galactocerebrosidase                           | Galactocerebrosides                                 | Mental retardation, myelin deficiency                                                                                       |
| GM1 gangliosidosis           | $\beta$ -Galactosidase-1                       | GM1 ganglioside                                     | Mental retardation, skeletal abnormalities, hepatomegaly                                                                    |
| Metachromatic leukodystrophy | Arylsulfatase A                                | Sulfatides                                          | Mental retardation, metachromasia of nerves                                                                                 |
| Fucosidosis                  | $\alpha$ -Fucosidase                           | Pentahexosylfucoglycolipid                          | Cerebral degeneration, thickened skin, muscle spasticity                                                                    |
| Farber granulomatosis        | Acid ceramidase                                | Ceramides                                           | Hepatosplenomegaly, painful swollen joints                                                                                  |

Cross-References

- Carnivore (diet)
- Catarrhine Diet
- Feline Diet

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List Memory Effects (Primacy and Recency)

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List memory has been studied since the experimental study of behavior began (Ebbinghaus 1902). List-memory results are displayed as a serial position function, usually showing best memory for items at the beginning of the list (the primacy effect) and at the end of the list (the recency effect) – a U-shaped serial position function. These serial position effects and their changes over time (retention delay) have had a profound impact on concepts and theories of how human memory works (e.g., Crowder



1976). List-memory studies can be more informative about how memory works than single-item memory studies because in the real world events are almost never encountered in isolation and are imbedded in a surrounding stream of other events. In order to further extend the role of list memory in understanding memory generally, nonhuman animals need to be tested in these same list-memory tasks for direct species comparisons.

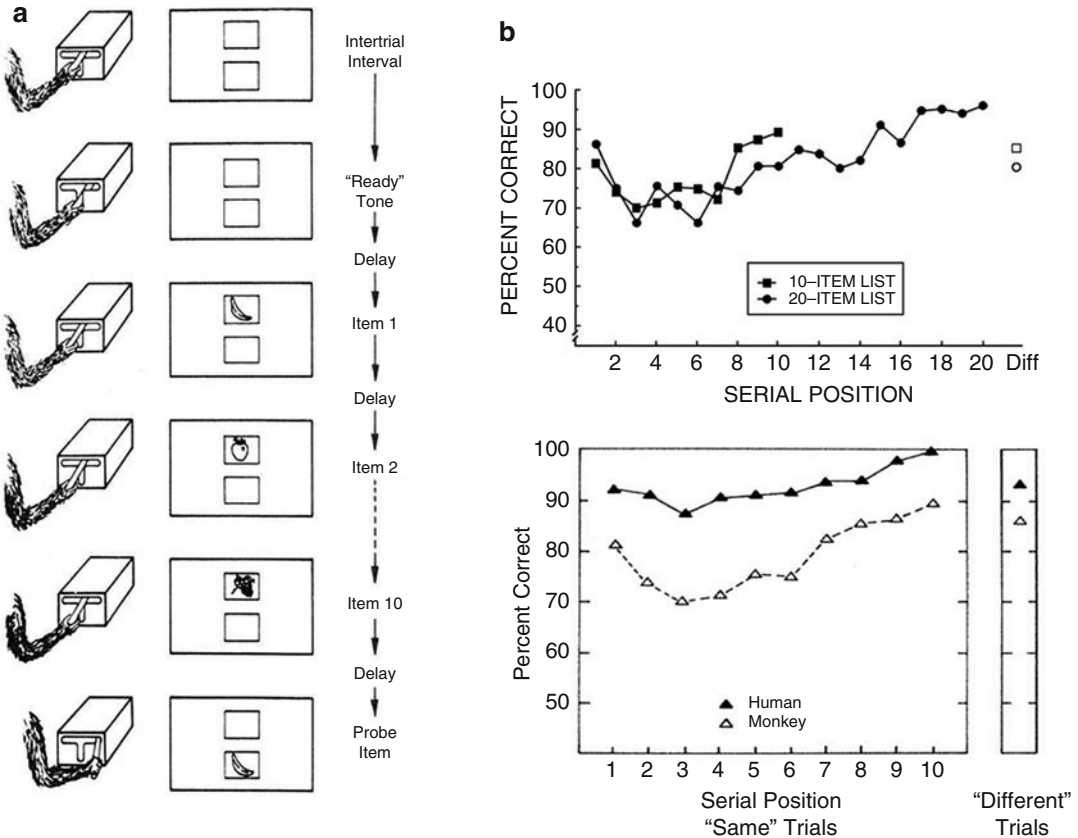
The major impediment to testing animals in list-memory tasks has been their inability to remember even single items for more than a few seconds. Accurate memory is essential to interpret changes that occur over time in the form of the serial position functions and what these changes might reveal about the underlying processes of memory. The conundrum about animal's fleeting memory is how they could have survived in the natural environment if they could not remember food locations, mates, alpha conspecifics, nesting sites, and predator locations for hours and days, let alone a few minutes.

As it turns out, the issue of fleeting animal memory was more due to the use of a small number of experimental stimuli than anything related to the duration of the animal's memory. The rationale for using a small number of testing stimuli was to use very simple stimuli and maintain high familiarity, which in turn was reinforced by commercially available testing apparatus that came with limited numbers of simple stimuli (e.g., colored geometrical shapes). In studies of memory (delayed matching to sample or delayed *same/different* tasks), the small number of testing items would have been seen dozens of times during any individual session and hundreds of times across sessions. When a test stimulus did not match the sample item on an individual trial, the animal could easily become confused because that test stimulus had been seen many times in previous trials. Research has since shown that with systematic increases in the number of testing stimuli memory accuracy dramatically increased, resulting in *same/different* abstract concept learning, accurate memory for lists of as many as 20 stimuli, and maintained accuracy over substantial delays between the list presentation and the test presentation (see entry ► [“Interference”](#)).

An advantage of studying list memory as opposed to single-item memory is the ability to study changes in memory for different list positions as the retention interval is increased, similar to human memory studies where extending the delay prior to a test produced a dissipation of the human recency effect. Originally, dissipation of the recency effect was thought to be due to passive “decay” through a lack of rehearsal of those items. Moreover, the primacy effect was thought to be due to active rehearsal of the first list items as presentations of subsequent list items were being made (Atkinson and Shiffrin 1968; see also entry ► [“Memory”](#)). Primacy effects had been considered to be unique to humans because no non-human animal had shown primacy effects. Such logic made good sense at the time because non-human animals were thought incapable of cognitive abilities to actively rehearse (initial) list items and therefore were not expected to show list-memory primacy effects, only list-memory recency effects.

## Visual List Memory

Contrary to common wisdom at the time that nonhuman animals were incapable of accurate list memory and could not produce serial-position primacy effects, a rhesus monkey was trained with 211 unique picture items (scenes, objects, people, animals, etc.) and tested with lists of 10 and 20 pictures. Each item of the ten-item list was presented for 1 s, with a 0.8 s interstimulus interval (ISI) and a 1.0 s retention interval (Sands and Wright 1980a, b). If the test item (in the lower screen) matched any one of the list items shown in the upper screen, then a *same* response (right lever movement) was correct, Fig. 1a. If it matched no list item, then a *different* response (left lever movement) was correct (see entry ► [“Same/Different Learning”](#)). These changes from a simultaneous *same/different* task to 10-item and 20-item serial probe recognition (SPR) task caused only slight disruption of performance. Performance was 86% correct with these ten-item lists. Performance was even a respectable 81% correct with 20-item lists. Shown in Fig. 1b are



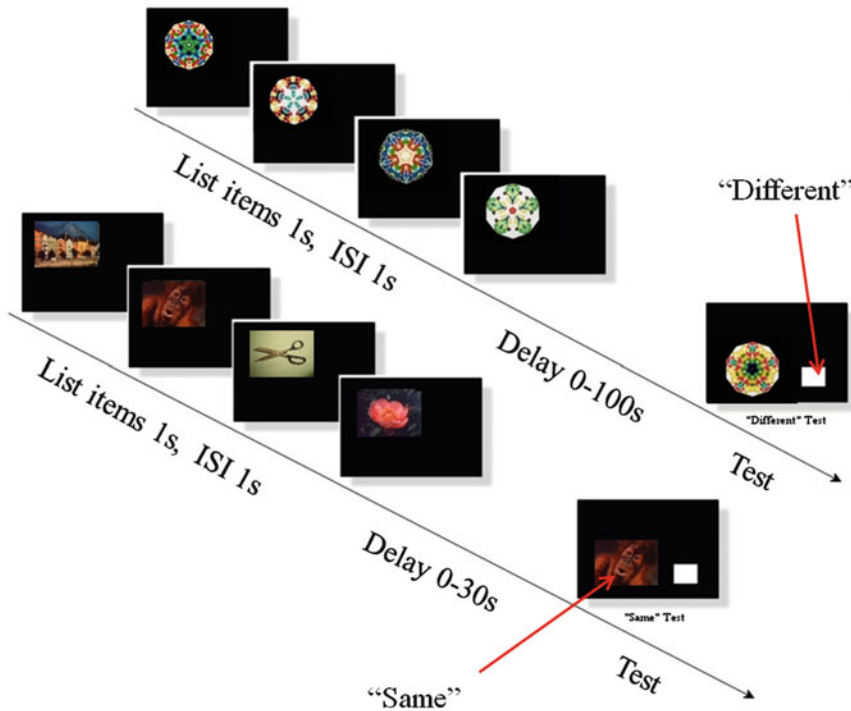
**List Memory Effects (Primacy and Recency), Fig. 1** (a) Schematic of a ten-item list-memory testing procedure. A monkey hand and arm is shown starting a trial by pressing downward on a lever. List pictures are then sequentially presented on an upper screen. Following a delay, a single test picture is presented on a lower screen. The subject moves the lever to the right, a correct response

this monkey's serial position functions (SPFs) with ten-item lists compared to a human in the same task. The monkey's 10-item SPF is compared to its 20-item SPFs in Fig. 1c.

These serial position functions show both primacy and recency effects and were the first evidence of both these characteristic signatures of human list memory. These signatures of serial list memory have been replicated many times since with a variety of species including: apes, rhesus monkeys, squirrel monkeys, capuchin monkeys, and pigeons (see Wright 2007 for a review). Thus, animals show at least some of the important characteristics of list memory as do humans. Nevertheless, there was plenty of skepticism

("same"), indicating that the test picture was in the list. (Left lever movements would indicate that the test picture was not in the list). (b) Serial position functions for a rhesus monkey tested with 10- and 20-item lists and showing primacy effects good memory for the last list items and recency effects for the last list items. (c) Comparison to a human tested with the same ten-item lists as the monkey in (b)

about whether the rhesus monkey in the Sands and Wright (1980a, b) studies (or any animal subject) was actively rehearsing the pictures and therefore whether rehearsal was the root cause of the primacy effect. Rehearsal is a process that is very difficult to test objectively with human participants, let alone nonhuman animals. Nevertheless, procedures such as lengthening the interstimulus interval that should have allowed more time for rehearsal of travel slide pictures did not enhance the monkeys' primacy effect, (Cook et al. 1989) nor did such manipulation for rehearsal of kaleidoscope pictures enhance the humans' primacy effect. But by teaching names (codes) for 40 kaleidoscope pictures to



**List Memory Effects (Primacy and Recency), Fig. 2** *Top*: an example of a four-item list-memory *same* trial with kaleidoscope pictures for testing humans. *Bottom*: an example of a four-item list-memory *different* trial

with travel-slide pictures for testing monkeys and pigeons. Pictures and the white rectangle were presented on a computer screen with a black background

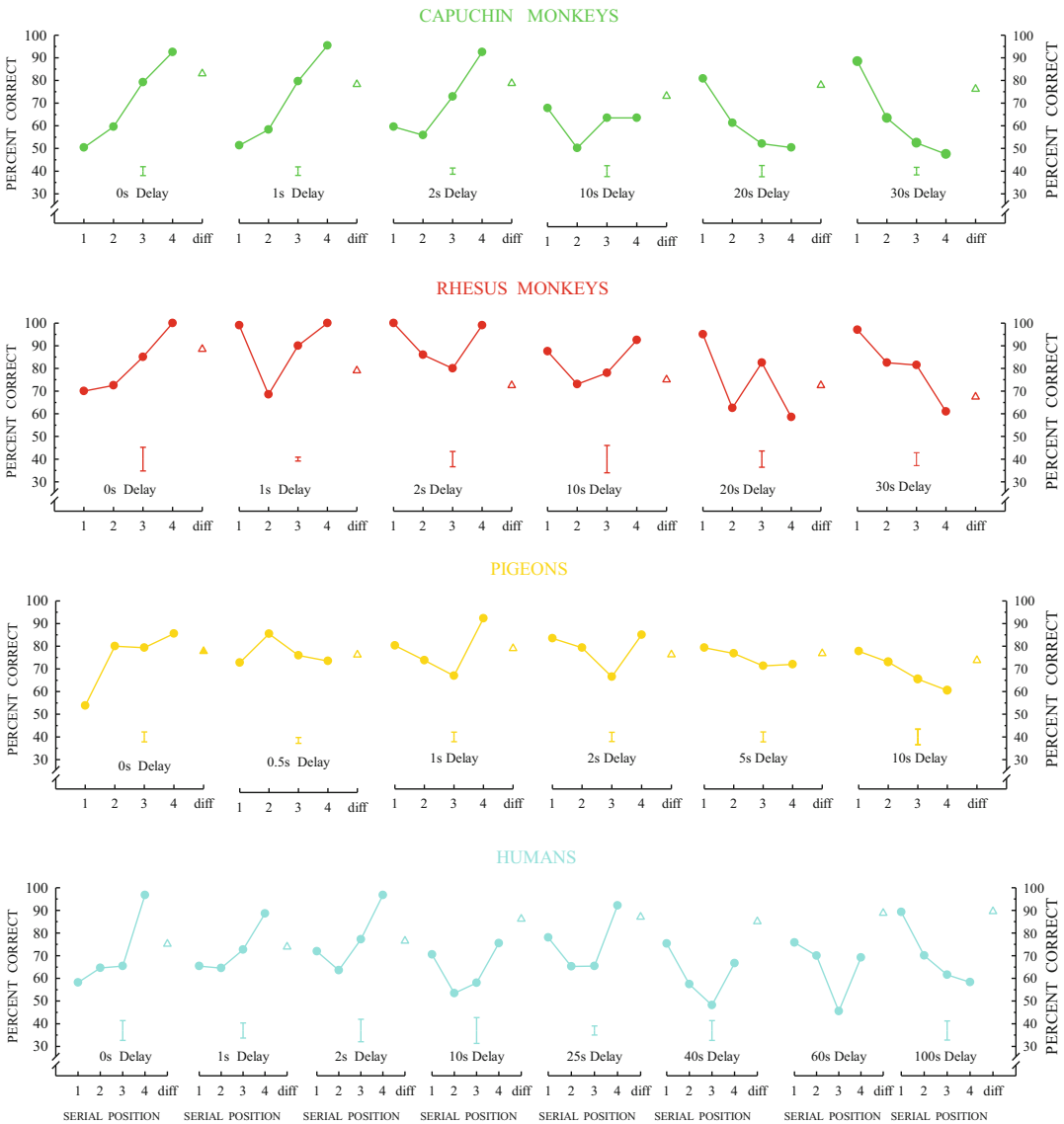
humans, these same participants then showed ISI effects, and the magnitude of the ISI effect was related to their rehearsal strategy as shown by overt rehearsals and from posttesting interviews (Wright et al. 1990). Most important, however, was that rehearsal did not affect the magnitude of the primacy effect, but instead it improved memory performance for the middle items (the dip in the serial position function). Together these results and findings suggest that many of the same processes that produce serial position effects found in humans can be found in rhesus monkeys – a nonverbal, nonrehearsing animal.

To explore what was responsible for primacy and recency effects, different species were tested with short four-item memory lists to accommodate pigeons, which had difficulty with lists longer than four items (e.g., Santiago and Wright 1984; Wright 1989, 1998b, 1999a, 2007; Wright et al. 1984, 1985). Lists of four “travel slide”

pictures were used to test rhesus monkeys, capuchin monkeys, and pigeons (Fig. 2, bottom). Lists of four kaleidoscope pictures were used to test humans (Fig. 2, top) to avoid ceiling effects and level the “playing” field for comparisons to the (nonhuman) animals (Wright 1999a; Wright et al. 1985). Four pictures were each presented for 1.0 s with 1.0 s interstimulus intervals between list items, and one of six retention intervals that varied from 0 to 100 s depending on the species. Typically, retention intervals were fixed for blocks of 20 trials with two 20-trial blocks with different retention intervals tested daily; all randomized combinations the six retention intervals were tested.

The serial position functions for four different species are shown in Fig. 3. All species showed changes in their serial position functions with retention interval. At the shortest delay, the serial position function was upward-sloping, showing virtually pure recency performance. As retention





**List Memory Effects (Primacy and Recency), Fig. 3** Serial position functions showing primacy and recency effects that change as a function of retention delay for monkeys, pigeons, and humans. (The fourth item is the last list item.) Mean group error bars are

shown below each serial position function. Different-trial performance is shown to the right of each serial position function. Animals were tested with travel-slide pictures, and humans were tested with kaleidoscope patterns as per Fig. 2.

delay increased, a primacy effect appeared, giving the function its characteristic U-shape. At the longest delays, the recency effect dropped out, and the serial position function was downward-sloping, showing virtually pure primacy performance. These same qualitative pattern of changes occurred in the serial position functions of all

species, but there was a time course difference for species. The dissipation of the recency effect took place in about 30 s for rhesus and capuchin monkeys, 10 s for pigeons, and 100 s for humans. The primacy effect began to appear in only 1 or 2 s after the end of the list presentation and was somewhat more rapid for rhesus monkeys and

pigeons than it was for capuchin monkeys and humans. These different time courses for the different species are quantitative differences. The similar pattern of SPF changes for the different species is a qualitative similarity showing similar visual memory processes for these species.

These systematic changes in the serial position functions serve to constrain the possible explanations for these memory changes as a function of the retention delay. Consider the consistent result that memory for the first list item (primacy effect) improves with retention delay. The appearance of the primacy effect with increasing delay is counterintuitive to the hypothesis that memory decays with time and has impacted explanations of how memory changes over time.

### **What the Delay Changes Reveal About Memory**

The increase in primacy memory with retention delay is difficult for most memory theories to handle. As previously mentioned, memory according to most theories is supposed to decay with time – a so-called law of disuse – otherwise known as forgetting. Such forgetting is often portrayed as a passive decay process – as the dissipation of the recency effect was portrayed for humans. The waning of the recency effect, like all forgetting, is a hallmark of most memory theories. Indeed, the passive decay of the recency effect in human memory contributed to the rising popularity of the study of short-term memory and the so-called cognitive revolution. The time course of the recency effect was supposed to be a measure of the short-term memory buffer. But even this (theoretical) concept has not survived the test of time. Recency effects have been shown for greatly extended time scales such as recall of United States Presidents (Roediger and Crowder 1976), and rugby scores by pub patrons (Baddeley and Hitch 1977). Notwithstanding any lingering debate over whether dissipation of the recency effect is brought about by passive decay, the same cannot be said about the primacy effect. If memory decays with time, then how can primacy memory (primacy effect) increase with delay time? Such increases with delay point to inhibitory processes that change with delay.

### **Visual List-Memory Conclusions**

Nonhuman animals show the important characteristics of primacy and recency list-memory effects, as do humans. In addition, the four species tested in the four-item visual list-memory task showed similar dynamic changes in their primacy and recency effects as the retention delay was increased – a qualitative similarity across species with widely differing evolutionary histories and neural architectures. Quantitative differences across species were shown in differences in time courses of these serial-position-effect changes with retention delay. If only one retention delay had been tested, then the conclusions would likely have been different. A single delay would have sampled a different point along the continuum of serial-position-function changes for the different species and dissipation of the recency effect or appearance of the primacy effect would have been a chance finding.

These similarities and differences in memory were made apparent by using short memory lists and investigating list memory over a substantial range of the effective retention delay. If longer lists (e.g., >10 items) had been used, then the early serial-position-function changes (e.g., emergence of the primacy effect) would have been lost because other items would have been presented during the time that these serial position function changes were taking place. Other tests of human list memory with short lists and difficult-to-code memory items (like kaleidoscope patterns) have shown similar serial-position-function changes (e.g., snowflake patterns, Neath 1993a, b; Neath and Knodler 1994; and antique car drawings, Korsnes 1995; Korsnes and Gilinsky 1993).

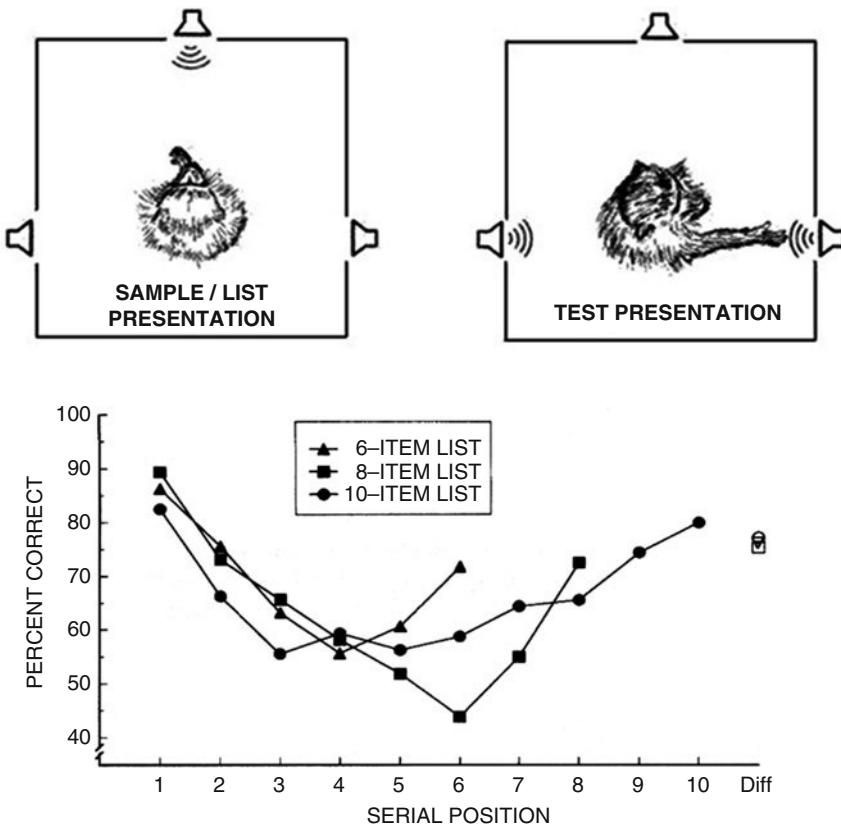
### **Auditory List Memory of Rhesus Monkeys**

The changing shape of the visual serial position functions as a function of delay produced similar patterns of change for the different species. Does all memory work this same way? For example, would auditory memory show similar serial-position-function changes? One could possibly point to the modality effect in human memory

(prolonged recency memory) that might be expected to extend the recency effect. Like with visual list memory, auditory list memory with monkeys has encountered severe impediments, including a string of failed attempts by several laboratories to train rhesus monkeys on even single-item auditory memory tasks. A breakthrough came when monkeys were required to touch and contact the source of the sound – the speaker. In that task, three speakers were positioned on different walls of an experimental chamber (Fig. 4).

Two rhesus monkeys were trained to touch copper screens in front of the speakers mounted in wooden cabinets (Fig. 4). By touching the center speaker, a sample sound was played (2 s),

followed by a second sound played from the two opposing speakers on the two sides of the experimental enclosure. They then selected one of the two side speakers to touch. If the test sound matched the sample, then the correct response was a touch to the right-side speaker (*same* response). Otherwise, the correct response was a touch to the left-side speaker (*different* response). Correct responses were reinforced with 3.5 cc of Tang orange drink. Sounds were selected from a 520-item set of natural/environmental sounds (e.g., steamboat whistle, wood chopping, pig grunts, bongo drums, water gurgling, reveille, insect buzzing, cash-register bell, toy train whistle, girls giggling, coins dropping, ducks quacking, xylophone, yodeling, geese, lion roar,



**List Memory Effects (Primacy and Recency), Fig. 4** Schematic of an auditory list-memory procedure for testing rhesus monkeys. *Top left:* Lists of auditory items (different sound effects) were presented from the front speaker. *Top right:* Following the list presentation and a delay, a single test sound was played (simultaneously)

from both side speakers. A right speaker touch was a *same* response, indicating that the test sound matched one of the list sounds. A left speaker touch would indicate that the test sound was did not match any list sound. *Bottom:* Mean auditory serial position functions for two monkeys with lists of 6, 8, or 10 sounds

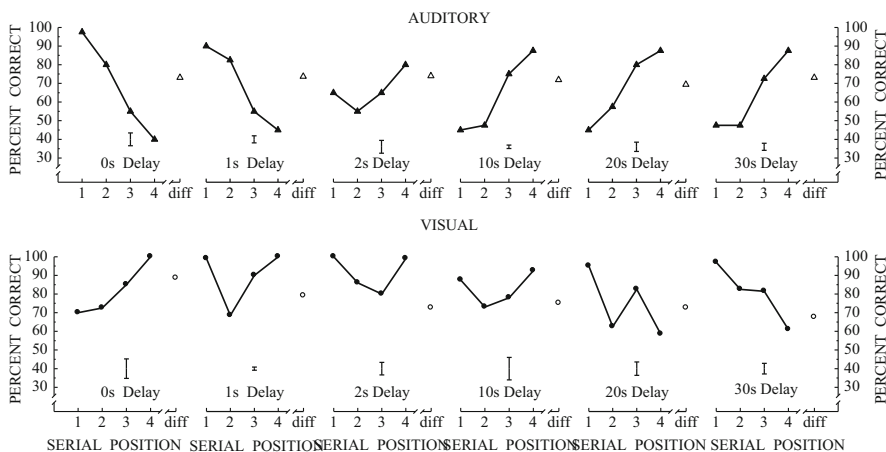
electric drill, children's piano, motorcycle, squeaky door, sneezing, crumpling paper, frogs, Big Ben chimes, glass breaking, horse whinny; see Wright 1998a, b; Wright and Rivera 1997, for additional sounds). The serial position functions shown in the lower portion of Fig. 4 for lists of 6, 8, and 10 sounds show primacy and recency effects, similar in this respect to those for visual memory in Fig. 1. Visual SPFs, however, tend to emphasize recency effects, whereas auditory SPFs tend to emphasize primacy effects more than recency effects.

The monkeys' auditory memory emphasizing primacy effects is shown even more dramatically with delay manipulations following four-item auditory memory lists. Delays of 0, 1, 2, 10, 20, and 30 s tested in 32-trial blocks like in the visual-memory tests (Fig. 5, top).

The rhesus monkey's auditory four-item serial position functions revealed primacy and recency effects that changed with delay of the test item as they did in the rhesus monkeys visual list-memory tests, but surprisingly the auditory serial position effects were opposite and changed in opposite ways compared to the rhesus monkey's visual serial position functions, as shown in Fig. 5. Immediately following presentation of the sound list, the auditory serial position function showed a strong primacy effect and only a primacy effect. As the retention interval was increased to around

10 s, the auditory serial position function gradually took on the typical U-shaped form with primacy and recency effects. At 20- and 30-s retention delays, the auditory serial position functions showed only recency effects; performance was worst on the first item and rapidly rose to very good performance on tests of the last list item. There was as much as a 40% change in accuracy. These auditory serial position functions and their changes with retention delay were replicated in more than 13 independent experiments including: testing familiar versus unfamiliar items, eliminating center-speaker touches, varying the intertrial interval (time between trials) across four experiments (1.0 s, 0.5 s, 1.0 s, and variable 12.0–27.0 s), trial-by-trial intermixing of the six retention delays and retesting after 4 years of layoff from the task (Wright 1998a, b, 1999b, 2002; Wright and Roediger 2003).

The change from a primacy-dominated function to a recency-dominated function for monkey auditory memory was rapid, and the ability to recognize the fourth (last) item in the list dramatically increased in just a few seconds. Such recovery of recency information strongly implicates the presence of inhibition coupled with spontaneous recovery or some sort of release from inhibition over time. If such inhibitory processes were instrumental in these serial-position function changes, then proactive inhibition of memory



**List Memory Effects (Primacy and Recency), Fig. 5** Comparison of auditory and visual four-item serial position functions for rhesus monkeys tested at the same

six retention delays. The auditory and visual serial position functions are opposite in form and are shown to change in opposite ways with changes in delay

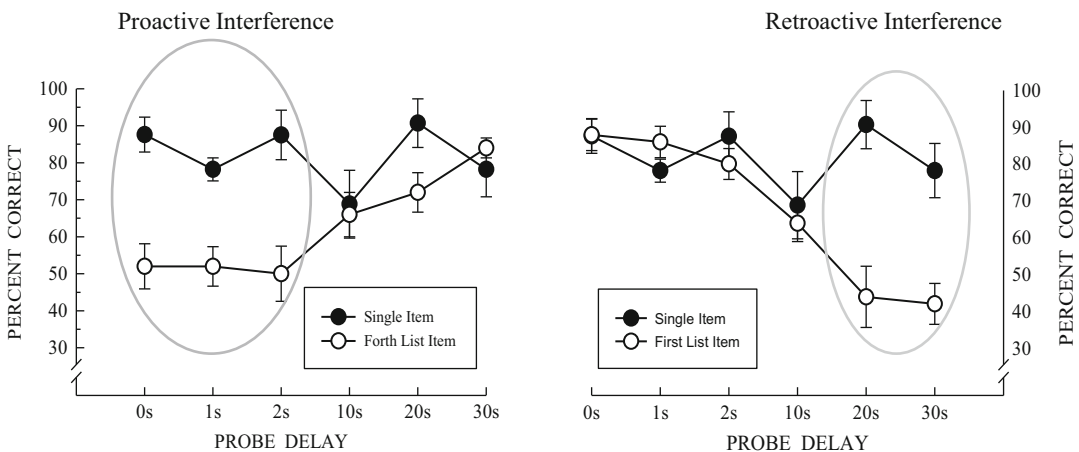
(e.g., memory retrieval) of the last list items would be strong initially, but such proactive inhibition would need to dissipate as the delay increased in order for memory retrieval of the last items to recover (see also entry “Retrieval”). Furthermore, when retrieval of memories of the last list items were recovered, then those retrieved memories might in turn retroactively inhibit memory retrieval of the first list items as the delay was extended further.

### Inhibition Effects in Auditory List Memory

One inhibition experiment most clearly draws comparisons between single-item memory and four-item memory by eliminating either the first three list items or the last three list items and with tests across all six of the delays (Wright and Roediger 2003). The logic of comparing list-memory performance to single-item performance might be best understood by considering the following: If proactive inhibition from the first items of the list dissipates with retention interval, then fourth-item performance from four-item lists should rise with longer retention intervals and eventually equal single-item performance. And the same logic should hold for retroactive

inhibition from the last three list items on first item performance at short retention intervals.

The list-memory functions for four-item lists shown in Fig. 6 are similar and they replicated those shown in Fig. 5. The left-hand panel shows fourth-item performance compared to mean single-item performance. Single-item performance is much more accurate than fourth-item performance over the shortest (0 s, 1 s, 2 s) retention delays. This large performance difference further demonstrates the considerable effect of proactive interference from the first three items on the monkey’s memory of the fourth item of the auditory list at these short delays. This is compelling evidence because otherwise fourth-item performance would be just like single-item performance at these short delays. Fourth-item performance did rise as delay increased and became equivalent to single-item performance at the longest retention intervals, demonstrating that proactive interference from the first three items largely dissipated as retention delay increased. Thus, proactive interference at short delays appears to be the primary factor contributing to the shape of the short-delay auditory serial position functions.



**List Memory Effects (Primacy and Recency), Fig. 6** *Left:* Single-item auditory memory compared to fourth (last) item of a four-item auditory memory list showing a performance “gap” (circled) in accuracy produced by proactive interference from the previous three list items on memory of the fourth (last) list item at shorter

delays. *Right:* Single-item auditory memory compared to the first item of a four-item auditory memory list showing a performance “gap” (circled) in accuracy produced by retroactive interference of retrieval memory of the first list item from the subsequent three list items at longer delays



There was also evidence that retroactive interference contributed to the shape of these serial position functions at the long retention intervals by showing that retroactive interference adversely affects the monkey's memory for the first list items. The right-hand panel of Fig. 6 shows performance for the first item of the list compared to the mean single-item performance across delays. In this case, single-item performance is much more accurate than first-item performance over the longest (20 and 30 s) retention intervals. This large performance difference at the longer delays demonstrates the considerable effect of retroactive inhibition at these delays. Retroactive inhibition must have occurred, otherwise performance would have been just like it was with the single item across all delays. The equivalent performance for the first list item and the single item at the shortest retention intervals demonstrates that retroactive interference from the last three items is largely absent at these short retention delays. As the retention delay increases, retroactive interference builds and eventually eliminates the primacy effects of the serial position functions. Thus, retroactive interference at long delays is the second process to explain the shape of these serial position functions and is the major factor contributing to the shape of the long-delay auditory serial position functions.

Other tests of inhibition among list items (but results not shown) include: (i) Separating list items (increasing the interstimulus interval from 1 to 2.5 s) to decrease interaction and inhibition among item memory which reduced 0-s delay primacy effects from 98% to 63% and was accompanied by an increase in recency effects from 40% to 79%; (ii) Adding just 2 s to the middle interstimulus interval (between the second and third list item) produced similar results; (iii) Substituting frequently repeated sounds for either the first two list items or the last two list items and testing with delays of either 0 s or 20 s, dramatically improved memory for sounds not frequently repeated independent of delay (Wright 1999b). These results show that by making the first two items familiar and not associated with any one list, these items generated little or no inhibition of retrieval memory for the last two items. When

the list position of the familiar items was exchanged, that is when the last two items were from the small (frequently repeated) set and were tested at the 20-s delay, memory of the first two list items increased to the similar accuracy level when all four items were from the large set. This latter result shows the powerful retroactive inhibition of the last items on retrieval memory for the first list items at these comparatively long retention delays. These effects cannot be due to encoding differences because the subjects have no way of knowing whether the last two items would be comparatively familiar or unfamiliar. Thus, it appears that retroactive inhibition is the major mechanism controlling auditory memory performance at long retention delays, whereas proactive inhibition is the major mechanism at short retention delays.

### Theoretical Implications of Visual and Auditory List Memory

There have been, to be sure, accounts other than inhibition to explain the shape of the serial position function. The popular and venerable dual-store models (e.g., modal model) claim that the recency effect represents short-term memory, which decays with time (e.g., Atkinson and Shiffrin 1968; Gillund and Shiffrin 1984; Haarmann and Usher 2001). But the monkey's auditory recency effect cannot represent short-term memory because a recency effect is not present initially; its later appearance is more like a long-term memory effect than a short-term memory effect. Other accounts of dynamically changing serial position functions have included temporal distinctiveness (e.g., Knoedler et al. 1999; Neath 1993a, b; Neath and Knoedler 1994) and storage versus retrieval strength (Bjork 2001). An item's temporal distinctiveness is thought to change with time like a receding row of telephone poles, with those in the distance less distinct than those closer by (Crowder and Neath 1991). But, as Bjork (2001) has pointed out, temporal distinctiveness cannot account for absolute (as opposed to relative) memory recovery, as shown by the visual primacy effect. To account for absolute recovery, Bjork (2001) proposed a storage-strength versus retrieval-strength model.

However, Bjork's (2001) model depends on learning with repetitions of the same list and would not apply to absolute recovery following a single presentation of each list, like those used to test the monkey's auditory (and visual) memory.

In conclusion, no explanation fares as well as inhibition to account for the auditory list-memory results. The evidence presented here is that retrieval failure underlies the monkey's auditory list memory. The auditory list-memory results show that proactive interference is strong just after an auditory list is presented, thereby causing retrieval failure and depressing recognition of the last items. Release from proactive inhibition causes an absolute increase in recency performance as the retention delay was lengthened. This is a substantial performance increase with retention delay and is counterintuitive because memory is commonly thought to decay with time. But as shown here, inhibition is dynamic and very different from decay.

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## Lithic Technology

- [Stone Tools](#)

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## Little Brain

- [Cerebellum](#)

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## Livestock Feed

- [Feed Industry](#)

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## Lizards and Snakes

- [Squamate Life History](#)

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## Local Bias

- [Bottom-Up Processing](#)

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## Local Geometry

- [Geometric Encoding](#)

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## Locomotion

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## Synonyms

[Animal mobility](#); [Animal movement](#); [Animal progression](#)

## Definition

Locomotion refers to an organism's ability to translate itself from one place to another. This can be accomplished by active and passive means. It spans from the use of simple molecular machines to complex multi-organ systems acting in concert.

## Introduction

All organisms share a common ancestry along with a set of enduring biological directives reflecting their relatedness. Chief among these is the drive to persist by temporarily overcoming overwhelming physical and energetic obstacles. Organisms large and small, simple and complex, labor to survive long enough to produce viable offspring. To accomplish this, they evolved abilities to exploit beneficial resources and environments. Some eventually became able to seek new resources when local supplies became exhausted, transporting themselves to new environments.

Locomotion refers to an organism's ability to transport itself from one place to another. This is a task fraught with uncertainty and danger. Trading a known environment for an opportunity to find a

better one is risky at best. Many animals are particularly vulnerable during locomotion. Their available resources and attention become repurposed to the completion of this goal, making them particularly vulnerable to energy depletion and predation. Therefore, locomotion is a dangerous behavior not undertaken lightly. As such, it is often goal-oriented and used to increase fitness (e.g., securing nourishment, avoiding death/predation, reproduction). Because of the associated risks, many animals locomote in short bouts when approaching potentially dangerous environments. This allows them to sample their environment for dangers. The same animals, however, increase their bout durations when traveling back toward safety.

The evolutionary race for survival resulted in the production of highly diverse and complex sensory systems to probe environments and locomotor systems to convey animals to their destinations quickly and safely. How animals accomplish locomotion, and translate themselves from one place to another, depends on factors such as their evolutionary history, the physics of their environment, and the biological drive being satisfied.

Many animals living near the interface of distinct physical environments (e.g., land and water) evolved the ability to exploit multiple environments (e.g., one for sustenance and another for locomotion). For example, many insects and birds walk when foraging but switch to flight when traveling between feeding sites as a more energetically efficient form of locomotion. Crayfish and young lobsters walk on the bottom of springs and oceans but will swim away from predators using their powerful tails. Each distinct type of locomotion is made possible by dramatic feats of specialization in the animals' nervous system, skeleton, and musculature. While there are many examples of transition between environments over evolutionary time, most animals are specialized for locomotion through one physical niche throughout their lives. Those capable of locomotion through multiple environments must reconfigure their motor outputs to match the properties of each environment.

When studying simple processes, it is often possible to divide them into their components

and to dissect and understand the role of each part independent of the whole. Often, single chains of cause-and-effect hierarchies make easy work of understanding the process by sequentially dealing with each aspect of the whole. Animal locomotion defies this type of approach. Locomotion is not the final output of a chain of events; rather, it emerges from the tightly concerted interaction of numerous organismal systems (Alexander 2003). Thus, our compartmentalized approach to its study is more a reflection of our own limitations than a characteristic of the process we will now discuss.

Thus, while the following sections attempt to simplify our task by dealing with intuitive (dissectible) aspects of animal locomotion, the reader should remain aware that these separations are artificial and for our benefit. Furthermore, animal locomotion is not the product of a machine optimized for the performance of a task, but rather the survivable output of the cumulative history of a species. As such, it can only be fully understood in the context of an animal's life history challenges and of its inheritance passed down through evolution. We will next look at some of the challenges this behavior evolved to surmount before looking within organisms at its mechanics.

## Goals of Animal Locomotion

Why do animals move? As mentioned above, one of the primary drives common to all life forms is the directive to survive to reproduce. Thus, locomotion can be understood as an animal's attempt to improve the odds of this outcome. Some overarching goals driving locomotion include (i) avoiding death (self-preservation), (ii) finding mates (for sexually reproductive animals), and (iii) ensuring the survival of offspring. These are certainly not all the reasons why animals move. Additionally, some of these goals (e.g., self-preservation) include unique locomotor goals within them. For example, self-preservation includes escaping predators but also energy procurement. We will discuss some of these goals, as the (often competing) demands they place on animals have

driven the evolution of the distinct types of locomotion we appreciate in the natural world.

### Self-Preservation

Many distinct locomotor activities have the goal of maintaining an organism's viability. The exact locomotor behaviors depend on the animal, but minimally they involve (a) procuring and ingesting other organisms, (b) avoiding ingestion by other organisms, and (c) avoiding environmental risks (e.g., temperature extremes). Each of these tasks presents unique challenges that are often in conflict with one another. For example, searching for food often places animals at increased risk of predation.

Animals are unable to manufacture their own complex organic compounds for nutritional purposes (i.e., they are heterotrophic). Instead, they must obtain their nutrients by ingesting other organisms in their environment. Some animals, such as sponges, corals, and tunicates, are sessile and able to capture sufficient nutrients as they move past them. Even here, most of these animals have short motile stages where their larvae seek promising environments before becoming sessile. Large, complex animals are unable to reliably capture sufficient resources without investing energy to seek them out regularly.

Each vital locomotor activity often requires distinct neural specializations. Finding food (or mates) requires extreme feats of sensory detection involving computationally expensive specialized search strategies. For example, moths use a strategy called *casting* when following pheromone plumes in search of mates. Similarly, dogs tracking scents employ active sensing, sampling their environment at regular intervals. In both examples, sensory inputs are integrated over time to deduce the scent's source.

Locomotion during the search phase of mate or food procurement needs to be slow enough to allow the nervous system enough time to sample the environment and resolve (often tenuous) gradients. During this type of locomotion, sensory processing can be the rate limiting factor. Increasing the organism's investment in its sensory system can result in higher neural acuity, sampling speed, and resolution. However, this also carries

heavy energetic costs, which animals must balance with their needs.

While searching for food might be slow and involve large sections of the central nervous system acting in concert, avoiding predation is often more straightforward. During predator avoidance, an animal's reliance on its sensory system comes down to a single vital piece of information: locating the threat. This information is used to trigger often stereotypical escape behaviors that remove the animal from danger. Because escape speed is often the variable that separates life and death, nervous systems show adaptations that optimize the speed of these behaviors. These include:

- (a) Using as few cells as possible to sense and trigger the escape response (minimizing delay associated with synaptic communication).
- (b) Using electrical synapses whenever possible. Chemical synapses, while malleable and effective, are also the slowest (each adds at least 1–5 ms to signal conduction time). Therefore, many escape behaviors rely on a few, fast ( $<0.3$  ms), electrical synapses.
- (c) Using large diameter nerve fibers and myelination to maximize the impulse velocity.

There are many examples of escape behaviors making use of these neural optimizations. The Mauthner cell in fish and amphibians is a large neuron that makes extensive use of electrical synapses to produce fast escape responses. Similarly, large diameter neurons and/or electrical synapses also mediate the tail-flip escape response in crayfish, escape jet propulsion of squids, escape jumps in fruit flies, and more. Similarly, myelination of escape neurons in some copepod species allows these animals to perform faster, energetically efficient, escapes than they could perform otherwise.

Animals that succeed in consuming (and avoid being consumed by) other organisms are still faced with the task of surviving changing environmental parameters. The magnitude of this task varies significantly across species. For animals unable to regulate their temperature (i.e., ectotherms), or those living in harsh environments (e.g., deserts), the task might pose greater risk than predation or starvation. Because many



environmental parameters change between day and night, or across different seasons, animals often relocate to avoid environmental extremes. Locomotion in response to cyclical environmental fluctuations are responsible for many of the great animal migrations occurring across the world, from the daily vertical migrations of jellyfish in the ocean to the yearly migrations of the monarch butterfly in North America.

However, some environmental parameters change too fast for animals to successfully relocate once change is underway. Faced with this challenge, some animals initiate their locomotion before environmental variables begin to change. Nervous systems thus evolved internal (biological) clocks allowing them to predict and behave in anticipation of impending environmental changes. Accurately anticipating environmental variations is of paramount importance in survival. In addition to these predictive computations, animals often use environmental cues (e.g., photoperiod) to decide when to initiate their migrations.

### Finding and Securing Mates

Solitary organisms that rely exclusively on sexual reproduction must travel to find potential mates. Finding a mate can involve returning to a natal site or group (philopatry) or dispersing to new areas and populations (Greenwood 1980). Animals that disperse must seek out and find mates in isolation. For example, moths will orient to chemical signals (pheromones) to find a mate. However, philopatric animals often engage in group migrations which increase their odds of finding suitable mates. Examples include crabs, polychaete worms, salmon, and migratory birds. Regardless of their strategy, searching for mates often increases the chances of predation.

### Ensuring Offspring Survival

Following reproduction, animals must sometimes protect and feed their young until they are independent. Some animals travel to find a suitable place to rear their offspring and then to a place to forage for them. Emperor penguins, for example, can travel up to 500 km to forage for food to bring to their offspring.

## Molecular Motors

We discussed above some of the reasons why animals elect to translate themselves from one place to another. We now turn to how animals accomplish these feats. In this section we discuss the molecular motors powering all forms of animal locomotion (Schliwa and Woehlke 2003).

Cells maintain their shape by means of structural proteins polymerized into rods and tubes that form their cellular skeleton (cytoskeleton). To shuttle proteins and other payloads around, some proteins evolved the ability to use chemical energy (in the form of ATP) to walk their cargos along these cytoskeletal fibers. A key development in the evolution of animals came when these molecular motors (e.g., dynein and myosin) became harnessed not just to pull a cargo along a polymerized fiber but also to move these fibers against each other. This endowed these molecules with the ability to generate locomotion by stirring fibrous projections in the surrounding environment (e.g., flagella) or to reversibly reshape cells to produce locomotion (e.g., muscle contractions).

### Cilia and Flagella

Cilia and flagella are strictly the same cellular organ (henceforth flagella), although they are discerned by their length and number. Eukaryotic cells may have only a few ( $<10$ ) large flagella but may have thousands of cilia. While both prokaryotic and eukaryotic cells evolved flagella, and use them in locomotion, these organs are structurally distinct. Eukaryotic flagella are powered by dynein ATPase motors and have a cylinder (i.e., axoneme) containing two single microtubules surrounded by nine microtubule doublets (Woolley 2000). The entire assembly lies perpendicular to the cell surface and is surrounded by flexible extensions of the cell membrane. Many additional proteins, both in the flagella and at their base (called centrioles), are responsible for the generation and control of its motion. Movement at the base of these structures produces a wave that travels distally and can be either two or three dimensional. Unlike its eukaryotic counterpart, prokaryotic flagella are composed of a hollow

cylinder made of flagellin. At the base of these flagella, a small protein assembly creates an electric motor driven by atomic currents derived from ( $\text{Na}^+$  or  $\text{H}^+$ ) ions entering the cell.

Cells typically have only a few long flagella but may have thousands of short cilia. Whereas flagella generate propulsion by beating in a continuous corkscrew fashion, cilia generate metachronal waves during which their action is divided into the power-generating stroke phase and the recovery phase when there is no propulsion generated. These differences may reflect their favored use. Flagella are well suited for generating large, propulsive forces (e.g., spermatozoid's flagellum), but cilia can be differentially controlled within a single cell, resulting in highly precise movements.

For billions of years, bacteria, archaea, and later eukaryotes used flagella to seek out viable environments. These molecular propellers and oars continue to translate these microorganisms to hospitable environments. In animals, flagella and cilia fulfill a myriad of roles: from propelling sperm and moving oocytes along to removing debris in the respiratory system or detecting light, sound, and gravity. The rise of multicellular organisms, and their consequent increase in size, weight, and drag, reduced the effectiveness of these motors due to their ever-heavier payloads. Thus, as animals grew in size and complexity, they evolved alternative means for propulsion better suited to their larger scales. However, some small gastropod snails (and even some not-so-small sea slugs) remain able to achieve propulsion purely by the action of their cilia. They accomplish this by sliding over their mucus secretion. However, unlike their unicellular counterparts, the beating of cilia in these animals is under neural control.

### Myosin II

To achieve propulsion, cilia and flagella must be exposed to the environment. A second type of molecular motor evolved from the novel rearrangement of core proteins. It allowed single-celled organisms, and eventually multicellular animals, to move through their environment by causing entire cells to act as motors.

Myosin heavy chain II is a molecule capable of transforming chemical energy (ATP) into mechanical energy (Rayment et al. 1993). Myosin is comprised of two light chains and two heavy chains that combine to give rise to the molecule's characteristic two heads, neck, and tail domains. The N-terminal halves of the heavy chain give rise to the globular heads, while the tail of myosin is assembled from the C-terminal halves. The tails of the molecule can polymerize together to form a filamentous backbone lined with the globular heads along its surface. Each head of myosin II consists of a motor domain that binds to the thin filament actin when allowed to hydrolyze ATP. Myosin successively binds, deforms, and releases an ordered lattice of actin proteins. These additively transfer the combined mechanical deformation of all myosin molecules to effectors such as membranes, tendons, and skeletons, thereby generating propulsion.

Myosin II predates animals and is found in amoeba and fungi, as well as in primitive animals lacking muscles such as sponges and cnidarians. Amoebas are large unicellular organisms that locomote through the protrusion and retraction of cellular pseudopodia and rely on the activity of the actin-myosin II complex. Besides locomotion, myosin also functions in cell division, migration, and shape.

## Cellular Motors

### Muscles

Cilia and flagella are feats of evolution, allowing (mostly) small unicellular organisms to move effectively in their native aqueous environments. To be propulsive, these structures must act at the interface of the animal and its environment. For mostly sessile animals (e.g., sponges), flagella function by propelling food particles into digestive cavities. However, as many organisms grow in size and cell numbers, their surface area to volume ratio rapidly drops. Under these conditions, fluid flow changes from laminar to turbulent (see Reynolds numbers below), reducing the propulsive effectiveness of flagella.

Unlike flagella, myosin II acts within cells. Their numbers and effective forces can therefore scale with the volume of cells, rather than just with their surface area (i.e., flagella). This allows these molecules to generate forces strong enough for large cells to deform (and even divide), allowing them to interact physically with other cells and their environment to generate propulsion.

One limitation to the use of myosin in propulsion is the necessity to effectively transfer these large forces to the environment without structurally compromising the cells themselves in the process. This challenge becomes significant in multicellular animals, where myosin and actin allow many cells, even those buried deep within an animal, to become motors and generate combined forces far greater than those previously possible. When the structural elements responsible for transferring these forces are absent (e.g., loss of dystrophin in Duchenne muscular dystrophy), the powerful forces generated by the actomyosin complex are strong enough to rip muscle cells apart (Nowak and Davies 2004). Arguably, when properly harnessed, the versatility and scalability of the actomyosin complex can give rise to the enormous diversity of animal forms, sizes, and locomotion we observe in the animal kingdom.

### Skeletal Muscle Structure

In vertebrates, three types of muscles are recognizable by their structure, their function, and the forces they generate. Skeletal muscles are responsible for locomotion and are discussed below (Lieber 2002); cardiac muscles are structurally similar to skeletal muscle but are capable of myogenic contractions (i.e., able to initiate contractions autonomously); and smooth muscles are also capable of myogenic contractions but possess unique myosin organization (see below). We will restrict our discussion to skeletal muscles as they are responsible for producing locomotion.

In vertebrate skeletal muscles, each myosin filament is surrounded by six actin filaments. Actin filaments are fixed to a z-disk (comprised of a vast array of interlinked proteins and fibers) at one end. The ends of the actin filaments not bound to the z-disk bind to one of the distal ends of the centrally located myosin fibers. The sarcomere is

the smallest contractile unit of a muscle, and the z-disks themselves are ultimately responsible for transferring the force generated by actin and myosin within the sarcomere. Sarcomeres are aligned in series (end-to-end) within elongated threads called myofibrils. In humans, myofibrils can be up to 1 cm in length. Myofibrils are like threads in a rope; they are bundled together to form thicker and longer fascicles.

The head of the myosin molecule has two binding sites (one for ATP and one for actin). When ATP binds to a myosin head, it causes it to release an actin filament. Following the release of the previously bound actin filament, myosin hydrolyzes the bound ATP to ADP + P<sub>i</sub> and uses the energy released to change conformation and weakly bind to an actin filament. On the actin filament, two free Ca<sup>2+</sup> ions bind to troponin, causing the protein tropomyosin to slide and allowing actin filaments to fully bind to the myosin head. Finally, myosin releases the inorganic phosphate and initiates the power stroke in which it changes conformation and slides the actin filament toward the center of the sarcomere, shortening the sarcomere as a consequence. Myosin then releases the bound ADP and remains in this (rigor) state until a new ATP binds to its free site, restarting the contractile cycle.

Animals can alter their muscle architecture in a variety of ways to generate different types of forces. At the ultrastructural level, long series of sarcomeres activated simultaneously generate quick muscle shortening and allow animals to generate fast motion. Conversely, arrangements of sarcomeres in parallel allow the generation of large powerful forces. In vertebrates, myosin can be found polymerized into thick filaments with their long axes aligned with the fiber and their globular heads pointing away from a bare center zone (e.g., striated muscle). Alternatively, myosin can be at an angle to the filaments' long axis with their globular heads, covering the whole length of the filament. This arrangement is found in smooth muscle.

Invertebrate muscles display even more diversity. Many species alter their myosin diameter, length, and myosin-to-actin ratio even within a single muscle cell. A type of invertebrate muscles

termed “asynchronous muscles,” found in flying insects, are capable of contraction rates an order of magnitude faster than is possible through other muscles. Used to power flight, these muscles are driven by mechanical stretch rather than neural stimulation.

### **Additional Function of Muscles during Locomotion**

The most intuitive role for muscles during locomotion is that of generating propulsive force. Besides acting as motors, muscles can perform other functions during locomotion (Dickinson et al. 2000). For example, muscles can stiffen to become force transmitters rather than generators. This “strut” function allows the optimal transmission of force from multiple muscles into a single effector organ. For example, in fish that use their caudal fin for propulsion, posterior muscles become stiff and act as struts to convey anteriorly generated forces to the tail. Once these forces pass, the muscles resume their propulsive role to generate force by contracting, then conveyed to the (still stiff) posterior muscles of the tail.

Many invertebrate muscles possess a myosin binding protein (i.e., paramyosin), which allows them to display a property called “catch” in which they can maintain force in the absence of actomyosin activity. The best-known examples of catch muscle fibers are those of bivalve mollusks, which they use to hold their shells tightly closed for long periods of time.

Another role muscles can perform during locomotion is that of brakes. During running, extensor muscles in the legs of cockroaches do not act to generate power, but rather to slow the velocity of the swing phase of the motion. This type of activity provides a metabolically inexpensive way to slow down locomotion.

### **Muscle Contraction**

Contractions are initiated when calcium ions are released from intracellular storage compartments and bind troponin. In order for the many sarcomeres in a muscle to act in synchrony, the release and removal of calcium ions must be under precise control. As mentioned above, muscles that achieve this endogenously are known as

myogenic. Cardiac, arterial, and intestinal muscles are examples of myogenic tissues. It is likely that the ancestral muscle was similarly myogenic and able to independently respond to environmental stimuli. Myogenic contractions work well for (relatively) independent organs such as arteries or guts (Horowitz et al. 1996). While hormonally regulated, these organs function in partial autonomy. However, myogenic contractions are not well suited for most forms of animal locomotion, where different muscles acting remotely from one another must achieve precise timing to produce accurate locomotor patterns. For these complex muscular ensembles, endogenous or reflexive activation could not produce the fast, reliable, and diverse array of activities associated with locomotion. Therefore, around the same time muscles evolved, a second type of specialized excitable tissue evolved which could coordinate muscle activity. These cells could detect meaningful environmental information, compute appropriate responses, and mount an appropriate organismal activity by synchronizing patterns of muscular activation. They gave rise to the nervous system.

### **Neural Control of Locomotion**

The movements of charged atoms (i.e., ionic currents) are important drivers of prokaryotic flagella and eukaryotic muscular contractions. In muscles, the magnitude and speed of intracellular calcium release allow quick and synchronous activation of millions of myosin molecules throughout these large cells. Around the same time as muscle cells were getting their evolutionary start, a second type of specialized cell evolved to also harness ionic currents to communicate distant parts of large multicellular organisms. Neurons are specialized cells that can detect and integrate environmental changes as well as select and elicit adaptive patterns of muscular activity.

Neurons can communicate with one another (and with muscles) using chemical molecules released across intercellular approximations called (chemical) synapses (Jessell and Kandel 1993). Chemical synapses are by far the most

common way by which neurons communicate. Because of the large number of proteins involved in this type of communication, they lend themselves to the modification and modulation characteristic of learning. Most forms of proactive locomotion, that is, locomotion initiated in response to internal drives, rely primarily on chemical synapses coordinating the activation of different muscle groups.

A second form of neuronal communication is the electrical synapse or gap junction (Bennett 1997). Gap junctions rely on proteins creating physical channels between adjacent neurons. These allow ions and small molecules to travel freely between cells. By connecting the cytoplasm of two cells electrically, gap junctions are responsible for the fastest form of cell-to-cell communication. This speed, however, comes at the cost of plasticity. Electrical synapses lack the degree of modulation that chemical synapses champion. However, the velocity of these synapses makes them ideal for synchronizing different cells and for driving reactive locomotion or locomotion that is initiated in response to external perturbations. For example, electrical synapses are responsible for coordinating many escape behaviors in the animal kingdom such as the C-star escape in fish or the tailflip of crayfish.

A third way in which neurons control locomotion is by the action of molecules released into systemic circulation (Harris-Warrick and Marder 1991). The release of chemical modulators by neurons is a way of altering the function of multiple and remote locomotor systems in an organism. Whereas diffusion of chemicals across an organism makes this the slowest form of neural control, its global effects (simultaneously reaching multiple tissues), coupled with its combinatorial potential (using multiple signaling molecules), make this one of the most diverse and robust ways of generating behavioral diversity. For example, the simple stomatogastric ganglion driving mastication in crustaceans is comprised of about 30 neurons interconnected by electrical and chemical synapses. Although the number of neurons may seem small, the patterns of muscular activation this network can produce are vastly increased by an even larger number of modulatory

substances, which can act singly or in combination to produce many behavioral patterns.

### Central Pattern Generators

Whether it is the crawling of a worm, or the swimming of a whale, successful locomotion relies on the appropriate pattern of muscular activation, which must be initiated and maintained throughout the duration of the behavior. This necessitates synchronization of distant muscles, which must be contracted and relaxed in precisely the correct order and with the appropriate duration and intensity. In addition, sensory information about changing environmental and internal conditions must be allowed to modify the initial motor output. For example, a strong gust of wind, a change in terrain inclination, or a misstep could prevent the completion of a locomotor goal unless the animal used sensory feedback to correct motor outputs to match new available information. In the next section, we discuss sensory modulation of locomotion, but first we will consider the generation of motor outputs.

Most forms of animal locomotion rely on the rhythmic activation of groups of muscles. These cyclical patterns of activity are often the product of specialized neural tissues dedicated to the production of these rhythms. They are known as central pattern generators (CPGs), and they are capable of producing rhythmic outputs in the absence of rhythmic inputs (Marder and Bucher 2001). Extensive work on cats demonstrated that the mammalian spinal cord houses CPGs for the production of walking and running. Similar central rhythmic centers have been identified across taxa, including nematodes and jellyfish.

Motor patterns are usually produced by one or several cells, which act as pacemakers for the rhythm. Pacemakers can consist of a single rhythmically active neuron, a pair of mutually inhibiting neurons, or a group of three or more cells. Although CPGs do not require inputs to generate an output, sensory feedback is crucial for modifying outputs and obtaining rhythms that reflect the changing needs of an animal. For this reason, rhythms recorded from isolated nervous systems (termed “fictive”) generally match rhythms observed in intact animals only partially.



In the absence of sensory feedback, rhythms tend to be faster and less variable than those recorded in intact preparations. The importance of sensory feedback to modulate motor output is exemplified in box jellies. These animals, among the simplest to possess nervous systems, use CPGs to produce locomotion. Nevertheless, the activity of their CPGs is modulated by input from rudimentary sensory organs (eyes), which help the animal steer their locomotion.

### **Locomotor Gaits**

Simple pattern generators such as the jellyfish's may be restricted to the generation of one or, at most, a few patterns of activity. This places limits on the behavioral repertoire they are able to produce. As animals increased their number of neurons, the number of possible synaptic connections between them grew exponentially. Increased interconnectivity permitted finer modulation of motor outputs and led to the evolution of alternative motor circuits animals could now select between. The neural networks responsible for these distinct programs could be independent or partially overlapping. Many of these circuits are highly conserved between species, and only minor modifications are needed to produce profound changes in outputs. In the case of distinct locomotor outputs, these are referred to as gaits (Alexander 1989).

The term gait is historically associated with the patterns of leg movements in pedestrian locomotion on land. Work pioneered by Eadweard Muybridge and his stop motion photography in 1878 allowed the study of the patterns of limb movements in freely moving animals. The study of animal locomotion has since expanded from animals walking on land to all animals (limbed or limbless) moving in every kind of environment by means of rhythmic movements. Locomotion researchers modified the usage of "gait" to include other types of locomotion. In general, two patterns of animal locomotion are considered to be distinct gaits if their production represents the output of nonidentical neural circuits. Animals thus may produce flying, swimming, crawling, walking, burrowing gaits, etc.

The production and selection of different gaits is associated with the distinct energetic costs of locomotion in different environments or speed ranges. For example, a person on an accelerating treadmill can increase their pace as the treadmill speeds up. However, beyond roughly 2 m/s, most people become unable to keep pace and are forced to switch from walking to running. This transition occurs at the point where walking faster would consume more energy than running slow. Walking and running gaits are optimized to minimize energy expenditure for a particular range of velocities. We discuss the energetics of locomotion in a later section.

While the transition between walking and running might be subtle and occurs within the same environment (on land), some gait transitions are more dramatic and involve different environments. For example, crawling and swimming involve the activity of the same muscles, but using distinct patterns of activity. These patterns of muscle activity involve different pattern generators and often rely on distinct sensory feedback. The ability to appropriately select and transition between distinct motor patterns is of paramount importance to survival. For many animals, getting this transition wrong once spells demise. Because of this, the mechanisms employed to effect these transitions tend to be highly conserved across evolution. For example, leeches and nematodes are evolutionary distant animals that use the signaling amines dopamine and serotonin to trigger transitions from swimming to crawling (dopamine) and vice versa (serotonin). Dopamine is an ancient molecule universally used to modulate locomotion. Loss of dopamine in Parkinson's disease, or through other insults, results in the inability to initiate locomotor patterns in worms just as much as it does in humans. Natural selection does not act on all processes equally. While the genes involved in the synthesis and use of signaling molecules are highly conserved across taxa, genes coding the receptors for these molecules have been free to diverge and increase in number. They are key contributors to the diversity of locomotor programs we see in the natural world.

### Sensory Feedback

The production of meaningful locomotion depends on an animal's ability to monitor (a) changes on its environment, (b) the position of its limbs during the performance of the behavior, and (c) its changing orientation and position with respect to its intended trajectory (Ausborn et al. 2009). Higher-order sensory systems, such as the olfactory, visual, and auditory systems, modulate the direction and speed of locomotion. These are instrumental in achieving the locomotor goal of translating an animal to its destination. At a more basic level, internal organs such as the inner ear (or statocysts in invertebrates) allow animals to maintain appropriate body orientation during the performance of locomotion. Lastly, proprioceptor organs distributed throughout the organism provide ongoing feedback to central motor centers that allow the continuous adjustment of motor outputs. It is through the continuous and combined inputs of these sensory streams that locomotion becomes relevant and meaningful to the survival of the organism.

### Physical Variables Influencing Locomotion

Animals adapted to move in every niche afforded by our planet. These include environments with physical properties that place unique demands or constraints on the strategies available. For example, demands faced in aquatic and aerial locomotion are distinct from those encountered during terrestrial or subterranean locomotion.

#### Environment

Our planet is lush with diverse environments animals can exploit in their quest to survive and reproduce. The seas were the first biotic environment and remain home to millions of animal species. Locomotion through a fluid (liquid or gaseous) is dominated by the friction and inertia experienced by an animal as it collides with the molecules in the fluid around it (Sfakiotakis et al. 1999). To minimize resistive (drag) forces experienced while swimming (or flying), animals often

evolved hydrodynamic (or aerodynamic) shapes that reduce the number and intensity of collisions with the particles making up their environment. In physical terms, the primary distinction between aquatic and aerial locomotion resides in the relative density of animals to their environment. Animals that are denser than their environment sink and must continually spend energy to remain air- or waterborne. Both aerial and aquatic animals often possess adaptations that allow them to mitigate the effects of this differential density. For example, birds have hollow bones that considerably reduce their weight, while most bony fish have swim bladders that allow them to control buoyancy without having to swim continuously. These adaptations reduce the energy required to maintain the animal within its locomotor substrate.

The familiar shape and locomotor strategies of swimming animals evidence their commitment to a single physical environment (Gleiss et al. 2011). The similarities between aquatic and aerial environments allowed many birds to become apt swimmers without compromising their flight abilities.

Subterranean locomotion places unique physical demands on animals. We define subterranean locomotion as locomotion through solids such as soils, sands, or even other organisms. These environments are characterized as being overwhelmingly dominated by resistive forces and the absence of inertia. Although mostly understudied, burrowing is one of the most commonly used forms of animal locomotion (Gans 1973).

Like swimming and flying, the physical demands that burrowing places on animals have resulted in the evolution of an optimal burrowing shape adopted by most animals that burrow regularly: the vermiform or wormlike shape. Like fish and birds, most worms are bilaterally symmetrical. However, because their density is often lower than that of their environment, worms often adopt a cylindrical shape that allows them to exert forces equally well in every direction. For example, peristaltic waves allow worms to maximize propulsion by generating thrust in every direction. For burrowing animals, the relative density of the media determines the optimal burrowing strategy.

Swimming and burrowing are modes of locomotion in which animals inhabit and locomote through a single physical environment. However, many animals evolved the ability to exploit the interphase between distinct physical environments as a way to reduce the energetic cost of locomotion. Terrestrial and benthic animals take advantage of the differences between different physical environments to effectively locomote at their interface. For example, walking animals exploit the resistive differences between soil and air, using the high resistance in the ground to generate propulsion and the lower resistance of the air to move large, heavy payloads. Walking evolved multiple times in aquatic and terrestrial animals. Tetrapod walking first evolved in sarcopterygian fishes. Arthropods, including crustaceans and insects, produced some of the most sophisticated walkers nature has to offer. Even apt swimmers like cephalopods can produce bipedal walking under certain conditions.

Birds and insects are the most proficient and prolific users of multiple physical environments. Many species spend considerable time locomoting in two or more distinct media. Locomotion in multiple physical environments poses distinct challenges depending on the environments in question. For example, as discussed above, aquatic and aerial locomotion share some similar challenges that allow many flying animals to swim effectively using the same machinery they use for flight. However, there are limits to this overlap. Other forms of locomotion are considerably less synergistic. For example, the demands placed by walking and flying are so different that animals must maintain distinct neuromuscular and skeletal machineries dedicated to each type of locomotion. The high energetic costs of maintaining two independent locomotor systems result in animals dedicating more resources to one form of locomotion over another. As such, many birds are better flyers than they are walkers or swimmers. Alternatively, there are examples of birds where walking or swimming is preferred over flying; however this usually leads to the loss of flight (e.g., ostriches and penguins). An alternative to this type of compromise or commitment is found in arthropods. Insects often have

complex life histories that allow them to sequentially specialize for distinct forms of locomotion during different life stages. For example, dragonfly larvae are voracious aquatic predators capable of walking, swimming, and even jet propulsion, while their adult form is one of the most effective flying hunters in nature. Therefore, dragonflies and other insects can exploit distinct environments by using them during different life stages. Of course, before some swimming larvae can become an aerial adult, they must invest a considerable amount of energy and time undergoing the process of metamorphosis with all the dangers and costs associated with it.

The physical properties on an environment clearly place unique challenges and opportunities for animal locomotion. We now discuss the challenges and opportunities associated with the animals themselves and with their locomotor strategies.

### Stability and Maneuverability

Stability refers to the ability of a system to withstand perturbations that would bring it away from equilibrium (Full et al. 2002). For standing animals, *static stability* is dictated by the interaction between an animal's center of mass and its base of support. We will use the analogy of a painter's folding ladder to visualize how this interaction works. In the opened position (with the legs placed well apart), the ladder is in its most stable configuration. Considerable force can be applied to it before this stability is compromised. This is because the ladder's center of mass lies well within a base of support. As long as destabilizing forces do not move the center of mass outside of their base of support, the ladder will remain stable. If the legs of the ladder are brought closer together, the base of support decreases in size, and the ladder becomes less (stable) able to withstand perturbations. Most ladders have rectangular bases of support (wider than long). Therefore, ladders can withstand greater perturbations in one direction (it is easier to tip a ladder sideways than forward or backward). Animals follow the same rules of stability as the ladder in the analogy above. For example, standing quadrupeds with narrow bases of support (e.g., a horse) are less stable than animals with wider base of support.

One of the most consequential properties of stability is that it is independent of the source of the perturbations. A system that is highly stable will resist environmental perturbations (e.g., wind) as much as they will resist perturbations they themselves cause (e.g., locomotion). Because of this, animals must carefully balance an equation where on one hand they have their ability to withstand unwanted perturbations and on the other is their ability to disrupt their stability to achieve locomotion. One way by which many animals solve this problem is by altering their posture depending on their changing needs. For example, many animals adopt a sprawled stance when engaged in withstanding environmental perturbations and a more upright stance during locomotion.

Once locomotion is initiated, stability is not discarded. Instead, the challenge increases in complexity as it must be achieved for a body in motion. This is termed *dynamic stability*, and it pertains to the ability of a moving body to withstand perturbations. Like the static stability discussed above, an animal's dynamic stability is realized as a compromise between competing needs, namely, the animal's need to resist unwanted perturbation versus its need to produce quick, intentional disruptions such as turning, dodging, abrupt breaks, etc. (e.g., maneuverability).

It is easy to underestimate the challenge that animals face to achieve both high stability and maneuverability. On first approach, animal locomotion can seem simple: an animal exerts force on its environment and produces acceleration (locomotion) in the opposite direction. However, this bears little resemblance to reality. Locomotion in most animals is accomplished by the oscillation of bodies or appendages that exert nonlinear forces on their environment. Indeed, if animal locomotion consisted of straight, steady-state motion, one would not expect to see animals invest in the large number of muscles, neurons, or appendages they often have for the purpose of propulsion. The heavy investment in the generation and control of locomotion can only be understood in light of both the important role of locomotion in survival and in the unpredictable

nature of the external and internal perturbations that challenge its completion.

### Energetics of Locomotion

Locomotion in animals requires the expenditure of large amounts of energy (Schmidt-Nielsen 1972). Due to its energetic cost and incurred risks, animals do not generally engage in locomotion unless there is a physiological need being served that justifies the expenditure. When animals do move, only part of the energy spent is transformed into propulsion. A significant fraction of the energy spent in locomotion is converted into unproductive motion or lost entirely to the environment.

The locomotor strategy employed by animals depends on the most energy-efficient options available in a given environment. Walking animals use the high friction conditions of the ground to generate propulsion but must minimize ground contact to not lose energy to this very friction. For example, at low speeds, walking animals use an inverted pendulum strategy where the body mass moves up over each leg in a motion reminiscent of an inverted pendulum. Part of the energy spent in propulsion is transformed into forward displacement, while part of it is saved as potential energy as the body moves up. The potential energy is then harvested during the second part of the stance phase when the body falls forward toward the next step. The maximal velocity walking animals can achieve is constrained by the earth's gravity, as this force field powers the second half of each step. For animals that are able to temporarily generate accelerations greater than that of the earth's gravity, a second type of motor gait becomes available. At faster speeds, these animals transition to a form of locomotion called running (or hopping, trotting). Here, motion by the center of mass resembles a pogo stick. All muscles are used to generate forward and upward propulsion (which might lead to an aerial phase). During the second part of the stride (as an animal accelerates downward), tendons, muscles, and ligaments absorb vertical forces and store them as elastic energy, ready to propel the first part of the next stride. The use of elastic body components to store energy is also in use in the horizontal plane. Many

animals such as lizards and crabs have sprawled postures that generate significant lateral motion while walking. The energy spent in lateral displacement is stored and partially recovered during successive steps. For slower walkers, this strategy is useful in more than one way. It also enhances stability by allowing the animal to absorb and use disruptive forces such as those experienced when pushed. Because these strategies are based on physical constraints posed by the environment, they are observed in most walking animals (Full and Koditschek 1999).

The energy-saving or recovering strategies described above are not only used by walkers but also by swimmers and fliers. As they push against a fluid (air or water), these animals impart forces on their environment, causing it to move in vortices. Many animals ranging from insects to salps, fish, and birds control the shape and distribution of these vortices to recover part of the energy lost in their generation. For example, generation of tightly packed vortex rings allows swimmers higher velocities and efficiencies. Similarly, flying insects generate lift with their wings in large part due to the vortices created above at the leading edges of their wings.

### Size and Reynolds Numbers

Organisms locomoting through fluids constantly crash with the particles in their surrounding media. They therefore must spend energy to move the fluid out of their way, and they must overcome the internal friction of the fluid (i.e., its viscosity). Osborne Reynolds determined that flow patterns in fluids could be predicted by the ratio of the inertial forces over the viscous forces present in a system (Reynolds 1883). This relationship turned out to predict a great deal of natural phenomena from flow through pipes to the locomotor strategies available to animals. The ratio of these forces (Reynolds number) is a widely used, dimensionless number. For animals (solids) moving through a fluid, the Reynolds number ( $Re$ ) can be calculated as the product of the density of the media ( $\rho$ ), the velocity of the animal ( $V$ ), its length factor ( $L$ ), and the inverse of the viscosity ( $\mu$ ) of the medium:  $Re = (\rho VL)/\mu$ .

For biological systems, this number ranges from  $\sim 10^{-6}$  (bacteria) to  $\sim 10^{14}$  (whales).

At high Reynolds numbers, inertial forces dominate animal locomotion. However, as the fluid viscosity increases ( $Re = 1$ ), viscous forces dominate, and animals produce purely laminar patterns of flow over their bodies. Above  $Re = 40$ , turbulence develops in the wake of the animal (see above). Beyond  $Re = 10^6$ , the cost of overcoming turbulence to increase speed becomes challenging. Animals can push the velocity at which turbulence becomes insurmountable by streamlining their shape. This is a widely used strategy by larger swimming and flying animals (e.g., fish, birds), but that would present no advantage for small swimmers operating in the absence of turbulence (e.g., bacteria). Many animals exist within Reynolds numbers characterized by both viscous and inertial components (e.g., the nematode, *C. elegans*). Others can span Reynolds numbers posing distinct physical demands as they grow in size or transition between different environments.

## Survey of Locomotor Forms

Animals adapted distinct forms of locomotion to best suit their physical environment and to accomplish the goals of self-preservation, finding and securing mates, and ensuring the survival of offspring. We discuss a few examples of the numerous types of locomotion that animals use to achieve these goals relative to their physical environments: aquatic, terrestrial, and aerial (Alexander 2003).

### Aquatic Locomotion

Aquatic environments lend themselves to several types of locomotion, from walking and swimming to sailing and jet propulsion.

**Walking** is accomplished by the cyclical motion of body appendages against a solid substrate. Many aquatic species evolved the machinery required for this type of locomotion. Because walking entails generating force against a solid substrate, most walking is performed using rigid limbs (e.g., arthropods and some fish). Some



animals, however, evolved the ability to walk using different means. Echinoderms such as starfish walk by means of tube feet, which rely on a water vascular system to inflate and deflate them during locomotion. Nudibranch sea slugs and other mollusks walk by means of their foot cilia, and some octopus use their arms to walk on the ocean floor.

**Burrowing** is a form of locomotion that takes place through solid media. Many aquatic species tunnel through the benthos using peristaltic waves of body contractions. Most of these animals developed vermiform (wormlike) shapes. Examples of this type of animal are nematodes and annelids. Their locomotion usually relies on the presence of a hydrostatic skeleton capable of precise rhythmic deformations. There are, however, many burrowing species that rely on other means for burrowing. For example, bivalves use their muscular foot to dig themselves into the substratum.

**Swimming by undulation** is one of the most commonly used forms of aquatic locomotion. Animals across taxa, from platyhelminths to mollusks and annelids, nematodes, arthropods, and chordates, evolved the ability to move through water by undulations generated along the longitudinal axis of their bodies. These undulations can be lateral, as in the case of most fish and reptiles, or dorsoventral, as in the case of marine mammals like dolphin, whales, or seals (Sfakiotakis et al. 1999).

**Swimming with appendages** is the main manner by which organisms inhabiting the low Reynolds number space generate thrust (Purcell 2014). When viscous forces dominate locomotion, symmetrical (reciprocal) forces such as body undulations become ineffectual. Many small animals rely on nonreciprocal motion generated by flagella or on swimming appendages that evolved multiple times in most animal groups. Appendages generate propulsion through nonsymmetrical motion that is divided into the power-generating phase (when interaction with the medium is maximized) and the recovery phase (when interaction with the medium is minimized). Many cartilaginous fish, arthropods, and other animals locomote through water (and other environments) using

their appendages. Examples of swimming appendages include fins (e.g., fish), swimmerets (e.g., krill), wings (e.g., penguins), and legs (e.g., cormorants).

**Sailing** is a passive form of locomotion used by some aquatic animals. Cnidarians are among the most prolific sailors with several species taking to this form of locomotion. For example, the by-the-wind sailors form disks that dwell on the water surface on top of which a triangular fin sits able to harness wind force in locomotion. Another sailing cnidarian is the Portuguese man-of-war, which, unlike the permanent stiff sail of the by-the-wind sailor, has an inflatable gas-filled sail it can use to travel.

Just like cnidarians are able to exploit the water-air interface for locomotion, many animals exploit the benthos (the water-ground interface) to the same end. Like swimming, benthic locomotion can be achieved by body undulations or by the motion of specialized appendages.

**Jet propulsion** evolved convergently in many aquatic animals as a mechanism for evading predators and approaching prey. The most well-known example of jet propulsion comes from jellyfish, which propel themselves by ejecting water from their oral cavity. Cephalopods (e.g., squid and octopus) draw water into their mantle cavity under low pressure; water is quickly expelled through the siphon under high pressure. The generated force propels the animal in the opposite direction, which can be controlled by movements of the siphon. Additional examples of jet propulsion come from scallops and dragonfly larvae, which are capable of jet propulsion by using their rectal chamber to hold and expel water. Jet propulsion is limited by the volume of water used for reaction mass (which is dependent on the animal's cavity size). Many coleoids adapted undulatory fins for fish-like locomotion.

## Terrestrial Locomotion

Many animal orders transitioned from aquatic to terrestrial environments. Whereas some locomotor approaches used in aquatic environments are ineffective on land (e.g., jet propulsion and swimming), many approaches that first evolved in aquatic environments remain effective.

**Burrowing** is a widely used locomotor strategy for many animals including nematodes, annelids, arthropods, and vertebrates.

**Walking** is one of the most effective forms on locomotion on land. Terrestrial environments offered walkers decreased drag and buoyancy compared to aquatic walking. This increased their ability to generate greater propulsive forces (due to their increased effective weight) and to experience less resistance. The result of these improved conditions was the evolution of the fastest forms of pedestrian locomotion for both vertebrates and arthropods.

**Crawling** is mostly performed by limbless animals that produce either axial bending to produce propulsive forces as in the case of snakes and some fishes or by peristaltic waves as in the case of many arthropod larvae.

**Jumping** or hopping involves the simultaneous retraction or extension of the hind legs, followed by an aerial phase of movement. Jumping is the dominant mode of terrestrial locomotion in frogs, and it is also found among mammals and arthropods. Whereas most animals use muscular contractions to power their jumps, some arthropods evolved additional mechanisms, enabling them to attain greater accelerations and improved jumping performances. For example, jumping spiders use hemolymph pressure to extend their legs, and planthopper insects evolved biological gears to power their ballistic jumps.

Most terrestrial animals locomote on, or through, the ground; however, some terrestrial animals evolved the ability to locomote through the air.

### Aerial Locomotion

True flight has evolved independently at least seven times among insects, birds, and mammals. By sheer number of species, and flight modes, insects are the most prolific aerial group.

**Active flight** refers to flight produced by muscular exertion of an animal's flight machinery. Insects, the undisputed champions of this form of locomotion, began flying during the Carboniferous (~350 mya). In insects, flight can be produced by the action of direct, or indirect, muscles. With *direct flight*, muscles attach directly to the

wings. Examples of this arrangement are dragonflies and mayflies. Most insects, however, use *indirect flight*. Here, flight muscles attach not to the wing, but rather to the thoracic skeleton. Compressions of the thoracic cavity result in the (indirect) movement of the attached wings. In birds, active flight dates back to the earliest avian ancestors (e.g., Archaeopteryx) some 150 mya and is responsible for the great success and diversity of this group. Among mammals, bats alone evolved the ability for powered flight. Unique among animals, squids are capable of flight by means of rocket propulsion. This involves the generation of lift by means of forceful ejection of water from their mantle cavity during flight.

**Gliding** refers to the use of gravity to power forward locomotion. By harnessing and controlling the drag forces experienced during free fall, gliding animals travel with only minimal energy expenditure. Birds are the champions of this type of locomotion, with albatrosses being able to harvest up to 20 times in horizontal displacement what it invests in falling vertically. Gliding also occurs among mammals (e.g., flying squirrels), amphibians (e.g., gliding frogs), reptiles (e.g., geckos), fish (e.g., flying fish), and mollusks (e.g., squid).

**Ballooning** refers to the passive aerial dispersal of animals using silk threads to harness the wind. This process is best understood in spiders that use it to disperse following hatching, but it also takes place among mites and some insect larvae.

### Cross-References

- [Adaptedness of Behavior](#)
- [Behavior Systems](#)
- [Bird Migrations](#)
- [Catarrhine Locomotion](#)
- [Cetacean Locomotion](#)
- [Escape Response](#)
- [Fitness](#)
- [Fixed Action Patterns](#)
- [Gait](#)
- [Motivation](#)

- ▶ [Mustelidae Locomotion](#)
- ▶ [Natural Selection](#)
- ▶ [Perception-Action Theory](#)
- ▶ [Pinniped Morphology and Locomotion](#)
- ▶ [Platyrrhine Locomotion](#)
- ▶ [Predation Risk](#)
- ▶ [Predator Defense](#)
- ▶ [Prosimian Locomotion](#)
- ▶ [Proboscidea Navigation](#)
- ▶ [Terrestrial](#)

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## Locus

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## Synonyms

[Gene locus](#)

## Definition

Location on a chromosome of the DNA sequence for a gene.

## Introduction

A locus is the physical location of a gene on a chromosome. There may be one or more alleles at a single gene locus. In diploid organisms, there are two copies of each locus on the autosomal chromosomes. An individual can have two copies of the same allele at a locus and have a homozygous genotype or have two different alleles at a locus and have a heterozygous genotype.

## Pleiotropy and Complex Traits

Pleiotropy occurs when a gene at a single locus effects multiple traits. For example, one allele of the *tb1* gene in corn not only causes the plant to have multiple branches instead of a single stalk, but also results in increased numbers of leaves, smaller leaves, and smaller ears of corn (Losos et al. 2017). In contrast, complex traits are those that are influenced by multiple genes at multiple loci.

## Recombination and Linkage Disequilibrium

The law of independent assortment states that individual genes assort independently during gamete formation, so that the allele a gamete receives for one gene does not influence the allele received for another gene. Not only can genes on different chromosomes be independently sorted into gametes but also genes on the same arm of a chromosome can assort independently through the process of recombination. Recombination during meiosis via chromosomal crossing over differs from site-specific recombination, which can alter gene order and/or add new information to the genome (Alberts et al. 2002).

An important exception to the law of independent assortment occurs when the loci for two genes are too close together for recombination to occur frequently. Alleles at these loci appear together more often than expected by chance, causing linkage disequilibrium. Phenotypic traits at these physically close loci are considered to be linked.

## Mapping Gene Loci

The frequency of recombination for two loci is dependent on the physical distance between them. Loci that are closer together have a lower frequency of observed recombination, while loci

that are more distant have higher rates of recombination. Loci that are very distant may recombine at the frequency expected by chance.

The differences in frequencies of recombination can be used to determine the sequence of genes and their relative distances from each other (Becker et al. 2003). This distance is expressed in map unit or centiMorgans, where one centiMorgan corresponds to a 1% recombination frequency. One centiMorgan is roughly equivalent to one megabase of sequence on the physical map of the genome (Jobling et al. 2004).

More recent advances in genetics allow us to use quantitative trait loci (QTLs), loci that influence a quantitative phenotype of interest and contribute to a complex trait, to map gene locations. QTL mapping identifies associations between phenotypes and genotypes on a genome-wide scale, giving information not only about the genomic location but also the number and effect sizes of the loci that influence a phenotype.

## Nomenclature

Loci are expressed as *4q21.3*, where *4* is the chromosome number, *q* is the chromosome arm (*p* for the short arm, *q* for the long arm), *2* is the region, *1* is the band, and *3* is the sub-band. Bands are counted out of the centromere (center) of the chromosome to the telomere (end) after the chromosome has been stained with Giesma stain (also known as G-banding).

## Cross-References

- ▶ [Alleles](#)
- ▶ [Gene](#)
- ▶ [Law of Independent Assortment](#)
- ▶ [Pleiotropy](#)
- ▶ [Quantitative Trait Loci \(QTL\)](#)
- ▶ [Recombination](#)

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of obtaining the test data if the two gene loci in a chromosome are indeed linked to the likelihood of observing the same data purely by chance. If the LOD score is positive (high LOD score), it means that the gene loci are closely linked and therefore usually inherited together. If the LOD score is negative (low LOD score), it means a low linkage. LOD stands for “logarithm (base 10) of odds,” means that the number is expressed logarithmically.

## LOD Score

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## Synonyms

Log of odds; Logarithm (base 10) of odds

## Definition

A statistical test used for linkage analysis in human, animal, and plant populations.

## Introduction

The search for a method to detect linkage of major loci took 25 years, beginning with Bernstein (1931) and ending with LOD scores. In 1955, Newton Morton developed a statistical test (named LOD score) for linkage analysis (Morton 1955). When two gene loci are located on the same chromosome, the chance of a cross-over producing recombination between the gene loci is related to the distance between the two gene loci. Therefore, recombination frequencies have been used to develop linkage maps or genetic maps. In genetics, the LOD score has been applied to test whether two gene loci are likely to be located near each other on a chromosome and are therefore likely to be linked. The LOD score compares the probability/likelihood

## How to Calculate LOD Score

The calculation of a LOD score needs a large data of samples, which tend to yield more statistically meaningful information, because a large number of samples reduce the risk of flukes and clusters which twist the data (Morton 1996).

The LOD score is calculated as follows:

LOD score =  $\log_{10}(\text{probability of birth sequence with a given linkage value} / \text{probability of birth sequence with no linkage})$

To calculate the LOD score, a pedigree for two gene loci of interest should be established first. That is to say, the genotypes of parents and offspring are needed. Second, the number of recombinants and number of nonrecombinants are determined according to the genotypes of parents and offspring observed.

The third step is to calculate the probability of obtaining the results assuming the two loci are linked. This is given by

$$P_{\text{linked}} = \left( \frac{R}{R + NR} \right)^R * \left( 1 - \frac{R}{R + NR} \right)^{NR},$$

where R = number of recombinants and NR = number of nonrecombinants.

The fourth step is to calculate the probability of obtaining the results assuming the two loci are not linked. This is given by  $P_{\text{non-linked}} = \left( \frac{1}{2} \right)^{NR+R}$ , where R = number of recombinants and NR = number of nonrecombinants.



The fifth step is to divide the probability of obtaining the results assuming the two loci are linked by the probability of obtaining the results assuming the two loci are not linked. This is given by  $\frac{P_{\text{linked}}}{P_{\text{non-linked}}}$ .

At last, take the base 10 logarithm of the ratio obtained above. This is given by  $LOD \text{ score} = \log_{10} \frac{P_{\text{linked}}}{P_{\text{non-linked}}}$ .

A lower LOD score (negative) indicates less likelihood of genetic linkage (Nyholt 2000). A LOD score of 3 or higher generally means that two genetic loci are located close to each other on the chromosome, indicating 1000 to 1 odds that the linkage being observed did not occur by chance. A LOD score of 3 translates to a  $p$ -value of approximately  $0.05^3$  (Risch 1991).

## Conclusion

Recombination frequency, a measure of genetic linkage, is the frequency with which a single chromosomal crossover will take place between two genes during meiosis. LOD scores provide a method to unify linkage tests based on identity by pedigree and identity in marker state while permitting selection of the most informative individuals through their phenotypes and genetic markers in relatives. The LOD score is determined by taking the base 10 logarithm of the ratio of the linkage likelihood to the likelihood of no linkage. LOD score is a simple method to analyze complex family pedigrees in order to determine the linkage between two genetic markers.

## Cross-References

► [Linkage Analysis](#)

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## Log of Odds

► [LOD Score](#)

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## Logarithm (Base 10) of Odds

► [LOD Score](#)

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## Long Interspersed Nuclear Elements

► [Repeat Sequences](#)

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## Long-Delay Conditioning

► [Inhibition of Delay](#)

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## Longevity

► [Lagomorpha Life History](#)

► [Lifetime Expectancy](#)

## Long-Lasting Strengthening

### ► Long-Term Potentiation

## Long-Term Memory

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### Synonyms

Autobiographical memory and procedural memory; Declarative memory; Episodic memory; Explicit memory; Semantic memory

### Definition of Long-Term Memory

Long-term memory is, conceptually, the process by which events, skills, procedures, and concepts are stored indefinitely in the mind. That is not to say that forgetting is impossible, just that there is no precisely defined point when that will happen (Greene 1987). The model most people are familiar with involves the movement of concepts from short-term or working memory into long-term memory with rehearsal or practice (Atkinson and Shiffrin 1968). It is thought that information moving through short-term memory is encoded into long-term memory through a process called synaptic consolidation which leads to the formation of a permanent change in the brain defined as an engram (Dudai 2004; Liu et al. 2012). This change in brain connections is thought to materialize physically as increased synaptic strength (increased dendritic formation) that is the result of cellular consolidation; however, recent research has illuminated this further, as it seems a specific pattern of connectivity of engram cells may be the crucial element for long-term storage (Ryan et al. 2015). Sleep is also considered to be an

important process for memory consolidation (see day night cycles in this volume; Ruch et al. 2012).

### What Is Remembered?

Long-term memories can be subdivided into explicit and implicit categories. Explicit memories are those that we have conscious reflections of and are further subdivided as semantic, autobiographical, and episodic memory. Semantic memory involves the facts one knows. When you are remembering information for a test or the meaning of words, that is semantic memory (Wood et al. 2012). Autobiographical memory involves the knowledge one has of the personal events that have impacted his or her own life (Conway and Pleydell-Pearce 2000). It contrasts with episodic memory in that autobiographical memory can only apply to personal events, whereas episodic memory can apply to events that have involved others and is more altered by the ravages of time and age than the other two subdivisions of explicit memory (Spaniol et al. 2006). Implicit memory, by contrast, deals with the mechanics of the body. This is where one's procedural ability to ride a bike or drive a car is centered (Foerde and Poldrack 2009). Considered a subconscious memory system, implicit memory is considered non-associative (Eysenck 2012). As we get better with these types of tasks, like writing or mechanical activities we are "primed," our performance is accompanied with greater speed and dexterity.

### What Is Forgotten?

Many neurodegenerative diseases, like Parkinson's disease, Alzheimer's disease, dementia, multiple sclerosis, Huntington's disease, and schizophrenia, are related to forgetting things. It is the associated damage to neuronal tissue that causes the lapses rather than normal forgetting processes. Even menopause in women can be associated with memory loss (Drogos et al. 2013). According to some, it is the process of sleep that helps us prune our

memories (Poe 2017). In normal functioning, forgetting is as important as remembering, and understanding what we remember and what we forget helps determine what things are ecologically relevant to both people and animals alike.

### **Long-Term Social Memory: An Evolutionary and Ecologically Relevant Test of Comparative Cognition**

In 1976, Nicholas Humphrey published a seminal paper on the “social function of intellect.” He argued that the problems faced by primates related to food acquisition or general survival could not explain the evolution of intelligence differences between species facing similar ecological pressures (Humphrey 1976). Humphrey argued that sociality accounted for the observed aptitude differences. It was the processing of social information, like recognizing and remembering individuals as well as tracking relationships of both self and others as well as between others, which proved to be the most relevant tasks of learning and memory faced by primates. Humphrey argued that the ability to perform match-to-sample tasks, sustain long-term memories for decades, or even engage in abstract problem-solving stems from the social demands that lead to complex behaviors such as tactical deception and tactical coalition formation (Dunbar 1998; also see Emery et al. 2007; Humphrey 1976).

To associate cognition with sociality, one needs a cognitive task that can be tested across species as an indicator of relevant cognitive evolution driven by the needs presented by a complex social system (such as fission fusion, see Aureli et al. 2008). Associating memory (or demonstrating recall, as a behaviorist might point out) with social recognition provides just such a task, because it leads naturally to the prediction that as social systems get more and more complex, the duration of conspecific memory retention should increase. This is a direct, semi-easily quantifiable cognitive measurement (not something as intractable and loaded as deceit or theory of mind), applicable to all species that have social recognition capabilities, and relates directly to the main ecological problem of a complex social

system: needing to remember more individuals for longer periods of time (Bruck 2013b).

Long-term social recognition is potentially necessary in the few species that exhibit fission-fusion dynamics where changes in the social group size and composition occur regularly (Connor et al. 2000; Isbell and Van Vuren 1996). Availability of food often causes dolphin pods to break up and reform, leading to separations that could last hours, days, or possibly even years (Connor et al. 2000; Connor and Whitehead 2005). Using signature whistles, dolphins advertise their individual identity and location to pod-mates after such separations (Caldwell and Caldwell 1965; Caldwell et al. 1990; Harley 2008; Janik 2009; Sayigh et al. 1998). In terms of nonkin long-term social recognition in nonhuman animals, dolphins have been systematically shown, so far, to have the longest social memory retention of more than 20 years (Bruck 2013a). Anecdotally, later tests performed on a 47-year-old dolphin using a signature whistle playback of a social partner she had not seen in 42 years indicated that dolphin social memory most likely rivals our own limits of approximately 50 years (Bruck, unpublished data; Bahrack et al. 1975). Individual-level recognition systems are found outside of cetaceans as well, and in many cases, we not only know that nonhuman animals can recognize individuals but also how long these social memories persist. For example, elephants are able to distinguish between the acoustic signals of over 100 different individuals from distances extending 1–1.5 km and can potentially remember olfactory cues of individuals for a decade or more (Hart et al. 2008; McComb et al. 2000, 2003; Rasmussen 1995; Rasmussen and Krishnamurthy 2000). In fur seals, mothers and pups are often separated as the mother hunts for food. When the mother returns, she uses her offspring’s call to reunite with the correct fur seal pup. Over time, however, this call changes as the pup grows. The mother not only remembers the specific call of her pup at the time; she also maintains long-term memories for the various different versions of her offspring’s call (Charrier et al. 2003; Insley 2000). As mentioned previously, humans maintain face memory for almost 50 years, even of unrelated individuals (Bahrack et al. 1975; Dasser 1985). For other fission-fusion species most likely to

**Long-Term Memory, Table 1** Duration of long-term social memory by species, length of memory social system, and kin-based familiarity vs. generalized familiarity

| Species                        | LTSR duration (years) | Modality | Study                       | Kin only | Fission-fusion | Concerns                                 |
|--------------------------------|-----------------------|----------|-----------------------------|----------|----------------|------------------------------------------|
| Belding's ground squirrels     | 6 months              | Odor     | (Mateo and Johnston 2000)   | y        | n              | Not based on familiarity (armpit effect) |
| Hooded warblers                | 8 months              | Acoustic | (Godard 1991)               | n        | y              |                                          |
| Spotted hyenas <sup>a</sup>    | 1                     | Odor??   | (Holekamp et al. 2007)      | n        | y              | Anecdotal                                |
| Australian sea lions           | 2                     | Acoustic | (Pitcher et al. 2010)       | y        | n              |                                          |
| Ravens                         | 3                     | Acoustic | (Boeckle and Bugnyar 2012)  | n        | y              |                                          |
| Japanese monkeys               | 3                     | Visual   | (Murai et al. 2011)         | n        | y              | No adults tested                         |
| Cotton-top tamarin             | 4 +                   | Acoustic | (Matthews and Snowdon 2011) | y        | n              |                                          |
| Campbell's monkeys             | 4                     | Acoustic | (Lemasson et al. 2005)      | n        | y              |                                          |
| Northern fur seal              | 4                     | Acoustic | (Insley 2000)               | y        | n              |                                          |
| Bonobo                         | ~5–8                  | Acoustic | (Keenan et al. 2016)        | n        | y              |                                          |
| African elephants <sup>a</sup> | 2–12                  | Acoustic | (McComb et al. 2000)        | n        | y              | Anecdotal                                |
| Bottlenose dolphins            | >20                   | Acoustic | (Bruck 2013a)               | n        | y              |                                          |
| Asian elephants <sup>a</sup>   | 2–27                  | Odor     | (Rasmussen 1995)            | y        | y              | Anecdotal                                |
| Humans                         | 46                    | Visual   | (Bahrick et al. 1975)       | n        | y              | Yearbook photos                          |

<sup>a</sup>Denotes anecdotal observations, low sample size, and/or non-peer-reviewed publication

have persistent social memories, systematic studies have been conducted on corvids (3 years of long-term social recognition, Boeckle and Bugnyar 2012; Marzluff et al. 2010) and Japanese monkeys (3 years, Murai et al. 2011), and there is anecdotal information for hyenas (1 year, Holekamp et al. 2007) and elephants (2–27 years, sons to mothers, Rasmussen 1995), but there is little information for most nonhuman apes and parrots (see Table 1).

Long-term social recognition bridges the studies of cognitive science, comparative psychology, and evolutionary biology in an ecologically meaningful way. It is not possible to rank animal intelligence, despite the public pressure to do so. Comparative tests across taxa on ecologically

relevant cognitive tasks allow us, however, to make informed predictions about how evolution shapes animal minds. This is important, because it allows us to consider evolution in the study of animal minds.

**Cross-References**

- [Attention](#)
- [Cognition](#)
- [Learning](#)
- [Memory](#)
- [Short-Term Memory](#)
- [Working Memory](#)

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## Long-Term Potentiation

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## Synonyms

Long-lasting strengthening; Long-time acquaintance

## Definition

The continuous increase in conductivity and efficacy of synaptic transmission induced by

appropriate activation of the same synapses to carry out the action

## Introduction

The formation of declarative memory (e.g., memory required to remember the content for the next day exam) involves the activation and collaborative working of the neocortex, medial temporal lobe, and hippocampus. Memory formation requires the strengthening of synapses and is studied by *Hebb's rule* (Hudspeth et al. 2013). It is believed that synaptic potentiation is an efficient pathway for learning and formation of memories by the release of neurotransmitters. This activity leads to flexibility of synapses (Marieb and Hoehn 2007), and such plasticity is called Hebbian plasticity.

Hebb postulated: "When the pre-synaptic axon of Cell 1 is in close association with postsynaptic dendrite/cell body/axon of Cell 2, it continuously fires in order to elicit the response. Some growth or metabolic alterations take place in both Cell 1 and 2 to generate the action potential. In order for a stronger response and strengthened synapses, it is mandatory for both pre and post parts of the synapse to be active at the same time" (Squire et al. 2012).

An important phenomenon is seen during the formation of declarative memory in the hippocampus. Timothy Bliss and Terje Lømo in 1973 at Norway discovered high-frequency electrical stimulation (HFS) of an excitatory pathway to the hippocampus. It produced a long-lasting enhancement in the strength of the stimulated synapses in anesthetized rabbit (Squire et al. 2012). Such an effect or the synaptic phenomenon is termed as long-term potentiation (LTP) (Bear et al. 2007; Squire et al. 2012; Tortora and Derrickson 2008). It is the long-last strengthening of postsynaptic nerve cell for stimulation across the synapse. It occurs with repeated stimulation (Bear et al. 2007). However, it is only possible to potentiate the depolarized synapses and not the polarized ones.

Other than hippocampus, LTP has been observed in other brain regions such as cerebellum, neocortex, subcortical regions like amygdala, etc. (Hudspeth et al. 2013). In addition to mam-

mals, LTP is observed in other classes such as in neuromuscular junction of an arthropod, sensorimotor synapse of *Aplysia*, etc. (Squire et al. 2012). Interestingly, there is no such single method to induce LTP in all cases, but there are multiple mechanisms known that depend on the type of synapse and neuroanatomical position (Squire et al. 2012).

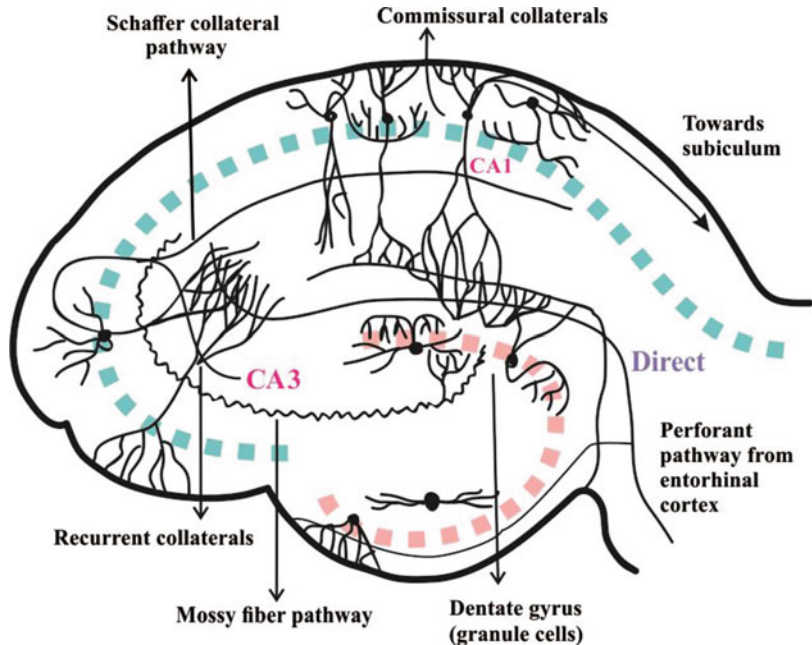
## Neuroanatomy of Hippocampus

Hippocampus is a folded structure of archicortex constituting dentate gyrus and areas of CA1 and CA3 (CA stands for *cornu ammonis*), which are two thin neuronal layers folded onto each other along with subiculum – a transitional cortex. The information gets relayed from one part of hippocampus to the other regions via various pathways that are made up of different fibers. Hippocampus receives its one of the major inputs from six-layered neocortex known as entorhinal cortex via perforant pathway. This pathway is an axon bundle directly stimulating the glutamatergic synapses of granular cells of dentate gyrus (Brady 2011; Hudspeth et al. 2013). It is called perforant because it perforates the dentate gyrus after traversing the hippocampal fissure. From dentate gyrus, the mossy fibers carry the information to the CA3 region forming again the excitatory glutamatergic synapses, and from here the branching occurs in various directions (Fig. 1):

- (a) Commissural fibers from CA3 region pass to the other side of hippocampus.
- (b) Efferents from hippocampus relay information to the hypothalamus or thalamus via fornix.
- (c) Recurrent collaterals form the association between the same and neighboring cells of CA3 region. They are the backward connections.
- (d) Schaffer collaterals pass on the information from CA3 to pyramidal cells of CA1 region.
- (e) The fimbria carries the information to the septum.
- (f) CA1 then sends its axons further to the subiculum and entorhinal cortex (Bear et al. 2007; Squire et al. 2012).

**Long-Term Potentiation,****Fig. 1** Microcircuits

within the hippocampus:  
The flow of direct information starts from the entorhinal cortex to dentate gyrus (granule cells) through perforant pathway. From here it gets relayed through mossy fiber axons to the pyramidal neurons of CA3 region. The information then gets transferred with the help of Schaffer collaterals to the pyramidal neurons of CA1 region. CA1 neurons also receive the input from contralateral hippocampus through commissural collaterals. The message is further carried by CA1 axons to the subiculum



Additionally, there is a direct pathway for the connectivity of many of these regions. It starts from layer III neurons of the entorhinal cortex and terminates into the glutamatergic synapses of CA1 (Brady 2011).

Second, LTP is long-lived. If it is induced in CA1 region in an awake animal, it can last for weeks to months to years and possibly for a lifetime (Bear et al. 2007).

Apart from these LTP has three other properties:

**Properties of LTP in CA3-CA1 Region**

Hippocampal LTP is input specific, i.e., process and conduction of LTP is only seen when the neurons are stimulated with appropriate input. The effectiveness of synapse conductivity is seen once the presynaptic neurons are externally stimulated by an electrical stimulus. Apart from generating LTP through tetanizing, it can also be generated by antagonizing the actions of inhibitory neurotransmitters like GABA, serotonin, etc. (Kandel et al. 2014).

Main function of LTP is to keep the synapse active for a longer period of time when the presynaptic neuron is releasing neurotransmitters and postsynaptic neuron is highly depolarized. This type of synaptic plasticity has two remarkable features. First, it can be induced by brief exposure of tetanus for even less than a second. It will produce frequencies within a normal range.

1. Input specificity: EPSP is not generated when an untetanized low-frequency stimulus is delivered. The only synapse triggered with tetanus shows the properties of LTP.
2. Cooperativity: Strong stimulatory response is only possible when many afferent fibers are elicited by the stimulus displaying spatial summation. It implies that the magnitude or change in the response is only generated when high- and low-frequency-stimulating afferents *cooperate* in order to generate LTP.
3. Associativity: This property is displayed by the synapse when a weak tetanic stimulus fails to elicit a response. The tetanic stimulus from the contralateral or ipsilateral side from other pathways pairs up with a weak response and tends to elicit the response of LTP (Bear et al. 2007).

These Hebbian properties are not universal form of LTP and are not displayed by the mossy

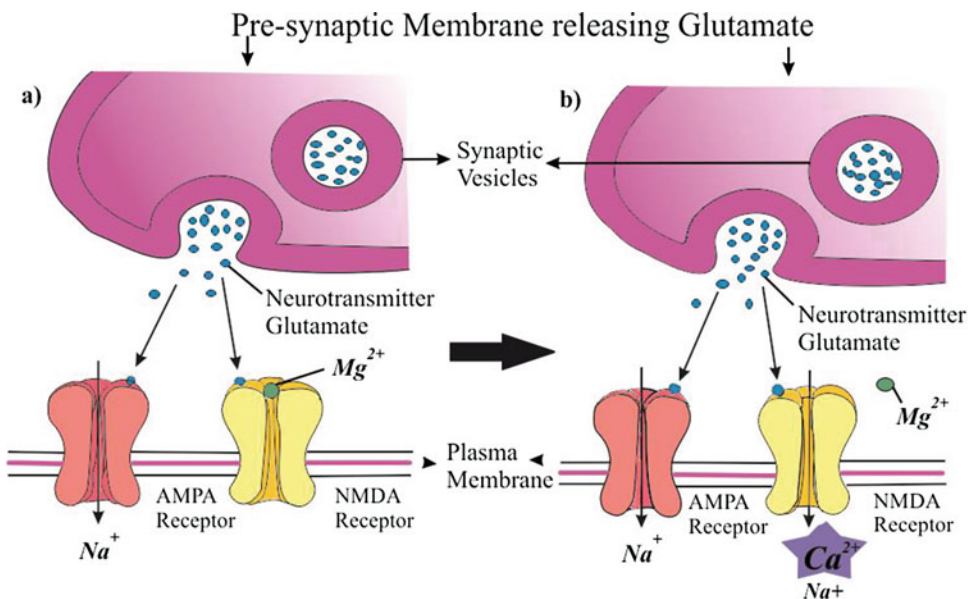
fibers of CA3 synapse or by the Purkinje cell synapse in the cerebellum (Bear et al. 2007). They are unique to the CA1 region.

### Mechanism of LTP in CA1 Region

The amino acid glutamate is responsible for the excitatory synaptic transmission in hippocampal region. Glutamate receptors are of two types: AMPA ( $\alpha$ -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid receptor or AMPAR) and NMDA (N-methyl-D-aspartate receptor or NMDAR) receptor subclasses. The process of LTP follows the following processes. It begins by passing of  $\text{Na}^+$  (sodium) ions through the AMPA receptors in order to generate EPSP at the synapse of pyramidal cells (Bear et al. 2007). NMDA receptors are present on the postsynaptic part. They are of two types: (a) voltage-gated and (b) ligand-gated ion channels. They are in the blocked condition and don't permit the passage of  $\text{Ca}^{2+}$  (calcium) ions (Marieb and Hoehn 2007).

Soon after the transmission of  $\text{Na}^+$  ions and binding of glutamate that is released from the synaptic vesicles of the presynaptic region, their sole purpose is to conduct the  $\text{Ca}^{2+}$  (calcium) ions (Hudspeth et al. 2013) (Fig. 2).

Accumulation of these  $\text{Ca}^{2+}$  ions results in activation of two types of protein kinases: (a) protein kinase C and (b) calcium-calmodulin-dependent protein kinase II (CaMKII) (Hudspeth et al. 2013). Their activation sends signal to the nucleus that huge amounts of proteins are required by a molecular messenger called CREB (cAMP response element-binding protein). The BDNF (brain-derived neurotrophic factor) helps in the formation of these proteins (Marieb and Hoehn 2007). These two protein kinases are known to cause an increase in the ionic conduction of the channel via two pathways: (a) by phosphorylation of existing AMPA receptors (GluR1 subunits) and (b) by inserting entirely new AMPA receptors into the postsynaptic membrane leading to its "AMPAfication" (Hudspeth et al. 2013; Morris 2003). Soon after the release of  $\text{Ca}^{2+}$  ions and protein kinases, NMDA receptors help the



**Long-Term Potentiation, Fig. 2** Simultaneous activity of pre- and postsynaptic neurons leads to activation of NMDA receptors. (a) Activity at postsynaptic membrane during resting potential: Glutamate neurotransmitter binds to AMPA and NMDA receptors allowing the entry of sodium ions. This results in depolarization of polarized

membrane, which then displaces magnesium ions from NMDA channel. (b) Activity at postsynaptic membrane during depolarized (action) potential: Soon after the displacement of magnesium ions, calcium enters through NMDA channels and activates secondary messenger pathways. (Adapted from Bear et al. 2007; pp. 718)

membrane to depolarize and displace  $Mg^{2+}$  ions that were clog the ion channels (voltage-dependent blockade) (Bear et al. 2007). NMDA receptors are also known as Hebbian detectors as they provide correct measure of activation of pre- and postsynaptic parts simultaneously (Hudspeth et al. 2013).

The  $Ca^{2+}$  influx is possible via two ways:

- The inflow of calcium ions through ionotropic GluRs, especially N-methyl-D-aspartate receptor (NMDAR).
- The  $Ca^{2+}$  rush through voltage-gated calcium channels (VGCCs) (Squire et al. 2012).

## Maintenance of LTP

For LTP to take place for a long period of time, it is very important for the synapse to remain active for prolonged periods. There are two documented processes that bring such alterations:

- (a) There are four subunits that make up CaMKII. Activation of  $Ca^{2+}$  leads to their phosphorylation, and even after the return of  $Ca^{2+}$  ions to their resting phase, these subunits remain phosphorylated. This is helpful in reviving the subunit which gets dephosphorylated. The neighboring subunits come and activate it again thus keeping the LTP live for long duration (Bear et al. 2007).
- (b)  $Ca^{2+}$  ions also stimulate an isoform of adenylyl cyclase for increasing the concentration of AMP (adenosine monophosphate) available for LTP (Hudspeth et al. 2013; Kandel et al. 2014).

A retrograde messenger is also needed to travel in backward direction and enhance the glutamate release. This is performed by NMDA  $Ca^{2+}$  ions that signal and generate one such molecule – nitric oxide (NO). This molecule is synthesized by nitric oxide synthase (NOS). NO diffuses through the synaptic cleft into the presynaptic membrane and stimulates the guanylyl cyclase for the release of glutamate (Hudspeth et al. 2013). Endocannabinoids are also a type of retrograde messengers (Marié and Höhn 2007).

Importance of these  $Ca^{2+}$  ions and its proteins can be evaluated after inhibiting the accumulation of  $Ca^{2+}$  ions or any of the two kinases. Inactivating them or blocking their path doesn't permit the formation of LTP (Morris 2003).

## Can LTP Be Termed as Memory Formation?

There are ongoing discussions, and experiments are being carried out to ascertain whether LTP coincides with learning and memory formation. Experiments in a gene knockout mice suggested that LTP is severely impaired at the synapses present in the pathway of entorhinal cortex to dentate gyrus. But the spatial memories that tend to include this particular region for its formation show no signs of disturbance. This proves that there is no relativity between LTP and spatial navigational memory. Alternatively, it can be said that LTP doesn't take the charge of formation of such type of memory (Hudspeth et al. 2013).

It is also suggested that LTP contributes to the formation of declarative memories. The evidence to this statement comes from the fact that the same molecules that are involved in the mechanism of LTP are also responsible for learning and memory formation of declarative memories. Both of these processes have a common requirement of the activation of NMDA receptors after the AMPA receptors.

## Cross-References

- [Dentate Gyrus](#)
- [Entorhinal Cortex](#)
- [Episodic Memory](#)
- [Hippocampus](#)
- [Long-Term Memory](#)
- [Memory](#)
- [Neocortex](#)
- [Neurogenesis](#)
- [Neuron](#)
- [NMDA Receptors](#)



- Parahippocampal Cortex (PHC)
- Perirhinal Cortex
- Short-Term Memory
- Temporal Lobe

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## Long-Time Acquaintance

- Long-Term Potentiation

## Loris

- Prosimian Cognition
- Prosimian Communication
- Prosimian Life History

## Loss of Care

- Primate Orphans

## Louis Leakey

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Louis Leakey (b. 1903–d. 1972) was a prominent paleoanthropologist who paved the way in the field of primate and human evolution in Africa.

## Personal Life

Louis Seymour Bazett Leakey was born on August 7, 1903, in Kabete, Kenya. His parents, Harry and Mary Leakey, were English missionaries to the Kikuyu tribe. In 1921, Leakey traveled back to England and matriculated at Weymouth and St. John's College, Cambridge University, reading in anthropology and archaeology. In 1930, Leakey received his doctorate in African prehistory based on findings near Lake Elmenteita in northwest Kenya.

In his personal life, Leakey married his first wife, Frida Avern, in 1928 and had a son Colin Leakey. They divorced in 1936, and Leakey later remarried that year to fellow archaeologist and illustrator, Mary Nicol. They moved to Kenya and had three sons, Jonathon (1940), Richard (1944), and Philip (1948).

## Works

After he completed his studies in 1924, Leakey traveled back to East Africa to begin his archaeological expedition. Leakey strongly believed that humans originated from Africa and that East African fossils were far older than was previously believed (Isaac and McCown 1976). At the time, this idea was incredibly controversial as species origins were believed to be from Asia or Europe. Leakey's excavation in 1931 at the Olduvai Gorge in Tanzania marked his first and most prominent excavation which shifted the theory of evolution

to be centered in Africa. There, Leakey uncovered animal fossils and ancient stone tools, which were called Oldowan tools. However, it took some time until 1969 before the site developed into a major excavation site.

In 1948, Mary Leakey and the Leakey team made a significant discovery of the complete fossil remains of *Proconsul africanus* on Rusinga Island. This fossil was found to be an ancestor of apes and humans over 18 million years ago (Leakey 1948). Furthermore, in 1962 in east Lake Victoria in Fort Ternan, Leakey's team discovered the remains of *Kenyapithecus*, which provided another link between apes and early man dated 14 million years ago (Leakey 1961). One of the most prominent findings at the Olduvai Gorge excavation site occurred in 1959 by Mary Leakey, who discovered the renowned fossil *Australopithecus* (*Zinjanthropus*) *bosei*. This hominin fossil was nicknamed the "Nutcracker Man" as its jaw was evolved for heavy repetitive chewing (Leakey 1959). The cranium fossil was dated 1.8 million years old.

In 1959, the Leakey excavation team which now included Mary and Leakey's first son, Jonathan, discovered a fossil of a juvenile hominid. The lower jaw and partial top of the skull piece belonged to *Homo habilis* or the handyman. The partial skeleton, dubbed "Johnny's Child," was dated 1.8 million years old and speculated to have created Oldowan stone tools which were found nearby. These findings led Leakey to theorize that the *H. habilis* and *Z. bosei* fossils originated from coexisting, but separate hominid lineages. In fact, Leakey and two other paleoanthropologists, Philip Tobias and John Napier, proposed that *Z. bosei* was not a direct ancestor of modern man due to differences when compared to *H. habilis* (Leakey et al. 1964). This new proposition suggested that the Olduvai fossils met a defining criterion for "homo," which included an upright posture, bipedal gait, and dexterity to stone tools. Furthermore, it was proposed that *H. habilis* was an advanced hominin which lived contemporaneously with *Z. bosei* in east Africa and represented an evolutionary step between *Australopithecus* and *H. erectus* (ancestor of *H. sapiens*) (Leakey et al. 1964). Although the

significance of the findings were widely accepted, the proposed theory faced with skepticism since its proposal in the 1960s until this day as an ongoing debate about the origins of modern humans.

Mary and Leakey were among the pioneers in their field in using newly developed tools and techniques such as isotopic dating in researching Stone Age artifacts (Leakey 1971). Analysis of Oldowan artifacts showed that it was significantly older than any known stone tool technology in Europe. This backed the idea that human predecessors originated in Africa, rather than Europe or Asia.

## Other Works

Throughout his career, Leakey's numerous various books include *The Stone Age Cultures of Kenya Colony* (1931), *Adam's Ancestors* (1934, rev. ed., 1953), *White African: An Early Autobiography* (1937), *Stone Age Africa* (1936), *White African* (1937), *Olduvai Gorge* (1951), *Mau Mau and the Kikuyu* (1952), *Olduvai Gorge, 1951–1961* (1965), *Unveiling Man's Origins* (1969, with Vanne Morris Goodall), and *Animals of East Africa* (1969).

Later in his career, Leakey focused on his academic path where he held appointments at British and American universities while also fundraising for projects. Mary Nicol and their second son, Richard, continued excavations in Africa. From 1945 to 1961, he was appointed as a curator of the Coryndon Memorial Museum in Nairobi. In 1961, he established and became the director of the Centre of Prehistory and Paleontology. In 1958, Leakey founded the National Primates Research Center with Cynthia Booth (previously known as Tigon Primate Research Centre) which became a main center for primate research.

Leakey believed that our understanding of human evolution can be enhanced through our understanding of behaviors of early ape-like ancestors. He was instrumental in support prominent mentees which include Jane Goodall and her research of chimpanzees in Gombe, Dian Fossey and her studies of mountain gorillas in Rwanda,

and Biruté Galdikas insights of orangutans in Borneo. The research of apes in the wild was formative and revolutionary in the course of primate research.

## Legacy

Leakey passed away on October 1, 1972, in London, England. The work led by Leakey and his team was groundbreaking and formed the vital understanding of the earliest origins of human life. The contribution of the Leakey family to natural sciences in the fields of primatology, paleoanthropology, and wildlife conservation continues to this day. In 1968, the Leakey Foundation was established to ensure the legacy of the Leakey family work in the study of human origin. The International Louis Leakey Memorial Institute for African Prehistory located in Nairobi, Kenya, remains a fossil repository, which includes laboratory and research facilities, and stands today as a testament to Leakey's accomplishments.

## Cross-References

- [Jane Goodall](#)
- [Paleontology](#)

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## Louis M. Herman

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## Introduction

The renaissance period of animal cognition in the early 1970s (Hulse et al. 1978) witnessed the emergence of several notable figures that championed an effort to describe the cognitive characteristics (i. e., abilities, specializations and limitations) of different species. Louis M. Herman was among these pioneers whose findings ushered in a new view of animal cognition that extended beyond the restrictive stimulus-response lens of the past. Considered by many to be the “father” of dolphin cognition, Dr. Herman spent nearly 50 years with his many students and colleagues conducting groundbreaking studies that revealed the remarkable cognitive capacity of bottlenose dolphins (*Tursiops truncatus*). In parallel with these efforts, he pioneered the scientific study of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. The marine mammal laboratory Dr. Herman created became world renowned not only for its scientific studies and breakthroughs in the study of dolphin cognition and whale behavior but also for the unique applied learning opportunities it provided to students of all ages through volunteer apprenticeship programs, college-level internships, and higher level degree programs. On August 3, 2016, after five decades of research and publishing about dolphins and whales, Dr. Herman passed away. Full biographies of Dr. Herman's life and remarkable career in marine mammal science can be found in Herman (2012) and Pack et al. (2017).

## Background, Education, and Early Career Directions

Louis M. Herman was born in Queens, New York, in 1930. He earned his bachelor's and master's

degrees in Psychology at City College of New York. After serving as an intelligence officer in the US Air Force and studying concept learning in rhesus monkeys at Emory University in Atlanta, Georgia, Dr. Herman entered the doctoral program at Pennsylvania State University where he investigated human information processing. His dissertation, awarded in 1961, explored how humans process information when confronted with competing cognitive demands from two simultaneous auditory tasks. The American Institutes for Research honored Dr. Herman's work with first prize in their inaugural "Creative Talent Award" in Psychology. In their citation of Dr. Herman's work, eminent psychologists Harry Harlow, James Miller, and Theodore Newcomb wrote "This thesis, beautifully conceived and executed, displays a wealth of knowledge and historical documentation on a modern problem of great significance in psychology" (Harlow et al. 1962, p. 681). Dr. Herman continued his studies of human information processing and performance at North American Aviation in Columbus, Ohio, from 1961 to 1963 and at Queens College in New York City as an assistant professor from 1963 to 1966 (see Pack et al. 2017 for references to some of these studies). In 1966, he joined the Psychology Department at the University of Hawaii at Manoa where he remained for the rest of his career. In his personal life, he was an avid long distance ocean swimmer and most importantly a devoted husband and father to his wife Hannah and their daughter Elia.

### **Founding the First Laboratory Fully Devoted to Dolphin Cognition**

When he joined the University of Hawaii, Dr. Herman's research plans were to continue his studies with humans; however, his attention was soon diverted to another large-brained social mammal, the bottlenose dolphin, whose cognitive capacities he realized had received surprisingly little scientific investigation (see Herman 2012 for examples of some early work). An intriguing summer study on dolphin rule learning at Hawaii's Sea Life Park in 1967 serendipitously

turned into an opportunity to have dolphin pupils at a laboratory of his own creation that could be fully devoted to the study of dolphin sensory perception, cognition, and language comprehension. In 1969, after locating and converting an abandoned shark display facility to house dolphins, Dr. Herman launched the Kewalo Basin Marine Mammal Laboratory (KBMML). There, together with his dolphin pupils (Keakiko, Nana, Puka, Akeakamai, Phoenix, Hiapo, and Elele), 38 graduate students, and scores of undergraduates, he produced numerous groundbreaking studies in dolphin cognition and humpback whale behavior. Following the close of KBMML in 2004, Dr. Herman continued his innovative studies of humpback whale behavior until his passing (summarized in Herman 2016).

### **Dolphin Sensory Perception and Cross-Modal Abilities**

Recognizing that little was known about dolphin sensory perception, Dr. Herman's earliest studies at KBMML explored dolphin hearing and vision as a foundation for future inquiries into dolphin cognition. Starting with dolphin hearing, Dr. Herman demonstrated the dolphin's ability to detect small degrees of frequency modulation and its sensitivity to other types of sounds as well as temporal differences in sounds (summarized in Herman 1980b). Dr. Herman next tackled dolphin vision, performing pioneering studies of dolphin visual acuity that showed that dolphins see well (about 8–12 min of arc) both in air and underwater (Herman et al. 1975). He also explored the dolphin's sensitivity in different areas of the visible spectrum and characterized its limitations in discriminating different colors (Madsen and Herman 1980). Much later, Dr. Herman and his students revealed that dolphins could immediately recognize complexly shaped objects across echolocation and vision (Herman et al. 1998; see also summary in Pack et al. 2004). For the latter work, Dr. Herman and his coauthors received the American Psychological Association Division 6's F.A. Beach Comparative Psychology Award for best paper published in the *Journal of Comparative Psychology* in 1998.

## Dolphin Rule Learning and Concept Formation

In the 1970s, Dr. Herman began investigating the efficiency with which dolphins could acquire and apply generalized rules and concepts, in keeping with other animal cognition studies of the times. His work with learning sets showed that dolphins could learn and apply a “win-stay, lose-shift” rule across numerous novel problems after a single trial with arbitrary sounds and also that they could immediately shift response strategies within problems after reward contingencies were reversed. They performed both of these tasks at levels comparable to what had been shown with nonhuman primates (Herman 1980b). Dr. Herman and his students also investigated the dolphin’s ability to develop a concept of same/different and apply this to novel problems in different modalities. Using matching-to-sample (MTS) tasks as well as tasks involving symbolic judgments of similarity and difference using either simultaneously presented stimuli or successively presented stimuli, the dolphins performed accurately on first trials across numerous problems with novel auditory and visual materials (Herman 1980b; Herman et al. 1993b; Mercado et al. 2000). With one dolphin, acquisition of the same/different concept was near instantaneous suggesting that when confronted with tasks requiring judgments of similarity and difference, dolphins, like chimpanzees, may be predisposed toward cognitive solutions involving concepts rather than memorizing stimulus-specific rote associations (Herman et al. 1993b). Finally, in the mid-1990s, Dr. Herman and his students began to investigate the types of mental representations of objects dolphins formed through echolocation. The results of these studies revealed that complexly shaped objects inspected by the dolphin through echolocation were represented holistically rather than through individual features. They also showed that objects that had never previously been experienced simultaneously through echolocation and vision, as well as novel objects, could be matched across these senses (summarized in Pack et al. 2004). Collectively, these studies demonstrated that dolphins can abstract a same/different

concept from relatively few exemplars and can readily apply that concept on first trials across numerous pairs of novel stimuli in different modalities and even across the senses at levels comparable to those demonstrated with some non-human primates.

## Dolphin Memory Abilities and Processes

In the 1970s, recognizing that memory is the bedrock upon which all cognition rests, Dr. Herman and his students also investigated for the first time dolphin short-term memory abilities and processes. Early work is summarized in Herman (1980b). In studies of auditory MTS in which various delays were interposed between the offset of the sample sound and onset of the alternative sounds, Dr. Herman showed that matching accuracy remained at or near ceiling levels across hundreds of pairs of novel sounds for nearly all delays tested up to 120 sec (the longest delay tested), a finding comparable to what has been found in several species of nonhuman primates (Herman 1980b). He also showed that like visual short-term memory in primates, short-term memory for sounds in MTS tasks was subject to both proactive interference (i.e., interference from earlier experienced sounds on the memory of later sounds), as well as retroactive interference (i.e., interference from noise inserted during the delay period on the memory of sounds experienced prior to the delay). In some of the first serial-probe-recognition tasks run with animals, in which a list of sounds was followed by a probe sound which the dolphin judged symbolically as either on or absent from the list, Dr. Herman showed that memory span for lists of novel sounds was between four and five sounds. He also demonstrated a recency effect with increasing list length, as had been shown in humans and nonhuman primates. Later, Dr. Herman and his students extended these studies by demonstrating that short-term memory retention abilities for various types of visual materials were comparable to those witnessed with auditory materials and that the dolphin was also capable of maintaining representations of motor behaviors either performed by



another dolphin or behaviors that were self-performed (Herman et al. 1993b; Herman 2002). In a unique variant of the latter task, Dr. Herman and his students taught a dolphin to respond to a “repeat” command by repeating the last behavior it performed and also to an “any” command by performing any one of five behaviors except the one that it last performed. The dolphin was tested on different sequences of four commands. Each sequence began with a command to perform a specific behavior. The next three gestures were different combinations of “any” and “repeat.” The dolphin performed with high accuracy, including on those trials in which it was required to repeat self-selected behaviors (Herman 2002). The dolphin’s ability to correctly carry out these sequences demonstrated important aspects of the management of working memory including maintaining, monitoring, and updating mental representations. Collectively, these studies showed that dolphins have well-developed short-term memory capabilities and working memory processes that can flexibly handle material in different modalities and which are critical for supporting higher-level cognitive tasks.

### Dolphin Imitative Abilities

In many ways, Dr. Herman was ahead of his time in terms of recognizing the significance of particular aspects of animal cognition. For example, prior to a renewed interest in animal imitation and the recognition of its complexity and importance in social learning in the 1990s, Dr. Herman and his students had already conducted groundbreaking laboratory studies of imitation in dolphins, who in the wild demonstrate a natural ability to copy the signature whistles of close companions and closely coordinate similar behaviors with these individuals (Herman 2002). They showed for the first time that a dolphin could imitate with high fidelity a variety of arbitrary computer-generated familiar and novel sounds (Richards et al. 1984) and also that it could imitate a variety of familiar and novel arbitrary behaviors produced by either another dolphin or by a human (either in the dolphin’s habitat or at

tank-side or displayed on a small television monitor placed behind an underwater window) (Herman 2002). The ability of the dolphin to imitate both novel sounds and motor behaviors, and to respond to an “imitate” signal (in contrast to other signaled commands), demonstrated that it could develop a broad and generalized concept of imitation thus far unmatched in studies with other nonhuman animals.

### Studies of Dolphin Social Awareness and Self-Awareness

In the 1990s, Dr. Herman and his students began to investigate forms of social awareness beyond imitation. These studies focused on the management of joint attention between an informant and a receiver toward objects of interest by testing the dolphins’ understanding of human pointing and/or gazing. Joint attention is recognized as an essential component of social cognition (Pack and Herman 2006). Early work with nonhuman primates showed that they had difficulty in comprehending pointing cues, unless the tip of the informant’s pointing finger was positioned nearly touching a focal object (reviewed in Pack and Herman 2006). In contrast, Herman et al. (1999) demonstrated that dolphins could respond accurately on first trials to dynamic brief human pointing cues toward distal objects including those placed behind the dolphin. The dolphin could also immediately understand sequences of pointing cues when these were substituted for gestural references to objects that instructed the dolphin to create relationships between two objects (see section on sentence comprehension below). Later work extended these discoveries by demonstrating that dolphins could immediately understand static human pointing cues as well as both static and dynamic human gazing cues at objects (Pack and Herman 2006). Together, these studies showed that the dolphins understood the referring function of pointing and gazing, and they complemented other work performed at Epcot’s Living Seas facility in Florida by some of Dr. Herman’s former students and colleagues showing dolphins spontaneously producing

pointing behaviors (by aligning their rostrum and body toward an object) and understanding the importance of attentiveness of a receiver (reviewed in Pack and Herman 2006). Dr. Herman and his students also studied various forms of self-awareness. They showed that a dolphin could on command recall its own actions including those behaviors of its own choosing or creation (summarized in Herman 2002). They also showed that a dolphin could both understand human-directed references to its own body parts and could use referenced body parts in different ways (e.g., to touch or toss an object) (Herman et al. 2001). This work adds to the understanding of dolphin self-awareness, which has also been demonstrated in mirror self-recognition studies (Reiss and Marino 2001).

### Studies of the Interpretation of Television Displays

One of the most unexpected and remarkable abilities shown in dolphins by Dr. Herman was their capacity to spontaneously (i.e., without training) understand television displays as representations of the real world. When confronted for the first time with the small, 20 cm image of a trainer on a television monitor placed behind an underwater window in their habitat, both the dolphins Phoenix and Akeakamai (Ake) immediately understood gestural signs given by this trainer including, for Ake, imperative sentences within her language (see section below on sentence comprehension) (Herman et al. 1990). The immediacy with which the dolphins interpreted these television displays as representations of the real world stands in contrast to the initial difficulty common chimpanzees had with this understanding (Savage-Rumbaugh 1986). In addition to understanding the gestural signs from the small image of a trainer, the dolphins also understood gestural signs that were reduced to point-light displays (i.e., points of light against a black background moving about in place of the trainers arms and hands) (Herman et al. 1990). Further studies showed that they also understood the relationship between a small, televised image of an object and

the same real-sized object inspected through echolocation (Pack et al. 2004), and could imitate televised behaviors of a human (Herman et al. 1993b; Herman 2002).

### Studies of Comprehension of Sentences by Dolphins

Arguably, the most notable of Dr. Herman's contributions to the field of animal cognition have been in language comprehension (Herman 1986, 1987, Herman and Forestell 1985; Herman et al. 1984, 1993a,b). Dr. Herman created two artificial language systems in which either human-generated gestural signals (taught to Ake) or computer-generated acoustic signals (taught to Phoenix) were used to express individual "words" in various semantic categories (agents, objects, actions, modifiers, relationships). Sequences of words were used to compose sentences up to five words in length according to various syntactic frames and constraints. A "sentence" was defined as "a sequence of words that expressed a unique semantic proposition" (Herman et al. 1984, p. 135) and was given in the imperative or interrogative mode. Imperatives required the dolphin to take named actions to named objects taking into account their named modifiers or asked the dolphin to construct a relationship between two named objects. To illustrate the complexity of some of the imperatives, the five-word relational sentence *Right Hoop Left Ball Fetch* asked Ake to take the ball on her left to the hoop on her right, with pairs of hoops and balls present as well as other named objects. The modifiers *Left* and *Right* could exchange positions in the sentence as could the objects *Hoop* and *Ball*, and the relationship term *In/On* could be exchanged for the relationship term *Fetch* to create a variety of new instructions, all of which Ake understood. The findings (see earlier citations) established the ability of Phoenix and Ake to take account of both the semantic and syntactic features of their separate language systems to carry out the instructions embedded in the sentences. Among other things, the dolphins could understand instructions new to their experience, derive the meaning of new

syntactic frames that were extensions of existing frames, understand the different meanings of novel sentences in which the same words were placed in different orders, decode semantically or syntactically anomalous sentences, and immediately generalize the lexical references to objects to include different exemplars of those objects. The only other nonhuman species that has shown similar capabilities for comprehension of novel sentences using a variety of objects and in different contexts is the Bonobo (*Pan paniscus*) (Savage-Rumbaugh et al. 1993). In addition to understanding imperative sentences, Ake could report accurately (by responding on *yes* or *no* paddles) whether a named object was present in or absent from her habitat (interrogative sentences). For example, the interrogative *Frisbee Question* asked whether the named object *Frisbee* was present or not in the dolphin's habitat. The ability of the dolphin to report that a symbolically referenced object was absent from the habitat as well as to understand the same symbol in a variety of different sentence types and contexts was strong evidence that language symbols were understood referentially (Herman and Forestell 1985; Herman et al. 1993b).

### Field Studies of Humpback Whale Behavior

The multitude of diverse and innovative studies described above could alone characterize a remarkable career. However, as noted earlier, Dr. Herman was also prolific in the studies he and his students conducted on humpback whale behavior in their Hawaiian breeding grounds and Alaskan feeding grounds. In 1976, when most people were unaware of the presence of humpback whales in Hawaiian waters, Dr. Herman pioneered their scientific study with the first aerial and boat-based surveys of their numbers, association patterns, and habitat use (see Herman 2012). He then created one of the longest continuous field studies of the behavioral ecology of humpback whales ever conducted and through this was able to trace the life histories of individual whales for over 30 years (Herman et al. 2011). The work of Dr.

Herman and his students produced a wealth of new information on humpback whale behavior, which Dr. Herman summarized in his final publication on humpback whales produced in the last year of his life (Herman 2016). Some of these findings were the description of the behavioral role and coining of the term “escort” to describe the whale(s) accompanying a mother-calf pair; that males demonstrate mate guarding in the breeding grounds; that male-male competition over single females in the breeding grounds can escalate from dramatic displays to blood-shedding fights; that male size confers an advantage in competition; that affiliations between humpback whales in the breeding grounds (other than mother-calf pairs) are best characterized as transient; that playback of humpback whale song is much less attractive than playback of a feeding call in the breeding grounds (a finding that later served to help rescue “Humphrey the Wrong Way Whale” from San Francisco Bay in 1985); that males prefer to associate with females without calf (i.e., those with a higher reproductive potential), rather than females with calf (i.e., those with a lower reproductive potential); that across years, females vary their migratory timing depending on their reproductive status; that larger females produce larger calves and tend to attract greater numbers of male escorts than do smaller females; that mature females prefer associating with larger sized adult males; that females with calf tend to segregate into shallow water to avoid male harassment; that both mature and immature males sing in the breeding grounds; and that the mating system in humpback whales has the essential requisite characteristics of a lek mating system.

### Conclusions

Dr. Herman's collective works are documented in 181 scientific publications including two edited books (Herman 1980a; Roitblat et al. 1993). His discoveries have been featured nationally and internationally in over 230 newspaper and magazine articles, radio broadcasts, television documentaries, and IMAX films. At a point in history when much of animal cognition research was

focused on rats, pigeons, and nonhuman primates, Dr. Herman's findings compelled researchers to take notice of the similarities in cognition between dolphins and apes despite their divergent evolutionary lines. Dr. Herman's genius was also in his creative approach to designing scientifically rigorous and unique methods to ask each research question of *dolphins* (in contrast to humans or nonhuman primates) and to continuously adapt his approach in response to the dolphins' behaviors. From the outset, Dr. Herman's goal was to describe dolphin cognition within a comparative framework and "to understand eventually the pressures selecting for intellect and how particular cognitive specializations are adaptive" (Herman 1980b, p. 364). Dr. Herman continued working diligently to reach this goal until his passing. His revelations reinforced his earliest ideas that aside from the dolphin's relatively large brain size, a major evolutionary impetus for the development of its broad, flexible, and sophisticated suite of higher cognitive skills appears to be the elaborate social matrix and communication network typical of wild dolphin societies in which cooperation and competition play roles, the strengths of individual relationships are constantly being assessed, and young calves enjoy a protracted period of parental care through which to observe and learn (Herman 1980b, 2006). In 2004, Dr. Herman was honored as an American Psychological Association's President's Program Featured Speaker, and in 2008, his work with dolphins as well as humpback whales was recognized among the top 100 pioneering accomplishments in the history of the University of Hawaii. Beyond these and many other accolades, Dr. Herman will always be remembered as a pioneer who led one of the most productive long-term field studies of any whale species and advanced the field of dolphin cognition from virtual ignorance to a well-established position in the history of animal cognition research.

## Cross-References

- [Cetacean Cognition](#)
- [Cetacean Communication](#)

- [Cetacean Life History](#)
- [Cetacean Sensory Systems](#)
- [Cognition](#)
- [Imitation](#)
- [Intelligence](#)
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## Lowering

### ► Need Reduction

## Lower-Level Representation

### ► Bottom-Up Processing



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## Lucky Finding

### ► Serendipity

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## Lucy

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## Synonyms

AL 288-1; *Australopithecus afarensis*  
(*A. afarensis*)

## Definition

A notable female specimen of an early hominid classified as *Australopithecus afarensis*. Upon discovery, Lucy's fossilized remains were coded as AL 288-1.

## Introduction

Lucy is the name given to a female specimen of *Australopithecus afarensis*, a relatively early variety of the hominid lineage that ultimately gave rise to the currently existing human species of *Homo sapiens* (modern humans). Lucy's fossilized remains were uncovered at a Pliocene (~5.3–2.6 MYA) site in Hadar, Ethiopia, in 1974. Other fossils of *Australopithecus afarensis* were also found in Laetolil, Tanzania, during the same period, resulting in the initial classification of the species, as well as its placement in the genus *Australopithecus* (from Latin: *southern ape*). The genus is defined by its combination of distinctively human and ape-like features, such as human-like skeletal features well adapted for bipedalism (walking on two legs), ape-like skeletal features adapted for life in the trees, and

relatively ape-like dental properties and brain size (Pontzer 2012). The specimens found at Hadar and Laetolil clearly belonged to the *Australopithecus* genus but differed significantly from previously known species, resulting in it being designated as the new species *A. afarensis* (Johanson et al. 1978).

## Bipedalism

One of the traits that made the discovery of “Lucy” and her conspecifics very interesting is the apparent adaptation for habitual bipedal locomotion (walking on two legs) that was exhibited by their remains. Even though *A. afarensis* seemed to have been able to walk on its hindlimbs, *A. afarensis* also retained elements of skeletal morphology in the forelimbs that are typical of knuckle walking such as seen in modern day African great apes (Richmond et al. 2001). The presence of adaptations suggesting divergent movement strategies makes it difficult to draw definite conclusions about locomotive habits of this early hominid. Still, examination of skeletal morphology suggests that *A. afarensis* was well adapted for bipedal locomotion. However, the hypothesized gait of this species shows relatively few similarities with that of modern humans. Instead, evidence suggests the species' strides were shorter and its walking velocity lower than that of modern humans, despite the relatively larger amount of energy used (Jungers 1982).

## Ecology

Despite the ostensibly more “primitive” walking gait of *A. afarensis*, evidence uncovered recently shows that the species showed adaptations considered to be more directly related to effective bipedalism. The morphology of a newly discovered fossilized metatarsal (middle foot) bone suggests that the foot of *A. afarensis* was nearly identical in function to that of modern humans, making it ideally suited for walking on the hindlimbs (Ward et al. 2011). This discovery

supported the hypothesis that *A. afarensis* was an obligatory terrestrial biped but is in itself not enough to rule out a partially arboreal ecology.

When looking at the morphology of the scapula in this species, it appears that *A. afarensis* was generally well adapted for climbing (Jungers 1982). A range of specimens of different ages shows that throughout development, *A. afarensis* retained scapular properties typical of suspensory primates, whereas these properties are lost during maturation in commonly ground-dwelling species (Green and Alemseged 2012). Evidence thus suggests that *A. afarensis*' behavioral repertoire consisted of a substantial amount of climbing (Green and Alemseged 2012; Stern and Susman 1983). Interestingly, sexual dimorphism in uncovered fossils shows that males were commonly larger and seemingly less well adapted to an arboreal lifestyle and thus likely engaged in terrestrial locomotion more often than females did (Jungers 1982). Ultimately, given that this hominid's anatomy appears well adapted for both arboreal and terrestrial lifestyles, *A. afarensis*' may have had the lifestyle and anatomy of a generalist ape (Stern and Susman 1983).

## Intelligence and Social Structure

Evidence regarding intelligence in early hominids often remains circumstantial and indirect, making it difficult to make any legitimate claims about intelligence in *A. afarensis*. Still, when looking at skull morphology in *A. afarensis*, it is clear that encephalization, being the relative size of the forebrain and therefore an indirect measure of "thinking capacity," was similar to or slightly larger than that of modern great apes (Begun and Kordos 2004). The amount of encephalization in *A. afarensis* relative to that of modern great apes may be indicative of similar levels of intelligence, making tool use not entirely impossible. However, both the absence of adaptations for precision grasping in *A. afarensis*, as well as the absence of stone tools in the fossil record

anywhere before two million years ago make it highly unlikely that this early hominid was an avid tool user (Susman 1994).

As with intelligence, evidence of the social structure of *A. afarensis* can only be inferred from indirect evidence. In this case, sexual dimorphism, or size difference between males and females, has been the dominant lead. Analyzing skeletal size of male and female specimens has suggested that sexual dimorphism in *A. afarensis* was similar to that in modern humans, providing evidence that male–female dynamics in this species were similar to that of *H. sapiens* and thus predominantly monogamous (Larsen 2003; Reno et al. 2003). However, this claim may be debated due to the fact that different methods have shown that sexual dimorphism in *A. afarensis* may have closer resembled that of modern day great apes (Lee 2005), which suggests a social structure that is more reminiscent of chimpanzees, with males competing over females in cooperative communal groups (Larsen 2003).

## Conclusion

The fossilized remains of both Lucy and her conspecifics have provided novel insights into the realms of human evolution and paleoanthropology. Still, notable information, like that regarding Lucy's mode of locomotion and ecology, remain open for debate. Despite the secrets that Lucy has unraveled about early hominins, specifically *A. afarensis*, uncovering further unpreserved traits such as intelligence, social structure, or mating rituals remain to be uncovered, due to the elusive nature of the evidence provided in the fossil record.

## Cross-References

- [Bipedalism](#)
- [Hominid](#)
- [Hominoidea Locomotion](#)
- [Hominoidea Morphology](#)
- [Knuckle-Walking](#)

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## Ludwig Huber

Ludwig Huber

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## Personal History and Overview of Research

Ludwig Huber was born in Neunkirchen, Lower Austria, on 25 July 1964, but raised in Ternitz. He attended Sachsenbrunn, a classical grammar school near Kirchberg/Wechsel for 8 years, where he was educated in traditional humanistic studies, including Latin and ancient Greek. Despite this catholic-humanistic education, Huber nourished interest in biology from an early age. As a child he dreamed of becoming a biologist, mainly due to his fascination with African fauna (actually by watching TV documentaries and reading books about the work of Jane Goodall, Diane Fossey, and Bernhard Grzimek). Shortly before starting his biology studies at the University of Vienna, he participated in a symposium celebrating the 80th birthday of Konrad Lorenz in Laxenburg (south of Vienna). It was here that he got his first hands-on lessons in ethology from well-known scholars of Lorenz, including Bernhard Hassenstein, Sverre Sjölander, Wolfgang Schleidt, Iräneus Eibl-Eibesfeldt, and Antal Festetics. Still, he was most fascinated by Rupert Riedl, a professor of theoretical biology at the University of Vienna, who was not a scholar but a companion of Lorenz in his later years. His speech drew Huber's attention away from classical ethology and toward evolutionary and cognitive biology.

During Huber's biology studies (major, zoology; minor, philosophy and philosophy of science) at the University of Vienna (1983–1988), he broadened and deepened his interests with a focus first on comparative morphology (homology) and later on evolutionary theory (the debates about group selection, exaptation, and constraints). His latent interest in behavioral biology

was nourished by an excursion to the Maldives, where he compared different foraging strategies of coral reef fish. Nevertheless, he was taken by Rupert Riedl's lectures and seminars on evolutionary epistemology, the most interesting of which being dedicated to an interdisciplinary inquiry into the theoretical foundations of biology. This motivated him to study the philosophy of science (Erhard Oeser) as an accessory discipline with a focus on the Viennese strand of evolutionary epistemology following Ernst Mach, Ludwig Boltzmann, and Karl Popper. Still, the major influence on his later career arose from writings of Konrad Lorenz and Rupert Riedl, most notably the books "Behind the Mirror" and "Biology of Knowledge," and two conferences on evolutionary epistemology, organized by Rupert Riedl at the University of Vienna, with Karl Popper and Konrad Lorenz as keynote speakers.

Shortly after these influential events, Huber started his diploma thesis project, which examined the power of associative learning as a means of anticipating events that do not follow alternation sequences. Indeed goldfish (*Carassius auratus*) proved able to adapt to a complex sequence of reinforced and non-reinforced events. This study was part of Rupert Riedl's larger project dedicated to applied questions of evolutionary epistemology, namely, the parallel working of rational and irrational (called "ratiomorphic") processes in human thinking. Inspired by vivid discussions during two visits of Konrad Lorenz in autumn 1988, Riedl and Huber tested several populations of humans, varying in age and education, on how they distinguish between foreseeable and unforeseeable event series. Surprisingly, with the exception of mathematicians, most participants relied on the "negative recency effect," also known as the "gambler's fallacy."

After completing his diploma studies in biology and philosophy in 1988 (academic title Mag. rer. nat.), Huber turned to a completely different topic for his doctoral thesis, namely, pigeons' (*Columba livia*) ability to categorize complex visual classes. In comparison to students, pigeons solved a polymorphous classification problem (the so-called m-out-of-n problem) by learning to combine the four class-defining feature

dimensions of an artificial stimulus set (so-called Brunswick faces) in an additive manner. Humans have difficulties solving such problems as quickly as pigeons because we tend to try combinations of conjunctive and disjunctive rules. Here again evolutionary epistemology offers an answer in terms of the parallel existence of simpler and more advanced, or in evolutionary terms older and more recent, processes of human cognition. Huber's work on categorization (prototype formation, feature learning) and concept formation (including abstraction and rule learning) remained the focus of his research for more than a decade after graduating (Dr. rer. Nat.) in 1991.

Ludwig Huber had the good fortune to be offered the position of university assistant to Prof. Riedl at the Institute of Zoology (Faculty of Natural Sciences) in 1991 and, after his retirement, became head of the Department of Theoretical Biology for almost 8 years (1995–2003). Huber received the postdoctoral lecture qualification (habilitation) for zoology together with the professional upgrade to associate professor in 2000. Thanks to a successful period of raising third-party funding, and by means of international advertisements, Huber was able to hire qualified young postdocs and PhD students. These enthusiastic colleagues arrived with broad interests and helped to widen his research agenda and raising awareness of the steadily growing unit, its scientific output, and its international visibility, especially through an EU-funded international research project that he coordinated. As a result, his lab received the status of priority research program "Cognition" of the Faculty of Life Sciences in 2005.

Huber's purely noninvasive research program at the University of Vienna (1991–2011) involved many aspects of comparative cognition, clustering mainly around perceptual, social, and technical cognition. Rather than using animals as "model systems" to understand humans, he aimed at understanding the cognitive worlds of animals within an evolutionary context (Heyes and Huber 2000). Perhaps the most fundamental component of cognition is *categorization*. Using improved methodologies, Huber and his co-workers demonstrated that pigeons, though

lacking language and presumably also the associated higher cognitive capacities, can categorize photographs or drawings as complex as those encountered in ordinary human experience (Huber et al. 2005). The underlying cognitive mechanisms include picture memorization, feature learning, prototype formation, and the abstraction of concepts. These topics had already been addressed in Huber's doctoral thesis, but he later added studies on the perception of biological motion (with Niko Troje, Kingston, Canada) to serve social recognition, picture-object equivalence, inference by exclusion, and the functional asymmetry of the pigeon brain (with Onur Güntürkün, Bochum, Germany). In addition to pigeons, the researchers investigated the link between perception and cognition in kea (*Nestor notabilis*), domestic dogs (*Canis familiaris*), red-footed tortoises (*Geochelone carbonaria*), lizards (bearded dragon; *Pogona vitticeps*), archer fish (*Toxotes chatareus*), and giant pandas (*Ailuropoda melanoleuca*).

A second research focus clustered around social learning. This ability is considered an important manifestation of cognitive behavior in both humans and nonhuman species. Huber's main interest focused on the mechanisms underlying learning through conspecific observation and their contribution to the horizontal and vertical transmission of innovations. Rigorous experiments were conducted with marmosets (*Callithrix jacchus*) to investigate *imitation*, i.e., learning some part of the form of a demonstrated behavior (Voelkl and Huber 2000). Imitation, it is said, not only demands the most sophisticated cognitive processes but also enables the most elaborate form of social information transfer, "cultural transmission." The formation of behavioral traditions and possible effects of conformity and habit formation were studied in wild marmosets (with Nicola Schiel and Antonio Souto, Recife, Brasil). Other forms of nongenetic transmission, like *emulation* (i.e., learning about the properties or the function of objects), were studied in kea (with Michael Taborsky, Bern, Switzerland) (Huber et al. 2001). The functional role of observational learning and the learning of sequences was investigated in marmosets as well as dogs (Huber et al. 2009). In addition to evidence for automatic

imitation (with Cecilia Heyes, London, UK) and *deferred* imitation (with Adam Miklosi, Budapest, Hungary), Huber and his team found evidence for *selective imitation* in dogs (with Gyorgy Gergely, Budapest, Hungary) (Range et al. 2007). Cooperation and some underlying social factors (like scrounging tolerance, inequity aversion) were studied in dogs, kea, and marmosets (Range et al. 2009). Concerning the evolution of social learning, they also found surprising evidence for social learning in nonsocial tortoises and lizards (Wilkinson et al. 2010).

The third research focus was directed at physical intelligence. In the inanimate environment, problems arise from the interaction with objects, the understanding of physics (*folk physics*), time, space, and causality. Using the kea as a model, the team investigated how birds manipulate objects in a flexible manner by learning how the objects affect the environment (Huber and Gajdon 2006). Comparisons with marmosets, but also ravens (*Corvus corax*) (with Thomas Bugnyar, Vienna), New Caledonian crows (*Corvus moneduloides*) (with Auguste von Bayern, Oxford, UK), and Goffin's cockatoos (*Cacatua goffiniana*) (with Alice Auersperg, Goldegg, Austria) provided important insights into the selective pressures for the evolution of technical intelligence. Both kea and Goffin's cockatoos showed flexible and innovative behavior, with the individual invention of using a stick tool to act in a goal-directed manner on objects. In collaboration with Elisabetta Visalberghi (Rome), Huber and his colleagues investigated causal understanding in capuchin monkeys (*Cebus apella*) using stones as percussors for nut-cracking behavior.

This extensive research agenda could not have been realized without the establishment of excellent facilities in cooperation with highly motivated collaborators. Firstly, Ulrike Aust and Michael Steurer helped establish a huge pigeon testing facility equipped with half- and fully automatized indoor conditioning units connected to outdoor aviaries for 120 pigeons. Ludwig Huber, along with Thomas Bugnyar and Bernhard Voelkl, established a marmoset lab with indoor/outdoor enclosures for two to three families of up to eight individuals each. Huber and Gyula



Gajdon improved the outdoor facilities for kea (the mountain parrots of New Zealand) at the Konrad Lorenz Institute for Ethology. In 2007 Huber founded, with colleagues Friederike Range and Zsófia Virányi and the generous help of a private sponsor, the first Clever Dog Lab in Vienna. And finally, Anna Wilkinson's vision and enthusiasm made possible the creation of the "Cold Blooded Cognition" Lab in 2008, including indoor facilities for tortoises, lizards, and tadpoles.

In parallel to his research, Huber's teaching interests were also broadened, with lectures and courses ranging from animal behavior and cognition to comparative morphology, evolutionary biology, and even bioethics. He gave comparative cognition lectures not only at the University of Vienna but also as a guest professor at the Charles University in Prague (2005–2011) and at the University of Salvador de Bahia, Brazil (2012). Of course, supervision comprised the majority of his teaching work, helping students on their way to becoming young scientists in more than 80 diploma or master projects and 30 doctoral or PhD projects.

In 2009, he helped recruiting two professors of cognitive biology (Tecumseh Fitch and Thomas Bugnyar) and with them established a new organizational unit, the Department of Cognitive Biology at the Faculty of Life Sciences. As its head from January 2010 to September 2011, Huber was responsible for founding a new research facility 40 km south of Vienna (the Haidlhof Research Station for Cognition and Communication Research) in cooperation with the University for Veterinary Medicine Vienna. In huge aviaries, altogether comprising 1300 m<sup>2</sup>, Thomas Bugnyar's and Huber's groups began comparative investigation of the social and technical abilities of corvids and kea (with Gyula Gajdon and Raoul Schwing). Furthermore, Tecumseh Fitch established research on the vocal production and perception of birds and mammals in specially equipped bioacoustics facilities.

In September 2011, Ludwig Huber was appointed professor of the Natural Science Foundations of Animal Ethics and Human-Animal Interactions at the new Messerli Research

Institute, an interdisciplinary institution of the University of Veterinary Medicine Vienna, the Medical University of Vienna, and the University of Vienna. He was the head of comparative cognition and acted as the institute's spokesperson from its founding until 2014. This appointment allowed him to extend his previous work to the study of emotional processes like empathy, as well as to applied research, in particular on human-animal interactions and ethical issues (e.g., Müller et al. 2015). The range of study species extended to include some exotic species, which Huber and his team investigated in the lab and the field (Goffin's cockatoos with Alice Auersperg in Indonesia and poison frogs with Eva Ringler in French Guiana) and finally also farm animals (pigs, horses, chicken), which they started to investigate in semi-natural conditions (with Marianne Wondrak). Finally, Huber's theoretical interests opened the question of how our understanding of cognitive and emotional processes in animals contributes to our concern and responsibility for them. He became convinced that the better people understand how animals think, decide, suffer, cooperate, reconcile, have empathy and theory of mind, etc., the more they will be inclined to respect and take care of them, i.e., take responsibility in the various forms of human-animal interactions and include them in our moral universe.

## Cross-References

- ▶ [Behavioral Flexibility](#)
- ▶ [Canine Cognition](#)
- ▶ [Comparative Cognition](#)
- ▶ [Cooperation](#)
- ▶ [Discrimination Learning](#)
- ▶ [Domestication](#)
- ▶ [Emotional Contagion](#)
- ▶ [Empathy](#)
- ▶ [Emulation](#)
- ▶ [Guesser-Knower Paradigm](#)
- ▶ [Imitation](#)
- ▶ [Inequity Aversion](#)
- ▶ [Human-Animal Interaction](#)
- ▶ [Konrad Lorenz](#)
- ▶ [Means-End Reasoning](#)
- ▶ [Operant Chamber](#)

- Pigeon (*Columbidae*)
- Primate Cognition
- Problem-Solving
- Reasoning by Exclusion
- Social Intelligence Hypothesis
- Social Learning
- String Pulling
- Swine Cognition
- Technical Intelligence Hypothesis
- Tool Use
- Touch Screen

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## Lunate Sulcus

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## Introduction

Sulci are defined as deep portions on the surface of the cerebral hemisphere. The cerebral cortex is divided into the five lobes with the help of the major sulci present on the surface. The central sulci divide the cortex into frontal and parietal lobe, the lateral sulcus or fissure divides the superolateral surface into upper parietal and lower temporal lobe. The imaginary line joining the parieto-occipital sulcus and pre-occipital notch, situated 5 cm anterior to the occipital pole mark the occipital or the posterior region. The major concern of the occipital lobe is the visual information receiving and processing.

Lunate sulcus also called as “ape sulcus” was first identified by the anatomist Grafton Elliot Smith on the posterolateral part of the brain. It was identified to be a feature of the ape brain but not exclusively persistent with them instead can be markedly present in human brains also. In its typical forms, lunate sulcus is situated just in front of the occipital pole which may or may not be joined by the calcarine sulcus and oriented vertically (Allen et al. 2006). However, the frequency of description differs between right (26.4%) and left side (32.7%) (Allen et al. 2006).

The location of lunate sulcus as compared to the apes is located more posteriorly. According to Smith Elliot, this lunate sulcus forms important landmark to identify the band of Gennari. According to his observation, the sulcus is not a permanent and symmetrical feature of the ape as well as the human brain.

## History and Evolution

Lunate sulcus has been linked as an important milestone with the discovery of Taung baby, *Australopithecus africanus*, in the evolution by the Raymond Dart, the former student of Elliot Smith. In his evaluation, he identified that the location of lunate sulcus is more posteriorly placed in humans than apes, suggesting the increased surface area for the parietal, temporal, and occipital lobe. Thus the position of the lunate sulcus forced data to conclude that Taung baby was not simply an extinct ape but the evolutionary modified early hominid.

Some evidence to confirm its evolutionary profile was given by Falk et al. in 2005. He also identified the location of the lunate sulcus more posteriorly placed in the homo floresiensis specimen and also argued that despite such a small brain volume; there were high cognitive processing abilities.

In order to assess the actual evolutionary profile of the lunate sulcus, the same sulcus was studied the contemporary species, i.e., chimpanzee. In them, the sulcus is a prominent feature with a particular location and present as a deep sulcus and thus marking the position for the anterior extension of the occipital lobe. However, after recent finding in the two chimpanzees, the lunate sulcus is more posteriorly placed as compared to the fellow chimps, correlating the human-chimpanzee common ancestral evolutionary origin with more cognitive capabilities. Thus, it is evident that posteriorly positioned lunate sulci in the fossil hominis is an indicator for reduction in the volume of primary visual cortex and this is due to the evolutionary up gradation of the visual association areas. Presumably, this would have resulted from the functional reconfiguration since the period of *Australopithecus africanus* (Holloway et al. 2001). Larger brains having significant number of visual association areas process the primary information obtained by visual cortex and delegate them to visual association areas for further processing.

Holloway RL performed a profound research regarding the lunate sulcus and found that it was much better defined in the anthropoid humans other

than humans and in those species, it demarcates the anterior boundary of primary visual cortex (Holloway 1975). When compared to anthropoid brains, human lunate sulci are fragmented in nature with a significant posterior displacement (Holloway et al. 2001, 2003). Studies have shown that the human brains which lacked prominent lunate sulcus had reduced volume of primary visual cortex (Ono et al. 1990).

## Shapes of the Lunate Sulcus

The variability in the occipital sulcus is more and extensive. It may appear as a continuous structure or fragmented or segmented in some of the specimens. The combination of these fragmented segments was referred to as composite lunate sulcus. According to Allen et al., lunate sulcus were classified as complete, composite, or no lunate sulcus. The composite sulcus is much more common than the individual complete sulcus. Connolly's also grouped the lunate sulcus into various groups depending upon the segmentation or continuous nature. In general, Elliot's Smith observed that there was a rare similarity in the two cerebral hemispheres of the same individual. In some of the research articles showed the presence of lunate sulcus is more in the left side as compared to the right side of the cerebral hemisphere. In addition, lateral occipital sulcus, otherwise known as pre-lunate sulcus is crucial for defining the overall morphology of the lateral surface of occipital lobe and divides the lobe into superior and inferior portions (Smith 1904).

Malikovic and colleagues (2012) found that out of 30 hemispheres, lunate sulcus can be observed as a variable but continuous impression near the occipital pole and mostly there were either seen as continuation of inferior lateral occipital sulcus (6/10 hemispheres) or superior lateral occipital sulcus (4/10 hemispheres). They concluded that lunate sulcus is not homologous among humans and primates.

In some of the great apes, the lunate sulcus is so deep that it will form an occipital operculum, but in

humans, the finding is not evident. Initially it was thought that lunate sulcus is related to the visual cortex, but later extensive studies were done to map the visual areas in the cerebral cortex. However, it needs to be remembered that in contrast to the higher degree of gyrification in rest of the human cortex, occipital lobe of apes have similar degree of gyrification as humans (Armstrong et al. 1991).

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## Lung

- [Respiratory System](#)

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## Luteotropic Hormone

- [Prolactin](#)

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## Luteotropin

- [Prolactin](#)

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## Lying

- [Turing Test](#)

# M

## Machiavellian Intelligence

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### Synonyms

[Social intelligence](#)

### Definition

The hypothesis that an important contribution to the evolution of intelligent behavior was the adaptive challenge of dealing with the complexities of living in a social group: striking a balance between cooperation and competition with a range of other individuals, often requiring subtle social skills rather than brute power.

### Introduction

Before the 1980s, it was generally accepted that intelligence, in the sense of that package of useful skills that impress people as being in some way “smart,” evolved to deal with the physical challenges of the environment: finding and getting access to food, remembering safe places, noticing

signs of danger, etc. (For human evolution, a special form of this hypothesis was labeled “Man the tool maker.”) Complex societies were considered a by-product of intelligence.

Radically different views were occasionally expressed, pointing instead to the problems set by social living. Chance and Mead (1953), impressed with the social maneuvering of male baboons, suggested that social challenges might select for greater intelligence in general. Alison Jolly (1966), pioneering the study of highly social lemur species whose members seemed technically inept, suggested reversing the common view of primate society as a product of intelligence, postulating instead that general intelligence might result from the complexity of social living. Nicholas Humphrey (1976), a psychologist highly experienced with the skill of captive monkeys in dealing with experimenters’ gadgetry, could see nothing remotely as challenging in their natural environment and made a strong case that they met greater problems simply by living socially; he therefore proposed that intelligence might result, as an adaptation to group living, itself driven by other factors such as reduction of predation risk. Noting that these radical proposals had emerged at roughly decade intervals, Byrne and Whiten (1988) argued that this was an idea whose time had now come and put together a book which reprinted those seminal theory papers plus a range of current studies that gave support to the hypothesis, which they labeled “Machiavellian intelligence” and used as the book’s title.



The apposite nature of Niccolo Machiavelli's maxims to describe the social maneuverings of nonhuman primates was first pointed out by Frans de Waal, who chose Machiavelli quotations to explain the logic of chimpanzees' "political" decisions about social alliances (de Waal 1982). In giving advice to an aspiring prince, Machiavelli (1532/1979) had stressed the importance of being friendly, cooperative, kind, and generous – just until it paid not to be so. Similarly, the Machiavellian intelligence (MI) hypothesis applies just as much to the social sophistication shown in friendship formation, reconciliation, coalitions and alliances, kin support, and reciprocal altruism, as it does to deception and overtly political manipulation. Old World monkeys, for instance, use grooming to build up relationships with unrelated individuals who later come to their aid in conflicts (Dunbar 1991); if important monkey friendships are disrupted by a fight, one of the combatants will soon make friendly overtures which usually result in repairing the relationship (Cords 1992); if a monkey's relative or ally is attacked by a high ranker, then they may still respond – by attacking a (lower-ranking) relative of the attacker, in a sort of monkey vendetta (Seyfarth and Cheney 1984). Individuals sometimes use deception tactically, such as when a young monkey, frustrated by seeing a larger individual monopolizing a good food source, gives a scream that causes his higher-ranking mother to rush to his aid and displace the other monkey: "coincidentally" leaving the food source for the youngster to monopolize (Byrne and Whiten 1985; Whiten and Byrne 1988). All this implies a great deal of social knowledge, about who's a friend or relative of whom, and this knowledge is often acquired indirectly, by "eavesdropping" on conflicts among third parties, as primatologists have shown by simulating conflicts with artfully constructed sequences of monkey calls (Kitchen et al. 2005). The ultimate benefits are selfish; the proximate means may be altruistic, or not. MI should therefore not be conflated – though it sometimes has been – with the human personality trait of "Machiavellianism" (Christie and Geis 1970), which refers specifically to an ability

to detach from conventional morality and emotionality in order better to deceive and manipulate other people. MI is not about morality and not restricted to "nasty" actions. Using the synonym "social intelligence" does avoid such confusion, but brings in turn the risk of missing the importance of selfish benefit to the agent or its kin in MI – unlike the case of so-called "pro-social" actions – which would be equally misleading.

## Testing the MI Hypothesis

There is no doubt that MI gave impetus over the last 30 years to the great burgeoning of studies on animal social complexity and maneuvering, and it became accepted as a central explanation for the evolutionary origins of intelligence. Clear evidence in support of that position has been more elusive. Part of the difficulty with testing the MI hypothesis relates to ambiguities of its scope (Byrne 1996a; Whiten 1997). Is MI required to be the primary driver of cognitive advance and therefore refuted by any clear cases where it is not? If, instead, MI is just one of many factors that may select for intelligence, interpreting findings is more problematic. Is MI supposed to select for a specific "module" of advanced social intelligence, contrasting with primitive abilities in other domains? If, instead, the result is going to be general intellectual advance, then tying it back to a social origin is much more difficult: how can we be sure which arena was the evolutionary driver of intelligence manifest in many correlated ways? Separating "arenas of expertise" is itself tricky: if acquiring a valuable feeding skill is aided by observational learning from a companion, is that a social or a physical aptitude? At its most general, MI must surely predict that any highly social species should be more intelligent than an asocial one, other things being equal: but when are they equal? If the relatively solitary orangutan consistently outperforms the obligate social baboon, does that refute the MI hypothesis because both are primates – or not, because one is an ape and the other a monkey? To cap these difficulties, the long history of trying to measure differences of

intelligence among animal species gives little confidence that even clear formulations can be tested against reliable data (Macphail 1985).

Researchers instead turned to brain measurements, as a proxy measure of intelligence; but this approach also has its problems. While few would doubt that brain size has some relation to cognitive abilities, pinning down any such relationship so that it can be used as a measure is not straightforward. Like many biological parameters, brain size increases with body size; the relationship is generally curvilinear in group of related species, so plotting on logarithmic coordinates has been used to produce a straight line (allometric scaling). Larger or smaller brain sizes than expected are deduced from (1) the intercept with the Y-axis (height of line), compared with that of other taxonomic groups plotted, and (2) by deviations from the averaged line of a single taxonomic group under examination. As if this were a sort of IQ test, the ratio of observed to expected brain size – the “encephalization quotient” EQ – has sometimes been treated as species intelligence, on the assumption that the brain is in some way an “on-board computer” and bigger is better. Using EQ, it appears that it is diet complexity – among primates, frugivory rather than folivory – that correlates with brain enlargement, rather than any measure of social complexity (Clutton-Brock and Harvey 1980; DeCasien et al. 2017).

However, experience with man-made systems suggests that the upper limit of computing power is given by the *absolute* number of components, whereas the EQ measures brain size *relative* to body size (Byrne 1996b). In consequence, two species with identical EQs but different body sizes can vary massively in the number of extra neurons they possess, above or below that predicted from their body size. Rather than giving a direct indication of intelligence, EQ seems instead to measure cost. The brain is a metabolically expensive organ and requires energy remorselessly at normal temperatures, so the larger the brain the higher the risk to an animal. Larger-bodied species can “afford” larger brains, since their basal metabolic rate will in general be higher, but any species with a brain larger than expected from its body (i.e., high EQ) must have been

under selection for brain size increase; those species with low EQ have been able to manage with smaller brains and thus reduce their costs. Powerful selection for larger or smaller brains certainly gives a clue about the need for cognition, but potential intellectual power is better measured by absolute number of computing components.

Numerous studies in a range of mammalian taxa have found positive correlations between absolute brain size (or absolute size of the neocortex or the ratio of neocortex size to the rest of the brain) and measures of social complexity, which are taken to support the MI hypothesis (Barton and Dunbar 1997). For species that live long-term in stable social groups, the average size of semi-permanent social groups is typically used as a rough-and-ready index of the social complexity confronting any individual. Much of the early work was carried out on primates, whose groupings are typically long lasting and in which researchers have shown that relationships are differentiated: an individual knows others as individuals and behaves quite differently toward them according to their kin relationships, friendships, and history of past interactions with them. These characteristics are critical for the Machiavellian intelligence hypothesis, because it is only when relationships are differentiated among individuals that there is any real possibility of social complexity. Many groupings of mammals and birds are temporary aggregations, such as a winter flock of sparrows and finches foraging near a grain store or a herd of deer feeding on a flush of young grass. Their typical group size is not predicted by MI to relate to any measures of brain size, and indeed they do not (Dunbar and Shultz 2007; Emery and Clayton 2005). But for primates, and for several other mammalian families which live in semipermanent groups, such as cetaceans and chiropteran bats, correlations with brain measures have regularly been found.

Unfortunately, absolute brain size is itself flawed as a proxy measure of intelligence. Many brain functions do not contribute to the package of abilities we recognize as intelligence, but rather regulate the somatic and sensory functioning of the body; those functions are presumably responsible for the strong relationship between brain size

and body size, so often noted. Harry Jerison (1963, 1973), the pioneer of the allometric approach to intelligence, was well aware of the problem. He tried to devise a measure of “spare neurons” – the computing capacity, measured in neural components, beyond that which an animal needs minimally for regulatory functions and therefore available for cognitive computations. So far, no generally accepted measure of spare neural capacity has been found. The size of individual neurons and their packing density vary across species and larger taxonomic groups, and these variations can be compensated for: but the fundamental problem remains that neither the brain nor any specific brain part is a dedicated “thinking machine,” and we have no principled way of taking account of all the other demands on neural capacity in addition to any cognitive computing. Until one is found, claims that the MI hypothesis has been proven or refuted must be taken with a large pinch of salt.

### What Is Social Complexity?

At the heart of the MI hypothesis lies the idea of social complexity and the belief that we can compare it with other kinds of complexity confronting individual animals (Byrne et al. 2001; Cochet and Byrne 2014; Sambrook and Whiten 1997). Traits accepted as indicating social complexity among primates, and increasingly discovered in other taxonomic groups, include acquisition of rank by kin support; the use of grooming to cultivate “friendships” with potentially useful individuals, friendships that persist over long time scales and predict the distribution of mutual help; as a consequence, the important role of third parties in deciding the outcome of conflicts; informed choice of potential allies on the basis of individual characteristics; and the repair of these relationships by targeted reconciliation after conflict. These traits are generally species-typical, so likely to be strongly channeled genetically. To benefit from such “hard-wired” traits, individuals must possess certain fundamental cognitive capacities: (1) distinguish conspecific group members as individuals and respond differently to kin,

(2) remember relative ranks and past affiliations, and (3) remember the personal histories of help given and received from various others (Byrne 2016). Manipulation by tactical deception is reported only among certain individuals and varies in precise form even within a species. Nevertheless, most records of deception can be explained as learning from natural coincidences, provided individuals first possess a rich database of social knowledge and can learn new tactics over only a very few trials (Byrne 1997b). Success essentially demands good visual perception and discrimination, attention to social attributes, and a good memory. Confronting situations of increased social complexity is therefore likely to select for enhanced social discrimination and memory efficiency, including rapid learning of socially relevant information.

The word “understanding” is conspicuously absent in this account. Of course, an individual able in some way to represent and compute with what is going on in the mind of a competitor or an ally would be viewing a more complex situation. Evidence that such mentalizing or “theory of mind” understanding is found in animals has been controversial, but is now becoming accepted for a few animal species, including all great apes and some corvid and psittacine birds, and possibly also toothed whales and elephants (Byrne 2016). It does not appear possible to explain such a distribution by invoking the MI hypothesis (Byrne 1997a). Using the rough-and-ready metric of the average size of semipermanent groups, great apes cannot be confronting greater social challenge than many monkey species, several of whom live in larger groups than any ape. Similarly, corvids and parrots do not live in particularly large groups: monogamous pairs are typically the largest long-term associations among birds, and those few species living in larger groups, often cooperative breeders, seem in any case to have smaller brains (Fedorova et al. 2017).

### Conclusion

The Machiavellian intelligence hypothesis that social complexity is a powerful driver of selection

for cognitive power in animals is consistent with the social sophistication and manipulative tactics that have been increasingly documented among animals in the last 50 years. Direct testing of the hypothesis will require good measures of intelligence that can be applied across species and clearer statements of what exactly MI and competitor hypotheses predict, both of which have been lacking. Most social complexity among animals can be underpinned simply by good skills of memory and perception, allowing rapid learning of nuanced distinctions among social companions. While a good case can be made that this quantitative variation matches the challenge of living long-term in larger social groups, that is not the case for mentalizing about others (theory of mind), whose distribution does not particularly correlate with living in large groups.

## Cross-References

- Allometry
- Cooperation
- Deception
- Encephalization
- Intelligence
- Technical Intelligence Hypothesis
- Theory of Mind

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## Machine Learning

- [Bioinformatics](#)

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## Machine Thinking

- [Turing Test](#)

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## Magnetic

- [Electromagnetic Fields](#)

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## Magnetoreception

- [Accipitriformes Sensory Systems](#)
- [Cetacean Sensory Systems](#)
- [Falconiformes Sensory Systems](#)

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## Major Histocompatibility Complex

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### Synonyms

[Human leukocyte antigen \(in humans\) and H-2 \(in mice\)](#)

### Definition

A tightly linked cluster of genes present in every mammalian species called as major histocompatibility complex (MHC).

The functions of the products of this complex are intercellular recognition and discrimination between self and non-self. MHC genes are of fundamental significance in both types of immune responses (i.e., humoral and cell-mediated) to foreign proteins. Recognition of antigens by T cells happens only when it is combined with an MHC molecule whereas antibodies react with antigens alone. The repertoire of antigens recognized by T helper ( $T_H$ ) and T cytotoxic ( $T_C$ ) cells is influenced by expression of particular set of MHC molecules in an individual.

### Mouse and Human MHC Loci

The MHC is a collection of genes located on the short arm of chromosome 6 in humans and on chromosome 17 in mouse. The MHC is referred to as the HLA (human leukocyte antigen) complex in humans and as the H-2 (histocompatibility-2) complex in mice (MHC sequencing consortium 1999). The organization of MHC genes into regions encoding three classes of molecules in the mouse and human is shown in simplified form in Fig. 1.

The products of different classes of MHC genes are as follows:



| Complex   | H-2 (in mice)       |                     |                     |                     |       |       |       |
|-----------|---------------------|---------------------|---------------------|---------------------|-------|-------|-------|
| MHC Class | I                   | II                  |                     | III                 | I     |       |       |
| Region    | K                   | IA                  | IE                  | S                   | D     |       |       |
| Products  | H-2K                | IA $\alpha\beta$    | IE $\alpha\beta$    | TNF- $\alpha/\beta$ | H-2L  | H-2D  |       |
| Complex   | HLA (in humans)     |                     |                     |                     |       |       |       |
| MHC Class | II                  |                     |                     | III                 | I     |       |       |
| Region    | DP                  | DQ                  | DR                  | C4,C2,BF            | B     | C     | A     |
| Products  | DP<br>$\alpha\beta$ | DQ<br>$\alpha\beta$ | DR<br>$\alpha\beta$ | TNF- $\alpha/\beta$ | HLA-B | HLA-C | HLA-A |

**Major Histocompatibility Complex, Fig. 1** Simplified organisation of MHC genes in mice and humans

Class I MHC genes encode glycoproteins which are expressed on the surface of nearly all nucleated cell. These molecules are encoded by the K and D regions in mice and A, B, and C loci in humans and referred to as classical class I molecules. Other genes which also encode class I molecules within the H-2 or HLA complexes are referred to as nonclassical I genes. Class I MHC molecules play a role in presentation of peptide antigens to T<sub>C</sub> cells.

Class II MHC genes encode glycoproteins which are expressed on antigen-presenting cells (macrophages, dendritic cells and B-cells). These molecules are encoded by the IA and IE regions in mice and DP, DQ, and DR regions in humans. Class II MHC molecules play a role in presentation of peptide antigens to T<sub>H</sub> cells.

Class III genes encode molecules that function in immune responses which includes complement components and inflammatory cytokines (TNF) and cytokines.

### Inheritance of Alleles of MHC Genes in Linked Groups

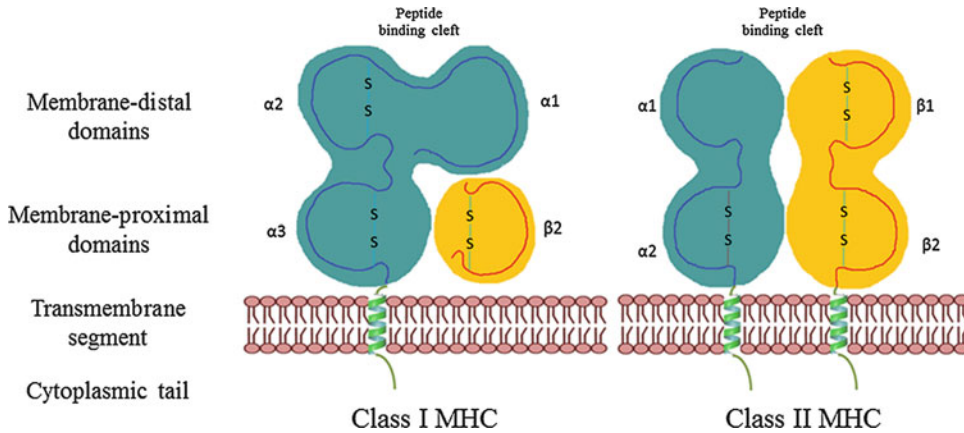
MHC locus is highly polymorphic which means there are many forms of the genes or alleles existing at each locus among a pool of population. The recombination frequency within the complex is  $\leq 0.5\%$  indicating the linkage of genes of MHC locus. Inheritance of set of these genes occurs in

linked groups referred to as haplotype (a single set). A person inherits one haplotype from the father and other one from the mother. MHC locus is generally heterozygous in outbred population and codominant, i.e., both maternal and paternal alleles are expressed in an individual. If mice are inbred (having identical alleles at all loci), H-2 locus will be homozygous and both maternal and paternal haplotypes are identical.

## MHC Molecules

### Class I MHC

The structure of both class I and II molecules have been determined by x-ray crystallography. Class I MHC molecule is composed of a 45 kilodalton (kDa)  $\alpha$  chain and a 12 kDa  $\beta$ 2-microglobulin molecule. The  $\alpha$  chain is a transmembrane glycoprotein encoded by genes in the A, B, and C regions of the human HLA complex and K and D/L regions of the mouse H-2 complex.  $\beta$ 2-microglobulin is a protein encoded by gene present on a different chromosome. For expression of class I MHC molecules on cell membranes, association of the  $\alpha$  chain with  $\beta$ 2-microglobulin is required. The  $\alpha$  chain is organized into three external domains ( $\alpha$ 1,  $\alpha$ 2 and  $\alpha$ 3), a hydrophobic transmembrane domain and a hydrophilic cytoplasmic anchor segment. The  $\beta$ 2-microglobulin shows similarity in organization to the  $\alpha$ 3 domain, lacks a transmembrane



**Major Histocompatibility Complex, Fig. 2** The pictorial representation of MHC molecules

region, and binds to the class I glycoprotein noncovalently (Fig. 2). The peptide binding cleft is formed by the interaction of  $\alpha 1$  and  $\alpha 2$  domains and located on the top surface of the class I MHC molecule and it is large enough to bind a peptide of 8–10 amino acids as this is blocked at both ends (Natarajan et al. 1999).

### Class II MHC

Class II MHC molecule consists of two different polypeptide chains, a 33 kDa  $\alpha$  chain and a 28 kDa  $\beta$  chain. Both  $\alpha$  and  $\beta$  chains have two external domains ( $\alpha 1$ ,  $\alpha 2$  in one chain and  $\beta 1$ ,  $\beta 2$  domains in the other), a transmembrane segment, and a cytosolic anchor segment (Fig. 2). The  $\alpha 1$  and  $\beta 1$  domains interact to form antigen binding cleft. This cleft present as an open-ended groove and binds to a peptide of 13–16 amino acids (Owen et al. 2013).

### MHC-Peptide Interaction

Allelic forms of class I and II MHC genes are polymorphic and in humans several hundred different allelic variants have been identified. But only 6 different class I molecules and up to 12 different class II molecules are expressed, despite of this number MHC molecules are able to present a wide variety of different antigenic peptides to T cells. The binding between a peptide and an

MHC molecule is referred to as promiscuous because a given MHC molecule can bind numerous different peptides and some peptides can bind to several different MHC molecules.

Class I MHC molecules present peptides to CD8<sup>+</sup> T cells. These peptides are derived from endogenous intracellular proteins that are digested in the cytosol, and then transported from the cytosol into the cisternae of the endoplasmic reticulum, where they interact with class I MHC molecules. This process is known as the cytosolic or endogenous processing pathway (Abbas et al. 2014).

Each allelic variant of a class I MHC molecule binds a distinct set of peptides and about  $10^5$  copies of each class I MHC molecules are expressed on the surface of a single nucleated cell enabling it to present different peptides simultaneously. The peptides which bind to these MHC molecules have two features:

- Peptide length is 8–10 amino acids.
- They contain specific amino acid residues which anchor the peptide into groove and called as anchor residues.

Class II MHC molecules presents peptides to CD4<sup>+</sup> T cells. It also binds to a variety of peptides which are derived from exogenous proteins (either self or nonself), internalized by phagocytosis or by receptor-mediated endocytosis, and

processed by the endocytic processing pathway. Peptides binding to class II MHC molecules are generally 13–18 amino acids and contains internal conserved motif unlike anchor residues in class I MHC molecules (Hennecke et al. 2000). This internal sequence comprises of 7–10 amino acids that provide the major contact points. This sequence has aromatic or hydrophobic residues at the amino terminus and three additional hydrophobic residues in the middle portion and carboxy-terminal end of the peptide (Owen et al. 2013).

## Conclusion

A wide range of different MHC molecules are expressed in an individual and within a species. The source of diversity in antibodies and T-cell receptors is somatic process including gene rearrangement and somatic mutations whereas MHC molecules diversity originates from polymorphism. Sequence variation among alleles of the MHC within a species is very high but not randomly distributed along the entire polypeptide chain, rather clustered in short stretches, mainly within the membrane distal  $\alpha 1$  and  $\alpha 2$  domains of class I molecules. Interestingly,  $\alpha 1$  and  $\beta 2$  domains of class II molecules also show similar patterns of diversity. Some alleles occur at a much higher frequency in those suffering from certain diseases than in the general population. The diseases associated with particular MHC alleles include autoimmune disorder, some viral diseases, several allergies, disorders of complement, and neurological system. A relative risk is a value which is calculated by determining the frequency of the HLA alleles expressed by the patient and then comparison of this data with the frequency of the same alleles in the normal population. This value basically tells the association between HLA alleles and a given disease.

## Cross-References

- [Mutations](#)
- [Population](#)

- [Protein](#)
- [Recombination](#)

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## Make-up

- [Karyotype](#)

## Maladaptive Behavior

- [Sign Tracking](#)

## Male Androphilia

- [Fraternal Birth Order Effect](#)

## Male Gametogenesis

- [Spermatogenesis](#)

## Male Hormone

- [Androgens](#)

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## Male Sexual Orientation

- ▶ [Fraternal Birth Order Effect](#)

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## Male Sexual Refractory Period

- ▶ [Coolidge Effect, The](#)

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## Male-Male Competition/Combat

- ▶ [Intra-sexual Selection](#)

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## Mammal

- ▶ [Haplorhini](#)
- ▶ [Primate Sensory Systems](#)

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## Mammotropin

- ▶ [Prolactin](#)

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## *Mammuthus primigenius*

- ▶ [Woolly Mammoth](#)

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## Manager

- ▶ [Signaller](#)

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## Manatee

- ▶ [Sirenia Navigation](#)
- ▶ [Sirenia Sensory Systems](#)

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## Manatee Diet

- ▶ [Sirenia Diet](#)

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## Manatee Movement

- ▶ [Sirenia Locomotion](#)

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## Manipulator

- ▶ [Signaller](#)

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## Map Unit

- ▶ [CentiMorgan \(cM\)](#)

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## Margaret Floy Washburn

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Margaret Floy Washburn (July 25th, 1871 – Oct. 29th, 1939) played a major role in the advancement of Comparative Psychology, in regard to humans and non-humans. In addition, she assisted in the revolution of women in the field of psychology. She was the second woman to serve as the American Psychological Association (APA) president in 1922 and also was the second woman to be named as a Fellow of the National Academy of Sciences in 1931 (Woodworth [1949](#)).

She first began her undergraduate degree at the age of 16 at Vassar College (1891). When she completed her degree she was interested in attending Columbia University under the guidance of James McKeen Cattell. During this time women

were not able to apply for the graduate program. She spent one year as a student auditor learning under the direction of Cattell. He suggested that she apply to Cornell University. Cornell accepted her in 1892 and she worked under the direction of Edward B. Titchener not only as his first female student but also his first graduate student in his lab. Within her first year in the program she was able to use the research she had collected with Cattell to get a Master's degree from Vassar College. She was the first woman to be awarded her PhD, studying cutaneous perceptions from the perspective of distance and direction, a few years later from Cornell in 1894. After graduating she worked as the Chair of Psychology, Philosophy and Ethics at Wells College from 1894 to 1900. She then spent two years back at Cornell as a lecturer of Psychology in addition to being a warden at Sage College for women. In 1902 she spent one year at University of Cincinnati before she became a professor at Vassar College and stayed there for 36 years (Woodworth 1949). Her areas of interest were not only in psychology but a variety of other disciplines such as philosophy, chemistry, biology, and art.

One of Washburn's major contributions included consciousness in humans and non-humans (*The Animal Mind*, 1908). Throughout this book she summarized experimental studies on a variety of topics such as sensory perception, consciousness, and attention. This contribution was successfully used by other professors for many years later. The book was updated and published in later editions (in 1917, 1926, and 1936) as new research was explored in the field. Another contribution was related to motor development as it pertained to the Motor Theory. In the book, *Movement and Mental Imagery* (1916), the question was asked about how consciousness plays a role in motor movement. More specifically, how is this related to the perception of movement from a distance and modification of the responses to that perception? Within the topic she explored the importance of motor movements in the context of learning and attention. From a retrospective view she contributed to knowledge on spatial perception, binocular rivalry, afterimages, memory of hand movement

and emotions, individual differences, color vision motivation, and orientation across a variety of species (Woodworth 1949). Her contributions to experimental research, editorial and reviewer roles, and leadership have displayed her insight and determination.

## Cross-References

- [Comparative Psychology](#)
- [Edward B. Titchener](#)

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## Margaret Ruth Kuenne Harlow

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Margaret Ruth (nee Kuenne) Harlow (August 8, 1918 – August 11, 1971) was a child psychologist and primatologist best known for her decades of research collaboration with husband Harry F. Harlow. She also contributed extensively to the field through editorial work and helped to establish the American Psychological Association Publication Office, serving as its first director. Her expertise in child development was critical in the Harlows' well-known studies on the effects of maternal separation, social deprivation, and contact comfort on infant monkeys' social, cognitive, and behavioral competencies. Margaret Harlow's research not only illuminated the importance of parental care in the development of



primate infants but also served as a model for the integration of developmental and comparative frameworks in psychological science and theory.

Margaret Ruth Kuenne was born in St. Louis, Missouri. Her parents were Edward S. (a newspaper compositor) and Margaret E. Kuenne (a milliner). She was the eldest of three siblings, each of whom would grow to attain academic prominence: brother Robert E. Kuenne (1924–2005) would become a noted economist at Princeton, and sister Dorothy J. (Kuenne) Stearns (1927–1972) would earn her doctorate in chemistry before working in atomic physics at Washington University. Among the siblings, Margaret Ruth Kuenne was first to obtain a Ph.D., earning hers in psychology from the State University of Iowa (1944). Previously, she received bachelor's and master's degrees at Washington University in St. Louis (1938 and 1940, respectively). She was a member of national honor societies both at Washington (Phi Beta Kappa) and at Iowa (Pi Lambda Theta). In her dissertation, directed by Kenneth W. Spence, Kuenne reported an experiment she conducted as a research assistant in the prestigious Iowa Child Welfare Research Station. The study, subsequently published in the *Journal of Experimental Psychology* (Kuenne 1946) was an investigation of transposition by 56 preschool and kindergarten children (3–6 years of age). The work provided an important theoretical bridge between the animal research in the Spence tradition on the one hand and the verbal behavior thought to mediate transposition by human adults on the other. She found that as mental age increased, and thus verbal labels like “bigger” and “smaller” became more available, children were more likely to pass the most difficult of transposition tests. The dissertation has been described as “a classic in the area of children's learning” (Graham et al. 1971). University of Michigan educational psychologist Harold W. Stevenson described Kuenne's doctoral project as “. . . a lucid example of how theoretically based research could be conducted with children” to bridge the chasm between developmental and comparative literatures (quoted in Graham et al. 1971, p. 1312).

During her time at Iowa, Kuenne also trained as a clinical psychologist and worked in this area after earning her doctorate (Pelcowitz 2012). Her first academic appointment was at the University of Minnesota (1944). In 1946, she moved to the University of Wisconsin in Madison as an assistant professor of psychology. There, Dr. Kuenne quickly published her dissertation, as well as two book reviews in *Psychological Bulletin*. She also began a collaboration with fellow faculty member Harry Harlow, testing children to complement data he was collecting with monkeys. Professor Kuenne remained at the University of Wisconsin for the remainder of her too short but remarkable life and productive career.

However, her career trajectory was not to be without detour. The challenges so often faced by women scholars with respect to academic-/personal-life balance are well illustrated in Dr. Kuenne's biography. A growing mutual attraction with her collaborator and colleague would force Dr. Kuenne to make a choice. As Deborah Blum (2002) wrote about Harlow and Kuenne: “They were natural collaborators, and after Harry's first marriage fell apart, their relationship shifted almost effortlessly into something more intimate.”

On February 3, 1948, Kuenne married Harlow at a quiet ceremony in Anamosa, Iowa. The elopement was in strategic deference to the strict anti-nepotism policies at Wisconsin that forbade such relationships. Harry and “Peggy” (as he called her) Harlow would spend the next 23 years together, until her death. Together, they would have two children: Pamela (1950) and Jonathan (1953). However, the secret marriage became public long before the child psychologist gave birth to children of her own. (Indeed, their “Harlow & Harlow” publication together – a 1949 *Scientific American* article titled “Learning to Think” – described them as husband and wife, both with faculty appointments in the same department.) Soon after the wedding, the Harlows were informed by the university that at least one would be required to resign. Consequently, Dr. Margaret Harlow yielded her faculty position, although she remained professionally active as a project associate in the University of Wisconsin

primate laboratory that her husband directed. She assumed the role of laboratory editor (and, in many ways, day-to-day lab manager) for Harry and his students. When Professor Harlow became editor of the *Journal of Comparative and Physiological Psychology* in 1951, she expanded this role to assist with the editorial duties of that journal, for the duration of his tenure. “Harry always said that Peggy was the more ruthless editor. He told his students that it sometimes took him weeks to persuade her to approve what even he had written” (Blum 2002).

It would be 17 years before Dr. Margaret Kuenne Harlow would again hold an academic appointment. In 1965, she was permitted to return to teaching as a lecturer in the Department of Educational Psychology at Wisconsin. In 1970, she was promoted to professor – achieving her goal of teaching as a full professor before her untimely death.

Despite these professional challenges, Dr. Margaret Harlow contributed richly to the field of psychology, both with achievements in scholarship as well as in administration. In addition to the publications discussed above, she co-authored a paper showing that monkeys learn to solve puzzles in the absence of traditional rewards, suggesting that monkeys have a powerful and primary “manipulation drive” (Harlow et al. 1950). Harlow et al. (1960) published a report of infant monkeys’ performance on learning set and other tasks. Her most impactful scholarly publications, however, came as part of the long-time collaboration for which her husband is principally famous. The studies of maternal separation, social deprivation, contact comfort, and filial affection were critical, if controversial, contributions. Demonstrations of the deleterious behavioral, cognitive, social, and psychological consequences of maternal separation are as important today as they were a half-century ago when they were first and widely reported by Harlow and Harlow. Co-authored publications with titles like “Social deprivation in monkeys” (1962), “The effect of rearing conditions on behavior” (1962), “The affectional systems” (1965), “Maternal behavior of rhesus monkeys deprived of mothering and peer associations in infancy”

(1966, with Dodsworth & Arling), “Developmental aspects of emotional behavior” (1970), and “Psychopathology in monkeys” (1971) showed how effectively and productively science could be advanced through the marriage of developmental and comparative psychology. Summarizing many of the findings from this research tradition – and reflecting Margaret Harlow’s longtime interest in clinical psychology, Harlow et al. (1971) published “From thought to therapy: Lessons from a primate laboratory” in *American Scientist*.

Professor M. Harlow’s last sole-authored publication was a 1971 apparatus paper, describing methodological innovations permitting her to study the developmental consequences for monkeys of rearing in nuclear (mother-father-child) families. About her efforts to study the paternal effects on development, Frances Graham (a former Division 6 President) and her co-authors wrote, “Once again, an important area of behavior, generally thought not to be amenable to laboratory study, succumbed to Harlow ingenuity” (Graham et al. 1971, p. 1314). Sadly, Margaret Harlow did not live to see this work completed.

In addition to these scholarly achievements, Professor Margaret Kuenne Harlow had a lasting professional impact from her service to the discipline. Already discussed was her many years of assistance as editor of *JCPP*. She is also credited with establishing the American Psychological Association Publications Office in 1950, serving as its first director. From 1966 until her death, she was Executive Officer of the Society for Research on Child Development.

Margaret Kuenne Harlow died on August 11, 1971, following a 4-year battle with breast cancer. Even in death, her career was overshadowed by her famous husband, as her obituary in the *Madison Capital Times* newspaper (August 12, 1971, p. 35) carried the title, “Mrs. Harry Harlow Dies”! However, the Wisconsin newspaper continued with the apt subtitle describing her as a “Noted Primate Psychologist.” The obituary further indicated that “. . . in 1968 [Harlow and Harlow] were jointly awarded National Medals of Science. The award was given for 10 years of research into the love relationships of primates.”

In actuality, the National Medal of Science was awarded only to Harry Harlow, but the newspaper story was not wrong about Margaret Harlow's importance to the work, and about the "love relationship" that she had with the fellow primate that she married and with whom she collaborated for 25 years.

## Cross-References

- [Comparative Psychology](#)
- [Harry Harlow](#)
- [Kenneth Spence](#)
- [Primates](#)
- [Transposition](#)

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## Mark Test, The

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## Synonyms

[The mark-mirror test](#); [The mirror test](#)

## Definition

**A method for testing whether an individual is capable of mirror self-recognition (MSR).**

Self-awareness is a cognitive trait that has fascinated philosophers and psychologists throughout history (Keenan et al. 2004). Self-aware individuals are cognizant of their own actions and how they may affect the world around them, and this trait is closely associated with consciousness and theory of mind (Gallup 1970; Keenan et al. 2004). Self-awareness allows an individual to compare its own situation to the situations of others, making it capable of empathy, gratitude, and pretence (Gallup 1998; Keenan et al. 2004). In spite of the great interest in this trait, there are few nonverbal means for psychologists and behavioral biologists to test self-awareness. Studying self-recognition using *the mark test* has become a popular method for assessing whether an individual is capable of self-awareness. In theory, self-recognition is only possible for self-aware individuals, as the subject needs to be aware of their actions in order to understand that their reflection in a mirror is not another individual (Bekoff and Sherman 2004; Gallup 1998).

The mark test involves the application of a mark on the body of the test subject, in a place

not directly visible to them, such as the face or chest (Gallup 1970; Plotnik et al. 2006; Prior et al. 2011). It was independently invented by Gallup (1970) and Amsterdam (1972) and has become the predominant way of testing the presence or absence of mirror self-recognition (MSR) in nonhuman animals and human children. While there are similarities between Amsterdam's and Gallup's methods, the Amsterdam method is more widely used in the field of developmental psychology to test individual development of human infants (Mitchell 1993), and Gallup's method is commonly used by behavioral biologists in studies on nonhuman animals and comparative studies on the species level (Mitchell 1993). When applying the mark, it is recommended that the subject is not aware of the application taking place. In nonhuman animals, this is sometimes achieved by using anesthesia while applying the mark (Gallup 1970, 1998). In children, the mark is applied by a parent rubbing a spot of rouge (hence the test sometimes being referred to as "the rouge test") on the side of the nose of the child (Amsterdam 1972).

After the mark has been placed, the subject is allowed to interact with a mirror (Prior et al. 2011). If the introduction of the mirror results in the subject inspecting or trying to remove the mark, this is considered evidence that the subject is capable of MSR (Prior et al. 2011). Self-directed behavior, such as grooming and inspection of the individual's own body, can also be considered an indicator of MSR (Gallup 1970). Both of these behaviors display that the subject has identified its own reflection and can use the information in the mirror to examine its own body (Gallup 1970; Prior et al. 2011).

All nonhuman animals require training with a mirror before they can pass the mark test (Gallup 1970, 1998; Shettleworth 2010). Initially, most animals behave socially (aggressively or otherwise) towards the reflection (Gallup 1970, 1998; Shettleworth 2010). However, after some time, the animal may begin to inspect the reflection more closely and perform self-directed behavior (Gallup 1998; Prior et al. 2011).

There are some key differences between the Amsterdam and Gallup tests. Firstly, the subjects in the Amsterdam experiments have a parent present during the test. The parent pretends to wipe the infant's nose in order to apply the mark and may ask "who's that?" while looking at the mirror, thus guiding the child towards inspecting the reflection (Amsterdam 1972; Mitchell 1993). The subjects in Gallup's experiment are isolated from conspecifics during the test in order to motivate mirror exploration and are sometimes sedated when the mark is applied (Gallup 1970). Secondly, the two methodologies differ in their interpretation of the subject's behavior. Gallup's method only considers changes in social behavior, self-directed behavior, and time looking at the mirror image as indications of MSR (Gallup 1970; Prior et al. 2011). According to Amsterdam's methodology, infants saying their own names or "nose" are also considered as touching the mark and indicate self-recognition (Amsterdam 1972).

In addition to methodology, there are differences in how the mark test is used between developmental psychology and behavior biology. In developmental psychology, MSR is seen as one of several milestones towards true self-consciousness (Zahavi et al. 2004). The mark test is, therefore, used to examine the mental development of young children, alongside tests that indicate the presence of other aspects of self-awareness (Zahavi et al. 2004). Traditionally, MSR has been used in behavioral biology to test the presence or absence of the MSR trait in species or populations and not to place individuals on a continuous scale of self-consciousness (Bekoff and Sherman 2004; Mitchell 1993).

However, some behavioral biologists consider MSR as one point on a continuous spectrum of self-consciousness (Bekoff and Sherman 2004). The biologists do not use the mark test to assess self-awareness as a dichotomous trait, but rather to interpret MSR as one of several traits that could indicate that the animal has some form of self-consciousness (Bekoff and Sherman 2004; Shettleworth 2010). Although there are inconsistencies in how the mark test is used, the method is still an important tool to investigate

self-awareness in both developmental psychology and behavioral biology today (Plotnik et al. 2006; Prior et al. 2011).

## Cross-References

- [Consciousness](#)
- [Self-Awareness](#)

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## Marsupial Cognition

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## Introduction

Marsupials are all the members of the infraclass Marsupialia which diverged from the main radiation of placental mammals around 130–160 mya. They exhibit a myriad of adaptations to different habitats, wide array of diet, locomotor modes, and social and mating systems. Even though their point of origin is contested, the earliest metatherian fossil record (comprising marsupials and their closest fossil relatives) has been discovered in Asia and dated to the Early Cretaceous (stretching from 146 Ma and 100 Ma). The earliest common ancestor of eutherians (modern placentals) and metatherians is thought to be *Juramaia sinensis*. Dated back to the Jurassic (160 Ma) and discovered in China, it exhibits scansorial (adapted for climbing) forelimb anatomy, weights around 15–17 g, and based on tooth morphology, was an insectivore. It is more closely related to most modern day placentals than all metatherians including the earliest known *Sinodelphys* and *Deltatheridium*.

All extant marsupials are native to Australia, New Guinea, and the Americas, but the fossil record shows that they have been present on all continents at different points in time. Over 330 extant species of marsupials had been described, with around 100 in the Americas and the rest in Australia and New Guinea.

The main difference between placentals and marsupials regarding cognition can be expected due to difference in their developmental mode (the specific type of developmental stages and conditions that an organism undergoes). Despite their name and designation, the marsupial infraclass does undergo placentation but it is relatively short, and some marsupials do not even have a pouch (marsupium), like the short-tailed opossum

## Marriage

- [Consort](#)



(*Monodelphis domestica*). Besides the confusing naming nomenclature, most marsupials do have a very different developmental mode to placentals. They have very short gestation periods (typically between 2 and 5 weeks) and most of the fetal development takes place in the marsupium. This exposes both the developing offspring and the mother to an array of very different developmental/parental conditions as compared to placentals. This also predisposes differences in cognitive and behavioral development.

The striking difference in developmental mode and early phylogenetic divergence, and the subsequent morphological convergence between the two infraclasses of mammals presents a wonderful opportunity for studies on comparative/convergent cognitive evolution. Despite that marsupials are remarkably understudied from psychological perspective. There are only a handful of studies assessing the cognitive abilities of the infraclass, either purely descriptive or in comparative perspective.

What follows is a summary of the current state of understanding of marsupial cognition, starting off by defining cognition and its neuroanatomical correlates. Some differences in neuroanatomy which might be underlying further differences in behavior and cognition between placentals and marsupials are described, followed by a review of the current literature – starting from the initial interest in marsupial behavior and cognition in the beginning of the twentieth century and summarizing the current state of research on different aspects of cognition – perception, learning, memory, attention, decision-making, and executive functions (flexibility, categorization, problem-solving).

## What Is Cognition?

*Cognition encompasses the abilities of an organism to decode, encode, store and process information from the environment (endogenous and exogenous) in (almost) real time.* This usually results in adaptive or flexible behaviors that maximize the species' fitness. These abilities had emerged and evolved as an assembly of different

properties of the nervous system in combination with other receptive and perceptive systems multiple times in evolution.

## On Neuroanatomical Differences with Placentals

Placentals and marsupials show surprising convergence in neuroanatomy (Karlen and Krubitzer 2007). One major difference is the fact that while all marsupials are relatively lissencephalic (exhibiting smooth cortical surface), placentals do exhibit gyrencephaly (folded cortical surface) more often. It is not clear whether the last common ancestor had a gyrated or smooth cortex, but a case has been made that proposes a secondary loss of gyrencephaly in mammals. If so, this might be an example of secondary loss, that is, lissencephaly might be a derived trait in marsupials and not an indication of “primitiveness” (Kelava et al. 2013).

One notable aspect of marsupial neuroanatomy which sets them apart from placentals is that they lack corpus callosum (Suárez et al. 2018). Most connections between the hemispheres are initiated through the hippocampal tracts or the anterior commissure (diprotodont marsupials, such as kangaroos and koalas have an additional axonal tract called *fasciculus aberrans*), which is more typical of reptiles and birds.

Besides these two significant neuroanatomical differences there is a striking convergence between placentals and marsupials in neuroanatomy, morphology, and behavior in species occupying similar habitats. This indicates a possible set of constraints or limits to the developmental bias on the evolution of the nervous system, resulting in similar solutions to similar pressures of the environment.

## On Perception

### Vision

Visual acuity in marsupials is quite poor compared to more derived placental mammals. This is mostly explained due to their nocturnal or

crepuscular activity pattern which relies more on sensitivity to UV instead of resolution or color vision (Arrese et al. 2006).

Until recently, all marsupials were thought to have dichromatic vision (possessing only two types of cones). Recently, it has been discovered that there are many trichromatic species (i.e., fat-tailed dunnart, honey possum, quenda, and quokka, among others), but up until now it has been impossible to identify the third cone's photopigment unambiguously. The observation that around 20% of the photopigments in the retina of the fat-tailed dunnart (*Sminthopsis crassicaudata*) do not react to short or middle wave opsins has been backed up with behavioral experiments (Arrese et al. 2006). Previously thought to be unique to primates, the third class of cones allow for red–green color discrimination. Interestingly, trichromacy in marsupials is not linked to the X-chromosome, and all cones express a type of rod opsin.

The evolution of trichromacy in marsupials presents an interesting case, where this trait might have evolved at least twice in the infraclass (in polyprotodonts and diprotodonts) if it is assumed that the ancestral marsupial was dichromatic. The explanation as to what might the evolutionary pressures behind that be is challenging – for example, species from similar habitats were shown to have different visual ability. Wallabies have been shown to be dichromats while quokkas trichromats. Further research is needed in order to establish the exact evolutionary pressures behind that phenomenon.

### Audition and Vocalization

Marsupials use vocalization, mostly directed to conspecifics during mating, agonistic territorial encounters, and mother–young interactions (Aitkin 1998). The size and habitat of different species appears to drastically affect calls. Vocal communication seems to be more important and thus more developed in arboreal species (Aitkin 1998). For example, opossums' calls cover very broad spectra (0.5–8 kHz – growl; 1–16 kHz – screech), while dasyurids' calls are usually in the spectral frequencies below 3 kHz. In contrast, the arboreal striped possum's call (*Dactylopsila*

*trivirgata*) has a tonal peak at 2.5 and 5.5 kHz. There is evidence that some small, terrestrial carnivorous species can use ultrasonic frequencies, but most such calls lack harmonic structure. Brushtail possums' (*Trichosurus vulpecula*) hearing sensitivity increases from 2 to 15 kHz, and they could still hear tones between 20 and 35 kHz. The hearing range in northern quolls (*Dasyurus hallucatus*) has been shown to lie between 8 and 10 kHz, while the best frequency of hearing in the American opossum (*Didelphis virginiana*) was shown to be between 16 and 32 kHz which is much higher compared to the quoll.

Low-frequency hearing and calls are related to recognition of conspecifics, mid-frequency ranges are related to interactions with pouch-young, while upper ranges are mainly used during predator–prey encounters (Aitkin et al. 1994).

Finally, similarly to placental mammals, there seems to be broad diversity of spectral sensitivity in different species of marsupials, corresponding to wide array of vocalization frequencies. This probably reflects the variety of adaptations to habitats that these species occupy. These findings strengthen the argument that auditory perception and production are as diverse in marsupials as they are in placentals, reflecting their ability to perceive, process, and react to complex stimuli in the environment.

### Olfaction

Similarly to placentals, marsupials possess main and vomeronasal olfactory system, where the later exhibits pronounced sexual dimorphism in some species, and high structural conservation (Aland et al. 2016). The structure and development of the vomeronasal organ in marsupials indicates that, as in other mammals, the importance of pheromones in reproduction is crucial. This might be especially important for some small dasyurid species, as females from these species are monestrous (only a single estrus in a lifetime) while males are semelparous (sudden death of all males after one reproductive season). Thus, the cost of reproduction in such species is extremely high, and an evolved ability to correctly assess a potential

mate should necessarily rely on highly developed olfactory perception for recognition.

In regards to olfactory cognition, there are no studies up to date addressing questions related to olfactory memory, attention, or categorization in marsupials, despite it being a popular topic of research in other mammals (Zucco et al. 2014).

## Cognition in Marsupials

In lieu of the fact that most extant marsupials can be found in Australia and New Guinea, one of the most studied species of marsupial in the psychological literature is the common opossum (*Didelphis marsupialis*). Most marsupials are understudied in terms of cognition and behavior and little progress has been made in this area of inquiry since a series of pioneering attempts in the 70s (Kirkby 2015). Before that, it was popularly held that marsupials were a primitive mammalian radiation, representing an intermediate form between sophisticated eutherians and primitive reptiles. Even though that notion is no longer supported, almost no advance has been made in the field of marsupial cognition, and the view that marsupials are somewhat primitive is still widely and wrongly accepted.

## Exploration and Problem-Solving

Platt and James (1967) were able to show that adult opossums exhibited preference for novelty, by training them in T or Y mazes with different colors of the different arms. When both arms were changed to congruent color choice, most opossums showed tendency to explore the arm that had changed color. In a larger comparative study Russell and Pearce (1971) exposed 30 animals from 6 different marsupial species to a set of four novel objects with different odor, shape, and texture. Their findings showed similar response to novelty to placental mammals, where repeated exposure led to habituation, with some species showing higher level of reactivity (brush-tailed marsupial rat – *Dasyuroides byrnie*) while others had very quick habituation (i.e., red

kangaroo, *Macropus rufus*, or the Tammar wallaby, *Macropus eugenii*). Other studies had also pointed to similarity in exploration toward novelty between mammals and marsupials (Kirkby 2015) with the little differences been attributed mainly to differences in habitats and diets.

One striking example of problem solving, where possums outperform even primates involves retrieval of a food reward tied to string when the only solution to the task requires the animal to face away from the goal object (Wynne and McLean 1999). In terms of spatial learning, marsupials, and especially opossums, have been shown to be especially apt. On specific maze tasks they seem to perform better than rats, chickens, and even dogs. In rare study in wild animals (Morrant and Petit 2012) the nectar feeding western pygmy possum (*Cercartetus concinnus*) were shown to exhibit very complex exploratory behavior in their natural environment, combined with diet-switching in order to cope with fluctuation in resource availability. Pygmy possums have been detected to travel up to 4.7 km in a single night in search of flowering plants, and when certain food sources were unavailable, they could identify alternative flowering plants to feed on.

## Conditioning and Learning

Attempts for classical conditioning in marsupials had been more controversial in their outcomes. Initially, researchers could not successfully train animals to respond to conditioned stimuli but recent attempts have shown that this is possible, concluding that a suitable choice of stimuli is crucial for conditioning in marsupials (Papini 2005). On the other hand, several species of marsupials had been shown to react very similarly to placentals in regards to acquiring both positive and negative operant responses (Angermeier et al. 1987; Powell and Doolittle 1971). Red opossums (*Lutreolina crassicaudata*) were even shown to acquire similar preference to a box with sugar solution versus an empty box, after only a few daily training trials (Papini et al. 1987).

This was not the case in Virginia opossums, which exhibited better performance with more trials per session (Friedman and Marshall 1965), indicating variation in context learning in marsupials.

In another study (Bonney and Wynne 2004) both herbivorous quokkas (*Setonix brachyurus*) and carnivorous fat-tailed dunnarts (*Sminthopsis crassicaudata*) showed impressive cognitive flexibility. Both species were successful in learning discriminations, learning sets and reversal sets. Dunnarts showed exceptionally fast learning abilities successfully learning reversal sets in one trial, and were the only species which succeeded in transverse patterning tasks (in which each stimulus has a different property contingent on other stimuli with which it is presented) and negative patterning tasks (tasks in which an animal is conditioned to respond to one of two stimuli, but not to the simulations presentation of both). This difference between the two species might be due to the better developed cortical association areas in dunnarts as compared to quokkas.

Such findings lead to the conclusion that operant learning ability does not appear to have evolved after the split between eutherians and metatherians, and that more encephalized animals do not show improvement as compared to less encephalized ones. This might be related to the fact that experimental operant and classical conditioning mostly rely on food as reward. It is a very basic stimulus related to survival, that even the most basic vertebrates should be capable of efficient conditioning to.

## Lateralization

Lateralization of behavior (preferential usage of one side of the body during execution of certain repertoires like extracting fruit, offspring care, etc.) has been shown to be a property of most bilaterally symmetrical vertebrates. It has many implications for behavior and cognition and has been suggested to be a result of an evolutionary stable strategy under social pressures, where asymmetrical organisms need to coordinate their

behavior with other conspecifics or other species (Vallortigara and Rogers 2005).

In a study on southern hairy-nosed wombats (*Lasiorhinus latifrons*) right auditory bias was detected when the animals were presented with eight sounds from different contexts (Descovich et al. 2013). Interestingly, once used to the sounds, the animals reversed their bias to the left side. This is in concert with other studies, indicating that most vertebrates exhibit left hemisphere/right sensory bias for vigilance (Vallortigara and Rogers 2005) and right hemisphere/left sensory bias for familiar objects (Robins and Phillips 2010).

Strong manual lateralization had also been shown to be present in some bipedal marsupials both on individual and on population level (Giljov et al. 2017). Left-limb preference was observed in several species of macropods, and it was shown to be present from the pouch-young stage. These findings suggest that manual preference and lateralization in this group is not determined by habitual bipedality, but it is a result of developmental processes precluding postural and locomotor bipedality. This is in stark difference to most studied placental mammals, where manual lateralization usually manifests with advancing age, with the one exception in primates, where the scenario resembles marsupial's early development. In that sense, both humans and macropods manifest handedness before the adult stage which becomes evident before the development of bipedality.

## Avoidance Learning and Generalization

Predator avoidance in marsupials is one of the best studied areas of cognitive ability in that group with all observations and experiments suggesting that learning processes in marsupials might be convergent with those in placentals. One of the largest members of the Macropodoids, the eastern grey kangaroo (*Macropus giganteus*) was shown to flee if there are dingos or farm dogs in proximity. The fear response toward the farm dogs had also been shown to generalize toward the vehicle the dog always appears around (Jarman and Wright 1993). Several other marsupial species

had been shown to successfully learn to recognize introduced predators. Rufous hare-wallabies (*Lagorchestes hirsutus*) could learn to recognize a stuffed model of a fox and a cat, and quokkas (*Setonix brachyurus*) had been shown to be able to generalize their fear toward dogs to a stuffed model of a cat (McLean et al. 2000). Tamar wallabies (*Macropus eugenii*) were shown to become fearful of a model fox then generalize the response to a cat, but not to a non-predator (goat) (Griffin et al. 2002). The authors interpret this finding as an adaptive predisposition to acquire a fear of predators, based on their subsequent experiments with an array of control stimuli.

### Social Cognition and Play

Tammar wallabies (*Macropus eugenii*), a highly gregarious and social species, can socially transmit knowledge on avoiding a predator model (fox) and can generalize between contexts (Griffin and Evans 2003) – they subsequently avoid cats, but not goats. This was the first instance where social learning was demonstrated in a marsupial species. Another study (Cordonni and Norscia 2014) demonstrated that in the red-necked wallaby (*Macropus rufogriseus*) reconciliation was not only present, but it was also modulated depending on the intensity of the conflict. While low intensity conflicts were reconciled, high intensity ones were not. These findings indicate that the red-necked wallaby can evaluate the costs of conflict and reconciliation and can engage actively in peace-making in an attempt to maximize the pay-offs.

Play has been considered one of the indicators of complex cognition in mammals and birds (Iwaniuk et al. 2001). Despite the scarcity of data, a survey of play behavior among marsupials revealed that play was common in larger-bodied members of Dasyuridae, in *Myrmecobiius*, in Vombatidae, and in all Macropodoidea (Watson 2009). They exhibit a diverse range of social (play fighting, sexual play, and parallel locomotion), nonsocial (locomotor or object play), and inter-specific play. It was shown that the presence of play was related to relative brain mass, but a point

was also made that there might be a confusion in classification of play fight versus real fight, for example in macropodoids (Watson 2009). Some ritualized behaviors in fights categorized as real ones, might have been indicators of play fight instead.

The evolution of play in marsupials, and macropods more specifically, has been analyzed from the scope of their specific social system. Most of the playing macropodoids are polygynous, which necessitates a certain level of competition between both males and females, which can be “rehearsed” while playing. Another contributing factor might have been predation pressure, as macropodoids have been preyed upon by a range of mammals, avians, and reptilian predators throughout their evolution. Training different predator avoidance strategies through locomotor play might be an adaptation alternative to crypsis in some non-playing species (e.g., potoroids).

### Conclusion

The area of marsupial cognition is remarkably underexplored, and despite many potential species that can be studied as model animals the infraclass remains poorly understudied. For example, in species that show evidence of enhanced learning abilities and cognitive flexibility, studying pouch young in their early development provides a great opportunity for research on development and evolution of cognitive abilities. Many species had never been studied in terms of cognition, and there is a substantial gap in our knowledge of memory, cognitive flexibility, social learning, innovation or most types of complex cognition in the group, such as emotions, moral judgment, prospection and planning, theory of mind, and consciousness. Metatherians in general provide a wonderful study system for research on convergence in cognitive ability, and given their differences and similarities in neuroanatomy, they deserve more attention from scholars interested in evolutionary comparative studies, such as neuroecology and cognitive ethology.



## Cross-References

### ► Cognition

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## Marsupial Diet

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## Synonyms

[Feeding behavior](#); [Metatherian](#); [Nutrition](#)

## Introduction

The marsupials are a varied and diverse group of mammals, with specialized dentition and digestive physiology for each specific niche they occupy. Their dietary strategies include carnivores, insectivores, nectarivores, omnivores (of varying degrees), folivores, frugivores, fungivores, browsers, and grazers. Marsupials have a basal metabolic rate that is about 30% below eutherian mammals. Though, McNab (1978) challenged whether this is due solely to phylogeny or just life history in general, as frugivory and folivory are also associated with

sedentary arboreal habits in both mammal groups. However, this strategy is commonly encountered across the marsupials and can be possibly explained by a survival strategy to overcome the unpredictable environments across their range. Withers et al. (2006) noted that species from arid and unpredictable environments, generally, have lower metabolic rates. Hume (1999) compiled a detailed account of the marsupial diet, nutrition, and physiology. Here the diets and foraging behaviors have been summarized and more recent findings included as well as a consideration of how we can use these diet choices to better understand the cognition of some of the marsupials.

## Diet Strategies

The marsupials can be classed into two groups the Australasian marsupials and the American marsupials. Carnivores of the former have a simple digestive tract with no caecum, whereas a caecum is present in the latter suggesting a more omnivorous diet, although several of these species have a much greater proportion of animal matter in their diet and a dentition that can allow them to be considered as carnivores (Hume 1999).

## Dasyuromorphia

The order Dasyuromorphia includes the family Myrmecobiidae, with the sole species the numbat (*Myrmecobius fasciatus*) and the family Dasyuridae, which ranges from the small planigales to the large Tasmanian devils. The numbats feed principally on termites, scratched from the top soil layers of the forest floor, and scooped up with their long tongue (Cooper and Withers 2004).

The dasyurids have a primitive dentition and a simple digestive system with a rapid passage rate, indicative of typical carnivores with no caecum. The prey choice correlates with body size, whereby the smaller members eat small invertebrates, but larger species can predate on vertebrates too (Hume 1999). The largest carnivorous marsupial the Tasmanian devil (*Sarcophilus harrisii*) is a generalist predator, taking animals ranging from small invertebrates up to large

vertebrates such as seabirds, wallabies, or wombats, which they will either ambush or chase over short distances to catch prey (Jones 2003). They also scavenge on the carcass of wallabies, wombats, quolls, or livestock. The spotted-tailed quoll (*Dasyurus maculatus*) consumes medium-sized mammals and, being particularly good climbers, are well placed to prey on arboreal species such as gliders. They will also supplement this diet with rabbits other medium-sized marsupials as well as some invertebrates and a little plant material (Glen and Dickman 2008). Whisker-like vibrissae on their paws allow them to reach into the dens of their prey, and they can stalk their prey, catching and holding them down with their front paws and will also scavenge on the carcasses of larger animals (Jones et al. 2001). Several of the small to medium-sized dasyurids weighing 6–1000 g can use daily or short-term torpor to help combat food shortages in an unpredictable environment (Munn et al. 2010). Though Pavey et al. (2009) found that the high energetic content of vertebrate prey allows for less frequent and shorter torpor duration. This torpor behavior is also observed in other carnivorous/insectivorous Australian marsupials such as the numbats and marsupial moles.

### Notoryctemorphia

Due to their elusive subterranean and solitary nature, there is very little information on the diet and feeding behavior of the marsupial moles. There are two extant species the southern marsupial mole (*Notoryctes typhlops*) and the northern marsupial mole (*Notoryctes caurinus*). Living in the sandy deserts of Australia, they tunnel rapidly into the sand with their forelimbs and fill in the space behind them with their hind limbs (Pavey et al. 2012). They have been observed in captivity to use their protrusible tongue to lick larvae and eggs of invertebrates from the ground surface, and it is thought that they have a similar feeding behavior underground (Benshemesh and Johnson 2003). A well-developed olfactory sense is likely to allow the moles to locate social invertebrate nests (Benshemesh and Johnson 2003). Museum samples offer an insight into their diet, finding that marsupial moles not only consume social insects

but that beetle larvae are also an important food source (Pavey et al. 2012).

### Microbiotheria

More closely related to Australian marsupials Microbiotheriidae is the only neotropical marsupial family in the superorder Australidelphia. Only one species remains living, *Dromiciops gliroides*, which occupies arboreal forests in Chile. It is primarily insectivorous with a diet of predominately arthropods and insect larvae (Vieira and Moraes 2003). In particular, insects are thought to be important energy sources when they emerge after hibernation (Amico et al. 2009). Though crests on their molars are indicative of an insectivorous diet, their broad molars and flat incisors are more representative of a frugivorous diet (Amico et al. 2009). They are well adapted for climbing (Vieira and Moraes 2003) allowing them to consume fruit to supplement their diet throughout the summer and most probably in the spring, and thus the species is an important seed disperser of mistletoe and other shrubs and trees in Chile (Amico et al. 2009).

### Paucituberculata

The family Caenolestidae are shrew-like insectivores that feed on a variety of animal material from invertebrates to frogs and dead rodents (Martin and González-Chávez 2016). They possess peculiar lip flaps that are thought to prevent their sensory vibrissae and fur being clogged with blood and dirt (Hume 1999). Their dentition is made up of well-developed lower incisors that protrude to the front. Captive animals were noted to stab their prey with these teeth (Vieira and Moraes 2003). Dusk shrew opossum (*Caenolestes fuliginosus*) can climb and jump well using a prehensile tail for balance. No intra-specific aggression in the captive group was observed, and group huddling and non-agonistic feeding bouts were noted suggesting they are not exclusively solitary animals in the wild (Martin and González-Chávez 2016).

### Didelphimorphia

The extent of carnivory in the neotropical marsupials and in the Didelphidae family, specifically,

varies with arboreal lifestyle in that the more arboreal the species is, the less carnivorous the diet that it follows (Vieira and Moraes 2003). This is a large order of marsupials with over 60 small- to medium-sized species. The Patagonian (*Lestodelphys halli*), lutrine (*Lutreolina crassicaudata*), and water opossum (*Chironectes minimus*), which eats crustaceans, fish, and amphibians, are the most carnivorous of the didelphids. Patagonian opossum dentition suggests a carnivorous diet, having very long canines and molars. Apart from the more carnivorous Didelphidae, the rest of the family are omnivores. The Brazilian gracile opossum (*Gracilinanus microtarsus*) opportunistically feeds on both plant and invertebrates, though its diet is primarily made up of insects (Martins et al. 2006). Much work has been carried out on the Virginia opossum (*Didelphis virginiana*), whose dietary range has, in part, allowed them to successfully expand their range across North America (Hume 1999). The species can survive cyclical food availability and low winter temperatures by reducing activity, sheltering in dens, and using up fat reserves, which can result in body weights falling by 27% (Gardner 1982). They have been known to predate on rattlesnakes and show immunity to their toxins. Woolly opossum (*Caluromys* sp.) and bushy-tailed opossum (*Glironia venusta*) and black-shouldered opossum (*Caluromysiops irrupta*) are the least carnivorous of the Didelphidae family.

### Peramelemorphia

The order Peramelemorphia is indicative of the main omnivorous marsupials, comprising of bandicoots and bilbies. Bandicoots are too small to be fully herbivorous and too big to be a generalist insectivore so the omnivorous strategy has been adopted. The diets of all the species vary but include invertebrates, plant material, and fungi (Hume 1999). The greater bilby (*Macrotis lagotis*) is a small omnivorous marsupial with a diet that mainly comprises of beetles, termites, and ants. They show digestive flexibility being able to adapt to seasonal variation, in the cooler months' roots and seeds are also consumed (Navnith et al. 2009). They can dig through the soil to get their food and possess very long

tongues to reach their prey. They have relatively low basal metabolic rate and a low requirement for nitrogen which helps them to adapt to changes in an unpredictable arid environment (Hume 1999).

### Diprotodontia

#### Petauridae

Though some species of the Petauridae can be considered herbivores, many consume a mixed diet that includes invertebrates. This superfamily includes the ring-tailed possum, gliders, and honey possums.

The striped possum (*Dactylopsila trivirgata*) and sugar glider (*Petaurus breviceps*) both have a long fourth digit to pull out insects from bark and enlarged incisors to chew bark and reveal sap. The sugar glider diet varies geographically and seasonally, in summer they eat pollen and nectar from *Eucalyptus* trees and in autumn they change to arthropods (Dobson et al. 2005). Yellow-bellied gliders are the largest glider species; they are exudivores that live socially with vocal communication to help maintain large home ranges. Eucalypt sap is important in the diet of yellow bellied glider (*Petaurus australis*), and they will make a notch in the tree to extract the sap. The Leadbeater's possum (*Gymnobelideus leadbeateri*) is also an exudivore; they are very rare and only found in one specific area of Australia. It is thought that they have microbes in the digestive system to help break down the polysaccharides in the gum. Eucalypt nectar is important to squirrel gliders (*Petaurus norfolcensis*) (Hume 1999).

Reduced dentition and a specialized tongue have allowed the honey possum (*Tarsipes rostratus*) to become unique nonflying pollen and nectar consumers (Bradshaw and Bradshaw 2012). They do not have a caecum and instead digest pollen in the intestines; their stomach is bilobed with a well-defined diverticulum (Bradshaw and Bradshaw 2012).

Encephalization quotas were compared across marsupials and found the honey possums as well as some of the gliders to have an encephalization quota similar to prosimians, suggesting spatial

memory is important for their arboreal lifestyle and dietary requirements (Ashwell 2008).

The rock ringtail possum of the Pseudocheiridae has a mixed diet of fruit, flowers, and leaves; their digestive tract has a small caecum (Hume 1999).

Of the more folivorous species, common ring-tailed possums (*Pseudocheirus peregrinus*) consume the leaves, shoots, and flowers of *Eucalyptus* and other available trees. The green ringtail possum is also highly folivorous, in particular, feeding on *Ficus* leaves. They possess a very large caecum with hindgut fermentation to help digest the high quantity of leaf material. The New Guinean ring-tailed possums are smaller and therefore adapted to a more mixed diet, but all still possessed a large caecum and are thought to be chiefly folivores (Hume 1999).

The greater glider relies almost solely on *Eucalyptus* foliage. Due to this low-quality food resource, it has adapted with shearing teeth to break the leaves into small particles to allow better fermentation in their enlarged caecum. They also have a very low reproductive rate.

#### Phalangeridae

The pygmy possums from the family Burramyidae are more closely related to the *Phalangeridae* family and are included together in the superfamily Phalangeridae. The mountain pygmy possum (*Burramys parvus*) eats moths as well as alpine fruits; the other pygmy possums (*Cercartetus* sp.) primarily consume nectar and pollen but will also eat arthropods and small vertebrates.

The Phalangeridae family are more frugivorous, and the common brushtail possum (*Trichosurus vulpecula*) is a particularly successful species. As with many invasive species, its high fecundity and low reproductive age has allowed it to rapidly establish in new areas. The adaptability it shows to new diets has helped it to maximize resources in new environments. Of the eight New Guinean phalangerids, the ground cuscus is thought to be the most frugivorous, filling the same ecological niche as eutherian sloths and hyrax with extremely low metabolic rate; unlike tree hyrax they spend the day in

burrows or under tree roots and climb tree at night to feed. The dentition is made up of small bunodont molars and very large premolars like other frugivorous mammals (Hume 1999). They have a long small intestine and short caecum, where cell wall digestion takes place. The stomach is unilocular and so can stretch to accommodate large food items (Hume 1999).

#### Hypsiprymnodontidae

The rainforest dwelling, musky rat kangaroo (*Hypsiprymnodon moschatus*), formerly classed within the Potoroidae, has more recently been placed with the extinct rat kangaroos (Burnett et al. 2016). It is now the sole surviving species within the family. Unlike other Macropodiformes it has a simple stomach suited to a lower fiber diet (Hume 1999). They are primarily frugivores eating the fruits and seeds of a large number of plant species and preferring large, fleshy fruits with soft seeds (Dennis 2002). They will also eat fungi when in season (Arman and Prideaux 2015).

#### Potoroidae

The family Potoroidae have been classed as herbivores, omnivores, and fungivores. Bennett and Baxter (1989) observed long-nosed potoroos (*Potorous tridactylus*) to have a seasonal diet variation feeding in the autumn on fungi and seeds and in spring on arthropods. They have long claws on their front feet that help to excavate deep rooted fungi, and as there is a high proportion of fungi (>40%) in the diet of all species in this family with the exception of the burrowing bettong (*Bettongia lesueur*), they should be considered as fungivores. The burrowing bettong has adaptations to allow the consumption of tougher food. This thought to be an ancestral trait to cope with their arid habitat (Vernes and Lebel 2011).

The potoroid digestive system comprises of a sacciform stomach, which allows the storage of high energy foods and a small tubiform stomach. Dentition is that of a basal macropod adapted to a low fiber (seed and fungi) diet where the premolars can cope with large food items such as fungi and can be used to open seed cases before their low crowned molars crush the seeds. Potoroids do not need fibrous material, as the small capacity of



their stomach restricts bulky, low energy, fiber intake (Hume 1999). Their fungal dietary intake is also shared with several browsing macropods.

#### Macropodidae

Arman and Prideaux (2015) reassessed the dietary classification of the macropods putting the quokka and the red-necked wallaby as browsers (with more than 70% browse consumption) and pademelons, swamp wallabies, rock wallabies, and the nail-tailed wallaby as mixed feeders. The brush wallabies, hare wallabies, wallaroos, and kangaroos were combined as grazers (with more than 70% grass consumption).

Tree kangaroos (*Dendrolagus* sp.) are strictly folivorous foregut fermentation, browsers consuming the leaves and stems of a wide range of trees and vines (Hume 1999). The quokka (*Setonix brachyurus*) eats leaves and stems of succulent small trees and shrubs that grow in the swamp shrubland habitat (Hayward 2005).

Very little is known about the diet of the New Guinea forest wallabies. This group of five, currently identified, species has a basal dentition similar to the potoroids and given their small size are expected to consume a mixed variety of vegetation and fungi (Vernes and Lebel 2011).

Pademelons and wallabies (with the possible exception of the rock and nail-tailed wallabies) also consume and disperse a wide range of truffle-like fungi. They scrape away leaf litter from the forest floor, with their front feet to reveal shallow fruiting fungi (Vernes and Lebel 2011). Hare wallaby is considered to be a seed specialist grazer (Arman and Prideaux 2015).

As body mass increases, there is an increasing reliance on a larger intake of grass (Arman and Prideaux 2015). This has resulted in a change to their digestive system. Except for the red-legged and red-necked pademelon, which rely more on the sacciform stomach for digestion, the highly folded tubiform forestomach is the largest gastric region which helps to slow the passage of the higher fiber food and thus aid digestion (Hume 1999). In the larger kangaroos, the tubiform region is much larger relative to the sacciform region. Incisors bring food in and rows of uniform large ridged molars are used for cutting and chewing grasses.

#### Vombatidae

Wombats are the largest burrowing mammals, weighing up to 50 kg; this is even more unique when the combination of herbivory is considered. They forage on low nutritional perennial grasses and so have distinct adaptations to extract enough energy from their food source in order to expend the energy and time to dig their burrow. However, once a burrow is created, living underground is an energy-saving strategy, with less need to be alert for predators and the thermoregulatory properties of a burrow help to keep the animal cool in the shade and protected from the cold (Finlayson et al. 2005).

They are the only marsupials to possess continuously growing teeth and as these teeth wear, they are left with sharp cutting edges. The molars are left particularly sharp on the cheek side of the lower jaw and the tongue side of the upper jaw allowing food to be reduced to very small particles and thus facilitating the extraction of higher nutritional content from their diet (Hume 1999). Southern hairy-nosed wombats (*Lasiornhinus latifrons*) feed in halo-like circles from their burrow, obtaining the most nutritionally valuable new shoots as they emerge. Very little is known about the diet of the highly endangered Northern hairy-nosed wombat (*Lasiornhinus krefftii*). Common wombats (*Vombatus ursinus*) are generalist feeders, foraging on any available tussock grasses in the mosaic habitat that they occupy (Evans et al. 2006). The digestive system of both these species reflects the differences in their diet. The Southern hairy-nosed wombats have a relatively large small intestine and small proximal colon, whereas the common wombat has a relatively short small intestine (Hume 1999).

#### Phascolarctidae

Koalas, though arboreal folivores, feeding almost entirely on *Eucalyptus* species, still share many features with wombats, they both have a backward facing pouch and a vestigial tail, a specific gland in the stomach, and a diastema between the incisors and the premolars.

*Eucalyptus* has a low nutritional value and is high in toxins (Hume 1999). Koalas are exposed to gut microbes as joeys, through the feeding of

pap as a mechanism to overcome the toxic substances in the *Eucalyptus*. Koalas need to have large digestive system to cope with enough food in order to get enough energy, but they need to be small enough to be mobile so they have developed physiological and metabolic adaptations (Moore and Foley 2000). They have very low energy requirements, resting for a large proportion of the day. They have a simple stomach and an extremely large caecum and proximal colon where fermentation takes place with specific mechanisms to allow particle separation in the stomach; large particles will pass through and smaller particles are retained in the caecum and proximal colon for further digestion.

Olfactory cues are important for koalas who will often scent mark the base of a tree with urine or sternal gland (in males). Koalas will also sniff the base of a tree before climbing. When selecting leaves, koalas will grasp the branches with their front paws and sniff the leaves before they are stripped and eaten.

Out of the 600 species of *Eucalyptus*, koalas have been recorded using up to 120 different species (Moore and Foley 2000). Their dietary preference varies geographically, and while this is in part due to the geographical variation of tree availability, there has been some evidence of a difference in preference between koala populations. For example, a study in New South Wales found that koalas would eat *Eucalyptus radiata* but that koalas in Victoria actively avoided it even to their own detriment (Moore and Foley 2000).

Koalas and other sympatric folivores have been shown to actively select against high plant secondary metabolites such as tannins and phenolics, especially formylated phloroglucinol compounds (FPC) (Foley et al. 2004). The act of sniffing the leaves before consumption is seen as a method of determining FPC concentrations and that prior learning plays a part too (Moore and Foley 2000). This could be through negative past experiences such as the post ingestive consequences of secondary metabolites of *Eucalyptus*-like FPC's and other substances or pre-ingestive experiences, for example, exposure either in utero, via lactation, by social observation or through pap feeding. Though learning through

foraging consequences or conditioned food aversions has not been seen in koalas; there is evidence for this in common ringtail possum and brushtail possum (Lawler et al. 1999).

## Conclusions

Marsupials, with the exception of the honey possum, have a low basal metabolism, and suggestions have been made that this low metabolic rate results in lower cognitive abilities. Evidence suggests that some marsupials' diets and lifestyles have resulted in encephalization quotients that are equivalent to that of similar-sized eutherians. Many marsupials have evolved unique physiological and cognitive strategies to cope with the challenges that they are faced with, be it unpredictable environments or specialized dietary niches. With such a highly specialized group of animals, it is likely that more will be revealed about how they navigate through their habitat in search of food, choose the best food to maximize their energy intake, or learn to avoid predators. However, with pressure from eutherian invasive species and human disturbance, many of these unique species are under threat. We can only hope that important information about their ecology, behavior, and cognition comes to light before it is too late.

## Cross-References

- [Catarrhine Diet](#)
- [Classical Conditioning](#)
- [Marsupial Cognition](#)
- [Marsupial Life History](#)

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## Marsupial Gaits

► [Marsupial Locomotion](#)

## Marsupial Life History

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### Definition

A marsupial life history refers to the series of changes a species in the marsupialia infraclass undergoes throughout its lifetime. These events include age and stage patterns associated with reproduction, growth, and survival.

### Introduction

Marsupials are part of the mammalian class; however, they are then further categorized into the clade Metatheria and infraclass Marsupialia. The main difference between a marsupial mammal and other mammal species is the manner in which they carry their young. Marsupials will give birth to a very immature fetus, which then crawls up the mother's abdomen to a pouch or pouch-like area where it attaches to a teat, then continues its development. In comparison a placental mammal will undergo much of its development internally in the uterus (Archer and Kirsch 2006).

**Kingdom:** Animalia  
**Phylum:** Chordata  
**Class:** Mammalia  
**Clade:** Metatheria  
**Infraclass:** Marsupialia

There is a wide variety of marsupials, overall there are 7 extant orders, which include over 330 species. Figure 1 depicts the two major

divisions of marsupials which are Ameridelphia (3 orders) and Australidelphia (4 orders), ones found in the Americas and those in Australasia, respectively (Archer and Kirsch 2006).

Marsupial are very diverse in all aspects, and they range in size from the long-tailed planigrade (*Planigrade ingrami*) weighing just 4.5 g to the largest the red kangaroo (*Macropus rufus*) weighing around 90 kg (200 lbs) and can grow to be 2.18 m (7.2 ft) tall (Dickman and Vieira 2006).

They occupy a diversity of terrestrial habitats, but there are no truly aquatic marsupials. There are however two South American species which are closely associated to water, the lutrine, and water opossums. The majority of Ameridelphia marsupials are forest dwelling species. The woolly opossums are arboreal animals preferring tropical forests, whereas the slender mouse opossums dwell more on the forest floor and occasionally intermediate levels. There are some species that are quite adaptable to many habitats and are even found in urban areas, such as the American opossums (*Didelphis spp.*) and the Australian common brushtail possum (*Trichosurus vulpecula*) (Dickman and Vieira 2006).

Marsupials also vary in their activity patterns and diets. Some are entirely nocturnal like the sugar glider (*Petaurus breviceps*), whereas others are diurnal like the numbat (*Myrmecobius fasciatus*). Diet wise they range from specialist herbivores such as the koala (*Phascolarctos cinereus*) to carnivorous species such as eastern quolls (*Dasyurus viverrinus*) and Tasmanian devils (*Sarcophilus harrisii*) (Dickman and Vieira 2006).

The wide variety of niches that they fill has an effect on their various life history strategies. A life history strategy is an adaptive set of traits that has evolved over time that allows a species to maximize their fitness. Throughout this entry, there will be examples of key species that have specific physiological and behavioral adaptations linked to their life history.

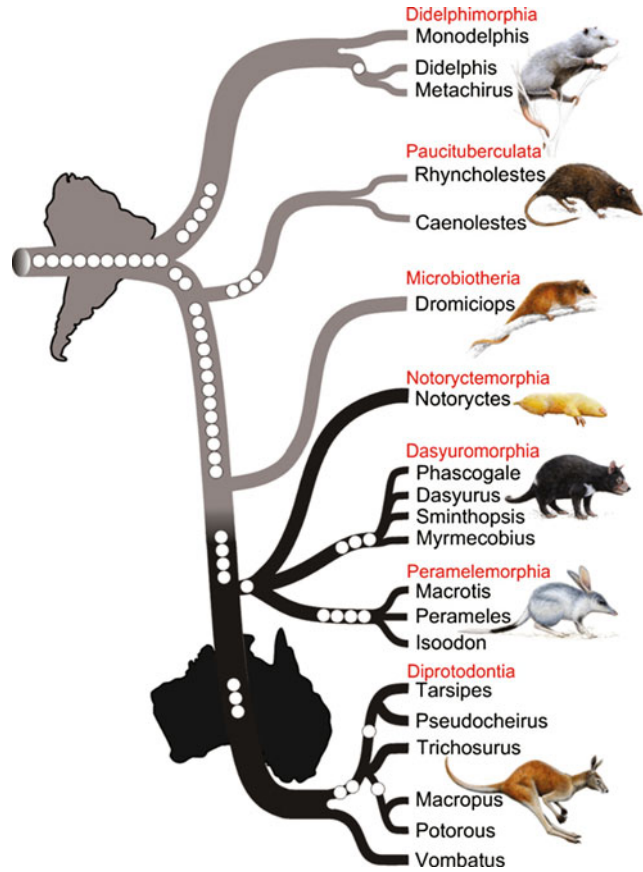
### Reproduction

#### Mating

The niche of marsupials play a role in determining the social systems of each species, and this is then

### Marsupial Life History,

**Fig. 1** Phylogenetic tree of marsupials depicting orders in red, genus in black with representative species from selected genus in that group (Nilsson et al. 2010)



connected to their seeking, finding and mating behaviors.

When male and females live solitary lives, it is likely that they will use vocalizations and/or odors to attract a mate (Fig. 2). In American opossum species (didelphids), both sexes emit short clicking sounds prior to physical interactions, *Planigale*, and *Antechinus* females also produce clicks or “tstitts” sounds that the males may then join in with to create a duet (Croft 1982).

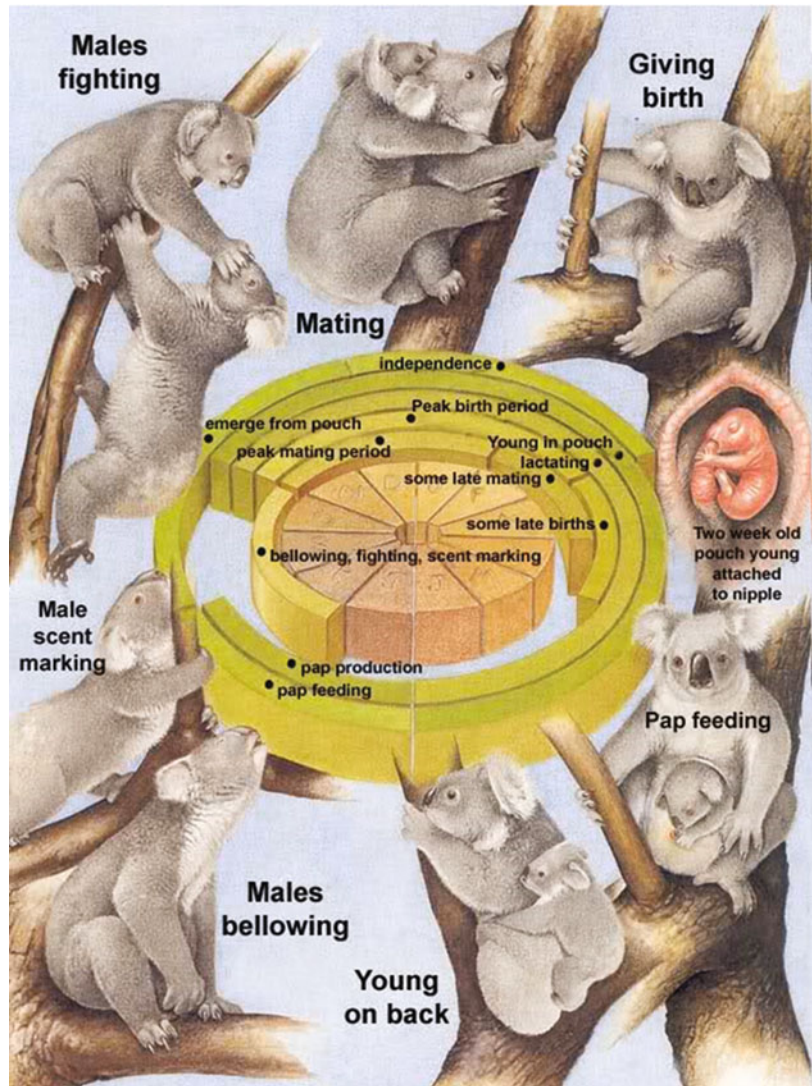
In dasyurids like the spotted tail quoll (*Dasyurus maculatus*), females have been known to produce extended “cp-cp” calls during estrus, whereas female common spotted cuscus (*Spilocuscus maculatus*) will emit loud braying calls. Male marsupials such as the fat-tailed dunnarts (*Sminthopsis crassicaudata*), Tasmanian devil (*S. harrisii*), and common brushtail possum (*T. vulpecula*) all make distinctive sounds when pursuing females for mating. Some species also vocalize while intromission is taking place (Croft and Eisenberg 2006).

Research into odor producing glands in marsupial has found that 40 out of the 73 genera have such glands. Marsupials have a large olfactory bulb and a well-developed vomernasal organ suggesting that olfactory communication is an important part of their sexual behavior repertoire (Russell 1985). Further evidence to support the notion that scent is relevant to mating is when males encounter females they will attempt to sniff her cloaca and pouch, urine taste, and flehmen (Coulson 1989).

In many marsupial families, including didelphids, phalangerids, and petaurids, there is a sternal gland which is used for scent marking. In some species, the gland is more prominently seen in the males like with the sugar glider (*Petaurus breviceps*), whereas in koalas the gland is completely absent in the females (Fig. 3) (Croft and Eisenberg 2006). All odor producing glands may not be associated with attracting a mate; however, they are honest



**Marsupial Life History,**  
**Fig. 2** Koala life cycle,  
depicting courting  
behaviors to maternal care,  
illustration by Peter  
Schouten



signals for potential mates and rivals (Zala et al. 2007).

In marsupials mate competition can be fierce and violent. Populations are generally made up of choosy females and roaming males. Male North American opossum (*D. Virginia*) travel greatly during breeding seasons to find multiple receptive females. When they find one, as many as three other males may be in direct competition with him, disputes are settled through aggression and inter-male dominance. Male to male competition is common among marsupials and not only takes the form of fighting for access to females but mate

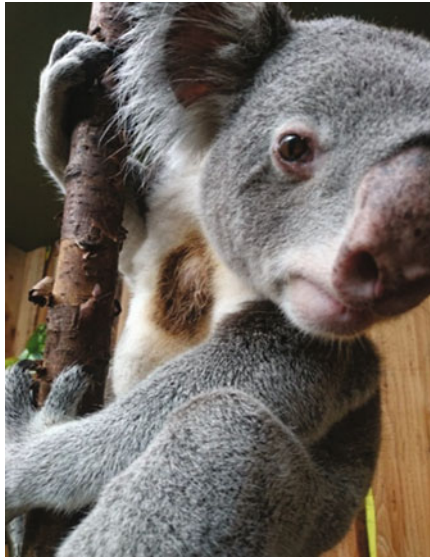
guarding as well. In several dasyurids, coitus can be many hours long and he will then stay with the female until her estrous has passed (Croft and Eisenberg 2006).

Although many marsupials are fairly solitary and practice a promiscuous mating system, small groups or even monogamous pairs can occasionally form in petaurids (Fig. 4), macropods, and phalangerids (Russell 1984).

Males can choose monogamy when a female and her range are defendable. In the short-eared possums (*Trichodurus caninus*), the male and female will have exclusive use of a core area that

**Marsupial Life History,**

**Fig. 3** Picture of male koala sternal gland and female koala without the gland – Photos by Lucy Petrie – RZSS

**Marsupial Life History,**

**Fig. 4** A pair of sugar gliders (*Petaurus breviceps*)



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will only marginally overlap home ranges of other possums.

Another scenario that can occur is stable female groups can form when female home ranges are not defendable. A male may gain access to a group of females and defend them from other males, in a loose harem style system. This can occur in species such as the Greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*).

In the macropods, you will generally have aggregations of individuals in high resource areas, with males forming a hierarchy based on size. Male Eastern grey kangaroo (*M. giganteus*)

may even hold the alpha position for up to 2 years (Croft and Eisenberg 2006).

**Parental Care**

The gestation period in marsupials is very short, just 9–45 days and the young that are born always weigh less than 1% of the mother's body weight (Dickman and Vieira 2006; Mills et al. 2012). When the tiny babies are born, they will have to climb their way to the mother's pouch. In the hopping Macropodidae family, the pouch opens upward so the young have a fair way to climb to get there. In burrowing type species that belong to the family Vombatidae, the pouch opens towards

**Marsupial Life History,**  
**Fig. 5** Female numbat  
 with young. (Photo  
 courtesy of Gary Blagden  
 and Project Numbat)



the rear so it is a shorter journey. The opening position can be directly related to the species locomotor behaviors.

Not all species of marsupial have a fully developed pouch, and members of the numbat family (Myrmecobiidae) do not have a pouch as such, but rather the young are protected by extra hair and swollen skin in the abdomen area. The babies will attach to a teat just like other marsupials and stay attached for up to 6 months (Fig. 5). After which she builds a nest and continues to suckle them until they wean at about 11 months. Other pouchless, nest building marsupials include the kowari (*Dasyuroides byrnei*) who have simple grass nests and the brush tailed phascogale (*P. tapoatafa*) who builds an elaborate nest with bark strips and fibrous materials (Croft and Eisenberg 2006).

In general, body size and lifespan will play a role in determining litter size and weaning age. Larger longer lived animals will have smaller litters (1 joey) and longer weaning times (12 months) as in the Red kangaroo (*Macropus rufus*), whereas species that have relatively short lifespans of just 1 year like the Robinson's mouse opossum (*Marmosa robinsoni*) will have larger litters (10–14 joeys) and shorter weaning times (9–10 weeks). Table 1 draws upon two reviews and additional sources to give examples of a variety of species in connection with their life history traits.

In grazing herbivore species, like the kangaroos that only produce one joey in a litter, it is

possible for them to be caring for and carrying more than one joey at various life stages. One that is out of the pouch yet still nursing, one attached to a teat in the pouch. The two young that are nursing have their designated teats, with each producing the right nutrient level milk with regards to their stage of growth. She may also be carrying a fertilized ovum that remains in embryonic diapause until the oldest joey has weaned (Dickman and Vieira 2006).

In general male marsupials do not play a role in the care and rearing of the joeys. There are a few exceptions to this rule, however, like the male sugar gliders (*P. breviceps*). They will huddle, guard, and even groom their young. So other than the few exceptions, the sole care of marsupial young is the responsibility of the female, she will be the one who nourishes them and protects them from environmental conditions and predators.

In 1982, Russell categorized marsupial maternal care into three types that were determined by the pouch anatomy, the nesting habits, and mobility of the young once they permanently exited the pouch.

Type I strategy is exemplified by the fact these females have rudimentary or are lacking pouches; this category includes mothers of the didelphid, most dasyurids, and myrmecobiids families. Some genera in these families will have a more defined pouch when lactating like the large American opossums (*Didelphis*), monito del monte (*Dromiciops*), and some species of woolly



Marsupial Life History, Table 1 Life-history traits of marsupials categorized by dietary group

| Species                                                   | Mean male mass | Mean female mass | Age of first reproduction (months) | Seasonality of reproduction | Weaning age (weeks) | Bouts of reproduction per year | Interval between litters (days) | Litter Size | Life span                      |
|-----------------------------------------------------------|----------------|------------------|------------------------------------|-----------------------------|---------------------|--------------------------------|---------------------------------|-------------|--------------------------------|
| <b>Carnivores</b>                                         |                |                  |                                    |                             |                     |                                |                                 |             |                                |
| Sandstone antechinus ( <i>Pseudantechinus bilarni</i> )   | 40 g           | 30 g             | 11                                 | Seasonal: short             | 12                  | 1                              | 365                             | 5           | M – 24 months<br>F – 36 months |
| Paucident planigale ( <i>Planigale gilesi</i> )           | 52 g           | 52 g             | 12                                 | Seasonal: long              | 9–10                | 1–2                            | 365                             | 6–8         | < 36 months                    |
| Fat-tailed dunnart ( <i>Smithopsis crassicaudata</i> )    | 15 g           | 15 g             | >5                                 | Seasonal: long              | 9.5                 | 2–3                            | 85                              | 6–8         | > 18 months                    |
| Eastern quoll ( <i>Dasyurus viverrinus</i> )              | 1300 g         | 880 g            | 11                                 | Seasonal: short             | 19–20               | 1                              | 365                             | 6           | 30–32 months                   |
| Tasmanian devil ( <i>Sarcophilus harrisi</i> )            | 8 kg           | 6 kg             | 24                                 | Seasonal: short             | 21–40               | 1                              | 365                             | 4           | 6 years                        |
| <b>Omnivores</b>                                          |                |                  |                                    |                             |                     |                                |                                 |             |                                |
| Robinson’s mouse opossum ( <i>Marmosa robinsoni</i> )     | 95 g           | 50 g             | 9–12                               | Seasonal: long              | 9–10                | 2                              | 85                              | 10–14       | > 12 months                    |
| Sugar glider ( <i>Petaurus breviceps</i> )                | 140 g          | 115 g            | 8–15 (F)<br>12 (M)                 | Seasonal: long              | 16–17               | 2–3                            | 140                             | 1–2         | > 7 years                      |
| Long-nosed potoroo ( <i>Potorous tridactylus</i> )        | 1180 g         | 1020 g           | 12                                 | Non-seasonal                | 24                  | 2–3                            | 140                             | 1           | 7 years                        |
| North American opossum ( <i>Didelphis virginiana</i> )    | 2.35 kg        | 2.35 kg          | ?                                  | Seasonal: varies            | 14–15               | 1–3                            | 110                             | 6–9         | 24 months                      |
| <b>Herbivores</b>                                         |                |                  |                                    |                             |                     |                                |                                 |             |                                |
| Koala ( <i>Phascolarctos cinereus</i> )                   | 9.2 kg         | 6.5 kg           | 24–36                              | Seasonal: long              | 48–52               | 1                              | 365                             | 1           | 15 years                       |
| Common brush tail possum ( <i>Trichosurus vulpecula</i> ) | 3.5 kg         | 2.5 kg           | 12                                 | Seasonal: long              | 26                  | 1–2                            | 200                             | 1           | 12.5 years                     |
| Quokka ( <i>Setonix brachyurus</i> )                      | 3.6 kg         | 2.9 kg           | 18                                 | Non-seasonal                | 39                  | 1–2                            | 185–365                         | 1           | 5 years                        |
| Eastern grey kangaroo ( <i>Macropus giganteus</i> )       | 50 kg          | 27 kg            | 18                                 | Seasonal: long              | 78                  | 1                              | 362                             | 1           | > 16 years                     |

Table comprised of information from Dickman and Vieira 2006; Jackson 2003; Dooley 2004; Kimble 1997; Phillips et al. 2017; Tyndale-Biscoe and Renfree 1987; Kahn 2005; Menhorst 1995; Jackson et al. n.d.; and Smith, 2004

opossums (*Caluromys*), whereas other genera are completely lacking a pouch regardless of lactation like the mouse opossums (*Marmosa*) and fat-tailed mouse opossums (*Thylamys*). These females will commonly produce large litters that stay in the pouch for only a short amount of time before they are deposited in a nest in a fairly immature state of having eyes closed, little fur, and unable to control their own thermoregulation. It is likely that this strategy has been adapted due to the poor protection from the basic pouch, but also the mass of the growing young would impede upon the mother's foraging and predator evasion (Croft and Eisenberg 2006).

The type II strategy has been adopted by members of the peramelidae, petauridae, and vombatidae families. The abdomen area of these females is completely covered by a flap of skin, with an opening that can be to the anterior, as is the case for some cuscus and brushtail possum (phalangerids) and honey possum (tarspedids), or it can open towards the posterior as it does in bandicoots (peramelids) and wombats (vombatids) (Fig. 6).

Young of these mothers leave the pouch further developed than those of Type I. They will have their eyes open and be fully furred and able to move about in the nest/burrow. There may be a transitional phase where they only stay in the nest area, but full emergence will be classed as when

they go with their mother for the first time. Some will follow behind like bandicoot and some will be carried on the mother's back like in the gliders and possums.

Finally, the type III strategy is seen in the macropodids, potoroids, and phascolarctids families. These females have a well-developed pouch and carry their young for relatively longer periods of time with full emergence and weaning taking place later than type I and II species. At the age of permanent emergence from the pouch, they are a little heavier than equivalent precocial placental mammals at birth (Croft and Eisenberg 2006).

Overall, the young of Type I are emerging from the pouch and being weaned at a greater maternal body mass (MBM) than in type II or III. For example, in the common planigale (*Planigale maculata*) young are left in a nest at about 70% of the MBM, and when the litter reaches weaning age they are 300% of her MBM. Whereas in a type II species such as the Southern hairy nosed wombat (*L. latifrons*) young leave the pouch at approximately 20%MBM, in a type III species like the red kangaroo (*M. rufus*) are weaned at 44% MBM (Croft and Eisenberg 2006).

## Growth

The most amazing adaptation to marsupials is the fact they give birth to such tiny immature young in comparison to placental mammals (Fig. 7).

All marsupial species start off life at less than 1% of that of their mother's body mass and many species are much less than 1%. Eastern grey kangaroo female weigh on average 27 kg and the weight of their joey is approximately 4 g; therefore, her young is 0.01% of her body weight. Comparatively, a North American white tailed deer doe weighs on average 65 kg, and her fawn at birth weighs 3.6 kg, thus having a baby at 5.5% her body weight (Haugen & Davenport, 1950).

As an example of the growth process we will look at the stages of macropodids. After birth, the joeys will spend a long time attached to a teat and developing in the pouch before their first emergence. The next stage will be for permanent



**Marsupial Life History, Fig. 6** Wombat joey in rear facing pouch. (Photo by Tapio Salmel)



**Marsupial Life History,**

**Fig. 7** Cleared-and-stained marsupial (grey short-tailed opossum, *Monodelphis domestica*; left) and placental (four-striped grass mouse, *Rhabdomys pumilio*; right), showing differences in development at time of birth. Bony elements are highlighted in pink. (Image from Goswami et al. 2009)



emergence from the pouch and then weaning and postweaning (Croft and Eisenberg 2006).

For the Eastern grey kangaroo, a chart of progression has been produced to assist in the rehabilitation of joeys that have lost their mothers. In the guide, it states that joeys under 250 g are usually not viable for hand rearing.

A joey that is 250–550 g is less than 4 months old, will still be furless, and have its eyes closed and ears down. By 5 months the ears will come up and the eyes will open. By 6–7 months they will have a fine covering fur and weigh about 1380–1700 g and possibly start poking their heads out of the pouch. At 7–8 months they are fully furred and they will make their first emergence from the pouch at an approximate weight of 1700–2240 g. By the age of 9–10 months they weigh 3.3–5 kg and have no trouble in grazing outside of the pouch during the day. When they reach 5–10 kg, they are about 10–13 months old and are ready for permanent emergence; however, it is advised they will not be fully weaned and ready for release until they are 15–18 months old and in the weight range of 15–20 kg (Dooley 2004).

Once fully grown, many marsupial species show sexual dimorphism with the males being the larger sex. In phascolarctids and dasyurids, the males can outweigh the female by approximately 70% as is the case in of the koala and Eastern quoll (Table 1). Interestingly, the wild growth rate of male and female littermates of *Phascogale tapoatafa* and *Dasyurus geoffroii* is

the same until the young start to forage for themselves, after which the males will increase in size to be greater than that of their female siblings (Soderquist 1995).

## Survival

### Longevity

As depicted in Table 1, you will have seen the marsupial life span varies greatly from the short lived species, like the antechinus to the relatively long lived species like the kangaroo.

Many males in the antechinus species are semelparous, which means they only breed once in their lifetime. For example, the subtropical antechinus reach sexual maturity at about 11 months then die at about 12 months old after an exhausting breeding season where they do little else than mate, females may live long enough to see a second breeding season. Robinson's mouse opossum (*M. robinsoni*) also have a short life span of just 12 months for both sexes; however, the female may be able to deliver two litters in that year.

For most marsupial species, body size does correlate well with lifespan, i.e., the larger the body size the longer the lifespan. One of the exceptions to this rule is in the large American opossums (*Didelphis sp.*). They have an unusually low survivorship given their size (2.3 kg) as less than 20% survive to a second breeding season (Dickman and Vieira 2006).

The Robinson's mouse opossum, antechinus, and the large American opossums are known as R selected organisms, which means they mature and reproduce quickly, produce large litters with low survivorship and have relatively limited parental investment. On the other hand, koalas and kangaroos tend to be more akin to a K-selected species, meaning they have longer lifespans and mature slower, their young have a low mortality rate and higher survival rate, and the parental investment tends to be higher than that of r selected species (Post & Thompson, 2018).

Senescence is the process of aging or physiological deterioration over time. For some marsupials like the antechinus, this happens very quickly and predictably, whereas in others the process can be much slower with more variation. A study into northern brown bandicoot (*Isodon macrourus*) examined the lifespan, weight, and litter sizes of wild bandicoot. They found that lighter females were less fecund in their third reproductive season than heavier females; this result indicated that reproductive senescence had a greater impact on smaller females (Price-Rees et al. 2011).

### Predation

Antipredator behaviors are based on a variety of variables ranging from animal size, to resource distribution to habitat type.

Larger marsupials like the macropodids that occupy open pastures are able to congregate and form groups known as mobs for increased predator detection but also for the affect that central individuals will have a higher chance of escape than periphery ones. In western grey kangaroo (*M. fuliginosus*), the size of the group will correlate with the habitat type; the more open the habitat the larger the group; thus, the groups found in woodland areas will be smaller (Croft and Eisenberg 2006). Larger kangaroo species have few natural predators, today mainly dingos and man however in the past they would have been a main prey source for the thylacine (Figueirido and Janis 2011).

Smaller species who lack the ability to out run a predator will tend to live concealed lives and rely more on avoiding detection. Gumnivore species like the yellow bellied glider (*Petaurus*



**Marsupial Life History, Fig. 8** Virginia opossum in death feigning behavior. (Photo by Bruce MacQueen)

*australis*) live in forests and are exclusively nocturnal as their main food source of plant exudates tend to be found in uncovered areas.

Finally, one of the most famous antipredator behaviors of a marsupial is death feigning. Although many species will freeze on predator detection, few will “play dead,” there are only two known marsupial species to do this: the Virginia and the white-eared opossums. When a serious predator threat arises, the opossum will flop over on its side and assume a position with its tail curved in, eyes open, mouth open, and tongue extended (Fig. 8). It will also urinate and defecate and its heart rate and respiration will go down. When a study was done on the behavior, the dogs used to illicit this response did lose interest when the death feigning behavior occurred (Kimble 1997).

### Conclusions

Although there is an extensive diversity of marsupial species with many varying life history strategies, in regards to growth, survival tactics, and reproduction they do all share some commonalities. They must all seek a mate, give live birth to immature young, and all find a way to survive in their own niche.

The marsupial infraclass and our knowledge of it is expanding all the time; in 2014 two new

species of antechinus were added to the genus (*Antechinus vandycki* and *Antechinus swainsonii mimetes*). These dusky antechinus species were discovered in Tasmania and the Australian eastern mainland, and they too exhibit the extreme life history trait of males mating themselves to exhaustion and death (Baker et al. 2015). We are also still learning new things about the species that we do know exist, as it has just been recently discovered through fossil records that the marsupial moles (*Notoryctes*) of Australia were not originally desert dwelling species as they are today in fact prehistorically they were rainforest species (Archer et al. 2010). So with each new discovery we will be able to build up a bigger picture and greater understanding of the fascinating life histories of marsupials.

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## Marsupial Locomotion

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## Synonyms

Marsupial gaits; Metatherian locomotion; Pouched mammal locomotion

## Definition

Movement used by pouched animals (e.g., opossums, possums, koalas, kangaroos) to traverse their environment.

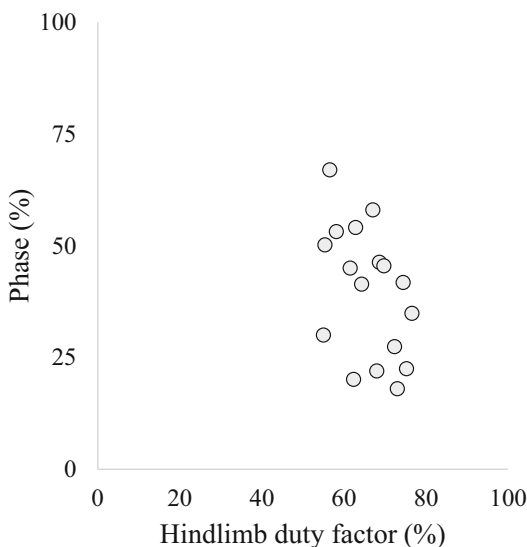
Marsupials, also referred to as the metatherians, are classified as mammals that typically carry their young in an abdominal pouch. The pouch (also known as the marsupium) is an external flap of skin that encases the nipples. The pouch is supported by the epipubic bone. Not all marsupials have this external covering. The marsupials differ from most other mammals because they give birth to very underdeveloped young that are still in the embryonic stage. Marsupials tend to spend less time growing in the womb and more time in the pouch. Due to the short gestation period, a placenta is not required to nourish the young. Instead, a large yolk sac is developed to provide nutrients to the embryo for three to seven weeks. Once the embryo enters the pouch, it is nourished through the mammary glands sometimes for nine months depending on the species (Cardillo et al. 2004; Horovitz and Sánchez-Villagra 2003).

There are roughly 300 different species of marsupials, and today are endemic to Australasia and the Americas. Marsupials are endothermic like placental mammals; however, they maintain a slightly lower core body temperature. Some marsupial exemplars include the kangaroos, wombats, koalas, wallabies, opossums, and possums. Australian marsupials can be further categorized with their diet. Dasyurids are meat consuming marsupials. This group includes the Tasmanian devil, dunnart, and mulgara. Peramelemorphs (e.g., bilbies and bandicoots) consume meat and plants. Diprotodonts (e.g., kangaroos, wallabies, and koalas) primarily consume plants (Cardillo et al. 2004). Syndactyly is a curious morphology of the foot found in many marsupials species (Horovitz and Sánchez-Villagra 2003). It is traditionally defined as a condition in which digits II and III of the foot are bound by skin and are reduced. From a locomotor perspective, the marsupials demonstrate a wide range of locomotor modes. This chapter will introduce terrestrial and arboreal locomotion, swimming, and gliding.



## Terrestrial Locomotion

The terrestrial gaits of marsupials can be divided broadly into quadrupedal and bipedal locomotion. The quadrupedal gaits of marsupials are consistent with other mammals. At low speeds, the lateral-sequence diagonal-couplet walk is most common (Fig. 1). This footfall sequence is inherently stable due to the generally low proportion of the stride spent as a unilateral bipod (~22%), and the relatively high proportion of the stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support). In general, foot positions arranged as diagonal bipods and large tripods are thought to be highly stable (Cartmill et al. 2002; Granatosky 2018b). It should be noted that both lateral-sequence lateral-couplet and diagonal-sequence diagonal-couplet gaits (see “[Arboreal Locomotion](#)” section below) are also present in marsupials. At higher speeds, trots (i.e., diagonal limb pairs move together with a slight aerial phase) and half-bounds (an asymmetric gait in which the hind left-right pair are in phase while the fore left-right pair are somewhat out of phase) are common (Pridmore 1992; Santori et al. 2005). Limb-loading is



**Marsupial Locomotion, Fig. 1** Hildebrand plot showing the relationship between hindlimb duty factor (%) and phase (%) for seventeen marsupial species

generally consistent across the quadrupedal marsupials. The forelimb serves a net-braking function and supports a majority of body mass. In contrast, the hindlimb serves to propel the body forward. Both limbs have low mediolateral forces, despite the semi-sprawling postures of many quadrupedal marsupials (Granatosky et al. 2020).

The natural habitats of most small marsupials are filled with heterogeneous substrates, including sloped terrain, rocks, and fallen and growing vegetation. However, most studies of marsupial locomotion have been conducted on flat runways. Lammers et al. (2006) collected data from gray short-tailed opossums (*Monodelphis domestica*) moving along level, inclined, and declined trackways instrumented with a force platform to understand how small terrestrial quadrupeds deal with the challenges of substrate heterogeneity. Patterns on the level terrain were typical for nonprimate quadrupeds: the forelimbs supported most of the body weight, forelimbs were net braking and hindlimbs net propulsive, and both limb pairs exerted small laterally directed impulses. On sloped substrates, *M. domestica* moved more slowly, suggesting a need for cautious locomotion. On inclines, both limb pairs were more protracted at touchdown and more retracted at liftoff, fore- and hind limbs had equal roles in body weight support, and the forelimbs exerted greater propulsive impulse than hind limbs. On declines, only the forelimbs were more protracted at touchdown. Additionally, forelimbs supported the great majority of body weight while they generated nearly all the braking impulse. These findings highlight that terrestrial locomotion is not always as simple as is often portrayed in the literature (see Granatosky 2018a), especially for small animals, and that the marsupials are capable of an impressive level of intrinsic locomotor plasticity in the face of mechanically challenging substrates.

The bipedal gaits of marsupials are most notable in the macropods (i.e., kangaroos and wallabies). The locomotion of a kangaroo is described as a hopping behavior. The two hind limbs are synchronized with each other and the forelimbs do not contact the substrate. The long tail is outstretched behind the animal and serves as a counterbalance. This type of locomotion



exemplifies the ability of the limbs to store and recover energy. At high speeds, kangaroo hopping ranks among the most energy efficient means of terrestrial locomotion. Much of this energy recovery has been attributed to the unusual set of anatomical features observed in the macropods. Tendons and ligaments located in the hind limbs and the tail of kangaroos provides the storage for elastic energy return. Furthermore, when kangaroos speed up, they do not increase the frequency of their hops, but rather stride length. The greater the length, the more energy they harness in their muscles and tendons after they touch down (Kram and Dawson 1998).

While the kangaroos and wallabies are best known for their hopping ability, these grazing animals spend much of their time moving slowly (Kram and Dawson 1998), and when they do so, the tail has an entirely different function. They plant it on the ground in sequence with their front and hind legs in a distinctive gait referred to as “pentapedal” locomotion, with the fifth point of contact being the tail. O'Connor et al. (2014) found that the tail is responsible for as much propulsive force as the front and hind legs combined. It also generates almost exclusively positive mechanical power, performing as much mass-specific mechanical work as does a human leg during walking at the same speed. Kangaroos use their muscular tail to support, propel and power their pentapedal gait just like a leg.

## Arboreal Locomotion

The exploitation of an arboreal environment provides access to diverse resources and minimizes risk from terrestrial predators. However, the diversity of available arboreal substrates (i.e., variable size, inclination, length, fragility, etc.) presents a demanding, discontinuous, and unpredictable three-dimensional environment that imposes important and differing constraints to arboreal marsupials. As such, arboreal marsupials have evolved a range of anatomical and biomechanical adaptations that have allowed them to navigate in trees safely and effectively (Karantanis et al. 2015; Schmitt and Lemelin 2002; Shapiro and Young 2010).

In an arboreal context, gait patterns may serve as a behavioral mechanism to enhance stability and safety (Granatosky et al. 2019). These gaits can be either symmetrical, when the left and right limbs of a pair alternate, or asymmetrical, when the left and right limbs move more synchronously. Diagonal-sequence gaits [hindlimb footfall is followed by a contralateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb)] contribute to dynamic stability in arboreal substrate navigation and reduce the periods of the stride where the limbs are arranged as unilateral bipod. These gait sequences have been observed in Woolly opossums (*Caluromys philander*), feathertail gliders (*Acrobates pygmaeus*), and koalas (*Phascolarctos cinereus*) (Gaschk et al. 2019; Karantanis et al. 2015; Schmitt and Lemelin 2002). In contrast, lateral sequence gaits may be functionally linked to static stability in substrate navigation and maximize the proportion of the stride where the limbs are positioned as a wide polygon of support. This is the strategy used by the sugar glider (*Petaurus breviceps*) (Shapiro and Young 2010). During arboreal locomotion, duty factor usually decreases on larger substrates (i.e., longer swing phase) along with an increase in the frequency of asymmetrical gaits (Granatosky et al. 2019; Karantanis et al. 2017).

Asymmetrical gaits, including gallops, half-bounds, and bounds, are commonly used by arboreal marsupials at high speeds and frequently include a whole-body aerial phase (Granatosky 2018b; Hildebrand 1980). It has been proposed that asymmetrical gaits may be preferable over symmetrical gaits during faster locomotion as they confer a reduction in the peak reaction forces, decrease the strain on the musculoskeletal system, and may optimize metabolic costs, at least at the trot-gallop transition (Hoyt and Taylor 1981). For small arboreal marsupials (e.g., *Dromiciops australis*, *M. domestica*, and *Lutreolina crassicaudata*), asymmetrical gaits further confer advantages in stability by limiting center of mass oscillations (Lammers and Zurcher 2011; Pridmore 1994; Santori et al. 2005).

Beyond categorical gait sequences, arboreal stability is also influenced by speed, which is a

function of stride frequency and stride length (Granatosky et al. 2019; Karantanis et al. 2017). Increased velocity during arboreal locomotion can be achieved either by increasing stride frequency, and decreasing stride length, by increasing primarily stride frequency and, at a lesser rate, stride length, or by reducing stride frequency while increasing stride length. Increasing velocity through increased stride length is often encountered in medium-sized and larger arboreal mammals. This enhances safety during arboreal locomotion as the longer reach of the forelimbs minimizes branch sway. In contrast, increasing velocity by stride frequency may be better suited for smaller arboreal marsupials, which are subject to insignificant branch sway, as it decreases body oscillations at limb touchdowns (Delciellos and Vieira 2007; Karantanis et al. 2015).

## Gliding

Some marsupials evolved the ability to glide using a membrane of skin called a patagium. Gliding is a simple and efficient form of gap-crossing that allows marsupials to reach substrates that can be quite far apart. There are four separate phases of gliding. At the first stage, the animal either drops in free-fall, or springs roughly horizontally and then drops in free-fall, with both cases having the purpose of obtaining air speed. In the next stage, the marsupial then exerts control over its movement through the air. Shortly after this point, locomotion may be unstable, but after the animal loses more height and raises its air speed, it can maintain steady aerial locomotion. An animal may fail to maintain constant velocity if either glide is short, or in longer glides an animal begins to shift in a different direction. In the final phase, as the animal prepares for landing, it begins to alter the air speeds of its body and adopts a body orientation suitable for landing. Gliding is usually considered to be quite energetically efficient. Work on sugar and feathertail gliders reveal that the cost of gliding is relatively higher than the cost of quadrupedal locomotion. However, when one considers the energy required to descend, cross the gap, and then ascend again, gliding likely

still has energetic benefits (Bishop 2007; Flaherty et al. 2008; Pridmore and Hoffmann 2014). Furthermore, gliding behavior likely reduces the risk of predation.

## Swimming

The thick tailed opossum *L. crassicaudata* is a semiaquatic species of the family of Didelphidae. During a swim cycle, *L. crassicaudata* uses all four limbs in a parasagittal plane, with emphasis on the hind limbs for propulsion. Forelimbs, however, are commonly used for rotational motion and balance. In the power phase, the hind limbs accelerate posteriorly and ventrally, while the digits are abducted and extended. During paddling motion, *L. crassicaudata* shows a homolateral gait; power phase of the forelimb is followed by power phase in the hind limb of the same side of the body. Fur bearing species such as *Didelphis* are presented with a number of issues when swimming. The most apparent of which is the lack of proper buoyancy, due to uptake of water by the fur. Ultimately, this results in horizontal displacement of the body, with compensation needed from the forelimbs to counteract the effect of reduced buoyancy. To ensure adequate breathing during the power phase, *Didelphis*' movement of the forelimbs resulted in upward movement of the nose above water as well (Fish 1993; Santori et al. 2005).

## Conclusion

As a group, the marsupials have evolved a range of locomotor behaviors almost consistent with placental mammals (i.e., no powered flight, obligate swimming, brachiation, or striding bipedalism). They use both quadrupedal, bipedal, and even pentapedal (tail acting as a fifth limb) gaits when moving terrestrially. They are adept at arboreal locomotion, and even use many of the same gait characteristics as the primates (Granatosky 2020). Some marsupial species are even capable of swimming and gliding. Despite this wide range of locomotor

behaviors, the marsupials have largely been ignored as a group compared to their placental counterparts. As such, there remains much to be learned about the locomotor behaviors of this mammalian group.

## Cross-References

- Activity Budget
- Adaptation
- Adaptedness of Behavior
- Adaptive Radiation
- Arboreality
- Basal Metabolic Rate (BMR)
- Canopy
- Captivity
- Common Ancestor
- Dispersal Ability
- Dispersal Patterns
- Diurnality
- Ecology
- Evolution
- Extinction in Learning
- Gait
- Herbivore
- Home range
- Homology
- Homoplasy
- Locomotion
- Marsupial Cognition
- Marsupial Diet
- Marsupial Life History
- Marsupial Morphology
- Morphology
- Muscular System
- Natural Selection
- Navigation
- Paleontology
- Pets
- Phylogeny
- Quadrupedal
- Species
- Taxa
- Terrestrial
- Vertebrate Nervous System
- Zoo
- Zoology

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## Marsupial Morphology

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## Definition

- |            |                                                                                    |
|------------|------------------------------------------------------------------------------------|
| Marsupial  | Group of mammals which may have a marsupium pouch to carry their young             |
| Morphology | The biological category concerning size, shape, and general structure of organisms |

## Introduction

Marsupials are a group of mammals mainly characterized by their distinct reproduction. They have a short gestation period followed by an extensive lactation, sometimes inside a pouch, also called marsupium. Despite what the group name implies, several marsupials do not have a pouch. Another interesting characteristic is that all marsupial neonates are altricial, which means that they have an incipient state of development at birth. Young are born excessively small, blind, and without fur but with the ability to climb the mother's inguinal region until they find a teat to attach to and complete its development.

The earliest fossil known of metatherians (mammals most closely related to marsupials than placentals, besides modern marsupials) is from the early Cretaceous of Asia (Kielan-Jaworowska et al. 2004). However, there are few well-preserved records of late Cretaceous metatherians with complete skulls and/or skeletons; most are composed only by jaw fragments and teeth, which already show similarities with modern marsupials. After the mass extinction at the Cretaceous-Paleogene boundary, several metatherian families were extinct. Still in the late Cretaceous, North American opossums from the Didelphimorphia order have a rich fossil record until the middle Miocene. During the Cenozoic, marsupials migrated to southern continents and

spread throughout South America, probably including Antarctica and Australasia regions. The Oceania isolation in late Eocene allowed a great diversification of marsupials, with animals of very different sizes, shapes, habits, and habitats. At first glance, it looks like marsupials are phylogenetically split due to geographical distribution: the cohort “Ameridelphia” (a paraphyletic group that occurs in the Americas) and cohort Australidelphia (a monophyletic group that mainly occurs in the Australasia region). In fact, this division was first proposed by the tarsal morphology of calcaneum and astragalus bones (Szalay 1982), lumping one order found in South America with the Australian marsupials. This classification is still used today and is corroborated by several morphological and molecular phylogenetic analyses.

The cohort “Ameridelphia” is represented by two orders, Didelphimorphia and Paucituberculata. The first one occurs in diverse habitats ranging from southern Canada to Argentinian Patagonia, and the latter occurs in high altitudes of the Andes Mountains, northern and western South America (Astúa 2015; Patterson 2015). The cohort Australidelphia is represented by five orders: Dasyuromorphia, Diprotodontia, Notoryctemorphia, Peramelemorphia, and Microbiotheria. Most of them occur in the Australasia region (Wilson and Mittermeier 2015), except for the Microbiotheria order, which belongs to the Australidelphia cohort although it is present only in South America, in southern Andean forests. This latter is also considered an Australian or Antarctic radiation survivor.

This entry will be categorized into three important topics of (I) morphological design; (II) dentition; and (III) reproductive system and biology. In each topic, the group identification could be by the cohorts or by the orders of marsupials, to facilitate the understanding of their general morphology. The information provided in these sections were mainly based on Vaughan et al. (2000), Szalay (2006), Gardner (2007), Flores (2009), Pough et al. (2012), Feldhamer et al. (2015), and Wilson and Mittermeier (2015). Additional or specific data will be presented with its respective reference.

## Morphological Design/General Morphology

### Skull

The marsupial skull is generally characterized by its tight and small braincase and a flared narrow long nose. When the bone is present, they have ossified auditory bullae that are formed predominantly by the alisphenoid bone instead of the tympanic, basisphenoid bones and/or petrosal, similar to most eutherian mammals. Marsupials do not present the postorbital bar (bone bar behind the orbit), while the jugal bone comprises portions of the jaw glenoid. The palate is very distinct, with a characteristic large vacuity in the posterior part. The angular process of the dentary bone is normally inflected medially and is not present in eutherian mammals, being a synapomorphy of marsupials.

### Skeleton

Most marsupial skeletons barely resemble eutherian skeletons and their morphology are often compared. Notwithstanding, there are a few important differences between them.

In the Australian marsupial foot, a strong unification of digits II and III by the skin, also known as syndactyly, is present in all species from the Diprotodontia and Peramelemorphia orders. The true ecomorphological function of this phenotype is still subject to discussion.

Another feature frequently considered as unique within marsupials are the epipubic or marsupial bones, paired bones articulated in the pubic symphysis, in the pelvic girdle. These bones are ventrally projected to the front of the belly and were considered, for a long time, to function only as a marsupium pouch support. However, there are registers of epipubic bones in monotremes (platypus and echidnas) and also the cyodonts, the non-mammalian group that originated modern mammals. The latter were and oviparous species that did not carry their young during development. Besides that, it is known that these bones, in addition to two extra muscles, perform a cross-couplet linkage during marsupial locomotion (Reilly and White 2003). These two non-



excluding hypotheses for epipubic bone function continues in discussion.

### Ameridelphia Morphology

The Ameridelphia group is composed of two orders, Didelphimorphia and Paucituberculata. They are small to medium size opossum-like marsupials with very conserved characteristics. Considering the Didelphimorphia order (Fig. 1), they have a long snout with many vibrissae, round eyes, and big flattened ears. The coloration is variable, with individuals presenting dark gray or brown tones, with some having a cream-colored belly. Some species with lighter shades may be brownish-orange and white, with details in black or gray, especially in eye masks. Body length ranges from 10 to 95 cm and can be as light as the 30 g *Tlacuatzin* or as heavy as the 5.9 kg *Didelphis*. Body shape may be associated with its locomotion habit. Terrestrial and scansorial species tend to be elongated while walking and form a lumbar curve when sitting, standing, or jumping. Arboreal species are likely to walk with the limbs flexed because of their gravity point, which needs to be closer to the substrate (Argot 2001). The contrasting animal in this group is the unique and truly semiaquatic marsupial species, *Chironectes minimus*. With a hydrodynamic body, dense and -water-repellent fur and also a webbed feet, is the most adapted didelphid to swim. There are no fossorial or gliding marsupials in this group. All

Didelphimorphia have a prehensile tail, but it may be short, as in the short-tailed opossums *Mondelphis*, long or fat as in the fat-tailed opossum *Thylamys*, and especially thick, as in the thick-tailed opossum *Lutreolina*. In Didelphimorphia, the skull is homogeneous, with a few differences related to size and shape, preserving their general morphology. The rostrum is long and the sagittal crest is prominent. *Caluromys* shows a rounded palate, where a shift in orientation occurs between the upper post-canine rows and the development of a strongly curved post-palatine torus, which are not known for any other marsupial so far (Flores et al. 2010). Their feet are plantigrade, and all species have an opposable and clawless thumb, being probably inherited from arboreal ancestors.

The Paucituberculata order (Fig. 2) is known as a small and terrestrial shrew-like opossum due to its long snout and small eyes. They have a distinct lip flaps right below and anteriorly from the vibrissae, and also flattened ears smaller than Didelphimorphia. Their feet are unspecialized (not fused) and do not have opposable thumbs. The tail is not prehensile and can store fat seasonally, expanding from 4–5 mm (in diameter) during summer to 9–11 mm in the winter. Their size generally ranges 15–25 cm, and they can weigh 25 g as in the Dusky shrew opossum (*Caenolestes fuliginosus*) and up to 53 g as in the Sangay shrew opossum (*Caenolestes sangay*). The dorsal coloration does not diverge from black, gray, and dark brownish and they could or could not present a whitish belly.

M



**Marsupial Morphology, Fig. 1** White-eared opossum, *Didelphis albiventris*, representing the Didelphimorphia order. Photo: Fernando Perini



**Marsupial Morphology, Fig. 2** Shrew-opossum *Lestoros inca*, representing the Paucituberculata order. Note the unique lip flaps. Photo: Bruce Patterson

### Australidelphia Morphology

As mentioned earlier, the Oceania isolation during the Cenozoic Era supports the significant diversification of Australian marsupials, when compared to American marsupials. In Australian marsupials, their entire body can be remarkably different, even in the same order or family. They also have huge differences in size. The smallest ones are the pygmy possums, ranging from 5 to 12 cm, and they could weigh between 10 and 50 g. The largest ones are the red kangaroos, with up to 2 m height and a body mass up to 90 kg. To comprise all these distinct designs, this section will be divided according to their orders and main differences.

#### Dasyuromorphia

This order comprehends two families, Dasyuridae and Myrmecobiidae. Dasyuridae (Fig. 3) are known as carnivorous marsupials, and some of them have similar skull to Didelphimorphia order. Their forefoot has five digits, and the hindfoot can have four or five digits, with a clawless thumb that could be vestigial or absent in some cursorial genera, such as the Tasmanian devil, *Sarcophilus*. Except for the long-limbed jumping kultarr (*Sminthopsis laniger*) and the cursorial quoll (*Dasyurus viverrinus*), they all have plantigrade posture. The tail is never prehensile. Their sizes range from 10 cm and 3.6 g in

very small possums as Planigale, with 10 cm and 3.6 g to Tasmanian devils (*Sarcophilus*) that can reach 131 cm and weights up to 14 kg. Myrmecobiidae is represented for only one species, the numbat. It is a slender and small long-nosed anteater, with a long, narrow and sticky tongue to capture termites. The species have a colorful dorsum with an orangish, black, and gray gradient, with well-marked lighter strips and a non-prehensile tufted tail.

#### Diprotodontia

The most diverse order of marsupials have several and extensive radiations. It is comprised of 11 very distinct families (Wilson and Mittermeier 2015), organized in 3 suborders: Vombatiformes, Phalangeriformes, and Macropodiformes (Fig. 4).

Vombatiformes comprise the koalas and the wombats. Koalas can range up to 82 cm length, and males can be two times heavier than females. The species significantly changes between South Australia population, which are heavier and darker than North and East Australia population. They have rounded tufted ears, a large and flat nose, and eyes with a vertical iris. They have opposable clawless thumbs and a rudimentary tail. The fur is mostly gray on the dorsum and white belly, with dark brownish tones on the rump in southern populations. Wombats resemble a terrestrial and burrowing koala, with smaller ears and short and large nose. They could be up to 115 cm in length and 30 kg, and pelage can be gray or brown, some with yellowish tones. In contrast with the koala, they have a poorly developed cecum and produce cubic feces.

Phalangeriformes have five families which include arboreal primate-like forms as cuscuses and large opossums; great, lesser, and feather-tailed gliders; pygmy possums; and the exclusive nectarivorous marsupial, the honey-possum. They are medium-small sized, ranging from 10 cm to 1.2 m length, and can weight up to 4.5 kg. The fur color greatly varies between the families, and they can be dorsum-striped as gliders and honey-possums, or with exceptionally different spotted patterns as several cuscuses, white with gray, black, and also brown yellowish stains on



**Marsupial Morphology, Fig. 3** Tasmanian-devil, *Sarcophilus harrisii*, representing the carnivorous marsupials from Dasyuromorphia order. Photo: Gabby Guilhon



**Marsupial Morphology, Fig. 4** Vombatiformes as the koala (*Phascolarctos cinereus*) and Macropodiformes as the red kangaroo (*Osphranter rufus*), representing the Diprotodontia order. Photos: Gabby Guilhon

the dorsum. Some of them have a prehensile tail as in the ring-tailed opossum. In the two glider forms, the gliding membrane is formed by strong connective tissue from the elbow to the ankle, comprising all the lateral side of the body.

Macropodiformes are the hopping marsupials, including bettongs, potoroos, musky rat-kangaroos, wallabies, and kangaroos. They all have short forelimbs and large hindlimbs and hindfeet. The first two represents the Potoroidae family; they are small, ranging from 55 to 85 cm and up to 3 kg. It can present greyish, brownish, or yellowish dorsum fur, with a lighter belly. They have medium furred ears, small eyes, and naked nose. The tail can be prehensile. The third mentioned, musky rat-kangaroos are the smallest macropodiformes ranging up to 45 cm and 0.5 kg. The body fur is mostly orangish brown, with a prehensile naked tail, short naked ears, and small rounded eyes. The rostrum is short. The last two forms, wallabies and kangaroos, are lumped in Macropodidae, the largest family in the order Diprotodontia. They can reach up to 2 m in height and weigh 90 kg in the red kangaroos. They could be terrestrial or arboreal, with a huge variation on pelage color, varying from homogeneous gray to flashy yellow and brownish as in some tree-

kangaroos. Sexual dimorphism of size is notable, with males significantly heavier than adult females. Males can also be very muscularized, which serves the purpose of being able to box with other males, for sexual competition. The rostrum is long, usually, and they have movable large ears, and eyes size can vary. The tail is robust and provides equilibrium during rapid bipedal hopping locomotion. Their big rump is useful as low gravity center to help them maintain balance while jumping.

#### Microbiotheria

In this order, there is only one extant species, the monito del monte *Dromiciops gliroides* (Fig. 5). The species is small, 15–25 cm in length and weighing up to 32 g. Their snout is short when compared with other opossums, with medium-sized ears and eyes, the latter with a rounded well-marked mask. They have dense body fur with a blended pattern color with a white venter and a mixed cream, yellow, brown, and grayish dorsum. The tail is semi-prehensile, and it stores fat, in case of food scarcity and/or cold temperatures to enter in a period of hibernation (Rageot 1978; Palma and Valladares-Gómez 2015). They have a greatly enlarged tympanic bullae which





**Marsupial Morphology, Fig. 5** *Dromiciops gliroides*, the only extant member of the Microbiotheria order. Photo: P. L. Meserve, ASM Image Library



**Marsupial Morphology, Fig. 7** Long-nosed bandicoot *Perameles nasuta*, representing the Peramelemorphia order. Photo: J. Hall, ASM Image Library



**Marsupial Morphology, Fig. 6** Marsupial mole, *Notoryctes* sp. representing the Notoryctemorphia order. Photo: P. Aitken, ASM Image Library

includes an ectotympanic bone, an unknown feature among other marsupials (HersHKowitz 1992).

#### Notoryctemorphia

This noteworthy order is represented by the unique marsupial mole (Fig. 6), presenting many congruent characteristics with eutherian moles. The species is small, completely blind with vestigial eyes covered by skin, the ear does not have a pinnae, and the nose is similar to a hard shield with a slim incision. Limbs are robust, spread positioned and closer to the ground, like a “sand-swimmer”, with their main specializations concentrated in (but not restricted to) the forelimb (Warburton 2006). The fore claws of digits III and IV are greatly expanded and spade-shaped, while in the hindfeet the first digit has a nail; the II,

III and IV digit are enlarged; and the fifth digit is vestigial. Five cervical vertebrae are fused to stiffen the neck while digging and epipubic bones are reduced. The fur is long and bright white or yellowish red due to sand stains (Aplin 2015).

#### Peramelemorphia

This order comprises bandicoots and bilbies (Fig. 7). Both present non-prehensile tails and lack clavicles. Bandicoots have a slender rostrum with very lengthy nose. The smallest bandicoot can weigh up to 100 g and the largest up to 5 kg. In general, they have dorsum fur darker than the belly, and the dorsum can vary from gray to orangish brown. They present short forelimbs with the II, III, and IV digits well developed with claws and elongated hindlimbs with a very prominent fourth digit. Bilbies can range from 50 to 85 cm in length, and sexual dimorphism in size is evident; males can range to twice the size of females, up to 2.5 kg. Due to its hopping habits, and long nose and ears, they resemble a rabbit. Therefore, they are a surrogate of Easter bunnies. Australians celebrate the “Easter Bilby” instead. They have silky and mostly gray fur on the dorsum and a white belly, with a tufted tail abruptly divided anteriorly in black fur and posteriorly in white fur.

#### Dentition

The marsupial molar teeth are tribosphenic or tritubercular, due to three sharp and large cusps

disposed in a triangular pattern. Upper molars are formed by the paracone, protocone, and metacone cusps. Lower molars, otherwise, have a paraconid, protoconid, and metaconid as sharp cusps. Nevertheless, particularities of marsupial dentition different from eutherians are a well-developed styler shelf present only on the upper molars in the labial side.

Marsupials have a particular pattern of dentition, with distinct numbers of upper and lower incisors. Primary (deciduous, “milk-teeth”) incisors and canines are vestigial and never erupt, being reabsorbed when the secondary teeth (“permanent-teeth”) erupt. The first and second premolars are deciduous and caniniform, the permanent form does not develop. The third premolars have two forms, the first is a deciduous (“milk teeth”) molariform teeth and also represented as dP3. This form helps the young to shift their feed pattern from liquid to solid and starts mastication activity. As the animal grows up and other molars develop, the second form appears as a permanent caniniform premolar (or P3), that erupts and takes place in the occlusal plane. Sometimes the dP3 is not lost immediately after the P3 eruption, so it is common to find both teeth coexisting for a while in the jaw. The four molars are unreplaced primary teeth (Cifelli and Muizon 1998). The general dental formula of the cheek teeth in marsupials is three premolars and four molars, usually represented by  $P3/3$  and  $M4/4$  or  $P_3^3$  and  $M_4^4$ .

### Ameridelphia

The dental formula of Didelphimorphia is I 5/4, C 1/1, P 3/3, M 4/4 = 50. They have small, delicate and unspecialized incisors, canines are robust and large, and molars do not have critical changes. Although their feed habits are highly diverse, it is not strong enough to override the pre-existing morphological differences in molar shape that occur among didelphids (Chemisquy et al. 2015).

In Paucituberculata, the dental formula is I 4/3-4, C 1/1, P 3/3, M 4/4 = 46 or 48. The distinguishing feature about them is their first lower incisors that are strongly procumbent and

large, while the others incisors, the canine, and the first premolar are narrow and unicuspid. Their lower incisors are used like rapiers to stab prey (Kirsch 1977), and it appears to be homologous with the second lower incisors of didelphids.

### Australidelphia

#### Dasyuromorphia

The dental formula is I 4/3, C 1/1, P 2-3/2-3, M 4/4 = 42 or 46. They have small, pointed or blade incisors with large sharp-edge canines. Their upper molars have three sharp cusps that are adapted to an insectivorous and carnivorous diet.

#### Diprotodontia

The name of Diprotodontia order is due to their modified lower incisors, which are procumbent and project forwardly, similar to rodents (Greek *di* = two, *proto* = first and *dont* = tooth). This order is comprised of herbivorous and omnivorous extant forms. Their dental formula is variable within the families.

In Vombatiformes, the dental formula of koalas (Phascolarctidae) is I 3/1, C 1/0, P 1/1, M 4/4 = 30 and in wombats (Vombatidae) is I 1/1, C 0/0, P 1/1, M 4/4 = 24; in the latter, teeth are open-rooted and grow continuously, unique in marsupials and similar to rodents.

In Phalangeriformes, the pygmy possums (Burramyidae) dental formula is I 3/1-3, C 1/0, P 2-3/2-3, M 3-4/3-4 = 30-42, with the first incisor much larger than the other two. In cuscuses and possums (Phalangeridae), dental formula is I 3/2, C 1/0, P 2-3/2-3, M 4/4 = 36-40, with a second deciduous premolar. Ring-tailed and greater gliders (Pseudocheiridae) have I 1-3/1-2, C 1/0, P 1-3/1-3, M 4/4 = 26-40, while lesser gliders (Petauridae) have I 3/1-2, C 1/0, P 3/1-3, M 4/4 = 34-40, with the three premolars single-cusped and crest-shaped crowns in molars. The tiny honey possums (Tarsipedidae) have fragile jaws that are not able to chew, and the dental formula is reduced due to its nectarivorous habit, I 2/1, C 1/0, P 1/0, M 3/3 = 22. Feather-tailed gliders (Acrobatidae) have uncertain dental formula, usually I 3/1, C 1/1?, P 3/3?, M 3/3 = 36, and can differ from feather-tailed possums.



In Macropodiformes, the dental formula in the Potoroidae is I 3/1, C 1/0, P 1/1, M 4/4 = 30, with first incisors larger than the other two and short diastema, with well-developed upper canine and a large blade-like premolar. In Macropodidae the dental formula is variable, I 3/1, C 0-1/0, P 1/1, M 4/4 = 28-30, with upper incisors and procumbent lower incisors usually well-developed. They have a long diastema and are lophodont, with high-crowned molars.

#### Microbiotheria

The dental formula is the same as the American order Didelphimorphia, but their lower canines are smaller than the didelphids. The four lower incisors are uncrowded and evenly spaced in line (Hershkovitz 1992).

#### Notoryctemorphia

Their teeth are unusually separated from each other. The dental formula is variable, I 3-4/3, C 1/1, P 2/2-3, M 4/4 = 40-44. Incisors, canines, and premolars are unspecialized, unicuspid, and little sharp, while the last upper premolars have two cusps (bicuspidate). The upper molars are tritubercular and the lower molars lack a talonid.

#### Peramelemorphia

They are characterized in general by their insectivorous sharp dentition and also are polyprotodont, with four or more incisors on each side of the jaw. The general dental formula is I 5/3, C 1/1, P 3/3, M 4/4 = 46-48, but *Echymipera* bandicoots have only four upper incisors. Peramelemorphians have small incisors and well-developed canines and molars which can be tritubercular or quadritubercular, with fewer cusps.

## Reproductive System and Biology

Marsupial general anatomy is commonly compared with some eutherians, due to size and shape similarities. The reproductive apparatus of these two groups, however, is remarkably different.

In females, the oviducts are separated by the ureters, in other words, the ureters pass in between the oviducts. This impedes the oviducts from meeting in the middle to form a single median uterus and vagina, one of the limiting features that possibly explains the small size of marsupial neonates (Renfree 1993). The reproductive tract consists of two lateral vaginae only for sperm passage, and it is connected anteriorly, following the end of the uteri. During the first birth, a median vagina or pseudovagina is formed, a canal only for the neonate passage. Concerning the placenta, it is commonly stated that marsupials do not have one. In fact, all marsupials and some eutherians have a rudimentary choriovitelline placenta, which is developed from the yolk sac and considered as a primitive placenta. Bandicoots, koalas, and wombats develop an intermediary chorioallantoic placenta in late gestation, formed from the union of chorionic and allantoic amniote membranes, similar with eutherians placenta.

In most males, the penile glands is bifid, to fit in the two lateral female's vagina. Unlike eutherians, peduncular testicles from marsupial males are in front of the penis. An interesting exception occurs in the marsupial mole (Notoryctemorphia). Due to its digging habit, the testes are located inside the body, between the abdominal wall and the skin, so there is no visible scrotum. In American marsupials, males do not have seminal vesicles, ampullary, or preputial glands, as seen in eutherians. In *Didelphis*, the gonadal differentiation occurs early, with 9 days in the marsupium as altricial neonates. At this same time, the scrotum and the marsupium (in females) are visible in the young (Nogueira 2006). In Microbiotheria, the scrotum has a very short peduncle, being almost sessile.

Both sexes present an external cloaca instead of a separated reproductive and excretory apparatus, except the male of the American water opossum (*Chironectes*), which lacks a cloaca and has separated anal and urogenital openings (Nogueira et al. 2004). In Microbiotheria, the cloaca is significantly different, opening on the ventral side of the base of the tail, as occurs in monotremes (platypus, equidnas) and also in reptiles.

## Pouches

The name marsupial comes from the marsupium/pouch, a structure in the abdomen to keep and protect the litter during external development. Although it is expected that all marsupials have pouches, due to iconic kangaroos with their well-developed pouch, many of them do not have a marsupium, especially the American marsupials. This structure has several morphological changes during reproduction, such as change in color, size, and shape, and could secrete fluids (Hesterman et al. 2008). This variation also occurs in pouchless species but in the female inguinal region in both Australian and American marsupials (Calaby and Taylor 1981; Guilhon et al. 2019).

In Didelphimorphia, the pouch is present only in medium-large opossums (6/18 genera) as *Didelphis*, the woolly-possum *Caluromys*, the black-shouldered opossum *Caluromysiops*, thick-tailed opossum *Lutreolina*, and the black four-eyed opossum *Philander*. The brown four-eyed opossum *Metachirus* has a similar size but lacks a pouch. The water-opossum *Chironectes* is the only American marsupial in which both sexes have pouches and it is notably specialized: a sphincter is responsible for closing females' pouches, sealing it entirely and preventing incoming water. On the other hand, male pouches protect their scrotum from water and cooling, keeping spermatogenesis at the optimum level. No other species in the Didelphimorphia and Paucituberculata orders have pouches, maintaining their litter in the inguinal region during the teat-attachment phase, and avoiding moving long distances with the neonates. After this first development phase, the female leaves the nestlings unattended while foraging. In Microbiotheria, females of the only extant species *Dromiciops gliroides* possess a pouch with four nipples. A further characteristic of this order is that pouch-young males lack mammary anlagen (the first discernible group of cells destined to form a mammary gland) during development, classified as another morphological feature shared only with Australian marsupials (Frankham and Temple-Smith 2012).

Most of the Australian marsupials, however, have pouches, in variable forms. It could be well-developed as in several diprotodonts (e.g.,

kangaroos, wallabies, koalas, wombats, etc.), poorly developed (e.g., some dasyurids) or absent (e.g., sugar gliders, mouse opossums, honey-opossum). The extinct Tasmanian tiger *Thylacinus* had pouches in both sexes. In females, the pouch opening was faced posteriorly, while males had a rudimentary pouch, believed to protect the penis and scrotum during cursorial running. Posteriorly oriented pouch openings in females can have several functions, as in wombats, who can continue to dig with pouch-young, protecting them from the dirt entering. This also occurs in the mole *Notoryctemorphia*, in which a fold in the abdominal wall divides the pouch into two compartments, and each one contains a nipple (Grassé 1955). In males, the marsupium is sometimes inconspicuous, consisting of a slight transverse skin fold that resembles the internal conformation of the female's pouch.

## Neonates

Marsupial newborns are altricial (Fig. 8), which is characterized by the pup being blind and hairless, with a very reduced mobility and with a high chance of not surviving without maternal parental care. The neonate is born with the minimum anatomical development necessary to live outside the uterus: mouth, forelimbs and deciduous claws, being able to climb the female's inguinal region to find a teat and attach to it until its development is completed. This teat-attachment phase is variable among



**Marsupial Morphology, Fig. 8** Altricial neonates from *Didelphis albiventris*, blind, hairless and with a very reduced mobility. Photo: Diego Astúa

species but always exceeds the gestation period. The number of nipples and litter size are not always compatible. The number of nipples varies from 2 in Notoryctemorphia and some Dasyuromorphia to more than 12 in Didelphimorphia species. Individual variation in this number also occurs within a species. This expresses a very selective phase for the newborn, in which only the first one able to find a teat will survive.

## Conclusions

Marsupials are a group of mammals characterized by their peculiar reproductive strategy, with a short gestation period and a long period of post-partum development and lactation, which could happen inside a marsupium pouch. They are commonly divided in two groups, American and Australian marsupials. The first represents the generalized opossum-like forms, weighing from 30 g to 5.9 kg, terrestrial, arboreal, scansorial and containing the only truly water-adapted opossum. Most of them are small and pouchless species with similar skull/skeleton and dental formula, usually appropriate to an omnivorous diet. Australian marsupials, however, are more diverse in size and shape, including kangaroos, koalas, sugar gliders, marsupial rats and marsupial moles, weighing from 10 g in the honey-opossum to 90 kg in the red kangaroo. Their skull and skeleton can be significantly different from each other. Most of them have pouches, which could be well or poorly developed, with posterior or anterior openings. All female marsupials possess two lateral vaginae for reproduction, and one medial pseudovaginal canal developed only for the neonate birth, while most male marsupials have a bifid penile gland, positioned posteriorly to their scrotum. The marsupial young are born in a very altricial state, blind, hairless and with very low mobility, highly dependent of the maternal care to survive.

## Cross-References

- [Marsupial Life History](#)
- [Marsupial Locomotion](#)
- [Suckling/Nursing](#)

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## Martens

### ► [Mustelid Communication](#)

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## Martha Alice Helson

### ► [Martha Helson Wilson](#)

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## Martha Helson Warren

### ► [Martha Helson Wilson](#)

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## Martha Helson Wilson

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## Synonyms

[Martha Alice Helson](#); [Martha Helson Warren](#)

Martha H. Wilson (1929–2010) was a member of one of the most influential families in psychology. Her father was Harry Helson (1898–1977), who received the Distinguished Scientific Contribution Award of the American Psychological Association in 1962, among other career awards, in part for his development of Adaptation Level Theory. Her husband of 62 years was William August (Bill) Wilson, Jr. (1924–2017), who earned M.D. and Ph.D. degrees before a long and productive career in biopsychology and

neuroscience. Martha's older brother Henry, a professor of mathematics, married Ravenna Mathews Helson (1925–), a leading scholar in the psychology of women and the study of personality across the lifespan. As for Martha Wilson, she made significant and lasting contributions to physiological and comparative psychology, both through scholarship and leadership. She was a long-time professor of psychology and behavioral sciences at the University of Connecticut who studied the physiology of vision, discrimination learning, and category learning in rhesus monkeys (*Macaca mulatta*) and bush babies (*Galago*). She was also elected to lead the discipline in numerous roles, including as the 1986–1987 President of the Division of Physiological and Comparative Psychology (Division 6) of the American Psychological Association.

## Personal and Professional History

Martha Alice Helson was born January 7, 1929, 18 months after her brother Henry, to Dr. Harry and Lida G. (nee Anderson) Helson (1900–1979?). Martha Alice was practically raised on college campuses, principally at Bryn Mawr where her father was professor of psychology for many years. Her mother had earned undergraduate and master's degrees in French literature before marrying; later, she authored several published remedial-reading texts, workbooks, and teacher manuals. When World War II broke out, Dr. Helson moved his family to Foxboro, MA, for several years to work on Navy-funded human-factors research. Martha Alice was sent back to a Quaker boarding school in Pennsylvania, where she would graduate from Westtown Friends School in 1946 before enrolling in Bryn Mawr College.

Martha was encouraged by her father to prepare for a career as a psychiatrist to bring scientific rigor to the area that was still dominated by psychoanalytic thought, and indeed she completed all of the coursework required for admission into medical school. However, Martha gravitated to psychology, which used research methods from the natural sciences for investigating the behavior

of living organisms. Her own independent research program began during these years, as she undertook a study of color vision under the supervision of physics professor Walter C. Michaels. In 1950, Martha H. Warren – prior to her senior year, she had married Robert Warren, Jr., whom she had met at a Quaker work camp – graduated with honors with a degree in psychology from Bryn Mawr.

The years between undergraduate and graduate school were momentous for Martha, both professionally (e.g., she worked on a research project that resulted in her first two scholarly publications: Helson et al. 1952, 1956) and personally (e.g., she gave birth to a daughter, her marriage ended). In 1952, she enrolled at Yale University for doctoral study in psychology, working initially there with Dr. Lloyd Beck and Dr. Walter Richard Miles. In her second year at Yale, Martha met Dr. Burton S. Rosner, an assistant professor in need of a research assistant to help with a funded project to study the neural signals corresponding to tactile stimulation in guinea pigs and rabbits. Although physiological psychology was a new area for Martha, she embraced the topic without hesitation. After a year in this research project, Martha planned to develop a dissertation project under Professor Rosner's direction on somatosensory mapping; however, an opportunity to develop her skills in electrophysiology at the Hartford (CT) Institute for Living changed those plans.

At the Institute, Martha met a powerhouse team of scientists at the Laboratory of Neurophysiology, directed by Dr. Karl Pribram. Other scientists in Pribram's laboratory included new Ph.D.'s Mortimer Mishkin and Larry Weiskrantz, and a new M.D. named William A. (Bill) Wilson, Jr., who would receive his Ph.D. from Berkeley the following year. Each of these men would profoundly impact the science of brain and behavior, but two would have a particularly large influence on Martha herself: Dr. Pribram became her mentor, collaborator, and friend across her career. Dr. Wilson, also a life-long collaborator, became the love of her life, husband of 62 years, and father of her children. Martha and Bill married in 1954. Martha worked at the Institute for Living from that same year until 1959.



After learning neurosurgery in Hartford, Martha changed her dissertation topic to an attempt to link structure and function in the posterior association cortex of the rhesus monkey brain. Her 1955 dissertation, titled *Effects of circumscribed cortical lesions upon somesthetic and visual discrimination in the monkey*, was approved by a committee consisting of Professors Rosner, Pribram and Frank A. Beach. The study linked the inferior temporal region to visual but not somatosensory discrimination learning, and posterior parietal cortex to tactual but not visual discrimination. The work was subsequently published in *Journal of Comparative and Physiological Psychology* (Wilson 1957).

In 1958, Bill accepted a faculty position at the University of Colorado, and so Martha and Bill moved with the children to Boulder. Martha was appointed Visiting Professor and began teaching while writing-up data collected in Hartford (Wilson et al. 1960). Research facilities were not ideal, however, and an offer to Bill from Dr. M. E. Bitterman, chair of psychology at Bryn Mawr brought the Wilson family “home” to Martha’s alma mater. Martha accepted a research associate position on Bill’s NIMH-funded project, studying visual and tactual learning-set formation in a laboratory with nearly 100 monkeys (Wilson and Wilson 1962; Wilson et al. 1963; Wilson and Wilson 1964). She also taught at nearby Rosemont College. The research and publications continued when the Wilsons moved the project, and their family, to the University of Connecticut in 1964 (e.g., Oscar and Wilson 1966; Wilson et al. 1968).

Dr. Martha Wilson spent the remainder of her career at the University of Connecticut, until her retirement in 1987. For the first 9 years, she remained in a full-time research position, conducting experiments in the rhesus monkey laboratory that UConn had built for the Wilsons in Storrs. When the Wilsons returned from Bill’s 1972 sabbatical-year visit to Duke University – during which time Martha worked as a NIMH research fellow with Dr. Irving Diamond on a study of the neural mechanism of visual attention in bush babies (e.g., Soper et al. 1975) –, Martha was appointed as Professor of Psychology at the

University of Connecticut. The faculty position allowed Professor M. Wilson to teach and mentor students, and to apply for grants as principal investigator. Soon, she had obtained a large grant from the National Science Foundation, established a bush baby colony in Storrs, and began studying the behavioral consequences of lesions in the visual cortex of the prosimians. She also continued to study visual processing in rhesus monkeys.



Dr. Martha Wilson with one of the monkeys at the laboratory in Storrs, CT

In the late 1970s, Professor Wilson began to consider whether the kinds of research she had conducted with monkeys and prosimians could be applied fruitfully to human populations. She invested her 1979 sabbatical in learning the protocols for working with people who had suffered brain damage. Always ready to learn from the leaders of the field, Dr. Wilson traveled to the Montreal Neurological Institute to work under the supervision of famed neuropsychologist Dr. Brenda Milner and her team. From her first day at the Institute, Dr. Wilson was engaged in neuropsychological assessment – both as a clinical researcher, and also by serving as a normal-control volunteer participant in all of the ongoing studies. The lessons about studying brain-behavior relations in humans, often applying the testing paradigms and questions (if not the physiological methods) of her own work with nonhuman primates, were taken back to Storrs after Professor Wilson’s sabbatical. There, she began studying how organisms (humans,

monkeys, prosimians) organize or categorize sensory information. Together with her graduate advisee Barbara Streitfield, Dr. Wilson challenged the popular “speech is special” view of categorical perception, which argues that language allows humans to distinguish stimuli across category boundaries better than stimuli that are equally different but within category boundaries (e.g., to discriminate better between a blue stimulus and a green stimulus than between two blue stimuli that differ by the same amount of hue, but share a linguistic label). For Streitfield’s dissertation studies (subsequently published as Streitfeld and Wilson 1986), she and Dr. Wilson showed these same category-boundary effects with non-linguistic stimuli. Human participants’ visual and kinesthetic discrimination performance was better between than within categories. Critically in this work, category boundaries were computationally determined by applying the logarithmic formula that had been theorized in Gestalt-psychology inspired “Adaptation-level Theory” – one of the primary contributions championed by Martha Wilson’s father Harry Helson. This application of Adaptation-level Theory has important ongoing implications for a wide range of topics in psycholinguistics and cognitive psychology, including for the comparative study of cognition.

### Selected Significant Accomplishments

Dr. Wilson retired from the University of Connecticut and professional responsibilities in 1987, at just 59 years of age, but invested great energy over the subsequent 33 years of her life into community service and advocacy for social and political causes. For example, she volunteered her time, effort and expertise at the Northeast Correctional Institute, visiting the Connecticut prison three times per week for 8 years to teach inmates literacy skills, psychology classes, GED preparation, and other topics. She also remained active in anti-war and social-justice issues until her death on April 6, 2020 at her home in Block Island, RI.

Although her professional career lasted less than four full decades, Dr. Wilson authored 40 publications, attracted significant federal grant support,

taught and mentored students, and invested heavily in disciplinary service, particularly for the American Psychological Association (APA). For her scholarly work, Dr. Wilson was recognized as a Fellow of APA Divisions 1 (General Psychology), 3 (Experimental Psychology), and 6 (Physiological and Comparative Psychology).

As the name suggests, APA’s Division 6 represented two different but complementary sub-fields. In its 75-year history, few scholars served the division as extensively as did Dr. Martha Wilson, and arguably no one’s program of scholarship better represented *both* of its membership constituencies. Dr. Wilson was a physiological psychologist who studied the neural mechanisms of vision in monkeys and prosimians. Her behavioral investigations of intersensory learning were mainstream comparative psychology, as were her innovative studies of category learning that bridged animal research with human clinical neuropsychology. In a definitive history of Division 6, Dewsbury (1996) described Martha Wilson (along with Brenda Milner, Karl Pribram, Mortimer Mishkin, and a few others) as “regulars who kept Division 6 alive” (p. 55). Dr. Wilson served as the organization’s temporary Secretary-Treasurer when Division 6 was reestablished in 1963, after its 14-year period of merger with Division 3, and she was elected to this office again for 1969–1971. She subsequently served the division in elected offices of Member-at-Large on the Executive Committee (1974–1977) Representative to Council (1977–1980), President-elect (1985–1986), President (1986–1987), and Past-president (1987–1988). For her 1987 presidential address, Professor Wilson discussed brain mechanisms in categorical perception. A chapter *Categorical Perception: The Groundwork of Cognition*, edited by Stevan Harnad, reviews this research (Wilson 1987).

Included in this legacy is Dr. Wilson’s record of accomplishment during an (ongoing) era in which women faced challenges beyond those of their male peers. Like other female scholars, Martha Wilson made difficult choices and sacrifices in professional development in order to have children. Her long, happy, and successful marriage to Bill Wilson came with academic costs, both from institutional biases and anti-nepotism rules and

also from less overt negative attitudes and treatment. Although she benefited from strong and effective mentors and collaborators, academic and professional opportunities and recognitions were likely slower to come to Martha Wilson and other female scientists than to males with comparable academic and research records. Nevertheless, Dr. Wilson expressed gratitude for the support, acceptance, and honors she received from psychology, and noted in the foreword of her memoir that she was writing “in the context of an era that allowed me, if somewhat painfully at times, to become a different person than most women who lived in past times” (Wilson 2010).

## Cross-References

- [Categorization](#)
- [Discrimination learning](#)
- [Division 6, American Psychological Association \(APA\)](#)
- [Frank Ambrose Beach](#)
- [Morton Edward Bitterman](#)
- [Parietal Lobe](#)
- [Prosimian Cognition](#)
- [Primary Somatosensory Cortex](#)
- [Temporal Lobe](#)

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## Martin Daly and Margo Wilson

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## Synonyms

[Aggression](#); [Crime](#); [Homicide](#); [Intimate Partner Violence](#)

## Definitions

Martin Daly is an evolutionary psychologist who received his Ph.D. from the University of Toronto. Margo Wilson was an evolutionary psychologist who received her Ph. D from University College

London. Together, Daly and Wilson applied an evolutionary perspective to crime statistics to provide an explanation for patterns of violence and homicide in modern human societies.

Martin Daly and Margo Wilson were a husband-wife research team who, together, investigated the evolved functions of human aggression until Wilson's death in 2009. A great deal of Daly and Wilson's work focused on human aggression and, in particular, homicide. Their 1988 book *Homicide* applied an evolutionary perspective to violent crime statistics from urban cities and offered explanations for these patterns of violence in the context of evolved psychology. Daly and Wilson dispelled a number of supposed inconsistencies between evolutionary logic and observed crime statistics in industrialized, Western cities like Chicago and Detroit. They argued that available data on violent crime are vulnerable to misinterpretations and erroneous conclusions, such as the belief that the majority of homicides are committed against kin. However, the factual basis of this claim relies largely on one's definition of kin. The kin altruism hypothesis predicts that, because individuals share roughly 50% of their genes with full siblings, biological children, or parents, an individual may aid copies of his or her own genes by behaving altruistically toward these individuals (Hamilton, 1964). Therefore, if humans regularly engaged in the killing of genetically related kin, this would pose a considerable contradiction between patterns of human aggression and the theory of evolution by natural selection (Darwin, 1859). Daly and Wilson explain that crime statistics like those from Chicago and Detroit do not present a conflict with evolutionary theory because many of the homicide victims reported as "kin" in police records are not genetically related to the perpetrator. In fact, many of these homicides are perpetrated by husbands, against their wives. Daly and Wilson take caution to avoid the implication that wife-killing may be adaptive. Rather, they explain that the supposedly high frequency of kin-killing suggested by violent crime statistics may be explained, at least in part, by men killing their spouses. Although killing one's intimate partner may certainly incur adaptive costs, Daly and Wilson argue that wife killing is likely an unintended byproduct of spousal

abuse which, itself, is intended to prevent or punish partner infidelity.

Another contentious aspect of human behavior addressed by Daly and Wilson in *Homicide* was infanticide, specifically the killing of infants by their mothers. At first glance, infanticide might appear to be in conflict with evolutionary logic, as not only are women killing an offspring who shares half her genes, but also they have seemingly wasted the time and investment involved in gestating and birthing the child. However, as Daly and Wilson explain, for women who find themselves giving birth under especially unfavorable conditions, the costs of keeping the child might be much greater than committing infanticide and may be outweighed by the potential benefits of waiting to raise a child under more favorable conditions. Daly and Wilson also point out that women are much more likely to kill their infant children when they are young and/or unmarried, suggesting that women who are poorly provisioned might be better off in the long term by committing infanticide and having another child when they have secured investment from a male partner.

Daly and Wilson's body of work represents a landmark contribution to the literature on evolved human psychology; however, their research is also notable for inspiring numerous subsequent studies investigating violence and aggression using an evolutionary perspective. For example, many studies have investigated intimate partner violence from an evolutionary perspective and have consistently found that men are more likely to use violence against their partner when they suspect her of committing infidelity (e.g., Buss & Shackelford, 1997). Further, researchers have observed that younger women appear to be at increased risk of being killed by their partners (e.g., Shackelford et al., 2000). The researchers suggested that, for men, the reproductive costs associated with a female partner's infidelity are much greater when the female partners are relatively younger. As a result, a young woman's infidelity might elicit greater sexual jealousy, and subsequently more severe violence by her male partner. As a whole, these findings support several of Daly and Wilson's main arguments in *Homicide*, such as that selective pressures in the

ancestral environment likely favored violent, aggressive responses from males when they suspected their partners of infidelity, and that such responses reduced the likelihood that men would unwittingly invest resources in genetically unrelated offspring.

Daly and Wilson have also published several papers on nonhuman animals (e.g., Daly et al., 1990). Martin Daly, in particular, has conducted research on foraging habits in kangaroo rats (*Dipodomys*, Heteromyidae). One such study observed that kangaroo rats are more selective in their foraging habits when predation risk in their environment is relatively high (Leaver & Daly, 2003), and a separate study reported that kangaroo rats expend greater effort to store more desirable food items (Leaver & Daly, 1998). Additionally, Daly et al. (1984) conducted a descriptive study, in which they detailed the living conditions and breeding procedures of their captive, kangaroo rats, and in another study, Wilson et al. (1985) described the estrous cycle of captive kangaroo rats.

Recent published works by evolutionary scientists have emphasized the downward trend in violence (Pinker, 2011) as well as the relative lack of aggression in humans compared to other species, and especially compared to our closest living primate relatives (Wrangham, 2019). Nevertheless, aggression is undoubtedly part of human evolutionary history, and Daly and Wilson's research on violent human behavior and cognition has yielded substantial contributions to evolutionary psychology.

## Cross-References

- [Aggression](#)
- [Infanticide](#)
- [Kin Selection](#)

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## Masseter Muscle

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## Synonyms

[Muscle of mastication](#)

## Introduction: The Muscle and Its Fascia

Masseter belongs to the group of the muscles for mastication (others are temporalis, lateral pterygoid, and medial pterygoid). The epimysium of masseter along with the superficial lamina of the deep cervical fascia of the neck covering the parotid gland forms a thickened unyielding parotid – masseteric fascia or parotido – masseteric fascia. This fascia separates structures overlying the surface of masseter, the parotid



duct, the buccal branch of the facial nerve, and interconnecting branches from the mandibular nerve. Anteriorly, the parotid – masseteric fascia blends with the epimysium of buccinator muscle after crossing the surface of buccal pad of fat and below the lower border of mandible, parotid – masseteric fascia is continuous with the deep cervical fascia (Gleeson 2016).

Masseter is quadrilateral in shape and is situated on the lateral surface of the ramus of the mandible. The muscle has three layers with different origin and insertion. The superficial layer of masseter has fibers in oblique direction (going downwards and backwards at 45°) originating from anterior 2/3rd of lower border of zygomatic arch and adjoining zygomatic process of maxilla. The insertion is at lower and posterior part of lateral surface of ramus of the mandible. The middle layer originates from the deep surface of anterior 2/3rd and lower border of posterior 1/3rd of zygomatic arch, and inserts at the middle of ramus of the mandible. The third layer, also called as the deep layer originates

from deep surface of zygomatic arch and inserts on the upper and anterior part of lateral surface of ramus of the mandible including the coronoid process (Sinnatamby 2011) (Fig. 1. Shows origin and insertion of superficial and deep fibers of the masseter muscle.).

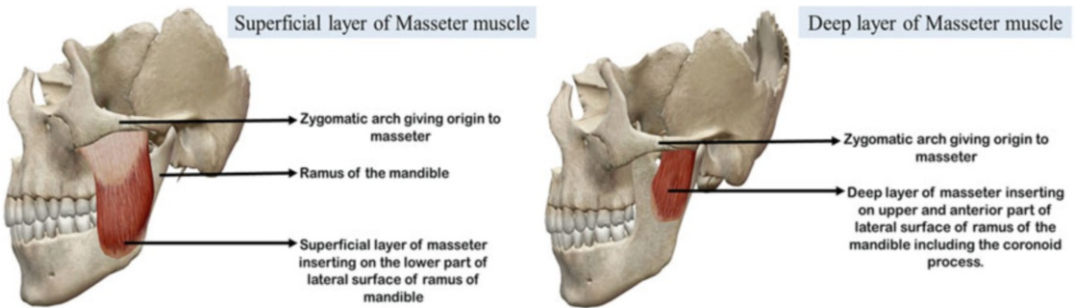
The middle and deep layers cross the superficial layer in “X” – like manner forming a cruciate muscle (Wigley 2016). Intramuscular tendinous septa in superficial layer are responsible for the ridges on the surface of the ramus.

Relations of Masseter

Masseter has got two surfaces and two borders/margins.

- 1. Surfaces – Superficial and deep
- 2. Borders – Anterior and posterior

The structures related to the surfaces and borders are mentioned in Table 1 (Gleeson 2016).



Masseter Muscle, Fig. 1 Different layers of masseter muscle

Masseter Muscle, Table 1 Structures in relation to masseter muscle

| Superficial                                             | Deep                                                   | Anterior margin        | Posterior margin |
|---------------------------------------------------------|--------------------------------------------------------|------------------------|------------------|
| Skin                                                    | Temporalis muscle                                      | Buccinator muscle      | Parotid gland    |
| Platysma                                                | Ramus of mandible bone                                 | Buccal nerve           |                  |
| Risorius                                                | Masseteric nerve branch from trunk of Mandibular nerve | Buccal pad of fat      |                  |
| Zygomaticus major                                       | Masseteric artery branch of maxillary artery           | Facial artery and vein |                  |
| Parotid gland                                           |                                                        |                        |                  |
| Branches of facial nerve                                |                                                        |                        |                  |
| Transverse facial branch of superficial temporal artery |                                                        |                        |                  |

## Vascular Supply of Masseter

The vessels supplying the masseter muscle are:

1. Masseteric branch from the pterygoid part of maxillary artery
2. Masseteric branch from facial artery
3. Transverse facial branch of the superficial temporal artery

The masseteric artery accompanies the masseteric nerve as it passes behind the tendon of temporalis through the mandibular notch to enter the deep surface of masseter. The masseteric artery anastomoses with the masseteric branches of the facial artery and with the transverse facial branch of the superficial temporal artery. It also supplies the temporomandibular joint via its branch (Gleeson 2016).

## Nerve Supply of Masseter

The muscles of mastication develop from the first pharyngeal arch and hence are supplied by the nerve to this arch, the mandibular nerve. Specifically, the masseteric branch of the anterior trunk of the mandibular nerve supplies the masseteric muscle. The nerve enters the deep surface of the masseter by passing through the mandibular notch, immediately anterior to the capsule of the temporomandibular joint (gives articular branches to the joint, following the Hilton law) (Koshi 2018).

## Action of Masseter

1. Masseter elevates the mandible and clenches the teeth.
2. Its superficial fibers help to protract the mandible.
3. Acting alternately, the two muscles (right and left) move the chin from side to side, producing a grinding movement of the teeth.

The combined jaw closing action of masseter and temporalis pulls the condyle backwards,

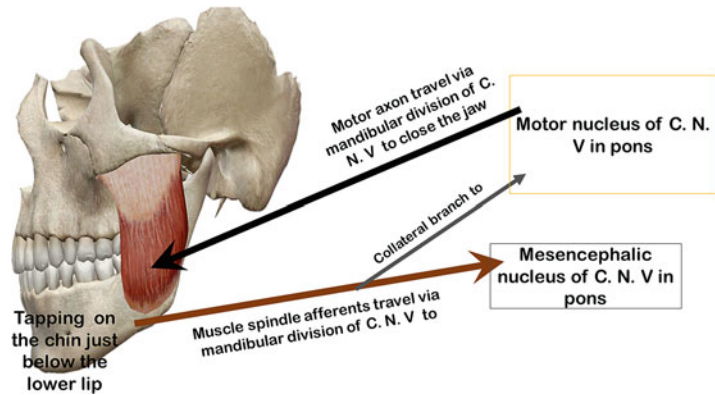
as the pull of temporalis is greater than the associated forward pull of (superficial) masseter. The backward pull of the mandibular condyle is prevented by the simultaneous contraction of the upper head of lateral pterygoid, which stabilizes the condylar head against the articular eminence during closure, particularly during biting and mastication.

A pterygo-masseteric sling is formed by the masseter and medial pterygoid together to support the angle of the mandible. The robust attachments of these two muscles resists the surgical lengthening of the ramus (Evans 2016).

## Applied Anatomy

1. **Submasseteric space infections:** A series of spaces between the lateral surface of the ramus of the mandible and masseter, which are formed due to multiple insertions of fibers of masseter on the lateral surface of the ramus. Sporadically, infection around the mandibular third molar tooth tracks backwards and lateral to the mandibular ramus; pus localizes deep to the attachment of masseter in the submasseteric tissue space. Such an abscess produces negligible swelling but is accompanied by profound muscle spasm and severe limitation to opening of jaw (a clinical condition known as trismus) (Sinnatamby 2011).
2. **Palpable pulses:** Facial artery pulsation can be palpated anterior to masseter muscle on the lower border of mandible and on the face approximately 1 cm lateral to the angle of the mouth (Wineski 2019).
3. **Jaw jerk reflex or Masseter reflex (Fig. 2):** A dynamic stretch reflex is used to test the status of a patient's trigeminal nerve (C.N. V), as it regulates both the sensory and motor aspects of this reflex. It also helps in distinguishing an upper cervical cord compression from lesions occurring above foramen magnum.

**Procedure:** The mandible or lower jaw is tapped at a downward angle just below the lips at the chin while the mouth is held slightly open.

**Masseter Muscle,****Fig. 2** Pathway for jaw jerk reflex

**In response**, the masseter muscles will jerk the mandible upwards.

**Interpretation of the response** – Normally, this reflex is absent or very slight. However, in individuals with upper motor neuron lesions, the jaw jerk reflex can be quite pronounced.

**Reflex pathway:** it is a monosynaptic pathway where a tap on the chin below the lower lip activates muscle spindle afferents, which travel via the mandibular division of the trigeminal nerve to the brain stem. The cell bodies of these primary afferent neurones are located in the mesencephalic trigeminal nucleus. Collaterals project monosynaptically to the motor nucleus of the trigeminal nerve in the pons. Motor axons arising in the nucleus travel via the mandibular nerve to innervate the muscles that act on the temporomandibular joint and closes the jaw (Gleeson 2016).

4. **Spasm of masseter:** When in spasm, masseter holds the head of the mandible tightly against the articular tubercle of zygomatic arch causing anterior dislocation of temporomandibular joint. To perform the reduction of the joint back into the fossa, pressure is applied first downward and then backward on the mandibular molar teeth. The downward pressure helps in overcoming the spasm of the masseter and the backward force pushes the head back into the fossa by overcoming the spasm of the lateral pterygoid muscles (Sinnatamby 2011).
5. **Palpation of masseter:** Anterior border of the masseter is made prominent and palpable by

clenching the jaw (Charalampidou et al. 2008). This procedure is also used to test the integrity of trigeminal nerve (C. N. V) (Wineski 2019).

## Cross-References

- [Muscular System](#)
- [Reflex](#)

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## Mastering

### ► Learning

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## Matched Countersinging

### ► Countersinging

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## Matching-to-Sample

### ► Delay Neurons: Comparative Overview ► Oddity

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## Matching-to-Sample: Comparative Overview

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### Synonyms

Behavioral neuroscience; Comparative cognition;  
Delay cells; Delayed matching-to-sample; Mem-  
ory; Memory cells; Prospective processing; Same/  
different concept; Transitivity

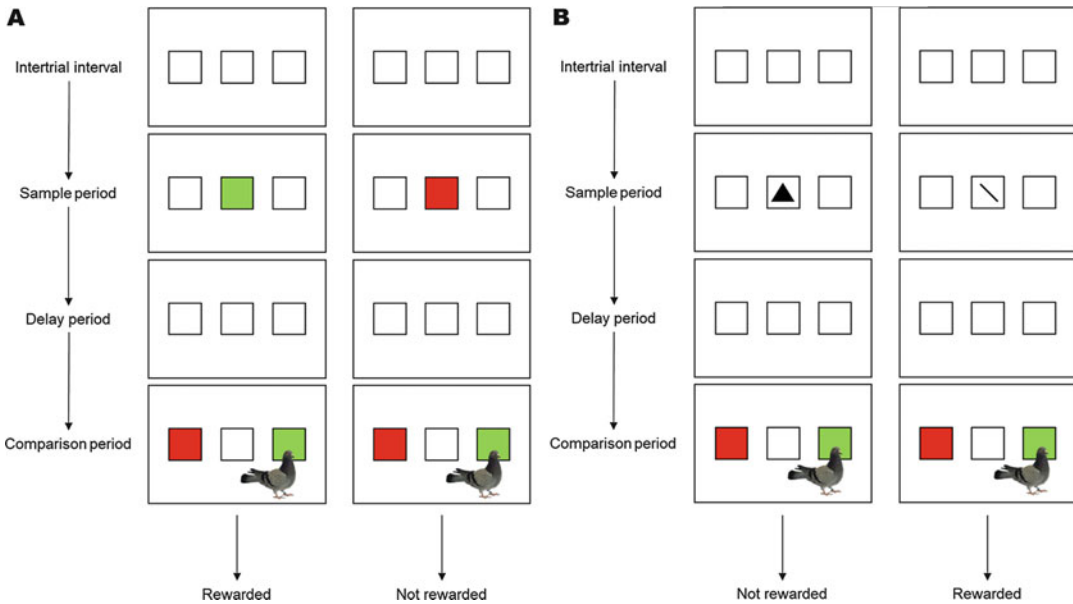
### Introduction

The matching-to-sample task is widely used in behavioral neuroscience and comparative cognition as a means of examining the underpinnings of working memory and testing a variety of cognitive processes. The most common version of the task is delayed matching-to-sample (DMS). On a typical DMS trial, following an intertrial interval, a subject is presented with a sample stimulus, followed by a delay period in which the sample is turned off (see Fig. 1a). After the delay, two

comparison stimuli appear, and the subject is required to select the stimulus that matched the sample stimulus they saw before the delay. If the chosen comparison stimulus is what had appeared as the sample stimulus then the subject is rewarded (Fig. 1a, left panel). If the subject chooses the comparison stimulus that is different to what had appeared as the sample stimulus they are not rewarded (Fig. 1a, right panel), and may be punished with a time-out from playing the task. Following either reward or punishment is the intertrial interval, signalling the start of the next trial. An animal may complete dozens of such trials in a daily session.

Konorski (1959) first proposed the matching-to-sample method as a means of investigating working memory in nonhuman animals, arguing that working memory was composed of a dynamic memory trace, and that previous methods did not sufficiently test this type of memory. Instead, previous methods of testing nonhuman animals could be easily solved without actively remembering information. For example, take the case where an animal is shown a sequence of three stimuli and is trained to respond if the sequence is different from the previous sequence. Rather than evaluating the position of each individual stimulus in the current sequence against its position in the previous sequence, it is possible to solve this task by only looking at whether the first or last items are the same across the two sequences. That is, an animal could solve these kinds of tasks by using other cues, or simpler forms of memory, than actual working memory. To examine true working memory, Konorski (1959) proposed that pairs of stimuli from the same modality should be presented one after the other, and that in order to be rewarded, the animal should respond when the stimuli match (go response). If the stimuli do not match, then the animal should withhold responding (no-go response). It is from Konorski's (1959) go/no-go paradigm that the matching-to-sample procedure evolved.

The first use of the matching-to-sample method with animals was by Blough (1959). While the method Konorski (1959) created displayed the sample and comparison stimuli one at a time,



**Matching-to-Sample: Comparative Overview, Fig. 1** An example of a trial from a (a) basic DMS task and a (b) conditional DMS task. For the basic DMS task, in order to be rewarded, the animal must select the comparison stimulus that is the same as the sample stimulus they saw just before the delay period. Note that the animal in the left panel makes a correct response, whereas in the right panel it makes an incorrect response. For the conditional DMS task, in order to be rewarded, the animal must select the comparison stimulus that is associated with the sample stimulus they saw just before the delay period. For the

example shown, the animal is trained to respond to the red comparison stimulus if the triangle served as the sample stimulus, and the green comparison stimulus if the sample stimulus was a line. Note that the animal in the left panel makes an incorrect response, whereas in the right panel, it makes a correct response. For both the basic and conditional DMS tasks, within a session the two sample stimuli would appear an equal number of times and would be followed by an equal number of presentations in which red would appear on the left and green on the right, as well as green on the left and red on the right

Blough (1959) displayed a sample stimulus followed by two simultaneously-presented comparison stimuli. Four pigeons were trained with light stimuli that were either flickering or steady. On each trial, pigeons were presented with one of these stimuli as the sample stimulus, followed by a delay. After the delay, both a flickering light and a steady light were presented, and the pigeons had to peck the one that matched the sample they had seen. The delay length started at 0 s (no delay), and, if pigeons performed at a suitable level, was gradually increased to 10 s. Blough (1959) found that two of the birds were able to perform the task well even at the longer delays, while the other two birds did not progress to the longer (5 and 10 s) delays during the study. For the two birds who performed poorly at long delays, performance nevertheless appeared to be a function of delay length, displaying a classic forgetting curve as

observed in humans (White et al. 1996). However, the birds that performed well at the longer delays did not seem to “forget” and appeared to use other strategies for remembering the sample. Overall, Blough’s original use of the DMS paradigm demonstrated the task’s usefulness in assessing working memory with animal subjects, despite the fact that some animals seemed to adopt non-memorial strategies.

## Variations of the DMS Task

The most common form of the DMS task is similar to the one used by Blough (1959) with two simultaneously-presented comparison stimuli, and has been used with many different species such as primates (D’Amato et al. 1985a), birds (Johnston et al. 2017a, b), fish (Goldman and



Shapiro 1979), and even bees (Giurfa et al. 2001). The other form is the successive go/no-go form proposed by Konorski (1959), in which stimuli are presented sequentially and the animals are trained to respond in one way when the comparison stimulus matches the sample stimulus, and withhold responding when it does not match (Miller et al. 1996; Miyashita and Chang 1988).

Beyond these two basic forms, there are many other variations of the matching-to-sample procedure. In delayed nonmatching-to-sample (DNMS, also known as oddity-from-sample), animals must respond to the comparison stimulus that does not match the sample (Zentall and Hogan 1974). It is also possible to structure the matching task such that the sample and comparison stimuli bear no physical relationship to each other. For example, in a conditional DMS task (also known as symbolic DMS, or delayed paired associate task; DPA), the sample stimuli may be shapes and the comparison stimuli may be colors (Fig. 1b). On each trial, animals are presented with one of the sample stimuli, followed by a delay. After the delay, the comparison stimuli are presented, and the animal must choose the comparison stimulus that is mapped onto the sample they just saw. For example, take the case where the sample stimuli can be either a triangle or a line, and red and green are the comparison stimuli. When the animal sees the triangle as the sample stimulus, it must choose the red stimulus during the comparison period (Fig. 1b, left panel). On the other hand, if it sees the line as the sample stimulus, then it must choose the green comparison stimulus (Fig. 1b, right panel). Symbolic DMS/DPA tasks can use comparison stimuli either from the same modality as the sample stimuli (Rainer et al. 1999) or from another modality (Colombo and Gross 1994).

The number of stimuli that are used within a session can also vary depending on the type of DMS procedure. For example, a DMS task can use trial-repetitive stimuli, in which the same set of (most often two) stimuli are used for every trial in a session. Alternatively, a DMS task can use trial-unique stimuli, in which each trial has a unique set of stimuli (Mishkin and Delacour 1975). DMS performance with trial-unique stimuli is typically better than performance with trial-

repetitive stimuli because the levels of proactive interference are higher with trial-repetitive tasks. Essentially, the DMS task is a complex discrimination procedure in which the animal must determine which stimulus appeared most recently as the sample stimulus. In the trial-repetitive version of the task, with only two stimuli serving as sample stimuli, determining which comparison stimulus served as the sample most recently is a far more difficult task than in a trial-unique version, where the stimuli change on every trial (D'Amato 1973).

## Matching-to-Sample Tasks and Comparative Cognition

In a simultaneous matching-to-sample (SMS) task, the sample stimulus remains on when the comparison stimuli appear. One of the most common uses of the SMS tasks is to study whether animals possess a matching concept, that is, an understanding of the concepts of same and different. The method is relatively straightforward. An animal is trained on a SMS task with two stimuli, say red and green. All animals tested can acquire such a task, but the important question is: *What exactly has the animal learned?* The “behavioral” interpretation is that the animal has learned a set of stimulus-response rules such as “press the red comparison if red was the sample” and “press the green comparison if green was the sample” (Carter and Werner 1978). The alternative “cognitive” view is that the animal learns a matching concept such as “press the comparison that matches the sample” (Zentall and Hogan 1974). One can distinguish between these two views by delivering a transfer test whereby novel stimuli, such as a circle and a plus sign, are used. According to the behavioral interpretation, in which the rules were learned specifically with the training stimuli (red and green), an animal should do poorly with the novel stimuli. On the other hand, if the animal’s behavior was driven by a cognitive rule, then testing the animal with novel stimuli should pose no difficulty, since the learned rule “press the comparison that matches the sample” is independent of any stimulus. Although a

brief review could never capture the complexities of the numerous studies that have explored whether animals possess a matching concept, monkeys (D'Amato et al. 1985a), birds (Wright 1997), and even bees (Giurfa et al. 2001) all do well when presented with novel stimuli.

Another use of the SMS task comes in studies investigating whether animals have the capacity for transitivity. For example, if  $A > B$  and  $B > C$ , we conclude that  $A$  must be greater than  $C$ . Can animals perform such logical operations? D'Amato, Salmon, Loukas, and Tomie (1985b) used an SMS task and trained animals on a first SMS relation with  $A$  and  $B$  as sample stimuli mapped onto  $C$  and  $D$  as comparison stimuli, such that when  $A$  was the sample stimulus, the correct comparison choice was  $C$ , and when  $B$  was the sample stimulus, the correct comparison choice was  $D$ . Once this first relation was learned, the animals then learned a second relation whereby the comparison stimuli of the first relation,  $C$  and  $D$ , became the sample stimuli of the second relation.  $C$  and  $D$  were then mapped onto a new set of comparison stimuli,  $E$  and  $F$ . Once the second relation was learned, the animals were tested for transitivity by using the sample stimuli of the first relation ( $A$  and  $B$ ) and the comparison stimuli of the second relation ( $E$  and  $F$ ). Although the animals had never experienced these pairings, the monkeys in the study fared quite well in that they selected  $E$  if  $A$  had appeared as the sample, and  $F$  if  $B$  had appeared as the sample. Such an outcome implies an underlying transitive relation guiding the monkeys' behavior.

The matching concept and transitivity are just two of the many uses of the versatile SMS/DMS procedure, which has also been used to investigate metacognition (Hampton 2001) and episodic memory (for an overview, see White et al. 1996; Griffiths et al. 1999). Another use of the DMS procedure has been to explore issues relating to whether animals engage in prospective processing, a form of mental time travel. Take the case of a standard DMS task that uses red and green stimuli. During the delay period, does the animal engage in retrospective processing and remember what it saw as the sample stimulus, or does it engage in prospective processing and

remember which stimulus it should press as the comparison stimulus to get a reward? Naturally, in the standard DMS task where the sample stimuli are the same as the comparison stimuli, it is not possible to untangle these two options. For example, if red was the sample stimulus, then a retrospective processing account (remembering the sample) would mean that an animal remembers "red," but a prospective processing account (remembering the correct comparison stimulus) would also mean that the animal remembers "red." One can get around this problem by using conditional DMS tasks where the sample stimuli are mapped onto physically different comparison stimuli, much like in the case of the previously described transitivity study (see also Fig. 1b). For example, take the case of Fig. 1b where the sample stimuli are a triangle and a line that are mapped onto the red and green comparison stimuli, respectively. Let us assume a trial where the animal sees the triangle as the sample stimulus. If the animal is retrospectively processing, then it must be remembering "triangle," whereas if it is prospectively processing, it must be remembering "red." Using such a conditional DMS task, with either physically different visual sample and visual comparison stimuli, or auditory samples and visual comparison stimuli, it is possible to show that animals do indeed engage in prospective processing (for an overview of animal studies showing prospective processing, see Colombo et al. 2017).

## Matching-to-Sample Tasks and Behavioral Neuroscience

The DMS task has been a cornerstone task used in almost all studies that have examined the neural basis of memory, from early lesions studies, to later electrophysiological studies. The DMS task was used extensively throughout the 1980s and 1990s to explore the role of the hippocampus in learning and memory (for a review, see Colombo and Broadbent 2000). The advantage of the DMS task is that by using delays of various lengths, one can simultaneously explore the impact of a lesion on memory, as well as basic discriminatory

abilities. For example, if a structure was involved in memory, then one might expect the impairment to be minimal at a short delay where the memory load is minimal, and increase for longer delays, as memory load becomes more noticeable. Such might have been the case with damage to the hippocampus (see Colombo and Broadbent 2000, and references therein). Alternatively, damage that encroaches on the visual system will cause perceptual impairments that manifest as impairments at both the short and long delay (see Colombo and Broadbent 2000, and references therein).

Electrophysiological studies of memory have also relied heavily on the DMS procedure. One of the most common ways to explore the neural mechanisms of memory is to study what is known as delay activity. Fuster and Jervey (1981, 1982) were the first to notice delay activity, initially in the prefrontal cortex (PFC), and later in the inferior temporal (IT) cortex. Fuster and colleagues noticed that some cells in PFC and IT cortex continued to fire during the delay period, a time in which the animal is presumably remembering information either about the sample stimulus or the anticipated correct comparison stimulus. Miyashita and Chang (1988) argued that delay activity represents a neural correlate of memory. Evidence that an animal's performance on the DMS tasks is correlated with aspects of delay activity seems to lend support to this notion (see also Colombo and Gross 1994). Delay activity has now been identified in many regions of the brain across many different species including rats (Sakurai 1990) and birds (Johnston et al. 2017a, b).

The DMS task has been used to explore the possible role of delay activity in coding aspects of behavior other than memory for the sample stimulus. For example, both studies with monkeys (Rainer et al. 1999) and studies with crows (Moll and Nieder 2015; Veit et al. 2015) have shown that delay activity may represent a neural code of a prospective stimulus. Additionally, studies of categorization (Freedman et al. 2001), numerosity (Ditz and Nieder 2016), and abstract rule learning (Veit and Nieder 2013) have all utilized versions of the DMS task to understand what information animals are processing during a delay period.

## Conclusions

Since its conception by Konorski in 1959, the DMS task has been widely used in comparative cognition studies exploring the cognitive abilities of animals, and neuroscience studies exploring the neural basis of learning and memory, both in a variety of different animals. In fact, it is its ease of use across so many different species that makes matching-to-sample procedures such powerful tools.

## Cross-References

- Cognition
- Comparative Cognition
- Corvids
- Discrimination Learning
- Episodic Memory
- Learning
- Neural Impulse
- Neuron
- Operant Chamber
- Pigeon (*Columbidae*)
- Primates
- Reinforcement
- Vision
- Visual Recognition in Birds
- Working Memory

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## Mate Choice

### ► Female Choice

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## Mate Guard

### ► Mate Guarding

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## Mate Guarding

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## Synonyms

Mate guard

## Antonyms

Mate searching

## Definition

To guard a mate, or to prevent a mate from (re) mating with other mates/partners; to stay with partner longer than the time required for mating.

## Evolutionary Context

Although mate guarding mechanism has evolved to ensure paternity of the one guarding, evolution should also confer some selective advantage to the guarded partner. Before understanding it fully, it is important to understand the reproductive context in which it is included.

Mate guarding can be observed in both sexes, but is more frequently reported among males within a variety of species. This sex bias is possibly a response or consequence to male gamete evolution in Animal Kingdom. Animal male gametes ARE tiny and numerous tiny and numerous, outnumbering the female's by many folds, which are large and rare. These different morphologies

between gametes (anisogamy) oppose to gametes of equal sizes (isogamy), a much rarer condition but believed to occur in the first sexual organisms (Bell 1982).

Anisogamy is also thought to be the origin of asymmetry in gender roles. According to Trivers (1972), the gender that invests less in the offspring should be the competitive one, and the one who invests more should be choosy. Since the actual sperm contribution to the zygote survival is nearly absent, males are more likely to be the sex that invests less in offspring as they provide little more than just semen. Conversely, females produce fewer gametes and they devote a great deal of resource on them, so that zygote survival is highly dependent on her. Thus, female contribution to the next generation is directly related to the number of eggs released and/or matured at the time of ovulation, while male contribution to the next generation is much more variable (Bateman 1948). Since female gametes are a scarcer resource, almost every male must compete for an egg at least once in their lifetime. If females are rare, competition will be even stronger. There must be competition in order to mate guarding to occur.

High gamete productivity yields an advantage through sperm competition and anisogamy sets up the conditions since the highly abundant male gametes will compete to fertilize the limited female gametes (Bjork and Pitnick 2006). Interestingly, mate guarding males are predicted to produce less sperm than males that are always in sperm competition. However, it is whether not clear if sperm reduction is a cause or consequence from mate guarding.

The general scenario that mate guarding should occur as means of high gamete competition is broadly accepted, but the lack of body literature regarding its evolution possibly indicates that it has multiple origins. Among insects, Parker (1970) has shown a neat evolutionary trend of internal fertilization to external fertilization. The evolution of internal reproduction without copulation, observed among terrestrial insects, but also in marine animals (such as crustaceans), provides a shorter fertilization time by placing the protected sperm as closer to the eggs as possible. Internal reproduction can be dissociated from



copulation when the sperm is not free, but encapsulated somehow. This means that males will spend more energy in producing capsules and spend more time in placing the capsules along the females' path. Consequently, these males are slightly choosier due to its increase in gamete investment. Yet, the male does not need to be present for the fertilization to happen. On the other hand, females produce hundreds to thousands of eggs and there is a delay between sperm placement and the actual eggs' fertilization, with plenty of opportunity for multiple matings. Therefore, there is an absent male that has dedicated time and energy to a single female, and the possibility of multiple males to copulate with this same female, handicapping all the first male's effort. At this point, mate guarding will boost the male's outcome and fitness if he manages to protect the female and, consequently, his sperm.

Still following Parker (1970), further selective pressures brought internal fertilization associated with copulation. The male introduces the sperm (usually free) even closer to the female's eggs, inside her reproductive tract and, consequently, there is now the need for him to be present. This is probably one of the most familiar reproductive systems that possibly led to the evolution of a copulatory organ, such as the penis or phallum. Although this system bestows the sperm closer to the eggs, the negative consequence is that the male needs to spend even more time and energy with a single female. By reaping his chances to further mate with more females, he needs to assure that his sperm will not be replaced nor displaced by subsequent males, should a second mating occur. That is, if there is a high probability of losing fertilizations through sperm competition or if probability of finding another mate is low, such dedication may constitute time waste.

In insects, there is the "last male favoritism" and the male that mates last fertilizes more eggs than the previous one, while the female produces a fixed amount of eggs irrespective of how many matings she had. At this point, there will be two opposite evolutionary directions. At one end, the second male tries to displace as much sperm as possible from the first male (increased sperm competition), producing an even greater amount of

sperm to displace any possible previous sperm and still have plenty to fill storage organs (the spermatheca) with a single ejaculation in insects, such as the fly *Drosophila melanogaster*. At the other end, there is the first male that is able to avoid or reduce sperm competition by preventing a second male to mate (increased mate guard). Extended copulation is a common form of mate guarding. In dung fly *Scatophaga stercoraria*, if copula duration is prolonged, there is an increase in fertilization rates by the male. Parker (1970) emphasized that this strategy is disadvantageous in two ways, first the male will reduce the number of females mated and, secondly, there is a high chance of takeover from other males when attached the female.

No similar review has been done to other invertebrates nor vertebrates. However, most species (e.g., mammals) show polygamous breeding systems with a high male competition and mate guarding has been intensively studied in this group. Mate guarding among vertebrates is diverse in both type and duration. Duration is extremely variable and may start many days before conception and finish many weeks after it. When reaching the maximum time and energy expenditure in one female, it is believed that this have been a precursor of monogamy. Monogamy, in turn, might be serial (temporary, during a single breeding season) or last for a lifetime (more frequent among birds). The wide variety of forms include pre- or postcopulatory; physical, chemical, behavioral; solo or cooperative. Each will be presented separately, followed by the taxonomic examples observed in the Animal Kingdom.

## Female Mate Guarding

The female mate guarding hypothesis is much rarer and was proposed to explain the frequent copulation observed in birds (Petrie 1992). Females may copulate regularly (even outside the fertile period) to reduce the likelihood of her partner to mate with other females. She may accomplish her goal by reducing his sperm stocks and depleting his energy reserves. In birds, copula is important in establishing a pair bond and by

reducing the chance of her partner to mate with other females, she is also reducing the chances of another female to establish a pair bond with him. Mate loss is particularly important if the male is of high quality and low quality ones will be less solicited, as seen in wild American kestrel *Falco sparverius*. Another important feature in birds that might have helped the evolution of such tactics is that many species are monogamous, with biparental care. Thus, females will suffer a cost from her partner having multiple mates, reducing his care toward their young. This form of mate guarding has not been described for any other group besides birds.

### Cooperative Mate Guarding

Another exception among mate guarding types. Solo mate guarding is the rule while its cooperative counterpart is the exception. Therefore, solo mate guarding will not be presented in a singular session but will be addressed throughout sessions.

Within some species, males form coalitions or alliances that may coercively maintain consortships (or herding) with females, sometimes considered as cooperative mate guarding. Both chimpanzees *Pan troglodytes* and bottlenose dolphins *Tursiops truncatus* males mate guard in alliance with other males. In the case of the bottlenose dolphins, this is possibly because of the high energetic cost of guarding highly mobile female (see “[Mammals](#)” section below). However, both species aggressively herd females and consortships are longer than the receptive period because competition is high when female is the most attractive (e.g., during the fertile period). If the alliance waits for maximal attractiveness before start consorting, other males (or coalitions) may confiscate her.

### Precopulatory Mate Guarding

Precopulatory mate guarding may have evolved if female receptivity is low or if mate searching costs are higher than the cost of guarding. Precopulatory mate guarding is a very common

form and usually includes following up a female until she becomes receptive. Within the mechanical version of precopulatory mate guarding, the male adopts a what-so-called passive phase, when the male stays attached to the female and physically impedes other males to reach her. Many insects, such as beetles’ families, show this behavior. A not so passive phase consists of competing aggressively with other males and, thus, precopulatory mate guarding may overlap with male-male competition.

The behavioral version of precopulatory mate guarding includes a looser phase, although Parker (1970) still considers it as “passive,” as observed in the male termite, which follows closely the female that is in search of an adequate nest site. Some Odonata show this behavior, with females ovipositing on submerged vegetation while the male partner attacks any approaching male. Some males even guard more than one female, placing the second one closer to the first and guarding both.

Territory defense is a possible version of extended precopulatory noncontacting guarding as the males protect likely areas in which a female will enter. A similar strategy is present in harem defenders ungulates. Amid these hoofed animals, males are territorial and females are gregarious, and a male will defend females until they become receptive to his attempts.

### Postcopulatory Mate Guarding

This form is the most widely studied and observed. In many taxons, postcopulatory mate guarding is so long that male presence and protection against other males may function as parental care and protection of the brood.

Tactics are numerous. Chemical agents present in seminal fluid may induce unreceptivity in Diptera female, while many mammals present copulatory plugs that function as “chastity belts.” Copulatory plugs are chemical constituents that cause seminal coagulation immediately after ejaculation. Although it is mainly associated with further mating impedance, they may also function to minimize sperm loss and promote their survival

within the alkaline environment of the vagina. Harvestmen and some dipterans have developed anatomical adaptations such as spined femora or adapted antennae to grasp the female during copulation. Acrinoid males emit sounds against searching males. Cerambycids males produce disturbance stridulation as a reaction to attack from other males.

Parker (1970) assigned this version of mate guarding to the high density of males. In dung flies *Scatophaga stercoraria*, the male remains close to the female while she oviposits. If he fails, other males might take over and will copulate with her until the moment she has laid her last egg. The familiar “tandem position” observed in many dragonfly species of Odonata occurs after mating and while the female is ovipositing. Like the dung fly, takeovers have been observed if the male is not in contact with the female. Nonetheless, protection during oviposition is also positive to the female as she will be protected during oviposition and will avoid attacks of rival males.

Prolonged postcopulatory mate guarding can be costly for males as increased copula duration is associated with reduction of food reserves. In locusts, males can reach nearby food while mounting or protecting the female, and mature males have greater fat reserves, guarding for longer periods. Crickets are also among the taxons that present prolonged postcopulatory behaviors. In this case, the male keeps the pair immobile and, thus, he prevents her from removing the spermatophore, ascertaining multiple copulation with the same female. In Hemipterans, passive phases are linked with parental care. When the female has laid all her eggs and left, the male continues caring for the laid eggs, even after they have hatched. However, other females may visit the egg mass and add their own, increasing fertilization rates for the brooding male.

## Mate Guarding and Sexual Conflict

Although mate guarding has obvious advantages for males, females may also benefit from guarding. Firstly, they may be protected from harassment of other males (as seen in colonial breeders birds, where females may be followed

by up to six males). Secondly, they may be protected from potential predators and, thus, females can focus on foraging and increase their foraging success. Thirdly, if guarding results from competition, females may benefit from the increased fitness from high quality males.

However, sexual conflict stands for opposing interests in mating between sexes. Male interests may contradict the female’s concerning feeding or predation avoidance. Females cannot be regarded as inert and passive beings. Therefore, their collaboration plays an important role in the success of mate guarding. If she is not willing to mate with the one guarding her, she may actively look for other mates and, thus, configure extra-pair copulation if in a monogamous mating system (see “► [Extra-Pair Copulation](#)” entry).

Female isopods *Idotea baltica* resist attempting males by many behavioral mechanisms, such as kicking and bending their bodies for days. Larger males, on the other hand, were better in overcoming their resistance. The lesser waxmoth *Achroia grisella* shows an extended mating time as a form of prefertilization mate guarding, but it also decreases mobility and renders the pair more vulnerable to predation. This species is short lived and nonfeeding as adults, so the whole reproductive bout needs to be fast and functional. Female Seychelles warbler *Acrocephalus sechellensis* scape their mates’ guard to seek partners either for indirect genetic gains or for direct phenotypic gains. Unattractive male blue tits *Cyanistes caeruleus* will guard a female more intensively and she will take advantage of his guarding as she will spend less time fending off against intruding males while she will copulate with a higher quality male.

Prolonged guarding increased the likelihood of aggressive encounters with unpaired males (and possible injuries) and reduced feeding opportunities for the final molt in blue crabs. However, this species copulates only once and, if the female does not collaborate, she might miss this mating opportunity. Females have some control on when the mate guarding begins. Pairing was easier with late pre-molted females suggesting that those females are seeking for mates, while early pre-molted females avoid being guarded.

Summarizing when a male guards and the female copulates with him, it is not possible to deduce that the female prefers this male or if she was coerced by him or if she has no other choice as he chases other males away. Connor et al. (1996) hypothesized that extended cycling period is a counterstrategy to herding by males. Females will reduce alliance monopolization by increasing the number of times they cycle.

## Mate Guarding and Hormones

Sexual and aggressive behavior are usually androgen dependent in males. Aggressiveness as means of mate-guarding behavior should, then, be affected by alteration in circulating testosterone levels in males and has been observed to do so in birds and mammals. Testosterone is also associated with the development of male secondary sexual characteristics, leading them to have bigger bodies and/or larger weaponry, brighter colors, etc. enhancing his guarding abilities.

A study with male barn swallows *Hirundo rustica* (Saino and Møller 1995) showed that circulating testosterone levels were positively correlated with the intensity of mate guarding. Thus, if mate guarding is dependent on testosterone levels, then additional costs of mate guarding arise because of immunosuppressive effects of high testosterone levels. Everything else being equal, males with higher testosterone concentrations are more likely to pay the costs of time, energy, and immunosuppression caused by this hormone.

Pheromones are also decisive for mate guarding. The blue crab *Callinectes sapidus* female produces a urinary-origin pheromone released several days prior to molting that signalize to males that her molting approaches.

## Mate Guarding and The Evolution of Male Alternative Strategy

Size usually defines which males win contests and competitions. Large males consistently guard females better and for longer periods. Smaller males, on the other hand, will not be capable of

keeping this duty for long. The smaller male will be outcompeted and displaced by larger males. Therefore, the evolution of alternative “types” (named as strategies) of males is a counterstrategy to win competitions against larger males by other means. While LARGER males are able to guard females and other resources, SMALLER ONES rely on “sneaky” matings. There can also be an intermediate male, presenting a mixed and plastic strategy, playing in either one side or the other, depending on the situation and depending on the male that he is competing with. This is common among cuttlefishes, lizards, and many bone fish.

In lizards, such as *Psammodromus algirus*, body size is age dependent and, henceforth, old males are the ones who guard, while young males are small and ill-equipped to guard females and seek forced copulation.

## Mate Guarding Examples Among Taxa

### Asexual Reproductive Animals

Animals of obligate asexual reproduction (vegetative or parthenogenetic) are rare, less than 1,000. In some animals, such as bdelloid rotifers from Phylum Rotifera, sexual reproduction has never been recorded. Mate guarding has not been described for any of these animals.

### Hermaphrodites and Aquatic/Sea Animals

Michiels (1998) presented a table showing that many phyla have at least one hermaphroditic representative. Among hermaphrodite individuals, selection on male traits is not independent from the females as they coexist in the same individual. Additionally, gonochorists (just one sex in one individual organism) differ from hermaphrodites in mating opportunities. Whereas in gonochorists females limit mating opportunities, in hermaphrodites donor individuals (equivalent to males) are limited by its own capacity to inseminate partners and receiving is costly (e.g., parasite transmission), leading researchers to classify donors as choosy instead. One nearly universal aspect among hermaphroditic animals is their low density. Thus, partners are too rare to be selective and promiscuous matings in outcrossing

hermaphrodites are likely to occur. Michiels (1998) also states that the physical removal of sperm from sperm storage organs is absent from hermaphrodites, although part of autosperm and allosperm is likely to be digested. Adding, for instance, the reluctant donation to the low population densities, hermaphrodites may not benefit from sperm exclusivity and mate guarding. There seems to be nothing that a partner can offer that the receiver does not already have. In species where multiple individuals participate in mating, on the arrival of a third individual, previous partners may start competing for the new one, instead of protecting each other.

Phyla in which hermaphroditism is almost ubiquitous comprise those mainly of aquatic and marine environments (sponges, corals, bryozoans, ctenophorans) with an ancestral condition of mating behavior. Among these sessile species, adults release gametes into the external medium (called “spawners”), fertilization can be either external (e.g., some corals and ctenophorans) or internal (e.g., sponges and bryozoans), and these individuals mate assortatively (matching phenotypes, as in, larger individuals will prefer to mate with a larger partner). Sea turbulence diffuses gametes concentration to a point that their encounter is rare. Competition among gametes is furious, and there has been no report on mate guarding for such species. Since in marine environment chemical substances play an important role in communication, we have no reason to think that chemical mate guarding should not occur.

Some non-sessile animals, such as the slug *Ariolimax columbianus*, frequently lose their penis during copulation and could be interpreted as means of reducing mating opportunities. Similarly, the flatworm *Dugesia gonocephala* remains in copula for up to 10 h, almost 5 h after sperm transfer is completed. Mate Guarding has not been described for them either.

## Invertebrates

### Aranea

Arachnid females are usually larger than males. Large and heavy females are more fecund, carrying a greater number of eggs and, thus, are of

greater values for males than smaller light females. During breeding season, male *Metellina segmentata* guard female webs for several days prior to mating, which occurs when a pray of suitable size is trapped in the guarded web. It is important that the male is able to gather information on the resident female receptivity so that he does not waste time guarding immature females. Assessment may be tactile, chemical signaling, and web vibration.

### Crustaceans

Regarding other invertebrates, mate guarding is also common among Crustaceans. In this group, female is receptive during a brief period after molting, a period in which carapace is soft and she is vulnerable to predators and injuries from struggles. Thus, precopulatory mate guarding has evolved as males compete intensively for these scarce females and they, in turn, benefit from protection during this delicate stage. The precopulatory mate guard is energetically costly since males use energy reserve to carry females or when the pair spends time in a low-quality refuge during this phase. Since males reduce drastically their feeding rate while precopula mate guarding, a key point is that males are able to detect the molt stage of females accordingly.

**Copepoda** Copepods also have copulation restricted to a very brief period, soon after the female molts. Mate guarding behavior includes close physical association with clasping or carrying to defend females. This is reflected in the evolution of special characteristics that helps them sequestering females, such as increased body size (at least the same size of the female counterpart), enlarged cheliped weapon, and aggressive behavior toward other males.

As reported many times previously, guarding females longer than the time needed represents a significant investment that could be used searching for receptive females. Should the probability of encountering receptive females be low and males mate only once in their lifetime, it would be advantageous for males to guard unmated and even immature females until their terminal stage. Pheromones play an important role



in mate seeking among copepods (shrimps, lobsters, crabs).

Mate guarding in copepods is defined as when males clasp to the females at terminal molting stage. The female reaches sexual maturity after the last copepodid stage, and one copulation seems to be sufficient for the complete fertilization of eggs. After she has finished molting, male clasping is classified as true copulatory behavior. However, some calanoid copepods remate during the gravid phase so that a greater egg mass is produced. In this case, female receptivity is less predictable since fertilization window is larger.

***Isopoda and Amphipoda*** In isopods and amphipods, there is an operational sex ratio bias toward males, reducing severely the mating opportunities per male. In extreme cases of very low female density, permanent mate guarding (or partner fidelity or even monogamy) will be selected for. Precopula mate guarding would not be adaptive if receptive females were numerous and encountering rates were extremely high. A model was proposed for crustaceans by Wickler and Seibt (1981), stating that if female inter-spawn interval was greater and 3–4 days (most crustaceans) and if a male meets up to two females a day, then precopulatory mate guarding is predicted. If encounter rate is higher, mate searching is favored.

***Decapoda*** Several species lack obvious traits that help mate guarding. *Heptacarpus* spp., *Palaemon* spp., and *Palaemonetes* spp. are all highly gregarious species with males smaller than females, not particularly aggressive and weakly armed. In *Palaemonetes pugio*, however, there was no support that mate guarding occurred as males did not exhibit either morphological or behavioral indicative. Despite the fact that there was an increase in male contacts with the molting female, it was too short (1 h before she molted) for Bauer and Abdalla (2001) to consider it as mate guarding. This conservatism was due to Ridley (1983) definition that premating guard needs to last more than 1 h. The former authors interpreted that this species was able to detect pre-spawning females only shortly before her molt.

Hermit crabs occupy empty gastropod shells, and there is individual difference in shell size preference based on past experience of shell availability. Thus, much of the studies with hermit crabs address their memory. Male hermit crabs *Pagurus middendorffii* can assess sex ratio and operational sex ratio (proportion of sexually mature males to inseminated females) in order to extend their mate guarding. Assessment can be through counting both the number of competitors and the number of receptive females or even by memorizing encounter frequencies. Small hermit *P. middendorffii* guarded females earlier than larger males, though the big ones could take over at any time in Wada et al. (1999) lab experiment, so that guarding was unserviceable.

### Cephalopoda

Cuttlefishes are all about number. Usually, population is male biased. They are spawners and form large aggregations in which the female lays 1 egg at a time, reaching up to 39 a day, while mating 17 times with 2 to 8 males a day. Guarding males account for 64% of matings and the remainder by extrapair males. Mate guarding behavior of cuttlefishes manifests in many ways. The large males hover above females or place themselves between the female and other males. If the female is under a rock, the guarding male stays at the entrance. Challengers draw agonistic displays and very rarely it escalates to physical combats. The guarding male is persistent, maintain pre- and postcopulatory guard, and, thus, it may occur last male precedence. Indeed, this long mate guarding does not translate into high fertilization success due to strong sperm competition and/or cryptic female choice.

Octopuses also present mate guarding, and different categories were classified based on its arm's reach, being either adjacent (male and female within arm's reach of each other) and temporary (not adjacent). Like cuttlefishes, size determines which males win contests. If a small male is guarding a female, it is very likely that he will not be able to do so. The large males usually displace the smaller ones.

## Insects

Insects perhaps show the widest array of mate guarding for two main reasons: (i) sperm longevity, allowing enough time for multiple males to compete for the eggs fertilization; (ii) mating occurs in conditions of high densities, where searching males fight for the possession of females, resulting in “gregarious mating.” Therefore, mate guarding has been observed and well studied in this group. One of the most common features among insects is that copulation duration is often longer than the required for transmission of full seminal fluids and sperm. The presence of the male’s genitalia acts as copulatory plugs and prevents other males from inseminating the female. The most commonly shared type of mate guarding in this group is the postcopulatory one and the last male to mate with a female fertilized the greatest proportion of eggs (last male precedence) is usually the norm among insects (see Alcock 1994).

**Lepidoptera** Butterflies and moths follow a well-known mating system, in which the female remains close to its emerging site, emits a long-distance chemical calling, while males search persistently those females by means of sensitivity to their pheromones. The lesser waxmoth *Achroia grisella* shows an extended mating time as a form of prefertilization mate guarding. Conversely, other moth species, such as *Pectinophora gossypiella*, males enter a refractory period, becoming sexual inactive for approximately 24 h after mating. This difference might result from the virtually absent cost of a second mating trial. Additionally, flying has a high energetic cost and, for such a short living creature, attempts to remate or stay in a refractory period and avoid flying is advantageous.

**Hemiptera** Prolonged postinsemination copulation is also common in Hemipterans species with dense aggregations where encounter probability among individuals is high and population is male biased. Additionally, in *Lygaeus equestris*, the last male to fertilize may sire up to 90% of the subsequent eggs.

Most species with prolonged insemination, such as the cotton stained *Dysdercus* sp., *Nezara viridula*, water striders *Gerris remiges* and *G. lateralis*, departs soon before oviposition. Water strider males ride passively on the back of the females after copulation and its function as mate guarding has been discussed over the years. Females may storage sperm up to 30 days and stay fertile up to 60. Hence, one or a few matings are sufficient for the complete fertilization of her eggs and multiple matings may have little benefits in terms of increased fertility. As for the males, the last one to mate will sire about 90% of the upcoming brood in many species from the *Gerris* genus (Arnqvist 1988). Additionally, since many water striders are polyandrous, there should be minor gains to the male in providing protection to the female and, instead, mate guarding serves mainly as paternity insurance.

However, in the soapberry bug *Jadera haematoloma*, male stays with the female even after she has laid her eggs, guarding her and eventually recopulating afterwards. Female soapberry bugs take 25 days (for single copulation) for complete sperm depletion. Paternity loss for females that copulated with multiple males accounted for 60%. Carroll (1991), however, considered as “enigmatic” that males guarded only during one oviposition, hypothesizing that the time taken to find another mate and guard her until oviposition must be greater than the time required for waiting the first female to produce another brood.

**Orthoptera** Crickets complete their copulation when the male transfer a spermatophore, a small sperm-containing ampulla that hangs outside the female’s body. Females usually dispose the spermatophore by consuming it and often do it before it has been emptied. Thus, one of the hypotheses for the evolution of postcopulatory mate guarding in crickets accounts for the prevention of early removal of spermatophore and presenting the female with a nutritious part of the spermatophore (the spermatophylax) so that she remains close and occupied. Another hypothesis is that while the male maintains close proximity to the female, he has enough time to produce an extra

spermatophore, allowing him to recopulate with the same female. The third hypothesis is that mate guarding functions to impend the approach of other males and reduce sperm competition. Mated females will mount intruder males and the thrusting actions may increase the risk of dislodging the previous' mate ampulla. Although it also prevents premature ampulla removal, unlike the first hypothesis, this one excludes other males approach rather than controlling the female.

Males initiate mate guarding immediately after copulation by maintaining close proximity to their mates through many tactics, such as standing right next to the female, frequently antennating the female, searching rapidly if she becomes unreachable, producing aggressive chirps upon movement from an intruder male, and physically attacking this intruder.

In decorated crickets *Gryllobates supplicans*, mate guarding did not prevent premature removal of the sperm ampulla. Yet, duration was positively correlated with the ampulla retention. However, males that manage to deflect courtship attempts of intruder males reduced the molting frequency of their mates and concomitantly reduced the risks of ampulla displacement.

## Vertebrates

### Fish

“Bone Fish” Females are almost universally correlated with fecundity and males engage in parental care. Most of the studies with fish thus relate mate guarding with the actual guard of the brood and nest. Therefore, much of the observed mate guarding is overlapped with parental care. Still, if mate guard is a strategy to increase paternity, deserted or unattended eggs are likely to die, becoming a waste of time and energy.

Among Amazonian cichlids, both parents rear the young, with the male being more assiduous than the female. However, Yamamoto et al. (1999) has emphasized that male-male aggression serves both offspring protection and territory protection. The latter, in turn, is elementary to partner acquisition and retention.

In Mediterranean wrasse *Symphodus ocellatus*, males may experience no sperm competition even with as many as 20 males vulturing nests. Three independent male mating strategy occur in this species, similar to the pattern observed in lizards: (i) larger males build nests (“nesting males”) and guard females, with lower production of sperm; (ii) intermediate-sized males (“satellite males”) does not guard and produce a similar amount of sperm as the nesting males, and iii) smaller males (“sneakers”) are incapable of guarding nests and are specialized in sperm competition with their increased gonad mass. Thus, males may switch strategies between allocating more resources to sperm competition or to mate guarding, depending on which conditions are worthwhile endeavor in each season. Satellite males decrease the number of sneaker males by joining their spawn and may allocate energy to mate guard. Sneakers, on the other hand, contribute significantly more to sperm as they are unable to guard against large nesting males or larger satellite males. Interestingly, both males and females of the monogamous butterflyfish *Elacatinus evelynae* are aggressive toward same sex intruders and are consistent with mate guarding by both sexes.

Several fish are sequentially hermaphroditic (individuals first functioning as one sex and then changing to the opposite sex). Sex change control is influenced by the dominant individual that aggressively overt others. Although there are other exogenous and endogenous factors that control sex change in fish, social control has been observed in anemone fish *Amphiprion*, in which females control the production of other females by means of dominant aggression over males. Some species within this genus such as the skunk clownfish *A. akallopisos* are monogamous in pairs or in groups, of which the largest individual is always a female that is dominant over other group members. The largest male prevents other males from spawning, maintaining the monogamy of the group. The removal of the dominant female leads to one subordinate male (beta) taking over the alpha position and change his sex. Such system may have evolved due to low density population of host anemones.

**“Cartilaginous Fish”** Male sand tiger sharks *Carcharias taurus* have been reported to present mate guarding behavior in captivity, with the usual scenario of the dominant male physically excluding rivals from females until he has copulated with them.

### Amphibians

Most of amphibians are polyandrous with sequential polyandry. Sequential polyandry is when the female mates with one male and produces a clutch of eggs of this one male, then leaves the eggs either being incubated by him or unprotected, while moving on to another male in a different nesting place. In the most common anuran mating behavior, the male stays mechanically attached to the females (amplexus) until she has laid the eggs, eventually releasing his own sperm. Some males even developed nuptial pads on their forearms, a morphological adaptation to ensure a tight grip on the female. Females are usually larger than males and similar to what has been observed in spiders; larger females produce larger clutches of smaller ova. Hence, these larger females are also of greater value for males.

The amplexus may be considered as mate guarding behavior as unpaired males try to access females by dislodging amplexant males. Attempts of multiple males to participate and mate with a single female occur frequently. In many explosive breeding ranids, availability of female is brief due to its abbreviated breeding seasons. Among these species, prolonged amplexus is considered as a mate guarding mechanism. The term “mate guarding monogamy” has been applied for frog species such as *Atelopus* sp., in which male remains amplexed to the female as long as 32 days prior to the egg release. Male-female duetting of the South African clawed frog *Xenopus laevis* serves, among other functions, as pair bond maintenance, territory defense, and acoustic mate guarding.

### “Reptilians”

Long-term mate guarding is apparently rare in ectothermic vertebrates (usually referred as “cold-blooded” vertebrates), consisting of periods shorter than 24 h.

The largest *Ameiva* males attain the right to guard females, when the male fights with other males and the winner stays in close proximity to her. The male guards the female and copulates with her just before she returns to the burrow at the end of the day, though he carries on guarding for a while before he returns to his burrow. When she emerges the next day, the cycle repeats, with guarding lasting until the end of her receptive period. In a population from the Lesser Antilles, females spend more time foraging while being guarded by males, suggesting that mate guard also serves as extra protection for her, expelling males but also alerting for potential predators. While *Ameiva plei* is a nonterritorial species and, thus, males neither control nor monopolize resources, old *Psammudromus algirus* males are territorial. These elderly males court females for long periods, copulate with them, and guard them afterwards.

Side-blotched lizards *Uta stansburiana* present three male morphotypes. The ultradominant males are orange throated, sneaker males are yellow throated, and intermediate dominant males are blue throated. The ultradominant males have naturally high plasmatic testosterone levels. Conversely, yellow-throated males present lower plasma levels and mimic females in order to avoid agonistic encounters with these ultradominant males. They also do not defend territories but have large home ranges that include many orange males, copulating with some females that the ultradominant did not manage to monopolize. Yellow-throated may transform into blue throated individual within the dearth of territory defenders. Intermediate blue-throated males have intermediate testosterone levels and bear modest territories, efficiently protecting fewer females from the sneaker yellow males. They are, though, incapable of winning contests against the ultradominant orange males. Their relative reproductive success may change throughout time and change morphotype frequency in populations.

In the snow skink *Niveoscincus microlepidotus*, males and females form pairs, males are highly aggressive toward other approaching males, and therefore, it is considered as a type of

mate guarding. It is unclear if males guard reproductive females that they have already mated or if they guard females that are in the imminence of birth giving and becoming receptive shortly (within a few weeks). They use their chemosensory ability to recognize mates and prolong pair formation.

### Mammals

Poligamy is almost ubiquitous to mammals. More specifically, polygyny is the prevailing mating system, where male mammals control access to many females. Hence, guarding male is a common scenario within this group of animals.

**Monotremata** Echidnas hibernate and males emerge from hibernation before females. As soon as 30 days after the end of hibernation, males are ready to mate. Males remain reproductive active for about 60 days but stay with females up to 7 days. There have been males that stayed in close proximity with up to four females. It appears that males are promiscuous rovers that guard promiscuous females before and after mating. In Tasmanian echidnas, some males were found mating repeatedly with hibernating females thus insuring high probability of successful paternity since females appear to be induced ovulators (copulation triggers ovulation).

**Marsupialia** Many Australian marsupials are semelparous (breed once in their lifetime and then die). Mate guarding thus presents an extra energy load to this costly reproductive strategy. The brown and the agile antechinus, *Antechinus stuartii* and *A. agilis*, are semelparous marsupials and present extended copulation periods that are considered as a form of mate guarding. This tactic, although not effective in obtaining exclusive paternity, reduces sperm competition and/or displacement.

Among platypuses *Ornithorhynchus anatinus*, females seems to actively control encounters with possible mates. The female may alter their activity patterns until she becomes receptive and males had little capacity to control courtship, and, therefore, unable to mate guard her (Thomas et al. 2018).

**Small Mammals – Rodentia, Chiroptera, and Lagomorpha** Rodents have variable mating systems, from monogamy to promiscuity. Prairie voles *Microtus ochrogaster* have been extensively studied and males can be either monogamous or polygynous. Those monogamous long-term bonders guard females from other males. Within dominance hierarchies, dominant males Cape ground squirrels *Xerus inauris* enjoy greater reproductive success as they are more outstanding in guarding females.

Precopulatory mechanisms include overtaking conflicts, such as vigorously preventing rivals to access females by guarding them. Postcopulatory mechanisms include copulatory plugs to delay female remating. Precedence for matings is also common among rodents. Mate order effects influence the male strategy. If there is a first male advantage, such as Belding's ground squirrel *Urocitellus beldingi*, males resume search as soon as copulation is completed. However, if there is a last male advantage, like Idaho ground squirrel *Spermophilus brunneus*, mate guarding is likely to be a mechanism to reduce sperm competition. Male maras *Dolichotis patagonum* typically mark estrous females by urinating on them. Some researchers agree that male urination on females could be olfactory mate guarding, but the diverse context of this behavior leaves plenty of room for other theories. In many prairie dog species (*Cynomys ludovicianus*, *C. parvidens*, and *C. gunnisoni*), the male sequesters the estrous female in a burrow with only one exit and he protects the burrow, preventing her from exiting and preventing other males from entering.

Among bats, polygynous species such as *Uroderma bilobatum*, *Vampyressa nymphaea* and *Artibeus* sp., males defend critical resources that are important to females and they defend these resources in order to gain reproductive access to those females. Therefore, this represents a form of mate guarding. In other species, such as *Myotis daubentonii*, sperm is stored and ovulation and fertilization occur seasons later, making mate guarding practically impossible.

Interestingly, the brown hare *Lepus europaeus* hybridize with the mountain hare *L. timidus* and different guarding behaviors have been observed in



interspecific sexual interactions. Dominant brown hare males mate guard females that is close to oestrus. If males from both species court a mountain hare female, the brown hare male simply chase away the mountain hare male. The mountain hare female will be limited to interact with the brown hare male as she approaches oestrus.

**Ungulata** Ungulates present a territorial harem defense, in which males are territorial and females are gregarious. The male, usually one, guards and protects the females, mating with all (or most) of them. Yet, association does not last long, remaining until parturition. The formation of harem is associated with a lot of stress for the male that, not infrequently, is depleted at the end of the mating season. Some bucks reduce up to 20–30% of its body mass during breeding season and some even die of starvation and wounds caused by fights. However, both sexes benefits from mate guarding: males defend their own reproductive interests and, consequently, they augment foraging and reproductive success of his harem.

**Cetacea** High mobile females, such as cetaceans, may limit opportunities and benefits of mate guarding. Monitoring female movement, maintaining proximity, and supervising potential rivals are energetically costly. For these reasons, mate guarding is an uncommon male tactic among cetaceans. Dall's porpoise *Phocoenoides dalli* males present close proximity with females and of lengthy nature (several hours and possibly days). These guarding males show shorter dives, suggesting that they spend less time foraging deep and more time guarding. Factors that facilitate this lasting mate guarding behavior remain unknown. Female odontocetes are spontaneous multiovulators. Theory suggests that either they stay receptive for long periods or males are unable to anticipate the timing of ovulation (or both), favoring extended mate guarding. Guarding may have substantial costs for male weight and general condition, but male Dall's porpoise increases its body mass at the onset of female oestrus, supporting that they buffer energetic deficit and curtail condition decline over the breeding period.

In bottlenose dolphins *Tursiops truncatus*, male duos and trios formed consortships with

single females up to several weeks. A consortship is an association between a dyad (in this case, the male coalition and the single female). These male pairs and triples traveled up to two body lengths away from the female, behind or flanking her. The female is coerced to stay close, with males using vocal or physical threats to keep her close.

**Carnivora** There are several social representatives in carnivorans and many societies show high reproductive skew, with a dominant pair (or alpha pair) Monopolizing up to 90% of the breeding opportunities within a group. Dominant males are thus capable of guarding the dominant female due to its high-ranking hierarchy. It is not uncommon, though, that dominant males are cuckolded, or, in other words, that his female partner seeks for other male (see “► [Extra-Pair Copulation](#)” entry). Despite the amount of time spent alone, many dominant males do not monopolize entirely the paternity of a litter, as seen in dwarf mongoose *Helogale parvula*, African wild dogs *Lycaon pictus*, and meerkats *Suricatta suricatta*. Many pinnipeds (walruses, sea lions, and true seals) have harems. One male protects and guards a large set of females by competing, sometimes aggressively, with male invaders.

**Primates** Copulatory plugs are common among mammals and even more so among primates. Moreover large testis size is correlated with high sperm competition since they are required to sustain an increased volume of sperm production in order to outcompete mates. Some groups are composed of multiple individuals of each sex (named multimale-multifemale mating systems), such as macaques (*Macaca* spp.) and chimpanzees (*Pan troglodytes*); females usually copulate with two or more males when conception is imminent. Non-gregarious primates such as nocturnal prosimians also show large testes and females are too expected to mate with more than one male. Conversely, monogamous species such as the owl monkeys *Aotus* and gibbons or polygynous species tend to have relatively small testes because females mate with a single male and sperm competition is not as likely to occur. Even with this variety of strategies, nearly all primates present

copulatory plugs, from a more rudimentary type (seminal coagulation) to a more complex type (semisolid plug that molded to the female's vagina). Although the copulatory plug serves well as "chastity belt," it may also function to help sperm survival and leakage.

Although no primate sperm seems to be completely fluid, neotropical primates still needs further research to confirm this general trend. For instance, some howler monkey species have fluid semen and small testes. Nonetheless, males are notorious for its high volume howls emitted by its utterly adapted hyoid bone and larynx. Louder males are more capable of female monopolization, and selection pressure is relaxed on testes among *Alouatta* genus, limiting the need of sperm competition. Could vocalization be a sonorous way to mate guard?

**Humans** The strong desire for privacy during sex could reflect guarding intentions by humans. Despite their serial monogamous behavior, half of men and half of women have or wish to have engaged in extra pair encounters. Moreover, women are usually referred as "concealed ovulators" due to lack of obvious signals of her fertile period. Subtle changes, such as increased symmetry and odor alterations, follow up their menstrual cycle. However, men cannot discern consciously and it usually takes a considerable amount of time spent together for men to perceive these alterations. Both issues favors long pair bonds and high paternal reliability among humans. Buss (2002) stated that there are currently about 20 different mate guarding tactics among humans, such as vigilance (calling at unexpectedly to check up on partner); violence (beat up rivals); mate concealment (be not accompanied in public by the partner); time monopolization (spending all free time with partner); verbal threat; rival denigration; physical signs of possession (hold hands); resource display (expensive gifts); appearance enhancement; sexual inducement; and possessive ornamentation (wedding rings).

### Birds

Birds have an interesting energetic feature. Flying is 15 times higher than basal metabolism, when

compared to walking that is only 1 to 2 times higher. Thus, it is less energetically costly to stay on the ground than fly to flight. Additionally, many birds are monogamous, a mating system considered as an extended mate guarding. Therefore, extra pair copulation is also commonly observed among birds and most of the studies focus on both. Male birds have then evolved a wide array of tactics to avoid cuckoldry, such as frequent mating and mate guard. Mate guarding determination of a male is directly related to the risk of extra pair copulation.

Conspicuous large birds that feed in the open are more likely to present mate guarding, such as the rheas *Rhea americana*, combe ducks *Sarkidiornis melanotos* and the red junglefowl *Gallus gallus*. Not surprisingly, female pheasants *Phasianus colchicus* remain with a single male as he relies on vigilance to escape from predators and to detect other males, a system similar to those of ungulates. Males are too large to hide in vegetation, and like many other large birds and mammals that live in the open, vigilance takes a good proportion of their actions. While, again, males spend less time feeding when accompanying their females, females gain protection. Escorted females spend three times more feeding, a system indeed similar to those observed in ungulates.

Female passerine birds are not gregarious, and males, instead of guarding individuals, guard areas or territories that contain females, with bonding persisting through incubation. Unlike polygynous mammals, polygynous male birds try to attract females instead of controlling them. Therefore, mate guarding is not as common in this group as it is in large ground-dwelling polygynous species, such as pheasants.

Procellariiforms seabirds such as the colonial *Fulmarus glacialis* are among the longest living birds and present high fidelity to both mate and nest site. Both parents care for the single laid egg and share similar portions of parental care. However, this species store sperm for several weeks after mating and the female stays without any contact with the male for a long period (up to 38 days) for the pre-laying foraging period. This susceptibility is a perfect scenario for sperm competition and extra pair copulation,

so that males need to be resourceful to counterbalance it. Males are the first to arrive and last to leave in nesting sites to keep an eye on his partner.

Among cooperative breeders such as woodpeckers, the presence of multiple males in a social unit sharply increases the likelihood of kleptogamy and selection for more intense mate guarding is strong. Groups with single males present very low frequencies of attendance and following behaviors, considered as by-products of sociality and not true mate guarding. In other words, mate guard functions as within-group mating prevention rather than between groups. If a group presents two breeding males, both will probably share their mate guarding intensity. However, if one of the two copulated first with the female, the other would apply a takeover maneuver to prevent cloacal contact, such as flying into the pair, mounting both, or pecking them. Presence of helpers also plays an important role as workload is diluted among the group individuals. Helpers free breeding males from territory defense and tree maintenance duties allowing breeding males to focus on mate guarding. Acorn woodpeckers *Melanerpes formicivorus* mate guard way earlier than expected and their social system may again explain this observed behavior as the costs of taking too long to start mate guarding are high.

White crowned sparrows *Zonotrichia leucophrys gambelii* are also monogamous and, although males do not incubate eggs, they contribute to parental care by feeding offspring. While his mate is sexually receptive, the male increase territorial defense. Conversely, bank swallows (*Riparia riparia*) guard their mates when they are sexually receptive but seek extra pair matings when the female is incubating.

Communal species (or colonially breeding species) are unable to guard efficiently their mates because at least one of the two must guard the nest site against conspecifics intruders. Extra pair copulation in these species is highly frequent and is considered as the main disadvantage of colonial breeding.

Many bird species imprint (young birds' mode of learning any specific characteristics that enables it to find conspecifics, separated between filial and sexual imprinting). Ducks are among the most familiar imprinters, but there are other representatives, such as great tits *Parus major* and blue tits *Cyanistes caeruleus*. In an interesting study between these two species, Hansen et al. (2009) cross-fostered males. Although cross-fostered great tits guarded, they guarded less than control males, both in terms of distance and degree of following, regardless of the female species. Cross-fostering clearly affected their guarding behavior as they failed to perceive conspecific partners. Imprinting behavior partially explains why many bird species end up forming same-sex pair bonds or engaging same-sex sexual behavior (male geese *Anser anser*, mallard ducks *Anas platyrhynchos*, and Japanese quails *Coturnix coturnix japonica*).

## Conclusions

Mate guarding enhances paternity of the one guarding, but the guarding individual suffers from decreased body condition. Mate guarding is consistently reported in males due to differences in reproductive strategies between the two sexes: males produce tiny and numerous sperm and females produce large and rare ova. Thus, nearly every male will compete for an egg at least once in their lifetime. Mate guarding is more pronounced when availability of females is brief, either due to short breeding seasons or due to short fertile period. Mate guarding evolved to reassure paternity of the guarding male, although evolution should also confer some selective advantage to the female. Guarded females will be more protected against predators and against other males, whose attempts may constitute energy waste and injuries to the female and/or her eggs. Conversely, the female's interest may not be aligned to her guarding male's, and his presence may interfere with her foraging success. In species in which males are larger than

females, larger males guard more efficiently. However, in species where females larger than males is the rule, larger females are generally associated with higher fecundity and, thus, those are the ones more likely to be guarded and competed for. Mate guarding may be of sonorous nature, as observed in frogs; chemical by means of copulatory plugs; mechanical by the grasp of male beetle, or behavioral, when the male fights with other males and follow up an oestrus female until she becomes receptive. Mate guard can occur many days prior to fertilization and last for a lifetime after copula (monogamy). Female mate guarding has been only observed in birds (so far). Mate guarding tactic of female birds is to request frequent copula. By this, she will lead the male to exhaustion, emptying his sperm stock and energy reserves.

## Cross-References

- [Extra-Pair Copulation](#)
- [Sexual Selection](#)
- [Sperm Competition](#)

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## Mate Protection

- [Mate Provisioning](#)

## Mate Provisioning

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## Synonyms

Mate protection; Nuptial gift; Resource provisioning; Sexual cannibalism

## Definition

Providing one's sexual partner, or a prospective sexual partner, with material resources (such as food) or protection from predators or intrasexual competitors.

In many sexually reproducing species, one sex often will provision a member of the other sex with protection, food, or other resources to gain or maintain sexual access. Females are typically the sex with a larger obligate parental investment for offspring production, and as a result, males exert greater mating effort to gain sexual access to females. Males of many species exert mating effort by provisioning females with protection or material resources, sometimes in the form of a "nuptial gift."

## Nuptial Gifts

Nuptial gifts often are provisioned as a nutritional resource. For example, males in several avian species engage in courtship feeding, wherein they feed prey to their female partner (Jawor and Breitwisch 2006; Mougeot et al. 2006), and male scorpion flies gift females with dead insects or secretions from their salivary glands (Liu and Hua 2010; Thornhill 1981). In several species of spider, including the fishing spider, males offer themselves as a nuptial gift, being devoured by the female while and after they deposit their sperm in the female's reproductive tract (Arnqvist and Henriksson 1997).

Evidence from tribal and postindustrial societies suggests that humans also provision resources to prospective mating partners, though the type of resource provisioned varies across cultures. Several articles reviewing evidence from tribal societies suggest that men may provision food, and in particular meat, to attract mating partners (Bird 1999; Hawkes and Bird 2002; Jaeggi and Gurven 2013). Evidence from a Western, industrialized population suggests a similar pattern, with participants judging displays of resource potential to be the most effective strategy for men pursuing a long-term, romantic relationship (Schmitt and Buss 1996). However, participants from the same study judged immediately giving resources to be the most effective strategy for men pursuing a short-term sexual partner, indicating that the type of relationship pursued is important when considering the effectiveness of different provisioning strategies.

## Protection

Males may also provision their current or prospective mating partners with protection, either from predators or from sexually coercive males. Protection against rival males (also referred to as mate guarding) has the dual adaptive benefit of protecting against cuckoldry for males and protecting against copulation attempts from undesirable mates for females. Research involving mate protection behaviors in several avian species provides evidence for the adaptive benefits to females of protection by a male partner (Hogstad 2015; Lemmon et al. 1997). Specifically, partnered female willow tits received less aggression and experienced a higher foraging rate relative to unpartnered female willow tits (Hogstad 2015). A study of black-capped chickadees found similar results, observing that females paired to alpha males experienced less frequent aggression and a higher feeding rate (Lemmon et al. 1997).

Mate protection behaviors have also been observed in humans; however, these protection strategies have mostly been researched in the context of mate guarding against rival men, rather than protecting one's partner from nonsexual



harms. Several studies have identified a range of strategies that men report using in their long-term romantic relationships to guard against mate poaching by rivals (Buss 1988; Buss and Shackelford 1997). There has also been research investigating the potential benefits that women may receive as a result of mate guarding. Hughes et al. (2004) found that, among college students, women are more likely to initiate sleeping with their sexual partner after intercourse. Hughes and colleagues suggested that, similar to other forms of mate guarding, sleeping with one's sexual partner may serve the adaptive function of guarding against cuckoldry for men and protecting against forced copulation from other men for women.

Males of many sexually reproducing species, including humans, exert mating effort in order to gain sexual access to females. This mating effort often takes the form of provisioning gifts or protection to the female. Mate provisioning is one method by which males compete with one another for access to mating opportunities, and therefore, a male's ability to provision protection or resources can have considerable consequences for his reproductive success.

## Cross-References

- [Mate Guarding](#)
- [Mating Effort](#)
- [Nuptial Gift](#)

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## Mate-Finding

- [Mustelidae Navigation](#)

## Mate-Guarding

- [Territory Defense](#)

## Material Culture

- [Tool Use](#)

## Maternal Behavior

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## Synonyms

Mother's behavior

## Definition

Set of behavioral patterns exhibited by the female parent.

## Introduction

Maternal behavior encompasses all the responses and behaviors displayed by the mother towards her offspring. These behaviors ensure the survival of the offspring and its effective development and growth, both mentally and physically (Wang and Storm 2011). Mothers are often the primary caregivers in mammals. However, in many other species, fathers contribute substantially to parental care. Providing food, warmth, shelter, protection from predators, and grooming are some of these behaviors. Maternal care entails prolonged interaction with the offspring, usually spanning days, months, or even years. Variation, with respect to intensity and frequency, is observed when relating these behaviors to the temporal stage of offspring development. During gestation, aggression towards intruders and nest building behaviors are observed. At parturition, many mothers, especially mammalian mothers, consume amniotic fluids and placenta (placentophagia). These

behaviors provide nutrition to the mother, facilitate lactogenesis, and have many other benefits. After the birth of offspring, two types of behaviors are observed, those directed at the offspring and those indirectly correlated with the offspring. Active nursing, retrieval of pup, licking, and grooming are few examples of offspring-directed behaviors. Protection of offspring from threats, nest building, lactational hyperphagia, or elevated levels of food consumption are few examples of indirectly associated offspring directed behaviors (Bridges 2015). Maternal behaviors in oviparous animals include egg-laying site selection, egg-attending, burrowing, nest building, brooding, etc. In viviparous animals, provision of food, nursing, defense of offspring, and teaching of sustaining skills are some distinctive maternal behaviors (Dulac et al. 2014).

## Types

There are various types of parental care among mammalian neonates that differ with respect to the maturity of the newborn like altricial, intermediate, and precocial. Nature of care is further determined by the postnatal growth rate, litter size, social structure, etc. In the altricial type, the mother gives birth to immature young ones. They are characterized by blindness and deafness, with limited locomotor and sensory capabilities. The offspring are overly dependent on their mothers for basic processes such as urination and defecation. The mother licks the anogenital area, thereby stimulating it, and this stimulation facilitates urination and defecation in the young. In addition, the offspring lack fur and are unable to regulate their body temperatures. Nesting patterns are crucial to the altricial type of animal rearing. The mother gives birth to many offspring at the same time; hence, the one-on-one emotional bonding between the mother and each offspring is infrequent. Some examples of animals in which altricial type of maternal care is observed include mice, rabbits, rats, hamsters, squirrels, etc. (Kendrick et al. 1997; Levy 2016).

Precocial is another type of rearing in which the mothers give birth to fully developed young.

The offspring are characterized by relatively mature locomotor and sensory capabilities and are able to regulate their body temperatures and stand up, after some time, if not immediately. Nesting behaviors are almost never detected. The mother gives birth to a small litter (one or two offsprings). This helps the mother distinguish her offspring from other infants. The mother forms an attachment with her offspring and may show hostile behavior towards other infants who approach her for milk. Hence, they develop discriminative maternal care, whereby they reject other infants and favor their offspring. Some examples include sheep, goat, horse, deer, and cattle (Kendrick et al. 1997; Levy 2016).

The third type is termed as the intermediate type. Maternal care in this type can be classified as semi-altricial and semi-precocial. They are characterized by functional hearing and vision modalities but limited locomotion and thermoregulation. Some species do build nests, while some carry their young ones. The litter size is small, and the mother gives birth to one or two offspring. The mother shows maternal care only towards her own offspring but doesn't necessarily reject other infants like the ungulates. Such type of maternal care is observed in primates, humans, and suids (e.g., pigs) (Kendrick et al. 1997; Levy 2016).

## Neurobiology Behind Maternal Behavior

Maternal care often comprises detection and processing of offspring-related cues and indulging in behaviors such as licking, grooming, nest building, etc. (Kohl et al. 2017). There are two neurobiological circuits underlying maternal care, one that suppresses and the other that promotes maternal care.

Offspring-directed aggression has neurobiological correlates such as detection of cues by vomeronasal organ (VNO) and processing of these cues by medial amygdala and bed nucleus of stria terminalis (Kohl et al. 2017). Inhibition of maternal care and initial avoidance behaviors in virgin rats are linked to the medial amygdala that receives direct projections from accessory olfactory bulb.

Stimulation of main olfactory epithelium (MOE), tactile, and auditory pathways by a stimulus that is generated by offspring leads to constructive maternal behaviors. An important brain region underlying positive parental care is the median preoptic area (MPOA). Lesions in this area result in diminished motor activity on the caregiver's part, e.g., offspring retrieval. Onset and maintenance of maternal behavior are disturbed by deafferentation, chemical inactivation, and excitotoxic lesions in this area (Fang et al. 2018). Studies show that maternal behavior is aided by direct hormonal stimulation of MPOA. Pregnancy-related hormone receptors and modulators are highly exhibited in this area (Kohl et al. 2017).

The MPOA neurons are GABAergic, and therefore they exert their control via inhibition. Multisensory offspring cues are integrated at the MPOA neurons, which then send their projections directly to nucleus accumbens or indirectly via the ventral tegmental area (VTA) or retrorubral field. The dopaminergic neurons of the VTA mediate motor activities such as pup retrieval. This one-to-many organization of projections helps coordinate the complex expression of maternal behaviors. The paraventricular nucleus (PVN) of hypothalamus and dorsal raphe (DR) regulates this motivational pathway. The neuronal circuits mediating onset and maintenance of maternal behaviors are disparate, with the PVN more directly involved in maternal care induction (Kendrick et al. 1997). MPOA neurons expressing the neuropeptide galanin are essential in regulating the proper execution of parenting behaviors. Ablation of these neurons leads to impairment of crouching behavior, pup retrieval, nest building, and other critical maternal care behaviors (Kohl et al. 2017).

## Endocrinology

Multiple similarities and differences have been observed across species with respect to hormonal influences in mediating maternal behavior. It is debatable as to whether these hormones are essential for exhibiting maternal care. The peripartum period is distinguished by fluctuations in steroidal

hormones. During gestation, levels of estrogen and progesterone rise. These hormones, along with protein hormones such as oxytocin and prolactin, are known to activate maternal behavior. When progesterone levels fluctuate, uterine contractions are induced, and that is further boosted by the release of oxytocin. Prolactin levels rise in concordance with parturition thereby facilitating milk production. Oxytocin mediates milk ejection in response to offspring's suckling. Neuropeptides and steroidal hormones have both short-term and long-term effects. Short-term effects include membrane potential modulation, whereas long-term effects include gene expression modulation (Kohl et al. 2017). These hormones work closely with MPOA neurons to regulate maternal expression.

Estradiol 17 beta, the active form of estrogen, plays an important role in stimulating maternal behavior in various species such as sheep, mice, nonhuman primates, etc. These behaviors are mediated by estrogen receptor alpha (ESR1). One of the brain regions that express the highest levels of ESR1 is the MPOA, thus implying that estrogen is crucial in motivating maternal care (Bridges 2015).

Progesterone promotes gestation and regulates lactogenesis as well as maternal expression. It primes the brain to be sensitive to the offspring's cues at parturition and regulates the timing of this heightened sensitivity (Bridges 2015). Progesterone activity is mediated by progesterone receptor-mediated ligand-dependent nuclear transcriptional factors.

Intracerebroventricular (ICV) infusions of oxytocin in rat brain demonstrate short-latency maternal responses in virgin females. Delayed postpartum maternal behavior is demonstrated to be associated with lesions in this area. Oxytocin antagonist infusions into the olfactory bulb negatively affect the onset of maternal behavior (Levy 2016). MPOA and VTA are other sites of oxytocin action. Oxytocin's action is more evident in estrogen-primed or anosmic females (Kendrick et al. 1997). Maternal responsiveness is stimulated by prolactin in prior steroidal-primed virgin rats. Rapid onset of maternal care is observed in

such rats after infusions of prolactin and placental lactogens into the MPOA. Offspring retrieval and crouching behavior are known to be promoted by prolactin.

Neurotransmitters such as dopamine, norepinephrine, serotonin, galanin, etc. are implicated in maternal behavior. Dopamine is associated with both induction and maintenance of maternal care. The onset of maternal care has been linked to dopamine D1 receptor in the nucleus accumbens. Blockage of dopamine D2 receptor hampers maternal care but fails to prevent the establishment of maternal memory. Studies show that olfactory learning of offspring recognition in ewe is mediated by beta-adrenergic receptors of the olfactory bulb. Selected aspects of maternal expression are correlated to relative noradrenergic tone. Serotonin is another decisive neurotransmitter regulating maternal care. Lesions of median raphe impair offspring-associated responses and postpartum care (Bridges 2015).

## Stress

Experiencing stress while carrying out the duties of a parent is a common phenomenon. Parenting stress is a set of processes that result in detrimental physiological and psychological reactions in response to attempts at adapting to parenthood. Moderate levels of this type of stress can be correlated with effective maternal motivation. However, high levels have a myriad of detrimental effects. Negative parent-offspring relationship, harsh and reactive parenting, and impairment of the well-being of the mother are some examples of deleterious effects of maternal stress. Studies have shown that maternal love is mediated by brain regions such as the right orbitofrontal cortex, anterior insular cortex, periaqueductal gray region, and basal ganglia. Chronic and acute stress hinders functions of these regions, especially the orbitofrontal cortex causing emotion dysregulation, etc. Therefore, it is inferred that the orbitofrontal cortex is related to stress resilience (Noriuchi et al. 2019).

In addition, maternal distress is closely linked with infant developmental delay. Studies conducted on rat and monkey elucidate this relationship. If the gestating mothers are exposed to stressors such as electric shock and loud noises, many permanent alterations are observed in the offspring. Alterations in social and sexual behaviors, reduced adaptive and exploratory behaviors, delayed motor development, and impaired attention and learning are some of the effects (Mulder et al. 2002).

## Diet

Diet is commonly acknowledged to be closely correlated with behavioral outcomes. Moderate and severe vitamin B12 deficiency is known to result in negligent maternal behavior in mice. The occurrence of anxiety and depression phenotypes is observed in such micronutrient-deficient mothers (Ghosh et al. 2018). Severe maternal undernutrition during pregnancy affects glucose metabolism in the offspring. In rats, impairment of insulin sensitivity and hypertension are detected in offspring in response to restricted maternal protein intake. In the presence of limited nutrient availability in the environment, the mitochondria in the fetus greatly enhance its activity. Consequently, reactive oxygen species (ROS) levels also rise, causing oxidative stress buildup inside the cell. This leads to metabolic changes in offspring.

Conversely, increased nutrient availability during pregnancy leads to obesity in offspring. Obesity is correlated with inflammation and oxidative stress. In addition, it is known that it exerts its detrimental effects via mitochondrial dysfunction (Rando and Simmons 2015).

## Animals in Focus

### Domestic Sheep

Immediately after parturition, a bonding period is observed between the ewe and the lamb that is characterized by intensive grooming behavior

and frequent low-pitched vocalization. However, this behavior declines after a few hours of parturition. Sheep are precocial animals, i.e., the lambs are mature and are able to perform most of the essential functions on their own. There are differences among species of sheep in relation to maternal “styles” of parenting. The Suffolk ewes are predominantly rejecting, whereas the Blackface ewes are infrequently rejecting mothers. Maternal experience differentially affects few features of maternal behavior, such as a reduction in aggression towards offspring, noncooperation with sucking behavior, etc. These effects are independent of other maternal behaviors such as grooming (Dwyer and Lawrence 2000).

### Cattle

Prior to calving, the female cow separates from the herd and selects a nesting site. Cattle, like other precocial animals, invest little effort in building a nest. Standing bouts increase by 80%, and they become restless. Calving is accomplished in a recumbent position.

Licking and grooming behaviors are observed in the first hours after parturition. These behaviors help dry the calf's coat to reduce evaporative heat loss and help establish a familial bond. Lack of licking is associated with impaired maternal behavior, due to the fact that the mothers haven't learned the calf's odor. Maternal experience is a strong determinant of the occurrence of such behaviors. Ingestion of the placenta (placentophagia) postparturition is often observed (von Keyserlingk and Weary 2007).

### Wild Orangutan

Young Bornean orangutans are solely dependent on their mother's milk for nutrition. Solid foods are incorporated in diet after 12–18 months. Increased fruit availability lessens infant demand for mother's milk and allows the mother to replenish energetic reserves. Infants usually suckle and nest inconspicuously in their arboreal environment. They are characterized by late ages at weaning, female growth cessation, and reproductive maturation (Smith et al. 2017).



## Old-World Monkey

Regular allomaternal care such as playing with infants, carrying, protecting, socializing, handling, etc. is generally absent in old-world monkeys. Nonetheless, there are some exceptions such as the golden snub-nosed monkey (*Rhinopithecus roxellana*, Colobinae). Approximately 87% of infants are allonursed, and this behavior is broadly confined to the first 3 months of an infant's life. Allomaternal nursing was further characterized by kin selection and reciprocity hypotheses that state that the allonursers are related to the infants and the mothers reciprocally nurse each other's offspring (Xiang et al. 2019).

## Conclusion

All types of behavior exhibited by the mother towards her offspring(s) that ensure their survival constitute maternal behavior. Maternal care varies along a wide spectrum of behaviors that are usually unique to a specific species. Maternal behavior is regulated by an integrated neural circuitry, the median preoptic area (MPOA), which promotes active maternal behavior. This is also highly dependent on the hormone levels, such as estrogen, progesterone, oxytocin, prolactin, etc. High levels of parenting stress and inadequate diet can hamper effective maternal care expression. Maternal behavior is critical for upholding the welfare and grooming of the offspring and, hence, is crucial for the perpetuation of species.

## Cross-References

- ▶ Evolution
- ▶ Hormones and Behavior
- ▶ Hormones and Cognition
- ▶ Hormones and Face Preferences
- ▶ Neural Control of Behavior
- ▶ Neural Network
- ▶ Parenting
- ▶ Paternal Behavior
- ▶ Prolactin
- ▶ Sensory Receptors

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## Maternal Immune Hypothesis

### ► Fraternal Birth Order Effect

## Mathematical Modeling

### ► Model Fitting

## Mating

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### Introduction

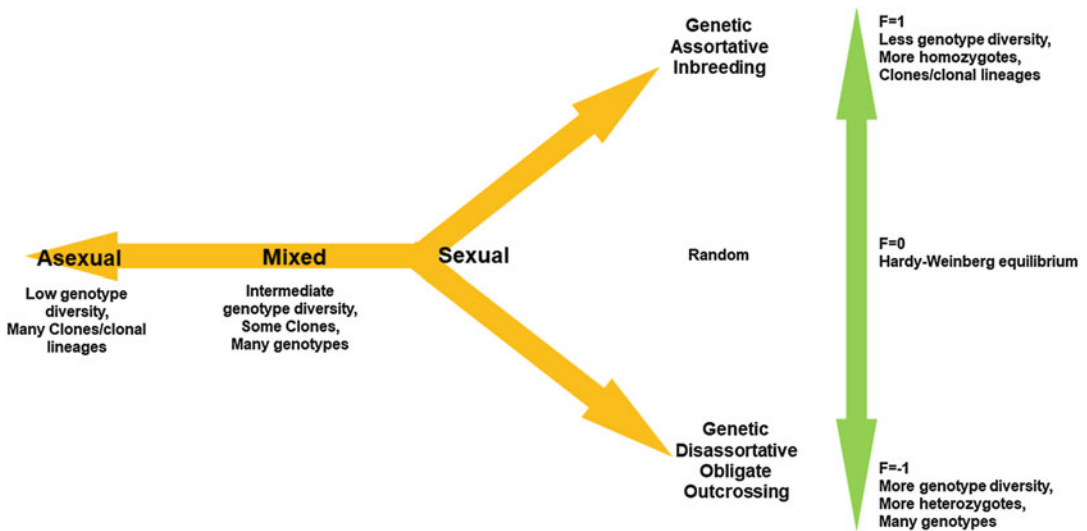
Reproduction is the obligatory process to uphold the gene pool from generation to generation for any existing species. Among the other reproductive processes, mating fulfills the purpose of sexual reproduction by pairing of either two opposite sexually reproducing animals or hermaphrodite organisms in terms of copulation for insemination and subsequent internal fertilization. The term mating not only applied for higher vertebrates but also for bacteria, archaea, and viruses where formation of recombinant progeny occurs from the exchange of genomic information from the involved paired individuals. To understand mating, we must focus on its all arms, i.e., mating system, sexual selection, and sexual conflict.

## Mating System

Mating is initially dependent upon the mating system which itself is a circumstance based on which an organism shows its sexual behavior and further mate choice or sexual selection occurs. This mating system includes monogamy, polygamy (i.e., polygyny, polyandry, and gynandry), and promiscuity. Reproductive system can be asexual, sexual, or mixed type. Mating is only relevant to those organisms which undergo sexual reproduction. Thus, mating system possesses a possible span of continuum that ranges from 100% inbreeding to 100% outcrossing. Basically, the mating system follows Hardy-Weinberg law and thus gives chance to combine the allele within the individual in a population. In outcrossing organisms, new combination of genes occur, which further lead to different genotypes with high frequency of genotype diversity within populations. This outcrossing also put higher potential for rapid adaptations in changing environments. Due to homozygosity or derived from common ancestors, the inbreeding organism doesn't show diverged genotype. Mating systems confirm further the sexual selection processes in the species by affecting mate choice outcomes. In case of plants, the mating system refers to the degree and environments of the crossing, while in case of humans, mating system encompasses the formation of social relationships such as marriage. The mating system can further divide into plant, microorganisms, and animal mating system (Fig. 1).

### Plant Mating System

Plant mating system is mainly of two types, primary mating systems and mixed mating system. In primary mating system, plants can be outcrossed or cross-fertilized, autogamy or self-fertilized, and apomixis or asexual reproductive. Mixed mating system of plants follows mixed mating model which is more basic model; it reduces the complicity of other mating assumption models and assumes that any plant is either autogamy or randomly outcrossed. According to mixed mating model, plants use two or all three



**Mating, Fig. 1** Type of mating system in general

primary mating systems (Brown et al. 1989). Other than the basic mixed mating model, plant mating probability can also be assumed more efficiently by effective selfing model, developed by Kermit Ritland on the 1980s, which recognizes that closely related plants mate more effectively than that of with distantly related plants (Brown et al. 1989).

### Microorganism Mating System

Microorganisms also show three types of mating systems; asexual (by mitosis), mixed, and sexual (by meiosis). Bacteria and viruses reproduce asexually, while fungi and oomycetes can reproduce either asexual, sexual, or mixture mating.

Mating in bacteria mostly occur as homologous recombination where DNA of the donor bacteria transfer and incorporate into the genome of the recipient bacteria. This transfer of the DNA occurs either by transformation or transduction (bacteriophage mediated) or conjugation (plasmid mediated) (Chen and Dubnau 2004). Transformation basically depends on the products of the numerous bacterial genes which crosstalk with each other in a complex way to perform this process and the recipient bacteria accept the transferred DNA (Chen and Dubnau 2004). Before taking up and recombining the donor DNA into its own chromosome, the recipient bacteria enters

its natural competence. For example, *Bacillus subtilis* requires crosstalk of about 40 of its own gene products to procure natural competence, and then the bacterium introduces one third of the whole recipient genome inside its own chromosome (Saito et al. 2006). Among the different varieties of the bacterial species, at least 60 species can naturally able to procure their own competences (Bernstein et al. 2012).

Viruses (animal virus and bacterial virus or bacteriophage) also reproduce through mating and form recombinant virus progeny which ensures the mating interaction at the DNA level. Multiplicity reactivation (MR), a very known term in virology, is the mating between two viral genomes. In MR interaction occurs between two virus genomes, each containing inactivating genome damage within an infected cell. This way MR increases population of viable progeny viruses. For example, gene required for MR in T4 bacteriophage is same as the gene required for allelic recombination (Bernstein 1981). Many previous reports also state about the genes for MR in animal viruses such as herpes simplex virus (Michod et al. 2008), *Adenoviridae* virus (Yamamoto and Shimojo 1971), simian virus 40 (Yamamoto and Shimojo 1971; Hall 1982), *Reoviridae* (McClain and Spendlove 1966), *Vaccinia* virus (Abel 1962), etc.

## Animal Mating System

Animal mating system can be subdivided into following two mating relationships.

(a) **Monogamy:** Monogamy refers when one male shows exclusive mating relationship toward single female which often called as “pair bonding.” Two types of monogamy are facultative monogamy and obligate monogamy. When the species density is very low, mating occurs with a single member of opposite sexes is called facultative monogamy. In case of obligate monogamy, solitary female breeds within the habitat with small carrying capacity. They lack the ability to rear its litter alone and thus receive help from conspecifics (Kleiman 1977).

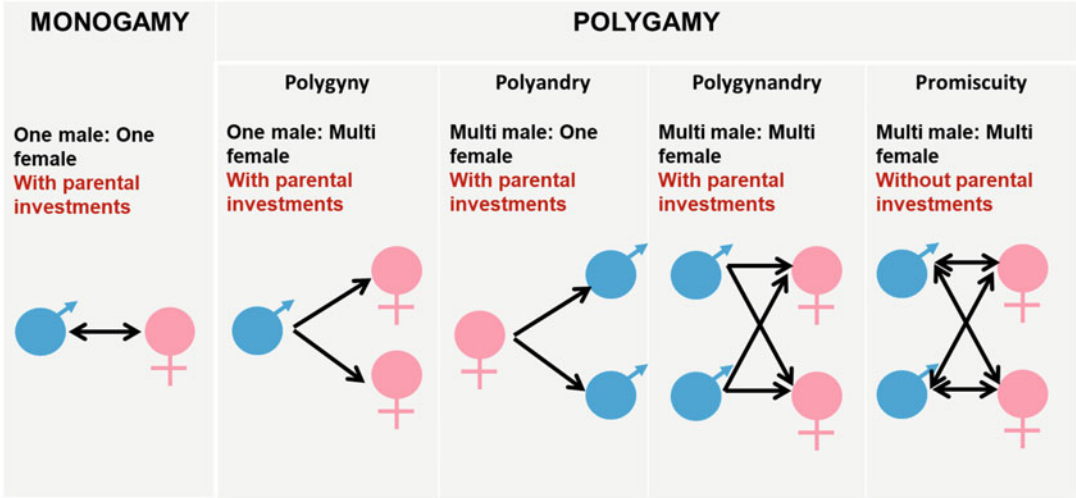
(b) **Polygamy:** The word polygamy is derived from Greek word *polygamia* meaning “state of marriage to many spouses,” i.e., practice of relationships among multiple opposite sexes (Brown et al. 1989; Pickett et al. 2001). According to the relationship type, polygamy can be divided into following subtypes:

(i) **Polygyny:** This type is the most practiced mating system in vertebrates where one male exclusively has relationships with two or more females. Based on organism, polygyny is of different types such as lek polygyny, resource defense polygyny, sororal polygyny and non-sororal polygyny. Lek polygyny is a polygamic mating system of insects and birds, forming lek of flock, where female especially peruse her mate choice and males neither scrutinize females before mating nor show any parental care to its offspring. Among the lek forming males, this mating system endorses profound skewed mating success (Akamatsu and Taguchi 2001). In resource defense polygyny, based on the best oviposition sites, females tend to choose a male based on male territory. Thus, male having best territory has several female partners (Dreisig 1995). For example, grayling butterflies (*Hipparchia semele*) show resource defense polygyny.

(ii) **Polyandry:** Polyandry is the exclusive relationship of one female with two or more males. This rare type of mating system is the composition of multi-female and multi-male and very commonly found in some insects, e.g., among honey bees (*Apis mellifera*), red flour beetles (*Tribolium castaneum*), desert spiders (*Stegodyphus lineatus*), field crickets (*Gryllus bimaculatus*), etc.; maximum pipefishes (*Syngnathidae phycodurus* and *S. phyllopteryx*); 1% of bird species, e.g., Jacana (*Parra jacana*) and dunnock (*Prunella modularis*); and also in few primates, e.g., marmosets and some marsupials (*Antechinus stuartii*, bandicoots). In case of honey bees, the queen use to mate with multiple drones (male) and store the sperms in her spermatheca and further use specific sperms on her will, throughout her reproductive life to fertilize eggs.

(iii) **Polygynandry:** This type of mating system is an association of multi-male, multi-female but with slight modifications, i.e., in this type of mating system, two or more males show their exclusive relationship with two or more females, and the number of partners is necessarily not to be the equal. In maximum cases the males are usually in less number than female partners. This type of mating system is common in alpine accentor (*Prunella collaris*) and red paper wasp (*Polistes carolina*) which is assumed to be the consequence of ecological and social stochastic (randomly determined) reproductive conflicts. The adults of the relationships show parental care to their child, and thus this mating system is more usually called as “communal breeding.”

(iv) **Promiscuity:** In this multi-male multi-female mating system, one sex of a social group mates with any other member of opposite sex, without showing any social relationship further, i.e., males of this mating system doesn't become the parenting partner (Fig. 2).



**Mating, Fig. 2** Types of animal mating system with schematic diagram

**Human Mating System**

The above described mating systems are idealized, but if one compares the mating system of human to other animals, humans possess a greater variety. Humans show all types of mating systems such as polyandrous relationships, polygynous, promiscuity, and monogamous. As human is a social animal, thus 83% of human societies are polygynous, and 0.05% are polyandrous (Low 2007). Hippies and some taboo culture peoples are often show promiscuity mating relationships where they believe in extra-pair copulations. Most interestingly in promiscuity relationship of new generation cultured people are believing in short-term relationship where they practice “sexual activity without emotional commitment or future involvement” (Turner 2009). Moreover, from the evolutionary perspective, females are more likely to practice monogamy, while males are polygamous. This is all due to the type of reproductive success they produce such as, in case of female, the acquired resources are more important for her reproductive success than that of the quality offspring she produces. Likewise, reproductive success is based on the number of offspring she can produce rather than the parental investments (Cartwright 2002). As culture always been affecting human lifestyle, starting from feeding habit to mating choices, the

ascertained “natural” human mating system is becoming increasingly difficult to maintain from zoological perspectives, and thus the level of genetic and societal promiscuity is highly varied across cultures (Marlowe 2003) (Fig. 3).

**Sexual Selection**

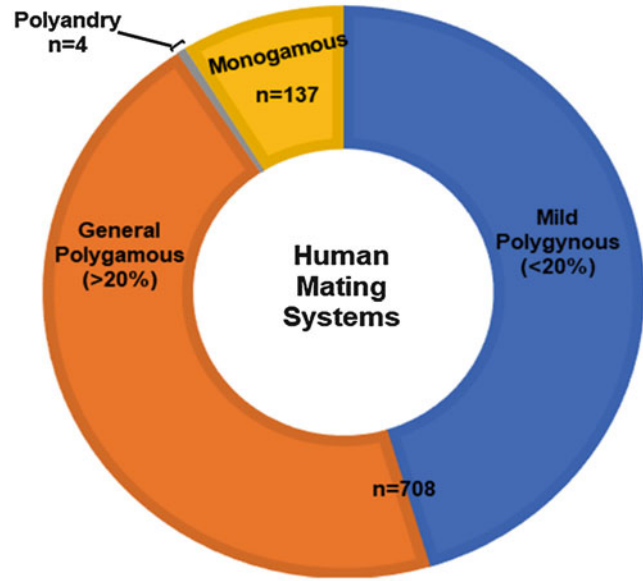
Among the evolutionary forces, sexual selection is the most powerful where individuals of one sex secure their mates in terms of offspring production at the costs of other folks of the same sex. In the description of sexual selection, in his book, Charles Darwin proposed “when the males and females of any animal species have the same general habit of life, but differ in structure, color or ornament such differences are called sexually dimorphic traits, which have been mainly caused by sexual selection” (Darwin 1859).

**Sexual Selection Induced Variance in Reproductive Success**

Darwin recognized two distinct patterns of sexual selection in nature, one is the micro-evolutionary pattern, and the other is the macro-evolutionary pattern. Micro-evolutionary sexual selection pattern is common within almost all species with separate sexes starting from plant to higher



**Mating, Fig. 3** Schematic diagram of the marriage pattern data of 849 societies collected from (Flinn and Low 1986)



animals, and this pattern affects males in a greater degree than females after specifying the sexes separately. In many species, males are perceptibly different from females and the common species name describes only the male sex, e.g. red-winged blackbird (*Aegialius phoeniceus phoeniceus*) are black with red chevron patterned wings where females are unobtrusive with dull brown in color (Searcy 1979; Weatherhead and Robertson 1979). Darwin also stated that, the exaggerated plumage, coloration, behavior, and morphology of males are correlated to each other but not necessarily to the male and female reproduction, i.e., sperm production or other physiological features of reproductive purpose. These males differ from the females of their own species in a rather random suite of phenotypic traits when considered across taxa. Darwin called these male-limited characters as “trivial” or insignificant because of the lack of correlation to the reproductive fitness.

The second pattern, i.e., macro-evolutionary sexual selection, is pragmatic across the male species within genera or families of almost all taxa, and thus these large differences in male phenotypes are the signature of a robust and rapid evolutionary force. In this pattern, the exaggerated males possess large phenotypic differences among the closely related male traits, and thus the sexual selection is rapid and strong.

As we understand from the micro-evolutionary theory and pragmatic studies of artificial selection and Mendel’s genetic theory that sexual selection acting on one sex is always slower and weaker than that of sexual selection on both sexes, because half of the genetic information in any generation comes from both parental sexes (half maternal and half paternal) (Falconer 1989).

We may consider an experimental condition to understand the micro-evolutionary perspective on both-sex selection and single-sex selection in which a captive or laboratory mice population is subjected to artificial sexual selection for increased body length in males of same age groups. Let’s first consider the artificial selection for both-sex, where males and females of same age group are taking part one by one for the selection process. Firstly, the body length of all the males are measured from that population, and higher body length males have been selected for further breeding, whereas other males with shorter body length prevented to be the parents. The strength of the selection of males can be calculated by using standardized selection differentials practiced by males or Sm, i.e., the difference in average body length between selected ( $Y^*$ ) and unselected ( $Y$ ) males divided by standard deviation (SD) of male body length. Thus, the equation will be as follows:

$$Sm = \frac{(Y^* - Y)}{SD}$$

Similarly, if we consider female selection, then the selection strength ( $Sf$ ) will be same as  $S_{\text{males}}$ , i.e., the difference in average body length between selected ( $X^*$ ) and unselected ( $X$ ) males divided by standard deviation ( $SD$ ) of male body length. So, the equation will be as follows:

$$Sf = \frac{(X^* - X)}{SD}$$

Now, we can calculate the total selection strength ( $S_{\text{total}}$ ) on present hypothetical population which is the average of the two selection differentials =  $\frac{(Sm+Sf)}{2}$ . If our both selections in males and females are equally strong, then the equation will be  $Sm = Sf = S$  or  $St = S$ .

Now, consider an example of artificial selection for single-sex, where selection occurs only on males, not on females. The male breed selection is followed by the same procedure as mentioned previously. However, females have been chosen randomly regarding body length. Due to the same mean body length values of the breeding and non-breeding females, the selection differential in females will be zero, i.e.,  $Sf = 0$ . Although, the actual selection differential in females is always less than zero, i.e.,  $Sf < 0$ , because the exaggerated traits preferred in males are selected against in females (Wallace 1868). In our hypothetical population, in the male gene pool, we selected for those genes that increase body length and thus  $Sm > 0$ , but in the female gene pool, we selected against these very same genes, so  $Sf < 0$ . Thus, the sex-specific selection differentials are always of conflicting sign, i.e.,  $Sf < 0 < Sm$ .

If we contemplate genetic information regarding body length in the  $F_1$  generation of the above selected male parents and unselected female parents, they will get only half of the genes affecting body length descending from male parents, whereas not from the female parents, as they were chosen randomly. Thus, the total selection differential is  $St = \frac{Sm}{2}$ , and if we elect on males as strongly as we did above then,  $= \frac{S}{2}$ . Thus, we

can conclude that single-sex selection is weaker half than that of both-sex selection or  $\text{sex selection} = \frac{\text{Both sex selection}}{2}$ .

As we mentioned earlier during the hypothetical experimentation, males taken were of same age groups because micro-evolutionary pattern suggests sexual selection as age-limited or stage-limited. Subjecting that male population again for artificial-sexual selection but this time supposing that the selection is executed on males at two diverse stages in the life cycle i.e., young or immature stage and adult or mature stage. At young or immature stage, the selection may favor small body length and act against males with larger body, and males only with the smallest body at this stage are permitted to mature, so in this early stage selection differential,  $Sm(\text{early}) < 0$ . Further, at adulthood of those permitted mice, selection as parents occurs to only those with the largest tails, and thus in this late stage selection differential,  $Sm(\text{late}) > 0$ . If we concentrate in understanding the genetic view of this selection, genes that upsurge the body length at all ages will experience conflicting selection pressures, and specifically they will be rejected at the first event of selection. Only those genes that incidentally act later in male life to increase body length will experience an articulate selection pressure and avoid the opposing juvenile selection. Thus, we can summon up that the total selection differential in males is the blend of these opposing components which further weakens and slower the overall strength of selection for these traits in the male sex.

Table: Sex-specific viability, reproduction, and total selection differential

| Selection | Viability              | Reproduction           | Total selection differential |
|-----------|------------------------|------------------------|------------------------------|
| Male      | $Sm(\text{early}) < 0$ | $Sm(\text{late}) > 0$  | $St > 0$                     |
| Female    | $Sf(\text{early}) < 0$ | $Sf(\text{early}) < 0$ | $St < 0$                     |

### Sexual Selection in the Reproductive Fitness

Sexual selection is correlated with reproductive fitness as well as sexual viability. Darwin argued that sexual selection depends on the struggle

among the males for possession of the female and is strong enough to pledge the opposing forces of male and female viability selection. Darwin provided justification while identifying the specific cause of sexual selection, and he mentioned, “if each male secures two or more females, many males cannot pair” (Darwin 1871, 1874). This relationship provided an intangible solution to the quantitative paradox due to the documentation of an evolutionary process responsible for the sexual divergence. Let us consider  $P_m$  as the fraction of males who are capable of mating and  $P_{nm}$  is the fraction of non-mating males. Thus, we can write as  $P_m = (1 - P_{nm})$ . If  $H$  is the average number of mates (females) per mating males ( $P_m$ ) then, the average fitness off mating males will be  $P_m(H)$ , and the average fitness off non-mating males will be  $P_{nm}(H)$  which will be zero, i.e.,  $P_{nm}(H) = 0$ , because non-mating males cannot have mates. Now, if the sex ratio ( $R$ ) is the average number of mates ( $N_f$ ) available for all males ( $N_m$ ), i.e.,  $R = \frac{N_f}{N_m}$ , where  $N_f = P_m(H) + P_{nm}(H)$  and  $N_m = P_m + P_{nm}$ ; so, rewriting the whole equation:

$$R = \frac{\{P_m(H) + P_{nm}(H)\}}{(P_m + P_{nm})}$$

or,  $1 - P_{nm} = \frac{R}{H}$ ; [because,  $P_m = (1 - P_{nm})$  &  $P_{nm}(H) = 0$ ]

or,  $P_{nm} = (1 - \frac{R}{H})$

If, we now consider sex ratio,  $R = 1$ , the equation will be as follows:

$$P_{nm} = (1 - \frac{1}{H})$$

From the above equation, it can be concluded that as the value of  $H$  increases, the value of  $P_{nm}$  will automatically increase, and this is the quantitative expression that captures what Darwin proposed.

Such conflicts between the fitness components of male viability and male reproduction may exist for many exaggerated male traits. It is often hypothesized that exaggerated male traits lower male viability by making males more conspicuous to predators (e.g., bird territorial calls, plumage,

and displays) or by imposing high energetic costs on males (e.g., male vocalizations in frogs and toads). In some species, these costs to males have been well documented. For example, only male frogs call, and calling has been shown by ecological physiologists to be extremely costly in energetic terms (Tuttle and Ryan 1981). Males of many anuran species expend large amounts of energy calling and, although more than 90% of mating will take place over three or four nights, the males might call every night for 2 or 3 months. Also, in one species, *Physalaemus pustulosus*, males are victims of frog-eating bats that use the sex-specific calls to locate their prey (Tuttle and Ryan 1981; Ryan 1983).

### Mechanism of Sexual Selection

As discussed earlier that according to Darwin, sexual selection is a special mode of natural selection where evolutionary selection occurs over the extreme sexual phenotypes. From his viewpoint of one sex micro-evolutionary selection pattern, females act as the scarce resources and to access to the females, males of that species compete among themselves. Thus, the winner male shows the higher mating success (more mates) than the males who lost the competition. To achieve this higher mating success, the selected male also improves their extreme phenotypes which also increase the fitness of that male solely, and thus the next generation blessed with these exaggerated phenotypes from the male parent. But, according to Wallace (1868), these exaggerated phenotypes can be unfavorable to the viability of that particular sex of species (mostly male).

For example, firstly, for achievement of higher mating success, only male competes with the other males of the same population, but the females do not get engaged in such activities. If, this kind of activities is necessary for the survival, then it must be expressed by both the sexes. Secondly, if the male-limited exaggerated, phenotypes are displayed only during the breeding season which comes once or twice in a year and after that those phenotypes disappear for the rest of the year (e.g., the appearance of antlers of some deer and other ungulates during breeding time and shed off after the mating season).

Wallace (1868) argued that why these exaggerated phenotypes display year-round, if these traits are advantageous, e.g., if the antler of male deer is useful for repelling predators, then why do the shed after mating time? Darwin conditionally stated about the function of extreme male traits in mate procurement but was not clear whether these traits were disadvantageous to both sexes or not as Wallace argued. For these reasons and following Darwin's view of sexual selection, we can anticipate three mechanisms of sexual selection to summon up the higher mating success:

- (I) **Male-male competition for mates:** From the viewpoint of Darwin, male-male competition for mates is the direct competition among the males of one species population during mating season for the achievement of high mating success, as he stated for sexual selection that it stands for the struggle for possession of the mates, not for the struggle for existence. The abovementioned struggle doesn't always lead to the death of loser, but can result in his few or no progeny. Therefore, 'sexual selection' is less rigorous than 'natural selection' (Darwin 1859).

Male-male competition is a common sexual selection mechanism for deer, elk, or horned beetles (Emlen 1996). Prior to the breeding season, males of these species use their antlers or horns in prolonged head-to-head combat in their own territory. The winning male then copulates with many females because of his higher reproductive fitness. In some other species, certain structures in male persist for reproductive combat but are not use in face-to-face combat, and these structures are less apparent than the abovementioned physical face-to-face combat structures. For example, in damselflies copulatory and seminal combat between males occur where they employ their caudal structure during the mating time (Eberhard 1996). These structures remove sperms of other males from the female reproductive tract (Waage 1979). Interestingly, some male species transfers a "mating plug" along with sperms which

have the capability to impede copulatory efforts of subsequent mating males (Gwynne 1984).

It is obvious that one successful male of fifty-fifty Mendelian sex ratio, if have several mates, then several males will have no mates at all. Thus, this type of sexual selection establishes the fundamental relationship between the variance in male fitness and the variance in female fitness.

- (II) **Female choice of mates:** As Wallace (1868) argued that the male exaggerated phenotypes are against the viability of those traits. Darwin believed that the male-male combat is insufficient to explain the evolution of these male-limited characters, and thus he proposed about another type sexual selection via female choice of mates. Darwin postulated "female choice for mates" as the process by which females select certain males as mates among other males. Darwin stated the reason as, "if man can in a short time give elegant carriage and beauty to his bantams, according to his standard of beauty, I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect" (Darwin 1859). But same possibility will arise just as raised in combat-related male sexual selection, i.e., if female choice of mates alone comes in the operation, then only the preferred male trait will be exaggerated which will be again against the evolutionary viability.

Now question may arise where female mate choice occurs as well as how and why it becomes operative. Basolo (1990) and Andersson (1994) reviewed experimentally in natural population that extreme ornamentations in males act as a strong preference signal for female mate choice. These studies also revealed that the reproductive fitness of a preferred male indicated by the extreme values of mating achieved by the preferred male throughout his lifetime rather than male-male combat. Here again

the same condition of having no mating for those “unsuccessful” males increase the variance in male mating success, which in turn increase the variance of male fitness. Burley and Foster (2006) performed an experiment on zebra finches, *Taeniopygia guttata castanotis*, to study the variation in female choice of mates by altering the physical condition of female zebra finches, i.e., by modest trimming of their flight feathers. After observing the results of sensitivity and companion experiments, they communally concluded as “female’s mate selectivity is dynamically adjusted based on her assessment of her own condition or mate-getting ability.”

- (III) **“Chase-away” sexual selection:** Above we discussed about two different types of sexual selections: (1) One was about the male displayed traits developed as the incidental by-product of viability selection, i.e., development of static female attraction toward the winning male (male-male combat for mate). (2) Second was the female-mate selection procedure where preferred male trait are been exaggerated by females when females get influenced by male secondary sexual traits. Here both the male display trait and female attraction increased concurrently from their positive coevolutionary feedback.

The “chase-away” sexual selection is another mode of intersexual selection which is not dependable on these above two types of selection and based on antagonistic coevolution between sexes (Holland et al. 1998). In “chase-away” sexual selection, males evolve some initial rudimentary display traits to enhance their own attractiveness toward females and among them the exaggeratedly attractive male influence females to mate in a suboptimal manner (e.g., too often, less than ideal time or ideal manner) (Holland et al. 1998). These variances further counter-select females to evolve their resistance to the male display traits, rather than preference for it. To overcome this increased threshold of female pre-existing sensory system, males further

advance more extreme display traits, and this way the “chase-away” sexual selection ensures cyclic antagonistic coevolution. This type of selection is common in peafowl (*Pavo cristatus*).

## Sexual Conflict

First question that arise about sexual conflict is what it is. Sexual conflict or sexual antagonism is the skirmish of reproduction associated optimal fitness strategies, i.e., mode and frequency of mating between male and female, leading to an evolutionary arms race (Parker 2006; Danchin et al. 2008). Now if we consider the type of sexual conflict, then it takes two major forms:

- (I) **Interlocus sexual conflict:** When a set of antagonistic alleles interact at one or more loci in both sexes, it is called as interlocus sexual conflict (Chapman et al. 2003). A well-documented example of this interlocus sexual conflict has been observed in *Drosophila melanogaster*, where a male *Drosophila* secretes its seminal fluid which not only induce females to lay eggs but also reduce her re-mating desires with another male along with shorten her life span by tumbling her fitness. This type of selection act as perpetual cycle which initiates with favored male reproductive traits which establishes male perseverance, resulting in reduced female fitness. This reduction in female fitness further maintains the evolutionary concept and evolves a counter-adaptation which is called as female resistance, leads to a co-evolutionary arm race.
- (II) **Intralocus sexual conflict:** Intralocus sexual selection is the tug of combat between natural selection on both sexes and sexual selection of either sex. As we see above in female mate choice, males of the population produce ornamentations to attract females for mating which is not only costly but also make males vulnerable to predators. The alleles which support the above phenotypic trait belong to antagonistic selection which



is basically a sexual dimorphism, maintains sexually antagonistic alleles within the population (Arnqvist and Rowe 2005).

### Different Types of Sexual Conflict

- **Infanticide:** Infanticide is a common sexual conflict observed where adults or parents predate their own juvenile or eggs. Sometime this phenomenon may be sex biased like either only male can be biased in eating the offspring or only female can predate their own juvenile or eggs. For example, male *Stegodyphus lineatus* sometimes eats their offspring, (Schneider and Lubin 1996) while females *Jacana jacana* predate their own juveniles (Emlen et al. 1989). This type of conflict is costly for both sexes, and thus they evolve some counter-adaptations in the exaggerated sex such as abortion of existing offspring upon the arrival of a new male (the Bruce effect) from obliging resistance of their young to loss minimization approaches.
- **Traumatic insemination:** Traumatic insemination is another type of sexual conflict to ensure paternity success where males pierce a female abdomen using their needlelike intromittent organ and directly incorporate sperms along with the accessory gland fluids into the female's blood. This is very commonly found in bed bug (*Cimex lectularius*, *Hesperocimex cochimiensis*) (Reinhardt et al. 2005), bat bugs (*Afrocinemex constrictus*) (Reinhardt et al. 2011), and spiders (*Harpactea sadistica*) (Milan 2009). If we consider example of *C. lectularius*, male *C. lectularius* climb up onto female *C. lectularius*, and by piercing her abdomen, male directly injects his sperm resulting in females with distinct melanized scar in the pierced region. The male not only pierce females but also other males and nymphs to lower the probability of other mating and thus increasing its own paternal success. As a result of this conflict, the females often suffer from blood leaking, wounds, the risk of infection, and the immune system having difficulty fighting off sperm in the blood which becomes detrimental to its own life span (Stutt 1999).
- **Toxic semen:** Sexual conflict by introducing toxic semen is mostly associated with fruit fly family member, i.e., *Drosophila melanogaster* and *D. hibisci* (Bretman et al. 2010). As we discussed earlier, this sexual conflict is an interlocus sexual conflict where male *Drosophila* pierces his intromittent organ within the inner wall of female genitalia and introduces toxic semen which is a mixture of sperm and accessory gland proteins (Acps) (Findlay et al. 2008) which is found in male seminal fluid. Male *Drosophila* may benefit from transporting toxic semen inside the females by keeping other males away from that mated female, but this changes the behavior and physiology (Ravi and Wolfner 2007) of those females, resulting in decreased life span (Chapman et al. 1995) and fitness (Wigby and Chapman 2005). Therefore, we can assume that male *D. melanogaster* matures other male adaptations to reimburse for mating plug deficiency and direct intra-genital traumatic insemination.
- **Spiky genitals:** This is another type of sexual conflict where extra-genital traumatic insemination in females occurs by males through his intromittent organ having spines which is used to pierce reproductive tract. This is common in bruchid beetle or bean weevil (*Callosobruchus maculatus*), but the insemination process and harm is the same as other discussed inseminations except that females that mate with virgin males were less likely to suffer genital damage than those who mated with sexually experienced males (Eady et al. 2007) and thus we may assume that some factors are present in male virgin seminal fluid which contributes less harm due to ejaculate size and the amount of sperm contained.
- **Love darts:** Love darts is a sharp "stiletto" like structure, created by males of hermaphroditic gastropod snails while copulation. Due to lengthy regeneration procedure, a single love dart is shot forcefully at a time at the female during courtship (Koene and Schulenburg 2005). It has been observed that love dart doesn't ensure mating success (Arnqvist

and Rowe 2005), but a successful love dart penetration ensures higher paternity assurance (Rogers and Chase 2001). Many snails suffer from open wounds, and sometimes death imposed by love darts (Baur 1998).

- **Forced copulation:** Forced copulation or sexual coercion is very common in a wide range of species which elicit aggression, harassment (Arnqvist and Rowe 2005), and grasping (Yong-Hong 2015) during both prior and at the time of copulation and make females suffer from detrimental effects including mental and physical loss due to forceful mating tactics. Moreover, we can say forced copulation as “rape” which is very common term use in case of human where females are forced to copulate against their will.
- **Sexual cannibalism:** In terms of sexual conflict, sexual cannibalism is an exception of traditional male-female courtship behavior where female homicides and devours males during copulation (Arnqvist and Rowe 2005). A very common example of sexual cannibalism is sexual interaction between male and female funnel-web spider, *Hololena curta* (Yong-Hong 2015). After sperm exchange, female kills and consumes the male to increase “parental investment,” i.e., female spiders consume male which serves as a blood meal since they volunteer their soma and thus increase in quality of offspring. Some male gift-giving spiders provide edible gifts to the females before sexual intercourse just to manipulate females to not kill them.
- **Anti-aphrodisiac:** Anti-aphrodisiac is a volatile compound produced only by the males of several *Heliconius* butterflies, i.e., *H. melpomene* and *H. erato*, and serves as a beneficial for both sexes. Male *Heliconius* butterfly transferrers this anti-aphrodisiac inside the females so that she smells like that male resulting in prevention of future copulation with other males as well as benefits from post-mating harassments to from males to decrease reproductive success by disturbing the production of eggs. Thus, anti-aphrodisiac increases the paternity success of the male by preventing introduction of sperms of other males resulting

in fertilization of the egg by his own sperm (Schulz et al. 2008).

## Conclusion

In this chapter we have emphasized on the basic concepts of various parameters on which a successful mating depends. The cost and benefits of mating rely on different mating systems, mating behaviors, mate selections, and sexual conflicts which are likely to vary widely within and between species. Charles Darwin clinched that the effect of cross robustness or complementation “is amply sufficient to account for the . . . genesis of the two sexes.” Meanwhile the advent of the modern evolutionary fusion in the twentieth century, numerous biologists have suggested rival explanations for this vast array of different living species maintain sexual reproduction. This diverse cost and benefits of mating possess an important consequence both on population dynamics and on the genetic structure of populations (Clutton-Brock 1985). But one may be curious about the advantages and disadvantages of mating. The main disadvantage of mating or sexual reproduction is the population expansion cost, i.e., sexual reproduction takes more investments such as energy and time, while asexual population grows in multiplication form each generation. Not only that sometimes for mate selection or mate attraction, some members of the population become vulnerable to predators, and chances become higher toward population decrease. Both in this case the natural selection theory maintains, i.e., the higher the fitness, the higher the genetic quality. Now if we consider the advantages of mating or sexual selection,

- (i) Mating can syndicate the effect of valuable mutations in the individual. Thus, mating aids to the spread of advantageous traits in the population.
- (ii) Deleterious mutations come together by mating and generate severely unfit individuals which are then eradicated from the population. Thus, mating promotes removal of deleterious genes.

- (iii) Mating also creates new gene combinations which ensures more fitness than existing ones or may simply lead to condensed competition among relatives.
- (iv) Mating is an abrasive filter, tidying out chromosomal rearrangements like major genetic changes but also authorizing minor variation, i.e., changes at the nucleotide or gene level to pass through the sexual sieve. Thus, mating promotes genetic variations via protecting population from major genetic mutations.
- (v) Mating ensures combinations of advantageous genes from two individuals. Thus, mating is a novel genotype creator.
- (vi) Mating also ensures the increasing resistance to parasites by coevolution which is also known as the Red Queen hypothesis.

## Cross-References

- [Assortative Mating](#)
- [Conjugation](#)
- [Female Choice](#)
- [Internal Fertilization](#)
- [Intersexual Selection](#)
- [Psychopharmacology of Sex Steroids](#)
- [Reproductive Fitness](#)

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## Mating Effort

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## Synonyms

Intra-sexual Competition; Parental Investment Theory

## Definition

Mating effort encompasses all the investment of resources in order to gain sexual access to a conspecific, the time and energy expended during copulation, and all the sex cells expended as a result of copulation.

Mating effort refers to the time and energy an organism invests to gain sexual access to another organism, the energy expended during sex, and the gametes (sex cells) invested. In sexually reproducing species, the sex that invests more resources in its offspring is more selective when choosing a mating partner (Trivers 1972). As a result, the sex that invests fewer parental resources will experience greater intrasexual competition for mating partners and will exert greater mating effort to reproduce sexually. The sex with lower obligate parental investment needed to produce offspring may achieve greater reproductive success by copulating with a greater number of partners. There is a range of evolved strategies expressed in mating effort, with some individuals being more competitive in terms of gaining sexual access and others having adaptations resulting in a more competitive contribution of sex cells (sperm).

## Intrasexual Competition

One way in which organisms can exert mating effort is by directly competing with same-sex

conspecifics to gain sexual access to opposite-sex conspecifics. In some species, such as peafowl, males (peacocks) display prominent physical characteristics to advertise their genetic quality (Petrie et al. 1991; Petrie and Halliday 1994). In this case, females (peahens) select as mating partners males with the most vibrant plumage. In other species, males may possess ornamentation, or “weaponry,” such as the antlers used in intrasexual competition by deer (Andersson 1994). Physical characteristics like weaponry and colorful displays of plumage constitute one type of mating effort, wherein organisms directly compete to gain sexual access.

Evidence for sex differences in mating effort has been observed in humans. Relative to women, men report a higher ideal number of lifetime sexual partners, indicate that they need less time to know someone before having sex with them (Buss and Schmitt 1993), and express greater desire for casual sex (Schmitt et al. 2001). Similar to males in many nonhuman species, men also exert mating effort to gain sexual access; however, the ways that men advertise their desirability as a mating partner often corresponds to their ability to provision the female and/or her offspring with resources. For example, both men and women in one study judged “showing resource potential” to be most effective for men pursuing a long-term partner and judged immediately gifting resources to be the most effective strategy for men pursuing a short-term sexual partner (Schmitt and Buss 1996). Whereas males of other species may exert mating effort using direct competition, including physical displays of genetic quality such as the peacock’s train, men may exert mating effort by displaying their ability to provision resources to a woman and her children. In this sense, human mating effort may be unique because, in most other species, mating effort is often framed as an alternative to parental effort. To further complicate this distinction, there is debate about whether altruism may be better understood as mating effort or as a way in which men display their ability to provision resources. Whereas some have argued that men use altruistic behavior as a means to display their genetic quality (e.g., Gintis et al. 2001), others have argued that men use altruistic



behavior to indicate their ability to provide parental care (e.g., Kokko 1998). Still others have argued that the framing of parental and mating effort as a trade-off may be misleading (Stiver and Alonzo 2009), as certain behavioral characteristics may simultaneously serve both functions.

## Sperm Competition

Males can also exert mating effort without engaging in direct competition with one another for sexual access. Adaptations for sperm competition facilitate males of some species to compete to fertilize a female's ova. Some sperm competition adaptations result in the production of higher-quality ejaculates. Chimpanzees have a larger testes-to-body weight ratio compared to many other primates, and because larger testes are capable of producing larger ejaculates, this implies an evolutionary history of frequent sperm competition (Møller 1988). Alternatively, some adaptations to sperm competition involve the removal of rival sperm. For example, one study of *Drosophila melanogaster* observed that sterile males could displace semen from the reproductive tract of females who had previously mated (Harshman and Prout 1994). In humans, the male penis has evolved a shape that is effective at removing semen from a woman's reproductive tract (Gallup et al. 2003). Research investigating sexual behavior in humans has also revealed a number of behaviors that may reflect adaptations to sperm competition. For example, men who have spent more time away from their partner since the couple's most recent copulation report greater interest in sex with her, even after controlling for time since the last copulation (Shackelford et al. 2007), potentially to displace or to compete with the sperm of rival males in the woman's reproductive tract.

Mating effort encompasses a range of physical, behavioral, and cognitive adaptations that individuals use to increase their reproductive success. In particular, males of many sexually reproducing species often face greater intrasexual competition for access to mating partners and, thus, have adaptations for intrasexual competition.

## Cross-References

- ▶ [Intra-sexual Selection](#)
- ▶ [Mate Guarding](#)
- ▶ [Mate Provisioning](#)
- ▶ [Sexual Selection](#)

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## Matrilines and Patriline

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### Definition

**Matriline** a line of descent in which the intervening generations are mothers

**Patriline** a line of descent in which the intervening generations are fathers

### Social Organization via the Matriline

The organization of animal and human societies depends on kinship ties that persist either through the female line, deemed “matrilines,” or the male line, deemed “patriline.” In many animal societies, the most common form of kinship social structure is via the matriline. Matrilineal social systems commonly occur in multimale/multifemale groups in which females are promiscuous, mating with several males. Males disperse from their birth (natal) group to reduce inbreeding (mating with relatives) and due to local mate competition in which males compete for access to the females. Given the high degree of female promiscuity, the certainty of paternity is low, whereas maternity is readily identifiable. This leads to an organization where individuals tend to interact primarily with their maternal relatives, or their matriline, rather than their paternal relatives, or patriline. Matrilineal social organizations are predominant in baboons (e.g., *Papio anubis*), macaques (e.g., *Macaca mulatta*), hyenas (e.g., *Crocuta crocuta*), lions (e.g., *Panthera leo*), and many other animal species.

The support for matrilineal kin recognition is abundant, with individuals preferentially affiliating with kin via grooming interactions, proximity, and other affiliative behaviors. Individuals have also been shown to respond to vocalizations of matrilineal kin during playback experiments. During playback experiments, individuals respond, generally via enhanced looking time, to the

vocalizations of matrilineal kin. This recognition eventuates via familiarity (i.e., familiarity through associations) and phenotypic matching, the process by which individuals match similar visual and/or acoustic components to their own. Matrilineal kinship also manifests itself in the structure of the dominance hierarchy. Maternal rank inheritance is the process by which individuals attain adjacent ranks to their mothers via the cumulative support of mothers and matrilineal kin in aggressive interventions. Matrilines can therefore be ranked among one another, and individuals are also ranked within the matrilines, all of which is highly predictable via kinship relationships and highly stable over time. Occasionally however, lower ranking matrilines will jointly challenge higher ranking matrilines, resulting in a matrilineal overthrow. These violent events are rare and result in the dramatic social reorganization of a large number of individuals. Given the consequences for the social group, it is not surprising that individuals respond more strongly to the vocalizations corresponding to a matrilineal overthrow (Bergman et al. 2003), suggesting that individuals classify entire matrilines as entities, recognizing not only individual ranks, but matrilineal ranks.

The highly complex social structure of matrilines, which can have as many as four generations, can depend on matriarchs, or old females. In a number of species, matriarchs can be instrumental in survival through ecological knowledge, group leadership, stability, and grandmothering. Indeed, the loss of a matriarch can lead to group fissions along the matriline, fighting, family disputes over money, and reduced vitality of offspring and grand-offspring in a number of species. Accordingly, the “grandmother hypothesis” (O’Connell et al. 1999) poses that the long postreproductive life in humans (and some animals, e.g., orcas, *Orcinus orca*) has evolved to enhance reproductive success by caring for and helping raise grandchildren, with maternal grandmothers having the most significant influence. Indeed, matrilineal lineages can be lost at considerable rates in wild populations (Gompper et al. 1997), and the loss of grandmothers, or matriarchs, can therefore have considerable impacts on the survival of the matriline.

## Social Organization via the Patriline

Contrary to matriline, patriline generally occur in multimale/multifemale groups in which males reside in their birth group and females disperse, such as in chimpanzees (*Pan troglodytes*), African wild dogs (*Lycaon pictus*), and some birds. Females disperse either due to local resource competition in which males compete for access to a territory to attract females or when the average tenure of the male exceeds the age of females at first conception (to prevent daughters from mating with their fathers). Whereas matrilineal social organizations are predominant in animal societies, patrilineal organization is predominant in many human cultures. Cattle may have led to the transformation from matrilineal to patrilineal societies in some human cultures (Holden and Mace 2003), as the inclusion of livestock as an indicator of bride wealth may have provided more benefits for sons than daughters. Accordingly, whether males or females have greater reproductive success generally explains whether matriline or patriline occurs in human cultures. The evidence of patriline influencing the structure in many human societies is relatively ubiquitous with family name, property inheritance, and political or royal titles generally transmitted via fathers. Ancestry too is predominantly measured by genealogical markers such as the Y chromosome to detect ancestry through the paternal line (Calafell and Larmuseau 2017), although mitochondrial DNA (mtDNA) is also used to detect maternal ancestry.

While some animal species have patrilineal-like social structures, such as chimpanzees, African wild dogs, gorillas (e.g., *Gorilla gorilla*), red colobus monkeys (e.g., *Colobus badius tephrosceles*), and sac-winged bats (e.g., *Saccopteryx bilineata*), it is suggested that the only truly patrilineal social structure is in humans. Patriline requires some level of paternal kin recognition, which may require monogamy (see Chapais 2016 for a comprehensive overview) to ensure paternal certainty. While some behaviors consistent with a patrilineal society exist in animals, others appear to be absent, such as paternal rank inheritance and paternal kin recognition past primary paternal kin (see Chapais 2016). Non-human primates laid the basic foundation for

patriline, with monogamy contributing to the patrilineal kinship structures seen in humans currently.

Research is however increasingly supporting the hypothesis that animals may discriminate vocalizations of unfamiliar paternal kin, even without social experience, indicating that phenotypic matching may play a role in acoustic kin recognition. However, age proximity in individuals with social experience with one another is also likely an important social cue of paternity as well, with individuals less likely to mate with individuals of a similar age as they may have been sired from the same father. However, inbreeding is still relatively more common in patriline compared to matriline given the uncertainty of paternal relationships. Paternal lineages can also influence infant development, genetic diversity, productivity, and fitness in a number of species.

Contrary to grandmothers or matriarchs, grandfathers or patriarchs may derive little benefits of long life in monogamous human societies (Lahdenperä et al. 2007), with the patriline deriving little added reproductive success, contrary to the effect grandmothers have on their matriline, although old men may benefit the patriline in other ways (Strassmann and Kurapati 2016). The long lifespan of females has also been hypothesized to be a byproduct of male longevity (“the patriarch hypothesis,” Marlowe 2000). In this case, the benefits of grandmothers to their grandchildren are hypothesized to be indirectly related to grandfathers, or aged men. A patriline may generally be less vulnerable than a matriline, but group fissions along the patriline have been reported in some nonhuman primates and humans.

## Conclusion

Whether social groups develop matrilineal or patrilineal social organizations depends on a number of factors including sociosexual behavior, reproductive success of males and females, and paternal certainty. The kinship structure of social groups then gives rise to an interesting social structure, which can influence the development of behavior and cognition across the lifespan.

## Cross-References

- [Affiliative Behaviors](#)
- [Coefficient of Relatedness](#)
- [Friendships in Animals](#)
- [Grandmother Hypothesis](#)
- [Heredity](#)
- [Heritability of Behavior](#)
- [Kinship](#)
- [Monogamy](#)
- [Phenotype Matching](#)
- [Philopatry](#)
- [Polyandry](#)
- [Polygamy](#)
- [Polygyny](#)
- [Primate Social Structure](#)
- [Promiscuity](#)
- [Resource Defense Polygyny](#)
- [Sociosexual Behavior](#)

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## Matutinal (Active at Dawn)

- [Crepuscular](#)

## Max Planck Institute for Evolutionary Anthropology

- [Josep Call](#)

## Maximal Longevity

- [Lifetime Expectancy](#)

## Means-End Behavior

- [Means-End Reasoning](#)

## Means-End Reasoning

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## Synonyms

[Means-end behavior](#); [Means-end understanding](#)

## Definition

Broadly speaking means-end reasoning is concerned with finding means for achieving

goals (Pollock 2002). More specifically, it involves the deliberate and planned execution of a chain of actions to achieve a goal and occurs in situations where an obstacle (e.g., a distance between the subject and a desirable item, person) preventing the achievement of the goal must initially be removed (Willatts 1999).

## Introduction

In everyday life, we are regularly facing situations which require elaborate sequences of mediating actions to reach a distant goal at the end. For example, imagine a person opening a drawer to take a key to unlock a storeroom to get a ladder needed to reach the door to an out-of-reach vitrine where there is a candy box that can be opened to get some sweets. As this hypothetical problem-solving sequence illustrates (modified from Santos et al 2005), the individual steps within a sequence are often separated from the final goal both in time and space. To complete the sequence, problem solvers must initially ignore the primary goal (e.g., reaching the sweets) to focus on first completing the individual subgoals (e.g., getting the stepladder). Moreover, means-end behavior often requires an extensive knowledge of the causal relations between objects. In other words, an individual needs to understand both the connection between the individual steps of a chain of action (a key can open a locked door, a ladder can be used to access things that are out-of-reach, etc.) and how they relate (finding the key to the storeroom is necessary for eventually eating the sweets).

When performing a goal-directed behavior, understanding these consecutive sequences of mediating actions as the means to an end can be of significant advantage for any individual (Schmidt and Cook 2006). In fact, without such an understanding, it will be impossible for an individual to transfer an intention into an action, and arguably impossible to form an intention at all (Osthaus et al. 2005). The understanding of functional relations between an action and its consequence is thus a crucial step in cognitive development.

## Means-End Reasoning in Human and Nonhuman Animals

In human cognitive development, understanding of means-end relations develops in early infancy (Piaget and Cook 1952). Piaget was among the first to develop a task assessing this specific kind of problem-solving. In the so-called “support task,” the infant must try to obtain an object, (e.g., a toy, that is out of direct reach) by pulling a piece of cloth placed underneath the toy towards itself. In this task, the piece of cloth serves as a support and correctly using the support is the means to accomplish the end of obtaining the toy. Piaget found that the infants first acquire the ability to pull supports, but they persist in doing so even when the goal does not rest on the support (on/off condition). At a later stage (after 12 months), the infants gain conceptual knowledge about the relationship between the means and the end, the spatial relationship between the two, and the features of the support used. Furthermore, they develop cognitive processing that allows subjects to have a definite goal, to persist in trying to achieve it, and thus to produce a goal-directed behavior. Even though later work massively improved and refined the model of infant cognitive development, Piaget’s original model remains valid (Willatts 1999).

The question if and how animals develop means-end understanding remains one of the central questions of the modern comparative cognition research (e.g., Schmidt and Cook 2006). Analyzing the understanding of means-ends relationships in nonhuman animals requires problem-solving tasks in which a solution to the problem can in principle be perceived directly, without trial and error or previous experience of similar tasks. Means-end understanding is thought to be most clearly demonstrated if the subject shows an “insightful” solution to the problem on the first trial, ruling out possible operant conditioning. Usually, relying on means-end connections is assessed by offering a choice of two options, one of which is in physical connection to an out-of-reach object of desire. Widely used paradigms in this context include the “string-pulling task,” originally applied by Köhler (1927), as well as the “support problem,” originally introduced by



Piaget (Piaget and Cook 1952). Both tasks involve offering a possible physical connection to an out-of-reach object of desire. In the string-pulling task, a string is attached to a piece of food. The food itself is out of reach of the animal, but the near end of the string is accessible. In the “support problem”, an object is out of the subject’s reach but is placed on a cloth which the subject can pull towards it. Both tasks – the string pulling as well as the support problem – are based on the assumption that if the animal understands the physical properties of the string or the cloth, it uses it as a means to an end, i.e., pulls the food into reach with the string or cloth on its first exposure to the task. In contrast, subjects who do not understand that pulling the string is the “means” for achieving the desired “ends” of bringing the reward within reach, will only be able to succeed via repeated exposure and associative learning (Range et al. 2012).

When offering a choice of two options, one of which is in physical connection to an out-of-reach object, the physical situations of these choice discriminations then can be varied in many ways. In each case, the food is out of reach, so the subjects need to recognize which of the physical arrangements would yield a reward. By analyzing the subjects’ performance in such simultaneous discriminations, it can be assessed whether an animal is relying on perceptual features rather than attending to the relevant functional features of the task. In the support task, subjects can choose between pulling a cloth with a piece of food on it versus pulling another piece of cloth with the same reward closely next to it (“on/off problem”). In the “connected problem”, subjects can choose between a piece of food resting on an intact piece of cloth versus a second reward resting on a cloth that is divided into two pieces and hence separated by a small gap. The nature of string-pulling task allows for a higher number of conditions since the strings can be arranged in a number of different patterns (e.g., slanted, parallel, convergent, crossed, pseudo-crossed, double-crossed and so on), commonly referred to as “patterned-string problems.”

So far, animals as diverse as monkeys, great apes, dogs, cats, elephants, pigeons, corvids, parrots, and bumblebees have been tested with the string-pulling task and/or the support problem.

Spontaneous apparently “insightful” solutions were found in just a few species, for example, in a number of nonhuman primates (Hauser et al. 1999; Herrmann et al. 2008), large-brained birds such as corvids and psittacids (e.g., Auersperg et al. 2009; Heinrich and Bugnyar 2005; Krasheninnikova et al. 2013), and elephants (Irie-Sugimoto et al. 2008). Various cognitive mechanisms underlying the pulling of strings and/or supports have been proposed for other animals, for example, associative learning (e.g., pigeons, *Columba livia*, Schmidt and Cook 2006, and bumblebee, *Bombus terrestris*, Alem et al. 2016), relying on perceptual feedback (New Caledonian crows, *Corvus moneduloides*, Taylor et al. 2010), or attending to perceptual contact but not necessarily connectivity (great apes, Povinelli 2000). Dogs as well as domestic cats (*Felis catus*), although able to learn to obtain food that is out of reach by means of an attached string, have failed to show understanding of means-end relationships when tested in a two-choice paradigm involving various patterned-string tasks (Osthaus et al. 2005; Whitt et al. 2009).

Other tasks requiring an understanding of means-end relationships involve tool use, but they also require other cognitive capacities as well, so that they are sometimes considered to be less appropriate as tests of means-end understanding as such (Osthaus et al. 2005). Nevertheless, an obvious parallel to the hypothetical problem-solving sequence, as described at the beginning of the chapter, is the sequential tool use, where a tool is used to acquire another tool (Santos et al. 2005). There are three difficulties arising from sequential tool using: (1) the subject must recognize that one object can be used as a tool that can be used on another nonfood item, (2) the subject also must forego the immediate motivation to use the first tool to attempt to access the food directly, and (3) the subject must be capable of hierarchically organized behavior (Wimpenny et al. 2009). Such sequenced behavior is exceptionally rare in the nonhuman animals. The only evidence of using tool sequences comes from nonhuman primate and large-brained birds (corvids and parrots). For example, wild chimpanzees have occasionally been observed using an additional

stone to adjust poorly positioned stone anvils; the additional stone thus provides a leveler for the anvil (Matsuzawa 2001). These observations suggest that chimpanzees can use a means, in this case the additional stone, to act on another means, the stone anvil, even in the absence of an immediate food reward. The New Caledonian crow, *Corvus moneduloides*, a habitual tool-manufacturer and tool-user in the wild, has shown sequential tool use by using a short tool to extract a longer tool that could then be used to obtain a reward (Wimpenny et al. 2009). However, it has been shown that sequential tool use is not restricted to habitual tool users only. The rooks, *Corvus frugilegus*, a non-tool-using corvid, could use a large stone to access a small stone that could be used to release an out-of-reach food (Bird and Emery 2009). In parrots, the other large-brained avian group, sequential problem-solving has been documented in the Goffin's cockatoo (*Cacatua goffiniana*). The birds could solve a five-step sequence of multiple locking devices blocking one another demonstrating that they can execute a chain of intermediate actions unaffected by the fact that the goal was very distant (Auersperg et al. 2013).

## Do Nonhuman Animals Really Perform Means-End Reasoning?

However, despite the recent impressive findings involving apparent understanding of means-end relations found in various animals, the pivotal question remains: to what degree do states of cognition characterized by terms like “means-end reasoning”, “insight”, “understanding”, and “problem solving” contribute to an animal's behaviors as opposed to “simpler” mechanisms based on experience and associative learning (Hanus 2016; Shettleworth 2012).

Obviously, mere acquisition of the reward by pulling at the string or the cloth does not necessarily reflect means-end understanding. For example, successful performance in string-pulling tasks might be based on perceptual feedback, i.e., forming an association between pulling the string and the reward coming closer, resulting in

repeated pulling (Taylor et al. 2010). Another common strategy subjects may employ when faced with patterned-string tasks or support problems is the proximity rule, i.e., pulling the string or cloth closest to the reward. Thus, it has been claimed that an animal can reasonably be said to possess means-end understanding only when pulling the support (string or cloth) is goal-directed and not dependent on such perceptual features (Jacobs and Osvath 2015).

For example, in the support task study on tamarins, the authors conclude that the subjects solved these tasks by understanding the general means-end relations mediated by the functionally relevant properties of their physical arrangement (Hauser et al. 1999). Later, this claim has been questioned by Povinelli (2000), proposing instead that primates only learn about the perceptually salient features of the task rather than about any more profound understanding of mean-ends relations. In other words, the animals were learning only how to obtain the food, based on the visually observable features of the task such as the continuous nature of the cloth or gap placement. As such, the observed transfer across different task conditions in Hauser's et al. (1999) study has been suggested to reflect the direct generalization of what was learned about these perceptual features rather than any reasoning about means-end relations. Accompanying experiments testing chimpanzees in various support and connection problems supported Povinelli's (2000) perceptual interpretation.

There are other related situations in which an animal's behavior may also suggest a failure to represent means-end relations adequately or to understand how a particular sequence of means contributes to an end (Woodward 2011). For example, animal's behavioral recipe may contain elements not necessary or superfluous for the achievement of the goal. An adequate means-end understanding would allow the animal to recognize when these superfluous elements are present and can be omitted. First evidence for such a recognition capacity comes from Goffin's cockatoos successfully responding to the functionality of each step in the chain in the five-step sequence problem-solving task. When one or more locks

were missing, the birds directed their attention to the first relevant one, ruling out a rigid learned routine (Auersperg et al. 2013). Alternatively, an animal that behaves as if it recognizes that employing a means in specific situation is sufficient for achieving the desired goal, (like a crow obtaining a short tool to use it on a longer stick to obtain the desired food reward) may, in fact, may, in fact, just employ a specific behavioral recipe or routine sufficient for reaching the goal in this specific situation. However, the animal may fail to recognize that there may be alternative means besides the employed one for the achievement of the goal, or, when a changed situation has the consequence that the original means is no longer appropriate. Furthermore, some claim that most animals, maybe even all except humans, can only deal with causal information which features their own actions as causes and outcomes as effects. In other words, an animal that only has a representation of the form “If I do action A, desired outcome O results” with no general representation of intermediate steps leading from A to O (Woodward 2011).

Probably the most challenging part of animal cognition is to rule out all the alternative explanations for “intelligent” behavior, and whether or not one or the other researcher adequately do so may remain open to debate. Nevertheless, recent findings in the context of means-end reasoning in animals provide promising and tractable empirical paradigms for investigating this challenging topic of animal cognition.

## Conclusions

Human behavior regularly involves elaborated sequences of means-end actions, but such sequences are quite rare in the natural behavior of nonhuman animals. Given recent reports about the performance of various nonhuman animals in different means-end tasks, it seems that at least some species may potentially possess a basic concept of means-end reasoning that is not directly reliant on perceptual features. However, given the likely perceptual origins of learning about means-end relations, researchers, in general, should be cautious in interpreting how animals

solve such problems, especially when the visual characteristics of the task are salient.

## Cross-References

- Analogical Reasoning
- Associative Learning
- Comparative Cognition
- Comparative Psychology
- Decision-Making
- Embodied Cognition
- Goal-Directed Behavior
- Insight
- Intelligence
- Intentionality
- Planning
- Problem-Solving
- String Pulling
- Tool Use

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## Means-End Understanding

### ► Means-End Reasoning

## Meat-Eater

### ► Carnivore (Diet)

## Mechanoreceptors

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## Introduction

Mechanoreception has roots in the Greek word “mechano,” meaning “machine,” and the Latin “receptiō,” meaning “to receive.” Mechanoreceptors are sensory organs that carry impulses from touch, pressure, and sound waves along nerves to the central nervous system (CNS), including the

brain. When a given mechanoreceptor is activated by external stimuli, such as touch, pressure, and/or sound waves, positive ions (electrically charged atom(s)) flow into the relevant cell. Net depolarization, or a positive change in charge, generates action potentials (APs) or electrical impulses. As the impulse travels along the nerve cell membrane, the AP synapses (connects) with nuclei (eukaryotic organelles containing genetic material) in the dorsal column of the spinal cord. Nerve fibers from this region travel upward, eventually forming synapses with nuclei in the thalamus of the brain, which relays sensory information to the cerebral mantle and somatosensory cortices. The somatosensory cortex interprets tactile (touch) information. In contrast, auditory (sound) information travels to, and is interpreted by, the primary auditory cortex. Thus, mechanoreceptors transduce mechanical energy from external stimuli (outside of the body) to biologically useful neural information for the body to use to respond to stimuli (French and Torkkeli 2009).

There are three types of mechanoreceptors. The first are mechanoreceptors that respond to tactile sensation (e.g., hair cells). The second are proprioceptors that respond to positional changes and movement of the body (e.g., muscle spindles and Golgi organs), and the third are baroreceptors that respond to changes in pressure (e.g., volume receptors). There are more tactile mechanoreceptors than proprioceptors or baroreceptors, perhaps in part because the skin constitutes the largest sensory organ in the body and provides a physical barrier and conduit between an organism's external and internal milieu. Indeed, in mammalian vertebrates, there are at least four known types of tactile mechanoreceptors, including but not limited to bulbous corpuscles, lamellar corpuscles, tactile corpuscles, and Merkel's discs.

Proprioceptors play a role in an individual's sense of balance and work with the vestibular system. In mammals, birds, reptiles, and most fish species, vibrational pressures are detected by hair cells in the cochlea of the ear. Hair cells are specialized receptors equipped with stereocilia, or small fingerlike projections. Vibrational forces induce movement of the stereocilia, which causes mechanically gated ion channels within the

sensory epithelium to open, allowing ions to enter the cell. Cations (positively charged ions such as  $\text{Na}^+$ ) enter the cell and change the cell's voltage, making it more positive. This change in voltage creates APs that are sent to the CNS and ultimately form the basis of spatial orientation. Like the vestibular system, the auditory system is also modulated by hair cells. The mechanisms of these two senses differ though primarily in the arrangement of hair cells. In proprioceptors, stereocilia in vestibular hair cells form an apex cilium (kinocilium), while auditory hair cells lack kinocilia and are arranged in a staircase-shaped formation.

## Evolution of Mechanoreceptors

The location and distribution of mechanoreceptors differ across taxa, but most types of mechanoreceptors share the same basic physiological principle: the presence of a specialized neuron that depolarizes in response to external stimuli. This indicates that throughout vertebrate evolution, mechanoreceptors have been evolutionarily conserved (Coffin et al. 2004). For example, both lampreys (agnathans or jawless fish) and gnathostomes (jawed vertebrates) have hair cells. Sensory hair cells are also found in invertebrates, but their similarity may merely reflect convergent evolution (Coffin et al. 2004). Also, ion channels sensitive to mechanical stimuli exist in bacteria, suggesting the ancient nature and function of mechanoreceptors (Manley and Ladher 2010). However, no basal ancestor of mechanoreceptors has been identified nor is the evolution of mechanoreceptors comprehensive or well understood.

## Vertebrates

Mammalian mechanoreceptors are located along the body, with clusters in locations particularly sensitive to mechanical stimuli, such as the fingertips. Tactile mechanoreceptors are located within or beneath the epidermis, the topmost layer of the skin, while Meissner's corpuscles lie just below the dermis in smooth skin, such as in



elephant trunks (Verendeev et al. 2015; Hoffmann et al. 2004). In contrast, Pacinian corpuscles are found in deeper layers of the skin in subcutaneous tissue. Meissner's corpuscles have a smaller receptive field than Pacinian corpuscles and are active when a stimulus first occurs and when the stimulus ends. Also, their response threshold is lower than that of Meissner's corpuscles, which means that Pacinian corpuscles respond faster to stimuli (Purves et al. 2001). Pacinian corpuscles are activated when they detect high-frequency vibrations (Purves et al. 2001). Both Merkel's discs (unencapsulated nerve endings) and Ruffini's corpuscles (encapsulated nerve endings) respond slowly and remain activated longer while a stimulus is occurring (Purves et al. 2001).

Bird beaks, or bills, interact with the external environment and are capable of detecting changes in pressure and velocity. Bird bills have internal mechanoreceptors with clusters of afferent neurons at the tips in some species (Cunningham et al. 2013). Afferent neurons carry nerve impulses from sensory stimuli to the central nervous system and brain. There are two types of mechanoreceptors in bird beaks, Herbst corpuscles and Grandry corpuscles, both of which detect external mechanical stimuli (Cunningham et al. 2013). The locations of the receptors within the bill depend upon multiple factors, including the species' diet, as a function of bird mechanoreceptors includes prey detection (Cunningham et al. 2013). The mechanoreceptors in primate fingertips function similarly to those in bird beaks, though they are not considered the same type of receptor, as they are morphologically different (Cunningham et al. 2013; Verendeev et al. 2015).

## Aquatic Vertebrates

Fish and other vertebrates adapted to aquatic life, such as amphibians, have evolved the lateral line system (LLS) to detect vibrations in water. The LLS allows aquatic organisms to identify objects in the surrounding environment and to respond to stimuli such as pressure gradients, vibrations, and movement of potential predators/prey. Named for a series of characteristic epithelial pores running

from the gills to the tail of the animal, the LLS consists of neuromasts or specialized hair cells located beneath the skin. Neuromasts are roughly analogous to the hair cells found in the mammalian auditory system. Some cartilaginous fish, notably sharks, have evolved electroreception and employ specialized organs, known as ampullae of Lorenzini, to detect electric potentials in water (Freitas et al. 2006; Winther-Janson et al. 2012).

## Invertebrates

Invertebrates, mostly arthropods (insects, spiders, crustaceans), also use mechanoreceptors to sense changes in their environment. One of the best-studied examples of invertebrate mechanosensation is that of the roundworm, *Caenorhabditis elegans*, whose six touch cells (ALML, ALMR, AVM, PLML, PLMR, PVM) are used to detect both internal and external forces. The intensity of the worm's withdrawal response from stimuli depends on the strength of the force. Mechanoreceptors also play a role in *C. elegans* reproduction. In order to facilitate mating, male *C. elegans* must utilize nine pairs of sensory rays to detect the position of a hermaphrodite's vulva. Genetic knockout males with faulty or absent rays cannot reproduce, emphasizing the importance of mechanosensation in *C. elegans*. Likewise, spiders belong to another invertebrate order (Araneae) with highly developed mechanosensory organs, including slit sensilla that detect vibrations, and tactile hairs, which enable spiders to navigate their webs (in web-building species) and locate prey (Mutai and Heller 2003).

## Conclusion

Impulses from touch, pressure, and sound waves travel along nerves to the central nervous system. Once the signal reaches the brain, the body can react to the stimulus. Thus, mechanoreceptors transduce mechanical energy from external stimuli into internal biologically useful neural information that the body uses to respond to stimuli.

Simple forms of mechanoreception have likely been present since the evolution of bacteria (approximately 3.5 bya). The ubiquity of mechanoreceptors across different domains of life suggests that they are of great evolutionary importance. Without mechanoreceptors, organisms would not have the ability to successfully navigate and/or respond to the outside world. This has been demonstrated by the high mortality rates seen in individuals with congenital analgesia, a disease characterized by nonfunctional nociceptors, which are specialized sensory neurons.

## Cross-References

- ▶ [Action Potentials](#)
- ▶ [Chemoreception](#)
- ▶ [Electroreceptors](#)
- ▶ [Evolution](#)

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## Mechanosensation

- ▶ [Accipitriformes Sensory Systems](#)
- ▶ [Falconiformes Sensory Systems](#)

## Medial Entorhinal Area (MEA)

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## Synonyms

[Medial entorhinal cortex \(MEC\)](#)

## Definition

Medial entorhinal area (MEA) refers to the medial subfield of the entorhinal cortex (EC) of rodents, bats, and a number of mammals with similarly structured brains. Its homologue in human and nonhuman primates is more accurately defined along the posterior, rather than medial, region of the entorhinal cortex. This brain area consists of a six-layered network of interconnected neurons whose patterns of electrical activity are thought to support spatial cognition.

## Introduction

To understand the role that the medial entorhinal area (MEA) plays in cognition and behavior,

investigators have attempted to identify the principles of structural and functional organization that govern the electrical activity of this brain region. Efforts toward characterizing the cellular organization, or microcircuitry, of the MEA have notably succeeded in identifying a range of morphologically distinct cell types and in describing how these neurons' cell bodies, dendrites, and axons are organized across the six layers of the MEA. Results from electrophysiological studies have additionally revealed neurons with markedly distinct patterns of electrical activity during behavior, leading investigators to functionally define a number of cell types in the MEA. To date, however, the relationship between morphologically and functionally defined cell types – as well as the contribution of these neurons to cognition and behavior – remains an open question.

## Current Knowledge

**Microcircuitry.** Neurons in the MEA are distributed along six cortical layers, designated I–VI, with larger numerals corresponding to layers located further from the surface of the brain. Superficial (I–III) and deep (IV–VI) layers are peppered to different degrees with a variety of morphologically distinct neurons that either excite or inhibit their postsynaptic targets.

The major known classes of excitatory neurons in the MEA are stellate and pyramidal cells. As their name suggests, **stellate cells** exhibit a roughly star-shaped appearance. The primary dendrites of these neurons emerge from the superficial portion of the cell body, or soma, and extend perpendicularly toward the surface of the brain. Dense arborization characterizes the length of the dendritic trunk. **Pyramidal cells'** somata and dendrites are similarly oriented, but they exhibit relatively sparse branching along the dendritic trunk, resulting in a more streamlined appearance that distinguishes these neurons from the starburst morphology of stellate arborization (Klink and Alonso 1997). The axons of stellate and pyramidal cells located in layers II and III project out of the MEA to form the perforant path, a dense array

of fibers that innervate each major subfield of the hippocampal formation (Witter et al. 2017). A subset of pyramidal cells found in layer V direct long-ranging axons toward various cortical and subcortical areas, while others innervate neurons in the superficial layers of the MEA and have been shown to particularly synapse onto layer III pyramidal cells (Kohler 1986; Witter et al. 2017).

Inhibitory neurons, which tend to suppress the electrical activity of their postsynaptic targets, can be further subdivided according to whether they issue local or long-ranging axonal fibers. An intricate network of locally projecting interneurons exerts inhibitory control over the excitatory cell population across the six layers of the MEA. This class of neurons includes **basket** and **chandelier cells** (Witter et al. 2017). These types of neuron vary in their somatic and dendritic morphology, yet they are more frequently differentiated by their axonal targets, as each type distinctly innervates either the soma or the initial axon segment, respectively, of excitatory cells located in the MEA. As far as the available evidence suggests, stellate and pyramidal cells do not directly innervate each other within the MEA. Instead, groups of interneurons provide direct synaptic contacts onto excitatory cells and coordinate their activity through a dense, recurrent inhibitory network (Couey et al. 2013; Witter et al. 2017). In contrast, the axons of long-ranging inhibitory neurons project out of the MEA to primarily innervate neurons in the hippocampus (Melzer et al. 2012), a finding that led to the realization that the entorhinal projection to the hippocampus is not exclusively excitatory.

Layers I and IV consist mainly of myelinated axonal fibers and glial cells and are only sparsely populated with neurons and their dendrites (Kohler 1986).

**Neural Correlates of Behavior.** Electrophysiological recordings carried out in awake, behaving animals have developed in parallel with the meticulous characterization of the microcircuitry of the MEA. While the bulk of these studies have been performed in rodents, a growing body of work has focused on data acquired from bats and nonhuman primates. Extracellular recordings in

these model species have overwhelmingly targeted the superficial layers of the MEA, largely due to their increased accessibility to recording electrodes relative to the deeper layers. According to results from various experiments, neurons located in layers II and III appear to exhibit strong spatial modulation that manifests as several complementary phenotypes, defined in the literature as **border**, **grid**, and **head-direction cells**. These patterns of electrical activity have lent credence to the hypothesis that functionally differentiable neurons may uniquely contribute to information processing in the MEA.

**Border cells**, which are thought to make up a small percentage of the neuronal population of the MEA, are neurons whose firing rates selectively increase as animals travel along segments of the physical boundaries of an environment (Solstad et al. 2008; Savelli and Knierim 2014). A larger proportion of MEA neurons, estimated at 50% in layer II (Sargolini et al. 2006), have been labeled **grid cells**. These neurons emit bursts of action potentials at spatial coordinates that coincide with the vertices of tessellated triangles (Hafting et al. 2005). The multiple, spatially distributed firing fields that each grid cell generates ultimately result in a gridded patterning of the surface area of an environment (Hafting et al. 2005). Rather than anchoring their activity to the boundaries of an enclosure, **head-direction cells** reflect vestibular and proprioceptive information by increasing their activity when an animal's head is oriented toward a preferred direction, regardless of the animal's allocentric position in the environment (Sargolini et al. 2006).

While the patterns of electrical activity used to define a given cell type are demonstrably robust, they have also been shown to be malleable. For example, some grid cells additionally exhibit head-direction modulation (Sargolini et al. 2006; Solstad et al. 2008), and a handful of neurons in several studies meet quantitative criteria for functional categorization as border and grid cells (Solstad et al. 2008). Moreover, Bonnevie et al. (2013) probed the impact of hippocampal inputs onto the MEA by pharmacologically suppressing

the CA1 region of the hippocampus and simultaneously recording electrical activity in the MEA. Over the period of hippocampal inactivation, grid cells simultaneously lost their grid fields and began exhibiting tuning to head direction, demonstrating the importance of available inputs in shaping MEA neuronal activity patterns during behavior. The ability of neurons to exhibit flexible patterns of activity suggests that there is no direct one-to-one mapping between morphology and functionality.

**Future Directions: Relating Structure to Function.** Neural activity depends on an intricate and highly dynamic interplay between the intrinsic properties of neurons and the connective structure in which they are embedded. Attempts to map neuronal morphology to function are ongoing (reviewed in Savelli and Knierim 2014). Additional efforts aim to identify the mechanisms whereby the organization of neuronal connections in the MEA fundamentally constrains and shapes the patterns of activity that its constituent cells manifest under a given set of circumstances. For instance, emerging data suggests that grid field generation may critically rely on the recurrent inhibitory circuitry that connects stellate and pyramidal cells in layers II and III (Couey et al. 2013). Moreover, computational simulations of the MEA network have provided a promising platform for experimenters to manipulate simulated physiological variables (e.g., neuronal morphology, network connectivity) and test the contributions of these variables to the resulting patterns of activity (Couey et al. 2013). Moving forward, the combination of empirical work and computational modeling will continue to elucidate the principles of structural and functional organization that ultimately shape the role of the MEA in cognition and behavior.

## Cross-References

- [Afferent and Efferent Impulses](#)
- [Entorhinal Cortex](#)
- [Hippocampus](#)

- [Medial Temporal Lobe](#)
- [Neuron](#)

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## Medial Entorhinal Cortex (MEC)

- [Medial Entorhinal Area \(MEA\)](#)

## Medial Striatum

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## Synonyms

[Associative striatum](#); [Caudate nucleus](#); [Dorsomedial neostriatum](#); [Dorsomedial striate nucleus](#)

The dorsal striatum is composed of two sub-regions, the dorsomedial and dorsolateral striatum, that, although thought to be generally similar in terms of their internal microcircuits and cell types, are now known to differ in a number of important ways. Among these is their connectivity; recent evidence suggests that, whereas the cortical inputs to the dorsolateral striatum are largely from sensorimotor cortices, the dorsomedial striatum receives the most heterogeneous cortical input of all striatal regions (Hunnicutt et al. 2016), and additionally receives glutamatergic inputs from the thalamus and basolateral amygdala. Both regions receive rich dopaminergic inputs from the substantia nigra pars compacta. Importantly, these distinct inputs have been found to play quite distinct functional roles in learning and behavior; whereas the dorsomedial striatum is involved in behavioral flexibility generally and in goal-directed action in particular, the dorsolateral striatum has variously been linked to relatively inflexible or automatic skilled motor movements and to the formation or “chunking” of action sequences or, more generally, to the control of habitual actions. Taken together, therefore, the medial and lateral regions of the dorsal striatum are currently thought to mediate two of the primary forms of action control composing the adaptive behavior of animals; i.e., goal-directed actions and habits.



## Background

Classical views of striatal function centered on its role in motor control, according to which striatal regions gathered information from widespread cortical areas and funneled this information through the basal ganglia and ventrolateral thalamus to the primary motor cortex to control movement (e.g., Kemp and Powell 1971). Alexander et al. (1986) were among the first to observe that the basal ganglia anatomy only superficially accorded with this view and went on to describe multiple parallel corticostriatal feedback loops, involving both motor and nonmotor regions of the cortex, which they felt could enable striatal involvement in a broad range of movement typographies. The authors reviewed the results of tracing studies and identified five parallel corticostriatal loops, originating from distinct cortical regions; skeletomotor, oculomotor, dorsolateral prefrontal, lateral orbitofrontal, and anterior cingulate (Alexander et al. 1986). Subsequent neuroanatomical and functional interrogation of striatal circuitry has refined the descriptions of these circuits and the involvement of other cortical and limbic regions, such as the temporal cortex (Middleton and Strick 1996) and the amygdala (Kelley et al. 1982), and has suggested that, rather than supporting heterogeneous motor movements, these parallel loops actually mediate heterogeneous forms of behavioral control process (Balleine and O'Doherty 2010).

## Anatomy

The dorsomedial striatum contains two populations of spiny projection neurons, which together make up 95% of all striatal neurons. Approximately half of the medial striatal projection neurons are striatonigral neurons and are the source of a direct monosynaptic projection to the substantia nigra pars reticulata (SNr). These direct pathway neurons preferentially express the neuropeptides substance P and dynorphin and express the dopamine D1 receptor. The remaining spiny projection neurons in the dorsomedial striatum also project to the SNr indirectly via a

multisynaptic pathway within the basal ganglia that includes the external part of the globus pallidus (GPe) and the subthalamic nucleus. These indirect pathway neurons preferentially express enkephalin, the adenosine A<sub>2A</sub> receptor and the dopamine D2 receptor. The remaining 5% of neurons are made up of a number of different interneurons, including the giant aspiny cholinergic interneurons that modulate striatal output neurons through the release of acetylcholine, and other interneurons that express somatostatin, neuropeptide Y, or nitric oxide synthase and regulate striatal output through the release of gamma-aminobutyric acid (GABA).

## Function

**Rodent** The anterior region of the dorsomedial striatum (aDMS) in the rat extends from approximately 2.76 mm anterior to bregma to the end of the ventral striatum, approximately 0.48 mm anterior to bregma. The aDMS is involved in cue-guided behavioral flexibility (Ragozzino et al. 2002), which is thought to be regulated by cholinergic activity (Ragozzino et al. 2009). Cortical projections from the prelimbic region of the medial prefrontal cortex to the aDMS have been associated with regulating cost-benefit choice behavior (Friedman et al. 2015). The anteriomedial quadrant of the DMS is involved in feeding; surges in enkephalin occur during feeding, and increases in mu-opioid receptor signaling induce feeding behavior (DiFeliceantonio et al. 2012). In contrast, the posterior dorsomedial striatum (pDMS), beginning around 0.24 mm anterior to bregma, has been implicated in several aspects of goal-directed learning and decision making. The pDMS is necessary for learning the specific action-outcome associations required for goal-directed learning and for the performance of goal-directed actions following learning (Yin et al. 2005a). This learning relies on N-methyl-D-aspartate (NMDA) receptors in the pDMS (Yin et al. 2005b) and phosphorylation of mitogen-activated protein kinase (MAPK), thought to occur as a result of coactivation of NMDA receptors and D1 receptors (Shiflett et al. 2010). The

glutamatergic input to the pDMS from the pre-limbic cortex is thought to be necessary for acquiring the specific action-outcome association during goal-directed learning (Hart and Balleine 2016), whereas the glutamatergic input from the parafascicular thalamus to cholinergic interneurons in the pDMS is not required for initial learning, but necessary for updating new action-outcome learning (Bradfield et al. 2013). The glutamatergic input from the BLA to the pDMS is necessary for goal-directed learning and performance (Corbit et al. 2013); however, this input is thought to contribute information about outcome value, embedded within the sensory-specific properties of the outcome (Balleine and Killcross 2006; Fig. 1).

**Humans** Homologies between rodent and human striatum have been drawn along more general lines, suggesting that the dorsomedial striatum in rodents is homologous to the caudate nucleus in humans (Balleine and O'Doherty 2010; Balleine et al. 2007). From this perspective, decision making in humans reflects much the same division as observed in rodents; flexible, reward-related action control involves the more medial caudate whereas relatively inflexible, habitual actions involve the more lateral putamen. For example, fMRI studies have shown that there is an increase in activity in the anterior caudate when the contingency between an instrumental response and reward is high (Tanaka et al. 2008), and similar to the dissociation between the rodent aDMS and pDMS, the activity in the posterior

caudate is associated with detecting noncontingent reward delivery (Liljeholm et al. 2011). There are also homologies in the role of the cortical input to the striatum in rodents and humans; the ventromedial prefrontal cortex in humans is considered homologous to the prelimbic cortex in rats (Balleine and O'Doherty 2010), and as with rats, this pathway has likewise been implicated in goal-directed actions, whereby the strength of input to the caudate predicts individual differences in the degree of flexible goal-directed action demonstrated by people (de Wit et al. 2012).

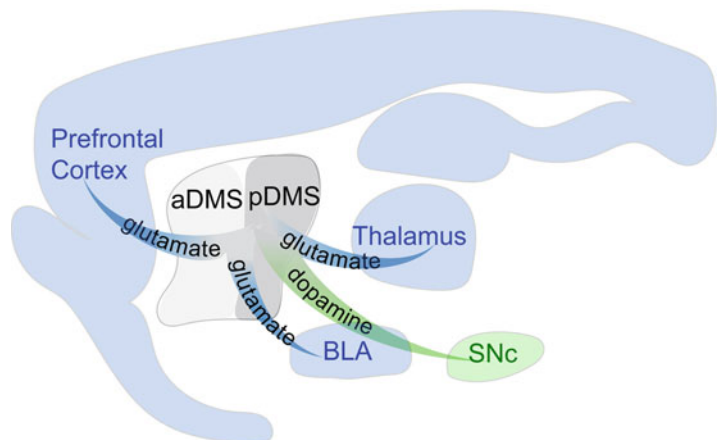
## Dysfunction

Given its intrinsic structure and its known functions, it is perhaps unsurprising that the dorsomedial striatum has been closely linked to executive functions and that, as with its afferent regions in frontal cortex, changes in the activity of this region, whether induced by stroke; neurodegenerative conditions, such as Parkinson's disease dementia; psychiatric conditions such as schizophrenia, major depression, or addiction; and even normal aging have been found to result in a common set of symptoms called collectively dysexecutive syndrome. The symptoms of this syndrome involve cognitive, affective, and behavioral changes reflecting increased inflexibility; cognitive rigidity and emotional and behavioral disinhibition. Interestingly, this is similar to that observed with habitual action control, in which

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### Medial Striatum,

**Fig. 1** Sagittal representation of the rat brain showing primary input pathways to the dorsomedial striatum. *aDMS*, anterior dorsomedial striatum; *pDMS*, posterior dorsomedial striatum; *BLA*, basolateral amygdala; *SNc*, substantia nigra pars compacta



performance is stimulus bound, motivated by general activation and associated with behavioral repetition. In essence, many disorders are partially characterized by a loss of goal-directed action control and the intrusion of habits. There is some evidence in clinical populations that some aspects of dysexecutive syndrome may be the result of reduced activity in the caudate; for example, patients with schizophrenia show intact sensitivity to changes in outcome value, but deficits in using those changes to flexibly alter choice, and this deficit is associated with a reduction in activity in the anterior caudate nucleus (Morris et al. 2015). Adolescents with major depressive disorder show reduced caudate activity, relative to healthy controls, during reward anticipation and reward outcome (Forbes et al. 2009). Dopamine release in the caudate and putamen is suppressed by drug-associated cues in drug addicts, and the magnitude of dopamine reduction is associated with cravings (Volkow et al. 2006), and patients with Parkinson's disease dementia show a significant reduction in caudate activity during a working memory task, relative to patients with Parkinson's disease without dementia (Lewis et al. 2003).

## Cross-References

- Amygdala
- Associative Learning
- Contingency
- Decision-Making
- Dopamine Receptor
- Executive Function
- Free Operant Response
- Goal
- Goal-Directed Behavior
- Instrumental Learning
- Motivation
- Nucleus Accumbens
- Operant Conditioning
- Reinforcement
- Stimulus Control

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## Medial Temporal Lobe

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## Structure and Connectivity

The medial temporal lobe (MTL) corresponds to the amygdala and the fifth temporal convolution of the human temporal lobe. The MTL cortex can be subdivided in the hippocampal formation and the surrounding cortex, the parahippocampal gyrus. The latter includes the entorhinal cortex, perirhinal cortex, and parahippocampal cortex (Squire and Zola-Morgan 1991; Zola-Morgan and Squire 1993). Important bidirectional pathways are established between high-order associative areas of the cortex and the MTL (Lavenex and Amaral 2000; Qin et al. 2016). The perirhinal cortex receives more prominent projections from unimodal associative areas such as the inferior temporal cortex and has efferents toward the lateral entorhinal cortex. The parahippocampal cortex receives inputs from multimodal associative areas such as the posterior parietal lobe and projects toward the medial entorhinal cortex. These two routes, commonly referred in the literature as the “what” and the “when” streams, finally converge in the hippocampus (Eichenbaum and Lipton 2008).

The hippocampal formation is a complex region with different cytoarchitectonical subregions including the subiculum, the hippocampus (also referred as the hippocampus proper or the Cornu Ammonis), and the dentate gyrus (Insausti and Amaral 2003). This structure has great synaptic plasticity properties, and it is the main site of adult neurogenesis in the brain (see chapter on the “► Hippocampus”). The hippocampus can be considered an information hub at the top of the hierarchy of the MTL system. Information can flow in and out the hippocampus from two main

routes: (a) via subiculum (mediated by the entorhinal cortex) (Lavenex and Amaral 2000) and (b) via fornix (Aggleton et al. 2010). After hippocampal processing, information can be then output back to the parahippocampal gyrus through the subiculum and from there to the cortex. The fornix connects the hippocampus with subcortical areas including septal nuclei (particularly nucleus basalis of Meynert), mammillary bodies, anterior thalamic nuclei, ventral striatum, ventral tegmental area, locus coeruleus, and raphe nuclei. Additional direct afferents are received from the amygdala, which also has a connection to the hippocampus through the entorhinal cortex. Both hippocampi are connected through the commissure of fornix (also called hippocampal commissure), and the anterior commissure connects both medial temporal lobes.

Taking all together, these circuits and the particular cytoarchitectonical characteristics of the MTL allow establishing feedback and feedforward connections with the cortex, which are essential for memory.

## The Role of MTL on Memory Processes

The pioneering work by Brenda Milner and colleagues evaluating patients with lesions in the MTL, including the iconic case of patient Henry Molaison (1926–2008), opened avenues for the investigation of the various aspects of memory that are causally linked to this area (Scoville and Milner 1957). H. M. had followed bilateral MTL removal for the relief of intractable temporal lobe epilepsy at the age of 27. Due to this treatment, he developed a severe amnesia. H. M. was unable to learn new information or form new memories – a condition called *anterograde amnesia*. Additionally, access to memories of events and facts occurring prior to the surgery was impaired to some extent – a condition called *retrograde amnesia*. This retrospective memory retrieval deficit occurred in a temporally graded manner, such that he was unable to recall almost anything from the 3 years prior to the surgery, but he was able to retrieve older memories. Such chronological pattern of impairment for autobiographical

memory following MTL insult is known as the Ribot's Law (for a review, see Frankland and Bontempi 2005). Strikingly, general intellectual and perceptual functions were preserved as well as working memory, procedural memory, and *priming* (an implicit memory facilitation effect, whereby the exposure to certain stimuli affects the later response to other stimuli or tasks).

The publication of H. M.'s case, as well as other MTL lesion studies that followed, established the causal role of the MTL in *declarative memory* (explicit and conscious memory for facts and events). However, these studies were limited since lesions extended broadly to the anterior temporal lobe. Hence, such evidence did not allow isolating the specific contribution of each MTL structure. This fact prompted the development of animal models, followed by the use of neuroimaging techniques, which shed light on the functional properties of this region and fostered the distinction between different memory systems.

Soon it was established that the memory deficits observed were related to the hippocampus and the surrounding parahippocampal gyrus, which will be hence referred to as the MTL memory system, excluding the amygdala and the lateral anterior temporal lobe (Squire and Zola-Morgan 1991; Zola-Morgan et al. 1991).

Today, the role of the MTL in long-term *episodic memory* (explicit encoding, consolidation, and recollection of experienced events including contextual details such as where, when, why, or with whom) is well established. For many years, a dominant view of memory recognition proposed subdividing recognition in two qualitatively distinct processes: familiarity and recollection (for a review see Yonelinas 2002). On the one hand, *familiarity* is a distributed process that follows the rules of signal detection, targeting a sense of knowing or having had previously experienced something. On the other hand, *recollection* is defined as an all-or-nothing process that may require the identification of details of an object or scene. Familiarity, recollection, and novelty processes were suggested to depend in different structures within the MTL (Daselaar et al. 2006). Accumulated evidence has shown that while the



hippocampus is engaged in processing the details that lead to recollection, the surrounding perirhinal and parahippocampal cortex can support familiarity (for items and context, respectively) with certain independence of the hippocampus.

More recently, the growing interest on describing the particular elements that differentiate MTL structures' roles has led to a new approach. It considers that the core function performed by the MTL is the establishment of arbitrary associations, relational processing, or binding. Instead of building up on the psychological distinction between familiarity and recollection, researchers have begun to focus on the qualitative differentiation of MTL structures and a functional specialization dependent on the kind processed information (for a review, see Eichenbaum et al. 2012). One of the most influencing MTL function models in this vein is the Binding Item and Context (BIC) model (Davachi 2006; Diana et al. 2007; Eichenbaum et al. 2007).

Based on neuropsychological and neuroimaging findings, the BIC model stresses the importance of binding during both encoding (Davachi 2006) and retrieval (Diana et al. 2007). According to this model, the perirhinal cortex supports the encoding of items and item features (intra-item associations) and plays a role in certain complex perceptual tasks (for a review, see Graham et al. 2010). On the other hand, the parahippocampal cortex supports the processing of the context in which items are presented. This context can include spatial (the "where"), temporal (the "when"), or even emotional information. All this information is finally transmitted through the entorhinal cortex into the hippocampus, which is the key structure that binds items and context across time and space into a single memory trace (inter-item associations).

## Spatial Navigation

Nevertheless, many different aspects and specifics of MTL function are still under debate. The exclusively long-term memory function of the MTL has been challenged. For instance, it has been suggested that the region also plays an important

role in short-term memory (Ranganath and Blumenfeld 2005) and perception (for supporting and contrasting views see, Baxter 2009; Suzuki 2009).

One of the most relevant debates rises from specifying the main hippocampal function as spatial navigation in contrast to declarative memory (Eichenbaum and Cohen 2014). A long tradition in the rodent literature has focus on the spatial navigation function of the MTL including in the human (for a review see, Moser et al. 2008) since the discovery of place cells (in the hippocampus and parahippocampal cortex) (O'Keefe and Dostrovsky 1971) and grid cells (in the entorhinal cortex) (Fyhn et al. 2004). *Place cells* are neurons that fire when the animal is positioned at a specific spatial location. *Grid cells* are neurons that provide a position-in-space signal such as a cognitive representation of the space. From this perspective, the MTL has a main role for both spatial memory and spatial navigation (Sanders et al. 2015).

More recently, neurons that fire at particular moments within a relevant time period have been identified in the hippocampus, namely, *time cells* (for a review, see Eichenbaum 2014). This has led some authors to suggest that the ultimate goal of the MTL may not be specific to the spatial navigation per se but rather reflect the integration and encoding of multiple details of the spatiotemporal context and the content of a given event that allows its differentiation from other events, whether they are pathways, sequences, or autobiographical memories (Eichenbaum and Lipton 2008; Eichenbaum et al. 2012).

## Amygdala

From an anatomical viewpoint, the amygdala is part of the medial temporal lobe. However, this independent nucleus is often excluded in most studies addressing the MTL function, which focus on the medial temporal lobe cortex (Squire et al. 2004). This is due in part because the amygdala does not directly contribute to episodic memory or spatial navigation. Instead, the amygdala has received greater attention for its role in emotional processing, fear conditioning, and

modulation of memory consolidation (LaBar and Cabeza 2006). More information on the function of this structure can be consulted in the appropriate chapter.

## Cross-References

- ▶ [Amygdala](#)
- ▶ [Declarative Memory](#)
- ▶ [Encoding](#)
- ▶ [Entorhinal Cortex](#)
- ▶ [Episodic Memory](#)
- ▶ [Hippocampus](#)
- ▶ [Navigation](#)
- ▶ [Parahippocampal Cortex \(PHC\)](#)
- ▶ [Perirhinal Cortex](#)

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## Medulla Oblongata

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## Synonyms

Myelencephalon

## Definition

The medulla is a funnel-shaped structure located between the pons and spinal cord. It is responsible for regulating the heart rate, arterial blood pressure, autonomic functions, and transmission of sensory and motor signals between the spinal cord and the cortex of the brain.

## Introduction

The medulla or medulla oblongata, synonymously known as myelencephalon, is a stem-like, funnel-shaped structure and is located posterior to the midbrain. It extends from the foramen magnum up to the pons-medullary junction [as shown in Fig. 1] (Haines 2018).

The medulla regulates the body's motor function by ascending and descending fiber tracts that pass forward and backward through the spinal cord by traversing the medulla. The medulla also contains neuronal cell groups extending from medullary reticular formation, which play a fundamental role in regulating visceral sensory processing, heart activity, gastrointestinal, and other physiological functions, thereby maintaining homeostasis of the body (Verberne 2014). Medulla is present among different animal species (Fig. 2). Lamprey and hagfish possess a fully developed medulla (Nishizawa et al. 1988), which is thought to be evolved around approximately 505 million years ago (Haycock 2011).

## Development

During the initial stages of embryonic development, medullary neurons emerge from the caudal section of the neural tube known as rhombencephalon, which further differentiates into two structures called metencephalon (forming the pons and cerebellum) and myelencephalon (forming the medulla), as shown in Fig. 3 (Verberne 2014).

The basal plate and alar plate during the development phase differentiate into **somatic afferent [SA]**, **somatic efferent [SE]**, **visceral afferent [VA]**, and **visceral efferent [VE] nuclei** (Fig. 4).

The basal plate gives rise to the **hypoglossal nucleus [SE]**, the inferior **salivatory nucleus [VE]**, the **dorsal motor vagal nucleus [VE]**, and the **nucleus ambiguus [SE]**.

Furthermore, the alar plate forms the cranial nerve nuclei such as the **vestibular nuclei [SA]**, the **cochlear nuclei [SA]**, and the **spinal trigeminal nucleus [SA]**, along with the **solitary nucleus [VA]** (Haines 2018).

## Anatomical Structure

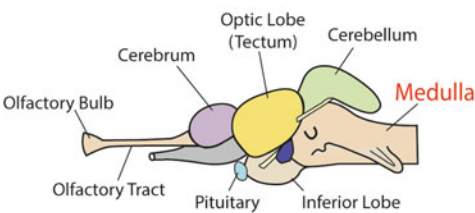
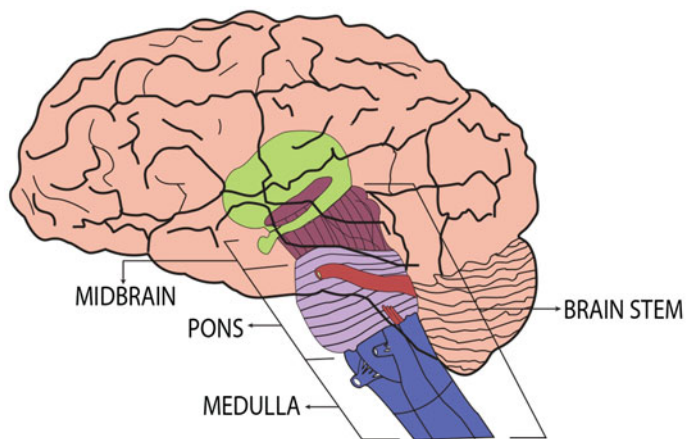
### External Anatomical Features

#### Anterior Medulla

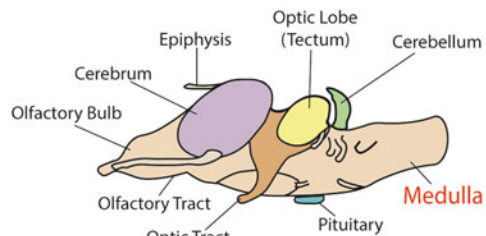
The anterior portion of the medulla can be distinguished by a median fissure (anterior) that has two

**Medulla Oblongata,**

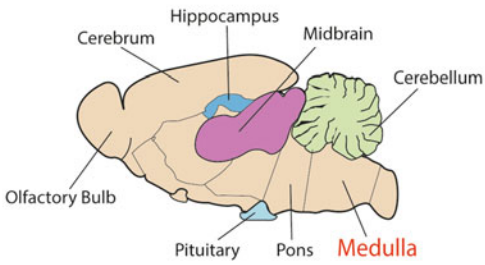
**Fig. 1** Position of the brainstem inside the cortex of human brain



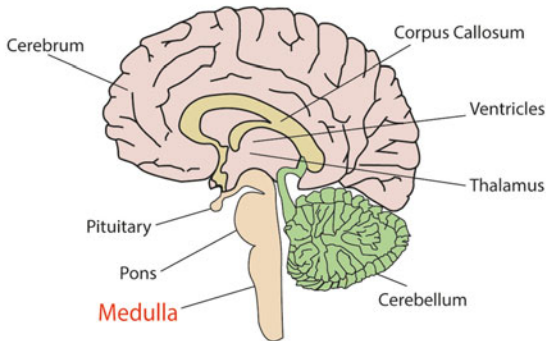
(a)



(b)



(c)

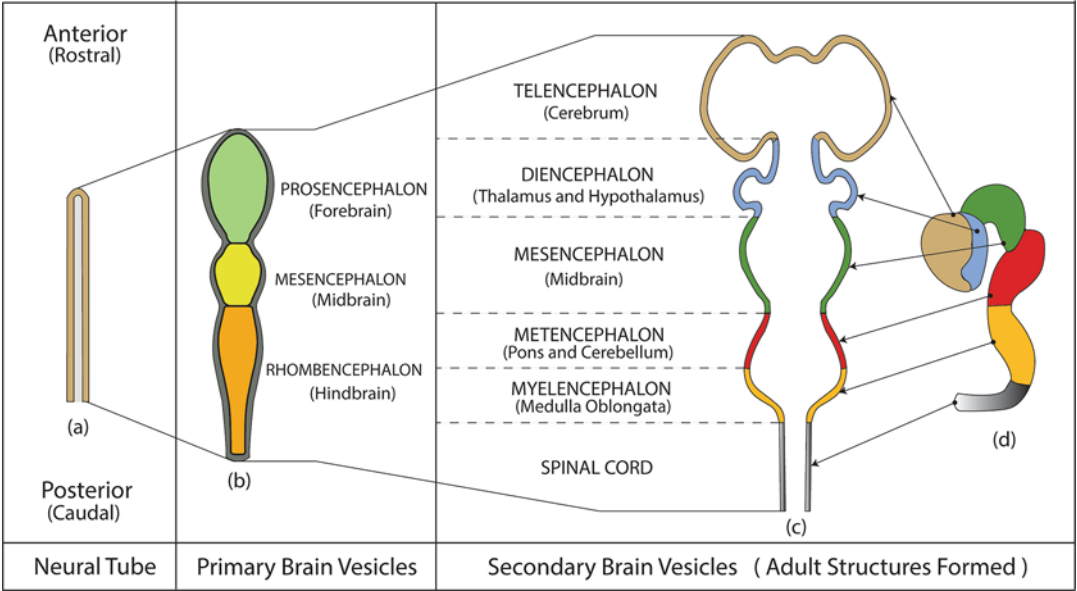


(d)

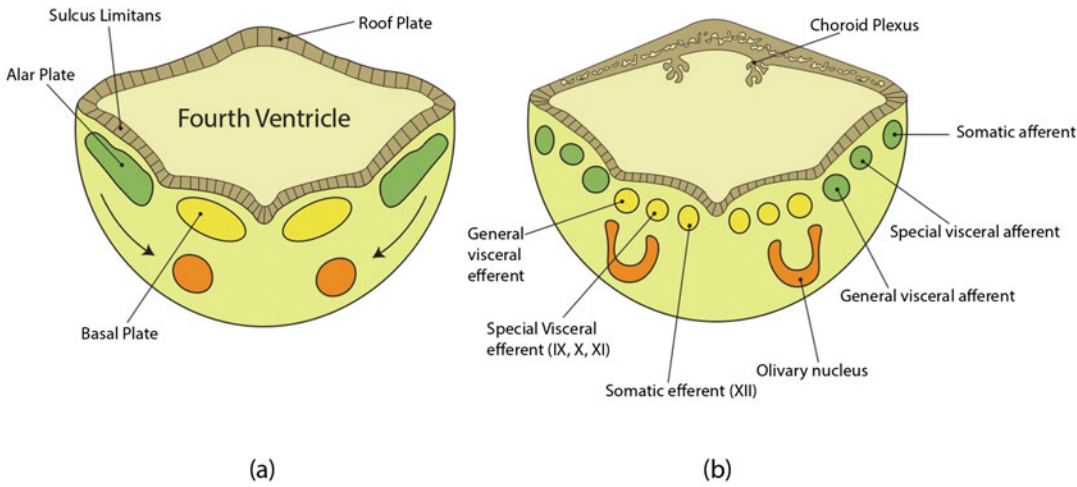
**Medulla Oblongata, Fig. 2** Location of the medulla among different animal species: **a)** fish, **b)** frog, **c)** rat, **d)** human

longitudinal ridges located adjacent to the inferior olivary eminence and the pyramids. The pyramids emerge from the basilar pons and stretch caudally toward the pyramidal decussation, and about 90% of these fibers traverse through the midline. Most of these fibers have their origin in the motor cortex as corticospinal fibers; hence, this crossing is also

known as motor decussation. The hypoglossal nerve leaves the medulla from a deep groove present between the pyramid and olive, known as the preolivary sulcus. In addition, the abducens nerve surfaces at the pons-medullary junction, in line with the rootlet hypoglossal nerve (Haines 2018).



**Medulla Oblongata, Fig. 3** Development of different structures of the brain during the course of embryonic development: **a)** neural tube, **b)** primary brain vesicles, **c** and **d)** represent secondary brain vesicles of the developing embryo and corresponding adult structures that are formed



**Medulla Oblongata, Fig. 4** Cross section through the developing medulla: **a)** early stage, **b)** later stage

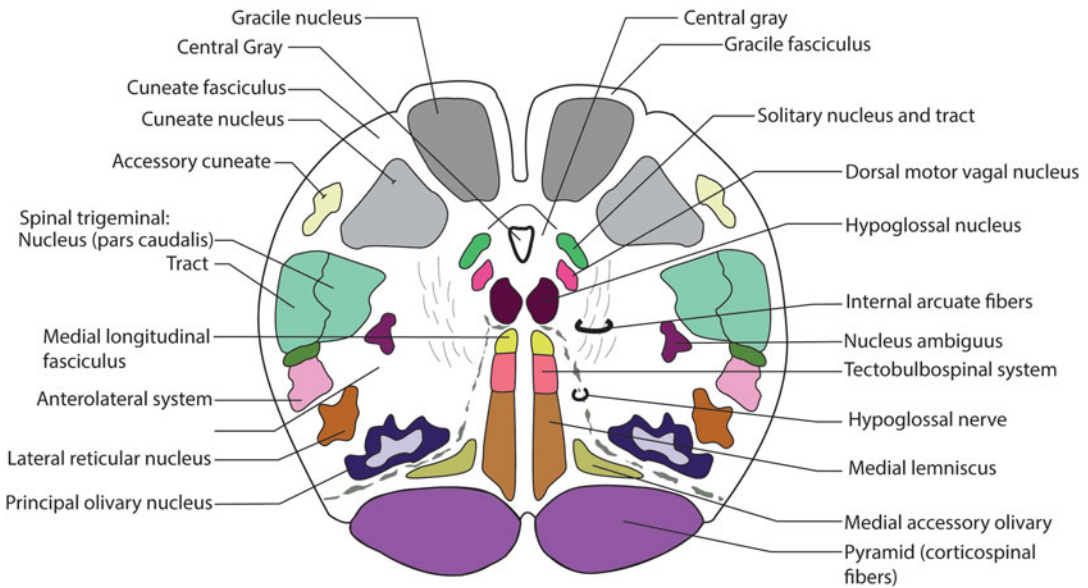
**Lateral Medulla**

The lateral segment of the medulla has a deep groove, known as the postolivary sulcus. It is located medially between two structures, the restiform body and the inferior olivary nucleus. Cranial nerves, for example, the vagus and glossopharyngeal nerves, emerge from this

region. In comparison, the facial and vestibulo-cochlear nerves arise from the posterolateral medulla. However, the structures that are served by the accessory nerve do not have any projections from the medulla (Haines 2018).

The brain and the fourth ventricle contract to form the central canal of the spinal cord at a point





**Medulla Oblongata, Fig. 5** Transverse section of the medulla at the level of the caudal medulla showing the fasciculus, tracts, and nucleus

called obex. Anterior to this point lies the restiform body, whereas the trigeminal tubercle (tuberculum cinereum) is located posteriorly (Haines 2018).

#### Posterior Medulla

The posterior segment of the medulla is characterized by the cuneate fasciculi and gracile nucleus (Fig. 5) located caudal to the obex and their respective tubercles (Fig. 5). Anterior to these tubercles lies a protruding elevation on the posterolateral region of the medulla, called the restiform body. This structure continues to elevate up to the pons-medullary junction and holds a range of cerebellar afferent fibers. At the pons-medulla junction, the restiform body joins with a much smaller juxtarestiform bundle to form the inferior cerebellar peduncle (Haines 2018).

#### Internal Anatomy

The internal anatomy of the medulla is commonly studied at the following levels:

##### Spinal Cord-Medulla Transition

The transition between the medulla and spinal cord takes place at the caudal level of pyramidal

decussation. The gray matter of the spinal cord is replaced with motor decussation, substantia gelatinosa, and posterolateral tract fused into the spinal trigeminal tract and nucleus, and the central gray matter enlarges (Haines 2018).

The central canal of the spinal cord extends until the caudal half portion and then expands into a cavity of the fourth ventricle, in the rostral half of the medulla (Snell 2010).

##### Level of Decussation of Pyramids

At the level of pyramidal decussation (motor decussation), approximately 90% of the corticospinal fibers pass through the anterior midline and continue down to the spinal cord as the lateral corticospinal tract. Posterior to the central gray matter, the gracile and cuneate nuclei first appear in their respective fasciculi, collectively known as posterior columns.

Laterally, the spinal trigeminal tract appears as the trigeminal tubercle or tuberculum cinereum on the surface of the medulla.

The caudal segment of medulla contains the remnants of medial motor cell column of C1, nucleus ambiguus, tectobulbospinal system (Fig. 5), and medial longitudinal fasciculus,

whereas remnants of the medial motor cell column of C1 and accessory column can be seen at the spinal cord medullary junction, but they do not innervate the medulla (Haines 2018).

#### Level of the Sensory Decussation

At this level, a major ascending sensory pathway traverses through the midline, known as posterior column-medial lemniscus, and because of which, it is known as sensory decussation. The posterior columns are mainly replaced by the gracile and cuneate nuclei, onto which the fibers responsible for conveying vibratory and tactile sensations from the upper and lower parts of the body terminate.

The axons from these nuclei traverse anteromedially to form the internal arcuate fibers and then decussates in a contralateral manner to form the medial lemniscus. Axons of the gracile nucleus and cuneate nucleus convey information coming from the lower and upper extremities to the anterior and posterior regions of the medial lemniscus (Haines 2018).

In the anterolateral region of the medulla, the vestibulospinal, spinocerebellar, and rubrospinal tracts are situated. Lateral to the internal arcuate fibers lies the nucleus of the spinal tract of the trigeminal nerve, and collectively, they are known as spinal lemniscus (Snell 2010).

#### Level of the Olivary Nucleus

A transverse section through this region reveals the floor of the fourth ventricle. At this level, the amount of gray matter increases due to the presence of the vestibulocochlear, glossopharyngeal, hypoglossal nerve, vagus, accessory, olivary nuclear complex, and arcuate nuclei (Snell 2010).

#### • Olivary Nuclear Complex

The complex contains nuclei-like inferior olivary nucleus and dorsal and medial accessory olivary nuclei, out of which the inferior olivary nucleus is the largest. Here, the medially facing gray matter is present in the shape of a crumpled bag (Fig. 5), which is responsible for the protruded structure called the olive, located on the surface of the medulla (Snell 2010).

#### • Vestibulocochlear Nuclei

The vestibular nuclear complex is composed of the following nuclei: (1) inferior vestibular nucleus, (2) superior vestibular nucleus, (3) lateral vestibular nucleus, and (4) medial vestibular nucleus.

There are other two nuclei: the anterior cochlear nucleus located on the anterolateral portion of the inferior cerebellar peduncle and the posterior cochlear nucleus on the posterior region of the peduncle and lateral to the floor of the fourth ventricle (Snell 2010).

#### • The Nucleus Ambiguus

It consists of large motor neurons located deep within the reticular formation (Fig. 5). Nerve fibers emerging from this nucleus synapse with the vagus, glossopharyngeal, and cranial part of the accessory nerve and are dispersed to the voluntary skeletal muscle (Snell 2010).

#### Rostral Medulla and Pons-Medulla Junction

The structures that occupy the position at the central portion of the medulla oblongata continue at same locations in the rostral medulla. However, structure like the inferior salivatory nucleus and prepositus (hypoglossal) nucleus appears (Haines 2018).

#### Ascending Tracts

##### Dorsal Column Tracts

The tracts of dorsal column or medial lemniscal system carries the sensory information for delicate touch, vibration, positioning, and point discrimination from skins and joints.

The medial lemniscal system consists of ascending axons of cuneate and gracile fasciculi, which receives the sensory input from the upper and lower of the body and terminate in the cuneate and gracile nucleus, traversing through the medial lemniscus and relaying the information to the thalamus and ultimately to the somatosensory cortex (Verberne 2014).

##### Spinothalamic Tracts

Spinothalamic tracts originate from the neurons of the spinal dorsal column, receiving its sensory

input from afferent fibers of Lissauer's tract of the spinal cord. It has two subdivisions; the lateral branch carries temperature and pain information, while the anterior part conveys the information about fine touch (Verberne 2014).

#### Spinoreticular Tracts

The axons of spinoreticular tract convey the information about intense pain and arise from the ventrolateral spinal cord neurons and terminate onto neurons of the rostral ventrolateral medulla and midline medullary raphe (Verberne 2014).

#### Spinal Trigeminal Tract

The trigeminal nerve is responsible for the conduction of sensory information from the nose, face, and mouth to the brain. The medulla receives one-third projection from the caudal segment of the spinal trigeminal nucleus (Fig. 5), terminating in the subnucleus caudalis, and conveys the information about pain and temperature (Verberne 2014).

#### Spinocerebellar Tracts

Spinocerebellar tracts pass through the lateral medulla into the cerebellum via cerebellar peduncles. This tract transmits the information from tendon organs, muscle spindles, pressure, baroreceptors, and control movement (Verberne 2014).

#### Cranial Nerve and Nerve Nuclei

The medullary structure contains the fibers and nucleus of cranial nerves such as facial nerve, glossopharyngeal nerve, vagus nerve, accessory nerve, and hypoglossal nerve that originate and project from the medulla (Verberne 2014).

**Facial Nerve** The facial nerve (cranial nerve IX) originates from the anterior surface of the pons-medullary junction and has motor, sensory and parasympathetic nuclei (Snell 2010).

The motor segment of the facial nerve supplies the muscles of the scalp, face, stylohyoid muscle, and digastric muscle through somatic motor axons, responsible for voluntary muscle control and facial expressions as its motor neurons project to and control the muscles of the lips, cheeks, and forehead (Snell 2010).

The taste fibers originating from the floor of the mouth, anterior two-third of the tongue, and palate innervate the sensory nuclei and are responsible for the sensation of taste (Snell 2010; Verberne 2014).

The parasympathetic nuclei is located posterior to the motor nucleus and consist of lacrimal and superior salivatory nuclei. Both nuclei receive their projections from hypothalamus. The lacrimal nuclei receive information about emotional response, reflex lacrimation through the trigeminal nerve and the superior salivatory receives information about taste from the mouth cavity through the nucleus of the solitary tract (Snell 2010).

**Glossopharyngeal Nerve** The glossopharyngeal nerve (cranial nerve IX) exits the anterolateral surface of rostral medulla as a string of rootlets, in a fissure located in between the olive and the inferior cerebellar peduncle. The glossopharyngeal nerve has three nuclei: (1) the main motor nucleus, (2) the sensory nucleus and (3) the parasympathetic nucleus.

The motor nucleus is located deep within the reticular formation of the medulla and emerges from the anterior end of nucleus ambiguus. The stylopharyngeus muscle is responsible for the elevation of laryngeal and pharyngeal muscles that receive its motor input from the efferent fibers of the glossopharyngeal nerve.

The sensory nucleus emerges as a part of the nucleus of tractus solitarius and receives its input from the carotid sinus (responsible for the control of arterial blood pressure), pharynx, and caudal one-third of the tongue (responsible for taste) (Snell 2010).

The parasympathetic nucleus receives its afferent projections from the hypothalamus through the autonomic pathways, which are believed to receive the olfactory information via reticular formation.

The preganglionic efferent parasympathetic fibers extend up to the otic ganglion via the lesser petrosal nerve, tympanic branch of the glossopharyngeal nerve, and the tympanic plexus. The postganglionic fibers progress towards the parotid salivary gland.

**Vagus Nerve** The vagus nerve exits the anterolateral surface of the rostral medulla as rootlets, from the middle of the olive and cerebellar peduncle.

The vagus nerve also has both motor and sensory nuclei:

The motor nucleus is located deep within the reticular formation of the medulla and emerges from the nucleus ambiguus.

The parasympathetic nucleus of the vagus nerve is a subdivision of the motor segment that receives the afferent projections from the hypothalamus and glossopharyngeal nerve. The efferent fiber innervates involuntary muscles of the heart (heart rate), bronchi, stomach, small intestine, and large intestine and extends to the distal one-third of the transverse colon (peristalsis).

The sensory nucleus emerges as a caudal portion of the nucleus of the tractus solitarius and the incoming afferent input that enters the brain stem and terminates in the spinal nucleus of the trigeminal nerve. The sensory input conveys information from mechanoreceptors; chemoreceptors of the GI tract, lungs, and heart; and hepatic glucoreceptors (Snell 2010; Verberne 2014).

**Accessory Nerve** The accessory nerve (cranial nerve XI) is a motor nerve formed by the fusion of a spinal root and a cranial root.

The axons of nerve cells lying in nucleus ambiguus form the cranial root. The motor fibers emerge anteriorly from the medulla between the inferior and olive cerebellar peduncle. The spinal root is formed from the axons of nerve cells lying in the spinal nucleus, located in the gray column of the upper five cervical segments of the spinal cord.

The accessory nerve is responsible for the voluntary movement of the larynx, pharynx, and trapezius muscle (Snell 2010).

**Hypoglossal Nerve** The hypoglossal nerve (cranial nerve XII) is a motor nerve that emerges anteriorly from the medulla, innervating the extrinsic styloglossus, genioglossus, hyoglossus, and intrinsic muscles of the tongue. It is responsible for the voluntary control of the shape and movement of the tongue (Snell 2010).

### Spinal Trigeminal Tract

The sensory input from mouth, face, and nose is carried to the nervous system by the afferent cell bodies of trigeminal nerve found within the trigeminal ganglion.

The neurons of trigeminal ganglion enter the brainstem at the pons level and have two main components, (1) principal sensory nucleus and (2) spinal trigeminal nucleus, situated in the lateral medulla and the posterior one-third in subnucleus caudalis of the medulla (Verberne 2014).

### Descending Tracts

Most of the axonal bundles pass through the medulla in a rostrocaudal manner. These bundles may not synapse with the medullary region, but a traumatic lesion can significantly impair the functions for which they are responsible (Verberne 2014).

### Corticospinal Tract

Corticospinal tracts are responsible for conducting motor signals from the premotor and precentral motor cortex to the spinal cord descending through the medullary pyramids in the medulla and controlling the body's voluntary movements (Verberne 2014).

### Corticobulbar Tract

The axons of the corticobulbar pathway travel through the primary motor cortex; project into the nucleus of cranial nerve such as hypoglossal, ambiguus, facial, and trigeminal nucleus; and control muscles of the face, head, and tongue regions. The facial, ambiguus, and trigeminal nuclei receive the cerebral cortex's input in an ipsilateral manner (Verberne 2014).

### Medial Forebrain Bundle

It contains the axons from neurons projecting to and from the hypothalamus and the other structures. They also contain the neurons from the paraventricular hypothalamic nucleus that projects to the dorsal medulla such as the dorsal motor nucleus of vagus and solitary tract (Verberne 2014).

### Vestibulospinal Tract

The vestibulospinal tract axons originate from the lateral and medial vestibular nucleus into the spinal cord's white matter. The vestibulospinal pathway is responsible for controlling antigravity muscles and facilitates the rapid movements in response to the change in body position (Verberne 2014).

### Rubrospinal Tract

The fibers of rubrospinal tract are responsible for the somatic motor function, originate from the midbrain's contralateral red nucleus, and go down into the spinal cord via lateral medulla (Verberne 2014).

### Reticulospinal Tract

The reticulospinal tract emerges from the midbrain, medullary reticular formation, and pontine and plunges into the gray matter of the spinal cord in both contralateral and ipsilateral manner. The axons projecting to these structures originate from the ventral midline raphe neurons and modulate the somatosensory transmission, e.g., pain, and some of them are responsible for the production of the neurotransmitter serotonin (Verberne 2014).

### Tectospinal Tract

The axons of tectospinal tract arise from the neuronal cell bodies of tectum and superior colliculus descending through the medulla and are responsible for rotatory movement of the head in response to the auditory and visual stimuli (Verberne 2014).

### Medial Longitudinal Fasciculus

It is responsible for carrying out the head and eye movements and consists of neurons found in vestibular nuclei, where it forms an additional fiber tract that descends near the tectospinal tract (Verberne 2014).

## Vasculature

The medulla is supplied with two main vertebral arteries, the anterior spinal artery and the posterior inferior cerebellar artery (PICA), and an

additional artery known as the posterior spinal artery, a subdivision of PICA.

The anterior spinal artery serves all the medial structures of the medulla, including the hypoglossal nucleus and roots, the medial lemniscus, and the pyramid through its innervating branches.

The posterior spinal artery serves the posterior region caudal to the obex. Significant structures in this area include the spinal trigeminal tract, nucleus, and posterior column (gracile and cuneate) nuclei.

The branches of PICA serve the entire posterolateral medulla, located rostrally to the obex, including the anterolateral system, vestibular nuclei, spinal trigeminal tract and nucleus, nucleus ambiguus, solitary tract, and nucleus (Fig. 5).

Apart from the medulla, PICA also serves the fourth ventricle's choroid plexus, and the anterior inferior cerebellar artery serves structures like the cochlear nuclei, pons-medulla junction, and a small adjacent part of the restiform body (Haines 2018).

## Function

### Physiological Functions

#### • Arousal and Nociception

The medulla is a major site for the processing of pain (nociceptive), where neurons within raphe magnus nucleus play a fundamental role by controlling the activity of nociceptive ascending pathway and, in turn, are controlled by neurons in the midbrain periaqueductal gray area.

Apart from pain processing, the raphe magnus nucleus controls a range of motor and sensory functions, including sympathetic vasomotor control, some aspects of sexual organ function, nociception, and thermoregulation.

The sensory neurons of the solitary tract nucleus are organized in a topographical manner so that its rostral segment receives significant gustatory input. In comparison, the intermediate and caudal segments receive general visceral and respiratory inputs. These neurons not only synapse with intramedullary neurons but significantly contribute to the ascending projection as well (Verberne 2014).



- **Eating and Digestion**

The medulla is implicated in the process of digestion. Various signals such as hunger, visual stimuli, and nutrients in intestinal lumen trigger responses like salivation, changes in gastrointestinal blood flow, motility, and release of cholecystokinin (CCK) from endocrine cells via afferent fibers of the vagus nerve, which synapse in the nucleus of solitary tract of the medulla. These signals are then conveyed to the hypothalamus by ascending pathways, where they further regulate the groups of neurons that control food consumption (Verberne 2014).

- **Taste**

Gustatory (taste) signals perceived by the taste buds are transmitted to the nucleus of the solitary tract by primary efferent fibers. These signals are relayed to higher regions such as the somatosensory thalamus and parabrachial nucleus, which in turn transmits it to the gustatory region of the postcentral gyrus and insular cortex (Verberne 2014).

- **Salivation**

The neurons that control the production of saliva, by stimulating salivary glands (sublingual, lingual, and submandibular glands), are in the salivatory nucleus near the dorsal pons-medullary junction. These neurons also control the secretion from lacrimal, nasal, and palatine glands (Verberne 2014).

- **Vestibular Function**

The vestibular system perpetuates functions like posture, body stance, and movements of the head and eye in response to vestibular signals. The inferior olivary complex located in the ventral part of the medulla directs the fiber inputs from components of the vestibular system via the olivocerebellar tract to the Purkinje cells of the cerebellum (Verberne 2014).

- **Cardiovascular Regulation**

The neuronal networks within the medulla provide negative feedback by relaying the afferent information to the brain through cranial nerves, to regulate the homeostatic bodily function of the body such as arterial baroreceptor reflex, maintenance of the heart rate, and sympathetic vasomotor discharge.

The neurons of rostral ventrolateral medulla are implicated in several processes such as cardiovascular reflexes, glucose homeostasis, and epinephrine secretion and are targeted by the antihypertensive drugs to exert its effect by inhibiting it (Verberne 2014).

- **Respiration**

The Bötzing and pre-Bötzing complexes found in the rostral ventrolateral medulla and the rostral-caudal ventral respiratory groups of neurons are responsible for the generation of rhythmic respiratory activity (timing and depth of respiration) and are also known as a central respiratory generator.

The central respiratory generator regulates the timing and depth of respiration, and its function remains unaltered even under the influence of anesthesia, except in case of deep anesthesia or overdose of drugs, which causes respiratory arrest (Verberne 2014).

## **Disorders**

- **Wallenberg Syndrome**

The Wallenberg syndrome or lateral medullary syndrome is characterized by clinical features such as falling toward the site of the lesion, vertigo, diplopia (double vision), Horner syndrome (ipsilateral), loss of nociceptive (pain) and temperature sensation on the opposite side, nystagmus, dysphonia, dysarthria, dysphagia, and decreased gag reflex.

This condition can occur as a result of insult to the lateral medulla, and condition such as infarct of the posterior inferior cerebellar artery is among

the most common cause of Wallenberg syndrome (Sciaccia et al. 2019).

- **Dejerine Syndrome**

The Dejerine syndrome or medial medullary syndrome is characterized by a contralateral weakness and hemi-sensory defects with hypoglossal palsy on the ipsilateral side, caused by an injury to the medial portion of the medulla.

This condition can occur as a result of infarct affecting the hypoglossal nerve nucleus, due to obstruction of the anterior spinal artery or small branches of the proximal or vertebral artery (Sciaccia et al. 2019).

- **Babinski-Nageotte Syndrome**

The Babinski-Nageotte syndrome or hemimedullary syndrome is caused by lateral and medial medullary infarction due to the obstruction of intracranial portion of the vertebral artery.

The clinical features include symptoms of both lateral and medial medulla, cerebellar ataxia (ipsilateral), Horner syndrome, contralateral hemiplegia, hemianesthesia, and sensory deficits of the face (Sciaccia et al. 2019).

- **Hypertrophic Olivary Degeneration**

Hypertrophic olivary degeneration is a rare condition marked by a lesion in the triangle of Guillain and Mollaret (dentato-rubro-olivary pathway), a structure formed by the inferior olivary nucleus, red nucleus, and contralateral dentate nucleus. The hypertrophy affecting the inferior olivary nucleus occurs as a result of transsynaptic degeneration of the central tegmental tract or dentatorubral tract. The clinical features include palatal myoclonus and a rapid spasm of the palate (roof of the mouth) (Sciaccia et al. 2019).

## Conclusion

The medulla oblongata is both anatomically and functionally, a crucial part of the nervous system

located anterior to the spinal cord and forming the lower portion of the brainstem. It contains several ascending and descending tracts that pass through the structure responsible for conveying sensory and motor information between the cortex and the spinal cord. Moreover, several nuclei situated in the medulla give rise to cranial nerves such as the vagus nerve, hypoglossal nerve, and facial nerve that contribute to important functions such as perception of taste, pain, and touch; regulation of the heart rate and blood pressure; and voluntary muscle control. Any damage to the structure may lead to loss of sensory and motor functions, which is also seen in disorders such as Wallenberg syndrome and Babinski-Nageotte syndrome.

## Cross-References

- [Cerebellum](#)
- [Homeostasis](#)
- [Homunculus](#)
- [Nerve Cells](#)

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## Megabat Locomotion

### ► Megachiroptera Locomotion

## Megachiroptera Locomotion

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## Synonyms

Fruit bat locomotion; Megabat locomotion; Old  
World fruit bat locomotion

## Definition

Pattern of movement observed in Megachiroptera.

Megachiroptera (also known as fruit bats, Old World fruit bats, or megabats) is a suborder of Chiroptera. As of 2018, 197 megachiropteran species have been noted (Almeida et al. 2011). Due to the gracile anatomy of megachiropterans, genetic records have been more reliable than fossils in determining the evolution and lineage of megachiropterans. Based on genetic records, it is suspected that the megachiropterans evolved from Australia or Melanesian Island. The lineage eventually dispersed to mainland Asia, the Mediterranean, and Africa (Almeida et al. 2016). Today, you can find megachiropterans in the subtropical parts of Eurasia, Africa, and Oceania (Almeida et al. 2011). The vast range in megachiropteran migration may be due in part to their adaptive locomotion and anatomy.

Megachiropterans have distinct dog-like faces and have clawed second digits that allow them to climb and walk (Adams and Carter 2017; Granatosky 2018). Megachiropterans vary considerably in size with many species weighing less than 50 gram while some can weigh up to 1.45 kilograms and have a wingspan up to 1.7 meters (Nowak and Walker 1994). Beyond the forelimbs that have been modified into wings, the megachiropterans have large lung capacity (Maina and King 1984), high heart rates (Carpenter 1986), and increased oxygen consumption that permit efficient flight (Maina and King 1984).

Other notable general characteristics of the megachiropterans include sharp eyesight and smell. Unlike microchiropterans, megachiropterans are not known for their echolocating ability (Müller et al. 2007). These bats are typically frugivores or nectarivores (Dumont and O'Neal 2004). Megachiropterans have low reproductive rates (i.e., they produce one offspring at a time) and gestation is generally 4–6 months (Nowak and Walker 1994). Unfortunately, megachiropterans are at potential risk of extinction due to overhunting and habitat destruction.

## Flight Biomechanics

Flight is the primary mode of locomotion in bats, and species can perform complex aerial behaviors, such as hovering or landing head-under-heels (Bergou et al. 2015). The forelimb wing architecture is a major contributor to megachiropteran motion capacity, flight behaviors, and kinematic plasticity. A bat wing is divided into two sections: inner wing and outer wing (Fig. 1). The inner wing, proximal to the first and fifth digits, is formed by propatagium (the leading edge) and the plagiopatagium (membranous structure found between the last digit and the hindlimb). The outer wing has four subdivisions: the dactylopatagium major, dactylopatagium medius, dactylopatagium minus, and dactylopatagium brevis. Proximally to distally, the trailing edge of the wing consists of the plagiopatagium, dactylopatagium major, and dactylopatagium medius (Hedenström and Johansson 2015a, b).

**Megachiroptera****Locomotion, Fig. 1**

Bat wing morphology:

(A) inner wing; (B) outer wing;

(C) propatagium;

(D) plagiopatagium;

(E) humerus; (F) radius;

DM: dactylopatagium

major; DMD:

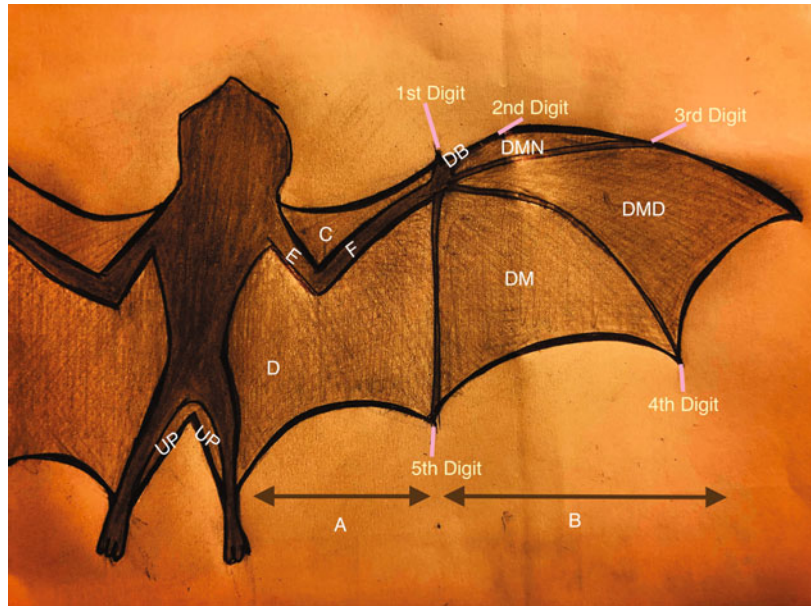
dactylopatagium medius;

DMN: dactylopatagium

minus; DB:

dactylopatagium brevis;

UP: uropatagium



Bat wing skin is thin, soft, anisotropic, and highly deformable. As wing skin is malleable parallel to the trailing edge, it deforms in response to aerodynamic forces (Hedenström and Johansson 2015a). Bat wing skin membrane is stretched by elongated arms and fingers, giving bats the ability to effectively change the overall shape of the wings by flexing and extending their metacarpophalangeal joints and interphalangeal joints (Bahlman et al. 2016). The skin on the wing is composed of living tissue that contains sensors, elastic fibers, and specialized muscles (Hedenström and Johansson 2015b). Tiny hairs on bat wings serve as transmitters of neural signals to provide bats with information on the speed and direction of airflow near the wing. These specialized sensors are most sensitive to the airflow from the trailing edge going toward the direction of the leading edge (Hedenström and Johansson 2015a). Large, well-organized, pre-stretched elastin fibers allow for significant extensibility and efficient packing and unfurling of wings (Cheney et al. 2014; Cheney et al. 2015). Bat wings have long, slender muscles called *m. plagiopatagiales proprii* which are embedded in dermis. These intramembranous muscles are not attached to any bones (Hedenström and Johansson 2015b). The contraction and relaxation

of *m. plagiopatagiales proprii* adjust the curvature of bat wings by tuning the membrane stiffness, thus allowing for support and deformation when aerodynamic load is applied (Cheney et al. 2014). Recent studies demonstrate that aerodynamic performance is improved when artificial wing membranes have electrically controlled compliance (Curet et al. 2014).

Bat wings are framed by bones with varying densities and relative compositions of mineral and protein, thus resulting in varying mechanical properties (Voigt et al. 2017). However, compared to other similar sized mammals, bat wing bones have reduced mineralization, resulting in decreased total weight of the wings (Hedenström and Johansson 2015b). Since the bat skeleton is located close to the wing's leading edge, the wing's center of pressure at which aerodynamic forces act is located posterior to the major bony support (Swartz et al. 1992). As a result, forces applied upwards at the center of pressure produce a torsional force toward the direction of pronation which is then transmitted through the wing membrane and the extended digits (Swartz et al. 1992). Based on analysis of bone deformation patterns during free flight in large bats, researchers proposed that the large cortical diameter and thin walls of the humerus and radius in bats allow

them to reduce weight and withstand large torsional stresses during propulsive downstroke movements (Swartz et al. 1992).

In discussing the wing shape of bats and its relationship with flight biomechanics, the terms wing chord, wingspan, wing area, aspect ratio, and wing loading must be considered. Wing chord, measured parallel to the direction of flight, is the length of the bat wing from the leading edge to the trailing edge. Wingspan is measured from one wingtip to another, while the wing area may be calculated by multiplying the values of wingspan and wing chord. The aspect ratio of a wing is equal to the square of the wingspan divided by the wing area. The wingspan and wing area of megachiropterans increase with body mass, while the aspect ratio rises only slightly with increasing body mass (Norberg and Rayner 1987). Wing loading is equal to the weight of the bat divided by the wing area. Megachiropterans generally have a shorter wingspan, smaller wing area, lower aspect ratio, and higher wing loading in contrast to microbats. Megachiropterans usually fly in straight paths quickly (Norberg and Rayner 1987). Some megachiropterans have been observed to have good maneuverability and slow flight in cluttered environments (Norberg and Rayner 1987). Maneuverability is defined by the space required for a bat to alter its path while flying at a constant speed. Bat wing morphology evolved to be highly specialized to meet the survival needs of the species.

Unlike other flying animals, bats are capable of modulating their wing inertia to produce sophisticated aerodynamic forces (Bergou et al. 2015). This is primarily due to the bat wing's morphological features that allow them to respond efficiently to aerodynamic demands. In evaluating aerodynamic forces produced by flying animals, researchers measure and analyze the structure and motion of wake shed during flight in wind tunnels by using a technique called particle image velocimetry. According to fluid dynamic principles, the wake reflects the magnitude of forces on the wing (Hedenström and Johansson 2015a, b). Studies on wake vortices of bats have demonstrated that the majority of aerodynamic force in bats is produced during the downstroke (Voigt et al. 2017).

As bats flex and extend their digits to different degrees, the wing membrane stiffness changes, affecting the overall three-dimensional shape of the wing. The overall wing shape is defined by camber and angle of attack. In aerodynamics, angle of attack refers to the angle between the wing chord line and the flight direction. Camber, the curvature of bat wings, can be controlled by bats through various ways, such as flexing the fifth digit, deflecting the legs, and elevating or lowering the second digit relative to the main wing surface (Hedenström and Johansson 2015a, b). When bats adjust the wing camber by moving their second digit, the outer wing membrane in front of the third digit functions as a leading-edge flap that modulates the leading-edge vortices (Hedenström and Johansson 2015a, b). In bat wings, the leading edge forms a sharp edge, which facilitates the formation of leading-edge vortices (Hedenström and Johansson 2015a).

Flying animals use leading-edge vortices in close proximity to their wings to help them stay floating in the air. Leading-edge vortices function to improve force generation to maintain vortex lift. Vortex lift increases with greater angle of attack. At slow speeds, bats increase wing force production by controlling leading-edge vortices through adjusting their wing's camber. This increase in force production allows bats to maintain stable flight at slow speeds. To maintain stable leading-edge vortices at the wings, bats need to be able to efficiently control the angle of attack, camber, and wing twist. The leading-edge flap is stabilized by a mechanical locking system (Norberg mechanism) that provides stiffness to the wing's leading edge (Hedenström and Johansson 2015b). Changes in camber and angle of attack determine the lift coefficient, which refers to the capacity of the wing to generate lift. Lift coefficient is defined as  $C_L = 2 L / \rho U^2 S$ , where  $L$  is the lift force,  $\rho$  is air density,  $U$  is local speed about the wing, and  $S$  is the surface area of the wing (Hedenström and Johansson 2015a, b). The speed of the wing relative to the air, the dynamic changes in wing shape, and the lift coefficient determine the magnitude and orientation of aerodynamic forces produced by the



wing (Bahlman et al. 2016; Hedenström and Johansson 2015a).

For flight to occur, bats must produce sufficient lift and thrust by flapping the wings to tilt the lift forward. Thrust is required to reduce the induced drag during flight. Bats adjust the shape and motion of their wings by controlling the strength of the lift, angle of attack, camber, and the speed by which the wing moves through air (Hedenström and Johansson 2015a). When bats change flight speed, they adjust these kinematic parameters to enhance flight stability and performance. The downstroke is responsible for generating both lift and thrust at most speeds, while the function of upstroke changes with forward flight speed (Hedenström and Johansson 2015a). The power required for flight in bats follows a U-shape mechanical power curve (Norberg and Rayner 1987). This curve describes the changes in kinetic energy during the passage of a flying bat. The bottom point of the U-shape mechanical power curve refers to the minimum power speed that should be used by the bat to maximize flight time with a given amount of energy (Norberg and Rayner 1987). An example of a flight behavior representing this point in the U-shape mechanical power curve is nectarivores hovering as they wait their turn to feed. The maximum range speed in the curve represents the energy required to transport the unit weight of the animal through unit distance (Norberg and Rayner 1987). For example, a bat's long-distance flight during mass migration is represented by the maximum range speed in the U-shape mechanical power curve.

When bats fly at slow speeds or hover, such as during foraging in confined spaces for hover-feeding nectarivores, the wake is primarily dominated by downstroke. Three major mechanical constraints on slow flight and hovering performance have been identified: power, wing inertia, and lift generation (Norberg and Rayner 1987). In nectarivore megachiropterans, lift ability during hover-feeding and flight in clutter is enhanced by their large, rounded wingtips, and relatively high wingbeat frequency. During slow speeds and hovering, bats utilize leading-edge vortices to improve lift and an inverted wing during upstroke for additional weight support (Hedenström and Johansson 2015a, b). Since hovering lacks the aerodynamic force from forward speed, flapping

the wings at a higher angle of attack is required. To prevent loss of lift, bats develop leading-edge vortices that enhance the lift and remain stable throughout most of the downstroke (Hedenström and Johansson 2015a, b). During slow flight, there are two simultaneous leading-edge vortices formed at different wing positions and running in different rotation directions. In kinematic upstroke occurring during slow flight, the angle of attack of the outer wing results in leading-edge vortex formation on the underside of the wing concurrently present with another leading-edge vortex formed on the inner wing (Hedenström and Johansson 2015a, b). In contrast, at cruising speeds, where a relatively high drag is experienced, bats often generate two vortex loops at the transition from upstroke to downstroke, reflecting forward thrust and negative weight support (Hedenström and Johansson 2015a, b).

Acceleration and take-off are flight behaviors that do not have a direct relationship with bat wing morphology (Norberg and Rayner 1987). In bats with long and high aspect ratio wings, the energetic cost of acceleration is not high because they are able to generate more force to propel their bodies forward (Norberg and Rayner 1987). On the other hand, acceleration is more energetically expensive among megachiropterans since they generally have a shorter wingspan, smaller wing area, and lower aspect ratio. The presence of high wing loading in megachiropterans gives them the ability for fast but not enduring flight. Take-off from the ground requires movement from rest to overcome inertia. Thus, due to their high wing loading, take-off is also energetically demanding for megachiroptera species (Norberg and Rayner 1987).

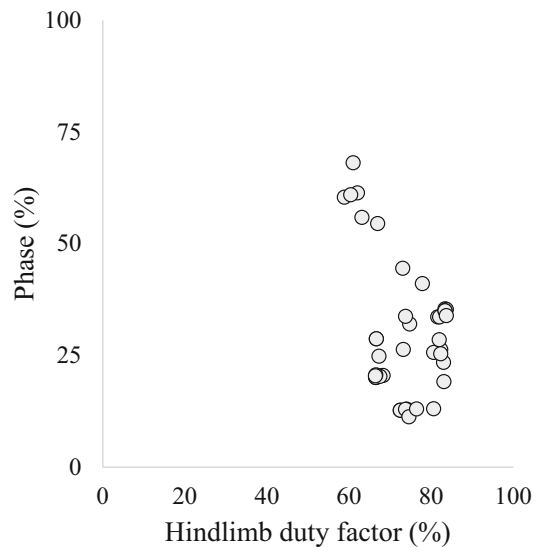
### **Terrestrial Walking, Suspensory Walking, and Climbing**

In addition to flight, megachiropterans use quadrupedal gaits during terrestrial walking, suspensory walking, and climbing. Below-branch walking and climbing locomotion are used by the megachiropterans for movement along cave walls, tree trunks and branches, and roosting sites

(Adams and Carter 2017). Compared to terrestrial mammals of similar size, the forearms of bats are long and curved with the radius larger relative to the ulna. Elongated digits support the membranous wing. In the hindlimb, the femur and tibia are long and slim with a fibula either reduced or absent. The hindlimb bones of bats are rotated 90–180° from the typical mammalian pattern. This structure results in the femora extending laterally or caudally and flexor surfaces of knees facing ventrally. As such, terrestrial locomotion is considered awkward and nonlinear when hindlimbs are utilized and energetically expensive. Megachiropterans may attempt to mimic climbing locomotion when placed on the ground. Individuals of *Pteropus pumilus* were seen to utilize a bounding type of locomotion where they pulled themselves along the ground using their forelimbs and thumb claws. Overall, compared to ground dwelling animals of similar size, megachiropterans have poor terrestrial locomotion (Adams and Carter 2017).

In suspensory locomotion, the hindlimbs are used for weight bearing and braking, while the forelimb is the primary propulsive limb with a reduced role in weight bearing. As a limb touches down upon the substrate, the limb applies a propulsive force to the substrate followed by a braking force prior to lift-off. Megachiropterans may shift their body away from their forelimbs as a mechanism to limit the load onto the forelimb. In addition, mediolateral forces help maintain the megachiropteran's "grip" upon a surface when moving below the support (Granatosky 2018). Gait sequences during suspensory walking vary from diagonal-sequence diagonal-couplet all the way to lateral-sequence lateral-couplet (Fig. 2).

Climbing techniques of megachiropterans align with other fully arboreal mammals. Megachiropterans tend to climb in a head-up posture on a vertical surface utilizing an ipsilateral gait with one point of contact to a surface. Megachiropterans are able to cycle their limbs faster when climbing than walking (Adams and Carter 2017). During climbing, the hindlimb is swung through a greater travel arc between fore and aft foot positions relative to the body axis. This allows for foot placement next to or ahead of the



**Megachiroptera Locomotion, Fig. 2** “Hildebrand” plot displaying phase against hindlimb duty factor collected during suspensory quadrupedal walking in *Pteropus vampyrus* ( $n = 43$  strides). Collected from Granatosky (2018)

rostrum, as compared to microchiropterans. In addition, the humerus can extend past the shoulder plane in a swing of  $\geq 180^\circ$ , while microchiropteran rotate their humerus up to the shoulder plane with climbing. Overall, the hindlimbs have been shown to be the generator of climbing thrust with forelimbs utilized for stability (Adams and Carter 2017).

## Bioinspiration

Bats have been used as a source of bioinspired robotics due to their unique wing flexibility and complex wing kinematics. Scientists and engineers have created the Bat Bot, a full self-contained, autonomous flying robot that weighs approximately 93 grams utilizing the morphology of bat wings. An ultrathin silicon membrane is stretched across the skeleton robot that was designed to mimic the bats' membrane. The researchers were able to simplify the 40-joint structure in a way to retain the bats' flight mechanics (Ramezani et al. 2017). Bat-inspired robots have an advantage over current aerial robots, such as the

quadrotors, in that the soft wing of the bat robots offer increased safety when interacting with humans. The bat-like robot flaps its wings at a lower frequency and is created with a flexible material, which allows for collisions with little or no damage. It is hypothesized that constructing bat robots may offer an alternative method of research when studying bat flight biomechanics as opposed to vision-based motion capture systems (Ramezani et al. 2017).

Additionally, bat algorithms, which are meta-heuristic algorithms for global optimization, are being used to develop, something known as, swarm intelligence. Swarm intelligence is the use of simple robotics agents used in groups, or “herds,” to develop a system that can tackle complicated problems and complex situations. Unlike drones, which use a main central intelligence to dictate rules and behaviors of other robots, swarm robotics use multiple simple robots to work together to create a superior system. Members of the swarm communicate with each other and their environment, almost behaving as a flock of birds or a colony of bats, to increase the intelligence of the swarm (Suárez and Iglesias 2017). Possible future applications of swarm robotics include self-driving vehicles used in the military or replacing drone technology with the more comprehensive and less expensive approach of swarm robotics. Among possible swarm robotic models, the bat algorithm has become popular due to its application in solving complex multimodal nonlinear continuous optimization problems with increased variables (Suárez and Iglesias 2017).

## Conclusion

This chapter explores the versatility in megachiropteran locomotion behaviors. The intricate anatomy of their wings has allowed megachiropterans to adapt various forms of flying, hovering, and landing. Megachiropteran flight has also evolved to fit their dietary lifestyle and appropriately balance their energy expenditure in relation to their diet. Due to their ability to acutely modify their wing shape to suit their current

needs, megachiropterans have become of interest to scientific engineering and robotics.

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Radiation](#)
- [Arboreality](#)
- [Basal Metabolic Rate \(BMR\)](#)
- [Canopy](#)
- [Captivity](#)
- [Common Ancestor](#)
- [Dispersal Ability](#)
- [Dispersal Patterns](#)
- [Diurnality](#)
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- [Species](#)
- [Taxa](#)
- [Vertebrate Nervous System](#)
- [Zoo](#)
- [Zoology](#)

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## Megachiroptera Sensory Systems

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## Definition

Auditory, visual, and olfactory capacities of fruit bats.

## Introduction

The order Chiroptera (bats, “hand wing”) comprises over 1000 species, nearly 25% of all mammals. Traditionally, Chiroptera have been classified into two suborders, the Microchiroptera (microbats or echolocating bats) and the Megachiroptera (megabats or fruit bats). This classification has been reconsidered based on new phylogenetic data (Teeling et al. 2005). Bats in the family Pteropodidae (Old World fruit and nectar bats) are discussed in this entry. There are over 180 different species within this family, including the largest known bats, the flying foxes. Some flying foxes can weigh over 1 kg, with wingspans over 1.5 m. The pteropids inhabit Old World tropical forests, as well as grasslands and even desert areas in proximity to fruit or palm agriculture in Africa, Asia, Australia, and the Indian subcontinent. They commonly are encountered in cities in these continents, where they roost in plain sight, typically in trees although sometimes even in buildings or ruins. Fruit bats have doglike faces with elongated muzzles, large frontally facing eyes, and large external ears (Hill and Smith 1984). Most pteropods eat fruit, while others are specialized for feeding on nectar. They play a crucial role in dispersing seeds and pollen within their tropical habitats (Hill and Smith 1984). Fruit bats are also vectors for human diseases; for example, they are the natural hosts for the Nipah and Ebola viruses (World Health Organization 2018, 2019). Understanding the biology and behavior of fruit bats is important for devising control measurements for transmission of these and other zoonotic diseases.

## Audition

Many species of fruit bat are highly vocal, with a rich repertoire of communication sounds. Egyptian fruit bats, *Rousettus aegyptiacus*, are social animals that live in large roosts, typically in caves; roost sizes of up to 10,000 bats have been reported (Prat et al. 2016). To study the social communication of these bats, Prat

et al. (2016) recorded social interactions and concurrent vocalizations of mixed sex groups of 10–12 bats housed in laboratory enclosures for 75 days continuously. The spectral content of 14,863 vocalizations produced by seven adult females fell within the high-frequency range from 5 kHz to 30 kHz. Many of these vocalizations were harmonically structured and consisted of multisyllabic sequences of sounds. By comparing social behaviors with vocalization parameters, the authors were able to classify calls as mating calls, isolation calls, aggressive calls, and distress calls (Prat et al. 2016). Aggressive calls occurred in four different contexts (while mating, while feeding, while competing for perch sites, and while in sleeping clusters). These data indicate that Egyptian fruit bats utilize a complex communication repertoire and highlight the importance of hearing in mediating social interactions within roosts.

Egyptian fruit bats, like some other species of *Rousettus*, echolocate, but by producing short clicks with their tongues rather than by producing tonal or frequency-modulated sounds with their larynx, as do the echolocating microbats (Holland et al. 2004). These clicks contain energy across the frequency bandwidth of 12–70 kHz with peak energy at 20–40 kHz (Holland et al. 2004). Although this click-based echolocation is not as precise as the laryngeal echolocation of the microbats, it is effective in guiding landing on a perch, and it allows the fruit bats to detect the presence of medium-sized objects even in total darkness (Yovel et al. 2011). Some other megabats (the cave nectar bat, *Eonycteris spelaea*; the lesser short-nosed fruit bat, *Cynopterus brachyotis*; and the long-tongued fruit bat, *Macroglossus sobrinus*) produce clicks using their wings rather than their tongues. These species can detect large objects in the dark with these clicks (Boonman et al. 2014).

Psychophysical measurements of the hearing sensitivity of Egyptian fruit bats (Koay et al. 1998) show that their range of hearing extends from about 2 to 64 kHz (measured at a criterion level of 60 dB SPL), overlapping the spectral content of both communication sounds and echolocation clicks. The audiogram shows a



region of best sensitivity between 8 and 25 kHz, at a low threshold of 4 dB SPL. This low threshold is comparable to that of echolocating bats within their best region of sensitivity (Tuninetti and Simmons 2019).

Fruit bats have large external ears (which are often scaled with the length of the muzzle), but their external ears are smooth, without the ridges and folds characteristic of the ears of echolocating bats (Hill and Smith 1984). In addition, their ears lack a tragus, a structure important for vertical sound localization in insectivorous echolocating bats (Lawrence and Simmons 1982). The general structure of the inner ear in adult fruit bats is similar to that of non-echolocating mammals and without the specializations typically seen in the inner ears of echolocating bats (Tuninetti and Simmons 2019). The cochlea is smaller, and the basilar membrane is shorter than those of echolocating bats, even after accounting for the larger body size of the fruit bats and even when the click-based echolocators are included in the comparisons (Habersetzer and Storch 1992; Davies et al. 2013). In addition, the volume of the auditory midbrain (inferior colliculus) in the fruit bat brain is smaller than that in the insectivorous bat brain, again after controlling for body size (in 63 species, Hutcheon et al. 2002; in 7 species, Liu et al. 2015).

## Vision

Most fruit bats leave their roosts shortly before dusk in order to forage, although some species are also active at higher light levels. As expected from these daily activity patterns, their eyes are specialized for scotopic (low light) vision. The greater Indian flying fox, *Pteropus giganteus*, has large eyes with large spherical lenses and a wide binocular field (Neuweiler 2000). Even when corrected for body size, eyes of fruit bats are larger than those of insectivorous bats (Bojarski and Bernard 1988; Neuweiler 2000). The eyes of some species of fruit bat [the greater Indian flying fox; Madagascar rousette (*Rousettus madagascariensis*); Madagascar straw-colored fruit bat (*Eidolon dupreanum*);

and Gambian epauletted fruit bat (*Epomophorus gambianus*)] also include a tapetum lucidum (“shining layer”). The tapetum is the reason for the “eyeshine” observed in the eyes of nocturnal animals (Ollivier et al. 2004). This structure operates to reflect light not captured by the retina back into the photoreceptor layer, and so it works to increase sensitivity of vision, but at the cost of resolution.

Structural studies of the retina of Egyptian fruit bats reveal other adaptations for vision in low light. In these bats, the retina is thick and folded in such a way so as to increase its surface area, and thus the number and density of photoreceptors can be packed into it (Bojarski and Bernard 1988). Large numbers of photoreceptors can transduce more light and thus increase sensitivity. There is no fovea and thus no region of improved spatial resolution (Müller et al. 2007). The vascular layer (choroid) of the eye contains protuberances, called papillae, that extend into the retina, making “its surface look like a volcanic landscape” (Neuweiler 2000, p. 215). This organization appears to be unique among mammals. The function of these papillae is still debated. One possibility is that they improve the oxygen supply to the retina, which is not itself vascularized (Müller et al. 2007).

The fruit bat retina was until recently believed to contain only rod photoreceptors, which are specialized for detecting dim light (Neuweiler 2000). Müller et al. (2007), using immunocytochemistry for opsin antibodies, uncovered the presence of cone photoreceptors in the retinas of six different species [the Madagascar rousette; Madagascar straw-colored fruit bat; Gambian epauletted fruit bat; Madagascar flying fox (*Pteropus rufus*); greater Mascarene flying fox (*Pteropus niger*); and Rodrigues flying fox (*Pteropus rodricensis*)]. Retinas of all of these species were indeed dominated by rods, but between 0.25 and 0.6% of the total photoreceptors were cones. Two types of cone photoreceptors (“blue” and “green”) were identified in the three species of *Pteropus*, while only one type (“green”) was present in *Rousettus*, *Eidolon*, and *Epomophorus*. Melin et al. (2014) identified two cone types in the retina of Samoan flying foxes

(*Pteropus samoensis*), confirming that some fruit bats have the retinal substrates for dichromatic color vision. The presence of only one cone type in *Rousettus*, *Eidolon*, and *Epomophorus*, on the other hand, suggests that these species are color-blind.

There is little information on the organization or function of central visual pathways in fruit bats. Studies mapping out neural responses to visual stimulation determined that almost one-half of the entire neocortex of the grey-headed flying fox (*Pteropus poliocephalus*) is related to visual processing, a much greater proportion than in insectivorous bats and even larger than expected for mammals of similar body weight (Rosa 1999). Another study based on manganese-enhanced multiple resonance imaging showed that the visual midbrain (superior colliculus) is larger in fruit bats than in insectivorous bats, which is opposite to the pattern seen when comparing the sizes of the auditory midbrain in these animals (Liu et al. 2015).

Field observations suggest that visual acuity and sensitivity differ between fruit bat species based on their activity patterns and roosting sites. *Pteropus* often forage during the day and live in tree roosts that can be exposed to sunlight. They also use postural displays for conspecific communication (Kunz 1982). Thus, these bats should have better vision at higher light levels than *Rousettus*, which roost in caves. Psychophysical data quantifying these possible species differences in visual sensitivity are few. When tested at low light levels, the visual acuity of the greater Indian flying fox in some visual tasks seems to exceed that of humans. These bats were able to discriminate black from white stripes at down to stripe widths of 9 mm, compared to the 15 mm limit of human performance (Neuweiler 2000).

## Olfaction

Fruit bats forage on ripe fruits, typically at dusk but sometimes also during daylight hours. Olfactory acuity of some species has been tested

in several laboratory experiments. Luft et al. (2003) questioned whether little golden-mantled flying foxes (*Pteropus pumilus*) and greater musky fruit bats (*Ptenochirus jagori*) could discriminate between an empty dish and one containing fruits (banana, mango, or fruits from local wild plants and shrubs) by odor alone. Even though visual cues were eliminated by covering the dishes with gauze in these two-choice tests, both species chose the fruit dish consistently (choice ratios of 7–10). In addition, the bats were able to discriminate ripe from unripe fruits (choice ratios of 9–10). In these experiments, bats were tested in laboratory cages where the distances to the dishes were small (0.5–1.5 m), so the distance from which bats may be able to detect the odors of ripe fruit in natural foraging could not be determined. Hodgkison et al. (2007) examined the role of odor cues in foraging in four different species [the short-nosed fruit bat (*Cynopterus brachyotis*); spotted-wing fruit bat (*Balionycteris maculata*); black-capped fruit bat (*Chironax melanocephalus*); and Horsfield's fruit bat (*Cynopterus horsfieldii*)]. Bats were housed in a large flight cage in the laboratory and foraged in the dark for figs. Foraging behavior, quantified by landing and then feeding, was strong (95–100% correct performance) to ripe figs, but significantly less to unripe figs (5%). These data suggest that the odors of the figs were more important in foraging than any visual cues that may have been available.

Fruit bats may also use odors for conspecific communication. Indian short-nosed fruit bats (*Cynopterus sphinx*) form tight clusters in their roosting spots and groom one another. Bats in these grooming clusters were observed to be wet with saliva and with secretions from sebaceous glands and the anogenital area (Neuweiler 2000). Laboratory assays showed that these secretions contain several volatile organic compounds, suggesting that they may function as pheromones. But the presence of pheromonal communication has not been directly tested in this species.

Consistent with the reliance on odors for foraging and their possible use in chemical communication, fruit bats have large nasal cavities,

with the olfactory epithelium considerably thicker than that of insectivorous bats (Neuweiler 2000). Olfactory bulbs of fruit bats are larger than those of insectivorous bats, even after correcting for body size; comparatively, the differences in sizes of the olfactory bulbs exceed those of the auditory midbrain (Hutcheon et al. 2002). Nothing is known, however, about receptor sensitivity, either for olfactory or for taste receptors.

## Conclusion

Fruit bats rely on both visual and olfactory senses to guide their foraging behaviors, with olfaction seemingly the predominant sense. Odors allow bats to discriminate ripe from unripe fruits, a task that would be difficult using visual cues only. And although fruit bats forage on many different kinds of fruits and flowers, there is no quantitative data on their taste sensitivity. Fruit bat eyes are specialized for seeing in low light levels, with adaptations for sensitivity but at the expense of resolution. Although some species seem to have the capacity for color vision, it is not known if they can behaviorally discriminate objects based on color cues. Because echolocation is limited to only a few species, and the acuity of this click-based echolocation is poorer than that of the laryngeal echolocators, it is likely that fruit bats rely on vision rather than hearing to navigate through their environments and to find food sources over large distances. The large external ears and the large vocal repertoire of several species of fruit bats suggest that hearing mediates social communication. It is also possible that chemical cues play a role in mediating social behaviors, particularly in roosts, but this has not been studied systematically. Most of our information on the sensory capacities of the more than 180 species of fruit bats comes from field observations, and there is very little quantitative psychophysical data available on their sensory acuity.

Fruit bats play crucial roles in tropical ecosystems by their activities in dispersing seeds and pollinating plants. They are also vectors for

many pathogens that can affect humans and domestic animals. Understanding fruit bat behavior, including their sensory capacities, will facilitate informed decisions about regulating human-bat interactions to decrease disease transmission and devising conservation measures critical to maintaining their role as pollinators.

## Cross-References

- Auditory Processing and Perception
- Microchiroptera Morphology
- Microchiroptera Sensory Systems

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## Melanin

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## Introduction

Melanin refers to a group of natural pigments found in the animal kingdom and fungi. Melanin is responsible for the color of skin, hair, and iris.

## Types and Distribution of Melanin

There are three types of melanin namely eumelanin, pheomelanin, and neuromelanin. Eumelanin is the most common type. Pheomelanin is a cysteine derivative responsible for the red hair. As the name suggests, neuromelanin is found in the brain and produced by dopaminergic and noradrenergic neurons located in the substantia nigra and locus coeruleus.

## Melanogenesis

Melanogenesis is the process of synthesis of melanin. It takes place in the melanosomes found inside melanocytes. Melanosomes are small, membrane-bound, specialized organelles related to lysosomes. Melanosomes are transported from melanocytes to the adjacent keratinocytes through the finger-like (dendritic) projections of melanocytes. Melanin protects the skin from the DNA-damaging effect of UV light.

Melanocytes are derived from melanoblasts which themselves are derived from neural crest cells. Melanogenesis takes place in the skin, hair, eyes, ears, and leptomeninges. The UV radiation

is the primary stimulus for melanogenesis. This is the basis of tanning of skin (increased melanin synthesis) after prolonged sun exposure. People with less melanin are more susceptible to sunburn. Fitzpatrick scale is a numerical classification system based on the susceptibility for tanning and sunburns (Altieri et al. 2017). People with Fitzpatrick type I skin contains less melanin so that they always get sunburns and never get tanned whereas people with Fitzpatrick type VI skin contains more melanin so that they never get sunburns.

In animals, melanocytes are located at the basal layer of the epidermis of the skin. Eumelanin and pheomelanin are produced from the oxidation and polymerisation of the hydroxyl group-containing amino acid tyrosine. Tyrosinase is the rate-limiting enzyme of melanogenesis. The enzyme first hydroxylates tyrosine to dihydroxyphenylalanine (DOPA) and then oxidizes it to dopaquinone. Further reactions yield various types of melanin.

## Melanin and the Iris Color

The amount of melanin does not only determine the color of the skin, but also the iris. The high amount of melanin produces black or dark brown iris whereas the low amount of melanin leads to blue colored iris (Sturm and Larsson 2009). Melanin in the iris serves to protect the retina from the damaging effect of light.

## Albinism

Overproduction, as well as underproduction of melanin, can happen. Albinism is a group of congenital hypopigmentation disorders inherited in recessive mode. Albinism produces white fur and red eyes in mammals and white plumage, red eyes, and white claws in birds. Many zoos keep albino animals for the purpose of visitor attraction. Albino rats have been used as laboratory animals for the past 150 years, and in fact they were the first animals to be domesticated for

the purpose of scientific research (Kuramoto et al. 2012).

In humans, when albinism is limited to skin and hair, it is known as cutaneous albinism. People with cutaneous albinism have melanin in their eyes. Oculocutaneous albinism (OCA) refers to the absence of melanin in skin, eyes, and hair. People with OCA suffer from skin cancer, nystagmus (involuntary eye movement), photophobia (aversion to light), and poor eyesight. Skin cancer is due to loss of protective effect of melanin against DNA-damaging UV radiation.

## Fungal Melanin

Melanin is not only produced by animals but also by fungi. Fungal melanin is different from animal melanin. 1,8-dihydroxynaphthalene (DHN) is the major melanin of fungi. It is synthesized from acetyl-CoA through the polyketide pathway. Some pathogenic fungi like *Cryptococcus neoformans*, *Candida albicans*, and *Paracoccidioides brasiliensis* can produce eumelanin also. Fungal melanin is involved in the virulence (disease-causing ability) of the pathogenic fungi (Nosanchuk and Casadevall 2006).

## Cephalopod Ink

In the animal kingdom, melanin is not just a body pigment. Animals have evolved to use melanin for various other purposes. When threatened, many cephalopods release dark-colored ink. The major constituent of the cephalopod ink is melanin. The ink is secreted by the ink sacs located between the gills. The release of ink is accompanied by the water jet and creates a smoke screen and allows the escape of cephalopod.

## Cross-References

- [Amino Acid](#)
- [DNA](#)
- [Fungi](#)



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## Membrane Lipid

- [Lipid](#)

## Memory

- [Arthropod Cognition](#)
- [Cognition](#)
- [Delay Neurons: Comparative Overview](#)
- [Entopallium](#)
- [Matching-to-Sample: Comparative Overview](#)
- [Parahippocampal Cortex \(PHC\)](#)
- [Proactive Interference](#)
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## Memory Awareness

- [Metamemory](#)

## Memory Cells

- [Matching-to-Sample: Comparative Overview](#)

## Memory Interference

- [Cognition](#)

## Mendel's Law

- [Mendelian Crosses](#)

## Mendel's Laws

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## Synonyms

[Mendelian inheritance](#)

## Definition

The set of three laws, proposed by Gregor J. Mendel in the mid-1860s, to explain the biological inheritance or heredity is known as Mendel's laws. These laws are the law of segregation, law of independent assortment, and law of dominance, and they form the core of classical genetics to date.

## Introduction

Gregor Johann Mendel (1822–1884) was a friar-cum-science teacher in Brno (Austria-Hungary), and known as the father of genetics due to his groundbreaking genetics experiments on sweet pea plants. Though he performed and published his scientific work in the 1860s, significance of his work was not widely recognized until 1900. His scientific results describe the transmission of hereditary information from parent generation to

progeny generation. These results helped him to frame three laws of biological inheritance, which led to the foundation of classical genetics. Mendel's contribution is significant in genetics as he framed these laws during a time when even words like “chromosomes” or “genes” were not discovered (Hartl and Ruvolo 2011).

Mendel crossed white flower and purple flower pea plants (parents or P generation) and found out that the progenies (F1 generation) were purple-flowered plants rather than a blend. Interestingly, when he self-fertilized these progenies, he got both purple flower and white flower plants (F2 generation) in the ratio of 3:1. The results of this cross are summarized in Fig. 1.

### First Law: Law of Dominance

When individuals with one or more sets of contrasting characters (now known as phenotypes) are crossed, then the characters that appear in F1 generation are called dominant characters, and the characters that remain hidden are called recessive characters. The above example, where P generation plants were crossed together and only purple-colored flower F1 generations were

obtained, shows that the dominant purple flower allele (B) will hide the phenotypic effects of the recessive white flower allele (b). This is known as the law of dominance (Hartwell et al. 2017). White phenotypes will appear only in the absence of dominant purple flower alleles. The uppercase letters are used to denote dominant alleles, whereas the lowercase letters are used to denote recessive alleles. Mendel used the term “factors” instead of alleles during that time.

### Second Law: Law of segregation

This law is also referred to as *law of purity of gametes*. During the formation of male and female gametes (generally sperm and ova in animals or pollen grains and ovule in plants), factors (alleles) responsible for a particular character separate and are passed into different gametes. This process implies that the gametes are either pure for dominant alleles or for recessive. These gametes can unite randomly in different possible combinations during fertilization and produce the genotype for the traits of the progenies (Pierce 2017). In a zygote, the two members of an allele pair remain together without being contaminated. This is known as law of segregation.

In Fig. 1 above, both pollen and pistil form male and female gametes, respectively, with either B or b allele. These male and female gametes combine randomly during fertilization to produce F1 generation of purple flower and white flower plants in the ratio of 3:1.

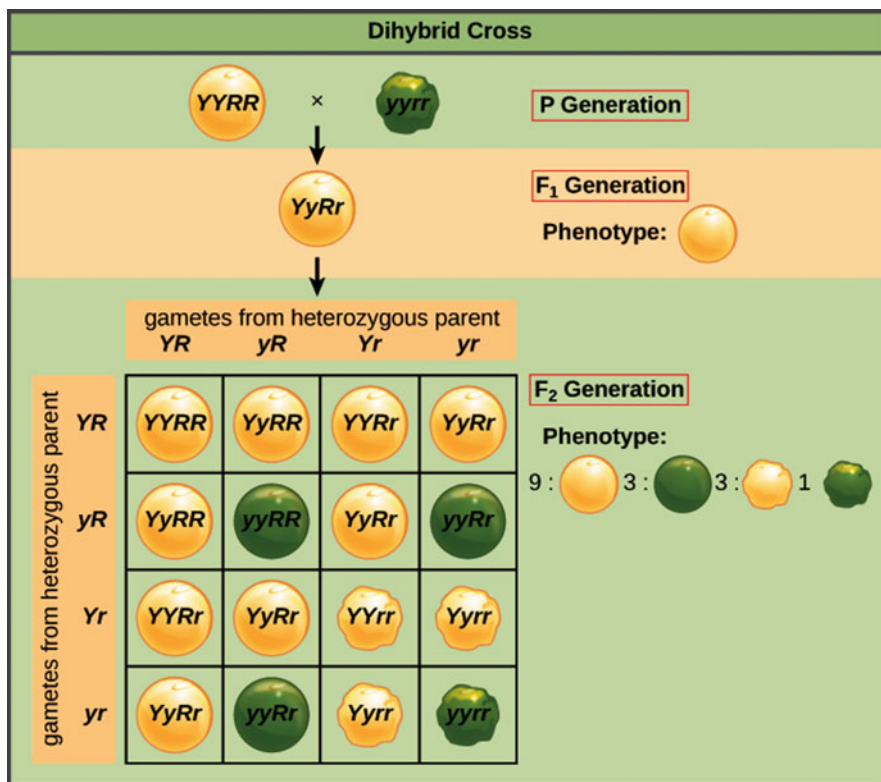
### Third Law: Law of Independent Assortment

This law is also known as *inheritance law* and is defined as alleles of different genes which distribute independently of one another during gamete formation (Watson et al. 2013).

As shown in Fig. 1, mixing a single trait (monohybrid cross) in Mendel's experiment constantly resulted in a 3:1 ratio between dominant and recessive phenotypes. However, when he performed experiments on two traits (dihybrid

|             |   |                                                                                           |                                                                                           |
|-------------|---|-------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------|
|             |   | pollen<br>♂                                                                               |                                                                                           |
|             |   | B                                                                                         | b                                                                                         |
| pistil<br>♀ | B | BB<br> | Bb<br> |
|             | b | Bb<br> | bb<br> |

**Mendel's Laws, Fig. 1** Punnett square describing self-fertilization of F1 pea plants (both purple). Here B and b represent the factors (now known as alleles). (Image credit: Madeleine Price Ball, CC0 licensed)



**Mendel's Laws, Fig. 2** Dihybrid cross between yellow round seed plant and green wrinkled seed plant. Here, Y (yellow) R (round) is the dominant allele over

y (green) r (wrinkled). (Image credit: <https://opentextbc.ca/biology/chapter/8-2-laws-of-inheritance/> CC license)

cross), he obtained F<sub>2</sub> generation in the ratio of 9:3:3:1 (Fig. 2). These results led Mendel to conclude that different traits (e.g., seed shape and color) are inherited independently of one another and there is no relation between two traits.

## Conclusion

Historically, biologists in the nineteenth century believed in the apparent blending of inherited traits in the overall appearance of the progeny, which proved to be a major roadblock for the understanding and acceptance of Mendel's work. It was only in the year 1900 (16 years after Mendel first published his studies) where three European scientists, i.e., Hugo de Vries, Carl Correns, and Erich von Tschermak, rediscovered Mendel's work by performing similar experiments independently (Snustad

and Simmons 2015). William Bateson was a huge promoter of Mendel's work later in Europe and also coined the terms genetics, gene, and allele to describe the basic constituents of Mendelian genetics.

With the advancement in the field of genetics, scientists observed few deviations from Mendel's laws of inheritance. These include incomplete dominance, codominance, and lethal genes.

## Cross-References

- ▶ [Alleles](#)
- ▶ [Assortment](#)
- ▶ [Chromosomes](#)
- ▶ [Genes](#)
- ▶ [Heredity](#)
- ▶ [Homozygosity](#)
- ▶ [Mendelian Crosses](#)

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## Mendelian Crosses

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## Synonyms

[Mendel's law](#); [Mendelian inheritance](#)

## Definition

A set of breeding experiments and carefully augmented observations, performed on sweet pea (*Pisum sativum*) to understand the pattern of inheritable characters or traits, which led to three basic principles that are the pillars of classical genetics.

## Introduction

Gregor Johann Mendel (1822–1884) was an Austrian (now Czech Republic) priest-cum-scientist who is known for his extraordinary work on sweet peas and is essentially considered as the father of

modern genetics. In 1853, upon completion of his studies from the University of Vienna, he joined a monastery in Brno (called *Brünn* in German) as a science teacher and began his groundbreaking work on sweet peas to understand the basic mechanism of heredity. To understand the mechanism, he chose sweet pea plants considering few essential and critical points. Peas are easy to cultivate, easily available, have shorter generation time, produce large number of progeny in terms of seeds, and possess distinct and easily observable external characters and, more importantly, fertilization between two plants can be easily controlled. Peas possess both male reproductive structure (stamens) and female reproductive structure (pistils) and self-fertilize normally; i.e., anthers located at the end of the stamen produce pollen (germinates to form male gametophyte) that falls on the pistils (containing female gametophyte) of the same flower and undergo fertilization. Thus, fertilization could be selectively controlled through removal of the stamens (emasculation) from a developing flower before it starts producing mature pollen and transferring the pollen from one pea plant to pistils of emasculated desired flower with a small paint brush. Mendel started with 34 strains of pea plant having different traits and allowed them to self-fertilize for a number of generations to get pure-breeding or true-breeding strain – which shows the same traits generation after generation (Russel 2010). Based on the strains, Mendel selected seven traits that were clearly distinguishable from each other and went for cross-fertilization that are as follows:

| Traits                 | Phenotypic features for crosses                                                 |
|------------------------|---------------------------------------------------------------------------------|
| <b>Coat color</b>      | <b>Seed coat:</b> Grey versus white<br><b>Flower color:</b> Purple versus white |
| <b>Seed color</b>      | Yellow versus green                                                             |
| <b>Seed shape</b>      | Smooth versus wrinkle                                                           |
| <b>Pod color</b>       | Green versus yellow                                                             |
| <b>Pod shape</b>       | Inflated versus pinched                                                         |
| <b>Stem height</b>     | Tall versus short                                                               |
| <b>Flower position</b> | Axial versus terminal                                                           |

Mendel extensively used breeding experiments or genetic crosses to get ideas about the inheritance pattern. Certain terminologies are very

much essential to start with breeding experiments. The Parental generation, with which the experiment or breeding started, is P generation. The progeny of the p generation are referred as F<sub>1</sub> or *first filial generation*. The subsequent progeny produced by the interbreeding of F<sub>1</sub> generations are called *second filial generation* or F<sub>2</sub> and so on. The filial word originally came from Latin word *filia* (daughter) and *filius* (son).

Monohybrid Crosses

Mendel started his experiment considering a single trait at a time or Monohybrid crosses, i.e., crossing between those pure lines that differ by a single character. While doing so, he simultaneously examined reciprocal crosses to check whether sex has an influence on inheritance or not. Mendel carried out 60 such experiments but, in all his reciprocal crosses, he never encountered any differences in F<sub>1</sub> generation (as all the genes/traits were autosomal fortunately). Not only that, he also observed that F<sub>1</sub> progeny of all the pure breed monohybrid crosses showed only one of the parental phenotype.

In one such experiment, he crossed pure breed of *round seeds* with pure breed of *wrinkled seed* plants and found that all the progeny showed round seed phenotype F<sub>1</sub> generation; even in reciprocal crosses. But when he allowed F<sub>1</sub> generation for self-fertilization, both the parental trait (i.e., round and wrinkled seeds) was recovered in F<sub>2</sub> generation. So he counted the total 7324 seeds and found 5474 seeds were rounded and the rest of the 1850 seeds were wrinkled which typically resemblances 3:1 ratio (~ 2.96:1); that is, three-fourth of the seeds were round and one-fourth of the seeds were wrinkled phenotypically. He did the same experiment with all seven pure breeds and obtained the same ratio of distribution in F<sub>2</sub> generation (Griffiths et al. 2015).

| Parental phenotype              | F <sub>1</sub> phenotype | F <sub>2</sub> phenotype     | F <sub>2</sub> ratio |
|---------------------------------|--------------------------|------------------------------|----------------------|
| Round seeds<br>X wrinkled seeds | All round seeds          | 5474 round;<br>1850 wrinkled | 2.96:1               |

(continued)

| Parental phenotype                | F <sub>1</sub> phenotype | F <sub>2</sub> phenotype     | F <sub>2</sub> ratio |
|-----------------------------------|--------------------------|------------------------------|----------------------|
| Yellow seeds<br>X green seeds     | All yellow seeds         | 6022 yellow;<br>2001 green   | 3.01:1               |
| Purple petals<br>X white petals   | All purple petals        | 705 purple;<br>224 white     | 3.15:1               |
| Green pods<br>X yellow pods       | All green pods           | 428 green;<br>152 yellow     | 2.82:1               |
| Inflated pods<br>X pinched pods   | All inflated pods        | 882 inflated;<br>299 pinched | 2.95:1               |
| Axial flower<br>X terminal flower | All axial flower         | 651 axial;<br>207 terminal   | 3.14:1               |
| Long stems<br>X short stems       | All long stems           | 787 long;<br>277 short       | 2.84:1               |

Outcome of Monohybrid Crosses

In such crosses, Mendel clearly observed that one of the parental traits disappears in F<sub>1</sub> but reappears in F<sub>2</sub> generation – also in 3:1 ratio consistently. Reappearance of both of the parental characters in F<sub>2</sub> could only be explained if F<sub>1</sub> possess both the factors controlling round and wrinkled seed character – inherited from P generation. So, Mendel concluded that each trait is controlled by the *two inheritable factors* and such factors are now called alleles.

Mendel, by convention, designated traits with single letters with upper and lower case. So, he used *R* for round seeds and *r* for wrinkled seeds. As the parental lines were true breeding, they possessed both the identical alleles of the same character (*homozygous condition*); *RR* for round seeded and *rr* for wrinkled seed P-generation (now called *genotype*).

The second conclusion drawn by Mendel on such monohybrid crosses was that during gamete formation, two alleles get segregated and one gamete receives only one allele. One such gamete from the male and another one from the female fuse to form the zygote, and thus, it contains both the contrasting alleles for the same character or trait (*heterozygous condition*). Thus, all the progeny of F<sub>1</sub> generation received both *R* and *r* alleles. Surprisingly, only *R* alleles expressed in the form of round seeds though *r* alleles were also there

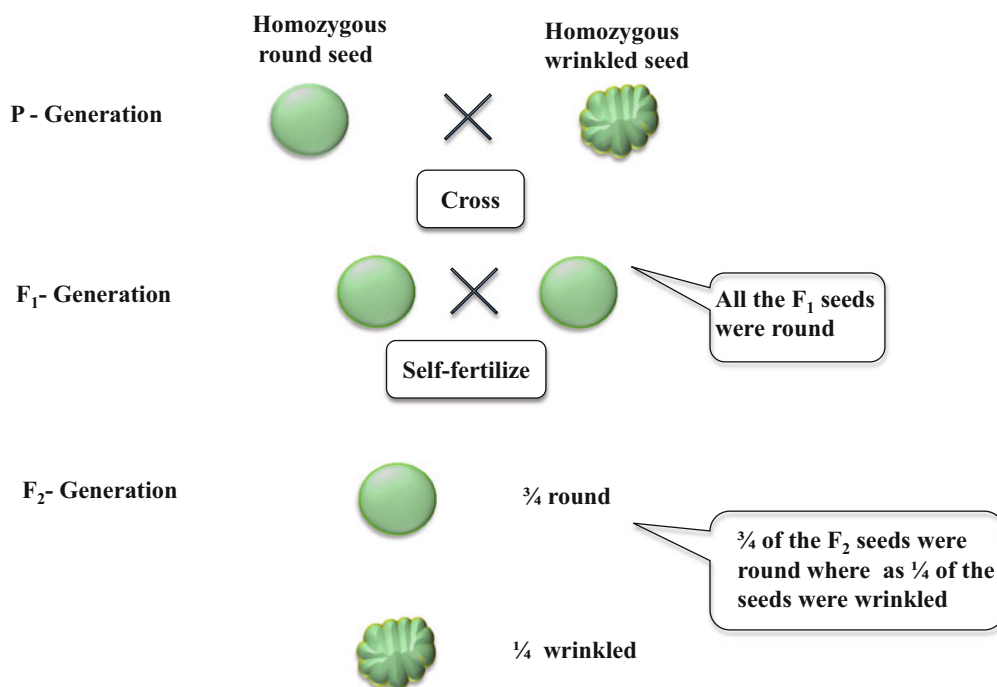


with  $R$  allele simultaneously – but  $r$  failed to express. Mendel considered such characters as *dominant* that expressed in  $F_1$  generation in heterozygous condition and the counterpart as *recessive*. Essentially, the dominant allele suppresses or masks the effect of recessive allele in heterozygous condition, which helped Mendel to draw another important concept of heredity – *i.e.*, *dominance*. It was the third important concept concluded from monohybrid crosses by Mendel.

Mendel drew a fourth conclusion from here that alleles of the same trait get equally separated during gamete formation and randomly pair with allelic partners during zygote formation – coming from another mating partner. So all the progeny of  $F_1$  generation received  $R$  from round seeded parent ( $RR$ ) and  $r$  from wrinkled seeded parent ( $rr$ ) and they were heterozygous ( $Rr$ ). As  $R$  was found to be dominant over  $r$ , all the  $F_1$  progeny became round seeded. But during self-fertilization among  $F_1$  progeny, all of them produced two types of gamete,  $R$  and  $r$ . Hence, in  $F_2$ , genotypically four different types of progeny –  $RR$ ,  $Rr$ ,  $rR$ , and  $rr$  –

were produced in equal proportion because of random pairing among gametes. As  $R$  is dominant over  $r$ ,  $RR$ ,  $Rr$ , and  $rR$  progeny were round seeded and  $rr$  was the only one with wrinkled seeded phenotype ( $Rr$  and  $rR$  are same both genotypically and phenotypically – by convention both of them represented as  $Rr$  considering dominance of  $R$  over  $r$ ). Moreover, distribution of round to wrinkled seed progeny in 3:1 ration in  $F_2$  reconfirms third conclusion and random pairing of alleles occur during gamete formation.

Based on such conclusions, Mendel formulated the principle of segregation and concept of dominance. Principle of segregation is referred as *Mendel's first law*, and it states that each diploid organism possesses two alleles for a particular character or trait. Such alleles get separated during gamete formation and segregate in equal proportion and each gamete receives only one allele for a particular trait. According to the concept of dominance, when two different alleles for a particular trait present together, only one allele expresses by masking the expression of other allelic partner.



**Mendelian Crosses, Fig. 1** Monohybrid cross: Parental traits do not blend with each other. Dominant traits are expressed in  $F_1$  generation, but both the parental phenotypes are found in  $F_2$  in 3:1 ration

The allele that masks or suppresses the expression of other allele is referred to as dominant and the counterpart is called the recessive allele (Snustad and Simmons 2015).

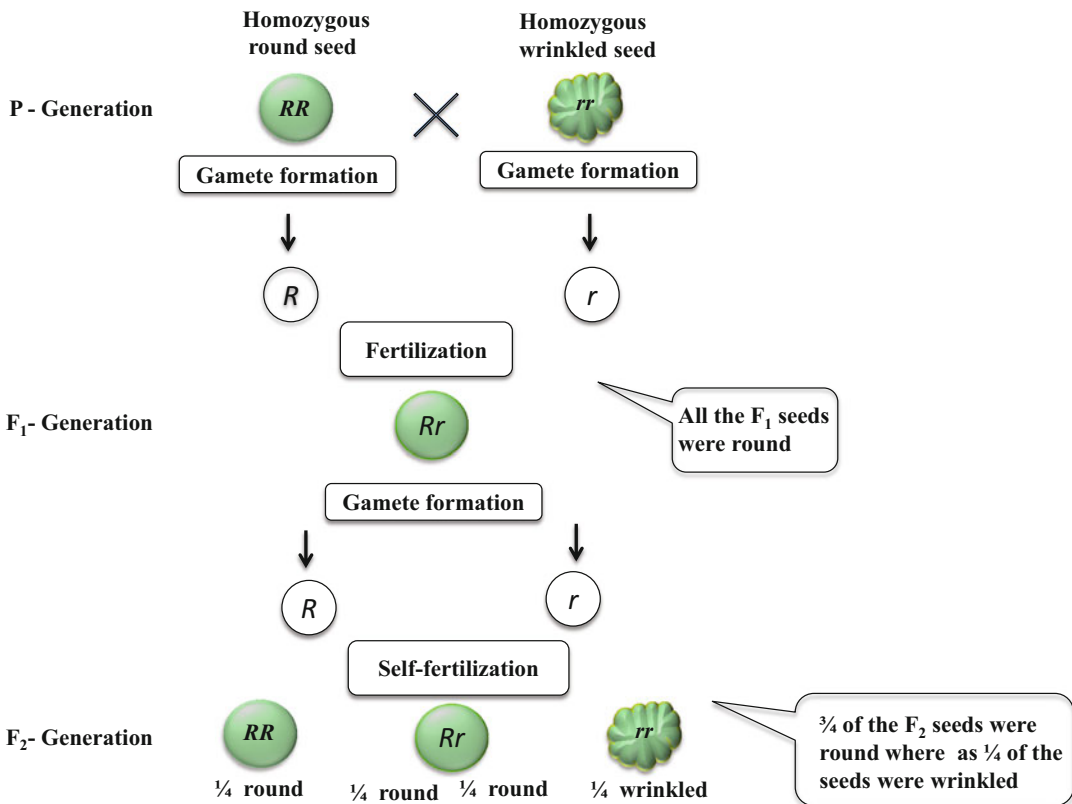
Mendel further confirmed his results by extending up to  $F_6$  generations by allowing self-fertilization of progeny and observing similar phenotypic ratio of round and wrinkled seeded plants in consistency, as found in  $F_3$  (Figs. 1 and 2).

### Di-hybrid Crosses

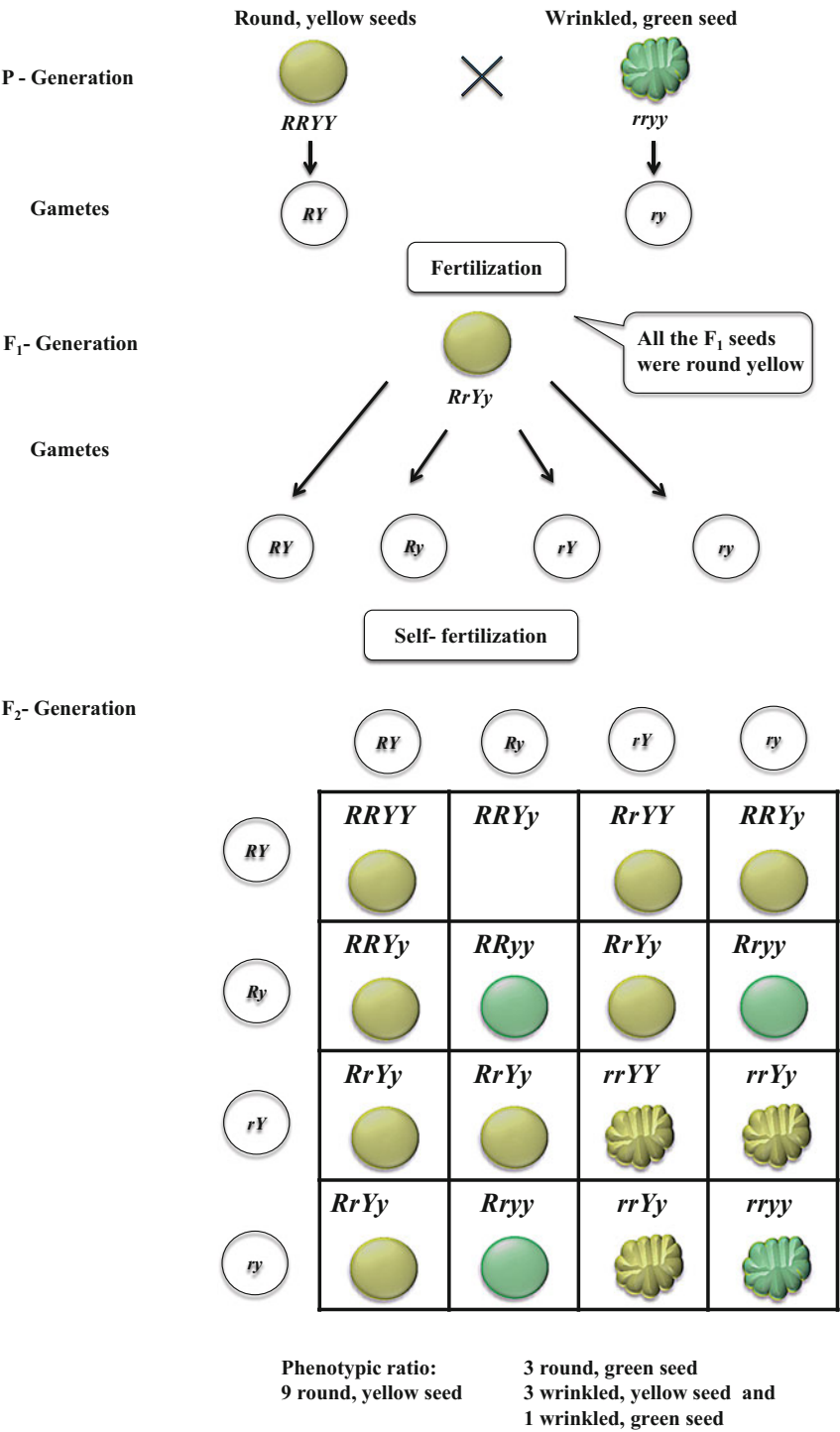
Mendel extended his work into more complex forms to understand the hereditary dynamics of two traits when they are present together in a single parent. He crossed one homozygous parent having round and yellow seed ( $RRYY$ ) with homozygous plants showing wrinkled and green seed ( $rryy$ ). In  $F_1$  generation, he found all the progenies showed round and yellow seed phenotype ( $RrYy$ ), similar to

the outcome of monohybrid crosses. Then he allowed self-fertilization of  $F_1$  progeny and found four different phenotypes in  $F_2$  generation: round and yellow seeds ( $RRYY$ ) – 315, wrinkled and yellow seeds ( $rrYy$ ) – 101, round and green seeds ( $Rryy$ ) – 108, wrinkled and green seeds ( $rryy$ ) – 32. When Mendel calculated the results, he obtained 9:3:3:1 ratio of phenotypic distribution. He observed that among total progeny  $\frac{9}{16}$  of them round and yellow seeded,  $\frac{3}{16}$  of them were having wrinkled and yellow seeded,  $\frac{3}{16}$  were round and green seeded, and rest  $\frac{1}{16}$  of them were wrinkled and green seeded. He observed similar  $F_2$  phenotypic ratio in all other di-hybrid crosses as well.

Such a result perfectly satisfies the principle of segregation and concept of dominance along with another fundamental aspect of heredity – the *principle of independent assortment*. This is referred to as the *third law of Mendel* and it states that



**Mendelian Crosses, Fig. 2** Monohybrid crosses satisfying principle of segregation and concept of dominance



M

**Mendelian Crosses, Fig. 3** Dihybrid cross: Alleles responsible for seed color and seed shape assorted independently during gamete formation and producing 9:3:3:1 phenotypic ratio in F<sub>2</sub> generation

during gamete formation all the alleles from different traits assorted independently of one another (Pierce 2012).

The first law of Mendel essentially refers to the separation of alleles of the same trait, whereas the principle of independent assortment reflects the separation of alleles of different traits independently from one another. Indeed, the first law of Mendel is an extension of the later one.

Besides that, it was significantly found that alleles of different traits are separated independently and finally combine with all possible combinations during zygote formation. Thereby, during gamete production, P generation produced two types of gamete  $RY$  and  $ry$ . They fused to form  $RrYy$  progeny in  $F_1$  generation. When  $F_1$  progeny were allowed for self-fertilization, they produced four different types of gametes –  $RY$ ,  $Ry$ ,  $rY$ , and  $ry$  – and formed zygotes with all possible combinations equally. As  $R$  is dominant over  $r$  and  $Y$  over  $y$ , all  $F_1$  progeny were round and yellow seeded. But in  $F_2$ , as alleles were independently assorted during gamete formation, they combined to produce two new phenotypes showing mixed parental traits. But because of independent assortment, both the parental traits were recovered along with heterozygous parental phenotypes. Mendel further confirmed heterozygous and true breeding parental phenotypes via self-fertilization  $F_2$  progeny for successive generations. External features of traits are now called *phenotype*, and genetic makeup or genetic constituent of an organism is called *genotype*. Essentially, because of dominance and independent assortment, 9:3:3:1 phenotypic ration was obtained in  $F_2$  generation (Hartl and Ruvolo 2011, Fig. 3).

## Discussion

Understanding of inheritable traits or characters provides an idea about the dynamics and flow of the characters over generations. Mendel provided experimental support and mathematical explanation about the dynamics of such inheritable traits for the first time way back in nineteenth century when almost nothing was known about that. Later on, such inheritable traits were defined as genes (named by W. Johannsen) that are located in a

specific location on the chromosome (*loci*) and regulate traits via their expression. But till 1900, the significance and impact of Mendel's work was not recognized until three different scientists – Hugo de Vries, Eric von Tschermak, and Carl Correns – derived similar results independently while working with plants. Not only that, understanding of meiosis and gametogenesis further clarified Mendel's principles. Although Mendel worked on plants, such principles are applicable on all chromosomal inheritance, which made him the father of genetics. But detailed understanding of complex molecular genetics hint that Mendel was a bit lucky to obtain such consistent results as pea is a diploid organism and all the characters chosen by Mendel were located on different chromosomes, including the fact that he did not encounter any extra chromosomal inheritance. Nevertheless, his work revealed a new dimension of understanding genetics and eventually he laid the foundation for the most remarkable principles of inheritance.

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## Mendelian Inheritance

- [Mendel's Laws](#)
- [Mendelian Crosses](#)

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## Mental Abilities

- [Platyrrhine Cognition](#)

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## Mental Capacities

- ▶ [Platyrrhine Cognition](#)

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## Mental Disorders

- ▶ [Animal Psychopathology](#)

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## Mental Functions

- ▶ [Platyrrhine Cognition](#)

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## Mental Image

- ▶ [Top-Down Processing](#)

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## Mental Processes

- ▶ [Platyrrhine Cognition](#)

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## Mental Time Travel

- ▶ [Stuck-in-Time Hypothesis](#)

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## Mesocortex

- ▶ [Perirhinal Cortex](#)

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## Messages

- ▶ [Communication](#)

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## Messenger RNA

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### Synonyms

[mRNA](#); [Template RNA](#); [Informational RNA](#)

### Definition

The form of RNA which carries information from nuclear DNA to the ribosomal sites of protein synthesis in the cell.

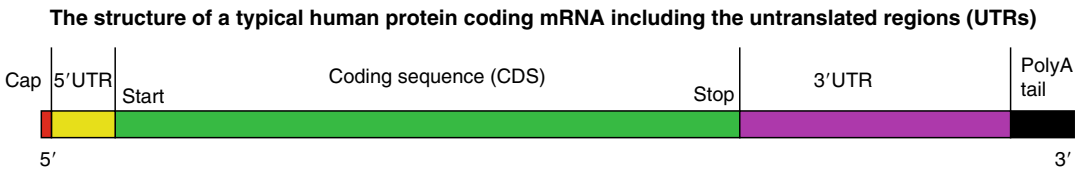
### Introduction

Messenger RNA (mRNA) is a single-stranded nucleotide sequence that carries genetic information from the master molecule DNA in the form of codons (series of three bases which specifies a particular amino acid). It comprises only about 5% of the total RNA in the cell and is the most heterogeneous RNA which varies in the coding region. It was discovered in the year 1960 at the California Institute of Technology by Sydney Brenner, François Jacob, and Matthew Meselson (Ullmann [2011](#)).

### Messenger RNA Structure

The mRNA molecule also known as the “transcript” is generally 300–50,000 nucleotides in length and varies in prokaryotes and eukaryotes. mRNA forms in the nucleus of eukaryotic cells; however, owing to the absence of nucleus in prokaryotes, the mRNA is made directly off of the DNA in the cell’s cytoplasm. The backbone of mRNA contains five-carbon sugar ribose which includes nucleotide bases uracil instead of thymine in the prokaryotes (Kozak [1983](#); Shabalina et al. [2006](#)). Structurally, it consists of Cap,





**Messenger RNA, Fig. 1** Representative image of an mRNA codon

noncoding region, an initiation codon, and coding region (Fig. 1).

### 5' Cap

A 5' cap is also called as RNA cap or RNA 7-methylguanosine cap. A modified guanine nucleotide which is added to 5' end of a eukaryotic messenger RNA immediately after transcription starts forms the RNA cap. The terminal 7-methylguanosine residue which constitutes RNA cap is linked through a 5'-5'-triphosphate bond to the first transcribed nucleotide. This modification facilitates the recognition and attachment of mRNA to the ribosome, as well as protection from degradation by 5' exonucleases. Besides, it is also crucial for other functions such as splicing and transport (Kozak 1983).

### Coding Regions

Coding regions consist of codons, which are decoded and translated by the ribosomes into one (mostly eukaryotes) or many (mostly prokaryotes) proteins. Coding regions have a start codon as the beginning sequence and end with a stop codon. Generally, AUG triplet is the start codon and UAA, UAG, or UGA are the stop codons. The coding regions are made stable by the internal base pairs which prevents their degradation (Katz and Burge 2003; Shabalina et al. 2006). Codons not only act as protein-coding regions but may also serve as regulatory sequences in the pre-mRNA as exonic splicing enhancers or exonic splicing silencers.

### Untranslated Regions (5' UTR and 3' UTR)

Untranslated regions (UTRs) are sections of the mRNA before the start codon and after the stop codon that are not translated and are termed as 5' UTR and 3' UTR, respectively. Since these

regions are transcribed with the coding region, they form a part of the exons and present in the mature mRNA. Various functions in gene expression, mRNA stability, mRNA localization, and translational efficiency have been attributed to untranslated regions (Kozak 1983; Shaw and Kamen 1986). The capability of UTR to perform such functions is sequence dependent and can vary. UTRs have variable affinity toward ribonucleases and ancillary proteins that promote or inhibit RNA degradation. Proteins or microRNAs that bind to either the 3' or 5' UTR modulate the translational efficiency by affecting the ribosome's ability to bind to the mRNA.

3' UTR also functions to determine the cytoplasmic localization of the proteins. UTRs also form characteristic secondary structures when transcribed into RNA which are responsible for mRNA regulation and also form targets for protein binding (e.g., SECIS element). Another class of mRNA elements, the riboswitches, modify the levels of transcription or translation by directly binding small molecules and changing their fold expression, thus regulating themselves (Copeland et al. 2001; Ren et al. 2017; Shabalina et al. 2006).

### Poly(A) Tail

The 3' poly(A) tail is a long sequence of several adenine nucleotides located at the 3' end of the pre-mRNA which facilitates the export from the nucleus, promotes translation, and hinders mRNA degradation (Shabalina et al. 2006).

### Monocistronic Versus Polycistronic mRNA

An mRNA molecule is monocistronic when it translates into a single protein which mostly

occurs in eukaryotes (Kozak 1983). Polycistronic mRNA carries information of several gene proteins and is translated into several proteins. These multiple proteins share related functions and are regulated together in an operon which mostly occurs in prokaryotes.

## Processing and Function

The life of mRNA molecule begins with transcription and ultimately ends in degradation. During its existence, the mRNA molecule can possibly undergo processing, edited and transported before being translated. This process is more common in eukaryotes than prokaryotes.

## Transcription

The process of transcription is similar in both prokaryotes and eukaryotes where the enzyme RNA polymerase makes a copy of a gene from the DNA to mRNA as required. However, the eukaryotic RNA polymerases are associated with mRNA processing enzymes while transcription is undergoing so as to speed up the processing of the mRNA (Gerber and Shilatifard 2003; Sims et al. 2004a, b). The unprocessed or partially processed mRNA, also known as pre-mRNA, is degraded, while mature mRNA is the completely processed mRNA.

## Eukaryotic Pre-mRNA Processing

Even though the prokaryotic mRNAs are essentially mature upon transcription, the eukaryotic mRNA needs extensive processing to promote their maturation. One of the important pre-mRNA processing techniques utilized to mature eukaryotic mRNA is 5' cap addition which is coupled to transcription and is critical for recognition by the ribosome and protection from RNases, splicing by which pre-mRNA is modified by removal of noncoding sequences called introns, editing where sometimes the sequence of the mRNA is edited and results in

modification of its nucleotide composition, and polyadenylation which is the covalent linkage of a polyadenylyl moiety to an mRNA molecule at 3' end mostly. It aids in protecting mRNA from degradation by exonucleases, transcriptional termination, and export of the mRNA from the nucleus. Prokaryotic mRNA polyadenylation however facilitates exonucleolytic degradation (Gerber and Shilatifard 2003; Jurado et al. 2014; Xiang et al. 2014).

## Transport

Another difference between eukaryotes and prokaryotes is mRNA transport. Because eukaryotic transcription and translation are compartmentally separated, eukaryotic mRNAs must be exported from the nucleus to the cytoplasm. Mature mRNAs are recognized by their processed modifications and then exported through the nuclear pore.

## Translation

Translation is initiated just after transcription in prokaryotes because they do not require processing or transporting. Thus, prokaryotic translation is coupled to transcription and occurs co-transcriptionally. Nonetheless, eukaryotic mRNA is first processed and thereafter transported to the cytoplasm which is then translated by either free floating ribosomes or those attached to endoplasmic reticulum by signal recognition particle (Dever and Green 2012; Hinnebusch et al. 2016; Kozak 1983). Therefore, unlike prokaryotes, eukaryotic translation is not directly coupled to transcription.

## Degradation

After a certain amount of time, the message is degraded by RNases. The limited lifetime of mRNA enables a cell to alter protein synthesis rapidly in response to its changing needs. Different mRNAs within the same cell have distinct

lifetimes (stabilities). In bacterial cells, individual mRNAs can survive from seconds to more than an hour; in mammalian cells, mRNA lifetimes range from several minutes to days. The greater the stability of an mRNA, the more protein may be produced from that mRNA. The presence of AU-rich elements in some mammalian mRNAs tends to destabilize those transcripts through the action of cellular proteins that bind these motifs. Rapid mRNA degradation via AU-rich elements is a critical mechanism for preventing the overproduction of potent cytokines such as tumor necrosis factor (TNF) and granulocyte-macrophage colony-stimulating factor (GM-CSF) (Shaw and Kamen 1986). Base pairing with a small interfering RNA (siRNA) or microRNA (miRNA) can also accelerate mRNA degradation (Nilsen 2007).

## Applications of mRNA

Application of mRNA in its native and modified form is colossal, and recently the concept of mRNA pharmacology has been introduced which involves ex vivo and direct vaccination of in vitro transcribed (IVT) mRNA into the cell. These methods can be used for genome engineering, genetic reprogramming, T cell and dendritic cell mRNA-based immunotherapies to treat cancer and infectious diseases, replacement of proteins, telomerase regiments to treat allergies, and other protein replacement therapies (Grimm and Kay 2007; Sahin et al. 2014; Vallazza et al. 2015; Van et al. 2015). The introduced mRNA is translated by the cells' own translational machinery; however, the introduction of mRNA does not alter the physiological state of the cells due to its transient and non-mutagenic effect. Moreover, while protein synthesis, there is no intervention in the human genome because mRNA does not integrate into the genome and basically does not even require entering the nucleus to get translated. Therefore, mRNA has rightly been called the next-generation therapeutics.

## Conclusion

The mRNA of several bacteria and bacteriophages is polycistronic, whereas in eukaryotes, it is monocistronic in nature. Posttranscriptional modification of prokaryotic mRNA is very little; on the other hand, eukaryotic mRNA undergoes major posttranscriptional modification which includes polyadenylation at 3' end of mRNA, capping at 5' end by condensation of guanylate residues and splicing of introns from heterogeneous mRNA. Life span of prokaryotic mRNA is very short in comparison to eukaryotic mRNA, and like all other biomolecules, RNA also undergoes degradation after its useful life.

## Cross-References

- ▶ [Codon](#)
- ▶ [DNA](#)
- ▶ [Exon](#)
- ▶ [Genes](#)
- ▶ [microRNA](#)
- ▶ [Ribosome](#)
- ▶ [RNA](#)

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## Meta-cognition

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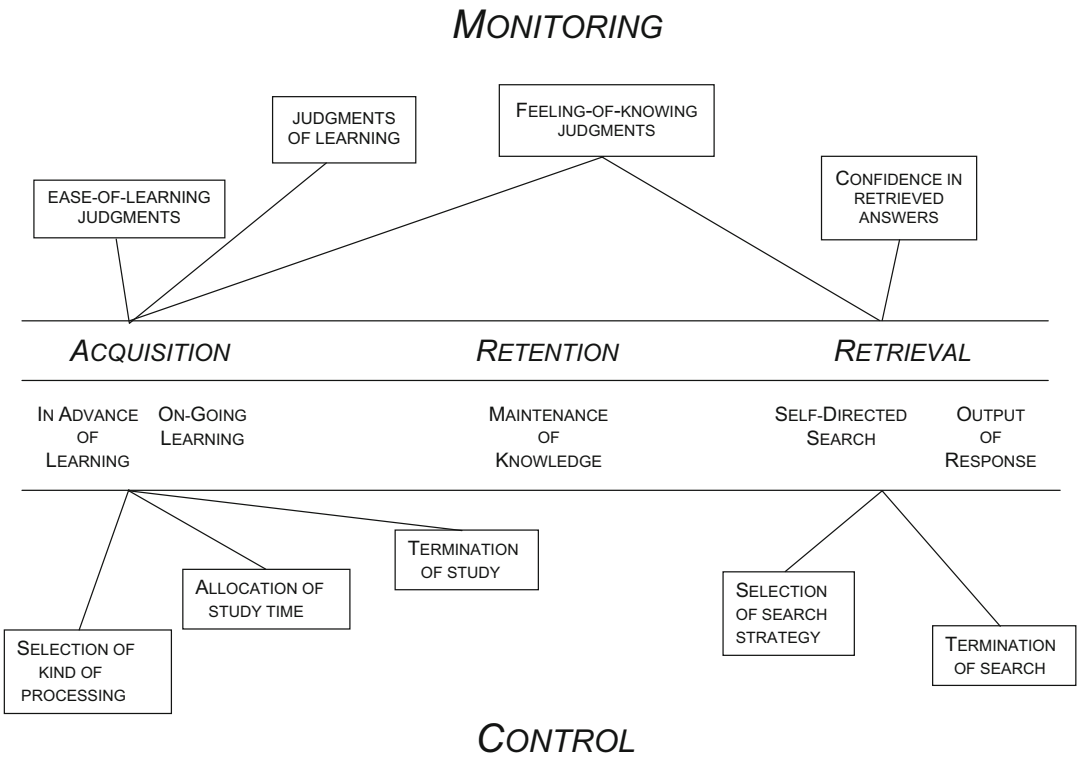
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Humans feel doubt and uncertainty. They often respond adaptively to these feelings by seeking additional information. In essence, they *GOOGLE™*. Humans' responses to mental states like uncertainty have grounded an enormous research literature on metacognition (Benjamin et al. 1998; Dunlosky and Bjork 2008; Flavell 1979; Koriat 1993; Nelson 1992; Schwartz 1994).

Metacognition occurs when cognitive processes oversee and guide other cognitive processes. Nelson and Narens (1990) provided a useful theoretical perspective on metacognition (Fig. 1). They differentiated cognitive processes at a first-order, object level and a second-order, meta level. The object level registers stimuli, retrieves memories, and so forth. The meta level monitors the first-order processes to judge their accuracy, relevance, and sufficiency to the task at hand. It also controls the first-order processes, directing them toward perhaps more productive and facilitating approaches. The monitoring processes (feelings of knowing, judgments of learning, confidence judgments, etc.) and the control processes (time allocation, strategy selection, etc.) are shown in Fig. 1 (top and bottom, respectively). The animal-metacognition literature has begun to explore both these monitoring and control functions of metacognition within nonhuman animals (hereafter, animals).

Metacognition clearly reveals the sophistication of human cognition. It shows hierarchical levels in mind, as second-order metacognitive processes regulate first-order cognitive processes.



**Meta-cognition, Fig. 1** A theoretical framework for research on metacognition, showing examples of process-monitoring capacities above and process-control capacities

below. (From Nelson and Narens 1990. Copyright 1990 by Elsevier Ltd, Reprinted with permission)

It shows humans’ conscious awareness of their own cognitive processes (Nelson 1996; Koriat 2007) – metacognitive states often reside within awareness and can be declared to others. In fact, research on human metacognition depends on these declarations. Metacognition is also intimately linked to humans’ self-awareness (Gallup 1982), because mental states like uncertainty are distinctly personal and self-owned (*I* don’t know; *I* can’t decide). Indeed, Gallup thought that a cognitive-awareness like metacognition was one of the fundamental cognitive capacities revealed by success in the mirror-dye test. Thus, readers should note that the area of animal-metacognition research is closely allied to the research areas on animal consciousness and animal self-awareness.

Yet because metacognition is such a sophisticated capacity, mightn’t it be a uniquely human achievement? Given this question’s importance, Smith and colleagues inaugurated a new area

of research on animal metacognition (Smith et al. 1995, 1997, 1998, 2003). The field has grown enormously and achieved substantial theoretical success (e.g., Basile et al. 2015; Beran et al. 2013; Call 2010; Couchman et al. 2010; Foote and Crystal 2007; Fujita 2009; Kornell et al. 2007; Paukner et al. 2006; Roberts et al. 2012; Smith et al. 2013; Suda-King 2008; Sutton and Shettleworth 2008; Templer and Hampton 2012; Washburn et al. 2006; Zakrzewski et al. 2014). Many innovative, distinguished colleagues have contributed to this research area. This listing can only be illustrative. In this entry to the encyclopedia, we summarize the research area of animal metacognition, discussing empirical progress, theoretical challenges surmounted and remaining, and the relationship of this work to other areas in comparative psychology.

The original researchers in this area faced the problem that human metacognition paradigms



do not suit animals, for their phenomena are based in verbal self-reports about feelings of knowing (FOKs in the literature), judgments of learning (JOLs), and tip-of-the-tongue experiences (TOTs) (see Brown 1991; Hart 1965; Smith et al. 1991). As matters stand presently, such self-declarations cannot be a viable part of the empirical dialog between animal participants and human practitioners.

Therefore, early animal metacognition research focused on a comparative uncertainty paradigm. There are two basic requirements for creating such a paradigm. The first is to create perceptual/cognitive/memorial difficulty for the animal – using difficulty to stir up something like an uncertainty mental state in animals' minds. This requirement caused an interesting conflict in the original dolphin-metacognition research, because the dolphin's trainers did not want to cause the animal the stress of difficulty and uncertainty. This was solved by opening the animal's enclosure to the Gulf of Mexico during testing sessions. He could relieve any trial stress by going for a walkabout in the Gulf – all the way to Dry Tortuga if he wished. But always, he quickly came back to join his trainer, the task, and the fish (Smith et al. 1995).

Presenting difficult trials is not sufficient for exploring animal metacognition. Many times animal psychophysicists have brought animals to their discrimination thresholds, the point where animals cannot know which stimulus event is occurring and which primary response to make. At threshold, their response curves for the two primary responses cross, demonstrating clearly that they do not know. These tasks feature difficulty. They show animals facing response conflict given balanced response strengths. They might reflect an animal feeling something like uncertainty. But, they can't show metacognition. This capacity is hidden by allowing only primary responses that map to the two perceptual input classes, and by denying the animal any way to comment on mental states like uncertainty or to respond to them effectively.

One solution is to hope that animals make ancillary behaviors, making observable their uncertainty or conflict on threshold trials. These ancillary behaviors do occur sometimes. They even made behaviorists somewhat uncomfortable

because they seemed to show that animals were in mental turmoil on difficult trials. Tolman even suggested that these ancillary behaviors – that he called “lookings or runnings back and forth” (Tolman 1938, p. 27) – could operationalize animal consciousness for the behavioral researcher (Tolman 1927).

However, it is hit or miss to depend on ancillary behaviors like these. Uncertain/puzzled humans might scratch their heads, uncertain monkeys might not, and uncertain dolphins would not! The behaviors might not be observable across species or comparable across species. Surely animals in different species may react differently when facing uncertainty. Accordingly, the best strategy in comparative metacognition research has been to give animals of different species the same behavioral response, letting them report on or deal with the difficult situation. This becomes the second requirement of an animal-metacognition paradigm – to give animals a third response that lets them cope with trial difficulty by declining to complete any trials they choose. This third response has now come to be called the Uncertainty Response (UR) in the literature. With this response available, one may see the animal adopt this reasonable strategy: to use the UR selectively when error or failure on the primary perceptual or cognitive task seems likely. To carry out this strategy, animals must identify, if they can, the occasions on which failure is likely.

The early history of this literature has been well reviewed (e.g., Smith et al. 2003; also entry *The Uncertainty Paradigm in Animal-Metacognition Research* in this Encyclopedia). Still, one example of the early paradigms will be described here to establish the literature's theoretical context. Smith et al. (1997) placed rhesus macaques (*Macaca mulatta*) in a psychophysical threshold task. Their use of a threshold task may be theoretically important. Macaques saw unframed boxes on their computer screens that could vary in their internal density of lit pixels. True Dense trials (exactly 2,950 lit pixels) occurred about half the time. Sparse boxes (ranging from 450 to 2949 pixels) occurred about half the time. Macaques used a joystick to

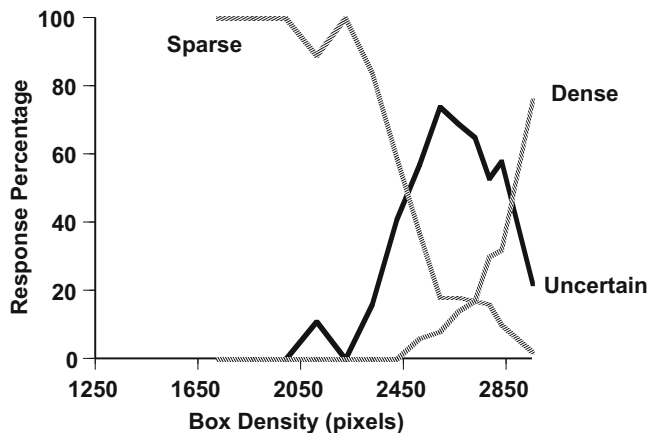
move a cursor to touch the pixel box (Dense response) or an S (Sparse response) to positively identify members of these two perceptual classes. Approaching threshold, as Sparse trials grew much denser, they became hard to identify. In turn, Dense trials became confusable with these Sparse trials, and also grew difficult. So, macaques were also allowed to make URs by moving the cursor to a Star. This let them decline to complete the present trial, end it, and receive a new, easy trial.

In Fig. 2, the Sparse and Dense discrimination curves cross at about 2,650 pixels. Here, macaques demonstrably could not tell Sparse from Dense. They didn't know. They couldn't know. But the question is whether they were in touch with some psychological signal that would let them monitor this uncertainty and manage it. And they were. The bold UR curve shows that they correctly assessed when they were at risk for error in the primary discrimination, and they selectively declined to complete those trials. The peak of the UR performance curve lies just over their threshold region. If their performance was metacognitive, then we could say that animals were monitoring the difficulty of trials and appreciated that at threshold they were in decisional trouble. But there are other possible signals

macaques might have been reacting to, and we will discuss these shortly.

Humans performed highly similarly (Smith et al. 1997). There is an isomorphism between humans' and monkeys' URs that is potentially theoretically meaningful. The main difference is that humans tend to use the UR less generously and somewhat reluctantly. The interesting explanation for this is that humans view the UR as a cop-out compared to a strong, affirmative Sparse or Dense response. It is interesting that the UR feels psychologically distinctive to humans – less affirmative, weaker – and this also has theoretical significance. Humans also explicitly declared that their URs were based on their conscious uncertainty on difficult trials. They knew they didn't know – consciously. To them their three responses meant: That's Sparse, That's Dense, I don't know. The UR in this task is an index of humans' meta-cognition. Macaques use the UR identically. The theoretical foundation was laid to consider whether that response can index metacognition in animals, too.

So what were macaques thinking or reacting to? Did they self-reflect on mental states like doubt? This would be a high-level psychological signal akin to metacognition. Or had they simply grown avoidant of the threshold stimuli that



**Meta-cognition, Fig. 2** A monkey's performance in the uncertainty paradigm used by Smith et al. (1997). The horizontal axis indicates the density of the trial. For 2,950-pixel trials – those trials plotted to the far right of each curve – the Dense response was correct. For all trials with lesser densities/fewer pixels, the Sparse response was

correct. The percentages of Dense and Sparse responses are shown (dashed lines). The percentage of trials receiving the uncertainty response at each trial level is shown in the solid line. (Adapted from Smith et al. 2003. Copyright 2003 by the Cambridge University Press)

often brought errors, time-outs, and reduced rewards? This stimulus aversion would be a low-level stimulus cue. If this were the explanation, then low-level explanations were possible for the macaques' "metacognitive" performances. That is, they could be explained associatively, by reinforcement learning, if animals' URs are cued by stimuli or shaped by reinforcement. Therefore, the early animal-metacognition paradigms were debated sharply. Indeed, one will see in this entry that the animal-metacognition literature has been dominated by the associative-metacognitive debate (Basile and Hampton 2014; Basile et al. 2015; Carruthers 2008, 2014; Hampton 2009; Jozefowicz et al. 2009a, b; Le Pelley 2012, 2014; Smith 2009; Smith et al. 2008, 2009a, b, 2012a, 2014a, b; Staddon et al. 2007).

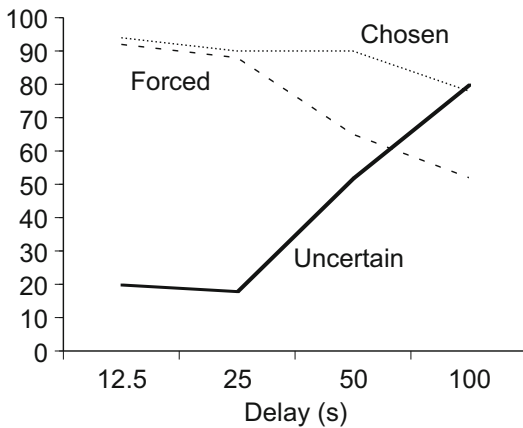
The story of this literature, in the hands of many inventive colleagues, has been one of dramatic empirical progress, and notable theoretical development in resolving this debate. Research has progressively lifted the phenomena of animal metacognition above traditional notions of stimulus control and beyond traditional ideas of reinforcement-based learning. It has raised the possibility of higher-level systems and processes in animal learning. It may have even grounded the development of methods to explore animals' conscious awareness. It has refined theoretical ideas in comparative psychology, and bent the arc of the field's theoretical discourse. This entry summarizes briefly the story of the literature.

Given early results like those shown in Fig. 2, associative-learning theorists were quick to supply various possible low-level explanations. However, these associative accounts soon met difficulty. For example, one sees immediately that a threshold stimulus – by definition – is terribly indeterminate. Because it equally suggests either of two responses (e.g., Sparse, Dense), it recommends neither. It is a very difficult kind of a stimulus to envision triggering a low-level reactive response. Moreover, it is most unclear whether the region at threshold could in any way be considered a third, intermediate stimulus between Sparse and Dense to which animals might react associatively. In fact, behavioral analysts had already grappled with the difficult

stimulus-control problem presented by threshold stimuli, concluding that the threshold state changes profoundly the nature of stimulus control and associative behavior (Boneau and Cole 1967; Commons et al. 1991; Davison et al. 1985; Miller et al. 1980; Terman and Terman 1972). So, is responding to a threshold state still associative responding, or have we already taken a step toward higher-level cognitive processing? Even though the early studies fairly deserved the criticism they received, it was quickly clear that stimulus-based accounts were less transparently available than it had first seemed.

Complementary research took uncertainty paradigms still farther from traditional ideas of stimulus control. In Shields et al. (1997), for example, macaques responded uncertain when they judged they were not able to complete trials in an abstract, simultaneous Same-Different task. This task is known to be cognitively sophisticated and derived – organisms are not responding to the concrete stimuli presented, but to the abstract relation instantiated by the combination of the two stimuli. Just for this reason, true Same-Different performances occur in only a handful of cognitively sophisticated species. Sameness is not a stimulus; neither is Differentness. Yet macaques were able to make URs selectively for the same-different trials that were most difficult because they were poised at their threshold for discriminating Same and Different. Their performance profiles correlated up to 0.97 with human performance in the equivalent task. Possibly relational-judgment uncertainty transcends associative responding, crossing a threshold to demonstrate animals' higher-level uncertainty-monitoring capability.

The associative-learning construct was challenged more strongly when the "stimulus" to be judged was present only in the animal's memory. In Hampton's (2001) elegant study, monkeys declined to complete tests of their memory when they judged that their available memory traces were faint or questionable. Figure 3 shows that at longer delays, as sample memory became fainter, monkeys made URs more often, as though they were monitoring the metacognitive signal of fainter memory and responding to it



**Meta-cognition, Fig. 3** A macaque's performance in the uncertainty paradigm used by Hampton (2001). The horizontal axis indicates the length of the retention interval before matching could occur. The percentages correct are shown for memory tests completed when the memory test was required (dashed line) or optional and intentionally chosen by the macaque (dotted line). The percentage of trials receiving the uncertainty response is shown in the solid line. (Adapted from Hampton 2001. Copyright 2001 by The National Academy of Sciences)

appropriately. Hampton also showed that at longer delays, when monkeys did not respond uncertain, but rather chose to complete the memory test, their performance was quite high. This result is consistent with the monkeys' following a metacognitive signal that told them they still remembered the sample on that trial. This performance difference between Chosen trials (selected for completion by the animal) and Forced trials (fended off by the UR) has become an important finding in the memory tasks in this literature. In these experiments, there was no objective stimulus that could control behavior. Rather, animals had to consider whether they remembered the previous sample. It is quite doubtful that a monitored, faint memory should be considered an associative stimulus that controls behavior. Performance in this task seems to depend instead on some cognitive process like memory monitoring.

Washburn et al. (2010) gave the Hampton task a telling twist. They presented shapes far in a monkey's left or right visual periphery, so that the to-be-matched sample might be represented more quickly and fully in the opposite cerebral hemisphere. The macaque sometimes received

transcranial magnetic stimulation (TMS) to the left or right cortex during the forgetting interval. The TMS disrupted visual working memory temporarily. With no TMS, the macaque matched well and made few URs. With sample presentation and TMS concordant (stimulus left periphery, TMS left cortex), the result was the same, because the TMS had largely spared the relevant memory contents. But with sample presentation and TMS opposed (stimulus left periphery, TMS right cortex), the monkey matched poorly and made many URs. In a sense, the TMS stole the contents of the animal's visual working memory after stimulus presentation was complete. The remarkable result is that the monkey noticed the theft, and made URs adaptively in that case. Clearly, he was monitoring an internal signal regarding a psychological state of lost memory.

Through this period of research, it gradually became clear that the normal mechanisms of associative learning could simply not explain the phenomena of uncertainty responding in the animal-metacognition literature. Rather, it seemed that animals might be bringing some higher-level cognitive strategies to bear on the tasks being studied. In one capstone comment summarizing this literature, Carruthers and Ritchie (2012, p. 76) concluded that "this body of work, taken as a whole, cannot be explained in low-level associationist terms, as involving mere conditioned responses to stimuli." In a capstone experiment, Basile et al. (2015) systematically explored 7 possible associative hypotheses about macaques' URs in memory-monitoring tasks. They found no evidence supporting these hypotheses. Rather, they consistently found evidence supporting the metacognition or memory-monitoring hypothesis. Basile et al. (2015, p. 85) concluded that monkeys "can use memory strength as a discriminative cue for information seeking, consistent with introspective monitoring of explicit memory."

Accordingly, researchers began to establish the diagnostic features of these higher-level strategies, which appeared to show many aspects of controlled and deliberate cognition by animals. Smith et al. (2010) showed that monkeys could make adaptive URs in four different tasks simultaneously when trials of these tasks were

interleaved randomly. URs were apparently responsive to a general psychological signal of uncertainty that was not restricted to one stimulus domain at a time. Washburn et al. (2006) showed that macaques would make URs on the first trial of novel tasks, showing that the signal of uncertainty they were monitoring was available in new stimulus domains that had never been trained or reinforced. In another indication of the cognitive flexibility grounding monkeys' confidence/uncertainty judgments, Morgan et al. (2014) tested the transfer of these judgments between retrospective and prospective versions of an uncertainty task. One monkey was able to transfer immediately, from reporting lack of confidence after a trial response had already been completed, to reporting unwillingness to engage the trial before a trial response was made. Finally, Zakrzewski et al. (2014) showed that monkeys could flexibly, from trial to trial, adjust their willingness to complete difficult trials, or to decline those trials, based on the number of reward tokens they stood to lose from an error. That is, monkeys, just like humans, made a modified form of UR differentially based not only on trial difficulty but also on the risk they faced. In psychophysical terms, they widened their uncertainty region as their accumulated rewards increased, so that they protected themselves more generously against a possible error that would cost them all those rewards. Haun et al. (2011) showed a similar flexibility in ape species.

Gradually, the theoretical climate changed, so that theoretical consensus emerged that animals were not only bringing high-level cognitive strategies to bear on the literature's tasks, but possibly also sometimes bringing metacognitive strategies. Sutton and Shettleworth (2008, p. 266) concluded that "metamemory, the ability to report on memory strength, is clearly established in rhesus macaques (*Macaca mulatta*) by converging evidence from several paradigms." Fujita (2009, p. 575) concluded that "evidence for metacognition by nonhuman primates has been obtained in great apes and old world monkeys." Roberts et al. (2009, p. 130) concluded that "substantial evidence from several laboratories converges on the conclusion that rhesus monkeys

show metacognition in experiments that require behavioral responses to cues that act as feeling of knowing and memory confidence judgments." Our theoretical judgment is that this consensus is clearly justified. However, this judgment does not imply that nonhumans share all aspects of humans' metacognitive capacity, or that animal metacognition is self-imbued and self-conscious in the ways that human metacognition is. There can still be important differences across species that remain to be investigated.

Only a few times in comparative psychology has there been such a careful and systematic evaluation made of the sufficiency of associative-learning processes in explaining animals' behavioral performances. This evaluation has been especially influential within comparative psychology because of the clear lessons it teaches: Associative interpretations are sometimes insufficient to capture a field's phenomena, animals sometimes transcend associative mechanisms, showing higher-level, deliberate cognitive strategies instead. Therefore, comparative psychology must also turn to the problem of characterizing the nature and cognitive level of those higher-level strategies.

In fact, Smith and his colleagues tried to characterize these cognitive strategies (Smith et al. 2012a, b, 2003). This was a difficult problem because comparative psychology lacked models and descriptions that transcended associative learning. So they began with an admittedly questionable analogy to human cognition. In uncertainty tasks, the essence of the information-processing problem is to be facing an uncertain threshold stimulus or an indeterminate memory trace. By definition, the animal will then experience equivalent response tendencies and reward expectations regarding both primary responses. Response in this case cannot be adjudicated by reinforcement-based, conditioned response tendencies. The animal will be frozen between responses like the philosophical donkey facing two haystacks. Some other decisional process would have to step in to referee the behavioral close call and break the tie. Shiffrin and Schneider (1977) described the cognitive processes that could do so. They agreed that because ambiguous



mental representations map equally to multiple behavioral responses, those representations cannot be the organism's behavioral indicator. Accordingly, they thought responses made under uncertainty could not reflect low-level, automatic processes. Instead, they thought the organism would adopt higher, controlled cognition to resolve the indeterminacy and choose adaptive behavioral solutions. These controlled processes would be slow, deliberate, and serial in nature by Shiffrin and Schneider's theoretical description. Atkinson and Juola (1974) made the analogous claim about the resolution of indeterminate memory traces. This analysis applies even to the threshold phenomena shown in Fig. 2, another reason why one should not too quickly dismiss these early performances as purely associative and reactive.

In interesting ways, this higher-level description of animal-metacognition performances has proved out and is being clarified with more operationalizable cognitive constructs. For example, Smith et al. (2013) reconsidered monkeys' performance in the Sparse-Uncertain-Dense task already described in this entry (Fig. 2). However, in some conditions, they gave monkeys a concurrent working-memory load to sustain while they performed the Sparse-Dense trials. The memory load possibly served to occupy macaques' active cognitive resources, diverting those resources away from the discrimination task. Smith et al. hypothesized that URs, if they are a higher-level decisional response, might be especially vulnerable to this manipulation, as they would depend on these cognitive resources. But they suggested that Sparse and Dense responses could be low-level, associative, stimulus reactive, and not affected by the memory load. These results obtained. Concurrent tasks disrupted macaques' URs far more than their Sparse or Dense responses. Interestingly, Schwartz (2008) found that for humans, too, memory load strongly interfered with metacognitive judgments, above all sharply decreasing tip-of-the-tongue experiences. It is a significant theoretical insight if monkeys' metacognition and working memory use similar cognitive resources, as proposed by Schwartz for humans.

Smith et al. (2013) presented an additional notable dissociation when they gave monkeys an allied Sparse-Middle-Dense task. In this case, the Middle response was correct for an objective range of intermediate density impressions – in essence the same range that should also occasion the UR in the other task. But Middle responses to Middle stimuli were immediately rewarded, clearly supporting reinforcement-based, associative learning. And now, Smith et al. found that Middle responses, just like Sparse and Dense responses, were minimally affected by the cognitive load. Monkeys can react automatically to identifiable stimulus impressions, even with memory resources occupied. What they seem less able to do without those resources is to monitor the still, small psychological signal that indicates they don't know.

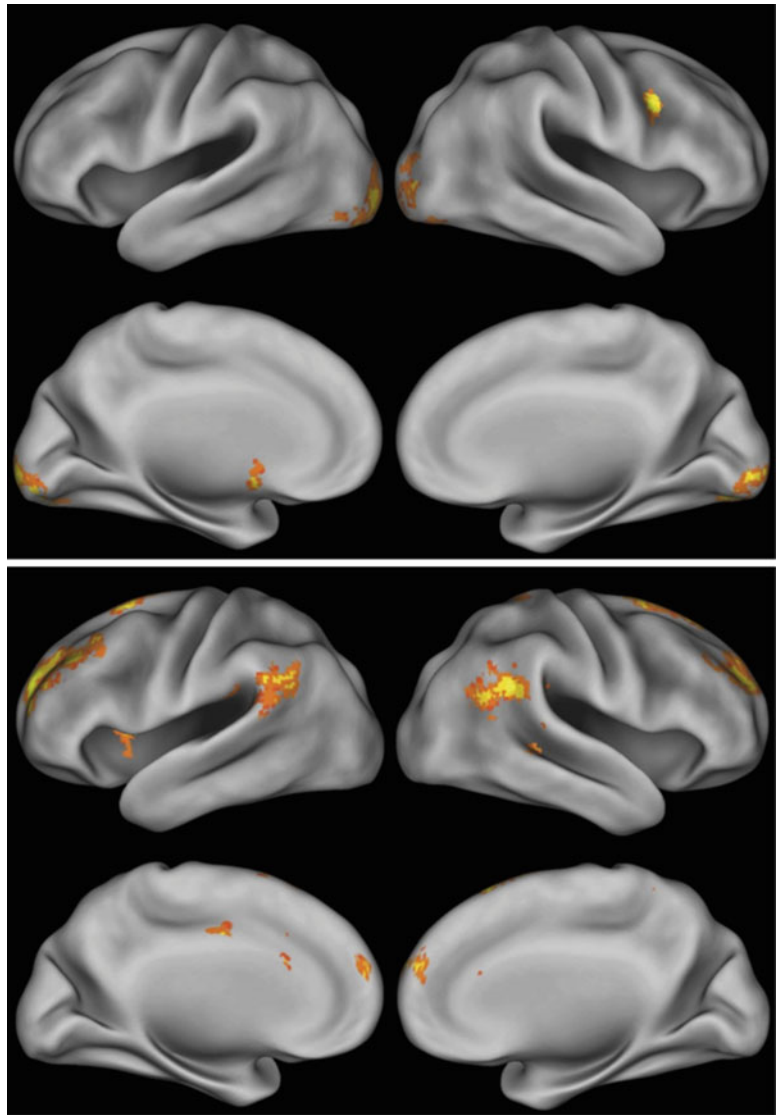
A significant benefit of the newer theoretical perspectives on animal metacognition is the synergy it creates with human research, and in particular with the literature on human cognitive neuroscience. For example, Paul et al. (2015) described the distinctive psychological circuits underlying uncertainty responding using rapid event-related fMRI. They used the Sparse-Uncertain-Dense task once again. They showed that the neural activity patterns recruited during humans' URs are distinctively different from those recruited during humans' primary perceptual responses (Sparse, Dense).

Figure 4 (top) shows the simple activation pattern when participants chose correct Sparse or Dense responses instead of making URs. The activity pattern was elementally simple, consistent with the interpretation that Sparse and Dense responses are first-order behaviors in which identifiable visual stimuli elicit well-associated behavioral responses.

In contrast, Fig. 4 shows the complex activation pattern when participants chose URs instead of Sparse-Dense responses. Uncertainty responding activated a much more elaborate cognitive-control network. This result is consistent with the idea that URs are the output of controlled, decisional cognitive processes – the idea to which cognitive experiments were already pointing. Of course, this is a human experiment

**Meta-cognition,****Fig. 4** Humans'

performance in an uncertainty paradigm depicted from an fMRI perspective. Top. Whole-brain results from the contrast Correct Sparse–Dense Response > Uncertainty Response projected on an inflated lateral and medial cortical surface. Table 2 in Paul et al. (2015) gave the coordinates and voxel numbers for significant clusters. Images were cluster thresholded (correcting for multiple comparisons) at  $z > 3.54$ ,  $p < 0.01$ . Bottom. Whole-brain results from the contrast Uncertainty Response > Correct Sparse–Dense Response projected on an inflated lateral and medial cortical surface. Table 3 in Paul et al. (2015) gave the coordinates and voxel numbers for significant clusters. Images were cluster thresholded (correcting for multiple comparisons) at  $z > 3.54$ ,  $p < 0.01$ . (From Paul et al. (2015). Copyright 2015 Elsevier Ltd. Reprinted with permission)



only. But it exhorts comparative psychologists toward eventual replication with monkeys. It also starts to map the field's cognitive-science constructs to their neuroscientific architectures, explaining why the response to uncertainty is so distinctive psychologically.

Smith and Church (2017) contributed a theoretical review to this area. They described instances in which small task changes (just like the change from Uncertain responding to Middle responding discussed above) alter sharply the cognitive psychology of tasks – sometimes affecting in concert the level of awareness, the

declarative nature of knowledge, the dimensional breadth of knowledge, and the brain systems that organize learning. These changes reveal dissociable learning processes that a unitary associative construct cannot explain but that a multiple-systems framework can explain. They urged comparative scientists to bring this multiple-systems approach to comparative studies, even though it means acknowledging that animals may have systems of cognitive processing that are parallel to humans' systems of declarative and explicit cognition. Work by Robert Hampton and his colleagues is proceeding along similar, dissociative

lines (Anderson et al. 2014; Basile and Hampton 2013; Tu and Hampton 2012). It is interesting that two laboratories focusing on this new multiple-systems theoretical perspective in comparative psychology have emerged from long practice in the animal-metacognition literature.

From the original associative criticisms of the UR by monkeys, to new systems perspectives in comparative psychology, to possibly explicit-declarative levels in animal minds, the animal-metacognition literature has traced a constructive journey and fostered theoretical development in comparative psychology.

This entry would not be complete without discussion of metacognition research on other vertebrate species. One can see the theoretical utility behind cross-species research. If, as one theoretical possibility, uncertainty responding were simply associative and stimulus reactive, then we could expect to observe metacognitive performances (so-called) spread broadly across species, because many animals condition and learn associatively, and should do so in metacognition tasks as well. However, if, as another theoretical possibility, some animals monitor uncertainty states like uncertainty and doubt in higher-level ways, then we could expect to observe these performances spread narrowly across species. And, of course, this cross-species research would also illuminate the emergence during cognitive evolution of capacities like cognitive self-awareness.

With the clear demonstration of successful uncertainty monitoring in Old-World rhesus macaques, research quickly turned to examining monitoring abilities in New-World monkeys, like capuchins. Evidence for the ability of these monkeys to monitor their uncertainty has been harder to find, and the field has largely come to the consensus that their monitoring ability is weaker than that of macaques (e.g., Beran et al. 2009, 2014; Fujita 2009).

Fujita (2009) gave capuchin monkeys a variation of the delayed matching task along with the UR on some trials. In one experiment, two capuchins made URs more often after longer forgetting intervals, consistent with the idea that they knew they had forgotten the sample they were to match.

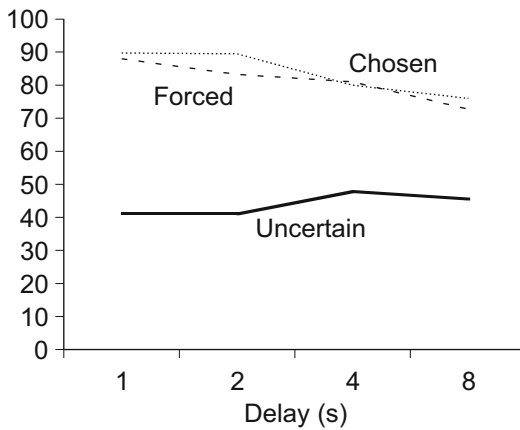
One of the two showed the advantage of Chosen trials over Forced trials that has already been discussed. However, Fujita conducted additional experiments, and in the end he concluded that these monkeys are expressing a faint and fragile metacognitive capacity.

Beran et al. (2009) tested capuchin monkeys in a Sparse-Uncertain-Dense psychophysical uncertainty paradigm and found that even with extremely long time-outs for incorrect answers only one capuchin showed any sign of ever using the UR to fend off difficult trials. However, when they used the Sparse-Middle-Dense paradigm described earlier, the capuchins had no problem learning to correctly discriminate the middle items. They concluded that capuchins do not have a robust metacognitive ability to monitor their uncertainty.

In follow-up work, Beran et al. (2014) used a six-choice psychophysical discrimination (in contrast to the usual two-choice discrimination) in both capuchins and macaques. This reduced the probability of randomly guessing the correct answer from 50% to 17%. Under these circumstances, all the macaques used the UR on the difficult trials, and multiple capuchins also used the UR appropriately. The researchers concluded that capuchins potentially have the ability to monitor uncertainty, but it is harder for them than for the Old-World monkeys, perhaps because they are more impulsive and less risk averse.

Pigeons and their researchers have also made a strong contribution to research in this area. For example, Inman and Shettleworth (1999) evaluated pigeons' metamemory capacity using an approach like that in Hampton (2001). Pigeons given longer forgetting intervals in matching trials demonstrably forgot what they should match (Fig. 5, dashed and dotted lines). Yet they barely made more URs after long delays, though avoiding the long-delay trials would have been optimal (bold line). The pigeons don't seem to have access to a psychological signal indicating that they have probably forgotten the sample and they should respond uncertain to decline the trial.

Inman and Shettleworth also analyzed the trials that pigeons chose affirmatively to complete (by NOT responding uncertain). A metacognitive



**Meta-cognition, Fig. 5** Pigeons' performance in the uncertainty paradigm adopted by Inman and Shettleworth (1999). (Data graphed with permission from Inman and Shettleworth 1999. Copyright 1999 by American Psychological Association)

animal ideally would be monitoring some psychological signal that told them that the relevant memory trace was still present and active, so that it was safe to complete the memory test. Yet pigeons did not show stronger matching performance when they chose to complete matching trials than when they were forced to complete them (Fig. 5, dashed and dotted lines). In these aspects of performance, pigeons hardly expressed any metacognitive capacity. Comparing Fig. 5 to Fig. 3, one sees that pigeons, evidently not expressing a metacognitive capacity in these tasks, were quite different than monkeys, who do express that capacity.

Sutton and Shettleworth (2008) replicated the pigeon findings in several experiments using converging methods. They still found that pigeons were a strong comparative NO in the area of metacognition. Shettleworth and her colleagues made a very strong contribution by systematically building this negative evidence – sometimes the rewards of our field obstruct this important kind of research. At least one must conclude that pigeons have great difficulty expressing the key features of metacognitive performance. Nonetheless, research continues to find the right contingencies under which pigeons may show a semblance of monkeys' metacognitive performances. These efforts are highly appropriate, for

they might suggest the very earliest forms that ancestral cognitive self-awareness assumed, and how it arose from purely associative processes (Adams and Santi 2011; Zentall and Stagner 2010, 2011).

Similar studies with rats have produced results more indicative of metacognition within a non-primate mammal. For example, Foote and Crystal (2007) conducted a study akin to the psychophysical perceptual studies described earlier in this entry. Rats performed a discrimination among temporal durations. On some trials, rats could make a UR to decline to complete it, which they should do if the trial was difficult because it is near the Short-Long break point of the duration continuum. On other trials, rats were required to complete the discrimination trial. This technique of comparing performance on Forced and Chosen trials is a very innovative and revealing approach that we have seen adopted by several researchers already.

Foote and Crystal found that rats did respond Uncertain most on the durational stimuli nearest the Short-Long break point of the discrimination. They also found that rats performed more accurately on Chosen trials than on Forced trials, as though they were monitoring a felicitous psychological signal indicating an appropriate expectation of responding correctly. This was the first demonstration of possible metacognition by rats in the perceptual tasks of this literature.

The experiment by Foote and Crystal (2007) remains an extremely interesting, sophisticated experiment. It is fair to say that Crystal later became skeptical about the results that they had obtained. He was influenced by Smith et al.'s (2008) theoretical article in which they noted some cautions necessary before fully and safely concluding metacognition from performance in tasks like theirs. We note that we do not necessarily share Crystal's skepticism, given what we have said about the special character of threshold tasks and about the special psychological character of the threshold state.

Templer et al. (2017) adopted a delayed matching-to-sample paradigm akin to those tested by Hampton with macaques and by Shettleworth with pigeons. The rats performed an odor memory

task. They could make a UR to decline the memory tests they wished. Templer et al. also compared trials on which rats chose to complete the test to trials when they were forced to complete the test. Rats did show a performance advantage on chosen trials, possibly an important symptom of cognitive monitoring. Rats also showed continued appropriate use of the UR under conditions that were designed to strengthen or weaken their memory traces. This was the first demonstration of possible metacognition by rats in the matching-to-sample tasks of this literature. Probably the convergence of the results in Foote and Crystal (2007) and Templer et al. (2017) suggests the reasonable likelihood that rats are expressing the beginning form of cognitive self-awareness.

If the cognitive origins of metacognition lie before the primates, perhaps one can see why. There must be times when animals face difficulty and uncertainty in the natural ecology. Those cases, by definition, are when there hasn't been training, or when there is response conflict, or when the balanced forces of conditioning can't resolve an adaptive behavior. Instead, the adaptive behavior must be selected using some other mechanism, perhaps at a higher cognitive level. It is simply logical that some animals would have benefited from having – that is, from evolving – an uncertainty-monitoring mechanism like that macaques clearly have. Even James (1890/1952) noted the particular advantage that conscious uncertainty could confer on organisms facing difficult, dangerous, and uncertain situations. Now, to be sure, the potential benefits from evolving metacognition do not guarantee that animals would have evolved metacognition. It isn't known how difficult it is for cognitive systems to arrive at forms of decisional response selection – or perhaps forms of mental self-reflection – that are above and beyond stimulus reaction and reinforcement learning (Smith et al. 2003).

This entry would also not be complete without addressing the elegant research that has explored animals' metacognitive control over cognition, the bottom of the metacognitive capacity expressed in Fig. 1. The question here is whether animals, beyond realizing in a sense that they are in cognitive difficulty, can also change

and guide their information processing down more facilitative pathways.

Research in this area is typified by the elegant information-seeking paradigm of Call and his colleagues. For example, Call and Carpenter (2001, also Call 2010; Suda-King 2008) used a naturalistic uncertainty task (i.e., which opaque tube contains food) in tandem with an information-seeking response (i.e., visually checking to find out where the food is). Sometimes apes saw the food placed in the containers. On those trials, they retrieved the food without seeking additional information. On other trials, they did not see the placement of the food. On those trials, they made information-seeking responses (bending down to inspect the barrels of the food tubes). It is a notable feature of this design that the two situations are identical in the perceptual and potentially associative cues that are presented to the animal – the setup, the tubes, everything is identical. The only distinguishing feature lies in the animals' self-awareness of knowing where the food is. These tasks come close to logically requiring animals to respond to their state of knowledge.

In an engaging extension of this research, Call (2010) showed another very human thing about chimpanzees' information seeking. He found that when the food tubes contained a very highly desired food item, the chimpanzees would check the tube to make sure they had it right **EVEN IF THEY HAD CLEARLY SEEN THE HIDING**. Call likened this to the human in an international airport terminal who checks their passport in their pocket for the 14th time, because it is really important not to spend your vacation time in some country's detention facility because you forgot a travel document.

Beran et al. (2013) confirmed the cognitive sophistication of chimpanzees' information seeking by raising the ante on Call's task to the symbolic lexical level. Chimpanzees were given a task in which they had to identify on their lexicon keyboards the identity of a hidden food in order to obtain it. They got the food if they supplied its correct lexical label. They could report the food's name directly on their nearby keyboard. Or, they could take a significant route detour in order to



first inspect the opaque container in which the food item was hidden. On some trials, they saw the food placed in its container. Then they often immediately labelled it. On other trials, they did not see the food's placement. Then they often detoured to look inside the container before naming. They sought additional information just when they knew they lacked sufficient information to complete the trial correctly.

The research area on metacognitive control has also produced strong and intriguing species differences. For example, Basile et al. (2009) tested capuchin monkeys (*Cebus apella*, a New World monkey species) in Call and Carpenter's (2001) food-tube paradigm. In an interesting failure to express the expected metacognitive capacity, they found in one experiment that only one of five monkeys showed the pattern of searching more often when the food-hiding event had not been seen. In later experiments, capuchins were slightly more successful. But Basile et al. concluded that overall capuchins were showing dubious evidence of having this metacognitive capacity.

In Paukner et al.'s (2006) converging study, some capuchin monkeys did show evidence of visual inspections before food-tube selection. Yet capuchins also showed evidence of visual inspections for transparent tubes in which the food was clearly visible. They also searched bent tubes, even though these searches were futile because they could not yield any useful information. Paukner et al. judged that, unlike humans, apes, and macaques in related studies, capuchin monkeys showed a relatively weak expression of this metacognitive capacity.

Roberts et al. (2009) conducted fascinating information-seeking studies with pigeons. The birds participated in a matching-to-sample task. However, the sample was initially occluded, and pigeons needed to make a sample-reveal response to see it. Clearly, if you don't see the sample, you will be at chance in trying to match it. Remarkably, pigeons had a controlling tendency just to attempt the match, even though the match now occurred without their having seen the sample and without any relevant information to support the match. Roberts et al. (p. 129)

concluded that "The findings of all of these experiments suggest the absence of metamemory in pigeons."

We were extremely interested in this strong negative result, and we saw a chance to confirm by this converging paradigm the macaque–pigeon species difference that has already been discussed in this entry. So we studied information seeking by capuchin monkeys and rhesus macaques in a task much like that of Roberts et al. (2009). Rhesus monkeys immediately understood that if you want to match correctly, you have to wake up the sample. Even capuchin monkeys were substantially successful at making this basic information-seeking response. In more detailed testing, though, the capuchins exhibited definite weaknesses in information seeking compared to macaques (Beran and Smith 2011).

Once again, the pigeon–macaque dissociation testifies to the distinctive cognitive sophistication of metacognitive responses like information seeking. If the situation contained a patent temporal, or stimulus, or other associative cue, pigeons might well learn to respond reactively to that. In fact, the matching task did contain a strong stimulus of an occluded sample, yet still that did not cue successfully the sample-reveal response. It did not do so even after extensive training in which the birds were required to wake up the sample, and got to see how much their matching performance improved. Pigeons just aren't finding the internal signals of not knowing, of needing information, and so forth. Macaques appear to find and respond to those psychological signals easily and naturally. Evidently, the voice of uncertainty is still, is small, and not all species hear it.

We close this entry with outreach to other areas of comparative psychology that have important connections with our own.

First, this area has close ties to research on mirror self-recognition. The mirror paradigm devised by Gallup (1982) has had extraordinary influence, and promoted important debates, including whether animals other than primates have sophisticated forms of reflective mind, and whether primates other than apes do. The animal-metacognition studies in this context can be seen as complementary to those of Gallup.

They explore animals' cognitive self-awareness, whereas Gallup explored animals' bodily self-awareness. They also make a distinctive theoretical contribution, for showing robust cognitive self-awareness in monkey species, when those species have normally shown mirror self-recognition with great difficulty.

Second, this area raises crucial questions about what self-awareness is, and about how it is to be operationalized. There are dye-mark studies, metacognition studies, and so forth. The dye-mark studies can be questioned because low-level body-grooming utilities could underlie those phenomena. But the metacognition studies can be questioned as measures of self-awareness also, because the mental monitoring that monkeys show might not require the knowing of self, a feeling of selfness, and so forth.

Third, animal-metacognition research has close ties to work on self-control and agency. In Metcalfe and Son (2012), the highest level of auto-noetic metacognition was restricted to cases in which metacognition is imbued with self-awareness. For Metcalfe, this raised the question of whether animals understand the idea of their own agency within a task, and of whether they can report having or not having agency within a task as they perform it. Accordingly, researchers have begun to explore declarative reports of agency by humans. Metcalfe and her colleagues (Miele et al. 2011; Metcalfe et al. 2013) have used a video game in which mouse movements let one reach targets descending on the screen. By disrupting, fuzzing, or lagging the cursor control, one can reduce humans' effective agency in the task and they report this loss of agency sensitively. Couchman (2015) contributed perhaps the first comparative study of agency judgments across humans and monkeys. Humans and monkeys were trained to move a computer icon with a joystick while a distractor icon partially matched their movements. Both humans and monkeys were able to recognize and identify the icon that they were controlling. This suggests that they may have some understanding of self-agency. More research is certainly warranted on this facet of self-awareness and on its relation to metacognition.

Fourth, our research bears on animals' higher-level capacity for declarative memory and declarative cognition generally. In animal-cognition research, there has been a scourge of scare quotes surrounding constructs – traditionally forbidden in the behavioral zeitgeist – like “episodic memory,” “declarative memory,” “explicit cognition,” and so forth. However, many of the animal-metacognition paradigms have begun to show that animals are transcending the bounds of associative learning as it has traditionally been understood. Accordingly, it is sharply time to take all the scare quotes away, and use the sophisticated paradigms available now to explore animals' explicit and declarative cognitive capabilities systematically (Smith and Church 2017).

Fifth, the animal-metacognition literature seemingly presents paradigms that can bring comparative researchers close to the threshold of demonstrating animal consciousness. This idea extends back to Tolman (1927), who thought that animals' hesitating-vacillating behaviors at threshold could become “The Behaviorist's Definition of Consciousness.” This theme was expressed eloquently again when Weiskrantz (1986, 1997) presented a thought experiment in which animals were offered a commentary key so that they could express their mental states, a response beyond the responses devoted to the primary task. The metacognition paradigms are good instantiations of his thought experiment, and their metacognitive responses are good instantiations of his commentary key.

Indeed, in Cowey and Stoerig (1995), a kind of metacognitive response by blindsight monkeys essentially let them make declarations about their conscious awareness. The researchers gave monkeys a visual-detection task. When forced to answer, monkeys could successfully localize targets by pointing to their location, even within their impaired hemifield. This is consonant with the phenomena of blindsight. But Cowey and Stoerig also gave these monkeys a response that meant: The trial was Blank, or “I didn't see anything.” Remarkably, the animals used that response to comment on the trials presented in their impaired hemifields, even though they could answer those

trials correctly when required. They may well have been saying: “I didn’t see anything.”

Sixth, this literature on cognitive self-awareness presents an extraordinarily important bookend to the literature on other awareness (Theory of Mind) that explores whether animals know about the other minds in other bodies. The relation between self- and other-awareness has been an important topic in comparative theory. Humphrey (1976) made the famous proposal that metacognition arose to support social animals’ reading of the other minds around them. He called these mind readers Nature’s Psychologists. Carruthers (2009) took the stronger view that mind reading – the theory of the other’s mind – evolved first to serve social functions, and then only later was directed inward to ground metacognition.

The animal-metacognition literature makes important contributions to this ongoing theoretical discussion. For it is quite clear that in a variety of tasks monkeys show robust forms of cognitive self-awareness. Yet in many theory-of-mind tasks, monkeys display almost no capacity for showing other awareness. These findings, taken collectively, present a strong case that cognitive self-awareness has sometimes evolved on its own, not as a slave system to mind reading. Moreover, this evidence shows that cognitive self-awareness sometimes evolved first in the evolutionary progression. Given this evidence, perhaps we can understand why this evolutionary progression from self- to other awareness may even be mandatory and inevitable. If other-awareness evolved first, then one must assume that these creatures appreciated the mental states of others without appreciating their own. However, animals with no understanding of their own mind and mental state would have no basis for judging another’s mind and mental state. This would be like trying to judge what keys a conspecific has in its pocket, even though it has no conception of what keys and pockets are. Instead, if cognitive self-awareness evolved first, then the animal would understand mental states and mind, or keys and pockets. And then it would only be a small step to inferring that other animals have keys and pockets, too. This evolutionary progression seems more possible

and workable in preadaptation terms, and this evolutionary progression seems to be the one borne out by the animal-metacognition literature.

Seventh, broadening out, discussions like these encourage theorists to consider the overall factor structure of reflective mind in animals. Gallup (1982; see also Gallop and Suarez 1986) was very influential for his proposal that mirror awareness, self-awareness (metacognition), and consciousness all emerged together when, in some evolutionary transition to apes, all the facets of reflective mind began to shine brightly together. He took a g-factor approach to the emergence of reflective mind. However, it hasn’t been confirmed that this occurred. It is not clear whether reflective mind is all-or-none or unitary in Gallup’s sense. In fact, the animal-metacognition literature, especially regarding metacognition versus TOM, appears to speak against that possibility. No doubt these discussions will continue.

Eighth, the animal-metacognition literature has begun to make a constructive contribution to discussions about animal rights, and animal care/husbandry. The literature shows that many animals monitor their mental states, like uncertainty, confidence, and recollection. Therefore, it is perfectly plausible that they may monitor other aspects of their personal mental experience, including pain, discomfort, fear, and so forth. Thus, joining other research areas on high-level aspects of animal cognition, this literature systematically elevates comparative psychology’s view of animals’ reflective minds. It must also, therefore, elevate the level of care and respect that is owed to those animal minds and animal lives. For this reason, and for many other reasons, too, we are in the debt of many extraordinary research animals who have produced performances that have fostered profound theoretical development in this area, and who have been extraordinary ambassadors for their species.

## Cross-References

- [Cognitive Control](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)

- ▶ Computerized Testing Paradigm in Primates
- ▶ David Washburn
- ▶ Edward C. Tolman
- ▶ Georgia State University's Language Research Center
- ▶ John David Smith
- ▶ Metamemory
- ▶ Michael J. Beran
- ▶ Sara Shettleworth
- ▶ Self-Awareness
- ▶ Uncertainty Paradigm

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## Metacommunication

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### Synonyms

[Framing](#); [Simulative communication](#)

Metacommunication is a term developed by Gregory Bateson (1955/1972, 1956) to refer to signals that (intentionally or not) simulate other signals and, in obviously simulating, refer to those other signals for the signaler, the recipient, or both. Bateson conceived of some signals as natural indicators of some state, e.g., a baby's crying as an indicator of distress. If a baby simulated or re-created its cry when it was not upset (say, to play with making the sounds of crying or to get its caregiver to nurture it), the baby might emit the simulated cry in such a way that it was distinguishable (by the infant, by another, or by both) from a natural cry. Bateson viewed this evidence of the fact of simulation between the natural and simulated signals (i.e., this recognition of difference amid similarity or pretense) as itself a signal, communicating that the natural signal is being simulated. Critiques of Bateson's ideas argued that animals need not be aware of any simulation in play, and, indeed, many play behaviors are apparently not simulations (Mitchell 1990; Pellis 1988), though it seems likely that, e.g., some primates and canids are aware when they or others are simulating (see Mitchell 1991 for critiques and discussion). Almost identical ideas focusing on communicative simulations were developed apparently independently by Grice (1957) in his discussion of the development of Non-natural meaning (i.e., intending to communicate). Both authors viewed salient simulations as important in the evolution of human language, in that signals came to be used beyond their original ("natural") meaning and thus came to have a potentially dual meaning or function.

Although Bateson (1955/1972, 1956) viewed the term as applicable to a variety of simulations (including deception, imitation, pretense, threat: see elaboration in Mitchell 2002), he specifically singled out animal play as suggestive of metacommunication, as players simulate other activities, yet (apparently) recognize that these activities referred to in the simulations are not enacted, but instead playful versions are (e.g., when playfighting simulates fighting). Consequently, metacommunication in the animal literature has been almost exclusively used in discussions of play. In his elaboration of metacommunication, Bateson (1955/1972) developed the notion that implicit assumptions or signals that designate how to interpret messages are metacommunicative, calling these assumptions or signals "frames": "as in the case of the play frame, the frame is involved in the evaluation of the messages it contains, or the frame merely assists the thinker in understanding the contained messages by reminding the thinker that these messages are mutually relevant and the messages outside the frame may be ignored. In [this] sense... the frame is metacommunicative" (p. 188). In using Bateson's ideas to understand animal communication, Bekoff (1975) and others focused on metacommunication as framing, rather than as based on simulation (though such framing is only necessary if simulative metacommunication is not effective, i.e., if the simulation is not recognized as such). Metacommunication, in this view, was present when a signal that occurred prior to a behavior influenced the interpretation of that behavior. For example, a playface shown by a lunging primate just prior to the lunge allowed the lunger's play partner to expect play, rather than a fight. By this interpretation, metacommunication becomes indistinguishable from signaling. It is this use of the term "metacommunication" to refer to signaling in relation to other signals that remains prominent: e.g., even with simulative metacommunication present in "aggression-like elements" during play, authors take prior behavior that changes the meaning of subsequent behavior as evidence of metacommunication (Špinka et al. 2016). The playface is conceived to be necessary specifically because of the fact that the play

simulates fighting and might be misconstrued as fighting (although play faces are not always present during playfighting – Pellis and Pellis 1996). The playface is thus viewed as a natural signal of playful desire, much as crying is a natural signal of distress. Play signals themselves may be simulatively metacommunicative when they are used to signal play amid aggressive uses of playfighting (see Mitchell 1991; Pellis and Pellis 1996). Questions continue to arise as to whether play signals are natural (“emotive”), intentional (“cognitive,” “manipulative”), or both (Palagi et al. 2016; Pellis and Pellis 1996), suggesting that ideas about metacommunication in play still resonate with researchers unconcerned with Bateson’s formulations.

## Cross-References

- [Play](#)
- [Pretend Play](#)

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## Metamemory

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## Synonyms

[Memory awareness](#)

## Definition

The awareness of one’s own memory system through the monitoring and control of memory strength for previously acquired events or information. This awareness results in the knowledge of what one does and does not remember.

## What Is Metamemory?

Memory systems allow individuals to store and retrieve information that is gained through their senses. Like many cognitive processes, memory is prone to error and can be inconsistent and undependable. This is shown during daily experiences such as going to the store or trying to remember work to-do lists, and even in cases of eyewitness testimony. Humans, and potentially other species, recognize and understand this truth and are able to compensate for some of the fallibility of memory by developing an understanding of their own personal memory systems. This capacity to be self-aware of one’s memory

processes is known as metamemory. Metamemory allows someone to recognize what they are cognizant of and recognize the limits of that knowledge. It is a system that enables one to monitor and consider the strength of their own memory and plays a crucial role in situations that involve strategy, planning, and performance evaluation.

The term “metamemory” was first coined by Flavell (1971) and was analyzed in depth a few years later (Flavell and Wellman 1977). It could broadly be described as “knowing about knowing” (Brown 1975). When detailed by Flavell and Wellman, metamemory was separated into two major components: sensitivity and variables. Today, the variables category can be referred to as declarative metacognitive knowledge, while sensitivity is generally associated with procedural metacognitive knowledge (Schneider 2001). Declarative knowledge describes the explicit awareness of how variables may impact one’s memory. In humans, this can be assessed through interviews and questionnaires. The procedural component of metamemory is the capacity to monitor and regulate memory and can be evaluated by asking participants to describe the process they used to complete a memory task (Schneider 2001).

Each of these two major divisions of metamemory may then be further subdivided. Declarative (variables) memory knowledge can be categorized into three subsections: person, task, and strategy (see Flavell and Wellman 1977). More relevant to animal research on metamemory, procedural (sensitivity) memory knowledge can be subdivided into two categories: monitoring and control. Monitoring allows one to make self-assessments during information acquisition and retrieval of memories. This enables greater comprehension about what has been retained and how reliable recall and recognition of the information may be (i.e., retrospective monitoring). Monitoring of memories further allows recognition of information that will need to be remembered as well as understanding the boundaries of one’s future recall performance (i.e., prospective monitoring). Prospective monitoring may appear in multiple forms such as ease-of-learning judgments, judgments of learning, and feeling-of-

knowing judgments (Nelson 2001). On the other hand, control enables the regulation of information at points of acquisition and retrieval to aid in processes such as planning, decision-making, and presenting relevant memory enhancing strategies. As in prospective monitoring, feeling-of-knowing judgments can play a role in control, allowing one to quickly make a decision about whether or not a piece of information is stored within one’s memory before memory monitoring initiates (Nelson 2001).

In humans, metamemory is not an ability present at birth. Like many cognitive capacities, metamemory develops with age through continual exploration and learning about the world. Research has shown that metamemory appears around the age of 4–5 years and continues to improve throughout the formative years (Lockl and Schneider 2006). Longitudinal studies on metamemory have produced interesting results, such as demonstrating a decline in older age as well as gender differences. Gender differences include women reporting greater levels of strategy use, memory efficacy, and control (Hertzog et al. 2019).

Procedural metamemory appears to have gained a larger focus over the years. Common studies on metamemory in humans include feeling-of-knowing judgments, tip-of-the-tongue phenomena, source-monitoring judgments, and confidence judgments (Schwartz 1994). As one may expect, all of these tasks rely heavily on the use of language. This greatly impacts the ability to test preverbal and nonverbal humans as well as nonhuman primates and other species. The language barrier has been a constant struggle within comparative studies; however, researchers working with nonhuman animals have designed numerous approaches to answer questions about metamemory. The following sections will summarize and describe a portion of this work on metamemory.

## Assessing Metamemory in Animals

The study of metacognitive processes in animals began when abilities of a bottlenose dolphin were

investigated (Smith et al. 1995). From this study, metacognitive capabilities and subsequently, metamemory research, took off. While limited by the inability to use language as a tool to assess the memory system in animals, researchers have found many creative ways to explore some of the same judgments of memory that have been studied in humans. Today, there is a large focus on pigeons (*Columba livia*; Inman and Shettleworth 1999; Roberts et al. 2009) and primates (Call 2010; Fujita 2009; Hampton 2001) in nonhuman metamemory research. Other species, such as rats (*Rattus norvegicus*; Templer et al. 2017) have also been tested for this ability, albeit not as extensively.

A significant number of animal studies assessing metamemory aim to observe judgments of knowing and uncertainty. Many such studies utilize delayed-matching-to-sample (DMTS) or categorization techniques. Typical matching-to-sample studies present a subject with a stimulus and the subject must then choose the image or item they were just shown out of an array of distractor stimuli. DMTS incorporates an additional element where the subjects must wait a predetermined length of time after initially seeing the target stimulus and before seeing the stimuli they must choose from. This delay in time encourages subjects to use their memory system and has helped researchers to judge levels of uncertainty in subjects by allowing them to either provide an answer to a DMTS trial for a desired reward or opt out of the trial for a lesser reward (Hampton 2001; Sutton and Shettleworth 2008). Further assessing certainty, researchers have also developed categorization tasks with the same element of allowing subjects to answer or opt out of trials (Adams and Santi 2011; Smith et al. 2009).

Other common tasks to assess metamemory include information-seeking tasks that enable subjects to fill their gap in knowledge or confirm an answer by searching for the solution before solving (Basile et al. 2009; Call and Carpenter 2001; Hampton et al. 2004). This type of study allows researchers to observe whether subjects recognize if they are unaware of the answer and that it is not stored within their memory. Evidence of metamemory in this task would appear as subjects

participating in a solution search when they are uncertain of the answer but foregoing this search in times when they are already aware of the answer. Results are indicative of one's faculty to use memory as a prompt to seek information.

## Metamemory in Apes

In one of the earlier tests of metamemory involving nonhuman species, Call and Carpenter (2001) tested 2.5-year-old children, chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*) with an information-seeking task. The participants' goal was to locate a hidden food or sticker reward within one tube when presented an array of opaque tubes. In randomized trials, participants were able to see the tubes be baited or the baiting of the tubes was blocked by a barrier. Once baited, participants had the opportunity to look through the open ends of the opaque tubes in order to gain information about the contents of each tube. Overall, participants across species utilized efficient search strategies. In other words, when they observed the tubes get baited, participants tended to forego the search. However, during uncertain trials when baiting was blocked from view, participants were more likely to search the tubes.

In two independent studies, Suda-King (2008) and Suda-King et al. (2013) tested orangutans and gorillas (*Gorilla gorilla*) on object choice spatial memory tasks to observe decisions to opt out of responding during uncertainty. If individuals chose to decline a test, they would receive a guaranteed, but lower-valued food reward than if they chose to participate and gave a correct response. Researchers defined two criteria in their search for metamemory. First, subjects should have declined the test more often if the trial was considered to be difficult. Second, on trials where subjects may have chosen to decline the test (as opposed to forced trials), they should have shown higher accuracy in memory tests that they agreed to participate in. Supporting the first criterion, individuals of both species chose to not participate in more difficult memory tests during times when they were uncertain of the preferred reward location. Additionally, one individual



from each species satisfied the second criterion and performed significantly better during choice trials.

These promising results have not been without critique. Concerning uncertainty response tasks in which one may decline a test, Smith et al. (2009) believe subjects are able to recognize when it is effective to opt out by associating sets of stimuli in more difficult trials with the decline key, not because they can monitor their own mental state. In a critique of information-seeking tasks, Hampton et al. (2004) cited the generalized search hypothesis, stating that subjects may simply be searching for the reward until it has been located. In order to address these criticisms, Call (2010) utilized similar methods to the previously described Call and Carpenter (2001) study and tested all nonhuman great ape species (chimpanzees, bonobos (*Pan paniscus*), gorillas, and orangutans). In this three-experiment information-seeking task, researchers manipulated the information received (presenting auditory information via tube shaking or increased difficulty of visual searches with angled tubes), the interval between baiting the tube and choice selection to increase the potential of forgetting (and thus increasing uncertainty), and food quality (high versus low desired). As expected, auditory information and increased difficulty in visual search decreased information-seeking behaviors. Additionally, visual search increased when subjects were presented with higher stakes and with longer durations of time between baiting and retrieval. Results of this study further support the claims of metamemory and metacognitive abilities in apes.

Similarly, Beran et al. (2013) tested three enculturated chimpanzees in an information-seeking task. Utilizing the chimpanzee's training to name people, places, and items (including food) using pictorial symbols, the chimpanzees were tasked with naming food items placed in a container to receive the food as a reward. Critically, the subjects had the option to name the food immediately when asked or check the container where the food had been hidden before responding. When the food was made visible to the subjects, the chimpanzees were more likely to name the food item immediately without seeking any additional information. However, when the

food was not made visible to the subjects, they searched the container for the food item prior to naming it. Overall, the chimpanzee's information-seeking behavior suggested that they accurately remembered what they had or had not seen.

## Metamemory in Monkeys

Smith et al. (1998) had humans and rhesus macaques complete a serial probe recognition task in which they needed to decide whether a given stimulus had been or had not been in a serial list of two, four, or six images. As in previously described tasks (Suda-King 2008; Suda-King et al. 2013), the participants were given the opportunity to decline the presented test. Differing from the other studies, Smith et al. (1998) put a cost on their decline option in the form of time. For instance, the more an individual would decline a test, the longer the time delay would be before they would receive their reward. By giving the participants this punishment for using the option to opt out, the researchers assumed the chance to decline would be more sparse and more strategic. The results showed that the monkeys were sensitive to the fluctuating cost of the choice to decline. Additionally, they made more errors for stimuli in middle list positions, and this was also where they tended to decline taking the test most often. This suggested the monkeys recognized that they did not have a good memory for items in those list positions.

During a DMTS task, Hampton (2001) also allowed rhesus monkeys to opt out of completing the matching task. Here, the subjects would receive a lesser reward for declining a trial, as opposed to it resulting in punishment (Smith et al. 1998). Results showed that longer delays between the initial viewing of the target and the time when a matching choice needed to be made led to a decrease in accuracy and that the macaques chose to decline the tasks with longer periods of delay. Finally, high levels of accuracy were present when macaques chose to answer after long delays, compared to when they were forced to take the memory test. In combination with Smith et al.'s (1998) study, it appears that

macaques are sensitive to and can strategically utilize declining a test to optimize task outcome in both costly and beneficial scenarios. Overall, the shown pattern between decline responses and accuracy, combined with the increase of accuracy on chosen compared to forced trials, has been widely interpreted as a strong indicator of metamemory in nonhuman animals and the results have been held as a standard to indicate prevalence in other species as well.

Adapting the methods of Call and Carpenter's (2001) study with children and apes for rhesus macaques, Hampton et al. (2004) found similar abilities to those reported for the apes. When asked to locate a food reward between four opaque tubes, the rhesus macaques would strategically peer into the tubes when they were uncertain about the food's location (because they had not seen the baiting). In an impressive computerized study, Kornell et al. (2007) showcased both monitoring and control aspects of metamemory. Experiment 1 presented subjects with the chance to signal high or low certainty on various memory tasks, resulting in monkeys showing high-confidence on correct trials and low-confidence on incorrect trials. In Experiment 2, when given a sequence remembering task, macaques had to touch images in the order they were presented and could request hints at the cost of a food reward. Results showed that the subjects possessed control strategies and would request fewer hints when they could possess greater certainty. Together, these results indicated that rhesus macaques are able to differentiate what they know from what they do not know.

In another adaptation of Call and Carpenter's (2001) methods, researchers observed the tendency for capuchin monkeys (*Cebus apella*) to seek information (Basile et al. 2009). As before, the monkeys were given the chance to peek in opaque tubes and were tasked with picking the one containing a reward. Unlike young children, apes, and rhesus macaques, the capuchins did not increase their rate of information seeking when they did not see the experimenter bait the tube, signifying they are unaware of what they do not know. In another version of a DMTS task with a chance to opt out due to uncertainty, capuchin monkeys potentially showed some ability to

monitor memory trace strength (Fujita 2009). However, these results do not demonstrate strong evidence of metamemory as in apes and rhesus macaques. It is generally acknowledged that, to date, capuchins have not been able to show a solid representation of this ability. However, more research will need to be conducted to determine if this is a failure in task design or if there is a divide within primates and truly indicative of the absence of ability.

## Metamemory in Non-Primate Species

As in rhesus macaques, pigeon metamemory is highly studied, although the results are not nearly as conclusive. Some of the more prominent studies using pigeon subjects also involved DMTS tasks (Inman and Shettleworth 1999; Sutton and Shettleworth 2008). Inman and Shettleworth (1999) presented pigeons with a DMTS task that permitted subjects to gain six food pellets for the correct answer on a memory test or opt out of the memory test and choose a safe key, rewarding them with three pellets and the chance to bypass potential failure. The pigeons occasionally opted out of difficult trials; however, alternative interpretations could not be ruled out and the inconsistent results across individuals were deemed to be not indicative of metamemory.

Another DMTS task presenting pigeons with the chance to opt out of a problem came to a similar conclusion, as uncertainty responses that were made were not aligned with the strategies expected as a result of metamemory (Sutton and Shettleworth 2008). Combining methods conducted with primates, one study consisted of a computerized test that allowed pigeons to seek information before being given a DMTS task (Roberts et al. 2009). This four-part task asked whether pigeons would choose to "study" the target stimulus in a DMTS task by choosing an option indicating desired information or choose to move directly to the DMTS task without seeing the stimulus they would need to select after the delay to obtain a reward. Roberts et al. (2009) found the pigeons would continually forego seeing the target stimulus, which ultimately suggests the absence of metamemory.

Producing similarly weak results of metamemory, Adams and Santi (2011) trained pigeons on a duration matching-to-sample task to peck response buttons to classify short 2-s and longer 8-s light durations or indicate uncertainty and opt out of answering. During select trials, the pigeons would complete (or opt out of) memory tests after a retention interval (ranging from zero to 60 s) was inserted between the light duration and their classification task. This study further opposed the results found in rhesus macaques and overall, it appears no study thus far has supported this ability in pigeons. While it is easier to say pigeons don't possess the capability, like with capuchins, it is possible that this is a methodological failure to find an appropriate task to showcase the species' potential.

Studies with rats have expanded the possibilities of metamemory testing and its implications. Using uncertainty response experiments adapted for rats, researchers tasked their subjects with memory monitoring and observed the rats' responses when given the chance to opt out of a difficult task (Templer et al. 2017; Yuki and Okanoya 2017). Both studies offered subjects the choice to solve the presented problem for a greater reward or choose to decline answering, receiving a lesser reward while potentially signaling a diminished confidence in memory. Templer et al. (2017) tested subjects with a DMTS task while Yuki and Okanoya (2017) utilized delayed matching to position methods where subjects were required to remember a specific location and relocate it in a two- or six-choice task after a short time delay. Results from both experiments show that rats would participate in the tests they could have more confidence in and declined the memory tests where confidence would have been lower. However, in the case of the delayed matching to position task (Yuki and Okanoya 2017), these results were only seen in rats that completed the six-choice task. Rats given the two-choice task did not strategically use the possibility to decline tests.

In summary, there is varying strength of evidence for the potential capacity of metamemory in multiple species, including rhesus macaques, apes, and rats (Call 2010; Hampton 2001; Templer et al. 2017). Conversely, capuchin

monkey and pigeon studies have provided equivocal evidence indicating limited metamemory, if present at all (Fujita 2009; Roberts et al. 2009). The deficit of demonstrated metamemory in these two relatively intelligent species speaks to the complexity of metamemory. Overall, if the goal is to simply find evidence of metamemory processes that have developed in nonhuman animals independent of language, it does appear that there are positive results. Continued testing is needed to better understand the abilities within the animal kingdom, especially within the primate order, which shows mixed results between species. Further research may uncover a greater indication of capacity and whether these are legitimate species differences or task-specific.

## Controversies in Studying Metamemory in Animals

Across the various studies of metamemory, there is disagreement about the mechanisms behind this behavior in nonhuman animals. The longstanding debate is around whether positive results of metamemory should be explained by associative or cognitive principles (e.g., Crystal and Foote 2011; Hampton et al. 2004; Kornell et al. 2007; Smith et al. 2009). Some argue that reinforcement history (Crystal and Foote 2011) and memory trace strength of the primary representation (Adams and Santi 2011) are the mechanisms that should be attributed to metamemory behaviors. These associative explanations rely on a default response rule that selects for the behavior with the highest response strength. Sometimes this behavior appears metacognitive in nature (e.g., opting out of difficult trials), but does not posit the awareness necessary for metamemory. Crystal and Foote (2011) believed that researchers must be conservative and parsimonious when explaining the root of metamemory in nonhuman animals. According to Crystal and Foote, cognitive explanations are more complex than associative ones and, aligning with Occam's razor, cognitive explanations should be reserved until all associative principles have been eliminated as possible explanations. Like Crystal and Foote's position, hypotheses drawn from work done with pigeons

(e.g., Inman and Shettleworth 1999) also credits associative principles as the mechanism for metamemory behaviors in these nonhuman animals. They also put forth that memory trace strength acts as a discriminative stimulus (Inman and Shettleworth 1999), which allows pigeons to use a signal detection model to maximize rewards during metamemory tasks – an associative explanation of metamemory.

On the other hand, researchers such as Call (2010) and Smith et al. (2009) argue that metamemory (and metacognition more broadly) is a higher-order and controlled cognitive process. They view metamemory as a flexible decisional process in nonhuman animals (monkeys, apes, and a dolphin) and related to humans' reflective mind and consciousness (e.g., Smith et al. 2009). Other researchers (e.g., Basile et al. 2015; Hampton 2009) do not take such a hard stance in this debate and argue that metamemory in nonhuman animals is driven by multiple mechanisms to varying degrees. From their perspective, whether metamemory behavior derives from an associative or cognitive mechanism is less important than identifying the specific cues that support this behavior. They argue that the mechanisms for metacognitive behavior, including metamemory, can be both internal and external. Although, similar to Crystal and Foote (2011), internal cues should only be inferred once external stimulus control can be ruled out as the driving force for behavior (Hampton 2009). Hampton and colleagues (e.g., Basile et al. 2015; Hampton 2009; Templer et al. 2017) hold the position that both *public* cues and *private* cues may elicit metamemory behavior. Potential public cues prompting metamemory include response competition (including a generalized search strategy; e.g., Call 2010; Hampton et al. 2004), environmental cue associations, behavioral cue associations, and rote response learning, while private cues involve introspective monitoring of explicit memory or fluency effects (Basile et al. 2015). After ruling out various external sources of stimulus control, Basile et al. (2015) argued that metamemory in rhesus macaques can likely be attributed to an internal memory monitoring hypothesis. This hypothesis involves memory

strength serving as a discriminative cue for monkeys' metamemory behavior and is both associative (memory trace strength as a discriminative cue) and cognitive (monitoring of memory trace strength) in nature. Templer et al. (2017) suggested that metamemory in rats is also likely based on internal cueing from memory strength and not solely external stimulus control.

Kornell et al. (2007), however, took a different intermediary viewpoint of what the mechanisms of metamemory are. They do not support that metamemory behaviors can be explained simply by stimulus control, but also do not support metamemory as a conscious and self-reflective behavior in monkeys (or humans). Instead, they argue that metacognitive errors in memory tasks with monkeys result from unconscious inferences from task fluency while completing tasks.

## Conclusion and Implications

As described in the previous section, there are multiple contrasting opinions about the psychological mechanisms that best explain the presented results across a variety of species. Despite these differences, studies of metamemory in nonhuman animals have led to a variety of methods to test for this phenomenon in nonverbal ways. Continued metamemory research with nonhuman animals will help facilitate new methods to test explicit memory and the neural basis of metacognition in humans (Basile et al. 2015; Templer et al. 2017). These studies also provide a means to better understand the evolution and phylogenetic organization of metacognition. Further testing will determine if memory awareness is a widely distributed cognitive capacity among primates (i.e., human adults and children, apes, and monkeys) and its potential to have evolved multiple times through convergent evolution in other distant species (e.g., rats and dolphins; Hampton et al. 2004; Smith et al. 2009). Adaptively, metamemory would facilitate optimal foraging behaviors in these nonhuman animals, as just one example.

Studying metamemory in nonhuman animals also shines a light into the nature of animal minds

and intelligence. Given that metacognition is believed to be an aspect of self-awareness (Sutton and Shettleworth 2008), metamemory may broadly reflect animals' ability to understand their own and other's minds (Suda-King 2008). Additionally, studying metamemory from a comparative lens potentially provides information about nonhuman animals' consciousness, reflectiveness, and subjective experience (Basile et al. 2015; Smith et al. 2009). Overall, metamemory behaviors in nonhuman animals are functionally similar behaviors to the verbal, reflective processes in humans, and potentially the precursors of human metacognition and consciousness.

## Cross-References

- [Consciousness](#)
- [Episodic Memory](#)
- [Memory](#)
- [Meta-cognition](#)
- [Self-awareness](#)
- [Theory of Mind](#)

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## Metatherian

### ► Marsupial Diet

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## Metatherian Locomotion

### ► Marsupial Locomotion

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## Methylation

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### Definition

Methylation is defined as the addition of a methyl group to proteins and DNA by a group of enzymes called methyltransferases.

## Introduction

Methylation occurs both on DNA as well as on proteins. The reaction is catalyzed by group of enzymes known as methyltransferases. Methylation marks are reversible. Methyl marks are removed by another group of enzymes known as demethylases. Methylation is also involved in modification of heavy metals. Balance between level of methylation and demethylation regulates expression of genes, regulation of protein function, and processing of RNA. S-adenosylmethionine (SAM) acts as a donor of methyl group for addition by methyltransferases.

## DNA Methylation

DNA methylation is a process by which methyl groups are added to the DNA molecule. Methylation can change the activity of a DNA segment without changing the sequence. When located in a gene promoter, DNA methylation typically acts to repress gene transcription by preventing the binding of transcription factors either directly or through recruitment of methyl binding proteins and formation of repressor complex. DNA methylation takes place on those cytosine residues which are followed by guanine, generally known as CpG islands. It is catalyzed by DNMTs (DNA methyltransferases) that transfer methyl group from S-adenosylmethionine to cytosine residues. DNMTs are broadly categorized into de novo DNMTs and maintenance DNMTs. The de novo DNMTs, DNMT3a and DNMT3b, establish initial methylation patterns on previously unmethylated DNA, and the maintenance DNMT, DNMT1, establishes methylation patterns on hemimethylated replicating DNA. DNA methylation is an important regulator of various neuronal functions like memory formation and stabilization.

DNA methylation is also essential for normal development and is associated with a number of key processes including genomic imprinting, X chromosome inactivation, repression of transposable elements, aging, and carcinogenesis.

## Protein Methylation

Methylation of histones is widely studied among protein methylation. Methylation occurs at N-terminal tail of histone lysine and arginine and involves three different possible variations – mono-methylation, dimethylation, and trimethylation. These different forms of methylation influence chromatin structure differently and regulate expression either positively or negatively. Histone methylation is catalyzed by histone methyltransferases (HMTs) which add methyl group, while histone demethylases (HDMs) remove methyl group from specific arginine or lysine of histone H3 and H4. HMTs have a conserved SET (Suppressor of variegation, Enhancer of zeste, Trithorax) domain and are divided into seven families SUV39, SET1, SET2, EZ, RIZ, SMYD, and SUV4-20. This classification is based on the presence of different domains of protein along with the conserved SET domain. HDMs are divided into two classes: amine oxidase type lysine specific demethylases (LSD) and JumonjiC domain containing histone demethylases (JMJC). Histone methylation is implicated in memory and central nervous system (CNS) function. Methylation of histones can either increase or decrease transcription of genes, depending on which amino acids in the histones are methylated and how many methyl groups are attached. Methylation events that weaken chemical attractions between histone tails and DNA increase transcription by enabling the DNA to uncoil from nucleosomes due to which transcription factors, proteins, and RNA polymerase can access the DNA. This process is critical for the regulation of gene expression that allows different cells to express different genes.

## Cross-References

- [Amino Acid](#)
- [DNA](#)

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## Michael Domjan

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## Biography

Michael Domjan is a prominent figure in the field of animal learning and comparative psychology, with major contributions spanning a 40-year period. Domjan's area of expertise is Pavlovian conditioning and its ecological and evolutionary bases. His empirical studies have focused primarily on conditioned taste aversion in rodents and conditioned sexual behavior in birds. His work is highly significant in that it bridges two areas of inquiry – animal learning and evolution – that have historically lacked empirical and theoretical synthesis. Furthermore, he has challenged many long-held assumptions about how humans and nonhumans learn.

Domjan was born in 1947 in Budapest, Hungary. In the aftermath of the Hungarian revolution in 1956, his family fled to Austria. After spending a year in Switzerland, the family settled in the United States with the help of a Rockefeller Foundation grant to his father, who was a prominent artist. Soon after arriving in New York, he and his brother were enrolled in the preparatory division of the Juilliard School of Music. However, his parents were concerned about him making a living as a musician and encouraged him to consider alternatives. He became fascinated with conditioning and learning at the Behavior Science Institute, a summer science program for high school students sponsored by the National Science

Foundation. Domjan spent the next five summers as a staff member of the Behavior Science Institute at Western Michigan University, working with Neil Kent and many of the pioneers of Applied Behavior Analysis. He also spent some time on the staff of the Fort Custer State Home, where Louise Kent had started an Applied Behavior Analysis program.

At the advice of Dr. Ron Hutchinson, Domjan entered the biopsychology doctoral program at McMaster University in 1969, where his focus turned to studies of Pavlovian conditioning. McMaster had a vibrant community of scholars working on issues of learning. Domjan worked in the laboratory of Shepard Siegel but was also heavily influenced by Bennett G. “Jeff” Galef and Herb Jenkins. Domjan began graduate school soon after Garcia’s groundbreaking discoveries of selective associations and long-delay taste aversion learning (Garcia and Koelling 1966), both of which were topics of extensive debate in the learning labs at McMaster.

### Early Work on Conditioned Taste Aversion

What made conditioned taste aversion (CTA) such a seemingly unusual phenomenon is that it did not conform to the characteristics of other types of conditioning. Conditioned taste aversion has unique features, such as its single-trial requirement and long CS-US delay. Another unique feature, identified by Domjan, was that, in CTA, the participant initiates contact with the CS (the flavored solution), rather than the CS being experimentally controlled and unavailable for direct interaction. Domjan speculated that the unique features of taste aversions could be due to this, instead of CTA being a specialized form of learning, as was proposed at the time. Domjan tested this hypothesis by developing experimental protocols that allowed him to present taste stimuli in the absence of active approach and ingestive responses. For example, Domjan and Wilson (1972a) found that rats that did not directly interact with the CS, due to paralysis

induced by curare injection, developed weaker aversions to saccharin paired with lithium than did rats that were not paralyzed. Domjan subsequently improved the technique of testing the role of ingestion in CTA by developing an oral infusion procedure using a cannula. Bypassing the process of ingestion using this technique resulted in reduced aversion conditioning to saccharin, as was found with the curare experiment (Domjan and Wilson 1972b). Domjan subsequently utilized the oral infusion technique to study numerous CTA related and Pavlovian phenomena. Among Domjan’s greatest early contributions was his discovery of the roles that ingestion-related physical sensations play in the acquisition of CTA. These ingestion-related experiences seem to act as “gating” mechanisms that bind sensory cues to eating and drinking.

Domjan’s important work on CTA coincided with growing interest among learning researchers into the functional and adaptive features of conditioning. Garcia and Koelling’s (1966) work on CTA complemented the work of Paul Rozin on specific hungers. Rozin suggested that the forms of learning that investigators were studying at the time constituted adaptive specializations (Rozin and Kalat 1971). Martin Seligman (1970) suggested a complementary notion of preparedness of learning. In many circles, the field of animal learning was shifting away from general process examinations of learning and toward more ecologically informed conceptualizations. However, in the decade that followed these claims, relatively little data emerged that could actually support these new perspectives (Domjan and Galef 1983). Domjan’s next research program on conditioned sexual behavior sought to address this deficit.

### Conditioned Sexual Behavior

Domjan accepted a tenure-track position at the University of Texas at Austin in 1973. In the middle 1980s, he shifted his focus to studying Pavlovian conditioning of sexual responses using Japanese quail (*Coturnix japonica*) as a

model species. Leaving CTA work did not mean leaving behind the major theoretical issues that he had been working on. In fact, studying conditioned sexual behavior, which had received very little attention to that point, was very much related to the topic of adaptive specializations of learning. The past 30 years of work in this area has brought the field much closer to making direct, causal links between conditioning and reproductive fitness.

*Coturnix* quail turned out to be an ideal species for these studies. The full range of copulatory behaviors readily occurred, and could be recorded, in the laboratory. When introduced to a female quail, males will approach (sometimes pursuing aggressively) until contacting her, often by grabbing her neck feathers with his beak. Receptive females squat and allow the male to mount her back, and, while using his outspread wings for balance, the male will contact his cloaca with that of the female and engage in a brief, stereotyped thrusting movement that culminates with delivery of sperm into the cloaca of the female. The unconditioned sexual stimuli and responses they elicit were readily measureable. Keeping with the same approach as his CTA work, Domjan developed a CS with which the birds could directly interact. In many of his experiments, Domjan and colleagues used a CS consisting of a foam pad covered with terry cloth that was roughly the size of a female quail body mounted on a small piece of plywood. Adjacent to the “body” of the CS model was an elongated “neck” made of the same material. This model could be paired with copulatory access to a female quail, typically for a 5-min period. A CS object consisting of the model just described, but with a taxidermically prepared head of a female quail attached to the neck piece, was used to examine how a CS object that included a naturalistic cue or “sign stimulus,” and could support the full range of sexual behavior, influenced conditioning relative to a CS object that lacked any naturalistic features.

Falih Köksal, who was working in Domjan’s lab while on sabbatical from his position at Bogaziçi University in Istanbul, tested whether

the naturalistic CS would resist the blocking effect. The blocking effect is a highly repeatable, standard phenomenon observed in laboratory studies of learning in which conditioning to a CS is attenuated if a different CS that was previously paired with the same US is also present during conditioning. However, Köksal and Domjan found that the naturalistic CS was highly resistant to the blocking effect: Male quail showed strong conditioned responses toward it even when encountering it along with a previously conditioned arbitrary CS. This was a highly unusual finding. The blocking effect had been demonstrated in countless laboratory experiments using stimuli such as audio or visual cues: It was regarded as a well-established general learning process. So too were the phenomena of extinction, habituation, and attenuation of responding with second-order conditioning and other processes. However, results from studies that implemented the naturalistic CS often ran counter to general process learning theory predictions (reviewed in Domjan et al. 2004; see also Domjan et al. 2000). It would seem that Pavlovian conditioning of sexual behavior occurs in relation to its ecological relevance. That is, it is adaptively specialized. Ecological relevance also plays a role in fear and appetitive conditioning (Domjan and Krause 2017).

A widely cited and influential review by Domjan (2005) examined the functional utility of Pavlovian conditioning. Specifically, this work discusses how, in natural circumstances, CSs have a preexisting relation to the US, and, importantly, learning about responding to the biologically significant US is of greater evolutionary importance than is responding to the CS. Domjan (2005) applied this notion to numerous conditioning phenomena including lactation, poison-avoidance learning, drug tolerance, and eyeblink, sexual, and fear conditioning. These examples demonstrate the adaptive significance of Pavlovian conditioning without requiring a creative story to explain how the results make biological sense. The results make biological sense because the learning itself occurs in a biologically relevant context to begin with, and the learning directly

modifies how organisms interact with biologically relevant stimuli. Even more direct evidence for the adaptive significance of Pavlovian conditioning was demonstrated by Domjan and colleagues in numerous experiments showing that quail exposed to a Pavlovian cue prior to mating opportunities has fertility advantages over unsignaled animals (Domjan et al. 2012).

## Other Contributions and New Directions

In addition to his numerous research achievements, Domjan has generously served his university and professional psychological organizations. He was the psychology department chair (1999–2005) and the founding director of the Imaging Research Center at the University of Texas (2005–2008). He served as president of APA division 6 (Behavioral Neuroscience and Comparative Psychology) from 1999 to 2000, was president of the Pavlovian Society of North America (2006–2007), and was editor for the *Journal of Experimental Psychology: Animal Behavior Processes* (1986–1991). Domjan was also co-director of the NIMH training program in Neurobiology and Behavior at the University of Texas (1993–2003). Domjan's dedication to education and teaching throughout his career is evident from his authoring two widely adopted textbooks on conditioning and learning. His primary textbook, *The Principles of Learning and Behavior*, has been a staple of the field since 1982 and is now in its seventh edition (c 2015). His book *The Essentials of Conditioning and Learning* has been translated into Spanish, Turkish, and Arabic and is now in its fourth edition (c 2018).

In recent years, Domjan has rekindled his interest in music. After a 35-year hiatus, he went back to playing his Tertis viola and started teaching an undergraduate seminar in music and psychology. He also initiated the Tertis/Pavlov Project in which he explores connections between music and psychology through a series of instructional videos that are available on YouTube. These videos include titles such as “How is Pavlovian

conditioning relevant to music” and “What I learned in a music conservatory that made me a better scientist.”

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Bennett G. Galef](#)
- ▶ [Biological Preparedness](#)
- ▶ [Classical Conditioning](#)
- ▶ [Ivan Pavlov](#)
- ▶ [Taste Aversions](#)

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## Michael J. Beran

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### Early Life and Educational Background

Beran was born to Ellen L. and Robert A. Beran on August 11, 1973, in Middlefield, OH, but he grew up in Birmingham, AL, with one brother, Matthew. He received his B.A. in Psychology from Oglethorpe University in 1995, after some time as an accounting major, a business major, and a political science major (as well as at least one semester where he was undeclared!). Apparently what was required was the time needed to take courses in cognitive psychology and animal learning, and the realization that people could study both. He discovered this and his broader enjoyment of psychology because of the guidance of three faculty members, Nancy Kerr, Timothy Hand, and Adrian Brock. He received his M.A. (1997) and Ph.D. (2002) in the Department of Psychology at Georgia State University. His dissertation research focused on mathematical operations by chimpanzees and was conducted under the supervision of David A. Washburn, who he also routinely defeated at racquetball, basketball, and ping-pong, or at least that is how he remembers things. Additional mentors during his graduate career were Duane Rumbaugh and James Pate, and he is grateful to these three people for all they have done for him. He tries every day to pay that forward through work with his own students and other students who he works with. In his career, he is most proud of who those students have become.

### Professional Career

Beran took a research staff position at Georgia State University during the latter part of his graduate training, with support from NICHD and

support as the inaugural Duane M. Rumbaugh Fellow at Georgia State. He has remained at Georgia State University throughout his career, although he also spent time as a Visiting Lecturer at Spelman College from 2003 to 2007. He was a Research Associate and then Senior Research Associate at the Language Research Center of Georgia State before joining the Psychology Department at GSU as Associate Professor in 2015. He has authored more than 250 publications during his career including more than 150 peer-reviewed journal articles, which have appeared in outlets such as *Proceedings of the National Academy of Sciences*, *Psychological Science*, *Current Directions in Psychological Science*, *Current Biology*, *Journal of Experimental Psychology: General*, *Journal of Experimental Psychology: Animal Behavior Processes*, *Journal of Comparative Psychology*, *Animal Cognition*, and *Animal Behaviour*.

Beran has received several awards and recognitions. He is a Fellow of the American Psychological Association (APA Division 3 and Division 6) and the Psychonomics Society. He served as the President of the Southern Society of Philosophy and Psychology (SSPP), as well as serving as the Treasurer of that organization. He has served on the Executive Councils of the Southeastern Psychological Association and Division 3 and Division 6 of the APA, and he has been elected as President of the Southeastern Psychological Association. He received the Brenda A. Milner Award from the APA and the Richard M. Griffith Memorial Award from the SSPP.

Beran serves as the current co-editor of *Animal Behavior and Cognition* and is on the editorial boards of *Cognition*, *Frontiers in Comparative Psychology*, *Journal of Comparative Psychology*, *Comparative Cognition & Behavior Reviews*, *Learning & Behavior*, *Journal of Experimental Psychology: Animal Learning and Cognition*, *Animal Cognition*, and the *International Journal of Comparative Psychology*. His research has been supported by grants from the National Science Foundation, the National Institute of Child Health and Human Development, the European Science Foundation, and the Templeton Foundation.

## Research Interests

Beran and his students and collaborators focus on comparative cognition with an emphasis on nonhuman primates, particularly chimpanzees, capuchin monkeys, and rhesus monkeys, and human children and adults (Beran 2015; Beran and Heimbauer 2015; Beran et al. 2015a, 2016; Heimbauer, Beran, and Owren 2011). They sometimes work with other species, such as elephants, bears, gorillas, and orangutans.

Beran has assessed counting and arithmetic skills in nonhuman primates, human adults, and human children. His research has contributed to the notion that other species share with human an Approximate Number System (ANS), in which quantitative information including the numbers of items in sets can be encoded and represented, but with a degree of increasing inexactness as a function of true size, amount, or number (e.g., Beran 2001, 2007; Beran and Beran 2004; Beran and Parrish 2016). Among the many things that chimpanzees and monkeys have shown is that they can learn the values of Arabic numerals. They also can compare sets of items on the basis of numerosity, even when items are presented one at a time and the whole set can never be seen at once, and even when they have to compare auditory sets (hearing dropped items) compared to static visual sets (seeing all items at once). Sometimes, however, they show perceptual illusions about size similar to those seen in humans (Parrish and Beran 2014).

Beran also has made contributions to the study of metacognition in nonhuman animals (Beran, Brandl, Perner, and Proust 2012). Here, the question is whether animals may experience some sense of knowing what they do or do not know when faced with a decision. This is a difficult thing to assess in animals given the role of verbal reports in our understanding of human metacognition. However, certain experimental procedures have provided insights into the metacognitive skills of nonhuman animals (e.g., Beran and Smith 2011). For example, monkeys can be presented with various psychophysical and memory tasks for which stimuli can be categorized objectively as more difficult or less difficult for the animals based on task

performance. Animals also are given an additional response option, called the uncertainty response, that allows the animals to “escape” from choices that are too difficult or error-risking. In many cases, the animals use that response on exactly those trials for which the primary response is made least efficiently. This suggests that animals may monitor their own knowledge states when faced with decisions about how to respond to stimuli. Beran has focused particularly on chimpanzee metacognition (e.g., Beran, Smith, and Perdue 2013), demonstrating that these animals seek information based on what they know (or do not know), and they also provide measures of confidence in their own memory abilities. They do this by anticipating food reward for correct responses even before any external feedback is given to them – in essence by responding as if they know they are going to be correct or are not sure about that (Beran et al. 2015b).

Beran has studied future-oriented cognitive processes in animals and children. The ability to flexibly plan for the future has long been reserved for humans, and some have argued that animals are “stuck in time,” and they cannot think about the past or future because their behavior is affected only by their current needs and surroundings. However, animals may show capacities for mental time travel. Beran and his students and colleagues test nonhuman primates’ ability to anticipate future situations and plan future actions so as to determine continuities and discontinuities in the prospective memory and planning abilities of humans and other primates. This research has shown that nonhuman animals do have prospective memories and can anticipate future needs and remember to make responses in the future (e.g., Beran, Evans, Klein, Einstein 2012).

Beran also has spent his career learning about how nonhuman primates demonstrate self-control by delaying gratification. Delay of gratification occurs when one chooses to wait for something bigger or better rather than taking something that is available more immediately. Beran devised a way to use with nonhuman primates a task originally presented to children. In this task, animals learn that food items continue to pile up before them as long as they do not eat any. Thus, the

longer they wait, the more they get by delaying gratification. This simple technique has provided compelling evidence that chimpanzees show excellent delay of gratification (sometimes for periods in excess of 20 minutes with highly preferred food accumulating in front of them). Even rhesus monkeys and capuchin monkeys, traditionally viewed as more impulsive species, show some success with this task. Beran and his colleagues also have shown that chimpanzees can even use self-distraction to help aid delay of gratification (Evans and Beran 2007).

Ultimately, the “lab culture” that Beran tries to instill in these and other research programs is inspired by this quote from Edward Tolman in 1959 – “Since all the sciences, and especially psychology, are still immersed in such tremendous realms of the uncertain and the unknown, the best that any individual scientist, especially any psychologist, can do seems to be to follow his own gleam and his own bent, however inadequate they may be. In fact, I suppose that actually this is what we all do. In the end, the only sure criterion is to have fun.”

## Cross-References

- Addition
- Approximate Number System (ANS)
- Arabic numerals
- David Washburn
- Duane Rumbaugh
- Georgia State University’s Language Research Center
- Sarah, Lana, Sherman, and Austin)

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## Michael Tomasello

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## Introduction

Michael Tomasello (b. 1950) is an American psychologist known for his ground-breaking experimental studies of communicative development, cultural learning, and cooperation in humans and nonhuman primates. Since 2016, he has been Professor of Psychology and Neuroscience at Duke University. Tomasello's program of research has focused on the social-cognitive origins of uniquely human abilities and cultural inventions, such as language, complex tool use, advanced technologies, and social institutions. Several key themes have been emphasized. First, human language and gestural communication are acquired in contexts of social interaction and shared attention. Within these contexts of joint engagement, children are aware of their partner(s) and what they are doing together and can make sensible inferences about what their partner has in mind when communicating via speech or gesture. This ability to infer their partner's communicative intentions allows children to work out the meanings of words and their complex patterns of usage. As such, language development relies on children's use of sophisticated social-cognitive abilities rather than an innate knowledge of grammar.

Second, humans are experts in cultural learning and collaborative activity. Young children

grasp that interactions with their caregivers are generally cooperative, and they are motivated to help or play along. Children quickly come to understand that human social conventions, such as games and table manners, follow rules that are mutually agreed upon, and they are interested in learning to do things in culturally appropriate ways. Tomasello has contrasted children's apparent motivation to cooperate, share attention and mental states, and enforce socially established rules and moral codes with the more independent, problem-solving orientations of nonhuman primates, such as chimpanzees and orangutans. He has argued that human social interactions differ from those of other animals in that they are based on "shared intentionality," which includes the motivation to mutually understand conspecifics and share collaborative goals (Tomasello et al. 2005). Such collective, shared aims allow humans to work together on a daily basis in myriad ways, large and small, and provide the foundations for human culture and social institutions.

Tomasello's research contributions have been honored with numerous awards and prizes, including the Fyssen Foundation Prize for Cognitive Science (2004), Sir Frederic Bartlett Prize and Lectureship (2009), Heineken Prize for Cognitive Science (2010), Wiley Prize in Psychology for Lifetime Achievement from The British Academy (2011), and the Distinguished Scientific Contribution Award from the American Psychological Association (2015). Tomasello received the William James Book Award from the American Psychological Association for *The Cultural Origins of Human Cognition* (Tomasello 1999), the Cognitive Development Society Book Award for *Constructing a Language: A Usage-Based Theory of Language Acquisition* (Tomasello 2003a), and the Eleanor Maccoby Book Award from the American Psychological Association for *Origins of Human Communication* (Tomasello 2008). He received the Jean Nicod Prize for Philosophy of Cognitive Science (2006) with his lectures published with commentaries in a volume titled *Why We Cooperate* (Tomasello 2009).

## Biography

Tomasello obtained his Bachelor of Arts degree in Psychology from Duke University in 1972 and his Ph.D. in experimental psychology from the University of Georgia in 1980. His dissertation, conducted under the supervision of Ernst von Glasersfeld, was a diary study of his daughter's acquisition of verbs, later published as a monograph titled *First Verbs: A Case Study of Early Grammatical Development* (Tomasello 1992). In this monograph, Tomasello proposed the “verb island” hypothesis, which posits that grammatical development hinges on children's initial acquisition of individual verbs. As their vocabularies develop, young children begin to notice recurrent grammatical constructions associated with semantically related verbs, which they gradually redescribe in the form of more abstract rules and categories. Tomasello's proposal that grammatical knowledge is acquired in an item-by-item, piecemeal fashion from verbal input was a direct challenge to the nativist proposal, endorsed by Noam Chomsky and Steven Pinker among others, that an innate Universal Grammar (UG) underlies all human languages. In lieu of UG, Tomasello highlighted other cognitive abilities crucial for language learning, such as children's ability to partition complex events into constituent parts for word-to-world mapping. Tomasello emphasized children's ability to link expressions together, insert nouns into slots in verb argument structures, and draw analogies between words with similar combinatorial properties as providing the basis for linguistic generativity. In developing his Usage-based Theory of Language Acquisition, Tomasello borrowed ideas from cognitively oriented linguists, such as Ronald Langacker and Adele Goldberg, whose views he promoted in a series of edited volumes (Tomasello 1998, 2003b).

Upon completion of his doctoral studies in 1980, Tomasello joined the faculty of Emory University, where he remained until 1998. While at Emory, Tomasello initiated a series of studies exploring the social bases of communicative development, with a focus on joint attention,

imitation, and gesturing as precursors to language. Tomasello's socio-cultural framework was influenced by Jerome Bruner and Lev Vygotsky, who emphasized the social and cultural context of communicative development and viewed caregivers as providing a support system that scaffolded language acquisition. Under this view, children participate with others in routinized activities, such as reading picture books, which provide predictable formats for identifying the referents of words. In such contexts of joint engagement, children share their interests with others, while caregivers offer linguistic descriptions of direct relevance to what the child sees and has in mind. Over time, the dynamic of joint engagement shifts: young infants are supported by caregivers who “follow into” their activities (e.g., commenting on what the child is looking at), whereas at older ages children can effectively initiate bouts of joint engagement by proactively using gestures like pointing and showing, as well as vocalization, to share attention (Carpenter et al. 1998). Tomasello's studies highlighted how young children come to view others as intentional agents who engage in purposeful communication and how children gradually co-opt the communicative devices used by others for their own communicative purposes. For Tomasello, the child's ability to infer the intentions of others is the cornerstone of successful joint action and knowledge transmission and is an early manifestation of their tendency to view routine social interactions as inherently cooperative.

While at Emory, Tomasello became affiliated with the Yerkes Primate Research Center and began conducting comparative research on tool use, learning via imitation, gestural communication, and theory of mind in young children and apes, culminating in the volume *Primate Cognition* (Tomasello and Call 1997). Tomasello's observations of cross-species differences in the social transmission of knowledge led to the hypothesis that uniquely powerful forms of cultural learning in humans serve as a ratchet to prevent slippage of technological knowledge and accumulated wisdom over human history. Thus, according to Tomasello's “ratchet effect,” each



new generation assimilates the collective cultural wisdom and cultural tools developed by previous generations (Tomasello et al. 1993). These collectively created cultural settings and artifacts then form the milieu in which succeeding generations further develop their cognitive capacities through social learning in cooperative activities. In studies of tool use and gestural communication, Tomasello highlighted the ways in which non-human primates' problem-solving methods are akin to trial-and-error, with less attention or interest in the specifics of *how* someone else has solved the problem. Human children, in contrast, are especially interested in the means to the end, as evidenced by their propensity to "over-imitate" by including irrelevant actions in their efforts to perform tasks exactly as adults have modeled them (cf. Whiten et al. 2009).

Tomasello moved to Leipzig Germany in 1998, where he served as Co-Director of the Max Planck Institute for Evolutionary Anthropology and Co-Director of the Wolfgang Köhler Primate Center (appointment ending in 2018). Around this time, Tomasello began a new line of research on the social-cognitive abilities of dogs (e.g., Hare et al. 2002), advancing the "Social Dog, Causal Ape" Hypothesis that dogs have enhanced skills in reading humans' social and communicative behaviors (e.g., using human pointing to help locate hidden food) relative to apes. Tomasello posited that during the domestication process humans exerted selection for social communication skills in companion dogs, whereas in the absence of domestication, apes developed adaptations for individual foraging, which were more focused on physical causation than social-communicative processes.

Over time, Tomasello's research program shifted its focus from language acquisition toward greater emphasis on cooperation and collaborative activity as the foundation of human cognitive and cultural development. Tomasello illustrated the human propensity towards cooperativeness with findings that infants spontaneously offer altruistic help to adults who, for example, drop a book or need help opening a door (Warneken and Tomasello 2006). Nonhuman primates, in contrast, engage in rudimentary forms of cooperation,

yet rarely demonstrate altruistic resource sharing. In addition, during cooperative activities, when a partner stops collaborating (as an experimental manipulation), human toddlers make communicative attempts to reengage the partner in the shared goal, while chimpanzees do not, suggesting that a unique human form of shared intentionality is already evident in the second year of life.

In addressing the question of what separates human and animal cognition, Tomasello pitted the "general intelligence" hypothesis, which proposes that humans developed superior general cognitive functioning across all domains, against the "cultural intelligence" hypothesis, which argues that humans have species-specific social-cognitive skills that enable groups to invent cultural tools, symbols, and social practices. In comparing human toddlers with apes (chimpanzees and orangutans), Tomasello and colleagues observed similarities across species in cognitive skills for analyzing the physical world, but superior skills among children in cognizing the social world (e.g., social learning, communication, and theory of mind), which supported the "cultural intelligence" hypothesis (Herrmann et al. 2007).

Frans de Waal and others (2008) have questioned the "cultural intelligence" hypothesis, citing studies suggesting that nonhuman primates have greater cultural learning skills than apparent in Tomasello's research. In addressing this debate, Tomasello has never denied that nonhuman primates engage in social learning, while maintaining his argument that humans have evolved qualitatively more powerful forms of cultural intelligence and social learning that "bootstrap" the development of other cognitive capacities, such as language, from a young age. In recent years, Tomasello has acknowledged that non-human primates can exercise formidable theory of mind and intention reading. In considering human uniqueness, Tomasello argues that apes engage their social cognition in a competitive social milieu, reading the intentions and assessing the knowledge of other primates in order to better compete with them for limited resources such as food. Humans, in contrast, are an "ultra-social animal," far more adept than apes at developing shared goals and working toward them collaboratively.

## Conclusion

Working at the intersection of child development, cultural-historical development, and human evolution, Tomasello has made extensive and innovative use of comparative experimental methods to advance his hypothesis that powerful forms of social cognition distinguish humans from other species. His work emphasizes shared intentionality, defined as the ability and motivation to establish mutual understanding and shared goals in cooperative activities, as the critical factor underlying successful transmission of complex forms of knowledge, such as human language, over generations with sufficient stability to support cumulative cultural advancement.

## Cross-References

- [Andrew Whiten](#)
- [Cultural Transmission](#)
- [Frans de Waal](#)
- [Josep Call](#)
- [Primate Cognition](#)
- [Primate Communication](#)
- [Pro-Social Behavior](#)
- [Social Learning](#)
- [Wolfgang Köhler Research Center](#)
- [Yerkes Primate Research Center](#)

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## Microarray

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## Synonyms

[DNA array](#); [DNA chip](#); [Genechip](#)

## Why Do We Need a Microarray?

Biological systems are one of the most complex systems known to mankind. Thousands of gene and protein expressions change in tandem in

response to external and internal stimuli. For a biologist to be able to track all these changes simultaneously is no small task. Conventional techniques to track one gene or protein at a time are inefficient at best.

There is need for techniques that can track thousands of genes or proteins simultaneously. Time-efficient high throughput techniques are the need of the hour. Microarray is one technique that serves the purpose.

## What Is a Microarray?

A microarray refers to a technology in which “probes” (which detect “targets”) are arranged on a solid surface in the form of a two-dimensional array (Bumgarner 2013). Such an arrangement of multiple probes coupled with suitable detection method allows high throughput, multiplexed, parallel processing of samples to enable the researcher to detect changes in multiple analytes at the same time.

## How Does a Microarray Work?

The heart of the functionality of a microarray lies in its arrayed assembly. Multiple probes are arranged in the array in a position-specific manner so that exact location of each probe is known. Samples containing targets are labeled with a suitable detection reagent, like a fluorophore. When labeled samples are added to the array, probes would bind to their respective targets, in a specific manner. This arrayed assembly and specific binding is what makes a microarray “work” (Primrose and Twyman 2010).

Thus, the specifically bound target gets immobilized and the intensity of its fluorescent label indicates the abundance of that target. If more amount of a target is present in the sample, it would be bound and immobilized to a greater extent and would give a higher fluorescence reading. As the position of each probe in the array is known, the fluorescence coming from a certain position can be attributed to that particular probe and its specifically bound labeled target.

Probe and target depends on the type of microarray. DNA microarray is the most common. In a DNA microarray, short nucleotide sequences serve as the immobilized probe. Target comprises of labeled cDNA or genomic DNA or RNA depending on the application (Brown 2010). In protein microarray, capture proteins (including antibodies), ligands, or antigens form the immobilized probe while labeled proteins or small molecules form the target.

## History of Microarray

The idea of microarray was born with the development of antibody microarrays by Tse Wen Chang in 1983. This provided the base for the initial framework and concept of microarrays. Advancement continued at a slow pace till 1995, when Ron Davis and Pat Brown of Stanford University published a path-breaking paper in Science entitled “Quantitative Monitoring of Gene Expression Patterns with a Complementary DNA Microarray” (Schena et al. 1995). This gave impetus to the industry to develop “gene chips,” a fancy name for microarrays. Later, the microarray industry flourished with establishment of big-money companies and made innovative additions to the repertoire of microarray formats.

## Types of Microarray

There are different types of microarrays available in the market. DNA microarray, protein microarray, reverse phase protein microarray, carbohydrate microarray, antibody microarray, and transfection microarray are some of the well-known microarray types (Wilson and Walker 2005). Irrespective of the type, the underlying principle remains the same. The difference lies in the choice of probes and targets.

## Model Workflow of a Microarray Experiment:

The following workflow is a typical example of how a microarray experiment is executed. This example deals with gene expression profiling

using a DNA microarray, which is one of the most common uses of the microarray technique.

1. mRNAs are extracted and purified from control and treated samples.
2. mRNAs are reverse transcribed to cDNA (complimentary DNA).
3. cDNAs are labeled with detectable tags like a fluorophore. For single channel detection, all samples are labeled with the same fluorophore. For two-channel detection, distinguishable tags are necessary.
4. Labeled cDNAs are loaded on to the microarray chip to allow them to hybridize to corresponding probes.
5. Unbound and nonspecifically bound targets are washed off.
6. Bound cDNAs(targets) are detected using a laser scanning system.
7. Acquired data is normalized against reference standards and then analyzed to find out fold up-regulation or down-regulation in gene expressions.

### One-Channel Versus Two-Channel Detection

In the one-channel method, all the samples are labeled with the same tag. Only one sample is hybridized and detected at a time. Comparison is made between two samples that are detected separately.

In the two-channel method, samples to be compared are labeled with distinguishable tags. Two samples having dissimilar tags are mixed and simultaneously hybridized to the chip (which contains the arrayed probes). Abundance of both the tags (representing the two samples) is measured at the same time. Ratio of the signal from the two tags tells us about the relative changes in target expression between the samples.

Single-channel detection method suffers from batch variation and saturation effect. Samples are detected separately and the experimental condition for different samples may not be exactly identical. Thus comparing data from separate hybridization experiment may lead to erroneous

findings. In two-channel system, samples to be compared are used in a single experimental set up and hence can overcome this drawback.

Probes can also get saturated by targets in such a way that the difference in expression levels of targets goes unnoticed. Any difference in expression levels beyond the saturation level of probes would go undetected. In two-channel system, the ratio of the two tags provides information about the relative changes in gene expression and hence, there is no such issue.

One limitation of the two-channel system lies in the number of experiments needed to be performed. For comparing  $i$  number of samples, the number of experiments to be performed is  $i(i - 1)/2$ .

This means that two-channel system is not feasible if a large number of samples are to be compared, unless a reference sample is present (in which case number of experiments to be performed is  $i - 1$ ). One-channel system is the only option in such cases.

Accuracy of two-channel system may suffer due to difference in labeling efficiency between two fluorescent tags. One tag may label more efficiently than the other, leading to over-estimation of targets in that sample. One-channel system does not suffer from this limitation.

Moreover, in one-channel system, a single aberrant sample cannot affect the raw data derived from other samples, because each array chip is exposed to only one sample. In two-channel system, single aberrant data may obscure raw data of the second sample.

### Applications of Microarray

The basic principle of microarray has been expanded to put it to use for a multitude of purposes. By choosing appropriate probes and targets, a wide range of applications has been made possible.

- Gene expression profiling allows the researcher to find out relative changes in mRNA expression levels between samples.

Small nucleotide sequences are used as probes and cDNA derived from mRNA are used as targets.

- Comparative genome hybridization helps in analyzing copy number variations (CNVs) and genome content of patient samples or between closely related organisms.
- Single nucleotide polymorphisms can be detected by using probes that are specific to different variant forms of a gene. Such mutant forms may have implication in predisposition to diseases, drug response, and other physiological factors, and their detection can help in providing better medical care.
- ChIP-on-chip allows one to find out the genome-wide binding sites of transcription factors and DNA-binding proteins.
- Alternative spliced forms of genes may be detected using probes specific to exon junctions or individual exons. Fusion genes can also be detected using probes specific for chimeric transcript junction. Fusion gene detection is important in several cancers, such as BCR-ABL fusion gene.
- Protein microarray may help in discovery of novel biomarkers associated with certain conditions. Protein expression profile under different conditions may be explored. Protein-protein interactions, protein-ligand interactions can also be studied. Another important application of protein microarray is in detection of posttranslational modifications like phosphorylation, acetylation, and others.
- Reverse phase protein microarray uses immobilized cell lysates as the target and labeled antibodies serve as the probe. Cell lysates from different biological samples are arrayed on the chip, and antibody is used to probe and compare the abundance of any specific protein between the arrayed cell lysates.
- Peptide microarray uses short peptides as probes to pinpoint the position of epitopes or discovering key residues involved in protein-protein binding.

### Alternate Formats

Apart from the standard chip-based formats, bead-based microarrays are also available. Each bead contains a specific probe and is distinguishable by its unique ratio of two or more dyes that allows it to produce a characteristic and distinct color signature.

### Synthesis of Microarrays

Fabrication of microarrays can be done by a variety of methods. For DNA microarrays, there are two approaches. In spotted microarrays, the probes are presynthesized and then spotted on to the chip surface using robots. Alternatively, in situ manufacturing process is employed in which the oligonucleotide probes are directly synthesized on the chip.

### Future of Microarray

Microarray faces tough competition from RNA-Sequencing and mass spectrometry-based quantitative proteomic techniques. Microarray has a few significant limitations:

1. It is an indirect measure of the target abundance.
2. Signal is linearly proportional to the abundance only over a limited range.
3. It can only detect targets for which probes are available.
4. Mismatches are likely for sequences with high sequence homology or highly variable genomes. Different genes having high sequence homology may bind to the same probe. In genomes with high degree of variability, the designed probe may not be able to bind to its target due to sequence variation between the reference target and actual target.

All these factors make direct detection of target abundance a more sensible choice. RNA-Sequencing is able to directly read the nucleotide bases. Mass spectrometry-based quantitative



proteomic techniques allow simultaneous comparison of up to 10 samples.

With alternative techniques becoming more and more economical, microarray usage is bound to witness a slowdown. But still, microarray provides simplicity, versatility, customizability, and economy that are yet unparalleled. In all likelihood, microarray will still have its own niche usage and continue to be an important technique at the disposal of a researcher.

## Cross-References

- [Alleles](#)
- [Alternative Splicing](#)
- [Base Pair](#)
- [Bioinformatics](#)
- [Candidate Gene](#)
- [Chromosomes](#)
- [Copy Number Variant \(CNV\)](#)
- [DNA](#)
- [Gene Expression Profiling](#)
- [Genetic Variation](#)
- [Messenger RNA](#)
- [Primer](#)
- [RNA](#)

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## Microchiroptera Cognition

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## Definition

Cognitive abilities of laryngeal echolocating bats viewed through perception, learning, and memory.

## Introduction

Echolocating bats have been traditionally classified in the suborder Microchiroptera (microbats) within the order Chiroptera, although this classification has been recently modified on the basis of new molecular findings (Teeling et al. 2005). There are over 1000 species of echolocating bats including the sac-winged bats, the mouse-tailed bats, the horseshoe bats, the leaf-nosed and vampire bats, the free-tailed bats, the mustached bats, and the evening bats. These bats are smaller in body size than the nonecholocating fruit bats and flying foxes (formerly Megachiroptera) and have diverse diets, including insects, blood, fruit, nectar, and small animals. They use echolocation to identify and classify objects as prey or non-prey and to avoid obstacles in their flight paths. Because echolocating bats are nocturnal, hearing is their primary sense for orienting and foraging. Their cognitive capacities can be understood through how they use echolocation to learn about and perceive their environment. This review will approach the issue of cognition through studies of perception, learning, and memory; communication and navigation are addressed in other entries.

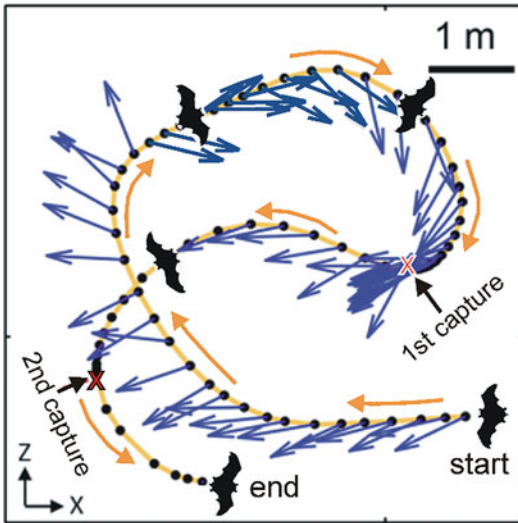
## Active Perception

Echolocation is an active sense by which bats make ultrasonic (20–100 kHz) sounds in their larynx, beam them into the environment through their nostrils or open mouths, and then process the returning echoes to form an image of (to “see”) their surroundings (Griffin 1958). Bats modify their echolocation calls in order to adapt to their immediate situation. They change the rate at which they emit these calls as they simultaneously pursue insects and avoid obstacles, and they change the direction in which they point their echolocation sound beam to ensoundify (“look at”) different objects in the environment. When and whether bats make these modifications depend on how much clutter (background or irrelevant objects) they must contend with (Moss et al. 2011). When many objects are present in the environment, for example, when chasing an insect in vegetation, the flying bat must separate out numerous echoes from various sources (the insect, the vegetation, other objects in the environment) arriving at its ears from multiple directions. This means that the bat must decide which echoes are relevant for foraging (those that represent the insect) and those that are relevant for orientation (those that represent vegetation and obstacles), and then coordinate its perception of these echoes with its control of flight in order to be able to make a successful capture without crashing.

Big brown bats (*Eptesicus fuscus*) pursuing a flying insect in an open, uncluttered environment will call progressively faster and faster, emitting from 10 up to 200 sounds per second with shorter and shorter interpulse intervals (100–20 ms) as they progress through the basic prey-interception sequence of search, pursuit, and capture (Simmons et al. 1979). Bats modify this basic sequence of sound emissions when flying and foraging in cluttered surroundings. In one experiment, big brown bats were challenged with flying in a large, dark flight room with multiple obstacles impeding their flight paths (Petrites et al. 2009). As the environment became more and more cluttered with obstacles, the bats called more and more rapidly, and the standard interception sequence changed as a result. When few obstacles

impeded their flight paths, bats made echolocation calls with interpulse intervals of about 40–100 ms, which are indicative of search and pursuit phases. Conversely, when many obstacles were present, interpulse intervals decreased to 15–65 ms, indicative of pursuit and capture phases. The duration of interpulse intervals is a metric of how perceptually challenging or difficult the bat finds its environment, and how rapidly it must update its image of the environment to stay on its flight path. Moreover, when flying in a cluttered environment but not in an open environment, bats emit their calls in discrete groups called “sonar sound groups” rather than in one smooth decreasing sequence. In a sonar sound group, groups of two, three, or four sounds are emitted close together at very short interpulse intervals (15–25 ms), and these groups alternate with groups of other sounds made at longer interpulse intervals (25–60 ms). Thus, a bat may make a cluster of four sounds separated by very short interpulse intervals followed by a cluster of two sounds separated at longer intervals. The bat repeats this alternating sequence of clusters of short interpulse intervals flanked by longer interpulse intervals until it reaches its goal. These sonar sound groups have been compared to strobe groups in vision and act in much the same way – to provide a burst of rapid images to allow continual updating of the internal percept of the environment (Moss et al. 2011).

The direction towards which the bat points its echolocation beam is another index of its percept of its surroundings. Bats can rapidly change the direction of their beam when hunting and orienting simultaneously in cluttered environments. For example, studies have shown that Japanese house bats (*Pipistrellus abramus*) can manage to hunt insects in a busy urban environment by directing their beam at multiple targets (insects, buildings, telephone poles, bridge supports) while simultaneously navigating in-flight (Fujioka et al. 2014). The bats were able to point their echolocation beams both in the momentary direction of their own flight and also towards the direction of the flying insect (Fig. 1). Moreover, they were able to direct their echolocation beam to new insects appearing in the immediate vicinity,



**Microchiroptera Cognition, Fig. 1** Horizontal-plane view of a looping flight path (start to end) followed by an individual Japanese house bat pursuing two small flying insects outdoors. The bat's flight path is traced by the orange line; its flight direction is shown by the orange arrows and the successive silhouettes of the bat. The blue arrows show the direction in which the bat pointed its echolocation beam each time it made a call. In this example, the bat captured two insects (1st capture, 2nd capture). The rapid change in direction of the echolocation beam shows evidence of the bat planning its flight to capture the second insect after it has encountered and captured the first insect. Total duration of the flight is less than 4 s. (Data are adapted and replotted from Fujioka et al. (2014))

suggesting that the bats were simultaneously planning their flight towards these new prey while still keeping the original prey and surrounding obstacles in view. These rapid shifts in the direction of the echolocation beam suggest that bats are able to divide their attention between separate objects and can anticipate when and where new objects might appear. Bats have an awareness of their environment and modify their echolocation behavior as a result.

### Individual Variability in Perceptual Strategies

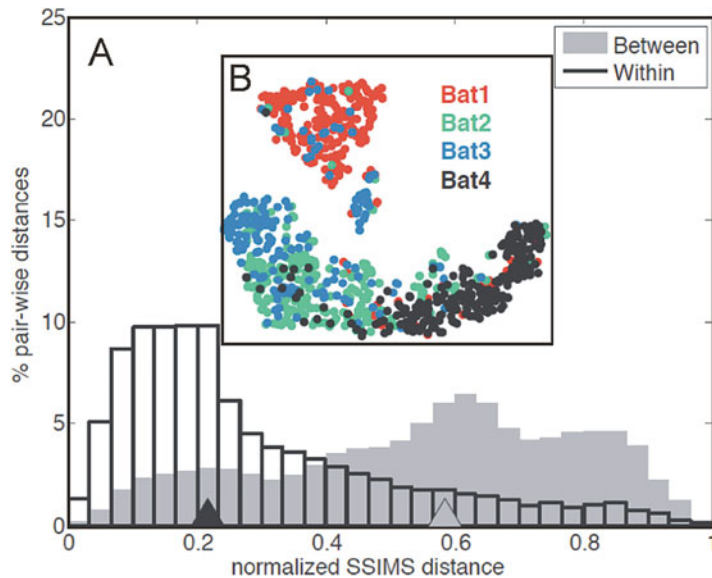
Individual bats face the challenges of their environment in unique ways. Even though all bats modify their echolocation behavior in the ways

described above – changes in interpulse intervals and in direction of the echolocation beam – individuals differ in the extent to which they make these modifications. For example, four bats flying through the same cluttered environment altered the pattern of interpulse intervals of their echolocation calls in different ways, even though all bats solved the orientation task successfully (Fig. 2). Some bats made sonar sound groups consisting of alternations of four calls with two calls, while other bats made sonar sound groups consisting of alternations of two calls with one call. Moreover, the bats' expectancy of their environment was reflected in how rapidly they made their calls. When the bats were challenged with flights through expected (matching that on the previous trial) compared to unexpected (new) obstacle arrays of different configurations, both their interpulse intervals and the pattern of sonar groups differed in the two environments (Accomando et al. 2018). All four bats made unique modifications, indicating that their individual expectancy of the environment altered their percept. This shows the flexibility of their behavior.

### Associative Learning

Echolocating bats have demonstrated the ability to learn in various instrumental tasks. They are readily trained in two-choice or go/no-go procedures for food reward. Using echolocation alone, bats can learn to discriminate objects differing in size, shape, orientation, and distance. They can also learn to associate a virtual (phantom) object with a specific location in space based solely on echo information. Bats can discriminate simple echoes (that is, containing one main reflection or "glint") from more complex echoes (containing many glints). This is likely achieved by analyzing and comparing the acoustic information in these echoes rather than by simply counting glints.

Bats' ability to learn is correlated with the complexity of their natural foraging behaviors. One study compared behavioral flexibility and rule-learning strategies in three species of the



**Microchiroptera Cognition, Fig. 2** Individual big brown bats emit echolocation calls in different patterns (sonar sound groups) while flying in the same challenging environment. **A** shows the output of a similarity (SSIMS) algorithm applied to the analysis of echolocation call patterns (interpulse interval timing and sonar sound groups) of individual bats. Lower values of the normalized SSIMS distance (x axis) show greater similarity. In this example, the normalized distance is more similar within (black outlines and triangles) than between (gray outlines and triangles) individual bats. The y axis shows the percentage of the total between-trial comparisons made (i.e., the relative

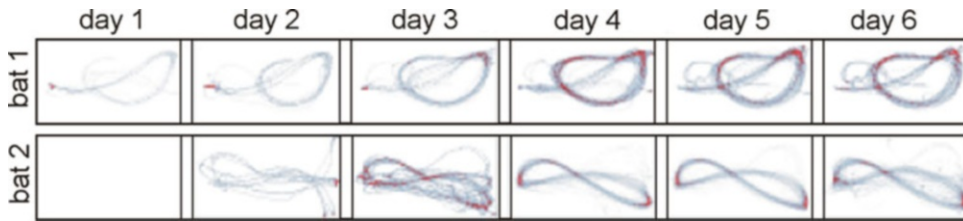
frequency of each normalized distance). The black and gray distributions are significantly different, showing that individual bats were internally consistent in their calling patterns, but that these patterns differed across bats. All bats completed the flights successfully. **B** shows the individual results for each bat (red = Bat 1, green = Bat 2, blue = Bat 3, and black = Bat 4). It is clear that the echolocation calls of each bat clustered differently in the similarity space, with very little overlap. (Data are modified from Accomando et al. (2018) by a Creative Commons Attribution License)

genus *Myotis* challenged with the same experimental tasks (Clarín et al. 2013). All three species learned a simple maze at the same rate and with the same success. But the performance of these three species differed when faced with a complex maze and when the rules for solving the maze changed. In the complex maze, the long-fingered bat (*Myotis capaccinii*), a species that hunts insects over open water, showed poorer performance than did Geoffroy's bat (*Myotis emarginatus*), a species that hunts insects in dense vegetation. When the rules for solving the complex maze were changed, Geoffroy's bat learned these new rules more quickly than the long-fingered bat. Hunting in dense vegetation is a more complex foraging strategy than hunting over open water because it requires bats to avoid more obstacles, to segregate more echoes, and to implement more complex flight paths. Bats using

the more complex strategy may require increased cognitive flexibility to find and locate prey.

## Social and Observational Learning

Bats are able to solve problems and gain information about the environment by observing other bats. Big brown bats, little brown bats (*Myotis lucifugus*), and pallid bats (*Antrozous pallidus*) can learn a novel feeding task simply by watching other bats perform this task (Gaudet and Fenton 1984). Bats can learn novel tasks from watching other bats perform, even when these novel tasks require reversal of a previously learned discrimination. Fringe-lipped bats (*Trachops cirrhosus*) prey on túngara frogs (*Physalaemus pustulosus*) and locate these edible prey by listening to the frogs' advertisement



**Microchiroptera Cognition, Fig. 3** Big brown bats flying in an unfamiliar flight room form individualized flight paths. The bats had to avoid obstacles in the room to maintain a steady flight path. Both bats were flown for 60 trials on each of 6 consecutive days. The flight paths (blue lines, red dots) were quantified by marking when and

where the bats made echolocation sounds. As time progresses from Day 1 to Day 6, the flight paths of the two bats become more distinct and more stereotyped. Although both bats flew successfully in the same environment, their flight paths are different. (Archival data from Barchi et al. (2013))

(mating) calls. The bats learn to associate the sound of the frogs' calls with edible food. Similarly, in the natural environment, these bats learn to avoid the advertisement calls of cane toads (*Bufo marinus*) because these toads are toxic. However, studies were able to show that fringe-lipped bats can learn to associate cane toad calls with edible prey instead of toxic prey, if they are rewarded with edible prey for approaching those calls. Moreover, naïve bats were able to learn this novel association between food and cane toad calls after observing bats who had already been trained, without having been explicitly trained themselves (Page and Ryan 2006). Neotropical short-tailed fruit bats (*Carollia perspicillata*) can also learn a preference for a novel food, this time from observing tutor bats within their roosts (Ratcliffe and ter Hofstede 2005). Because bats are social animals that roost, fly, and forage in groups, social learning is likely widespread across species.

## Memory

Because the operating range of echolocation is short and constrained by the physics of the attenuation of ultrasonic sounds in air, and because bats can fly quickly, having a sense of and memory for space would be extremely advantageous for orientation and flight. Many bats follow predictable routes when flying between their roosts and their foraging grounds. But, if novel obstacles are placed along these familiar routes or if familiar

objects are removed, the bats will crash into these objects or turn back. These behaviors suggest that bats have an internal map of their environment (Griffin 1981). How big brown bats might form such an internal map was examined in a series of experiments in which naïve bats were released over a series of days into a large, dark, unfamiliar flight room containing obstacles that the bat needed to avoid to maintain a steady flight path (Barchi et al. 2013). Each bat quickly developed an individualized, stereotyped flight path around the flight room that persisted over days (Fig. 3). When the bat was reintroduced into the flight room after a long absence, it immediately flew along this same flight path, indicating that it recognized the space and remembered its flight path through the space. These data are consistent with the hypothesis that bats have a spatial memory and an internal cognitive map of space. They also show individual variability in this spatial memory.

Even though insect-eating bats can form a spatial memory for orientation, when foraging, echo cues from prey (which give information on prey size and shape) take precedence over spatial (location) cues. Studies have shown that the insect-eating Natterer's bat (*Myotis nattereri*) bases its foraging decisions on echo cues rather than on spatial location cues when these two cues are put into opposition (Hulgard and Ratcliffe 2014). Because insects fly, their specific locations change continually, and so learning their spatial locations will not be as beneficial a strategy as learning their echo signatures and anticipating their flight paths. Spatial memory for location is



more salient for bats foraging on flowers and fruits. Pallas' long-tongued bat (*Glossophaga soricina*) feeds on nectar. These bats learn the locations of patches of flowers, likely using visual and olfactory cues, but will not revisit a particular flower within a patch until after sampling the other flowers in that patch. In this way, they can avoid foraging from a flower whose nectar has been recently depleted. When location (spatial) cues are put into conflict with echo (size/shape) cues, Pallas' long-tongued bats pay more attention to the spatial cues than to the echo cues (Thiele and Winter 2005). Foraging strategies impact the extent to which a bat uses its spatial memory.

## Conclusion

Echolocating bats learn to identify objects and to distinguish edible from inedible prey by associating echoes from these objects with their physical characteristics. While flying, they can shift their attention between simultaneous and sequential moving insect prey while still maintaining a flight path around obstacles. They can create and update internal maps of space. They can learn to respond to virtual echoes (that is, ones in which no objects are physically present). They can remember which flowers they have recently visited and which may still contain nectar. These are all important aspects of cognition. Other aspects of cognition have not been examined systematically in echolocating bats. It is not known, for example, if bats form categories of events apart from their ability to recognize and discriminate echoes.

Echolocating bats were used by the philosopher Thomas Nagel (1974) as an example of a mammalian species that experience their world and therefore have conscious mental states, even though these experiences are not directly accessible to humans. It is not known if bats are conscious or if they experience metacognition. But because echolocation is an active sense, bats must have an awareness of their surroundings in order to implement the dynamic changes in their calls and in their echolocation beams that occur in complex environments. The presence of strong individual differences between bats in how and

when they modify their echolocation calls and in how they represent space also suggests that these animals have individual awareness.

## Cross-References

- [Auditory Processing and Perception](#)
- [Auditory Signals](#)
- [Echolocation](#)
- [Foraging](#)
- [Memory](#)
- [Microchiroptera Life History](#)
- [Microchiroptera Morphology](#)
- [Microchiroptera Sensory Systems](#)

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## Microchiroptera Diet

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## Introduction

Microchiroptera is a traditional suborder of bats that includes all species that echolocate. No longer recognized as a suborder, the microbats are now split into Yangochiroptera (14 families, 158 genera, and 866 species) and Yinpterochiroptera, being represented in the latter by Rhinolophoidea (6 families, 17 genera, and 183 species) (Amador et al. 2016). Microbats encompass representative species from all bats' acknowledged diet categories. Most of the families are insectivores, but a lot of species feed on fruits (and seed/leaves), nectar

(and pollen), small vertebrates (including fish and other bats), several arthropods (e.g., scorpions, centipedes, spiders, crustaceans), and blood (Neuweiler 2000). The difference in feeding habits is so marked that in the earliest classifications proposed for Chiroptera, the former suborders Megachiroptera and Microchiroptera were, respectively, called Fructivorae, Carpophagen, or Frugivora and Insectivorae, Entomophagen, or Animalivora (Gardner et al. 1977). In Yangochiroptera, the largest variety of dietary specializations occurs in the family Phyllostomidae that, besides insectivory, includes frugivory, nectarivory, carnivory, and sanguivory. Curiously, the etymology of some bats' genus of this family reflects their feeding habits: *Diaemus* (*diaimos* (Gr.): blood-stained), *Musonycteris* (*musa* (Ar.): banana), and *Glossophaga* (*gloss-glossa* (Gr.): tongue + *phag-phago* (Gr.): to eat). The epithet *mordax* (La.) in *Lonchophylla mordax* and *Sturnira mordax* refers to biting. Many names (e.g., *Vampyrum*, *Vampyrops*, *Vampyrodes*, and *Vampyressa*) are associated with the initial idea that all bats fed on blood (Gardner et al. 1977). Vernacular names often refer to feeding habits as well. Some examples are “Common Vampire Bat” (*Desmodus rotundus*), “Great Fruit-eating Bat” (*Artibeus lituratus*), and “Vieira's Nectar-feeding Bat” (*Xeronycteris vieirai*).

## Dietary Categories

Despite the general classification of bats into several dietary categories, many of them do not restrict their diet just to one type of food (Table 1). Many insectivores, for example, also feed on other arthropods and may complement their diet with fruits and small vertebrates. Similarly, the frugivores may consume nectar, floral parts, and even insects (Rex et al. 2010; Monteiro and Nogueira 2011; Reis et al. 2017). Rex et al. (2010) demonstrated that phyllostomids are “opportunistic omnivores” and complement their primary diet with nutrients from many different food sources, which is important to satisfy the protein and carbohydrate requirements for growth, tissue synthesis, and

**Microchiroptera Diet, Table 1** Primary diet of microbats' families, including phyllostomid subfamilies

| Family           | Diet                     | Family          | Diet                     |
|------------------|--------------------------|-----------------|--------------------------|
| Cistugidae       | Insectivory              | Phyllostomidae  |                          |
| Craseonycteridae | Insectivory              | Carollinae      | Frugivory                |
| Emballonuridae   | Insectivory              | Desmodontinae   | Sanguivory               |
| Furipteridae     | Insectivory              | Glossophaginae  | Nectarivory <sup>a</sup> |
| Hipposideridae   | Insectivory              | Glyphoncterinae | Insectivory              |
| Megadermatidae   | Insectivory <sup>b</sup> | Lonchophyllinae | Nectarivory              |
| Miniopteridae    | Insectivory              | Lonchorhinae    | Insectivory              |
| Molossidae       | Insectivory              | Macrotinae      | Insectivory <sup>c</sup> |
| Mormoopidae      | Insectivory              | Micronycterinae | Insectivory <sup>d</sup> |
| Mystacinidae     | Omnivory                 | Phyllostominae  | Insectivory <sup>e</sup> |
| Myzopodidae      | Insectivory              | Rhinophyllinae  | Frugivory                |
| Natalidae        | Insectivory              | Stenodermatinae | Frugivory                |
| Noctilionidae    | Insectivory; piscivory   | Rhinolophidae   | Insectivory              |
| Nycteridae       | Insectivory <sup>f</sup> | Rhinopomatidae  | Insectivory              |
| Vespertilionidae | Insectivory <sup>g</sup> | Thyropteridae   | Insectivory              |
|                  |                          | Rhinonycteridae | Insectivory              |

<sup>a</sup>*Glossophaga soricina* is an example of omnivore specie

<sup>b</sup>Some *Megaderma* and *Cardioderma* eat small vertebrates

<sup>c</sup>Species of *Macrotus* can eat some fruits

<sup>d</sup>*Lamproncyteris brachyotis* is an example of omnivore specie

<sup>e</sup>There are some examples of carnivorous and omnivorous bats

<sup>f</sup>*Nycteris grandis* eats small vertebrates

<sup>g</sup>Some *Myotis* eat fish

reproduction. This ability to switch among several food types also helps them survive in periods of scarcity of their preferred food (Rex et al. 2010). Even so, some species are more food specialized and have a more restrict diet (e.g., *Dermanura*, *Pygoderma*, *Desmodus*) or consume just occasionally other resources (e.g., *Macrotus*, *Lonchorrhina*, *Trinycteris*) (Monteiro and Nogueira 2011; Reis et al. 2017). In these cases, the over-consumption of the same sources, such as fruits by herbivorous bats, may allow them to meet their protein requirements when eating a protein-poor diet. Bats also may adjust their diets to local and seasonal changes in resource availability (Rex et al. 2010).

The diet has been used, together with habitat and foraging mode, to classify bats into ecological guilds. According to Root (1967), “a guild is defined as a group of species that exploit the same class of environmental resources in a similar way.” This classification varies among authors, from simpler categories to more complex ones (e.g., Norberg and Rayner 1987; Kalko et al.

1996). More recent studies, however, do not take into account the diet on the guild classification “because echolocation and foraging behavior are mainly influenced by habitat type and foraging mode but not by the prey type” (Denzinger and Schnitzler 2013). Considering the importance of earlier guilds classifications, below we present data for the main dietary categories of microbats, classifying them primarily according to their predominant food consumed, but also addressing their foraging strategies and correlated morphological characteristics.

## Insectivores

Most bats feed on insects, but other invertebrates, such as crustaceans, spiders, and scorpions, may also be part of their diet. The taxa of insects most consumed by bats are Lepidoptera, Coleoptera, Diptera, Hemiptera, Hymenoptera, and Orthoptera (Kunz and Fenton 2005; Reis et al. 2017). The hardness of the prey eaten varies from soft (e.g., lepidopterans) to hard (e.g., coleopterans),

and the capacity of these bats to feed on harder prey depends on their skull size, teeth morphology, and bite force. Larger bats may consume a wider range of insects' sizes, including the hard-bodied ones (e.g., beetles) since they have more robust skulls and larger teeth (Freeman 2000; Aguirre et al. 2003).

The way bats capture their prey also varies; some species catch insects on the wing during flight (aerial insectivores) and others take prey from the substrate (gleaning insectivores). The gleaners generally locate their prey using the sound generated by them while the aerials use oral echolocation (Kunz and Fenton 2005; Santana and Cheung 2016). A more specific classification was proposed by Norberg and Rayner (1987) that described five foraging strategies for the insectivore's bats. The *fast hawking* comprises bats which rely on speed and agility to catch insects away from clutter, at high speeds and altitude, using echolocation to detect the prey at long range. As examples are some molossids, emballonurids of genus *Taphozous*, vespertilionids of genera *Nyctalus* and *Lasiurus*. The *slow hawking* comprises bats with a sustained flight, slow speed maneuverability, and agility that locate their prey by echolocation at short range. Some examples are *Emballonura* and *Rhynchonycteris* (Emballonuridae), many mormoopids, natalids, thyropterids, nycterids, megadermatids, rhinolophids, *Macrotus* (Phyllostomidae), and some vespertilionids (e.g., *Lasionycteris*, *Nyctophilus*, *Eptesicus*). The *trawling* comprises species that feeds opportunistically on many insects that swarm over water and species that actually have a more specialized pattern of trawling for aquatic insects. This is seen in many species of *Myotis* (e.g., *M. albescens*, *M. daubentonii*, *M. capaccinii*, *M. velifer*), in the noctilionid *Noctilio albiventris*, and in the phyllostomid *Macrophyllum macrophyllum*. The *gleaning* and *hovering* include bats that glean from the ground, requiring the ability to handle prey on the ground and often to fly off with it, and bats that hover briefly while searching for food or while gleaning from vegetation or trunks. Many vespertilionids present hover-gleaning (e.g., *Myotis evotis*, *Myotis myotis*, *Plecotus auritus*), some nycterids, *Craseonycteris thonglongyai*

(*Craseonycteridae*), and many of the smaller insectivorous phyllostomids. For the ground-gleaners, some examples are *Nycteris thebaica* (Nycteridae), *Antrozous pallidus* (Vespertilionidae), *Cardioderma cor*, *Megaderma lyra*, *Macroderma gigas* (Megadermatidae), and larger insectivorous phyllostomids (e.g., *Macrotus californicus*). This strategy allows bats to catch insects and other terrestrial arthropods before they run away and, like the hover-gleaners, they need slow and maneuverable flight. The large ears of some gleaners enable them to use low-intensity echolocation calls or to hear sounds from prey. The *flycatching* and *perch hunting* comprises bats that hawk flying insects by making short flights from a perch or use a perch while seeks non-flying prey, respectively. These bats have a good maneuverability, increased agility and, like gleaners, have large ears. The *perch hunting* is seen in some vespertilionids (e.g., *Nyctophilus bifax*) and megadermatids (e.g., *Cardioderma cor*, *Macroderma gigas*). The *flycatching* is seen in some rhinolophids (e.g., *Rhinolophus* sp.) and larger hipposiderids (*Hipposideros* sp.).

## Carnivores

Bats that regularly feeds on vertebrates (frogs, reptiles, small birds, and terrestrial mammals, including other bats), except fish, using a wide range of hunting strategies, including ambushing prey, capture in continuous flight and gleaning from substrates (Norberg and Rayner 1987; Kunz and Fenton 2005; Santana and Cheung 2016). All carnivorous bats are osteophagous, consuming the bones of their prey along with the soft tissues (Santana and Cheung 2016). They do not always rely on their nasal echolocation for prey discrimination and search in the passive mode (listening and vision) for prey moving on the ground (Denzinger and Schnitzler 2013; Santana and Cheung 2016). Kalko et al. (1999) noted that *Trachops cirrhosus* hunts in continuous flight, changing gradually to perch hunting, and capturing frogs by mouth. It includes few species, some of which are only partly carnivorous (e.g., *Nycteris grandis* (Nycteridae) and the phyllostomids *Phyllostomus hastatus*, *Trachops*

*cirrhusus*, *Chrotopterus auritus*, and *Vampyrum spectrum*; Norberg and Rayner 1987; Reis et al. 2017). Santana and Cheung (2016) highlighted that large body size is not a requirement for the consumption of vertebrate prey in bats, once *Micronycteris microtis* (a small phyllostomid bat; 7 g) has been documented to feed on small lizards.

## Piscivores

Some bats, such as *Noctilio leporinus* (Noctilionidae), *Myotis vivesi*, and *Myotis capaccinii* (Vespertilionidae), regularly eat fish, but also supplement their diets with arthropods, like aquatic and nonaquatic insects, and some crustaceans (Norberg and Rayner 1987; Ferrarezzi and Gimenez 1996; Kunz and Fenton 2005; Aizpurua et al. 2015). They have a greatly enlarged hind feet and sharp claws that they use to trawl the water surfaces (Norberg and Rayner 1987). Piscivores bats find their prey using oral echolocation, but fish can only be detected when they break the water surface, as bats cannot echolocate entirely submerged targets (Schnitzler et al. 1994). Schnitzler et al. (1994) show that *Noctilio leporinus* can discriminate between the acoustical glint pattern produced by a fluttering insect and from a jumping fish, which can also produce low-frequency splashing while leave and enter the water, and could alert the bats. Aizpurua et al. (2015) demonstrated that *Myotis capaccinii* “react only to targets protruding above the water and discern fish from insects based on prey disappearance patterns.”

## Frugivores

Although some bats eat fruit as an alternative food (e.g., *Mystacina tuberculata* (Mystacinidae), *Noctilio albiventris* (Noctilionidae)), frugivores belong primarily to Phyllostomidae, more specifically to Stenodermatinae, Carollinae, and Rhinophyllinae. *Carollia* and *Rhinophylla* feed on fruits of *Piper*, *Solanum*, *Vismia*, *Cecropia*, *Ficus* and complement their diet with insects

and other plant resources (Monteiro and Nogueira 2011; Reis et al. 2017). The dietary preferences of stenodermatines vary among genus, where some have most of the diet composed of fruits (*Enchistenes*, *Dermanura*, *Ariteus*, *Stenoderma*, *Centurio*, *Pygoderma*, *Sphaeronycteris*, and *Ametrida*) and other are more generalists and complement their diet with pollen/leaves/nectar and insects (*Artibeus*, *Sturnira*, *Chiroderma*, *Vampyriscus*, *Vampyressa*, *Vampyrodes*, *Platyrrhinus*, *Uroderma*, and *Mesophylla*) (Monteiro and Nogueira 2011; Reis et al. 2017). A specialized type of frugivory is seen in some species of *Chiroderma* (*C. doriae* and *C. villosum*) that feeds on seeds of *Ficus*, “ingesting the rich nutrient content of seeds and discarding most of the coat fragments as compact oral pellets” (Nogueira and Peracchi 2003). Some stenodermatines feed on leaves – *Artibeus planirostris* feeds at least 16 species of plant leaves in Caatinga (Cordero-Schmidt et al. 2016) and *Platyrrhinus lineatus* regularly consumes leaves in dry and wet seasons in a fragment of Atlantic forest (da Rocha et al. 2017). The size of the specimen is reflected in diet – smaller species tend to eat smaller fruits and larger species tend to eat larger fruits (Kalko et al. 1996).

Frugivorous species can be classified in three foraging guilds, “canopy frugivorous” (forage above 3 m from the ground, on fruits in the trees of the canopy and subcanopy; e.g., *Artibeus*, *Uroderma*, *Chiroderma*), “groundstory frugivores” (forage on fruits of shrubby plants, from 0 to 3 m above ground level; e.g., *Carollia* spp.), and “scavenging frugivore (or juicers)” (feed on very soft ripe fruit) (Kalko et al. 1996).

As in gleaning insectivores, they use sensory cues, mostly olfaction, to detect and glean fruits from foliage of trees and shrubs, and use echolocation mostly for orientation in space (Kalko et al. 1996). Some stenodermatines (e.g., *Sturnira* and *Artibeus*) are also reported to feed on ripe fruit fallen on the ground (Gardner et al. 1977). They usually must commute long distances between foraging and roosting places, thus contributing to seed dispersal, and most species cling or perch while feeding (Norberg and Rayner 1987).



## Nectarivores

Nectar-feeding bats are found in Phyllostomidae, more specifically in Glossophaginae and Lonchophyllinae. These bats are excellent hoverers, typically hovering while feeding, and are distinguished by their greatly elongated rostrum and tongues, which are used to access the nectar of plants (Kunz and Fenton 2005; Fleming et al. 2009). They pollinate flowers with particularly characteristics that “appear to have evolved to attract relatively large, nocturnal, color-blind, volant pollinators” (Fleming et al. 2009). These characteristics, called “chiropterophilous syndrome,” include musty/fetid odor (given by sulfur-containing compounds), drab coloration (e.g., white, brown, green, pink, fuchsia, yellow), which may function to stand out the flowers against foliage at the night or as a camouflage from other visitors, and nocturnal anthesis (“opening of flower buds in the late afternoon or at night”; Fleming et al. 2009).

The flowers visited by nectar-feeding phyllostomids are often large and robust, more tubular in shape, and produce relatively large amounts of hexose-rich nectar. An important characteristic that allows bats to access the flowers is their placement away from foliage, emerging on branches or tree trunks (cauliflory) or suspended on long stalks (flagelliflory), allowing bats easily find, approach and depart from them (Fleming et al. 2009). Among the families of plants visited by nectar-feeding bats are Bromeliaceae, Brasicaceae, Fabaceae, Lythraceae, Magnoliaceae, Malvaceae, and Solanaceae (Reis et al. 2017).

An interesting behavior is recorded to some species that can forage in groups and exploit the resource more efficiently by following leader bats, saving energy, since just the leader appears to use echolocation (Kunz and Fenton 2005). Besides nectar, many species (e.g., *Anoura geoffroyi*, *A. caudifer*, *Brachyphylla* sp., *Glossophaga soricina*, *Leptonycteris curasoae*) also consume and digest pollen and parts of the corolla of flowers. Fruits and insects are usually present in their diet (Gardner et al. 1977; Ferrarezzi and Gimenez 1996; Fleming et al. 2009; Monteiro and Nogueira 2011; Reis et al. 2017).

## Sanguivores

Also known as vampire bats, the sanguivores are represented only by three species, *Desmodus rotundus*, *Diaemus youngi*, and *Diphylla ecaudata*, from the subfamily Desmodontinae (Phyllostomidae). They feed nearly exclusively on blood, being perhaps the most specialized feeding habit found in bats (Ferrarezzi and Gimenez 1996) and, as a consequence of this specialization, they are also the most agile quadrupedal bats (Schutt and Simmons 2006). *Diphylla* and *Diaemus* are arboreal foragers, feeding preferentially on avian blood, which is obtained from perching birds, stalked from below as they sleep. *Desmodus* feeds on mammals' blood (e.g., bovids, equids, porcines, and domestic animals), foraging both on the ground and trees, approaching the prey from above (Ferrarezzi and Gimenez 1996; Schutt and Simmons 2006). These bats have “trigeminal nerve fibers that innervate specialized pit organs” on their face, providing “the ability to detect infrared radiation as a mean of locating hotspots on warm-blooded prey” (Gracheva et al. 2011).

According to Neuweiler (2000), *Desmodus* locates a highly vascularized area of its prey, as the neck and throat, wets it with its saliva, and then presses its lower jaw against the skin. It then brings the upper jaw teeth down and cuts away a piece of skin. The wound reaches down into the dermis and bleeds for a considerable time because the vampire continually prods the wound with its rough keratinized tongue, opening new capillaries, and their saliva contains substances that prevent clotting. When vampire licks, the lower lip rests against the edge of the wound and the grooves on the left and right underside of the tongue allows the blood to flow through the split in the lower lip. A blood meal lasts about 25 min and the vampire can ingest about half of its body weight.

An interesting behavior seen in vampire bats is the altruism. Vampires do not accumulate large fat reserves and can survive no more than 3 days without blood meal, so vampires that have fed will regurgitate a part of their blood meal not only for their young, but for other adult members

of the colony that have failed to obtain a meal (Neuweiler 2000).

## Morphological Characterization

The morphology of the skull and teeth in bats is strongly linked to their diet (Neuweiler 2000; Santana et al. 2011). Microbats are almost exclusively insectivorous, except for Phyllostomidae. In insectivorous bats, the premolars and molars are located far back in the jaw, just under the muscles of mastication, where the greatest force can be applied. The molars are dilambdodont (W-shaped), the upper are sharply serrated, with narrow triangular ridges and grooves that fit tightly on the lower teeth (Neuweiler 2000; Santana et al. 2011). The morphology of the skull is also relevant and is correlated with the degree to which hard (robust skull) or soft (gracile skull) items occur in their diet (Freeman 2000). The durophagy (*duro* = hard + *phagous* = feeding) evolved independently in five families (Molossidae, Vespertilionidae, Emballonuridae, Noctilionidae, and Phyllostomidae) that share some morphological features: “stout dentaries, tooththrows with fewer but larger teeth, the development of cranial crests, usually longer canines relative to maxillary tooththrow length, and usually wide skull widths relative to skull lengths” (Freeman 2000). On the other hand, the soft-items specialized bats present “long thin jaws, gracile skulls with little or no cranial crest development, more but smaller teeth, and smaller canines” (Freeman 2000). Piscivorous bats have a teeth morphology similar to those of insectivores and a short, broad, and tall rostrum (Santana and Cheung 2016).

The greatest variation of skull and dental morphology is observed in Phyllostomidae. From an insectivorous ancestor, four major ecomorphological novelties evolved – carnivory, nectarivory, frugivory, and sanguivory. Carnivorous bats have enlarged cusps on their molars and teeth that are larger relative to the size of the palate, features that may aid mastication of endoskeleton items (soft outside, hard inside). The skull is generally robust, with well-developed

sagittal crest (Freeman 2000). Nectarivores have the rostrum narrow and elongated, the teeth reduced (in number and size), and a specialized protractible tongue that may even exceed their body length and are covered with long hair-like papillae (in Glossophaginae) or have deep longitudinal grooves running laterally along their entire length (in Lonchophyllinae) (Reis et al. 2017). Frugivorous bats from Stenodermatinae have short and wide rostrum and specialized teeth for processing fruit, with the molars large and broad (enlarged transversely); Carollinae is less specialized, with a tooth morphology resembling those of insectivorous bats (Freeman 2000). Sanguivorous bats have large and sharp incisors, large canines, and a great reduction in size and number of molars. The rostrum is extremely short and they have lateral grooves on their tongues, which allow the blood to flow during the feeding (Neuweiler 2000; Reis et al. 2017).

## Ecological Importance

Due to their food habits, bats can play several important roles in the ecosystems where they live. Fruits and flowers, for example, are important components in the diet of many phyllostomids and some species, such as *Phyllostomus hastatus*, play an important function in both flower pollination (chiropterogamy) and plant dispersion (chiropterochory) (Gardner et al. 1977).

Indeed, bats can be considered the most important seed dispersers among mammals, which is associated with their great mobility and foraging habits (Reis et al. 2007). According to Galindo-González (1998), frugivorous phyllostomids usually forage long distances searching for food. Once the fruits are collected, they go to refuges to consume and digest them. They are able to consume and disperse seeds of several sizes; when eating fruits with small seeds, the bat can easily swallow the fruit and the seeds will be expelled, after digestion, at the refuge or somewhere else. On the other hand, bigger seeds that cannot be swallowed will be released at the refuge after the consumption of the fruit pulp. In both

cases the seeds are released far from where the fruit was obtained, favoring its dispersion. The chiropterochory occurs in several families of plants (e.g., Moraceae, Piperaceae, Arecaceae, Anacardiaceae, Sapotaceae, Solanaceae, Meliaceae) and several frugivorous phyllostomids (e.g., *Carollia perspicillata*, *Artibeus lituratus*, *Vampyroides caraccioli*) are responsible for neotropical forests regeneration, once they help plants with their reproduction, colonization, and settlement (Galindo-González 1998). Some species (e.g., *Carollia sowelli*, *Artibeus jamaicensis*) are also important in perturbed areas (e.g., affected by forest fires), contributing to the germination of pioneer and persistent plant species, such as *Solanum erianthum* and *Psychotria* sp., which in turn generate microclimates for the short-term establishment of other plant species, encouraging the succession process (Preciado-Benítez et al. 2015).

The chiropterogamy is extremely important for plants and some bats have a deep relationship with the plants they pollinate (Kunz and Fenton 2005; Fleming et al. 2009). *Glossophaga longirostris* has a mutualistic relationship with columnar cacti (e.g., *Stenocereus griseus*, *Pilosocereus tillianus*), acting as their main pollinator, and *G. soricina* is an important pollinator of endemic plants of Atlantic forest, such as *Dysochroma viridiflorum* (Solanaceae) and *Pitcairnia albiflos* (Bromeliaceae). An interesting example occurs with *Anoura fistulata* (subfamily Glossophaginae). This bat can extend its tongue twice as far as those of other nectarivorous bats, being the unique species that can reach and pollinate the 8–9 cm long corollas of the *Centropogon nigricans* (Campanulaceae), which appears to be an example of plant-pollinator coevolution (Muchhala 2006). In general, bats have an important role on pollination of nearby 500 species of plants in Neotropics, a lot of them with commercial value, as food (e.g., *Caryocar* sp., *Psidium* sp., *Musa* sp.) or as ornaments (Reis et al. 2007).

Insectivorous bats are important in the insect's population control. Some species can eat a huge number of insects on a single night, corresponding sometimes to almost twice its weight, and some phyllostomids can capture up to 500 insects per hour. Thereby, bats that usually feed on dipterans

can help on control of some diseases' vectors (e.g., *Aedes aegypti*) (Reis et al. 2007). Additionally, some bats (e.g., *Rhinolophus*, *Plecotus*, *Nyctalus*, *Myotis*, *Eptesicus*) act as natural pest controllers, eating many lepidopterans that are considered important agricultural pests (e.g., Noctuidae and Nymphalidae). This can provide a decrease of pesticide applications, also reducing the development of pesticide resistance, and some farmers in North America have been installing artificial roosts, such as bat boxes, trying to attract these bats for this service (Ricucci and Lanza 2014).

## Cross-References

- ▶ [Microchiroptera Locomotion](#)
- ▶ [Microchiroptera Morphology](#)
- ▶ [Microchiroptera Sensory Systems](#)

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## Microchiroptera Life History

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## Synonyms

[Bats](#); [Yimpterochiroptera](#); [Yangochiroptera](#); [Life cycle](#)

## Definition

Life history refers to the life cycle of an organism (how they are born, grow, reproduce, and die) and aspects that maximize their chance of survival and

reproduction, including morphological, physiological, and ecological traits.

## Introduction

Bats are mammals that belong to the order Chiroptera, which is the second most speciose group within the class Mammalia, only outnumbered by rodents. Bats can be found in nearly every part of the world inhabiting forests, savannas, tundras, mountains, deserts, urban and rural areas in temperate, subtropical and tropical latitudes, with the exception of polar regions and some oceanic islands (Vaughan et al. 2015). Bats are undoubtedly the most diverse group of mammals when it comes to feeding habits; their diet includes insects, other arthropods such as scorpions, spiders and centipedes, fruits, nectar, small vertebrates (e.g., fish, frogs, lizards, birds, and small mammals), and even blood (Vaughan et al. 2015).

Two features are responsible for the astonishing success of bats: they possess a sophisticated echolocation system and are the only mammals capable of true (or powered) flight. These traits promote good mobility and lead to the exploration of nocturnal niches that are largely unoccupied by other vertebrates (Altringham and Senior 2005). There are currently more than 1300 bat species classified in 21 families (Fenton and Simmons 2014; Foley et al. 2015; Amador et al. 2018). This number tends to increase at a rapid pace, and at least ten new species are described every year (Fenton and Simmons 2014). This great diversity is also reflected on morphology, ecology, social behaviors, and different attributes associated with the life history of bats.

## Microchiroptera x Megachiroptera

The order Chiroptera has been traditionally divided into the suborders Megachiroptera and Microchiroptera. Megachiroptera (megabats) contains just flying-foxes and fruit bats of the family Pteropodidae, usually large-bodied, non-echolocating species; while Microchiroptera

(microbats) comprises all remaining families of small-sized, laryngeal echolocating bats. However, this classification is outdated and does not reflect the evolutionary relationships of bat families, as shown by molecular studies (Springer et al. 2001; Teeling et al. 2005; Foley et al. 2015). Six families of microbats are more closely related to flying-foxes and fruit bats (Pteropodidae) than to the remaining families of microbats, what make Microchiroptera paraphyletic, hence Megachiroptera and Microchiroptera are artificial groups.

Bats are now classified based on molecular evidence into the suborders Yinpterochiroptera (containing the families Craseonycteridae, Hipposideridae, Megadermatidae, Pteropodidae, Rhinolophidae, Rhinonycteridae, and Rhinopomatidae) and Yangochiroptera (containing Cistugidae, Emballonuridae, Furipteridae, Miniopteridae, Molossidae, Mormoopidae, Mystacinidae, Myzopodidae, Natalidae, Noctilionidae, Nycteridae, Phyllostomidae, Thyropteryidae, and Vespertilionidae) (Springer et al. 2001; Teeling et al. 2005; Foley et al. 2015). The terms Megachiroptera/megabats and Microchiroptera/microbats are used in an informal way to distinguish and refer to Pteropodidae and the small-sized laryngeal echolocating bats, respectively.

## Natural History

Microchiropteran bats come in different shapes and sizes. The Kitti's hog-nosed bat, *Craseonycteris thonglongyai* (Craseonycteridae), is one of the smallest mammals in the world, weighting 2 g and with a wingspan of less than 20 cm, while the Spectral Bat, *Vampyrum spectrum* (Phyllostomidae), can weight more than 200 g and reaches a wingspan of nearly 1 meter (Vaughan et al. 2015).

Most microchiroptera families are insectivorous (e.g., Cistugidae, Craseonycteridae, Emballonuridae, Furipteridae, Hipposideridae, Megadermatidae, Miniopteridae, Molossidae, Mormoopidae, Mystacinidae, Myzopodidae, Natalidae, Noctilionidae, Nycteridae, Rhinolophidae, Rhinonycteridae, Rhinopomatidae, Thyropteryidae, and



Vespertilionidae). Greater Bulldog Bats, *Noctilio leporinus* (Noctilionidae), and some Mouse-eared Bats, *Myotis vivesi* and *M. macropus* (Vespertilionidae), use their large feet and claws to capture fish for food. Other vesper bats (*Ia io* and *Nyctalus spp.*) seasonally prey upon migratory birds, and Slit-faced Bats (Nycteridae) and False Vampire Bats (Megadermatidae) eat small vertebrates (Vaughan et al. 2015). New World Leaf-nosed Bats (Phyllostomidae) calls attention because they are the family with the most diverse feeding habits amongst all mammals: there are more than 200 phyllostomid species with several adaptations to frugivory (e.g., carolines, stenodermatines), nectarivory (e.g., lonchophylines and glossophagines), insectivory (e.g., micro-nycterines), carnivory (e.g., phyllostomines), omnivory (phyllostomines), and hematophagy (desmodontines) (Vaughan et al. 2015; Baker et al. 2016).

Microbats live in a great variety of natural environments, and some species can also adapt to inhabit urban areas. The urban landscape provides conditions for the establishment of bats, such as food resources (especially for insectivorous bats), and roost sites at human-made structures. Microbats are found in the wild roosting in caves, crevices, tree cavities, under tree bark, foliage, exposed on tree branches, or in any suitable shelters they find (Kunz 1982). Neotropical Disk-winged Bats (Thyropteridae) and Madagascar's Sucker-Footed Bats (Myzopodidae) possess suction discs and pads on their hind feet and wrists/thumbs to help roost inside the smooth surfaces of rolled leaves. Bamboo Bats, *Tylonycteris spp.* (Vespertilionidae), roost inside slits and cavities on bamboo stems, while the Hardwicke's Woolly Bat, *Kerivoula hardwickii* (Vespertilionidae) roosts inside modified leaves of pitcher plants. Some stenodermatine bats (Phyllostomidae) such as *Uroderma spp.*, and *Ectophylla alba*, modify leaves to make tents, and some phyllostomine bats (Phyllostomidae) such as the Greater Spear-nosed Bat, *Phyllostomus hastatus*, and Round-eared Bats, *Lophostoma spp.*, use their teeth to excavate arboreal termite nests where they may roost (Fenton and Simmons 2014).

As nocturnal animals, microbats forage mostly at night, but the time they emerge from their roosts

is variable among species; most emerge in the first hour after sunset, some a little earlier, and others later (Altringham and Senior 2005). Emergence time is related to vulnerability to predation, flight performance, feeding habits, and foraging strategies according to the species. Insectivorous bats usually emerge before dark when there is still some light available, and they can access diurnal and nocturnal insects (Altringham and Senior 2005).

The foraging area that bats use is also variable among species. Some microbats forage in small areas close to their roost, while others cover great distances every night when searching for food. Brown Long-eared Bats, *Plecotus auritus* (Vespertilionidae), forages only 1 km from its roost, while Brazilian Free-tailed Bats, *Tadarida brasiliensis* (Molossidae), forage up to 50 km away from their roosting sites (Altringham and Senior 2005). Bats can also forage alone or in small co-ordinated groups (e.g., *Phyllostomus hastatus*, *Rhynchonycteris naso*, and *Saccopteryx leptura*), according to the species (Altringham and Senior 2005).

## Life History

Life histories of microbats are very diverse in terms of life cycles, social systems, and mating strategies. Despite small in size, many aspects of their life history resemble those of large-bodied mammals: longevity, multiple reproductive events, few offsprings per pregnancy, intense parental care, and delayed onset of sexual maturity (Racey and Entwistle 2000). These traits are unusual for small mammals of similar size as bats (such as rodents), since they have rapid reproduction and high mortality rates.

## Social Systems

Sociability is a feature common to most microchiropteran bats, and social structure and social interaction play fundamental roles in their life history. Bats interact with each other using a wide array of sensory cues that include auditory,

**Microchiroptera Life**

**History, Fig. 1** A colony of Woolly False Vampire Bats (*Chrotopterus auritus*), a species that live in small family groups. (Author: Hugo Villela)



olfactory, tactile, and visual displays; and, although some microbats may be solitary, the majority of species are colonial (Fig. 1). Roosting in colonies may reduce predation risk through dissolution effect, reduce thermoregulation costs, and be beneficial in terms of cooperation and information transfer (Altringham and Senior 2005).

Colony size typically varies from few bats to a few hundred individuals, and larger colonies are found especially amongst cave-dwelling insectivorous species. Brazilian Free-tailed Bats, *Tadarida brasiliensis* (Molossidae), currently held the title of the largest mammal aggregations found in nature, and may form colonies of several millions bats in North, Central, and South America (Altringham and Senior 2005).

Colony size and composition may vary over time and suffer influence from many aspects such as mating strategies, seasonal changes in climate, food availability, reproductive status, and roosting ecology (Altringham and Senior 2005). Besides, social structures can be modified through fragmentation and fusion of groups, migration between harems and other types of colonies, spatial and temporal segregation of sexes and ages, weaning of juveniles, and other countless possibilities (Altringham and Senior 2005).

Some temperate zone species live in small groups formed by females and males (e.g., *Plecotus auritus*), and most species roost in

small colonies formed exclusively or mostly by females, with males living in small groups or solitary roosting (Altringham and Senior 2005). However, during hibernation, bats can roost alone, in mixed-sex or single-sex groups, and sometimes even in mixed-species groups (Altringham and Senior 2005). In many tropical and subtropical species, males form harems with females, such as in several New World Leaf-nosed Bats (Phyllostomidae) and Sac-winged Bats (Emballonuridae). On the other hand, a small number of species roost in pairs or extended family groups with their offsprings, such as some animalivorous False Vampire Bats (Megadermatidae) and New World Leaf-nosed Bats (Phyllostomidae).

The type of roost bats uses also influences the size a colony can reach (Altringham and Senior 2005). For example, thyropterids and myzopodids roost in temporary roosts such as rolled leaves, therefore they form nomadic small-sized colonies that must frequently relocate to new roosts when leaves unfurl. In contrast, bats that roost in permanent (e.g., caves) or long-lasting shelters (e.g., hollow trees) may form colonies of larger sizes (e.g., molossids, mormoopids, and vespertilionids).

Developed social behaviors are observed in the Common Vampire Bat, *Desmodus rotundus* (Phyllostomidae). They roost in colonies and die of starvation if they fail to feed in two nights, and,

### Microchiroptera Life

**History, Fig. 2** A colony of Common Vampire Bat (*Desmodus rotundus*), a species with highly developed social behaviors. (Author: Gabriela Rezende)



to avoid colony members from starving, bats share blood through regurgitation (Wilkinson 1990) (Fig. 2).

### Mating Systems

Like other aspects of their life history, microbats also have an astonishing diversity of mating systems. However, mating behaviors of bats, in general, are hard to be categorized because some classifications may be compartmentalization of a continuum instead of nonoverlapping categories (McCraken and Wilkinson 2000; Altringham and Senior 2005).

Mating systems can be categorized using many criteria such as the number of females and males within the mating group (composed either by single male/multiple females, multi-male/multiple females, or single male/single female), duration of association (e.g., groups are seasonal or persist year-round), compositional stability (e.g., a more or less stable female composition within harems), mating sites (e.g., in or away from the roost), and spatial distribution of sexes (e.g., in some species roving females visit males that roost alone) (McCraken and Wilkinson 2000).

Harems seem to be a common system for bats in general, and although most species show some form of polygyny (male mates with multiple females), polyandry (females mate with multiple males), promiscuity and monogamy are also present. In some species, there are even records

of multiple paternity and paternity outside mating groups. Besides, some species are not restricted to a single mating system, such as the Lesser Sac-winged Bat, *Saccopteryx leptura* (Emballonuridae), that is frequently monogamous but can also form harems (Altringham and Senior 2005).

Monogamy is reported for few microchiropterans and includes species that may roost in stable pairs, such as the Spectral Bat, *Vampyrum spectrum* (Phyllostomidae) and the Yellow-winged Bat, *Lavia frons* (Megadermatidae), but also gregarious species such as the Heart-nosed Bat, *Cardioderma cor* (Megadermatidae), that forms monogamous pairs within the colony (McCraken and Wilkinson 2000; Altringham and Senior 2005). In some species, the male and female remain together throughout 1 year, but during mating seasons new pairs are formed such as in the Benito Roundleaf Bat, *Hipposideros beatus* (Hipposideridae) (McCraken and Wilkinson 2000).

### Sexual Dimorphism and Mating Displays

Pronounced sexual dimorphism is rare among bats in general, and males and females are very similar in appearance. Usually, females are a little larger than males in most species of microbats. The size difference is remarkable in the Little White-shouldered Bat (*Ametrida centurio*), where males are much smaller than females

(17% of size difference) that they were once described in a separated species (Lee Jr. and Dominguez 2000).

Marked sexual dimorphism on qualitative external traits is also rare, and when present, males have more developed structures than females. On short-faced bats (a group of fruit-eating phyllostomids that also includes *Ametrida centurio*), it is common to find examples of notable sexual dimorphism: Visored Bats (*Sphaeronycteris toxophyllum*) has large fleshy protuberances above and between their eyes that are larger on males (Fig. 3). Wrinkle-faced Bats (*Centurio senex*), as its name suggests, have a naked face ornated with dermal outgrowths that are more prominent on males than those seen on females. Males Visored Bats and Wrinkle-faced Bats also possess a skin fold under their chin that extends to cover their faces, a feature rudimentary on females.

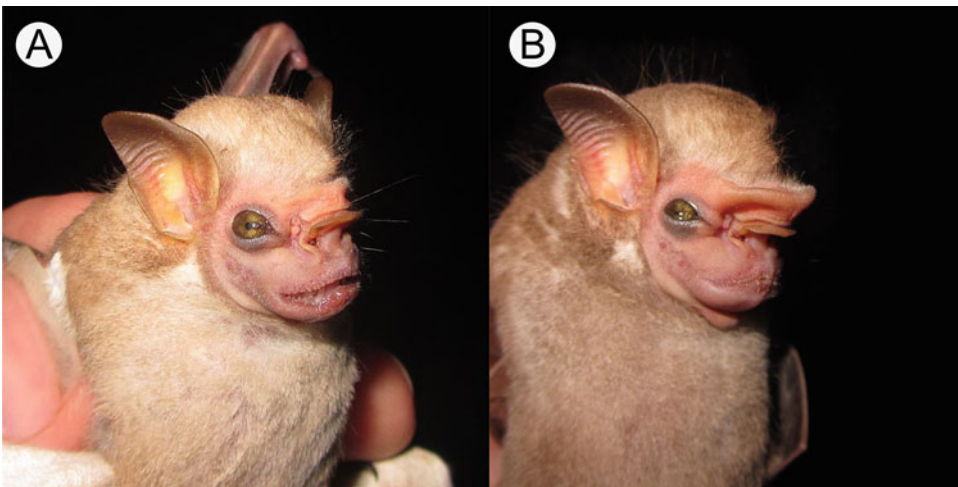
In microbats, males have several strategies to attract and mate with females, including vocalizations, olfactory clues, and visual displays according to the species. Territorial males can be aggressive with other males, and mark their territories with scents. In some species, however, males gather together to compete for female's attention using vocal and visual displays. In this behavior, known as lekking, the female chooses

the most attractive and healthier male to mate. Mating can be quiet and peaceful, but there are reports of males aggressively pulling females from a group and forcing them to copulate (e.g., *Tadarida brasiliensis*) (McCracken and Wilkinson 2000).

Scents play an important role in mating and also for communicating purposes. Glandular scent organs are present on the face, gular region, chest, ears, and other regions according to sex and the species (e.g., natalid organ in males Funnel-eared Bats (Natalidae) and eversible glandular organs in front of the noseleaf of males of some Old World Leaf-nosed Bats (Hipposideridae)) (Scully et al. 2000).

In some species, hairs associated with scent glands may retain and disperse glandular secretions. In Chapin's Free-tailed Bat, *Chaerephon chapini* (Molossidae), males possess a tuft of conspicuous hairs on their head, more prominent during reproductive seasons, that disperse scents produced by a gland at its base. Male Yellow-shouldered Bats, *Sturnira* spp. (Phyllostomidae), have shoulder glands associated with specialized shoulder hairs that retain and disperse glandular secretions, giving these bats their characteristic shoulder spots (Fig. 4).

A different strategy is seen on Sac-winged bats (Emballonuridae) that have sacs on their



**Microchiroptera Life History, Fig. 3** Visored Bats (*Sphaeronycteris toxophyllum*), a sexually dimorphic microbat. (a) Female and (b) Male. Note the size difference of the fleshy protuberance in their faces. (Author: Guilherme Garbino)





**Microchiroptera Life History, Fig. 4** Male (a) and female (b) Little Yellow-shouldered Bat (*Sturnira lilium*) captured during the reproductive season. Note the

conspicuous spots in the male's shoulder, where glands are associated with hairs that retain and disperse glandular secretions. (Author: Fred Victor de Oliveira)

propatagium and/or uropatagium, which do not have a glandular function but acts as fermentation chambers instead. In these sacs (less pronounced in females), males store and ferment saliva, urine, and other body secretions to produce scents. Males spread the scent during hovering flights to mark their roost surfaces and even females of its harem. This behavior, in addition to visual and vocal displays, serves to attract females and also to repel rival males (McCracken and Wilkinson 2000; Scully et al. 2000).

## Reproduction

Most bat species reproduce seasonally, and the timing is determined by climate and periods of optimal food availability. Reproduction is timed to ensure that lactation (or weaning in some species) occurs at the same time as the peak of food available (Racey 1982; Racey and Entwistle 2000). Bats from more stable environments where food sources fluctuate less throughout the year (as in tropical forests) may have aseasonal reproductive patterns. On the other hand, bats from regions where food supplies vary markedly throughout the year show pronounced seasonality in reproduction and may reproduce only during

periods of maximum food availability (Racey 1982; Racey and Entwistle 2000).

The reproductive activity of some species (insectivorous and frugivorous) in tropical environments may be associated with rainfall seasons (when food availability reaches its peak). Contrasting to sympatric bats of different feeding habits, reproduction of nectarivorous species, however, may mirror the flowering of plants, and females may give birth during the dry season instead (Racey and Entwistle 2000). In temperate zones, where climate varies markedly between winter and summer, the reproductive activity of bats is constrained by climate and food availability, since most species are insectivorous and insect availability reaches its peak during summer. Bats that inhabit seasonal environments but rely on stable food resources, such as vampire bats, may also be able to reproduce year-round (Racey and Entwistle 2000). The timing of male reproduction may also correspond with climatic and food seasonality. At temperate latitudes, spermatogenesis corresponds with the peak of insect availability, and in tropical species, it corresponds to rainfall season with high food availability (Racey and Entwistle 2000) (Fig. 5).

There are many reproductive patterns reported for microbats. Temperate species (mostly





**Microchiroptera Life History, Fig. 5** Male Pale Spear-nosed Bat (*Phyllostomus discolor*). In many tropical species, spermatogenesis occurs during rainfall seasons, when food availability reaches its peak (note the conspicuous testicles). (Author: Fred Victor de Oliveira)

Horseshoe Bats (Rhinolophidae) and Vesper Bats (Vespertilionidae) have seasonal monoestry, where females have a single litter during one specific climatic season. (Racey and Entwistle 2000). However, in tropical species, there are at least ten different patterns that range from restricted seasonal monoestry (e.g., *Nycteris thebaica* (Nycteridae)) to aseasonal polyoestry (e.g., *Molossus ater*, *Chaerephon pumilus* (= *Tadarida pumila*) (Molossidae)). Aseasonal polyoestrous species have a variable number of litters per year, and females estrous is not synchronized, hence young are born throughout the year instead of in a single climatic season (Happold and Happold 1990; Racey and Entwistle 2000). The cycles of males and females may also be synchronized; males may have a single peak of spermatogenesis when females are monoestrous, two peaks when females are dioestrous, and an extended period of spermatogenesis or be fertile the whole year when females are polyoestrous or aseasonal breeders (Racey and Entwistle 2000).

As in other mammals, during copulation, males will transfer sperm to fertilize the egg released by females during ovulation. In some species, males may store sperm after spermatogenesis and, after mating, females may store



**Microchiroptera Life History, Fig. 6** A pregnant Riparian Myotis (*Myotis riparius*). (Author: Nathália Louzada)

viable sperm within their tracts for even periods of several months (Crichton 2000). Most sperm-storing species are seasonal breeders from temperate regions, where their reproductive cycle is interrupted by hibernation. The sperm stored by hibernating species retains its viability through the course of the hibernal period (for up to 10 months), and some nonhibernating tropical species may also store sperm. Sperm storage is reported in the families Rhinolophidae, Vespertilionidae, Miniopteridae, and Molossidae, but it may also occur in other families such as Rhinopomatidae and Emballonuridae (Crichton 2000; Racey and Entwistle 2000).

The cells will start to divide after fertilization, and the process of implantation connects the embryo to the circulatory system of its mother, which will provide nutrient and oxygen support and the removal of metabolic wastes. Embryo implantation may occur a few days after fertilization (e.g., Vespertilionidae) up to almost 2 weeks (e.g., Noctilionidae) (Fenton and Simmons 2014). If fertilization and implantation take place correctly, the female will then be pregnant (Fig. 6).

Pregnancy in bats is considered long for mammals of their size. Gestation length varies among species but also within a single species due to developmental delays (Fenton and Simmons 2014; Badwaik and Rasweiler 2000). Female bats from temperate latitudes (Rhinolophidae

and Vespertilionidae) and some species in the tropics (e.g., Miniopteridae and Phyllostomidae) display some form of delay in their reproductive cycle. They are capable of delaying ovulation, fertilization, implantation, and even the development of embryos (Racey 1982; Racey and Entwistle 2000). These strategies, and also sperm storage, are used to ensure that the timing of birth coincides with the season of optimal resources for lactation and growth of newborns.

Embryo development is delayed in temperate species once bats enter torpor or hibernation, but, in tropical/subtropical species, delays may occur by alternative mechanisms (Tuttle and Stevenson 1982). In light of these circumstances, lengths of gestation range widely among microbats, from circa of 40 days up to 11 months (Tuttle and Stevenson 1982).

Female bats give birth to large pups, and the average body mass of the neonatal microbat is more than 20% of the maternal body mass. Horse-shoe Bats (Rhinolophidae) have the highest neonatal body mass among microbats, and newborns weight an average of 28.8% of their mother's body mass (Kurta and Kunz 1987). Despite their relatively large size at birth, young microbats are functionally altricial: most species are born naked, with eyes closed, have limited thermoregulatory abilities, and are dependent on their mothers for nutrition (Kurta and Kunz 1987; Kunz and Hood 2000) (See [Thermoregulation Challenges and Postnatal Growth](#)).

Most bat species give birth to a single offspring per pregnancy, and few species frequently produce twins (e.g. *Eptesicus fuscus*) (Fig. 7). However, bats from the genus *Lasiurus* (Vespertilionidae) have the largest litter sizes among Chiroptera and give birth up to four offsprings per gestation. While bats from temperate latitudes tend to have a single reproductive event within a year, many species from less constraining environments (tropical regions) increase their reproductive potential by exhibiting postpartum oestrus, hence increasing the number of offsprings they can produce in a year (Badwaik and Rasweiler 2000; Racey and Entwistle 2000). Some species, as the Indian Pigmy Bat, *Pipistrellus tenuis* (= *Pipistrellus mimus*) (Vespertilionidae), constantly produce



**Microchiroptera Life History, Fig. 7** A male and two females Seba's Short-tailed Bat (*Carollia perspicillata*), each with its offspring. (Author: Daniele Pedrosa)

twins and can give birth up to six young within a year (Suthakar Isaac et al. 1994)

## Lactation and Parental Care

After pups are born, the female microbats provide parental care until weaning age, in the form of nutritional and non-nutritional forms of care. Non-nutritional care includes protection, sensory stimulation, thermal influence, pup retrieval and transport, while nutritional care involves lactation and provision of other food supplies for the young (Kunz 1982; Kunz and Hood 2000).

Female bats possess a pair of mammary glands and nipples located close to their armpit, which serves to feed milk to the young (Fig. 8). In *Lasiurus* spp. and *Otonycteris* spp. (Vespertilionidae), however, there is an additional pair of nipples (Simmons 1993). In the Thumbless Bat, *Furipterus horrens* (Furipteridae), the pair of nipples is located in the abdominal region, just above the genitalia, unlike all other chiropterans (Uieda et al. 1980).

Juveniles also use nipples as an attachment point to their mother's body (Fig. 9). In some species, females also possess an additional pair of pubic nipples to serve as anchoring points. Pubic nipples are present on females of several families of microbats: Craseonycteridae, Hipposideridae, Megadermatidae, Rhinolophidae,



**Microchiroptera Life History, Fig. 8** The nipple of a lactating female Seba's Short-tailed Bat (*Carollia perspicillata*). (Author: Nathália Louzada)



**Microchiroptera Life History, Fig. 9** A female Seba's Short-tailed Bat (*Carollia perspicillata*) hanging upside down with its young attached. (Author: Daniele Pedrosa)

lactating purposes, they are associated with lacteal tissue in at least some species of Rhinolophid, Hipposiderid, and Rhinopomatid bats (Simmons 1993). Pubic nipples are polymorphic for males in some species, where they can be present or absent.

In many species, juvenile bats may remain attached to its mother almost continuously, have multiple suckling events, and females even transport them while foraging (e.g., many New World Leaf-nosed Bats (Phyllostomidae)). This behavior is uncommon in other species (mostly small insectivores), where young are not constantly attached to their mothers, and suckling events are not frequent. In these species, females leave their offsprings at roosting sites when emerging to forage and feed them after returning and later on a regular schedule (Kunz and Hood 2000). When foraging, some females often leave their young at sites that are different from their day roosts (e.g., Slit-faced Bats (Nycterids) (Fenton and Simmons 2014)).

Most females only allow pups to suckle if recognized as their young. Nursing mothers roosting in large colonies may rely on spatial memory, acoustic, tactile, olfactory, and visual clues to distinguish their offspring from others (Kunz and Hood 2000) (Fig. 10). Some pups may try to steal milk from unrelated females and, in some species, females sometimes nurse unrelated offsprings as they approach weaning age (e.g., *Nycticeius humeralis*) (Kunz and Hood 2000).

Young bats use milk teeth (deciduous teeth) shaped like small hooks to attach to their mothers. This shape is unique among mammals, where milk teeth usually have form and function similar to permanent teeth that replace them later. In bats, permanent teeth are different in shape, size, and function from milk teeth and the number and form of permanent teeth vary from species to species and are also related to feeding habits. Vampire Bats (*Desmodus rotundus*, *Diphylla ecaudata*, and *Diaemus youngi* (Phyllostomidae)), for example, use large blade-shaped incisors to cut through the skin of their prey to access blood. On the other hand, their molars and premolars are small, simplified in shape, and reduced in number because these bats do not need to chew their food.

Rhinonycteridae, and Rhinopomatidae (Simmons 1993). Although pubic nipples do not serve for



### Microchiroptera Life

**History, Fig. 10** A female mustached-bat (*Pteronotus rubiginosus*) roosting with multiple young. Females rely on spatial memory and sensory clues to recognize their offspring among others. (Author: Daniele Pedrosa)



Females undoubtedly play the major role in raising the juvenile, and paternal care is rare among bats in general. Direct evidence of paternal care comes from monogamic species where males defend territories where young bats learn to feed, and offsprings remain with their parents for an extended period (Kunz and Hood 2000). In Yellow-winged Bats, *Lavia frons* (Megadermatidae), the juvenile remains with its parents for up to 50 days after learning to fly. Spectral Bats, *Vampyrus spectrum* (Phyllostomidae), are carnivorous bats that live in pairs or extended small groups with their newborn and an older offspring. Both parents and older offspring take care of the young, and at least one bat stays in the roost with the juvenile while the others forage. The foraging bats bring prey back to the roosting site, provisioning food to both young and the bat that remained in the roost (Kunz and Hood 2000; McCracken and Wilkinson 2000; Altringham and Senior 2005).

In most species from temperate zones, males assume little to no responsibility in parenting, since maternity roosts comprises mainly nursing females and their offspring. In contrast, males from tropical zones may display some form of parental care when constructing tents for roosting (e.g., many fruit-eating phyllostomids), defending roosting sites and groups of pregnant and lactating females from other males and predators (Kunz and Hood 2000; McCracken and Wilkinson 2000).

The weaning age differs from species to species; less than 3 weeks in small vespertilionids to over 7–9 months in the Common Vampire Bat (*Desmodus rotundus*) (Fenton and Simmons 2014). At the onset of weaning, mothers and young of several species are reported flying and even foraging together (Kunz and Hood 2000). After weaning, the age of reproductive maturity is highly variable among species, between males and females of the same species and even between same-sex individuals of a single species (Tuttle and Stevenson 1982).

Most bats reach sexual maturity at 1 or 2 years of age, but some species only in few months (e.g., 3 or 4 months in some vespertilionids) (Racey 1982; Tuttle and Stevenson 1982). However, the onset of reproductive maturity is delayed even further in some species such as the Lesser Horseshoe Bat, *Rhinolophus hipposideros* (Rhinolophidae), where some females may give birth to their first young at 3–7 years of age (Racey 1982).

### Age Estimation

Estimating the age of a bat can be difficult, because, when it reaches adulthood, there are few ways to differentiate age classes. In some well-known species, juveniles and adults are distinguished by the length of long bones with linear growth rates, such as forearm, metacarpals, and

digits (Brunet-Rossini and Wilkinson 2009). However, a common way to tell apart young bats from subadults and adults is by looking at the closing patterns in the epiphyseal growth plates of their phalanges. In very young bats, the tissue on their epiphyseal plates is less mineralized, and the epiphyseal plates eventually close as the bat grows, until they are fully fused. In many species, juveniles' pelage is usually darker, less dense, and thinner from that seen in adults, and only after the first molt it will have the same aspect as the adult's fur (Brunet-Rossini and Wilkinson 2009).

### Thermoregulation Challenges and Postnatal Growth

The increased surface area of bats' wings leads to passive thermal conductance when flying and roosting, which increases the energetic demands of thermoregulation (Ochoa and Kunz 1999). Bats can minimize thermoregulation costs by selecting roosts that approach thermal neutrality and clustering.

Clustering modifies the microclimate of the environment because a large number of bats roosting within the same site increases local ambient temperature (Altringham and Senior 2005). In the Neotropics, some cave-dwelling bats roost in large aggregations of hundreds of thousands of individuals in subterranean chambers called hot caves. This term is applied to caves with constant

high ambient temperatures that are caused by body heat emanating from the high bat density, and also from decomposing guano (some caves can reach approximately 40° C) (Ladle et al. 2012). Mustached Bats (Mormoopidae) are the main species associated with Hot Caves, and many mormoopids and some Funnel-eared Bats (Natalidae) have limited geographic ranges or are restricted to hot caves environments year-round or during parturition (Ladle et al. 2012).

Since young bats are born altricial and have limited ability to regulate their body temperature, thermal conditions also play a role in their development (Racey and Entwistle 2000; Kunz and Hood 2000). Mothers help maintain the body temperature of their young sharing body heat through conduction and radiation, and warmer roost temperatures enhance young survival and promote rapid pre- and postnatal growth (Racey 1982; Racey and Entwistle 2000; Kunz and Hood 2000). In many species, females form maternity colonies, and the dense clustering of juveniles assists in heat exchange (e.g., mormoopids, molossids, some nectar-feeding phyllostomids) (Fig. 11).

### Torpor and Hibernation

For bats from temperate regions, it is difficult to remain active year-long and maintain endothermy because cold temperatures demand an increased

**Microchiroptera Life History, Fig. 11** A maternity colony of the mustached-bat (*Pteronotus rubiginosus*). Young bats have limited ability to regulate their body temperature, and clustering assists in heat exchange. (Author: Daniele Pedrosa)





rate of heat production and food consumption (McNab 1982). The majority of temperate species are insectivorous, and besides colder temperatures, they also face a shortage of food availability during winter. Frugivorous and insectivorous bats only enter marginally in temperate latitudes and do not face the same challenges as insectivorous species, which are widely distributed in temperate zones (McNab 1982).

To avoid or minimize changes in climate and food resources, temperate bats must migrate to warm climates to retain endothermy or enter in torpor/hibernation for extended periods. Although tropical species do not hibernate, some may enter torpor when temperatures are too low.

Bats achieve torpor lowering their body temperature to ambient levels (as long as the ambient temperature does not approach to or fall below freezing) and lowering their metabolic rates to reduce their daily energy requirements (Racey and Entwistle 2000; Kunz and Hood 2000). During hibernation, bats spend much or all winter in extended periods of torpor, and the length of these periods vary in response to environmental conditions, body size, and species (torpid periods are longer at low temperatures and small-bodied species) (McNab 1982).

Although there is reduced rate of metabolism and energy expenditure, long hibernal periods require significant amounts of energy that is provided by fat accumulated before hibernation (Fleming 2019). During hibernation, bats may still show some levels of activity that is influenced by temperature, clustering behavior (if they hibernate alone or in clusters), energetic demands, and species (McNab 1982). Hibernation is also closely associated with reproduction in temperate bats; mating occurs before or during hibernal periods, sperm is stored, delayed reproductive processes (ovulation, fertilization, implantation, and gestation), and parturition and lactation occur after the end of hibernation.

## Migration

Migration is an essential feature on the life history of many microbats, and species migrate to deal

with seasonal changes in climate, food availability, and also to find hibernation or nursery roosts (Altringham and Senior 2005; Fleming 2019). Unlike birds, bats are relatively short-distance migrants, and intercontinental migration is uncommon (Fleming 2019).

Many bats from temperate and subtropical zones are migratory. In temperate species migration and hibernation are closely associated, and bats may migrate and/or hibernate to overcome a seasonal shortage of food resources during winter when the energetic demands of homeothermy increase (Altringham and Senior 2005). These species accumulate fat before or during migration, which will provide energy later during hibernation.

Among temperate bats, there are a variety of migratory behaviors: (1) nonmigratory species that breed and hibernate within a 50-km radius or less (e.g., *Rhinolophus* spp., *Corynorhinus rafinesquii*), (2) regional migrants that migrate 100–500 km between seasonal roosts (e.g., *Myotis* spp., *Perimyotis subflavus*), and (3) long-distance migrants, which migrate 1000 km or more between seasonal roosts (e.g., *Lasionycteris noctivagans*, *Nyctalus* spp.) (Fleming 2019). Migration may also not apply to all individuals in some species, and while some populations are sedentary, others are migratory (*Vespertilio murinus*, *Tadarida brasiliensis*) (Fleming 2019).

Bats from temperate zones may form swarms during late summer when hundreds of thousand bats visit roosts that are used for hibernation later during winter (Altringham and Senior 2005). Throughout the swarming season, bats from different populations may fly to the same sites to mate (which can reduce inbreeding), and this behavior may also act as an introduction of hibernation sites for young bats born early in the year (Fenton and Simmons 2014).

Migration is less common among tropical and subtropical species, and, when present, is not associated with hibernation but with food gradients or seasonal food resources instead (Fleming 2019). The Lesser Long-nosed Bat, *Leptonycteris yerbabuenae* (Phyllostomidae), for example, is a nectarivorous, long-distance migrant species that migrate following a “nectar corridor” of flowering

columnar cacti in Mexico and southeastern United States of America (Fleming 2019).

Sex-biased migrations and seasonal spatial segregation occur in some temperate and tropical/subtropical migrant species, and males and females may differ in the distance each sex migrates and also to where they migrate. For example, during summer, male Hoary bats, *Lasiurus cinereus* (Vespertilionidae), are found in western North America while females are in north-central and northeastern United States and Canada (Fleming 2019). Females tend to be more migratory than males and migrate long distances to find nursery roosts where their maternity colonies are formed (see [Thermoregulation Challenges and Postnatal Growth](#)) (Altringham and Senior 2005; Fleming 2019).

## Lifespan

The lifespan of microbats is, on average, at least three times greater than nonflying mammals of similar size (Wilkinson and South 2002). Data on the longevity of microbats are scarce, and most come from studies with banded animals recaptured over the years in the wild (Fig. 12). Greater Horseshoe Bat, *Rhinolophus ferrumequinum* (Rhinolophidae) and some vespertilionids (*Myotis* spp., *Plecotus* spp.) are known to live more than 30 years, while one specimen of Brandt's Myotis, *Myotis brandtii* (Vespertilionidae), is known to live at least 44 years after its banding (Fenton and Simmons 2014).

Hibernation seems to be involved in the extended longevity of bats, since it allows them to escape severe weather conditions and food shortages, thereby delaying physiological deterioration (Brunet-Rossini and Wilkinson 2009). Several hibernating species have lifespan 6 years longer than that of species that do not hibernate when comparing the average maximum lifespans of microbats (Wilkinson and South 2002). Bats live long and have a low mortality rate relative to their body size. Flight and the use of protected roosts may reduce extrinsic mortality, providing secure shelters and agility to avoid and



**Microchiroptera Life History, Fig. 12** Banding of a Flat-faced Fruit-eating Bat (*Artibeus planirostris*). Banded animals help scientists keep track of their movement and life history throughout the years. (Author: Fred Victor de Oliveira)

escape predators (Kunz 1982; McCracken and Wilkinson 2000).

## Conclusion

Bats, in general, are a diverse group of mammals, which reflect in the variety of natural histories and life histories found among the order Chiroptera. Bats' life history includes a range of social systems, mating systems, spatial behaviors, reproduction strategies, and tactics to overcome environmental challenges. Despite such diversity and complexity of known and unknown life histories, all bats must find ways to grow, reproduce, and survive in their own environment.

## Cross-References

- [Life History](#)
- [Microchiroptera Diet](#)
- [Microchiroptera Morphology](#)
- [Microchiroptera Sensory Systems](#)
- [Microchiroptera Locomotion](#)
- [Microchiropteran Communication](#)
- [Microchiroptera Cognition](#)
- [Megachiroptera Sensory Systems](#)

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## Microchiroptera Locomotion

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### Introduction

The name “Chiroptera,” derived from the Greek words *cheir* (=hand) and *pteron* (=wing), refers to the hand-like wings of bats, feature related to their unique ability, among all mammals, to perform true flights. Flight confers bats the access to exclusive resources (food, places to roost), not available to animals that walk, run, burrow, or climb; helps them to avoid and escape from potential predators; and gives them a higher mobility that allows some species to migrate long distances. Part of their diversity success (c.a. 1300 species), being the second largest order of mammals, is attributed to that (Fenton and Simmons 2014). The forearm (radius and ulna), metacarpals, and fingers of bats are elongated, and, with the patagium, they form the strong structure of the wing (Neuweiler 2000). The wing morphology varies among taxa and can be associated to different ecological guilds and flight patterns (Norberg and Rayner 1987). Despite these incredible modifications associated to flight, some bats have also a great ability to crawl, performing several movements on the ground (Schutt and Simmons 2006).

The traditional suborder Microchiroptera (=echolocating bats) is not recognized nowadays, because evolutionary studies have shown that some “microbats” (e.g., Rhinolophoidea) are more closely related to “megabats” (Fenton and Simmons 2014). Currently, bats are classified in suborders Yangochiroptera and Yinpterochiroptera (Amador et al. 2016). In this sense, the expression “microbats” includes representative of both currently recognized suborders. An efficient aerial locomotion is present in all taxa,

but the quadrupedal one has evolved independently in some lineages of Yangochiroptera (Riskin et al. 2016). A detailed review of aerial and quadrupedal locomotion of bats is made below.

### Aerial Locomotion

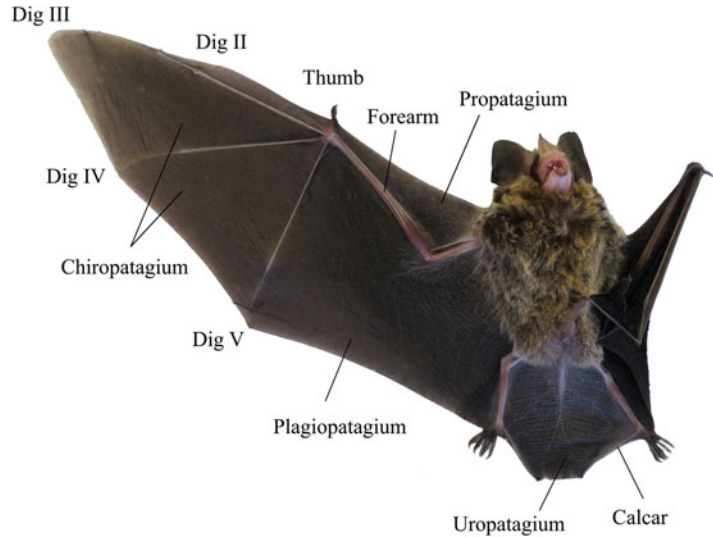
#### The Wing Structure and Morphology

The wing of a bat (Fig. 1) consists of the same elements of the mammalian forelimb but has passed through some modifications: the humerus is large, strong, and suspended from the scapula; the arm is elongated and consists of two bones, the sturdy radius and the thin ulna; the hands include six carpals, five metacarpals, and five sets of phalanges. The first metacarpal, or thumb, is the only digit with a functional claw in extant “microbats” and retains its functions as a freely moving grasping tool. The second to fifth metacarpals are greatly elongated and form a supporting structure to the wing membrane. The wing membrane, or patagium, is very thin and almost lacks a fur cover; it is stretched between the side of the body and the arm (plagiopatagium), between the fifth finger and the wing tip (chiropatagium), between the shoulder and wrist (propatagium), and between the legs and the tail (uropatagium). The patagium have several intrinsic muscles, and fibers of several muscles pass into it (e.g., *coraco-cutaneus*, *humeropatagialis*, *tensor plagiopatagii*). The plagiopatagium and propatagium support the weight of the body during flight; the chiropatagium functions mainly to propel the bat forward; and the uropatagium acts during horizontal takeoffs and very slow flight by producing important thrust and also aids in complicated maneuvers of aerial insectivorous bats (Vaughan 1966; Neuweiler 2000; Gardiner et al. 2011; Adams et al. 2012).

The patterns of flight in bats depend partially on the size and form of the wings (Fig. 2). For this reason, the morphology of the wings provides an evidence about bats’ preferred flight style and foraging strategies, and flight performance indices can be inferred from wing measures of the

**Microchiroptera**

**Locomotion, Fig. 1** Wing profile of *Gardnerycteris crenulatum* (Phyllostomidae) showing the modified bones and patagium that constitute the wing. Note the large forearm and elongated digits (Dig. II to Dig. V) and the membranes that are stretched between the hands, the leg bones, and the body. (Figure: Nathália Siqueira Verissimo Louzada)



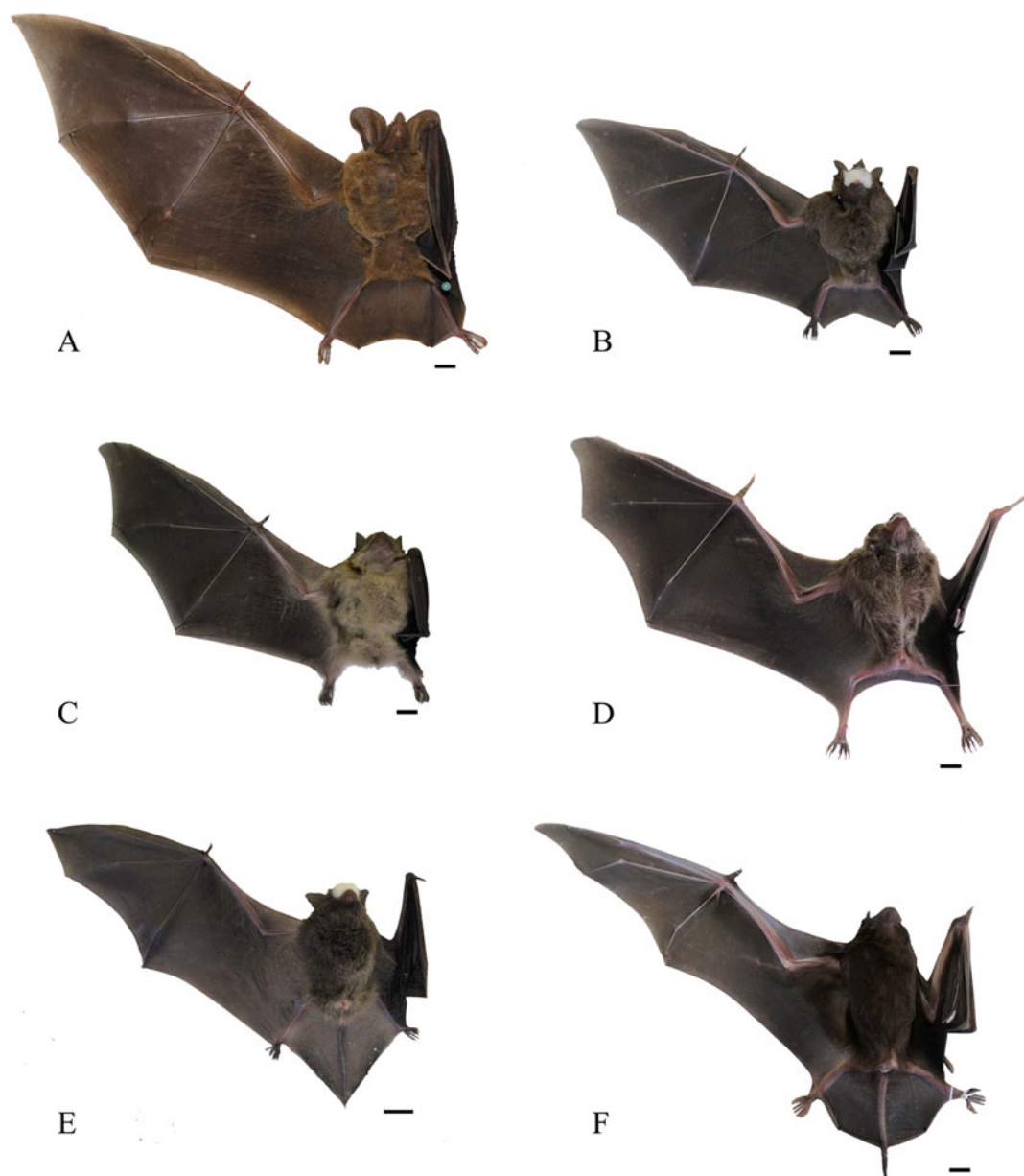
species – wingspan (B), wing area (S), length of the hand-wing (lhw), length of the arm-wing (law), hand-wing area (Shw), and arm-wing area (Saw) – plus the body mass. The main indices are the wing loading (WL), which is the specimen's weight divided by the wing area ( $Mg/S$ ) and is related to the mean pressure on the wings, and the aspect ratio (AR), which is the square of the wingspan divided by the wing area ( $B^2/S$ ), and correspond with aerodynamic efficiency and energy losses in flight. Additional indices are the tip length ratio ( $TL = lhw/law$ ), related to maneuverability, tip area ratio ( $Ts = Shw/Saw$ ), and tip shape index ( $I = TS / (TL - Ts)$ ) (Norberg and Rayner 1987; Neuweiler 2000).

The wings of bats can vary from narrow to wide and long to short (Fig. 2). Narrow wings usually have small wing area and high wing loadings, and the bat with this morphology must fly fast to obtain sufficient weight to support (e.g., Molossidae). Bats with long wings (high wingspan) of high aspect ratio usually have low or average wing loading and fly slowly (e.g., Mormoopidae, Vespertilionidae), which should be advantageous by migratory bats, whose goal is to minimize the energy consumed covering a given distance. Bats with short, broad wings (low aspect ratio) and large wing area (low wing loading) can fly slowly within vegetation (e.g.,

Phyllostomidae). The size and shape of the uropatagium also vary, from reduced (e.g., *Sturnira*, *Desmodus*) to well-developed, and may completely enclose the tail (e.g., Vespertilionidae) or just a part of it (e.g., Molossidae). The presence of a well-developed tail membrane may contribute to lift and to help on the stabilization of the body during turns and other maneuvers when bats are flying (Norberg and Rayner 1987; Neuweiler 2000; Feldhamer et al. 2007).

The wing morphology and flight are also correlated to the use of the space (open, edge, and narrow) and the functional guilds that bats occupy (Table 1). Open space foragers have a wing adapted for fast aerial-hawking flight – they have high aspect ratio and pointed wings. Edge space foragers have a slow and maneuverable flight with low cost – they have average aspect ratios, average wing loadings, and rounded wing tips. In this category are the trawling foragers, with long wings, average wing loading, and high aspect ratio, which allow them to forage above water surface with an economic flight. Narrow space bats have short and broad wings, with rounded wing tips, that give them high maneuverability in confined spaces – the aspect ratio and wing loading are low (Norberg and Rayner 1987; Kalko et al. 1996; Denzinger and Schnitzler 2013).





**Microchiroptera Locomotion, Fig. 2** Wing profile of species of bats representative of Phyllostomidae ((A) *Trachops cirrhosus*, (B) *Carollia perspicillata*, (C) *Sturnira lilium*, (D) *Desmodus rotundus*), Vespertilionidae ((E) *Myotis nigricans*), and Molossidae ((F) *Molossus rufus*). Note the variation from wider (A–D) to narrower (E, F) wings; the aspect ratio increases as wings become longer and thinner, while the wing loading increases as wings become wider. Note the variation in the

uropatagium shape and the tail development: in *Sturnira* (C) and *Desmodus* (D), the uropatagium is poorly developed, and the tail is absent; in *Trachops* (A) and *Carollia* (B), the uropatagium is well-developed, with a notch in *Carollia*; and in *Myotis* (E) and *Molossus* (F), the uropatagium is developed, in V-shape, but the tail in *Myotis* is enclosed on the membrane, while in *Molossus* its distal part is free. Scale bar: 1 cm. (Figure: Nathália Siqueira Veríssimo Louzada)

**Microchiroptera Locomotion, Table 1** Flight characteristics of families of bats. Due to great morphological diversity of Phyllostomidae, their subfamilies are

considered separately. (Data from Norberg and Rayner (1987), Kalko et al. (1996), and Marinello and Bernard (2014). ND: no data available on literature)

| Taxa                    | Wing design                                            | Foraging habits                                   | Taxa                   | Wing design                                      | Foraging habits                                    |
|-------------------------|--------------------------------------------------------|---------------------------------------------------|------------------------|--------------------------------------------------|----------------------------------------------------|
| <b>Cistugidae</b>       | ND                                                     | ND                                                | <b>Phyllostomidae</b>  | Low to high wing loading and aspect ratio        | Narrow and edge spaces                             |
| <b>Craseonycteridae</b> | Average wing loading and aspect ratio                  | ND                                                | <b>Carollinae</b>      | Low to average wing loading and low aspect ratio | Narrow space passive/ active gleaning              |
| <b>Emballonuridae</b>   | Low to high wing loading, average to high aspect ratio | Open and edge space aerial                        | <b>Desmodontinae</b>   | High wing loading, low to average aspect ratio   | Highly cluttered space gleaning                    |
| <b>Furipteridae</b>     | ND                                                     | ND                                                | <b>Glossophaginae</b>  | High wing loading, low to average aspect ratio   | Narrow space passive/ active gleaning              |
| <b>Hipposideridae</b>   | Low wing loading, average to high aspect ratio         | Narrow space flutter-detecting                    | <b>Glyphoncterinae</b> | Low wing loading, average aspect ratio           | ND                                                 |
| <b>Megadermatidae</b>   | Low to average wing loading and aspect ratio           | Narrow space passive gleaning                     | <b>Lonchophyllinae</b> | High wing loading, average aspect ratio          | Narrow space passive/ active gleaning              |
| <b>Miniopteridae</b>    | Average wing loading, average to high aspect ratio     | Edge space aerial                                 | <b>Lonchorhininae</b>  | ND                                               | ND                                                 |
| <b>Molossidae</b>       | High wing loading, average to high aspect ratio        | Open and edge space aerial                        | <b>Macrotinae</b>      | Low wing loading and aspect ratio                | ND                                                 |
| <b>Mormoopidae</b>      | High wing loading and aspect ratio                     | Edge space aerial, narrow space flutter-detecting | <b>Micronycterinae</b> | Average to high wing loading, low aspect ratio   | Narrow space active gleaning                       |
| <b>Mystacinidae</b>     | Low wing loading and aspect ratio                      | ND                                                | <b>Phyllostominae</b>  | Low to high wing loading and aspect ratio        | Edge space trawling, narrow space passive gleaning |
| <b>Myzopodidae</b>      | ND                                                     | ND                                                | <b>Rhinophyllinae</b>  | Average wing                                     | Narrow space passive/                              |

(continued)

**Microchiroptera Locomotion, Table 1** (continued)

| Taxa                    | Wing design                                    | Foraging habits                                                                    | Taxa                   | Wing design                                    | Foraging habits                      |
|-------------------------|------------------------------------------------|------------------------------------------------------------------------------------|------------------------|------------------------------------------------|--------------------------------------|
|                         |                                                |                                                                                    |                        | loading and aspect ratio                       | active gleaning                      |
| <b>Natalidae</b>        | Low to high wing loading, average aspect ratio | Edge space aerial                                                                  | <b>Stenodermatinae</b> | Average to high wing loading, low aspect ratio | Narrow space passive/active gleaning |
| <b>Noctilionidae</b>    | Low to average wing loading, high aspect ratio | Edge space trawling                                                                | <b>Rhinolophidae</b>   | Low to average wing loading and aspect ratio   | Narrow space flutter-detecting       |
| <b>Nycteridae</b>       | Low wing loading and aspect ratio              | Narrow space passive gleaning                                                      | <b>Rhinopomatidae</b>  | High wing loading, average aspect ratio        | Open space aerial                    |
| <b>Vespertilionidae</b> | Low to high wing loading and aspect ratio      | Open and edge space aerial, edge space trawling, and narrow space passive gleaning | <b>Thyropteridae</b>   | Low wing loading, average aspect ratio         | Edge space aerial                    |
|                         |                                                |                                                                                    | <b>Rhinonycteridae</b> | ND                                             | ND                                   |

## Aerodynamics

Flight requires production of two forces combined that allow a bat to rise, to fly at a constant speed and elevation, and to move forward through the air – the lift, a vertical force that counterbalance the bat’s mass, and the thrust (propulsion), a horizontal force that counterbalance the drag (resistance of the body and wing), both produced by the wingbeat (Neuweiler 2000; Fenton and Simmons 2014). The air traveling across the upper surface of the wing moves faster than in the lower surface, which result in lower air pressure above the wing, sucking the wing upward and higher pressure below the wing, pushing the wing up. These different pressures – high under the wing and low above – generate lift. The thrust is provided by the movement of the air across the top of the wing, producing vortices that generate most of the aerodynamic force required to propulsion (Neuweiler 2000; Fenton and Simmons 2014).

While flying, bats continuously change the position of their body and limbs and adjust the position of the wings by the flexion and extension

of the structures that support them (e.g., arm and hand bones, hind limbs, thumbs, calcar), dynamics that are critical to produce changes in flight direction. The lift and the thrust are influenced by the curvature of the airfoil and their angle of attack – if the angle is too shallow, the less lift is produced, and if is too steep, stalling may occur (Fenton and Simmons 2014). The airfoil section of the wings in bats is located between the body and the fifth finger, and this finger can be stretched causing the entire wing membrane to curve upward, adjusting the camber of the wing. A steeper angle of attack is produced by an adjustable leading-edge flap in the propatagium that is made through movements of the thumb – when the bat is flying slowly or executing difficult maneuvers, the angle of propatagium is increased, thereby improving lift (Neuweiler 2000; Fenton and Simmons 2014).

The speed that bats can reach during flight depends on the species and the situation – bats hunting flying insects, for example, have flight speeds between 10 and 34 kph (e.g., 18 kph in *Myotis lucifugus*, 34 kph in *Tadarida*

*brasiliensis*), while migrating bats can approach over 50 kph (e.g., *Lasionycteris noctivagans*). Bats flying over water, however, adjust their wingbeats and move more slowly (8 kph). The metabolic rate and relative costs of different activities of bats are dynamic – a bat (e.g., *Myotis lucifugus*) hibernating has a pulse about 5 beats per minute (bpm), while a bat hanging in a roost has about 200 heartbeats per minute, and a bat flying over an insect has 1000 bpm (Fenton and Simmons 2014).

When a bat is flying straight ahead in a horizontal course, both wings move forward at the same time, from about 60° above the long axis of the body to about 30° below, and, to stay airborne, they require 8–15 wingbeats/s. The wing tips have a propeller-like action, describing a path shaped like a figure eight during each wingbeat cycle. During the upstroke, the surface of the wing is reduced to about 65% of its full size – the chiroptagium remains fully outstretched, while other wing surfaces are slightly bent. The downstroke is primarily responsible for generating lift and takes up 50–60% of the wingbeat cycle. To achieve fast speeds, the amplitude of the wingbeat is reduced, and the wings are sustained almost passively by the air pressure under the wing membranes, saving energy by maintaining airborne as long as possible. This type of flight would be important to migration bats, which can travel the longest possible distance using a limited energy supply (Neuweiler 2000; Fenton and Simmons 2014). When a bat hovers, there is no horizontal propulsion to provide the air flow through the wing (the flight speed is zero), and the air flow must be generated by the wingbeat. Thereby, this flight consumes a great deal of energy and can only be maintained for short periods of time. Bats with short, broad wings, such as nectarivorous bats (*Glossophaga soricina*; Phyllostomidae), are best suited for this type of flight, using the upstroke to generate lift – the plagiopatagium remains folded to reduce air resistance, while the chiroptagium is extended and supinated, and the wings are raised high relative to the body so that they beat in a forward direction rather than a downward one, which generates lift rather than

thrust, thus keeping airborne (Neuweiler 2000; Fenton and Simmons 2014).

The takeoff and flight of bats are facilitated by their elevated hanging upside-down position in twigs or ceilings of caves, which means that “taking off only involves letting go and spreading your wings – gravity does the rest” (Fenton and Simmons 2014). This posture does not require any energy, due the presence of unique tendons and tendons sheaths that allow their feet to lock closed when the bat is roosting. In this means, the legs of bats are considered to serve mainly as a framework to support the wing membranes during flight and thus are small, thin, and not very muscular (Neuweiler 2000; Fenton and Simmons 2014). Some recent studies, however, have been demonstrating that this is not true for all bats. Louzada et al. (2019), for example, showed that the femurs of bats that have functional demands associated to an active use of the legs (e.g., in quadrupedal and trawling behavior) are more robust than the femurs of bats that do not present such functional demands. Similar patterns can be observed in other structures of the bat’s legs (Celeita et al. 2018), and the reduction of the hind legs is not seen in all lineages (see section “[Quadrupedal Locomotion](#)”).

### **Skeleton and Musculature Adaptations to Flight**

The skeleton of bats comprises several morphological specializations associated to an efficient flight. The manubrium, the first two ribs, and the last cervical and first two thoracic vertebrae are fused and form the pectoral ring, which anchor the wings. The column is rigid, with the thoracic vertebrae tightly connected to one another, the sternum presents a keel for the insertion of strong pectoral muscles, the clavícula is robust, and the scapula is parallel to the vertebral column, holding the muscles that controls the wingbeat cycle during flight. The rib cage is large and often broader than deep, and the cervical vertebrae are twisted so the bat’s head can stand raised during flight. The ilium and the sacrum are fused together up to the level of the acetabulum, limiting the mobility at the iliosacral joint and producing stability during flight. The shape of the bone of the upper arm

(humerus) and shoulder blade (scapula) shows great diversity among bats and probably reflects differences in their flight abilities (Vaughan 1970; Neuweiler 2000; Feldhamer et al. 2007; Fenton and Simmons 2014).

There are nine pairs of muscles involved in powering flight of bats. The wingbeat is provided by elevator and depressor muscles (located on the back and on the chest, respectively), most of them acting to adjust the position of the wing and a few more powerful being responsible for the wingbeat itself. This gives the bats agility and maneuverability that could never be achieved by birds, which have just two pairs of muscles (“elevator” and “depressor”) to control wingbeat. The thin profile of the chest observed in bats, when compared to birds, given by the attachment of the musculature both in back and front, probably allowed them to squeeze into crevices and through small openings, facilitating the access to exclusive roosts. Bats also have at least five exclusive muscles associated to the control of the wing membranes: the *m. occipito-pollicalis*, which pulls the propatagium and increases the area of camber of the plagiopatagium; the *m. coraco-cutaneus*, which anchors the elastic fibers of the plagiopatagium to the axilla, helping to reinforce this membrane; the *m. depressor ossis styloformis*, which spreads the uropatagium by pulling the calcar laterally; the *humeroptagialis*, which tightens and braces the distal parts of the wings membrane; and the *m. tensor plagiopatagii*, which strengthens the connection between the plagiopatagium and the lower leg and helps maintain the tautness of the posterior part of the plagiopatagium when the wings are spread (Vaughan 1959; Neuweiler 2000; Fenton and Simmons 2014).

The set of muscles that act during flight varies in the downstroke and in the upstroke of the wing. During the downstroke, the muscles that act in the most control are *pectoralis*, *serratus*, and *clavodeltoideus*. The last two are supporting muscles, acting on the ribs and scapula, and the first one, *pectoralis*, is originated on the sternum and is inserted on the humerus, providing the main power for the downstroke and, in some bats (e.g., *Eumops*), weighting four times as much as

the next largest muscle, the *serratus*. The adjustments of the angle of the wing according to different flight conditions are also made by *m. pectoralis*. Their contraction pulls the wing downward and forward, and, depending on which part contracts more strongly, the humerus may assume different rotational positions. Another important muscle to the downstroke is the *subscapularis*, which controls the position of the wing during rotational movements (Vaughan 1959, 1970; Neuweiler 2000).

Regarding the upstroke of the wing, four muscle groups accomplish the action, the *rhomboideus*, the *trapezius*, the *deltoideus*, and the *serratus*. The first two act pulling the shoulder blade across the torso in the direction of the spine, the third one lifts and rotates the humerus, and the last one provides fine control at the beginning of the upstroke. Usually, little force is required for upstroke because the air pressure under the wing surface passively forces it upward. For reverse the wing direction, however, it requires more energy than any other phase of flight, and several muscles need to act, mainly the *latissimus dorsi* and the *infraspinatus*. In general, the flight muscles of bats are adapted for the metabolism of fatty acids rather than glycogen, which contributes to reduce the weight during flight – fat reserves contain eight times as much energy as a glycogen reserve of equal weight (Vaughan 1959, 1970; Neuweiler 2000).

## Quadrupedal Locomotion

The quadrupedal ability has evolved independently in three lineages of Yangochiroptera: in Desmodontinae (family Phyllostomidae), which occurs in Central and South America and is represented by three species, *Desmodus rotundus*, *Diaemus youngii*, and *Diphylla ecaudata*, all hematophagous; in Mystacinidae, represented by a single living species, *Mystacina tuberculata*, omnivorous and endemic from New Zealand; and in Molossidae, represented by 17 genera and more than 100 insectivorous species with pantropical distribution (Gregorin and Cirranello 2015;



Amador et al. 2016). In Desmodontinae, the quadrupedal locomotion is employed to approach the food resource – blood of mammals or birds; in Mystacinidae, it is used to forage on the forest floor, searching for flowers, fruit, and soil insects. In Molossidae, on the other hand, this habit is associated with roosting behavior, allowing them to access narrow spaces in rocks, trees, roofs, or hollows, and facilitating movement within these locations. As a common strategy, all groups can use the quadrupedal habit to avoid possible threats (predators) during roosting and foraging behaviors (Schutt and Simmons 2006; Riskin et al. 2016).

### Morphological Adaptations in Quadrupedal Bats

The quadrupedalism is a consequence of a series of changes in both the appendicular skeleton and the external morphology of these groups. Externally, these bats have modifications that help and increase contact with the surfaces on which they walk, including metacarpal pads, developed thumbs, reduced calcaneus and uropatagium, in Desmodontinae; lateral pockets in the body where the wing tips are inserted, secondary claws at the base of the thumb and foot, and adhesive discs in *Mystacina*; and lateral pockets, spatulate bristles on digit I of the foot, and inclination of the thumb relative to the other digits, in Molossidae (Schutt and Simmons 2006).

The position of the hind limbs, anterolaterally oriented in specialized quadrupeds, appears to be determinant to the quadrupedal ability – the femur is directed anterolaterally and the tibia vertically, allowing greater and more efficient limb mobility during terrestrial locomotion. The lower limbs (femur and tibia) are known to be more robust, and the fibula is developed in quadrupedal bats. The femoral head is displaced from the main axis of the shaft, condition that is typically found in terrestrial mammals but absent in most bats. This gives the femur a pronounced “neck” and allows a frontal rotation with respect to the anterior tab of the acetabulum, which is limited in most bats because the femur head is aligned with the shaft, restricting the anterior movement of the femur and then the hind

limbs. This arrangement, coupled with changes in the musculature, allows the hind limbs to have greater efficiency during terrestrial locomotion (Vaughan 1959, 1970; Schutt and Simmons 2001; Louzada et al. 2019).

More recently, Louzada et al. (2019) have shown noticeable differences in femoral features, comparing a wide diversity of yangochiropteran bats. From their comparative analysis, they noted that quadrupedal bats have a sturdier femur than other bats and a set of anatomical characteristics that are exclusive or more developed: the shaft is straight; the trochanters are well-developed; the trochanteric fossa is deep; there is a tubercle in the greater trochanter, specially developed in *Mystacina* and molossids; and have associated this features to a greater musculature insertion and thus improved mobility of the hind limbs during crawling behavior. Another interesting result was observed in noctilionoids, which share some characters with quadrupedal bats, such as the sturdy femur, the straight shaft, and the developed trochanters; for them, however, the functional link is related to the use of the legs in trawling behavior (Celeita et al. 2018; Louzada et al. 2019).

Some modifications associated to quadrupedal habit are also described in the humeral morphology. Desmodontinae, for example, has a humerus with a spherical central capitulum, which allows considerable rotational movement (anteroposterior and lateral) in the elbow joint, while *Mystacina tuberculata* shares with the molossids a more restrictive bone joint between the humerus and radius, and presents a more pronounced radial inclination. Hand et al. (2009) showed that in *Mystacina*, the humerus has a deep supraepicondylar notch that is occupied by a tendon of the *extensor carpi radialis longus* muscle, which acts directly on the extension of the entire distal part of the wing and also aids in lifting the flight from the ground, which is important for quadrupedal species. Therefore, humerus morphology also reflects specializations in muscle morphology and muscle action and can be used to infer both flight mode and terrestrial capacity in extant bats (Schutt and Simmons 2001; Hand et al. 2009).

## Cross-References

- [Locomotion](#)
- [Microchiroptera Diet](#)
- [Microchiroptera Life History](#)
- [Microchiroptera Morphology](#)
- [Microchiroptera Sensory Systems](#)

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## Microchiroptera Morphology

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## Introduction

The name Chiroptera is derived from the Greek words *cheir* (=hand) and *pteron* (=wing), referring to the hand-like wings of bats, the primary adaptation for flight (Feldhamer et al. 2007). The wing is

formed from skin (patagium) stretched between the arm, wrist, and finger bones, which are light and slender. The forearm (radius and ulna), metacarpals, and fingers are elongated and, with the patagium, they form a structure that is “strong like an umbrella” (Neuweiler 2000). The thumb remains free and is the only digit that retains a claw in extant microbats. The wing membranes usually attach along the sides of the body and, besides their primary function in flight, they also aid bats in thermoregulation – the thin, vascularized membranes dissipate excess body heat generated during flight (Feldhamer et al. 2007).

Many skeletal features are associated with a need for strong or specialized attachments for the powerful flight musculature, which has influenced the architecture of the vertebral column, pectoral girdle, sternum, and first rib (Vaughan 1970). On the other hand, the hindlimbs are smaller than the forelimbs, presenting a 90-degree or more rotation around the longitudinal axis of the body, so the knees point backwards (Czaplewski et al. 2008). This is important to the upside-down roosting posture and aids in several flight maneuvers. A special locking tendon allows bats to cling surfaces without spending energy (Feldhamer et al. 2007).

Microbats encompasses representatives of the suborder Yangochiroptera plus Rhinolophoidea (Yinpterochiroptera) and are differentiated from megabats (Pteropodidae; Yinpterochiroptera) by the following features: tragus often well developed; nose or facial ornamentation often evident; no claw on second digit; cervical vertebrae modified; head is flexed dorsally from main axis of body when roosting; tail and tail membrane often evident; generally small body size; eyes generally small; mandible with well-developed, long, and narrow angular process; postorbital process usually absent; palate usually does not extend beyond the last upper molars; and presence of a neomorphic calcar (Gunnell and Simmons 2005; Feldhamer et al. 2007).

## External Morphology

There is a great range of size variation among microbats, from the small *Craseonycteris*

*thonglongyai* (2–3 g) to the large *Vampyrum spectrum* (130–235 g). Since they are nocturnal animals, a living coloration would be worthless and therefore most bats present only variations between black and brown, with some reddish or yellowish species (e.g., *Lamproncycteris brachyotis*, *Noctilio leporinus*). Even white fur may occur in some species (e.g., *Diclidurus* spp., *Ectophylla alba*) although this does not appear to increase its predation (Reis et al. 2007). The pattern of coloration is an important taxonomic tool that helps on the identification of some species, such as the tufts of white hair on the dorsal part of the forearm and the longitudinal stripes on the dorsal fur in *Rhynchonycteris naso* (Emballonuridae), the different facial strips patterns on some stenodermatines (e.g., *Platyrrhinus* spp.), the remarkable pattern of body fur coloration in *Nimbapha superba* (Vespertilionidae), and the stunning pattern of wing coloration in *Kerivoula picta* (Vespertilionidae) (Fenton and Simmons 2015; Reis et al. 2017). Besides taxonomy, the color pattern may function as a camouflage in roosting situations, potentially protecting bats from visually oriented predators. An example occurs in some reddish and yellowish lasiurine bats (*Lasiurus borealis* and *L. intermedius*) that roosts in the foliage of deciduous trees (Kunz and Fenton 2005).

Microbats usually have small eyes, large ears, well-developed tragus, nasal, and facial ornamentations, features primarily related to their echolocation system. The pronounced nose leaf of phyllostomids, for example, is important on the orientation of the ultrasonic pulses that come out from their nostrils. A projection from the lower margin of the ear, called tragus, is also important in echolocation (Feldhamer et al. 2007). On the other hand, the larger ears of gleaning bats, including some phyllostomids, are important to hear the sounds generated by insects or small vertebrates (Kunz and Fenton 2005; Reis et al. 2017). As the coloration patterns, the facial features are important to taxonomy: the flesh nose leaf present in Phyllostomidae, Nycteridae, Rhinolophidae, and Megadermatidae; the lips with folds and hairs around the muzzle that look like a mustache in *Pteronotus* spp.; the upper lip divided by two vertical grooves in Noctilionidae (Feldhamer et al. 2007; Gardner 2008).

Important structures to flight, the wing and uropatagium morphology also varies in bats. When viewed from above, wing shape varies from short and broad, to long and thin, being important to aerodynamics of flight. The uropatagium is the membrane between the hindlimbs that encloses the tail and may contribute to lift and to help on the stabilization of the body during turns and other maneuvers when bats are flying. A cartilaginous process, the calcar, helps to support the uropatagium. The size and shape of the tail membrane varies from extremely reduced (e.g., *Desmodontinae*) to well-developed, being sometimes even greater than the body length (e.g., *Natalidae*), and may completely enclose the tail (e.g., *Vespertilionidae*) or just a part of it (e.g., *Molossidae*) (Feldhamer et al. 2007; Reis et al. 2017).

## Skeleton

The bats skull is generally long and low with a rather long and narrow rostrum and somewhat inflated braincase. However, the configuration of the skull and jaws varies greatly in some species, reflecting primarily the strikingly diverse feeding habits, but also roosting habits, echolocation and flight styles, and other morphological correlates (Vaughan 1970; Czaplewski et al. 2008). The rostrum of nectar-feeding bats (e.g., *Glossophaginae* and *Lonchophyllinae*), for example, is narrow and elongated, while in frugivorous bats (e.g., *Stenodermatinae*), it is short and broad. Some bats have the skull strongly flattened which facilitate the access to small spaced roosts (e.g., *Tylonycteris robustula* lives inside of bamboo culm; molossids roosts in rock crevices) (Kunz and Fenton 2005), while bats that roost by hanging have skulls with well-rounded braincases (Vaughan 1970). Regarding to dentition, bats do not have the 44 mammalian pattern teeth, being 38 the greatest number of teeth that are usually present in most insectivorous groups (e.g., *Natalidae*, *Vespertilionidae*) and 20 the fewest number of teeth, present in the vampire bat *Desmodus rotundus* (Vaughan 1970). The incisors and canines retain their typical form in most bats,

but the former can be absent in some species (e.g., *Megadermatidae*). The first premolars are absent and additional lost occurs in many genera. The molars are W-shaped in most insectivorous species, being probably a primitive condition for bats (Czaplewski et al. 2008). The large neotropical family *Phyllostomidae*, however, presents a wide variety of molar morphology, according to its diet. The last molar is greatly reduced or lost in some members, usually associated with frugivorous and sanguivorous habits (Vaughan 1970). Like most mammals, newborn bats have a set of deciduous teeth that are precursors of the incisors, canines, and premolars. These teeth are slender, pointed, and sharply recurved and are used by the young bats to grip the mothers' nipples (Vaughan 1970; Neuweiler 2000; Fenton and Simmons 2015).

The axial skeleton of bats is similar to that of other mammals. In bats, the spine is usually made of 7 cervical vertebrae, 11 thoracic vertebrae, and up to 10 caudal vertebrae. The pectoral area is highly developed and modified, and some features seem to be related to flight in these mammals. The pectoral ring, which anchor the wings, is formed by the fusion of the manubrium, the first two ribs, and the last cervical and first two thoracic vertebrae. The thoracic vertebrae are tightly connected to one another to form a rigid column. The articulating scapula and proximal end of humerus are also highly modified for flight. The sternum presents a keel for the insertion of strong pectoral muscles, the clavicle is robust, and the scapula is parallel to the vertebral column, holding the muscles that controls the wing-beat cycle during flight. The body of bats is short and broad, due to both an anteroposterior compression of the cervical and thoracic vertebrae, and to a strong dorsal arching of the thoracolumbar section of the vertebral column. Therefore, their rib cages are large and often broader than deep. Also, the cervical vertebrae are twisted so the bat's head can stand raised during flight. The pelvis has undergone several adaptations that make it specially well suited for flight. In microbats, the ilium and the sacrum are fused together up to the level of the acetabulum (the socket into which the head of the femur fits), limiting the mobility at the iliosacral joint

(Vaughan 1970; Neuweiler 2000; Feldhamer et al. 2007; Reis et al. 2007).

The bones of the forelimbs form the wings of bats. The large and strong humerus is suspended from the scapula. The elongated lower arm is consisted of two bones: the radius, which is thick and sturdy, and the ulna, which is thin. There are six carpals, five metacarpals, and five sets of phalanges. The second to fifth metacarpals are greatly elongated and the thumb is free and is the only clawed digit of the manus. The hindlimbs primarily serve to support the wing membranes, so they usually are small, thin, and not very muscular, but there are few exceptions from species that have quadrupedal behavior (e.g., desmodontines, molossids, mystacinids). The femur is roughly the same length as the tibia, its head is large and slightly offset from the long axis of the shaft, which allows a great freedom of movements at the hip joint, important during hanging, fighting, and crawling behaviors. The tibia is the only bone in the lower leg, once the fibula is vestigial in most bats. The feet are usually short, the phalanges and claws are laterally compressed, and the calcar is usually well developed and projects into the adjacent border of the uropatagium, which is important to keep the posterior part of the tail membrane extended (Vaughan 1970; Neuweiler 2000).

It is worth noting that studies on the postcranial anatomy may increase and improve the descriptions and identifications of bats that usually are made based on cranial characters. Recent researches on this area have been showing a great potential on taxonomic, phylogenetic, evolutionary, and morphofunctional studies (Gardner 2008; Gaudioso et al. 2017). From the paleontological view, such studies are also noteworthy, allowing the identification of extinct and extant specimens from fossil records, which many times are composed by fragmented bones (e.g., Czaplewski et al. 2008).

## Families Characterization

Despite the general description given above for both external and skeleton morphology of bats, each family presents a set of features that allow

their differentiation from other families. Below, we describe a brief characterization of each family of microbats, based on Hill (1982), Hooper and Van Den Bussche (2003), Garbutt (2007), Feldhamer et al. (2007), Lack et al. (2010), Happold and Happold (2013), Fenton and Simmons (2015), Stuart (2015), Armstrong et al. (2016), and Reis et al. (2017).

**Cistugidae:** The wing-gland, pimple-winged, or hairy bats formerly were grouped in the large genus *Myotis* (Vespertilionidae). The unique feature that distinguishes them from other bats is the presence of one or two pronounced pimple-like glands on the plagiopatagium of each wing, just near the forearm, that are evident in living animals, but may not be observed in dried museum specimens. There are only two species representing this family: *Cistugo lesueuri* and *Cistugo seabrae*. They are small bats and have a great color variation of their dorsal dense pelage. The tragus is long and narrow but not sharply pointed. Their tail is long and enclosed in the uropatagium.

**Craseonycteridae:** This monotypic family comprises the smallest species of bat, the hog-nosed bat *Craseonycteris thonglongyai*. They have large ears and tragus, and a distinctive plate on the nose. The tail and the calcar are absent, the uropatagium is large, and the wings are broad.

**Emballonuridae:** The sac-winged bats have this name in association to their most remarkable feature – wing sacs on the ventral surface of the wings, near the elbow. These sacs, that are more developed in males, exude a red, odiferous substance that is probably important in pheromone production and attraction of females. The ears are short and the long uropatagium is drilled in the upper face by the tail, which has its end free.

**Furipteridae:** The species of this family are known as smoky or thumbless bats. They have large and well-separated ears with a small triangular tragus, and dense fur. Their thumb appears to be absent, once it is very small and mostly enclosed in the wing membrane. The tail is long and enclosed in the long uropatagium.

**Hipposideridae:** They have an elaborate nose leaf (leaf-nosed bats), which consists of fleshy protrusions above the nostrils. These ornamented



nose leaf present a great diversity in size and shape, varying among species. The size of the ears varies and the tail can be absent.

**Megadermatidae:** Known as false vampire bats by the false belief that they feed on blood, megadermatids have large ears that are united on the forehead, a divided tragus, and a large, erect nose leaf. All species lack upper incisors. The uropatagium is extensive, but the tail is short or absent.

**Miniopteridae:** They are known as long-winged or bent-winged bats and were first considered as vesper bats. However, some apomorphies distinguish them from all other vespertilionids. They have a prominent rostrum, the second phalanx of the third finger is about three times as long as the first, the baculum is absent, and there is a supplementary vestigial tooth between the upper canine and the first premolar. They have a long tail that is enclosed in the long uropatagium.

**Molossidae:** The free-tailed bats have a long and robust tail that extends well beyond the outer edge of the uropatagium. They have large ears that point forward and a tragus that is nearly rounded. The wings are long and narrow, the thumbs are short and thick, with a swollen base.

**Mormoopidae:** The species of this family are known as mustached, ghost-faced, or naked-backed bats. They have reddish-brown or dark brown coloration, the ears are short, and the tail projects dorsally from near middle of the long interfemoral membrane. The lips are enlarged and surrounded by numerous stiff hairs ("mustached"). Some species have the wings meeting middorsally, obscuring the fur ("naked-backed") and some have conspicuous, leaflike appendages on the chin ("ghost-faced").

**Mystacinidae:** The New Zealand short-tailed bats have a long snout, and their slit-like nostrils are located in a pad covered with bristles. The ears are moderately developed with a long and pointed tragus. They have very sharp claws on the hind feet and thumb, and a thick membrane along the side of the body where they can hide their wings when walking on the ground. The short tail projects from midpoint of dorsal surface of a medium-sized uropatagium.

**Myzopodidae:** The sucker-footed bats have suction disks on their wrists and ankles, not related with those in thyropterids. They have a unique mushroom-shaped process at the base of their large ears. Their toes have only two phalanges, and the thumb is small with a vestigial claw. The tail is long and extends beyond the well-developed uropatagium.

**Natalidae:** The funnel-eared bats are small bats with a long dorsal pelage that varies from yellow to reddish-brown. The tragus is short, and the large ears are funnel-like, giving these bats their common name. The forehead region is domed, and there are no ornaments on the face, although the males have a mass of glandular sensory cells (called natalid organ) on their muzzle. They have a well-developed uropatagium, which encloses the long tail.

**Noctilionidae:** Known as bulldog bats, noctilionids have a remarkable yellow to brown pelage coloration and a cleft upper lip. The hindlimbs are well developed, as the feet and claws, and the tail extends halfway through the long uropatagium. The ears are separated, narrow, and pointed.

**Nycteridae:** The slit-faced bats have this name due to the unusual longitudinal groove throughout the facial region, given by the deep concavity between the eye orbits. They have large ears and small tragus. The uropatagium is long and encloses the tail, which forms a unique T-shape on the tip.

**Phyllostomidae:** The leaf-nosed bats have a nasal ornament usually in the form of leaf or lance, that varies from highly developed (e.g., *Chrotopterus* and *Lonchorhina*) to extremely reduced and modified (e.g., *Desmodus*, *Diaemus*, and *Diphylla*, which have a horseshoe-shaped nose leaf). Their ears vary greatly in size and shape, and the tragus is always present. The tail may or may not be present, but when present is completely enclosed in the uropatagium. Some species have a well-developed uropatagium (e.g., *Macrophyllum macrophyllum*), but it can be almost absent in another species (e.g., *Desmodus rotundus* and *Sturnira lilium*).

**Rhinolophidae:** The horseshoe bats are named by their distinctive facial ornamentation,

which varies from simple to very ornate, and includes a nose leaf above the nostrils, and horseshoe-shaped flaps below and on the sides of the nostrils. Between the horseshoe and the nose leaf there is a median projection called sella, which differs them from hipposiderids. The ears are large and pointed, lacking the tragus. The wings are broad and rounded, the uropatagium is well-developed, with the tail extending up to its end.

**Rhinonycteridae:** The trident bats and the diamond-faced bats are named by one of their most conspicuous external features, a complex nose leaf, which have three dorsally oriented fleshy processes in the posterior rhinarium in most genera (trident bats), and a diamond-like nose leaf, with the anterior leaf more or less pentagonal in outline in *Rhinonycteris* (diamond-faced bats). They have a flattened muzzle, and the ears can be short or large, usually pointed. The tail is long and its tip may exceed the margin of the long uropatagium in some species.

**Rhinopomatidae:** Also known as mouse-tailed bats, they have a long tail, nearly equal to their body length and even longer than their forearm. The uropatagium is short and most of the tail is free. The ears are large and connected across the forehead by a flap of skin. They have dark dorsal fur and paler ventral fur, being some areas of the face, rump, and abdomen, naked.

**Thyropteridae:** The disk-winged bats have this name due to their round and concave suction disks at the base of the thumbs and on the soles of the feet. They are small bats with a long and slender snout and have small warts above their nostrils. The ears are moderately large and funnel-shaped, and the tragus is present. Their feet are tiny, with fused toes. The tail is long and extends beyond the well-developed uropatagium.

**Vespertilionidae:** The vesper bats present a great variation of size, pelage coloration, and morphology features. They have small eyes and ornaments on the nose are usually absent, although their face may be adorned with swollen glands and other structures. The ears vary in size and shape, some species with small rounded ears (e.g., *Lasiurus*

*cinereus*) and other ones with elongated ears (e.g., *Histiotus*). A well-developed tragus is usually present. Their tail is well developed and extends to the edge or beyond of a V-shaped uropatagium.

## Functional Morphology

Morphological characteristics of bats may represent functional adaptations related to the habitat use, foraging strategies, styles of terrestrial locomotion, and roosting behavior. The wing morphology, for example, is related to the flight pattern and habitat use of bats. A long and narrow wing, with small surface area, adapts a species for sustained, relatively fast flight, as is seen in noctilionids and many molossids, that forage high above the ground, predominately in open unobstructed environments, as the region above the forest canopy or over water. A short and wide wing, with large surface area, is present in bats with slower, more maneuverable flight, as seen in carnivorous bats (e.g., *Chrotopterus auritus*, *Vampyrus spectrum*, *Nycteris grandis*, *Cardioderma cor*), that forages more often in habitats with dense, obstructing understory vegetation. Intermediate patterns of wing morphology, present in some gleaning frugivores (Stenodermatinae and Carollinae), indicate flexibility in the use of space and resources (Feldhamer et al. 2007; Marinello and Bernard 2014).

Some bats have specializations related to roosting behavior, having morphological features that allow them to occupy different habitats. *Neoplatymops mattogrossensis*, for example, have the forearm with small wart-like granulations on dorsal side, which is related to their crevice-dwelling habits. Specimens of Thyropteridae and Myzopodidae have rounded, concave, suction disks at the base of the thumbs and on the soles of the feet that make possible for them to cling to stems, furled leaves, and other smooth surfaces; these disks, however, differ anatomically, and evolved independently in each family, being an example of convergent evolution (Kunz and Fenton 2005; Feldhamer et al. 2007).

Regarding to foraging strategies, *Noctilio leporinus* and *Myotis vivesi* have very long and large hindlimbs, rake-like feet with well-developed claws to scoop up aquatic and terrestrial prey. Among sanguivorous bats, *Diphylla ecaudata* is the only one that retains a functional calcar. The behavior of this vampire indicates that it is an arboreal hunter, and its calcar can be used as an opposable sixth digit to facilitate branch-grasping during arboreal locomotion, while they are stalking its prey (Schutt 1998).

Some features are related to the quadrupedal habit of some bats. Desmodontines and molossids have metacarpal pads to support the hindlimb during the terrestrial locomotion (Schutt and Simmons 2006). Mystacinids have very sharp claws on the hind feet and thumb, each with a small, basal talon. They also have a thick membrane along the side of the body, where the wings can be folded up, during the quadrupedal behavior (Feldhamer et al. 2007).

## Cross-References

- [Microchiroptera Diet](#)
- [Microchiroptera Life History](#)
- [Microchiroptera Locomotion](#)
- [Microchiroptera Sensory Systems](#)

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## Microchiroptera Sensory Systems

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### Definition

Auditory, visual, and olfactory capacities of echolocating bats.

### Introduction

Bats are one of the most evolutionarily successful mammalian groups, occupying a wide variety of ecological niches and adapted to a range of lifestyles. As members of the order Chiroptera, they have traditionally been categorized as either Microchiroptera (microbats) or Megachiroptera (megabats), although this categorization has been updated and revised (Teeling et al. 2005). This entry concentrates on the microbats, of which there are nearly 1,000 recognized species. These bats use laryngeal echolocation to perceive their surroundings by emitting ultrasonic sounds from their mouth or nostrils and then listening to the returning echoes reflected back from nearby objects. Hearing is the primary sense that echolocating bats use for short-distance orientation, obstacle avoidance, and foraging. Bats are not blind, but their vision is adapted to seeing at low light levels and for navigating on large spatial scales. Nectar- and fruit-eating bats use their vision and their sense of smell to locate flowers and fruits; for these bats, these senses supersede echolocation in foraging but not in obstacle avoidance. Bats also use their sense of smell to recognize conspecifics in crowded roosts. This review will summarize current understanding of auditory, visual, and olfactory senses in guiding the behavior of laryngeal echolocating bats.

### Audition

Echolocation is a unique and specialized perceptual system that has evolved as an adaptation to support nocturnal behaviors. It allows bats to navigate spaces that other visually adapted nocturnal mammals cannot take advantage of, such as deep cave systems where no ambient light reaches, and to perceive the distance, size, shape, horizontal location, and vertical location of objects. For the purposes of echolocation, the auditory and vocalization systems of bats have evolved to use ultrasonic frequencies (i.e., above 20 kHz, the limit of the human range of hearing). While these high-frequency sounds do not propagate through the environment as far as do sounds of lower frequency, high frequencies with their short wavelengths are much better suited to provide information about the shape, size, and texture of small objects such as insects. Though there are some prominent similarities in the auditory systems of all echolocating bats, there is nonetheless considerable variability in the precise auditory capabilities across species. Each species has its own calls and emission patterns as an acoustic adaptation to its lifestyle and the unique challenges it faces in the wild (Griffin 1958; Neuweiler 2000). This section aims to give an overview of the auditory systems of this group as a whole while highlighting the unique characteristics that have arisen in certain species as a function of their echolocation.

### Anatomy

If a bat's mouth or nostrils is its biosonar "transmitter," then its two external ears, or pinnae, are its signal receivers. Pinnae are the only externally evident component of the auditory system, and the bat's pinnae, as in all mammals, act to amplify sound and direct it efficiently toward the eardrum for optimal sensitivity. Though all echolocating bats have relatively large pinnae – a clear indicator that they rely heavily on audition – differences in the complicated pinnae shape and size across species reflect variability in bat ecology and what sounds they produce and hear.

One of the central purposes of the pinnae is to amplify the external sounds entering the ear

canal before they hit the eardrum. The amount of amplification, or gain, depends partially on the size of the pinnae. Larger pinnae capture more acoustic energy from the air and more effectively amplify lower sound frequencies, because the longer wavelengths of low frequencies can interact more with the larger pinnae surface areas. This is illustrated by the fact that gleaners (such as the greater false vampire bat, *Megaderma lyra*, and the fringe-lipped bat, *Trachops cirrhosus*) have very large pinnae. These bats detect their prey (insects, frogs, small mammals) not by active echolocation but by remaining perched and passively listening for the low frequency sounds that these prey make while moving on the ground or vocalizing. The massive pinnae of these gleaners disproportionately amplify these prey-generated low frequencies (Obrist et al. 1993). In contrast, nectar-eating and fruit-eating bats tend to have relatively small and simple pinnae.

Pinnae also act to increase the directionality of sounds reaching the ear, selectively amplifying or attenuating (decreasing) the amplitudes of sounds entering the ear from specific angles. This gives the bat additional cues for sound direction. The amount of directionality exerted upon a particular sound varies with the size and geometry of the pinnae as well as with the sound frequency; in general, pinnae show increasing directionality at frequencies greater than 5 kHz (Obrist et al. 1993). Directionality also changes based on the type of echolocation calls a particular species emits. Frequency-modulating (FM) bats emit short duration broadband echolocation calls sweeping downward from 100 kHz to 20 kHz, and their pinnae generally exert moderate directionality across a broad range of frequencies. Constant-frequency (CF) bats emit much longer duration echolocation calls that consist of only a narrow band of ultrasonic frequencies; the pinnae of these species display very sharp directionality at the specific frequencies of these calls (Obrist et al. 1993). Echolocating bats have an additional structure in their pinnae called the tragus, a small leaflike structure that stands upright in front of the pinna. The tragus selectively changes the amplitude of incoming sounds based on the vertical angle with which they enter the

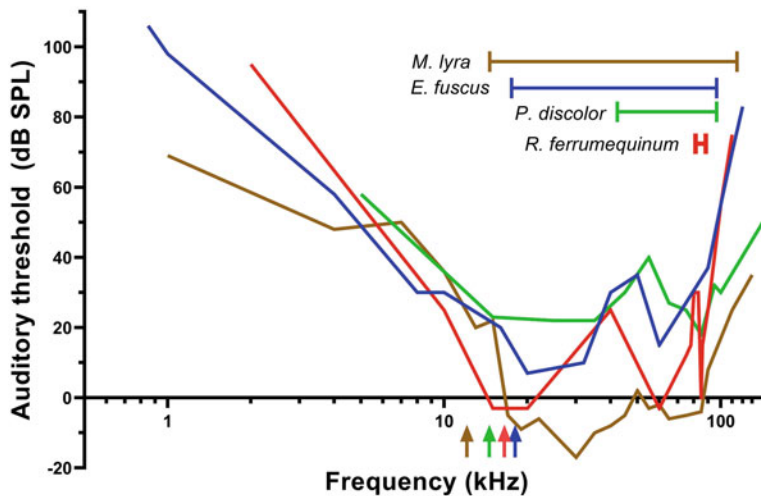
pinnae. This effect acts to provide information to the bat on the vertical position of sound (Lawrence and Simmons 1982).

The remainder of the auditory system of bats follows the typical mammalian pattern: sounds are transmitted to the tympanic membrane, through the middle ear, and then to the cochlea, where hair cells transduce incoming vibrations into neural signals that are then transmitted to the brain. Bats have relatively huge cochleae compared to similarly sized mammals. The width of the cochleae in greater horseshoe bats (*Rhinolophus ferrumequinum*) ranges from 2.6 to 4.3 mm, while the cochleae of similarly sized mice average 1.15 mm (Habersetzer and Storch 1992). There is another adaptation in the cochlea which greatly affects the bat's sense of hearing. The cochleae of the FM bats represent equally well all frequencies of sound to which the bat is sensitive. In contrast, many CF bats have an "acoustic fovea" – their cochlea disproportionately overrepresents the small range of frequencies in their CF echolocation call, making the bat's hearing much more sensitive to those frequencies than to others in their audible range. For example, in the greater horseshoe bat, a full 25% of the cochlea's hair cells are sensitive to frequencies of 80–86 kHz, which is just 6% of the bat's frequency hearing range but represents the frequencies in its CF echolocation call (Bruns and Schmieszek 1980).

### Hearing Sensitivity

All echolocating bats hear ultrasonic frequencies, but how sensitive their hearing is within this frequency range varies across species. In addition, bats use hearing for purposes other than active echolocation. The gleaners must be able to hear the low frequencies emitted by their prey in order to hunt (Neuweiler 2000). Furthermore, bats have extensive repertoires of social communication calls used for individual identification, mother-pup recognition, and communication of emotional state. Social calls typically contain frequencies lower than those in echolocation calls and in some cases extend below the ultrasonic range (Bohn et al. 2006). To perceive echolocation calls and echoes, sounds made by prey





**Microchiroptera Sensory Systems, Fig. 1** Behavioral audiograms showing the frequency sensitivity of hearing of four species of bats, as indicated by different colors. The big brown bat (*E. fuscus*) and the pale spear-nosed bat (*P. discolor*) are FM bats; the greater horseshoe bat (*R. ferrumequinum*) is a CF bat; and the greater false vampire (*M. lyra*) is a gleaning bat. Each colored plot indicates for each species the threshold for detection of pure tones at the indicated frequencies. Valleys indicate the frequency ranges of heightened auditory sensitivity (lowest thresholds) for each species. The colored bars next to the species names indicate the frequency range of

that species' emitted echolocation calls. The two FM bats emit echolocation calls with broader frequency ranges than the CF bat. The greater false vampire bat has better hearing sensitivity than the FM and CF bats in the low-frequency region below 10 kHz. Colored arrows below the x-axis indicate the peak frequencies of contact calls or isolation calls emitted by pups of each species. These frequencies are below those in echolocation calls but remain within the range of good hearing sensitivity. (Adapted from Esser and Daucher (1996), Esser and Schmidt (1989), Koay et al. (1997), Long and Schnitzler (1975), and Neuweiler (1984, 2000))

and social calls, the bat's auditory system must function over a wide range of frequencies.

Figure 1 plots behavioral audiograms for one primarily CF bat (the greater horseshoe bat), two FM bats [the big brown bat (*Eptesicus fuscus*) and the pale spear-nosed bat (*Phyllostomus discolor*)], and one gleaning bat (the greater false vampire bat). Each species hears with greatest sensitivity (lowest thresholds) the frequencies in its echolocation calls. The greater horseshoe bat shows an extremely sharp peak in hearing sensitivity at the 86 kHz component in its CF echolocation call, and another region of broader sensitivity around the frequencies contained in the isolation calls of its pups (Long and Schnitzler 1975). The big brown bat's echolocation calls extend from 20 to 90 kHz, and the bat shows greatest sensitivity within this range. The increased thresholds within the range of 45–50 kHz are due to filtering by the pinnae (Koay et al. 1997). The pale spear-nosed bat has

less sensitive hearing than the other bats, but with two regions of good sensitivity. The high-frequency peak of sensitivity around 60–90 kHz covers the range of its echolocation calls, and the low-frequency peak between 20 and 40 kHz covers the range of its social communication sounds (Esser and Daucher 1996). Pale spear-nosed bat pups emit isolation calls with frequencies around 16 kHz (Esser and Schmidt 1989). The greater false vampire bat emits brief broadband (20–120 kHz) echolocation calls and is very sensitive within this frequency range. Contact calls of this species have energy concentrated at 20 kHz. The comparatively good hearing sensitivity below 20 kHz allows these gleaning bats to detect sounds made by moving or vocalizing prey (Neuweiler 2000).

### Detection and Identification of Echoes

The identification of objects based on their reflected echoes is crucial for the survival of

echolocating bats. Not only do bats need to identify general properties of spaces and surfaces for navigation and roosting purposes, but their environments also require discriminating between different objects for successful foraging – whether they eat insects, vertebrates, fruits, or nectar. Bats are able to hear weak echoes from small insect prey or from small obstacles in the environment, even though these echoes are much fainter than those returning from large obstacles such as trees or buildings. Their hearing sensitivity is so high that they can detect thin wires as much as 50–60 times smaller than the wavelength of their echolocation call. For example, the greater horseshoe bat can detect wires with a diameter of just 0.08 mm, while the Mediterranean horseshoe bat (*Rhinolophus euryale*) and Mehely's horseshoe bat (*Rhinolophus mehelyi*) can detect wires of 0.05 mm diameter (Schnitzler and Henson 1980).

Bats can readily discriminate between objects of different sizes, textures, and shapes. North American insect-eating bats will pursue small pebbles thrown into the air but desist after a few attempts (while still hunting insects), demonstrating they can clearly distinguish between edible and inedible objects of similar size (Griffin 1958). To discriminate objects of different size, a bat must perceive differences in the amplitudes of returning echoes. When ensonified, two objects of equal shape and texture will reflect echoes with identical frequency compositions, but the larger object will simply reflect more acoustic energy than the smaller one. Greater bulldog bats can discriminate between cylinders of different sizes if their returning echoes differ by just 1 dB, and big brown bats can discriminate triangular targets of different sizes when echo intensity differences are 1.5–3 dB. Beyond an object's size, bats can discriminate objects of different shapes, textures, and materials based on differences in their reflected echoes. Spectral bats (*Vampyrum spectrum*) are able to discriminate between spheres and elongated spheres that reflect echoes of equal amplitude; serotine bats (*Eptesicus serotinus*) can discriminate between targets covered in glass and targets covered in velvet; and lesser mouse-eared bats (*Myotis blythii*) and greater horseshoe bats can discriminate between

aluminum, plexiglass, plywood, and resinous plates. Big brown bats can discriminate between metal plates with small holes drilled partway into them, even when the depth of the holes differ by as little as 0.6 mm. Bats use acoustic cues in returning echoes to make these behavioral discriminations (reviewed in Moss and Schnitzler 1995).

### Localization of Echoes

Ranging refers to a bat's ability to perceive the distance to an object. With echolocation, this is a matter of precisely measuring the amount of time that passes between the emission of an echolocation call and the reception of any echoes. Big brown bats and greater spear-nosed bats (*Phyllostomus hastatus*) can accurately distinguish between two identical surfaces whose distances are only 12 mm apart, even when these surfaces are presented at different overall distances from the bat and thus reflect echoes at different intensities (reviewed in Moss and Schnitzler 1995).

In addition to target distance, CF bats can detect a target's relative velocity from a single reflected echo – that is, whether the target is moving toward or away from them. They do this by detecting the Doppler shift in the returning echo and comparing it to their original echolocation call. When a CF bat approaches a target, the narrow band of frequencies in its echolocation call is compressed by the bat's forward motion, causing an upward Doppler shift in the frequency of the echoes that are then detected by the bat. Similarly, if a target is flying quickly away from the bat, a reflected echo's frequencies will be Doppler shifted downward. Greater horseshoe bats can detect Doppler shifts as small as 10 Hz, allowing them to accurately determine the velocity of a target relative to themselves (Schnitzler and Henson 1980). Moreover, these bats can adjust their CF broadcasts to emphasize objects moving at a particular velocity.

Determining a sound's position in three-dimensional space requires measurement of both its azimuth (horizontal position) and elevation (vertical position). Bats can determine the azimuth of a returning echo by comparing cues

from the two ears. Big brown bats can detect differences in the time of arrival of sounds at the two ears with an accuracy of 1  $\mu$ s, corresponding to an azimuth difference of 1.6° (Masters et al. 1985). Differences in intensity of echoes at the two ears are caused by the sound shadow produced as sound travels around the head. The small heads of the Indian roundleaf bat (*Hipposideros lankadiva*) cast enough of a shadow to significantly reduce the intensity for echoes of its high frequency sounds as they travel from the closer ear to the farther ear by as much as 40 dB SPL (Obrist et al. 1993). The elevation of a sound is determined with the help of acoustic cues caused by the tragus. Big brown bats are able to discriminate thin metal rods separated vertically by 3°, but this accuracy decreases to 12–14° separation when the tragus is physically moved out of the way (Lawrence and Simmons 1982).

### Vestibular Sensing

Mammals use their vestibular systems to monitor balance and the body's position in space in relation to gravity. Precise vestibular input through the semicircular canals and the otolith organs in the inner ear is extremely important for animals who use powered flight to navigate and maneuver in three dimensions. But, unlike birds, echolocating bats do not have larger semicircular canals than expected on the basis of their body size (Davies et al. 2013). This may be due to space constraints in the bats' inner ear caused by their disproportionately large cochleae.

Big brown bats can maneuver with great agility through static or rotating arrays of obstacles. If they are given deuterium oxide (heavy water) rather than tap water to drink, they fly more slowly, more erratically, and they collide with obstacles more frequently, even though they continue to echolocate (Horowitz et al. 2004). Heavy water disrupts the mechanical responses of the otolith organs, the inner ear organs that provide information about linear acceleration through space, without disrupting hearing. Bats may rely on vestibular cues in combination with

echolocation to keep their bodies correctly oriented when performing complex flight maneuvers.

### Vision

Echolocating bats are not blind. Many species have eyes adapted for vision in dim light, as shown by their small eyes, large corneas, and retinas densely packed with rods (Suthers and Wallis 1970). Insect-eating species typically begin foraging at dusk, when low levels of ambient light are still present. Little brown bats (*Myotis lucifugus*) will echolocate across a range of ambient light levels, but they will collide more often with obstacles having little visual contrast as light levels increase (Orbach and Fenton 2010). This suggests that in some environmental conditions, some species may pay attention to visual cues, even when this disrupts orientation by echolocation. The California leaf-nosed bat (*Macrotus californicus*) hunts desert insects by hovering above the ground. It can locate its prey with comparable success using vision (at moderate levels of ambient illumination) and using echolocation (in total darkness). When light is available, this bat echolocates less than it does in darkness. The visual acuity of California leaf-nosed bats is 3' of arc, while that of big brown bats, which hunt insects in the air, is 60' of arc (Bell and Fenton 1986). But other species continue to rely on echolocation even in moderate light levels. Kuhl's pipistrelle (*Pipistrellus kuhlii*), a bat that hunts insects near vegetation, and the greater mouse-tailed bat (*Rhinopoma microphyllum*), a bat that hunts insects in open space, use echolocation in preference to vision when hunting small prey at different levels of ambient illumination (Boonman et al. 2013). Big brown bats can maneuver through complex arrays of small obstacles using echolocation alone. Their performance does not improve when visual cues are provided, unless their vestibular senses have also been disrupted (Horowitz et al. 2004).

Bats that forage on fruits and nectar rather than on insect prey rely on visual cues rather than on echolocation for detecting and localizing their

food sources. The fruit-eating bats Seba's short-tailed bat (*Carollia perspicillata*) and Pallas' long-tongued bat (*Glossophaga soricina*) have in their retinæ cone receptors that are sensitive in the ultraviolet range (Müller et al. 2009). The ability to detect ultraviolet light may help these bats find flowers that reflect in the ultraviolet range and to orient at twilight, when ultraviolet cues are visible in the sky (Winter et al. 2003).

Common vampire bats (*Desmodus rotundus*) feed by drinking blood from large warm-blooded prey such as cattle and pigs. These bats use echolocation for orientation and initial approach to the prey. They then land on the animal and search for a suitable place to feed by detecting maximal regions of heat (infrared radiation) on the skin. Vampire bats can detect temperature differences between warm and cold objects at distances of up to 16 cm using a group of three pits located on their face around their nose leafs (Kürten and Schmidt 1982). These pits function as simple "pinhole" sensors for detecting the long wavelengths of radiated body heat. The array of receptors inside each pit organ supplies to the bat a degree of directional information about nearby warm surfaces.

## Olfaction

Fruit- and nectar-eating bats also use odors rather than echolocation to find food. These bats tend to have larger olfactory bulbs than do bats that forage via echolocation, although nasal cavities and olfactory areas of the brain are highly variable in size and structure across different bat species (reviewed in Bloss 1999). Even so, fruit- and nectar-feeding bats have acute senses of smell, and olfactory cues alone can guide choice of flower or fruit in these species. Seba's short-tailed fruit bat can distinguish ripe from unripe fruit and natural from synthetic food odors. Pallas' long-tongued bat prefers sulfur-containing floral scents that are the natural components of the flowers that this species pollinates (Bloss 1999; von Helversen et al. 2000).

Insectivorous species forage using echolocation rather than by detecting odors; however,

these bats use olfactory cues to recognize conspecific bats in the large, often crowded roosts (maternity colonies) in which they live and give birth. The sources of these odors could be from specialized glands, urine, feces, or metabolic byproducts of diet (Bloss et al. 2002). Female big brown bats can distinguish between the smells of females from their own colony and those of females from other colonies. In two-choice tests, they spent more time in the arm of a Y-maze containing the odor of a familiar than that of an unfamiliar female (Bloss et al. 2002). Bats living in the same roost have similar bacterial compositions in their body secretions, and these may serve as a sort of odor signature. Greater sac-winged bats (*Saccopteryx bilineata*) have scent pouches on their wings that contain odorants that they secrete during courtship displays. These odorants differ in chemical composition from those found in the scent pouches in the closely related species, the lesser sac-winged bat (*Saccopteryx leptura*) (Caspers et al. 2009), suggesting that each species has its own olfactory signature. Female sac-winged bats prefer the scents of males of their own species over the scents of the males of the lesser sac-winged bat.

Olfactory cues are also important in mediating mother-pup recognition in maternity colonies. In two-choice tests, female Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) can discriminate between the odors of their own nursing pups and those of unrelated pups. These females mark their pups with odors from their own muzzles as a way to recognize them in these large colonies (Gustin and McCracken 1987).

## Conclusion

The sensory systems of echolocating bats have developed in specialized ways to allow these species to occupy a unique ecological niche as nocturnal foragers. Their auditory systems are tuned to hear faint ultrasonic frequencies (>20 kHz) and allow them to distinguish fine detail in their surroundings by sound rather than by sight or smell. Bats that are aerial insectivores are more reliant on echolocation than are those species

that forage on fruits and flowers, but even those species echolocate to orient and avoid obstacles. Even within the nocturnal niche, sensory capabilities of bats differ depending on their particular ecology and foraging habits. The vision of echolocating bats is in general not as well-developed or sensitive as their hearing, but is nevertheless well-adapted to low-light situations and quite suitable for long-range navigation. Still, some bats have better visual capabilities than others. The use of vision is of particular importance considering that the effective range of echolocation is no more than several tens of meters. For bats roosting in large colonies (up to tens of millions of conspecifics), olfaction is required for distinguishing between conspecifics and close relatives. The sense of olfaction is arguably even more important for fruit- and nectar-eating bats, who often rely on their sense of smell to find food among vegetation. Finally, though little is known concerning the vestibular sensitivities of bats, these are undoubtedly highly developed and sensitive. Like other flying animals, bats rely on an acute sense of balance, acceleration, and spatial positioning in order to remain airborne while executing complex and sudden maneuvers. In short, exploring the sensory systems of echolocating bats provides a unique look into the lives of these fascinating animals, the ecological pressures present in their environments, and the strategies they have developed to overcome these difficulties.

## Cross-References

- [Auditory Processing and Perception](#)
- [Echolocation](#)
- [Megachiroptera Sensory Systems](#)
- [Microchiroptera Morphology](#)

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## Microchiropteran Communication

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### Definition

Communication occurs when a signal produced by an animal provides information to conspecifics (animals of the same species).

## Introduction

Nearly all microchiropterans are highly social; whether living in small tight-knit clusters or large aggregations or even complex societies (see Kerth 2008), they continuously interact with conspecifics in their roost sites. This entry presents an overview of *social communication signal transmission* in bats. Social communication signals can be *olfactory*, *visual*, *tactile*, or *acoustic*. Bats use all four modalities for social communication but rely most heavily on acoustic and olfactory communication signals.

## Acoustic Communication

One defining feature of microchiropterans that is rare among animals is reliance on acoustic *auto-communication*, meaning communicating with oneself, by actively producing signals in the form of *echolocation* calls to navigate (see Box 1). Not only can these calls be used by other eavesdropping bats, to determine the presence and location of the caller (including potential food); reports on various species indicate that echolocation calls can also provide social information such as individual identity, group membership, or sex (reviewed in Bohn and Gillam 2018). Specializations for the sophisticated auditory-vocal system required for echolocation have also had a large impact on the evolution of acoustic social communication, which is by far the most common modality of communication in bats. Considering the degree of sociality in bats, it is not surprising that every species studied uses social communication calls in addition to echolocation. These range from modified echolocation-like calls to simple “squawks” during confrontations to complex hierarchical songs used in courtship.

In addition to echolocation signals that can provide social information, specialized vocalizations for social communication are produced by most if not all bat species with acoustic properties that are distinct from echolocation. Social calls are extremely common if not ubiquitous in roost sites. Some species also produce distinctive social calls in flight. The acoustic range of vocal

communication signals is extremely diverse, varying greatly within and among individuals and species. Commonly but not always, social communication calls are lower in frequency and longer in duration than echolocation. Frequencies range from the audible range (approximately 5 kHz) to ultrasonic (up to 80 kHz). The form of syllables (individual sound elements) can be “noisy” such as “squawks” or “screams,” to clicks, to tonal signals that sound like whistles. In many species, some calls are multisyllabic, that is, they consist of multiple elements; these signals vary from a few to hundreds of syllables. For example, one of the most common multisyllabic signals across microchiropteran species are “buzzes” – rapid successions of short *frequency-modulated sweeps*. Given the diversity of microchiropterans and long evolutionary history of the order Chiroptera, it is not surprising that repertoire size and complexity vary immensely. Relatively complete repertoires have only been documented on a small percentage of bat species, and given the difficulty in observing bats in their natural habitats (such as dark caves or in flight), the functions of many vocalizations are poorly understood. Generally, however, communicative vocalizations can be grouped into the following functional categories: *conflict resolution, mating, and social integration*.

#### Box 1

Microchiropteran bats use auto-communication in the form of echolocation signals. Other bats can eavesdrop on these signals. In social communication systems, the production of signals evolves to evoke a favorable behavioral response from the receiver.

### Conflict Resolution

Conflict resolution vocalizations are produced in adverse situations either from an external threat (distress calls) or during conflicts among individuals (agonistic calls). All bats, like most mammals, produce distress calls. In bats, these calls are predominantly low-frequency, noisy “scream-

like” calls that are often produced in bouts. These bouts may repeat and are thought to carry redundant information. Agonistic calls are also common in bats and take the form of low-frequency, noisy “squawks,” buzz-like calls (i.e., a rapid set of downward frequency-modulated sweeps), trills, and warbles. In roost sites, these commonly occur when bats quarrel over roost space. Mildly aggressive encounters between bats of either sex may start with down sweep vocalizations switching to more noisy screech-like calls as aggression escalates. In some species, during mating seasons, males use extensive agonistic calls and/or songs while maintaining roost site territories where they permit females to reside but aggressively defend against males. In some species, these vocalizations are accompanied by specific postural displays such as wing flapping or boxing.

Agonistic calls are also produced in flight in many species. For example, “honks” have been well noted across taxa to avoid midair collisions. “Buzzes” are frequently heard at foraging sites for many species. More complex agonistic calls are common in those species that defend foraging territories (e.g., *Pipistrellus* species reviewed in Bohn and Gillam 2018). Finally in competitive foraging contexts, some species produce food claiming calls (e.g., big brown bats, *Eptesicus fuscus*, Wright et al. 2014) or calls that directly interfere with the echolocation of competitors (Brazilian free-tailed bats, *Tadarida brasiliensis*, Corcoran and Conner 2014).

### Mating

During the mating season, males of a handful of bat species produce elaborate songs to attract females and repel conspecifics. Singing behavior is not ubiquitous in bats but has evolved in at least five families (reviewed in Smotherman et al. 2016), making it far more common than in other mammalian groups. Songs can be composed of hundreds of syllables and have multiple types of phrases. In some cases, syllables used for other communicative purposes such as aggressive buzzes or isolation calls (see below) may be combined to build songs used during mating (Bohn et al. 2008). For example, in the Brazilian

free-tailed bat, songs are comprised of syllables that are combined to form phrases, phrase order typically follows precise syntactical rules, and specific phrase combinations are preferred over others depending on social context (Bohn et al. 2013). Nevertheless, songs are flexible, varying in syllable number, phrase order, and phrase repetitions. In another species, *Saccopteryx bilineata*, songs are composed of over 20 types of syllables, can contain multiple types of information such as geographic and individual signatures, and are at least partially vocally learned (reviewed in Knoernschild 2014; Smotherman 2016). The fundamental frequency of syllables and length of buzzes in songs contain information on male quality and competitive ability and are correlated with reproductive success (Voigt et al. 2008).

### Social Integration

Social integration signals are used to facilitate social cohesion predominantly among group mates and kin or between parents and offspring. One feature that is common to social integration signals across species is that they have either an individual or group signature (i.e., each individual or group has a relatively unique signal). The majority of these calls are long and tonal with frequency modulations that are unique to the individual or group. The most widespread social integration signals in bats and indeed most mammals are termed infant *isolation calls*. Young bats go through a non-volant period where, in the majority of species, mothers leave their pups behind while they forage and must find and identify their pup among others in the roost site upon their return. Infants produce isolation calls, and in some species mothers produce maternal directive calls to facilitate reunions. In at least one species, *Phyllostomus discolor*, vocal learning plays a role in the development of maternal directives (Esser 1994, reviewed in Knoernschild 2014; Vernes 2017). As in many other mammals, mothers can discriminate among isolation calls from different pups and respond preferentially to their own offspring. Females can rapidly track and update their template of infant isolation calls, as these rapidly change during ontogeny (reviewed in Gillam and Fenton 2016).

The second main category of social integration calls are *contact calls* that serve to identify and recruit group mates and/or family members (beyond just mother/pup reunions). In a number of species, bats have individual- or group-specific calls that allow bats to identify and join group members within roost sites often while bats are returning from foraging. For example, Spix's disc-winged bats (*Thyroptera tricolor*), which roost in furled leaves that require constant roost switching, produce group-specific calls from roost sites that are then "answered" by flying bats looking for the roost (reviewed in Bohn and Gillam 2018; Gillam and Fenton 2016). Vocal communication is particularly important in species where cooperation is common particularly among non-kin (see review Wilkinson et al. 2016). For example, in greater spear-nosed bats (*Phyllostomus hastatus*), bats learn social group-specific social calls to coordinate foraging and cooperatively defend food sites from other groups (Boughman 1998), and in common vampire bats (*Desmodus rotundus*) where bats cooperate via reciprocal blood sharing, bats identify conspecifics using contact calls and during playback experiments preferentially responded to previous blood donors more than kin (Carter and Wilkinson 2016).

### Neurobiology of Acoustic Communication

Although vocal learning is relatively rare among mammals apart from humans, at least three species of microchiropterans from distinct evolutionary lineages show evidence of vocal adaptation/learning of communication signals in social contexts, making them a compelling taxon for investigating the neurobiology of vocal production and perception (reviewed in Knoernschild 2014; Salles et al. 2019; Vernes 2017). Echolocation requires constant real-time audiovocal feedback, which may provide a basis for the evolution of social modification of communication signals.

Different areas of the brain of bats have been implicated on the control of vocalization production. Communication or echolocation vocalization can be elicited from bats when different regions of the brain are stimulated, either electrically or chemically. The periaqueductal gray

(PAG) and the amygdala may be necessary in the production pathway of social communication.

The neuronal processes involved in the decoding of the semantic content of different types of vocalizations have yet to be fully understood. Some communication calls may share commonalities with echolocation sounds, such as signal duration and bandwidth, which makes neural discrimination of species-specific calls by the bat brain a challenge. Several brain areas appear to play a role in the discrimination of communication and echolocation calls, and these regions include the amygdala, the auditory cortex, and the inferior colliculus. The brain of bats appears capable of successfully interpreting the content of social vocalizations, regardless of spectrotemporal overlap with echolocation calls (reviewed in Salles et al. 2019).

### Olfactory Communication

Bats, being nocturnal, are expected to rely heavily on olfaction in addition to acoustic signals. There is very little research on chemical signals in bats, especially when compared with acoustic communication (reviewed in Dechmann and Safi 2005). The common presence of specialized glands for pheromone production supports its role in communication. However, while most mammals use specialized vomeronasal organs and accessory olfactory bulbs specifically for pheromonal communication, the majority of bats appear to have lost this ability (Yohe et al. 2017). Experiments in the laboratory on a number of species have shown that bats can use scent to identify roost mates from unfamiliar bats or individuals. Olfaction is also used in parent-offspring recognition in addition to isolation calls. Chemical signals are especially important in mate selection. For example, males of many molossid and phyllostomid species have *gular glands*, large glands on their throats that produce compounds applied to roosting surfaces or conspecifics. Male emballonurid species have wing sacs where they deposit secretions, and in the singing *S. bilineata*, they wafted odors toward females while performing wing-flapping displays. Research has shown that chemical signals can

provide information on identity, sex, reproductive condition and status.

### Visual Communication

Microchiropteran bats are nocturnal and usually roost in dark areas, making vision constrained and nearly impossible for communication depending on the roosting habitat of the species. Multiple species perform visual displays, particularly those that roost in lighted areas, like *S. bilineata* that roost on the sides of trees in the neotropics or wing-flapping displays in *T. brasiliensis* that commonly roost under bridges. For most bats, their appearance usually mimics their roosting environment, with reddish, brown, or black fur; and there does not seem to be a strong sexual dimorphism in most species. Only few species have facial colorations including yellow and white pigments that may have a function in communication (see Chaverri et al. 2018); however, whether they are used in communication is not well understood.

### Tactile Communication

Tactile communication occurs in affiliative behaviors as it requires close contact. These types of interactions often happen in roosts and are mediated by fur and different types of touch receptors common in mammals. Some bats also have specialized hairs called vibrissae that are present in the muzzle and, in some species, feet that gather precise information about the tactile surroundings of the animal. The most common form of tactile communication is social grooming. Licking, rubbing, and scratching a conspecific may carry information regarding identity, health, and status. Most microchiropteran bats will huddle when roosting, reinforcing social bonds within colonies.

### Cross-References

► [Echolocation](#)

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## MicroRNA

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## Definition

MicroRNAs or miRNAs are small noncoding RNAs, which regulate gene expression at post-transcriptional level through RNA-protein interactions and thus influential for varieties of biological processes.

## Introduction

MicroRNAs (miRNAs) are small, functional non-coding RNAs of ~22 nucleotides – which are integral part of gene expression regulation at post-transcriptional level. They are involved in a wide array of biological processes such as cellular growth, proliferation, and differentiation and other fine-tuned developmental processes (Ameres and Zamore 2013). Such small RNAs were first discovered in *Caenorhabditis elegans* while finding the role of *lin-4* in postembryonic cell lineage formation. Interestingly it was found that *lin-4* does not code for any protein but represses *lin-14* expression for proper lineage progression. Surprisingly, nothing much could be deciphered except the fact that both of them share high degree of sequence complementarity (Lee et al. 1993). Genome-wide studies based on computational analysis showed huge variability in



their number from very few in sponges to more than 1,500 in humans (Ameres and Zamore 2013). Apart from this, *in silico* studies also indicated that they can target more than half of the protein-coding genes in human and in turn can regulate their function, which possibly evoked through evolutionary selection pressure (Friedman et al. 2009). Therefore, miRNA dysfunction is also associated with various human diseases including cancer.

## Biogenesis of miRNAs

Both biogenesis and mode of action of miRNAs are well-coordinated and cumulative interplay of RNA and proteins (especially **Argonaute** family proteins). miRNAs are derived from longer double-stranded RNAs which are cleaved and trimmed to form mature and functional ones through sequential steps. Much longer, double-stranded RNA (intramolecular) called primary miRNA (pri-miRNA) starts the proceedings for biogenesis, which is trimmed and processed sequentially by RNase III enzyme (e.g., Drosha, Pasha) and dsRNA-binding proteins (Lee et al. 2003). Similar to regular transcription, pri-miRNAs are also produced by RNA Pol II from distinct miRNA-coding transcriptional unit as well as introns of the protein-coding genes (Lee et al. 2004). Then **Drosha** as a part of ~600 kDa complex along with another heterodimeric protein complex called **DGCR8** (in mammals) or **Pasha** (in other animals) cleaves the stem-loop structure of the pri-miRNA at their base to produce ~60-nucleotide-long pre-miRNA at the nucleus. Because of the polycistronic organization of the miRNA genes, multiple pre-miRNAs can be produced from a single pri-miRNA (Kim et al. 2009; Denli et al. 2004). Further processing of pre-miRNA occurs at the cytoplasm, which necessarily requires transport of the pre-miRNA from the nucleus to cytoplasm – mediated by a Ran GTP-dependent double-strand binding protein **Exportin5**. In the cytoplasm, another RNase III enzyme called **Dicer** does further processing of pre-miRNA into ~22-nucleotide-long duplex with the help of **TRBP** (transactivation response RNA-

binding protein) and **PACT** (protein kinase R-activating protein) in mammals and **Loquacious** in *Drosophila*. In flies, miRNAs are generated by **Dicer 1**, whereas **Dicer 2** is associated with siRNA biogenesis, but in mammals, single **Dicer** does so. AGO proteins are then loaded into miRNA duplex in association with chaperone machinery to form pre-RISC (RNA-induced silencing complex). AGO does the final trimming of the miRNA duplex to produce “seed sequence” – which provides specificity for target mRNA 3' UTR (Ameres and Zamore 2013).

*Seed sequence:* Generation of “seed sequence” is very essential for miRNA function as it provides the high affinity binding with target mRNA and thus provides target specificity. Any mutation or alteration in seed sequence results in disruption of repressive activity of a particular miRNA. Structural and functional analysis of AGO proteins throughout plant and animal kingdom, including archea and bacteria, shows impeccable impact of seed sequence modification by AGO proteins. Structural and ITC (isothermal titration calorimetry)-based studies revealed that AGO does structural rearrangement of the seed sequence for stronger affinity with target sequence via their PIWI/MID domain through reduction of entropic penalty (Wee et al. 2012; Parker et al. 2009).

*Self-regulation of miRNAs:* Amplitude of miRNA-mediated mRNA repression is fine-tuned by directing bound miRNA destruction. Studies on miRNA degradation in fly and mammals showed that target mRNA itself induces miRNA destruction following binding to their complimentary sites, in order to restrict particular miRNA – which shows cooperative mode of regulation. Such destructive action involves trimming (3'-5' exonucleolytic resection) as well as tailing (addition of A or U) of the miRNA. However, clear and detail mechanisms including involvement of additional proteins are still a matter of research. On the other hand, such destructive action is exclusive in miRNA pathway in *Drosophila*, but not in the case of siRNA. siRNA in flies can escape this action because **HEN1** (HUA enhancer 1) cannot introduce 2'-*O*-methylation of the seed sequence while AGO1

loading. In flies, siRNA pathway is mediated by AGO2, and thus HEN1 cannot exert such action – thus such distinctive regulation can do self- and non-self-recognition too (Ameres et al. 2010).

*isomiRs*: As miRNA-mediated repression depends on the seed sequence, sequence heterogeneity at seed sequence can provide more diverse target range. Small RNA sequence-based studies on diverse group of organisms including tissues and cell types have provided astonishing dimension of miRNA diversity via generation of isoforms of miRNAs – referred as *isomiRs*. Such isomers can be generated due to improper trimming or dicing of pri-/pre-miRNA including further addition of nucleotides. Alteration in 5' end of the miRNA is an efficient way of making *isomiRs* as 5' end defines the target signature. Such editing can be a result of adenosine deamination via ADAR (adenosine deaminase acting on RNA) – which can also edit dsRNAs (Kawahar et al. 2007). Surprisingly in *Drosophila melanogaster*, 3' trimming is profoundly observed in Ago1-bound miRNAs irrespective of the source of the pre-miRNA. But this process requires another protein called nibbler which has 3'–5' exonuclease activity. Following Ago1 loading, Nibbler does so to fit the miRNA in the PAZ domain of Ago1 and in turn come up with heterogeneity. Apart from this, 3' heterogeneity can also arise due to addition of extra nucleotides commonly referred as tailing. TNTases (terminal nucleotidyl transferase) exerts such tailing via 3' uridylation of the miRNA (Liu et al. 2011).

*RISC formation and target destruction*: Mature miRNAs exert their functional impact of posttranscriptional gene silencing via formation of **RISC** (RNA-induced silencing complex) in collaboration with *Argonaute* family proteins and their associated partners via perfect or imperfect base pairing with the target transcripts followed by catalytic activity of the Ago proteins or additional functions of recruited partners (Ameres and Zamore 2013). Several repressive strategies including decapping, deadenylation and 5'–3' mRNA degradation, and translational repression are utilized by RISC either singly or in combinations. Ribosome profiling and genome-wide miRNA-mediated repressive studies showed that

target mRNA decay is the dominant form of repressive strategy (66–90%) in comparison with translational repression (6–26%) in mammalian cells. miRNA utilizes same indigenous 5'–3' mRNA decay machinery for the target mRNA degradation. During this process, **PAN2-PAN3** along with **CCR4-NOT** deadenylase complex causes deadenylation of the target mRNA, followed by decapping through **DCP2** (decapping protein 2) along with additional partners like **DCP1**, **EDC3** (enhancer of decapping3), **EDC4** (**Dcp1** *Drosophila melanogaster*), **DDX6**, and **PATL1**. Finally, cytoplasmic nuclease **XRN1** (5'–3' exoribonuclease 1) degrades the deadenylated and decapped target mRNA (66). Besides this, **GW182** family proteins {having multiple tryptophan (W) containing motifs} interact with Ago family proteins and deadenylase complexes to assist the degradation pathway (Ameres and Zamore 2013; Jonas and Izaurralde 2015).

Besides robust and more effective mRNA degradation-mediated repression of mRNA, translational repression is also another strategy used by miRNAs. This process is a much weaker one and found during early expression of miRNAs. Artificial mRNA reporter-based assay showed that such mode of repression can be independent of mRNA decay pathway and also helpful for those mRNAs which do not possess distinctive poly A tail and are resistant to deadenylation (Mathonnet et al. 2007).

*Multiple targeting by single miRNA*: As miRNA utilizes 3' UTR of the target mRNA and imperfect pairing of seed is sufficient to exert the repressive action, thus single miRNA can target multiple genes simultaneously. For example, miRNA-200b can regulate cell motility and cell invasion via targeting of cytoskeletal genes at multiple levels as well as by regulating structures called focal adhesion and invadopodia. Conversely, multiple miRNAs can regulate common biological processes as found in regulation of actin cytoskeleton by miR-200 family. Surprisingly, such miRNAs are produced from polycistronic clusters and thus act as cooperative functional unit of miRNAs. Similar to multi-strategic action of miRNAs, mRNA 3' UTR also

restricts robust action of miRNAs. Specially functioned genes produce mRNA with longer 3' UTR with higher density of miRNA target sites as compared to housekeeping genes – thus provides further prominent landscape of regulation evolutionarily (Bracken et al. 2014).

miRNA-mediated repression can be indirect as they can target downstream effector of a gene or even downstream transcription factors to mediate indirect action. Typically miR-200 family exerts such effects in regulation of EMT, where such miRNAs target EMT regulator ZEB1 and SNAIL1 to control EMT indirectly (Perdigão-Henriques et al. 2016).

Till now miRNA has shown their role in mRNA repression either directly or indirectly, but they can be linked to gene activation also. miRNA-mediated gene activation is an indirect mode of activation where repression of the repressor of certain genes can result in activation of particular gene as found in neuronal differentiation of vertebrate groups. miR-128 has found to do so for neuronal differentiation and proper brain function (Bruno et al. 2011).

So, miRNA has enormously wide landscape of function and strategy to fine-tune different biological processes. Despite our detail knowledge about their structure and mode of action, still newer areas are there to be open.

## Cross-References

- [Exon](#)
- [Gene Expression](#)
- [Intron](#)
- [Noncoding RNA](#)
- [RNA](#)

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## Microsatellite Marker

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## Synonyms

Short tandem repeats (STR); Simple sequence repeats (SSR)

## Definition

Microsatellites are very short nucleotide (two to seven) sequences repeated many times, number of repetition varying depend on the type of species which is used to determine genetic diversity, paternity studies, and population studies in identification of genetic traits and also in forensic studies.

## Introduction

The term “microsatellite” was first of all given by Litt and Luty (1989). A microsatellite is a region of the repetitive DNA sequence localized in both prokaryote's and eukaryote's genome. The length of the microsatellite marker is one to six base pair and is repeated, typically 5–50 times. Additionally, microsatellites are found in thousands of the location in the whole genome of the organism. The rate of mutation in the microsatellite marker is very high as compared to other region of the genome or DNA. Microsatellite markers are also known as simple sequence repeats (SSR), short tandem repeats (STR), and

simple sequence length polymorphisms (SSLP), which are found in both prokaryotic and eukaryotic organisms.

## Location and Structure of Microsatellite

They are widely distributed throughout the genome, especially in the transcriptionally active region, i.e., euchromatin of eukaryotic genome as well as coding and noncoding nuclear and organelle DNA (Pérez-Jiménez et al. 2013; Phumichai et al. 2015). Additionally, they are located at noncoding as well as regulatory site of coding region of genome. However, microsatellites of the noncoding regions have not been explored yet; these noncoding regions lead to accumulation of mutation that are involve in the formation of variation from one generation to another generation which use in DNA finger printing. Microsatellite mutation at the regulatory region of coding region leads to phenotypic changes and diseases like fragile X syndrome and Huntington's disease.

## Features of Microsatellite Marker

- Microsatellites are repeated mono-, di-, tri-, tetra-, and pentanucleotide unit sequence which are widely distributed in genome (Powell et al. 1996).
- They are found in the genome of both prokaryotes and eukaryotes.
- They are also found in organelle genome such as mitochondria and chloroplast (Powell et al. 1995).
- These are widely distributed throughout the genome with high rate of mutation as compared to other regions of genome. The mutation rates estimated in the microsatellite marker range between  $10^{-4}$  and  $10^{-2}$  per generation.
- The microsatellite region in genome leads to high diversity.
- They are most potentially powerful informative molecular marker with easily operated and low cost PCR analysis.

## Origin of Microsatellite

The origin of microsatellite marker in genome can be nonrandom and take place due to the imbalance between the processes that promote microsatellite formation and the process that prevent microsatellite initiation. At present, there are two non-mutual exclusive hypotheses to explain the origin of microsatellite.

- (i) **De novo microsatellite:** According to this hypothesis proposed by Messier et al. (1996), the origin of microsatellites was a consequence of creation of proto-microsatellites, a short region with three or four repeated units. Proto-microsatellites originate by the base substitution or indel events and latter supported by observation that insertions tend to copy adjacent bases (Gemmell 2006). Once proto-microsatellite is initiated, its maintenance and multiplication is favored by its tendency to undergo strand slippage during replication.
- (ii) **Adopted microsatellites:** According to this hypothesis proposed by Wilder and Hollocher (2001), the origin of microsatellites was from the other region of genome through transposable elements. These transposable elements composed of two or more than two site which is involve in microsatellite formation. Transposable element is a DNA sequence that can move from its position within a genome that lead to creating or reversing mutation and later the cell genome identity as well genome size.

## Type of Microsatellite Markers

Many authors classified marker according to the presence of nucleotide bases: short repeats (30 nucleotides) are microsatellite marker and long repeats (10–100 nucleotides) are minisatellite markers. Moreover, microsatellite marker is further classified according to the type of repeat sequence present.

- (a) **Perfect microsatellite marker**, when sequence show only perfect repetitions, e.g., (AT)<sub>20</sub>
- (b) **Imperfect microsatellite marker**, when repeated sequence interrupted by different nucleotides which are not further repeated, e.g., (AT)<sub>12</sub>GC(AT)<sub>8</sub>
- (c) **Composite microsatellite marker**, when there are two or more than two different repeats motif present in *tandem*, e.g., (AT)<sub>7</sub>(GC)<sub>6</sub>

However, the composite marker has been categorized as both perfect and imperfect microsatellite marker. The di, tri, and tetra repeated nucleotide sequences are most commonly used in molecular genetic studies (Selkoe and Toonen 2006).

## Application of the Microsatellite Marker

From the last few years, microsatellite marker has been used in the characterization screening and to appraise the genetic diversity between the different species.

- I. **Forensic lab studies:** From the last few decades, microsatellites have become a very powerful technique in the forensic studies. It has been used as genetic fingerprinting for the differentiation of individual of the same species. The microsatellite's principle is based on the analysis of all tetra- and pentanucleotide repeat and it gives high degree of error-free data. Shorter repeat sequence has a tendency to suffer from artifacts such as PCR shutter as well as several genetic diseases that are associated with trinucleotide repeat such as Huntington's disease (Angel Carracedo 2010).
- II. **Population genetic study:** Microsatellite markers were also useful in population genetics study during the 1990s. It became ubiquitous in research laboratories. This study, based on the PCR, allowed researchers to design primers and analyzed set of microsatellites at minimum cost (Manel et al.



2003). Microsatellite marker are also applicable for interfering or measuring bottlenecks, population size gene flow, all allelic fixation index, and local adaptation.

III. **Conservation biology:** Microsatellite markers are crucial tool to analyze the rapid change, effect of population fragmentation, and interaction of the different population. It is also used in the identification of incipient and new population. Additionally, there markers are also useful to identify adaptation of population in new environment condition.

IV. **Genome mapping:** It is a very important technique which helps in mapping the genome as well as in identification of the location of the significant portion in the genome. Additionally, they are also widely applicable in the area of publicized human genome mapping (Moxon et al. 1999).

V. **Cancer detection:** In cancer cells, the rate of microsatellite expansion (increase in the number of repeats) and microsatellite contraction (decrease in the number of repeats) increases due to defect in the enzyme that is involved in the correction of the copy DNA. Initial clinical detection of some type of colon and bladder cancer has been successfully identified by the use of the alteration in microsatellite repeats (Yonekura et al. 2002).

VI. **Biological/evolutionary context:** Microsatellite markers are also used to address the degree of relatedness between the individual and groups. In case of endangered or captive species, microsatellite is used as a tool to evaluate the level of inbreeding. Microsatellite marker is used to admission the demographic history (e.g., to look for evidence of population bottlenecks), and to access the effective population size as well as the direction of the gene flow between population. They are also used for fine-scale phylogenies up to the level of closely related species.

VII. **Diagnosis and identification of human disease:** Microsatellite markers are also widely used as marker in the biomedical diagnosis of the certain disease. Microsatellite alleles are also associated with the occurrences of mutation in the coding region of DNA that

lead to variety of disease. Microsatellite is associated with change in length of the early development of cancer. Therefore, it is used as a marker for diagnosis of early cancer. These markers have polymorphic nature; therefore, they are useful in linkage studies which attempt to identify the location of the genes responsible for various disorders (Kashi and Soller 1999).

There are some examples of diseases associated with microsatellites trinucleotide repeats (<http://www.woodrow.org/teachers/esi/2002/biology/projects/p3/diseases.htm>).

### Limitations of Microsatellite Markers

Even though microsatellites have many advantages over other molecular markers, all data sets might include some errors and genotyping errors remain a subject in population genetics because they might bias the final conclusions (Bonin et al. 2004). Microsatellite genotyping errors result from many variables (reagent quality, Taq polymerase error, or contamination), as reviewed by Pompanon et al. (2005).

- (a) Null alleles: Mutation or deletion of locus in the annealing primer inhibits heterozygous identification and locus amplification that leads to inaccurate estimation of allele segregation and frequency rates.
- (b) Homoplasmy alleles: Alleles identical in state (length) but not by descent are homoplasic alleles. They can be identical in length but not in sequence with different evolutionary history (Anmarkrud et al. 2008). Because homoplasmy is disregarded, the actual divergence between populations is underestimated. Sequencing could be used to identify differences in sequences, but differences in evolutionary history can only be identified by mutations documented in known pedigrees.
- (c) Linkage disequilibrium: It is deviations from the random association of alleles in a population, which are primarily caused by population substructuring and high levels of

| S. no | Name of the disease            | Symptoms of the disease                                                                                                                                                                                                                      | Involvement of microsatellite                                                                                                                                                                                                                                                |
|-------|--------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1.    | Huntington's disease           | Late onset dementia and loss of motor control, motor disorder accompanied by the loss of memory or cognitive deficit, juvenile onset is rare, patient show rigidity, epilepsy and severe dementia                                            | Occurs due to alteration in CAG coding repeat in the first exon of HD gene. Normal gene is composed of 6–36 repeats and affected gene is composed of 36–121 repeats. The microsatellite adds a string of glutamine amino acid to the Huntington protein (Bailer et al. 2002) |
| 2.    | Fragile X                      | Mental retardation, long and prominent ears and jaws, high-pitched speech, Hyperactivity, poor eye contact, and stereotypic hand movements                                                                                                   | The repeat is CGG in a noncoding region of the FMR2 gene. Normally this gene is composed of 6–53 repeats and the affected gene is composed between 60 and 200 repeats                                                                                                        |
| 3.    | Myotonic dystrophy             | Involving hypotonia, respiratory distress at birth, and developmental abnormalities. Adult onset. Includes variable loss of mental function, myotonia, muscle weakness, and progressive muscle wasting                                       | It involves CTG repeats in a noncoding region of the DMPK gene. Normal gene is composed between 5 and 37 and the affected gene may involve 50–1000 repeats                                                                                                                   |
| 4.    | Spinal bulbar muscular atrophy | Neurological degeneration associated with difficulties in speech, articulation and swallowing, muscle weakness and atrophy Signs of mild androgen insensitivity are typically seen at adolescence                                            | It involves CAG repeat in the first coding exon of the androgen receptor (AR) gene. Between 9 and 36 repeats is normal, and people with 38–62 repeats develop the disease                                                                                                    |
| 5.    | Friedrich's ataxia             | Ataxia, diminished tendon reflexes, loss of position and vibratory senses, dysarthria (slurred speech), cardiomyopathy, diabetes mellitus, optical atrophy, scoliosis, and skeletal abnormalities. Age of onset is typically early childhood | It involves GAA repeat in noncoding region of gene X25. Normal gene contains between 7 and 34 repeats. The disease gene has 34–80 repeats (Santos et al. 2010)                                                                                                               |

inbreeding (Weising et al. 2005). It is especially problematic for population studies and paternal exclusion. This problem could be detected by the computer programs or an offspring analysis.

exchangeable data format to allow users to access different kinds of analyses and computer programs easily (Excoffier and Heckel 2006) and the best understanding about microsatellite evolution and mutation mechanisms.

## Perspectives

The application of microsatellite markers has been validated by a large number of studies and different areas that apply microsatellite for different purposes. Additionally, novel technologies have allowed the improvement of markers for previously neglected species over the generation of new sequences and a more developed search in databases. However, there are some bottlenecks that need to be overcome as they hamper the best and widespread use of SSR data, e.g., an

## Conclusion

Over the last few decades, the use of molecular marker has been playing a vital role in the analysis of genetic diversity and genetics. Out of the different types of molecular marker, microsatellite marker has been extensively used because they can be easily amplified by PCR and also used in the analysis of large amount of the genetic variation (allelic variation at each locus). Microsatellite markers are simple sequence repeats and typically composed of one to six nucleotide repeats. These

markers are abundant and distributed throughout the genome. Microsatellite markers are highly polymorphic as compared to the other molecular markers as well as species specific and codominant. Due to this, microsatellite markers have become increasingly important genetic markers in the amplification of genetic diversity, population genetics, and disease diagnosis. This scenario confirms the current relevance of microsatellite marker and indicates their continuous utilization in different studies.

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## Microsatellites

### ► Simple Sequence Repeats

## Migration

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## Synonyms

Diaspora; Exodus; Flight; Journey; Movement; Shift; Transfer

## Alternative Words

► Displacement; ► Exodus

## Introduction

The cause of migration is specific for each individual or group of individuals. Some migrate

in search of food, and some migrate to avoid unfavorable climatic conditions such as extreme cold and hot conditions, etc., while others migrate to carry out their reproductive functions such as searching mate, spawning, etc. Migration occurs in response to some internal and external cues – external cues include photoperiod, food/water availability, changing seasons, earth's magnetic field, etc., while internal cues include low fat reserves, circadian rhythms, etc. Apart from the external cues, some portions of the migratory mechanism have a genetic basis. Variations in migratory phenotype are observed in migrants within the same species as well as in closely related species, and these variations are genetically and epigenetically controlled. However, the genetic and epigenetic control mechanisms are not well understood and are still under investigation. Diadromous and catadromous migrations occur through water, while some migrations occur through drift carried out by wind, current, etc.

Migration allows migrants to exploit a greater range of resources and to use the favorable environmental factors present in a different environment to their own advantage for survival and greater reproductive success but also has a great effect on communities and ecosystems. Migrations result in competitions for resources between migrants and local inhabitants which sometimes lead to scarcity of resources in that particular zone. Migration exerts top-down effects on residents by affecting predation pressure. The migrants often increase the predation risks for the nonmigrants in their absence. The migrants also act as vectors for diseases and carry these diseases to the new environment thereby affecting the communities. Migration also helps in transfer of genetic information and affects the gene pool. It has been seen that migration has the capability to enhance and weaken community stability. Even the effect of migration on nutrient cycles and primary productivity in ecosystems is worth mentioning.

Various forms of migrations are seen in animals, and these are categorized on the basis of the organism, space, time, as well as the medium through which the movement takes place. The various types of migration include the

following: obligatory, a regular, consistent, and predictable migration; facultative, an optional migration in response to specific conditions; partial, when some individuals migrate while others remain in the breeding area; differential, when migratory differences are seen in individuals based on age and sex; to-and-fro, migration of animals between two areas; round trip/loop, when migrants return to their breeding ground passing through succession of non-breeding areas; one-way, when migrants are translocated from their native environment to another where they breed and produce successive generations before dying; altitudinal, migration from lower altitudes and higher altitudes; vertical, migration between different zones of water bodies; nomadic, an irregular migration linking temporary breeding sites which host suitable conditions; seasonal, long-distance migrations on a seasonal basis; and irruptive, when portions of population migrates while other members remain on their breeding.

The earliest documented observation on migration was that by Aristotle who noticed that the birds around him changed with season and concluded that a species gave rise to the other with change of season. Others noted that birds disappeared in winter and probably hibernated deep down the earth. With time and careful scientific observation, these earlier explanations gave way to a deeper understanding of the fact that migration is widespread in the animal kingdom and has basically emerged as a mode of survival (Lohmann 2018).

## Definition

In a general sense, the word migration refers to the movement of biological entities from one place to another with specific motives or due to some external or internal influence. However, migration in ethology and ecology refers to the large-scale movement of individual animal or animal groups to a different environment. This movement may be cyclical, frequently occurring, and sometimes on a daily basis, and the reason of migration also varies in different species. Most animals migrate to avoid

unfavorable conditions and to enjoy better opportunities with respect to food availability, less competition, safety from predators, better reproductive success, and utilization of necessary resources. The complex nature of animal migration due to its variability in different animal groups (birds, mammals, fishes, insects, etc.) makes the process difficult to explain. One of the commonly used definition is migratory behavior defined as “persistent and straightened out movement effected by the animal’s own locomotory exertions or by its active embarkation upon a vehicle. It depends on some temporary inhibition of station keeping responses but promotes their eventual disinhibition and recurrence.” The fact that migration mainly occurs seasonally and is followed by a return journey distinguishes it from other types of animal movements including emigration.

In a strict sense, the term migration encompasses four distinctive but overlapping concepts: (i) a tenacious locomotory practice; (ii) a resettlement of an animal which is an outcome of longer periods of movement excluding those which are a part of daily routine; (iii) a seasonal to-and-fro movement of populations between regions hosting alternately deleterious or beneficial conditions, including the breeding ground; and (iv) movements leading to redistribution within a spatially extended population. These concepts include the various components of migration of individuals as well as of populations such as cause of migration, cues of migration, types of migrations, and its effects on the ecosystem.

## General Description

Migration is the movement of animals from one place to another. The main reason an animal hibernates or migrates is due to the lack of food, which occurs during the winter months due to the cold weather. In contrast hibernation is when animals rest or remain asleep during the entire winter. Hibernation and migration are adaptations for animals to survive winter months when food is not available.

There are different kinds of hibernation. Some animals sleep so deeply, they are impossible to wake up, like the woodchuck and bat. Some of them are light sleepers like raccoons, skunks, and opossums that wake up during the winter to eat. Many bears take long rests and also lightly sleep during the winter months.

Animals also migrate to other areas during the winter months. Many birds fly long distances to escape the cold winter, like the Arctic tern from the North Pole that flies South to Antarctica. Some birds in the far south of South America, Australia, and Africa migrate to the North, and others from east to west to coastal climates. The monarch butterfly travels south during the winter where there are flowers. A few animals must avoid the extreme heat, so they migrate to cooler areas. Animals may also migrate to find a good habitat to raise their young ([softschools.com](http://softschools.com) 2018)

## Types of Migration

Migration is the movement of people from one place to live in another. Emigrants leave their country, while immigrants enter a country. Migration impacts on both the place left behind and on the place where migrants settle. People have many reasons why they might want to move from one place to another. These reasons may be economic, social, political, or environmental. For migration to take place, there are usually push factors and pull factors at work. Push factors are the reasons that make someone decide to move. This is their own experience of life in one place which gives them good reasons to leave it.

There are different types of migration such as counter-urbanization, emigration, immigration, internal migration, international migration, and rural-urban migration.

## Factors Influencing Migration

### In Birds

All birds do not migrate, but all species are subject to periodical movements of varying extent. The



birds which live in northern part of the hemisphere have greatest migratory power.

Migration may be:

- (i) Latitudinal
- (ii) Longitudinal
- (iii) Altitudinal or vertical
- (iv) Partial
- (v) Total
- (vi) Vagrant or irregular
- (vii) Seasonal
- (viii) Diurnal
- (ix) Nocturnal

**Latitudinal migration:** The latitudinal migration usually means the movement from north to south and vice versa. Most birds live in the land masses of the northern temperate and subarctic zones where they get facilities for nesting and feeding during summer. They move towards south during winter.

An opposite but lesser movement also occurs in the southern hemisphere when the seasons are changed. Cuckoo breeds in India and spends the summer at Southeast Africa and thus covers a distance of about 7250 km.

**Longitudinal migration:** The longitudinal migration occurs when the birds migrate from east to west and vice versa. Starlings (*Sturnus vulgaris*), a resident of east Europe and West Asia, migrate towards the Atlantic coast. California gulls, a resident and breed in Utah, migrate westward to winter in the Pacific coast.

**Altitudinal migration:** The altitudinal migration occurs in mountainous regions. Many birds inhabiting the mountain peaks migrate to lowlands during winter. Golden plover (*Pluvialis*) starts from Arctic tundra and goes up to the plains of Argentina covering a distance of 11,250 km.

Birds migrate either in flocks or in pairs. Swallows and storks migrate a distance of 9650 km from northern Europe to South Africa. Ruff breeds at Siberia and travels to Great Britain, Africa, India, and Ceylon thus traveling a distance of 9650 kms.

**Partial migration:** All the members of a group of birds do not take part in migration. Only several

members of a group take part in migration. Blue jays of Canada and northern part of United States travel southwards to blend with the sedentary populations of the Southern United States of the USA Coots and spoonbills (*Platalea*) of our country may be an example of partial migration.

**Total migration:** When all the members of a species take part in the migration, it is called total migration.

**Vagrant or irregular migration:** When some of the birds disperse to a short or long distance for safety and food, it is called vagrant or irregular migration. Herons may be an example of vagrant or irregular migration. Other examples are black stork (*Ciconia nigra*), glossy ibis (*Plegadis falcinellus*), spotted eagle (*Aquila clanga*), and bee-eater (*Merops apiaster*).

**Daily migration:** Some birds make daily journey from their nests by the influence of environmental factors such as temperature, light, and humidity also. Examples are crows, herons, and starlings.

**Seasonal migration:** Some birds migrate at different seasons of the year for food or breeding, called seasonal migration, e.g., cuckoos, swifts, swallows, etc. They migrate from the south to the north during summer. These birds are called summer visitors. Again there are some birds like snow bunting, red wing, shore lark, gray plover, etc. which migrate from north to south during winter. They are called winter visitors.

## In Fishes

**Migratory pattern in Chinook salmon fish:** It is the largest of the Pacific salmon and has black spots on its tail and the upper half of its body. They have black pigment along the base of teeth. The weight (pounds) of largest Chinook documented is about 126 pounds.

**Distribution:** In the western Pacific, the distribution ranges from northern Japan in the south to the Arctic ocean.

**Classification:**

Kingdom: Animalia  
 Phylum: Chordata  
 Class: Actinopterygii  
 Order: Salmoniformes

Genus: *Oncorhynchus*

Species: *O. tshawytscha*

Fish status: Nine populations of Chinook salmon are listed under the US Endangered Species Act as either threatened or endangered.

Type of migratory fish: These fishes are anadromous meaning they are born in freshwater, migrate to sea, and return to freshwater to spawn.

Migration: Homing instinct is strongest among salmons and generation after generation. They return to the same river. The Chinook salmon provides a legendary example of this homing instinct. Every year, countless millions of salmon carry out one of the greatest animal migration on earth. The longest and most remarkable of these journeys runs the entire length of the Yukon River by Chinook fishes across interior Alaska and into northwestern Canada.

Beginning of migration: The Yukon River Chinook migrates upstream during the fall of a distance of about 2,000 in miles.

The first migration: Chinook spend a full year in the Yukon River before migrating to the first summer, building up enough fat to carry them through the long boreal winter. The little Chinooks now begin their first great journey – swimming and drifting downstream, urged by the current.

Life in the ocean: As they grow; juvenile Chinooks move into the northern. The Bering Sea ranges from about 60 degrees latitude up through the Bering Strait.

The second migration: In the second migration, a king salmon heading back to its home river cover a tremendous distance – perhaps a thousand miles or more.

Some experts speculate that salmon might use the position of the sun or its polarized light as a compass.

Biologists also have known that a salmon has flecks of magnetite in its snout, so possibly it uses the earth's magnetic field as a compass.

Migratory pattern in European eel: The European eel is a species of eel, a snake-like fish.

Distribution: The European eel inhabits the Atlantic Ocean from Europe to North America.

This eel is native to the Atlantic Ocean off the coast of Europe.

Classification:

Kingdom: Animalia

Phylum: Chordata

Class: Actinopterygii

Order: Anguilliformes

Genus: *Anguilla*

Species: *A. anguilla*

Fish status: The European eel is a critically endangered species.

Migratory pattern: These fishes are catadromous, those migrating from freshwater to the sea for spawning.

Migration: The spawning migration of the European eel to the Sargasso Sea is one of the greatest animal migrations. Adult European eels begin their spawning migration from European rivers and coasts during the autumn of each year [predominantly October to December] and must migrate a distance of between 5,000 and 10,000 km (depending on their departure locations) to presumed spawning area in the Sargasso Sea.

### Migratory Behavior

**Vertical Migrations** Eels that reached oceanic depths exhibited a stereotypical vertical migration, moving from shallow water between night and day. Vertical migration resettled in a diel temperature change with experienced temperature being cooler during the day than at night. Eels released from Swedish west coast and the Baltic outlet experienced extreme ambient temperature below 0 °C, whereas eels released from the Celtic Sea (Ireland) rarely experienced temperature lower than 9 °C.

### Migration Route

It has been observed that migration routes are not simply error-free great-circle routes (i.e., the shortest possible route to the Sargasso Sea from the departure points); instead many of the routes are in the reverse direction of the northern part of the subtropical gyre in the Northern Atlantic Ocean which is consistent with the hypothesis

that eels follow olfactory cues originating in the spawning areas or that eels navigate using oceanic cues imprinted or learned during the leptocephalus phase.

**Migration speed:** The speed of migration was estimated in European eels about 37 km per day.

**Migratory pattern in carps:** Carps are various types of oily freshwater fish which belongs to the family Cyprinidae which are found in abundance native to Europe and Asian subcontinents. Most cyprinid forms have scales and teeth on the inferior pharyngeal bones which may be modified in relation to the diet.

**Distribution:** The various species of carps (common carp, *Cyprinus carpio*, etc.) is widespread freshwater fish of eutrophic waters in lakes and large rivers in Europe and Asia. Several species of carps are considered invasive in the USA and worldwide, and large sums of money are spent on carp control.

**Classification:**

Kingdom: Animalia  
Phylum: Chordata  
Class: Actinopterygii  
Order: Cypriniformes  
Family: Cyprinidae  
Genus: *Cyprinus*  
Species: *C. carpio*

**Fish status:** IUCN Red List status has listed the common carp under the vulnerable category.

**Migratory pattern:** These fishes are potadromous because these fishes move and complete their life cycle entirely within freshwater.

**Migration:** Potadromous fishes exhibit complex life cycles and habitat use pattern that are integrated with the diversity of their various life stages and associated body sizes. The migratory behavior in carps arises from spatial, seasonal, and ontogenetic separation of optimal habitats for growth, survival, and reproduction.

Schlosser in 1991 described the basic migrations of stream fishes among three types of habitat (feeding, overwintering, and spawning).

After hatching, most carps migrate during each of the four subsequent mobile life stages (larvae,

juvenile, subadult, and adult). The diversity of destination habitat and movement patterns by carps in riverine and lacustrine system reflect seasonal habitat preferences as well as shifts in preferred habitats as fishes develop among life stages. After larval fish emerge, some may drift passively with stream or lake currents. Others may begin feeding, even before their yolk sac is absorbed.

After fish attain the juvenile stage, the diversity of movement may further increase, if there is an abundant food supply, if cover is adequate (i.e., water depth, overhead cover), and if other rearing conditions are favorable like temperature and move within that range until winter.

**Distance range of migration:** Migration and movement of carps range from short distances approximately 1–2 m to long distance >650 km.

#### Migratory Pattern in Atlantic Herrings

**Description:** Atlantic herring is a herring in the family Clupeidae. It is one of the most abundant fish species in the world. Atlantic herring can be found on both sides of Atlantic oceans congregating in large schools.

Atlantic herring have a fusiform body. Atlantic herrings are in general fragile. They have large and delicate gill surfaces, and contact with foreign matter can strip away their large scales.

**Distribution:** Atlantic herrings can be found on both sides of the ocean. They range across North Atlantic waters such as the Gulf of Maine, the North Sea, Irish Sea, etc.

**Classification:**

Kingdom: Animalia  
Phylum: Chordata  
Class: Actinopterygii  
Order: Clupeiformes  
Family: Clupeidae  
Genus: *Clupea*  
Species: *C. harengus*

**Conservation Status:** Least Concern (LC)

**Migratory pattern:** Herring species are anadromous, traveling up coastal river to spawn. Atlantic herrings are fully marine and migrate to coastal and offshore spawning grounds. In late summer

and early fall, Atlantic herrings aggregate into massive schools and move into coastal water at various rotations in the Gulf of Maine to spawn. They also spawn on offshore bank such as the Georges Bank and Brown Bank south of Nova Scotia. Spawning times vary for different populations of Atlantic herrings.

**Migration:** Herrings are small fishes, the adults being about 25–30 cm in length. Baltic herrings are smaller and somewhat larger. They mature at about 3 or 4 years of age, and their annual fecundity amounts to 40,000–10,000 eggs. They live and swim in large shoals, each of which may be many kilometers across. They migrate towards the surface at night and then tend to disperse in shoals. They make long migration each year from spawning ground to feeding ground and back and have to travel distances of up to 2000 km to do this; they usually swim down tide or current. The herrings of any spawning group spawn at the same season each year to within about a week.

In the North Sea, there are two autumn spawning stocks, Buchan and Dogger, in the northern and central North Sea and a winter spawning stock, the Downs, in the south of the North Sea. The North Sea herring migrate in a clockwise circuit in the North Sea.

In general, the spawning pattern of herring conforms to the typical triangular migration pattern common in pelagic schooling. Adult fishes migrate against currents from feeding ground to spawning grounds. Larvae drift passively away with currents, and juveniles eventually swim back out to join adults at feeding grounds.

**Factors in human:** Many people choose to migrate. These are voluntary migrants. Many are economic migrants. Other voluntary migrants include older dependents who want to live somewhere warm and sunny in their retirement. However many other people have no choice and are forced to leave their homes. These are involuntary migrants. Their lives and homes may be in danger due to war or a natural disaster. These people are also called refugees.

**Importance of migration in humans:** Often push factors are negative things such as unemployment, crop failure, droughts, flooding, war, poor education opportunities, or poor services and

amenities. Pull factors, on the other hand, are the expectations which attract people to the new place. They are usually positive things such as job opportunities, a better standard of living, better education, or better healthcare. Push factors are the reasons that make someone decide to move. This is their own experience of life in one place which gives them good reasons to leave it. Often push factors are negative things such as unemployment, crop failure, droughts, flooding, war, poor education opportunities or poor services and amenities. Pull factors, on the other hand, are the expectations which attract people to the new place. They are usually positive things such as job opportunities, a better standard of living, better education or better healthcare.

**Evolutionary significance of migration:** Migration in animals significantly contributes towards selective advantages leading to evolution of species. Although migration in birds have been more fascinating and widely studied, migration is a phenomenon widely present across species which include insects, fishes, amphibians, as well as mammals. Migration is an adaptive response integrated with the survival needs for less competition, ambient temperature, avoidance of harsh weather conditions, and availability of resources. It is also critically associated with the need to find the right geographical conditions that support breeding. The process and consequence of migration have considerable evolutionary significance. For example, migrating population of birds lack information on the weather/environmental condition at destination and utilize length of day as a guiding mechanism. Length of day helps these birds adjust the timing, intensity, and choice of place for migration and breeding. Photoperiodic response of migratory birds pre-determines juvenile development and expression of reproductive features (Coppack and Pulido 2004). This ability to respond to daylight may be completely lacking in birds that do not depend on photoperiodic response for food or other survival mechanism.

Migration is also a common feature in fishes, although less explored compared to their avian counterparts. Young salmon migrate to the sea to take advantage of abundant food but returns to

rocky tributaries to spawn (Dingle 2014). It has been observed that migratory species are better adapted to utilize available resources and grow faster but may sexually mature later compared to nonmigratory species (Roff 1988).

Genetic variation in migratory vs non-migratory population is an important factor leading to evolution of species better adjusted to the prevalent environmental conditions. Due to high energy demands and exposure to varied pathogens during migration, certain genes related to higher innate immune response may be favored and expressed. If the migrating population ends up mating with the residents, this brings greater variability in the gene pool. Any favorable combination will be selected, thriving genetic drift and emergence of a population genetically different from the original species.

**Methods of studying migration:** Migration is a complex behavioral phenomenon that has several other associated factors such as genetics, physiological, biomechanical, ecological, and evolutionary aspects. Hence scientific study of migration demands a broad and integrative approach that includes empirical and theoretical approach. This section of the chapter will focus on some of the current methodologies employed in the study of migration.

**Field method** – This method employs direct counting of birds/animals as spotted in a particular area or field which could be a natural landmark in the path of migration or a man-made object. This method has been popularly used to study bird migration but also has been employed to study butterflies and other organisms. Although this method can lead to detail information on the population and their relationship with the environment, this can be very time-consuming and not a cost-efficient method (Boccagni and Schrooten 2018).

**Tracking method** – Migrating animals have been studied by tracking them down their migratory path. Tracking employs extrinsic and intrinsic markers present in the animals. Extrinsic markers uses capture-recapture/resighting data where animals are captured and data collected on their unique recognition markers and released only to be recaptured at a different geographical

location to validate its migration. This method heavily depends on the number of sites at which data is being collected. It also depends on animal behavior and use of the site. Natural markers have been successfully used to distinguish migrants from residents and identify the link between migrating population at either ends of route and the source of migration. Some natural markers used are footprints in large terrestrial animals and head and plumage details in birds. Song dialect in birds, e.g., the white crowned sparrow (*Zonotrichia leucophrys*), has also been used to separate migrants from residents (Milligan and Verner 1971). Man-made markers such as the use of metal rings have also been employed to study migration in birds for more than 100 years, and the ring recovery data has been compiled in bird migration atlases. Satellite tracking through radio transmitters has greatly revolutionized this method of studying migration using external markers; however radio transmitters can only be used on relatively large animals. The smallest transmitter is about 10gm which restricts the use of transmitters on animals weighing 250 gm or above. This criterion alone excludes about 80% of world's birds and 70% of mammals. The fundamental flaw in the use of extrinsic markers to study migratory animals is that it can be employed only on marked individuals and the probability of their recapture/resighting (Dingle 2014).

Intrinsic markers have great advantage in understanding the migratory path and migration in animals as these markers are integrated tissue features in the animals. Measure of stable isotopes of hydrogen (H), oxygen (O), nitrogen (N), carbon (C), and sulfur (S) has routinely been used to study migration particularly in aquatic or airborne animals. Stable isotopes are like footprints of where the animal has been and a unique tool in the study of migration. The isotopes are records of the dietary sources of animals, and provided a database of environment specific isotope is available, the migratory path of the animals can be easily tracked. The O and H isotopes are geographically preserved and are related to the hydrological and meteorological over thousands of years for a particular geographical region,



hence enabling interpolation of regional isotope data. The “hydrogen cycle” and the measure of H isotope composition are used to evaluate the migratory path in aquatic animals. Various processes in water cycle lead to large-scale geographic patterns of hydrogen isotopes in water, which can be quantitatively used to study migration. The choice of food available to the migrating animals offer unique composition of stable isotope that is integrated in the body and can be biochemically analyzed from small tissue samples to identify the geographic pathway of migration. Two types of tissue samples are usually used to measure stable isotopes. The first type is fixed tissue that is metabolically and hence isotopically inert. This includes keratinous materials such as feathers, claws, nails, hair, etc. Metabolically and isotopically inert tissue materials are used to determine the local environment where the tissue was initially formed (Coiffait et al. 2009). However, caution should be exerted while analyzing slowly growing keratinous tissue. Feathers and claws that grow slowly as the animal migrates will incorporate isotopes from the diet of the animal en route and therefore may show a variation in isotope composition. The second type of tissue sample used is dynamic and metabolically active and directly depends on the dietary habit of the migrating animal. The samples are blood, muscles, organ tissue, and even feces. The turnover rate for isotopes varies a few days in the blood and liver, weeks in the muscle, and lifetime in bone collagen. A comprehensive manual for sampling wild birds has been documented by Whitworth, et al. (2007) and needs to be particularly referred when dealing with highly pathogenic avian influenza (HPAI).

**Radiotelemetry** – Radiotelemetry is a powerful tool to study migration in animals that move in air or in aquatic environment and surface to breathe. This method employs attaching a device either externally (noninvasive) or implanted in the body of the migrating animal (Hay and Nebel 2012). Signals from the device can then be collected to understand the pattern and pathway of migration. Ambient temperature of the environment the migrant is in and even water pressure for aquatic animals. In addition, physiological

information of the migrating animal, such as rate of wing beat in birds, respiration rate, heart rate, etc., can also be accessed using radiotelemetric devices. Choice of device may vary depending on the environment and the range of movement of the migrating animal. Radio transmitters are typically used to collect long-distance signal transmissions, whereas ultrasonic devices are normally used for short-range transmissions (Bowlin et al. 2005; Leon et al. 2004; Wolcott 1995). Currently the ocean tracking network with its headquarter at Dalhousie University, Canada, is monitoring movements of more than 150 species of aquatic animals around the globe. International cooperation for animal research using space (ICARUS) is another organization that aims to develop a telemetric system based on low-orbiting satellites in order to track numerous migratory species (Dingle 2014). The biggest hurdle in the use of radiotelemetric method of migration study is the impact on energy budget and the size requirement of the devices. An ideal radiotelemetric device should not exceed 2–5% of the total body mass of the animal. Most often, the devices fail due to small-sized battery dying out or because the transmitter was destroyed due to the fact that the animal was either hunted or harvested. As such the researcher can never track down the reason for device failure without tracking down the animal.

## Conclusion

Migration is classically defined as the regular movement of animals each year between separate breeding and wintering grounds. There are many different types of migratory behavior, ranging from completely sedentary populations to populations that are completely migratory (obligate migrants). There are three kinds of natural selection that can cause evolutionary change: directional selection, disruptive selection, and stabilizing selection. The study of Darwin’s finches illustrates how rapidly natural selection can result in a change in phenotype. Homeostasis is an important mechanism for maintaining internal balance. In achieving homeostasis,

animals maintain a relatively constant internal environment even when the external environment changes significantly. Birds use both internal maps and compasses to find their way during migration. Olfactory maps and magnetic maps are believed to help birds locate themselves in space. Three internal compasses allow birds to sense the direction in which they are flying. These are the sun compass, the star compass, and the magnetic compass. The fishes also show potential migratory patterns with special reference to their change in habitats. The mechanisms used by different organisms to orientate during migration are still largely unknown and are currently the subject of ongoing research.

## Cross-References

- [Artiodactyla Navigation](#)
- [Bear Navigation](#)
- [Canine Navigation](#)
- [Caudata Cognition](#)
- [Chondrichthyes Navigation](#)
- [Navigation](#)
- [Proboscidea Navigation](#)
- [Sirenia Navigation](#)
- [Zoology](#)

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## Mimicking

- [Copying](#)

## Mimicry

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Mimicry as an inherited adaptation is very widespread and can be found even at molecular level, mimicking viral antigens (Rose and Mackay 2000; Shahrizaila and Yuki 2010). Some plants and flowers display visual mimicry (van der Niet et al. 2011; Lev-Yadun 2017). Among insects (Lepidoptera), the butterflies and moths offer

plentiful examples of mimicry of colors and patterns. The large group of invertebrates with exoskeletons from scorpions, crabs, and others to spiders (Herberstein and Wignall 2011), grasshoppers, and even cockroaches (Vršanský et al. 2018) furnish examples of mimicry. Fishes (Randall 2005), octopi (Norman et al. 2001; Gómez-Moreno 2019), and other creatures in the seas may mimic by supplementing colors and patterns with species-typical movements (usually locomotion patterns) of other, more dangerous species. Mimicry of most forms, be this visual or olfactory, is absent in mammals, but there are other land vertebrates such as lizards, frogs (Rojas 2017), and even snakes, in which such mimicry is present.

Mimicry is thus an important biological phenomenon that occurs for a number of reasons. In general, it may enable undetected invasion as is possible in some predatory wasps or spiders that invade ants' nests by means of mimicry of ant pheromones or body shape in order to gain access to food (Allan et al. 2002; Malcicka et al. 2015). Mimicry may be a method of self-protection for an otherwise defenceless organism by adopting the colors or patterns of another species. The ones being mimicked are most often unpalatable or even toxic, and the more convincing the mimicry, the greater the protection from potential predators. Adaptive mimicry of shape and color

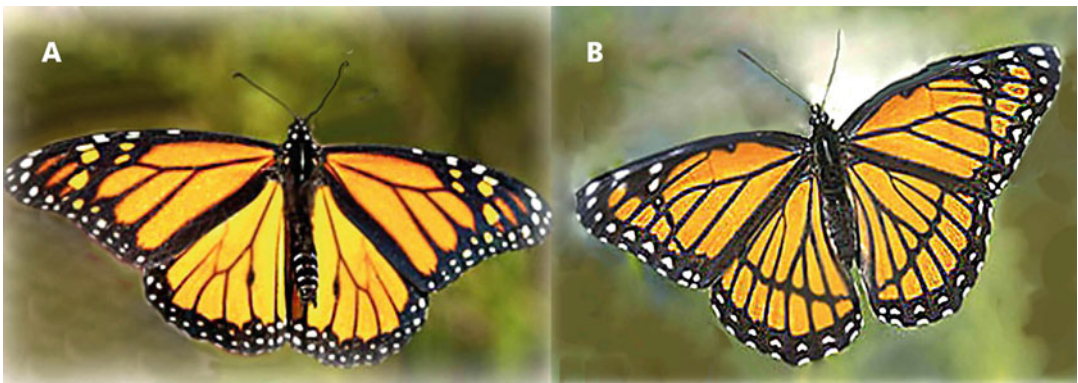
thus tends to be protective (Krajewski et al. 2004) and, in some contexts, may provide safer or the only access to a food source (Pereira et al. 2013).

The mimics have no direct way of making themselves more or less camouflaged. It is a permanent mimicry that is genetically inscribed and thus adaptive. There are many variations and shades to such bodily mimicry – in some, the mimicry is not all too convincing (sparingly defended prey species), while in other cases, the mimicking animals may be very well-camouflaged by having taken on rather accurate markings and shapes of their toxic counterparts (Fig. 1).

Mimicry, as H. Bates originally argued in the nineteenth century, involves three parties: the true identity of the species being mimicked; the mimicker; and the predator that is deceived by the mimicker and will not eat it because it looks like the unpalatable model (Wickler 1968). Müllerian mimicry formulated usually involves at least two parties, both of which are unpalatable or toxic. The two share common predators and mimic each other to their mutual benefit, leading to the predator's avoidance of both (Sherratt 2008).

Adaptive signals of mimicry are not confined to visual signals. Some species utilize the recipients' ability to perceive vibrations, scents, or flashing lights that can serve equally well to

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**Mimicry, Fig. 1** Left, monarch butterfly (*Danaus plexippus*); right, viceroy butterfly, (*Limenitis archippus*), both of North America. Note their similarity in color and patterns. These two species were often cited as classic Batesian mimicry adaptations (the harmless viceroy

mimicking the toxic monarch butterfly). However, the viceroy is now known to be poisonous too, giving each butterfly twice the protection from predators; thus are examples of Mullerian mimicry

deceive, i.e., stop potential predators from eating them, but the mimicry can also be used to attract potential partners either as honest courtship signals or to be deceptive in order to attract potential prey.

In fishes and invertebrates in the sea, such as salmon (Weir et al. 2016), sunfish (Rios-Cardenas and Webster 2008), peacock blenny (Gonçalves et al. 2003), squid (Hanlon et al. (2002), and many others, it is relatively common to find so-called sneaker males that are not only substantially smaller but mimic females and often succeed precisely because they are perceived by the dominant male as constituting no direct and immediate threat.

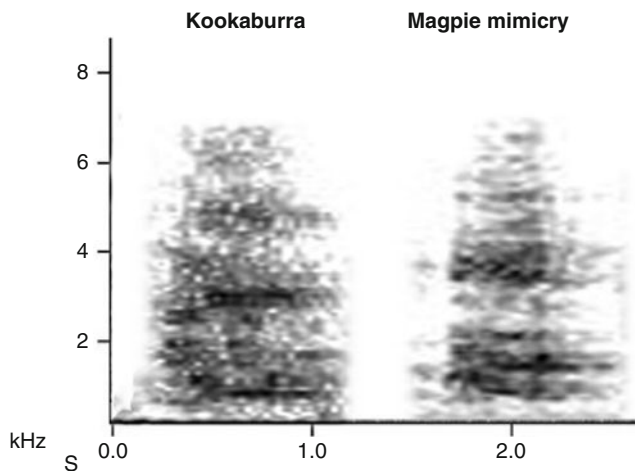
### Vocal Mimicry in Birds

Sound signals from different species or between male and female can be or become convergent or more similar. This may be an indication of a - well-tuned and well-matched pair, as, for instance, in magpie-larks, *Grallina cyanoleuca* (Hall and Magrath (2007). They duet, and these duets may overlap, but usually the calls of two birds follow each other closely and are so very similar and so precisely timed that apart from physical distance

of the two birds (and possible localization of different sound sources), they may sound like the vocalizations of one bird. This is called convergence, not mimicry.

Vocal mimicry is not convergence of sounds within its own species and its own vocal repertoire. Unlike mimicry of shape, color, and/or patterns, vocal mimicry does not exist as part of the species' own specific repertoire but only as a potential capacity. Mimicked sound signals are thus in a class of their own. As long as they are produced via the syrinx (not air sacs or wings), such sound signals have to be learned. The ability to produce identifiably mimicked sounds is one that each bird has to learn and acquire individually. For physiological and other reasons, some songbirds may not be able to mimic another bird very well (such as frequency range), but, in general, mimicry of another bird or even of mammals (dog barks, horse neighing, and of human speech) may be surprisingly accurate (Kelley and Healy 2011; Kaplan 2000, 2015).

The ability to mimic tends to exist only in songbird species that are lifelong learners and are able to integrate new sounds into their own repertoire at any time in their adult lives (unlike songbirds with fixed song learning periods and crystallized song, as in the zebra finch) (Fig. 2).



**Mimicry, Fig. 2** Sonograms: (a) one element of the loud and noisy typical kookaburra “laugh” and (b) the magpie’s rendition. Although the magpie’s own song is largely tonal and melodious, the bird successfully rendered the noisy

quality of the sound (gray fuzzy) and its loudness (energy to 5 kHz). Australian magpies, *Gymnorhina tibicen*, are among the most accomplished Australian songbird mimics, apart from lyrebirds (see also Kaplan 2000)



In general, vocal mimicry in birds could be regarded as a paradox. Vocal behavior in birds is species-specific and identifies a species, while any mimicry blurs or contradicts species identification (Hausberger et al. 1991).

According to Goller and Shizuka (2018), vocal mimicry is widespread among songbirds and parrots but perhaps not as widespread as was once thought. Goller and Shizuka identified 339 species out of their sample of 4,410 songbirds. Importantly, unlike the mimics of color and patterns in a wide variety of non-vertebrates and some vertebrates, vocal mimicry is not a stable behavioral attribute. It apparently evolved independently at least 237 times and was lost at least 52 times (Goller and Shizuka 2018).

### Functions of Vocal Mimicry

In animal behavior one expects to be able to identify functions that serve the species in its survival. Vocal mimicry, however, extends over a wide range of different functions, some of which may be adaptive (Baylis 1982), while others have no obvious function, and there is little consistency across species. Some parasitizing cuckoo chicks learn to approximate the food-begging calls of the host chicks, as do channel-billed cuckoos (imitating nestling currawongs and magpies; Kaplan 2015). This has also been evident in common cuckoo chicks raised by various warblers (Butchart et al. 2003). The ability of these cuckoo chicks to approximate the food-begging calls of the species raising them may well have survival value, and thus it is an adaptive behavior.

When birds mimic their own parents or members of their group, accuracy about a specific sound profile may ensure vocal recognition and also facilitate and enhance communication within groups (Wheatcroft and Price 2013).

Another type of mimicry is connected with territoriality. Birds may copy sounds of neighbors of the same species (Putland et al. 2006). Territorial birds tend to share part of their repertoire with permanent neighbors.

In the above cited contexts, the mimicked sequences are still part of the natural repertoire even if partly adopting a neighbors' set of sounds. In the latter context, it is thought that sharing repertoire reduces competition between neighbors, but such sharing can also be deceptive in certain circumstances (Wilson and Vehrencamp 2001).

Other examples of mimicry in the wild are reported cases of pink cockatoos raised by galahs adopting the vocalizations of their host parents (Rowley and Chapman 1986). The African grey parrot also mimics in the wild (Cruickshank et al. 1993), furnishing at least some anecdotal evidence that parrot mimicry is not just an artifact of captivity and of living in human company (Fig. 3).

Particularly in lyrebirds, mimicry is used as embellishment in the male's courtship display. It can involve calls and song sequence of other avian species, sometimes even sounds of mammals or inanimate objects, the purpose being to make the song more attractive for a female to choose the courting male over other males.



**Mimicry, Fig. 3** Red-lored parrot, *Amazona autumnalis*, of Central and South America may be one of the few cases of mimicry observed in the wild (pers. observation in Guatemala)



## Vocal Mimicry and Cognition

The cognitively interesting aspects of vocal mimicry, be they short or relatively long, demonstrate very clearly that vocal mimicry is the result of learned behavior. In human babies, the acquisition of human speech also begins with mimicry that is constantly socially shaped by parents who give signals of strong social approval when babblings such as “mamama” eventually turn into “mama,” meaning that syllables are beginning to be shaped into words. In a study of juvenile magpie babblings, it was found that the stages of vocal development match human babbling stages (Kaplan 2017). As in human babbling, the sounds produced are initially not intentional, but, in human social contexts, the mimicry gradually turns into socially meaningful words.

Vocal mimicry in birds was said not to have reached the stage of sounds developing into independent (no longer mimicked) stable and identifiable signals (language). In birds, vocal mimicry is said to remain just that: mimicry. As has been shown above, even such mimicry can be used to deceive and thus be an intentional act. Moreover, this has been proved incorrect in some instances of wild, untrained songbirds. In one case, an Australian magpie had learned to call a dog at the very moment when a cat approached the bird, roosting on a tree trunk in a hostile manner. Instead of fleeing, the bird called the dog by name. On being called, the dog came running chasing the cat away (Kaplan 2019). The magpie’s calling signifies a new context for the mimicked name and represents an intentional act. The interaction between cat/dog/magpie suggests that the bird had learned to associate the word/sound not just with a specific animal but that the word could call in help. Cognitively, this is quite a complex process.

In another context, African drongos had learned alarm calls of other species in order to frighten groups of birds away and then access the bounty of flying insects (Munn 1986). Similar reports aiding the acquisition of food resources



**Mimicry, Fig. 4** The fork-tailed drongo, *Dicrurus adsimilis*, furnishes one of the best and most complex examples of mimicry. Their varied deceptive alarm calls make other species flee and leave behind valuable food sources for drongos to exploit (Attis 1979, Creative Commons/Wikipedia)

have also been reported in great tits (Møller 1988; Satischandra et al. 2010) (Fig. 4).

The fork-tailed drongo of South America even varies deceptive mimicked alarm calls so that other birds are tricked every time. It causes them to flee while the mimicking bird is able to collect and even steal food (Flower et al. 2014). Clearly, vocal mimicry can reflect not just learning ability but additional cognitive abilities if such mimicry is effectively applied in new situations. Both adaptive and vocal mimicry continue therefore to be of great interest to science. The latest discoveries suggest that both, adaptive and cognitive mimicry, have long evolutionary trajectories and still produce surprising and novel applications and contexts.

## Cross-References

► [Cuckoo Brood Parasitism](#)

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## Mind

### ► Cognition

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## Mind Reader

### ► Receiver

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## Mind-Body Problem

### ► Reductionism

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## Mind-Brain Problem

### ► Reductionism

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## Miniaturization

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### What Is Miniaturization?

Miniaturization represents a morphological phenomenon that leads to the extreme body reduction of a lineage in comparison to a non-miniaturized and larger ancestral (Hanken and Wake 1993). This phenomenon has independently evolved several times among metazoans, including several vertebrate and invertebrate lineages (Hanken and Wake 1993; Hedges 2008; Weitzman and Vari 1988). The evolution of such a reduced body size is associated with dramatic changes in anatomy, ecology, and physiology for the lineages (Hanken and Wake 1993), most likely favoring and/or increasing the lineage fitness, for instance, the occupation of new niches, to explore new food resources, to avoid predators, to reduce intra- and interspecific competition, and to promote rapid reproductive maturity (Hanken and Wake 1993).

Miniaturization might be especially common in certain environments (Hanken and Wake 1993), and the fact that several of the smallest and largest animals are found in islands has historically raised

the attention of several biologists. This curious phenomenon is known as “the island rule” (Van Valen 1973) and depicts the traditional scenario in which large animals tend to become smaller (=insular dwarfism), and small animals tend to be larger (=insular gigantism) on islands. For instance, most of the smallest vertebrates in the world are island inhabitants (e.g., Glaw et al. 2021; Hedges 2008; Ocampo et al. 2018; Rittmeyer et al. 2012). Even though there has been a long debate whether such a trend applies to all vertebrates, insular dwarfism might be, in most cases, a result of taxa miniaturization, most likely associated with natural selection forces toward an optimal size (Van Valen 1973).

As miniaturization occurs in very different ways in vertebrates and invertebrates, this entry will address this phenomenon for the former group. When applicable, data for invertebrates will be included as examples.

## The Lowest Limits of Size

Given the wide diversity of metazoan body plans, it is not simple to establish an absolute value for the lowest size of an animal. While several invertebrate phyla might attain microscopic sizes, vertebrates with the lowest sizes reach an average body size of about 7–35 mm (Kottelat et al. 2006; Rittmeyer et al. 2012). Extremely reduced body sizes in ectotherm vertebrates include, for instance, the fish genus, *Paedocypris*, with a total mean length of 7.9 mm; the frog *Paedophryne amauensis*, with a mean of 7.7 mm (Rittmeyer et al. 2012); the hummingbird of Cuba (total length of about 64 mm, *Mellisuga helenae* Ocampo et al. 2018); the snake *Tetracheilostoma bilineata* (total length of about 100 mm; Hedges 2008); and the lizard, *Brookesia nana* (total length of about 21 mm; Glaw et al. 2021). Extreme size reduction seems to occur more drastically in ectotherms and is directly associated with body energetic demands.

Decrease of the body size also involves structural modifications to maintain functional efficiency at a strongly reduced size (Hanken and Wake 1993; Rieppel 1996). The reduction in

body size is associated with a change of structural proportions and may lead to the transformation of structures that are possibly attained by the reduction of tissue cell layers and/or reduction of cell volume (Rensch 1948). However, there is a minimum critical size that the species can reach in order not to impair its biological functions, such as feeding, locomotion, and reproduction (Hanken and Wake 1993; Rieppel 1996), with such a lower limit being constrained by the maximum volume that organs can fill in the body cavity (Rensch 1948). For instance, the number of clutch size and egg shape seem to be constrained by the extreme reduction of the miniaturized snake *Tetracheilostoma carlae* (Hedges 2008). In this species, the clutch size is of one, a result of the tradeoff between clutch size and relative offspring size, in combination with the tubular body shape of snakes (Hedges 2008). Such a tradeoff seems to also occur in other small-sized snake species (Hedges 2008).

## Morphological Consequences of Miniaturization

Miniaturization is rather much more than attaining a very reduced size (Hanken and Wake 1993). Besides evaluating the general morphological alterations that occur in miniaturized lineages, the phylogenetic position of such miniaturized clades must be evaluated to distinguish derived characters that were a result of miniaturization, from synapomorphies that precede the size reduction (Pérez-Ben et al. 2018). Three general consequences of miniaturization have been previously identified for tetrapods, although it might sometimes be applied to other metazoans: (i) structural simplification or reduction; (ii) emergence of morphological novelties; and (iii) increased intraspecific morphological variation (Hanken and Wake 1993).

Structural simplification or structural reduction is one of the best documented consequences of miniaturization among metazoans, being associated with the reduction or complete loss of organs and/or systems (Hanken and Wake 1993; Rieppel 1996). In vertebrates, for instance, these

consequences have been identified in the loss of several skull and appendicular skeleton elements (Rieppel 1996). Most morphological simplifications and reductions are associated with the skull because it houses several fundamental organs for the organism survival, such as the brain, inner ear, and eyes, and must not decrease in size beyond a specific limit (Hanken and Wake 1993; Rieppel 1996).

The emergence of morphological novelties is intimately associated with size decrease and seem to compensate for the reduction of organs and/or systems of vital function (Hanken and Wake 1993). This consequence is widespread among vertebrates and invertebrates, with the emergence of several remarkable structures, such as hyperossified skulls, the subcephalic copulatory organ of phallostethid fishes, and the ciliated wings of a few beetles (Hanken and Wake 1993; Yeh 2002). Osteological novelties among tetrapods are highly variable; however, miniaturized lineages of tetrapods are known for their proportionally large sense organs and their skeletal elements (Rieppel 1996). These changes might be a result of the conservative negative allometry between the brain, eyes and otic capsules in vertebrates, as well as the constraints imposed on nervous and sensory systems to maintain functional efficiency even at a small-sized head. Given such alterations, the skull (mostly the braincase) must go through an extensive “packaging effect” due to the need for spatial arrangement to maintain fundamental skeletal functions such as feeding (Rieppel 1996).

Increased morphological variability within species is the third morphological consequence of miniaturization, being a direct result of the reduction or morphological novelty of the lineage. Among vertebrates, it is usually associated with late-development skeletal structures, leading to variations that may occur intra-individually or within a population (Hanken and Wake 1993). Such an evolutionary consequence has been thoroughly detailed for the salamander of the genus *Thorius* (Hanken and Wake 1993), with the presence/absence of elements such as the septomaxillary bone.

## The Role of Heterochrony in Miniaturization

Miniaturization has been historically associated with the developmental consequences of heterochrony, which can be defined as changes in the rate or timing of developmental events over evolutionary time (Gould 1977; Hanken and Wake 1993). Two main heterochronic phenotypes are associated with miniaturization: (i) paedomorphism and (ii) peramorphism (Gould 1977; Hanken and Wake 1993; Rieppel 1996).

Paedomorphism occurs when later stages of ontogeny of an organism retain characteristics of earlier stages of development of its ancestor (Gould 1977). Such characteristics might be retained due to the truncation of growth period (known as progenesis), by the decrease of the growth rate (neoteny) or by a delayed onset of developmental processes (postdisplacement; Gould 1977). In this sense, it seems that elements that appear in later stages of ontogeny suffer greater variation in miniaturized species if compared to the ones that emerge earlier (Hanken and Wake 1993). Some examples include the loss or extreme simplification of skull elements in anurans, the reduction of number of digits in salamanders (Hanken and Wake 1993), loss of skull and post-cranial elements/simplification in Squamata (Rieppel 1996), the loss of cranial crests in mammals (Rieppel 1996), and the distinct skeletal morphology in a few fish species (Britz et al. 2009). For instance, skull bones that are frequently lost in miniaturized anurans – palatines, columellae, and quadratojugals – are among the last to ossify in frogs, being consistent with paedomorphosis (Yeh 2002). However, paedomorphosis is not necessarily strictly correlated to the miniaturization of a lineage and might be independently responsible for the generation of morphological novelties and simplifications (e.g., Pérez-Ben et al. 2018). For instance, this phenomenon might have been fundamental in generating the avian skull bauplan with large brains and to enable beak elongation and cranial kinesis along with the evolution of the lineage (Bhullar et al. 2016).



On the other hand, peramorphic organisms exhibit developmental processes that extend beyond the developmental stages of their ancestral lineage, producing adults with exaggerated characteristics (Gould 1977; Hanken and Wake 1993). Some examples include the hyperossified skull of a few lizards (e.g., Daza et al. 2008) and anurans (Paluh et al. 2020). These exaggerated characteristics play an important role in the generation of morphological novelties, one of the main consequences of miniaturization. On the other hand, peramorphism might also act to generate large body sizes, as its fundamental role in the evolution of multiple fossil lineages including non-avian dinosaurs (Foth et al. 2016), and to the general bauplan of the avian skull (Plateau and Foth 2020).

## Miniaturization in Vertebrates

Miniaturization is extensive and well-documented for several major vertebrate clades, such as fishes (e.g., Weitzman and Vari 1988), amphibians (e.g., Hanken and Wake 1993), lizards (e.g., Glaw et al. 2021), snakes (e.g., Rieppel 1996;), birds (e.g., Ocampo et al. 2018), and mammals (e.g., Rowe 2020). Indeed, this phenomenon has been historically hypothesized as a key feature in the evolution of many major taxa among vertebrates, including snakes (Rieppel 1996), lissamphibians (but see Pérez-Ben et al. 2018), birds (Lee et al. 2014), and mammals (Rowe 2020), as well as the origin of several morphological simplifications, as the simple anatomy of the lung in the first amniotes (Lambertz et al. 2015), and also by favoring the evolution of endothermy in the theropod lineage leading to birds (Rezende et al. 2020). However, as the endothermic metabolism of birds and mammals dictates a larger minimum adult body size compared to ectotherms, consequently, miniaturization is more common – and certainly more extreme – in fishes, amphibians, and reptiles (Hanken and Wake 1993).

Miniaturization has independently occurred several times along fishes evolution, being a common phenomenon among teleosts, with such a group exhibiting several examples of the

reduction, structural simplification, morphological novelties (e.g., hyperossification), and increased morphological variability (Weitzman and Vari 1988; Hanken and Wake 1993; Britz et al. 2009). While larger fishes seem to occur in marine environments, smaller lineages – specially miniatures – are most likely to occur (but not exclusively) in more complex environments, such as the South American streams (Weitzman and Vari 1988). For instance, representatives of the genus *Paedocypris*, a cyprinid fish of about ~10 mm long, is one of the smallest vertebrates currently known (Britz and Kottelat 2008). This lineage exhibits a number of unique specializations that consists of a mixture of truncated characters resembling larval stages of other members from the family, as well as several novel autapomorphic features, as a hypertrophied genital papilla in males that are most likely consistent with their extreme miniaturization (Britz and Kottelat 2008). Indeed, as *Paedocypris* spp., other freshwater fishes (e.g., *Danionella dracula*; Britz et al. 2009), specially characiforms and siluriforms, represent a model for the study of the evolution of miniaturization in the group (Britz et al. 2009; Weitzman and Vari 1988). However, the phenomenon of miniaturization might occur under poor environmental conditions, pushing the population to rapid miniaturization. For instance, recent studies (e.g., Esin et al. 2020) have detected paedomorphic miniaturization in a population of cyprinid fishes (*Salvelinus malma*) as an adaptation of volcanic impact, with the occurrence of changes in the lifestyles, physiological characteristics, shortening of lifespan, and anatomical simplification in the expressive short period of about 25 years. Thus, under the volcanic impact, the species attained, through paedomorphic miniaturization, an evolutionary mechanism that enabled the successful reproductive cycle under high risks (Esin et al. 2020).

As fishes, amphibians represent the group with best documented processes that result from miniaturization (Hanken and Wake 1993). This phenomenon has figured in discussions of the evolution of the three extant amphibian orders from their much larger temnospondyl ancestors, although such a phenomenon has been recently

unrelated to their evolution (but see Pérez-Ben et al. 2018). Despite that, several instances of miniaturization have occurred in salamanders – as the genus *Thorius* (Hanken and Wake 1993) – in several lineages of anurans (Yeh 2002), and caecilians (Hanken and Wake 1993) with several morphological novelties, variation and the reduction or digit loss, and/or simplification of the skull and nervous system (Hanken and Wake 1993). Among amphibians, life history traits are also associated and constrained by miniaturization. For instance, among several miniaturized brachycephalids, leptodactylids, and microhylids, the laryngeal apparatus is highly simplified, clutch sizes are smaller, and miniaturization might have also played an important role in other life history strategies (Estrada and Hedges 1996), as the high incidence of direct development (Rittmeyer et al. 2012; Fig. 1).

Although skull hyperossification has previously been hypothesized as a byproduct of miniaturization in anurans, such a view has recently been rejected for anurans as a whole, with hyperossification most likely representing a peramorphic trait possibly associated with accelerated ontogenetic trajectories and morphological change unrelated to size reduction (see Paluh et al. 2020). However, the relatively large braincase and sensory capsules present in miniaturized anurans seem to indicate that the neurocranium is subject

to a minimum constraint (Paluh et al. 2020) as observed in other vertebrates (Rieppel 1996).

The occurrence of miniaturization among non-avian reptiles is undoubtedly more extensively detailed for squamates – specially for lizards and snakes (Rieppel 1996; Hedges 2008). Even though there are several small-sized lineages of Testudines that have been assigned as miniaturized species (= small taxa in Vlachos and Rabi 2018), recent studies found no direct relation with small size and the phenomenon of miniaturization in these taxa (Angielczyk and Feldman 2013). There seems to be no evident miniaturized living lineage of Crocodylia, although a few extinct taxa exhibit reduced sizes most likely associated with miniaturization (Pinheiro et al. 2013). The most speciose of all miniaturized lizard species is possibly comprised by the species from the genus *Sphaerodactylus*, with miniaturized species exhibiting several morphological novelties/simplification of their skull related to the closure of the post-temporal fossae, reduced skull length and diameter, and bone arrangement (Daza et al. 2008). Among snakes, extreme cases of miniaturization are found in blind snakes, threadsnakes, and worm snakes traditionally known as “Scolecophidia.” Recent works have hypothesized that several characteristics of the group are a result from miniaturization possibly driven by paedomorphosis, including the loss/reduction of



**Miniaturization, Fig. 1** Photos of *Brachycephalus bufonoides* (a) and *B. garbeanus* in life (b). Both species are miniaturized (~12–20 mm of body length in adults) and are restricted to areas of the Atlantic Forest in Brazil. The taxa exhibit several morphological novelties and

simplifications as the hyperossification of their skull, and emergence of new bones in the skull and post-cranial skeleton, and also exhibit direct development. (Photos: J. Perez Pombal Jr)

several skull bones in comparison to alethinophidian snakes (Strong et al. 2020).

Many of the miniaturized living lizards and snakes are found in islands worldwide (e.g., Hedges 2008), leading several authors to associate such a reduction to the island rule phenomena. Additionally, extreme size reduction in these lineages has also been postulated as a direct effect of fossoriality (Hanken and Wake 1993; Rieppel 1996). In such a view, hypotheses suggest that miniaturization represent a consequence of headfirst burrowing, in order to reduce the energy for soil burrowing, therefore generating convergent reinforced skulls with reduced mobility. This might seem the relation for the evolution of such miniaturized body sizes in blind snakes, threadsnakes, and worm snakes traditionally known as “Scoleophidia” (Hedges 2008). Regardless the relation of extreme body reduction to fossoriality, miniaturization in lizards and snakes are reported as structural simplification in the appendicular skeleton as well as morphological novelties in the skull and their associated muscles (Rieppel 1996).

Miniaturization in the lineage of birds is extensively reported for several extinct taxa, being considered as a major event in the origin and diversification of birds in relation to their closest theropod relatives, as well as the possible evolution of arboreality (Lee et al. 2014; Benson 2020). Indeed, many traits that accompanied the reduction of size are associated with developmental truncation, generating, in this lineage, more robust and fused bones, short snouts, enlarged brains and eyes, and smaller teeth (Lee et al. 2014; Benson 2020). However, studies on the miniaturization of living lineages seem to be scarce in the literature. In this lineage, the tiniest bird currently known – the Cuban bee hummingbird, *Mellisuga helenae* – represents a species with several morphological novelties and simplification due to its extreme body size decrease (Ocampo et al. 2018). Hummingbirds, in general, include the smallest species of birds currently known, with the smallest species exhibiting a series of morphological simplifications and novelties, as a lower level of skull ossification, a highly compact skull (Ocampo et al. 2018). These skull traits are a direct result of body and brain size to accommodate disproportionally larger brain and

eyes without the need of increasing overall head size (Ocampo et al. 2018).

Miniaturization represented important milestones for the evolutionary process of mammals, being a key factor for the evolution of endothermy in the group, development of nocturnal habits, and other relevant ecological adaptations as lactation (Rowe 2020). Early mammals might have attained miniaturization by accelerated maturation of the skeleton at smaller sizes, with reduction in size being accompanied by remodeling of the skull and postcranial skeleton (Lautenschlager et al. 2018). For instance, recent studies suggest that the evolution of the mammalian jaw and middle ear are a result of the selective regimes imposed by extremely reduction during the mammaliaform transition (Lautenschlager et al. 2018). Miniaturization has occurred in a few mammal lineages, including rodents, shrews, moles, lemurs, and bats. As very small mammal species have very high mass-specific metabolic rates, miniaturized lineages thus require highly caloric and nutritious food. Therefore, small lineages are associated with highly caloric diets of seeds and insects, with no miniature mammalian species (below 15 g) being strictly herbivorous (Gliwicz and Taylor 2002).

## Cross-References

- Allometry
- Evolution
- Morphology
- Neoteny
- Ontogeny
- Salientia Morphology
- Testudines morphology
- Vertebrates (Chordata)
- Zoology

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## Minority Advantage

- [Frequency-Dependent Selection](#)

## *Mirounga angustirostris*

- [Elephant Seals](#)

## *Mirounga leonina*

- [Elephant Seals](#)

## Miroungini *Mirounga*

- [Elephant Seals](#)

## Mirror Recognition

- [Visual Self-Recognition](#)

## Mirror Self-Recognition

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## Synonyms

[Self-awareness](#); [Self-recognition](#)

## Definition

The ability to recognize oneself in a mirror.

## Introduction

Mirror self-recognition (MSR), the ability to recognize oneself in a mirror and “the ability to become the object of your own attention” (Gallup 1982, pp. 242–243) is considered to be a reliable indicator that humans and some other animals recognize their reflection in a mirror as an external representation of self (Amsterdam 1972; Anderson 1984; Gallup 1970; Rochat 2003). Researchers have used mirrors as tools to study the development and perception of self in human and nonhuman species. Developmental studies of MSR in humans indicate that the earliest age children first show self-directed behavior is 12–15 months and mark-directed behavior (passing the mark test) first emerges between 18–24 months (Amsterdam 1972; Anderson 1984; Bard et al. 2006; see review in Reiss and Morrison 2017). It has been theorized that proprioceptive awareness may be an antecedent of the onset of MSR and some of the proposed developmental correlates of MSR in children include sensorimotor intelligence, prosocial behavior, synchronic imitation, and pretend play (see review in Reiss and Morrison 2017). In an early paper, Gallup (1982) suggested both an



ontogenetic and phylogenetic link between MSR and empathy. MSR studies have been conducted with a variety of species and most fail to show unequivocal evidence of self-recognition (e.g., squid, manta rays, ants, pigeons, African grey parrots, dogs, horses, sea lions, killer whales, and monkeys) (see a review of some of these studies in Reiss and Morrison 2017).

Only a limited number of nonhuman species have demonstrated MSR: chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla gorilla*), bottlenose dolphins (*Tursiops truncatus*), Asian elephants (*Elephas maximus*), and the Eurasian magpie (*Pica pica*). Most of these species have either large brains and/or higher encephalization quotients (EQ - ratio between actual brain mass & predicted brain mass for an animal of a given size) than species lacking the capacity for MSR (see review in Parker et al. 1994; Reiss and Morrison 2017).

In MSR studies with mirror naïve humans, great apes, dolphins, elephants and magpies, it has been reported that during mirror exposure these phylogenetically divergent species progress through three strikingly similar stages of behavior: (1) social behavior (e.g., reacting as if viewing a conspecific) and mirror exploratory behavior (e.g., attempting to look over, under, or behind the mirror), (2) contingency-testing (e.g., producing repetitive behaviors at the mirror allowing the individual to perceive a corresponding relationship between its own behavior and the mirror image), and (3) self-directed behavior (e.g., viewing parts of their body or monitoring actions they perform that have been previously unobservable in the absence of the mirror) (Amsterdam 1972; Anderson 1984; Bard et al. 2006; Gallup 1970; Morrison and Reiss 2018; Plotnik et al. 2006; Povinelli et al. 1993; Prior et al. 2008; Reiss and Marino 2001).

## MSR in Nonhuman Primates

Gordon Gallup (1970) developed and utilized the first paradigm for testing MSR in nonhuman primates, the mirror test. In this groundbreaking

study, four chimpanzees were exposed to a full-length mirror and their behavior was documented over time. At the start of the study, the chimpanzees vocalized and performed social displays towards the mirror but over time these responses declined and were replaced by self-directed behaviors. Gallup considered the performance of self-directed behavior at the mirror as evidence of MSR in chimpanzees, but created what he considered a more objective experimental procedure, “the mark test,” to further confirm the presence of this ability. The mark test was conducted only after observing self-directed behavior in the chimpanzees (Gallup 1970). The chimpanzees were anesthetized and marked with a red dye devoid of odor or tactile cues above the uppermost portion of their eyebrow ridge and the upper part of the opposite ear, locations that could only be seen when at the mirror. Upon recovery from anesthesia, they were observed for 30 min in the absence of a mirror and then for 30 min when the mirror was reintroduced. The chimpanzees passed the mark test by exhibiting more mark-directed touching in the mirror condition than in the previous condition in which the mirror was absent. In some later studies with great apes, the animals were not anesthetized for the mark test (e.g., Bard et al. 2006; Lin et al. 1992). A similar test, “the rouge test,” was created by Amsterdam (1972) for use in developmental studies with children; however, children are never anesthetized prior to conducting the mark test. Studies with children have used less stringent criteria and passing the rouge/mark test typically requires that the child only touch the mark once or touch their face near the mark without comparing the frequency of touching to that area in the pre-mark condition (Amsterdam 1972; Bard et al. 2006; see review in Reiss and Morrison 2017).

Notably, in past studies with species that have shown the capacity for MSR, not all individuals tested pass the mark test, indicating that caution should be used when assuming that mark test results are the only indicator of MSR. The standard paradigm used in conducting MSR tests with nonhuman species involves exposing an individual to the mirror and only after self-directed behaviors are observed, mark tests are conducted.

Importantly, the performance of self-directed behavior during the period of mirror exposure itself is an indicator of MSR and the mark test is further confirmation (Gallup 1994; Morrison and Reiss 2018; Povinelli et al. 1993; Reiss and Morrison 2017). As previously stated by Gallup (1994),

I have never maintained that the mark test is the *sine qua non* of self-recognition. Appropriate behavior in response to unobtrusively applied facial marks that can only be seen in a mirror constitutes a means of validating impressions that arise out of seeing animals use mirrors in ways that suggest they realize that their behavior is the source of the behavior depicted in the reflection. In trying to demonstrate self-recognition in other species, some people appear to have lost sight of this and have focused almost exclusively on the mark test (p. 42).

MSR has been well documented in all great ape species; however, studies with lesser apes and both old world and new world monkeys have not reported evidence for the spontaneous development of MSR (see reviews in Anderson and Gallup 2015; Reiss and Morrison 2017). Studies of the development of MSR in chimpanzees have reported the ages at which they exhibit social, contingency testing, self-directed and mark directed behavior. Chimpanzees have been observed to exhibit social behavior towards a mirror between 7 and 9 months of age and contingency-testing commenced at about 10 months of age (Robert 1986). Self-directed behavior has been reported to first emerge between 24 months (Bard et al. 2006; Lin et al. 1992) to 3 years, 3 months (de Veer et al. 2002; Povinelli et al. 1993) and mark-directed behavior to be exhibited between 2 years 4 months (Bard et al. 2006; Lin et al. 1992) and 3 years 9 months (de Veer et al. 2002; Povinelli et al. 1993). Different criteria used by Povinelli et al. (1993), de Veer et al. (2002), Lin et al. (1992), and Bard et al. (2006) when judging the performance of self-directed behavior and when determining mark test results may partially explain the discrepancy in age of onset reported in the literature for chimpanzees.

Reports of MSR in ape species led to the speculation and theory that MSR was rooted in common aspects of primate social ecology,

neurobiology, and cognition and led to the assumption and perspective that this ability was confined to humans and their closest relatives, the great apes. However, Gallup (1979) suggested that other large-brained social mammals, such as dolphins, other cetaceans, and elephants that showed empathy (e.g., care-giving, or targeted helping-behavior towards others), would be good candidates to test for MSR.

## MSR in Dolphins

Fifteen years after Gallup's suggestion to conduct mirror tests with dolphins, Marino et al. (1994) conducted a study in which they exposed two mirror naïve 7-year old captive-born, male bottlenose dolphins to a mirror. Gallup's basic procedural approach for testing MSR in apes was used but slightly modified to test the non-handed dolphins that were unable to touch the mark. As in MSR testing with apes, the criteria for demonstrating MSR in dolphins was the demonstration of self-directed behavior during mirror exposure, but the criteria for passing the subsequent mark tests required that the dolphin show mark-directed behavior by orienting its body in a manner that exposed the mark to the mirror. The dolphins remained together during mirror exposure and testing and were marked and tested individually within the social context. During the period of mirror exposure, the dolphins showed evidence of similar stages of behavior as reported in mirror studies with great apes, which was suggestive of MSR. However, the results were inconclusive due to the inability to conduct a sufficient number of mark tests. Each dolphin was only marked once with zinc oxide, a white visible mark, and their adverse reactions to being marked resulted in no further mark tests being conducted. Marten and Psarakos (1994) reported similar suggestive yet inconclusive findings with four out of five dolphins in another test of MSR.

Reiss and Marino (2001) demonstrated the first conclusive evidence for MSR in dolphins. They reported that two captive-born male bottlenose dolphins, ages 13 and 17-years old, exhibited self-directed behavior at a mirror and passed

multiple mark tests. Similar procedures were used as those described in Marino et al. (1994), but this study used the requisite combination of control and test situations. Multiple mark tests were conducted in which the individuals were marked on different areas of their body that could not be viewed in the absence of the mirror. Dolphins were observed in the presence of a mirror in the pre-mark condition for 30 min and then in the post-mark condition for 30 min. The criteria for passing the mark tests required that the dolphin show mark-directed behavior by orienting its body to the mirror such that the mark was exposed to the mirror and that these orientations occurred more frequently in the post-mark versus the pre-mark condition. It was reported that during mirror exposure, the dolphins showed behavioral responses consistent with those reported in chimpanzees. Both dolphins exhibited self-directed behaviors at the mirror (i.e., repetitive body movements, open mouth & close eye viewing, & varieties of bubble production) and in the mark tests, after being marked, the dolphin's first mirror orientations exposed the marked area of their bodies to the mirror. Both dolphins passed multiple mark tests.

Reiss and Marino (2001) reported that their findings provided evidence for cognitive convergence in evolutionarily divergent species, large-brained primates, and dolphins. Bottlenose dolphins, like great apes and humans, have brains that show high degrees of encephalization and neocortical expansion; however, the dolphin brain also differs from those of primates in many ways including aspects of the cortical cytoarchitecture and organization (Marino et al. 2008; Reiss and Marino 2001). Showing MSR in dolphins provides evidence that the ability is not a byproduct of factors specific to humans and their close relatives the great apes but may be linked instead to a high degree of encephalization and cognitive ability more widely distributed than previously thought (Reiss and Marino 2001).

Using similar methodology as Reiss and Marino's (2001) study with dolphins, Morrison and Reiss (2018) conducted a study to investigate the age of emergence of MSR in two young

bottlenose dolphins to identify how humans, great apes, and dolphins compare developmentally with regards to MSR. Young dolphins show precocious sensorimotor and social development, factors that appear to correlate with the emergence of MSR in humans, thus it was predicted that this species might show the early development of MSR. Confirming prior findings of MSR in dolphins, it was reported that one dolphin demonstrated self-directed behavior at 7 months of age, an age earlier than reported for humans, and self-directed behavior was exhibited by both dolphins at a younger age than reported for chimpanzees. Both dolphins passed mark tests at a comparable age reported for children and at a younger age than chimpanzees. The authors suggest that the precocious development of MSR in this species may be attributed to the precocious development of their motor skills, muscle development, coordination, and social awareness at birth, skills that occur later in development in children and great apes.

## MSR in Elephants

Elephants were optimal candidates for MSR studies. They have large brains and relatively high EQ values, are socially complex, and show evidence for empathy (Plotnik et al. 2006) and consolation behavior directed towards conspecifics (Plotnik and de Waal 2014). Povinelli (1989) exposed two adult female Asian elephants to a mirror positioned outside of the bars of the elephants' enclosure and just beyond the reach of the elephants' trunk. Neither elephant exhibited self-directed behavior and both failed to pass the mark test; however, both elephants demonstrated spontaneous mirror-guided behavior to gain access to food that could only be seen in the mirror. Plotnik et al., (2006) tested three adult female Asian elephants that were exposed to a large-sized acrylic mirror affixed to a wall of their outdoor holding yard that the elephants could approach and touch. The elephants followed a similar progression of behavioral stages during mirror exposure as described in chimpanzees (Gallup 1970; Povinelli et al. 1993) and dolphins (Reiss and Marino 2001). All three

elephants exhibited self-directed behavior at the mirror and mark and sham mark tests were simultaneously conducted to control for possible olfactory and tactile cues resulting in only a visual component to differentiate between the mark and sham-mark (see Plotnik et al. 2006). Using the same criterion for passing the mark test as used with chimps, one out of the three elephants tested, passed the test.

Plotnik et al. (2006) suggested that the disparity between their findings and those reported by Povinelli (1989) could be attributed to methodological differences. Povinelli (1989) used a smaller mirror that was placed at an angle outside of the elephant exhibit and the elephants could not touch the mirror. The reflected image of the elephant would have been smaller in comparison to their actual body size. The size and placement of the mirror in the Plotnik et al. (2006) study afforded the elephants the ability and opportunity to see their entire body in the mirror and at its normal size. The mirror was mounted on a wall in the elephants' exhibit allowing the elephants to touch the mirror and determine their proximity to the mirror and the optimal viewing distance. In the majority of studies demonstrating MSR in other species (apes, dolphins, and magpies), the animals had direct access to mirrors as well.

## MSR in Avian Species

Corvids were considered to be good candidates for studying MSR because they exhibit novel foraging behaviors using tools and show evidence of advanced planning and visual perspective-taking (Emery and Clayton 2004; Lefebvre et al. 1997). Magpies and other corvids (e.g., crows, ravens, jackdaws, nutcrackers, & jays) have especially high EQs (Rehkämper et al. 1991) and have developed a relatively large forebrain pallium, although they lack a neocortex. Prior et al. (2008) reported the first evidence of MSR in a non-mammalian species of corvid, the Eurasian magpie. They tested five birds for MSR and three of the five birds showed social behavior that decreased with mirror exposure and instances of contingency-testing

behavior were observed. Sham mark tests (black sticker) and mark tests (colored stickers) were conducted and three of the five birds tested exhibited mirror-mediated mark-directed behavior towards the colored stickers, but not the sham mark (Prior et al. 2008).

Soler et al. (2014) attempted to replicate Prior et al.'s (2008) study by using the same methodology with nine adult jackdaws (*Corvus monedula*). During initial mirror exposure, the jackdaws did not exhibit social behavior; however, they explored the mirror by looking behind it and pecking at it, and they exhibited self-contingent behaviors (Soler et al. 2014). In both the mirror and the control (cardboard, no mirror) conditions, the jackdaws touched and tried to remove the sticker; therefore, it was reported that none of the birds passed the mark test. The authors suggested that using stickers with birds is a methodological flaw because of tactile feedback from the birds' feathers.

More recently, Clary and Kelly (2016) developed what they considered to be an ecologically relevant test of MSR in which Clark's nutcrackers cached alone, in front of a conspecific, in the presence of a blurry mirror, or in the presence of a regular mirror and mark tests (red sticker) were also conducted in each of the mirror conditions. When caching, the nutcrackers did not treat the image in the blurry mirror as a conspecific and they were more likely to investigate the mark in the blurry mirror condition. The authors suggest that these results reveal that nutcrackers may be demonstrating a degree of self-recognition.

Although there are some interesting results with corvids, only the study with magpies (Prior et al. 2008) reported the occurrence of self-directed behavior during mirror exposure prior to being marked, but it was not quantified or described. Further studies with these species should be conducted to determine if they will demonstrate spontaneous mirror mediated self-directed behaviors and to describe such behaviors prior to conducting mark tests with the birds, which has been the standard approach with other species (Gallup and Anderson 2018; Morrison and Reiss 2018).

## Controversy Regarding MSR Research

MSR studies with nonhuman species have stimulated much interest, discussion, and debate regarding the methodology, implications, and significance of these findings (Suddendorf and Butler 2013). Suddendorf and Butler proposed that mark test results have been overinterpreted and the current evidence does not support MSR as indicative of self-awareness, as Gallup and others have proposed. Some discussions have centered on determining what type of data replication and methodologies may be required to provide more conclusive evidence for MSR in other species (Gallup and Anderson 2018). Other discussions have focused on the importance of the emergence and demonstration of self-directed behavior prior to being marked, as well as during mark tests, as requisite evidence for MSR (Morrison and Reiss 2018; Reiss and Morrison 2017) and the use of more nuanced ecologically relevant approaches to investigating MSR (Clary and Kelly 2016).

## Conclusion

MSR in nonhuman species has been a provocative topic in comparative cognition and the wider field of psychology. The discovery of the capacity for MSR in an evolutionarily divergent group of other large-brained highly social species has profound implications regarding the continuity of self-awareness in the biological world. MSR has been correlated with proprioception, social awareness, spatial awareness, EQ level, and with the capacity for empathy (in great apes, dolphins, & elephants), but a comprehensive understanding of all the factors that contribute to MSR remain unclear. The extant studies of MSR in other species have provided insights into the level of self-awareness in some nonhuman minds, although we remain at the periphery of understanding its full dimensions.

## Cross-References

- Cetacean Cognition
- Cognition

- Intelligence
- Primate Cognition
- Primates
- Self-Awareness
- Self-Directed Behavior
- Social Intelligence Hypothesis
- Theory of Mind
- Visual Self-Recognition

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## Misidentification

### ► Turing Test

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## Mismatch Hypothesis

### ► Oddity

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## Mitochondrial DNA

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## Synonyms

Eve gene; mtDNA

## Definition

Mitochondrial DNA is a small circular DNA found in mitochondria.

## Introduction

Mitochondrial DNA (mtDNA), discovered in 1963 by Margit and Sylvan Nass, is a small circular DNA present in the power house (mitochondria) of the eukaryotic cells. It was believed that the mtDNA is only found in the egg and is passed down to both sons and daughters from their mothers until it was found that the copy number of mtDNA is extremely high in oocytes ( $\geq 10^5$ ) as compared to the sperm (50–75), thus explaining the maternal inheritance which could have been a result of dilution of paternal contribution wherein the mitochondria from sperm are lost during embryogenesis. Since mtDNA is a nonrecombinant DNA, it passes down virtually unchanged through the direct maternal line over the generations (Giles et al. 1980; Pakendorf and Stoneking 2005). Therefore, it is also known as the “Eve gene.”

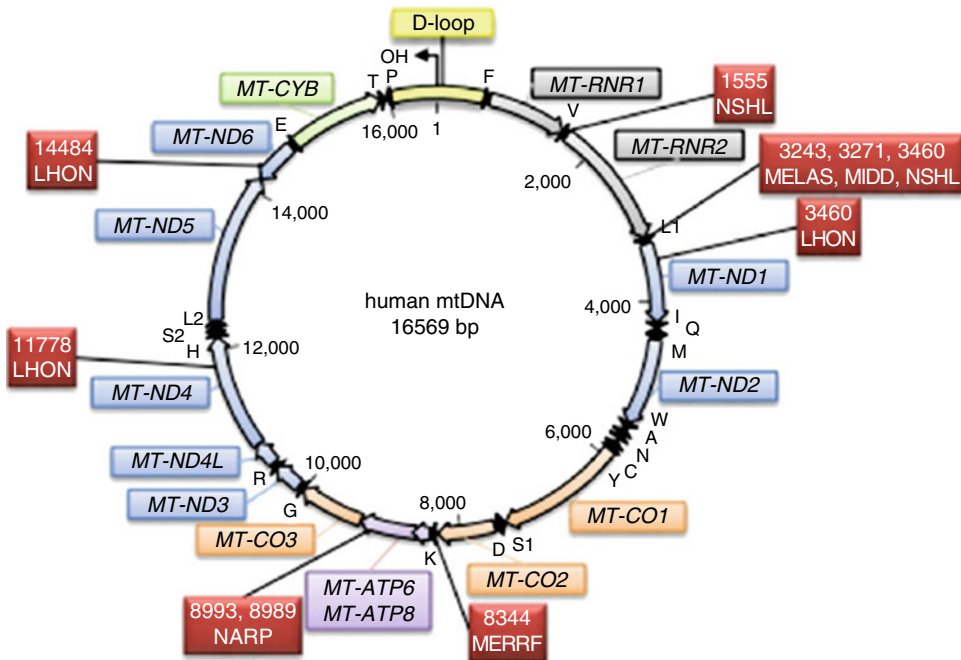
## Need for Mitochondrial DNA

The need for mitochondria to possess its own DNA is still debatable. However, many scientists

proposed “theory of endosymbiosis” which suggested that, billion years ago, mitochondria used to be independent single-celled organisms before they were swallowed by larger cells. Nevertheless, these mitochondria were not digested by these cells and developed a mutually beneficial relationship with the host cells. This mutualism further gave rise to more complex life forms over time (Brown et al. 1979). Another group of scientists also believe that mtDNA is present only to provide local control to mitochondria because pivotal proteins that regulate mitochondrial function are created in mitochondria itself and allow quicker and efficient regulation of energy production by the cell (Picard et al. 2013).

## Structure of mtDNA

Human mtDNA was the first significant portion of the human genome to be sequenced by Sanger’s laboratory, Cambridge, in 1981. There are 16,569 base pairs of mitochondrial DNA in human beings which encode for 37 genes. It also comprises of the control noncoding region (Fig. 1). Thirteen genes coded by mtDNA are essential for



**Mitochondrial DNA, Fig. 1** Representative image of human mitochondrial DNA (Adapted from Pinto et al. 2013)

normal mitochondrial function and involved in making enzymes for oxidative phosphorylation (a process that uses sugar and oxygen to produce ATPs), and the rest of them provide instructions for manufacture of transfer RNA (tRNA) and ribosomal RNA (rRNA) that help in assembly of amino acids into functional proteins. Mutations in mtDNA are generally heteroplasmic, and the wild-type and mutated mtDNA coexist in the same cell. These mutations can be associated to diverse forms of diseases and aging (Pakendorf and Stoneking 2005; Shuwen et al. 2017).

### mtDNA Inheritance

Though mtDNA are inherited through generations from mother to child, it still maintains its variability by the occurrence of high mutation rates due to lack of repair mechanisms and proofreading capabilities. The mutation rates of mitochondrial DNA are ten times higher than in nuclear DNA which may be a result of nucleotide imbalance in mitochondria that causes compromised DNA polymerase gamma fidelity and higher mitochondrial DNA mutation rates (Kujoth et al. 2007). This variability in mtDNA can be utilized in human identity tests, to map out ancestry and migration of a population and to evaluate the evolutionary phylogenetic by analyzing the short variable sections present in the noncoding region of mtDNA. Recently, it has been discovered that mtDNA plays crucial role in innate immune responses and inflammatory pathology and can also act as a novel marker for the prognosis of various diseases including cancer (Lee et al. 2016; Mills et al. 2017; Shuwen et al. 2017; West and Shadel 2017).

### mtDNA Replication

Mechanism of replication in mitochondrial DNA is still being investigated. It was considered for long that the maintenance of mitochondrial genome was simpler than nucleus for many years. Mammalian mitochondria lack all DNA repair systems and possess an eschewed DNA recombination. Mitochondria have only a single DNA polymerase, polymerase- $\gamma$ , and it was

suggested for long that Poly replicates mtDNA exclusively via one mechanism, involving only two priming events and a few proteins which is also referred to as “strand-displacement model.” A mechanism of replication for mammalian mtDNA was elaborated in the early 1970s from EM images of DNA isolated from rodent mitochondria by cesium chloride density centrifugation (Kasamatsu and Vinograd 1973). The EM images of mouse mtDNA suggested a model, whereby leading strand synthesis started at a specific site and advanced approximately two-thirds of the way around the molecule before second-strand DNA synthesis initiated (Kasamatsu and Vinograd 1973). Although it was earlier thought that displaced strand was coated with protein, RNA has more recently been proposed in its place. Furthermore, mtDNA molecules have now been demonstrated to possess all the features of conventional bidirectional replication, suggesting that the process and regulation of replication in mitochondria are complex, as befits a genome that is a core factor in human health and longevity.

### Regulating mtDNA Copy Number

A central question in organelle biogenesis is to determine the mechanism by which the cell controls mtDNA copy number. Based on the mechanism of replication found in mtDNA, it is suggested that the rate of mtDNA replication is determined by a balance between transcription initiation from the lagging strand and subsequent RNA processing steps to provide replication primers. It has not been proved yet that mtDNA copy number is regulated by the levels of mtDNA polymerase or other proteins associated with DNA strand elongation; however, mutations in these proteins may not result in less, or even loss of, mtDNA. It has been suggested that direct activation of the nuclear transcription factor NRF-1 results in stimulation of mitochondrial biogenesis coincident with increased synthesis of mtTFA (mitochondrial transcriptional factor A) owing to the interaction of NRF-1 as an activator of the nuclear gene for mtTFA. This result, along with studies in which loss of mtTFA results in loss of mtDNA and mitochondrial function, raises the

probability that mtTFA is a central feature of not only mtDNA transcription and replication but of organelle biogenesis itself (Holt et al. 1988).

## Conclusion

Human mitochondrial DNA (mtDNA) typically forms 5- $\mu$ m circles, or 16.5 kilobases, one genome in length. The mtDNA varies largely in size and form outside animal kingdom, yet it exists without fail to provide the cell with essential components of the respiratory chain (and ATP synthase). Therefore, any mutation caused in mtDNA can lead to respiratory chain dysfunction, which results in rare diseases in plants (Levings and Pring 1976; Newton and Coe 1986) and humans (Holt et al. 1988). Since budding yeast can grow anaerobically, hence, it can survive without mtDNA (Goldring et al. 1970). Also, the vertebrate cells cultivated in the laboratory on a diet of glucose far less concentrated than soda can achieve the same feat (Desjardins et al. 1985). Nevertheless, it is impossible for even a simple free-living multicellular organism, such as the nematode worm, to survive without mtDNA (Brown et al. 1979; Pakendorf and Stoneking 2005).

## Cross-References

- DNA
- Mutations
- RNA

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## Mitosis

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## Synonyms

Cell division; Equational division; Somatic cell division

## Definition

Mitosis is the process where a parent cell divides into two daughter cells and each receives an exact copy and number of the chromosomes (genetic material) and is called as equational division. It maintains cell growth and repair.

## History

In the seventeenth century, cellula was discovered as a building block of many organisms by Hooke, Van Leeuwenhoek, and others (Hook 1665; Leeuwenhock 1662). In the first half of the nineteenth century, Schleiden and Schwann established the cell theory, according to which all organisms are composed of tiny units, the cells (Schleiden 1838; Schwan 1839). In 1875, Strasburger published a comprehensive book about cell formation and cell division (Strasburger 1875). Strasburger's colleague Walther Flemming started detailed studies on dividing cells in different organs and organisms, mainly from animal kingdom. In 1873, Schneider drew the different steps of cell division (Schneider 1873). In between 1874 and 1876, Flemming described in more details whereas Schneider had postulated that the nucleus undergoes deformation during cell multiplication (Flemming 1874, 1875, 1876). Flemming showed that the scaffold and network within the nucleus transformed into "threads" which then separated into two groups. These two groups in turn formed two skeins, from

which the scaffold of the nuclei reappeared. By carefully studying wounds and scars, Flemming and his students found an accumulation of dividing cells in these tissues and concluded that the regeneration of tissues and organs occurs by cell division. In 1878 and 1879, Flemming coined the term "indirect nuclear division" because he had observed that a transformation of nuclear content had to take place before fission could occur. A cleavage of the nucleus and protoplasm which until then had been generally assumed was called direct nuclear division (Flemming 1878, 1879). The methods that Flemming had developed allowed to recognize a fibrous scaffold in nucleus which could easily be stained and was therefore named chromatin (stainable materials). In 1882 Walther Flemming introduced the term (derived from the Greek word, meaning thread).

## Stages of Mitosis

One round of DNA replication is followed by single round of chromosomes segregation to generate two genetically identical daughter cells.

Mitosis starts with the nuclear division (karyokinesis), corresponding to the formation of daughter nuclei, and usually ends with division of cytoplasm (cytokinesis). Mitosis is continuously divided into four stages: prophase, metaphase, anaphase, and telophase.

### Karyokinesis

#### Prophase

The first stage of mitotic cell division is prophase. At prophase the replicated chromosome with two closely related sister chromatids starts condensing. The mitotic spindle assembles outside the nucleus, between the two replicated and moved apart centrosomes (Fig. 1).

### Events Involved in Prophase Stage

1. The chromatin, which is visible in interphase, slowly condenses into well-defined chromosomes.
2. Each chromosome has duplicated during preceding S phase, and each of these sister



chromatids is held together at a centromeric region (constricted region).

3. At centromere, the sister chromatids are kept together by a member of the SMC (structural maintenance of chromosomes) family of proteins called cohesin. Cohesin is a protein complex composed of four subunits (Smc1 and Smc3 with two ATPase domains and two additional subunits Scc1 and Scc3, with ATPase domains forming a ring structure).
4. Prophase ends with the disappearance of nucleolus and breakdown of nuclear envelope. Nuclear envelope disruption is a complex multistep process that begins when M-CDK phosphorylates several subunits of the nuclear pore complexes present in the nuclear envelope, and this initiates the disassembly of nuclear pore complexes.
5. M-CDK phosphorylates components of the nuclear lamina which lies beneath the envelope. The phosphorylation of nuclear lamina components results in disassembly of the nuclear lamina and breakdown of membrane envelope into small vesicles.
6. In most cells, the disruption of the nuclear envelope marks the end of the prophase of mitosis. However, this disruption of the nuclear envelope is not a universal feature of mitosis and not found in all cells.
7. In some lower eukaryotes (e.g., yeasts), the nuclear envelope remains intact and chromosomes migrate to opposite poles within the nucleus. This is termed as closed mitosis. The cells of higher eukaryotes undergo the breakdown of the nuclear envelope at the end of the prophase which is known as open mitosis.
8. At the end of the prophase, the cytoplasmic microtubules are disassembled, and the mitotic spindle begins to form. Mitotic spindle is a bipolar structure composed of microtubules and associated proteins.
9. The spindles assemble outside the nucleus between separating centrosomes.
10. The nuclear division in mitosis is mediated by a microtubule-based mitotic spindle which separates the chromosomes. Spindles are also called microtubules each of which made up of polarized tubulin polymer from one

end, the minus end, embedded in a spindle pole and the other end, the plus end, pointing outward from the pole. The mitotic spindle is of three types: kinetochore microtubules, polar microtubules, and astral microtubules.

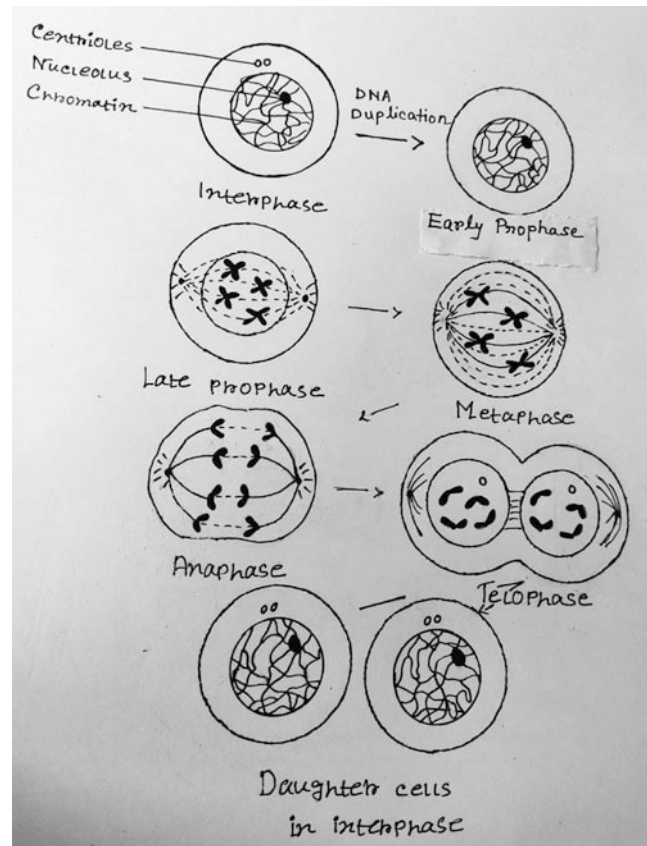
### Metaphase

The chromosomes are aligned at the equator of the spindle or midway of the spindle poles in metaphase. The kinetochore microtubules attach sister chromatids to opposite pole of the spindle (Fig. 1).

### Events Involved in Metaphase

1. Metaphase is an extremely dynamic part of the cell cycle. The completion of spindle assembly in animal cells requires nuclear envelope breakdown, and prometaphase starts abruptly with breakdown of the nuclear envelope.
2. The event of assembly and disassembly of spindle fibers occurred once they originate from MTOC to reach the required length.
3. Spindle fibers attach to a specialized structure, the kinetochore, at the site of chromosome. Kinetochores are of two types facing in opposite directions on each chromosome.
4. Chromosomes make attachment with the spindle fibers by the process known as "search and capture" in which the plus ends of some microtubules radiating out from the MTOC attach to kinetochore. Some microtubules randomly hit kinetochore and subsequently stabilized to form kinetochore microtubules. Eventually the opposite kinetochore on the other sister chromatid is captured by the free end of a microtubule from the opposite pole. This leads to bipolar orientation of chromosome.
5. The movement of chromosomes during metaphase depends on numerous microtubule-dependent motor proteins. These proteins belong to two families – the kinesin-related proteins (such as kinesin-5, kinesin-14, kinesin-4, and kinesin-10) and dynein.
6. Kinesin-5 protein (plus end-directed motor protein) interacts with the plus ends of anti-parallel polar microtubules in the spindle midzone and pushes the poles apart.

**Mitosis, Fig. 1** Linear diagram showing the different stages of mitosis starting from parent cell in interphase to early prophase, late prophase, metaphase, anaphase, and telophase which produces two daughter cells after cytokinesis



- Kinesin-14 proteins are minus end-directed protein (toward pole from kinetochore). The heavy chain of kinesin consists of motor domain (head), the helical coiled coil domain (neck), and the carboxy-terminal tail domain attached to light chain. Once ATP hydrolysis occurs in the motor domain (ATP-dependent microtubule-binding domain), it helps in changing the conformation and orientation of the neck with reference to head results in the motion. Kinesin-14 family member motors can bind to, crosslink and slide of microtubules which helps in spindle assembly and to pull together (She and Yang 2017).
- Kinesin-4 and kinesin-10 proteins (also called chromokinesin) are plus end-directed motors that associate with chromosome arms and push the attached chromosome away from the pole.
  - Finally, the minus end-directed dynein motors link the plus ends of the astral microtubule to the cytoskeleton component of the cell cortex. The dynein motors pull the spindle poles toward the cell cortex.
  - At metaphase stage, chromosomes aligned at the midpoint between the two spindle poles. During this process chromosomes often oscillate backward and forward before arriving at the midpoint. Multiple forces move chromosome at the equator. One major force pulls the chromosome along the kinetochore microtubule toward the spindle pole. It is produced by proteins at the kinetochore itself.
  - Depolymerization at the plus end of the microtubule somehow generates such force that pulls the kinetochore poleward. Kinetochore-localized kinesin-13 (a class of microtubule-depolymerizing protein) and CENP-E (a member of kinesin-7) play an important role.
  - Apart from poleward forces, each chromosome is simultaneously subjected to

anti-poleward forces. The force acting on chromosomes is the polar ejection force. Plus end-directed motor proteins kinesin-4 and kinesin-10 located on the chromosome arms interact with polar and astral microtubules to produce the anti-poleward polar ejection forces. This force pushes the chromosomes toward the equator. The combination of these forces makes the chromosome alignment on the metaphase plate. The alignment of chromosomes at the metaphase plate, midpoint between the two spindle poles, is called congression.

### Anaphase

This is the third phase of mitotic cell division in which chromosomes move away from one another to the opposite of the spindle poles (Fig. 1).

#### Events Involved in Anaphase

1. At metaphase two sister chromatids attach to the kinetochore microtubules which pull two kinetochores toward the opposite pole.
2. Sister chromatids are tightly attached together at their centromere by multiple protein complex which is called cohesin.
3. During anaphase separase degrades cohesin molecules in between two sister chromatids.
4. Before anaphase a securin protein binds with separase protein and keeps it in inactive state.
5. After degradation of securin, it releases separase which is then free to cleave cohesin complex.
6. M-cdk activates APC complex and then initiates ubiquitination and degradation of securin.
7. Each chromatid is pulled slowly toward the poles by two independent and overlapping process. The separated chromatids are now called chromosomes.
8. Anaphase can be divided into two processes: anaphase A and anaphase B.
9. In anaphase A, the initial poleward movement of chromosome and shortening of kinetochore microtubules occur. In this phase the force is generated by microtubule depolymerization at the kinetochore which results in the loss of tubulin subunits at the plus end as the kinetochore moves toward the pole. Kinesin-7 and kinesin-13 that are located at the kinetochore help in the movement toward the spindle poles.
10. Three basic processes help in the separation of the poles in anaphase-B (Lodish 2013).
  - (a) Pushing force – kinesin-mediated sliding of polar microtubule past one another.
  - (b) Pulling force – cortex-associated cytosolic dynein.
  - (c) At the minus end, polar microtubules lengthen.
11. Kinetochore dynein helps in segregation of chromosome acutely by delaying anaphase to properly attach the chromosome to the spindle (Foley and Kapoor 2012).

### Telophase

1. In telophase the separated daughter chromosomes are located at the poles, and the kinetochore microtubules disappear.
2. The polar microtubules elongate even further, and a new nuclear envelope re-forms around each group of daughter chromosomes.
3. The condensed chromatin expands and the disappeared nucleolus starts reappearing again at the end of mitosis (Fig. 1).

### Cytokinesis

1. Cytoplasm of the cell is divided by cytokinesis; it begins in anaphase and ends in telophase reaching completion as the next interphase begins.
2. During cytokinesis, the cytoplasm is divided by a process called cleavage.
3. Cleavage is accomplished by contraction of circumferentially oriented contractile ring which is made up of actin filament and myosin II.
4. This contractile ring which is known as cleavage furrow generates force required for cleavage.
5. The function of the contractile ring at the site of cleavage is controlled by RhoA (a small GTPase of the ras superfamily).
6. The myosin II assembly and contraction require other protein kinases, including Rho-activated kinase ROCK.

7. This kinase phosphorylates the regulatory subunit of myosin light chain and promotes the assembly and contraction of the actin myosin ring.
5. Apical and lateral cambium growth occurs through mitosis in meristematic tissue in plant throughout the life.
6. It maintains cytoplasmic growth in the cells.

## Mitosis-Related Abnormalities

In mitosis, cells can divide, and it creates two identical daughter cells that carry an original copy of parental DNA, and error of this process results in incorrect DNA copies. These errors result in the health of organisms.

| Diseases      | Causes                                                                                                                                                                                                                                                                                                                                                               |
|---------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Cancer        | Two types of errors occurred during DNA replication in the form of missense or silent mutation which can multiplies over times and go through cell cycles and lead to tumors. Cancer occurs when mutated cells are ignored by checkpoint and begin to reproduce uncontrollably                                                                                       |
| Down syndrome | Due to failure of chromosomal attachment to the spindle, the poleward movements of chromosome get hampered. Consequently, non-disjunction produces cells with abnormal copies of chromosome as aneuploidy. Down syndrome occurs due to such abnormalities in chromosomes 14 and 21 (trisomy 21)                                                                      |
| Alzheimer     | Trisomy 21 exhibits Alzheimer neuropathology by the time they are 30–40 years old because the gene for APP (amyloid precursor protein) resides on chromosome 21 and its consequent overexpression in trisomy 21 cells presumably contributes to the development of Alzheimer's disease in Down syndrome. Mis-segregation of chromosome in mitosis is the reason here |

## Significance of Mitosis

1. This biological process helps in growth and development of multicellular organism.
2. It helps in maintaining the proper size of somatic cells.
3. It helps in repairing of damaged tissues.
4. It is responsible for maintaining the same number of chromosomes in daughter cells after division.

## Conclusion

Mitosis is the process of duplication of cells with equal number of chromosomes in daughter cells as compared to parent cells. It helps in normal growth and development of individuals and repairing of tissue. The abnormalities in the division cause different disease pathologies in the individual.

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## Mixed Species Group

- ▶ [Polyspecific Associations](#)

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## Mnemonic

- ▶ [Adaptive Memory](#)

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## Mnemonic Device

- ▶ [Survival Processing](#)

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## Mobility

- ▶ [Mustelidae Locomotion](#)

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## Modal Action Pattern

- ▶ [Unconditioned Response](#)

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## Modal Action Pattern (MAP)

- ▶ [Fixed Action Patterns](#)

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## Modal Action Patterns

- ▶ [Innate Behaviors](#)

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## Modality

- ▶ [Catarrhine Communication](#)
- ▶ [Mustelid Communication](#)

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## Model Fitting

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## Synonyms

[Best-fit models](#); [Mathematical modeling](#)

## Definition

Mathematical model fitting of animal behavior and cognition constitutes mathematical expressions which accommodate key variables involved in particular behavior under the certain condition of environment or stimuli presented.

## Introduction

Animal behavior involves a complex mixture of sensory, biomechanical, and neuronal restrains. Because of the complexity of behavior schema, it is impossible to account for all the factors which have their role in the particular behavior. So, the mathematical models are the tools which regress out the certain variables associated with the behavior, and thus mathematical abstractions based on that present the key to assessing quantitative prediction about behavior in certain conditions. Though these models do not present the full array of factors, the model itself if fitted well to behavior can predict the behavior with precision and accuracy resulting to less ambiguity of modeling and easier testing in silico.

Organized movement displayed by an organism is termed as behavior. Some behaviors are individualistic in nature, while some behaviors are of the collective type. Behavioral organization involves:

- (a) Sensors (receptors) which act as an input for the internal milieu



- (b) Channels for information flow, i.e., neuronal pathways, conducting information, etc.
- (c) Effectors

And to predict the outcomes, model fitting is done for the behaviors which help to assess the cognitive parameters behind it. Mathematical modeling is an investigative technique which uses a mathematical expression of a system accounting, may be all or some of its known properties. Modeling for researchers is the powerful tool of scientific analysis. The simpler the model accounting for variables essential for the behavior, the better it is. Also, it is important to distinguish the rational mathematical models based on hypotheses from the empirical mathematical models, as empirical models do not support knowledge acquired based on scientific theories. Rational theories are derived from a number of basic theories and provide good fitting with the observed experimental data. If the model fitting fails for particular behavior, then it proves that the tested theory cannot be applied to the data set available.

**Model fitting of animal behavior can be based on one of the given based strategies/models:**

- A. **Deterministic:** In deterministic modeling observations can be defined by a limited well-defined set of an outcome, and the prior outcomes of some experiments can be represented by their representative different outcomes.
- B. **Stochastic:** In stochastic modeling the probabilities are assigned to each of the event in a paradigm. If the probabilities observed are close to unity, then the model can be termed deterministic.
- C. **Statistical Models**

## Mathematical Models of Behavior

- (a) **Teleological determinism:** In teleological determinism the subject chooses behavior based on the assumption that this behavioral outcome will be beneficial.

Two groups of theories to define it: (i) game theories, based on Nash equilibria principle, and (ii) reinforcement theories, based on Skinnerian reinforcement principle or matching law (Coley and Tanner 2015).

Here the parameters used are dimensionless or represented by per second.

- (b) **Causal determinism:** In causal determinism subjects do not choose from the set of possibilities/available opportunities, but rather they are prompted to do what is prefixed in hypothesis, doing so in response to a specific stimulus. Here, behavior occurrence is the result of sufficiently strong stimuli being presented.

Here the parameters are in SI metrics system.

## Game Theory

Game theory is special for researchers when they have to model the influence of evolution over strategies and tactics, since choosing the right strategies (natural selection helping winners to combat in adverse situations) is the key point deciding success in life. The theory of human games applies to animal behavior; it gives a scaffold over which behavioral choices made by animals can be analyzed.

**Nash equilibrium (NE):** John Nash proposed an optimal model for collective strategy involving two or more players; he has defined the terms where if each player in the game has strategy fixed and none of the player is benefitted by changing the strategy while the other players choose to stay with their fixed choices, the set of strategy choices and corresponding leads in game constitutes Nash equilibrium (NE).

In Nash's game it can have a pure strategy NE or the mixed extension in NE, where pure strategy is chosen stochastically. In the latter, mixed strategies (players choosing strategies in random according to preassigned probabilities), for every n-player game, every player can make a choice from the finite number of strategies leading to at least one Nash equilibrium.

**Evolutionary stable strategy (EES):** Strategies by animals which cannot be perturbed by the other strategies. Concept of an EES is the crucial

and important part dealing with game theory. EES is able to withstand the budding new strategies over evolution. So, here the natural selection will provide for the base over which different strategies can be tested, and computational biologists simulate the behaviors in the best possible fitting manner (Brown 2016).

Applying game theory for analysis of an animal behavior is the most plausible approach for mathematical modeling. Though teleological determinism is the best suited to explain the outcomes, same time they are quite useful.

### Matching Law

Matching law states that the choice made is neither solely an internal decision nor an isolated output of an internal decision processes; here the choices are rated based on overt events strung over time. So according to matching law, the model will predict alternative activities PL or PR, and allocation of their behavior to activities in proportions corresponding to the relative rates of reinforcement, RL and RR, e.g., time spent by animal in mating, eating, etc. (Kubaneck and Snyder 2015):

$$PL/(PL + PR) = RL / (RL + RR)$$

### Modeling Individual Animal Behavior

Individual behavioral mechanisms are defined by their respective individual's probabilities to display the behavioral outcome, whether it is some action or change in the state (Buhl et al. 2005).

**Optimality models:** These models quantitatively predict the consequences faced by an animal when presented to the conditioned environment. According to this model strategy, the animal will behave to maximize their fitness. Optimality model evaluates fitness benefits (B) and the fitness costs (C) for the different values presented on the decision scale. Optimality model using calculus and logical tool helps to evaluate minima and maxima of a particular function  $f(x)$  by assessing its derivatives  $df(x)/dt$ . The model aims to optimize "decision variable." "Constraints" are barriers in the relationship between decision variable and "currency: to

check the outcome of decision variables." This approach is key to access sensitivity to changes of decision variables determining what type of information are valuable for the currency-decision variable relationship.

#### 1. Optimal Foraging Theory: Model examining choice of food items

Selection of food item is a behavior which every animal shows, and this is based on the basic instinct of an organism to maximize its currency; currency here is a number of calories present in particular food item. E1 and E2 refer to the caloric energy contained in two different food items/prey. H1 and H2 are the handling time needed to access the caloric content of food. So, the model prefers food/prey for which estimates of energy gained per unit of time are higher,  $E1/h1 > E2/h2$ . This model defines the behavior of the predator either as a specialist or the generalist (Sayers and Menzel et al. 2012).

#### 2. Marginal Value Theorem (MVT)

MVT is an optimality model that usually describes the behavior of an optimally foraging individual in a system where resources (often food) are located in discrete patches separated by areas with no resources.

This model attempts to optimize a cost/benefit ratio; it is an optimality model describing the behavior of an individual in a system where the resources are dispersed in discrete patches with the areas of void, i.e., without resources (Calcagno et al. 2014).

### Modeling Collective Animal Behavior

Diversity and complexity observed in the behavioral patterns of swarms, flocks, and crowds are the examples of collective behavior shown by the population; they may be the result of relatively simple interactions happening between the individuals. Collective behavior is displayed as dynamical patterns grouped by the self-organizing processes involving simple individual behaviors. Temporal and spatial characteristic lengths of dynamical patterns formed during collective animal behavior are much larger than the typical ranges observed under individual interactions.

Modeling of collective animal behavior will lead us to causally link these studies with the studies dealing with neural and cognition basis of individual behavior and collective behavior in which these neuronal and cognitive processes are involved (Weitz et al. 2012).

For evaluation of cognitive capabilities based on modeling of collective animal behavior, the key basis is to sort out all possible biological parameters involved in determining individual behaviors and then deduce the relative collective outcome. And it provides for the simplest way where self-organization of an individual behavior is seemed as the components of an observed collective behavior.

### Collective Behavior of Corpse Clustering in Ants

Ants *Messor sancta* show behavior, clustering broods, leaf fragments, sand pellets, and corpses of their dead conspecifics. While looking for their collective behavior ant movement, picking of corpse and dropping it in pile of high density or low density are seen as one action (Jost et al. 2007).

For exemplifying and for better resolution, the three different protocols based on segregation of an action involved in performing a collective behavior task is used for:

- (a) Movement of ants
- (b) Picking up
- (c) Deposition

Three model ingredients and their corresponding cognitive significance in corpse clustering tasks can be parameterized based on:

- 1. Influence of the perceived object density
- 2. Importance of interindividual variability
- 3. Role of individual temporal correlation

How the interactions between individuals work in order to control the collective behavior is still not resolved. Individual behavioral mechanisms refer to the individuals' probabilities to perform an action, determining the causal link between neural and cognitive processes with the

individual behaviors helping to further resolve enigma of collective behavior.

### Modeling and Its Rationale, Difficulties, and Possible Solutions

A very demanding task is to have a clear demarcation separating different behavioral models based on the defined combination of biological concepts and their formal translation into mathematical representations.

Mathematical expressions depend on the limited set of quantitative variables involved in fitting the functional dependencies for the behavioral outcomes seen under a task/stimuli presentation, and complete model translation requires arbitrary choices to be made for the state variables and stimuli that can be deduced as direct consequence of the model.

Understanding of mathematical modeling in biology fluctuates:

1. One according to which the equation is the essence, pure ideal design of a complex biological process
2. Second, that a simple equation is a crude approximation, a formal representation of a hypothesis which is only valid if its assumptions agree with empirical data obtained under certain conditions

Equations though inherent are perturbed by many factors in nature. Theory of deterministic chaos, dealing with nonlinear parameters, things effectively impossible to predict/control, capturing infinite complexity of nature. Fluctuating power spectrum with exponential frequency dependency of behavior will help to model nonlinear parameters.

In movement ecology linking animal movement patterns, chaotic dynamics are linked to underlying biological processes, including those operating at neurobiological level. Hallmarks of chaotic dynamics are seen in movement patterns of mud snails (*Hydrobia ulvae*), moving in controlled conditions, observed in temporal dynamics of turning behavior.

Levy walks (LW) are made by mud snails with their mechanistic origin in chaotic neuronal processes, opening window for new research over coupling between neurobiology and motor properties helping to distinguish intrinsic movement behavior of animals from observed movement patterns, affected by various environmental factors. Levy search, a complex scale-free behavior – alternate clusters of many short steps with longer steps between them – creates fractal movement patterns having no characteristic scale (Andy Reynolds 2015). LW is important for random searches. Hayashi et al. provided the first evidence of neurons having chaotic dynamics. Findings by the researcher have focused on chaotic dynamics, and with the results we know, spontaneous flight patterns seen in *Drosophila melanogaster* are linked to spontaneous neuronal firing in central complex (Chang et al. 2017). **Pacemaker neurons** in molluscs observed to show chaotic temporal dynamics linked to the chaotic behavior in movement pattern seen in molluscs.

## Flaws in Study of Animal Behavior and Thus the Models Proposed

Uncritical adaptationist thinking is the major flaw (Gould and Lewontin 1979); the appropriate approach is to formulate optimal hypotheses for the particular function of the complex behavior; once it is selected, the controlled assessment of hypotheses is a must.

## Cross-References

- Behavioral Genetics
- Self-Directed Behavior

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## Modelling

- Shaping

## Moderate Behavior

- Restraint

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## Modern Human

► *Homo sapiens*

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## Modern Synthesis

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## Synonyms

Modern synthetic theory

## Definition

The modern synthetic theory of evolution describes the evolution in terms of genetic variations in a population that leads to the formation of a new species.

## Introduction

Darwin's book, *The Origin of Species by Means of Natural Selection*, founded a strong ground for evolutionary theories that favored the idea that all the organisms have descended from a common ancestor. Darwin proposed natural selection as a mechanism of evolution. Then came the neo-Darwinian theory of evolution that explained the significance of mutations and variations within a population, as a driver factor of evolution. This perspective was followed for many decades.

Ronald Fisher and his colleagues set Darwin's concept of natural selection on a new foundation of genetics. They left an equally major project open for later biologists: to explain in the language of genes what species are and how they originate. While the Darwin's theory largely demonstrated the "facts" of evolution, the

"mechanism" of evolution was still unexplained. The answer only began to emerge in the 1930s, thanks in large part to the work of a Soviet-born geneticist named Theodosius Dobzhansky, who proposed the idea of modern synthesis.

However, a quiet majority of geneticists thought of species' origin as the gradual accumulation of small mutations, and in 1940 this allowed for propagation of "the synthetic theory of evolution" by geneticist Theodosius Dobzhansky (1900–1975) and other zoologists.

The neo-Darwinian view was then replaced by a new concept which considered several other mechanisms in addition to natural selection. These ideas on evolution are usually referred to as the modern synthesis which is described by Futuyma as "The major tenets of the evolutionary synthesis, then, were that populations contain genetic variation that arises by random (i.e. not adaptively directed) mutation and recombination; that populations evolve by changes in gene frequency brought about by random genetic drift, gene flow, and especially natural selection; that most adaptive genetic variants have individually slight phenotypic effects so that phenotypic changes are gradual (although some alleles with discrete effects may be advantageous, as in certain color polymorphisms); that diversification comes about by speciation, which normally entails the gradual evolution of reproductive isolation among populations; and that these processes, continued for sufficiently long, give rise to changes of such great magnitude as to warrant the designation of higher taxonomic levels (genera, families, and so forth)" (Futuyma 1986).

## Modern Synthetic Theory of Evolution

The modern synthetic theory of evolution describes the evolution in terms of genetic variations in a population that leads to the formation of a new species. It explains the contribution of factors such as genetic variations, reproductive and geographical isolation, and natural selection. It also describes about the Mendelian population, gene pool, and gene frequency. It merges the concepts of Darwinian theory of evolution and



Mendelian genetics to form a unified theory of evolution. Synthetic theory of evolution was introduced by few renowned evolutionary biologists naming T. Dobzhansky, J.B.S. Haldane, R.A. Fisher, Sewall Wright, G.L. Stebbins, and Ernst Mayr in the years 1930–1940.

The modern synthetic theory of evolution proposed a new definition to the evolution as “the changes occurring in the allele frequencies within the populations,” which accentuates on the genetics of evolution.

### Aspects of Modern Synthetic Theory of Evolution

Some of the factors describing the modern theory of synthetic evolution can be explained as follows.

#### Recombination or Variation

Recombination occurs between the existing genes to form a new genotype. It is an exchange of the chromosomal pairs of alleles during the meiosis at the time of sexual reproduction to form new gene combinations. Cytogenetic events such as mutations (including deletion, inversion, duplication, translocation, and polyploidy) result in the recombination.

#### Mutation

A mutation is a change in DNA, the hereditary material of life. An organism’s DNA affects its phenotype, its behavior, and its physiology. Mutations are the raw materials of evolution. Evolution is categorically dependent on mutations because it enables the formation of new alleles and new regulatory regions.

#### Heredity

The transmission of variations from the parents to their offsprings is a principal mechanism in the evolution. The organisms which retain hereditary characteristics are preferred in the struggle for the existence.

#### Natural Selection

Natural selection is a phenomenon by which species adapt to their environment. Natural selection results in an evolutionary change when

individuals with certain characteristics have a greater survival or reproductive rate than other individuals in a population and pass on these inheritable genetic characteristics to their offspring.

#### Reproductive Isolation

It is one of the crucial factors responsible for the synthetic theory of evolution. Reproductive isolation helps in preventing the interbreeding of related organisms. Additionally, some other factors that contribute to the synthetic theory of evolution include migration of individuals from one form of the population to another and hybridization between the races of species which increases the genetic variability within the population.

It differs from Darwinism in three important aspects:

1. In addition to natural selection, it considers several mechanisms such as random genetic drift to be an important element of evolution.
2. It describes that the characters are inherited as discrete units called genes. Occurrence of multiple alleles of a gene within a population gives rise to variation.
3. It postulates that speciation is (usually) due to the gradual accumulation of small genetic changes. This is equivalent to saying that macroevolution is simply a lot of microevolution.

Modern synthesis was one of the utmost accomplishments of evolutionary biology. By combining the concepts of Darwin and Mendel, it expounded that diversity within a population ascended from random occurrence of mutations and environment acted to select the phenotype that is more fit. Potential reproducing animals transmitted the genes that were advantageous. These types of genes included those coding for enzymes with better rates of synthesis and globins with better oxygen-carrying capacity. It was presumed that the genetic variations, that caused evolution within a species, also caused evolution of a new species. If a new phenotype is to be produced, it is essential that there should be an accumulation of these mutations followed by reproductive isolation. The theory of modern synthesis not only did explain the evolution within

species but also explained many relevant questions such as why some alleles that seem to be deleterious get selected in certain populations, for example, one of the hemoglobin gene variants results in sickle cell anemia. The population genetic approach to evolution was summed up by Theodosius Dobzhansky, who stated that “Evolution is a change in the genetic composition of populations. The study of the mechanisms of evolution falls within the province of population genetics” (Dobzhansky 1951).

Thus, some of the core assumptions of modern synthesis include five major postulations which include:

1. Phenotypic variations of evolutionary significance arise from genetic mutations occurring at a low rate and independent of the strength and direction of natural selection.
2. Most of the advantageous mutations show small phenotypic effects which progressively lead to the change in phenotype.
3. Inheritance is genetic in nature.
4. Natural selection is an exclusive explanation for adaptation.
5. Accumulation of variations that arise through microevolutionary processes results in macroevolution.

### Significance of Developmental Biology in Modern Synthesis

At the time when the concept of modern synthesis was formulated, developmental biology and developmental genetics was at a naive stage. Significance of embryology was neglected and was kept out of modern synthesis by most of the geneticists and evolutionary biologists (Hamburger 1980; Gottlieb 1992; Dietrich 1995; Gilbert et al. 1996). It was earlier assumed that population genetics is enough to explain the evolution; hence, developmental biology seemed to contribute almost negligible in the modern evolutionary theory (Adams 1991). However, it is not well accepted that “developmental genetics approach to evolution concerns more the *arrival* of the fittest than the *survival* of the fittest” (Gilbert 2000). Even the critics of modern synthetic theory agreed that macroevolution, which refers to the large morphological changes that are

seen between species, classes, and phyla, is based on mutation and recombination. Nevertheless, these macroevolutionary variations occur in developmental regulatory genes in the embryo and larvae, and not in adults competing for reproductive success (Waddington 1953; Gilbert 1998).

Developmental biology has brought a new platform to understand the relationship between genotype and phenotype in the light of evolutionary biology. Also, it enables us to understand the genetic relationships between diverse organisms. Developmental biology thus provides a population genetic approach to understand gene regulation (Arthur 2000; Macdonald and Goldstein 1999; Zeng et al. 1999). It opens questions as to how various paracrine factors, transcription factors, and signal transduction pathways were modified during the evolution.

Evolutionary developmental biology also provides answers to many classical evolutionary questions such as those of the examples of mimicry and industrial melanism. Now that the genes responsible for such phenomena have been identified, the mechanism can be very well explained (Koch et al. 1998; Brakefield 1998). Thus, to explain the mechanism of evolution, both the population and developmental genetics should be taken under consideration.

### The Extended Synthesis

The concept of modern synthesis emerged in first half of the twentieth century and flourished for many years. However, as the evolutionary biology research progresses, several research subjects emerged that transcended the boundaries of modern synthesis. Major thrust areas that challenged the theories and concepts of modern synthesis included epigenetics, phenotypic plasticity, evolutionary developmental biology, and systems biology. This new conceptual framework of evolution was termed as extended synthesis, as it was an extension, rather than contradiction, to the modern synthesis (Pigliucci 2007). An excellent description of this is provided in the book “*Evolution—The Extended Synthesis*” (Pigliucci and Müller 2010).

Epigenetics has been one of the major thrust areas in extended synthesis. The term “epigenetics” was first introduced by Conrad Waddington in the

early 1940s (Waddington 2011). He defined epigenetics as “the branch of biology which studies the causal interactions between genes and their products which bring the phenotype into being”. However, as the field of genetics expanded, it is now defined as, “the study of changes in gene function that are mitotically and/or meiotically heritable and that do not entail a change in DNA sequence” (Morris 2001). Epigenetic mechanisms include interactions among various genetic, physiological, and morphological systems and serve as an important constituent of organism-environment interactions (Angers et al. 2010; Richards et al. 2010; Schrey et al. 2012).

The significance of epigenetics at molecular level has been well elucidated and appreciated for, e.g., its function in cell determination and cell recognition; however the role of epigenetics in evolution is recently under attention. Some epigenetic characters are known to stably transmit across generations, which highlights that it includes some mechanisms of heredity which was not considered in the framework of modern synthesis.

Epigenetic mechanisms play critical roles and several mechanisms such as in phenotypic plasticity, invasive species biology, soft inheritance, response to environmental variations, and conservation biology. Epigenetic variations such as DNA methylation provide an evolutionarily significant source of phenotypic variation among individuals. DNA methylation is the most studied molecular epigenetic mechanism. It is actively involved in mechanisms such as DNA imprinting, X-chromosome inactivation, silencing transposable elements, and response to environmental stressors. DNA methylation is a basis for interindividual variation and is studied to regulate various phenomena such as phenotypic variation in shape of flower and fruit pigmentation, shape of mouse tail, body size and coat color, and numerous traits differentiating queen and worker honeybees. For example, *Viola cazorlensis* shows a high level of interindividual DNA methylation variation that differentiated populations (Schrey et al. 2012).

Nevertheless, DNA methylation serves as the most comprehensively studied mechanism in ecology and evolutionary perspectives; several

studies have described other epigenetic mechanisms also. Modifications of histone, small and long noncoding RNAs, and genome structure are shown to regulate gene expression and contribute to phenotypic variation in diverse taxa.

Epigenetics continues to prove as a remarkable phenomenon in evolutionary biology. A great deal of work, however, remains to be done. Pragmatic studies that established the significance of epigenetic variation in evolution will likely explain some of the empirical questions of evolutionary epigenetics, which will further help in development and enhancement of a foundational theory of evolutionary epigenetics. Thus, epigenetics studies seem to be very promising in providing information about the individual and population processes both at the ecological and evolutionary timescales.

## Cross-References

- [Evolution](#)
- [Genetic Variation](#)
- [Heritability](#)
- [Population](#)

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## Modern Synthetic Theory

- [Modern Synthesis](#)

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## Modification

- [Mutations](#)
- [Recombination](#)

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## Modular Cognition

- [Mosaic Cognition](#)

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## Mole, Hedgehog, or Shrew Locomotion

- [Insectivore Locomotion](#)

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## Molecular Marker

- [DNA Marker](#)

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## Molecular Scissors

- [Restriction Enzyme](#)

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## Mollusca

- [Mollusk](#)

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## Mollusk

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## Synonyms

[Mollusca](#)

## Definition

Mollusks are the members of a diverse group of invertebrates with a thin fleshy soft unsegmented body, divisible into a head, visceral mass, and foot. Members of this phylum exhibit an “organ system” grade of the organization (Anderson 2001), e.g., snails, octopus, squids, oysters, chitons, mussels, etc.

## Etymology

The term mollusk was coined by the French naturalist Lamarck. This term is originated from the Latin word *molluscu*, meaning “thin shelled,” derived from the root Latin word *Mollis*, meaning “soft.” Cuvier first used the term in 1798 to describe the animals with reduced shells, such as cuttlefish, snails, squids, etc. The study of mollusks is known as malacology, whereas mollusks’ shell study is called conchology. Due to the vast diversity of species and many fossil forms, they are considered the largest marine phylum and comprise about 23% of all marine organisms (Amsler et al. 2001). They constituted the second-largest phylum of non-chordate after arthropods and were believed to appear during the Cambrian period (Ruppert and Barnes 1994).

## Present Taxonomical Status

The phylum Mollusca is considered one of the most conspicuous of the invertebrate group, consisting of about 220,000 living species. The fossil record also indicates a long and extensive history (Telford and Budd 2011). Mollusks are one of the largest metazoan phyla, which includes about 130,000 described extant species and about 70,000 described fossil species (Haszprunar et al. 2008). As per Ponder and Lindberg (2008), Mollusk fauna’s total living species diversity comprises 20,000–30,000. According to modern taxonomists, the following classes include the mollusk phylum: the Gastropoda (slugs, snails, etc.), the Bivalvia or pelecypods (mussels,

clams, etc.), the Cephalopoda (sepia, cuttlefish, octopus, etc.), the Polyplacophora (chitons), the Scaphopoda (dentalium), the Monoplacophora (univalves), and the Aplacophora (Barth and Broshears 1982).

## Habit, Habitat, and Ecological Importance

Mollusks’ habitat ranges from the deepest ocean to intertidal/abyssal zone, freshwater, and lands. A few members form a significant part of freshwater fauna, and the others include terrestrial habitat. They are found on rocky, sandy, or muddy substrata, and some members are burrowing, some are crawling, few members become attached to a substratum, or some are free-swimming forms. Among all classes, Gastropoda is the most important and comprises more than 80% of all mollusk species (Fortunato 2015). Cephalopods such as squids, cuttlefish, etc. are considered the most neurologically advanced invertebrates (Amsler et al. 2001).

Mollusks are bilaterally symmetrical and sluggish invertebrates (Apte 2015). Their size ranges from microscopic organisms to 20 m long. They are considered important ecosystem engineers to frame and protect the aquatic habitat’s bottom (Fortunato 2015). These animals play an essential role in stabilizing many marine ecosystems and keeping the algal and bacterial levels balanced. They play a crucial role in recycling nutrients, soil generation, and water filtration due to their abundance. Most bivalve members contribute to the organic turnover in the intertidal (littoral) zones of marine and freshwater ecosystems because of their active filtering. However, this filtering activity may also seriously interfere with the various invertebrate larval populations or planktons found suspended and free swimming in water. They also form an essential trophic level in the aquatic food chain and act as good bioindicators for the ecological quality in all types of aquatic habitats (Avila et al. 2000, 2004). Most members form food sources to a wide variety of other taxonomic groups like humans, birds, fish, mammals, and other invertebrates.



Mollusks play a crucial role in the lives of humans. They form a rich source of protein, good fat, and minerals (e.g., lime from the shells is used in poultry food and building material). In many regions, mollusk shells are used to manufacture ornaments and jewelry. This phylum plays a significant role in the pearl industry. Pearl oysters (*Pinctada margaritifera* and *P. mertensi*), which inhabit the Indian and Pacific Ocean's warmer parts along the coast of China, India, Sri Lanka, and Japan, form the most valuable natural pearls. Pearls are produced by most bivalves (pelecypods), including freshwater calms and marine oysters. When a small foreign object such as a particle of sand or parasite lodges between the shell and mantle, the foreign object becomes a nucleus around in which concentric layers of nacreous are laid by mantle to form a pearl (Avila et al. 2000).

A few members of this group are used as a medicine, especially for sore throat and cough. A recent research shows that a wide variety of secondary metabolites from mollusks possess anticancer, anti-inflammatory, and antimicrobial abilities. Most of these compounds are in clinical trials. The extracts from the shells and bioactive compounds of some mollusks act as growth inhibitors of cancer cells in mice (Beckendorf et al. 2005; Cohan et al. 2003).

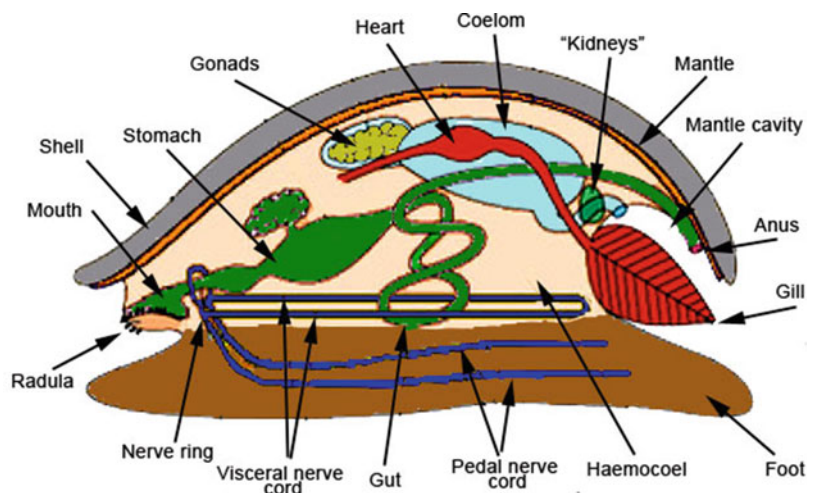
Some mollusks, such as slug, shipworm, etc., act as pests and destroy garden and agriculture cultivations by eating leaves and cutting up roots and stems. Moreover, a few members of gastropod species are intermediate hosts for disease-causing parasites such as liver fluke (phylum Platyhelminthes, class Trematoda), which causes fascioliasis or liver rot in cattle. The zebra mussel *Dreissena polymorpha* is considered a harmful exotic invader. They were carried from Europe in ship ballast water to the Great Lakes and caused commercial damage by clogging the water pipes of power plants as well as cooling systems. They are driving many native freshwater bivalve species to extinction. Tereido worms, commonly called shipworms, burrow into the wooden structures immersed in the sea and cause severe damages to ships, piers, etc. (Avila et al. 2004).

## Mantle and Mantle Cavity

One of the unique features of mollusks is the presence of the mantle and mantle cavity. A thin fleshy double fold of tissue that lies beneath the shell and the part of the epidermis/skin is known as the mantle. This mantle secretes calcium carbonate layers, which form the mollusk's shell (Canti 2017) (Fig. 1). The mantle is rigidly

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**Mollusk, Fig. 1** Mantle cavity. [http://www.mesa.edu.au/molluscs/molluscs\\_01.asp](http://www.mesa.edu.au/molluscs/molluscs_01.asp)



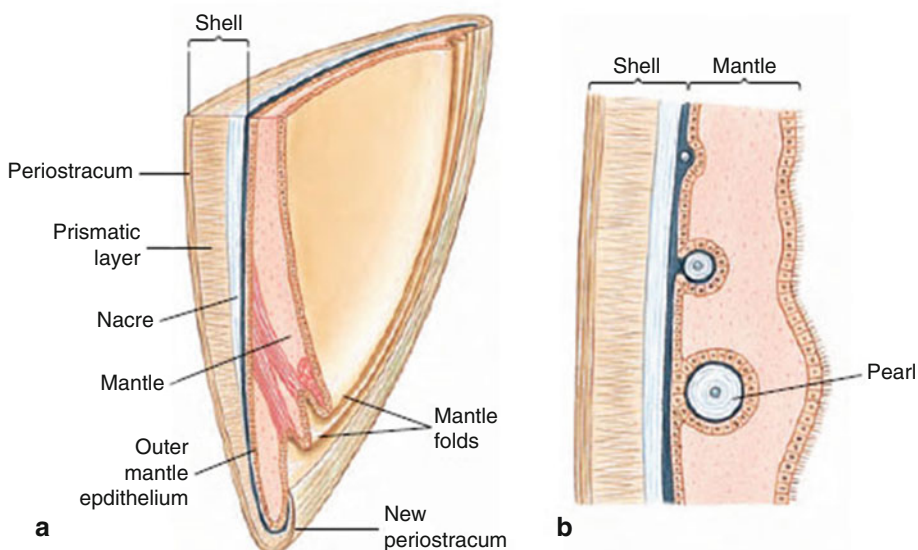
attached to the shell only at the outer edges and covers the visceral organs. The mantle also encloses a cavity called the mantle cavity between the mantle and the body. The mantle cavity functions as a respiratory chamber in most of the mollusks. The mantle's own exposed surface serves for gaseous exchange. In addition to that, the mantle cavity also possesses anus, osphradium, nephridia, and gonophores. So products from the digestive, excretory, and reproductive systems are emptied into the mantle cavity. In aquatic mollusk, there is a continuous water current, which kept moving by the surface of cilia or by muscular pumping, brings in oxygen and in some forms flushes out the food waste, and carries reproductive products (egg/sperm) out to the environment. In aquatic mollusks, the mantle is usually equipped with sensory receptors to detect the quality of environmental water current. In cephalopods, the muscular mantle and mantle cavity create a jet propulsion, which helps in locomotion. In cephalopods (squids and octopuses), the muscular mantle and its cavity create a jet propulsion used in locomotion. Many mollusks can withdraw their head or foot into the mantle cavity, surrounded by the shell, for protection.

## Shell

Mollusks possess a calcareous exoskeleton known as a shell, which encloses, supports, and protects their visceral organs. There is great variation in shell structure. The first shell appears during the larval period and grows continuously throughout life. Most of the members have an external shell, whereas the members, like a slug, cuttlefish, squid, etc., have an internal shell, but it is absent in octopus (Linstädter and Kehl 2012). The mantle secretes the shell made up of several layers consisting mainly of chitin and a protein hardened with calcium carbonate called conchiolin (Barnes et al. 2009).

Typically the shell consists of three layers (Fig. 2):

- a) The outer layer periostracum – It is the horny layer composed of an organic substance called conchiolin consist of quinone-tanned protein, which helps protect underlying calcareous layers from erosion by boring organisms. A fold of mantle edge secretes this, and growth occurs only at the shell's margin, and at the older parts of the shell, this periostracum often becomes worn out.



**Mollusk, Fig. 2** (a) Diagrammatic vertical section and mantle of a bivalve. (b) Formation of a pearl. [https://biocyclopedia.com/index/general\\_zoology/form\\_and\\_function02.php](https://biocyclopedia.com/index/general_zoology/form_and_function02.php)

- b) The middle layer prismatic layer, composed of densely packed prisms of calcium carbonate, is laid down in a protein matrix that is strengthened due to more calcium carbonate crystals made of columnar calcite. The mantle's glandular margin secretes this layer, and the increase in shell size occurs at the shell margin as the animal grows.
- c) The inner layer called the nacreous layer, made of laminated calcite, is responsible for pearl formation. This layer lies next to the mantle and is secreted continuously, so it increases in thickness during the life of the animal. The calcareous nacre is laid down in thin layers. Fragile and wavy layers produce the iridescent mother of pearl. A freshwater mollusk usually has a thick periostracum, whereas it is very thin, or in some members, it is absent in marine forms.

When a foreign body or microbe/stone enters and touches the mantle, the mantle's shell secretes cells that build up layers of the nacreous layer around it, and pearls are formed. To protect itself, the mollusk secretes the substance, a mineral called aragonite and conchiolin, a protein that is the same substance it secretes to form its shell. The composite of all these is called nacre or mother of pearl. The layers are deposited around the foreign body, and it grows over time, and a pearl is formed.

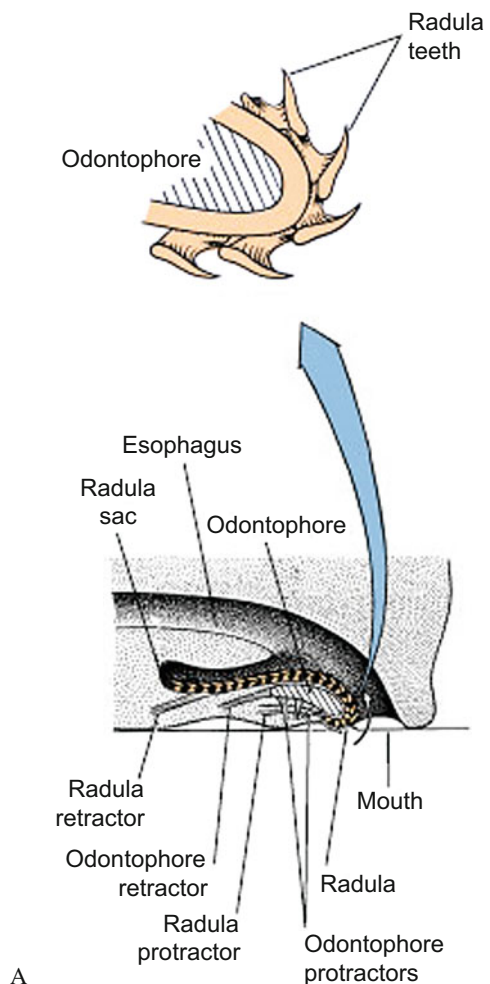
## Foot

The ventral body wall of mollusks is modified as a muscular foot. It varies in shape and function in different classes of mollusks. In gastropods, the foot is broad and expanded with a creeping sole. Rhythmic contractions of the muscular foot perform the locomotion. Moreover, the mucus-secreting glands present in the foot secrete mucus on which the animal slides. In bivalves (Pelecypoda), the foot is a large plow or wedge-shaped adapted for burrowing. A cephalopod's foot is used for jet propulsion, and the tentacles and arms are derived from the foot.

In polyplacophora, the foot is the broad flat muscular, glandular creeping sole and ventral in position. In scaphopods, the foot is long, narrow protrusible spade-like, and is used for digging. For mollusks such as limpets, the foot acts as a sucker attaching the animal to a hard surface (Kotpal 2009).

## Feeding and Digestion

Most members of this family enjoy intracellular digestion. The buccal cavity's interior region has a tongue-like organ called a **radula** (Fig. 3). The



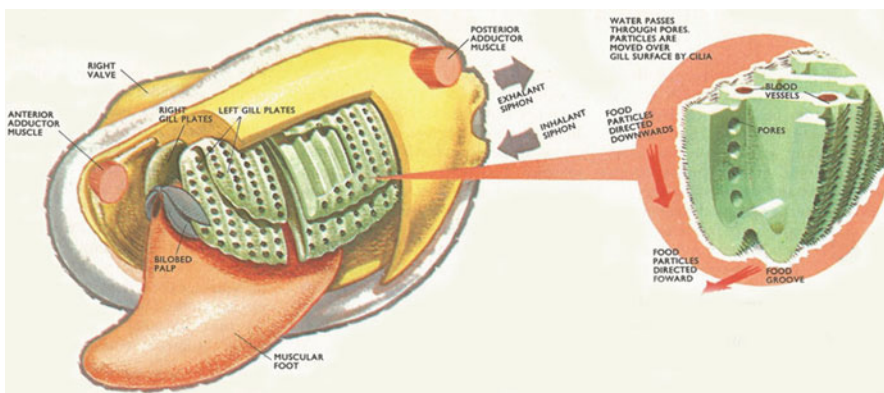
**Mollusk, Fig. 3** Lateral section of a gastropod head showing the radula and radula sac. [https://biocyclopedia.com/index/general\\_zoology/form\\_and\\_function02.php](https://biocyclopedia.com/index/general_zoology/form_and_function02.php)

radula bears a ribbon of chitinous tooth-like ornamentation, supported by a muscular structure known as odontophore. The teeth are pointed backward. There are complex muscles that move the radula and its supporting cartilages. There may be a few or as many as 250,000 teeth. When the radula wears away, new rows of teeth are continuously replaced by secretion at its posterior end. The pattern and number of teeth in a row are species-specific. The movement of the radula is back and forth over the odontophore cartilage. During feeding, the animal opens the mouth; the odontophore is thrust forward, and the radula gives a strong scrape backward, brings food into the pharynx, and closes the mouth. This process is repeated rhythmically. The radula is generally used for feeding and is present in many species and serves to shred or scrape food like bacteria and algae of rocks. The mouth of mollusks is provided with slimy mucus-secreting glands to which the food particles are trapped. The trapped food enters the stomach by ciliary action in such a way that the mucus forms a long string called food string (Alison et al. 2020). The stomach has some acidic nature, which makes the mucus less sticky and frees the food particles from it, and reaches the structure called pyrostyle at the region of the hindgut. The pyrostyle is rotated by another set of cilia, which act as a bobbin and send the smaller particles, mainly minerals, to the pyrostyle to get excreted. Compared to the smaller particles, the large food particles are sent to the stomach's cecum for digestion and absorption. Excretory

organs consist of paired nephridia, which filter the waste products and open to the mantle cavity and push them out with the help of water current produced by ctenidia (Jordan and Verma 2001).

## Respiration

In mollusk, the process of gaseous exchange occurs through the body surface, particularly through the mantle and in specialized respiratory organs such as ctenidia, secondary gills, and lungs. Respiration in aquatic members of mollusks is performed by gills or ctenidia. The members of the terrestrial habitat perform pulmonary respiration. The feather-like gills are filamentous and provided with cilia. The ctenidia/gills are located on opposite sides of the mantle cavity and are arranged so that the cavity is functionally divided into an incurrent chamber and an excurrent chamber where the water enters through the bottom exit near the top (Fig. 4). There are three cilia sets, one set makes the water current into the mantle cavity, and two other sets keep the ctenidia clean. If the osphradia detects any unfavorable entry, the ciliary beating stops and prevents current water entry. The gills are supplied with blood vessels connected to the hemocoel (Jordan and Verma 2001). Cilia between gill filaments propel many leaf-like gill filaments project from the central axis, and water and blood diffuse from an afferent vessel in the central axis through the filament to an efferent vessel. The direction of



**Mollusk, Fig. 4** Respiratory system. [https://www.daviddarling.info/images3/bivalve\\_section.jpg](https://www.daviddarling.info/images3/bivalve_section.jpg)

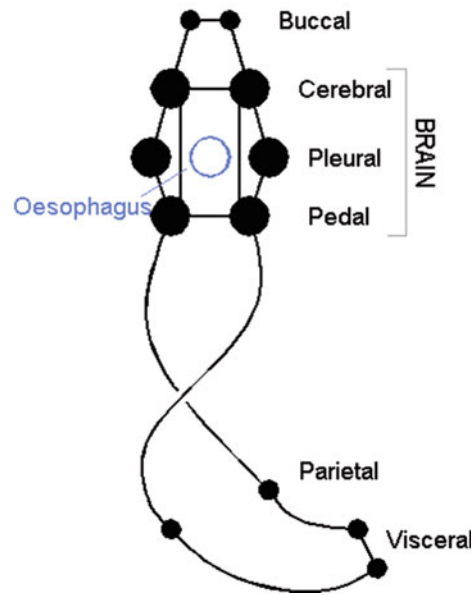
blood flow is opposite to the water current, thereby establishing a counter current exchange mechanism.

## Nervous System and Organs of Sensation

In general, their nervous system has paired cerebral pleural, pedal, and visceral ganglia and simpler than annelids and arthropods. Typically a mollusk consists of a pair of cerebral ganglia (mass of nerve cells bodies) that innervate the head, mouth, and associated sense organs. Arising from the dorsal ganglia, two pairs of longitudinal nerve cords arise: a pair of lateral (pleural) nerve cords often forming pleural ganglia which innervate the mantle and a pair of pedal nerve cords that often include pedal ganglia which innervate the foot. In primitive forms, both nerve cords are interconnected by lateral branches of nerve fibers. A buccal nerve loop with paired ganglia generally supplies the radular apparatus in the head. Posterior paired visceral ganglia innervate the viscera. Because of torsion (twisting of the body during development), special nerve configurations are found in gastropods. In cephalopods, a cartilaginous capsule encloses the concentrated mass of ganglia. The cephalopods have two pairs of nerve cords with four paired ganglia. The visceral nerve cord serves the internal organs, whereas the pedal nerve cord serves the foot. The ganglia located above the esophagus are cerebral, pleural, and visceral, and the ganglia situated below the esophagus are the pedal (Jordan and Verma 2001). Monoplacophora and Aplacophora have a very primitive ladder-like nervous system (Fig. 5). The cephalopod members possess well-developed vertebrate-like eyes, and there are photoreceptors on the mantle margins of some bivalves.

## Circulatory System

Most mollusks' circulatory systems are mainly open type, where the blood or hemolymph pumps into the open space around the visceral organs and nourishes the visceral organs. As



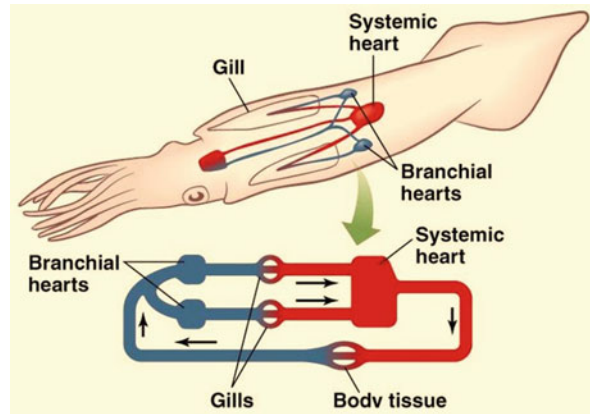
**Mollusk, Fig. 5** Nervous system of gastropods. [https://commons.wikimedia.org/wiki/File:Gastropod\\_nervous\\_system.gif](https://commons.wikimedia.org/wiki/File:Gastropod_nervous_system.gif)

mollusks are true coelomates, the main body cavity is called hemocoel, through which the coelomic fluid and blood circulate (Pechenik 2015). The hemocoelic spaces act as a hydrostatic skeleton. The heart possesses one or two atria/auricle pairs that receive the gills' oxygenated blood and pumps it into ventricles. From there, it enters into the main blood vessel called the aorta that opens into the hemocoel. The auricle/atria perform the excretory system's function partly by filtering waste products out of the blood and dumping them into the coelom as urine (Ruppert et al. 2004). The body fluids are transported largely within sinuses devoid of distinct epithelial walls; the heart is posterior-dorsal, enclosed in a pericardium that typically consists of a ventricle and two posterior auricles. The blood or hemolymph is drained from ctenidia, gills, or the specialized respiratory epithelia into respective chambers. The ventricle pumps the hemolymph through the middorsal sinuses (in solenogasters and scaphopods) or vessel (aorta) into the body tissues. Hemocyanin is the respiratory pigment that contains copper rather than iron: in more advanced forms, hemoglobin is bound to blood



**Mollusk, Fig. 6**

Circulatory system



cells. In chiton and some members of monoplacophorans, the heart is also the site of purification discharged waste into the pericardium and via a pair of pericardial outlets (modified kidney/nephridia) (Fig. 6).

## Excretory System

The anatomical structure of the renal gland varies from species to species. Still, a common plan is evident. The atria/auricle of the heart also functions as part of the excretory system by filtering waste products known as the organs of Bojanus. The renal gland is a relatively wide tube opening from a sac (pericardium) that surrounds the heart at one end and to the mantle cavity at the other end. Some mollusks possess Keber's organ, otherwise called the pericardial gland. It is a large reddish-brown glandular mass situated anterolateral to the pericardium into which the waste materials are excreted. A majority of mollusks are aquatic, so they excrete nitrogen in the form of ammonia (Baeumler et al. 2012). In octopus the excretion is in the form of ammonium chloride. Terrestrial snails and slugs excrete uric acid and excrete ammonia when the animal is in moist surroundings. In all mollusks, the primary urine production appears to be filtration of blood. This may take place through the heart walls into the pericardium or from blood vessels that supply the glandular part of the renal gland. These are located

at the rear of the coelom, extract any reusable material from the urine, dump additional waste products into it, and then eject it via tubes that discharge into the mantle cavity (Brusca et al. 2014). In most freshwater mollusks, the reabsorption process takes place by glandular tube and in the wide tubule. So the final urine is more dilute than the blood.

## Reproduction

Most mollusks are dioecious, and fertilization occurs externally, except terrestrial mollusks such as snails, slugs, and cephalopods (Furuhashi et al. 2009). In adult cephalopods and other representatives, the paired dorsal gonad retains the developmental connection with the pericardium. Some solenogasters egg and sperms are discharged into the pericardial cavity and through pericardial outlets discharge to an environment where the fertilization takes place. In more advanced mollusks, separate gonoducts (oviducts for female gametes vas deferens for male gametes) produce the egg and sperm respectively to the mantle cavity. In some mollusks, the zygote hatches and undergoes two larval stages – **trochophore** and **veliger** – before becoming a young adult; bivalves may exhibit a third larval stage, **glochidia**. Eventually, the larva sinks to the seafloor and metamorphoses into an adult form (Buchsbaum et al. 2013).

**Mollusk, Fig. 7** *Pila*.  
<https://pixabay.com/photos/snail-garden-snail-shell-1634852/>



### Classification of Phylum Mollusca

There are seven living classes and two extinct groups. First, we will see the living classes:

1. **Gastropoda** (Gr. *gaster*-belly+*podios*-foot): This is the largest class of mollusks and includes snails, conchs, abalones, and whelks sea hares, garden slugs, etc. Because their stomach is situated on foot, they are named gastropods. The member's habitat includes marine, freshwater, or terrestrial. Their body is asymmetrical with a distinct head, which is well developed with tentacles and eyes. The foot is broad and expanded with a creeping sole. Rhythmic contractions of the muscular foot perform the locomotion. Some mucus-secreting glands in the foot secrete mucus on which the animal slides (Ruppert et al. 2004). The body is asymmetrical due to the "rotation of visceral mass in its axis" (torsion). There is a lid at the opening of the shell called the operculum. Respiration is by gills or pulmonary sac. The mantle encloses the visceral mass. The buccal cavity contains the radula with odontophore, which works as a file to scrape and tear food materials. The nervous system is well developed with paired ganglia and their connectives and commissures, with distinct cerebral and pleural ganglia besides pedal and visceral ganglia. Sexes are separate, and the development is indirect through a veliger larva or trochophore larva. The animal is very active during the night or dim light. As the

slugs have no shell, the mucus layer gives protection to the body, enabling the animal to live in wet and moist areas. Slugs and land snails cause severe damage to plants and agricultural cultivations as they eat leaves and stems (Jordan and Verma 2001; Louise 2006). Examples include *Pila* (Fig. 7), *Xancus*, *Aplysia*, *Doris*, and *Dolabella*.

2. **Pelecypoda (Lamellibranchiate or Bivalvia)**: Pelecypodes (Gr *pelekus*-hatchet+*podos*-foot) are bilaterally symmetrical, laterally compressed mollusks with a two-lobed mantle. The body is enclosed within two valved shells, hence the name bivalve. The head is rudimentary without eyes and tentacles but with a pair of labial palps. The foot is large plow or wedge-shaped, adapted for burrowing. The respiratory organs are plate-like gills called ctenidia. The intestine is highly coiled and devoid of the radula. Excretory organs consist of paired nephridia. The nervous system includes three pairs of nerve ganglia – cerebropleural, pedal, and visceral (Ruppert et al. 2004). Sexes are separate, gonads are single, and development includes a parasitic glochidium larva (freshwater mussel) or free-living veliger larva (Pinctada). This group includes clams, oysters, and scallops. They are the food sources for other living beings, including humans. This group of animals is well adapted for living in the water. For protection, clams burrow deep into the sand by contracting and relaxing their muscular foot. Mussels and oysters attach themselves with a



**Mollusk, Fig. 8** Pinctada. [https://en.wikipedia.org/wiki/Pinctada#/media/File:Pinctada\\_margaritifera\\_MHNT.CON.2002.893.jpg](https://en.wikipedia.org/wiki/Pinctada#/media/File:Pinctada_margaritifera_MHNT.CON.2002.893.jpg)

strong thread or cement to solid surfaces, called byssus threads. Examples include *Lamellidens*, *Milieus/Perna*, *Pinctada* (Fig. 8), and *Solen*.

3. **Polyplacophora (Loricata or Amphineura)** (Gr. Amphi-both+nervous-nerve): This group is considered as most primitive of existing mollusks. The members of this group include chitons. They are exclusively marine, bilaterally symmetrical, and dorsoventrally flattened animals. They have an articulated shell composed of eight hinged and overlapping longitudinal/transverse plates or valves (Budd and Jensen 2000). A thick leathery mantle covers the body. They have an indistinct head without eyes and tentacles. They have a well-developed radula mounted on an odontophore. The foot is the broad, flat muscular, glandular creeping sole and ventral in position. The mantle cavity is restricted to mantle grooves on either side of the ventral side. Numerous bipectinate gills occur on either side of the body in the mantle groove. The nervous system is primitive and ladder-like, which resembles the Platyhelminthes (turbellarians). They have

a cosmopolitan distribution, from cold waters through to the tropics (Jordan and Verma 2001). They live on hard surfaces, such as on or under rocks or in rock crevices, inhabit intertidal or subtidal zones, and are exposed to the air and light for long periods. They feed on algae and seaweeds that grow on rocks by their radula. Examples include *chitons* (Fig. 9), *Leptochiton*, and *Chaetopleura*.

4. **Cephalopoda** (Gr kephale-head+podos foot): The word cephalopod means “head-footed.” All are exclusively marine, most specialized, and complex animals such as squid, octopuses, and cuttlefish. The members possess a large head, a crown of oral arms, a well-developed nervous system with centralized brains, and large eyes similar to the human eyes. They are the only mollusks having an advanced circulatory system, an accessory bronchial heart, and closed blood vessels. Their foot is divided into many tentacles with strong suction cups or hooks, capturing the prey. They feed on crustaceans, worms, and other small mollusks (Canti 2017). They have thick muscular, and



**Mollusk, Fig. 9** Chiton. <https://www.flickr.com/photos/jsjgeology/15947947127>

**Mollusk,**

**Fig. 10** Octopus. [https://www.flickr.com/photos/joachim\\_s\\_mueller/6775462987](https://www.flickr.com/photos/joachim_s_mueller/6775462987)



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leathery mantle. There is an external or internal shell, which can be absent in some species. They have a cartilaginous endoskeleton for supporting the body, attachment of muscles, and protection of nerve centers. They possess ink glands as a defensive adaptation. These glands secrete melanin-containing dark color ink to discolor the surrounding water and escape enemies (Stoger et al. 2013). Examples include *Sepia*, *Loligo*, *octopus* (Fig. 10), and *Nautilus*.

5. **Scaphopoda (Solenoncha):** Scaphopoda (Gr. Shapha-boat+podos-foot) includes elephant tusk shells. A group of aberrant marine mollusks of very low grade of organization. According to the fossil record, it is believed that scaphopods from the youngest mollusks and appeared from Mississippian onwards. The members of this class are exclusively marine. The shells' size ranges from about 0.5 to 15 cm in length, and they like to live in soft substrates offshore. Long cylindrical and



bilaterally symmetrical body without eyes, sensory tentacles, and gills (David and Winston 2001). Tubular and tusk-like shell open at both ends. Mantle edge fuses to form a mantle tube open anterior and posterior. The foot is long, narrow protrusible spade-like and is used for digging. The mouth is surrounded by lobular outgrowths, cephalic filaments, or protrusible tentacular processes called captacula, which serve as tactile organs to capture food particles. As gills are absent, the respiration is by the exchange of gases through the mantle surface. The circulatory system is simple, and the heart is rudimentary or absent. The nervous system has a pair of cerebral and pleural ganglia. Sexes are separate, and development includes a veliger larva. According to molecular data, it is suggested that the scaphopods are considered Cephalopod sister group (Ruppert et al. 2004). An example is *Dentalium* (Fig. 11).

6. **Aplacophora:** Aplacophora is the animal group popularly known as Solenogasters or mud moles. They are primitive degenerative marine mollusks that inhabit marine habitat with cosmopolitan distribution with long, narrow, bilaterally symmetrical, and vermiform bodies (Scheltema 1993). There is the absence of head, foot, mantle, shell, and nephridia (Ruppert et al. 2004), but they have calcareous spicules in the skin. The digestive tract is straight with toothed radula in the mouth. They have the presence of a pair of

coelomoducts, which serve as gonoducts. The heart consists of a single auricle and a ventricle. Hemocoel has two portions, namely, dorsal hemocoel and pedal hemocoel separated from each other by septum. The aplacophorans are traditionally considered as an ancestral mollusk (Buchsbaum et al. 2013). They are found at all depths of the sea, usually absent in the littoral zone. Some of them burrow in the mud while some are live in association with certain colonial coelenterates, and still, others are predators. The group comprises the two clades Solenogasters and Caudofoveata. The aplacophorans are traditionally known as ancestral mollusks (Budd and Jensen 2000; Amelie 1993). Examples include *Neomenia* (Fig. 12) and *Chaetoderma*.

7. **Monoplacophora (Tryblidiida):** A small group of mollusks with primitive features. Body bilaterally symmetrical flat and oval body with a minute head foot, mantle, and radula. The body is internally segmented. The shell is univalved, conical or cup-shaped, and symmetrical. There is the presence of segmentally paired external gills, segmentally repeating nephridia, and gonads. They have a primitive ladder-like nervous system. The sexes are separate in almost all forms. At present, a monoplacophoran is represented by a single genus, namely, *Neopilina*. It is a very primitive form and considered a living fossil and thought to have become extinct over 380 million years ago. The shells of many



**Mollusk, Fig. 11** Dentalium. [https://commons.wikimedia.org/wiki/File:Dentalium\\_octangulatum\\_01.JPG](https://commons.wikimedia.org/wiki/File:Dentalium_octangulatum_01.JPG)





**Mollusk, Fig. 12** *Neomenia*. [https://commons.wikimedia.org/wiki/File:Neomenia\\_yamamotoi.jpeg](https://commons.wikimedia.org/wiki/File:Neomenia_yamamotoi.jpeg)

**Mollusk, Fig. 13**

*Neopilina*. [https://digit.snm.ku.dk/www/inv/full/MON-000001\\_shell-mo.jpg](https://digit.snm.ku.dk/www/inv/full/MON-000001_shell-mo.jpg)



monoplacophorans are limpet-like in shape. They were not recognized as such until 1952 (Ruppert et al. 2004). An example is *Neopilina* (Fig. 13).

**Some Extinct Groups of Mollusks**

- a) **Rostroconchia:** These are extinct mollusks from the early Cambrian period to the late Permian period. This group was mistaken as bivalves because the larval stage is univalve, but the adult typically has a pseudo-bivalve shell that encloses the mantle and muscular foot. This group consists of more than 1,000 species of members (Budd and Jensen 2000).
- b) **Helcionelloida:** They are also an extinct group of mollusks, consisting of the oldest

conchiferan mollusk with mineralized shells (Budd and Jensen 2000).

**The Fossil Records**

Mollusks are considered some of the oldest metazoans. The evolutionary history and origin of mollusks from the ancestral group Lophotrochozoa and their evolution into modern living form and fossil form are still a debated subject. Some of the fossil record obtained from the south region of Australia and North Russia shows close resemblance with mollusks. There is good evidence available for the appearance of gastropods and bivalves (Parker 2017). Most familiar members of living members of this phylum, such as the Gastropoda, the Bivalvia Cephalopoda, the

Polyplacophora, the Scaphopoda, the Monoplacophora, and the Aplacophora are believed to originate from the Cambrian period (Budd and Jensen 2000). Now itself, the debate occurs about *Kimberella*, a mollusk-like organism from 555 million years ago, and some Ediacaran and early Cambrian fossils (Ruppert et al. 2004).

## Cross-References

- [Bilateral Symmetry](#)
- [Digestive System](#)
- [Jean Baptiste Lamarck](#)
- [Nervous System of Invertebrates](#)
- [Phylum](#)

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## Mollusk Cognition

### ► Cephalopod Cognition

## Molting

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## Synonyms

[Ecdysis](#); [Eclosion](#); [Shedding](#)

## Definition

The process of casting off outer coverings.

## Introduction

Protection from the constant assault of environmental harms is a basic need of all living organisms. Whether they are physical or biological,

such challenges pose a threat to survival. Defense takes shape in the way of barriers like skin, scales, feathers, and hair which shield the inside environment from the outside one. Like all defenses, these “suits of armor” incur costs to maintain integrity and consequent effectiveness. Skin cells die and are constantly shed and replaced, feathers are lost and new ones grow in, and likewise scales and hair are renewed. Instead of such constant and gradual turnover, some vertebrate animals shed their entire protective covering abruptly as when a snake or frog sheds its skin, or a bird changes plumage. In contrast, most invertebrate animals – lacking an internal skeleton – are encased in a protective coating called an exoskeleton that is very durable and frequently hard in texture. There, growth and renewal happens only through the process of molting, also known as ecdysis, when the entire covering is shed in a single event. Molting has been recorded as far back as the Cambrian in fossils of early arthropods (García-Bellido and Collins 2004). The diverse groups of invertebrate animals that molt their exoskeletons are collectively named the Ecdysozoa (Aguinaldo et al. 1997).

## Molting and Molt Phases

Exoskeletons are effective shields and vary in ways they function as skeletons. They can form points of attachment for muscles or function solely to maintain an animal’s shape. As with all adaptations that increase survival, there are trade-offs, and for being coated with an effective nearly impenetrable encasement, one trade-off is more limited motion and flexibility. Perhaps most importantly, exoskeletons restrict growth because such coatings cannot gradually and continuously stretch and expand. Therefore arthropods such as insects, crabs, shrimps, and lobsters as well as other ecdysozoans, the nematodes, nematomorphans, kinorhynchs, priapulids, onychophorans, and tardigrades must molt in order to grow. This limitation has obvious implications for overall size but also a less apparent consequence: mouthparts eventually become too small for efficiently meeting an animal’s increasing

energy demands and need to be included in the molting process. Having said that, molting may not always be associated with growth in all ecdysozoans since some species of tardigrades can be smaller after molting when they are starved beforehand (Baumann 1961).

Among insects and crustaceans, the entire molting process consists of three phases, premolt, molt, and post-molt with behavioral changes associated with each. In general, preparations for ecdysis occur during the premolt phase when the muscular connections to the old exoskeleton loosen and the exoskeleton cracks along defined lines called sutures. The molt phase follows with the animal wiggling out of the old exoskeleton. During the post-molt phase, the animal swells in size and the new soft exoskeleton sclerotizes. Until such hardening completes, some crustaceans are supported by a hydroskeleton (Taylor and Kier 2003). As Ecdysozoa are a diverse animal group, duration and complexity of molt phases vary greatly among members. For example, the entire molting process is accomplished in a matter of hours for nematodes (Singh and Sulston 1978) but can take as long as 16 weeks in some land crabs (Fletcher et al. 1990). Changes in physiology during molting are complex, as are some of the behaviors associated with them discussed next.

## Molting Hormones and Behavior

The cellular changes during premolt, molt, and post-molt phases are orchestrated by a variety of molting hormones. Best studied are the ecdysones and juvenile hormones of arthropods, major hormones involved in growth, molting, and metamorphosis, which appear to be structurally and functionally similar to thyroid hormones (Flatt et al. 2006). These hormones and their analogs might be expected in some other ecdysozoans, as in the case of the onychophoran *Euperipatoides leuckarti* (Hoffman 1997). And still, free-living nematodes lack ecdysteroids (Chitwood 1999), and no orthologs of ecdysone receptors are found in the complete genome of *Caenorhabditis elegans* (Sluder and Maina 2001). Genetic

evidence supports the idea of an endocrine control for molting in *C. elegans* (Frand et al. 2005), so some other steroid(s) must be involved as inferred by the requirement for cholesterol to molt successfully (Yochem et al. 1999).

Molting hormones can produce neurophysiological effects on behavior. Among insects, feeding stops, and locomotor activity declines with decreased juvenile hormone or a surge of ecdysterone near the onset of the molt phase (Raabe 1982). The premolt loosening of connections to the exoskeleton and shedding of the old exoskeleton by peristaltic contractions during the molt phase are regulated in insects by a neuropeptide cascade (Gammie and Truman 1997). Similar to insects, crustacean molting appears to be regulated by neuropeptides. Behavioral features of molting similar to those of insects (positioning, wiggling, shedding) are correlated with a rise and fall of crustacean cardioactive peptide (Phlippen et al. 2000). In lobsters, increased levels of aggression and greater inclination toward escape characterize pre- and post-molt behavior, respectively (Cromarty et al. 1991). Presumably, these behavioral changes are under hormonal regulation.

## Molting and Predator Avoidance

When the protective function of the exoskeleton is considered, the vulnerability of an animal to environmental attack during molting is immense. The loss and reformation of an exoskeleton is physiologically challenging, energetically expensive, and time consuming. By losing their protective shell, a molting animal must endure a period of time, often days, when it is soft-bodied and defenseless. Moreover, such animals have limited mobility since most of its musculature for locomotion is attached to the exoskeleton. Therefore, molting animals cannot escape or show aggression toward an attacker. To survive the process of molting, many animals have evolved adaptations for protection. For example, some animals become cryptic through adaptations that are physical, behavioral, or both. In all cases known, establishing some form of protection during

premolt is crucial, and there are a variety of ways safety can be achieved.

Vulnerability to attack during molting is most commonly thought of in terms of visual predators, and these might be deterred by camouflage or concealment. So, for example, premolt caterpillars of moths and butterflies often search for protected out-of-view microhabitats like the undersides of leaves for building camouflaged cocoons or attachment spots for pupation from chrysalides (James and Nunnallee 2011). Concealment underground has evolved in a diversity of species that establish burrows during premolt. For example, some caterpillars of moths drop from host plants to burrow underground and molt (Janzen 1984), as do hymenopteran caterpillars (Smith and Janzen 2003). Coconut crabs, *Birgus latro*, seek out soft ground away from their usual rocky habitats to dig molting burrows, which can be 1 m long at 0.5 m depth (Fletcher et al. 1990). Finally, nocturnal molting is common among a number of insects (Lindgren and Wolf 1982; Wallace and Anderson 1996).

Many predators are not so visual and instead use scent to find their food. Prey have evolved adaptations for chemically cloaking their location, a strategy particularly effective during molting. For instance, some caterpillars incorporate chemicals from their food plants that make them chemically “invisible” to predaceous ants (Akino et al. 2004). Larvae of the European lycaenid butterfly species *Maculinea rebeli* are inquilines or tenants that live and molt in *Myrmica* ant nests while disguised as chemical mimics (Dettner and Liepert 1994). Chemical adaptations for protection can also be defensive as in *Pycnogonum littorale*, a sea spider that releases molting hormones, ecdysteroids, to deter predators before and during molting (Tomaschko 1994).

Lobsters, *Homarus americanus*, have evolved adaptations that physically, temporally, and chemically decrease vulnerability during molting. Lobsters are nocturnal and seek cover during daylight hours in shelters they excavate in rocky areas. In the weeks prior to molting, a lobster utilizes more than one shelter, which it barricades with carefully selected rocks, pebbles, and seaweeds. Lobsters molt in the early morning allowing them time to

start hardening their shell before the next nocturnal activity period when other lobsters can find and evict them. Once outside the shelter, they are vulnerable to predation. In the first post-molt days, they can hardly walk and avoid fights by jetting away. It may take a male several months to regain his old dominance status despite the fact he is now much larger than before molting. Mature females employ a remarkable strategy for survival and reproduction: they join a dominant male in his shelter by emitting a pheromone that subdues his natural aggression to any other lobster who tries to enter (Atema and Steinbach 2007). The pair cohabits for several days during which he inseminates and protects her when she molts. This gives her time to harden her new shell, and it reduces chances for other males to inseminate her. The dominant male practices serial monogamy and can receive a series of premolt females, one at a time (Cowan and Atema 1990). When his own time to molt arrives, he has no protection and drops down the dominance hierarchy.

## Molting and Feeding Behavior

Many ecdysozoans do not feed immediately following molting. This post-molt delay lasts until their mouthparts harden (Greenway 1985). The length of time varies widely for a group as diverse as the Ecdysozoa, and focusing on its composite phyla does not help to narrow the variation. For example, among the Crustacea, feeding can resume within 24 h to a week following ecdysis (Steel 1982; Greenway 1985). Their first meal is usually the old exoskeleton, the exuviae, which are consumed to replenish calcium stores and other minerals (Paul and Sharpe 1916; Auzou 1953; Steel 1982; Graf 1978). In lobsters (*H. americanus*), the male consumes the cast shell of his cohabiting female (Atema, personal observation). Fletcher et al. (1990) speculate that much of the 3–4 weeks before coconut crabs emerge from molting burrows is occupied by the consumption of the old exoskeleton. Not all ecdysozoans eat their exuviae. For example, the nematode *C. elegans* does not eat its old exoskeleton yet begins feeding as soon as it molts and



begins crawling out of its old cuticle (Singh and Sulston 1978). While feeding is delayed in the priapulid *Priapulius caudatus* for nearly a week, the exuviae are not consumed presumably because it does not contain essential minerals like calcium (Trott 2017).

## Conclusion

All animals have a protective coating to shield them from the environment. For ecdysozoans, that barrier restricts growth, and increase in size comes with the expense of shedding their exoskeleton in its entirety through the process of molting, a complex process requiring physiological and behavioral changes, orchestrated by a variety of hormones. The Ecdysozoa encompasses a diverse group of invertebrates, which are equally diverse in their behavioral adaptations required to survive a most vulnerable time in their life histories. These include visual and chemical concealment from predators and frequent use of burrowing which accomplishes both. A cyclic physiologically and physically transformative process, filled with chances for failure, molting is certainly one of nature's amazing evolutionary wonders.

## Cross-References

- [Arthropod Life History](#)
- [Mimicry](#)
- [Predation Risk](#)

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## Monitor

- [Touch Screen](#)

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## Monkey

- [Haplorhini](#)  
 ► [Parieto-occipital Sulcus \(POS\)](#)

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## Monkeys

- [Catarrhine Cognition](#)

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## Monochorionic Dizygotic Twins

- [Dizygotic \(DZ\)](#)

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## Monocular Depth Cues

- [Cognition](#)

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## Monocular Vision

- [Cognition](#)

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## Monogamy

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## Synonyms

[Pair-bonding](#); [Pair-living](#)

## Definition

A mating system in which two individuals consistently and primarily mate within their pair.

## What Constitutes Monogamy?

Monogamy is a mating system in which two individuals consistently and primarily mate within their pair. Measuring the consistency and exclusivity of monogamous pairs can be challenging, and there is currently a lack of agreement regarding what frequency of extra-pair copulations, if any, should still constitute a monogamous mating system. Accordingly, while this system is often associated with pair-living and pair-bonding, these arrangements do not necessarily indicate monogamy. Pair-living, also referred to as social monogamy, is a social organization in which two adults of opposite sex occupy the same home range with their nonreproducing offspring. Pair-bonding represents a long-term social relationship between two unrelated individuals of the opposite sex which is characterized by affiliative interaction, close proximity, and reciprocity (Tecot et al. 2016).

## Distribution and Prevalence

Throughout the animal kingdom, monogamous species are relatively rare compared to those characterized by other mating systems. This pattern is expected because, in most species, males have access to several breeding females, and offspring can survive without paternal care. In such contexts, males can increase their reproductive success (i.e., number of offspring) by associating and mating with more than one female. Thus, monogamy is not an advantageous mating strategy for males of most species (Trivers 1972).

Lifelong monogamy is particularly rare among pair-living animals, which typically practice serial monogamy. In the latter case, monogamous bouts

are separated by divorce, which is defined as having occurred when both previously paired individuals are alive during a subsequent breeding season and at least one of them consistently mates with a new partner. Divorce has evolved as an adaptive behavioral strategy since it is triggered by low breeding success (relative to other individuals of their species) and often results in increased breeding success for the initiating individual (Culina et al. 2015). Divorce rates vary across species and usually increase as adult sex ratios become more skewed. In humans, divorce rates peak at 4 years of marriage. This may reflect an adaptation to serial monogamy in which the pair-bond duration is similar to the age at which infants are weaned (Fisher 1989).

Interestingly, the prevalence of monogamy varies greatly between animal groups. While 90% of bird species are classified as socially monogamous, this is true for only 9% of mammals (Lukas and Clutton-Brock 2013). This difference is likely to be driven by disparities in infant care and parental investment. In mammals, only mothers can provide nourishment for nursing offspring. Consequently, a lack of paternal investment is less costly to mammalian offspring survivorship, and mammalian males can benefit relatively more from investing in mating rather than parenting (Opie et al. 2013). Furthermore, in contrast to socially monogamous birds, extra-pair mating is relatively low in socially monogamous mammals. This is likely to reflect adaptations to bi-parental care and/or mate guarding (Lukas and Clutton-Brock 2013). Infidelity rates are higher for bird species which nest in colonies, as colony-dwelling individuals have more opportunities to find a mate of higher quality than their partner (Moller and Birkhead 1993).

Primates are unusual among mammals in that approximately 29% of species are monogamous (Lukas and Clutton-Brock 2013). This mating system has evolved independently in all major primate clades (Opie et al. 2013). Humans represent an interesting case, as about 17% of human cultures are considered monogamous,

meaning that in these cultures, polygyny is either prohibited or extremely rare. However, although the remaining majority of human societies exhibit slight or general polygyny (Marlowe 2000), most marriages within those societies are nonetheless socially monogamous (Dixson 1998).

## Evolutionary History

The selective pressures that lead to monogamy are still debated. Male infanticide may lead to monogamy, with protection against infanticidal rivals selecting for paired males who can offer protection to offspring. This may explain the high prevalence of monogamy in primates, since they are relatively altricial and exhibit long lactation periods, which can increase infant vulnerability to infanticide (Opie et al. 2013). Furthermore, although most mammals are seasonal breeders, many primate species reproduce all year round. Nonseasonal breeding increases the likelihood of infanticide since females in these species can be brought back into estrus sooner following the loss of an unweaned infant. Monogamy may have also evolved as a way for males to secure access to females who are dispersed due to low food density. This could also explain the high frequency of monogamy in primates since many species depend on high quality, low abundance food resources (Lukas and Clutton-Brock 2013). Other theories have been proposed to explain the evolution of pair-living and/or pair-bonding, but such ideas do not necessarily explain monogamous mating. These include predation-driven optimal group size and resource defense (Tecot et al. 2016).

Many monogamous species have subsequently evolved cooperative breeding or paternal care (Lukas and Clutton-Brock 2013; Opie et al. 2013). In cooperative breeding systems, females usually stay in their natal group and, rather than producing their own offspring, provide care for the offspring of their dominant relatives. Since

monogamy increases sibling relatedness, this makes cooperative breeding potentially beneficial for nonbreeding individuals (Lukas and Clutton-Brock 2013). Monogamy also provides the opportunity for paired males to provide infant care, which can decrease parenting costs for females. This may allow females to increase resources dedicated to lactation, potentially leading to shorter lactation periods, shorter inter-birth intervals, and higher reproductive rates. Consequently, paternal care can improve the reproductive success of both males and females in monogamous species (Opie et al. 2013).

## Neurobiological Mechanisms

Neurobiological studies on monogamous organisms have identified the proximate mechanisms underlying monogamy. Pharmacological and neuroimaging studies have identified the involvement of specific brain areas, such as the nucleus accumbens, lateral septum, and ventral pallidum. These regions are associated with reward processing and stress responses. Key neurotransmitter systems have also been identified which are critical in the formation and/or maintenance of pair-bonds. These include dopamine, opioids, oxytocin, and vasopressin. Across taxa, these systems are associated with regulating sociosexual behavior and reward learning (Johnson and Young 2015).

Most of our current knowledge regarding the neurobiology of monogamy is the result of laboratory studies of monogamous prairie voles (*Microtus ochrogaster*). Individuals of this species form long-term social bonds with their mates and produce multiple litters in these pairs. However, within populations, not all prairie voles exhibit the same inclination for monogamy. Interindividual neurobiological differences have been linked to the observed differences in pair-bonding behavior. Furthermore, a closely related species, the montane vole (*Microtus montanus*), is asocial and promiscuous. Comparative studies of these species have illuminated the neurobiological differences underpinning this mating

behavior variation. This work has facilitated studies in other monogamous animals which are also relatively easy to maintain and breed in laboratory settings. These include species of primates (titi monkeys: *Callicebus cupreus*; marmosets: *Callithrix penicillata*), birds (zebra finches: *Taeniopygia guttata*), rodents (deer mice: *Peromyscus californicus*), and fish (cichlid fishes: *Amatitlania nigrofasciata*). Overall, these studies suggest an evolutionarily conserved role for many neurotransmitters in modulating monogamy-related behaviors (Johnson and Young 2015).

## Cross-References

- [Extra-Pair Copulation](#)
- [Mate Guarding](#)
- [Mating](#)

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## Monophyletic

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## Definition

A monophyletic group is a set of taxa descended from a single (“stem”) taxon (*i.e.*, a ► [common ancestor](#)), which includes all taxa descended from this single common ancestor, as well as the ancestor itself. Monophyletic groups are defined by the sharing of apomorphic (“derived”) conditions and, for that reason, the taxa contained in a given monophyletic group are considered more closely related to each other than to any taxon classified outside of this group.

## Introduction

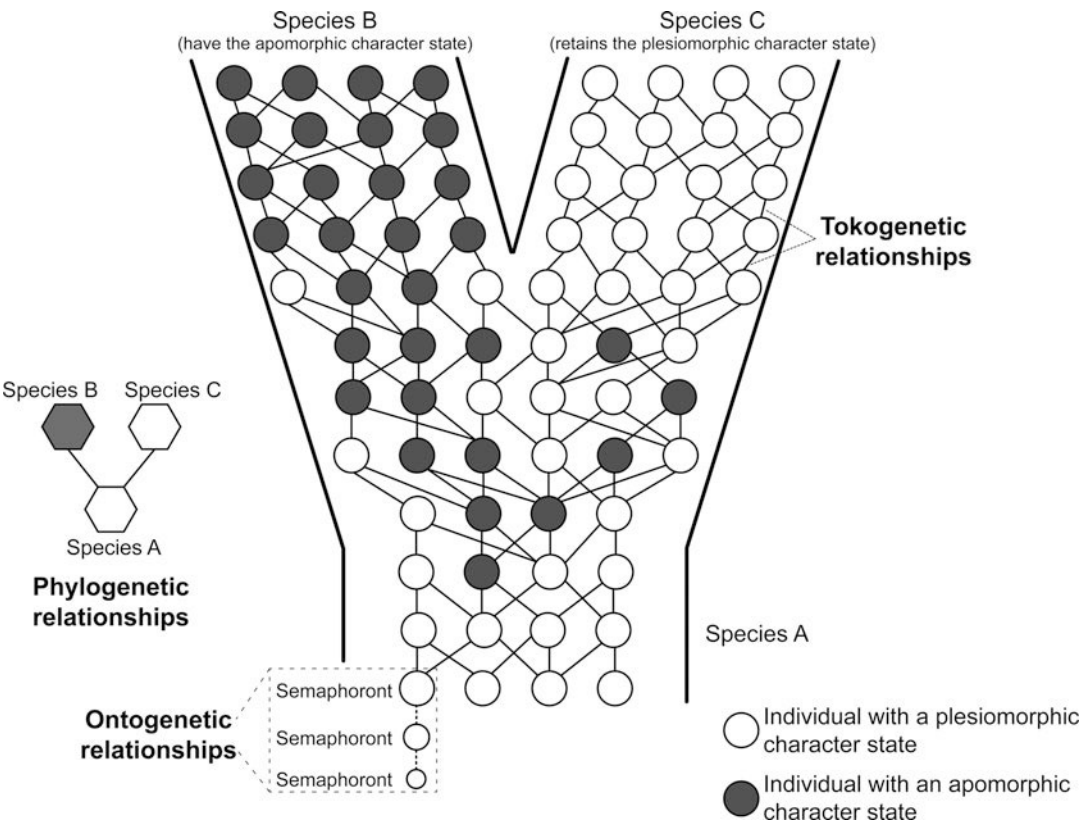
Phylogenetic systematics (or Cladistics) is a field in biology that aims to reconstruct the evolutionary history and patterns of relationship among extant and fossil organisms. It consists of a method of character analysis for studying the evolution and relationships among organisms based on observed heritable characteristics (phenotypes or genotypes), which are tested under specified models of evolution. The results of a phylogenetic analysis are represented by a ► [phylogeny](#) (or phylogenetic tree), which graphically symbolizes the evolutionary history of a group of taxa. Phylogenetic trees are obtained through a congruence analysis (like ► [parsimony](#), maximum likelihood, or Bayesian inference), their tips represent the “end” or the “present time” in an evolutionary lineage and are constituted by the terminal taxa that are being studied (either extant or fossil organisms). The pattern of connections between



these taxa hypothesizes the phylogenetic relationships among them.

Phylogenetic systematics was first proposed by Emil Hans Willi Hennig (1950, 1966, 1968) as a biological reference system that not only investigates and expresses the evolutionary relationships among organisms but also offers a rationalization of the phenomena leading to these relationships. Hennig's initial step was to consider an individual organism in a specific period of its life history—named semaphoront—as the fundamental unit of systematics. This individual would be the “character-bearing specimen,” which is an organism in a definite, brief interval of its life span (Hennig 1966). His proposition was based on the evidence that the morphology of a given individual could not only vary when compared to different taxa but also as a function of time (ontogeny) and in various lineages, as among sexes and between seasons

(Hennig 1966; Sharma et al. 2017). Therefore, Hennig established the idea of semaphoront as a solution to standardize the interval in life in which the specimens representing the different taxa in a phylogenetic analysis should be studied. In order to make valid comparisons, taxa selection for phylogenetic analyses should preferably contain comparable semaphoronts (*i.e.*, individuals sharing similar ontogenetic stages, sex, etc.). According to Hennig (1966), semaphoronts would be connected by ontogenetic relationships and form individuals; individuals by tokogenetic (*i.e.*, population genetic or genealogical) relationships and form species; and species by phylogenetic relationships, represented as cladograms (Fig. 1). From these, only the phylogenetic relationships among semaphoronts would constitute a “hierarchic system,” in the mathematical sense, and thus be used for biological classification purposes as a result of phylogenetic analyses.



**Monophyletic, Fig. 1** Modification of figure 6 of Hennig (1966), indicating the differences between ontogenetic, tokogenetic and phylogenetic relationships. Colored

individuals exemplify the origin and maintenance of an apomorphic state for a certain character

The relationships between the different hierarchies contained in a phylogenetic tree are determined by the existence of shared novel characteristics (**apomorphies**) between the analyzed taxa (Fig. 1). These characteristics are acquired during the phylogenetic separation of a common ancestor into two taxa, and kept in the new population by means of tokogenetic relationships among its individuals. Natural groups are delimited by apomorphic characters states and called **monophyletic** groups. It is important to note that it is not enough for organisms to share characteristics; in fact, two organisms may share several characteristics and still not be considered members of the same, less inclusive, group. That is because these characteristics may represent unmodified features (**plesiomorphies**) inherited from their ancestors, and sharing of these with other phylogenetic hierarchies is not used as evidence of phylogenetic relationships.

Below, we provide detailed explanations of a few topics in order to further explore the presented concepts.

### What are *Characters* and *Character States* in a Phylogenetic Systematic Context?

Despite the term “character” being central to phylogenetic analyses, its precise meaning was often neglected in theoretical phylogenetic studies. This was changed in 2007, after the publication of a revisionary study by Paul Sereno. His study focused on the logical basis for morphological characters and provided formal definitions for the terms *characters* and *character states* to be used in a phylogenetic systematics’ context. Sereno (2007) proposed that **characters** should be the term applied for *independent variables* (i.e., ► [Homology](#) parts that vary across the different semaphoronts), while **character states** should be *mutually exclusive conditions* of a given character (i.e., different ways in which a specific character may vary). For example, when studying the different ways that the anterior limb of mammals may vary, the independent variable (thus, the character) would be *anterior limb*, and the exclusive conditions (character states) are the different ways in which this character is observed:

as a *wing* (in bats), as *fins* (in aquatic mammals), as *arms* (in apes), or as the *front legs* (in quadrupeds).

The necessity of a formal definition comes from the confusion caused by the interchangeable operational use of the terms “character” and “character state,” which started with Hennig (1966), but persisted in several subsequent works (e.g., Platnick 1979; Patterson 1982). In the pursuit of well-delimited definitions, Sereno’s (2007) circumscriptions of *character* and *character state* are used hereafter.

### Natural Groups of Species and Evolution

The basic idea behind phylogenetic systematics is that members of a certain hierarchy group share a common evolutionary history. They are more “closely related” to members of the same group than to other organisms, because they share unique characteristics that were not present in distant ancestors. The term **natural group** describes these groups of taxa that exist in nature and are connected hierarchically by past evolutionary events.

Despite our ability (or lack thereof) to recognize natural groups, we accept a single origin for life on earth. Thus, all organisms are related to each other in some way or another and, because of that, we can retrieve the pattern of relationships among any organisms. We only have to use the right kind of information in order to do so. In this sense, the phylogenetic system tries to provide an idea of how these natural groups are connected and hierarchically organized by successively shared common ancestors. These groups are subordinated one to the other according to the temporal distance between their origins and the present time, and the sequence of subordination corresponds to the recency of common ancestry (Hennig 1966).

These natural, hierarchically disposed groupings are named **monophyletic** groups. A monophyletic group is a set of taxa descended from a single (“stem”) taxon, and which includes all taxa descended from this stem’s common ancestor, besides the ancestor itself (Hennig 1966). Therefore, every terminal taxon contained in a given monophyletic group is considered more closely related to each other than to any taxon classified outside of this group. Recognition

of monophyletic groups requires identification of characteristics that demonstrate the sequence of temporal subordination among those groups.

### Apomorphic and Plesiomorphic Character States in the Understanding of Natural Groups

Evolution is a transformation of organisms through which the descendants accumulate differences from their ancestors. Consequently, the split of a given taxon into two mutually isolated communities (cladogenesis) implies the existence of a transformed (“changed”) character state in at least one of the daughter taxa (Hennig 1966) (otherwise, those communities would not be different). This transformed character state, shared by the new community, is termed **apomorphy**. On the other hand, the opposing character state, inherited from the common ancestor (thus not transformed) and presented by the other daughter taxon, is named **plesiomorphy** (Fig. 1).

*Only apomorphic character states provide necessary and sufficient evidence to identify a natural (monophyletic) group.* They are the only traits that identify a change in the original state of a given character, which is kept by a population after the split of a given taxon and, therefore, indicate the occurrence of cladogenesis. The sharing of plesiomorphic character states among different taxa, on the other hand, does not provide evidence of monophyly. The presence of these characters in a given population after a splitting event may be due the inheritance of unaltered (not transformed) states from a common ancestor. Therefore, the *sharing of plesiomorphic characteristics does not delimit a natural group.*

In order to determine the genealogical relationships among taxa, several character states common to these organisms must be listed. However, these character states must vary among these taxa in a way that some, but not all taxa being studied, share a given state. The next step is to compare these states to the ones found in taxa outside the group of interest, in order to determine which represents a novelty (thus, an apomorphy), and which was inherited from the common ancestor (thus, a plesiomorphy).

Given a group of taxa expressing two different character states, only the sharing of apomorphic states indicates a shared evolutionary path of a subpart of this group. For example, among actinopterygian (ray-finned fishes), eye of Pleuronectiformes (flatfishes, flounders, soles, and halibuts) migrates ontogenetically from one side of the head to the other. Accordingly, eye asymmetry is an exclusive characteristic of adult Pleuronectiformes. In contrast, all other actinopterygians retain eye symmetry in adults. Since eye symmetry is also present in all lineages of ► [Vertebrates \(Chordata\)](#), it is recognized as the **plesiomorphic state**. In this context, eye symmetry is a shared plesiomorphy (**symplesiomorphy**), and cannot be used to delimit ► [“Actinopterygii \(Bony Fish\)”](#) as a monophyletic group. On the other hand, the presence of a migrated eye in adults is the *transformed condition*, putatively present in the common ancestor of Pleuronectiformes and shared among all flatfishes. This is a shared apomorphy (**synapomorphy**) that can be used to delimit a monophyletic group encompassing all flatfishes, the Pleuronectiformes.

However, a particular plesiomorphic character state can, and will, correspond to an apomorphic, informative character state at a higher level of inclusion. For example, since the presence of a vertebral column is common to all vertebrates, it cannot be used to delimit one of its subgroups (like Gnathostomata) because it is a symplesiomorphy of gnathostomes in the phylogeny of Vertebrata. However, the presence of a vertebral column in all vertebrates, and of its absence on the other groups of Chordata, indicates that this is a synapomorphy of Vertebrata in the Chordata phylogeny.

As noted above, symplesiomorphies offer no evidence for the recognition of monophyletic groups, as they represent an unchanged, inherited character state. However, there is a second set of character states that do not add information during the reconstruction of the evolutionary hierarchy among taxa, **autapomorphies**. These are modified characteristics (apomorphies) that are unique to a single taxon. For example, when considering the interrelationship among the extant great apes (group that includes orangutans, gorillas, chimpanzees, and humans), bipedalism would be an exclusive characteristic of *Homo sapiens*. This

trait distinguishes humans from other ► **primates** rather than indicating their relationship to the remaining apes, and therefore it does not provide information about the hierarchical relationships among humans and the remaining primates (*i.e.*, which of the other primates' lineages are more closely related to the humans).

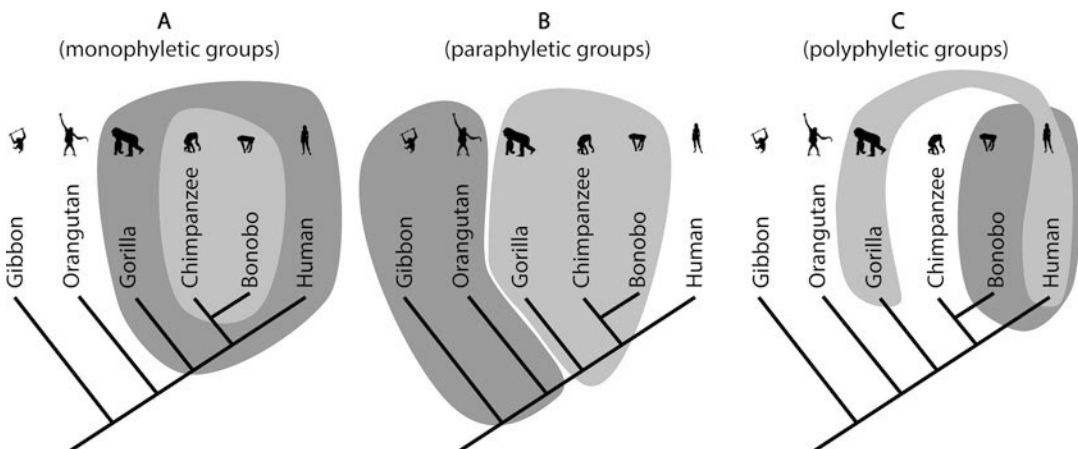
Finally, what determines if a particular character state is apomorphic or plesiomorphic is its comparison with the condition observed at the root of the cladogram. When a phylogenetic tree is obtained through a congruence analysis, the root is a taxon included in the phylogenetic analysis to represent the character states presented outside the group of interest (*i.e.*, the root would carry unaltered conditions for the characters). In the example focusing on the relationships among great apes, a good choice for a root would be the primate that is most similar to the great apes, but still not considered one of them, which in this case is the gibbon.

The root (the gibbon) should bear the unaltered conditions for some characters, meanwhile the ingroup (great apes) present new conditions. What is displayed by the gibbon will then indicate the *direction of transformation of each character, from one state to the other*. In the case of bipedalism, comparing the character state

found in the gibbon (absence) with the one found in great apes (presence) indicates that a non-bipedal primate started walking on two feet. Therefore, any character states of the ingroup (great apes) that differ from the gibbon (the root) are considered apomorphies. In other words, the root *polarizes the character states*, and enables the identification of character states as apomorphic or plesiomorphic. The root might even help (despite not being required) in the recognition of convergences among different groups (*i.e.*, similarities that are not the result of common ancestry).

### Monophyletic Versus Merophyletic Groups

As mentioned above, only apomorphic characteristics can be used to infer natural (**monophyletic**) groups. However, there are also groups of species that are not monophyletic. **Merophyletic** (or partial groups, *sensu* Bernardi 1981) is a term indiscriminately used to refer to nonmonophyletic taxa, including both **paraphyletic** and **polyphyletic** groups. **Paraphyletic** refer to groups of taxa based on shared plesiomorphies, and **polyphyletic** describe groups of taxa based on



**Monophyletic, Fig. 2** Hominoidea cladogram highlighting: (a) **monophyletic groups**, which include an ancestor and all its descendants (Chimpanzee + Bonobo in light gray; Gorilla + Chimpanzee + Bonobo + Human in dark gray); (b) **paraphyletic groups** (in light gray, grouping Gorilla, Chimpanzee, and Bonobo but excluding Human;

in dark gray grouping Gibbon and Orangutan but excluding remaining Hominoidea); (c) **polyphyletic groups** (in light gray a group formed by Gorilla and Human, and in dark gray a group containing Bonobo and Human. Both groups exclude remaining Hominoidea)

convergences (Hennig 1966). Both paraphyletic and polyphyletic groups are artificial, and distinguished from monophyletic ones by not having a natural history, thus not possessing either reality or individuality (Hennig 1966).

Another useful way to think about paraphyletic and polyphyletic groups is as follows: a paraphyletic group corresponds to a monophyletic group after the withdrawal of one or more monophyletic subgroups; and a polyphyletic group corresponds to a monophyletic group after the withdrawal of a paraphyletic subgroup (Fig. 2) (Nelson 1971; Bernardi 1981). For both groups, the resultant cladogram does not correspond to one ancestor and all its descendants (otherwise, it would be monophyletic). This second definition allows us to distinguish monophyletic and non-monophyletic groups without reference to any real characters, but conditional on a specified phylogeny (Farris 1974).

Merophyletic groups have no place in the phylogenetic system, since they are not natural groupings and do not satisfy the condition of exclusive common ancestry. However, they are still frequently used in textbooks and classrooms, since their names are traditional and can help us retrieve information. For example, the term “fishes” (Pisces, in the Latin name) corresponds to a paraphyletic group, which includes all Vertebrata except the monophyletic group of tetrapods. Therefore, in order for “Pisces” to be a monophyletic group, it would have to also encompass the Tetrapoda and thus all vertebrates would be “Pisces.” Although “fishes” retain several plesiomorphic conditions when compared to tetrapods, the use of this traditional name helps us to recover several characteristics (anatomical, physiological, behavioral, etc.) common to most of its taxa. Therefore, in order to keep the traditional name, but also provide an indication that we are aware that the group is not monophyletic, we write the name between quotes, as done above.

## Cross-References

- [Actinopterygii \(Bony Fish\)](#)
- [Cladistic Analysis](#)
- [Common Ancestor](#)

- [Homology](#)
- [Parsimony](#)
- [Primates](#)
- [Phylogeny](#)
- [Vertebrates \(Chordata\)](#)

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## Monotreme Sensory Systems

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## Synonyms

[Echidna](#); [Electroreception](#); [Olfaction](#); [Platypus](#); [Prototheria](#)



## Introduction

Monotremes are a unique group of mammals confined to Australia and New Guinea. The lineage leading to modern monotremes probably diverged from that leading to therians (modern placental and marsupial mammals) as much as 220 million years ago (Yu et al. 2012), so there has been abundant time for independent evolution of sensory systems and the brain. Modern monotremes cannot be considered primitive or relict, and they are certainly not models for the ancestors of placental mammals. Monotremes have undergone just as long a period of evolution as have therians. Furthermore, although they do exhibit some primitive characteristics, living monotremes are also highly specialized animals with some remarkably advanced neural adaptations (e.g., electroreception and isocortical expansion). Like all mammals (including humans), they are therefore the result of mosaic evolution, where primitive and derived characteristics co-exist in the one species.

## What Are Monotremes?

Monotremes are egg-laying mammals and are represented in the modern world by the platypus of eastern and southern Australia (*Ornithorhynchus anatinus*, of the Ornithorhynchidae) and the echidnas (*Tachyglossus aculeatus* – the short-beaked echidna of Australia and New Guinea; several species of long-beaked echidna from New Guinea – *Zaglossus bartoni*, *Zaglossus bruijni* and *Zaglossus attenboroughi*; all within the Tachyglossidae). The platypus and long-beaked echidnas are rather confined geographically, but short-beaked echidnas occupy a strikingly diverse range of habitats across the entire continent of Australia and parts of New Guinea. Monotremes lay soft, leathery-shelled eggs about 12–18 mm in length, from which the embryonic young hatch, in contrast to therian mammals that bear live young. Dependence on the mother is prolonged in all monotremes, with lactation continuing up to 140 days post-

hatching in the platypus and 200 days in the short-beaked echidna.

One might say that monotremes have always been Australian (or at least Gondwanan), because monotreme fossils are confined to the Early Cretaceous and Cenozoic of Australia (Oligocene to Recent), the Pleistocene-Holocene of New Guinea, and the early Paleocene of Patagonia, Argentina. The fossil record for Ornithorhynchidae is better than that for Tachyglossidae, probably due to the different habitats of the two groups (aquatic vs. desert/scrub/open woodland) and hence dissimilar opportunities for fossilization.

Monotremes have normal body temperatures of 30–32 °C, generally lower metabolic rates than therians, and live long lives for their body size. The platypus can be very active when hunting in cold water, so its metabolic rate approaches that of therians of the same body size. On the other hand, the short-beaked echidna exhibits a lower level of activity than the platypus and is able to use torpor and hibernation to reduce energy expenditure even further during cold months, but there is no evidence that long-beaked echidnas or the platypus employ torpor (Nicol et al. 2008).

## Monotreme Electroreception

Electroreception is a useful sense for aquatic animals living in murky water and it has evolved independently several times among vertebrates. It evolved probably once in agnathids, twice in teleosts, once in non-teleosts, and either once or twice in amphibians (Butler and Hodos 2005).

Monotremes are most famous for being the only mammals with electroreception, although this sense should be considered a complement to somatosensation in the platypus, and to somatosensation and olfaction in the echidnas. Indeed, electroreception on its own would be unlikely to provide sufficient information for prey detection in either the platypus or echidnas, because of sensitivity problems. The electro-sensory apparatus is the bill of the platypus (both upper and lower) and the snout tip in the short- and long-beaked echidnas.

Electroreceptive function is confined to the trigeminal pathway in all monotremes. This pathway is particularly striking in the platypus, where it is estimated that 1,344,000 myelinated axons of the trigeminal nerve supply the upper and lower bill (Manger and Pettigrew 1996). Approximately half of those innervate the putative electroreceptors (see below), while the rest innervate mechanoreceptors of the bill. The trigeminal nerves of the echidnas are much smaller (only 7% of the area of the platypus nerve).

The electroreceptors in the platypus are of the ampullary type, meaning that they are open to the skin surface through a fluid-filled duct and respond to low-frequency electrical rhythms, such as are produced by the regular muscle contractions or tail flicks of prey animals (0.1–50 Hz). Electroreception in the platypus is most closely associated with the mucous sensory glands of the upper and lower bill, estimated at 30,000 to 40,000. When viewed from the bill surface, these glands have a peony blossom-like appearance due to the presence of many epithelial “flakes” surrounding the duct pore (Andres and von Düring 1988). The duct provides a low resistance pathway for electrical fields to reach the sensory nerve endings at the papillary part of the gland (Iggo et al. 1988). In contrast to non-mammalian electroreceptors, the electrosensory terminals of the mucous sensory glands of the platypus are naked and do not contact a sensory cell (Manger and Pettigrew 1996). This may account for the short latency of electroreceptor activation in the platypus (0.8 ms) compared to ampullary electroreceptors of fish (see discussion in Gregory et al. 1989).

The mucous sensory glands are arranged in parasagittal stripes along the external surfaces of the upper and lower bill (Andres and von Düring 1988). The platypus sweeps its bill through the water from side to side when hunting, so these stripes may act as an antenna, detecting the movement of electrical field lines across the stripe (Manger and Pettigrew 1996).

The platypus spends a significant portion of the day out of the water, so a mechanism is needed to prevent fluid loss from the ducts of the mucous sensory glands. The pores of mucous sensory

glands open when the bill is exposed to cold water and close when exposed to dry air, protecting the duct contents from drying. This reflex is stimulated by exposure to cold and mediated by sympathetic nerve fibers to the gland.

The echidnas also have putative electroreceptors in their snout tips, but these are far fewer in number than the platypus. The short-beaked echidna has only a few hundred and the long-beaked echidna about 3,000 sensory glands (Manger et al. 1997). Much like in the platypus, the sensory apparatus is associated with an elongated dermal mucous gland of about 0.3 mm diameter (Manger and Hughes 1992). Axons innervate the modified epidermal portion of the gland to form a sensory cuff. In the real world, the snout is used as a push probe, thrust into loose soil, or leaf litter in search of invertebrates.

## Monotreme Somatosensation

Somatosensation, principally the detection of mechanical and thermal stimuli at the skin surface, may be just as behaviorally important as electroreception for the monotremes and models of real-world behavioral use of electroreception require integration of electro- and mechanosensory input at the cortical level.

Monotreme bills and snouts have highly specialized sense organs called push-rod mechanoreceptors. In the platypus, this consists of a mobile epidermal rod of stratified keratinocytes, about 400  $\mu\text{m}$  long and 70  $\mu\text{m}$  wide. When the complex is viewed from above, the rod tip looks like a dome bulging from the epidermal surface and surrounded by rings of flattened keratinocytes (Andres and von Düring 1988; Manger and Pettigrew 1996). Three types of mechanosensory assemblies are located within the rod itself (central vesicle chain, peripheral vesicle chain, and Merkel cells), and a further three to six Paciniform corpuscles are located in the dermis immediately deep to each rod. Collectively, these give the platypus bill a suite of slowly and rapidly adapting mechanoreceptors to detect both sustained and vibratory indentation of the bill surface. Push-rod mechanoreceptors are scattered

across all four surfaces of the bill, but concentrated at the lateral and rostral borders (Andres and von Düring 1988; Manger and Pettigrew 1996).

In the short-beaked echidna, the most sensitive part of the beak is the distal 1–2 cm. Mechanoreceptors in the echidna beak include: free nerve terminals; lamellated receptors; intra-epidermal discoid, vesicle chain, and cluster receptors; and Merkel cell receptors (Andres et al. 1991; Manger and Hughes 1992). The push-rod organ of the echidna is shorter than in the platypus. More significantly, the push-rod of the echidna is linked to surrounding epidermal cells by desmosomal junctions, so its mobility and sensitivity to shearing movement are greatly limited compared to the platypus (Manger and Hughes 1992).

### Integration of Electoreception and Somatosensation in the Cerebral Cortex

How do electro- and mechanoreception work together in the real world? The mechanics are undoubtedly different in the platypus and the echidnas as reflected in bill and beak shape. The platypus bill is a large flat electrical antenna and mechanosensory device to be swept from side to side while swimming, whereas the beaks of the echidnas act more as push probes.

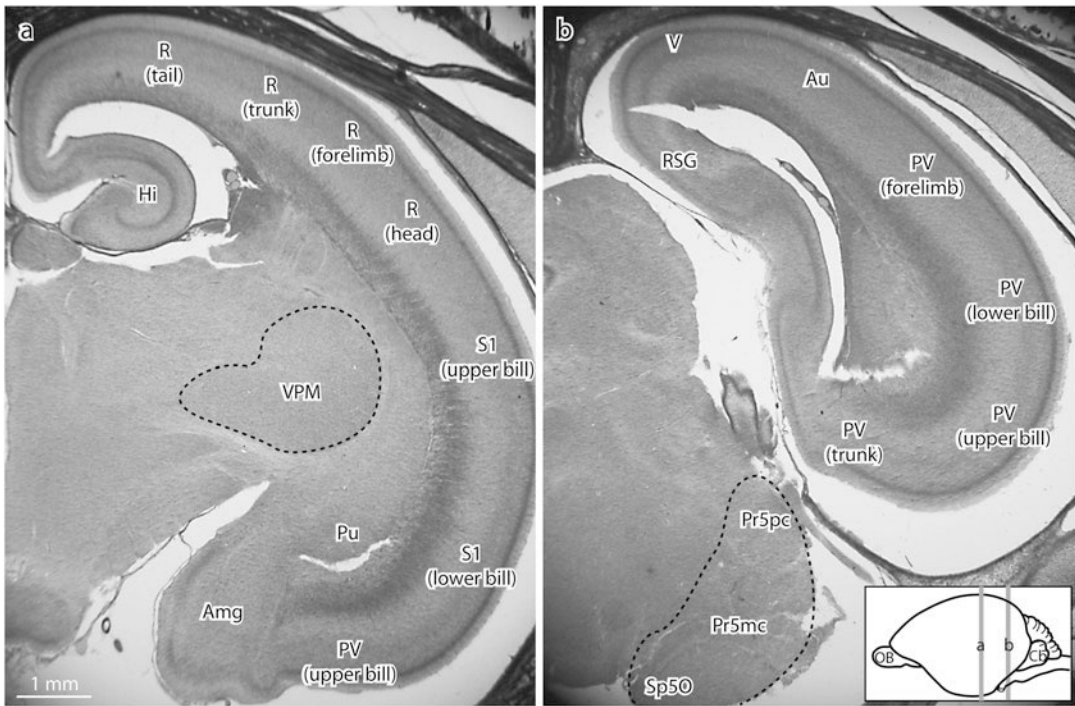
Each individual sensory channel of the platypus bill is of limited sensitivity, so there must be significant spatial and temporal summation to achieve a behaviorally useful input. Captive platypuses engage in a continuous sweeping of the bill from side to side at about 75 cycles per min. This appears to be important in locating the direction of an electrical target by reorientating the head relative to the source, perhaps to present the more sensitive part of the bill towards the stimulus (Proske et al. 1998) or to sample electrical field-lines sweeping across the bill. When a captive platypus is exposed to a novel electrical stimulus, it produces automatic head movements towards the source and snaps at the electrode (Manger and Pettigrew 1995), even when the source is inedible. These studies suggest that there are both voluntary and reflexive elements in the alignment of the platypus to electrical sources.

Electro- and mechanosensation most probably work in concert to detect both the direction and distance of the prey. Although the electrophysiology of these central pathways is poorly understood, it has been suggested that a comparator system functions within the enlarged primary somatosensory cortex of the platypus (Fig. 1). Electrical signals propagate through the environment at the speed of light, whereas the pressure waves detected by the mechanoreceptors are substantially slower. For example, the tail flick of a prey crustacean at a distance of 15 cm from the bill would generate a mechanical disturbance in the water that is delayed by approximately 10 ms after the electrical signal (Pettigrew et al. 1998). A neural system that is sensitive to the delay between the electrical and mechanical stimulus could be used to assess range to prey. Pettigrew and colleagues have suggested that activation of cortical bimodal neurons that facilitate optimally at a variety of different time delays between electrical and mechanical signals could provide such a system (Pettigrew et al. 1998), but this has never been tested experimentally.

### Monotreme Olfaction

No behavioral or physiological studies of olfaction have been carried out in captive monotremes, but several observations indicate the behavioral importance of this sense in tachyglossids. During the mating season, usually solitary echidnas gather to form trains of males following females, suggesting that olfactory signals are critically important for finding mates and assessing reproductive status of conspecifics. Behavioral observations of wild short-beaked echidna also suggest that olfaction plays an important role in detecting ants, termites, and other invertebrates.

The two living groups of monotremes have very different olfactory capacities, and this is reflected in the very different structure of their olfactory systems. The poorly osmotic, semi-aquatic platypus has a greatly reduced main olfactory system but a surprisingly large



**Monotreme Sensory Systems, Fig. 1** Somatosensory system structures as seen in frontal sections through the brain of a juvenile platypus (240 mm body length). Note the extensive somatosensory regions in the cerebral cortex (**a**, **b**; PV – parietoventral somatosensory area, R – rostral somatosensory area, S1 – primary somatosensory area; names in parentheses indicate body regions represented here). The electrosensory areas are located in S1. The somatosensory nucleus of the dorsal thalamus (VPM – ventral posteromedial thalamic nucleus), concerned with mechano- and electroreception from

the bill, is also very large (**a**), as are the trigeminal sensory nuclei in the brainstem (**b**; Pr5mc – magnocellular part of principal trigeminal sensory nucleus, Pr5pc – parvocellular part of principal trigeminal sensory nucleus; Sp50 – oralis part of spinal trigeminal sensory nucleus). Amg – amygdala; Au – primary auditory cortex; Hi – hippocampal formation; Pu – putamen; RSG – retrosplenial gyrus; V – primary visual cortex. The line diagram shows the position of the two sections (**a**, **b**) in the extent of the brain from olfactory bulb (OB) in the front to cerebellum (Cb) in the rear. Scale bar in (**a**) applies to both photomicrographs

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collection of vomeronasal chemoreceptor genes, as great as any placental mammal studied so far. This suggests that although the main olfactory pathways of the platypus are unlikely to make a significant contribution to prey detection, the accessory or vomeronasal olfactory system may be very important in courtship and recognition of offspring (Griffiths 1978). On the other hand, the long- and short-beaked echidnas both have highly specialized main olfactory systems, although very little is currently known about olfactory receptor genes in the echidnas. The main olfactory system in both types of echidna shows signs of convergence with myrmecophagous xenarthrans and

probably acts as an important sensory complement to the electrical organs of the snout tip.

The nasal cavity of the platypus is relatively simple in structure, with tiny nasal and ethmoidal turbinates (Griffiths 1978), but the vomeronasal organ is large, with a pair of pouches that open into the front of the nasal cavity, rather than the nasal cavity. By contrast, the nasal cavities of both long- and short-beaked echidnas are structurally complex, with seven endoturbinates suspended vertically from the ethmoid, many ectoturbinates, and groups of naso- and maxilloturbinates. The cribriform plate of the short-beaked echidna is approximately 300 mm<sup>2</sup> in area and reaches 440 mm<sup>2</sup> in *Z. bartoni* (*diamondi*).

Olfactory receptor genes (main olfactory pathway – OR, TAAR; vomeronasal pathway – V1R and V2R families) have been studied in the platypus, but not the echidnas. The platypus has only a few intact OR and TAAR genes (261 and 4, respectively), compared to 1037 and 15 in the laboratory mouse (Niimura and Nei 2007). By contrast, the vomeronasal pathway genes are abundant in the platypus. The V1R family detects odorants in the air, whereas V2R detect chemicals in water. Despite its poor main olfactory system ability, the platypus V1R family has 270 intact genes and 579 pseudogenes; and the V2R has 15 intact genes, 55 potentially intact genes, and 57 pseudogenes (Grus et al. 2007).

The main olfactory bulb, anterior olfactory area, olfactory tubercle, and piriform cortex are all quite small in the platypus, although the accessory olfactory bulb is of substantial size (Ashwell 2006). By contrast, the main olfactory bulb of both short- and long-beaked echidnas is large and folded, presumably to increase the available surface area for synaptic input to glomeruli. The short-beaked echidna has a complex piriform cortex, with regional differences of cellular structure and chemical architecture around the circumference of the large piriform lobe (Ashwell and Phillips 2006).

The function of the large frontal cortex that lies rostral to the primary motor cortex of the echidnas has always been a mystery. Divac and colleagues (Divac et al. 1987) showed that the frontal cortex of the short-beaked echidna receives abundant input from the piriform cortex, medial, and cortical (olfactory) parts of the amygdala, and the medial and lateral entorhinal cortex. This pattern of input suggests that the expanded frontal cortex receives a rich source of olfactory input, as would be anticipated if it were serving as a chemical sense integration center.

## Monotreme Audition

The middle and inner ear of monotremes show some remarkable differences from therian mammals, but these are of an underived nature, indicating that hearing is poorly developed in the

group. In fact, hearing is unlikely to be of major behavioral importance in the semiaquatic platypus, although it may be important for the echidnas in detecting invertebrates. In both the tachyglossids and the platypus, hearing is optimal around the relatively low frequency of 4–5 Hz. Hearing among echidnas may actually be best for bone conduction, consistent with the use of their long, pointed snouts as push probes for detecting low-frequency vibrations produced by invertebrates in the soil.

Middle ear structure in monotremes suggests relatively poor functional capacity of the auditory system. The tympanic membrane of the short-beaked echidna is supported by a hook-shaped tympanic bone and is relatively loosely supported, but the malleus and incus are rather tightly bound to the periotic bone (Aitkin and Johnstone 1972) and do not move freely. Unlike many placental mammals, where the stapes is stirrup-shaped, the stapes in monotremes is a columnar bone expanded distally to cover the oval window, which is actually round in these mammals. Mechanical amplification across the auditory ossicle chain is probably poor.

The monotreme inner ear is like other mammals, in that there are distinct inner and outer hair cells in the organ of Corti (Griffiths 1978). However, the cochlea is shorter than therians of a similar body weight and is only loosely coiled in the monotremes, achieving a curvature of only 130 to 180° (Gray 1908; Fox and Meng 1997) in contrast to the 720° or more found in therians. The total number of inner hair cells is similar in the monotremes and therians, but the outer hair cells (which engage in the cochlear amplifier mechanism) appear to be fewer (Ladhams and Pickles 1996). There is also an unusual structure known as the macula lagena (a distinct sensory area at the end of the cochlear duct and separated from the organ of Corti) present in both the platypus and short-beaked echidna (Ladhams and Pickles 1996). Its role is unclear, but it shows some structural features (i.e., opposing stereocilia polarity) that are similar to the vestibular sense organs.

The area of the primary auditory cortex is relatively small in both the platypus and short-



beaked echidna (Krubitzer et al. 1995), consistent with less behavioral reliance on auditory function compared to other senses.

## Monotreme Vision

Vision is not a major sense used by monotremes and visual acuity of monotremes is poor. Behavioral studies of the short-beaked echidna by Gates (1978) showed that discrimination of vertical from horizontal lines is possible only at a line width greater than  $0.499^\circ$ , comparable to that in rodents. Nevertheless, there are some interesting aspects of monotreme vision related to cone photoreceptor evolution.

All the monotremes are adapted to a crepuscular lifestyle, with retinas that are dominated by rod photoreceptors, with cones making up only 10% even in central retina. Some distinctive features of the monotreme eye include cartilage reinforcement of the sclera, double cone photoreceptors, and the presence of oil droplets in the cone photoreceptors (at least in the platypus) (Zeiss et al. 2011). The distributions of photoreceptors and retinal ganglion cells across the retina of the short-beaked echidna are relatively flat (i.e., minimally concentrated), meaning that there is only poor development of a zone for higher acuity vision.

All monotremes are dichromats. This means that they determine colors by comparing the input from two types of cone photoreceptors. In the platypus, the peaks of the SWS2 and LWS pigments of the platypus cone photoreceptors are at 451 nm and 550 nm, respectively. The peak for the LWS pigment of 550 nm is similar to that found in many marsupial and placental mammals for their LWS pigments. The peak at 452 nm for SWS2 is at only a slightly longer wavelength than the violet-sensitive SWS1 pigments of some placental mammals (Hunt et al. 2007). The *SWS1* opsin gene found in therians may have been deleted during monotreme evolution (Wakefield et al. 2008).

All monotremes have poor binocular vision, because there is minimal overlap of the visual fields of the two eyes, and 99% of retinal ganglion

cell axons cross at the optic chiasm (Campbell and Hayhow 1971, 1972). Nevertheless, there is good interhemispheric transfer of information through the large anterior commissure. The retinorecipient nuclei of the thalamus are unusual in monotremes, in that the pregeniculate of the prethalamus is widely separated from the lateral geniculate nucleus of the true thalamus (Campbell and Hayhow 1971, 1972).

The visual cortex is small in both the platypus and short-beaked echidna. Krubitzer (1998) identified at least two visual field representations in the cortex of the platypus (caudal and rostral). The caudal visual field representation may be homologous to primary visual cortex of therians but is so unspecialized that visual field magnification on the platypus visual cortex (0.03 mm per degree; Pettigrew et al. 1998) is no better than the tiny laboratory mouse. It may be that the midbrain is a much more important visual processing center in the platypus than the visual cortex. Krubitzer also reported that there are two visual field representations in the short-beaked echidna (Krubitzer 1998), but the physiological evidence for this is not well-documented.

## Conclusions

Although monotreme electroreception has received the most scientific attention, somatosensation and olfaction are also very important behaviorally for the group and there is evidence of striking cortical adaptation for those senses in the platypus and echidnas. Monotremes should therefore not be seen as primitive or relict mammals, because they are clearly successful mammals with advanced nervous systems with derived characters. Although the platypus is clearly a trigeminal somato- and electrosensory specialist, the olfactory centers of the echidnas are large, complex, and laminated, much like that seen in other myrmecophagous mammals. The large frontal cortex of the echidnas may act as a chemosensory integration center and store detailed information about home range topography.

## Cross-References

- [Biological Rhythms](#)
- [Electroreceptors](#)
- [Encephalization](#)
- [Evolution](#)
- [Evolution of Animal Color Vision](#)
- [Evolutionary Psychology](#)
- [Olfactory Perception](#)
- [Thermoregulation](#)

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## Monty Hall Dilemma

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### Synonyms

Monty hall problem; Three box problem; Three Prisoners Problem

### Introduction

Beginning in 1963, contestants on the American television program *Let's Make A Deal* competed to win prizes. In one game, a contestant was confronted with three closed doors. One of these doors concealed a prize (such as an automobile), while the other two doors did not (they often

concealed a goat). The contestant began by picking one of the three doors, which remained unopened, in the hope that it concealed the prize. Then the host of the program, Monty Hall, opened one of the other doors to reveal a goat. To end the game, the contestant had to finally decide whether to stay with their original choice or instead to switch their choice to the remaining unopened door. After the contestant decided to “stay or switch,” the location of the prize was revealed.

Why might this game be of interest to comparative psychology? One reason is that when human participants are presented with the standard version of this task (described in more detail below), they perform very poorly on it. Generally speaking, people believe that after the host reveals the goat behind the door, there is a 50–50 chance that the prize is hidden by the door that was originally selected and (for a variety of reasons) are likely to stay with their original choice. However, this belief is false: it can be shown in a variety of ways that a contestant is twice as likely to win the prize by switching their choice to the other door (Rosenhouse 2009). A second reason is that some animals may outperform humans on this task. For instance, some studies have shown that pigeons quickly learn to always switch their choice in order to maximize reward (Herbranson and Schroeder 2010), which is the optimal strategy (Stephens and Krebs 1986).

This article introduces the Monty Hall dilemma and its psychological implications. It begins by considering the properties of the standard version of this task. It describes variations of this standard version and how these variations can be used to study the processes used to play the game. It also briefly reviews some of the psychological studies of the Monty Hall problem as well as the implications of this research.

### The Standard Monty Hall Dilemma

The Monty Hall dilemma is a mathematical brain teaser because while mathematics proves that switching from the initial choice actually doubles the probability of winning, human intuition strongly indicates that switching door choice

should not affect the likelihood of winning. Importantly, the proof that switching from the initial choice doubles the likelihood of winning requires that the game have particular characteristics which define its standard version (Rosenhouse 2009).

The standard version of the Monty Hall dilemma requires that the probability that the prize could be behind any of the three doors is equal. It also requires that the host never opens the door selected by the contestant and never opens the door that conceals the prize. Finally, if the contestant's first pick is the door that hides the prize, the standard version requires that the host randomly choose which of the two remaining doors to open. Of course, if the contestant's first pick is a door that hides a goat, then the host is forced to open the other door that does not conceal the prize.

If the characteristics of the game conform to those of the standard version described above, then the optimal strategy for winning is to switch choices. Informally, one can argue for this strategy by noting that when the contestant makes their first choice, they have a one in three chance of being correct. This means that there is a two in three chance of the prize being behind a door that the contestant did *not* choose. This is not changed when the host opens a losing door. In other words, after the losing door is opened, there is still a one in three chance of success with the original choice, but the likelihood that the prize is behind the other unopened door is now two in three, because it is the only remaining member of the set that had a 2/3 probability of concealing the prize.

The Monty Hall dilemma is challenging because this informal account of the situation runs counter to strong (and incorrect) intuitions (Piattelli-Palmarini 1994). When the host reveals a losing door, the contestant is faced with two closed doors, one of which hides the prize. Intuition strongly suggests that each remaining door must be equally likely to be the winner. However, this intuition fails to realize that the host's choice is constrained by the contestant's first choice: if this first choice is of a losing door, then the host is forced to open the other losing door. This makes the dilemma one based on conditional

probabilities, which means that the only door whose probability of winning changes is the door not picked by either the contestant or the host.

There are a number of formal methods that can be used to prove that switching is the best strategy for winning the standard version of the game (Rosenhouse 2009). One approach is to simply enumerate all of the possible ways that the game can proceed. An examination of the resulting table of possibilities quickly indicates that the probability of winning by staying is 1/3 while the probability of winning by switching is 2/3 (Selvin 1975). Another approach is to use Bayes' theorem to use equations involving conditional probabilities (Krauss and Wang 2003). A third approach is to run Monte Carlo simulations, which again quickly demonstrate the underlying probability structure of the task as well as the advantage of switching from the initial choice.

The Monty Hall problem is particularly interesting because human intuitions about the puzzle prevent its mathematical solution from being readily accepted. As a result, this problem is one of the best examples of a mathematical brainteaser and was originally presented as such in the 1950s by Martin Gardner as the "Three Prisoners Problem" (Gardner 1959a, b). When the Monty Hall dilemma was reintroduced to the public in *Parade Magazine* in 1990, it caused thousands of readers – many of whom were professional mathematicians – to write letters that challenged the (correct) solution of the problem that had been provided by columnist Marilyn vos Savant (1990a, b, 1991). Indeed, famed mathematician Paul Erdos was extremely reluctant to accept the correct solution to the dilemma because it ran counter to his intuitions (Rosenhouse 2009). The formal logic of the Monty Hall dilemma is so difficult to accept that Massimo Piattelli-Palmarini uses it as his "grand finale" example of cognitive illusions (Piattelli-Palmarini 1994).

## The Psychology of the Monty Hall Dilemma

The skepticism held by professional mathematicians concerning the correct solution to the Monty

Hall dilemma is further reflected and magnified in the performance of average human participants on this task. A wide variety of studies show that people have a strong preference to stay with their original choice in the standard version of the task.

Consider one illustrative study (Granberg and Brown 1995) that presented a written description of the standard version of the dilemma to introductory sociology students. After laying out the basic nature of the problem, the description told participants that they had initially selected Door 1 and had then been shown a goat behind Door 3. Given this information, they were then simply asked to decide between staying with Door 1 (the non-optimal decision) and switching their choice to Door 2 (the optimal decision). In this study, only 13% of the participants indicated that they would switch their choice. A follow-up study employed a similar method to compare performance from participants from different cultures (Brazil, China, Sweden, the United States) (Granberg 1999a). On average, only 17% of the participants switched their choice, and there were no statistical differences between the performances of participants from different countries. In general, the psychological literature suggests that only between 9% and 21% of human participants in a typical Monty Hall experiment will decide to switch from their original choice (Mazur and Kahlbaugh 2012).

The typical behavior of human participants on the Monty Hall dilemma is so well established that psychologists now focus on explaining its irrationality. Why do people stay with their original choice when switching would double their probability of winning? A variety of explanations have been proposed.

Social psychologists have suggested that regrettable actions have more impact than do regrettable inactions; as a result participants will feel better about the Monty Hall dilemma if they lose after staying than they would if they lost after switching (Gilovich et al. 1995; Granberg and Brown 1995). A related theory is to appeal to what is known as the endowment effect, which is the hypothesis that people assign more value to objects merely because they own them (Thaler

1980). In the context of the Monty Hall dilemma, the endowment effect predicts that participants assign a higher value to the door they choose first choice more merely because it has been chosen and is therefore less likely to switch away from it.

Cognitive psychologists argue that the poor performance on the Monty Hall dilemma reveals poor probabilistic reasoning (James et al. 2018; Shimojo and Ichikawa 1989; Tubau et al. 2015). This position is consistent with other studies that show that human performance improves if information about the problem is presented in terms of frequencies instead of probabilities or if more detailed feedback about behavior is provided (Krauss and Wang 2003; Saenen et al. 2015).

## Variations of the Monty Hall Dilemma

Psychologists are interested in the Monty Hall dilemma because it can be easily presented to participants, it produces a robust and counterintuitive effect, and it stimulates a wide-ranging discussion about why humans have problems with this task. A second reason for psychology's interest is that the task can be easily manipulated in order to alter the optimal approach to dealing with the dilemma. This means that psychologists can explore numerous variations of the dilemma in order to attain better understanding of how participants approach it.

Many of the possible variants of the problem, and their mathematical implications, are discussed in detail by Rosenhouse (2009). For instance, one simple variant assumes that the host is unreliable because they randomly choose the door to reveal after the contestant has picked first. This means that sometimes the host will open the door that conceals the prize, which abruptly ends the game. In this variant, there is no advantage to switching if the host opens a door that reveals the prize. This is because the host's choice is random, and therefore not constrained by the contestant's selection. This means that the prize is equally likely to be behind the two remaining unopened doors.

Another simple variation of the dilemma is to use more than three doors. In general, assume that



there are  $N$  doors in the game, where  $N \geq 3$ . As in the standard version of the game, the contestant chooses one of the doors, which has a  $1/N$  probability of concealing the prize (as do the others). The host then opens  $N - 2$  doors, each of which reveals a goat. It seems that the structure of this task is identical to the standard version, because once again the contestant is faced with two closed doors and must decide whether to stay or switch. However, as  $N$  increases in size, staying with the initial choice is more and more irrational. This is because the probability of winning by switching is  $1 - 1/N$ . Thus a simple way to alter the probability of reward associated with choice behavior is to increase the number of doors in the game.

Of course, a more direct approach to manipulating rewards associated with choice is to alter the probability structure of the dilemma by not requiring the doors in the game to have equal probabilities of hiding the reward. In this case, the optimal solution is to initially choose the door that has the smallest probability of concealing the prize (Granberg 1999b). Then when the host (who is assumed to know where the prize is) reveals a goat, the winning strategy is to switch.

Of course, one issue with the optimal strategy to use when the doors have unequal probabilities of hiding the prize is that the contestant does not know in advance which door has the least likelihood of being the winner. Experimental psychologists have developed a variation of the dilemma that permits this obstacle to be overcome in principle. Instead of having participants solve a single instance of the problem, one can provide multiple instances of the dilemma and have the participant solve each one in sequence. This permits the participant to receive feedback about their choices and permits them to learn about how to solve the task, for instance, by learning that one strategy is better than the other or by learning that one door is less likely to hide the prize than are the others.

To provide an example of this approach, consider one study that trained human participants on the task and which also adopted other variations of the problem by using four doors and by assigning unequal probabilities of reward to each door in one of the conditions (Granberg 1999b). Granberg

used a computer to present the dilemma to participants, who then were trained by playing the game 60 different times at their own pace. All of the participants had a strong preference to stay with their first choice at the beginning of their training – only about 9% of the 192 participants began the study by switching from their first choice. As training continued, there was a significant increase in the number of switches made by participants. However, this increase plateaued midway through training, suggesting that participants learned something as they were trained but in general did not learn the optimal strategy.

One advantage of training participants by presenting them with a number of trials of the Monty Hall dilemma is that researchers can explore the factors that affect what is learned about the task. For example, one study provided 80 trials of training and manipulated the kind of feedback that participants received (Saenen et al. 2015). The feedback was either in the form of the participant's probability of winning or in the form of the frequency of the rewards that had been received. As well, feedback could either be unconditional (i.e., participants were simply informed about their overall performance) or conditional (i.e., participants were informed about their performance when they stayed and about their performance when they switched). It was found that the participants who learned to switch the most (on approximately 85% of the last 20 trials) were those who were provided conditional feedback in frequency format. However, while choice behavior was altered by the feedback, it did not appear to alter participants' understanding of task probabilities which were also measured at the end of the study.

## The Comparative Psychology of the Monty Hall Dilemma

A second advantage of training participants by presenting them with a number of trials of the Monty Hall dilemma is that this permits human performance to be compared with the performance of other species. This is because while animals cannot be told the basic structure of the

problem, they can be trained in a fashion that mimics the constraints of the task. One reason that animal performance on the Monty Hall dilemma is of interest is because the problem is an example of foraging task in which predictions are being made about the location of rewards (Herbranson and Schroeder 2010).

The most influential comparative study of the Monty Hall dilemma studied the performance of pigeons to that of humans (Herbranson and Schroeder 2010). Pigeons were trained in an apparatus that contained three pecking keys that could be illuminated. The animals would peck one key, and then one of the two unselected keys would darken. This was analogous to the host opening a door to reveal a goat. The pigeons were then faced with two illuminated keys: the one that they had pecked originally and one other. Their choice in this situation was in essence “stay or switch.” When they were rewarded in accordance with the standard Monty Hall dilemma, they learned to switch. On the first day of the study, pigeons would only switch on about 36% of their trials. However, after 30 days of training, the pigeons would switch their choice on over 96% of the trials. In other conditions, the reward structure of the task was altered so that pigeons were rewarded for staying instead of switching. Herbranson and Schroeder found that the birds quickly learned to approximate the optimal strategy in these non-standard conditions.

Of particular note is that when Herbranson and Schroeder (2010) trained human participants in a fashion that was analogous to the pigeons, they discovered that human performance differed markedly from that of the birds. Human participants did not quickly learn to adopt the optimal strategy. For instance, in a condition that mirrored the structure of the standard Monty Hall dilemma, by the end of 100 trials of training, human participants would be expected to switch only about two thirds of the time. Thus, instead of learning the optimal strategy, their behavior suggests that they learned to match probabilities (Estes 1964), with their likelihood of staying or switching becoming roughly equal to the probability of reward associated with each of these choice behaviors. Similar results – with pigeons learning optimal strategies

but humans failing to do so – were produced in a follow-up study in which the probability of reward associated with each of the three choices was not equal (Herbranson and Wang 2014). In general, these results raise the possibility that some animals are smarter than humans when confronted with the Monty Hall dilemma.

Other pigeon studies have attempted to vary the experimental conditions in a fashion that permits the exploration of other factors that have been raised to account for human performance. For example, some have attempted to create an endowment effect in birds by requiring pigeons to peck their first choice 20 times before proceeding to the next stage of the Monty Hall dilemma (Stagner et al. 2013; Zentall et al. 2015). These experiments found no evidence of an endowment effect. However, they are also of interest because the performance of the pigeons is less optimal than that observed in other studies (Herbranson and Schroeder 2010; Herbranson and Wang 2014).

Similar results (i.e., poorer performance in animals than that described by Herbranson and Schroeder) have been reported in other studies. For example, in one experiment (Mazur and Kahlbaugh 2012), pigeons performed poorer, and humans performed better, than was found by Herbranson and Schroeder (2010). Another study found similar performance in both pigeons and rats, where both species learned to switch (Stagner and Zentall 2015). Interestingly, this study found that both species learned to perform less optimally than did the pigeons trained by Herbranson and Schroeder. An experiment that compared the performance of humans and monkeys found similar performance in each species (Klein et al. 2013). While some learning to switch was evident in both groups of participants, there was no indication that learning of an optimal strategy occurred.

In short, the comparative psychology of the Monty Hall dilemma suggests that some species of animals, in comparison to humans, may be able to better learn an approach to the task that approximates the optimal strategy. However, this evidence is incomplete, suggesting that more comparative explorations of the problem are required.

## Conclusion

In summary, the Monty Hall dilemma is a mathematical brainteaser in which participants are confronted with a choice to find a prize: stay with an initial pick or switch to the other available. In the standard version of this problem, the best strategy is to switch, which doubles the probability of winning. However, this strategy is not favored by people who have an extremely strong tendency to stay with their initial pick and who often mistakenly believe that staying and switching are equally likely to yield a reward. This less than optimal strategy is resistant to explanations about the underlying probability structure of the dilemma and is also difficult to change when participants are provided numerous trials of training on the problem. The Monty Hall dilemma is easily presented to participants, and many variations of it exist that permit its nuances to be investigated and also permit human performance on the dilemma to be compared to animals. These latter investigations suggest that some species of animals quickly learn to perform much better on this task than do humans, although this difference has not been completely confirmed. In short, the Monty Hall dilemma appears to provide a flexible experimental medium that can be used to explore issues that include the social psychology of regret, Bayesian reasoning, probability learning, and optimal foraging strategies.

## Cross-References

- [Cognition](#)
- [Comparative Cognition](#)

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## Monty Hall Problem

- [Monty Hall Dilemma](#)

## Mood

- [Animal Emotion in Farmed Animal Welfare Assessment](#)

## Morality

- [Pain and Ethics of Animal Care and Use](#)

## Morgan's Canon

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## Synonyms

[Morgan's principle](#)

## Introduction

“Perhaps the most quoted statement in the history of comparative psychology is Lloyd Morgan’s canon” (Dewsbury 1984, p. 187). “To this it can be added that perhaps the most misrepresented statement in the history of comparative psychology is Lloyd Morgan’s canon” (Thomas 1998, p. 158). Conwy Lloyd Morgan (1852–1936) did not refer to it as a “canon” but as a “principle.” However, it quickly became known as “Morgan’s canon,” and that is how it will be identified here, unless Morgan is being quoted. Morgan’s canon was intended to guide choice among alternative explanations of animal behavior. This entry emphasizes at least 12 decades of misrepresentation of Morgan’s canon as a guide and provides fundamental guidelines for constructing the best explanations in animal cognition and psychological science.

## Morgan's Canon

The most cited version of Morgan’s canon is in his *Introduction to Comparative Psychology* (Morgan 1894, p. 53):

In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale.

Realizing early misunderstanding of the canon, Morgan (1903, p. 59) refined it as follows:

In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development.

### Misrepresentations of Morgan's Canon

The most frequent misrepresentation of Morgan's canon occurred as early as 1896 when Stanley equated it with Sir William Hamilton's (1788–1856) "law of parsimony." In turn, Hamilton had equated parsimony with William of Ockham's (c. 1285–1349) "razor." Generally, Morgan's canon, Hamilton's law of parsimony, and Ockham's razor, often incorrectly, have been interpreted as advocating that when two or more explanations are available to explain natural phenomena (including animal behavior), one should choose the simplest (see Thomas, 1998, 2001, 2007 and the references contained within).

The second most frequent misrepresentation is that Morgan's canon opposed anthropomorphism, and the third most frequent is that it opposed the use of anecdotes to describe and explain animal behavior. Morgan's alleged opposition to anthropomorphism and using anecdotes as evidence for animal intelligence typically were linked erroneously to George John Romanes (1848–1894) and his book, *Animal Intelligence* (1882).

### Ockham's Razor

The main point to be made about Ockham's (also known as Occam's) razor is that Ockham meant it to be only a methodological stricture for choosing among alternative logical formulations; that is, he did not intend that it be applied to natural phenomena. Interestingly, scholars (Moody 1967 and others) have not located among Ockham's writings its most frequently cited version, "*Entia non sunt multiplicanda necessitate*" (Entities are not to be multiplied without necessity). However, comparable strictures have been found among Ockham's writings, such as "What can be done with fewer [assumptions] is done in vain with more." (Moody's translations). To conclude this brief account of Ockham's razor, it would be remiss to (a) fail to note that Ockham never referred to his stricture as a "razor" or (b) fail to

recognize that Ockham was not the first to suggest such a stricture. Aristotle, and others between Aristotle and Ockham, proposed similar strictures. Aristotle intended that his stricture be used to choose among explanations of natural phenomena.

### Hamilton's Law of Parsimony

Sir William Hamilton equated the law of parsimony with Ockham's razor as follows:

Without descending to details. . .there exists a primary presumption of philosophy. This is the law of parsimony; which prohibits without a proven necessity, the multiplication of entities, powers, principles or causes; above all the postulation of an unknown force where a known impotence can account for the phenomenon. We are therefore entitled to apply "Occam's razor" to this theory of causality, unless it be proved to explain the causal judgment at a cheaper rate. . . (Hamilton 1855, p. 580)

Pearson (1892) explained that Hamilton also extended the law of parsimony to natural phenomena. Pearson first reported that Hamilton added some scholastic axioms that were valuable as canons for economy of thought.

When, however, Sir William Hamilton adds to them, *Natura horret superfluum*, and says that they only embody Aristotle's and Newton's dicta that God and Nature never operate superfluously and always through one rather than a plurality of causes, then it seems to me we are passing from the safe field of scientific thought to a region thickly strewn with the pitfalls of metaphysical dogma. (p. 482)

### Morgan's View of Simplicity

As noted above, Ockham's razor, Hamilton's law of parsimony, and Morgan's canon in general use have in common the assumption that the simplest explanation (e.g., of an animal's behavior) is preferable. However, Morgan (1894) explicitly disavowed that assumption. Immediately after stating the canon on page 53, Morgan began anticipating some objections that might be raised against it. On page 54 Morgan wrote:

A second [anticipated] objection is that by adopting the principle in question, we may be shutting our eyes to the simplest explanation of the



phenomena. . . But surely the simplicity of an explanation is no necessary criterion of truth.

Regarding parsimony, Morgan (1890, p. 174) had previously written, "We do not know enough about the causes of variation to be rigidly bound by the law of parcimony." "Parcimony" is how Morgan and Hamilton spelled it.

### Was Morgan's Canon Anti-anthropomorphic?

Anthropomorphism as applied to animal cognition and behavior means attributing purportedly uniquely human abilities to nonhuman animals. Early on, as will be shown below, many authors wrote that Morgan's canon was anti-anthropomorphic. Such assertions prompted Wozniak (1993, p. x) to write:

Even worse [than equating Morgan's canon with the law of parsimony, Morgan's canon] is consciously anthropomorphic and based squarely on the adequacy of the psychologist's personal introspection.

*What was Morgan's view?* Two pages after stating his principle, Morgan (1894, p. 55) wrote.

As we have already seen, we are forced as men to gauge the psychical level of the animal in terms of the only mind of which we have first hand knowledge, namely the human mind. But how are we to apply the gauge?

Morgan continued on pages 56–59 to consider how to apply the gauge, and it clearly involved anthropomorphic reasoning by introspection and analogy.

### Was Morgan's Canon Anti-anecdotal and Anti-Romanes?

As will be shown below, many authors erroneously believed that at least part of Morgan's motive for the canon was to oppose Romanes' use of anecdotes as evidence for animal intelligence.

*Who was Romanes?* He was, perhaps, the first to consider animal intelligence in the context of Charles Darwin's theory of evolution. They were

friends, and when Darwin's editor for *On the Origin of Species* (1859) insisted that he reduce the manuscript's length, Darwin gave Romanes his chapter on "Instinct" intended for *On the Origin of Species* to use as he wished. Romanes included it as an Appendix to his book, *Mental Evolution in Animals* (1883).

*Mental Evolution in Animals* was Romanes' major theoretical work, and he based it primarily on data from *Animal Intelligence* (Romanes 1882). As few experimental data were available, Romanes had to rely mostly on published anecdotes. Romanes was aware of the pitfalls of anecdotes, and in the Preface to *Animal Intelligence* (p. vii), he wrote:

If the present work is read without reference to its ultimate object of supplying the facts for the subsequent deduction of principles, it may well seem but a small improvement upon the works of anecdote-mongers. But if it is remembered that my object in these pages is the mapping out of animal psychology for the purposes of a subsequent synthesis [viz., *Mental Evolution in Animals*], I may fairly lay claim to receive credit for a sound scientific intention, even if the only methods at my disposal may incidentally seem to a minister to a mere love of anecdote.

Also, in the Preface to *Animal Intelligence*, Romanes included a rigorous set of guidelines to be followed in selecting anecdotes. His main misstep was that he felt an obligation to quote observers' anecdotes as fully as possible, which usually included the observers' interpretations of the observed behavior. Such interpretations were rarely ones that Romanes accepted. Most of the observers were amateurs devoid of formal education in scientific methods.

For example, Romanes wanted to establish the fact that some ant colonies bury their dead. Romanes quoted several observers (including Sir John Lubbock, the eminent author of *Ants, Bees, and Wasps*, 1882) who reported seeing ants bury dead ants, which was all that Romanes wanted from the observations. However, in his perceived duty to quote observers' accounts fully, when feasible, he often also quoted their interpretations. One observer suggested that ants burying ants was a form of a funeral including a funeral procession; another observer's interpretation was that some

ants killed ants that shirked their duties and then buried them. Romanes' interpretation (*Animal Intelligence*, 1882) was, "This habit [ants burying ants]. . . is no doubt due to sanitary requirements, thus becoming developed as a beneficial instinct by natural selection" (p. 89). This is a reasonable interpretation, as sanitary colonies likely had better survival and reproductive rates than unsanitary ones.

Nevertheless, prominent early psychologists such as Margaret Washburn in her book, *The Animal Mind* (1908), cited and ridiculed the interpretation that ants hold funeral processions to bury their dead. Similarly, Wilhelm Wundt, the acknowledged founder of experimental psychology, in his book *Human and Animal Psychology* (translated from German to English in 1894) criticized Romanes' as follows:

While we admire the diligence with which the author [Romanes] has observed and collected the observations of others, we cannot but notice the unfortunate absence of the critical attitude in a field where it is especially desirable. Turn to the chapter on ants. . . (p. 343)

It seems clear that neither Wundt nor Washburn read Romanes' Preface to *Animal Intelligence* or his explanation of ants burying ants on page 89.

Regarding Morgan's opinion of using anecdotes, in his book, *Animal Life and Intelligence* (1891, p. 362), he wrote:

I do not propose to bring forward a number of new observations on the highly intelligent actions which animals are capable of performing. . . Mr. Romanes has given us a most valuable collection of anecdotes on the subject in his volume on *Animal Intelligence*.

Following Romanes' death in 1894, Morgan gave a eulogy for Romanes before the Royal Society of London in 1895 that included the following:

. . . by his patient collection of data, by his careful discussion of these data in the light of principles clearly formulated. . . Mr. Romanes left a mark in this field of investigation and interpretation which is not likely to be effaced.

His choice of words showed clearly that Morgan had read and respected Romanes' Preface to *Animal Intelligence*. It is ironic that Romanes'

name would be effaced as a result of the misuse of Morgan's canon.

## How Morgan's Canon Has Been Perceived by Historians of Psychology

Leading the pack, the most eminent twentieth-century historian of psychology, E. G. Boring, best known for his *A History of Experimental Psychology* and using the same words in both editions (1929, p. 464; 1950, p. 473), wrote: "For this reason [Romanes' alleged tendency to anthropomorphize]. . . the anecdotal method of Romanes has not only been discarded, but has become a term of opprobrium in animal psychology."

Thomas (2007) reviewed 32 history of psychology textbooks published from 1991 to 2005 (including multiple editions of a few of them), and he found that 18 misrepresented Morgan's canon as a canon of parsimony. Some of these and others misrepresented Morgan's canon as being anti-anthropomorphic and/or anti-anecdotal always referring to Romanes' use of anecdotes. Combining all three types of misrepresentation (or four if one counts being anti-Romanes separately), Thomas found only three textbooks (including two editions of one of them) among the 32 examined that provided generally accurate coverage of Morgan's canon. Additionally, Costall (1998, p. 18) wrote, "*The extent to which the intentions of Morgan's canon have been misinterpreted is astonishing.*" Wozniak (1993, pp. ix) wrote, "*It would be an interesting study in itself to trace the distortion of Morgan's views, in particular the attribution to Morgan of the principle of parsimony.*"

## A History of Misrepresentation of Morgan's Canon

Thomas (2001) conducted a study such as Wozniak suggested, and the main results are shown below. Intended to be representative and not exhaustive, this section includes quotations from researchers spanning at least 12 decades

who misrepresented Morgan's canon (full references for these quotations may be found in Thomas (1998, 2001, 2007). Section "[A History of Efforts to Correct the Misrepresentation of Morgan's Canon](#)" which follows has quotations from researchers spanning nine decades who tried to correct the misrepresentation of Morgan's canon. These sections may seem unduly tedious, but it is important to emphasize by examples the persistence and variety of misrepresentations of Morgan's canon as well as the largely disregarded efforts of scholars to correct the misrepresentation of Morgan's canon.

**Stanley (1896, p. 541)**

"His [Morgan's] caution is also admirable, but we do not think the law of parsimony is positive proof as he seems to urge."

**Mills (1899, p. 271)**

[In the context of Morgan's canon Mills wrote:] "Nor can I agree with those who maintain that we must always adopt the simplest explanation of an animal's action."

**Washburn (1908, p. 25)**

[After quoting Morgan's canon...] "In other words, when in doubt take the simpler interpretation."

**Holmes (1911, p. 159)**

"...it is well in general to be guided by the principle enunciated by Lloyd Morgan, which is a sort of special case of the law of parsimony."

**Warden (1927, p. 155)**

"The canon of Morgan... was an attack against the prevailing anthropomorphism... The canon is merely the law of parsimony applied to animal psychology."

**Adams (1928, p. 241)**

[After quoting Morgan's canon...] "This is plainly intended as an adaptation to the problems of animal psychology of the general Law of Parsimony..."

**Boring (1929, pp. 464–465)**

[Morgan] "...who undertook to offset the anthropomorphic tendency in the interpretation of the animal mind by an appeal to the 'law of parsimony.' This law applied to animal psychology is often known as 'Lloyd Morgan's canon.'"

**Pillsbury (1929, p. 283)**

"He [Morgan] is deserving of credit for urging what he calls the law of parsimony in the interpretation of mental phenomena in animals. . ."

**Flugel (1933, pp. 123–124)**

The reaction started with Lloyd Morgan, who, in the [eighteen] nineties, endeavored to combat the dangers of the anecdotal method by the "law of parsimony," according to which we must always explain animal behavior in terms of the simplest mental processes that will account for the facts.

**Waters (1939, p. 534)**

Morgan's canon was offered as just such a check [against the use of anecdotes and anthropomorphism]. Its immediate effect was to outlaw at once any description of animal behavior as due to mental processes.

**Harriman (1947, pp. 225–226, 255)**

[These definitions appeared in Harriman's *The New Dictionary of Psychology*.]

Morgan's canon: C. Lloyd Morgan's axiom to the effect that the simplest explanation of all known facts is the best hypothesis or theory. It is a restatement of the principle expounded by William of Occam (c. 1325) and known as Occam's razor. Parsimony, law of: Lloyd Morgan's statement (1900) that animal behavior should be described in the simplest possible terms. It is an application of Occam's razor to animal psychology. Occam (1280–1349) had said that entities should not be multiplied beyond necessity [sic]; and Morgan accepted this view, indicating that anecdotes, attribution of human mental activities to animals, and projection of introspections have no place in animal psychology.

**Munn (1950, pp. 1–2)**

"Lloyd Morgan... advocated a curb on anthropomorphic speculation... His well known principle of parsimony for students of animal behavior read as follows:..."

**Caldwell (1960, p. 401)**

Morgan gave comparative psychology his interpretation of the law of parsimony, which curbed the tendency of observers of animals to anthropomorphize.

**Dewsbury (1973, p. 9)**

He proposed a law which has been variously termed Occam's razor, the law of parsimony, and Lloyd Morgan's canon. . .Lloyd Morgan's canon seems applicable today. If alternative explanations appear truly equal, the simpler is to be preferred until data require postulation of more complex processes.

**Dewsbury (1978, p. 10)**

Morgan is best known for opposing unbridled anthropomorphism. According to the often-cited "law of parsimony" or "Lloyd Morgan's canon. . ." The admonition that we should strive to accept the simpler of two equal alternative explanations is certainly good advice for many situations.

**Denny (1980, p. 4)**

"C. Lloyd Morgan, author of the famous Canon of Parsimony, dealt explicitly with animal behavior."

**Griffin (1981, p. 118)**

[Below and elsewhere (p. 99), Griffin accepted the interpretation that Morgan's canon is a canon of parsimony. However, Griffin (p. 131) also accepted Miller's view (1962) that the canon was not anti-anthropomorphic.]

This [Morgan's canon] has been widely interpreted as requiring that complex functions should not be postulated if a simpler explanation will suffice. That is the widely accepted principle of parsimony. . .

**Boakes (1984, p. 40)**

The canon can be seen as simply the application of the general law of parsimony to explanation of behavior. Nevertheless, Morgan did not justify it on these terms but on the grounds of evolutionary theory.

**Dewsbury (1984, p. 188)**

"The law of parsimony and Morgan's canon are two closely related principles."

**Epstein (1984, pp. 122–123)**

Morgan was a British psychologist and biologist who, in *An Introduction to Comparative Psychology*, published in 1894, challenged the tendency of some naturalists of his day to attribute human characteristics to animals. . .Morgan was no less a mentalist than Romanes, but he took a more conservative stand. Just as evolution had produced organisms that varied from the simple, to the complex, he argued, so must it have produced minds that varied from the simple to the complex. It would therefore be presumptuous of us to infer higher mental activities in animals where simpler ones would do. He expressed this in his famous Canon, sometimes called the Canon of Parsimony.

**Grier and Burk (1990, p. 52)**

Among his other contributions, he rejected anecdotalism and undisciplined anthropomorphism in the interpretation of behavior in other animals. He called for a principle of theoretical parsimony (i.e., the simplest explanation) which became known as Morgan's canon. . .

**Baenninger (1994, p. 805)**

[Baenninger's was a book review titled "A Retreat before the Canon of Parsimony." The book being reviewed was Donald R. Griffin's book, *Animal Minds*.]

"C. Lloyd Morgan's Canon of Parsimony is not mentioned in the index but it casts a long shadow over this important book."

**Barrows (1995)**

[Barrows' quotations appear in his book, *Animal Behavior Desk Reference*, which may be compared to a dictionary or an abbreviated encyclopedia. Relevant to the present work were the entries for "Morgan's canon," "Ockham's razor," and "law of parsimony." The citations of Dewsbury were Barrow's.]

[p. 308] Morgan's canon. [after quoting the canon, the entry continued]. . .that is, one should interpret data using the most parsimonious explanation (Dewsbury, 1978, 10). . .Syn. Law of parsimony, (Lloyd) Morgan's canon (Dewsbury 1978, p. 10). See law: law of parsimony. Cf. Ockham's razor. [p. 358] Ockham's razor. [included] Cf. Law: Law of parsimony; Morgan's canon; simplicity. [p. 385] law of parsimony. [included] Cf. Morgan's canon, Ockham's razor.

**Bekoff and Allen (1997, p. 326)**

[After quoting Zabel et al. who wrote, "One must be cautious about inferring complex cognitive processes when simpler explanations will suffice," Bekoff and Allen considered Zabel et al.'s statement to be equivalent to Morgan's canon. With the aid of an anonymous reviewer, Bekoff and Allen tried to distinguish Morgan's canon from parsimony, but they did not acknowledge that the anonymous reviewer was wrong.]

The statement by Zabel et al. is a paraphrase of Morgan's (1894)

Canon. . . It is possible that Morgan's Canon which is concerned with the complexity of processes should be distinguished from parsimony which is concerned with the number of processes needed to explain a given behavior (as an anonymous reviewer noted).

**Knoll (1997, p. 20)**

Those with a fondness for neatly organized historical eras might say that Morgan's Canon, as it is called, marks the end of the anthropomorphic strategy in psychology and the beginning of twentieth century behaviorism. [Paragraph break] However, Morgan's Canon is a double-edged sword. . . It can cut up as well as down. . . if we cannot anthropomorphize the animals, we cannot anthropomorphize ourselves either.

**Macphail (1998, p. 80)**

What animal psychology needed, then, was. . . the theoretical discipline to interpret the results in as parsimonious a way as possible – a discipline crystallized by the British psychologist Conwy Lloyd Morgan (1852–1896) in his well known canon. . .

**Dewsbury (2000, p. 751)**

In his classic textbook, Morgan (1894) outlined his famous canon that an animal's behavior should be interpreted in terms of the psychologically simplest processes consistent with the data. Morgan's canon, and its related concept, parsimony, spread widely during this period.

## **A History of Efforts to Correct the Misrepresentation of Morgan's Canon**

Again, intended to be representative and not exhaustive, Thomas (2001) presented quotations

across nine decades by those who tried to correct the misrepresentations of Morgan's canon (quoted here from Thomas 2001, where, again, references for the quotations may be found). In a few instances, the following were modified slightly when appropriate to fit the present context.

**Adams (1928, pp. 241–242)**

[Given the Adams' (1928) quotation in the previous section, this may be a dubious example of an effort to correct the misrepresentation of Morgan's canon.]

Morgan's canon, however, instead of being as commonly considered, a special case of the law of parsimony, is not related. . . and may on occasion work to exactly opposite effect. . . Here is Morgan trying to adapt the law of parsimony to psychology and violating it in the same breath by "multiplying entities" making quantities of unnecessary assumptions.

**Nagge (1932, pp. 492–493)**

[Nagge appropriately explained the canon and also addressed issues related to the law of parsimony. The phrases "undergone a transformation" and "come to be known. . . as the law of parsimony" was seen by Nagge as misrepresenting Morgan's canon.]

Lloyd Morgan. . . has laid down a canon of interpretation which has come to be known to psychologists as the law of parsimony. . . This canon seems to have undergone a transformation in general psychological usage until it might now be tentatively expressed thus: of any possible number of explanations of an animal act the simplest possible explanation should be employed. . .

**Newbury (1954, p. 73)**

[Before concluding as quoted below, Newbury cited ten references where the canon had been misinterpreted as a version of the law of parsimony, seven references (including five of the parsimony-10) interpreted the canon as a doctrine of simplicity, and four (all in the parsimony-10) related Morgan's canon to Occam's razor. Newbury also cited other forms of misinterpretation, and he provided a detailed analysis of how Morgan's canon should be interpreted.]



Aside from their historical inaccuracies, many current misinterpretations of Morgan's Canon have *sui generis* failed to take advantage of possible logical developments. Without contending that Morgan's methodology represents the last word, one can recognize in it some of the essentials for integrating modern introspective and comparative psychology. Whether this gain through historical continuity can be realized depends upon an accurate and significant interpretation of that methodology, including the Canon.

### Miller (1962, pp. 214–215)

Subsequent generations of psychologists have called this Lloyd Morgan's canon and have assumed that what he must have meant was that anthropomorphism – attribution of human characteristics to gods or, as in this case animals – is unscientific. A glance into Morgan's books, however, is enough to refute this assumption. Like all of his contemporaries, Morgan took it for granted that since the only psychical faculties we can know anything about directly are our own, "introspection must inevitably be the basis and foundation of all comparative psychology."<sup>3</sup> [Footnote 3 is Miller's, and it referred to "Morgan (1894, p. 37)."] Any human introspection would necessarily be anthropomorphic; all that Morgan hoped for were a few reasonable rules for playing the game.

### Gray (1963, pp. 221–222)

[Gray provided a reasonable analysis of what Morgan intended, identified some of the misinterpretations of Morgan's canon, and ridiculed them as follows.]

Boring, Flugel, and Skinner have referred to the Canon as a law of parsimony. Had it been such a law, surely it would have reduced Morgan's entities; instead, it was compatible with their multiplication. [Paragraph break] Likewise, Thorpe's assumption that the Canon is related to Occam's razor is merely gratuitous. [Paragraph break] Waters' statements [e.g., Waters 1939, in previous section] are not only contrary to historical fact, but are also incorrect.

### Singer (1981, p. 268)

[Singer's parenthetical "*Animal Behavior*" below referred to Morgan's book with that title published in 1900. Unfortunately, Morgan's emendation of Morgan's canon in *Animal Behavior* has been almost totally ignored, and errors of one kind have been replaced by errors of the other.]

Some workers took this principle too seriously and would not allow any interpretation of an advanced process, even if suggested by the evidence, and in 1900 Lloyd Morgan was obliged to add the following rider to his canon: 'To this it may be added – lest the range of the principle be misunderstood – that the canon by no means excludes the interpretation of a particular act as the outcome of higher mental processes if we already have independent evidence of their occurrence in the agent (*Animal Behavior*)'.

### Costall (1993, pp. 116–117)

[Costall's entire paper, listed among the references here, is a discussion of the misrepresentation of Morgan's canon. Hence, selecting excerpts to quote is difficult. Please consult Costall for footnotes omitted from the following quotations.]

Later commentators have consistently represented this [Morgan's canon] as an appeal to Occam's razor, a principle of parsimony; they have taken it as an outright prohibition against treating animals as anything other than mechanical automata; and they have characterized it as a rejection of anthropomorphism. [Six paragraphs later.] Morgan's canon as currently misconstrued has very much the character of a myth. Indeed, many of those wishing to counter the implications of this myth have themselves managed to perpetuate the myth itself. It has evidently been highly resistant to several attempts at correction. Indeed the two most informative recent accounts of Morgan's work make no attempt to question the accepted view of the canon.

### Wozniak (1993, pp. ix–x)

[After quoting examples where Skinner (1938), Griffith (1943), and Harriman (1947); see previous section) associated Morgan's canon closely with the law of parsimony, Wozniak wrote:]

One thing is virtually certain – neither Skinner, nor Griffith, nor Harriman could ever have read Lloyd Morgan. Even if one set out deliberately to distort the meaning of Morgan's canon, it would be virtually impossible to do so with greater success. Morgan's canon is not a principle of parsimony, it was not formulated as a guide to the description of behavior, it does not dispense with mental faculties, it is not an appeal to the observable, and it is not meant to be specific to animal psychology. Although earlier writings may also have misinterpreted Morgan in this fashion, it seems likely that Boring [Boring, E. G. (1929). *A history of experimental psychology*. New York: Century] was one of the more influential culprits. See especially pp. 464–465.

### Costall, Clark, and Wozniak (1997, p. 66)

Morgan's canon has been consistently overinterpreted. It was not a prohibition against the application of intentionalistic descriptions to animals, but rather an attempt by Morgan to put 'anthropomorphism' on a more secure scientific footing. (Costall 1993)

### Costall (1998, p. 18)

When Morgan realized his intentions were being misinterpreted, he added the clarification that "the Canon by no means excludes the interpretation of a particular activity in terms of the higher mental processes, if we already have independent evidence of the occurrence of these higher processes in the animal under observation" (Morgan 1903, p. 59). Nor, contrary to most accounts, was the canon, in any simple sense, an appeal to the principle of parsimony – an invitation to be economical with the truth... His serious point was that there were very good Darwinian reasons for supposing that animals should vary in the nature of their mentality. The canon was, therefore, Morgan's attempt to put "anthropomorphism," the psychological approach to animals, on a secure scientific footing (Costall 1993). [Paragraph break.] The extent to which the intentions of Morgan's canon have been misinterpreted is astonishing.

### Thomas (1998, p. 156)

Clearly Morgan's canon was intended to be a stricture to guide the interpretation of evidence pertaining to psychological processes in animals, but the misrepresentation of that canon that occurred early...and that continues in the present...is that it was a canon of parsimony or simplicity.

## A Proper Approach to Use Morgan's Canon

As noted earlier, Morgan realized early that his intended use of the canon was being misunderstood, so in 1903 he revised it for clarification. It is useful to repeat it here.

In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development.

"Higher" and "lower" meant "newer" and "older," respectively, in terms of the evolutionary development of psychological processes. Unfortunately, Morgan was not clear about what the components of scale of psychological processes were. One may get weak hints from some of his chapter titles (identical in the 1894 and 1903 editions) and the order in which they appear. However, other chapter titles [e.g., "Memory" and "The Sense-Experience on Animals"] are mixed among the ones that give the best hints of a scale of processes, namely, Chapters IV "Suggestion and Association," XII "Instinct and Intelligence," XIII "The Perception of Relations," XIV "Do Animals Perceive Relations," XV "Conceptual Thought," and XVI "Do Animals Reason?." In 1894 and 1903, Morgan appeared to have concluded that the evidence then did not show that animals perceived relations, had conceptual thought, or were capable of reason. However, he acknowledged that future research may provide confirming evidence for one or more of these, as is the case (e.g., Thomas 1996).

Meanwhile, Romanes' *Mental Evolution in Animals* (1883) included a foldout chart that shows his self-admitted, tentative construction of "The Psychological Scale" as well as "Products of Emotional Development" and "Products of Intellectual Development." Each of these headed a column with many rows with content entries (more below). The chart also includes an illustrative "tree" that is too complex to summarize here. The column headed "Products of Intellectual Development" has 17 numbered categories where 1 was intended to be the earliest and 17 was intended to be the most recent in evolutionary development. A few examples will be listed below in order of their numbers in the chart from the column headed "Products of Intellectual Development" together with examples from the adjacent row in column headed "The Psychological Scale." The latter consisted of Romanes' identification of representative animal classes, orders or, in some cases, examples of animals that he believed to have achieved a particular level in the scale of "Products of Intellectual Development." Following are a few examples:

- 08. Association by contiguity – Mollusca
- 10. Association by similarity – Fish and Batrachia [Amphibia]
- 13. Communication of ideas – Hymenoptera
- 16. Use of tools – Monkeys and Elephant

If 13 seems generous, recall that later research showed that bees use the “waggle dance” to communicate distance and location of sources of nectar.

Romanes' foldout chart follows the Table of Contents, and one must read the book to better understand his reasons for the entries he made in the chart. Boakes reproduced Romanes' chart in his book, *From Darwin to Behaviorism: Psychology and the Minds of Other Animals* (1984), as did Murray (1989) in his *A History of Western Psychology*. Murray wrote:

Romanes. . .book, *Mental Evolution in Animals*, is now being recognized as one of the most important books in the history of psychology because it attempted to unify all the research on animal instincts and animal intelligence into a single evolutionary scheme. (p. 263)

Morgan (1891) commented on Romanes' chart in a footnote on page 478 as follows:

I ought not pass over without notice the ‘psychological scale’ which Mr. Romanes introduces to a table prefixed to ‘Mental Evolution in Animals.’ It would be unjust to criticize this too closely, for it is admittedly provisional and tentative. If such a scheme is to be framed, I would suggest that the various phyla of the animal kingdom be kept distinct. I question, however, whether anyone can produce a scheme which any other independent observer will thoroughly endorse.

## A Modern Role for Morgan's Canon?

Karin-D'Arcy (2005) provided critical discussion of modern roles for Morgan's canon as seen by numerous well-known contemporary researchers, and she provided commendable recognition of the history of the misrepresentation of Morgan's canon. Risking overgeneralization here, most modern roles for Morgan's canon as reported by Karin-D'Arcy are reasonably consistent with Morgan's and Romanes' views in section

“A Proper Approach to Use Morgan's Canon” here pertaining to the evolutionary development of a psychological scale of intellectual processes. However, some modern investigators insist on a role for simplicity even when they acknowledge that was not what Morgan meant by the canon. The view here, to be documented in the next section, is that *determining simplicity* is so fraught with pitfalls and limitations that it is useless in psychological science.

## Simplicity in Philosophy

Emblematic and representative of articles and books by philosophers of science on the subject of simplicity as a basis for choosing between or among alternative explanations, theories, etc., 50+ years ago was Bunge's (1963) *The Myth of Simplicity: Problems of Scientific Philosophy*. For psychological science, perhaps, the most recurring problem with simplicity as a criterion for choosing among alternative explanations is that most explanations involve unrecognized or hidden assumptions that confound being able to determine which is the simplest explanation. Bunge's view that simplicity was a myth or, at least, that simplicity is almost forbiddingly capable of being defined or applied continues 50+ years later. For a recent example, Fitzpatrick (2015, pp. 39–40) wrote:

The putative role of considerations of simplicity in the current practice of science gives rise to a number of philosophical problems, including the problem of precisely defining and measuring theoretical simplicity, and the problem of justifying preferences for simpler theories. As this survey of the literature on simplicity in the philosophy of science demonstrates, these problems have turned out to be surprisingly resistant to resolution, and there remains a live debate amongst philosophers of science about how to deal with them.

Scorzato (2013, p. 2867) addressed some problems associated with assumptions and language that prohibit the ability to decide which explanation is simplest.

Simple assumptions represent a decisive reason to prefer one theory to another in everyday scientific praxis. But this praxis has little philosophical

justification, since there exist many notions of simplicity, and those that can be defined precisely strongly depend on the language in which the theory is formulated. The language dependence is a natural feature – to some extent – but it is also believed to be a fatal problem. . . in fact, the concepts that enable a very simple formulation, are not necessarily measurable. . . precisely those concepts that make the theory extremely simple are provably not measurable.

If Fitzpatrick's and Scorzato's observations and conclusions are not enough to make a working behavioral scientist dizzy with uncertainty about using parsimony or simplicity as a criterion to choose among alternative explanations of behavior, Sober's (2015) *Ockham's Razors: A User's Manual* should persuade behavioral scientists to surrender completely any attempt to use simplicity to choose among alternative explanations.

### **Simplicity Aside: How to Approach Explanation in Animal Cognition Research**

As mentioned above, mere perusal of a few issues in 2018 of the journal, *Animal Cognition*, revealed that researchers are studying animals ranging from insects to apes, and I am confident that further perusal will reveal research on animals taxonomically lower than insects. In that quick perusal, topics being investigated included "vigilance decrement" (spiders), "boldness" (fish), "jealous behaviors" (dogs), "causal reasoning" (crows), "facial recognition" (monkeys), and "intuitive optics" (chimpanzees) to mention only a few.

Sir Francis Bacon's (*Novum Organum*, 1620) consideration of "idols of the market place" showed the hazards for science that are inherent in the fallibilities of language, and Gregory Bateson (*Steps to An Ecology of Mind*) wrote critically about "linguistic muddling." If they were alive, they would be overwhelmed by the linguistic morass that psychological science has created. It may be hopeless, but to begin to hope to reduce this morass, the following are recommended.

### **Understanding Intervening Variables (IVs) and Hypothetical Constructs (HCs)**

An important article that all psychological scientists should read and incorporate into their understanding regarding concepts and explanations is McCorquodale and Meehl (1948). Seventy years later it seems apparent that most psychological scientists do not understand their distinction between IVs and HCs. Here is a fundamental quotation.

At present the phrases 'intervening variable' and 'hypothetical construct' are often used interchangeably, and theoretical discourse often fails to distinguish what we believe are two rather different notions. (p. 106) [Later]. . . the only rule for intervening variable is that of convenience, since they have no factual content surplus to the empirical functions they summarize. . . In the case of the hypothetical constructs, they have a cognitive, factual reference in addition to the empirical data, which constitute their support. (p. 107)

Elsewhere in the article, it is clear that the meaning of an IV is limited to observables, and as concepts or explanations, an IV's meaning is no more or less than the observations that support an IV's existence as a concept. At most, IVs are shortcut terms invented or adopted from common language whose meanings are defined by a multiplicity of observables. On the other hand, a HC as an explanatory concept implies something beyond the observables, something that is presumed to exist. Atomic and subatomic particles in physics are HCs, and a good example in biology was the "gene." The HC "gene" came into use in 1909, long before its physical makeup as DNA had been determined.

One is challenged to identify any concept in animal cognition research that is not an IV. As such and despite common practice, IVs cannot be reified. For example, they cannot be causes or effects, because their existence is limited to the observables that define them. Examples used here for illustrative purposes of IVs in animal cognition research, "boldness," "causal reasoning," and "facial recognition" (chosen among several others listed in first paragraph of section "[A Modern Role for Morgan's Canon?](#)"), were gathered via a quick survey of a couple of 2018 issues in the electronic journal *Animal Cognition*. Other IVs ad

nauseam may be seen in *Animal Cognition* and other contemporary journals that publish research in animal cognition.

### The Brain and Intervening Variables (IVs)

Close study of functional neuroanatomy textbooks (e.g., the several editions of Alf Brodal's *Neurological Anatomy* or Malcolm B. Carpenter's *Human Neuroanatomy*; over the years Brodal had a successor, and Carpenter had coauthors and a successor), other textbooks in functional neuroanatomy, and articles such as Diamond (1979) should result in the conclusion that all brain functioning reduces to three fundamental types of processing: sensory, memory, and effector. *All other processes reduce to one or combinations of these three.* These three processes interact continuously in the brain and effect physicochemical changes in the brain. The brain is never exactly the same physicochemically from moment to moment, nor are the associated IVs exactly the same from moment to moment.

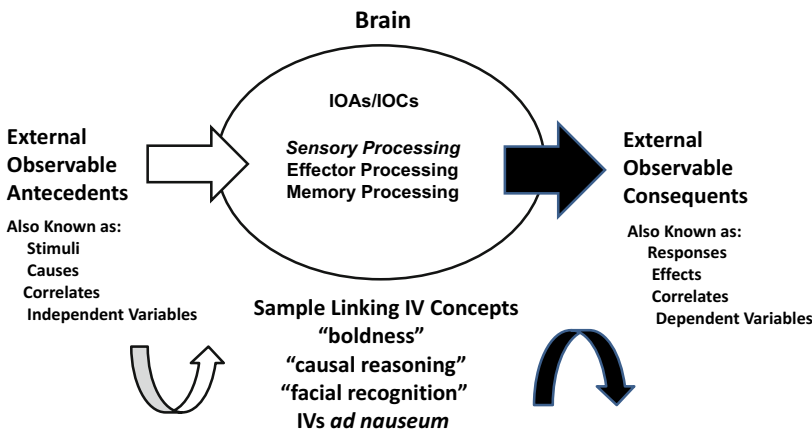
Figure 1 shows how IVs exist only as shorthand terms to summarize each IV's associated antecedent and consequent observables.

Figure 2 emphasizes that the brain and the IVs used in this example (and all other IVs) are never exactly the same from moment to moment.

Strictly speaking, a radical behaviorist might insist correctly that the precise meaning of each IV is limited to the antecedents and consequents associated with a specific experiment or controlled observation. However, to cite but one example, we know that many IVs (e.g., "fear") may be used more generally based on many different experiments or controlled observations involving different observables. Such different uses of "fear" have in common antecedents and consequents associated with potential bodily harm or death. Of course, one does not have to be bitten by a poisonous snake to fear being bitten by a poisonous snake, because memories associated with learning about the experiences of others provide us with sufficient information to be fearful of being bitten by a poisonous snake. It cannot be iterated enough that an IV's meaning is limited to the observable antecedents and consequents that define it and that IVs can never be reified as causes and effects or have any other characteristics of entities that have material existence.

### Hazards of Emergentism in Psychological Science

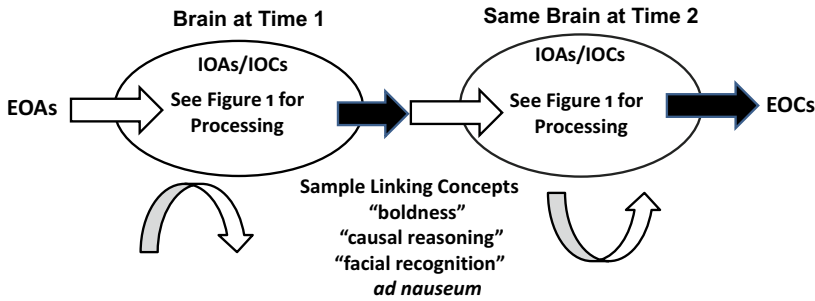
In her aptly titled critique, "Clever Animals and killjoy explanations in comparative psychology," Shettleworth (2010, p. 477) quoted Holldobler and Wilson as follows:



**Morgan's Canon, Fig. 1** The brain at a moment in time when physico-chemical events associated with sensory, memory and effector processing are constantly interacting and effecting new physico-chemical changes. To an extent, these internal observable antecedents, IOAs, or consequents,

IOCs, may be observed via chemical sampling, electrical recordings or brain imaging, or manipulated via chemical or electrical stimulation or targeted ablations. "Tagging along" with the brain's activity are the Linking IV Concepts





**Morgan's Canon, Fig. 2** A dynamic representation of the brain and its associated External Observable Antecedents (EOAs) and Internal Observable Antecedents (IOAs) symbolized as open arrows and External Observable Consequents (EOCs) and Internal Observable Consequents (IOCs)

symbolized as solid arrows. As indicated, the EOCs at one moment in time become part of the EOAs at the next moment in time. The brain, physically, is never exactly the same from moment to moment, thus the meaning of linking concepts are not exactly the same from moment to moment

The extremes of higher-level traits may at first appear to have a life of their own, one too complex or fragile to be reduced to their basic elements and processes by deductive reasoning and experiment. But such separatist holism is in our opinion a delusion, the result of insufficient knowledge about the working parts and processes.

This raises nicely the issue of the hazards of emergentism.

Emergentism, although not by that name, developed most strongly with the nineteenth-century British associationist philosopher, John Stuart Mill. John Stuart Mill argued against his father's, John Mill's, "mental mechanics" using a paradigm the younger Mill named "mental chemistry." This was illustrated by John Stuart Mill's example of water. He argued that water has emergent properties, namely, that water has properties that cannot be reduced to its constituent elements, hydrogen and oxygen. As opposed to John Mill's "the whole is equal to the sum of its parts," John Stuart Mill asserted that "the whole is greater than the sum of its parts." If water seems to have emergent properties, it is likely because we do not yet understand the complete physical and chemical properties of oxygen and hydrogen.

That "the whole is greater than the sum of its parts" was perpetuated by the Gestaltists Max Wertheimer, Wolfgang Kohler, and Kurt Koffka beginning early in the twentieth century and has been advocated for animal cognition research in recent years by Duane Rumbaugh and colleagues among others. Thomas (1999) presented a rebuttal

of Rumbaugh and colleagues in 1999 in a symposium in which Rumbaugh and two colleagues participated at the Southern Society for Philosophy and Psychology.

A quotation from Guyer (1931) used by Thomas (1999) is also useful here. It is slightly modified here as explained below to show that "emergentism" in animal cognition is deemed parallel to the role that "vitalism" once had in biological science. Before significant progress could be made in biology, biology had to rid itself of vitalism. In the portions quoted here from Guyer (1931), "emergentism" or related terms have been added in brackets to make explicit the parallels between the hazards of "vitalism" for biological science and the hazards of "emergentism" for psychological science.

Are the characteristics which mark off living from nonliving matter explainable by physics and chemistry and the known laws of matter or is there something else?... Two opposing interpretations have been suggested; one known as vitalism [emergentism], the other as mechanism. By vitalism [emergentism] is meant a directive tendency beyond the inherent properties of mere molecules or chemical elements which manifests itself in and is peculiar to the living organism. . . They [vitalists and emergentists] believe they find evidence of purpose in life-activities and that such activities are inexplicable on the basis of mere physics or chemistry. . . admitting that many of the phenomena seen in living things are yet unexplained or are even inexplicable in terms of our present knowledge of chemistry and physics, the mechanist points out that with our advancing knowledge in these fields many

of the processes originally claimed by vitalists [emergentists] to be distinctively vital [emergent] have been shown to be physical or chemical and that continual progress is being made by mechanistic methods. . . . Mechanists believe it is simpler and more accurate to regard life as process or function rather than as a separate essence, and to consider living matter as ordinary matter so arranged as to become a metabolic mechanism. . . .

The controversy, though changing its form from time to time, has been carried on ever since the days of Aristotle and there seems no prospect of agreement in the near future. The problem may be insoluble. As our knowledge of fundamental life processes has advanced, the vitalist [emergentist] has been forced to abandon one position after another, but there is still such a great unexplained residue of facts relating to the constructive and coordinating processes of living matter that he still has abundant material for argument. As a practical working program, however, it is well to note that the science of biology has advanced mainly as it has been able to explain its phenomena in mechanistic terms, and that there is undoubtedly much yet that can be so explained. To rest content with merely attributing vital [emergent] phenomena to some sort of "vital principle" [emergent] is in effect to give up the problem, and such an attitude of mind can lead only to scientific stagnation. (Guyer 1931, pp. 22–23)

## Concluding Remarks

It is hoped that all misrepresentations of Morgan's canon (equivalency with Ockham's razor, parsimony, and simplicity; being anti-anthropomorphic, anti-anecdote, and anti-Romanes) can now cease and rest in peace. Greater consideration of Morgan's canon's association with a study of the evolutionary development of cognitive abilities, together with Romanes *Mental Evolution of Animals*, might lead to a useful way to assess and rank cognitive abilities in animal cognition research.

Finally, it is hoped that researchers in animal cognition will pay greater heed (a) to the futility of using simplicity as a criterion to choose among alternative explanations; (b) to the importance of McCorquodale's and Meehl's distinction between intervening variables, IVs, and hypothetical constructs, HCs; and (c) to the limitations of what we can and cannot know about the brain and IV concepts in animal cognition research.

## Cross-References

- Aristotle
- C. Lloyd Morgan
- Charles Darwin
- Comparative Psychology
- Evolutionary Psychology
- George Romanes
- Gestalt
- Intervening Variables
- Margaret Floy Washburn
- Ockham's Razor
- Origin of Species
- Parsimony
- Reductionism

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## Morgan's Principle

### ► Morgan's Canon

## Morphemes

### ► Cognition

## Morphology

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## Synonyms

Animal structure; Body type; Difference of form; Shape; Zootomy

## Introduction

The word morphology derives from the Greek μορφή, morphé, meaning “form,” and λόγος, lógos, meaning “word, study, research.” In biological sciences, morphology is responsible for the study of form, shape, and structure of extinct and extant organisms. Even though studies on morphology have been conducted far before the eighteenth century, the term was first publicly employed by W. Goethe in a medical handbook in 1800, with the underlying meaning of study in organic design or form (Richards 2008; Kardong 2008). However, the term morphology (=morphologie) was already used by Goethe in 1796 in a correspondence with his personal friend, the poet Friedrich Schiller. In the first number of the first volume of Goethe's classic publications

named *Zur Morphologie* (1817), he meant especially by the term as the study of organic forms, both external and internal, and the development of such structures (Richards 2008).

Inspired mostly by Goethe's studies and definitions, several physicians and naturalists (e.g., K. Friedrich, L. Oken, C. Carus, R. Owen, E. Haeckel) have posteriorly complemented and advanced several concepts, terms, and theories that are currently used in morphological studies (Richards 2008). Morphological studies have been complemented by several fields in sciences, such as histology, anatomy, cytology, and embryology (Kardong 2008). Above all definitions given to the term since its proposition, morphology raises questions about structure and offers a method to address these questions, seeking to explain organisms design by elucidating the reasons and processes that produce their basic structural plan (Kardong 2008).

## Morphology Versus Anatomy

The concepts and utilizations of the terms “morphology” and “anatomy” have been used interchangeably in biological sciences. For some, internal morphology may represent a synonym of anatomy, contrasting with external morphology, which does not demand any invasive procedure for structure visualization. However, they represent distinct, yet similar areas of study considering an organismal structure and organization and should not be considered as synonyms. The term anatomy is composed of two Greek words that mean cutting up. In other words, the term anatomy should be used to refer to the organismal structure, based on observations of structures capable of demonstration (Snodgrass 1951). For instance, when analyzing the structure of an animal intestine, one should report the tissue components, cell organization, microstructures, etc. that demanded any kind of technique for its acquisition. On the other hand, morphology includes several hypotheses and background theories associated with the animal structure and shape, such as evolutionary assumptions that are highly multidisciplinary. Morphology, therefore, should be applied to studies that consider

the animal structure – derived from evidence based, for example, on anatomy and embryology – and might discuss the evolutionary means that lead to those structures. Such evolutionary means might include several concepts that associate the anatomy of individual to the means that lead to such body plans.

## Form and Function

Animal bodies and design must address physical and biological demands. For instance, gravity acts on all structures of terrestrial animals, as a consequence, heavy vertebrates must exert much effort in locomotion. Differences in size necessarily lead to differences in performance and design. As body size changes, the demands on various body parts change disproportionately.

Form is solely the appearance, configuration, or shape of a structure, while the function of this structure is its action or how it works (Bock and Wahler 1965). Size and shape are necessarily linked, and the consequences affect everything from metabolism to body design. Thus, change in size inevitably requires a change in form, known as scaling, a compensatory adjustment in proportion to maintain performance with changes in size. Furthermore, a surface area increases rapidly with increase in size, scaling in proportion to the square of the linear dimensions. Volume (mass) is even more affected, increasing by the cube of linear dimensions. Inevitably, larger organisms have relatively greater mass with which to contend and, consequently, the supportive and locomotor systems must be built differently and stronger to meet the accompanying physical demands (Kardong 2008).

Shape changes in proportion to size, termed allometry, are common during the growth of an organism. Shape is important, for example, in aquatic animals. Thin shapes help reduce drag in aquatic environment, while specific position like turning broadside allows a fin or flipper to use profile grad to generate forces. A streamline shape encourages smooth, non-separating flow.

The study of the function of structural features of organisms opens up a new realm in the analysis

of biodiversity. Much attention has been focused on the morphological parts of organisms and on the geographic distribution of species, but in comparison, relatively little is known about function diversity. Although the form-function relationship is one of the oldest areas in biology, relatively little attention has been paid to the function side of this dichotomy. Accordingly, disciplines analyzing organismal function are traditionally reductionist, mechanistic, and experimental. Such analyses have provided insights into many features of organismal design and have been instrumental in the spread of new ways of thinking about how organisms are built. For example, the use of dimensional analysis and scaling to evaluate mechanistic hypotheses about musculoskeletal function has contributed to a number of significant insights into how birds fly. Also, the now widespread awareness of the importance of fundamental physical relationships such as surface-area-to-volume ratios for understanding organismal design is in large measure due to the contributions of comparative physiologists.

## Basic Morphological Concepts

Several concepts have been developed in order to analyze design, as the concepts of form, function, and evolution. Even though terms associated with such concepts have just been proposed in the nineteenth century, their meanings as currently applied have only been defined after Darwin's theory on common ancestry (Kardong 2008). Some of the most useful of these terms address (1) similarity, (2) symmetry, and (3) segmentation (Kardong 2008).

Regarding similarity, the terms homology, analogy, and homoplasy have been proposed mostly based on three criteria: ancestry, function, or appearance. Homologous structures which similarity are due to common ancestry. Homoplastic structures look alike, but that is not due to common ancestry, while analogous structures do not feature a common ancestor, and may not be similar but exhibit similar functions. As an example, wings of butterflies are analogous to bat wings as they both perform the same function (=fly),

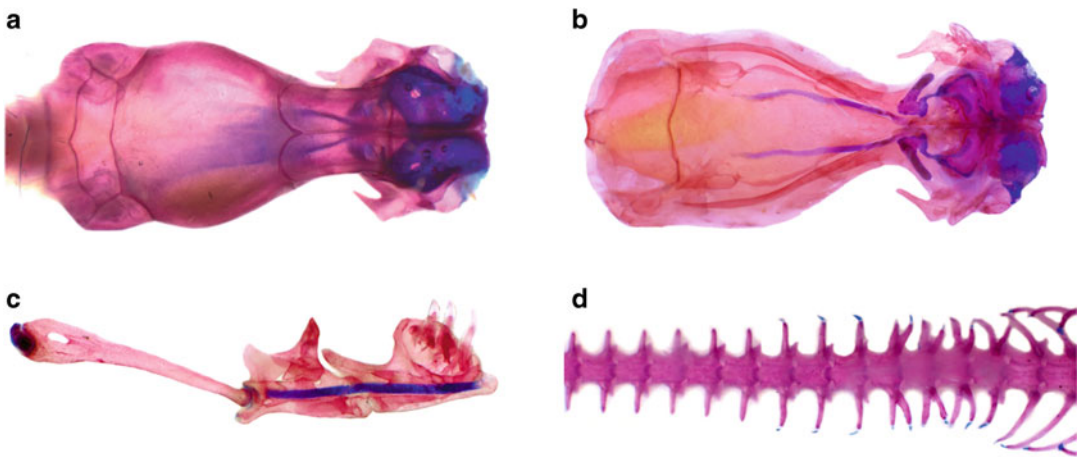
but do not have a common winged ancestral. Thus, parts may be similar in ancestry, function, and/or appearance; however evolutionary evidence might contribute on relevant data for their understanding.

With respect to symmetry, it refers to the plan of the organism in relation to the environment, as well as its distinct regions. The two main types of symmetries applied in zoology regard radial and bilateral symmetries, with the former representing a body laid out equally from a central axis (e.g., starfish) and the latter regards individual that only the midsagittal plane divides the body into two mirrored images (e.g., whale). Organismal regions are described in many ways, frontal planes divide bilateral organisms in dorsal and ventral sections, a sagittal plane splits into left and right, and a transverse plane (=coronal) divides into anterior and posterior portions. Finally, segmentation deals with a body plan that includes repeating or duplicated sections in the organism structure. Examples are the backbone composed of repeated vertebrae (vertebrates) and the body of several arthropods (Hannibal and Patel 2013).

## Assessing Morphological Data: Fields of Study, Methods, and Techniques

Several tools have been developed since the first studies conducted on organismal morphology, which can be conducted depending on the researcher goal (Kardong 2008). The earliest tool developed by morphologists was direct **dissection** (Kardong 2008). First dissections were conducted in humans and can be traced back thousands of years ago, at least to 1600 BC in two ancient Egyptian papyri that distinguishes organs such as the heart, liver, spleen, kidney, and others. Even though the dissection practices conducted by Egyptians did not directly aim to contribute on the knowledge on the human anatomy, the continuous practices of mummification contributed to it. It was only in 500 BC that Alcmaeon of Croton, an ancient Greek philosopher and medical theorist, dissected the first human body, providing the first insights on the origin of physiological processes of feelings, mostly associated with the





**Morphology, Fig. 1** Cleared and stained skull of a threadsnake (*Trilepida salgueiroi*) in dorsal (a) and ventral (b) view, lower jaw in medial view (c) and ventral view of the posterior trunk vertebrae, cloacal vertebrae and caudal vertebrae (J. J.)

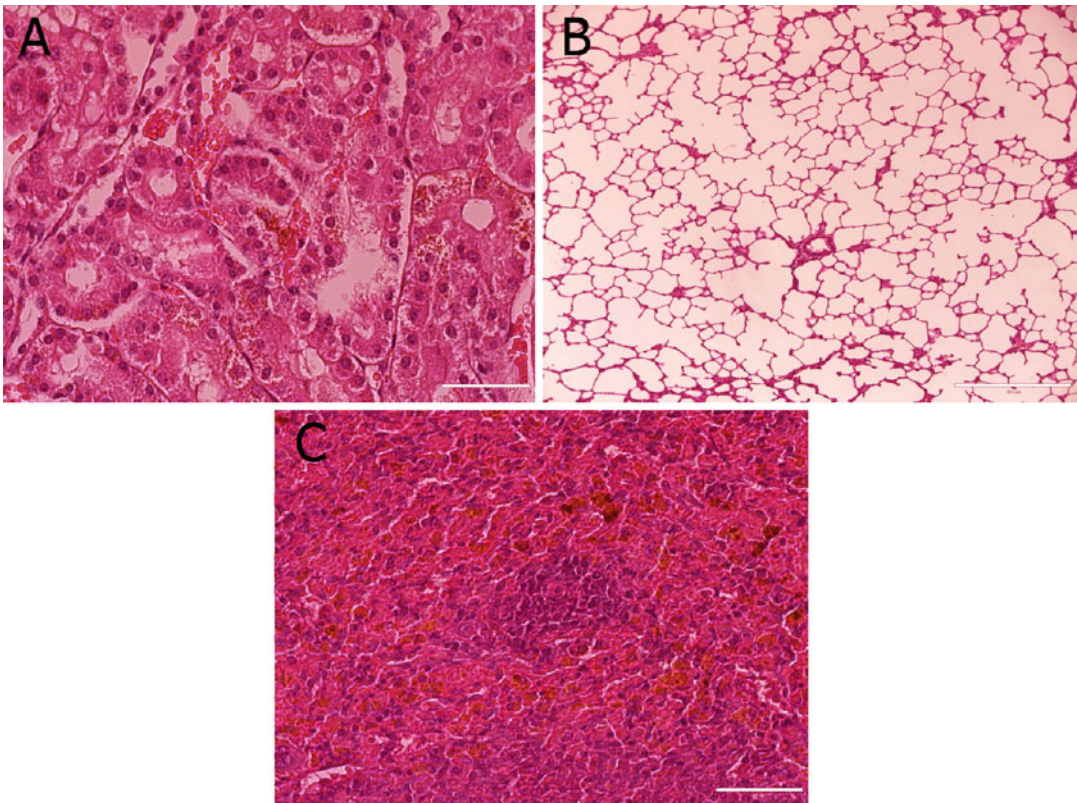
brain (Singer 1957). The earliest animal dissections were performed by Galen, who dissected several mammals (e.g., monkeys, cows, and dogs) in 150 AC. Much has been improved regarding organismal dissection, and different methods/techniques have been developed for specific elements in the body. For example, techniques for bone examination involve soft tissue removal and bone cleaning, with a wide variety of methods or techniques for bone preparation (Dawson 1926; Onwuama et al. 2012). Bone preparation might be accomplished by maceration, by removal of soft tissues with the aid of water/reagents, or by the exposure to flesh-eating bugs – *Dermestes* spp. In maceration, specimens are left in sealed containers to the natural effect of putrefaction, with constant removal of putrefied tissue. In manual removal of soft tissues, specimens might be immersed in water, sodium hypochlorite or potassium hydroxide. Such reagents will soften tissues in order to facilitate its removal with the aid of tweezers. While maceration and manual dissection consume a large amount of time (especially in large animals), the use of flesh-eating bugs of the genus *Dermestes* might represent a valuable tool for osteology. Chemical preparation with sodium hydroxide was found to be the best method in terms of time required to complete the procedure, number of bones

recovered, color of the bones, and odor of the preparation. However, the chemical method has the disadvantage of dissolving and cracking the bones if the concentration used is high and prompt attention is not given to the preparation (Onwuama et al. 2012). Another method for analyzing bone structure is known as clearing and staining (Taylor and Van Dyke 1985), in which the specimen is subject to several stages and reagents in order to have its muscles and most tissues translucent, while bones are dyed red and cartilage dyed blue (Fig. 1). This method can be modified to stain simultaneously nerves (Song and Parenti 1995). However, all the aforementioned techniques are highly invasive, damaging all tissues and structures associated to bone. Recently, new techniques were developed to cope with the limitation posed by morphological studies of anatomy in live or rare specimens, such as computed tomography (Schaefer and Fernández 2009) or magnetic resonance. These techniques allow 3D images of hard tissues, and with proper staining techniques also low-density structures such as muscles and glands (Dickinson et al. 2018). They are particularly valuable in paleontological studies where fossils cannot be extracted from the matrix or to visualize internal structures of the fossils (Racicot 2017). More recent techniques such as the images from

synchrotron light source have proven to be a promising tool in virtual dissections at an impressive resolution of 30 nm (Lu et al. 2019). This resolution is able to provide data at a level similar to histological dissections in organisms.

Microscopic studies on organism morphology were only made possible with the origin of the microscope, in the seventeenth century. At that time, even though lenses that amplified vision already existed, they were not implemented in such a way as the microscope to visualize structures at a microscopic level. The earliest record of the existence of a microscope is from 1622, in a letter by Constantijn Huygens in London (Huygens 1622; Bardell 2004). However, the earliest records of microscopic observations date from 1625 and 1630 and are investigations of a bee and a weevil by Federico Cesi and Francesco Stelluti (Bardell 1983, 2004). After its invention, improvement of the microscope quality went by,

associated with quality of images assessed and greater magnification (Bardell 2004). The invention of the microscope allowed the investigation of parts of organisms, mostly by specific cuts of their organs, tissues and elements. It was in the nineteenth century that **histology** was then recognizable a discipline, with the concept of tissue being introduced by Bichat in 1801. As its definition, the field of histology aims to study the structures of tissues and organs of an organism. Also called microscopic anatomy for some, modern histology is not merely descriptive but also includes many aspects of molecular and cell biology in order to contribute on the cell organization and function (Pawlina 2016). Even though methods used for histological methods vary, much of the area deals with techniques that involve light microscopy (Fig. 2). Past studies have dealt with several methods involving electron microscope, but current studies usually



**Morphology, Fig. 2** Histology of different organs of wistar rat (a) kidney, (b) lung, and (c) spleen. Scale 50  $\mu$ m, 400  $\mu$ m, and 50  $\mu$ m, respectively. (Photos by Fernanda Paulini)

include atomic force microscopes that can provide images with much higher resolution (Pawlina 2016). Additionally, auxiliary techniques as histochemistry, cytochemistry, and immunocytochemistry allow visualization of different structures. The goal of histochemistry is to provide color and contrast to microscopic images by the use of techniques to accomplish the specific labeling of biological structures (Davis 2011). Comparably, cytochemistry involves specific reagents to identify biochemical content of cells. Finally, immunocytochemistry aims to anatomically visualize specific protein or antigen in specific cell spots by the use of primary antibodies under a fluorescence microscope (Pawlina 2016).

Not only histology was made possible with the origin of the microscope but also a few areas that are directly related to morphology studies. For instance, while histology deals with organismal tissues, **cytology** is the field that studies the structure and function of the cell. Also called cell biology, it focuses on studying the basic unit of life, in order to understand its its physiology, metabolism, life cycle, and chemical composition. As histology, cell biology directly contributes on understanding the morphology of an organism through its structure and function. The explosion of new imaging and computer technologies continues to provide fresh and spectacular views of the inner workings of living cells (Alberts et al. 2014). Finally, **Embryology** deals with the prenatal stage of animals by investigating the formation and development of the embryo and fetus. It is intrinsically linked with cell biology and histology, as these fields aid on the clarification of several developmental issues.

## Morphology and Evolution

Animal morphology has been slowly shaped over millions of years, and an understanding of evolutionary history can aid on the comprehension of patterns observed in living organisms. Anatomy evolves often through changes in developmental genes, but the causal mutations, and their effects, remain largely unknown (Frankel et al. 2011). Thus, understanding the phenotypic effect of

size and mode of action of genes that contribute to these complex traits is an important challenge for evolutionary biologists.

In general, rates of morphological evolution vary among different taxonomic groups, thus variations in rates of evolution has been proposed as one of the main drivers for the great diversity of organisms on Earth (Sherrat et al. 2017). The subarea of evolutionary biology focuses on the documentation of the variability of organisms in the tempo and evolution, identifying extrinsic and intrinsic factors pertaining to such variabilities, such as lineage biology, ecology, and development (Sherrat et al. 2017). Such goals are currently being assessed by recent methods as the phylogenetic comparative methods that include huge phenotypic datasets with an evolutionary purpose.

Additionally, an evolutionary insight into morphology can offer ways of understanding some human disorders and diseases. Understanding how a structure evolved, and how structures are linked during evolution and development can therefore shed light on why and how abnormalities arise.

## Morphology and Systematics

Classifying is probably an endeavor as old as our species. The activity of grouping certain living beings based on their attributes, and naming those groups is a powerful tool to convey information about them. Even before science as we know, the relevance to the survival or thriving of a community could depend on the ability to recognize certain attributes of organisms as an indication of danger or food. The placement of an organism to a group in detriment of another group was based on phenotypic characteristics, for the most part, its morphology. For this reason, the birth of biological classifications is hand in hand with the birth of comparative morphology.

The first attempt of a more thorough classification was by the Greek philosopher Aristotle. Aristotle's classification was followed by other ways to classify organisms, but the birth of the modern taxonomy and our still used scheme of

classification was proposed only in the eighteenth century by Carl Linnaeus. In his scheme of classification, the basic unit was the species, in which morphologically similar organisms would be grouped. To this species, a binomial name would be attributed. Similar species would be grouped in a given genus, and similar genera in a given family, and so forth. In this hierarchical scheme of classification, each of these taxonomic ranks (e.g., species, genera, family, and order) was arranged by degree of inclusiveness. The degree of morphological similarity among other taxa is determinant for placing the species in each of these taxonomical ranks. For Linnaeus, some classes of morphological characters were more important for a given taxonomical group than to others, as an example, his entire plant classification was based on the morphology of reproductive structures (Linnaeus 1753). The Linnean system of classification is so practical and simple, that is still used with few modifications, even though it was conceived in a distinct paradigm. In this paradigm, known as fixism, it was believed that each and all species were created exactly like what we see today.

In the nineteenth century, the understanding of the natural world was profoundly changed by the proposal of the theory of biological evolution (Darwin 1859). Breaking with fixism, Darwin proposed the evolutionary process as a branching tree of descents with modifications. This phylogenetic pattern gave the theoretical framework for the hierarchy of similarities observed by Linnaeus and which formed the basis for his classification. Linnaeus' observed morphological similarities used in the classification are now interpreted as the result of shared common ancestry. For Darwin, morphology is the path to understand evolution and "is the most interesting department of natural history and may be said to be its very soul" (Darwin 1859, p. 434).

One century later, Hennig (1966) proposed that not all similarities are equal. And that classifications should reflect the evolutionary history of the group and consequently, only similarities due to common exclusive ancestry should be considered. Similarities not reflecting this common ancestry, as convergences, should not be used. This

methodology, named by Hennig (1966) phylogenetic systematics and later known as cladistics, became quickly the paradigm in biological classification (Schuh and Brower 2009). In the following decades, many classifications were proposed based on this methodology with morphological characters, until molecular characters became increasingly more used in phylogenetic analysis.

However, at the end of the twentieth century and beginning of the twenty-first century, there was a heated debate on the utility of morphological data for biological classifications in face of the growth of the molecular data (Hillis 1987; Hillis and Wiens 2000). The discussion centered on if one dataset had an advantage per se over the other, and how congruent they were. While the molecular data could be much larger than the morphological data, it could be applied only to a small portion of the diversity, since museum specimens and fossils could only provide morphological information (Hillis 1987). Several authors at that time advocated a combined analysis using both molecular and morphological data as a way to provide an improved estimate for the phylogeny in question (Wiens 1998). However, in recent years new sequencing technologies were developed making available genomic-scale datasets easily and at low cost (Lee and Palci 2015). In this phylogenomic age, molecular datasets surpass the morphological datasets many folds. As a consequence, morphological information has been increasingly relegated to a secondary role in phylogenetic analysis, usually excluded from it altogether with a few key characters optimized and discussed in the topology generated solely by the molecular data (Mooi and Gill 2010; Giribet 2015). The reasoning for excluding morphological characters is that the putative huge asymmetry between both kinds of datasets causes the morphological data to contribute little, if at all, to the phylogenetic structure when in a combined analysis and that morphology is more prone to convergences (Giribet 2015; Lee and Palci 2015). However, it has been shown that even with a very asymmetric data matrix, the morphological dataset can still change the position of taxa in comparison with the analysis without the morphological characters (Wiens et al. 2010).



Furthermore, the use of morphological data in a combined analysis allows the inclusion of fossil taxa which are crucial to understanding diversification and lineage origin and extinction (Giribet 2015; Pyron 2015).

## Cross-References

- Bilateral Symmetry
- Charles Robert Darwin
- Cognition
- Crocodilia Morphology
- Evolution
- Homology
- Homoplasy
- Radial Symmetry

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## Morris Water Maze

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## History and Application

The Morris water maze is one of the most widely used methods for testing spatial learning and memory. Developed by Richard Morris at the University of St Andrews in the 1980s (Morris 1981, 1984), experiments using the Morris water maze have made vital contributions to theoretical and methodological advancements in behavioral neuroscience and animal cognition.

The logic behind the Morris water maze is simple: subjects are placed in a circular pool of opaque water and must swim in the pool until they find a small hidden platform submerged beneath the surface of the water that they can stand on. The Morris water maze was initially developed for use with rats, which are natural swimmers yet intrinsically motivated to find and stand on the hidden platform in order to get out of the water. In the

classic version of the Morris water maze, the position of the hidden platform is constant in relation to the visual cues outside of the maze (e.g., posters located on the wall), so subjects can find the approximate location of the hidden platform by using these cues. After several learning trials, normal subjects become faster at finding the hidden platform, both in terms of speed (latency) and the distance taken to reach and stand on the platform. Once subjects have learned the location of the hidden platform, they are able to find the platform from any of the designated start locations, which are often at the edge of the pool. In test trials, the platform is removed and the time spent in the different areas of the pool are measured, with the assumption that subjects that have learned the location of the platform will spend more time searching in the area where the platform once was (Morris 1981). Other behavioral measures, such as the proximity measure (i.e., the distance between the subject and hidden platform, calculated every second throughout a trial), have additionally been developed to assess a subject's spatial learning and memory in greater detail (see Pereira and Burwell 2015). Development of accurate methods to quantify performance in the maze is important to properly control for the influence of factors unrelated to spatial learning, such as a subject's inability to swim towards the platform, sex, species (i.e., rats versus mice), age, health, and stress levels (reviewed by Vorhees and Williams 2006). For instance, prelearning trials are often included at the start of the experiment: in these trials the platform is not hidden but elevated above the water and visible to subjects. This is so subjects learn that there is a platform somewhere in the pool and will try to find it in later trials when it is hidden beneath the surface of the water. The prelearning trials also allow experimenters to see whether a subject has difficulty swimming in the maze and exclude any subjects from the experiment if necessary.

In any trial, different strategies can be used to find the location of the hidden platform (Brandeis et al. 1989). Subjects can remember the sequence of movements required to reach the platform or learn to locate the platform based on a cue

(purposely or unintentionally) present in the pool or room. Both of these strategies are inflexible, however, and may be ineffective if subjects start their search from a different point in the maze. When a subject finds the platform by learning the position of the visual cues relative to each other, they are thought to be forming a mental map of their environment and employing a place learning strategy (also known as a spatial strategy), which is a flexible strategy that enables the subject to find the platform from any starting point in the maze. Place learning strategies rely heavily on a brain region called the hippocampus (e.g., Morris et al. 1982), although neural systems distributed throughout the brain are involved in spatial learning and memory in the Morris water maze (D’Hooge and De Deyn 2001).

Even though it was originally designed for rats, the Morris water maze is ideally suited for comparing spatial learning and memory in different animals because navigating efficiently through environments is a natural and important behavior for practically every animal. A few adjustments allows the Morris water maze to be used with mice (Vorhees and Williams 2006), and variants of the Morris water maze have already been successfully developed for humans and songbirds. Virtual simulations of the Morris water maze are used for testing humans (e.g., Astur et al. 2002), while a “dry version” of the Morris water maze is used for songbirds (Mayer et al. 2013). These studies involving both humans and songbirds show that, like rats and mice, the hippocampus plays a key role in supporting place learning strategies, which suggests that function of hippocampus for spatial learning and memory is conserved across animal taxa.

## Cross-References

► [Hippocampus](#)

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## Morton Edward Bitterman

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## Synonyms

[Jeff Bitterman](#)

Morton Edward “Jeff” Bitterman (1921–2011) was an American comparative psychologist—in the most literal sense of the term! His research, which was focused on fundamental learning processes, was distinctive for the number of different species that he compared across a productive career that spanned almost 70 years. This comparative breadth served as the catalyst for many methodological and apparatus innovations that Dr. Bitterman developed for the field. He also served in academic and disciplinary leadership roles. For these methodological, empirical, and

theoretical contributions, Professor Bitterman was recognized with numerous awards and honors.

## Personal and Professional History

On January 19, 1921, the former Stella Weiss, wife of Harry Michael Bitterman, gave birth to a son in the same Brooklyn house where she herself had been born. The Bittermans, who had married in Brooklyn in 1917, named their only child Morton Edward—although he would be called “Jeff” throughout his life. Jeff’s father owned a fur business in the Garment District of New York City, whereas his mother was a practical nurse. As for young Bitterman, he planned to pursue a career as a lawyer. After high school, he enrolled in New York University with that goal; however, encounters with two assistant professors of psychology at NYU changed Bitterman’s career plans (Balsam 2012) and, ultimately, psychology’s understanding of animal learning. Jeff became interested in psychology through an introductory course taught by the behaviorist George Benjamin Vetter, who studied personality and social psychology. Bitterman’s love for animal psychology was sparked by University of Michigan-educated Theodore Christian Schneirla, whose detailed studies of the behavior of ants (particularly the army ants of Panama) resulted in dozens of published articles and a book (Schneirla and Topoff 1971). Bitterman earned his B.A. in psychology from NYU in 1941, followed by an M.A. from Columbia University in 1942. His research at Columbia in Professor Carl John Warden’s Laboratory of Comparative Psychology resulted in Jeff’s first publication (Bitterman and Warden 1943), a study of inhibitory effects of conditioning on the seizure behavior of white rats. (It is interesting that Vetter’s own graduate work at the University of Washington had also involved the study seizure behavior, albeit in humans with epilepsy.)

For his Ph.D., Bitterman traveled upstate to Cornell University. Balsam (2012) noted that Jeff conducted research there on Pavlovian conditioning in sheep and other animals at Cornell’s “Behavior Farm” (see also Kirk and Ramsden 2018), directed by Dr. Howard S. Liddell.

Professor Liddell was a psychobiologist who examined the relation between mental illness and the Pavlovian phenomenon of experimental neurosis. However, Bitterman’s Ph.D. research was conducted in a very different domain: His dissertation, *Studies in Visual Fatigue and Efficiency* (Bitterman 1945a) was directed by Dr. Thomas Arthur Ryan, who had himself earned the Ph.D. in psychology from Cornell 8 years earlier. Professor Ryan’s own research program was focused on real-world applications of psychology (e.g., Ryan 1947), so it is unsurprising that Bitterman’s topic was rather applied, involving a series of studies testing whether psychophysiological measures such as heart rate, squinting, and blink rate are valid and sensitive measures of eye fatigue during reading (see also Bitterman 1945b). These data were published a short time after a related note Bitterman authored in the *American Journal of Psychology*, in which he argued that fatigue could be objectively measured by the ratio of performance to expended effort (i.e., efficiency; Bitterman 1944). By the end of 1946, five other related articles authored by Bitterman had appeared in the literature (Bitterman 1945b, 1946a, b; Bitterman and Soloway 1946a, b). Within another year, Dr. Bitterman had a total of 21 publications, and others forthcoming, to his credit, including collaborations with Cornell Professor Dr. Frederick Lawrence Marcuse on psychophysiological indicators of posthypnotic amnesia (Bitterman and Marcuse 1945) or of guilt or innocence (e.g., Bitterman and Marcuse 1947), and a classroom demonstration (Marcuse and Bitterman 1944). Dr. Marcuse (1940) had earned his Ph.D. in 1940 from Queen’s University with a dissertation titled *A Study of Abnormal Behavior in the White Rat*, so it is easy to imagine that the two scientists might have found common research interests to discuss beyond the topics they published collaboratively.

With this early record of scholarly output, Dr. Bitterman was offered employment by Cornell University in 1945. He served on the psychology faculty until 1950, before being recruited to the University of Texas in Austin by Professor Karl M. Dallenbach, himself a Cornell Ph.D. recipient (1913) and a professor of Bitterman’s, who in 1948 had moved after 30 years on Cornell’s

faculty to become chair of the psychology department at Texas. Bitterman joined the faculty as an associate professor. He was also named co-editor (1955–1973) of the *American Journal of Psychology*, which Dallenbach had purchased from G. Stanley Hall in 1921 (see Evans 1987). Dallenbach served as a lifelong mentor to Bitterman, and the two remained very close until Dallenbach's death in 1971. Dr. Bitterman served on the psychology faculty at Texas from 1950 to 1955, followed by 2 years (1955 to 1957) at the Institute for Advanced Study at Princeton, NJ. The Institute was directed by Dr. J. Robert Oppenheimer, the famed physicist. In a letter recommending Bitterman for a NATO Fellowship, Oppenheimer described Jeff as “an unusually imaginative, fertile, active and clear headed psychologist, with a long record of good work done” and a “most agreeable scholar, clear, humorous, and with wide interests” (Oppenheimer, unpublished letter of recommendation, January 23, 1956). In 1957, he moved to Bryn Mawr College to become the department chairperson at the rank of associate professor. Bitterman was promoted to the rank of professor in 1961. He remained at Bryn Mawr until 1970, and then had a brief stint on the faculty of the University of South Florida (1970–1971). In 1971, Georg von Békésy recruited Professor Bitterman to the University of Hawai'i at Mānoa (Balsam 2012). von Békésy, who had been awarded the Nobel Prize in Medicine in 1961 for discovering the function of the cochlea in mammals, valued Bitterman's expertise in animal behavior to complement ongoing work at Békésy's Laboratory of sensory sciences. This research unit would later merge into the Pacific Biosciences Research Center and become known as the Békésy Laboratory of Neurobiology, for which Bitterman served as Director beginning in 1990. Dr. Bitterman retired and became an emeritus professor at the University of Hawaii in 2001.

Ten years into an active retirement from academic duties—he published at least 10 articles after 2001—Dr. M. E. Bitterman died on May 10, 2011 in San Francisco, CA. He is survived by his wife of nearly 44 years, Mary Gayle Foley Bitterman, three daughters (Joan, Ann, and Sarah

Fleming), and two grandchildren. Jeff's first marriage to Shirley Subke, mother of his two older daughters, ended in divorce. With Hawaii and California being his two residences for many years, his ashes were scattered in the Pacific Ocean (M.G.F. Bitterman, personal communication, August 23, 2020)

## Professional Contributions

Jeff Bitterman was a creative and tireless researcher and a prolific writer. Ten years after earning his Ph.D., Bitterman had already published 74 empirical papers, reviews, replies, and other works. His 1960 article, *Toward a comparative psychology of learning* (Bitterman 1960) was a classic in our field. He first challenged the field to be truly comparative: Updating the famous critique of Beach (1950) that psychology too exclusively studied rats and pigeons, to the exclusion of other animals, Bitterman wrote that “It is our willingness to *assume* that the process of learning is essentially the same in all animals which has been responsible in large measure for our concentration on the rat” (pg. 704, emphasis his). Rather than being a field built on assumption, Bitterman argued that comparative psychology should be true to its name and determine empirically whether the similarities (and differences) across species are merely superficial. He wrote, “The resemblances may, in fact, be more than superficial, but we shall never know until our level of inquiry becomes more than superficial” (pg. 705). Bitterman illustrated this willingness to study learning in a truly comparative way by discussing his own research with human adults and children, rats, fish, crabs, blowflies, and earthworms. To be sure, research with such a wide range of species presents methodological challenges seldom faced by the scientist studying learning by pigeons, rats, and monkeys. Accordingly, Bitterman (1960) described apparatus innovations for studies of these atypical animal species—just a few of the creative methodological contributions that characterized his remarkable career (e.g., Couvillon et al. 2003; Horner et al. 1961; Longo and Bitterman 1959, 1963; Pert and

Bitterman 1969; Potts and Bitterman 1968; Woodard and Bitterman, 1974).

Bitterman (1960) further described two broad (and complementary) strategies for comparative psychology. The first, and most common, follows the tradition of Yerkes, Harlow, and many other scholars who develop a particular standardized test, administer the assessment to multiple species, and then rank or otherwise compare the animals in terms of performance on the measure. The second, described favorably by Bitterman, involves the study of multiple species not by comparing performance on a particular test or apparatus, but rather by extensive investigation of the principles of learning of each species “as an attempt to determine whether learning in different animals may be understood in terms of the same set of laws or whether different laws are required” (pg. 707). Arguably, no comparative psychologist in history has better illustrated this second strategy of inquiry than Dr. M. E. Bitterman.

It is impossible to provide a comprehensive review of all of Bitterman’s research publications, but several other key contributions merit particular attention for the impact they had on the field and the ways that they illustrate chapters of Jeff’s scholarly interest. Bitterman (1965) investigated manipulations of hunger in spatial and habit reversal learning by rats and fish, not comparing absolute performance itself across species, but rather the functional models of the relation between hunger and learning by the two species. The primary distinction between rats and fish, according to this review, was that rats demonstrated progressive improvement in tasks such as habit reversal (whereas fish failed to demonstrate this tendency) and fish showed random matching in probability learning trials (a response pattern demonstrated by decorticated but not typical rats). Bitterman then extrapolated these findings to monkeys, pigeons, turtles, cockroaches, and earthworms. This paper has been highly cited, contributing to later comparative work (e.g., Cambraia 2019; Cauchoix et al. 2017; Bobrowicz 2019).

In 1975, Professor Bitterman again called out comparative psychology, criticizing its lack of theoretical foundation (Bitterman 1975). He

suggested that this deficiency was due to the failure of animal psychologists to explore evolutionary theories of learning, and to the overgeneralized acceptance of Pavlov’s and Thorndike’s work in comparing animal learning. As in his earlier critiques, Bitterman observed that there is a common assumption that all animals follow the same law of learning. Thus, two views contrast with regard to animal learning: the view stemming from Thorndike and Pavlov suggesting that learning among animals is fairly universal, and the second view related to ethology, treating animal learning as ecological specializations specific to each organism and its niche. Bitterman provided empirical examples to illustrate the significant differences between diverse animals, and echoed his earlier views on the ideal strategy for comparative psychology (i.e., by seeking to answer the question, “Can the performance of multiple species of animals be described by a common set of psychological principles?”). This frequently cited *Science* publication continues to be discussed as important for setting a research agenda for comparative psychology (e.g., Cabrera et al. 2019; Muszynski and Couvillon 2020).

Contemporary comparative psychologists probably best remember Professor Bitterman for the innovative studies that characterized the most recent chapter of his incredible research career: investigations of learning by honeybees (e.g., Bitterman 1976, 1983, 1996; Cooke et al. 2007; Couvillon and Bitterman 1980). His systematic studies, using paradigms from Pavlovian conditioning, habituation, discrimination learning, spatial learning and memory, and symbolic matching, established that bees demonstrate many similarities with vertebrates with regard to behavior and performance. For example, in terms of parameters of reward, honeybees demonstrated similar patterns of incentive contrasts that have been reported in studies with rats and opossums. Across publications, this research (much of it conducted with collaborator Patricia Couvillon) is impressive not only for the patterns of behavior demonstrated by the bees, but also for the number of standard comparative psychology testing paradigms, developed for vertebrates, that were



successfully employed with the insects. For all of these reasons, the honeybee publications are among Dr. Bitterman's most impactful, and continue to be extensively cited by other scientists who study bee behavior (e.g., Dawson et al. 2016; Daniel 2020; Muszynski and Couvillon 2020; see also Macphail 1987).

Across his career, Professor Bitterman generated over 300 publications in scholarly literature. This work attracted grant funding from the Office of Naval Research, the National Institutes of Health, and the National Science Foundation. For his contributions to psychological science, Dr. Bitterman was recognized with numerous honors, including fellow status in the American Association for the Advancement of Science and the American Psychological Association (APA), the latter of which recognized Bitterman with the D. O. Hebb Distinguished Scientific Contribution Award (2001, from APA Division 6) and the Ernest R. Hilgard Award for Lifetime Career Contribution to General Psychology (2004, from APA Division 1); membership in the Society of Experimental Psychologists, which awarded Bitterman their Howard Crosby Warren Medal (1997); the Humboldt Prize from the Federal Republic of Germany (1981); and the Regents' Medal for Excellence in Research from the University of Hawaii (1992). Across his career, Professor Bitterman was awarded more than 30 visiting professorships and research positions, including by the University of California at Berkeley, Princeton U., U. Pennsylvania, the Bermuda Biological Station, the Lerner Marine Laboratory, Naples Zoological Station (Italy), Moscow University and the Sechenov Institute of Evolutionary Morphology (USSR/Russia), U. Michigan, U. Brasila (Brazil), Campeche Biological Station (Mexico), U. California at Davis, U. Dusseldorf, Weizmann Institute of Science (Israel), Simon Fraser U. (-Canada), U. Freiburg and U. Frankfurt (Germany), U. Sydney and the Edward River Crocodile Station (Australia), Brain Research Institute (Yugoslavia), Georgetown U. School of Medicine, U. Auckland (New Zealand), and other universities in Japan, Spain, and Germany. Dr. Bitterman held Fulbright Professorships in Argentina and Germany and Humboldt Research

Fellowships in Germany. In addition to his long service as co-editor of the *American Journal of Psychology*, Bitterman was appointed to the editorial boards of the *Journal of Comparative Psychology*, *Animal Learning and Behavior*, *Psychonomic Science*, and *Behavior Research Methods, Instruments and Computers*. In these and similar roles, his expertise, insight, unyielding standards, and candor served to promote the rigor, sharpen the arguments, and challenge the assumptions of the field of comparative psychology.

Professor Bitterman also contributed to the field through his mentorship of students and collaborators. Some of the most important scholars in the field of comparative psychology have benefited from the opportunity to work with and learn from Jeff. For example, Dr. William Roberts, who earned master's (1962) and doctoral (1965) degrees under Bitterman's direction, described his advisor as a brilliant scientist and a charming man, but someone who did not suffer fools gladly—and who defined fools broadly (W. Roberts, personal communication, August 6, 2020). The razor-sharp intellect that kept Bitterman's research on the cutting edge of science could also lead to harsh and cutting criticism of others' work. Dr. Mauricio Papini, who was strongly influenced by Bitterman's published work (particularly the 1960 paper discussed above), communicated with Jeff for years and received fellowships to work with him. Dr. Papini remembered that Bitterman treated his advisees more like colleagues. For example, when Papini worked in Bitterman's lab, the senior scholar would ask Papini what his vision for certain experiments was. Papini explained, "the work we were doing in Hawaii was brand new, so we had to design the lab from scratch. I had a lot of freedom with the design" (M. Papini, personal communication, August 8, 2020). Reflecting also on Dr. Bitterman's capacity for incisive criticism, Dr. Papini notes that, to this day, he asks himself "What would Jeff say about this?" whenever he writes something speculative.

Professor M. E. Bitterman was a giant in the study of animal behavior. His scholarly interests and contributions spanned the animal kingdom, including arthropods and nonarthropod

invertebrates, crustaceans, fish, birds, and a wide range of mammals including human children and adults, and his methodological innovations served as catalysts and heuristic inspiration for the contributions of other scholars. If comparative psychology is to be truly comparative, and to produce a science of animal (versus of “some animals”) behavior, then Bitterman provided both the theoretical foundation and also an enduring example of how the discipline should proceed.

## Cross-References

- ▶ Associative Learning
- ▶ Associative Mechanisms
- ▶ Classical Conditioning
- ▶ Comparative Psychology
- ▶ Frank Ambrose Beach
- ▶ Invertebrates
- ▶ Reversal Learning
- ▶ William Roberts

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## Mosaic Cognition

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## Synonyms

Modular cognition; Mosaic brain; Mosaic evolution

## Definition

Mosaic cognition refers to the fact that the mammalian brain is composed of various functionally separate morphological systems which have evolved, in part at least, by means of processes of mosaic evolution (modular evolution) or selective evolutionary changes on individual parts of the brain that were (in some degree at least) developmentally and historically distinct.

## Introduction

It has been outlined that modularity (or a mosaic design) is found at every level of an organism's structure, including the brain, although anatomical and functional modularity should clearly be distinguished from each other, as they by no means always coincide. In addition, brain modularity exists in tandem with the tailored functional and developmental integration of brain structures, as modules link with other local (and even some remote) modules at various hierarchical levels of connectivity (Lieberman 2011). Perhaps the most basic modular distinction in any primate brain is that between the left and right hemispheres, which are in many ways functionally specialized (or lateralized).

It has been suggested that these two features of organisms taken together – brain modularity and the localized integration of these modules – contribute to the emergent property of covariant evolvability, as the flexible and independent nature of a modular system facilitates many

## Mosaic Brain

### ► Mosaic Cognition

small transformations over time, leading to the prevalence of so-called evolutionary tinkering. This evolvability feature is especially prominent in relation to the high degree of complexity of many brain structures, although it is debatable whether evolvability and modularity are capacities that are directly selected for. But, as distinct from the functional modules themselves, how exactly does mosaic evolution progress as a process?

## Mosaic Evolution

As has been explained about mosaic evolution, “brain structures with major anatomical and functional links evolved together independently of evolutionary change in other structures” (Barton and Harvey 2000, p. 1055), and evolution in these sub-structures also involves dynamic interrelationships among different brain components, this being a type of functionally independent mosaic progression. For example, the size of the neocortex – the largest and most recently evolved part of the cerebral cortex – shows a fivefold difference comparing primates and insectivores (insect-eating animals), even after scaling with the rest of the brain.

Mosaic evolution also involves various social and ecological (or environmental) factors that have different effects across distinct cognitive domains and in different periods of time, with cladistic branching patterns of evolutionary development being the result. These ecological contexts all vary both spatially and temporally. Mosaic evolution is the opposite of concerted or coordinated evolution, in which an individual part is evolved in correlation with the evolution of the whole of the structure that is involved.

## History of the Term

One of the earliest uses of the term “mosaic evolution” was in the field of paleontology, in relation to the well-known so-called missing link (or transitory form) of *Archaeopteryx*

*lithographica*. Charles Darwin had originally called the *Archaeopteryx* “that strange bird” (Darwin 1872 [1859], p. 284), while elsewhere it was labelled as a “misbegotten-bird-creature”: now it is regarded as the very first known bird. While the paleontologist Richard Owen had noted the “enigmatic character” of *Archaeopteryx* (Owen 1863, p. 44), he declared it unequivocally to be a bird soon after the first fossil of it was discovered in 1861. It is now known that birds are small flying theropod dinosaurs, but because of Owen’s skepticism about the overall theory of evolution, he downplayed the transitional significance of *Archaeopteryx*.

T.H. Huxley was the first commentator to use what he elsewhere called “comparative zoological reasoning” in order to explicitly highlight the intermediate nature of the skeletal form of *Archaeopteryx* (Huxley 1863, p. 85). In addition, Huxley compared *Compsognathus longipes*, a chicken-sized bipedal meat-eating theropod (another birdlike dinosaur), to *Archaeopteryx* as a dinosaur-bird intermediary, the two animals having some definite structural similarities/evolutionary homologies. As has been explained on this topic, nearly a full century later:

De Beer (1954) studied the five known [fossil] specimens and pronounced *Archaeopteryx* to be an example of what he termed “mosaic evolution.” In De Beer’s view, *Archaeopteryx* is an anatomical mosaic because it presents a mixture of character states that are (1) “reptilian” (e.g., it has teeth and a bony tail), (2) intermediate between reptilian and birdlike (e.g., its weakly developed sternum), and (3) fully birdlike (e.g., it possesses feathers). (Eldredge 1989, p. 49)

Sometime later, the mosaic evolution concept was further applied to the mandible of *Archaeopteryx*, which was also seen to have both reptilian and avian characteristics (Cracraft 1970). Here the term “mosaic evolution” is being used to refer to an anatomical mosaic of physical features that had their evolutionary origins in multiple animal taxa. The concept then became popular within the field of macroevolution as specifying independent evolutionary change of various portions of the phenotype (Stanley 1979).

## Variant Meanings

More recently, various different variant meanings of the mosaic evolution concept have been articulated, for example, as follows: (1) morphological instability in a certain phase of a branched phylogeny, or the staggered evolution of a mosaic of different ancestral and descendent characteristics; (2) multiple trajectories of the same trait in a branched phylogeny, or the same trait appearing in different species over time; and (3) a trait itself as a mosaic of sub-traits, or a combination of different functional elements (Parravicina and Pievani 2019). Meaning number one is by far the most common in the literature but the other two meanings sometimes appear as elements of wider analyses.

Elsewhere, mosaic evolution has been defined somewhat differently as “the evolution of different components of a phenotype at highly unequal rates” (Lock and Peters 1996, p. 372), a conception that can here be termed temporal mosaic evolution. A related concept of modular evolution has been outlined, in which selection mechanisms act on each carrier of modular-contained information at various levels of biological organization and complexity (Vinicius 2010). Finally, evolutionary change in one body part without any simultaneous changes in other body parts is a simpler definition that is sometimes encountered. These are all variants on what might be termed the functionally independent morphology concept, given previously as mosaic evolution meaning number one.

It has correctly been pointed out that mosaic and concerted evolution are not mutually exclusive, as both can occur in relation to different physical features (D’Aniello et al. 2019), similar to how domain-specific and domain-general cognitive mechanisms are also not mutually exclusive. In addition to considering the brain of *Homo sapiens*, there are various different neuroanatomical components and structures that are found across different animal species; for example, mammalian brains are composed of some different components to those of birds (van Horik et al. 2012). This latter point leads neatly into a consideration of mosaic brain evolution, rather than the more general concept of mosaic evolution.

## Mosaic Brain Evolution

Mosaic brain evolution is simply mosaic evolution applied to the various regions of the brain, which has been categorized as “the most modular part of the body” (Lieberman 2011, p. 183). One of the first researchers to implicitly identify temporal sequences or “successive waves of circumferential differentiation” in brain evolution was Raymond Dart, who identified subdivisions in the reptilian brain such as the oldest identifiable neocortex (Dart 1934). This then led to the idea developed by Paul MacLean of the so-called triune human brain, with three separate evolutionary layers: (1) the reptilian or primal brain (brain stem and midbrain); (2) the paleo-mammalian or emotional brain (limbic system); and (3) the neo-mammalian or rational brain (neocortex), although this is now known to be a significant oversimplification of *Homo* brain structure (Ploog 1971).

One of the first researchers to explicitly apply the mosaic evolution concept to the brain was Ralph Holloway, who investigated the evolution of hominid brain size and how this could be measured in relation to “interpretations of time-related shifts in the nature of hominid mosaic evolution” (Holloway and Post 1982, p. 73). Holloway concluded that neuronal structural reorganizations and brain size increases likely involved each other and/or occurred in tandem, implying that mosaic cognition had both overall volume and specific component features.

As has been explained, the contemporary hypothesis of mosaic brain evolution involves selective forces acting on specific regions of the brain, whose adaptive reactions do not then involve other parts of the brain (D’Aniello et al. 2019). Correspondingly, individual elements of the brain are grouped within structurally and functionally separated neural systems that are devoted to particular cognitive tasks. For example, as has been outlined regarding the neural generation of emotion: “emotions can be decomposed into more basic psychological processes that correspond to large-scale networks in the brain” (Fugate et al. 2014, p. 44). Taken as a whole, these neural networks constitute a set of reference areas for particular emotions.



Specific to this is a hypothesized principle of proper mass: the mass of neural tissue controlling a particular cognitive function is appropriate to the amount of information processing involved in performing that function (Falk 2002). It has been concluded about the processes influencing brain enlargement that “primate brain structure is largely driven by selection on sensory and cognitive specializations that develop in response to divergent sociological niches” (DeCasien and Higham 2019). Correspondingly, different primate brain components have altered their size to varying extents, at varying times and in varying ways in relation to these niches (Barton 2007). In addition, selection processes can act on various different features of the brain: the number of neurons as illustrated by overall brain size and surface structural convolutions, and then the level of connectivity of neurons and the corresponding connection patterns (Stone 2007), this mirroring Holloway’s previously articulated distinction between volume and component.

Of course, just because that human brain is divided into numerous separate systems, does not mean – in and of itself – that mosaic evolution rather than concerted evolution was the dominant force at work in its recent evolutionary phases. However, there is some good evidence that mosaic evolution was indeed a force in operation to a significant degree. For example, one study on patterns of brain covariation (correlated variation) in chimpanzees and humans concluded that both types of brain had modular structures and that spatially adjacent regions in both types of brain covaried much more than spatially separated regions (Gomez-Robles et al. 2014).

Another study of the avian cranium concluded that it was highly modular, with the presence of seven independently evolved anatomical regions (Felice and Goswami 2018), while a study of a series of primate brains concluded that corresponding brain regions were expanded in correlation with both diet quality and either nocturnal or diurnal behavioral needs (DeCasien and Higham 2019). In general, the existence of some degree of mosaic brain evolution is now commonly accepted in the literature on cognition, although this does not mean that concerted

evolution of some closely interconnected brain systems has never occurred. In the case of primate brains, a mosaic of neurological systems is most extensively developed within the cerebral cortex.

## The Cerebral Cortex

A key evolutionary development in the higher primates was a large increase in the size of the cerebral cortex (the outer surfaces of the two cerebral hemispheres) and the underlying thalamus; in *Homo sapiens*, the cerebral cortex is 76% of brain weight and about 0.23 m<sup>2</sup> in area, whereas in the gorilla it is only 68% of brain weight (Holloway 2000). The cerebral cortex is composed mostly of neocortex, the overall size of which in primates has been shown as coevolving with group size and language use (Dunbar 1993) and which is found only in mammals.

Neocortex has its own distinct six-layered structure and numerous layer-specific connections, and it is divided into three basic parts: sensory, motor, and association areas, with numerous mosaic subdivisions. As has been explained, the *Homo sapiens* cerebral cortex contains relatively more parietal and temporal lobe association cortex compared to other primate species, this association cortex facilitating complex intermodal cognitive functioning (Holloway 2000).

Consequently, the cerebral cortex plays a central role in various different aspects of *Homo* cognition, including many of the complex abilities that have reached their apogee in *Homo sapiens* such as communication skills, tool manipulation, and abstract thought processes; hence its evolution was closely linked to the development of the higher *Homo* cognitive functions. The neocortex plus the basal ganglia is sometimes called the executive brain (Stone 2007). The thalamus operates as the communicative sensory gateway to the cerebral cortex for subcortical regions of the brain.

The cerebral cortex as a large collection of neural circuitry is perhaps the most significant brain feature that separates *Homo sapiens* from the earliest *Australopithecines*. In terms of the forces that may have driven its mosaic evolution,

various different hypotheses have been advanced in the literature as explanations. The most commonly encountered are the Machiavellian intelligence hypothesis (social manipulation abilities), the technical intelligence hypothesis (tool/shelter construction abilities), the social intelligence hypothesis (group living abilities), and the cognitive buffer hypothesis (insurance against environmental variation), but some staggered combination of them is another definite possibility. Social transmission intelligence as a specialized behavioral adaptation has been directly linked to mosaic brain evolution, but behavioral flexibility and problem-solving ability can also be so linked (Brown 2008; Vonk 2016).

## Mosaic Cognition

So far the implicit assumption has been made that mosaic brain evolution is synonymous with “mosaic cognition” – which is the actual title of this entry – but might it not actually be so? Mosaic cognition – the existence of numerous functionally separate neurological systems – has (in an important sense) been generated by mosaic brain evolution, and hence it is morphologically and evolutionarily inseparable from it. However in perceptual terms, the fact that cognition takes place across a mosaic of different neural systems could have important consequences for how it operates in performance and reliability terms.

In reality, “perception” is much more accurately described as a series of separate and neurologically distinct perception processes – the modularity of perception – and this fact needs always to be kept in view. The nature of mosaic cognition means that there must also be specific neural systems devoted to combining different types of perception-derived information (as a form of meta-cognitive synthesis) when this is required for additional computational or behavioral reasons. This is a particular type of meta-cognitive processing and regulation and may involve the functioning of several hierarchically organized interlinking neural networks (Smith et al. 2018; Gibson 1990).

For example, auditory and visual perceptions are often employed in tandem: when finding the precise source of a sound in a visual field by listening for the direction of the sound and checking for other visual clues to its origin for instance. In turn this means that the possibility of generating meta-cognitive errors may exist through these types of combinations, at least in some instances. Individual perception systems are also subject to various types of processing distortions and perceptual illusions, as the central nervous system sometimes makes educated guesses using only partial data plus a degree of extrapolation. In these senses, mosaic cognition can be employed as a general term that refers to various types of meta-cognitive combinations of the inputs from individual neurological and perceptual systems.

## Conclusion

In this entry, three distinct but related concepts of mosaic evolution, mosaic brain evolution, and mosaic cognition have been presented in outline, and some of their connections have been traced. The link to wider anatomical modularity and localized functional integration patterns has also been briefly considered. However, there is a wider sense in which all living organisms are constituted from mosaic morphological systems. As has been explained in this respect:

The fact that genes influence and are influenced by behavior is exactly what an evolutionary psychologist would expect if information-processing bundles are the products of a mosaic evolution at different levels (genes, cells, neurons, structure, cognitive mechanisms, and outward behavior) . . . [all] organisms are not necessarily cohesive wholes but rather bundles of interests with common and conflicting goals. These bundles are subject to selection and include catalytic reactions, biochemical cascades, neuronal firing, structural components, neuro-cognitive activation, behavior, and learning (individual to social). (Brown 2008, pp. 130–131)

Multilevel mosaic evolution is, therefore, a new meta-level concept that arises out of the fact that in the development of such organic bundles of interests, mosaic cognition is one

expression of the various different types of mosaic evolutionary change.

## Cross-References

### ► Technical Intelligence Hypothesis

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## Mosaic Evolution

### ► Mosaic Cognition

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## Mosaicism

### ► Mosaics

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## Mosaics

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## Synonyms

### Mosaicism

## Definition

Mosaics describe a mixture of two or more cell populations with different genotypes in one individual.

## Introduction

Mosaics were discovered by German-born American geneticist Curt Jacob Stern in the early 1930s showing that genetic recombination not only happens during meiosis but can also take place during mitosis resulting in somatic (body) mosaics containing genetically distinct types of tissue (Stern and Sekiguti 1931; Stern 1936). The term “somatic mosaicism” was later coined in the 1950s by C. W. Cotterman.

## Genesis of Mosaics

Genetic mosaicism can derive through different mechanisms like anaphase lag (failed connection

of chromosomes (meiosis) or chromatids (mitosis) to the spindle apparatus), chromosome nondisjunction (improper segregation of homologous chromosomes or sister chromatids), endoreplication (replication of nuclear genome in the absence of cell division), and mutation in one cell during development (mutation only passed on to daughter cells) (Fitzgerald et al. 1979). Chimerism is often mistaken as genetic mosaicism, where two different genotypes arise during early embryonic development by fusion of more than one fertilized zygote resulting in two or more genotypes (which is similar to mosaicism). Mosaicism can be divided into somatic or germline/gonadal (restricted to gametes) mosaicism. Both can be individually present or occurring at the same time.

## Somatic Mosaicism

Somatic mosaicism describes somatic cells with more than one genotype most commonly arisen through mitotic errors from a single fertilized egg cell. They are prevalent in early and late phases of (human) life and underlie various mechanisms. Mitotic recombination or somatic crossover are basic mechanisms for mosaic tissue. Somatic mosaicism is common in embryogenesis through retrotransposition (position change of DNA sequence within a genome creating or reversing mutations) as undifferentiated cells contain long stretches of unmethylated genomic regions and are therefore more susceptible to transposable elements (De 2011). There are further endogenous and exogenous factors contributing to somatic mosaicism like DNA polymerase slippage and unbalanced chromosomal segregation (endogenous) or UV radiation and nicotine (exogenous). In addition, increasing DNA damage and DNA copy errors through life naturally increase mosaicism and therefore could lead to cancer development. Somatic mosaicism is also commonly found in cells underlying chromosome abnormalities like trisomies or Turner’s syndrome (around 30% of cases show mosaicism). Although most cases of trisomy develop during meiosis, there are mitotic cases through nondisjunction with occurrence in only a few cells with a loss of a

chromosome in these trisomic cells. Consequently, these patients, for example, with Klinefelter syndrome (46/47 XY/XXY mosaic), with some XY cells containing the normal number of 46 chromosomes and some containing XXY and 47 chromosomes show a milder phenotype than people with full trisomy (Strachan and Read 1999). Rever- tant somatic mosaicism as an opposite is a rare nondeleterious mitotic recombination event leading to a spontaneous correction of the mutant.

## Germline Mosaicism

Germline mosaicism or gonadal mosaicism occurs when more than one genotype is found specifically in gametes. This can derive from a mutation arising after conception (Orva and Orva 1998) or through epigenetic DNA methylation (Laurentino et al. 2014). Germline mosaicism can lead to hereditary carriers of diseases which show no phenotype themselves. Gametes are difficult to obtain and in pure germline mosaicism the somatic cells should not contain the mosaicism which makes diagnosis troublesome for genetic counselling. Various diseases are reexamined for hereditary germline mosaicism as disease onset was often mistaken for being induced through *de novo* mutations (Armaroli et al. 2015). As the nature of mutations is sporadic the frequency of germline mosaicism is not known, although higher occurrence is given with earlier mutation during development.

## Experimental Biology

Mosaics allow for multifold purposes in biological research. They can be intentionally created in a variety of model organisms and are powerful tools for studies of biological systems. Naturally, mosaics are valuable for experimentation in gene studies during early development (transplantation from blastula stage embryo into another one with different genotype) to obtain adult organisms with given perturbations. In addition, genes can be examined for tissue specificity, requirement for specific cell types, and cell autonomy

(if unaffected cells do take on the specific phenotype through environment differentiation).

Mosaics are commonly created in the model organism of the fruit fly (*Drosophila melanogaster*) through mitotic recombination originally induced through irradiation. The resulting DNA strand break could result in homozygosity for one of the two alleles leading to mutant cell clones after replication rounds. Modern methods incorporate transgenes selectively through Flip Recombinase (FLP) which recognizes Flip Recombinase Target (FRT) sites and allows recombination between them. CRISPR/Cas9 as a state-of-the-art system for gene editing creates mosaic mutations as an unwanted side effect with its underlying mechanism still elusive. Recent studies from Abyzov et al. (2012), for example, in induced pluripotent stem cells (iPS cells) show in addition that somatic mosaicism happens frequently and that the cells of origin for reprogramming (e.g., skin cells) show mosaicism as well, leading to differences between iPS cells and cells of origin (due to differences in fractions of cells).

## Conclusion

Mosaics consist of two or more cell populations with different genotypes in one individual. The underlying mechanisms are manifold and can be endogenous or exogenous and occurrence can be in germline cells (gametes) or somatic cells or both. Mosaicism can be undetected, have mild implications, or lead to disease phenotypes. In addition, mosaics are commonly used in experimental biology for studies of genes in model organisms or whole biological systems.

## Cross-References

- ▶ Alleles
- ▶ Chromatid
- ▶ Chromosomes
- ▶ Crossover
- ▶ Embryo
- ▶ Genotype



- [Homozygosity](#)
- [Nondisjunction](#)

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## Motivation

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## Causality and Motivation: What Moves Behavior?

Motivation is a construct that refers to the underlying causes of behavior. These causes have been analyzed as mechanisms that explain how behavior is controlled and changes, and the survival and reproductive advantages of behavior. Motivation

is often understood as a state that controls behavior. It is temporary and may be variable and reversible. This is one of the central aspects of the construct, as it accounts for the immense variation there is in the direction and scale level in all the different dimensions of behavior among individuals.

Niko Tinbergen (1963) proposed four questions to address the causes of behavior at these two levels: proximate and ultimate. These questions refer to mechanistic, developmental, functional, and phylogenetic causes and continue to be a useful guide in understanding the different types of factors that explain behavior.

Much of psychology literature has centered on proximate causes of behavior, describing in great detail physiological, developmental, cognitive, and social phenomena, associated with motivation. Psychology and other social sciences have placed a great emphasis on how changes in the environment affect our behavior, and how behavior changes over the lifespan of individuals, leaving the study of ultimate causes of behavior mostly unexplored. Similarly, evolutionary theorists emphasize ultimate causes and often ignore proximate causes of behavior that explain mechanisms common to different species. An approach integrating proximate and ultimate causes is very important for a clear and complete understanding of behavior (Wong 2000). An integrative, as opposed to a reductionist approach is more likely to cross-fertilize any discipline in this time of high specialization.

Motivation is inferred from behavior as it cannot be directly observed. This means that different measures may be used as indicators of motivation. For example, choice, magnitude, latency, frequency, and duration of response are all measures that have been used to determine the level of motivation of an individual. No single unit of behavior can be used as a general measure of motivation, as the response quality and structure (i.e., sequence and topography) may vary across different behavioral systems.

Motivational systems can be regulatory or non-regulatory. Regulatory systems are based on homeostatic mechanisms and usually control life processes such as feeding, thirst, and temperature

regulation. Most of the literature on motivational factors of behavior has mainly considered the feeding system. As feeding is a regulatory system, some methodological problems may appear when motivational mechanisms are to be studied. For instance, in order to study motivation, we often use an instrumental paradigm; under those conditions, changes in the balance of calories, fat, glucose, or water are induced by the experimenter, and, through its behavior, the subject is able to restore that balance. Deprivation must be carefully planned if a stable and motivated response is to be obtained without the subject's health being put at risk. In addition, any measure of behavior must be carefully planned in order to properly evaluate the motivational value of the stimulus, because as the subject becomes satiated there is change in the value of food, as well as the value of any stimulus associated with it. This issue, however, is not limited to regulatory systems and constitutes a challenge in any motivational study.

Nonregulatory systems are not vital in maintaining homeostatic levels of nourishment, excretion, or systems maintenance but can be powerful sources of motivational control of behavior and are also essential for the individual's fitness: survival and reproduction. For instance, sexual behavior is nonregulatory, yet it is one of the most powerful sources of motivation for species that reproduce sexually. Similarly, defensive behavior is nonregulatory but it is crucial for survival, and consequently, a powerful source of motivation.

Historically, motivational concepts such as instinct and drive have received much attention and have been used to explain the source of forces that account for the magnitude, timing, and direction of behavior. Those concepts resulted in controversies derived from theoretical approaches with differential emphasis on nomothetic vs. idiographic explanations, mechanistic vs. cognitive approaches, innate vs. learned behavior, and external vs. internal influences.

Instinct refers to an organized behavioral pattern, common to the members of a species, and independent of learning and experience. The concept was very popular early in the twentieth century as an explanation for behavior that was not

clearly explained by environmental influences. Konrad Lorenz and Niko Tinbergen developed models of motivation based on the concept of *fixed action pattern*, a development of the idea of instinct. These models, however, were not supported by behavioral and physiological evidence and are not currently driving research in the study of animal behavior, despite their usefulness for the development of behavior theory during the twentieth century (Burghardt and Bowers 2017).

The concept of instinct was the subject of controversy between ethologists and comparative psychologists. Behavioral psychologists questioned the distinction between “innate” and “acquired”, pointing to a series of findings on development that showed that the criteria used to distinguish between the two were not empirically supported, and the influence of genetics on behavior was expressed through developmental processes, far more complex than argued by nativistic theories. We now have extensive evidence showing that species-typical behaviors appear at times different from birth, that experience and learning influence this behavior in indirect ways, that isolation does not warrant exclusion from environmental influences, including the stimulation of the individual itself, and that the so-called instinctive behavior is plastic in response to environmental variation. New developments also provide hypotheses on how learning may become assimilated and develop as “innate” behavior, and how differences in motivation and expression of behavior are often more the result of epigenetic than genetic differences (e.g., Jablonka and Lamb 2005). A better understanding of the role of development in the integration of genetic input and experience has built on the concept of instinct refining its use in current scientific explanation of behavior.

After the debate on instinct, psychologists adopted the concept of “drive” as an internal force activated by deprivation that energizes a motivational system, resulting in the performance of an organized set of behaviors in response to specific environmental stimuli. Many authors considered drive as the force moving an animal to obtain a consummatory stimulus; that is, the motivation for appetitive behavior. The empirical

evidence, mostly based on hunger, thirst, and circadian rhythms, was difficult to interpret and the concept grew confusing because different authors used it as behavior, as a motivational construct, or as a physiological state; however, the three meanings were often not in agreement in a single set of observations. Despite the efforts of theorists like Clark Hull to make effective use of the concept, it was vague, and not easy to integrate with the knowledge of mechanisms for different motivational systems (Bolles 1975, p. 217).

A universal measure of motivation is the approach/withdrawal response thought of as an organizing principle to understand biphasic processes in all phyletic levels, allowing the integration of simple and complex adaptive responses. In addition to approaching or withdrawing, motivated behavior is often expressed through choice. These and other more complex responses are expressed as an organized and hierarchical structure that may be inferred from the observation of behavior in time and space. This has been recognized in ethology and comparative psychology and has given place to a scheme of organized behavior that integrates the role of genetic and environmental information through cognitive mechanisms such as perception, memory, learning, and motivation (Shettleworth 2010, pp. 33–35).

A simple organization of motivated behavior uses two categories: appetitive and consummatory responses. Appetitive behavior increases the probability of a functional outcome and includes the display of some preparatory responses, as well as providing signals to competitors or conspecifics. In contrast, consummatory behaviors terminate a motivational sequence and relate more closely in time and space to the functional role of behavior. For example, in feeding, appetitive responses include an increase in motor responses, general search for feeding areas, prey/food selection, and others. Consummatory responses include capture, food handling, chewing, and food ingestion. The use of this simple model to understand the behavioral organization of the sexual response shows a more complex sequence that includes an additional category of responses

linking appetitive and consummatory responses: precopulatory responses (Pfaus et al. 2001). Appetitive responses include motor activation, searching, and grooming; precopulatory responses include arousal, solicitation, pursuit, and in general courtship responses; and copulatory responses include mounting, copulation, lordosis, squatting and other receptive behaviors, and orgasmic responses such as ejaculation. Appetitive responses are more flexible and more likely to be influenced by learning, whereas consummatory responses tend to be more species-specific and stereotyped (Burghardt and Bowers 2017). The appetitive-consummatory distinction has been useful to organize empirical questions at all levels of Tinbergen's explanatory taxonomy.

### **Sexual Behavior: An Integrated Model for the Study of Motivation**

In this entry, sexual behavior will be used to illustrate the main concepts of motivation. Unlike feeding or drinking, sexual behavior is not regulated. Most of the literature on regulatory systems, such as feeding, is very detailed in explaining behavioral and physiological mechanisms, but mainly centers on the proximate causes of behavior; thus, showing the possibility of integration between proximate and ultimate causes of behavior is a more challenging task. Sexual behavior, a nonregulatory system, allows for this possibility.

All organisms have evolved and behave to maximize reproductive success (Wong 2000, p. 221). Given the variety of ecological conditions in nature, there are multiple solutions to this general principle of evolution. Sexual reproduction is one solution to the reproductive problem; it has been argued that the main advantage of sexual reproduction is its capacity to produce variability in offspring that allows them to respond to variations in environmental conditions.

Males and females of many species show differences in morphology, physiology, and behavior. Darwin developed Sexual Selection Theory to explain the evolution of such dimorphism. According to his theory, certain dimorphic traits result from two processes: competition among

same sex individuals for sexual partners (intrasexual selection) and preference for certain characteristics in the opposite sex (intersexual selection).

The combinations of these processes derive traits that may be incompatible with traits resulting from natural selection. Sexual selection not only results in exaggerated morphological traits but also in behavioral specializations such as acoustic signals, visual displays, and olfactory cues that attract potential reproductive partners (Alcock 2001, pp. 348–351).

Differences in the characteristics of sexual gametes between males and females have been thought to promote sexual differences in reproductive behavior. Limited quantity and immobility of female sexual gametes make them a valuable resource for males, leading to the evolution of differential reproductive strategies. The interaction of male and female strategies results in a variety of mating systems, associated with variations in motivation and behavior (Wong 2000, p. 17).

### **Sexual Differences in Reproductive Behavior**

The differences between male and female sexual behavior have often been described in terms of their relative contributions to the production and rearing of offspring. This approach has emphasized the role of males in courtship and copulatory behavior, and the role of females in nesting and caring for their offspring. Nevertheless, both males and females participate in most aspects of sexual reproduction, and thus, a comparison of their roles, behavior, and motivation should be done on the basis of equivalent categories of behavior. Frank Beach (1976) developed a taxonomy of sexual behavior that can be used to analyze differences between males and females using similar criteria. Sexual behavior is expressed in attractivity, proceptivity, and receptivity which represent the interrelated stages of reproductive interaction between males and females. They have some correspondence with the previously presented taxonomy of appetitive, precopulatory,

and consummatory behavior; despite a tremendous variety in these characteristics among taxonomic groups, this categorization is helpful to understand male-female differences in sexual behavior and their underlying causes.

*Attractivity* is inferred from the behavior of the pair mate and represents the value of an individual as a reproductive partner. *Proceptivity* refers to responses indicating the attraction to a potential sexual partner; some indicators are orientation, approach, solicitation, and contact behavior. Courtship responses are generally considered proceptive behavior and tend to elicit proceptive and receptive responses in the mating pair. *Receptivity* refers to consummatory responses to solicitation and stimulation by the sexual partner.

A behavioral repertoire in all three categories has been described both in males and females across many species, and differences in their expression are observed between both sexes. It has been found that female attractiveness can be determined by characteristics that indicate reproductive condition and their capacity to invest and care for their offspring. Male attractiveness can be determined by characteristics indicating their ability to provide direct resources (i.e., protection or parental care) or indirect ones (i.e., genes) to the female or the offspring (Alcock 2001, pp. 341–353). Hormones may affect the level of attractiveness of an individual by influencing both their appearance and their behavior. Hormonal fluctuations are associated with changes in the coloration of feathers, vocal patterns, and other secondary sexual characteristics (Adkins-Regan 2005, p. 61).

The expression of proceptivity is also different in males and females. For instance, it has been observed that male Japanese quail (*Coturnix japonica*) approach and remain close to a window that provides visual access to a female conspecific, but under equal conditions, the same response was not detected in females (Mills et al. 1997). Nonetheless, when females are visually exposed to a male quail and later removed from an experimental arena, females are more likely to go to the area where the male was previously seen (Gutiérrez and Domjan 2011). A similar effect has been observed in rats (*Rattus norvegicus*), especially when females have been allowed to pace

their approach responses to males (see Pfaus et al. 2001). Frequently, the issue at hand is that selected behavioral measures can sometimes be insensitive to variations in motivation and may be mistakenly interpreted as the absence of motivation, rather than as a methodological artifact. Along these lines, it is necessary to explore multiple behaviors to identify measures of motivation. For example, in addition to approaching an area where a male has been previously observed, other proceptive behaviors (e.g., pacing in front of males) have been identified in birds and rodents (Carter 1992, p. 73). Hormones may also influence levels of proceptivity. For instance, in female mammals, elevated concentrations of estrogen increase their sexual interest in males; females approach males and show precopulatory behaviors toward them (Carter 1992, p. 72).

Receptivity may be expressed in either an active or a passive way and may also be affected by hormonal changes (e.g., Lee and Gorman 2000). Active receptivity has been studied in the lordosis response in rodents and other mammals as well as squatting in birds. Both lordosis and squatting are described as the female lowering her body, raising her back toward the male, and remaining in this position long enough to facilitate the mounting and sperm delivery into the female reproductive tract. Lordosis and similar responses such as squatting are indicators of motivation of the female toward sexual interaction. A measure called the Lordosis Quotient has been developed to measure the magnitude of such responding (Carter 1992, p. 74); related measures might be developed for squatting and other receptive responses. Passive receptivity is interpreted as the female remaining in an area where a male is present. The proper evaluation of this response, however, requires that the female is not constrained by other variables such as essential resources, offspring, or other factors that motivate her to remain in the area, confounding sexual and other sources of motivation.

Other reproductive behaviors such as response to courtship and nest construction are often seen as receptive behaviors. For instance, in ring-necked doves the reproductive sequence starts with the male courtship behaviors directed towards the female. The female responses to



courtship are followed by the selection of a nesting site, building of a nest, and copulatory interaction. After this interaction, the female lays eggs and starts the incubation process (Silver 1992, pp. 417–418). Although the behaviors of males and females previously described are categorized as receptive behaviors resulting from the social stimulation produced by the reproductive partner, it is not always easy to differentiate between proceptive and receptive responses due to the fact that the sequence includes behaviors common to both stages of sexual behavior.

Male sexual responses in many species are more easily observed and measured than female sexual responses, and sexual behavior is often studied in the laboratory in situations in which subjects are deprived of sexual interaction. Under these conditions, males tend to copulate readily after being presented with female partners, whereas females do not show the same type of response or immediate proceptive or receptive behaviors. Furthermore, under laboratory conditions, females are not usually given the opportunity to avoid or escape exposure to a male or to select their mate. Therefore, lack of female responsivity can be misinterpreted as lack of motivation. However, changes in experimental protocols to study sexual behavior have clearly shown that females are motivated to sexually interact with males, but their behavior is often subtle and depends on their possibility to control their access to males. Thus, the understanding of differences between males and females should take into account possible differences in expression rather than the level of motivation (Gutiérrez and Domjan 1997; Pfaus et al. 2001).

## Sexual Competition and Mate Choice

According to Sexual Selection Theory, males tend to be more competitive than females, and females tend to be more sexually selective than males. This seems to be the case in polygynous species, but in relatively monogamous species, these differences tend to decrease, and competition and selection become relatively common in both sexes. Competition and choice complement each other, and result from a balance of interests and

strategies of males and females to increase their fitness. Courtship behavioral patterns play a special role connecting those interests. They attract a mate, provide information to the selecting partner, elicit sexual responses, and synchronize those responses as well as the physiological mechanisms supporting them (Ryan and Jordan 2017).

Sexual competition, courtship, and mate selection result in behaviors that are indicators of sexual motivation; thus, the mechanisms responsible for these responses are ultimately, motivational ones. Whether competition and selection directly result in measurable gains for males and females is not always easy to determine empirically; however, courtship and mate choice lead to sex and its rewarding properties. Sometimes, motivational systems may influence behavior in different directions. The resulting trade-off may increase mating success, but at the same time, it may decrease survival of the individual (Wong 2000, p. 222). In male-male sexual competition, for example, males sometimes incur high risks of predation, injury, or starvation.

Male-male competition may occur before, during, and after copulation. Competition at each of these moments is motivationally controlled by mechanisms at proximate and ultimate levels, as will be explained later in this entry. In some species, males compete for and defend a territory during the mating season. Females then select males on the basis of the quality of those territories. For example, Japanese quail form territories at the beginning of the reproductive season and females select a male to form a pair during the season (Mills et al. 1997). Male-male competition can take other forms as well, including scramble competition, resource defense, harem defense, social hierarchies, and mate guarding, among others (Alcock 2001, pp. 327–340).

Male and female mate selection are often established according to different criteria; females select males on the basis of resource production and physical as well as behavioral traits associated with survival and reproduction capacity, whereas males select females based on their reproductive capacity and health. In species in which both males and females provide parental care, reciprocal mate selection is common (Ryan and Jordan 2017). In any case, the selective partner must

compare among possible mates, based on information provided by physical and behavioral characteristics. In some cases, the information is provided by the results of a contest between competitors. In other cases, however, the information provided is an indirect measure of the quality of the sexual partner. For example, pied flycatchers (*Ficedula hypoleuca*) prefer males with a jet black and white plumage that show better parental care, over males with a less defined plumage color and lower parental qualities. Similarly, male house finches (*Haemorrhous mexicanus*) with a bright red patch in their plumage are more likely to resist parasites and are preferred over males with a duller plumage (Alcock 2001, pp. 345–346). The relative roles of direct and indirect benefits on motivation of mate choice and sexual behavior constitute an unresolved issue and require empirical evaluation.

The genetic and epigenetic mechanisms of sexual selection have not been extensively studied. For some species, mate choice is likely the result of developmental processes. Animal behavior researchers have described the role of early learning in mate selection in a number of species, especially birds. For example, female Japanese quail prefer males with some phenotypical similarity (cousins) but not closely related males (brothers) (Bateson 1982). It is unclear which male physical characteristics determine this decision. In a more recent study, it was found that in a choice situation, female quail preferred males different from those they had previously encountered during rearing (Pérez and Gutiérrez 2006).

Motivation for and choice of mates might also be influenced by social factors. For instance, female quail are more likely to choose males that have been selected by other females, and these males are more likely to fertilize the female's eggs than nonpreferred males (Persaud and Galef 2005).

Sexual selection may influence other reproductive behaviors and physiological responses in the female. For example, females of a number of bird species are likely to make a larger investment on offspring of a more attractive male, before and after hatching. Female zebra finches (*Taeniopygia guttata*) have been found to lay eggs with higher levels of testosterone when those eggs have been

fertilized by a preferred male (Alcock 2001, p. 341). The proximate mechanism for this effect seems to be activated during the yolk phase, and it results in increased growth and begging rates after hatching, giving chicks an edge in their survival and reproduction. This phenomenon has not been extensively explored but shows motivational effects on developmental and evolutionary mechanisms of behavior.

## The Role of Learning in Sexual Motivation

As many other motivational systems, sexual behavior is more likely to be effective if flexible to changes in the environment. Learning provides the basis for that flexibility in several ways. As previously pointed out, appetitive responses (and even consummatory ones) are likely to be influenced by learning. Changes in responsivity to stable sexual stimuli (i.e., habituation and sensitization), capacity to predict a sexual partner (i.e., Pavlovian conditioning), changes in behavior to the environment in order to obtain an outcome (i.e., instrumental learning) and learning from others to select a sexual partner or a sexual response (i.e., social learning) have all been investigated using animal and human models and have important implications on how we understand the role of motivation in sexual behavior.

Sexual learning phenomena have been investigated in a variety of species, including insects and other invertebrates, fish, reptiles, birds, and mammals (see Domjan and Holloway 1998, for a review). Sexual learning has been studied following a Pavlovian conditioning procedure. Hollis et al. (1989) studied the conditioning of sexual behavior in the blue gourami fish (*Trichopodus trichopterus*). They presented each fish of a male-female pair with a light followed by visual access to the other fish. As a consequence, both males and females showed an increase in frontal displays; males increased their courtship appeasement responses and decreased aggressive responses to their pair-mate. This suggests that learning has a functional effect and provides an adaptive value to individuals who are able to

predict the presence or availability of a conspecific.

Pavlovian conditioning makes appetitive and consummatory responses more effective. For example, male rats copulate quicker if they encounter a copulation partner after the presentation of a conditioned stimulus previously paired with exposure to a female (Krause and Domjan 2017). Similarly, male quail presented with a conditioned stimulus preceding the release of a sexually responsive female, copulate faster and more often in a sexual competition situation than a male without the same learning experience (Gutiérrez and Domjan 1996).

The role of learning on other competition situations has also been explored. The effect of dominance on reproductive access has been extensively documented (Alcock 2001, p. 331); the clearest effect is that dominant males of many species, which tend to have more access to females, have more copulations and fertilize more eggs. A general correlation of dominance with steroid production has been found but the relation is not simple and may be modulated by other factors such as social experience and learning (Adkins-Regan 2005, pp. 94–98). Subordinate males often have to use alternative strategies if they are to sire offspring. Montoya et al. (2016) explored the possibility that learning may be one of these alternative strategies; they showed that subordinate male quail improve their copulation efficiency in a competition with other dominant males, after learning to predict the presence of a female conspecific.

Pavlovian conditioning may also increase the production of sperm in terms of volume and number, fertilization in a sperm competition situation, and fertilization rate in noncompetition situations (see Krause and Domjan 2017, for a review). All these findings show that learning may have important effects on appetitive and consummatory responses, including copulation and fertilization. A shorter latency to copulate, assuming the costs of learning, seeking new opportunities for sexual interactions, changing the hierarchical organization of social and sexual responses, and physiological changes in response to challenging situations are all indicators of motivational

change, but further explorations are necessary to determine the interaction of learning and motivation in these situations.

Instrumental learning also affects sexual motivation; male rats trained in a runway increase their running speed to have access to a female rat, and press a lever for access to sexually receptive female rats; a similar effect has been demonstrated for females trained to press a lever to selectively have access to one of two males. In a choice situation, females in estrus prefer a male over a female. This preference decreases during pregnancy and increases again during lactation. An instrumental response of choice has also been observed in pigeons (*Columba livia*), Rhesus monkeys (*Macaca mulatta*), and other species in a number of instrumental paradigms (see Pfau et al. 2001, for a review).

Male Japanese quail increase their running speed in a straight alley when reinforced with copulatory access to a female quail (Baquero et al. 2009). The similarity of the instrumental response to the approach response using a Pavlovian paradigm suggests a similar motivational structure. The magnitude of the Pavlovian response and the choice response is related to the amount of sexual reinforcement and is mediated by testosterone (Domjan and Holloway 1998).

One important effect observed in the study of the sexual system is that learning seems to affect both appetitive and consummatory responses. As pointed out before, in other behavioral systems, the role of learning has been documented mostly on appetitive responses. It is still unknown if this indicates that reproduction may be somehow different from other motivational systems (i.e., regulatory systems).

## Hormones, Sexual Motivation, and Ecology: The Case of Birds

For many animal species, especially those in regions with more extreme climate variability, reproduction occurs at certain times of the year, usually timing the availability of resources. This timing in breeding has been selected over hundreds of thousands of years; that is, animals who

bred and raised their offspring when food resources were scarce or weather conditions were extreme were less likely to have surviving offspring and vice versa. Selection of certain behaviors implies the selection of anatomical structures, physiological mechanisms, and other biological characteristics associated with those behaviors. In this section, I will show how hormonal changes are related to multiple environmental factors associated to the onset and maintenance of sexual motivation, especially in birds.

In species living in mid and high latitudes, the most important environmental factor regulating reproduction is photoperiod. Taking into account the rate of change regarding the day's length is the same every year, it constitutes a reliable cue for many animals living at those latitudes to predict changes in the availability of resources and other conditions necessary for successful reproduction. There are, however, other factors such as temperature, humidity, social signals, and others that are used as additional cues at different stages of reproduction and serve as tuners of these activities (Wingfield et al. 2000).

In species living close to the equator and in deserts, photoperiod is not relevant as a proximate factor associated to reproduction. For instance, zebra finches living in the South Australian desert remain sexually inactive most of the time despite being pair-bonded, but when it rains in that region, reproduction is activated, and they begin nesting and egg laying. In this particular case, humidity is the major factor involved in triggering reproductive behavior (Adkins-Regan 2005, pp. 68–69).

Most research on the effects of light on sexual behavior in birds has been performed on passerines species, some domestic species such as the fowl and the pigeon, and the Japanese quail. Males are usually studied because their physiological and behavioral responses are more easily observed, but as noted elsewhere, a better understanding of parallel processes in females is important and should be of continued interest to researchers.

In mid and high latitudes, reproduction occurs during spring and summer for most species. When the day length reaches a certain level, some

changes associated with reproduction take place. In the wood pigeon, the testicular weight is very low (close to 0) between the months of November and March. During April, however, the testicular weight increases dramatically, then it increases at a steady rate and reaches its peak between July and September, after which it decreases very fast (Gwinner 2012). These changes in testicular weight are symmetrical to the photoperiod. When the day photoperiod is at about 12–13 h of light and 11–12 h of darkness, the wood pigeon starts its increase in testicular size.

The symmetry between the pattern of testicular size and day length does not apply to all species. Some birds show a pattern of rapid increase, a relatively short peak period, and then a rapid decrease even though there is still enough photostimulation to support their reproductive state. This phenomenon is called *refractoriness*, and it has been observed in the rook (*Corvus frugilegus*), the mallard (*Anas platyrhynchos*), and some sparrows. Good examples of this effect are observed in the house sparrow (*Passer domesticus*) and the white-crowned sparrow (*Zonotrichia leucophrys*).

During the breeding season, male white-crowned sparrows arrive early to the breeding area and establish territories that later will be visited by the females. The hormonal and sexual activities of males and females are not synchronized at that time. Males arrive to the breeding area when their testes are almost fully grown. This corresponds to high levels of testosterone and LH. Light stimulates follicular development in females, but when the females arrive, the follicle is still not completely mature and only fully develops as a result of interactions with the males in the breeding area (Wingfield et al. 2000). High plasma levels of testosterone in that moment may contribute to keep relatively high aggression levels in the males in order to defend the territory formed by the pair. High levels of male-male aggression are observed during that time. When the female reaches reproductive condition and sexual receptivity, males mate-guard the females to prevent extra-pair copulations, common to many species of birds (Adkins-Regan 2005, pp. 102–108). After the first brood,

the sparrow shows spontaneous testes regression even though there is still enough photostimulation to maintain this bird in reproductive condition, followed in some occasions by a second breeding period.

The phenomenon of refractoriness contributes to the repetition of reproductive stages across the mating season and a response to unpredictable variation in environmental conditions, migration, and other life-cycle changes (Ramenofsky 2011). Some species such as the Californian quail (*Callipepla californica*), the bobwhite quail (*Colinus virginianus*), and the Japanese quail do not show a pattern of gonadal growth characteristic of refractory species. In fact, in a laboratory setting it is possible to keep Japanese quail in fully reproductive conditions by maintaining a stable photoperiod of 16 h of light and 8 h of darkness (Mills et al. 1997).

Temperature changes may have direct and indirect effects on different aspects of reproductive motivation and behavior in many species. In some cases, the effect of temperature on sexual behavior has been argued to be direct. In the domestic fowl, extremely low and extremely high temperature affects fertility in both males and females (Huston 1975). In the *pugetensis* variety of the white crowned sparrow, an increase in temperature promotes gonadal growth in females, whereas in the *gambelii* variety it does not. This is likely related to ecological conditions of the two populations. *Z. l. pugetensis* is a migrant species and the onset of the breeding season shows a variation; thus, it is more susceptible to other environmental cues such as temperature (Wingfield et al. 2000). In Japanese quail, for which light is the most important trigger of sexual behavior, it has been observed that an important increase in temperature, even during short-day photoperiods, may stimulate gonadal growth and subsequently, sexual behavior (Mills et al. 1997).

Indirect effect of temperature on the reproductive conditions of birds is observed in the nesting of the great tit (*Parus major*). Changes in temperature affect leafing of birch and the availability of caterpillars, the main supplies of food for the great tit. This supply allows females to store enough fat

necessary for egg formation. Changes or stability in the food supply may also affect fattening, molting, and migration in white crowned sparrows (Ramenofsky 2011).

The preceding studies suggest that food availability and quality might be important cues in the development of certain reproductive behavior in some species. Certain elements in the diet of birds might be essential for specific aspects of reproduction, such as oviposition. Various researchers have shown that food quality may affect gonadal development in several species (Lee and Gorman 2000). For example, during the fall, a time in which photoperiod is unable to maintain gonadal growth, Payne (1969) fed tricolored blackbirds (*Agelaius tricolor*) with insects, a diet rich in protein. As a result of this particular diet, the subjects grew their testes to levels that were significantly higher than the ones maintained before the diet manipulation. Similarly, pinyon jays (*Gymnorhinus cyanocephalus*) fed with cones of the pinyon pine show gonadal growth; for this species, the availability of food is a reliable signal for sexual and reproductive motivation and action, allowing the individuals to cope with variations in food supply in a changing environment (Visser et al. 2004).

Besides temperature and food availability, other environmental cues are believed to be responsible for motivation and the activation of sexual behavior. As previously mentioned, in Australia, the zebra finch shows gonadal growth with increases in atmosphere humidity, and also in laboratory conditions with the introduction of fresh water after deprivation. In tropical species, the main factor determining the onset of sexual activity seems to be the changes in humidity. Some tropical species are photosensitive and may show endocrinological changes to slight photoperiod variations. The final trigger for courtship, copulation, and nest-building, however, seems to be rainfall changes; studies in tropical Africa (see Adkins-Regan 2005, p. 70) showed that in male blue-eared glossy starlings (*Lamprolornis chalybaeus*) changes in rainfall from the dry season to the wet season were associated with increases in plasma LH and testosterone, and territoriality. Since rainfall in many regions of the



tropics does not occur on a strict schedule every year, it is believed that it is not the rain itself that produces the hormonal changes, but that the change from the dry season (which is inhibitory) to the wet season is what elicits those changes. When the rainy season is not strong enough, such a disinhibitory effect does not take place. It is important to note that hormonal changes from the dry to the wet season are not universal in males of tropical species; for example, male stonechats (*Saxicola rubicola*) do not show significant LH and testosterone changes from the dry to the wet season. Rainfall might also control reproductive behavior in other ways. In the jungle fowl (*Gallus gallus*), which inhabits some regions of southeast Asia, sexual behavior occurs during the dry season. Since this species nests on the ground, the inhibitory activity of rainfall has a clear adaptive effect (Nishida et al. 2000).

Signals that are not related to environmental changes, but indicate the presence of conspecifics, may have an effect on the hormonal state, motivation, and sexual behavior of birds and other species. General sexual experience may affect hormonal levels of some birds at the beginning of the next mating season. For example, visual exposure to a female but not a male induces an increase in testosterone level in ring doves (*Streptopelia capicola*) (Silver 1992). In general, the presence of a sexual partner induces gonadal growth in males and ovarian development in females of many vertebrate species. This effect may result from the presentation of acoustic and other social signals (Wingfield et al. 2000).

Sexual experience may affect the level of the sexual response of male Japanese quail to females, as well as signals associated with them (Cornil and Ball 2010). This effect is evaluated by measuring responses such as the approach to those signals or to females, and copulation with females. It has been found that Japanese quail are able to learn complex relations between neutral signals and access to a sexual partner (Domjan and Holloway 1998). Changes in hormone production are flexible and occur in response to changes in the environment. For example, male mice (*Mus musculus*) exposed to females increase the production of LH and testosterone. This

response can be learned; using a classical conditioning procedure in rats, a conditioned stimulus (previously neutral) induced the production of LH and testosterone, before the presentation of the unconditioned stimulus (a female rat) (Adkins-Regan 2005, p. 22).

Although hormonal changes produced by learning have not been extensively studied, the effects of hormonal changes over learning and performance are better known. For example, in Japanese quail, a decrease in sexual motivation produced by functional castration disrupts the performance and learning of the approach response to an arbitrary stimulus associated to a sexual partner (Domjan and Holloway 1998).

In some cases, the behavior of the mate may elicit the onset of certain aspects of reproductive behavior. When female ring doves are exposed to courtship behavior by males in reproductive conditions, they ovulate, while the exposure to castrated animals does not have a similar effect. In this case, the courtship behavior seems to act as a cue of the reproductive condition of females. Similarly, latency of egg-laying might be reduced by exposure to the male's courtship sounds and display in barbary doves (Silver 1992).

Male white-crowned sparrows maintain high levels of LH and consequently of testosterone in the presence of females that are laying eggs. Additionally, males of this species keep high levels of LH and testosterone if their female mates are treated with estradiol and maintained sexually active and receptive (Wingfield et al. 2000).

Interactions with conspecifics of the same sex may also increase other behaviors associated with sexual activity in some species. For instance, white-crowned sparrows show increased levels of testosterone when exposed to other males whether the stimulus males are sexually active or not. In those cases, aggressive behavior increases for some time and then decreases to baseline levels (Wingfield et al. 2000). This suggests that the introduction of new males in the territory of males represents a motivational change, particularly an increase in sexual competition that could explain the increase in testosterone levels. This has been called "The Challenge Hypothesis."

This idea was tested in song sparrows (*Melospiza melodia*) by introducing a caged male in the territories of other males and by playing territorial songs; this procedure induced attacks by the residents on the intruder. When captured (later on), males of those challenged territories showed higher levels of testosterone than males of other nonchallenged territories. Competition with other males might explain why higher levels of LH and testosterone have been found in free-living animals than in laboratory subjects. This effect is dynamic, as the removal of the social challenge is followed by a decrease of testosterone levels and aggression (Wingfield et al. 2000).

A relation between testosterone levels, sexual motivation, and mating systems has been found. Species with a polygynous mating system maintain, in general, higher levels of testosterone, while species with a monogamous mating system keep lower levels of testosterone, but induced changes in androgen levels might induce a change in mating system. This relationship between mating systems and hormone expression is not simple, but is modulated by parental care; males of species that provide parental care show lower levels of testosterone when caring for eggs or young, but this androgen level and related aggressive behavior increases if exposed to competing males (Wingfield et al. 2000).

The previous findings would suggest that in polyandrous species, females would have higher levels of testosterone than males, since in many of those species females keep large territories with several males in them. Studies on the hormonal levels of polyandrous females, however, do not support this idea. Goyman and Wingfield (2004) have found that female black coucals (*Centropus grillii*), a polyandrous species, mate with more than one male. They are larger than males, are more vocal, defend territories, and have a higher reproductive rate than males. However, they do not present higher levels of gonadal steroids than males. The pattern of prolactin production for sex-role reversed species differs from the androgen production. In these species, the level of prolactin (a hormone that regulates incubation in birds) is higher in males than in females (Eens and Pinxten

2000). The implications of these pattern differences for behavior and reproductive motivation remains to be fully understood.

## Conclusions

The study of motivation has been central to psychology for the last century. The main theories of behavior have attempted to explain what moves individuals to action. Those explanations have centered on variables, internal and external to the organism, on levels that can be organized in time (from synchronous to evolutionary), and structure complexity (from molecular to social).

Comparative psychology provides a strategy to evaluate motivation at different levels of explanation as the ones proposed by Tinbergen. It provides a systematic approach to identify mechanisms of motivation at behavioral and physiological levels; it offers a strong body of knowledge to understand the relationship between development and behavior, and it provides a systematic approach to study the origin and functionality of behavior across species.

An integrative approach is demanding because it requires the extension of mechanistic understanding, to ecological and evolutionary views. Usually this starts by following a heuristic exploration of how mechanism relates to adaptation, but it must move to empirical evaluation of such speculation. The study of learning has recently achieved that step. After decades of speculation on the adaptive value of conditioning, recent empirical evaluation has shown that learning affects proceptive and receptive responses in several species of vertebrates, improving fitness both in males and females. This is possible through changes in motivation, memory, perception, and other behavioral and physiological processes. Similarly, the study of the relations between hormones, ecological conditions, and behavior, all isolated fields of study in the past, are becoming integrated to show a fascinating picture relating behavioral and physiological mechanisms, environmental constraints, and evolutionary history. Endocrine processes are critical mediators of motivated behavior. They not only contribute to

organize anatomy, physiology, and behavior but also activate the proper behavioral sequence under specific environmental conditions. Clearly, they are not the only motivational force in sexual behavior, but a solid understanding of their mechanisms can be a great basis for an integrative view of reproductive behavior.

## Cross-References

- ▶ [Appetitive Response](#)
- ▶ [Clark L. Hull](#)
- ▶ [Frank Ambrose Beach](#)
- ▶ [Hormones and Behavior](#)
- ▶ [Instinct](#)
- ▶ [Nikolaas Tinbergen](#)

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## Motivational State

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## Introduction

Motivational states are physiological internal states in the organism that play an important role in initiating behavior, selecting actions to perform, and orienting the actions to achieve desired goals. Motivational states are critical because they help the organism prioritize behaviors oriented to obtain access to resources that are required to maintain a balanced well-being and, in extreme situations, for survival. Some of the better known motivational states include the states of hunger and thirst, and they can activate specific behaviors oriented to obtain food and drink.

In the laboratory, a motivational state can be inferred by assessing the effect it has on the performance of certain actions. For instance, we can restrict access to food for some animals (food deprivation) and compare how this manipulation affects the performance of pressing a lever that delivers food, relative to animals that were not food-deprived. We can also study the motivational state at a physiological level, for instance, by determining the brain structures and circuits involved in its activation and termination as well as the groups of neurons and neurotransmitters that play a role in these processes.

Motivational states can be regulated by not only homeostatic mechanisms that aim to maintain a biological balance in the organism, for instance, blood glucose levels, but also by non-homeostatic mechanisms, for instance, social events or emotional states. Learning processes are also deeply involved in the development and activation of motivational states, contributing to the acquisition and performance of behaviors oriented to terminating them. Here is a brief review of some of the motivational states of hunger and

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thirst, the mechanisms responsible for them, and their relationship with learning processes.

## Hunger

Early accounts of the motivational state of hunger gave particular attention to stomach contractions as an indicator of hunger and the initiation of eating behaviors (e.g., Cannon and Washburn 1912); however, this idea was discarded. Instead, evidence supports the existence of homeostatic mechanisms that keep track of the levels of blood sugar and fat, which stimulate the initiation or cessation of eating in order to maintain an optimal state in the organism. In the digestive system, including the stomach, duodenum, liver, and pancreas, there are receptors that detect fluctuations in the level of glucose. When glucose levels decrease, these organs send signals to the central nervous system (CNS) to initiate eating behaviors, and when the glucose levels increase, signals are sent to stop eating (Cumming et al. 2004; Thorens 2011).

In the CNS, the hypothalamus has been shown to play an important role in eating. According to the influential “dual center model,” there would be a specific center for feeding and another separated for satiety, the former located in the ventrolateral hypothalamus (VLH) and the latter in the ventromedial hypothalamus (VMH). The dual center model was based on early studies showing that lesions in the VMH resulted in animals eating excessively, whereas lesions in the VLH resulted in animals that did not eat. Contemporary studies show that the role of the hypothalamus in feeding and satiety is more complex, involving areas such as the arcuate (ARC) nucleus in the hypothalamus, as well as projections to other brain regions, for instance, those in the reward pathway, e.g., ventral tegmental area (VTA) (Farr et al. 2016; Saper et al. 2002; Timper and Brüning 2017).

The motivation to eat might also be regulated by long-term processes. According to the set point theory, each individual has a body weight determined by its genes, and feeding and satiety depend on this set point. The organism could regulate and determine the state of the organism

by receptors of specific hormones such as leptin and insulin. When we lose weight, our levels of leptin and insulin decrease, whereas the opposite can be observed when we gain weight (Farias et al. 2011; Weinsier et al. 2000).

Although these homeostatic processes can explain part of the motivational state of hunger and eating behaviors, humans also eat in circumstances in which homeostasis is not disrupted, for instance, in social circumstances or in response to learned stimuli associated with food. The effects of learning on the motivational states and behavior are described below.

## Thirst

The motivational state of thirst can be activated by at least two different types of homeostatic mechanisms: volumetric and osmometric thirsts. Volumetric thirst is caused by mechanisms related to the fluids located outside the cells of the body (extracellular) and osmometric thirst by a mechanism related to water levels inside the cells (intracellular).

Volumetric thirst occurs when the volume of extracellular (but not intracellular) fluids decreases, for instance, because of blood loss, diarrhea, or vomiting, in the state known as hypovolemia (Stricker et al. 1992). This reduction of the blood volume is detected by the kidneys, which start producing and secreting the enzyme renin into the system. This enzyme interacts with the liver resulting in the release of vasoconstrictor angiotensin II, which increases blood pressure by narrowing the blood vessels. Angiotensin II also stimulates the adrenal glands to produce aldosterone, causing the organism to reabsorb sodium and water resulting in an increment of blood volume and blood pressure (Stanhewicz and Larry Kenney 2015).

Osmometric thirst occurs when the solute concentration in the extracellular fluid increases, causing the body cells to lose water via osmosis. This can happen because of the increased ingestion of salty foods and loss of body fluids via evaporation (as in respiration and sweating), urination, and defecation. Changes in the solute



concentration are detected by cells known as osmoreceptors, which can detect changes in their own volume caused by the loss of water, and send signals to activate drink consumption. The osmoreceptors are located in a brain region that surrounds the third ventricle known as the organum vasculosum of the lamina terminalis (OVLT). Because the OVLT does not have a blood-brain barrier, its neurons can detect changes in the solute concentration of extracellular fluid. When this happens, it activates the median preoptic area, resulting in the sensation of thirst and the activation of drinking behaviors (Stricker and Sved 2000).

Although these homeostatic mechanisms can induce thirst and initiate drinking behaviors, animals do not require being thirsty in order to drink. Just like for hunger and eating behaviors, there are other non-homeostatic mechanisms involved in drinking behaviors.

## Learning and Motivational States

At the beginning of the twentieth century, Pavlov demonstrated that behaviors in anticipation of food delivery, such as salivation, can be learned. He noticed that the external events that preceded the delivery of food began to produce behaviors similar to those naturally produced by food itself but before the animals had access to the food (Pavlov 1927). This first demonstration that physiological events can be learned started a field that has significantly advanced in the last century. Since most of research has been conducted using food deprivation techniques, we will provide examples for the motivational state of hunger, although similar processes are found to be involved in other motivational systems, such as thirst.

As described above, hunger is characterized by many physiological factors, such as a drop in the concentration of glucose in the blood and an increase in body temperature shortly before eating (de Vries et al. 1993; Thorens 2011). Although it has been proposed that these physiological changes initiate food-seeking and food consumption in an environment in which food is readily available or

periodically provided, it is more likely that external cues, such as the time of the day or the amount of light, initiate the internal processes to prepare the organism to eat and digest food (Woods and Seeley 2002). Cues that are consistently present before or during eating become capable of eliciting physiological changes in the organism by increasing levels of insulin (Woods et al. 1977) and dopamine (Mark et al. 1994), which serve to anticipate food and trigger anticipatory behaviors such as salivation. These external cues also become capable of initiating food-seeking responses, and they invigorate eating behaviors even in sated animals (Petrovich et al. 2007).

The interoceptive cues that characterize a motivational state provide information about the delivery of a relevant consequence, and they can also become discriminative stimuli that inform the animal that, by performing a certain range of actions, access to a reward will be granted. Interestingly, internal cues from a particular motivational state, such as cues that signal hunger, can also be used by the animal to anticipate events from a different motivational system, for example, the occurrence of aversive events. For instance, animals can use the information provided by different levels of food deprivation to anticipate the delivery or non-delivery of a foot shock, as indicated by a conditioned freezing response (Benoit et al. 2010).

Importantly, the interaction between motivational states and learning is bidirectional. For instance, a particular motivational state, such as hunger, can be triggered by learned cues, but what an animal learns at any given time is also modulated by the current motivational state of the animal. There is evidence that the value that an animal assigns to a reward will depend on the current motivational state of the animal (e.g., a food pellet will have a larger value if consumed while hungry than sated; Bolles 1972) and that the prediction error, that is, the difference between what the animal expects and what actually occurs, is modulated by the motivational state of the subjects (Laurent et al. 2018).

A motivational state can also shape the content of what is learned, facilitating new learning about motivationally relevant stimuli. Examples of this can be found in conditioned preference

experiments, in which a stimulus, such as a flavor or an odor, is paired with a nutritional reward like sucrose. Learning is evaluated by measuring animals' preference in a test in which they have a choice between two solutions: one with the trained cue and another with a control cue. Animals will consistently prefer the solution containing the cue that was earlier paired with the nutritional reward. This paradigm has shown that at least two types of associations can be established: one between the flavor/odor and the calories of the reward and another between the flavor/odor and the taste. The expression of the animal's preference will depend on one of these associations, which in turn will depend on the motivational state of the animal. For instance, animals will prefer a flavored solution that has been paired with sucrose, but the preference will be larger in animals that were trained in a food deprivation state relative to those trained with free access to food. Interestingly, this difference is maintained regardless if the animals are tested hungry or sated. In contrast, when animals are trained with saccharin, which has no nutritional value, rather than sucrose, the animals' preference for the solution paired with saccharin is not affected by the motivational state of training (Capaldi et al. 1994).

This type of experiment has also shown differential effects of extinction on animals' preference. In extinction, a stimulus that has been paired with a relevant consequence (a conditioned stimulus) is then consistently presented in the absence of the reward, resulting in a loss of its learned properties (Delamater 2004). There is evidence that the animals' preference for a flavored-solution that has been paired with a reward, either with a nutritional value or not, persists after multiple tests, in which the animals are exposed to the flavored solution without the valuable component (Capaldi et al. 1983). However, this preference for a flavored solution paired with a nutritional reward decreases if the animals are either trained or tested in a food-deprived state (Harris et al. 2004).

Another example of the effect of the motivational state on the content of learning can be found in cue competition phenomena, which have been critical for development of the most influential learning models. One of them is latent inhibition,

in which learning about the predictive relationship between a cue and a reward is slowed down if animals have prior experience with the same cue in the absence of any reward (Lubow 1973). Latent inhibition also depends on the motivational state of the animals: if the cue is preexposed to the animals while they are hungry, then learning about this cue as a predictor of rewards relevant to the motivational state of hunger, such as foods, will be retarded. However, learning about this cue and the delivery of a non-nutritional reward, such as saline, will not be affected. In contrast, if pre-exposure is conducted to thirsty animals, then this will slow down learning about this cue and saline, but not between this cue and food (Killcross and Balleine 1996).

## Behavior and Motivational States

Perhaps the more direct link between a motivational state and behavior can be observed on goal-directed actions. As the name implies, a goal-directed behavior is an action oriented to obtain a goal, and its expression depends not only on previous learning about the relationship between the behavior itself and the access to the goal but also on the desirability of that goal (Dickinson and Balleine 1994). A rat will press a lever to obtain food if the animal has learned a relationship between the action of pressing the lever and the delivery of food, but it is also important that the animal is hungry. One commonly used technique to assess if a behavior is goal-directed is to reduce the value of the "goal," which can be achieved by pairing the goal with an aversive consequence. For instance, Adams and Dickinson (1981) trained hungry rats to press a lever to obtain one type of food, and separately, the same animals were exposed to a different type of food. After training, half of the animals received pairings of the food that served as a reinforcer and lithium chloride, which produces illness, while the other half received pairings of the food that was merely exposed with the aversive consequence. In the test, the first group of animals showed a lower rate of responding than the latter, demonstrating that the

desirability of the outcome is necessary for goal-directed behavior.

However, the role of the motivational state on goal-directed behavior is slightly more complicated. As described above, the current motivational state of an animal has a direct impact on the value of an outcome; for instance, food is more valuable when hungry than when not. Thus, motivational shifts from hunger to satiety, for example, should result in a reduction of the outcome value, while shifting from satiety to hunger should result in an increment in the outcome value. However, for this to happen, animals need to have prior experience with the outcome in the corresponding motivational state. For instance, Balleine (1992) trained rats to press a lever to obtain a nutritious reinforcer (different from the maintenance food), and after this, he measured the rate of lever-pressing in a test in which the reinforcer was not delivered. Importantly, before training, all the animals were food-deprived for a period in which half of them had the chance to consume the reinforcer, while the other half did not. Then, all the rats regained access to the maintenance food in their home cages throughout training. Before the test, half of each group of animals were food-deprived again, while the other half were not, and in the test, the hungry rats that had experienced the reinforcer while hungry were the ones that showed a higher rate of lever-pressing relative to the other three groups. The performance of the group that was also food-deprived but that did not experience the reinforcer while hungry did not differ from those groups that were not hungry at test. Balleine (1992) also conducted similar experiments by training animals in a hungry state and then tested them either hungry or sated, finding no differences between these two conditions. However, animals that received exposure to the reinforcer prior to training while sated showed a reduction in the rate of responding relative to the other groups. This phenomenon is known as “incentive learning,” and it refers to the fact that the value assigned to an outcome depends on the animal experiencing this outcome in the relevant motivational state (Dickinson and Balleine 1994).

In contrast, motivational state does not play the same role in habitual behaviors, such as behaviors

that do not depend on the desirability or value of the goal and may develop through extensive training (Dickinson 1985). Habits can be performed when the animals are in an opposite state to the motivational state that corresponds to them; for instance, an animal may perform food-seeking behaviors in a state of satiety and even if the “goal” is harmful to the animal. Several studies have demonstrated that animals will continue pressing a lever that was trained with a food reward even if the food has been paired with an aversive consequence, once the lever pressing behavior has become habitual (Adams and Dickinson 1981).

There is another situation in which behavior does not seem to be affected by the current motivational state of the animal. In some cases, a learned stimulus, such as a light that signals food delivery, can invigorate certain actions, such as pressing a lever to obtain food. In other cases, these stimuli can affect decision-making processes, biasing action selection. For instance, the sound that signals the delivery of a solution can result in animals pressing a lever that gives access to this solution more than a lever that gives access to food (Alarcón and Delamater 2019). This selective effect on behavior persists even after the motivational state of the animal has been shifted or when the value of the goal has been reduced by pairing with an aversive consequence, demonstrating that the control over behavior by learned cues is in some degree independent on the motivational state of the animal (Cartoni et al. 2016).

## Summary

Motivational states are important in the initiation, maintenance, and termination of behaviors that aim to obtain resources necessary to maintain an organism’s physiological balance and survival. Motivational states can be studied from different levels of analysis, for instance, from a behavioral or a physiological perspective. The mechanisms involved in these states are in part homeostatic, such as regulation of glucose in the blood for the state of hunger, but there are also non-homeostatic mechanisms that keep the organism balanced in the long term. Motivational states are influenced

by learning processes, and they can also affect the acquisition of new learning as well as the performance of goal-directed behaviors. However, motivational states do not seem to play the same role in the performance of habitual behaviors or in the invigorating and biasing effect that some learned cues have on behavior.

## Cross-References

- Drive State
- Goal
- Homeostasis
- Hypothalamus

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## Motor-Related Cells

- [Parieto-occipital Sulcus \(POS\)](#)

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## Movement

- [Artiodactyla Navigation](#)
- [Bear Navigation](#)
- [Canine Navigation](#)
- [Cetacean Locomotion](#)
- [Chondrichthyes Navigation](#)
- [Lagomorpha Navigation](#)
- [Migration](#)
- [Mustelidae Locomotion](#)
- [Mustelidae Navigation](#)
- [Newton's Third Law](#)
- [Plantae](#)
- [Proboscidea Navigation](#)
- [Sirenia Navigation](#)

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## Movement Patterns

- [Sirenia Navigation](#)

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## mRNA

- [Messenger RNA](#)

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## mtDNA

- [Mitochondrial DNA](#)

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## Müllerian Mimicry

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## Synonyms

[Honest mimetic signal](#)

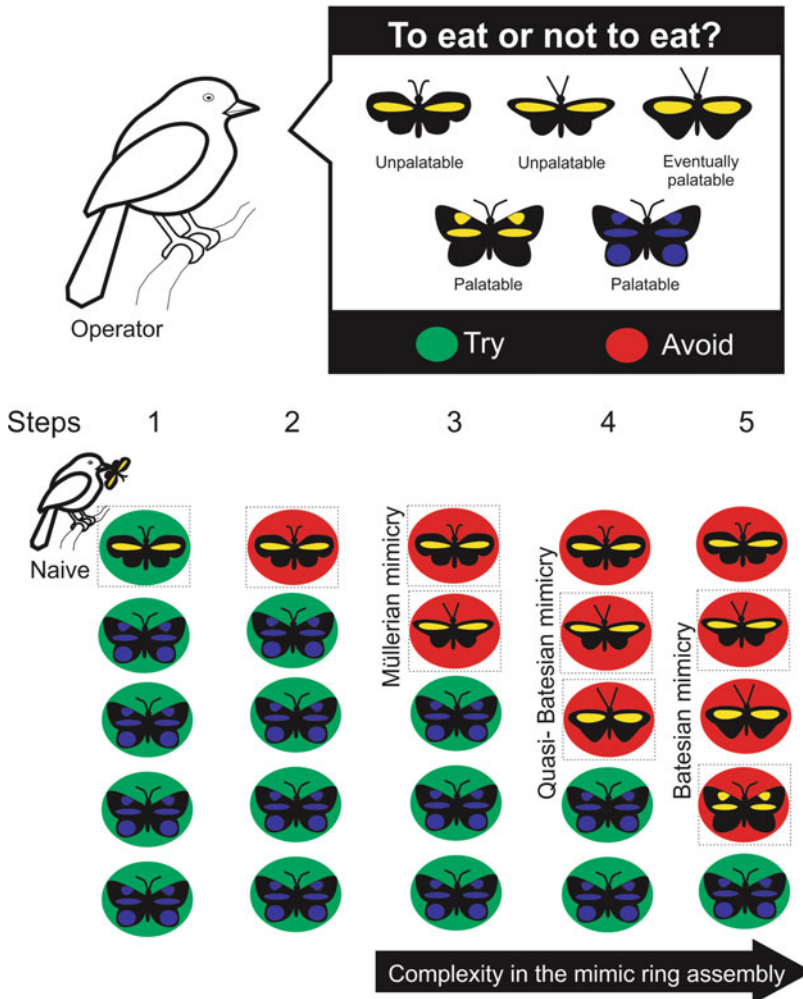
## Definition

A convergent pattern of morphological and/or behavioral traits in organisms that signal aposematism for predators.

## Introduction

Predators exert strong selective pressures on prey, therefore shaping their defensive strategies. According to the theory of optimal foraging,





**Müllerian Mimicry, Fig. 1** The mimicry ring assembly is modulated by predator decision over time. The prey-predation interrelationship is an important interaction for shaping mimicry ring formation. Some information about the butterfly prey such as palatability level and coloration pattern (on the top) help the operator decide to try (green) or avoid (red) the prey, which changes the community frequency. The capacity to associate the palatability of prey to a black-yellow pattern is beneficial for the operator and the emitters. Furthermore, prey frequency and capacity to know about the unpalatable prey (either learned or innate) are important aspects. The naive predator that does not know about the unpalatability of prey tries all prey in the community, including the unpalatable (Step 1).

After an unpleasant experience, the operator can recognize the unpalatable prey and avoid the aposematic prey (Step 2). Other unpalatable prey are protected by the same coloration pattern (honest signal) and form a **Müllerian mimicry** (Step 3). Some variable and eventual unpalatable prey forms a **Quasi-Batesian mimicry** (Step 4). Finally, when the palatable prey mimics the unpalatable model, a false signal, this forms a **Batesian mimicry** (Step 5). The warning signal increases in efficiency when the frequency of the signal increases; however, the palatable prey that resemble the warning signal decreases the efficiency of the warning signal, and this false signal allows predators to disassociate the palatability from the warning signal (morphological and behavior convergence)

predators tend to maximize their energy absorption per unit of time. During the first step of the assessment phase of a potential prey, the predator needs to distinguish palatable and easy prey from

unpalatable, dangerous or difficult to capture prey (Fig. 1). A naive predator trying the unpalatable prey (Step 1, Fig. 1). The decision to attack or not depends on the animal's cognition through

instinctual behavior (innate) and/or previous experiences (learning). These decisions must be made quickly and accurately, as mistakes can result in high costs including unpleasant experiences, injuries or even death. On the next attempt, the experienced predator starts to avoid conspicuous aposematic prey (Step 2, Fig. 1). To maximize time and minimize costs involved in the manipulation, subjugation and digestion of prey, predators use indirect sensorial cues as colors, smells and sounds. The choices based on these cues select for generalized convergent patterns between prey through natural selection. This scenario explains the origin of conspicuous warning signs (aposematism) and displays of intimidation (e.g., false eyes) (Ruxton et al. 2004; Janzen et al. 2010) (see Steps 3–5, Fig. 1). In this sense, mimicry can be classified as a “meme” (sensu Dawkins 1976), a piece of symbolic information that exists only from the perspective of the operator’s cognition. This interaction has evolved under different selective pressures and sometimes in conflicting ways with other animal demands, such as sexual selection, environmental changes, host plant distribution, phenotypic plasticity and dispersal (Rossato et al. 2018a). These are the adaptive bases for understanding the evolution and maintenance of the different types of mimicry in biological systems (see Fig. 1).

While many different types of mimicry have already been proposed, Müllerian mimicry is a special case. It was first proposed by the naturalist Johannes Friedrich (‘Fritz’) Müller (1821–1897) after he immigrated to Brazil. He formulated an explanation for the similarity between unpalatable species that is now so widely accepted that it is often considered synonymous with the phenomenon itself. In 1879, Fritz Müller proposed the first formal model of mimicry, which was the first mathematical demonstration of the fitness consequences of ecological traits where two unpalatable prey could benefit from mutual resemblance (Müller 1879; Mallet 2001).

In Müllerian mimicry the prey are called co-mimics, which are two or more aposematic organisms that share a similar appearance and together reduce antagonistic interactions by sharing the mortality costs of educating naive or

forgetful predators (see Step 3, Fig. 1). Therefore, Müllerian mimicry includes at least three agents: two or more emitters of the true warning signal and one operator, respectively representing the co-mimetic prey and the predator (Joron 2009). The co-mimic’s signal information could be visual, chemical, tactile, acoustic, electric, or kinetic, depending on the sensorial universe in which the operators and emitters are found. The strong similarity between unpalatable prey results in the reinforcement of the warning signals, which decreases the predation risk and consequently increases the survival rate of the co-mimics (Franks and Noble 2002; Endler 1988). Consequently, individuals with the same signal have a reduced mortality rate, forming a mimicry ring in the same geographical areas or resource-based microhabitats through natural selection (Willmott and Mallet 2004).

Batesian mimicry is another important type of interspecific interaction and is generalized as a tripartite system, in which a sensitive signal-receiver (operator) misidentifies the mimic (false signal emitter) as the model (honest signal emitter) (Vane-Wright 1976). There may be intermediate cases between Batesian and Müllerian mimicry. Quasi-Batesian mimicry (Speed 1993) (Step 4, Fig. 1) is seen when co-mimics, like Müllerian, have different levels of unpalatability, like Batesian. In this case, some prey (emitters) in a mimicry ring are eventually unpalatable or have populations that contain some palatable individuals (see Step 4, Fig. 1). For example, some mimetic ithomiines species acquire defensive pyrrolizidine alkaloids (PAs) only as adults by feeding on certain flowers (Brown 1984). Therefore many ithomiines have little or no PAs and this increases the costs of interaction for unpalatable prey, as in Batesian mimicry. As mimetic rings in tropical sites can be composed of rich assemblages of species, it is more realistic to analyze them as a spectrum of variation in costs and benefits (Step 5, Fig. 1).

Mimicry rings have evolved under different selective pressures between interacting species. Some aspects of animal cognition and behavior evolved into mimicry in distinct scenarios, such as the predator-prey relationship and the coevolution

between co-mimics (Cuthill and Charleston 2012) and between co-mimics and host plants (Ehrlich and Raven 1964).

Considering the ecological aspects of interaction between co-mimics, Müllerian mimicry is comprehended as a kind of mutualistic relationship between aposematic emitters. Moreover, predators and prey are benefited in this interaction, and therefore survival increases for the predator that better associates the aposematic signal to unpalatable prey information, and the convergence of prey on the aposematic signal, thus avoiding the risk of attacks. On the other hand, rare individuals with new variants in the prey population are not recognized as unpalatable by the predator, thus suffering a greater risk of predation (Joron 2009). Therefore Müllerian mimicry evolution is based on the tendency toward a uniformity of aposematic signaling, which signifies coevolutionary convergence. The prey signal is honest in Müllerian mimicry, which means both co-mimics belonging to the same mimicry ring are unpalatable (see Step 3, Fig. 1). On the other hand, the signal is dishonest when one palatable species mimics an unpalatable species, as seen in Batesian mimicry (see Step 5, Fig. 1). In this case, the palatable mimic is benefited by the unpalatable model species.

Another important force to modulate mimicry selection is predation. In predator-prey systems, the dynamics are modulated by the mimicry signal emission of the prey and by the recognition of this sign by the predator. In addition to predator density, the survival of the predator from this interaction consequently regulates prey density, which could decrease a species' dominance through competition and could strongly affect the species composition in one place. This process is called apparent competition (Holt 1977) where predation prevents the monopolization by the most competitive species in the habitat. Just as predators evolved a more efficient predation through the development of certain behavior and structures, prey also evolved to avoid predation threats through mechanisms such as mimetic rings. The defensive strategies adopted by prey when they cannot hide or escape include the production of strong odors due to a chemical secretion or by

pain in addition to chemical substances that make them unpalatable. The association between toxicity and interspecific aposematic displays found in co-mimics reduces the mortality costs of predators and enhances accurate discrimination between edible and unprofitable prey.

Beyond this, the convergent evolution from mimicry could evolve into conflict with other forces during its evolution (Rossato et al. 2018a), including, for example, intraspecific coevolution by female choice and secondary sexual traits. The phenotypic similarities between species from the same mimetic ring could impose disadvantages stemming from mimicry due to possible mistakes in identifying a mate during courtship (Rossato et al. 2018b). Therefore, the mimetic appearance evolves under a trade-off between natural selection of mimetic traits and sexual selection in mimetic species. Wing color is indeed used as an important visual cue in both sexes of butterflies, as is observed in the aposematic *Heliconius erato*'s courtship (Crane 1955).

Visual characteristics associated with chemical defenses are widely used to avoid predation. Whereas camouflaged individuals tend to have patterns that make them imperceptible in their environment, individuals in the mimicry system show a conspicuous aposematic signals. Therefore, mimicry in the environment presents a warning signal to the predator due to its association with unpalatability (Joron 2009).

## Examples of Müllerian Mimicry

According to an informal survey of the scientific journal literature since 1960, mimicry is predominantly a lepidopteran phenomenon (Sherratt 2008). However, this phenomenon has already been reported for other fascinating animal groups such as bumblebees, frogs, coral snakes, bees, birds, ants and fishes, in addition to being suggested for some plants.

The first and most famous case of Müllerian mimicry occurs in the Neotropical butterflies *Heliconius* (see Benson 1972). This is an evolutionary model in biology due to the large intra- and interspecific variation in color pattern and

especially for presenting various mimetic associations, at both specific and sub-specific levels. Four different mimicry rings are typically recognized as “tiger”, “red”, “blue” and “orange” (Mallet and Gilbert 1995). The members of each mimicry ring co-occurring in a similar habitat overlap in the spatial-temporal distribution of distinct mimicry rings, with the most famous case between *H. erato* and *H. melpomene* (Brown et al. 1974). Their spatial distribution in South America shows the occurrence of selective pressures working to generate similar forms, which could not possibly be explained as a coincidence. For example, in these systems birds are recognized as the main agent for mimicry selection, including the maintenance of spatial polymorphisms of the wing color in butterflies. Birds learning to associate the wing color and patterns of co-mimics with unpalatability require a sacrifice from both co-mimics. Therefore, co-mimics must share the burden of the learning predator. Many distinct ways in which the predator learns about the unpalatable butterflies have previously been described for these groups, such as the level of unpalatability (Ihalainen 2006) and co-mimic frequency (Rowland et al. 2010). In addition, the warning signals inherent in wings could be described in terms of coloration (Svádová et al. 2009), pattern (Ihalainen et al. 2008), size (Marples 1993), asymmetry (Forsman and Merilaita 1999), wing shape (Rossato et al. 2018b) and the wing movement pattern used for flight (Srygley and Ellington 1999).

## Conclusion

Müllerian mimicry systems are interesting models for exploring the interface between behavioral ecology and evolution. These complex systems have evolved under different interactions, which modulate the main aspects of similarity between the co-mimics, from coevolution with host plants, with the co-mimics and interactions predator-prey. Additionally, a conflicting force like sexual selection could change some aspects of resemblance. Much information has evolved in this system and could provide opportunities for understanding animal cognition and behaviors. Finally,

Müllerian mimicry in butterflies, first described by Fritz Muller over one hundred years ago, continues to be a system of interest for understanding important aspects of animal cognition and behavior.

## Cross-References

- ▶ [Batesian Mimicry](#)
- ▶ [Camouflage](#)
- ▶ [Mimicry](#)
- ▶ [Natural Selection](#)
- ▶ [Optimal Foraging Theory](#)
- ▶ [Sexual Dimorphism](#)

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## Multi-agent Systems

### ► Agent-Based Modelling

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## Multiday Torpor

### ► Hibernation

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## Multigenic Effects

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## Synonyms

Polygenic effect

## Definition

Polygenic inheritance is described as an inherited characteristic that is governed by more than one gene.

## Mendelian Inheritance

Heritability of human characteristic is often discernible. When we observe a family, we often



notice characters of our parents and grandparents. There are some traits in which one gene controls one character or one phenotype. This is called classical Mendelian trait. However, the mode of inheritance of these traits is not always simple. In fact there are numerous human characteristics whose inheritance is governed by multiple genes also called as multigenic traits. The most classical example of this is height in humans. Height is a trait that is genetically regulated; however we observe many families in which height of the children does not follow height of their parents. Another very example of this is skin color. We often see many families in which skin color of children does not resemble to that of their parents. Remarkably, most of the traits in humans and other organisms are polygenic. These types of non-Mendelian characters are the result of intricate interactions among genes that modify the characteristic of a phenotype.

This is rather interesting to note that these complex gene interactions are observed in diseases as well. It has been observed that a large number of human diseases and disorders are multigenic in nature, that is, a single phenotypic trait is expressed due to mutations in multiple genes. There are basically two classes of trait: monogenic trait and multigenic trait.

### Monogenic Traits

Monogenic traits are characters that are governed by single gene only. For several years, many diseases are known that result from mutation in a particular gene. These diseases are known as monogenic (“single gene”) diseases. The most common example is cystic fibrosis that occurs due to mutation in *CFTR* gene. As monogenic diseases are severe in nature, they are usually rare in population. Selection pressure helps in reducing the prevalence of mutations that are deleterious in nature.

The dominant mutations are effectively eliminated by selection pressure before sexual maturity. However, some monogenic disorders that are caused due to recessive mutations tend to persist in population. Selection pressure acts only of the individuals that are homozygous for those alleles.

In such cases, a reservoir of such genes always persists in the population.

Monogenic disorders are caused due to autosomal genetic mutation. These kinds of mutations can be spontaneous with no family history, or they can follow Mendelian pattern of inheritance also called as Mendelian disorders. The inheritance pattern of Mendelian disorders may be autosomal dominant; autosomal recessive; X-linked dominant; or X-linked recessive. These are described below.

### Autosomal Dominant Inheritance

The term “autosomal” denotes that the gene is present on any of the numbered non-sex chromosomes (Chromosomes 1 through 22). The word “dominant” expresses that even a single copy of the disease-linked mutation will suffice to cause the disease. As this pattern of inheritance involves autosomes only, it effects both males and females equally. The most common examples of this include Huntington’s disease, Ehlers-Danlos syndrome neurofibromatosis, achondroplasia, and Marfan syndrome.

### Autosomal Recessive Inheritance

The term “recessive” refers to alleles which are not expressed in an individual unless an individual inherits both the copies of the mutated gene, one from each parent. Usually, in these cases parents are the carriers of that disease. The most common examples of diseases that follow autosomal recessive mode of inheritance include Huntington’s chorea, polycystic kidney disease, and tuberous sclerosis.

### X-Linked Dominant Inheritance

X-linked dominant inheritance occurs when the gene responsible for the trait is present on the X chromosome. Furthermore, only one copy of the allele is sufficient enough to cause the disease.

Male cells carry one X and one Y chromosome, while female cells consist of two X chromosomes. In X-linked dominant inheritance, a mutation in one copy of an X-linked gene is enough to express the disease. Thus in this condition, both the sexes can be affected, but

males are more severely affected than females. Moreover, in this condition the father is not able to pass on the X-linked dominant condition to the male offspring (due to inheritance of only X chromosome from their mother); however all the daughters will express the disease and will be able to pass on the condition to their children. Some of the examples of diseases that shows X-linked dominant pattern include hypophosphatemic rickets, oral-facial-digital syndrome type I, Rett syndrome, Aicardi syndrome, fragile X syndrome, the X-linked lissencephaly and double-cortex syndrome, and incontinentia pigmenti type 1 (Johnson and Hisama 2007).

### X-Linked Recessive Inheritance

In X-linked recessive inheritance, the males would express the disease phenotype if they inherit the X-linked mutation. Thus, in males, a mutation in the copy X-linked gene can express the disease. However, females must have a mutation on both X chromosomes to express the trait. As sons inherit Y chromosome from their father and daughters inherit X chromosome from their father, affected men will not be able to pass on the trait to their son but to all the daughters. Hence, all their daughters will be the carriers. Some of the most common examples of disorders showing X-linked recessive inheritance are hypohidrotic or anhidrotic ectodermal dysplasia, Duchenne muscular dystrophy (DMD), hemophilia, and Hunter disease. Rarely, female carriers may show mild characteristics of an X-linked disorder. For example, fragile X syndrome.

### Multigenic Traits

In contrast to monogenic traits, the phenotype of multigenic or polygenic traits is regulated by multiple genes present at different loci. This type of genetic defect arises from interaction between multiple genes. Thus, mutation in more than one gene gives rise to multigenic diseases or disorders. It is interesting to note that any one of these mutations alone are not sufficient to cause the disease but together they can result in severe phenotypic changes. These type of genes show

cumulative effect and show a continuous distribution pattern for, e.g., height or skin color. Multigenic inheritance does not follow phenotypic ratios typical to Mendelian inheritance.

The inheritance pattern in which mutation in two different genes results in manifestation of a phenotype is referred to as digenic inheritance. The most common examples of digenic inheritance include retinitis pigmentosa, a disease which occurs due to heterozygous mutation in two genes, viz., *PRPH2* (peripherin-2) and *ROM1* (retinal outer segment membrane protein 1). Notably, mutation in either *PRPH2* or *ROM1* alone is not sufficient enough for manifestation of the disease phenotype (Harel et al. 2015). The following studies established that interaction between proteins encoded by these genes is essential for photoreceptor disk formation (Goldberg and Molday 1996). Interestingly, a more complex digenic model tri-allelic inheritance (resulting from mutation in three alleles, two at one locus and the third at other locus) was evidenced in Bardet-Biedl syndrome (BBS), a genetically heterogeneous ciliopathy that affects many parts of the body. People with this syndrome show primary characters of obesity, visual impairment due to cone-rod dystrophy, extra fingers or toes (polydactyly), hypogonadism, renal malformation, congenital heart disease, and learning difficulties. Mutations in three alleles at two loci are essential to express a BBS phenotype in some familial cases (Katsanis et al. 2001; Eichers et al. 2004; Harel et al. 2015).

When a polygenic trait is subjective to environmental influence, it is called as a multifactorial trait.

Plate L was perhaps the first who used the term “polygenic” (Plate 1932). Later on, Fisher (Fisher 1918) and Mather (Mather 1941) augmented the significance of term “polygenic inheritance” (Guo 2005).

The key characteristics of polygenic inheritance were extensively reviewed by Lerner in 1968 (Lerner 1968). It described the following properties:

1. Multiple genes influence most of the polychotomous traits.
2. Similar phenotypes can be expressed by a great variety of genotypes.

3. Environmental factors are able to considerably influence the phenotypic manifestation of a trait.
4. The genetic pool of the population often contains great reserves of genetic variability.
5. Polygenic traits tend to follow a continuous distribution pattern.
6. The genes regulating polygenic inheritance are no biochemically exceptional.

The terms “polygenic” and “multifactorial inheritance” are sometimes used interchangeably. Nevertheless, in the exact sense, polygenic denotes to the sum total of many genes; however multifactorial also involves the interaction of environmental and genetic determinants. Some of the commonly observed multifactorial diseases include infertility, epilepsy, asthma, diabetes, high blood pressure, epilepsy, hypertension, arthritis, cancer, manic depression, and schizophrenia (Laitinen et al. 2004). Some other examples include certain developmental abnormalities such as neural tube defects (NTDs), cleft lip/palate, isolated hypodontia, and congenital heart defects (Taipale et al. 2003). A complex multifactorial trait tends to show a low heritability (proportion of total variance that is genetic) compared to single gene disorders, for example, the heritability of schizophrenia is around 81%. Similarly, the heritability of diabetes is around 40%. Also, it is observed that only 2–5% of the close relatives of diabetes also suffer from diabetes. These examples indicate that for a multifactorial disease, no single genetic factor is sufficient enough to cause the disease and it takes a complex interaction between many factors to affect the susceptibility towards the disease. This may include exposure to various environmental toxins and an individual's own genetic predisposition towards the disease.

### Characteristics of a Multifactorial Disease

A multifactorial disorder has a combination of distinctive characteristics that can be

differentiated from Mendelian or sex-limited conditions (Lobo 2008). These are as follows:

1. Multifactorial disorders are relatively common in population and fail to show a clear Mendelian pattern of inheritance.
2. The frequency of the disease display sex predilection, and it may occur more frequently in one sex than another. However, it is not sex-limited trait in which the disease is present in both, expressed in one while it remains switched off in other. Furthermore, for some diseases, the threshold of the disease is variable in both the sexes. For example, systemic stenosis disease shows a significant female preponderance than girls. Another example is congenital dislocation of the hip, which is more frequently observed in women than men.
3. Environmental factors can influence the disease risk.
4. The concordance rates in monozygotic and dizygotic twins refute Mendelian proportions.
5. The diseases are ethnically biased and appears more frequently in a specific ethnic group.

### The Threshold Model for Discontinuous (Disease) Traits

A large number of multifactorial traits such as height and intelligence show continuous variation; nevertheless, there are some disorders such as diabetes mellitus and autism that display discontinuous variation with people either being affected or not with no intermediate state. This can be explained by threshold model. However, to understand that we should first understand the term “liability.”

#### Liability

Liability is a term used to collectively explain all the genetic and environmental influences that contribute to the development of a multifactorial trait. Though it is almost impossible to estimate the liability of an individual, the liability of a group can be ascertained depending on the number of affected individuals in that group. Liability is represented as a standard distribution curve, as

most of the unaffected individuals will have some degree of liability and only a small percentage of a population will show a liability that is very low or that surpassing the threshold level.

### Threshold Model

For discontinuous traits, it is assumed that there is a liability threshold; individuals whose genetic predisposition surpasses the above will manifest the disease.

## Genomic Approaches to Decipher Multifactorial Disorders

### Traditional Approaches

Classical approaches to study multifactorial disorders involve pedigrees analysis or preparation of family trees which gives an idea of the inheritance pattern of the disease. Subsequently, the use of linkage mapping became more prevalent, and single-nucleotide polymorphism (SNP) markers along the genome were being used as reference points to investigate the DNA sequences that were co-inherited with a particular disease. These co-inherited regions were referred to be in linkage disequilibrium (LD) (Ralston 2008). However, the approach of linkage mapping had some limitations as these were typically ineffective in analyzing diseases with low heritability and those traits that are limited to small families.

### New Approaches

With the advent of omics era, novel techniques such as whole genome sequencing were used to identify disease loci. This method was utilized for comparing the genome of affected cases versus unaffected controls. The comparison was exploited to locate the potential risk causing genes or “hot spots” for a particular trait (Ralston 2008).

## Genetic Counseling in Multifactorial Disorders

For genetic counseling in multifactorial disorders, the counselor has to carefully detect the recurrence risk of the disease in the relatives of an

diseased individual. If the counselor observes that more than one children in a family is born with a multifactorial condition, it indicates either that the couple has high genetic predisposition towards the disease or they have suffered chronic environmental insult or both. Thus, the genetic counseling in multifactorial disorders is contingent upon a thorough pedigree analysis and a relevant up-to-date empirical data (Bijanazadeh 2017).

## Cross-References

► [Polygenic Inheritance](#)

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## Multigravida

- [Multiparous](#)

## Multimodal

- [Catarrhine Communication](#)
- [Mustelid Communication](#)

## Multimorbidity

- [Comorbidity](#)

## Multiparous

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## Synonyms

[Multigravida](#); [Parous](#)

## Definition

Having given birth on two or more occasions.

## Introduction

Animals that reproduce repeatedly across their lifespan face trade-offs between current reproductive investment and future potential reproductive opportunities (Stearns 1992). As such, the probability that a female reproduces at a given time, and the resources she then allocates to a reproductive event, is contingent upon her current condition, her prior reproductive experience, and the likelihood that she will survive to reproduce subsequently. Prior reproductive experience (parity) is particularly important in animal societies where offspring are heavily dependent on parents for nourishment and protection, with multiparous mothers tending to be more adept at raising offspring than first-time mothers (primipares). As such, variation in maternal behavior according to reproductive experience can affect the survivorship of offspring and profoundly influence their physical and social development. Since the term multiparous is largely restricted to mammalian literature, this entry draws heavily on mammals. Nonetheless, age-related increases in reproductive performance are widespread across other taxa (birds, reptiles, fish), the underlying causes of which are likely to have parallels with those operating in mammals (see Curio 1983; Forslund and Pärt 1995).

## Experienced Mothers

It is common for multiparous females in natural populations to produce larger litters and raise more resultant offspring to independence than primiparous females (Clutton-Brock 1991). As mammals are often still growing at the time of first breeding, the lower success of primiparous mothers is thought in part to reflect a trade-off between allocating energy to current reproduction versus ongoing growth and somatic maintenance. Even so, smaller females tend to produce smaller



offspring with lower survival rates independently of reproductive experience (Clutton-Brock 2016), which can make it difficult to disentangle parity effects per se from differences in female size or condition at different reproductive stages. Similarly, inexperienced mothers are more likely to occupy socially subordinate positions within animal societies, which is also associated with lower reproductive outputs. To fully understand the causes of parity-related changes in reproductive output, it is therefore necessary to quantify the behavioral, social, and physiological contributions to parental care in mothers at different stages of development.

Rather than being entirely instinctive, maternal behavior is modified by experience gained through rearing young, with the quality of care tending to improve over successive reproductive events. Notably, time spent in the proximity of offspring does not necessarily translate into improved maternal care and increased offspring survival. Instead, multiparous mothers appear to be more efficient in allocating their time to offspring, targeting their investment to periods when offspring care is most needed. For example, in feral horses in New Zealand, older mares were more protective over foals in their first 20 days of life, but were less diligent subsequently (Cameron et al. 2000). As foal mortality is highest in early life, offspring from older mares enjoy higher survivorship despite their reduced contact with foals thereafter. Support for such targeted investment is also found in wild primates such as chimpanzees (Stanton et al. 2014) and baboons (Nguyen et al. 2012). In both species, it is typical for inexperienced mothers to display closer and more prolonged contact with infants, but this does not translate into improved offspring survival. That age-related increases in reproductive success occur without increases in reproductive investment is at odds with models of residual reproductive value, which predict that females should invest more effort into each successive reproductive event as her number of potential future offspring declines. Even so, no study in a wild mammal population has accurately quantified

energy expenditure during lactation across repeated reproductive events, which would provide a stronger footing on which to compare hypotheses concerning age-related maternal investment.

Maternal investment also includes the defense of young against predators or conspecifics, the latter being particularly important in cases where females are territorial or where conspecific infanticide is commonplace. As with other behaviors, it might therefore be expected that the detection and recognition of threats to offspring, and their subsequent handling improves with reproductive experience. This was found to be the case in Belding's ground squirrels, as levels of vigilance and aggression during gestation and lactation increased with parity (Nunes 2014). Additionally, multiparous ground squirrels reacted less strongly to an introduced, caged conspecific male, more quickly recognizing the intruder as nonthreatening. Thus, the discriminatory capacity of multiparous mothers is better, allowing them to act appropriately given social circumstance.

Experience-related improvements across such a broad range of maternal behaviors imply an active role of social learning in modulating parental investment. An association between learning and maternal experience has been explored in mice and rats, where the propensity for learning, working memory, and long-term memory are all augmented in multiparous mothers compared to primiparous mothers (Pawluski et al. 2006). The strong component of learning to the expression of maternal behaviors could confer an adaptability to females, allowing parental investment to be responsive to the conditions mothers experience across their development. At a proximate level, the increased learning ability and improved competence of care in multiparous mothers is reflected in significant changes in neural biochemistry. One of various hormones implicated in such changes is oxytocin, which mediates key maternal behaviors in rats such as pup licking and pup nursing (Pedersen and Prange Jr 1988) while also being

directly involved in improving long-term spatial memory during motherhood (Tomizawa et al. 2003).

The improved targeting of maternal behaviors by experienced mothers is mirrored by improved physiological competence. In captive rats, the efficiency of energy allocation to reproduction amounts to 25% in primiparous females versus 38% in multiparous females, despite similar pup growth rates and survival from litters of standardized size (Künkele and Kenagy 1997). Supported with additional evidence such as increased milk quality and yields in primates (Hinde and Milligan 2011), it is apparent that multiparous females have greater energetic reserves available for mobilization during pregnancy and lactation than primiparous females. Hence, novice mothers often need to invest more resources per unit of reproductive output to compensate for physiological inefficiencies.

## Parity in Humans

In humans, unlike in other animal societies, offspring born to multiparous females are frequently considered to be at a disadvantage. Ideas concerning “firstborn advantage” can be traced to Francis Galton, who noted a preponderance of firstborn sons in eminent positions in 1874 (Galton 1874). More recent treatments similarly support an association between birth order and intelligence and importantly, provide good evidence that this association arises through social rank effects rather than through gestational effects; later-born Dutch conscripts that lose an elder sibling as a child attain an adult IQ score comparable to men of higher birth order (Kristensen and Bjerkedal 2007). Firstborn advantage in contemporary human populations is reflected in various other metrics, such as increased nourishment (Ballweg and Pagtolun-An 2002), better schooling (Black et al. 2005), and improved healthcare (Kaplan et al. 1992). Consequently, although human mothers encounter problems of physiological inefficiency when

breeding for the first time as in other mammal species (offspring born to multiparous mothers are heavier at birth (Kaplan et al. 1992)), this initial deficit is compensated for by reduced sibling competition and increased parental attention. Theoretically, firstborn children are favored even if parental resources are distributed equally among children at any given time (Hertwig et al. 2002).

Yet, despite many studies highlighting the reduced performance of offspring born to multiparous females, in various human societies the pattern is absent or reversed. For example, in the hunter-gatherer !Kung communities of Southern Africa Draper and Hames (2000) found a positive relationship between birth order and reproductive success. Among population differences in birth order effects are regularly attributed to differential patterns of land and wealth inheritance, patterns that can be understood under Darwinian considerations of the resource-holding and reproductive potential of individuals (Hrdy and Judge 1993). In this regard, it is easy to see how the historically widespread practice of primogeniture, the right of firstborns to parental wealth, would tend to disfavor offspring born to multiparous mothers. In contrast, the !Kung lack divisible material wealth, meaning that lastborn individuals in !Kung families might benefit from a larger number of siblings, and thus kin-directed assistance, across their reproductive lifespan (Draper and Hames 2000). Clearly, both cultural and biological factors must be taken account of when thinking about multiparity in humans (Hrdy and Judge 1993; Draper and Adams 2000; Myrskylä et al. 2013; Savage et al. 2013; Derraik et al. 2016; Rohrer et al. 2015).

## Cross-References

- Fraternal Birth Order Effect
- Life History
- Matrilines and Patrilines
- Parturition
- Reproduction

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## Multiple Gene Inheritance

- [Complementary Genes Hypothesis](#)
- [Polygenic Inheritance](#)
- [Polygeny](#)

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## Multisensory Integration

- [Cross-Modal Transfer](#)

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## Muscle of Mastication

- [Masseter Muscle](#)

## Muscular System

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### Definition

Muscle tissue is a specialized structure in the body of animals that acts by contracting myosin and actin, creating movement when stimulated by nervous tissue, specialized conducting fibers, or hormones.

### Introduction

Muscle tissue is found throughout the body and allows for movement by contraction. There are three different types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle. The name given to muscle tissue is usually related to its location or characteristic appearance microscopically. When muscle tissue contracts or becomes shorter, the body or organ in the body move in a given direction. While each of these muscle types shares similar functions, they individually possess unique characteristics. “Locomotion, movement through the environment, is the behavior that most dictates the morphology and physiology of animals” (Dickinson et al. 2000, p. 100).

### Muscle Contraction

For the purpose of understanding general muscle contraction, it is important to know that muscle fibers are composed of smaller units that are grouped in a longitudinal fashion where portions interlock with one another at a microscopic level. Two proteins make up the contractile elements of striated muscle: the thick filamentous fibrous

protein cluster named myosin and the thinner filamentous protein named actin. Striated muscle includes cardiac and skeletal muscle and is distinguished as striated because the myosin and actin proteins are organized in a striped fashion. Smooth muscle, as the name suggests, organizes its contractile proteins differently and does not produce the striated appearance.

The interaction of myosin and actin filaments is regulated by other proteins (aptly called regulatory proteins). These proteins determine when actin-binding sites are available for myosin binding. Myosin-binding site regulatory proteins (troponin & tropomyosin) are found along the actin filaments and cover the actin-binding sites, preventing them from binding to myosin. In turn, these regulatory proteins are controlled by calcium ions. Contraction occurs when the myosin and actin bind together to produce movement.

When nerves within the muscle receive electrical signals that travel through muscle cells, calcium is released. As calcium ions increase around the contractile filaments, they bind to a portion of troponin, one of the regulatory proteins, allowing actin to bind with myosin causing muscle contraction. Muscle contraction typically ends when electrical signals stop being sent and calcium is resorbed.

Adenosine triphosphate (ATP) is the chemical molecule that powers muscle contraction. At the beginning of contraction, the myosin head is bound to actin molecules and Adenosine triphosphate (ATP) is absent. In order for release to occur, ATP must bind to the myosin head, which in turn causes a change in shape of the actin-binding site. This conformational change loosens the bond and causes the myosin head to release from the thin actin filament. The ATP-binding sites undergo further conformational shape shifting, causing the myosin head to bend. The myosin head movement is caused by the breakdown of ATP into Adenosine diphosphate (ADP) and inorganic phosphate; both of these products remain bound to the myosin head. This causes the myosin head to linearly displace relative to the thin filament. Once the myosin heads weakly bind to its new sites, inorganic phosphate is released, which has two effects. First, the bond increases with strength

and, second, the myosin head generates a force as it returns to its original unbent state forcing the thin filament to move along the thick filament. During this step, ADP is lost from the myosin head. To fully understand this concept, imagine the actin molecules as marbles that run along the length of a rope – the rope being the thin filament, which allows a numerous amount of binding sites for the myosin head to continually progress the thin filament forward to further the contracture.

A practical application of the above text helps us understand the phenomenon of muscle rigidity or muscular contraction experienced after death, known as rigor mortis. When an animal dies, ATP production is terminated, and thus no energy is produced. Since it requires more ATP for muscle relaxation than contraction, this explains why rigor mortis occurs following death.

### Three Main Types of Muscle Tissue

#### Skeletal Muscle

Skeletal muscle is attached to bone (or the skeleton) and is responsible for the majority of body movements, its position, and posture. These muscles perform functions such as walking, swallowing, and urination. “Skeletal muscles also protect internal organs by acting as an external barrier or shield to external trauma and by surrounding the weight of the organs” (Kaufmann et al. 2018, 10.1). Skeletal muscles are under voluntary or conscious control in contrast to smooth muscles, which are under involuntary or unconscious control.

“Each skeletal muscle has three layers of connective tissue that enclose it, provide structure to the muscle, and compartmentalize the muscle fibers within the muscle” (Kaufmann et al. 2018, 10.1). An individual muscle is surrounded by a thick connective tissue termed the *epimysium*, “which allows a muscle to contract and move powerfully while maintaining its structural integrity. The epimysium also separates muscle from other tissues and organs in the area, allowing the muscle to move independently” (Kaufmann et al. 2018, 10.1). Moving within the epimysium, there are individual bundles of muscle fibers termed

fascicles. These individual bundles are organized within another connective tissue termed the *perimysium*. “This fascicular organization is common in muscles of the limbs; it allows the nervous system to trigger a specific movement of a muscle by activating a subset of muscle fibers within a fascicle of the muscle” (Kaufmann et al. 2018, 10.1). Lastly, each fiber has its respective connective tissue covering termed the *endomysium*.

At each end of the skeletal muscle, the connective tissues merge to form connective tissue tendons, which is how each muscle is attached to a particular place. Tendons are usually understood to connect muscles to bone; specifically, the tendon fuses with the periosteum covering of the bone. The periosteum is described as a vascularized connective tissue that surrounds bones, except at joints. As muscle fibers contract, tension is distributed through the connective layers, through the tendon, and finally to the periosteum, which pulls on the bone allowing movement of the skeleton (Kaufmann et al. 2018). Tendons hold such impressive tensile strength that when exposed to extreme forces, a tear in a portion of muscle or a break of bone where the tendon attaches is more likely to occur (Dyce et al. 2010).

Muscles receive blood supply and innervation from nearby arteries and nerves, which travel through the various layers of connective tissue. They branch into even smaller extensions as they travel inwards, toward the endomysium and underlying fibers. An important distinction skeletal muscle has from other muscle tissues is its innervation by the somatic nervous system (SNS). The SNS is under conscious voluntary control and allows movement from skeletal muscles to be controlled consciously. “Unlike cardiac and smooth muscle, the only way to functionally contract a skeletal muscle is through signaling from the nervous system” (Kaufmann et al. 2018, 10.1).

Skeletal muscle can vary in color and appearance which is partly determined by the amount of myoglobin within the fibers. “Myoglobin is an oxygen-binding protein that closely resembles hemoglobin found in erythrocytes (red blood cells) and occurs in varying amounts in muscle



fibers. It provides a ready source of oxygen for muscle metabolism” (Ross and Pawlina 2011, p. 313). Most skeletal muscle is composed of three fiber types, of which the proportions vary. Of these three, type I fibers (slow oxidative fibers) are colored red and are small in size. They contain many mitochondria and high levels of myoglobin concentration; explaining why type I fibers exhibit impressive endurance and take longer to fatigue. “Importantly, type I fibers are the primary fibers of the long muscles of the back in humans, explaining how maintaining an erect posture is possible for long periods of time” (Ross and Pawlina 2011, p. 313). Type IIa (fast oxidative glycolytic fibers) fibers also contain high levels of myoglobin and mitochondria; however, they contain high levels of glycogen and therefore are capable of anaerobic glycolysis. These components allow type IIa fibers to be termed fast-twitch fatigue-resistant motor units. Type IIb (fast glycolytic fibers) are larger fibers, which are also red in color. They contain less myoglobin and mitochondria than the previously discussed fibers. They contain high levels of anaerobic enzymes in addition to a large amount of glycogen. While their ability to utilize energy is the fastest of the fibers, they also fatigue rapidly due to lactic acid production. This explains their adaptation for rapid contraction and accurate movements, such as dexterous movements like playing the piano. An interesting example of the importance of the contribution of these fibers can be observed in the instinctive rapid swim movement of shrimp. “Forty percent of the body mass of a shrimp is devoted to the large, tasty abdominal muscles that produce a powerful tail flick during rare, but critical, escape behaviors. During escape, rapid acceleration, rather than energy minimization, is the relevant aspect of performance” (Dickinson et al. 2000, p. 102).

### Cardiac Muscle

Cardiac muscle makes up a majority of the heart. As discussed earlier, cardiac and skeletal muscle have the same organization and types of contractile filaments. A difference cardiac muscle has when compared to skeletal muscle is its intercalated disks that connect individual cardiac muscle

cells. These intercalated disks serve as an important component of the synchronized contraction that cardiac muscle exhibits. Gap junctions are found within the intercalated disks and “provide ionic continuity between adjacent cardiac muscle cells, thus allowing informational macromolecules to pass from cell to cell” (Ross and Pawlina 2011, p. 330), ultimately enabling cardiac muscle fibers to behave as one, while retaining cell-self. The heart beat exhibits continuous contraction by unique cardiac muscle cells and conducting fibers known as Purkinje fibers.

Sympathetic and parasympathetic nerves communicate with these parts of the heart by stimulating the heart to increase, or decrease in rate, conduction, and contractility. The sympathetic nervous system, most commonly referred to as “fight or flight,” typically happens in situations of panic. The parasympathetic system is referred to as “rest or digest.” An example of sympathetic drive would be a gazelle running from a cheetah. The gazelle’s sympathetic nervous system would take over the parasympathetic, increasing cardiac contractions. This would allow more blood to flow through vessels, resulting in more oxygen delivery throughout the body, giving the gazelle a chance to endure the race for life.

Trauma to an area of the heart resulting in injury can cause that portion of cardiac muscle tissue to die and eventually be permanently replaced with fibrous connective tissue. Fibrous connective tissue, commonly termed scar tissue, is responsible for repairing injuries to many tissues of the body. Unfortunately, when a portion of the heart dies or becomes scar tissue, cardiac function is lost at that site. This type of cardiac injury is commonly referred to as myocardial infarction or heart attack.

### Smooth Muscle

Smooth muscle is termed so because of how its contractile proteins are organized in appearance at the microscopic level. They surround blood vessels and internal organs, such as the digestive tract. Smooth muscle is under involuntary control and can be stimulated by hormones and conduction from the autonomic nervous system (Kaufmann et al. 2018). The autonomic nervous

system can be further broken down into the sympathetic and parasympathetic nervous system. As described earlier, the parasympathetic nervous system is critical for digestion. Parasympathetic stimulation encourages oxygen delivery and other useful materials to support the energy required for digestion, such as the propulsive movements by smooth muscle directing ingested material through the intestinal tract. If sympathetic stimulation were to occur, oxygen delivery would be directed toward other areas of the body in need. Smooth muscles are able to operate with coordination because of the gap junctions found between its cells. “Single-unit smooth muscle produces slow, steady contractions that allow substances, such as food in the digestive tract, to move through the body” (Kaufmann et al. 2018, 10.7).

## Conclusion

Muscle tissue is made up of muscle cells grouped together in the body of animals. The proteins that make up muscles is comprised of actin and myosin. Contraction or movement by muscles occurs when the proteins slide past each other forming tension that changes the shape of muscle cells and can create significant or subtle force for motility. Contraction requires energy or ATP to occur. Muscle tissues are either voluntary (striated) or nonvoluntary (smooth) and are divided into skeletal, cardiac, and smooth. Muscle tissue is responsible for locomotion, posture, shape, heartbeat, and other organ movement such as intestinal contractility to help pass food throughout the gastrointestinal tract.

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## Mustelid Communication

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## Synonyms

Acoustic communication; Badgers; Communication; Martens; Modality; Multimodal; Mustelids; Olfaction; Otters; Scent; Sensory channel; Signal; Social organization; Sociality; Vision; Vocalization; Weasels

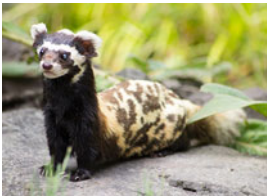
## Introduction

Mustelids are a large family, with 60 species found in Eurasia, Africa, Asia, North and South America (Koepfli et al. 2008). As shown in Table 1, the family contains eight subfamilies, with many fascinating species like the European badger (*Meles meles*), the sea otter (*Enhydra lutris*), and the wolverine (*Gulo gulo*), to name but a few.

Communication in mustelids is closely related and dependent on the species' respective social system and habitat (Buesching and Stankowich 2017). The social and spatial organization of mustelids is highly variable between species, but there may be also variation in different populations of the same species (Kruuk 2006; Newman et al. 2011). Divergence of a pure solitary lifestyle is induced by environmental

**Mustelid Communication, Table 1** Subfamilies and number of genera and species in the family of mustelids. Each genus is shown with one exemplary species. The number of all genera and species is given in the

subheadings for each subfamily (genera/species). All subfamilies are depicted with one representative species. Taxonomy following Koepfli et al. 2008

|                                                              |                                                                                                                                                                                                                                                                            |                                                                                                              |
|--------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------|
| Subfamily: Galictinae (4/6)                                  |                                                                                                                                                                                                                                                                            |                                                                                                              |
| Galictis<br>Ictonyx<br>Poecilogale<br>Vormela                | Greater grison ( <i>G. vitatta</i> )<br>Striped polecat ( <i>I. striatus</i> )<br>African striped weasel ( <i>P. albinucha</i> )<br>Marbled polecat ( <i>V. peregusna</i> )                                                                                                | <br>Marbled polecat        |
| Subfamily: Helictidinae (1/5)                                |                                                                                                                                                                                                                                                                            |                                                                                                              |
| Melogale                                                     | Chinese ferret-badger ( <i>M. moschata</i> )                                                                                                                                                                                                                               | <br>Chinese ferret-badger  |
| Subfamily: Lutrinae (6/13)                                   |                                                                                                                                                                                                                                                                            |                                                                                                              |
| Aonyx<br>Enydra<br>Lontra<br>Lutra<br>Lutrogale<br>Pteronura | Asian small-clawed otter ( <i>A. cinerea</i> )<br>Sea otter ( <i>E. lutris</i> )<br>North American river otter ( <i>L. canadensis</i> )<br>European otter ( <i>L. lutra</i> )<br>Smooth-coated otter ( <i>L. perspicillata</i> )<br>Giant otter ( <i>P. brasiliensis</i> ) | <br>Eurasian otter        |
| Subfamily: Martinae (3/10)                                   |                                                                                                                                                                                                                                                                            |                                                                                                              |
| Eira<br>Gulo<br>Martes                                       | Tayra ( <i>E. barbara</i> )<br>Wolverine ( <i>G. gulo</i> )<br>European pine marten ( <i>M. martes</i> )                                                                                                                                                                   | <br>European pine marten |
| Subfamily: Melinae (2/4)                                     |                                                                                                                                                                                                                                                                            |                                                                                                              |
| Arctonyx<br>Meles                                            | Hog badger ( <i>A. collaris</i> )<br>European badger ( <i>M. meles</i> )                                                                                                                                                                                                   | <br>European badger      |

(continued)

**Mustelid Communication, Table 1** (continued)

|                                 |                                                                                                                 |                                                                                                       |
|---------------------------------|-----------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------|
| Subfamily: Mellivorinae (1/1)   |                                                                                                                 |                                                                                                       |
| Mellivora                       | Honey badger ( <i>M. capensis</i> )                                                                             | <br>Honey badger    |
| Subfamily: Mustelinae (3/20)    |                                                                                                                 |                                                                                                       |
| Lyncodon<br>Mustela<br>Neovison | Patagonian weasel ( <i>L. patagonicus</i> )<br>Stoat ( <i>M. erminea</i> )<br>American mink ( <i>N. vison</i> ) | <br>Stoat           |
| Subfamily: Taxidiinae (1/1)     |                                                                                                                 |                                                                                                       |
| Taxidea                         | American badger ( <i>T. taxus</i> )                                                                             | <br>American badger |

Picture credits: Marbled polecat by Volker Röhl on Wikipedia; Chinese ferret-badger by Chien-Jen Wang; Eurasian otter by Gellinger on Pixabay; European pine marten by Maxmann on Pixabay; European badger by Chris Parfitt on Flickr; Honey badger by Derek Keats on Flickr; Stoat by Jo Garbutt on Flickr; American badger by Northwest Power and Conservation Council on Flickr

factors such as habitat, geographical distribution, ecomorphology, resource dispersion, or season (Johnson et al. 2000). The socio-spatial organization of mustelids is based on the “classical” system of one male territory encompassing distinct female territories. Several variations of and exceptions from this basic pattern exist as well (Kruuk 2006).

As knowledge on mustelids accumulates, several species which formerly have been described as purely solitary turn out to be more social, or have at least a much more flexible social lifestyle (e.g., Newman et al. 2011).

Each communication channel has its advantages and disadvantages. One may be more useful than the others, depending on when, where, and which information needs to be transmitted. Compared to acoustic signals, chemical markings

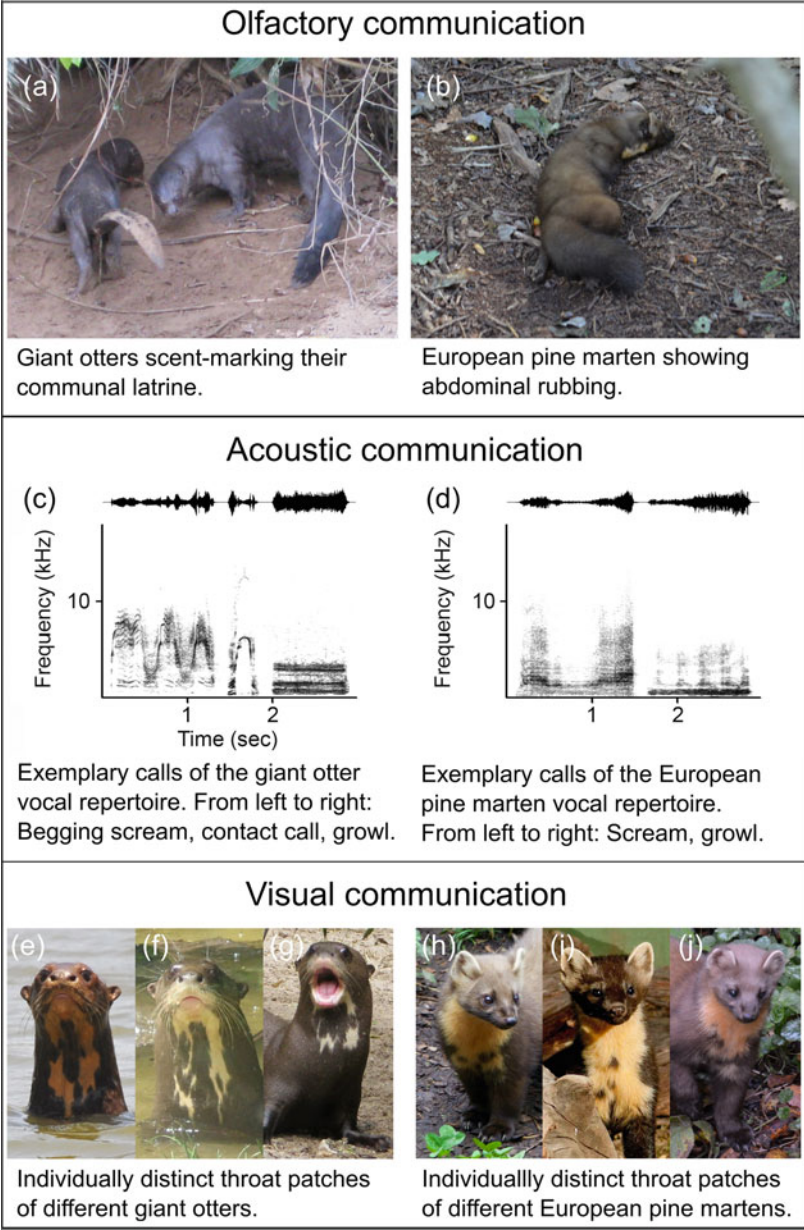
persist for an elongated time, thereby allowing conspecifics or co-occurring species to gather information even in the physical absence of the sender. In a habitat where olfactory cues cannot be deposited, acoustic communication may be favored (Fig. 1). This is especially true for the subfamily of otters. With the exception of sea otters (see below), they show a semiaquatic lifestyle and only use scent-marking on land (Kruuk 2006).

### Olfactory Communication

Olfactory communication has a multipurpose function. It is regarded as the most important communication channel for mustelids, probably because all mustelids are territorial and scent-

**Mustelid Communication,**

**Fig. 1** Mustelid communication in three sensory channels. Olfactory communication: two examples of scent-marking postures; acoustic communication: spectrograms of vocalizations showing frequency over time; visual communication: throat patterns likely used for visual (Picture credits **a**, **c**, **d**, **f**, and **g** by Christina Mumm, **b** and **j** by Pia Weidenmüller (written license), **e** by Hannah Heitherr (written license), **h** by user 422737 on pixabay (CC0 license), **i** by user Ellis Lawrence on flickr (CC BY-SA 2.0 license). Recordings: **c** by Christina Mumm, **d** by Tierstimmenarchiv Berlin)



mark their territories to announce ownership. It further allows mustelids to signal information on reproductive state, as well as information on identity and food resources. To exchange more detailed information, the animals may vary frequency and location of markings.

Territorial scent-marking can be done by the deposition of feces, urine, or a combination of both (i.e., excremental marking, see Fig. 1a), as

well as through gland secretion (i.e., secretional marking). Secretion may be produced in anal, ventral, foot, or subcaudal glands and applied by body rubbing, anal drag, or scratching (see Fig. 1b). Gland secretions can also be used to mark conspecifics. In some species, territorial scent-marking is enhanced by visually marking the surroundings, e.g., by scratching the ground or trees (e.g., Hutchings and White 2000;



Leuchtenberger and Mourão 2009). Otter spraints consist of feces, anal gland secretion, and often of a third compound, the “jelly.” Not much is known about this slimy substance, the only available information is that it “is secreted somewhere in the intestine itself” (Kruuk 2006). Chemical composition varies among feces, urine, and gland secretion, thereby allowing for the transmission of differential information (Clapperton 1989).

Deposition of scent is not random in time and space (Kilshaw et al. 2009). For scent-marking, the animals select prominent places, on stones, under bridges, or on other landmarks, which are frequently revisited (Hutchings and White 2000). Otters may even choose marking places which are relatively far and visit them repeatedly (Kruuk 2006). Furthermore, European badgers do not only carefully select marking places, but also the positioning of scent inside each place (Stewart et al. 2002). As badger territories contain more than one latrine site, the animals systematically revisit several places to refresh their scent marks (Kilshaw et al. 2009).

Social species like European badgers and giant otters (*Pteronura brasiliensis*) make use of communal latrines – enlarged areas for the deposition of excremental and secretional marks from all group members. Giant otters regularly clear off the vegetation at communal latrines. Otters in general show an elaborate marking behavior because the deposition of excremental and secretional marks can be accompanied by a scent-marking “dance.” Giant otters, as well as spotted-necked otters (*Lutra maculicollis*), and North American river otters (*Lontra canadensis*) show dance-like stepping postures, accompanied by intense sniffing. Giant otters use their forepaws for dancing, while spotted-necked otters and North American river otters use their hind legs. Some species may also smear feces from different individuals with their paws or tail to create a typical group odor (e.g., Buesching et al. 2016; Leuchtenberger and Mourão 2009; Rostain et al. 2004).

In several mustelids scent-marking frequency shows seasonal changes, mainly with a peak in the mating season. Mustelids scent-mark within their territory (“hinterland latrines”) or at territorial

borders (“boundary latrines”). Both types have different functions, which are best described in badgers. The use of different latrine sites depends on population density and season. In high-density populations, European badgers form social groups, whereas in low-density populations, groups mainly consist of a pair and their offspring. Larger groups have more latrines inside their home range, but space is limited in high-density populations, so that these groups usually occupy smaller areas. They invest mainly in boundary latrines; however, their function in territorial defense is not fully understood (Buesching et al. 2016). Nevertheless, European badgers can discriminate between feces from neighboring and alien groups and react more aggressively towards the scent of alien groups. Smaller badger groups in low-density populations may use larger areas, but their ability of marking is limited by the number of individuals. Therefore, small groups may neglect boundary latrines and the use of hinterland latrines peaks during mating time. Latrine use is even abandoned seasonally, when home range size is enlarged. This shows a trade-off between group size and the area a group is able to defend, either in terms of limited space or in terms of limited number of individuals marking the latrines (Buesching et al. 2016). Population density also affects the main information provided at latrines: they likely function to signal territoriality in high-density populations, but reproductive state and other individual information in low-density populations (Zhou et al. 2015). In low-density populations of Japanese badgers (*Meles anakuma*), information provided at both latrine types eases information exchange about presence, identity, and hormonal state of females, and Japanese badgers visit boundary latrines most often during mating season (Kaneko et al. 2009). Hog badgers (*Arctonyx collaris*), which are described to be solitary, use latrines for a different reason: they signal the location of food resources (Zhou et al. 2015). This behavior is also found in coastal Eurasian otters (*Lutra lutra*), which mark food patches and freshwater pools to signal their use of these resources (Trowbridge 1983). Scent-marks allow them to inform conspecifics that the resource is already depleted, and avoid direct

competition and confrontation. Besides its importance for signaling territoriality and reproductive state, excremental markings may also aid in spatial orientation. For instance, Eurasian otters mark locations where their trails change direction (Trowbridge 1983).

The only mustelid in which excremental marking is absent is the sea otter. This exception is due to its exclusive aquatic lifestyle, differing from all other otters, which have a semi-aquatic lifestyle. Instead of scent marking, male sea otters defend their marine territories during the mating period by patrol swimming, splashing, and direct chases of rivals (Kruuk 2006).

Secretional marking is also important in territoriality, spatial organization, and individual information exchange. Dominant males of European badger groups intensify secretional marking of females during mating season (Kruuk et al. 1984). Individually distinct odor cues are found in several mustelids. Ferrets (*Mustela putorius furo*) do not only distinguish the deposition time of conspecific odor, but also discriminate between different individuals because the composition of volatiles is individually distinct. The combination of this information enables ferrets (and likely all other mustelids) to learn movement patterns of conspecifics, adjust their activities accordingly, and thereby avoid direct aggressive encounters.

Even though mustelids may encode individual identity in all available signal modalities, most studies focus on olfactory communication. Experiments on olfactory discrimination or recognition in mustelids are restricted to a few species, and older studies often tested only one focal animal, thereby providing descriptive indications rather than reliable statistical data for further comparisons.

Volatile compounds produced by mustelids differ between species, and show sufficient variation to encode sex, age, and individual identity (Brinck et al. 1983). Identity cues can either be encoded by presence or absence of certain compounds and/or through the amount and composition of the chemical compounds. For instance, gland secretions of Siberian weasels (*Mustela sibirica*) and the urine of ferrets contain sex-specific chemical compounds, while steppe

polecat (*Mustela eversmanni*) secretions encode sex in the relative abundance of different compounds (Zhang et al. 2002; Zhang et al. 2005).

Group or family odors can be created by secretional marking of conspecifics; cubs, mates, or other group members are normally labeled by body rubbing (Duplaix 1980). Group odors can be combined with individual distinct odors as well. For instance, European badgers use the scent from their subcaudal gland to create a group odor and to share individual information, especially about their reproductive state (Buesching et al. 2003). They distribute their group odor through mutually marking each other, but deposit their individually distinct odor by sequential allo-marking, i.e., one badger rubbing its scent onto the fur of other group members (Buesching et al. 2003).

The function of scent cues may also be influenced by composition of social groups. North American river otters, for instance, show a flexible social organization. When females rear their young, they may build family groups, sometimes with elder helpers, or stay solitary, while males may form temporary groups of up to 30 individuals (Larivière and Walton 1998). Group-living females use scent cues for territorial maintenance and solitary individuals use them for avoiding direct encounters with conspecifics (Ben-David et al. 2005). Whereas in male groups, scent cues help to maintain a dominance hierarchy (Rostain et al. 2004).

In areas where different mustelid species co-occur, interspecies competition seems to be low due to different habitat and dietary preferences or foraging strategies (Hussain et al. 2011). Nevertheless, interspecific territoriality and social dominance are most likely communicated via olfactory cues.

Several mustelid species, e.g., the striped polecat (*Ictonyx striatus*) and the African striped weasel (*Poecilogale albinucha*), can produce chemical defensive sprays (Apps et al. 2015; Larivière 2001), comparable but not as strong as those known from skunks (*Mephitidae*). Other mustelids, such as the American mink and the honey badger (*Mellivora capensis*), do not directly spray, but also produce deterrent secretion when threatened (Brinck et al. 1978; Vanderhaar

and Hwang 2003). The respective volatile compounds are produced in anal glands, and are foul and strongly smelling (Apps et al. 2015; Larivière 2001).

Currently, no information on the mustelids' sense of smell is available but it is conceivable that their olfactory perception is highly sensitive, given the importance of odor cues for social communication.

## Acoustic Communication

Many mustelids are extremely vocal and often engage in screaming, hissing, chuckling, squeaking, and squealing. Mustelids may signal identity cues, intention, stay in contact or beg for food via the acoustic channel. Some vocalizations also play a role in territorial defense. Nevertheless, peer-reviewed publications of the vocal repertoire exist for only 12 species and anecdotal descriptions are available for only 14 more (for an example of European pine marten calls see Fig. 1d). The acoustic communication of the remaining 34 species has not been studied so far (Table 2). There are no publications on acoustic communication in Helictidinae, and Taxidiinae. Most descriptions are found for the subfamily of otters. Outstanding in terms of vocal complexity are two representatives of the otters: the Asian small-clawed otter (*Aonyx cinerea*) and the giant otter (*Pteronura brasiliensis*).

To date, giant otters are the best studied mustelid concerning acoustic communication. Several authors described the vocal repertoire to consist of 15–19 distinct vocalizations (see some examples in Fig. 1c). This elaborate repertoire is further enlarged by gradations between calls. Like in many other otter species, such as sea otters, or Asian small-clawed otters, several giant otter vocalizations show enough variation in acoustic cues to provide individual differences and the potential for vocal discrimination and recognition (Leuchtenberger et al. 2016; Mumm and Knörnschild 2014). Giant otters use contact calls and hums for group cohesion and can discriminate between different individuals based on these

vocalizations alone (Mumm et al. 2014). Correspondingly, Asian small-clawed otters derive sufficient information from their contact calls to distinguish their mates from unknown individuals (Lemasson et al. 2013). Group screaming (a territorial vocalization) and snorts (a type of alarm call) provide acoustic information on group identity, thereby aiding giant otters in territorial defense. Moreover, acoustic parameters of snorts encode the sex of the calling individual, an aspect which is not prominently reflected in the physical appearance (Leuchtenberger et al. 2016; Mumm and Knörnschild 2017).

Some studies describe vocalizations of cubs. Apparently, innate precursors of the adult vocal repertoire are found in all species studied to date. Giant otter cubs emit adult-like vocalizations from birth on and combine them in long babbling bouts, presumably to practice. Some cub calls are age-specific and disappear during development (Mumm and Knörnschild 2014). American mink cubs are also vocally active from birth on. However, studies on hearing development in ferrets and mink cubs could show that hearing starts not earlier than around 30 days of age (Brandt et al. 2013; Moore and Hine 1992).

Hearing ranges and thresholds are known for six mustelid species. The hearing ranges of semi-aquatic otters and minks are largely comparable, while ferrets and stoats have a broader range. Best hearing lies between 1 kHz and 16 kHz (compare Brandt et al. 2013; Ghoul and Reichmuth 2012; Heffner and Heffner 1987). Overall, the hearing capacity of mustelids is comparable to other carnivores (Ghoul and Reichmuth 2012; Heffner and Heffner 1985). In tests for hearing and sound localization accuracy, least weasels performed better than their prey species (rodents), which underlines the selective pressure on carnivores for good sound detection abilities in order to localize their prey (Heffner and Heffner 1987).

## Visual Communication

Fur coloration and body postures are apparent in several mustelid species, but vision is poorly

**Mustelid Communication, Table 2** Publications describing the adult vocal repertoire of mustelid species

| Subfamily    | Species                                                 | Nr. of vocalizations | Detailed description of vocalizations | Reference                                               |
|--------------|---------------------------------------------------------|----------------------|---------------------------------------|---------------------------------------------------------|
| Galictinae   | Marbled polecat ( <i>Vormela peregusna</i> )            | 3                    | No                                    | Gorsuch and Larivière (2005)                            |
|              | African striped weasel ( <i>Poecilogale albinucha</i> ) | 6                    | Yes                                   | Channing and Rowe-Rowe (1977)                           |
|              | Greater grison ( <i>Galictis vittata</i> )              | 6                    | No                                    | Yensen and Tarifa (2003)                                |
|              | Striped polecat ( <i>Ictonyx striatus</i> )             | 6                    | Yes                                   | Channing and Rowe-Rowe (1977)                           |
| Lutrinae     | Smooth coated otter ( <i>Lutrogale perspicillata</i> )  | >3                   | No                                    | Larivière and Hwang (2005)                              |
|              | Hairy-nosed otter ( <i>Lutra sumatrana</i> )            | 3–8                  | No                                    | Wright et al. (2008)                                    |
|              | Congo clawless otter ( <i>Aonyx congicus</i> )          | 7                    | No                                    | Jacques et al. (2009)                                   |
|              | European otter ( <i>Lutra lutra</i> )                   | 7                    | Yes                                   | Gnoli and Prigioni (1995)                               |
|              | Sea otter ( <i>Enhydra lutris</i> )                     | 10                   | Yes                                   | McShane et al. (1995)                                   |
|              | African clawless otter ( <i>Aonyx capensis</i> )        | 11                   | No                                    | Larivière (2001)                                        |
|              | North American river otter ( <i>Lontra canadensis</i> ) | 11                   | Yes                                   | Almonte (2014)                                          |
|              | Spotted-necked otter ( <i>Hydrictis maculicollis</i> )  | 12                   | No                                    | Reed-Smith et al. (2014)                                |
|              | Asian small-clawed otter ( <i>Aonyx cinerea</i> )       | 7–17                 | Yes                                   | Lemasson et al. (2014), Tramm (2012)                    |
|              | Giant otter ( <i>Pteronura brasiliensis</i> )           | 15–19                | Yes                                   | Leuchtenberger et al. (2014), Mumm and Knörmisch (2014) |
| Martinae     | Fisher ( <i>Martes pennanti</i> )                       | >3                   | No                                    | Powell (1981)                                           |
|              | Tayra ( <i>Eira barbara</i> )                           | >4                   | No                                    | Poglayen-Neuwall (1974)                                 |
|              | Beech marten ( <i>Martes foina</i> )                    | 5                    | Yes                                   | Lodé (1991)                                             |
|              | American marten ( <i>Martes americana</i> )             | 7                    | Yes                                   | Belan et al. (1978)                                     |
|              | European pine marten ( <i>Martes martes</i> )           | 8                    | No                                    | Kvalheim (1982)                                         |
| Melinae      | European badger ( <i>Meles meles</i> )                  | 10                   | Yes                                   | Wong et al. (1999)                                      |
| Mellivorinae | Honey badger ( <i>Mellivora capensis</i> )              | >6                   | No                                    | Vanderhaar and Hwang (2003)                             |
| Mustelinae   | Long-tailed weasel ( <i>Mustela frenata</i> )           | 3                    | Yes                                   | Svendsen (1976)                                         |
|              | American mink ( <i>Neovison vison</i> )                 | >4                   | No                                    | Larivière (1999)                                        |
|              | Steppe polecat ( <i>Mustela eversmanni</i> )            | 6                    | Yes                                   | Farley et al. (1987)                                    |
|              | Black-footed ferret ( <i>Mustela nigripes</i> )         | 7                    | No                                    | Clark et al. (1986)                                     |
|              | European polecat ( <i>Mustela putorius</i> )            | 9                    | Yes                                   | Gossow (1970)                                           |
|              | Stoat ( <i>Mustela erminea</i> )                        | 9                    | Yes                                   | Gossow (1970)                                           |
|              | Weasel ( <i>Mustela nivalis</i> )                       | 9                    | Yes                                   | Gossow (1970)                                           |

studied, with only seven publications on five species (three otter species, European polecat, and ferret). Only one, but a very interesting study deals with visual cues in mustelids (Newman et al. 2005).

The otter eye is equivalent to that of other terrestrial mammals. Same visual acuity in air and underwater is achieved by an accommodation process which offsets loss of corneal refractive power underwater. The retinal resolution angle is about 14' in Asian small-clawed otters (Balliet and Schustermann 1971), and 7' in sea otters (Mass and Supin 2000), which is close to the angle of 5' in pinnipeds. European polecats and ferrets have a resolving angle of 16' (Neumann and Schmidt 1959). The amplitude of accommodation in sea otters is 60D and thereby comparable to that of humans (58D) (Murphy et al. 1990). Thus, we think that the often proposed poor visual abilities of mustelids can no longer be supported.

Fur coloration in mustelids reaches from inconspicuous unicolor (as in the Lutrinae), over contrasting black-and-white (as in the Galictinae) to a vivid coloration in the marbled polecat or the yellow-throated marten (*Martes flavigula*). Several species have facial masks, e.g., grisons and badgers, or individually distinct throat markings, e.g., giant otters and European pine martens (Fig. 1e–j) (Newman et al. 2005). Facial masks and throat markings may have different functions: facial masks are most likely a warning signal since they are found in species which produce defensive sprays and anal gland secretion in threatening situations (Newman et al. 2005). Throat markings, on the other hand, probably play a role in individual communication. Many mustelids stand on their hind legs when monitoring their surroundings, and giant otters periscope out of the water when detecting unknown or threatening objects (Duplaix 1980). This behavior gives conspecifics ample opportunity to see the throat pattern. Nevertheless, it remains to be tested whether mustelids make use of throat markings for visual or multimodal individual recognition.

## Multimodal Communication

Not much is known about the information mustelids can derive by combining signals in different modalities. Asian small-clawed otters are the only mustelid species for which multimodal discrimination of conspecifics has been tested experimentally (Lemasson et al. 2013). Females are able to discriminate their male partners from unfamiliar males based on scent and vocalizations. They did not react to life-size photographs, which may either show the minor importance of visual cues or their inability of visual discrimination.

## Conclusion

Mustelids use different modalities for communication. Like many mammals, they exchange information about territorial ownership, hormonal state, and individual cues like group membership, or sex and age. The mostly solitary lifestyle in this family may account for the importance of signals which do not require direct contact for communication. This is achieved via olfactory markings. Nevertheless, visual communication in terms of fur coloration and body postures also plays a role in mustelid communication. The more social the species, the more important becomes the acoustic channel, allowing group members a fast and direct information exchange.

Despite the growing literature on social communication in mustelids, there is an obvious lack of knowledge about perception and processing of olfactory, acoustic, and visual cues. There are many limitations hampering experimental approaches for the study of communication and cognition in mustelids: several species are elusive, solitary, and/or protected; basic data on behavior and ecology is lacking; captive holdings have only a few or one individual; and animal training strongly depends on cooperation and attention span of focal animals. Furthermore, experimental design needs to be sophisticated, and properly adjusted to the respective species



(compare Mumm et al. 2014; Trowbridge 1983). Nevertheless, mustelids are a highly promising family for future studies, especially regarding multimodal communication and self-recognition. Moreover, the variety of social organization in mustelids is well suited to investigate the positive feedback loop between social and communicative complexity.

## Cross-References

- Acoustic Communication
- Mustelidae Cognition
- Mustelidae Life History
- Olfaction
- Scent-Marking
- Vision
- Vocalization

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## Mustelidae Cognition

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### Introduction

Due to their apparent intelligence and adaptability, mustelids typically thrive if introduced into new ranges and increasingly they live among us even in urbanized areas (e.g., stone martens (*Martes foina*): Hisano et al. 2016). Yet, despite our general acquaintance with some members of this family, many aspects of their behavior, and particularly their cognitive abilities, remain more mysterious than those of their canid and felid cousins. This is likely due to their smaller size and more nocturnal lifestyle as well as being less amenable to being domesticated (with the singular exception of the domesticated ferret *Mustela putorius furo*). In this chapter we explore why this should be, identifying that despite being unified as “long, thin, and stinky,” they exhibit a diversity of cognitive traits linked to their form and function, powers of perception, and communication, resulting in disparate extents of social behavior and cognitive abilities.

### The Constraints of Form, Function, and Physiology on Cognition and Behavior

Mustelids have short, tough limbs ending in five-toed paws attached by a highly flexible wrist/ankle, and they exhibit greater paw variation than any other carnivore family (Kitchener et al. 2017). Iwaniuk et al. (1999) caution that – in fissioned carnivores – brain size is not correlated with forelimb dexterity, and that disparate ecological and phylogenetic factors act in concert to promote or constrain neural development and behavior in different species. Nevertheless, having free “hands” able to manipulate objects opens

up a range of ecological possibilities, ensuing specific intellectual and brain-developmental characteristics. Indeed, sea otters are one of the few nonprimate mammals known to use tools on a regular basis (Fuji et al. 2014), employing a specially chosen rock held in their forepaws to break open shellfish and clams collected under water. Similarly, in captivity, Asian small-clawed otters (*Aonyx cinerea* syn. *Amblonyx cinereus*) appear capable of understanding the application of specific tool use ahead of feeding bouts in behavioral enrichment trials, pulling hooks to activate levers to release fish (Frick et al. 2016). Other mustelids, such as martens and tayra use their strong dexterous paws to climb, where the balance and three-dimensional spatial awareness required to move along thin and bendy branches resulted in extremely rapid information processing (Taylor 1989). Crucially, however, because these typical stubby limbs preclude figuratively “running with the pack,” and thus predatory mustelids tend to be solitary, limiting the opportunity for direct social behaviors (and related social intelligence) to manifest (Table 1).

### Sensory Perception, Recognition, and Communication

Cognition is highly dependent on sensory perception (Pecher and Zwaan 2005) and is intimately linked to the evolution of life-history strategies. Because many mustelids are nocturnal, or very short-legged, their range of vision is generally limited. Instead they tend to rely on their hearing and especially on olfaction for orientation, hunting, and communication (Buesching and Stankowich 2017). The receiver’s “psychological landscape,” which determines detectability, discriminability, and memorability of the cue after it reaches his sensory organs (Guilford and Dawkins 1991) is particularly important in our context of cognition, as it allows, for instance, conspecifics to recognize each other’s vocalizations or scent marks even after periodic absence (e.g., Buesching and Stankowich 2017).

**Mustelidae Cognition, Table 1** The relationship of cognitive abilities with diet, habitat use, communication and social behaviors in Mustelids

| Genus (species or broad group)                                              | Habitat use/special cognitive abilities                                                                                                        | Social system                                                                               | Diet/foraging strategy                                                                                                                                                                      | Communication                                                                                                                                                                                                            | Cooperative/key behaviors                                                                                                                                                          |
|-----------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Mustela, Poecilogale, Vormela, Ictonyx, and Lyncodon (weasels and polecats) | Cursorial/subnivean weasels; fossorial polecats/ferrets (cathemeral, linked to prey availability)                                              | Solitary                                                                                    | Carnivorous/predatory                                                                                                                                                                       | Predominantly via scent, including feces, urine, and anal and dermal gland secretions, involving body dragging and rubbing. Vocalizes only in aggression/distress                                                        | None. No mutual interactions outside of mating, maternal care, and territorial defense                                                                                             |
| Martes and Pekania (martens)                                                | Climbing (scansoriality) and subnivean predation, with adaptations to deep snow. Activity patterns relate to prey availability and temperature | Solitary – some species will congregate at rich feeding sites (fruit trees/carcasses)       | Omnivorous/opportunistic generalists. Can assess need for protein in diet (vs. fruit) during cold conditions. Fisher map porcupine dens/trees                                               | Predominantly via scent, including feces, urine, and anal and dermal gland secretions, involving body dragging and rubbing. Vocalizes only in aggression/distress                                                        | None. No mutual interactions outside of mating, maternal care, and territorial defense. Will congregate around rich food sources (carcass scavenging, fruiting trees) <sup>a</sup> |
| Meles (European and Asian badgers)                                          | Fossoriality (nocturnal)                                                                                                                       | Continuum from solitary to group living with increasing population densities – forage alone | Omnivorous/opportunistic generalists (some populations specializing on earthworms – with availability mapped to weather and microclimate). Can map out rabbit nests and grub-rich dead wood | Predominantly via olfaction, including specialized subcaudal gland secretion used to mark objects and conspecifics. Feces (anal gland) and urine used in territory marking. A range of intraspecific vocalizations noted | In social-group living populations, allo-grooming, allo-marking, some suggestion of occasional allo-parental care. Purely reciprocal                                               |
| Arctonyx (hog badgers)                                                      | Fossorial (nocturnal)                                                                                                                          | Solitary                                                                                    | Omnivorous/opportunistic generalists                                                                                                                                                        | Predominantly via olfaction, including specialized subcaudal gland secretion used to mark objects. Feces (anal gland) and urine used in territory marking. A range of intraspecific vocalizations noted                  | None. No mutual interactions outside of mating, maternal care of offspring                                                                                                         |

(continued)

**Mustelidae Cognition, Table 1** (continued)

| Genus<br>(species or<br>broad group)     | Habitat<br>use/special<br>cognitive<br>abilities                        | Social system                                                                                                             | Diet/foraging<br>strategy                                                                                                             | Communication                                                                                                      | Cooperative/key<br>behaviors                                                                                                                                                                                                                                   |
|------------------------------------------|-------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Melogale<br>(ferret<br>badgers)          | Fossorial – but<br>also strong<br>climbers<br>(nocturnal)               | Solitary – new<br>evidence of<br>extended<br>philopatry and<br>possibly group<br>living                                   | Omnivorous/<br>opportunistic<br>generalists                                                                                           | Predominantly<br>via scent (anal<br>gland/urine).<br>Occasional<br>intraspecific<br>vocalization                   | Groups seen<br>foraging together<br>and cohabiting in<br>dens – social<br>behavior under<br>ongoing<br>investigation                                                                                                                                           |
| Taxidea<br>taxus<br>(American<br>badger) | Fossorial (well<br>innervated<br>foreclaws for<br>sensitive<br>digging) | Solitary                                                                                                                  | Carnivorous.<br>Occasionally,<br>pairs with<br>coyotes to<br>predate prairie<br>dogs but little<br>apparent<br>advantage to<br>badger | Predominantly<br>via scent (anal<br>gland/urine)                                                                   | Noted for intense<br>aggression                                                                                                                                                                                                                                |
| Mellivora<br>(honey<br>badger/<br>Ratel) | Fossorial                                                               | Solitary<br>(occasional pair<br>hunting)                                                                                  | Carnivorous<br>(noted also to<br>take honey and<br>insensitivity to<br>bee stings)                                                    | Predominantly<br>via scent (anal<br>gland/urine).<br>Cubs vocalize                                                 | Noted for intense<br>aggression. <sup>b</sup><br>Seen to move a<br>log to stand on to<br>reach chicks in<br>cave roof (tool<br>use). Also pair<br>documented to<br>use sticks, a rake,<br>heaps of mud and<br>stones to escape a<br>captivity pit <sup>c</sup> |
| Gulo gulo<br>(wolverine)                 | Cursorial tundra<br>specialist/<br>subnivean dens                       | Solitary<br>(paternal<br>investment<br>polygyny, with<br>males<br>associating<br>amicably with<br>their own<br>offspring) | Carnivorous                                                                                                                           | Predominantly<br>via scent (anal<br>gland/urine)                                                                   | Noted for intense<br>aggression                                                                                                                                                                                                                                |
| Galictis<br>(Grisons)                    | Terrestrial<br>(predominantly<br>diurnal<br>~catheymeral)               | Solitary<br>(occasional<br>pairs) –<br>temporary<br>maternal-<br>offspring groups                                         | Omnivorous<br>(solitary hunters)                                                                                                      | Grunts/snarls<br>when threatened.<br>Strong anal gland<br>musk, which can<br>be sprayed, used<br>to mark territory | No mutual<br>interactions<br>outside of<br>mating, maternal<br>care. Social<br>grooming not<br>observed                                                                                                                                                        |
| Eira brabara<br>(Tayra)                  | Climbing<br>(scansoriality)                                             | Solitary<br>(diurnal) –<br>possibly<br>temporary<br>maternal<br>offspring groups                                          | Opportunistic<br>omnivorous.<br>Hunt primarily<br>by scent – poor<br>eyesight                                                         | Mostly via<br>scent –<br>occasional intra-<br>specific calls                                                       | Caching green,<br>unripe plantains<br>until they ripen. <sup>d</sup><br>Uses tail as<br>counterbalance<br>when climbing                                                                                                                                        |
| Neovison<br>vison                        | Cursorial/<br>aquatic                                                   | Solitary                                                                                                                  | Opportunistic<br>carnivore –<br>rodents, fish,                                                                                        | Territory<br>marking with<br>anal gland/feces.                                                                     | (From<br>experimental<br>testing) Good                                                                                                                                                                                                                         |

(continued)



**Mustelidae Cognition, Table 1** (continued)

| Genus<br>(species or<br>broad group)                                                         | Habitat<br>use/special<br>cognitive<br>abilities                         | Social system                                                                                                                                                             | Diet/foraging<br>strategy                                                                                          | Communication                                                                                                                                                                                    | Cooperative/key<br>behaviors                                                                                                                                                                                                       |
|----------------------------------------------------------------------------------------------|--------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| (American<br>mink)                                                                           |                                                                          |                                                                                                                                                                           | crustaceans,<br>amphibians,<br>birds                                                                               | Vocal calls when<br>encountering<br>conspecifics                                                                                                                                                 | ability to<br>recognize objects<br>and make object<br>selections from<br>memory <sup>e</sup>                                                                                                                                       |
| <i>Lontra</i> (New<br>World otters)                                                          | Predominantly<br>aquatic<br>(nocturnal –<br>summer/<br>diurnal – winter) | Social groups,<br>based on<br>maternal-<br>offspring<br>associations<br>form<br>temporarily,<br>sometimes<br>including mature<br>males. Also<br>gregarious male<br>groups | Piscivorous –<br>fish,<br>supplemented by<br>crustaceans.<br>Occasionally eats<br>small terrestrial<br>vertebrates | Anal gland<br>sprainting to<br>mark territory.<br>Vocal<br>communication<br>within groups                                                                                                        | Conspicuous<br>play among<br>siblings. Allo-<br>grooming. Den<br>cohabitation by<br>groups                                                                                                                                         |
| <i>Lutra</i> (Old<br>World otters)                                                           | Predominantly<br>aquatic                                                 | Solitary<br>(temporary<br>maternal-<br>offspring<br>groups). No male<br>involvement                                                                                       | Piscivorous –<br>fish,<br>supplemented by<br>crustaceans.<br>Occasionally eats<br>small terrestrial<br>vertebrates | Anal gland<br>sprainting to<br>mark territory.<br>Maternal-pup<br>vocalizations<br>(12 calls)                                                                                                    | Conspicuous<br>play among<br>siblings                                                                                                                                                                                              |
| <i>Aonyx<br/>capensis</i><br>(African<br>clawless<br>otter)                                  | Predominantly<br>aquatic (diurnal)                                       | Solitary<br>(temporary<br>maternal-<br>offspring<br>groups)                                                                                                               | Shellfish, fish,<br>amphibians,<br>worms                                                                           | Anal gland<br>sprainting to<br>mark territory.<br>Maternal-pup<br>vocalizations                                                                                                                  | Use vibrissae<br>(whiskers) to<br>navigate murky<br>water. Use<br>forepaws to<br>search for prey.<br>Moves between<br>water, muddy<br>banks, and<br>burrows to<br>thermoregulate                                                   |
| <i>Amblonyx<br/>cinerea</i><br>(formerly<br><i>Aonyx</i> )<br>(Asian small-<br>clawed otter) | Predominantly<br>aquatic (diurnal)                                       | Social groups,<br>built on<br>maternal-<br>offspring<br>associations,<br>with father<br>present to also<br>provision pups                                                 | Mainly<br>crustaceans and<br>mollusks – some<br>small fish<br>(seasonally<br>mudskippers)<br>and insects           | Strongly social<br>(12 call), also for<br>territorial<br>defense. Also<br>anal gland<br>sprainting +<br>rubbing,<br>scratching<br>against objects.<br>Group members<br>allo-groom and<br>posture | Use vibrissae to<br>detect prey<br>movement in<br>water and<br>forepaws to<br>locate and<br>capture prey<br>(rather than<br>mouths).<br>Incomplete<br>webbing gives<br>manual dexterity<br>to dig in mud for<br>shellfish. Playful |

(continued)

**Mustelidae Cognition, Table 1** (continued)

| Genus<br>(species or<br>broad group)                            | Habitat<br>use/special<br>cognitive<br>abilities | Social system                                                                                                                         | Diet/foraging<br>strategy                                                                                                                                                                                    | Communication                                                                                                                                                                                                     | Cooperative/key<br>behaviors                                                                                   |
|-----------------------------------------------------------------|--------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------|
| <i>Hydrictis<br/>maculicollis</i><br>(spotted neck<br>otter)    | Predominantly<br>aquatic                         | Groups<br>(especially<br>maternal-<br>offspring) under<br>some<br>environmental<br>conditions – hunt<br>alone. Cohabit<br>burrow      | Piscivorous – fish<br>subsidized by<br>crustaceans                                                                                                                                                           | Very vocal –<br>whistles and<br>chatters.<br>Sprainting well-<br>used paths                                                                                                                                       | Playful                                                                                                        |
| <i>Lutragale<br/>perspicillata</i><br>(smooth-<br>coated otter) | Predominantly<br>aquatic                         | Social groups –<br>also group<br>hunting                                                                                              | Coordinated<br>group hunting of<br>fish, subsidized<br>by crustaceans                                                                                                                                        | Very vocal –<br>whistles, chirps<br>wails. Also<br>olfactory<br>(sprainting)<br>communication                                                                                                                     | Tamed otters<br>trained to work<br>with fisherman<br>by chasing fish<br>into nets<br>(Bangladesh) <sup>f</sup> |
| <i>Enhydra<br/>lutris</i> (sea<br>otter)                        | Marine (rarely<br>on land)                       | Rafts' (separate<br>congregations of<br>each sex but not<br>socially<br>integrated)                                                   | Uses forepaws<br>(uniquely within<br>group) to catch<br>shellfish                                                                                                                                            | Exclusively<br>vocal<br>(no olfactory<br>component at<br>sea) – coo, grunt,<br>whistle hiss                                                                                                                       | Carries and uses<br>rock to break<br>open shellfish                                                            |
| <i>Pteronura<br/>brasiliensis</i><br>(Giant otter)              | Predominantly<br>aquatic (diurnal)               | Social (family)<br>groups –<br>dominant pair,<br>highly cohesive,<br>and cooperative.<br>Cooperative<br>(aggressive)<br>group defense | Highly<br>piscivorous<br>(specializing on<br>chiclids,<br>characins, and<br>catfish). Solitary<br>and group<br>hunting (using<br>vision) –<br>depending on<br>prey type. Grasp<br>fish in forepaws<br>to eat | Vocalizations –<br>up to 22 distinct<br>adult and pup<br>calls. Olfaction –<br>anal gland<br>territorial<br>latrines.<br>Excellent<br>vision – may<br>recognize<br>conspecific throat<br>patches<br>(periscoping) | Entire group<br>(including<br>nonreproductive<br>adults and<br>siblings)<br>provisions pups<br>with fish       |

All Information from: Biology and Conservation of Musteloids. Eds. D.W. Macdonald, C. Newman & L.A. Harrington. OUP, and pertinent chapters therein, except specific studies cited

<sup>a</sup>Newman et al (2011). *Mammal Study*, 36: 169–188

<sup>b</sup>“Honey badger Houdini – Honey badgers: Masters of Mayhem – Natural World” BBC2: Video. *BBC*

<sup>c</sup>India Land of the Tiger. Archived 21 June 2011 at the Wyaback Machine

<sup>d</sup>Soley & Alvarado-Díaz (2011). *Naturwissenschaften*, 98: 693–698

<sup>e</sup>Doty et al.(1967). *Science*. 155: 1579

<sup>f</sup>Feroz et al. (2011). *IUCN Otter Spec. Group Bull. A*, 28, 14–20

## Eyes and Vision/Ophthmoception

Most mustelids are nocturnal, but many *Mustela* species and lutrines are cathemeral (i.e., no bias toward diurnal vs. nocturnal activity). While more diurnal species, such as various *Martes* species, have greater acuity enabling them to resolve fine spatial detail through reduced retinal summation

(i.e., the ratio of photoreceptors to ganglion cells: Kitchener et al. 2017), nocturnal species have relatively larger and more curved eyeballs with high rod/cone ratios, making the most of available light to summate retinal images, but at the cost of acuity. Certainly the nocturnal European badgers (*Meles meles*) react to the unfamiliar silhouettes of

human observers, even if sitting perfectly still, whereas the cathemeral American mink and ferrets can be taught to discriminate successfully between different objects with an ability rivaling primates (Doty et al. 1967). Semi-aquatic lutrines on the other hand can see in both air and under water and can learn to discriminate submerged targets for food rewards equally in both environments (Balliet and Schusterman 1971). Because many lutrines, *Mustela* species, and martens have evolved distinct throat patches that are highly visible when the animal is scanning its environment – a typical response to contact calls from conspecifics – and which provide a useful aid for human observers to distinguish individuals (e.g., Sirén et al. 2016), Buesching and Stankowich (2017) suggested that these throat patches may also aid in individual recognition among conspecifics.

### Ears: Hearing/Audioreception

Interestingly, mustelid sound localization acuity is typically lower than that of larger carnivores. Heffner and Heffner (1987) propose that this acuity may be limited by their interaural distance, thus shifting the cognitive bias toward other senses. Yet, many mustelids use vocalizations as interspecific communication signals, although this is typically limited to aggressive or maternal-offspring calls in solitary species, with more complex repertoires evident in those few group-living species. For example, Asian small-clawed otters can recognize vocalizations from individual conspecifics in experimental playback experiments (Lemasson et al. 2014), indicating a high level of social cognitive abilities. Scheifele et al. (2015) found that these Asian small-clawed otters can even infer negative (aggression, separation anxiety, pain, hunger) and positive (feeding, training, playing) emotional states of captive otters by pairing vocalizations to social context and circumstance. Overall, the complexity of vocalizations across the Mustelidae, interactive with group-living and degrees of social integration within groups, may support the social intelligence hypothesis (Leuchtenberger et al. 2014); although recent re-analyses have cast doubt on the robustness of the “social brain” hypothesis

(Dunbar 1988), where earlier work was heavily biased by encephalization traits among canids, and neglected extinct species (Finarelli and Flynn 2009).

Aside from communication, ability to detect sounds also serves to warn mustelids of danger. Clinchy et al. (2016) used experimental sound playbacks to observe that European badgers exhibited increased vigilance and reduced foraging on artificially provisioned sites when the sounds of bears and dogs (but not wolves) were broadcast. Crucially, the sound that caused badgers greatest anxiety was that of people talking, suggesting a learned fear of humans when prone to persecution.

### Smell and Taste: Chemoreception

Mustelids rely extensively on scent, and many have a functional vomeronasal organ (VNO) (Kitchener et al. 2017), although the VNO has not been investigated systematically across species. Signals from the VNO are processed in a discrete, but tiny (0.15% by volume), part of the olfactory bulb of the anterior brain. The VNO is often used in detecting the reproductive status of conspecifics, where animals generally lick scent marks, such as urine or glandular secretions, to take up nonvolatile semiochemicals, which are then transferred through the typical flehmen behavior into the VNO (e.g., European badger: Tinnesand et al. 2015).

In parallel to their acute sense of smell, mustelids exhibit a multitude of scent-marking behaviors, and many species have been confirmed to recognize individual conspecifics from their olfactory profiles (reviewed in Buesching and Stankowich 2017). Interestingly, in scent provisioning experiments in the field, European badgers have even been shown to react differently to anal and subcaudal gland secretions of conspecifics according to the spatial context in which they are provided. This highlights an acute socio-spatial awareness. If, for example, scent from a badger belonging to a neighboring group was positioned at the territorial border between the respective groups (i.e., “in context”), scent marks were largely ignored, whereas if the same scent was positioned “out of context” at a border

latrine with a different social group, the scent was frequently investigated and overmarked (Tinnesand et al. 2015).

The hierarchical group structure of giant otters, with a dominant breeding pair, and sometimes as many as 20 subordinates present, leads to some very directed scent-marking behavior, showing cognizance of social status in relation to sexual status and territorial defense. Leuchtenberger and Mourao (2009) report that 62% of marking was performed by alpha males, followed by alpha females. Almost half of alpha male scent-marking events involved overmarking of other group members, but only one-third of those from alpha females were deposited as overmarks, specifically focused on other females. Interestingly, these observations reflect object-marking patterns in European badgers although no obvious dominance hierarchies are evident in this species (Macdonald et al. 2015).

Taste reception has generally received little attention among scientific studies. While strict carnivory results in a fairly stenophagous diet, more generalist euryphagous species, common among the mustelids, must be able to discriminate between different food types and qualities, implicitly through recognizing flavors. A trainable cognitive link between smell and taste has been developed in the context of conditioned taste aversion for the European badger (Baker et al. 2007). Nevertheless, as predicted by the encephalization theory, proposing that carnivores following a strict predatory diet need more brain power than those with an omnivorous diet due to the challenges of capturing live-prey (Gittleman 1986), badgers proved to be comparatively difficult to dissuade to consume certain foods. Trialing three irritants, Cinnamamide, Capsaicin, and Ziram, Baker and Macdonald (2015) discovered that badgers continued to eat familiar food baits, despite these foul tastes (Macdonald et al. 2015). Notably, some individuals were much more persistent than others. Only Ziram acted as a successful deterrent and even then only gradually. By night seven, badgers began to reject baits without tasting them, presumably based on the smell of Ziram alone – where this most likely occurred through second order conditioning to the odor cue.

Exploiting this association, Baker and Macdonald (2015) developed a conditioned taste aversion by presenting an odorless form of Ziram along with pungent clove oil. This combination could produce learned aversion to even untreated baits in the presence of the clove odor cue.

A similar example of instrumental learning has been observed in sea otters. Kvitek et al. (1991) showed experimentally that sea otters actively reduced their capture and consumption rates of butter clams (*Saxidomus giganteus*) high in saxitoxin (the causal agent of paralytic shellfish poisoning resulting from dinoflagellate blooms), or discarded highly toxic clam siphons and kidneys. This behavioral response is likely highly adaptive, given the importance of butter clams in sea otter diets even in areas where toxic dinoflagellate blooms occur.

### Touch: Somatoception

Mustelids use their whiskers (vibrissae) to fine-tune their navigation, or position within confined spaces. Vibrissae are particularly abundant, and rather stiff, among river otters, which may aid in foraging in murky water (Carss 1995), resulting in an expansion of the coronal gyrus in the brains of *Lutra* and *Pteronura* (Radinsky 1968). In contrast, *Aonyx*, and, in a different way, *Enhydra*, exhibit an enlargement of the primary somatic sensory projection area which is associated with the forelimb, indicating increased tactile sensitivity of the hand in these otter species, which reflects their above-mentioned ability to manipulate rocks as tools to pound open shellfish (see above). The American badger (*Taxidea taxus*), in contrast, has high densities of tactile nerves in the lips, nose, and paws, which are likely a functional adaptation for poking through substrate with their noses when digging (Bourlond and Winkelmann 1966).

Having thus far explored the physiological adaptations and constraints acting to focus the cognitive abilities of mustelids, and how their senses of perception relate to their behavior, we next explore how key life-history factors contribute to the way they think and interact with each other and their environment; noting that the more sociable the species concerned, the more

specialized the ethology involved (Holekamp and Benson-Amram 2017). These social interactions, and thus also the cognitive abilities of mustelids, however, are not only influenced by their anatomy, but particularly also by their formidable temperament. Their renowned fierceness is exemplified by honey badgers and wolverines; but even a 100 g weasel can prove a formidable adversary if caught inadvertently by an unsuspecting researcher performing a rodent survey. Macdonald and Newman (2017) speculate that this ferocity may arise from a type of “eco-physiological inertia,” limiting sociability among the mustelidae: many mustelids (e.g., badgers) can use adaptive torpor to cope with periods of food scarcity, where they rely upon high levels of the hunger-alleviating hormone leptin, which in turn stimulates catecholamine secretion (Rousseau et al. 2003). Because inhibited ability to oxidize catecholamines speedily among men carrying the monoamide oxidase A gene mutation is associated with the aggressive “warrior gene” personalities (McDermott et al. 2009), this led Noonan et al. (2015a) to propose that this biochemical pleiotropy might foster fearlessness in mustelids. Along similar lines, several mustelid species exhibit degrees of delayed implantation, which requires the inhibition of oxytocin, the affection, or “antipsychotic,” hormone (Douglas et al. 1998), possibly to the detriment of a sociable nature (Caldwell et al. 2008).

## Diet and Foraging Behavior

Cognitive abilities play a direct role in selection pressures governing the acquisition and consumption of key food resources (McLean 2001). Unable to figuratively “run with the pack,” predatory mustelids tend to be solitary, limiting the opportunity for direct social behaviors to manifest. Cooperative hunting is thus rare among the mustelids; indeed, even when high prey patch richness causes individuals to aggregate, there is scant evidence of musteloids hunting collaboratively – largely because they can dispatch their small prey without assistance. It is likely only the giant otter that is the true cooperative

hunter among mustelids. Although giant otters can hunt alone successfully, groups have been seen to corral fish to improve hunting efficiency (although this has not been quantified), and to tackle prey that they could not manage alone, such as juvenile black caiman (*Melanosuchus niger*) and anacondas (*Eunectes murinus*) (Ribas et al. 2012), apparently able to anticipate the role conspecifics will play in the pursuit and understanding the benefits to collaboration.

Nevertheless, omnivory and opportunism also require memory skills, the ability to weigh multiple criteria, and well-developed declarative maps of foraging ranges (Tversky 1993). For instance, unprecedented cold and snow in subtropical China in January–February 2008 caused yellow-throated martens (*Martes flavigula*) and Chinese ferret badgers (*Melogale moschata*) to shift from a typical seasonal diet dominated by fruit, which still remained available, to consume more small mammals (Zhou et al. 2013) – showing an understanding of the need to increase protein consumption during cold conditions.

Even dietary specialists exhibit keen cognitive abilities linked to foraging success. European badgers mainly eat earthworms in the UK, and research by Stewart et al. proposed that rather than latrines between social groups acting as defensive borders, badgers were instead making “notes to self” marking the isopleth of peak earthworm availability; apparently cognizant that beyond that point badgers foraging toward them from the neighboring group would have diminished earthworm availability (Macdonald et al. 2015).

This European badgers research also provides an example of conditioned foraging responses. In a pilot experiment where food was concealed under paving slabs, to slow down consumption and permit social interactions to be observed (Macdonald et al. 2015), badgers came to associate paving slabs with hidden food generally and began excavating patios at residences adjacent to the woodland research site. The strength needed to casually upturn 10 kg paving slabs belies the way in which badgers combine brute force with intellect to solve problems.

An application of similar abilities for spatial reasoning was recorded by the BBC TV series



*Land of the Tiger* (1997), where a honey badger (*Mellivora capensis*) exploring a cave in India rolled a log to where it could use this “tool” to climb up and reach a kingfisher fledgling, lodged among roots in the cave ceiling. Similarly, honey badgers have been seen to relocate objects (logs, rocks, rakes, spades, tires, etc.) to enable them to escape from walled captivity pits. In this amazing display of spatial cognizance, clearly the honey badger was planning repeat escapes through various combinations of items and strategies, and exhibited genuine insight (Sutherland and Mackintosh 2016) into how to solve the problem of scaling a concrete wall.

Of course, the ability to understand orientation and navigation in confined spaces is fundamental to archetypal elongate mustelids, which hunt rodents through tunnels. Relatively little is known about fossorial activity, because it proves difficult to track and study underground behavior (but see Noonan et al.’s (2015b) development of magnetic inductive tracking methods). Clearly, species such as black-footed ferrets (*Mustela nigripes*) can hunt within prairie dog burrows with considerable efficiency (Biggins & Biggins and Eads 2017). Interestingly, Perreault and Plowright (2004) have proven experimentally that ferrets can take short cuts between two points, implying they follow more complex declarative cognitive maps, rather than simple procedural rules. Noonan et al. (2015b) have also redressed the assumption that when European badgers use their setts (burrow systems) by day they are “at rest.” Instead they engage in a variety of underground relocations, often linked to social bonds, implying that they make informed decisions on tunnel and chamber use.

The omnivorous tayra shows highly developed prospective thinking linked to foraging success. It is the only nonhuman mammal reported to cache green unripe fruits, specifically native sapote fruit as well as cultivated non-native plantains, apparently in the knowledge that these climacteric fruits will then ripen (Soley and Alvarado-Diaz 2011). Not least, the different developmental rates of these two fruits require that tayra understand their respective ripening processes. By harvesting unripe fruit tayra gain a selective advantage over

other sympatric frugivores that must wait until fruits are edible. European badgers display a similar understanding of time effects when predating rabbits (Martin et al. 1995). They patrol past rabbit warrens until the kits underground are large enough to provide a substantial meal, but still too young to flee predation, and then dig down to unearth their prey. This involves acute spatial awareness, where badgers do not dig into warrens along rabbit tunnels, but directly into the nesting chamber from above.

Interesting reports of feeding mutualisms among mustelids involve the apparent understanding of the benefits that interspecific cooperation can bring. Most often quoted being the association between honey badgers and honey-guides (*Indicator indicator*). This arose from hearsay reported by Sparman in 1785, and today many consider this a fallacy. Nevertheless, honey badgers have been reported to hunt commensally with black-backed jackal (*Canis mesomelas*) and pale chanting-goshawk (*Melierax canorus*), although without any apparent costs or benefits (Begg 2006). American badgers will also hunt phoretically (accidentally and nonobligatorily) with coyotes (*Canis latrans*) for ground squirrels (Lehner 1981); although the greater benefit is likely to coyotes that chase down squirrels flushed from their underground burrows by the badgers’ excavations (Minta et al. 1992).

Of course collaborations between humans and mustelids also require an advanced understanding of the resultant benefits. Examples are few, but in Sundarbans region of Bangladesh a traditional fishing method involves two trained smooth-coated otters (*Lutrogale perspicillata*) and an immature trainee otter working with three fishermen from a boat. Otters herd fish into a net and greatly enhance capture success – indeed around 2000 people depend on this fishing method for their livelihoods in the region. Even our interaction with the most tractable of mustelids, the domestic ferret, stems from their traditional use by human hunters to help flush rabbits (*Oryctolagus cuniculus*) from warrens (Cowan 1984); again illustrating that ferrets can comprehend complex roles and social relationships.

## Collaborative Behaviors: Den Use, Parental Care, and Cooperative Defense

Cooperative breeding is rare among mustelids, although giant otters present a notable exception (Groenendijk et al. 2017). In this species pups are produced only by the groups' dominant breeding pair, although subordinate nonbreeding adults of both sexes provision these pups with fish. The greater the number of these nonbreeding helpers, the more likely pups will survive. Interestingly, giant otters also appear to care for elderly group members, with Davenport (2010) reporting multiple forms of assistance given to the declining group matriarch. Perhaps this suggests an altruistic understanding of "acquired credit," beyond utilitarian reciprocity.

Despite group living, European badgers do not seem to provide any substantive allomaternal care to cubs (Fell et al. 2006), with cubs being largely left to their own devices when old enough to emerge from the underground sett. One curious and informative facet of badger reproduction involves whether fathers can recognize their own offspring. Certainly, infanticide by males that know they are not related to offspring can be an issue in carnivore societies (Agrell et al. 1998), and so when badger populations reach very high densities strategies to avoid infanticide have a selective advantage. To these ends, high-density badger populations exhibit highly promiscuous and noncompetitive polygynandry (Macdonald and Newman 2017), which combined with 10 months of delayed implantation in this species sufficiently confuses and dislocates mating from birth, so that paternity is confused. To what extent females understand and plan that their promiscuity confuses males is unknown; however, this strategy would be undermined if males could recognize their own offspring in some way, possibly via scent (Porter et al. 1986). In this regard, work by Fell et al. (2006) found that while cubs are still too immature to produce their own subcaudal scent secretion, they anoint themselves with the subcaudal secretion of other adult group members, by ducking under the belly and squeezing out under their scent glands, in what they termed "scent theft."

Relating to this, and likely linked to a lack of reliance on visual senses in musteloids, Buesching and Stankowich (2017) emphasize that, unlike most other Carnivore families, young mustelids lack the distinct neotenic "kindchenschema" that would usually solicit care-giving; those features that cause people to find kittens and puppies appealing.

Because the majority of mustelid species forage alone, and are often disproportionately fierce and thus relatively unworried about threats from predators and competitors (Newman et al. 2005), instances of cooperative defense are few, and largely restricted to the social otters. Certainly groups of giant otters use display and attack to repel rival groups and marauding caiman (Ribas et al. 2012); similarly, Cape clawless otter groups defend against conspecifics. There is even a plausible, if unproven, suggestion that sea otters may attempt to confuse sharks and orca (Hatfield et al. 1998) by forming large rafts.

## Mutual Interactions

Giving care to another individual requires cognizance of the benefits afforded by this generosity. These may be reciprocal, or involve inclusive fitness, or may simply serve just to appease aggression (e.g., Rankin and Taborsky 2009). The possibility of mutual interactions outside of maternal care is again restricted to very few, more social species. Social otters not only play but also allogroom one another, arising from the need to remove ectoparasites (Green et al. 2015). But perhaps one of the most detailed studies of the precise understanding and weighing of reciprocity relates to mutual grooming in paradoxical European badgers, only just on the cusp of evolving secondary benefits from group-living. Badgers groom mainly to alleviate itching from their large host-specific flea, *Paraceras melis* (Cox et al. 1999). When alone, they focus on their chest and belly, but they appear to understand that they must elicit the assistance of conspecifics to de-flea harder to reach areas. Cooperative grooming involves reciprocity, and badgers give very little credit, defecting within just 1.2 seconds if the

recipient does not respond in kind (Macdonald et al. 2015). Once initiated, cooperative grooming bouts continue until one individual defects, whereupon the other generally stops within half a second, in a classic tit-for-tat arrangement. This rather Machiavellian cooperation seems entirely self-serving and evidences a distinct lack of trust or altruism between actors.

Badgers also allomark each other with their subcaudal gland scent secretion (Buesching and Stankowich 2017) to create a shared group-odor. Marking can either be mutual, with two badgers pressing their subcaudal pouches against each other simultaneously to maintain a cohesive group smell, or sequential, with one badger marking the body of another individual, likely as social appeasement as well as an individual advertisement signal, being strongly influenced by sex, age, and reproductive status. Strong correlation in the frequencies of sequential and mutual allomarking, combined with allogrooming, point to particular cliques within broader badger groups of more closely interacting individuals, highlighting that badgers discriminate with whom to invest in socializing.

## Conclusion

When examining the way such a diverse group as the mustelids acquires knowledge, interprets experiences, and thinks about situations, it is difficult not to slip into interpretative bias (Wilder 1996), or to make inferences about their societies flavored by our own human cognitive biases (Harding et al. 2004). How much mental processing power does it take for an otter to catch a fast-moving fish in three-dimensional space? Or for a honey badger to plot an elaborate escape from a zoo pen? Indeed, what fine-tuned cognitive skills are required for a weasel to simply catch a mouse? Even comparing the intellect needed to undertake solitary practical skills is incomparable with the social mind required to deal with group-living situations.

Neurophysiological experimentation can elucidate some of these points, but such studies are lacking for the mustelids. This leaves us to

interpret observations, guided by the certain knowledge that natural selection weeds out inefficiency, and so the cognitive abilities of species are just as highly tuned as their more evident specialized anatomies. What is clear is that whatever the mustelids do, they do it well, with ecological niches spread far more widely than in any other carnivore family; arguably more diverse than in any other mammalian taxa.

## Cross-References

- [Communication](#)
- [Mustelidae Diet](#)
- [Mustelidae Life History](#)
- [Mustelidae Morphology](#)
- [Mustelidae Navigation](#)
- [Scent-Marking](#)

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## Mustelidae Diet

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## Synonyms

### Feeding habits



## Introduction

Diet is one of the most important dimensions of the ecological niche of an animal (Hutchinson 1959). Knowledge of the feeding habits of an animal allow us to understand how it deals with the food available in the environment, and how it changes in space and time as a function of fluctuations and distribution of food resources, in terms of the stability and predictability of the environment (Kruuk 2006; Ruiz-Olmo and Jiménez 2009). Within the Carnivores, as is the case of the Mustelids, the abundance, quality, and distribution of food has a first order of importance in body condition, survival, reproductive capacity, socialization, and size of the groups, as well as to determine the use of space and time and home range size, among others (see also Gittleman 1989; King and Powell 2007).

Mustelid energy needs (basal rate and food) are 20% higher than those of other terrestrial Carnivores (McNab 1989). According to this author, the energy needs of otters (subfamily *Lutrinae*) are even 20% higher than those of other terrestrial representatives of the mustelids. Thus, Mustelidae constitutes a group in which obtaining a sufficient and quality food is of great importance. For instance, Kruuk (2006) considers that Eurasian otter *Lutra lutra* is food-limited species, as it is the case of the other species of otters, mainly in high mountains or colder waters.

Food acquisition can be understood as an active process where the animal chooses from the different available resources. The comprehension of how a species choose from the available prey is very important to conservation biology, and habitat and species management, once it allows the selection of priority areas and the elaboration of conservation plans and the recovery of degraded areas (Miller et al. 1996; Manly et al. 2002).

The Mustelidae is the largest and the most diverse family of the order Carnivora. The 59 recognized species (following Wilson and Reeder 2005), also called weasel-like family, are widely distributed through all continents besides Antarctica and Australia. They show great variation in size (from 30 g to 40 kg) and can occupy nearly

every habitat, both terrestrial (subdesert, burrow, arboreal, humid, snow-covered, and agricultural), aquatic (salt and fresh water), and even man-made or urban (Griffiths 2000; Nowak 2005; Wilson and Mittermeier 2009). Not surprisingly, with this wide range of habitats and body length, the mustelids present a wide range of feeding habits, ranging from omnivory to strict carnivory, from terrestrial to aquatic prey, from living animals to carrion. Mustelids are agile, usually are flesh hunters, feeding mainly on mammals, birds, amphibians, reptiles, fish, crayfish or crabs, and molluscs or insects. Some mustelids can feed on plants, fruits, eggs, honey, and be omnivores (Nowak 2005). Most of them eat nothing but meat, with teeth highly adapted to predation and to dilacerate their prey (Macdonald 1995).

The plasticity in the feeding behavior, with a wide niche breadth, is one of the reasons that helps to explain their huge distribution range (for examples, see Clevenger 1994; Martin 1994; Clavero et al. 2003; López-Martín 2006; Ruiz-Olmo and Jiménez 2009; Zhou et al. 2011; Rheingantz et al. 2017). Even within the same species, the diet may vary spatially or temporarily according to the prey and food available. There are some exceptions of this plastic behavior, as in the case of the endangered black-footed ferret *Mustela nigripes* (Miller et al. 1996; Belant et al. 2015). This ferret feed mainly upon prairie-dogs, depending of habits occupied by those rodents as they also depend of their burrows for shelter and denning (Ludwig et al. 2008). This is often also the case of the least (*M. nivalis*) and long-tailed weasels (*M. frenata*), and the stoat (*M. erminea*), often depending on one-two rodent species (King and Powell 2007).

The diet of Mustelids is heavily affected by the abundance and biogeography of their prey as was demonstrated for otters and martens (Clavero et al. 2008, 2003; Clevenger 1994; Martin 1994; Rheingantz et al. 2017; Ruiz-Olmo and Jiménez 2009; Zhou et al. 2011). Mustelids prey on a wide trophic spectrum, which depends on the temperature. In warmer areas, mustelids presents wider niches and prey more often on plants, fruits, insects, fish, and reptiles, while in the colder areas, the main preys are carrion, mammals, and

birds. In the case of otters, marine and estuarine habitats provide the wider prey species availability, resulting in the wider trophic niche width (see Kruuk 2006).

### Strategies of Food Acquisition by Mustelids

The mustelids, as opportunists and occupying wide range of environments, adopt many strategies of food acquisition, depending on the habitat and prey types available. They have slim fusiform body shape, short legs, often very long tail and well-developed senses that work well both in aquatic and terrestrial environments, as vision, hearing, smelling, and touch. There are several species of mustelids that are semiaquatic; they forage in the water but also depend on the land to rest and breed (Dunstone and Gorman 1998). There are degrees of water dependence, but semiaquatic mustelids usually catch their food from the water, by swimming or diving. Otters, for example, prey mainly upon aquatic animals as fish and crustaceans but can also prey upon amphibians and other vertebrates and invertebrates (Dunstone and Gorman 1998; Kruuk 2006). Due to its dependence for both environments, terrestrial and aquatic, semiaquatic mammals, as the otters, some polecats and minks, occur mainly alongside rivers, streams, lakes, bogs, marshes, lagoons, coastal zones (Kruuk 2006), and even reservoirs. River otters and minks use their vibrissae and vision to locate prey movement underwater (Dunstone and Gorman 1998), either during the day or at night. The semiaquatic mustelids are considered single-prey loaders, catching one prey per dig (Houston and McNamara 1985), and they usually prey in shallow water to enhance the searching efficiency of prey. As they are not so adapted to the water as the otters, minks can locate a part of their prey outside the water to maximize the success rate in catching it (Dunstone and Gorman 1998). These animals are found close to rivers or small pools, or near the surface in open areas, in places with higher densities of prey and where the prey are easier to catch (Kruuk and Moorhouse 1990).

The 13 species of otters are top-chain predators that forage mainly on the water, looking mainly for aquatic prey (Kruuk 2006). The

river otters encompass 11 species. Four of them live in groups, in part or all the year. As they forage in groups, they predate upon fish clusters and they can catch bigger fish than other species that usually forage individually. The group besiege the prey shoal, make a semicircle, and each animal catch its prey by itself. The smooth-coated otter forage in groups, with everyone having its task to help in the hunt. The South-American giant otter *Pteronura brasiliensis*, the longest mustelid, that can reach two meters long, are also social, that forage in groups. However, differently from the Asian smooth-coated otters, each animal usually hunts by its own prey lonely. They can predate in groups when chasing large and dangerous preys as black caiman, as occurs in Brazilian Pantanal, even though they usually do not share it.

Most of river otters are solitary animals and look preferentially for slow mobility prey such as suckers, cyprinids, cichlids, salmonid, eels, catfish, crayfish, and crabs, but they can prey upon other aquatic invertebrates (i.e., molluscs), anurans, snakes, or aquatic insects (Kruuk 2006) when they become more available or easier to catch in relation to fish. They can also prey in coastal shallow waters and river margins and pools, using their touch, hearing, and vision when possible to locate prey underwater.

The teaching process is very important in Carnivores, and the mustelids are not an exception of it. The parents, and the brothers when they are social, teach the juveniles how to hunt. For the semiaquatic otters, they teach how to dig and to prey underwater, for example.

An interesting behavior was observed for both Eurasian and Neotropical otters: the predation upon toads (*Bufonidae*). These animals have toxins in their skins produced by the serous glands, mainly in the back and head. When preying upon toads, the otter start eating them by slicing the ventral part and skinning to avoid the contact with the toxins. This behavior appears to be innate, once captive Eurasian otters that never saw a toad before show the same behavior as the wild ones (Morales et al. 2015).

There are two otters that live exclusively in salt water environments: the sea otter *Enhydra lutris*,

in the Northern Pacific, and the marine otter *Lontra felina*, in the Southern one (Doroff and Burdin 2015; Kruuk 2006). The sea otter usually dives in waters with less than 30 m in depth to look for its prey (Estes et al. 2003). As it lives in cold waters, it spends a lot of daily energy intake (eats 20% of total body weight daily) just to maintain the body heat. This mustelid is a kelp-system top-chain predator that digs up to 4 min looking for its prey. When it comes to the surface, it uses a tool, usually a stone, to break the hard parts of sea urchins, mussels, crabs, and clams. Each animal carry its own stone in the hind foots during the period it does not use the artifact (Kuuk 2006). *L. felina*, however, lives on the shore and around, looking for prey as freshwater otters do. Some “inland” otters inhabit coastal habitats as *Lutra lutra*, *Lontra canadensis*, *L. longicaudis*, or *L. provocax*, foraging and catching the prey both in the shore in shallow waters and diving in deeper waters as sea otter does (Kruuk 2006).

Among the terrestrial species, there is also a great variety of strategies. The wolverine *Gulo gulo* lives in low-productive tundra/taiga zone habitats of northern Holarctic and is active all year around. The species is the largest terrestrial mustelid (Nowak 2005), and is polyphagous. In the winter, some of these animals use their excellent smell to feed mainly upon carcasses of large herbivores as reindeers and caribous that die in avalanches or during cold winters (Lofroth et al. 2007). They can be also an active predator, capturing also deer.

Due to their agility, high metabolism and strong bite, weasels can prey upon animals with larger sizes than themselves. The weasels, polecats, and ferrets (least, long-tailed, stoat, black-footed ferret, European, steppe, and marbled polecats, for example) can eat preys with two or three times its size, as voles, rats, lemmings, prairie dogs, rabbits, or ground squirrels (King and Powell 2007). These animals can hunt underground or inside the snow (burrows, tunnels, stone, and rocky habitats), and by using the smell and touch, they forage both during the day and at night. A common hunting strategy of these animals is to follow their prey to their holts or burrows, killing and eating them inside there.

The stoat is a fast-opportunistic predator that looks for preying inside burrows and is also good climber. These characteristics allow it to prey upon bigger rodents and lagomorphs, and birds and eggs in nests. The weasels, stoats, and ferrets commonly bite the prey on the back, by the spine/throat.

The martens are medium-sized carnivores that are good climbers, some of them climbing mainly on trees (American marten, pine marten, yellow-throated marten, Japanese marten), but some climb rocks, stones, or even buildings (stone marten). They are opportunistic species with a wide trophic spectrum, including a high consumption of fruits in summer, autumn, and even winter (Clevenger 1994; Martin 1994; López-Martin 2006). They are also very good hunters, having a strong bite that immobilizes the prey at the back of the throat. In the case of fruits, martens look for trees or bushy areas during the appropriate season. In this case, they can take fallen fruits from the ground or climb on the trees and take directly the fruits.

The fisher is a “large marten” that displays an interesting behavior to prey upon porcupines, by biting their faces several times when the prey is cornered. The fisher starts to consume the prey even alive, once it is immobilized.

Grisons (genus *Galictis*) are good climbers and swimmers but are mainly terrestrial predators. During the hunting, the grison moves in a zigzag pattern and can prey as a cat, moving silently with the body very close to the ground.

The badgers use their long claws and strong jaws to hit the prey; the European badger is one of the few species that can prey the hedgehog. As they are very good in digging and have good smell, most badger species look for earthworms in habitats plenty of them, caving holes on the earth. As the martens, badgers also look for fruits rich patches, but they cannot climb up trees or high bushes.

### Variation in Feeding Habits within Mustelids

With practically 60 mustelid species, and living in practically all kind of habitats, this family presents an enormous variety of feeding patterns. However, there are some few general strategies, all of

them involving the capture of animals as must be expected in a carnivorous origin group:

- Omnivorous, eating animals (vertebrate and invertebrate), fruits, honey, and other (martens, sable, badgers, ferret-badgers, tayra, grisons)
- Strictly carnivorous, eating mainly mammals (weasels, including Patagonian; stoat; ferrets; fisher; wolverine)
- Strictly carnivorous, eating mainly aquatic or semiaquatic preys (otters)
- Strictly animal eaters, but wide spectrum including insects, crustacean, amphibian, and other (polecats, minks, zorillas)

Among the omnivorous, the martens *Martes* sp. are medium-sized carnivores that occur in boreal and temperate habitats of the Northern Hemisphere, being distributed widely over the Holarctic. They show broad habitat flexibility, occupying several types of habitats, what is reflected in the plasticity of their feeding habits, where small mammals (principally rodents), fruits, and insects provide primary or secondary food resources (Clevenger 1994; Martin 1994; López-Martin 2006). As expected for opportunistic animals, as many other mustelids, they show differences in the diet between areas and even seasons. When the main prey becomes scarcer, martens change their main prey to another. Temperature, rainfall, and other factors can affect the ecosystem dynamics, what changes the prey availability and consequently the diet of *Martes* sp. (Wilson and Mittermeier 2009). Northern martens consume large amounts of carrion in winter and spring time (Clevenger 1994; Selva 2004).

The badgers (genera *Arctonyx*, *Taxidea*, *Meles*, and *Melivora*) inhabit both pristine and farmland habitats, and even cities (Wilson and Mittermeier 2009). The broad habitat types occupied by those animals can be justified by the broad niche of badgers. They are generalist omnivores that eat vertebrates, invertebrates (worms, insects), cereals, fruits, roots (honey), and even snakes. As generalists, they have different primary food sources between regions. The European badger *Meles meles* eat primarily earthworms in humid

habitats, but in some human-modified locations, the species can increase the ingestion of cereals and fruits. In more forested areas, with great availability of fruits and insects, those items were consumed more frequently by the badger, while in open areas the rodents or lagomorphs are preferentially eaten. The honey badger *Melivora capensis* can vary the diet between seasons, maintaining daily intake in weight, but switching items and varying niche breadth from summer to winter. The exception of this generalist behavior of badgers is the American badger (*Taxidea taxus*). This badger is specialized in rodents as prairie dogs and squirrels in many areas (as the European badger in some areas). The predator excavates the burrows of the prey and preys it inside the hole. Some of them can store the prey not eaten immediately to consume later.

The tayra *Eira barbara* is another opportunistic polyphagous omnivore, with a very diverse diet, including fruits, vertebrates, and also carrion. It can also prey upon insects and feed honey, being called in Portuguese as “papa-mel,” which means honey-eater. Its plastic behavior is probably associated with the wide variety of habitats that the tayra occupies, from forests to disturbed areas. The knowledge of the feeding habits of this mustelid rises from opportunistic observations, without a systematic study aiming to describe the seasonal and spatial differences in its diet. Its predation upon mammals, reptiles, and birds and the consumption of coffee, mamey, palm, genipapo, and *Cecropia* were reported.

The grisons, genus *Galictis*, are agile hunters, swimming and climbing very well. The lesser grison *Galictis cuja* preys mainly upon small mammals but can also eat birds, reptiles, amphibians, and their eggs. There are few studies focusing in its diet, but the main preys of the species seem to be rabbits and hares (Delibes et al. 2003). This behavior of predating upon invasive species can hire the species as a potential biological control of these two Lagomorph species. The greater grison *Galictis vittata*, as the smaller one, is opportunistic, eating almost everything it can obtain from predation. The main preys are small-medium sized vertebrates as agoutis and other rodents and lagomorphs, but

it can prey upon birds, lizards, amphibians, and their eggs too.

Weasels and ferrets can eat different vertebrate species, but they prey specially on small mammals, from mice or voles to rabbits and marmots (King and Powell 2007).

More aquatic the animal, more dependent from aquatic preys, as shown by the differential dependence of the sea otters, river otters, minks, and polecats for aquatic preys (Wilson and Mittermeier 2009). The most aquatic mustelids, the otters, prey mainly upon aquatic animals. River otters as Eurasian and Neotropical otters are generalist predators that show variation in their diet between areas and seasons. They prey preferentially upon fish, crustaceans, and frogs. Usually, fish constitute the main prey, but in certain areas and seasons, in situations with limited fish abundance or with restriction to small-sized fishes, or even with high availability of alternative prey, the otter can change the main prey to crustaceans, toads, frogs, or other aquatic species. More dependent on the terrestrial environment, minks *Neovison vison*, and *Mustela lutreola* eat aquatic prey, but less frequently than otters. They can prey upon aquatic birds as the water fowl and small mammals as rabbits and rodents. Polecats *M. putorius* are the most terrestrial of these three Mustelids, and they prey mainly upon terrestrial prey as woodland rodents and rabbits, and anurans are also common. These differences allow these Mustelids species to coexist in the same region, with exception of the two minks. The invasive American mink is a better competitor than the native European one, and in areas where they coexist, usually the European mink end up disappearing.

The sea otter *Enhydra lutris* can live all its life inside the water. Not surprisingly, it preys exclusively upon aquatic prey. They are top-chain predators of kelps and can prey upon several animals, but the main preys are benthic invertebrates as sea urchins, abalones, and mussels and clams. The Neotropical otter *Lontra longicaudis* and the giant otter *Pteronura brasiliensis* coexist in parts of their distribution. In those areas, although preying upon aquatic slow-mobility prey, they hunt different animals and with different sizes. The giant otter has a narrow food niche,

preying upon larger prey, mainly fish with 20 cm size or more. The Neotropical otter has a wider niche, preying on smaller fish (10–15 cm) and other categories of prey as crustaceans and anurans.

### Differences of the Diet between Size, Ages, and Sex of Mustelids

Most of the mustelid species present sexual dimorphism, the males being larger and heavier than the females (Holmes and Powell 1994; Kruuk 2006; King and Powell 2007). This provides different opportunities due to differential feeding specialization. This situation is more extreme within weasels, stoats, ferrets, and polecats, displaying differences in the type of species taken and in the prey size, between both sexes (King and Powell 2007). This can be a strategy to avoid intraspecific competition, especially during food shortages and to prevent the affection or event depletion of food stocks. There are other mustelid species that present differences in prey choices between sexes. As for example, in Shetland, UK, the Eurasian otters show differences in the feeding habits of solitary females, females with cubs, and adult males (Kruuk 2006). Usually, the males eat larger fish than females and cubs.

It was observed in Canada that mountain wolverines also show differences in the diet preferences between sexes (Lofroth et al. 2007). During the winter, females usually prey upon smaller animals, while larger males prey upon large ungulates as reindeer. Also, differences within sexes were observed. Caribou, hoary marmots, and porcupines were found in significantly higher frequencies in the diet of reproductive females than other females. However, there are exceptions. Despite marked sexual size dimorphism, male and female honey badgers do not show differences in daily intake and prey sizes (Wilson and Mittermeier 2009).

Mustelids also present differences in diet among age classes. This is the case again of the Eurasian otters in Shetland islands (Kruuk 2006). Cubs eat larger prey (more mass carried in a single way) during the first months of life than mother.

The type of prey consumed may be learnt from the parents, what explain the complex strategy



adopted for predation. In California sea otter, individuals from the same population specialize in different food items, with this behavior being passed from mothers to sons (Estes et al. 2003). The sons hunt in the same way as their mothers, with the main prey being the same.

## Conclusion

In this chapter, it was described how the mustelids get food from different sources and what are the main food items in their diets. They are usually highly mobile generalist predators that have different strategies depending on the environment where they occur. The animals of this highly diverse family can also feed upon fruits and other vegetables, honey, and can predate upon several species of animals, from aquatic to terrestrial ones. The comprehension of how each Mustelidae species deals with the food available, being more specialist or generalist, many times helps to adopt right strategies for its conservation. The black-footed ferret, one of the most specialist Mustelids, experiences conservation challenges, as it only occurs where its main and almost unique prey occurs, the prairie dog (Miller et al. 1996). Conservation decisions must consider the flexibility in habitat use and diet to project how the species would deal with food shortages and habitat modifications.

## Cross-References

- Carnivora
- Carnivore (Diet)
- Digestive System
- Food Calls
- Foraging
- Optimal Foraging Theory
- Predator Defense

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## Mustelidae Life History

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## Synonyms

Delayed implantation; Reproductive strategies; Weasel family

## Introduction

The Family Mustelidae includes a diverse group of small-to-medium-sized carnivores, adapted to a wide range of habitats and distributed worldwide. The 22 genera and 59 species range in body size from the least weasel (*Mustela nivalis nivalis*, 30–70 g), the smallest living carnivore, through the martens and sables (*Martes*, 0.5–5 kg), river-otters (*Lutra*, 5–30 kg), and badgers (*Meles*, *Taxidea*, 2–12 kg), to the bear-like wolverine (*Gulo gulo*, 25 kg) and the sea otter (*Enhydra lutris*, 45 kg).

The latest (Koepli et al. 2008) phylogeny of the family has identified four major clades (otters, weasels, martens, and galictids) plus three separate lineages of badger-like animals, mostly originating in Eurasia as a result of two bursts of diversification during the Tertiary era. The first, about 12–9 mya (million years ago) was

correlated with a global change in faunal composition as climate cooled, forests retreated, and the grasses evolved; and the second accompanied the start of the glacial cycles at about 5–2 mya. The earliest of the living lineages to reach the New World (extinct American badgers) arrived in the Miocene (about 7 mya) via the Bering Land Bridge.

These diversification events were set off by major environmental changes driven by the cooling climate, e.g., the spread of vast dry grasslands and the evolution of the voles and lemmings. These changes created new ecological niches determining the type and distributions of prey for mustelids, and correspond with similar events in other vertebrate groups. The global diversity of living mustelids is due to repeated dispersal from the Old World south to Africa and east to the New World, followed by local adaptation.

The Mustelidae as a group offer a clear example of adaptive radiation, defined as the evolution of multiple lineages of descendants adapted to different lifestyles and habitats, all traceable back to a common ancestor in the Oligocene (before 24 mya). The smallest species form a size-graded set of co-existing small, specialized searching predators, which share habitat and morphology but partition prey resources by size. At the other extreme, the larger species are generalized predators, dissimilar in morphology because of their advanced adaptations to different arboreal, aquatic or fossorial habitats. Body size is one of the most important parameters linked to life history characters; hence, we can observe an unusually wide range of life history characters within this one family. Complicating these general patterns is the fact that all members of the Mustelidae have some degree of sexual size dimorphism, whereby the males are larger – in the smaller species, much larger – than the females.

### Body Size, Habitat, and Population Dynamics

Body size, habitat, and the interaction between them profoundly influence life history and

population dynamics. Size affects energy requirements, metabolic rate, reproductive effort, generation time and population rate of increase, and therefore also home range and population density.

Habitat can be defined as that part of the total environment available to the individual (King 1983) and for carnivores the most important aspects of a habitat are the type and extent of vegetation cover, which determine the species and distribution of prey. For example, a strip of long grass full of field voles (*Microtus* sp.) may offer a short-term habitat for a weasel, which its offspring will probably have to leave. By contrast, a whole woodland and many of the surrounding fields may be a stable and permanent home for generations of badgers (*Meles meles*). Hence, mustelids of different sizes must have different life-history characters and population dynamics even when sympatric (King and Moors 1979).

When considering life histories, it is useful to make a distinction between evolutionary and ecological time. At the species level, life histories have evolved over millions of years and can be labelled as long-term *strategies*. In this context, the term “strategy” does not imply any forethought or planning; it simply describes the predictable results of a coordinated assemblage of reliable species-specific characters (e.g., average age-specific fertility and survival rates, and life expectancy) which are generally not changeable by individuals. The most important factor determining long-term life-history strategy is habitat stability.

But within those strategies, there is room for some flexibility at the individual level to variable environmental conditions. Short-term individual responses changeable in ecological time can be labeled as *tactics*. A similar contrast between long-term and short-term effects is summarized by the comment that: “Climate is what you expect; weather is what you get.”

### Life History Strategies

In short-lived and changeable habitats, the living conditions enjoyed by successive

generations may be very different – for example, in boreal grasslands and tundra, where voles and lemmings go through 3–4 year cycles of numbers ranging from sparse to super-abundant. In such a precarious environment, natural selection has favored the combination of reproductive characters which most strongly increase  $r$ , the population rate of increase, so they are called “ $r$ -selected” or “opportunistic” species. The key characters of such species are: early maturity, large litters, more than one litter per year, small young, minimal parental investment, short period of learning before independence, and a short average life span, in that order. Opportunistic species typically have small body size, short generation time, unstable populations, high and variable annual mortality and dispersal rates, and considerable resistance to total (though not to local) extinction. All the smallest mustelids are solitary and strictly carnivorous (King and Powell 2007).

By contrast, in long-lived and stable habitats such as a climax forest or undisturbed major waterways (preindustrial rivers, lakes, and the sea), the living conditions for successive generations are likely to be broadly similar. Forest predators such as pine martens, fishers, and sables, and for aquatic species such as river-otters and sea-otters, depended, for much of their evolutionary history, on broader food supplies less liable to feast-or-famine fluctuations. Some, e.g., stone martens and badgers, are omnivorous, extending the breadth of their dietary options. In such a (relatively) steady environment, natural selection has favored the combination of reproductive characters which most strongly affect  $K$ , the population density, so they are called “ $K$ -selected” species. Their key characters are (compared with  $r$ -selected species): later maturity, smaller litters, only one litter per year, large well-developed young, maximal parental investment, long period of learning before independence, and a long average life span, in that order. Equilibrium species typically have larger body size, longer generation time, stable populations, low annual mortality of adults, and greater vulnerability to extinction. Where the net marginal benefits of mutual association exceed the costs of

competition, some of the larger mustelids, e.g., European badgers and giant otters, have become sociable.

Of course, there are all gradations between these extremes, so there is a recognized  $r$ - $K$  spectrum of selective advantages generally correlated with reproductive effort, even though the combinations of life-history characters are somewhat flexible. This effect can best be seen by examining a set of sympatric species belonging to one mustelid assemblage. For example, the six members of the family Mustelidae resident in Britain can be ranged along the spectrum, as shown in Table 1. Similar tables could be compiled for other mustelid assemblages.

### Life History Tactics

The key challenge for all breeding animals is to minimize the risks of leaving no surviving young, thereby failing to pass on copies of their genes (King et al. 2003). Opportunistic and equilibrium species tend to use different tactics to respond to this problem. For parent animals belonging to opportunistic species, the chances of producing surviving young range from very high to practically nil, depending on the fluctuations of resources during the current breeding season and the dispersal capabilities of their offspring.

By contrast, for parent animals belonging to equilibrium species, the chances of success depend more on their social position within an established population, which in turn determines whether they can maintain possession of a viable territory and produce strong and competitive offspring.

Specialist vole predators such as least weasels face the greatest variation in resources between years, because the population fluctuations of their primary or only prey create alternate feasts and famines over periods longer than the average life span of breeding adults (1–2 years). In such a precarious environment, the best chances of parent weasels achieving reproductive success are to make a great effort to produce large numbers of small young capable of growing rapidly, dispersing widely and maturing quickly enough to

**Mustelidae Life History, Table 1** Relative positions of native British mustelids along the r-K spectrum, from strongly r-selected at left to strongly K-selected at right. Figures in parentheses following a mean give the range;

figures in square brackets are rough estimates. (Adapted from King and Moors 1979, updated from Harris and Yalden 2008)

|                                                       | <i>Mustela nivalis</i> | <i>Mustela erminea</i> | <i>Mustela putorius</i> | <i>Martes martes</i> | <i>Lutra lutra</i> | <i>Meles meles</i>  |
|-------------------------------------------------------|------------------------|------------------------|-------------------------|----------------------|--------------------|---------------------|
|                                                       | Weasel                 | Stoat                  | Polecat                 | Pine marten          | River otter        | European badger     |
| Earliest age (y) at first littering <sup>a</sup>      | 0.33–0.42              | 1                      | 1                       | 2–3                  | 1.5–2              | 2                   |
| Mean litter size                                      | 6 (4–8)                | 9 (6–9)                | 5–10                    | 3                    | 2–3                | 2.7 (1–5)           |
| # litters/y                                           | 1 or 2                 | 1                      | 1                       | 1                    | 1–1.5 <sup>b</sup> | 1                   |
| Mean female life span, y                              | <1                     | 1–2                    | 4–5                     | [3–6]                | 3                  | [1–4]               |
| Delayed implantation?                                 | No                     | Yes                    | No                      | Yes                  | No                 | Yes                 |
| Mean body weight female, kg                           | 0.068                  | 0.242                  | 0.689–787               | 1.3                  | 6–7                | 10.1                |
| Mean birthweight (g)                                  | 2–4                    | 3–4                    | 9–10                    | 30                   | [100]              | 75–132 <sup>c</sup> |
| Ratio reproductive <sup>d</sup> to somatic biomass, % | 18–35                  | 11–13                  | 6–13                    | 7                    | 3–4                | [2–3]               |

<sup>a</sup>Not age at first conception, which is distorted by delayed implantation

<sup>b</sup>No fixed breeding season

<sup>c</sup>Strongly influenced by social status and environmental conditions

<sup>d</sup>Ratio of total birthweight of young to weight of adult female, a measure of reproductive effort. Full reproductive biomass includes maternal genitalia, placentae and mammary glands, but data are not available

produce their own offspring at an early age. Young female least weasels born in the spring of a year with abundant voles are the only members of the Family Mustelidae capable of mating in the summer of their birth (at 3–4 months old), while at the same time, their mothers can produce a second litter. The combination of good juvenile survival and summer litters borne by both mothers and their early-born young results in a sudden huge increase in least weasel numbers at the peak of the vole cycle. During vole crash years, the local population of least weasels simply disappears, until restocked by young wanderers dispersing from more favored habitats elsewhere.

By contrast, equilibrium species have fewer options. Martens, otters and badgers take longer to mature and produce fewer, larger and slower-growing young. None can breed more than once a year (Table 1). Their best chances of achieving reproductive success are to produce small numbers of strong and well educated young capable, once mature, of competing with resident adults for social acceptance and living space. For established adults, the chances of living through more than one breeding season are relatively good. In years when few young are likely to survive, a resident adult can reduce the number

of young in a litter, or even skip breeding altogether, meanwhile holding on to their territory. For the parent, it is a better tactic to save wasted effort this year if there is the chance of better luck next year, so the parents put less effort into each litter. Variation in juvenile survival still causes fluctuations in population density, but over a smaller range than in opportunistic species.

This general pattern can be illustrated from the density data for mustelids recorded on Polish farmland through a population irruption of field voles in 1970–72 (Ryszkowski et al. 1973). The numbers of voles were low but increasing in the winter of 1970–71; they peaked during the summer of 1971, and the decline started in the winter of 1971–72. During this time the density of weasels varied threefold (15–46 hectares per weasel); the density of pine martens varied twofold (221–443 hectares per marten); and the density of European badgers remained at 510 hectares per badger throughout. Such contrasts in population density are due to age-specific variation in fertility and survival in all species, but the variation is controlled differently: by food resources in opportunistic species, but by density-dependent competition and social status in equilibrium species.



## Delayed Implantation

Of the 59 species in the family Mustelidae, the life history patterns of at least a third include some form of delayed implantation (DI), compared with 0.05% of all mammals (Thom et al. 2004). Under DI, the normal progression of reproductive processes from fertilization to birth is interrupted by a period of diapause (suspension of development). The fertilized zygote develops as far as the blastocyst stage, a hollow ball of cells, but it cannot implant until the uterus is ready to receive it and to cooperate with it in establishing a placenta. So the blastocyst simply floats free in the uterus, for periods varying from a few days in American mink to 10 months in the stoat. Only after a complex series of signals are exchanged between uterus and blastocyst can implantation and development proceed in the usual way. The period of delay therefore lengthens the reproductive cycle by disconnecting the season of mating from the season of littering.

DI is distributed patchily through the family, and is not a simple correlation with *r* or *K* type population dynamics. For example, of the six species ranging along the *r*-*K* spectrum shown in Table 1, three have periods of delayed implantation of different lengths, and three do not have it at all. Habitat and environment are not always reliable correlates either, since there are several pairs of similar small carnivores in which one has delayed implantation and the other has not. For example, the North American river otter, the stoat and the western spotted skunk all have delayed implantation, while their ecological equivalents the European river otter, the common weasel and the eastern spotted skunk do not.

The evolutionary origin and selective advantage of DI have been debated for years (Thom et al. 2004). The remarkably high incidence of this character among the Mustelidae suggests some kind of phylogenetic explanation. On the other hand, the *origin* of such an important feature of reproduction is a separate question from that of its *maintenance* in living animals over evolutionary time. No ancestral character could be so consistently retained among descendant lineages if it

were not associated with a significant adaptive advantage. The great diversity in size, habitat, and life span among mustelids and the great variation in hormonal mechanisms starting and ending the period of delay make any proposed advantage unlikely to apply to all species.

If DI was present in the common ancestor of the Mustelidae, variations in presence/absence or length of DI in descendant species could be accounted for by flexibility in the required endocrinal pathways controlling the mechanism and timing of implantation. Such flexibility is certainly visible in living species which have facultative and/or variable periods of delay, or none at all. Potential explanations for the advantages of DI in living species include the following:

1. Because DI separates the mating and birth seasons by longer than one cycle of gestation, each activity can be undertaken at the most favorable season for mating success and for the survival of offspring (Sandell 1984). It should therefore be an adaptive advantage in short-cycle species living in seasonal environments, allowing young to be born in early spring when food first becomes abundant, without requiring the adults to search for mates in mid-winter – the time when they need all their energy to keep warm. If so, DI should be more common in species living in more severe climates further north, whose young benefit from having a full summer to grow and mature before facing their first winter, and this is generally true.
2. The disadvantage of DI to the adult female is that it lengthens the total gestation period, meaning that a pregnant female must survive for longer before she can birth her pups. Therefore, one would expect DI to be more common in longer-lived (and generally larger) species, and this too is generally true. One conspicuous exception is the small, short-lived stoat, but in that case there could be a special reason (King 1984). The stoat has a unique combination of DI with an extraordinary precocity of the juvenile females: they pass puberty as infants, and are fertilized by an adult male

while they are still blind and unweaned. This surprising capability confers an extra advantage to the young females, balancing the obligate delay against their short lives: virtually all of them are fertilized before they leave the nest (King et al. 2003). It is also a massive benefit to the adult male, who is guaranteed a harem of young mates and huge reproductive success for his genes. (The stoat's similar but independently evolved North American cousin, the long-tailed weasel, also has juvenile precocity but in a less extreme form: the young females are already dispersed and independent by the time they become receptive).

The common weasel is not as closely related to the stoat as it looks, and besides, it is too short-lived for this strategy to work, so it has neither feature. Instead, young weasels born early in a season of exceptional food supplies can produce their first litters at 4 or 5 months of age (Table 1). If combined with high survival rates and second litters by adult females, the density of a weasel population can increase fivefold over a single summer (King and Powell 2007).

3. In species in which the female remains receptive for several days, DI could enable more than one father to contribute to a single litter. Where the two genders live on large and separate home ranges and may encounter each other infrequently, this effect, known as multiple paternity, allows the female to mate with a higher-ranked male even after having been served by a lower-ranked one. Later blastocysts join the earlier ones in delay, and at the right time they all implant together and produce an even-aged litter. This extra degree of mate choice benefits the female's chances of finding the best possible father for her offspring, and incidentally increases their genetic diversity. Alternatively, in sociable species like the European badger, mating activity goes on all year, in part as a guarantee of social acceptance. Delayed implantation at around the time of the winter solstice ensures that all cubs are born at about the same time in spring, mostly to the older, more dominant females (Yamaguchi et al. 2006).

## Conclusion

The various members of the Family Mustelidae are widespread and successful carnivores which have adapted to almost all habitats available around the world, in ways that enable them to avoid competing with rival Carnivores, the felids (cats) and canids (dogs). Instead, they specialize in a great variety of predatory niches all of their own. Their trademark long bodies and short legs are perfect tools for solitary burrowing, climbing, and swimming, and these hunting methods are reflected in their habitat choices and diets, which in turn decide their life histories.

## Cross-References

### ► Mustelidae Morphology

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## Mustelidae Locomotion

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### Synonyms

[Mobility](#); [Motion](#); [Movement](#)

### Definition

Movement of the family of carnivorous mammals that includes weasels, otters, marten, ferrets, badgers, and wolverines.

### Introduction

Members of the family Mustelidae share a similar morphology that involves an elongated body and short legs relative to mammals of similar body mass. This morphology facilitates hunting in unique or under-utilized ecological niches and may be a compromise between the abilities to exploit specialized habitats and to overpower relatively large prey (King and Powell 2007). While the differences in habitat specialization are associated with additional morphological adaptations to maximize success in ecological niches including aquatic, terrestrial, semiarbooreal, and fossorial habitats, it also translates into differences in locomotion among the species. For instance, otters use their elongated body for dorsoventral propulsion through water (Williams 1983a; Williams et al.

2002). American (*Mustela americana*) and Pacific martens (*M. caurina*) and fishers (*Pekania pennanti*) search for prey within subnivean space (spaces located underneath the snow between the snow and the ground) and in tree cavities (Buskirk et al. 1989). Other species including ferrets, weasels, and badgers hunt prey underground in fossorial habitats (Zub et al. 2011). However, there are common challenges for these species related to this body morphology: gaits are influenced by the short legs resulting in elevated stride frequency (Tayler et al. 1982), energetic economy is impacted because of the cost of supporting a long body with short limbs and by other morphological adaptations to exploit a specific habitat, and the higher surface area to volume ratio related to the long body also results in high energy expenditure during locomotion (Williams 1983b). Thus, understanding locomotion in Mustelidae includes consideration of four major variables: ecological niche or habitat, morphology, gait and posture, and energetic economy related to locomotor performance.

### Aquatic Mustelids

Mustelids that occupy aquatic habitats include 13 extant species of otters and 2 species of mink (*Mustela* spp.). These species' lifestyles include semiaquatic, aquatic, freshwater, and marine habitats with some species, like the North American river otter (*Lontra canadensis*), utilizing a range of these. For this group, body morphology strongly influences locomotor performance both in water and on land. All aquatic or semiaquatic mustelids have reduced cervical segments in their vertebral column (compared to other carnivores) to streamline the body (Taylor 1989). Adaptations for aquatic locomotion vary from mink (*Neovison spp.*), which have very few adaptations despite spending considerable time in aquatic habitats, to sea otters (*Enhydra lutris*) that possess many adaptations for a marine environment and rarely visit terrestrial habitats.

In aquatic habitats, the long body and reduced limb length of this group results in a stream-lined shape that reduces body drag, increases speed

during swimming locomotion, and consequently decreases the energetic costs of locomotion (Fish 2000). Otters use dorsoventral propulsion, a wave-like undulatory movement, as an energetically efficient means of locomotion in water. When using undulatory movements, the muscles in the lumbar region of the back provide most of the energetic movements, the forelimbs are held close to the body to reduce drag, and the hind limbs are extended parallel to the tail (Tarasoff 1972). The toes of otters are webbed to increase thrust generation while swimming, although this aquatic adaptation may reduce agility on land (Williams 1983b). Otters also have short forelimbs (Tarasoff 1972) because most of their forward propulsion originates in the lumbar and caudal regions of the body (Taylor 1989). However, mink, a more semiaquatic group of mustelids, do not use dorsoventral propulsion and, instead, swim at the surface of water and propel themselves with leg strokes. Mink are capable of diving and swimming while completely submerged but primarily dive when in pursuit of prey. The toes of mink are only slightly webbed, and they have relatively smaller feet compared to otters. The smaller foot size results in low surface area for forward propulsion while in water but has greater benefits for terrestrial locomotion. In water, mink compensate for their smaller and less effective feet with longer stroke lengths, a higher stroke frequency, and use both fore- and hind paws for propulsion, result in an energetically costly form of aquatic locomotion (Williams 1983a). Sea otters use both surface and submerged swimming and spend the majority of their time in the ocean (Estes 1980). The large size of the hind feet and even shorter hind legs (relative to other mustelids) of sea otters are effective adaptations for aquatic locomotion but decrease terrestrial locomotor performance. Submerged swimming in sea otters is half as energetically expensive as surface swimming at the same speed because of a decrease in form drag achieved through body morphology (Williams 1989). Unlike mink but like river otters, sea otters use dorsoventral undulation of the body and tail for forward propulsion during submerged swimming, and while it may not provide an energetic benefit,

it does increase swimming performance in terms of maneuverability and speed (Williams 1989). Sea otters also use movements originating in the pelvic region and their dorsoventrally flattened tail to move while floating on their back (Tarasoff 1972).

Most otter and mink species also use terrestrial habitats to varying degrees. Sea otters are capable of limited terrestrial locomotion and are the most aquatic species in this family. For some of these species, the flexible, elongated body can reduce locomotion costs on land. However, at lower speeds energy costs are high because of the high stride frequency associated with short legs. At higher speeds, otters and mink experience reduced transport costs through spinal flexion (Williams 1983b; Williams et al. 2002). Spinal flexion accelerates the front half of the elongated body during rebound movement and propels the animal forward like a spring during bounding locomotion, (Williams 1983b, Williams et al. 2002). When using spinal flexion, bound/stride length increases without increasing stride frequency (Williams 1983b). Mink exploit this economy by transitioning to a bounding gait at a lower speed than would be predicted based on body mass to maximize energy economy during locomotion (Williams 1983b).

## Terrestrial Mustelids

Terrestrial mustelid species include the stone or beech marten (*Mustela foinea*), grisson (*Galictis* spp.), and many of the weasels (*Mustela* spp.) Mustelids that spend the majority of their time in terrestrial habitats do not possess specific adaptations for locomotion beyond the general mustelid morphology. Grissons, however, possess webbed toes and will swim and climb trees although they are considered primarily terrestrial (Yensen and Tarifa 2003). Indeed, many primarily terrestrial mustelids also use fossorial, arboreal, and aquatic habitats to some degree.

During terrestrial locomotion, most mustelids skip the trotting gait that involves the opposite front and hind leg moving in unison and suspending the body between alternations of legs

(Hildebrand 1977; Williams 1983b). Instead, weasels and martens are more likely to transition from walking directly to a half-bound gait possibly because of the challenges related to the physical dynamics of a trot with the arched back and short legs of mustelid morphology (Gambaryan 1974; Williams 1983b). During the half-bound, the front feet contact the ground individually followed by the hind feet contacting the ground together. This movement then allows for spinal flexion in some species. This flexible form of locomotion allows weasels and other terrestrial mustelids to increase speed quickly by using muscles to propel the front limbs forward (Hildebrand 1982) and well-developed back and abdominal muscles to forcefully extend, flex, or contract the back during locomotion (Alexander and Jayes 1981). Many mustelids have higher cost of transport at low speeds, with increased energetic economy at higher speeds (Williams et al. 1983b) likely as a result of this spinal flexion. Greater grissons use intermittent locomotion (frequently pausing between movements) (Kaufmann and Kaufmann 1965), while bounding most likely as a predation strategy to pause and search for prey but possibly as a strategy to reduce energetic costs. Because of the general body morphology of mustelids and the related high surface area to volume ratio, these carnivores generally use or lose a large amount of energy even at rest. Therefore, maximizing and reducing energy use by limiting locomotion or exercise is yet another strategy to conserve energy (Chappell et al. 2013).

### Semiarboreal Mustelids

Semiarboreal mustelids include martens, fisher, and tayra (*Eira barbara*). These species use both terrestrial and arboreal habitats while hunting for prey and are skilled at climbing and moving above the ground through trees. Semiarboreal mustelids have been described as pursuit predators that pounce on prey, unlike other arboreal predators including felids that often use sit-and-wait predation and are quite agile at pursuing prey like birds and squirrels through trees. In order to use arboreal habitats, these species possess strong fore-

and hind limbs for climbing quickly, and in some species, the hind feet can be supinated or completely rotated (Powell et al. 2003) to increase control and grip when moving up and down tree trunks. Leaping movements between branches requires rapid and powerful extension of hind legs while using the tail for balance but possibly also as a parachute to increase control over downward movements (Taylor 1989).

Semiarboreal mustelids are also known to move through subnivean spaces in search of prey as well as use terrestrial habitats more generally. During terrestrial locomotion, these semiarboreal species also appear to either skip or minimally use the trot gait. Unlike the aquatic mustelids, these species have less curvature in the spine and either do not use spinal flexion during locomotion or use it very minimally. Pacific marten experience reduced spinal curvature during locomotion at high speeds. This curvature is considerably less pronounced and more posterior than in river otters or mink suggesting minimal benefits from spinal flexion during locomotion (Flaherty et al. 2014). Even without spinal flexion, these species still display greater energetic economy at higher speeds compared to lower speeds. Instead, the shift to a bounding gait reduces stride frequency and likely saves energy through mechanical energy recovery. Similar to locomotion in long-bodied canids, energy saving occurs during the natural rise and fall of the center of gravity of body mass during locomotion (Williams et al. 2002).

### Fossorial Mustelids

Fossorial mustelid species include badgers (*Meles* and *Taxidea* spp.), ferrets (*Mustela* spp.), and polecats (*Vormela peregusna*). The morphological adaptations for fossorial lifestyles in mustelids occur primarily in the feet (Taylor 1989). Badgers use their feet to dig and move soil and have developed large claws, heavily muscled bodies (Hildebrand 1985), and enlarged and strong leg bones to increase stability as well as surface area for attachment of the large muscles, especially shoulder muscles, used in digging (Taylor 1989).



The long claws influence the gait used by fossorial mustelids; the European badger (*Meles meles*) places more pressure on the toes using a digitigrade stance (Yalden 1970), while the American badgers' (*Taxidea taxus*) weight rests on the lateral portions of the paws resulting in a more plantigrade stance and removing weight from the large claws. Both species of badgers are also able to hyperextend their wrists (Taylor 1989). The overall body morphology is relatively short and flat with minimal bending or movement in the wide trunk. In the honey badger (*Melivora capensis*), trunk movement is reduced to the point of little to no lateral bending or sharp turns during locomotion; instead the honey badger rears on its hind legs to rotate the trunk perpendicular to the ground and returns to a four-legged stance oriented in a new horizontal direction (Eilam 1994).

Badgers use ambulatory locomotion and rarely use faster gaits. While the European badger has been observed running using a gait that involves overlap of hind feet and fore feet (Neal 1948), it is unlikely that the American badger uses a fast gait and relies primarily on a variable speed walk when searching for food. The large mustelids, like American badgers and honey badgers, likely do not use the half-bound or bounding gait because of a more rigid spinal column (Dagg 1973) and wider trunk. Faster gaits in these larger mustelids may not be necessary for pursuing fossorial prey. However, locomotion in badgers is relatively unstudied and little is known about the use of faster gaits in these species.

Ferrets and polecats are smaller-bodied than the badgers. These species use similar gait patterns when walking in a tunnel and when walking above ground despite the reduced body profile, and differences in pelvic height and limb extension in the two habitats (Horner and Biknevicius 2010). The crouched position during fossorial locomotion likely leads to increased energetic demands in response to the metabolic cost of maintaining this posture. While in tunnels, ferrets only use symmetrical gaits (walking, trotting, running) and no asymmetrical gaits (bounding, semi-bounding). The low ceiling and the crouched position likely limits movement of spine and

body axis, eliminating the opportunity to employ spinal flexion and other movements observed during half-bounds and gallops (Horner and Biknevicius 2010).

## Conclusions

Mustelid locomotion, both in terms of gait and energy economy, is heavily influenced by body morphology, which reflects adaptations to optimize habitat use and exploit unique ecological niches. As a result, there is considerable variation in the forms of locomotion used by members of this mammalian family.

Some mustelids cannot easily be classified into one of the four groups described above and have morphological adaptations for exploiting aspects of >1 habitat. For example, the Chinese ferret-badger (*Melogale moschata*) has webbed digits, long and robust claws, and while primarily terrestrial, occupy burrow systems and will use arboreal habitats (Storz and Wozencraft 1999), clearly suggesting additional unique locomotor abilities. Currently, only research on minks has investigated how adaptations for using multiple habitats may impact locomotion (Williams 1983a, b).

Locomotion is still relatively unstudied in this diverse carnivore family. Because mustelids and other carnivores disperse long distances and are capable of sustained locomotion, understanding this aspect of natural history and animal biology has important implications for conservation and wildlife management.

## Cross-References

- ▶ [Bear Locomotion](#)
- ▶ [Canine Locomotion](#)
- ▶ [Caudata Locomotion](#)
- ▶ [Dispersal Ability](#)
- ▶ [Energy](#)
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- [Mustelidae Morphology](#)
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- [Pinniped Morphology and Locomotion](#)
- [Quadrupedal](#)
- [Terrestrial](#)

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## Mustelidae Morphology

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## Introduction

Despite recent molecular data evidenced that skunks do not lie within the mustelid group (Sato et al. 2012), Mustelidae, bearing 56 species in 22 genera, are the largest and oldest family in

the order Carnivora (Nyakatura and Bininda-Emonds 2012). The family originated in Eurasia in the middle-late Miocene and underwent a rapid evolution and diversification, resulting in a remarkable ecomorphological diversity (Koepfli et al. 2008). Koepfli et al. (2008) identified two major clades, Lutrinae and Mustelinae, and eight minor clades of Mustelidae. American and honey badgers (genera *Taxidea* and *Mellivora*) are monotypic lineages basal to all other mustelids. The clade Martinae, including taira, wolverine, hog badger, Eurasian badgers (genus *Meles*), and martens (genus *Martes*), is in turn basal to the clades Helictinae (ferret badgers), Galictinae (spotted and striped aposematic species: grisons, zorillas, the marbled polecat, and the African striped weasel), Mustelinae (minks and true weasels), and its sister clade Lutrinae (otters).

## Coat

Mustelids have a dense and rich underfur, and overharvesting for pelt trade led many species to the brink of extinction in the last century. Ermines, sables, martens, fishers, otters, and minks were among most harvested species, while hairs of badgers have been long used as paint brushes (Domingo-Roura et al. 2006). The trapped air in the underfur helps both to retain body heat and to maintain a stable body temperature. Aquatic and semiaquatic mustelids like otters and minks have the densest underhairs, i.e., highest number of underhairs per bundle, which facilitates the hair interlocking and increases the efficiency of the insulating air barrier during prolonged submergence in cold waters (Liwanag et al. 2012). The fur of the sea otter *Enhydra lutris* is the thickest among mammals, with up over 1,000,000 hairs per square inch. According to Liwanag et al. (2012), the ancestral form of mammal insulation depending on the external fur became the primary thermal barrier in water in aquatic and semiaquatic mustelids, while in other marine carnivore lineages (Pinnipeds) primary insulation relies on internal blubber layer (Liwanag et al. 2012). Insulation in otters is also promoted by geometric scale patterning of the underhairs, which favors interlock of hairs (Fig. 1).

Despite a dense underfur functions as a good insulator, insulating value is diminished by water vapor, water penetration of the fur, and the altered position of the fur relative to the body during swimming and diving (Kuhn and Meyer 2009, 2010). To overcome these drawbacks, guard hairs of aquatic and semi-aquatic mustelids are flattened so that the air layer trapped by the underfur is maintained also during swimming. Flattening of guard hair is especially efficient in sea otters, as this species lacks arrector pili muscles (Liwanag et al. 2012). Flat and elongated scale patterning on the guard hairs is found in otters and ermines and is likely an exaptation of mustelids hairs (Liwanag et al. 2012). Specialized oil glands further increase insulation by waterproofing of the hair. The three layers of the mammalian hair, i.e., cuticula, cortex, and medulla, can be used for species identification (Teerink 1991). However, Toth (2002) has shown that only combinations of hair traits allow a reliable identification of species.

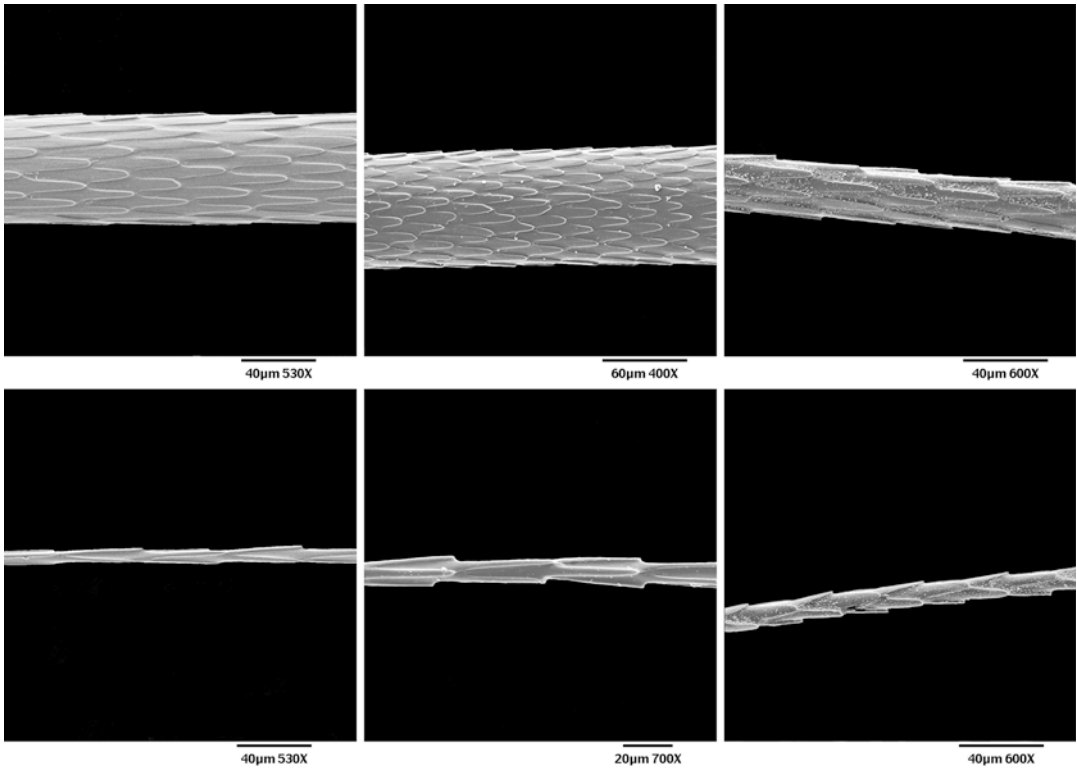
Mustelid pelage is generally uniform in color, with exception of the clade Galictinae, including species with spotted and striped aposematic pelage (genera *Vormela*, *Poecilogale*, and *Ictonyx*). At high altitudes or latitudes where snow cover is common in wintertime, the ermine *Mustela erminea*, the long tailed weasel *M. frenata*, and the least weasel *M. nivalis* undergo a complete change of their coats from brown to white (“ermine” morph). In the Japanese weasel (*Mustela itatsi*), the pale yellowish winter pelage turns to dark brown in summer.

The black tail tip shown by ermine and long-tailed weasel in winter is likely useful to focus the attention of potential predators away from the body.

Facial and throat markings occur in many species, like polecats, martens, badgers, and giant otter, and are often used in field studies for individual recognition (see for example Groenendijk et al. 2014; Fig. 2).

## Body Shape and Postcranial Skeleton

In spite of little variation in body shape, i.e., small head, long neck, and body, Mustelids are highly



**Mustelidae Morphology, Fig. 1** Scanning electron micrographs showing the cuticular scale patterns of dorsal guard hairs (top) and dorsal underhairs (bottom) of a sea otter *Enhydra lutris*, a North American river otter *Lontra*

*canadensis*, and a least weasel *Mustela erminea* (Courtesy H. Liwanag, after Mostman Liwanag 2008 and Liwanag et al. 2012)



**Mustelidae Morphology, Fig. 2** Different throat marking in giant otters. Left: Courtesy © Rob Williams, Manu National Park, Peru; Right: Courtesy © Caroline Leuchtenberger

variable in size, from 30 cm and 24 gr of a least weasel (*Mustela nivalis*) – the world’s smallest carnivore – to 130 cm and 45 kg of a sea otter (*Enhydra lutris*) (Fig. 3).

However, most members of the family show a similar size, a phenomenon that according to Meiri et al. (2007) can be explained by similar prey selection rather than by competition.

Mustelids are skilled hunters, exploiting a great diversity of both vertebrate and invertebrate prey (King et al. 2010). They often hunt in burrows and crevices, and some species chase their preys on trees (e.g., marten) or in water (e.g., sea otters, minks). The short-legged, long and flexible body and tail of most species are considered ancestral traits of the family, evolved to run after and chase rodents in burrows, whereas the squat shape with short tail of badgers and wolverine is believed considered a derived trait (Ercoli and Youlatos 2016; Fig. 4).

In accordance, Koepfli et al. (2008) suggested the main driver of mustelid radiation was the spread of fossorial preys that followed the replacement of forests with open environments, as a consequent of aridity turnover of the global climate during the middle-late Miocene.

Limbs of Mustelids have five digits each, usually provided with strong curved and nonretractile claws that are often shown in prints (Halfpenny

and Biesiot 1986). Most members of the family are digitigrade although few are plantigrade (Fig. 5). Some species like otters are normally plantigrade but can be digitigrade when running (Halfpenny and Biesiot 1986). In most otters, minks, and two South American weasels, the digits are webbed to facilitate swimming.

The family shows a wide range of locomotory adaptations, including ground dwelling (weasels and wolverine), arboreal (martens and ferret), fossorial (badgers and black footed ferret), as well as aquatic and semiaquatic (sea and marine otters, freshwater otters, minks) species. Whereas gravity and inertial forces are the principal constraints on locomotion in terrestrial species, drag forces are dominant in water (Fabre et al. 2015).

To reach relative high-speeds during running with their short limbs, Mustelids adopt a bounding locomotion, in which jumping is performed by an extended axial phase synchronized with limb movements (Ercoli and Youlatos 2016). The high



**Mustelidae Morphology, Fig. 3** Skull of a least weasel *Mustela nivalis* (left, Muséum National d'Histoire Naturelle Coll.N. MNHN-ZM-MO 2006-261) and a sea

otter *Enhydra lutris* (right, Muséum National d'Histoire Naturelle, Coll. N MNHN-ZM-MO 1962-2678), showing extremes of size variation in Mustelids. © Anna Loy



**Mustelidae Morphology, Fig. 4** Body shapes of Mustelids. Left: a short-legged and long tailed river otter (from Chanin P. 1985 The natural History of otters,

Academic Press). Right: a squat short tailed badger (Photo credit: Tierbildergalerie.com, [http://www.tierbildergalerie.com/data/media/91/otter\\_skelett.jpg](http://www.tierbildergalerie.com/data/media/91/otter_skelett.jpg))





**Mustelidae Morphology, Fig. 5** Fore (above) and hind (below) paws of a badger (left) and a polecat (right). Courtesy © Brian Ecott – Hainault Forest

speed runs of the wolverine and the undulating swimming of otters are taught to be derived from such ancestral traits. Moreover, in semi-aquatic animals, drag is minimized by streamlining body shape and appendages.

Limbs adaptation and convergence in long bone morphology in mustelids were recently investigated by Ercoli and Youlatos (2016) and by Botton-Divet et al. (2017). According to Ercoli and Youlatos (2016), the forelimb of most Mustelids shares a well-developed epicondyle and supinator crest of the ulna, this latter oriented in the proximodistal direction and flaring laterally. In the majority of scansorial and arboreal species, the scapula has an ample acromion process that tilts cranially with respect to the spine, the humeral head is located more proximally than the lateral and medial tuberosities, and the radial head is elliptical to rounded. In scansorial species, the olecranon process of the ulna is moderately to poorly developed. In most arboreal species, including the tayra, characterized by a mosaic of autopodial specializations to arboreal locomotion and less modified ancestral proximal elements, the anterior surface of the distal ulna bears a distinct pronator

crest (Ercoli and Youlatos 2016). In terrestrial species and in the scansorial boulder *Martes*, the acromion process of the scapula is reduced and/or with a lesser tilt. As to the hind limbs, the femoral head of terrestrial species possess more abrupt limits and a more medial position in respect to the major axis of the diaphysis. In scansorial and arboreal species is slightly more elevated or similar in height in respect to the major trochanter. The calcaneum has a well-developed trochlear process, and the metatarsals are long in relation to the rest of the hind foot. The pelvis of both scansorial and terrestrial musteloids possesses a relatively long ischium. High specialization of mustelids limbs is found in fossorial badgers and aquatic otters. In the fossorial *Meles* sp., the forefeet are provided with strong claws that enable to dig complex tunnels systems, the scapula has a prominent ridge acromion process, the deltoid ridge is prominent, and like in scansorial species, the supinator crest is relatively well developed in the proximodistal direction while the medial epicondyle is well developed (Ercoli and Youlatos 2016).

Otters and the two minks (*Mustela lutreola* and *Neovison vison*) represent three independent

returns to the aquatic environment among the Musteloidea (Sato et al. 2012). Adaptations to water followed different pathways and reached different efficiency in Mustelinae (minks) and Lutrinae (otters) (Botton-Divet et al. 2017). Minks retain the four limb terrestrial locomotor patterns of the Mustelinae, swimming by a drag-based propulsion with paddling appendages, whereas otters use a more efficient lift-based propulsion with oscillating hydrofoils. Also, otters show various swimming gaits depending on the species (Botton-Divet et al. 2017), and their limbs display more robust bones than Mustelinae (Fabre et al. 2015). This latter trait was interpreted as an adaptation to both support body weight during terrestrial locomotion and to stabilize the body during swimming (Nakajima and Endo 2013). Lutrinae shows a large diversity in all bones but the humerus, likely as a consequence of diversity in swimming gaits (Botton-Divet et al. 2017). The sea otter shows the most derivative traits, as it extensively uses its forepaws to manipulate objects, and not for aquatic locomotion. Also, it seldom walks on land, and has lost the ability to run (Botton-Divet et al. 2017). The peculiar feeding behavior of the sea otters, using forepaws to dig, gather, hold, and often manipulate prey with tools, is testified by its unique radial and ulnar shape, which are slender and with a shorter and straighter olecranon process compared to that of other mustelids (Botton-Divet et al. 2017). In contrast, minks display a high degree of convergence in the shape of their long bones, likely as the result of same functional pressures on the forelimb. Convergence is especially significant in the humerus. This bone is characterized by an expansion of the cranial part of the diaphysis, a wide area between the greater trochanter and distally expanded deltoid crests leading to greater insertion areas of the shoulder flexor, the abductors, and the retractor muscles (*m. deltoideus*, *m. pectoralis major*, and *m. pectoralis minor*) (Ercoli et al. 2015; Botton-Divet et al. 2017). However, despite their similar shape, the forelimbs of the two minks differ in some traits. The shape of the long bones in European minks *Mustela lutreola* is closer to that of Lutrinae. They show an antero-distal displacement of the

shoulder retractors implying an extended in-lever and therefore a more powerful retraction of the shoulder, likely related to the mechanical requirements of padding when moving in a denser medium (Botton-Divet et al. 2017). Also, European minks have a wide epicondylar crest reminding that of otters, even if less developed. This crest provides origin for the *m. anconeus*, which assists elbow extension on the caudal side, and is also the origin for several digital and carpal extensors and the wrist flexor on its laterocranial side (Botton-Divet et al. 2017). American mink *Neovison vison* has a longer olecranon process of the ulna compared to its terrestrial relatives, providing a longer in-lever for the elbow extensor. This trait seems to be linked with body mass, suggesting a role for sustaining larger mechanical load during terrestrial locomotion (Botton-Divet et al. 2017). The American mink tends to converge with the Lutrinae for the shape of the ulna, femur, and tibia, in accordance with the larger size of this species. Ercoli et al. (2015) recognized some muscular traits of the limbs shared by all mustelids, such as the presence of *rhomboideus profundus*, an angular head of *triceps brachii*, and, apparently, the absence of a *flexor digitorum brevis manus*. The lesser grison *Galictis cuja* possesses an unexpected *articularis humeri* and lacks the *tensor fascia antebrachii* (Ercoli et al. 2015). Also, according to Ercoli et al. (2015), *Ichthyonychia* and *Mustelinae* possess traits related to a high resistance in landing during bounds and to the increase of gait length during epigeal and subterranean crouched. These traits include a strong and subdivided protractors, a sagittal rotators of the forelimbs, and shoulder and elbow extensors. Powerful neck musculature assists during hunting and carrying of prey. Ercoli et al. (2015) found that the configuration of the *rhomboideus* and the absence of *coracobrachialis* are diagnostic of subfamilies.

## Skull Morphology

As for most vertebrates, the skull of mustelids is a highly informative structure, retaining both phylogenetic and adaptive signals (Hanken and Hall

1993). Adaptive significance is linked to the deep involvement in many critical functions, such as the protection of the brain and the special sensory organs, food acquisition and manipulation, as well as breathing and communication skills (Hanken and Hall 1993). Recently Dumont et al. (2016) also highlighted differences in skull traits of the Musteloida related to locomotor adaptations, such as the orientation of orbit, cranial base, and occipital condyles. Mustelids share with ursids, canids, viverrids, and herpestids an “arctoid” skull design, whereas a “feloid” skull is characteristic of felids, hyaenids, and some viverrids. The typical “arctoid” skull has a large head and long snout housing large cheek teeth suitable to exploit a variety of feeding resources, including vegetables (Van Valkenburg 1988). Mustelids skull partially deviate from the arctoid skull in that it has generally a long braincase (Fig. 6).

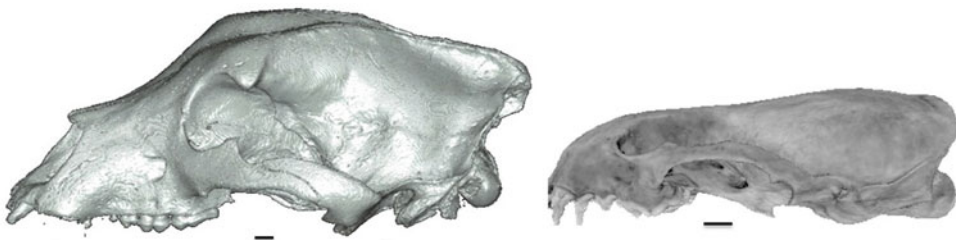
Trophic adaptation is a main driver of skull morphological changes in Mustelids skull, and evolutionary response to feeding pressure can be very rapid, even at subspecific level (Timm-Davis et al. 2015). Also, the high degree of morphological divergence observed in strictly related species suggests feeding adaptive pressures and intraguild competition having a more relevant role in shaping skull morphology of Mustelids than phylogenetic constraints (Abramov et al. 2016). As an example Abramov et al. (2016) suggested resource partitioning and reduction of ecological niches’ overlap as main factors explaining the differences in skull morphology between the sympatric and closely related polecats *M. putorius* and *M. eversmannii*. Also, a different degree of

hypercarnivory was claimed to explain the differences in the skull design of the closely related *Martes martes* and *M. foina*, with selective forces acting to either increase the bite force at the expense of gape or vice versa (Loy et al. 2004). Finally, Timm-Davis et al. (2015) found significant differences in the skull shape of Lutrinae, also within foraging types.

Thus, we can affirm that the shape of the mustelid skull markedly reflects their diets.

Mustelids should consume a large amount of food to maintain their basal metabolism; as a consequence, animal prey is a major component of their diet (King et al. 2010). Only few species include vegetables in their diet: badgers (genera *Taxidea*, *Arctonyx*, *Mellivora*, and *Meles*), pine marten *Martes foina*, beach marten *M. martes*, and tayra *Eira Barbara*. The European badger also relies heavily on earthworms, which can make up nearly two-thirds of its diet (Roper 1994). Some mustelids, such as wolverines and fishers, may also feed on carcasses of animals killed by other predators (Landa et al. 1997; Zielinski et al. 1999).

Timm-Davis et al. (2015) provided an extensive and accurate analysis of the morphology and functional performances of otters’ skull in relation to feeding adaptations. Otters have evolved two feeding specializations. Mouth-oriented piscivores use raptorial biting to capture elusive prey in open water, while hand-oriented otters chase nonelusive, benthic organisms (e.g., crustaceans, mollusks) which armors require high crushing capabilities. Mouth oriented habit is considered the basal feeding mode of otters (Berta



**Mustelidae Morphology, Fig. 6** Comparison of the typical “arctoid” skull of a brown bear (left, *Ursus arctos*, 3d scanning, Coll.N. C60 National Park of Abruzzo, Lazio and Molise, courtesy Centro Radiologico Potito,

Campobasso, Italy) and that of an Eurasian otter (right, Swedish Museum of Natural History Coll.N. NRM-20115598, 3D photogrammetric reconstructions by A. Loy). © Anna Loy

and Morgan 1986), and it is typical of North American river otter (*Lontra canadensis*), neotropical river otter (*Lontra longicaudis*), giant river otter (*Pteronura brasiliensis*), smooth coated otter (*Lutrogale perspicillata*), Eurasian river otter (*Lutra lutra*), spotted-necked otter (*Hydrictis maculicollis*), and hairy-nosed otters (*Lutra sumatrana*). Hand-oriented predators include the sea otter (*Enhydra lutris*), the African clawless otter (*Aonyx capensis*), the Congo clawless otter (*Aonyx congicus*), the Asian small-clawed otters (*Aonyx cinerea*), the marine otter (*Lontra felina*), and the Southern river otter (*Lontra provocax*) (Medina-Vogel et al. 2004; Medina-Vogel and Gonzalez-Lagos 2008; Timm-Davis et al. 2015). These specializations have profound influence on skull morphology, as jaw motion velocity (required in mouth-oriented species) and biting capabilities (required in hand-oriented species) cannot be simultaneously maximized (Timm-Davis et al. 2015). Thus, jaws are designed to either increase velocity at the expense of biting capability. In mouth-oriented predators, longer, narrower skulls and long mandibles position the resulting bite force farther from the temporo mandibular joint, providing jaws with greater velocity at the expense of bite force

capability. Hand-oriented predators have shorter skulls and mandibles providing a high bite force and further modified dentition (e.g., wide, flat occlusal surfaces) (Timm-Davis et al. 2015). Extreme skull morphologies are shown by the mouth-oriented giant otter and the hand-oriented sea otter, having blunt mandible and concomitantly wide skull (Fig. 7).

Mouth-feeding river otters have hypertrophied jaw muscles even compared to terrestrial mustelids. The temporalis muscle and the zygomatico-mandibularis muscle are responsible for exerting the main force when jaws are fully open, while enlarged digastric muscles allow the rapid jaw motion necessary for catching elusive fish underwater (Timm-Davis et al. 2015). These characteristics are reflected in the skull, having broad mastoid processes where the digastric muscles originate. Rapid motion of the jaws is especially favored in the giant otter that has the longest skull and mandibles and the smallest temporalis and masseteric mechanical advantages among otters, and a bite point (at all bite locations; e.g., canines, molars) positioned farther from the temporal-mandibular joint (Timm-Davis et al. 2015). Conversely, the skull of sea otters is deeply shaped by durophagy, possessing taller and wider



**Mustelidae Morphology, Fig. 7** Left: ventral view of the skull of a sea otter *Enhydra lutris*, deeply shaped by durophagy and hand oriented feeding (Museum National d'Histoire Naturelle de Paris, coll. N. MNHN-ZM-MO

1962-2678); right: ventral view of the skull of a giant otter *Pteronura brasiliensis*, a piscivore and mouth oriented feeder (Museum National d'Histoire Naturelle de Paris coll. N. MNHN-ZM-MO 2006-550). © Anna Loy



mandibular rami, and shorter, blunter skulls than other otters (Fig. 7). Great width of both braincase and rostrum, great interorbital distance and the corresponding differences in jaw adductors likely explain the increased zygomatic length.

The great masseteric mechanical advantage, the height of the mandibular ramus, and depth of the mandibular fossa relate to increased bite force, while a greater moment arm of the masseter also generates more control over mastication (Timm-Davis et al. 2015). Sea otter mandibles have relatively tall and vertically oriented rami combined with a long zygomatic arch for masseter attachment. A long zygomatic length allows muscles to attach more anteriorly, thus improving bite force while allowing a larger gape (Timm-Davis et al. 2015). Otter adductor muscle architecture and physiology are modified to allow for a wide gape while maintaining a high bite force. Sea otters also possess a higher rostrum, offering an increased area for muscle attachment. Shorter and wider skulls increase the bite force and bring the canines closer to the fulcrum, which increases the mechanical advantage of the masseter even at the tip of the jaw, resulting in increased bite force at this position as well.

North American, Neotropical, and Eurasian river otters, smooth coated otter, spotted-necked otter, and hairy-nosed otters primarily feed on fish, but also incorporate crustaceans, amphibians, birds, and mollusks in their diet. Their skull shape is thus expected to be intermediate between the

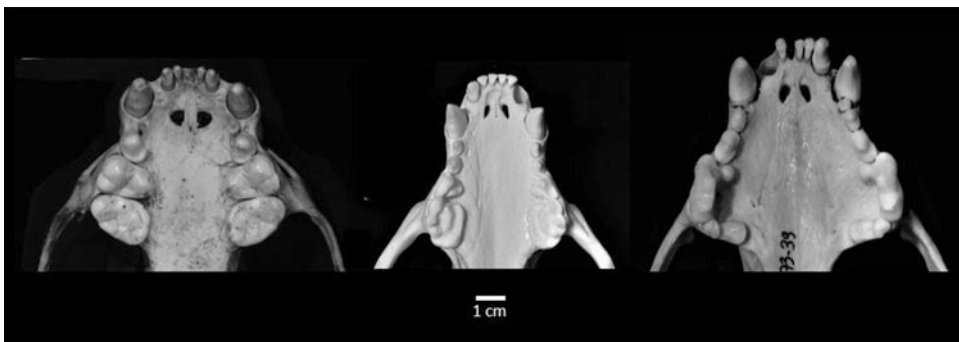
strictly piscivorous giant otter and hand-oriented invertebrate specialists (Fig. 8).

Timm-Davis et al. (2015) showed that in the North American river otter the relatively long mandibles and higher temporalis and lower masseteric mechanical advantage position bite force at the anterior mandible at the canines, which favors a mouth-oriented predator that also may consume large fast moving fish like salmonids.

Similarly, the Asian small-clawed otter *Aonyx cinereus* is a hand-oriented predator that consumes a broader spectrum of prey than sea otters. In this species, the mechanical advantage of temporalis, which large mass is witnessed by a long zygomatic fossa, is significantly greater than the masseter's, suggesting increased force at the anterior jaws near the canines, allowing to catch fast prey by this hand-oriented feeder.

Timm-Davis et al. (2015) suggest that trophic differentiation in otters may be either deeply or shallowly rooted in phylogeny, and is at least partly replicable.

The transverse condyle of the mandible is locked into the postglenoid process partially enclosing the glenoid fossa, so that in some species the condyle of the dentary bone is difficult to disengage from the fossa (Van Valkenburg 1988). This enables the animal to maintain it firmly hold, but limits jaw movements. Other cranial features of Mustelids are the absence of alisphenoid canal, a single-chambered auditory bulla, and a supra-meatal fossa in the middle ear (Wolsan 1993).



**Mustelidae Morphology, Fig. 8** Palatal view of a sea otter *Enhydra lutris* (left, Museum National d'Histoire Naturelle de Paris, coll. N. MNHN-ZM-MO 1962-2678), an Eurasian badger *M. meles* (Museum National d'Histoire

Naturelle de Paris, coll. N. MNHN-ZM-MO 1998-1247) and a wolverine *G. gulo* (Museum National d'Histoire Naturelle de Paris, coll. N. MNHN-ZM-MO 1873-39). © Anna Loy



**Mustelidae Morphology, Table 1** Dental formula of Mustelidae

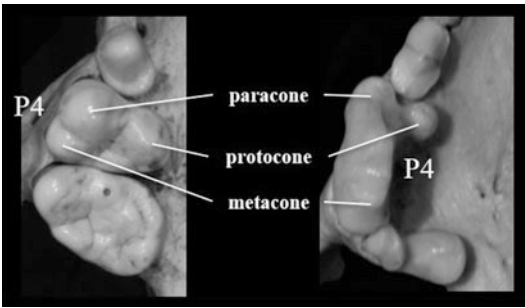
| Dental formula                         | Species                                                                                                                                                                                                                                                                       |
|----------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| I3/3, C 1/1, PM4/4,<br>M1/2 = 38       | <i>Gulo gulo</i> , <i>Martes foina</i> , <i>M. americana</i> , <i>M. zibellina</i> , <i>M. martes</i> , <i>M. pennanti</i> , <i>Lutra lutra</i> , <i>Meles sp.</i> , <i>Arctonyx collaris</i> , <i>Martes pennanti</i> , <i>Aonyx cinereus</i> , <i>Melogale sp.</i>          |
| I3/3, C 1/1, PM 3-4/3,<br>M1/2 = 36    | <i>Lontra canadensis</i> , <i>L. provocax</i> , <i>L. felina</i> , <i>Lutrogale perspicillata</i> , <i>Pteronura brasiliensis</i> , <i>Lutra sumatrana</i> , <i>Aonyx capensis</i> , <i>A. congicus</i> , <i>Hydrictis maculicollis</i>                                       |
| I3/3, C1/2, PM3/3,<br>M1/2 = 36        | <i>Mustela felipei</i>                                                                                                                                                                                                                                                        |
| I3/3, C1/1, PM3/4,<br>M1/1 = 34        | <i>Galictis cuja</i>                                                                                                                                                                                                                                                          |
| I3/3, C1/1, PM3/3,<br>M1/2 = 34        | <i>Mustela nivalis</i> , <i>M. putorius</i> , <i>M. frenata</i> , <i>M. erminea</i> , <i>M. lutreola</i> , <i>M. nigripes</i> , <i>M. nudipes</i> , <i>Vormela peregusna</i> , <i>Taxidea taxus</i> , <i>Ichthyonyx sp.</i> , <i>Galictis vittata</i> , <i>Neovison vison</i> |
| I3/3, C1/1, PM3/3,<br>M1/1 = 32        | <i>Mellivora capensis</i>                                                                                                                                                                                                                                                     |
| I 3/2, C 1/1, PM 3/3,<br>M1/2 = 32     | <i>Enhydra lutris</i>                                                                                                                                                                                                                                                         |
| I 3/3, C 1/1, PM2-3/2,<br>M1/2 = 30-32 | <i>Mustela africana</i>                                                                                                                                                                                                                                                       |
| I3/3, C1/1, PM2/2,<br>M1/1 = 28        | <i>Poecilogale albinucha</i> , <i>Lyncodon patagonicus</i>                                                                                                                                                                                                                    |
| I3/3, C1/1, PM3/3,<br>M0/0 = 28        | <i>Eira barbara</i>                                                                                                                                                                                                                                                           |

Teeth

The mainly carnivorous diet of Mustelids is reflected in their teeth: canines and molars are large and sharp, while incisors are usually small. The dental formula is quite variable, from I3/3, C1/1, P4/4/, M1/2 = 38 to I3/3, C1/1, PM3/3, M0/0 = 28 (Table 1).

Mustelids that crush their prey or feed on vegetable though food possess broad flat occlusal surface areas of the cheek teeth (Timm-Davis et al. 2015). These include wolverines, fishers, badgers, and sea otters, these latter showing the largest relative occlusal surface areas among mustelids, and the only possessing bunodont dentition (Fig. 9).

Specifically, the carnassials (P4 and m1) are either trenchant or modified into crushing teeth. In the sea otter and other otter species specialized to feed on hard shelled mollusks (*Aonyx congicus*, *Aonyx cinerea*, *Lontra felina*, and *Lontra provocax*) have carnassials with rounded cusps adapted to crushing and broad postcarnassials (M1 and m2).



**Mustelidae Morphology, Fig. 9** Crushing (left) and trenchant (right) cheek teeth of the upper jaw of a sea otter (left, Museum National d’Histoire Naturelle de Paris, coll. N. MNHN-ZM-MO 1962-2678) and an Eurasian badger (right, Museum National d’Histoire Naturelle de Paris, coll. N. MNHN-ZM-MO 1998-1247). (© Anna Loy)

Sexual Dimorphism

The evolution of sexual dimorphism in body size and morphology of animals has been related to sexual selection, intersexual food competition, and differential investment in parental care (Hedrick and Temeles 1989). Therefore, sexual

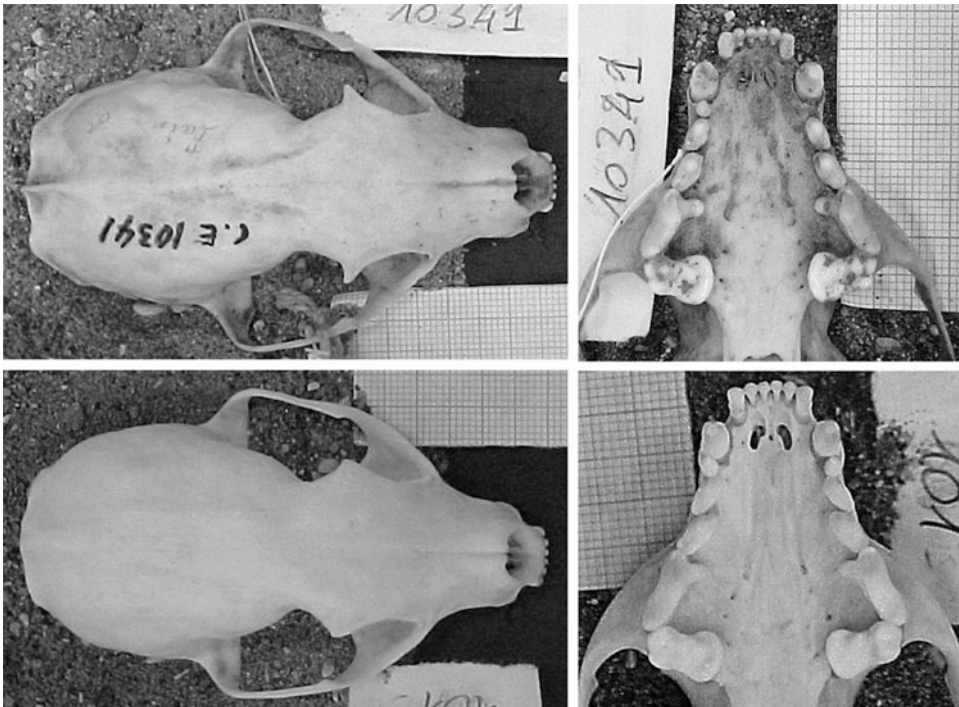
dimorphism is the result of evolutionary changes and constraints posed on each of the sexes independently (Fairbairn 1997).

As in most Carnivora, sexual dimorphism in Mustelid is mainly sexual size dimorphism (SSD), with males larger than females. As an example, in sea otters males are 34% heavier and 8% longer than females. SSD has been explained either by a strategy to avoid intraspecific competition (males and females adapted to catch different preys) or related to polygynous mating system, where small females are favored because they need less energy for daily maintenance and can channel more energy into reproduction, while male's larger size is favored by sexual selection and ability to exploit a wider range of prey (Moors 1980). Loy et al. (2004), by adopting a geometric morphometric approach that allows to disentangle the variation in shape versus variation in size, found significant differences in both the size and the shape of the skull of males and females of the

closely related pine marten *Martes martes* and beech marten *M. foina*. Shape differences were similar, although more marked in the stone marten, with males bearing a larger and shorter skull, larger carnassial teeth PM3 and M1, and more marked postorbital constriction than females (Loy et al. 2004; Fig. 10).

Interestingly, a more marked postorbital constriction in males was also described by Lynch et al. (1996) for the Eurasian otter *Lutra lutra*, while Dayan et al. (1989) found sexual dimorphism in the canine size of three species of weasels from North America.

Sexual size dimorphism of mustelids has been interpreted either as a mechanism to reduce intersexual competition for food by enabling each sex to exploit different prey (Loy et al. 2004) or as a consequence of sexual selection that in polygynous mustelids favors larger males (Moors 1980). As an example, Loy et al. (2004) suggested that sexual dimorphic traits probably



**Mustelidae Morphology, Fig. 10** Dorsal view (left) and palate (right) of a male (top) and a female (bottom) stone marten *Martes foina*. The female skull is smaller and more elongated than that of males and has a wider

postorbital constriction. Also, the palate of females is more elongated than in males, likely due to a different orientation of PM2 and PM3, and to the smaller carnassial PM3 and M1 teeth. © Anna Loy

act on *M. foina* and *M. martes* as a mechanism to avoid both intraspecific competition between sexes and interspecific competition between these ecologically overlapping species. Wiig (1986) found that SSD in skulls of otters, minks, and badgers is also functionally related to the jaw mechanism, as larger males have larger jaw muscles and larger absolute gape. Berdnikovs (2005) found sexual dimorphism in body mass within mustelids to be a consequence of unequal rates of male and female body size evolution, with male body mass being less constrained in its evolution than female mass. In contrast, Gliwicz (1988) suggested extreme body size dimorphism in small mustelids has been constrained by the diameter of the borrows of their common preys. Despite SSD is widespread in Mustelids, there are some exception. Rozhnov and Abramov (2006) found a low dimorphism in cranial characters of *Vormela peregusna* compared with other similar sized mustelids, likely related to low intraspecific competition in habitat and food selection.

## Cross-References

- Cetacean Locomotion
- Cetacean Morphology
- Muscular System
- Mustelidae Cognition
- Mustelidae Diet
- Mustelidae Life History
- Mustelidae Locomotion
- Mustelidae Navigation
- Pinniped Morphology and Locomotion

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## Mustelidae Navigation

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## Synonyms

[Audition](#); [Cognitive map](#); [Cues](#); [Dispersal](#); [Foraging](#); [Landmarks](#); [Latrine](#); [Mate-finding](#); [Movement](#); [Olfaction](#); [Route following](#); [Territoriality](#); [Vision](#)

## Definition

Causes for and mechanisms by which mustelids move from one location to another.

## Introduction

Navigation, or the process by which an organism moves from one place to another, is a critical behavior for the success of most vertebrates. Organisms accomplish such movements by adapting to cues produced either externally in the environment or internally through physiological or neurological processes. Navigation can be as simple as an individual moving toward or away from a stimulus, or cue. More advanced behavior may include following an established route through one's territory. In its most complex form, animals construct a cognitive map, or a spatial representation of the landscape, which provides the ability to navigate using potentially novel routes based on the locations of positions or landmarks stored in memory (Tsoar et al. 2011; Wiener et al. 2011). Much is known about how some groups of animals use these various techniques to navigate their environment (e.g., birds, insects), but less is known about the mechanisms used by mammals (Gould and Gould 2012).

Members of Mustelidae make up the most diverse family in the Order Carnivora. They can be divided into two primary subfamilies: Lutrinae (otters) and Mustelinae (all other members of the family). Located on five continents and at nearly all latitudes, the adaptive radiation of Mustelidae resulted in the occupancy of a wide diversity of ecoregions and habitat types from oceans and rivers to tropical forests and arctic tundra (Koepfli et al. 2008). Mustelid evolution has thus resulted in an assortment of ecological lifestyles, including aquatic, fossorial, arboreal, and terrestrial. Not surprisingly, they have also evolved a diversity of methods by which they navigate these environments. The application of these methods provides unique benefits while incurring costs related to life history actions such as territory maintenance, prey location, conspecific identification, and juvenile dispersal.

## Sensory Modality of Navigation

Despite their phylogenetic diversity, many species use common techniques and sensory systems to

navigate their environment. For example, olfaction is important for navigation throughout the family. All mustelids possess anal scent glands and many have additional glands on the feet, torso, and elsewhere that produce odiferous chemical secretions unique to each species and often unique to the individual (Brinck et al. 1983; Thom and Hurst 2004). These secretions, usually in combination with other types of scent-marks, are deposited throughout an individual's home range (i.e., area of regular use) on a regular basis. Purposes of the scent-marking behavior vary across species, but the recognition of these glandular secretions via olfaction is an important tool utilized by mustelids to navigate landscapes. For example, individuals may navigate toward scent marks that signal resource abundance and away from scent marks that signal the territory of a conspecific. Olfactory signals such as those produced by scent-marking behavior provide a number of advantages over other methods such as visual or auditory signals. Olfactory signals can be effective in situations or habitats where visual or auditory contact is not possible and can provide a record through space and time of an individual's movements or behavior. Perhaps most importantly, these signals are capable of persisting long after the individual that produced the signal has left the area (Gorman 1990).

Latrine establishment and subsequent use is a specialized form of scent-marking that is common among many of the mustelids. A latrine is a location on the landscape where one or more individuals regularly returns to urinate, defecate, and/or scent-mark. The spatial distribution of latrines varies by species and habitat type, but latrines are most often established strategically to perform functions such as establishing territoriality, signaling resource availability, or promoting sociality. Latrines therefore provide long-lasting cues that can serve as navigational landmarks for individuals in search of resources, a home range, or a mate (Gorman 1990).

In addition to olfaction, mustelids generally possess excellent hearing (i.e., audition) but weaker visual acuity, though all three senses may be used for navigation (Gillingham 1986). Vision tends to be more helpful in navigation at



close distances or for identifying moving objects, while hearing is used for both social and ecological purposes across greater distances. For the more fossorial and aquatic species, tactile senses accessed through vibrissae or forelimbs are also important for navigation. These senses tend to be less relevant to long-distance navigation through the environment, however, and more relevant to close-range processes such as prey capture.

## Territoriality

A key feature of mustelid navigation is the ability to maintain a territory and defend it from conspecifics who would exploit its available resources. A territory is an area defended by an occupying individual or group of individuals. A common strategy is for solitary individuals to maintain territories between members of the same sex, but overlap between members of the opposite sex (Powell 1979). Often a single male's territory will encompass multiple female territories. Thus, individuals must be able to navigate and defend their own territory while avoiding intrusion onto the territories of their neighbors. Other factors such as the sex of the occupant and their relative position in a dominance hierarchy may factor in to territorial movements as well. This generic social pattern may be flexible within species and may be dependent on factors such as resource distribution and availability (Powell 1994). Other social patterns also exist. Some species or populations live in intersexual social groups (e.g., *Pteronura brasiliensis*, *Meles meles* in the UK), others may exhibit territoriality in only one sex (e.g., *Enhydra lutris*), and still others may consist of solitary males and small family groups composed of an adult female and her young (e.g., *Lontra canadensis*). Despite the diversity of social structures, all species likely display some form of territoriality.

Resident and dispersing mustelids use established territorial systems to navigate their environment while mutually avoiding direct encounters. Territoriality in the mustelids is most commonly maintained through scent-marking behavior. Scent marks can be from one or more

of glandular secretions, feces, or urine. For conspecifics, compounds in these scent marks can be complex enough to signal the individual identification of the depositor along with its sex, age, and reproductive status (Brinck et al. 1983; Service 1997). Scent marks are commonly distributed along the edges of territories and at the core of the home range (Hutchings and White 2000), and individuals will follow regular routes to maintain scent marks. These marks are often placed on prominent objects on the landscape such as rocks, trees, logs, or mounds, thereby maximizing exposure to the olfactory signal. Thus when a neighboring or dispersing individual approaches a scent mark, they can readily identify the sex, dominance status, or individual identity of the owner of the mark. Producing scent marks and defending a territory are energetically costly, but potentially less costly than a physical encounter (Gosling and Roberts 2001). When individuals do come in close proximity, visual signals such as facial expressions and body posture, and auditory signals in the form of aggressive vocalizations serve as navigational cues for the intruding individual to avoid the territory of the owner and prevent a physical confrontation. For many species, particularly the Lutrinae, movements and territories tend to follow linear water features on the landscape. This unique pattern of movement may yield higher encounter rates with conspecifics and therefore lead to increased competition and territorial behavior (Quaglietta et al. 2013).

## Foraging

Mustelids are highly active foragers, continually navigating to locate their next prey item. This is partly due to their elongate body shape, which is advantageous for living and foraging in tight spaces or for swimming, but yields a high surface area to volume ratio relative to other mammals in the order Carnivora (Brown and Lasiewski 1972). This pattern of morphology results in rapid loss of body heat and corresponding high rates of metabolism. Thus mustelids must navigate to, capture, and consume a large proportion of their body mass each day to maintain consistent weight. This need

is met by frequent, active bouts of foraging for prey items, driving the need for advanced navigational capabilities. For most of the Mustelinae, primary prey items consist of mobile prey such as small vertebrates or invertebrates including rodents, lagomorphs, birds, amphibians, reptiles, insects, and earthworms. For the Lutrinae, prey are almost exclusively aquatic and can include fish, crayfish, crabs, eels, mussels, insects, sea urchins, and any other aquatic or semiaquatic animal small enough to be handled by an otter. A minority of species are omnivorous or seasonally omnivorous (e.g., *Martes americana*, *Eira barbara*, *Melogale moschata*), but the general rule is carnivory. Navigational processes during foraging therefore vary throughout the family for the detection, pursuit, and capture of prey.

Mustelids do not forage randomly, but in selected directions and locations (Powell 2005). While foraging, the Mustelinae will navigate their home range following a general route or direction that may be used multiple times per day. Along with this route-following behavior, fine-scale foraging movements may consist of short zig-zag motions characterized by high sinuosity where individuals frequently cross their own path checking every cavity, burrow, tree, or other location that may potentially contain prey. During this search phase, the primary senses involved in detecting and navigating toward prey items are hearing and olfaction, especially when prey items are hidden from sight. Vision is generally not acute enough to detect stationary prey items and may not be useful for navigation until prey is in close range. Some species (e.g., *Poecilogale albinucha*, *Mellivora capensis*) will forage with their nose close to the ground, often rooting through debris as they navigate their territory. Another common behavior is to pause frequently and sit back or stand on the hind legs while surveying for signs of predators or prey. Upon detection of a prey item, a chase and attempted capture ensues. Mustelids rarely ambush or stalk their prey, preferring to rush the prey item and quickly end the encounter with a lethal bite to the back of the skull or neck. For the Lutrinae, foraging takes place at relatively stationary locations as opposed to constant traveling, and navigation is required to

move between feeding locations. The process of capturing prey is similar to that of the terrestrial mustelids, except that prey are detected primarily by vision or tactile senses using facial vibrissae that are sensitive to perturbations in the water. The latter sense is especially useful when foraging at night or in murky water. Several species of otters also have highly adapted forelimbs for tactile sensitivity that aid in searching for and handling prey in aquatic substrate (Radinsky 1968). In addition to navigating their environment spatially, navigation of the temporal environment (i.e., choosing when to forage) is also required. Daily activity patterns often align closely with activity patterns of prey items, and such patterns may vary seasonally as well.

Mustelids are capable of maintaining a spatial network (i.e., a cognitive map) of suitable foraging locations for navigating within their home range (Powell 2005). Memory therefore plays an important role in navigation while moving between sites within the cognitive map. For the terrestrial mustelids, such sites are revisited regularly and often lie along established routes followed by the individual throughout the home range. These routes may connect multiple foraging sites, burrows, or otherwise protected locations that can be used for resting between bouts of foraging. For smaller species, overhead cover (e.g., forest canopy, woody debris) is an important component of established routes and may guide navigation, possibly because it reduces risk of predation by aerial predators. Travel through open clearings is rare for such species. Mustelids commonly kill more than they are capable of eating and some may cache their prey along routes or near rest sites. This behavior requires the ability to both remember and navigate to the location of the cache in the future. In addition to route-following, latrines or other scent marks may be used to identify and mark foraging locations. Latrine behavior is more common among the Lutrinae than the Mustelinae, and evidence suggests that otters may use latrines both to signal areas of high resource availability (Prenda and Granado-Lorencio 1996), and to signal locations where resources have been recently exploited (Kruuk 1992). For coastal otters in the UK, these

sites serve to identify locations of freshwater pools important for drinking water (Gorman 1990). In terms of navigation, latrines serve as navigational landmarks that contribute to the cognitive map used by otters and other species to navigate their environment.

## Mate-Finding

As most Mustelids, males in particular, are solitary throughout most of the year, the ability to navigate to the locations of females becomes crucial for reproductive success. For species that occur at higher latitudes, breeding takes place once per year, usually during spring and/or early summer. As one moves toward the tropics, species tend to be more plastic in their breeding schedule and may mate at any time during the year. During breeding periods, territorial boundaries may dissolve as males begin to search both within and beyond their home range for receptive females (Johnson et al. 2000). Males often mate with more than one female (polygyny), but promiscuity is common as well. Monogamy may be observed among the more social species (e.g., *Pteronura brasiliensis*), but extra-pair copulations may occur as a result of bachelor males expanding the range of their movements during breeding season (e.g., *Meles meles*) (Dugdale et al. 2007; Sandell 1989).

During breeding periods, males usually navigate to females, while females maintain their territories. Initially, navigation is guided by a combination of the male's previous knowledge of the locations of females within their home range and by scent-marks deposited by females in estrus. Latrines can be important indicators of location and reproductive status during this period (Stevens and Serfass 2008). For navigation to receptive females to be successful, males must navigate not only through space but through time as well. If mate-searching behavior fails to align with female receptivity, or daily activity patterns fail to align between the sexes, mating may not occur. Seasonal timing of breeding is likely a result of syncing reproduction with either environmental cues such as photoperiod or

temperature, or syncing with resource availability (Ben-David 1997). When a reproductive male and a receptive female come into close proximity, the female may indicate her location and status through a variety of auditory and visual signals. Males are guided by these signals to approach the female and attempt to mate. In more social species or populations, males and females occupy the same dens and share the same territory. In these cases, navigating to a mate is simpler, though extra-group males may navigate into unfamiliar territories to mate with a receptive female.

## Dispersal

The dispersal of juveniles from their natal home range consists of three processes: emigration from the natal home range, movement between habitat patches, and establishment or immigration to the new home range. Timing of dispersal is inexorably linked to reproduction. After young are weaned they spend time with the mother learning skills such as locomotion, foraging, and how to minimize risk of predation. Eventually they leave their natal grounds in search of a new home range. Considerable variation exists in the timing and distance of dispersal events within a species, and this variation may be explained by factors such as population density and resource availability (Powell 1994). For example, high population densities and low resource availability may result in increased dispersal rates and distances. After leaving their natal grounds, juveniles enter a search phase during which they travel from patch to patch in search of suitable, unoccupied habitat. This search may take the form of exploratory forays or an individual may leave its natal grounds permanently. Mustelids are capable of dispersing great distances relative to their size. For both terrestrial and aquatic species, navigation may be accomplished by following linear features such as fencerows or riparian corridors (Sheffield and King 1994). While searching, perceptual range, or the distance at which suitable habitat may be detected, plays an important role (Lima and Zollner 1996). The ability to detect scent-marks of conspecifics and suitable habitat at greater

distances increases navigational efficiency and may reduce time to home range establishment and risk of predation during dispersal. For home range establishment, search criteria for males may differ from those of females, given their respective needs for defendable territory or habitat suitable for raising young. Ultimately, the location and size of the selected home range is dependent on the availability of resources that contribute to increased fitness for the disperser (Powell 2005).

Causes for dispersal behavior are many, but they can be summarized as either evolutionary or ecological in nature (Bowler and Benton 2005). Mustelid dispersal is usually sex-biased, in which males travel further from their natal grounds than females. This behavior is driven by an evolutionary need to maintain gene flow, reduce inbreeding, and regulate population dynamics throughout species ranges (Bowler and Benton 2005). Ecological drivers of dispersal behavior contribute to the regulation of more proximate factors such as population density, food availability, and resource distribution. Once the decision to disperse is made, navigation plays a central role in how individuals select a home range as well as the timing of the dispersal event.

## Risk Minimization

Navigation is required to facilitate the avoidance of circumstances that are perceived as risky to the individual. Important risk factors for mustelids include predation, interference competition, and anthropogenic disturbance. All species are at risk of predation for at least a portion of their life cycle, but predation tends to be more important for the population dynamics of smaller species (e.g., *Mustela*, *Martes*, *Vormela* spp.) than larger species (e.g., *Gulo gulo*, *Lutra* spp.). Predators include raptors and larger carnivorans. When the predator is a competitor that kills to reduce the sharing of resources rather than to consume prey, this is known as interference competition. This type of competition occurs particularly when the species ranges of several members of the family – and sometimes of a single genus – overlap. In such cases, the subordinate species may navigate

away from the dominant species in both time and space. For example, fishers (*Pekania pennanti*) occasionally kill American martens (*Martes americana*), and martens may respond to fisher presence by adjusting their periods of activity to avoid direct encounters (McCann et al. 2017). Regardless of whether the purpose of the predation event is consumption or competition, vigilance and escape behaviors from the prey species are similar. For example, while traveling some species frequently pause to use audition and olfaction to survey for predators. Upon detection of a perceived risk, the individual may remain in a state of heightened vigilance or may immediately navigate away from the source of the risk and toward a refuge such as a forest canopy, a body of water, or an underground burrow.

Anthropogenic sources of disturbance are often perceived as risky and responses to such disturbance can be similar to responses to predators (Clinchy et al. 2016; Frid and Dill 2002). Regardless of whether the stimulus is benign or harmful, mustelids tend to respond negatively to such disturbances (Cervinka et al. 2015). They rarely occur in urban or human-dominated landscapes (though exceptions do occur e.g., *Martes foina*), and species commonly shift behaviors and/or alter their patterns of space use in response to the alteration or degradation of their habitat (Pereira de Oliveira et al. 2014; Stewart et al. 2016). Avoidance behaviors and mortality events resulting from human disturbance likely contribute to the decline of species ranges and population sizes throughout the family (Ceia-Hasse et al. 2017). Ultimately, navigation in response to risky stimuli plays a critical role in driving the individual-, population-, and species-level responses to changing landscapes.

## Conclusion

Navigation is a critical aspect of the success of many mustelids much as it is for many other vertebrate and invertebrate species. The noteworthy diversity found across the members of Mustelidae is reflected in their approaches to navigation. However, common themes such as a

typical emphasis upon olfaction and the importance of latrines as features used in navigation are apparent. In summary, whether it is used in territory maintenance, foraging, mate-finding, or other capacities navigation is an important consideration in the life history of all members of the family.

## Cross-References

- Auditory Signals
- Dispersal Ability
- Dispersal Patterns
- Foraging
- Home Range
- Mating
- Mustelidae Cognition
- Mustelidae Diet
- Navigation
- Olfactory Discrimination
- Olfactory Perception
- Predation Risk
- Scent-Marking
- Sensory Receptors
- Territoriality
- Territory Defense

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## Mustelids

### ► Mustelid Communication

## Musth

### ► Rutting

## Mutations

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## Synonyms

Alterations; Change; Modification

## Introduction

Errors may occur in every process of molecular biology, although at a low rate. A mutation is an error in genetic material. Generally, mutations do not affect the survival of an organism, but there are lethal and beneficial mutations. The accumulation of beneficial mutations leads to the evolution of a species with different environmental conditions.

Mutations may be variations in DNA/RNA sequences or alterations in the coding sequence of a gene. Subsequently, the replication of DNA carries forward the mutation to the next generation in unicellular organisms. In multicellular organisms, only germ cell mutations are passed to the next generation. A mutation in somatic cells transfers to the next descendants of those cells; it is also responsible for the advent of cancer. Because DNA passes a message to RNA and RNA passes it proteins, an alteration in DNA leads to the synthesis of a defective protein.

## Types of Mutations

Alterations of DNA molecules occur in many different ways. The major types of mutations include the following:

**Insertion:** the addition of one or more bases into a DNA sequence

**Deletion:** the removal of one or more bases from a DNA sequence

**Base substitution:** replacement with another base in DNA sequence

**Translocation:** a segment of DNA transferred from one location to another location, on the same or different DNA molecules

**Duplication:** a copy of a segment of DNA is pasted into another location, with the original copy remaining at its original position

However, mutations also occur in gene codes for tRNA, rRNA, and other non-translated RNA molecules. Mutations in these genes have more drastic effects in RNA processing. Furthermore, mutations can also occur in the regulatory regions of a gene. Mutations in these regions can upregulate or downregulate the expression of a protein and lead to distinguished phenotypes.

### Insertion

A gene can be inactivated by the addition/insertion of a foreign base/segment of DNA, which leads to disruption of the reading frame. This inactivation of a gene also depends on the insertion location. If the insertion occurs in the extreme ends of the gene, then a functional protein can still be made; however, an insertion in the middle will be non-functional. An insertion mutation is divided into two parts: one through the mobile genetic element (natural condition) and the second through chemical mutation or an error by DNA polymerase (Frost et al. 2005).

In natural conditions, the insertion is of a mobile genetic element (transposons or retrotransposons) or viral genome. A transposable element has multiple transcriptional termination sites. Therefore, RNA polymerase cannot pass through it without termination of the transcript, which is known as a **polarity effect** (Baba et al. 2006). Occasionally, insertion also activates genes. If the insertion is a repression region of the transcript, binding of the repressor is prevented and the gene is activated. However, some transposon elements have promoters at their extreme ends (facing outward). Therefore, the

insertion is in the upstream of a gene and the genes are activated. An example of a “cryptic gene” is found in *Escherichia coli*, which is inactive in the wild-type and active in the mutant.

### Deletion

The removal of one or more bases from a sequence is known as a deletion mutation. The lethality of this mutation depends on how many bases are deleted. A point deletion has a more drastic effect because it disrupts the reading frame. It is indicated by the symbol  $\Delta$  or DE; for example,  $\Delta(\text{LigA-LigB})$  indicates deletion of a region from LigA to LigB. Obviously, there is no gene, no mRNA, and no protein. If this gene is essential for survival, then the deletion will be lethal. A deletion is not site-specific; that is, the deletion may occur in a regulatory region or a non-essential region between or within the gene (introns).

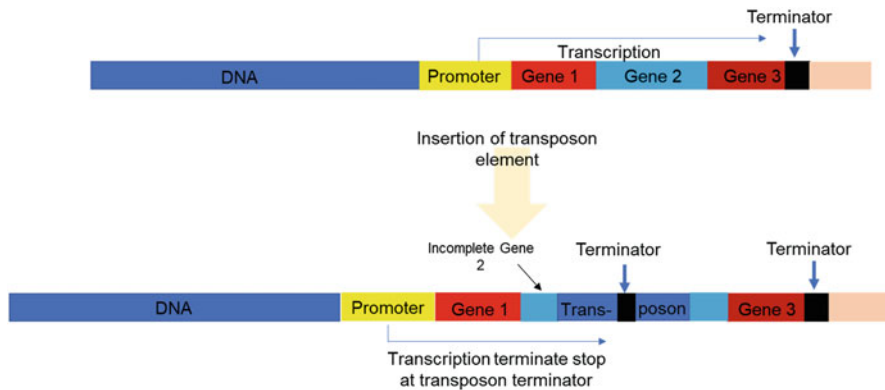
### Base Substitution

The replacement of one base with another base is a substitution mutation. There are two types of substitutions: **transitions** and **transversions** (Topal and Fresco 1976). In a transition mutation, purine is replaced by purine and pyrimidine is replaced by pyrimidine (i.e., T replaced by C or vice versa). In the case of a transversion mutation, purine is replaced by pyrimidine or vice versa.

When DNA polymerase replicates, this mutated site (mismatched site) is incorporated, such that there is one wild-type daughter and one mutated daughter.

### Duplications, Inversions, and Translocations

A duplication is a simple copy-and-paste of a sequence from one location to another location; the original copy and location are unchanged. A eukaryotic gene is full of tandem repeats, which are generated by either slippage of DNA polymerase or transposon elements (Viguera et al. 2001). During replication of a repetitive sequence, DNA polymerase may skip or revert back and replicate the same sequence again. In the case of a transposon element (retrotransposon), enzymes are required for integration; hence, it integrates into the genome. Our genome is full of retrotransposons (Fig. 1)



**Mutations, Fig. 1 Effect of an insertion mutation.** Immature termination of an operon in a bacterium after the insertion of a transposon element inside gene 2. Only

gene 1 transcribed completely. Gene 2 immaturely transcribed, and gene 3 did not transcribe

As the name suggests, an inversion is the inversion of a segment of DNA. The inversion of a gene discontinues it from a regulatory region (promoter) and has highly detrimental effects. If an inversion fragments all the regulatory and open reading frames, then it has an only mild effect. Sometimes, a chromosome rotates  $180^\circ$  after a double-strand break; when it rejoins, the segment becomes inverted.

A translocation is a change in location of a gene or DNA segment from its original position to another position. Translocation can be intrachromosomal or interchromosomal. If a complete gene is moved from one place to another, it would not cause any issue. However, if a gene is inserted between another gene, then it causes insertional inactivation of that gene and results in double chaotic.

### Missense Versus Nonsense Mutations

In a substitution mutation, a gene coding region leads to a change in codons followed by a change in the amino acid sequence; that is, one amino acid is replaced by another amino acid at the protein level. The severity of a mutation depends upon the replaced amino acid. If the replaced amino acid is similar to the previous one, then it has a very low or non-significant effect; however, if the changed amino acid is different in nature, then it has a drastic effect. Severity also depends on the position of the mutation. A mutation in the active site of the enzyme is more severe in a one-letter code

abbreviation mutation; for example, G153R or Gly153Arg indicates that glycine in the 153rd position was replaced by arginine.

The chemical properties of the replaced amino acid play a significant role in a missense mutation. Suppose the codon GUG, which codes for valine amino acid, changed into GCG, which codes for alanine. If both amino acids are hydrophobic in nature (i.e., have similar chemical properties), then the conversion of GUG into GCG has a minor effect. The replacement of one amino acid with a different amino acid having similar physical and chemical properties is known as a **conservative substitution**, whereas replacement with an amino acid having different physical and chemical properties is known as **radical replacement**.

In a type of substitutive mutation known as a **temperature-sensitive (ts) mutation**, a protein is folded properly at a low temperature (permissive temperature) and unfolded at a higher temperature (restrictive temperature) (Game and Mortimer 1974). This type of mutation is very essential to study the functional properties of essential proteins. If the knockout of that gene is generated, then the organism does not survive. Therefore, in this case, a ts mutation is generated and the organism survives at permissive but not restrictive temperatures.

There are three codons (UAA, UAG, and UGA) that do not code for any amino acid; they are known as **stop codons**. When a substantive mutation converts a codon into any of these stop

codons, it is called a **nonsense mutation**. For example, if the codon UAC code for tryptophan undergoes a substitution mutation and is converted into UAG, this is a stop codon (Liaw et al. 1997). Therefore, when ribosome reads this transcript during translation, it terminates at the tryptophan site that was converted into a stop codon. Thus, this type of mutation is also known as a **chain termination mutation**. Such a truncated protein is detected and degraded by a proteasome complex. If a nonsense mutation is an essential gene, then it has a lethal effect.

### Silent Mutation

When there is a change in the DNA sequence but no change in the protein sequence, this is called a **silent mutation**. Suppose UUU codes for phenylalanine and U is converted into C; therefore, it becomes UUC, which also codes for phenylalanine. When one amino acid is coded by multiple codons, it is called **degeneracy** of the genetic code, which plays a major role in silent mutations. Very often, changes in the third position of a codon have no change in an amino acid sequence; this is called **third-base redundancy**. In addition, a substitution mutation at the third position of a codon may be silent. Third-base redundancy causes no changes in protein sequence but affect the translational level due to a shortage of charged non-preferred tRNA in the tRNA pool. For example, suppose there are six codon codes for leucine, but only one or two codons are preferred in our genome/genes; due to this preference, the concentration of charged tRNA inside a cell is present at different levels. Therefore, if a high-frequency codon is converted into a low-frequency codon for the same amino acid, it may slow down due to a shortage of charged tRNA translation (although sometimes it may speed up).

A mutation in an intervening region of a gene that causes no change in the protein sequence is also a type of silent mutation. If a mutation is at the splicing site of an intron and results in a failure of splicing of intron, it has drastic effects and initiates an evolutionary phenomenon known as **alternate splicing**, which results in a slightly abnormal splice product (Modrek and Lee 2002).

### Mutagens

Agents that cause mutations in DNA are known as **mutagens**. There are three types of mutagens: chemicals, radiation (ionizing), and heat. Chemicals and radiation cause direct and indirect effects that change/modify DNA bases, which further lead to mutations. In an indirect effect, the mutagen directly reacts with nucleotide bases; the product of a mutagen reacts with DNA (like free radicals) (Liaw et al. 1997). A mutation may be **induced** or **spontaneous**. Sometimes, mutation may occur even when there are no mutagens, which is called spontaneous mutation. The enzymes involved in replication and repair may make mistakes.

### Induced Mutations

The most common mutagens are chemical mutagens. They react with a nitrogen base and modify it. DNA polymerase may misidentify these modified bases and add a wrong base in the newly replicated strand. Some examples of chemical and radiation mutagens include the following.

#### Chemical:

Hydroxylamine

Base analog (e.g., bromodeoxyuridine)

Alkylating agents (e.g., N-ethyl-N-nitrosourea (ENU))

DNA adducts (e.g., ochratoxin A)

DNA intercalating agents

DNA crosslinkers

Oxidative damage

Nitrous acid (converts A to C)

#### Radiation:

Non-ionizing radiation (ultraviolet light), which causes the dimerization of two constitutive pyrimidine bases and forms a pyrimidine dimer.

Ionizing radiation. Exposure to any ionizing radiation causes strand breakage and lysis of water molecules, which release free radicals that react with DNA. Alpha has a maximum **linear energy transfer**, so it produces more double-strand breaks; due to the short range, it is less effective. Although gamma has a lower linear energy transfer than alpha and beta, it has

maximum penetration and range, thus making it more harmful.

### Spontaneous Mutations

Spontaneous mutations are very rare but very helpful for evolution. The following changes may occur:

- Depurination: The loss of purine (only nitrogen base) and formation of an apurinic site, which is repaired by base excision.
- Deamination: Hydrolysis of a normal amino group into a keto group in a nitrogen base, such as adenine to hypoxanthine.
- Slipped-strand mispairing: Denaturation and then renaturation of the newly synthesized strand in a different region, causing insertion or deletion.
- Replication slippage: During replication of a repetitive sequence, the DNA polymerase slips backward or forward and changes the number of repeats.
- Tautomerization: Repositioning of a hydrogen atom that changes the hydrogen bonding pattern.

than average, and the type of mutation is also the same; these sites are called **hotspots** (Brash and Haseltine 1982). Most hot spots sites are methylcytosine in genes. After replication, methylation of a newly synthesized strand occurs by methyltransferases; for example, cytosine is converted into methyl-cytosine and pairs with guanine. After deamination, methyl-cytosine is converted into thymine, which pairs with adenine, not guanine. Therefore, when DNA polymerase replicates, it adds adenine instead of guanine and causes a transversion mutation (Fig. 2).

### Detection

The mutagenic effects of a mutagen are checked by the rate of conversion of mutant to wild-type. The **Ames test** uses well-characterized mutants (in the histidine gene) of *Salmonella typhimurium* and the rate of revertant screened on a negative histidine background (Ames 1975). All cosmetics, hair dyes, drugs, food colorings, and preservative are screened by government agencies using this technique.

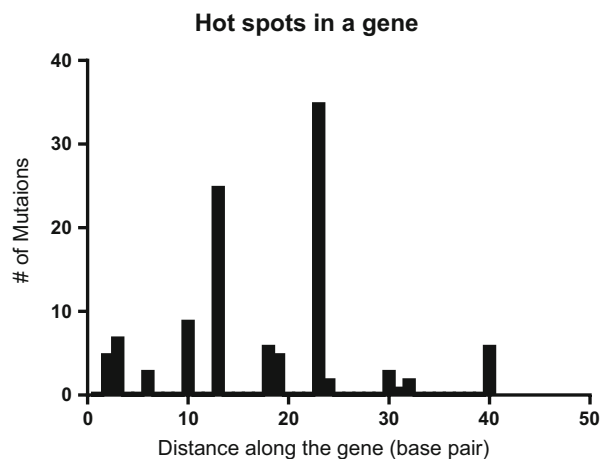
### Hotspots

A gene may mutate a thousand times, but all the mutations are not on different sites. There are certain sites where the rate of mutation is higher

### Conclusions

Mutations have both advantages and disadvantages in evolution. Without mutations, the evolution of species is not possible. A single mutation

**Mutations,**  
**Fig. 2 Mutation**  
**distribution in a gene.** The frequency of mutations versus the positions of nucleotide bases in a gene. Locations around 12 and 23 base pairs receive more mutational events than other regions





leads to the extension of a species or the emergence of a new species. The rate of mutations (known as the **molecular clock**) varies from organism to organism. The rate of mutations in viruses is high, whereas it is very low (and very difficult to even determine) in humans (Ames 1975). Mutations occur not only at the gene level but also at the chromosome level, affecting the structure, function, and inheritance of the whole DNA.

## Cross-References

- [Amino Acid](#)
- [Base Pair](#)
- [Chromosomes](#)
- [Codon](#)
- [DNA](#)
- [Evolution](#)
- [Exon](#)
- [Gene](#)
- [Gene Expression](#)
- [Genetic Code](#)
- [Genetic Variation](#)
- [Genotype](#)
- [Intron](#)
- [Recombination](#)

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## Mutual Aid

- [Mutualism](#)

## Mutualism

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## Synonyms

[Cooperation](#); [Facilitation](#); [Mutual aid](#); [Proto-cooperation](#); [Reciprocal altruism](#)

## Definition

Mutualism is a positive reciprocal relationship between two individuals where both may live together in close physical association.

## Introduction

Every other organism on the planet is an intricate part of the ecosystem and has to interact with various other organisms in the environment for

their requisite survival. This biological interaction not just encourages the survival of species but ensures the smooth functioning of the ecosystem as a whole. Margulis (1971) described the basis of all eukaryotic life, i.e., endosymbiotic mutualism between independent microbes and their cells. Mutualism is one of the three fundamental ways of interaction between two different species of organisms, the two other being commensalism and parasitism. The term “mutualism” was introduced by Pierre-Joseph van Beneden in 1876. This relationship can be within the species, between living things from two different species, between individuals in a society, and between two societies. Each participant in the mutualistic relationship is called a symbiont. Mutualism is a type of symbiosis. Symbiosis is a broad category, defined to include relationships that are mutualistic, parasitic, or commensal. Mutualism involves either the exchange of resources, such as nutrients, food, and shelter or may involve the exchange of services, such as protection or transportation.

### Role of Mutualism

Mutualism is a type of symbiotic relationship where, in brief, it can be defined as a  $+/+$  interaction whereas commensalism and predation are, respectively,  $+/0$  and  $+/-$ . However, not all symbiotic relationships are mutualistic (Boucher et al. 1984). Mutualism occurs in both terrestrial and aquatic ecosystems; as ecologists now believe that each and every species on earth is directly or indirectly involved in one or more of these interactions. Most modern terrestrial ecosystems are critically dependant on mutualism: 90% of land plants exhibit a symbiotic relationship with mycorrhizal fungi, and significantly, all mammalian and insect herbivores inhabit cellulose-digesting symbionts (Smith 1991). The influence of mutualism dates back to the levels of biological organization from cells to populations, communities, and ecosystems. The significance of mutualistic symbioses is linked to many key events in the history of life on earth, including the origin of the eukaryotic cell, invasion of the land, and radiation

of the angiosperms. Mutualism has surely played a crucial role in the ecology and evolution of various life forms on earth.

### Benefits of Mutualism

Mutualisms have long been acknowledged as exchange of benefits among which comprises: (1) nutritional, involving breakdown of compounds by digestion for the partner or supply of nutrients and growth factors by synthesis; (2) providing energy, generally from photosynthesis; (3) protection, either from enemies or from environment; and (4) transport, either from an unsuitable to a more suitable environment or by dispersal of propagules or gametes (Boucher et al. 1984). Symbiotic mutualists usually exchange the first two services, seldom third, and rarely the fourth. Nonsymbiotic usually exchange all four.

### Direct and Indirect Mutualism

Mutualism can be categorized into direct and indirect mutualism. The former involves direct physical association between the two species, and then indirect mutualism, in which each species benefit from the other's presence but there is no direct contact. Direct mutualism is divided into symbiotic and nonsymbiotic, using physiological incorporation as basic criterion. Within mutualism, there are three types: (i) trophic mutualism, (ii) dispersive mutualism, and (iii) defensive mutualism. Each of these three with examples is discussed below.

#### Direct Mutualism

**Symbiotic Mutualism** In case of mutualistic symbioses, the two species lives in close proximity to each other for part or all of their lives. They tend to be coevolved and obligate and thereby cannot lead an independent life. This is the case with the fungus-algae symbiosis called lichens. A lichen is a mat of fungal hyphae inside which dwells a thin layer of cells of photosynthetic algae or cyanobacteria. The algae gains protection from drought and solar radiation from fungus, while the latter receives products of photosynthesis from the algae. Thus lichens can withstand extreme environmental conditions in which neither algae nor

fungus could (Mackenzie et al. 2002). Intestinal flagellated protozoans and termites display obligative mutualism, in which the protozoans digest the food ingested by the termites, where neither can survive without the other under natural conditions. Another example comes from mycorrhizae, the symbiotic association of fungal hyphae with the roots of many species of higher plants, particularly significant in poor soil types. The fungi help plants in the uptake of nutrients (essentially phosphate) while receiving nutrients from the plants.

Gut microbiota in mutualism with many vertebrates (Backhed et al. 2005), termites, and other arthropods are involved in degradation of cellulose and related substances and toxic secondary plant compounds. In numerous associations, they are involved in the synthesis of all of the B-complex vitamins, vitamin K, and sulfur containing amino acids. However, some non symbiotic mutualisms are also obligate, such as those formed by fungus-farming ants, in which neither can survive without the other, and another one being cleaner fish and the “customer” fish from which they remove dead skin and parasites. Endozoic algae harboring in coral zooxanthellae supply ammonia from seawater and bacterial symbionts in green hydra increase uptake of phosphate from the medium. In return, these organisms take up waste products from their hosts and use them for their own growth.

**Nonsymbiotic Mutualism** These are facultative and not coevolved. Both the partners may coexist without a dependence on each other and exhibit opportunistic mutualism. However, exceptions arise in case of anemone-dwelling fishes, which show some physiological habituation to the mutualist. They may be diffuse, involving varying number of species, example being pollinators and their plants. Honey bees visit many different species of flowering plants during the course of the season and many of these plants will be visited by a number of insect pollinators. Similarly, interaction between nitrogen fixing bacteria and plants, such as between legumes and *Rhizobium*, is facultative. Leguminous plants benefit immensely from the nitrogen-fixing activities of the bacteria,

which form nodules in plant roots in nitrogen-poor soils (Mackenzie et al. 2002). However, when soil nitrogen levels are optimum, the plants thrive in their absence.

#### Indirect Mutualism

Theories on indirect mutualism have established that species that never come into close physical contact with each other may however positively affect each other's physical fitness (Connor 1995).

#### Types of Mutualism

##### Trophic Mutualism: Resource-Resource Benefit

Mutualism where both species acquire benefit in the form of resources. Substantial evidence comes from the relationship between the coral polyps and zooxanthellae – a single celled alga which lives within the coral polyps. In this case, coral polyps depend on the photosynthesis process carried out by zooxanthellae, while the latter depend on nitrogen, which the coral polyps derive from hunting at night.

##### Dispersive Mutualism: Resource-Service Benefit

Mutualism in which one partner is dedicated in harvesting a food resource traded for a service. An explicit example is pollination, in which nectar or pollen are traded for dispersal or ant protection of aphids, where the latter trade sugar-rich honeydew in exchange for defense against insect predators such as ladybugs (Bailey 2018).

##### Defensive Mutualism: Service-Service Benefit

Mutualism in which one partner protects the other against predators or parasites and the other returns favor by providing food and shelter. The best example is mutualism between anemone fish (family Pomacentridae) and sea anemones: The anemones provide fish with protection from predators and the fish in return defend against butterflyfish (family Chaetodontidae). Acacia ants (*Pseudomyrmex ferruginea*) reside in bull-horn acacia (*Vachellia cornigera*), wherein the ants obtain food and shelter inside the plant's thorns and acacia depends on the ants for protection from browsing animals.

## The Evolution of Mutualism: Considering the Alternatives

Since past few years, ecologists have acknowledged the connection between global change and ecological species interaction (Kiers et al. 2011), notably plant-pollinator interactions. While mutualistic interdependence has paved way for many evolutionary opportunities, it also becomes a necessary evil: because mutualisms aggregate multiple species to a common fate, the significant breakdown of these interactions will amplify the effects of global environmental degradation and other causes of species extinction. For example, the intensely debated topic “Adaptive Bleaching Hypothesis” which signifies coral bleaching (i.e., exclusion of zooxanthellae partners from their coral reef hosts) (Jones et al. 2008). However, exclusion of the mutualistic zooxanthellae and increased susceptibility to fast growing symbionts reflects flexibility in mutualism management. Sometimes mutualism leads into unbalanced exploitation of one symbiont to the benefit of the other-parasitism. For example, many orchids tender no reward for their pollinator and instead use them to perch on the flower to mimic female insects by using scent and color patterning. Mutualisms are dynamic and scientists wonder the indefinite persistence and stability of many mutualisms. However, many have been formed and dissolved over evolutionary time scales undergoing changes in the important trajectories of mutualism: (1) shifts from mutualism to antagonism, (2) evolutionary changes of novel partners, and (3) mutualism desertion (i.e., extinction of the interaction, but not necessarily partners).

## Cross-References

- [Coalition Enforcement](#)
- [Cooperation](#)
- [Evolution](#)
- [Symbiotic relationship](#)

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## Myelencephalon

- [Medulla Oblongata](#)

## Myelination

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A thick insulating structure derived by the glial cells around the axons of neuron cells in the nervous system is called myelin. The overall event of myelin formation is called myelination.

Myelin was first described by Rudolf Virchow in 1864. It is made up of 70% of lipid (neutral

lipids, phosphoglycerides, sphingolipids) and 30% of proteins (majorly glycoproteins). Myelin sheath is derived from the plasma membrane of the glial cells. In the central nervous system (CNS), it is formed by oligodendrocytes, while in the peripheral nervous system (PNS), it is formed by Schwann cells. It is not that all the axons of vertebrate is myelinated, even the non-myelinated axons have their role in nervous system. The fundamental role of myelin sheath is to fast conduction of action potential along the neurons which it insulates (Fields 2014). There will be a periodic gap in the myelin sheath between adjacent myelin segments – node of Ranvier. These gaps or nodes are rich in sodium and chloride ion channels. Action potential is triggered at these nodes and passively move to the next node where the next action potential is generated; this jumping of action potential from node to node results in rapid conduction of nerve impulses (Kettenmann and Verkhratsky 2011).

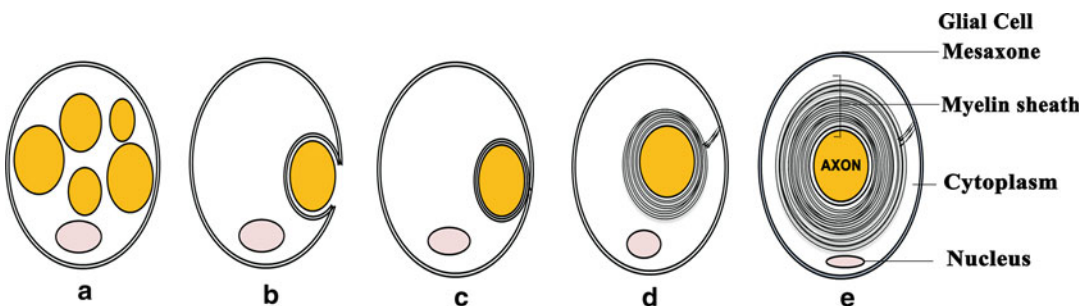
### Early Events in Myelination

Myelination is a complex molecular process that requires precious coordination between several cellular signaling molecules and cascades. Glia-axon interactions are potentially vital throughout the event of myelination. Signaling molecules like neuregulins, neurotrophic factors, transcription factors, and survival factors are required in myelinating of axons (Feltri et al. 2016).

Early events in myelination involve different morphological stages, where every stage is highly controlled and well executed by the specific signaling molecules both in the central and peripheral nervous system (Fig. 1).

### Myelination in CNS

In the CNS, myelination process is carried by the oligodendrocytes and their precursor, where single oligodendrocyte can myelinate multiple axons; therefore, it is called as multipolar glia. Myelin sheath is formed by the plasma membrane of oligodendrocytes that spirally wrap around the axon that have a diameter of more than 0.2  $\mu\text{m}$ , to form thick insulating structure of around 40 segments (Simons and Trajkovic 2006). Oligodendrocytes are developed from oligodendrocyte progenitor cells (OPCs) that divide and migrate to the appropriate destination from their germinal region, and then initiation of myelin component's synthesis will take place. Later myelin wrapping will be initiated, followed by compaction of myelin structure by mature oligodendrocytes. Many extrinsic and intrinsic signals control the oligodendrocyte differentiation and myelination (Emery 2010). Signaling molecules like neuregulins-1 (NRG1), laminin, PDGF, IGF, NT, and Notch-1 (Barres and Raff 1999) are expressed during the myelination in the CNS. Recent studies on the role of oligodendrocytes have proven that initiation and continued myelination can be done



**Myelination, Fig. 1** Early events of myelination in the CNS and PNS. (a) Bundles of axons are closely associated with glial cells. (b) Glial cells surround the single axon. But the mesaxon is not yet completely fused but portion of

axon is engulfed. (c, d) The mesaxon is fused in the initial stage; later the glial cells begin to rotate around the axon to form few layer of myelin. (e) Myelin completely wraps around the axon to form tightly packed myelin sheath



by oligodendrocytes in the absence of neurons. This proves the major function of oligodendrocytes in myelinating the axons of CNS.

## Myelination in PNS

Schwann cells are the glial cells of the PNS; their plasma membrane differentiation forms the myelin sheath around the axons of peripheral neurons. In PNS, a single Schwann cell will myelinate a single axon. Neuronal crest cells are the stem cells which generate the Schwann cell precursors that migrate along the axons extending to their target. In the next step, this Schwann cell precursor gives rise to immature Schwann cell which performs the radical sorting of axons. This allows the axons to build one-to-one relationship stable contact between the axons and Schwann cells. Later Schwann cells which are in promyelinating stage will form the tight wrapping of myelin around the axon to form myelinated Schwann cell. The signaling molecules like nucleic acid-binding (NAB) protein, Sox-10, Krox-20, Oct-6, Brn1, and Brn2 are involved in the myelination of peripheral neurons (Jessen and Mirsky 2005).

## Conclusion

Myelination is a step-by-step event that is highly coordinated by several intrinsic and extrinsic factors. Many neuropathic diseases exhibit the

demyelinated morphological characteristic that fails in normal conduction of nerve impulse. Thus myelin development and their maintenance are considered very crucial in healthy individuals. Still the cellular and molecular mechanisms involved in myelination and their maintenance are likely to be key area for further research.

## Cross-References

► [Axon](#)

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## NAc

- [Nucleus Accumbens](#)

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## NAcc

- [Nucleus Accumbens](#)

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## Naïve Physics

- [Folk Physics](#)
- [Hood's Gravity Rules](#)

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## Napoleon Chagnon

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## Synonyms

[Anthropology](#); [Social ethology](#); [Sociobiology](#)

## Main Text

Bodies donned in black pelts and beaded necklaces swarm in a hostile crowd. Shrill invectives

are hurled across a dirt courtyard encircled by thatched longhouses. The tension between groupings around this courtyard heightens, weapons are brandished, and violence ensues, one man striking another on the head with the blunt side of an ax. This is the opening scene of “The Ax Fight,” one of the best-known works of anthropologist Napoleon Chagnon, then a graduate student at the University of Michigan. By initially providing no interpretation, Chagnon intended to create for the viewer the experience of observational naïveté upon watching the behaviors of an unfamiliar group of people, much as a naturalist might watch a pride of lions. This unfamiliar group was the Yanomami, an Amazonian indigenous group living on the border of Venezuela and Brazil. Chagnon researched the Yanomami from the mid-1960s to the late 1990s and was both applauded for his in-depth study of the cultural group and groundbreaking analyses of its members and denigrated for his resultant conclusions about “human nature.” Utilizing observational strategies from ethology and applying Darwinian theory to human behavior, Napoleon Chagnon has concluded that “nature, red in tooth and claw” holds for humans as well as the other organisms on Earth, that competition is the primary directive of human action and, therefore, violence is fundamental to social groups.

In the film, Chagnon, a student of Leslie White who reintroduced theories of cultural evolution to anthropology in the mid-1900s, displays kinship diagrams after the unedited footage of the

Yanomami conflict plays and then replays the footage in slow motion, describing the familial relationships between the main actors. He demonstrates, drawing on kin selection theory from animal behavior studies, that this fight is structured by kinship; combatants choose sides based on genetic relatedness. This is not merely a chaotic brawl. Kin selection theory posits that an individual's behavior will support other closely related individuals, as those actions will ensure the reproduction of the individual's genetic material in the next generation. In "The Ax Fight," Chagnon reveals to his viewers that the fight results from long-standing hostility between a group of closely related individuals in the village and another visiting group of related individuals. In a published 2013 interview with Napoleon Chagnon, he stated, "I began using commonly known ways to 'measure' relatedness between organisms – Sewall Wright's coefficient of inbreeding and its extended concept, the coefficient of relatedness. This was very unusual in cultural anthropology" (Iannone 2013, p. 260).

Not only was Chagnon's work unusual in cultural anthropology at the time, it was extremely controversial. Two of his major works – an early 1968 monograph, *The Yanomamö: The Fierce People*, and a 2013 retrospective, *Noble Savages: My Life among Two Dangerous Tribes – the Yanomamö and the Anthropologists* – sent shock waves through the discipline. Chagnon was denounced as a biological determinist and dismissed by many. However, in 1975, biologist Edward O. Wilson published *Sociobiology: The New Synthesis*, which explained the evolutionary basis behind such social behaviors as altruism and aggression. Wilson's formidable text argued that there really is no distinction between social and biological aspects of human life. Due to the rise in popularity of sociobiology following Wilson's publication, Chagnon's work garnered more respect in scholarly circles. In the 2013 interview, he said, "Wilson's Sociobiology brought to anthropology – and other social sciences – a new and fresh way of looking at human behavior and attempted to make it more comprehensible in the context of primate evolutionary tendencies" (Iannone 2013, p. 262).

Critics of Chagnon's research methods and analyses include anthropologists, natural scientists, and journalists. A relatively small faction of anthropologists have gone on to use evolutionary theory to explain human behavior in recent decades, leading to influential theories like optimal foraging theory and costly signaling theory, but many cultural anthropologists disagree with pushing culture and social learning to the background, except where these processes are individually adaptive. Furthermore, many critics are uncomfortable with the axioms about human nature that result from sociobiological explanations of human behavior – humans are inherently selfish, human behavior is driven by self-interest and profit maximization, competition and violence are innately human. Anthropologist Brian Ferguson (1995) refutes Chagnon's assertion that humans are inherently or "naturally" violent, arguing that Yanomami warfare is a more recent cultural artifact of the violence of European colonialism. Others question the veracity of Chagnon's data, critiquing his statistical methods (Albert 1990) and the effect of his presence on the behavior of the people he observed, particularly because he and his film crew distributed highly-prized and sought-after goods like machetes and other steel wares to individual Yanomami. Anthropologist Marshall Sahlins (2000) went so far as to say that Chagnon's trade of goods for genealogical information amounted to "participant-instigation."

Despite these controversies, Chagnon continues to be an active scholar, contributing to social ethology and cultural anthropology. He retired from the University of California, Santa Barbara in 1999 and was elected to the National Academy of Sciences in 2012. He then joined the faculty of the University of Missouri's Anthropology Department as a "Distinguished Research Professor and Chancellor's Chair for Excellence in Anthropology" and became an adjunct research professor at the University of Michigan's Institute of Social Research. His work with the Institute involves digitizing and archiving his papers in a permanent data repository and translating decades of Yanomami audio recordings into English. Further, in a 2014 publication alongside colleagues at

the University of Missouri, Chagnon compares and contrasts Yanomami patterns of coalitionary violence to that of chimpanzees. In this recent work, the results of the testing “support the strategic alliance model of coalitionary aggression, demonstrate the complexities of human alliance formation, and illuminate key differences in social structure distinguishing humans from other primates” (Macfarlan et al. 2014, p. 16662). While again humans are viewed through a lens typically reserved for the study of animal groups and behaviors, Chagnon and team ultimately conclude that humans are distinct from other primates at least insofar as there are social structural explanations for coalitionary aggression as well as genetic explanations. Just how distinct humans are from the rest of the animal kingdom and the relationship between cultural and genetic drivers of behavior are important questions in the discipline of anthropology, and Napoleon Chagnon has had a long career of pushing the boundaries of investigation.

## Cross-References

- ▶ [Coefficient of Relatedness](#)
- ▶ [E.O. Wilson](#)
- ▶ [Optimal Foraging Theory](#)
- ▶ [Sociobiology](#)

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## Nash Equilibrium

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## Synonyms

[Predicting rational behavior](#)

## Definition

In an  $N \in \mathbb{N}$  player normal form game, a Nash equilibrium is a set of strategies for which no player has an incentive to deviate from their current strategy.

## Introduction

Game theory can best be described as the study of interactive decision-making through the use of a variety of mathematical analytic methods (Osborne and Rubinstein 1994a). Game theory lends itself to a number of applications, including life sciences such as conservation, the study of evolutionary biology, and the study of animal cognition and behavior.

A Nash equilibrium, a cornerstone term that appears throughout game theory is used to predict a strategy profile for a given game, or interaction, between  $N \in \mathbb{N}$  decision-makers. In game theory, the term “strategy profile” refers to the strategies used by each player in a given game. Most importantly, at the Nash equilibria, no player has an incentive to deviate from their current strategy.

In order to fully understand the term Nash equilibrium, it is first essential to understand some of the simplest terms associated with game theory.

### Normal Form Games

An  $N$  player normal form game can be defined as a game consisting of:

- A finite set of  $N$  players
- A finite set of strategies available to each player  $i \in N$ ,  $S_i$
- A payoff function for each player  $i$ ,  $u_i: S_1 \times S_2 \times \dots \times S_N \rightarrow \mathbb{R}$ , which maps a strategy profile to a real number corresponding to the utility received

The representation of such normal form games will become more clear in the subsequent section.

### Common Knowledge of Rationality

A key aspect of game theory is the assumption that all players are rational. The following chain of assumptions is known as common knowledge of rationality and is essential in attempting to predict rational behavior (Knight 2017a):

- All players are rational.
- All players are aware that all other players are rational.
- All players are aware that all other players are aware that they are rational.
- And so on.

### Pure Strategies and Mixed Strategies

In a decision-making game, players have the option of adopting a pure strategy whereby the strategy that they choose to use in a given game will be identical for any iteration of that same game. An alternative is for players to adopt a mixed strategy. A mixed strategy is a probabilistic distribution of the player's strategies.

Mathematically, we define a mixed strategy for a player  $i$  as  $\sigma_i \in [0, 1]_{\mathbb{R}}^{|S_i|}$ , where  $\sigma_i$  is a probability distribution over the pure strategies of a player (Knight 2017b). With this definition, it follows that:

$$\sum_{i=1}^{|S_i|} \sigma_i = 1$$

Since probabilities are continuous, there are infinitely many mixed strategies available to all decision-makers.

### Best Responses

A best response in a given game of pure strategies is a strategy that maximizes or minimizes, depending on the game, a player's utility given the opposing player's strategy. Subsequently, a pair of best responses identified in a game of pure strategies is defined as a Nash equilibria.

Mathematically, "in an  $N$  player normal form game, a strategy  $s^*$  for a player  $i$  is a best response to some strategy profile  $s_{-i}$  if and only if

$$u_i(s^*, s_{-i}) \geq u_i(s, s_{-i})$$

for all  $s \in S_i''$  (Knight 2017c, ¶2). Here,  $s_{-i}$  represents an incomplete strategy profile for all other players considered in the game. For example, in an  $N$  player normal form game where  $S_i = \{A, B\}$  represents the strategies available to player  $i$ , a valid strategy profile is  $s = (A, B)$ , for all  $i$ . Therefore,  $s_{-2} = (A)$  denotes the incomplete strategy profile where the first player utilizes the strategy A, and the strategy utilized by player two is undetermined (Knight 2017a).

### Nash Equilibria

According to Knight (2017d, ¶2), "in an  $N$  player normal form game, a Nash equilibrium is a strategy profile  $\tilde{s} = (\tilde{s}_1, \tilde{s}_2, \dots, \tilde{s}_n)$  such that:

$$u_i(\tilde{s}) \geq u_i(\tilde{s}_i, \tilde{s}_{-i})$$

for all  $i$ ." Again, at the Nash equilibria no player can deviate their chosen strategy in such a way that benefits their utility given the actions of the other players (Osborne and Rubinstein 1994b).

### Examples

With the use of the preceding definitions, the Nash equilibria of the following normal form games can be obtained.

### Nash Equilibria in Pure Strategies

Consider the following version of the classic hawk-dove game, first developed by J.M. Smith and G.R. Price (1973), to illustrate how the Nash equilibria is obtained in a game of pure strategies:



There are two birds of prey, who are assumed to have equivalent attributes, and who have both identified a potential food source. The birds of prey have the option of acting like a hawk or a dove. It is assumed that hawks are willing to fight relentlessly over the resource, leading to injury to both themselves and their opponent. In contrast, doves are much more passive and are willing to share a single resource (Table 1).

The arbitrary figures in this example can be interpreted as follows: if both birds are to act like hawks, the birds yield a negative utility through injury inflicted by the other bird. In the case that one bird acts like a dove whilst the other acts like a hawk, the dove retreats and the hawk eats the entirety of the prey. When both birds take on the role of a dove, the resource is shared equally.

Through identifying best responses to each possible strategy, it is possible to predict a rational outcome of this game. If the first bird is to act like a hawk, the best response for the second bird is to act like a dove, since  $0 > -1$ . In the instance that bird 1 acts like a dove, the utility is highest for bird 2 when taking on the role as a hawk, since  $1 > 0.5$ . Since in this case the utilities yielded by each player are independent of which player chooses the action, the best responses are identical for both players. Therefore, this game yields Nash equilibria in pure strategies, those being (Hawk, Dove) and (Dove, Hawk). Hence, in a population of birds of prey who primarily take on a role as a hawk, an individual would yield the highest utility by taking on the role of a dove. In contrast, in a population of birds of prey who primarily take on a role as a dove, an individual would yield the highest utility by taking on the role of a hawk.

### Nash Equilibria in Mixed Strategies

Now, consider the same game with the same payoffs, but where both bird 1 and bird 2 adopt

mixed strategies. In order to obtain best responses against mixed strategies, it is required to first obtain the player's expected utilities. In order to do so, the utility function is relied upon. Knight (2017b) defines the utility function for a two-player normal form game as follows:

$$u_i(\sigma_1, \sigma_2) = \sum_{r \in S_1, c \in S_2} \sigma_1(r) \sigma_2(c) u_i(r, c)$$

Assume that the first bird takes on the role of a hawk  $x$  percent of the time and takes on the role of the dove the remaining  $(1 - x)$  percent of the time. This can be defined by  $\sigma_1 = (x, 1 - x)$ . Then it follows that:

$$\begin{aligned} u_2(\sigma_1, \text{Hawk}) &= x(-1) + (1 - x)(1) \\ u_2(\sigma_1, \text{Hawk}) &= 1 - 2x \end{aligned}$$

and that,

$$\begin{aligned} u_2(\sigma_1, \text{Dove}) &= x(0) + (1 - x)(0.5) \\ u_2(\sigma_1, \text{Dove}) &= 0.5 - 0.5x \end{aligned}$$

Using the mixed strategy algorithm, any mixed strategy that exists that makes the other player's decision over which strategy to play indifferent can be identified (Spaniel 2012). Therefore, it follows that the expected payoff for a player will be the same regardless of the strategy adopted by the opposing player. Hence:

$$\begin{aligned} u_2(\sigma_1, \text{Hawk}) &= u_2(\sigma_1, \text{Dove}) \\ 1 - 2x &= 0.5 - 0.5x \\ x &= 1/3 \end{aligned}$$

and therefore,

$$1 - x = 2/3$$

yielding that,

$$\sigma_1 = (1/3, 2/3)$$

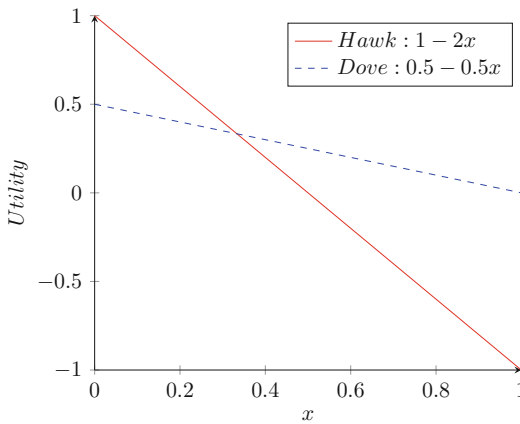
This can be illustrated graphically as follows (Fig. 1):

Here,

- If  $x < 1/3$ , then acting like a hawk is a best response for bird 2 since it will yield a higher utility.

**Nash Equilibrium, Table 1** Hawk-dove game, with expected payoffs

| Bird 1 | Bird 2     |              |
|--------|------------|--------------|
|        | Hawk       | Dove         |
| Hawk   | $(-1, -1)$ | $(1, 0)$     |
| Dove   | $(0, 1)$   | $(0.5, 0.5)$ |



**Nash Equilibrium, Fig. 1** Graphical representation of the expected payoffs for bird 2

- If  $x > 1/3$ , then acting like a dove is a best response for bird 2 since it will yield a higher utility.
- If  $x = 1/3$ , then bird 2 is indifferent.

Since the game is symmetric, it is clear that:

$$\sigma_2 = (1/3, 2/3)$$

Therefore, a Nash equilibria has been identified in mixed strategies. That is to say that both birds adopt the role of a hawk one third of the time, and adopt the role of a dove two thirds of the time, denoted  $((1/3, 2/3), (1/3, 2/3))$ . At this point, neither bird has an incentive to deviate from their strategy.

### Nash's Theorem

Nash's theorem states that any game with two or more players and a finite number of strategies available to the players has at least one set of strategies where no player is able to improve their utility by independently changing their strategy (Weisstein 2019). That is, a Nash equilibrium exists for every such game. Therefore, if a pure strategy Nash equilibrium does not exist, one must exist in mixed strategies.

### Conclusion

As highlighted, the concept of Nash equilibrium is incredibly useful in attempting to predict an

outcome for a given interaction between rational decision-makers. For example, in more complex dynamic games than those outlined in this paper, the Nash equilibria can be used to attempt to predict potential evolutionary adaptations whereby organisms who adopt "successful" strategies will out compete those who do not (Gintis 2009). This notion is incredibly powerful and effectively highlights the fact that Nash equilibria, along with numerous other game theoretic tools, can be utilized to provide insight into the cognitive processes in animals which lead to their behaviors, and even an overall insight into how the natural world operates and adapts.

### Cross-References

- [Game Theory](#)
- [Prisoner's Dilemma](#)

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## Nathan Emery

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Nathan Emery is a comparative psychologist with a strong background in neuroscience. He was one of the first UK students to take a Bachelor's degree in Neuroscience, at the University of Central Lancashire, Preston (1990–1993). In 1994, he worked on his PhD with David Perrett on neurons in the superior temporal sulcus of rhesus monkeys tuned to social signals, such as eye gaze direction and intention movements. After completing his PhD in 1997, he moved to the University of California, Davis, working with David Amaral on the role of the amygdala in primate social behavior. Here he met his future wife and collaborator, Nicky Clayton, and his research interests started to change from the brain to cognition and from primates to birds, specifically corvids. In 2000, Emery and Clayton moved to the University of Cambridge; Emery continued his research on the neurobiology of primate social behavior with Barry Keverne at the famous Sub-Department of Animal Behaviour working on the role of the amygdala and prefrontal cortex in marmoset parental and sexual behavior, but he increasingly devoted more of his time to studies of caching behavior in western scrub jays with Clayton. This latter work resulted in a paper published in *Nature*, which may be a first in science. The two authors are married and share the same birthday and the paper was published on their joint birthday! In 2002, Emery was awarded a prestigious University Research Fellowship from the Royal Society. This gave him 8 years of funding and freedom to pursue research to support his now celebrated theory that corvids are “feathered apes” because of their similar cognitive abilities with the great apes.

In 2007, Emery moved to Queen Mary University of London to become Senior Lecturer in Cognitive Biology and assist with the development of a new Bachelor's degree in Psychology, as well as establish a research center in psychology with a strong comparative and evolutionary focus.

During this time, Emery started a new research program on parrot cognition with his student Jayden van Horik, establishing groups of Hahn's macaws and black-headed caiques. He has also worked with the iconic Tower of London ravens. He has served on the editorial boards of *PLoS ONE*, *Communicative & Integrative Biology*, *Frontiers in Comparative Psychology*, *Journal of Comparative Psychology*, *Current Directions in Behavioural Sciences* and *Animal Cognition*. Recently, he wrote and illustrated a popular science book called *Bird Brain: An Exploration of Avian Intelligence* (Emery 2016) which has now been translated into German, Spanish, Korean and Japanese. A long bout of ill health prevented Emery from taking a more significant role in experimental research, but he continues to play an active role in the comparative psychology community, especially with respect to public engagement.

Although he started as a neuroscientist and later switched to comparative cognition, he has always maintained an active interest in the brain, especially in how our understanding of neuroscience can inform our understanding of animal minds and vice versa. There are a number of areas to which he has made important contributions:

### Eye Gaze as a Complex Social Signal

When Emery started his PhD, Perrett had already found that some neurons in the monkey temporal lobe were selectively responsive to the perception of another's gaze direction; some tuned to gaze looking right, others to gaze looking left, and others to gaze directed at the viewer. However, these neurons were strange because monkeys did not seem capable of using eye gaze as a social cue, for example, to locate hidden food. This was important, because studies of the primate brain were being justified ethically for their utility as a model of the human brain. For example, understanding the system involved in computing where another is looking may be used to model social deficits in individuals with autism. Emery therefore attempted to resolve the issue of why monkeys had failed to respond behaviorally to eye

gaze direction cues, when their brains responded automatically to such cues. Through using conspecifics as stimuli, presented as short video clips, as well as recording the subjects' eye movements, he found that monkeys used eye gaze direction to look at objects viewed by another monkey (Emery et al. 1997). He followed this up with a comparative review on gaze processing, breaking it down into subcategories, as well as reviewing the neurobiology of eye gaze. This review has been cited over 1250 times (Emery 2000). Emery continues to work on eye gaze but in birds. He and his PhD student, Auguste von Bayern, found that jackdaws distinguish between different human attentional states when making decisions about when to steal food but only when the human is a stranger, not a caregiver (von Bayern and Emery 2009). Jackdaws can also use eye gaze and pointing cues to locate hidden food from both humans and conspecifics, but only when the cues are deliberately communicative, such as when moving attention from the viewer to the attended object.

### **Role of the Amygdala in Primate Social Behavior**

Studies by Arthur Kling in the 1960s and 1970s had focused the idea that the amygdala plays an important role in primate social behavior. Amygdala-lesioned monkeys acquired devastating social deficits; losing their dominance status and becoming socially isolated. However, such studies were fraught with interpretational problems, as the lesions were crude, damaging more than the amygdala, including fibers of passage, and the surrounding cortex, hippocampus, etc. A more selective procedure was required to destroy only the amygdala, leaving everything else intact. Ibotenic acid, a selective neurotoxin, fulfilled this role, with MRI-guided lesions to make sure that only the amygdala was damaged. Finally, the behavioral analyses performed by Kling (who was a psychiatrist, not an expert in primate behavior) were rather simplistic. David Amaral therefore assembled a team of neurosurgeons, anatomists, and primatologists to determine the detailed

behavioral deficits resulting from precise amygdala lesions. Emery had a detailed knowledge of primate brain anatomy and function, as well as an in-depth knowledge of primate social behavior, and so facilitated communication between the neuroscientists and primatologists on the team. They found that amygdala lesions did not cause the social isolation previously described. Conversely, the amygdalectomized monkeys were more socially attractive, being more approachable, perceived as less threatening, and more likely to elicit affiliative behavior in others (Emery et al. 2001). The lesions appear to have dampened the natural inclination for adult rhesus monkeys to attack strangers. Studies in larger social groups found similar effects, and this research has continued to focus on social development (albeit without Emery).

### **Cache Protection Strategies as Social Cognition**

Although the exceptional long-term memories of caching birds had been a popular target of ethological research, very little was known about another threat to successful cache recovery: cache pilfering. Evidence suggested that corvids were different from other caching animals, as they could observe another bird caching, and remember the location of their caches when they came back to them later without the original cacher present, i.e., they had observational spatial memory. Such a skill meant that caching corvids had to implement strategies to minimize cache theft. Following on from Clayton's seminal studies on episodic-like memory in scrub jays, Emery and Clayton found that scrub jays would cache when observed by another bird but attempt to reduce potential cache theft by coming back alone and moving their original caches to new sites (Emery and Clayton 2001). Most intriguingly, this re-caching was only seen in birds that had previous experience of being thieves themselves. The implications for this are that the caching jays may be capable of projecting the specific past experience of pilfering onto another bird with the potential to steal their caches. This is akin to

simulation theory of mind, where an individual models another's future actions based on their own experience, using this model to make predictions about what they may be thinking, "putting oneself in another's shoes [when they have worn the same shoes themselves]." In a series of follow-up experiments, Emery, Clayton, and PhD student Joanna Dally found that scrub jays utilized a number of different cache protection strategies, such as caching at a distance, caching behind barriers, and caching in darkened areas. They also appeared aware of who was watching and what they had observed, being more selective in their strategies when specific individuals had spied specific caches being hidden or the individual spy had changed (Dally et al. 2006).

### Convergent Evolution of Cognition

A trickle of studies on corvid cognition over the last 30 years, primarily on complex forms of memory, suggested that corvids were vastly more intelligent birds than had previously been appreciated. Corvid brain size, relative to their body size, was found comparable to that of the great apes, with crows having brains relatively the same size as chimpanzees. Emery and Clayton reviewed evidence from studies of tool-using New Caledonian crows, social cognition in western scrub jays, and long-term memory in pinyon jays and Clark's nutcrackers, amongst others, and concluded that the cognitive abilities of members of the corvid and ape families were strikingly similar. They suggested these similarities had arisen independently in the two groups separated by 300 million years, as thousands of close relatives do not demonstrate the same cognitive skills (Emery and Clayton 2004). It is very likely, but not yet known, whether both families had to face similar socio-ecological problems in their recent evolutionary histories, and whether specific selection pressures, such as trying to locate hidden food distributed across wide swaths of time and space, would have driven the evolution of brains and intelligence capable of overcoming such pressures. Studies on corvid cognition, and direct comparisons with great apes, have

blossomed in the years following Emery and Clayton's hypothesis.

### Tasks for Testing Physical Cognition in Non-tool-Using Birds

Emery has been at the forefront of designing cognitive tasks to specifically test physical problem-solving in species that do not use tools. Tool use has been proposed as a specific driver of cognitive evolution, as the ability to use tools is said to require skills in causal reasoning and object manipulation not found in species that do not use tools to procure their food. However, one problem with this assertion was that all tests for physical cognition, such as the classic trap tube task, were designed to only test tool-using animals, i.e., subjects had to insert a tool into an apparatus in order to procure the treat inside. Emery, Clayton, their PhD student Amanda Seed, and Sabine Tebbich designed a new version of the trap tube task which included a pre-inserted tool, so that the subject only had to decide which side to pull (i.e., the side that would lead to the treat being removed from the tube or the other side that would result in the treat falling into a trap). They also included a number of elegant additional designs, such as a nonfunctional trap and a series of controls to remove the use of simple rules as a winning strategy, such as pull from the side furthest from the trap. They found that rooks, a crow that does not use tools in the wild, rapidly learned to pull the inserted stick from the correct side and did so much faster than tool-using chimpanzees. They transferred immediately to novel designs, with one rook passing all controls (Seed et al. 2006). Emery and his student, Chris Bird, then went on to design a number of other physical cognition tasks that could be used to test non-tool-using species for different aspects of their physical cognition, such as the collapsible platform task (Bird and Emery 2009a), *Aesop's Fable* (or water displacement; Bird and Emery 2009b) task, and the peephole task, measuring looking time in birds. These tasks revealed hitherto unknown abilities in rooks. Bird and Emery (2009a) also found that rooks could make



complex tools, such as bending wire into hooks to reach food located in a small bucket at the bottom of a vertical tube (Bird and Emery 2009a). This had only been previously demonstrated in one captive New Caledonian crow, whereas four rooks solved the task on the first trial it was presented, with no natural propensity to make hook (or any) tools.

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## Cross-References

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- [Comparative Cognition](#)
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- [Corvids](#)
- [Nicola Clayton](#)
- [Psittacine Cognition](#)
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- [Zoology](#)

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## Natural Selection

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Natural selection is a process by which organisms that are better adapted to specific pressures of their environment tend to survive longer and produce more offspring, thus ensuring the preservation and multiplication of those favorable traits through generations, at the expense of the less advantageous ones. It is one of the key mechanisms of evolution, which affects organisms in every aspect, from their physiology and morphology, to behavior and ecology. The term was popularized by Charles Darwin (Darwin 1859).

Natural selection has been incorrectly called “survival of the fittest,” but rather than to the survival, it refers to a *differential reproductive success* of organisms who do and do not carry

beneficial traits that affect how many descendants they will leave.

## The Maturation of the Idea of Natural Selection

The idea of species changing over time long predates Darwin's theory of evolution by natural selection, and it is possible to follow its development back to the ancient Greece. Anaximander suggested that all life forms, including human ancestors, came from water. Empedocles believed that both animals and plants were formed from disconnected parts that would come together in different combinations. Those combinations that were the most adapted survived, while the strange ones became extinct. Plato believed in essentialism and proposed a *theory of Forms*, or *theory of Ideas*, which argued that non-physical forms (ideas) represent the most accurate reality (Ross 1951). Aristotle created *scala naturae* (also known as the *Ladder of Life* or the *great chain of being*), which he used to explain the relationships between all living organisms, placing them on this scale hierarchically, with regard to their structural and functional complexity. He believed that all organisms were designed for a purpose, thus rejecting Empedocles' view of all organisms originating by chance (Charlton 1983).

While Middle Ages philosophy emphasized the role of divine guidance in the creation and development of life, renaissance naturalists maintained that this development was mechanical (Bowler 1989). In the Age of Enlightenment, these ideas were further developed. Carl Linnaeus, a Swedish botanist and taxonomist who came up with the taxonomic system of binomial nomenclature, believed that God created a small number of species, which then interbred and produced hybrids that became new species (Bowler 1989). Comte de Buffon, a French naturalist, rejected Linnaeus' ideas, proposing that species and even individuals within them differed. He defined a species as a group of animals that were able to produce fertile offspring. He was also the first to suggest a possibility of all animals descending from a single breeding pair. James Hutton, Scottish naturalist and the

father of modern geology, advocated uniformitarianism – the assumption that the laws of the universe that operate at present are stable across time and space – for all living organisms, suggesting natural selection as a mechanism that may be affecting them. He believed that species formed varieties, some of which made them better adapted to particular environments, distinguishing between heritable and nonheritable variations. Traits that are passed down from parents to offspring are referred to as *heritable traits*. On the other hand, *non-heritable* or *acquired traits* are obtained through individual's actions (e.g., developing large muscles or higher flexibility through exercise) or are a result of learning (e.g., certain food type preferences or seeking a particular hiding place to avoid a predator).

Erasmus Darwin, an English physician and Charles Darwin's grandfather, suggested that all living organisms, from plants to animals, have a common origin. He believed that a “living filament” is the cause of all organic life. This “great first cause,” as he called it, granted the organisms the power to acquire new parts and improve their inherent activity over generations (Darwin 1794). His most important publication is *Zoonomia* (Part I published in 1794, Part II published in 1796), wherein he explains how species should be spread through the proliferation of the strongest and most active animals in order to improve. This view is today regarded as the *survival of the fittest*.

In 1809, a French biologist Jean-Baptiste Lamarck proposed a theory of the *transmutation of species*. Lamarck believed that living organisms were continuously created by spontaneous generation, and that their increasing complexity was prompted by an innate life force. He did not believe that all organisms shared a common ancestor, but he recognized the adaptedness of species to their environment. However, he presumed that the organisms changed depending on the organs they used or disused, and these changes would be passed down to the next generation, producing adaptations to the environment. This idea that organisms can pass on the acquired characteristics to their offspring is known as *Lamarckism* or *Lamarckian inheritance*, or *soft inheritance*.

In 1813, William Charles Wells read a paper before the Royal Society in which he explained the principle of natural selection in humans. Studying how different breeds of production animals are bred through an artificial, human-orchestrated selection of the best individuals, he realized that an equally efficient, albeit a slower, process is carried out by nature on humans. Wells was interested in the emergence of human races. He proposed that they arose from accidental varieties and those that were best suited to a particular country's climate and diseases became the most prevalent (Wells 1818). Charles Darwin and Alfred Russel Wallace were not aware of Wells' work at the time of publishing *On the Origin of Species*, but Darwin later acknowledged Wells for being the first to recognize the principle of natural selection. He, however, also recognized the limits of Wells' conclusions, as he only noted the natural selection in humans, and only in respect to race.

Edward Blyth, an English zoologist, also discussed artificial selection of production animals, as well as recognized the within-species variation in nature, but he did not see it as a potential for formation of new species, but rather as a way to preserve the one that already exists (Blyth 1835). He believed that natural selection operates on within-species variations by removing those that were less suited for the species' natural habitat than the "original" form, which was without modifications. He also did not believe in a shared ancestry of species.

In 1844, Robert Chambers, a Scottish publisher and author, anonymously published *Vestiges of the Natural History of Creation*. Herein he argued a similar view of evolution to that proposed by Lamarck. Chambers proposed a cosmic theory of transmutation, suggesting that all currently existing forms, from the solar system to all living organisms, including humans, have developed from earlier forms (Chambers 1844). He argued that life originated by spontaneous generation and that the reason behind extinction lies in flawed designs – however, a supernatural force is, according to Chambers, unnecessary. The book was received with praise, and even Charles Darwin believed that its publication may have facilitated the acceptance of his "Origin of

species," due to bringing attention to the subject of evolution and removing prejudice. Alfred Russel Wallace found the book ingenious, but in need of more evidence.

## The Theory of Evolution Through Natural Selection

The theory of evolution through natural selection was independently developed by two British naturalists – Charles Darwin and Alfred Russel Wallace. Wallace believed that every species emerged from a closely related one that had already existed. Unaware of Darwin's at the time still unpublished work, he autonomously reached similar conclusions. He wrote them in an essay, which he mailed to Darwin, asking his opinion. His effort resulted in the jointly written publication entitled *On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection* (Darwin and Wallace 1858). The two scientists presented their work to the Linnean Society of London on 1 July 1858, which was organized by Joseph Dalton Hooker and Charles Lyell. At the time, Darwin had not yet written his ideas as a paper, so he read parts of his drafts of the *On the Origin of Species*, which he had already began writing, as well as parts of his correspondence with Professor Gray. Asa Gray, who Darwin met in 1839, was one of the most notable botanists of the nineteenth century. Darwin considered him a kindred spirit. Wallace's and Darwin's presentation was published as a science paper on 20 August 1858. This publication was the first revelation of their theory of evolution by natural selection. The following year, Darwin published his world-renowned book *On the Origin of Species*.

### On the Tendency of Species to Form Varieties; And on the Perpetuation of Varieties and Species by Natural Means of Selection

"Extract from an Unpublished Work on Species"  
(by Charles Darwin)

This essay contains a portion of a few chapters ("On the Variation of Organic Beings in a State of

Nature,” “On the natural means of selection,” and “On the comparison of domestic races and true species”) later published in his *On the Origin of Species*. Darwin began his essay with a reference to De Candolle’s argument of all nature being at war, “one organism with another, or with external nature” (p.46). Darwin agreed, stating, however, that this war is not a constantly ongoing one, but instead recurs at short periods (to a lesser degree) and occasionally (to a more severe degree). He further explained that it is also a result of seasonal differences in climate and food abundance. Species differ in their favoring of particular seasons, which Darwin saw as an application of Malthus’s doctrine “with a tenfold force”. He believed that mankind could double in size more quickly with more available resources; however, since animals do not have these “artificial means,” the average amount of their food is constant, but their increase will in most cases be enormous. If unexpected factors – for instance, drought – are at play, it is possible that some species will perish, while others will flourish. Darwin explained that this higher than normal increase is likely a result of more organisms surviving to the age of reproduction, and reproducing. Once the environment of the flourishing species returned to normal, the numbers would decrease. However, Darwin proposed that this decrease would still occur regardless once the environment was completely full and could not support more individuals.

Noting that most environmental changes tend to be to a fairly small degree, and therefore causing only a small change in the inhabitants, Darwin drew the attention to an example in which the population is small and isolated from others on an island, with their secluded environment undergoing a progressing change in a way that its original inhabitants would soon no longer be perfectly adapted to it. Since all individuals have to struggle for resources, and against their conspecifics, even the smallest variation of a trait that puts them at advantage could ensure success. If this variation is heritable, the offspring of the individuals carrying the variation would also have better chances. If the species continued to breed, and if the more suitable characteristics were selected for over a number of generations, it will result in a similar change

observed previously in domestic animals after the identical principle of selection.

In addition to the “natural means of selection,” Darwin recognized another similar effect – the battle of the males for the females. He believed, however, that this selection was less rigorous, as it does not require the death of the less successful individual: it just gives them fewer offspring. Darwin noted that this struggle usually occurs at times of food abundance, and it does not have an impact on traits related to food acquisition or predator avoidance. Instead, it affects secondary sexual characteristics, therefore carrying implications for intrasexual competition. These mechanisms comprise sexual selection.

#### “Abstract of a Letter from C. Darwin to Prof. Asa Gray” (by Charles Darwin)

Darwin’s essay is followed by the abstract of the letter he wrote to Professor Gray. Darwin wrote about a human-orchestrated selection of useful animals. He believed that, regardless of the degree of intention with which such selection was carried out, it was the main force behind the production of domestic animals. He explained to Gray how selection only works through the accumulation of variations and argues that humans have adapted particular races within a species for different purposes. Darwin also wrote about how the main reasons for children not completely resembling their parents are “the changed conditions of existence” (p. 51). He explained that natural selection exclusively selected for the good traits. He backed his claim by saying that any species could, given enough time, cover the entire earth, if it was not for the “check” that occurs during some part of organism’s life or during a shortly recurrent generation. He explained that this is why only a small number of organisms born each year survive long enough to propagate their species.

If a change in the environment occurs, it will likely cause a variation of the inhabitants. While some will die out, others will be exposed to the “mutual action” of a different set of inhabitants (those remaining in the population). Darwin explained to Gray his belief that the latter is of a much higher importance to each individual’s life than an environmental change. He also stated that

variation can be accumulated in any part of organism's structure, as well as useful during any part of its life. This abstract of Darwin's letter also includes an explanation of how the occurrence of new varieties, new subspecies, or even new species (i.e., speciation) will typically exterminate the previous, less well-fitted parent species. Darwin believed his letter to be very imperfect, inviting Professor Gray to use his imagination to fill up the "very wide" blanks.

Darwin and Gray continued an extensive correspondence. Gray originally did not believe in the concept of simpler species becoming more complex over time and even tried to convince Darwin that all life forms had an inherent, unmistakable design. Gray later wrote a collection of essays entitled "Darwiniana," which were published in 1888. Herein, he defended the theory of evolution, reconciling it with theology by stating that the two are not mutually exclusive. His other work focused on the morphological similarities between eastern Asian and eastern North American plants, a phenomenon that is now known as the "Asa Gray disjunction."

"On the Tendency of Varieties to Depart Indefinitely from the Original Type" (by Alfred Russel Wallace)

Wallace began his essay by stating the, at the time, generally accepted belief that the varieties, both in domesticated species and in the wildlife, are typically unstable and over time show a tendency to return to the "normal form" of the species. In his part of the paper, Wallace aimed to show that the opposite was true: His belief was that in the nature many varieties will survive, causing successive variations progressively departing from the original type, while in domesticated animals the tendency will be to return to the parent form.

Similarly to Darwin, Wallace believed that wildlife struggle to survive and reproduce, and those processes require them to fully utilize all their capacity. The main challenges the wild animals face come from environmental conditions, which affect not only the survival of individuals within a population but of entire species. Wallace further explained that large animals will not be as

abundant as small ones, and that carnivores will be less numerous than herbivores. He proposed that the prevalent view of his time that species' abundance is directly caused by their fecundity is not true. Wallace believed that entire world's population of animals is, despite the fluctuations, stationary or possibly decreasing by the influence of humans. He also suggested that every species reaches its maximum population size within just a few years of its emergence. For a population to stay stable in size, equal numbers of organisms that are born also die. If every parent pair breeds two offspring, twice the number of the new born organisms must die. In his opinion, large broods were, for this very reason, superfluous, as the majority of the offspring are likely to either become prey, or die due to environmental conditions (i.e., hunger or harsh climate). Wallace suggested that a species can increase its population size rapidly if there is a constant supply of wholesome food. Some species can tackle the problem of this condition not being met by migrating. Those that are unable to do so will, in Wallace's view, remain scarce. The organisms that die are the weakest and the least perfect.

Wallace thought that all variations have a "definite effect, however slight, on the habits or capacities" of an individual (p.57). Furthermore, if a variation offered advantages, it will over time become superior, occurring in the majority of the population. In addition, he recognized that some variations would never reach that level of prevalence. The advantageous variation will over time completely replace the original form, and the new species will be better adapted to the environment. The new form would not be able to return to its original, as the organisms carrying the original form would never be able to compete for existence. The new form would instead continue to emerge new varieties, the superior of which would again follow the same principle of replacing the currently prevalent form. Wallace referred to this as a *progression and continued divergence*. He also noted that variations that arise in aspects of no perceivable effect on the life preservation do not follow the same patterns. They can instead coexist, progressively diverge, or return to the previous form.



Unlike wild animals, domesticated animals do not have to struggle for survival and have everything provided for them. Potentially advantageous variation that occurs in these species is therefore useless and could exist without the animal's awareness. All variations emerging in domesticated animals have an equal chance of being passed on to the offspring, until humans artificially select for the preferred traits. Many of the artificially selected traits would very likely never be selected for in nature due to them being disadvantageous and thus a step towards "inferior forms" (p.60). Wallace provided the examples of these, in his opinion abnormal and irregular animals, in dog breeds and quickly-fattening pigs. If domesticated animals turn wild, they will therefore either return to the original form of the species or die out. Because the selection mechanisms worked so very differently among wildlife and domesticated animals, Wallace believed that very little can be inferred about variation in the nature from simply observing domestic animals.

In the last parts of his essay, Wallace commented on the Lamarck's theory of evolution. He believed that his hypothesis was unnecessary, as similar results are achieved by the constantly occurring variation, and those variations that ensure the most success will survive. He saw this as proof of the nature's tendency for continued progress of the varieties that successively distinguish the species from its origins, while the opposite mechanism is at play in domestic animals, which show a tendency to revert to the original form. Although these changes occur in small steps, they are continually "checked" and balanced out.

### **The Mechanism of Natural Selection, as Proposed in *On the Origin of Species***

According to Charles Darwin's conclusions published in the *On the Origin of Species*, natural selection is the inheritance of genetic traits that are more suitable to the environment. The process is, however, not driven by superiority of one organism over another in an absolute sense but by a comparative advantage that certain individuals have over their conspecifics. Natural selection is based on four principles: variation, inheritance,

population growth, and differential survival and reproduction.

#### **Variation**

Variation in traits is the precondition of natural selection. According to Darwin, organisms do not adapt to the environment – the variation in their traits is a preexisting state, and the environment simply favors organisms with certain variants of these traits. The favored traits enable the individuals who possess them to survive and reproduce in greater numbers, thus passing them on to the next generation. Over time, this process produces new species. While some characteristics can be highly variable (e.g., body size or hair color), others show very little to no variation – for example, the number of eyes or limbs among animals of the same species.

Darwin was an externalist and believed that variation was generated by environmental changes, which were its necessary prerequisite (Winther 2000). He also proposed natural selection as an external mechanism for adaptation. Darwin suggested two different ways in which the environment can cause variation: indirectly – through an altered embryonic development, or a malfunction of parents' reproductive systems, causing variation in the subsequent generation, or directly – through an action on the organism's body through the use and disuse of its organs, with the variation displayed in the same generation (Darwin 1859). In addition, Darwin offered two internal mechanisms for variation: crossing between organisms of the same species and crossing between organisms of different species, which he referred to as hybridism.

#### **Inheritance**

Inheritance is the process of genetic information being passed on from parent to offspring. Darwin's hypothetical mechanism of heredity was *pangenesis*. He presented the idea of pangenesis in his 1868 book *The Variation of Animals and Plants under Domestication* (Darwin 1868). This hypothesis was originally conceived by two ancient Greek philosophers, Hippocrates and Democritus. They postulated that an entire organism of a parent participates in heredity. Darwin's

theory was almost identical to theirs. He believed that tiny heredity particles, which he called *gemmules*, were transmitted from parent to offspring (Holterhoff 2014). These gemmules were tiny contributions from every tissue and organ of the parents, collected in their gametes, and transmitted to the offspring. They were responsible for the configuration of offspring's every tissue and organ. Since Darwin regarded gemmules as similar to plant spores and seeds, he believed it was possible for some variations to be expressed by the majority of offspring, while others could remain dormant for generations before being expressed. Darwin offered an explanation of one parent's characteristics dominating over those of the other's, considering this to be the result of that parent's gemmules being more numerous or vigorous. However, the theory failed to account for the preservation of variations through generations, as this type of inheritance would rapidly reduce the original variation to the average of the original (parents') traits (Liu 2008).

Not unlike the majority of the nineteenth-century scientists, Darwin was convinced in the idea of *blending inheritance*. This theory posited that traits from each parent were averaged and the genetic composition of offspring was a uniform, intermediate blend of their parents'. One of the problems with this theory was the lack of explanation for the propagation of beneficial mutations: according to the blending inheritance theory, favorable, new traits would be unable to spread through a population since they would be blended out in the subsequent generation.

After Darwin's 1868 publication, Francis Galton, an English statistician, conducted a series of experiments involving blood transfusion between a common lop-eared rabbit and a silver-grey rabbit. His experiments negated the pangenesis theory (Galton 1871). Darwin reacted by explaining that his theory does not state that gemmules occur are conveyed by blood. Despite this, Galton's results were the main reason why the pangenesis theory was long disregarded (Liu 2008). However, the experiments of blood transfusion carried out in the 1950s and 1970 on poultry by Sopikov, Gromov, and many other Soviet researchers yielded positive results. A possible explanation is that heritable changes are easier to detect in

poultry than in rabbits, as it can take many generations for a trait to be expressed in rabbits. Experiments using *parabiosis* – surgical joining of anatomical parts of two animals involving a blood transfusion – that Boriachok-Nizhnik (1951) conducted on Angora rabbits and Flanders rabbits resulted in the so-called vegetative hybrids of the two species, confirming that blood transfusion alters hereditary traits. Later studies suggested that another important role may be that of DNA. Experiments on ducks revealed that vegetative hybridization was possible using erythrocytic DNA (Benoit et al. 1960), and the treated parent was affected as well. It has since been shown that DNA integration is a mechanism of horizontal gene transfer through blood transfusion. A proposition that gemmules could include RNAs, circulating DNAs, and other mobile elements has been broadly accepted since the discovery of circulating DNA and RNA molecules, as well as prions in plant sap and in the blood plasma and serum of both living and deceased animals. One of the biggest critiques of the pangenesis theory is its Lamarckian hypothesis that allowed for the heredity of acquired traits. Darwin discussed the effects of use and disuse, drawing a comparison between production animals and wildlife, suggesting that some changes in traits that were commonly attributed to these processes could be results of natural selection. He related the processes that occur in the nature to artificial selection or selective breeding of domestic animals and plants, aimed towards a development of particular (desired) traits.

#### Population Growth

Darwin and Wallace believed that natural selection is dependent on a high-population growth. Darwin originally thought that a population will increase until its size is in accordance with the available resources, at which point it will become stable. However, he refined his ideas after reading an essay published in 1798 by an economist Thomas Robert Malthus entitled the "Essay on the Principle of Population." Malthus's central premise was that a growth of population will always overpower the growth of food supplies, thus creating perpetual states of struggle, hunger, and disease. Human population, is left

unrestrained, would increase beyond their means and struggle to survive. Darwin and Wallace extended this incurable struggle for survival to the evolutionary scheme, as they realized that animals and plants are likely to experience the same pressures. They proposed that the organisms that were better equipped to survive will thrive and pass those more desirable traits on to the following generation, while the organisms that were less able to cope with the inherent inequality of the environment would die out. As offspring numbers are sometimes higher than what could be supported by the local environment, they must compete. This often unconscious competition for resources will cause the mortality of less-fit offspring. Traits that ensure more successful coping with environmental challenges (e.g., harsh winters or droughts) will become more common in the next generation, which will result in an ongoing progression of the species. Darwin believed that this competition for resources will be the harshest between closely related forms sharing environmental niches, a concept he anticipated.

#### Differential Survival and Reproduction

Variation occurs among any population causing individual differences in traits. Some of the variants can enhance individual's chances of survival and reproduction. Individuals who possess traits that enable them to prevail in the struggle for resources will contribute more offspring to the next generation. If these traits are heritable, these beneficial effects will be reflected in a differential reproduction – there will be a higher proportion of organisms carrying those traits in the following generation. In some cases, the survival or reproductive advantages will be very slight. However, over many generations, they will nevertheless become predominant in the population. Even though natural selection is without a purpose, traits that carry reproductive advantages will be selected for.

### Types of Selection

There are different types of selection in regard to the effect they have on traits: *directional selection* favors a single extreme phenotype, *stabilizing*

*selection* favors an intermediate phenotype over the extremes, and a *disruptive selection* favors extreme phenotypes over an intermediate and can be a precursor of speciation. If selection acts to remove the genetic variation from the population, it is considered a *negative selection* (also known as a purifying selection). If, however, selection acts to maintain the genetic variation, it is referred to as *balancing selection*. Selection that acts to increase chances of survival is known as *viability selection* (or survival selection), while that which increases organisms reproduction rates is called *fecundity selection* (or fecundity or reproductive selection).

Types of selection that act on an individual organism are jointly referred to as *individual selection*, while *gene selection* acts on the genes. Examples of gene selection include kin selection (an evolutionary strategy that favors the reproductive success of organism's relatives, even at a cost to the organism's own survival and reproduction) and the intragenomic conflict (a situation when genes inside a genome not being transmitted by the same rules, due to a single gene causing its own transmission to the detriment of the rest of the genome). Selection that acts on groups of organisms is called *group selection*, but its mechanisms are not yet fully understood. For a group selection to take place, the trait or behavior that is being selected for needs to spread out through the entire group. Group selection has mostly been proposed in humans and eusocial species (mainly Hymenoptera). Finally, with regard to the resource that the organisms are competing for, selection be classified as sexual selection (resulting from mate competition) or ecological selection (also known as environmental or survival selection, of asexual selection), which refers to strictly ecological processes operating on species' inherited traits.

Factors that reduce survival or reproductive success within a population are called *selection pressures* or *evolutionary pressures*. If they decrease the occurrence of a trait, they are called negative selection pressures, while those that increase the proportion of a trait are called positive selection pressures. Some selection pressures are dependent on the density of a population (for examples, predators, resource availability, supply

of nutrients, or spread of pathogens and diseases), while others are not (e.g., weather conditions, changes in temperature or carbon dioxide levels, or natural disasters).

### Alternatives of the Theory of Evolution by Natural Selection

While the majority of Wallace's and Darwin's contemporaries were relatively promptly persuaded by their theory of evolution, few of them accepted natural selection as the prime driving force of evolution. The late nineteenth century brought forward a couple of alternatives to natural selection.

*Theistic evolution*, also known as *evolutionary creationism*, advocates that God guided the process of evolution. It is a middle-ground between Darwinism and religion. Supporters of theistic predetermination believed that God created the universe, as well as the natural laws within it. This view is very similar to deistic evolution (a position encompassing the belief that God created the universe but has not interfered with it since). Another form of theistic evolution proposed that God was involved in the creation process, either to start abiogenesis (spontaneous generation of life from nonliving matter) or to ensure that some mutations would have beneficial effects. Guided evolution posited that God used evolution so that humans could evolve. This view, similar to progressive creationism, comprised belief that God extensively intervened in the process of evolution, either by generating species or by modifying gene sequences, and helping beneficial mutations gain selective advantage. By the beginning of the twentieth century, theistic evolution was rarely a part of scientific discussions, but it kept a following among laymen.

*Orthogenesis*, or orthogenic (progressive, straight-line) evolution, proposed that all organisms carry an innate tendency to evolve towards a predetermined, fixed goal. This teleological hypothesis of a unilinear change of species towards perfection was supported by many eminent scientists who found proof for the argument in the seemingly constant and gradual

unidirectional change within the fossil records. The term was introduced in 1893 by Wilhelm Haacke, a German zoologist. Orthogenesis was largely discarded with the emergence of the modern synthesis, but the idea that evolution represents progress remained popular. Although this is not true, evolution does proceed in a seemingly linear way, which is in accordance with the neo-Darwinism.

*Vitalism* proposed that all living organisms are fundamentally different from the nonliving matter due to containing a non-physical element (sometimes referred to as the vital spark or energy), or regulated by different principles (Bechtel and Richardson 1998). The idea has been discussed since ancient Egypt and ancient Greece, through the Middle Ages to the nineteenth century. Among the supporters of this theory was Louis Pasteur who, after conducting several experiments, concluded that fermentation was a vital action. By mid-twentieth century, the majority of scientists had abandoned vitalism.

*Saltationism* or *mutationism* offered a faster alternative to the Darwinian concept of gradual change of natural selection, suggesting that new species emerge as a result of large mutations. This hypothesis was the basis of the mutation theory of evolution. The central premise was that species go through periods of fast mutation, possibly due to environmental stress. These mutations could produce subspecies or new species in a single generation. Modern science accepts the role of mutation in evolution, albeit only as a supplier of variation, which is then acted upon by natural selection.

*Catastrophism* is a theory that hypothesizes that the Earth was affected in the past by sudden violent events (Turney and Brown 2007). A French paleontologist Georges Cuvier proposed that the various extinctions and the patterns of faunal succession in the fossil record were caused by these large-scale natural catastrophies. He found evidence in the stratigraphic record that such catastrophic events occurred but were separated by long periods of stability. Modern biology allows for catastrophism due to the evidence of a large extinction event at the end of the Cretaceous period, which led to a loss of approximately 70% of all species (Renne et al. 2013).

*Structuralism* (biological or process structuralism) argued that evolution is not solely driven by natural selection, but that important roles are played by other mechanisms, which can in some cases completely override natural selection. Structuralism comprises several theories. Etienne Geoffroy Saint-Hillarie's *law of compensation* suggests that all animals share an ideal pattern, as evidenced by their homologous morphology. This is not a result of evolution, but a product of the law of nature. As certain parts become more developed, others are reduced in compensation. D'Arcy Wentworth Thompson's *universal laws of form* explain that the morphology of living organisms often echoes inorganic structures. Adolf Sellacher's believed that fossils were the so-called *pneu structures* and were determined by mechanical inflation rather than natural selection. Gunter P. Wagner argued that homology and biological novelty can be explained by a developmental bias of structural constraints on embryonic development. Stuart Kauffman proposed that *self-organization* plays a role alongside natural selection in population dynamics, molecular evolution, and morphogenesis. Michael Denton argued the existence of the so-called *Types* – the basic forms in nature, which were determined by the laws of form. He believed that these universal, recurring patterns were not shaped by natural selection but by the self-organizing properties of matter and the laws of nature. Stephen J. Gould and Richard Lewontin suggested that many biological features, which they compared to architectural *spandrels*, do not always arise as direct results of adaptation but can be consequences of evolutionary changes, or even exaptations. Brian Goodwin proposed that natural patterns can be created by spatial oscillations of chemical signals, similar to the way in which morphogenetic fields operate (Webster and Goodwin 1996). Extreme structuralists G.B. Muller and S.A. Newman held the view that diversifications of species are dictated by the physical laws of structure. They believed that a relatively unconstrained, “pre-Mendelian” phase in animal evolution existed in the early stages of the multicellular life, suggesting possible explanations of how organisms evolved genetic mechanisms (Newman et al. 2003).

The most popular alternative to Darwin's theory at the end of the nineteenth century was *neo-Lamarckism*. In addition to Lamarck's original ideas, neo-Lamarckism included a proposition that environment can directly alter organic structures. This was used as an explanation to why organisms are adapted to their environments. However, the largest flaw of this theory was the complete lack of solid evidence suggesting the inheritance of acquired traits. As the genetics field progressively developed, neo-Lamarckism began to lose support.

## The Modern Synthesis (the Neo-Darwinism)

The Modern Synthesis is the modern theory of evolution that arose in the 1930s and 1940s from the merger of Darwinian theory of evolution and Mendelian genetics. It advocates the genetic basis of evolution, describing it as a change in the allele frequency within a population. The theory is also based in the population genetics, and the work of such as Ronald Aylmer Fisher, an English biologist and statistician, Sewall Wright, an American geneticist, or John Burdon Sanderson Haldane, an English-born Indian biologist and biostatistician.

### Central Contributors of the Modern Synthesis

Several distinguished scientists contributed to the development of the Modern Synthesis. Theodosius Grygorovych Dobzhansky, a Ukrainian-American geneticist and evolutionary biologist, greatly influenced the development of the Modern Synthesis with his 1937 publication *Genetics and the Origin of Species*. He proposed that evolution is a change in the allele frequency within a gene pool, explaining that natural selection works through mutation (Dobzhansky 1937).

Ernst Walter Mayr was an evolutionary biologist and a taxonomist. His main contribution to the Modern Synthesis theory came from his re-definition of the term species so as to include a group of not only morphologically similar individuals but those who can breed only among themselves. He also developed a theory of peripatric speciation – explaining the speciation that



arises from an isolated peripheral population (Mayr 1954), which was the basis of the theory of *punctuated equilibrium*, developed by Stephen Jay Gould and Niles Eldredge (Eldredge and Gould 1972). This theory proposed that most changes that occurred in the evolutionary history happened very rapidly, in short bursts of branching speciation (i.e., cladogenesis) typically lasting less than 100,000 years. After a species has appeared in the fossil record, it will show very little evolutionary change for the rest of its geological history, which they called *stasis*. The opposite idea, proposing that evolution typically occurs smoothly and uniformly, by the steady gradual change of entire lineages is called phyletic gradualism.

George Gaylord Simpson, an American paleontologist, integrated paleontology with genetics and natural selection. He developed methods of analysis of the rates of evolution through time and showed their variability. Furthermore, he introduced the term of *quantum evolution* to explain sudden emergences of lineages (Simpson 1944). He suggested that microevolution of population genetics offered an adequate explanation of the macroevolution patterns observable by paleontology. In his book *Tempo and Mode in Evolution*, published in 1944, he defined *tempo* as the evolutionary acceleration and deceleration, the evidence of which could both be found in the fossil record. Simpson described *mode* as the pattern of evolution, more encompassing than evolutionary rates that were its basic factor. Simpson noted that Gould's and Eldredge's punctuated equilibrium theory is a reiteration of his idea of quantum evolution.

George Ledyard Stebbins Jr. was an American botanist and geneticist, and one of the leading evolutionary biologists of the twentieth century. In his work he combined genetics and Darwin's theory of evolution by natural selection to describing the speciation of plant species (Stebbins 1950). He was the first to discuss natural selection in plants.

Julian Huxley, a British evolutionary biologist and T.H. Huxley's grandson, coined the terms *modern synthesis* and *evolutionary synthesis*. In his 1942 publication *Evolution: The Modern*

*Synthesis*, he integrated Darwin's theory of evolution with Mendelian genetics and population genetics. He believed that different groups will differ in the nature of their evolution, depending on the various factors, for example their reproductive strategies and genetic material (Huxley 1942). He published numerous books in collaboration with many of his eminent peers and worked on the popularization of science and evolutionary biology through many public appearances on television and the radio.

Bernhard Rensch, a German evolutionary biologist, popularized the Modern Synthesis in Germany. He studied environmental impacts on the evolution of geographically isolated species. Moreover, in his book *Evolution above the species level*, published in 1947, he aimed to prove that the major evolutionary trends and the formation of species and races are governed by the same factors (Rensch 1960).

### Differences Between the Modern Synthesis and Darwin's Theory

According to the premises of the Modern Synthesis, natural selection remains a driving force of evolution, but its power is joined with that of gene flow (the transfer of alleles or genes between populations, which happens as a result of immigration or emigration of individuals), genetic drift (the random change in allele frequency in a population caused by random sampling), and mutation (a change in the DNA sequence, which can involve deletions, duplications, insertions, or inversions (translocations)). The Modern Synthesis provides an explanation of how genetic variation (i.e., variation in the alleles) persists. As Darwin supported the theory of blending inheritance, he struggled to explain this. Mendelian inheritance gave a new perspective for tackling this issue. Gregor Mendel was an Austrian scientist and a monk who, after experimenting with pea plants, showed that genes play a role in the traits of an organism, and that those traits can be statistically predicted using the knowledge of genetic makeup of organism's parents. According to Mendel's laws, alleles (i.e., DNA segments of genes) do not merge and blend out. In reference to traits, Mendel created the terms "dominant,"

describing the allele whose effect on organism's phenotype masks the contribution of the other allele, and "recessive," describing the allele whose effect is masked by that of the other allele. While Mendel's work is the cornerstone of modern genetics, his views were not broadly accepted or known until the beginning of the twentieth century. Mendel was aware of Darwin's work, which he studied in great detail. There are a few indications that Darwin could have been familiar with Mendel's work – portions of Mendel's publications and references to them made by other authors were included in books later found in Darwin's library and were thus likely available to him. Mendel sent a copy of his 1865 paper "Versuche uber Pflanzen-Hybriden" ("Experiments in Plant Hybridization") to 40 of the most renowned nineteenth-century scientists, but it is not known for certain whether or not Darwin was one of the 40 scientists who received a copy, or whether he read it.

According to Mendelian genetics, genetic variation can occur both within populations and among them. It allows the natural selection to decrease or increase the frequency of alleles that already exist. Genetic variation arises from the formation of new alleles, alteration of the number or position of genes, rapid reproduction, and recombination between chromatids of homologous chromosomes during meiosis (a process also known as the *crossing over*) in sexually reproducing species. Some genetic variations that arise can have a neutral effect, in which case they will be neither selected for or against, and are likely to remain in the population. In addition to the variation within a population, species can also exhibit geographic variation – variation in the genotype of geographically separated populations. These distinctions can arise either due to a separation by environmental barriers or because of the different selection pressures caused by different environments. When a change in an environment generates new available resources, creates new challenges or opens new niches, adaptive radiation (also known as divergent evolution) can take place. It is a rapid diversification of species into a multitude of new forms. One of the most famous examples of an adaptive

radiation is the so-called *Darwin's finches*. Occupying fragmented landscape of the Galapagos islands, they have diversified in their ecology and morphology – most notably the size and shape of their beaks, which provided Darwin with evidence for his theory of evolution.

## The Second Synthesis: Evolutionary Developmental Biology

As molecular genetics continue to advance, a new field of *evolutionary developmental biology* started to emerge. The research of this field, informally referred to as "evo-devo," aims to explain evolution in terms of the genetic regulatory network – a collection of molecular regulators governing the gene expression of mRNA and proteins, through the interaction with each other and other cell substances. They have a central role in the creation of body structures (morphogenesis). The central premise of the field is the existence of a subset of genes that control the organism's embryonic development, called the *evo-devo gene toolkit*. These genes are conserved among phyla and thought to date back to the last common ancestor of all bilaterally symmetric animals (animals that have mirror symmetry in the sagittal plane vertically dividing their bodies into left and right halves, with each side comprising one of each sense organ and limb pair). These genes also tend to convergently (independently) evolve the same function. According to evolutionary developmental biology, variation does not arise from mutation of gene sequences but from mutation-driven changes in gene regulation. Variation can thus result from a toolkit gene being expressed in a different pattern (i.e., under-expressed or non-expressed) or from it acquiring a new function.

Darwin's theory also left a mark on the development of cell-biology and molecular-biology. The so-called *cellular Darwinism* proposes that stochasticity (or random variation) at the molecular level generates diversity in cell types, whereas cell interactions import a characteristic order on the developing embryo (Kupiec 2010). It is based on the work of Wilhelm Roux, a German

zoologist and embryologist, who believed that a Darwinian competition occurs at all levels of organisms, from molecules to organs, during embryonic development.

## Social Darwinism

Darwin's theory of evolution by natural selection had implications for the social sciences. The term *social Darwinism* refers to theories that apply his concepts of natural evolution to human society. Social Darwinism emerged in the late 1880s and was first described by Oscar Schmidt, but the term was used fairly rarely until 1944 when Richard Hofstadter, an American historian, published a book entitled *Social Darwinism in American Thought*. Social evolution and cultural evolution hypotheses were common during the Enlightenment, as well as seventeenth-century thinkers, but social Darwinism differs from the other theories of social change as the ideas are drawn from biology. In addition to believing that humans also struggle for resources and that advantageous physical and psychological traits are accumulated over time, Darwin proposed that social instincts also evolve through natural selection, which strengthens societies in which they occur (Darwin 1871).

## Universal Darwinism

*Universal or generalized Darwinism*, also known as the *Darwinian metaphysics* or the *universal selection theory*, comprises a variety of extensions of Darwin's original theory of evolution, aiming to explain evolution in an array of other disciplines. These extensions can be grouped depending on whether they focus on the biological implications of evolution (i.e., psychology or medicine) or whether they discuss the evolution of entities other than genes (i.e., computer science). Gene-based extensions include evolutionary psychology, evolutionary aesthetics, evolutionary anthropology, evolutionary musicology, sociobiology, human behavioral ecology, evolutionary

epistemology, evolutionary medicine, Darwinian literary studies, Darwinian happiness, molecular evolution, evolutionary linguistics, and other. Examples of non-gene-based extensions include quantum Darwinism, cosmological natural selection, memetics, cultural selection theory, evolutionary economics, evolutionary ethics, evolutionary art, evolutionary music, genetic algorithms, dual inheritance theory, and neural Darwinism.

## Cross-References

- [Adaptation](#)
- [Bear Life History](#)
- [Charles Darwin](#)
- [Directional Selection](#)
- [Divergent Evolution](#)
- [Evolution](#)
- [Fisher](#)
- [Fitness](#)
- [Gene Flow](#)
- [Genetic Drift](#)
- [Genetic Variation](#)
- [Genotype](#)
- [Gregor Mendel](#)
- [Jean Baptiste Lamarck](#)
- [Mendel's Laws](#)
- [Mendelian Crosses](#)
- [Mutations](#)
- [Origin of Species](#)
- [Phenotype](#)
- [Population](#)
- [Quantitative Genetics](#)
- [Runaway Selection](#)
- [Sexual Selection](#)
- [Stabilizing Selection](#)

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## Naturalistic Stimuli

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## Synonyms

Biologically significant stimuli; Ecological stimuli; Evolutionarily relevant stimuli; Functionally relevant

## Definition

Naturalistic stimuli are cues that reliably precede biologically significant events (e.g., an unconditioned stimulus, US) that animals have encountered recurrently in their evolutionary histories. Thus, a natural precursor of a US is regarded as

a naturalistic stimulus given its inherent relationship with the US.

## Introduction

From the traditional associative perspective, conditioned responses should develop regardless of the preexisting relations between the conditioned stimulus (CS) and unconditioned stimulus (US). Accordingly, any stimulus could be paired with any US as effectively as any other stimulus to produce conditioned responding. This view calls forth the idea that prior to conditioning the CS, by definition, is “neutral” and therefore the CS is arbitrary with respect to its potential to elicit a CR after being paired with a US. As Pavlov once assumed, any cue an animal could sense could be used as a conditioned stimulus for any response (Lakoff and Johnson 1999). Similarly, Skinner (1938) maintained that any arbitrary associative link could be formed between a response and the outcome. They assumed that the same laws of learning operated in all species and learning was about making connections between arbitrarily chosen stimuli and responses. This purely mechanistic-associative view has changed as behaviorist principles have undergone significant revision, particularly in light of findings from functional perspectives on animal learning (Domjan 2000). Curiously, as one of the fathers of behaviorism, Edward Thorndike himself believed that stimuli were not potentially equal in their effects on behavior and introduced the notion of “belongingness” in his formulation of the “Law of Effect.”

In contrast with traditional, general process approaches to learning, functional perspectives on conditioning have examined the inherent relationships between stimuli in naturalistic settings. According to functional views, learning provides organisms with an effective way of dealing with the particular kinds of problems they have recurrently encountered in their environments; hence learning mechanisms are specialized. According to this view, learning cannot be accounted for by a single, general process, but rather by many processes that relate to specific problems. Learning

mechanisms are thus been seen as responses by ecological opportunities and challenges, and therefore influenced by natural selection. Given the biological significance of the US, a CS would not likely be something arbitrary under natural circumstances. According to Domjan and Krause (2017) “. . . stimuli and responses that are a part of that ecology will activate the learning process more effectively” (p. 10). After all, arbitrary stimuli do not occur often enough with ecologically relevant USs to result in their becoming CSs. For this reason, it has been hypothesized that learning is more likely if the CS has a preexisting relation to the US (Domjan et al. 2004).

Ecologically relevant cues are readily associated with their resulting counterparts. For example, rats were able to associate audiovisual cues with a foot shock, but not so with illness; moreover, they were able to associate taste cues with illness, but not so with the foot shock (Garcia and Köelling 1966). Similarly, Foree and LoLordo (1973) found that pigeons predominantly use auditory cues as discriminative stimuli for avoidance behavior as opposed to visual cues. The functional perspective provides us with a glimpse into the ultimate causation of learning, in addition to its proximate underpinnings. Cole et al. (1982) elegantly showed how ecological relevance of stimuli affects conditioning. Hummingbirds were provided with two artificial flowers: one containing food and the other empty. The experiment consisted of two types of learning conditions. In the win-stay condition, subjects were trained to search for food in the same flower that they had received food in during a preliminary phase of the trial. In the win-shift condition, the subjects were required to visit an artificial flower at a location that differed from the preliminary trial in order to receive reinforcement. Results showed that the birds learned the win-shift condition significantly faster than the win-stay condition. More interestingly, opposite results were obtained when they used water as the biologically important stimulus. This time, birds tended to learn the win-stay strategy more readily than the win-shift strategy. Although these findings are highly puzzling from the traditional associative perspective, they make sense from the functional



view of learning and memory, especially given the relative constancy of the food and water sources in the birds' ecological niche. This study presents an example of the inherent relationship between ecological variables. This idea is quite compatible with the Behavior Systems approach formulated by Timberlake and his colleagues (1989).

According to the Behavior Systems approach, behavior is the product of functional systems (e.g., feeding, reproduction, predatory defense), and behavioral outcomes of conditioning are shaped by these functional systems. Each of those functional systems has evolved to achieve some important biological goal. For a food deprived animal, a piece of food is a desired US, and it activates an appetitive feeding behavior system which generally includes approach responses, while an unpleasant US such as presentation of a brief foot shock activates a defense behavior system which generally includes aversive responses. Thus, in a Pavlovian conditioning procedure a conditioned stimulus (CS) is integrated into the behavior system that is activated by the US. A brief foot shock causes rats to jump in the experimental cage. However, contrary to the stimulus substitution approaches to associative learning, the cues (punctate or contextual CSs) preceding the shock (US) elicit a freezing response as the CR (e.g., Bolles and Collier 1976; Fanselow 1980). The signaling CS gains conditioned properties and becomes a part of the defense behavior system of the animal. Therefore, the nature of the resultant conditioned response is determined by the behavior system relevant to the US involved. For that reason, the CR is not jumping, but rather freezing. The ease of learning a particular task depends on the extent to which the task is consistent with the behavior system that is activated by that conditioning procedure. In natural circumstances, ecological CSs that are already parts of the relevant behavior system reliably precede the occurrence of USs.

On the one hand, traditional mechanistic associative accounts of conditioning claim indifference between arbitrary and naturalistic stimuli, and on the other hand functionalist approaches to learning argue for the importance of naturalistic learning paradigms. Michael

Domjan and his colleagues (2004) have recently proposed an overarching approach that differs from general process learning perspectives.

More than 30 years ago, Domjan and Galef (1983, p. 160) stated, "carefully designed comparative investigations of learning can add a biological dimension and help integrate the study of learning with behavioral ecology and phylogeny without rejecting the general process tradition." Although there is strong agreement with the general idea that the primary function of the CR is to help the organism respond to the US more effectively, actual tests comparing naturalistic and arbitrary stimuli are relatively rare. Öhman and Mineka (2001) demonstrated that fear was acquired more readily to ecologically relevant cues, such as the sight of a snake, than to ecologically irrelevant cues, such as the sight of flowers. Over the years, Domjan and his colleagues have been able to build the empirical and theoretical bridge between the general process and naturalistic views of learning. A tenet to this approach is that the study of ecologically relevant stimuli will help us better understand how learning interacts with the preexisting organization of behavior. Domjan (1994) attempted to integrate stimulus and response factors into a general theory of learning and was able to test this attempt in an animal model of sexual conditioning in Japanese quail. This research program also provided insight into the ecological relevance of learning, since it requires comparing stimuli used during testing with those encountered in natural circumstances.

In the sexual behavior system of Japanese quail (*Coturnix coturnix japonica*), conditioned responses to a naturalistic CS (e.g., head-neck model of a female), compared to an arbitrary stimulus, were substantially enhanced if it was paired with a US (live female). The naturalistic CS was resistant to the blocking effect and the response attenuating effects of extinction procedures. Conditioned responding developed more rapidly toward the naturalistic CS, and a greater range of conditioned responses came to be elicited. The presence of naturalistically relevant features in a CS object increased the effectiveness of that CS in producing second-order

conditioning. Learning with the naturalistic CS was not easily disrupted by increasing the CS-US interval, and vigorous responding to naturalistic CS was observed, even with very low I/T ratios (for review see Domjan 2008).

It is worth mentioning some interesting observations and implications of the functionalist approach to conditioning. First, it establishes a continuum consisting of entirely unrelated, purely arbitrary stimuli at one end, and US-related, highly naturalistic stimuli at the other. Second, it nicely accommodates Timberlake's Behavioral Systems approach, the Biological Constraints View, the concept of Preparedness, and Naturalistic Learning paradigms. Third, it does not exclude the general process learning perspective but does challenge some basic tenets. Finally, the functionalist perspective is heuristically valuable, is supported on both empirical and theoretical bases, has supportive evidence from behavioral systems such as sexual and aversive conditioning, and it stimulates future studies integrating ecological analyses into traditional learning approaches.

In conclusion, traditional views of conditioning generally underestimated the significance of naturalistic stimuli on animal learning and conditioning. Implicitly or explicitly, they postulated that the CS has no inherent relation to the US prior to conditioning. Functional perspectives, on the other hand, actively acknowledge the role of preexisting relationships between stimuli in naturalistic settings. Thus, learning about naturalistic cues preceding a biologically important event would occur more readily and produce different conditioning phenomena. This idea has been supported by several lines of work that has added to our understanding about the interaction between the conditioned and unconditioned organization of behavior.

## Cross-References

- [Arbitrary Stimuli](#)
- [Associative Learning](#)
- [Behavior Systems](#)
- [Classical Conditioning](#)

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## Nature

- [Hominoidea Navigation](#)
- [Temperament](#)

## Nature Versus Nurture

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## Synonyms

Nature: [Character](#); [Condition of birth](#); [Quality](#); [World](#)

Nurture: [Bring up](#); [Nourishment](#)

## Definition

The word “Nature” is originated from the Latin word *nātūra*, which means conditions of birth, quality, character, natural order, world, etc. In other words, nature is the material world that surrounds individuals and may exist independently, even if there is no human activity. In another aspect, nature also refers to the specific features, characters, or qualities of something or someone which is inherited and transferred from one generation to another generation. In concern to the human being, nature is the genetics that determines one’s behavior like personality traits and abilities.

On the other hand, the word “Nurture” is originated from the Latin word *nutrire*, which means to nourish. The surrounding environment of a person, his upbringing, and life experiences

determine his behavior in a certain way. In other words, nurture can be defined as the one who nourishes, giving food, or helps to develop someone or something. For example, a bird feeding her baby is the nurture of the baby bird.

## Introduction

Diversification leads to uniqueness or individuality. Although being the same in all aspects, every individual on the globe is yet different from one another. These kinds of differences in race, intelligence, behavior, etc. are governed by certain factors that may include the one we might be focusing on. In a huge, vast, and diversified population of life on earth, the exactness or commonness has no more significant role to play. From the past few decades, the workers are trying hard to reveal the reasons behind such diversifications in behaviors. One of the most common connections revealed through several studies done in the past includes those between the surrounding environments with that of the behaviors. The outer space or the place of harbor plays a major role in shaping up the character of an individual or lining of their behaviors. Many times providing the same environment to different groups of people shows different behavioral patterns. The 50% of one’s actions or any act of intelligence or related to learning and cognition depends upon the genetic material that we receive from our parents (Plomin 2018).

The commonly used term for all types of human behaviors is their “nature.” It may be referred to as the genes that are pre-wired and influences the innate characters irrespective of their place of birth. Nurture, on the other hand, is related to the learned aspects of nature, i.e., influences of exposures of the surrounding environment directly or indirectly on the behavior of an individual. The theory of nature versus nurture initially came into the light in 1869 and the psychologist Sir Francis Galton was credited to use the term for the first time in history (Bynum 2002). The topic of nature versus nurture becomes the cause of debate among scientists, doctors, behaviorists, and many others. So this is very

clear that it is going to be difficult to understand the relation of nature and nurture with human behavior and personality, correlation and/or differences between nature and nurture, etc. Prior to understanding the topic of nature versus nurture, we have to know what human behavior is. Various research on mirror neurons, automatic imitation, mimicry, etc. is explaining human behavior as fundamental behavior which has a very important role for human beings to understand who they are and for what they born in this world, their responsibility toward the community. The studies are explaining fundamental human behavior as an immediate, uncertain, and difficult to control, which should be adjusted according to the objectives of our society (Lakin and Chartrand 2003; Corballis 2010; Heyes 2011).

An individual person is a unit of society; so to adjust us into a society, it is important to understand that what individuality is and the factors affecting it. The individuality refers to the way a human behaves differently in different situations. The diversity of single individuals depends upon many factors involving some common ones such as the surrounding environment, genetic factors, parenting styles, inborn intelligence, etc. These have some or the other effects on a newborn child during its growth phase. The growth phase of a child is considered as the most crucial phase of its development and sometimes future consequences are also decided based on one's growth.

In a book titled as "The Developing Genome" written by psychologist David S. Moore, it has been explained that in this fast-growing world with a burgeoning population it is important to know that genes are playing a crucial role and what these are doing is somehow influenced by the changeable environment in which these genes are sustained. Expression of genes can also get affected by some other factors like one's nutrition, stress, toxin exposure, etc. The above explanation indicates that genes (nature) and the surrounding environment (nurture), both are playing an important role in the development of human beings and are correlated with each other. But in another book "Gene and Behaviour" by Michael Rutter, it has been summarized that there is not a single factor or gene that is responsible for the sort of behavior

a human shows, rather it is a multifactorial existence of behavioral genetics, i.e., polygeny influence the pleiotropy, particularly in the area of psychiatric disorders. The occurrence of many neurodegenerative disorders is influenced by the genes irrespective of the environmental conditions provided. The primary environmental or genetic disorder is one that is independent of any of the other factors. If the disorder is of genetic type, the outer surroundings or the social factor doesn't provide any impact on the disease and vice versa (Simon et al. 2002).

From the above discussion, this is very clear that the topic nature versus nurture will be difficult to explain, which is more important as either nature or nurture, both are interrelated or independent to influence one's behavior and many more. Nature versus nurture is the topic of argument for several decades which concerns the relative contribution of human biology and behavior such as personality development, intellectual capacity, cognitive trait, scientific temperament, mental illness, and biopsychology. According to researchers, nature is the human behavior which evolves from heredity, gene, and other factors (Levitt 2013). On the other hand, nurture is the method by which behavior can develop. Nurture is controlled by external factors (Plomin et al. 2014). For example, the physical character is determined by one's gene with respect to their birth and growth, but nurture refers to one's childhood or how they were taught. So nature is fixed and cannot change but nurture is a kind of learned behavior that is changeable.

The debate on nature versus nurture is based on the discussion between one's learned and acquired behavior. There is a disputing explanation about behavior. According to some scientists, behavior is evolved from own gene or nature, meanwhile some other scientists are there who believe that behavior is the result of the environment or nurture. It is assumed that living mechanisms and thoughts of a person depend on their nature and nurture, but actually it is not clear how much of human traits are influenced by nature and nurture. According to Mullen (2006), unique individual feature is determined by unique gene and genomic or biological feature while nature presumably

refers to one's behavior in relation to his social and physical environment both. So here upon, as the theory of human behavior, nature describes cognitive trait, personality aggressiveness, and intelligence. Human behavior varies from person to person depending upon the genetic make-up of a person. Thought of a person and his vision around him or his opinion about the particular situation is determined by his own biological make-up (Ekelund et al. 1999). Scientists found that human traits such as hair color are acquired from parents. Further, they elaborate the point of contents that an individual's personality, sexual orientation, intelligence, and aggression are decided by their genes (Bleidorn et al. 2010). The personality of an individual is different from child to adult. But the question arises that what nature is, either personality of human being, his intelligence, or the natural world around humans. On this, there are many opinions of different scientists. To know what exactly nature is all about, we have to understand more about nature.

## Nature

As already mentioned, nature refers to the pre-wired information stored in the genes inside the cell and is hereditary, i.e., it gets passed on to their successive generations. Besides this, there exist several other aspects to define "nature." Many workers define nature according to their field of interests. The broad aspect of defining it has its own uniqueness and diversification.

According to Psychology, nature is the personality and physical appearance of a person which results from the specific genes he has and their characters which are inherited generation by generation (Cherry 2017).

According to Ecology, it refers to all forms of life on earth that have their origin ranging from subatomic to cosmic. Also, the natural environment includes all those areas that have not been altered by humans or those that persisted despite human interventions.

The above-mentioned aspects are interrelated as both are including humans as an entity that is being affected. Both the genetic factors as well as

the surrounding environment influence the development of behavior in an individual human being.

Certain theories support the development of an individual depends entirely on nature regardless of the environment provided. This was supported strongly by two great philosophers Plato and Descartes. They also believed that inherited characters decide almost all kinds of behaviors that an individual shows.

According to the Language Acquisition Device (LAD) theory of Chomsky, the capacity of children to learn and speak a language is governed by their instinctive mental ability obtained from their parents.

The biopsychology researchers supports nature's view of human eugenics by conducting experiments related to the working of neurotransmitters in shaping one's behavioral patterns.

If the theories mentioned above explain what nature is, then the question is what the nurture is and how it is different from nature.

## Nurture

Nurture refers to the surrounding culture, childhood experiences, and other social relationships that played a significant role in building up the behavioral characters of an individual. The impact of surrounding one's personality development is commonly referred to as a nurturing pattern.

Supporting statements giving critical place to nurture in defining one's behavior includes John Locke's belief that the mind begins as a blank state, i.e., the knowledge is acquired by the experiences of life.

According to a theory by John B. Watson, each individual has the ability of becoming whatever they want if proper conditioning is done regardless of the genes obtained from their parents.

The behavior of a person is highly influenced by parenting styles as well as the experiences that the one has gone through. For example, the manners of thanking and regretting by saying "thank you" and "sorry" is learned by the children from their surrounding only. This environmental surrounding supports the view that behaviors are governed by conditioning, i.e., nurture.



A more interesting theory in Psychology by Bandura (1977), i.e., Social Learning Theory, extensively provides a strong view in support of nurture's involvement in shaping the behavior of an individual. He conducted the "Bobo-doll experiment" with one most critical conclusions that the aggressive behavior in children is acquired by their surrounding environment observations (McLeod 2018).

The area of social psychology supports the nurture side view of the human behavior development enclosing crucial entity, i.e., peer pressure.

One of the common forms of human disorders is depression which is likely to be caused in almost all parts of the globe regardless of the environmental conditions. The contribution of such a common disorder is at least 38%, which is thought to be caused due to genetic factors or heritability (Kendler et al. 2006).

Nature accounts for about 30% and 60% of the total physiological traits of human behavior and the rest 40–70% depends upon the surrounding in which the person harbors, i.e., the higher percentage favors the nongenetic view of human behavioral development patterns (Plomin et al. 2013). It seems to be difficult to evaluate the argument about nature versus nurture that which is more important but this is quite clear that nature defined the gene and nurture refers to the surrounding environment.

## Nature–Nurture: Gene and Environment

The interaction between genes and the environment is all about phenotype. Phenotype is the physical appearance of the trait in real life and experimental condition. Phenotype is measured by questionnaire, test, and interview.

### Gene

Gene is the factor that represents the unit of inheritance. An allele is the alternative form of the gene that is present at the same locus on the chromosome. The position of a gene on the chromosome is the locus of a gene. The alleles are represented by "R" or "r" simplest system for a locus. A genotype is the set of chromosomes of an allele

for an individual. At a single locus, genotype may be represented as RR, Rr, or rr and for multiple-locus it may be symbolized by RRRY, RRYy, RRyy, RrYY, RrYy, Rryy, rrYY, rrYy, or rryy in case of two loci. A similar allele at corresponding loci on the homologous chromosome is termed as homozygosity while heterozygosity refers to different alleles at corresponding loci on the chromosome.

There are two kinds of genetic effects distinguished by Geneticists as an additive and nonadditive genetic effect (Neale and Cardon 1992). An additive effect is the effect of different genes that add together in their effect on trait while nonadditive is the genetic effect that does not add together in their effect on the trait. Nonadditive are dominance and epistasis. Intercommunication between two alleles at the same locus on the chromosome represents dominance. On the other hand, epistasis represents the intercommunication between two alleles at a different locus on the chromosome. The variety of epistatic interactions in animals depends on the number and effect the interacting loci have shown (Montooth et al. 2003; Andresson and Georges 2004; Williams et al. 2004). However, epistatic effect in human studies is not yet identified because of the absence of specific loci (Purcell and Sham 2004). When looking at outcomes for twins studies, it is realized that the epistatic effect cannot impure the heritability.

Heritability is the difference in a particular population at a particular time due to the genetic difference of an individual. It is defined as broad sense as well as narrow-sense heritability. Broad sense heritability is additive and narrow-sense heritability is nonadditive (dominance). Most twin's study is taken in a narrow-sense heritability because they show resemblance of offspring to their parents (Plomin et al. 2000). The concept of heritability is to observe differences among genetic factors of the individual.

### Environment

The environment is the nongenetic biological and noninherited factor and is influenced by other than inherited factors (Plomin et al. 2000). It is influenced by the shared and nonshared

environmental factors. Factors that are shared between the members of the twin pair are shared environmental factors, for example, a twin living in the same place and sharing their problems and hobbies. The factors which are not shared between the individuals of twin pair are nonshared environmental factors, for example, having different friends living in different places and having different interest. The theoretical and empirical tradition concludes that psychological behavior is influenced by shared rather than nonshared environmental factors, while according to behavioral genetic research, psychological traits are influenced by nonshared environmental factors rather than shared environmental influences (Plomin and Daniels 1987). It is concluded that phenotype is influenced by genetic factors, shared, and nonshared environment. As genetic factors and shared environmental factors involved in the same family are more similar to each other and different from other families influencing the phenotype. The nonshared environmental factor is the difference between the same family influencing phenotype.

According to the above studies, it is not necessary to be similar in personality, cognitive abilities, or schizophrenia-like disease even if two persons are physically similar. Physical similarity and personality are totally independent of each other (Kendler et al. 1993). The above studies conclude that genetic and environmental factors influence one's phenotype independently. But some of the studied cases didn't follow the above conclusion, so it is also important to understand the correlation between nature and nurture.

## Interrelations between Nature and Nurture

Researchers working in the field of science with specific approaches to reveal the interrelationship of nature with that of nurture have conducted several studies. The most common studies are the Twin and the Adoption study (Plomin et al. 2001). In this study, the differences between the two groups were taken into considerations. One group comprises of twins whose genetic materials

resemble one another. The other group consists of those whose genetic profile doesn't resemble at all. After providing the same environmental conditions, the changes in the behavior of each group were analyzed. Genetic researches have shown that heredity influence mental illness, personality, cognitive disabilities, etc. (Plomin and Asbury 2005). These two studies are the examples of a broader class of methods that are commonly used for the observation of nature–nurture relationship and are coming under the area of science known as “quantitative genetics,” the scientific discipline which analyses the similarities among persons depending on the percentage of biological interrelation between them. Quantitative genetics work on behalf of the number which is varying from 0 to 1 and called a heritability coefficient. The heritability coefficient evaluates the differences between two individuals based on the differences between their genes. These studies can be applied to siblings and half-siblings, cousins, and twins who got separated at the time of birth and grown separately (Plomin et al. 2012). The twin study observing the nature and nurture by the means of comparison of similarities between the two kinds of twins as monozygotic (MZ) also known as “identical twins” and the dizygotic twins (DZ) also called “fraternal twins.” Another study known as the Adoption study explains some interesting things like if a child of tall parents will be adopted by the family with short height then this is possible that the child will be taller or if the language of the biological parents of an adopted child was not similar to that of his present parents, possibly he speaks in the language of his parents with whom he lives for several years after adoption rather than his biological parents. The Twin and Adoption study concluded that both the genes and the surrounding environment affect the behavior of a person but the more weightage has been given to the genes rather than the environmental surroundings. But two drawbacks are there with the study as it fails to explain the adoption theory and if the theory can be applied to individuals rather than groups. But later in one of the great books of an American psychologist and geneticist Robert Plomin named “Blueprint: How DNA Makes Us Who We Are,” it has been

explained that these studies are not necessarily related to individual differences. He explained it with the help of average differences among a group of individuals. According to Plomin, this might be possible that heritability of a trait is high individually but if the average differences are higher in an ethnic group or a specific gender, then this can be possible only because of environmental factors.

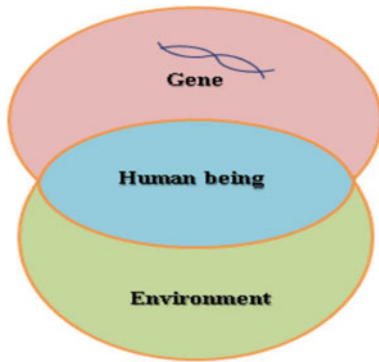
The differences in the genetic material are consistent and are the source of all kinds of psychological individuality. DNA is the blueprint of who we are, i.e., our behavior depends on the genes more than the surroundings. The encoded genes are responsible for the kind of action we perform up to some extent. But it's not necessarily mandatory that only the genes take the responsibility of all behaviors. The behavioral differences are observed when the exposure of an individual is studied at different surroundings. For example, there is a perception about the IQ that children born in highly educated families are more educated than the children born in comparatively less educated families. According to research, it was found that if the family income play as an environmental factor, then in about 70–75% cases ability (which measured as IQ) affects the educational emoluments which can be termed as genetic effects. Although the study remains complicated to find which factor is dominant, either nature or nurture as it fails in adoption theory, two points come into the light. One is that ability to avail facilities can play an important factor in educational achievement by children only to a certain extent. But the inheritance is more responsible for educational achievement by the children (Plug and Vijverberg 2003). The quality of behavior alters with factors such as parenting, education, life-shaping events, friend goals, area of living, quality of life living, etc. The more time one is exposed to the mentioned attributes, the more effective it shows. It might be supposed that human being has a greater capacity to achieve many things than any other species because they have greater sense and IQ than others. The developed qualities and life goals of a person are partially determined by his societal systems in which he is assigned for development. This social

system provides a competitive atmosphere, strong efficacy, opportunity, platform, aidful resources, etc. for the self-realization of their wishes (Bandura 1999). The above explanation is giving direction also toward the importance of nurture (environment).

The differences between nature and nurture do not have a clear picture and understanding but epigenetic mechanisms have shown that permanent changes or mutagenesis can be caused due to environmental exposures. Also, the effect of mutagens is long lasting and is at the level of genes. According to Randy Jirtle (an epigenomist), the debate on “nature versus nurture” is quite irrelevant because it was found that both of the forces interact in such a specific way that can switch the gene behavior (Miller nad Jones 2014). The best example of the above explanation is Darwin's theory of evolution by natural selection which is taking the side of survival of the fittest as the theory states that the organisms which are congruent with the surrounding environment will survive and reproduce. On the other hand, the organisms which are comparatively less compatible with their environment will die off. Giraffe's long neck is the best example as they evolved such an uncommon and helpful trait for reaching toward the leaves on height for their nourishment and survival.

To understand more about the interrelation between nature and nurture, a group of researchers found that the ability of understanding music is linked to a single gene but this cannot work alone. For a child to become a master of his field, the perfect training of that interest is also required the most. These views support the interactive theories of nature with that of nurture in deciding the future actions of a child. Another interesting example of the interaction between the two can be analyzed in families with healthier parents having undernourished children. It's not only the genes that are responsible for the physique of a child, the nourishment also plays a central role in ruling it (Fig. 1).

Human behavioral development nowadays doesn't have a monotonous view, i.e., either nature or nurture, rather it shows a dichotomous view focusing on both the aspects. A new research



**Nature Versus Nurture, Fig. 1** Interrelation between nature and nurture

area influencing human behavior has come up, which lies somewhat in between the genes and the environment or includes interactions of both of them. The area is popularly known as “Epigenetics” (Griffiths and Stotz 2013; Jablonka 2016). Human behavior is referred to as the response of an individual against a particular stimulus. It might be external or internal or both. For example, some aspects of human behavior depend on the other’s behavior while some of the behaviors are not causative and meaningless (Bandura 1986). Some traits of human behavior are social and depend on one’s individuality and temperament and are immutable (Skinner 1957). Torgersen (2009) told about the theory of nature that human behavior like aggression is totally depending on a person’s genes. Depending on the developmental stages, it might be possible that children’s behavior is calm, polite and responsible rather than their aggressive parents. According to two great philosophers Descartes and Plato, without any external factors like atmospheric forces or personal experiences innate traits never changed (Myres 2013). Here it can be anticipated that both nature and nurture have an equal role in building one’s behavior.

## Conclusion

Nature and nurture are all about genes and the environment respectively. Genetic fitness and the surrounding environment both are very important

for the proper development of a person. So this is not right to give priority to one of both, nature and nurture, as both are equally responsible for one’s personality, health, intelligence, social aspects, etc.

The debating topic of nature versus nurture in determining the person’s individuality never ends with one view. It always supports the interactive approach of determination, i.e., a vice versa relationship between both nature and nurture. Also, diversification among the huge population is not limited to these two factors, the behavior and character of the individual is a multifactorial approach.

After going through several examples and theories, the debating issue between nature and nurture got more entangled. One group of science, dealing with the inherent characters of an individual, targets the nature side for the kind of actions an individual performs, while the other side of science, i.e., psychology, moves its attention toward the nurture-targeted human behavior development. The third view of some of the researchers points out the collective approach in evaluating the behavioral patterns of an individual, i.e., both the genes as well as the surrounding environment influence common acts.

Hence, we can conclude that around 50% of the behavior might be governed by the genes that we inherit from our parents as each gene has codes for a particular type of action and in total internally masks the individual’s way of presenting themselves to the society. The other half is a learned behavior that is conditioned by interacting with the environment provided to them. Therefore, both nature as well as nurture present their crucial places in influencing the individual’s behavior.

The interaction between the genes and environment is a two-way criteria that defines the pattern of the act and the character as such. The social responsibilities of an individual are also headed under the vice versa interaction of these two entities. This topic tests one’s intelligence and thoughts for giving importance to one of these two approaches and decide whether nature governs their behavior or nurture. But with the help of several studies and different theories of great

researchers from different areas of science, it can be concluded that both nature and nurture play a crucial role in maintaining one's life well. Both are related to each other. If either one will be affected, the other will automatically get affected. For example, the current situation which is the worldwide pandemic attack of Covid-19 (a deadly virus) can be spread by touch, sneezing droplets, and even nearby air of an infected person. At this time, peoples are suffering from such a huge problem of health issues, starvation, economic crisis, etc. because of a virus named Corona. This virus is infecting our community. It can attack easily the person with weak immunity, so in this condition one should try to not go out and just stay at home and take the necessary precautions; only by this one can change this environment and get rid of this problem. On the other hand, people with good immunity can become a carrier of the said virus. Possibly they can't get affected but they can affect the related community as this virus can spread with touch or even via a close environment. In this case, such a person should also avoid going out. At present, this is the only possible solution for breaking the chain of infection and saving our community as well as the environment. This is as simple as Darwin's theory which explains that adaptations according to that of the environment can raise the rate of survival. Further with the help of a said example, we can summarize that nature (one's physical condition) and the nurture (one's surrounding environment) are interrelated and play a crucial role not only in one's development but his survival also. If one gets affected, then others will definitely be getting affected and the results will be frightening.

Compiling the above studies of the topic named "nature versus nurture," it should be notified that instead of trying to find which is more important either nature or nurture, one should try to understand the importance of both the nature and the nurture with respect to human development as well as the survival of other animals. The environment can exist without the presence of humans but human beings can't survive without it. Being on top of the animal kingdom, it is the responsibility of human beings to understand the importance and follow the rules of the natural world.

## Cross-References

- ▶ Alleles
- ▶ DNA
- ▶ Epistasis

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## Navigation

- [Hominoidea Navigation](#)
- [Spatial Orientation](#)

## Navigation by Honey Bees

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## Definition

Navigation by honey bees refers to the cognitive and behavioral mechanisms bees of the genus *Apis* use to move between a location and one or multiple goals. These involve the evaluation and integration of direction and distance cues as well as the learning of specific places. For honey bees, goals can be as diverse as the colony nest, a foraging site, a new nesting site, or an open-air mating area.

## Introduction

The vast majority of the about 20,000 known bee species are central place foragers: adults collect and bring back resources (flower nectar and pollen, water, resins) in a stable nest where they raise their progeny (Michener 2007). Foraging requires navigation skills to locate resources, travel between them, and return to the nest. Many bees

must also navigate at some point in their life to find mating partners, a new suitable nesting site, or even to orient inside their dark nests.

About a century of research on insect navigation, starting with pioneering work of Turner (1908) and von Frisch (1967), shows that these navigation behaviors are sustained by a cognitive “toolkit” (Wehner 2009) involving celestial cues (typically a **sun compass**), a distance estimator (**odometer**), a system for integrating both information (**path integrator**), and the ability to learn **visual landmarks** and specific places (see Fig. 1a and Glossary). For bees, these mechanisms sustain the expression of different types of spatial behaviors that change as individuals learn and gain experience with their environment.

In this entry we describe these spatial behaviors in honey bees (Fig. 2), a group of 11 species and 44 subspecies (Lo et al. 2010) exhibiting some of the most advanced levels of social forms in the animal kingdom, characterized by a reproductive division of labor (fertile queens and drones, sterile workers), cooperative breeding, and overlapping generations of adults. Navigation skills are required by individuals of the different castes (Seeley 2010). The foragers collect food, water, and resins from plants. The scouts must find new nesting sites. The reproductives must find mating partners for reproduction. And the in-hive workers move between important places in the nest, such as brood cells, honeycombs and the nest entrance. All these tasks require the ability to explore the environment, identify and learn places of interest, and sometimes communicate spatial information to nestmates.

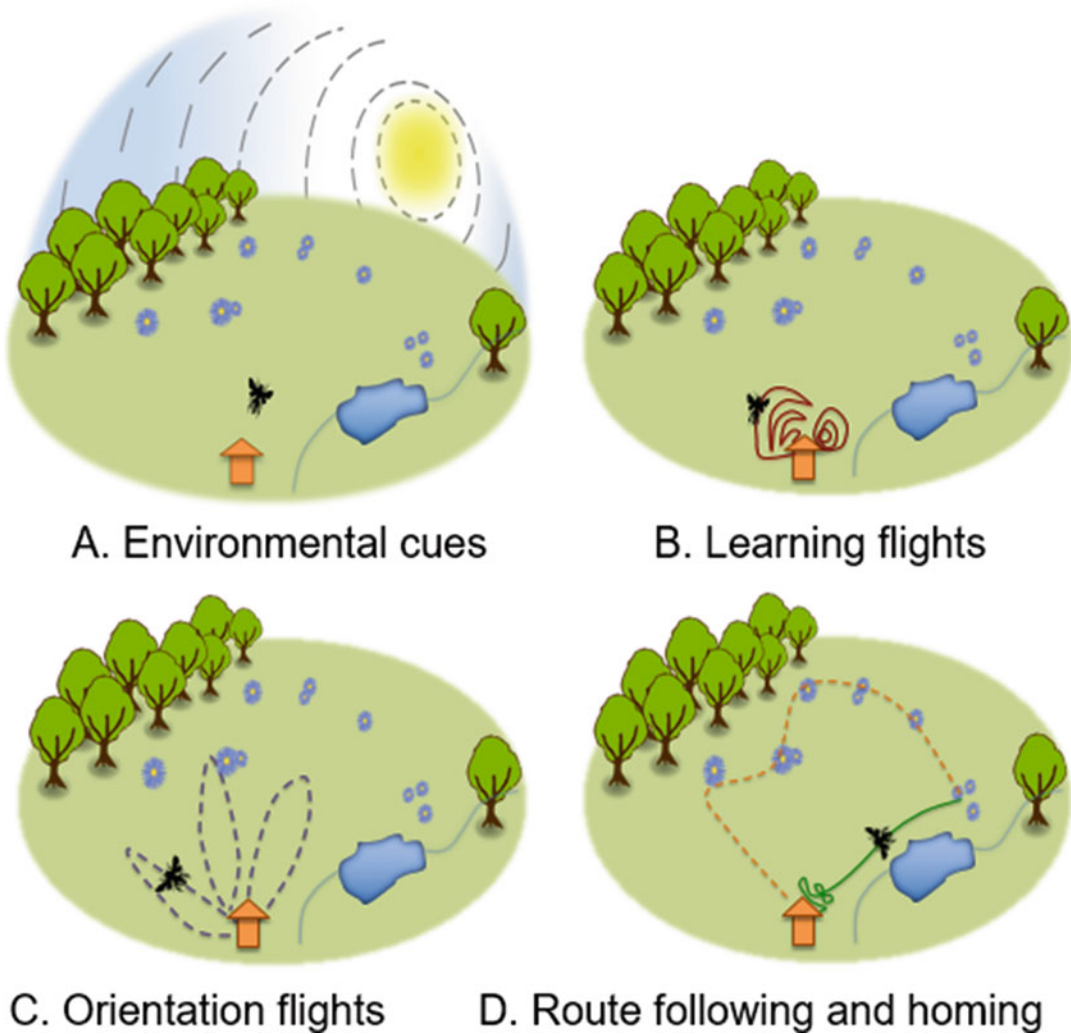
Here we focus in particular on the Western honey bee (*Apis mellifera*) as this species has a long history of domestication for honey production and crop pollination and is a model for the study of insect navigation. We discuss the different types of flights exhibited by foragers because they have been best described, especially since the development of automated tracking systems that record bee movements over several hundred meters (e.g., harmonic radar: Riley et al. 1996). However similar behaviors are expected by scout and reproductive bees. In-hive navigation has been less studied and is therefore not discussed.

## Exploration Flights

Western honey bees hatch in a dark nest, visually isolated from the outside environment. After about 2 weeks, they become foragers, which mean that they collect plant resources, sometimes scattered over several kilometers around the nest, to provision the colony. While foraging, the bee engages in different types of exploration flights during which it acquires visual memories of salient features of its environment, presumably in the form of **snapshot memories** (Collett et al. 2013), to guide future foraging trips.

On its first few excursions outside the colony nest, a bee engages in peculiar flight sequences known as “learning flights” (Fig. 1b), during which the bee learns the skyline **panorama** and **visual landmarks** associated with its nest location (Zeil 2012). Learning flights are composed of many convoluted maneuvers, loops, arcs, and zigzags facing the nest. During the initial learning flight, the bee slowly increases the radii of the loops and arcs, distancing itself from the colony nest until a point when it returns home without bringing back any resources. On the next few flights, the bee flies a bit further, slowly gaining experience with the outside environment.

Once a visual memory of the nest location is acquired, the bee engages in “orientation flights” (Fig. 1c), this time turning back to the nest. The bee flies along extended loops anchored at the nest location and covering a narrow angular sector in a given direction. Successive orientation flights are longer loops covering other sectors of the environment until every direction has been covered (Capaldi et al. 2000). During this process, the bee orients itself and searches for flower sites. If the bee is caught and released at an unfamiliar location outside the area covered by its previous flights, it engages in an extended search for its nest. By contrast, if the bee is released at a familiar location, it flies straight back home (Degen et al. 2016). Drones (males) have also been shown to be faster to relocate the colony nest after several exploration flights, allowing them to come back home from the drone congregation area if they failed to mate a queen.

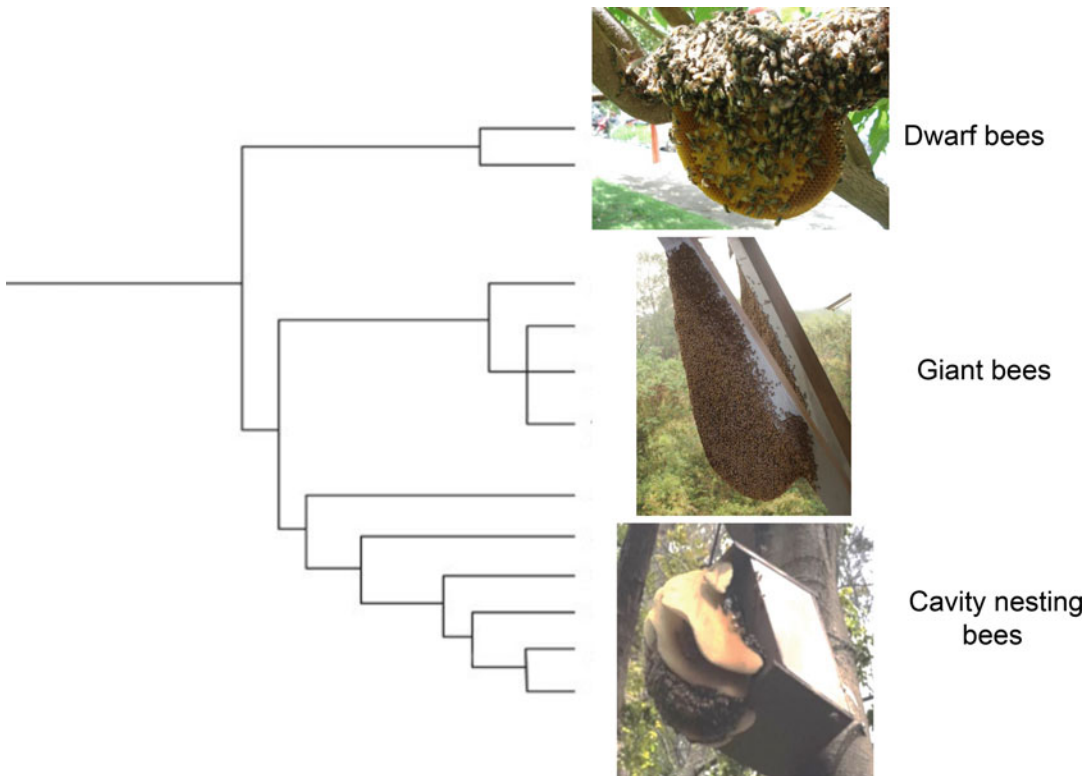


**Navigation by Honey Bees, Fig. 1** (a) Environmental cues used by honey bees to navigate. Bees use the position of the sun in the sky (or polarized light dashed lines under cloudy conditions, dashed lines) as compass. They learn visual landmarks (e.g., trees, rivers, paths) and views of broader visual cues like panoramas and skyline (i.e., snapshots). When closer to the goal, bees use local available information to pinpoint the goal (e.g., shape, color, odors). (b, c, d) Hypothetical examples of flight sequences performed by a forager as it gains experience. (b) Learning flights: during its first excursions outside the hive the bee learns the visual scene characterizing the nest entrance

using concentric circles increasing in size (red plain lines). (c) Orientation flights: after a few trips, the bee starts exhibiting sequential exploration of sectors around the nest (orange dashed line) to find flower patches. (d) Route following and homing: once experienced, the bee follows a multi-destination route (trapline) learnt from previous foraging trips (dashed orange line). The bee returns home following a home vector computed through path integration (inbound in green). At the end of this homing flight the bee corrects eventual path integration errors through small search loops to precisely locate the nest entrance

Exploration flights are not exclusive to first trips outside the nest, but also occur during the foraging process. For instance, once a food resource is found, a forager may exhibit learning flights to learn the visual scene surrounding this

new site so that it can more easily return to this site on subsequent foraging trips (Robert et al. 2018). When a resource is depleted, the bee searches for an alternative site through longer flights centered at the familiar depleted location. These



**Navigation by Honey Bees, Fig. 2** Honey bees contain 11 species. Dwarf open nesting honey bees like *Apis florea* are the most basal group and live mostly in Asia and Middle East. The open nesting giant honey bees like *Apis dorsata* are found only in Asia. The most recently derived group are the cavity nesting honey bees represented by six species: five of which are distributed in Asia. *Apis*

*mellifera* has a natural distribution in Africa, Europe, and the Middle East, but has been domesticated and distributed throughout the world. It is now found in the wild on all continents except Antarctica. Photo credits: Dwarf and cavity bees from Naila Even, giant bees from Benjamin Oldroyd. Phylogeny modified from Lo et al. (2010)

exploration flights, composed of straight segments and turns, have Lévy characteristics, meaning that there is a larger proportion of long flight segments than one would expect from a normal distribution (i.e., a Brownian search) (Reynolds 2008). This type of random search pattern is expected to be optimal to locate patchily distributed food sources, like plants, for animals with little knowledge of their environment.

## Homing Flights

At the end of every foraging trip, a forager must navigate back to its nest to unload its crop and feed the colony. “Homing flights” are composed

of two phases: a straight line flight to return to the nest area, and a convoluted flight to pinpoint the nest entrance (Fig. 1d).

To return home, the bee uses its estimation of directions and distances of the often tortuous inbound path toward a goal (e.g., feeding site) and integrates both information using a **path integrator**. In honey bees, directions are primarily estimated through the position of sun in the sky, constituting a **sun compass**. When the sun is not directly visible (e.g., during cloudy days), this information can be retrieved from the pattern of **polarized light**. Distances are estimated using an **odometer** through the quantity of visual information perceived on the retina of the compound eye while flying. It is possible to study this mechanism

in bees by making them fly in narrow tunnels with black and white strips of different widths, thereby making them under- or overevaluate their real flight distances (Srinivasan 2011).

When the crop (stomach) of the bee is full of nectar or its tarsi are packed with pollen grains, its motivation to return home sets a new directional aim: the nest. A straight line return (also called “beeline”) is then indicated by the opposite of the integrated vector during the inbound journey. During the homing flight, the bee also integrates the distance and direction traveled, shrinking the integrated vector pointing to the nest. A central part of the bee brain, called the “central complex,” receives and integrates inputs of directions and distances from diverse internal senses like eyes, body hair, wing muscles, and other brain parts, and allows all these neural computations (Stone et al. 2017). The integration process is subject to noise accumulation during the journey of the bee. To reduce this error, foragers also refer to **visual landmarks** learned during previous flights to pinpoint directions and goals (Srinivasan 2011). Anything salient in the environment can be used as visual landmarks, even elongated structures on the ground such as rivers, edges, and paths (Menzel et al. 2019).

The last bit of the homing flight (also known as “view-based homing”) is guided by visual landscape cues. Since the seminal experiments of Bouvier (1900), showing that bees locate their nest entrance with surrounding visual cues, bees have been challenged to pinpoint their home in a plethora of scenarios. Objects may be displaced closer to or further away from their nest, displaced to a new location, replaced with smaller or differently colored one, or even camouflaged (Dittmar et al. 2010). Based on these studies, we know that bees learn relations between a myriad of visual cues and their nest entrance. These relations are not necessarily explicit. Indeed, the use of **panoramic skyline snapshots** around the nest entrance is sufficient to guide a simulated bee toward its home (Towne et al. 2017).

Two navigational routines, **path integration** and visual guidance, jointly lead a bee home (Hoinville et al. 2018), but the importance of the routines depends on the context, such as the

foraging experience of an individual bee. For instance, **path integration** tends to be preferred over **visual landmarks** in a novel environment. However when both navigational routines are conflicting, **visual landmarks** are favored (Kheradmand and Nieh 2019).

## Route Following

After several foraging trips, foragers tend to develop routes to efficiently return to known profitable feeding sites. Bees can famously be trained to learn straight line outbound paths between the nest and a feeder providing large amounts of sucrose solution (von Frisch 1967). However, in many natural conditions, bees may visit hundreds of flowers, sometimes dispersed over several kilometers, to fill their crop with nectar (honey bees have been observed homing after being released 11 km from their nest (Pahl et al. 2011)). When this is the case, foragers therefore need to develop more complex circuits between multiple goals, a routing challenge analogous to the well-known Traveling Salesman Problem (TSP) in mathematics.

A naive honey bee forager first visits flowers in an unordered sequence as it discovers them. However with experience, the bee can develop a stable route linking multiple flowers, a behavior described in many other pollinators (e.g., bumblebees, bats, hummingbirds) and known as **trapline** foraging (an analogy of the routes used by trappers to check their traps; Fig. 1d). This behavior was discovered by observing individual bees foraging in small arrays of artificial flowers within 100 m from the hive (Buatois and Lihoreau 2016). As long as the artificial flowers were regularly replenished with a sucrose reward, the bees learned to revisit them and adjusted their visitation sequence in order to minimize overall travel distances, ultimately selecting the shortest possible route (i.e., thus solving the TSP).

Computational models attempting to decipher the cognitive mechanisms underpinning this navigational feat show that trapline development and optimization can emerge based on the ability of bees to learn sequences of places using visual



memories (Collett et al. 1993) and estimate travel distances with **path integration** (Srinivasan 2011). According to these models, at the end of its foraging trip the bee may sum the straight line distances between successively visited flowers and derive the net length of the entire route. By comparing successive routes, the bee could thus increase its probability of reusing the vectors composing the shortest experienced route (Lihoreau et al. 2012). Through trial and error, this simple learning process may enable the development of good (if not optimal) routes in environments with different numbers and spatial configurations of feeding sites (Reynolds et al. 2013).

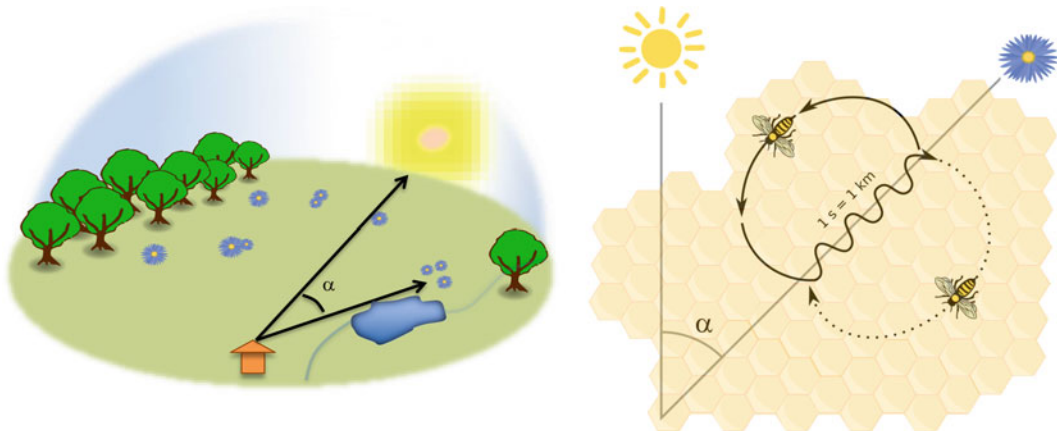
### Place Communication

Once back in the hive, the honey bee forager can communicate the direction, distance, and quality of a discovered feeding site via a sequence of movements known as the “waggle dance” (von Frisch 1967; Fig. 3). Scout bees also use this communication system to indicate the location of a suitable nesting site (e.g., cavity, hive) to reach a

consensus about the best available site before swarming (Seeley 2010).

While this ability to recruit nestmates for profitable places was discovered by naturalists long ago (e.g., Aristotle), the symbolic meaning of the dance was finally decoded by Karl von Frisch. In 1919, von Frisch trained bees to forage on feeders containing sucrose solution placed around the hive. He observed that the foragers returning to the hive performed energetic rounds and were occasionally followed by other bees who would then fly to the communicated feeder. von Frisch described two types of behaviors referring to them as “dances” depending on the distance of the food source to the hive. For feeders within 90 m the hive, foragers performed a round movement, where for longer distances they performed a wagged movement following an eight-shaped figure. It is now accepted that both dances are in fact a single behavior, whose precision varies with the distance of the food source to the hive (Griffin et al. 2012).

During the waggle dance, the forager waggles its abdomen and moves toward the direction of the food relative to the sun. In cavity nesting honey bees, like the Western honey bee, the invisible sun



**Navigation by Honey Bees, Fig. 3** The waggle dance. Upon returning to the colony nest following a successful foraging trip, a honey bee forager can communicate the location of the discovered food site to its nestmates by performing a waggle dance. The bee communicates the direction of the resource by wagging in the direction of the resource relative to its angle with the sun ( $\alpha$ ). The duration of the wagging movement is proportional to the distance of the food. The bee repeats the wagging

movement coming back from the left and then from the right drawing the figure height. The more the dance is repeated the higher the quality of the resource. Any bee following the dance can thus integrate the information and leave the hive using the instruction from the dance. The waggle dance is also performed by scout honey bees to communicate the location of a new nest site before swarming. Modified from Emmanuel Boutet (CC BY-SA 2.5)

in the dark hive is encoded by the vertical vector facing up (i.e., against gravity). Therefore, the angle between the waggle trajectory and the vertical of the comb represents the angle of the food source and the sun. In open nesting honey bees, however, the dance occurs horizontally on the top of the single frame and the dancing bee faces directly the direction of the food or the future nest. In both open nesting and cavity nesting honey bees, the distance of the food source is communicated via the duration of the waggle movement that correlates with a distance in meters. This correlation and the precision of the duration slightly varies between species and subspecies of honey bees (Beekman et al. 2015). The rewarding value of the resource is communicated by the total duration that the bee performs repeating the eight-shape dance. Dancing for a longer time increases the probability to recruit foragers susceptible to be interested by the navigation instructions for a new resource (Seeley 2010).

## Migration

Several *Apis* species from tropical Asia, such as the cavity nesting honey bee (e.g., *Apis cerana*), the giant honey bee (*Apis dorsata*), or the dwarf honey bee (*Apis florea*), do not remain in a stable nest but can abandon the nest or migrate over long distances to respond to local food shortage (Oldroyd and Wongsiri 2009, Fig. 2). Giant honey bees, for instance, have been reported to migrate to destinations up to 200 km away, stopping over in bivouac congregations to rest and forage. These bees can even sometimes return to the exact same tree after the migration period. During migration, Asian honey bees use dance communication to orient the swarm departure in the correct direction toward a new nest. In the case of long distance migrations, especially in open nesting giant honey bees, the direction is communicated but the distance is only indicated by a very long waggle signaling (Dyer and Seeley 1994). Sensory mechanisms used to migrate to a new location are similar to those used by honey bee foragers, including the **sun compass**, the **optic flow**, and the learning of visual landscape cues.

## Concluding Remarks

Honey bees show a unique diversity of spatial behaviours but share numerous sensory abilities and navigational strategies with other insects (see Glossary). Thus, they are key model species to study insect navigation. Understanding how a tiny brain, with about one million neurons, uses computations to navigate efficiently in three dimensions over large spatial scales, finds direct applications in algorithmic and robotics and may help understand how these mechanisms evolved in the more complex brains of vertebrates (Chittka and Niven 2009). Some features described in mammal navigation studies, like the hypothesis of the representation of the global surrounding in a single mental map (i.e., cognitive map), influence debates about mental representations of space in insects (Menzel 2019). Even though no consensus has been yet reached, most studies show that **path integration** and visual guidance are sufficient to explain the complex spatial behavior exhibited by honey bees and other insects (Webb 2019).

The study of the neural mechanisms underlying navigation in the insect brain may address this important knowledge gap and clarify whether honey bees use cognitive maps. Deep brain structures start to be linked to navigational functions such as the central complex for **path integration** and the mushroom bodies for visual memories (Webb and Wystrach 2016). Exploring brain function in vivo in a flying insect in its natural environment is still out of reach. However, recent advances in virtual reality setups (e.g., Buatois et al. 2018) and onboard neuron-stimulator or recorders (e.g., Sato et al. 2015) increase the possibilities to study navigation under tightly controlled, yet ecologically relevant, conditions while exploring brain function.

## Cross-References

- ▶ [Central Place Foraging](#)
- ▶ [Cognitive Map](#)
- ▶ [Dead Reckoning](#)
- ▶ [Foraging by Honeybees](#)
- ▶ [Insect Navigation](#)
- ▶ [View-Based Homing](#)

## Glossary

**Central place foraging** Foraging behavior consisting in collecting resources in the environment and carrying them back home. In the case of honey bees, foragers make back and forth trips between resource sites (food, water, resin) and their nest to feed the colony.

**Odometer** Mechanism enabling animals to estimate travel distances. In honey bees, distance estimation is mediated by the apparent motion of surrounding objects on the retina of the compound eye, also called “optic flow.”

**Panorama** Piece of visual information corresponding to a global visual cue, such as a landscape or a skyline. A panorama can also correspond to a combination of several visual landmarks (e.g., trees, buildings, rivers). Honey bees use panoramas for learning places such the location of their colony nest or a profitable food site.

**Path integration** Method used by an animal for knowing its current position from a reference point, also known as “dead reckoning”. Honey bees integrate odometry cues (distances) and sun compass (directions) to compute the vector pointing to a reference point (e.g., the nest) from their current position. This computation allows a honey bee to come back to the nest in a straight line.

**Polarized light patterns** Rayleigh scattering creates patterns of polarized sunlight, which are distributed in the sphere of the sky following concentric circles with the sun as a center (see Fig. 1a). With photoreceptors located in the dorsal area of their compound eyes, honey bees can detect direct sunlight as being the unpolarized area of the sky and can sense that polarization increases when the e-Vectors (electric vectors of light) are further away from the sun along the concentric circles.

**Snapshot** Learning of a 2D image at one point in time. For a honey bee, the memorized view corresponds to a specific orientation of the bee relative to the image, similar to a camera objective taking a snapshot from a specific angle.

**Sun compass** Utilization of the sun’s position in the sky as a directional guide. For honey bees, the position of the sun can be perceived directly (when the sun is visible) or indirectly through the pattern polarized light (when the sun is not visible). To orient when the sun is visible, bees can use the light intensity (higher closer to the sun) and the chromatic gradients (toward green in solar region to UV in the antisolar region).

**Trapline** Repeatable sequence of flower visits, starting and ending at the nest. With experience, honey bee foragers tend to develop traplines minimizing overall travel distances between familiar feeding sites. These routes are based on individual experience.

**Visual landmark** Salient feature in the visual scene. Honey bees can use many types of landmarks spanning from 3D trees or buildings to 2D elongated patterns on the ground (e.g., paths, edges, rivers, roads).

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## n-Back Task

► [Back-Test](#)

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## NCL

### ► Delay Neurons: Comparative Overview

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## Need Reduction

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## Synonyms

**Need:** Necessity; Desire; Wish; Indispensability  
**Reduction:** Decrease; Diminution; Lowering;  
Lessening

Like most of the terms they use, psychologists have purloined “need” and “reduction” from ordinary language. According to the *English Oxford Living Dictionary* (<https://en.oxforddictionaries.com/definition/need>), the ordinary term “need” could be a verb or a noun. As a verb, it means “to require (something) because it is essential or very important rather than just desirable” and “Be necessary.” As a noun, the term means “Circumstances in which something is necessary; necessity,” “A thing that is wanted or required,” and “The state of requiring help, or of lacking basic necessities such as food.” The term “reduction” means “The action or fact of making something smaller or less in amount, degree, or size,” and “The amount by which something is made smaller, less, or lower.”

Psychologists’ uses of the expression “need reduction” have preserved these ordinary meanings. Generally, psychologists view a need as a state (a temporary condition) that results from the relatively prolonged absence or lack of something, but can be lessened by its reappearance. Widely studied examples are basic biological needs such as hunger. Psychologists have defined hunger as a need for food that results from a relatively prolonged food deprivation, and is

reduced by the return of food, or so many psychologists have assumed.

Theorizing about the role of this reduction in psychological phenomena was central to classical learning theory. Hull (e.g., 1943) was the first to propose a theory of reinforcement learning as need reduction. His observations came primarily from maze learning (typically T mazes), where animals, typically hungry rats, had to learn to navigate through a maze following a certain required path, from a start box to a finish or goal box (see “goal,” this volume) where food was available. Intuitively, Hull’s proposal was that hunger motivated or drove rats to navigate through the maze to obtain food. Obtaining the food as a result of this navigation reduced the need for food, which reinforced the stimulus-response (S-R) associations that the animal had learned from previous successful navigations, and allowed it to navigate the maze ever more efficiently and effectively.

Hull formulated his theory of reinforcement as need reduction in terms of his famous (abridged) state equation  $sE_R = sH_R \times D$ , where  $sE_R$  denotes the reaction potential (which determines the probability of occurrence of a response  $R$  to a stimulus  $S$ ),  $sH_R$  the habit or S-R associative strength (determined by conditioning), and  $D$  the drive level (determined by the level of food deprivation). As  $D$  increases (thanks to a stronger need),  $sE_R$  also increases,  $sH_R$  being equal. Getting the food at the finish box, after navigating the maze in a certain required way, reduced the need by some amount, which in turn reduced  $D$ . This reduction, in turn, increased  $sH_R$ , which maintained  $sE_R$  relatively high. When there was no food in the finish box,  $sH_R$  decreased but  $D$  increased again, also maintaining  $sE_R$  relatively high.

Reinforcement as need reduction is squarely framed within the *drive* theory of motivation (see “drive state,” this volume), according to which needs drive or *push* the animal from the inside to perform certain actions conducive to reducing the need. Another theory is *incentive* theory, according to which behavior is determined by incentives, external stimuli that create needs (e.g., as when someone says “I need that car”



upon seeing a brand new car) and *attract* the animal towards the stimuli. The causes of behavior in this theory, then, are extrinsic to the animal. The two theories are compatible.

Incentive theory has promoted theorizing about needs other than hunger, and to speak of “need satisfaction” instead of “need reduction.” As part of this further theorizing, psychologists have distinguished between lower needs and higher needs. This distinction became important because lower needs, in and of themselves, did not suffice to explain the persistence of learned behavior without primary reinforcement (i.e., without need-reduction). Higher needs were thus introduced to explain behavior that does not seem to be directly and immediately motivated by the reduction of basic biological needs.

Drive theorists too made this distinction, or something close enough. Hull (and many others) postulated the notion of “secondary reinforcement” to explain the maintenance of maze-movement behavior in the (temporary) absence of reinforcement. The food served as a “primary reinforcement” of the immediately preceding S-R association, and this association as a “secondary reinforcement” of the immediately preceding association, and so on. Hull thus viewed maze learning as the formation of a chain of S-R associations, much of which consisted of secondary reinforcement that kept the animal moving through the maze in the temporary absence of reinforcement. In effect, rats learned to need to, say, turn right upon seeing the right corner of the maze. This learned need was reduced by performing this response, which served as a secondary reinforcement of other, antecedent learned needs.

Hull explicitly framed his theory of reinforcement as need reduction within an adaptive, Darwinian account of behavior. Hull also formulated his theory in terms of “neural mediating structures” and “mechanisms,” which inspired the study of the neural substrates of reinforcement in more empirical detail. Unfortunately, the neuroscience of learning was very incipient in Hull’s time, which did not allow a study of specific neural mechanisms of learning.

These mechanisms are now known in much more detail, and, ironically, have unraveled a far

more complicated story than classical learning theorists ever imagined. Just a little over a decade after Hull’s 1943 book, Olds and Milner (1954) reinforced rats for pressing a bar by just electrically stimulating the septal area (stimulating other brain structures did not have a positive reinforcement effect), *without any deprivation of food or water*. The acquisition curves were comparable to those obtained with food as reinforcer. Clearly, there is no need or drive here, just electrical stimulation of certain brain areas, and yet, there was significant learning.

Moreover, given a *choice*, hungry rats prefer direct brain electrical self-stimulation over food, to the point of starvation, a phenomenon known as “self-deprivation” (for a review, see Frank and Stutz 1984). Need reduction, then, is not necessary for learning. These early studies led to many others that have yielded identification of *dopaminergic* structures (e.g., ventral-tegmental area, nucleus accumbens, medial forebrain bundle, etc.) as key to associative learning, operant as well as Pavlovian. These structures have also been shown to underlie the effects of addictive drugs such as cocaine (for a review, see Wise 2006).

Choice complicates the matter, leading to another field where talk of need satisfaction has gone well beyond basic biological needs. This field is known as “economic psychology” or “behavioral economics,” the interdisciplinary relations between economics and psychology. At the heart of this field is the study of the determinants (external, internal, social, cultural, biological, etc.) of economic choices or decisions, where agents must decide which action to perform, among a set of alternative actions, based on cost-benefit judgments. To be sure, a rat in a T maze must decide whether to go left or right, but in the classical studies there was no choice between different kinds of foods (e.g., sweetened vs. salty). When animals, human and nonhuman alike, are faced with this kind of decision situations, needs and their satisfaction become exceedingly complex affairs where incentives play a more central role.

One insight this field has led to is that, in such kinds of situations, humans do not seek to satisfy needs like the ideal, perfectly rational agent, the *Homo economicus*, economists have postulated.

The research of Daniel Kahneman and colleagues, which earned him the Nobel Prize in 2002, was instrumental in this regard. Their results suggest that humans, when seeking to satisfy economic needs, repeatedly fall prey to a number of logical fallacies. For example, the conjunction fallacy (e.g., Tversky and Kahneman 1983) is to infer that a conjunction (e.g., “I will get paid today and tomorrow”) is more *probable* than either of its conjuncts individually (e.g., “I will be paid today” *or* “It will be paid tomorrow”). What makes it a fallacy is the multiplication rule of probability, according to which the joint probability  $p(A \& B)$  for independent events  $A$  and  $B$  (where “&” or “and” take their strict logical sense) equals  $p(A) \times p(B)$ . Since probabilities are numbers between 0.0 and 1.0,  $p(A) > p(A \& B) < p(B)$ . Another fallacy is the gambler’s fallacy, the belief that occasional highly frequent occurrences are more probably followed by lower frequent occurrences. Committing these and other fallacies, Kahneman and colleagues argued, leads to unsound economic decisions to satisfy economic needs. However, as Gigerenzer et al. (2008) have pointed out, Kahneman’s conclusion arises from too strict an interpretation of the term “probability” (and “and,” in the case of the conjunction fallacy) that does not always obtain in ordinary language and common sense.

Another important phenomenon is delay discounting (for a review, see Odum 2011). In this phenomenon, the reinforcing value of a reward decreases hyperbolically with its delay relative to a required response. This function predicts behaviors like impulsivity, the preference for a smaller but immediate over a larger but delayed reward. This kind of behavior is yet another challenge to the classical learning theorists’ rather simplistic view of the role of reward magnitude in need reduction. Contrary to such view, animals do not necessarily seek greater rewards.

There has also been much research on the neuroscience of economic decisions, or neuroeconomics (for a recent review, see Glimcher and Fehr 2013). This research has shown that some of the same neural substrates of simple animal learning also underlie complex economic decision-making under risk (where some

decisions could lead to significant losses) and uncertainty (where relevant information is unavailable). For example, increases in the activity of parts of the prefrontal cortex such as the frontomedian cortex (e.g., Volz et al. 2003) and frontoparietal cortex (e.g., Paulus et al. 2001) have been linked to decision-making under uncertainty. Increases in the activity of the insular cortex have been linked to decision-making under risk (e.g., Paulus et al. 2003).

Talk of “needs” remains widespread in neuroeconomics and behavioral economics research, although, again, with a much wider meaning beyond basic biological needs like hunger, to include many other kinds of needs (e.g., the need to say, do, buy, know, ignore, change, learn, or decide things that do not directly or immediately involve getting food). Talk of “need reduction” has declined significantly, giving way to talk of “need satisfaction” and becoming more historically than theoretically or empirically relevant.

## Cross-References

- [Clark L. Hull](#)
- [Decision-Making](#)
- [Genetic Fallacy](#)
- [Goal](#)
- [Instrumental Learning](#)
- [Learning](#)
- [Nucleus Accumbens](#)
- [Operant Conditioning](#)
- [Reinforcement](#)

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## Need: Necessity

### ► Need Reduction

## Negative Reinforcement

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### Definition

Negative reinforcement is a concept within operant conditioning which involves the strengthening of a behavior via the removal of negative stimuli as a consequence of the behavior. Such negative reinforcement increases the probability of the behavior being repeated.

For example, the behavior of visiting a dentist is negatively reinforced by the removal of toothache. Such negative reinforcement increases the probability that an individual will repeat the behavior and go to the dentist again in the future.

## Introduction

It is natural to adjust behavior in response to good and bad consequences. Throughout life individual behavior is constantly shaped by reinforcement and punishment. Experiments by the American psychologist Edward Lee Thorndike (1911) were among the first to highlight how the consequence of a given behavior can affect the likelihood of it being repeated in the future. The concept being that in a given situation, without thought process, an organism will exhibit a range of behaviors, and a behavior followed by a desired outcome is more likely to be a behavior that the organism will repeat. He coined this the “Law of Effect.” Thorndike uses the example of a cat escaping a box via unlatching a door and noted that each time the cat was placed in the box, the behavior which led to unlatching the door occurred earlier.

Later American psychologist, Burrhus Frederic Skinner, likewise conducted research on how consequences of behavior affect the probability of individuals repeating such behavior. In 1937 B. F. Skinner coined the term “Operant Conditioning” – meaning changes in the probability of responses as a result of changes in the consequences of such responses. In one of his books, B. F. Skinner described the following example: a pigeon is fed via a food tray immediately after raising its head above a predetermined point; this leads to the frequency that the pigeon’s head is above the point increasingly, very quickly the bird’s posture has changed, and its head very rarely falls below the predetermined point. Within operant conditioning the unit of behavior is known as “the operant” which in this case would be “the pigeon raising its head.” Initially this response is a spontaneous behavior but reinforced (strengthened) via being rewarded with food (the reinforcer) and thus increases in frequency.

Reinforcing events were described by B. F. Skinner as those which increase the probability of a given response occurring again, and he described two types of reinforcing events: those which involve adding a positive stimuli (positive reinforcement) and those which involve removing negative stimuli (negative reinforcement). He also described two other forms of operant conditioning: those which involve adding negative stimuli (positive punishment) and those which involve removing positive stimuli (negative punishment).

## Negative Reinforcement

One particular form of behavioral learning is via negative reinforcement. Negative reinforcement consists of the removal of negative stimuli as a consequence of a behavior. Both escape and avoidance behaviors remove negative stimuli. Behaviors which involve the organism getting away from an existing negative stimuli are known as escape behaviors. Whereas behaviors which prevent the onset of negative stimuli are known as avoidance behaviors. For example, a child may touch a hot cooker and feel burning and therefore remove their hand from the surface. The behavior of removing the hand was cued by the feeling of burning, which was negatively reinforced by the burning feeling stopping. This is an escape behavior. However, over time the child learns not to touch the cooker, a negatively reinforced avoidance behavior.

## Antecedent Cue

The negative reinforcement of a behavior will increase the frequency at which it occurs in the future. However, behaviors do not have the same effects in all situations, and therefore situational cues are important. Cues which precede behaviors are known as antecedent cues and are used by organisms to decide if a given behavior is likely to have a positive or negative consequence. Thus, antecedent cues come before a given behavior, and consequences proceed it. When a behavior is

reinforced, it is more likely to be repeated in the future in response to the correct antecedent cue, that being a stimulus that cues an organism to perform a reinforced behavior in order to receive an associated reinforcer. For example, the onset of illness is an antecedent cue for going to the doctors in order to receive medication, which removes the symptoms of illness. From a young age, we are negatively reinforced to seek help from a parent, pharmacist, or medical professional in order to remove symptoms of illness, and therefore symptoms of illness become the antecedent cue for the behavior of seeking help. The consequences of a given behavior both influence the likelihood that behavior will happen again and the ability of an antecedent cue to result in a given behavior in the future.

## Contingent Consequences

Operant conditioning is the most effective when consequences immediately follow the behavior or are directly related to the behavior and the association between the behavior and consequence can be detected by the individual, i.e., the consequences are contingent. For example, the immediate removal of intense pain after moving your hand off a hot surface negatively reinforces this behavior as there is an immediate and direct link between the behavior and the consequence. However, while the behavior of quitting smoking is negatively reinforced by improving health, an individual may not see immediate removal of related health issues such as coughs and shortness of breath. Despite this the long-term health improvements are negatively reinforcing as they are a contingent consequence detectable by the individual. Generally, consequences not related to the behavior but immediately following will not affect the frequency of the behavior as the individual may be aware the two are not associated, i.e., winning the lottery directly after quitting smoking is not going to positively reinforce the behavior of not smoking, as the individual can detect the two are not related.

## Negative Reinforcement and Punishment

Punishment works in the opposite direction to reinforcement. It involves a negative consequence following a behavior, reducing the frequency at which the behavior occurs over time. Many behaviors are learned via a combination of both reinforcement and punishment. For example, the behavior of driving at a speed above the limit is positively punished by the addition of a fine or negatively punished via the removal of a driving license. This addition of negative stimuli, or removal of positive stimuli, as a result of the behavior of driving above the speed limit reduces the probability the individual will repeat the behavior in the future. Equally, the behavior of driving below the speed limit is negatively reinforced by the consequence of not receiving a fine, and thus the individual is more likely to repeat the behavior of adhering to the speed limit in the future. Punishment often occurs alongside negative reinforcement. Negative consequences can both punish behaviors and cause a reduction in their frequency and result in escape and avoidance behaviors to be learned via negative reinforcement.

## Extinction and Punishment

The frequency a given behavior occurs at, as a result of positive or negative reinforcement, can reduce over time, as a result of processes such as extinction and punishment. Reinforcement increases the frequency at which a given behavior occurs and maintains that behavioral frequency. If such reinforcement is stopped, the frequency of the behavior is likely to decrease over time, and this process is known as extinction. Likewise, if an alternative behavior now results in greater reinforcement, the individual may switch to that behavior. Operant behaviors learned via negative reinforcement to avoid or escape negative stimuli can reduce in frequency should such negative stimuli no longer be present. However, avoidance behaviors learned as a result of negative reinforcement can persist long after elimination of the

negative stimuli. This is due to individuals avoiding behaviors linked to negative stimuli and therefore not learning that the negative stimuli are no longer present. Punishment usually works faster than extinction in reducing the frequency of a behavior, especially if the punishment is strong and not counteracted by reinforcement. Likewise, punished behaviors can recover (increase in frequency) once punishment ceases, and the rate at which this occurs is linked to the severity of punishment, with milder punishment linked to quicker recovery. If both punishment and reinforcement are acting on a behavior, the cost-benefit ratio, and frequency of each, affects the outcome on the behavior. An alternate behavior may be switched to if it offers a more favorable cost-benefit ratio.

## Conclusion

Negative reinforcement is an effective way to alter the frequency an individual exhibits a behavior and is naturally encountered and forms part of behavioral learning in individuals throughout their lifetime. In addition it is now actively used by scientists and captive animal professionals as a behavioral training technique to study and shape animal behaviors. Antecedent cues are important in stimulating such learned behaviors, contingent consequences essential in consequences being reinforcing, and reinforced behaviors do not persist indefinitely if reinforcement is not sustained, or behaviors are acted on by opposing forces such as punishment or more reinforcing alternatives.

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Classical Conditioning](#)
- ▶ [Conditioned Inhibition](#)
- ▶ [Conditioned Place Preference](#)
- ▶ [Delay of Reinforcement](#)
- ▶ [Free Operant Response](#)
- ▶ [Habituation](#)
- ▶ [Observational Conditioning](#)



- [Operant Chamber](#)
- [Operant Conditioning](#)
- [Partial Reinforcement Extinction Effect](#)
- [Passive Avoidance Learning](#)
- [Positive Reinforcement](#)
- [Punishment](#)
- [Reinforcement](#)
- [Schedules of Reinforcement](#)
- [Shaping](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Neighbor-Stranger Discrimination

- [Dear Enemy Effect](#)

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## Neocortex

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## Synonyms

[Isocortex](#); [Neopallium](#)

## Definition

The neocortex is a portion of the cerebral cortex found exclusively in mammals. It is a six-layered structure, broken into distinct areas, each with their own laminar appearance, connectivity, and functional properties. Its organization, accessibility, and

size (particularly in primates) have made it one of the most studied portions of the brain.

## Laminar Structure

Perhaps due to its prominence in humans, the neocortex has been the subject of extensive research for well over 100 years. As part of the cerebral cortices, the neocortex is a bilateral structure, distinct from the basal ganglia, amygdala, olfactory bulb, and hippocampus because of its extensive connectivity with the thalamus, as well as its six-layered structure. From superficial to the deep, these layers include:

- I. Molecular layer
- II. External granule cell layer
- III. External pyramidal cell layer
- IV. Internal granular cell layer
- V. Internal pyramidal cell layer
- VI. Multiform layer

These layers vary in their thickness in different parts of the neocortex, but increasingly there is evidence that all layers can be identified across the entire cortical sheet. Further, while the specific connections differ across the neocortex, these cortical layers form an essential part of a general thalamocortical circuit, with layer IV receiving thalamic input, layers II/III involved in cortical processing, and layer VI projecting back to the thalamus. Layer V projects to subcortical structures other than thalamus and more broadly allows for subthalamic cortical output.

## Areal Structure

Grossly, the neocortex is divided into the frontal, parietal, occipital, and temporal lobes, after the names of the bones of the skull covering these portions of the brain. These lobes are often associated with different functions, with the frontal lobe being involved in motor planning and execution, the parietal lobe processing somatosensory inputs, and the occipital and temporal lobes processing visual and auditory inputs, respectively.

Within each lobe, the neocortex is further divided into different cortical areas, with its own distinct laminar appearance, cortical and subcortical connectivity, and functional characteristics. The neocortex's modular structure has long been appreciated; however, the importance of differences in the laminar structure of different cortical areas as a marker for functionally different cortical areas gained prominence in 1909, when German anatomist Korbinian Brodmann published the location of 52 different areas in humans, based on observed laminar structure using the Nissl method of staining cell bodies (Garey 2006). Today, the exact number of cortical areas can vary greatly, depending on the species being investigated, and sometimes, the scientist being asked. However, the smallest mammals, with the simplest brains, are generally agreed to have at least 15 distinct cortical areas, while humans are thought to have over 200 (Kaas 2017).

## Sensory Areas

Each sensory modality represented in the neocortex has a primary sensory area, along with numerous secondary, or association areas. Primary sensory areas (including primary visual, auditory, and somatosensory cortex) form the most distinct laminar boundaries with the surrounding cortex, due to the density of thalamic inputs to layer IV. Generally, these primary sensory areas represent the sensory environment of the contralateral side of the body, with highly organized topographic representations of sensory space.

Primary somatosensory cortex (in the parietal lobe) represents the contralateral body surface, with the head and face represented laterally, and the legs and (when applicable) tail represented medially. This topographic representation of the body is referred to as a somatotopic representation. Importantly, adjacent parts of the body are represented next to each other in cortex. Ecologically important portions of the body often show cortical magnification, with a greater portion of the somatotopic representation taken up by these body parts compared to other, less ecologically important body parts. In humans, the hands, as

well as oral structures, show cortical magnification, reflective of the ecological importance of tool use and language production. Rodents, including rats and mice, show cortical magnification of the whiskers, as these species primarily use their whiskers to interact with the environment.

Primary visual cortex (in the occipital lobe) represents the contralateral visual field, displaying a form of topography referred to as retinotopy. Just like the adjacent parts of the skin being represented next to each other in primary somatosensory cortex, adjacent parts of the retina are represented next to each other in primary visual cortex. Further, ecologically relevant parts of the retina show cortical magnification in primary visual cortex, with primates and humans showing extensive cortical magnification of the central part of the visual field, called the fovea. In contrast, prey animals (such as antelope) often show cortical magnification of the entire horizon (called a visual streak), rather than a single point, reflecting the need to use vision to detect predators across the whole visual field.

Primary auditory cortex (in the temporal lobe) represents the auditory sensory environment by frequency, thus primary auditory cortex is said to contain a tonotopic representation. Frequency ranges represented vary by species and, like the somatosensory and visual systems, display cortical magnification of important frequency ranges.

Secondary sensory areas (also called association areas) are often conceptualized as part of a hierarchy of sensory processing. Unlike primary sensory areas, topographic representations in these areas are often more abstract and are not always complete. Additionally, association areas often show various degrees of multimodal sensory processing, with neurons in these areas maximally responding to simultaneous presentations across multiple modalities.

## Motor Areas

Primary motor cortex (in the frontal lobe) is located immediately rostral to primary

somatosensory cortex. Originally identified by intercortical microstimulation experiments at the end of the nineteenth century, it is the region of cortex where electrical stimulation, using a relatively small amount of electrical current, results in movements of muscles on the contralateral side of the body. Broadly, it is organized using a similar form of somatotopy as somatosensory cortex; however, unlike primary somatosensory cortex, this somatotopy is not present on a fine scale. Motor cortex is also called agranular cortex, because it was long thought to lack the inner granular layer (layer IV, the thalamic recipient layer). More recent work suggests that primary motor cortex, like the rest of the neocortex, does have all six cortical layers (Yamawaki et al. 2014); however, layer IV is more difficult to identify with classical methods, such as a Nissl stain.

Layer V of motor cortex contains Betz cells, the largest neurons in the neocortex. The axons of these neurons project down to the spinal cord, synapsing directly onto anterior horn cells, and forming the corticospinal tract. These neurons are thought to be responsible for the direct motor output of primary motor cortex, and are the neurons that, when activated electrically via intracortical microstimulation, cause movement. Betz cells are involved in producing dexterous movements, particularly in the arm and digits, and damage to the corticospinal tract produces a permanent deficit in these types of movements. However, lesions to motor cortex, particularly in nonprimates, do not result in paralysis but instead produce motor learning deficits, with previously learned movement patterns remaining intact. This hints at a second, but arguably equally important role of motor cortex, in directing motor learning of subcortical motor centers (Peters et al. 2017).

Anterior to motor cortex exists a large region of cortex termed prefrontal cortex. This region of the brain greatly expanded in primates, especially humans. Involved in motor planning and executive control, the exact function of many prefrontal areas has been difficult to determine. Having expanded so rapidly in human evolution, homologies with other, particularly nonprimate species, are difficult.

## Cross-References

- [Auditory Processing and Perception](#)
- [Entorhinal Cortex](#)
- [Parahippocampal Cortex \(PHC\)](#)
- [Primary Somatosensory Cortex](#)

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## Neopallium

- [Neocortex](#)

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## Neophobia

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## Definition

Neophobia is the fear of the novel (neo = new, phobia = fear).

## Introduction

Neophobia elicits avoidance of novelty and protects an organism from danger. An organism

categorizes something as novel when it deviates from an innate template or what it has experienced before (Greenberg and Mettke-Hofmann 2001). Novelty can include unfamiliar space, situations, organisms (conspecific and heterospecific such as novel predators and prey), food, fluids, items, etc. Neophobia varies with the degree of novelty and organisms show more avoidance reaction the more the currently experienced deviates from what they know (Greenberg and Mettke-Hofmann 2001). However, repeated exposure to the same stimulus without negative consequences results in habituation or attenuation of neophobia (Ramos 2015) and either disregard of the formerly novel stimulus or finally approach and investigation (neophilia – attraction to novelty) to learn about the stimulus.

Several brain areas are involved in neophobia reactions though this is an active area of research; one of the main areas involved is the amygdala which is responsible for emotional reactions such as fear, whereas the perirhinal cortex and ventro medial prefrontal cortex (in mammals) are important in detecting novelty (Ramos 2015; Burns et al. 1996). The hippocampus, particularly the ventral subiculum, is another area involved in neophobia and often linked to spatial neophobia. The amygdala, hippocampus, and prefrontal cortex all communicate novelty to the nucleus accumbens (Burns et al. 1996).

Neophobia often has a genetic component and species differ in their avoidance reactions which have evolved over evolutionary times in interaction with their environment. However, experience also affects neophobia and the avoidance response expressed results from an interaction of genes and environment in most cases.

### Types of Neophobia and Brain Areas Involved in Neophobia

The distinction between novel versus familiar is a fundamental process in categorizing the environment and items therein. However, the context in which novelty is encountered seems to matter. For example, rooks (*Corvus frugilegus*) show year-round consistently high neophobia toward novel objects presented near familiar food. In contrast,

neophobia toward unfamiliar humans (which may be perceived as a predator) standing beside familiar food decreased during the breeding season maybe due to higher energy demands during this period resulting in higher risk-taking. This indicates that different mechanisms are underlying these two types of neophobia (Greggor et al. 2016). The notion that context is important is supported by brain studies as lesions to specific brain areas affect some types of neophobia but not others (Walker and Winn 2007; Burns et al. 1996). Moreover, different brain areas seem to be involved in the initial avoidance reaction and the process of attenuation during repeated presentation (e.g., Ramos 2015).

Overall, how organisms categorize novelty is an active area of research. From an evolutionary point of view, different selection pressures may act on different types of novelty. Miscategorizing food or predators can have catastrophic effects, whereas unfamiliar habitats or objects may have less drastic consequences.

**Food neophobia** is possibly one of the most researched types of novelty reactions and important in identifying how new resources are incorporated into a species' diet. It also links to eating disorders in humans – a highly researched area at the moment. When encountering unfamiliar food, animals initially try small quantities and wait for any negative digestive consequences. When there are none, they start incorporating more of the novel food. In experimental testing, familiar and novel food are presented simultaneously and the time to approach each and the amount eaten is compared. Food neophobia is closely linked to dietary conservatism – the refusal to incorporate palatable food into its own diet even after thorough investigation. While neophobia describes the initial avoidance of unfamiliar food due to its novelty, dietary conservatism refers to the time it takes to fully incorporate the food into the diet which can take months in some cases (Marples et al. 2007). Likewise, **taste neophobia** extends to the avoidance of fluids and is investigated the same way as food neophobia.

**Object neophobia** is another well-researched area and can be linked to how animals respond to changes in their environment. In an increasingly faster changing world due to global warming and

human activities, the ability of an organism to respond to environmental change is critical for population development and provides important information for conservationists how a species may fare in the future (Mettke-Hofmann 2017). To test object neophobia, a novel object is often presented besides familiar food and the animal is in conflict between the motivation to feed and the motivation to avoid the novel object. The time to start eating with and without the novel object is measured with the difference between the two representing the strength of the neophobia reaction (Mettke-Hofmann et al. 2002). Alternatively, food is substituted with a resource regularly visited such as nest boxes, water holes, etc. Repeated presentation leads to attenuation of neophobia and latencies to approach with objects converge with latencies without objects. Consequently, the novel object is either ignored or individuals start exploring the novel object.

**Spatial neophobia** represents the avoidance of unfamiliar areas and can be linked to the willingness of an animal to venture into unfamiliar habitats, range expansion, and invasion. However, it should be mentioned that the decision to enter and explore an unfamiliar environment is driven by spatial neophilia: the attraction to novelty that leads to approach and exploration of an unfamiliar environment (Mettke-Hofmann et al. 2009). Experimentally, spatial neophobia is often measured as the proportion of time spent in open (dangerous) versus closed (safe) arms of a T-maze or in the center of an open arena in rodents (Walker and Winn 2007). In birds, spatial neophobia has also been measured as the frequency of approach attempts to the novel environment from a familiar cage representing the conflict between the motivation to enter and explore the novel environment and the motivation to avoid the novel environment (Mettke-Hofmann et al. 2009).

**Neophobic predator avoidance** is a relatively new research area and specifically investigates how organisms respond to new predators. Misidentifying an unfamiliar species can result in death when encountering a predator and neophobia toward unfamiliar species can reduce this risk (Brown et al. 2016). Neophobic predator

avoidance is investigated by presenting the study species with unfamiliar species which can be other predators or nonpredatory species (control) or extracts of such species, e.g., odor or vocalization and measuring the duration of freezing, reduced activity, or time to resume feeding before and after the presentation of the stimulus.

## Ecology Shapes Neophobia

As outlined above, neophobia often has a genetic component meaning that selection can act on neophobia. While neophobia protects an organism from danger, it also prevents access to possibly useful resources such as food or other habitats. Extreme neophobia while safe would not be advantageous for an organism and selection may act on balancing costs and benefits of neophobia resulting in different degrees of neophobia between species.

Different hypotheses have been brought forward to explain neophobia reactions. The neophobia threshold hypothesis (NTH) states that experiences made during early life are later protected by neophobia (Greenberg 2003). Few early experiences result in increased neophobia later in life, whereas ample early experiences would lead to lower neophobia reactions as many situations are already known. The NTH has been confirmed in wild-caught generalist and specialist species; habitat and diet generalist species showed lower object neophobia by feeding earlier from familiar food presented in novel objects or microhabitats than closely related habitat and diet specialists (Greenberg 2003). The generalists had gained more experience with a variety of situations during young age than the specialists. Strong food neophobia has also been shown in snail kites (*Rostrhamus sociabilis*) which are extreme dietary specialists (Beissinger et al. 1994).

Another hypothesis linked to neophobia is the dangerous niche hypothesis (DNH) which predicts that animals exposed to dangerous environments are more cautious, i.e., neophobic, than animals living in a safer environment (Greenberg 2003). Support for this hypothesis comes again from comparing specialists and



generalists. In this case, hand-raised diet and habitat generalists showed more object neophobia than specialists, possibly as a consequence of the former expecting to encounter dangerous situations more often (Greenberg 2003). As hand-raised individuals were used in Greenberg (2003), intrinsic neophobia was measured as opposed to functional neophobia as in the example provided for the NTH.

Movement patterns – being year-round resident or conducting seasonal migrations – also affects object neophobia with residents being less neophobic toward novel objects placed around familiar feeding locations compared to migrants. Residents are possibly more familiar with local risks and can categorize the risk around novel objects faster than migrants that only spend a few months on the winter ground (Mettke-Hofmann et al. 2013). In contrast, migrants have been found to show less spatial neophobia than residents in concordance with the migrant-neophobia hypothesis which predicts a higher willingness and lower hesitation of migrants to enter unfamiliar environments. This helps during migration when encountering many unfamiliar habitats (Mettke-Hofmann et al. 2009).

Neophobia has also been shown to differ along an urbanization gradient but with conflicting results; in some studies, urban birds displayed less object neophobia than suburban birds, whereas in other studies, urban birds showed more object neophobia even though experimental setups were similar with placing novel objects besides familiar feeders.

Finally, food neophobia has been linked to invasion history in house sparrows (*Passer domesticus*) with actively invading populations showing lower neophobia toward novel food than established populations (Martin and Fitzgerald 2005).

## Experience Changes Neophobic Reactions

While neophobia often has a genetic component, animals develop in a given environment which results in gene–environment interactions and

the behavioral output is a mixture of both. Evolutionary this makes sense as some species may generally live in more dangerous environments, hence having a genetic predisposition to be more neophobic. However, at the same time, danger may vary between locations or change between generations. The ability to adapt neophobic reactions to such variation on the individual level is advantageous. A variety of studies on fish and amphibians have demonstrated that variation in predation risk (either naturally or experimentally induced) affects neophobic responses in different populations of the same species. Individuals from high predation backgrounds often express a heightened predator avoidance response toward any novel odor (whether from a predator or nonpredator) and also show spatial neophobia, i.e., take longer to enter an unfamiliar environment. In contrast, individuals from low predation backgrounds often do not avoid novel odors at all and enter novel environments quickly (e.g., Brown et al. 2013). For individuals living under high-predation regimes, neophobic predator avoidance reduces encounter rates and improves survival. Such predator avoidance can be rapidly induced experimentally but also fades when predation risk decreases providing a flexible mechanism to respond to local predation (Chivers et al. 2016). Brown et al. (2013) expanded the dangerous niche hypothesis (see above) to this phenotypic plasticity in neophobic predator avoidance that allows context-specific expression of neophobia toward predators. Under high predation risk, neophobia provides maximum protection, whereas under low risk, exploitation of new resources is not compromised.

However, predators also express neophobic responses when encountering unfamiliar prey (food neophobia). Mutations are often avoided by predators even when they stick out due to their oddity, i.e., novelty. This gives mutations an advantage and increases their abundance which eventually reduces their novelty effect. Over time, predators learn that this unusual prey is not dangerous and predation on them increases. It is assumed that the evolution of aposematic prey is based on initial neophobia reactions which are then maintained by toxicity

(Thomas et al. 2003). Interestingly, studies in several bird species ranging from chickens (*Gallus domesticus*) to hand-reared songbirds have shown that positive experience with novel prey (different color) can dramatically reduce neophobic reactions toward novel food even when the novel food also differs in shape and size indicating generalization (Adamova-Jezova et al. 2016). However, it is unclear whether such generalization would also happen in wild individuals which may have encountered already noxious prey.

Developmental conditions also affect neophobia reactions. Birds raised in barren environments show greater object neophobia when combined with familiar food than birds raised in enriched environments (Greenberg and Mettke-Hofmann 2001) and pigs (*Sus scrofa domesticus*) from barren environments show stronger food neophobia (Oostindjer et al. 2011). Neophobia also follows a developmental curve in many species including humans with high neophobia early in life, lower neophobia as adults, and again increasing neophobia at the end of the lifetime (Ray and Hansen 2005). The initial high neophobia may be due to their vulnerability but also inexperience resulting in most situations being novel. As an organism grows, it accumulates knowledge and it may also be in its best body condition favoring the reduction of neophobia. While knowledge further accumulates as an organism ages, body condition may deteriorate leading to higher neophobia again. Such age effects are known for object, food, and spatial neophobia in a range of species (e.g., Ray and Hansen 2005).

The social environment possibly not surprising affects neophobia responses. Animals are often less neophobic in the presence of conspecifics and are more likely to test novel food (Oostindjer et al. 2011). This may be due to social facilitation (even though other group members may eat familiar food), protection from other dangers due to the group which allows focusing on the novel food or competition to get access to a possibly new resource first. The latter is supported by findings that subordinate individuals often show less food and object neophobia which allows

them exploiting new resources before they are displaced by dominant individuals (An et al. 2011). Moreover, group size itself affects neophobic reactions with lower object neophobia in larger groups (Mettke-Hofmann et al. 2013).

## Neophobia as Part of Personality

In recent years, research has accumulated ample evidence that individuals differ consistently and predictably in their reaction to environmental challenges; this is often referred to as animal personality. This means that animals are consistent over time, i.e., when tested at time point A and respond in a particular way, they will do so again when retested at time point B. Furthermore, behaviors are often correlated with each other and form behavioral syndromes. Neophobia is often part of personality and linked to the neuroticism dimension in the human big-five personality scale. This means that individuals across the animal kingdom express different degrees of neophobia and do so consistently. It is important to mention that such behavioral polymorphism (e.g., more or less neophobic individuals) requires equal fitness to persist over evolutionary times. Different behavioral types can persist in a population due to occupying microniches, the existence of temporal environmental variation favoring different types or morphological/physiological differences between individuals. Most of the neophobia tests used in conjunction with personality have tested for object neophobia. An exception is the study by Bokony et al. (2012) who showed that object and food neophobia were correlated on the individual level, whereas predator response measured as the time to feed when a predator model is shown was not correlated with the former. Therefore, object and food neophobia formed a behavioral syndrome with those individuals approaching the novel objects quickly, also sampling the novel food quickly. These behavioral differences were consistent over time. Spatial neophobia has been shown to be consistent over time in laboratory rats though juveniles, and mature adults were more neophobic to enter a novel and open area than young adults (relative

consistency; Ray and Hansen 2005). Neophobia is often investigated together with neophilia and exploration. Neophilia is the motivation to approach and investigate novelty and exploration is usually the behavior that results from this motivation. Neophobia and neophilia are two independent motivations (Mettke-Hofmann et al. 2002) and can occur in four combinations in an organism: (a) high neophobia coupled with low neophilia resulting in not approaching novelty due to high fear; (b) low neophobia coupled with high neophilia resulting in fast approach of novelty and little neophobia; (c) high neophobia coupled with high neophilia resulting in ambivalent approach and avoidance behavior; and (d) low neophobia coupled with low neophilia resulting in no approach due to lack of interest in the novelty despite low neophobia (two-factor model; Greenberg and Mettke-Hofmann 2001). With respect to personality, some studies find positive correlations between object neophobia and object exploration (approaching a novel object at a neutral location in the cage), i.e., individuals that start foraging beside a novel object fast also approach and investigate a novel object quickly (Miranda et al. 2013), whereas other studies find a negative relationship with individuals that hesitate long to feed besides a novel object approach a novel object at a neutral location fast. This latter case can be interpreted as generally responding to novelty strongly but depending on the situation with different reactions (Mettke-Hofmann et al. 2005). Finally, some studies do not find a relationship between neophobia and neophilia. Neophobia has also been linked to reproductive success with breeding pairs responding neophobic to objects attached to their nest box having fewer successful nests and lower survival of females. Such pairs also showed less mobbing behavior toward predators (Vrublevaska et al. 2014).

## Neophobia and Cognition

Neophobia can be seen as one of the first steps in the sequence of cognitive processes after a stimulus has been perceived. Due to its function of protecting individuals from danger and keeping

organisms away from novelty, it can have far reaching consequences how animals interact, learn, and incorporate novelty into their repertoire. Eventually, neophobia can affect an organism's ability to adapt to environmental change. The consideration of neophobia in learning processes is relatively new but has been shown to considerably affect learning. For example, object neophobia often delays problem-solving as a neophobic animal interacts less with a novel item (Sol et al. 2011). While this is interesting in its own right, neophobia may overshadow differences in problem-solving ability further down the line such as the ability to combine behaviors in a new way. To exclude neophobia as a factor affecting problem-solving abilities, the focal animal first has to be made familiar with the test apparatus before setting up the problem-solving task. For instance, when an animal is tested on its ability to find a way to get access to hidden food, then it should be habituated to the apparatus which will later hide the food. This way neophobia can be excluded and, e.g., learning speed be compared between groups of animals. However, neophobia is not always correlated with problem-solving ability as some studies find higher problem-solving abilities in highly neophobic animals (Audet et al. 2015). Moreover, contrasting results have been found regarding a relationship between neophobia and different types of learning. While neophobia and associative learning (i.e., the initial acquisition of a task) are often unrelated, there is increasing evidence that reversal learning is negatively related to object neophobia with more neophobic individuals reversing learning faster (Guido et al. 2017).

A mechanism to overcome neophobia is social learning by which an animal observes others in unfamiliar situations. This is a powerful and save way to accumulate information about a novel possibly dangerous situation. However, from whom is learned and the type of neophobia concerned matters. Social learning about unfamiliar food is widespread in the animal kingdom and particularly important for young inexperienced individuals. Many organisms learn from their mother which food is safe. In social species such as pigs, food neophobia in young individuals is

reduced by observing other familiar group members but not unfamiliar ones (Figueroa et al. 2013). However, adult individuals also use social learning to assess unfamiliar situations but with interesting differences. Wild jackdaws (*Corvus monedula*) were more likely to use social information to overcome food neophobia and did so throughout the year, whereas they used social information to overcome object neophobia only during the breeding season (Greggor et al. 2016).

There is ample evidence of generalization processes with neophobia reactions. Positive experience with novel food is often generalized toward other novel food regarding a similar stimulus. Individuals of a range of species that have learnt about the palatability of a food of a particular color often readily accept similar food of a different color indicating generalization with the result of no or very low neophobia (Adamova-Jezova et al. 2016). The same is true for odors. For some species, this can even be extended to novel food that not only differs in the specific stimulus but additionally may have a different shape. Negative experience with novel food also leads to generalization but with an increase in neophobia toward novel food. Generalization of neophobic predator responses has been observed to occur across modalities. Fish from high predation backgrounds experienced with a chemical or visual predator cue generalized their neophobic response to any new stimulus whether chemical or visual (Brown et al. 2016). Generally, irrespective whether food or predator neophobia is involved, generalization is more likely to occur the more similar a novel item is to what has been experienced before. Tadpoles familiar with a predator cue (odor) of a particular predator generalized their neophobia response toward closely related predator cues (via odor) and avoided these new predators, but they did not produce a neophobia response to distantly related predator or nonpredator cues (Chivers et al. 2016).

Finally, with repeated exposure to the same new stimulus without negative consequences, neophobia changes over time, termed habituation or attenuation. Examples have been provided above in various sections for food and object neophobia that eventually leads to approach and

sampling of the novel food in case of food neophobia or approach and continuation with other activities close-by, e.g., eating familiar food or entering nest boxes in case of object neophobia. However, prolonged absence of the now familiar food or object reinstates the initial neophobic reaction. Examples in birds show that object neophobia is fully reinstalled after a period of 1 month, whereas in tadpoles, predator neophobia wanes after a few days when kept in low-predator regimes.

## Conclusion

Neophobia is an important mechanism to protect organisms from danger and has far-reaching consequences how animals interact with unfamiliar situations. It differs between species as an adaptation to the riskiness of the environment and can also be modulated via learning according to local risks. Neophobia is context-specific and different brain areas are involved in different types of neophobia. Neophobia is often considered a personality trait and as such often consistent within individuals but at the same time differs between individuals and can form behavioral syndromes with other behavioral traits. Finally, neophobia affects cognitive processes how organisms learn about their environment which can affect their ability to respond to environmental change.

## Cross-References

- ▶ [Amygdala](#)
- ▶ [Aposematism](#)
- ▶ [Avoidance](#)
- ▶ [Categorization](#)
- ▶ [Escape Response](#)
- ▶ [Familiarity](#)
- ▶ [Fear Response](#)
- ▶ [Novelty](#)
- ▶ [Open-Field Test](#)
- ▶ [Taste Aversions](#)
- ▶ [Tonic Immobility](#)
- ▶ [Xenophobia](#)

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## Neoteny

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## Synonyms

Juvenilization; Paedomorphism; Paedomorphosis

## Definition

Neoteny is the deceleration of the rate of somatic development, resulting in paedomorphism (or paedomorphosis).

Neoteny is the deceleration of the rate of somatic development, resulting in paedomorphism (or paedomorphosis). Paedomorphism is a form of heterochrony characterized by the retention of ancestral juvenile traits in descendent adults (McNamara, 2012). Paedomorphism can be the result of neoteny or progenesis (acceleration of sexual development) and it is important to distinguish whether apparently juvenile reproduction is better explained by neoteny or progenesis. The term “neoteny” was introduced by German zoologist Julius Kollmann (1885) to describe the retardation of physiological development in species of amphibians that results in the retention of larval traits in sexually mature adults (Gould, 1977). In neotenic animals, growth and sexual maturation progress but with certain arrests in physiological development.

Neoteny is arguably demonstrated in many modern animals such as species of gobies, termites, mayflies, cicadas, crustaceans, jellyfish, and the Mexican axolotl (*Ambystoma mexicanum*) (Skulachev et al., 2017). An axolotl is an aquatic salamander that retains its gills and remains in water throughout its life. Most salamanders have an aquatic larval stage and emerge from the water as metamorphosed terrestrial adults capable of reproduction and with lungs instead of gills, whereas axolotls reproduce while exhibiting features characteristic of juvenile salamanders (Ridley, 2003). The age at which an axolotl reproduces is not abnormally early for a salamander, suggesting that axolotl age of reproduction remained consistent with non-neotenic salamanders while somatic development slowed down – evidencing neoteny rather than progenesis (Ridley, 2003). Other amphibians display features of neoteny similar to the Mexican axolotl, including the olm (*Proteus anguinus*) and the American mudpuppy (*Necturus maculosus*); however, debate is ongoing as to whether these features are the result of neoteny, progenesis, or both (Wakahara, 1996). Similarly, research has not yet identified the mechanistic basis of neoteny in axolotls, and outstanding questions remain about the functions of variations in salamander life history strategies (Crown et al., 2019).

Although the etiology and function of neoteny in axolotls remains unclear, research indicates that neoteny evolved in various nonhuman animals to facilitate coexistence with humans as a result of artificial selection. Neoteny is a feature of the domestication syndrome, and many neotenic mammals are domesticated. Common physical and behavioral traits of domestication in mammals (and animals, more generally) were identified by Darwin (1868) and include reduction of body mass, shortening of the face, smaller tooth size, reduced sexual dimorphism because of feminization, and reduced skull volume (Wrangham, 2019). Humans have selectively bred animals for docility, and Belyaev (1969) demonstrated that selection for lowered propensity for aggression in foxes produced a suite of phenotypic traits characteristic of neoteny and domestication syndrome such as smaller jaws, skulls, and teeth

(Wrangham, 2019). Exemplary features of neoteny visible in many domesticated mammals are thus the unintended downstream consequence of artificial selection for docility. Animals such as dogs, cats, fancy rats, hamsters, ferrets, and rabbits exhibit neoteny related to the domestication syndrome produced by selective breeding by humans. Natural selection presumably contributed to the development of the domestication syndrome and neoteny in these species since coexistence with humans affords survival and reproductive benefits, such as access to human food and shelter.

Bonobos also demonstrate neoteny related to the domestication syndrome, likely a result of sexual selection. Bonobos evolved from a shared ancestor with chimpanzees between one million and 1.8 million years ago and, despite many shared features, appear to demonstrate the domestication syndrome whereas chimpanzees do not (Wrangham, 2019). Adult bonobos exhibit physical and behavioral similarities to juvenile chimpanzees, suggesting that bonobo development is delayed or occurs at a slower pace than in chimpanzees. Compared to adult chimpanzees, sexually mature bonobos have thinner limb bones, smaller teeth, and narrower faces (Wrangham, 2019). Bonobo females do not face the feeding competition from gorillas that chimpanzee females face and are therefore able to form alliances with other females to dominate an aggressive male and prevent sexual coercion. Female chimpanzees are routinely subject to sexual coercion and unprovoked attacks apparently related to male control of food sharing (Wrangham, 2019). Female alliances facilitate female mate choice, which appears to be the mechanism by which bonobos self-domesticated. Throughout bonobo evolutionary history, females apparently chose to mate with males exhibiting lowered aggression, leading to the unintended downstream consequence of neoteny.

There is strong evidence that humans exhibit neoteny. When a human is sexually mature, it has the bulbous cranium, small jaw, and flat face of a developmentally immature ancestor (Bogin, 1999). Compared to other primates, adult humans demonstrate neotenous traits such as a lack of

body hair, central position of the foramen magnum (which migrates backward in most other primates), a high relative brain weight, persistence of cranial structures to an advanced age, absence of brow ridges, thin skull bones, small teeth, later eruption of teeth, lactose tolerance into adulthood, and no rotation of the big toe (Skulachev et al., 2017). Other neotenous features in humans include the form of the pelvis, the labia majora in females, prolonged growth, prolonged infant dependency, a long lifespan, and short extremities relative to body size (Skulachev et al., 2017). *Homo sapiens* reaches sexual maturity at a later age than ancestral humans, demonstrating neoteny rather than progenesis (Bogin, 1999). Studies have reported that neotenous features illicit more help, render babies cute, and that neotenized female faces are more attractive (Jones, 1995; McArthur & Berry, 1987; Montagu, 1989). The role of neoteny in human ontogeny and phylogeny is a rich area of research that has produced a wide array of theories and findings.

## Cross-References

- ▶ [Adolescence](#)
- ▶ [Artificial Selection](#)
- ▶ [Coevolution](#)
- ▶ [Common Ancestor](#)
- ▶ [Developmental Arrest](#)
- ▶ [Domestication](#)
- ▶ [Domestication Hypothesis](#)
- ▶ [Domestication Syndrome](#)
- ▶ [Female Choice](#)
- ▶ [Hominid](#)
- ▶ [Homo Sapiens](#)
- ▶ [Human-Animal Interaction](#)
- ▶ [Husbandry](#)
- ▶ [Life History](#)
- ▶ [Natural Selection](#)
- ▶ [Parenting](#)
- ▶ [Pets](#)
- ▶ [Phenotype](#)
- ▶ [Phylogeny](#)
- ▶ [Primates](#)
- ▶ [Richard Wrangham](#)
- ▶ [Self-Domestication Hypothesis](#)

- Sexual Dimorphism
- Sexual Selection
- Species

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## Neruoeneration

- Neurogenesis

## Nerve Cell

- Neuron

## Nerve Cells

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## Synonyms

Neurons

## Definition

Basic structural and functional unit of the nervous system.

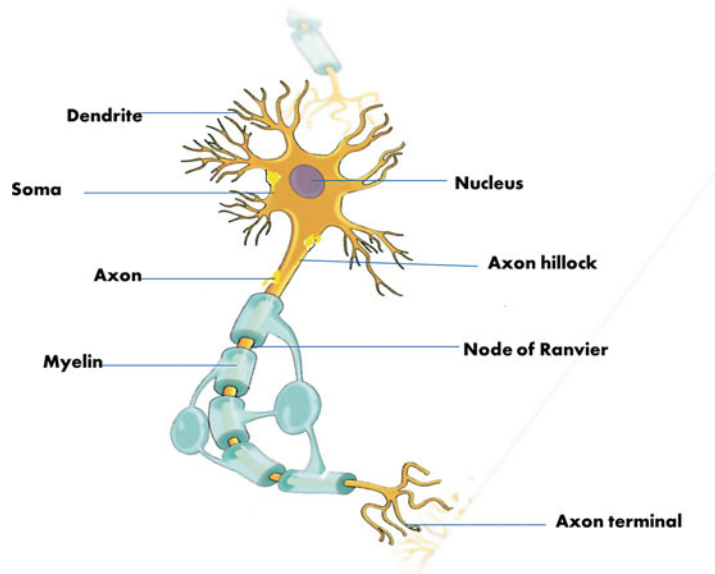
## Introduction

Nerve cells or neurons are the signaling cells of the nervous system. They are involved in the generation of action potential and transmission of nerve impulses across the whole length of the body. Nerve cells are considered as the longest and oldest cell in one's body. Glial cells are the other cells (non-neuronal cells) in our brain, which provide support and protection to these nerve cells (Ganong 2005).

## General Structure

Nerve cells contain all the organelles of a general animal cell (like a nucleus, cell membrane, ribosomes, endoplasmic reticulum, Golgi apparatus, mitochondria, etc.). However, the specialized function of electrochemical signaling in nerve cells is provided by the presence of dendrites and axon, attached to the soma (or cell body)

**Nerve Cells, Fig. 1** Nerve cell (Image adapted from: [https://cnx.org/contents/GFy\\_h8cu@9.87:c9j4p0aj@3/Neurons-and-Glial-Cells](https://cnx.org/contents/GFy_h8cu@9.87:c9j4p0aj@3/Neurons-and-Glial-Cells))



(Fig. 1). The cell body in human nervous system can measure from 10–100 micrometers in diameter. Dendrites are thin and short branch-like structures, whereas axon forms a long tail-like structure which originates from the soma at a swelled point known as axon hillock. Axon is covered by a protecting covering of myelin sheath, which is secreted by Schwann cells (a type of glial cell). Axon ends in numerous small terminal buttons. Nerve impulse moves from axon terminals of one neuron to the dendrite of another neuron via synapse (Baars and Gage 2010).

## Functions of Nerve Cells

Main function of nerve cell is to relay electrochemical signal from/to other cells in the body. The generation of action potential across the membrane of nerve cell is interplay of concentration gradient of sodium and potassium ions inside and outside of the cell. (For more information, see “► Neural Impulse”). The general nerve cells send its signal by firing spikes from the cell body down to the axon to the terminal buttons. At the terminals, neurotransmitter is released from this nerve cell (presynaptic neuron) at synapse to trigger a

postsynaptic potential in the next nerve cell (postsynaptic neuron) (Fig. 1) (de Robertis and de Robertis 2001). The connections of nerve cells and their pattern of interactions with each other are the major study points in cognitive neuroscience.

## Classification of Nerve Cells

Nerve cells have a great variety of shapes, branching patterns, and synapses. They can be classified into different ways:

- (a) On the basis of polarity:
  - (i) **Unipolar**: Axon or dendrite (either of them) emerges from the soma
  - (ii) **Pseudo unipolar**: Axon and dendrite emerge from the same side of soma
  - (iii) **Bipolar**: Axon and dendrite emerge from the opposite ends of soma
  - (iv) **Multipolar**: One axon and many dendrites emerge from the opposite ends of soma
- (b) On the basis of direction of neurotransmission:
  - (i) **Sensory**: conduct neurotransmission from tissues/organs to the brain, also known as afferent neurons

- (ii) **Motor:** conduct neurotransmission from brain to the tissues/organs, also known as efferent neurons
- (iii) **Association:** Nerve cells which connects sensory and motor neurons, also known as interneurons
- (c) On the basis of their firing pattern:
  - (i) **Tonic:** constantly active in discharge pattern
  - (ii) **Phasic:** fire in bursts or phase
  - (iii) **Fast:** rapidly fire with a fast rate
- (d) On the basis of their neurotransmitter:
  - (i) **Glutamatergic:** produce glutamate
  - (ii) **GABAergic:** produce gamma amino butyric acid
  - (iii) **Cholinergic:** produce acetylcholine
  - (iv) **Dopaminergic:** produce dopamine
  - (v) **Serotonergic:** produce serotonin
- (e) On the basis of myelination:
  - (i) **Myelinated:** axon is covered by myelin sheath
  - (ii) **Nonmyelinated:** axon is not covered by myelin sheath

## Cross-References

- [Action Potentials](#)
- [Afferent and Efferent Impulses](#)
- [Axon](#)
- [Cell Membrane](#)
- [Neural Impulse](#)
- [Neuron](#)
- [Neurotransmitters](#)

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## Nerve Fiber

- [Axon](#)
- [Dendrites](#)

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## Nervous System

- [Nervous System of Invertebrates](#)
- [Vertebrate Nervous System](#)

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## Nervous System Function

- [Serotonin](#)

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## Nervous System of Invertebrates

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## Synonyms

[Brain; Nervous System](#)

## Neurons and the Nervous System

Neurons or nerve cells feature specialized *elongated structures* that allow for high speed



(up to 100 m/s or 223 mph) transmission of signals via electrical impulses (action potentials) from receptor sites or other neurons to effectors or other neurons (Ramon y Cajal 1906). These elongated structures (or processes) are known as dendrites (branched structures) and axons (long fibers some of them can extend along the length of the body), together called neurites. The Nervous System (NS) is an organized network of neurons that transmit signals between different parts of the body to generate adaptive responses. In many animal NSs, neurons are accompanied by a specialized class of cells, called glia. Glial cells support and protect neurons, in addition to wrapping processes of their own in a sheath-like manner around neurites for insulation and better propagation of action potentials. NSs can be found in all animals except the placozoa and porifera phyla, which lack neurons.

In early evolved animals, neurons form diffuse networks, referred to as nerve nets, mainly associated with the body wall. In some of these animals, neurons tend to be clustered around sensory structures and the sites of higher physiological activity – forming round shape neuronal conglomerations referred to as ganglia (singular: ganglion), and elongated structures called nerve rings or nerve cords. The centralized NSs of bilaterians are likely to have evolved from such local clusters of neurons. With the rise of bilateral animals, sensory organs better coordinate the two halves of the body concentrated in the anterior end of the body (head). The brain formed around these sensory structures by concentration of ganglia involved in receiving and processing sensory input. This organization often divides the NS into two parts: the brain and the associated nerve cord extending throughout the body form the Central Nervous System (CNS), and the peripherally located sensory neurons, nerve nets, and the nerve fibers (axons) communicating between the CNS and the periphery form the Peripheral Nervous System (PNS).

## Nervous Systems of Invertebrates

Invertebrates being the most extensive and diverse group of animal life (comprising 90% of all existing animals) have evolved with a variety of NSs.

Cnidarians (hydra, sea anemones, and corals) are the earliest animals with NSs, organized as nerve nets. The cnidarian body is formed along an oral-aboral axis with two layers of tissues. The epidermal (outer) layer forms skin, while the endoderm (gastrodermis or inner layer) forms the gut, and nerve nets are sandwiched between them and form the NS (Davis 1974). This is a basiepithelial NS, separated from the interior of the animal by the epidermal basement membrane. The NS is composed of sensory and ganglion neuronal cells. They form chemical synapses with both epithelio-muscular cells and neighboring neurons – performing both sensory and motor functions, which in higher animals are performed by two different neuron types. Neurons conglomerate near the mouth, foot, and base of the tentacle. In many hydra species, sensory neurons condense at the opening of the mouth forming a nerve ring. Some cnidarians have light- and gravity-sensing organs called ocelli and statoliths respectively at the bases of marginal tentacles. They may be integrated into larger sensory organs called the rhopalialia. The ocelli contain ganglion-like clusters of light-sensitive neurons, connected by nerve tracts to the nerve rings of the bell margin, where the signals are integrated and transmitted to the motor neurons (muscles) to control the pace of swimming by muscle contraction.

The phylum Platyhelminthes (class Turbellaria) comprises unsegmented, soft-bodied flatworms, commonly known as planarians, which are phylogenetically close to cnidarians. They represent the most primitive known extant animals exhibiting a bilateral symmetric body layout common to vertebrates and many invertebrates, and an anterior concentration of sensory organs in the head (cephalization), including a pair of simple eyes. Flatworm NSs are composed of a basiepithelial nerve net which innervates the ciliated epidermis,

bilobed anterior ganglia (brain), and bilaterally symmetric nerve cords (Morita and Best 1966). The neurons forming the brain ganglia and nerve cords are separated from the epidermis by a basement membrane and concentrated within the body cavity. Their cell bodies encircle their neurites and synapses called the neuropil. The outer layer of cell bodies is called rind (in invertebrates) or cortex (vertebrates). This organization is called subepithelial NS. The cell bodies of the brain are intermingled with the neurosecretory cells and accessory cells that resemble neuroglia. The nerve fibers of the neuropil are closely packed, mostly unmyelinated, and terminate in close contact with endings of other nerve fibers to form synapses. The nerve fibers emanating from the brain are initially arranged into tracts, and then cables of parallel fibers, and extend in a caudal direction to form the longitudinal nerve cords along the length of the body. The two largest ventral nerve cords ensure rapid signal conduction from head to tail. They further extend as peripheral nerve fibers to form subepidermal and submuscular plexuses throughout the body – resembling two sides of the vertebrate spinal cord. There is a closer resemblance of these neurons to the neurons of vertebrates than to those of higher invertebrates, even though the glial sheath is absent. Planarian neurons are multipolar with a single axon, excessive dendritic branching, the presence of dendritic spines, and the predominance of chemical synapses compared to electrical ones. These features are rarely observed even in higher invertebrates but are reminiscent of the vertebrate brain. Therefore, planarians are considered a living example of the early evolutionary stages of the vertebrate brain.

Adult *Caenorhabditis elegans* hermaphrodites (phylum nematoda) are composed of exactly 959 cells, 302 of which are neurons that belong to two distinct and independent NSs known as somatic (282 neurons) and pharyngeal (20 neurons) (White et al. 1986). The somatic NS is also supported by 56 nonneuronal cells called sheath cells, socket cells, and GLR cells. These NSs communicate through a single pair of ring-pharynx interneurons. The neurons of somatic NS and their neurites are mainly positioned

between the hypodermis and the hypodermal basal lamina that separate them from the body wall muscles. In contrast, the neurons of pharyngeal NS are positioned directly along the pharyngeal muscles. Several head ganglia surrounding the pharynx constitute the bulk of neurons and form a brain of basiepithelial type. Most of them are sensory neurons (69 in total) that detect various soluble volatile chemicals, tactile stimuli, and temperature. The brain neuropil encircles the axially placed esophagus, associated cells, and center of the pharynx isthmus and forms a nerve ring. Neurites of sensory and interneurons form synapses as they run next to each other in the nerve ring. Sensory neurons extend their dendrites to the sensory organs such as sensilla, while their axons join the nerve ring, where they form synapses with interneurons. Some neurons also extend their long axons along the ventral cord, which runs the entire length of the animal. Motor neurons are scattered around the ventral nerve cord and innervate muscles allowing the animal to respond to sensory input by changing its movement pattern. Sensory organs called sensilla (singular sensillum) are composed of dendrites from one or two bipolar sensory neurons surrounded by a glial-like single sheath cell and one or more socket cells. Sensilla are predominantly situated in the head and the tail of the animal. Sheath cells envelop neurons' endings, and some part of the neuropil and ventral cord.

Arthropods have a segmented body in an exoskeleton with paired, jointed limbs at all or several of the body segments. Arthropods possess subepithelial NSs with an anterior brain, and a series of ventrally located ganglia in most body segments making up the ventral nerve cord running down the abdomen. These ganglia appear physically fused (but are connected by commissures) at the midline in pairs in bilateral symmetry, and their lateral nerves innervate each side of the body segment and/or appendages. Most arthropod brains (called supraesophageal ganglion) are formed by three dorso-anteriorly paired ganglia in the head segments. The subesophageal ganglion, another fused complex of ganglia, lies ventrally in the head, just below the brain, and

innervates mouthparts, salivary glands, and some muscles. In posterior direction, it is followed by the thoracic, abdominal, and specialized terminal ganglia. The thoracic ganglia innervate appendages and control walking and flying-like activities. The abdominal ganglia innervate pleopods, reproductive organs, and anus, and control several activities including swimming. Each ganglion can process sensory information in its own body segment and pass it on to neighboring ganglia without input from the brain. Sensory neurons are mostly located outside ganglia in the periphery (integument) and constitute the PNS. The longitudinal compression of ganglia is a common variation in arthropod NSs. For example, brain and thorax ganglia are compressed as a single unit in scorpions, locusts, and lobsters and are called synganglion. The arthropod brain has three anatomic divisions. The protocerebrum is a pair of ganglia in the foremost head segment, which innervates vision-related sensory structures (compound eyes and ocelli). In some social insects such as bees and ants, the protocerebrum contains thousands of specialized neurons called mushroom bodies (Ito et al. 1998). They are the centers of higher-order sensory integration involved in sophisticated learning and decision-making. The deutocerebrum innervates antennae, labial palps, and parts of the tegument (body wall) and controls chemo-sensation and tactile sensation. The tritocerebrum innervates the labrum and integrates sensory input from proto- and deutocerebrum, in addition to linking the brain to the rest of the ventral nerve cord.

Mollusca phyla have the most intriguing invertebrate NSs, which comprise a subepithelial CNS, and basiepithelial peripheral nerve nets. Most molluscan NSs are composed of (five to) six paired ganglia. Sensory and motor information from the sensory organs is processed by the largest and most lobed anterior cerebral ganglia. The buccal ganglia innervate the muscular feeding organ, called the buccal mass, and control eating-related activities. The pedal ganglia control locomotion and conjoint muscle movements involving the shell in snails. The pleural ganglia supply nerves to the mantle cavity, and their functions are generally unknown. The abdominal/parietal ganglia innervate internal

organs. Many complex actions that require the integration of whole-body movement involve more than one ganglion.

Some molluscan NSs have remarkable features. For example, the *Aplysia* (class gastropoda) NS is composed of 20,000 neurons arranged in four pairs of head ganglia and a single abdominal ganglion (Kriegstein 1977). Some of these neurons represent the largest nerve cells in the animal kingdom (up to 1 mm) and can be seen with the naked eye. Their giant size makes a single neuron an extremely powerful center in controlling multiple complex behaviors and tasks. Cephalopod NSs are the largest of all invertebrates. Their brain-to-body weight ratio exceeds that of most fishes and reptiles. Octopuses are among the most intelligent and behaviorally diverse soft-bodied invertebrate animals, with excellent vision, and a mouth located at the center point of eight highly efficient, flexible limbs (arms). The CNS is composed of the brain and optic lobes that contain about 40 and 130 million neurons, respectively. The brain size surpasses many vertebrate brains in terms of cell number and complexity. The PNS consists of two-third (~350 million) of the total neurons located in the body and arms (Gray and Young 1964). Most neurons are organized in the nerve cords and ganglia of the arms and act as lower motor centers to coordinate the movements of arms and suckers. The ganglia of head and trunk are fused into one large brain around the esophagus and anatomically divided into a supraesophageal and a subesophageal part, connected laterally. Each of these parts is further subdivided into a varying number of lobes depending on the Cephalopod species. Almost all brain nerves project to, and/or originate from, more than one of these lobes, and almost all lobes, including the subesophageal lower motor centers, have two-way connections. Therefore, many of these lobes (the supraesophageal ones in particular) do not have a single precise function.

Octopuses have a large number of chromatophores distributed across their entire skin. Each chromatophore consists of a membranous sac containing a pigment, which can be red, yellow, brown, or black in color. Each pigment sac is

surrounded by about 15–25 radial muscle cells. When the muscles contract, the sac expands, and the color becomes visible on the octopus' skin. Conversely, the respective pigment becomes less visible when the muscles relax, and the pigment sac shrinks back to its original size. These muscles are controlled by nerve fibers projecting directly from a brain region called chromatophore lobe. The muscle fibers form synapses with glutamatergic motor neurons. Historically, it was this synaptic connection where the neuromodulator action of acetylcholine and serotonin was first demonstrated (Messenger 2001). Perhaps, this Cephalopod neuromuscular image generation system is the only example of chromatophores in animal kingdom, which is neuronally controlled and allows for an unprecedented, fast, localized change in body color, which is often used to trick prey and confuse predators. Octopus arms can, without bones, move in infinite directions. The arm movement is controlled by higher motor centers in the brain, which send global commands to the neuronal centers in the arm. These then control the entire spatiotemporal details of the movement. The arm NS is extensive and works independently. Many cephalopods also have giant nerve fibers for achieving extremely fast conductance of action potentials for the rapid activation of the mantle muscles during jet-propelled escape.

Lancelets (amphioxus) and tunicates are the only two groups of invertebrates belonging to the Chordata phylum. Tunicates NSs have an invertebrate layout consisting of ganglia with nerves that innervate siphons, mantle, and muscles. Amphioxus is the closest living relative of vertebrates with a similar body and NS plan. The amphioxus CNS consists of a hollow dorsal cord that closely resembles the vertebrate NS. Amphioxus has a cerebral vesicle that shows some similarity to vertebrate brains. *Nervous System*, and ► [Vertebrate Nervous System](#) chapters describe such NSs in detail.

In summary, invertebrate NSs consist of nerve nets, ganglia, and nerve cords with a variation in organization across species. Ganglia of considerable size at the anterior (or head) end of the body in many invertebrate species can be considered a

primitive brain. Molluscan NSs evolved with remarkable unique features.

## Cross-References

- [Action Potentials](#)
- [Axon](#)
- [Dendrites](#)
- [Nervous System, The](#)
- [Neuron](#)
- [Neurotransmitters](#)
- [Vertebrate Nervous System](#)

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## Nervous System, The

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## Synonyms

Brain; Central nervous system; Peripheral nervous system

## Introduction

Living organisms sense the changes in the external environment and respond accordingly to maintain homeostasis. The survival of organisms depends on how they sense and respond to their surroundings. The quicker the responses, the better the chances of survival. Early in evolution, animals acquired a system which helped them to integrate multiple sensory inputs and produce directed responses at a speed of hundreds of kilometers per hour. This system is referred to as the nervous system (NS) – an organized network of cells having processes extended throughout the body, which can sense external cues and direct responses from simple voluntary or involuntary movements of the body to managing emotions or solving complex survival problems. Even simple NS of primitive animals have staggering complexity in the way they process information, store it, and decode it based on the stimulus. Humans have a marvelously complex NS, which allows us enormous cognitive capacity and helped us to conquer every part of the planet and beyond.

## Fundamental Units of the Nervous System

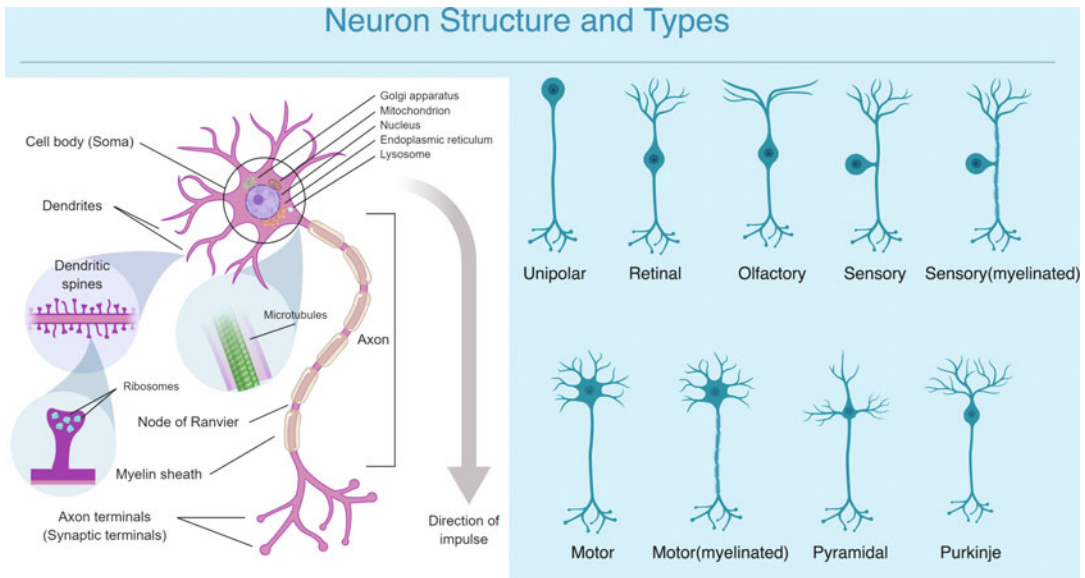
The NS is a diffused or centralized network made up of a specialized cell called neuron and its projection in every part of the body, often supported by another specialized cell called neuroglia.

### Neurons

Neurons evolved with the ability to engage in electrical communication with each other. Each neuron has three specialized structural parts, which are called dendrite, soma (also called cell body, plural somata), and axon (Fig. 1). Dendrites are projections of the soma which receive signals from other cells and transmit to the soma (in many cases, directly to the axon). The soma contains typical subcellular organelles found in eukaryotic cells. It processes and transmits signals along the axon. The axon is a single long fiber branched into fibrils at its distal end. The terminal end of each fibril has a bulb-like structure called synaptic knob, which contains synaptic vesicles filled with chemicals called *neurotransmitters*. The axons projecting from the somata can run through the length of the animal's body in a bundle called fiber, and multiple fibers form a nerve trunk. The function of an axon is to carry signals away from the soma toward an anatomical site referred to as the *synapse* or to a neuromuscular junction (Golgi 1906; Ramon and Cajal 1906). The synapse is the region formed between the membranes of two neurons (called pre- and postsynaptic neurons), which may or may not be separated by a fluid-filled small space called synaptic cleft (Fig. 2).

Neurons are divided into three major groups: sensory, motor, and interneuron, based on the way they communicate among themselves and with other cells. Sensory neurons typically have a long dendrite and short axons and carry signals from sensory receptors to the NS. Motor neurons have a long axon and short dendrites and transmit signals from the NS to a muscle or to a gland. The third type of neuron is called interneuron or short-axon neuron, found only in the central NS where they connect with projecting neurons.





**Nervous System, The, Fig. 1 A general structure of a neuron and its types.** The cell body receives signals via converging dendrites. The axon, a cylindrical elongation of the cell body, conducts action potentials out of the cell via synaptic terminals and releases neurotransmitters into the synaptic cleft influencing other neurons. Each dendrite contains spines which increase the contact surface in order to form synaptic contacts. The tip of the dendrite is a highly active site for protein synthesis due to the high concentration of ribosomes as compared to the rest of the neuron. The dendritic extensions are usually variable, decreasing in diameter, but axonal extensions, also

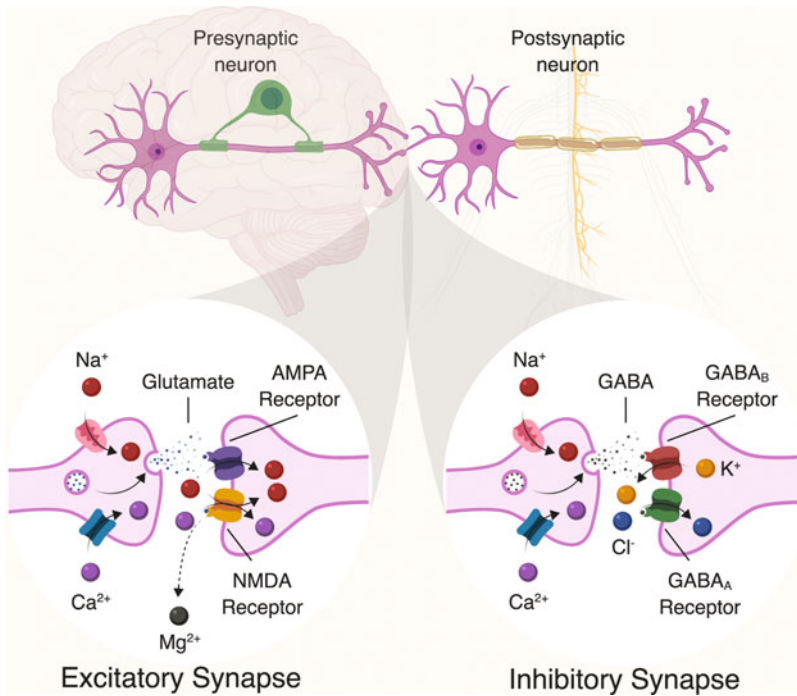
known as axis cylinders, have uniform diameters and branched terminations that make contact in a region-dependent way with nerve, muscle, glandular cells, etc. The axon can span a few hundred micrometers or much longer distances. For example, neurons of the spinal cord have very long axon projections, while very short ones are part of local circuits in the brain. The branched end of the axon dilates to form the synaptic buttons or terminals. These participate in the communication either through electrical activity or through neurotransmitters. Nine common types of neurons can be observed (right panel)

Axons can be wrapped by several glial cells disposed side by side. The spaces between these cells on axons are known as the *nodes of Ranvier* and facilitate signal conduction along the axon. Nerve impulses jump from one node to another traveling hundreds of times faster than impulses traveling continuously along the surface of the axon. Neurons can be further classified based on different criteria such as their function, activity, location in the body, electrochemical properties, and morphology, including the axonal and dendritic patterns (Fig. 1).

### Neuroglia or Glial Cells

In many animal groups neurons are accompanied by a second class of cells, called glia or neuroglia. Glial cells nourish, support, and maintain neurons

as well as form sheath-like processes around neuronal cell bodies and nerve fibers. Glial cells are of four types – oligodendrocytes, Schwann, microglia, and astrocytes. Oligodendrocytes and Schwann cells produce a layer of a fatty substance called myelin in the central and peripheral nervous systems respectively. Myelin wraps around axons, providing electrical insulation that allows neurons to transmit nerve impulses much more rapidly and efficiently. Microglia and astrocytes may also act as resident immune cells to protect the brain since the cells of the dedicated immune system usually cannot cross the blood-brain barrier (Hickey and Kimura 1988). These cells are involved in phagocytosis during development, and in the mature and diseased NSs. Glial cells also provide guidance cues for directing the axons



**Nervous System, The, Fig. 2** Diagram of signal transmission between neurons. The upper part shows two cells communicating by a chemical synapse. The presynaptic neuron releases neurotransmitters as a result of an action potential entering its axon terminal. In response to binding neurotransmitters, the post synaptic neuron discharges a new action potential. In the lower part, excitatory and

inhibitory synapses are exemplified. Glutamate is an amino acid which serves as the most common excitatory neurotransmitter in the mammal CNS. Gamma-aminobutyric acid (GABA) is the most abundant neurotransmitter present in mammalian inhibitory synapses. Ion channels participate in changing the membrane potential in both excitatory and inhibitory synapses

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to their targets or extending branched processes that interact with terminal nerve fibers and synapses. Hence, they play a critical role in development and the establishment of neuronal signal transmission. The total number of human glial cells is roughly proportional to the number of neurons present in the brain. The proportions may vary in different areas of the brain, indicating that glial cells play pivotal roles, as neurons do, in shaping the brain structure and nerve responses.

## The Signal Transmission Between Neurons

In metazoans, neurons evolved as specialized cells capable of conducting electric signals, also termed nerve impulses, enabling neurons to

communicate between each other (Hodgkin et al. 1952). Like any other cell, neurons maintain different concentrations of certain ions across their membranes. Ions that are important in building nerve impulses include sodium and potassium. More positively charged ions flow out of the neuron than those which flow inward. This imparts a positive charge on the outside of the neuronal membrane and a negative charge inside. It creates a voltage difference across the membrane referred to as the membrane potential, and the membrane is said to be polarized. Neurons are said to be at rest when they are not conducting a nerve impulse. The resting potential of a neuron is approximately  $-70$  mV, during which the neuron has an overall negative charge. Membrane potential is transiently modulated by electrochemical signals from nearby cells. The fast and temporary

reversal of the membrane potential is called the action potential. This takes place extremely rapidly, in about 0.002 s, thus allowing neurons to fire action potential in series, a common feature in neuronal communication or signal transmission.

Since the cell membrane is almost impermeable to ions, there are two types of specialized proteins located on the membrane of a neuron, which allow selective passage of ions to maintain the membrane potential. They are called sodium-potassium ATPase pumps (or ion pumps) and ion channels. The transport of ions through a cell membrane against their concentration gradient requires energy expenditure since ions have to be transported against their flow. Ion pumps are equipped with ATPases which break down ATP molecules to generate the energy required for the transport. In contrast, ion channels transport ions along their natural flow in favor to the concentration gradient, hence not requiring energy for this process. Ion channels are highly specialized to the specific type of ion they transport. Ion pumps and channels are usually closed, but they open in response to differences in ion concentrations across the membrane. Sodium channels respond to slight membrane depolarization and, once they are open, allow a quick influx of sodium ions, thereby switching the resting potential. The membrane is depolarized locally, and this depolarization triggers the opening of adjacent ion channels. Thereby, the impulse of an action potential spreads across the neuronal membrane and along the axon. In order to restore the net electrical charge across the membrane, potassium channels open to release potassium into the extracellular milieu. Both channels close after the action potential has passed. Ion pumps then work continuously to transport ions back to their respective locations against their concentration gradients to restore the original resting membrane potential and ion concentrations.

Action potentials spread anterogradely, away from the soma, because once the ion channels close, they cannot be opened again for a short time called refractory period and will be opened again only by an extraordinarily strong depolarization during this period. Not only does this mechanism ensure directionality of the impulse, but it also determines the maximum frequency

at which nerve impulses can be passed down the axon.

Nerve impulses generated by an action potential are transmitted from one neuron to another through synapses (Fig. 2). The nerve impulse may directly transmit from one neuron to another through a synapse when they are close to each other leaving no room for synaptic cleft formation. Such synapses are called electric synapses. In this case, neurons electrically excite other cells by the changes in the membrane potential elicited by the passage of ions and small molecules through the specialized proteins linking their membranes at synapse (Hodgkin et al. 1952).

Nerve impulses may also be transmitted indirectly when neurons are farther apart, forming a synaptic cleft at the synapse between them. This type of synapses are called chemical synapses. In this case, the nerve impulse crosses the synaptic cleft with the help of neurotransmitters that are small molecules or ions stored in small synaptic vesicles clustered at the tip of the axon (Dale et al. 1936). When an action potential increases, some of the vesicles move to the axonal membrane and discharge their contents into the synaptic cleft via exocytosis. Neurotransmitters therein diffuse across the cleft and bind to their specific receptors on the next cell, causing ion channels on that cell to open, thereby transmitting or interfering the nerve impulse along the membrane. Neurotransmitters released in the synaptic cleft are active only for a short period of time. They are either inactivated or broken down by specific enzymes in the cleft or reabsorbed into the axon of the cell which released them for recycling. Neurotransmitters are generally small (often amino acids), and some are even hormones. Neurotransmitters act in between 0.5 and 1 ms; some trigger an action potential, while others inhibit it.

## Embryonic Development of the Nervous System

In the course of animal embryonic development, a single fertilized egg cell undergoes division to form a sphere of cells called blastula that differentiates into layers of cells called germ layers.

Animals with just a single layer of germ cells (homoblastic) evolved early on, followed by animals with two (diploblastic) and three (triploblastic) germ layers. In diploblastic animals, the inner layer of cells is called endoderm, and an outer layer is called ectoderm. In triploblastic animals, a third germ layer called mesoderm develops between endoderm and ectoderm. The process of germ layer formation is called gastrulation and exists perhaps in all animals except in sponges. These germ layers differentiate into various organs as the embryo develops.

Of the three germ layers, the ectoderm (in some animals the endoderm) gives rise to the NS during embryonic development. Some regions of the ectoderm express specific transcription factors influenced by the signaling molecules (morphogens) secreted by nearby embryonic cells. These transcription factors are called neural determinants, and the ectodermal region where they are expressed is called neuroectoderm. In these regions, neuroectodermal cells are maintained in the proliferative state. These cells then express a second set of transcription factors to become neural progenitor cells. These progenitor cells proliferate, migrate, and differentiate in a stereotypic pattern along the gradients of morphogens and neural determinants to form various parts of the NS.

The embryonic development of the NS is tightly regulated spatio-temporally by a gene expression program influenced not only by intrinsic determinants from within the developing NS but also by extrinsic determinants from other regions of the developing embryo. The genetic mechanisms underlying neural progenitor specification and formation of neurons are fairly similar among all the well-studied model organisms.

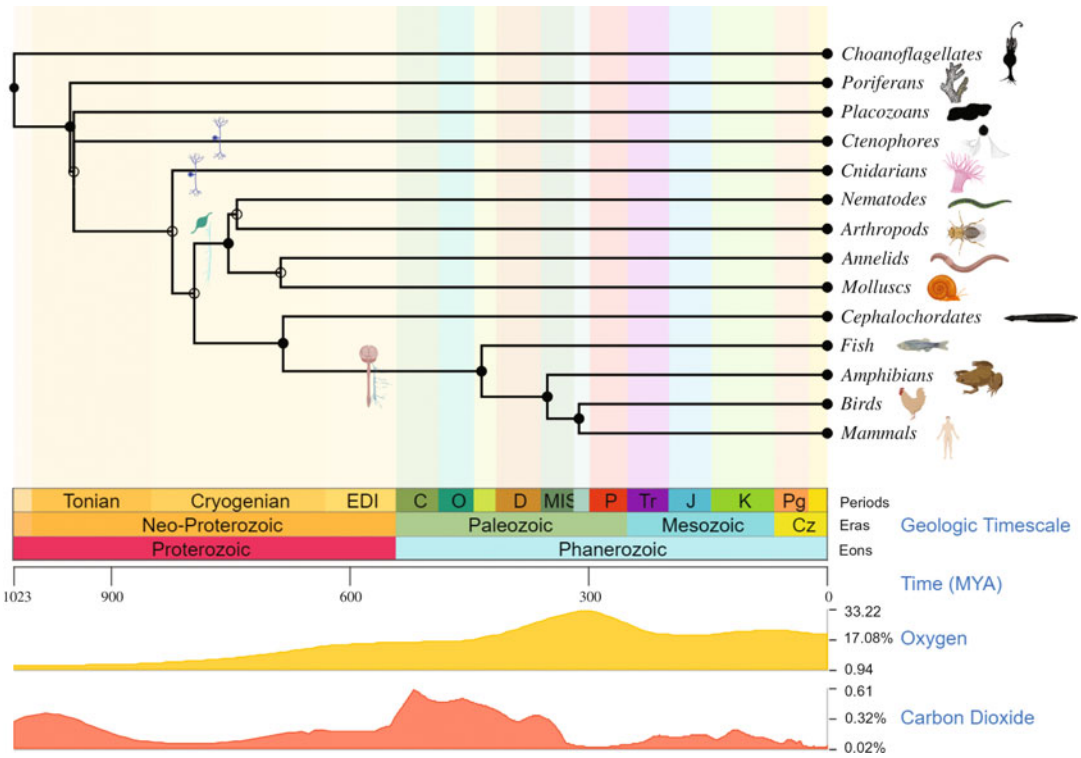
## Evolutionary Origin of the Nervous System

Animals have a relatively recent evolutionary origin compared to remaining living organisms. They are likely to be evolved from a group of free-living, single-celled, colonial choanoflagellate-like eukaryotes having a sophisticated toolkit for

sensing and responding to the environment. Early evolved animals have been placed in four major groups, Porifera (sponges), Placozoa (flat animals), Ctenophora (comb jellies), and Cnidaria (hydra, corals, and sea anemones). The phylogenetic placement remains contentious for these groups.

Porifera and Placozoa taxa branched off the phylogenetic tree at an early stage of animal evolution. Neurons and synapses are absent in extant members of these groups. Ctenophores and cnidarians have neurons and synapses, which constitute a simple, diffused NS. There are two schools of thought on the origin of neurons in these phyla (in other phyla too). Traditionally, it was thought that neurons have monophyletic origin – the primordial neuron evolved into all neurons found in extant animals. Current molecular evidence, however, suggests that neurons evolved multiple times. For instance, neurons in ctenophores and cnidarians may have independent origin. The assumption here is that the molecular building blocks of neurons, such as ion channels, ion pumps, neurotransmitters, and vesicular transporters, can be found in choanoflagellates, sponges, and placozoa. Neurons could have possibly evolved from the cells having these building blocks just by rearranging certain components of their cytoskeleton to form elongated processes. This event could have happened multiple times during animal evolution.

A significant step toward the centralization of the NS from a diffused network took place approximately 700–600 million years ago with the appearance of the bilateral symmetric animals. The ancestral cnidarians are likely to have branched off from the other animals, and some animals evolved with bilateral symmetry. Bilateral animals are triploblastic and include all organisms from tiny worms to humans (Fig. 3). Their NS is characterized by two major components – the central and the peripheral. In many cnidarians and ctenophores, regions of higher neuronal density are detected at the mouth opening and at the base of tentacles. Such conglomerates of neurons can take a rounded shape to form ganglion (plural, ganglia) or elongated structures to form nerve rings or nerve cords. It is likely that



**Nervous System, The, Fig. 3** A timeline tree depicting the evolution of the nervous system and its components.

The phylogenetic tree was created using representative species of each of the lineages shown in the figure. The position of each taxon in the tree is based on the morphological and molecular data available to date. The positions of lineages that diverged before cnidarians are contentious. First neurons are likely to have appeared in the ancestors of

ctenophores and cnidarians, with simple NSs in the form of nerve nets. Bilateral symmetric animals were then branched off from Cnidarians and evolved with nerve cords, agglomerates of sensory structures in the ventral side of the body, and the brain. Cephalochordates have a notochord in addition to a brain. Eyes and most olfactory systems evolved in ancestors of fish and also spinal cords. An enlargement of the brain occurred in mammals

from such local densities or ganglia, true centralized NSs evolved in bilateral animals.

The bilateral animals have defined top, bottom, front, and back. The appearance of bilateral animals followed an evolutionary trend, which is called cephalization. It means the concentration of the neurosensory organs at the anterior end of the body formed the head and the brain during evolution. Flatworms are the most primitive bilaterians and belong to the Platyhelminthes phylum of unsegmented, soft-bodied invertebrates, which are phylogenetically close to cnidarians. Platyhelminths are the first animals of organ-grade construction with an anterior concentration of neurons and sensory systems, accompanying the first signs of cephalization. They are also the first animals to have a true centralized NS, which

constitutes a ganglionic mass in the head of the animal as a sort of primitive brain. There are multiple paired nerve chords that extend from the ganglia along the length of animal body. Flatworms serve as the basal stock from which all higher animal phyla are thought to have evolved. In some more evolved invertebrate bilaterians, particularly within the nematode, annelid, and arthropod phyla, ganglia are segmented anteriorly with the nerve cords running down the ventral plane of the body (i.e., bottom side of the body as opposed to back).

Chordates evolved with a more elaborate NS which includes a dorsal NS rather than a ventral one, continuation of cephalization in the form of larger and more complex brain, and appearance of the characteristic feature defining



the phylum – the notochord, which provides physical support for the development of NS in the embryo. More specialized brain regions arose with the appearance of vertebrate animals – characterized by the presence of vertebral column containing neurogenic tissue outside of the brain called the spinal cord.

The fossils from the beginning of the Precambrian period provide potential reasons for the evolution of complex NS in animals. Animals likely evolved with fast-conducting systems like neurons for keeping different parts of the body coordinated and making quick movements to obtain food and to avoid predators.

## The Architecture of the Nervous System

NS organization is diverse in modern animals. The simplest NS can be found in early evolved cnidarians and ctenophores. Cnidarians are important for understanding the evolution of the NS since most phylogenetic criteria place them at the base of bilateral animals. They have a radially symmetric body formed around an oral-aboral axis by two tissue layers. An outer layer, the epidermis, forms the skin, and an inner layer, the endoderm (gastrodermis), forms the gut. The network between the epidermis and the endoderm is similar in structure to a cobweb and is referred to as the *nerve net*. A cnidarian polyp typically has several independent nerve nets, which tend to be condensed near the mouth opening forming a nerve ring in adults. There are two types of neuronal cell types found in a nerve net called sensory and ganglion neurons. The ganglion cells connect different neural structures within the NS. Sensory cells detect different stimuli such as light, touch, or temperature. Davis and Koizumi et al. carried out a detailed anatomical study of the nerve nets and rings of *Hydra* (Koizumi et al. 1992; Davis 1974). The nerve net is associated with the inner or basal side of epithelial/epidermal layer of the body wall, with no signs of centralization. The nerve net-based NSs can also be found in ctenophores and echinoderms. All these animals are characterized by a radial symmetric body around a central digestive cavity.

## The Nervous System of Animals with Bilateral Symmetry

In early bilateral animals, the conglomerates of neurons (ganglia) began to cluster around sensory organs (near the mouth and primitive eyes) in the anterior part of the animal – forming the first brain-like structure – the sign of cephalization, enabling animals to move and respond to the environment in even more sophisticated ways. When neurons are clustered their cell bodies form a processing center, and nerve cords running through them can innervate various parts of the body to receive sensory inputs. In this way, information could be further processed rather than merely relayed as in the case of nerve nets. Many biologists suggest that the last common ancestors of bilateral animals – probably worm-like animals – had such a primitive brain. The presence of regions with higher neuronal density in cnidarians supports this notion. The brain and the nerve cords form the central nervous system (CNS). The nerve net and/or sensory neurons located in the periphery, and the nerve fibers communicating between the CNS and the periphery, constitute the peripheral nervous system (PNS).

NS is further organized between bilateral animals that are vertebrates and invertebrates. The major notable difference between vertebrate and invertebrate NSs is the degree of centralization.

In invertebrates, the CNS constitutes an aggregation of neuronal components organized into longitudinal or ring-like nerve chords usually near the midline of the body. A planarian (Platyhelminthes) has two nerve cords running along the length of its body from the two ganglia at its anterior end. Likewise, two nerve cords are fused and run down the ventral surface of the body in earthworms belonging to annelid phyla. Arthropods such as the crayfish also have a double ventral nerve, in addition to ganglia in the head. Some organisms have more than one nerve cord connected by transverse nerves, resembling a ladder.

In many invertebrates such as annelids, arthropods, and molluscs, a CNS and a PNS can be distinguished. In these animals, a series of ganglia are usually located along the animal's midline. The peripheral component of the NS is formed

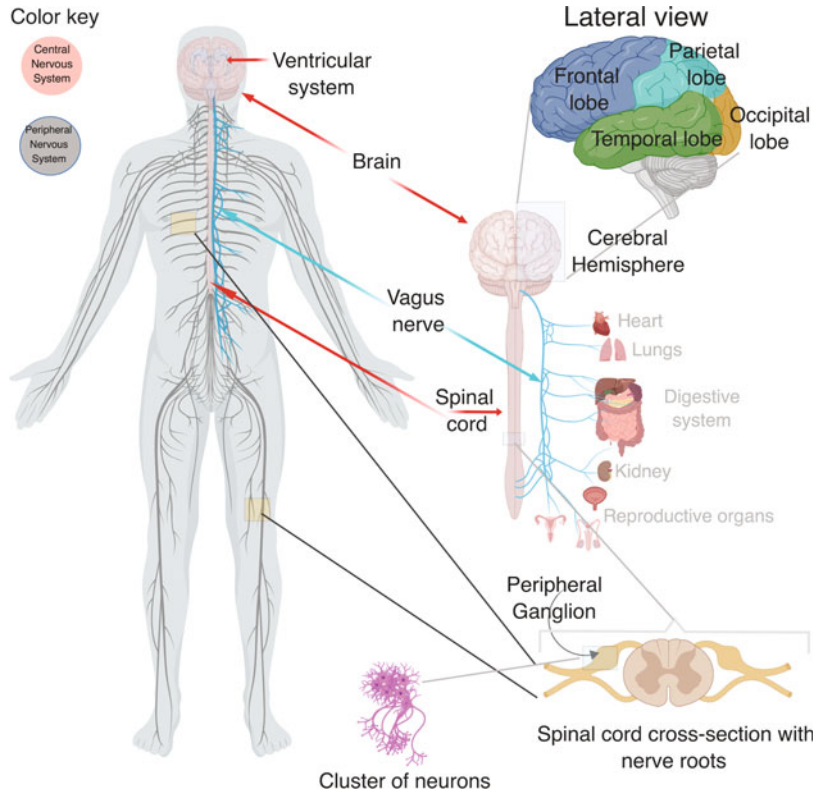
by the extensions of the cells in the ganglia. Some of these cells carry sensory information from the environment to the ganglia, while others carry signals from the ganglia afferently to produce a response (such as movement). Each ganglion along the midline responds to, and controls, an individual segment of the body. Ganglia connected to each other coordinate the segments in a chain-like fashion by a nerve cord, which runs throughout the length of the body. The nerve cord is enlarged at the anterior (or head) end in many invertebrates and can be considered a primitive brain. In squids (molluscs), this primitive brain enables visual information processing and rapidly generates coordinated responses in order to escape or capture preys. This invertebrate NS is so specialized that it closely resembles some vertebrate NSs. Two groups of invertebrates, the tunicates and the lancelets (protochordates), are grouped with the vertebrates as chordate. The NS of an adult tunicate is fairly like other invertebrates in layout, in that it consists of a ganglion

with nerves that radiate out to innervate the siphons, mantle, and somatic muscles. In contrast, the NS of adult lancelet *Amphioxus* is a hollow dorsal cord that much more closely resembles a vertebrate NS. The front end of the dorsal cord clearly has a great homology with vertebrate brain structure. There is also a simple anterior eyespot likely to be homologous with vertebrate eyes. The vertebrate NS is much more centralized and cephalized as compared to the invertebrate NSs and is described in detail below.

## Vertebrate Nervous System

In the vertebrate NS, the CNS and the PNS are clearly defined anatomically. The CNS comprises the brain and the spinal cord, whereas the PNS is formed by ganglia and nerves (Fig. 4). Conventionally, a cluster of neuronal cell bodies within the CNS is called a *nucleus*, while a cluster outside the CNS is called a *ganglion*.

**Nervous System, The, Fig. 4** The organization of the nervous system and its parts in the human body. The central nervous system is composed of the brain and spinal cord (pink). The brain is anatomically organized into the frontal, temporal, parietal, and occipital lobes. The peripheral nervous system (gray) is formed by spinal nerves that arise from the peripheral ganglia (cluster of neurons) and innervate different organs



## The Central Nervous System

The CNS is enclosed and protected by three-layered membranes called meninges. The outer, tough, and leathery layer is called *dura mater*, whereas the delicate innermost membrane layer is called *pia mater*, which is pierced by blood vessels that supply the CNS with oxygen and nutrients. The *arachnoid mater*, a middle membrane layer, provides a cushion between the *dura mater* and *pia mater* layers. In addition to the meninges, the brain is also protected by the skull which houses the brain and certain sensory organs – including the cranial cavity and mandible. Like the brain, the spinal cord is enclosed by meninges and further protected by the vertebrae, a set of interlocking bones that, together with intervertebral discs, form the spinal column. A third mechanism of protection of the CNS is provided by the cerebrospinal fluid, which surrounds the brain in the skull and lies between the spinal cord and vertebrae, thereby offering a buffer to impact in the brain and spinal cord. In addition to these mechanisms of physical protection, the selectively permeable blood-brain barrier further protects the CNS from toxic substances and pathogens (Abbott et al. 2006).

At the tissue level, the CNS is divided into areas of gray and white matter. The gray matter contains a high proportion of neuronal cell bodies and their dendrites, glial cells, and capillaries. The gray matter is mainly composed of clusters of neurons in the brain and spinal cord and in outer layers that line their surfaces. The white matter is mainly composed of myelinated axons and appears white due to the myelin sheaths and scarcity of blood vessels.

The brain controls almost all the processes carried out in the CNS and has three anatomical subdivisions: *prosencephalon* (forebrain), *mesencephalon* (midbrain), and *rhombencephalon* (hindbrain). The forebrain is a frontal part of the brain, which is covered with a large, wrinkly, outermost layer of the brain – the cerebral cortex (Fig. 4). It consists of a left and right hemisphere, each of which is further divided into four major lobes: frontal, parietal, temporal, and occipital lobes. There is a portion of the cerebral cortex folded deep within the fissure separating the temporal lobe from the parietal and frontal lobes. These lobes together constitute the largest site

of neural integration in the CNS and play key roles in memory, attention, perception, awareness, thought, and language.

The midbrain is a vital connection point between the forebrain and the hindbrain. This is the topmost part of the brain stem, which connects the brain to the spinal cord. The upper portion of midbrain has two principal pairs of structures called the superior and inferior colliculi. The superior colliculus processes visual signals before they are passed on to the occipital lobe through the thalamus. The inferior colliculus processes auditory signals before they are passed, through the thalamus, to the main auditory processing center in the cortex.

The hindbrain is the lowest portion of the brain stem, and it is composed of the medulla oblongata, pons, and cerebellum. The medulla oblongata contains cardiorespiratory centers that can increase or decrease the cardiac and respiratory rates depending on the physiological needs. The pons is responsible for conducting signals from the brain to the cerebellum and down to the medulla, and has tracts that carry the sensory signals from the spinal cord up into the thalamus. The small cerebrum, or cerebellum, is a rounded structure hosted in the posterior fossa of the cranium, behind the pons and medulla oblongata, and underneath the occipital lobe. The cerebellum is an integration center which processes sensory information for movement-related functions.

## The Peripheral Nervous System

The PNS is organized as clusters of neurons or ganglia and nerves outside the CNS. Nerves form several branches that innervate every sensory ending of the body, linking them with the CNS (Fig. 4). The PNS is further subdivided into two parts: the somatic and the autonomic. Nerves are also classified as sensory, motor, or mixed nerves if they contain axons from both sensory and motor neurons. Based on the signal transmission, toward or away from the brain, nerves are termed afferent or efferent respectively. The afferent nerves arise from the sensory neurons, which receive inputs from sensory organs, such as the ears, eyes, nose, tongue, and skin, and pass the signal to the CNS. There, nerve impulses are processed to elicit the appropriate sensation. The efferent nerves transmit signals from the CNS to motor neurons and

are responsible for putting the organs and muscles into action to execute voluntary movements of the limbs (Sherrington 1906). The somatic NS innervates the skin, joints, and muscles. It regulates the movement of skeletal muscles. The autonomic NS contains nerves that innervate the internal organs, blood vessels, and glands. It controls involuntary actions such as heart rate, digestion, and perspiration.

## Closing Remarks

The NS is substantially similar within vertebrates, with subtle differences in specialized structures and their functions. However, early evolved invertebrate animals show staggering diversity of NSs, even within various phyla. Despite the complex diversity of NSs across metazoans, their NSs coordinate and control bodily functions in a relatively similar manner. Nonetheless, appearance of NSs in animals bestowed them the ability to respond faster and attentively, which in large part can be attributed to their success on the planet.

## Cross-References

- Action Potentials
- Embryo
- Gene Expression
- Nervous System of Invertebrates
- Neuron
- Neurotransmitters
- Vertebrate Nervous System

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## Nest Building

- Nest Construction
- Susan D Healy

## Nest Construction

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## Synonyms

Animal Architecture; Nest Building

## Definition

Nests are structures built by animals, typically for the purpose of holding the animal's eggs or live offspring.

There is considerable diversity in nest construction across species. Nesting occurs in a wide variety of species, and there is great variety in how nests are constructed within phyla and even within genera. Dinosaurs built nests that often consisted of simple depressions in the ground, and in which eggs were laid and incubated (Chiappe et al. 2004; Norell et al. 1995). Birds are the living descendants of dinosaurs and, although some living species do construct ground nests (Angelstam 1986; Manolis et al. 2002), there are many different strategies of nest building among the various bird species. As seems to be the case in dinosaur nests, bird nests typically function as structures for keeping eggs, and later chicks, safe from predation (Heenan and Seymour 2011).

Because bird nests function to keep eggs and chicks safe from predation and environmental hazards such as rain, there is a sense in which natural selection has shaped the structures and building materials of nests. Dawkins (1982) argued that various aspects of nest construction may be best understood as extended phenotypic effects. Dawkins suggested that, whereas the forces of natural selection directly act on the physical characteristics of a given nest, the downstream consequence is that those genes responsible for more well-constructed nests become more abundant in the gene pool. Hansell (2007) extended Dawkins's argument, suggesting that by imposing selective pressures on populations of nest builders over time, natural selection is responsible for the wide variety in the materials used to build nests, as well as the differences in the architectural designs of nests among closely related avian species. Those individuals that build stronger nests, nests better at insulating eggs and chicks, or nests that better protect against predation will have more surviving offspring. In this sense, natural selection acts on both the physical composition of different nests and the behavior responsible for nest construction. Zebra finches may even use information about past breeding success to inform subsequent decisions about nesting materials (Camacho-Alpizar et al. 2021), and a separate study of zebra finches found

that experimental manipulation of early-life exposure to different colored nesting material influenced the materials preferred by adolescents during the construction of their first nest (Breen et al. 2020).

Sexual selection may also play a role in nest construction for some species. Male weaver birds build nests that will eventually hold eggs without the assistance of the female, and in fact, male weavers construct these nests before they are even chosen as a mating partner. It seems that male weavers construct their nests, at least in part, to display their quality as a mate. Indeed, one study of baya weavers observed that the number of female visits to an incomplete nest predicted whether that nest would eventually be completed (Quader 2005). The same study also observed that females were more likely to choose nests that were built higher up, connected to thinner branches, and that were more neatly woven. The results of this study provide evidence that, at least for this species of weaver, nest construction is subjected to sexual selection, with better nest builders being more likely to attract a mate.

Nest building also occurs in many non-avian species, including several primate species. One study of nesting behaviors in chimpanzees (*Pan troglodytes*) found that chimpanzees preferred to nest above 1000 m, under dense canopies, and in relatively less humid areas (Koops et al. 2012). A study of nesting materials in western lowland gorillas reported a preference for specific species of plant, with individuals using an average of 4.9 different species per nest, but no seasonal shifts in preferences for different materials (Willie et al. 2014). Similar to avian species, nest-building primates also show preferences for certain nest characteristics, including both material and location, suggesting that in both aves and primates, selective pressures have likely shaped nest building behaviors.

Despite the large degree of variation in species that construct them, nests almost universally appear to serve a similar purpose: holding and protecting eggs and offspring. And although nests serve similar purposes, there is



considerable variation in the materials used to construct nests, and in the architectural designs of the nests.

## Cross-References

- [Brooding](#)
- [Clutch](#)
- [Paleobiology of Dinosauria](#)

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## Nest Sharing

- [Huddling](#)

## Nesting of Sea Turtles

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## Nesting Behavior

Female sea turtles have a unique characteristic of returning to the same beaches on which they were born in order to nest (Brothers and Lohmann 2018). Upon leaving the nest early in life (after about 2 months in-nest incubation), sea turtle hatchlings will swim vigorously to escape predator-rich shallow waters and will never return until they reach sexual maturity about 20 years later.

Sea turtles are generally solitary, and in most species, individual female turtles nest on their own. However, out of the seven species of sea turtles worldwide, two species – the olive ridley (*Lepidochelys olivacea*) and Kemp's sea turtle (*Lepidochelys kempii*) – exhibit mass nesting, called *arribada*, the Spanish word for “arrivals.”

Nesting activity typically happens on sandy beaches with sediment types ranging from fine to coarse sands (Kelly et al. 2017). Most of the time, the nest is constructed above the high tide waterline to secure the incubating eggs for the approximately 2 month-long (range, 45–70 days) incubation period. The incubation process depends on temperature where the higher incubation temperature will shorten the time to hatching (Booth and Astill 2001; Jong et al. 2009). However, incubation temperature above 33–35 °C of sea turtle eggs might be causing low-quality and impaired locomotion of hatchlings produced to escape from their nests (Segura and Cajade 2010). Therefore, the behavior

of sea turtles constructed their nest under shaded or open area will result in variation in phenotype and performance of an individual.

## Nesting Period

Sea turtles are known as a highly reproductive species as one female can produce several clutches within a nesting season (Miller 1997). However, nesting activity seldom occurs annually. Typically, the interval between nesting seasons is between 2 and 4 years (Broderick et al. 2001; Chaloupka 2001; Chan 2010; Sims et al. 2008). Some scholars believe that this interval period occurs because sea turtles spend so much time in the open ocean, foraging and migrating from one feeding ground to another.

Within any particular nesting season, a female turtle will remain within the vicinity of a nesting beach and spend several months there in order to deposit multiple clutches. A single female may nest up to six times with interval of 10–14 days before the next nesting activity (Hart et al. 2010). The nesting period for a typical female lasts about 3 months before she heads back out to the sea.

Nesting activity typically occurs at night as sea turtles are very sensitive to disturbance from light and potential predators. Night nesting also helps turtles avoid dehydration from the long arduous crawl from the water to the beach and back again. The complete process may take between 2 and 4 h depending on the species and beach characteristics. Occasionally females also crawl out from the water but do not nest. This phenomenon is known as a “false crawl” (Talbert et al. 1980).

Sea turtles are likely to nest during high tide, probably to reduce the crawling distance from shoreline to the nesting spot. Due to the high drag of her heavy body weight (60–600 kg depends on species), nesting is energetically costly and seems exhausting to human observers. Teardrops can often be seen during the nesting process as a mechanism to excrete excess salt in blood (Lutz 1997).

## Nest Construction

Nesting activity starts when a mature female emerges from the water and crawls up to her nesting spot. When the appropriate spot is reached above the high tide level, a turtle will move both left and right flippers synchronously back and forth and start lowering her body until it reaches the same level of beach surface. This sand throwing behavior, termed “body pitting” may later help rear-flippers to reach deeper level. Hence, the depth of nest chambers is dependent on the size of a female’s rear-flippers.

When the turtle has stopped using its front-flippers, she begins to use her rear-flippers, which act like shovels to scoop the sand out of the nest cavity. This is known as “egg chambering.” During this activity, the turtle moves the rear-flippers alternately between left and right. The turtle is typically seen trying to maximize the depth of nest chamber by lifting up her body with the support from her front-flippers. The nest chamber is constructed in a shape similar to a flask, which is thought to equalize temperatures among all of the incubating eggs. Depending on the species, the nest chambers typically highly related to maternal morphology and the reproductive output (Bjorndal and Carr 1989).

Sea turtles often abort the nesting process if they found any hard surface such as roots, dead coral, or gravel while chambering. She may then move to another spot and start with body pitting again as described above or may return back to the water immediately, likely returning to the same beach the next night.

Once the nest chamber construction is completed, turtle lays eggs through ovipositor by dropping two to three at a time until there are about a hundred eggs per clutch. It is believed that when the eggs touch the tail of the turtle, this serves as a cue that the nest chamber is full enough. However, Hailman and Elowson (1992) suggested that this tactile feedback is not the only cue for termination of eggs laying as some of turtle had stop earlier. The whole process takes around 10 min, depending on the species.

Upon completion of egg deposition, a turtle will conceal the nest cavity with her rear-flippers. Then, the turtle will rest for about 5 min. During this short window, conservation workers can safely measure morphological characteristics and attach identification tags, before the turtle starts using both front flippers to continue covering the nest. While dispersing the sand over the covered egg chamber by using their front flippers, turtles moved gradually a few meters forward. This camouflaging behavior created an elongated mound of sand on the origin nest chamber hence will confuse potential predators (this is typically known as creating a “false nest”). When the nest is covered, the turtle will crawl immediately back to the sea.

## Cross-References

- [Homing](#)
- [Maternal Behavior](#)
- [Nest Construction](#)

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## Nests

- [Cuckoo Brood Parasitism](#)

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## Neural Architecture

- [Neural Network](#)

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## Neural Circuit

- [Neural Network](#)

## Neural Control of Behavior

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## Introduction

The way in which an individual acts in response to a stimulus or situation is called “behavior.” Behavior is chiefly controlled by the central nervous system (i.e., brain and spinal cord). Behavior can be innate (present since birth) or is learned during a lifetime. Further it can be simple or complex. The simplest forms of the behavior are the “reflexes” which are innate in nature. For a reflexive behavior, the individuals may fail to perceive a conscious appraisal, as it primarily gets executed from the motor centers in the brain stem or spinal cord. Complex behavior, a varying motor action or response adjusted to the need of a situation, involves more than one component of the brain and is intricately regulated. A stimulus which is received at the sensory receptors is carried by the nerves to the sensory cortex which generates perception and further sends it to the cognitive and the effectors domains of the brain

where complex neural processing constructs a behavior from the substrate, in response. The comprehensive cortical processing of sensory feedback is essential for the conscious appraisal of a complex behavior. Reflex behavior is common to all the organisms, while complex behaviors are unique to the animal kingdom and denote their intellectual ability and hierarchy in the living system.

Complex behaviors can be innate or learned. Innate behaviors (as feeding or sexual behavior) are genetically determined. Innate behaviors involve hypothalamus and other subcortical centers and are associated with limited cortical processing in comparison with the learned behaviors. Emotional behaviors, which are largely innate, are regulated by limbic system which presents a unique set of cortical and subcortical centers. Learned behaviors may be driven by reward – a phenomenon called conditioning – or may not involve any reward at all, called nonassociative learning. A reward pathway which connects aminergic nuclei of the brain stem to the specific nuclei group in the forebrain has been considered as the driver of any reward-based behavior (Kiernan et al. 2014). Aminergic nuclei in the brain stem are known as the prime determinants of the adaptive behavior – which is largely a learned behavior helping the individuals in adapting to the environmental challenges.

How brain generates behavior has been an all-time curiosity of the human which has now developed into a distinct stream of the neuroscience, called *neuroethology*. In recent years, knowledge of the neural control of the behavior has got extensive research updates revolutionizing the existing understanding of the neuroethology. Behavioral roles have been found for many new brain regions which were earlier either not or little known. Recent research suggests extensive role of *anterior cingulate cortex* in decision-making. Basal nuclei and cerebellum have been found to bear important roles in behavior, in contrast to their earlier known roles which limited to the movement control. There are also updates regarding the role of the *insula* (a cortical island) and *claustrum* (a strip of gray matter), for which any cognitive/behavioral functions were earlier little

known. Uniquely, *habenula* – a subcortical set of nuclei which connects with brain stem – has been noted crucial in regulating adaptive behavior (Kumar et al. 2017b). Other than the central nervous system, two other nervous system types, i.e., “autonomic” and “enteric,” are also known to bear important roles in complex behavior. The current research adds extensively into their behavioral functions.

Present chapter takes a comprehensive look on the role of the three nervous system types involved in regulation of the animal behavior, and behavior-specific neural circuitries comprised of them, with a focus in human.

## Methods for Study of Neural Regulation of Behavior

Animal behavior is either studied by direct observations of its response to a given stimulus in a natural setting or through modeling of a behavior in laboratory settings. In laboratory settings, interventions like creating a lesion or inserting an implant, or the introduction of a pharmacological agent into the nervous system of an animal, can be done to model a behavior. These models can be further assessed by the standard neuropsychological tests.

For long, creating a lesion in the brain to know its impact remained a primary method to study a behavior. Implying the electrodes in targeted brain parts to record the local field potential (LFP – an electrophysiological signal created by summed up electric current arising from large population of neurons from the recording site) in the behaviorally activated neurons or to observe effect of an electrical stimulation, or pharmacological interventions, had been the next prevailed methods to study animal behavior in laboratory settings. These methods when combined with the neuroimaging modalities have brought revolution in the understanding of neural control of behavior.

There have been significant advances in neuroimaging (and recording) methods in recent years which have made structure-function coupling for the brain parts possible. Multimodal neuroimaging and data integration from chosen

combinations of the magnetic resonance imaging (MRI), positron emission tomography (PET), single-photon emission computed tomography (SPECT), near-infrared spectroscopy (NIRS), magnetoencephalography (MEG), electroencephalography (EEG), diffuse optical tomography (DOT), etc. have given edge to the behavioral research. The advances have given rise to a new stream of behavioral study, neuroeconomics – an interdisciplinary field which seeks to explain how decisions are made in the brain (Xue et al. 2010).

Structural magnetic resonance imaging (sMRI) has now got resolution of 7 and 9 tesla which is able to provide the structural details of the brain parts in living closer to that histological study in postmortem brain tissue. Use of contrast-based sMRI (mainly iron oxide) can detect the activity of targeted molecules with high sensitivity and specificity.

*Diffusion tensor imaging (DTI)* has revolutionized the knowledge on the fiber connections of the brain parts. DTI is a sub-modality of the structural MRI that encodes diffusion effects of the water molecules in the nuclear magnetic resonance signal by using bipolar magnetic field gradient pulses. The fiber tracts can be delineated in vivo based on the fractional anisotropy. *Constrained spherical deconvolution (CSD)* tractography is a modification of DTI which can provide better three-dimensional model of the neural tracts due to its ability to detect crossing fibers in the tracts.

*Functional magnetic resonance imaging (fMRI)* can depict brain activity by detecting the associated changes in brain hemodynamics by using blood-oxygen-level-dependent (BOLD) contrast. BOLD reflects cerebral blood flow (CBF) as brain function requires blood flow to supply oxygen for energy consumption by neurons. Event-related fMRI can also be used to label specific molecules with contrast agents called molecular MRI. A statistical method called *multi-voxel pattern analysis (MVPA)* implies feeding of fMRI data into a computer algorithm that automatically learns the neural patterns associated with specific thoughts or experiences.

*Single-photon emission computed tomography (SPECT)* is a functional nuclear imaging method often used to image awake behaving animals



(where a targeted brain part is stimulated using invasive electrodes or some other physical means). It uses an intravenous radiotracer to detect cerebral perfusion during activity and in turn neuronal activity (which depends on cerebral perfusion rate).

*Positron emission tomography (PET)* is the best to study neurotransmitter/receptor interactions. It has lower spatiotemporal resolution when compared to MRI. It is exquisitely sensitive for detecting the targeted molecules or processes.

*EEG* and *MEG* detect synchronized activity of an assembly of neurons by measuring LFP or magnetic fluxes. EEG and MEG can be used to explore brain cortical activation pattern with ultra-high temporal resolution and real-time recording of the event-evoked neural information flow. *Stereoelectroencephalography (SEEG)* uses *in-depth* electrodes (surgically implanted in the brain tissue) for recording electroencephalographic signals from desired subcortical nuclei in animal models.

Electrical recording of the cortex and *in-depth* brain parts has progressed much in recent years. Scalp electrodes have become more efficient. For intracranial recording, miniature multiplex electrode panels or multielectrode arrays (MEAs) can get surface recordings from large parts of the cortex very easily, and new hair-thin electrodes can reach *in-depth* brain parts without causing any significant brain damage. Wireless electrodes can be implanted in brain parts in behaving animals which can be operated from remote control to provide stimulation or recording. Magnetic transcranial and deep brain stimulation are now being frequently used to stimulate desired brain parts. Whole cell patch clamp (which can detect ionic currents in single neurons) can be used to detect neuronal activity at the level of single neurons in awake or behaving animals. Whole brain imaging of neuronal activity using fluorescent calcium indicators and multiphoton laser scanning microscopes in head-fixed behaving animals is a recent method for detecting behavior-specific neuronal circuitry.

*Diffuse optical tomography (DOT)* is an optical spectroscopy method which uses infrared

light to probe activity inside any organ. Light entering in the tissue can undergo multiple scattering, and as a result some photons are redirected back toward the tissue surface each time. The distance this light travels and the changes in its physical properties in that course carry information which can be decoded to measure events and map their locations within the brain tissue. Regional variations in oxy- and deoxy-hemoglobin concentrations as well as blood flow and oxygen consumption can be imaged by monitoring spatiotemporal variations in the absorption spectra of used light. DOT can be used to monitor brain activity; it can directly measure hemodynamic, metabolic, and neuronal responses to neurons and tissue and organ activations.

### Newer Methods

Use of inducible gene constructs for the membrane ion channels in model animals can provide high-quality information for the neural circuitry – behavior relationship. *Chemogenetics* uses systematically administered *Designer Receptors Exclusively Activated by Designer Drugs (DREADD)* targeted to the specific molecules (Kumar et al. 2018c). *Optogenetics* uses laser lights of specific wavelengths to control activation of ion channels in neurons that are genetically tagged with fluorescent biomolecules. Fine optical electrodes are inserted in the brain for light-induced manipulation of electrical activity in *in-depth* neurons and neuronal circuits. This method has revolutionized the study of animal behavior (Deisseroth 2010; Kumar et al. 2018a). *Sonogenetics* uses low-pressure ultrasound waves to activate the artificially ultrasonically sensitized neurons (Ibsen et al. 2015). *Brain-computer interface (BCI)* integrated with the neuro-recording methods like EEG is being used as a mode of study or manipulating a specific behavior based on the neurofeedback (Grau et al. 2014; Kumar et al. 2018a).

*Computational modeling (CM)* is a recent entry into the study of animal behavior. It uses computers to simulate and study the behavior of complex systems applying principles of mathematics, physics, and computer science.

The benefit of using this method is that it can predict the influence of numerous variables which characterize any system, in minuscule time, with minimum of efforts by creating simulation of the system (Pareek 2017). A simulation is created by manipulating the variables individually or in combination and observing how the alterations influence the outcomes – called in silico experiment. Computational models have the ability to study a system at multiple levels – known as multiscale modeling (Cipresso 2015).

CM is a unique tool to understand how individuals or groups influence each other's behavior in a social structure. *Virtual reality (VR)*-based experimental settings are used to manipulate behavior in a single or a small group of individuals, and information-based parameters are extracted to develop a basic computational model of the behavior dynamics. (*VR is a computer-generated simulation of the reality.*) These basic models are further used to develop simulations to understand and explain behavior dynamics at the social level in the context of the possible scenarios. CM can also be used to study behavioral pathologies in individuals or groups (Cipresso 2015).

### Neurodevelopmental Basis of Behavior

The earliest forms of behaviors in a growing fetus are simple sensorimotor reflexes when brain parts and neuronal tracts are still maturing. The primitive reflexes disappear after birth. Any return of the primitive reflexes in an adult is considered as the indicator of a neuronal lesion. Childhood and adolescent ages are the critical periods when an individual forms concepts about the environment surrounding it and develops “theory of mind, an ability to understand mental status of others,” which are very quintessential for learning social behaviors. As cognitive and behavioral domains are still maturing, children and adolescents are vulnerable to develop behavioral disorders. Poor rearing up conditions during childhood and adolescence are known to adversely affect social behavior of the individual. Certain individuals are considered more susceptible to develop such behavioral disorders due to their unique genotypic structure.

## Common Neural Mechanisms in Complex Behaviors

### Perception-Cognition-Action Triad

A behavior generates from the hierarchically arranged cortico-brain stem/spinal networks (top-down and bottom-up) of the central nervous system (CNS). Perception and cognition are the neural substrates for any behavior. Any given stimulus is received by a peripheral sensory organ which is further carried to sensory cortex of the brain through sensory pathways (entering either through the spinal cord or brain stem at the lowest hierarchical level and then through the midbrain and the diencephalon). In the sensory cortex, perception for the stimulus is generated (which can be further unified in a multimodal cortical area with the corroboratory perceptions from other sensory modalities). The perception is further encoded by cognitive domains of the brain in the form of a memory or learning, following which effectors domains generate a suitable response for the encountered stimulus based on the merits.

### Prediction Signaling, Error, and Response

It is a basic property of any neuronal ensemble that it would generate a prediction estimate against any incoming sensation or a motor command. This prediction (or *prediction signaling*) is further matched with the actual input to the nuclei. Any difference of the actual and expectant value is called *prediction error* which is used to correct the future predictions. Neuronal ensembles calculate saliency (strength) and valence (positive or negative character, which is important in reward predictions) of a stimulus. Any behavioral response is based on the prediction error values (den Ouden et al. 2012). Any behavioral response against a novel stimulus generates learning which can be stored in the specific parts of the brain as the memory patterns (or engrams), which will provide an experienced-based contribution to the future behaviors when a similar stimulus is encountered. A prediction error-based construction of the behavior will be further discussed in the section “*Behavior-Specific Neural Correlates*” of this entry.

### **Behavior-Induced Brain Plasticity and Vice Versa**

Behavior induces plastic changes in the brain components. The plasticity may involve brain part (like size of amygdala may increase in the anxiety disorders), connections, dendritic arborization and spine density, axonal sprouting, synaptic organization and formation, and neurogenesis (in hippocampus). Vice versa, the brain plasticity may have influence on cognitive abilities and behavior of the individual which in turn may induce further plasticity – a phenomenon known as meta-plasticity (Altenmüller and Furuya 2016) – and is regarded crucial for the behavioral modifications and learning motor skills.

### **Role of Neurotransmitters, Neuromodulators, and Neurohormones**

Neurotransmitters are the chemical messengers which facilitate communication of impulses at synapses. Neuromodulators (catecholamines derivatives such as dopamine, serotonin, noradrenaline, and many small peptides like enkephalin, endorphin, dynorphin, etc.) and neurohormones (which are secreted by neurons, like estrogen, oxytocin, and vasopressin) have the capacity to modulate transmission at the synapses. Though a behavior is not directly created at the synapses, synaptic communications create neural substrate for it. Along with the neurotransmitters, neuromodulators and neurohormones have critical roles in setting and maintenance of the mood. An intricately regulated cocktail of these neurochemicals not only determines the quality of synaptic communication but also sets the rate, rhythm, coupling, and synchronization of the oscillatory waves arising from cortical neurons – which is crucial for the construction of an appropriate response to the encountered stimulus (Kumar et al. 2018b).

### **Neural Basis of Sexually Dimorphic Behaviors**

We can distinguish the behavioral differences between male and female by looking at their varying responses to the same environmental stimuli, but neuroscientific basis of this is not very clear yet. The new research has gradually disapproved the earlier belief that some brain parts are sexually dimorphic. Accumulating evidence suggests the

sex-specific differences are not in the gross brain structures or neural connections but lie at the ultrastructural levels like transcriptomic and proteomic configuration of the specific brain parts and molecular arrangement and signaling at the neuronal synapses (Chen et al. 2019).

## **Salient Brain Parts/Nervous System Components and their Affiliated Behaviors**

### **Cerebral Cortex: Supreme Controller of Animal Behavior**

Ordinarily, the cerebral cortex is believed to have control over cranial and spinal regulation of motor actions. It also has limited control over basic/instinctive behaviors as hunger, thirst, or sex, which primarily involve hypothalamus. Brain has primarily four cortical lobes (frontal, parietal, temporal, and occipital lobes) controlling all kinds of behavior. Two minor lobes – insular and limbic – are also described which involve parts of the four primary lobes. (A detailed description on behavioral role of insular cortex has been provided later in this entry in segment “Emerging behavioral role for other brain parts and nervous system components.” Limbic cortex is further described with limbic system in section “[Emotional Behavior](#)” under section “[Behavior-Specific Neural Correlates](#).”) Prefrontal cortex (PFC) (anterior part of the frontal lobe) is the most important cortical part involved in the control of executive, social, emotional, or instinctive behaviors. Distinctive parts of the prefrontal cortex are involved in specific aspects of the behavior, e.g., dorsolateral prefrontal cortex (DLPFC) is involved in executive behaviors (showing intelligence) like planning, thinking, making judgments, and problem-solving. Ventrolateral and ventromedial/orbital (VLPFC and VMPFC or OFC) parts concern more to the control of social and emotional components of a behavior. Anterior cingulate cortex (ACC) is said to have crucial role in decision-making and personal/social conflict resolution. VLFC, VMFC/OFC, and ACC are also involved in fetching attention of the individual to a salient stimulus, hence working as a self-referencing center.

### Cortical Modularity-Based Cerebral Mechanisms

Cortical domains in the brain are arranged into large-scale structural and functional networks. A large-scale network can be decomposed into sets of densely connected small-world networks (based on the short average distances or closeness between connecting elements) and activated during a specific cognitive function or sensory perception (Meunier et al. 2010). Major cognitive cortical modules are saliency network (SN), default mode network (DMN), dorsal attention network (DAN) and ventral attention network (VAN), task-positive network (TPN), and central executive network (CEN). Each such small-world cortical network is defined as a module – which can be represented on a graph and contains dense structural/functional connections (called edges) between its components (called nodes). A cortical module is an evolutionarily conserved and functionally segregated network. There could be further levels of hierarchy within a module, where it can be decomposed into more densely connected clusters or subsets (Meunier et al. 2010). These cortical modules are delineated by the graph-theoretic study of fMRI connectivity pattern during rest- and task-related activity. DMN and executive/attention networks exist in anticorrelation (activation of one has deactivating influence on another) relationship and deal with “task-negative” and “task-positive” cognition, respectively. DMN gets activated when an individual is at rest, absorbed into autobiographical moments, or self-monitoring detached from the external world. Conversely, executive/attention networks get activated when individual follows a task or engages to the external world. The DMN grossly includes VMPFC, bilateral posterior cingulate cortex (PCC) and retrosplenial cortex (RspC), inferior parietal lobule (IPL), parts of the hippocampal formation, medial temporal lobes (MTL), and the angular gyrus. The CEN is anchored in DLPFC and PPC. The DAN is organized bilaterally and grossly comprises the intraparietal sulcus (IPS) and the frontal eye fields (FEF) of each hemisphere. The VAN which is said to be lateralized to the right hemisphere involves temporoparietal junction (TPJ) and the ventral

frontal cortex (VFC). Salient network (SN) comprises anterior insula (AI) and dorsal anterior cingulate cortex (dACC). SN detects relevant internal or external stimuli and also acts as a switch between DMN and ACN (and DAN/VAN).

Other than above described major cortical modules, there are many minor modules, like that for face, object, color identification, or memory recall. Major sensory perception cortical modules are that for visual, olfactory, tactile, and auditory perception.

Cortical modules hold key to specific neurophysiological processes or sensory perceptions, and cognitive functions (Hilger et al. 2017), and are building blocks for any behavior. Several of the cortical modules can be recruited to orchestrate behavioral response to any stimulus.

### Theory of Mind: A Basic Cortical Function in Social Behavior

Theory of mind is defined as a cognitive ability to understand mental status of others and develops during childhood and adolescence (as we described above). This ability is more evident in human, primates, and other animals showing higher engagement in social behavior. This is an essential ability for peaceful coexistence in a society which depends on strong social relationships and cooperations with each other. Neural correlates of *theory of mind* are not much understood though mainly cortical parts (prefrontal cortex, insular cortex, parts of parietal and temporal cortices (inferior parietal lobule, temporoparietal junction, posterior part of the superior temporal sulcus, etc.)) are said to contribute to this. A unique type of cortical neurons – “*mirror neurons* which activate when animals view others doing actions” (Carrillo et al. 2019) – is said to be crucial in developing this ability (has been described in detail along with “insula and mirror neurons” in section “[Emerging Behavioral Role for Other Brain Parts and Nervous System Components](#)”). Another type of neurons (similar to the *mirror neurons* in cortex) was recently reported in amygdala, called *simulation neurons*, which help in predicting and creating a mental simulation of others’ probable actions based on their observations (Grabenhorst et al. 2019) (further studies

will be necessary to develop a concrete concept in this regard).

### **Hypothalamus: Master Regulator of Innate Behavior**

Hypothalamus is also called as visceral brain due to its concern with the visceral functions like feeding, hunger, and thirst. It is also involved in the instinctual behavior like sex and reproduction. Hypothalamus is also the master regulator of endocrine organs, and it is the highest autonomic center in brain (Kumar et al. 2018c). Thus, hypothalamus presents a hub connecting the endocrine regulatory axis and autonomic nervous system to the rest of the brain.

### **Hippocampus: A Memory Base for the Cognitive Flexibility and Social Behavior**

The role of hippocampus has been considered important in creating cognitive flexibility and social behavior (Rubin et al. 2014). Hippocampus exerts its influence on behavior through memory. In hippocampus, registration and *long-term potentiation (LTP)* of the memory occur (Kiernan et al. 2014). Memory contents create a neural substrate for any experience-based behavior. Hippocampus has an exclusive role in learning which can create new experiences which in turn can amend an old behavior. Nearby parahippocampal region (entorhinal cortex) is known to register spatiotemporal details of the surroundings the animal resides in that creates important attribute to a learned behavior. Hippocampus has also an influence on the *hypothalamo-pituitary-adrenal (HPA) axis*, through which it regulates endocrine homeostasis, which in turn can influence behavior.

**Hippocampus Microanatomy (In Brief):** The hippocampus is located in the medial temporal lobe. It contains two parts: the hippocampus proper and the dentate gyrus. The hippocampus and dentate gyrus (DG) have the shape of a curved tube, which can be compared to a seahorse and a ram's horn (Cornu Ammonis – CA). Hippocampal subfields CA1, CA2, and CA3 are named by abbreviation of Cornu Ammonis. Hippocampus proper and DG present an allocortex bearing only three layers. The major neurons in the

hippocampus proper and DG are pyramidal neurons and granule cells, respectively. The hippocampus is reciprocally connected to various cortical and subcortical structures. Its prime cortical connection is from the entorhinal cortex (EC). The EC is located in the parahippocampal gyrus, a cortical region adjacent to the hippocampus bearing all six layers. The cortical transition zone (from three layers to six layers) between the hippocampus and EC is called subiculum. The entorhinal cortex (EC) is strongly and reciprocally connected with many cortical and subcortical structures as well as with the brain stem. Its major efferents to the hippocampus enter via perforant pathway bypassing the subiculum (Kiernan et al. 2014). Figure 1 provides a schematic description of the chief hippocampal microcircuitry connecting to EC. The reentrant signals through hippocampal-EC loop are associated with registration and long-term potentiation of the new memories.

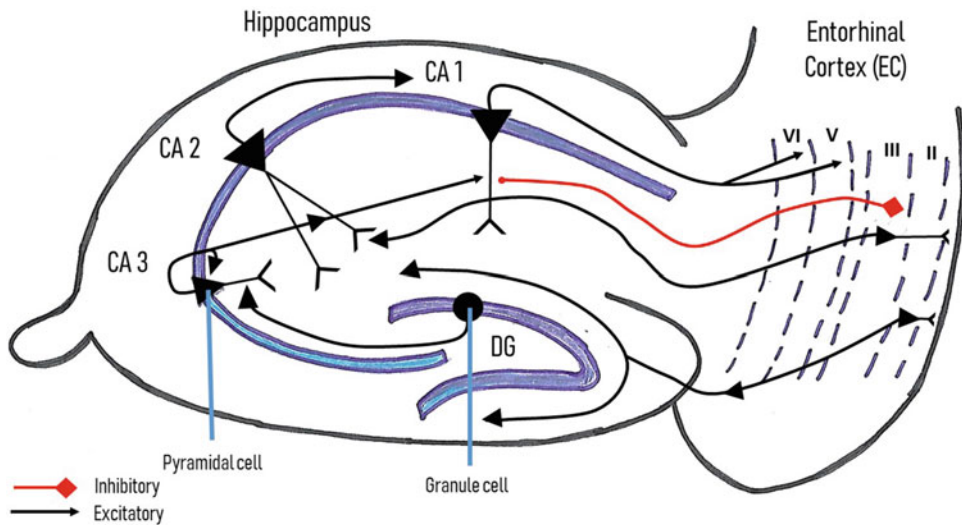
### **Basal Nuclei: A Tool for Selection of Appropriate Behavior**

Basal nuclei (BN, earlier known as basal ganglia) are a set of subcortical gray matter collections located in vicinity of the diencephalon (Kiernan et al. 2014). Earlier known roles of basal nuclei in behavior were limited to the motor functions like movement, but new research establishes its essential role in reward value-guided or motivated behavior – it helps to decide which choice will be more rewarding to follow (Hikosaka et al. 2014). Reward can be evaluated here for the short-term and long-term benefits – which give individual chance to switch from a choice based on its current value (Kim and Hikosaka 2015). Simply put, basal nuclei help to select most appropriate behavior among the available alternatives in response of an external or internal stimulus. The appropriateness of a choice is decided by competitive actions between three pathways in the basal nuclei neural circuitry, namely, direct, indirect, and hyperdirect pathways (Nambu 2009).

### **Basal Nuclei: Basic Anatomy (In Brief)**

The main components of the basal nuclei – as defined functionally – are the striatum (dorsal





**Neural Control of Behavior, Fig. 1 Hippocampal microcircuitry in behavior** (Sensory signals drive the perforant path (PP, black) excitatory inputs from EC II and III layer pyramidal neurons to granule cells in the dentate gyrus (DG, black), which in turn sends mossy fiber axons (black) to CA3, and then CA3 feeds excitatory inputs onto CA1 neurons through Schaffer collaterals (SC,

black). A major output of the hippocampus arises from CA1 pyramidal neurons, which projects back to EC (V and VI layers) thus completing the hippocampal-EC loop. Hippocampal microcircuitry also contains GABAergic interneurons (red) which modulate pyramidal neuron activity in a domain-specific manner)

striatum comprising of caudate nucleus and putamen and ventral striatum comprising of nucleus accumbens and olfactory tubercle), globus pallidus, substantia nigra, and subthalamic nucleus (STN). The globus pallidus is functionally divided into external (GPe) and internal (GPi) domains. The substantia nigra which is actually a part of the midbrain is functionally divided into two parts: the inner pars compacta (SNc) and the outer pars reticularis (SNr). The basal nuclei present a three-tier structure (input, caudate nucleus and putamen; intrinsic, GPe, STN, SNc; and output GPi, SNr nuclei) connecting cerebral cortex in a cortico-basal nuclei-thalamo-cortical (CBnTC) loop.

Basal nuclei microcircuitry in behavior is organized in CBnTC loops. There are four types of CBnTC loops which can be recruited for any behavior (Table 1) (Kiernan et al. 2014).

The three known basal nuclei pathways (direct, indirect, and hyperdirect) involve one of these CBnTC loops. Figure 2 presents a schematic diagram of the basal nuclei microcircuitry implied in behavior.

### Cerebellum: A Prime Moderator for all Behavioral Actions

Like the basal nuclei, the cerebellum was primarily known for its role in movement. New evidence suggests the cerebellum is involved in moderation of each of the functions of the cerebrum; hence supposedly it has a function to modulate the cerebral control of cognition and behavior. It was reported to be involved in the control of the reward-oriented behavior mediated by its projection to VTA – a brain stem dopaminergic nuclei which also gets projections from the prefrontal cortex (Carta et al. 2019). It gets activated several milliseconds prior to the cerebrum when we are to initiate an action or even in showing imaginary of an action (Kiernan et al. 2014). It assembles and provides experience-based feedback for correction of the prediction error (made by executive and motor centers in cerebral cortex) which brings perfection to a learned behavior (Rapoport et al. 2000).

### Cerebellar Microanatomy (In Brief)

A histological section of cerebellum would show an outer folded cortex (gray matter) surrounding

**Neural Control of Behavior, Table 1** Cortico-basal nuclei-thalamo-cortical loops in behavior

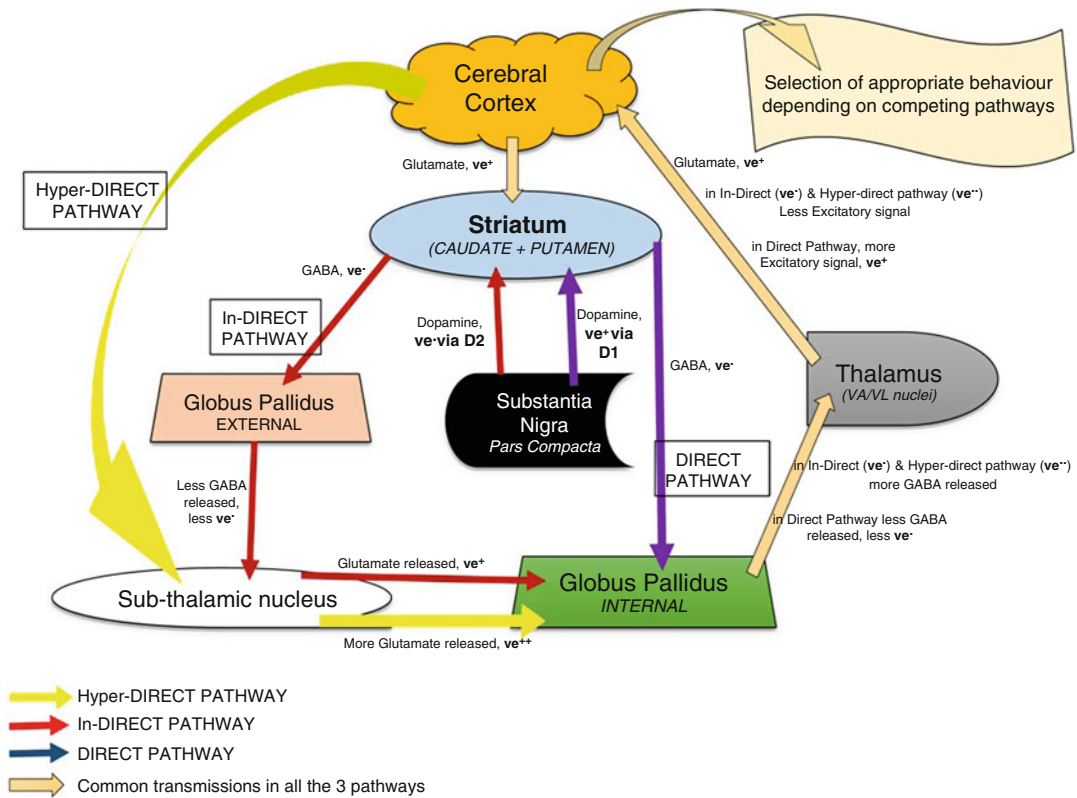
| Cortico-basal nuclei-thalamo-cortical (CBnTC) loops | Cortical input                                         | Part of striatum                     | Part of pallidum                                  | Thalamic nucleus                            | Cortical output                                         |
|-----------------------------------------------------|--------------------------------------------------------|--------------------------------------|---------------------------------------------------|---------------------------------------------|---------------------------------------------------------|
| Motor                                               | Primary somatic sensory and motor areas; premotor area | Putamen                              | Globus pallidus                                   | Ventral lateral and ventral anterior nuclei | Supplementary and primary motor areas and premotor area |
| Oculomotor                                          | Prefrontal and posterior parietal cortex               | Caudate nucleus                      | Globus pallidus; substantia nigra pars reticulata | Ventral anterior and mediodorsal nuclei     | Frontal eye fields                                      |
| Prefrontal                                          | Premotor area and posterior parietal cortex            | Caudate nucleus                      | Globus pallidus                                   | Ventral anterior and mediodorsal nuclei     | Prefrontal cortex                                       |
| Limbic                                              | Temporal lobe; hippocampal formation; amygdala         | Nucleus accumbens (ventral striatum) | Ventral pallidum                                  | Mediodorsal nucleus                         | Cingulate gyrus and orbital prefrontal cortex           |

Adapted from Bar’s The Human Nervous System: An Anatomical Viewpoint, Tenth Edition

an inner medulla (white matter) which contains deep nuclei embedded within it. There are three layers to the cerebellar cortex; from outer to inner, these are the molecular, Purkinje, and granular layers. The function of the cerebellar cortex is essentially to modulate information flowing through the deep nuclei embedded in the medulla. The molecular layer is outermost layer of the cerebellar cortex, containing two types of inhibitory interneurons: the stellate and basket cells. It also contains the dendritic arbors of Purkinje neurons and parallel fiber tracts (axons of granule cells), coming from the granular layer. The middle layer contains only one type of cell body – that of the large Purkinje cells. Purkinje cells are the primary integrative neurons of the cerebellar cortex and provide its sole output which is inhibitory in nature. The innermost layer contains the cell bodies of two types of cells: the numerous and smaller granule cells and the larger Golgi cells (Kiernan et al. 2014). Figure 3 provides a schematic description of functional cerebellar microcircuitry implied in behavior.

**Reticular Formation (RF): Center for the Generation of Consciousness, Arousal, and Behavioral Reflexes**

RF is a diffuse neural network comprising of neuronal cell bodies and nerve fibers located in brain stem core. RF contains diverse set of nuclei arranged in columns which send axons up and down to almost all brain parts including cerebral cortex and cerebellum and spinal cord segments. Their dendrites create an entangled network locally, contact with the cranial nerve nuclei which are located in the brain stem, and receive collaterals from ascending and descending tracts passing through the brain stem (except that in the posterior column for fine touch, pressure, and proprioception) (Kiernan et al. 2014). Among RF nuclei also are the aminergic nuclei which secrete adrenaline/noradrenaline, dopamine serotonin, acetylcholine, etc. and take part in reward-oriented and adaptive behavior. Ascending cortical projections from RF, called reticular activating system (RAS), relay through nonspecific midline nuclei of thalamus and then spread diffusely to all over the cortex. RAS is said to provide arousal to

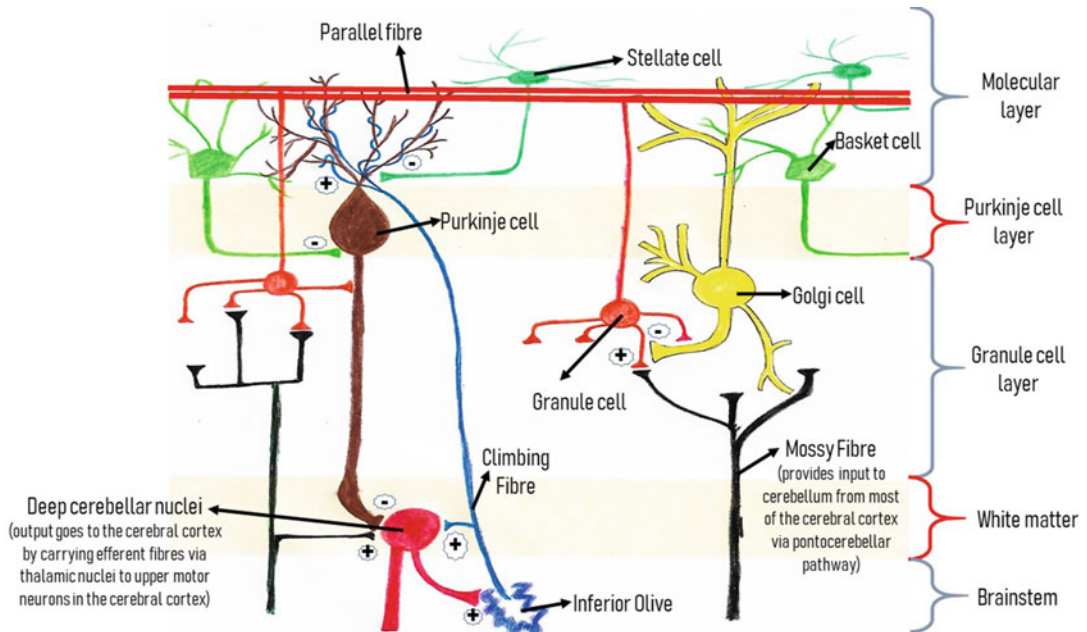


**Neural Control of Behavior, Fig. 2 Basal nuclei microcircuitry in behavior** (All the basal nuclei pathways begin with the cerebral cortex stimulating striatum by the glutamatergic efferents. Thereafter, striatum inhibits Globus pallidus “externa” in “In-Direct” and “interna” in “Direct” pathway by the GABAergic efferents. An inhibited Globus pallidus “interna” releases less amount of GABA to the adjacent Sub-thalamic nucleus, which is directly stimulated by the efferents from cerebral cortex in “Hyper-Direct” pathway. Subthalamic nucleus in turn stimulates the “interna” by more amount of glutamate

being released from it. Efferents from Globus pallidus “interna” now inhibit the thalamus, the extent of which depends upon the pathway being followed, more inhibition in In-Direct and Hyper-direct pathway as compared to that in Direct pathway. The thalamus by default stimulates the cortex by the glutamatergic efferents, which is more in Direct pathway (disinhibition) than the rest of the two pathways (inhibition). Depending upon the resultant stimulation of the motor cortex, appropriate behavior can ensue. The inhibition made by Hyper-Direct pathway is more than the In-Direct pathway)

the cortex hence to contribute to the alertness and attention. Secretions of aminergic nuclei which are mostly neuromodulators in function are also said to set the mood of the individuals. Owing to its reciprocal connections of RF to almost all brain parts similar to the claustrum, it is believed to be the “seat” of consciousness – from where the state of consciousness is controlled and maintained. Damage of RF creates coma-like conditions. RF also has reciprocal connections to autonomic centers like hypothalamus and in lateral horn of spinal segments, through which, it controls the ANS and the endocrine system. RF also has important role

in generation and maintenance of sleep, rhythmic control of respiration and cardiovascular functions, and maintenance of tone of the axial and limb muscles. Sleep is identified with reduced activity in RF neurons, in turn, less activation of the cortex through RAS. Sleep also helps to refill depleted store of aminergic neuromodulators. It has a modulatory role in pain as ascending spinothalamic fibers send collaterals to RF. Numerous nuclei of RF create polysynaptic circuits for certain reflex behaviors like chewing and eating, breathing, and head-neck movements in response of a visual or auditory stimulus.



**Neural Control of Behavior, Fig. 3 Cerebellar micro-circuitry in behavior** (The Climbing fibers and Mossy fibers are the two afferent fibers to the cerebellum. The Climbing fibers provide excitatory input from the inferior olivary nucleus of the medulla, on dendritic shafts of the Purkinje cells. The Mossy fibers are coming mainly from the cerebral cortex via pontine nuclei. The Mossy fibers synapse with the Granule cells in the granular layer of the cerebellar cortex, which in turn extend their axons into the molecular layer, where it divides and continues as the parallel fibers. The Purkinje cells are the only output of cerebellar cortex which project to the deep cerebellar nuclei. Since the Purkinje cells are GABAergic, the output of the cerebellar cortex is absolutely inhibitory. However, the deep cerebellar nuclei receive excitatory inputs from

the collaterals of the mossy and climbing fibers. The Purkinje cell inhibition of the deep nuclei serves to modulate the level of this excitation. This inhibitory activity of Purkinje cells is modulated by the interneurons like Basket cell (on the body) and stellate cell (on the dendritic shaft) from the molecular layer; both of the latter cells receive excitatory inputs from the parallel fibers. The molecular layer contains the apical dendrites of a cell type called Golgi cells; these neurons have their cell bodies in the granular cell layer. The Golgi cells receive excitatory inputs from the parallel fibers and in turn provide an inhibitory feedback to the granule cells. The output from the deep cerebellar nuclei reaches the thalamic nuclei and then to the motor cortex modulating their ongoing neuronal activity)

### Autonomic Nervous System (ANS): Prime Controller of Adaptive Behavior

Autonomic nervous system (ANS) is known to have very important role in innate as well as learned behavior. ANS has the sympathetic and parasympathetic components and bears a larger bodily spread than CNS. Hypothalamus presents the highest center of the ANS with vaguely distinguishable sympathetic and parasympathetic components. Brain stem contains the parasympathetic outflow only. Spinal cord contains thoracolumbar sympathetic outflow and sacral segment parasympathetic outflow. ANS is engaged in control of the animal behavior, by resetting hypothalamic circadian clock in

suprachiasmatic nuclei (SCN) and the neuroendocrine balance along the HPA axis, in turn, influencing neuroeffector communication at the peripheral targets in response of the external or internal stimulus. Hypothalamic autonomic nuclei send reciprocal connections to spinal autonomic centers. Innate behaviors like hunger, thirst, and sexual behavior are known to be regulated by contrasting influences of sympathetic and parasympathetic components of the ANS. Sympathetic component of the ANS is said to be greatly involved in the adaptive behaviors which present survival challenges like fight, flight, and fright situations (Kumar et al. 2018c). An activation of sympathetic component is associated with

aggression, anxiety, panic reaction, and disturbed appetite; in contrast an activation of parasympathetic component may be associated with ease of the mood, relaxation, good appetite, sexual excitation, and orgasm.

### **Emerging Behavioral Roles for Other Brain Parts and Nervous System Components**

#### **Insula and "Mirror Neurons": In Awareness of the Self-Action and That of Others**

Insular cortex which is anatomically buried between frontal, temporal, and parietal cortices is said to be involved in introspection and awareness of the "self-actions" (Namkung et al. 2017). A specific type of neurons, "mirror neurons," which are said to be present in anterior part of the insula (and also in frontal, temporal, and parietal cortices surrounding it), and ACC are believed to be principle to the awareness of the "self-actions" (Ramachandran 1995). Mirror neurons are also present in premotor regions of prefrontal cortex, temporoparietal junction (TPJ), or inferior parietal lobule (IPL). These neurons were first reported in macaque monkeys, when it was found that these neurons activated not only during performance of a task but also when a monkey was made to observe others doing it. Mirror neurons were also said to be behind social behaviors like understanding what others think or feel (hence in empathizing) (Carrillo et al. 2019), or learning by imitation of others' actions (Ramachandran 1995).

#### **Habenula: In Reward-Based Decisions and Adaptive Behavior**

Habenula is involved in the regulation of release of neurotransmitters and modulators from brain stem aminergic nuclei which is thought to be a central mechanism for developing an adaptive response to a persistent stimulus. Habenula is an evolutionarily conserved bilateral structure located at the interface of the diencephalon, basal nuclei, and brain stem which works as a gateway between cortical-subcortical and brain stem structures (Kiernan et al. 2014; Kumar et al. 2017b). It is thought to function as a switchboard for regulating emotional behavior in

conditions facing survival challenges (e.g., to avoid or approach or submission or freezing in response of a stimulus). Medial and lateral components of the habenular pathway are involved in positive and negative reward prediction, respectively, making their balanced action crucial for decision-making in reward-oriented behavior (Kumar et al. 2017b). Any adaptive behavior also involves modulation in the settings of the hypothalamo-pituitary-adrenal (HPA) axis.

#### **Clastrum: In Unified Perception and Consciousness**

Clastrum is a thin sheet of gray matter sandwiched between insular cortex and striatum (it is separated from the insular cortex by the extreme capsule and from the striatum by the external capsule). Its unique location allows it to connect to all parts of the cerebral hemisphere reciprocally. It also sends reciprocal connections to contralateral hemisphere and other brain parts as hippocampus, amygdala, basal nuclei, thalamus, brain stem, and nearly all other parts of the brain. Uniquely, contralateral claustrums also connect with each other through interclaustral fibers. Empirical studies are scarce on the functional role of claustrum. Any direct role in behavior is not known, but recently proposed functions to claustrum suggest that it creates a neural base for production of any behavior. A study in the epileptic patients which placed electrodes in at one site of the white matter tract beneath the claustrum made the patient to stare blankly ahead with no recall of event when stimulus was removed (Koubeissi et al. 2014). The above said observation suggested mechanistic role of claustrum in the generation of consciousness. Claustrum fibers topographically connect with the deeper layers of cortex (mostly layer six). Claustral efferents to the cortex mostly end at the interneurons hence indirectly bear inhibitory influence on the pyramidal neurons. Inhibition of the cortex by the claustrrocortical fibers is said to have modulatory effect on the electrical activation pattern of the cortical segments (Jackson et al. 2018). Studies also suggested its role in real-time synchronization of electric waves and oscillatory coupling of two cortical regions bound to a common



cognitive function (Narikiyo et al. 2018). Francis Crick, based on its universal cortical connections (and also to the other brain parts) and role in coordination of the cortical electrical activity, proposed its role in generation of consciousness and being conductor of the information flow through the cerebrum (like conductor of an orchestra who directs whole band!) (Crick and Koch 2005). Function of claustrum resembles to an electrical device which performs multimodal integration of the stimulus information across the brain parts hence helps to create a unified sense of perception and generates a continuous flow of consciousness.

#### Enteric Nervous System (ENS): Mediator of the Gut-Motivated Behavior

ENS-CNS connection has given rise to concept of gut-brain axis. ENS is predominantly autonomic in function, and in concert with the gut hormones, it helps to maintain mood and emotion of the individual. New research has established its role in reward-mediated behavior. Uniquely, enteroendocrine cells in the gut mucosa were found to connect to the vagus nerve which is a parasympathetic nerve supplying the gut (Han et al. 2018). Right vagus nerve which innervates gut was found to carry gut impulses to the dopaminergic nuclei in the brain stem – which present important component of reward pathway connecting to the forebrain (Han et al. 2018). Parkinson's disease, a neurodegenerative disease of nigrostriatal pathway in the brain, is believed to start in ENS neurons of the large gut. A dysregulation of gut-brain axis has also been found implicated in the psychological stress and mood disorders like anxiety and depression.

## Behavior-Specific Neural Correlates

### Simple Behavior

#### Limb Reflex

A reflex is a rapid and involuntary response to a stimulus or cue. It is controlled at the level of spinal cord and is considered as a protective mechanism to a suddenly presented threatening stimulus (which is either painful and/or can

potentially injure the organism). A reflex is generated by a sensory-motor circuit of spinal neurons (Fig. 4) and doesn't involve a cortical control. Certain of the reflexes are also controlled at the level of brain stem; these are head and neck movements, mastication, and vital bodily functions such as cardiovascular circulation and respiration.

### Complex Behavior

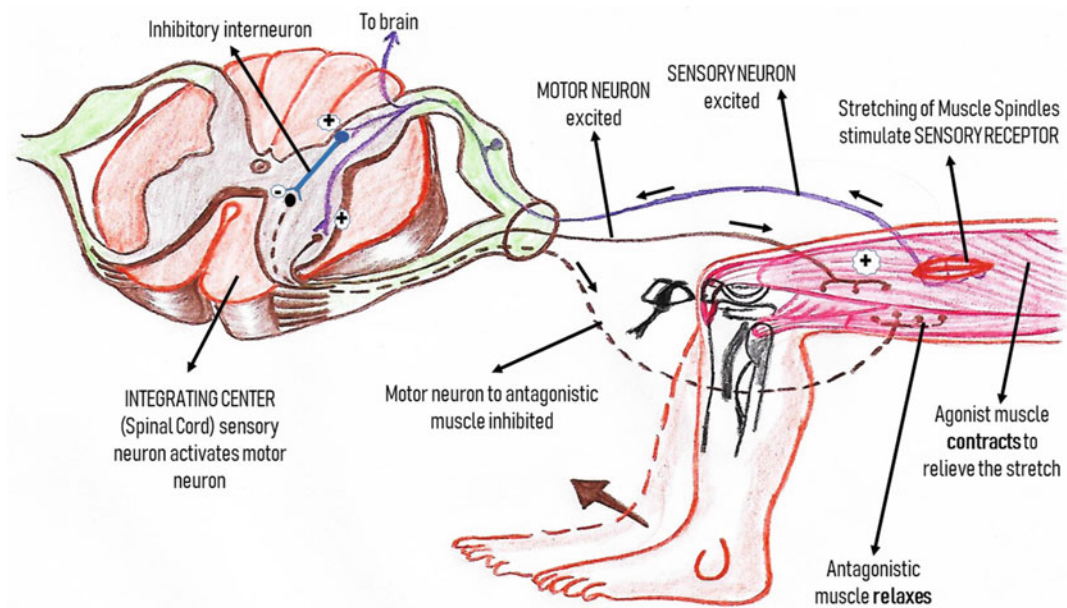
#### Emotional Behavior

Emotional behavior is said to be generated and controlled by the *limbic system* in the brain. *Limbic system* comprises a rim of cortical mass surrounding the diencephalon – also called as *limbic lobe*, a set of subcortical nuclei – and white matter connections between them (Fig. 5) (Kiernan et al. 2014). *Amygdala*, a quasi-cortical gray matter mass, is one of the main components of this system. Amygdala is also called a center for fear, aggression, anxiety, and panic, or more correctly, it predicts salience value for any emotional information (Janak and Tye 2015). A connection between amygdala and prefrontal cortex is said to exert control over impulsive behavior where prefrontal control is inhibitory to amygdala, and their relationship is antagonistic (Volman et al. 2011).

The neural circuitries related to memory, centered at hippocampus, are extensively connected to the limbic system (as memory contents make essential ingredients of any emotional behavior). Also, autonomic and endocrine systems, which are centered at hypothalamus, are intensively linked with the limbic system, and their associated activations contribute to the physical and psychological manifestations of any emotional behavior.

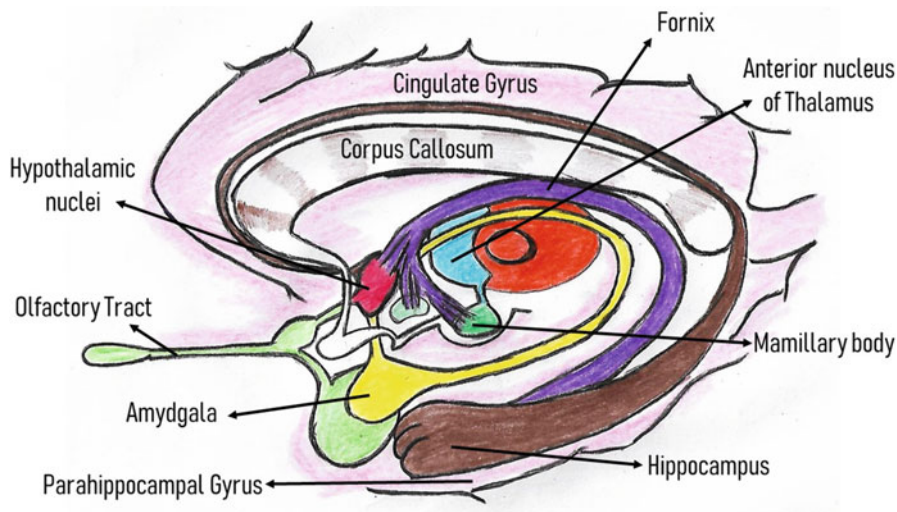
#### Reward-Driven Behavior

*Mesolimbic or reward pathway* – a dopaminergic circuitry – connects *ventral tegmental area (VTA)* in the midbrain to ventral striatum or *nucleus accumbens (NAc)* in the forebrain (Kiernan et al. 2014). This is the prime circuitry (VTA-NAc) involved in all kinds of reward-based behavior including natural responses for food and sex and social interactions (Fig. 6).



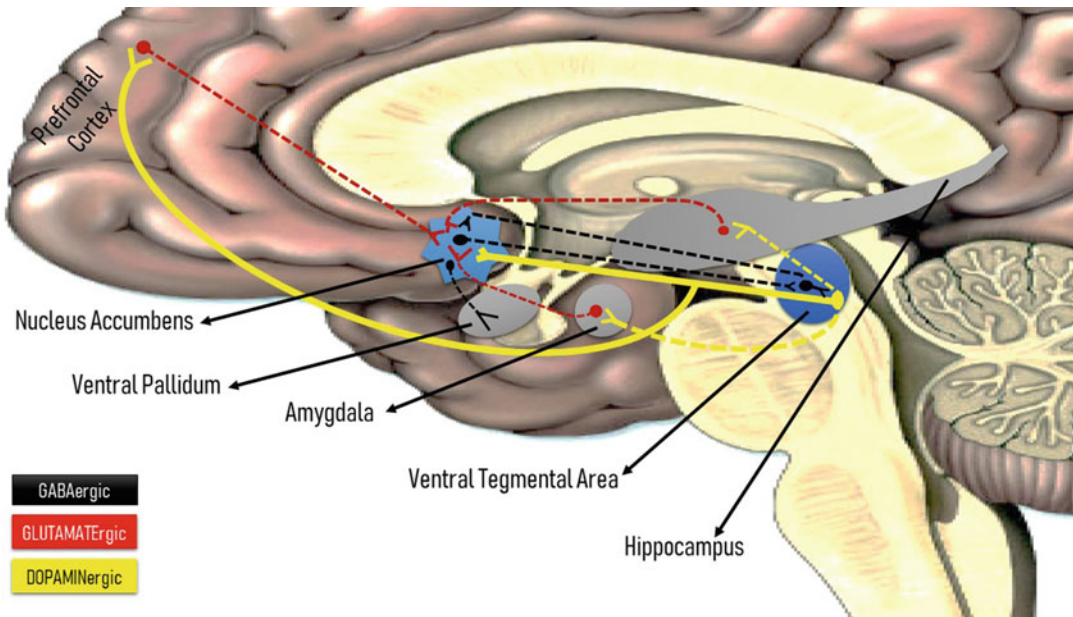
**Neural Control of Behavior, Fig. 4** A limb reflex arc (Hammer tap stretches tendon which in turn stimulates sensory receptors (spindles) in the agonist muscles. Sensory neurons (blue) synapse with and excite motor neurons (brown) in the ventral horn of the spinal cord. The motor neurons innervate agonist muscle fibers (brown, intact

line), and their stimulation causes immediate contraction of these muscles. Sensory neurons also excite spinal interneurons (purple) which in turn synapse to and inhibit motor neurons innervating the antagonist muscles (brown, broken line), causing their relaxation)



**Neural Control of Behavior, Fig. 5** Limbic system (The limbic system is a complex set of structures found on the central underside of the cerebrum, comprising inner sections of the temporal lobes and the bottom of the frontal lobe. It combines higher mental functions and primitive

emotion into a single system often referred as the emotional nervous system. The primary structures within the limbic system include the amygdala, hippocampus, thalamus, hypothalamus, basal ganglia, and cingulate gyrus)



**Neural Control of Behavior, Fig. 6 Reward pathway**  
 (The reward pathway is principally a dopaminergic pathway (yellow, solid line) that connects ventral tegmental area in midbrain to nucleus accumbens of ventral striatum and the prefrontal cortex of cerebrum. Apart from dopaminergic efferents, the nucleus accumbens also receives

inputs from the Glutamatergic neurons (red, broken lines) of the hippocampus, amygdala, and medial prefrontal cortex. After being activated by glutamatergic inputs, GABA release (black, broken lines) occurs onto the ventral pallidum, consequently causing cortical disinhibition)

This pathway is intensely connected to various cortical and subcortical regions, hippocampus, and brain stem nuclei. Prefrontal cortex keeps this circuitry inhibited and hence puts a break on reward-based behavior. This circuitry is involved in the addictive behavior and is also implicated in obsessive-compulsive disorders. Reward pathway is evolutionarily conserved among animal species which is based on the release of dopamine when presented with a desirable stimulus. Same circuitry is involved in aversive behavior and stress where a reduction in dopamine release brings displeasure.

*Reward system* works on the prediction error signaling (den Ouden et al. 2012). Reward centers, which contain dopamine-releasing nuclei, generate prediction for the expected reward following behavior. A prediction error is computed by these nuclei deducting the prediction estimate from the actual reward value (den Ouden et al. 2012). When this actual reward is more than what was expected, a positive prediction error is

generated which causes release of dopamine – causing pleasure and in turn enforcing/motivating the individual to repeat the behavior. When actual reward is less than expected, a decrease in dopamine release (depression) is to occur – causing displeasure and in turn aversion from that behavior. When expectation is fulfilled, there has to be a normal release, causing no/or little enforcement to repeat the behavior. There is hierarchical difference in coding of reward along the reward pathway. The neurons at the down most center, SNc/VTA, activate with any novel information irrespective of its nature (i.e., each novel information is rewarding to the subject) based on its saliency. Neurons in NAc encode both saliency and valence of any incoming information. PFC encodes saliency as well as valence of any incoming information though its components exert differential influence on the reward pathway. Neurons in VMPFC/OFC activate more in positive prediction signaling, i.e., reinforce a rewarding behavior, and in DLPFC activate more in the

negative prediction signaling, i.e., create aversion for a non-rewarding behavior (Fouragnan et al. 2018).

### Adaptive Behavior

Adaptive behaviors, like response of the individual to a threatening or rewarding stimulus or situation like success or failure, win or defeat, have a complex neural circuitry which chiefly involves medial and orbital PFC, ACC, and anterior portion of the insula. Also are involved in this, cortical and subcortical components of the reward pathway, septal nuclei, and anterior hypothalamic nuclei. Emerging evidence suggests master role of the habenula in regulation of the adaptive behavior (has been described in detail in section “Emerging Behavioral Role for Other Brain Parts and Nervous System Components”).

**Miscellaneous: Love, Lust, Hate, Disgust, Religious/Ideological Fundamentalism, and Crowd Behavior** Though available knowledge on neural correlates of these behaviors is still limited, functional neuroimaging studies put some light on the brain parts grossly involved. Affectionate love is known to activate specific cortical and subcortical components of the limbic system which is overlapped but effectively distinct from the sexual attraction. The core brain regions that activate in a loving behavior are medial PFC, ACC, anterior insula, head of caudate nucleus or putamen, and VTA (Diamond and Dickenson 2012). In sexual attractions, activation of caudate nucleus and VTA is less distinctive, and an additional activation of the amygdala and hypothalamus occurs (Diamond and Dickenson 2012). Showing hateful and disgust behaviors also causes activation of the amygdala. Hateful behavior similar to the loving causes activation of the putamen and insula but, in contrast, causes deactivation of frontal, temporal, and parietal cortices (Zeki and Romaya 2008). Reward (or aversion) pathway is activated both in loving and hateful (or showing disgust) behavior. More ventral regions of the striatum and pallidum get involved in rewarding behavior like lust or aversive behaviors like hate or disgust. Increase in secretions of oxytocin by the hypothalamic nuclei (Heinrichs et al. 2009) and neurotrophins by

cortical neurons is known during loving behavior (Emanuele et al. 2006). Religious and ideological fanaticisms (fundamentalisms) are known to cause more activation of medial/ventral prefrontal cortex with relative silencing of DLPFC. DLPFC is thought to have role of a critic and activates more in a rational behavior – when individual uses reasoning to select a response (Harris et al. 2009). Crowd behaviors involve complex interactions between prefrontal cortex and limbic system components, with a lesser prefrontal cortex-mediated inhibition of the amygdala (Huis in ‘t and de Gelder 2015). An added influence of oxytocin and vasopressin (secreted by supraoptic and paraventricular nuclei of the hypothalamus, respectively) on decision-making by individual members has been evidenced in such behaviors (Heinrichs et al. 2009).

### Neural Basis of the Pathological Behaviors

Brain parts involve differentially in various known pathological behaviors. A dysregulation of reward pathway is associated with many pathological behaviors like addiction, substance abuse, and gambling (Yun et al. 2016). An amygdala-prefrontal imbalance has been associated with aggression, anxiety, depression, and panic reaction and the diseases like major depressive disorder (MDD) and bipolar disorder (BPD) (Volman et al. 2011). MDD and BPD have also been linked with altered activity of hippocampal neurons. An abnormal activity at temporoparietal cortical junction (TPJ) has been associated with hallucinations in schizophrenia. A hyperactivity of the dopaminergic neurons in reward pathway has been noted in psychotic disorders. A dysregulated brain plasticity also has been attributed for the pathological behavior, like excess anxiety, aggression, panic, or post-traumatic stress disorder (PTSD) (Kays et al. 2012). Social defeat and self-harming behaviors involve experience induced dysregulated plasticity in the brain regions involved in adaptive behavior like prefrontal cortex, amygdala, and aminergic nuclei in the brain stem. Dysregulation of the basal nuclei circuitry has been suggested in obsessive-compulsive disorders (OCDs).



Dysregulation of the neural circuitry involved in adaptive behavior also can give rise to certain behavioral pathologies. Repeated social defeat may induce a state of chronic unpredictable stress (CUS) and learned helplessness (a behavioral state in which individual no more explores for a safer option) in the individuals. CUS may be a reason for self-harming behavior seen in some individuals – which supposedly give them some sense of release from a conflicting condition or mental strain (Blasco-Fontecilla et al. 2016).

Owing to the increasing daily life use of new information technology facilitated digital devices like computers and smartphones, certain new behavioral disorders have emerged. “Problematic use of the Internet (PUI)” is an umbrella term for such disorders which involves “Internet video gaming and pornography,” excessive social media network use, and selfitis – an excessive preference for selfie taking and posting it on social media. Though many of the PUI-affiliated disorders are still not recognized by Diagnostic Statistical Manual (DSM) of psychiatry, emerging research suggests these behaviors involve reward system of the brain quite similar to other recognized addictive behaviors (Kumar et al. 2017a).

## Cross-References

- Behavior Systems
- Endocrine System
- Heritability of Behavior
- Hormones and Behavior
- Model Fitting
- Theory of Mind

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## Neural Impulse

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In the 1880s, Santiago Ramón y Cajal made a series of significant observations using a histological staining technique developed earlier by Italian physician Camilo Golgi (1843–1926). These discoveries were based on his ability to demonstrate the extensive, and oddly branched, individual elements of all nervous systems. These basic elements are the neurons, considered the basic unit of the nervous system (Nichols 2001).

Cajal's discoveries led to the establishment of the “neuron doctrine,” which states that the nervous system, like other organs, is made up of individual cells, in this case “neurons.” These neurons process and exchange signals with one another at specific points of contacts called synapses, called so by the neurophysiologist Charles Scott Sherrington (1857–1952). The idea of “reticular” organization, in which the cells of the nervous system were supposedly fused into a multicellular, syncytium-like continuum, therefore had to make way for the extension of cell theory to the nervous system. The discovery of the

nervous system are really system of the neurons, provide the first step for a number of observations and scientific investigation about the function of the brain, and marked the birth of the modern neurobiology (Sherrington 1906).

Nowadays, it is well known that the nervous system is composed of two main types of cells: neurons and glial cells. Glial cells (from the Greek word that means “glue”) outnumber neurons by about 10–1, and they account for about half of the volume of the nervous system. Together, glial cells nourish the neurons, remove their wastes, and defend against infections. Glial cells also provide a supporting framework for all nervous system tissue. Individual neurons are organized into tissues called nerves, which are grouped into nerve bundles and surrounded by protective connective tissue. Like optical fiber cables, which carry many individual wires from one part of network to another, the nerves extend the neurons throughout the entire central and peripheral nervous system (Nicholls 2001).

Just like glial cells, neurons must fulfill metabolic functions and participate in the exchange of substances; they have the same genes, the same biochemical mechanism, and the same organelles as other cells. However, neurons differ from other cells in one important thing, they process information and transmit it in the form of electrical impulses to neighboring cells. Each single neuron contributes to information processing in several ways. As receiver unit, it takes up signal from other neurons and converts these signals into propagated electrical activity to other location and then transfers the electrically encoded information to receiving neurons. The process of signal conversion and conduction is favored by the anatomy of the cell structure (Purves et al. 2004).

The ability of neurons or nerve cells to process information is due to the properties of their cell membranes. The synaptic integration is based on the electrical properties of the neuronal membrane. Like other cells membranes, the neuronal cell membranes are made up of lipid bilayer into which various membrane proteins are incorporated. One can classify the membrane proteins either as structural receptors, enzymes, pumps, or channels, although these different classes are

not mutually exclusive. Structural proteins contribute to the maintenance of cellular structure and the formation of connections among neurons. Receptors allow the recognition of specific signals transmitting molecules. Enzymes facilitate chemical reaction in or near membrane. Receptor and enzymes control the production of a postsynaptic signal during transmission at chemical synapses. Pumps, by using metabolic energy, can establish ionic gradients or gradients of other molecules, such as water, across the membrane. Channels allow charged ions and molecules passage through the hydrophobic lipid bilayer of the membrane. The electrical activity in nerve cells results from the interaction between ion pumps and ion channels. Ion pumps and ion channels, working together, generate electrical phenomena such as resting potential, action potentials, and synaptic potential.

Therefore, due to characteristics of the neural membranes, they are capable to establish a voltage difference between the inside and outside of the cells membrane, and they use this voltage difference to generate a neural impulse.

A neural impulse consists of a series of action potentials, in response to a change in the resting membrane potential. To understand the process of neural impulse, it is imperative knowing the electrical bases of the neural excitation.

## Resting Membrane Potential

The presence of ion channels in the cell membrane and proteins, such as sodium-potassium exchange pumps ( $\text{Na}^+/\text{K}^+$  ATPase), allows the separation of ions (mainly  $\text{K}^+$ ,  $\text{Na}^+$ ) in the intracellular and extracellular compartment, generating ionic gradients. This process allows a more negative charge in the cytoplasm than in the extracellular space. This charge separation across the membrane is a form of potential energy, called membrane potential, and the potential difference across the membrane in resting neurons is called resting membrane potential. The resting membrane potential of most unstimulated neurons is  $-70$  mV (millivolts). The resting membrane potential provides energy for the generation of a neural impulse in response to appropriated stimulus. Thus, the resting potential maintains the

membrane of neurons in a condition of readiness for an impulse to occur. The energy of any eventual impulse is stored in the electrochemical gradient across the membrane (Wright et al. 2004).

## Graded Potential

As previously stated, the action potential is the major signal sent down the axon. By contrast, the graded potential takes place at the dendrites and cell body; this potential varies in size and determines whether an action potential will be sent or not. Graded potentials are small changes in membrane potential that are either excitatory (depolarize the membrane) or inhibitory (hyperpolarize the membrane). A certain level of excitatory graded potential must happen at once to depolarize the cell body enough to trigger the action potential (Wright et al. 2004).

## Action Potential

To understand an impulse, we first need to focus on an individual action potential taking place on one tiny segment of the axon membrane, called nodes of Ranvier. These nodes of Ranvier are myelin-free structure in the axonal membrane, where the presence of  $\text{Na}^+$  channels is higher. The action potential starts when the neural membrane is “depolarized,” this means that the membrane potential is reduced to less ( $-55$  mV) than the resting membrane potential of  $-70$  mV. The action potential can be divided into four phases:

1. Threshold potential: positive ions flow into the negative cell, generating a difference, decrease, in the cell's polarity (from  $-70$  to  $-55$  mV). If the cell body gets positive enough that it can trigger the voltage-gated sodium channels found in the axon, then the action potential will be sent.
2. Depolarization: makes the cell less polarized (membrane potential gets smaller as ions quickly begin to equalize the concentration gradients). Proteins called voltage-gated sodium channels at the part of the axon closest to the cell body activate, thanks to the recently

depolarized cell body. This lets positively charged sodium ions flow into the negatively charged axon and depolarize the surrounding axon. We could view the channels opening like dominoes falling down, once one channel opens and lets positive ions in, it sets the stage for the channels down the axon to do the same thing. Though this stage is known as depolarization, the neuron swings past equilibrium and becomes positively charged as the action potential passes through.

3. Repolarization: brings the cell back to resting potential. The inactivation gates of the sodium channels close, stopping the inward rush of positive ions. At the same time, the potassium channels open. There is much more potassium inside the cell than out, so when these channels open, more potassium exits than comes in. This means the cell loses positively charged ions and returns back toward its resting state.
4. Hyperpolarization: makes the cell more negative than its typical resting membrane potential. As the action potential passes through, potassium channels stay open a little bit longer and continue to let positive ions exit the neuron. This means that the cell temporarily hyperpolarizes or gets even more negative than its resting state. As the potassium channels close, the sodium-potassium pump works to reestablish the resting state.

Action potentials work on an all-or-none basis. This means that an action potential is either triggered, or it isn't, like flipping a switch. A neuron will always send the same size action potential. When the neuron is highly excited, it fires off multiple signals, with the rate of neural firing correlating with the intensity of the original stimulus: the more intense the signal, the higher the frequency of action potentials. There is a maximum frequency at which a single neuron can send action potentials, and this is determined by its absolute and relative refractory periods.

Absolute refractory period: during this time, it is absolutely impossible to send another action potential. The gates inactivation of the  $\text{Na}^+$  channels lock shut for a time, and make it so no sodium will pass through. No sodium means no depolarization, which means no action potential.

Absolute refractory periods help direct the action potential down the axon, because only channels further downstream can open and let in depolarizing ions.

Relative refractory period: during this time, it is really hard to send an action potential. This is the period after the absolute refractory period, when the gates are open again. However, the cell is still hyperpolarized after sending an action potential. It would take even more positive ions than usual to reach the appropriate depolarization potential. This means that the initial triggering event would have to be stronger than normal in order to send more action potentials along. Relative refractory periods can help us figure how intense a stimulus is; cells in your retina will send signals faster in bright light than in dim light, because the trigger is stronger (Barnett and Larkman 2007).

Refractory periods also give the neuron some time to replenish the packets of neurotransmitter found at the axon terminal, so that it can keep passing the message along. While it is still possible to completely exhaust the neuron's supply of neurotransmitter by continuous firing, the refractory periods help the cell last a little longer.

Because action potential is forced to "jump" from one node of Ranvier to the next due to the myelin sheath, the conduction of an impulse along a myelinated neuron is called *saltatory conduction*. A similar process occurs in unmyelinated neurons. In these neurons, however, action potentials can occur at all locations along a membrane. Therefore, they occur next to each other. As a result of so many action potentials occurring all along the axon, the transmission of an impulse along an unmyelinated axon is much slower than the saltatory conduction along a myelinated axon (about 0.5 m/s, compared with as much as 120 m/s in a myelinated axon) (Nicholls et al. 2001).

The nerve impulse, generated by action potentials, travels the length of the axon until it reaches the far end, called synaptic terminal (presynaptic terminal). In this structure, the nerve impulses induce the release of chemical messengers (neurotransmitters) that diffuse across the synaptic cleft, taking 0.5–1 ms to reach the next neurons (postsynaptic cell). These chemical messengers bind to specific receptor in the membrane of the

postsynaptic neuron, generate a depolarization of the membrane, and, if the threshold potential is reached, initiate an action potential and continue the nerve impulse.

## Cross-References

- [Action Potentials](#)
- [Neural Control of Behavior](#)
- [Neural Impulse](#)
- [Neural Network](#)

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## Neural Network

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## Synonyms

[Brain circuit](#); [Neural circuit](#); [Complex arrangement](#); [Complex system](#); [Connectionist network](#); [Interconnected structure](#); [Interconnected system](#); [Neural architecture](#); [Nexus](#)

The expression **neural network** is much more recent than its constituent terms. The adjective **neural** relates to the adjective **neuronal**, from

the noun **neuron** (see the entry “[Neuron](#)” in this encyclopedia). This noun originated with von Waldeyer-Hartz’ (2016) German **neurone**, coined in 1891, likely inspired by the Greek νεῦρον or νεῦρον, meaning “nerve,” which he used as synonymous with **nerve cell**. He proposed it as a technical term for a kind of cell that constitutes brain tissue, marking the birth of the *neuron doctrine* (see Shepherd 2016), the now universally accepted thesis that brain tissue, like any other tissue, consists of *discrete*, individual units called “cells.”

The noun **network** is much older, dating from the 1500s, and is a contraction of the nouns **net** and **work**. Skeat (1910, p. 334) defines **net** as “an implement made of knitted or knotted twine for catching fish” (p. 399), present in Middle English (roughly between 1200 and 1460) as **net** and **netten**. Current uses of **net** in **network** are reminiscent of this sense. The noun **work** is from about the same time but has a more complex etymology. According to Skeat (1910), the term comes from the Middle-English **werk**, meaning “thing done or written” (p. 722) and “to do.” Current usage is reminiscent of this origins, where a network is “an arrangement of intersecting horizontal and vertical lines,” “a number of interconnected computers, machines, or operations,” or “a system of connected electrical conductors” (<https://www.lexico.com/en/definition/network>).

## General Intuitive Initiation

These meanings lead to a very rough, preliminary notion of a neural network as a system of *units* (or elements, nodes, or vertices) that are *mathematical models* of neuronal activity, linked through *connections* (or edges) that are mathematical models of synaptic plasticity (changes in synaptic strength). Some uses of **neural networks** refer to systems of biological, natural, and organic neurons connected through biological synapses (e.g., brain circuits), but I will not follow these uses. In this entry, I will refer only to *theoretical* or *artificial* neural networks and call them just “neural networks” (NNs).

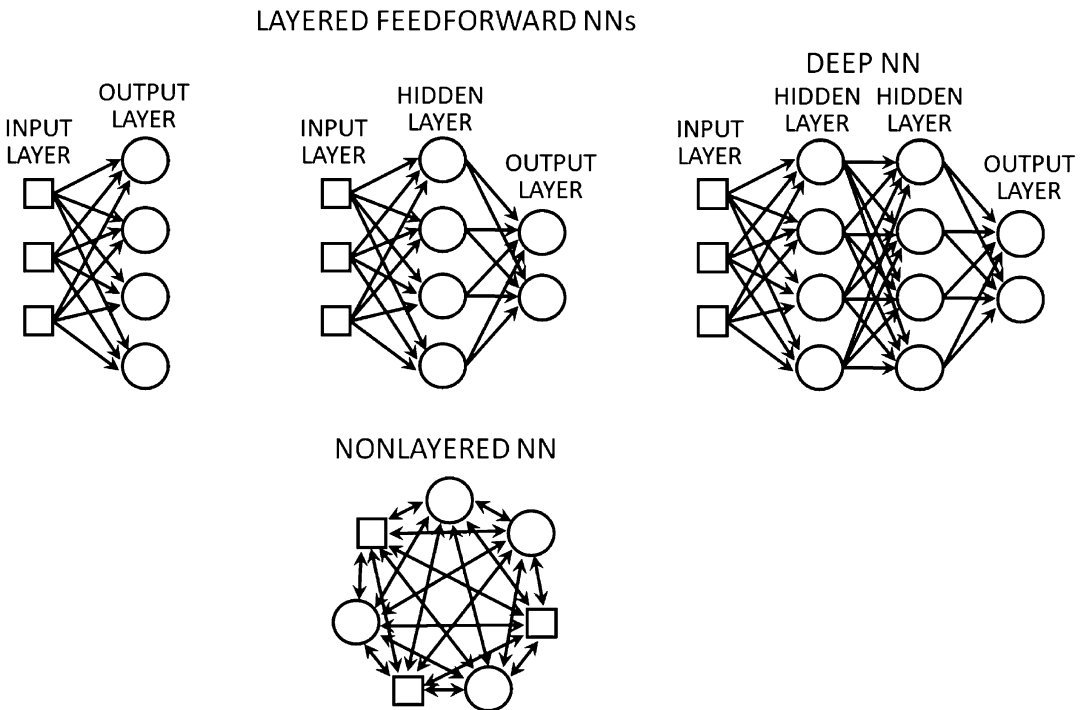


Figure 1 shows a few examples of very small NNs thus defined (I will elaborate some of the technical details in the third section). (NNs in most modeling research are much larger.) There are two types: layered (upper panel) and non-layered (lower panel). In layered networks, the most common, units are arranged into *layers*, depicted here as *columns* of units (it is also common to depict layers as rows). Layered NNs in early modeling had only two layers, input and output (upper left panel), but as I elaborate later, they suffered from critical insurmountable limitations.

An input layer consists of input units (squares) that function as detectors of external environmental

events (in depictions of layers as rows, the input layer is commonly placed at the bottom row). Each layered NN in Fig. 1 has three input units. The output layer consists of output units whose functioning represents a NN's performance or responding, the final stage of a NN's functioning (in depictions of layers as rows, the output layer is commonly placed at the top row).

Most layered NNs also have at least one *hidden* layer (middle upper panel) between the input and output layers, but many NNs have more (right upper panel) and are known as *deep* NNs, which have become quite popular during the last decade. Units in non-layered NNs do not have layers, so in principle any nonspatially contiguous units could



**Neural Network, Fig. 1** Examples of two types of NNs: layered (top panel) and non-layered (bottom panel). In layered NNs, units are arranged into layers depicted here as columns of units. These NNs have at least two layers of units, input and output (upper left panel), but most (middle and right upper panels) include at least one *hidden* layer between the input and output layers. The input layer consists of input units (squares) that detect external environmental events (the layered NNs here have three input units). Computational units are represented as circles. Connections are represented as arrows and typically have

changeable strengths numerically represented as *weights* that change according to a *learning* algorithm. Typically, connections in feedforward NNs are *unidirectional* in that a connection goes *from* a unit *i* to another unit *j*, but not vice versa. Therefore, *i* can affect *j* but not vice versa. In the input-output NN, the input units connect to and affect the output units directly. In contrast, connections in the non-layered NN are bidirectional. In this NN, then, the units are *completely interconnected*. Units in non-layered topologies have no particular arrangement

function as inputs. In the non-layered NN in Fig. 1, for example, I arbitrarily chose three separate units as inputs.

Neural units (circles) function according to a model of neuronal activity in the form of an *activation function*, used to calculate a unit's *activity* or *activation state* at some moment  $t$ . (I depict input units differently because their states are *assigned* according to a training protocol that defines the task a NN is to do.) Connections are depicted as arrows and usually have changeable *strengths* numerically represented as *weights* that change according to a *learning function*. Connections represent abstract, theoretical synapses or synaptic groups and are the means through which units *influence* each other's activation states, depending on the connection weights (the larger the weight, the greater the influence).

In layered NNs, connections are *unidirectional* in that a connection *projects from* a unit  $i$  to another unit  $j$ , such that  $i$  can influence  $j$  but *not* vice versa. In this sense, layered NNs have a layer-to-layer *feedforward connectivity*, for which they are called "feedforward NNs." Typically, this connectivity is *complete* in that all units in one layer connect to all units in the layer immediately adjacent (to the right, in layers depicted as columns). The connectivity of the non-layered NN in Fig. 1 is also complete, but its connections are often *bidirectional*. In this sense, units in these NNs are *interconnected* and, hence, mutually influence one another. I will not speak of this type of NN anymore, to focus on layered feedforward NNs, or just NNs, to abbreviate.

Unit activities *propagate* through connections from inputs to outputs (left to right in layers depicted as columns, as in Fig. 1), directly (without the mediation of other units) in NNs without hidden layers or indirectly in NNs with hidden layers. In the latter, hidden-unit activation states mediate between input and output activation states.

The above suggests a kinship between NN modeling and neuroscience, where NN modeling is *inspired* by brain structure and functioning as studied in neuroscience. This inspiration has taken various forms that differ in its closeness to neuroscientific laboratory data. On one end of this

spectrum, *computational neuroscience* follows the closest inspiration, where models seek to be *realistic* by fitting as accurately as possible experimental data about neuronal activity and synaptic plasticity. These models thus tend to be much more concrete. On the other side of the brain inspiration spectrum, models do not seek to be so accurate and are often called "connectionist." They are much more abstract and simplified than computational neuroscience models.

The two approaches have grown apart, to the point of becoming different, often warring scientific cultures. Computational neuroscientists dismiss connectionist models as too high-level and unconstrained by neuroscientific data, which makes them neuroscientifically invalid. Connectionists complain that computational neuroscience models are too low-level and lack generality, which makes them incapable of capturing psychological phenomena. Both sides have a point, but arbitrating between them raises a very difficult issue I cannot address here: model abstraction is a matter of degree, and it is unclear how much abstraction is too much or too little. I am a psychologist and, hence, partial to connectionist models, so they will be my focus in this entry.

Despite their important methodological differences, both sides share the general intuition that there is an important relation between the brain and "the mind" or "the mental," broadly conceived to include "phenomenal consciousness" (sensory and perceptual experiences), and "cognition," often associated with "intelligence" and "thinking." (I quote all these terms because they lack technical, universally agreed-upon definitions, and I will not even try to give any such definitions here.) This intuition is far from new. It was already present in Ancient Greece, well before the advent of the neuron doctrine and NN modeling.

Most NN modeling has a strong *engineering* or "tech" motivation to solve concrete practical problems. They are legion and include optimization tasks, various types of pattern recognition (face, voice, handwriting, etc.), natural language processing, image compression, marketing, stock prediction, banking-finance, robotics, gaming, self-driving vehicles, and medical diagnosis,

among many others. Tech NN modeling seeks effective efficient problem solutions that require flawless, superhuman performance, more than a *scientific understanding of natural* psychological phenomena and their underlying brain processes.

NN tech research is very important in generating technologies that improve the human condition, but will not be my focus here. Instead, I will focus on the minority of NN modeling, aimed at scientific understanding of behaviors indicative of mental state, process, or condition, as they actually occur and how they relate to brains, independently (without excluding the possibility) of practical applicability. In short, I will focus on *basic* connectionist NN modeling (NN modeling, henceforth). I do not mean to separate sharply between basic and tech research models, only a very fuzzy distinction between models uses. There is considerable overlap between the two kinds of uses. The same model could be used in both ways, and this will be the case of the models I discuss later on.

Before I elaborate, I will step back briefly to give some historical-conceptual context. For this, I will first summarize traditional cognitive science (TCS) as the approach that dominated the field for over a decade, before NN models became a viable alternative. After this, I will dedicate the rest of the entry to the foundations of basic NN modeling and illustrate with a few representative models.

## TCS

TCS had a strong tech motivation from its beginnings in traditional artificial intelligence (TAI) but also sought to understand scientifically human “intelligence.” (This term is very problematic, but its use is widespread, so I will follow suit.) Both fields arose from a series of related papers. In some of them, Church (1936a, b) and Turing (1936–1937) marked the beginnings of computer science as attempts to solve the so-called *Entscheidungsproblem*, German expression for “decision problem.”

The problem originated almost a decade earlier, in relation to *predicate logic*, the part of *modern formal* or *symbolic* logic to formalize the *grammatical structure* (subjects and predicates)

of statements, such as “All humans are mortal,” “Socrates is human,” and “Socrates is mortal,” and valid arguments with them. These three statements are classical examples of the constituents of a class of Aristotelian syllogisms, a kind of deductive (logically valid) argument where the first two are the premises and the third is the conclusion that follows from them. Logical validity in these arguments hinges on the grammatical structure of their statements. Symbols for statements in *propositional* logic ( $p$ ,  $q$ , etc.), another part of symbolic logic, conceal this structure and, hence, are unsuitable to formalize such arguments. Propositional logic only allows formalizing arguments whose logical validity does not hinge on symbolizing this structure.

In essence, the Entscheidungsproblem asks whether statements of a certain class in first-order predicate logic are *decidable*. That is to say, does an *effective method* or *algorithm* exist to decide whether any such statements is or not *tautological* (i.e., *necessarily true* or true *in all logical possibilities*)? Propositional logic has an algorithm, known as the *truth table*, to decide whether any statement in this logic is tautological (or whether any argument in this logic is valid). This algorithm was key to the origins of NN modeling, as I elaborate in the third section.

To solve the Entscheidungsproblem, Church and Turing formalized the notion of an algorithm. They proposed independently different but equivalent formalizations, effective  $\lambda$ -calculability and computability, respectively. With these formalizations, the authors demonstrated that the Entscheidungsproblem was unsolvable, for  $\lambda$ -noncalculable (in Church’s formalization) and noncomputable (in Turing’s formalization). These results led to the general Church-Turing hypothesis that any task doable through a finite sequence of rules is  $\lambda$ -calculable or computable. In particular, everything calculable is  $\lambda$ -calculable or TM-computable and vice versa.

## Turing Machines

The most influential formalization was Turing’s definition of computability (or not) in terms of

what he called an “automatic machine” and Church (1937) called “Turing machine” (TM). Figure 2 depicts a general informal sketch of a TM as often characterized today. It consists of left/right (arrows) moving read/overwrite head (trapezoid) and a two-way tape divided into indefinitely but finitely many cells holding one *token* of a prespecified symbol *type* from a finite set of symbol *types*  $\{Y_i, Y_j, Y_k, \dots\}$ . The required set depends on the task the TM is to do. Different tasks may or may not require different symbol-type sets, but the general notion defines all TMs and gives them their *symbolic* character.

Figure 2 shows three cells with symbol variables  $y_i, y_j,$  and  $y_k$  that can hold one *token* of the same or different members of the symbol-type set at a time  $t$ . The tape may have any required *finite* length as dictated by the task of interest. Different TMs could thus vary in the length of their tapes (ellipses). Also defining of a TM (not shown in the figure) is the set of its *possible internal states*. A TM can be in one and only one of these states at  $t$ , according to a *transition* table that instructs what state the TM should be in and what its head should do at  $t$  (read, write, move to the left, or move to the right). All this depends on the machine’s internal state and the symbol in the cell where the head is at  $t$ .

Different TMs can be defined for different computational tasks, but it is also possible to define a *universal Turing machine* (UTM) that can in principle do the tasks all different TMs can do. This possibility led to a technological breakthrough during the 1940s: the development

of *physical implementations* or *realizations* of a UTM that marked the beginnings of electronic personal computers, as we know them today. These implementations added components such as storage memory and a central processing unit (CPU) that do the actual computations in real time while the computer is on.

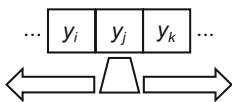
Three features of a UTM are central to this story. First, computation in a UTM is *symbolic* in nature: a UTM is defined partly by a set of symbols. Second, a UTM’s functioning is inherently (theoretically and physically) *serial* because it can be in one and only one internal state at a time. A UTM’s functioning thus consists of a *succession* of input – internal state – output triplets across different times, where different triplets *imply* different moments. Third, in physical implementations of a UTM in digital computers, the CPU makes computations *centralized*.

## The Imitation Game

The use of a UTM to model human intelligence began with Turing’s (1950; further references to Turing will be to this entry) other widely influential paper. In this paper, he used his concept of a UTM to reformulate the question of whether machines could think. He called his reformulation “the imitation game” or “question-and-answer method” (p. 435), more familiarly known as the “Turing test” (TT). I will summarize it very briefly, as this encyclopedia includes an entry for this topic (see ► “Turing Test”).

In a simple modern version, the TT involves human “interrogators” or participants engaging in a question-and-answer conversation with different input-output interfaces (e.g., computer keyboards and monitors). In separate rooms, confederate humans control one interface, and a UTM computer running a conversation app controls the other. The participants know this but not which is which, and their task is to choose. If a certain agreed-upon percentage of participants choose the UTM, it “passes” the TT or plays the imitation game “satisfactorily” or “well,” as Turing put it.

Turing proposed to replace the question of whether machines could think with the question



**Neural Network, Fig. 2** General informal sketch of a TM. Trapezoid: Left/right moving (arrows) read/overwrite head.  $y_i, y_j, y_k$ : Symbol-token variables. Squares: A tape’s cells that hold symbol tokens. The length of the tape is given by the number of squares, which can vary across different specific machines (ellipses), depending on the task the machine is expected to do, but must be finite. At any moment, the head can move one cell to the left or to the right, depending on the symbol in the current cell and the machine’s current state

of whether a UTM physically implemented in an electronic digital computer could play the imitation game well. He predicted that "... in about fifty years' time," computers would be sufficiently powerful to play the imitation game so well that "one will be able to speak of machines thinking without expecting to be contradicted" (p. 442), if a sufficiently clear and precise meaning of "thinking" arose (which he also predicted).

This prediction remains unfulfilled, at least in the way Turing envisioned his imitation game, which focused on *general* intelligence in *English-speaking adults*. A reason has been his lack of detail on the game's rules. The game analogy suggests clear, detailed, precise rules that leave little doubt about how to play. Games as different as chess, go, soccer, baseball, basketball, poker, and Monopoly© share this key feature, but not Turing's game, as innovative and inspiring as it was. This led to different ways to fill in the details, and there still is no agreement over which one is the best one.

## Logical Problems with TCS

In the meantime, I wonder counterfactually (a common exercise in basic science) *what if* a UTM passed the TT. With this exercise, I seek to reflect on how fulfillment of Turing's prediction *would* advance scientific understanding of human thinking. The answer from TCS arises from its core hypothesis that human thinking *is* UTM computing. A UTM passing the TT would thus advance such understanding by giving empirical support to this hypothesis. The standard rationale for this answer in TCS and TAI hinged on the assumption that intelligent behavior was a *sufficiently reliable* indicator (ideally, a *deterministic effect*) of covert functioning to warrant inference of a similarity in the latter from a similarity in the former. (It is unclear to me whether Turing followed this rationale. He likely viewed the covert workings of humans and UTMs that passed the TT as thinking, but it is not obvious that he viewed the two covert workings as being of the *same kind*.)

This assumption, however, is very debatable. A major issue arises from the widely held view

that thinking crucially involves *understanding* (Turing hinted this relation, but did not delve into it). In ordinary English, the adjective **thoughtful** is synonymous with **understanding**, often defined as "the power of abstract thought." Math teachers often admit the possibility that high schoolers could be quite good at solving certain standard high-school math problems without knowing their underlying principles. High schoolers can multiply without knowing that multiplications are abbreviated sums. They can also solve standard high-school algebra problems without knowing abstract algebra and standard high-school geometry problems using the Pythagorean theorem without knowing how to *prove it logically*.

Intuitively, understanding in these considerations includes knowing something *additional* about a task, such as its foundational principles, which is neither necessary nor sufficient for doing it correctly. To this extent, passing the TT does not even entail thinking period, let alone that human thinking is like machine thinking. At best, they only *indicate the possibility* of thinking, a much weaker, hypothetical proposal. A high schooler *could* be excellent at solving standard high-school problems with the Pythagorean theorem *and* know how to prove it logically, but the former does not *entail* the latter nor vice versa: someone could know how to prove the theorem logically but be very bad at using it in practical situations without the aid of a calculator.

In sum, there can be thinking behavior without covert thinking and vice versa. Therefore, even the existence of *humans* who pass the TT does not imply that they think. Searle (1980) famously argued this implication in his widely discussed Chinese room thought experiment. In this experiment, a human is entirely ignorant of Chinese in a room with access to an enormous database of correspondences among different Chinese expressions. This human does not need to know or understand any Chinese at all to use the database. A Chinese-speaking user outside introduces into the room a paper or card with something written in Chinese; the person inside the room searches for this expression in the dictionary, prints the proper reply stipulated by the dictionary, and sends it back out to the user, who understands the reply as meaningful.



Searle's point was that the person inside the room passes the TT for a meaningful Chinese conversation, but does not *understand Chinese*. Passing the TT, then, is not sufficient for thinking, a conclusion against TCS' core hypothesis that human thinking is TM computing ("strong" AI, as Searle called it), nor is it necessary, if widespread talk of *nonhuman* animal thinking is to be admissible. Turing envisioned his game as a linguistic task, so nonlinguistic creatures cannot play it, which precludes such talk.

All this suggests that thinking behavior does not warrant a strong argument by analogy of the kind behind the TCS' core hypothesis. Further support of this outcome came from Putnam's (1988) rejection of his own *functionalism* about the mind (Putnam 1960). His main hypothesis was that a type of mental state was a type of causal role that mediated a type of input-output relation. To do significant explanatory and predictive work, this hypothesis requires that computational states *individuate* mental states *unequivocally* and vice versa. However, Putnam concluded that this requirement was unfeasible in principle: different types of computational states could constitute the same type of mental state, and the same type of computational state could constitute different types of mental states. Both possibilities reduce functionalism's explanatory and predictive power.

Specifically, Putnam realized that being UTM computational was not exclusive to the mental, an obvious possibility he and his followers failed to appreciate (and many still do today). The old Galilean adage that "the book of nature is written in mathematical language," and, centuries earlier, the Pythagoreans, anticipated the possibility. Taken literally, this adage leads to *pancomputationalism*, the thesis that *all* reality is computational in nature.

The extreme version of this thesis, UTM-pancomputationalism, asserts that the universe is one giant UTM. The rationale behind this version is that all *true* mathematical scientific models are computational and, hence, programmable and executable by UTMs, and crucial to what makes them true is that the phenomena they model are UTM-computational in nature. However, these include myriad phenomena that are not mental in

any standard sense of the term, such as the Moon's revolution, billiard balls colliding and falling, water flowing inside a pipe, the shear resistance of concrete beams, crystallization, hurricanes, and radioactive decay, among many others.

If TCS researchers insist that UTM-computing is exclusive to the mental, they would have to restrict UTM-computing to the type of covert functioning that supposedly causes thinking behavior, but it is not obvious how to justify this restriction. If they embrace UTM-pancomputationalism and maintain UTM-computing is exclusive to the mental, they fall back to *panpsychism*, the thesis that all reality, the above phenomena included, are literally mental in nature, a very inconvenient outcome. The middle position, to accept UTM-pancomputationalism but view the mental as a special kind of UTM-computing, avoids this outcome but also lacks compelling justification.

## Connectionist Cognitive Science (CCS)

TCS thus seems to be sufficiently problematic to deserve a healthy dose of skepticism, and it has: TCS is no longer dominant in cognitive science, nor is TAI dominant in AI tech research. The obsession over the TT might have contributed to this, so lessening it might benefit future TCS and TAI research. NN modeling offers a different (not necessarily opposite) approach, often labeled "connectionist cognitive science" (CCS). Its tech manifestation is connectionist AI or CAI. The term **connectionism** also labels certain proposals in early psychology of learning (see ► ["Learning"](#) in this encyclopedia), but here I use it only to name the hypothesis that drives NN modeling.

Very succinctly and roughly, the main guiding hypothesis in CCS is this: NN models explain the mental better than UTMs do. The key reason is the NN models' greater emphasis on the mental as it naturally occurs, with its flaws and physical constitution. This emphasis contrasts sharply with Turing's focus on idealized perfect intelligent behavior in a UTM ("By definition ... we can truly say that 'machines can never make mistakes'," Turing 1950, p. 449). He thus excluded mistakes, even physical constitution, as

inessential to thinking (the latter exclusion was a major inspiration for functionalism about the mind). Thinking behavior remains a criterion in CCS, but mistakes and physical constitution are essential. CCS research has shown a greater interest in nonsymbolic behavior, allowing for a broader, more flexible concept of the mental that includes nonhuman animals.

Methodologically, computational modeling consists in *finding numerical solutions* to a model's equations. In most NN models, the equations are the activation and the learning functions. A common way to do this is to code the equations in a programming language and use the resulting application to run *simulation experiments* in electronic computers (there also are robotic, hardware applications). The use of electronic digital computers in this way is mainly practical: they are much faster and more reliable at doing the required calculations. This use, however, is quite suggestive when comparing NNs to UTMs.

## NNs and UTMs Compared

Conventional wisdom has it that NNs and UTMs are incompatible. It is customary, for instance, to view neural-network functioning as nonsymbolic, parallel, and distributed and contrast these features respectively to the symbolic, sequential, and centralized character of a UTM's functioning. (I prefer to speak of **functioning**, which relates more intuitively to **working**, than **representation** and **processing**; **representation** is infamously difficult to define technically in a way acceptable to most users; **processing** promotes the use of information theory, which is optional and complicates the matter considerably.)

The specialized literature is not entirely clear in these distinctions, but the intuitions behind them seem to be more or less like this. Nonsymbolic functioning is *analog* or *quantitatively continuous* in nature, where quantities are real numbers rather than symbols as traditionally conceived in linguistics (marks with certain conventional qualitative morphologies, connotations, and denotations). Parallel functioning consists in the simultaneous operation of a NN's constituent parts (units and

connections). Distributed functioning refers to their equivalent functioning.

But then again, these features are not as incompatible as they seem to be, in various respects. An obvious one is that all NN models are computational. Therefore, they are programmable and executable in UTM electronic computers that do numerical calculations in the binary system. The symbol set of this UTM is  $\{0,1\}$ , where "0" means "OFF" and "1" means "ON," in reference to the possible states of electronic switches in today's computers. The same set of symbols made symbolic logic key to the origins of NN modeling as well albeit in quite a different way, as I clarify shortly.

McCulloch and Pitts (1943) anticipated the UTM-NN affinity in what many regard as the first NN paper (not cited by Turing):

... every net, if furnished with a tape, scanners connected to afferents, and suitable efferents to perform the necessary motor-operations, can compute only such numbers as can a Turing machine ... each of the latter numbers can be computed by such a net .... (p. 129)

Relatedly, Siegelmann and Sontag (1991) proved that at least one kind of neural network exists that can simulate a UTM. Moreover, for decades there have been efforts to build *hybrid, neurosymbolic* models that combine NN quantitative and TM-style qualitative functioning (<https://www.microsoft.com/en-us/research/blog/next-generation-architectures-bridge-gap-between-neural-and-symbolic-representations-with-neural-symbols/>).

NNs resemble TMs also in that NN functioning is *physically* sequential. NNs' functioning is parallel only theoretically, depending on how they conceive time. In most NN models, like TMs, time is conceived as *discrete*, consisting of whole moments, times, epochs, or occasions (symbolized as  $t_1, t_2, \dots$ ) of *arbitrary* (often unspecified) but *nonzero* duration. NN functioning in these models is parallel only in that calculations occur in the same *theoretical* moment, but all moments have temporal extension, no matter how short, so calculations must be physically sequential.

NNs and UTMs, then, are less sharply different than often believed, although they still differ in

important respects. Perhaps the distributed-centralized distinction is more differentiating: it is unclear how NNs and UTMs are *conceptually* comparable in this regard. A related feature also viewed as distinctive of NNs is *graceful degradation*, a gradual performance deterioration with the gradual loss of units (provided a sufficiently large NN). Human brains have this feature: they can lose thousands of neurons daily to natural death without significant performance deterioration. In contrast, losing just one part, the CPU, would completely shut down a UTM computer.

In the introduction, I anticipated the defining feature of NNs that differentiates them more clearly from UTMs: automated learning. The difference is not one of *theoretical possibility* but *emphasis* (or lack thereof). Turing discussed the issue of learning in addressing the objection that a UTM could not think in ways that deviated from what it has been programmed to do. He dedicated the last section of his 1950 paper to this discussion, under the heading *Learning Machines* (pp. 454–460). His discussion relied heavily on rather convoluted similes, but my understanding is as follows.

He speculated that a UTM could learn *in principle* by having a changeable transition table where the rules of operation had “only an ephemeral validity” (p. 458), but did not *need* to *in practice*, for two reasons. One, his idealization of thinking behavior and thinking in the imitation game presupposed maximally effective and efficient means of acquiring the necessary knowledge to play the game well. Two, he viewed learning (and evolution) as too inefficient and uncertain a process to guarantee perfect results, as it inevitably involved randomness. He thus put learning aside, at least as a *temporary strategic simplification*, perhaps even as inessential to thinking. All this made TCS and TAI researchers indifferent to learning, which might have fed their adoption of *nativism* (the thesis that the mental is innate) and perhaps vice versa.

Not so in NN modeling. Although NNs could in principle work as expected without any learning (as I illustrate next), this possibility quickly became unviable in practice. I suspect that this (combined with a scientific interest in natural

intelligence) drove early NN modelers to focus on learning and give it a central role. This focus was compatible with (in fact, supported) the inspiration on brain structure and functioning, which historically came first.

## Some Fundamentals

As anticipated in the introduction, the basic concepts of NN modeling are task, neural unit, activation, connection, and weight. I now illustrate them the first and simplest NN model: the McCulloch-Pitts (MCP) model. It has more historic than scientific interest, but it sets some theoretical foundations of NN modeling. It also shows how symbolic logic was at the root of NN modeling although in a different way: using propositional logic as a model of brain functioning (What of *predicate* logic? This question motivated neurosymbolic models.) This use arose from the *all-or-none law* of neuronal functioning. According to this law, a neuron is either completely active or completely inactive, a key intuition that defined NN modeling from its beginnings.

Based on this law, MCP viewed neuronal functioning a “factually equivalent to a proposition” (p. 117), meaning that unit activations are *functionally analogous* to truth-values of standard bivalent propositional logic. A standard way to express this analogy is to symbolize the active (or ON) state as 1 and the inactive (or OFF) state as 0. With this symbolism, it is common to express the MCP model as the following activation function (MCP did not formulate it quite like this):

$$a_j = \begin{cases} 1, & x_j \geq \theta \\ 0, & \text{otherwise} \end{cases} \quad (1)$$

where  $a_j$  denotes the activation *state* *act* of target neural unit  $j$ , 1 and 0 denote “active” (or “ON”) and “inactive” (or “OFF”), respectively, and  $\theta$  denotes a threshold. Equation 1 is a *conditional* or *decision function* in that reads as follows: unit  $j$  is *either* active (its activation state is (1) *if*  $x$  is equal to or greater than ( $\geq$ )  $\theta$  *or* inactive (its activation level is 0) *if*  $x$  is less than ( $<$ )  $\theta$ . (Some use  $>$  and  $\leq$  instead, but I prefer the

present way because  $\geq$  captures *reaching*  $\theta$  as sufficient for neuronal firing.) It is also common to define  $x_j$  algebraically as

$$x_j = \sum_{i=1}^n a_i w_{i,j}, \quad (2)$$

where  $i$  denotes an *afferent* unit *connected* to  $j$ ,  $n$  the total number of afferents connected to  $j$  (at least one),  $a_i$  denotes the activation state of afferent unit  $i$ , and  $w_{i,j}$  denotes the weight of the connection from  $i$  to  $j$ .

In *linear algebra* (the part of mathematics about vectors and matrices, widely used in NN modeling), Eq. 2 is a product of two *vectors* (sets of values ordered usually as columns) with the same number of members. The two vectors in Eq. 2 are the vector of *input* activations and the vector of weights of the corresponding connections from the afferents. This product expresses a central assumption of all NN modeling: the relation between neuronal activations and synaptic strengths can be mathematically described as *linearly multiplicative*.

Equation 1 is a binary threshold or step activation function, where, following the all-or-none law, a unit's activation state at  $t$  could be either 1 or 0. It is the simplest activation function in NN modeling, but it has important limitations, as I show later. Before I do, I next illustrate very simply how the MCP model works, following modern depictions of it.

**A toy example.** The first steps in NN modeling are to define the task of interest and design a NN for this task. The usual order is to first define the task as clearly and precisely as possible and then design a NN that could do it (a NN designed for a certain task may or may not work with others). As tasks become increasingly complex, modelers need to test several NNs to find a suitable one, but here I will focus on very simple tasks and NNs. They are of very limited use for scientific understanding (let alone practical applications) but constitute theoretical foundations of basic NN modeling.

The tasks are defined by input-output relations functionally analogous to *truth tables* in

propositional logic (specifications of all the possible truth-values for any given proposition). In these tasks, the inputs are *possible activation states* of a NN's input units, and outputs are the *expected, desired, or target* output activation states for different possible input activations. The simplest truth table defines the *negation* of one proposition  $p$ , often symbolized as  $\sim p$ , where  $\sim p$  is false when  $p$  is true and vice versa. The input-output relation that defines the analogous task for a NN stipulates target output activation states of 0 and 1 for input activation states of 1 and 0, respectively.

The minimal MCP network for this task is the smallest NN possible, consisting of one input unit connected to one output unit. This network can do the task if at least one connection weight and one value of  $\theta$  exist that satisfy the task's definition, where the *actual* NN's output activation state, computed using Eq. 1, must equal the expected output activation state stipulated in the task. It is possible to demonstrate this algebraically by determining whether the system of *linear Boolean inequalities* for the task is *solvable*. They are linear inequalities because of Eq. 1, as explained above and Boolean after Boole (1847), who created this kind of algebra. Let  $w$  denote the weight of the NN's connection. The system for the negation task consists of two inequalities,  $1w < \theta$  and  $0w \geq \theta$ , or, simplifying,  $w < \theta$  (because  $1w = w$ ) and  $0 \geq \theta$  (because  $0w = 0$ ), which is solvable. There are infinite solutions, but one, for example, is  $\theta = 0$  and  $w = -0.1$ .

A larger set of tasks are functionally analogous to all possible truth tables for two propositions  $p$  and  $q$ . There are  $2^{2^2} = 16$  such tables the base and first power are the number of truth – values the second power is the number of propositions, all with  $2^2 = 4$  rows, where the power is the number of propositions. Among these tables, there are those that define some *logical connectives* taught in introductory textbooks of symbolic logic.

To illustrate, I will define only three tasks functionally analogous to the truth tables for the conjunction (&, “and”), inclusive disjunction ( $\vee$ , “and/or”), and conditional ( $\rightarrow$ , “if... , then...”) operators. Table 1 shows the three tasks

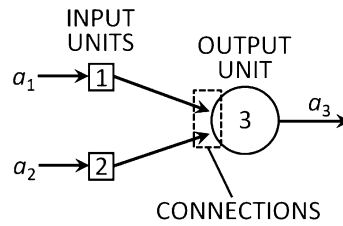
**Neural Network, Table 1** Tasks functionally analogous to the truth tables for conjunction (&, “and”), inclusive disjunction ( $\vee$ , “and/or”), and material conditional ( $\rightarrow$ , “if..., then...” or “only if”) in propositional logic. The rows of columns labeled as  $a_1$  and  $a_2$  specify all possible input activations, common to all the tasks. A pair of possible input activation states is an input *pattern* or *vector*. The rows of the other columns specify the *desired* or *expected* activations of the neural unit that will function as the output unit

| $a_1$ | $a_2$ | $a_1 \ \& \ a_2$ | $a_1 \ \vee \ a_2$ | $a_1 \ \rightarrow \ a_2$ |
|-------|-------|------------------|--------------------|---------------------------|
| 1     | 1     | 1                | 1                  | 1                         |
| 1     | 0     | 0                | 1                  | 0                         |
| 0     | 1     | 0                | 1                  | 1                         |
| 0     | 0     | 0                | 0                  | 1                         |

compressed into one table (the order of the rows makes no theoretical difference). The input-output relations that define these tasks consist of the first two columns and any one of the other columns. The first two columns specify all the possible input activation states, common to all the tasks, where a pair of possible input activation states is an input *pattern* or (more mathematically) *vector*. The other columns specify the target output activations for the corresponding input pattern.

The tasks differ only in the target output activation states. For example, the first row for the & task stipulates that the NN’s output unit should be active (have an activation state of 1) whenever its two inputs are active but inactive (have an activation state of 1) whenever one or both inputs are inactive. All the tasks stipulate only two possible output activations, either 0 or 1. This stipulation illustrates the simplest *classification* task, which requires a sharp discrimination between two categories of possible input patterns.

As the tasks suggest, the minimal NN for them needs two input units connected to one output unit. Tasks that are more complex would require larger minimal NNs, and this illustrates how differences in *basic* structural constitution or architecture *define* NN modeling. (All UTM computers have the same architecture.) Figure 3 depicts an example of this NN, labeled as MCP1. It is a three-unit NN with two input units (squares labeled as 1 and 2, where the 1 does not mean the same as the 1 for active) that form the input



**Neural Network, Fig. 3** MCP1, minimal NN necessary to do the tasks defined in Table 1. 1, 2: Input units that form the input layer. At  $t$ , both can be active, one active and the other inactive, or both inactive. 3: Neural output unit.  $a_1$ ,  $a_2$ ,  $a_3$ : 1’s, 2’s, and 3’s activations at  $t$ .  $a_1$  and  $a_2$  are not calculated but assigned by sampling input patterns or vectors (pairs of input activations from the rows of the first two columns of Table 1).  $a_3$  denotes MCP1’s *actual* output activation, calculated with Eq. 1, where  $j = 3$  and  $n = 2$  in Eq. 2. Different input and/or output activations occur at different times. MCP1 has two connections, one from Unit 1 to Unit 3 and the other from Unit 2 to Unit 3.  $w_{1,3}$ ,  $w_{2,3}$ : Connection weights, where the subindexes denote the units

layer and connect to one neural unit (circle labeled as 3) that functions as the output unit. For MCP1, then  $n = 2$  and  $j = 3$  in Eq. 2. MCP1 has two connections, one from Input Unit 1 to Unit 3 and one from Input Unit 2 also to Unit 3. Their weights can be labeled as  $w_{1,3}$  and  $w_{2,3}$ .

MCP1 simulates a *spatial structure* that *persists through time* (no neural development), for all possible input and output activations shown in Table 1. Thus, 1 labels the *same* input unit in different moments; 2 labels a *spatially* separate input unit but the same one in different moments; and 3 labels yet another spatially separate unit but the same one in different moments. As an output unit, 3 is also *functionally* different from 1 and 2, which are input units. For simplicity, I will ignore the time variable and assume that all unit activations and connection weights take particular values at a present theoretical moment  $t$  of constant but indefinite duration. Assume that different activations occur at different moments. In contrast to MCP, I will not assume a delay between input and output activations. In this sense, MCP1’s functioning is parallel *in theory*.

MCP1 can do these tasks if there is at least one set of values for  $w_{1,3}$ ,  $w_{2,3}$ , and  $\theta$  that allow MCP1 to “respond” (have the expected output activation) in *all* the ways specified by the task. It is possible



to determine this algebraically by defining the system of linear Boolean inequalities for each task. Table 2 shows the systems for the three tasks depicted in Table 1.

As before, I simplified by showing only weights multiplied by 1. The three systems are solvable. For example,  $\theta = 0.4$ ,  $w_{1,3} = 0.2$ , and  $w_{2,3} = 0.3$  solve the system for  $\&$ , whereas  $w_{1,3} = 0.4$ ,  $w_{2,3} = 0.5$ , and  $\theta = 0.3$  solve  $\vee$ . Therefore, MCP1 can also do both tasks, as well as  $\rightarrow$  (e.g.,  $\theta = 0.0$ ,  $w_{1,3} = -0.1$ , and  $w_{2,3} = 0.3$  solve the inequality system for this task).

A common geometrically equivalent way to say all this is that these tasks are *linearly separable*. That is to say, there is at least one straight line (defined by a linear function) that separates the 0 from the 1 expected output activations in a Cartesian coordinate system. Figure 4 illustrates this feature for the three tasks with hypothetical lines, where the black (0, analogous to a dark, unlit bulb) and white (1, analogous to a white, lit bulb) dots represent the possible expected

outputs. Most of the rest of the 16 tasks suitable for MCP1 are linearly separable in this sense.

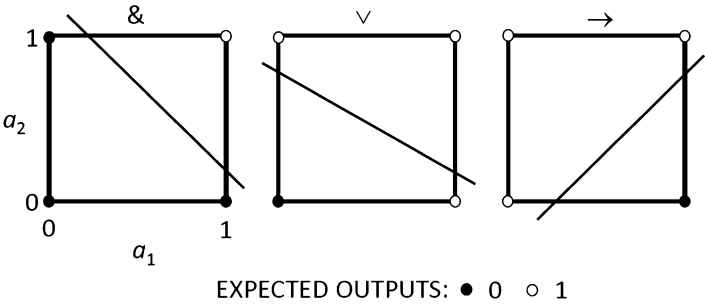
**The problem.** An exception central to this story, reported by Minsky and Papert (1988) in a widely influential book, is the *exclusive disjunction* task, often symbolized as  $\vee$  in propositional logic but more familiarly known in the NN literature as XOR. This task requires the NN’s output unit to be active whenever any of its input units is active but inactive whenever both inputs are either active or inactive. Table 3 depicts this task with its system of linear Boolean inequalities.

This system is unsolvable. The last row requires  $\theta$  to be positive, which means that both weights must also be positive (to satisfy the inequalities of the second and third rows), but the inequality of the first row requires their sum to be less than  $\theta$ . No set of values for  $w_{1,3}$ ,  $w_{2,3}$ , and  $\theta$  can satisfy all of these requirements. Therefore, MCP1 cannot do this task nor the biconditional task, where the target output activation state is 1 for the (1,1) and (0,0) and 0 for the (1,0) and

**Neural Network, Table 2** Linear Boolean inequality systems for the tasks defined in Table 1, simplified by leaving only weights that multiply by 1 and omitting this

value. The systems differ only in the  $\geq$  (for expected output activation states of 1) and  $<$  relations (for expected output activation states of 0), and all are solvable

| $a_1$ | $a_2$ | $a_1 \& a_2$ | Inequalities                    | $a_1 \vee a_2$ |                                 | $a_1 \rightarrow a_2$ |                                 |
|-------|-------|--------------|---------------------------------|----------------|---------------------------------|-----------------------|---------------------------------|
| 1     | 1     | 1            | $w_{1,3} + w_{2,3} \geq \theta$ | 1              | $w_{1,3} + w_{2,3} \geq \theta$ | 1                     | $w_{1,3} + w_{2,3} \geq \theta$ |
| 1     | 0     | 0            | $w_{1,3} < \theta$              | 1              | $w_{1,3} \geq \theta$           | 0                     | $w_{1,3} < \theta$              |
| 0     | 1     | 0            | $w_{2,3} < \theta$              | 1              | $w_{2,3} \geq \theta$           | 1                     | $w_{2,3} \geq \theta$           |
| 0     | 0     | 0            | $0 < \theta$                    | 0              | $0 < \theta$                    | 1                     | $0 \geq \theta$                 |



**Neural Network, Fig. 4** Linear separability of the  $\&$  (left panel),  $\vee$  (middle panel), and  $\rightarrow$  (left panel) tasks, using hypothetical lines. Possible input activations  $a_1$  and  $a_2$  are depicted in the horizontal and vertical axes, respectively.

The expected outputs 0 and 1 are depicted as a black dot (representing a dark, unlit bulb) and a white dot (to represent a lit bulb), respectively

**Neural Network, Table 3** A task MCP1 cannot do, known as XOR (symbolized as  $\vee$ ) and functionally analogous to the truth table that defines exclusive disjunction in propositional logic

| $a_1$ | $a_2$ | $a_1 \vee a_2$ | Inequalities                 |
|-------|-------|----------------|------------------------------|
| 1     | 1     | 0              | $w_{1,3} + w_{2,3} < \theta$ |
| 1     | 0     | 1              | $w_{1,3} \geq \theta$        |
| 0     | 1     | 1              | $w_{2,3} \geq \theta$        |
| 0     | 0     | 0              | $0 < \theta$                 |

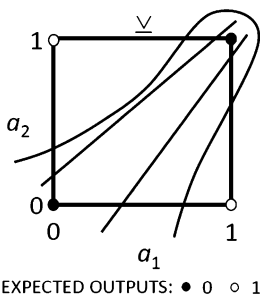
(0,1) input patterns. Tasks like these are *linearly inseparable* in that no single straight line separates the 0 from the 1 target outputs. Figure 5 illustrates this feature for  $\vee$  and how such separation requires at least two straight lines or a nonlinear (curved) function.

**Learning as Automated Weight Search: The Perceptron**

The above example demonstrates mathematically that MCP1 cannot do the  $\vee$  task. (I did not demonstrate it for the biconditional.) MCP1 can do all the remaining tasks (I only demonstrated it for three). The example’s simplicity facilitated specifying the required inequalities systems in table form (as in Tables 2 and 3), determining by visual inspection if they had a solution, and finding specific solutions. The example thus illustrates how a NN can do a task correctly without learning, in virtue of a human user (myself) finding weights that allowed for this.

The same applies to tasks and MCP NNs that are more complex, but it quickly becomes unviable, as the numbers and sizes of inequality systems grow exponentially with the number of input units. For example, adding just 1 input unit to MCP1 would result in  $2^3 = 256$  possible systems, each one with  $2^3 = 8$  inequalities. It would be very difficult to specify all of them in table form and determine by visual inspection which ones are solvable (never mind finding particular solutions).

One way around this problem is to use a *learning algorithm, function, or rule* to *automate* the search for weights that allow an MCP NN to do a task. MCP did not include a learning rule, but



**Neural Network, Fig. 5** Linear inseparability of the  $\vee$  task. The input-output relation that defines this task makes it impossible for a single straight line to divide the 0 from the 1 expected output activations. The separation can be achieved with two linear functions or a nonlinear function. Possible input activations  $a_1$  and  $a_2$  are depicted in the horizontal and vertical axes, respectively. The expected outputs 0 and 1 are depicted as a black and a white dot, respectively

Rosenblatt (1958) did. He called the resulting model “the perceptron” and characterized it as taking the “empiricist or ‘connectionist’ position” (p. 397), in opposition to the aforementioned nativism in TCS, implied by rationalism. Such opposition indicates a fundamental *epistemological* disagreement between TCS and CCS.

Rosenblatt formulated his model in terms that were more psychological and neuroscientific, in an effort to model how learned behavior and its brain substrates actually occurred. He strived to distance the model from the tidiness of symbolic logic (and TAI, although he did not cite Turing) and embrace the messiness of natural biological systems by formulating it “in terms of probability theory rather than symbolic logic” (p. 388). (The two are not mutually exclusive, as Carnap 1950, showed in his characterization of inductive logic using symbolic logic as a foundation of probability theory). The probabilistic aspect referred to “random connections” (p. 387), “random stimuli” (p. 405), and response probabilities given different stimuli. (As will become clear below, the learning rule, like the activation rule in Eq. 1, is deterministic.)

In identifying associations with connections, he anticipated an affinity with associationism in the psychology of learning but argued his model was more parsimonious, verifiable, explanatorily powerful, and general than models proposed by

learning psychologists of the time. He also concluded that “the memory of a perceptron is *distributed*” (p. 405), anticipating a defining feature of the connectionist concept of memory, but contrary to standard practice today, he did not speak of connections as representing synapses or weights as representing synaptic strengths (he used none of these expressions). Instead, he identified connections with “association cells” and postulated construct  $V$  as the value of an association cell that could represent “an amplitude, frequency, latency, or probability of completing transmission” (p. 391).

His mathematical formulation of the rule to change  $V$  was quite complex, but it is standard practice today to formulate it more simply and intuitively for a single binary output unit, as the following algorithm:

1. Choose an input *pattern* (vector of possible input activations) randomly.
2. Calculate the real activation of the output unit (according to Eq. 1).
  - a. If the real activation is correct (i.e., equals the target output activation), return to Step 1.
  - b. If incorrect and the real activation is 0, add each input activation to its corresponding weight.
  - c. If incorrect and the real activation is 1, subtract each input activation from its corresponding weight.
3. Return to Step 1.

This cycle is repeated until no weight changes for all the task’s possible input patterns. This repetition brings the temporal dimension into play, which I had ignored before, but now, for the sake of clarity, I will indicate by adding a temporal subindex  $t$  to activations and weights, where  $t$  denotes the run number of the cycle. For MCP1, then, the new notation is  $a_{1,t}$ ,  $a_{2,t}$ , and  $a_{3,t}$  for the activations, and  $w_{1,3,t}$  and  $w_{2,3,t}$  for the weights. Before running the algorithm, we need some *initial* weights. These can be randomly assigned, but as a conveniently simple example, assume that for MCP1 are  $w_{1,3,1} = 1.2$  and  $w_{2,3,1} = 1.3$ . Also assume, as before, that  $\theta = 0.4$  (this value remains constant across different

runs of the algorithm, so it does not need the time subindex).

For the & task, these weights satisfy  $w_{1,3,1} + w_{2,3,1} \geq \theta$  (fourth column, first row of Table 4, with the time subindex added, to indicate the first moment or run of the loop) and  $0 < \theta$  (fourth column, last row of Table 4), but neither  $w_{1,3,1} < \theta$  nor  $w_{2,3,1} < \theta$ . Using Eq. 1, these weights result in  $a_{3,1,1} = 1$ , the incorrect output activation for ( $a_{1,1} = 1$ ,  $a_{2,1} = 0$ ) and ( $a_{1,1} = 0$ ,  $a_{2,1} = 1$ ). In this case, the above algorithm stipulates going to Step 2c. If  $a_{1,1} = 1$  and  $a_{2,1} = 0$ , 2c instructs that  $w_{1,3}-1 = 1.2-1 = 0.2$  and  $w_{2,3}-0 = 1.3-0 = 1.3$ . This change in  $w_{1,3,1}$  ( $w_{2,3,1}$  did not change) means that MCP1 learned to satisfy  $w_{1,3,1} < \theta$ . For the next run ( $t = 2$ ), suppose that  $a_{1,2} = 0$  and  $a_{2,2} = 1$ . The algorithm instructs us to go to Step 2c again, instructing that  $w_{1,3,2}-0 = 0.2-0 = 0.2$  (using the new value of  $w_{1,3,2}$ ) and  $w_{2,3,2}-1 = 1.3-1 = 0.3$ . This change in  $w_{2,3,2}$  means that MCP1 learned to satisfy  $w_{2,3,2} < \theta$ .

I was able to use the algorithm manually, thanks to the example’s simplicity. In tasks and networks that are more complex, it is more viable to code the algorithm in a programming language and run the resulting application on a computer, for an automatic, fast, reliable weight search. This automated weight search makes learning in NNs somewhat more *autonomous* in that while the application is running, the weight search becomes independent of the programmer. Of course, it is not *completely* autonomous, as the programmer must still code the application but also for another, more specific reason.

The perceptron learning algorithm exemplifies the general definition of learning in NN modeling as a *change in one or more connection weights*. In this algorithm, learning thus defined occurs only when the perceptron *errs* (Steps 2b and 2c). Otherwise, the perceptron does not learn. Strictly, then, this algorithm only models learning by *failure*, not by success (Step 2a). In this sense, the perceptron learning rule is an *error-correction* rule and illustrates how erring *defines* a NN model, in sharp contrast to Turing’s characterization of his automatic machines as flawless.

This kind of learning is also known as *supervised* in that it implies an external.

“supervisor” or “teacher” that tells the system when it errs (in real teaching situations, the teacher would remain silent when the student succeeds). This implication obtains from the notion of a *desired* or *expected* output activation (as defined in the task), which prompts the question “Desired or expected by whom?” A natural answer is to assume an expectant agent that assists the perceptron in erring less frequently, another reason why this kind of learning is less autonomous (i.e., does not capture *autodidacticism*).

Minsky and Papert (1988) demonstrated that perceptrons with one input-unit layer and one output-unit layer could not learn tasks that were inseparable by a *hyperplane* (a general term that includes tasks with *any* number of inputs, defined as a subspace with one less dimension than its Cartesian coordinate system). About 88% of the possible tasks for a perceptron with the MCP1 structure are separable by a hyperplane, which is not bad at all. However, the percentage of these tasks tends exponentially to zero with the number of inputs (for a perceptron with just 9 input units, the percentage is  $1.075 \times 10^{-135}$ ), a major limitation. Most TCS and TAI researchers of the time mistook this limitation as *inherent* to *all* NNs, making them reject the connectionism hypothesis, which bolstered TCS and TM AI to become the dominant approach to theorizing about the mental for over a decade.

## CCS Vindicated: Backpropagation

A few scholars continued working on the CCS hypothesis and made important advances, but its decisive resurgence came with the publication of the PDP (“parallel distributed processing”) volumes (McClelland et al. 1986). This publication proved early rejections of NN modeling premature. A major development was the discovery that perceptrons with a hidden layer could do tasks that were inseparable by two hyperplanes (see Fig. 5). Another key advance was the use of a *continuous* activation rule.

A widely used continuous activation rule is the *logistic function* (which has a sigmoid shape that

resembles a stretched S), often expressed in abridged form as

$$a_{j,t} = \frac{1}{1 + e^{-x_{j,t}}}, \quad (3)$$

where  $x_{j,t}$  is defined in Eq. 2 and  $e \approx 2.71828 \dots$  is the base of natural logarithms. Its continuous character makes this function *differentiable*, meaning that it allows for the definition of a *derivative*, a fundamental concept in *calculus* (another part of mathematics that has been central to NN modeling). The derivative of a function is an equation to calculate the *slope* of a straight line that is *tangent* to the function at one of the function’s points. (The slope is a measure of how fast the function is/was changing at that point.)

By far, the most popular use of this concept in NN modeling is *backpropagation* (e.g.), in an error-correction learning algorithm known as *gradient descent*, which basically seeks to reduce a NN’s error, as part of this learning rule:

$$\Delta w_{i,j,t} = \alpha \delta_{j,t} a_{i,t}, \quad (4)$$

where  $\Delta w_{i,j,t}$  denotes the change ( $\Delta$ ) in the weight ( $w$ ) of the connection from  $i$  (an input or afferent) to  $j$  at  $t$ ,  $\alpha$  denotes the learning rate (a free parameter that influences how much  $w_{i,j,t}$  changes), and  $a_{i,t}$  denotes the *actual* activation state of  $i$  at  $t$  (computed according to Eq. 3, if  $i$  is a hidden unit connected to output unit  $j$ ).

The key term is  $\delta_{j,t}$ , the specific quantitative contribution of  $j$ ’s activation to an error at  $t$  in a feedforward NN with one hidden layer (e.g., upper middle panel of Fig. 1). Technically,  $\delta_{j,t}$  is the *partial* derivative of Eq. 3 with respect to  $x_{j,t}$ , computed differently for hidden and output units, *after* the *forward-propagation* phase (computation of the *actual* activations of *all* hidden and output units for a given input pattern at  $t$ , according to Eq. 3). If  $j$  is an output unit,  $\delta_{j,t}$  crucially includes a *prediction error* defined as  $a_{j,t} - d_{j,t}$ , where  $a_{j,t}$  denotes  $j$ ’s *actual* activation (computed according to Eq. 3) and  $d_{j,t}$  denotes  $j$ ’s *desired* activation for the current input pattern, as stipulated by the task. Once computed,  $\delta_{j,t}$  is sent *back* (hence the name “backpropagation”) to the

hidden units connected to  $j$  and used to compute  $\delta_{j,t}$  for them and change the corresponding weights. In general, the greater the value of  $\delta_{j,t}$ , the greater the weight change, everything else being equal.

## Concluding Remarks

Thanks to these and other developments, NN modeling has become dominant in cognitive science and AI tech research. This research has overcome the obsession TCS and TAI researchers have for the TT, moving beyond an anthropocentric and symbolic-centric view of the mental. All this has made for a more inclusive cognitive science that contemplates the possibility of non-symbolic cognition, human and nonhuman.

The foundations summarized above have had a strong engineering import, but they also inform scientific understanding of natural minds, although not without important modifications. For example, the view of learning as error correction has been very influential in computational modeling of *Pavlovian conditioning*, the simplest form of associative learning studied in animals (see ► “[Learning](#)” entry in this encyclopedia). According to a standard NN interpretation (e.g., Sutton and Barto 1981), error correction is at the core of the most influential model of Pavlovian conditioning, proposed by Rescorla and Wagner (1972). However, these interpretations do not include the kind of mechanism found in the back-propagation model.

I have only skimmed the surface of NN modeling, focusing on the fundamentals of supervised learning in feedforward NNs. As anticipated in the first section, there are other types of NNs and learning algorithms. Unfortunately, I can only mention a few very briefly, without doing them the justice they deserve.

In one important category of NN models, learning is *unsupervised*, which does not occur by error correction. As the name suggests, this kind of NN learning does not imply the presence of a teacher. Rather, weights change depending on the levels of co-activation of the connected units. In this sense, unsupervised learning is somewhat

more autonomous. A paradigmatic example is Hebbian learning (after Hebb 1949). In its simplest form, Hebbian learning occurs according to this rule (Hebb did not formulate it computationally):  $\Delta w_{i,j,t} = \alpha a_{i,t} a_{j,t}$ , where  $a_{i,t}$  denotes  $i$ 's (an afferent's) activation state at  $t$  and  $a_{j,t}$  denotes  $j$ 's activation state at  $t$ . Other unsupervised-learning NN models include the *self-organizing map* introduced by Kohonen (2001) and the *adaptive resonance theory* (e.g., Grossberg 2013).

Yet another category of NN models involves *reinforcement learning*. In their version, Sutton and Barto (2018) have drawn from experimental animal research on conditioning. They conceive Pavlovian conditioning as learning to *predict* that a certain biologically significant stimulus reliably follows a biologically nonsignificant cue. They also try to account for operant or instrumental conditioning, a more complex form of associative learning where animals are rewarded for acting in certain ways on their environment (see ► “[Learning](#)” entry in this encyclopedia), conceiving it as learning to *control* the environment through actions that have consequences. Recent NN models of conditioning have tended to maintain a sharp distinction between Pavlovian and operant learning algorithms. One exception is the model proposed by Donahoe et al. (1993), which seeks a more unified approach by using the *same* learning algorithm to simulate *both* kinds of conditioning. This model makes no distinction between operant and Pavlovian *learning*.

In sum, the pursuit of the CCS hypothesis through NN modeling has changed cognitive science significantly, and its AI tech achievements have been very impressive. At least some, perhaps most of it has been for the better, and the overall balance seems positive, but it still is too soon to know where it will lead. Only future research can tell. Meanwhile, the field will benefit from heeding a lesson from past research: avoid premature overenthusiasm. Enthusiasm motivates and inspires, but it is wise to keep it in check. Beware of the recent hype about CAI, especially machine and deep learning AI.

It thus is wiser to pursue CCS as a *working hypothesis* very much in need of further investigation. Despite significant progress, Smolensky's



(1988) assessment that “the connectionist approach is still quite underdeveloped” (p. 2) remains valid. Further progress requires continued discussion of the approach’s difficulties. Some are practical and more relevant to CAI tech research. Here I focus on a potentially more worrisome problem from a basic-scientific modeling perspective: it is very difficult to *explain thoroughly and intelligibly* why particular NNs function the way they do in specific tasks. CAI tech researchers too face this problem but care more about NNs doing their job effectively and efficiently than explaining why.

I gave a glimpse of the problem in the third section. There, I suggested that it would be impractical to explain thoroughly why a particular MCP NN with just three input units connected to one output unit *succeeds* at a particular task, *if* this explanation was a mathematical demonstration of the solvability of the corresponding system of linear Boolean inequalities. The perceptron learning algorithm makes this demonstration unnecessary, because it allows for an automated search of a solution with a computer. There also is the perceptron *convergence theorem*, a mathematical proof that the perceptron learning algorithm will find in finite time a solution for any *solvable* system.

However, it is not obvious exactly how all this would make a thorough explanation more intelligible or even viable. Much depends on the explanation’s form and the perceptron’s size as determined by the task. It would seem viable to explain thoroughly why a perceptron with three input units connected to one output unit succeeded at a particular task through a computer simulation that preserves the eight final weights. This explanation could show the eight final connection weights and appeal to the convergence theorem to assert that they solve the task’s system of linear Boolean inequalities, but how *intelligible* would this be? To begin with, understanding the theorem’s *proof* would seem necessary to understand the explanation, but this is not easy, especially for the non-expert. How intelligible or even viable would be a thorough explanation of why such a perceptron *failed* a particular task?

The problem arises from NN size *with unrealistic, simplified activation and learning functions* like

the perceptron’s. Therefore, simplifying them does not ease the problem. The search for realism in computational neuroscience also promotes the use of NNs too large for thorough explanations to be intelligible or even viable. A realistic NN of the *C. elegans* brain, one of the simplest known to neuroscience, would consist of about 300 units and 7,000 connections. It is far from obvious how intelligible or even viable would be a thorough explanation of why such a NN functions in particular situations. The search for realistic activation and learning functions only exacerbates the problem.

In general, then, NN model realism decreases the viability and intelligibility of explanations of why particular NNs function the way they do in particular situations. The problem is not exclusive to NN modeling but afflicts *all* computational modeling of complex phenomena that seeks realism nor is the problem new; it arose decades ago under the name of “Bonini’s paradox” (see Dawson 2004, pp. 17–18, 121–125), in reference to computer simulations that are as difficult to understand as the simulated phenomena are.

Avoiding this problem is necessary for progress in NN modeling, but particular ways vary across models and phenomena. The root of the problem is that two key virtues of explanations, parsimony and realism, relate inversely. The only options, then, are either to maintain realism and reduce explanation intelligibility or vice versa. The wisest strategy for the time being is to seek a judicious *balance*. Unfortunately, it remains unclear where such balance is, let alone how to achieve it.

## Cross-References

- [Action Potentials](#)
- [Associative Learning](#)
- [Cognition](#)
- [Consciousness](#)
- [Donald O. Hebb](#)
- [Edward Thorndike](#)
- [Functionalism](#)
- [Learning](#)
- [Neuron](#)
- [Turing Test](#)

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## Neuroanatomical Plasticity

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## Synonyms

Structural plasticity

## Definition

The ability of the brain to physically change and reorganize itself in response to learning and experience.

## Introduction

For many years, the idea that specific functions and behaviors were hard-wired and localized to one specific brain region was dogmatic throughout the scientific community. However, a shift away from the Doctrine of Localization was observed in the 1970s and 1980s when acknowledgement of the brain's ability for change as a result of experience first gained popularity. Since then, the development of modern technology has provided scientists with the tools to back up the speculation that behavioral changes are correlated with neuroanatomical changes with evidence at the structural level. Now, acceptance of the brain's ability to reorganize itself in response to stimulation, novel information, development, and damage has swept the neuroscience community and lead to the acceptance of neuroplasticity as a fundamental function of the nervous system.

## Neurobiology of Structural Plasticity

The overall ability of the brain to change is primarily a result of activity that occurs at synapses (the connections between neurons). There are two primary types of changes that can occur at the synapse. The first involves the formation of novel neuronal connections and is known as Synaptogenesis. The process of synaptogenesis is believed to begin when the dendritic spines (projections off of the cell body of a neuron) of one neuron reach out to the axons of nearby neurons and actively pull them closer to the cell body (McCallister 2000). Once the initial recruitment of nearby axons to dendrites has occurred, the solidifying of the neuronal connections is dependent upon neurochemical communication between the pre-synaptic neuron (axon) and the post-synaptic neuron (dendrite).

Once neurons are brought together and synapses are formed, the strength of the connection is subject to change as a direct result of activity. This phenomenon, known as Synaptic Plasticity, is the second type of change that can occur at the synaptic level and generally functions in line with the commonly known principal of “use-it-or-lose-it.” Each time that a neuron is stimulated, or “used,” by a pre-synaptic neuron, a strengthening in the connection between the two neurons is observed. In other words, repeated stimulation by a pre-synaptic neuron leads to the strengthening in response of a post-synaptic neuron resulting in the Long-Term Potentiation (LTP) of the connection between the two neurons.

On the flip side of this is a phenomenon known as Long-Term Depression (LTD). LTD is observed when a decrease in stimulation by a pre-synaptic neuron leads to a decrease in response of a post-synaptic neuron. This decrease in stimulation eventually causes the connection between the two neurons to be “lost.” Taken together, LTP and LTD make up the mechanism by which the brain is able to achieve cortical map reorganization.

Beyond changes at the synapse, the brain is also capable of changing through the formation of new neurons – Neurogenesis – and the eradication of existing neurons. The greatest rate of neurogenesis occurs in the womb and throughout development. However, neurogenesis can also occur into adult hood and be stimulated by hormones released after the brain experiences trauma (Wieloch and Nicolich 2006).

## When Does Neuroanatomical Plasticity Occur?

Plasticity is not just something the brain is capable of; plasticity is the constant state of the brain. From the onset of neuronal development to death, the brain persistently demonstrates its unparalleled plastic abilities. From the perinatal onset of neuronal development, the brain gains neurons at a rate of about 250,000 nerve cells per minute. At the time of birth, neurons in the cerebral cortex of the human brain form roughly

7000 connections each and, though the rate has decreased from that of perinatal development, nerve cells are still being added (Ackerman 1992). By the age of seven, the number of connections for each neuron increases to about 15,000. Following this rapid state of expansion in the brain, an event known as Synaptic Pruning occurs where the principles of “use-it-or-lose-it” are put into place and the synaptic connections that are being used are strengthened and the ones that are not are broken. At the end of this developmental process each neuron has somewhere between seven or eight thousand connections.

Though neurogenesis does greatly slowdown after the developmental stage, plasticity in the brain persists. Every time something new is learned or forgotten – be it a skill, a person, a task, a motor function, or anything else – the brain is capitalizing on its plastic abilities.

Another time where the brains plasticity is strongly capitalized on is following brain trauma. Often times, trauma to the brain can result in the loss of the function for which the damaged brain region was responsible. However, thanks to both functional and structural plasticity, the recovery of the lost behavioral function is possible. Following damage, the brain may structurally alter its neural maps and connections by temporarily entering into a state of neurogenesis as well as increasing the the connections between healthy – or undamaged – brain regions to compensate for or take over the role of the lost function.

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## Neuroanatomy

- [Sirenia Sensory Systems](#)

## Neurochemicals

- [Neurotransmitters](#)

## Neuroethics

- [Pain and Ethics of Animal Care and Use](#)

## Neurogenesis

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## Synonyms

[Neruogeneration](#)

## Definition

Neurogenesis is a process of generation of functional neurons from the precursors, which happen during the embryonic and prenatal stage in mammals.

## Introduction

Neurogenesis is a process where neurons are generated from precursors (neural stem cells and progenitor cells). Neurogenesis comes from two terms, neuro or nerve cells and genesis means creation or beginning of, combined it simply is the creation of new nerve cells. Adult neurogenesis is a process where new neurons are born after postnatal stage from adult neural precursors. A typical neuron generation takes place in three distinct stages, cell proliferation, cell migration, and cell differentiation.

## Neurogenesis

Neurogenesis is the most important phenomena during the embryonic development of any species. The main reason for this is that to develop a functional connection between neurons requires the generation of specific neuron types, and their correct migration and differentiation at the precise time in the development stage. During embryonic neurodevelopment, an embryo has three distinct layers (endoderm, mesoderm, and ectoderm), which give rise different part of the body. Ectodermal layer forms the nervous system and skin.

Neuron production in human begins on embryonic day 42 or E42, and differentiation of neural progenitor cells extends to late adolescence. These neurons migrate to different brain parts and begin making connections to form the primary neural networks. After the gastrulation period of embryo, neural stem cells emerge and they are capable of producing all different type of cells that are required in the central nervous system. Neural stem cells are also called neural progenitor cells. After formation of these progenitor cells, these cells are positioned along the upper layer (ectoderm) of the embryo and this region is called neural plate.

Next important step in development is formation of neural tube which forms along the two sides of the neural plate and later becomes a hollow tube and eventually forms the ventricular system of the brain. Neural progenitors are located in a region of the brain called ventricular zone (VZ) (Stiles and Jernigan 2010). At E42 stage neural progenitors go through asymmetrical cell division and give rise to one stem cell and one neuronal precursor cell (neuroblast) that never go for cell division again (Purves et al. 2004). Neuroblasts once exiting cell cycle leave the proliferative VZ to further differentiate into neurons and other specific cell types and subsequently migrate to target areas in the brain. These neuroblasts give rise to several neuronal cell types depending on brain area they are targeted and type of connections they will form. Neuronal differentiation is based on local cell-cell interaction and several transcription factors expressed in each cell.

Migration of postmitotic neuroblasts brings together the different class of neurons together

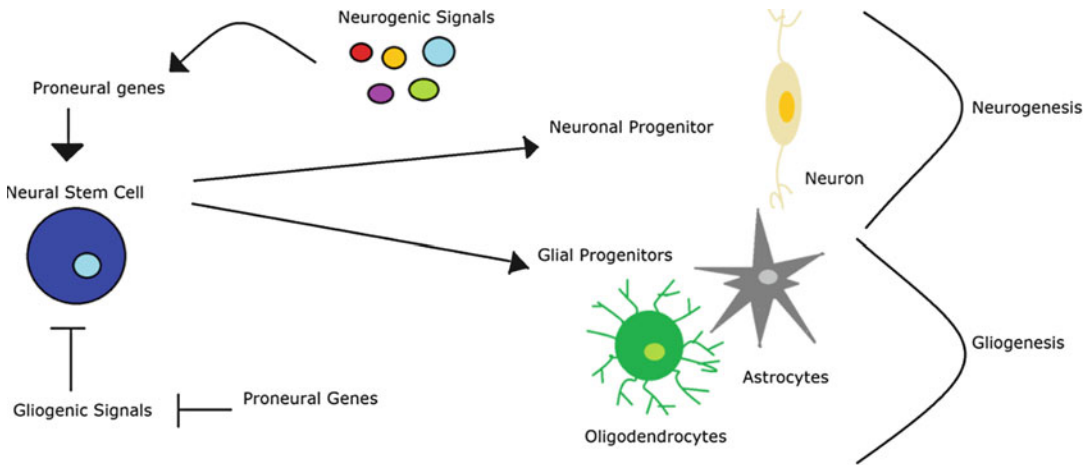
for dynamic interaction and development precise connection at the synaptic level. Some neuron migrates shorter distance whereas neurons that migrate greater distance require a special type of cells called “radial glial cells” to act as a guidance system. Neurons that leave the VZ earlier forms the deepest layer of cortex and later neurons make the superficial layers. This order of migration is termed as inside-out (Stiles and Jernigan 2010). After reaching at target location in cortex and elsewhere in brain, these neurons need to form connections and makeup the rudimentary neural network. In order to do so, they develop neuronal processes (axon and dendrites) with help of some signaling molecules that allow them to communicate with other neurons (Fig. 1).

Until last two decades, it was in consensus that once the brain has developed and neurons have settled in various networks, it is impossible to generate new neurons and adult neurogenesis does not occur. But this was challenged by few scientists who observed that few part of the brain still undergo neurogenesis in the adult state of the brain also, two discrete regions of the brain were identified, dentate gyrus of the hippocampal formation and subventricular zone (SVZ) and its projection to the olfactory bulb (Gage 2002). This new discovery was very important for two main reasons: first is that brain is capable of much more plasticity than previously thought, and second in the case of brain trauma, there are higher chances of brain repair now using stem cells from these regions.

## Conclusion

Neurogenesis is a critical part of brain development structurally and functionally. This development process requires availability and appearance of these neurons at the right time, which is ensured by the various stages of neurogenesis. Migration and differentiation of neural progenitor cells ensure this process goes smoothly. Adult neurogenesis, the amazing phenomena of the brain to generate new neurons in adulthood has opened doors to many opportunities to mitigate the brain degenerative processes in various disease





**Neurogenesis, Fig. 1** Neural stem cells differentiate into neuronal progenitor cells, which give rise to neuron, or glial progenitors, which give rise to glial cells (Image

credit: NCD Project/CC BY-SA 3.0 via Commons) (Ref What is neurogenesis? 2017)

conditions. New therapeutic treatments are available now and continue to develop using adult neural stem cells and promise a new dimension in disease treatment.

## Definition

A neuron is a specialized cell that transmits electrical impulses and is the basic unit of the nervous system.

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## Introduction

Neurons are the basic unit of the nervous system; when bundled together they create nerves, the spinal cord, and the brain. They can transmit information with electrical and chemical signals. This characteristic allows for processing in different brain structures and for sending information throughout the body. To do this, neurons form networks and communicate with each other via nerve impulses, also known as action potentials. Typically, a neuron has dendrites to receive electrical signals, a cell body, or soma, for integration, an axon for propagation, and axon terminals to release neurotransmitters into the synaptic cleft, a junction between two neurons.

All neurons have a relative negative resting potential that is maintained by the sodium-potassium pump. There are three major ions in the electrochemical activity of a neuron: potassium, sodium, and calcium. The concentration of potassium is higher inside the cell than outside, while the concentrations of sodium and calcium

## Neuron

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## Synonyms

Nerve cell

are higher on the outside than inside. The electrical activity caused by a stimulus will affect the permeability of a neuron causing these ions to change the cell's resting potential, allowing for the transmission of information. The aggregate activity of neuron action potentials accounts for nearly all the activity of the nervous system.

To create complex networks and circuits, there are different types of neurons within the nervous system, each varying in structure, function, and location. Some differ in their direction of firing, sending information from the peripheral nervous system (PNS) to the central nervous system (CNS), or vice versa. Neurons also have different structures that are driven by polarity, the projections that extend from the cell body. Lastly, there are neurons that, when fired, release primarily one neurotransmitter. These neurons are present in certain neuronal pathways that often have a specialized function, like dopamine pathways for controlling movement and reward.

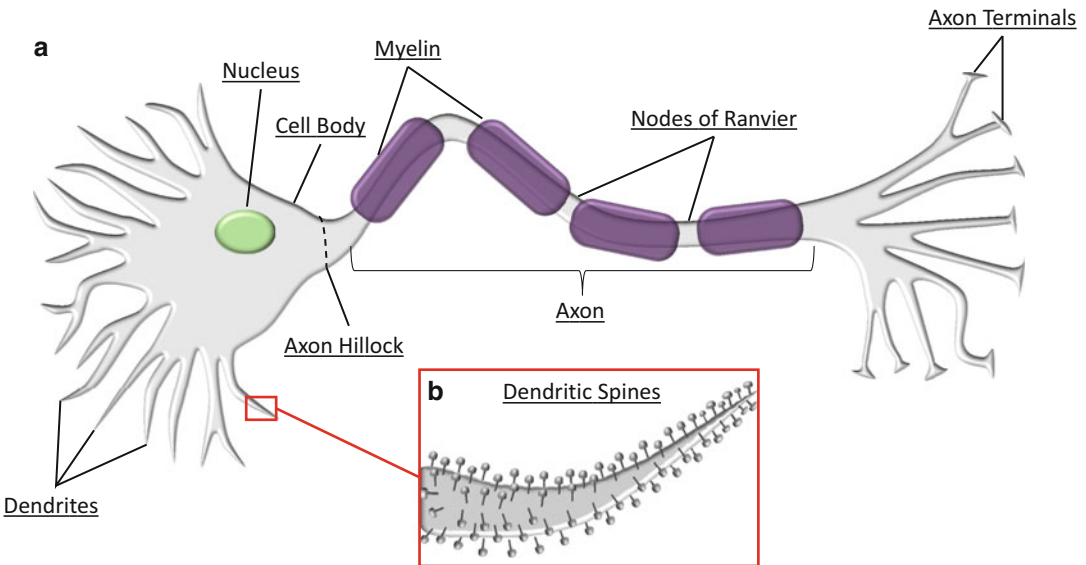
### Neurogenesis and Maintenance

Unlike most cells in the human body, neurons do not undergo cell division and their formation

typically stops at adulthood. Neurons are developed and maintained with support from differentiated cells, such as glial cells, and substances such as neurotrophins (Palmer et al. 1999). Neurotrophins are a class of growth factor that play an important role in the generation and overall health of new and existing neurons, both in newborn and adult animals. Neurotrophins interact with signaling pathways involved in the generation, maintenance, and differentiation of neurons (Takahashi et al. 1999).

### Structure and Function of a Neuron

A neuron is composed of dendrites, a cell body, an axon, and axon terminals (Fig. 1a). The dendrites contain receptors that bind to specific neurotransmitters released from the presynaptic neuron. Usually, this area is the starting point for an action potential. An important aspect of dendrites is their widespread layout and density, increasing their ability to synapse with many other neurons and brain regions (Lodish et al. 2000b). This property is known as arborization. Dendrites with greater arborization feature larger dendritic fields. To further increase neuronal connectivity, dendrites



**Neuron, Fig. 1** Structure of a neuron. (a) General structure of multipolar neuron containing dendrites, a cell body or soma with a nucleus, the axon hillock, axon, myelin,

nodes of Ranvier, and axon terminals. (b) Close-up of dendrite showing structure of dendritic spines. Image is not to scale

contain spines that receive most of the incoming excitatory signals (Kasai et al. 2003). Each of these spines represents another synapsing point. A dendritic spine is made up of a head and neck, with the former featuring a postsynaptic density (PSD) (Fig. 1b). The PSD is an area that contains many receptors and proteins that facilitate neural transmissions through increased neurotransmitter binding. Spines are highly plastic and react to the amount of input they receive. Maturation and increased cognitive processing, such as learning, can lead to well-developed dendritic spines, while diseases and lack of stimulation can weaken or destroy them (Wong and Ghosh 2002).

The cell body contains the nucleus, with all genetic information, and other life-sustaining organelles, such as the mitochondria, endoplasmic reticulum, ribosomes, and Golgi. The main function of this structure is to provide all necessary materials for the cell, such as proteins. The cell body also receives electrical signals from the dendrites and integrates them at the axon hillock, or initial segment. If the signal is strong enough, it is transmitted to the axon (Lodish et al. 2000b).

Attached to the cell body is a long projection called the axon. Once an action potential is initiated, it is conducted down this structure, away from the cell body. The axon contains many voltage-gated ion channels, mainly calcium and potassium, that are involved in an action potential (Lodish et al. 2000b). The axon is sometimes insulated by myelin to protect the signal from degrading and slowing down. Schwann cells and oligodendrocytes are two types of cells that produce myelin, with the former working in the PNS and the latter working in the CNS. Myelin does not completely cover the axon, instead only covering segments. Gaps in these segments are called nodes of Ranvier. These nodes allow for faster propagation by a process called saltatory conduction, in which a signal can pass quickly through the myelin, jumping from node to node. The axon diameter also plays a factor in the velocity of an action potential. As the axon diameter increases, so does the velocity of the action potential (Salami et al. 2003).

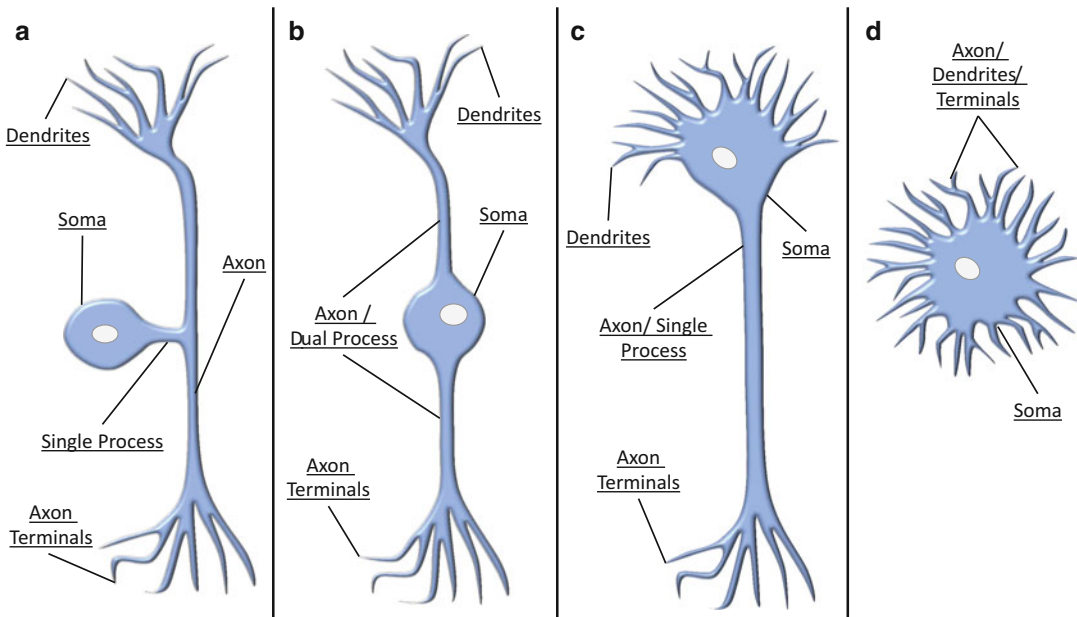
The end of a neuron features axon terminals that usually synapse with dendritic spines. These terminals contain vesicles filled with

neurotransmitters. When an action potential reaches the terminals, the positive charge activates voltage-gated calcium ion channels. Calcium ions rush into the cell and bind to proteins that initiate a series of events in which the vesicles fuse with the membrane to release the neurotransmitters. Presynaptic neurons can also repackage neurotransmitters in the cleft to be reused. The synapse marks the end of an action potential and the transmission of information (Lodish et al. 2000a).

## Types of Neurons

Neurons can be characterized by structure, such as polarity, and by function, such as firing direction or neurotransmitter production. Polarity refers to differences in the structural development of a neuron and is subdivided into categories: unipolar, pseudounipolar, bipolar, multipolar, and anaxonic. A unipolar neuron has only one projection from the cell body that splits into two axons, featuring dendrites and terminals at opposite ends (Fig. 2a). This type of neuron is primarily found in invertebrates and is used for touch and pressure sensation. Pseudounipolar neurons are similar to unipolar neurons in structure and function (Fig. 2a). However, they develop from a bipolar cell and are found primarily in vertebrates. In humans, the pseudounipolar neuron branches from the sensory organ to the spinal cord. Bipolar neurons have two projections extending from the cell body, one for dendrites and the other for terminals (Fig. 2b). These neurons are found exclusively in the olfactory bulb and retina. Multipolar neurons have a single process and numerous dendrites that project from the cell body (Fig. 2c). They are the most common type and makeup the bulk of neurons in the brain (Squire et al. 2008). An anaxonic neuron is one in which the axon is short and therefore cannot be differentiated from the dendrites or terminals (Fig. 2d). These neurons mainly work to integrate signals from many neurons and can be found in the retina and parts of the brain, like the olfactory bulb (Crespo et al. 2013).

Another way to characterize a neuron is by the direction of firing. A neuron that sends information from the CNS to organs and limbs is called an



**Neuron, Fig. 2** Structural differences of neurons dictated by polarity. (a) Structure of a unipolar or pseudounipolar cell with a single projection from the soma. (b) Structure of a bipolar cell with dual projections from the soma. (c)

Structure of a multipolar cell with a single projection from the soma. (d) Structure of an anionic cell with unidentifiable axon

effluent neuron. Motor neurons allow for movement, as they send signals from the brain to the PNS to control processes like muscle contraction and gland secretion. Conversely, a neuron that sends information from the sensory organs to the CNS is called an afferent neuron. Sensory neurons are those that respond to the environment. They gather information from sensory receptors and send it to the brain to be interpreted. Linking the sensory and motor neurons with the CNS are interneurons, which can be afferent or efferent. These neurons also serve as connections between brain structures, creating circuits, and are only found within the CNS (Squire et al. 2008).

Neurons can also be classified by their production of neurotransmitters and the effects on postsynaptic neurons. There are two main classes of neurotransmitters, excitatory and inhibitory. Excitatory neurotransmitters increase the likelihood for an action potential to occur while inhibitory neurotransmitters do the opposite. There are five main neurotransmitter classifications of neurons that have receptors for Acetylcholine, GABA, Glutamate, Serotonin, and Dopamine.

Cholinergic neurons work with receptors that can be excitatory or inhibitory, and are present in learning and memory pathways. GABAergic neurons produce inhibitory effects, as they hyperpolarize postsynaptic neurons. Glutamatergic neurons work with four types of receptors that produce excitatory effects in postsynaptic neurons, facilitating neural transmission. Serotonergic neurons can be excitatory or inhibitory, and play important roles in sleep, mood, sexual behavior, and anxiety. Lastly, dopaminergic neurons may be excitatory or inhibitory, depending on the neural pathway. Most commonly, dopaminergic neurons are implicated in movement and reward pathways (Lodish et al. 2000a).

## Circuits

Circuits are collections of interneurons that cluster in groups and form ensembles, which connect in series with others around the brain. These circuits carry electrical signals through brain structures and serve specific functions, from basic sensation

processing, like vision, to more complex processing, like emotions. Myelin is especially important in these circuits, as it allows for increased conduction velocity throughout distant brain structures (Salami et al. 2003). Destruction of these myelinated pathways, and the subsequent increase in transmission timing, can deteriorate healthy brain function and result in many neurodegenerative ailments, such as multiple sclerosis (Lodish et al. 2000b).

## Cross-References

- [Action Potentials](#)
- [Axon](#)
- [Dendrites](#)
- [Myelination](#)
- [Nervous System](#)
- [Neurogenesis](#)
- [Neurotransmitters](#)

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## Neurons

- [Nerve Cells](#)

## Neurosciences

- [Serotonin](#)

## Neurotransmitter

- [Serotonin](#)

## Neurotransmitters

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## Synonyms

## Neurochemicals

## Definition

Neurotransmitters are chemical messengers in the brain that transmit a signals from one neuron (nerve cell) to another neuron, muscle cell, or gland cell (Lodish et al. 2000).



## Synaptic Space and Neurotransmitter Mechanism

The synaptic space consists of three functional parts: the presynaptic membrane, the synaptic cleft, and the postsynaptic membrane. These highly specialized membranes ensure that vesicles containing neurotransmitters are released at its appropriate active sites (Patestas and Gartner 2016). Neurotransmitters are composed of amino acids, the basic building blocks of proteins. Neurotransmitters are stored and released from synaptic vesicles, which are found at the terminal end of a neuronal axon (Ikeda and Bekkers 2009). A neuronal signal is conducted after an action potential has been initiated by releasing neurotransmitters into the synaptic space, a microscopic gap that exists where the axon of one neuron meets the dendrite of another. During depolarization of the action potential, the synaptic vesicles will fuse with the presynaptic membrane (Purves et al. 2012). The influx of calcium from depolarization will cause the synaptic vesicle to attach to the presynaptic membrane allowing the neurotransmitters to release (Patestas and Gartner 2016). The neurotransmitters attach to corresponding receptors at the receiving neural, muscle, or gland cell (Thompson 2000). A released neurotransmitter exists in the synaptic space for a short period of time before it is either bound to a receptor or metabolized by enzymes. Neurotransmitters may influence neurons in an inhibitory or excitatory manner (Sapolsky 2005). They influence neurons by causing ion channels to either open or close in order to depolarize or hyperpolarize the target cell membrane (Patestas and Gartner 2016).

## Types of Neurotransmitters

Neurotransmitters must meet the following main criteria (Patestas and Gartner 2016):

1. Neurotransmitters must be present or synthesized within a neuron.
2. Neurotransmitters must be stored in synaptic vesicles.

3. Upon neural activation, the neurotransmitter must produce a response at the target cell receptor site.
4. An identical response must be produced when the neurotransmitter is experimentally placed at the target cell receptor site.
5. A removal mechanism must be intact to remove the neurotransmitter from its activation site after its release from the neuron.

The term “neurotransmitter” can also be used to define chemicals that:

1. Carry messages between neurons
2. May or may not have an effect on membrane voltage, but can change the synaptic structure
3. Communicate messages that affect the release or reuptake of other transmitters (Breedlove et al. 2013).

## Classification of Neurotransmitters

Neurotransmitters are classified into biogenic amines, neuropeptides, and small molecule neurotransmitters.

### Biogenic Amines

Biogenic amines are neurotransmitters made from amino acids, the building block of proteins. Norepinephrine, epinephrine, dopamine, serotonin, and histamine all fall under the biogenic amine category. These neurotransmitters are quickly digested after release and therefore are only responsible for a limited number of depolarizations or hyperpolarizations (Patestas and Gartner 2016).

### Neuropeptides

Neuropeptides are small neuronal proteins that are used by neurons to communicate with each other. They tend to be co-released during an action potential in order to enhance or inhibit the effect of other neurotransmitters. Endorphins are an example of neuropeptides (Patestas and Gartner 2016).

### Small Molecule Neurotransmitters

Small molecule neurotransmitters are low molecular weight proteins synthesized in the presynaptic terminals. Some examples are acetylcholine, gamma aminobutyric acid (GABA), glycine, and glutamate.

### Neurotransmitter Imbalance and Disorders

There are no standardized levels for each neurotransmitter in the body due to the inability to accurately measure the concentration of each individual neurotransmitter at any given time; often times, various neurotransmitters regulate the concentration of other neurotransmitters further deeming it difficult to measure (Trofimova 2016). Neurotransmitters can provide significant effects on the brain in smaller amounts (Sapolsky 2005). A consistent imbalance of neurotransmitters is responsible for various disorders like depression, schizophrenia, attention deficit hyperactivity disorder, autism, and obsessive-compulsive disorder. Most psychoactive drugs affect neurotransmitter activity in order to treat psychological disorders (Sapolsky 2005).

### Cross-References

- Action Potentials
- Amino Acid
- Axon
- Cell Membrane
- Chemical Signals
- Dendrites
- Dopamine Receptor
- Myelination
- Neural Impulse
- Neuron
- Neuron
- Oxytocin
- Protein
- Serotonin

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### Neutral

- Arbitrary Stimuli

### New World Monkey

- Haplorhini

### New World Monkeys

- Platyrrhine Cognition
- Platyrrhine Sensory Systems

### New World Monkeys Communication

- Platyrrhine Vocal Communication

## Newt

### ► Caudata Cognition

## Newton's Third Law

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## Synonyms

Force; Motion; Movement

## Introduction

Intuitively, a body's movement remains constant unless there is an external factor acting on it, which is called *force* (Halliday et al. 2012). In nature, it is observed that forces arise in pairs since for each existent force there's another with the same intensity but in the opposite direction. This phenomenon is known as *Newton's third law*. From this perspective, Newton's third law remarks that forces *always* arise in pairs. This can be verified in many different practical situations; as a person walks through a solid surface, for example, pressing their feet against the ground ( $F_1$ ), there's a so-called friction force ( $F_2$ ) propelling the person's body forward (Nussenzveig 2013; Taylor 2013) (Figure 1). For another example, in Figure 2, while an astronaut in the middle of space throws an object forward ( $F_1$ ), the same object will exert a force ( $F_2$ ) on the astronaut, launching him in the opposite direction.

## Animal Locomotion

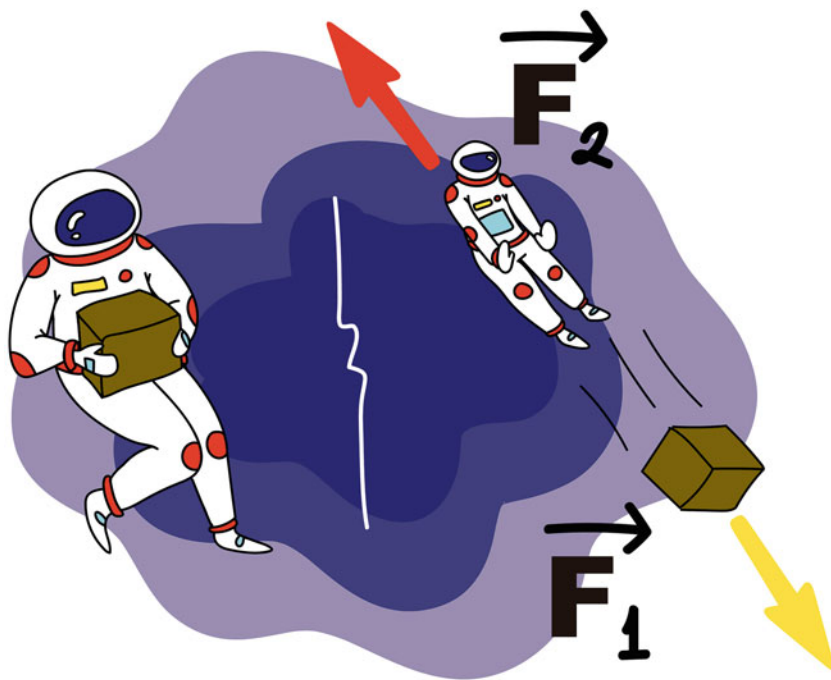
Analogous to the astronaut walking on the moon or throwing an object into space, Newton's third law

also applies in the movement of animals: in the flight of a bird, the wings make a force pushing the air downwards, and the air reacts with an equal and opposite direction force, pushing the bird upwards; when a fish is swimming, it pushes the water backward, and the water reacts and pushes the fish forward. Even though there are intricacies to the nature of the force in any example that can be observed, Newton's third law concerns only with the overall concept of forces, their direction, and intensity.

## Remarks

The examples presented in the previous discussion assumes one important point about the interaction between objects: any other forces acting on them have negligible effects, and it's only considered their overall effect. In the example of a bird flying, the air currents propel nontrivial individual forces through the bird's body; notwithstanding, when taking all contributions, there'll be a resultant force responsible for the bird's flight. The same reasoning can be applied to the fish swimming through the water or any other physical phenomena that it's observed in everyday life.

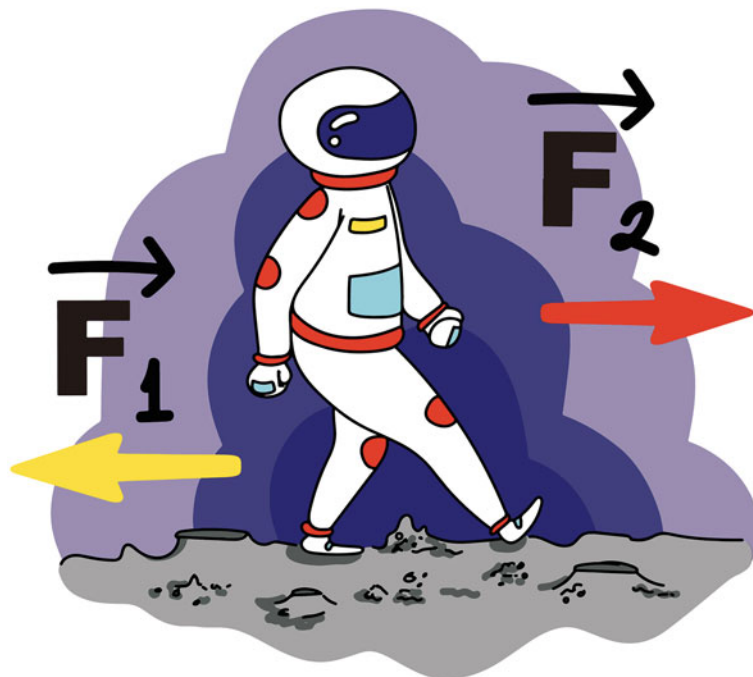
Another significant aspect is that, in these examples, the interaction between the objects occurs with contact forces; this means that the time of interaction between them is really small and the forces can be understood as instantaneous – the time interval between the force of the astronaut's feet against the lunar soil and the force propelling the astronaut forward is effectively imperceptible, for example. It's from this “instantaneous interaction” perspective that arises the idea that the forces always arise in pairs (Halliday et al. 2012). It's also important to remark that Newton's third law shouldn't be confused with the “action-reaction” erroneous perception of the influence of a posterior event due to initial and small conditions. An illustration of this is the famous metaphorical example of the “butterfly effect,” where the formation of a tornado could be influenced by the flapping of a butterfly's wings. The idea here is not to take this example literally but to illustrate that there are systems that are sensitive to small changes on the initial conditions and they have nothing to do with Newton's third law.



**Newton's Third Law, Fig. 1** Astronaut walking on the moon

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**Newton's Third Law, Fig. 2** On the left, the astronaut carries a cube and then, on the right, he throws it



## Cross-References

- [Folk physics](#)
- [Locomotion](#)

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## Next Generation Sequencing

- [Bioinformatics](#)

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## Next-Generation Sequencing

- [Gene Expression Profiling](#)

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## Nexus

- [Neural Network](#)

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## Niche Divergence

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### Definition

Any change in ecological niche (fundamental and realized niche) due to abiotic (climatic) and biotic (e.g., competition, predation, parasitism, etc.) constrains on a subgroup of population, and

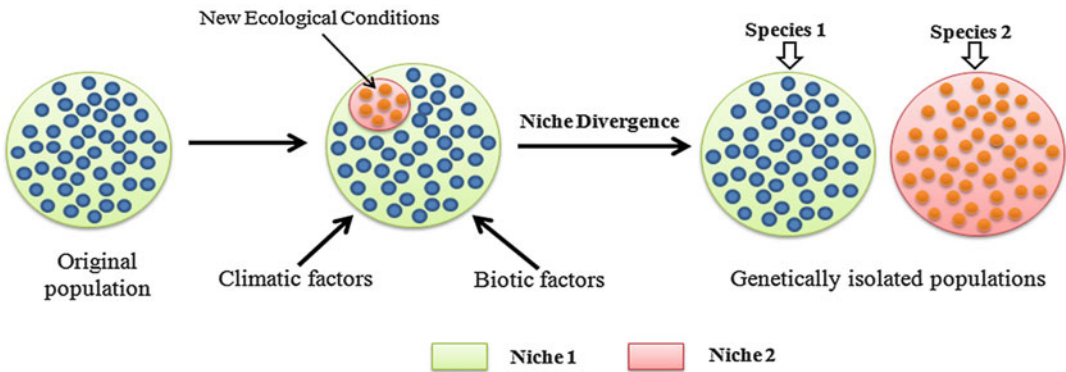
subsequent adaptation to this diverge niche is known as niche divergence.

## Introduction

The organisms tend to live and reproduce in a given set of environmental conditions, known as niche. Various abiotic and biotic factors determine the limit of occurrence range of a species. The niche can be further divided into realized and fundamental niche. Fundamental niche can be defined as the range of environmental (abiotic) conditions under which population of a species can survive and maintain a positive growth rate. The potential niche is the subsection of fundamental niche, which allows a species to survive and reproduce at specific point in time. The realized niche is a subsection of potential niche which is actually occupied by population of a species despite the biotic interactions like competition, predation, etc. (Hutchinson 1957; Jackson and Overpeck 2000). However, the environmental conditions are not always constant; the ever-changing interaction among populations and its abiotic and biotic components influence its growth and occurrence. These factors influence the behavior of organisms, which leads to change in their fundamental, potential, or realized niches. These changes in ecological niches lead to speciation by natural selection.

Evolutionary ecologists suggest that mutation-order and ecological speciation are the two marked mechanisms for speciation by natural selection. The mutation-order speciation involves the fixation of advantageous/neutral mutations among a subgroup of the population, which leads to increase in the frequency followed by genetic isolation in same ecological niche. On the contrary, ecological speciation occurs through the appearance of different environmental conditions within an ecological niche and adaptation of a subgroup of the population toward it followed by niche divergence, which ultimately leads to genetic isolation and speciation (Fig. 1). Mutation-order speciation is based on the principle of niche conservatism, while ecological speciation relies on the niche divergence. Both niche





**Niche Divergence, Fig. 1 Ecological speciation through niche divergence:** The abiotic and biotic factors exert pressure on existing population due to which new ecological conditions generated within the existing niche.

Some individuals of population are adapted to these new ecological conditions and in turn give rise a new niche accompanied by niche divergence followed by genetic isolation and speciation

divergence and niche conservatism plays crucial role in ecological speciation. The niche divergence refers to the any change in ecological niche of a population of a species due to abiotic and biotic factors including climate, inter- and intraspecific competition, and constrain in food resources which ultimately leads to speciation (Rato et al. 2015). On the other hand, niche conservatism is the conservation of ecological niche in due course of time by a population of a species which also leads to speciation (Wiens 2004).

## Causes of Niche Divergence

**Climate:** Climate is a key component in determining the ecological niche of species. As the organisms are well adapted to their habitat, any change in prevailing climatic conditions affects their normal behavior. The climatic conditions such as temperature, precipitation, and solar radiation are directly associated with the feeding and mating habit of organisms. All the terrestrial organisms have tendency to live in a set of climatic conditions (temperature and precipitation), known as climatic niche (Holt 2009). The climatic niche is crucial for determining the occurrence of a species in an ecosystem along with other abiotic and biotic factors and its response to the climatic changes at temporal and spatial scale. Every species has a range of climatic conditions

where it occurs, known as climatic niche width (e.g., maximum and minimum annual temperature and annual precipitation across a geographical area). However, the climatic variables may differ from one locality to another within a geographical area; this will lead to the adaptation of subgroup of a population to their corresponding climatic condition, which further leads to divergence of niche and genetic diversification from original population (Hua and Wiens (2013).

**Biotic interaction:** Biotic interactions such as inter- and intraspecific competition are major determinants of ecological niche of a species (realized niche). Interspecific competitions such as predation and parasitism have greater impact on niche occupied by the organisms. Predation and parasitism exert pressure on existing subgroup of a population, which results in niche divergence. The intraspecific competitions are fiercer among the population of a species as they compete for same resources. This will force the subgroup of population to change their habit to avoid competition and consequently gives rise to new niche characteristics which differs from the original and help the group of individuals to survive.

In natural ecosystems climatic and biotic factors work in combination to exert differential evolutionary responses and motifs of climatic tolerances which eventually leads to adaptation of populations in new habitats (niche divergence).

## Role of Niche Divergence in Speciation

Niche divergence plays key role in ecological speciation. The deviation from geographical range position and extent among species is caused by niche divergence. Due to differences in geographic range, the subgroups of population experience different environmental condition leading to niche divergence. The subgroup of population adapts to new environmental condition, which further leads to genetic/reproductive isolation and speciation through natural selection (Wiens and Graham 2005). Similarly, niche divergence due to inter- and intraspecific competition among species leads to speciation as the competing species tends to occupy different niches. This will lead to character displacement followed by natural selection and consequently speciation.

## Conclusion

Niche divergence is any displacement in niche characteristics due to abiotic and biotic interactions and consequently adaptation of group of individuals to this divergent niche. It is caused by several abiotic and biotic factors. In most of the cases, niche divergence caused by climatic factors is the main determinant of ecological niche. However, the biotic interactions are also an important factor contributing to niche divergence. Niche divergence caused by abiotic and biotic interactions leads to genetic and reproductive isolation of group of individuals in a population and in term speciation. Thus, niche divergence is a key driver to evolution and it plays key role in speciation.

## Cross-References

- [Competition](#)
- [Speciation](#)

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## Nicolous

- [Altricial](#)
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## Nicola Clayton

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## The Biography of Professor Nicola Clayton FRS

Known synonymously as The Bird Lady and The Dancing Professor, Nicky's work focuses on the behaviors and cognitive abilities of birds. Indeed it is her passion for birds that led to the development of her career as a scientist and her work in dance. Currently Nicky is the Professor of Comparative Cognition in the Department of Psychology at the University of Cambridge and a Fellow

of Clare College, Cambridge. She is also the first ever scientist in residence at Rambert, Britain's flagship touring dance company, a position she has held since 2011, and cofounder of *The Captured Thought*, a science-arts collaboration which explores the subjective experience of thinking, together with her tango partner, Clive Wilkins, who is artist in residence in the Department of Psychology at the University of Cambridge.

### Career History

Nicky spent her youth dancing and bird watching in and around Blackpool, a seaside town in the North of England, before going on to read zoology at Pembroke College, University of Oxford, from 1981 to 1984. This is where she met Lord John Krebs FRS, who was to become a highly influential figure in her scientific development. When applying to Oxford, she wondered whether to read zoology or PPP (Psychology, Physiology, and Philosophy). The clincher was when John Krebs explained that if she were to choose zoology, she could do research on birds at the Edward Grey Institute for Field Ornithology. Indeed her undergraduate research project investigated the role of memory interference in the food-caching habits of marsh tits – a species of titmouse that loves to live where the elm trees grow and obsessively hide food throughout the autumn and winter months and have long-lasting and highly accurate memories of where they have stashed their scattered stores of food.

For her PhD, Nicky went to St. Andrews University in Scotland to study how zebra finches and Bengalese finches learn their songs, focusing on the cues the birds use to decide which tutor(s) to copy, under the supervision of Professor Peter Slater, completing her PhD in just two and a half years. From there, Nicky went to the University of Bielefeld as a Royal Society postdoctoral fellow and was also awarded an Alexander von Humboldt-Stiftung to work with Professor Klaus Immelmann but sadly he passed away briefly before she arrived. Although she had no official mentor, Professor Joachim Bischof took her under his wing, and she very much felt part of his

wonderful academic family. She returned to Oxford to work with John Krebs on what was then called a Science and Engineering Research Council postdoctoral fellowship, before becoming the Department of Zoology's departmental demonstrator (akin to a temporary university lectureship) at Oxford University and taking up a Junior Research Fellowship at Linacre College coupled with a University Research Fellowship with the Agricultural and Food Research Council.

In 1995, she moved to California to take up an assistant professorship at the University of California Davis and rapidly rose through the ranks in the 5 years she was there – first as associate professor then full professor and Chair of the Animal Behaviour Graduate Group. It was a very special time – for that is when she met Dr. Nathan Emery, not only her key collaborator but also now her husband (since 2001). They share the same birthday (but not the same year), and arguably their most influential paper was published in *Nature* on Nathan's 30th birthday.

In 2000, she returned to the UK to take up a lectureship with tenure in the Department of Psychology at the University of Cambridge. In 2002, she was appointed a Reader, and in 2005, she was appointed to her current post as the Professor of Comparative Cognition. She was elected a Fellow of the Royal Society in 2010.

Her science-arts collaborations began in 2009 when she started to collaborate with Mark Baldwin, world-renowned choreographer and Artistic Director of what was then known as the Rambert Dance Company (formerly Ballet Rambert, and now Rambert), on *Comedy of Change*, a new choreographic work in honor of Charles Darwin's bicentenary and the 150th anniversary of "*On The Origin Of The Species*." She was appointed scientific advisor to Rambert the same year and the scientist in residence in 2011. One year later, she (together with Clive Wilkins) cofounded *The Captured Thought*, which explores the subjective experience of memory, perception, and consciousness by integrating science and the arts using their skills in tango and the performing arts. They have lectured, performed, and delivered workshops all over the globe – in science and arts venues alike.

## Research Contributions

Nicky's research in learning, memory, and cognition in birds has focused on three behaviors: bird-song, food caching, and food sharing.

Her first series of published endeavors for her PhD and initial postdoc focused on how estrildid grass finches, such as zebra finches and Bengalese finches, learn their songs and what the implications of this song tutor choice (Clayton 1987) was on sexual imprinting and mate choice (Clayton 1989). She then applied this way of thinking about behavioral development in birds to a new behavioral paradigm, food caching, to study how birds that rely on memory to hide food for the future develop these skills in hiding food and the effect this experience has on the development of both memory and the hippocampus (Clayton and Krebs 1994) and how this might not only be relevant to spatial memory but also the ability to episodically recall what happened where and when, an ability that had been previously assumed to be unique to humans (Clayton and Dickinson 1998). This finding led to the idea that these food-caching birds might also remember social aspects of caching, such as who was watching when they cached, and if so, whether they would be able to adjust their caching tactics accordingly to protect their stashes of food from being stolen by other birds that had watched them cache (Dally et al. 2006). The most remarkable finding was that only those birds that had had the opportunity to pilfer (steal) other birds' caches in the past engaged in these cache protection tactics (i.e., naïve birds that had not pilfered before did not do so) and that they only did so if they had been observed by a potential pilferer – they did not do so if they had cached in private (Emery and Clayton 2001). Taken together these series of findings about the extraordinary ability of corvids led to the idea that cognition must have evolved independently and probably convergently in the corvids and apes despite obvious differences in body morphology and the neuroarchitecture of their brains (Emery and Clayton 2004).

Subsequent work established that these birds can also plan ahead, not only for other times (Raby et al. 2007) but also for other minds (Ostojic et al. 2013). It was the latter research

that led to the development of the food sharing paradigm, showing that the jays can infer what their mate will desire in the future (Ostojic et al. 2013).

This work has also led to the development of new paradigms for testing humans that rely much less than conventional studies on verbal report, which have been particularly informative in bridging the gap between human cognitive development and comparative cognition (Clayton 2014) and inspiring new models for thinking about human cognition which have translational aspects – for example, the relationship not only between the hippocampus and memory but also obesity (Cheke et al. 2016; Cheke et al. 2017).

Finally, her science and art collaborations have also resulted in published papers that explore the evolution and manifestation of cognition, through the conduit of dance and with inspiration from the birds (Laland et al. 2015; Clayton and Wilkins 2017). Perhaps that is why Nicky has become known as both The Bird Lady and The Dancing Professor.

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## Nidifugous

### ► Precocial

## Nikolaas Tinbergen

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Nikkolas (Niko) Tinbergen contributed to the growth of the field of ethology, a branch of zoology (born April 15, 1907, The Hague, Netherlands – died December 21, 1988, Oxford, England) (Burkhardt 2005). Ethology is the scientific study of instinctive and learned animal behavior in a naturalistic environment. Tinbergen played a role in studying animal behavior with systematic field experiments.

Tinbergen grew up in the Netherlands within a family of five children. His father was a teacher of Dutch language and literature. His family shared

his interest in nature and being outdoors. In addition to Niko's impact in ethology, his siblings Jan Tinbergen became a Dutch economist and Nobel laureate and Lukas Tinbergen was an influential ornithologist and ethologist (Burkhardt 2005; Kruuk 2003; Tinbergen 1973a). Early in life his interests were exploring fauna and flora in their natural environment while his interest in school was scarce. He was influenced during his secondary education by several individuals, Dr. Schierbeek, and C. J. Tijnstra, to name a few. They promoted his interest in nature. He finished secondary school in 1925 and then spent 3 months exploring an area where bird migration fieldwork was occurring. He then started his education at Leiden University. Later Tinbergen pursued and obtained his Ph.D. in biology from Leiden University in 1932. During his time in college, he had a tedious educational disinterest as he did during his childhood school experience. He did appreciate teachers who exposed him to animals and promoted flexibility with his outside interests. His dissertation was a relatively short paper where he examined digger wasps orientation behavior. One of the reasons for such a small project was a 1 year expedition to Greenland where one of the topics he studied was snow bunting territorial behavior. He also examined birds and Eskimos during this time. During the year that he obtained his degree, he also married Elisabeth Rutten. After his short-term project in Greenland, he returned to Leiden University in 1933, where he taught and established a program examining animal behavior. In 1936, two events influenced his future in researcher. This was the first time a course in ethology was ever offered. He also met Konrad Lorenz, who came in as an invited speaker to Leiden. This was the beginning of a collaboration between the two in the field of ethology. Lorenz had provided the theoretical concept of the fixed action pattern and the innate releasing mechanism. This lead Tinbergen's interest in the experimental exploration of these concepts. In September, 1942, Tinbergen was held hostage during World War II. When he was released, he returned to work and in 1943 the university was reopened, and he was promoted as a full professor. While his first



experience of teaching and research began at Leiden University, he later moved to Oxford in 1949 and continued to influence this field of science in England.

Due to his unique study of animal behavior, he was awarded, along with Karl von Frish and Konrad Lorenz, the 1973 Nobel Prize in Physiology or Medicine “for their discoveries concerning organization and elicitation of individual and social behaviour patterns” ([http://www.nobelprize.org/nobel\\_prizes/medicine/laureates/1973/](http://www.nobelprize.org/nobel_prizes/medicine/laureates/1973/)). Specifically, he was recognized for his research on the adaptation of gulls to ecological settings. During his time he founded the *Behaviorism* journal (1947) and published several books, including *The Study of Instinct* (1951), *The Herring Gull's World* (1953), *Curious Naturalists* (1958), *The Time-Life Volume, Animal Behavior* (1965), and *The Animal in its World* (1972, 1973b) to name a few. His final contribution was a collaborative study with his wife on early childhood autism, *Early Childhood Autism – An ethological approach* (1972).

One of his main contributions explored behavior through the breakdown of proximate and ultimate mechanisms. Within these mechanisms a total of four possible causes of behavior were described: causation, development, phylogeny and adaptation (Tinbergen 1963; Shettleworth 2010).

Proximate – the immediate causes of behavior

- Causation (Mechanism) – How does this behavior occur in an individual? How do signals and mechanisms cause the behavior?
- Development (Ontogeny) – What can effect or influence the growth or development of behaviors.

Ultimate – the adaptive significance of behavior

- Phylogeny (Evolution) – How does this behavior arise in the species? How did the behavior evolve over generations?
- Adaptive Value (Function) – Why is the behavior adaptive for the species? How does this function contribute to survival and reproduction?

One example is related to bird song; how and why do birds sing. What mechanisms underlie song production (i.e., neural, sensory, hormonal, and motor systems)? How is the song acquired and modified throughout the lifespan of the bird? What are the differences in the acoustics across a comparison of species? How does the bird song play a role in defending a territory or in reproductive success?

Another example would examine the behavior of social grooming (e.g., allogrooming) in non-human primates. What triggers allogrooming behavior? What age does allogrooming begin and which animals engage in the behavior? Does this development change depend on the environmental habitat or the type of social group? Within the comparison of different social groups, when might it change from hygienic function to a social function? Is allogrooming used to increase social bonding and health and/or reduce tension in the social hierarchy?

Tinbergen's contributions expanded the understanding of behavior in a variety of species such as black-headed gulls, graylag geese, herring gulls, stickleback fish, and digger's wasps. In each of the studies, he created systematic observations and experiments to investigate animal behavior.

## Black-Headed Gulls

Black-headed gulls naturally take empty egg shells and drop or relocate them some distance from the nest. During this time the chicks are left alone in their nest. Why do black-headed gulls remove broken eggshells from the nest after the chick hatch? This is an example of an ultimate question. Tinbergen examined why the chicks would be left vulnerable by this behavior. He found through experimental studies that the function was to decrease the predation of their offspring which was the results of an adaptive mechanism (Tinbergen et al. 1962). Tinbergen also explored how the stimuli (i.e., egg) could alter the type of behavior that the gull exhibited. He manipulated a model egg in various ways such as the color, shape, size, and distance from the nest. In doing so he measured the frequency and

latency of the specific behavior that the gull was engaged in (e.g., rolling vs carrying).

## Graylag Goose

Tinbergen also worked with Lorenz on graylag geese and their stereotypical egg rolling behavior (Lorenz and Tinbergen 1939, 1970). An automatic response of the goose exists when an egg is located outside of the nest. The automatic response of rolling the egg back into the nest was discovered to be a complex instinctive behavior. If the egg was removed during the recovery response, the goose would continue with the complex response. This is when Tinbergen and Lorenz further examined this by using a variety of egg-shaped stimuli to discover that geese continued the “fixed action pattern” regardless of if the egg was removed. This fixed action pattern was the result of exposure to a specific sensory stimulus (i.e., sign stimulus) which created an innate sequence of reflexive responses. In the study the geese were also provided multiple varieties of “eggs” outside of the nest in which the size, pattern, shape, and color were modified. Through this investigation they determined there was a preferred egg but it was not the normal egg. The artificial egg they preferred was larger, had a more complex speckled pattern, and was darker in the green color. These unrealistic cues were labeled as “supernormal stimuli.”

## Herring Gull Chicks

Another one of Tinbergen’s classic studies examined herring gulls (Tinbergen and Perdeck 1950; Tinbergen 1960). Herring gull chicks display an automatic pecking behavior to a red spot located on the mother’s beak. The mother’s beak then produces an automatic response of regurgitation. In the classic experiments, Tinbergen explored how a “model,” the position of the red spot (distance above the ground), and alternated response time could influence the pecking behavior of the chicks. He found that the location sign stimulus (i.e., the red spot) on the model played a role in the

automatic response of the chick. When the red spot was toward the bottom and end of the beak, the chicks were more likely to peck. Tinbergen also explored how a narrow boldly colored vertical stick with horizontal movement would be perceived by the chicks. He found by intensifying the color and the contrast the model became a supernormal stimulus which elicited a supernormal response. The red stick shape and contrast created more pecking than to a real beak.

## Stickleback Fish

Tinbergen also explored this topic by examining how sign stimuli could control aggressive and sexual behavior of stickleback fish. During breeding season males displayed the fixed action pattern, which changed the color of their “belly” to red. Due to the competition of territory of the males, the color red appears to be the stimulus that triggers the notable difference in territory. If another red-bellied fish, male or female, came into their territory, it created an aggressive response. Tinbergen explored what aspect of the other fish created the automatic response and discovered it was the color red (Tinbergen 1951). This indicated that it did not have to be just a fish that had the color red on it but any object with the sign stimulus (i.e. color red) in the experiment created the fixed action pattern. In relation to courtship behavior, Tinbergen found that a swollen “belly” of a model fish, in addition to the posture, stimulated the “zigzag dance” of the male. Throughout the study it was indicated that there were multiple sign stimuli that were used in the sequence of the reproduction. During the building of the egg tunnel, by the male, is when the red belly indicated territorial aggressive behavior. However, after the egg tunnel has been completed, a female approached and became the trigger or the sign stimulus (i.e., the swollen abdomen of the female). The swollen abdomen creates the zigzag dance of the male. The female is then stimulated by the red belly of the male. In this case the size of the abdomen of the female will draw the attention and response of the male, and the red belly of the male will draw in the female to the egg tunnel.

Tinbergen examined this process using a variety of models throughout this process.

### Digger Wasps: It Relates to the Landmark Use to Lay Eggs

Tinbergen also examined the homing behavior in digger wasps, specifically the use of landmarks (Tinbergen and Kruyt 1972). How do digger wasps find their homes among a variety of nests in a location?

This is a proximate question. Digger wasps lay eggs in a burrow, for predator avoidance, after which they exit the burrow and fly around to possibly locate landmarks to assist in finding the burrow. Tinbergen first explored this aspect by creating a circle of pinecones around the entrance to the burrow. When the wasp was out foraging, they relocated the circle of pine cones. They found that the returning wasp went to the location where the pinecones were relocated. Tinbergen also explored if scents, type of object, or arrangement of the landmarks provided the burrow location. Through his studies he found that scent and the type of object were not used to locate the burrows. However, when the arrangement of the landmarks was examined, it was found that this did contribute to the landmarking principle. For example, when the wasp left the burrow, it had a circular arrangement of pinecones. Once the wasp left, a triangle of pinecones were put above the burrow and a circular arrangement of rocks were placed to the side of the burrow. When the wasp returned, it traveled to the circular arrangement of the rocks.

Tinbergen's research on patterns of behavior played a role in the development of ethology, the confirmation of field research, and the development of modern behavioral ecology. Tinbergen also contributed the connection between comparative psychologists and European ethologists. His classical studies are currently involved not only in biology but also in the field of psychology. He was not only a professor and researcher; he also became a writer and filmmaker. In addition to his research contribution, he also provided interest and concern in diplomacy, goodwill, and humanity.

### Cross-References

- ▶ Aggression
- ▶ Allogrooming
- ▶ Fixed Action Patterns
- ▶ Innate Releasing Mechanism
- ▶ Konrad Lorenz
- ▶ Ontogeny
- ▶ Orientation
- ▶ Phylogeny
- ▶ Sign Stimulus
- ▶ Zoology

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## Nipple Attachment

### ► Suckling/Nursing

## Nitrogenous Base

### ► Base Pair

## NMDA Receptors

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## Synonyms

[N-methyl-D-aspartate receptor](#); [NMDAR](#)

## Definition

N-methyl-D-aspartate receptor (NMDAR) is an ionotropic glutamate receptor which is found in nerve cells. NMDAR is named after the synthetic agonist to whom it is selectively sensitive, N-methyl-D-aspartate (NMDA).

## Introduction

NMDAR is a glutamate-gated positive ion-channel protein, so when activated it allows

positively charged ions to flow through the nerve cell membrane. These are found in postsynaptic terminals in communicating cells throughout the brain. It is nonselective to cations such as sodium ( $\text{Na}^+$ ), potassium ( $\text{K}^+$ ), and calcium ( $\text{Ca}^{2+}$ ).

NMDAR is critical in synaptic plasticity due to its high  $\text{Ca}^{2+}$  permeability, which is important in learning and memory. This makes it one of most extensively studied ion-channel in brain. Overstimulation of NMDAR causes excitotoxicity and abnormal NMDAR functioning has been implicated in various pathological conditions and disorders including hypoxia, ischemia, head trauma, Huntington's, Parkinson's and Alzheimer's diseases.

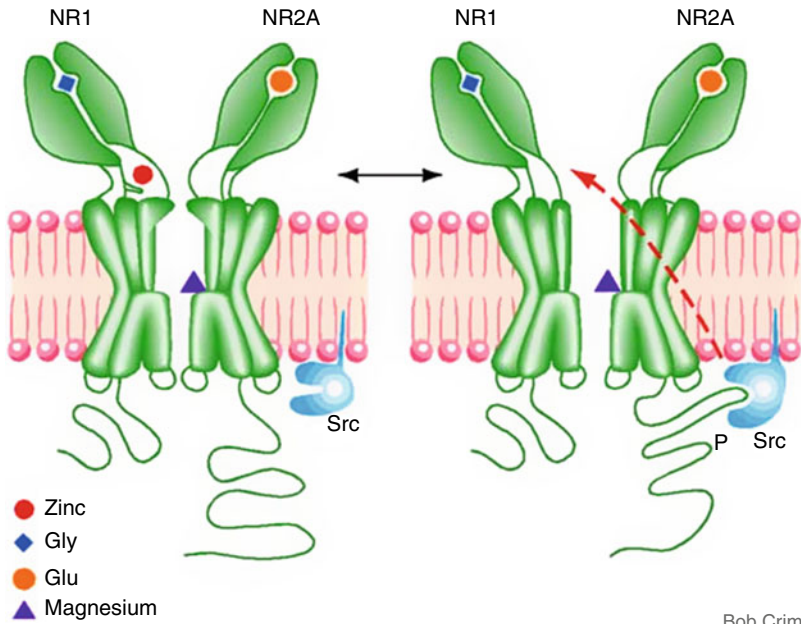
## NMDA Receptors

NMDARs generally have a heterotetramer structure made up of two GluN1 subunits and two GluN2 subunits, which bind to glycine and glutamate respectively. Thus activation of this receptor is dependent on both neurotransmitters to bind simultaneously, which gives it a unique property and tight control of activity. There are four functional domains of NMDAR, an extracellular N-terminal domain, a ligand-binding domain, an intracellular C-terminal domain, and a transmembrane pore-forming domain. In nervous system, GluN1 subunits are only of one subtype but GluN2 has four subtypes named GluN2A–D, and thus gives diversity to NMDARs throughout brain (VanDongen and Blanke 2008) (Fig. 1).

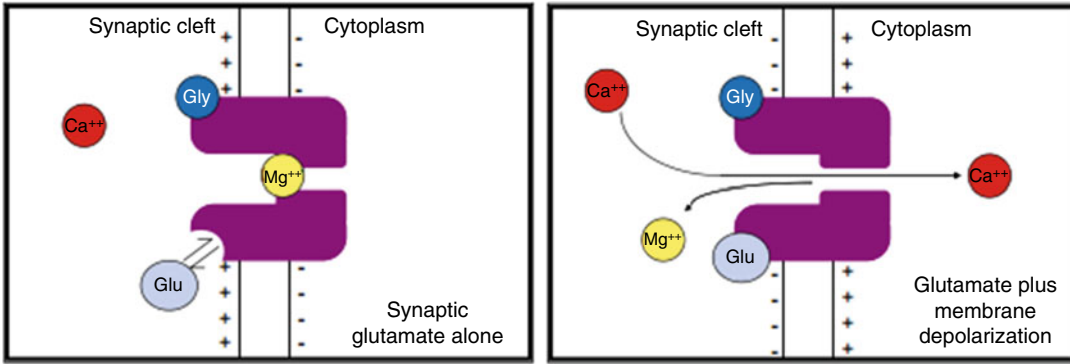
NMDA receptors has three very important properties which makes it high-throughput receptor and critical for proper functioning of nervous system. First is, opening of this channel requires a cofactor, glycine along with glutamate, so that this channel will only function in presence of extracellular glycine. Second, this receptor has multiple cation permeability including  $\text{Na}^+$ ,  $\text{K}^+$ , and most importantly  $\text{Ca}^{2+}$ . Third, this channel has dual mode of control among all transmitter-gated ion channels because opening of NMDAR requires ligand binding as well as membrane voltage. In the NMDA-activated channels, an extra particle  $\text{Mg}^{2+}$  binds to the pore of receptor and

**NMDA Receptors,**

**Fig. 1** NMDA receptor with its two subunits GluN1 (NR1) and GluN2 (NR2A) has been activated by binding of glycine to NR1 subunit and of glutamate to the NR2A subunit (Ascher 1998)



Bob Crimi



**NMDA Receptors, Fig. 2** Coincidence detection by the NMDA receptor. The simultaneous presence of glutamate and membrane depolarization is necessary for relieving Mg<sup>++</sup> blockade and allowing calcium influx (Sweatt 2010)

blocking the current flow. Ligand binding of glutamate to receptor and depolarization of membrane expels Mg<sup>2+</sup> from the channels by electrostatic repulsion, allowing sodium and calcium to enter and maximum current flows through receptor (Kandel et al. 2000) (Fig. 2).

The NMDA-type receptor opening and closing takes place relatively slowly than other receptors and it contribute to late phase of EPSP, and this is

carried out largely by Ca<sup>2+</sup>. Thus NMDA receptor activation further leads to calcium-dependent second messenger cascade activation in the post-synaptic cells. Long-term potentiation (LTP) is NMDAR dependent in hippocampus and many other regions of brain. These biochemical reactions are important for neuroplasticity and certain long-lasting modifications in neuronal networks important for learning and memory.



## Conclusion

NMDARs play important roles in processes of plasticity both functionally and structurally in nervous system. NMDARs have some unique properties which enable them to be very important contributor in events of synaptic plasticity, such as learning and memory formation. Most prominent of these are its dual mode of activation control, high permeability to  $\text{Ca}^{2+}$  ions, and slow deactivation kinetics which allow it to change neural patterns for extended period of time and affect plasticity. Due to these properties, NMDAR hypo or hyperfunctions results in many cognitive brain dysfunctions. All the unique properties and their malfunctions make these receptors key targets of therapeutic interventions in disease conditions.

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## NMDAR

► [NMDA Receptors](#)

## N-Methyl-D-aspartate Receptor

► [NMDA Receptors](#)

## Nomenclature

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## Synonyms

[Binomial nomenclature](#); [Biological nomenclature](#)

## Definition

Nomenclature is a system of naming any organism, based on certain a set of rules and regulations which are explicit worldwide.

## Introduction

The different life forms are known by their specific name. The term nomenclature is derived from the Latin word (*nomen + calare*) meaning assigning name to someone. Naming animals or plants is not like naming someone according to our wish, but it needs to follow ample scientific rules which biologists have formulated (Huxley 1940; Mayr 1969; Narendran 2006). Naming an organism is important for communication in order to specify the organism. Nomenclature is in fact part of taxonomy, especially in biological science. Scientific names are provided to any organism based on its taxonomy not haphazardly. For example, fruit fly *Drosophila* belongs to family Drosophilidae which include a huge number of its species distributed in different geographical conditions. Some of its commonly occurring species like *D. melanogaster*, *D. pseudoobscura*, *D. ananassae*, *D. bipectinata*, *D. malerkotliana*, etc. share taxonomically same criteria and are placed under same genus *Drosophila* and have

sufficiently been studied to explore several biological aspects.

The organization dealing with animal nomenclature is ICZN (International Code of Zoological Nomenclature) and for plants, algae, and fungi is ICNafp (International Code of Nomenclature for Algae, Fungi and Plants); previously it was known as ICBN (International Code for Botanical Nomenclature). ICNP (International Code of Nomenclature of Prokaryotes) is concerned with prokaryotes (including Archaea) nomenclature; formerly it was called as ICNB, i.e., International Code for Nomenclature of Bacteria. Since viruses have also been considered organisms, a separate body ICTV (International Committee on Taxonomy of Viruses) has been established to name them (Narendran 2006).

The term binomial nomenclature is quite popular to be used as naming to organisms; however, this should be known that the terms binomial and binominal have distinct sense in the modern scenario (Mayr 1969; Singh 2012). Now these terms do not mean same. Botany people use *binomial* term as they follow two-word nomenclatures which state that while naming a plant, one must use two separate words for genus and species. For Zoology discipline, *binominal* term is suggested that means to follow two-name patterns for naming the animals. This then allows even to use generic as well as species name by a single word (tautonym) like *Naja naja*. Thus binomial nomenclature is the correct term for botany, and binominal nomenclature is technically correct term in Zoology. A binominal name is also called a binomen (plural binomina) (Simpson 1961; Sokal and Sneath 1963; Schuh 2000).

## Binominal Nomenclature

Carolus Linnaeus in 1753 proposed the binominal nomenclature for the first time in his book *Species Plantarum* (Kapoor 1998). Conventionally every species of animal or plant must be named by using two separate names, one as generic and other as species name. Such names are always written in Latinized form.

Either the genus or species name can be derived from words in any language. While naming an animal, the following points must be taken into account (Simpson 1961; Kapoor 1998; Barrie et al. 2012):

1. Binominal names consist of two separate names, the genus name and the species name. For example, house sparrow is named as *Passer domesticus*, where *Passer* is genus or generic name and *domesticus* is species or specific name.
2. The generic name always begins with a capital letter, whereas the species name is always in lower case letters. The species name can be a noun or an adjective.
3. The binominal names are printed in italic form, and if handwritten, the generic and species names have to be separately underlined.
4. In the running text, the name may be repeated a number of times and in such condition, the generic name can be written in full the first time it is used, and then after it is written only by its first capital letter. For example, *Passer domesticus* will appear at the start of the text and then after it will be mentioned as *P. domesticus*.

The two major groups of organisms, animals and plants, are named considering certain criteria. One of them is to follow tautonym for animal's nomenclature but not for plants. Here tautonym refers to the use of same words for genus as well as species, for example, *Naja naja* (the cobra snake). None of the plant is named by using same generic and species words.

## Trinomial Nomenclature

Trinomial nomenclature refers to three-name pattern where the third name is of subspecies. Thus our own species is always named as *Homo sapiens sapiens* where *sapiens* coming after generic name is species name and the third word *sapiens* is subspecies name (Barrie et al. 2012).

## Author's Name

In several cases the name of species is followed by the name of the person who first described or reported it. For example, *Bactrocera cucurbitae* (Coquillett), here Coquillett is the name of the scientist who described *B. cucurbitae* for the first time. This method of terminology is the correct way to represent the species name.

**Use of Parentheses:** Sometimes after further research and study, some species are reassigned another genus after their first report. In case of reassigned species, the name of reviser is added after the name of original author in bracket, for example, *Hemilea bipars* (Walker 1862; Hardy 1959). This denotes that *H. bipars* was originally described by Walker in some different order, but Hardy in 1959 correctly assigned its order (Kapoor 1998). This methodology is strictly used in the field of plant science only but not in Zoology (Narendran 2006).

**Use of Square Brackets:** In Zoological nomenclature, if author's name has been taken from indirect source other than original publication, it is necessary to put in square brackets.

## Cross-References

► [Taxa](#)

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## Nominal Fallacy

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The nominal fallacy is the belief that by naming something, we have also explained it. The naming of a concept does not make the meaning of the concept a self-evident truth and does not confer any explanatory power. For example, animals that live in our homes and share our lives can be defined as pets, and pets can be defined as animals that live in our homes and share our lives. Yet, by assigning a singular label for a concept, we have not gained any further insight into what an animal that lives in our homes and shares our lives, is (Eddy 2003).

As another example, we can describe a behavior as being a product of “instinct” and assume that everyone will know what set of behaviors comprise an “instinct”. But clearly, this is not true, as Kuo (1921) put it, “no two psychologists will agree upon the definition of and what constitutes human instincts” (p. 646). The same can be said for the word “group.” While intuitively understood by everyone, it is difficult to define and operationalize across different contexts (Mudrack 1989). In all cases, the more we understand about a concept, the more we also understand that assigning a label does not take us beyond the concept itself. A particular feature of the nominal fallacy is that with knowledge, a concept can be reduced to finer and finer detail categories within the concept, i.e., different levels of instinctive behavior or different types of

groups, which may be related to different mechanisms and functions, thus rendering the overall concept label unhelpful to scientific investigation.

## Problems

Why may it be problematic if some labels are broad and serve as a placeholder for a range of explanations? A key problem with nominal fallacies is stereotyping or over-generalization. Take the example of “autistic.” Autism is a now known as Autism Spectrum Disorder to take into account the wide range of features the condition incorporates (APA 2013). Describing someone as autistic or as a person with autism creates a label where the range of behaviors ascribed to the individual depends on the observer’s familiarity with traits associated with ASD. In extreme situations, one individual may be perceiving one set of behaviors as indicative of ASD and another individual may be perceiving the same set of behaviors as neurotypical. The nominal fallacy creates a situation where it is possible to wittingly or unwittingly ascribe seemingly common sense or everyday labels to diverse sets of behaviors and definitions.

## Solutions

In most cases, there is no problem with nominal fallacies; they create cognitive shortcuts for us to broadly understand everyday terms. We don’t need to interrogate the meaning of every term we encounter because to do so we would spend most of our time speculating about definitions and fail to proceed to the higher-order issue we really want to address. For example, if policymakers had to define what constituted a “group” when discussing how to address homelessness, not much would get done about resolving homelessness.

However, researchers do need to carefully define their terms. In research, this is called “operationalization.” Labels such as “group,” “instinct,” and “autistic” need careful definition. There can be no ambiguity; there can be no self-evident truths. Nominal fallacies are the enemy of clarity and exactness. Every label needs to be

precise and this makes precise labeling a friend to the researcher. Grant awarding bodies will look unfavorably on nominal fallacies, so will journals and other publication outlets of high-quality research output. Identifying what is and is not a nominal fallacy in your own line of research will help you develop and conduct better research.

## Conclusions

Linguistically, all words are labels and so all words are open to the problem of the nominal fallacy. In everyday life, we can use phrases and words that have multiple meanings because we are often not interested about the exact meaning of the word, just the category-level shared understanding of, e.g., a group.

However, in research, we cannot afford to commit a nominal fallacy because research has to be precise. Ambiguous terms lead to ambiguous interpretations, which leads to ambiguous findings. It is beholden to researchers to carefully examine the labels they use. No researchers should commit nominal fallacies.

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## Nonassociative Learning

► [Habituation](#)

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## Noncoding DNA

► [Intron](#)

## Noncoding RNA

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## Synonyms

Junk RNA

## Definition

An RNA sequence not coding for a protein is termed as a noncoding (nc) RNA.

## Introduction

In general, the term noncoding RNA is used for RNA sequences that get transcribed from DNA but do not code for a protein. However, this does not imply that these RNAs do not code for any information or are devoid of any function. Studies have shown that the genome of mammals and other higher organisms gets transcribed into noncoding RNAs, which further undergo the process of splicing, leading to smaller products. The field of noncoding RNAs has progressed a great deal in the past decade due to the development of high-throughput sequencing tools and bioinformatic software (Delpu et al. 2016; <https://www.whatisepigenetics.com/noncoding-rna/>).

It is fascinating to know that a large chunk of the total RNA (around 60%) belongs to the class of noncoding RNAs. The functions of the noncoding RNAs involving complex mechanisms are gradually being understood. More or less, the

function of the noncoding RNAs has been identified as controllers of gene expression in physiology and development, including chromatin architecture/epigenetic memory, transcription, RNA splicing, editing, translation, and turnover, thus constituting a major class of epigenetic regulators. Apart from this, they are also being used as potent biomarkers for different human pathologies by pharmaceutical industries and biotechnology companies, making them a useful therapeutic approach against human pathologies like cancer (Delpu et al. 2016).

These noncoding RNAs are variable in length ranging from 20 nucleotides to a few hundred nucleotides. For an easy understanding, the noncoding RNAs will be divided here into two groups based on their lengths: small and long noncoding RNAs (Fig. 1).

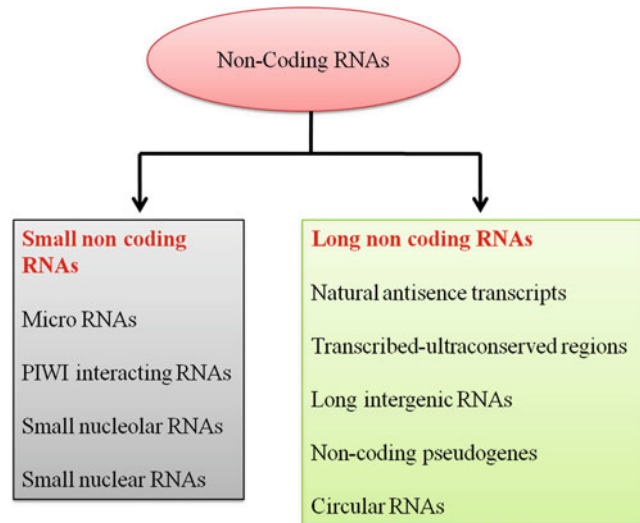
## Small Noncoding RNAs

### MicroRNAs

MicroRNAs, a recently discovered class of noncoding RNAs around 22 nucleotides in length, act at the posttranslational level and have been estimated to regulate the expression of approximately 30% of all mammalian protein-encoding genes.

MicroRNAs have been shown to be involved in a variety of diverse biological processes such as cell cycle control, cholesterol metabolism, ageing, immune responses, viral replication, apoptosis, several developmental and physiological processes including stem cell differentiation, hematopoiesis, hypoxia, cardiac and skeletal muscle development, neurogenesis, and insulin secretion. MicroRNAs also play a key role in tissue differentiation and maintenance of the tissue identity, which is evident from their highly tissue-specific and distinct temporal expression patterns during embryogenesis. Furthermore, their use as diagnostic and prognostic markers for a wide range of diseases such as cancers, heart diseases, and neurological diseases is underway. However, around 14,000 microRNAs have been annotated till now, but the functions of most of them remain undiscovered (<http://www.exiqon.com/what-are-microRNAs>).



**Noncoding RNA,****Fig. 1** Classification of noncoding RNAs**PIWI-Interacting RNAs**

PIWI-interacting RNAs or piRNAs is a class of small noncoding endogenous RNAs having a length of 24–31 nucleotides acting as guardians of the genome and protecting it from invasive transposable elements in the germ line. Their association with the PIWI proteins gives rise to an effector complex, known as piRNA-induced silencing complex which is responsible for repressing the transposons via transcriptional or posttranscriptional mechanisms, thus maintaining the germ line genome integrity (Ishizu et al. 2012; Iwasaki et al. 2015). Apart from transposon silencing, piRNAs play important roles in the regulation of cellular genes and trans-generational inheritance of the memory of “self” and “nonself.” It has also been observed that animals having nonfunctional piRNAs exhibit defects in gametogenesis and sterility. Apart from their activity in the gonadal cells, piRNAs have also been found to play crucial roles in the non-gonadal cells. Their activity in the multigenerational epigenetic phenomena in worms has also been identified (Ishizu et al. 2012). However, many piRNAs have been identified, but the mechanism of their maturation and the effector phase of gene silencing still remains to be explored (Iwasaki et al. 2015).

**Small Nucleolar RNAs (snoRNAs)**

Small nucleolar RNAs (snoRNAs) are one of the most abundant classes of ncRNAs, are 60–300

nucleotide in length, and are located in the nucleolus or in Cajal bodies (Delpu et al. 2016). Human genome comprises around 300 different snoRNA sequences generated after splicing, debranching, and trimming of mRNA introns. They have been further subclassified into two main classes (1) C/D box snoRNAs and (2) H/ACA box snoRNAs depending upon their role in methylation or pseudouridylation. Eventually, these snoRNAs interact with certain proteins to form a complex called small nucleolar ribonucleoproteins (snoRNPs), which get transported to nucleolus for 2'-O-methylation (Esteller 2011; Kiss-László et al. 1996) and pseudouridylation of rRNAs. These modifications have been reportedly known to facilitate finer folding and higher stability of rRNAs (Ni et al. 1997; King et al. 2003). Further, the role of snoRNAs in the regulation of alternative splicing has also been observed.

**Small Nuclear Ribonucleic Acid (snRNA)**

**Small nuclear ribonucleic acid (snRNA)**, or **U-RNA**, is the first class of noncoding RNA molecules identified and has an average length of around 150 nucleotides. Their location has been found to be in the splicing speckles and Cajal bodies of the nucleus in eukaryotic cells. Their transcription is governed by RNA polymerase II or RNA polymerase III (Henry et al. 1998).

snRNA and some specific proteins form a complex called as small nuclear ribonucleoprotein

(snRNP, often pronounced “snurps”), which is a spliceosome and aids in the pre-mRNA processing. Their role in the maintenance of the telomeres, regulation of the RNA polymerase II and other transcription factors, RNA biogenesis, and in guiding chemical modifications of ribosomal RNAs (rRNAs) and other RNA genes (tRNA and snRNAs) has also been reported.

## Long Noncoding RNAs

### Natural Antisense Transcripts

Natural antisense transcripts (NATs) are endogenous RNAs that are found in eukaryotes such as humans, mice, yeast, and *Arabidopsis thaliana* (Vanhée-Brossollet and Vaquero 1998). They have a striking feature of having transcript complementarity to several other RNA transcripts, thereby partially/completely overlapping those transcripts resulting in a positive/negative expression of the sense gene. Furthermore, they comprise of both protein-coding and noncoding RNAs (Lavorgna et al. 2004; Osato et al. 2007). Experimental studies have shown their role in RNA interference (RNAi), alternative splicing, genomic imprinting, and also X-chromosome inactivation (Zhang et al. 2006). On the basis of their location and site of action, they are broadly divided into two categories cis and trans. If the NATs are transcribed from a different location than their targets, they are called trans-NATs, and if the transcription takes place from the same genomic locus but from the opposite DNA strand, they are called cis-NATs. Additionally, it has been observed that the trans-NATs can target multiple transcripts with a few mismatches, whereas the cis-NATs form perfect pairs (Carmichael 2003; Wang et al. 2005).

### Transcribed-Ultraconserved Regions

Ultraconserved regions (UCRs), as the name suggests, are such genomic regions with a size of 200 bp and exhibit a 100% homology between eukaryotes such as human, rat, and mouse. UCRs are known to exist in clusters, and till now, 481 UCRs have been identified excluding the rRNAs (Bejerano et al. 2004). They are classified into (1) intergenic, (2) intronic, (3) exonic,

(4) partly exonic, and (5) exon-containing subclasses (Mestdagh et al. 2010). Expression profiles of these UTRs have been useful in identifying different types of cancers in humans. Furthermore, their conserved nature also portrays that they have important roles in cell physiology and interactions with the miRNAs (Bejerano et al. 2004; Calin et al. 2007). Nevertheless, the functions of these regions are just beginning to get discovered.

### Long Intergenic ncRNAs (lincRNAs)

Long intergenic ncRNAs are transcribed from a noncoding region of DNA that is present between coding genes. These genes have been found to be rich in transposable elements (Saey 2011; <http://www.rinnlab.com/>). More than 1000 lincRNAs have been identified in the human genome as of now, which majorly reside inside the nucleus or nucleolus. One of the most studied lincRNAs is HOTAIR, which functions as an epigenetic regulator and has an important role in cancer.

### Noncoding Pseudogenes

Pseudogenes are noncoding genomic regions that originate due to duplication or the retrotransposition of an mRNA sequence into different genomic loci and still remain homologous to an ancestral gene (Delpu et al. 2016). Pseudogenes are formed when a gene is affected in such a way that it loses its function. It is usually seen that frame shift mutation or mutations in the transcription and translation control regions lead to the formation of pseudogenes. Almost, 10,000 pseudogenes are already identified in mammalian genomes to date. Multiple studies indicate that the pseudogenes control the parental gene expression by producing natural siRNAs (Sasidharan and Gerstein 2008) or antisense transcripts and by competing with miRNA binding sites on mRNA targets (Poliseno et al. 2010). Further, it is also assumed that pseudogenes can have an important evolutionary role to play.

### Circular RNAs

Circular RNAs (circRNAs) are noncoding RNAs whose 3' and 5' end are joined together by covalent bonds resulting in the formation of closed continuous loops unlike the linear RNAs. Initially, they were regarded as the structures formed due to

errors occurring during splicing, but now they are considered as important factors in gene regulation. Their conserved nature, abundance, and also stability in the cytoplasm have increased the curiosity and interest of researchers toward them. These important characteristics provide the circular RNAs multiple functions like acting as miRNA sponges or binding to RNA-associated proteins to form RNA-protein complexes that regulate gene transcription. Further, studies also indicate the role of circular RNAs in interacting with miRNAs leading to the regulation of gene expression at transcriptional and posttranscriptional level (Delpu et al. 2016). A lot of research is still underway about their use in potential disease biomarkers and therapeutic targets in case of cancer.

## Conclusion

In the recent past, an enormous amount of research has been undertaken aiming at identification and annotation of new classes of noncoding RNAs along with deciphering their complex functions. They have been identified to play roles in multiple human disorders; the most important among them is cancer. The expression patterns of these noncoding RNAs can hence be used as a powerful biomarker against some diseases. The major challenges regarding their use in the clinical practice are in vivo delivery, off-target residual effects, and efficacy. Dedicated efforts are required to curtail these challenges and develop innovative methods and techniques to help the cause.

## Cross-References

- [DNA](#)
- [Genes](#)
- [Messenger RNA](#)
- [RNA](#)

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## Nondisjunction

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## Definition

Nondisjunction is the failure of chromosomes to disjoin during the meiotic division, which leads to formation of gametes with an extra or missing number of chromosomes.

## Introduction

In the normal process of cell division, the chromosome segregate and equal amounts of genetic material are distributed in each cell. When these chromosomes fail to separate properly, each daughter cell receives an abnormal number of chromosomes. One of the cells has many chromosomes while others have few. This improper segregation is known as **nondisjunction** that could result from improper chromosome movement, incomplete pairing, or centromere malfunction (Bridge 1913). This abnormality was discovered by Calvin Bridges in 1913 while working on *Drosophila* (Morgan 2012).

## Forms of Nondisjunction

There are various forms of nondisjunction that lead to different types of chromosomal abnormality.

### Failure of Homologous Chromosome to Separate in Meiosis I

In nondisjunction at meiosis I, a pair of homologous chromosome fails to separate and leads to production of four gametes, two will be  $n + 1$  and other two will be  $n - 1$  (Fig. 1) Fusion of normal gametes with  $n + 1$  would have trisomic ( $2n + 1$ ) zygote and with  $n - 1$ , monosomic ( $2n - 1$ ) zygotes are formed.

### Failure of Sister Chromatids to Separate in Meiosis II

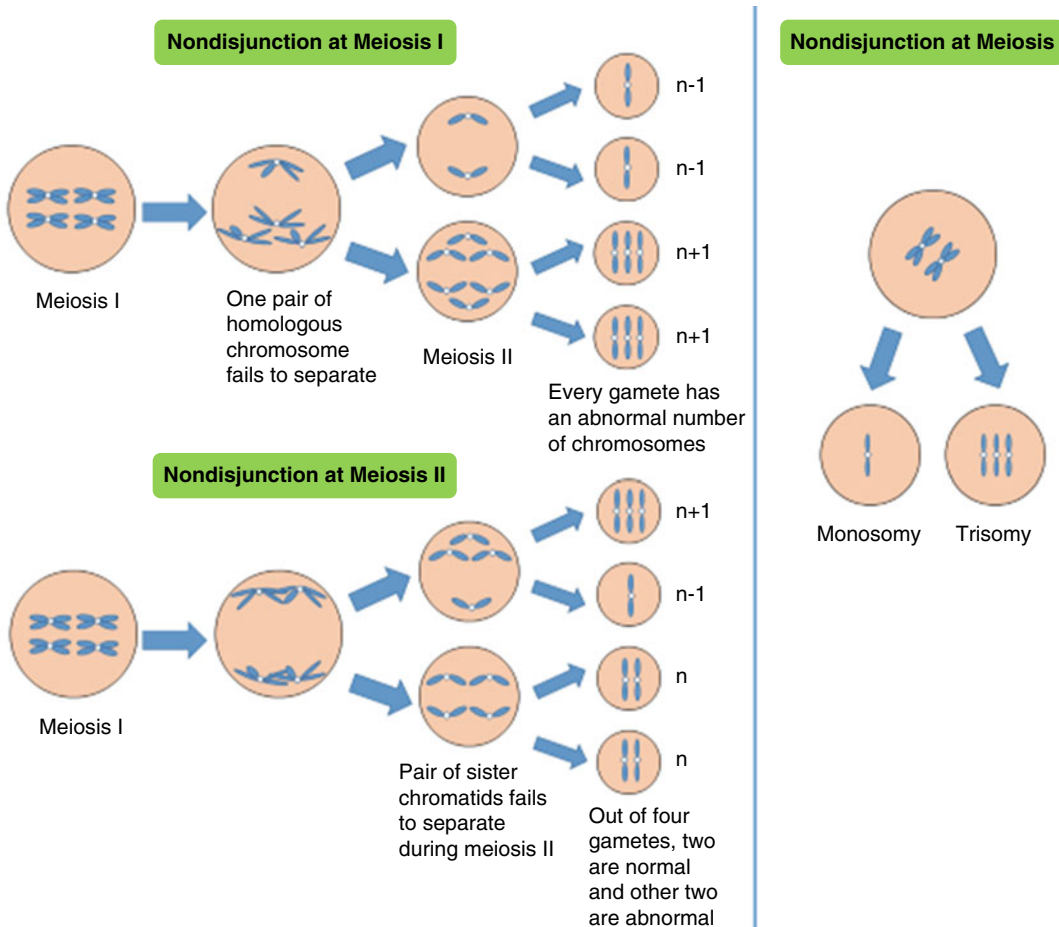
During meiosis II, each cell divides and get diploid (two pairs of each chromosome) to haploid (one of each chromosome) for fertilization. If a pair of sister chromatids fails to separate properly during anaphase of meiosis II, one daughter cell will have an extra chromosome and other daughter cell will be have some chromosomes missing and rest two have normal chromosomes (Fig. 1) Fusion of normal gametes leads to one monosomy, one trisomy, and two normal diploid cell.

### Failure of Sister Chromatids to Separate During Mitosis

During the anaphase stage of mitosis, the chromatids normally separate, and each daughter cell gets one chromatid. However, when nondisjunction occurs, one cell will receive an extra chromatid and becomes trisomic, while other will have a loss of chromatid and becomes monosomic (Fig. 1). In mitosis stage, nondisjunction may also lead to mosaicism in which a tissue may contain patches of cells with some cells having normal karyotype while the others may have abnormal chromosomes. It is commonly observed in cancer.

## Nondisjunction Disorders

Brief introduction to some of the important nondisjunction disorders is mentioned below:



**Nondisjunction, Fig. 1** Nondisjunction at various stages of cell division

### Trisomy 18 Edward Syndrome

It is the second most abundant autosomal trisomy found in the population of small children. This syndrome includes severe mental and growth retardation with frequent microcephaly, myelomeningocele, omphalocele, and cardiac and renal malformations, leading to 95% mortality rate within the first year of life (Edwards et al. 1960). Trisomy 18 is caused by meiotic nondisjunction that gives rise to a gamete with an extra copy of chromosome 18, thus has 24 chromosome. When it combines with partner chromosome the zygote chromosome will become 47. In some cases, only few cells of the body get extra chromosome 18 and this is called mosaic Edward syndrome.

### Trisomy 21 Down Syndrome

It is caused by trisomy of human chromosome no. 21. Individuals with Down syndrome have three copies of all genes on chromosome no. 21 (Patterson 2009). Trisomy 21 has a significant impact on the development of many tissues, including reduction in brain volume, the size of hippocampus, and cerebellum (Weis et al. 1991). People with Down syndrome have a high risk of early onset Alzheimer's disease (AD). By the age of 60, between 50% and 70% of the people with Down syndrome develop dementia (Aylward et al. 1997). It is also associated with a number of congenital heart defects.



### Trisomy 13 Patau Syndrome

Like all nondisjunction conditions (such as Down syndrome and Edwards syndrome), the risk of this syndrome in the offspring increases with maternal age at pregnancy, with about 31 years being the average (Holland et al. 2000). Individual with this syndrome have heart defects, brain and spinal cord abnormalities, very small or poorly developed eyes, extra fingers or toes, and weak muscle tone.

### Sex Chromosome Disorders

#### Klinefelter Syndrome

Klinefelter syndrome is the most common sex chromosome aneuploidy in humans that results from the presence of two or more extra X chromosome in human male. It represents the most frequent cause of hypogonadism and infertility in men. Most cases are caused by nondisjunction errors in paternal meiosis I. It is named after Harry Klinefelter who identified the condition in the 1940.

#### Trisomy X

In this syndrome, the females have an additional X chromosome and are also known as meta-females. It occurs in about one in every thousand female birth (Tartaglia et al. 2010). The affected individual is generally taller than normal female. It is a random event and not inherited usually.

### Diagnosis

#### Karyotyping

A conventional karyotyping method is preferable for studying the chromosomal complement of human oocytes. A fixation method is used in association with R banding technique to perform detailed survey on cytogenetics of human oocytes for aneuploidy diagnosis.

#### Preimplantation Genetic Diagnosis

In this diagnosis, only chromosomally normal embryo is selected and requires in vitro fertilization to obtain embryos for evaluation. This technique is used to identify embryos at risk.

### Polar Body Diagnosis

It is a new diagnostic method for the indirect genetic analysis of oocytes, which is carried out as part of *in vitro* fertilization. The biopsy of polar bodies can be accomplished either by zona drilling or laser drilling within a very short time period (Montag et al. 2009).

### Conclusion

Nondisjunction is the inability or failure of homologous chromosomes or sister chromatids to separate during meiosis. Depending on the stage of its occurrence, it may lead to various types of disorders. Among many autosomal and sex chromosomal disorders, Down syndrome and Klinefelter syndrome are the most common. There are some diagnostic techniques that can be useful for diagnosis and prevention of these disorders like preimplantation genetic diagnosis, polar body diagnosis, etc.

### Cross-References

- ▶ [Assortment](#)
- ▶ [Crossover](#)
- ▶ [Genetic Variation](#)
- ▶ [Homozygosity](#)

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## Nondisjunction of Chromosomes

- ▶ [Crossover](#)

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## Nonentrained

- ▶ [Free-Running Cycle](#)

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## Non-homologous End Joining

- ▶ [Targeted Mutation](#)

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## Nonhuman

- ▶ [Animal Psychopathology](#)

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## Nonhuman Intelligence

- ▶ [Alex the Parrot](#)

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## Nonhuman Primates

- ▶ [Josep Call](#)

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## Non-match-to Sample

- ▶ [Oddity](#)

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## Non-Mendelian Inheritance

- ▶ [Genomic Imprinting](#)

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## Non-motor Imitation

- ▶ [Cognitive Imitation](#)

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## Non-natural Meaning

- ▶ [Metacommunication](#)

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## Nonrandom Mating

- ▶ [Assortative Mating](#)

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## Norm of Reaction

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## Synonyms

[Reaction norm](#)

## Origin of the Term

The norm of reaction is a concept helping to explain the observation that individuals of the same genotype will produce different phenotypes if they experience different environmental

conditions. The term was originally coined by Richard Woltereck (1909), who studied environmental influences on the development of clonal lines of water fleas (*Daphnia*). He observed that those animals can develop a protective shell and spines that protect them from predators. They do so, however, only in environments where predators are present. Originally Woltereck referred to the relationship between one specific environmental parameter and the phenotype as a *phenotype curve* (Phänotypenkurven) and used the term *norm of reaction* to specify the collective influence of all environmental parameters on the phenotype. However, in the same article, Woltereck concedes that the number of potential environmental factors might be close to infinite and that, for practical reasons, one can apply *norm of reaction* also to a small subset of phenotype curves or even to a single curve. The latter use of the term has been widely adopted by the research community, and *norm of reaction* has superseded “phenotype curve” for describing the relationship between a single environmental parameter and the phenotype.

Woltereck argued that it is actually the norm of reaction that is inherited from one generation to the next and that hereditary change is a modification of the norm of reaction. As such, the norm of reaction is equivalent to the concept of “genotype” introduced by the Danish botanist Wilhelm Johannsen (Sarkar 1999). While the genome was sometimes portrayed as “the code of life” or “the blueprint of the organism,” suggesting a predominantly deterministic developmental process, the reaction norm perspective emphasizes that the genotype does not instruct for a single phenotype but for the ways how development responds to environmental variation.

### Categorization and Special Cases

The existence of fine-scaled spatial or temporal variation in the environment will favor the evolution of norms of reaction that allow for phenotypic plasticity. If it is unlikely that the environmental condition will change throughout the lifetime of an individual, then this will lead to developmental

plasticity, where a certain trait emerges during development and remains unchanged for the rest of the animal’s life. The size of helmets and spines of *Daphnia* in response to predator presence are a classical example for developmental plasticity. A polyphenism is a norm of reaction where two or more discrete alternative phenotypes can be produced contingent on environmental cues during a critical phase. The development of different color morphs of several butterflies during dry and wet season is a typical example for polyphenism, environmental sex determination in reptiles and fishes another one. If it is likely that the environmental conditions change several times within the lifetime of an individual, then norms of reaction will produce reversible phenotypic traits (Piersma and van Gils 2011). Life cycle staging, like the seasonal change of fur or plumage in many mammals or birds or the seasonal growth of antlers in deer, are examples where individuals repeatedly change between distinct phenotype.

### Mechanisms

The genetic architecture underlying norms of reaction is still poorly understood. In general, norms of reaction require an integrated system of components, including a mechanism for reception of environmental cues, a system for the transduction and interpretation of the cue, and finally the cue’s target: specific genes and their products (Schlichtig and Pigliucci 1996). Environmental transduction through immediate physiological responses and hormonal cascades can lead to the up- or downregulation of gene products such as transcription factors and micro-RNAs, which in turn influence expression patterns of genes in the gene network (Sultan 2015). The regulatory networks determining the norm of reaction can include cytoplasmatic and epigenetic factors which can be either direct responses to an individual’s past or present environment or inherited from the parent generation. A phenotype must therefore be seen as the product of a complex interaction between genotype, epigenotype, parental environment, and current environment.

## Conceptualization

Woltereck visualized norms of reaction as curves which immediately suggest conceptualizing them as functions, mapping environmental parameter values onto expected trait values. Formally the norm of reaction can therefore be defined as  $f: E \rightarrow T$ , where  $f$  is the norm of reaction, the domain  $E$  is the environmental parameter, and the co-domain  $T$  is the expected phenotypic trait. This generic formulation applies both to cases where the phenotypic trait can be measured on a continuous scale and to cases of polyphenisms where only a few discrete phenotypes exist. In the latter case, the norm of reaction can be accurately described by a step function.

## Consequences for Evolution

A reaction norm perspective on phenotypic traits unifies two concepts which have often been studied in isolation or even been seen as opposing mechanisms: phenotypic plasticity and canalization. Phenotypic plasticity describes phenotype diversification due to environmental variation, while canalization describes the limitation of phenotypic variation by mechanisms that buffer development against genetic and environmental variation (Stearns 1989). Representing the norm of reaction as a function, a plastic trait would be indicated by a steep slope, while a canalized trait would have a slope close to zero, but otherwise there are no qualitative differences between plastic and canalized traits.

Acknowledging the influence that the environment has on the development of the phenotype has important consequences for our understanding of the evolutionary process. Because norms of reaction vary among individuals and because each individual will encounter different environmental conditions, the environment is not only an agent of selection but also a determinant of the range of phenotypes exposed to selection (West-Eberhard 2003).

If environmentally induced developmental variation consistently leads to adaptive phenotypes over many generations, the produced phenotypes can become genetically assimilated, such

that the environmental input previously required to produce the trait is replaced by genetic cues. This process of genetic assimilation (Waddington 1942) has the effect that phenotypes might adapt to changes in the environment before the genotypes. This phenomenon of “genes as followers” (West-Eberhard 2003) of adaptive change rather than its sole origin is a direct consequence of the norm of reaction.

## Behavioral Reaction Norm

The concept of the norm of reaction has been applied to describe the relationship between the environments experienced by a single individual and its consistent behavioral responses. This has been dubbed *behavioral reaction norm* (Dingemanse et al. 2010). The behavioral reaction norm describes how an animal behaves on average and how its behavior changes over a gradient of environmental conditions. As such, the behavioral reaction norm is not a special case of a norm of reaction but an analogous concept, describing a property of an individual instead of a genotype.

## Norm of Reaction and Reproducibility

Finally, the norm of reaction has been recognized of having important implications for the reproducibility in bioscience – specifically for in vivo research. Laboratory experiments that are conducted with inbred animals under highly standardized conditions are testing only a very narrow range of one specific norm of reaction. Independent replicate studies often fail to reproduce the original findings, though this might not necessarily indicate that the original study was biased or underpowered but rather that the replicate study was probing a different region of the norm of reaction (Voelkl and Würbel 2016).

## Outlook

One important property of the norm of reaction is its regulatory complexity as environmental cue

response system (Sultan 2015). The regulatory complexity is a product of stabilizing selection (Schmalhausen 1949), which buffers the functioning of the organism against environmental and genetic perturbations. The consequence of such a regulatory system is that environmental information contributes to the formation of the phenotype. Environmental input is essential for the developmental phenotype. Thus, the genetic code does not contain a complete blueprint of an organism, but it carries only a part of the information, while the epigenome and the environment carry complementary information. Understanding the interplay between genetic code, epigenome, and environment and its consequences for inheritance and evolution will be the big challenge for the twenty-first century.

## Cross-References

- [Canalization](#)
- [Genetic Variation](#)
- [Genotype](#)
- [Phenotype](#)
- [Stabilizing Selection](#)

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## Norma Basalis

- [Cranial Base](#)

## Norma Internalis

- [Cranial Base](#)

## Nourishment

- [Canine Diet](#)
- [Nature Versus Nurture](#)

## Novelty

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## English Oxford Dictionary

1. The quality of being new, original, or unusual
2. A new or unfamiliar thing or experience
3. An object intended to be amusing as a result of its unusual design

## Cambridge Dictionary

1. The quality of being new and unusual
2. Something that has not been experienced before and so is interesting



## American Dictionary

1. The quality of being new or unusual, or a new or unusual experience

Novelty is defined as a stimulus (object or event) that has never been experienced before or as a deviation from the expected likelihood of an event on the basis of both previous information and internal estimates of conditional probabilities (Berns et al. 1997). Therefore, a reaction to such stimuli is a memory-dependent process, and any stimulus has to be compared with what is stored in memory to assess its novelty. Detecting novelty results in an arousal of the animal's attention and triggers a response (Berlyne 1950). Responses may take the form of simple reflexes, such as tropisms, kinesis, and taxis. In organisms with a more advanced organization of behavior, responses to novelty include an orienting response, startle response, and increased exploration aimed at the new object or situation (Pisula 2009). Exploring a new object or environment mostly involves locomotion through the new situation, approaching the unfamiliar elements in a familiar situation and sensory investigation.

Attention and response to novelty are particularly common in vertebrates. These behaviors are observed mainly in mammals and birds, but research shows that the tendency to be attracted to and explore novel objects is also present in some reptiles including turtles, varanid lizards, and crocodiles (Greenberg 2003). Reactions to novelty have also been tested in invertebrates such as octopuses or cockroaches.

In contrast to a situation involving hedonic stimuli (e.g., food or mate), the effect of novelty is self-limiting, and with time the animal becomes habituated to the resulting arousal (Staddon 2016). However, novelty has its own rewarding value, independent of other properties of the stimulus. Studies on animals show that rats are willing to endure an electric shock if they are rewarded by being able to examine an unfamiliar environment (Nissen 1930). Rats also prefer to spend more time in the experimental cage compartment previously associated with novelty. However,

animals generally prefer novel stimuli of low intensity (Pisula and Siegel 2005).

Novelty can be also viewed as a source of information. Organisms regulate their behavior based on information that is constantly available to their senses. Even simple organisms have the ability to use complex behavioral regulation based on external input. The information may be conveyed in various forms, e.g., as chemical, thermal, electric, or light stimuli. However, the ability to detect the novelty of a particular stimulus requires the ability to differentiate between various stimuli. This differentiation involves a negative (withdrawal) or positive (approach) response to a stimulus, a change of direction, or the animal resuming or stopping its locomotion. The animal receives information from the environment and reacts to it depending on the capabilities of its sensory and executive apparatus.

Surprise is also one of the possible responses to novelty. This kind of arousal may be induced not only by complete novelty of the stimulus but also by some unexpected feature in a familiar object or event, by something that is to some extent similar and to some extent dissimilar to what is well-known to the animal. In this sense, novelty can be viewed as a continuum from complete familiarity to complete unfamiliarity. Moreover, animals regulate the amount of novelty through their own activity, e.g., by approaching the novel stimulus or withdrawing from an unfamiliar situation. Therefore, in the natural environment, it is unlikely that an organism will be faced with completely novel stimulation. Complete novelty would have to be defined as complete lack of expectations with respect to future stimuli. It is only possible when such a situation is artificially created either intentionally or unintentionally by humans. It is unlikely that this type of unnatural situation has played any part in the development of a stable adaptive mechanism.

From an evolutionary perspective, a reaction to novelty which involves increased exploration has an adaptive value. An animal's response to novelty results from the interaction of behaviors motivated by curiosity about the novel object's potential value and fear of possible threat, or, in other words, the uncertainty of either the costs

or benefits of approaching the novel stimulus. Detecting a potential threat triggers neophobic reactions of varied intensity. Such reactions may take the form of latency to approach a new object or to start exploring a new environment. When confronted with high-intensity stimuli, the animal may freeze or flee. There is ample evidence to suggest that neophobia (caution toward novel stimuli) is a learned response; young individuals explore new objects and environments with lower latency and higher intensity than adults. In addition, research shows that animals reared in an enriched environment show reduced neophobia in comparison with those reared in an impoverished environment. Animals inhabiting a threat-rich environment (e.g., where the risk of predation or competition is high) exhibit more caution when exploring new objects or environments (Greenberg 2003).

The neurological mechanisms underlying reactions to novelty have not yet been thoroughly examined. However, the amygdala, the dentate gyrus, and the cingulate and parietal cortices may be involved in novelty detection and the associated cognitive events (Montag-Sallaz et al. 1999).

## Cross-References

- [Adaptation](#)
- [Curiosity](#)
- [Exploratory Behavior](#)
- [Food Neophobia](#)
- [J.E.R. Staddon](#)
- [Neophobia](#)

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## Nucleus

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## Synonyms

[Core/heart of the cell](#); [Pronucleus](#); [Storage site of nuclear material](#)

## Definition

Nucleus is one of the most dynamic membrane-bound organelle present in the cell. During the course of evolution, packaging of nuclear material in a separate membrane inside a cell was a turning point that distinguished eukaryotic from prokaryotic organisms. It is the most important structure of the cell as it contains the blueprint of life, DNA, responsible for storage and transmission of hereditary characters.

## Introduction

The term “nucleus” is derived from Latin word *nucleus* or *nuculeus*, meaning kernel or seed. Nucleus is equivalent to the eye of cell which

contains the DNA. It is one of the most important, prominent, and first ever discovered organelle that encompasses the genetic material of the cell in eukaryotic organisms. Prokaryotic cells do not have a nucleus; their genetic material is loosely bound to their outer membrane and is called nucleoid. The DNA is contained within the walls of the nucleus forever, never leaving it; the transcribed product of the DNA, however, comes out of the nucleus to make the functional proteins. The 2-m-long DNA thread is packed inside a 6- $\mu$ m nucleus of a 60- $\mu$ m-diameter mammalian cell owing to the compaction given by binding of DNA with various histone as well as nonhistone proteins (Alberts et al. 2002).

Nucleus was first observed by Antonie Philips van Leeuwenhoek in RBCs of salmon in seventeenth century. It was also analyzed by Franz Bauer in 1804 and Robert Brown in 1831 who coined the term “nucleus,” but all of them could not assign any function to the nucleus. Further in 1838 Matthias Schleiden called it cytoblast (cell builder) proposing that the nucleus function in cell generation. Later after the discovery of other cell organelles, and increasing number of studies on cell, nucleus was recognized as a key tenet of the cell (Pederson 2011).

## Structure and Components of the Nucleus

Nucleus has been proposed as one of the complete cell organelles having its own skeleton and organelles (Lamond and Earnshaw 1998). Nucleus is enclosed by a double-layered phospholipid nuclear membrane, outer and inner, separated by a perinuclear cisternal space of 10–50 nm and is in direct connection with the inner membrane of rough endoplasmic reticulum (ER) (Rowat et al. 2008). The nuclear membrane contains nuclear pores lined by nuclear pore complex and provides a way to maintain continuity between cytoplasm and nucleoplasm (Carmo-Fonseca et al. 2002). Nuclear membrane also works as a selective barrier separating cytoplasmic and nuclear content. The outer membrane is very much similar in composition as well as

function to rough ER, containing ribosomes on its cytoplasmic surface. The inner membrane is in direct contact with nuclear lamina. Nuclear pore is a circular membrane opening, occupied by eight spokes and the central granule; it allows the passage of small water-soluble molecules (Görllich and Kutay 1999). While for the transport of macromolecules, a specialized class of transporter factors known as karyopherins is responsible. RNA synthesized in the nucleus is exported to the cytoplasm with the help of karyopherin called exportin and proteins such as histones, DNA and RNA polymerases, and transcription factors are imported into the nucleus by importins.

Another major component of the nucleus which held together all the components of nucleus is nuclear matrix. It includes nuclear lamina, nucleolar remnants, structural components of the nuclear pore complex, enzymes, nuclear membrane proteins, and an internal nuclear meshwork of fibers and fibrils (Fey et al. 1984; Tubo and Berezney 1987; Miller and Forbes 2000). Nuclear matrix helps in maintaining the structural integrity of the nucleus (Cockell and Gasser 1999) and also in regulating the gene expression (Tetko et al. 2006). Nuclear matrix proteome analysis has revealed a great deal of variation in the types of factors that are associated with it, which varied according to the need of the cell during development (Kallappagoudar et al. 2010). These factors include structural proteins, chaperones, DNA/RNA-binding proteins, chromatin remodeling factors and transcription factors, and indicator of its structural and functional significance. Nuclear matrix provides the microenvironment for the optimum functioning of the chromatin.

Nucleolus is the densely stained largest structure present in the nucleus. It is a suborganelle as it is not bound by any membrane and is mainly responsible for the production and distribution of rRNA (Boisvert et al. 2007). The nucleolus is formed in the region of the ribosomal DNA (rDNA) repeats, which cluster at chromosomal loci called nucleolar organizers, and is the region in which ribosomal RNAs (rRNAs) are transcribed, processed, and assembled into ribosome subunits (Lamond and Earnshaw 1998). Various studies have linked the morphological changes of nucleolus with cancer progression (Quin et al. 2014).

Along with the nucleolus, various other sub-cellular structures are present in the nucleus including Cajal bodies, Gemini of coiled bodies, polymorphic interphase karyosomal association (PIKA), promyelocytic leukemia (PML) bodies, and nuclear speckles, specialized for different functions. Cajal bodies (CBs) or coiled bodies are mostly present in metabolically active proliferating cells as is mainly responsible for RNA processing and telomerase assembly. PML bodies or nuclear domain 10 (ND10) or Kremer bodies are spherical structure involved in DNA replication, transcription, or epigenetic silencing. Nuclear speckles or interchromatin granule clusters are nuclear domains enriched in pre-mRNA splicing factors and are involved in regulation of gene expression (Spector and Lamond 2011).

In a eukaryotic cell, DNA complexed with protein is present in the form of chromatin which is condensed during the cell division. In a cell, 10% of the chromatin is highly condensed and darkly staining called heterochromatin, while rest is transcriptionally active and lightly stained called euchromatin (Wolffe 1992) (Fig. 1).

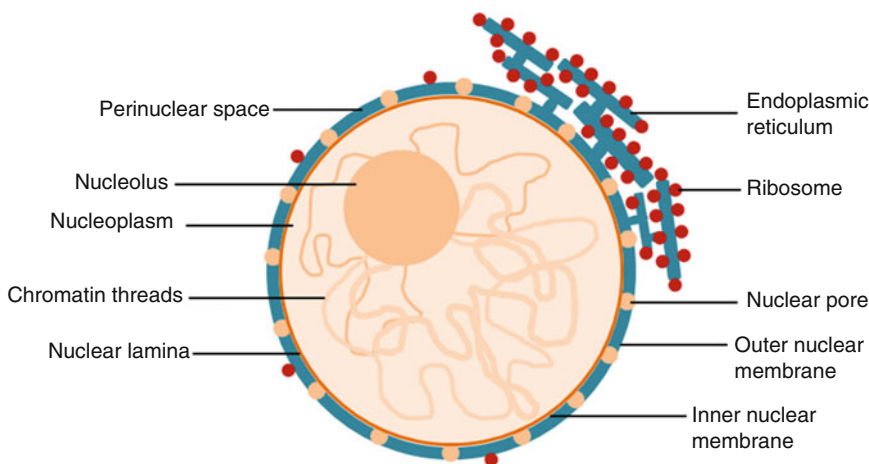
## Nucleus Number

The nucleus number in eukaryotes varies among different cell types and also sometimes with

different developmental stages of same cell type. Depending upon the number of nucleus in a cell, they can be categorized as anucleate, uninucleate, or multinucleate cell. Anucleate cell does not have any nucleus and thereby they are incapable of producing daughter cells. Most common examples include mammalian RBCs and sieve tube elements in plants. Abnormal cell division may also give rise to such condition in which one daughter cell has no nucleus, while the other has two. Most eukaryotic cells are uninucleate as they have a single nucleus. Multinucleate cells have multiple nucleus (two or more); examples include skeletal muscle cells and giant multinucleated cells in human, mycorrhizal cells, and some species of protozoans.

## Conclusion

The origin of nucleus in a cell was one of the landmarks in the history of evolution. Various theories revolve around the origin of nucleus, among which, the syntrophic model is the most famous, which suggests that the nucleus is a result of symbiosis between archaeon and eubacterium (Misteli 2011). The advances in the cell techniques have helped understand the dynamic roles of nucleus. It is a highly ordered structure containing various sub compartments separating proteins and other molecules to perform specialized functions. The



**Nucleus, Fig. 1** Diagrammatic representation of nucleus and its major structural components

importance of this cell organelle can be understood by the fact that removal of nucleus leads to the complete loss of structure and function of the cell.

## Cross-References

- [DNA](#)
- [Gene Expression](#)
- [Ribosome](#)
- [RNA](#)

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## Nucleus Accumbens

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## Synonyms

[Accumbens nucleus](#); [NAc](#); [NAcc](#); [Nucleus accumbens septi](#)

## Definition

Nucleus accumbens (NAc) is a brain area found in basal forebrain. It is present in between caudate and putamen nuclei of basal ganglia. NAc is also the main component of ventral striatum. Most importantly NAc is implicated in reward pathway of brain.

## Introduction

Nucleus accumbens is part of ventral striatum in basal forebrain area of our brain. It is present in both hemispheres. It is a key structure involved in motivational, reward processes associated with psychoactive drug use. Due to a central part of reward pathway in brain, this region has been



implicated in various psychiatric and neurological diseases such as depression, anxiety disorder, obsessive-compulsive disorders, and in drug abuse and addiction. Nucleus accumbens receives input from dopaminergic neurons of ventral tegmental area (VTA) and it results in increase in dopamine levels in the NAc (Salgado and Kaplitt 2015).

## Nucleus Accumbens

The nucleus accumbens (NAc), a part of ventral striatum, is mostly involved with reward, motivation, satisfaction, motor function, and learning. NAc itself is made up of two anatomical components, a central core and an outer shell and both has different contributions to the function of nucleus accumbens. NAc core controls the goal-seeking behavior and generic motivational value whereas the NAc shell looks for novelty and controls the enhancing effect of drugs (Shirayama and Chaki 2006) (Fig. 1).

Nucleus accumbens is an important component of mesolimbic pathway (VTA-NAc) which is a major dopaminergic pathway stimulated during all rewarding experiences. This circuit is key stimulator of reward experience. Activation of this circuit tells the brain to remember the activity which resulted in particular reward and repeat it in future. Along with VTA and NAc there are several other areas of brain which contributes

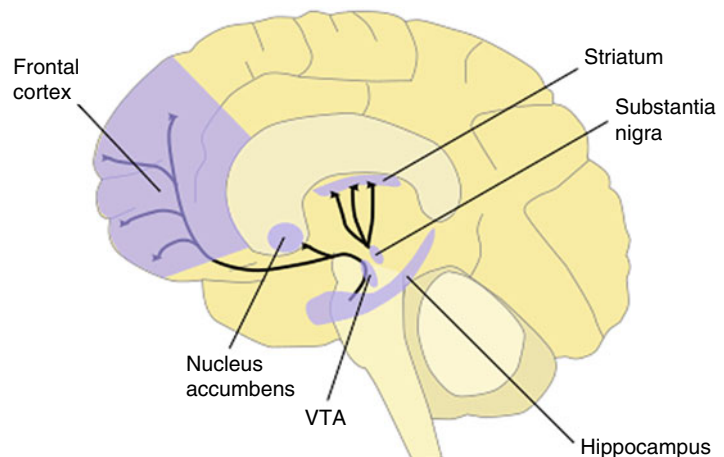
significantly to overall reward experience including hippocampus, amygdala, hypothalamus, and prefrontal cortex. All of these have their distinct role in reward-seeking behavior for individuals (Shirayama and Chaki 2006).

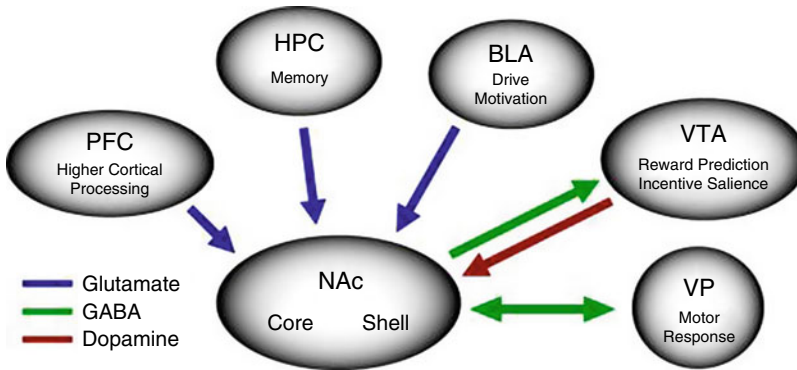
The primary neurons in NAc are medium spiny neurons and they get projections from dopaminergic neurons from VTA area. Also medium spiny neurons project to various areas of mesencephalon and basal ganglia. The main input nucleus of basal ganglia, NAc, gets afferent projections from VTA and substantia nigra in form of dopaminergic projections and direct input in form of glutamatergic projections from subiculum, amygdala, hippocampus, thalamus, and prefrontal cortex (Brain Reward Pathways n.d.) (Fig. 2).

In terms of functional diversity, nucleus accumbens plays critical role in locomotion, learning (both conditioned place preference and avoidance), and sexual motivation, feeding behavior as well as reward and incentive. NAc was the first structure of interest to study the dopamine (DA) and dopamine receptors in various pathological states (Brain Reward Pathways n.d.). A strong body of evidence suggested that DA in the NAc plays key role in addiction. Naturally with any rewarding stimulus such as food, there is increase in DA release in accumbens but it goes down with repeated exposure. However, in case of drugs of abuse the waning of DA release does not happen with repeated exposure to drugs and leads to abuse and addiction. Drugs of

### Nucleus Accumbens,

**Fig. 1** Location of nucleus accumbens (NAc) in brain along with projections to other brain areas (Retrieved from Neurosciencenews)





**Nucleus Accumbens, Fig. 2** General overview of key nucleus accumbens afferent and efferent projections. See text for more information on the anatomic organization of the nucleus accumbens. Note that placement of *arrows* does not necessarily indicate degree or precise location of

projection. *PFC*, prefrontal cortex; *HPC*, hippocampus; *BLA*, basolateral amygdala; *VTA*, ventral tegmental area; *VP*, ventral pallidum; *NAc*, nucleus accumbens (Day and Carelli 2007)

abuse also tend to change synaptic plasticity in accumbens and once an addictive behavior is learned the DA neurons fire with different spatial and temporal degrees. Dopaminergic pathway dysfunction in NAc is involved in depression-like behavior, and dopamine in NAc is prime target of therapeutic drugs for treatment in major depressive disorders (Volman et al. 2013) (Fig. 2).

## Conclusion

Nucleus accumbens is a prime area involved in major reward circuits and has influence over variety of human behaviors. It controls response to rewards such as food, sex, environments, and recreational drugs and implicated in their abuse. NAc is a major determinant of motivational and incentive-driven behaviors. It gets inputs from several regions of brain and projects to several others which makes it vulnerable to any insult or abuse and that leads to its involvement in major psychiatric and neurological disorders.

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## Nucleus Accumbens Septi

► [Nucleus Accumbens](#)

## Numerical Cognition

► [Approximate Number System \(ANS\)](#)

## Numerosity

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At the Fifth International Congress for the Unity of Science in Cambridge, Massachusetts, Stevens (1939, p. 1) proposed a distinction between the terms “numerousness” and “numerosity.” He proposed that numerousness refers to “a property or attribute which we are able to discriminate when we regard a collection of objects,” while numerosity is a “property defined by certain operations performed upon groups of objects.” For example, an operation to determine numerosity might be to count a group of objects. Twelve years later, in a footnote from chapter 1 of his *Handbook of Experimental Psychology*, Stevens (1951, p. 22) again suggested the distinction, stating that “numerousness refers to the subjective aspect or attribute that we observe when we look at, but do not count, a collection of objects.”

A perusal of the literature from mid-twentieth century to the present suggests Stevens’ distinction was never fully embraced by researchers. Numerosity is used routinely in papers from the 1950s onward to refer to the perception of the number of items in a set without counting, including studies using Stevens’ experimental methods (e.g., Abbey 1962; Cheatham and White 1952; Krueger 1972, 1982). Stevens himself, in his 1939 conference presentation, suggested the terms as a “possible distinction” and jokingly referred to both as “barbarous” (Stevens 1939, p. 5).

Krueger (1972) used the term “perceived numerosity” and in the footnote on page 1, Krueger thanks Stevens for commenting on an earlier draft of the paper. One might think that Stevens would have recommended that Krueger use “numerousness” instead of “numerosity,” and it would be interesting and informative to see what Stevens did share with Krueger in that correspondence. In Krueger’s (1972) abstract, he

also distinguishes between “apparent numerosity” and “absolute numerosity,” with the latter likely referring to what Stevens meant by numerosity and the former referring to what Stevens meant by numerousness.

In 1967, APA’s Psyc Abstracts introduced the search term “numerosity perception” to mean “perception of quantities in stimulus sets in visual, auditory, or other perceptual modes.” The term “numerousness” was apparently never added to Psyc Abstracts as a search term, and it’s also not used in the thesaurus of APA’s modern electronic database PsycINFO. A recent search for the two terms in PsycINFO (1950–present) returned 1128 abstracts containing the term “numerosity” but only 57 containing “numerousness.”

Dehaene (1997) in his book *The Number Sense* (p. 35) suggests the two terms are interchangeable: “. . . scientists, when they describe perception of numerical quantities, speak of ‘numerosity’ or ‘numerousness’ rather than number.” An example of a similar use of interchangeable terms in perceptual psychology might be “pitch” and “frequency perception.” Pitch refers to the perception of sound frequency; therefore “pitch” and “frequency perception” are referring to the same thing, and the two terms might be used interchangeably. Similarly, numerousness is the perception of numerosity (cardinal number through counting), so “numerousness” and “numerosity perception” are referring to the same thing, the perception (without counting) of the number of items in a countable set. Someone could determine the numerosity of a set by counting and then ask another person for their perception of that numerosity without counting. Some other terms encountered in the literature are “perceived numerosity,” “numerosity judgments,” “numerosity discrimination,” “numerosity estimation,” and “numerosity perception,” all of which refer to numerousness as Stevens (1939) used it. It seems that Stevens’ suggested distinction was never widely adopted, and most researchers have been using numerosity to refer to what Stevens called numerousness. It should be noted, however, that many researchers use numerousness as Stevens (1939) originally proposed (e.g., Beran 2017; Thomas and Chase 1980).

Numerosity perception has been studied and documented in a very large number of nonhuman animal species (Beran 2017) including insects (Giurfa 2019). Numerosity perception is likely a highly adaptive cognitive mechanism across a diversity of animal taxa. In several studies of animals in natural settings, researchers have concluded that numerosity perception likely enhances fitness (e.g., McComb et al. 1994), and it is easy to see how. If a fish is able to perceive numerosity and discriminate a shoal of 10 conspecifics from 15, it would make ecological sense to select the shoal with the larger number of conspecifics. Similarly, a prey animal capable of numerosity perception might be more inclined to avoid a trio of predators than a single predator. Of course, cues other than numerosity might be used in such behavioral decisions as well.

In studies of numerosity perception with nonhuman animals, it's important to attempt to rule out the possibility of other quantifiable stimulus cues correlated with numerosity, which could potentially be used instead of, or in addition to, numerosity perception. Such potential cues include the total volume of the items, the total surface area of the items, how densely packed together the items are, etc. In each of these cases, the larger the non-numerosity quantity cue, the larger the number in the set is likely to be. For example, a bowl of fruit with a large total surface area is likely to contain more individual pieces of fruit than a bowl with a smaller total surface area. Such nonnumerical quantity cues are difficult to control (Beran 2017), and compelling arguments have been made that any two sets of items differing in numerosity will always differ in one or more nonnumerical quantity cues as well, but attempts should be made to control for them. Of course, other nonquantifiable cues must also be controlled, such as the color or shape of the items. If a larger numerosity set contains only triangular or blue objects, while a smaller set contains only circular or red objects, then the two sets could be discriminated without reliance on numerosity perception at all.

Some have suggested that animals use non-numerical quantity cues readily and only resort to numerosity perception as a kind of “last resort”

when these quantity cues are not available (Davis and Memmott 1982). Cantlon and Brannon (2007) tested the last resort hypothesis in an experiment with monkeys in which color and shape could be used in addition to numerosity. The monkeys were more likely to use color or shape when the numerosity task was difficult. However, when the numerosity task was relatively easy (i.e., a large difference in numerosity between correct and incorrect responses), numerosity perception was more likely to be used, contrary to the last resort hypothesis. Beran (2017) suggested that experimental tests for numerosity perception in animals are especially difficult to design because of the task demands animals are required to learn (i.e., attending to numerosity rather than other cues).

Several mechanisms have been proposed for numerosity perception, with two receiving the most attention (Feigenson et al. 2004; Hyde 2011). One is the approximate number system (ANS; Parrish and Beran 2020). In the approximate number system, numerosity perception can be thought of as a continuous mental quantity, proportional to the absolute numerosity it represents. Smaller numerosities are easier to accurately perceive than larger numerosities, possibly because there is more “noise” in the mental representations of larger numerosities, generating more error (Gallistel and Gelman 1992). An alternative notion is that, as numerosity gets larger, noise does not increase, but the mental representations become closer together (less discriminable), making accurate numerosity perception more difficult (Dehaene 2003). Both of these ideas have received support in the research literature, and both predict the same kinds of data from experiments. Both predict that as numerosity increases, discrimination between numerosities will become more difficult, resulting in a ratio-dependent kind of performance. For example, both models predict that discrimination between a set of 6 items and a set of 12 items (ratio  $6:12 = 0.5$ ) will be easier than discrimination between a set of 9 items and a set of 12 items (ratio  $9:12 = 0.75$ ). As the ratio approaches 1.0, discrimination accuracy approaches chance level. This ratio-dependent performance is an example of Weber's Law. As long as the ratio

of the numerosities to be discriminated remains constant, performance remains constant. Ratio-dependent performance and Weber's Law have been observed in numerosity perception tasks in a variety of species (Merritt et al. 2012).

Another proposed mechanism for numerosity perception, limited to small sets of four and less, has come to be known by two names, the parallel individuation system and the object file system (Feigenson et al. 2004). In this mechanism, items are assigned mental indexes and represented as working memory files, with an upper limit of three or four files capable of being stored in working memory at any given time. Several studies have found that animals' numerosity perception is much better with very small sets of items ( $<4$ ) compared with more (e.g., Agrillo et al. 2014; Rugani et al. 2008). However, other studies have found no difference in the numerosity perception of small versus large numbers of items (e.g., Beran 2007).

The object file system shares similarities with another proposed mechanism for numerosity perception coined "subitizing" by Kaufman et al. (1949). These authors studied numerosity perception in humans and observed that, with briefly presented sets of items, response times (RTs) for up to around six items were substantially faster than for more than six. Kaufman et al. also observed that, in addition to faster RT in this range, the accuracy of participants' numerosity perception and their confidence in their accuracy were higher than with displays of more than six items. These three findings (faster RT, higher accuracy, and higher confidence) led Kaufman et al. to posit the existence of a unique numerosity perception process for small sets of items (one to six) which they called subitizing from the Latin *subitus* ("sudden") referring to the fast and accurate perception of numerosity in this range.

The existence of subitizing as a unique numerosity perception process with small numbers of items has been the subject of considerable debate and controversy. Mandler and Shebo (1982) undertook a comprehensive study to uncover the possible mechanism(s) for subitizing. In the range of one to three items, Mandler and Shebo concluded that humans quickly perceive and recognize canonical visual patterns formed

by the items (e.g., a point, a line segment, a triangle) and that it is these visual patterns that are the basis for fast, accurate, and confident numerosity perception in this range. Gallistel and Gelman (1992) theorized that subitizing in the range of one to four items is accomplished through use of a rapid, serial preverbal counting mechanism (Meck and Church 1983). The preverbal counting mechanism is prone to error, however, especially when the number of targets exceeds about four or five.

Other researchers have argued that there are no discontinuities in the RT function within the subitizing range (e.g., Balakrishnan and Ashby 1991). These authors base their conclusions on a series of statistical tests and line-fitting procedures done on the RT function for one to six items which show no significant discontinuities in the function. These authors concluded that subitizing is a capacity-limited process, and while more "mental effort" is required to perceive numerosity in larger displays compared with smaller displays, the actual mechanism is the same.

Thomas and Lorden (1993) proposed two processes for numerosity perception (they used the term "numerosness") both based on prototype matching. Relative numerosness judgments are used to discriminate the relative numbers of items in two or more sets. For example, a flock of ten birds would likely be perceived to be greater in numerosity compared with a flock of five. Absolute numerosness judgments are used when numerosity perception is applied to a single set of items, for example, a single bowl of fruit. For both relative and absolute numerosness judgments, Thomas and Lorden proposed that prototype matching is the underlying mechanism. Prototype matching occurs when an exemplar is matched against a prototype for a category acquired through experience with many other exemplars (e.g., Rosch 1975). Through training, animals may acquire prototypes for number as well and use those prototypes during absolute and relative numerosness judgments. Thomas and Chase (1980) demonstrated relative numerosness judgments, and Thomas et al. (1980) demonstrated absolute numerosness judgments, both using squirrel monkeys.



Several studies have investigated the underlying neural basis of numerosity perception in human and nonhuman animals. Two cortical areas in the parietal and frontal lobes have been most implicated (Dehaene 1997). Nieder and Miller (2004) review numerosity perception studies with monkeys where recording from neurons in the prefrontal and parietal cortices was conducted. Individual neurons were found that are “tuned” to the numerosity of items in the displays. These neurons fire faster to specific numerosities and slower to others. Parietal cortex neurons responded to numerosity more quickly than the frontal cortex cells suggesting that the parietal cells encode numerosity first and then pass that information on to the frontal cortex for subsequent decision-making.

Numerosity perception is widespread in the animal kingdom, evolving from an ancient common origin, or perhaps through more recent convergent evolution. Nonhuman animals appear to share with humans two core systems for the perception and representation of numerosity. Continued research on the mechanisms and neural bases of numerosity perception in nonhuman animals will likely provide insights regarding the phylogenetic history of this remarkable perceptual ability.

## Cross-References

- [Absolute Number Discrimination](#)
- [Approximate Number System \(ANS\)](#)
- [Plantae](#)

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## Nuptial Gift

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## Definition

Nuptial Gift: Materials beyond the obligatory gametes that are transferred from one sex to another during courtship or mating (Lewis and South 2012).

## Introduction

In nature, the race to reproduce is incredibly competitive. Success means an organism passes on its genes; failure means that the organism's specific genes are lost to the gene pool. One way in which an organism can increase its chance of reproduction is the presentation of a nuptial gift. Lewis and South (2012) define a nuptial gift as "...materials beyond the obligatory gametes that are transferred from one sex to another during courtship or mating." Note that this definition does not specify the sex of the giver or the receiver. Whereas male to female gifts are the most common variety of nuptial gift, some species show evidence of female to male gifts (Arnqvist et al. 2003). Male Zeus bugs (*Phoreticovelia disparata*) feed on female glandular secretions while mating. There is also precedence for nuptial gifts in hermaphroditic species (Koene et al. 2005). Earthworms (*Lumbricus terrestris*) inject their copulatory partners with a substance that increases sperm uptake.

## Diversity of Nuptial Gifts

Nuptial gifts are diverse; they can take the form of lipids, proteins, carbohydrates, peptides, uric acids, amino acids, water, pheromones, minerals, and anti-predator compounds, just to name few. Because of this diversity, it is helpful to categorize nuptial gifts in several ways. Gifts can be either endogenous or exogenous in nature (Lewis and South 2012). Endogenous gifts are gifts produced by the giver's body. Exogenous gifts are food items procured by the giver from the environment. Similarly, nuptial gifts can be oral, genital, or transdermal in nature. Oral gifts are consumed through the receiver's mouth (Gwyne 2008). Oral gifts assist the giver in mating by occupying the receiver and prolonging copulation (Lewis and South 2012). Genital gifts are consumed through the receiver's genitals. Transdermal gifts are gifts that are consumed neither orally nor genitally, but injected through the receiver's skin.

## Common Types of Nuptial Gift

**Exogenous Oral Gifts:** An exogenous oral gift is a gift that is received orally but is not created by the giver. An example of an exogenous oral gift would be food items, such as is displayed in nuptial feeding (Lewis and South 2012). In many species of bird, males provide females with food during courtship or incubation (Silver et al. 1985).

**Endogenous Oral Gifts:** An endogenous oral gift is a gift that is received orally and generated by the giver's body. Female sagebrush crickets (*Cyphoderris strepitans*) feed on wings of males during copulation (Eggert and Sakaluk 1994). Chewing on the male's wings occupies the female cricket and prolongs copulation.

**Endogenous Genital Gifts:** An endogenous genital gift is a gift created by the giver and given to the receiver through its reproductive tract. Male butterflies of the species *Heliconius melpomene* produce an antiaphrodisiac pheromone during copulation (Schulz et al. 2008). This pheromone prevents the female from re-mating by repelling would-be mates.

**Endogenous Transdermal Gifts:** An endogenous transdermal gift is a gift that is created by the giver and injected into the skin of the receiver. In some species, male squids are known to inject their spermatophores into the tissue of the female (Hoving and Laptikhovsky 2007). The spermatophore releases a structure known as a spermatangium, essentially sperm encased in a thin covering.

## Effects on Fitness

More often than not, nuptial gifts increase the reproductive fitness of the giver (Lewis and South 2012). This increase in fitness is not universal to receivers. Certainly, some receivers do increase in reproductive fitness after receiving a nuptial gift. Gifts can positively contribute to the size and number of eggs produced by a female, as well as the overall lifespan of that female (Lewis and South 2012). The longer a receiver lives, the more healthy offspring they can produce, leading to an increase in fitness. However,

some nuptial gifts decrease the reproductive fitness of the receiver (Lewis and South 2012). Male fruit flies (*Drosophila melanogaster*) prevent females from re-mating through use of a mating plug (Bretman et al. 2009). These mating plugs physically block a female's reproductive tract, with the purpose of retaining sperm. Mating plugs also prevent the females from re-mating, resulting in greater reproductive fitness for the male, allowing only his sperm to fertilize the eggs. This increase in fitness is not shared by the female, however; because she cannot re-mate, she incurs a loss in reproductive fitness.

The nursery web spider (*Pisaura mirabilis*) illustrates another form of nuptial gift that does not improve the reproductive fitness of the receiver (Ghislandi et al. 2014). Males in this species create nuptial gifts by wrapping insect prey in silk. However, male nursery web spiders have been known to deceive females by wrapping useless gifts, such as empty exoskeletons or plant materials. Whereas this behavior increases the reproductive fitness of the male without requiring a large degree of effort, the female is left without the nutritional content promised by the false nuptial gift.

## Conclusions

The need to pass on genetic material has led to many unique strategies to ensure reproduction. Nuptial gifts vary incredibly between the many species they occur in; they can be oral or genital, made by the organism or found by the organism, and can be beneficial or detrimental to the fitness of the receiver. Despite this variance, nuptial gifts share a common trait of an increase in the reproductive fitness of the giver.

## Cross-References

- [Coevolution](#)
- [Courtship Rituals](#)
- [Cuckoldry](#)
- [Deception](#)
- [Ejaculate](#)
- [Evolution](#)

- ▶ Extra-Pair Copulation
- ▶ Facultative Polyandry/Strategic Pluralism
- ▶ Fecundity
- ▶ Female Choice
- ▶ Fitness
- ▶ Genes
- ▶ Hermaphrodite
- ▶ Internal Fertilization
- ▶ Mate Guarding
- ▶ Mate Provisioning
- ▶ Mating
- ▶ Mating Effort
- ▶ Mollusk
- ▶ Natural Selection
- ▶ Parental Investment
- ▶ Polyandry
- ▶ Polygyny Threshold Model
- ▶ Promiscuity
- ▶ Species-Specific Behavior
- ▶ Sperm Competition
- ▶ Spermatogenesis

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## Nut-Cracking

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## Synonyms

Defended food/encapsulated food processing

## Introduction

Nut-cracking is one instance of predator-prey “arms race,” where plants mechanically defend their fruits’ endosperm, even when (or *especially* when) its outer layers are meant to be eaten by animals, for seed dispersion. Nut eaters, then, need to be able to apply the necessary force to access those endosperms, which can be accomplished by sheer bodily force alone, with the aid of gravity and hard substrates, or by using tools.

Some parrots simply crack nuts with their beaks, but tools may play a role in the technique: the oldest report of tool use by a parrot in the wild dates back to 1869, when Wallace described a black palm cockatoo (*Probosciger aterrimus*), in New Guinea, feeding from kanary nuts (*Canarium commune*). After starting to groove the nut with its lower mandible, the bird introduced a piece of leaf between the upper mandible and the nut before breaking the shell, apparently to prevent it from slipping.

Hyacinth macaws (*Anodorhynchus hyacinthinus*) exhibit a similar procedure when cracking nuts such as indaia (*Attalea dubia*), introducing leaves or pieces of wood between the nut and the beak. Borsari and Ottoni (2005) observed captive individuals holding the nuts in their beaks or feet, and slicing off a piece of wood from the perch, which was positioned, with the aid of the tongue, beneath the bird’s upper mandible. The nut was then held with the foot in contact with the fixed piece of wood. With its lower

mandible, the bird pushed the nut against the tool, grooving it with its lower mandible.

These tools may be serving as wedges, preventing the nut from slipping or rotating, or reducing the impact of the final cracking on the beak.

### Gravity-Aided Nut-Cracking

Dropping defended food, such as mollusk shells or nuts, on hard substrates is not an uncommon practice among birds. The dropping of nuts is particularly common among corvids. In most cases, it involves the selection of proper, hard substrates; there is evidence of adjustments in terms of dropping height or in the number of successive drops by the birds, as reported by Cristol and Switzer (1999), in a study on nut-cracking by American crows (*Corvus brachyrhynchos*). A typical hard substrate is asphalt roads' pavement. Nonetheless, despite a few anecdotal reports suggesting otherwise, Cristol et al. (1997) found no evidence that Western American crows (*Corvus brachyrhynchos hesperis*) deliberately used the cars to crack the dropped nuts.

In the case of Japanese carrion crows (*Corvus corone*) in Sendai, though, Nihei (1995) systematically observed the apparently intentional behavior of dropping or positioning walnuts in front of cars stopped at the red traffic lights of pedestrian crossings; after a car ran over the walnuts, the crows returned to eat the nut fragments. The author suggests the car-using behavior is an alternative invention to crack nuts too hard to be broken just by dropping (even from more than 10 m above the ground), or are still covered with pulp.

Another form of substrate use is securing the encased food in crevices to facilitate the extraction of the contents, a strategy exhibited by some seed eaters such as jays, nutcrackers, nuthatches, or pine warblers. New Caledonian crows (*Corvus moneduloides*) use these "vice-anvils" to extract the kernel of candlenuts cracked by dropping them on hard "anvils." New Zealand rooks (*Corvus frugilegus*), on the other hand, use crevices to secure walnuts while they break the shells with their beaks (Hunt 2014).

### Tool-Aided Nut-Cracking

Birds may also use stones as percussive tools to crack open defended food: Egyptian vultures (*Neophron percnopterus*) may kill lizard prey or break ostrich eggs, using stones they raise in their beaks. There are reports of American crows handling stones in their talons to hammer acorns (and of captive bald eagles doing the same to predate crickets; Shumaker et al. 2011).

The use of stone or wooden percussive tools – "hammers" and "anvils" – to access nuts' endosperm (or other defended food) is the most common form of tool use among nonhuman primates, being customarily observed in many wild populations of chimpanzees, tufted capuchin monkeys, or long-tailed macaques.

### Tool-Aided Nut-Cracking in Nonhuman Primates

*Tufted capuchin monkeys* (*Sapajus* sp.): Stone-aided nut-cracking by tufted capuchin monkeys was first studied in semifree, urban park populations (Otoni and Mannu 2001). The first direct and systematic observations in the wild were done with two populations of bearded capuchin monkeys (*Sapajus libidinosus*) in Fazenda Boa Vista (Fragaszy et al. 2004) and in Serra da Capivara National Park (Moura and Lee 2004; Mannu and Otoni 2009), both in the state of Piauí (northeastern Brazil). Tool use seems absent from forest-dwelling tufted capuchin monkeys' behavioral repertoire; the customary use of stone "hammers" to crack open palm nuts, though, is rather the rule than the exception for savannah populations (Mendes et al. 2015). The degree of terrestriality seems to be – rather than food scarcity – a stronger predictor of the use of stone percutors to process defended food in modern-day populations. The genus' evolutionary history, though – occupying savannah environments in times of intense climatic change, strongly suggests a potential role for hard-shelled fruit as fallback food in their past (Otoni and Izar 2008).

Stone tools can also be employed to process softer fruit, such as cashew nuts (*Anacardium occidentale*), to avoid contact with the irritating liquid surrounding the seed (Sirianni and Visalberghi 2013).



Field experiments have shown that tufted capuchin monkeys minimize transport costs (Corat et al. 2016); choose, transport, and use the effective tool to crack nuts when faced with stones differing in functional features (Visalberghi et al. 2009); and skillfully place the nuts so that they do not fall off the “anvil” when struck (Fragaszy et al. 2013).

*Long-tailed macaques (Macaca fascicularis)*: The only Old World species where customary use of stone tools has been observed in the wild are long-tailed macaques. Some populations of *M. fascicularis aurea*, the Burmese subspecies, use stones to detach or break oysters, gastropods, crabs, and crack open encapsulated fruit such as sea almonds (*Terminalia catappa*), transporting stones of up to 2 kg to use them as “hammers” (Gumert et al. 2009; Falótico et al. 2017).

*Chimpanzees (Pan troglodytes) and other great apes*: In captivity (or rehabilitation facilities), orangutans, gorillas, and bonobos frequently exhibit the use of percussive tools. Kanzi, the notorious, symbol-language-proficient bonobo, even produced blades by flaking stones in an experimental context, and bonobos in the “Lola ya Bonobo” sanctuary, in the Democratic Republic of the Congo, crack oil palm nuts with stone hammers; they are known to show nut-cracking behavior since the establishment of first nursery sanctuary, in 1995 (Neufuss et al. 2017). The customary use of stone tools by apes in the wild, though, seems to be restricted to chimpanzees.

Wild chimpanzees use objects as tools in a wide range of objects, usually while foraging, but also in communicative, bodily care, or other contexts. Nut-cracking with the aid of tools had already been reported in the nineteenth century; the first long-term field studies in the 1960s, such as Jane Goodall’s (1986), revealed not only the complexity of their social lives but also their technical skills – and the variation between populations (McGrew 1992; Whiten et al. 1999). The customary use of percussive tools for nut-cracking is common in West Africa (Guinea, Ivory Coast, Liberia, and Sierra Leone), though techniques and materials vary, but is virtually absent in Central and East Africa – even in places where nuts and stones are available. In sites like the Taï forest (Boesch and Boesch 1983), wooden

or stone “hammers” are usually employed to crack *Coula* nuts. For the harder *Panda* nuts, stone “hammers” are the preferred choice. Diécké chimpanzees and other populations crack these nuts with stone “hammers,” employing stone or wooden “anvils.” In Bossou (Guinea), where nut-cracking has been studied in a “field laboratory,” chimpanzees crack softer palm nuts with the aid of smaller stone tools (Matsuzawa et al. 2011). Tool use experiments have shown that captive chimpanzees actively choose appropriate stones to crack open nuts according to weight (Schrauf et al. 2012), and experienced tool users adjust their movements to optimize their performances according to the weight of the “hammer” (Bril et al. 2009). In the Ivory Coast, Taï chimpanzees transport lighter stone tools for longer distances from the source and reuse them more frequently (Luncz et al. 2016).

## Conclusion

The use of stone tools leaves lasting remains, allowing archaeological techniques to be applied in search of ancient evidence of nonhuman primates’ technology. According to archaeological evidence, Taï chimpanzees have been using stones as “hammers” and “anvils” for nut-cracking for at least 4,300 years (Mercader et al. 2007), and bearded capuchin monkeys have been using stone “hammers” to process cashew nuts for at least 700 years (Haslam et al. 2016). Although these techniques appear, thus, to be very conservative, the population differences in tool use among wild primates (McGrew 1992; Whiten et al. 1999; Ottoni and Izar 2008), along with developmental studies on nut-cracking (Resende et al. 2008; Biro et al. 2006; Eshchar et al. 2016), clearly point to, beyond genetic or ecological determinants, a socially biased learning dynamics underlying the spread and maintenance of tool use traditions among nonhuman primates.

## Cross-References

- Foraging
- Social Learning

- Stone Tools
- Tool Use

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## Nutrients

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## Definition

Nutrients are substances which we obtain from diet, and it provides nourishment, promote growth, maintenance, and repair of body tissues (Hendrich et al. 1994).

## Nutrients

Food is one of the most basic and fundamental part of living organisms. Food provides us with the essential nutrients, which are necessary for all the biological functions of a body. Nutrients are very crucial for maintaining the structural and functional integrity of the cells. Some nutrients also function as cofactors and substrates in various biochemical reactions and pathways proceeding inside the cells or in extracellular environment. Nutrients can influence the phenotypic expression of genes by affecting processes like transcription, translation, and posttranslational modifications. The genetic makeup of an individual can also influence the response to diet (Mutch et al. 2005). Hence, it is very important to include a variety of foods in our daily diet, which can fulfill all the nutritional requirements pertaining to a healthy body. Nutrients are of different types such as carbohydrates,

fibers, minerals, fats, proteins, vitamins, and water. All these nutrients can be subcategorized into two main categories:

**Macronutrients:** They are needed in large amounts, e.g., carbohydrates, fats, proteins, and water.

**Micronutrients:** They are needed in relatively small amounts, e.g., vitamins and minerals.

Nutrients are not found in isolation except water; whereas some pharmaceutical preparations can have purified forms mixed with adequate preservatives, as in the case of supplements. Nutrients interact with each other during various processes of digestion, absorption, and transport into the bloodstream, assimilation, and use in the cellular pathways.

## Nutrition, Health, and Disease

Many studies have shown that certain nutrients act as antioxidants and protect the cells from the harmful effects of oxidative damage (Evans and Halliwell 2001). Deficiency of a single micronutrient can be easily identified and treated. But, it is often difficult to determine the subclinical deficiency of multiple micronutrients (Shenkin 2006). Hence, many countries have made separate recommendations for dietary intake of nutrients in different age groups. The values of recommended intakes of each micronutrient are set, below which a clinical deficiency state will be considered, and for the upper limits, a state of toxicity is more likely to happen. These recommendations are made based on the intakes in the healthy population coupled with epidemiological/nutrition surveys conducted in that particular population over a period of time.

## Individuals with a Higher Risk of Getting Inadequate Intakes

There are certain groups in a population that are at a high risk of getting inadequate levels such as:

People of low socio-economic status, as they cannot afford a regular supply of fresh fruits,

vegetables and other staple foods rich in micronutrients (Hoare et al. 2004).

People with chronic alcohol abuse often have multiple micronutrients deficiency due to the negligence of proper food habits (Kirby 1990). Conditions like anorexia nervosa, bulimia nervosa, and Binge-Eating Disorder (BED) are consequences of extreme efforts to control weight or food intake and are often found in adolescents and teenagers. Such conditions can result in severe micronutrient deficiencies resulting in various health complications (Sharan and Sundar 2015).

The elderly often suffer from low appetite due to age-related conditions. This lower appetite can lead to lowered food intake and hence can easily cause micronutrient deficiencies (Smithers et al. 1998).

## Individuals with Increased Demand for Nutrients

Females require higher amounts of folic acid before conception and during pregnancy especially in first trimester (Institute of Medicine 1998).

People recovering from acute illness or who went through surgical intervention might need increased amounts of specific nutrients to help them recover better and fast (Payne-James 2001).

The demand for micronutrients increases tremendously when a patient is gaining weight after a prolonged period of catabolism (Kay et al. 1976).

Loss of body fluids as in case of excessive blood loss during menstruation or other reasons can cause iron deficiency anemia in that individual. Zinc deficiency in case of diarrhea can start a vicious cycle of worsening as a result of further loss (Castillo-Duran et al. 1988).

## Micronutrient's Deficiency and Disease

Deficiency of certain micronutrients is most common in low and middle-income countries. Deficiency in any essential micronutrients can have health complications but only a few are found commonly such as folic acid, vitamin B12, iron, vitamin A and D (Shenkin 2006).

**Deficiency of various B-vitamins (Vitamin B12, B9, B1, B2, B3 and B6):** Deficiency of Folic acid (B9) and Vit B12 alone or in combination is often found to be associated with various pregnancy complications such as early pregnancy loss, preterm birth, neural tube defects, anemia, and cognitive impairment. Hyperhomocysteinemia due to deficiency of these two micronutrients is an independent risk factor for cardiovascular diseases (Shenkin 2006). Vitamin B1 and B2 are associated with Beriberi and pellagra, respectively, whereas Vitamin B3 deficiency can cause fatigue, impaired iron absorption dermatitis, eye changes, and brain dysfunction. Deficiency of vitamin B6 is common in developing countries and can cause neurological disorders, anemia, dermatitis, convulsions, and elevated plasma homocysteine.

**Vitamin D:** Vitamin D deficiency is widespread and is found in all age groups. It is associated with rickets, osteomalacia, osteoporosis, and colorectal cancer.

**Iron and vitamin C:** Iron deficiency is most prevalent among adolescent girls and pregnant females and intervention studies are still not able to control it especially in low-income countries. It can cause iron deficiency anemia, increased maternal and infant mortality, and low birth weight. Prolonged severe anemia can cause left ventricular hypertrophy (LVH), which can require hospitalization and sometimes cause death. Deficiency of Vitamin C can reduce the absorption of iron. Vitamin C deficiency is known to cause scurvy, low resistance to infection and anemia.

**Vitamin A:** Vitamin A deficiency is most commonly found in preschool children and is associated with night blindness, xerophthalmia, increased risk of mortality in children and pregnant women.

**Calcium:** Calcium deficiency is widespread and more common in old age and lactating mothers. Decreased bone mineralization, rickets, and osteoporosis are some of the symptoms associated with it (Tulchinsky 2010).

**Iodine and Zinc:** Iodine and zinc deficiency is most common in low-income countries. Iodine deficiency is associated with goiter, increased

risk of stillbirth, hypothyroidism, iodine deficiency disorders, birth defects infant mortality, and cognitive impairment. Zinc deficiency can cause impaired growth (stunting), poor pregnancy outcome, genetic disorders, and decreased resistance to infectious diseases.

**Selenium and fluoride:** Selenium deficiency can cause cardiomyopathy, increased cancer, and cardiovascular risk, whereas fluoride deficiency is associated with increased dental decay and affects bone health (Tulchinsky 2010).

### Nutritional Deficiencies in Animals

Studies have shown that poor nutrition in farm animals can adversely affect the various stages of reproduction such as delayed puberty, reduced ovulation, poor rate of contraception, followed by decreased number of successful pregnancies (Smith and Akinbamijo 2000).

Deficiency of certain micronutrients in animals is associated with various effects such as: Zn (loss of appetite, poor growth, reduced immunity, and fertility in grazing livestock), Cu (poor growth, diarrhea, anemia, and loss of pigmentation in goat), Mn (lameness), As (poor growth and abnormal reproduction in rat, chicks, and goats), and Pb (anemia, depressed growth, elevated serum cholesterol, decreased liver glucose, phospholipids, and bile acids and disturbed Fe metabolism in pigs and rats) (Alloway 2013).

### Macronutrients and Disease

**Carbohydrates:** Carbohydrates are the main source of energy, and we consume carbohydrates in the form of sugars and starch. Diets rich in refined carbohydrates and sugars can increase the glycemic index (14) (Jenkins et al. 1987). Studies have shown that diet including <3 servings per week of whole grain foods can increase the risk of type 2 diabetes. Increased consumption of whole grain foods also decreases the risk of cardiovascular diseases. High fiber, low fat, and high carbohydrate diet were found to improve the blood lipid concentration and be useful in improving intestinal disorders (Venn and Mann 2004).

**Protein:** Protein deficiency can increase in chronic illness such as infections and inflammation due to significant loss of proteins.

Excess protein can cause acidosis, azotemia, hypercalciuria, increased risk of type 2 diabetes, and cancer (Levine et al. 2014; Van Nielen et al. 2014).

**Fat:** Polyunsaturated fatty acids (PUFA) play an important role as a structural component of cell membranes and signaling molecules (eicosanoids). Some studies have shown that omega-3 PUFA has anti-inflammatory properties and might play a significant role in the management of autoimmune and cardiovascular diseases (Kris-Etherton et al. 2002; Simopoulos 2002). The higher amount of saturated fats in diet can increase the levels of cholesterol and triglycerides.

### Conclusion

It is evident that nutrients play a significant role in cellular pathways and metabolism.

Micronutrient deficiencies are much common in the general population as compared to macronutrients. The majority of food preparations are rich in proteins, carbohydrates, and fats and processed foods generally have very low micronutrients content. Hence, it is important to recognize the reasons behind micronutrient deficiency and act accordingly. It is often advisable to take micronutrient supplementation along with proper food intake if daily requirements are not being fulfilled with food alone. But one should always take supplementation under the supervision of medical personnel only. Excess consumption of supplementation without prescription can have harmful effects.

### Cross-References

► [Nutrition](#)

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## Nutrition

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# O

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## Oats

- [Equine Diet](#)

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## Object Handling

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## Object Movement Re-enactment

- [Copying](#)

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## Object Perception

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## Object Permanence

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### Definition

Object permanence is the capacity to represent objects as persisting in time and space independently of perception.

### Introduction

Object permanence is one of the most studied abilities in animal cognition. In the early twentieth century, researchers investigated memory by hiding a food reward in one of several opaque containers and allowing the animal to retrieve it after a delay (e.g., Tinklepaugh 1928). This research on *delayed reactions* tacitly involved object permanence, which was not explicitly considered a separate cognitive capacity until the influential

studies of Piaget (1954). He found that children develop object permanence in stages throughout early childhood. Behavioral biologists and comparative psychologists later used the Piagetian framework to document the cognitive development of various species. They discovered that not all species reach all six stages of object permanence as humans do while acknowledging that the Piagetian tasks are not suitable for many species and that numerous other factors affect performance. The debate on optimal methods continues. Recent research tries to disentangle these confounds and test animals in multiple carefully controlled conditions, with the overarching aim to describe why some species perform better than others in the light of their respective natural histories.

Piagetian Stages of Object Permanence

Piaget (1954) observed the development of his children through spontaneous behavior and informal experiments. He concluded that children, from birth to 2 years of age, progress through six stages of object permanence, with increasing cognitive demands (Table 1). In general, object permanence is tested by letting a subject search for a hidden object, which is often a toy for children

and a food reward for animals. The ability to find these rewards under various conditions indicates how well the subject understands the concept of object permanence.

Stage 1: No Response to Objects

During Stage 1, subjects are not yet capable of recognizing and searching for objects (Piaget 1954). They do not show any visual or motor responses to a surrounding object or reward. Since this is the first stage that subjects possess from birth, the criteria for this stage is that Stage 2 of object permanence has not been reached yet. Precocial animals such as chickens are more active and independent from their first day and start life at a higher stage of object permanence (Doré and Dumas 1987).

Stage 2: Visually Tracking Objects

During Stage 2, subjects still do not actively search for a disappeared object. However, they do visually track the object or reward when it is moved in their visual field (Doré and Dumas 1987; Ujfalussy et al. 2013; Zucca et al. 2007). To test this stage, subjects are presented with an object that moves through a 180° arc. The passing criterion is that the subject visually pursues the moving object (with the eye, head, or full body movements).

Stage 3: Retrieving Partially Hidden Objects

During Stage 3, subjects can retrieve a partially hidden object (Doré and Dumas 1987; Singer and Henderson 2015; Ujfalussy et al. 2013). These tests are often done by covering half of a toy or food reward with a piece of cloth (e.g., Collier-Baker et al. 2004; Pepperberg et al. 1997; Piaget 1954; Zucca et al. 2007). The passing criterion is that the subject retrieves the partially hidden reward.

Stage 4: Retrieving Fully Hidden Objects

Understanding the permanence of object entails recognizing the persistence of objects independently of perception. Unlike earlier stages, Stage 4 involves tests with fully hidden objects. Typically, the reward is fully covered by one of several opaque *occluders*, and the subject is then allowed

**Object Permanence, Table 1** Summary of the Piaget stages in object permanence. (Adapted from De Blois et al. (1998))

| Stages                          | Description                                                    |
|---------------------------------|----------------------------------------------------------------|
| 1                               | No response to the object                                      |
| 2                               | Visually tracking the object                                   |
| 3                               | Retrieving partially occluded objects                          |
| 4a                              | Retrieving fully occluded objects with initiated motion        |
| 4b                              | Understanding single visible displacement (with A-not-B error) |
| 5a                              | Understanding single visible displacement (no A-not-B error)   |
| 5b                              | Understanding multiple visible displacements                   |
| <i>Simple object permanence</i> |                                                                |
| 6a                              | Understanding single invisible displacements                   |
| 6b                              | Understanding multiple invisible displacements                 |
| <i>Full object permanence</i>   |                                                                |

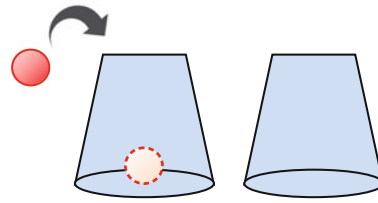
to search for it (Jaakkola et al. 2010; Piaget 1954). The occluder is usually a piece of cloth, box, cup, or screen. When presented with two occluders, of which only one is baited, subjects with object permanence are expected to select the baited occluder after observing the baiting procedure. This test is usually repeated multiple times with the same subject, such that performance is reflected in a score of X trials correct out of Y trials in total, which can be statistically compared to chance level (e.g., 50% correct when two occluders are used).

Two substages are recognized. In Stage 4a, a subject is able to choose correctly but only if it initiated its movement toward that occluder before the reward fully disappeared. In Stage 4b, the subject can select the correct occluder without such initial movement (Doré and Dumas 1987; Singer 2018; Ujfalussy et al. 2013). If the reward is moved from one location to the occluder during the procedure, this is called a *single visible displacement* (Fig. 1a). Delayed response tasks in which a reward is hidden behind an occluder, instead of an arbitrary cue such as a light, involve visible displacement. Performance differs strongly among primates, but overall, they always perform better when the delay between disappearance and search is shorter (Many Primates et al. 2019). The alternative method of placing occluders over the reward does not constitute displacement because the reward remains stationary.

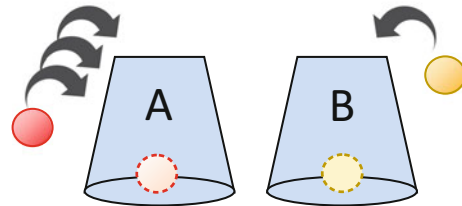
Piaget noticed a strange error occurring in infants of 8–12 months old. After correctly retrieving the reward at location A over several trials, subjects kept searching at location A in subsequent trials even after seeing the reward was now hidden at location B. This is called the *A-not-B error* or the *perseveration error*. Animals often make the same error (Cacchione and Rakoczy 2017; Doré and Dumas 1987; Osthaus 2017; Piaget 1954; Ujfalussy et al. 2013). Individually, these subsequent trials are still single visible displacements, but to distinguish them as a group, this procedure is called *sequential visible displacement* (Fig. 1b).

The A-not-B error becomes more prevalent with a larger number of preceding A trials, an

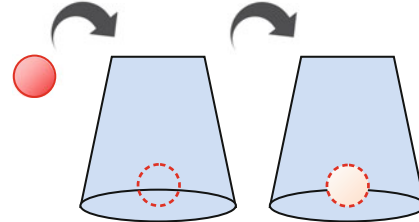
### A) Single visible displacement



### B) Sequential visible displacement



### C) Multiple visible displacement



**Object Permanence, Fig. 1 Visible displacements.** The most common visible displacement tasks. (a) The object is placed under an occluder. (b) The object is placed under occluder A in several trials followed by a trial where it is hidden under occluder B (as a test for the A-not-B error). (c) The object is first hidden under one occluder and then under the other occluder in the same trial. Dark objects are visible for the subject, transparent dots are intermediate positions, and light objects are in the final position

increased delay between hiding and retrieval, more complex motor requirements for retrieval, and generally if the subject is younger. This pattern suggests that the error arises from overburdened executive functions, which develop with age (Cacchione and Rakoczy 2017; Osthaus 2017). Importantly, a subject may accurately appreciate object permanence but still commit the A-not-B error because it fails to attend to the sequence, inhibit previously learned responses, remember the correct location, or perform the required actions. Methodological developments aim to reduce the impact of these confounding factors (see section “[Violation of Expectation Studies](#)”).

### Stage 5: Understanding of Multiple Visible Displacements

Stage 5 also consists of two substages. In Stage 5a, subjects successfully search the correct location in the sequential visible displacement task without making A-not-B errors. In Stage 5b, subjects perform above-chance level in a *multiple (or successive) visible displacement task* (Cacchione and Rakoczy 2017; Doré and Dumas 1987; Ujfalussy et al. 2013). Here, the reward is hidden multiple times in the same trial (Fig. 1c). Typically, the experimenter holds the reward, shows it to the subject, moves it behind occluder A, removes it, and finally places it behind occluder B. The subject should then understand that the reward is no longer at location A but at location B. A common error is searching in the first place of disappearance, resulting in below-chance performance. Animals generally perform worse on multiple compared to single visible displacement tasks (Cacchione and Rakoczy 2017). Subjects have the ability of *simple object permanence* when they passed tasks of both substages.

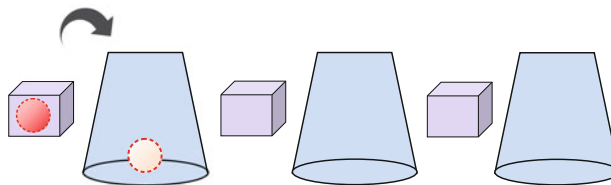
### Stage 6: Understanding of Invisible Displacements

In all earlier stages, the reward is always displaced in sight of the subject. In contrast, Stage 6 is tested by an *invisible displacement*; the reward is occluded during movement, and the subject has to track or infer its location (Doré and Dumas 1987; Piaget 1954; Singer and Henderson 2015; Singer 2018; Ujfalussy et al. 2013). Invisible displacements can be tested with the standard Piagetian task, the transposition task, or the rotation task.

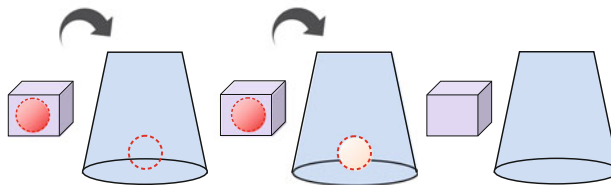
#### Standard Piagetian Task

The standard Piagetian task has been tested most often (Jaakkola 2014). It resembles the visible displacement tasks of Stage 5 except that the reward is hidden during movements and its location has to be inferred. In Stage 6a, the subject is presented with a *single invisible displacement*, in which the reward is moved only once per trial (Fig. 2a). In Stage 6b, the subject can successfully retrieve the reward in a *multiple invisible displacement task* when the reward is invisibly

A) Single invisible displacement (Piagetian)



B) Multiple invisible displacement (Piagetian)



**Object Permanence, Fig. 2 Standard Piagetian invisible displacements.** The two substages in invisible displacement tasks. (a) The object is hidden in the displacement device and then transferred to one occluder. After that, the displacement device is shown to be empty. (b) The object is hidden in the displacement device and

then transferred to one occluder. After that, the object is transferred with the displacement device and shown to the subject after which it is hidden at another occluder. Dark objects are visible for the subject, transparent dots are intermediate positions, and light objects indicate the final position



displaced multiple times during the course of a single trial (Fig. 2b). In general, multiple occluders and an opaque *displacement device* are used. This displacement device holds the reward during movement (Cacchione and Rakoczy 2017; Jaakkola et al. 2010; Piaget 1954; Singer 2018). Often, a small container or the experimenter's hand is used as a displacement device, as both can cover the reward and move it between locations. Tasks for both substages start by the experimenter visibly placing the reward in the opaque displacement device, after which the subject can no longer see the reward. The displacement device is then moved behind or under the first occluder. In tests for Stage 6a, the reward is deposited there, and the subject is shown that the displacement device is now empty. In tests for Stage 6b, the reward is either similarly deposited behind the occluder or kept in the displacement device to be moved to the next occluder(s). The subject is then allowed to search for the reward. By tracking and inferring the position of the reward, the subject should search the occluder after which the displacement device was shown empty and thus where the reward has been left behind. Subjects that passed tasks of both substages are said to have *full object permanence*.

This task has at least five key requirements: (1) understanding that the reward continues to

exist after disappearance (simple object permanence), (2) inferring that the reward moves with the displacement device, (3) inferring that the reward has been left behind after the displacement device is shown to be empty, (4) updating the location of the reward during its movements, and (5) inhibiting prepotent responses (Cacchione and Rakoczy 2017). The third requirement is called reasoning by exclusion, which entails representing multiple alternatives ("A or B") and then ruling out one alternative ("not A"), leading to the conclusion that the remaining alternative must be true ("therefore B"). Many animals that have simple object permanence struggle with such tasks (Klerk and Jacobs 2021). Thus, the standard Piagetian invisible displacement is much more cognitively demanding than a visible displacement (Jaakkola et al. 2010).

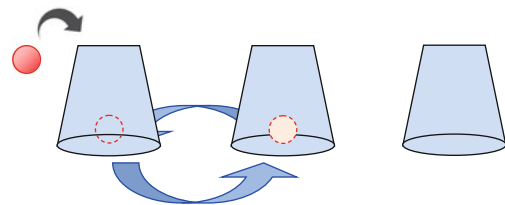
#### Transposition Task

No displacement device is needed in the transposition task. The experimenter visibly hides the reward under an occluder and then moves the occluder(s) around (Fig. 3a). The subject can choose the correct occluder by tracking the invisibly displaced reward. There are four typical sequences in which the occluders are moved, with increasing cognitive demands (Cacchione and Rakoczy 2017; Jaakkola 2014; Majecka and

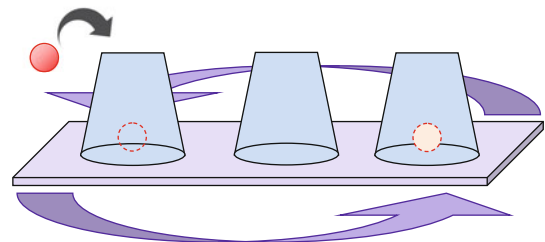
#### Object Permanence,

**Fig. 3 Invisible displacement: transposition and rotation.** The two alternatives to the standard Piagetian invisible displacement task. (a) After hiding the object under an occluder, two occluders switch positions. (b) After hiding the object under an occluder, the whole tray is rotated (180°). Dark objects are visible for the subject, transparent dots are intermediate positions, and light objects are in the final position

#### A) Single invisible displacement (Transposition, switch)



#### B) Single invisible displacement (180° Rotation)



Pietraszewski 2018; Singer 2018). The first is a *simple lateral* movement, where the occluders move laterally to a new location and the original location of the baited occluder remains empty (Fig. 4a). The second is a *lateral substitution*, where the occluders also move laterally and an empty occluder takes the original position of the baited occluder (Fig. 4b). The third is a *simple cross*, where the occluders cross during their movements and the original location of the baited occluder remains empty (Fig. 4c). The fourth movement is a *switch* or *shell game*, where the occluders also cross during their movements but an empty occluder is moved to the original location of the baited occluder (Fig. 4d).

### Rotation Task

All variations of the rotation task involve multiple occluders that are closed on all sides (e.g., cups or boxes) and do not use a displacement device. The

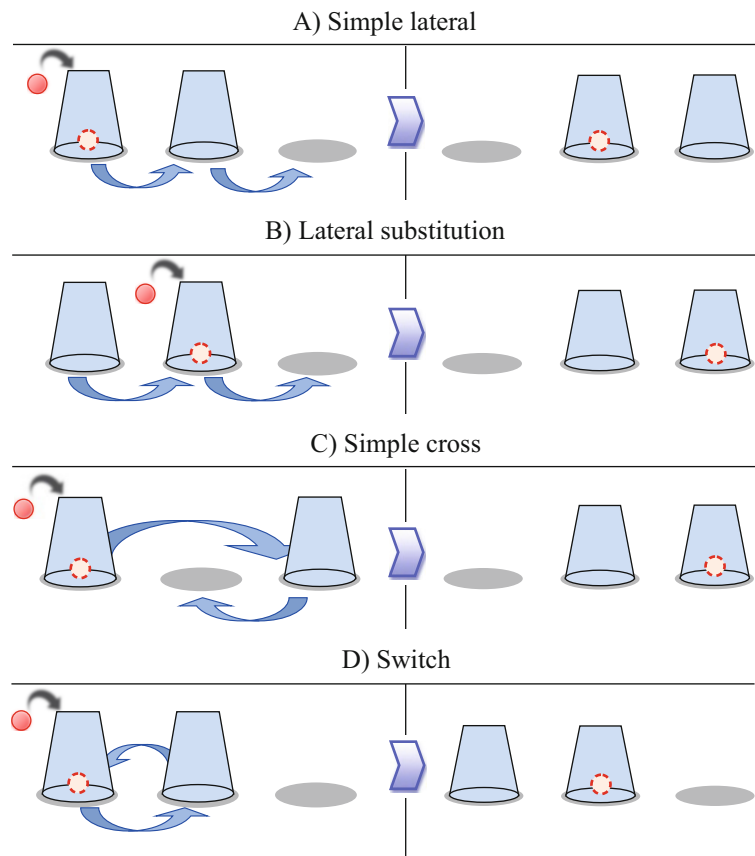
occluders are placed on a flat platform that can easily be rotated. One occluder is visibly baited with the reward. Instead of moving the occluders individually as in transposition tasks, the whole platform is turned (Fig. 3b). After it has been turned, the subject is allowed to search the occluders for the reward. The most common rotations are 90°, 180°, and 360°. Animals generally perform better after a 90° rotation, where both occluders move to new positions, than a 180° rotation, where the occluders switch positions (Jaakkola 2014; Singer 2018). However, a methodical disadvantage of the 90° rotation task is that one of the occluders is behind another and is therefore less visible and accessible (Jaakkola 2014).

### Task Comparisons

These different methods of invisible displacement appear to have different demands. The standard

### Object Permanence,

**Fig. 4 The four types of transpositions.** The initial setup with movements is presented in the left column, and the final situation is shown in the right column. (a) Simple lateral transposition, where the cups do not cross and the originally baited position remains empty. (b) Lateral substitution, where the cups do not cross and the originally baited position is taken by an empty cup. (c) Simple cross, where the cups cross each other and the originally baited location remains empty. (d) Switch, where the cups cross each other and the originally baited location is taken by an empty cup



Piagetian task is challenging as it involves complex nested movements with invisible transfer of the reward, and it requires inference that the reward was removed after observing the empty displacement device. Transposition and rotation tasks do not have this nested invisible transfer, but they involve more moving occluders. The sequential movements of transposition tasks may be easier to attend to than the simultaneous movements of rotations (Cacchione and Rakoczy 2017; Jaakkola 2014). Thus, the tasks differ along multiple dimensions that may have divergent effects on different species. Moreover, each task may be passed by using different cues and heuristics, which are discussed further below (see section “[Methodical Issues and Improvements](#)”). Children – but not great apes – perform better in the standard Piagetian task than the switch version of the transposition task. The 180° rotation task was found to be most difficult by both apes and children (Barth and Call 2006; Jaakkola 2014). Species comparisons on transposition tasks show that apes perform better than monkeys, which in turn outperform dogs, and that cross and switch conditions are overall most challenging (Majecka and Pietraszewski 2018).

## Development of Object Permanence

Piaget formulated the stages of object permanence as a developmental sequence in children. Uzgiris and Hunt (1975) further developed these methods with a clearer scoring system and split the different stages in 15 tasks. Each subject was repeatedly tested on a task and proceeded to the next task when successful in the majority of trials. As a result, these tasks were ordered by cognitive demands based on performance (Jaakkola 2014; Uzgiris and Hunt 1975).

Animals have been tested in similar developmental studies (Doré and Dumas 1987; Pepperberg et al. 1997). The focus lies less on when a species passes a certain stage, which is not a particularly meaningful measure, and more on whether a certain stage is passed and in what order (Pepperberg 2002). Knowing the “final stage” of multiple species can be used to

determine coupled abilities, ecological relevance, and evolutionary history. Studies have been done on many mammal and bird species (Barth and Call 2006; Collier-Baker et al. 2004; De Blois et al. 1998; Lambert et al. 2019; Pepperberg et al. 1997; Ujfalussy et al. 2013; Zucca et al. 2007). In general, adult great apes, parrots and corvids reach Stage 6 and perform better than their close relatives. Object permanence develops in a similar sequence across species, except that some species do not reach later stages and precocial species start life in a stage later than the first. Its developmental speed generally reflects the life history of the species, with faster developing species also reaching the final stage faster (Doré and Dumas 1987; Jaakkola 2014; Lambert et al. 2019; Pepperberg 2002).

Most studies focus on the visible and invisible displacement tasks and do not test the entire range of Uzgiris and Hunt’s or Piaget’s tasks (Cacchione and Rakoczy 2017). Thus, studies often neglect earlier stages, which complicates inferring the animals’ motivation and ability to track and retrieve objects. An animal with full object permanence may seem to lack this ability when not showing sufficient attention and motivation during testing. Similarly, inability to retrieve objects and remove occluders in experimental conditions may give the false impression that object permanence is lacking (see section “[Violation of Expectation Studies](#)”). Thus, these aspects should be addressed to avoid false negatives – especially for younger animals in developmental studies. Future studies should therefore test visual tracking for monitoring attention and use transparent occluders to document motivation and ability to retrieve the reward when it remains visible.

## Adaptive Significance

Although much research has focused on the maximal stage a species can reach, only little attention has gone to the potential adaptive significance of reaching a certain stage. Achieving the first stages, and doing so at an early age, is certainly crucial for various survival skills of visual animals. The later ability to represent temporarily

unperceivable agents and objects also has clear benefits in many situations, such as foraging, predator avoidance, and social behavior. An animal sticking its head in the sand to evade predators like the proverbial ostrich would not be long for this world. Nonetheless, empirical studies on the adaptive significance of object permanence are scarce, and explanations for its phylogenetic spread are speculative. Visible and invisible displacement have been discussed most in this context.

### Visible Displacement

Understanding visible displacements is an ability reached by species of many taxa, such as great apes, monkeys, dogs, cats, parrots, pigeons, chickens, corvids, and fish (e.g., Cacchione and Rakoczy 2017; Collier-Baker et al. 2006; Fiset and LeBlanc 2007; Jaakkola et al. 2010; Jaakkola 2014; Majecka and Pietraszewski 2018; Singer and Henderson 2015; Sovrano et al. 2018; Ujfalussy et al. 2013; Zucca et al. 2007). Simple object permanence thus seems common – if not universal – across mammals and birds, and a wider phylogenetic spread would not be surprising given its benefits. Moving prey visibly displaces themselves to an observing predator, which will hunt more efficiently when attending to this movement and correctly locating the prey in the new hidden location, such as behind a tree or in a burrow (e.g., Osthaus 2017; Sovrano et al. 2018). Similarly, prey species can evade predators better by continuously updating their location and movement. Representing visible displacements also has benefits for social animals, such as when avoiding competition or keeping track of offspring without the requirement for constant perceptual feedback (Jaakkola 2014). Memory is crucial in all these situations and is clearly a limiting factor in visible displacement tasks that impose time delays (Cacchione and Rakoczy 2017; Many Primates et al. 2019).

Caching birds store, remember and retrieve many hidden food items to survive food-scarce periods. Hypotheses on species differences in object permanence abilities often invoke caching propensity, but the results are mixed (e.g., Ujfalussy et al. 2013; Zucca et al. 2007), which

suggests that a different factor primarily drove the evolution of representing hidden objects. Animals may rely on various cues and heuristics that do not involve advanced levels of object permanence, as outlined in the next section. A possible explanation for species reaching later stages is that they may experience objects and agents disappearing in a large variety of contexts that warrants more flexible responses; a stereotypic or learned response might not suffice. Future studies should test such ecological and evolutionary hypotheses in more detail.

### Invisible Displacement

Understanding an invisible displacement means tracking the movements of an object even when it is not directly perceivable (Cacchione and Rakoczy 2017; Piaget 1954; Singer 2018). Its occurrence and significance in nature may be rare because target objects are not often concealed by a moving “occluder.” A baby marsupial in the mother’s pouch is one example. Prey species often move when not perceivable by a predator, but this does not constitute invisible displacement as defined in the literature. For instance, a vole escaping through a burrow is not invisibly displaced in this sense because the “occluder” (i.e., the burrow) does not move. Instead of invisible displacement, a predator could use *trajectory extrapolation* to predict where the vole might end up (Jaakkola 2014; Johnson et al. 2015). Under most circumstances, the most adaptive response to something disappearing out of view may be searching where it was last seen, which would be a failure in most invisible displacement tests. The adaptive significance of invisible displacement is more often viewed as arising from broader representation or abstraction abilities than as an isolated skill (e.g., Collier-Baker et al. 2006; Suddendorf and Whiten 2001).

Mental *secondary representation* of an object is required to understand it continues to exist and can move when not perceivable (e.g., Fiset and LeBlanc 2007; Suddendorf and Whiten 2001). For example, a subject needs to appreciate the continued existence of the reward in the displacement device and that it moves with it in the standard Piagetian task. It also needs to understand

that the reward can stay in the displacement device or move out of the device and stay behind the occluder (Cacchione and Rakoczy 2017). These are two hypothetical models that the subject needs to bear in mind and then infer which model is correct. Thus, this secondary representation adds the ability to mentally create hypothetical models, to conserve those multiple models, and to adjust them through deduction (Collier-Baker et al. 2006; Suddendorf and Whiten 2001). Secondary representation is defined as the capacity to consider multiple models of the world rather than relying only on immediate perception to guide behavior. It is a cognitively complex ability that only a few species have reached in Stage 6 object permanence tasks (e.g., Collier-Baker et al. 2006; Jaakkola et al. 2010; Jaakkola 2014; Singer and Henderson 2015; Zucca et al. 2007).

Many cognitive skills of humans have been linked to secondary representation, and it is therefore no surprise that they emergence at the same time during development (Cacchione and Rakoczy 2017; Suddendorf and Whiten 2001). Full object permanence develops in children around the age when they also develop mirror self-recognition, means-end reasoning, imitation, symbolic thought, and language (Collier-Baker et al. 2006; Jaakkola et al. 2010; Suddendorf and Whiten 2001). Most of these cognitive skills are also found to some extent in great apes and corvids, which is similar to the spread of full object permanence (Collier-Baker et al. 2004; Lambert et al. 2019; Suddendorf and Whiten 2001). Each skill is beneficial in a different way, but all fit under this wider representational umbrella. Although the adaptive significance of understanding invisible displacement is not well studied – and could be marginal due to such contexts being rare in nature – this perspective may better explain its evolution. However, it is also possible that these skills are a by-product of another cognitive skill that has not yet been recognized as such (Ujfalussy et al. 2013) or that successful test performance arises from cognitive “shortcuts” such as using cues and heuristics (see below). The methodology of object permanence tasks has therefore been regularly scrutinized.

## Methodical Issues and Improvements

Piaget created a useful framework to test object permanence in many species. Although it is still used, it is also frequently criticized. Critics mainly call for conceptual clarification and reduction of alternative explanations through control experiments and analysis of multiple variables (e.g., Cacchione and Rakoczy 2017; Jaakkola 2014). Without control conditions, the cognitive abilities of successful subjects may be overestimated (false positives); there are numerous reasons why a subject performs well on a task, with representation of object permanence being one of many. The risk for false negatives should also be considered; animals with the ability in question may still perform poorly when the testing procedure is unsuitable or unnecessarily complex (e.g., Cacchione and Rakoczy 2017; Pepperberg 2002). As in all experimental paradigms, these risks need to be understood and balanced. The four main critiques are nonvisual perception, social cues, associative learning, and sensorimotor incompetence.

### Nonvisual Perception

Humans are primarily visual creatures, so when we think of objects not being perceivable during tests, we intuitively think of them as being out of view sight. Although some cues are necessary for the subject to base the search on (e.g., perceiving the hiding process), other unintentional cues can still help subjects with perceiving hidden objects, which is a risk of any testing condition – especially when species are involved that have excellent nonvisual senses. These animals may appear to have outstanding object permanence abilities when they in fact perceive the hidden object in ways that experimenters failed to take into account.

### Olfactory and Auditory Cues

Sound and odor are probably the most influential nonvisual cues in comparative research. Preventing these cues can be done in three main ways. First, study designs can aim to *minimize the presence of a cue*. For example, occluders can be made airtight or soundproof. The subject



can also be separated from the experimental setup by a transparent wall that blocks these cues. Second, researchers can *oversaturate the setup with a cue*. In many studies, the scent of the reward is spread around all materials and will thereby mask the scent of the goal reward during testing (e.g., Zucca et al. 2007). Similarly, use of auditory cues can be minimized by playing ambient sounds during testing. Experimenters can also perform the same manipulations at each occluder, which should produce the same sounds in each case. Third, studies can actively *test for the influence of a cue*. This is typically done by secretly changing the location of the reward or by hiding it out of view of the subject. Thus, the subject cannot deduce the correct location with object permanence. Successful above-chance performance over repeated trials then suggests the subject located the reward through a nonvisual cue (e.g., Uzgiris and Hunt 1975; Zucca et al. 2007). These three methods of controlling for nonvisual cues can be used separately or combined (Collier-Baker et al. 2004).

#### Potential Influence of Other Senses

Smell and hearing are probably the most important senses to consider in a task design for object permanence. However, many animals have senses that humans do not possess or have a wider range and higher sensitivity of senses shared with humans (Keeley 2015). For example, some sharks and migratory birds can perceive magnetic fields, which makes it inappropriate to use magnets to hold and move objects and occluders (Jaakkola 2014). Echolocation is another sense that can distort results on object permanence tests (e.g., Keeley 2015; Singer and Henderson 2015). To minimize the use of echolocation, the test can be conducted in a different medium. For instance, testing materials were placed on land for cetaceans, so they could not use echolocation to find the hidden items (Jaakkola et al. 2010; Singer and Henderson 2015). Other potentially influencing senses are the ability of “remote touch” (where species use their specialized beaks to sense vibrations of nearby moving prey), detecting thermal infrared waves of objects, or sensing electric signals from the nerves of prey animals (Keeley

2015). The potential problem of these senses is species-specific, so it is important that experimenters are familiar with the sensory abilities of their study species. The kind of senses that representations are built on is another important line of enquiry: true object permanence means representing objects as permanent multimodal entities, but the question of whether animals recognize object cross-modally has received little attention.

#### Social Cues

Animals may also perform well on object permanence tasks by using social cues that are (unintentionally) produced by the experimenter. These cues are mainly found in gaze direction and body posture (Jaakkola 2014; Pepperberg 2002). Conspecifics may also provide inadvertent cues that reveal the location of a reward, so subjects should be tested in individual settings where possible. Controlling for social cues produced by humans and conspecifics is an important method to reduce the likelihood of false positives.

Four main methods are applied to prevent social cueing (Jaakkola 2014): shielding gaze direction, averting gaze, shielding body posture, and using multiple experimenters. First, experimenters can ensure that subjects cannot see their gaze by shielding their eyes. For example, the experimenter can wear mirrored sunglasses (Pepperberg et al. 1997) or a welding mask (Collier-Baker et al. 2006). This is also necessary for other people present, such as pet owners, who can be blindfolded (Collier-Baker et al. 2004). However, welding masks and mirrored sunglasses can distract or scare animals, which should therefore be well habituated to the shielding method. Some animals learn to find hidden food through reflections and mirror images, which needs to be avoided in this context. Furthermore, only humans appear to treat (human) gaze alone as a salient cue. Great apes tend to react more to head direction, whereas human infants focus mostly on gaze direction (Tomasello et al. 2007). Covering the experimenter’s eyes will remove only gaze direction but not head direction as a cue. Thus, while most studies cover the experimenter’s eyes to prevent gaze cues (Jaakkola 2014), this might

not be sufficient as subjects may use head direction as a cue instead. A second control method is to have the experimenter look away from the setup (e.g., Zucca et al. 2007). Averting gaze can help against social cueing for both eye and head directions, although unintentional glances might occur as the experimenter needs to monitor and control the test. Furthermore, body posture can still give cues to the subject with both methods.

Third, the body of the experimenter can be shielded with a screen or curtain to avoid cuing with body posture (e.g., Collier-Baker et al. 2004; Fiset and LeBlanc 2007). Although this method reduces many social cues, it may also distract subjects when they are not familiar with partially occluded humans. A decrease in attention to important events during the experiment brings about a higher risk of a false-negative result. Moreover, the position of the experimenter can still be used as a cue. A fourth method is to use a *conductor-asker* setup (Jaakkola 2014). The conductor performs the experiment as usual but then leaves the room. The asker then enters the room and prompts the subject to make a choice. This asker does not know where the reward was hidden and thus cannot provide cues – not even cues that do not involve gaze or body posture. Although this setup makes sure that social cueing does not happen, it also complicates the task. It might be hard to teach the subject the procedure and to have it understand when it is “asked” to select or search. The switch of researcher may also be confusing or distracting. Moreover, there is a longer waiting period before a selection can be made, which may decrease performance and requires more inhibitory control (Cacchione and Rakoczy 2017; Osthaus 2017). Experiments that do not involve humans or rely less on demonstrations by an experimenter carry a lower risk for social cuing (see section “[Violation of Expectation Studies](#)”).

### Associative Learning and Strategies

Animals can learn to choose the correct occluder without representing the location of the hidden object (Cacchione and Rakoczy 2017; Collier-Baker et al. 2004; Jaakkola 2014; Singer and Henderson 2015). They will appear to possess

object permanence but in fact merely act on learned associations, rules, biases, or heuristics. The ability to solve a task through these strategies risks a higher chance of false positives and should therefore be taken into consideration.

When representing object permanence, the subject is expected to solve each task rapidly with only a few trials to adjust to the setting. More trials will create a greater likelihood that subjects can learn an associative rule, which is a weakness of the Uzgiris and Hunt scales (Cacchione and Rakoczy 2017; Doré and Dumas 1987). Therefore, most studies use a minimal number of trials and look for learning effects, such as a positive correlation between trial number and performance (Doré and Dumas 1987; Jaakkola 2014). Learning may also explain better performance in conditions or stages that are tested later in a test sequence. This effect can be investigated by counterbalancing testing order across subjects. If they all perform better in later tasks, regardless of condition, a learning effect is apparent. Another suggested improvement to reduce associative learning is to never show the correct location of the reward after the subject has chosen the wrong occluder (e.g., Zucca et al. 2007). The advantage of this is that associative learning will become harder and there is a lower risk of carryover effects between trials (e.g., selecting the occluder that was correct in the previous trial). However, this method may also reduce motivation. A stronger case for object permanence can be made when success is maintained across context, with different materials, rewards, experimenters, positioning, and conditions. Next to these general suggestions, many studies have also aimed to directly control for known associative rules.

### Select the Occluder Manipulated by the Experimenter or Visited by the Displacement Device

Typical tests of object permanence are done by placing a reward in, under, or behind an occluder. Thus, only one occluder is manipulated by the experimenter or visited by the displacement device. In this context, a subject can be highly

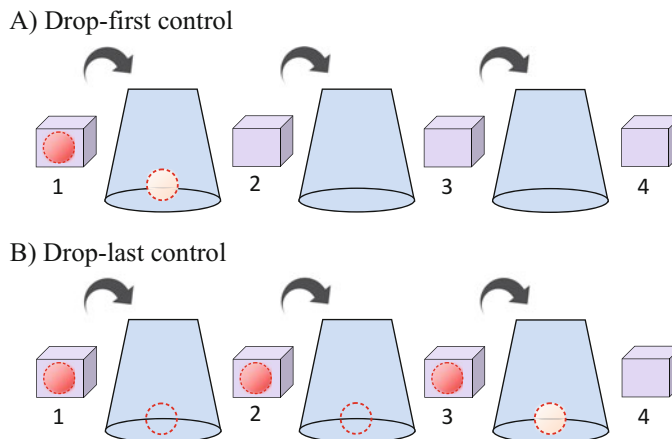
successful by always selecting the occluder that was manipulated last by the experimenter or visited by the displacement device (Doré and Dumas 1987). This can be avoided by manipulating all occluders and by letting the displacement device visit all occluders, preferably in a random order (Jaakkola 2014; Zucca et al. 2007). It is important that the experimenter performs a sham manipulation or transfer with every occluder, where similar actions to a normal manipulation or transfer are done, without actually transferring the reward. The saliency of the manipulation may also play a role. For instance, hiding a reward behind a stationary barrier or screen is likely a less salient cue than lifting an inverted cup, placing the reward, and then placing the cup over it. Placing two occluders simultaneously, with one thereby covering the previously visible stationary reward, is another approach. Nonetheless, subjects may still succeed by using associations or learned rules such as always searching in the general area where the reward was last seen, which would be an adaptive response under many natural circumstances. Similar to other methodological issues, eliminating potential cues is difficult – if not impossible – but they can be reduced.

#### Select the Occluder Last Visited by the Displacement Device

Using the order of events or manipulations can be another successful approach. Always selecting the occluder last visited will result in perfect performance when there are no movements after hiding the reward (Collier-Baker et al. 2004; Jaakkola 2014; Zucca et al. 2007). This can be countered with a *drop-first control* (Fig. 5a). For this control, the experimenter moves the baited displacement device behind an occluder, transfers the target reward behind the occluder, and shows the empty displacement device to the subject. The displacement device then continues to the next occluder where a sham transfer is performed, after which the subject is again presented with an empty displacement device. This sequence is repeated until all occluders have been visited by the displacement device (Collier-Baker et al. 2004; Jaakkola 2014; Zucca et al. 2007). A subject using the “select the last occluder visited” rule will never choose the correct location first.

#### Select the First Occluder Visited by the Displacement Device

Another frequently successful strategy is to choose the occluder first visited by the



**Object Permanence, Fig. 5 The drop-first and drop-last controls.** (a) The object is hidden in the displacement device and then transferred to one occluder. Then, the displacement device is shown to be empty, and it continues to the next occluder(s). (b) The object is hidden in the displacement device and then transferred to one occluder.

This sequence is repeated for each occluder, and the reward is deposited behind the last occluder, after which the displacement device is shown to be empty. Dark objects are visible for the subject, transparent dots are intermediate positions, and light objects are in the final position

displacement device. In the *drop-last control* (Fig. 5b), the experimenter moves the baited displacement device behind an occluder, then performs a “sham transfer,” and reveals the displacement device to be baited. This sequence is repeated at every location until the last occluder, where the reward is transferred behind the occluder. Following the *first-visited rule* will no longer be viable in this control. However, this control method is underrepresented in most studies, which weakens interpretations of full object permanence in invisible displacement tasks (Jaakkola 2014). Gaining more solid evidence is possible by testing an intermixed series of drop-first, drop-last, and maybe even drop-middle controls (Collier-Baker et al. 2004, 2006).

#### Select the Occluder Adjacent to the Displacement Device

Subjects that fail more complex object permanence tasks often attend closely to the location of the displacement device at the end of a trial (Cacchione and Rakoczy 2017; Collier-Baker et al. 2004). They tend to search the occluder adjacent to the displacement device first. These animals appear to link the displacement device to the reward and then search in its vicinity, using the position of the displacement device as a landmark that indicates the baited location (Fiset and LeBlanc 2007). The displacement device should be removed to reduce use of such spatial cues. Although results do not show consistent effects, chances of another possible associative strategy are reduced by removal of the displacement device before a choice can be made (Collier-Baker et al. 2004; Jaakkola et al. 2010).

These are some of the most common controls for associative learning, and more are possible. However, it should be noted that such tasks can become too complicated to solve and that subjects may not be attentive or motivated enough to participate in all conditions. Studies should be adjusted to the species, and a mindful balance between avoiding false positives and false negatives can be achieved by considering the effects of these confounding factors.

#### Sensorimotor Incompetence

The Piagetian tasks were originally designed for human children and proved a great inspiration for studies on other species. However, the difference between species in sensorimotor competences should not be neglected (Cacchione and Rakoczy 2017). These object permanence tasks are suitable only for visual species, even though understanding that objects endure is beneficial to less visually adept species, and tasks can be redesigned to suit them. These tasks also require animals to select an occluder or remove it. Selection by human infants is traditionally shown by uncovering an occluder with their hands (Piaget 1954). However, uncovering occluders is not always easy for animals that are less anatomically suited for such behaviors (e.g., Fiset and LeBlanc 2007). Therefore, the sensorimotor capacities of a species should be a key factor in study design. Selecting an occluder is generally easier than removing it. Each subject can first be trained to touch an occluder and receive the hidden reward before formal testing begins.

Although many researchers take the species-specific differences in physical competence into account, it is often overlooked how this competence differs within species, especially during development (Baillargeon 1987; Cacchione and Rakoczy 2017; Pepperberg 2002). These animals may fail on an object permanence task because they cannot remove or select their choice, but that does not mean they consider the hidden object to have vanished. Some studies have tried to minimize the demands on physical competence with a new group of methods: violation of expectation.

#### Violation of Expectation Studies

Contemporary theories of object cognition build on the Piagetian tradition but differ in substantial aspects. Core knowledge theorists postulate that cognition consists of several domain-specific core systems that represent fundamental aspects of the environment, such as objects, geometry, numbers, and agency. Much like adults, human infants represent objects as entities that are cohesive (enduring as discrete units), bounded (having a

boundary that cannot be occupied by other objects), spatiotemporally continuous (persisting over time and space), and material (consisting of matter with mass). Each aspect of core object cognition – particularly spatiotemporal continuity – corresponds to some degree with Piagetian object permanence. Thus, developmental research often specifies what aspect is under investigation, rather than using the less specific term “object permanence.” Compared to the Piagetian framework, examining core knowledge is not as dependent on sensorimotor interactions and search behavior and therefore employs less action-based measures – such as looking time – that have lower motoric and executive demands (Baillargeon 1987; Cacchione and Rakoczy 2017).

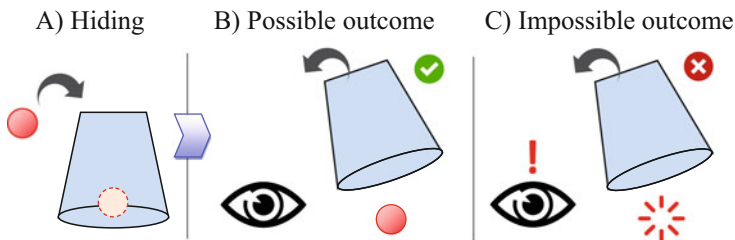
Violation of expectation (VoE) studies compare how long subjects look at possible and impossible outcomes of an event. The possible outcome follows the expected persistence of objects across space and time. The impossible outcome does not follow these principles and is orchestrated through various secret manipulations. Subjects are expected to look longer when “tricked” by the impossible outcome, compared to the possible outcome that closely resembles the impossible one (Baillargeon 1987; Müller et al. 2011). The rationale behind this method is that a subject will react similarly and look equally long to the possible and impossible outcomes when it does not have object permanence.

Developmental psychologists first designed VoE methods to study infants younger than the age at which they actively make choices in traditional Piagetian tasks. This benefit extends to

animals, especially when they are similarly early in development or when the species is not suited for choice tasks. Although this procedure is less common than the standard Piagetian tasks, it holds many advantages, such as lower sensorimotor demands and reduction of social cues, non-visual perception, and strategy use. Learning still occurs but forms an important component because subjects are expected to initially show great interest in the impossible outcome, which will diminish with increasing exposure (Baillargeon 1987; Cacchione and Rakoczy 2017). These benefits are especially welcome when studying infant animals; they merely need to attend to the event, which is possible after reaching Piagetian Stage 2. The VoE method is mainly applied in three components of object knowledge: continuity, constancy, and solidity.

### Violation of Object Continuity

Object continuity is the principle that an object continues to exist independently of perception. This principle is under investigation in most traditional tests of object permanence. In VoE studies, a standard displacement task is performed, but the reward is secretly removed or moved to another occluder. A subject with sufficient understanding of object continuity will expect the reward to be behind the original occluder (Fig. 6b). When the experimenter uncovers the empty occluder in the impossible event (Fig. 6c), the subject may be “surprised,” as revealed by longer looking times and other key behaviors such as strong arousal. In other words, its expectation was violated.



**Object Permanence, Fig. 6 Violation of object continuity.** (a) The target object (red circle) is hidden behind an occluder. The subject then watches either (b) a possible outcome, where the target object appears again, or (c) an

impossible outcome, where the target object has seemingly disappeared. This method can further be combined with manipulations from traditional tests, such as visible and invisible displacement



Although this paradigm comes closest to the standard Piagetian tasks, it has rarely been studied directly. Most comparative studies have used it as a control for nonvisual cueing, but few studies report the difference in reaction or looking times of the subjects between the possible and impossible outcomes (but see Zucca et al. 2007). Importantly, looking time is also used as a measure of expectation before the outcome occurs, which may or may not violate expectations. Here, the subject's predictions are revealed by where they look. For instance, this method has shown that bottlenose dolphins appear to predict the trajectory of occluded moving objects and the correct location of invisibly displaced objects (Johnson et al. 2015).

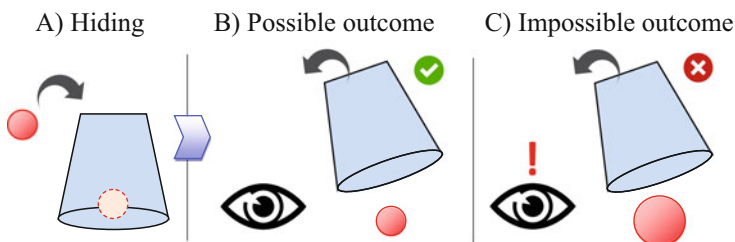
### Violation of Object Constancy and Identity

Object constancy is the principle that the features of an object remain constant independently of perception; they do not change their appearance or turn into other objects (i.e., change identity). Typical object permanence tasks ask the subject to choose the correct location of an object, not its correct identity. Nonetheless, a subject that appreciates object permanence should also encode its features and should therefore not expect these features to change when temporarily out of view. This principle is often tested with size constancy, where the size of the target object either remains the same size (possible outcome; Fig. 7b) or is secretly changed (impossible outcome; Fig. 7c). For instance, female dogs looked significantly longer when the size of a ball changed after disappearing compared to it remaining the same, which suggests they relied on size constancy (Müller et al. 2011).

Recognizing the constancy of object identity is tested in a similar matter, except that the object is substituted with a different kind. Rhesus macaques and African gray parrots act surprised and often angry when finding food type A in a location where food type B was hidden and often reject A even though they would eat it immediately under normal circumstances (Pepperberg et al. 1997; Tinklepaugh 1928). Thus, they appear to represent the specific identity of the occluded object and express surprise when its constancy is violated.

### Violation of Object Solidity

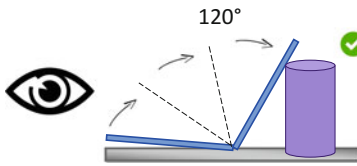
Object solidity is the principle that multiple solid objects cannot occupy the same space at the same time. This principle naturally also applies when not directly perceived, such as an out-of-view object colliding with a visible object. Failure to represent this principle may arise from a deficient concept of object permanence in which objects can suddenly disappear or come into existence. The *drawbridge paradigm* is commonly used in this context (Baillargeon 1987; Singer and Henderson 2015). Here, subjects are shown a flat screen that can rotate 180°, from horizontally flat, to vertically upright, to horizontally flat again (Fig. 8). An object is placed behind the screen in such a way that when the screen is rotated 90° (vertically upright), the object is no longer visible for the subject. If the subject understands object permanence, it should know that the object is still present and that when the screen will be rotated further, it should hit the object and thus will not be able to rotate any further (Fig. 8a). In the impossible outcome, the object is secretly removed, and



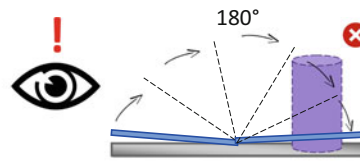
**Object Permanence, Fig. 7 Violation of object constancy.** (a) The target object (red circle) is hidden behind an occluder. The subject then watches either (b) a possible

outcome, where the target object appears again, or (c) an impossible outcome, where the target object has seemingly changed in size

A) Possible outcome



B) Impossible outcome



**Object Permanence, Fig. 8 Violation of object solidity (drawbridge paradigm).** The screen (blue) rotates away from the subject (looking from the left) toward the object (purple). (a) The  $120^\circ$  rotation is the possible outcome, as

the screen stops at the object. (b) The  $180^\circ$  rotation is the impossible outcome as the screen would have to move through the object (which had been secretly removed). (Adapted from Baillargeon 1987)

the screen fully rotates (Baillargeon 1987; Singer and Henderson 2015). The principle of object solidity prohibits such movements, which should surprise subjects that represent this principle when observing this seemingly impossible outcome (Fig. 8b). Surprise is again measured by increased looking time compared to the possible outcome. For instance, California sea lions and bottlenose dolphins look longer at the impossible event, just like human children, which suggests they have a concept of object solidity (Singer and Henderson 2015). Action-based versions involve a reward that is hidden out of view under one of two rigid boards. Reasoning about object solidity should lead a subject to choose the inclined board because the solidity of both the reward and board causes the inclination, and the reward cannot occupy the same space under a flat board. Some species have passed this test, but care should be taken to control for alternative explanations (Cacchione and Rakoczy 2017) and additional cognitive requirements, such as reasoning by exclusion (Klerk and Jacobs 2021).

Overall, these three VoE paradigms can test for different principles of object permanence (continuity, consistency, and solidity). They have been used to great success for investigating the object cognition of young infants and are promising yet underutilized tools in animal cognition.

## Conclusion

Object permanence is a cognitive skill that has been extensively investigated in humans and

other animals. The study of object permanence in animals builds on the foundational work of Piaget, who formulated a stepwise progression in the first years of a child's development. Although cognitive development is not frequently studied in animals, the six-stage Piagetian framework proved useful in documenting and comparing the highest stage that various species reach as adults. Through this comparison, we gain insight into the adaptive benefits of object permanence and its evolutionary history. However, the reliability of many results is heavily debated, which obscures the comparative power of this paradigm despite its widespread use. Therefore, conceptual clarifications are formulated, and methodological improvements are tested, with the resulting recommendations largely deviating from the Piagetian framework. Crucially, these changes in methodology should suit the species under investigation and aim to limit the effects of confounding factors and alternative explanations; the risks of false positives and false negatives form a trade-off that needs to be carefully navigated. Thus, the unique position of object permanence as a key cognitive ability has – with further conceptual and methodological development – a promising future after its long history.

## Cross-References

- ▶ [A-Not-B Problem](#)
- ▶ [Associative Learning](#)
- ▶ [Executive Function](#)
- ▶ [Invisible Displacement](#)
- ▶ [Modality](#)

- Reasoning by Exclusion
- Short-Term Memory
- Social Learning
- Visible Displacement

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## Object Recognition

### ► Cognition

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## Object Substitution

### ► Pretend Play

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## Object-Assisted Problem-Solving

### ► Tool Use

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## Object-Choice Task

### ► Object-Choice Test

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## Object-Choice Test

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### Synonyms

#### Object-choice task

The object-choice test (OCT) refers to a family of procedures used to examine nonhuman perceptual and cognitive abilities, in which animals are presented with objects from among which they select one. Correct choices are typically followed by food reward, and in order to make a correct

choice, the animal might be required to discriminate among different colors, remember which object contains hidden food, or properly respond to a communicative signal.

Early studies using the OCT (for review, see Tinklepaugh 1928; Yerkes and Yerkes 1929) examined whether monkeys (*Macaca mulatta*) or children could select the rewarding object based on its position among similar objects. Other studies with raccoons (*Procyon lotor*), for example, presented six differently colored cans to see if the animals distinguished colors; only one color was rewarded, and the animals were given repeated exposure to the variably arranged cans to see whether they could learn to select a particular color. Such OCTs transformed in diverse ways, remaining useful for psychological tests with animals. For example, after a gorilla (*Gorilla beringei*) and chimpanzees (*Pan troglodytes*) observed food being placed in one of four boxes, they selected the correct box after delays of up to 3 h (and could also remember where food was buried when tested 48 h later).

Further memory tests examined the influence of the number of containers from which the animal had to select, indicating that memory diminished as the number of containers increased; some animals (raccoons; dogs, *Canis familiaris*; primates) were able to accurately select the correct container after delay even though they did not maintain perceptual directedness toward that container, although primates showed the longest memories (see Tinklepaugh 1928). Tinklepaugh examined not only how long primates could delay before selecting the correct container but also the positioning of the containers (e.g., one in front of the other, rather than equidistant) and whether primates would be surprised when, upon selecting the correct container, they discovered a food item of lesser value (lettuce) than the one they had seen being baited under that container (banana); they were. Recent variants of these original OCTs include one study in which a bottlenose dolphin (*Tursiops truncatus*) was presented with (usually) 2–3 items associated with 0–6 fish that were presented sequentially after the dolphin selected an item. The dolphin accurately distinguished all possible pairings except that indicating 5 and

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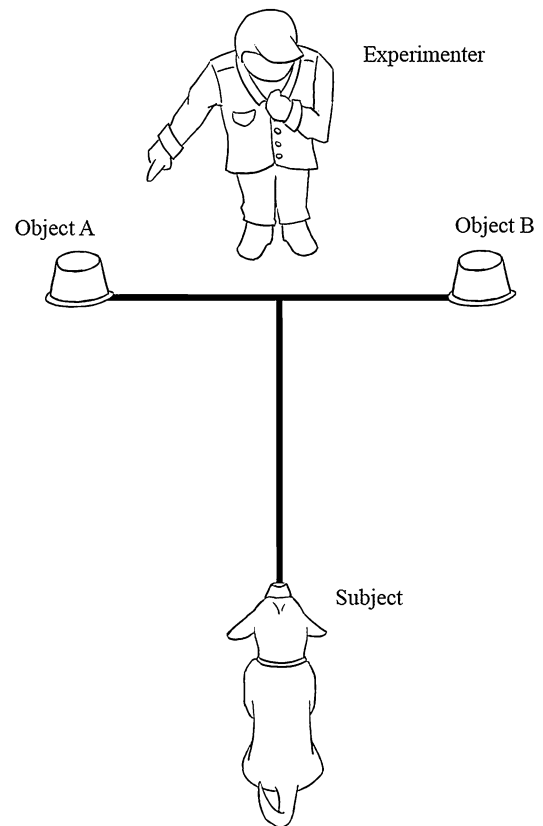
Mark A. Krause and Robert W. Mitchell contributed equally to this work.

6 fish (Mitchell et al. 1985). Another variant found in studies of numerical competence in chimpanzees required the animals to select a container holding a number of items matching the number of stimuli in a previously presented container, or corresponding to an Arabic numeral (see review in Boysen and Hallberg 2000).

OCTs became standardized for use with primates in the Wisconsin General Test Apparatus (WGTA; Harlow 1949). The WGTA separated animals from objects by a screen and required them to reach through the screen to touch an object. Harlow and others used the WGTA to assess the development of learning sets in diverse primate species. Tests included selecting, from among two or more items, the previously rewarded item or the right- or leftmost item, alternately selecting the left then right then left (etc.) item, selecting the previously unrewarded item on the second trial or later sessions (reversal learning), selecting the object that matched a previously observed object, and selecting the odd item from among three items (odddity learning). In some tests, the objects used were food items themselves, evaluating primates' skill at distinguishing the relative number or size (Menzel and Draper 1965). Menzel and Draper (1965) also manipulated whether both food items were visible or one known food item was hidden and the other visible, the latter resulting in only slightly diminished performance compared to the former. The WGTA was later modified for use with nonprimates. The OCT has been used to test hypotheses about the evolution of cognitive abilities (e.g., Harlow's theories about the evolution of learning sets) and, more recently, the evolution of sociocognitive abilities. Work on canids has employed the OCT to test for the roles of domestication and rearing history on the social behavior of dogs.

OCTs have examined animals' comprehension of human communicative cues and animals' behavior to influence human selections, and these are the focus of the rest of this entry. During the task, subjects use a human-facilitated social cue to find a food reward hidden in two or more containers, or humans interpret animals' gestures toward objects to decide which container has food

hidden in it. Manual pointing is among the most common cues used in the OCT; other cues include eye gaze and/or touching or placing markers on the "baited" container. Figure 1 presents a standard comprehension test; if the placement of the dog and human were reversed, it would present a standard production test, where the dog "produces" some indication of which object it chooses. Here we discuss some of the different versions of the OCT used in studies of communication and review the diversity of species examined and some hypotheses that have been tested using the procedure.



**Object-Choice Test, Fig. 1** The object-choice test is often used in studies of comprehension of human social cues. The experimenter provides a cue such as manual pointing toward (typically) the container that has food hidden within it. The subject is then given a chance to make a response, such as approaching the baited container, in order to receive the reward. (Drawing by Lyra Skopos)



## Methodological Variations in the Object-Choice Task

The OCT as a tool for studying communication is implemented in a variety of ways, with variations typically based on the hypotheses of interest, shaping and training procedures needed, and the range of perceptual and social behaviors of species tested. The commonality across most studies is that, for experimental trials, an object, typically food, is placed inside of one of two (or more) opaque containers (and thereby hidden). Then an experimenter provides a communicative signal to the animal or awaits a communicative signal from the animal, which indicates the location of the food.

Familiarization with the procedure is typically conducted prior to training and might consist of simply showing the subjects that one of two or more containers contains food and requiring some kind of indicating act by the subject (e.g., approaching, pointing, begging gesture) in order to receive the food. Following this procedure, positional, gestural, and eye-gaze cues become the only sources of information the subjects can use to determine which of the containers is baited. The containers are usually visually but not tactilely accessible during the cueing phases of the procedure, and correct choices are rewarded by offering the food reward to the subject, releasing the subject to retrieve the food, or moving the chosen container into the animal's enclosure. In studies of deception, however, if the animal selects or indicates correctly, the cooperative participant gives the animal the food, but the competitive (deceptive) participant keeps the food. With a competitive participant, the animal has to learn to indicate the unbaited container or select the container the participant does not point to in order to get the food.

Task difficulty may vary by the level of cue salience, such as having the indicating individual touching the container or briefly glancing at it, or in terms of memory required to make a selection, via the delay between signaling and opportunity to make a choice. Pointing gestures may take many different forms in terms of the distance between the experimenter and the objects, the

duration of the point, and the lateral dimension of the point (e.g., cross-body vs ipsilateral). Since eye-gaze changes typically accompany pointing gestures, the experimenter may look in the same direction of the point. Conditions, or entire studies, may involve eye gaze alone as a cue for which container is baited. The following descriptions are based on standard usage of terminology from the literature, especially Miklósi and Soproni (2006).

**Proximal and distal pointing.** In the proximal pointing condition of the OCT, containers are placed between the subject and the experimenter, and both are within reach of the latter. In the distal condition, the subject and experimenter also typically face each other, but the containers are separated by a greater distance. Miklósi and Soproni (2006) consider 10–40 cm spacing between point and container to be proximal and 50 cm and greater to be distal.

**Static, dynamic, and momentary pointing.** The duration of the pointing gesture can vary in duration and, relatedly, complexity. A point is already present when the animal first sees the pointer in static pointing, whereas the point is initiated while the animal observes the pointer in dynamic pointing; in both cases, the point continues until the animal makes a choice. Momentary pointing consists of pointing briefly (a couple of seconds) at the object before returning the arm to the side of the body. Unlike static or dynamic pointing, momentary pointing requires that the subject remember the location indicated.

**Flexibility of pointing.** The range of complexity of animal responses to pointing cues has been tested using points that are relatively ambiguous in comparison to those previously described. Pointing with the foot or elbow or with an arm and finger extended across the body toward a baited container on the contralateral side increases the complexity of the task. Another level of difficulty can be introduced by using asymmetric pointing, where the experimenter stands adjacent to the empty container and points toward to the baited one.

**Tap, touch, or mark.** The use of a touching or tapping cue involves local or stimulus enhancement, or the direct drawing of the subject's attention to a stimulus by physical contact. This might

be done to test whether local or stimulus enhancement accounts for selecting the baited container. A less direct option is placing an iconic cue (a photo or replica) or physical marker on or near the baited container in order to draw attention to it.

**Auditory cues.** The OCT is also used to test whether animals use auditory cues as a source of information about food location. For example, Rossano et al. (2014) showed that dogs respond to the direction in which a human speaks to make their choice.

**Eye gaze.** The OCT has been used in studies exclusively examining gaze sensitivity or studies examining multiple types of social cues that include eye-gaze direction. Gaze following, namely, using eye direction, could represent the capacity for understanding another's visual perspective.

What may seem like minor variations in methodology can elicit very different results (Miklósi and Soproni 2006). Thus, the methodology used must be carefully examined before any comparisons among species, ages, or other variables of interest are drawn. One of the most appealing elements of the OCT is its versatility and flexibility; small adjustments to the methodology open the opportunity to explore the gesture-following abilities of myriad species. Success on more complex variations of the OCT may be taken as evidence that the visual attention and gestural signals provided by humans were understood by the animals. We review a sampling of the various species tested and results from some of this work (for a complete inventory and citation list of species tested so far, as well as all uncited references, see Krause et al. 2018).

## Review of Species Tested

**Primates.** Chimpanzees; bonobos, *Pan paniscus*; gorillas, *Gorilla gorilla*; orangutans, *Pongo pygmaeus*; and a gibbon, *Hylobates lar*, have all shown evidence of comprehending human gestures in the OCT, but there are numerous sources of variation that could account for individual, task-related, and possible species-level differences in

performance. For example, chimpanzees, bonobos, and orangutans that have had extensive contact with humans, including learning an artificial or gestural language system, outperform nursery-reared, mother-reared, and/or wild-caught apes on the OCT (e.g., Lyn 2010). Results are ambiguous with regard to gorillas on the OCT, where fewer studies have been conducted.

The apparent difficulty that some chimpanzees and other apes have with pointing using the OCT has generated much discussion and debate in comparative psychology. It seems puzzling that chimpanzees, the closest living relative to humans, are outperformed in the OCT by domestic dogs. The role of domestication in canine cognition has been offered as an explanation (Kirchhofer et al. 2012), though there is by no means consensus on this issue (Leavens et al. 2017). After all, dogs with extensive human contact (pets) outperform dogs with less contact, such as those reared in kennels (D'Aniello et al. 2017), and apes with extensive experience interacting with humans likewise outperform apes with less human interaction (Lyn 2010). Also, the types of cues used in the OCT influence performance (Miklósi and Soproni 2006). If we measure performance using only the proximal pointing variation, then chimpanzees might be regarded as relatively poor at understanding human pointing. However, when tested with distal pointing, rather than proximal pointing, chimpanzee (and bonobo) performance exceeds chance levels (Lyn 2010). Why might this be? Food containers are high-interest objects to chimpanzees, and because both containers and social cues occupy the same visual space, the pointing and gaze cues must compete with the more salient and immediately interesting containers (the “distraction hypothesis”). The distal (“peripheral”) condition puts human experimenter and containers in a different visual space and in addition creates a situation in which an incorrect choice comes at a greater cost than the proximal (“central”) condition (e.g., latency between making a choice and receiving feedback is longer in the distal condition: see Mulcahy and Hedge 2012 for discussion). Interestingly, dogs performed better in the distal than the proximal condition (with performances similar to those of apes in the two

conditions in the Mulcahy and Hedge study), whereas cats (*Felis catus*) performed well in both conditions (comparable to dogs in the distal condition), though fatigue may have been a factor as dogs were tested on 1 day and cats across 2 days (Kraus et al. 2014). The authors suggest that cats are highly responsive to the movement involved in the pointing gesture in making their selection, whereas the dogs (like apes) may have been distracted by the closeness of the food bowls in the proximal condition.

Tests with iconic cues (photographs or replicas of food or containers) have been examined with apes (Herrmann et al. 2006). In this study, the authors in experiment 1 varied whether or not the apes saw the placement of the iconic image atop the container. Some of the 27 apes (including chimpanzees, gorillas, orangutans, and bonobos) performed at above chance levels when they saw (or when they did not see) the placement of the replica, others when they saw (or when they did not see) the placement of the photograph, and others when they either saw or did not see the placement of the replica (or the photograph); one ape (a bonobo) succeeded in all four conditions. Most apes failed to succeed under all four conditions, although on average the apes succeeded on all conditions except the one with the replica they had not seen being placed atop the container. (Note that, throughout this study, the authors mistakenly examined chance occurrence for individual subjects using a two-tailed binomial test; in fact, they should be using a one-tailed binomial test, a remarkably consistent error among this research group when testing apes, but not when testing dogs [see Mitchell et al. 2018, Appendix].) Similar findings occurred in experiment 2 when, testing 11 of the best performers, each container had a photo or replica of a (different) fruit atop them, or one container had a photo or replica of a fruit and the other had a photo or replica of a non-fruit on top, but one of the two iconic items was of the fruit the ape had seen before it was hidden (but in this case, a gorilla succeeded at above chance levels on all four conditions and was the only ape to succeed when fruit replicas were on top of both containers). Average performance was above chance for all conditions except the one with two

fruit replicas. The same apes (experiment 3) were then shown a photo of one of two containers which had been baited and were then provided with both containers; following two sessions of this, the same apes (experiment 4) were shown that one of two transparent containers containing different fruit was locked and were then shown a photo of the fruit in the unlocked box. In both experiments, all apes failed on the first session, and all failed on the second session except for one gorilla (the same one who had succeeded in experiment 2). (Note that the authors mistakenly depict the greater than chance performance of 13 out of 18 that the gorilla obtained in the second session in each of these final experiments as chance performance.) The data from this study indicate that some apes can use iconic cues to pick the correct container in OCTs but that with more things to remember for success, performance diminishes: a standard finding in tests of working memory.

At least ten monkey species have been tested using the OCT (see Krause et al. 2018), including capuchin monkeys, *Cebus (Sapajus) apella*, which reliably followed pointing and eye-gaze plus pointing cues toward baited containers but did not reliably use gaze cues alone. However, capuchin monkeys could learn to use gaze direction in the OCT through extensive training, but it is likely that head orientation, and not eye direction per se, was the salient feature used by the monkeys to determine the food location.

As with apes, performance on the OCT among monkeys is widely variable and dependent upon training, rearing histories, and procedural variation. For example, long-tailed macaques (*Macaca fascicularis*) reliably use proximal pointing cues, but not distal ones, to locate food in the OCT (Schmitt et al. 2014), which contrasts with what tends to occur with chimpanzees. The experimental trials included conditions in which the experimenter stood behind a curtain and reached out with only their arm, a doll arm, or even a stick to indicate the baited container. Interestingly, the monkeys performed best under conditions where the experimenter's face was blocked by a curtain, even if an inanimate object was used to indicate the baited container. Schmitt et al. (2014) suggest that face-to-face contact in a feeding context could

be interpreted as threatening by monkeys (as it may be with other species, including apes) and that removing this variable and introducing the most salient cue (outstretched arm or object) remove what would be a confounding variable if one wants to make meaningful comparisons with other species, including ones that may respond defensively to direct eye contact. As tempting and fascinating as species comparisons may be with the OCT, any interspecific differences found do not default to a sound, phylogenetic interpretation (see Leavens et al. 2017).

A naturalistic variant of the OCT examining chimpanzees' responses to a conspecific's knowledge of the locations of varying amounts of hidden and visible food was created by Menzel (1974). A chimpanzee was shown the location of the hidden food in a one-acre field and then was allowed into the field with conspecific comrades, all of whom saw an available piece of fruit. The knowledgeable chimpanzee usually led the group to the hidden food, which was shared by all. However, one chimpanzee became greedy, maintaining all the food for himself, and the knowledgeable chimpanzee attempted to avoid indicating the location of the hidden food for this chimpanzee. In addition, when there were two caches of food, one smaller than the other, the knowledgeable chimpanzee led the greedy chimpanzee to the smaller cache of hidden food, before herself going to the larger cache (a form of deception). The follower chimpanzee picked up on these maneuvers, creating distress for the knowledgeable chimpanzee. Similar "informed animal" studies involving mangabeys, *Cercocebus torquatus torquatus* (Coussi-Korbel 1994), and Tonkean macaques, *Macaca tonkeana* (Ducoing and Theierry 2003), showed similar findings.

Menzel's work led Woodruff and Premack (1979) to control more variables by using the OCT with chimpanzees and by having humans act as either cooperators or competitors (as described earlier). Each chimpanzee was presented with two containers, one of which was baited. If the chimpanzee knew which was baited and a human approached the containers who did not know which was baited (the production context), the chimpanzee needed to indicate the baited

container for the cooperator (who gave the food to the chimpanzee) and withhold information as to which was baited or indicate the unbaited container for the competitor (who kept the food). If the chimpanzee did not know which container was baited and a human who (the chimpanzee knew) knew which was baited approached the containers (the comprehension context), the chimpanzee needed to select the container the cooperator indicated and select the container other than the one the competitor indicated. Chimpanzees used a variety of methods of indicating a container, including combinations of frontal position toward the container, gaze from container to person, and whole arm or leg pointing; humans mirrored chimpanzee responses in the comprehension context, using similar positional, gaze, and whole arm or leg pointing. Chimpanzees eventually succeeded, after 100 or so trials, in generally acting appropriately in both production (indicating the appropriate container to get the food) and comprehension contexts (indicating the appropriate container to get the food or withholding information from the competitor, for which they were rewarded). Minor variations on the production version of this general experimental form were used with brown capuchin monkeys, *Cebus apella* (Mitchell and Anderson 1997); squirrel monkeys, *Saimiri sciureus* (Anderson et al. 2001); brown lemurs, *Eulemur fulvus* (Genty and Roeder 2006); and black lemurs, *Eulemur macaco* (Genty et al. 2008), with similar results. Some of the primates withheld information from the competitor, even when they were not rewarded for this withholding (Genty et al. 2008). Another variation employed both an informed animal and an OCT, where both a dominant and a submissive Tonkean monkey saw food atop a container, but only the submissive knew where hidden food was (Canteloup et al. 2017).

**Canids.** The OCT has been very popular among those studying canine social cognition. Domestic dogs are by far the most common species in studies using the OCT and comparative studies employing captive populations of wolves (*Canis lupus*), foxes (*Vulpes vulpes*), dingoes (*Canis dingo*), and coyotes (*Canis latrans*).

Since Miklósi et al.'s (1998) study using the OCT with dogs, dozens have followed. In fact, over 50 papers have examined pointing comprehension in over 2000 dogs (Krause et al. 2018). It was apes' skill at understanding pointing, and monkeys' lack of skill, that initially spurred Miklósi et al. (1998) to use the OCT to examine dogs' understanding of human pointing, which they viewed as comparable to that of apes. Researchers who believed that apes showed limitations in their responses to human pointing to find hidden objects were particularly intrigued by dogs' apparently immediate understanding of human points (Hare and Tomasello 1999), creating a view of ape inadequacy and dog skill in relation to human pointing (e.g., Kirchofer et al. 2012) that has been questioned on several fronts, particularly by presenting evidence of ape skill (Leavens et al. 2017) and dog inadequacy (D'Aniello et al. 2017; Udell et al. 2008).

In general, pet dogs respond appropriately to pointing in the OCT. Factors which influence dogs to respond inappropriately to human pointing in the OCT include side preferences, earlier reinforcements, early experience with little to no human interaction, and knowledge of the location of the reward (D'Aniello et al. 2017; Petter et al. 2009; Udell et al. 2008). For example, when dogs knew by sight which one of two containers was baited in the OCT, they were more likely to choose the baited container even if the human pointed to the other container than if they did not know which container was baited (Scheider et al. 2013); however, when their knowledge of which container was baited was based on smell, they tended to follow points to the empty container (Szetei et al. 2003). Human-raised wolves selected the baited one of two bowls based on human gestures in several studies, though the data conflict somewhat: wolves selected the baited bowl when a human touched or pointed proximally to it, but not when the human pointed distally to it (Miklósi et al. 2003; Virányi et al. 2008); and human-socialized wolves selected the baited bowl when the human momentarily pointed distally to it and did so either with no apparent training as adults (Udell et al. 2008) or only after extensive training as pups (Virányi et al. 2008).

There is great variability across wolves and dogs in their responsiveness to human social cues in the OCT.

Canids have also been used in replications of the Woodruff and Premack (1979) deception studies. Studies of deceptive pointing (and of extinction of responding to pointing toward the unbaited container) in standard OCTs examine dogs' responses to pointing when the dogs did not know under which object the food was hidden. Dogs generally selected one of two containers pointed to regardless of whether the pointer was cooperative or competitive. However, the dogs sometimes refused to respond or selected the other container, more often with the competitor than the cooperator (Petter et al. 2009). It requires many trials for dogs to avoid responding to pointing by a deceiver (Petter et al. 2009). Dogs respond to artificial human hands pointing toward or away from transparent containers to decide which to choose; surprisingly, when an artificial hand pointed toward an empty transparent container, and another artificial hand pointed away from a baited transparent container, most dogs selected the unbaited container that the artificial hand pointed to (Kundey et al. 2014).

Canids communicate differently depending on whether the human is cooperative or communicative. Following extensive experience with a human indicating cooperatively and competitively (the comprehension context), dogs were put into a production context, such that the dog now indicated which bowl a human should choose (Petter et al. 2009). Dogs usually indicated the baited bowl and sometimes the unbaited bowl or withheld information, for both the cooperator and competitor. In these studies, the standard OCT was used, but with the dog and human in Fig. 1 in reversed positions. To determine if dogs could learn to trust cooperators and avoid competitors through brief exposure to each, researchers gave dogs direct experience with a cooperative and a competitive human, by having each human independently lead the dog to two containers where the dog knew which container was baited and then either giving the dog the food (cooperator) or keeping the food for herself (competitor) when the dog indicated the baited bowl. Later, the



dogs were allowed to lead the cooperator or the competitor separately to one of three boxes: one containing a preferred food, one containing a less preferred food, and one empty (Heberlein et al. 2017). Over (usually) four trials each with each person, most of the dogs led the cooperator to the box containing the preferred food most of the time, and most led the competitor to the box containing the less preferred food or the empty box most of the time. In a similarly organized study with wolves and dogs (Heberlein et al. 2016), only one of the three boxes was baited with (a preferred) food, and the cooperator or competitor observed the canid when in a room with the three boxes and decided which box the animal selected. Both wolves and dogs exhibited almost identical frequencies of directing attention to the box containing the food and did so much more frequently for the cooperator than for the competitor.

Dogs are also attuned to nonsocial signals of a container's being baited or unbaited, analogous to social signals of cooperativeness and competitiveness, respectively. Petter et al. (2009) used either a black or white box as a marker to indicate that one of the containers near a box was baited or empty (for some dogs, white indicated the baited container and black, the empty one; for others, it was the reverse), thereby mimicking the cooperator/competitor context without a human present. Dogs responded appropriately to the markers, more often selecting a container when its box indicated it was baited and selecting the other container when a container's box indicated it was empty.

Whereas the domestication hypothesis of Hare et al. (2010) posits that dogs, as a result of domestication, are inherently appropriately responsive to human pointing (and other social signals) even without any exposure to humans prior to the pointing, an alternative hypothesis focusing on dogs' socialization by humans, the two-stage hypothesis, implicates dog's social interaction with humans and subsequent conditioning as necessary for appropriate responses to pointing (Udell et al. 2010). The evidence so far appears not to support the domestication hypothesis. Although domestication may provide dogs with

some predispositions necessary to understand pointing, they are not born with the ability to successfully use human cues. In contrast to pet dogs, research dogs raised in a kennel with limited human socialization experience failed to reliably use distal and proximal pointing to locate a hidden reward (D'Aniello et al. 2017). Free-ranging dogs in India were more likely not to follow points than to follow them in OCTs, with most (35%) juveniles and adults failing to follow and most (69%) pups following points (Bhattacharjee et al. 2017), suggesting that dogs may unlearn their responsiveness to pointing as they mature based on their experiences of humans. Thus, rearing history and early experience with humans are critical to the development of pointing skill in any individual dog, lending support to the two-stage hypothesis. Tamed dingoes (a type of dog which had been domesticated, had gone wild, but is often tamed as a pet) on average selected the baited of two containers following a variety of human indications, including diverse points, showing chance performance only when the human stood by one container but pointed to the other. Note that dogs who respond appropriately to human pointing will sometimes actually ignore such pointing (e.g., during play with a human; Mitchell et al. 2018), and the same may occur during OCTs.

Specific examples of human contact that may contribute to the development of a dog's (or wolf's) ability to follow pointing gestures include treat offering, filling food bowls, toy throwing and playing, or informal pointing to objects to direct the animal's attention in a daily context. Each of these interactions, intentional or not, exposes the animal to stimulus-response-consequence situations that increase the likelihood of repeating the corresponding behavior, such as following human hands in response to a pointing stimulus, reinforced in the past with food or toys, toward a new location or object (Miklósi et al. 2003; Udell et al. 2010). Canine choice performance is significantly influenced by ostensive communication with humans, such as calling the dog's name (e.g., Erdőhegyi et al. 2007).

An experimental study of domesticated and non-domesticated foxes interpreted as supporting the domestication hypothesis (Hare et al. 2005)

provides findings more consistent with the two-stage hypothesis (developed 5 years after the study). Domesticated foxes had been selected for breeding based on friendliness to humans, whereas non-domesticated foxes (which expressed fear and aggression toward humans) had not. Domesticated foxes and age-matched dog puppies, both presumably familiar with humans, used a human's pointing and gazing at one of two containers to select the baited one at levels greater than chance (on average, just over 15 out of 18 trials). However, non-domesticated foxes also used the human's pointing and gazing to select the baited container at levels greater than chance (on average, 12 out of 18 trials). Although the domesticated foxes used the point and gaze gestures more frequently than non-domesticated foxes did, it is surprising, if the domestication hypothesis is true, that the non-domesticated foxes followed the gestures at greater than chance levels. The methods indicate that the non-domesticated foxes experienced "weeks of exposure to humans" prior to the point and gaze study (p. 228), thereby indicating some human socialization, and, oddly, the non-domesticated foxes had interacted with the experimenter "for twice as long as the [domesticated] foxes" (p. 229), who had "far less experience with humans" than the non-domesticated foxes (p. 228), thereby increasing the chances of conditioning (p. 228). By contrast with the foxes, domestication shows a much more clear-cut beneficial effect on ferrets (see below).

**Other domesticated animals.** Inspired by the possibility that domestication has influenced social behavior in dogs, investigators have used the OCT to test whether other domesticated species understand human social cues. Pet cats showed skills comparable to that of dogs in responses to human momentary and dynamic distal and proximal pointing in OCTs and better than that of dogs in responses to momentary proximal pointing (Kraus et al. 2014). Pigs (*Sus scrofa domestica*) can spontaneously use proximal and, to some extent, distal pointing in the OCT. Goats (*Capra hircus*) can use touching and, to varying degrees, pointing and gaze cues during the OCT. Also, horses (*Equus ferus caballus*)

learn to follow even momentary distal points, particularly if they have extensive experience in communicative contexts with humans prior to the beginning of the experiment. The learning required by horses that had or lacked extensive exposure to human cues does not lend support to the domestication hypothesis.

A comparison of domestic ferrets (*Mustela furo*) and wild x domestic tamed *Mustela* hybrids in OCTs seems to offer support for the domestication hypothesis (Hernádi et al. 2012). Domestic ferrets (*Mustela furo*) were comparable to dogs in their ability to follow momentary pointing to or sustained touching of a container in OCTs, whereas the diverse set of *Mustela* hybrids performed at chance levels in relation to the pointing or touching to locate hidden food. However, the hybrids (unlike the domestic ferrets) avoided direct eye contact with their human owner, and the authors suggest that failure to engage in eye contact with familiar (and other) humans is the basis for animals' failure in pointing tasks. Thus, rather than domestication leading directly to understanding of human social signals, it may allow for tolerance of and/or preference for eye contact with humans, which is necessary for the development of understanding of human social signals (Miklósi et al. 2003). The two-stage hypothesis, linking animals' social interaction with humans and learning about human social signals to explain success on pointing and other OCTs, also seems insufficient, as the hybrids were extensively socialized with their owner.

**Non-domesticated species, tamed individuals.** Some studies have examined comprehension of pointing using the OCT with tame individuals of non-domesticated species. Bottlenose dolphins selected the appropriate object when points were stationary and dynamic proximal points and when points were direct or cross-body; some were also successful when stationary and dynamic eye gaze indicated the object to choose. None were initially successful at understanding that a same-sized "replica" of one of the two objects indicated which of the objects to choose, but two became successful after brief training. Similarly, South African fur seals (*Arctocephalus pusillus*) tested using the OCT

selected appropriately in response to whole arm pointing, eye gaze, both pointing and gaze combined, and cross-body pointing and gaze but did not respond appropriately to finger pointing, short gaze, or presentation of object replicas. Some of the African elephants (*Loxodonta africana*) tested on static as well as momentary direct and cross-body points selected the indicated objects, and one elephant was successful on all four point types. Some elephants later “generalized” their understanding to foot points. Human-reared and tamed megachiropteran bats (*Pteropus* species) successfully followed pointing gestures when they were captive born, but not wild born. As with the ferrets, findings once again suggest that neither domestication nor human rearing is necessarily enough to successfully respond to human pointing. Clark’s nutcrackers (*Nucifraga columbiana*) can use a look-point-touch gesture cue to choose food locations. Interestingly, the birds learned to successfully discriminate between gestures made by experimenters who were either naive or informed about the location of the food. By contrast, ravens (*Corvus corax*) appear to be relatively unresponsive to pointing and gaze cues in the OCT.

## Conclusion

The OCT has a long history in comparative psychology. The task is well-suited for studying perceptual and cognitive capacities among nonhumans. The OCT utilizes the ubiquitous motivation for food reward among animals to engage their attention to the specific experimental manipulations. Also, the OCT generally elicits a clear, overt behavior indicating choice. These are among the properties of the OCT that make it suitable for use with a wide array of species and research questions. Over the past few decades, the OCT has become a standard procedure for examining the capacities that animals have for following human communicative signals. Interestingly, comparative psychologists are often warned to avoid the Clever Hans effect, in which animals only appear to be solving the problems they are given but are instead responding to cues

unwittingly provided by humans. Contemporary research using the OCT is revealing that animals’ skills at reading human social signals, the basis of the Clever Hans effect, are itself worthy of study.

## Cross-References

- [Domestication Hypothesis](#)
- [Human-Animal Interaction](#)
- [Learning](#)
- [Pointing](#)
- [Wisconsin General Test Apparatus](#)

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## Objective

► [Goal](#)

## Obligate Trait

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### Definition

A trait exhibited by a species that persists in all environmental conditions and is necessary for survival.

### Description

When a trait so significantly increases the chances of a species' survival that it becomes a mandatory system, it is considered to be obligate. An obligate trait remains consistent in times of environmental change. Thus, it can not be lost or 'turned off' even if the environment undergoes a rapid change that would seemingly cause the trait to be futile.

Because such a system can be extremely restrictive, the evolution of an obligate trait is

only advantageous if it reduces a consistent opposition faced by a species. The energy exerted to maintain the trait cannot exceed its overall benefit to the species. Therefore, traits considered to be obligating usually effect circumstances that remain predictable throughout the lifetime of the species (Newton 2012). Some commonly observed obligate traits are discussed below.

### Obligate Parasite

An organism is considered to be an obligate parasite if at least one part of its life cycle is unable to proceed without the use of a host. The host may be used as a source of food, environmental protection or hold another function essential to the parasite. All viruses are considered to be obligate parasites because they replicate by invading a host cell (Hogg 2005). Although the survival of the invading virus itself is not directly affected by the host cell, the continuation of the viral species is impossible without such interaction.

### Obligate Aerobe/Anaerobe

Organisms classified as obligate aerobes require oxygen for survival. Exogenous oxygen molecules are used in the respiration pathway of these organisms and is essential for energy production (Hogg 2005). In contrast, obligate anaerobes are unable to survive in the presence of oxygen. These organisms are unable to break down exogenous oxygen, allowing the molecule to form free radicals within the organism and cause extensive cellular damage. Obligate anaerobes also respire, but do so through the use of inorganic electron acceptors such as sulfate or carbon dioxide instead of oxygen (Hogg 2005). An anaerobic lifestyle can be beneficial for organisms living in extreme environments such as deep in soil and within the human digestive system.

### Obligate Mutualism

Species considered to be obligate mutualists consistently engage in one or more mutualistic



relationships for survival and/or reproduction. A mutualistic relationship between two species can be obligate for one or both of the species involved. Mutualistic interactions between species are evolutionarily favorable to both parties but may differ in relation to degree of benefit and relationship dependence (Boucher 1988).

An example of an obligate mutualistic relationship is that of the yucca moth and the yucca plant. Yucca moths pollinate yucca plants, making them necessary for survival. In turn, yucca moths use the flowers of the yucca plants as a home for their eggs and the plants' seeds to nourish their young. Many years of evolutionary events have led this relationship to become obligate, such as the decrease in the amount of yucca plant pollinators. In addition, yucca moths have developed a distinct mouthpiece with which to carry the yucca plants' pollen, making their relationship even more efficient (Pellmyr and Huth 1994). This mutualistic relationship is obligate for both parties, as both the plants and the moths depend on it for survival.

## Cross-References

- [Behavioral Genetics](#)
- [Bird Migrations](#)
- [Facultative Trait](#)
- [Fixed Action Patterns](#)
- [Innate Behaviors](#)
- [Instinct](#)
- [Reflex](#)

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## Obliterative Coloration

- [Cryptic Coloration](#)

## Obliterative Shading

- [Countershading](#)

## Observational Conditioning

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Observational conditioning refers to the learned association between an environmental action and a desired consequence. An example might be the case of an observing rats that sees a demonstrator press a lever and soon after a pellet is delivered to the demonstrator. What makes this different from imitation is the behavior of the demonstrator may not be necessary for learning to occur. That is, the movement of the lever followed by pellet delivery, a stimulus-stimulus association, may be sufficient to increase the probability that the observer will press the lever (see Heyes 1994).

Observational conditioning is different from social facilitation (facilitation due to the mere presence of the demonstrator; Zajonc 1965), the effect of an increase in the observer's general arousal produced by the presence of the demonstrator (see section on social facilitation). It is also different from stimulus enhancement, attention drawn to the lever by seeing the lever move up and down (see section on stimulus/local enhancement). Observational conditioning can be thought of as a special case of learned affordances (see section on learned affordance). In learning the affordances of a particular context, one may learn that a barrier can be jumped over in order to escape from shock. More closely related to observational conditioning, a child may be given a marking pen with a cap over the felt tip. By

seeing a demonstrator pull the cap off the pen, the child may simply learn the affordances of the pen and cap. She may learn that a pen has a removable cap and there are actually two parts. In principle, one could accomplish the same thing by showing the child a video of the pen and cap moving in opposite directions. By doing that one would not consider it an example of imitation because there would be no one performing, thus nothing to imitate.

In observational conditioning, the affordance of the context consists of the temporal relation between the movement of the lever and the delivery of the pellet. One can think of observational conditioning as a presentation of a conditioned stimulus (the moving lever) followed by presentation of an unconditioned stimulus (the pellet or more specifically the sight and sound of the pellet). Thus, observational conditioning actually involves higher-order conditioning. It assumes that there is already conditioning between the sight and sound of the pellet appearing at the feeder and the unconditioned effect of consuming the pellet.

Perhaps the strongest case for observational conditioning can be found in fear conditioning (Mineka and Cook 1988). Laboratory raised rhesus monkeys are not naturally afraid of snakes but if they observe another monkey react fearfully to a snake, they will also react fearfully to the snake. But clearly there is a predisposition to acquire this fear because if the other monkey appears to react fearfully to a flower (the demonstrator is exposed to a snake but the observer sees only the flower) a fear reaction to the flower does not develop.

Observational conditioning should not be confused with observational learning. Observational learning has sometimes been used interchangeably with imitation (see e.g., Galef 1988), but at other times it has referred to deferred imitation. That is, imitation in which some time elapses between the period of performance by the observer and the period of observation (see Bandura 1977). Bandura's view is that imitation that occurs at the same time as observation may involve some kind of reflexive response (what Byrne 1994 calls response facilitation) but

observational learning requires an internal representation of the observed behavior that is recovered at a later time to be performed by the observer (see Dorrance and Zentall 2001).

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## Observational Learning

### ► Cognitive Imitation

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## Observational Methods

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## Introduction

Animal behavior is studied for many different reasons, and observations can take place in a variety of settings. The way one chooses to study animal behavior either in a laboratory, at a zoo, or in the wild depends on the research

question being asked. Questions often begin broadly and become more specific after preliminary observations. Once the research question is formulated, it is necessary to identify the behaviors that will be measured. For example, if the question is asking if males of a group are more aggressive than females, it is necessary to determine which behaviors will be defined as aggressive and how these behaviors will be observed and recorded. An ethogram is a comprehensive inventory with the purpose of providing a description of all behaviors known to exist in a particular species. A researcher can use this to determine which behaviors are appropriate for analysis in a study. A limited ethogram that only includes behaviors relevant to the current study may also be created.

## Events and States

Behaviors can be measured on a continuum from events to states. While all behaviors realistically require some amount of time to complete, behaviors can be categorized for observation based on their duration. Events are discrete behavior patterns that occur in a relatively short amount of time. Event behaviors are measured by the count, or number, of occurrences of the behavior. For example, each time a horse displays a foot-stomping behavior, it can be counted as an event. On the opposite end of the continuum, states are behavior patterns of relatively long duration or are prolonged activities. States are measured by the duration of the behavior. For example, the amount of time a horse spends sleeping can be a measure of state.

Since events and states are on a continuum, a researcher can choose to describe many behaviors as either events or states. The choice to define a behavior as an event or a state is at the discretion of the researcher and is based on the research question they are attempting to answer. A researcher addressing the number of times an individual engages in a specific behavior may define it as an event. In contrast, a researcher investigating the amount of time an individual engages in a specific behavior may frame the same behavior as a state. For example, a

researcher could count the number of times a lion is observed lying down if they were investigating the frequency of resting behaviors. These frequencies are obtained by counting the number of times a behavior or activity is initiated. Alternatively, the researcher could record the amount of time the lion spends lying down in order to investigate the duration of resting behaviors. The decision to define behaviors as either events or states should be given careful consideration based on the question of interest. Defining a behavior as an event not only is determined by the type of research question, but it also affects which method of observation should be used when observing and recording the behavior.

## Rates and Frequency

When events are being scored, the simplest way to quantify the results is by tallying the number of occurrences of a specific behavior. For example, a researcher may tally the number of times an individual performs a grooming behavior. Although the resulting count is informative, it does not provide results that are appropriate for comparisons, analyses, or conclusions. Describing the count per unit time produces a more meaningful metric. Rate (or frequency) is defined as the number of occurrences of a behavior per standard unit of time (e.g., per minute, per 5 min, per hour, or per day). Rate and frequency are synonymous terms of behavioral measurement that allow researchers to compare within and across experiments and provide useful information that count alone does not reveal. Rate is calculated by dividing the number of occurrences of a behavior by the unit of time. For example, a chimpanzee who has three occurrences of grooming in 10 min during the first observation and has one occurrence of grooming in 10 min during the second observation has response rates of 0.30 and 0.10 per minute.

In the previous example, a 10-min observation time is used for both observation periods. Ideally, observation times would be equal for each individual or group in the study, allowing for easy comparison due to the standard unit of time.

In many situations, however, an animal may not be visible to the researcher during the entire observation period. Rates also allow researchers to compare counts from observation periods of different lengths. Unequal observation times that are beyond the researcher's control can occur when an animal changes location to an area secluded from the researcher's view. For example, a chimpanzee who has five occurrences of grooming in 10 min during the first observation and has three occurrences of grooming in 8 min during the second observation has response rates of 0.50 and 0.38 per minute.

## Sampling Rules

In order to design a viable study, researchers need to engage in the systematic observation of behaviors. There are two components of recording methods that a researcher should examine when designing a research study. First, the sampling rules should be considered. Sampling rules dictate which subject or subjects should be watched and when their behavior(s) should be recorded. The second design consideration is the recording rules, which dictates how the behaviors should be recorded.

There are four widely used sampling rules: focal animal, focal behavior, scan, and ad libitum. Researchers must determine if a single animal, a subgroup, the whole group, or a specific behavior should be observed.

Focal animal sampling is a technique in which the observer records all instances of behavior of a previously selected individual for a specific period of time. The behaviors displayed by the other members of the group are not recorded. This sampling technique provides a flexible platform where solitary and social behaviors involving the focal animal can be recorded. The focal animal can be recorded as the actor or receiver of a behavior based on the study questions and ethogram. Generally, the activities of a single animal are recorded for a predetermined period of time, and then the observer moves to watch the next animal. This is repeated until all of the animals in the group or subgroup are observed. If

possible, focal animals should be selected for observation in a randomized order.

Focal behavior sampling is a technique in which all instances of a specific behavior displayed by any member of the group are recorded. This sampling rule is an effective recording method when the study question pertains to a specific scenario or when the behavior of interest is rarely exhibited. Within focal behavior sampling, a researcher may choose to only record the specific behavior of interest, or they may record both the focal behavior and the sequence of behaviors (displayed by the original actor or behaviors of others in response) that follow the focal behavior as well. For example, a researcher studying the use of aggressive kicking in African elephants may record only instances of forward or sideways foot thrusting in the direction of another elephant. This threat display by any individual in the group would be noted. Any of the chosen responding behaviors defined in the ethogram by the researcher may also be recorded.

Scan sampling is a sampling technique in which the observer surveys an entire group of animals at a single point in time to record the behavior of each individual and repeats the process at defined intervals. This sampling technique provides a representation of the overall distribution of behaviors and the behavioral repertoires of the group simultaneously. Ideally, scan samples are collected in such a rapid fashion that they represent a single snapshot or moment in time. Practically, without the ability to freeze frame live action, it takes a certain amount of time to record the data. The interval between scans should be substantial enough to record accurate observations before the next scan time point arrives. Scan data can be used to generate estimates of percentages of time engaged in different activities. This method can also be used to compare the behavioral patterns of one group (which can be based on social cohort, age, sex, etc.) to the behaviors of another group. Unlike focal behavior and focal animal sampling, scan sampling requires the use of the instantaneous recording rule (see below) to record behavior because behavior is only being observed instantaneously (at the single point of the scan). In this instance, a researcher

may be interested in evaluating the differences in behavior patterns between three male adolescent giraffes and three female adolescent giraffes. The observer may sample the behavior of the giraffes every 20 s for a 5-min period several times a day. After accumulating enough data, the researcher can compare the activities of adolescent male and female giraffes.

Ad libitum sampling is a sampling technique in which there are no systematic conditions placed on the behaviors of individuals/groups being recorded or a specific time interval in which the recording is completed. In this method, which is similar to note taking, the observer records behavior based on what is interesting or pertinent. Ad libitum sampling is prone to observer bias largely because the activities of interest tend to be charismatic and gregarious in nature. Mundane behaviors are easily overlooked despite their potential to be influential. For example, one way a chimpanzee may invite another to reconciliation after a recent conflict is by making eye contact (De Waal 2005). Because subtle yet important behaviors, such as brief eye contact, can be disregarded by an observer during ad libitum sampling, it is generally not suggested for use in scientific studies. Another potential issue with this sampling technique that must be addressed are discrepancies in how each behavior is described. As there are no behavioral definitions characterized prior to the observation, differences in how behaviors are categorized and detailed may arise throughout sampling. Despite these limitations, this sampling technique can still be used effectively when the study goal is to collect contextual information, make preliminary observations, record rare events, or note potentially impactful behaviors outside of the regular observation schedule.

## Recording Rules

Recording rules describe how the behavior is recorded. There are two categories of recording procedures: continuous recording and time sampling. Instantaneous sampling and one-zero sampling are two commonly used types of time sampling.

## Continuous Sampling

The purpose of continuous recording is to obtain a complete record of the behavior and provides the only means to understand sequences of behaviors. In continuous recording (often referred to as all-occurrence recording), every occurrence of the behavior and the time of each event is recorded. For states, both the time the activity began and the time it terminated are recorded, while only a single time point is recorded for an event behavior. Continuous recording is designed to provide accurate frequencies, latencies, and durations of all behavioral events and states. One problem that may arise with continuous recording is when a behavioral bout has a long duration. The longer the duration, the more likely the recording session will terminate before the end of the behavior and the record will underestimate the actual duration. In addition, the record can underestimate the duration of an activity if the animal goes out of view. Again, this is most likely to occur if the behavior typically has a long duration. One of the drawbacks of continuous sampling is its practicality. It is more difficult on the coder to record time and duration of every behavioral event or state. This means that only a limited number of behavioral categories can be accurately coded at any time. The likelihood of missing behaviors increases as the number of behaviors increases in the ethogram, resulting in decreasing reliability (Martin and Bateson 2007).

## Sequence Sampling

Sequence sampling is an observation technique used to describe an interaction sequence. It is necessary to use continuous recording procedures when using a sequence-sampling method. The sampling period begins as soon as the interaction of interest begins. The observer then records all behaviors in order of occurrence until the interaction is interrupted or terminated. The next sample period then begins upon the start of a new interaction sequence. In sequence sampling, the observer is focused on interaction behaviors rather than on any individual in the group. This type of sampling procedure can be used to study social behavior. Within a sample period, sequential sampling is similar to focal-animal sampling with



each member of the interaction acting as the focal animal. Each behavior performed by these individuals is recorded. Within an observation session, there will be differences from a focal-animal sampling procedure since the sampling period ends with any interruption or termination of the interaction. The next sequence then may be initiated by different members within the group.

There can be problems with this type of observation procedure. When the observer selects the next available interaction initiation or one that occurs in close proximity to the previous interaction, this new interaction might not represent a true independent sample. However, it is difficult to describe a procedure for selecting interaction sequences at random. It can also prove difficult to specify the beginning and ending of an interaction. One of the advantages of this technique is that it allows large samples of social interactions to be studied. During an interaction, the observer is able to direct attention to the focal animals. The observer then moves to the next available sequence creating little time in which data is not being recorded.

### Instantaneous Sampling

In the instantaneous sampling procedure, behaviors are recorded at specified time intervals. An example of this type of procedure would be observing an animal's behavior at a point in time every 5 min on the minute throughout a 12-h period. Typically, instantaneous sampling is used as a measure for studying states rather than events. This procedure can be used to study the behavior of an individual or a group. For groups in which all members are visible at the specified time point, the behavior of the group can be considered a simultaneous sample. The state of each individual should then be recorded at the same moment. It is not always possible for the whole group to be observable at the same time. In this case a scan sampling procedure should be used.

The instantaneous sampling score is the proportion of the total number of sampling points an animal was engaged in a particular activity. In the case above, in which a sample was taken every 5 min for 12 h, there would be a total of 144 sample points. If an animal was engaged in a certain

behavior on 50 of these sample points, the instantaneous sample score would be  $50/144 = 0.35$ . The instantaneous sampling score is a unitless score. Since individual sample points within a session cannot be treated as independent measurements, only one score is obtained for the entire session. Instantaneous sampling is appropriate for measuring percentage of time an animal engages in an activity. This is also a useful technique for measuring group synchrony. Instantaneous sampling is not an appropriate measure for studying rare behaviors, which have the risk of being missed at any given sample point. It is also possible for there to be bias in instantaneous samples because observers are often more likely to include noticeable or interesting activities that occur just before or after a sample point as occurring within that sample point.

### One-Zero Sampling

In one-zero sampling, behavior is observed during specified time periods, and the occurrence or non-occurrence of a behavior is recorded. Frequency is not observed, only whether or not a specific behavior occurred. A behavior can be considered as having occurred if it was in progress at any time during the sampling point. In one-zero sampling, typically only one individual or pair is recorded during each sampling point. Sampling periods are typically very short, only lasting a few seconds, with a series of sampling periods in succession. In interpreting data from one-zero sampling procedures, the number of sample periods in which a behavior occurred is reported as a percentage or proportion of the total number of sampling periods in a session (Altmann 1974). One-zero sampling is also used similarly to instantaneous sampling in which the presence or absence of a behavior is recorded at a definite time point (as opposed to time interval). These records are still calculated as a proportion of the total number of sampling points in a session. A single one-zero sampling score will be obtained for each sampling session, since, like instantaneous sampling, each sampling point within a session is not an independent measure (Martin and Bateson 2007).

One-zero sampling has been used to measure both states and events; however, there are certain

limitations with this observation technique. When using one-zero sampling to measure states, it is possible for an activity to start in one sampling period, continue into another sampling period, and end in a third sampling period. Using one-zero sampling, this single activity would be scored three separate times. It is also possible to observe an activity being initiated and terminated three different times within a single sampling interval. This would only be scored once as one-zero sampling does not take into account the frequency of the behavior during the sampling interval.

It is important to consider both the typical duration of the behavior as well as the typical interval between occurrences of the behavior. The sample intervals need to be shorter than both the typical behavior duration and the typical interval between behaviors. Many researchers do not believe that one-zero sampling provides an accurate measure of duration or frequency of behavior. This is true whether one-zero sampling is being used to measure states or events (Altmann 1974). Others have suggested that for behaviors that start and stop frequently and which last for very short periods of time (e.g., play behaviors), one-zero sampling is an appropriate measurement to use. The benefit of one-zero sampling is the ease of the scoring procedure.

### **Advantages and Disadvantages of Time Sampling**

One drawback of time sampling (both instantaneous and one-zero sampling) is that neither provide an accurate measure of frequency or duration. In one-zero sampling, because of the assumption that the behavior lasts the entire duration of the sampling interval, there is a tendency to consistently overestimate the duration of a behavior. Another disadvantage of time sampling procedures is that they cannot be used to describe the sequence of behaviors.

One of the benefits of time sampling procedures is the ease of the recording process. By reducing how often a behavior is recorded, the ability to record a greater number of behaviors

and behavioral categories increases. There must be a balance then between maximizing this benefit and obtaining the most accurate representation of frequency and duration. Instantaneous samples with short intervals produce a close approximation of the continuous record and can provide a more accurate measure of duration. As the sample interval is shortened, the benefits of time sampling are diminished. Time sampling procedures also provide the possibility of studying a larger number of animals, something that is difficult to do when using continuous sampling. In addition, time sampling procedures are more likely to have reliability and ensure that every sample point accurately describes what occurred during that time point. For certain behaviors that occur too rapidly to observe every occurrence, time sampling can provide a better means of observing these behaviors than continuous recording.

### **Sociometric Status Matrix**

A sociometric status can be constructed to describe the interaction between two individuals. A table, or matrix, is constructed with the behavior or outcome for the actor listed in rows and the behavior or outcome for recipients listed in columns. The objective of this type of procedure is to determine for each pair in a group the degree of one-sidedness that exists in the relationship. This type of procedure has been used to determine the outcome of aggressive encounters between two individuals. This type of matrix can describe whether one individual in the pair is more likely to be the loser.

### **Recording Medium**

Once the measurement procedure has been identified, the researcher must decide what process will be used to record the behaviors. There are several options available (i.e., video recordings, verbal descriptions, check sheets, automatic recording devices, computer event recorders) (Martin and Bateson 2007).

**Video recordings.** These provide an exact record of the behavior. Video offers flexibility in terms of repeated playback and slowed playback speed that can assist an observer in recording the behaviors present. Audio recordings of vocalizations and acoustic data provide the same benefits and are used in much the same way as videos of behavioral data. Video can also be analyzed in different ways at different times, which allows for multiple questions and studies to be developed from the same video data. It also aids in the processing of timing behaviors for duration and produces a more accurate measure than when coding live in real time. With video data, it is still necessary to code the behavior. Coding is the process of identifying and describing the behaviors that occurred during the recording. This can be done based on an ethogram developed for the study. Typically, an observer will record behaviors observed on the video on a check sheet or computer event recorder. Video recording should be used when there is a specific reason for doing so, as for example, if the behavior requires repeated or detailed analysis. This type of recording can be time stamped and can be helpful to have proof that what was described was actually observed. For studies on behaviors that are rare, it can be useful to have video as a permanent record of what was observed. One drawback to the use of video is that it can be time consuming. It may take hours of observation to code a few minutes of video recording. In addition, one is limited by the field that was actually captured on screen. There may be details that are missing from the video record that could have been captured during live observations.

**Verbal descriptions.** Descriptions can be provided through physical notes or through audio dictation. These recordings are beneficial during preliminary observations or as a means of describing rare events that are not a part of the current study. This type of recording is often coded similarly to video data. This has the same drawbacks as when using video data. This coding process can be time consuming and take up to ten times longer than the original observation.

**Automatic recording devices.** Technology advances have introduced devices and techniques

that can produce a signal when a particular behavior or vocalization is performed or when an animal moves to a specific location in a test chamber. These devices are designed to produce a digital record that can be used for analysis. Some of these devices include activity monitors that automatically record movements. These work through various means including infrared, ultrasonic, capacitive, and microwave detectors. There are physiological detectors that provide automatic measurements of heart rate, temperature, blood pressure, electromyograms, and electroencephalograms. These devices can work remotely which further facilitates the observation process and allows data to be collected more easily and efficiently.

**Check sheets.** In a typical check sheet, columns indicate categories of behavior and rows indicate successive sample intervals. It is important to include information such as date, time, and subject at the top of the sheet. Check sheets provide an inexpensive and flexible technique for easily recording behavior in real time. At the end of a sample period (typically denoted by a signal from a timer), the recorder simply moves to the next row and starts recording all behaviors that occur within that sample interval. This type of recording can be used with different types of observational methods (e.g., focal-animal, scan sampling, ad libitum sampling). It is common to use different parts of a single check sheet for different types of sampling procedures during a single observation period. Continuous recording, instantaneous sampling, and one-zero sampling can all be used in a single check sheet. Check sheets are not ideal when duration of behaviors is of interest since you do not indicate the precise time a behavior is observed, only the sampling period in which it was observed. In order to be analyzed, the data from the hand-written check sheet can be entered into a computer. Check sheets are typically done with paper and pencil, and the data is then entered into a computer. It can be a time-consuming and tedious process to convert this paper data into a digital record that can be used for analyses.

**Event recorders.** Computer event recorders and mobile software applications have been

developed that allow an observer to directly input behavior observations directly into a digital format. Typically, a specific keypress is associated with a certain behavior. The software recognizes the key and the time at which it is pressed. There is also the ability to build in modifier keys to provide further detail of the behavior (e.g., actor and recipient). Other programs allow users to directly input their ethogram into the program and record behaviors and times by selecting the appropriate item. A computer event recorder and software applications provide several advantages over a paper and pencil check sheet. Because the time is coded in the keypress, this data can be used to determine accurate durations of behavior. This is not possible with the paper and pencil check sheet which does not have precise times of behaviors. Limitations in size also prevent observations of larger numbers of behavioral categories on a single sheet. A computer event recorder is not limited in this way and can therefore collect data regarding more behavioral categories. It is also possible to observe more rapidly occurring sequences of behaviors. Computer event recorders have an additional advantage over the check sheet because they eliminate the need to convert the paper data into a digital format that can be analyzed on a computer. These recorders also eliminate the need to store large amounts of paper data that can take up substantial physical space. One of the drawbacks to these recorders is that they often do not offer the flexibility of a paper check sheet in terms of immediate modification of a glitch in the program may cause data loss. It is important for the recording device to fit the research question and the behavioral categories being studied rather than trying to alter the way behaviors are recorded to fit the device.

## Validity and Reliability

**Validity.** Validity refers to the ability of a measure to accurately measure what it claims. A researcher studying aggression needs to be confident that the behaviors being observed are the appropriate behaviors to assess aggression. Three things to consider when deciding if a measure is valid are accuracy, specificity, and scientific validity.

Accuracy refers to the extent to which the measured values correspond to the actual values, thus ensuring there is no bias in the measure. Specificity refers to the ability of a measure to describe only what is being measured and nothing else. Finally, scientific validity is the extent to which the measurement procedure reflects the processes being studied.

**Reliability.** Reliability describes how consistent and repeatable a measure is. There are four factors related to how reliable a measure is. Precision describes how free the measurement is from random errors. Sensitivity refers to the degree to which small changes in the true value are reflected by changes in the measured value. Resolution is defined as the smallest change in the true value that can be detected by the measurement. Consistency is the ability to produce the same results over repeated measurements. In studies on animal behavior, the observer is the measurement tool and therefore must be a reliable measurement instrument. There are two aspects of reliability that are important to consider when observing animal behavior. The first is intra-observer reliability or the degree to which one observer obtains the same results when measuring the same thing on multiple occasions. For example, the observer should code the same sample period on two or more occasions, with similar results for each observation time. This should be repeated multiple times throughout the study depending on its length. Interobserver reliability is the extent to which two or more observers obtain similar results when measuring the same time period simultaneously. When a study utilizes two or more coders, it is necessary that both intra-observer and interobserver reliability are ensured.

**Measuring reliability.** One common way of measuring reliability is through a correlation coefficient. A value of +1.0 represents a perfect correlation, and a value of 0 represents a complete lack of any association. A correlation coefficient can be obtained for each behavior category under investigation. The criterion used to determine what value is deemed "reliable" can vary; however, values between 0.70 and 0.80 are commonly used as criterion values. Correlation coefficients higher than these values would be considered indicative of good reliability. There are other

means of calculating reliability beyond the correlation coefficient. The index of concordance is a measure that can be used when nominal or categorical data is used. This technique compares the total number of agreements and disagreements and provides a percentage of agreement. Cohen's kappa is another procedure used to calculate reliability. This value corrects for agreements that are the result of chance alone.

In the event that two observers are not reliable, there are two options for correction. First, the measures can be redefined to make them more restrictive in order to resolve any ambiguity in the measure. Second, it is possible to combine two or more unreliable measures to determine if together they represent a reliable combined measure. This can eliminate redundancy and reduce the number of categories.

Observer bias (also referred to as experimenter bias) occurs when an observer sees what he or she expects to see. In order to avoid observer bias whenever possible, individuals coding for behaviors should not be aware of the research question and hypotheses of the specific experiment. It is also important to consider how the influence of the observer being present can influence the behavior of the animal. It is possible that repeated exposure to the presence of the researcher can habituate the animal to the observer and minimize the effect of the presence of the researcher. Use of automated equipment, discussed previously, provides another means to limit the effect the exposure to the observer can have on behavior. Whenever possible, measures should be taken to limit the likelihood animals will become aware of the researcher and alter their behavior.

## Cross-References

- [Ethogram](#)
- [Focal Animal Sampling](#)

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## Occipital Lobe

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## Definition

The occipital lobe is one of the four primary lobes of the cerebral cortex, which is largely responsible for visual processing. It is located in the posterior part of the brain.

## Introduction

The occipital lobe is the smallest of the four primary lobes of the cerebral cortex and contains the primary function of vision processing (Purves 2012). It is located in the posterior portion of the brain, behind the parietal and temporal lobes. The occipital lobe lies directly under the occipital bone of the skull. The occipital lobe is a part of the telencephalon, which is a division of the forebrain. The parieto-occipital sulcus lies on the medial surface of the brain and demarcates the occipital lobe from the parietal lobe (Mancall et al. 2011). The occipital lobe rests upon the tentorium cerebelli, a thick membranous layer of dura mater that is used to demarcate the occipital lobes from the cerebellum. It receives its blood supply from several branches of the posterior cerebral artery (PCA).

## Visual Processing in the Occipital Lobe

The occipital lobe can be divided into several anatomical regions, including Brodmann areas 17, 18, and 19, which are arranged hierarchically



within the occipital lobe (Mancall et al. 2011). The most notable region is known as the primary visual cortex (V1) or Brodmann area 17. The primary visual cortex is located on the medial side of the occipital lobe within the calcarine sulcus. If the V1 is stimulated, the person reports flashes of light. To understand the function of the primary visual cortex, it is helpful to understand the basic pathway of visual information (Tsuchitani n.d.). Visual information travels from the retina by the optic nerve, which becomes the optic tract after the optic chiasm, towards the thalamus (Grill-Spector 2015). The visual information arrives at the lateral geniculate nucleus of the thalamus where the axons synapse. The final stop of the basic visual pathway is the **primary visual cortex**, which is located on the medial aspect of the occipital lobe. Visual information may undergo further visual processing in the temporal and/or parietal lobes. There are two pathways for visual information to undergo further processing, which both originate in the occipital lobe: the ventral pathway and the dorsal pathway. The ventral stream projects information to the temporal lobe and results in knowing what the particular object is. The dorsal stream projects information to the parietal lobe and is involved in knowing the location of an object. Another notable area of the occipital lobe is the lateral occipital complex that has been found to hold distributed representations, which can be understood as the usage of spatial activity patterns to create a specific representation of objects (Ishai et al. 1999). The occipital lobe also contains peristriate regions, which are involved in the perception of shape and colors, discrimination of movement, and visuospatial processing.

## Damage to the Occipital Lobe

Damage to the occipital lobe results in visual defects, ranging from partial or complete blindness or visual agnosia, which can be defined as the inability to recognize or interpret visual information. The degree of blindness or visual agnosia depends on the exact location and the severity of the damage. Bilateral damage to the occipital

lobe, most often the result of cerebrovascular disease, can result in cortical blindness or Anton's syndrome, which is a form of anosognosia (Maddula et al. 2009). Anosognosia occurs when individuals have an unawareness of their own disorder or defect. In the case of individuals with Anton's syndrome, the patients behave and act as if they can see, despite their loss of sight, which usually presents with confabulation or the creation of false memories (Sacks 1985).

Injury to one side of the occipital lobe results in homonymous hemianopsia, which is loss of vision of the same field in both eyes. A lesion in the primary visual cortex results in a scotoma. A scotoma can be defined as an area of decreased light sensitivity on the retina (Cheung and Legge 2005). Some visual information is still available to those with scotoma so some people can still react to stimuli even though there is no conscious perception of them, which is known as blindsight (Danckert and Goodale 2000). Occipital lesions can cause visual hallucinations, while lesions in the parietal-temporal-occipital association area are associated with color agnosia, movement agnosia, agraphia, and alexia.

## Cross-References

- [Blindsight](#)
- [Parieto-occipital Sulcus \(POS\)](#)
- [Vision](#)
- [Visual Recognition in Birds](#)

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## Occlusion

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### General Information

Occlusion derives from the Latin *occludere*, a verb that means “to close up.” Its origin should provide an obvious hint regarding its utilization in the modern day: when something is occluded, it is blocked off or obstructed (McCoy 2013). Vascular occlusion, which occurs when a blood vessel is clogged, is responsible for many morbidities commonly associated with ischemia. Ischemia occurs when blood supply to tissues is restricted, depleting the downstream tissue of molecules like oxygen and glucose needed to keep the tissue alive through cellular metabolism. A common example of an occlusion is that of a coronary artery, called a myocardial infarction, that leads to heart attacks; the occluding agent in heart attacks is often a blood clot that blocks the passage through the artery, obstructing blood flow (Ferdinandy et al. 2014).

Common jargon related to occlusion includes terms like thrombus, embolus, ischemia, and infarction. A thrombus is a blood clot that forms in the blood stream or in the heart, while an

embolus can be anything that travels in the blood vessel until it reaches a vessel too narrow to let the object pass. When the object cannot pass through this smaller vessel, an embolus blocks blood flow and leads to occlusion. An embolus can be a myriad of objects such as fat, a tumor, or even a foreign object. When a piece of a blood clot breaks off and then gets stuck due to a narrow vessel, this agent is referred to as a thromboembolus because it is a blood clot that formed in the artery or vein and was too large to continue through the blood vessels. As expected, an embolus is more common in narrower arteries (Welch 1899). Recall that ischemia is the result of a decrease of blood supply to tissue that results in tissue dysfunction or even death due to the depletion of metabolic nutrients. An infarction results from prolonged ischemia and refers to the death of tissue due to the loss in blood supply (Fluri et al. 2015).

### Occlusion and Stroke

Stroke incidence and related fatality rates have been in a decline due to several implemented measures meant to control cardiovascular risk factors such as cholesterol or smoking cessation programs (Mozaffarian et al. 2016). In addition, the decline can be contributed to improved prevention and care once acute strokes occur (Jauch et al. 2013). While the decline in the number of stroke in the USA has fallen around 18.2% and the fatality rate has declined by 33.7%, this does not mean strokes are not as impactful on the population. This substantial decline has only lead to stroke becoming the fifth leading cause of death in the USA, instead of fourth. In fact, it has been reported that in 2013, 1 in 20 deaths in the USA were due to stroke, with a stroke occurring every 40 seconds and a death due to stroke occurring every 4 minutes in the USA alone (Mozaffarian et al. 2016). Still, this is a major improvement from just 5 years prior, as stroke was ranked as the third leading cause of death in the USA in 2008 (Jauch et al. 2013).

Like myocardial infarctions, large strokes are usually the result of at least one large vessel occlusion that leads to decreased blood flow and

eventually ischemic injury regions of the brain such as the ► [hippocampus](#) or the ► [hypothalamus](#). These ischemic strokes are referred to as cerebral infarctions. Brain imaging is often a priority to understand the location and size of the occlusion. Occlusion of a large vessel, such as the middle cerebral artery or MCA, leads to increased density in a CT scan of the brain. A large vessel occlusion often causes a severe stroke and helps predict neurological deterioration. A hyper-dense MCA can be seen in up to half of thromboses, or blood clotting (Jauch et al. [2013](#)).

### Animal Models of Ischemic Stroke Involving Occlusion

Due to the significant effect of strokes on society, there is a keen interest in the scientific community to study the effects of large vessel occlusion in arteries such as the MCA. Due to the nature of occlusion studies, it is easier to study the mechanisms of occlusion and stroke in animals than it is to experiment with the effects of large vessel occlusions on human participants due to concern for welfare. Studies using animal models have greatly expanding the knowledge around mechanisms of occlusion and have proven to be of great benefit to stroke patients. Rats and mice commonly serve as models of ischemic strokes, but there exist many different animal models. The use of animal models in stroke research has aided our understanding of the physiology and pathology of stroke in humans. Many of these animal models are considered induced models, a term that refers to animals in which the condition is caused experimentally. For the rats used in many occlusion studies, an occlusion is introduced that induces the stroke (Casals et al. [2011](#)).

There are many occlusion mechanisms to induce ischemia, such as blood vessel constriction, infarction, middle cerebral artery (MCA) occlusion, and macrosphere embolization. MCA occlusion is performed by injecting blood clots to obstruct circulation through a carotid artery into the head, which then go on to block blood flow. Artificial macrospheres between 100 and 400  $\mu\text{m}$  model occlusion of the MCA using sutures, while

microspheres around 20 to 50  $\mu\text{m}$  occlude smaller vessels. Macrospheres are injected into the internal carotid artery and lead to focal, or localized, ischemic lesions, while microspheres are inserted into either the MCA or the internal carotid artery and lead to multifocal infarcts. These artificial spheres are injected into vessels to obstruct blood flow and induce ischemia, like the injection of blood clots (Fluri et al. [2015](#)).

Endovascular filament middle cerebral artery occlusion is an animal model specific to rats and later adapted for mice of focal cerebral ischemia that was developed in 1986. It consists of a filament or intraluminal suture that obstructs blood flow when inserted into the vessel at the base, or origin, of the MCA; the occluding agent can be inserted and removed periodically at will to restore or obstruct blood flow, or left in the vessel permanently. When the MCA is reperused, or re-oxygenated, via the withdrawal of the suture, this is referred to as transient middle cerebral artery occlusion. The longer the artery is occluded, the more severe the ischemic change in the tissues that the artery leads to (Ansari [2011](#)).

### Other Forms of Occlusion

Occlusion is not specific to the blockage of blood vessels and is used in dentistry and visual psychology as well. Dental occlusion refers to how the upper and lower teeth touch each other when the jaw is closed, with malocclusion referring to when the teeth do not close properly (McCoy [2013](#)). The occlusion of a retinal artery slows blood flow to the retina, causing vision loss in the ischemic retina due to dysfunctional tissue (Moshiri [2015](#)). External of our body, visual occlusion occurs when a view is obstructed in some shape of form. Studies have shown that as occlusion increases, the ability to process visual movement, or ► [optic flow](#), deteriorates by having participants catch tennis balls while wearing spectacles that provided ► [vision](#) at specific frequencies. As the duration of occlusion increases, it becomes difficult for people to process the ► [perception](#) of ball movement accurately (Elliott et al. [1994](#)).

## Cross-References

- [Animal Welfare](#)
- [Death](#)
- [Dentition](#)
- [Hippocampus](#)
- [Hypothalamus](#)
- [Optic Flow](#)
- [Perception](#)
- [Vision](#)

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## Ocelli

- [Plantae](#)

## Ockham's Razor

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## Synonyms

[Morgan's Canon](#); [Parsimony](#); [Principle of simplicity](#)

## Definition

This epistemological principle states that, among a few solutions for a problem, the simplest explanation is usually the best.

## Introduction

Ockham was a Franciscan philosopher who lived in the late Middle Ages. Historical sources date his birth in Ockham, England, around 1290 and his death probably in Munich in 1349 (Leahey 2012). He formulated the Ockham's razor principle, a rule of thinking that considers the simplest explanations as more likely to be correct. The name comes from Ockham's reject of Platonism's ideas, cutting through the previous apogee of metaphysics and

opening the age of empiricism. Through the formulation “*Pluralitas non est ponenda sine necessitate*,” Ockham explained the need to discard superfluous interpretations first (Epstein 1984).

This principle is also called principle of parsimony (*Lex parsimoniae*), working as a synonym of this economic view of scientific explanations. Used in a scientific context, Ockham's razor has been employed to test the possible hypothesis that explains a phenomenon, finding an order from simpler to more complex explanations. Popper and the falsifiable method (Popper 1968) established that the assumption of theories is based on the occasions which a theory would fail. Considering the power of the Parsimony principle, the razor principle could be applied and then possible explanations proven false from simplest to more complex. Ockham's razor could serve as an epistemological guide to sort out between different theories that could explain a phenomena (Rodríguez-Fernández 1999).

### Ockham's Razor in Animal Cognition

The Ockham's razor had its own application in terms of animal cognition: it is the Morgan's Canon. Lloyd Morgan was an author who marked the early stages of comparative psychology in the late nineteenth century, investigating animal abilities outside the frame of a human perspective. Morgan applies the Ockham's razor in terms of how to understand psychological faculties in the animal kingdom. The Canon says that if any animal's ability can be explained by a simpler process, it is better than to assume higher faculties are involved. A perfect example of the Canon (in terms of Morgan) or the razor (in terms of Ockham), was the case of Clever Hans (Boakes 1984). Hans was a horse that lived in the early twentieth century, and his owner claimed that Hans possessed the ability of mathematical reasoning, showing that the horse could response correctly to sums through knocking the appropriate number with the hoof in the floor. Pfungst, the researcher responsible for elucidating Hans's abilities, proved that the horse did not reason in arithmetic terms by using the parsimony principle and

thus proving Morgan's Canon. The animal could read the nonverbal expression of its interviewers and detect when to stop knocking.

Parsimony marks the direction in which scientific knowledge explores nonhuman animal cognition, needing complex controls and experimental conditions to prove higher faculties in animals, avoiding humanistic and presentisms bias.

### Implications

The implications of Ockham's razor, apart from how we judge the capacities of other lifeforms, are the ways on how the scientific community accepts or rejects certain revolutionary ideas. This directly connects parsimony with Kuhn's theory of scientific knowledge (Kuhn 1957; Rodríguez-Fernández 1999).

At this respect, taking the simplest explanation as always valid can lead to the rejection of some theories that could be correct, despite being more complex (Gernert 2007). This trend of judgement could bias patterns of explanation in some fields of science, for instance, taking for granted that animals do not exhibit higher cognitive faculties, like numericity perception or language, without exploring all the empirical options and experimental dispositions to show them.

The parsimony was also reformulated in economy of cognitive efforts by Ernst Mach (1897). Mach applied Ockham's razor in his principle of simplicity. This principle says that the cognitive systems clearly prefer the simplest configurations of information, like plain descriptions and simple cognitive paths. Later, cognitive psychology took over from Mach. It is the case of human causal judgement research, in which several research lines have confirmed that humans prefer simplest explanations (Pacer and Lombrozo 2017), because it seems to bring more control of their causal environment.

Parsimony is still a central concept in the evolution of science that remains in effect from its formulation in the fourteenth century to the present day. Following Ockham's formulation of the power of simplest explanations, a few authors have proposed their own version of the razor



principle in different fields like comparative psychology or cognitive research, claiming the time-less relevance of parsimony.

## Cross-References

- [Clever Hans](#)
- [Comparative Psychology](#)
- [Morgan's Canon](#)
- [Parsimony](#)

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## Oddity

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## Synonyms

[Matching-to-sample](#); [Mismatch hypothesis](#); [Non-match-to sample](#); [Oddity concept](#), [Oddity problem](#), [Oddity task](#)

## Introduction

The easiest version of the oddity task requires an animal to choose among three discriminanda (typically objects, but sometimes two-dimensional illustrations, or computer images). Two objects are identical (the nonodd objects) and the third, odd object, differs in all properties (color, form, size, etc.) from the nonodd objects. Typically, objects are presented side by side in a row, and the animal learns to choose the odd one. Controls must include varying the position of the odd object (i.e., odd object must not appear predictably in a single position in relation to the nonodd objects). Also, when real objects are used, correct responses are usually reinforced with a bit of food hidden beneath the odd object, control must be use to prevent the animal from detecting the odd object based on the odor of the reinforcer. Inadvertent cueing by the experimenter must be controlled, and other controls may be necessary depending on the design of the oddity task. Assuming all necessary controls are used and the animal attains a statistically significant criterion of correct responses, one may conclude that the animal learned the oddity problem.

## The Oddity Concept

Oddity problems involving the same discriminanda on each trial can be learned by rote via trial and error, which is not of interest to most investigators. Rather, they want to know if an animal can learn the oddity concept. Investigation of oddity concept learning is achieved best by using new objects on each trial, although the same objects may be used more than once, provided the same odd and non-odd objects are never used together twice. Thomas (1996) discussed the kinds of evidence and control procedures necessary to show any kind of concept learning including oddity.

Many investigators using numerous avian and mammalian species have reported use of the oddity concept, but owing to methodological flaws, most conclusive studies with robust results have been limited to research using primates.

## The Oddity Concept: Theoretical Considerations

One of the twentieth century's most brilliant but mostly forgotten behavioral primatologists, Henry Nissen wrote:

Without taking the time now to elucidate the argument, let me categorically suggest that all reasoning reduces to three processes, responsiveness to identity and to difference, and, thirdly, the balance or relevant weight given to each of these. (Nissen 1958, p. 194)

Nissen did not suggest systematic ways to manipulate "the balance or relative weight given to each." However, Bernstein (1961) introduced dimension-abstracted oddity, which moved far beyond the easier oddity concept problems already described. Bernstein used five discriminanda per trial, and to illustrate with one example, five objects differed in sizes and shapes, but four had the same color, a color that differed from the color of the odd object. On other problems, size or shape might determine the odd discriminandum.

### Hierarchies of Oddity Concept-Learning Problems

Building on Bernstein, Thomas and Frost (1983) developed and tested squirrel monkeys on a six-level hierarchy of theoretically, increasingly difficult oddity problems based on variations of color, form, and size, together with manipulation of relevant, constant, and ambiguous cues; constant cues are identical for all objects and ambiguous cues vary among objects in noninformative ways. For example, level 1 (easiest) had three relevant cues; that is, the odd object differed from the nonodd objects in color, form, and size. Level 6 (difficult) might be a problem where all objects differed in form and size, but the odd object and nonodd objects differed in color. The hierarchy can be summarized as follows where R = Relevant cue, C = Constant cue, and A = Ambiguous cue.

#### A Hierarchy of Oddity Problems

1. 3R 0C 0A
2. 2R 1C 0A
3. 1R 2C 0A
4. 2R 0C 1A
5. 1R 1C 1A
6. 1R 0C 2A

Thomas and Frost's monkeys' performances confirmed the hypothesized levels of difficulty except performances were worse on level 3 than level 4. This was explained by squirrel monkeys being protanomalous (deficiency in the retinal cone pigment, erythopsin, which reduces the ability to discriminate wavelengths of light at the red end of the visible portion of the electromagnetic spectrum), and often the single relevant cue at level 3 was color.

Thomas (1996) extended the six levels to ten by adding numerosness as a cue. Thomas (1996) did not specify the ten levels (which the reader can do by following the logic used to develop the six-levels above), but Thomas illustrated an "easy" oddity problem with numerosness as an added cue with two sets of three small white circles as the nonodd discriminanda and two large black squares as the odd one; color, size, and number were relevant. For "difficult," he showed a set of four small white circles, a set of three small black triangles, and a set of two large striped squares. In that case, color, form, and numerosness were ambiguous; size was relevant.

Related to oddity, Thomas also described comparable levels of Sameness-Difference discrimination problems where, typically, two identical or more similar discriminanda must be distinguished from two more clearly different discriminanda. An "easy" example might be two red balls for "sameness" and a green cylinder and a yellow block for "difference." A "difficult" example might be a medium-size small red ball and a large green ball for "sameness" and a small blue block and a large yellow cylinder for "difference." Thus, form is relevant, and size and color are ambiguous.

### Oddity Concept and Learning Set Formation

Harry Harlow, a pioneering investigator of animal learning wrote,

... all concepts ... evolve only through LS [learning set] formation [and] insightful learning through LS formation is a generalized principle [that] appears ... in oddity learning. (Harlow 1959, p. 510)

In Harlow's typical experiment, learning set formation (LSF) was assessed by presenting animals

(usually monkeys) with two new objects for six trials. The experimenter determined which of two objects when chosen would result in a food reinforcer, and the reinforced object's position varied unpredictably to the left or right of the non-reinforced object. The animal had no way to know on trial 1 which of the two was correct. After six trials, two new objects were presented for six trials and the reinforced object's location was varied. The animal could choose only by chance on trial 1, but if it learned to use the information gained on trial 1, it could respond successfully on trials 2–6. Performance on trial 2 is typically used as the best measure of LSF.

Warren (1965) suggested that LSF might be a good way to compare species on learning ability, and he presented a graph where the ordinate was percent correct on trial 2 and the abscissa was the number of six-trial problems. His graph had data for six species. Rhesus monkeys were 85% correct on trial 2 after 400 problems, but rats were 55% correct after 1800 problems. Hodos (1970) presented a similar graph that included 2 human children and 16 additional species. One human child (age unspecified but IQ = 136) achieved 100% correct on trial 2 in 100 problems, a chimpanzee achieved about 95% correct in 150 problems, and a rat achieved 55% in 1000 problems.

However, Warren (1974) changed his opinion and concluded that success on LSF better reflected visual capability than learning ability. Almost all testing had been done with discriminanda based on visual cues, and color was usually an important cue. Old world primates and apes have trichromatic color vision comparable to humans with normal color vision, whereas many mammalian species have poor color vision, and rats have poor vision overall.

### Rats, Oddity, and LSF

Rats have significantly better olfactory than visual abilities, and Langworthy and Jennings (1972) used a simple and inexpensive way to present olfactory discriminanda to study oddity concept learning by rats. Their experiment might also show LSF. They used ping-pong balls saturated with the odors of one of eight food flavorings. Because a given odor might be odd on some

problems and nonodd on other problems, no odor could be associated exclusively with either odd or nonodd.

Three balls, two of the same odors and the third of a different odor, were presented side by side in a mostly open-air chute (please see Fig. 1 in Langworthy and Jennings, 1972, p. 88) in which the balls were inserted. Marks on the chute showed how far the rat had to nudge the ball aside to access the food cup beneath it. The rats' task was to nudge the "odd" ball aside sufficiently to get its food reinforcer. Langworthy and Jennings (1972) reported good results (which Thomas and colleagues later analyzed and found to be statistically significant), but it was unclear whether the food reinforcer was beneath only the odd ball. If so, it is possible that the rats detected the correct ball by smelling the food beneath it.

Bailey and Thomas (1998) also investigated oddity concept learning by rats using odoriferous ping-pong balls. They used 18 odors. With 18 odors used two at a time where either might be odd or nonodd, 306 odor-unique problems can be constructed. Furthermore, because a given odor might be odd on one trial and nonodd on another, no odor was reliably odd. They baited all food wells each of which was covered by a small sliding board. Only the board for the correct choice was moved to expose the food well upon a correct response; so, food odor could not influence the rats' oddity choices. They presented each new problem for 20 trials/day until a rat achieved 16 of 20 correct for two successive days, or until a maximum of 100 trials were presented, after which a new problem was presented. Bailey and Thomas found no evidence of oddity concept learning, because trial 1 performances were at chance levels. However, Bailey and Thomas (1998) found significant evidence of LSF. They found that their four rats averaged 87% correct on trial 2 on problems 16–30 which compares favorably to the chimpanzee's performance seen in the graph in Hodos (1970). Using only first-trial data, one rat had two statistically significant, near-perfect runs, but it did not sustain those performances. Nevertheless, those data suggest that rats might learn the oddity concept with alternative training methods.

## Concluding Remarks

The oddity concept appears to have been investigated in more species than any other concept-learning task, and, historically, it appears that few, if any, nonprimate species have been robustly successful. However, more nonprimate species might be successful with improved methods including that contextual variables (sensory, effector, motivation, environmental, etc.) are suitably adapted to each species (see Thomas 1996), such as, olfactory rather than visual discriminanda for rats.

Greater attention should be given to Nissen's theory (see above) of what most importantly constitutes reasoning, and the hierarchies of oddity tasks and sameness-difference tasks described here provide the means for further investigating Nissen's theory.

## Cross-References

- [Categorization](#)
- [Evolution of Animal Color Vision](#)
- [Harry Harlow](#)
- [Olfactory Discrimination](#)
- [Same/Different Learning](#)

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## Oddity Concept

- [Oddity](#)

## Oddity Learning in the Rat

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## Synonyms

[Difference](#); [Relational understanding](#)

## Definition

Oddity concept learning is an ability to identify an odd stimulus from two or more identical stimuli. If the subject can consistently pick the odd stimuli from the identical stimuli across different oddity training tasks and can apply this experience to the novel set of stimuli, it is considered that the subject has acquired oddity concept learning. For example, a stimuli set involves an odd stimulus “Blue circle” and two identical stimuli “Red squares.” Animals are required to discriminate an odd stimulus (blue circle) from the stimuli set

(one blue circle and two red squares). Transfer of the oddity discrimination to a novel oddity stimuli set (e.g., a purple star and two triangles) in the first trial of a transfer test can be interpreted as evidence of abstract oddity concept learning (Wright 1991).

## Introduction

Oddity concept learning has been studied to gain an understanding of comparative learning abilities and the evolutionary origin of animal intelligence (Thomas and Noble 1988). Oddity relates to the same/different (S/D) concept, which is an ability to identify a S/D stimulus from item pairs in discrimination training and its successful transfer [e.g., more than chance level or equivalent to baseline performances (performances of training stimuli during testing trials) that should be 80% or more than 80% correct performances] to novel stimuli in the first trial of the transfer test. Lazareva and Wasserman (2008) opined that responding to members of one stimulus class with a similar strategy and to members of another stimulus class with a different strategy as well as an accurate transfer of training tasks to novel members of the class forms an abstract concept. To study the inter-relations among complex learning, memory, information processing, and perception, an appropriate paradigm should be selected.

The oddity relation is considered abstract because the subject has to be able to store in memory a functional representation of relational understanding between an odd stimulus and identical stimuli (Langworthy 1971). To meet the criteria for evidence of the oddity concept, simply picking an odd stimulus from two or more identical stimuli in a set is not sufficient. Animal subjects are required to identify and retain logical relations among stimuli and to apply this relational understanding to sets of novel stimuli. This relationship does not exist in the physical environment and as concrete entities (Taniuchi et al. 2017). Therefore, to encode the abstract aspects of the discriminative stimuli, higher-order cognition is required.

Rats' abilities to acquire oddity concept learning have been misrepresented because of methodological issues. Past oddity studies (e.g., Koronakos and Arnold 1957; Thomas and Noble 1988; Wodinsky and Bitterman 1953) could not show evidence of oddity learning in rats due to the use of one-odd tasks or two-odd tasks or serial presentation of multiple oddity tasks. Conversely, recent oddity studies (e.g., April et al. 2011; Lazarowski et al. 2019; Taniuchi et al. 2017) were able to show evidence of oddity concept learning in rats by employing multiple concurrent oddity tasks. In this entry, the focus is on the improvement in rats' oddity performances from the original oddity studies (e.g., Koronakos and Arnold 1957; Thomas and Noble 1988; Wodinsky and Bitterman 1953) until today, and some critical parameters (e.g., concurrent presentation, the use of a large number of stimuli) that enabled various species (e.g., rats, monkeys, and pigeons) to demonstrate oddity concept learning. The fact that the same critical parameters also enabled other species (e.g., monkeys and pigeons) to acquire oddity concept learning suggests that these species employ a similar learning strategy to process the discrimination tasks. Testing whether similar neural mechanisms may be in operation across various species during the higher-order learning tasks may advance our understanding about comparative cognition.

Cook, Katz, and Cavoto (1997) concurrently trained pigeons to discriminate odd-item different displays from same displays using a two-alternative forced choice task in which a same and a different display were presented. Each display differed in terms of shapes, pictures, and other elements [e.g., six same pictures (same display) vs. five same pictures and a different picture (an odd-item different display)]. Cook and colleagues found that pigeons could discriminate odd-item different displays from same displays and apply this relational strategy across a variety of simultaneously presented visual items. Although the pigeons showed an acquisition of oddity concept learning with stimuli containing multielements, some perceptual cues became evident in pigeons forming oddity concept learning. The presentation of two or more identical stimuli



along with an odd stimulus in a trial might induce a perception (the process of recognizing and interpreting sensory stimuli) of sameness among identical ones that made an odd stimulus salient by contrast. The sense of sameness among identical stimuli and the salience of an odd stimulus might make the S/D tasks easier for pigeons. Lombardi et al. (1984) also provided evidence in support of pigeons' oddity concept learning. Ten pigeons were concurrently trained with multiple oddity problems dividing them into two groups. One group, the "Few examples group" was trained with five visual patterns. Another group, the "Many examples group," was trained with 20 visual patterns. Different oddity problems were exchanged trial-by-trial. The main training began with a pattern, the sample stimulus, being projected on the middle key. A peck at the middle key created two comparison stimuli, one that matched the sample and another one that had a different pattern. When pigeons responded to the odd pattern, they were reinforced. Whereas, when they responded to the identical pattern, they were punished with 3-s time out and the house light extinguished. After the successful acquisition training, two series of transfer sessions containing novel patterns were conducted. Pigeons of the "many examples" group demonstrated a concept-like rule in demonstrating better transfer than pigeons in the "few examples" groups, suggesting that a larger number of stimuli might facilitate the acquisition of oddity concept learning. Although Lombardi et al. (1984) did not analyze performance on the first trials of test problems, given that they gave no reinforcement feedback on the test trials (extinction test), the pigeons' performances could be attributed to abstract oddity concept learning. This evidence provided reliable evidence that a nonprimate animal could acquire oddity learning based on attending to the relation among stimuli.

In this study, one possible cue may have affected pigeons' discriminative behavior, that is, two presentations of the sample stimulus at every trial may enhance the differentness of nonmatching/odd stimuli that may facilitate pigeons to identify the nonmatching/odd stimuli correctly. Roitberg and Franz (2004) concurrently trained

17 African goats with visual oddity tasks (one odd and three identical nonodd stimuli in a set) simultaneously presented on a screen. The visual stimuli varied and gradually increased at different training phases. After the acquisition of training tasks, goats faced a transfer test involving 24 new discriminanda. Only one of 17 goats showed above chance level performances on the first trial of transfer tests involving new visual patterns. In testing oddity in a sea lion, Hille et al. (2006) suggest that the sea lion used different learning strategies, such as learning specific stimulus properties, the win-stay/lose-shift learning set, and the oddity concept learning, depending on the number of trials given for the oddity problem. When training with a single oddity problem was sustained until correct performance was attained, the sea lion seemed to learn specific stimulus properties because no progressive improvement in performance was observed for 10 consecutive problems. When the number of trials allowed for a problem was limited to 5, the sea lion seemed to use a win-stay/lose-shift strategy, because its performances progressively improved for trials 2–5 of a given problem but remained around chance for trial 1. This suggests that the sea lion's performance on trials 2–5 of a problem was based on the outcome of its response to specific features of discriminative stimuli on previous trials. When only one trial was given for each oddity problem and the win/lose information on previous trials became completely ineffective as a guide for correct responses on later trials, the sea lion appeared to use a relational oddity concept and to respond reliably on the first trials of novel problems. It becomes evident from the reviews of oddity studies with various species that concurrent training and the use of a larger number of stimuli may positively influence performance on oddity tasks.

Compared to monkeys and pigeons, the path of the attainment of oddity concept learning in rats was not so smooth. However, with the continuous efforts of researchers, robust evidence of an oddity concept has been found in rats (e.g., Lazarowski et al. 2019; Taniuchi et al. 2017). Hence, a question arises as to how rats acquired the oddity concept. Were the experimental procedures analogous to those testing other species

for oddity concepts? Monkeys and birds' cognitive abilities might evolve independently or concept learning abilities might evolve in common ancestors of monkeys and birds so that the ability is inherited (Pearce 2008). To compare these two possibilities, examination of concept learning abilities in nonprimate mammals, such as rats, is important. If much similarity in concept learning abilities is found among rats, monkeys, and pigeons, it would support the latter possibility of a common origin of concept learning. Rats can be used as a good animal model for relative class concept learning in pharmacological research. Developments in these areas may contribute to exploring the place of animal research in the study of emergent relations. Oddity discrimination learning has been measured using various experimental procedures. In common simultaneous oddity discrimination training, an odd stimulus and two or more identical stimuli are simultaneously presented in a row (e.g., ABB or BBA). Lashley (1938a) trained rats to choose a cross (X) presented with two circles (XOO) in a three window jumping apparatus or to choose a circle (O) presented with two crosses (OXX) in a stimuli set (concurrent presentation). After the third to fifth reversal, all rats were unable to consistently respond to the odd stimuli. In his subsequent experiments, Lashley (1938b) presented rats upright and inverted triangles on black and striated grounds in which the upright triangles were positive on the black ground and the inverted triangles were positive on the striated grounds.

Lashley's series of simultaneous oddity experiments revealed that rats could not learn the discrimination tasks on the basis that an item (e.g., A) which was correct in a trial might be incorrect in another trial. Rather, they learned the discrimination tasks based on a variety of specific configurations (e.g., XOO, XXO). In detail, rats might follow a strategy, for example, when an odd item X was presented with two identical stimuli OO, responding to item X led to correct solution. Conversely, when an odd item O was presented with two identical stimuli XX, responding to item O led to the correct solution. Simultaneous presentation of oddity problems was employed in other oddity studies with rats (e.g., Koronakos

and Arnold 1957; Wodinsky and Bitterman 1953). Recently, Taniuchi et al. (2017) simultaneously presented an odd stimulus and five identical stimuli (e.g., AAAAAB, BBBBBA) in a row in a wooden made discrimination box. After the presentation of multiple set of stimuli (e.g., ABBBBB, AAAAAB, CCCCCD, DDDDDC), rats were able to show significant test performances on novel tasks. One advantage of this procedure is that subjects have much opportunity to make comparisons between an odd stimulus and identical stimuli (as these ones are presented in a row), facilitating them to recruit some abstract properties from the oddity stimuli set. Non matching-to-sample (NMTS) discrimination task is another procedure to examine oddity discrimination learning in animals. As a measure of conditional discrimination and conceptual learning in humans and nonhuman animals, matching-to-sample (MTS) tasks have been used for over a half century. In MTS procedures, a sample stimulus (e.g., red) is shown to the subjects and then two comparison stimuli (e.g., red and green) appear on the screen. Subjects are typically reinforced for responding to one of the two comparison stimuli that matches the sample one (red). Alternatively, reinforcing responses to the non-matching stimulus is called oddity-from-sample (OFS), mismatching or nonmatching. In the example mentioned above, if subjects are reinforced for choosing one (green) of the two comparison stimuli (red and green) that does not match the sample one (red), it is called NMTS. Simultaneous NMTS implies that a sample stimulus (red) is, at first, presented and then two comparison stimuli simultaneously (red and green) appear. These three stimuli (red, red, and green) remain in view until a choice is made to one (green in case of NMTS) of the two comparison stimuli. Or a sample stimulus (red) is, at first, presented but disappears after some delay and then two comparison stimuli (red and green) are simultaneously presented. Lazarowski et al. (2019) examined identity and oddity learning in rats following the simultaneous MTS and NMTS procedures. In their studies, discrimination training began by inserting the sample tray into the chamber. After removing the sample tray, the

comparison tray was immediately placed simultaneously presenting two comparison stimuli, one of which matched the sample and the other did not match the sample (nonmatching/odd stimulus). In the case of oddity of nonmatching/oddity comparison, a response to one of the two comparison stimuli that did not match the sample was reinforced. In the case of matching comparison, a response to one of the two comparison stimuli that matched the sample was reinforced. Rats were divided into two groups; one was two-exemplar group and the other was 10-exemplar group. Each group was assigned to both MTS and NMTS conditions. For example, the first five training sessions of two-exemplar group belonged to MTS condition and the next five training sessions belonged to NMTS condition. A similar procedure was followed for the 10-exemplar group. After the discrimination training, rats were tested for generalized MTS/NMTS with novel stimuli. Their simultaneous NMTS procedures documented promising proof of oddity concept learning in rats trained with multiple exemplars.

In the case of NMTS procedures, acquisition may be accounted for in either of two ways. For example, if a sample is black and the comparison stimuli are black and red, it is expected that animal subjects may learn to avoid black on the side key, one of the two comparison stimuli (black and red) if sample stimulus (black) is presented in the center key and two comparison stimuli (black and red) appear in the left and right keys. In other words, the subject might follow a responding strategy "After pecking black on the center key, avoid pecking black on the side key." Such a rule (avoiding to peck black on the side key if black is presented as sample on the center key) is called  $S^{\Delta}$ .

But there is another possible candidate, that is, after pecking black on the center key, they may peck red on the side key. This is called  $S^D$  rule (Carter and Werner 1978). Hence, it is visible that in both MTS and NMTS experiments, the sample stimulus appears to function as a cue that facilitates to identify which one of the two comparison stimuli is the correct choice. If the animal subject learns the discrimination tasks on the basis of  $S^{\Delta}$

and  $S^D$  rule with a stimuli set of B (B,  $R^*$ ), his performances would not be better on a transfer trial with a green sample and a green and a blue comparison stimuli [G (G,  $B^*$ )], because he has not experienced these stimuli (green and blue) in previous sessions. According to  $S^{\Delta}$  and  $S^D$  rule, the acquisition of oddity discrimination learning might be limited to the specific features of the stimuli set, contributing to the formation of configural learning (learning the whole gestalt of each stimulus display and learning which comparison choice to make based on this global pattern). For example, oddity performance may drop after yellow has been substituted for blue or green as a sample, because the animal subject has not experienced these configurations involving yellow before. Even if the subject performs well on concurrent problems based on specific configural cues, he would not be able to respond appropriately to test problems consisting of novel stimuli, because when all stimuli are novel, features with already-learned stimuli will be ineffective in dealing with the new stimuli (i.e., transfer). Conversely, if learning is based on stimulus relations at the training phase, it is easy for the subject to apply this relational understanding to any novel stimuli set. Notably, to distinguish the oddity concept learning from configural learning, an examination of the transfer to novel stimuli is needed. According to Nakagawa (1993), concept formation in rats was influenced by some common responses (e.g., pressing the right lever or the left lever or choosing the right goal box or the left goal box), suggesting a responding strategy to associate configurations with lever pressing responses. Take for an instance, when rats went through the NMTS tasks, they might associate one configuration (e.g., ABB and BAA) with pressing the right lever and other configurations (e.g., AAB and BBA) with pressing the left lever. Thus, rats' discriminative choices were mediated by some common responses that might affect subsequent shift problems.

The oddity preference effect (OPE), a tendency to choose one of the two comparison stimuli that does not match the sample, has puzzled comparative researchers for nearly a half century. Wright and Delius (2005), in Experiment 1, trained two

groups of pigeons on matching-to-sample or oddity-from-sample tasks. Half of each group was given a sample reward and the other half received no sample reward. In Experiment 2, two transfer trials were intermixed (quasi-randomly) with six training trials. An oddity group without sample reward was tested with novel stimuli that differed in both color and texture from the training stimuli. Their studies showed that the oddity group without sample reward learned oddity tasks more rapidly than other groups (e.g., matching group with sample reward, matching without sample reward), suggesting that pigeons seemed to pay more attention on oddity comparisons without sample reward than matching with sample reward. In response to the question of how some aspects of experimental procedures contributed to producing OPE, Wright and Delius (2005) explained that, in oddity comparison, providing reinforcement for the selection of one of the two comparison stimuli that did not match the sample presumably increased the possibility to choose the oddity comparison and decreased the tendency to choose the sample comparison. The opposite phenomena might appear if comparison sample was rewarded.

It is worth noticing that discriminative choices are largely influenced by whether sample responding is rewarded. There may have been something common between OPE and the novelty preference in visual-paired comparison tasks. Zola and colleagues (2000) allowed monkeys to view a particular picture for a sufficient time and later gave them an opportunity to view the same picture and a novel picture. An interesting finding emerged; monkeys spent more time viewing the novel picture rather than the familiar picture. To decrease some concerns arising from NMTS, relational nonmatching-to-sample (RNMTS) tasks might be considered in which a pair of sample stimuli (e.g., AA) is, at first, presented and then two pairs of comparison stimuli (e.g., BB & CD) appear. After perceiving the relation between the pair of sample stimuli, the subject is required to respond to one of two pairs of comparison stimuli that does not indicate the same relation as that of the sample. As per the RNMTS, the subject is reinforced for responding to CD rather than

BB. In other trials, CD is presented as sample and EF and AA are presented as comparison pair of stimuli. The subject is reinforced for responding to AA that does not match the sample. In this procedure, no physical feature of the sample stimuli matches one of the two pairs of comparison stimuli. Internal relations between stimuli (e.g., relation between a pair of sample stimuli) rather than a representation of perceived stimulus are an indication of correct responding. So, relational matching rather than physical identity guides accurate choice responding. So far as it is known, RNMTS has hardly been studied with any animal species. Thus, RNMTS might be considered for future oddity studies with rats.

## Types of Oddity Tasks

One noteworthy aspect of previous oddity studies with rats is that animal researchers manipulated oddity tasks in different ways (e.g., one-odd task, two-odd tasks, and multiple oddity tasks). **One-odd task** allows an oddity task (e.g., AAB in which item A is an identical stimulus and item B is an odd stimulus) to be presented until the subjects meet the learning criteria (e.g., 80% correct response). A second task (e.g., CDD) is presented to the subjects in the same way as the first oddity task. In such manner, third, fourth, and so forth discriminations are presented. Koronakos and Arnold (1957) used 5-point discrimination oddity (in which rats had 5 options to make their discriminative choices) with 81-odd tasks to train rats in acquiring oddity concept learning. Rats were trained with each oddity task (one-odd task such as ▲●●●●) until they reached the learning criteria (e.g., 80% correct response). Following acquisition of learning criteria, rats were given second task (◆♣♣♣♣).

The next oddity tasks were presented in a similar manner. Research findings showed that five out of 20 rats could demonstrate gradually improved performances, which Koronakos and Arnold termed as learning set. Single-feature learning (learning based on the specific features of a single item) might be responsible for forming such learning set. It also became evident at the

initial stage of training with one-odd tasks (AAAAAB) in Taniuchi et al. (2017). This task can be solved by learning to respond to a specific item (e.g., item B in the case of AAAAAB), because one-odd task provides an opportunity to a specific item to be an odd item at every trial until the learning criteria is met. With this procedure, the subject may understand that responding to a specific item may lead to reinforcement. In Taniuchi et al.'s study (2017), rats went through the phase 1 training task consisting of one-odd tasks (AAAAAB). Although rats learned the one-odd task, when the same oddity task was reversed and presented as the second oddity task (BBBBBA) where item A was an odd stimulus and item B was an identical stimulus, their performances reached below chance level. It is not clear whether rats learned to approach item B or avoid item A in phase 1 training with the AAAAAB problem. Pigeons' NMTS studies (Zentall et al. 1981) showed that pigeons learned to avoid non-odd stimuli because their performances significantly deteriorated when replacing a matching comparison stimulus but not when replacing non-matching one with a novel stimulus. Similar tests would answer the question of whether rats learn to approach a correct odd stimulus or avoid incorrect identical stimuli in the one-odd task of Taniuchi et al.'s study (2017) with many identical stimuli. **Two-odd tasks** allow correct stimuli to be exchanged between two oddity problems (e.g., AAB and BBA in which item B and A are odd stimuli in the AAB and BBA oddity tasks, respectively) thereby discounting the possibility of learning by responding to a specific item. But there is an advantage of two-odd tasks that the subjects can solve these tasks by memorizing some configuration patterns of stimulus displays (e.g., AAB, ABA, BAA, BBA, BAB, and ABB). It is true that correct responding is limited to some configurations (e.g., AAB, ABA, BAA, BBA, BAB, and ABB) in AAB and BBA oddity tasks and it is possible for the subjects to work out the oddity problems by memorizing these configurations. But according to the criteria of oddity concept learning, the subjects must be able to transfer the training experiences to the first trial of transfer test with novel stimuli. If the subjects learn the

oddity training tasks by memorizing some configurations of stimuli, they cannot solve the novel tasks in the test trials because they will see the new configurations in the test trials that are different from training ones. However, two-odd tasks were reflected in Wodinsky and Bitterman's study (1953) who trained rats to choose a black card (positive) from two white cards (negative). The tasks were reversed [white card (positive) and two black cards (negative)] in the second tasks. Rats could concurrently learn four oddity problems in which positive and negative stimuli were exchanged among some problems. Although these authors found significant learning of four oddity problems, they did not examine transfer of oddity discrimination to novel stimuli, thus their findings could not eliminate the possibility of configural learning (a responding strategy based on the configurations of some specific items). Specific configural "patterns" of multiple stimuli presented together can be an effective cue for discriminative responses. If behavior is influenced by such a factor (control of stimulus configuration), the subject may show chance level performance when novel stimuli are substituted for the training stimuli, because he will see the new configurations in the novel set of stimuli in the testing phase.

**Multiple oddity tasks** involve many items as odd items in the discrimination training tasks. To confirm the acquisition of oddity concept learning, multiple oddity training tasks should be followed by test trials with novel sets of stimuli. Oddity studies with rats manipulated the presentation of multiple oddity tasks in some ways, for example, serial presentation of multiple oddity tasks and concurrent presentation of multiple oddity tasks. Thomas and Noble (1988) trained rats with multiple oddity problems (300 olfactory oddity problems in Experiment 2) serially changing problems every five trials. In particular, they presented rats a single task (e.g., AAB) at a time. Rats were required to discriminate an odd item from 2 identical items. When rats learned this task (e.g., AAB), the task was changed and shifted to the next task (e.g., CCD). In such manner, EEF, GGH, and so on were given to rats. These studies revealed chance-level performance on the first



trials of novel problems although there was progressive improvement of performances on trials 2–5 of a problem that could be attained by just win–stay/lose–shift strategy in which the subject stayed with a stimulus if it was reinforced (win). If rats could encode abstract relational properties of the stimuli set in the acquisition training, it would be evidenced in the first trial of the transfer test involving novel stimuli.

A single task could be solved simply by approaching a specific item. Take, for instance, an oddity task AAB could be solved by responding to item B. The same strategy was effective for the next task, CCD, where responding to item D led to the solution. In a sequential training procedure, learning by trial and error and responding to a specific item can be a simple and effective learning strategy. Abstract relational learning seems unnecessary for solving the task. However, serial presentation of multiple oddity problems resulted in configural learning. Recently, several oddity studies with rats (e.g., Lazarowski et al. 2019; Taniuchi et al. 2017) concurrently presented multiple oddity tasks, demonstrating evidence of oddity concept learning in rats. Taniuchi et al. (2017) trained rats to discriminate an odd object (B) from five identical objects (e.g., AAAAAB) in a row. After acquisition of the first task (e.g., AAAAAB), a second oddity task (e.g., ABBBBB) was added to the training, meaning that, AAAAAB and BBBBBA tasks were concurrently presented to rats (12 AAAAAB and 12 BBBBBA tasks in a session). The two-odd tasks (AAAAAB and BBBBBA) were followed by transfer test 1 involving novel stimuli sets CCCCCD and DDDDDC. Afterwards, novel tasks used in transfer test 1 were incorporated into the training tasks (12 oddity tasks consisting of 4 items A, B, C, and D) that were followed by transfer test 2 consisting of novel stimuli set EEEEEF and FFFFFE. They progressively increased the number of oddity tasks in different phases (e.g., one-odd task, two-odd tasks, and 12 oddity tasks). Their studies demonstrated that one rat (Rat 2) showed significant test performance for novel test sets EEEEEF and FFFFFE after concurrent learning of the 4 training problems with AAAAAB, BBBBBA, CCCCCD, and DDDDDC.

The discussions about the types of oddity tasks reveal that almost of all of the oddity studies with rats prior to 1990 examined oddity concept learning in rats with one-odd task (e.g., Koronakos and Arnold 1957) or concurrent presentation of two-odd tasks (e.g., Wodinsky and Bitterman 1953) or serial presentation of multiple oddity tasks (e.g., Thomas and Noble 1988) that resulted in single feature learning or configural learning. These studies did not use the concurrent presentation of multiple oddity tasks in a training phase and test the discriminative performances with the novel stimuli to confirm the acquisition of oddity concept learning. Recent researchers (e.g., Lazarowski et al. 2019; Taniuchi et al. 2017) made good use of the concurrent presentation of multiple oddity tasks in acquisition phases and tested rats' discriminative performances with the novel stimuli that yielded robust evidence in support of oddity concept learning in rats. Hence, it becomes clear that concurrent presentation of multiple oddity tasks and its transfer to the novel stimuli contributes to rats' oddity concept learning.

### Effects of the Number of Stimuli in Acquiring Oddity Concept

The number of training exemplars appears to be a critical parameter in the development of abstract concept learning. A limited set of training stimuli produces item-specific rather than abstract concept learning in animals, which may be reduced by the employment of a large set of training stimuli (e.g., Lazarowski et al. 2019; Taniuchi et al. 2017; Wright and Katz 2006). To understand which aspects of the procedures led to the acquisition of the abstract concept learning, Katz, Wright, and Bachevalier (2002) considered that the focus on which species had the cognitive capabilities to acquire abstract concepts should have been shifted to the process and mechanisms by which concepts were learned. Thus, Katz, Wright, and their colleagues (e.g., Katz et al. 2002; Wright and Katz 2006) developed the set-size expansion paradigm to employ multiple exemplar training in S/D concept learning. In Katz et al. (2002), monkeys were trained with

8-item sets in experiments 1, 2, and 3 following S/D procedure in which, if 2 pictures were the same, a touch to the bottom picture was reinforced, whereas, if different, a touch to the grey rectangle was reinforced. The set-size was increased from 8 to 16 pictures after six consecutive transfer test sessions. The set-size was further increased to 32, 64, and 128 pictures with transfer test on condition of criterion performances. The findings showed that monkeys' initial transfer was near chance (50%), indicating their dependence on the particular training items and the resulting stimulus displays.

However, transfer performances increased with increasing set-size. In particular, 57%, 71%, 82%, and 87% transfer performances were observed for 8-, 32-, 64-, and 128-item sets, clearly showing that set-size expansion played a critical role in acquiring abstract concept learning. Thus, the size of the training set was instrumental in producing S/D concept learning. Notably, monkeys showed full concept learning with the 128-item set, because their transfer performance (87%) was equivalent to baseline (89%). The role of set-size expansion was further strengthened by Wright and Katz (2006). They conducted experiments with monkeys and pigeons using S/D discrimination tasks in which animal subjects were reinforced to touch or peck the lower picture if two pictures were the same. If different, then a touch or peck to the white rectangle was reinforced. When an 8-item set was presented, subjects showed item-specific learning (learning based on specific physical features of stimuli or configurations of some stimuli). All monkeys and pigeons showed signs of some transfer (partial concept learning that was above the chance and below the baseline) after training with the 32-item set although monkeys showed 14% better transfer than pigeons. The training stimuli were further increased to 64-item sets that yielded improved transfer performances relative to that of 32-item sets. This improvement made the researchers believe that increasing the number of training stimuli might enhance the transfer to a further extent. Thus, they doubled the number of training stimuli and trained monkeys and pigeons with 128-item set followed by transfer test. Monkeys

showed full concept learning with the 128-item set. But pigeons' transfer performances were slightly less than baseline performances. Thus, to confirm acquisition of full concept learning, the stimuli set-size was further increased to 256 followed by transfer testing. Pigeons showed full concept learning. Wright and Katz (2006) proved again that set-size function for monkeys was the same as that of Katz et al. (2002). Set-size function may vary across different species. More specifically, expansion of stimuli set-size (e.g., 128-item set) does not affect various species' cognitive behavior similarly. Some species (e.g., pigeons) need more stimuli, whereas some species (e.g., rhesus monkeys) require fewer stimuli to attain full concept learning. Hence, it becomes clear that an expanded set of stimuli (e.g., 128-item set) may positively influence some species' cognitive behavior (e.g., rhesus monkeys) more rapidly than other species (e.g., pigeons). Thus, it can be said that set-size function might be highly functional for some species (e.g., rhesus monkeys), as a result of which they required comparatively less stimuli to attain full concept learning. Conversely, there are some animal species (e.g., pigeons) that needed a larger number of stimuli (e.g., 256-item set) to attain full concept learning, because set-size function did not seem to be highly functional in them.

From the discussions of Katz et al. (2002) and Wright and Katz (2006), two important factors emerge; full concept learning and partial concept learning. When transfer performances are equivalent to baseline performances (performance with training stimuli during test trials) and both are above 80% correct, it is considered acquisition of full concept learning (Wright and Katz 2006) and indicates that the subjects are making their discriminative responding realizing the relations between transfer stimuli as they are processing the training stimuli. Wright and Katz (2006) found that the larger number of exemplars might be a determinant of whether animal subjects would learn full concept learning or partial concept learning. The greater number of training stimuli may increase the possibility of some features of training stimuli to be shared with any given transfer stimuli. Thus, the number of exemplars during

the training phase has much importance for transfer performances.

It can be assumed that an expanded set of stimuli (e.g., 128 items, 256 items) enriches the categorical knowledge by increasing information on the generic features of the category (as many stimuli contain much information) or by reducing the possibility of some features of a particular stimulus becoming salient. In contrast, when test performances with novel items are intermediate, that is above chance but less than baseline, such a result can be regarded as partial concept learning (e.g., Katz et al. 2002). If animal subjects cannot fully grasp relational understanding among training stimuli or can partly understand which factors are differentiating the S/D item but their training performances still focus on the specific features of a particular item to some extent, partial transfer may be produced when they are tested with novel stimuli. Insufficient variations in the number of training stimuli may contribute to forming partial concept learning. When animal subjects are trained with a small number of training stimuli, they may pay attention to each individual stimulus pair (item-specific learning) rather than understanding the S/D relationship between stimuli of each pair. The animal subjects may learn the same/different aspects of training stimuli at the initial stage of the acquisition phase and associate these aspects with some responses that are reinforced. When novel stimuli are presented, they may utilize this rule more generally once they are able to grasp full understanding of relationships among stimuli. In the case of partial concept learning, they may grasp partial understanding among stimuli in training phase that is reflected in transfer performances with novel tasks. The full concept learning and partial concept learning can better be understood by stimulus control topography hypothesis (Dube and McIlvane 1996), which argues that, when stimuli were presented, stimulus-specific features and stimulus relations both competed to control behavior. Reinforcing a particular feature of stimuli enhanced the possibility of that particular feature to control behavior, because as a result of reinforcing that particular feature of stimuli, an association between reinforcement and that particular feature was formed.

The stimulus control topography hypothesis may be applicable to explain the partial concept learning in which responding to the novel stimuli seemed to be better controlled by generalization from specific properties of training stimuli previously encountered than the sample comparison stimuli. Training with additional sets of stimuli may reduce such control by decreasing reinforcement for responding to two training stimuli and may increase the possibility by the inter-stimulus relation consistently associated with reinforcement. The continuation of multiple exemplar training makes possible relational responding applicable to both novel and familiar stimuli and test performance equivalent to criterion performances: i.e., full concept learning (e.g., Lazarowski et al. 2019). Like monkeys and pigeons, set-size functions have also been found to control responding in rats. Lazarowski et al. (2019) trained 20 rats in a simultaneous MTS and NMTS learning paradigm dividing them into two groups using olfactory stimuli. One group was trained with two stimuli and another group with 10 stimuli as exemplars. Rats trained with 10 exemplars demonstrated high accuracy on the first and second transfer test, whereas rats trained with 2 exemplars did not perform significantly better than chance on initial transfer test. Interestingly, when set-size was expanded for rats originally trained with 2 stimuli and rats were retested with multiple exemplars, acquisition of full concept learning (where training and test performances are equal and both are 80% correct or higher during testing period) was observed. In Taniuchi et al. (2017), when rats faced transfer test 1 consisting of novel problem CCCCCD and DDDDDC after the concurrent presentation of two-odd tasks (AAAAAB and BBBBBA), they did not show transfer. But when they faced the transfer test 2 consisting of novel problems EEEEF and FFFFFE after concurrent presentation of 12 oddity tasks, they showed significant transfer to the novel problems, clearly suggesting that set-size expansion of stimuli plays an important role in the development of relational concept learning. This evidence is consistent with other recent studies (e.g., April et al. 2011) that also showed generalized identity and oddity matching

after training with 10 exemplars. These findings suggest that similar learning processes are functioning across different species in acquiring S/D concept learning.

The basis of stronger transfer with relatively few exemplars observed in rat studies may be that there may be variations in the capacities and the limits in associative memories across different species. For example, monkeys may have more capacity of associative memory as compared to pigeons (Cook et al. 2005). As compared to monkeys and pigeons, rats might have limited capacity to memorize multiple item-specific cues, as a result of which, they might abandon memorizing item-specific cues and start to learn relational cues. Why various species require different numbers of training stimuli to demonstrate evidence of relational concepts is not fully clear, thus requiring further investigation to clarify this issue.

A question arises as to why a larger number of stimuli contribute to concept formation in animals in general. One way to answer this question may be that rats seemed to adopt a memorization strategy to solve one-odd or two-odd tasks. But this memorization strategy would fail, or at least, make learning more difficult when rats faced a large number of discrimination tasks. In the case of 30 oddity tasks, for example, it should be far more difficult to memorize all of the configurations of so many stimuli. Therefore, the large number of tasks might make memorizing the correct responses more difficult (Cook et al. 2005) and contribute to increasing the memory load. This difficulty might have forced rats to give up the memorizing strategy and to switch to a more conceptual-based strategy, the application of an abstract rule that can contribute to reducing the increased memory load (Santiago and Wright 1984). Another reason may be that significant transfer may somewhat reflect generalization from training stimuli to transfer stimuli [if both belong to the same domain (e.g., object stimuli)]. More clearly, when the set-size of the training stimuli becomes sufficiently large, the training stimuli may share some of its common properties (e.g., size, shape, color) with testing stimuli. Animals may sometimes keep such common properties in their memory and transfer to the novel

stimuli on the basis of such similarity (stimulus generalization) rather than utilizing abstract concepts.

If animals constantly respond to the testing stimuli following such rules, their learning would be in a restricted domain [learning that is limited to a particular type of stimuli (e.g., familiar object stimuli–novel object stimuli)]. Therefore, it becomes difficult to rule out the possibility that transfer may be based on some common physical features shared between the novel stimuli and some of the stimuli used in training (Wright and Katz 2006). It should not be assumed that acquisition of S/D concept learning can only be attained by a large stimuli set. Transfer after few exemplars is also common after successive discrimination training with other species and stimulus modalities. Cook, Kelly, and Katz (2003) trained four pigeons in go/no-go successive S/D discrimination procedure in which either same (AAAA... or BBBB...) or different (ABAB... or BABA...) photographic stimuli were presented within a trial. Each array (same or different) was presented for a fixed period of time and was separated by a dark inter-stimulus interval. They were able to learn S/D classifications with up to five different multi-dimensional classes. They also learned and transferred a relational rule when they were trained and tested with photographic (color and gray-scale photographs) and video stimuli in Experiment 3 and Experiment 4, respectively. Cook et al. (2003) reported that successive training with only two exemplars allowed pigeons to transfer same/different responding to novel stimuli. Some possible factors might positively influence pigeons' S/D discriminative choices on novel problems. One of them may be that, in Experiment 3, the gray-scale test had two subtests. The first subtest employed familiar color photographs about which pigeons experienced before. The second subtest employed completely novel gray-scale pictures. The transfer of learning was higher with the familiar gray-scale displays than with novel ones, suggesting that prior experience with familiar gray-scale pictures might facilitate pigeons to show greater responsiveness to these picture stimuli. The other critical factors might be the amount of change occurring in the figures and

background elements of same/different displays. Pigeons faced little difficulty in learning to discriminate same displays from different displays in Experiment 3 and Experiment 4 in which moderate to large changes were brought out between successive items, but, in Experiment 1 and in Experiment 2, pigeons faced difficulty to relationally process the same/different photographs containing very small and centrally located changes. Rensink, Regan, and Clark (1997) found in humans that focused attention was required to direct particular changes or differences between successively presented pictures. Similar phenomena may occur to other species. Pigeons were found to be successful in successive S/D discriminations where large changes occurred from one interval to the next. Very large changes in display may remove the need for providing attention toward any specific place or feature within an image. Considering all of these possibilities, it seemed that pigeons were utilizing image-based memories of the successive stimuli across time. The findings, taken together, revealed that visual relations between elements can control pigeons' behavior. From the comparative discussions on S/D concept learning with various species [e.g., monkeys (Katz et al. 2002), pigeons (Cook et al. 2003; Wright and Katz 2006)], it can be said that S/D concept learning may emerge in animal subjects on the presence of an appropriate experimental procedure.

Although some studies (e.g., Lazarowski et al. 2019) showed generalized oddity learning in rats across a range of odors, it is a time-befitting argument that to confirm the true S/D concept learning, oddity studies across sensory modalities are necessary (Scholtyssek et al. 2013). Thus, it would be of interest to explore the possibility of generalized S/D concept using different stimulus modalities in future studies. Cross-modal transfer tests should be considered, meaning that, training tasks should employ visual stimuli and transfer tests should employ auditory stimuli such that training and test stimuli share no physical features. Several research studies were conducted across different modalities. Giurfa, Zhang, Jennet, Menzel, and Srinivasan (2001) studied bees in order to examine S/D concept learning with

MTS and NMTS procedures. They trained individual groups of bees across different modalities (from olfactory to visual) and found that bees could transfer the MTS or NMTS abilities to novel stimuli that shared no physical features of the stimuli specified in the training. Thus, it could be concluded that the ability of sameness and differences in bees was robust and broad. Such an experimental paradigm should be applied to rat studies in order to confirm their S/D concept abilities across different sensory modalities.

## Conclusion

Evidence demonstrating generalized S/D responding in a wide range of nonhuman species continues to emerge. This progress continues and has been enhanced by some techniques such as concurrent presentation and expanded set of stimuli that determine the efficacy of mediating behaviors, contributing to the development of S/D concept learning in animals. The present entry may guide future comparative cognition researchers on how to attain oddity concept learning in rats that is free from perceptual effect. Notwithstanding, a major challenge is to investigate what mechanisms are in operation in animals' concept formation.

## Cross-References

► [Same/Different Learning](#)

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## Oddity Problem

### ► Oddity

## Oddity Task

### ► Oddity

## Odds Ratio

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### Definition

The odds ratio is a statistical measurement that helps to understand the comparison of the combined effect of the parameter of each group into a single parameter scale. It is frequently used in medical science and behavior science, especially in control studies cases.

### Introduction

In clinical interventions or interpreting observations of diseases, many statistical tools are helpful in which *odds ratio* plays a frequent role (Montreuil et al. 2005). The ratio of odds ( $odds = \frac{p}{1-p}$ , where  $p$  is the *probability* of the event occurring) is said to be *odds ratio* and is a measure that quantifies the effectiveness of the association between two happenings or events (Szumilas 2010). It is also useful to determine

the odds of the outcomes for two groups (Montreuil et al. 2005). It can be easily evaluated whether the odds are the same or different (Szumilas 2010). *Odds ratio* measures the *odds* (events) in the presence of exposure to the *odds* (events) in the absence of the exposure (Martinez et al. 2017). The odds ratio and risk ratio are quite different in their applications and interpretations but there will be high chance of confusion between the *risk ratio* and *odds ratio*. If we are considering the case of any process of making some products in a company, then we will observe the impact of the newly applied process and existing process. Then, the *risk ratio* is the ratio of the probability of unsatisfactory results of the new process to the likelihood under the existing process. However, the *odds ratio* can be a better approximation in some specific cases. If there is a situation of some rare disease that spreads rarely and its data value is low, then the value of *odds ratio* is very close to the *risk ratio*, that is, both have the same approximate value and, in this case, the *odds ratio* can be a good approximation for the *risk ratio* (Montreuil et al. 2005). But otherwise, *odds ratio* and *risk ratio* are quite different.

Apart from betting (which is almost the odds), the *odds ratio* is explicitly used in many fields from a statistical point of view to compare the relative *odds* of outcomes with exposure such as *epidemiology*, *medicines*, control-decision problems, sports, and betting. The *odds ratio* in the field of statistics is the relative chance of an outcome under two or more different situations (Chen et al. 2010).

### Meaning of Odds

*Probability* is quite common and is defined as the ratio of numbers of *positive* concurrences divided by a number of *total* possible occurrences; however, the *odds* is the number of positive concurrences in relation to the number of nonpositive occurrences. The absolute or relative chance of an event of interest happening is generally expressed by *odds (event)* of that event happening and is given by:

$odds = \frac{p}{1-p}$ , where  $p$  is the probability of the event occurring.

When  $p$  is small, that is,  $p \approx 0$ , then  $1 - p \approx p$  and  $odds = \frac{p}{1-p} \approx p$ . But, when  $p$  is not small, then probability and odds are generally not the same, that is, they have different values for the event happening. *Probability* ranges between zero and one while *odds* are positive numbers ranging between zero and infinity. To understand the differences between probability and odds, consider the following simple example: Let us say that the probability of success of any event happening is 0.8, then the probability of failure of event happening is 0.2. But *odds (success)* and *odds (failure)* are calculated as  $odds (success) = \frac{0.8}{1-0.8} = \frac{0.8}{0.2} = 4$ , while  $odds (failure) = \frac{0.2}{1-0.2} = \frac{0.2}{0.8} = 0.25$ .

### How to Calculate the Odds Ratio?

*Odds* are determined with the help of probabilities, that is,  $p$  is the probability of any events, then *odds* can be calculated as  $\frac{p}{1-p}$  (McHugh 2009). Let us consider the number of exposed occurred events as  $a$  exposed non-occurred events as  $b$  not exposed occurred events as  $c$  and not exposed non-occurred events as  $d$  (Table 1).

The probability of exposed occurred events is given by  $p = \frac{a}{a+b}$

The probability of exposed non-occurred events is given by  $q = \frac{b}{a+b}$

Then, the *odds* of exposed cases are given by  $\frac{p}{q}$

$$\text{i.e., } odds(\text{exposed cases}) = \frac{p}{q} = \frac{a/a+b}{b/a+b} = \frac{a}{b}$$

Now, the probability of exposed occurred events is given by  $m = \frac{c}{c+d}$

The probability of exposed non-occurred events is given by  $n = \frac{d}{c+d}$

Then the odds of exposed cases are given by  $\frac{m}{n}$

$$\text{i.e., } odds(\text{not exposed cases}) = \frac{m}{n} = \frac{c/c+d}{d/c+d} = \frac{c}{d}$$

Now, the *odds ratio* is given  $\frac{p/q}{m/n} = \frac{a/b}{c/d} = \frac{ad}{bc}$ .

Also, since the *odds ratio* is invariant to the reversal of the orientation; therefore, the *odds ratio* for exposure  $\frac{a/b}{c/d}$  is mathematically the same as the *odds ratio* for the occurred events  $\frac{a/c}{b/d}$ , that is, both can be expressed as  $\frac{ad}{bc}$ . Depending upon the above scenarios the *odds ratio* may be interpreted as follows:

**Case 1. When  $OR = 1$ :** the *odds* of the outcome is independent of the exposure. There is no effect of exposure on the *odds* of the event.

**Case 2. When  $OR > 1$ :** The lower *odds* of the outcome is unlikely affected by exposure, that is, exposure is associated with higher *odds* of the outcome.

**Case 3. When  $OR < 1$ :** Higher odds of the outcome is very unlikely to be affected by exposure, that is, exposure is associated with lower *odds* of the outcome.

### Application of Odds Ratio

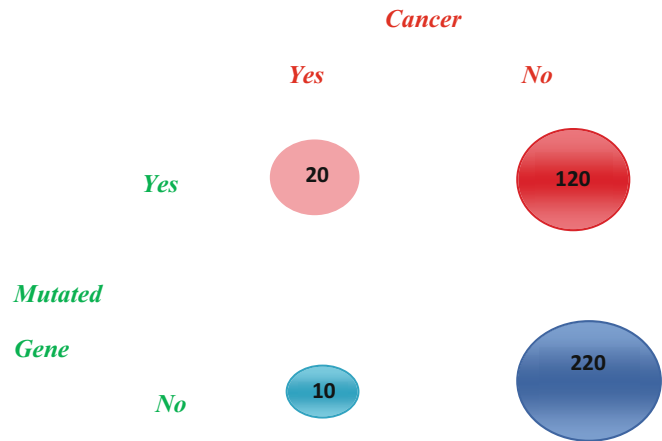
Behavioral science deals with the interaction and behavior of human beings. It helps us to understand the factors related to psychology or behavior in different case studies. The *odds ratio* is frequently used in the case-control study, which compares two groups of people in which one group has the disease, and the second group does not have a disease. Some examples exhibiting the concepts are listed below:

**Example 1** Suppose that we have data of 370 patients in which 20 of them are having cancer who have mutated genes and 10 who do not have mutated genes. Also, 120 are not having cancer but mutated genes and 220 who do not have a mutated gene.

**Odds Ratio, Table 1** Description of the outcomes and the possibilities

|             | Occurred | Non-occurred |
|-------------|----------|--------------|
| Exposed     | $a$      | $b$          |
| Not Exposed | $c$      | $d$          |

**Odds Ratio, Fig. 1** Data graph of patients



From the above data (Fig. 1), one can determine which fraction is exposed to cancer or not (with the help of probabilities). But the *odds ratio* helps us to find the relation between cancer and the mutated gene.

Case I: The patient has a mutated gene.

The *odds* of a person having cancer are  $20/120 = 0.1666$ .

Case II: The patient has not mutated gene.

The *odds* of a person having cancer are  $10/220 = 0.04545$ .

Therefore  $OR = 3.66 \sim 3.7$ . The *odds* of the person that has cancer are 3.7 times greater than that person will have cancer if they have a mutated gene.

The *odds ratio* is frequently used in a case-control study. In epidemiology *odds ratio* is very helpful to make a comparison with respect to the frequency of an exposure whose impact is evaluated (Cook 2002). Case subject is selected if the outcomes have disease and control subject is selected if the outcomes have not diseased for the case-control study, see *example number 2* (Montreuil et al. 2005).

**Example 2** Consider in lung cancer patients, red wine consumption is 47 among 132 patients (cases). Now, if among 187 patients without lung cancer (controls) in which only 101 patients

**Odds Ratio, Table 2** Description of Association between red wine consumption and lung cancer [7]

| Patients            | Red wine exposure |             |
|---------------------|-------------------|-------------|
|                     | Exposed           | Not exposed |
| Cases (lung cancer) | 47                | 85          |
| Controls            | 101               | 86          |

consume red wine, then Table 2 describes the details of exposed and not-exposed cases:

The *odds* of red wine consumption among cases are  $odds(lung\ cancer) = \frac{47}{132-47} = \frac{47}{85} = 0.55$ .

The *odds* of red wine consumption among controls are  $odds(control) = \frac{101}{187-101} = \frac{101}{86} = 1.17$ .

Thus, the *odds ratio* is (*Odds Ratio*) =  $(\frac{47}{85}) / (\frac{101}{86}) = \frac{4042}{8585} = 0.47$ .

This implies that the *odds* of being a red wine drinker if one has lung cancer are approximately half the *odds* of being a red wine drinker if one does not have lung cancer.

Here, the *odds ratio* is nothing but the ratio of the *odds* of exposure, but clinicians have more interest in the likelihood of diseases. Also, the *odds ratio* has a fascinating property that is invariant to the reversal of the orientation. But the risk factor does not satisfy such property. The *odds ratio* for exposure  $(\frac{47}{85}) / (\frac{101}{86}) = \frac{4042}{8585}$  is mathematically equivalent to the *odds ratio* for the outcome  $(\frac{47}{101}) / (\frac{85}{86}) = \frac{4042}{8585}$ . Therefore, the ratio of odds of

having lung cancer in red wine drinkers compared with nondrinkers is 0.47 (Ruano-Ravina et al. 2004).

## Cross-References

- [Anticipation of Future Events](#)
- [Genes](#)
- [Mutations](#)

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- Available evidence to date suggests that it is exhibited by desert ants (Wittlinger et al. 2006, 2007; Wohlgemuth et al. 2001), spiders (Barth 2002; Seyfarth and Barth 1972), honey bees (Tautz et al. 2004), fiddler crabs (Walls and Layne 2009a), dogs (Séguinot et al. 1998), and humans (e.g., Harrison and Turvey 2009; Mittelstaedt and Mittelstaedt 2001; Schwartz 1999; Turvey et al. 2009). A reasonable surmise is that it is exhibited in some form by all organisms.
- Figure 1 summarizes Schwartz's (1999) original investigation of human odometry conducted with blindfolded participants performing a simple homing task. On each trial, the participant went from a fixed starting point A to a variable terminus B – signaled during locomotion by the experimenter – and then attempted to return to A. The participant either walked from A to B with the aid of a long cane or jogged with the aid of a sighted partner. In both cases the participant was distracted so as to minimize the use of explicit strategies such as counting the number of steps. From B to A the participant walked alone without distraction and with the aid of a long cane. As Fig. 1 depicts, whereas jogging from A to B took less time (and involved fewer step cycles) than walking from A to B, the accuracy of the return trip from B to A for each of the distances traversed was the same. Unsighted distance traveled is apparently perceptible by locomotion regardless of duration and style of locomotion (see also Turvey et al. 2009; Abdolvahab et al. 2015).

That natural odometers may differ in significant ways from fabricated odometers is suggested by evidence of the varied means and context dependent nature of biological odometry. Wolf (2011) provides appreciation of the range of methods employed by insects for metering distance. Relatedly, odometric function is independently supported by various perceptual systems, including vision (Ellmore and McNaughton 2004; Kautzky and Thurley 2016; Srinivasan et al. 2000), the otolith organs of mammalian vestibular systems (Israel et al. 1997; Mittelstaedt 1999), and the haptic (i.e., kinesthetic, proprioceptive) system (Seyfarth et al. 1982; Schwartz 1999). For humans, the relative contributions of these perceptual systems can be flexibly adjusted, with the

## Odometry

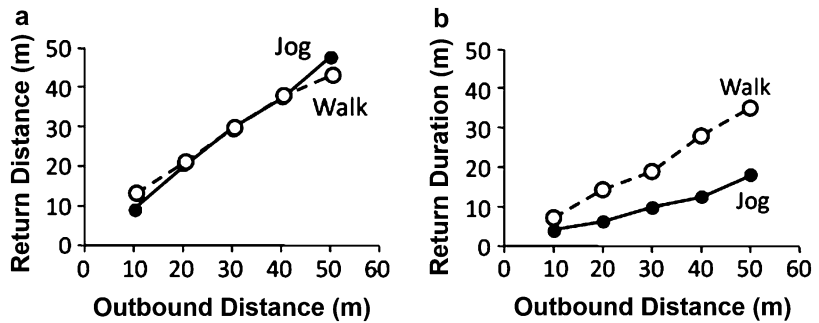
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Odometry refers to the implementation of a specialized procedure or instrument by means of which an organism measures distances traveled.



**Odometry, Fig. 1 (a)**

Homing task performance by blindfolded participants adopting either an outbound walk or jog gait pattern. (b) Patterns differ in the time to complete the outbound. (Adapted from Schwartz 1999)



contribution of vision shown to be greater in more complex environments supporting richer optical structure (Kearns et al. 2002).

Varieties of biological odometry can be interpreted with respect to the contextual constraints (i.e., the conditions of travel) that support the reliable measurement of distance traveled. For optical odometers, the detected rate of optic flow can vary with the properties of the terrain and the organism's height relative to the ground. Of special note, the duration of the so-called "waggle" aspect of the honeybee dance (in the capacity of an odometric measurement) increases at a slower rate when bees fly over water than when they fly over land. For route distances of equal magnitude over land and water, bee perception of distance flown (as indicated by their dances) is smaller for the flights over water. Of additional note, honeybees exhibit a tendency to fly at altitudes that produce a seemingly preferred degree of optic flow (Esch et al. 2001). The latter may relate to the observation on humans that in the driving of automobiles, perceived speed of motion varies as a function of eye height relative to the ground surface (Panerai et al. 2001).

For legged animals, mechanoreceptive organs sensitive to tissue deformation generated by the actions of the limbs during locomotion have been implicated in the measurement of distance traveled (Seyfarth et al. 1982). Haptic odometry of this variety is potentially dependent upon the specifics of legged locomotion, including adopted gait patterns, limb-segment lengths, step frequency, and step amplitude. For example, the haptic odometer of the fiddler crab appears to integrate information generated by limb movements (Walls and Layne 2009a). This stride integrator produces a measure

that depends upon the amplitude of steps (i.e., it is not a step counter) indifferent to slips between end-effector and ground surface suggesting that it is reliable only in measurement contexts supporting sure footing. By contrast, stride integration by the desert ant is sensitive to motion of the limbs relative to the environment, and as such accounts for both slips and stumbles (Steck et al. 2009), as well as undulations in the terrain (Walls and Layne 2009b). The haptic odometer of both desert ants (Wittlinger et al. 2007) and humans (Dominici et al. 2009) depends upon limb length, with lengthening of limbs (by attachments) producing overestimations of distance traveled.

For humans, the haptic odometer has been shown to produce a measure of distance traveled that is reliable across variations in the frequency and amplitude of steps (Schwartz 1999) and across subsets of the variations in gait patterns tested to date (Turvey et al. 2009). Manipulations of gait patterns across the outbound and return phases of simple homing tasks have revealed a human haptic odometer that is reliable across walking and jogging, walking and backwards-walking, and hesitation-walking and gallop-walking (Turvey et al. 2009). The latter two gait patterns are variants of step-to-gait patterns whereby one foot steps forward, followed by the trailing foot stepping next to the leading foot.

Other manipulations of gait patterns in homing tasks reveal a haptic odometer that depends upon the manner in which the limbs are coordinated. With gallop-walk as the outbound gait and walk as the return gait in a homing task, a systematic underestimation bias is observed. Moreover, when the ordering of gait patterns is reversed, so also is the direction of bias (Turvey et al., 2012).

The viewpoint of “gait as odometer” motivates an interpretation of haptic odometry in terms of the space-time structure of gait patterns (Turvey et al. 2009). Motivated by the group symmetry analysis approach of Golubitsky and colleagues (Golubitsky et al. 1999; Pinto and Golubitsky 2006), bipedal gaits can be divided into the so-called primary and secondary gaits on grounds of the group symmetry of the minimal network of identical differential equations required to model them. The spatiotemporal symmetry of primary bipedal gaits (e.g., walk) is dihedral, and that of secondary bipedal gaits (e.g., gallop-walk) is (a lower) cyclic symmetry. Gaits sharing a spatiotemporal symmetry classification are found to measure distance similarly.

The hypothesis of “gait as odometer” implicates a means of measuring distance that depends upon how the limbs are organized in the service of locomotion. Consistent with this hypothesis, in the case of Nordic-walking (handheld poles used to aid propulsion of the body), the manipulation of arm-leg coordination patterns systematically biases blindfolded homing tasks (Harrison et al. 2013). By contrast, matched manipulations of arm-leg coordination patterns in the absence of handheld poles do not produce systematic biases. The results suggest that limbs can be flexibly incorporated in human haptic odometry. The potential significance of such flexibility is evident in analyses of the reorganizations of limbs (in both coordination pattern and functional role) in desert ants dragging food back to the home nest by walking backwards (Pfeffer et al. 2016).

The relevance of the aforementioned faculties for odometry (e.g., Schwartz 1999; Seyfarth et al. 1982; Srinivasan et al. 2000) to the broader challenge of understanding animal navigation can be appreciated in two ways. First, in mathematical and neural models of path integration (Danafar 2012; Glasauer et al. 2007; Hinman et al. 2016; Kim and Dickinson 2017; Kropff et al. 2015; McNaughton et al. 1996, 2006; Ouarti and Berthoz 2008; Stone et al. 2017; Webb and Wystrach 2016) and second in insights into the contextual constraints – such as the ability to recognize places, landmarks, and other features of the environment – that can reset or obfuscate

path integration processes during the navigation of complex environments (Ardin et al. 2016; Warren et al. 2017).

## Cross-References

- ▶ [Arthropod Navigation](#)
- ▶ [Gait](#)
- ▶ [Homing](#)
- ▶ [Insect Locomotion](#)
- ▶ [Insect Navigation](#)
- ▶ [Landmark](#)
- ▶ [Navigation](#)
- ▶ [Navigation by Honey Bees](#)
- ▶ [Spatial Orientation](#)
- ▶ [Visual Perception](#)

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## Odor Detection

- ▶ [Olfactory Perception](#)

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## Odor Processing

- ▶ [Olfactory Perception](#)

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## Odor Representation

- ▶ [Olfactory Perception](#)

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## Oestrous

- ▶ [Estrous](#)

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## Offensive Behavior

- ▶ [Aggression](#)

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## Offspring Solicitation Behavior

- ▶ [Begging](#)

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## Old World Fruit Bat Locomotion

- ▶ [Megachiroptera Locomotion](#)

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## Old World Monkey

- ▶ [Haplorhini](#)

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## Old World Monkeys

- ▶ [Catarrhine Communication](#)
- ▶ [Catarrhine Life History](#)

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## Older Brother Effect

- ▶ [Fraternal Birth Order Effect](#)

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## Olfaction

- ▶ [Accipitriformes Sensory Systems](#)
- ▶ [Bear Communication](#)
- ▶ [Bear Navigation](#)
- ▶ [Catarrhine Communication](#)
- ▶ [Falconiformes Sensory Systems](#)
- ▶ [Hominoidea Sensory Systems](#)
- ▶ [Monotreme Sensory Systems](#)
- ▶ [Mustelid Communication](#)
- ▶ [Mustelidae Navigation](#)
- ▶ [Platyrrhine Sensory Systems](#)
- ▶ [Primate Sensory Systems](#)
- ▶ [Prosimian Communication](#)

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## Olfactory

- ▶ [Chemoreception](#)

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## Olfactory Adaptation

- ▶ [Olfactory Discrimination](#)

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## Olfactory Bulb

### ► Olfactory Discrimination

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## Olfactory Discrimination

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## Synonyms

Olfactory adaptation; Olfactory bulb; Olfactory epithelium

## Definition

The ability to differentiate between intensities of same odor as well as qualitatively distinguish among nonidentical odors.

## Introduction

The sensory process of response to chemical stimuli which gives rise to sensation of odors is known as olfaction. Two types of olfactory receptive areas are present, primary and accessory. The primary olfactory receptive area is the olfactory nerve (Cranial nerve I or C. N. I) innervated region of nose (Figs. 1 and 2) while the accessory olfactory receptive areas are those parts of nose, pharynx and larynx, which forms the respiratory tract and are innervated by chemoreceptive endings of the trigeminal (C. N. V), glossopharyngeal (C. N. IX), and vagus (C. N. X) nerves. The pungent or irritating odor sensation is being perceived by C. N. V but it is not certain that the nociceptive odorous sensation are the only ones being carried by the same, nonetheless it can be said that the part being played by the accessory areas help in olfactory discrimination (Engen 1982).

In humans, the patch of nasal mucosa having olfactory receptor cells are referred to as olfactory mucosa or olfactory epithelium (Figs. 1 and 2) lies in the summit of a constricted passageway termed as olfactory cleft or slit. The slit is 7 cm long as measured from the external nares and this constricted long passage heightens the probability for any inhaled molecule to reach the olfactory mucosal surface, which is being moistened to enable the trapping of the molecules (Moran et al. 1982a).

Olfaction is of utmost requirement for maintenance of life in kingdom Animalia. Phylogenetically, it serves vital purposes in vertebrates, namely, nutrition, communication for reproduction, identification of food (prey), and identification of members of their own species. The taste of the food that we eat is recognized in many instances by the smell of the food; this was documented by a study which asked subjects to identify 21 common food substances placed on the tongue. They noted that there was a decrease from an average of 60% correct to an average of 10% correct when the nasal cavity was made inaccessible to any vapor phase molecules given off by the substances. Even coffee and chocolate, which were correctly identified by over 90% of the subjects when the nose was accessible, were not identified correctly by any subject when the nose was made inaccessible (Moller 2003). This ascertains the fact that the sense of olfaction and its discrimination is essential for evolutionary processes.

## Anatomy of Olfaction

The olfactory pathway can be studied in two parts: olfactory mucosa & neural pathway of olfaction (comprising of olfactory bulb with tract and olfactory cortex).

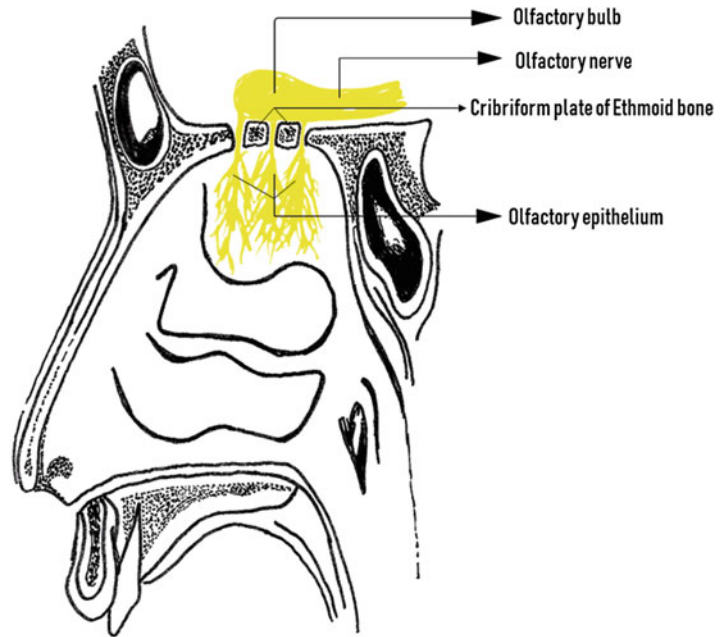
**Olfactory mucosa or epithelium** (Fig. 3): below the bony roof of cribriform plate of the ethmoid bone the olfactory mucosa has three histological layers, the lamina propria, a pseudo-stratified columnar epithelium, and finally, the mucosal covering.

The epithelium is composed of five principal cell types: olfactory receptor neurons (ORNs),

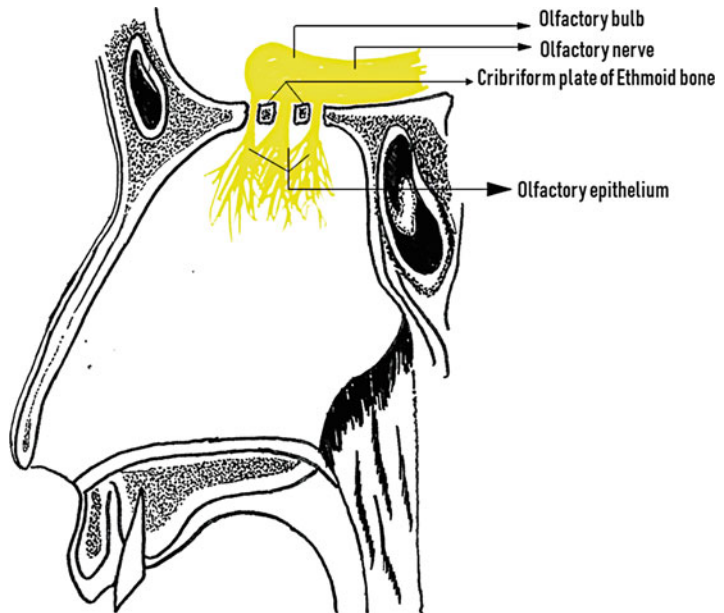


**Olfactory Discrimination,**

**Fig. 1** Showing primary olfactory receptive area in lateral wall of nose

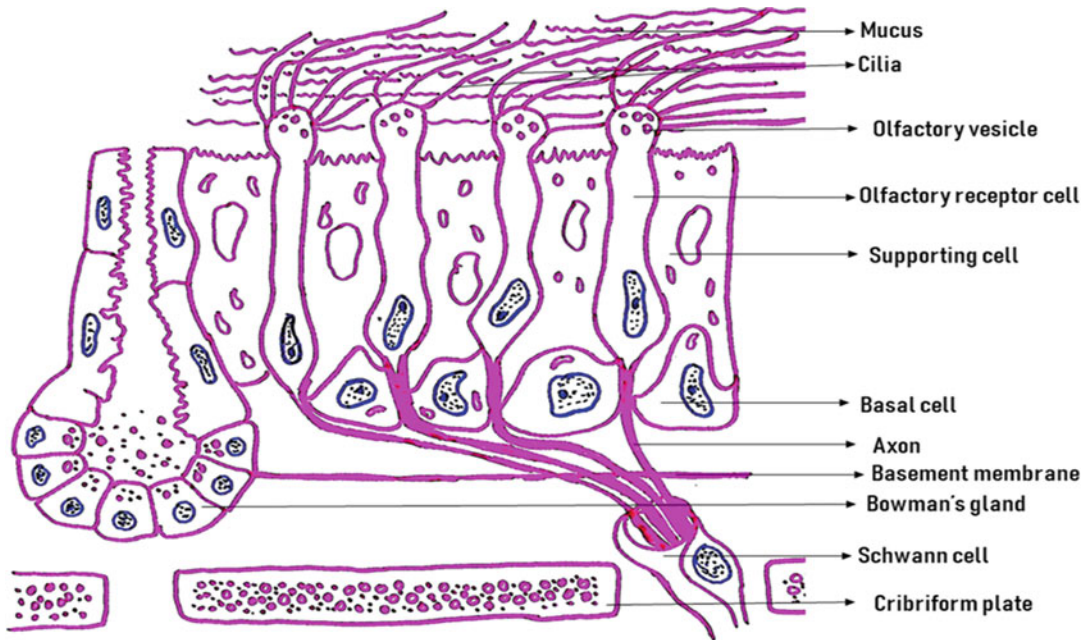
**Olfactory Discrimination,**

**Fig. 2** Showing nasal septum with olfactory epithelium



sustentacular cells, basal cells, microvillar cells, and finger-like microvilli cells (Polyzonis et al. 1979; Moran et al. 1982b; Morrison and Costanzo 1992; Jafek et al. 2002). The olfactory receptor neurons (ORNs) are sensory for odors and are interspersed with sustentacular cells at diversified stages of maturation in humans.

Sustentacular or supporting cells regulate the homeostasis and proliferation of ORN. Basal cells are the stem cells present above the basement membrane, which divides to form new neural and supporting cells, thus replenishes the steady loss of ORNs (Caggiano et al. 1994; Farbman 1994; Schwob 2005). The microvillar cells are flask-



**Olfactory Discrimination, Fig. 3** Schematic presentation of olfactory epithelium

shaped chemoreceptors with a tuft of microvilli that extends into the mucus layer of the epithelium, a thin axon-like cytoplasmic process extends from the basal pole of these cells and travels through the epithelium toward the lamina propria, rendering a bipolar morphology (Polyzonis et al. 1979). The fifth variety of cell, termed as finger-like microvilli cells were reported by Ota in 1998, who reported their presence only after the disappearance of the olfactory ciliary mat following resection of the olfactory bulbs. Transmission electron microscopy observation revealed that the microvilli of these cells are characterized by a specific core structure consisting of microfilament bundles absent in the microvillar cells, thus differentiating the two. Observing a disconnection between these cells and the postganglionic fibers of the trigeminal nerve and the olfactory bulbs, it was suggested that the fifth type cell could be a mechanoreceptor for a sensory system that is non-olfactory and can play a role in olfactory discrimination.

Among these five types of cells there can be seen two more components, i.e., Bowman glands (Fig. 3) and Olfactory ensheathing cells (OECs).

Bowman glands are branched tubulo-alveolar glands lying under the olfactory epithelium over which its secretion reaches via ducts. The dendritic endings and cilia of ORNs are immersed in the secretion which allows odorant diffusion to sensory receptors as well as the secretion is suggested to play important immunologic functions due to the presence of IgA, IgM, lactoferrin, and lysozyme (Chen et al. 2014).

The OECs were first described in the glial populations of olfactory bulbs in mammals (Golgi 1875; Blanes 1898). Recently, these have drawn much more attention due to their application in regenerative medicine. OECs from olfactory mucosa overexpress genes characteristic of wound healing and regulation of extracellular matrix, whereas OECs from olfactory bulbs express genes suggestive of nervous system development (Guérout et al. 2010; Rela et al. 2010).

**Neural Pathway of Olfaction:** The olfactory pathway is an exception to all sensory systems, as it sends direct impulses to cerebral cortex without relaying them in thalamus. The components of this pathway are bipolar ORNs, olfactory bulb

containing mitral cells, tufted cells and interneurons, olfactory tract, olfactory stria, pyriform area, anterior perforated substance, and septal area in paraterminal gyrus (subcallosal area).

As explained above, the bipolar ORNs have their peripheral processes in the olfactory mucosa while the central processes form the olfactory nerves, which will form synaptic glomeruli with mitral and tufted cells of the olfactory bulb (Halasz and Shepherd 1983).

The olfactory bulb rests upon the cribriform plate and has been highly conserved throughout vertebrate evolution, being absent only in the cetaceans (whales, dolphins) which lack a sense of smell. Its homolog in higher invertebrates (e.g., arthropods) is the antennal lobe. Its functions are to receive and process the information from the olfactory receptor neurons, to send this information to different parts of the olfactory cortex in the forebrain and to provide for integration and modulation of the information by means of pathways from midbrain and forebrain centers. A smaller structure is embedded in the bulb on the dorsal posterior surface and is called as accessory olfactory bulb which transmits information from the vomeronasal organ (Jacobson's organ) via the vomeronasal nerve. The cellular constituents of olfactory bulb include mitral cells, tufted cells (dendrites of both contribute in the formation of synaptic glomeruli with the olfactory nerves) and three interneurons, namely, periglomerular cells (PG), granule cells, and short-axon cells. The olfactory bulb receives a rich innervation of centrifugal fibres from the rest of the brain, which are of three main types: fibres arising from the anterior olfactory nucleus and other olfactory cortical areas, which function as feedback loops for sensory processing; fibres from the nucleus of the horizontal limb of the diagonal band (NHLDB) which are part of the basal cholinergic system innervating the fore brain; and fibres from the midbrain, which are part of the noradrenergic and serotonergic systems innervating the fore brain (McBurney 1984).

The axons of mitral and tufted cells are mainly responsible for the formation of olfactory tract, which extends as backward projection from the olfactory bulb and lodges in the olfactory sulcus.

Each tract has fibres from the opposite olfactory bulb and anterior olfactory nucleus via the anterior commissure. The tract flattens out and divides to continue as medial and lateral olfactory striae and forms an enclosed area in between called as olfactory trigone. The intermediate striae, if present terminates in olfactory tubercle via anterior perforated substance. The fibres of medial striae mostly end in para-terminal gyrus with few passing through anterior commissure to synapse with contralateral olfactory bulb and anterior olfactory nucleus. Whereas, fibres of the lateral olfactory striae makes synaptic contacts with neurons of anterior perforated substance, pre-pyriform region (formed by lateral olfactory gyrus and gyrus ambiens), and peri-amygdaloid region which collectively forms the primary olfactory cortex. The pre-pyriform region continues into entorhinal area (Brodmann's area 28) in the anterior part of para-hippocampal gyrus and projects to the olfactory cortex of uncus, these structures give rise to fibres towards hippocampus forming the perirhinal pathway. The pre-pyriform region, peri-amygdaloid region and entorhinal area are collectively termed as pyriform lobe. Primary olfactory cortex projects fibres to secondary (or association) olfactory cortex (which includes entorhinal area), amygdaloid body, dorsomedial nucleus of thalamus, hypothalamic nuclei and the septal nuclei in order to perceive the odor consciously. These fibers terminate at different levels within the olfactory bulb. The pathways through the medial dorsal portion of the thalamus that reach the orbitofrontal cortex may be responsible for perception and discrimination of odors, while the pathways that reach the amygdala and hypothalamus carry emotional response and physiologic reactions to odors. These pathways may also be responsible for the role of olfaction in eating and for sexually related behavior and reflexes (Shepherd 2006; Gottfried 2006).

Though the olfactory pathway is different from other sensory pathways but in some organisms where vomeronasal organ is active for chemical communication via pheromones between individuals of same species for reproductive behavior, the nonclassical pathway exists where the connections from the accessory olfactory bulb project to

the bed nucleus of the accessory olfactory tract, the medial nucleus, and the posteromedial cortical nucleus of the amygdala. There is no direct pathway from the vomeronasal organ to the cerebral cortex. Discrimination of pheromones and communication with pheromones may therefore occur without conscious awareness. That may be one reason why it has been difficult to establish the role of the vomeronasal system in humans (Bhatnagar 2001).

What Leads to Olfactory Discrimination?

There are a number of factors (Table 1) that has been studied on the part of both the odorant molecule and the animal that are inducing the phenomenon of olfactory discrimination (Table 1). It has been established by Moulton & Beidler in 1967 that the density of bipolar receptors varies from species to species and the boundaries of the olfactory mucosa are not distinct. The dendrites of these receptors extend to the epithelial surface and terminates in a swelling of olfactory knob. These dendrites provide a surface for interactions with molecules. It has long been believed (Parker 1922; Menco and Morrison 2003) that these olfactory cilia contain the olfactory receptor sites where this interaction takes place. The olfactory cilia move in different directions and more slowly than neighboring respiratory cilia, which move

in a more rapid and synchronized manner. This motion may be involved in the displacement of the odorant molecule from the receptor site (Bronstein and Minor 1973).

In 1971, Tucker explained that olfactory receptors are not alone in the nasal passages and are accompanied by the free nerve endings of the common chemical sense that responds to irritating chemical substances. Fibres from these receptors join fibres from other areas of the face and head in the trigeminal or fifth cranial nerve. These receptors are stimulated by many substances, such as automobile exhaust, which may also stimulate the olfactory receptors, and sensations from the trigeminal and olfactory receptors cannot always or easily be distinguished by a human observer but can help in discrimination of the odorants. Psychophysical data from studies clearly shows that what is judged to be odor intensity is partly the result of trigeminal stimulation. The olfactory and trigeminal systems also mutually inhibit each other, such that an odorant may mask an irritant and vice versa (Engen 1982).

In the absence of an accurate measuring entity for olfactory sensitivity as can be done in case of hearing by audiometer, it becomes difficult to establish the amount of an odorant causing a distinct sensory response. The branch dealing with this measurement is known as applied psychophysics. Fechner (1966) originated psychophysical methods for the purpose of describing the

Olfactory Discrimination, Table 1 Factors affecting olfactory discrimination

| Factors in odorants                                      |                                                                   | Factors in animals                                                                             |                                                                   |                                                                                     |     |                                                                  |                                                                                                     |                                                                                                                                                                                                   |                                                                                                                                                         |
|----------------------------------------------------------|-------------------------------------------------------------------|------------------------------------------------------------------------------------------------|-------------------------------------------------------------------|-------------------------------------------------------------------------------------|-----|------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------|
| Different molecular structure with                       |                                                                   | Mucous solubility of odorant                                                                   |                                                                   | Receptor density                                                                    |     | Nerve stimulated                                                 |                                                                                                     | Interaction                                                                                                                                                                                       |                                                                                                                                                         |
| Higher affinity to receptors                             | Lesser affinity to receptors                                      | Not soluble                                                                                    | Soluble                                                           | High                                                                                | Low | C. N. I                                                          | C. N. V                                                                                             | Between Cells of bulb                                                                                                                                                                             | Between Bulbs                                                                                                                                           |
| Elicits olfactory sensation easily and in lesser amounts | Large amount of odorant is required to elicit olfactory sensation | Can stimulate C. N. V to elicit noxious sensation and can also help in discrimination of odor. | Elicits response depending upon threshold of the odorant molecule | Depending upon the affinity and threshold of the molecule, the response is elicited |     | Will help to discriminate odors related to pleasurable feelings. | Helps to sense nociceptive odors and is involved in vice-versa inhibition of olfaction with C. N. I | Depending upon the neurotransmitters released in response to the odorant molecule these can either inhibit or excite each other and thus lead to different sensory response to different odorants | If one bulb is stimulated electrically, it tends to suppress the activity in the other bulb, whether the activity is spontaneous or evoked by odorants. |

relation between internal experience and external physical stimulation, between body and mind. The development of psychophysics is one of the key factors in the advancement made in the study of smell. Alas, in absence of an accurate measuring system of odor, the measurement of odor sensitivity and acuity is still made very crudely. Thus, one reads anecdotes about the sensitivity of special people such as Helen Keller, but one never sees any results from objective tests, because there are none (Engen 1982).

## Purpose of Olfactory Discrimination

One is not aware of how much the nonconscious sensory inputs of olfaction is important in daily life. This can be ascertained by an anosmic person who is deprived of more than pleasurable sensations, as the food turns into lukewarm mush, varying only in a few gustatory (taste) qualities and as has been argued that what the nose knows becomes more important in scenario of a hidden fire and increasing environmental pollution (Moncrieff 1949).

The main purposes of discriminating the odors is for

1. Perception of odors may actually dominate visual perception in the selection of food items (Beauchamp & Mailer, 1977). The food may appear to be tasty and fresh but the smell will make all the difference, if the food is actually pleasurable or spoiled.
2. Warning people of contaminated air (with invisible and obnoxious chemicals which can be harmful in small or large quantities)
3. Sexual arousal by pheromones – Although there are disagreements about the definition of a pheromone, there is no doubt that such odorants can initiate sexual activity, serve as warning signals, and delineate trails and territory.

One reason that the sense of smell has been given less consideration than other modalities, especially sight and hearing, is its characterization as the “subtle sense.” As presented in a popular account, odors tend to be concentrated near the ground. So, when our animal ancestors came

out of the water and became upright, they were preoccupied with vision and audition, therefore submitting to the poor olfactory acuity of ours. Olfaction, thus became more involved in visceral and emotional activities than the sensory information transmission (Droscher 1969).

## Cross-References

- Amygdala
- Chemical Cues
- Entorhinal Cortex
- Hypothalamus
- Pheromone

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## Olfactory Epithelium

### ► Olfactory Discrimination

## Olfactory Perception

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## Synonyms

[Elemental and configural perception](#); [Odor detection](#); [Odor processing](#); [Odor representation](#)

## Definition

Olfactory perception comprises the detection and processing of one or several odor molecules ending in the representation (sometimes identification) by the organism of a particular odor, which may be discriminated from another odor. Animals – including humans – detect odor molecules through receptor systems, in which higher organisms are expressed by receptor cells directly connected to the brain. The brain will analyze and interpret the incoming information and display a response if it is biologically relevant. The response may be physiological/neural, psychological (emotion), and/or behavioral. Responsiveness to the information may be either spontaneous (i.e., predisposed) or consecutive to a learning process. In the latter case, after acquisition, the information is stored by the brain and retrieved later on, therefore contributing to the animals' acquired knowledge of the world.

## Introduction

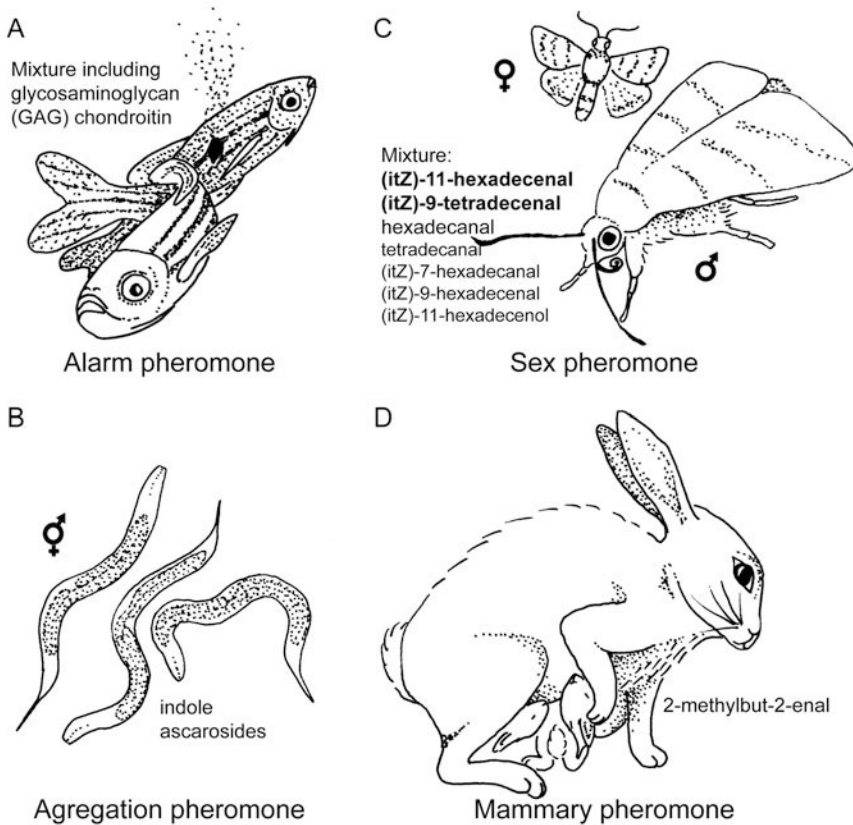
Chemical senses, which comprise olfaction and taste, are likely to be the oldest senses evolved as they are found throughout the animal kingdom. In olfaction, this is true from single cell to higher vertebrates and aquatic to terrestrial organisms. So far no species has been shown to be completely anosmic, underlining the pivotal role of olfaction in survival of all animals.

Odor signals are essential in the adaptation of organisms to their environment and often largely involved in the construction and conservation of social organizations such as flocks, packs, or colonies. Depending on the species: (i) they are used during hunting for prey, to detect its presence, to follow a trail, and to prepare for ambush; (ii) they help to avoid predators or other dangers such as poisoned food or toxic gasses in the surroundings; (iii) they may allow for responses to an alarm substance (alarm pheromone; see below for a definition of pheromone) inducing segregation, as observed, e.g., in fish (Mathuru et al. 2012; Fig. 1A); (iv) or on the contrary they may induce aggregation, e.g., in nematodes (Fig. 1B); mate localization, e.g., in moths (Fig. 1C); or resource exploitation, e.g., in beetles (Symonds and Gitau-Clarke 2016); (v) they are essential to define territories and help in finding back to the burrow or nest, e.g., in birds (Bonadonna 2009); (vi) odor cues emitted by a conspecific may convey information about its gender, kinship, social rank, and health status; (vii) such information, together with information of the owner's reproductive state, may influence mate choice, e.g., in rodents (Ferkin 2018); (viii) odor cues are also vital in mother-young bonding as they allow recognition and attachment of the mother and/or young; furthermore, they contribute in mammals to the orientation of the newborn toward the maternal body and to the location of the nipples (e.g., in mammals Lévy et al. 2004; Fig. 1D).

## Different Organs to Detect Odor Cues

Due to the overall importance of olfaction in the animal kingdom, organ systems have evolved

convergently and show some similarities across taxa, e.g., between vertebrates and invertebrates (Eisthen 2002). The detection systems may be as simple as receptors expressed on the surface of a single-cell organism (Valentine et al. 2008). In insects, the olfactory receptor cells and olfactory sensilla, mainly found on the antennae (Hansson and Stensmyr 2011), detect olfactory cues and transfer the information to the antennal lobe, which processes and relays the learned and non-learned information to the mushroom bodies and/or the lateral horn. In vertebrates, odor molecules reach the nose directly through the nares (orthonasal processing) or indirectly via the mouth (retronasal processing). The vertebrate olfactory system has two major olfactory epithelia, the main and the accessory ones (Brennan and Kendrick 2006). While the first one is typically situated at the back of the nasal cavity and devoted to the detection of volatile cues, the second – vomeronasal organ – involved in the detection of nonvolatile cues is situated at the front of the nasal cavity stretching along the sides of the septum; it may open into the mouth and/or the nose via the nasopalatine ducts. Two other olfactory epithelia have been described in some mammals, the Grüneberg ganglion, which is situated near the entrance to the nasal cavity, and the septal organ, located bilaterally at the ventral base of the nasal septum. The olfactory receptor neurons from the main olfactory epithelium project to the main olfactory bulb, which is the first to relay information to the brain, while the vomeronasal receptor neurons project to the accessory olfactory bulb. From the olfactory bulb, the signal is conveyed to the primary olfactory cortex but also to other brain regions such as hypothalamic nuclei involved in autonomic functions and the amygdala and hippocampus involved in learning and memory. While the vomeronasal organ and accessory olfactory system have long been considered as dedicated to the detection of pheromones, this dogma has been refuted over the last decades through studies showing that they can also process common odor cues and that, conversely, the main olfactory system can process both common odorants and pheromones (Wyatt 2015).



**Olfactory Perception, Fig. 1** Odor perception is important to all animals including humans. Here we are showing some examples of pheromones (composed by single odorants or mixtures) perceived by four different species in different contexts, i.e., fear response, aggregation, mating, and mother-young relationship/nutrition: (A) The perception of predators is essential to survival. In zebrafish (*Danio rerio*) skin damage causes the release of chemicals that elicit fear and escape in members of the shoal. The released alarm pheromone is a mixture that includes the glycosaminoglycan (GAG) chondroitin (Mathuru et al. 2012). (B) The nematode, *Caenorhabditis elegans*, hermaphrodites' aggregation behavior is induced through indole ascarosides (further studies are needed to understand how the chemical language used by this species mediates social communication) (Srinivasan et al. 2012). (C) Sex pheromones may be complex mixtures for which

the ratio of the components plays a key role in its detectability. The female tobacco budworm moth (*Heliothis virescens*) uses a seven-component pheromone blend to attract males of the same species (Vetter and Baker 1983). Among them, two components, (itZ)-11-hexadecenal and (itZ)-9-tetradecenal (in bold letters), are necessary for behavioral activity to occur, while among the remaining five compounds, hexadecanal is most consistent in elevating behavioral activity of males when added to test blends. (D) Olfactory perception is also essential for newborn's survival in mammals. The newborns of the European rabbit (*Oryctolagus cuniculus*), initially blind and deaf, and nursed only once a day for 5 min by the mother, search, locate, and grasp very rapidly the maternal nipples by responding to the mammary pheromone, 2-methylbut-2-enal, emitted by all rabbit females in their milk (Coureaud et al. 2010). (Drawings by N.Y. Schneider)

## Different Behaviors to Convey Odor Molecules to Sensory Organs

In order to make perception of odor molecules or odor mixtures possible, animals have developed diverse behaviors allowing sampling of the

information emanating from the surroundings. These behaviors may help to detect the odor source and the direction to the source or allow for transport of the odor stimuli to specific parts of the olfactory detection organ in species with multiple receptor sides.

Single-cell organisms such as paramecium are unable to detect chemical gradients by simultaneous comparison of the chemical concentration at two parts of the body as observed in multicell organisms. The former possess only one receptor side, while the latter have paired olfactory organs, e.g., two main olfactory epithelia (one per nostril) (Valentine et al. 2008). In order to locate a food source, single-cell organisms use chemotaxis behavior, e.g., they show periods of movement in a straight line interrupted at intervals by a turn. They may “remember” whether the concentration previously experienced was higher or lower than the current concentration.

Multicell organisms can use osmotropotaxis (Gaudry et al. 2012). This strategy depends on measuring instantaneous concentration at two spatially separated odor sensors and turning toward the side of the higher concentration; it was, e.g., described for the fruit fly, which uses its pair of antennae to detect and follow odor cues. A second strategy, which is known as optomotor anemotaxis, involves flying upwind when an odor is sensed (Gaudry et al. 2012). Another orientation strategy is the countertuning, for instance, extensively studied in moths. If the odor of interest is lost, moths switch to cross-wind flight, which may help them track down the odor again. Similar behaviors have been shown also in crustaceans.

Vertebrates appear to combine the use of bilateral chemosensory cue detection with active sampling to localize an odor source. To direct nonvolatile odor molecules to specific receptor sides, specific behaviors have been developed at the receiver level, e.g., the tongue-flicking behavior observed in snakes and other reptiles: The split tip of the tongue allows peaking up nonvolatile molecules and delivering them to the opening of the vomeronasal organ (Daghfous et al. 2012). Similarly, a number of mammals (ruminants, equids, felids, tapirs, and certain marsupials such as kangaroos and wombats) are known to use flehmen behavior which also involves picking up odor molecules with the tongue and applying the attractive nonvolatile substance to the opening of the vomeronasal organ while the head is held up high and the upper lip is retracted. The Asian

elephant uses its trunk to apply female urine to the opening of the vomeronasal organ. Furthermore, mammalian sampling of volatile odor molecules is carried out through a specific action, the sniffing behavior, which induces air entry (or amniotic fluid entry in fetuses) into the nostrils, then the nasal cavity, and, finally, the posterior part of the cavity, where fraction of the flow carrying odorants may reach the olfactory epithelium. Thus, a single sniff, a sniffing episode (successive sniffs), or sniffing cycles (successive episodes with number, frequency, velocity, and duration depending on the species, distance from the odor source, chemical complexity of the source, air turbulence, etc.) distribute the molecules to different populations of olfactory receptors. This allows for actively collecting odor information from the surroundings, analyzing complex olfactory scenes, and responding behaviorally to relevant stimuli (Coureaud and Datiche 2009). Importantly, sniffing also contributes to the temporal, spatial and mechanical coding of a stimulus, to the coding of its identity and intensity, and therefore to the representation of a particular percept for a given stimulus (Mainland and Sobel 2006).

## **Different Modes of Perception to Represent the World**

### **A Complex Olfactory Environment**

In ecological conditions, odors rarely result from single odorants but from mixtures of several – tens, hundreds, or more – odorants, and mixtures are themselves emitted among other mixtures coming from the same substrate or adjacent ones. Whatever the species and their aerial or aquatic living surroundings, animals therefore have to deal with an environment both chemically complex – in terms of number, nature, and diversity of volatile and nonvolatile molecules – and dynamic (e.g., daily, seasonal, anthropic and climatic variations). A common challenge shared by animals during their development, and crucial for survival and adaptation, is then to extract pertinent information from this complexity and to respond efficiently to the cues which are the most

important for them (i.e., those carrying positive or negative hedonic value) by displaying motor actions allowing to meet their needs.

### A Twofold Perceptual Strategy

In terms of perception, since odor mixtures constitute the common stimuli emanating from the physical (e.g., ocean, river, air, ground, rocks, etc.) and biological (e.g., plants, flowers, predators, preys, conspecifics, etc.) components of the environment, animals may simplify the amount of information contained in a mixture either by responding to certain of its elements only (elemental perception) or by responding to the mixture as a whole, i.e., by attributing a particular value to that odor object instead of its elements (configural perception). These two strategies are not necessarily exclusive, because for certain mixtures animals may respond both to a configural odor specific for the mixture and to the odor of one or several of its odorants (weak configural perception).

Elemental perception means that an organism will respond to one or several odorants of a mixture the same way as to the mixture itself or, at least for simple mixtures such as binary ones, that the sum of its responses to each constituent is equivalent to the responsiveness displayed to the mixture (while the level of response to each constituent is superior compared to control odorants) (Kay et al. 2005). This mode of perception makes it possible to reduce the complexity of a mixture by extracting only the information of interest. Elemental perception is, for instance, observed toward key odorants. By key odorants, here we mean particular odorants that convey by themselves, at least in part, the same odor quality as the mixture. For example, in a green apple, humans are particularly sensitive to hexyl acetate and trans-2-hexenal, two molecules that each appear to be strong contributors to the odor quality of that fruit (Bult et al. 2002). This elemental perceptual ability would allow for animals to respond to a complex stimulus through the rapid detection of one, some, or all of its constituents, in order to optimize its knowledge about that stimulus and capability to display preference for it among other stimuli contained in the same

surroundings. In addition, it may allow generalizing its responses from one stimulus to another emitting some common elements (e.g., from one food to another food sharing some odorants and both providing nutritional qualities). In certain cases, key odorants present pheromonal properties and correspond to monomolecular pheromones. By pheromone, we mean an odor cue with communicative value, released by a sender and perceived by a receiver, both from the same species, in which the pheromone triggers an adaptive response (physiological and/or behavioral) independently of previous learning. This is typically the case of 2-methylbut-2-enal, the so-called mammary pheromone emitted by rabbit females in their milk among more than 150 other volatile components: the pheromone strongly triggers in newborn rabbits stereotyped orocephalic movements allowing for the pups to search for the nipples when the mother comes into the nest and to orally seize the nipples during a nursing episode (Coureaud et al. 2010) (Fig. 1d).

Configural perception means, conversely, that the perception of mixture elements is restricted to the benefit of a new odor quality, specific of the whole mixture and clearly distinct from the odor qualities of the elements. It is a way to allow grouping individual stimuli into a perceptual unit – a gestalt – and attributing a specific value to a mixture as a whole (compared to its components), which is represented in the brain as a single unit of information, i.e., as an odor object (Kay et al. 2005). This object then becomes prominent in the environment and easily identifiable by the animal in the midst of other stimuli (Staubli et al. 1987). Configural perception may occur for complex odors emitted from food sources (e.g., flowers or preys in animals, meals in humans) or for odors which carry a social value, as for pheromones constituted by a small number of molecules that blend into a given mixture (Badeke et al. 2016). Configural perception is, for instance, at work in humans, when we perceive the typical odor of coffee, while no molecules of coffee effluvia (bouquet of molecules emanating from the substrate) evoke that odor quality by themselves (Czerny et al. 1999). More largely, it is observed in both aquatic and terrestrial organisms, and in



invertebrates (e.g., spiny lobsters, slugs, honeybees, moths) as in vertebrates (e.g., catfish, rabbits, rats, dogs). Configural odor perception has mainly been described in adults, but data in the rabbit pinpoint its functionality in the newborn (Coureaud et al. 2014; Schneider et al. 2016); the fact that very young organisms perceive certain mixtures as odor objects makes biological sense because of the chemical complexity of the perinatal environment and urgent necessity for individuals, during this early period of life, to extract information from complex odor substrates (amniotic fluid, maternal body, milk) in order to survive and learn about the surroundings. Interestingly, different species may process the same mixtures configurally, as it has been shown with binary and senary mixtures in rabbits and humans (Coureaud et al. 2014; Sinding et al. 2013), which suggests that the sensory systems of various animal species may have converged in the way they process certain complex stimuli, with a common goal: reducing perceptual complexity of their chemosensory environment (chemosensory Umwelt) to detect and behave selectively toward certain odor stimuli that contribute to their adaptation.

Differences in the neural processing supporting elemental versus configural odor perception, from the periphery of the olfactory system to central brain regions, remain to be clearly deciphered. However, certain results suggest that configural perception may occur as soon as odor molecules interact at the olfactory receptor/olfactory sensory neuron level, then in central regions where interactions between neurons occur (i.e., olfactory bulb in mammals and antennal lobe in insects, respectively) and in higher-order regions (i.e., piriform cortex in mammals and mushroom bodies in insects) (e.g., Rospars et al. 2008; Deisig et al. 2010; Gottfried 2010; Wilson and Sullivan 2011; Schneider et al. 2016; Singh et al. 2018).

Among factors that influence the mode of perception of odor mixtures is the number of components. If configural perception can occur even for very simple mixtures as binary mixtures, it is thought that the olfactory system presents elemental limits: when the number of odorants in a mixture becomes too high compared to that limit,

perception would switch from the elemental to the configural mode. In humans, this limit seems to be low (around 4–5 odorants); it appears to be higher in other species (e.g., Sinding et al. 2013). Other factors involved in the way odor mixtures are perceived may also depend on the stimulus, e.g., the chemical nature of the individual components and their ratio in the mixture, or on the receiver, e.g., the animal's experience of the mixture or its constituents. Thus, if certain mixtures are spontaneously processed in the elemental or configural ways, learning events may modulate this initial perception. The respective influences of all these factors in the final perception of odor mixtures remain to be clearly determined.

## Conclusion

From invertebrates to vertebrates and throughout ontogenesis, perception of odor cues is of vital importance to help animals to adapt to the environment in which they are living by displaying responsiveness to certain odorants or mixtures of odorants carrying spontaneous or learned biological values and to build representations about the social and nonsocial components of the environment. Further investigations, from chemistry to behavioral neurosciences, are required to better understand these remarkable sensory and cognitive abilities shared by all species, including humans, aiming to improve their integration into the world through the olfactory modality, alone or in interaction with the other sensory modalities.

## Cross-References

- ▶ [Attachment](#)
- ▶ [Chemical Cues](#)
- ▶ [Chemical Signals](#)
- ▶ [Chemoreception](#)
- ▶ [Chemotaxis](#)
- ▶ [Cognition](#)
- ▶ [Communication](#)
- ▶ [Escape Response](#)
- ▶ [Gestalt](#)
- ▶ [Information Processing](#)

- [Mating](#)
- [Olfactory Discrimination](#)
- [Pheromone](#)
- [Representation](#)
- [Scent-Marking](#)
- [Sensory Receptors](#)
- [Social Behavior](#)
- [Umwelt](#)

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## Olfactory Signals

- [Chemical Signals](#)

## Oligonucleotides

- [Primer](#)

## Oligos

- [Primer](#)

## Omics

- [Behavioral Genomics](#)

## Omission Training

- [Punishment](#)

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## Omnivore

Jacqueline Boyd

Skinner's Pet Foods, Stradbroke, UK

## Synonyms

[Consumer](#); [Heterotroph](#); [Scavenger](#)

## Definition

An omnivore is an organism with a dietary intake consisting of both plant- and animal-derived materials.

## Introduction

An omnivore is defined as an animal that consumes both plant- and animal-derived foods, the prefix being derived from the Latin words *omnis*, meaning “all,” and *vor*, meaning “to devour.” Omnivores can obtain their dietary energy and nutrient requirements from a mixed diet of plant and animal origin and will occasionally include other sources of nourishment in their diet such as fungi, algae, and bacteria. Omnivory can be characterized as behavioral and/or physiological, based on the spatial and temporal availability of foodstuff, combined with an organism's intrinsic ability to obtain energy and other nutrients from ingested material. Certain omnivorous species will demonstrate specific anatomical, physiological, and/or behavioral specializations and adaptations for the acquisition and processing of specific foodstuff.

Omnivores exploit a wide nutritional niche as a result of the diversity of foods consumed. Seasonality and availability of specific dietary components can vary, and some omnivores will demonstrate the opportunistic consumption of available material, either because of nutritional deficit or due to seasonal, temporal, and/or spatial availability. This impacts on both the qualitative and quantitative nutritional requirements of

omnivorous species. The digestive system and oral, dental, and other morphology of omnivores are also highly variable. As a result, generalized observations about the anatomy, physiology, and nutritional requirements of omnivorous species are problematic and tend to be best examined on an individual species level.

## Omnivorous Species

Omnivores are diverse and belong to several different taxonomic clades. Several mammals are acknowledged to demonstrate an omnivorous dietary strategy, with bears and many canid species (Landry and Van Kruiningen 1979) exhibiting a mixed dietary intake of plant- and animal-derived material, including that scavenged. The pig (*Sus scrofa domestica*) is a monogastric (simple, single-stomached) animal often described as a typical omnivorous mammal, with a dentition and digestive system considered intermediate to a typical carnivore or herbivore, whether ruminant or hindgut fermenter.

Several bird species are also considered to be omnivores, with consumed foods including fruits, berries, seeds, nectar, insects, worms, fish, and other animals including mammals, reptiles, amphibians, and other birds. Omnivory is also observed in marsupials such as the brushtail possum (*Trichosurus vulpecula*; Cruz et al. 2012), various reptiles, amphibians, fish, and invertebrate species. The diversity of species in which omnivory is observed supports the biological and evolutionary value of a mixed dietary strategy, where available dietary resources can be exploited in an otherwise inconsistent environment.

## Characteristics of Omnivores

The omnivore dietary strategy is diverse and observed across different taxonomic clades, often each independently evolving digestive capabilities for a mixed dietary intake. Consequently, in contrast to the easily identified physical characteristics of a typical mammalian carnivore such as dentition, identifying specific physical and

physiological characteristics of omnivores is less obvious. Behavioral characteristics will also relate to feeding behavior and how different foodstuffs are acquired and consumed by omnivorous species, and this may relate to both temporal and spatial availability of dietary components.

On this basis, classification of an organism as an omnivore is problematic as generalizations of fundamental biology are limited. For example, the domestic dog (*Canis lupus familiaris*) is recognized to exploit an omnivorous dietary niche and yet has the dentition and digestive anatomy of a typical carnivore. However, there are some characteristics that are common to many species with an omnivorous strategy.

The typical diet of omnivorous species will consist of a mix of plant- and animal-derived material, occasionally also including fungal matter. Consequently, the digestibility of ingested material will vary, and a greater proportion of indigestible, fibrous material will be consumed in contrast with carnivorous species. Physiological adaptations include the metabolic ability to manufacture specific nutrients from appropriate precursors supplied as nutrients, as well as the digestive capacity to deal with food of both plant and animal origin. As a result, omnivores typically have longer and more complex digestive systems, the provision of microbial fermentation in the caecum, and longer mean retention times (MRT) of digesta than observed in highly carnivorous species (Hume 2002). Indeed, the typical omnivore digestive system comprises aspects of both the typical carnivore and herbivore digestive systems, but without some of the extreme digestive specializations observed in the herbivorous ruminants and hindgut fermenters.

Omnivory is further complicated by the observation that species classified as either herbivores or carnivores on a physiological basis exhibit ingestive behavior that contradicts those classifications. For example, cats and dogs are known to occasionally eat grass. This has long been considered a behavioral response to elicit an emetic reaction, although evidence suggests this is not always the case (Hart 2008) and at least in dogs might be a gustatory preference (Ferrell 1984; Li et al. 2006).

Similarly, species typically considered to be herbivorous have been observed to consume animal material, sometimes in an opportunistic, scavenging capacity. This may arise from a physiological need for specific nutrients and/or a behavioral adaptation for nutrient acquisition from available resources during periods of limited dietary availability. Both domestic rabbits (*Oryctolagus cuniculus*) and snowshoe hare (*Lepus americanus*) have been observed to consume the carcasses of other animals, including those of their own species (Clauss et al. 2015; Peers et al. 2018).

Osteophagia (the consumption or chewing of bone) is also observed in otherwise herbivorous species. White-tailed deer have been seen to consume bone from carcasses in an opportunistic manner (Meckel et al. 2017), and osteophagia has been frequently reported in giraffe (Hampton 2002), potentially as an available source of phosphorus and calcium which might be otherwise deficient from their diet (Bredin et al. 2008).

While it is considered that the gnawing or chewing of bone (or other bony items such as antlers) by species predominantly considered to be herbivorous represents an opportunity to supplement dietary mineral inadequacy, boredom, habit, and taste may also contribute to this observation. However, the behavior can result in abnormal tooth wear and breakage, with both health and biological identification significance (Càceres et al. 2013). Rodent species have also been described as chewing on bone to address mineral inadequacies, and it appears to be a significant behavior in reproductively active female crested porcupine (*Hystrix cristata*), potentially to support the mineral demands of pregnancy and lactation (Mori et al. 2018).

## The Omnivore Diet

The proportion of animal and plant material in the diet of individual species will vary, and no set definition is ascribed to an omnivore based on dietary composition, beyond that of a mixed intake of plant, animal, fungal, algal, and bacterial material. Some species routinely consume a mixed diet, while others modify their dietary

intake of plant or animal material based on supply, culture, preference, behavioral adaptations, and seasonal availability. This has been observed in the dugong (*Dugong dugon*), where the seasonality of their usual seagrass diet leads to omnivory (Preen 1995). Other species display opportunistic scavenging behavior, resulting in a mixed dietary composition, such as members of the Canidae (Landry and Van Kruiningen 1979).

There may also be apparent behavior “preference” for specific foods, based on specific digestive system adaptations, and some species can be further classified into specific dietary niches based on the proportion of individual foodstuffs in their diet. This leads to classifications within the omnivore classification, such as the frugivorous (fruit-eating) maned wolf (*Chrysocyon brachyurus*; Motta-Junior et al. 1996), insectivorous (insect-eating), or granivorous (grain-eating). Such terms are useful in identifying what a large proportion of an otherwise omnivorous diet will consist of, and such dietary classifications can be observed across the range of species in which omnivory is observed.

## The Dentition and Digestive System of the Omnivore

Organisms demonstrating a mixed dietary strategy and intake encompass a number of different taxonomic clades and a wide number of species. Consequently, specific characteristics of the omnivore digestive system tend to be more species-specific than dietary intake-specific. However, omnivorous mammals will typically be monogastric with a simple digestive system and minimal reliance on bacterial fermentation of ingested foodstuff, compared to those species identified as herbivorous.

The omnivore gastrointestinal tract is typically more complex than that of carnivorous species, although the stomach remains simple. The omnivore small intestine is typically of moderate length, and the caecum and colon will permit a level of retention of digesta and may exhibit a degree of microbial fermentation (Hume 2002), greater than that of a typical carnivore.

Because of the mixed intake of dietary components by omnivorous species, they tend to have a diverse ability to digest specific nutrient groups (carbohydrate, protein, fat, and fiber). This leads to a diversity in the way that specific nutrients will also be metabolized and absorbed, in addition to specific nutritional requirements.

Bird species with an omnivorous dietary strategy will demonstrate a typical avian digestive system, with crop, proventriculus, gizzard, and duplicated caeca (McDonald et al. 2011), but may have intermediate beak morphology between that observed in birds with dietary specialties such as the raptors (typically carnivorous) and finches (with a typical intake of plant material).

The dentition of omnivorous mammals is typically intermediate to that of carnivorous species and the herbivorous species. Where there is a degree of dietary specialization, dentition may reflect this, although the dentition of most mammalian omnivores demonstrates a greater degree of grinding and crushing surfaces via the molars and pre-molars than would be observed in the typical carnivore dentition. This provides enhanced grinding and chewing ability and is typically combined with altered cranio-mandibular structures and musculature to facilitate prolonged food acquisition and processing.

## Omnivory and Evolution

While the ability to obtain nourishment from a mixed dietary intake, opportunistic and seasonal availability of dietary components may appear an adaptive survival strategy to support life in a changing environment, omnivory may represent a macroevolutionary sink, in birds at least (Burin et al. 2016). This supports the notion that the biological fitness of specialists tends to be higher than that of generalists (Wilson and Yoshimura 1994), although the very fact that omnivory appears to be such a widespread dietary form across a range of organisms does suggest a survival advantage, potentially as a result of inconsistent or unpredictable resource availability.

The evolution of individual species is characterized by the gradual acquisition of adaptations



that enhance reproductive survival. Dietary strategies are clearly integral to the evolution of a species due to the requirement for nourishment for survival, but also because of competition between individual species for dietary resources (Grant and Grant 2006). With omnivory typically representing a generalization and adoption of intermediate physical and physiological characteristics for this dietary niche, the lack of specialization may simply represent reduced biological diversification and, as a result, increased competition for dietary resources within an evolutionary timeframe.

In mammals, different diversification rates characterize the different trophic classifications, herbivore, carnivore, and omnivore, with transitions toward omnivory being more frequent than to either herbivory or carnivory (Price et al. 2012). This might be an indication of the biological value of a generalist dietary intake, although there are significant levels of diversification in the ruminant herbivorous species with different feeding styles (Cantalapiedra et al. 2014), further demonstrating the impact of diet on evolution.

However, birds are well understood to demonstrate specific physical adaptations to specific dietary niches, resulting in highly specialized feeders with physical adaptations in physical (e.g., beak morphology), behavioral, and other physiological characteristics. Species belonging to the Corvidae family tend to have more omnivorous, opportunistic diets (Kissling et al. 2012) and typically demonstrate intermediate physical characteristics in terms of size, beak morphology, and other adaptations, as well as a wider spatial distribution.

Omnivory may also have an impact on the evolution of body size, as is observed within carnivorous species (De Cuyper et al. 2019). Animals of larger body size tend toward herbivory and a greater intake of plant-based material, which is also associated with longer mean retention time for digesta (Hume 2002). In the common brushtail possum, subspecies with a smaller bodyweight appeared to consume more a mixed, omnivorous dietary intake than those of larger body size, supporting the shift toward omnivory or indeed even carnivory in smaller animals (Cruz et al. 2012).

## Conclusion

The omnivore dietary strategy is a generalist one, consisting of an intake of both plant- and animal-derived materials. Dietary intake can vary based on the availability of material either spatially or temporally, but also based on individual species physiological or behavioral preferences. While specific characteristics of omnivorous species are difficult to identify due to the variety of species in which the strategy is observed, at least in mammals and birds, omnivores typically demonstrate morphological, physiological, anatomical, and behavioral traits linked to ingestion, between those of typical carnivorous and herbivorous species.

Omnivory is observed and identified across a wide range of taxonomic orders and appears to be a significant factor in the diversification and evolution of some species. Omnivory represents a dietary niche that permits a range of available resources to be utilized for energy and nutrient acquisition. This can be of significant benefit in unpredictable or limited resource environments and, as such, can be considered a successful dietary strategy.

## Cross-References

- [Bear Diet](#)
- [Canine Diet](#)
- [Cannibalism](#)
- [Carnivora](#)
- [Feeding](#)
- [Herbivore](#)
- [Insectivore Diet](#)
- [Mustelidae Diet](#)
- [Omnivore](#)
- [Predator](#)
- [Prey](#)

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## On the Origin of Species

### ► Origin of Species

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## Ontogeny

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Ontogeny refers to the development and maturation of an organism or an organ from a fertilized egg. The term ontogeny first appeared in scientific literature in 1872 and is derived from 2 words – *onto* referring to individual/being and *genesis* meaning production.

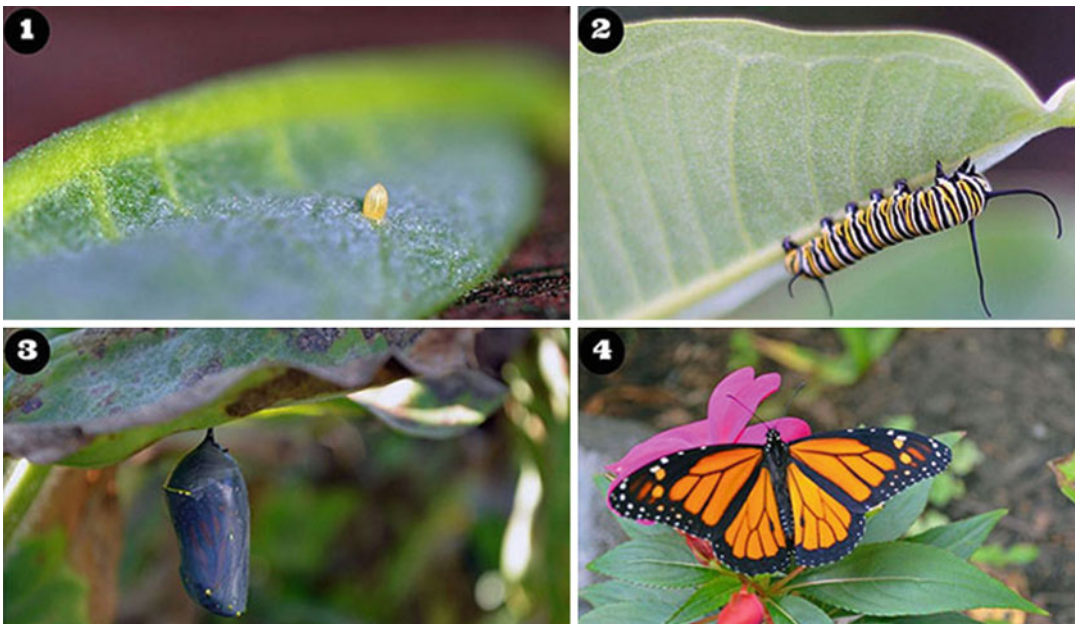
Ontogenesis is determined by various genetic and environmental factors. The stages that occur during ontogenesis are sequential and are extremely specific for a particular species (Cabej

2012). A deviation from the routine ontogenic process at a particular point in development is a major step in speciation (evolution into a new distinct species). Ontogenesis is usually associated with either of the two processes – metamorphosis and allometry.

Metamorphosis (*meta*: change; *morph*: form) is the drastic transformation that occurs to the form of an animal after it has completed the development as an egg. This has been observed in various classes like insects, amphibians and fish. Programmed cell death, also known as apoptosis, plays an important role in metamorphosis, where redundant cells undergo cell death in absence of inflammation, resulting in involution of body parts. Metamorphosis is also regulated by factors like hormones and growth factors (Fig. 1).

Allometry (*allo*: other; *metry*: measurement) is the relationship between the change in size of a body part in relation to the change in size of the organism. If the growth of the body parts of an organism occurs in equal proportions to one another throughout its development, the growth

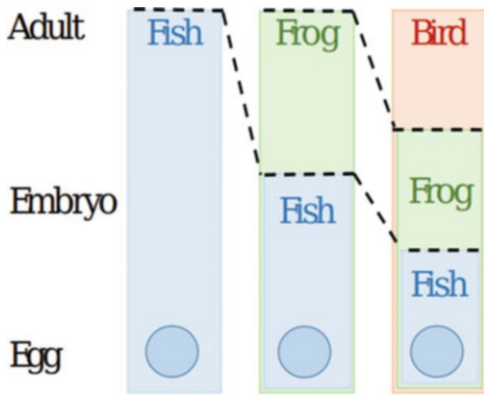
is considered as isometric (*iso*: same). This is observed in various organisms after metamorphosis, for example, in frogs. Any deviation from isometric growth pattern is referred to as allometric scaling. Allometric changes during ontogenesis are observed in a multitude of species including humans. An example of allometric growth is the size of head in humans during development – the proportion of head size with respect to the body size progressively decreasing, as the growth proceeds. Allometric growth pattern can be mathematically represented by the equation:  $f(x) = ay^b$ , where  $x$  and  $y$  are organ sizes/attributes, and  $a$  and  $b$  are scaling constants. The exponential scaling component of the above equation will be positive and high for an organ/attribute that is important in providing a survival trait for the organism. This is exemplified by the disproportionate growth of antennae and claws in lower animals. In humans, fetal weight is a function of femur length, head circumference, and biparietal diameter (length between two parietal eminences, which forms the part of the skull



**Ontogeny, Fig. 1** Metamorphosis in monarch butterfly (*Danaus plexippus*). Monarch completes its life cycle from egg to larva (caterpillar) to pupa (chrysalis) to adult in a

period of 28–38 days. (Courtesy: USFWS photos by Courtney Celley, Tina Shaw and Joanna Gilkeson)

bones), as determined by ultrasonography. Allometry can also be extrapolated across organisms, for example, metabolic rate in many organisms is a function of body mass raised to the power 0.75 (Kleiber's law).

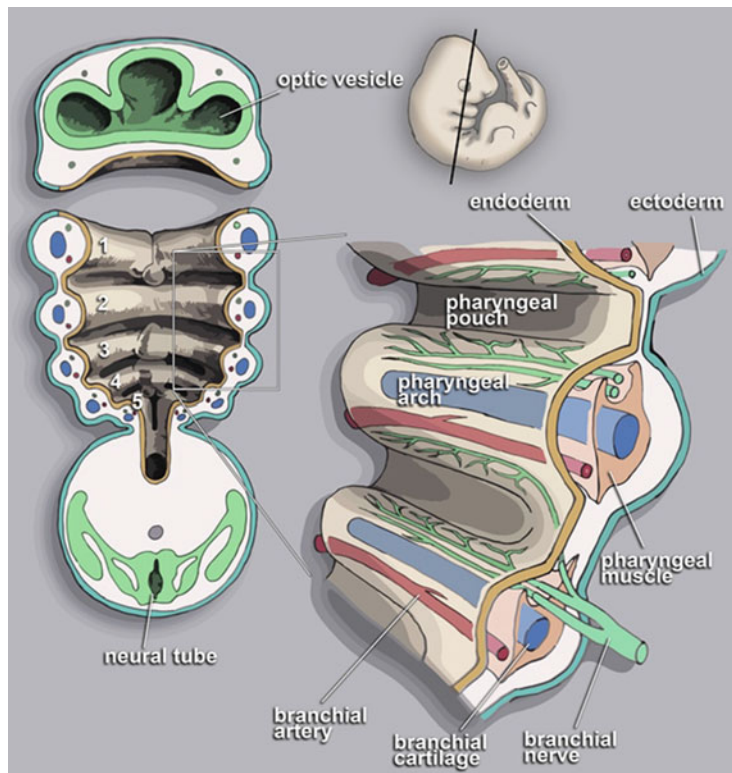


**Ontogeny, Fig. 2** Recapitulation theory. (Courtesy: Ian Alexander [CC BY-SA 4.0 (<https://creativecommons.org/licenses/by-sa/4.0/>)], from Wikimedia Commons)

Sometimes during the ontogenesis of an organism, features/traits that are otherwise observed only in the juvenile/larval growth stages are retained. This phenomenon is known as neoteny (*neo*: new; *teny*: prolong). A classic example of neoteny is observed in Mexican salamander, also known as axolotl (*Ambystoma mexicanum*), where the larval forms can reproduce and survive. Humans also exhibit neoteny during ontogenesis – development of human offsprings is much more prolonged than nonhuman primates, and this is thought to be the reason behind features like a larger brain and sophisticated emotional responses in humans compared to other primates.

Recapitulation theory proposed by Ernst Haeckel in early nineteenth century states that “ontogeny recapitulates phylogeny.” Phylogeny (*phylon*: tribe) is the evolutionary history of a species as a whole. According to the recapitulation theory, as an organism undergoes ontogenesis, it encounters various stages of

**Ontogeny, Fig. 3** Pharyngeal arches and pouches seen during human development. (Courtesy: Loki austanfell [CC BY-SA 3.0 (<https://creativecommons.org/licenses/by-sa/3.0/>)], from Wikimedia Commons)





development which closely resembles the organism's ancestral species along the evolutionary timeline. In the book *The Drama of the Oceans*, Elisabeth Mann Borgese mentions "Every woman's womb is a micro-ocean, the salinity of its fluids resembling that of the primeval waters; and every microcosm restages the drama of the origin of life in the gestation of every embryo, from one-celled protozoa through all the phases of gill-breathing and amphibian, to mammalian evolution" (Borgese 1975) (Fig. 2).

This concept of recapitulation is now being criticized and may not be as dramatic as Ms. Borgese explains or as Haeckel proposed. Since many organisms do not undergo embryonic stages that mimic all the ancestral forms, the concept of recapitulation is now defunct. Nevertheless, certain ancestral features are observed during ontogenesis, for instance, presence of pharyngeal arches and pouches during human development, and gill slits during the development of frogs, both reminiscent of evolution from aquatic organisms (Fig. 3) (Said 2018).

Reverse ontogenesis is the process by which an organism resorts to a larval stage from an adult stage. This was first described in 1913 in hydrozoans by H.C. Müller, where it acts as a protective mechanism against adverse environmental conditions.

## Cross-References

- [Evolution](#)
- [Neoteny](#)
- [Phylogeny](#)
- [Primates](#)

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## Open-Field Test

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## Alternative Words or Phrases Not Included in the Title

Anxiety, Animal fear, Sensorimotor test, Rodents, Locomotor activity, Exploratory behavior, Thigmotaxis

## Synonyms

[Test for analyzing anxiety-related behaviors](#)

## Definition

Open-field test is used to analyze the different aspects of anxiety-related behaviors, including locomotion and exploration in animals.

## Introduction

The open-field test (OFT) is a well-established and modest sensorimotor assessment employed to evaluate anxiety, basic locomotor-activity levels, and exploratory behavior in animals (Hall and Ballachey 1932). Traditionally it has been used for rodents like mice and rats, but the conceptual design is also used for other species including birds and humans (Uitdehaag et al. 2008; Walz et al. 2016).

The apparatus consists of a square arena where the animal is placed and allowed to freely explore



for a limited (predetermined) period of time. The locomotor and exploratory behavior is recorded using a camera. The video is then analyzed using appropriate software for multiple parameters like total distance covered and total time spent in demarcated areas (not visible to the subject animal). A comparatively decreased locomotion (less exploration) and overall preference to remain close to periphery near wall boundaries (thigmotaxis) imply increased anxiety in the animals (Crusio 2013).

### Usage of OFT

It is very useful in testing the effect(s) of various anxiolytic drugs or new chemical entities on central nervous system. It is also used for phenotyping different transgenic animals for the levels of anxiety. There have been multiple studies done to evaluate the effect of hormonal or nutritional deficiencies (Bale et al. 2000; Caldwell et al. 1970; Ghosh et al. 2018). Comprehending the practical glitches in studying animal behavior, OFT is generally used along with additional investigations such as the elevated plus maze and light-dark box test.

### Conclusion

To summarize, OFT can be used for the assessment of overall locomotor and exploratory activity to detect anxiety in animals.

### Cross-References

- Behavior Systems
- Cognition
- Locomotion
- Maternal Behavior
- Memory
- Paternal Behavior
- Rodentia Locomotion
- Species-Specific Behavior

### References

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### Openness

- Xenophilia

### Operant Box

- Operant Chamber

### Operant Chamber

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### Synonyms

Operant box; Skinner box

## Definition

An experimental apparatus used in the study of behavior.

## Introduction

An operant chamber is an experimental apparatus commonly used in psychological research with nonhuman animals, such as rats, mice, and pigeons. B.F. Skinner, a psychologist and behaviorist, invented the operant chamber (Skinner 1956). As a result, operant chambers are also referred to as Skinner boxes. Skinner invented the operant box to study operant behavior. Operant behaviors are behaviors that produce a consequence or outcome in the environment, such as positive reinforcement (e.g., food) or negative reinforcement (e.g., escape from shock) (Heron and Skinner 1939). The apparatus was invented in an attempt to increase experimental control over other apparatuses commonly used in the study of learning, such as mazes (Skinner 1957). Within the operant chamber, events can be delivered manually during an experimental session or sessions can be programmed so that all events are automated. This means that experimental variables such as the delivery of consequences are well controlled within an experimental session (Heron and Skinner 1939). In typical experiments using operant chambers, a subject learns to make some response for reinforcement. The operant chamber records when the subject makes the predetermined response. The response is typically a behavior that is easily observed and recorded, as well as easily repeated by the subject without the risk of immediate fatigue. The chamber allows for precise measurements of the frequency with which the subject makes a response. Researchers can use rate of responding to examine the effects of motivational states, reinforcement contingencies, and other manipulations on behavior while attempting to control for all other variables (Skinner 1957).

## Specifications

The operant chamber is typically placed within a sound attenuating cabinet to limit the effect of

any outside noise on the behavior of the subject. Most chambers are ventilated to filter the air and prevent excessive buildup of animal dander within the chamber. Typically, the chamber includes grated flooring for the subject to stand on and move freely about the box. The chamber is often illuminated by a dim light on the roof, which is commonly referred to as a house light. One wall of the chamber houses a food magazine that the subject can easily access. The magazine is capable of delivering reinforcement (e.g., food) to the subject contained within. Objects that can be manipulated such as pull chains, levers, or keys are often contained within the apparatus and serve as response manipulandum. These manipulanda allow for a subject to make multiple responses, allowing the experimenter to collect multiple data points at different times within the experimental session. Operant chambers often include additional components that can serve as stimuli that signal the availability or probability of a consequence or outcome. These stimuli often include lights that can be turned on and off, as well as varied in intensity, and speakers that can emit tones or white noise. Operant chambers may also be capable of delivering shock through the grated flooring. The delivery of these stimuli can be programmed so that their delivery is fully automated (Skinner 1957).

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [B.F. Skinner](#)
- ▶ [Operant Conditioning](#)
- ▶ [Reinforcement](#)
- ▶ [Skinner Box](#)

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## Operant Cognitive Bias

### ► Judgment Bias

## Operant Conditioning

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### Synonyms

Instrumental conditioning; Schedules of reinforcement

### Definition

Change in the frequency or probability of a response, caused by a change in the consequence or outcome of that response.

### Introduction

Research on how behavior is shaped by its consequences dates back to Thorndike (1911), who studied how cats and other species learn to escape various enclosures. Skinner (1935) further systematized this research, coining the term *conditioned reflex type I* to refer to responses that occurred because of their consequences. Conditioned reflex was a term used for responses that were conditional on previous experience. Whereas the conditioned reflex type II was dependent on the stimuli that *preceded* the response (commonly known as Pavlovian conditioned stimuli), the conditioned reflex type I was dependent on the stimuli that *followed* the response (the *outcome* of the response). Type I reflexes eventually came to be known as *operant behavior*, and the procedure and process by which they emerge, *operant conditioning*.

Skinner (1935) highlighted the point that, whereas Pavlovian responses to a stimulus (e.g.,

freezing to a tone) change in probability because of the pairing of that stimulus with another stimulus (e.g., tone with footshock), operant responses change in probability because these responses *mediate* the pairing of stimuli. If, for instance, pressing a lever in the presence of the tone resulted in footshock (i.e., lever pressing mediates the tone-footshock pairing), the tone would reduce the probability of pressing a lever.

Skinner investigated operant conditioning in subsequent publications and developed the basic nomenclature and technology for its investigation. Most basic research on operant conditioning is published in the *Journal of the Experimental Analysis of Behavior*, although several other journals have regularly published research on operant conditioning in the last few decades.

Skinner (1953) argued that most behavior, particularly human behavior, is the product of operant conditioning. Although this claim has been challenged, operant conditioning has been demonstrably useful in a wide range of fields. Operant conditioning in animals (typically small rodents and pigeons) is the dominant paradigm for the experimental study of voluntary behavior, including impulsive behavior. The field of behavioral pharmacology relies heavily on operant conditioning models to study the voluntary seeking and self-administration of drugs. Findings from operant conditioning research have been applied to education practices, particularly in populations with learning disabilities, and have informed public policy.

### Key Concepts

#### Experimental Design and Contingency

Operant conditioning involves a *causal relation* between a response-outcome relation (the fact that a specific response produces a specific outcome) and the probability of that response. Therefore, operant conditioning can only be demonstrated experimentally, by manipulating the response-outcome relation (the independent variable) and observing its effect on the probability of the response (the dependent variable).

Operant conditioning is often demonstrated by comparing between conditions in which the outcome is either present or absent. This approach has the limitation of confounding the presence/absence of the outcome with the presence/absence of the response–outcome relation. For instance, the outcome may elicit the response even when it is not caused by that response, such as when a psychostimulant drug elicits a locomotor response. In such situation, the mere removal of the psychostimulant outcome, and not necessarily the locomotion–psychostimulant relation, may reduce locomotion.

The *yoked-control* design prevents this kind of pseudoconditioning (Fig. 1). In this design, a pair of subjects is allowed to produce the target response, but only the response of one subject (the *experimental* subject) produces the outcome for both subjects (experimental and *control* subjects). In other words, both subjects are exposed to the outcome under similar conditions, but only the experimental subject is exposed to the response–outcome relation. Therefore, systematic differences in responding between subjects can only be attributed to the response–outcome relation, thus demonstrating operant conditioning. More technically, the outcome is said to be *contingent* on the response for the experimental subject and *noncontingent* for the control subject. A within-subject yoked-control design, in which a single subject alternates between experimental and

control conditions, may reduce intersubject variability. In this within-subject design, responses in an experimental condition produce the outcomes in both the experimental (contingent) and in the subsequent control (noncontingent) conditions.

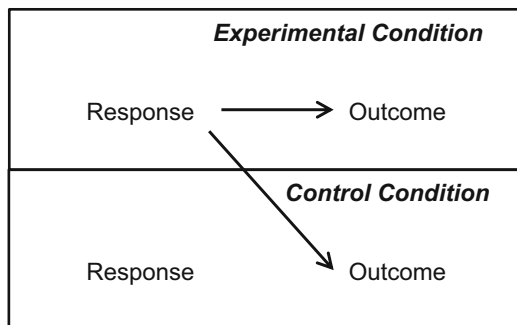
### Species and Materials

Operant conditioning is typically conducted in the laboratory, using specialized equipment that allows for strict control of variables. It is most often studied in small laboratory animals, such as rats, mice, and pigeons, because they are easy to house and handle. The prevalence of these species in operant research promoted the development of standard equipment for this research.

The equipment for operant research varies depending on the outcome and species under investigation. The typical apparatus for the study of *rewarding* outcomes was first developed by Skinner and is aptly called the *Skinner box*, or operant chamber. It is a small plastic and aluminum box, furnished with levers or keys (generically called *manipulanda* or *operanda*) to record responses, a device for delivering food outcomes, a houselight, a tone or noise generator, and a grid floor. When the outcome is a drug (primarily in rodents and nonhuman primates), it is often diluted in a solution and delivered through a catheter. The box is typically ventilated and enclosed in a larger, sound-attenuating box.

A common apparatus for the study of *aversive* outcomes in rodents is the active-avoidance shuttle-box. The shuttle-box is similar to the Skinner box, but elongated and lacking levers and food- or drug-delivery devices. The box is divided in two; the floor in each half can be independently electrified to deliver foot-shock. One side (the *shock* side) is sometimes electrified, while the other side (the *safe* side) is not. Operant conditioning is established as movement from the shock side to the safe side (or *shuttling*) when impending foot-shock is signaled.

Operant conditioning has been studied in a wide variety of other species, including humans and nonhuman primates. Unlike work with more typical laboratory animals, operant research with humans and nontraditional species relies on *ad hoc* equipment developed by the investigators.



**Operant Conditioning, Fig. 1** Schematic representation of the yoked-control design. Responses by experimental subjects produce outcomes for both experimental and control subjects. Differences in responding between the experimental and control conditions demonstrate operant conditioning

Human operant research is now typically conducted using videogame-like interfaces for collecting responses, with points exchangeable for goods or money as outcomes. Operant research with nonhuman primates often uses joy-sticks and touchscreen devices, with flavored pellets and juice as outcomes.

### Measuring Behavior

Operant conditioning procedures may be classified as *discrete-trials* and *free-operant* procedures. In discrete-trials procedures, access to a manipulandum is restricted, so that the response can only be emitted once per opportunity. For instance, an animal may be given access to a lever repeatedly, each time for 30 s; a single lever-press removes the lever, infuses a drug intravenously, and terminates the trial. In these procedures, response probability is readily measured as the number of responses emitted per opportunity to respond.

In the free-operant procedure, the manipulandum is continually available. Here the measurement of response probability is less intuitive and involves an indirect measure: the *rate of responding*, which will be signified with the letter *B* (other symbols and abbreviations are included in Table 1). Skinner (1938) proposed *B* as a surrogate for response probability and as the key dependent measure of operant conditioning. *B* is the number of responses produced per unit of time. To estimate response rate over multiple time scales, Ferster and Skinner (1957) proposed the use of the *cumulative record*. This record is obtained from a drum (or cumulative) recorder, in which a pen draws a horizontal line that extends at a constant speed, shifting upwards by a small fixed distance with each response, and resetting once it meets the edge of the drum (Fig. 2). The slope of that line is the response rate over a period of time. If vertical changes in the cumulative record are expressed as the proportion of total responses, the cumulative record is an empirical cumulative distribution function of responses over time. The slope of the cumulative record at any given time is, therefore, an estimate of the probability of a response at that time.

Cumulative records are still used today to track changes in behavior in individual organisms. However, these records are rarely obtained from drum recorders anymore. Instead, the activation of manipulanda is more often recorded electronically, through a computer interface that also controls the stimuli in the experimental environment. In fact, today it is fairly common for a single computer program to control the delivery of stimuli and the recording on responses in a fully automated way for multiple chambers, requiring minimal supervision.

### The Three-Term Contingency

Although the term *reflex* is now rarely used in the context of learning, it still highlights an important feature of operant conditioning: just like reflexes, the operant response occurs in the presence of a stimulus, the *discriminative stimulus*, or  $S^D$ . Prior to training, the rate at which the to-be operant response (e.g., lever pressing) is emitted in the presence of the to-be  $S^D$  (e.g., a light) is called the *operant level* of the response. Once operant conditioning is implemented, the operant response will produce the outcome mostly in the presence of the  $S^D$ . The efficacy of operant conditioning may be measured as the difference between the rate at which the operant response is emitted in the presence of the  $S^D$  and its operant level (albeit with the limitations already discussed). If this difference is positive (because its outcome is rewarding), the  $S^D$  is said to *set the occasion* for the response.

Along with the  $S^D$  (sometimes called the *antecedent*), the operant response (or behavior) and the outcome of that response (or consequence) constitute the *three-term contingency* (Fig. 3). A simple mnemonic to remember the components of the three-term contingency uses their first letters: Antecedent, Behavior, and Consequence, or ABC. The term *contingency* refers to the rules by which operant conditioning is implemented. The three-term contingency is the general rule that in the presence of  $S^D$  A, response B will produce outcome C.

The operant response is typically defined not in terms of the movements involved in the response, but in terms of its effect on the environment.



**Operant Conditioning, Table 1** Symbols and abbreviations

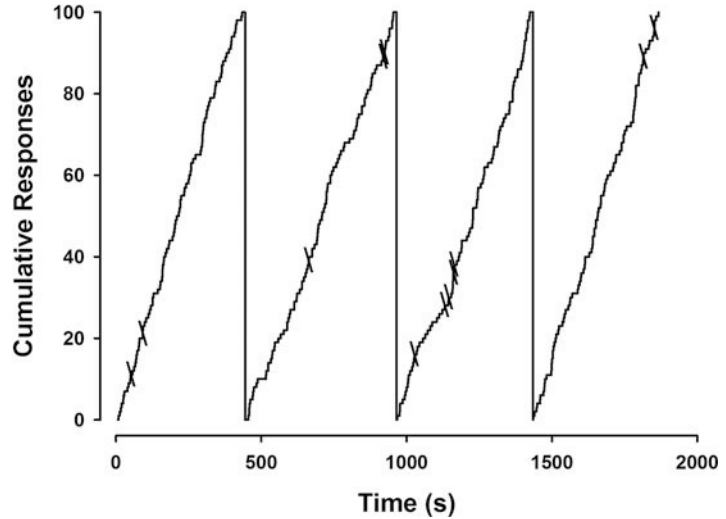
| Symbol/abbreviation               | Meaning                                                                              |
|-----------------------------------|--------------------------------------------------------------------------------------|
| <i>Responses</i>                  |                                                                                      |
| <i>B</i>                          | Rate of responding                                                                   |
| IRT                               | Inter-response time                                                                  |
| <i>Stimuli</i>                    |                                                                                      |
| $S^D$                             | Discriminative stimulus                                                              |
| $S^\Delta$                        | A stimulus in the presence of which the response does not produce the target outcome |
| $S^+$                             | Reinforcer (rewarding)                                                               |
| $SP^+$                            | Punisher (aversive)                                                                  |
| $S^-$                             | Stimulus removed by a negatively reinforced response (aversive)                      |
| $SP^-$                            | Stimulus removed by a negatively punished response (rewarding)                       |
| <i>Schedules of reinforcement</i> |                                                                                      |
| DRO                               | Differential reinforcement of other behavior                                         |
| CRF                               | Continuous reinforcement (also, FR1)                                                 |
| FR                                | Fixed-ratio schedule                                                                 |
| VR                                | Variable-ratio schedule                                                              |
| RR                                | Random-ratio schedule                                                                |
| PR                                | Progressive-ratio schedule                                                           |
| FI                                | Fixed-interval schedule                                                              |
| LH                                | Limited hold                                                                         |
| VI                                | Variable-interval schedule                                                           |
| RI                                | Random-interval schedule                                                             |
| DRL                               | Differential reinforcement of low rates                                              |
| DRH                               | Differential reinforcement of high rates                                             |
| NCR                               | Non-contingent reinforcement                                                         |
| FT                                | Fixed-time schedule                                                                  |
| VT                                | Variable-time schedule                                                               |
| <i>Schedule parameters</i>        |                                                                                      |
| <i>n</i>                          | Mean ratio requirement                                                               |
| <i>t</i>                          | Mean interval requirement                                                            |
| <i>r</i>                          | Rate of reinforcement                                                                |
| COD                               | Changeover delay                                                                     |
| <i>Matching law parameters</i>    |                                                                                      |
| <i>b</i>                          | Choice bias                                                                          |
| <i>s</i>                          | Sensitivity of choice to relative rate of reinforcement ( $r_1/r_2$ )                |

For instance, *lever pressing* is typically defined as the closure of a microswitch in the back of the lever. The lever-pressing *operant* does not indicate how the microswitch is closed, whether it is by pressing the lever with a paw or nose. The operant is not a single response, but a *class* of responses that share an effect on the environment. At any given time, the operant can only take one of two values: it either occurs (the micro-switch is closed) or it does not (the microswitch is open). In contrast, the particular action that results in the

operant, called the *topography* of the operant response, may take many forms.

A stimulus in the presence of which the operant does *not* result in the outcome is called the  $S^\Delta$  (*S-delta*). The operant is called a *discriminated operant* when *B* varies depending on whether the  $S^D$  or the  $S^\Delta$  is present. Under appropriate conditions, the discriminated operant may serve as evidence that the organism has the sensory capacity to detect the difference between the  $S^D$  and the  $S^\Delta$ .

**Operant Conditioning, Fig. 2** A (simulated) cumulative record. The hash marks indicate delivery of the outcome



**Operant Conditioning, Fig. 3** Schematic representation of the three-term contingency of operant conditioning

### Interaction with Other Learning Processes

The three-term contingency highlights some associative and nonassociative processes that may facilitate or hinder operant conditioning. Two processes are particularly informative of the structure of operant conditioning: outcome-related sensitization and habituation, and  $S^D$ -outcome association learning.

The unconditioned response to a stimulus may change merely because of the repeated presentation of that stimulus: a reflex, for instance, may become stronger (sensitization) or weaker (habituation) with repeated elicitation, even without muscle fatigue or sensory adaptation. It is in principle possible that the repeated presentation of the outcome sensitizes the ostensive operant (see the locomotion-psychostimulant example in the *Experimental design and contingency* section) or that it habituates a response that interferes with the operant (e.g., a neophobic response to food). There is evidence suggesting that the rewarding properties of an outcome may also sensitize and habituate (McSweeney and Murphy 2009).

Operant conditioning also implies a potential Pavlovian association between the  $S^D$  (or any other contextual stimuli) and the outcome of the operant response. For instance, a tone that sets the occasion for lever pressing for food may become a Pavlovian conditioned stimulus associated with the food. The conditioned response to the  $S^D$  may facilitate or suppress the operant. For instance, if the  $S^D$  is separately associated with food, the presence of the  $S^D$  would increase the rate at which a lever that yields food is pressed – this is an example of *Pavlovian-instrumental transfer*. In contrast, when food is programmed for a raccoon for depositing a coin into an enclosure, the coin-food association elicits instead a coin-rubbing response – this is an example of instinctive drift (Breland and Breland 1961).

### Reinforcement and Punishment

In operant conditioning, the outcome of the response may increase or reduce  $B$ . If the outcome increases  $B$ , it is called a *reinforcer*; if the outcome

reduces  $B$ , it is called a *punisher*. Reinforcement and punishment are thus defined by the change that the outcome causes on  $B$ .

The reinforcing or punishing outcome may be the introduction of a stimulus or the removal of a stimulus. Figure 4 shows the classification of operant procedures in terms of the nature of the outcome (introduction versus removal) and its effect on response rate (increase versus reduction). The procedures that involve the introduction of stimuli are fairly straightforward: the response produces an stimulus that is either rewarding and increases the rate of that response (*positive reinforcement*) or is aversive and reduces the rate of that response (*positive punishment* or simply *punishment*). The former stimulus is signified as  $S^{r+}$  (reinforcer); the latter is signified as  $S^{p+}$  (punisher). Increased lever pressing because it leads to food is an example of positive reinforcement, where food is the  $S^{r+}$ . Reduced lever pressing because it leads to foot-shock is an example of punishment, where foot-shock is the  $S^{p+}$ .

The procedures that involve the removal of a stimulus are less intuitive. In *negative reinforcement*, the outcome of a response is the removal of an aversive stimulus,  $S^{r-}$ , which increases  $B$ . The  $S^{r-}$  may be removed *after* its onset, such as when the rat shuttles to the safe side, of the shuttle-box when foot-shock (the  $S^{r-}$ ) is delivered. Such procedure is called an *escape* or *passive avoidance* procedure. Alternatively, the  $S^{r-}$  may be removed *before* its onset, such as when a stimulus preceding foot-shock elicits a shuttling response to the safe side. Such procedure, in which the  $S^{r-}$  may be prevented, is called an *active avoidance* procedure.

In *negative punishment*, the outcome of a response is the removal of a rewarding stimulus,

$S^{p-}$ , which reduces  $B$ . Negative punishment is a common procedure for reducing undesired behavior, such as acting out, in children. In that situation, the undesired behavior is the response that removes a rewarding  $S^{p-}$  (e.g., access to a preferred toy), thus reducing the rate of the undesired behavior. This example highlights the relative nature of reinforcement and punishment: negative punishment of a behavior is often described as the reinforcement of the omission of that behavior, or the differential reinforcement of other behavior (DRO).

Although operant conditioning may involve any of the cells in the matrix of Fig. 4, most variations in implementation and their effects on behavior have involved the top-left cell, positive reinforcement. The remaining sections will, therefore, focus on research on this procedure.

## Simple Schedules of Reinforcement

### Contingencies of Reinforcement

The rules by which a response produces a  $S^{r+}$  are called the *contingencies of reinforcement*. Contingencies of reinforcement may be thought of as models of naturally occurring positive feedback loops between behavior and environment (e.g., between foraging behavior and prey obtained), or as techniques to promote behavior (e.g., engaging in appropriate play behavior).

The simplest contingency of reinforcement is called *continuous reinforcement*, or CRF: every instance of the response is reinforced. Another way of stating this is that  $p(S^{r+} | \text{response}) = 1.0$  (the probability of the reinforcer given the response is 1.0). In contradistinction to CRF, in *intermittent reinforcement* only some

|               | Introduces Stimulus                                 | Removes Stimulus                                  |
|---------------|-----------------------------------------------------|---------------------------------------------------|
| Increases $B$ | Positive Reinforcement<br>[ $S^{r+}$ is appetitive] | Negative Reinforcement<br>[ $S^{r-}$ is aversive] |
| Reduces $B$   | Positive Punishment<br>[ $S^{p+}$ is aversive]      | Negative Punishment<br>[ $S^{p-}$ is appetitive]  |

**Operant Conditioning, Fig. 4** Classification of operant procedures in terms of the nature of the outcome (*introduces* versus *removes* a stimulus) and its impact on rate of responding (increases versus reduces  $B$ )

instances of the response are reinforced, so  $0.0 < p(S^{r+}|\text{response}) < 1.0$ . Whereas CRF can be implemented only in one way, intermittent reinforcement may be implemented in a virtually infinite number of ways. This section reviews the most frequently studied contingencies of intermittent reinforcement, most of them first introduced by Ferster and Skinner (1957). These schedules are arranged as a matrix in Fig. 5. All schedules are described in terms of responses and time; in all schedules, responses only count and time only passes while the  $S^D$  is present.

### Ratio Schedules

In *ratio* schedules of reinforcement, the reinforcer is contingent on emitting a number of responses since the last reinforcer. This number of responses is called the *ratio requirement*, and it may be fixed or variable (Fig. 5, top row). In *fixed-ratio* (or FR) schedules, the ratio requirement does not change between reinforcer deliveries. For instance, a rat may be repeatedly required to press a lever 5 times to obtain a reinforcer. In this case, the schedule is referred to as FR 5. More generally, an FR schedule is referred to as FR  $n$ , where  $n$  is the ratio requirement. Note that CRF is an FR schedule with  $n = 1$ , or FR 1. The FR schedule is akin to piecework, where the worker is paid per unit completed – each unit completed is the response, payment is the reinforcer, and the piece rate is the reciprocal of the ratio requirement.

Fixed-ratio schedules of reinforcement are widely used in behavioral economics. In this context, the FR requirement ( $n$ ) constitutes the *unit price*; the number of  $S^{r+}$  obtained constitutes the *demand* for  $S^{r+}$ . The function that relates the demand for  $S^{r+}$  to  $n$  is the *demand curve* for the  $S^{r+}$ . The slope of the demand curve is the *elasticity*

of the demand for  $S^{r+}$ , the sensitivity of demand to changes in  $n$ . The slope of the demand is typically negative; when it is steep, the demand for  $S^{r+}$  is *elastic* (sensitive to  $n$ ); when it is flat, the demand for  $S^{r+}$  is *inelastic* (insensitive to  $n$ ). Quantitative models of demand elasticity have informed key concepts in behavioral economics – particularly in the context of drug reinforcement – such as the essential value of reinforcers (Hursh and Silberberg 2008).

In *variable-ratio* (or VR) schedules, the ratio requirement changes randomly between reinforcer deliveries. For instance, a rat may be required to press a lever twice to obtain one reinforcer, but 8 times to obtain the next one, 5 times to obtain the one after that, and so on. A VR schedule is referred to as VR  $n$ , where  $n$  is the *mean* ratio requirement. There are several ways to implement VR schedules. For instance, a list may be made of equally spaced numbers with mean  $n$ ; after each reinforcer, a number is randomly sampled from the list, with or without replacement, and that number is the next ratio requirement. In this method, the probability of reinforcement given  $x$  responses since the last reinforcer,  $p(S^{r+}|x)$ , increases with  $x$ . Often times investigators prefer to keep  $p(S^{r+}|x)$  constant over  $x$ . To arrange for that, investigators rely on *random-ratio* (or RR) schedules of reinforcement, in which a computer samples a probability gate after each response, reinforcing it with probability  $p$ . The mean requirement of the RR schedule is  $n = 1/p$ . The main limitation of RR schedules is that they may yield very large ratio requirements, which may not support behavior. Variable- and random-ratio schedules are akin to slot machines, where each pull of the lever (or push of the button) yields a payoff probabilistically – pulling the lever is the response, the payoff is the  $S^{r+}$ , and the pay rate is the reciprocal of the mean ratio requirement.

Another ratio schedule commonly used in research is the *progressive-ratio* (or PR) schedule. In PR schedules, the ratio requirement increases over consecutive reinforcers, resetting between sessions either completely or partially. The first ratio requirement is typically very low, and the following requirements are often programmed to

|          | Fixed               | Variable               |
|----------|---------------------|------------------------|
| Ratio    | Fixed Ratio (FR)    | Variable Ratio (VR)    |
| Interval | Fixed Interval (FI) | Variable Interval (VI) |

**Operant Conditioning, Fig. 5** Simple schedules of reinforcement classified according to whether its requirement is a number of responses (Ratio) or the first response after an interval (Interval), and whether the requirement is the same (Fixed) or not (Variable) between reinforcers

increase geometrically (e.g., 8, 12, 18, 27), although arithmetic progressions of fixed step-size (e.g., 8, 12, 16, 20) and other progressions are fairly common. The key dependent measure in PR schedules is the *breakpoint* – the highest ratio requirement completed before the subject stops responding for a long period of time. The breakpoint is often used as a measure of the efficacy of the reinforcer (Hodos 1961).

### Interval Schedules

In *interval* schedules of reinforcement,  $S^{+}$  is contingent on emitting one response after some time since the last reinforcer. The time during which  $S^{+}$  is not available is called the *interval requirement* and is never signaled (if it were, the signal would constitute an  $S^{\Delta}$ ). Responses prior to the completion of the interval requirement are not reinforced. Like ratio requirements, interval requirements may be fixed or variable (Fig. 5, bottom row). In *fixed-interval* (or FI) schedules, the interval requirement does not change between reinforcers. For instance, a rat may be required to make one lever press after 3 min has elapsed since the last reinforcer to obtain the next reinforcer. In this case, the schedule is referred to as FI 3-min. More generally, an FI schedule is referred to as FI  $t$ , where  $t$  is the interval requirement. The FI schedule is akin to baking a cake that takes 45 min to be done: checking the cake before 45 min elapse has no effect (in terms of producing an edible cake), only checking it after 45 min is reinforced with an edible cake.

In the cake-baking example, however, waiting too long (e.g., 90 min) probably results in a ruined cake. Such constraint on the availability of the reinforcer may be incorporated to an FI schedule in the form of a *limited hold* or LH. The LH defines a maximum time after the interval requirement is completed during which the reinforcer is available. In the cake example, if the cake were ruined after 50 min in the oven, the edible cake would reinforce the checking on a FI 45-min LH 5-min schedule. Because of such short LH relative to the FI schedule, or simply because cake is typically preferred sooner rather than later, most people use a kitchen timer when baking a cake. The prevalent use of such external timers highlights the utility of FI

performance, without external timers, in assessing the intrinsic capacity of organisms to track the passage of time (Daniels and Sanabria 2017).

In *variable-interval* (or VI) schedules, the interval requirement changes between reinforcers. For instance, a rat may be required to make one lever press after 5 min to obtain one reinforcer, then after 1 min to obtain the next one, then after 3 min to obtain the one after that, and so on. A VI schedule is referred to as VI  $t$ , where  $t$  is the mean interval requirement. Like VR schedules, there are several ways to implement VI schedules. For instance, a list may be made of equally spaced times with mean  $t$ ; after each reinforcer, a time is randomly sampled from the list, with or without replacement, and that time is the next interval requirement. Nonetheless, in this method,  $p(S^{+}|t)$  increases with  $t$ .

There are two prevalent methods to keep  $p(S^{+}|t)$  approximately constant. The first one is to implement a *random-interval* (or RI) schedule. In this schedule, the computer samples a probability gate after every interval  $\tau$ , where  $\tau$  is typically short and fixed (e.g., 1 s), and completes the interval requirement with probability  $p$ . The mean interval requirement of the RI schedule is  $t = \tau/p$ . The main limitation of RI schedules is that they may yield very long interval requirements, which may not support behavior. The second method prevents very long intervals by setting up a list of times with mean  $t$ , on the basis of a progression of times where longer times are more spaced. After each reinforcer, a time is randomly sampled from the progression, with or without replacement, and that time is the next ratio requirement. Fleshler and Hoffman (1962) devised an equation for the precise length of consecutive times in this progression, so that the distribution of sampled times approximate the exponential distribution expected from a constant  $p(S^{+}|t)$ .

Variable- and random-interval schedules are akin to the delivery of interesting posts on your Facebook news feed. Checking the news feed has no effect on seeing an interesting post until an interesting post is posted (which happens at unpredictable times); once the interesting post is posted, checking the news feed results in seeing



an interesting post, which reinforces checking the news feed.

### Other Simple Schedules

There are other important schedules of reinforcement that do not fit into the matrix of Fig. 5. The *differential reinforcement of low rates* (DRL) schedule is usually implemented to train a slower pace of responding and to assess the capacity to withhold a reinforced response (e.g., Sanabria and Killeen 2008). In this schedule, reinforcement is contingent on an interval between consecutive responses (inter-response time, or IRT) longer than a criterion (e.g., 6 s); shorter IRTs are not reinforced. Like in FI schedules, a LH may be implemented in DRL, such that IRTs that are longer than the LH are not reinforced. The *differential reinforcement of high rates* (DRH) schedule is the opposite of DRL; it is often implemented to train a faster pace of responding. In this schedule, reinforcement is contingent on IRTs shorter than a criterion; longer IRTs are not reinforced.

Often times, performance at operant level contains too few responses that may be reinforced according to some schedule. For instance, a pigeon may rarely produce two consecutive pecks that are less than 300 ms apart, making it difficult for it to perform in a DRH 300-ms schedule any different than at operant level. In such cases, behavior may be put in contact with the contingencies of reinforcement through a *shaping* procedure. Shaping involves reinforcing successive approximations to a goal response, while discontinuing reinforcement of intermediate behaviors that are already acquired. There are many ways of shaping a response, but a particularly systematic one is the *percentile* schedule of reinforcement (Galbicka 1994). In this schedule, reinforcement is contingent upon a quantifiable dimension of behavior being either above or below some criterion established on the basis of recent performance. The pigeon in the previous example, for instance, may be trained on a percentile DRH schedule that only reinforces IRTs shorter than the median of the last 15 IRTs. This is expected to progressively reduce IRTs toward the 300-ms goal.

### Noncontingent Reinforcement, Induction, and Extinction

There are two response-stimulus arrangements that, although not strictly schedules of reinforcement (because no reinforcement is scheduled), they are often discussed in relation to schedules of reinforcement. These are *noncontingent reinforcement* (or NCR) and *extinction*.

NCR consists of presenting an otherwise contingent reinforcer in a noncontingent way. The yoked-control condition (bottom of Fig. 1) is an example of NCR, because the stimulus that serves as  $S^{r+}$  in the experimental condition is presented regardless of performance in the yoked-control condition. NCR is often implemented as *time* schedules of reinforcement. Time schedules are similar to interval schedules, except that once the interval requirement is completed, the  $S^{r+}$  is delivered whether responding occurs or not. Like interval schedules, time schedules can be fixed (FT) or variable (VT).

The terms “noncontingent reinforcement” and “time schedules of reinforcement” are somewhat oxymoronic. If the  $S^{r+}$  is noncontingent, by definition, it cannot serve as  $S^{r+}$ . Also, time schedules do not schedule  $S^{r+}$ , because the scheduled stimulus, rewarding as it may be, is noncontingent. There are, however, two reasons why this terminology has persisted. The first one is that NCR and time schedules are typically implemented to compare performance in these schedules relative to schedules in which the noncontingent  $S^{r+}$  is contingent. This is the case, for instance, in the yoked-control use of NCR. The second reason stems from an equivocal use of the term *reinforcement*. As defined here, operant reinforcement is the increase in the rate ( $B$ ) of the response *that produces* the  $S^{r+}$ . Reinforcement also increases behavior other than the operant through various mechanisms (e.g., unconditioned effects, context-outcome associations). These behaviors are not reinforced, they are *induced*. However, it is unclear whether or not the mechanisms that subserve induction overlap with those that subserve reinforcement. Some theories suggest, for instance, that induction and reinforcement depend on a single mechanism: the temporal proximity between behavior and  $S^{r+}$  (Skinner 1948). These

theories blur the distinction between induction and reinforcement – furthermore, they blur the distinction between procedure (reinforcement) and process (temporal contiguity). In that context, reinforcement can be noncontingent (Killeen and Pellón 2013).

Whereas NCR precludes reinforcement by removing the response- $S^{r+}$  contingency, extinction precludes reinforcement by removing  $S^{r+}$  altogether. Extinction is typically implemented following a schedule of reinforcement and without removing the  $S^D$ . Because prior to extinction  $S^{r+}$  maintained the operant, the removal of  $S^{r+}$  must result in a decline in  $B$ . Extinction thus implies a decline in  $B$  due to the removal of the  $S^{r+}$  that maintained  $B$ .

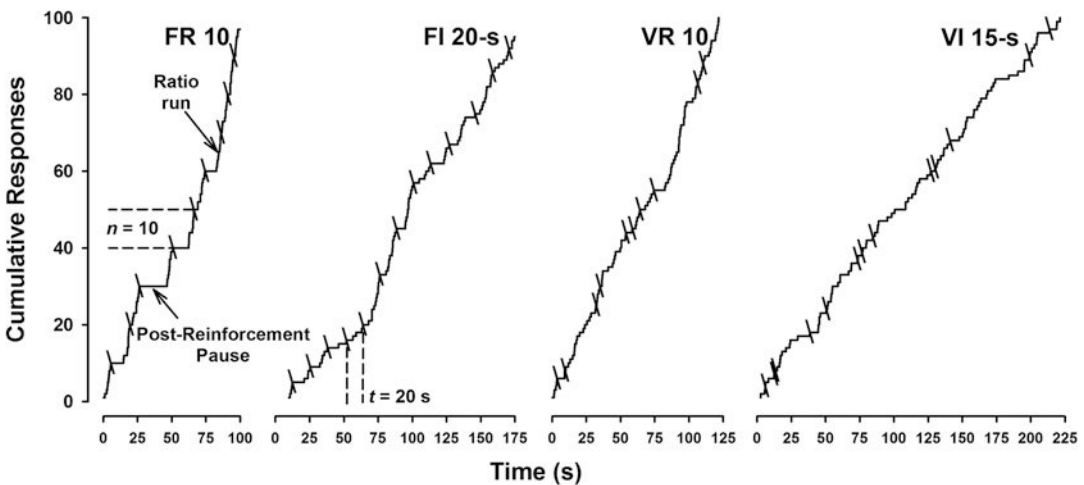
Recovery of an extinguished response can occur with relative ease after discontinuing the  $S^D$  (*spontaneous recovery*), changing it (*renewal*), extinguishing another response (*resurgence*), or implementing NCR (*reinstatement*). The fragility of extinction performance has informed theories of extinction learning that are crucial to understand the persistence of undesired behaviors (Bouton and Todd 2014).

### Schedule Control and Feedback Functions

Schedules of reinforcement vary substantially in their effect on behavior, as shown in the

cumulative records in Fig. 6. In FR schedules, responding between reinforcers typically consists of a *postreinforcement pause* (also called *pre-ratio pause*, or *latency to first response*) followed by a steady stream of responses (the *ratio run*). Similar performance is observed in FI schedules, but under some conditions the transition from pause to responding appears to be less abrupt; this pattern is called the *FI scallop*. Behavior in VR and VI (and RR and RI) schedules is typically more evenly distributed across the inter-reinforcer interval than in FR and FI schedules, but VR schedules maintain a higher  $B$  (steeper cumulative records) than VI schedules.

All else being equal, the systematic change in the pattern of responding – length of postreinforcement pause, curvature of scallop, response rate, etc. – as a function of schedule of reinforcement is called *schedule control*. To demonstrate schedule control, experimental and control training should be similar in every aspect, including rate of reinforcement ( $r$ ), except in the effective schedule of reinforcement.  $r$  is maintained invariant across conditions by yoking it. For instance, Catania et al. (1977) yoked  $r$  in VI and VR schedules by setting up the interval requirement in the VI-schedule condition to the observed inter-reinforcer interval in the VR-schedule condition.  $B$  was higher in VR than in yoked-VI schedules, indicating that response rate was under schedule



**Operant Conditioning, Fig. 6** Illustrative cumulative records for FR 10, FI 20-s, VR 10, and VI 15-s

control. This difference in  $B$  across ratio and interval schedules has motivated much theorizing on schedule control (e.g., Peele et al. 1984).

Operant conditioning research often relies on VI and RI schedules for two reasons. First, unlike FR and FI schedules, VI and RI schedules yield relatively steady streams of responding continuously (Fig. 6, rightmost record). Second, unlike ratio schedules, interval schedules allow adequate experimental control over the rate at which reinforcers are delivered,  $r$ . In ratio schedules, the investigator cannot fully control  $r$ , because it varies linearly with  $B$  (mathematically,  $r = B/n$ ). In interval schedules, an investigator can have fairly good control over  $r$ , because it reaches a flat maximum even with a modest  $B$ .

The relation between  $B$  and  $r$  in a schedule may be represented graphically as a *feedback function*. As the feedback functions in Fig. 7 show, the slope of the ratio feedback function is the reciprocal of the ratio requirement ( $n$ ), the asymptote of the interval and time feedback functions is the reciprocal of the interval requirement ( $t$ ), and  $r = 0$  in extinction. Interval and time schedules differ noticeably on  $r$  only when  $B$  is very low.

### Compound Schedules of Reinforcement

The schedules of reinforcement described so far model relatively simple relations between behavior and environment. More complex relations

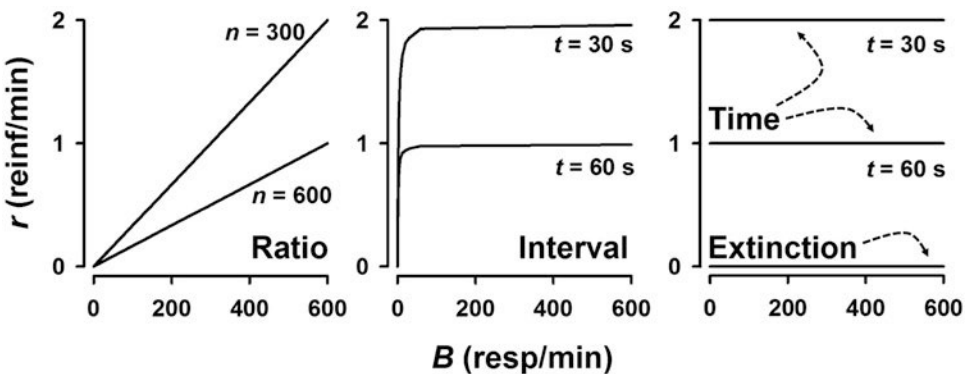
may be modeled by combining simple schedules. These combinations are called *compound schedules of reinforcement*. The *components* of a compound schedule – the simple schedules that make up the compound schedule – may be presented alternatively or simultaneously. Components may be implemented on different manipulanda (*heterogeneous* compound schedules) or on the same manipulandum (*homogeneous* compound schedules).

### Multiple and Mixed Schedules: Stimulus and Schedule Control

Components of a compound schedule may alternate on the basis of the passage of time. For instance, VI schedules with different interval requirements may alternate every 5 min on average. When a different  $S^D$  signals each alternating component (e.g., the color of the keys indicate the VI schedule in effect), the compound schedule is called a *multiple* schedule of reinforcement.

Multiple schedules may be used to establish and evaluate stimulus control. For instance, a higher  $B$  in the VR than in the extinction component of a multiple schedule would demonstrate that the  $S^D$  have gained control over performance. To distinguish stimulus control from schedule control, however, performance must be tested using the same schedule (same  $r$ , typically extinction) in the presence of each  $S^D$ .

When alternating components are not differentially signaled, the compound schedule is called



**Operant Conditioning, Fig. 7** Feedback functions for ratio (left panel), interval (central panel), and time schedules, and for extinction (right panel). The functions trace

changes in the rate of reinforcement ( $r$ ) with changes of rate of responding ( $B$ )

a *mixed* schedule of reinforcement. Unlike multiple schedules, in mixed schedules there is no  $S^D$  to potentially gain control over performance. Changes in  $B$  across components of a mixed schedule can only be due to the either (a) the passage of time in a component, if components alternate at fixed times, or (b) the difference in the contingencies of reinforcement across components (schedule control).

### Chained and Tandem Schedules: Conditioned Reinforcement

Components of a compound schedule may also alternate when they are completed. In these schedules, completion of the first component – called the *initial link* – is reinforced only with the transition to a second component and that second component may be reinforced with the transition to a third component, and so on. The last component in the schedule – called the *terminal link* – is reinforced with the *primary* reinforcer. The primary reinforcer is defined by its capacity to reinforce a response regardless to its relation to other reinforcers – food for a hungry animal, water for a thirsty animal, access to a conspecific, some drugs of abuse, among many others, constitute primary reinforcers.

Compound schedules of reinforcement in which a different  $S^D$  signals each link are called *chained* schedules. As in multiple schedules, the  $S^D$  of chained schedules may gain control over performance. More importantly, each  $S^D$  in a chained schedule may serve as a *conditioned* (or *secondary*) reinforcer for responding in the just-preceding link. A conditioned reinforcer reinforces an operant conditionally on some relation to another reinforcer. Secondary reinforcement is demonstrated to the extent that (a)  $B$  increases when access to the reinforcing  $S^D$  is contingent on the response, but not when it is noncontingent, and (b) this difference is reduced when the relation between  $S^D$  and the primary reinforcer is removed. A typical example of a conditioned reinforcer is money. An individual may work to obtain money (initial link) and then may spend that money on various goods (terminal link). Money constitutes a conditioned reinforcer for work to the extent that noncontingent money

(e.g., cash gifts) reduces work, and that a weaker relation between money and goods (e.g., inflation) reduces the impact of noncontingent money on work (e.g., an individual does not work less because of a cash gift in a currency she does not use).

The demonstration of conditioned reinforcement in chained schedules is challenging, because it involves isolating the primary-reinforcing effects of the terminal  $S^{r+}$  on responding that occurs in preceding links. For example, in a chained VI FR schedule of food reinforcement, food produced by the terminal FR link is contingent upon responding on the initial VI link; without those responses, neither the FR link nor the food reinforcer would occur. To the extent that such contingency increases VI responding, food serves as a primary reinforcer of VI responding. In general, responding on any link in a chained schedule may be a function of conditioned reinforcement (from subsequent links) and primary reinforcement (from the terminal  $S^{r+}$ ).

*Tandem* schedules of reinforcement may be used to isolate primary-reinforcer effects on the initial link of a compound schedule. Tandem schedules are similar to chained schedules, but no differential  $S^D$  signals each link. Therefore, in tandem schedules, there is no terminal-link  $S^D$  that reinforces initial-link responses; the only reinforcer operating is the primary reinforcer, i.e., the terminal  $S^{r+}$ . All other things being equal, then, differences in performance during initial links in chained versus tandem schedules are due to the conditioned-reinforcing effects of terminal links in the chained schedule (control conditions may be strengthened by noncontingent alternation of the  $S^D$  in the tandem schedule, yoked to the contingent alternation in the chained schedule).

## Choice Behavior

### Concurrent Schedules

A type of compound schedule, the *concurrent* schedule of reinforcement, has been so extensively studied that it merits its own section. In concurrent schedules, two or more schedules

operate simultaneously and independently of each other (often times they are referred to as *independent concurrent* schedules).

Concurrent schedules are often used in operant research to model a key aspect of natural environments – that they typically contain more than one schedule of reinforcement, each operating independently of others, and each supporting mutually inconsistent behavior. While a paycheck may reinforce working behavior, other stimuli are available to reinforce leisure behavior. Even in the operant chamber, lever pressing may be reinforced for food, but exploratory behavior away from the lever may yield its own reinforcers. In that sense, even simple schedules of reinforcement may be thought of as concurrent schedules, where responses on only one schedule are measured (Herrnstein 1970).

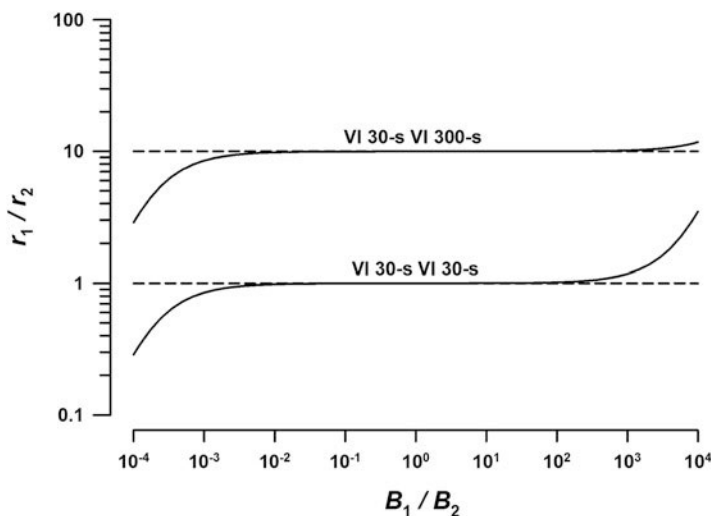
For over 50 years, research on choice behavior has relied heavily on concurrent schedules of reinforcement. In particular, concurrent VI VI schedules have been extensively used because they afford experimental control over a key independent measure, the *relative rate of reinforcement*, which is the ratio of reinforcers obtained from each component of the concurrent schedule ( $r_1/r_2$ ). In this research, the effect of  $r_1/r_2$  is measured on the *relative rate of responding* ( $B_1/B_2$ ), which is the ratio of responses allocated to each component of the concurrent schedule;  $B_1/B_2$  is the principal measure of choice. Concurrent VI VI

schedules attain control over  $r_1/r_2$  because this ratio depends primarily on the interval requirements (programmed by the experimenter) and substantially less so on  $B_1/B_2$  (emitted by the organism). This invariance (and its limits) is evident when feedback functions akin to those in Fig. 7 are constructed for concurrent VI VI schedules, but using relative – instead of absolute – measures of responding and reinforcement (Fig. 8).  $r_1/r_2$  diverges from the reciprocal of the ratio of interval requirements ( $t_2/t_1$ ) only when response allocation is extreme (very low or very high  $B_1/B_2$ ).

Other concurrent schedules do not provide the level of control over  $r_1/r_2$  shown in Fig. 8. For instance, in concurrent ratio schedules,  $r_1/r_2$  increases with more responses on components with lower requirements ( $n$ ), because of the linear relation between  $r$  and  $B$  in simple ratio schedules (Fig. 7). Concurrent ratio schedules may approximate the feedback function of Fig. 8 by scheduling them as *dependent* (or *nonindependent*) concurrent schedules (Stubbs and Pliskoff 1969). In these schedules, only one of the components is effective at any given time; the effective schedule is selected randomly after each reinforcer and is not signaled. Under these conditions,  $r_1/r_2$  may be controlled through the relative frequency of each component. Dependent scheduling is also useful to further reduce the small discrepancies between

### Operant Conditioning,

**Fig. 8** Feedback function, in log-log scale, for concurrent VI 30-s VI 30-s ( $t_2/t_1 = 1$ ) and concurrent VI 30-s VI 300-s ( $t_2/t_1 = 10$ );  $t_2/t_1$  is indicated with dashed lines. The continuous lines trace the relative rate of reinforcement ( $r_1/r_2$ ) as a function of relative rate of responding ( $B_1/B_2$ ). Over a broad range of  $B_1/B_2$  (from roughly 1/1000 to 1000),  $r_1/r_2 \approx t_2/t_1$





$r_1/r_2$  and  $t_2/t_1$  in concurrent VI VI schedules (Fig. 8). In dependent concurrent VI VI schedules, extreme relative response rates are not reinforced (because the preferred component is sometimes not effective) and are therefore discouraged.

An important variable in (independent) concurrent VI VI schedules is the cost of switching over from one component to another. This is typically implemented as a short interval ( $< 5$  s) during which the switched-to component is ineffective. This interval is called the *changeover delay* (COD); it starts either on the last response before or the first response after switching over. When concurrent VI VI schedules serve as models of foraging, where each component represents a patch of prey, the COD represents the time it takes to travel between patches (Dow and Lea 1987).

In order to facilitate rigorous experimental control over the COD and other switching contingencies, Findley (1958) developed an alternative implementation of independent concurrent schedules. Whereas the components of concurrent schedules are typically implemented in separate manipulanda, the *Findley procedure* arranges all components on a *main* manipulandum, each signaled by a different  $S^D$ , while responses to a *changeover* manipulandum change the effective schedule in the main manipulandum. In the Findley procedure, switching contingencies can be scheduled in the changeover manipulandum. For example, to implement a 5-s COD, an FI 5-s may be scheduled in the changeover manipulandum.

## The Matching Law

Regardless of its implementation (independently or dependently, two-manipulanda or Findley procedure), concurrent VI VI performance regularly shows that  $B_1/B_2$  is a power function of  $r_1/r_2$ ,

$$\frac{B_1}{B_2} = b \left( \frac{r_1}{r_2} \right)^s. \quad (1)$$

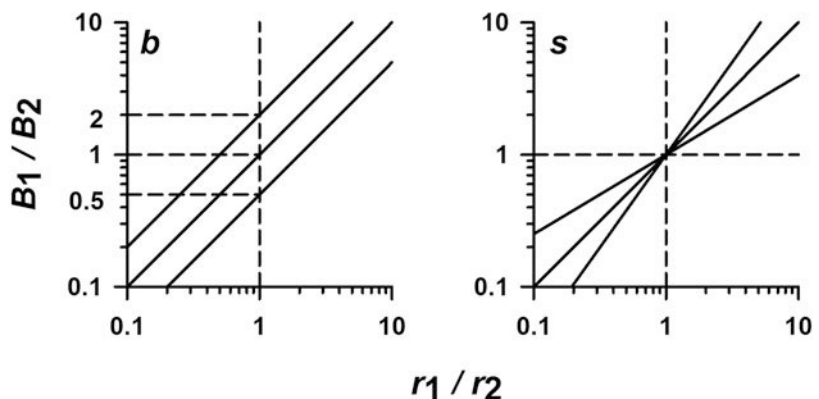
This equation is known as the *generalized matching law* (Baum 1974). When  $b = s = 1$ , Eq. 1 becomes a simple identity between  $B_1/B_2$  and  $r_1/r_2$ , a relation known as *strict matching*. In a plot relating  $B_1/B_2$  to  $r_1/r_2$  in log-log space (which linearizes Eq. 1), strict matching appears as an identity line (Fig. 9).

Parameter  $b$  in Eq. 1 is indicative of choice *bias*. If  $b > 1$ , component 1 is chosen more than expected from strict matching; if  $b < 1$ , component 2 is chosen more than expected from strict matching. It is as if  $B_1/B_2$  strictly matched  $r_1/r_2$ , but the preferred component provided additional reinforcers that are not measured. In a matching plot, choice bias appears as  $B_1/B_2$  when  $r_1/r_2 = 1$  (Fig. 9, dashed lines).

Parameter  $s$  is indicative of choice *sensitivity* to relative rate of reinforcement. If  $s > 1$ ,  $B_1/B_2$  changes faster with  $r_1/r_2$  than expected from strict matching; this is called *overmatching*. If  $s < 1$ ,  $B_1/B_2$  changes slower with  $r_1/r_2$  than expected from strict matching; this is called *undermatching*. In a matching plot, choice sensitivity appears as the slope of the function (Fig. 9). Steeper functions are indicative of overmatching,

## Operant Conditioning,

**Fig. 9** Traces of the matching law (Eq. 1). Left panel:  $s = 1$  and  $b = 0.5$  (bottom), 1.0 (middle: identity line), and 2.0 (top). Right panel:  $b = 1$  and  $s = 0.6$  (flatter), 1.0 (diagonal: identity line), and 1.4 (steeper). Note that these plots are similar to the feedback function of Fig. 8, but with the axes flipped



whereas flatter functions are indicative of undermatching. In concurrent VI VI performance, undermatching is more common than overmatching and is exacerbated by short or absent CODs (Davison and McCarthy 1988).

Reinforcers may differ between components of concurrent VI VI schedules not just in their rate, but also in their amount, quality, delay, etc. Larger, better, more immediate, and, in general, more efficacious  $S^{r+}$  in component 1 appear to increase  $B_1/B_2$  gradually. It thus appears that  $B_1/B_2$  is sensitive to a common factor across these dimensions: *value*. The outcome of one component is more valuable if it involves more frequent, larger, or more immediate  $S^{r+}$ .  $B_1/B_2$  in concurrent VI VI schedules may provide an objective measure of relative value of outcomes, such as brands of a product or opportunities to mate. Such feature has had important implications for behavioral economics and foraging theory (Herrnstein 1997).

Herrnstein (1970) also developed a key implication of the matching law for simple schedules of reinforcement. Behavior in a simple schedule may be thought of as a choice between the operant ( $B_1$ ) and every other behavior that is inconsistent with the operant ( $B_0$ ). The operant and every other behavior that is not the operant constitute the totality of behavior and that totality is a constant:  $B_1 + B_0 = k$ . It may be assumed that, whereas the operant is reinforced by the schedule at a rate  $r_1$ , inconsistent behavior is reinforced by an implicit schedule at rate  $r_0$ . When these assumptions are incorporated into Eq. 1 with  $b = s = 1$ , and it is solved for  $B_1$ ,

$$B_1 = \frac{kr_1}{r_1 + r_0}. \quad (2)$$

Equation 2 is called the *quantitative law of effect*. Assuming a constant implicit rate of reinforcement ( $r_0$ ), it predicts that response rate on a simple schedule ( $B_1$ ) increases fast as rate of reinforcement ( $r_1$ ) increases from zero, but it increases more slowly and toward an asymptote of  $k$  as  $r_1$  becomes very large. Aside from its quantitative predictions of simple-schedule performance, the quantitative law of effect has substantial implications for a theory of reinforcement. For instance,

it predicts that a response is reinforced not only by increasing the rate at which reinforcers are produced, but also by decreasing the rate at which other behaviors are reinforced (or induced). From this perspective, reinforcement is thought not as strengthening or energizing the reinforced behavior, but as shaping the allocation of a limited resource – time or responses – among alternatives.

### Concurrent-Chains Schedules: Choosing Between Schedules

Relative response rates may appear to index the preference of the organism for the components of a concurrent schedule. However, schedule control exerted by each component and global-maximization contingencies are likely to interfere with the expression of preference for that component. For example, in a concurrent VR 100 FI 30-s, an organism is likely to make most responses on the VR schedule and only visit the FI schedule around 30 s since the last reinforcer. This pattern of behavior may emerge because VR schedules maintain a steady and high  $B$  (Catania et al. 1977), whereas FI responding clusters around the interval requirement, and also because this pattern maximizes the global rate of reinforcement ( $r_1 + r_2$ ). Regardless of the cause, it does not seem reasonable to infer, from concurrent-schedule performance, which component the organism would stick to if it had to choose between them.

Choice between schedules of reinforcement is studied using *concurrent-chains* schedules. These schedules are similar to normal chained schedules, but the initial link is a concurrent schedule instead of a simple schedule. The components of the initial link do not yield a primary reinforcer, but instead each yields access to another simple schedule – the terminal link – signaled by a different  $S^D$ . Another way to describe concurrent-chains schedules is as concurrent schedules in which each component is reinforced with access to a simple schedule. Following a similar rationale as in concurrent schedules, the initial link of concurrent-chains schedules is typically a concurrent VI VI schedule with equal interval requirements. If  $B_1/B_2$  in concurrent VI VI schedules

measures the relative value of the outcome of each component, then  $B_1/B_2$  in the initial-link, equal-requirement VI VI of a concurrent-chains schedule measures the relative value of the schedules in the terminal link. Consider, for instance, a concurrent-chains schedule in which the initial link is VI 60-s VI 60-s and the terminal link is either VR 100 or FI 30-s. If twice the responses are allocated to the VI 60-s reinforced with the VR 100 than to the VI 60-s reinforced with the FI 30-s ( $B_1/B_2 = 2$ ), it may be inferred that the VR 100 schedule is twice as valuable as the FI 30-s schedule.

## Operant Conditioning and the Science of Behavior

### Complex Behavior

In concurrent-chains schedules, two forms of schedule compounding, chained and concurrent schedules, are themselves compounded. Such higher-order compounding highlights the unlimited number of ways in which simple and compound schedules may be further compounded and modified to model complex operant behavior. Indeed, one approach to complex cognition and social learning involves conceptualizing these processes as complex operant behavior.

One example of an operant approach to complex cognition involves attention. Discriminating between stimuli requires attending relevant features of those stimuli. To the extent that those relevant features serve as reinforcers, the attending response may constitute an operant. Indeed, an  $S^D$  may (conditionally) reinforce an *observing* response that produces it (Shahan and Podlesnik 2008). This may be demonstrated in a modified mixed schedule with positive reinforcement and extinction components, in which a separate observing response turns the mixed schedule (lacking differential  $S^D$ ) into a multiple one (with differential  $S^D$ ).

Operant approaches to language provide a similar example. For instance, something akin to semantic categories appear to emerge from conditional discrimination (or *matching-to-sample*)

training. Two  $S^D$  that set the occasion for the same response (e.g., the written word “APPLE” and a picture of an apple set the occasion for saying “apple”) may acquire *functional equivalence*, wherein any of the trained stimuli (e.g., the written word, the picture, and the spoken word) may serve as  $S^D$  for responses related to the other stimuli (e.g., selecting the picture of an apple from other pictures). Equivalence relations between stimuli may underlie important functions related to language and cognition (Sidman 2009).

A broader approach to social behavior – including language and communication – is embodied in the notion of *verbal behavior*, or “behavior reinforced through the mediation of other persons” (Skinner 1957, p. 2). Verbal contingencies involve responses from one organism that serve as  $S^D$  or as outcome for the response of another organism. Asking for an apple is both a response that is reinforced with an apple, and an  $S^D$  indicating to someone else that giving an apple would be reinforced with a “thank you.”

The maintenance and propagation of social practices are likely to rely on the imitation of such practices as observed in others. *Observational learning* involves the change in behavior because of the consequences observed when others produce that behavior (Greer et al. 2006). Observing the successful courtship behavior of conspecifics, for instance, may increase the probability of engaging in similar courtship behaviors. Such *vicarious reinforcement* involves overlaying observing contingencies directed to the model on otherwise simpler operant contingencies operating on the model.

These examples illustrate a key advantage of an operant-conditioning approach to complex behavior: its modularity. Even the most complex environment-behavior interaction, when modeled as a schedule of reinforcement, may be grounded on simple and tractable components. From an operant perspective, the complexity of complex behavior lies in the interplay between these simple components.

### Behavioral Mechanisms

The concept of operant conditioning identifies potential efficient causes of change in simple and

complex behavior. This concept, however, does not specify the mechanisms that underlie such change. Such mechanisms may be physiological or behavioral. The former identifies the material (neural) substrate of operant conditioning in particular species; the latter identifies more general processes that take place during conditioning, which may be implemented in various substrates. This section provides a succinct overview of the behavioral mechanisms of reinforcement.

Drawing a simile with natural selection, Skinner (1981) suggested that operant conditioning selects among populations of responses (*repertoires*), favoring those that are reinforced and hindering those that are punished. Reinforcement may select responses through local, contiguity-based mechanisms, such as assignment-of-credit algorithms (Staddon and Zhang 1991). Alternatively, Premack (1965) proposed a more global mechanism, based on the constraints that contingencies of reinforcement impose on the repertoire. According to this latter view, if freely available, (unreinforced) operants such as lever pressing are less likely than activities supported by the reinforcer, such as eating. Contingencies of reinforcement, such as FR 5, make access to the most likely activity dependent on the less likely activity, such that eating 1 pellet/min can only occur if the organism emits at least 5 responses/min. According to *Premack's principle*, reinforcement of relatively unlikely operants occurs because they are required for more likely activities supported by the reinforcer. Contemporary behavioral economic views on reinforcement are an elaboration of Premack's early proposition. These views conceptualize all the possible allocations of time across activities as a multivariate utility function; contingency constraints shifts the arg max of this function; such shift constitutes operant conditioning (Rachlin and Burkhard 1978).

Whereas the response-reinforcer association may select a response from the organism's repertoire, the Pavlovian  $S^D$ -reinforcer association may confer incentive-motivational properties to the  $S^D$  that energize the selected response (Killeen 1994). The Pavlovian-instrumental transfer demonstrates the capacity of stimulus-reinforcer associations to energize reinforced behavior.

## Conclusion

Operant conditioning is one of very few psychological concepts from early twentieth century that has not only persisted in research practices, but has infused itself into and grown in importance in a broad range of fields, including animal cognition, behavioral pharmacology, special education, artificial intelligence, and behavioral economics. Its ostensible simplicity and heuristic power are at the same time alluring and misleading. Although prevalent in animal behavior, strict experimental control is necessary to demonstrate operant conditioning, as potential confounds with unconditioned and induced behavior are everpresent. Perhaps its capacity to explain human behavior is narrower than what Skinner (1953) envisioned, but there is no question of the omnipresent role of operant conditioning in human behavior – the tweets and chatter feed that keep humans coming back to their mobile devices confirms the original insights of Skinner.

Operant conditioning provides a framework to ground and operationalize otherwise ambiguous constructs, such as *contingency* and *value*. In doing so, it guides the search for the mechanisms underlying learning and reinforcement and highlights unresolved conceptual issues regarding the distinction between these mechanisms and the procedures to study them. Furthermore, empirical research on stimulus control, induced behavior, schedule control, conditioned reinforcement, choice behavior, and other related topics has informed theory and broadened our models of instrumental behavior. This is reflected in the metaphors such models have spawned: behavior as a reservoir that can be filled or depleted, as musculature that may be strengthened or weakened, as a force that may be opposed, as a limited resource to be allocated, as a state that may be dwelled in or transitioned through. Operant conditioning remains the most powerful framework to put purposeful behavior under experimental control and to unveil the mechanisms that govern it. New developments in operant conditioning are likely to find applicability in new fields, spawn more sophisticated models, and inspire more compelling metaphors.

## Cross-References

- Associative Learning
- Attention-getting Behaviors
- B.F. Skinner
- Behaviorism
- C. Lloyd Morgan
- Categorization
- Contingency
- David Premack
- Decision-Making
- Delay of Reinforcement
- Delayed Matching-to-Sample
- Discrete Trials
- Discrimination Learning
- Edward C. Tolman
- Edward Thorndike
- Escape Response
- Extinction in Learning
- Feeding
- Foraging
- Free Operant Response
- Goal-Directed Behavior
- Incentive Relativity
- Instrumental Learning
- Intelligence
- John B. Watson
- Laboratory Research
- Law of Effect
- Learned Helplessness
- Learning
- Learning to Learn
- Matching-to-Sample
- Morgan's Canon
- Motivation
- Motivational State
- Nature versus Nurture
- Negative Reinforcement
- Operant Chamber
- Optimal Foraging Theory
- Partial Reinforcement Extinction Effect
- Passive Avoidance Learning
- Place versus Response Learning
- Positive Reinforcement
- Problem-Solving
- Reflex
- Reinforcement
- Relational Concepts and Symbolic Logic

- Schedules of Reinforcement
- Self-Administration
- Skinner Box
- Spontaneous Recovery
- Stimulus Control
- Time-Place Learning
- Timing
- Unconditioned Stimulus

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## Operant Conditioning Chamber

### ► Skinner Box

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## Operant Judgment Bias

### ► Judgment Bias

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## Operational Sex Ratio (OSR)

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### Definition

The operational sex ratio (OSR) is the proportion of fecund females to sexually active males in a population at a given time.

### Preface

Note that this entry discusses neither the primary sex ratio (sex ratio at conception) nor the secondary sex ratio (sex ratio at birth). For more information on factors that influence the primary and secondary sex ratios – factors such as temperature, level of inbreeding, and intensity of parasite infection – see another entry in this encyclopedia entitled *Sex Ratio* (Szala and Shackelford 2019).

### Introduction

Evolutionary approaches to biology have asked how sex ratio affects animal cognition and behavior (Fisher 1930). Sexual selection – a “special case” of natural selection – promotes traits that increase an individual’s ability to attract and retain

mates. Intrasexual competition – when members of one sex compete intrasexually to achieve sexual access to mates – is an important explanatory factor in the cognition and behavior of sexually reproducing species (Darwin 1871).

Sex differences in parental investment co-occur with sex differences in *potential reproductive rates* (Trivers 1972). A reliable indicator of reproductive rate is the minimum investment that each sex must contribute to produce offspring (i.e., obligate parental investment). Specifically, the sex whose minimum investment in parenting is larger will have the lower potential reproductive rate. In most sexually reproducing species, females' higher obligate parental investment is grounds for their sexual choosiness and selectivity, prompting males to compete intrasexually for access to mates (Trivers 1972). Both sexual selection theory and parental investment theory generate predictions concerning the effects of biased sex ratios on animals' cognition and behavior.

Biased sex ratios are expected to intensify intrasexual competition among members of the abundant sex that perceive cues to mate scarcity (i.e., when potential mates are scarce relative to the number of same-sex rivals). The more abundant sex experiences greater competition for mates. The members of the scarcer sex benefit from improved mating opportunities (Fisher 1930), along with the luxury of increased choosiness in their selection of a mate (Emlen and Oring 1977). For members of the abundant sex, mating prospects are more restricted because of the greater number of same-sex rivals (Emlen and Oring 1977). A male-biased environment, for example, limits men's mate choices and can intensify some aspects of male–male competition (Pedersen 1991).

## Working Definitions

The adult sex ratio (also known as the tertiary sex ratio) is the ratio of adult males to adult females in a population. The OSR is the proportion of fecund females who are available to mate to sexually active males (Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996). Different studies define OSR

in different ways. OSR is typically measured either as the ratio of males to females (Emlen and Oring 1977) or the ratio of males to (males + females) (Kvarnemo and Ahnesjö 1996). Using the former approach, an OSR of 1 is even, an OSR greater than 1 is male-biased, and an OSR below 1 is female-biased. Using the latter approach, an OSR of 0.5 is even, one higher than 0.5 is male-biased, and one lower than 0.5 is female-biased.

A third approach to measuring the OSR is “sex-neutral” and can be thought of as a ratio of competitors to potential mates or competitors to (potential mates + competitors); it is called the competitor-to-resource ratio (CRR). If the competitors to (potential mates + competitors) formula is used, then the CRR will equal 0 when the environment contains only opposite-sex others, the CRR will equal 1 when the environment contains only same-sex others, and the CRR will equal 0.5 when it is even. The CRR is a useful way to measure the OSR because it allows researchers to compare studies about male and female behaviors (Grant et al. 2000); CRR is equal to the OSR for males, and for females, the CRR equals  $(1 - \text{OSR})$ . This approach shares the benefits of log-transforming the ratio of competitors to potential mates (Weir et al. 2011) without the need for transformations.

In humans, the OSR is sometimes measured as the ratio of “marriage-age” men to “marriage-age” women in the local mating pool. Marriage age is typically considered to be between 15 and 49 years (Guttentag and Secord 1983).

## Is the OSR Usually Stable or Fluctuating?

A recent investigation of owl monkeys – a socially monogamous primate species – suggests that it may be erroneous to assume an equal OSR in monogamous species, as researchers have done in the past (Fernandez-Duque and Huck 2013). Rather, sexual selection models should assume unequal yet fluctuating OSRs, even in highly pair-bonded species, given the unmated “floaters” that may disrupt mating dynamics by affecting group composition. Many other factors have also been found to destabilize OSR. For example,

Del Giudice (2012) identified multiple factors that cause fluctuations in either OSR or adult sex ratio. These factors include the following processes. First, stochastic fluctuations in the adult sex ratio increase as the population size shrinks. These fluctuations are especially strong when populations have less than a few hundred individuals. Second, sex-specific mortality and geographic distribution destabilize the adult sex ratio via delayed feedback mechanisms. Third, if the mating age is different for each sex, OSR tends to fluctuate when populations shrink or expand. Fourth, OSR is destabilized when younger and older individuals compete over mates.

### Factors that Influence the Operational Sex Ratio

Many other factors may affect OSR, and these factors vary across species. They include the type of mating system, the stability of pair-bonds, and sex differences in potential reproductive rate (Clutton-Brock and Parker 1992; Del Giudice 2012). Factors that influence the potential rate of reproduction can indirectly affect the OSR. These factors may include contextual considerations such as food availability or nesting sites.

### The Cognitive and Behavioral Consequences of Changes in OSR

The ways in which OSR affects cognition and behavior vary across species. In some species, changes in OSR may even prompt sex role reversals (e.g., Fritzsche et al. 2016). A recent meta-analysis suggests that mate scarcity is related to increases in displays of mate-guarding, aggression, and courtship behavior (Weir et al. 2011). Another meta-analysis revealed that courtship competition and courtship propensity, but not courtship frequency, increased when fewer mates are available (de Jong et al. 2012).

Sex ratio theory predicts that intrasexual competition increases with mate scarcity (Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996). For example, aggressive female-female competition

occurs at most OSRs, but in several fish species, females become the more competitive sex in highly female-biased OSRs (Forsgren et al. 2004). The influence of mate scarcity on intrasexual competition has been documented in naturalistic and experimental observations of many species including fishes (e.g., Forsgren et al. 2004), amphibians (e.g., Lee and Park 2009), birds (e.g., Colwell and Oring 1988), rodents (e.g., Bonatto et al. 2015), hyenas (e.g., Curren et al. 2015), and nonhuman primates (e.g., Mitani et al. 1996).

### OSR Studies in Humans

Compared to other mammals, human males invest exceptional effort in caring for offspring (Geary 2000; Buunk and Fisher 2009). Rates of female competition are higher in species that engage in pair-bonding and biparental care like our own, because monogamy and paternal investment beget mate choosiness among males (Fernandez-Duque and Huck 2013). Consequently, women must also compete intrasexually to secure and retain high-value mates (Clutton-Brock 2007).

Male-biased sex ratios are associated with lower average marital age among women; the authors explain that when women are scarce, they have more bargaining power and are able to find commitment at an earlier age (Kruger et al. 2010). Some seminal evolutionary predictions concerning the effects of biased sex ratios in humans came from Pedersen (1991): in male-biased sex ratios, men increase the number of offspring that they produce as well as increase resource provisioning, parenting activities, and violence toward both men and women. Indeed, studies suggest that preliterate societies find it more permissible for a husband to severely punish his adulterous wife when the society has a male-biased sex ratio (Guttentag and Secord 1983).

In humans as well as other animals, sex ratios influence a wide range of social behaviors. A review of evidence linking surplus men to more violence sheds light on the theoretical and empirical challenges that remain (Schacht et al. 2014). The authors caution that expecting a

relationship between competition over mates and violence is likely based on untested assumptions and might be masking interesting patterns.

Seemingly paradoxically, both female-biased and male-biased sex ratios can increase violence and crime. These discrepant findings may represent manifestations of different dynamics (Del Giudice 2012). For example, male-biased sex ratios increase male-male competition, but the competition may manifest in circuitous ways (e.g., by increasing competition for status or access to economic resources; Barber 2009). A longitudinal study of the effects of varying sex ratios in three English-speaking nations found that rates of violent crime were predicted by male-biased sex ratios (Barber 2003). Some of the violence in male-biased sex ratio environments may, however, be explained by the relative surplus of men, not by the ratio itself (Messner and Sampson 1991). In female-biased sex ratios, the percentage of men who marry at a younger age diminishes on account of men's increased short-term mating opportunities and decreased incentive for commitment (Kruger and Schlemmer 2009). Men's aggression and violent crime may simultaneously increase to attain these casual mating opportunities (Barber 2011). Several studies support this hypothesis, finding cross-sectional associations between female-biased sex ratios and higher proportions of violent crime (Barber 2009, 2011). At least in modern-day societies, female-biased sex ratios seem to increase male violence (Del Giudice 2012). Further research is needed to determine under which specific conditions female- and male-biased sex ratios increase aggression and toward whom.

Relatedly, cross-sectional research suggests that sexual choosiness is correlated with sex ratios, such that members of the scarcer sex express greater selectivity regarding the *qualities* they desire in a mate (e.g., Stone et al. 2007). The relationship between mate scarcity and decreased selectivity in the mating domain has also been the subject of experimental investigation. Using doctored sex ratio cues to alter perceptions of mate availability, Watkins et al. (2012) found that females expressed less choosiness when men were perceived as scarce versus abundant. The

researchers also found evidence of another mating rule: if the sex ratio is unfavorable (i.e., mate scarcity), people pay more attention to cues that index the mate value of potential sexual rivals. This mating rule presumably increases the individual's vigilance to mating rivals under conditions of intense competition.

Experimental studies have also found that sex ratio could have wider implications, such as changing how men make financial decisions (Griskevicius et al. 2012). In particular, increasing the perceived sex ratio to be more male-biased led males, but not females, to: (1) favor immediate over delayed monetary gains, (2) increase their motivation to borrow money, and (3) decrease their motivation to save money. This evidence suggests that young single men might respond to increased mate competition by expending additional effort to attract a romantic partner.

A recent theoretical paper examined the potential links between male mate-guarding behaviors, mate scarcity, and the evolution of human monogamy (Schacht and Bell 2016). The authors argue that the adaptive problem of mate scarcity may represent one of the key selection pressures that paved the way for human monogamy. If mate-guarding behaviors were successful in solving the problem of mate scarcity, then we should expect a range of such mate-guarding behaviors – not just intrasexual aggression – to be upregulated in response to cues to this adaptive problem.

## Conclusion

The sex ratio is widely believed to be a key ecological determinant of not only the availability of potential mates but also the *intensity* of competition for those mates, thus affecting many types of behaviors (see Weir et al. 2011). Sex ratio theory predicts that animals will intensify the tactics they use to secure a mate under conditions of mate scarcity. Correlational research surveying trends within populations has shown that OSR is related to human mating and parenting patterns (Del Giudice 2012). Many of these patterns can be understood as resulting from the trade-off between parental investment and mating effort.

Individuals of a given species are expected to have flexible, context-sensitive adaptations that enable them to respond to environmental and contextual fluctuations in an adaptive manner (Al-Shawaf et al. 2019). Sex ratio is one key contextual factor that reflects the degree of intrasexual competition and plays an important role in animal behavior and cognition. Given that sex ratio is a widespread aspect of the social lives of many sexually reproducing species, hypotheses and theories involving sex ratio can yield insights in many different species and domains (Del Giudice 2012).

## Cross-References

- ▶ [Alternative Reproductive Tactics](#)
- ▶ [Intra-sexual Selection](#)
- ▶ [Parental Investment](#)
- ▶ [Sex Ratio](#)
- ▶ [Sexual Selection](#)

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## Opposable Thumb

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## Synonyms

Hand; Pollex; First digit; Prehensility; Grasping; Precision grip; Primates

## Definition

A complex term describing the anatomy and movements of the thumb of primates with specific meaning when applied to humans.

## What is an Opposable Thumb?

When asking a layperson to identify one feature that distinguishes humans from the rest of mammals, most people would likely move their first digit and say, “we have an opposable thumb.” In describing an opposable thumb (also known as the pollex), some people would stress how it sticks out on the side of the hand away from the other digits (a characteristic of most primates); others would emphasize the manner it contacts the index finger to form a pincer grip. Most people have been taught that the opposable thumb is a human character, though some would say it is found in nonhuman primates as well. The thumb of human beings is in fact capable of a very complex motion known as opposability, which allows the pulp or fleshy pad of the thumb to contact that of another digit, most often the index finger. This complex motion is promoted by a combination of bony, muscular, and touch reception and neural control features allowing the thumb to move in different planes and apply just the right amount of pressure, so that objects of different weight, shape, and texture can be sensed, held, and retained by a single hand (see Kivell et al. 2016 for in-depth reviews for each one of these topics). This ability to retain an object with one hand against the pull of gravity is what defines a hand capable of prehensility and typifies the hand of all primates (Napier 1961, 1993). Although prehensility can be achieved without opposition, a hand lacking prehensility cannot achieve opposition. In this way, the terms opposability and prehensility go hand in hand so to speak.

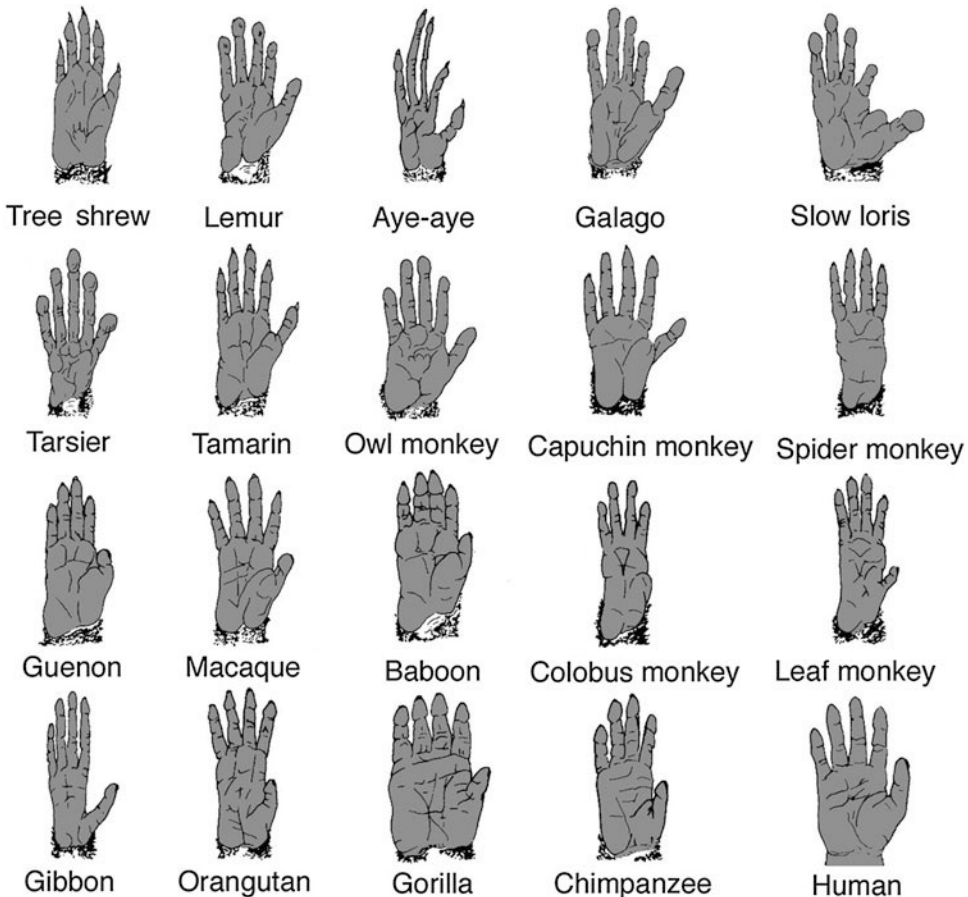
## Opposable Thumb: A Definition Based on Anatomy and Behavior

When examining and comparing the hands of different primates to each other and to

nonprimate mammals like tree shrews and rodents, key features can be easily identified: elongated fingers bearing flattened nails instead of claws and a long thumb diverging away from the other digits (Fig. 1). Historically, these features have been interpreted as adaptations for arboreal life and often used to classify the hand of primates as “opposable” (Haines 1958). In this context, the term opposable can be confusing. Anatomically, an opposable thumb can be defined as the first digit diverging away from the other digits. Behaviorally, an opposable thumb can refer to the ability of the pollex to converge toward the fingers using a motion known as opposability. Extensive variation exists within primates in these features, including thumb length and its degree of

divergence from other digits (Fig. 1) and the ability to achieve true opposition. Any attempt to define a thumb as “opposable” or capable of “opposability” requires careful consideration of both anatomical attributes and the behavior involved.

The broadest definition of opposability from both anatomical and behavioral perspectives involves a thumb diverging away or opposed relative to the other digits and the ability to assist the fingers in grasping an object securely with only one hand. However, a stricter and more precise definition of opposability more commonly used by human anatomists and clinicians focuses primarily on the thumb and its movements. Compared to most other primates, the human thumb is



**Opposable Thumb, Fig. 1** Hand diversity among primates and tree shrew. Compare the length and degree of divergence of thumb between different species. Hands not

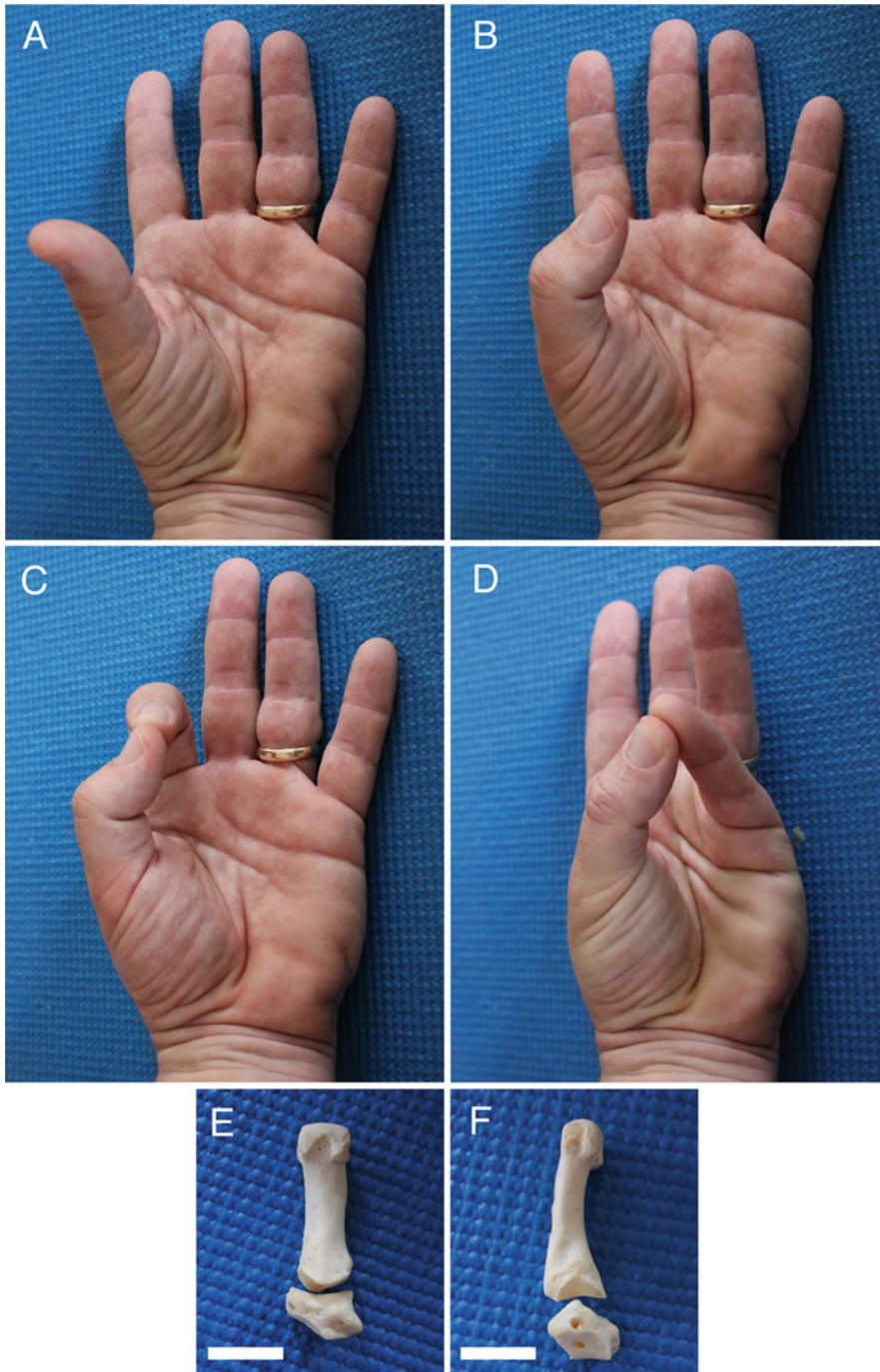
to scale (Reproduced from Lemelin and Schmitt (2016) with permission from Springer Science + Business Media LLC)

proportionally longer relative to the fourth digit or ring finger (Almécija et al. 2015), and its palmar surface is rotated out of plane from that of the fingers when the hand is at rest. As such, the pulp of the thumb and fingers (particularly the index finger) can be approximated to grasp a small object. In order to achieve opposition with the fingers, the thumb has to move in three different planes simultaneously: abduction (thumb moves away from the palm), flexion (thumb curls toward the fingers), and medially rotate (thumb undergoes rotation along its long axis toward the little finger) (Fig. 2). This compound movement of abduction, flexion, and medial rotation that results into opposition is promoted by a joint at the base of the thumb that has a unique shape that resembles a saddle (Napier 1961; Fig. 2). A group of short muscles crossing that joint (known as the thenar muscles) are primarily responsible for movement of the thumb during opposition. It is worth noting that this joint morphology and musculature allows the human thumb to make pulp-to-pulp contact with any of the fingers, including the little finger (which, like the thumb, has its own set of short muscles known as the hypothenar muscles). In parallel with this anatomical arrangement, large areas of the motor and sensory cortices of the brain are devoted to movement of the thumb and other digits, as well as sensation over the skin of the palm, and specialized nerve endings responsible for light-touch discrimination populate the palmar skin with disproportionately high numbers for the thumb and index (see relevant chapters in Kivell et al. 2016).

Applying this definition of opposability to the thumb of other primates in general can prove difficult as it overlooks the diversity of hand behavior observed in many different species, some of which showing striking similarities with humans. A comparative approach is vital to determining which aspects of hand movement and thumb opposability are unique to humans and which aspects are common to all primates. In turn, this comparative approach is necessary to test theories that emphasize tool use and other manipulative behavior as the major selective pressure for the evolution of thumb opposability in humans.

Many nonhuman primates such as chimpanzees have short thumbs relative to the index finger (what is described as a low opposability index or ratio of thumb length over index finger length) compared to humans (Napier 1960, 1993). As such, objects are often picked up between the pulp of the thumb and the side of the index finger rather than its pulp surface as in humans (Napier 1960; Christel 1993). This is also true for other apes, with gibbons being extreme in that regard. Thus, true opposability as defined above appears to separate humans from apes (Napier 1960). Interestingly, human-like opposition can be observed in African Old World monkeys such as baboons, which are characterized by opposability indices closer to those of humans (Napier 1993). Baboons can certainly achieve pulp-to-pulp contact of the thumb and index finger, but appear far more limited in opposing the thumb with the little finger. In nonhuman primates known as strepsirrhines (a group of primates including the lemurs from Madagascar), tarsiers (small primates from Southeast Asia), and New World monkeys (monkeys from Central and South America or platyrrhines), the thumb appears to lack the ability to undergo medial rotation (Napier 1961). Therefore, Napier (1961) invoked the term “pseudo-opposability” to describe thumb movements in these nonhuman primates (Napier 1961, 1993). It should be noted that most primates described as having “pseudo-opposable” thumbs also lack the ability to move the thumb and other digits independently, making opposability as defined in baboons, apes, and humans virtually impossible (Bishop 1964).

Broad categorization (i.e., “opposable” vs. “pseudo-opposable”) tends to mask the natural variation in anatomy and behavior found in primates. For example, capuchin monkeys – New World monkeys with so-called pseudo-opposable thumbs – are capable of thumb opposition comparable to that of their African cousins. Like baboons that collect seeds and other small objects using thumb opposition, capuchin monkeys are also capable of very refined grips involving pulp-to-pulp movements of the thumb and index finger when foraging on palm nuts, often involving tools (see Chapter 12 in Kivell et al. 2016).



**Opposable Thumb, Fig. 2** Typical movements and joint morphology of the thumb of humans. (a) abduction of the thumb (thumb away from the palmar plane); (b) flexion of abducted thumb; (c) opposition of thumb with index finger;

(d) opposition of thumb with little finger; (e, f) saddle-shaped joint between the trapezium (short carpal bone) and thumb metacarpal (palmar view on *left*, side view on *right*). Scale bars are 2 cm



## Conclusions

The term opposable thumb is not easy to define as it has different meanings depending on the scientific field (see Napier 1960 and Lemelin and Schmitt 2016 for a discussion on the topic). For a zoologist, an opposable thumb describes its positioning relative to the other digits and its ability to assist the fingers in grasping securely an object with only one hand. This definition is broad and imprecise as it encompasses wide anatomical and behavioral variation. For a human anatomist or clinician, however, an opposable thumb applies to the ability of the pollex of humans to achieve a combination of movements (i.e., opposition) resulting in touching between its pulp surface with the pulp surface of adjacent fingers, mainly the index finger. This is a narrower and more precise definition. As such, the term opposable thumb should be used thoughtfully and properly, with its meaning carefully defined when used in any anatomical or behavioral study, or in any discussion for that matter, involving the primate hand.

## Cross-References

- Adaptation
- Arboreality
- Mechanoreceptors
- Muscular system
- Precision grip
- Nonhuman primates
- Hominoid

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## Optic Flow

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## Introduction

When an animal moves, the image of its surrounding environment moves in the retinæ of the animal's eyes. The pattern of image motion (known as the “optic flow field,” OFF) bears rich information about the animal's own motion (termed “egomotion”), about the distance to various nearby objects, the speed of locomotion, the distance the animal has traveled, and several other parameters. This entry highlights some of the cues that are contained in the optic flow field and describes how they are used to control locomotion and enable safe and accurate navigation through the environment.

## The Relation of Optic Flow to Egomotion

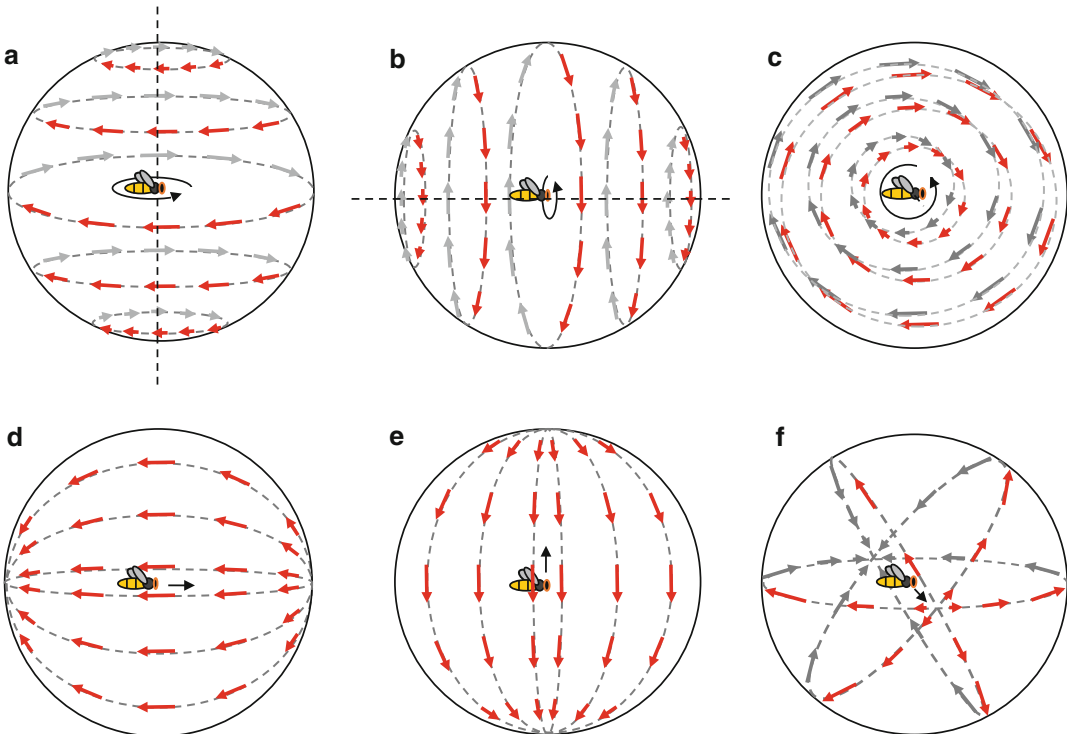
When a flying animal turns (yaws) to the left, the image of the world appears to move to the right



and vice versa. The OFF generated by a leftward yaw (counterclockwise rotation about the dorso-ventral axis) is shown in Fig. 1a, where the individual vectors depict the direction and magnitude of the image motion at each location in the animal's visual field (which is assumed to be panoramic). The image motion (optic flow, OF) is directed horizontally everywhere. Its magnitude is zero in the dorsal and ventral regions of the visual field (the "poles") and maximum in the horizontal plane (the "equator") – the plane perpendicular to the axis of rotation. Figure 1b shows the OFF generated by a counterclockwise roll movement (a rotation about the antero-posterior axis). A counterclockwise roll causes the image to rotate clockwise about the roll axis and vice versa. Here again, the OF is largest in the plane perpendicular to the axis of rotation and is zero in the frontal and rear regions of the visual field. Figure 1c shows the OFF generated by an upward pitch movement (a rotation about the medio-lateral axis). Here the OF is largest in the plane

perpendicular to the pitch axis and is zero in both lateral regions of the visual field. Thus, yaw, roll, and pitch produce OFFs that have distinct "signatures"; and a rotation about any other axis would induce an OFF that is an appropriately weighted combination of these three canonical OFFs.

When an animal rotates, it experiences an OFF that is independent of the distances of the various objects in the environment – and this is true irrespective of whether the rotation is about the yaw, pitch, or roll axis or some other axis. However, the OFF that is generated when an animal *translates* (moves in a straight line) in any direction depends upon the distances of the objects in the environment, as well as their bearings. In general, during translation the magnitude of the optic flow generated by an object is proportional to the sine of the bearing angle of the object relative to the direction of translation and is inversely proportional to the object's range. Figure 1d shows the OFF generated by a forward translation in an environment in which all of the



**Optic Flow, Fig. 1** Optical flow fields generated by various motions of a flying animal. (a) Counterclockwise yaw; (b) counterclockwise roll; (c) upward pitch; (d) forward translation; (e) upward translation; and (f) rightward translation

objects are assumed to have the same range. The image motion is zero in the frontal and rear regions of the visual field and maximum in a plane perpendicular to the direction of translation. Figure 1e, f depict the OFFs generated by an upward translation and a rightward translation, respectively. Given these six characteristic optic flow fields, a flying animal could, at least in principle, estimate its instantaneous rotation in 3D by monitoring the responses of motion-sensitive neurons that are selectively responsive to each of the three “canonical” OFFs illustrated in Fig. 1a, b, and c. The responses of these three neurons would then encode the rates of yaw, roll, and pitch, respectively. Similarly, the three components of the animal’s translation would be encoded by the responses of three further neurons that are selectively tuned to the three OFFs shown in Fig. 1d, e, and f. Interestingly, electrophysiological investigations of the insect visual pathway have revealed large-field movement-sensitive neurons that display some of the characteristics illustrated in Fig. 1 (Krapp and Hengstenberg 1996), suggesting that these neurons may play an important role in the visual computation of an animal’s instantaneous egomotion in six degrees of freedom (three of rotation and three of translation). There is now ample evidence to indicate that at least some flying insects use the OFF to (a) infer their egomotion (rotation and translation) to stabilize their attitude and flight direction, (b) control the speed of their flight, and (c) estimate how far they have traveled by integrating, over time, the vectors representing the moment-to-moment translations and rotations that have occurred during the journey, through a process known as “Path Integration” (Srinivasan 2011a).

In what other ways could animals use optic flow information? Most insects are unable to rely on stereo vision to estimate the range to objects or surfaces, because the two eyes are not sufficiently far apart to acquire reliable stereo cues. Consequently, they need to rely heavily on optic flow information to measure the distances to objects and surfaces. When an insect flies past an object at a given speed, the closer the object, the larger the magnitude of the optic flow that it generates. Honeybees avoid collisions with obstacles by

moving away from objects that generate strong optic flow (Srinivasan 2011a). They negotiate narrow corridors by balancing the magnitudes of the optic flows that are generated by the two side walls, thus ensuring safe flight through the middle of the corridor (Srinivasan 2011b).

Honeybees regulate the speed of their flight by holding constant the total magnitude of the optic flow that they experience in the two eyes. Thus, they fly at a constant speed in a corridor of uniform width, but slow down as they fly through a progressively narrowing tunnel and speed up as they fly through a progressively widening tunnel (Srinivasan 2011b). This strategy ensures that the speed of flight is automatically tailored to the nature of the environment – a tightly cluttered environment enforces flight at a low, safe speed, whereas an open environment encourages a high flight speed. Honeybees orchestrate smooth landings on surfaces by holding constant the magnitude of the optic flow that they experience as they approach the surface. This ensures that the flight speed is automatically reduced as the bee approaches the surface, reaching a near-zero value at touchdown (Srinivasan 2011a; Baird et al. 2013). The beauty of this strategy is that it does not require continuous information about the distance to the surface or the speed at which the surface is approached.

Optic flow information can be used in a number of different ways to guide an animal’s behavior as it approaches a surface or as an object approaches it. For example, the projected time to contact the surface (TTC) at any instant of time is given by the ratio of the angular bearing of a visual feature on the surface, to the radial optic flow that the feature generates in the retina. When gannets plunge into the ocean to catch fish, they close their wings to streamline their entry into the water at a *fixed time* prior to contacting the surface, irrespective of the speed of the dive (Lee and Reddish 1980), suggesting that the nervous systems of these birds are indeed computing the TTC to determine when to close their wings. When pigeons are shown movies of a football approaching them on a collision trajectory, one class of visual neurons in the tectofugal pathway displays an abrupt increase in firing rate

approximately 1 s prior to the projected time to contact (Sun and Frost 1998). Interestingly, these neurons respond only if the object is on a direct collision course (when the OFF is purely divergent) and not when the trajectory is a “near miss” (when it includes a translational component). Another class of visual neurons in the thalamofugal pathway of the pigeon commences firing when a large approaching surface is ~6 cm from the eye, suggesting that these neurons are computing the *distance* of the approaching surface, rather than the time to contact. Interestingly, the heart rate of the birds also accelerates when the surface reaches this distance (Liu et al. 2008). These findings suggest that natural visual systems are capable of analyzing the pattern of optic flow in sophisticated ways, not only to infer their owners’ motion in the environment but also to compute the distance of an approaching object or the time to contact it, if a collision is imminent.

Survival requires natural organisms to deal and interact with other objects that are moving in the environment; these may be prey, predators, or a potential mate. Animals are very adept at detecting moving objects, even when they themselves are in motion. This is a challenging task, because the visual system of a moving animal experiences not only the object’s motion, but also that of the environment. A moving object cannot be reliably distinguished on the basis of motion parallax (the motion of its image relative to that of the background), because even a stationary object can generate motion parallax when it is nearer than the background. One way to detect a moving object reliably would be to compare the direction of motion of the image of the object with that of its immediate background. If these directions are different, the object is in motion. While it remains to be seen whether natural visual systems indeed adopt such a strategy, it has been applied successfully in machine vision systems (Strydom et al. 2016).

Once a moving object has been detected, it may be necessary to pursue it, or avoid a collision with it, or flee from it – depending upon the context. In flying insects, the control of pursuit is based on measurement of the angular bearing of the target and the optic flow that it induces in the

eyes of the pursuer (Land and Collett 1974). Various pursuit strategies have been documented, ranging from (i) simple pursuit, where the pursuer continually reorients itself to move directly toward the target; (ii) predictive pursuit – a more efficient strategy, where the pursuer effectively predicts the point of interception of the target and moves directly toward that point; and (c) motion-camouflaged pursuit, where the pursuer conceals its motion by moving toward the target in such a way as to produce precisely the optic flow that would be induced by a stationary object (Srinivasan 2011b). Imminent collisions can be avoided by steering away from objects that generate purely divergent flow on the retina. Furthermore, in a close encounter with a moving object, the optic flow generated by the object can be used to predict the minimum separation and the time at which this minimum separation will occur (Gunasinghe et al. 2016).

Space does not permit detailed description of the above strategies. However, many of them rely critically upon the analysis of optic flow. How is optic flow actually computed by the nervous system? While movement-detecting neurons in the visual pathway have been characterized and modeled for some time (Borst and Helmstaedter 2015), they do not seem to provide a veridical estimate of the OF, because their responses depend not only upon the speed of the image in the retina but also upon its contrast and its visual structure (Srinivasan et al. 1999). Tackling this conundrum is a continuing theme of current research.

Another theme of research that is receiving increased interest is the application of the principles derived from understanding how animals use optic flow, to the design of vision-based guidance systems for aircraft (Srinivasan et al. 2013). Biologically inspired systems are being developed for flight stabilization, automated collision avoidance, speed control, landing, visual odometry, and navigation. Like an insect or a bird, these systems are completely self-reliant – they use purely vision-based information and do not require complex external infrastructure such as GPS (Franceschini 2014; Strydom et al. 2016; Gunasinghe et al. 2016).

## Cross-References

- [Bear Sensory Systems](#)
- [Dead Reckoning](#)
- [Depth Perception](#)
- [Insect Navigation](#)
- [Navigation](#)
- [Perception-Action Theory](#)
- [Stereoscopic Vision](#)

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## Optical Flattening

- [Countershading](#)

## Optimal Experience

- [Cognitive Flow](#)

## Optimal Foraging Theory

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Optimal foraging theory (OFT) predicts and evaluates how an organism behaves in response to problems encountered in its environment while searching for food (Commons et al. 1988). Motivated by a growing understanding of natural selection (Williams 1966), and the importance of energy in ecological systems, OFT was first introduced in the 1960s by two publications by MacArthur and Pianka (1966) and Emlen (1966). These seminal papers suggested that organisms' prey choices were selected for by evolution and guided by a tendency to maximize energy as a function of time spent feeding (Kamil et al. 1987). (Selection in biology is a natural process that results in the survival and reproduction of some organisms and not others with the result that inherited traits of the survivors are passed down to offspring, thereby

perpetuating those traits (“Selection,” 2017). The publication of Stephen and Krebs’ book *Foraging Theory* in 1986 further fortified and popularized the theory, inspiring many more publications on the topic that same year (Stephens et al. 2007). The most basic premise of OFT concerns efficiency and optimization: The organism that obtains food at the maximum possible rate will have a selective advantage over less efficient foragers of its species (Kurland and Beckerman 1985). Moreover, although acquiring food provides an organism with energy, it also *costs* time and energy to find, secure, and consume. Therefore, an organism that can minimize the time and energy required to acquire the maximum amount of energy from food increases its biological fitness (an organism’s relative capacity to survive and transmit its genes to offspring (“Fitness,” 2017). Also, referred to as Darwinian fitness). Consequently, according to the theory of natural selection, a species’ most efficient foraging pattern will be selected for (i.e., propagated).

To put this in perspective, let’s imagine that a species’ food source becomes limited. The members of this species that obtain food at the maximum possible rate, proportionate to their size, age, strength, and other physiological capacities (i.e., the optimal forager), will be better nourished than less efficient foragers of its species (Kurland and Beckerman 1985). Likewise, if an organism’s species faces other threats, whatever they may be, the optimal forager will have more time, energy, and strength to use in overcoming challenges associated with those threats. Even without any particular threat, an optimal forager will have more resources to dedicate to mating, parenting, and defending its offspring. In every one of these cases, the optimal forager will be more likely to survive and reproduce, thereby contributing to its species’ gene pool. OFT predicts then that (a) organisms will strive to acquire energy from food at the maximal possible rate and (b) optimal foraging behavior patterns will be perpetuated by being passed down from parents to offspring.

Optimal foraging is considered a multi-dimensional problem made up of several independent components including search, identification, handling, consumption, and utilization (i.e.,

digestion) (Commons et al. 1988). As an organism forages, environmental variations and other limitations affect each of these components in different ways (Commons et al. 1988). Consequently, the foraging process has been studied by isolating and manipulating each one of these components to analyze how various “constraints” (i.e., environmental variations and other challenges) affect them (Commons et al. 1988).

## OFT Model Components

Theoretical models are used to test hypotheses (i.e., possible explanations of phenomena). Models are formulated based on a hypothetical explanation of an observed phenomenon, idea, or process and then tested to see how accurate they are. That is, models enable predictions that can be compared with observable data. A successful model is one that can account for the relationships observed between factors of interest. Optimality and foraging models tend to share three common components: decision assumptions, currency assumptions, and constraint assumptions (Stephens and Krebs 1986).

### Decision Assumptions

Optimality models concern the “best” way to make a choice, whether that choice is made by the organism or by natural selection (e.g., What type of teeth should a shark have? What pattern should honey bees use to pollinate?). In optimality and foraging models, the forager’s “decision” that has been selected for analysis is often defined by translating that decision into one or more algebraic variables (e.g., speed, size, length, time, etc.). While decisions analyzed in “static models” are not dependent on time, and therefore can be represented by non-sequential lists of choices, dynamic models, on the other hand, involve decisions that depend on the timing of those choices. Because one choice in a dynamic model (e.g., honey bee pollinating path) can affect the organism’s future condition (e.g., amount of honey in the hive), which in turn can affect forthcoming decisions (e.g., number of larvae produced), dynamic models describe the optimal “path”



(i.e., sequence) of decisions. The decisions investigated by most OFT models focus on food exploitation: which food items to eat and when to leave a foraging area and move onto another (Stephens and Krebs 1986). Each of these questions is comprised of multiple decision variables that can be represented in different ways. For example, if we consider the latter problem, when to leave a foraging area, the decision variable is often “quantity of time spent in the foraging area” (e.g., the amount of time spent grazing a patch of grass). However, other decision variables could include the quantity or type of food ingested while foraging in that area.

### Currency Assumptions

A model’s currency is the variable that is optimized by the organism. In other words, it is the organism’s foraging “goal” or “payoff” (Hughes 1993; Stephens et al. 2007; Stephens and Krebs 1986). All OFT currencies concern long-term average energy rate maximization (i.e., how to acquire the most energy on average, over the long term, given the time and energy used to do so). The simplest OFT currencies can be defined as a food item’s value, less the cost of acquiring the food item (Stephens and Krebs 1986). For example, a popular currency used in OFT models is “energy intake per unit time spent foraging” (Shettleworth 1989). Once the decision variables and currency have been defined, the relationship between them must also be defined. For example, an investigator may analyze the relationship between the energy intake per time spent foraging (the currency) and the size of a food patch (the decision variable).

### Constraint Assumptions

A model’s constraints are variables that affect the relationship between the currency and the decision variable(s) (Stephens and Krebs 1986), that is, environmental, physiological, and informational factors that limit the forager’s available choices and the payoff obtained from those choices (Hughes 1993; Stephens et al. 2007; Stephens and Krebs 1986). Conventional OFT models assume three major constraints: (a) exclusivity of search and exploitation,

(b) sequential Poisson encounters, and (c) complete information. The first assumed constraint is straightforward; a forager cannot be two places at one time. That is, an organism cannot exploit prey or food patches while at the same time searching for food (Stephens and Krebs 1986). The second constraint concerns the timing of sequential foraging events; food items are encountered one at a time, and the probability of each food item in a short time period is constant (Stephens and Krebs 1986). The third constraint concerns the organism’s understanding of the rules of the model. OFT models assume that the forager knows or, at the least, behaves as if it knows the rules of the model, such as information about the foraging environment (Stephens and Krebs 1986).

### Conventional Models of Optimal Foraging Theory

Although, since its conception OFT models have advanced, expanded, and diverged, the most basic optimal foraging hypotheses stem from separating the act of foraging into “search” time and “handling” time and have been popular topics of study (Commons et al. 1988; Kurland and Beckerman 1985). “Search” includes behaviors dedicated to finding food, whereas “handling” refers to behaviors dedicated to obtaining and consuming food after it is found (e.g., pursuit, subduing, preparation, ingestion, etc.) (Kurland and Beckerman 1985). The two most influential examples include the prey and patch models (in foraging models, “prey” is conceived of as any distinct food item that a forager acquires (e.g., a mouse, a worm, a seed, grass, etc.)). Both are average-rate maximizing models, both focus on searching and encountering food, and both use Holling’s (1959) disc equation to calculate the average rate of energy intake (Stephens and Krebs 1986). However, they differ in that they analyze different decisions. The prey model analyzes the choice to *eat or continue searching* when a *food item* is encountered, and the patch model analyzes the choice of *how long* to forage when a *food patch* is encountered.



### The Prey Model

The prey model, also known as contingency theory, predicts what a forager will do when it encounters food in its environment. Will the forager stop and eat the food or continue searching for a more profitable food? To answer this question, each type of food is assigned an average handling time and an average value. The value of a food type is most often defined as its rate of energy intake (i.e., calories); however, other definitions, such as protein content, have also been used (Kurland and Beckerman 1985; Nakagawa 2009). For example, in herbivores, nutrient balance, digestion, inhibition, toxicity, and gut capacity have also been identified as important factors. Therefore, valuable herbivore food types are those that maximize intake of energy and nutrients while minimizing intake of digestion inhibitors and toxins (Freeland and Janzen 1974; Nakagawa 2009; H. R. Pulliam 1975; Westoby 1974). Nevertheless, for any organism, the “prey profitability ranking” or the “net yield” of a food type is defined as the ratio of its value to its handling time (Kurland and Beckerman 1985) (also referred to as “net payoff” and “net benefit”). When these factors as well as the net yield are known, an optimal foraging rule can be specified: A forager should stop searching for food and invest handling time for a food item only if, on average, it cannot maximize its food intake rate by passing up this food item to continue foraging and come across a more valuable food item (i.e., something better to eat). That is, a forager should only stop to eat when it finds a food item that has a small enough handling time, and a large enough caloric yield, that the forager is unlikely to do better by ignoring the food item to search for something better.

The results of the prey model make several predictions. The first as discussed above is *Ranking by Prey Profitability*: Food types are ranked based on the ratio of energy intake to handling time. The second is the *The Zero-One Rule*: Food item types are either always eaten when they are encountered or never eaten when encountered. If a forager encounters a high-ranking food item, and passes it up in search of another food item, the best possible scenario is that it will encounter *another*

high-ranking food. Therefore, there is no benefit to passing up a high-ranking food item; it should always be eaten. In comparison, when a low-ranking food item is encountered, and the opportunity loss due to consuming this food item outweighs the potential energy gain, then it never pays to eat a low-ranking food item. (Foraging opportunity loss is assessed by comparing potential gains from consuming a food item with the potential loss of the chance to consume a better food item.) In this way, The prey model predicts that it is always better to skip low-ranked food types in search of higher-ranked types, given how much time and energy it takes to consume them and their low caloric payoff. The last and most surprising prediction of the prey model is *Independence of Inclusion from Encounter Rate*: Whether a food type is included in an organism’s optimal diet is dependent only on the abundance of better food choices and not on that food’s own abundance (i.e., “encounter rate” or the likelihood a forager will come across a food type in its environment). That is, even if a low-ranked food item is abundant in a food patch, it should still be ignored. This prediction makes more sense when we consider that this model *only* asks *what* food should be eaten or ignored *within a homogenous* food patch. If a forager moves to a new patch, the model should be independently applied to the new patch scenario (Stephens and Krebs 1986). In this way, the prey model does not preclude the scenario in which an optimal forager might forage in a patch with unusually abundant low-ranking food items, if this abundance compensates for the low- value of the food.

### The Patch Model

Similar to food type selection, optimal foraging theory rules are also applicable to optimal “patch residence time” (Stephens and Krebs 1986), that is, predicting how long an organism will forage within a “patch” of food, among the patches available to them so as to maximize time and energy (Kurland and Beckerman 1985; Nakagawa 2009; R. H. Pulliam 1974; Pyke et al. 1977; Schoener 1971; Stephens and Krebs 1986). A patch is an area of an organism’s environment with a particular density and distribution of food. It differs

from the rest of the organism's environment based on food density; the patch is more, or less, dense with food than the surrounding environment. Originally proposed by Charnov (1976) as the marginal value theorem, the patch model hypothesizes that because most food patches contain limited resources, foraging a food patch will deplete it (Stephens and Krebs 1986) (also referred to as the patch choice theory). Consequently after a forager first enters a patch, it will experience diminishing returns, as the rate of energy intake decreases with time. Consequently, an organism should leave a patch it is foraging in when the average rate of energy intake in the patch (i.e., the calories available to be consumed) diminishes to match the average energy intake rate in the surrounding environment including the time it will take to search for and/or travel to a new patch (Nakagawa 2009; Stephens and Krebs 1986). In other words, although an animal can continue to increase its *total* caloric intake by foraging in a depleted patch, its time and energy could be more wisely used, by finding a new patch in which its rate of energy intake would be higher. It follows then that the patch model predicts that foragers will stay in (a) food patches with higher food density and/or higher value food longer than those that are less dense or contain lower-valued food types and (b) one food patch longer when surrounding food patches are scarce or far apart (Nakagawa 2009).

## Criticisms and New Concepts

Since the publication of Stephens' and Krebs' (1986) book and the flurry of publications inspired thereafter, OFT has become a focus of criticism and debate (Gould and Lewontin 1979; Pierce and Ollason 1987, so much so that by the mid-1980s, foraging scientists were hesitant to identify with OFT (Stephens et al. 2007). One of the most basic criticisms of this theory is that for the most part, OFT predicts inflexible and uncompromising behavioral responses. However, research indicates that animals are more likely to exhibit more gradual and incomplete responses, demonstrated via partial diet preferences and

variable patch residence times (Pyke 1984). Another popular area of debate surrounds how "optimality" is, or can be, defined (Stephens et al. 2007). Critics argue that natural selection is not sophisticated enough and does not have enough time to "perfect" traits. Moreover, many evolved traits may actually result as by-products of other traits that were selected for (Stephens et al. 2007). Ecologists in the field also questioned how applicable such simple OFT models are to the complex reality of natural environments.

Partly in response to these criticisms, new OFT hypotheses have developed. Stephens et al. (2007) identify some of the biggest conceptual advances to include (a) the recognition that foragers must weigh the trade-offs of compromised safety when foraging for food; (b) conceptual advances in "state dependence", the idea that a forager's choices may be influenced by state variables, such as level of hunger or fat reserves; and (c) consideration of the effects of group foraging and social foraging games between predator and prey, which takes into account the prey's behavior in addition to the predator's and proposes that the predator considers the consequences of its behavior and its prey's (Stephens et al. 2007).

## Cross-References

- Activity Budget
- Evolutionarily Stable Strategies
- Foraging
- Natural Selection
- Reproductive Fitness

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## Optimal Group Size

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Many animal species form groups for a portion or the entirety of their lives. Individuals benefit from forming groups when the advantages of aggregating – including foraging and hunting benefits, improved predator avoidance, increased conspecific threat avoidance (against infanticide and intergroup contests), cooperative infant care, and information sharing – outweigh the costs of group living – predominantly intragroup resource competition for food and reproductive opportunities, as well as increased exposure to disease.

Group size impacts access to food and the ability to respond to threats and has important fitness consequences (lifetime reproductive success). *Optimal group size* is the group size at which individual member fitness is maximized. Group size is influenced by ecological factors, namely food competition and risk of predation, which put pressure on the upper and lower limits of group membership until an intermediate, optimal size is reached. Intergroup competition is one such ecological constraint that favors larger groups as larger groups are better able to defend territory and food patches from other rival groups (the “resource defense model” (Wrangham 1980)). Even in situations where food patches or territories cannot be defended or when such

defense does not provide a net benefit, large groups may still be preferred over smaller groups to reduce the risk of predation, as larger groups are better able to detect predators and discourage attacks (Van Schaik 1983). Unfortunately, there are also costs associated with large group sizes. As group size increases, intragroup competition increases as limited food resources must be divided among more and more individuals (exploitation competition) and contests among group members over the limited food supply can prevent access to resources for some members (interference competition). Intragroup competition should thus favor smaller groups. It is this tension between intragroup competition, which encourages smaller groups, and intergroup competition and/or predation risk, which supports larger groups, that encourages group size toward an optimal, intermediate size.

A number of other ecological factors may directly or indirectly influence optimal group size. Seasonal food availability can impact optimal group size due to its effect on intergroup and intragroup competition. Generally, during times of food abundance optimal group size should increase. However, during times of food scarcity, optimal group size should decrease if food shortages cause increases in intragroup competition but increase if food scarcity causes increases in intergroup competition. The size, density, and distribution of food patches also impact group size (Chapman and Chapman 2000). Larger groups spend less time at a given patch as they deplete the patch more quickly and must move to the next patch sooner than smaller groups. When the density of patches is high, travel costs between food sources within a patch are low and thus larger groups should be supported. When large or small food patches are clumped together, travel costs are low between patches and larger group sizes can be supported (at least in the short term) as long as the clump of patches can support the group overall. When the distribution of patches is uniform, the density of the patches is expected to determine group size regardless of patch size, with higher densities supporting larger groups as travel costs are low and with lower densities supporting

smaller groups when patches are rare, as smaller groups can feed on one patch for longer periods. Threats of infanticide from rival conspecifics should encourage an increase in optimal group size as larger groups can better discourage and defend against attacks. Within a given group, optimal group size may differ for individuals of different ranks in the group's social hierarchy. Subordinate individuals are often responsible for group protection and thus generally benefit from larger groups that spread the costs of defense among a larger pool. Conversely, dominant individuals typically benefit from somewhat smaller groups that continue to provide efficient protection via subordinate members but have lower costs of intragroup competition.

Optimal group size will differ across species, populations, and even individuals within a given group due to the varying impact of the factors that affect the costs and benefits of group living. Understanding each group's optimal size will be important for conservation efforts both in terms of the expected survival of current species and populations as climate change and human encroachment force animals into areas that may not allow for optimal groupings and also in terms of the success of reintroduction efforts and captive breeding programs.

## Cross-References

- [Costs of Group Living](#)
- [Group Living](#)
- [In-Group](#)

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## Order Sirenia

### ► Sirenia Morphology

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## Ordinal Position

### ► Pecking Order

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## Ordinality

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## Synonyms

Position; Rank

## Definition

The numerical position of an object.

What knowledge do we acquire when learning a list of items? Ladd and Woodworth (1911) proposed that we encode ordinality, stating that “Associations are certainly formed, not only between successive members of a list, but also between individual members and their positions in the series” (p. 578). In contrast, Ebbinghaus (1913) argued that while associations were formed between adjacent items, associations were not formed between items and positions but “...beyond intervening members to every member... The strength of the threads varies with the distance of the members” (p. 94).

To test his hypothesis, Ebbinghaus (1913) developed the derived list paradigm. Ebbinghaus (1913) learnt six 16-syllable lists to the point where he could repeat each list without error. He then used the items in each list to construct derived lists of 1, 2, 3, or 7 degrees of remoteness. For example, if the original series was  $A \rightarrow B \rightarrow$

$C \rightarrow D \rightarrow E \rightarrow F \rightarrow G \rightarrow H \dots \rightarrow P$ , then a list of 1 degree of remoteness would look like  $A \rightarrow C \rightarrow E \rightarrow G \rightarrow I \rightarrow K \rightarrow M \rightarrow O$ , etc., and a list of 3 degrees of remoteness would look like  $A \rightarrow E \rightarrow I \rightarrow M \rightarrow B \rightarrow F \rightarrow J \rightarrow N$ , etc. Ebbinghaus (1913) reported that the speed with which a list was learnt was a decreasing function of the degree of remoteness. That is, derived lists with 1 degree of remoteness were learned faster than those with 2 degrees of remoteness, lists with 2 degrees of remoteness were learnt faster than those with three, and lists with 3 degrees of remoteness were learnt faster than those with seven. Importantly, all of the derived lists were learnt faster than a control list in which items from the original series were randomly arranged. Ebbinghaus (1913) used these data to conclude that remote associations play a key role in serial learning.

A potential problem with the Ebbinghaus (1913) method, however, was the control condition that he used. His control lists were composed of 16 items, taken from 6 lists he had previously learnt, and placed in a random order. In light of Ladd and Woodworth’s (1911) ordinal position hypothesis, a list constructed in this manner would lead to negative, rather than neutral, transfer. This is due to the fact that mixing the order of items for the control list creates interference between the old item-position associations and the new item-position associations that must be formed. To address this issue, Hakes et al. (1964) replicated Ebbinghaus’ (1913) derived list experiment with the exception that the control list was composed of novel items. On the derived lists, Hakes et al. (1964) reported no significant difference in the number of trials required to reach one perfect recitation for participants learning a derived list of 1, 2, or 3 degrees of remoteness and those learning the control list and concluded that “The present results are in accord with those of other recent experiments (serial to paired-associate transfer) in providing no support for the associative theory of serial learning” (p. 513).

Interestingly, a variation of Ebbinghaus’ (1913) method of deriving a list has provided the strongest evidence in support of the ordinal position hypothesis. Ebenholtz (1963) trained two



groups of subjects on a 10-item list composed of nonsense syllables ( $A \rightarrow B \rightarrow C \rightarrow D \rightarrow E \rightarrow F \rightarrow G \rightarrow H \rightarrow I \rightarrow J$ ). Once the participants acquired the list, Group 1 was trained on a derived list in which the even or odd items from the first list maintained their ordinal position (e.g., even items:  $X1 \rightarrow B \rightarrow X2 \rightarrow D \rightarrow X3 \rightarrow F \rightarrow X4 \rightarrow H \rightarrow X5 \rightarrow J$ ), while Group 2 was trained on a derived list in which the ordinal position of the even or odd items from the first list was changed (e.g., odd items:  $F \rightarrow X1 \rightarrow H \rightarrow X2 \rightarrow J \rightarrow X3 \rightarrow B \rightarrow X4 \rightarrow D \rightarrow X5$ ). Each X represents a novel list item. Ebenholtz (1963) found that participants in the maintained group learned the positions of the familiar list items significantly faster than participants in either the changed group or a control group. This finding suggests that participants encoded the ordinal positions of the list items during serial learning and used that information to guide responding on the derived lists.

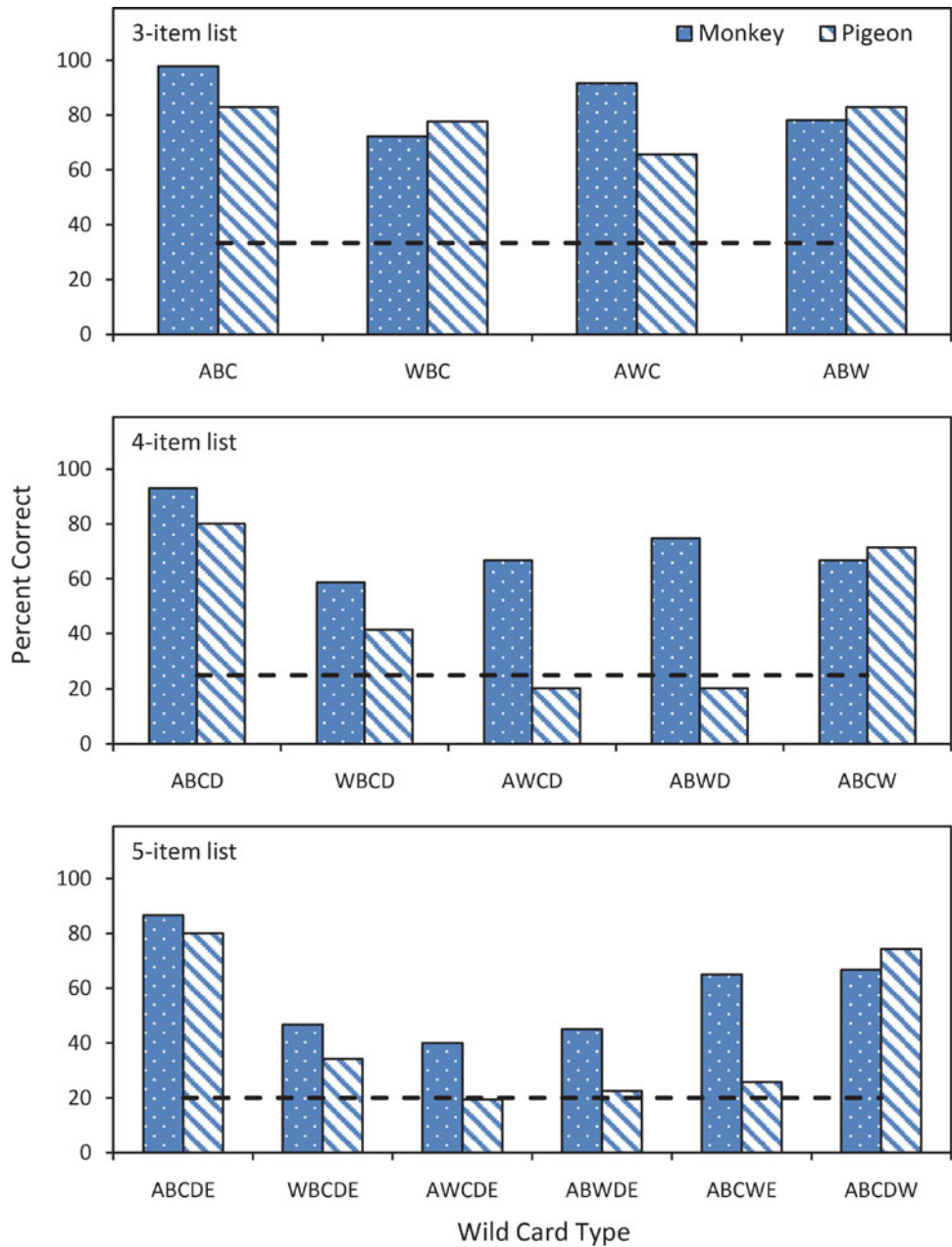
In nonhuman animals, studies have typically employed variations of the simultaneous chaining paradigm to investigate ordinality (Chen et al. 1997; D'Amato and Colombo 1989; Harris et al. 2007; Orlov et al. 2000; Scarf and Colombo 2011; Terrace et al. 1995). For example, D'Amato and Colombo (1989) trained monkeys on a 3-, 4- and 5-item list and, once subjects were performing above 75% correct in a single session, inserted "wild cards" on approximately half of a subject's daily trials. The "wild card" was a novel stimulus that was substituted for an existing list item. For example, on a 5-item list, a subject may be presented with the items A, W, C, D, and E, with W representing the wild card item. On this trial, the wild card has replaced the second item of a 5-item list, and in order to correctly complete the trial, the subject must respond to the wild card at the second position (i.e.,  $A \rightarrow W \rightarrow C \rightarrow D \rightarrow E$ ). The wild card was placed equally often in each ordinal position on the 3-, 4-, and 5-item lists. On the 3-item list, there were three types of wild card trials (e.g.,  $W \rightarrow B \rightarrow C$ ), on the 4-item list, there were four (e.g.,  $A \rightarrow W \rightarrow C \rightarrow D$ ), and, finally, on the 5-item list, there were five (e.g.,  $A \rightarrow B \rightarrow W \rightarrow D \rightarrow E$ ).

The performance of monkeys and pigeons on the 3-, 4-, and 5-item lists is shown in Fig. 1. The

monkeys performed above chance on the three 3-item, four 4-item, and five 5-item wild card lists. Although the performance of pigeons trained on the 3-item lists was comparable to monkeys, pigeons trained on the 4- or 5-item lists performed at chance, with the exception of performance on the 4-item  $A \rightarrow B \rightarrow C \rightarrow W$  and 5-item  $A \rightarrow B \rightarrow C \rightarrow D \rightarrow W$  lists. The performance on these wild card lists, in which the wild card replaces the end item, can be explained by the subject simply responding to the baseline items first (e.g.,  $A \rightarrow B \rightarrow C \rightarrow D$ ) and then responding to the wild card item (W) by default. The high performance by pigeons on the  $W \rightarrow B \rightarrow C$  and  $A \rightarrow W \rightarrow C$  lists is also easily accounted for without invoking knowledge of ordinal position.

The inability of Terrace et al.'s (1995) pigeons to place the wild card items correctly on the 4- or 5-item lists would suggest that they do not acquire knowledge of each item's ordinal position. However, the performance of Terrace et al.'s (1995) pigeons may also be attributed to a contextual variable. Indeed, when learning a 4- or 5-item list, it is common for pigeons to take 2000–2500 and 3000–3500 trials, respectively, to reach a 75% criterion. Given this extensive training, it is possible that when a novel item is substituted for an interior item, pigeons may have a strong tendency to first respond to within-list items before responding to the novel list item. Indeed, on the series  $A \rightarrow B \rightarrow C \rightarrow W$  and  $A \rightarrow B \rightarrow C \rightarrow D \rightarrow W$ , which represent 25 and 20% of total wild card trials, respectively, the subject is reinforced for responding to within-list items before responding to the novel item. Lists in which the wild card replaces the last item are also those on which the 3-, 4-, and 5-item groups perform at a comparable level. A similar within-list tendency has been found with human subjects (Stromer and Mackay 1993). This tendency would result in the same errors Terrace et al. (1995) suggest reflect an inability to position the wild card at the correct ordinal position. In summary, the wild card task may not be the best procedure with which to evaluate ordinal knowledge in pigeons.

To address this issue, Scarf and Colombo (2011) trained three pigeons on three 4-item



**Ordinality, Fig. 1** The performance of monkeys and pigeons on the 3- (top panel), 4- (middle panel), and 5-item (lower panel) wild card trials. The dashed line represents chance level of performance

lists (List 1, A1→B1→C1→D1; List 2, A2→B2→C2→D2; and List 3: A3→B3→C3→D3) and then presented them with maintained (e.g., A1→B2→C3→D1) or changed (e.g., A1→C2→B3→D1) lists. Scarf and Colombo’s (2011) pigeons not only performed significantly better on the maintained lists than the changed lists but also performed significantly above chance on their very first session on the maintained lists. These data suggest that similar to monkeys, pigeons also understand ordinality.

## Cross-References

► [Serial List Learning](#)

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## Organ Transplant

► [Xenotransplantation](#)

## Organization

► [Assemblage](#)

## Orgasm

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Unified definition of human orgasm is difficult: in spite of the intuitive individual recognition of the phenomenon, the research on orgasm has not converged on a broadly accepted definition. Rather, the definitions range from those focusing on the subjective sensation to the release of neural tension, or the bodily changes involved, such as muscular contractions (Mah and Binik 2001). This multitude of descriptions reveals the multifaceted, individually variable and thus highly subjective experience of human orgasm. For the purposes of this short description, we will delineate the orgasm here as a neuroendocrine event, alluding to the two main physiological signaling systems involved, i.e., the nervous and the hormonal, serving as the starting point. We will first focus on external description of male and female arousal and orgasm and its neurological and hormonal underpinnings, followed by its possible roles in the evolution. Finally we will briefly address some of the historical interpretations.

## Physiology of Human Orgasm

In both males and females, orgasm is preceded by the arousal stage, characterized by a rush of blood

into genitalia and triggered either by cognitive or tactile stimulation. In males, the rush of blood into penile corpus cavernosum, enabled by the relaxation of smooth muscles lining the blood vessel walls (see below), leads to penile erection. What is commonly addressed as ejaculation consists of two parts – the emission, during which the seminal fluid is collected in the prostatic part of the urethra, and the ejaculation from the penis. We equal here ejaculation with male orgasm, even though the field is not in complete agreement on this topic (Alexander et al. 1993). The fact that pathological disorders can affect each of these processes separately suggests that their regulation is at least to some extent distinct. Arousal, emission, and ejaculation are a complex coordinated interplay of several smooth muscles of the ducts connecting testes with urethra (epididymis and vas deferens), of the seminal vesicle, prostate, and several sphincters, which likely contribute to the pressure with which semen exits at ejaculation. Ejaculation also includes the involuntary action of striated pelvic muscle, anal sphincter, and perineal muscles. The trigger of ejaculation is likely not simply a matter of the degree of arousal; however, the actual mechanism is not understood so far. In females, the arousal and orgasm has traditionally been described in four stages: excitement, plateau, orgasm, and resolution (Masters et al. 1966). Plateau is the stage in which, similar to male arousal, blood flow into the genitalia is increased, leading to vaginal lubrication and vaginal dilation, as well as clitoral swelling. Clitoris is the female anatomical counterpart of penis and consists of external visible parts (glans and labia) and an appreciable internal portion (paired bulbs and crura with erectile corpora cavernosa; O'Connell et al. 2005; Puppo and Puppo 2015). Female orgasm similarly manifests itself as involuntary rhythmic muscle contractions of pelvis, uterus, and vagina as well as lower anus. As in males, also in females, it is not understood what underlies the transition from arousal to orgasm.

Some of the neurobiological mechanisms coordinating the above phenomena are known (reviewed in Komisaruk et al. 2006). Cranial and spinal nerves integrating parts of autonomous

(involuntary) and somatic nervous systems innervate genitalia. Most generally, it is thought that both parts of autonomous neural system are involved in control of sexual activity: the parasympathetic slow-acting system in arousal and the sympathetic quick-acting system in orgasm. The parasympathetic innervation of genitalia stems from cranial vagus (Komisaruk et al. 2004) and the sacral pelvic neural fibers, the later associated with pudendal spinal nerve (but see recent suggestion that the pelvic fibers may in fact be part of the sympathetic system; Espinosa-Medina et al. 2016). The established sympathetic innervation stems from the hypogastric plexus of lower abdomen, associated with lower lumbar spinal nerves. Neuroimaging studies of the brain during stimulation have shown activation of several brain regions. The somatosensory innervation of genitalia in both sexes maps to parts of medial cortex (Komisaruk et al. 2011), whereas the human orgasm itself has been shown to activate numerous additional brain regions. Mapping female and male orgasm (ejaculation) showed activity in the hypothalamic nuclei, cerebellum, preoptic area, bed nucleus of stria terminalis, amygdala, hippocampus, lower brainstem, and frontal cortex (Whipple and Komisaruk 2006; Georgiadis et al. 2007; Komisaruk and Whipple 2008; Komisaruk et al. 2011; Huynh et al. 2013). Thus at least to a great extent, male and female orgasm-associated brain circuits overlap. Interestingly, many of the same circuits have been also associated with male ejaculation in rodents indicating parts of homologous process across animal species (Baum and Everitt 1992) although there are also differences when compared to primates (Michael et al. 1999).

What we know about the neurotransmitters involved in signaling during arousal and orgasm is derived mainly from targeting of specific neurotransmitters to treat nervous conditions in other disease contexts, such as depression. Several drug classes have been shown to affect arousal and/or orgasm in humans. These include drugs that act directly on transmitter receptors, such as agonists of serotonin receptors or antagonists of inhibitory noradrenalin receptors, both of which enhance aspects of sexual behavior. Further, the use of drugs that inhibit degradation of transmitter in

the synapse, or inhibit its reuptake (e.g., SSRI), has indicated that serotonin and dopamine modifications significantly modulate sexual reaction and orgasm (Montejo-Gonzalez et al. 1997; Balon 2006; Higgins et al. 2010).

In addition to neural circuits in other brain regions, orgasmic activation of the hypothalamus also triggers a hormonal response of the pituitary. The pituitary is an endocrine gland, which functionally connects two signaling systems, the neural and the hormonal system. Its function is triggered by the neural signal to the brain, conveyed to pituitary either by direct neural connections (posterior pituitary) or by the signals secreted from the neurons to the hypothalamic vessel plexus, and transferred into pituitary by the blood (anterior pituitary). Orgasm triggers a surge of pituitary hormone secretion in humans, which is particularly pronounced in females (Exton et al. 1999, 2001). The strongest hormonal surge is that of prolactin; however, also a minor surge of oxytocin has been reported (Carmichael et al. 1987). The physiological significance of these surges is unknown. Because the long-term elevation of prolactin inhibits libido, the prolactin surge has been suggested to inhibit the promiscuous behavior in females (Kruger et al. 2002) after coitus. However, the fact that women (in contrast to men) lack refractory period after orgasm suggests that this explanation of the brief prolactin surge is unlikely (Bianchi-Demicheli and Ortigue 2007). An alternative suggestion is that the PRL peak is a remnant of evolutionarily older process that induces ovulation and therefore has had a reproductive function in the evolutionary past (see below). Indeed, prolactin peak is associated with normal ovulation in women (Vekemans et al. 1977; Braund et al. 1984). This will be discussed further in the section on evolution of orgasm. Mechanistically, the prolactin peak is likely a consequence of brief interruption of dopamine signaling in the hypothalamus, where dopamine constitutively inhibits prolactin secretion; thus, dopamine inhibition (e.g., due to transient increase in serotonin signaling) can account for the prolactin surge (Bianchi-Demicheli and Ortigue 2007). The existence of orgasm-associated surge of the second pituitary hormone,

oxytocin, has been variably reported (Kruger et al. 2003) and is likely rather due to projections of the separate neuronal signals from genitals and breast to the same brain region in hypothalamus (Cross and Wakerley 1977). The reproductive functional significance of oxytocin is likely found in causing the contraction of the myoepithelial cells in breast milk glands as well as in the reproductive tract, involved in milk ejection in the breast, and propagation of the egg cell (and, in labor, the fetus) through the reproductive tract. The social function that is often attributed to oxytocin is that of enhancing partner bonding, in analogy to what is observed in rodents (Carter 1992; Witt et al. 1992; Cho et al. 1999; Razzoli et al. 2003). However, the putative orgasm-associated surge reported for humans is not only variably detected, but very small (~1.3-fold change in female orgasm; Carmichael et al. 1987) compared to the experimental dosages in rodents (up to tenfold change in experimental settings showing effect on social behavior in rats; Witt et al. 1992). Given that oxytocin is suggested to reinforce future trust and sexual behavior also in humans, it is not clear whether orgasm (sex) contributes to this effect or whether it rather stems from other aspects of intimacy or relationship.

## Types of Female Orgasm

Whereas males perceive orgasm relatively uniformly, women report different types of orgasm associated with stimulation of different parts of genitalia (“vaginal,” “cervical,” vs. “clitoral” orgasm, Grafenberg spot). The innervation of genitalia mentioned above includes separate branches supplying parts of genitalia, and these all likely respond to stimulation. There is, in addition to spinal nerves, evidence for innervation independent of the spinal cord, which has been suggested to account for cervical orgasm (Sansone et al. 2002; Komisaruk and Sansone 2003; Komisaruk et al. 2004). Moreover, it is important to realize that the clitoris is an organ much larger than glans clitoris that is externally visible and extends internally dorsolateral, parallel to the urethra and also to the ventral vaginal wall (O’Connell et al. 2005;



Puppo and Puppo 2015). It is thus likely that vaginal penetration can achieve indirect stimulation of internal clitoral parts, leading to perception of the ventral vaginal side as “G-spot,” so-called after German physician Graefenberg (1950), who studied the role of urethra in female orgasm.

## Evolutionary Origin of Orgasm

To identify the evolutionary origin of any trait requires recognizing the corresponding trait in different species and then identifying the last common ancestor of the lineages in which the trait is present. Finding a corresponding trait of human orgasm is difficult, in part because research on orgasm has been primarily conducted in humans and primates, and therefore orgasm has been very narrowly characterized to capture human-specific characteristics, difficult to detect in other animals (Pfaus et al. 2016). For this reason, little is known about the presence, or the role, of corresponding traits across mammals. It is very unlikely that the physiological basis of orgasm has arisen only in human or primate lineage. However, it is likely that the trait has acquired human-specific modifications in human lineage.

It is useful here to focus separately on male and female orgasm for a moment. The orgasm in males is associated with ejaculation and sperm transfer and therefore crucial for reproduction. Prompt ejaculation of relatively large amount of sperm thus is generally assumed to be a sufficient explanation for the existence of orgasm-like impulse in species with internal fertilization. Indeed, erection and ejaculation are widely spread across animal kingdom, in particular in amniotes, that is, the reptiles and mammals.

In contrast to male orgasm, the human female orgasm is not required for reproduction, and in fact a high percentage of women do not experience orgasm during reproductive (penetrative) sex (Hite 1976; Lloyd 2005). To nevertheless explain its existence, various reproductive roles were suggested, by which the presence of female orgasm would still positively affect the number of offspring; ranging from mate choice (Alcock 1980; Puts et al. 2012), to bonding, to

enhancement of sperm transfer (Levin 2011a), to name a few. So far no evidence could be found for such effects of orgasm on reproductive fitness (Levin 2011b; Zietsch and Santtila 2013). However, whether the female orgasm presently has a (reproductive) function or not reveals little definitive about why it originated, as the function of a trait often changes during the trait’s evolution. An important critical review of existing theories of origination and maintenance, specifically of female orgasm, was published in 2005 by Elizabeth Lloyd (2005). Lloyd pointed out the difference between sexes in how closely reproductive sex is related to orgasm: whereas reproductive sex is effective in achieving orgasm in men, it is highly ineffective in women. This makes the explanations based on direct reproductive effect implausible. Lloyd systematically evaluated 21 theories based on the evidence their authors provided and rejected all but the *by-product* hypothesis (Symons 1979). This hypothesis states that the female orgasm is a side effect of male orgasm, meaning that it originated and is maintained (in spite of having no function), because the male counterpart is required for reproduction. To understand why female trait would be so dependent on male trait, it is useful to remember that the female clitoris is homologous to the male penis and therefore shares the very similar genetic basis. As this basis is passed sometimes to male and other times to female progeny, it becomes partially modified in the developmental context of particular sex to build either clitoris or penis. Whereas the adult morphology in males and females is different, not all the features of male and female physiology can be genetically decoupled, and physiology of orgasm could be one such feature. The necessity of orgasm in males is thus suggested to drive the origin and maintenance of the female orgasm.

In 2016, Pavlicev and Wagner proposed a new hypothesis for female orgasm (Pavlicev and Wagner 2016). The authors provided evidence that female orgasm may be a remnant of the neuroendocrine signal, which induces ovulation in some species. Ovarian cycles are spontaneous in women, meaning ovulation does not depend on environmental signals or the pheromones or

copulatory stimulation by a male, releasing a single egg cell periodically every ~28 days (ovulation). However, in many mammals, ovulation is not spontaneous but rather dependent on an external trigger, which is often tactile genital stimulation during copulation. These species are called induced ovulators and include many carnivores (cats, ferrets, etc.), camels, rabbits, etc. Pavlicev and Wagner suggested that the orgasmic neuroendocrine signal that triggers pituitary hormones in human female orgasm still carries a signature of the signal that triggers ovulation (via pituitary) in induced ovulators. Moreover, induced ovulation is phylogenetically older and thus may have been a predecessor of spontaneous ovulation. Many traits lose functions during evolution, but traces still stay around. Additional evidence is seen in female genital morphology: coincident with evolution of spontaneous ovulation, also the position of strongly orgasm-triggering glans clitoris has changed. In species, which require induction by copulation, the clitoris is positioned within copulatory canal where it gets directly stimulated, whereas in the species that ovulate spontaneously, the clitoris is removed from the copulatory canal. The latter at the same time may explain the rarity of female orgasm during reproductive (i.e., penetrative) sex.

## Historical Cornerstones of Research on Human Orgasm

The irregularity of female orgasm in particular has intrigued thinkers since the ancient times. Aristotle already has reflected on the question whether or not female orgasm is important for reproduction (reported in Leroi 2014). Early on, the female sexuality, including the lack of orgasm, has been strongly associated with psychological state, and the sexual massages were used as treatment for hysteria, *hysteria* standing for a very general description of female mental and behavioral disorders (psychosexual connotation is still reflected in *hysterectomy* for uterine removal). Particularly influential in this context up to the present day were the writings of Sigmund Freud, the Viennese founder of psychoanalysis. Freud in his work on

mental disorders laid great emphasis on the experiences during early development, as well as specifically on sexuality. With respect to female orgasm, he proposed a natural developmental succession from infantile clitoral to mature vaginal orgasm (Freud 1905). The grave consequence of this influential conceptualization was that the absence of vaginal orgasm during reproductive sex has become interpreted as a signature of mental immaturity, of women stuck in a childlike sexual state—quite overlooking that this is rather the norm than a deviation. One of the early remarkable woman sexologists was Marie Bonaparte (Bonaparte 1933). Herself a psychoanalyst, she opposed Freud's concept, proposing that glans clitoris remains the main source of mature female orgasm and that the lack of orgasm during reproductive sex is due to the lack of clitoral stimulation during penetrative sex, deriving from displacement of clitoris from the vagina, typical of human anatomy. In 1930s she collected over 200 individual measurements of the distance between vagina and clitoris and found a correlation between that distance and a decreased rate of copulatory orgasm (a dataset more recently re-evaluated by Wallen and Lloyd 2011). Best known empirical research on human sexuality and orgasm from the twentieth century is undoubtedly that by the zoologist Alfred Kinsey from Indiana University (Kinsey et al. 1948, 1953), followed by the rich work of William Masters and Virginia Johnson, at Washington University in St. Louis (Masters and Johnson 1960; Masters et al. 1966, 1974, 1993; Kolodny et al. 1979). An important contribution in particular in female sexuality came from Shere Hite. In a comprehensive review of female sexual experience, she first documented the high percentage of women that rarely or never experience orgasm in penetrative sex—thus considered dysfunctional in Freud's theory—however are perfectly able to do so in masturbation (Hite 1976). From the 1970s to 1990s, evolutionary theories of female orgasm were discussed by a wide variety of authors from the ethologist Desmond Morris (1967) to the behavioral biologist John Alcock (1980), to the paleontologist Steven J. Gould (1991). With the exception of the work of Symons, Gould, and

Lloyd, all attempts to explain the evolution of orgasm, discussed above, have been adaptationist, meaning that they attempt to explain the origin of female orgasm by its assumed current utility in humans (Wagner and Pavlicev 2016). This debate was synthesized in the influential book by Elisabeth Lloyd (2005). Finally, major contributions to the current knowledge of the physiology of female orgasm were made starting in the 1990s by Barry Komisaruk and collaborators.

## Cross-References

- ▶ Amygdala
- ▶ Arousal
- ▶ Evolution
- ▶ Evolutionary By-product
- ▶ Morphology
- ▶ Neurotransmitters
- ▶ Oxytocin
- ▶ Pheromone
- ▶ Phylogeny
- ▶ Pituitary Gland
- ▶ Upsuck Hypothesis

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## Orientation

- [Cetacean Navigation](#)
- [Chondrichthyes Navigation](#)

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## Origin of Species

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## Synonyms

*On the Origin of Species; The Origin of Species*

## Definition

*On the Origin of Species, The Origin of Species, or On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* is a book published in 1859 by English naturalist, biologist, and geologist Charles Darwin.

## Introduction

*On the Origin of Species* is a scientific book considered to be the first structured introduction to modern evolutionary biology. It popularized the process of evolution by natural selection. Much of the data inspiring and supporting Darwin's theory was collected during his voyages to the coast of South America (including Galápagos), Australia, and South Africa

(Desmond and Moore 1991). At the point of publishing the book, support for evolutionary ideas was already growing in the field of biology both in academic and public settings, and an evolutionary framework was used to explain novel biological findings. However, due to the close relationship the English academia had with the conservative Church of England, nontheological explanations were perceived as controversial because they claimed that humans are not unique or superior to other living organisms, and, therefore, it took several dozen years for the ideas described by Darwin to be widely accepted in academia.

One of the reasons for the popularity of *On the Origin of Species* was the fact that, despite describing complicated biological processes, it targeted readers who were not professional biologists. The book was written in a way that was both scientifically insightful and also relatively easy to read. Darwin was familiar with the scientific literature of the time, and he was able to compose the book in an engaging style. Darwin was a known scientist, and his ideas were used as strong supportive evidence of scientific naturalism by biologist and anatomist Thomas Henry Huxley, who promoted secularization of science. Approval of Darwin's and Huxley's ideas was not immediate; it took some decades before the theory of evolution by natural selection was accepted and approved by the majority of academia. The acceptance of evolution by natural selection as a unifying concept for all the life sciences was sealed around the middle of the twentieth century by the emergence of the extended evolutionary synthesis, which highlights the importance of two unifying concepts of an evolutionary approach to biology – reciprocal causation and constructive development.

## History of Evolutionary Thought

Before the presentation of Darwin's ideas, the main framework for understanding life was natural theology, which was based on a literal interpretation of the Bible according to which all species were perceived as God-made in their final form. Even Carl Linnaeus's taxonomy



considered species to be in their ultimate form. That understanding of life stood in opposition to a view favoring progressive, gradual development of species from their ancestral forms. The idea of transformism (transmutation of species) was popularized at the end of the eighteenth century by Erasmus Darwin, a grandfather of Charles Darwin, and then, at the beginning of the nineteenth century, further developed by Jean-Baptiste Lamarck. Lamarck introduced the process later called Lamarckism and explained that organisms are progressively transforming towards greater complexity. However, at that point, English scientists were still often Church of England clergymen, and, therefore, the abovementioned processes were construed as designed and executed by God (Bowler 2003).

Charles Darwin was exposed to Lamarckism from the early years of his childhood. He attended a school run by a preacher and then, in 1818, joined the Anglican Shrewsbury School (Desmond and Moore 1991). In 1825 he went to the Edinburgh University and studied medicine. In 1826, he abandoned his medical studies and, for 4 months, assisted Robert Grant's empirical research on marine invertebrates (Browne 1995). Then, he went to Cambridge University. Under the supervision of the botanist John Henslow, Darwin started studying science in a natural theology framework, and with the geologist Adam Sedgwick, he pursued the ideas of catastrophist geology, which understood transformation as a process of adapting to repeated worldwide catastrophes, such as the biblical flood (Bowler 2003; Browne 1995). An important event in Darwin's life was the expedition aboard the *Beagle* that he joined as a geologist and naturalist at the end of 1831. Reading the *Principles of Geology* by Charles Lyell and discovering fossils of *Glyptodon* (then considered extinct gigantic armadillos), Darwin understood that there is no gap between animals and humans and started to suspect that species might not be "fixed" and "final" (Bowler 2003; Keynes 2000; Larson 2004).

After returning to England, Darwin further analyzed empirical data from both living animals and fossils of extinct species and, by drawing conceptual evolutionary trees, started to drop

Lamarck's ideas about independent species transforming into their advanced forms and formed an idea about species evolving from a common ancestor. After seeing an orangutan, he acknowledged its similarity to humans (Desmond and Moore 1991). After comparing methods of professional breeders with the natural processes of specialization he observed, he became aware of the similarities between these phenomena. Then, while continuing his work, exchanging letters, and corresponding with scientists such as Joseph Hooker and Herbert Spencer, he began to write down and soon published his findings. By 1856, his theory of evolution by natural selection was almost fully formed.

Another English biologist, naturalist, anthropologist, geographer, and explorer, Alfred Russel Wallace, came to similar conclusions as Darwin and in 1855, published a paper with a theory that all species developed from closely related species (Wallace 1855). However, Darwin decided not to discuss his findings with Wallace and instead decided to work on his own project instead and in 1856 began formulating the first draft of a book (Quammen 2006). During the process of writing a book, Wallace sent Darwin a draft of his description of a process similar to the one described by Darwin; the difference was mainly due to Darwin perceiving the newly discovered process as similar to the one used by breeders and focused on competition, whereas Wallace placed emphasis on ecological pressures and described processes similar to the process nowadays called group selection. By arrangement of Darwin's friends and colleagues, and in order to preserve Darwin's precedent, a paper co-authored by Darwin and Wallace was read at a London scientific meeting, titled *On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection* (Bowler 2003; Darwin & Wallace 1858; Larson 2004; Quammen 2006). Neither Darwin nor Wallace was present, and this first public presentation of evolution by natural selection did not generate much interest or discussion.

In 1859, Darwin reached out to ask John Murray whether he would be interested in publishing his book, which he planned to title

*An Abstract of an Essay on the Origin of Species and Varieties Through Natural Selection*. Murray agreed, but after some discussions, they decided to modify the title; Darwin hoped the new title would include *Through Natural Selection or the preservation of Favoured Races* (Desmond and Moore 1991). An early draft of the book was entitled *On the Mutability of Species*. The title kept changing; the next version was *An Essay on the Origin of Species and Varieties*, then *An Essay on the Origin of Species*, and finally, with Murray's encouragement, the title became *On the Origin of Species*, with the subtitle *by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. The book with the final title was published on the 24th of November 1859. The book sold out quickly, so a second edition with corrections was soon published. Twelve years after the *On the Origin of Species* was published, George Mivart published a book called *On the Genesis of Species* in which he contested Darwin's ideas. The sixth edition of *Origin* – and the last one published during Darwin's lifetime – included an additional chapter addressing Mivart's opinions. In addition, in the sixth edition, the term "evolution" was used for the first time, and the title was changed to the simpler *The Origin of Species* (Darwin 1859). The book was published in several other countries, but some translations were inaccurate, often because the translators subverted the content of the book to support their own beliefs. That happened, for example, with the first German translation. While Darwin was still alive, his book was translated to German, Swedish, Danish, Polish, Hungarian, Spanish, and Serbian (Freeman 1977).

## Content of the Book

The main revolutionary message described in *On the Origin of Species* was that, in contrast to what was previously believed and accepted by learned peoples and the public, species did not appear as separate from each other and in their final, God-given form. Instead, they were changing from previous forms because of the process of *natural*

*selection*. Darwin first explained evolution by comparing it to artificial selection in animals and plants and then provided evidence from various disciplines that evolution is indeed happening (Darwin 1859).

The content of *On the Origin of Species* differs slightly depending on the edition of the book. The title page and introduction consist of quotes by several prominent thinkers. Darwin also mentions Wallace and highlights that he came to the same conclusions as the one presented in the book. In the third edition and beyond, Darwin provided a brief history of the development of the idea of evolution. In the book, Darwin explains the idea of variation under nature and domestication. He describes the process of breeding plants and animals, both in modern times and in the past, and introduces the idea of selective breeding, using the example of pigeons. Then he further clarifies how vague the distinction between varieties and species is and highlights how much variability there is in nature. He explains his concept of *natural selection*, or *the survival of the fittest*, and how a feature that is profitable will tend to be preserved and passed to offspring and therefore will become more frequent in the population. He draws the analogy with selective breeding that it sharpens the feature that is preferred by a breeder. He proposes the idea of competition-driven sexual selection to explain features that are sexually dimorphic. He highlights the complexity of adaptations and provides the first draft of an evolution-based taxonomy in a form of a "tree." He provides details about his ideas of heredity and variation, but at the point of writing the book, the field of genetics was not yet developed, and, therefore, Darwin did not understand how heritability works. Darwin also explained the idea of common descent and how, in sexually reproducing species, offspring express features of both their father and mother (Darwin 1859).

Darwin addresses possible problems with the theory, including that there often is no evidence for the existence of forms between two species. He did, however, present examples with

intermediate structures, e.g., flying lemurs or flying squirrels, explaining that they may share features of transitional forms of other flying mammals, such as bats. He also observed the unique behavior of honeybees constructing hexagonal cells, implying they must have evolved from bees making round cells, but the behavior of building hexagonal cells evolved to conserve space for honey. He also observed that hybrids of two different species occasionally are fertile, challenging the natural theological claim that hybrids are infertile by God's design (Darwin 1859).

In later editions of the book, Darwin added another section in which he addresses criticisms. Critics argued that some adaptations could not have appeared because of natural selection because they do not seem to have any adaptive purpose. Darwin replied that some features might either be by-products of the evolution of other features or adaptations we do not yet understand.

Darwin includes chapters addressing the geological record. He points out that many forms of fossils seem to appear suddenly. However, he argues fossils are relatively rare, and therefore the available fossils do not accurately reflect the past variability of species. Darwin was sure that, as geology progressed, more data would be collected and analyses that are more detailed would become possible. He also anticipated that changes happen at different paces, depending on how quickly the environment changes. Some species evolve more quickly, and some remain the same for a longer time. In the final sections of the book, he writes about geographic distribution of plants and animals. He points out that, despite environmental similarities between various geographical locations, fauna and flora differ between locations, e.g., in warm regions of Australia, Africa, and South America. He realized that migration barriers were important to explain the distribution of species on different sides of these barriers (e.g., mountains). He explains his thoughts about taxonomy and the way species are classified. Finally, in the last section, he reviews previous assumptions and highlights that he anticipates that evolution by natural selection will revolutionize biology (Darwin 1859).

## Reception of *On the Origin of Species*

Due to the fact that the book did not only have revolutionary biological, anatomical, and morphological assumptions, but also indirect implications standing in opposition to religion, it caused vigorous debates. There was massive resistance against the idea of evolution by natural selection. Some scientists, such as Joseph Hooker, Asa Gray, Thomas Huxley, Ernst Haeckel, and Henry Bates, supported the idea, but the resistance of some biologists was caused by the fact that they did not understand the idea, e.g., despite Darwin's arguments, they still believed that evolution is progressive and purposeful. Resistance among other readers was associated with the fact that accepting Darwin's idea might lead to social reformation; also, it was often the case that understanding of Darwinian ideas was superficial. There were many scientists in the field of biology that did not agree with Darwin's ideas, e.g., Richard Owen, British anatomist, perceived the gradual changes as a process that was caused by God or George Campbell, the Duke of Argyll, who argued that specific features of animals were designed by a Creator. Despite the fact that Darwin did not explicitly mention that humans also shared ancestry with all other species (and he did not do so until 1871 when he published his book, *The Descent of Man, and Selection in Relation to Sex*), heavy hints were dropped, and the idea could have been indirectly concluded from the rest of the text. The first widely popularized attempt to place humans on the phylogenetic tree belonged to Huxley, who, in 1858, noted similarities between the anatomy of apes and humans. Outside of England, evolutionary ideas faced similar challenges. As time progressed, more and more scientists were convinced and accepted evolution by natural selection as the explanation for all life (Bowler 2003).

Even the scientists that agreed with Darwin's ideas were sometimes skeptical or dubious about some of the processes he described. Carl Nägeli raised a concern that features that do not provide any adaptive benefit could not be retained by natural selection. Mivart agreed with Darwin that such features could have been linked with features

that were adaptive but then later criticized natural selection and supported the idea of “directed” evolution; his arguments were addressed by Darwin in later editions of *On the Origin of Species* (Bowler 2003; Mivart 1871).

Another wave of criticism came from readers alerted that the idea of evolution by natural selection supported secularism. Although Darwin did not explicitly discuss the origin of humans, the content of the book indirectly placed humans among animals, which was not in line with accepted dogma of religion. Evolution and recent findings in geology regarding the age of the Earth posed a direct threat to the standard biblical creationist view. Even those agreeing with Darwin often assumed natural selection is a mechanism directed by the Creator. To placate these critics, in the second edition of the book, Darwin added the phrase “by the Creator” to the sentence “Life, with its several powers, having been originally breathed [by the Creator] into a few forms or into one. . .” Despite taking that step, the book’s content deviated from established thinking of the time, and its implications irrevocably shifted the bounds of popular conversations, causing debates about issues regarding the origin of humans, the human soul, and spirituality, in general, that in some forms continue to this day (Bowler 2003; Larson 2004).

## Conclusion

*On the Origin of Species* authored by Charles Darwin argues that all species evolve by the natural selection of inherited, small variations increasing the individual’s ability to survive, compete, and reproduce. The data from Darwin’s notebooks, including the very early ones, suggests he perceived evolution as a process that links biological findings together, making it possible to understand life, and included humans in biological model of flora and fauna. In the conclusion of his book, he highlighted that evolution will be a foundation for other sciences, such as psychology and natural history. He was right; *On the Origin of Species* is widely considered the most innovative contribution to modern science, and Darwin himself is considered one of the most influential

individuals in the history of science. The book is centrally important in pursuing both scientific and humanist ideas.

## Cross-References

- [Adaptation](#)
- [Charles Robert Darwin](#)
- [Domestication](#)
- [Erasmus Darwin](#)
- [Evolution](#)
- [Evolutionary By-product](#)
- [Herbert Spencer](#)
- [Heredity](#)
- [Hybrid](#)
- [Jean Baptiste Lamarck](#)
- [Natural Selection](#)
- [Sexual Dimorphism](#)
- [Sexual Selection](#)

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## Ornamentation

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### Definition

A trait used to attract the opposite sex during mate choice.

### Introduction

Many animals exhibit conspicuous characteristics such as brightly colored body regions or exaggerated physical structures. When these traits function during mate choice to increase the likelihood of their bearer attracting a mate, they are referred to as ornaments. The quintessential example of an ornament is the peacock's tail: consisting of bright colors and patterns, and enlarged far beyond the relatively small tails of peahens, peacocks' tails are presented to females during mating displays. Peahens then accept or reject a male based in part on his tail characteristics (Petrie et al. 1991). Ornaments are often sexually dimorphic, with one sex ornamented and the other not, but mutual ornamentation is also observed (Andersson 1994).

Ornamentation is linked to reproductive success, with individuals that display more elaborate ornaments enjoying a selective advantage. Ornamentations are therefore defined not based on appearance but on function, and conspicuous traits are only considered ornaments when they have been shown to influence mate choice. The term ornamentation has generally been used to refer to visual characteristics such as colorful or elaborated body regions, and some authors explicitly define ornamentation as a morphological trait. However, other types of ornaments have also been reported, such as those that involve smell, vocalizations, or electric pulses, and ornaments can also be multi-modal (e.g., both visual and acoustic). This entry therefore defines ornaments as any traits that are used to attract the opposite sex during mate choice.

## Sexual Selection Dynamics

The extraordinary appearance of conspicuous traits such as the peacock's tail puzzled early biologists because such traits would seemingly make their bearer more vulnerable to predators. To explain the evolution of these ostentatious characteristics, Charles Darwin (1871) developed the theory of sexual selection, which posits that such traits can evolve when they increase individuals' reproductive success. Darwin separated sexually selected traits into two categories based on their function: armaments – such as large antlers or canines – facilitate competition with same-sex individuals for access to mating opportunities (via ► [Intersexual Selection](#), this volume), and ornaments aid in attracting mates of the opposite sex (via ► [Intersexual Selection](#), this volume). Ornamentation therefore results from a competitive regime in which mating decisions are influenced by characteristics of the opposite sex. Individuals with more impressive characteristics will be chosen more often and will therefore enjoy higher reproductive success, leading to an exaggeration of these traits over evolutionary time. Thus, the peacock's tail becomes more elaborate over time because this is linked to higher fitness. While ornaments by definition result from mate choice, it is important to note that intrasexual competition and intersexual mate choice can both support and oppose one another; therefore, a trait can be influenced by both selective processes simultaneously.

Many species are sexually dimorphic, with differential expression of traits like degree of ornamentation between sexes (Andersson 1994). Sexual selection acts on both sexes; however, the strength of selection is dependent upon which sex is the limiting resource in reproduction (see ► [“Parental Investment”](#), this volume). In many animals, females invest more in offspring and therefore tend to also be choosier in selecting mates. This generates a competitive regime in which males often compete for access to females and are therefore subject to stronger intersexual selection for attractiveness to potential mates. This results in males that are more ornamented relative to females. In ► [sex role reversed species](#)



(this volume) in which females tend to compete for access to males, this trend reverses and females are the more ornamented sex (Andersson 1994). This tendency for differential ornamentation is relative, however, and research is increasingly showing that there is scope for male choosiness and female ornamentation across species (Clutton-Brock 2007).

## Selective Advantages and the Evolution of Ornaments

Why are ornaments attractive to members of the opposite sex? The selective advantage and evolution of ornamentation has been a hotly debated and researched topic in evolutionary biology since Darwin's time, and several hypotheses have been presented on the topic (reviewed by Andersson and Simmons 2006).

Some hypotheses are based on nonadaptive mate choice and posit that the expression of ornaments is not linked to any adaptive trait in the individuals expressing them. Rather, they are meaningful only in a mating context. For instance, the sensory bias hypothesis (Ryan 1998) suggests that ornaments evolve because they exploit sensory-response systems in other behavioral domains, such as foraging. A species that forages on red fruit, for example, may have evolved a preference for red, and a red ornament could "piggy back" on this preference. Another commonly cited hypothesis is ► [runaway selection](#) (this volume), which predicts that ornaments evolve when an originally adaptive trait and a related mating preference are exaggerated via a self-reinforcing positive feedback loop. The mating preference (often considered to arise from a sensory bias) is initially selected for because it leads to offspring that tend to have more adaptive trait values. The runaway process then takes over, with the ornament and the mating preference both increasing proportionally, and often becoming genetically linked such that they are inherited together. Because each yields a mating benefit (i.e., attracting mates via the ornament or producing offspring with ornaments that are attractive to mates), both remain under positive selection. In

this way, the ornament becomes far more exaggerated than would be adaptive in a nonmating context. At some point, the costs of the ornament match any mating benefits, and the trait and preference stabilize. Runaway selection models are difficult to test empirically, but remain good candidates for the evolution of particularly elaborate ornaments.

Other hypotheses for the evolution of ornamentation focus on mate choice associated with adaptive traits. Closely tied to research involving signal honesty, these hypotheses focus on ornaments as signals of individual quality, with more elaborate ornaments indicating a higher quality mate. The underlying quality that is signaled can be of varying types. For instance, more elaborate ornaments may be associated with mates that provide direct benefits to the chooser, such as access to a high quality territory or absence of transmissible disease. Alternatively, the good genes hypothesis (this volume) suggests that ornaments evolve because they are associated with advantageous characteristics that are heritable (i.e., indirect benefits), such as good foraging skills or a strong immune system. The good genes hypothesis has been of particular interest to biologists because many species lack bi-parental investment, and therefore genetic contributions to offspring are often the only adaptive explanations for ornamentation. However, this hypothesis is theoretically problematic because mate choice based on a heritable trait should reduce associated genetic variability across generations (i.e., because many individuals are choosing the same mates), which would in turn lead to reduced selection on mating preferences. This contradiction is known as the lek paradox (Kirkpatrick and Ryan 1991). Many solutions to the lek paradox have been proposed, which mostly involve identifying mechanisms that can maintain variability in the face of mate choice and positive selection. These include solutions based on environmental change, mutation rates, and parasite co-evolution. A popular model is the genetic capture model (Rowe and Houle 1996), which suggests that ornaments linked to individual condition are influenced by many genetic loci, and this large target for selection helps to maintain variability.

Alternatively, trade-offs between selective pressures may maintain trait variability, such as opposing selective pressure from natural and sexual selection, or when a trait is beneficial for one sex but detrimental to the other. New work analyzing the genetic underpinnings of ornaments has helped to further clarify the ways in which trait variability can be maintained in the face of mating preferences (e.g., Johnston et al. 2013).

It is important to note that many proposed hypotheses for the evolution of ornamentation are not mutually exclusive. Different explanations are often supported by different biological systems, and given the diversity of ornaments observed in nature, it seems likely that they have evolved via a variety of mechanisms across the animal kingdom.

## Signal Honesty and the Costs of Ornamentation

A major question associated with adaptive explanations for ornament evolution is that of signal honesty (► [“Honest Signaling”](#), this volume). Many ornaments are condition dependent, with the strength of the ornament associated with individual quality, such that the ornament can be used as a proxy for individual characteristics (Andersson 1994). So what prevents cheaters from engaging in false advertising? In some cases, a signal is directly linked to some physical characteristic that cannot be faked; such signals are referred to as indices. For example, the tones of some acoustic calls are inherently linked to body size. Not all signals follow this pattern, however, so other explanations must be sought. Much of the research in this area has focused on ornaments as “handicaps,” which are costly to maintain and therefore more elaborate versions can only be produced by individuals in good condition. Emphasis is often placed on the physiological (e.g., energetic) costs of ornamentation, and from this perspective a particularly elaborate ornament can only be produced by an individual who has characteristics like strong foraging skills or a good immune system (► [“Handicap Hypothesis”](#), this volume). However, the overall costs

associated with producing an ornament are not actually very relevant to the maintenance of signal honesty, and the handicap hypothesis is neither necessary nor sufficient to explain many ornaments (Számádó 2011). Instead of focusing on the costs to each individual of producing their own signal, it is more useful to assess the cost differentials in ornament production. Honest signaling can be maintained when low quality individuals face higher costs to producing high quality ornaments compared to high quality individuals. Punishment of cheaters (e.g., via physical attack) is one such mechanism, although many others have been proposed (Számádó 2011). Ultimately, ornament quality is influenced by a variety of costs and benefits, not all of which are the same for all individuals within a species; in many cases, this can lead to an honest system where ornaments are generally indicative of some underlying individual quality.

## Conclusion

Ornaments are often conspicuous traits that would seemingly be costly in terms of avoiding predators, and as such have been of interest to biologists since the origin of evolutionary thinking. Indeed, such characteristics helped to provide the impetus for Darwin to develop his theory of sexual selection. Much of the research on ornamentation has focused on identifying ornaments across species via mate choice experiments, isolating the mechanisms by which ornaments can evolve, and identifying if and how ornaments can function as honest indicators of individual quality. In studying ornaments, biologists have learned about the nature of evolution and have helped to explain the existence of some of the most impressive phenotypes in the animal kingdom.

## Cross-References

- [Charles Darwin](#)
- [Female Choice](#)
- [Handicap Hypothesis](#)
- [Honest Signaling](#)

- [Intersexual Selection](#)
- [Secondary Sex Characteristics](#)
- [Self-Decoration in Dolphins](#)
- [Sexual Selection](#)

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includes the plated and spiked stegosaurs; the armored, spiked, and sometimes club-tailed ankylosaurs; the massive duckbilled hadrosaurian ornithopods; the thickly dome-headed pachycephalosaurs; the elaborately horned and frilled ceratopsians; and all of their respective basal relatives. Distinguishing features used to characterize ornithischians among other dinosaurs include a unique, midline jaw bone known as the prementary (forming the bottom half of the beak), a medially inset tooth row in most cases, and a caudally oriented pubis (a hip bone), among many others (Weishampel 2004).

With fossilized skeletal remains being the only glimpse into dinosaur biology, researchers use many different clues in skeletal morphology, brain endocast morphology (see below), footprints, dental wear patterns, and pathologies, among others, to speculate various aspects of their past behavior and cognitive abilities. Without the direct knowledge given by observational research and experimentation of live animals, speculation of ornithischian dinosaur behavior among many researchers is subject to countless debates regarding all of its attributes. In terms of intelligence and cognitive ability, it is quite clear that a majority, if not all, of ornithischians were largely unintelligent creatures based on relative brain size (see below). Discussions then usually resort to the question of how intelligent the dinosaurs were relative to each other and how would they use that certain amount of intelligence to perform based on instinct, to function properly, to evade predators, and possibly to communicate with one another in a herd setting (Hopson 1977).

## Ornithischia

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## Introduction

Ornithischian dinosaurs (Fig. 1) form an extinct group of diverse megaherbivores that dominated the Mesozoic Era roughly between 200 million and 66 million years ago. This extensive clade

## Brain Endocasts and Encephalization Quotient (EQ)

Due to the overall lack of actual dinosaur brains in the fossil record, researchers have relied on brain endocasts (i.e., endocranial brain cavity) to form a general understanding of brain morphology to, in turn, speculate on cognition and behavior. Because an endocast is an outer molding of a combination of the brain and all of the tissues



**Ornithischia, Fig. 1** Fossil skeletons of various ornithischian dinosaurs portraying distinguishing features. (a), *Stegosaurus* (a stegosaur) in oblique caudal view portraying four large tail spikes and plates along its back; (b), *Edmontonia* (a nodosaurid ankylosaur) in oblique rostral view portraying extensive body armor and large spikes protruding rostrolaterally; (c), *Parasaurolophus*

(a lambeosaurine hadrosaur) cast skeleton in oblique rostral portraying long, tubular crest used in enhanced vocalization; (d), *Pachycephalosaurus* (a pachycephalosaur) cranium in lateral view portraying large dome-shaped skull roof; (e), *Triceratops* (a ceratopsid ceratopsian) in oblique rostral view portraying large brow and nose horns as well as its large neck frill extending from its



that surround it (i.e., neural tissues [such as meninges], vasculature, etc.), it is not indicative of the absolute morphology of the brain itself (Edinger 1929). Also, due to the variation in the relationship between brain tissue size and endocast size, estimates of brain size can range anywhere between 50% and 95% in dinosaurs (Buchholtz 2012). With this in mind, comparative methods with living animals, either closely or distantly related, are used to make such inferences.

Regardless of the well-known setbacks, the morphology of the endocast is still greatly useful in predicting overall size and shape as well as more localized morphologies of individual anatomical features of the brain. Until recently, endocast studies have relied primarily on moldings and descriptions of cranial specimens that are broken such that the endocast is easily visible. Now, with the help of technological advances in computed tomography (CT) scanning, many are able to describe internal anatomy of dinosaur endocasts with digital volumetric data. For example, the variable relative sizes of the olfactory bulbs in the forebrain give indications of the degree of the sense of smell in these animals.

The primary method of speculation of ornithischian behavior with the use of endocasts is that of the encephalization quotient (EQ) (Jerison 1973; Hopson 1977; Buchholtz 2012). The EQ uses a regression of the relationship between brain size and body size to infer levels of cognitive function across animals of different clades relative to one another. Hopson (1977) performed the most extensive study of EQs across Dinosauria and interpreted a great deal regarding relative dinosaur intelligence. As dinosaurs are a member of the clade Archosauria, Hopson (1977) compares them to other archosaurs that are alive today, such as crocodilians and birds, as well as with mammals, to see comparatively where dinosaurs

are situated. In these analyses, larger brain sizes in dinosaurs ( $>1.0$ ) relative to body size are typically thought of as a proxy for a more advanced and complex cognitive ability and behavioral spectrum (Buchholtz 2012). Some of Hopson's (1977) results are used in the descriptions of EQs in various ornithischian clades below. With these studies, it is imperative to also be mindful of relative sizes of different regions of the brain as well, as these can also have an effect on the overall EQ.

## Functional Morphology

Studies in functional morphology of ornithischian dinosaurs also provide a great deal of insight into plausible behaviors among them. For instance, the diverse rounded-to-spade-shaped, denticulate, and often precisely occluding dentition of ornithischian dinosaurs has greatly informed paleontologists and functional anatomists of their past feeding behavior. In accordance with their morphological diversity, macro- and microscopic dental wear patterns have provided direct evidence of true feeding motions of the lower jaw during feeding, including orthal (i.e., dorsoventral, or up-and-down, jaw motion), palinal motion (i.e., caudally oriented, or backward, jaw motion while teeth are occluded), and long-axis rotation of each side of the jaw at the prementary joint (Mallon and Anderson 2014; Nabavizadeh and Weishampel 2016). These feeding motions vary both between and among clades of Ornithischia, and each gives a paleoecological context of the animals' respective time periods (Nabavizadeh 2016). Coprolites (i.e., fossilized dung) have also been used to assess plant material consumed by these animals (Chin 2012).

In addition to feeding mechanics, major evolutionary transitions in locomotive behavior have



**Ornithischia, Fig. 1** (continued) skull. Photographs of specimens were taken by the author at the American Museum of Natural History in New York City, New York (*Tegosaururus*, *Edmontonia*, *Pachycephalosaurus*,

*Triceratops*), and the University of Kansas Natural History Museum in Lawrence, Kansas (*Parasaurolophus*, which is a cast of a specimen at the Royal Ontario Museum in Toronto, Canada)



been described throughout the ornithischian clade as well. Convergent transitions from bipedality to quadrupedality have been described in all major subclades of Ornithischia, and numerous studies have explored the biomechanical nature of these transitions within each group, both with computer modeling (Maidment et al. 2014) and from fossil footprints or tracks. Track sites provide direct evidence of locomotive behavior, as it provides a true account of patterns in movements made by these animals (Farlow et al. 2012). This includes transitions from walking to running behaviors as well as sociality, such as that seen in ornithopod track sites.

Furthermore, distinctive and vibrant anatomical ornamentations adorning the external morphology of many ornithischian groups are also clear indicators of certain behavioral traits, specifically that of weaponry and defense used in intra-specific or interspecific combat (such as in defense against predators). Other external features could have been utilized for communication and display purposes, some of which may have been sexually selected. There has also been much broader speculation into various other plausible behaviors as well, such as those of breeding strategies (Isles 2010) and herd behaviors (Bakker 1986); although, these speculations mostly lack the evidence to support them. Many of the anatomical characteristics are noted in the descriptions of the diverse ornithischian dinosaurs below.

## Ornithischian Evolution

Ornithischians appeared roughly 200 million years ago and diversified rapidly throughout the Jurassic and Cretaceous Periods until their extinction 66 million years ago, at the end of the Mesozoic Era. Among the earliest forms were relatively small, bipedal animals that are believed to have already transitioned to at least a partially, if not fully, herbivorous diet. The basal-most major clade was Heterodontosauridae, which includes genera like *Heterodontosaurus* with specialized skull characteristics, including heterodont dentition (i.e., teeth that differ in shape along the tooth row) with a sharp caniniform tooth on each side

that has been speculated to have possibly been a weapon (Hopson 1977; Farke 2014). Along the ornithischian clade, body-type diversity differentiated, with forms such as the larger thescelosaurines, including *Thescelosaurus*, as well as the two major neornithischian clades, Ornithopoda and Marginocephalia (Boyd 2015).

Ornithopods initially conserved the basal ornithischian morphotype, with small, bipedal herbivores, such as *Hypsilophodon*. As the clade continued to diversify, however, they grew to be much larger, with many of them transitioning into partial or full quadrupedality. Iguanodontians were the major clade of ornithopods that gave rise to the well-known duckbilled hadrosaurs. Early iguanodontians included genera such as *Dryosaurus*, *Tenontosaurus*, and *Iguanodon*, each, respectively, larger than the previous. *Iguanodon* was first described by Mantell (1825) and was the first ornithischian to have ever been described. The duckbilled Hadrosauridae are divided into two major clades: the hollow-crested Lambeosaurinae (including such genera as the tube-crested *Parasaurolophus* as well as the round-crested *Lambeosaurus* and *Corythosaurus*) and the Saurolophinae (including such genera as *Prosaurolophus*, *Edmontosaurus*, *Maiasaura*, and *Gryposaurus*) (Prieto-Marquez 2010). Hadrosaurids included some of the largest ornithischian dinosaurs, some reaching over 40 or even 50 ft long, which would have likely been beneficial in lieu of any major anatomical weaponry when confronted with predators.

Marginocephalia is divided into two major clades. The first of these clades is the dome-headed Pachycephalosauria, which included such bipedal forms as the small *Stegoceras* and the much larger *Pachycephalosaurus*. Pachycephalosaurs possessed greatly thickened and vascularized skull roofs, which debatably might have been used for flank-butting (see below). The other much more diverse clade is the horned and frilled Ceratopsia. Ceratopsians ranged from very small, dog-sized beaked animals, such as *Psittacosaurus*, to moderately larger members with large frilled caudal margin of the skull, such as *Protoceratops* and *Leptoceratops*, to the much larger-bodied and highly derived

Ceratopsidae, divided into the Centrosaurinae (including such genera as *Centrosaurus*, *Styracosaurus*, and *Pachyrhinosaurus*) and the primarily longer-frilled Chasmosaurinae (including such genera as *Chasmosaurus*, *Pentaceratops*, and the most well-known ceratopsid, *Triceratops*).

The diverse groups mentioned above also each present many signs of diverse behaviors and cognitive functions that are specific to individual taxa as well as groups as a whole, and these are described below.

## Stegosauria

Stegosaurs (Fig. 1a), which include the well-known *Stegosaurus*, are Jurassic large-bodied, quadrupedal animals known primarily for their prominent, diamond-shaped plates and sharp, elongate spikes protruding from their backs, tails, and, in some cases, shoulders (e.g., *Kentrosaurus*). They were primarily graviportal animals (i.e., bearing a large amount of weight on thick legs), walking low to the ground and likely foraging on low plant material. A possible exception to this is *Miragaia*, possessing a much longer neck than other stegosaurs, which could have been used in reaching upward for plants. Previous speculation has stated the possibility of frequent upright posture for reaching higher vegetation; however, this has largely been argued against. Stegosaurs are thought to have exhibited a primarily orthal feeding mechanism (Barrett 2001) with possible slight rotation of the jaws at the predentary-dentary joint (Nabavizadeh and Weishampel 2016).

The flat, variably sized plates are large bones known as osteoderms (i.e., bones formed within the skin). These plates have been subject to extensive speculation as to their primary function and even their true arrangement along the midline of the spine. Because of their thin, almost sheetlike morphology, stegosaur plates are not believed to be used as any sort of defensive structure, as it is not suitable for forceful impacts of any kind. Researchers have suggested the plates to have possibly functioned for thermoregulation, due to

the presence of thin grooves along the plates indicating extensive vasculature. Others have challenged this assertion, however, arguing that the variable nature of plate morphology would not be suitable for thermoregulation and that the vasculature is merely indicative of growth of the plates. The plates have instead been suggested to have played a major role in visual display, given their prominence; however, this is also mere speculation.

The spikes projecting from the tails as well as backs and shoulders of stegosaurs are well accepted as having been used in combat. In fact, direct pathological evidence of the use of the four large tail spikes in *Stegosaurus* as weapons has been described with a puncture mark of a spike within the vertebrae of a predator's (*Allosaurus*) tail (Farke 2014). Biomechanical models of the spikes in *Stegosaurus* as well as the much more prominently spiked *Kentrosaurus* have shown that they are able to withstand great forces that would have occurred when struck in combat.

Stegosaurs typically present with relatively very small brains. Most notably, the brain of the large-bodied *Stegosaurus* has been described as being miniscule compared to the size of its body (Buchholtz 2012). This small brain size led early scientists to suggest that an enlarged space in the sacral region might have been evidence for a “second brain” for innervation to the limbs (Marsh 1881) – an assertion that has been since debunked (Giffin 1991; Buchholtz 2012). Hopson (1977) calculated the EQ of *Stegosaurus* to be quite low relative to other dinosaurs (0.56), corroborating with the assumption of a slow herbivorous lifestyle, especially in an animal that walked around low to the ground with lacked speed or agility.

## Ankylosauria

Ankylosaurs (Fig. 1b), best known for its largest taxon, *Ankylosaurus*, were large-bodied, quadrupedal animals that walked low to the ground and likely fed on low-growing vegetation. They are divided into the subclades known as ankylosaurids and nodosaurids, both of which

diversified during the Cretaceous Period. Dental microwear and morphological studies of their small, denticulate teeth and entire jaw system have shown their feeding mechanisms primarily consisted of a combination of palinal jaw movements with long-axis rotation of each side of the jaw at the predentary-dentary joint (Mallon and Anderson 2014; Ősi et al. 2014; Nabavizadeh 2016; Nabavizadeh and Weishampel 2016).

Ankylosaurs are known for their outer covering of thick armor, made up of heavily built, expansive osteoderms that covered the entire animal, from head to tail. This outer coating is nearly irrefutable evidence of a defense mechanism of some sort. It is likely that it is primarily used in defense against predators, as a predator's mouth would not have been able to surround the armor to bite into it. The only likely strategy in which a predator would have more easily been able to bite into an ankylosaur was to flip it over, as the ventral side of ankylosaurs was free of osteoderms. Still, the massively built nature of ankylosaur armor would have greatly reduced the chances of a predator to even attack an ankylosaur.

Ankylosaurs are also characterized by elongate spikes projecting laterally from the sides of their bodies and, in the case of ankylosaurids, a massive club tail. These characteristics are ideal for defense in combat behavior. The laterally projecting spikes in nodosaurids are especially prominent in many cases, and it seems intuitive that they would be amply helpful in combat situations, whether intraspecific or interspecific, especially in defense against predators of any size, although direct evidence is yet to be found. Depending on the taxon, nodosaurid spikes are oriented variable directions. For example, in *Edmontonia* the shoulder spikes are highly exaggerated in size and angled cranially, whereas in *Sauropelta*, the large shoulder spikes are angled dorsally (Carpenter 2012). Whether these variable spike orientations are indicative of differences in defense mechanisms is subject to speculation.

Ankylosaurid tail clubs are made up of extremely dense and enlarged, rounded bone at the tip of an already very ossified series of tail vertebrae. Arbour and Snively (2009) performed a computer modeling study testing the capacity of

an ankylosaur club tail to resist high forces and concluded that ankylosaurid tail clubs would have primarily been effective in later adulthood on impact when swung at a predator. Although club tails are variable, both between taxa and between ontogenetic stages within a taxon, there is still certain amounts of pain that the tail club likely would have inflicted (Arbour 2009; Farke 2014). The impact function of club tails in ankylosaurids would have been assisted by greatly enhanced hip and leg musculature (Arbour 2009; Farke 2014). Intraspecific combat could have also been possible among ankylosaurids. Other functions of the tail club could have been for display; however there is no direct evidence to support this.

In terms of brain morphology, nodosaurids and ankylosaurids show a diversion in hypertrophied sensory organs of the brain. Nodosaurids, such as *Silvisaurus*, show more prominent brain characters that would enhance vision, such as a rounded cerebrum and optic tectum (Eaton 1960; Buchholtz 2012). In contrast, ankylosaurids, such as *Euoplocephalus*, present with enlarged, divergent olfactory bulbs, which corroborate with enlarged and complex nasal passages. Hopson (1977) calculated the EQ of *Euoplocephalus* as even lower than *Stegosaurus* (0.52), also corroborating with an unintelligent, slow, herbivorous lifestyle in an animal that walked low to the ground with little agility.

## Ornithopoda

Ornithopods consist of a vast range of small- to large-bodied bipedal and quadrupedal herbivores, most notably the distinctive duckbilled hadrosaurs (Fig. 1c), such as *Parasaurolophus*, *Corythosaurus*, *Lambeosaurus*, and *Edmontosaurus*, as well as other iguanodontians, such as *Iguanodon*. The small-bodied ornithopods, such as *Hypsilophodon* and *Dryosaurus*, are bipedal animals with small, rounded teeth with primarily orthal feeding mechanisms with slight mandibular rotation (Weishampel 1984; Nabavizadeh and Weishampel 2016). As ornithopods diversified into the much larger iguanodontians, including hadrosaurs, there is a transition to a graviportal,

quadrupedal gait, and a major palinal component is implemented into their feeding mechanism in addition to long-axis rotation of the mandibles (Nabavizadeh and Weishampel 2016). Other studies have suggested the possibility of a form of cranial kinesis called “pleurokinesis” might have also been a key component in ornithopod feeding mechanisms (Weishampel 1984; Norman and Weishampel 1985), but more recent studies have challenged this notion (Rybczynski et al. 2008; Holliday and Witmer 2008; Cuthbertson et al. 2012). The immensely packed tooth batteries in the advanced hadrosaurs are also indicative of likely extensive feeding behaviors.

Notable characteristics of lambeosaurine hadrosaurs in particular are their incredibly diverse hollow cranial crests. Although these crests have previously been speculated to have been used in combat, it is now well known that they were used as resonators for vocalized communication between members of a specific taxon (Weishampel 1981). The long, tubular crest of *Parasaurolophus* is the most well-known case of this, with hollow cavities that pass through the crest and lead to the voice box, acting like a trumpet to amplify and enhance calls made by the animal (Weishampel 1981). Other morphologies of this crest also exist, such as the rounded nature of the crests in *Corythosaurus* and *Lambeosaurus*.

In terms of self-defense in an encounter with predators, most ornithopods do not possess any external anatomical features that could be used in combat. Basal iguanodontians, such as *Iguanodon*, are known for their conical thumb spikes that have been speculated to have been a special defensive structure against predators, although they could also have been used in feeding or mating aid (Farke 2014). Besides this exception, however, the lack of defense structures was likely compensated by the immense body size of many hadrosaurs, such as *Edmontosaurus* and, the largest of all, *Shantungosaurus*. Evidence from trackways and nesting sites of a hadrosaur known as *Maiasaura* have portrayed a great likelihood of sociality and communal living among these animals as well (Horner 2000), which would have

also been greatly beneficial in defense against predators.

Endocast morphology in ornithopods has offered clues into their active lifestyles and into their bipedal to quadrupedal nature, which has corroborated with inferences of stature using limb bone morphology (Buchholtz 2012). The ornithopod hypsilophodontid *Leaellynasaura* exhibits clear optic lobes that researchers speculate suggested high visual acuity in dark winters (Buchholtz 2012). Hopson's (1977) EQ calculations ranged from just below 1.0 in the earlier, mid-sized *Camptosaurus* to variably up to about 1.5 in the larger iguanodontian dinosaurs, such as *Iguanodon* and hadrosaurs. These results suggest a higher level of complex cognition compared to the armored thyreophorans (i.e., the stegosaurs and ankylosaurs). This is likely, again, due to the fact that ornithopods lack any defense mechanisms anatomically and therefore might have also needed to rely on sociality and communicative herd behaviors in order to survive, in addition to sensory acuity, faster running speeds, and much larger body sizes.

## Pachycephalosauria

Pachycephalosaurs, such as the well-known *Pachycephalosaurus* (Fig. 1d) and *Stegoceras*, are bipedal, orthal-feeding herbivores with characteristic dense, dome-shaped skulls. The dome is created by the frontal and parietal bones on the dorsal surface of the cranium and has been speculated to have been used in intraspecific head-butting combat, analogous to that of sheep and goats. One histological study argued against this due to certain distributional patterns of stress-induced bone cells within the dome (Goodwin and Horner 2004). However, other studies have noted there is still reason to believe that pachycephalosaurs could have used their domes for defense in some form (Farke 2014), such as possible flank-butting behavior (Carpenter 1997). Head-to-head butting combat is still plausible, although less so due to the small contact point required for accurate ramming (Farke 2014). Although complete cranial material of

pachycephalosaurs is relatively rare, braincase specimens of pachycephalosaurs are especially numerous due to their preservation within their thick-domed crania. Most prominently, pachycephalosaur braincases display large olfactory bulbs, suggesting a strong sense of smell.

## Ceratopsia

Ceratopsians (Fig. 1e) have arguably the most extravagantly ornamented skulls of any dinosaur. The most well-known ceratopsian by far is the three-horned *Triceratops*, which also happens to be the last and largest-bodied ceratopsian of all. Ceratopsians are known for their expansive frills that extend from the parietal and squamosal bones in the back of their skulls. The most basal ceratopsians, such as *Chaoyangosaurus*, *Yinlong*, and even the common *Psittacosaurus*, do not possess prominent frills; however, they do possess a characteristic rostral bone, which is a midline upper jaw bone unique to ceratopsians that opposes the prementary of the lower jaw. These basal ceratopsians were very small, bipedal herbivores ranging from the Jurassic into the Cretaceous, when the vast majority of ceratopsian diversity expanded. Notably, *Psittacosaurus* endocranial anatomy suggests an enhanced sense of smell (Buchholtz 2012), likely used for foraging. Furthermore, the hornlike structures projecting laterally from the cheeks of *Psittacosaurus* have been speculated as flank-butting weapons, although this is uncertain (Farke 2014). *Leptoceratops* and *Protoceratops* are two quadrupedal Cretaceous ceratopsians with much more distinctive frills extending caudally from their skulls. They were larger than their basal relatives and possessed much more robust beaks which, along with feeding, could have been used for biting predators in self-defense. They also possessed incipient nose horns that have been loosely speculated to have been used in combat (Farke 2014). These forms are predecessors to the derived and highly diverse ceratopsids and primarily fed with a palinal motion of the jaw (Varriale 2016).

The large-bodied, quadrupedal ceratopsids are divided into the Centrosaurinae (e.g.,

*Centrosaurus*, *Styracosaurus*, and *Pachyrhinosaurus*), which mostly have a relatively shorter frill and a single nose horn and short brow horns (with exceptions), and the Chasmosaurinae (e.g., *Chasmosaurus*, *Pentaceratops*, and *Triceratops*), which mostly have a relatively longer frill and two large brow horns and one short nose horn (with exceptions). Ceratopsids are known to have implemented a major palinal component into their feeding mechanisms in addition to orthal slicing (Varriale 2011; Mallon and Anderson 2014; Nabavizadeh and Weishampel 2016).

The elaborate cranial ornamentation worn by ceratopsids has been subject to a plethora of in-depth studies elucidating both their function and their role in phylogenetic relationships within the Ceratopsidae. Studies that have explored various possible functions of ceratopsian horns and frills include those exploring the possibility of intraspecific combat (Farke 2004; Farke et al. 2009), possibly in competition for mates in many cases and defense against predators (Farke 2014). The frills in ceratopsians could have been used for extra defense of the neck, as most were too large and wide for any predator to wrap their mouths around. In addition, they possessed hornlike knobs and spikes along the edges of their frill for extra defense, which is exaggerated especially in centrosaurines like *Styracosaurus*. The immense, keratin-covered, and sharp brow horns of most chasmosaurines like *Triceratops* are ideal for piercing any animal in combat and defense, as is the single large nose horn in centrosaurines like *Centrosaurus* and *Styracosaurus*. One unique centrosaurine known as *Pachyrhinosaurus* is characterized by a large plateau-shaped boss structure on its nose in place of a horn that was likely used in more forceful ramming behavior rather than piercing (Farke 2014). In terms of intraspecific combat, this type of behavior can be analogized to that of sheep and goats that ram heads in combat, just as it can also be analogized with pachycephalosaur fighting. Certain cranial pathologies of *Triceratops* and *Centrosaurus* specimens have been attributed to combat behavior as well, with variable patterns in bone growth suggesting varied fighting styles (Farke 2014).



Hopson (1977) calculated the EQ values of both *Protoceratops* and *Triceratops*. Although the exact values are not identified in the text for these two taxa, the two graphs provided show the EQ of *Protoceratops* to be roughly around 0.9 and the EQ of *Triceratops* to be roughly 0.7. At first glance, it seems counterintuitive that an earlier, much smaller ceratopsian would have a lower EQ value. However, *Protoceratops* did not possess nearly as effective of defensive structures as *Triceratops*' large horns. In turn, *Protoceratops* needed to rely more upon speed and sensory acuity to evade predators rather than fighting back with weaponry like *Triceratops* (Hopson 1977).

## Conclusion

Although it is extremely difficult to decipher behavior and cognition in the extinct ornithischian dinosaurs with direct evidence, there are still many clues that researchers have used to elucidate certain aspects of the lifestyle of these animals. Skeletal morphology, brain endocast morphology, tooth wear, footprints, and pathologies, among others, all play key roles in aiding in analyses of behavior and cognition, both directly and indirectly. Ornithischian dinosaurs, along with sauropodomorphs and a select few theropods, made up the vast majority of the megaherbivores of the Mesozoic ecosystems and contributed immensely to faunal and environmental fluctuations. Because of this, continued research elucidating aspects of their functionalities, sociality, and intelligence can help provide important insights and context for the state of the ecosystems of today.

## Cross-References

- [Herbivore](#)
- [Paleontology](#)

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## Ornithology

► [Language Research: Parrots](#)

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## Otters

► [Mustelid Communication](#)

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## Outfit

► [Safari](#)

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## Ova

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## Synonyms

[Eggs](#); [Female gametes](#); [Ovum](#) (singular)

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## Definition

Female reproductive cells that typically divide and develop to form a genetically distinct organism following fertilization by a male cell (e.g., sperm).

## The Female Gamete: A Highly Specialized Cell with Additional Components

Oogenesis – the development of the ova – is a dynamic process whereby germ cells undergo meiotic divisions to produce cells of a haploid state ( $n$ ). Evidence from studies of different species brings light to endless variations on the complex happenings during oogenesis. Despite variation in the process of ovum development among taxa, there is one common theme: the product is a highly specialized cell, which (when activated) commences the events of embryogenesis. Indeed, an ovum that took weeks to months to develop can be extraordinarily transformed within minutes during fertilization. In this entry, the term “ova” is restricted to an ovulated female gamete and, unless otherwise stated, the information provided is drawn from mammalian examples.

The ovum is ovulated as a “complex” that consists of three components: (i) the cumulus layer, consisting of several layers of ovarian follicular granulosa cells embedded in an extracellular matrix composed of hyaluronic acid; (ii) the specialized extracellular matrix, or zona pellucida (ZP), consisting of glycoproteins that are synthesized and secreted by the oocyte; and (iii) the oocyte (pre-ovulation) or ovum (post-ovulation), which is arrested at metaphase of meiosis II within the ovaries (Evans and Florman 2002).

Each of these three components has a specific function prior to and/or during fertilization. The thousands of cells that make up the cumulus layer support the oocyte before and ovum after ovulation. Postovulation, the “cloud-like” cumulus layer facilitates both the ovum’s transit into the oviduct and the passage of sperm to the ovum surface. As way of minimizing the risk of polyspermy (i.e., entry of the ovum by  $\geq 2$  sperm, which results in ovum mortality), the cumulus cells secrete substances that control the number of sperm that interact with the ZP via processes of chemotaxis and mediation of sperm motility (Oren-Benaroya et al. 2008). A prerequisite for sperm to be able to pass through the ZP is the acrosome reaction (AR), which is calcium-dependent exocytotic event that results in the

fusion of the sperm acrosomal membrane with the sperm plasma membrane. The widely accepted view that the AR is primarily induced by interaction with the ZP has recently been reconsidered with evidence suggesting that the cumulus cells “prematurely” induce the AR as a means of limiting the number of viable sperm that reach the ovum (Jin et al. 2011). AR sperm penetrate the ZP, enter the perivitelline space (i.e., the space between the ZP and the ovum’s plasma membrane), then adhere to and fuse with the plasma membrane (Evans and Florman 2002). Following this, ovum activation occurs and embryonic development is initiated. Research in ovum activation has focused on the mechanism by which sperm evoke oscillations of cytosolic calcium concentrations in the ovum; however, the specific mechanism through which a sperm activates an ovum remains largely unknown and highly controversial (Xu and Yang 2017). Ultimately, the fusion of the ovum and sperm results in the formation of a diploid ( $2n$ ) zygote. The second meiotic division of the ovum, with separation of chromatids, occurs shortly after fertilization. Later, the zygote will divide mitotically, eventually giving rise to a multicellular organism.

## Female Responses and Behavior: Implications for Ova Form and Function

Female behavior and physiological responses to their environment can profoundly influence ova form and function. For example, in many species, mothers are expected to adjust the size of their propagules to align with the environmental conditions to which those offspring will be exposed (Mousseau and Fox 1998). More specifically, life-history theory predicts that females should increase their investment in offspring quality if those offspring are at a high risk of encountering adverse environmental conditions. In several fish and amphibian species, larger offspring have been shown to fair better under adverse conditions and high predation rates. As a demonstration of phenotypic plasticity in ovum form, in these species females will adaptively tailor ovum size to match the environment that their offspring will

encounter after birth (Mousseau and Fox 1998). Remarkably, females may also mediate their investment in ova size based on the level of help that they will receive to care for their young (i.e., as demonstrated in a cooperatively breeding cichlid; Toborsky et al. 2007).

It has also been shown that female mating behavior can influence the evolution of ova function and the relative ease at which they may be penetrated and fertilized by sperm (reviewed: Firman 2018). Successful fertilization requires the co-occurrence of a sufficient number of competent sperm within the vicinity of the ovum. If females have mated polyandrously (i.e., with  $\geq 2$  males), they may be presented with the opportunity to “select” the sperm of a high quality or compatible male (“cryptic female choice,” a form of postmating sexual selection; Firman et al. 2017). In turn, this may lead to the production of better quality offspring and thus improve the evolutionary fitness of females. However, when females do mate multiply, rival males are often forced to compete for fertilizations (“sperm competition,” a form of postmating sexual selection), resulting in intensified selection for increased sperm number and quality. This scenario can lead to what is best described as “gametic sexual conflict,” whereby selection is driving the evolution of increased sperm numbers (“sperm competitiveness”), which in turn leads to an increased risk of reproductive failure resulting from polyspermy and a counteracting female response of increased resistance to fertilization (“ovum defensiveness”) (Firman 2018). Evidence in support of this gametic “coevolutionary arms-race” is accumulating both within and among different mouse species (e.g., Dean and Nachman 2009; Firman et al. 2014).

## Cross-References

- Ovaries
- Polyandry
- Sexual Conflict
- Sexual Selection
- Sperm Competition
- Zygote

## References

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## Ovaries

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## Introduction

In domestic animals, ovarian structures producing steroid hormones are integral to reproductive behavior. Although ovarian steroids have other

cognitive functions, these roles are less understood in domestic animals. The ovaries are ovoid, paired female gonads that are positioned anatomically in close proximity to the mammalian kidney. Ovarian size and shape is species dependent and relative to the functional structures present such as antral follicles or a corpus luteum. The ovary is comprised of an outer tunica albuginea, ovarian cortex, and ovarian medulla. In most species (except mares), oocytes and functional corpora lutea are found in the ovarian cortex. The medulla is composed of dense connective tissue and provides vascular, nervous, and lymphatic supply. The anterior portion of the broad ligament attaches to and supports the ovary; this portion of the ligament, the mesovarium, provides blood vessels, lymphatics, and nerves to the ovary. The utero-ovarian ligament provides structural attachment to the uterine horn. The ovary is partially or completely covered by the infundibulum of the oviduct at the time of ovulation to allow capture of the released oocyte.

## Main Text

Reproductive behavior is programmed during prenatal development and is the result of normal development chromosomal, gonadal, and phenotypic sex. The brain in mammals develops into a female phenotype unless exposed to hormones from the developing gonad. In female mammals, maternal estradiol and estradiol from the developing gonad is bound by  $\alpha$ -fetoprotein and prevented from crossing the blood-brain barrier preventing masculinization of the hypothalamus such that both tonic and surge centers develop. Thus, the female embryo brain becomes fully feminized. Historically, the feminization of the brain has been considered a default pathway, but recent evidence supports the active repression of masculinization via DNA methylation pathways (Nugent et al. 2015). Presence of gonadal steroids (estradiol, progesterone) is obligatory for normal female reproductive behavior which occurs in a cyclical fashion referred to as the estrous cycle.

The steroid hormones responsible for female reproductive behavior are estradiol and progesterone. Estradiol, produced by developing follicles on the ovary, either allows the expression of estrus or enhances the expression of estrous behavior. Estrus behaviors will vary dependent on the species, but the hallmark behavior is willingness to be mounted by the male (Senger 2012). In the cow, estrus may be preceded by increased ambulation, vocalization, mounting other periestrus females, and formation of sexually active groups. Mares exhibit characteristic behaviors such as tail raising, clitoral winking, tilting of the pelvis/leaning into the stallion, and urination. Sex hormones facilitate reproductive behavior via receptors in the hypothalamus; however, other brain functions and nonreproductive behaviors are also influenced by estrogens including fine motor control, motor coordination, pain, mood regulation, cognitive function, cardiovascular regulation, neuroprotection, and others (McEwen et al. 2012). Nonreproductive behaviors are produced through estrogen's actions on several other brain areas beyond the hypothalamus including the spinal cord, cerebellum, nigrostriatal and mesolimbic system, amygdala, hippocampus, cerebral cortex, and brainstem (McEwen et al. 2012).

In contrast, progesterone is produced by the corpus luteum formed after ovulation of a dominant follicle(s). Progesterone inhibits estrous behavior such that the female is not receptive to mating attempts during the luteal phase of the estrous cycle, even if other large follicular structures are present. The exception to this is the bitch; preludeinization of follicles results in standing estrus in the face of rising serum progesterone levels. Diestrus behavior may range from passive avoidance of males to outright aggression towards male animals to avoid mating attempts. If maternal recognition of pregnancy does not occur, luteolysis is initiated by the production and release of prostaglandins from the endometrium, allowing the female mammal to return to estrus and sexual receptivity.

Historically, it was accepted that prenatal development resulted in specific male or female



neural pathways that were activated by gonadal steroids to result in male or female reproductive behavior. This dogma has been questioned at least in part by studies that demonstrate that adult mice are capable of displaying reproductive behaviors of either sex and suggested that pheromones interpreted through the vomeronasal organ also play a significant role in expression of reproductive behaviors (Dulac and Kimchi 2007).

## Conclusion

Hormones produced by developing ovarian structures result in a cyclical pattern of reproductive behaviors in female mammals. In the event of pregnancy, this cyclical pattern is interrupted and the female is nonreceptive to further mating attempts until after parturition and resumption of ovarian activity. Understanding of the length of the estrous cycle in various species and subsequent interpretation of estrous behaviors is an important aid in breeding management of common domestic species.

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## Overdominance

### ► Heterozygote Superiority

## Overdominance Hypothesis for Male Homosexuality

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## Introduction

The complete definition of overdominance according to the Merriam-Webster dictionary is “the condition wherein a heterozygote produces a phenotype more extreme or better adapted than that of the homozygote.” In other words, overdominance produces a balanced polymorphism where the heterozygote has a greater phenotype value and it is more fit than the homozygous state for either of the alleles that it comprises. Hence, overdominance can also be described as heterozygote advantage, wherein heterozygous individuals have a higher fitness than homozygous individuals.

To clarify the effect of overdominance, the example of sickle cell anemia can be considered. Consulting the American Heart, Lung, and Blood Institute guidelines, it appears that this condition is determined by a single polymorphism. Sickle cell anemia results in an abnormality in the oxygen-carrying protein hemoglobin; homozygote carriers develop a specific syndrome with number of health problems. Carrier of these deleterious alleles has lower life expectancy, with homozygotes dying at early age.

It should be noticed that if a certain trait or behavior is detrimental to the reproductive success, or fitness, of an organism, one would not expect it to persist in the population. Natural selection should progressively eliminate it. Then, in an evolutionary perspective, the following population genetic question arises, why such deleterious disease does not disappear generation after generation, since the carriers of the alleles mostly die leaving less offspring than healthy individuals.

The answer is because this allele also yields resistance to malaria. Thus, in those population living in regions where malaria has exerted a

strong selective pressure, sickle cell anemia allele has been selected for its conferred in heterozygous individuals' partial resistance to malaria; these individuals have fewer physiological effects of sickle cell anemia; thus they survive better and leave more offspring than healthy individuals that on the contrary die of malaria. Hence the alleles for sickle cell anemia remain in balanced selection in the population due to the advantage carried by the heterozygote individuals on both homozygote ones. Alleles producing sickle cell anemia express themselves with an overdominance mechanism.

## Overdominance in Male Homosexuality

The hypothesis of a balanced selection has long been advocated by scientist trying to come to terms with the Darwinian paradox of human homosexuality and especially male homosexuality. Also in this case it has been since long clarified as a genetic component in our species. Homosexuality runs in families, and homozygotic twins have more than expected concordance in homosexual orientation. Homosexuality is not strictly genetically determined; however the heritability is between 0.3 and 0.7. However, genetic components can never be considered as strict determinants of homosexuality, and they should always be interpreted as acting within the frame of an environmental background that may also strongly contribute to sexual orientation in individuals (Camperio Ciani et al. 2015).

The more recent debate has considered a variety of selection mechanisms for homosexuality. Direct selection was rapidly dismissed in the case of male homosexuality homosexual reproduce far less than heterosexuals. The most promising mechanisms were then based on overdominance, on sexually antagonistic selection, and other selection modes including maternal effects and genomic imprinting, possibly involving epigenetic activity (Gavrilets and Rice 2006; Camperio Ciani et al. 2008).

At first Miller (2000) proposed an overdominance hypothesis for maintenance of male homosexuality in the population, hypothesizing that

individuals heterozygous for the feminizing alleles might make heterosexual carriers of the alleles better fathers and more attractive mates due to greater sensitivity, empathy, tendermindedness, and kindness, while homozygous individuals would develop homosexuality, but this was not further tested at the time. Meanwhile sexually antagonistic selection hypothesis came later suggesting that a gene that is detrimental to fitness in one sex could be maintained so long as it is beneficial to the other sex.

## Empirical Studies

Now it is difficult to trace directly genes influencing homosexuality in humans, even if recent studies seem to have identified some of them. However, without the need to genotype individuals, it is still possible to test the overdominance hypothesis on male homosexuals by verifying its predictions. For homosexuality being the expression of an overdominance mechanism, it should be expected to find an increased number of homosexual relatives and an increased number of individuals with increased fitness (heterozygotes) both in the paternal line and in the maternal line of the pedigree for a homosexual proband (King et al. 2005; Gavrillets and Rice 2006). The overdominance prediction contrast with the sexually antagonistic selection hypothesis that suggests that homosexuality is a male by-product of alleles than in females leads to an increase of fecundity (as compared to the population baseline fecundity under study) and that these genes are partially linked to the X chromosome (Camperio Ciani et al. 2004). In the sexual antagonistic hypothesis, it is expected to find an increased number of homosexuals and an increase in fecundity only in females only in the maternal line in pedigrees of the homosexual probands. The prediction generated by the competing hypothesis could be tested in pedigree analysis of homosexuals, through questionnaires.

Some empirical studies have indeed reported a generalized fecundity increase in other members in the pedigrees of male homosexual probands,

independently of the maternal or paternal line (King et al. 2005; Schwartz et al. 2010). Rieger et al. (2012), further based on the same dataset by Schwartz et al. (2010), found also a fecundity higher than expected in brothers of male HS as compared to brothers of the control group, leading some support to the overdominance hypothesis.

In contrast, Camperio Ciani et al. (2004) found that homosexuals are significantly more represented in the maternal line of homosexual probands and that only mothers and maternal aunts show a significant fecundity increase as compared to baseline population fecundity, hence supporting a sexually antagonistic mechanism for the maintenance of male homosexuality (Camperio Ciani et al. 2004). These results suggesting a sexually antagonistic hypothesis were replicated over again in different populations on male homosexuals (Camperio Ciani and Pellizzari 2012; Gavrillets and Rice 2006) and also in bisexuals (Camperio Ciani et al. 2009) and are opposed to the prediction for overdominance mechanism. Subsequently, also the data by Schwartz et al. (2010) were reanalyzed by Camperio Ciani and Pellizzari (2012), pointing also in this dataset to a previously unnoticed larger maternal-line female fecundity suggesting a sexually antagonistic selection rather than an overdominance mechanism.

## Population Dynamic Models

Mathematical models exploring the dynamic and equilibria of human male homosexuality were stimulated by some of these competing hypotheses and predictions. First, Gavrillets and Rice (2006) developed single-locus models (the effect of a single genetic factor), and then Camperio Ciani et al. (2008) developed multi-loci models (considering the effect of two or more genetic factors), either in the autosomes (the nonsexual chromosomes) or in the X chromosome. These authors have explored various selection modes in each case, under the assumption of random mating. They examined for each model the range of selection parameters which would guarantee a

stable polymorphism, hence the persistence of the trait in the population. The results showed that single-locus models are all largely unstable as their parameter ranges are too narrow to allow for stable polymorphism under the normal variability of population conditions (Gavrillets and Rice 2006). All these models due to their instability lead to either fixation or extinction of the genetic factors, contrary to the empirical requirement that suggests that homosexuality is relatively stable in human populations.

For multi-locus models, the overdominance models were shown to generate polymorphic equilibria compatible with the stability requirements for male homosexuality. However, these models always account incorrectly for the pedigree asymmetries highlighted in empirical studies, as they predict increased fecundities in both pedigree line (maternal and paternal) and regardless of sex. Fecundity enrichments in the families of male homosexual probands have been shown not to occur in such a generalized way but only asymmetrically in maternal-line females. Hence the overdominance selection mode was excluded from the possible maintenance mechanisms for male homosexuality in the population (Camperio Ciani et al. 2008).

Sexually antagonistic selection on the contrary met all empirical predictions (Camperio Ciani et al. 2008). The analysis of the sexually antagonistic model with an autosomal and an X-linked allele emerged as the simplest model, capable of meeting all the empirical requirements assessed in male homosexuality studies. In this mathematical model, the researchers found polymorphism stability at low frequency as predicted, with no extinction or fixation of the genetic factors in wide ranges of increased female fecundity and reduced reproductive success of homosexual males. The X-linked sexually antagonistic model describes all the correct pedigree asymmetries in the maternal line of homosexual males, resulting with a higher than patriline frequency of homosexuality in the males and a higher than patriline fecundity in the females (Camperio Ciani et al. 2008, 2015). Interestingly, a fecundity increase in paternal aunts of heterosexuals, as compared to

homosexuals, was also predicted in the sexually antagonistic models and later observed in empirical data (Camperio Ciani and Pellizzari 2012), strengthening the heuristics of these models. To further confirm the predictions of the sexually antagonistic model of two genetic factors one on the X chromosome and one on the autosomes, a large team of researchers screened a wide sample of homosexual brothers using genetic whole genome analysis (GWAS). The results confirmed, as predicted, a significant signal on chromosome number 8 (autosome) and the X chromosome (Sanders et al. 2015).

The overdominance model seems at present less probable in male homosexuality; however this is not so for female homosexuality. Recent data based on a pedigree analysis of over 30,000 individuals focusing on female homosexuality confirmed that female homosexuality runs in families and has a genetic influence and lesbians have a significant reduced fecundity. This study showed further that lesbians are more frequent in both sides of the pedigree of lesbian probands, and individual with increased fecundity are more frequent in both sides of the pedigree, thus balancing the reduced fecundity of lesbians. These results confirm empirically for female homosexuality the predictions of an overdominance mechanism (Camperio Ciani et al. 2017). It should be noted that in the case of females, an X-linked sexually antagonistic model and an overdominance model partly overlap since females contrary to males are diploid for the X chromosome.

## Conclusion

Male homosexuality is at present less likely explained by overdominance mechanisms. A sexually antagonistic selection model, for a multi-locus factor with at least an X-linked locus, provides a closest adherence to the empirically known patterns for male homosexuality. Overdominance, on the contrary, seems probable for female homosexuality where the patterns of generalized increase of homosexuality and increased fecundity that is expected in all the relatives of lesbians seem to be empirically confirmed.

## Cross-References

### ► Homosexuality

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## Overshadowing

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### Definition

Overshadowing may be defined by the consequences on behavior, the procedure that produces that consequence, and the mechanisms behind it. The following definition is at the level of behavior and procedure, for theoretical explanations, see below.

The phenomenon of overshadowing refers to a decrement in acquired conditioned responses produced by the training of two conditioned stimuli (CSs) together (i.e., in compound), followed by an unconditioned stimulus (US),  $CSa + CSb \rightarrow US$ , relative to training the stimulus apart,  $CSa \rightarrow US$  and  $CSb \rightarrow US$ . In this situation, the CS with more salience will be the one that generates higher conditioned responses at testing.

### Introduction

Overshadowing often represents how animals learn in the natural context when different stimuli presented at the same time compete for attention. An example of this is when a dog is fed, in front of him, the dog can see the food as it falls into his bowl, can smell it, and hear the sound it makes as it falls. All these stimuli compete to overshadow the others.

In addition to overshadowing, other interactions between CSs can also produce decrements in response (Miller and Escobar 2002). These situations can be classified as competition, when the reduction in responding results from training the CSs together in the same phase, as in

overshadowing, blocking (Kamin 1969), and relative validity of cues (Wagner 1968). Alternatively, interference rather than competition is called to the reduction in responding that results from training two CSs with an US, but at separate times (i.e., in different phases of training; e.g., Miguez et al. 2012).

In the case of overshadowing, two CSs are presented simultaneously followed by the US, one of these CSs will have the characteristic of being more intense or salient in comparison with the other CS. During the test phase, when they are presented separately, the more intense CS will generate a greater conditioned response (CR).

In some situations where two stimuli are presented at the same time, the overshadowing phenomenon fails to be found, contrary to what is expected, those stimuli end up potentiating. In potentiation (e.g., Urcelay and Miller 2009) the presented CSs, for example, smell and taste stimuli, can generate a higher CR compared to when they are presented separately, which is contrary to the overshadowing phenomenon.

Overshadowing is a phenomenon observed in different learning tasks and species, for example, instrumental conditioning with rats (Pearce and Hall 1978), aversive conditioning with rats (Wheeler and Miller 2007), spatial learning with rats (Sánchez-Moreno et al. 1999), landmark learning in pigeons and humans (Spetch 1995), appetitive conditioning with rats (Holland 1999), nictitating membrane response with rabbits (Kehoe 1982), taste aversions in humans (Okifuji and Friedman 1992), and antinociceptive response in rats (Illich et al. 1994).

### Overshadowing: From Pavlov to Today

Overshadowing was first observed by Ivan Pavlov (1927), who is considered one of the great exponents of psychology, responsible for the foundation of the theories of behavior and learning. In one of the many experiments carried out by Pavlov and his team, described in his text *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex*, they observed a phenomenon occurring in stimulus compounds.



When the compound's stimuli were presented individually, one of them was overshadowed by the other. This happened independently of the number of reinforcements.

For example, in one of Pavlov's experiments, a compound of stimuli was presented to a dog: a sound with a light, both were paired with food. When the light stimulus was presented individually it was ineffective because it did not produce any responses. On the contrary, the compound did produce a conditioned response. This was repeated in another experiment; in this case, thermal and tactile stimuli were used. When the two stimuli were presented separately, only the tactile stimulus provoked a conditioned response, while the thermal stimulus did not. Pavlov and his team determined that these differences in the conditioned response were related to the difference in the strength or intensity of the stimuli, so tactile stimuli should be considered stronger than thermal stimuli, and auditory stimuli stronger than visual stimuli. Thus, the stimuli with the characteristic of being stronger or intense overshadowed the stimulus characterized as less strong such that the latter does not generate an association. However, when the less intense CS was presented separately and was reinforced, over time, a conditioned response was generated (Pavlov 1927).

With the development of cognitivism, learning theories were adapted to integrate stimuli compounds in the associations between CSs and USs, attentional processes, and neural models, which impacted the theoretical models of overshadowing.

## **Overshadowing Research: Phenomena and Models**

Various models have tried to explain the phenomenon of overshadowing; these can be separated into two groups, those that focus on acquisition and those that focus on performance.

### **Acquisition-Focused Models**

Rescorla and Wagner (1972) explain overshadowing as a difference in acquisition rate between two CSs. According to this model, the

difference is due to the intensity or salience of each CS, so that faster conditioning would be expected to occur with a strong sound than with a weak sound. In this way, overshadowing occurred when one stimulus was conditioned faster than another during the first tests, so it is traditionally considered an acquisition phenomenon.

Mackintosh (1975) mentions that overshadowing is a consequence of training, since throughout the tests, the subjects learn to ignore the less salient stimuli that, according to his theory, do not contribute anything new to the prediction of the unconditioned stimulus. For this reason, overshadowing can be observed only when there is already training with several conditioning trials. According to the theory of selective attention, when two or more stimuli are present, they compete for the limited attention of the subjects who, on giving their attention to a specific stimulus CSa, will stop paying attention to another stimulus CSb (Mackintosh 1976).

Pearce (1987) stated that the overshadowing is a decrease of the conditioned response that would happen by the generalization that occurs when one of the two CSs presented as a compound is removed. According to this theory, this would occur during the test phase.

Pearce and Hall (1980) argue that the speed of association of CS will decrease as they become good predictors of US since it becomes unnecessary to learn more about the association of CS with US. In the case of overshadowing, the subject generates an association between the compound of CSs and the US, learning that the compound is a good predictor. Once the CSs are presented separately, the associative force of each one of the stimuli will decrease.

### **Retrospective Revaluation and Counteraction of Overshadowing**

Retrospective revaluation is the change of response to a stimulus when another related stimulus is trained (Kaufman and Bolles 1981). Traditional learning-centered acquisition models have problems explaining this phenomenon. For example, in the case of overshadowing, the extinction of one of the CSs will increase the

response to the other stimulus, representing a recovery from overshadowing (Amundson et al. 2008). Another result that challenged models of overshadowing was that this effect counteracted with other phenomena that also reduced responding. For example, training a cue as a blocked stimulus in a blocking training first reduces the ability to overshadow other stimuli later (e.g., Wheeler and Miller 2007). Acquisition-focused models can explain this effect (e.g., Wheeler and Miller 2007).

### **Performance-Focused Models and New Acquisition-Focused Models**

The comparator hypothesis (Miller and Matzel 1988) was the first learning model capable of accounting for retrospective revaluation. This model proposes that associative learning is determined by the contiguity and salencies of the stimuli, focusing on the processing of the information produced in the test and not during the acquisition. In this way, the response to a CS does not reflect the strength of the association between CS and US; instead, it represents the strength of the comparison between the CS-US association with the associative strength of the other stimuli present during training. In addition, this model proposes that at least three associations are learned, which are regulated by the principles of contiguity and salience of the stimuli (the more salient and contiguous the stimuli, the stronger the association). First is the association between the CS A presented in the test and the US. The second is between the CS A and its comparator stimulus (any stimulus present in the environment different from the US and with a strong association with the CS A). And finally, the third association is between the comparator stimulus and the US.

According to the comparator hypothesis, stimuli competition, as in the case of overshadowing, does not arise from a learning deficit but is explained through an error in the expression of the association between the CS A and the US, despite having been encoded during training; i.e., a diminished response to a CS is observed when a second stimulus is present during training and strong CS A-comparator and comparator-US associations are established.

Van Hamme and Wasserman (1994) proposed an associative learning model designed to respond to retrospective revaluation. Their model has similarities with the model of Rescorla and Wagner (1972); for example, both of them focus on the learning processes occurring during acquisition but reject the presumption of the obligatory presence of the CS for the occurrence of changes in associative strength, putting forward the idea that a subject can learn about a CS simply by the presence of a stimulus associated with it. Therefore, it can explain phenomena such as recovery from competition, although it has difficulties explaining counteraction effects of overshadowing (e.g., Wheeler and Miller 2007).

### **Conclusions**

Overshadowing is a key phenomenon when it comes to learning processes and stimuli competition, which has been demarcated with the development of experimental psychology and the study of basic learning processes. This phenomenon has been studied experimentally in both human and nonhuman animals through different tasks and preparations, as well as with different combinations of stimuli. Overshadowing has allowed us to understand how human and nonhuman animals learn from their environment and deal with an enormous number of stimuli present in the context by discerning which CS is the best predictor of the US, saving energy. In that sense, organisms could evolve to learn to ignore stimuli that are not good predictors.

Although almost a century has passed since Pavlov's discoveries, overshadowing continues to be present in the scientific contingency, allowing us to know more about the learning processes through the generation of new research and new lines of investigation.

### **Cross-References**

- ▶ [Associative Learning](#)
- ▶ [Blocking](#)
- ▶ [Classical Conditioning](#)

- [Conditioned Inhibition](#)
- [Contingency](#)
- [Ivan Pavlov](#)
- [Learning](#)
- [Ralph Miller](#)
- [Retrospective Revaluation](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Overt Attention

### ► Cognition

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## Ovum

### ► Gametes

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## Ovum (Singular)

### ► Ova

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## Owls

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## Introduction

Owls are raptors that make up the order of Strigiformes, subdivided into the “typical owl” (Strigidae) and “barn owl” (Tytonidae) families. There are over 200 species, which can be found on every continent except Antarctica. Species vary in size from the elf owl (*Micrathene whitneyi*), which is the size of a sparrow, to Blakiston’s fish owl (*Bubo blakistoni*), which is the size of a large eagle.

## Morphology and Perception

Nearly all owl species are nocturnal and consequently have eyes that are specialized for vision in poor light. Some species have been demonstrated to have color vision, but there is currently no evidence that any can see in UV or infrared spectra. Owls have forward facing eyes, which provide them with binocular vision. There is evidence that barn owls (*Tyto alba*) structure figure-ground

relationships similarly to primates, indicating some convergent evolution of visual perception (Van der Willigen et al. 2003). However, owls are unique in that their large eyes are tubular shaped and consequently nearly immobile, which is compensated for by a flexible neck able to rotate 270°.

Owls have exceptionally acute hearing. Species of owls with asymmetrical ears, such as barn owls, have been found to be capable of hunting with extraordinary accuracy even in total darkness. Similarly, great gray owls (*Strix nebulosa*) can hunt voles under half a meter of snow using only sound. In order to direct sound toward itself more effectively, the heart-shaped face common to the owl is walled with thick and densely packed feathers, making its face a type of satellite dish. The wing feathers are also specialized for sound reduction in flight, allowing them to surprise their prey (Bachmann et al. 2012).

It has been hypothesized that the ear tufts found on a large portion of nocturnal owls have a camouflage function, giving the appearance of broken branches (Perrone 1981). Most owls are colored in grays and browns with speckling, spotting, and bars to cryptically blend in with their environment. Some owls, like the Northern pygmy owl (*Glaucidium gnoma*), also have “eye spots” on the back of their heads, which appear to confuse mobbing birds (Deppe et al. 2003). Within a single owl species, there can be a wide range of colorations, and there is evidence that these different morphs possess distinct behaviors, differing in a range of dimensions including prey preferences, breeding habitats, dispersal distance, and reactivity (Van den Brink et al. 2012). Some morph types are also more predominant in one sex than the other and change in frequency according to latitude.

## Prey

Owls consume a wide variety of prey, including small mammals, birds, amphibians, reptiles, and invertebrates. However, the majority of owl species’ diets consist primarily of mammals, particularly rodents. Diets also vary seasonally, for

example, with more amphibians or insects consumed at times of the year when mammalian prey is less plentiful.

Compared to females, males consume more birds. This is due to the increased agility of most males, which have a shorter wing length than most females (Lundberg 1986). Some owl species prey on other owl species, for example, Eurasian eagle-owls (*Bubo bubo*) hunt tawny owls (*Strix aluco*), making Eurasian eagle-owls an intraguild predator, as both species predate on the dormouse. In response, tawny owl nest sites are located in Eurasian eagle-owl-free areas or as far as possible from Eurasian eagle-owl nests, resulting in a negative relation of tawny owl density to Eurasian eagle-owl density (Sergio et al. 2007).

Large fluctuations in prey numbers can have a substantive effect on owl population and density. For example, in the boreal forest, the snowshoe hare (*Lepus americanus*) has a population cycle of 10 years. Because the snowshoe hare is the primary prey of great horned owls (*Bubo virginianus*), great horned owls raise larger broods with higher survival rates when snowshoe hare numbers increase (Rohner 1996). This increase in predator numbers is a contributing factor toward a decline in snowshoe hare numbers, which in turn results in a great horned owl population decline. Similarly, vole cycles in Europe affect owl density. It has also been found that Tengmalm's owls (*Aegolius funereus*) adjust their brood sex ratio according to vole cycles, producing more females in low vole density years and more males in high density years, as males have higher mortality when food is limited (Hippkiss and Hörnfeldt 2004).

Unlike most bird species, owl females are heavier than males. According to Lundberg's (1986) starvation hypothesis, females are heavier in order to withstand periods of harsh weather and food shortages when incubating eggs, as they completely rely on male provisioning which may be irregular depending on food availability. Indeed, Lundberg (1986) found that sexual dimorphism was more marked in European owl species according to northerly latitude, where cold weather and food scarcity increases.

## Territoriality

Prey type and density can determine home range size and preferred habitats, resulting in wide variation within and between owl species. However, most owl species live in wooded or forested areas and are sedentary, settling down in one territory after dispersal from their natal area. Still, there are a few select species that are known to be nomadic, such as the short-eared owl (*Asio flammeus*), and others that seasonally migrate large distances, such as the Eurasian scops owl (*Otus scops*).

The ownership of a territory is usually advertised by hooting or visual displays. In years with increased owl population in an area, often due to the prey cycle, the number of owls without territories, or "floaters," increases. Territorial owls appear to prevent floaters from breeding and keep them from entering their territories. The occupation of a territory allows access to prime nest holes and superior spatial knowledge of an area and thereby increased hunting and reproductive success. When the best sites are already occupied, floaters are forced to range over larger and less valuable areas (Rohner 1997). Although leaving a territory is unusual, some owls may relocate ("breeding dispersal") if they are single or have lost their mate, have a low-quality site, or fail to reproduce (Blakesley et al. 2006). Breeding dispersal may also occur during crashes of a prey cycle (Korpimäki 1993).

## Mating

Male owls typically attract mates by singing and may offer nest sites or food. The pair may engage in courtship flights or mutual preening. Most owl species are socially monogamous, at least for the breeding season, and a growing number of studies indicate that they are also genetically monogamous, with nestlings sired by other males extremely rare. It has been suggested that because of the high male parental investment involved in raising owlets, female owls are not willing to risk extra-pair copulations that could lose the support of a mate (Marks et al. 1999). However, in times of great prey abundance, some females will "double brood," that is, start another brood later in the



season with another male, sometimes abandoning care of the first brood to her male partner.

Bigyny, a male with two female partners, is slightly more common in owl males, particularly in high prey availability years. Typically, the male has a “primary” female partner, the first he reproduces with that season, and a “secondary” partner. In Tengmalm’s owls, this secondary partner receives far less prey for her nestlings and consequently has poorer nestling survival, leading some researchers to argue that these secondary partners have been deceived into breeding with a male they believed to be unpaired (Carlsson et al. 1987). Others contend that the females are not deceived as to the mating status of the male but are willing to be a secondary female to a higher-quality male than the monogamous partner of a poorer-quality male, especially as she may receive all of his investment if his primary nest is lost to predation (Sonerud 1992).

## Parental Care

Owlets are born asynchronously over the course of 2 weeks, as eggs are laid and hatched at different times. The result is that nestlings at varying stages of development will be in the same nest. According to Lack’s brood reduction hypothesis (1947), this strategy allows for the greater overall survival of nestlings if food becomes scarce for a period, as only the youngest nestlings will die. Some species will also vary the order of laying male and female eggs, with at least one species (the Eurasian eagle-owl, *Bubo bubo*) preferring to lay females last. As the oldest and largest nestlings have an advantage over the youngest and smallest, there is usually a hierarchy in the nest. According to Penteriani et al. (2010), sibling competition in Eurasian eagle-owls may be reduced by having females born last, since they are larger and heavier.

Most owlets in a nest are full genetic siblings, due to the rarity of extra-pair fertilizations. This means that while owl siblings are in competition for food, their inclusive fitness can be increased by the survival of their siblings through kin selection, since they will share an average of 50% of their genes. Altruism toward kin has been seen among co-nestlings. Satiated owlets will share food with each other, particularly older siblings

with younger (Roulin et al. 2012). Owlets are also known to engage in “sibling negotiation” in the absence of their parents, in which they signal vocally to each other their willingness to compete for food (Roulin et al. 2000). Consequently, nestlings will reduce their own vocalizations in the presence of their parents if one of their siblings has signalled its urgency to be fed, as parents often respond to begging signals to determine which nestling to feed a prey item.

Care of owlets is biparental. While nesting and brooding, the male will provision the female with food. After the female has completed the brooding period, she will join the male in provisioning the chicks by hunting prey, except in the rare cases she begins another brood. Once the owlets have fledged, both parents will continue to aid in their provisioning for several months. During this period, fledglings will occasionally “nest switch,” where they are not only tolerated but fed similarly as their foster siblings (Roulin 1999). Because natural selection should act against the rearing of unrelated nestlings, it is yet unclear why this behavior is tolerated, though it appears to be quite rare.

Several months after fledging, activity levels begin to increase in what has been termed “dispersal restlessness” (Ritchison et al. 1992), and the young owls rapidly disperse away from their natal area, sometimes up to hundreds of kilometers. After this initial dispersal, owls may again make smaller dispersals until they permanently settle into an area. Many species will reproduce after their first year, but others not until their second or third.

## Cognition

Cognitive testing of owls has been very limited. There is some indication that owls have a rudimentary numerical ability, as barn owl nestlings can discriminate between one to four nestmates based on vocalizations (Ruppli et al. 2013). Barn owl nestlings can also discriminate between their mother and father and adjust begging accordingly (Roulin and Bersier 2007). Similarly, several owl species can discriminate between the hoots of neighbors and strangers, which is an important distinction to make as a stranger poses a greater territorial threat (Galeotti and Pavan 1993; Hardouin et al. 2006).

# Conclusion

Most research on owls has taken place within the fields of perception, neuroscience, and ecology, although these investigations have largely been

limited to a few dozen species of Eurasian and North American owls (see Fig. 1). The cognition of these ubiquitous avian predators is a rich and almost entirely unexplored area for future research.



**Owls, Fig. 1** Commonly studied species of owls. (1) Barn owl (*Tyto alba*) located on every continent except the polar regions, (2) Tengmalm's owl/boreal owl (*Aegolius funereus*) located in northern Eurasia and North America, (3) great horned owl (*Bubo virginianus*) located in North and South America, (4) snowy owl (*Bubo scandiacus*)

located in the arctic regions of Eurasia and North America, (5) Eurasian eagle-owl (*Bubo bubo*) located in Eurasia, (6) tawny owl (*Strix aluco*) located in western Eurasia, (7) Ural owl (*Strix uralensis*) located in Eurasia, (8) spotted owl (*Strix occidentalis*) located in western North America. (© Joel Colbourne. Used with permission)

## Cross-References

- [Brooding](#)
- [Extra-pair Copulation](#)
- [Inclusive Fitness](#)
- [Kin Selection](#)
- [Monogamy](#)
- [Parental Investment](#)
- [Territoriality](#)

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## Oxytocin

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## Synonyms

Pitocin; Syntocinon®

## Definition

A mammalian peptide hormone, produced in the brain, with wide-ranging effects on numerous aspects of animal physiology and behavior, including reproduction and social interactions.

## Introduction

The physiological importance of oxytocin (OT) was first described in the early 1900s, when biologists discovered that the compound stimulates uterine contractions and lactation. It would take nearly another half century to uncover OT's molecular structure – a nine-amino-acid sequence – and 30 years more to demonstrate OT's potency in regulating social behavior (Lee et al. 2009). Research on OT's behavioral impacts would accelerate substantially in the 1990s, when investigations using rodents implicated OT in pair bonding, parental care, and the evolution of mammalian mating systems. By 2015, this field of study had grown considerably and covered a more diverse range of species – including not only rodents but humans and other primates (Ondrasek 2016). This surge in research revealed OT's contributions to a striking array of physiological, neurobiological, and behavioral

processes. The following entry summarizes some of OT's most well understood functions, as well as its emerging promise as a therapeutic for neuropsychiatric conditions in humans.

## Evolution of the Oxytocin System

Found in mammals, OT is one member of an evolutionarily ancient family of peptides – each consisting of nine amino acids, and thus called nonapeptides – found across invertebrate and vertebrate groups (Lockard et al. 2017). Vertebrate nonapeptides are all derived from vasotocin, which diverged into the vasopressin and oxytocin nonapeptide lineages following a gene duplication event that occurred in early jawed fishes (Goodson 2013). Substitutions at position 8 in the amino acid sequence produced the vasopressin-like and OT-like nonapeptides. The former contain a basic amino acid (lysine, arginine) at position 8, while the latter contain a neutral amino acid. Nearly all vertebrates examined thus far possess at least one OT-like and one vasopressin-like nonapeptide (Gimpl and Fahrenholz 2001).

More than 15 nonapeptides have been identified, suggesting multiple divergence events, but perhaps more notable is the evolutionary stability apparent in nonapeptide structure. For instance, both mesotocin and Leu<sup>8</sup>-OT – the OT variants most commonly found in nonmammalian and mammalian vertebrates, respectively – differ from vasotocin and each other by only one amino acid (Goodson 2013). Such observations suggest that evolution of OT occurred under strong selective pressure to retain the basal amino acid sequence found in vasotocin, possibly due to the integral roles played by OT in critical reproductive functions, which are discussed further below (Anacker and Beery 2013; Gimpl and Fahrenholz 2001). In addition to the structure of the OT peptide, other facets of the OT system are evolutionarily conserved, including the locations of OT-containing neurons and fibers, and the structure of mammalian OT receptors, which are more similar to OT-like receptors in birds and fish than to the mammalian vasopressin receptors (Gimpl and Fahrenholz 2001).

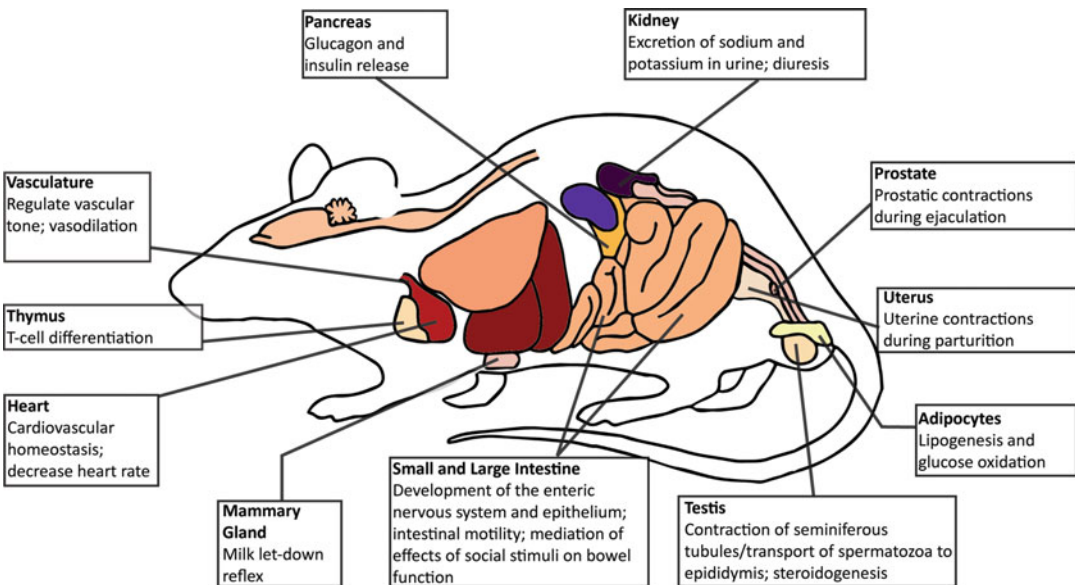
## Structure of the Oxytocin System

### Actions in the Periphery and in the Brain

In most mammals, OT is one of two peptide hormones (the other being vasopressin) that are secreted from the pituitary. Large neurosecretory cells (neurons modified to secrete peptide hormones into the blood) in the supraoptic (SON) and paraventricular (PVN) nuclei of the hypothalamus are major producers of OT, which they release into peripheral circulation via projections to the posterior pituitary (Wilkinson and Brown 2015). From there, OT circulates throughout the periphery, acting upon receptors located in a wide range of target tissues, including the gonads, uterus, mammary glands, heart, large and small intestines, and kidneys (Gimpl and Fahrenholz 2001; Fig. 1). The precise function of OT in many of these tissues has received scant attention, with the primary exceptions being the uterus and mammary glands. Cervical stretching and suckling induce pulsatile release of OT, which binds to receptors in uterine and mammary tissue and elicits contractions that facilitate parturition and milk ejection. These functions of the OT system

are highly conserved across mammalian species, including humans (Gimpl and Fahrenholz 2001).

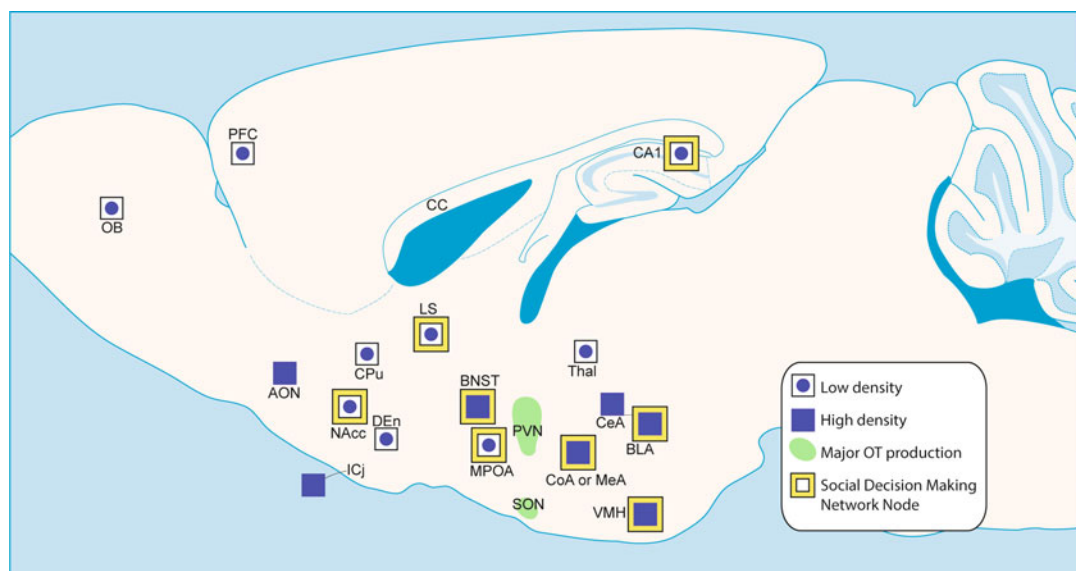
In addition to functioning as a hormone in the periphery, OT regulates a variety of behaviors by acting as a neuropeptide signal in the central nervous system, comprised of the brain and spinal cord. Although the SON and PVN are the primary sites of OT production in the brain, other regions, including the hippocampus and septal area, also release OT in response to external stimuli (Landgraf and Neumann 2004). Furthermore, OT-containing neurons have been documented in extra-hypothalamic sites, including spinal cord and brainstem areas, as well as key nodes of the “social decision-making network,” a group of reciprocally interconnected brain nuclei that regulate multiple forms of social interaction, including parental, sexual, and aggressive behaviors (O’Connell and Hofmann 2011, 2012; Veening et al. 2015; Fig. 2). OT receptors are present throughout this network, though the distribution and abundance of receptors varies widely – often in conjunction with differences in social behavior – across seasons, species, and individuals (O’Connell and Hofmann 2012; Ondrasek 2016).



**Oxytocin, Fig. 1** Widespread distribution of OT receptors in the periphery of the rat, with purported or known functions included for each site. Both male and female sex

organs are shown (adapted with permission, Ondrasek 2016)





**Oxytocin, Fig. 2** Sites of OT production, as well as distribution and relative densities of the OT peptide, in the rat brain. OT-containing regions that are also components of the social decision-making network (SDM) are highlighted to emphasize extensive integration of the OT system throughout the network (SDM network nuclei were identified based on a neural network model proposed by O’Connell and Hofmann 2012). *Abbreviations:* AON anterior olfactory nucleus, BLA basolateral amygdala, BNST

bed nucleus of the stria terminalis, CA1 cornu ammonis 1 of the hippocampus, CC corpus callosum, CeA central nucleus of the amygdala, CoA/MeA cortical or medial amygdala, CPU caudoputamen, DEN dorsal endopiriform nucleus, DG dentate gyrus, ICj islands of Calleja, LS lateral septum, MPOA medial preoptic area, NAcc nucleus accumbens, OB olfactory bulb, PFC prefrontal cortex, PVN paraventricular nucleus, SON supraoptic nucleus, Thal thalamus (adapted with permission, Beery 2015)

Oxytocin’s action at receptors in both the brain and periphery is likely important for coordinating physiological and behavioral processes. For instance, during lactation, suckling stimulates the release of OT into peripheral circulation, which subsequently induces milk letdown; at the same time, OT is released in extra-hypothalamic areas, where it regulates the expression of maternal behavior (Landgraf and Neumann 2004). These complementary functions – the production of milk and expression of parental care – are both critical for the survival of young mammals. In light of such observations, it seems reasonable to predict that OT’s peripheral and central functions are integrated, and in some cases even synergistic. However, little is known regarding interactions between the peripheral and central divisions of the OT system, or, more generally, how OT actions in the brain are influenced by peripheral processes or stimuli (Goodson 2013; Landgraf and Neumann 2004).

### Structure and Function of the Oxytocin Receptor

Like the majority of peptide hormones, OT binds to a G-protein coupled receptor. Briefly, these receptors consist of a single folded polypeptide that is embedded in the cell membrane and composed of three major regions: an extracellular series of loops that engage in ligand binding; a transmembrane portion consisting of seven helical domains; and an intracellular portion that is bound to the G-protein, a trimer made up of three subunits. These receptors function by transducing an external signal (binding by a ligand) to the interior of the cell, where a subunit of the G-protein complex responds by dissociating and subsequently activating intracellular second messengers. These messengers activate protein kinases and the release of calcium ions, which, among other things, activate other chemical messengers and proteins that act as transcription factors (Wilkinson and Brown 2015).

In the brain, OT receptors have been identified not only at synapses but also on neuronal axons and glial cells (immune cells that support and protect the brain's neurons; Mitre et al. 2016). Oxytocin may reach these receptors through two broadly defined means – via classical synaptic transmission, where peptides are released into a synapse and facilitate localized, point-to-point communication, or via a more recently described process known as volume transmission, in which peptides are secreted into and diffuse throughout the surrounding extracellular fluid, allowing them to reach more distant target sites (Ludwig and Leng 2006). Several brain regions that are involved in mediating social behaviors express OT receptors but lack innervation by OT-containing neurons (such areas include the amygdala, ventromedial nucleus of the hypothalamus, and olfactory bulbs); these observations suggest that both synaptic and volume transmission are important for communication within the OT system (Landgraf and Neumann 2004; Ludwig and Leng 2006).

## **Oxytocin and Behavior (I): Social Behavior in a Reproductive Context**

The fundamental drive to reproduce underlies many social interactions, as individuals variously seek each other out to mate, cooperatively rear their young, or compete for access to resources critical for reproduction (e.g., food, territory, or mates). Oxytocin plays a key role in mediating a variety of reproductive social behaviors in mammals – that is, social interactions that directly impact the production or rearing of young (Anacker and Beery 2013). The influence of OT on specific types of reproductive social behaviors – namely, sexual behavior, maternal care, and pair bonding – are summarized below.

### **Sexual Behavior**

In 1992, it was suspected, but not yet known for certain, that OT regulates mammalian sexual behavior (Carter 1992). Today, a sizeable literature on rats (*Rattus norvegicus*), and more recently on humans, confirms that OT influences

multiple phases of male and female sexual behavior, including sexual excitement, orgasm and ejaculation, and sexual satiety (Veening et al. 2015).

In humans, peripheral OT increases in both sexes prior to copulation and following orgasm, although it is unclear whether this change in OT is a direct mediator or byproduct of sexual arousal and orgasm (Borrow and Cameron 2012). Nonetheless, the observed rise in OT prior to mating has led to the suggestion that this hormone prepares reproductive organs for subsequent sexual behaviors (Borrow and Cameron 2012; Veening et al. 2015). Multiple lines of evidence support this conclusion, including reports that OT receptors in epididymal and uterine tissues are linked to ejaculation and uterine contractions that occur during orgasm (Borrow and Cameron 2012). Furthermore, the PVN – one of the primary sites of OT production in the brain – receives sensory input from the genital regions in both sexes and contains OT-rich cells that project to spinal neurons involved in generating male genital reflexes (Normandin and Murphy 2011).

Additional evidence for OT's contributions to sexual behavior derive from reports that exogenous OT administration – that is, OT delivered either peripherally (e.g., intraperitoneally) or centrally (i.e., directly into the brain) – modify sexual interactions in males and females. For instance, in male rats, both peripheral and central OT treatments decrease ejaculation latency, time between mating bouts, and facilitate erections (Lee et al. 2010). Similarly, in female rats, central and peripheral OT treatments facilitate lordosis, a stereotyped posture (characterized by back arching, hind leg extension, and lifting of the head and rear) that females display during copulation, although this effect varies with environmental light cycles and the specific site of central infusion (Veening et al. 2015). Interestingly, despite the effects of exogenously administered OT on sexual behavior, male and female transgenic OT-knockout mice, which cannot produce OT, display a complete suite of sexual behaviors that yield successful impregnation. These findings raise important questions about the specific contributions of endogenous OT to the normal expression of sexual behavior (Lee et al. 2010).

### Maternal Care

By acting in both the periphery and brain, OT plays an evolutionarily conserved role in regulating several facets of maternalism, including lactation, parturition, and maternal behavior (Broad et al. 2006). Because they display strikingly different patterns of maternal behavior, rats and sheep (*Ovis aries*) serve as particularly important models for understanding OT's role in different aspects of maternal care. While female rats indiscriminately nurture any conspecific infant throughout the postpartum period, female sheep and other precocial mammals develop a highly selective preference for their own offspring; thus, rats have been used to investigate maternal attraction to offspring, while sheep have been used to examine the processes underlying selective maternal recognition (Numan and Young 2016).

In general, virgin female rats are averse to interacting with young and will only provide maternal care after an extended period of acclimation to pup stimuli, or if they are primed with hormones (Pedersen and Prange 1979). In the absence of such treatments, female rats giving birth to their first litters display full maternal behavior – characterized by grouping, licking, crouching over, and retrieving pups, as well as nest-building – in response to the hormonal changes that occur around parturition, including increased estrogen, decreased progesterone, and the release of OT into the brain (Numan and Young 2016). That OT plays an important role in mediating the onset of maternal behavior is underscored by reports that central infusions of OT and OT receptor antagonists promote and inhibit, respectively, the display of maternal care in female rats (Pedersen and Prange 1979; Pedersen et al. 1994). Critical to the expression of postpartum, maternal behavior is a neural circuit beginning with OT projections from the PVN to the medial preoptic area (MPOA), followed by subsequent projections to the ventral tegmental area and then to the nucleus accumbens (NAcc; Numan and Young 2016; Pedersen et al. 1994).

Like rats, female sheep will care for any infant immediately after parturition. However, maternal recognition and an enduring mother-offspring bond, concurrent with aggressive behavior

towards unrelated lambs, emerge within hours of birth. The onset of maternal selectivity involves the development of an olfactory preference for one's own offspring; OT's possible involvement in this process is supported by the finding that, during birth, OT is released into the brain's olfactory bulbs, which in turn project to other brain areas that mediate maternal behavior (Numan and Young 2016). In addition, central OT infusions promote maternal behavior and decreased aggression towards novel lambs in estrogen-primed ewes (Kendrick et al. 1987).

The above discussion of maternal behavior presents a convenient opportunity to briefly address the importance of interactions between OT and other neural systems. In the brain, OT operates within a complex milieu comprised of numerous compounds, including classical neurotransmitters (e.g., dopamine, serotonin, epinephrine, norepinephrine), steroid hormones (e.g., testosterone and estrogen), and other peptides (e.g., vasopressin). Although it is known that the OT system can both influence and be modulated by other neural systems, the behavioral consequences of such interactions are, in many cases, not as well understood as the actions of individual systems (Baskerville and Douglas 2008). Nonetheless, communication among these systems has important behavioral implications. For example, interactions between OT and dopamine – a neurotransmitter that plays a key role in coding the salience (either positive or negative) of social experiences and regulating reward-seeking behaviors – are important for establishing and maintaining maternal attraction to young after birth (Numan and Young 2016).

### Pair Bonding

The mother-infant relationship is a defining and evolutionarily conserved feature in mammalian taxa. In contrast, *pair bonds* – social bonds between unrelated, adult sexual partners who often share parenting responsibilities – are rare, occurring predominantly in the 5% of mammalian species that display monogamy. However, striking similarities between pair and mother-infant bonds exist; for instance, both types of relationships endure following prolonged periods of

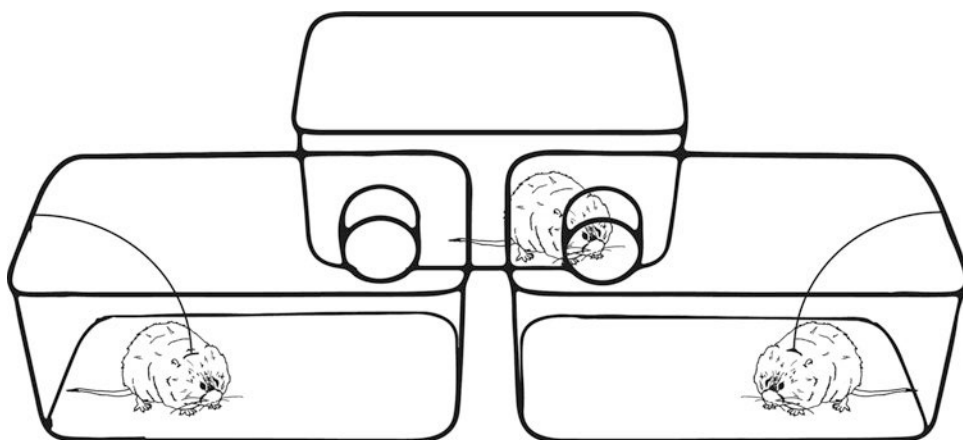
separation. Similarities between these two types of social relationships, combined with the widespread incidence of maternal care across mammals, suggest that the mechanisms underlying maternal-infant bonds may have provided the neurobiological framework for the evolution of pair bonding (Numan and Young 2016; Williams et al. 1994).

A great deal of effort has been invested in elucidating the proximate causes of pair bonding, perhaps because monogamy often co-occurs with other intriguing social behaviors – including the assembly of family groups and altruism. Comparisons among closely related vole species (members of the Arvicoline subfamily of rodents) with different mating systems, either monogamy or polygamy, have been particularly revealing. These comparisons have relied heavily upon use of the partner preference test, a standardized approach for identifying pair bonds. In this experimental paradigm, a focal individual has the option of interacting with a stranger or a familiar conspecific (usually a cagemate or “partner”); individuals that spend significantly more time in contact with the familiar cagemate are said to have a *partner preference*, which is assumed to indicate the existence of a pair bond (Fig. 3; Numan and Young 2016).

In the monogamous prairie vole (*Microtus ochrogaster*), mating facilitates the formation of

pair bonds between males and females, although bonding can occur without mating following 24 h of cohabitation (Adkins-Regan 2009). Neuropharmacological studies demonstrate that OT influences the pair bonding process, whether bonds emerge following mating or simply cohabitation. In female prairie voles, brain infusions of OT promote bonding after a brief cohabitation of 6 h – a period normally too short for pair bonding to occur (Williams et al. 1994). Furthermore, infusions of an OT receptor antagonist inhibit the development of a partner preference in females after mating, indicating that OT also facilitates the effect of mating on pair bonding (Insel and Hulihan 1995). Such studies were thought to suggest that males and females rely on different peptide systems for the establishment of pair bonds; specifically, males and females were believed to be more sensitive to vasopressin and OT, respectively. However, more recent neuropharmacological studies in prairie voles challenge this view by showing that vasopressin modulates pair bonding in females, and conversely that OT receptor antagonists impede pair bonding in males (Young et al. 2008).

Elucidation of the neural circuits underlying pair bond formation emerged from neuroanatomical comparisons of peptide, receptor, and gene expression in monogamous versus promiscuous voles, such as the meadow (*Microtus*



**Oxytocin, Fig. 3** The partner preference test, a key experimental paradigm used to identify social bonds between familiar individuals, usually cagemates. The partner and a

novel individual are tethered in opposing forechambers, while the focal individual is placed in the rear chamber and allowed to investigate both stimulus animals freely

*pennsylvanicus*) and montane voles (*Microtus montanus*), which do not form pair bonds (Numan and Young 2016). For instance, in females the distribution and density of OT receptor and mRNA expression differ, such that they are higher in monogamous versus promiscuous species across several brain regions, including the NAcc and bed nucleus of the stria terminalis (BNST; Young et al. 2008). Particular importance of the NAcc in OT-mediated pair bonding in females is highlighted by a report that infusion of an OT receptor antagonist directly into the NAcc blocks mating-induced partner preferences in female prairie voles (Numan and Young 2016).

## **Oxytocin and Behavior (II): Nonreproductive Social Affiliations**

As described above, OT plays a critical role in mediating many of the physiological and behavioral processes that are key to successful reproduction. However, animals also interact in nonreproductive contexts, participating in relationships that do not immediately impact the production or rearing of young. For instance, individuals in numerous bird, fish, and mammalian species gather in large aggregations during the nonbreeding season; in addition, females in several mammalian species engage in long-term same-sex relationships that persist during nonreproductive periods. Such nonreproductive affiliations often occur in promiscuous species, underscoring the importance of recent efforts to revise the classical view that equates monogamy and polygamy with social and asocial behaviors, respectively (Anacker and Beery 2013; Goodson 2013).

Compared to OT's contributions to pair bonding and maternal behavior, far less is known about the peptide's role in regulating nonreproductive social behaviors, though recent discoveries address this disparity. Work involving species aside from the common rodent models – rats and mice – has revealed a great deal about OT's influence on behaviors that support group-living outside of the reproductive context. For instance, female meadow voles – which are

asocial during the breeding months, but group-living during winter – show variations in same-sex huddling behavior that are associated with OT receptor expression in the lateral septum (LS), such that receptor density in the LS declines as huddling time increases (Anacker and Beery 2013). This negative correlation between LS binding and huddling time mirrors interspecific differences between social and solitary species of rodents known as tuco-tucos. Specifically, colonial tuco-tucos show lower OT receptor expression in the LS than their solitary counterparts. Intriguingly, although female meadow voles show seasonal differences in OT receptor density in the NAcc – a region that is critical in pair bonding, as discussed previously – these differences are not associated with seasonal variations in same-sex social affiliation, nor is OT receptor expression in the NAcc correlated with huddling behavior, more generally (Beery and Zucker 2010). In combination, the above reports suggest that the neural circuits mediating group-living are distinct from those underlying pair bonding and implicate OT function in the LS as a mediator of rodent grouping behavior (Anacker and Beery 2013).

## **Oxytocin and Neuropsychiatric Disorders in Humans**

In humans, social relationships have a striking impact on physical and psychological wellbeing. Adults engaged in supportive relationships with their spouses, and children with secure attachments to their parents, have better long-term prospects – their overall sense of “happiness” is higher, and their health outcomes are improved relative to individuals without these types of relationships (Waldinger et al. 2015). Thus, efforts to uncover the neurobiological bases of human social behavior are of great value, not only for understanding inter-individual relationships but for identifying causes, and treatments, for human psychosocial disorders.

Studies of the OT system using rodents and nonhuman primates laid the foundation for similar investigations in humans. Efforts to elucidate



function of the OT system in humans have relied heavily upon two minimally invasive approaches: (1) assessment of the behavioral and cognitive consequences of intranasal administration of OT, and (2) identifying associations between behavioral phenotypes and polymorphisms in the genes encoding OT and/or its receptor. Polymorphisms in the OT receptor gene are associated with variations in several aspects of human social behavior and cognition, including empathy, facial recognition, separation anxiety, attachment phenotypes, and responsiveness to social exclusion (Johnson and Young 2017).

Reports such as those described above provide strong evidence that, as in other mammals, OT in humans plays an integral role in regulating social behavior. This conclusion prompted considerable excitement about the use of OT as a therapeutic for human neuropsychiatric disorders in which social dysregulation is a key issue, including autism spectrum disorders (ASD), schizophrenia, social anxiety disorder, and obsessive-compulsive disorder. Thus far, a case for OT's role in these conditions has been made most strongly for ASD. Promising findings include reports that polymorphisms in the OT receptor gene are associated with ASD across several different populations, and that OT treatment reduces repetitive behaviors and improves social communication in persons with ASD (Romano et al. 2016). However, it should be noted that interpretation of these outcomes has been met with some caution, in part because the mechanisms underlying the effects of intranasally administered OT remain unclear. Specifically, it is unknown whether intranasal OT can cross the blood brain barrier and thus gain direct access to socially relevant brain areas, although recent discoveries suggest that this is the case (Neumann et al. 2013). Furthermore, work in prairie voles demonstrates that while short-term administration of intranasal OT promotes social contact, chronic treatment inhibits social bonding (Bales et al. 2013); this finding raises concerns that treating neuropsychiatric disorders with repeated doses of intranasal OT may worsen, rather than improve, symptoms in the long term (Beery 2015; Romano et al. 2016).

## OT: More Than Just a “Pro-social” Hormone

After the early 1990s, the subsequent two decades of OT research focused heavily upon the peptide's pro-social effects, leading to its characterization as the “cuddle” hormone. However, recent discoveries involving multiple species reveal that OT promotes a spectrum of social behaviors, including not only affiliation but aggression, fear, and social exclusion. For instance, in prairie voles, OT not only facilitates affiliative interactions between mothers and pups, but aggression towards conspecifics; the latter is presumably a tactic for protecting young from infanticide. While OT receptors in the NAcc appear to promote pair bonding, elevated levels of the same receptor type in the LS have been associated with enhanced fear, decreased alloparental care, and reduced huddling behavior (Beery 2015). Furthermore, in humans, OT increases not only in-group favoritism and cooperation but racial biases and outgroup derogation as well. Such findings demonstrate that function of the OT system is highly context and circuit dependent and prompted Anacker and Beery (2013) to suggest that OT's mediation of both affiliative and agonistic behaviors, while seemingly contradictory, may actually help preserve group structure by establishing social order and maintaining stable group membership.

## Conclusion: Future Directions

Originally thought of as a “female” hormone that primarily regulates lactation and parturition, OT is now recognized as a versatile peptide with wide-reaching effects, not only on reproductive physiology but on numerous social behaviors (Anacker and Beery 2013; Beery 2015; Carter 1992). By 2015, OT studies numbered in the tens of thousands and revealed the diverse range of OT's neurobiological, endocrine, and behavioral functions; yet, many important questions regarding this peptide system still exist. For instance, much of what is currently known about the OT system derives from work conducted almost exclusively

in rodent and primate taxa, a bias that makes it difficult to determine how broadly conclusions about OT's role in the evolution of social behavior may be applied across mammalian species. Other unknowns include the OT system's sensitivity to environmental stimuli that impact social behavior (e.g., food availability), how or whether OT's functions in the periphery and the brain are integrated, and how the OT system mediates inter-individual variations in social phenotype (Ondrasek 2016). Given OT's likely role in social evolution and its promise as a therapeutic for human neuropsychiatric disorders, there is strong reason to predict that OT research will continue to grow and that many of these unknowns will be addressed in the coming years.

## Cross-References

- Aggression
- Alloparental Care
- Maternal Behavior
- Neural Control of Behavior
- Neural Network
- Paternal Behavior
- Parental Investment
- Pro-social Behavior
- Sex Differences
- Social Behavior

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## Packet Theory

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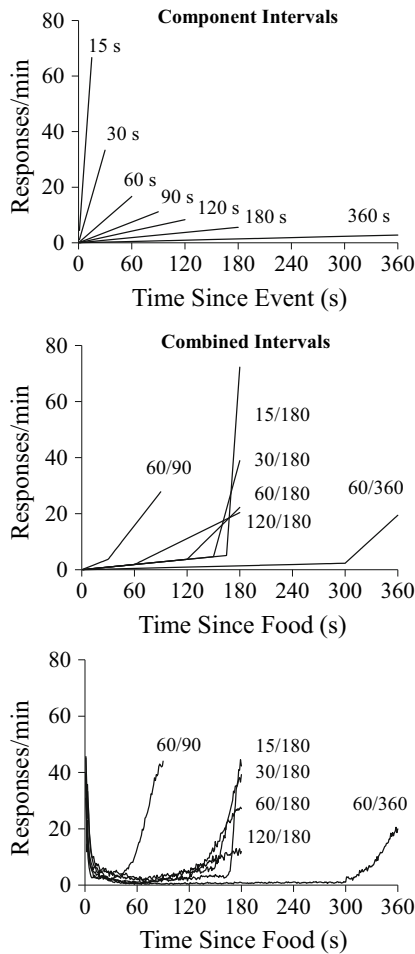
### Introduction

Packet theory (Kirkpatrick 2002; Kirkpatrick and Church 2003) was originally developed to provide a bridge between classical conditioning and interval timing. These two fields historically developed largely independently even though there is considerable overlap in the methods used to study the key phenomena in each field. Classical conditioning involves presenting a stimulus for a set duration, followed by an outcome that is usually biologically relevant. Initially, the stimulus evokes little or no response, but over the course of repeated pairings, conditioned responses (CRs) emerge and increase in strength. Although the stimulus is often presented for several seconds, CRs are usually measured collapsed over the whole period. Timing studies involve presenting a stimulus for a set duration followed by an outcome. Timing is typically studied within classical or instrumental conditioning paradigms, wherein the latter case a response is required to produce the outcome. Timing studies focus on the pattern of responses over the course of the stimulus. Both paradigms involve closely related procedures, and the primary difference is the

dependent variable for analysis (rate versus pattern of responding).

Prior to the creation of packet theory, Kirkpatrick and Church examined different theories of timing, conditioning, and some hybrid theories (Church and Kirkpatrick 2001). They reported that the hybrid theories performed best in accounting for both the rate and pattern of responding. Subsequently, it was found that appropriately timed responses were present at the earliest stage of learning (Kirkpatrick and Church 2000; Kirkpatrick and Balsam 2016), suggesting the need for a fully integrated hybrid model.

While these previous findings provided an important foundation, the most critical precursor to packet theory was the discovery of a general framework for determining the rate and pattern of CRs. Kirkpatrick and Church (2000) gave groups of rats a stimulus that lasted for different durations followed by food and with different times between foods or cycle times. They measured the head entries into the food cup (the CR) as a measure of anticipation of the upcoming food delivery. The response patterns over the whole cycle duration for the six groups are shown in the bottom panel of Fig. 1, with each function labeled with the stimulus/cycle durations. The shape of these functions reflects: (1) head entries following the previous food delivery to collect the food pellet, (2) an anticipatory gradually ramping response rate during the ITI, and (3) a sharper anticipatory ramping response rate during the stimulus.



**Packet Theory, Fig 1** (Top) A family of interval functions relating the mean stimulus or cycle duration to the mean response rate during the stimulus or cycle. (Middle) Arithmetic combination of the component functions to produce the predicted response rate gradients for each of the six groups. (Bottom) Actual response rate functions for each of the six groups (Adapted from Kirkpatrick and Church (2000))

The set of four groups with the 180 s cycle durations, but with stimulus durations of 15, 30, 60, or 120 s, shows that the ramping functions during the ITI are highly similar, but that the responding during the stimulus is determined by the stimulus duration, with shorter stimuli resulting in higher rates of responding and steeper increases. Comparisons of the set of three groups with 60 s stimulus durations, but with cycle durations of 90, 180, or 360 s, show that responding during the stimulus is similar, but the ITI responding differs. Using curve fitting to

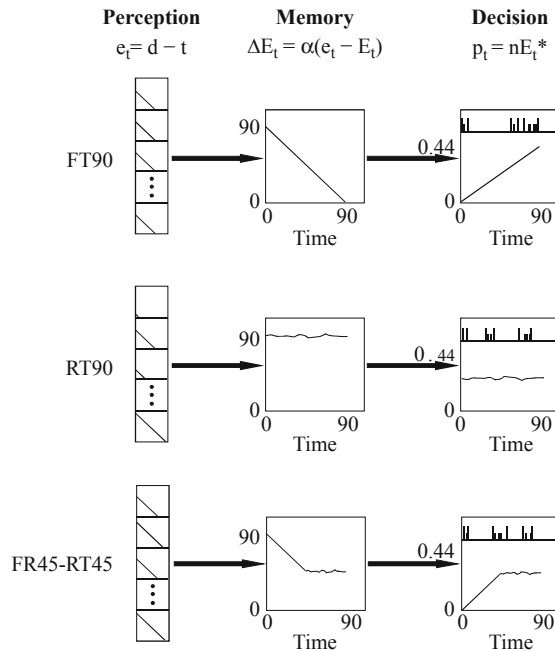
determine a generating function for the response rates, Kirkpatrick and Church created a family of ramping functions for each of the different stimulus and cycle durations (Fig. 1, top panel). They then created combined functions (middle panel), in which the ITI response was determined by the function for the relevant cycle and the stimulus response was the arithmetic combination of the relevant cycle and stimulus functions. The linear combined functions are generally similar to the anticipatory response rate functions, minus the head entries at the very beginning of the interval.

## Packet Theory

Packet theory grew out of the linear curve fitting model of Kirkpatrick and Church (2000), but with some important extensions. Kirkpatrick and Church (2003) implemented different schedules of food deliveries (with no stimuli) in which the mean and variability of the cycle duration was manipulated across groups of rats using a fixed time (FT) schedule. They found that the mean cycle duration determined the mean rate of the response function, which mirrored the previous findings of Kirkpatrick and Church (2000). Moreover, the distribution of the cycle durations determined the pattern of responding. In addition, they reported that the head entry behavior occurred in response bouts or packets. The packets were invariant across different interval durations and distributions, but the pause times between packets were directly controlled by the cycle times. Thus, the packets of responding became the key unit of behavior that was predicted by packet theory.

The model is diagrammed in Fig. 2, with separate components for perception, memory, and decision. The perceptual module of Packet theory consists of ramping functions associated with individual intervals. In an FT 90 s, the ramping functions would all be the same and would span the 90 s duration, but for random (RT) or combined FT–RT functions, the ramping functions would vary across cycles according to the distribution of intervals. The memory module in packet theory is a weighted sum of the individual ramping functions from the perceptual module, with the weights determined by the free parameter





**Packet Theory, Fig 2** The perception, memory, and decision components that comprise packet theory, with application to fixed time (FT), random time (RT), and combined FT–RT schedules. The perception module consists of linear ramping functions ( $e_t$ ) that are determined by the experienced intervals. Each ramping function is determined as a function time ( $t$ ) and spread across the duration ( $d$ ) of the interval. The conditional expected time function

in memory ( $E_t$ ) is a weighted combination of the individual ramping functions ( $e_t$ ), with the effect of relatively recent intervals determined by the weighting parameter,  $\alpha$ . The decision module issues packets of responses, with the probability of packet generation ( $p_t$ ) determined by a transposed conditional expected timing function from memory ( $E_t^*$ ) multiplied by a responsiveness parameter,  $n$  (Adapted from Kirkpatrick and Church (2003))

$\alpha$ . This is a conditional expected time function, which is the expected time until food, given that food has not yet been delivered. The decision module determines the probability of packet occurrence, which is inversely related to the conditional expected time function in memory. The packets of responding contain a random number of responses with random interresponse times. The functions for generating the model packets were determined by fitting functions to the packets generated by the rats. The number of packets per interval,  $n$ , is the second free parameter in the model, which determines overall response rates regardless of interval duration.

Kirkpatrick (2002) demonstrated several applications of packet theory in the timing and conditioning domains, showing quantitatively correct predictions of the following phenomena. (1) The scalar property, a key feature of interval timing (Gibbon 1977). (2) The rate of CRs during the

stimulus across a range of stimulus durations, a measure of the strength of conditioned responding. (3) The rate of CRs during the ITI across a range of cycle durations, a potential measure of contextual conditioning. (4) The rate of CRs during the trace interval, when there is a gap between the stimulus and outcome. (5) The effect of stimulus: cycle duration (Gallistel and Gibbon 2000) on the relative rate of CRs during the stimulus. Packet theory also makes a novel prediction that organisms time all distributions of durations, which does appear to be the case, at least in rats (Kirkpatrick and Church 2003). Timing of exponential random intervals occurs because the conditional expected time is flat and thus the model predicts randomly distributed packets of responding. Thus, timing of fixed and random intervals is accomplished with a single process rather than assuming that organisms time fixed intervals, but do something different with variable intervals.

## Evaluation and Extensions of Packet Theory

Compared to many timing and conditioning models, packet theory has a benefit of being relatively inflexible and parsimonious. The perceptual and memory components are driven by the stimulus inputs, with the only free parameter being the memory weighting parameter which affects the relative influence of recent events. The response output is driven by the memory component, but with an added response rate parameter. The packets are determined by the properties of previous data. Yet, despite these constraints, the model offers unique and accurate predictions of response rate and pattern in basic interval schedules that bridges the fields of classical conditioning and timing. However, all models have weaknesses, and one major weakness of the original version of packet theory is that it did not include a mechanism for learning nor did the model include any mechanism for the occurrence of extinction when outcomes are withheld. This is a serious challenge of the model for application to many classical conditioning phenomena.

More recently, Guilhardi et al. (2007) developed an extension of packet theory, known as the modular theory, designed to build on the strengths of the original model but also overcome the major weaknesses. The most noteworthy change in the modular theory is the separation of the memory into two components: pattern and strength memories. The pattern memory closely resembles the original packet theory memory function and is only influenced by reinforcement. A new strength memory component was added, based on the Rescorla–Wagner model (Rescorla and Wagner 1972), in which the associative strength of the stimulus is increased or decreased dependent on outcome delivery or omission, respectively. This change allowed the modular theory to explain basic acquisition and extinction phenomena. Most importantly, because pattern memory is only updated when reinforcement occurs, the response pattern and the maintenance of associations are maintained during extinction, consistent with several findings in the literature (Guilhardi and Church 2006). However, these improvements in the model were

accompanied by an increase in complexity and flexibility of the model, thus losing some of the original strengths of packet theory, although it is possible that the model implementation could be simplified for some applications by fixing a subset of the free parameters.

## Conclusion

Packet theory and the modular theory are attempts at building models that bridge classical conditioning and timing. This is an important venture that can spark new research, and new model development should continue in this area. In addition, more research is needed at the intersection of these two fields to provide unique data to guide and constrain future model development.

## Cross-References

- [Acquisition](#)
- [Cognition](#)
- [Delay of Reinforcement](#)
- [Inhibition of Delay](#)
- [Perception](#)

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## Paedomorphism

► [Neoteny](#)

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## Paedomorphosis

► [Neoteny](#)

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## Pain and Ethics of Animal Care and Use

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## Synonyms

[Animal suffering](#); [Animal welfare](#); [Morality](#); [Neuroethics](#); [Painience](#)

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## Definition

Responsible regard and treatment of nonhuman animals based in part upon their capacity to experience pain and manifest some form of sentience.

## Introduction

Neuroscientific assessment and definitions of mechanisms of sensation, cognition, emotion, and behavior have engendered a view of neural systems – and their functions – as embodied within organisms-in-environments. Understanding the neural bases of organisms’ ecological interactions has two-fold value: first, it fosters insight to the neurocognitive capabilities of individual beings and various species; and second, it prompts deeper reflection and more thorough address of what such functions and capacities *mean* relative to the ways that organisms are regarded and treated. As history reveals, the use of even simple forms of neurocentric criteria to shape categorical distinctions of what types of organisms, and which individuals may claim particular social goods is not new (Aristotle 1966). The scope and pace of contemporary neuroscientific advancement(s) has only fortified this trend, in part through heuristics that have been influential to establishing theories of mind. But, a theory of mind is a powerful tool, and with this power comes considerable responsibility (Giordano 2010; Giordano and Benedikter 2012; Giordano et al. 2012).

Much of the information gained from neuroscientific research has been derived from animal models. Increasingly, scientific evidence confirms that many animal species (e.g., mammals, several species of vertebrates, cephalopods, certain insects) have nervous systems of sufficient structural and functional sophistication to sustain complex cognitive processes. This challenges long held beliefs about animals’ capacity for experiencing consciousness, pain, and emotions, and contests rather dogmatic philosophical distinctions between humans and animals (Griffin 1994; White 2007).

A deepening understanding of the ways that nervous systems and brains are involved in (or evoke) those characteristics—valued within individuals, groups, and a species—should compel and sustain the ways that the organisms possessing such characteristics are regarded and treated. But, it is not clear whether humanity will be willing and able to embrace such knowledge to revise the moral attitudes and the ethics and policies affecting nonhuman animals. The relatively new field of neuroethics may be useful to address these challenges in that it grounds the discipline and its practices to: (1) a naturalistic philosophy; (2) the current epistemological capital of neuroscience; (3) the moral issues, problems, and solutions arising in and from neuroscientific research and its applications; and (4) a neurocentric criteria to define and resolve ethical questions and decisions (Giordano 2011, 2012; Giordano et al. 2012).

### **Painience as a Fundamental Neuroethical Criterion**

The recognition of sentience as a basis for establishment of ethical and legal codes for animals represents an explicit departure from arbitrary speciesism, and a noteworthy advancement toward the employment of neurocentric criteria. However, there is still much that remains unknown about the neurocognitive function(s) of animals, which tends to complicate determinations of what species of animals are sentient, the nature of such sentience (e.g., shifting definitions of “higher” and “lower” consciousness), and if and what particular properties of sentience should be relevant. This makes it difficult to discern the extent of moral regard and level of good that should be afforded (i.e., ranging from what might be considered obligatory to that which is supererogatory).

An organism’s capacity to feel pain as noxious (injurious) and explicitly hurtful (viz., pain *qua* pain; not simply nociception, but noci-perception) represents a minimum criterion upon which to base and predicate moral consideration and actions (Bentham 1823; Giordano 2009, 2010). But this too, is not without complication. The formal definition of pain as “...an unpleasant

sensory and emotional experience...” (IASP 2009) obtains that for an objective neural event to be subjectively experienced as pain (and not merely a high intensity, aversive stimulus), it would necessarily involve the combinatory qualities of sensation, cognition, and emotion. To be sure, pain is a multidimensional event that involves and is derived from “...a sensation in a part of the body...and an emotional experience...” (IASP 2009).

Some have claimed that animal pain is not as significant as that of humans, given that certain areas of the cortex and neural pathways that have been shown to be responsible (in humans) for the associative linking of sensations to cognition and emotion are not present in all animals (IASP 2010). These assertions are objectionable on several grounds. First, these positions fail to acknowledge the most current perspective(s) regarding the structure–function relationship of nervous systems; these can be colloquially summarized using a computer analogy to posit that the presence of the “wetware” (i.e., the neural substrates) is often a reliable predictor that the “program” (e.g., pain) can and will be executed. This is strengthened by comparative studies of mammalian species as anatomical, physiological, and behavioral models of human development, neurophysiology, and pain (Bekoff 1995). Perhaps what is more important is the recognition that the experience of pain, while involving a number of higher neuroanatomical loci (e.g., the somatosensory and associative cortices), is also reliant upon subcortical structures. These structures likely do not function site-specifically, but are engaged as and within hierarchical networks, the properties of which contribute to mental process(es) (Baars 1998; Edelman 2004).

Thus, the second flaw in arguments that attempt to negate the experience and profundity of animal pain is that they tend to attribute the function of networked hierarchies of neural structures (if not the whole brain) to particular parts (i.e., what has been called the “divisional” or mereological fallacy) (Bennett and Hacker 2003).

Third, is that 1-to-1 representation of neural structure–functional relationships between humans and animals need not be present for the

occurrence of cognitive, emotional, and behavioral processes. The networks involved in pain processing are not necessarily identical (i.e., homologous) to those of humans, but instead may – and often do – function analogously to conjoin distinct neural substrates to obtain the pain event and experience. This speaks in return to the second point – namely, that brains are embodied within an organism and this individual neural structure and function gives rise to differing subjective experiences.

At present, we cannot know the phenomenological characteristics of animal pain; and while an understanding of organisms' nervous systems' capacity to subtend pain is necessary and important, argument-by-analogy supports the use of behavioral expressions of pain such as increased vocalizations, agitation, writhing, reluctance to move and decreased locomotion, attending to and guarding parts of the body, and huddled postures. In mammals, such behaviors have been shown to represent more than merely “pseudo-affective” responses, and are now regarded as manifestations of cognitive and emotional processes, and abstract dimensions of fear, and (some form of) suffering (Sufka et al. 2009).

Such types of attending, guarding, and writhing responses have also been identified in crustaceans, and certain insects and other invertebrates. Additionally, it has been shown that these creatures have nocisponsive nerve endings, specialized nociceptors, and defined neural pathways to subserve high intensity noxious stimuli. Taken together, these findings would allow the possibility that such organisms experience at least nociception, and some type of noci-perception may also be plausible. Therefore, recognition of the neuroscientific fact that pain *can* occur in a particular organism is a necessary and sufficient condition to afford that organism moral consideration and respectful treatment. This is not inconsistent with a number of ethical traditions that base human action upon premises of non-harm and/or some version of a “golden rule” maxim (i.e., “do unto others”) that begins from a presumption that said others can experience “hurt” as similar or analogously to the way(s) that humans know it. To take this argument a step

further, the obligation to exercise this modicum of consideration and care reflects, and is derived from, the existential vulnerability of painient non-human animals that positions them as the subjects of human responsibility and care.

### Ryder's Painism Reconsidered

In this context, Richard Ryder's thesis of “painism” offers a number of precepts (i.e., what Ryder called “rules”) for the prevention and treatment of pain that may be worthwhile to a neuroethical approach to the moral regard and treatment of animals (Ryder 2001). Ryder's core thesis defines the nature and purpose of morality and ethics as relative and relevant to pain and the painient. The imperative to recognize animals' capacity to experience pain, and the human responsibilities that arise thereupon are obtained in the claim that “...*moral standards should apply equally to all painient individuals, regardless of species*” (Ryder 2001).

From these fundamental premises follow prescriptions against the infliction of “*unconsented pain*,” and pain “...*for trivial purposes*” (Ryder 2001). These assert responsibility for the stewardship of contemporary knowledge of neural mechanisms of animal pain and the power to inflict, prevent, and/or mitigate pain, which should undergird the ethical treatment of animals, in general. Explicit to these statements is the importance of a more finely grained analysis of the ways that animal welfare is imparted in other utilitarian agendas of human society.

### Painience and Precautionary Conduct

This argument may stand as a basis for both individual reflection and to contribute to guidelines and policies for the treatment of animals. This aim does not deny human needs and motives for flourishing. Nor is this a call for strict veganism, the abandonment of all animal products, and divorce from keeping pets, zoos, and the use of service and work animals. This is not an exhortation of extremism in the moral consideration and treatment of animals. But, it is important to use the most current evidence from neuroscience to inform epistemology, the generation of useful neurocentric criteria in the formulation of



ontologies, and the regard for both human and nonhuman beings. Simply put, recognition of pain in nonhuman animals dictates human responsibilities to minimize or prevent the infliction of pain in these creatures.

### Pain Research Involving Animals

But it is in this spirit of inquiry that yet another potential conundrum is encountered: Given that research is the principal tool that enables the articulation of science and acquisition of knowledge, there is a rational and defensible argument for continued studies to further elucidate the neurocognitive functions and capabilities of animals. Yet, the goals of such investigations, how such studies are undertaken, and how findings are utilized are equally important if science is to remain ethically sound. Pain research involving animals provokes particular ethical discussion and controversy, since it axiomatically is intended to elicit pain in the research subject, and a full presentation of this discussion exceeds the limits of this entry (see, for example, the work of Greek and Greek 2010; and Regan 2001).

To reiterate, while the phenomenology of pain cannot be objectively measured in animals (including the human animal) (Giordano et al. 2010), behavioral and physical responses to painful stimuli can lead to strong inference(s) regarding accompanying and resultant unpleasant emotional experience. So, while it is possible, and in some cases likely, that the perception and meaning of animal pain is different from that of humans (given distinctions in ecology, lived body, and life world), it is important to acknowledge that neural systems are in place and operational that allow many animal species to experience such stimuli as “noxious,” and this noxiousness is fundamental to the cognitive-emotional event, and hurtful nature of pain.

Animal studies have been important to guide and complement investigations involving human subjects (Mogil et al. 2010). However, a number of limitations and criticisms of animal models of pain have been brought to the fore, including a lack of ecological validity, narrow emphasis upon sensory events, lack of correlation to clinical pain

states in humans, inadequacies when addressing the epidemiology of chronic pain (in both human and animal populations), and inferiority of design and reporting standards (Mogil et al. 2010; Herrmann and Jayne 2019).

Identifying these gaps and inadequacies is crucial to the iterative reappraisal of the scope, conduct, and value of pain research in animals (if not animal research, overall). Questions essential to such reappraisal reflect the well-known “Three R’s” (reduction, revision, replacement), as proposed by Russell and Burch, and pose: (1) whether painful methods can be replaced with other, less invasive protocols; (2) if and how protocols and methods can be refined to minimize the painful nature of the research; and (3) whether and how the numbers of animals – and perhaps overall number of studies – can and should be reduced (Russell and Burch 1959).

There is continued uncertainty and debate within the scientific community as to whether animals provide a realistic model of human pain (Bennett and Xie 1988; Mogil 2009; Herrmann and Jayne 2019). This reflects a type of “extrapolation dilemma” (Steel 2007), which elicits two potential scenarios that are important to the ways that results from research studies are used. In *Scenario A*: the model is “distant” and therefore, while providing some information, remains “insufficient” for direct comparative applications due to differences and gaps in the structures and functions of systems studied. The *Resulting Implication*: is to abandon the model in favor of others that are more proximate and applicable. In *Scenario B*: the model is “proximate” and therefore “sufficient” given the similarity of structures and functions of those systems studied to the comparative target. The *Resulting Implication* is that information from the model should be applied both to the comparative target *and* to the model. If it is (rightly) assumed that current animal models of pain fulfill criteria of being proximate and sufficient sources for information that may be directly relevant, and translate to knowledge about human systems, then what is learned from studying animals – to gain information about humans – is applicable to both humans, *and*

those animals (i.e., the species) that are the object of study. If this is so, then the good of research could be maximized through the application and use of such knowledge to inform and direct subsequent actions toward both humans *and* animals.

From this, a foundational stance for the conduct of animal research and care could be derived from, and based upon a version of Rawls’ principle of *maximin*: Given (a) the unequal distribution of knowledge, capability, and power between humans and animals, and (b) reasonable expectation that any organism with the anatomical and physiologic capabilities for pain will manifest this experience, then (c) ethical probity can be achieved and sustained by maximum prevention and mitigation of such pain, as a minimum benefit that should be allocated by those in power toward the provision of the welfare of those organisms over whom such power is exercised (Rawls 1971).

Conclusion

It is important to recognize the potential benefit of animal pain research to both human and veterinary medicine, but it is equally important to question how, and to what effect research findings will be utilized. In light of knowledge about pain gained from such investigations to date, continued pain research in animals is acceptable if and only if any and all such studies: (1) adhere to practical and ethical guidelines that are consistent with the most contemporary understanding of comparative and cognitive neuroscience, (2) adopt a frank precautionary stance when the welfare of any painient creature is at risk, and (3) attempt to directly employ research findings to benefit animal species (i.e., reciprocal and/or reverse translation), writ both small (i.e., within veterinary practice) and large (i.e., as applied to the care and treatment of wild, captive, livestock, and domestic animals). Toward such ends, an expansion of the 3 Rs may be useful (i.e., 3 Rs + 3) to include broader precepts that are applicable both to research and more general regard and treatment of animals, see Table 1.

**Pain and Ethics of Animal Care and Use,**  
**Table 1** 3Rs + 3 Precepts and Practices

|                                                                                                                                                                   |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Reflective and Precautionary Process                                                                                                                              |
| 3 Rs + 3:                                                                                                                                                         |
| <b>Respect:</b> For knowledge to date, as well as the animal subjects (of research) and animals in general,                                                       |
| <b>Reciprocal Translation:</b> Of animal research toward human trials to veterinary and animal welfare applications when/where appropriate,                       |
| <b>Responsibility:</b> To appreciate and use the most current information about animal painience and cognition to guide regard and treatment of nonhuman species. |

Although painience may be a minimum criterion for neuroethical regard, this is but a first step, as further understanding of animal consciousness, emotions, and higher cognitive functions should instantiate stricter moral standards for animal research and welfare. As shown in Table 1, these neuroethical premises are not merely confined to the laboratory, but extend into the public sphere to affect social conduct, as well.

An important element in the social acknowledgment and embrace of new concepts will be the development of neuroethically informed and neuroethically based programs of primary, secondary, and post-secondary education. Such programs would inculcate more meaningful apprehension of the ways that neuroscience may foster a nonanthropocentric appreciation of animals, and strengthen the notion of human/animal differences as distinctions of degree, rather than natural kind, and in so doing weaken anachronistic dualisms that have guided human treatment of animals. This will be evermore necessary as (1) society becomes more neuroscientifically and technologically capable, dependent, and oriented; (2) neuroscience and technology become increasingly powerful forces of social construction and/or deconstruction; and (3) humanity confronts the growing, incumbent responsibility to use such knowledge and technology in ways that are morally sound.

In conclusion, the aim is not to prescribe a form of neuroethical absolutism, for individuals’ moral compasses differ, and cultural norms and mores vary. But any ethical analysis must begin from

fact(s), and it is hoped that neuroscientific information about the cognitive capabilities of other species will dispel dated apologia for the mistreatment of animals, and foster a sense of awareness and responsibility to inform and guide the ethical reflections, choices, and actions of both individuals and societies.

## Cross-References

- [Animal Welfare](#)
- [Consciousness](#)
- [Empathy](#)
- [Ethics](#)
- [IACUC](#)
- [Laboratory Research](#)
- [Morality](#)

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## Painience

- [Pain and Ethics of Animal Care and Use](#)

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## Pair Bond

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### Definition

A selective and enduring relationship between two unrelated adults that can be characterized by affiliative interactions, spatial proximity, distress to separation, aggression toward unfamiliar individuals, and/or sexual fidelity.

### Introduction

Animals from a broad array of taxa, ranging from parakeets to humans, form stable, lasting associations known as pair bonds. While pair bonds have been observed across the animal kingdom, most information about this phenomenon originates from studies of voles, birds, and primates. These taxa have provided key insights about the mechanisms responsible for the formation and maintenance of pair bonds. Additionally, this research has been critical for understanding the ecological and evolutionary processes associated with pair bonds.

### Social Versus Sexual Pair Bonds

Animals that form pair bonds interact socially as well as sexually. However, sexual exclusivity is quite rare for many species (Lukas and Clutton-Brock 2013). Researchers sometimes fail to specify which component of pair bonds, social or sexual, is being investigated. Imprecise terminology creates challenges for comparisons of pair bonding in different species. Such ambiguity also impedes comparisons across disciplines (e.g., psychology, ecology, and medicine). As such, studies of pair bonding should specify whether the relationships of interest are social or sexual (or both) (Fuentes 2002). These

clarifications will bolster efforts to understand the ecological and evolutionary implications of pair bonds.

### Evolutionary and Functional Origins of Pair Bonding

Several hypotheses aim to explain the evolutionary origins and adaptive significance of pair bonds. These proposals share a unifying supposition – pair bonds likely originated from a sustained male-female association following mating. Mechanisms strengthening these relationships might have been favored if stable, lasting partnerships conferred adaptive (i.e., survival and reproductive) advantages over unstable or ephemeral associations. Several of these hypotheses are outlined below:

*Infanticide prevention* (van Schaik and Dunbar 1990). Pair bonds may have evolved as a means to mitigate the threat of infanticide. In systems where males regularly kill unfamiliar infants, pairs may have been able to protect offspring better than single parents. If bonded individuals experienced reductions in offspring mortality, pair bonding could have evolved as an adaptive strategy to maximize reproductive success within these populations.

*Mate guarding* (Parker 1974). Males that maintained close spatial proximity to females may have monopolized matings by forestalling females' reproductive attempts with other individuals. Additionally, ecological contexts may have constrained males' abilities to locate additional females. If so, males that stayed close and guarded females may have produced more offspring than males that departed after mating.

*Females as limited resource* (Wrangham 1980). Pair bonding may have evolved because ecological conditions limited males' abilities to secure a home range productive enough to support multiple females. What is more, constrained dispersal may have generated a situation in which males that maintained close associations with females produced more offspring than males that roved across territories.

*Parental care* (Kleiman 1977). Pair bonding may have evolved because biparental care (e.g., provisioning, carrying, huddling, thermoregulation, or grooming) was critical for the survival of offspring. Additionally, closely bonded individuals might have provided superior care, thereby promoting the survival of their offspring.

## Neuroendocrinology of Pair Bonding

Behavior and physiology are inextricably linked. The neuroendocrinology, i.e., the neural and hormonal mechanisms, of pair bonding has been most thoroughly described for a single species – the prairie vole (*Microtus ochrogaster*) (Aragona and Wang 2004). Prairie voles are small, territorial rodents that often form monogamous social bonds for life. Prairie vole partnerships are characterized by clear social preferences for mates, selective aggression toward conspecifics (i.e., members of the same species), and biparental care of offspring (Aragona and Wang 2004). These traits, in addition to high fecundity and amenability to captivity, make prairie voles excellent models in which to investigate the causal mechanisms of social attachment and pair bonding.

Research with prairie voles has uncovered several hormones that are fundamental for pair bonds. These include oxytocin (OT), arginine vasopressin (AVP), dopamine (DA), and corticotropin releasing hormone (CRH) (Aragona and Wang 2004; French et al. 2017). These hormones work in concert to regulate pair bonding and promote the maintenance of bonds once they have formed. However, the action of these hormones is not uniform across the sexes. The binding of OT is critical for pair bonding in female voles, whereas AVP is essential for males. Differences in the distribution and density of hormone receptors, rather than levels of the hormones themselves, best explain this sexual dimorphism (Aragona and Wang 2004).

Evidence from other species, including some birds and primates, suggests that OT, AVP, DA, and CRH are important regulators of pair bonding (Klatt and Goodson 2012; French et al. 2017). For

example, approximately 60% of neotropical monkeys exhibit behaviors characteristic of social monogamy and pair bonding, whereas only 29% of all primates are socially monogamous (Lukas and Clutton-Brock 2013). Preliminary evidence from several species (i.e., titi monkeys, marmosets, macaques, and humans) suggests that differences in the OT and AVP systems may explain these differences in the behaviors associated with pair bonding (French et al. 2017). In birds, hormones related to OT and AVP also influence pair bonding behaviors. For example, inhibiting vasotocin (VT), the compound from which OT and AVP are thought to have evolved, hinders pair bonds in zebra finches (*Taeniopygia guttata*). Finches with blocked VT receptors take longer to form bonds and have more unstable bonds than do finches with functional VT receptors (Klatt and Goodson 2012).

## Development and Pair Bonds

Early experiences can have lasting consequences for behavior. For many species, the quality and quantity of parental care can have lifelong impacts on social repertoires. In prairie voles, parents that provide high levels of care raise offspring that are typically more affiliative than offspring whose parents provided less care (Arias del Razo and Bales 2016). These sustained differences were evident when young voles matured and formed pair bonds themselves. Voles that had received high levels of care as infants spent more time in contact with their mates than did voles that had received low levels of care (Arias del Razo and Bales 2016). This suggests that attributes of pair bonds may have consequences that extend across generations.

## Conclusion

Pair bonds are complex and curious. They stimulate a wide range of questions, including: Why should animals prefer one, rather than many, social partners? What ecological and social pressures favor the evolution of selective relationships? Why do some animals pair for life whereas others



separate after one breeding season? What are the neurobiological mechanisms modulating prolonged associations? How do pair bonds develop? What shapes an individual's propensity to bond with others? These questions have been addressed only for a few species. As such, studies from across the animal kingdom are needed to acquire a comprehensive understanding of this phenomenon. What is more, inputs from myriad disciplines, including social psychology, evolutionary biology, ecology, and anthropology, will ultimately strengthen explanations of the proximate and ultimate mechanisms underlying pair bonds.

## Cross-References

- [Consort](#)
- [Monogamy](#)

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## Pair-Bonding

- [Affiliative Bond](#)
- [Monogamy](#)

## Paired-Associated Learning

- [Proactive Interference](#)
- [Retroactive Interference](#)

## Pair-Living

- [Monogamy](#)

## Paleobiology of Dinosauria

*Ecology, Life History, and Neuroanatomy*

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## Introduction

Richard Owen coined the term Dinosauria in 1841. Ever since, paleontologists and laypeople alike have been fascinated by these extinct creatures. In the past three decades, the number of academic publications on Dinosauria has increased considerably, providing the scientific community with a better understanding of life in the Mesozoic. Moreover, current studies have moved beyond anatomical and geological descriptions toward a clearer portrayal of various

behavioral, physiological, and neuroanatomical traits. In addition to discussing recently altered classifications in phylogeny and cladistics, this encyclopedia entry will describe the implications of multiple paleobiological studies on describing growth, reproduction, parental behavior, sociality, and ecology in Dinosauria. The entry will also briefly mention the various extinctions, both major and minor, that occurred during the Mesozoic. While the evolutionary repercussions of the Cretaceous–Paleogene event are indisputable, other extinctions generated similarly vast ecological shifts. For instance, the rise of Dinosauria itself is due in part to the Late Triassic mass extinction that vacated numerous ecological niches. Consequently, this entry's final section will address several factors that led to the dramatic elimination of hundreds of species during different periods of the Mesozoic.

## Cladistics and Evolution

Archosauria evolved as a clade around 250 million years ago, after the Permian–Triassic extinction which eliminated over 90% of all species on Earth (Brusatte 2012). This ecological catastrophe vacated numerous ecological niches, enabling the rapid spread and diversification of species. Most archosaurian lineages emerged toward the end of the Early Triassic (Brusatte 2012). Paleontologists classify Archosauria into two main subclades, Crurotarsi and Avemetatarsalia (also known as Ornithodira). Crurotarsi encompasses lineages such as Phytosauria, Crocodylomorpha, Rauisuchia, and Aetosauria. Alternatively, researchers generally divide Avemetatarsalia into Pterosauria (flying reptiles), Dinosauriomorpha (small-sized archosaurs including *Silesaurus*, *Asilisaurus*, *Marasuchus*, and *Lagerpeton*), and Dinosauria. Traditionally, Dinosauria is classified into two main subclades: Saurischia and Ornithischia (Brusatte 2012).

### Saurischia

Akin to other Dinosauria clades, Theropoda evolved during the Late Triassic as small- (*Eoraptor*) or

medium-sized (*Herrerasaurus*) animals. Hence, in contrast to their descendants, theropod species in the Triassic faced a constant struggle with larger competitors such as Rauisuchidae (*Postosuchus*, *Polonosuchus*) and Prestosuchidae (*Prestosuchus*, *Saurosuchus*) archosaurs, wherein it was not uncommon for early theropods to fall prey to these massive quadrupedal predators. It was only with the extinction of rauisuchids and prestosuchids (among others) and the subsequent release of previously occupied ecological niches at the end of the Triassic that this clade diversified, leading to the rise of large-bodied predators in the Jurassic and the Cretaceous. Theropoda is subclassified into three major groups, Neotheropoda, Tetanurae, and Coelurosauria (this last one is usually described as a branching node emerging from Avetheropoda within Tetanurae). The first clade includes families such as Coelophysidae (*Coelophysis*), Dilophosauridae (*Dilophosaurus*), Noasauridae (*Noasaurus*), and Abelisauridae (*Abelisaurus*). In turn, Tetanurae contains, among other groups, the families Megalosauridae, Spinosauridae, Allosauridae, Carcharodontosauridae, and Neovenatoridae. Lastly, the derived group of Coelurosauria includes tyrannosauroids, compsognathids, ornithomimosaurs, alvarezsauroids, therizinosauroids, oviraptorosaurs, scansoriopterygids, deinonychosaurs, and Paraves.

Phylogenetic reconstructions have traced Sauropodomorpha's evolution to the Late Triassic, with prosauropod species such as *Massospondylus*, *Plateosaurus*, *Riojasaurus*, and *Lufengosaurus* (Brusatte 2012). Additionally, although paleontologists originally described Prosauropoda as a distinct clade, contemporary phylogenetic classifications no longer support this position. Comparative morphological analyses indicate that this "lineage" encompasses various sauropodomorph taxa featuring sufficient morphological differences to be considered a unified clade (Brusatte 2012). The persistence of basal sauropodomorph traits in early sauropods further calls this claim into question (Brusatte 2012). Beyond these caveats, the term prosauropod remains in use due to the observable variation between these Late Triassic species, with more

derived sauropod taxa generally found in Late Jurassic geological formations.

Sauropodomorph diversity increased substantially during the Jurassic. Mamechisauridae taxa, including *Mamenchisaurus* and *Omeisaurus*, evolved between the Middle and Late Jurassic in Asia. The derived clade of Neosauropoda contained two main subclades: Diplodocoidea and Macronaria. Concerning Diplodocoidea, three main families comprise this superfamily: Rebbachisauridae, Dicraeosauridae, and Diplodocidae. Of these three families, the Rebbachisauridae taxa (e.g., *Nigersaurus* and *Rebbachisaurus*) are the most basal clade, whereas Dicraeosauridae and Diplodocidae are generally viewed as more derived lineages. Dicraeosaurids are characterized by elongated neural spines, as observed in *Amargasaurus* and *Dicraeosaurus*. The Diplodocidae family covers large-bodied sauropod species commonly found in Late Jurassic North America. Well-described taxa include *Diplodocus* and *Apatosaurus*. Concerning Macronaria, this clade contains the tallest and heaviest sauropod taxa. *Argentinosaurus* and *Paralititan*, part of the subclade Titanosauria, are among the largest animals observed in earth's evolutionary history. Brachiosauridae (*Brachiosaurus*, *Sauroposeidon*) and Camarasauridae (*Camarasaurus*) are other macronarian families of the Jurassic, with the former clade found in Gondwana and Laurasia and the latter endemic to Laurasia.

### Ornithischia

The clade of Ornithischia is divided into two major groups, basal species and Genasauria. Basal taxa emerged as small-sized bipeds in the Early Jurassic that generally occupied either an herbivorous or omnivorous dietary niche (Heterodontosauridae: *Fruitadens*, *Heterodontosaurus*). Alternatively, Genasauria includes more derived clades such as Thyreophora and Cerapoda. With regard to the former, thyreophorans usually exhibit bony armor, such as osteoderms, plates, spikes, or clubs. Modern phylogenetic reconstructions suggest this clade evolved during the Early Jurassic, with some

small-bodied species such as *Scutellosaurus* and *Scelidosaurus* (a potential out-group species) displaying some morphological commonalities with the more derived thyreophorans (Brusatte 2012). Thyreophora is subdivided into Stegosauria (e.g., *Kentrosaurus*, *Dacentrurus*, and *Stegosaurus*) and Ankylosauria (*Ankylosaurus*, *Euoplocephalus*, *Nodosaurus*, and *Edmontonia*). Unfortunately, to this day, there is little agreement regarding the phylogeny of Stegosauria, with multiple phylogenetic trees providing different classifications. In contrast, paleontologists tend to agree on the phylogenetic structure of Ankylosauria, a clade divided into Nodosauridae (characterized by bony ornamentations above the eyes and around the snout; Brusatte 2012) and Ankylosauridae (featuring a club at the end of the tail and heavily armored craniums; Brusatte 2012).

Concerning Cerapoda, this clade branches into Marginocephalia and Ornithopoda. Marginocephals usually display either a bonny frill or skull dome (comparative anatomical analyses indicate these structures originate from parietal and squamosal regions). While domes are a common feature of Pachycephalosauria (e.g., *Pachycephalosaurus* and *Stegoceras*), frills and horns are frequently observed in the clade Ceratopsia. Paleontologists attribute the evolution of domes, frills, and horns in Marginocephalia to either natural (marginocephals may have used these osteological structures as antipredator defense) or sexual selective (as armaments during intrasexual contests or as ornaments aimed to attract the attention of a female) pressures. Akin to other Dinosauria, ceratopsians evolved as small-bodied animals (*Psittacosaurus*). Eventually, ceratopsians increased in diversity during the Early Cretaceous, with the emergence of several families in North America, Europe, and Asia (basal lineages such as Protoceratopsidae and Leptoceratopsidae and more derived clades as in the case of Ceratopsidae). For the rest of the Cretaceous, Ceratopsia experienced a significant increase in its number of species. Consequently, paleontologists subclassify Ceratopsidae into Centrosaurinae (e.g., *Centrosaurus*, *Pachyrhinosaurus*) and Chasmosaurinae (e.g., *Chasmosaurus*, *Triceratops*).

A second Cerapoda lineage, Ornithopoda, originally featured small bodies and typically walked in an upright position (e.g., *Hypsilophodon*, *Thescelosaurus*, *Dryosaurus*). The majority of these lineages are found in Jurassic geological formations. In the Cretaceous, however, multiple derived lineages reached larger sizes and adopted a quadrupedal stance, as in the cases of Iguanodontia (e.g., *Iguanodon*) and Hadrosauria species, such as *Tenontosaurus*, which featured an increase in body mass and the abandoning of a bipedal stance (Brusatte 2012). Akin to Ceratopsia, Hadrosauria also experienced a burst in its total number of species during the Cretaceous. Two main lineages originated during this period: Saurolophinae and Lambeosaurinae. Even though some saurolophine species displayed different types of skull decorations, lambeosaurines (*Parasaurolophus*, *Lambeosaurus*) exhibited more complex forms of cranial ornamentations. Paleontologists continue to debate these crests' evolutionary function, with some suspecting these bony structures acted as resonating chambers, facilitating communication with conspecifics and other organisms (interspecific competitors and predators) (citation needed). Other researchers claim that sexual selection could be the main force behind the evolution of these ornaments (citation needed). Although researchers initially thought hadrosaurs were endemic to North America, Asia, and Europe, contemporary evidence suggests this clade also inhabited various ecologies in South America, Oceania, and Antarctica (Brusatte 2012).

### Paleobiology

After describing the main cladistic classifications of Dinosauria, the upcoming sections will cover four areas of paleobiological research: (1) paleoneurology, (2) life history theory, (3) socioecology, and (4) biogeography. The first section will describe current inquiry into the neuroanatomy of nonavian Dinosauria as well as metrics, such as the encephalization quotient, which are frequently used as proxy variables for emergent cognitive abilities. The second section will offer a brief summary of life history theory and discuss its implications for the understanding of

dinosaurian growth patterns, body size, and life span. The third section, on socioecology, covers several studies on the parental and social behavior of this extinct clade. Lastly, section four reviews multiple analyses exploring the ecological diversification of Dinosauria. This final section will also discuss evidence of niche partitioning involving dinosaurian species found occupying different dimensions of an ecospace.

**Paleoneurology and the Encephalization Quotient.** The encephalization quotient (EQ) is a relative measure for brain size with consideration of a given species' body mass and allometric conditions. It was first expressed formally by H.J. Jerison in 1973 (Jerison 1973) but preceded by the original observation of patterns that Snell speculated to exist when scaling brain mass with body mass (Snell 1891). Later, Dubois' "index of cephalization" increased the specificity of Snell's initial observations and reduced the exponent used for scaling by nearly a third (Dubois 1897). Jerison would go on to challenge Dubois' exponential value but preserve much of the initial framework of his "index of cephalization," eventually yielding the following equation (Jerison and Barlow 1985; Boddy et al. 2012).

$$EQ = (\text{brain mass}) / \left( 0.12 \times \text{body mass}^{(2/3)} \right)$$

0.12 represents a biological constant of average growth. The contested 2/3 exponent provides a value for allometric growth. As seen, this mathematically prioritizes predicted brain size over both observed brain mass and body mass, providing support for the typical usage of EQ in relevant literatures (Boddy et al. 2012).

One of the main issues with this approach to measuring EQ, and thus EQ at large, is the handling of outliers. Since a regression line is produced in the measurement of EQ, researchers must theoretically posit that all species represented underwent comparable evolutionary histories in the development of, and selection for, their particular brain size. Any potential species that may have undergone a different path from their surrounding taxa and therefore today have substantially smaller or larger ratios

of brain-to-body size are automatically excluded from analysis, since lone species cannot be studied using this method. It is only in comparison with evolutionarily similar extinct species, if no other living ones can be identified, that such outliers can be studied using EQ.

Accurate measures of brain size across phylogenies can be challenging to obtain and thus leave researchers with few well-studied species and many that are unknown. EQ attempts to alleviate this problem through a combination of multiple variables, leading to a calculable ratio between known brain mass in observed species and predicted brain mass in unobserved species, as well as the inclusion of allometric predictors. Having been originally designed for the study of mammals, EQ is most commonly used in the analysis of vertebrate species, but some have applied it when studying invertebrates as well.

The EQ measure provides many useful applications. Most fundamentally, EQ refines the understanding of scaling effects on body size for between-species comparisons. Selective explanations can then be proposed for measured differences of quantities that would otherwise be unavailable, allowing researchers to more comprehensively represent physiology, behavior, and other allometric relations in species of interest. Due to a lack of reliable neuroanatomical indicators for intelligence and cognitive complexity in nonhuman species, EQ is also used in studies on cognition and its evolution across phylogenies. Given that all of the variables relevant to EQ can be studied or approximated in both living and extinct species, it has also become a common measurement tool in paleobiology.

A common method employed in paleoneurological studies of EQ first involves the generation of a three-dimensional model of the internal cavity of the skull where the brain is located (Larsson et al. 2000). This rendering, known as an endocast, provides essential data on the volume and structure of different neuroanatomical regions. Carabajal and Canale (2010), for instance, described the endocast of *Giganotosaurus carolinii*, a South American theropod from the Albian-Cenomanian (Coria and Currie 2003). The authors calculated the endocast

volume of *Giganotosaurus* to be 275 mL. The study identified that the endocast achieved its maximum width, 64 mm, at the level of the cerebral hemisphere. The olfactory bulb's length to the foramen magnum measured 29 mm (Carabajal and Canale 2010). Similar to the forebrain of *Carcharodontosaurus*, in *Giganotosaurus*, the cerebrum is located above the cerebellum (Carabajal and Canale 2010). The study also reported that the endocast of *Giganotosaurus* was considerably longer relative to the models described in *Carcharodontosaurus iguidensis* (30% difference) and *C. saharicus* (19% difference).

Franzosa and Rowe (2005) estimated that the endocast of *Acrocanthosaurus atokensis* (Lower Cretaceous, Aptian-Albian) measured 14.88 cm long and exhibited a volume of 190.8 cm<sup>3</sup>. Franzosa and Rowe (2005) calculated the maximum width of the cerebral hemispheres at 4.35 cm. The endocast of *A. atokensis* did not exhibit a pronounced sigmoidal shape but instead resembled the general neuroanatomical appearance of extant crocodylians (Franzosa and Rowe 2005). From these analyses, Franzosa and Rowe (2005) concluded that the brain of *A. atokensis* retained several of the neuroanatomical characteristics observed in ancestral archosaurs. Their study also found that the olfactory bulbs occupied a sizeable portion of the rostral endocranial fossa and reached 6.6 cm in longitude. The olfactory tract started as independent entities merging at the ventral and lateral expansion of the forebrain. The authors determined that *A. atokensis*'s olfactory tract and bulbs' structural organization is consistent with the reported neuroanatomy of other genus of Carcharodontosauridae, such as *Giganotosaurus* and *Carcharodontosaurus*, further supporting the inclusion of *A. atokensis* within this cladistics family. The position of the horizontal semicircular canal indicated that *A. atokensis* tilted its head slightly downward to facilitate the animal's orientation in movement (Franzosa and Rowe 2005).

Brusatte's (2012) review of the literature describes noticeable neuroanatomical differences among Dinosauria clades. According to the author, the endocasts of sauropodomorphs, early



theropods, and ornithischians display morphological similarities with those of extant reptilians. Alternatively, the neuroanatomy of later theropod species resembles, to some extent, those of avian species. In terms of general morphology, endocasts are often classified as either Z-shaped (or S-shaped) or globular. While Z-shaped brains are found across clades of Dinosauria, globular endocasts are generally observed in derived species of theropods, akin to modern birds. For Brusatte, most endocasts in Dinosauria follow a morphological organization which includes the olfactory bulbs and canals occupying the anterior areas, the cerebrum occupying the midpoint, and the cerebellum and brain stem occupying the posterior regions of the brain. The olfactory bulbs' size, measured relative to body size, enabled paleoneurologists to determine that Tyrannosauridae and Dromaeosauridae taxa had exceptional olfactory abilities (Brusatte 2012). In terms of the evolution of olfactory regions, comparative estimations across theropod species concluded that, while some clades had a remarkable sense of smell, this ability was considerably limited in other species, indicating olfaction followed different evolutionary routes in Theropoda (Brusatte 2012). In addition to studies exploring the sensorial abilities of theropods, other researchers have examined the association between neuroanatomy and sociality, wherein estimating the volume of different neural regions has provided insight into the degree of social complexity exhibited in Dinosauria. According to Isles (2009), for example, the telencephalic volume of large theropods, such as *Allosaurus*, *Carcharodontosaurus*, and *Tyrannosaurus*, is equivalent to that of extant reptiles.

Paleoneurologists typically follow the generation of a species' endocast with the computation of its EQ. This metric remains popular because of its ability to consider the positive association between body size and brain size, a link that often confounds an interpretation of correlation with sensory and cognitive functions. Franzosa (2004), for instance, calculated EQ for various theropod and sauropod species. Given that EQ estimates vary depending on the allometric slope associated with different clades, his study

employed two formulas: one based on extant reptilian data (REQ) and a second extracted from extant avian species (BEQ). Consistent with previous publications, the sauropod *Diplodocus* exhibited an REQ value that was slightly lower than that of the extant genus *Crocodylus* (Brusatte's research also identified that sauropodomorphs featured low EQ estimates; 2012). Overall, all theropod species in the sample (including *Ceratosaurus*, *Allosaurus*, *Carcharodontosaurus*, *Acrocanthosaurus*, *Tyrannosaurus*, *Dromiceiomimus*, *Citipati*, and *Troodon*) featured REQ estimates above that of *Crocodylus* but below some avian species (e.g., *Apteryx* and *Anas*). According to Franzosa's calculations, in addition to *Troodon*, *Dromiceiomimus* also displayed high REQ values (relative to other dinosaurs). Franzosa's analyses reached similar conclusions in terms of dinosaurian BEQ. Other publications have reached similar conclusions, wherein maniraptoran theropods, such as *Troodon*, displayed estimates similar to that of some extant avian species (Brusatte 2012).

**Life History and Growth.** Life history refers to how an organism reaches certain milestones during its development (Figueredo et al. 2020). Classical life history perspectives classified species as either *r*- or *k*-strategists (Paul 2016). According to these views, while *r*-strategists feature high reproductive output, leading to population growth, *k*-strategists have few offspring and inhabit populations at carrying capacity (the maximum population size sustained by an ecology). Some researchers have proposed that differential mortality schedules, wherein ecological pressures increase the mortality of a demographic group (e.g., younglings or adults), could explain the observed variation in life history across species. Environments exhibiting high youngling mortality are associated with having multiple offspring, increasing the probability that at least some younglings would survive and reach adulthood.

Alternatively, ecologies displaying considerable adult mortality relate positively with species having relatively few offspring and delaying sexual maturity (van Schaik and Isler 2012). In contrast to large eutherian mammals (exhibiting a long gestation period, a small litter size, and large

neonates), oviparous species, including most reptiles and birds, circumvent the additional costs known to be associated with an internal gestation and are capable of laying large clutches.

Based on the number of eggs per clutch, the literature classifies dinosaurs as *r*-selected species, inferring that young dinosaurs, including hatchlings and juveniles, experienced substantial mortality rates promoting a fast growth to counter the risk of predation (Paul 2016). However, in the past two decades, the *r-k* paradigm has been called into question (van Schaik and Isler 2012). Instead, life history researchers are now exploring alternative theories, including dimensions such as the neoteny-precocial and the fast-slow dimensions (van Schaik and Isler 2012). While the first factor considers the level of developmental immaturity, the second factor encompasses life history indicators such as maximum longevity and fertility (van Schaik and Isler 2012).

Organisms may also allocate resources to at least one of two developmental facets: somatic effort and reproductive effort (van Schaik and Isler 2012). Somatic effort comprises the individual's investment in tissue maintenance, growth, and repair (van Schaik and Isler 2012). Reproductive effort is subdivided into two main subcomponents. The first subcomponent concerns the animal's capacity for searching, courting, and copulating with sexual partners and competing with sexual rivals (i.e., mating effort). The second subcomponent engulfs the individual's parental behavior, including food provisioning and offering protection against predators, parasites, and conspecifics. Consequently, animals continuously face the dilemma of allocating a finite amount of bioenergetic resources to at least one of these life history efforts (somatic effort vs. mating effort, mating effort vs. parental effort, somatic effort vs. parental effort). While little is known in terms of the various types of efforts in extinct Archosauria, it is still feasible to determine some general life history patterns in Dinosauria.

Estimating life tables and calculating the corresponding growth patterns could also explain gigantism in some species of Dinosauria. Erickson et al. (2004) obtained medullar bone samples from juvenile, subadult, and adult specimens of

*Albertosaurus sarcophagus*, *Daspletosaurus torosus*, *Gorgosaurus libratus*, and *Tyrannosaurus rex*. Histological line counting identified that somatic maturity in *T. rex* occurred at approximately 19 years of age, with some individuals reaching maximum longevity at 28 years of age (Erickson et al. 2004). Relative to *T. rex*, *A. sarcophagus*, *D. torosus*, and *G. libratus* attained an earlier somatic maturity (14–16 years) with a slightly shorter maximum longevity (24 years). After computing a series of logistic growth curves, the authors concluded that even though all four species experienced an equivalent duration of the exponential stage, they differed in their growth rates (Erickson et al. 2004).

Erickson et al. (2007), assessed the life history patterns of five nonavian theropods (*Deinonychus antirrhopus*, *Troodon formosus*, *Oviraptor philoceratops*, *Oviraptor* sp., and *Citipati osmolskae*). The authors estimated that *D. antirrhopus* and *T. formosus* reached longevity at 14 and 18 years of age, respectively. The analyses indicated that at least two of the three oviraptorids in the dataset featured similar longevity values (*C. osmolskae* = 13 years; *Oviraptor* sp. = 18 years). *Oviraptor philoceratops* displayed a shorter life span, 8 years, given the specimen perished before attaining full somatic maturity. Because paleontologists discovered the remains of this individual in a brooding position, the results from the osteohistological analyses suggested that *O. philoceratops* attained sexual maturity before reaching somatic maturity.

Erickson's review (2005) of the literature identified considerable variations in the estimated longevity of different species of Dinosauria. Small theropods, such as *Shuvuuia*, had relatively short life spans (approximately 4 years). According to Erickson, saurischian species of moderate size, such as the prosauropod *Massospondylus* or the coelophysid *Coelophysis rhodesiensis* (formerly classified as *Syntarsus*) lived for approximately 7–15 years. For Erickson, larger theropods, as in *Albertosaurus*, nearly doubled the longevity of moderately sized species (24–30 years). Lastly, large sauropods (e.g., *Brachiosaurus*) reached longevity of 50 years of age. Even though additional data is required to conduct statistical

significance tests, Erickson's compendium suggests a positive association between body mass and longevity, a life history covariation observed in other clades.

In addition to saurischian studies, several publications have also examined the growth rates of ornithischians. Noticeable variation existed within this clade in both longevity and growing speed. Brusatte's (2012) assessment of the literature identified that faster growth was not limited to small ornithischians (e.g., *Lesothosaurus*). According to the author, the evidence obtained from ornithopod and ceratopsian specimens also indicates rapid growth. It is worth noting that not all ornithischians followed this life history pattern. Brusatte's (2012) review concluded that thyreophorans, relative to other ornithischians, grew slower. For instance, the limited presence of fibrolamellar tissue in *Scutellosaurus* indicates this species followed a growth pattern akin to that of crocodilians (Brusatte 2012).

Heated debate persists among paleontologists concerning the growth speed in Dinosauria. To date, three main perspectives have been described in the literature. The first hypothesis claims that dinosaurs grew following a general reptilian pattern. Alternatively, the second hypothesis favors avian or mammalian-like growth. The third approach takes a moderate stance, wherein dinosaurs grew faster than reptiles but slower than birds and mammals (Erickson 2005). Erickson's examinations (2005) concluded that, relative to extant reptiles, dinosaurs grew at a faster rate (the analysis accounted for body size). Moreover, larger species tended to reach their fully mature size faster. Hence, Erickson (2005) inferred that dinosaurs featured unique physiologies, as evidenced by their growth rates.

**Parental Behavior.** Given that parental care (such as parents attending to their clutches or investing in their young) is widespread across avian, crocodilian, and mammalian taxa, it is expected that at least some species of Dinosauria actively invested in their offspring. The fossil evidence collected in the past six decades indicates that a set of species akin to extant Archosauria performed parental behaviors. Notably, the fossils of at least two genera of

oviraptorosaurs – *Citipati* and *Oviraptor* – have been found nesting (Varricchio 2011). Paleontologists have also inferred parental care based on the physical proximity between the remains of adults and juvenile individuals, including the genus *Patagosaurus*, *Psittacosaurus*, and *Tenontosaurus* (Varricchio 2011). This pattern extends to maniraptoran theropods, whereby paleontologists discovered adult specimens of the genus *Troodon* and *Deinonychus* close to their respective nests (Varricchio 2011). Other dinosaurian species known to form assemblages of older juveniles include the theropod *Sinornithomimus* and the ornithopod *Edmontosaurus* (Varricchio 2011).

Debate persists concerning the prevalence of parental behaviors in other theropods. According to some publications, the osteological and taphonomic evidence supports the presence of parental behavior in *Allosaurus fragilis*, wherein adult and juvenile teeth have been recovered near skeleton prey, indicating that adults dragged the carcass to a lair to be consumed by younger individuals (Isles 2009; Varricchio 2011). Other researchers remain unconvinced by this evidence. Isles (2009) proposed that multiage *Allosaurus* congregations, rather than providing compelling evidence of parental behaviors, suggested cannibalism. Additional data is required to settle the enigma of parental care in large theropods.

Despite the absence of adult remains, some researchers have interpreted hatchling assemblages as an indication of parental care (Varricchio 2011). For instance, Horner discovered multiple *Maiasaura* eggs and hatchlings, a cretaceous ornithopod, within nest-like structures (Horner 1999). The younglings' osteological immaturity indicated a semi-altricial development and limited levels of autonomy (Varricchio 2011). This pattern, generalized to other ornithischian species, such as the ceratopsian *Protoceratops*, wherein hatchlings recovered from Late Cretaceous strata in Mongolia, displays signs of an altricial development (Varricchio 2011; Weishampel et al. 2000). Given that avian altricial and semi-altricial species often exhibit parental care (Shultz and Dunbar 2010), it is probable

that *Maiasaura* and *Protoceratops* also exhibited this behavioral phenotype.

Sauropod parental care remains a topic of intense scrutiny. The debate persists partly due to the current ichnological record supporting the hypotheses that at least some sauropod species were gregarious, with groups ranging from three to approximately 20 animals (Myers and Fiorillo 2009). Paleontologists have found sauropod trackways worldwide, including parts of modern-day China, Portugal, Brazil, Bolivia, the United Kingdom, and the USA (Myers and Fiorillo 2009). The literature also describes noticeable variation in the composition of these groups. While some trackways exhibit signs of adult and juvenile aggregations, the footprints described in other paleontological sites are exclusively of adults. Myers and Fiorillo (2009) assembled a comprehensive ichnological database suggesting age-segregated groups such as (1) at least 40 adults in the United Kingdom; (2) six adults in Colorado, the USA; (3) approximately ten adults in Texas, the USA; and (4) ten adults in Arkansas, the USA. The authors also reported juvenile and subadult assemblages: (1) five juveniles in Colorado, the USA; (2) three juveniles in Utah, the USA; (3) four juveniles in China; (4) seven subadults in Portugal; and (5) 11 subadults in Bolivia. According to Myers and Fiorillo's database, the ichnological data also supports mixed-age groups in some sauropod species: (1) five individuals in Brazil; (2) 23 animals in Texas, the USA; and (3) eight individuals in Bolivia.

The fossil evidence also supports the fact that some sauropod species lived in age-segregated groups (Myers and Fiorillo, 2009). Some examples include (1) at least six adult *Barapasaurus* in India; (2) more than 12 adult *Kotasaurus* in India; (3) at least four adult *Paluxysaurus* in Texas; (4) approximately 17 juvenile *Bellusaurus* in China; (5) eight juvenile *Diplodocoidea* in Montana, the USA; and (6) more than three juvenile *Alamosaurus* in Texas, the USA. Alternatively, evidence of mixed-age groups consists of (1) the remains of five *Patagosaurus* uncovered in Argentina, (2) over 12 *Europasaurus* in Germany, and (3) approximately five *Brachiosaurus* in

Tanzania. In light of this evidence, Varricchio et al. (2008) estimated the probability of paternal care in Dinosauria. The authors obtained life history data (body mass and clutch volume) on 433 extant avian and crocodilian species and three extinct maniraptoran theropods, *T. formosus*, *O. philoceratops*, and *C. osmolskae*. The data were disaggregated based on the type of parental care: (1) bird maternal, (2) bird paternal, (3) bird biparental, and (4) crocodilian maternal. Subsequently, the authors computed a series of bivariate regressions between log body mass and log clutch volume and used the Akaike information criterion (AIC) to determine which model fitted the maniraptoran values. The model comparison identified the avian paternal care model as having the best fit.

**Social Behavior.** Currie and Eberth (2010) considered five primary sources of evidence supporting the presence of gregarious behavior in Dinosauria: morphology, fossil assemblages, trackways, phylogenetic reconstructions, and inferences based on modern ecologies. According to the authors, the presence of morphological ornamentation in numerous dinosaur species suggests at least occasional interactions (intrasexual competition, intersexual selection, socialization) between conspecifics. For instance, numerous ornithomorphs (Hadrosauria) and marginocephalians (pachicephalosaurians and ceratopsians) feature cranial protrusions that could have been used in sexual contests or displays. This pattern also appears to have extended to various theropod species. Coelophysoids (*Dilophosaurus*, *Zupaysaurus*, *Monolophosaurus*), abelisaurids (e.g., *Carnotaurus* and *Majungasaurus*), ceratosaurids (*Ceratosaurus*), tyrannosauroids (*Proceratosaurus*, *Guanlong*), spinosaurids (*Spinosaurus*, *Irritator*), oviraptorosaurs (*Oviraptor*), and allosaurids displayed cranial crests, ridges, and horns (Currie and Eberth 2010).

Although the subject of theropod fossil assemblages as an indicator of dinosaur gregariousness remains a controversial topic, the physical proximity of conspecifics in the absence of other species suggests some theropod species behaved gregariously (Currie and Eberth 2010). For example, the authors discovered at least 12 *Albertosaurus*

in Dry Island, Canada. Given that large adult carnivores, as in the case of tyrannosaurids, required a vast home range (approximately 200 km<sup>2</sup> per individual), Currie and Eberth concluded that gregariousness, rather than the independent congregation of individuals, offers a more parsimonious explanation to the observed fossil assemblage. The absence of taphonomic markings in the remains of the 12 specimens falsified alternative hypotheses, such as cannibalism. Likewise, the authors remained unconvinced regarding perspectives claiming that these assemblages were the product of solitary individuals flocking around carrion. In addition to *Albertosaurus*, the literature describes at least four instances of tyrannosaurids found close to each other. The first two correspond to Mongolian quarry sites featuring at least two specimens of *Tarbosaurus*; the third quarry, found in South Dakota, the USA, contained the fossils of four *Tyrannosaurus*. Similarly, paleontologists extracted three *Daspletosaurus* from a bone bed located in Montana, the USA.

Dinosaur gregariousness is not exclusive to Cretaceous tyrannosaurids. The literature describes (Currie and Eberth 2010) three Triassic sites containing the bodies of coelophysoids. At Ghost Ranch, the USA, researchers identified approximately 1000 *Coelophysis bauri*. Similarly, paleontologists unearthed 26 *Syntarsus rhodesiensis* (nowadays relabeled as *Coelophysis rhodesiensis*) close to Zimbabwe's Chitake River. Lastly, researchers recovered two *Liliensternus liliensterni* from the Knollenmergel, Germany. Early Jurassic theropods retained their ancestor gregariousness. In Arizona, researchers described two *Dilophosaurus wetherilli* in relative proximity (Currie and Eberth 2010). Four *Syntarsus kayentakatae* were also recovered from another Jurassic Arizonian location. Conspecific congregations were not exclusive of small- and medium-size theropods. The literature describes two sites featuring Late Jurassic animals. In Kenton, Oklahoma, paleontologists identified four *Saurophaganax maximus*, a large allosaurid (some estimations indicate some animals could reach up to 14 meters long; Currie and Eberth 2010).

In a similar vein, the paleontological literature describes skeletal assemblages of other theropod species, including carcharodontosaurids. In

Argentina, a paleontological expedition identified nine *Mapusaurus* in Cañadón del Gato (Currie and Eberth 2010). This finding still generates intense debate regarding the presumed sociality of large theropods. Currie and Eberth (2010) clarified that multiple individuals' presence does not suggest that all theropod species lived gregariously. On the contrary, Currie and Eberth (2010) emphasize that researchers should examine any claim of sociality on a case-by-case basis, an essential recommendation considering that even closely related taxa occasionally feature different social organizations.

Trackways are yet another source used for inferring conspecific gregariousness and demographic compositions of groups behind the fossilized footprints. The Toro Toro site in Bolivia, a Late Cretaceous paleontological site, is a clear example of multiple individuals traveling together (Currie and Eberth 2010). This paleontological site features two trackways, each one displaying the coordinated movement of early theropods. The ichnological analyses estimated that approximately 60 animals of the same species generated the footprints at Toro Toro. Other Cretaceous theropod trackways include the Ponta da Guia site in Brazil, where at least four individuals seem to have traveled together, and Fuente Salvo, in Spain (12 conspecifics; Currie and Eberth 2010). This pattern extends to other geological periods. For example, two Middle Jurassic sites, the Chewore formation in Zimbabwe and the Isle of Skye site in the United Kingdom, display the footprints of multiple individuals (current calculations estimate at least five individuals on each site; Currie and Eberth 2010).

**Paleoecology and Biogeography.** Zoogeography, a subdiscipline of biogeography, comprises the study of species distribution and variety in past and present land regions. Sclater (1858) and Wallace (1876) provided foundational hypotheses that would later develop into the present field, considering such topics as regional variation in ecology, such as temperature and altitude, and its effects on the evolution of traits, such as predation, competition, and parasitism, across species. Further, species distribution was found to involve matching between species and environment, as



geographical barriers and species-specific traits both impact the likelihood of non-native species succeeding in novel environmental conditions (Wallace 1876). Hertler et al. (2018) recently built upon Wallace's view, finding that full assemblages of symbiotic species can be impacted by environmental pressures, not solely native species.

The early study of physical ecology comprised the use of latitude and longitude alone as indicators (Johnston 1850). Sclater (1858) crucially added species variation to demarcate regions in further depth. This began with a study of the regional prevalence of avian species across observable land areas, leading to the specification of six unique zoogeographic regions. Wallace (1876) expanded Sclater's construction, placing four additional subregions within each main region, based on whether or not transition zones were present and the degree of within-region variation. These original categories have largely stood the test of time, despite differing perspectives from some in zoogeography and relevant literatures (Figueroa et al. 2020).

In a recent review, Morrone (2015) hierarchically classified modern-day regions cited within the biogeographic, zoogeographic, and phytogeographic literatures from 1850 through 2010. His findings indicated, first, consensus around the naming of three kingdoms and nine regions: the Holarctic kingdom (containing the Nearctic and Palearctic regions), the Holotropical kingdom (containing the Neotropical, Ethiopian, and Oriental regions), and the Austral kingdom (containing the Cape, Andean, Australian, and Antarctic regions). Further, Morrone (2015) identified five transition zones, which, following Wallace's original conception of their importance, continued across time to permeate relevant literatures. Those zones were the Mexican (Nearctic-Neotropical transition), Saharo-Arabian (Palearctic-Ethiopian transition), Chinese (Palearctic-Oriental transition), Indo-Malayan (Oriental-Australian transition), and South American (Neotropical-Andean transition) (Morrone 2015). It is necessary to note that in a paleogeographical setting, the naming and relative locations of these regions are subject to substantial modification across time. However,

affirmation of the principles dictating Wallace's contributions to their classification – namely, the addition of transition zones and within-region variation – is unavoidably established using contemporary regions because of the relative ease with which one can study many organismic variables that are not easily investigated using ancient fossil records.

Wallace's original conception of species distribution relied on the documentation of ancestral relationships across species. More recently, however, species distribution is studied through the analysis of phylogenetic effects (Avice 2008). Holt et al. (2013) classified, according to phylogenetic proximity between species, the zoogeographic distribution of 21,037 species of amphibians, birds, and mammals. The study resulted in the identification of 20 distinct zoogeographic regions, which were further grouped into 11 overarching realms (Holt et al. 2013). These findings, among others, continue to largely support findings resulting from the hypotheses of Wallace and Sclater centuries before. Some differences in the characterization of certain areas did persist, however, such as insular regions of the Oceanian realm as well as the Saharo-Arabian realm and its intermediate positioning between the Afrotropical and Sino-Japanese realms (Holt et al. 2013).

The concept of an ecological niche revolves around the behaviors of organisms – both individuals and social groups – within a specified environment and the relationships among relevant biotic and abiotic components of that environment with those organisms (Pocheville 2015). These relationships impact the types of, and competition rates for, resources among inhabitants of the environment. Further, the organism's individual capacity to compete within, and thus preferentially construct, their niche determines the variety of resources they are able to utilize. This principle is known as their *niche width* (Roughgarden 1972). Smaller niche widths demarcate *specialist* species, whereas larger niche widths demarcate *generalist* ones (Roughgarden 1972).

Species appear to evolve toward either a specialist or a generalist strategy for a variety of reasons. First, the fitness consequences of the

variety of resources used by a species appear to depend on the trade-off between performance with one resource and the performance cost when introducing a second resource (Levins 1968). Generalist strategies are considered favored when a species is adapted somewhat equivalently to the utilization of multiple resources. Specialist strategies, in contrast, are considered favored when a species is primarily adapted to the utilization of one resource or resource type, meaning that they lack the capacity to productively forage for, or make use of, other available resources nearby. Therefore, minute alterations to the availability of resources negatively impact specialist species substantially more than generalist ones, who possess a buffer to such ecological fluctuations (Bonsall and Wright 2012). Fry (1996) argues that, as a result, selection for specialist strategies depends on positive selection for the traits underlying use of one resource and concurrent weaker positive, or neutral, selection on those traits involving other resources.

The nature of the coexistence between consumers of the same resource also impacts the likelihood of selection favoring generalist versus specialist strategies (Bonsall and Wright 2012). For those species favoring generalist strategies, cooperation with other consumers of the same resources increases the likelihood of preserving continued access to multiple resources, for all participating species (Chaneton and Bonsall 2000). In the opposing scenario, competition may decrease the success of cooperative behaviors, thus favoring both specialism and decreased competition (Platt and Bever 2009; Bonsall and Wright 2012). One tactic influencing this form of coexistence is resource partitioning (Miller 1967). Exclusive resource rights, herein, decrease the likelihood of competition between species and increase that of coexistence (Hunt and Bonsall 2009). Further, coexistence among multiple specialist species relies on life history trade-offs favoring diversification and constraining similarity in morphology or strategy. This is often, but not universally, a result of disruptive selection (Bonsall and Wright 2012). Phylogenetic analyses have provided support for this notion of an

increase in likelihood of specialist strategy with diversification processes (Schluter 2000).

**Dinosaur Zoogeography and Niche Partitioning.** Recent paleontological publications have also explored the distribution of dinosaur species across the globe. The phylogenetic proximity of taxa found in different continents offers some insight into the potential continental location of the last common ancestor of particular species. A classic example is the presence of abelisaurids, spinosaurids, and carcharodontosaurids in Africa and South America, indicating the ancestors of these clades probably originated in the southern supercontinent Gondwana, after the fragmentation of Pangea (Brusatte 2012). For species found in the continental remnants of Laurasia (constituting modern-day North America, Europe, and Asia), cladistic estimations identified that North American taxa (e.g., Tyrannosauridae) are phylogenetically closer to Asian, rather than to European, species (Brusatte 2012). This pattern is expected because, contrary to contemporary Europe, encompassing a large continental mass attached to Asia, Europe during the Cretaceous was mostly composed of numerous islands occasionally interconnected through shallow waters and temporary land bridges during the Cretaceous.

Farlow and Planka (2002) offer a compelling case regarding habitat partitioning and morphological variation in extinct Dinosauria. The authors reviewed the literature and gathered body mass and skull size information on various predatory species, including Australian varanid lizards, crocodilians, extant avian raptors, carnivorous mammals (their review encompassed both extant and Plio-Pleistocene carnivores), and theropod dinosaurs. The author's examination with the non-dinosaurian species determined that taxa inhabiting the same environment featured noticeable differences in body mass. The authors also concluded that large-bodied species occupying similar dietary niches exhibit other morphological differences associated with predatory behavior. Interestingly enough, smaller species, members of the same trophic guild, were less dissimilar to each other in skull and body size than larger species occupying similar ecological niches. The study also concluded that similar-sized species could

coexist in the same habitat under certain conditions as long as their dietary niche did not overlap. Lastly, the study concluded that they tend to either occupy specialized microhabitats or segregate geographically in circumstances wherein guild members feature similar body size and predatory morphology.

Following the identification of these evolutionary patterns, Farlow and Planka proceeded to explore similar dynamics in extinct theropod taxa. Their study included seven Late Cretaceous species: *Gorgosaurus libratus*, *Daspletosaurus* sp., *Chirostenotes pergracilis*, *Troodon formosus*, *Dromaeosaurus albertensis*, *Avimimus* sp., and *Sauronitholestes langstoni*. The analyses estimated a large skull length ratio for the pairs *Gorgosaurus-Troodon* (~4.5 ratio) and *Dromaeosaurus-Avimimus* (~3.0 ratio). Alternatively, the remaining pairs *Daspletosaurus-Gorgosaurus* and *Troodon-Chirostenotes* exhibited skull size ratios below 1.5. Regarding body size, Farlow and Plank calculated a substantial ratio between *Daspletosaurus* and *Chirostenotes* (~35.00). Based on these results, the authors determined that large carnivores, such as *Daspletosaurus* and *Gorgosaurus*, displaying similar morphologies, avoided direct competition by either specializing on different prey (*Daspletosaurus* preferred to hunt ceratopsians, whereas *Gorgosaurus* hunted hadrosaurs) or occupying nonoverlapping micro-niches. The more significant number of *Gorgosaurus* ( $n = 23$ ), relative to *Daspletosaurus* ( $n = 7$ ), found at the Dinosaur Park Formation in Canada, suggests these species did not interact frequently. Additional biogeographic studies have found that *Daspletosaurus* generally inhabited Southern North American ecologies, whereas *Gorgosaurus* preferred Northern regions. These results are consistent with Farlow and Planka's discovery of niche partitioning in extant predators.

In more recent publications, researchers have explored the relation between various lithological formation types and different species of dinosaurs. Lyson and Longrich (2011) reviewed the paleontological literature and assembled a comprehensive database containing information on

the sediment conditions found close to recovered dinosaur specimens in Late Cretaceous North America. The sample includes 343 individuals, 149 associated with mudstone and 194 with sandstone. The authors computed a series of chi-square tests and identified a positive association between the frequency of hadrosaurs and sandstone. Alternatively, most ceratopsian specimens were found in mudstone sediments. The analyses, however, did not detect a significant association between ornithomimosaurids and particular lithological formation. The number of *Tyrannosaurus rex* specimens did not differ in either sandstone or mudstone sediments. These results strongly suggest that populations of *T. rex* persisted and thrived across a variety of environments.

Further publications have also explored the presence of niche partitioning among herbivorous dinosaur species extracted from the Dinosaur Park Formation. Mallon and colleagues (2013) considered the hypotheses that folivorous species avoid direct competition by feeding at different heights. The study, however, did not detect evidence of feeding stratification based on height. Most of the species in the sample forage near the ground. Hadrosaurs were the only clade able to feed on small trees. The authors also concluded that the bipedal and quadrupedal stance of sympatric species of Hadrosauria reduced the intensity of feeding competition. Overall, the analyses concluded that, besides feeding stratification, other forces favored niche partitioning across Late Cretaceous ecosystems in North America.

In addition to complete remains, taphonomic and morphological studies offer further evidence of niche partitioning. Frederickson, Engel, and Cifelli (2018) assessed the diversity of North American Cretaceous predators at the Mussentuchit formation in Utah, the USA. The researchers compared the tooth morphology of multiple theropod species. The study gathered samples from six sites and identified four tooth morphotypes including Richardoestesia-like teeth and those of a small-sized dromaeosaurid, medium-size dromaeosaurid, and a large-bodied theropod. The analyses identified that Richardoestesia-like teeth were generally found close to water channels. The teeth of medium-

size dromaeosaurids were more frequently found in floodplains, whereas the teeth of both large-bodied theropods and small-sized dromaeosaurids were more abundant in channels and floodplains. According to the authors, this evidence supports the hypothesized division of the ecospace among Mussentuchit's theropods.

Isotopic assessments further support the division of ecospace among species of Dinosauria. Fricke and Pearson (2008) calculated the ratio of isotopes in a single element ( $\delta$ ) found in the enamel of various dinosaur species. This value conveys information on the water and plants each animal consumed during its lifetime. The authors computed  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  for multiple species of Ceratopsia and Hadrosauria recovered from the Hell Creek Formation in the USA. The project determined that these two clades displayed different isotopic signatures, supporting the hypothesis that the dietary niche of these clades did not overlap. Fricke and Pearson's review of the literature determined that, whereas high isotope estimates are often associated with open habitats, low values are found in canopy-type habitats. Based on these ecological and chemical patterns, the authors inferred that ceratopsians and hadrosaurs also inhabited different environments, with hadrosaurs preferring closed canopy settings and adult ceratopsians preferring open habitats.

Paleontologists have likewise found evidence of niche partitioning in Upper Jurassic Dinosauria. Henderson (1998) contrasted the skull and tooth morphology of large carnivorous dinosaurs collected from the Upper Jurassic Morrison Formation in the USA. Henderson's sample included various specimens of *Allosaurus* and *Ceratosaurus*. The comparative exploration identified two *Allosaurus* morphs. The first one featured a short and robust skull, whereas the second one exhibited a longer crania. *Ceratosaurus*, a medium-sized theropod, also displayed a compact skull. The authors interpreted the anatomical variation between *Ceratosaurus* and long-skulled *Allosaurus* to be an indication that these species relied on different predatory strategies. This pattern did not, however, extend to *Ceratosaurus* and robust-skull *Allosaurus*. Henderson interpreted the presence of robust-skull *Allosaurus* and the

absence of *Ceratosaurus* in certain locations as evidence of ecological competition and displacement. Besides their exploration of interspecific ecological interactions, Henderson's study provides further proof of niche splitting occurring within theropod species.

## Evolution of Dinosauria and Mesozoic Extinctions

Even though the Cretaceous-Tertiary mass extinction (i.e., KT event), leading to the demise not only of nonavian Dinosauria but also of Pterosauria, Plesiosauria, and Pliosauria clades, still captures the public's imagination, at least six additional extinctions occurred during the Mesozoic. Researchers dated the earliest event, referred to as the Carnian Pluvial transition, around 234 million years ago (Dal Corso et al. 2012). The sedimentological evidence suggests that both global climate variations, geological uplifting, and volcanism (e.g., flood basalts in Wrangellia, a terrane located in Northwestern North America) led to the disappearance of a multitude of invertebrates and primitive chordates. Paradoxically, basal species of Dinosauria, including *Eoraptor*, evolved under these challenging conditions (Brusatte 2012). Approximately 201 million years ago, almost 50 million years after the massive Permian-Triassic extinction (an event that eliminated over 90% of all marine life), the earth once again face a major extinction. This time, the Triassic-Jurassic mass extinction (TJ) eliminated close to 40% of all terrestrial tetrapods. The elimination of numerous archosaur and mammal-like reptiles enabled dinosaurs to occupy these recently vacant ecological niches. Current explanations claim that either volcanic eruptions (flood basalts associated with Central Atlantic Magmatic Province; Tanner et al. 2001) or climate change caused the TJ event (Quan et al. 2008). Although some researchers have also considered an asteroid or comet collision as an alternative explanation, to this date, no extraterrestrial crater matches the dates of the TJ extinction.

The Toarcian event, dated approximately 180 million years ago (Early Jurassic), mainly affected marine fauna (e.g., fish, crustaceans, and

marine reptiles), sparing most dinosaurian clades. The elimination of oceanic species suggests that changes in marine oxygenation or acidification, perhaps linked to volcanism (Karoo-Ferrar flood basalt; Pálffy and Smith 2000), caused this extinction. Close to 40 million years after the Toarcian, the Tithonian transition during the Late Jurassic (145 ma) saw a reduction in the number of theropod species (Tennant et al. 2017). Interestingly, contemporary research found noticeable continental differences in diversity loss, with Laurasia, relative to Gondwana, exhibiting a more pronounced decline in the number of species. Fossil counts also suggest that medium-sized, large-bodied theropods were especially susceptible to extinction, as was the case for megalosaurids, ceratosaurids, piatnitzkysaurids, and allosaurids (Tennant et al. 2017). Alternatively, carcharodontosaurids, neovenatosaurids, spinosaurids, tyrannosauroids, troodontids, and dromaeosaurids managed to survive into the Cretaceous. In contrast to other theropod clades, Paraves experienced accelerated radiation leading to multiple novel species during this transition. Even though paleontologists estimate sauropods reached their diversification maximum in the Late Jurassic, the fossil record evidences a sudden reduction in the number of species during the Jurassic-Cretaceous boundary (Tennant et al. 2017). Except for North America, the number of Brachiosauridae taxa fell dramatically worldwide (Tennant et al. 2017).

Around 117 million years ago, corresponding to the Aptian age (Early Cretaceous), India's Bengal region experienced a significant increase in volcanic activity (i.e., Rajmahal traps; Singh et al. 2004). Additionally, a second Cretaceous mass extinction occurred approximately 95 million years ago (Cenomanian-Turonian boundary). Some paleontologists and geologists claim that a rise in volcanism of two igneous provinces, located in the Caribbean and Madagascar, matches a decline in oxygenation during this time. These fluctuations caused the loss of numerous marine reptiles, including ichthyosaurian and pliosaurian taxa (Sachs and Grant-Mackie 2003).

The last Cretaceous extinction, the KT event, has been described in great detail over the past three decades; paleontologists have generated

multiple hypotheses concerning the causes of Cretaceous-Paleogene extinction, including gradual climate change, volcanism, and cosmic collisions. The current scientific consensus posits that nonavian Dinosauria, along with other archosaurs such as pterosaurs, plesiosaurs, and non-archosaurian marine reptiles, disappeared along with 75% of all life on earth approximately 65 million years ago.

Alvarez and colleagues detected high concentrations of iridium in KT sediments (Schulte et al. 2010). Given this material's rarity close to the earth's crust, the authors hypothesized a collision with a 15 km-wide asteroid occurred during the Cretaceous-Paleogene transition. Although initially considered a controversial claim, the subsequent discovery of a Late Cretaceous crater in Chicxulub (100 km in diameter), close to the Yucatan peninsula, provided strong support for Alvarez and colleagues' hypothesis (Schulte et al. 2010). The immediate consequence of this collision included severe earthquakes with a magnitude above 11 points on the Richter scale, megatsunamis covering coastal lands, and the ejection and spread of geological material to the atmosphere, reentering as spherules leading to the ignition of local wildfires around the Gulf of Mexico (to this date, the evidence does not support the claim of large fires occurring at a global scale; Schulte et al. 2010). The collision also expelled gases, dust, and water into the atmosphere, substantially modifying the climate. According to Schulte and collaborators (2010), the ejection of sulfur produced acid rain and led to a global decline in temperature (10 °C) for several years. Despite these alternations, the oceanic sediment did not exhibit an increase in marine acidification (Schulte et al. 2010).

## Discussion

Paleobiological reconstructions offer strong evidence of similarities the clade Dinosauria shared with extant tetrapods, from similar neuroanatomical organizations with reptilians and avian taxa to parental and social behaviors. To this date, the paleontological record supports the hypothesized



presence of paternal care in at least some theropod and ornithopod species. Likewise, it also suggests that dinosaurs differed in numerous aspects from contemporary species. Although researchers generally classify Dinosauria as an *r*-selected clade, the growth rate and gigantism of certain species have not evolved in other taxa during the evolutionary history of this planet. Similarly, osteological and histological analyses indicate the metabolism of these creatures did not follow either a strict reptilian or mammalian pattern. Concerning the multiple mass extinctions that occurred during the Mesozoic, the literature reveals that, while the Cretaceous-Paleogene event brought the reign of Dinosauria to a close, other ecological disruptions laid the foundations for their evolutionary success. The Late Triassic extinction, for example, eliminated multiple predators and competitors of Dinosauria, vacating many ecological niches and facilitating the rapid species radiation of this clade. Additional, environmental changes also accelerated species turn-out, leading to the noteworthy diversity of this now extinct clade.

## Cross-References

- [Crocodylia Cognition](#)
- [Paleontology](#)

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## Paleontology

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Paleontology, the study of ancient life, is a multi-disciplinary science. The fossil record provides a unique long-term view of the evolution of our planet and its biosphere, an insight into the extraordinary extinct organisms that have inhabited the Earth; it also informs us about global change through deep time and helps provide predictions for the future of life. Paleontology is a unique dimension of human thought, involving planetary evolution through deep time and speaks to our origins and place in the Universe. It has advanced as a science from a mainly descriptive subject based on careful taxonomy of fossil animals and plants by specialists to one relying heavily on the newest technologies to scan and analyze fossil material, from microscopic plankton to the skulls of the largest dinosaurs. Data on the morphology of fossils and their geographic and temporal ranges are now the components of

big databases; these form the basis for the reconstruction of phylogenies, and their calibration against geological time scales, as part of the Tree of Life. They also provide information to frame and test hypotheses on the long term and large-scale patterns and processes of the evolution of life in deep time. Nevertheless, our understanding and use of fossils have also provided fundamental evidence for tectonic processes, the movement and collision of continents through time, and the assembly of mountain belts.

How do we comprehend these alternative worlds in deep time, populated by animals and plants quite different from those of today? Worlds populated by dinosaurs with colored feathers; giant rats, weighing a ton; miniature human species; and frightening millipedes and sea scorpions exceeding the size of the tallest humans. The cast of a science fiction movie? No, the products of some four billion years of evolution. It is a story that only humans can attempt to unravel. Our understanding is based on scientific methodologies. Thomas Kuhn (1922–1996) proposed that science advances by paradigm shifts; in earth sciences the formulation of the theories of evolution and plate tectonics and possibly the meteorite impact at the end of Cretaceous sparked scientific revolutions. However, Karl Popper (1902–1994) argued that in science, proof is impossible; the best we can do is to continue to frame and test hypotheses that corroborate the available data and cannot be falsified. That is very much the methodology of paleontological research where data are generally incomplete.

## History

The early Greek historians and natural scientists, for example, Xenophanes (576–480 BC) and Herodotus (484–426 BC), recognized that some fossils were the remains of marine organisms. Xenophanes concluded that water must have once covered the Earth, whereas Herodotus suggested that the fossils in the hills of Egypt indicated that an arm of the Mediterranean extended southwards over the country. The

Romans, however, preferred to record fossils instead as magical objects.

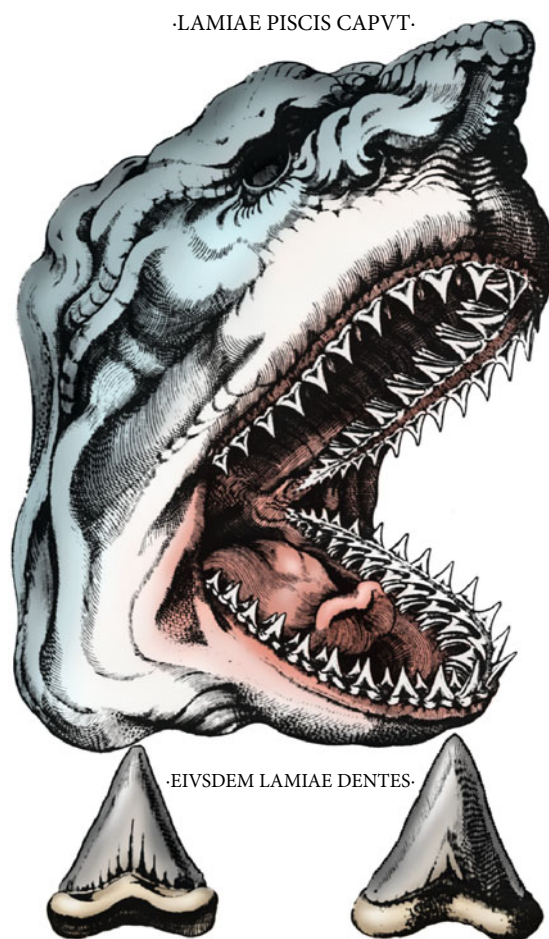
During the Renaissance, Leonardo da Vinci (1452–1519), the supreme polymath, used his knowledge of living animals and plants to explain the occurrence of shell beds in the hills of Lombardy in terms of once living shell banks now preserved, at four levels, in sandstones. Elsewhere, already fossils were being captured in cabinets of curiosity in the homes of the aristocracy; Conrad Gesner (1516–1565) displayed his fossil objects to good effect, whereas Johann Kentmann's (1518–1574) Ark or Cabinet resembled a well-organized museum with fossils recorded under stones and wood embodied in rocks. The notion that fossils somehow grew in the rock propagated by plastic forces continued to

prevail and was promoted by Robert Plot (1640–1696) and some of his contemporaries.

Nicolaus Steno (1638–1686), better known to geologists for his law of superposition of strata, established without doubt that fossil teeth or glossopetrae (tongue stones) he collected in the Tertiary rocks of the Italian Apennines were in fact identical to those of modern sharks landed from the nearby Ligurian Sea (Fig. 1). While in Britain, Robert Hooke (1625–1703) compared the structures seen in fossil wood (charcoal) with those seen in living trees, under the lens of a crude but effective microscope. Hooke also recognized the fact that organisms, such as ammonites, were now extinct. A critical component is the understanding of deep time. The planet did not originate thousands of years ago, but rather

#### Paleontology,

**Fig. 1** Nicolaus Steno's (1667) comparison of the head of a living shark (above: "head of a sea fish") and fossil shark teeth (below: "its teeth")



billions of years ago. James Hutton (1726–1797) provided the basis for understanding the planet's long and eventful history (Repcheck 2003). Paleontology picked up pace in the nineteenth century. George Cuvier (1769–1832) recognized horizons of mass extinctions or catastrophes in the Tertiary rocks of the Paris Basin. A significant part of Charles Darwin's *On the Origin of Species* (1859) was devoted to geology and the fossil record, whereas a year later John Phillips (1860) published a database of fossil ranges and diversity curves through time in *Life on Earth*. From these key discoveries sprang a number of key concepts not least those of evolution, extinction, and mass extinctions and subsequent studies built on these fundamental works. During the latter part of the nineteenth century and early part of the twentieth century, a continued focus on taxonomy and classification of fossil organisms was supplemented by some studies of the life modes and habitats of fossil organisms together with the recognition of recurrent assemblages and associations of animals and plants.

From the mid-1960s onwards, the science of paleontology began to change; there was a greater emphasis on community ecology and large-scale change through time. With the wider availability of computers, big databases were assembled for morphological analysis and for fossil range data throughout the Phanerozoic (Hammer and Harper 2006). X-ray scanning revealed much of the internal structures and the composition of many fossil organisms, particularly vertebrates, and molecular data were aligned with fossil data to construct and calibrate phylogenies. New discoveries and new techniques allowed paleontologists to pursue a much more scientific agenda and tackle much more interesting questions.

## Preservation

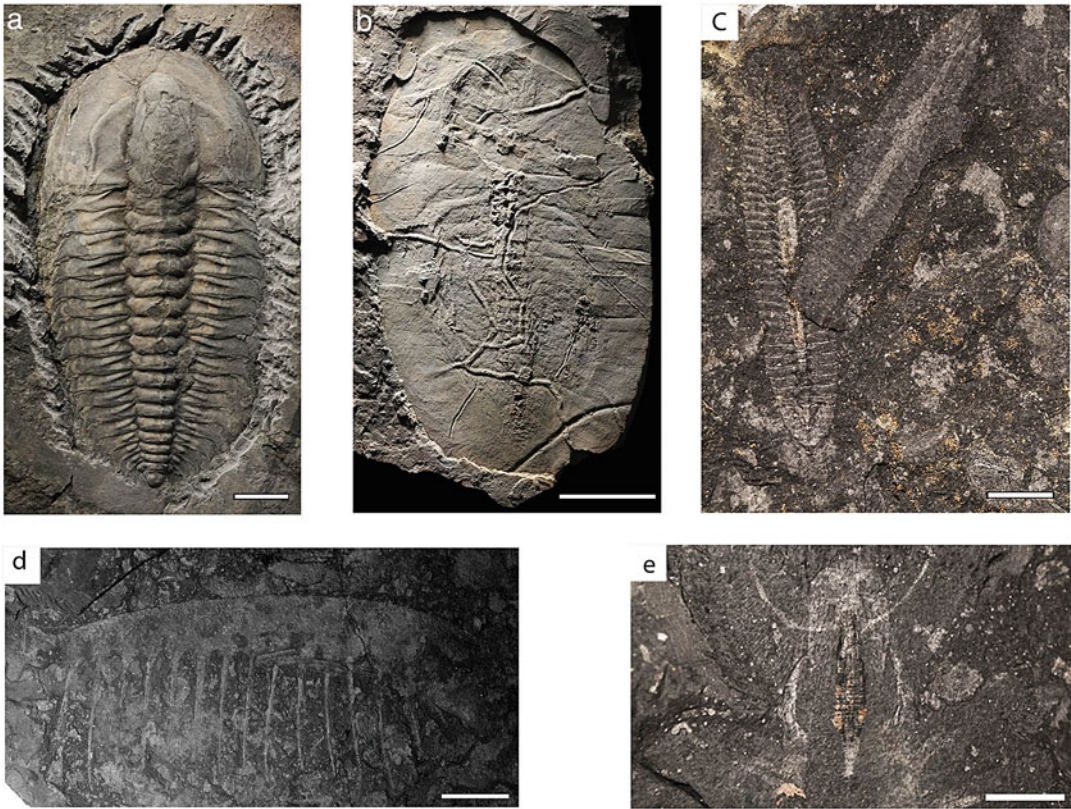
The fossil record is manifestly incomplete and biased but is more than adequate to document the key patterns and processes of the history of life. The eminent Victorian zoologist Thomas Huxley described the fossil record as “the skimmings of the pot of life.” Some 250,000 fossil

species have been described in contrast to the tens of millions of living species we have today. There is clearly a major disparity in numbers accounted for by the vagaries of fossil preservation. The science of preservation is normally called taphonomy and targets the processes of decay and preservation of an organism following its death (Allison and Bottjer 2010). The hard tissues of animals and plants are most usually preserved in the fossil record, since soft tissues and soft-bodied organisms rapidly decay during the transport and subsequent of dead organic material. Hard tissues commonly skeletons are preserved as molds, when the shell is dissolved or may be recrystallized as another substance or be partially or completely replaced by mineral material.

Occasionally, however, entire communities are preserved including the soft parts of skeletal organisms and soft-bodied organisms themselves (Briggs 2003). These exceptionally preserved biotas or Konservat-Lagerstätten preserve snapshots of the history of life. The life modes of these organisms, their affinities with other groups, and their place in food chains can be much better understood and graphically reconstructed. A large number of Lagerstätten are clustered around the lower and middle Cambrian, the most famous being the Burgess Shale (Canada), Chengjiang (China), and Sirius Passet (Greenland). In some fossils not only the guts and their contents are preserved but also muscle and nerve tissues and portions of the brain (Fig. 2). These discoveries expose much information about the origins and diversification of early animal-dominated, marine communities.

Paleontology is traditionally considered a sub-discipline of geology and is usually located in earth science departments and institutes. Paleontological data are derived from a number of sources: body fossils, the preserved bones and shells of organisms, and the behavior patterns left in the sediments (Fig. 3). The increasing relevance of fossils, however, to understanding biological processes and a greater alignment with the work of molecular biologists and paleontologists has seen a greater association with biological science departments.





**Paleontology, Fig. 2** Types of preservation in the early Cambrian Sirius Passet Lagerstätte, North Greenland. **a**, Trilobite *Buennellus*, hard parts preserved, sometimes in silica; **b**, a giant trilobitomorph *Arthroaspsis*, mold of soft parts showing a central gut and mining burrows produced by organisms feeding on the carapace; **c**, onychophoran

*Kleptothule* showing central gut trace; **d**, fine hairs preserved on the frontal appendage of the radiodont *Tamasiocaris* a sweep-net feeder; **e**, onychophoran *Kerygmachela* showing the head region displaying parts of the brain, nervous system, and eyes. (From Harper et al. 2019). Scales: measured in centimeters

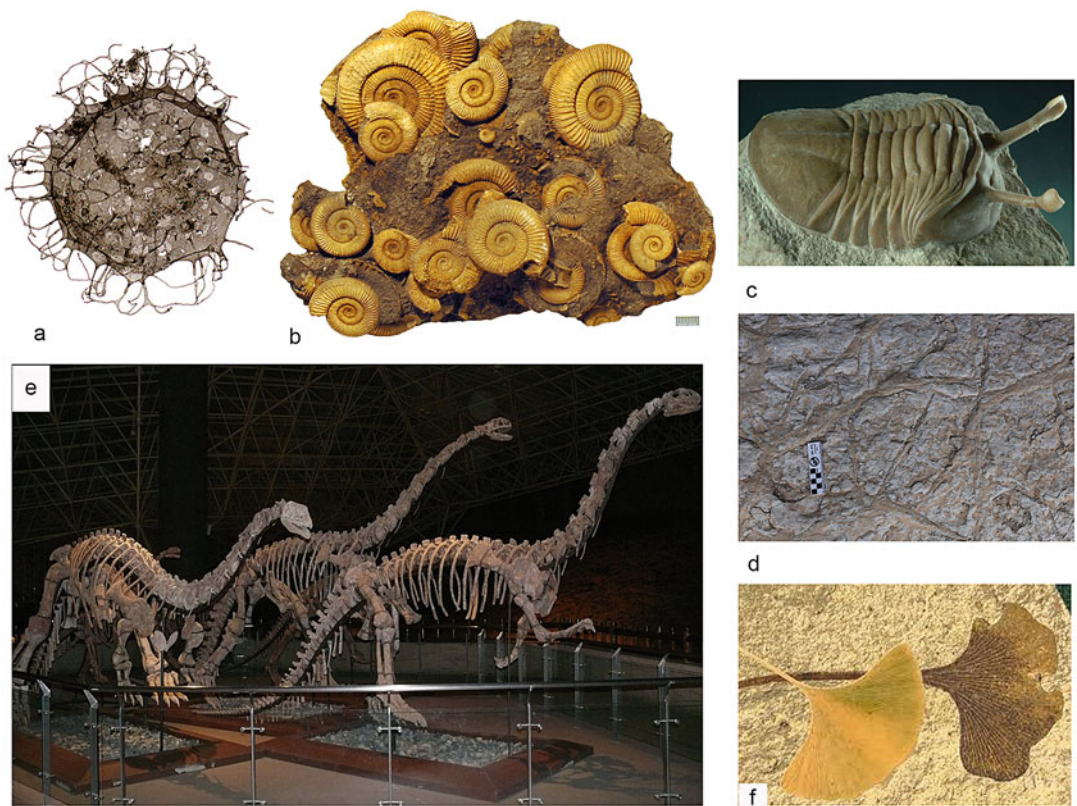
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## Evolution

Life has been diversifying and evolving on Earth for at least 3.8 billion years. The key model of natural selection, championed by Charles Darwin (1859), has been validated and hardened in all branches of biology (Futuyma and Kirkpatrick 2017). His observations on the fossil record that animals and plants changed through time by natural selection, progressing from simple forms to more modern forms in the Pleistocene, suggested that all species extinct and living are parts of a single Tree of Life. The ToL records relationships between organisms, and the tree itself is rooted in a single ancestral species. Fossil evidence is fundamental to understanding evolution, based on the

taxonomy and classification of fossil organisms, and their distribution in time and space. The ToL is, like any natural tree, composed of roots, a trunk, and branches. The dividing of the branches simulates speciation events. Speciation generally involves the splitting of a population into two perhaps by a physical or ecological barrier. The most common mechanism is that of allopatric speciation with populations normally split by a geographic barrier and isolated populations, perhaps stranded on islands form the the basis of the founder effect (MacArthur and Wilson 1967), associated with rapid and unusual evolution.

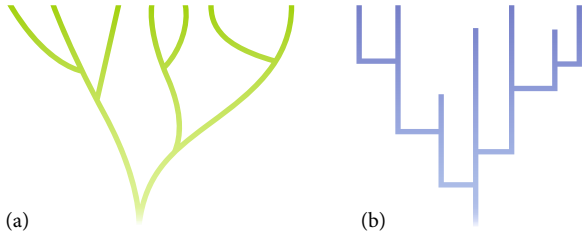
Two modes of speciation remain under debate (Fig. 4). Phyletic gradualism is characterized by sloping stems and branches, where speciation



**Paleontology, Fig. 3** A diversity of fossils; the evidence for the history of life (d is a trace fossil; all others are body fossils). **a**, Microscopic Precambrian acritarch composed of chitin (Nick Butterfield); **b**, block of Jurassic ammonites with calcium carbonate shells (Christian Klug); **c**, an Ordovician trilobite with eyes on stalks and composed of

calcium carbonate; **d**, horizontal trails of a Miocene crustacean in an ancient lagoon; **e**, giant Jurassic dinosaurs made of phosphatic bone; **f**, Cretaceous plant leaves (Wikipedia). Scales: **a** measured in microns; **b**, **c**, **d**, and **f** measured in centimeters; **e** measured in tens of meters

**Paleontology, Fig. 4** Two models of speciation. **a**, Phyletic gradualism and **b**, punctuated equilibria



takes place along lineages. On the other hand, punctuated equilibrium posits that lineages are in stasis but periodically speciation occurs as a rapid jump, indicated as lateral shift. There have been a number of tests of these hypotheses using fossil data. Because demonstration of the these models requires evolution within a single geological section, free from gaps and migrations of species in

and out of the area, punctuated equilibrium can be difficult to prove and easy to falsify.

Fossil data have been critical in understanding the relationships between organisms on the Tree of Life. Using cladistics methodologies based on morphology, there are now many phylogenies or trees available for most animal and plant groups, constructed using a range of computer software.

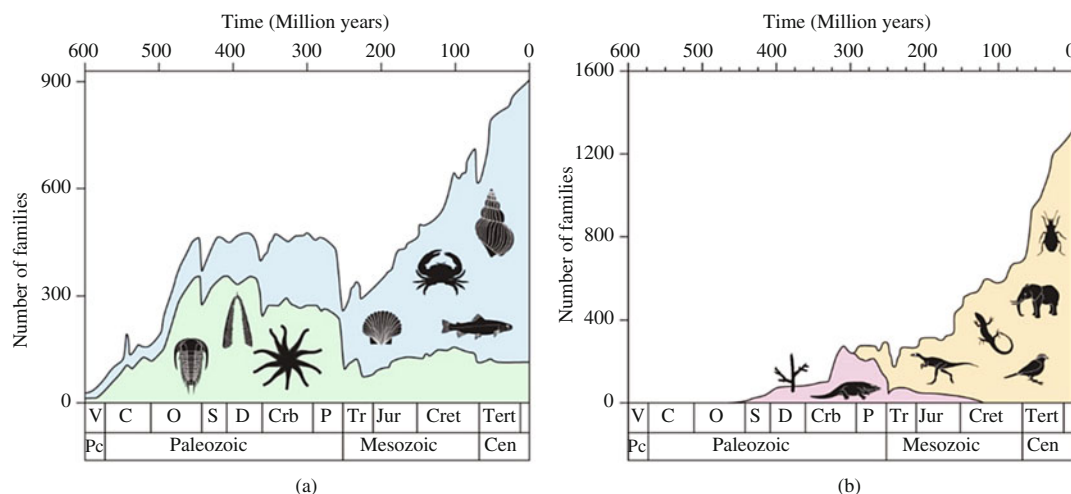
Other attributes can be mapped onto trees such as the paleobiogeographic distributions, age-range data, and the paleoecologies of organisms on parts of the tree. More recently trees have been reconstructed using molecular data or phylogenomics, and a molecular clock can be applied based on understanding the rates of change of particular proteins such as hemoglobin. Fundamental, however, is the calibration of such trees, and this can only be achieved by accurately dating the first occurrence of fossil members of those investigated clades (Donoghue and Benton 2007).

## Diversification and Extinction

Life has diversified from a single species deep in the Precambrian to between 2 and 20 million species today, a massive increase in species richness over some 4 billion years of Earth history. It is uncertain if there is a distinct pattern to this diversification; only a relative small number of species have ever been preserved; moreover estimates suggest that about 99% of organisms that ever existed are now extinct. Various models have been applied to this diversification, linear, logistic, and exponential, but there is no consensus. Rather

organisms have diversified through deep time, finding ways to adapt to new ecospace, changing conditions, and environments and balancing speciation with extinction to generate a highly irregular pattern.

Analysis of the fossil record demonstrates there were five major intervals of mass extinction, when over 30% of organisms went extinct during each event (Fig. 5). The animals and plants included a broad range of ecologies, attached to many different habitats, and the extinctions were global over a very short interval of time. The “big five,” the End Ordovician, Late Devonian, Permian-Triassic, End Triassic, and the Cretaceous-Paleogene, marked the turning points in the history of life but also set life off in different directions (Bambach 2006). For example, at the end of the Cretaceous, dinosaurs (excluding the birds) disappeared, but as life recovered the mammals gained diversity and dominance on land. Many causes have been advanced for the big five, each has its own peculiarities. The End Ordovician is associated with an ice age; the Late Devonian witnessed major cooling and anoxia; the Permian-Triassic (by far the most severe with the extirpation of some 95% of species) is associated with a run-away greenhouse; the End Triassic with anoxia and global warming; and an asteroid



**Paleontology, Fig. 5** The diversification of (a) marine life and (b) life on land. Life changed forever across the largest extinction of them all, at the Permian-Triassic boundary; the Paleozoic faunas (green and pink) were

replaced by “Modern” animals and plants (blue and beige). (From various sources summarized in Benton and Harper 2020)



impact (evidenced by an iridium anomaly, shocked quartz, melted glass, and a crater) is implicated in the End Cretaceous event (Hallam and Wignall 1997). The fossil record allows us to pinpoint these intervals of catastrophic change but also permits estimates of the rates of extinction in deep time, which habitats are most prone and which organisms are the most resilient. These data may help predict current extinctions and their consequences during what many term the “sixth extinction” with reported extinctions of amphibians, birds, and mammals far exceeding expected background levels.

## Paleoecology

An exciting part of paleontology is the ability to reconstruct the life modes of ancient organisms and their communities. These form two distinct avenues of study: autecology, the ecology of a single organism, and synecology, the investigation of associations or communities of organisms and their relationships to the environment (Brenchley and Harper 1998).

Autecology focuses on the form and function of organisms. There are three main lines of evidence: functional morphology (biomechanics), comparisons with modern analogues, and geological evidence. The functional morphology of an organism may be investigated through the use of biomechanical modelling, with real models consisting of man-made materials or computer simulations. Simple models can, for example, be constructed to understand how dinosaurs walked and ran, how brachiopod shells opened and closed, and how carnivorous reptiles chewed flesh. Comparisons with modern analogues is usually simple if there is a living group with which to compare. The biomechanics and function of limbs were probably similar between those of the fossil horse *Hyracotherium* from the Eocene and those of the genus *Equus*, today. Similarly, a Cambrian brachiopod may have functioned much the same as its modern counterparts. Those without obviously similar descendants such as the dinosaurs might be better compared with analogous though unrelated animals, such as elephants. Finally, the

environmental context is often key: dinosaurs and mammals often occur in sandstones associated with river systems, whereas graptolites are identified with dark mudstones and shales, testifying to deep-water marine environments. Associated biotas provide clues as do trace fossils, the preserved remains of animal and plant behavior, such as burrows, trails, and trackways.

Synecology involves community paleoecology, describing and analyzing the composition and structure of paleocommunities, how species related to each other and the environment and combined together to form food webs (Brenchley and Harper 1998). Most studies commence with intensive, usually bulk sampling of a biota, the careful identification and counts of the absolute abundance of each species and analysis, first using rarefaction curves to test sample size and then measures of diversity, dominance, and evenness to characterize the community. Graphic reconstruction such as those for the Jurassic Period can depict life on land and in the sea based on these data (see Benton and Harper 2020). Jurassic Park is no longer a sense of wonder but a testable hypothesis framed by the collection and analysis of fossils from different ancient environments (Fig. 6).

Relationships between organisms and their environment can be recorded for modern ecosystems by direct observation. For obvious reasons this is simply not possible for fossil organisms. Nevertheless bite marks and borings occur on and in bones and shells, the remains of animals and plants occur in coprolites (animal fossil feces), and increasingly gut contents can be analyzed, demonstrating predator-prey relationships. Commonly the relationship is less aggressive, and commensalism in the form of encrusting organisms such as bryozoans, corals, and serpulite worms on shells is relatively common in the fossil record.

## Biostratigraphy

Fossil organisms have evolved and preserved their temporal ranges in the geological record. The average range of a species is 5 myr; thus fossil-based successions are uniquely useful in



**Paleontology, Fig. 6** Jurassic Park and seas reimagining ancient environments in the early Jurassic on (a) sand, (b) muddy sand, and (c) associated with bitumen; in the late

Jurassic on (d) mud, (e) a reef, and (f) a lagoon. (From McKerrow 1978, modified in Benton and Harper 2020)



correlating geological strata. If, for example, a species of graptolite occurs at a particular level in black shales in Scotland, when found in Central Australia, perhaps in a sandstone, nevertheless the strata are of the same age. Characteristic fossils are typical of given intervals of time; for example, graptolites evolved rapidly during the Ordovician and Silurian, corals are commonly associated with the Carboniferous, whereas ammonites had their acme in Mesozoic strata. These fossil successions form the basis of biozones, the key operational units of biostratigraphy, and thus a stratigraphy can be established based on sequences of evolving organisms.

William Smith had already recognized the use of fossils as a proxy for geological time in the early 1800s as he accumulated data for the first geological map published in 1815, a survey of the geology of England and Wales. Thus, along his transect from northwest Wales to Thames Estuary, the older Cambrian rocks of North Wales were characterized by trilobites, the Carboniferous rocks typified by plants and the younger Neogene sediments of the London Basin, locally packed with mollusk shells and mammal bones. On this basis, British, French, and German geologists, between 1790 and 1840, scrambled to divide geological time each naming periods or systems with distinctive fossils and strata. These pieces of geological time were assembled in order, with the Cambrian at the base and the Tertiary (Paleogene and Neogene) at the top. This provided a very crude way of correlating rocks, but scientists needed much more precision and finer time zones for accurate correlation.

In order to correlate geological strata more precisely, fossils are normally organized into assemblage or range zones, based on the work of Albert Oppel (1831–1865). Oppel's methodology was modern and rigorous and formed the basis for correlation. His zones were lithological units with unique associations of species and were aligned with stages, which could be recognized regionally and occasionally, globally. These units functioned well, but modern practice would define each stage and zone in terms of a measured range in a rock succession (Doyle 2001). A number of more sophisticated numerical methods are now

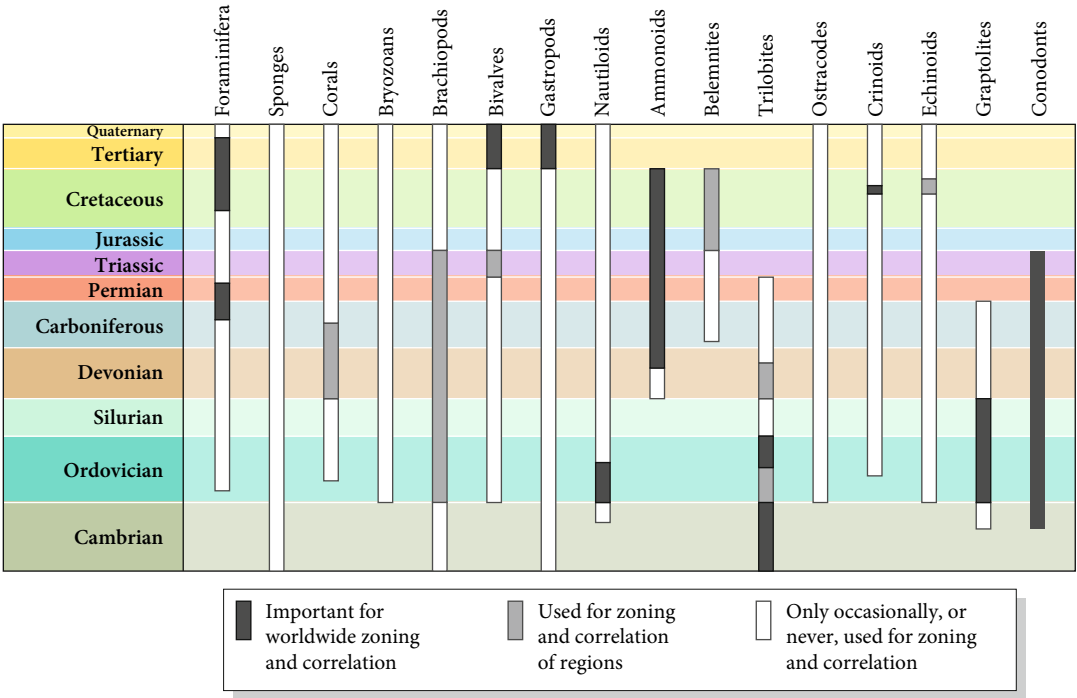
available to accurately compare and correlate two or more geological sections based on zonal ranges (Hammer and Harper 2006).

Some organisms are better than others as zonal fossils; those which are widespread are easily preserved and evolve rapidly. And different fossils characterize best particular time intervals (Fig. 7). Correlation, primarily by fossils, allows us to differentiate local events in a single marine basin of a river system from those truly global events such as mass extinctions.

## Paleobiogeography

Tectonic plates have moved throughout geological time, associated with island arcs and microcontinents, and so too have the positions, shapes, and sizes of biotic provinces. Fundamental evidence for continental drift was provided by not only the fit of the African and South American continents but also the continuity of faunas and floras across these and the continents of Australia and Antarctica (Fig. 8). It was not until the paradigm shift of the 1960s with the theory of plate tectonics that a realistic explanation for the movement of continents, that is, continental drift, could be adequately explained.

Fossil data have been essential in reconstructing the past positions of the continents and the oceans, barriers on land and in the sea, and migrational routes and biodiversity hot spots (Benton and Harper 2020 for summary and sources). Climate has changed dramatically through time. Many animals and plants are climatically sensitive; their distributions today commonly track altitude, latitude, or the movement of cold and warm air and water currents; these properties can further aid paleogeographic reconstructions. The Ediacara biota of the Late Precambrian already demonstrated some provinciality. The Early Paleozoic animal communities were clearly structured into provinces particularly within the brachiopods and trilobites together with the graptolites and mapped out the extent, margins, and positions of ancient continents (Harper and Servais 2013). By the Carboniferous and Permian, life on land was well established, the



**Paleontology, Fig. 7** Ranges of key fossil groups used in biostratigraphic correlation of different parts of the geological timescale. (From Benton and Harper 2020)

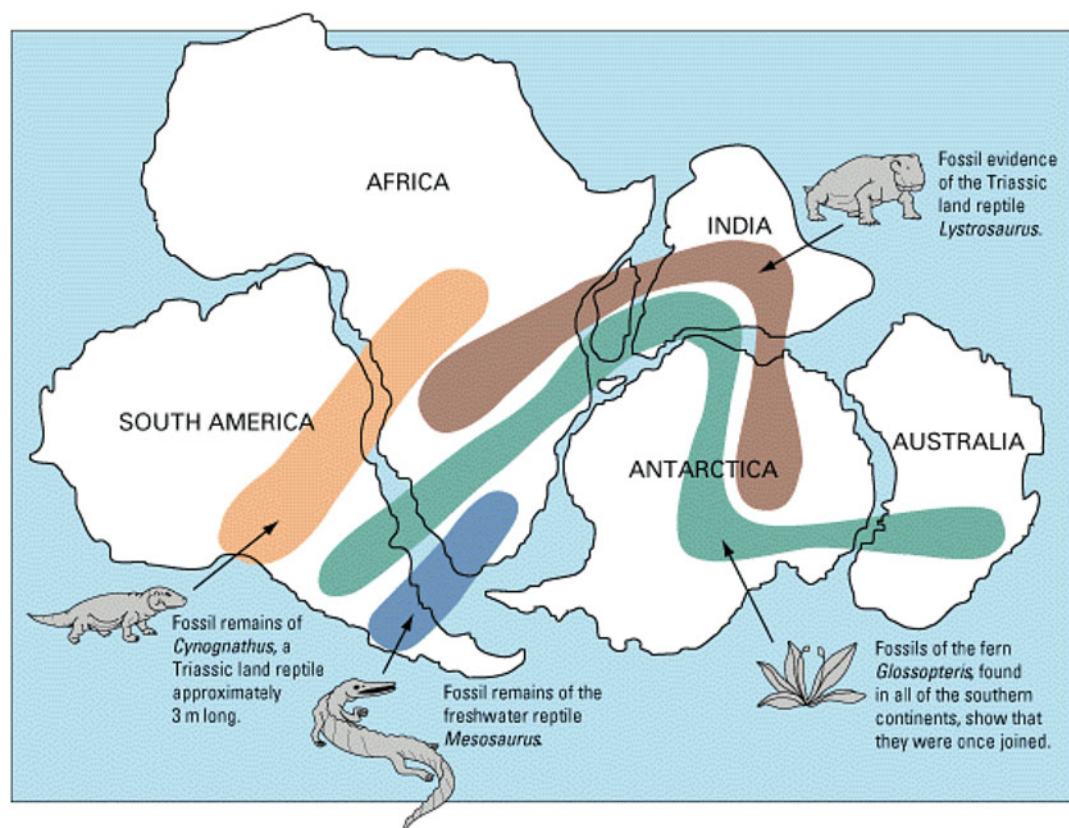
continents dispersed, and ancient floral provinces were clearly identifiable; the *Glossopteris* floral province is one of the best known, linking the southern continents. During the Mesozoic provincial patterns in the oceans were relatively simple, with marine life organized into Boreal (high-latitude) and Tethyan (low-latitude) provinces. On land, more complex ecosystems and bioregionalization patterns were provided by the rise of the dinosaurs during the Triassic and the appearance of flowering plants in the Cretaceous. In the Paleogene and Neogene, the configuration of the continents approached those of the present day, and our map of the provinces converged on modern biotic regions.

**Fossils in Mountain Belts**

The stratigraphy of mountains is fundamental to understanding global tectonic processes, and their distinctive faunas and floras had key roles to play, commonly as isolated island environments, in the

evolution of life on Earth (Harper 1998). Fossils have proven immensely useful in dating sedimentary rocks in mountain belts, assessing their provenance and the finite strain recorded in the rocks. “One bad fossil is worth a good working hypothesis.” This key statement from the eminent Alpine geologist Rudolf Trümpy reflected the fact that the discovery of a single fossil can literally turn a mountain belt on its head. Fossils in mountain belts are, however, generally rare, metamorphosed, and tectonized. Nevertheless when identified, fossil material can pinpoint the age and provenance of rock units. For example, large-scale mass horizontal movements of slabs of crust, or thrust sheets, in the Swiss Alps, Northwest Scottish Highlands, and the Scandinavian Caledonian mountains were detected over a century ago by the discoveries and utility of fossiliferous successions.

Both Steno and Darwin, in their respective studies during the late 1600s and early 1800s in the Apennines and the Andes, recognized shells on the tops of mountains and speculated about



**Paleontology, Fig. 8** Carboniferous and Permian distributions of plant and reptiles linking the southern continents; this fit suggested to Alfred Wegener that

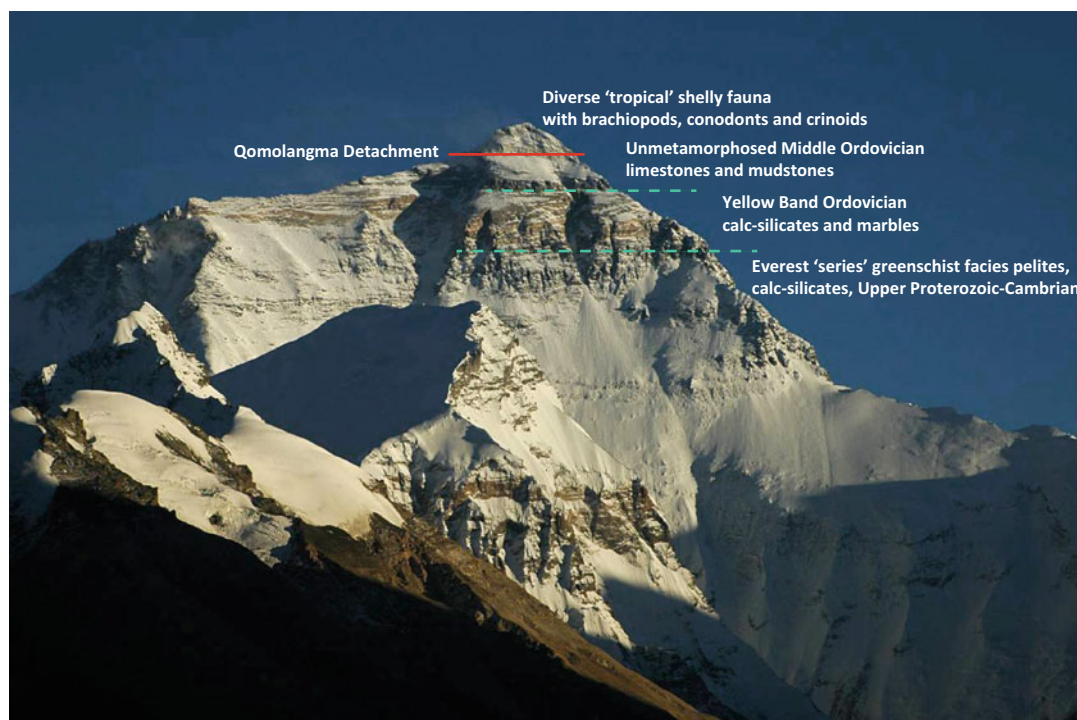
subsequently the continents drifted apart to their present positions today. (From Benton and Harper 2020)

large vertical movements in the Earth's crust. During the early ascents of Mount Everest, rock samples collected from at and near the summit were submitted for analysis. Fossil data initially suggested a range of ages. During the 1960s expeditions to the Everest Ranges focused on dates within the Ordovician based on shelly faunas such as brachiopods and cephalopods, confirmed more recently by conodonts (Stouge et al. 2020). The limestones capping Everest were indeed Middle Ordovician in age, and the summit of the roof of the world lay within warm tropical seas, rich in animal life, some 465 million years ago (Fig. 9). The region was uplifted and amalgamated into the Himalayan mountain belt, when India collided with the rest of Asia 55 million years ago.

Paleontological data have predicted and evidenced the existence and positions of ancient

oceans. The present day Atlantic Ocean separates Europe from North America, but did the Atlantic Ocean open, close, and reopen (Wilson 1966)? Examination of the brachiopods and trilobites within the Caledonian mountain belt suggests a suture existed within the belt, stretching from the north of Norway to Florida, indicating that during the Early Paleozoic an ancient ocean separated Europe from North America. Preserved in the ancient Caledonian Orogen are the remains of oceanic crust but, more significantly, islands which contained locally diverse fossil faunas contrasting with those of the continental margins of Europe and North America. The roles of such islands as ancient analogues of the Galapagos Islands today have been hypothesized.

Rates of geological events and processes have been constrained by paleontological data. The



**Paleontology, Fig. 9** The roof of the world. The rock formations displayed on the north face of Everest indicating that fossils from the summit provide crucial evidence to

date these rocks and indicate their origin before uplift in shallow-water tropical seas around an ancient equator. (Photo of Everest from Wikipedia)

Banda Arcs form a Neogene and Quaternary tectonic belt along the northern continental margin of Australia. Detailed biostratigraphy, based on foraminiferan microfossils, indicates the start and termination of folding and the age of emplacement of the thrust sheets, their imbrication, and the timing of the uplift of the tectonic belt as a whole. The thrust sheets travelled some 50 km southwards during 4–5 million years, to overthrust the Australian plate. Estimates based on the foraminiferan zonal stratigraphy suggest the thrusts were emplaced at between 6.25 and 12.5 cm per year, while the belt was uplifted at rates of about 1.5 cm per year.

Fossils thus can help reconstruct complex plate movements, but they can also quantify the amount of strain in rocks (see Benton and Harper 2020). Many fossils, originally symmetrical, are deformed in tectonic belts, the amount of strain in the rocks can be assessed and the fossil returned to their normal shape by the use of simple drawing software. Moreover, since some fossils change

color during metamorphism, the thermal maturation of strata can be estimated. Conodonts, for example, are useful thermal indicators, changing color from light amber through gray, black, and white eventually becoming translucent at temperatures of about 600 °C. Other fossils such as acritarchs, graptolites, and plant materials (vitrinite) also display color changes. In addition, paleotemperatures are commercially useful, predicting the so-called oil and gas window, where reservoirs hold extractable hydrocarbons.

## Conclusion

Almost certainly unique to ourselves, *Homo sapiens*, is consciousness, and part of that property is a curiosity about our origins, where we came from, and where we fit into the history of a unique planet and its biosphere that is over a billion years old. Humans can think about our existence, its past and its present, and plan for our



future. That brings knowledge but also a massive responsibility.

## Cross-References

- [Cenozoic Era](#)
- [Convergent Evolution](#)
- [Endemism](#)
- [Natural Selection](#)
- [Origin of Species](#)

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## Panbanisha and Panzee

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## Synonyms

### Panpanzee

Bonobo Panbanisha (*Pan paniscus*, November 1985 – November 2012) and chimpanzee Panpanzee (known as Panzee; *Pan troglodytes*: December 1985 – February 2014) were apes co-reared from early infancy by E. Sue Savage-Rumbaugh and colleagues at the Language Research Center (LRC) in Atlanta, GA. They were reared in a language-rich environment by a stable team of human caregivers in order to illuminate the nature and extent of species differences and environmental influences on the development of language skills in the nonhuman primates most closely related to *Homo sapiens*. Their primary means of symbolic communication with their caregivers was through touching “lexigrams,” which are arbitrary visual symbols that are equivalent to printed words. Different lexigrams denoted types of foods, objects, individuals’ names, locations, actions, adjectives, and other concepts (e.g., yes, no) that were prevalent in the



young apes' world. Panbanisha and Panzee had access to about 256 lexigrams during their co-rearing period.

Chimpanzees and bonobos are closely-related species; both are believed to have diverged from the human lineage approximately six million years ago and, therefore, serve as our closest evolutionary relatives as well. Prior research with chimpanzees Lana, Sherman, and Austin and bonobos Kanzi and Mulika had resulted in a confound between species, age of initial symbol learning, and symbol-teaching strategies that made it difficult to draw conclusions about non-human primates' learning of language skills. Specifically, the chimpanzees had been enrolled in the language research projects after they were 1 year of age and had been taught to use and respond to lexigram symbols primarily through trial-based reinforcement learning. The bonobos had been exposed to lexigrams and rich spoken English earlier in infancy and had learned symbol use through a more naturalistic enculturated rearing process in which human caregivers used speech and symbols to communicate with the bonobos throughout daily routines, much as is done in human families. The bonobos demonstrated more extensive and flexible symbol use than did the chimpanzees, and surprisingly, also exhibited substantial comprehension of spoken English. However, it was not clear whether these disparities represented true species differences, or were facilitated by different rearing environments and practices. Detailed information on the projects with these chimpanzees and bonobos can be found in Rumbaugh (1977: Lana), Savage-Rumbaugh (1986: Sherman & Austin), and Savage-Rumbaugh, Murphy, Sevcik, Brakke, Williams, and Rumbaugh, (1993: Kanzi).

Panbanisha and Panzee were reared together from the age of a few weeks until they were approximately 4 years of age, when Panzee was moved to the chimpanzee colony at the LRC. During their early years, Panbanisha and Panzee were immersed in an environment designed to facilitate comprehension and production of symbolic communication. The LRC laboratory facility in which they were raised included several ape-safe rooms with kitchen, bath, sleeping, and play

areas as well as over 50 acres of woods with countless trees to climb and several trails leading to sites baited daily with a variety of foods. A small team of caregivers accompanied the young apes throughout the day, using English and lexigram communication as they participated in daily routines of care, play, feeding (both outdoor foraging and indoor food preparation), household chores, and bedtime. Most days also included some type of assessment session or quiet time during which the young apes were expected to sit calmly and focus on the task at hand. Thus, their first years were structurally and linguistically as similar as possible to those experienced by young human children given that Panbanisha and Panzee were not allowed to leave laboratory property.

Caregivers recorded all instances of lexigram use and demonstrations of English or lexigram comprehension and production during daily activities and also conducted experimentally-controlled studies of English word comprehension. The resulting data indicated that both Panbanisha and Panzee understood several spoken English words and visual lexigram symbols and used symbols appropriately to communicate with their caregivers. The bonobo, however, began using lexigrams at an earlier age; had a larger, more flexible vocabulary; and appeared to be less context-dependent when interpreting complex utterances. Between 3 and 4 years of age, Panbanisha's receptive vocabulary, tested under controlled conditions matching English words to lexigram symbols, included approximately 186 words, while Panzee's included around 97 (Brakke and Savage-Rumbaugh 1995). Panbanisha's productive vocabulary, including lexigram symbols used spontaneously at least once per month, included approximately 140 symbols; Panzee's included approximately 90 symbols (Brakke and Savage-Rumbaugh 1996).

Later analyses of Panbanisha's and Panzee's symbol comprehension and use supported these early findings of vocabulary size with some growth over time (e.g., Beran and Heimbauer 2015), and also suggested that both apes combined symbols in ordered ways suggestive of a primitive grammar or "protogrammar"

(e.g., Lyn et al. 2011). Notably, both apes engaged in conversational turn-taking with their caregivers in ways that let them negotiate their daily life in much the same way as young human children. Panbanisha's performance across many linguistic measures corroborated that of bonobo Kanzi (See Savage-Rumbaugh et al. 1993) and provided insight into the possible foundations of early human language acquisition as well. Panzee – although not as adept with symbolic communication as were the bonobos – was the first, and to date only, chimpanzee to demonstrate extensive English speech comprehension under experimentally controlled conditions and to engage in symbolic communication using lexigrams without repetitive trial-based training.

Panbanisha's and Panzee's skills with English comprehension and use of communicative symbols also facilitated inquiry into other cognitive skills and interactions. Both apes demonstrated the ability to plan and navigate computer-mediated mazes using a joystick and to manipulate sets of objects in ways that reflected an underlying logic. In addition, after relocating to the chimpanzee colony, Panzee also participated in Michael Beran's (e.g., Beran and Evans 2012; Beran et al. 2013) and others' studies of chimpanzee cognition along with Sherman, Austin, Lana, and Mercury. In these studies, Panzee demonstrated skill with enumeration and quantification, self-control, prospective memory, and several other cognitive skills.

In a notable series of studies on spatial memory led by Charles Menzel (e.g., Sayers and Menzel 2012), Panzee regularly and accurately used lexigrams and gestures to communicate to experimentally naive caregivers that specific foods or other items had been hidden earlier by another person in the woods around her enclosure. She then used gestures, eye gaze, and vocalizations to remotely direct the caregiver to the buried cache. In extensions of this work, Panzee rank-ordered her preference among multiple hidden caches based on food type, food quantity, and ease of access in a way that related to the energy- and time-efficiency of obtaining the food (Sayers and Menzel 2012). Panzee lived with the other

chimpanzees at the Language Research Center until her death in February 2014.

Panbanisha was enrolled in the bonobo Species Survival Plan and gave birth to sons Nyota and Nathan. She and her offspring moved in the year 2005 with Kanzi and the other LRC bonobos to the Great Ape Trust of Iowa in Des Moines (now known as the Ape Cognition and Conservation Initiative). In November 2012, Panbanisha died after a brief illness.

The research with Panbanisha and Panzee has contributed to our understanding of the evolution of human language and cognition in several ways. In both species of *Pan* – as represented by Panbanisha and Panzee – many of the cognitive and social bases of language skills appear to be present at least to some degree, particularly in human-enculturated environments that support the development of these capacities. The work with these and other apes, through extension to our own species, also highlights the remarkable neural specializations in humans that have resulted in the capacity to elaborate on these higher cognitive and communicative skills as well as to leverage culturally-transmitted knowledge passed along over thousands of generations to yield powerful systems of cognition and language.

## Cross-References

- [Ape Cognition and Conservation Initiative \(ACCI\)](#)
- [Charles R. Menzel](#)
- [David Washburn](#)
- [Duane Rumbaugh](#)
- [Georgia State University's Language Research Center](#)
- [Kanzi](#)
- [Language](#)
- [Language Research: Great Apes](#)
- [Lexigrams](#)
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## Pangolin

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## Synonyms

*Pholidota*; *Scaly anteater*

## Definition

The pangolin family is comprised of a variety of scaly, armored terrestrial mammals that in appearance somewhat resemble armadillos and anteaters. Depending on the exact species, pangolin size ranges between that of a rabbit and a medium-sized dog. Due to similarities in morphology and diet, pangolins may be referred to as “scaly anteaters.”

## Introduction

The order of Pholidota, to which the pangolin belongs, contains only a single extant family of animals. This family, Manidae, in turn contains the three genera *Manis*, *Smutsia*, and *Phataginus*, to which the eight currently living species belong (Gaudin et al. 2009). Besides being the only extant species within their lineage, pangolins feature a full-body scaly keratinous armor that is unique among mammals. Functionally similar to the armored bands of the armadillo, the pangolin’s scaly armor makes it relatively impervious to predator attacks when curled into a ball, and the scales’ sharp edges additionally deter attempts to circumvent this defensive mechanism (Ganguly 2013; Robinson 1983; Wilson 1994). Correspondingly, the name “pangolin” derives from the Malay “Pengguling” which roughly translates to “rolling,” as per the animal’s defensive mechanism (Lexico 2019).

## Behavior and Ecology

Pangolins are found in the southern regions of Asia as well as in sub-Saharan Africa and prefer a range of predominantly vegetated habitats where their main dietary components of ants and termites are abundant (Choo et al. 2016; Gaudin et al. 2009; Robinson 1983; Save Pangolins 2019a; Wilson 1994). Apart from their characteristic scaly armor, pangolins may use a foul-smelling odor secreted from their anal glands as a further defensive measure (Ganguly 2013; Wilson 1994). Pangolins boast a variety of

specialist adaptations that make them well-equipped for their particular ecological niche. Their powerful clawed front legs are ideally suited for burrowing or climbing trees, as well as breaking open ant hills and termite mounds so as to reach their prey items (Ganguly 2013; Robinson 1983; Wilson 1994). Tree-dwelling species tend to use their prehensile tail to add to their climbing prowess (Ganguly 2013; Robinson 1983). As all but one species are nocturnal, pangolins rely on their acute sense of smell to pinpoint food items (Ganguly 2013; Wilson 1994). Indeed, genetic research has shown that both the Asian and African pangolin varieties bear genetic markers associated with a highly developed sense of smell (Choo et al. 2016). Their extremely elongated and extendable tongue is used to lap up insects and is unique among mammals in that it extends into the abdominal cavity (Chan 1995; Ganguly 2013; Wilson 1994). In order to prevent insects crawling into their facial orifices, pangolins use a set of membranes to protect their eyes and are able to close off their nostrils and ears during foraging (Ganguly 2013; Wilson 1994), making them well-equipped to deal with the challenge of eating ants and termites.

## Lineage and Subspecies

Although both extant and extinct species of pangolin fall within the order of ‘*Pholidota*’, the detailed resolution of their phylogeny has long remained a point of dispute. Part of the issue in resolving the pangolin family tree lies in the animals’ morphology and ecology. The lack of teeth, preference for vegetated environments, and low population densities characteristic for *Pholidota* are believed to have resulted in a relatively poor fossil record, making detailed morphological studies challenging (Gaudin et al. 2009). Currently, the most accurate subdivision of extant species appears to be across three separate genera: ‘*Manis*’, ‘*Phataginus*’, and ‘*Smutsia*’. Within this division, the four extant Asian species are classified as ‘*Manis*’ and include the “Indian pangolin” (*M. crassicaudata*), “Chinese pangolin” (*M. pentadactyla*), “Sunda pangolin” (*M. javanica*), and “Philippine pangolin” (*M. culionensis*). The

four extant African species are divided between the *Phataginus* and *Smutsia* genera, the first of which contains the predominantly arboreal “tree pangolin” (*P. tricuspis*) and “African black-bellied pangolin” (*P. tetradactyla*), while the latter contains the more terrestrial “giant pangolin” (*S. gigantea*) and “ground pangolin” (*S. temminckii*) (Gaudin et al. 2009).

## Conservation Status

Although the pangolin’s natural predators do not extend beyond leopards and pythons (Wilson 1994), all species are under heavy threat from human activity. In fact, pangolin varieties are now the most trafficked mammals in the world due to the value of their meat and scales in Chinese traditional medicine. As such, all pangolin species are currently experiencing population collapses due to poaching activity (Aisher 2016; Save Pangolins 2019b). Because a single pangolin is estimated to consume up to 70 million individual insects per year, they play a vital role in the control of social insect populations, thus balancing the ecosystems they live in (Durojaye and Olufemi 2015; Save Pangolins 2019a).

## Concluding Remarks

Due to their many specialist adaptations, these animals make for a somewhat strange, yet fascinating group. Sadly, the pangolin’s intrinsic value, as well as its role in maintaining social insect populations within ecosystems, is currently under heavy threat from poaching and trafficking. In order to ensure the future of pangolins outside of captivity, more concerted and global conservation measures must be attempted (Durojaye and Olufemi 2015; Save Pangolins 2019b).

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## Panpanzee

- [Panbanisha and Panzee](#)

## Panthera

- [Feline Life History](#)

## Pantherinae

- [Feline Life History](#)

## Paradoxical Extinction Effects

- [Partial Reinforcement Extinction Effect](#)

## Parahippocampal Cortex (PHC)

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## Synonyms

[Anatomy](#); [Hippocampus](#); [Memory](#)

## Definition

Parahippocampal cortex, termed postrhinal cortex in the rodent brain, is a region in the medial temporal lobe that is involved in processing visuo-spatial and contextual information in the service of episodic memory or memory for the events of our daily lives.

## Introduction

More than half a century ago, Scoville and Milner were the first to determine the importance of the hippocampus in memory as a result of involvement in the influential case of HM, the famous amnesiac patient whom we now know as Henry Molaison. Over the next few decades, it became apparent that memory processes were also supported by distinct cortical areas surrounding the hippocampus. Decades of research have shown that these parahippocampal structures are not merely conduits of information for the hippocampus, but that they have specific functions with regard to memory. It is now widely accepted that



the interaction between the hippocampus and these surrounding areas is necessary for associative learning and episodic memory.

The hippocampal memory system, also called the medial temporal lobe memory system, includes the hippocampal formation and the parahippocampal region. The hippocampal formation includes the dentate gyrus, the hippocampus proper (fields CA1, CA2, and CA3), and the subiculum. The parahippocampal region comprises the perirhinal, parahippocampal (PHC), and entorhinal cortices, as well as the presubiculum and parasubiculum. The PHC is located on the ventral surface of the temporal lobe bordered rostrally by the perirhinal cortex and entorhinal cortex and laterally by area temporal cortex (Suzuki and Amaral 2003). The situation is similar in the rodent brain, except that the region homologous to the PHC is termed the postrhinal cortex (POR). In the rat and mouse, Burwell and colleagues defined the POR as the area caudal to the perirhinal cortex and dorsal to the rhinal sulcus (Beaudin et al. 2013; Burwell 2001). The rodent POR wraps obliquely around the caudal pole of the brain and is bordered dorsally by the temporal association cortex and ventrally by the EC. The POR is subdivided into dorsal and ventral subregions. Likewise, the monkey PHC is composed of two subregions, areas TH and TF.

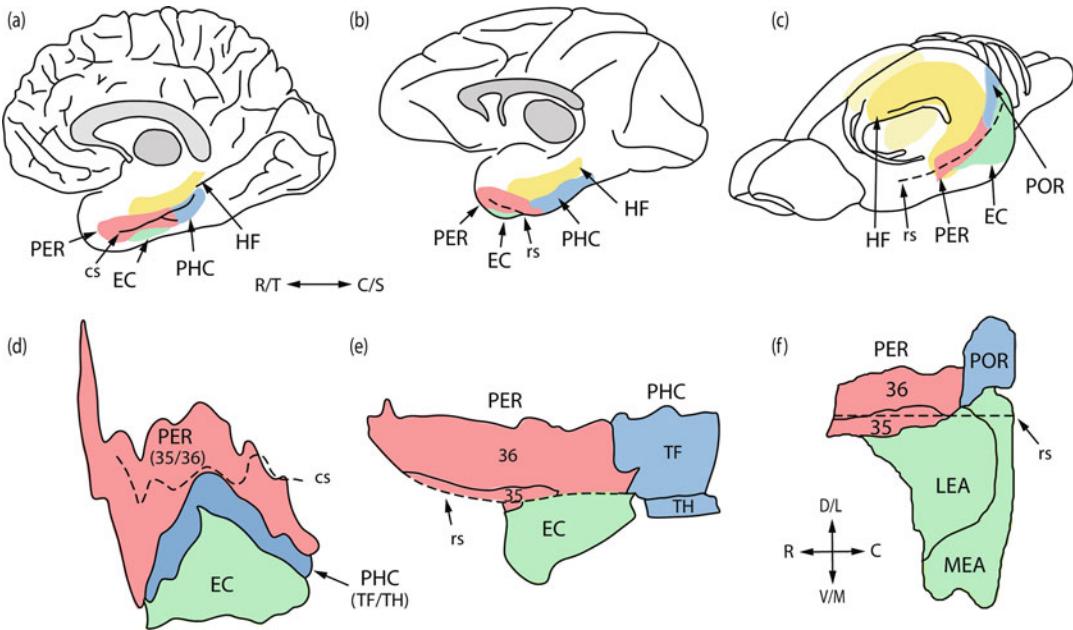
In the primate brain, it is important to realize that the word “parahippocampal” is used in four different anatomical and functional phrases: the “parahippocampal region,” the “parahippocampal cortex,” the “parahippocampal gyrus,” and the “parahippocampal place area.” Unfortunately, these terms are often used interchangeably, especially in the functional imaging literature. Again, for clarification, the parahippocampal regions include five anatomical structures, one of which is the PHC. The parahippocampal gyrus includes parts, but not all of the perirhinal cortex, the entorhinal cortex, and the PHC. The parahippocampal place area is not an anatomical structure, but rather is a region that is functionally defined in human imaging studies and varies across individuals. In rodents, this ambiguous nomenclature is avoided as the area homologous to the PHC is termed the POR. The rodent brain is

smooth, and so there are few sulci and no gyri. Thus, in rodents “parahippocampal” is used only to designate the parahippocampal region.

## Structure

Comparisons of the hippocampal memory system across humans, monkeys, rats, and mice show strong structural similarities. For example, the perirhinal, PHC/POR, and entorhinal cortices are associated with the caudal portion of the rhinal sulcus and show similar adjacencies in rodents and primates (Fig. 1). Neuroanatomical studies show substantial connectional homology of the PHC and POR across primates and rodents for both hippocampal, cortical, and subcortical structures. As might be expected given the role in memory, PHC/POR is connected with hippocampus both directly and via the entorhinal cortex. PHC/POR has direct and reciprocal connections with hippocampal field CA1 and the subiculum (Agster and Burwell 2013; Suzuki and Amaral 1990). Indirect projections are through EC to the dentate gyrus and hippocampal field CA3. The PHC/POR is strongly interconnected with the perirhinal cortex, although the inputs from the perirhinal cortex may be stronger than the reciprocal connections.

Both PHC and POR receive substantial visual and spatial input, which supports their role in visuospatial functions. For both PHC and POR, this input arises predominantly from visual association, retrosplenial, and posterior parietal cortices. The outputs are also similar. In the PHC, both TF and TH largely receive input from visual areas. TH, however, also receives input from auditory regions. The situation is similar for the POR in that both subdivisions receive input from visual and visuospatial areas, but the ventral subdivision also receives auditory input. The return connections are also strong to visual and visuospatial areas. Additionally, both areas have strong connections with the thalamic pulvinar in primates and the homologous lateral posterior nucleus in rodents (Agster et al. 2016; Baleyrier and Mauguier 1985). Notably, the pulvinar is implicated in visuospatial attention. Taken together,



**Parahippocampal Cortex (PHC), Fig. 1** Comparative views of the hippocampal memory system. Shown are surface views for the in the human, monkey, and rodent brains (a-c). The upper panel shows a lateral view of the hippocampal formation (HF), as well as parahippocampal structures including the perirhinal cortex (PER), parahippocampal/posrhinal cortex (PHC/POR), and entorhinal cortex (EC). The lower panel shows flattened maps of these regions in the human, monkey, and rodent (d-f). These

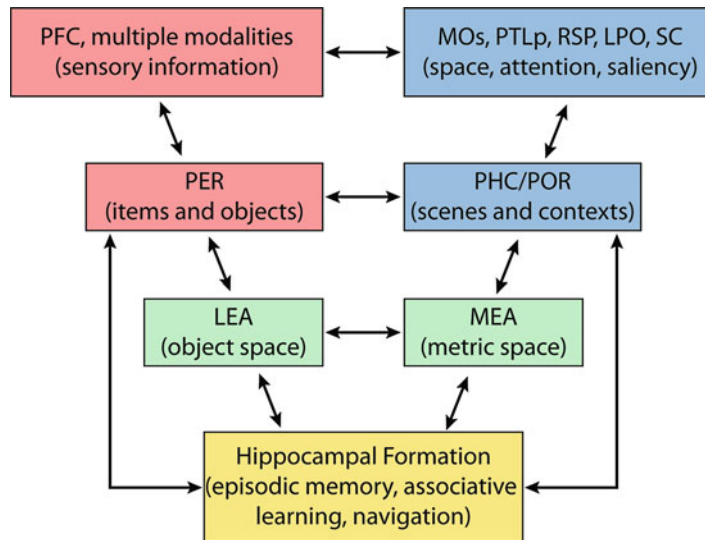
unfolded maps show PER areas 35 and 36, PHC subregions TH and TF in the monkey, as well as the lateral and medial entorhinal areas (LEA and MEA) in the rodent. Although not shown here, the primate EC is also subdivided into lateral and medial subdivisions. This figure was adapted from Burwell and Agster (2008) with permission (Elsevier, Inc.). Abbreviations: *cs*, collateral sulcus; *rs*, rhinal sulcus; *D/L*, dorsal/lateral; *R*, rostral; *C*, caudal; *V/M*, ventral/medial; *S*, septal; *T*, temporal

this pattern of connections suggests roles for POR/PHC in visual information processing and visuospatial attention.

## Function

Current views of medial temporal lobe function tend to emphasize that spatial and non-spatial information reach the hippocampus through segregated parahippocampal pathways. Spatial and contextual information is conveyed by the PHC/POR and the medial entorhinal area, and non-spatial information is conveyed by the perirhinal cortex and the lateral entorhinal area. There is, however, considerable cross-talk between these pathways at multiple levels (Fig. 2). Of importance, here, the perirhinal cortex and PHC/POR are directly connected.

Substantial evidence indicates the PHC/POR is involved in some, but not all, spatial functions. Rats with POR damage perform normally on most navigation tasks, but they are impaired on tasks that require processing of contextual information, that is, the local environmental context. This is consistent with findings of human imaging studies in which the PHC was shown to be involved in processing information about the environment, or context, but not in navigation (Epstein et al. 1999). Human imaging studies also implicate the PHC in a variety of higher-order cognitive functions including visual scene processing, binding of objects and contexts, and episodic memory (Aminoff et al. 2013). In addition, activity in the PHC increases when individuals are presented with objects that have strong contextual associations, regardless of whether the associations are spatial or non-spatial.



**Parahippocampal Cortex (PHC), Fig. 2** Pathways for nonspatial and spatial information into the hippocampal memory system. The nonspatial pathway is on the left and the spatial pathway is on the right. Sensory and prefrontal (PFC) information arrive in the perirhinal cortex (PER) and are used to identify individual items and objects. PER projects directly to the hippocampus and indirectly through the lateral entorhinal area (LEA). LEA likely uses this information to represent how objects are arranged in space possibly for the purposes of navigation. Visual and spatial information arrive in the parahippocampal/

postrhinal cortex (PHC/POR) which projects directly to the hippocampus and indirectly through the medial entorhinal area (MEA). The MEA likely uses this information for representing Euclidian or metric space. The PER also projects directly to the PHC/POR, likely providing object information so that the PHC/POR can represent the spatial layout of the objects and patterns that define the current environmental context. Spatial/contextual and nonspatial information are combined in the hippocampus for the purposes of associative learning and episodic memory

One question of interest is why the PHC/POR connections with perirhinal cortex are so robust. Abundant evidence indicates a role for perirhinal cortex in recognition and identification of individual objects. If one considers what comprises an environmental context, it becomes obvious that information about objects would be important. Most contexts are not empty rooms or bare environments, but are filled with objects and items that define the space. One interpretation that accommodates available evidence is that the PHC/POR encodes the physical features of environmental contexts including place, position of objects, and non-spatial feature information, for example, the furniture in a room and the pattern of the floor. Interestingly, neurons in the POR signal the location of objects in particular places (Furtak et al. 2012). If PHC/POR is representing the spatial layout of the objects and patterns in a particular environment, such

object location conjunctive coding would be expected.

## Conclusion

The conventional view of parahippocampal-hippocampal circuitry proposes that visuospatial information from multiple cortical regions converges in the PHC/POR on its way to the hippocampus and that nonspatial information is transmitted through the perirhinal cortex. This concept of parallel-processing streams is widely accepted; however, there is evidence that the PHC/POR is not simply accruing and transmitting spatial information. A modified view is that the PHC/POR relies on object information from the perirhinal cortex for the representation, identification, and discrimination of specific environmental contexts. Accordingly, the perirhinal cortex

supplies object information to the PHC/POR for representation of context and to the hippocampus for associative learning and episodic memory. Taken together, available evidence suggests that the POR/PHC encodes representations of specific contexts, monitors the current context, and updates these representations when a change occurs. This information would then be transmitted to the hippocampus for forming episodic memories and for associative learning.

## Cross-References

- [Declarative Memory](#)
- [Entorhinal Cortex](#)
- [Hippocampus](#)
- [Medial Temporal Lobe](#)
- [Perirhinal Cortex](#)

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## Parallel Distributed Processing

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## Introduction

The modern understanding of biological cognition has been heavily influenced by the computer metaphor or the idea that cognitive processes can be construed in terms of information processing. This idea was conceived in the early 1950s of the twentieth century when it was realized that the inventory of newly discovered digital computers provides a powerful framework for understanding the mind. Cognitive scientists readily grasped the idea that performance in tasks such as problem solving or visual object recognition can be described by drafting an algorithm of a series of distinct computations operating on well-defined data structures. The advantage of this approach was that it allowed the development of formal theories of cognition and the generation of testable predictions about behavior. However, it was soon realized that there are aspects of cognition which are hard to be accounted for in this manner. For example, the high granularity of the computer-inspired operations and data structures made it difficult to explain how a living organism gradually acquires new knowledge and adapts to the environment.

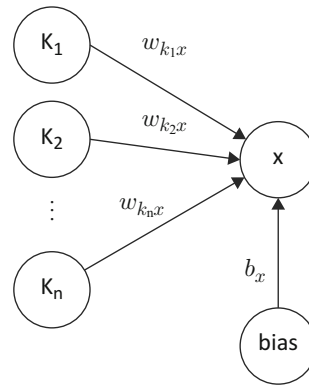
Discoveries in neuroscience (Hubel and Wiesel 1959; Hebb, 1961) as well as the pivotal work of McCulloch and Pitts (1943) on

mathematical modeling of the neural system provided an alternative way to formally account for cognition. In this framework, known as neural network modeling or connectionism, the incoming signal is processed by the simultaneous activation of a number of interconnected uniform computational units, artificial neurons, each of which performs a very simple task, such as the linear transformation of a number. Connectionism, therefore, assumes that any cognitive computation can be expressed as propagation of activation in a neural network, and the task of the modeler is only to find the right neural network architecture which can support a given task.

The first neural network models, such as the perceptron (Rosenblatt, 1957), consisting of just a few neurons, initially showed promising results, but it was soon demonstrated that such simple models have severe limitations (Minsky & Papert, 1969). It took about 20 years to overcome the problems and to develop theories and tools which allow researchers to build more complex and scalable neural network models. A turning point was the publication of the parallel distributed processing (PDP) volumes (Rumelhart et al., 1986) which set the foundations of modern connectionist modeling.

## Principles of PDP

A PDP neural-network model consists of a network of units which are usually organized in layers (Fig. 1). At each moment in time, the state of a unit is characterized by its level of activation, given by a real number. The connections between artificial neurons let the activation spread through the network, a process known as *spreading of activation*. The activation values of all units – a vector of real numbers – describe the knowledge currently encoded by the system. The spreading of activation is modulated by the pattern of connectivity – not all units are connected to each other and the strength (or *weight*) of the connections can vary. The level of activation of a given unit is a function (known as *activation function*) of the net amount of activation received by other units and a threshold parameter (a *bias term*) (Fig. 2). One of



**Parallel Distributed Processing, Fig. 1** An artificial neural network unit connected to  $n$  other units ( $k_1 - k_n$ ). The strength of the connection between unit  $k_i$  and  $x$  is indicated by the value of connection weight  $w_{kix}$ . A negative weight would indicate that unit  $k_i$  inhibits  $x$ . Units in hidden layers are usually also connected to a constant source of activation called bias. The effect of bias depends on the weight of the connection to the bias node ( $b_x$ ). Connection weights are considered parameters of the model and their optimal values and subject of learning

$$act(x) = f\left(\sum_{i=1}^n act(k_i)w_{k_ix} + b_x\right)$$

**Parallel Distributed Processing, Fig. 2** Calculating the level of activation of unit  $x$ . The net input to the unit is determined by taking the activation of each unit connected to  $x$  and multiplying it by the corresponding connection weight. The activation function  $f$  is then used to compute the level of activation of  $x$ . Activation functions vary across models but typical choices are s-shaped nonlinear transformations which keep the resulting value capped in a certain interval, such as  $[0, 1]$  or  $[-1, 1]$ . Importantly, the activation functions must be differentiable in order to be able to apply the back-propagation algorithm for finding the optimal values of the network parameters

the breakthroughs of the PDP approach was the introduction of nonlinear activation functions, such as sigmoids.

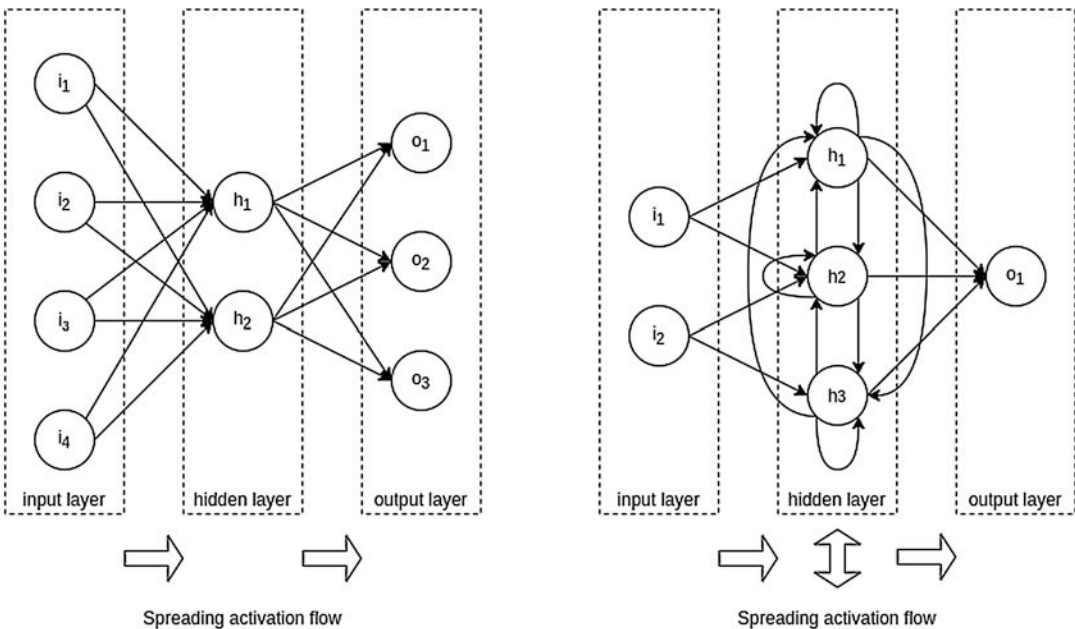
The operation of a PDP neural network model starts by manually setting the activation levels of some of the units in the “input” layer. The activation is then propagated to the rest of the network. The output of the model is determined by the activation levels of another layer of special units – the “output.” All the other units, which are neither externally activated nor considered an



output of the model, are referred to as “hidden” units. The number and the connectivity of hidden units determine the computational power of the model and is what defines the characteristics of neural network architecture.

There are two main types of PDP neural network architectures (Fig. 3). In feed-forward networks, the activation flows in a single direction and the computation is completed in a single time step. Typical applications of feed-forward networks include modeling tasks such as pattern recognition and classification. Recurrent architectures are time-sensitive and involve circular connectivity meaning that the activation of a unit at a given time may depend on its activation at a previous moment. They are particularly suitable for modeling cognitive processes requiring the capacity to store items in short-term memory, such as language comprehension and planning.

The main reason why the PDP modeling paradigm turned out to be so successful is that it provided a compelling account of learning. Learning in a PDP model can be viewed as finding the optimal values of the model parameters – the connection weights – with respect to a particular objective. The objective is defined by an *error* (or “*loss*”) function which quantifies the discrepancy between the desired and the actual output of the model. This kind of learning is referred to as “supervised” as it assumes that for each input to the model we know what the right output pattern should be. An important moment in the history of neural network modeling was the invention of the back-propagation algorithm for supervised learning which allowed researchers to train models (i.e., to find the optimal values of their connection weights) with varying complexity.



**Parallel Distributed Processing, Fig. 3** A sample feed forward (left) and recurrent (right) PDP model. In the feedforward model, activation flows unidirectionally from the input layer towards the output layer. The levels of activation of the output layer can be computed in just one iteration so there is no notion of time. The recurrent model has circular connectivity within the hidden layer,

and therefore a single input pattern may lead to multiple activation patterns within the hidden layer (and varying outputs) as the activation in the hidden layer is allowed to circulate. Recurrent architectures have much more computational power and are capable of modeling the dynamics of cognitive processes

## PDP as a Theory of Cognition

The PDP approach is not just a collection of modeling tools and formalisms but also a framework for understanding cognition. It imposes constraints on cognitive modeling which extend far beyond technical details.

A central assumption of the PDP approach is that information is processed in parallel, implying that there is no central processor controlling the computation, and it is not possible to pinpoint a set of discrete algorithmic steps which are executed in serial order. Such a view is incompatible with the computer metaphor and pushes theorists to thinking about cognition as a dynamic system rather than a computer program.

The second most important stipulation of the PDP framework is that knowledge representation is *distributed*, suggesting one cannot identify particular neural structures (such as neurons) which are responsible for a given fact or feature. For example, if a neural network model is currently representing a brown domestic cat, you can't figure out what the patterns of activation of individual features such as "brown," "cat," or "domestic" are. According to PDP theorists, distributed representations are essential for enabling generalization – the ability to process novel information – because the representation of novel inputs will always overlap to some extent with existing representations. Other advantages of distributed representations include context-sensitivity (the representation of a cat sitting on a sofa will be very similar but still different from the representation of a cat on a roof) and *graceful degradation*. The latter means that damaging a neural network leads to gradual loss of functionality, just as in aging animals, rather than in abrupt changes. However, the distributed representational format also makes predictions which can be described as problematic. For example, having continuous representations with blurred boundaries is incompatible with the symbolic view of knowledge – the idea that there exist atoms of knowledge which can be combined productively to form new meaning (Dietrich & Markman, 2003; Hummel, 2016).

A prime example of symbolic knowledge is natural language – we can produce and comprehend sentences we've never heard before by processing known words in novel combinations. The question of whether and how PDP can account for symbolic thought was the source of a fierce criticism (Fodor & Pylyshyn, 1988) and is still a hot topic for debate (e.g. Vankov & Bowers, 2020). There are also studies showing that under certain conditions PDP models actually tend to develop highly selective nondistributed representations (Bowers et al. 2014).

One of the most valuable contributions of connectionism to cognitive science is that it lets researchers explain how cognition develops through small incremental steps. For example, Elman, Bates, Johnson, Karmiloff-Smith, Parisi, and Plunkett (1996) argued that connectionist models can provide an empiricist development account of natural language and thus pose a serious challenge to the innateness hypothesis of language acquisition. Moreover, the PDP paradigm, which views learning as a relatively slow process of gradually updating the connection weights, imposes theoretically important constraints on models which adopt it. Many cognitive processes are consistent with this view, for example, learning to make fine-grained perceptual discriminations, detecting statistical regularities, or acquiring motor skills. However, there are also forms of learning which can't be accounted for in this way. For example, humans are capable of fast mapping (Carey & Bartlett, 1978), that is, learning a new category by being exposed to just a few examples. Similar results have also been reported for dogs (Kaminski et al. 2004). Another problem for the PDP account of learning, known as *catastrophic forgetting*, is related to how new information is stored without overwriting the existing knowledge. The problem arises because knowledge in PDP systems is distributed and therefore any change in the connection weights, which is needed to encode new information, will also affect existing representations. In order to address this problem, PDP researchers have proposed the *complimentary learning hypothesis*

(McClelland et al. 1995), which postulates that there exist two distinct systems for learning, one for long-term storage of distributed representations and the other one for quickly encoding new information.

## Biological Plausibility

One of the reasons for the wide adoption of connectionism in the cognitive sciences is that it lets researchers formulate models in a seemingly biologically plausible way. One can easily find biological counterparts of the basic PDP concepts such as a computational unit (nerve cell), level of activation (firing rate), adjustable connection weights (synaptic plasticity), and positive and negative activation flow (excitation and inhibition). The core ideas behind PDP – parallelism and distributing knowledge – are also intact with what we know about biological cognition. However, there are major components of PDP whose physiological plausibility is debatable (e.g. the back-propagation algorithm, Lillicrap et al. 2020) and many important neurobiological mechanisms which are just not accounted for in PDP models (e.g. myelination). It should be kept in mind though that the ultimate goal of cognitive modeling, including connectionism, is to explain cognition. Therefore, the value of PDP models should be judged by how well they account for cognitive phenomena and the theoretical insights they generate and not by how well they mimic the biological neural system. There are other modeling frameworks which explicitly set the goal of describing the operation of real neurons as close as possible (Gerstner & Kistler, 2002), but they are usually not applicable to studying high-level cognitive processes and therefore less popular among cognitive scientists.

## Deep Learning

Connectionism has recently experienced a renewed surge in interest due to the introduction

of a set of artificial neural network models collectively known as *deep learning* (Bengio et al. 2015). Major innovations in deep learning include the ability to efficiently train models with millions of parameters, tens (or even hundreds or thousands) of hidden layers and specific connectivity constraints. Some of the most important deep learning concepts, such as the convolutional neural network (LeCun et al., 1989) and the long-short term memory circuit (Hochreiter & Schmidhuber, 1997), have been proposed much before the deep-learning era, but had not been widely adopted until appropriate hardware and software became available.

Deep learning has achieved spectacular results in various fields of artificial intelligence, surpassing human performance on tasks previously considered to be particularly hard for computers (Silver et al. 2016). It has also affected the study of biological cognition by providing researchers with new tools and letting them complicate and scale up their models. Progress has been made by developing neural network models of cognitive functions which can be applied to real-world data and thus enable direct comparison with human or animal performance (e.g. Abudarham et al. 2019). Indeed, before deep learning, one of the main criticisms of the PDP modeling approach had been that it could only be used to address toy problems. At the same time, deep learning cannot be viewed as a conceptual breakthrough in understanding cognition, as long as it is based on the same fundamental principles of PDP and therefore exhibits similar computational, cognitive, and biological limitations (Bowers, 2017; Forbus et al. 2017).

## Conclusions

The PDP approach has had a profound effect on the study of cognition. It has provided researchers with a modeling framework which is powerful enough to be applied to almost all domains of cognition and at the same time is sufficiently constrained to not allow turning cognitive

modeling into a computer programming exercise. Importantly, PDP constraints on modeling are not arbitrary or just technical, but they reflect theoretical positions with far-reaching implications. Since its introduction, connectionism has been involved in some of the greatest debates in the cognitive sciences and has led to important theoretical advances, driven by both its proponents and its opponents. Recent progress in deep learning has extended the range of problems which can be addressed by PDP modeling and has opened new promising interdisciplinary lines of research, bringing together results from the study of artificial intelligence, cognitive psychology, and neuroscience.

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## Paralysis Agitans

### ► Parkinson's Disease

## Paraphyletic

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## Etymology

From the Greek words *para*, meaning “near,” and *phyletic*, meaning “tribe”

## Synonyms

Paraphyly

## Definition

A group of organisms that includes the most recent common ancestor and some – but not all – of its descendants.

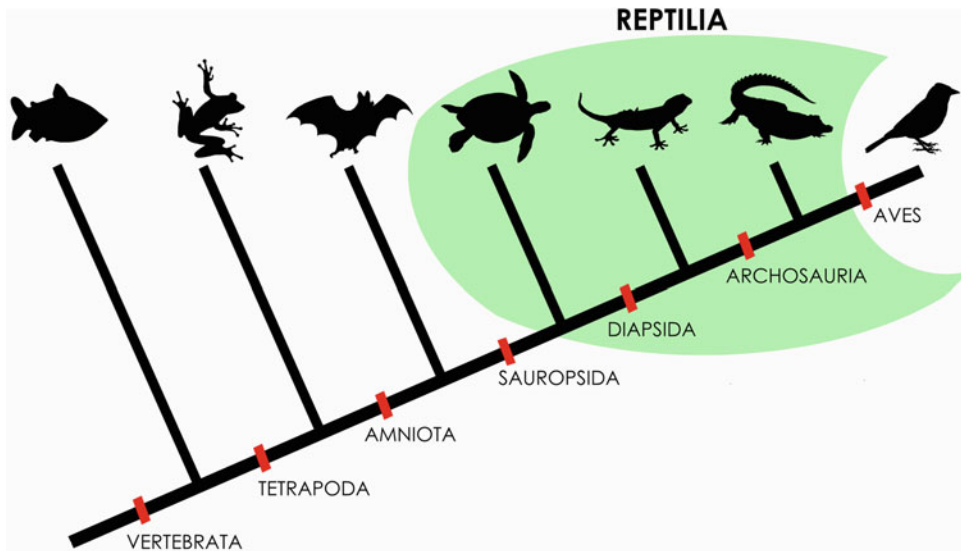
Taxonomic groups (treated here only as groups) can be classified according to the kinship between the ► [taxa](#) that compose them, which is the main goal of phylogenetic systematics. In the phylogenetic systematics context, a kinship relationship between taxa is established by the presence of a ► [common ancestor](#) *exclusive* of the group. For example, considering the Mammalia taxon, all species included in Mammalia must be

derived from an exclusive ancestor. In this case, all mammal species and their exclusive ancestor form a ► [monophyletic](#) group. Being so, the members of this group necessarily share exclusive features, called synapomorphies, such as the presence of hair, mammary glands, and others. However, it is common to find in the literature historical groups defined not based on an exclusive ancestor and its descendants but only considering similar features among taxa. These features are often used to categorize and order diversity, as typological Linnaean characteristics, or to demonstrate evolutionary grades, as does the Gradism approach (*see* Brief Historical Perspective section). In the phylogenetic context, these groups that are not recognized based on exclusive shared ancestry are considered unnatural groups and do not represent the evolutionary history of the organisms within.

We can classify unnatural groups into two types: para- and polyphyletic. These two terms were defined by Hennig (1966) and redefined later by other authors. Paraphyletic groups result from the exclusion of small monophyletic groups from a larger monophyletic group. For instance, in Fig. 1, the exclusion of Aves from the larger monophyletic group denotes the paraphyletic group Reptilia. To be recognized as a monophyletic group, Reptilia would have to include Aves (Fig. 1). On the other hand, polyphyletic groups include taxa descendants from two or more different immediate ancestors. An example is the former phylum Radiata, which was mainly created to classify animals with radial symmetry, such as cnidarians, ctenophores, and echinoderms. Since echinoderms have a different immediate ancestor of cnidarians and ctenophores, they do not form neither a monophyletic group nor a paraphyletic one (*see* ► [Monophyletic](#) chapter for more examples). Therefore, the radial symmetry of those taxa arose more than once and is so called homoplasy.

The pursuit to organize the biodiversity based on monophyletic groups is the goal of the phylogenetic systematics (also known as cladistics). However, reference to unnatural groups is commonly found in the literature. Some of the most classic examples are reptiles (explained above),





**Paraphyletic, Fig. 1** Phylogenetic hypothesis of Vertebrata, including Actinopterygii (fish), Amphibia (frog), Mammalia (bat), Testudines (turtle, here considered

as anapsid), Squamata (lizard), Crocodylia (crocodile), and Aves (bird). The paraphyletic group “Reptilia” is highlighted in green

invertebrates (which include all animals, but vertebrates), and gymnosperms (which include all spermatophytes, but angiosperms). Most cladists do not agree with the recognition of non-monophyletic groups since they are not considered real phylogenetic units (i.e., natural groups derived from the process of evolution). However, some authors argue that paraphyletic groups might be recognized as a group of taxa diagnosed by symplesiomorphies (symplesiomorphies are plesiomorphies, i.e., features that maintain their ancestral state, shared with two or more taxa) or by the *absence* of apomorphies (apomorphies are novelty features present in the ancestor and in one or more of its descendants) (Hennig 1966).

### Brief Historical Perspective

The organization and classification of biological entities have been always an activity of interest to humankind. Different criteria of biological classification have been created throughout history, mainly based on the morphological similarity between species, as the Aristotelian system and Linnaean classification. After the emergence of Darwin’s idea of common ancestry, a kinship-

based classification method, called Gradism, was proposed. This method organizes the organisms in levels, i.e., grades, based on the genealogical history of the taxa and their similarities and adaptive capacity (see Wheelis et al. 1992 for details). The Gradism represents one of the first attempts to include the kinship among taxa into a system of organism classification.

The phylogenetic systematics was implemented by Hennig (studies between 1950 and 1970), and consequently, a lot of methods for constructing phylogenetic trees arose. An important contribution of this method was its classification premisses, which state that all taxa must be monophyletic and all information between sister groups (Parallel groups that share a common ancestor) must be expressed. Different from the gradists, Hennig (1966) believed that non-monophyletic groups should not be considered in organism classifications because they do not have an independent history and thus possess neither reality nor individuality. Nevertheless, the author considered that non-monophyletic groups could still be defined based on similarities. For Hennig, a group would be considered para- or polyphyletic depending on the diagnostic feature shared by the taxa in it: paraphyletic are those

groups whose similarities are symplesiomorphies, while polyphyletic groups are those whose similarities are the result of convergence (i.e., homoplasies).

After to Hennig (1966), other authors expanded the definition of para- and polyphyletic groups to include information regarding the phylogenetic relationships among taxa, not relying exclusively on its similarities (e.g., Nelson 1971; Platnick 1977). Therefore, the second half of the twentieth century is filled with discussion on how to designate unnatural groups and the terms to delimit them. In 1981, Bernardi published a work that expanded the definition of these terms and coined the term merophyletic (from the Greek word *mero*, meaning “part”). A merophyletic group corresponds to a larger monophyletic group, from which one or more smaller groups, natural or not, have been removed. According to Bernardi (1981), paraphyletic groups are merophyletic groups that result from the exclusion of one or more smaller monophyletic groups from the larger monophyletic group to which they belong. For example, “Reptilia” is a merophyletic-paraphyletic group, since Aves was excluded from the larger monophyletic group Sauropsida (Fig. 1). Still according to the author, polyphyletic groups are merophyletic groups that result from the exclusion of at least one paraphyletic group from the smallest monophyletic group of which they are part.

Paraphyletic groups, although not being recognized as natural groups, are still being used, especially in didactic perspective, in an attempt to keep traditional names. Therefore, the name of the group should be written between quotes in order to provide an indication that it is not monophyletic.

## Cross-References

- [Charles Darwin](#)
- [Common Ancestor](#)
- [Homoplasy](#)
- [Monophyletic](#)
- [Species](#)

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## Paraphyly

- [Paraphyletic](#)

## Pareidolia

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## Introduction

Pareidolia is the phenomenon of recognizing a meaningful pattern, shape, or object from ambiguous forms in visual scenes. We experience pareidolia when an object is perceived even though it is not actually there (Kato and Mugitani 2015; Liu et al. 2014; Mamiya et al. 2016; Proverbio and Galli 2016). When we recognize an animal’s form in the clouds, a pattern of a leaf in a cup of coffee, or the figure of a reaching arm in the shadow of the tree, we are experiencing pareidolia. More notable examples include seeing a man’s face on the moon or Jesus’ portrayal on a piece of toast (Liu et al. 2014). Most studies focus on a specific type of pareidolia – face pareidolia – in which faces or face-like patterns are recognized in the absence of an actual face (Liu et al. 2014; Proverbio and Galli 2016; Ryan et al. 2016; Takahashi and Watanabe 2013; Wardle et al. 2017). Although examples of face pareidolia

emerge spontaneously in the environment, there are also examples of face pareidolia present in various forms of art. For example, Guiseppe Arcimboldo's work depicts human portraits composed of various items such as fruits, vegetables, and flowers.

The experience of face pareidolia is likely caused by our sensitivity to certain categories of importance. Faces are inherently one of the most socially relevant stimuli we encounter (Palermo and Rhodes 2007). They convey socially important information such as an individual's identity, sex, emotional state, etc. On a day-to-day basis we encounter hundreds of faces, resulting in our extreme sensitivity to facial structure, ultimately promoting the rapid detection and identification of different individuals (Crouzet 2010). Their relevance is likely the cause of our ability to so easily recognize face-like patterns even when they are not present (Ryan et al. 2016). From an evolutionary perspective, our threshold for detecting faces could be low in order to avoid any potentially dangerous situations, resulting in an increased number of false positives for seeing faces when they are not actually present (Takahashi and Watanabe 2013). Our susceptibility to such instances of face pareidolia could also be a result of our tendency to anthropomorphize objects (Proverbio and Galli 2016).

Several studies have investigated pareidolia using neurological measures such as event-related potentials (ERPs), functional magnetic resonance imaging (fMRI), or magnetoencephalography (MEG) to see whether activation resulting from illusory faces is associated with activation caused by seeing real faces. For example, the presentation of illusory faces results in activation of the fusiform face area (FFA) – an area of the brain related to face perception (Wardle et al. 2017; Liu et al. 2014). Similarly, Proverbio and Galli (2016) found that images of face pareidolia elicited ERP responses in brain areas involved in face processing, an effect that was stronger in females than in males. Finally, a study using MEG to measure the response to face pareidolia found activation in the ventral fusiform cortex, an area also activated by the perception of real faces. An important aspect to that experiment was that the

presentation of illusory faces resulted in an activation pattern that was not only similar in the brain regions activated but also similar in response times from stimulus onset to activation signal. These results suggest that our perception of face pareidolia is not a post-recognition phenomenon but is rooted in the early stages of visual analysis (Hadjikhani et al. 2009).

Other research has used behavioral measures such as looking time to assess perception of illusory faces. This method builds off research indicating that humans have an innate preference for looking at faces or face-like objects (Farroni et al. 2005). In a study presenting illusory faces to infants ranging in age from 8 to 12 months, researchers found that fixations were most concentrated on the "mouth" areas of images during the simultaneous presentation of sounds (Kato and Mugitani 2015). This behavior is consistent with infants' sound-mouth association or their tendency to look at one's mouth as a source of sound. Infants who were 7- to 9-months old showed a preference for upright Arcimboldo images, but not their inverted counterparts, indicating that they recognize these images as faces (Kobayashi et al. 2012). Beran et al. (2017) presented three and a half to five-year-old children with Arcimboldo images after training them to categorize images of foods and faces. Their results showed that preschool-aged children were successful in categorizing this type of illusory face as a face more often than scattered images, suggesting that, even at this young age, children are susceptible to face pareidolia. And, Takahashi and Watanabe (2013) found that examples of face pareidolia elicited shifts in gaze only when the illusory face pattern was explicitly recognized. Therefore, when illusory faces were perceived, an attentional response similar to that of true faces was triggered.

Several studies, including the fMRI study discussed above (Proverbio and Galli 2016), have investigated whether there are gender differences in perceiving face pareidolia. Gender differences have previously been shown in the perception of other social signals such as reading body language (Krüger et al. 2013) or emotional valence (Kret and De Gelder 2012). For example, two studies investigating gender differences in face pareidolia found

that females recognize Arcimboldo-type illusory faces more readily than males, and that females perceive these illusory faces as more likeable than male perceivers (Pavlova et al. 2016b).

Perception of face pareidolia has also been used as a platform for studying specific aspects of visual processing such as form perception or the underlying mechanism of face processing. For example, humans tend to process stimuli, especially faces, in a global or holistic manner. That is, we view and discriminate objects from each other based on their overall form rather than by their individual parts. For example, Navon (1977) presented stimuli that consisted of smaller letters forming the shape of a larger letter. Adults responded faster to the global form (the larger letter) rather than the local properties (the smaller, individual letters).

Our inherent tendency to process stimuli, especially faces, holistically also makes face pareidolia an ideal platform for studying social disorders in which these perceptual processes are disrupted. For example, individuals with autism spectrum disorder (ASD), in addition to having deficits in discriminating and interpreting social stimuli, typically show a local bias in which they discriminate objects by their individual features instead of global form (Happé and Frith 2006). In general, individuals with ASD are less likely to identify pareidolic faces than typically developing controls (Pavlova et al. 2017; Ryan et al. 2016). Similarly, adults with prosopagnosia (also referred to as “face blindness”) are unable to discriminate faces from each other and have marked deficits in the holistic processing of faces (Avidan et al. 2011; Busigny et al. 2010). However, evidence suggests that despite this impairment in face processing and a bias for local processing, global processing remains intact and allows for the perception of global Navon figures as well as illusory faces (Avidan et al. 2011; Busigny et al. 2010). This is also true for patients with simultanagnosia, who have an extreme local processing bias but are still able to recognize a face-like configuration in Navon and Arcimboldo images (Dalrymple et al. 2007). Individuals with Williams syndrome – who typically exhibit greater attention to faces and social stimuli – were unable to identify faces in pareidolic images

(Pavlova et al. 2016a). Thus, studying whether or not individuals with social disorders such as these perceive illusory faces (in which the local features are not face-like but the global form is face-like) allows for a greater understanding of what perceptual mechanisms underlying face processing are impaired in these populations.

## Comparative Research

Forms of pareidolia in nature may be recognizable to animals. For example, eye-spot patterns are sometimes used by prey species as a method of deterring potential predators. Although eye-spot mimicry has been shown to successfully deter predators, it is unclear whether this is due to the explicit recognition of the eye-like pattern by other animals or more simply due to the conspicuousness of the markings (Kelley and Kelley 2014).

However, comparative research has shown that many species of nonhuman animals experience various visual illusions, some in a similar manner to humans (Fujita et al. 2012; Kelley and Kelley 2014). This research has continued to explore the similarities and differences among human and nonhuman animal perception. Therefore, it is a natural progression of this field to investigate animals’ experience of the pareidolia illusion, especially of face pareidolia given a shared emphasis on the importance of face stimuli across species.

Pareidolia has only recently been studied in nonhuman animals. Faces are an important and socially relevant stimulus to many animal species. For example, multiple species show an inherent tendency to look at faces or the head regions of other individuals (Salva et al. 2011; Sugita 2008). Further, despite typically being local processors for other forms of visual information, the importance of faces is demonstrated by evidence that monkeys process faces holistically (see Parr 2011, for a review). Thus, research has investigated whether the salience of faces is strong enough to elicit this illusion as well as the holistic processing of these illusory faces.

A few recent studies have investigated whether nonhuman primates experience this illusion. In one study with rhesus monkeys and capuchin monkeys,

subjects were first trained to categorize images on a computer as either faces or foods (Beran et al. 2017). After learning this task, monkeys were then presented with Arcimboldo images as well as scattered Arcimboldo portraits, real faces, and object images. Monkeys were just as likely to categorize Arcimboldo images as faces as they were to classify their scattered image counterparts as being faces. These results seem to indicate that the monkeys were unable to perceive these illusory faces, perhaps due to their tendency to process environmental stimuli in a more local manner (i.e., attending to the individual components rather than its whole). If this is the case, then monkeys would fail to recognize the face-like configuration, suggesting instead that face pareidolia is a phenomenon unique to humans.

A second study of nonhuman primates' ability to experience face pareidolia used eye tracking to measure the gaze behavior of rhesus macaque monkeys during the presentation of illusory faces (Taubert et al. 2017). Images of conspecific faces, illusory faces, and content-matched non-face-like objects were presented in a visual paired comparison task in which monkeys were able to freely view images. Because of the monkeys' preference for viewing faces, researchers investigated whether the looking patterns typical of viewing a true face would also be evident when the monkeys viewed images containing illusory faces. The results showed that rhesus monkeys spent more time looking at illusory faces than at objects that did not contain any face-like configuration. In addition to this finding, viewing patterns revealed an increased number of fixations on the "eye" and "mouth" regions of pareidolia images. These viewing patterns are consistent with how nonhuman primates look at images of conspecific faces (Dal Monte et al. 2015), and they suggest that nonhuman primates do possess the ability to perceive illusory faces. Finally, in a similar experiment using rhesus macaque monkeys with bilateral amygdala lesions (an area of the brain involved in face and emotional valence processing), these viewing preferences were no longer apparent, emphasizing the importance of specific brain areas in responding to faces and face-like images (Taubert et al. 2018).

More work in this area will continue to focus on the nature of nonhuman animals' experience of this phenomenon. Specifically, the question remains as to whether the experience of this phenomenon in monkeys is more implicit (like the innate preference to look at face-like patterns) or whether nonhuman primates explicitly recognize the face-like aspects of these images.

## Conclusion

Overall, face pareidolia is a well-established visual phenomenon in humans. The similarity between neural and behavioral responses to real and illusory faces have elucidated the value in studying inanimate objects with illusory facial structure to better understand the neural basis of face perception and its development. Studying this phenomenon in animals will inform our understanding of the mechanisms underscoring face perception in humans as well as illustrate how these mechanisms may have evolved throughout time. Current comparative research has led researchers to draw preliminary, contrasting opinions regarding the perception of illusory faces in nonhuman primates. Therefore, more work is needed to better understand the experience of animals when presented with this illusion. By learning more about illusory perception in other species, we will gain insight into the mechanisms underlying our own perception of real and illusory faces.

## Cross-References

- [Face Processing in Different Brain Areas and Face Recognition](#)
- [Gestalt](#)
- [Mimicry](#)

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Parental Care

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Parental Investment

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Glossary of Terms

Evolution      Change in gene frequencies in populations/species over time via genetic drift, mutation, gene flow, and natural selection.

Fitness (biological)      Extent to which organisms contribute genes to future generations. Often measured as the

|                      |                                                                                                                                                                                                                                          |
|----------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                      | number of offspring surviving to reproduce.                                                                                                                                                                                              |
| Function             | Adaptive significance of a trait, i.e., how it leads to increased fitness.                                                                                                                                                               |
| Mating effort        | Effort allocated to mate attraction and/or exclusion of sexual competitors. Separate from parental effort.                                                                                                                               |
| Mechanism            | Machinery enabling behaviors to be expressed, particularly neuroendocrine systems.                                                                                                                                                       |
| Ontogeny             | Development of an individual over its lifetime (conception to death).                                                                                                                                                                    |
| Parental behavior    | Behavior that originated and/or is currently being maintained to enhance offspring fitness. Costs to parents not considered.                                                                                                             |
| Parental care        | Any parental trait (behavioral or non-behavioral) that enhances offspring fitness. Costs to parents not considered. The trait may have originally evolved to serve functions other than increasing offspring fitness.                    |
| Parental effect      | Casual effects that a parent’s phenotype has on an offspring’s phenotype over and above direct genetic effects (i.e., an environmental source of variation). Called maternal or paternal effects (female or male parents, respectively). |
| Parental effort      | Combined fitness costs (sum of parental investment) incurred by parents due to the production and care of offspring produced in a given period. Separate to mating effort and incorrectly synonymized with parental expenditure.         |
| Parental expenditure | Usage of parental resources (energy, time, mass) on parental investment. Incorrectly synonymized with parental effort. Calculated as a proportion of the parent’s total resource budget allocated to investment.                         |

|           |                                                                                |
|-----------|--------------------------------------------------------------------------------|
| Proximate | Ontogeny of a trait or mechanisms that result in the expression of that trait. |
| Ultimate  | Evolution of a trait or function of that trait.                                |

## Definition

Any behavioral and/or physiological contribution by a parent in an offspring that increases the survival/fitness of that offspring at a cost to the parent's ability to invest in other offspring (Trivers 1972).

## Introduction

Sexually reproducing animals invest in offspring metabolically through the generation of gametes (eggs and sperm). Beyond this initial energetic investment, the majority of animals provide no additional investment in their offspring. However, in species that do provide parental investment following conception, the quantity, quality, form, and duration of investment vary dramatically between species, as well as between the sexes within species (Clutton-Brock 1991). In vertebrates, females often show a disproportionately higher metabolic level of investment than males through the generation of yolk or placenta that provides nourishment for the developing embryo (Clutton-Brock 1991; Trivers 1972).

Confusion over what constitutes “parental investment” has occurred due to the use of diffuse terminology (see Glossary of Terms), the inclusion or exclusion of particular behaviors at the discretion of different authors, and difficulties associated with assessing the relative costs and benefits to both offspring and parents (Alonso-Alvarez and Velando 2012). Furthermore, confusion has arisen because of the variety of approaches adopted to understanding parental investment. Nikolaas Tinbergen (1907–1988), a Dutch biologist who studied the behavior of animals in their natural environment, suggested that behavior could be studied from four aspects, namely, the proximate (i.e., ontogeny and mechanisms) and ultimate (i.e., function and evolution). While parental investment

has been extensively studied, studies tend to focus on only one of Tinbergen's (1963) approaches. For example, Trainor and Marler (2002) focused on the mechanisms associated with paternal care in California mice *Peromyscus californicus*, while Gubernick and Teferi (2000) focused on the function of paternal care. Consequently, there is a need to integrate these approaches to afford a unitary understanding of parental investment.

## Behaviors Associated with Parental Investment

A physiological contribution to investment can often be directly measured (e.g., quantity of yolk supplied to an egg). However, the categorization of behavior is more difficult because behaviors may serve multiple functions. For example, a bird may build a nest for shelter for itself, but the nest may also house offspring at a later stage. Thus, nest building could be viewed either as having no influence on offspring fitness or having a direct influence. For a behavior to be considered investment, the survival of offspring must be increased in response to the performance of the behavior, and the parent must suffer a cost that reduces its ability to invest in other offspring (Trivers 1972).

Behaviors can be classified as either indirect or direct (Table 1). Indirect behaviors are performed while away from the young (i.e., no physical contact) but still influence offspring survival, growth, and/or development (Fedy and Martin 2009). In contrast, direct behaviors are performed in the presence of the young and directly influence offspring survival, growth, and/or development (Gubernick and Teferi 2000). Both types of behaviors can vary between and within taxa (Table 1), and their roles in offspring development and fitness can vary over time.

Behaviors can also be categorized based on the timing of occurrence, occurring either pre- or post-birth/hatching (Table 1). Several indirect behaviors typically occur before egg deposition or birthing of young. Generally, a suitable site must be selected (Fetherston et al. 1990). Following site selection, nest/den/burrow-building

**Parental Investment, Table 1** Categories and types of parental investment and timing of occurrence. Example species and their associated behaviors are provided, along with key references

| Category                           | Type            | Timing of occurrence         | Example species                                           | Example behaviors                                                                                                                                                | Key reference                 |
|------------------------------------|-----------------|------------------------------|-----------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|
| Nest/den/site selection            | Indirect        | Pre-birth/hatching           | Burying beetles<br><i>Nicrophorus orbicollis</i>          | Active seeking of a suitable carcass in which larvae can be interred during development.<br>Active seeking of a suitable burial site                             | Fetherston et al. 1990        |
| Nest/den/burrow building           | Indirect        | Pre-birth/hatching           | Foam-nest frogs<br><i>Chiromantis petersi</i>             | Female ejects a pale viscous fluid from the cloaca<br>Female and males beat the foam fluid with vigorous swimming movements until a stiff white foam is produced | Coe 1974                      |
| Nest/den/site / burrow maintenance | Indirect/direct | Pre- and post-birth/hatching | Blue tits<br><i>Cyanistes caeruleus</i>                   | Parents collect and line their nests with aromatic plants that have anti-bacterial properties                                                                    | Mennerat et al. 2009          |
| Nest/den/site/burrow defense       | Indirect/direct | Pre- and post-birth/hatching | Shell-brooding cichlids<br><i>Lamprologus callipterus</i> | Resident male assumes a head-down posture toward an intruder, tilting his back and undulating the body                                                           | Sato 1994                     |
| Egg maintenance and defense        | Direct          | Pre-hatching                 | Two-spotted gobies<br><i>Gobiusculus flavescens</i>       | Male undulates pelvic, dorsal, and/or caudal fins to generate current over the eggs<br>Adopting a threatening position, chasings, and/or biting                  | Skolbekken and Utne-Palm 2001 |
| Egg transport                      | Direct          | Pre-hatching                 | Pipid frogs<br><i>Pipa carvalhoi</i>                      | Female carries the eggs on her back as she moves around                                                                                                          | Trueb and Cannatella 1986     |
| Egg incubation                     | Direct          | Pre-hatching                 | Grey-headed juncos<br><i>Junco hyemalis caniceps</i>      | Female sits over the eggs                                                                                                                                        | Fedy and Martin 2009          |
| Female guarding                    | Direct          | Pre-hatching                 | Grey-headed juncos                                        | Males guard females during incubation (allows females to increase foraging efficiency)                                                                           | Fedy and Martin 2009          |
| Female provisioning                | Indirect        | Pre- and post-birth/hatching | Reed warblers<br><i>Acrocephalus scirpaceus</i>           | Male brings food to the female                                                                                                                                   | Požayová et al. 2009          |
| Offspring defense                  | Direct          | Post-birth/hatching          | Reed warblers                                             | Males mob and guard nests against parasitic cuckoos <i>Cuculus canorus</i><br>Females check nests and eject foreign eggs                                         | Požayová et al. 2009          |
| Territory maintenance              | Indirect        | Pre- and post-birth/hatching | Rock-haunting possums<br><i>Petropseudes dahli</i>        | Scent-mark by rubbing or pressing cloacal-caudal region or chest against a substrate                                                                             | Runcie 2000                   |
| Offspring provisioning             | Direct          | Post-birth/hatching          | African wild dogs<br><i>Lycaon pictus</i>                 | Lactation<br>Pups approach subadults and adults and start vocalizing<br>Subadults/adults regurgitate partially digested food for pups to eat                     | Malcolm and Marten 1982       |

(continued)

**Parental Investment, Table 1** (continued)

| Category                                         | Type     | Timing of occurrence | Example species                                   | Example behaviors                                                                                                                                                                   | Key reference                 |
|--------------------------------------------------|----------|----------------------|---------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|
| Huddling                                         | Direct   | Post-birth/hatching  | California mice<br><i>Peromyscus californicus</i> | Parent/s lie or stand arch-backed over the young                                                                                                                                    | Gubernick and Teferi 2000     |
| Offspring maintenance (e.g., grooming)           | Direct   | Post-birth/hatching  | California mice                                   | Parent/s gather the pups under their bodies and then lick pups with their tongue, or groom them by pulling their teeth through the fur                                              | Gubernick and Teferi 2000     |
| Offspring retrieval                              | Direct   | Post-birth/hatching  | California mice                                   | Parent/s grasp infants behind the shoulders or neck using their teeth and return them to the nest/den/burrow                                                                        | Gubernick and Teferi 2000     |
| Carrying/transport                               | Direct   | Post-birth/hatching  | Goeldi's monkeys<br><i>Callimico goeldii</i>      | Young grasp around the belly or ride on the back of mothers or other group members                                                                                                  | Schradin and Anzenberger 2001 |
| Sentinel behavior and alarm calling (or similar) | Indirect | Post-birth/hatching  | Rock-haunting possums                             | Individual stationed in a fixed position on an exposed surface, facing outward with eyes wide open<br>Tail beating: Rhythmic beating of the underside of the tail against a surface | Runcie 2000                   |
| Babysitting                                      | Direct   | Post-birth/hatching  | Meerkats<br><i>Suricata suricatta</i>             | Individuals remain at the den with pups, while other group members go out to forage                                                                                                 | Sharpe 2005                   |
| Play                                             | Direct   | Post-birth/hatching  | Meerkats                                          | Numerous types, e.g., mock-biting, jumping, pouncing, or chasing                                                                                                                    | Sharpe 2005                   |

species then construct the “home” in which offspring grow and develop (Coe 1974). The site, inclusive of the “home,” must then be maintained by removing pathogens, parasites, and fungi (Mennerat et al. 2009), and parents must also defend the site from conspecifics that would usurp the parents (Sato 1994).

For egg-laying species, following egg deposition, parents continue to defend the eggs from predators and conspecifics and also continue to maintain the eggs, removing dead or diseased eggs, parasites, pathogens, and fungi to maintain egg health (Skolbekken and Utne-Palm 2001; Table 1). Some animals forgo nest construction, rather transporting eggs in (e.g., gastric-brooding frogs *Rheobatrachus silus*) or on (e.g., pipid frogs *Pipa carvalhoi*) their bodies (Trueb and Cannatella 1986). Birds and some reptiles incubate the eggs, providing an appropriate thermal environment to ensure proper embryonic growth and development (Fedy and Martin 2009). For

birds, in particular, males can expend considerable energy in provisioning the female and protecting the eggs during the incubation period (Požayová et al. 2009). In contrast to egg-laying animals, most female mammals provide direct investment through internal gestation, which provides all the nutrition and protection the embryo needs (Gittleman and Thompson 1988).

Other behaviors are performed following the hatching/birthing of young (Table 1). Typically, parents protect offspring from conspecifics, predators, and kleptoparasites (Požayová et al. 2009). Territory maintenance can also be critical for ensuring offsprings gain access to high-quality resources or are protected from predation (Runcie 2000). Parents also continue to maintain the site (as for pre-hatching/birthing). Parents with dependent young spend considerable amounts of time provisioning young, either through lactation, regurgitation, or the presentation of food items (Malcolm and Marten 1982).



In some species (e.g., canids), males may also continue to provision females following the birthing/hatching of young. Huddling to provide warmth is especially important in mammals and birds, particularly when young are unable to thermoregulate at birth (e.g., rodents; Gubernick and Teferi 2000). Other direct post-birth behaviors include cleaning (grooming and licking, which can also be important to stimulate evacuation of waste), retrieval of young that have strayed from the nest/burrow (Gubernick and Teferi 2000), and carrying or transportation of young (Schradin and Anzenberger 2001). For social animals, additional behaviors that occur following birth include sentinel behavior and alarm calling to alert young of approaching predators (Runcie 2000), babysitting, and socializing, which can include play (Sharpe 2005).

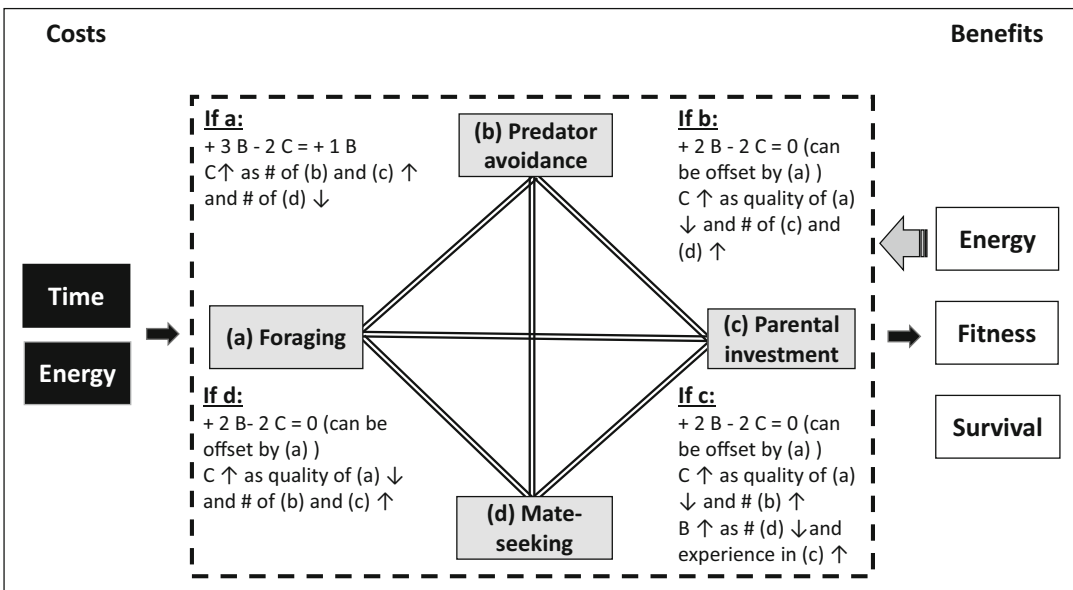
**Costs Associated with Investing in Offspring**

Parents spend energy, time, and body mass on investment (i.e., parental expenditure).

Consequently, the ability to invest in offspring is often not shared equally among parents and is also dependent on various factors, including, but not limited to, environmental hazards and mating opportunities (Woodroffe and Vincent 1994). The main costs of parental investment manifest as a reduction in fecundity, decreased parental survival (Clutton-Brock 1991), and a reduction in future mating opportunities (Woodroffe and Vincent 1994). Therefore, because behaviors associated with self-maintenance (e.g., foraging/feeding, mating, avoiding predators) and parental effort are functionally discrete (i.e., behaviors are mutually exclusive), parents must trade off between these behaviors using cost-benefit strategies (Fig. 1; Alonso-Alvarez and Velando 2012).

**Trade-Offs Between Foraging and Investment**

Animals require energy to grow, develop, repair tissues, and maintain behaviors. Therefore, animals must invest time and energy in foraging (Fig. 1a). Energy acquired from foraging can be diverted directly to the parent for its maintenance, increasing its survival and fitness (Fig. 1a). Alternatively, the energy can be diverted to other behaviors,



**Parental Investment, Fig. 1** Costs (C) and benefits (B) of engaging in different mutually exclusive behaviors. Trade-offs indicated by double lines with cost-benefit

relationships explained in each of the four corners (assuming animal engages in a particular behavior). Individual points explained in the text

namely, predator avoidance, parental investment, or mate-seeking (Fig. 1b, c, d). Energy diverted to parental investment can increase offspring survival, growth, and development but at a direct cost to the parent, and this cost only increases as the number of offspring in a clutch/litter increases (Fig. 1a). Gestation, lactation, egg incubation, and food provisioning are energetically expensive and time-consuming (Gittleman and Thompson 1988) and can lead to a reduction in parental body condition. For example, two-spotted goby *Gobiusculus flavescens* males guard and fan eggs until the fry hatch, showing a reduction in feeding behavior as eggs age, resulting in decreased male body condition (Skolbekken and Utne-Palm 2001). As offspring grow, they place increasing demands on parents for nutrients and resources. Parents must either increase their food intake to meet these growing demands, which can increase their likelihood of predation (Fig. 1a), or must accept this loss in body condition, which can further lead to increased susceptibility to diseases, parasites, and pathogens as they become immunocompromised (Alonso-Alvarez and Velando 2012). This trade-off between parental investment and parental self-maintenance, however, can still lead to an increase in parental fitness through increased offspring survival.

### Trade-Offs Between Predation Risk and Investment

Adults are exposed to increased predation risk during foraging and mate-seeking. However, the presence of offspring can also attract predators, increasing the risk of predation to both adults and young (Fig. 1b). Predation risk can be increased by the physical activity of the young (e.g., begging calls) and increases as clutch or litter size increases (Fig. 1b). The activity of parents also provides sensory cues to predators, increasing the likelihood that young may be predated. These factors lead parents to trade off between caring for fewer, current offspring against caring for more offspring in the future (Alonso-Alvarez and Velando 2012). This trade-off is also impacted by other factors (Fig. 1b), including the quality of the external environment (e.g., high resource availability = reduced time needed for foraging = reduced predation risk to parent = greater

investment in young = reduced predation risk to young), the mating/social system of the species (e.g., social species = more eyes to spot predators = reduced predation risk to young), and the experience of the parents (e.g., more experience = better quality investment = reduced predation risk to young).

### Trade-Offs Between Mate-Seeking and Investment

Animals expend time and energy finding a suitable mating partner (mating effort; Fig. 1d). For species that engage in physical competition, the costs (e.g., energy required for fighting and investment in testosterone, loss of body condition, injury, or death) can be significant. These costs may be offset by foraging, where energy is diverted to mate-seeking (Fig. 1d), or by the production of offspring, where energy is diverted to parental investment (Fig. 1c). However, because mate-seeking and investing in offspring are mutually exclusive, adults must trade off between investing energy in young or securing additional matings (Fig. 1d; Alonso-Alvarez and Velando 2012). In mammals, males are not constrained to invest in young before their birth. Therefore, the opportunity for males to desert females is high (Woodroffe and Vincent 1994). However, multiple matings can also incur significant costs, such as increased predation risk (Fig. 1d). Furthermore, when environmental conditions are harsh and unpredictable, resource limitation may constrain adults to invest in offspring to ensure offspring survival (Rymer and Pillay 2018), even if this comes at a significant cost due to lost body condition of adults. However, by trading off parental effort against mating effort under stressful conditions, parents may ultimately benefit via increased offspring survival (Fig. 1c).

### Understanding Parental Investment from Tinbergen's Perspective

Distinguishing between Tinbergen's (1963) proximate questions is challenging because of the complex interactions between ontogeny and the mechanisms driving the expression of behavior.

While the brain and central nervous system (i.e., the behavioral machinery) are critical for allowing behaviors to be expressed, ontogenetic factors can modify this machinery, leading to behavioral changes (Rymer and Pillay 2018).

### Proximate Questions: Ontogeny and Mechanisms

The neuronal complexes involving the medial preoptic area, bed nucleus of the stria terminalis, amygdala, vomeronasal organ, accessory olfactory bulb, lateral preoptic area, substantia innominate, and ventral tegmental area provide the behavioral machinery responsible for the expression of parent-typical behaviors (Rymer and Pillay 2018). This neural network is laid down by organizational hormonal effects (permanent, nonreversible changes in neural substrates) during early development (pre-, peri-, or early post-natal) and is activated later during adulthood by activational hormonal effects (nonpermanent, reversible changes due to modification of neural activity; Schradin and Anzenberger 1999). The neuroendocrinological regulation of parental investment thus begins early in development and is likely to be homologous between the sexes because it is easier to construct a single neural complex (in an evolutionary and functional sense) than evolve different neuroendocrine circuits for males and females (Rymer and Pillay 2018).

However, sex-specific patterns of gonadotropin secretion, principally testosterone and estradiol, during ontogeny affect the neuroendocrine circuitry differently, leading to sex-specific differences in parental investment in adulthood, although these responses are likely to be species-specific (Rymer and Pillay 2018). For example, in prairie voles *Microtus ochrogaster*, overexposure to testosterone while females are still in the womb leads to a reduction in parental responsiveness as adults (Lonstein and De Vries 2000). The male testes begin steroid production while the offspring are still in the womb, whereas the female ovaries remain inactive during this period. This leads to differential exposure of neonatal male and female

brains to testosterone and estrogen, which may ultimately influence sex differences in parental responsiveness during adulthood (Lonstein and De Vries 2000).

As individuals grow and develop, testosterone and estrogen continue to influence patterns of parental investment, particularly in paternal males, where paternal behavior is promoted through aromatization of peripheral testosterone into estradiol in the medial preoptic area (Trainor and Marler 2002). However, other hormones, particularly vasopressin, oxytocin, and prolactin, may also influence the expression of parental investment. Vasopressin, which may be stimulated by testosterone via activity of estradiol, and oxytocin are structurally similar neuropeptide hormones that are secreted by the posterior pituitary into the general circulation, and both are associated with parental investment. Both oxytocin and vasopressin can mediate the release of prolactin, which is a gonadotropic hormone that can cross the blood-brain barrier exerting a direct influence in the brain and affecting the central control of parental investment (Schradin and Anzenberger 1999). Circulating prolactin is correlated with parental investment in fish, birds, and mammals (Schradin and Anzenberger 1999), suggesting that the underlying neural circuitry governing its regulation is organized early in development but activated later in life. Social stimuli and cues from offspring (particularly tactile cues) have been suggested to influence prolactin secretion, although other factors (e.g., environmental factors) may also play a role (Schradin and Anzenberger 1999). Finally, other hormones, including cortisol, dopamine, progesterone, and serotonin, also influence parental investment through their influence on prolactin and vasopressin secretion.

Parental investment is not wholly an innate property of endocrine-specific events. In particular, components of parental investment may be heritable (e.g., maternal care in African striped mice *Rhabdomys pumilio*, Rymer and Pillay 2011a). Parental investment is also mediated by genetic mechanisms, where several candidate

genes/loci associated with the expression of vasopressin, oxytocin, serotonin, estrogens, glucocorticoids, dopamine, prolactin, and progesterone influence parental behaviors, including nursing in rats *Rattus norvegicus*, maternal infanticide in pigs *Sus scrofa*, and paternal retrieval in house mice *Mus musculus* (Champagne and Curley 2012). Parental investment may also have an epigenetic component. For example, variation in parental behavior (e.g., licking/grooming and arched-back nursing) during the early post-natal period can cause long-term changes in neuroendocrine function in offspring, with parental investment of these offspring being altered, as a consequence, in adulthood (Champagne and Curley 2012). These effects could be driven by changes in neural structure or regulation of the hypothalamic-pituitary-adrenocortical (HPA) axis or could occur via DNA methylation or histone acetylation (Champagne and Curley 2012).

The development of parental investment is also influenced by the exposure of individuals to conspecifics. Indirect genetic effects (IGEs) occur when the genotype of an individual affects the phenotype of a conspecific via environmental influences (Wolf et al. 1998). Maternal and paternal effects are specific IGEs that occur when the parents are influenced by environmental factors (e.g., pesticides or resource availability), which then impacts the development of offspring/grand-offspring, or when the investment of one parent is influenced by the behavior of the other parent or by the offspring themselves (Wolf et al. 1998). For example, the absence of the father leads to increased maternal care (compensation) in African striped mice females, resulting in sons raised by mothers alone providing more care to their offspring as adults (Rymer and Pillay 2011b). Consequently, the ontogeny of parental investment could result from a net effect of the interactions between proximate and social factors.

### Ultimate Questions: Function and Evolution

The primary benefit of parental investment to parents is increased offspring survival because this increases parental fitness (Clutton-Brock

1991). Investment affords protection from the external environment and supports development and growth in multiple ways (Table 1). Variable or unpredictable environments may result in increased predation risk, food shortages, pathogens, and desiccation, which could negatively impact offspring survival and growth. However, these negative environmental factors may be mediated or buffered by the parents. For example, foam-nest frogs *Chiromantis petersi* build a foam nest with a hard exterior over small seasonal pools (or even animal mud wallows; Coe 1974). The nest protects from desiccation and predation until the tadpoles are ready to be released to the pond below, and tadpole release can be delayed if the weather remains dry for some time (Coe 1974).

Some aspects of investment are essential for offspring survival (obligate). For example, the deposition of energy and nutrients into eggs is essential for growth and survival at the time of hatching in egg-laying species (Clutton-Brock 1991). However, other aspects of investment may be expressed only conditionally (facultative). For example, while male burying beetles *Nicrophorus orbicollis* usually provide paternal care for a short time after eggs hatch, females can raise young alone, and brood mass may decrease if males remain with the brood for an extended period (Fetherston et al. 1990). While facultative investment may not be essential for survival, it may provide other benefits to parents and offspring, such as improved reproductive competitiveness of offspring later in life.

The fitness consequences associated with parental investment will determine if it will spread in a population (i.e., natural selection). Parental investment is thus expected to evolve when the benefits of investing in offspring outweigh the costs (Klug et al. 2012). Kin selection theory (i.e., Hamilton's rule) may be suitable for explaining the evolution of parental investment because of the close genetic relationship shared by parents and offspring, as any selection on offspring impacts selection on parents and vice versa (Kölliker et al. 2010). Parental investment should, therefore, evolve in situations where the indirect/

inclusive fitness of the parent/s is increased by investing in the current brood/litter. However, including inclusive fitness benefits is problematic because attempting to assign indirect fitness benefits across generations confounds selection effects (e.g., increased offspring survival as a consequence of investment received) with inheritance effects (e.g., inheritance of traits that increase survival until recruitment). Furthermore, the evolution of parental investment is likely linked with other forms of social behavior (e.g., mate attraction, competition, and group-living, suggesting that investment is also likely under antagonistic selection (Kölliker et al. 2010). That is, selection favors offspring receiving investment because this can increase growth and survival, but there is also selection against parental investment because the costs can be very high (Kölliker et al. 2010).

Parental investment evolved independently in different lineages. However, the evolution of investment within lineages is debated, and patterns of parental investment are likely specific to species and life-history strategies (Klug et al. 2012). Parental investment may evolve when individuals have a reduced capacity to reproduce in future breeding attempts, resulting in increased investment in the current litter/brood. This is likely a consequence of ecological (e.g., food availability) and social (e.g., population density) factors. In harsh environments, where resource competition may be intense, parents may be constrained in their investment of current young to ensure their survival (Klug et al. 2012). However, the environment cannot solely explain the evolutionary origins of investment, and numerous hypotheses (e.g., paternity certainty, mating effort, and physiological constraints) can all explain the evolution of parental investment in different taxa (Rymer and Pillay 2018).

The social environment may also have been important for the evolution of investment because behavioral interactions can shape the development of phenotypes. Parents transfer numerous non-genomic resources (e.g., proteins and hormones) to offspring that may be essential for development, and these parental effects may

result in phenotypic accommodation (adaptive adjustment of the phenotype, without genetic change, following a novel genetic or environmental stimulus occurring during development, West-Eberhard 2005). This variation underlying phenotypic accommodation could ultimately be shaped by selection (genetic accommodation) if it had an underlying heritable component (West-Eberhard 2005), leading to the establishment of parental investment. In addition, other behaviors used in different contexts (e.g., aggression toward conspecifics) could have provided a starting point from which parental investment could be modified (e.g., aggression co-opted into guarding of offspring). Once investment originated, co-evolutionary feedback loops may have led to the maintenance, further evolution, or even diversification of parental investment traits (Klug et al. 2012).

## Conclusion

Parental investment is widespread in the animal kingdom and varies between taxa, within taxa, and between the sexes. Parental investment is costly. The benefits associated with increased offspring survival and fitness are traded off against these costs. Trade-offs occur between self-maintenance, foraging, mate-seeking, and antipredator behaviors. Parental investment can be studied from any one of Tinbergen's (1963) four approaches. However, a complete understanding of parental investment requires that all four aspects be integrated.

## Cross-References

- ▶ [Alloparental Care](#)
- ▶ [Biparental Care](#)
- ▶ [Evolution](#)
- ▶ [Maternal Behavior](#)
- ▶ [Mating Effort](#)
- ▶ [Nikolaas Tinbergen](#)
- ▶ [Parenting](#)
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- ▶ [Ultimate Causation](#)



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## Parental Investment Theory

- Coolidge Effect, The
- Mating Effort

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## Parenting

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### Synonyms

Parental care; Parental investment; Rearing

### Definition

Parenting is the investment by caregivers in their offsprings' survival to the age of reproductive viability, and to assure that the offspring possess the social skills necessary to compete for resources and reproduce. According to Trivers, the quality and length of the investment is shaped by a series of tradeoffs between the caregivers' needs to invest in additional offspring and each individual offspring's desire to optimize their own survival by exploiting their parents' resources. Parental goals include raising reproductively - viable offspring to adulthood, with minimal cost to their own reproductive capability. Offspring goals include obtaining as much care from their parent(s) as possible. These goals are, at times, in conflict, but at the root of successful parenting behavior lies the task of increasing offspring probability of survival to an age at which they are independent from their parent for survival, possessing the behavioral skills to attract a mate and successfully reproduce.

### Introduction

From an evolutionary perspective, one of the defining characteristics of a mammal, particularly females, is that they engage in parenting. While all mammals provide milk to their newborn offspring, parenting involves far more than the provision of calories and nutrition through lactation. As newborns, most mammals are relatively helpless, or altricial. They need protection from predators and, in the case of most non-ungulate mammals, they also require external warmth to

thermoregulate, both of which are typically provided by mothers. Even ungulates, who are capable of adult-like locomotion within hours of birth, require the protection of a parent as they respond to their native curiosity and explore their surroundings.

### Offspring-Caregiver Conflict

A primary feature of mammalian infants is an inherent curiosity (Harlow 1958), which drives them to learn about their environment, oftentimes leading to offspring-caregiver conflict. Young infants are driven to discover their environment and, in social species, to find agemates that will assist in their critical learning through play. Caregivers, on the other hand, tend to focus on keeping their offspring in close proximity to prevent injury or predation, an evolutionary-driven goal, as infancy is the period when the greatest loss of life occurs in most species. These diverging goals lead to conflict between the parent and the offspring (Trivers 1974). Indeed in rhesus macaques (*Macaca mulatta*), it is not unusual to see a mother grasping her curious infant's tail in a leash-like fashion to prevent it from leaving her side to explore. Parents must attend to and, at times, intervene to prevent their infants' incursion into novel and sometimes dangerous situations, while offspring recklessly seek out novel experiences and playmates, inherently trusting that their caregiver will keep them safe from harm and danger.

With increasing offspring age, this conflict reverses. As offspring develop the motor maturity and skills to fend for themselves, they become increasingly capable of independence from their parent, which is a primary parental goal. In line with this, as offspring age, their caregiver provides a decreasing amount of "hands-on" care and begins seeking new reproductive opportunities to invest in new offspring. Offspring, on the other hand, continue to seek resources from their parent(s) and tend to become distressed when their parent(s) focus on future reproductive opportunities.

As their mother becomes focused on mating and future offspring, and as offspring maintain their interest in their own needs and the resources a parent provides, weaning becomes a central feature

of offspring-caregiver conflict (see section “[Parental Investment Theory](#)” below). For example, while most Old World primate species are allowed continuous access to their mother’s nipple during the first weeks of life, as the infant ages and is more likely to survive without this care, and as the mothers’ continued investment in lactating leads to her missing out on reproductive opportunities, maternal carrying of and nursing infants are gradually reduced (Hinde and Atkinson 1970). The infant however, tends to continue to seek out nourishment and to have its psychological needs met by its mother. Thus, the weaning period can be a stressful period of time for both parties, as mothers reject their infant’s attempts to nurse and, consequently, infants become distressed and increase their attempts to maintain contact (Berman et al. 1993), with individual differences in both the parent and infant in the relative ease or difficulty of weaning. During the breeding season (the period when weaning is at its peak (Hinde and Spencer-Booth 1967)), of nonhuman primates such as rhesus monkeys it is not unusual to hear a cacophony of infant cries from the trees while their mothers engage in consort relationships (personal observations of author JDH from both the Morgan Island and Cayo Santiago free-ranging populations). Among some nonhuman primate species, the distressed infant may be comforted by siblings or fathers (e.g., tamarins (*Saguinius*) (Cleveland and Snowdon 1984), barbary macaques (*Macaca sylvanus*) (Deag 1980), and gorilla (*Gorilla*) species (Smuts et al. 1986)), and in some New World species, the father may increase his role significantly, acting as the primary caregiver (see section “[Fathering](#)” below).

## Parental Investment Theory

For caregivers, cost of reproduction is high, particularly for species whose young require care for an extended period of time following birth. As caregivers are typically limited in the amount of time and resources they can devote to any one offspring, parents must make decisions that will maximize the likelihood of offspring survival to sexual maturity, and therefore, the likelihood of extending the parents’ initial genetic contributions

to future generations, while balancing their own interest in reproducing again and investing in future offspring. Parental investment theory, proposed by Robert Trivers (1972), suggests that as parental investment into offspring involves expenditure of energy by the parent (i.e., time spent rearing offspring, energy spent carrying and protecting offspring, energy spent producing milk, etc.), each investment reduces the parent’s own reproductive fitness (i.e., possibilities of conceiving more offspring). While parents make a series of decisions about how much they will invest in the present offspring this must be balanced by potential investment in and the offspring themselves grapple for as much parental investment as possible, securing their own survival to an age of reproductive viability. Thus, parental investment is shaped by the demands of the offspring and the goals of the parent and must be optimized to meet the needs of both. While some species have opted for a higher birth rate, providing minimal parenting to their offspring beyond stashing eggs in a secure location (i.e., turtles, fish, frogs) (termed *r*-selection), others have opted for *K*-selection, having a lower birth rate and expending a substantial amount of time and energy rearing, feeding, and protecting their young (i.e., elephants, cats, primates) (MacArthur 1962), with the manifestation of *r*-vs.-*K*-selection not always clear. For example, among humans in societies where infant mortality is high and a lower percentage of the population live to a reproductive age, families tend to be larger than in modern or western societies where infant mortality is low and the vast majority live to reproductive age. It is clear that the type and quality of parenting invested into offspring is a reflection of our evolutionary history, and the current environmental demands, and that the cost of parenting is carefully assessed to promote reproductive success, and, therefore, the survival of the species.

## Parenting and Brain Development

A large brain requires a long time to grow. Consequently, growth must occur post-parturition. If not, mothers would likely die giving birth to large-

headed offspring as the birth canal is not equipped for such stress. Thus, a large brain arrives into the world underdeveloped, and appropriate input must be available for the brain to attain species-typical maturity. This phenomenon requires mammalian parents to devote more time and energy to parenting than do cold-blooded species, and primates take this to the extreme, with the vast majority of development of higher level brain functioning occurring postnatally. Even across primate taxa, there is wide-variation in infant needs, for example, infants of Old World primate species (i.e., chimpanzees (*Pan*), orangutans (*Pongo*), macaques (*Macaca*)) tend to have longer developmental periods of infancy in which they require maternal care, when compared to New World (i.e., marmosets (*Callitrichidae*), squirrel monkeys (*Saimirinae*), owl monkeys (*Aotus*)) or prosimian species (i.e., lemurs (*Lemuroidea*), lorises (*Lorisoidea*), aye-aye (*Chiromyiformes*)). This prolonged altricial period of Old World species is likely an evolutionary adaptation to their more complex adult brains, the complexity of social groups, and the requisite behaviors necessary for social living (Allman and Martin 1999), and a tendency toward a longer inter-birth intervals, and thus, a longer maternal investment.). With their long process of learning and development, primates possess certain features that set them apart from other mammals, including long lifespans (Charnov and Berrigan 1993) and bigger brains in relation to body size (Allman and Martin 1999).

From an evolutionary perspective, these features appear to be interrelated to the extent that altricial offspring require longer periods of post-natal development, in which a larger and more complex brain develops, allowing more rapid adaptation to changing and varied environments later in life. Furthermore, species with a longer lifespan and greater intelligence typically show comparatively more multifaceted behaviors and are capable of living in large societies that provide defense from predators and greater safety to developing infants. Such societies are typically organized around infant survival and are, in many ways, a macrocosm of the offspring-caregiver relationship, with males responsible

for troop defense and mothers bonding with other females to support one another. In this protective social setting, parents provide the input in which the immature infant's brain learns how to adapt to a vast number of circumstances, social challenges, learning to solve difficult social problems.

Infants, are born with a specific set of needs and expected inputs that must be met for normative neurodevelopment to occur, a concept called the experience-expectant brain in the developmental literature. Sensitive and attentive caregivers provide infants with the expected experiences, assuring that the right input is received by the under-developed brain at the right time. This parental input "wires" up the brain to develop to survive in its present environment, with the consequence of an immature brain requiring an oftentimes extensive period of investment to ensure survival to adulthood. *K*-selected species opt for a larger and longer parental investment to ensure their offspring's safety and physical health, as well as prepare them for a life as an adult member of the species. For example, observations of a mother cat (*Felis*) and her kittens indicate that, initially the mother produces energy-rich milk for her offspring, which declines in quality with time, and when her offspring are more mature, the mother teaches them to hunt to obtain their own food. In particular, for species living in complex social groups, parents provide critical opportunities for offspring to practice social skills, wiring up the brain to survive in a complex, social world. An underdeveloped brain at birth also provides for parenting that is calibrated to individual differences in offspring needs and to differences in environmental requirements, promoting the adaptability and survivability of the species as a whole.

To develop normally, infants must achieve an optimal level of arousal. That a parent reduces infant arousal via parenting behaviors is central to the development of mother-infant attachment bonds (arousal regulation theory) is grounded in the Yerkes-Dodson Law, proposed in the early 1900s by Robert Yerkes and John Dodson. The law posits that an optimal level of arousal is preferred for optimal performance. For an extensive

discussion on this theory and its relation to development, see ► [“Attachment”](#) entry.

Briefly, while adults are mature enough to regulate their own arousal, altricial infants' brains are not equipped to do so due to their immature emotional neural circuitry. The brains of species in which natural selection has favored a prolonged process of post-natal brain development form and maintain synapses if they are useful and prune them when they are not ecologically necessary. Through the formation of attachment bonds, adequate experiences occur and expected inputs are received, largely by repeatedly “turning off” the anxiety circuit in the brain as the caregiver nurtures and cradles their infant. By responding to the infant's over-arousal, the caregiver modifies their own behavior, with a goal of maintaining the infant's arousal at the optimal level. Optimal arousal is most readily achieved when a caregiver sensitively responds to their infant's needs, with individualized care. Similarly, when an infant is under-aroused, a caregiver will allow them to explore and play, with a goal of increasing arousal to the optimal level. By so doing, the caregiver sensitively engages the immature neural pathways in an experience-expectant manner until the infant matures to point that it can adequately regulate its own arousal.

## Transmission of Culture

A prolonged period of development with close parental oversight allows for the occurrence of the intergenerational transmission of extensive information concerning how to exploit the environment and solve problems. Observational learning of skills unique to a species, or specific to an ecological niche, or that provide insight into how to solve a problem that better adapts an immature individual to exploit a resource is an asset that provides an advantage to the developing offspring as it learns the skills that adults use. Outside of humans, direct tutoring and active teaching is rare, but the passive transmission of information (termed cultural transmission) via observation occurs frequently in the animal world and is one of the fundamental aspects of parenting in

primates as well as other species with long developmental periods (e.g., elephants, dolphins, whales) and is likely one of the major reasons for primates' success, as each generation gains access to knowledge honed and refined by earlier generations.

One salient example of this transmission of culture is that of the chimpanzee termite-fishing. Chimpanzees are a particularly-altricial species, relying on their mothers until they are between 8 and 10 years of age (Goodall 1967), closely observing their mothers to learn the skills they need to exploit their environment. Termite fishing is one such skill. Chimpanzee offspring observe their mothers insert a stick into a termite mound and extract termites to eat. As offspring are typically clumsy when they first begin applying this skill, chimpanzee mothers give them ample opportunities to observe and practice, and tend to be tolerant of their offspring's behavior, even when it disrupts the termite-fishing bout (Lonsdorf 2006).

Another example of this intergenerational transmission of culture is the washing of sweet potatoes by Japanese macaques (*Macaca fuscata*) found on Koshima Island. In 1953, one female was observed washing a sweet potato before consuming it. Over the next decade, this behavior spread through the troop. Over the next decade, all but four of the infants born into the troop learned the behavior from their parents. Such transmission of knowledge from parent to offspring is a fundamental parental function that has great benefit to species with long developmental periods (Hirata et al. 2001).

## Alloparenting and the Kin Selection Hypothesis

In some species, members of the social group beside the mother provide care for related offspring, in a process called alloparenting or aunting (Wilson 1975). Alloparenting is most clearly expressed in primates (Hrdy 1976), though it is seen in some other mammals, like porpoises and elephants, as well as in some insects and birds. A few hypotheses propose explanations as to why



**Parenting, Table 1** This table shows the proportion of genetic-relatedness between individuals in a family. Darker colors (and higher percentages) indicate greater genetic-relatedness

|               | Offspring | Mother/Father | Sibling | Step-sibling | Aunt/Uncle |
|---------------|-----------|---------------|---------|--------------|------------|
| Offspring     | 100%      | 50%           | 50%     | 25%          | 25%        |
| Mother/Father | 50%       | 100%          | 50%     | 50%          | 50%        |
| Sibling       | 50%       | 50%           | 100%    | 25%          | 25%        |
| Step-sibling  | 25%       | 50%           | 25%     | 100%         | 25%        |
| Aunt/Uncle    | 25%       | 50%           | 25%     | 25%          | 100%       |

alloparenting occurs. One of these states that, for nulliparous (no experience as a biological mother) females, alloparenting provides an opportunity to practice motherhood and gain experience caring for an infant (Lancaster 1971).

While this learning-to-mother hypothesis has been cited by many, there are clear drawbacks to this vein of thinking. For instance, what about males that participate in alloparenting? They are clearly not learning to mother. The kin-selection hypothesis accounts for this, suggesting that, as the primary goal of parenting is to promote the survival of one’s own offspring to an age of reproductive viability, parental investment is based on getting one’s own genes into the next generation. Fathers that care for their offspring increase the probability of their sons’ and daughters’ survival; thus getting their genes into the next generation. As mothers care for their offspring they are investing primarily in an individual that is 50% genetically related to them (her offspring – see Table 1) rather than an individual that is 100% genetically related to her (herself – see Table 1). If she were to only invest in herself, she may well ensure that she has enough resources for survival but as she will one day die, if she has no offspring, her genes will cease to appear in the next generation, assuming she has no siblings and therefore no nieces or nephews. It is proposed that in species which alloparent, those providing the care are investing in offspring that are their genetic relatives. For example, as a male sibling cares for their infant sibling, they are investing in an individual that is 50% genetically - related to them (see Table 1). As an aunt or an uncle cares for their infant niece or nephew, they are

investing an individual that is 25% genetically - related to them (see Table 1).

Therefore, as an individual cares for an infant that is related to them by some degree, they are ensuring their own genetic survival into the next generation.

**Parenting Styles**

Among most mammals, mothers are the primary, if not the sole caregiver, with males showing disinterest and, in some cases, engaging in infanticide (see Hrdy 1977), particularly when the infants are not sired by him. For rhesus monkeys, mothers play a primary role in parenting and infant development. This is thought to be because, when compared to males, females make a greater investment in the developing fetus and infant. Beginning with her investment of an ovum at conception, to her body’s dedication to house the developing fetus, to her investment in feeding and caring for the infant, the energetic costs are substantial, and much greater than that of the father. Put another way, sperm is cheap; ova are costly, and while males can produce multiple offspring in a year with little cost, females, particularly most primate females, are only able to produce approximately one infant in a year. That mothers are the main caregiver in most Old World species is largely a function of that initial investment. The intensive care that altricial infants require following birth necessitates that parenting play a crucial role in the survival of primate offspring to an age of reproductive viability. While primate parents invest differentially in their infants across species, parenting quality has been demonstrated to have

lasting effects on infant outcomes, including survival, social skills (Pereira and Altmann 1985), and normative development (Harlow 1958).

Because mothers are the primary caregiver in most species, their skillfulness, temperament, and style of care matters. While all mammalian females show certain similarities, largely centered around feeding, there are wide individual differences in the quality of care and maternal restrictiveness. For example, studies of the maternal behaviors of monkeys reared without mothers demonstrate that, for female primates, the complexities of maternal behavior are not merely a set of hardwired fixed-action patterns, but rather something that must be learned (Seay et al. 1964). Studies have investigated the role of mothering styles on development, suggesting that sensitive parenting (i.e., attentive, calibrated to the infant's individual needs) is linked to healthy, normative brain development, whereas less involved or insensitive parenting (i.e., permissive, abusive, restrictive) is linked to abnormal brain development (Maestripieri et al. 2006).

Early maternal experiences may also explain the evolutionarily-old phenomenon of offspring abuse in human and nonhuman primates as mothering styles are believed to be transmitted intergenerationally. For example, Widom and colleagues show that maternal child abuse in humans is often transmitted from one generation to the next (2015) in a process called the intergenerational transmission of abuse. In nonhuman primates, Fairbanks and McGuire (1988) identified two general maternal traits, protectiveness and rejection. Protectiveness is behaviorally - characterized by frequent maternal approach, making contact, restraint, and infant inspection. Rejection is behaviorally - characterized by high rates of rejection, breaking contact, and maternal leaving her infant. Such treatment tends to be stable and studies show the female infants mirror their mothers' parenting style when they care for their own infants. For example, Maestripieri (2005) identified rhesus monkey mothers with a history of abusive parenting and rhesus monkey mothers with no history of abusive care (control group). When the abusive monkey mothers and the control mothers gave birth, their

infants were cross-fostered to one another (i.e., the abusive mothers adopted the offspring of the control mothers and the control mothers adopted the offspring of the abusive mothers). As expected, the abusive mothers abused their cross-fostered infants and the control mothers did not. When the abused and the non-abused infants became adults and had their own offspring, the researchers observed that the mothers that were abused as infants were more likely to abuse their own infants, while none of the non-abused, cross-fostered mothers abused their own infants, despite their genetic-relatedness to an abusive mother. Other studies of nonhuman primate abuse suggest that propensity of mothers to engage in offspring abuse is tempered or exacerbated by genetic background (McCormack et al. 2009).

Beyond abusive parenting, studies investigating the role of maternal presence on offspring development derive from Harry Harlow (see ► [“Attachment”](#) entry). In these paradigms, infants are removed from their biological mothers at birth and raised with a warm, cloth-covered surrogate mother or a wire surrogate mother to which they can cling and from which they can feed (Harlow 1958). The results of these studies show that certain inherent maternal features make a mother a desirable maternal figure to the infant (see ► [“Attachment”](#) entry). For example, the cloth-covered surrogates provide warmth, softness similar to a mother's touch, and are universally preferred by the infants, which seek comfort from the surrogates in times of distress through clinging to the soft surrogate “bodies.” These studies suggest that, at least for primates, infants need more than milk, and that mothers are preprogrammed to fill those needs.

## Fathering

While mothers tend to be the primary caregiver of most nonhuman primate species, fathers play a role in parenting to varying degrees (see Mitchell 1969 for a review). For most Old World species, mothers are the primary caregiver and fathers play, at best, a limited role (Snowdon and Suomi 1982). For example, in the classic 21-month field

study of rhesus macaques, Lindberg (1971) only observed 66 incidents (less than 2 minutes total time) of an adult male carrying an infant. Some have suggested, however, that this may be a function of the restrictiveness of the mother that generally does not allow a male to approach her infant, but instead quickly retrieves her infant when a male approaches (Lindberg 1971). Two studies assessed adult males' interest in and psychological capacity to care for infants when the mother was not present. In both studies, the adult male carried and performed all the behaviors characteristic of the mothers, except nursing (Redican and Mitchell 1973; Gibber and Goy 1985). Remarkably, when the females were returned to the groups, mothers quickly retrieved their infants and the males ceased to exhibit infant care, suggesting that the male rhesus monkeys are capable of caring for an infant, but do not engage in infant care due to maternal restrictiveness, likely a product of evolution. However, in monogamous species, such as gibbons (*Simiiformes*) and siamangs (*Simiiformes*), some prosimian species, as well a variety of New World species, biparental caregiving is more readily observed and, in the case of *Callitrichidae*, fathers and siblings play a primary role in infant care (Cleveland and Snowdon 1984).

Across most Old World species and in many New World species that live in large social groups, males are more likely than females to take a role in the infant's macroenvironment, protecting and defending the infant as a member of the larger troop against outsiders and predators. Adult males do, however, tend to engage in play more often with infants and juveniles than do adult females (Brockelman et al. 1998), something that the infants and juveniles seem to enjoy, as they often elicit these interactions. Adult males will also break up a fracas when juveniles and adolescents become overly-rowdy. Fathers tend to play an indirect role in their offspring's overall survival. For example, in species that show limited paternal caregiving, when the father of a male offspring remains in the troop, the rhesus macaque son grows faster and is less likely to be injured (Huchard et al. 2013), and in yellow baboons, both male and female offspring tend to mature to

an age of reproductive viability more quickly (Charpentier et al. 2008) when their father is present.

Not all fathers in Old World species are uninvolved in their infants' lives. For example, the barbary macaque spends considerable time interacting with infants, with infant play, infant carrying, and infant grooming all central features of barbary macaque society (Deag and Crook 1971). Similarly, in species, where the male is more likely to be certain that they are the sire or in species that live in harems (e.g., *Hamadryas* baboons (*Papio hamadryas*), gorillas), males are not only tolerant of their offspring but will even engage their offspring in co-sleeping.

While males in New World species that live in large groups exhibit behaviors toward infants that parallel the behaviors of Old World species, monogamous *Callitrichidae* species show a great deal of paternal care, with the male often acting as the primary caregiver (Mitchell 1969). This unusual pattern of male-infant care is explained as a unique adaptation to the species-typical twinning behavior (i.e., bearing two infants at once), where the energetic cost of carrying and feeding the infant precludes a female from caring for her twins by herself. To put this in perspective, two infant marmosets weigh as much as 25–30% of the mother's total body weight. If this were to occur in a human, a mother weighing 54 kg would be carrying twins weighing about 14 kg, an enormous energetic cost that would hinder her ability to both feed and carry the twin infants. Thus, for a female marmoset to care for twins, help is necessary and a male cooperates both because as a father he gets twice as many of his genes into the next generation with each pregnancy and because they are monogamous, and the male is more certain of paternity than if he lived in a large society where promiscuous matings are the norm. In marmoset and other monogamous New World species, it is not unusual for the father to carry the infant more than the mother, particularly for the first birth (Ingram 1977); although, with subsequent offspring, caring for the infant becomes a family affair, with siblings often carrying the infant as much as the father. This has dual benefits: the infant gets the care it

needs, and the siblings get practice parenting (Cleveland and Snowdon 1984). Studies show that without such practice, as male and female offspring reach adulthood and give birth to their own infant, they are inept as parents and their offspring often perish (Pryce 1993), again illustrating the importance of learning in developing appropriate parenting skills.

Monogamous Old World males of species like gibbons and siamangs also play a significant role in caring for their offspring; however, unlike the *Callitrichidae*, they do not engage in overt parenting from the first day of infant birth. While siamangs begin engaging in parenting earlier than do gibbons, in neither species do males play a primary role during the first year of life. In siamangs, for example, males do not carry their offspring until it is about a year old. However, once siamang males begin carrying the yearling, they may do so more often than the female (Chivers 1972). Among gibbons, fathers have not been observed carrying their infants or sleeping with their infants until they are weaned (Gittins and Raemaekers 1980). In at least one study (Clemens et al. 2008), after the infant gibbon was weaned, fathers spent more time than mothers interacting with their offspring (i.e., showing more play behavior and sharing food) after the first year of life, but mothers were still more likely to retrieve the infant when it cried, while siblings play only a limited role. Unlike the monogamous *Callitrichidae*, gibbon and siamang species do not twin, so it is difficult to find a compelling reason for the increased male involvement. Some have suggested that males invest more in these species because their paternity is more certain than it is in the more promiscuous Old World species.

## Conclusions

With the goal of survival until an individual is capable of reproduction, parenting is considered an investment in continuing the genetic line of an individual. Thus, as Trivers postulates, parenting is a balance between offspring goals of obtaining all the resources they can to promote their survival

and caretaker goals of balancing the investment of their resources to promote offspring survival as well as their own survival. Parenting can be understood in the context of the relative development of offspring at birth and age of reproductive viability, with species that are born with large brains that mainly develop post-natally, that are highly altricial requiring a larger parental investment for a longer period post-natally when compared to species that are born precocial. While there are certainly neurodevelopmental needs that an experience-expectant brain requires, there are wide individual differences in parenting behaviors within a species, with sensitive parenting generally resulting in typical developmental outcomes and abusive parenting leading to negative outcomes, including psychopathologies. While mothers are typically thought of as the primary caregiver across mammalian species, fathers are also known to play a role to varying degrees, dependent on ecological context. Parents are a crucial part of the altricial infant's early experience, with the developmental signature of their caregiving lingering well into adulthood and across generations.

## Cross-References

- Altricial
- Attachment
- Human Infancy and Childhood
- Parental Investment
- Psychopharmacology of Sex Steroids

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## Parent-Offspring Conflict

- [Daughter Guarding](#)
- [Discriminative Parental Solicitude](#)

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## Parietal Lobe

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### Definition

The parietal lobe is a region of the human brain defined by anatomical landmarks. Within it are brain areas that process somatosensory information, spatial attention, visual-motor transformations, numerical computations, and language, including reading.

### Introduction

The aim of this entry is to provide an overview of the parietal lobe of the brain. It will cover the basic

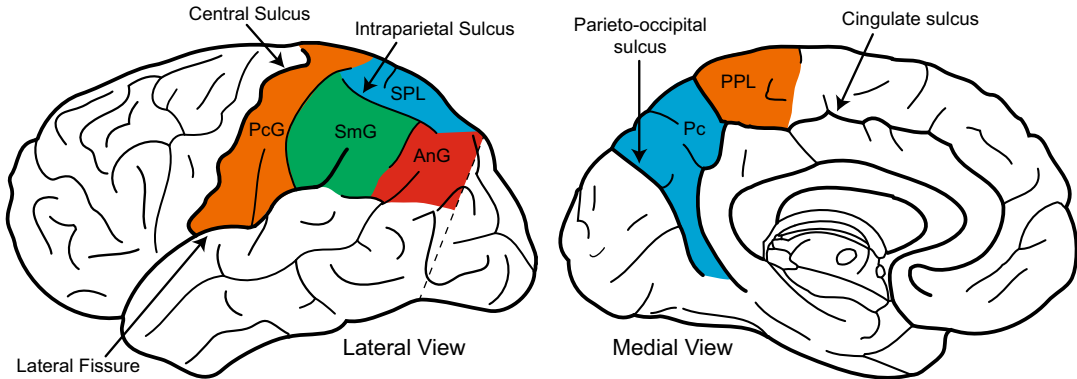
anatomy in the human and non-human primate and general neural processing, briefly highlighting the effects of lesions in the human brain and neuronal processing in the non-human primate brain.

## The Parietal Lobe in the Human Brain

### Anatomy of the Parietal Lobe

In the human, the parietal lobe is situated posterior to the frontal lobe, anterior to the occipital lobe, and superior to the temporal lobe (Fig. 1). Several of its margins are defined by clear landmarks. On the lateral surface, it lies posterior to the central sulcus, which separates it from the frontal lobe, and superior to the lateral fissure (also called the Sylvian fissure), which separates it from the temporal lobe. On the medial surface, it lies superior to the cingulate sulcus, which separates it from the limbic lobe, and anterior to the parieto-occipital sulcus, which separates it from the occipital lobe. At the posterior end on the lateral surface, it is separated from the occipital and temporal lobes by two imaginary lines. The first runs from the tip of the parieto-occipital sulcus, which is on the medial aspect of the brain, to the preoccipital notch and separates the parietal lobe from occipital lobe (dashed line, Fig. 1). The second is an imaginary extension of the lateral fissure, which separates the parietal lobe from the temporal lobe.

Within the parietal lobe, there are six main regions: four on the lateral surface and two on the medial surface. On the lateral surface, between the central sulcus and the postcentral sulcus, is the postcentral gyrus (PcG). Poster to this, the parietal lobe is divided by the intraparietal sulcus to form the superior parietal lobule (SPL) and the inferior parietal lobule. The latter is typically divided into two regions: the supramarginal gyrus (SmG) and the angular gyrus (AnG). On the medial aspect of the brain, the postcentral gyrus is contiguous with the posterior paracentral lobule (PPL), which ends at the marginal limb of the cingulate sulcus. Posterior to the cingulate sulcus is the precuneus (Pc), which is an extension of the superior parietal lobule and ends at the parieto-occipital sulcus.



**Parietal Lobe, Fig. 1** The parietal lobe in the human brain. The extent of the parietal lobe is indicated by the colored areas, which are coded based on the regions within

the lobe. *PcG* Postcentral gyrus, *SPL* superior parietal lobule, *SmG* supramarginal gyrus, *AnG* angular gyrus, *PPL* posterior paracentral lobule, *Pc* precuneus

### Functions of the Parietal Lobe

Primary somatosensory cortex lies in the postcentral gyrus, adjacent to the central sulcus. This is the main cortical area to receive information from the body about proprioception (information about body and limb position) and touch. The rest of the parietal lobe is composed of association areas: cortical areas that further process sensory information from one sensory source (unimodal) or from several sensory sources (multimodal). The unimodal association areas tend to be close to their respective primary sensory cortical areas. So somatosensory association areas are close to the postcentral gyrus, and visual association areas are close to the occipital lobe. The remaining areas within the parietal lobe are multimodal association areas.

The parietal lobe is one of the more lateralized lobes within the brain. Many of the multimodal association areas in the human parietal lobe have different functions on the left and right side of the brain. In most people, the left side is the *dominant hemisphere*. Together with the temporal lobe, regions of the inferior parietal lobule in the dominant hemisphere are involved in language comprehension. Lesions of this area produce *Wernicke's aphasia*: patients can have difficulty reading, comprehending speech, writing, or speaking. Deficits in writing or speaking are not motor related, but are due to an inability to put the correct words into a written or spoken sentence.

Lesions around the angular gyrus can also cause computational difficulties.

More dorsal lesions, around the intraparietal sulcus, can produce deficits in visually guided movements. These can include forms of *apraxia*, in which patients have difficulty executing learned and skilled movements, and *optic ataxia*, in which the patient has difficulty in making accurate and appropriate visually guided movements, including the grasping of objects they can recognize and describe. While these deficits are usually seen after lesions of the dominant hemisphere, they can follow from lesions of the nondominant hemisphere.

Lesions in the parietal lobe of the nondominant (usually the right) hemisphere tend to have a striking effect on the awareness of space. Thought to be due to deficits in the mechanisms underlying visual attention, patients can exhibit signs of *hemispatial neglect* or *extinction*. A patient with neglect tends to ignore the spatial world on the contralateral side (usually the left side of visual space). For example, they may draw a clock with the numbers 1 to 12 all on the right side of the circle or they may draw an object, but leave out features on the left side. In severe cases, patients can be unaware that the left side of their body belongs to them. Extinction is a more subtle deficit in which patients do not notice a visual or tactile stimulus on their affected side (usually the left) when simultaneously presented with a similar

stimulus on their intact side, but they are able to notice it when presented alone.

## The Parietal Lobe in the Nonhuman Primate Brain

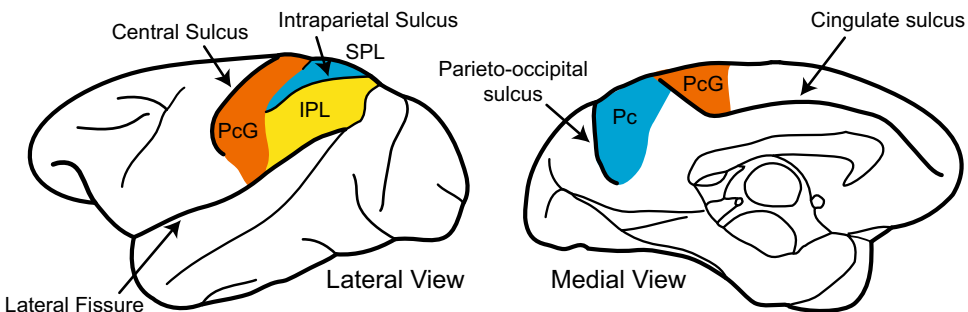
### Anatomy of the Nonhuman Primate Parietal Lobe

Aspects of the parietal lobe in the nonhuman primate are quite similar to the parietal lobe in the human (Fig. 2). Laterally, the anterior boundary is the central sulcus and the inferior boundary is the lateral fissure; medially, the posterior boundary is the parieto-occipital sulcus. However, the remaining boundaries are not as well established. On the medial aspect, the cingulate sulcus in the nonhuman primate does not curve inferiorly as it does in the human, so we have defined the inferior anterior boundary of the parietal lobe based on where cingulate cortical areas, as defined functionally and cytoarchitectonically, end and parietal cortical areas begin. Laterally, we have placed the posterior boundary of the lobe at the extension of the superior temporal sulcus. The area posterior to the superior temporal sulcus has been identified as the angular gyrus (Martin and Bowden 2000), which in humans is part of the parietal lobe. While this does appear to be the gross anatomical homologue, in terms of cortical areas, it is more homologous with the occipital lobe in the human, so we have not included it as part of the parietal lobe here.

The major regions within the parietal lobe of the nonhuman primate are similar to those in the human. Adjacent to the central sulcus is the postcentral gyrus, the intraparietal sulcus divides the superior parietal lobule from the inferior parietal lobule, and on the medial aspect posterior to the cingulate sulcus is the precuneus. Areas within the SPL and IPL are frequently described as being part of posterior parietal cortex. A key advantage of the nonhuman primate over the human is the ease with which physiological and histological mapping can be done. The regions labeled in Fig. 2 are all made up of multiple brain areas defined in these ways. In the following section, we will list some of the major and better understood brain areas with a brief note about their functions.

### Functions of the Nonhuman Primate Parietal Lobe

Functionally, the nonhuman primate lacks the lateralization seen in the human parietal lobe, but the basic foundations remain. Primary somatosensory cortex is found in the postcentral gyrus along with a number of areas involved in processing somatosensory information. The superior parietal lobule is primarily composed of area 5, which itself can be broken down into a number of areas (PE, PEC, PEip, MIP) based on cytoarchitecture and connections (Pandya and Seltzer 1982). These areas all appear to play important roles in visually guided movements, including visually guided reaching (Breveglieri et al. 2006; Snyder et al. 2000). In some studies, several of these areas close to the intraparietal



**Parietal Lobe, Fig. 2** The parietal lobe in the nonhuman primate brain. The extent of the parietal lobe is indicated by the colored areas, which are coded based on the regions

within the lobe. *PcG* Postcentral gyrus, *SPL* superior parietal lobule, *IPL* inferior parietal lobule, *Pc* precuneus

sulcus are grouped and termed the parietal reach region (PRR). Area AIP, which seems to have a similar function for grasping actions (Sakata et al. 1995), is found at the anterior end of the lateral/posterior wall of the intraparietal sulcus. These areas are likely to be nonhuman primate homologues of the areas that, when lesioned, create apraxia and optic ataxia.

Deep in the intraparietal sulcus is area VIP, a multimodal area which receives visual inputs, somatosensory inputs that appear to come from areas of the body with congruent receptive fields to the visual inputs, and vestibular inputs (Chen et al. 2011; Duhamel et al. 1998). Further, neurons in this area appear to encode numerosity as well. Part of the lateral/posterior bank of the intraparietal sulcus is area LIP, which is thought to be involved in the processing of visual information for the guidance of attention – both covert attention and eye movements (Bisley and Goldberg 2010). It appears to be a more specialized region within area 7, which encompasses much of the IPL. It is likely that these areas are the nonhuman homologues of the areas that, when lesioned, create neglect and extinction.

On the medial aspect of the parietal lobe are continuations of areas within the somatosensory cortex as well as area 7 and PEc. In addition, there are a number of multimodal association areas (such as V6, V6A, and LOP) that integrate visual and somatosensory information (Galletti et al. 1999a; Galletti et al. 1999b). Areas V6 and the ventral aspect of V6A appear to be high level visual processing areas providing visual information for movements. The dorsal aspect of V6A is affected more by somatosensory inputs and is thought to be more closely related to visually guided grasping movements. Each of these areas has strong connections with regions within area 5, including MIP and AIP.

Although the parietal lobe, as seen in the human, is not obviously present in species with lissencephalic brains – that is, brains that do not have prominent sulci – many primate and lower species have homologous somatosensory cortices and posterior parietal cortex areas with multimodal sensory processing to aid in driving motor commands.

## Cross-References

- [Lateral Intraparietal Region \(LIP\)](#)
- [Occipital Lobe](#)
- [Parieto-occipital Sulcus \(POS\)](#)
- [Superior Parietal Lobule \(SPL\)](#)
- [Superior Temporal Sulcus](#)
- [Temporal Lobe](#)

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## Parieto-occipital Areas

- [Parieto-occipital Sulcus \(POS\)](#)

## Parieto-occipital Sulcus (POS)

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### Synonyms

Grasping; Monkey; Motor-related cells; Parieto-occipital areas; Reaching; Visual cells

### Introduction

Among the areas of the monkey parietal cortex, those lying inside the parieto-occipital sulcus (POs), especially in its anterior bank and fundus, have been of particular interest for neuroscientists in the last decades. In fact, while the areas in the posterior bank show simple low-level visual responses, areas of the anterior bank and on the fundus have complex high-level visual and visuomotor functions. In this chapter, we will describe the main properties of neurons of the areas located in the POs.

### Localization of Areas in the POs

Figure 1 shows in different colors the areas located in the POs. All these areas have been traditionally considered as visual, because all of them contain visual cells. Thus, the names of all these areas start with the letter “V.” In the posterior bank, there are areas V2 and V3 (see Fig. 1a). In the fundus, there is a part of area V6. Areas of the anterior bank include the remaining part of V6 and area V6A. Areas V2, V3, and V6 are part of Brodmann’s area 18 (Brodmann 1909), whereas area V6A is part of Brodmann’s area 19 (Brodmann 1909, see Fig. 1a).

While the localization of areas in the posterior bank of POs is a proved concept (Zeki 1969; Gattass et al. 1981, 1988), the correct localization of areas in the fundus and in the anterior bank of the POs is a challenging issue, because POs has a

very complex and irregular shape. Thus, it is more subject to individual variability of the pattern of brain convolutions. Given these difficulties, there is not a consensus about the nomenclature and borders of these areas (Galletti et al. 2005).

In the 1980s, the anterior bank of POs was considered a single functional area, called PO (Gattass et al. 1985). One year later, Ungerleider and Desimone (1986) called “PO” a region occupying the fundus and part of posterior bank of POs (see Fig. 1b, blue line). Three years later, Colby et al. (1988) reduced the extension of PO to the lower part of the original PO (see Fig. 1b, green line). Later on, Lewis and Van Essen (2000) called “PO” mostly the dorsal part of the anterior bank of POs (see Fig. 1b, red line). Most of the discrepancies between these nomenclatures were because these definitions of PO were based in some cases on functional properties and in others on anatomical grounds.

In the same period of time, another nomenclature was used to define areas in the fundus and in the anterior bank of POs. In 1986, Zeki (1986) used the term “V6” to describe an area containing visual inputs by delimiting it by strong callosal connections. This area occupied almost the entire anterior bank of the POs, thus overlapping considerably with the PO of Gattass et al. (1985). A few years later, Galletti et al. (1996) divided the V6 of Zeki et al. (Zeki 1986) in a dorsal region containing visual and nonvisual cells (called V6A, see magenta area in Fig. 1a) and a ventral region containing only visual neurons (called V6, see green area in Fig. 1a). This latter one is the nomenclature currently used in literature, from 1999 on, also thanks to a wealth of functional and anatomical studies performed in this cortex (Fattori et al. 2017; Gamberini et al. 2015).

### Functional Properties of Areas of POs: Visual Properties

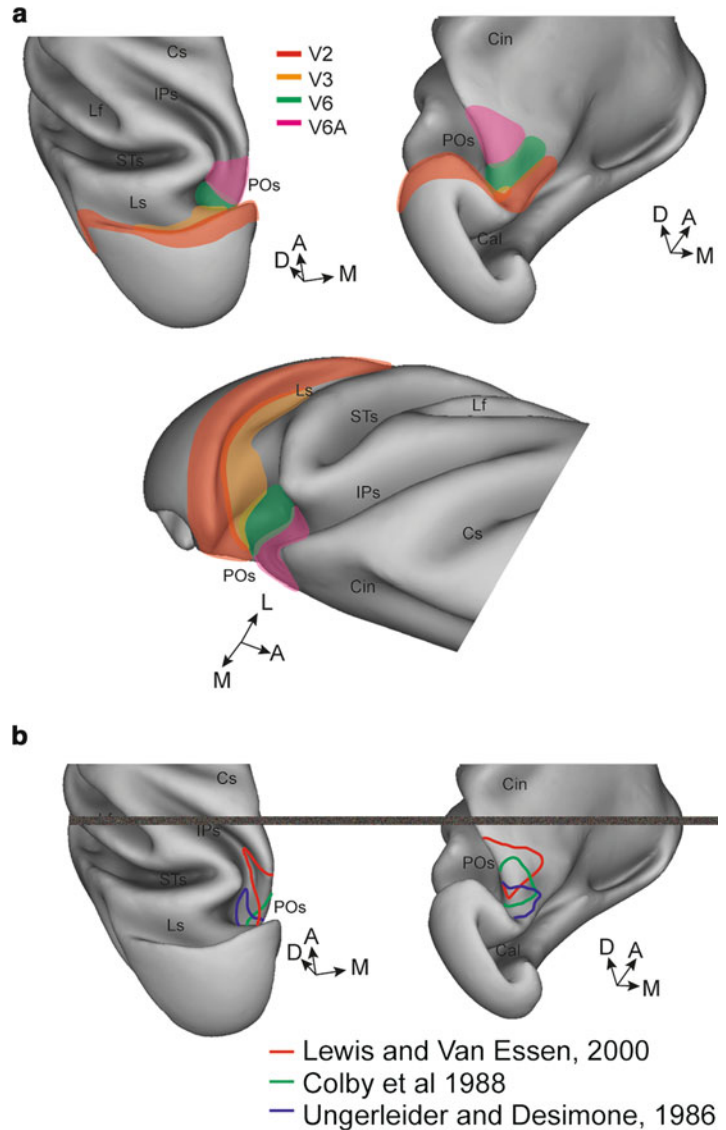
#### Area V2

Area V2 is the secondary visual area and occupies almost all the posterior bank of POs (Zeki 1969; Van Essen and Zeki 1978; Gattass et al. 1981) (see red area in Fig. 1a). All the cells in V2 are visual,



**Parieto-occipital Sulcus (POS), Fig. 1**

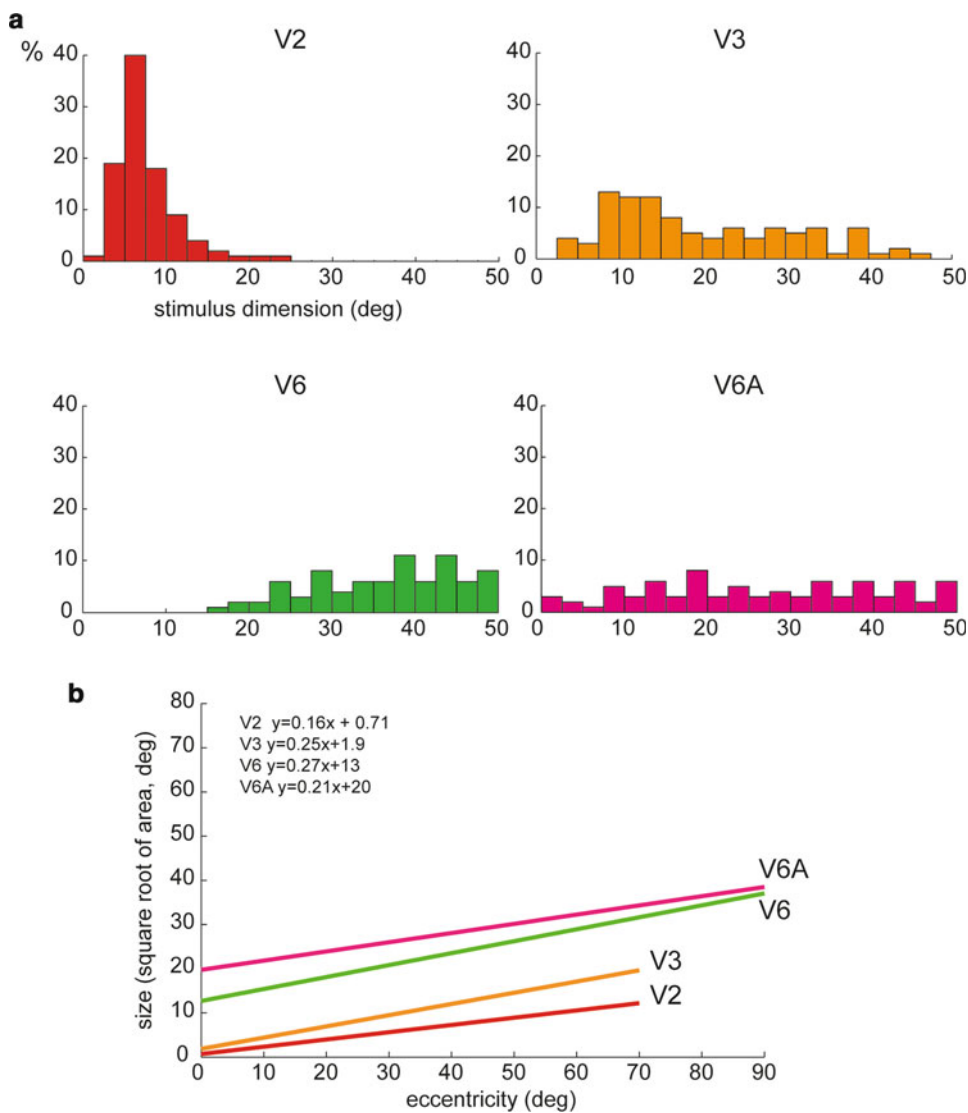
Brain location of areas located inside the parieto-occipital sulcus. **(a)** Modern subdivisions of the parieto-occipital cortex. Areas V2, V3, V6, and V6A are shown on 3D reconstructions of a macaque left hemisphere. *Top left and bottom: dorsal view; top-right: postero-mesial view.* Area V2 is represented in red, V3 in orange, V6 in green, and V6A in magenta. **(b)** Historical overview of the location of area PO according to different authors showed in dorsal (left) and on mesial (right) views of a macaque left hemisphere. Abbreviations: *POs* parieto-occipital sulcus, *Ls* Lunate sulcus, *STs* superior temporal sulcus, *Lf* Lateral fissure, *IPs* Intraparietal sulcus, *Cs* Central sulcus, *Cin* cingulate sulcus, *Cal* Calcarine fissure, *a* anterior, *m* medial, *d* dorsal, *l* lateral



and they are mostly activated by small light bars. Overall, the length of the light bars activating V2 is from 0.1° to 15° (Galletti et al. personal communication), but the overwhelming majority (94%) of cells were activated by bars with a length within 5°. The preferred stimulus size of area V2 cells is reported in Fig. 2a. Area V2 is topographically organized (Zeki 1969; Van Essen and Zeki 1978; Gattass et al. 1981) and contains the representation of the entire visual field. As in all striate and extrastriate visual areas, also in V2 there is a strong correlation between the size of the visual

receptive field and the eccentricity, as shown in Fig. 2b (red line).

Besides the sensitivity to the stimulus dimension, V2 neurons are also sensitive to the orientation, to the color (Gegenfurtner et al. 1997) and to the shape of the stimulus (Hegd  and Van Essen 2000; Anzai et al. 2007). V2 neurons respond also to complex visual features, like the orientation of illusory borders and binocular disparity (Thomas et al. 2002; Anzai et al. 2007). Moreover, V2 neurons show choice-related activity (Nienborg and Cumming 2006). A small incidence of V2



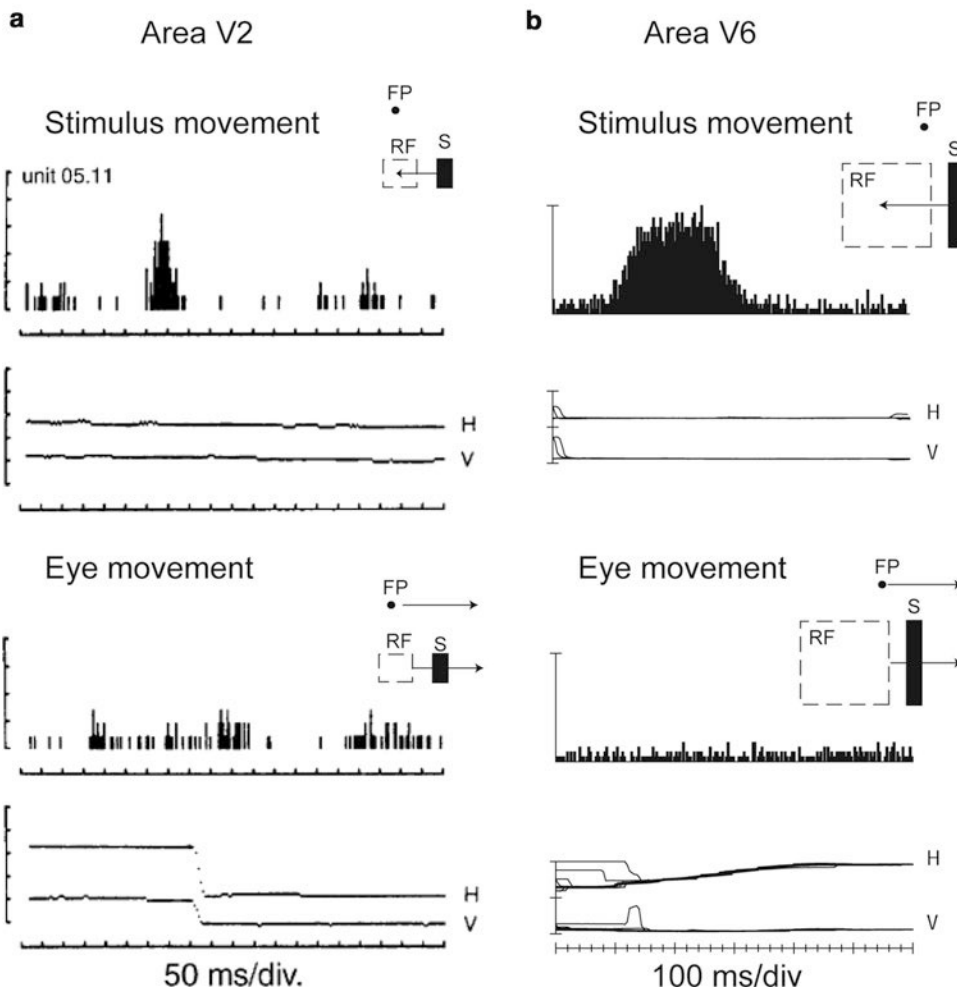
**Parieto-occipital Sulcus (POS), Fig. 2** Features of visual receptive fields of areas of the POs. (a) Distributions of the dimensions of the stimuli activating V2, V3, V6, and V6A visual cells. From V2 to V6A, an increase of the effective visual stimuli is evident. (b) Relation between

visual receptive field size and eccentricity in each of the areas of POs. Equations of the regression lines are shown for each area. Receptive field size increases with eccentricity in all the areas, with an increasing trend of the receptive field size from V2 to V6A. Other conventions as in Fig. 1

neurons (14%) are able to distinguish the real motion of a visual stimulus from the self-induced motion (real-motion cells, Galletti et al. 1988). An example of one of these cells is shown in Fig. 3a. It gives a strong response when a visual stimulus moves across the receptive field (Fig. 3a, top), whereas no response is present when the eyes pursue the fixation target moving in the opposite

direction with respect to the stimulus in the previous condition, while the visual stimulus is maintained still (Fig. 3a, bottom). It is noteworthy to highlight that the visual stimulation is the same in the two conditions. Thus, these visual cells are activated by a visual stimulation, but are not responsive if the same visual motion is present on the retina but in presence of eye movements. It

## REAL-MOTION CELLS



**Parieto-occipital Sulcus (POS), Fig. 3** Real-motion cells of areas V2 (a) and V6 (b) (Modified from Galletti et al. 1988; Galletti and Fattori 2003). For each area, a comparison of neural activity evoked by stimulus movement during steady fixation (*top*) and by eye movement against a stationary stimulus (*bottom*) is reported. Spike activity is shown as peri-stimulus time histograms (PSTHs); Horizontal (H) and vertical (V) components of a

typical record of eye movement are reported below spike activity. Scales: neural activity (y-axis), two spikes/division (area V2); 150 Spikes/s (area V6); eye position;  $4^\circ$  per division; time (x-axis), 50 ms/div (a), 100 ms/div (b). Real motion cells respond to a real movement of the stimulus in the visual field, but not to the same retinal movement evoked by eye movements

has been proposed that cells of this kind are involved in the detection of visual motion, taking into consideration also ocular motility (Galletti and Fattori 2003; Galletti et al. 1988).

### Area V3

Area V3 is generally considered a transitional or relay station in the extrastriate pathways and

borders area V2 ventrally (Van Essen and Zeki 1978; Gattass et al. 1988, see Fig. 1a) in the posterior bank and fundus of POs. Like V2, also V3 cells are all visual. The stimuli activating V3 cells are light bars like V2, but their size is generally higher than that effective for V2 (see Fig. 2a). Differently from V2, the dimensions of effective stimuli for V3 cells spread over a larger range of

values (from  $0.4^\circ$  to  $40^\circ$ , see Fig. 2a), and the receptive field size is overall higher than in V2 (see Fig. 2b) at any given eccentricity. Like all the extrastriate areas, in V3 too there is a strong correlation between receptive field size and eccentricity: the higher is the eccentricity, the wider is the receptive field.

Area V3 is retinotopically organized (Van Essen and Zeki 1978; Gattass et al. 1988; Arcaro and Kastner 2015); however, its ventral and dorsal parts, representing the two different visual hemifields (ventral part: superior hemifield; dorsal part: inferior hemifield), have different afferences and functional properties (Desimone and Ungerleider 1986).

Most of V3 neurons (80%) are orientation selective and a minor incidence (about 40%) is directional selective (Gegenfurtner et al. 1997). About half of V3 neurons are sensitive to color (Gegenfurtner et al. 1997). These data suggest that V3 is important in processing higher-level visual signals dealing with motion and also with other visual attributes.

### Area V6

V6 is a visual area located in the fundus and in the ventralmost part of the anterior bank of POs (Galletti et al. 2005) (see Fig. 1a, green surface). All its cells are visual. The strong correlation between eccentricity and receptive field size holds true also for V6 (see Fig. 2b), but the receptive fields are bigger than those of V3. V6 cells are sensitive to light bars and to dark-light borders whose dimensions are widely distributed from  $1.2^\circ$  to  $50^\circ$  (see Fig. 2a).

Area V6 is topographically organized and contains the representation of the entire visual field (Gamberini et al. 2015). V6 cells are very sensitive to the direction, orientation, and speed of motion (Galletti et al. 1996) and elaborate visual information at a high-level order. Indeed also in V6 there are real-motion cells, one example of which is shown in Fig. 3b (Galletti and Fattori 2003). In this cell, there is a strong activation when the visual stimulus moved from right to left, whereas similar retinal stimulations obtained by rightwards pursuit movements, with the stimulus stationary on the screen facing the animal, did not activate the cell. Another complex

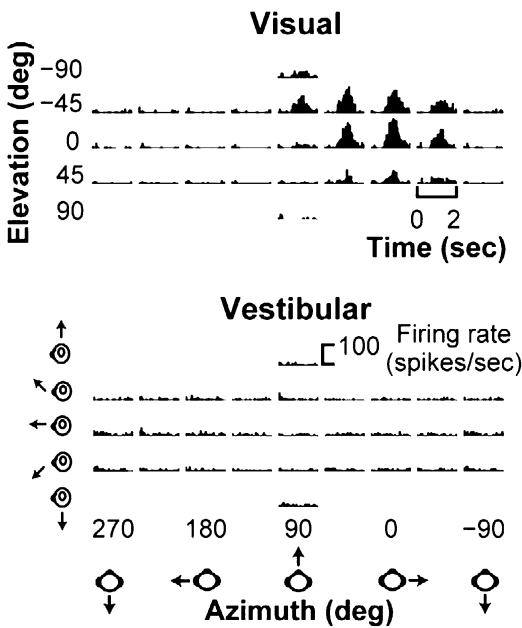
elaboration of visual information performed by V6 is the elaboration of heading signals, which are signals about the direction of self-motion (Fan et al. 2015). The majority of V6 cells (91%) are sensitive to heading defined by optic flow stimuli, that is, the pattern of apparent motion of objects, surfaces, and edges (e.g., dots or stars) in a visual scene caused by the relative motion between an observer and a scene. However, almost all V6 cells are unresponsive to inertial motion in the absence of optic flow; thus, they are not modulated by vestibular stimuli (Fan et al. 2015). An example of a V6 cell tested for visual and vestibular stimuli evoking heading sensation is shown in Fig. 4. The example neuron responded most vigorously to optic flow stimuli that simulated rightward translation (Fig. 4, top) but showed no significant sensitivity to vestibular stimuli (Fig. 4, bottom) evoking the equivalent heading sensation. However, V6 does not perform multisensory integration but extracts heading signals basing only on visual information (Fan et al. 2015). Overall, these data confirm that V6 is a high-level visual cortical area.

### Area V6A

Area V6A occupies almost all the anterior bank of POs (Fig. 1a, magenta area) and is the only visual area of POs that contains also non-visual cells (see next paragraph). V6A contains about 60% of visual cells (Gamberini et al. 2015), activated by dark-light borders whose dimensions span from  $3.2^\circ$  to  $50^\circ$  (see Fig. 2a). The receptive field size increases with eccentricity, although less strictly than in V6 (see Fig. 2b). Area V6A contains a coarse visual topography, with the representation of the central visual field in the dorsal part and the periphery mainly in the ventral part (Gamberini et al. 2015). Differently from V6, V6A does not contain real-motion cells (Galletti and Fattori 2003).

### Functional Properties of Areas of POs: Properties Other Than Visual

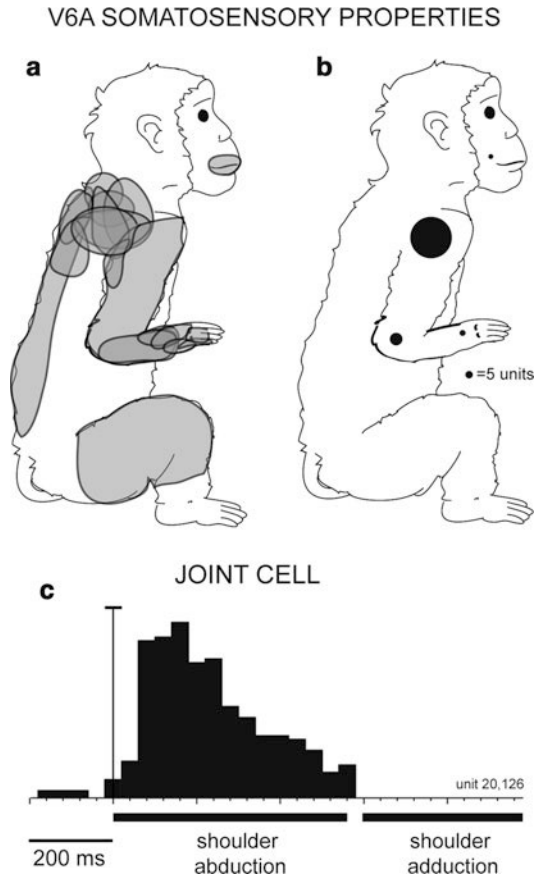
Despite the majority of V6A cells are visual, V6A is currently more considered as a visuomotor area



**Parieto-occipital Sulcus (POS), Fig. 4** 3D heading tuning for an example neuron of area V6. *Top*, visual stimuli. PSTHs of responses of the neuron to optic flow stimuli simulating 26 heading trajectories in 3D space. *Bottom*, vestibular stimuli. PSTHs are shown for responses of the same neuron to vestibular heading stimuli. Modified from (Fan et al. 2015). The cell discharges for heading information derived uniquely from visual stimuli, being insensitive to equivalent heading signals

rather than a purely visual region. In fact, it contains cells with somatosensory properties and motor-related properties. Figure 5 shows the sensitivity of V6A to passive somatosensory stimulations. Tactile receptive fields are mainly located on the arm, similarly to the location of joints whose rotation activates V6A cells (Fig. 5a, b). An example of a cell modulated by the passive rotation of the shoulder is depicted in Fig. 5c. There is a strong response when the shoulder was passively abducted (the elbow goes far from the trunk) and no response when the shoulder was passively adducted (elbow close to the trunk). About 30% of V6A cells showed somatosensory properties (Fattori et al. 2017).

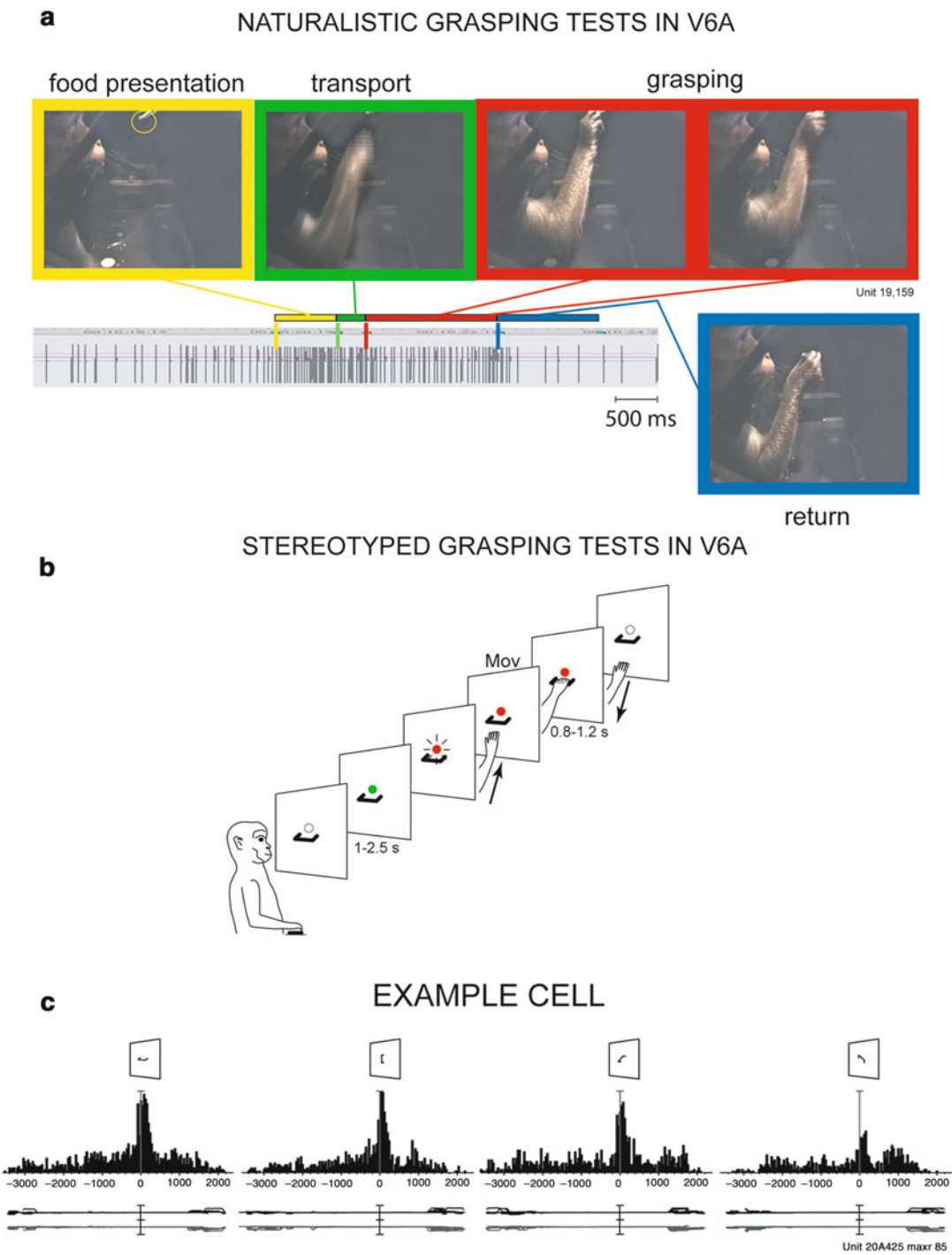
However, the most effective signals modulating V6A cells revealed to be those related to arm/hand actions to reach objects in space and at interacting with objects. In fact, about 70% of



**Parieto-occipital Sulcus (POS), Fig. 5** Somatosensory properties of area V6A. (a) Body locations of V6A tactile receptive fields. Above the animal, the internal surface of the left arm is reported to show locations of tactile receptive fields in that part of the body. Note that receptive fields are all reported on the right part of the body. (b) Location of joints modulating V6A cells. Each black dot indicates the joint that modulates V6A cells. The size of the dot is proportional to the number of modulated units. (c) Example of a cell modulated by the abduction of the contralateral shoulder. The activity of the recorded cell is shown as PSTH. Bars below the PSTH indicate the duration of shoulder abduction and adduction. Modified from Fattori et al. 2017. Other conventions as in Fig. 3. Area V6A is the only area in the POs showing also responses to passive somatosensory stimulations

V6A cells are reach-related, and most of them show directional tuning (Fattori et al. 2017). Also reaching actions performed at different depths have been shown to influence the discharge of V6A (Hadjidimitrakakis et al. 2014). Besides being a reach-related area, V6A is deeply modulated also by grasping actions. The first





**Parieto-occipital Sulcus (POS), Fig. 6** Grasping neurons in V6A. (a) Episode of naturalistic grasping of food from pliers. The audio band of the video clip below animals' pictures indicates the activity of the recorded cell (vertical bars are action potentials). Horizontal thick bar

over the audio band indicates the period during which the food was presented to the animal (yellow), the period when the animal transported the arm towards the food (green), the time when the animal grasped the food (red), and the period when the monkey brought the food to the mouth

evidence at this regard was obtained by Galletti's lab (Fattori et al. 2004) that tested V6A neurons while monkeys reached to grasp food using naturalistic, nonstereotyped actions. Figure 6a shows an example of one of V6A grasping cells documented in this way. The discharge of this neuron was modulated during the entire act of prehension, as shown in the video frames reported in Fig. 6a. Spike-train frequencies were higher than the baseline activity during food presentation (yellow frame), and a strong discharge rate was maintained during hand transport and finger extension (transport phase, green frame), as well as during finger flexion and food grasping, in the last phase of prehension (grasping phase, red frames). This phase was exaggeratedly long because the monkey made several attempts to grab the raisin in the pincer, continuously trying to catch the food. Neural discharge drastically decreased when the arm began the return movement to the mouth (blue frame). More than 50% of tested neurons were modulated by the entire act of this naturalistic prehension (Fattori et al. 2004). These were the first data about the involvement of V6A in grasping action and paved the way to new experiments to understand more precisely the role of V6A in grasping.

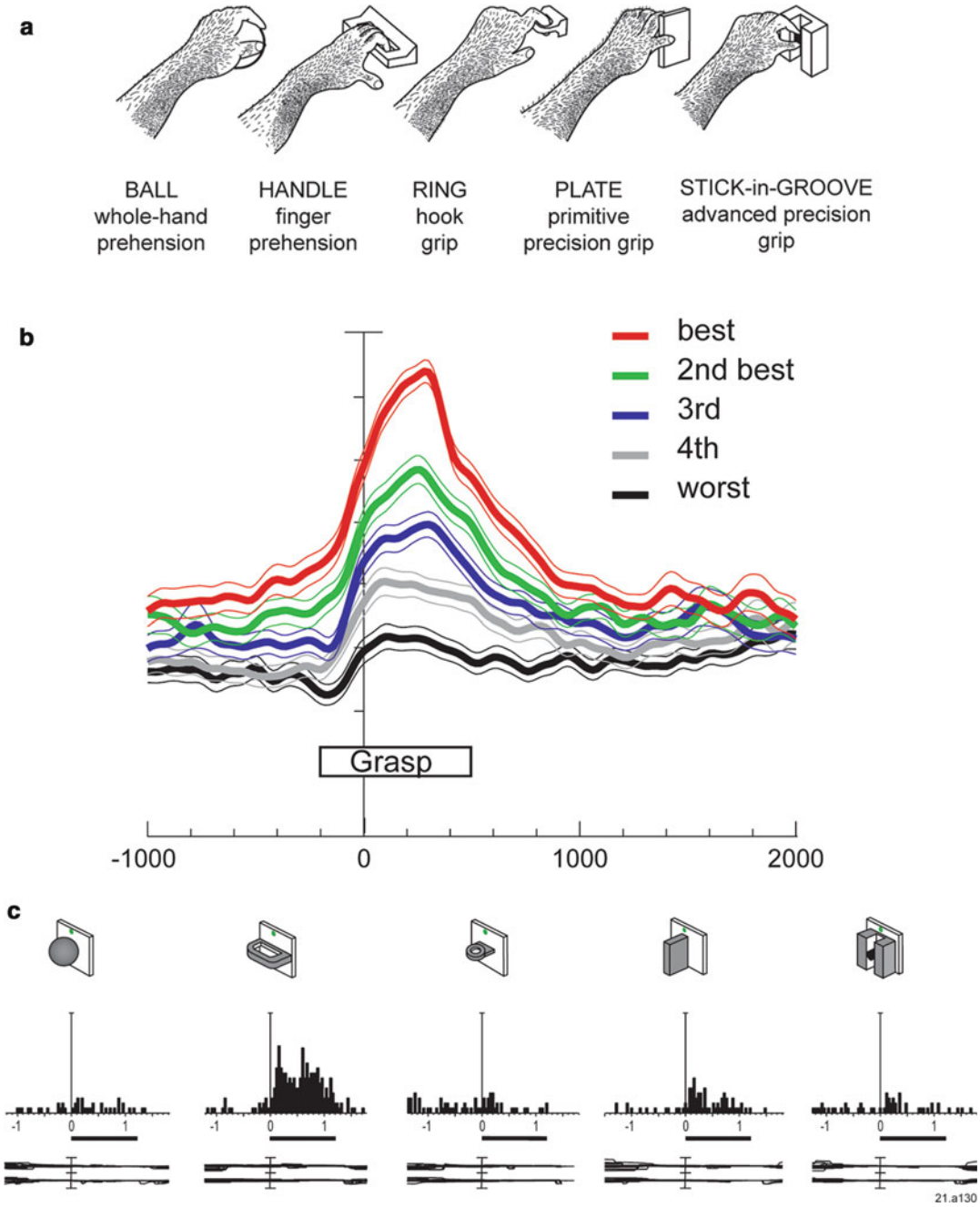
The first quantitative experiment was made when the monkey performed stereotyped movements to grasp a handle that could have different orientations within a instructed-delay grasping task in darkness, so to test neurons with different wrist orientations (Fig. 6b, Fattori et al. 2017). The majority of the tested cells (54%) turned out to be sensitive to the wrist orientation. An example of a V6A cell tested for grasping in light – a

phenomenon recently investigated (Breveglieri et al. 2016) – is shown in Fig. 6c. This cell was tested for four wrist orientations and fired vigorously as soon as the movement started (alignment time) and suddenly decreased the discharge once the handle was grasped. The neural discharge depended on the orientation of the handle (and therefore of the wrist orientation), strongly discharging when the handle was oriented horizontally (hand pronated) and vertically (hand half pronated), and weakly when it was oriented at 135° (halfway half pronated/pronated). As this cell was tested in light, it can be suggested that the vision of the hand-handle interaction, in given wrist orientations, strongly activated the cell.

The study of the involvement of V6A in encoding distal components of prehension continued by testing its neurons when the animals in darkness performed grasps requiring different grip types (Fattori et al. 2017): about 50% of tested cells displayed grip selectivity. Their population discharge, when five different grips are used (Fig. 7a), is shown in Fig. 7b. The activity of each grasping neuron for each of the five tested grips was ranked in descending order to obtain the population response for the best grip, the second best one, and so on, up to the fifth (worst) grip. The plot shows a clear distinction among the activations during the execution of grasping actions (Grasp in the figure). The fact that the curves are already separated before grasping suggests that the neurons began to code the impending reach-to-grasp movement well before the occurrence of the movement itself. The absence of visual information and the occurrence

**Parieto-occipital Sulcus (POS), Fig. 6** (continued) (blue). This cell was modulated during all these phases of the prehension action. Scale bar, 500 ms (Modified from Fattori et al. 2004) (b) Stereotyped grasping test. The monkey was in front of a panel containing an handle and pressed a button close to its chest. Then, a green fixation point was illuminated on the panel and the monkey was instructed to fixate it. Then, when the color of the fixation point changed to red, the monkey had to reach and grasp the handle (Mov) on the panel until the fixation point was illuminated. Then, the monkey came back to the starting

position. (c) Example V6A cell tested with this task in light when the handle was presented with four orientations, requiring four different wrist orientations. This cell shows a strong discharge when the handle is grasped, especially when the wrist is pronated, and half pronated. Scale bar: 85 Spikes/s. Other conventions as in Fig. 3. These demonstrations of modulations in V6A from distal components of prehension were obtained when the grasping was performed in the light, so when the motor-related signals may be added to the visual ones to monitor prehension



**Parieto-occipital Sulcus (POS), Fig. 7** Grip modulations in area V6A. (a) Drawing (derived from videoframes) of the five objects used by the monkey to grasp objects of different shapes. The orientation of the objects was chosen so that wrist orientation was similar in all cases. The different object to be grasped required different hand pre-shaping for the accomplishment of the grip: the ball with the whole hand (leftmost drawing), the handle with fingers only, the ring with the index finger only (hook grip), the

plate with a primitive precision grip with fingers/thumb opposition, and the stick-in-groove with an advanced precision grip with precise index-finger/thumb opposition (rightmost drawing). (b) Grip discrimination in V6A. Population neuronal activity, expressed as averaged normalized Spike density functions (SDFs, *thick lines*) with variability bands (Standard error of the mean; *light lines*), constructed by ranking the response of each neuron for each grip type in descending order according to the

of these modulations even before action execution point to a corollary discharge hypothesis.

Besides being modulated during grasping preparation and execution (grip tuning), V6A cells display also object tuning. In fact, 25% of V6A cells discharges differently depending on the object observed without a subsequent grasping (Fattori et al. 2017). An example of one of these cells is shown in Fig. 7c. This neuron was highly selective for the object, because its discharge was maximal during the presentation of the handle and very weak during the presentation of all the remaining objects. It has been suggested that the analysis of visual features of the object performed by V6A cells may serve to analyze object affordances, which are the potential actions that we can perform on each object. In fact, V6A cells are modulated by the contextual grasping information, that is, the grip type that is evoked by the visual feature of an object (Fattori et al. 2017).

The interplay between visual information on the object and on grasping and motor-related information during grip was studied only recently. V6A cells were tested when monkeys grasped a handle with different orientations, requiring different wrist orientations for grasping, in the dark and in the light (Breveglieri et al. 2016) or grasping objects of different shapes, requiring different grip types (Breveglieri et al. 2017). It was found that the activity of about 80% of V6A cells is influenced by visual information. An example of a cell containing both visual and motor-related signals for grasp is shown in Fig. 8. This cell was strongly activated during preparation and execution of grasping both in light and in dark

conditions, although it discharged more in the light. The cell showed a clear grip sensitivity, discharging more strongly for the preparation and execution of finger prehension, whole-hand prehension, and primitive precision grips (2nd, 3rd, and 4th panels). Like this cell, the majority of V6A neurons incorporate both visual and somatosensory/motor efferent copy signals and integrate them in guiding prehension.

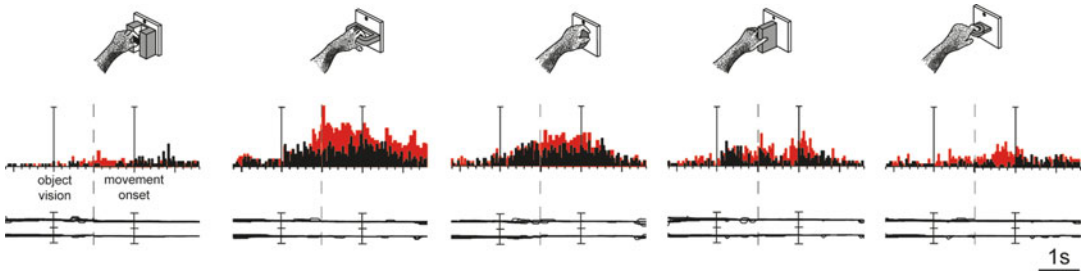
The grasp-related properties of V6A were recently confirmed by the results of decoding analyses that showed that V6A signals could be used to reliably decode objects and grips (Filippini et al. 2017). This is a further confirmation of the involvement of V6A in high-level elaboration of visual and somatosensory information for guiding hand actions. Moreover, these results add area V6A in the list of brain regions that can be used as a source of signals that can drive brain machine interfaces such as robotic arms/hands capable to grasp objects.

## Conclusion

Functional features of neurons of areas located inside the POs show a caudo-rostral trend from the simplest visual properties posteriorly (area V2) to the multisensory and complex motor-related ones anteriorly (area V6A). While areas V2-V3 are typical extrastriate visual areas, areas V6 and V6A show a higher degree of complexity. Area V6 analyses motion information for the purpose of recognizing real motion of objects and self-motion derived from visual signals.

**Parieto-occipital Sulcus (POS), Fig. 7** (continued) intensity of the response elicited during the movement (Grasp). Neuronal activities are aligned with the onset of grasping movement. V6A grasp-related neurons are able to discriminate the different types of grips, as demonstrated by the huge separation between the *red* and *black curves*. It must be noted that grasps were performed in the dark, so the observed modulations have to be ascribed to somatosensory/motor-related signals and not to visual ones. **(c)** Object selectivity during object observation. *Top*, objects tested. *Bottom*, one example V6A neuron selective for objects. Below each display is a record of

horizontal (*upper trace*) and vertical components (*lower trace*) of eye movements. Neural activity and eye traces are aligned (long *vertical line*) on the onset of the object illumination. This cell is selective for objects, preferring the vision of the handle and being mostly unresponsive to all the remaining 4 objects. *Black bars* below PSTH indicate the time of object illumination. *Vertical scale bars* on histograms: 50 spikes/s. Eye traces: 60°/division. Other conventions as in Fig. 3. Object selectivity and grasping selectivity are phenomena demonstrated for V6A, so far unique at this regard in the superior parietal cortex



**Parieto-occipital Sulcus (POS), Fig. 8** Example of the discharge of a V6A grasping neuron to five different grips and to 2 visual backgrounds. *Top*: type of handgrips. *Middle*: PSTHs. Horizontal scale: 200 ms/div. Vertical scale bar on histogram: 60 spikes/s; eye traces: 60°/division. Data collected in the dark are depicted in *black*, those collected in the light are in *red*. *Bottom*: record of horizontal (*upper* trace) and vertical components (*lower* trace) of eye movements, shown with the same alignment as the neural activity. The activity of cells in each plot was

aligned twice, on fixation onset and on arm movement onset (2 continuous vertical lines), with a dashed vertical line indicating the interruption of the trials to obtain the double alignment. The cell contains a grasp-related response influenced by the type of grip and by the presence of visual input. Neurons like this demonstrate the interaction of visual information and of hand movement signals occurring in the same V6A single cell. Modified from Breveglieri et al. 2017. Other conventions as in Fig. 3

Area V6A contains all the neural apparatus to monitor prehension actions. Specifically, V6A is modulated by prehension from object presentation up to action preparation and execution, with an evolution indicating that V6A processes vision for action (Fattori et al. 2017). Recent works suggest that arm movement sensitivity is higher than visual-related sensitivity and this may suggest that despite its name starting with the letter “V,” V6A should not be counted among the extrastriate visual areas, but among the posterior parietal grasping areas.

## Cross-References

- [Dorsal Pathway](#)
- [Dorsomedial Area](#)
- [Lateral Intraparietal Region \(LIP\)](#)
- [Neuron](#)
- [Occipital Lobe](#)
- [Parietal Lobe](#)

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## Parkinson's Disease

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## Synonyms

Paralysis agitans; Parkinsonism; PD; Shaking palsy

## Definition

A progressive and degenerative neurological disorder of movement marked by tremors, postural instability, rigidity, and slow movements.

## Introduction

Parkinson's disease is a chronic and relentlessly progressive disease marked by tremors, muscular rigidity, slow movement, and postural instability. Psychiatric problems, such as depression, dementia, and psychosis, may be comorbid to the illness or to a side effect of treatment. Parkinson's is idiopathic and there is no cure, though pharmacological therapy and potentially brain surgery may lessen symptoms (Binder et al. 2009).

## Symptomatology

Parkinson's is recognized for its classic triad of motor symptoms: a resting tremor, rigidity, and bradykinesia (slow movement). The tremors tend to start in the hands, feet, or jaw at 4–6 Hz, start

on one side of the body, but eventually progresses to encompass the whole frame. Tremors in the hands are notable for what is called a “pill-rolling tremor”, a rhythmic rubbing and shaking of the forefinger and thumb. Tremors are present at rest and dissipate with intentional movement; sometimes, they can be aggravated by stress. Muscle rigidity in swinging arms presents as short and jerky movements as opposing muscle groups fail to communicate properly and thus remain contracted. This results in stiffness and pain for the patient. Facial rigidity can inhibit the communication of emotions and present as a taut, mask-like face. This triad of bradykinesia, muscle rigidity, and tremors makes daily activities such as dressing and brushing one's teeth very difficult for the patient. In advanced PD, postural instability and issues with balance can lead to frequent falls. Moreover, the progression of Parkinson's leads to the worsening of motor symptoms over time. As patients attempt to keep their balance in later stages, they may present with festination, or the hurrying of steps as they propel themselves forward in walking. Freezing, or the sudden cessation of movement, may also occur in later stages. Though Parkinson's is primarily considered a disorder of movement, other non-movement symptoms can present themselves and do often complicate the lives of PD patients. Autonomic dysfunction, a decrease in olfaction and taste, mood disorders, sleep disturbances, diminished elements of cognition, and a high risk to dementia in later stages have all been as issues in those with PD (Double and Finberg 2016).

Parkinson's Disease Dementia (PDD) indicates a decline of cognitive functioning that develops over 1 year post-diagnosis, and may be related to Lewy bodies dementia. It is estimated that some 40% of Parkinson's patients struggle with dementia. Risk factors for developing this dementia include advanced age, a later disease onset, a history of smoking, a history of depression, and a poor response to L-Dopa. Deficits in executive functioning and bradyphrenia, or a slowness of thought processes, have both been noted as prominent issues (Kraybill and Suchy 2011).

## Etiology

The etiology, or cause, of Parkinson's disease is very complex and involves multiple factors that may differ widely across patients. Environmental factors have long been suspected, and at one point, viral infection was hypothesized as a cause of idiopathic PD due to a similarity of symptoms involving viral encephalitis. Though the etiology of Parkinson's as related to a number of diverse environmental risk factors remains controversial, a convincing link to a family history of Parkinson's has been demonstrated, suggesting a possible genetic component. Parkinson's disease as a result of one of six genetic mutations has been seen to develop, yet the treatment for genetic Parkinson's is the same as the treatment for common idiopathic Parkinson's. Nevertheless, studies of genetically-transferred Parkinson's patients and their affected family members have provided considerable insight into the neural mechanisms behind the idiopathic form of the disease (Double and Finberg 2016).

## Pathology

Parkinson's neurological presentation is rooted in the dysfunction of the basal ganglia and cerebellum. Subcortical changes, such as the slow loss of dopaminergic neurons in the substantia nigra region of the basal ganglia, are more notable first, followed by cortical changes later in the disease process, which supports the evidence that demonstrates motor symptoms arising earlier than other symptoms. A deposition of Lewy bodies in both subcortical and brainstem areas, such as the substantia nigra, locus ceruleus, nucleus basalis of Meynert, dorsal medial nucleus of the vagus nerve, and hypothalamus, has been recorded in PD patients, though Lewy bodies are certainly not a unique feature in Parkinson's. Alpha-synuclein accumulation in the basal forebrain and ascending pathways, leading to changes in acetylcholine, has been implicated in the cognitive changes in Parkinson's and the onset of Parkinson's dementia (Cook 2017).

## Prevalence

The prevalence of Parkinson's approaches 1% of the total population by age 65, and 2–3% by age 80. Early-onset Parkinson's, diagnosed before age 40, accounts for around 10% of all Parkinson's cases, a statistic that often goes overlooked (Baron 2011). The gender split is roughly 1:1.5, female to male, and as suggested above, age is a major risk factor. Smoking tobacco has been shown to reduce the risk of developing PD (Schwarz and Storch 2009).

## Assessment

A clinical diagnosis of Parkinson's is made after an examination of patient history plus an important physical and neurological battery, conducted by a neurologist, that involves tests for retropulsion and gait monitoring among other diverse measures. Making a differential diagnosis involves weeding out some of the following illnesses, with their distinguishing features in parentheses: cortical basal degeneration (often with unilateral apraxia and reflex myoclonus), multiple system atrophy (prominent ataxia and autonomic disturbances), progressive supranuclear palsy (issues with vertical eye movement), Wilson's disease (dystonia and liver disease), and Huntington's disease (choreiform movements and family history). A diagnosis of Parkinson's becomes increasingly more probable especially after positive response to levodopa treatment (Cook 2017).

Some presentations of parkinsonism may not be caused by Parkinson's itself, but rather by a psychogenic or pharmacological stimulus. Parkinsonism may stem from a conversion or somatoform disorder or be caused by neuroleptic (dopamine antagonist) therapy used to treat psychotic disorders. However, the Parkinson-like presentation of those who ingest neuroleptics over a long period of time is often bilateral as opposed to the asymmetrical presentation of Parkinson's. Diagnosis of the disease and the gauging of severity are facilitated by one of two standard rating scales: the modified Hoehn and

Yahr Scale or the Unified Parkinson's Disease Rating Scale (UPDRS). Post-mortem examination for Parkinson's tends to confirm the diagnosis at a rate of about 80% of those diagnosed with Parkinson's in life (Cook 2017).

## Treatment

Treatments for Parkinson's disease include a wide range of pharmacological therapies, as well as surgery.

### L-Dopa

Levodopa is the amino acid precursor to dopamine that is synthesized by many plants and animals, including humans. Whereas the neurotransmitter dopamine cannot cross the blood-brain barrier, L-Dopa can. It was first implemented in the 1960s and has remained the first-line treatment for PD to this day. L-Dopa works to increase the levels of dopamine in the surviving nigrostriatal neurons of the basal ganglia. It cannot cure PD, yet it can mitigate motor symptoms in the mild to moderate stages of the disease. The short half-life of L-Dopa necessitates that the patient take regular, evenly-spaced doses throughout the day. Historically, L-Dopa was prescribed orally on its own, with only minimal transference across the blood-brain barrier, thus necessitating very high doses and causing unpleasant side effects like vomiting and nausea. Today, either carbidopa or benserazide, two inhibitors of DOPA decarboxylase, are combined with levodopa to increase its absorption into the brain and reduce these side effects. After some years of symptom reduction with levodopa treatment, the disease progresses and the dosage must be increased to compensate for a continual death of dopaminergic neurons. Elevated levodopa doses are also associated with such side effects as constipation, hypotension, lethargy, hallucinations, and confusion. Dyskinesia, involuntary twisting movements of the arms, legs, and trunk, can result after long-term levodopa therapy. Duodopa pumps that continually pump levodopa into the body have been implanted in recent years to some success (Double and Finberg 2016).

### Glutamate Receptor Antagonists

Glutamate receptor antagonists may be beneficial in the treatment of LID, the dyskinesia associated with levodopa therapy, yet not without a number of pronounced side effects. Nevertheless, with the wide diversity in glutamate subtypes and their distribution across the brain, researchers have not stopped the search for new and selective drug possibilities on this front. The main drug of this class currently in use to treat PD is amantadine, an antiviral with anti-glutamatergic properties (Double and Finberg 2016).

### Dopamine Agonists

In order to alleviate motor symptoms in the later stages of the disease and compensate for the lack of surviving dopaminergic neurons, dopamine agonists are used to directly stimulate the dopamine receptors themselves. Dopamine agonists work by stimulating D2 and also D1 receptors and are primarily taken orally. The side effects associated with dopamine agonists are virtually analogous to those associated with levodopa, though levodopa is considered more effective at treating symptoms than any dopamine agonist. However, elevated doses of L-Dopa combined with long-term treatment have been associated with increased cell death due to the presence of uncontrolled free radicals. To combat this phenomenon, dopamine agonists and levodopa are sometimes given in tandem in order to reduce the dosage of levodopa and transfer some of that burden onto the stimulation of dopamine receptors by the dopamine agonists (Double and Finberg 2016).

### COMT Inhibitors

Catechol-O-methyl Transferase, or COMT, is a widespread enzyme that serves to break down dopamine, and COMT inhibitors impede this breakdown as a second-line medication for the treatment of Parkinson's (Binder et al. 2009; Double and Finberg 2016). Tolcapone and entacapone are the two drugs available of this type. Entacapone inhibits COMT only peripherally and thus does not cross the blood-brain barrier, unlike tolcapone. The inhibition of COMT in the periphery reduces the metabolism of L-Dopa

there, which augments the availability of the drug to the brain. Though tolcapone can cross the barrier and improve the brain's response to L-Dopa by reducing the metabolism to dopamine, there is a significant risk of toxicity to the liver that limits the non-clinical diffusion of this medication. Thus, a common combination of medications for the treatment of Parkinson's is entacapone, L-Dopa, and a previously-mentioned peripheral inhibitor of AAAD, like carbidopa (Double and Finberg 2016).

### Deep Brain Stimulation

Deep Brain Stimulation (DBS) involves the implanting of electrodes to stimulate the important areas of the basal ganglia that are most affected by Parkinson's. Detailed electrophysiological studies of the brain's circuitry and interaction between the pallidum, thalamus, and the motor cortex allowed for the development of this technology, as it became apparent that high-rate electrical stimulation could correct the hallmark motor symptoms of the disease. With the proper equipment, the procedure can be performed in any department of neurosurgery. The implanted electrodes connect to a battery-operated stimulator under the patient's skin, which can be controlled by the patient with a remote, much like a pacemaker for the heart. The procedure is best-suited for those who suffer from an early onset, who are in an advanced stage of the disease, or who do not respond satisfactorily to L-Dopa, and can tolerate the stress of neurosurgery. There are great improvements for many, but the complications can include hardware difficulties and some psychiatric and neurological side effects (Double and Finberg 2016).

### Future Directions in Treatment

Attempts have been made to introduce human embryonic dopamine neurons to be implanted into the Parkinson's brain as a form of treatment. Results in this area have been frustrated by ethical concerns and a lack of satisfactory clinical trials, with side effects that include dyskinesia. Nonetheless, developments in the ideas of stem-cell research continue to be made (Double and Finberg 2016).

Gene therapy, by way of a gene transfer that increases dopamine synthesis or protects the already-existing dopaminergic cells, is a major new frontier in the fight against Parkinson's. This therapy avoids the inherent problem of L-Dopa needing existing presynaptic neurons to encourage dopamine stimulation and involves using a viral vector to introduce new genes into relevant areas of the brain. Early clinical trials are promising and import some benefits to patients. Alternatively, neurotrophic factors such as glial cell line-derived neurotrophic factor (GDNF) can be delivered through genes to bolster dying neurons, yet concerns about safety have led to cautious progress (Double and Finberg 2016).

## Conclusion

Parkinson's disease is a debilitating and pervasive neurodegenerative condition and, while pharmacological and surgical treatment can slow progress, there is no cure. The restoration and protection of neurons affected is a primary target of investigation, and developing a response to the disease pre-clinically, before symptoms occur, is of particular attention to researchers.

## Cross-References

- [Dopamine Receptor](#)
- [Locomotion](#)
- [Neuron](#)
- [Neurotransmitters](#)

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## Parkinsonism

- [Parkinson's Disease](#)

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## Parous

- [Multiparous](#)

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## Parrot Cognition

- [Alex the Parrot](#)

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## Parrot Locomotion

- [Psittaciformes Locomotion](#)

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## Parsimony

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## Synonyms

- [Frugality](#); [Prudence](#); [Thrift](#)



## Definition

Parsimony is a principle used as a means of keeping explanations as simple as possible by providing the simplest of explanations to describe an observation or an understanding.

## Introduction

Behavior is the way in which a living organism reacts to a particular situation. In psychology, behavior is thought of as an organism's external reactions to its environmental stimuli. The analysis of behavior is a science based on the foundations and principles of behaviorism. It can be said that behavior is that particular response of an organism which reflects the kind of stimuli received from the environment. This behavior may be modified by using either positive or negative or manipulating reinforcements from the organism's environment or according to self-directed intentions or impulses. Human behavior is more complex than animal. Society and culture plays a vital role in shaping human behavior although it is difficult to quantify the extent to which it influences behavior.

Behaviorism is a learning theory that only focuses on objectively observable behaviors and discounts any independent activities of the mind. Behavior theorists define learning as nothing more than the acquisition of new behavior based on environmental conditions (Philips and Soltis 1998). So here, we will discuss the role of the most established principle of parsimony in making conclusion regarding the causes of behavioral and cognitive/learning modifications.

Behaviorists identified conditioning as a universal learning process in different experimental efforts and found two different types of conditioning; each yields a different behavioral pattern. The first one is classical conditioning in which a natural reflex responds to a stimulus. Ivan Pavlov (1890) discovered it during his famous experiment with dogs. Every time Pavlov fed a dog, he rang a bell. Pavlov then rang the bell without feeding the dog, and the dog salivated at the sound of the bell. Pavlov had conditioned the

dog to respond to the bell by salivating. Pavlov's experiment served as the one of the cornerstones of behaviorism (Powell et al. 2001). The other one is behavioral or operant conditioning sometimes also called as instrumental conditioning where a response to a stimulus reinforces or operates through reward for good behavior and punishment for bad behavior.

An eminent behaviorist, B.F. Skinner, in 1977 used reinforcement techniques to teach pigeons to dance and bowl a ball in a mini-alley. Therefore, operant conditioning is a simple feedback system where reinforcement follows the response to a stimulus and then the response becomes more probable in the future (Epstein and Medalie 1983). Thus, behaviorism is based upon the idea that all behaviors are acquired through conditioning, via interaction with the environment. For example, in behavioral psychology, by applying the basic principle of conditioning, people who suffer from psychological disorders are retrained, while cognitive psychology deals with the acquisition, processing, and storing of information in the mind. These mental functions include learning, attention, memory, reasoning, conceptual development, language acquisition, perception, and decision-making.

According to Division 25 of the American Psychological Association, analysis of behavior can be done in three different ways:

- Firstly, through the experimental investigation of behavior, i.e., by manipulating the environment under control conditions
- Secondly, through applied behavior analysis (ABA), i.e., by applying the learning behavior principles to real-world situations to change the behavior
- Finally, through the conceptual analysis of behavior which addresses the philosophical, historical, theoretical, and methodological issues in behavior analysis

All of these three areas of behavioral analysis implicate the fundamental principles, theories, and concepts, which are already well illustrated in the area of animal cognition and behavior. In each area of analysis, to test the economy of

explanations involved in the analysis, parsimony plays its pivotal role instantaneously.

## What Is Parsimony?

Parsimony is the well-established basic principle in the study of animal behavior, and in science, this principle is applied as discovery tool that guides researcher for the development of scientific models (Epstein 1984). The law of parsimony is introductory to all scientific disciplines and philosophy and in other applications that use logic (Anderson 1978). Parsimony is frequently equated with Occam's razor, the law which stresses choosing simpler explanations if that simpler explanation fits in totality to the collected data. Therefore, the term parsimonious means the simplest explanation or theory with the least assumptions and variables but with the greatest explanatory power.

Further, the law of parsimony is accepted as an important criterion in science for judging the merits of a theory or an explanation, but it is not the only one. A theory, which is parsimonious, need not be "right" – that is to say, it may not be the most effective or useful description of the body of facts for which it is said to account (Sober and Lewontin 1982).

## Examples

If one finds that, while exploring the causal factors that generate phenomenon Z, causal factor A accounts for 30% of Z, causal factor B accounts for 50%, and causal factor C accounts for 20%, we can conclude that  $Z = A + B + C$  and not worry over additional causal factors so long as the observed evidence is fully accounted for. To elucidate this idea, let's take one more concrete example. Suppose Meera is trying to understand why her pencil falls to the ground when she lets it go from her hand. After some basic research, she concludes that Newton's laws of gravity can fully explain this phenomenon of interest. Meera's friend Danny, however, suggests that while the

laws of gravity are responsible for some of the pencil falling to the ground, there also exist millions of invisible leprechauns that catch falling objects and guide them toward the ground. Danny and Meera both provide explanations of the same natural phenomenon, but Danny's explanation adds unnecessary causal factors. In addition, Danny's explanation is also very difficult to falsify, even though there is no evidence to support it. One hundred percent of Z can be accounted for by A (gravity), thus adding B (invisible leprechauns) adds nothing to our understanding of why the pencil falls to the ground. Because it adds nothing, parsimony suggests we drop it from our equation (Benjamin 2018).

Hence, parsimony is economy in the use of explanation in conformity with Occam's razor. Thus, scientifically, parsimony dictates that any example of animal behavior should be interpreted at its simplest and at the most immediate level. It can be done by adding the smallest number of unsupported assumptions, by postulating the existence of the fewest entities and finally by citing the fewest unobservable constructs the simplest explanation

The law of parsimony is also termed as principle of economy or principle of parsimony. The principle of parsimony argues that the simplest of competing explanations is the one that is most likely to be correct. Moreover, this simplest explanation is not considered an undeniable means of deriving the logic or scientific results but affects the importance of simplifying explanations.

The first statement about this principle is credited to a fourteenth-century English scholastic and philosopher William of Ockham. He proposed a rule of logic that is called "Ockham's razor" (Sober 1994).

By illustrating, an example of pet's responsive behavior in specific circumstances could be better explained by behaviorists with the principle of parsimony (Thorndike 1911).

For example whenever a person goes out of town leaves her dog, Mason, with a close friend. Mason always defecates overnight in one particular spot in friend's house. Mason will

occasionally do this at her home, but not on a regular basis, and the dog is quite familiar with both friend's and her home. She could not figure out any possible reason why Mason would be doing this and therefore concluded that it had to be because Mason was mad at her for leaving him. The reason behind this common tendency to jump on anthropomorphic explanations as the most likely reason for a pet's behavior could be because they believe that these are the simplest explanation for their pets' behaviors while in the point of behaviorists view it is the most complex one.

What might be some simpler explanations for Mason's behavior? Mason's schedule might be different in friend's home, causing his patterns of elimination to shift. Her friend might not be in the habit of giving Mason a last potty break right before bed, or perhaps Sarah is giving him more treats than he usually gets at home. Mason might be afraid to go outside at friend's place because of even one experience with a startling noise. Mason might be a bit anxious away from owner, even though Sarah is familiar to him. Perhaps, Mason doesn't like the texture of what is available for elimination in the yard (Cherry 2018).

Therefore, the principle of parsimony emphasized that the simplest explanations are more straightforward than the other higher thought processes, which could be thought for nastiness to be the motivation for Mason's defecation.

Debate on nature vs. nurture is one of the oldest philosophical issues within psychology. However, while we discuss about parsimony, nature versus nurture argument empowers the explanation of parsimony principle. The debate starts with certain basic question on behavior like the following: Do genetic or environmental factors have a greater influence on our behavior? Do inherited characters or life experiences play a greater role in shaping our personality?

To get answers to these queries, one must understand the meaning of nature and nurture. Nature refers to all of the genes and hereditary factors, while nurture refers to all the environmental variables including our childhood experiences, how we raised our social relationships, and our surrounding culture. It focuses on the relative

contributions of genetic inheritance and environmental factors in human evolution (Breed and Sanchez 2010).

Earlier, a very one-sided approach suggested nature was more important which played pivotal role in the development, while other side suggested that nurture was more significant. Certain philosophers like Plato and Descartes in 2001 suggested that certain things are inborn that they occur naturally regardless of environmental influences, while according to John Locke everything that we are and all of our knowledge are determined by our experience. Theorist John B. Watson in 1915 believed that people could be trained to do and become anything regardless of their genetic background.

An instance of nature versus nurture argument could be that if a man abuses his wife and kids, is it because he was born with violent tendencies or is it something he learned by observing his own parent's behavior? Another example is that all children are born with an instinctive mental capacity that allows them to learn and produce language but the behavior of a child is influenced by parenting styles and by learning through observation and reinforcement. While considering the views of both sides, the simplest and meaningful explanation of this argument is that genetic factors and environmental factors do play their role together and affect each other in a significant way, and researchers are looking forward for the factors and processes that influence their interactions. The reality is that there is no simple way to unravel the intermingled interactions of genetic factors and environmental factors such as social experiences and overall culture. The genetic factors interact with one another and modulate the influences of environmental factors.

As one school of thought, all differences between men and women are believed to be caused by societal and patriarchal forces. Again, societal influences on behavior are evident, and varying cultural gender labels have had profound and often negative impacts (particularly for women) on individuals throughout history. However, to suggest that all gender differences are the result of societal pressures lacks both parsimony and is

factually wrong. What's more, it offers the potential to be a useless and unproductive interpretation to adopt in many situations. Additionally, for example, the defensive behavior of women avoiding driving in risky areas can be explained by the fact that males of nearly all species are more likely to engage in risky behaviors in all facets of life. There would no need to change what is objectively a very smart and rational behavioral decision. The thought arguing about societal factors that they claim cause gender differences in this specific instance is simply wrong and reflects poorly on the general validity of the feminist movement and the important issues the movement seeks to address. Thus, viewing through the lens of law of parsimony, it must be suggested that the gender-specific protective and defensive behavior of women is the main behavioral cause for this and not any other (Benjamin 2018).

There are occasions where one can predict with confidence that a parsimonious theory is likely to be wrong. For example, Anderson in 1978, a cognitive psychologist, has noted that the most "parsimonious" computer program will probably not be the best one to represent cognition. There is no criterion of parsimony in evolution; redundant and supernumerary organs and mechanisms abound in nature. Further, there is no reason to believe that human cognition – or its counterpart in the real world, the nervous system – has been spared nature's disinterest.

## Conclusion

The principle is itself, ironically, an assertion, one that pervades science but that remains, for the most part, unexamined by scientists themselves. Since it is a criterion by which a theory is judged to be better or worse than another, it may have more value (Walsh 1979).

The principle of parsimony may be nothing more than an instantiation of the principle of "least effort," and hence we might interpret Mach's "least possible expenditure of thought" literally (Walsh 1979).

The argument in above examples is about gender differences where parsimony must be

considered in the reasoning. It is also suggested that it should not add causal factors that add nothing to explain the phenomena, especially if the behavior can be fully explained in their absence.

## Cross-References

- [Behaviorism](#)
- [Bioinformatics](#)
- [Ockham's Razor](#)
- [Phylogeny](#)

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## Parsing

### ► [Chunking](#)

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## Parthenogenesis

### ► [Asexual Reproduction](#)

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## Partial Reinforcement Extinction Effect

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## Synonyms

[Intermittent reinforcement](#); [Paradoxical extinction effects](#); [Resistance to extinction](#)

## Definition

The use of partial (i.e., intermittent) reinforcement tends to strengthen both the target behavior and its persistence in the absence of reinforcement. The result is that behaviors that produce only periodic reinforcement tend to be more resistant to extinction than behaviors that have been reinforced continuously.

## Introduction

Partial reinforcement (PR) means responses are only reinforced periodically; continuous reinforcement (CRF) means that every response is reinforced. There are a variety of PR schedules that have different effects on response patterns (see ► [“Instrumental Conditioning”](#)). The partial reinforcement effect (PREE) occurs when operant responses that have been reinforced

only occasionally become resistant to extinction compared with behaviors that have been reinforced continuously. This effect is considered paradoxical since intuition would suggest that behaviors that are reinforced less often should be easier to extinguish.

In the real world, intermittent reinforcement is associated with very persistent responding in extinction. Gambling is the classic example of unpredictable PR and resistance to extinction. Chronic gamblers only receive “payouts” periodically and they may not be particularly large. But the gambler persists despite long stretches with no reinforcement at all. This phenomenon allows gambling houses to bias the profits in their favor. Small to medium payouts in the short run are sufficient to maintain the persistent risk-taking behavior that results in long-term profits for the gambling house.

Several theoretical explanations have been offered and tested to determine the underlying mechanism that produces the PREE.

## The Discrimination Hypothesis

One possible cause of the PREE could be the difference in discriminability of the change in contingency from CRF or intermittent reinforcement to extinction. If a reinforcer follows every response in a one-to-one ratio, the shift to extinction would be very salient. The change in the response-reinforcer contingency would be easily and rapidly detected. Frustrated by the sudden absence of reinforcement, the subject gives up and stops responding. On the other hand, PR is characterized by non-reinforcement on many trials. Only occasionally does a response produce a reinforcer. During training, the subject gradually learns to expect reinforcement less frequently and less reliably. When the contingency shifts away from PR to extinction, it is less discriminable, more difficult to detect, and, as a result, extinction proceeds more slowly.

Jenkins (1962) and Theios (1962) tested the discrimination hypothesis using different species (domestic pigeons, *Columba livia*, and rats, *Rattus norvegicus*, respectively). In both studies,



one group of subjects was trained to respond using CRF. A second group of subjects was initially trained using PR and then moved to a CRF schedule. Once both groups were responding reliably under CRF, an extinction schedule was imposed. Jenkins and Theios reasoned that if the ability to discriminate the change to extinction determines the rate of extinction, responding for both groups should decline at the same rate. Furthermore, extinction should be relatively rapid because the discrimination is an easy one. In both studies, those animals initially trained with PR showed significantly slower extinction than those with CRF experience only. Discriminability differences in the shift from CRF or PR to extinction were not sufficient to explain the PREE phenomenon.

### The Frustration Theory

The frustration hypothesis of PR (Amsel 1958, 1962, 1967, 1992) suggests that extinction is generally the result of emotional frustration that arises when reinforcement is terminated. It proposes that the individual who experiences PR learns to deal with the frustration of non-reinforcement during training. Typically, intermittent schedules are thinned gradually; inter-reinforcement intervals are initially short and gradually lengthen over time. Learners working on a CRF schedule only (e.g., lever pressing or keypecking) do not have the opportunity to learn about non-reinforcement. They become easily frustrated when the reinforcer is omitted. This frustration usually results in a decrease or complete cessation in responding, perhaps due in part to the learner engaging in exploratory or alternative foraging-related behavior (Adelman and Maatsch 1956). PR learners experience the same frustration early in training, but they are quickly moved to and maintained on increasingly leaner intermittent reinforcement schedules. These participants learn that some trials are followed by reinforcement while others are not. Every new trial has a certain probability of reinforcement or not, but reinforcement eventually does occur. When a

reinforcer is delivered, it strengthens both the response itself and the persistence of that response in the absence of reinforcement. As a result, subjects learn to replace the initial frustration with response persistence until reinforcement does occur.

Recently, frustration theory and its effects on persistence during appetitive extinction have been applied to alcohol self-medication during extinction. Manzo et al. (2015) tested rats in a discrete trials runway study. Rats ran for either continuous (CRF) or partial reinforcement (PR) at the end of the runway. After completing the runway test, they were returned to home cages where they freely chose between two water bottles: water/water or water/2% ethanol solution. At baseline, all of the rats showed no preference for ethanol over water. Following initial testing, trials were conducted in which food was removed from the end of the runway. Termination of food reinforcement in the runway (aka extinction) produces emotional frustration, according to Amsel's frustration theory. Rats trained using PR food schedules showed greater runway persistence than the CRF group. Furthermore, the CRF rats developed stronger preferences for the ethanol during extinction than the PR rats. These data suggest that the anxiety or frustration associated with extinction from a CRF schedule will likely produce more self-medicating behavior than a PR schedule would. Torres and Papini (2016) suggest that individuals who experience negative emotions like frustration may self-medicate. In a review of studies like the Manzo et al. (2015) study, they established connections between reward loss, frustration, and self-medication in animals. Such findings are clinically relevant for humans with drug and alcohol addictions.

### The Sequential Theory

The sequential theory (Capaldi 1967, 1971, 1994) proposed a more cognitive explanation for the PREE. It assumes that subjects remember whether or not their behavior has been reinforced

on recent trials. CRF learners recall only that their behavior has always produced reinforcement. They never develop a memory for what happens after non-reinforced trials (because they don't have those experiences). On the other hand, PR subjects remember the sequence of events that follow non-reinforced trials. The probability of reinforcement increases with each successive non-reinforced trial. As such, non-reinforcement becomes an excellent predictor that the next response has an increasingly higher probability of reinforcement and that the next response will pay off increases with each successive no-food trial. The sequential theory argues that it is this ability to remember reinforcement patterns and to be sensitive to reinforcement probabilities that leads to response persistence during extinction with PR subjects. CRF subjects never develop a memory for reinforcement following no-food trials. In this scenario, no-food trials predict nothing about future reinforcement for the CRF subjects. But for the PR learner, no-food trials are highly predictive of future reward.

Haddad et al. (1980) tested the sequential theory using both a CRF group and two partial reinforcement groups that differed only in the sequence of reinforced (R) and non-reinforced (N) trials (e.g., NRRR or RRRN). The sequential theory predicts the formation of an association between non-reinforced responses and subsequent reinforcement for continued responding. This association is not possible in the RRRN condition. Therefore, the sequential theory predicts greater resistance to extinction in the NRRR condition. The results were consistent with the theory's predictions for both the rats and the pigeons.

### **Momentum Theory of Extinction Resistance**

Nevin and Grace (2005) and Nevin et al. (2001) have offered an alternative theory of response persistence under conditions of extinction. Borrowing from momentum theory in physics that says that an object with greater momentum is

harder to stop than one with less momentum, Nevin and Grace suggest that a behavior with greater momentum will resist extinction more than a behavior with less momentum. Behavior momentum is directly related to rate of responding, but not to the rate of reinforcement. Put simply, there is an analogy between velocity in physics and response rate in behavior. A high rate of responding produces greater momentum, and will be more resistant to change. Other findings show that momentum is also sensitive to other factors, such as response-reinforcer relations (Lattal 1989), delayed reinforcement (Bell 1999), and preference (Bell & Williams 2002).

### **Other Paradoxical Extinction Effects**

Two other paradoxical extinction effects have been noted (Domjan 2015): the magnitude reinforcement extinction effect and the over-training extinction effect.

### **The Magnitude Reinforcement Extinction Effect (MREE)**

The magnitude reinforcement extinction effect (MREE) is paradoxical because larger reinforcers do not lead to greater resistance during extinction; rather the opposite appears to be true. Hulse (1958) and Wagner (1961) reported that the use of larger reinforcers led to faster extinction when compared with smaller reinforcers. Similar to Haddad et al. (1980), Capaldi and Lynch (1968) found that N-R transitions with large reinforcers produced greater resistance to extinction than similar N-R transitions with smaller rewards.

While initially seeming paradoxical, it can be easily understood when we think about it in human terms. If your old boss was in the habit of giving very large holiday bonuses, you are likely to respond badly when your new boss only sends out holiday cards. In fact, you might not work as hard or may even change jobs (aka complete extinction). But, for those workers whose bosses give small bonuses, the change to cards only is small and unlikely to result in a

decline in work effort or resignations. The same is true with animals: the degree of contrast in the change from “large to none” is likely to produce more rapid extinction in the first case and slower extinction than when the change is from “small to none.” Although paradoxical at first glance (e.g., larger is better and should make behavior stronger), it is easy to see how the opposite may be true in terms of resistance to extinction.

## The Overtraining Extinction Effect

Overtraining is characterized as a long period of extended training, typically with high levels of precision for the instrumental response. At first glance, it would appear that extended training should establish a strong resistance to extinction. For example, consider the dolphin trained extensively on a complex series of behaviors (e.g., a behavioral chain). Early in training, non-reinforcement will encourage response variability that can be used to shape the desired behavior and increase precision of the response (s). But as the animal masters the behavioral sequence, non-reinforced trials occur less frequently or not at all. Extended training consists of long bouts of behavioral responses with few errors and a virtually continuous pattern of reinforcement. One might predict that it would produce very strong behavior. But when faced with extinction following extensive training with nearly perfect precision, non-reinforcement is a huge contrast. A rapid decline in responding during extinction is not surprising. Because overtraining leads to greater expectation of reinforcement, sudden non-reinforcement produces greater frustration and much more rapid extinction of the behavior than is observed with shorter, less frequent training sessions (Ishida and Papini 1997; Senkowski 1978; Theios and Brelsford 1964; Thombaugh 1967; Pert and Gonzalez 1974).

## Limitations

The paradoxical effects of PR on extinction have been observed in many mammal species, including rats, gerbils, opossums, pigs, monkeys,

and humans (Papini 2003). Papini argues that response persistence during extinction after PR is specific to mammals. He offers neurological correlates of emotion, frustration, and aggression as mediating variables for the effect, specifically the activation of the hypothalamic-pituitary-adrenal axis. He argues that there is an absence of both the PREE and those same neurological structures in fish, amphibians, and reptiles. Behaviorally, resistance to extinction following PR is well established in birds, specifically in laboratory pigeons (*Columba livia*) (Jenkins 1962; Nevin and Grace 2005; Nevin et al. 2001; Roberts et al. 1963). Furthermore, Romero and colleagues have studied the same neural structures in avian species (Romero 2006; Romero and Wikelski 2006; Romero and Wingfield 2001). Thus far, the evidence of PREE effects appears to be restricted to mammals and birds only.

With the magnitude reinforcement extinction effect and the overtraining effect, inverse relations between the amounts of reward and overtraining and extinction also seem to be primarily localized to mammals. Attempts have been made to establish MREE effects of PR in non-mammals, including goldfish, *Carassius auratus* (Gonzalez et al. 1967a, b, 1972; Mackintosh 1971); painted turtles, *Chrysemys picta picta* (Pert and Gonzalez 1974); and terrestrial toads, *Bufo arenarum* (Muzio et al. 2006; Papini et al. 1995), but they do not show the same inverse relationship between reward magnitude and resistance to extinction. The same is not necessarily true for overtraining; overtraining extinction effects have been observed in mammals such as rats (Senkowski 1978; Theios and Brelsford 1964; Thombaugh 1967; Thombaugh and St. Jean 1972), but also in birds (Williams 1967) and in pond turtles (Ishida and Papini 1997; Pert and Gonzalez 1974), and in the octopus (Mackintosh and Mackintosh 1963).

## Cross-References

- [Extinction in Learning](#)
- [Instrumental Conditioning](#)

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## Parturition

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## Definition

Parturition is the process of expelling a fully formed fetus from the uterus of the mother after the gestational period (38 +/– weeks in human females) is completed (Mijovic and Olson 1996).

## Parturition: A Complex Interplay of Various Physiological Processes

Parturition is a complex physiological process, which needs the precise interaction of various physiological events between maternal and fetal side. It's a millennial old concept that a fetus is a master of its own destiny and can sense when the placenta is no longer able to provide the sufficient oxygen and nutritional need of the fetus. In response to this stress, fetus activates a series of mechanisms to initiate labor and parturition (Mijovic and Olson 1996). Main physiological events involved in parturition are ripening and dilation of cervix, myometrium contractility, rupture of fetal membranes, separation of placenta, and uterine involution (Olson et al. 1995). Three main mediators such as steroid hormones, paracrine molecules, and inflammatory molecules control these events (Kamel 2010).

## Control of Parturition by Hormones, Paracrine, and Inflammatory Molecules

### Progesterone and Estrogen

Progesterone and estrogen are the main hormones involved in the maintenance of pregnancy as well as parturition. Levels of these hormones remain unaffected, but the sensitivity of the myometrium changes during various stages of pregnancy



via changes in their receptor expression. At the time of parturition, there is a functional withdrawal of progesterone by increasing the progesterone receptor A expression (myometrial contraction) as compared to progesterone receptor B (myometrial relaxation). Progesterone withdrawal also positively regulates the expression of estrogen receptor  $\alpha$  (ER- $\alpha$ ) at parturition, which increases myometrial sensitivity to estrogen (Pieber et al. 2001). Increased estrogen levels are also found to generate the action potential in myometrium by increasing the number, size, and permeability of gap junctions. Recent studies have also shown the genomic and non-genomic effects of various progesterone-responsive genes via nuclear factor kappa-B (NF-KB) promoter sites and 5 $\beta$ -dihydroprogesterone, respectively (Brown et al. 2004; Sheehan et al. 2005).

### Oxytocin and Vasopressin

Increased estrogen levels and expression of ER- $\alpha$  due to progesterone withdrawal stimulate the secretion of oxytocin and vasopressin, although the sensitivity of myometrium is lower to vasopressin than oxytocin (FUCHS and FUCHS 1984). The sources of intrauterine oxytocin are placenta, endometrium, and amnion. Oxytocin mRNA expression was found to increase in decidua with onset of labor at term (Mijovic and Olson 1996). The release of oxytocin is also stimulated by the diffusion of fetal hormones into the maternal circulation. Expression of oxytocin and vasopressin receptors in myometrium also increases before labor, which results in initiation of forceful contraction of myometrial smooth muscle cells (Akerlund 2004). When oxytocin binds to its receptors, phospholipase C gets activated, and there is an accumulation of intracellular calcium. Interaction of estrogen and oxytocin suggests the paracrine control of oxytocin and subsequent initial prostaglandin (PG) production in the intrauterine tissues such as decidua, chorion, and amnion (Fuchs et al. 1982).

### Prostaglandins

Prostaglandins have a role in cervical ripening and labor. The estrogen-mediated expression of

oxytocin receptors is enhanced by the PGs, which serves as a positive feedback in this cascade. The oxytocin gene expression is increased in hypothalamus due to stimulation by estrogen. In myometrial cells, oxytocin stimulates the hydrolysis of phosphatidylinositol resulting in the generation of second messenger inositol triphosphate (IP3) and diacylglycerol (DAG). Generation of IP3 activates a signal cascade leading to myometrial contraction, while cellular lipases act on DAG to release arachidonic acid, which is a substrate of PGs. Hydrolysis of phosphatidylinositol results in the release of intracellular calcium, which further helps in the mobilization of arachidonic acid. Oxytocin also helps in the production of endothelin-1, which helps in the calcium influx into myometrial cells resulting in uterine contractions (Mijovic and Olson 1996). Some reports have also suggested that during parturition, prostaglandins E2 (PGE2), PGF2- $\alpha$ , and thromboxane control uterine contractions via their specific receptors (Fischer et al. 2008).

Relaxin is another hormone present in the maternal decidua and chorion, but its exact role in human parturition is still under investigation. Few studies have shown its possible role in cervical ripening and rupture of membranes. It might have a paracrine effect and inhibit PGE2 production during pregnancy (Bernal et al. 1987).

Role of some other regulators of PG synthesis has also been postulated in labor. These molecules help in suppression of labor or uterine quiescence by inhibiting PG biosynthesis. Molecules such as phospholipase A<sub>2</sub> inhibitors, prostaglandin endoperoxide H synthase (PGHS), and nitric oxide have been found to inhibit the PG synthesis through various mechanisms (Wilson 1993; Garfield et al. 1995).

### Adrenocorticotropin, CRH, and Cortisol

Studies have shown that fetal adrenal and pituitary gland and the nervous system have a role in triggering the onset of labor. Fetal adrenal gland plays a role in parturition by synthesizing C<sub>19</sub> estrogen precursors and dehydroepiandrosterone (DHEA), as placenta is a major site of steroid

production and converts  $C_{19}$  estrogen precursors into estrogen and is closely related to the secretion of DHEAS from fetal adrenal gland (FUCHS and FUCHS 1984). In late gestation, mature fetal adrenal secretes cortisol resulting in increased levels of cortisol in fetal plasma. Onset of cortisol production is related to fetal adrenocorticotrophic hormone (ACTH), but studies have found that surge in cortisol occurs in spite of decreased ACTH levels. This was supported by the facts that not all anencephaly fetuses are born late. The role of fetal pituitary as well as placenta-derived factors such as corticotrophin-releasing hormone (CRH) and proopiomelanocortin-derived peptides (POMC) has been found in parturition (Riley and Challis 1991). Increased levels of CRH have been found in amniotic fluid and maternal circulation with advancing gestational age; however, there is a decrease in CRH-binding proteins. CRH synthesis is stimulated by prostaglandins, oxytocin, and stress (Kamel 2010).

Increased levels of glucocorticoids positively regulate CRH gene expression and mRNA levels. CRH also increases PG synthesis in myometrium, fetal membranes, and placenta, hence affecting the myometrial contractile response. CRH receptor expression also increases with gestational age and by two- to threefold at onset of labor (Speroff and Fritz 2005).

This suggests that estrogen, cortisol, CRH, prostaglandins, and oxytocin establish a positive feedback loop system and regulate the onset of labor as well as initiation of parturition.

### Inflammatory Molecules

It is a known fact that maternal-fetal tolerance is very necessary for the successful pregnancy. In addition to this, the role of inflammatory molecules and immune modulators in placenta and fetal membranes is well known in labor suggesting the contribution of regulated inflammatory reactions toward the initiation of labor or parturition (Keelan et al. 2003). These inflammatory molecules help in the release of PGs. Expression of various inflammatory molecules

such as IL-6, IL-8, and IL-1 $\beta$  was found to be increased at term labor. Various inflammatory changes such as increased levels of inflammatory cytokines, chemokines, and matrix metalloproteinases (MMPs) help in cervical ripening and myometrial activation during labor (Romero 1988). Expression of a highly conserved transcription factor nuclear factor kappa B (NF- $\kappa$ B) is associated with inflammatory responses. Expression of this gene is increased at the initiation of labor and starts a signal cascade leading to the expression of cyclooxygenase 2, contributing to functional withdrawal of progesterone, increased estrogen levels, and synthesis of PGs (Lindstrom and Bennett 2005). Levels of tumor necrosis factor-alpha (TNF- $\alpha$ ) and transforming growth factor-beta 1 (TGF- $\beta$ 1) were found to be elevated in amniotic fluid during labor (Hayashi et al. 2008). Some other studies have shown the role of cellular adhesion molecules {intercellular adhesion molecule-1 (ICAM-1), vascular cell adhesion molecule-1 (VCAM-1) and endothelial leucocyte adhesion molecule-1 (ELAM-1)} in association with inflammatory reactions in labor (Steinborn et al. 1999).

Proteolytic enzymes such as plasminogen and MMPs play very significant role in extracellular matrix remodeling during pregnancy as well as at parturition. Increased expression of MMPs was observed in preterm birth (Tsatas et al. 1999). Higher level of inflammatory cytokines such as IL-8 was found to induce the infiltration of cervix by neutrophils, which promotes the release of proteinases helping in parturition (Winkler et al. 1999).

### Conclusion

The etiology of parturition is multifactorial. Various maternal and fetal hormones as well as inflammatory molecules function in a controlled way before the onset of labor subsequently leading to the initiation of labor followed by parturition. Synchronized interactions of these pathways lead to the cervical ripening,

myometrial activation and contractility, and rupture of membranes. Any disturbances in the balance or regulation of these mechanisms due to genetic, physiological, or environmental factors can affect the timely initiation of labor as well as parturition.

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## Passerine Anatomy

### ► Passerine Morphology

## Passerine Cognition

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### Definitions and Features

It may seem counterintuitive to have to begin by talking about feet when the subject is cognition. However, the question of what passerines are has been determined by taxonomists, who classified birds with three unwebbed toes facing forward and one toe facing backward as passerines, or perching birds. With a few notable exceptions, most birds have four toes, but some have vestigial toes and effectively live with two or three toes; quite a few have two facing forward and two backward, but birds of the particular group known as “passerines” have three toes facing forward (called an anisodactyl foot), meant to promote perching.

Beak shape is not a good way to identify passerines. Beak shapes vary widely from short compact beaks as in finches to straight all-purpose beak as in flycatchers, sometimes massive beaks as in ravens to delicate and sometimes curved beaks of the honeyeaters.

To complicate matters, the labels “passerines” and “songbirds” have, at times, been used interchangeably, but this is not quite accurate. “Songbirds” (also called the true oscines) are defined by their vocal organ, the syrinx, and the number of muscles that operate this vocal organ, at least four pairs as shown in the second panel of Fig. 1. There are some passerines, such as the suboscines, which have three toes facing forward but not enough pairs of syringeal muscles (usually two pairs) to classify them as true songbirds. There are other birds with three toes facing forward, but they may have no syringeal muscles at all, and they are certainly not songbirds (such as tawny frogmouths). The distinctions are not altogether tidy because there are anatomical overlaps between the various groupings, but these are the currently accepted taxonomical distinction.

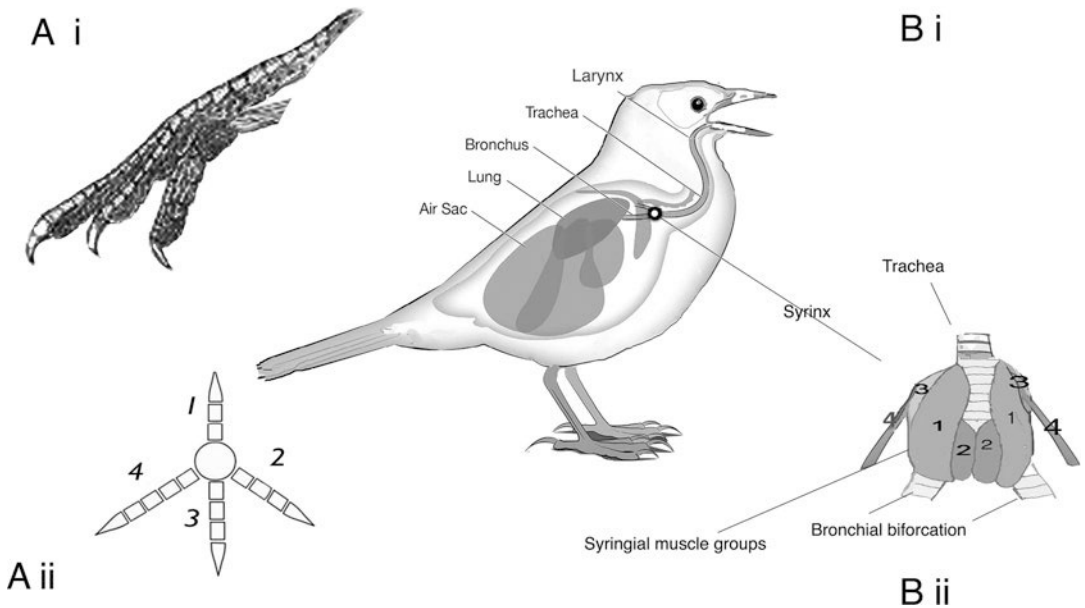
Apart from the toes, passerines have in common a quality that is of some considerable importance for the topic of cognition, namely, their immaturity at hatching (called altricial). When passerines hatch, they are helpless, often blind, featherless, and often not even able to stand on their feet and are thus completely dependent on adult care. This, for the parent bird (or both parents or even more than two adults), involves feeding and raising them, often well beyond the time when the offspring fledge.

While being altricial makes the newly hatched offspring much more vulnerable initially, biologically it has an advantage, namely, the opportunity for the offspring to develop as cognitively advanced a brain as possible. Indeed, the longer adults can care for their offspring, the greater the chances for optimal brain development. The brain is also a luxury. It is the most “expensive” organ in the body because, more than any other part of the body, it requires extensive high-quality nutrition and careful nurturing to develop fully. The interesting question is why some species, indeed families, have developed very large brains while others have not.

### How Many Are There

According to the most recent IOC World Bird List (Gill and Donsker 2017), there are 10,681 currently living species of birds (many more when subspecies are counted), and they are taxonomically subdivided by relatedness, their respective origin, and their categorization into superfamilies and eventually to species. Over half of them are passerines, thus an extremely large and diverse group of birds that have colonized every part of the globe.

As Fig. 2 shows, even the relevant part of the taxonomic bird tree is already quite complex just for tracing passerines. Panel I shows the ancient ancestors of songbirds; Panel II lists landbirds, among many others, and from those derive all perching birds. Passeriformes appear only in the third panel, and, of those, only the true songbirds have been included here, which are again subdivided into large groupings in Panel IV.



**Passerine Cognition, Fig. 1 Anatomical characteristics used in taxonomy for defining passerine birds. A, Ai:** The anisodactyl foot that gave perching birds their name. Three toes face forward and one backward. **Aii:** The toes are called digits and are numbered so that species with other foot configurations can be examined for their relative position. **B, Bi:** Showing the position of the syrinx in the body – the black circle indicates the location of the syrinx well inside the bird's chest. Songbirds also have a larynx, as marked, but it is of secondary importance in sound production. **Bii:** An enlargement of the outside of the syrinx – the tracheal and the lower bifurcation of the trachea into the two bronchial tubes is covered by muscles

organized in pairs to either side of the syrinx. Represented are the minimum number of pairs of muscles – four pairs – for a songbird. Many songbirds have five pairs, and some species may have as many as seven. The suboscines/Tyranni have at least two pairs, but many non-songbirds do not have any syringeal muscles. They may still produce sounds but to do so have to utilize the air sacs – as marked (Segment of Figure Bi adapted from Cornell Lab Animal free downloads, itself adapted from Rod Suthers, a former collaborator of the author of this entry, and Bii adaptation from a diagram of online site for Birds of South America II-Passerines by Ber van Perlo). For details of the syrinx proper and its functions, see Kaplan (2017)

P

An enlargement of Panel V highlights the superfamilies of Passerida, Corvoidea, and Meliphagoidea, but these groupings (and which species belong to them) certainly get revised quite regularly and change as we learn more about their deep relationships.

### Development of the Field of Avian (Passerine) Cognition

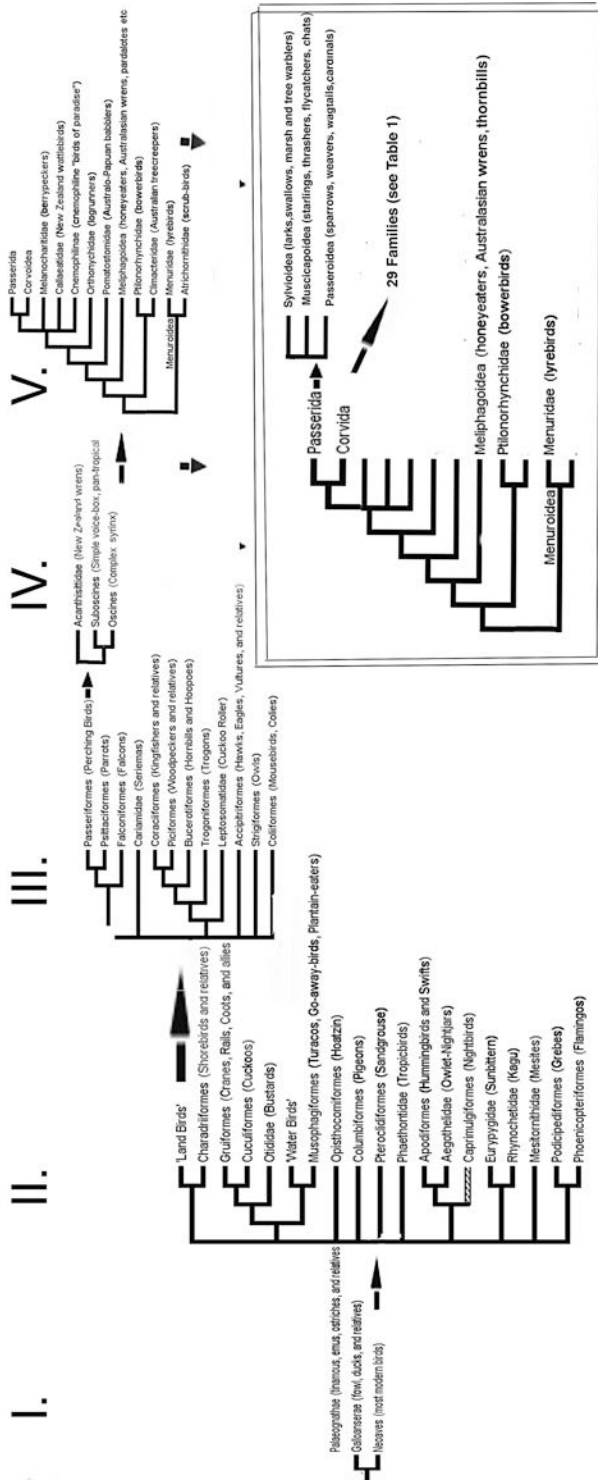
Cognition is a relatively new topic in science, first proposed for vertebrates in general in 1985 (Kummer and Goodall 1985). The idea of passerine cognition evolved slowly in the 1990s. The very idea of passerine cognition had been dismissed by most as anthropomorphizing, and,

for a long time, it was considered unscientific. The study of cognition in birds required an entirely new way of thinking, of asking new questions and conceiving of new research designs (and having the courage to think that this may be fruitful).

Some 20 years before Kummer and Goodall pleaded for some systematic investigations into vertebrate intelligence, guided by their work on chimpanzees, neuroscientists like Kuhlbeck (1967) had started systematizing comparative brain sizes. It is worth noting at the outset that, as early as the 1960s, birds were shown to have the largest brains relative to body size of any vertebrate (Table 1).

Hence, it has been known for a considerable time that birds have substantially larger brains relative to body size than mammals and





**Passerine Cognition, Fig. 2 Taxonomy of the passerines.** The passerines are thought to have begun to speciate only after the mass extinction 65 mya, whereas there is some evidence that some of its “sister” group developed much earlier. All songbirds and many other lineages of modern birds are now known to, or are suspected to, have evolved in East Gondwana, a kind of Noah’s arch for birds during the mass extinction events of 65 mya, which caused the extinction of dinosaurs and all other lineages of birds elsewhere in the world and of whose existence we have fossil evidence but no living descendants. The lineages that survived in East Gondwana (now Australia) are the ancient lineages on which all extant modern songbirds are based (Cracraft 2001). While passerines are just one of all orders of landbirds, they form the majority of all living birds. Note that the groups that are *not* passerines, even if they may share some features with passerines, are very diverse and form separate orders – these are the ratites such as ostriches, emus, and cassowaries and then the ducks, chickens, geese, swans, and other pond swimmers, such as moorhens and coots; grouse, quail, turkeys, and pheasants; seabirds such as albatrosses, shearwaters, skuas, and petrels and wading birds such as flamingos, herons, ibises, and egrets; swifts, swallows, and martins; shorebirds such as plovers; gulls and terns; and also raptors such as hawks, eagles, owls, and falcons and landbirds such as nightjars, kingfishers, hummingbirds, woodpeckers, barbets, and the large group of psittacine birds (cockatoos, parrots, lorikeets, and parakeets) that in new taxonomical assessments are considered a sister group of passerines (see [“Psittacine Cognition”](#) entry in this volume)

**Passerine Cognition, Table 1** Cuvier’s fraction for select vertebrates. Using simple ratios (Cuvier’s fraction E/S; E stands for brain weight and S for body weight),

| Species     | E/S ratio | Species      | E/S ratio |
|-------------|-----------|--------------|-----------|
| Small birds | 1/12      | Lion         | 1/550     |
| Human       | 1/40      | Elephant     | 1/560     |
| Mouse       | 1/40      | Horse        | 1/600     |
| Cat         | 1/100     | Shark        | 1/2496    |
| Dog         | 1/125     | Hippopotamus | 1/2789    |
| Frog        | 1/172     |              |           |

Kuhlenbeck (1967) noticed that these ratios did not necessarily match body weight. The larger the denominator, the less brain size had kept up with body size

vertebrates generally, foregrounding the topic of cognition and encouraging further exploration of brains and brain sizes of birds and vertebrates (see Fig. 3).

Such models have since been overtaken by more detailed assessments, but these first attempts threw some light on the evolution of the brain in animals generally, and the fascination with comparing brain sizes has never quite ceased since that time.

**Nonpasserine Avian Cognition**

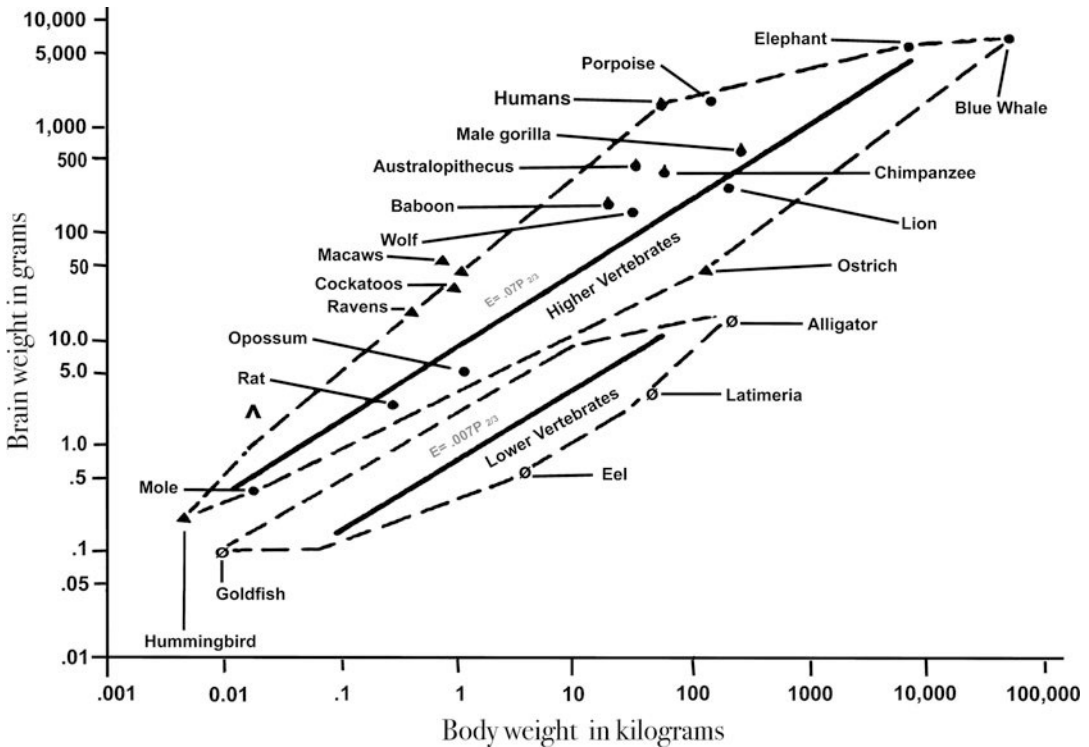
Interestingly, passerine cognition was largely foregrounded and, at times, intercepted by cognitive studies of pigeons and chickens, belonging to two families that are not passerines. There are probably more papers written on pigeon cognition in the last five decades than on any other birds. Güntürkün and colleagues suggested in 2014 that pigeons ought to be used as an avian model species for cognition rather than any of the typical passerines – mostly zebra finches, but also canaries, sparrows, and, among the larger passerines, chiefly those that belong distantly or directly to the large group of Corvoidea and corvids.

The reasons for suggesting pigeons as a model species for avian cognition are persuasive. They live long, learn fast, and can easily be trained in captivity. They have a highly developed visual system and excel in complex visual discrimination tasks even as abstract as distinguishing between paintings such as Monet and Picasso solely on the basis of previous experience with different pictures of paintings by these artists. Pigeons are also better than humans in performing a discrimination task involving rotation and

volume changes of objects relative to other shapes. They are equally excellent in spatial ability and memory. Yet most of the experiments with pigeons were performed with captive, domesticated stock of rock pigeons (*Columba livia*) and were often not seen as suitable examples for telling us anything general that would be transferrable to passerine cognition, although this is of course highly debatable.

The study of chicken cognition is perhaps even more noteworthy because the group of fowl and their relatives (Galloanserae) are an ancient lineage separate from most modern birds (Neoaves; see Fig. 2, left panel) serving as a powerful reminder that implicit assumptions of *scala naturae* are incorrect. All songbirds first evolved in East Gondwana (now modern Australia), and fowl arose well before the last mass extinction of 65 million years ago, and they belong to the precocial species capable of independent feeding from day 2 post-hatching.

Chickens were mostly considered to be particularly lacking in anything approaching cognition. Yet a good deal of research has established that chickens can do astonishing things across a range of fields (auditory, visual, and social). For instance, a study of object permanence showed that even in their first week of life, domestic chicks are able to conceptualize the presence of an object that has disappeared from sight. If the chick is imprinted on a specific object, say a colored ball, it will follow the ball and stay close to it. If the ball is moved out of sight behind a screen for a little while, the chick will retain a concept of the ball and find it. When presented with two identical screens, it will approach and go



**Passerine Cognition, Fig. 3** Body weight versus brain weight – calculations in the 1960s. Symbols: black circles, mammals; black teardrops, primates including humans; black triangles, birds; hollow/crossed circles, amphibians, reptiles, and fishes (open triangle = budgerigar). The diagram above is adapted from an older summary of ratios between brain and body weight for all vertebrate groups (accessible on the Internet [www.neurophys.wisc.edu](http://www.neurophys.wisc.edu)) with the addition of some birds (cockatoos, macaws, and ravens) to reflect latest research insights. Upper bold

black line indicates mean values for trend lines in “higher” vertebrates – note that some passerines and psittacines, as well as dogs, great apes, humans, and cetaceans (dolphins and whales) have brain sizes well above the mean, while many nonpasserines and waterbirds are well below the mean (see entry for ostrich). Note that the black trend line for “lower vertebrates” (fishes, reptiles) is well below that of any birds or mammals. Based on Kuhlbeck (1967). (Adapted from the original Jerison, H. J. 1973. *Evolution of the brain and intelligence*. New York, Academic Press)

behind the screen around which it had seen the ball disappear. Children achieve this ability usually only between 7 and 9 years of age. Researchers arrived at the then radical conclusion that all animals that locomote independently and need to find their food by processes of identification and discrimination would have to be equipped with a minimal perceptual apparatus and a basic cognitive “software” to survive (Vallortigara in Rogers and Kaplan 2004). Astonishingly, they suggested that such software consists of rudimentary knowledge of physics (gravity, physical causality), mathematics (basic numeral understanding), geometry (spatial ability and landmarks), and psychology (distinguish

between friend and foe). Indeed, such traits have also been found in invertebrates. Honeybees (*Apis mellifera*), for instance, also have spatial memory and relational concepts; indeed, they have a basic numerical cognition that has now even been found in other insects.

### Passerine Cognition

When speaking of passerine cognition, one tends to refer to species that have actually been studied in detail. Most of our knowledge of passerine cognition derives from three groups but largely, although by no means exclusively, from Corvoidea (Table 2) and only a small number of families among those (a separate list of the corvids is provided in Table 3

**Passerine Cognition, Table 2** The superfamily of Corvoidea (within the passerine group of birds) consisting of 29 superfamilies. A family or superfamily marked “red” indicates that we have substantial amounts of published information about the cognitive abilities of a family or of some species within a superfamily. Blue indicates that we

have some, albeit generally sparse, information about species within this superfamily – unmarked are those superfamilies that may have very few if any studied examples of cognition, but this does not preclude that there are not some that contain species of which we have occasional observations or single incidents of cognitively advanced behavior

| Numbered | Species Names in Latin | Common names                                  |
|----------|------------------------|-----------------------------------------------|
| 1        | Paramythiidae:         | tit berrypecker and crested berrypeckers      |
| 2        | Psophodidae:           | whipbirds, jewel-babblers and quail-thrushes  |
| 3        | Platysteiridae:        | wattle-eyes and batiss                        |
| 4        | Tephrodornithidae:     | woodshrikes and allies                        |
| 5        | Prionopidae:           | helmetshrikes                                 |
| 6        | Malaconotidae:         | bush-shrikes                                  |
| 7        | Machaerirynchidae:     | boatbills                                     |
| 8        | Vangidae:              | vangas                                        |
| 9        | Pityriaseidae:         | Bornean bristlehead                           |
| 10       | Artamidae:             | Australian magpies, butcherbirds, currawongs, |
| 11       | Rhagologidae:          | mottled whistler                              |
| 12       | Aegithinidae:          | ioras                                         |
| 13       | Campephagidae:         | cuckooshrikes, trillers                       |
| 14       | Mohouidae:             | whiteheads                                    |
| 15       | Neosittidae:           | sittellas                                     |
| 16       | Eulacestomidae:        | ploughbill                                    |
| 17       | Oreoicidae:            | Australo-Papuan bellbirds                     |
| 18       | Pachycephalidae:       | whistlers, shrike-thrushes, pitohuis          |
| 19       | Laniidae:              | shrikes                                       |
| 20       | Vireonidae:            | vireos                                        |
| 21       | Oriolidae:             | orioles, figbirds                             |
| 22       | Dicruridae:            | drongos                                       |
| 23       | Rhipiduridae:          | fantails                                      |
| 24       | Monarchidae:           | monarchs and allies                           |
| 25       | Corvidae:              | ravens, crows and others (see also Table 3)   |
| 26       | Corcoracidae:          | white-winged chough, apostlebird              |
| 27       | Melampittidae:         | melampittas                                   |
| 28       | Ifritidae:             | ifritabirds                                   |
| 29       | Paradisaeidae:         | birds of paradise                             |

later) and just a smattering of species from other species, including bowerbirds. In toto, our knowledge base thus far may amount to possibly just 2–3% of extant passerine birds. But perhaps, at least in some superfamilies, the knowledge that we now have may be regarded as representative and significant of songbirds, certainly of some families. The very least that can be said is that never before in natural history or in science have we had so much data and evidence of passerine

cognition and never before has the idea of passerine cognition received so much in-depth research. Although, occasionally, there are some publications involving species belonging to Passerida or the Meliphagoidea, the Corvoidea are by far the most prominent group used in studies on passerine cognition (Table 1). Hence, what we know about passerine cognition tends to derive from a fraction of passerine birds but what a remarkable group of birds it is.

**Passerine Cognition, Table 3** Corvid species worldwide. Ravens, rooks, crows, and jackdaws have a firm. Presence on every continent, and usually with several species, excepting South America

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**Africa/Middle East**

1. *Corvus albus* – pied crow (Central African coasts to Southern Africa)
2. *Corvus albicollis* – white-necked raven or Cape raven (Southern, Central, and Eastern Africa)
3. *Corvus capensis* – Cape crow or Cape rook (Eastern and Southern Africa)
4. *Corvus crassirostris* – thick-billed raven (Ethiopia)
5. *Corvus edithae* – Somali crow (eastern Africa)
6. *Corvus monedula* – jackdaw or western jackdaw (British Isles, Western Europe, Scandinavia, Northern Asia, Northern Africa)
7. *Corvus rhipidurus* – fan-tailed raven (Northeast Africa, Middle East)
8. *Corvus ruficollis* – brown-necked raven (North Africa, Arabian Peninsula, Afghanistan, Pakistan) – plus *Corvus ruficollis edithae*, Somali crow or dwarf raven (Northeast Africa)
9. *Corvus splendens* – house crow or Indian house crow (Indian subcontinent, Middle East, East Africa)

**Europe and Eurasian**

1. *Corvus corone* – carrion crow (Europe and Eastern Asia)
2. *Corvus frugilegus frugilegus* – rook
3. *Corvus monedula* – jackdaw or western jackdaw (British Isles and Western Europe, Scandinavia, Northern Asia, Northern Africa)
4. *Corvus corax* – common raven or northern raven (Holarctic regions of the Northern Hemisphere)
5. *Corvus cornix* – hooded crow (Northern and Eastern Europe and Northern Africa)
6. *Corvus corone* – carrion crow (Europe and Eastern Asia)
7. *Corvus dauuricus* – Daurian jackdaw (Eastern Europe to Eastern Japan, occasionally Scandinavia)

**Arctic Regions**

1. *Corvus caurinus* – northwestern crow (Olympic Peninsula to Southwest Alaska)
2. *Corvus cornix* – hooded crow (Northern and Eastern Europe and Northern Africa)
3. *Corvus corax* – common raven or northern raven (the Holarctic regions of the Northern Hemisphere)

**America (North)**

1. *Corvus brachyrhynchos* – American crow (United States, southern Canada, northern Mexico)
2. *Corvus corax* – common or northern raven (Holarctic regions of Northern Hemisphere)
3. *Corvus cryptoleucus* – Chihuahuan raven (Southwestern United States, Northwestern Mexico)
4. *Corvus ossifragus* – fish crow (Southwestern US coast)
5. *Corvus sinaloae* – Sinaloan crow (Pacific coast from Sonora to Colima)

**America (Central)**

1. *Corvus imparatus* – Tamaulipas crow (Gulf of Mexico coast)
2. *Corvus jamaicensis* – Jamaican crow (Jamaica)
3. *Corvus leucognaphalus* – white-necked crow (Haiti, Dominican Republic, Puerto Rico)
4. *Corvus nasicus* – Cuban crow (Cuba, Isla de la Juventud, Grand Caicos Island)
5. *Corvus palmarum* – palm crow (Cuba, Haiti, Dominican Republic)

**Pacific Ocean**

1. *Corvus hawaiiensis* (formerly *C. tropicus*) – Hawaiian crow (Hawaii)

**Asia**

1. *Corvus corone* – carrion crow (Europe and Eastern Asia)
  2. *Corvus enca* – slender-billed crow (Malaysia, Borneo, Indonesia)
  3. *Corvus florensis* – Flores crow (Flores Island)
  4. *Corvus typicus* – or Celebes pied crow (Sulawesi, Muna, Butung)
  5. *Corvus frugilegus* – rook
    - a. *Corvus frugilegus* (wide range across Europe and Mediterranean to Russia)
    - b. *Corvus frugilegus pastinator* – oriental rook (East Asia to Mongolia)
  6. *Corvus kubaryi* – Mariana crow (Guam, Rota)
- 

(continued)



**Passerine Cognition, Table 3** (continued)

|                                                                                                                                        |
|----------------------------------------------------------------------------------------------------------------------------------------|
| 7. <i>Corvus splendens</i> – house crow or Indian house crow (Indian subcontinent, Middle East, Eastern Africa)                        |
| 8. <i>Corvus macrorhynchos</i> – jungle crow (Eastern Asia, Himalayas, Philippines)                                                    |
| a. <i>Corvus macrorhynchos macrorhynchos</i> – large-billed crow                                                                       |
| b. <i>Corvus macrorhynchos levaillantii</i> – eastern jungle crow (India, Burma)                                                       |
| c. <i>Corvus macrorhynchos culminatus</i> – Indian jungle crow                                                                         |
| 9. <i>Corvus monedula</i> – jackdaw or western jackdaw (British Isles and Western Europe, Scandinavia, Northern Asia, Northern Africa) |
| 10. <i>Corvus torquatus</i> – collared crow (Eastern China, south into Vietnam)                                                        |
| <b>Australia/New Zealand/Oceania</b>                                                                                                   |
| 1. <i>Corvus coronoides</i> – Australian raven (Eastern and Southern Australia)                                                        |
| 2. <i>Corvus bennetti</i> – little crow (Australia)                                                                                    |
| 3. <i>Corvus mellori</i> – little raven (Southeastern Australia)                                                                       |
| 4. <i>Corvus tasmanicus</i> – forest raven or Tasmanian raven (Tasmania and adjacent south coast of Australia)                         |
| 5. <i>Corvus boreus</i> – relict raven (New South Wales, Australia)                                                                    |
| 6. <i>Corvus orru</i> – Torresian crow or Australian crow (Australia, New Guinea, and nearby islands)                                  |
| 7. <i>Corvus tristis</i> – gray crow or bare-faced crow (New Guinea and neighboring islands)                                           |
| 8. <i>Corvus fuscicapillus</i> – brown-headed crow (New Guinea)                                                                        |
| 9. <i>Corvus insularis</i> – Bismarck crow (Bismarck Archipelago, Papua New Guinea)                                                    |
| 10. <i>Corvus meeki</i> – Bougainville crow or Solomon Islands crow (Northern Solomon Islands)                                         |
| 11. <i>Corvus unicolor</i> – Banggai crow (Banggai Island)                                                                             |
| 12. <i>Corvus validus</i> – long-billed crow (Northern Moluccas)                                                                       |
| 13. <i>Corvus violaceus</i> – violet crow (Seram)                                                                                      |
| 14. <i>Corvus woodfordi</i> – white-billed crow or Solomon Islands crow (Southern Solomon Islands)                                     |
| 15. <i>Corvus moneduloides</i> – New Caledonian crow (New Caledonia, Loyalty Islands)                                                  |
| 16. <i>Corvus frugilegus</i> – rook (New Zealand)                                                                                      |

## Scientifically Acceptable Wish List of What Passerine Cognition Should Be

What is special about passerine cognition, if anything, needs to be carefully delineated from this basic “tool kit” of vertebrates and even some invertebrates generally. And one needs to bear in mind that some of the traits we once considered uniquely human are, in fact, not only shared by a few other mammals and birds but also by vertebrate and even invertebrate species in the distant evolutionary past.

Having said so, cognition, as applied to passerine cognition, is not a unitary term but involves many gradations – encompassing physical, core, and abstract knowledge as well as specific social knowledges. Scientists have carefully isolated areas of individual performances of passerines on very specific tasks.

Many researchers have made long catalogues of expectations that passerines would have to

meet before; they feel the term “cognition” could reasonably be applied to birds. Birds ought to show manifestations of complex memory (both making and maintaining memories, be this spatial, acoustic, seasonal, social), abilities for concept formation and categorization, remembering things that have gone out of sight (called object permanence), as well as being able to be a “time traveler”: that is, not only be able to remember the past but also plan for the future in the short term and possibly even the long term. Further, an individual ought to be able to judge what another may feel or think, which is called “inferring the state of another.” This may include behavior such as eye-gaze following (“I want to see what you see”), pointing, or responding to pointing (“I want to show you something”) in which expressions of intentionality and coordination should be apparent. Pointing and eye-gaze following involve not so much reading the behavior of another but interpreting what the other might

think it sees as important. Body movements, particularly when only showing pretended actions, can also serve as important markers that require an observer to interpret an intention. For instance, when a flight intention movement by a bird is not executed in order to set off on a flight itself but to encourage another bird to attempt flight, it is up to the second bird to read the intention as a signal for itself to take that action. It is the onlooker who has to make the important cognitive leap to perform an act that it is not the behavior that the demonstrator itself is actually doing but one that the demonstrator wants the observer to undertake.

Further, as others have identified, bird cognition should encompass abilities such as delay of gratification, reasoning, mirror self-recognition, and specific affiliative attitudes to others that show meaning is involved in the relationship, such as consoling a partner who may have lost a food item or, in a squabble, helping or defending a partner or group member in difficult situations, third-party interventions in serious fights (Güntürkün and Bugnyar 2016), or even more difficult emotions such as grieving, which perhaps might presuppose a concept of death or at least loss.

To complicate matters, debates on animal cognition, largely of primates, but at times including birds, have been framed in terms of theoretical debates on what is termed “theory of mind,” which not only includes attributing mental states to others but also an understanding that others can see, feel, and know which, in turn, is inextricably linked with a capacity for consciousness, insight, a concept of self, and such emotions as compassion (empathy) and even pride and shame as Charles Darwin had already outlined (Darwin 1904). While most researchers on passerine cognition have preferred not to get involved in debates on “theory of mind,” latest research results have shown that it may be increasingly difficult to avoid concluding that some passerine species may have a sense of consciousness and self.

While the bar was set very high as to what qualifies as “cognition” in birds, evidence of all of the above has been found in passerines.

## Evidence-Based Research Evaluating Cognition

The problem about regarding specific cognitive feats as a sign of cognitive complexity has remained and for good reason. Many species show one or the other trait that one might term “cognitively complex” but not all of the facets that together would make the organism seem so in all or most regards. As has been implied or argued by skeptics, avian brains are too small compared to, say, those of great apes or humans to be able to produce any noteworthy intelligent behavior. Even the most astounding documented feats of passerine behavior have, at times, been dismissed as examples of adaptations meant to indicate that not all complex behavior may not satisfy our understanding of cognition, and sometimes rightly so. The latter may well be true when a bird has shown a special skill, such as clever proto-tool use of opening walnuts in the great spotted woodpecker (*Dendrocopos major*), but shows few or no highly developed qualities in other facets of cognitive behavior. Of course, sometimes this impression of limited abilities is created when such findings are not followed up by new questions and experiments. For instance, as in the case of the Clark’s nutcracker (*Nucifraga columbiana*), it was always noted that its ability to hide and find some 30,000 pine nuts much later (recall of location of nuts exceeds 200 days) was extraordinary, but since Clark’s nutcrackers belong to scatter-hoarding taxa of relatively low phylogenetic diversity (i.e., various species of jays also scatter-hoard their food, and all belong to the corvid family), this was largely seen as an adaptive skill. Indeed, specialized skills may have been part of natural selection and encoded in the species’ genome: if Clark’s nutcrackers were unable to retrieve the nuts hidden in autumn and do so from under a blanket of snow in winter, they simply would not survive. Those who could not secure a safe food supply for the lean winter months might instead have been forced to migrate to wintering quarters with more easily accessible food sources. A different problem for birds, but just as potent, is the importance of remembering the ebb and flow of a food supply such as nectar. If

small honeyeaters should forget when and where a food source might be replenished, they would quickly deplete their own energy resources, already run at an exceptionally high metabolic rate, and die.

Hence, a good deal of seemingly cognitive behavior might indeed be the result of natural selection or thought of as being based on associative learning. Each case that is observed needs to be assessed rigorously, sifting through the possibilities of alternative explanations and, instead of speculating, opt for the explanation that is the most parsimonious and plausible in terms of its biological, behavioral, and environmental underpinnings.

### Risks and Pitfalls in Cognitive Research

The risks of over- or under-interpretation of behavior patterns that appear to be cognitive have always been great in this field. Historically, cognitive abilities tended to have been too readily dismissed or not even recognized as such, while, in current research, cognitive abilities at times may be at risk of being over-interpreted. Even now, however, cognitive abilities are often misused. A very telling example is the case of Clark's nutcracker. The assessment of finding nuts as an adaptive skill largely foreclosed further investigations for almost 30 years until Magnotti et al. (2015) tested Clark's nutcrackers in abstract concept learning in the laboratory, a task that capuchin and rhesus monkeys were known to have failed but human subjects were known to have solved. Superior learning by nutcrackers was shown to be due to their ability to learn an abstract concept, which can be determined only by transfer to novel stimuli. The researchers also pointed out, convincingly, that studies had previously failed to find evidence of such abstract cognition because of research designs that would have been unable to reveal it.

Another pitfall in the study of bird cognition is to treat an individual bird of a specific species as if it were representative of all individuals of the same species or even of the same order.

We now know that, as in humans, talents may be exceptional in one and not another individual

and circumstances may lead to the expression of certain skills while they cannot be demonstrated in others of the same species. The problem of variation has recently been addressed (Rowe and Healy 2014). Woodpecker finches, the first reported by Darwin and thus famous, are noted for their tool using, but, as research found, not all individuals of this species use tools, nor are non-using adults able to learn this skill by observation later in life. Tebbich et al. (2001) suggested that tool using in woodpecker finches may well be subject to being confined to a sensitive phase, just as is the case of vocal learning in some songbirds. This may demonstrate an important general point that not all clever skills may be evenly distributed among species or even within the same avian species or family group. There may also be learning opportunities that can be missed even if the potential for their expression exists, be this because of poor nutrition or a generally impoverished environment or because some catastrophic events undermined the time-tabling of receptiveness for certain intellectual or skill acquisitions – very much as we know is the case in humans.

Finally, we may at times still be haunted by assumptions about vertebrate cognition as an imaginary clear trajectory from lesser to greater cognitive ability coinciding with the size of brain/body ratio and an evolutionary timetable (a view that the brain/body ratio tables enforced rather than dispelled – see Fig. 3 above). And the order was simple: invertebrates as the lowest creatures, then fish, followed by amphibians and reptiles, then birds, and finally mammals and, at the apex, nonhuman primates and humans. This assumption is as old as Aristotle and referred to as *scala naturae*. However, as researchers on fish have discovered, many of the debating points about cognition discussed in primates could be discussed and found in fish (see chapter in Rogers and Kaplan 2004). Work on bees has more recently shown that bees form memories, and another invertebrate, the octopus, has problem-solving abilities.

The point made here is twofold: during the process of evolution, traits can be gained and lost and regained again. The second point is that

environmental niches impose their own challenges, risks, and prerequisites and survival in any of them will foster physical adaptations, skills, and problem-solving abilities that fit such challenges best – no more and no less. Even the bird's ability of flight is lost when environmental circumstances make it pointless to possess flying ability.

## Key Areas of Interest in Passerine Cognition

Research on passerine cognition has concentrated on three entirely different areas: (1) song development and/or vocal learning, (2) brain and brain functions, and (3) behavioral studies revealing cognition.

These three areas have increasingly begun to overlap and grow together. This third cluster of research interests (cognition), relatively later on the scene than the previous two, investigated aspects of bird behavior that fell into a very varied basket of “cognitive behavior” – starting perhaps with tool using, innovation, and insightful problem-solving and a raft of other special abilities extending to mental time travel (ability to remember past events and conceive of events that have not yet taken place) and awareness of others and many more abstract cognitive abilities.

In the following sections, the directions and details of interest and extraordinary findings in passerine cognition are briefly outlined. From the relatively few species studied, it is clear that those species researchers have studied in great detail have astonished the researchers and the world with a wide range of abilities and surprising characteristics that were all once, and often until very recently, thought to be the province of humans as the only species, or one of the few (such as great apes), to show advanced cognitive abilities and behavior.

### Song and Vocal Learning

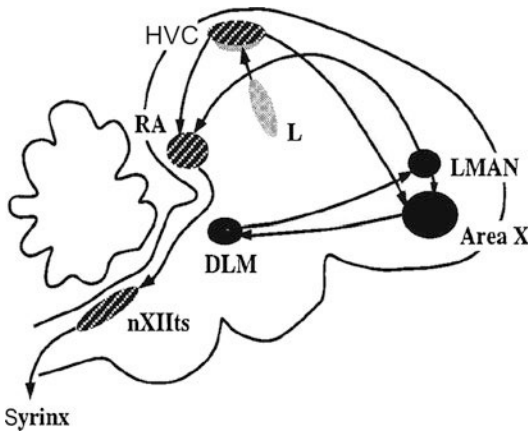
The most outstanding feature of most passerines is that they can sing. The study of passerine cognition received significant impetus and was also foregrounded by extensive work on birdsong

and birdsong acquisition generally and by the neuroscience of birdsong that dealt specifically with forebrain activity required for vocal learning and thus with significant aspects of passerine cognition. By far the most favored species in neuroscience for birdsong learning and memory have been zebra finches, canaries, and a smattering of others, while those more interested in the social aspects of vocal behavior of passerines have concentrated on well-known songbirds such as starlings, nightingales, mockingbirds, lyrebirds, and Australian magpies, and generally a wide range of songbirds have been studied in these regards.

Many of the songbirds such as mockingbirds, drongos, orioles, starlings, jays, bowerbirds, pipits, bush larks, warblers, towhees, Australian magpies, brown thornbills, and brown thrashers, to name just a few, can even mimic other species. The latter ability was incontrovertible proof that mimicry had to be learned since it was not accessible from an inherited template but had to be acquired during the lifetime of an individual. Very few other orders and species can learn vocalizations let alone mimic other species. Vocal learning is thus a rare quality in the animal kingdom that has so far only been discovered in very disparate groups such as cetaceans (e.g., whales/dolphins), in elephants, in some hummingbirds, in psittacine (parrot/cockatoo) species, and first and foremost in songbirds and humans. In songbirds, parrots, and humans, such capacity for learning sounds has often developed to highly sophisticated levels.

Most of the processes associated with song learning required discovery of an enabling neural network for hearing sounds, remembering them, and then reproducing what was heard. Further, song production and variations, indeed any vocal utterances, raised the question of memory as to how and what was stored and could be recalled when needed and how learning occurred so that vocal signals were used appropriately and in the correct context (Fig. 4).

A large cluster of singers belong to species in which song is exclusive to males that sing to attract a female in competition with other males. They tend to be migratory and, for reasons of climate and rapid seasonal changes, have little



**Passerine Cognition, Fig. 4** Schematic (simplified) representation of the anatomy of the song system. The crosshatched nuclei, HVC, RA (robust nucleus of the arcopallium), and nXIIts (the tracheosyringeal portion of the hypoglossal nucleus), form part of the descending motor pathway for song. Black: The nuclei of Area X, DLM (medial subdivision of the dorsolateral nucleus of the anterior thalamus), and LMAN (lateral magnocellular nucleus of the anterior nidopallium, shown in solid black) form a pathway indirectly connecting HVC to the RA and play a special role during song learning. The primary sources of auditory input to the song system are the field L complex (large area (light gray) subdivided into L1, L2, and L3) and its projections to the shelf underlying HVC (stippled areas)

time to reproduce and rear young that are then strong enough to also leave their nesting grounds and fly to wintering grounds, often thousands of kilometers away. Many of these males with elaborate song (and sometimes pronounced and colorful plumage) tend not to co-rear their young. Their song may be long or short and often may not vary much from year to year, and, however dazzling the performance may be at the time of the breeding season, the actual contents may be modest, saying no more than that the individual singer has stamina and is healthy. Beyond this capacity to have learned a song, it is no indication of any other cognitive skills.

Another cluster of species, sometimes also exclusively male, uses song to announce territorial ownership, and quite often such song may not need to be very elaborate.

In many songbirds, as has recently been researched in detail (Hall and Langmore 2017), female song is also ancestral and can be found in



**Passerine Cognition, Fig. 5** The zebra finch song control system is used as a model case. The male zebra finch is probably the most intensely studied songbird and has yielded the most detailed data on song learning. The zebra finch learns song mostly and best from a male tutor but needs to have completed the learning phase during “a sensitive period,” and this process is usually completed by 90 days post-hatching, when song crystallizes

hundreds of passerine species, such as in most species of the shrike family, in all Artamidae (Australian magpies, butcher-birds, currawongs), orioles, drongos, various corvids, cuckoo shrikes, and many more songbirds across different families of passerine birds such as wrens, gerygones, and thornbills (Odom et al. 2013). Many of these have not been studied in detail or not at all neither has the function of song (not used in a reproductive context) been examined nor song learning been investigated in the light of cognitive power than does male-song learning and practice for which the functions are well-known and studied.

Very careful consideration has been given to male-only (sexually dimorphic) song used during the breeding season. Model species usually chosen are zebra finches (*Taeniopygia guttata*) and less so canaries and sparrows. In the zebra finch (Fig. 5), song is learned from a male tutor, usually the father, and the zebra finch juvenile has only limited time to acquire the song (called the “sensitive period”), and then the song “crystallizes,” meaning that it takes its final form at the end of the



sensitive period. The zebra finch model of song acquisition is very useful because of its applicability to quite a number of songbirds. At least research for this group was able to show beyond doubt that birds need the forebrain in order to learn, need a memory to store what has been learned, and retrieve it in contexts that are meaningful to others.

Yet it would be wrong to assume that acquiring a mate is the major or even the only function of song. The zebra finch song learning model already breaks down in contexts of song being used to guard territory. Quite typically, in pairs that settle in one specific plot and are in the position to hold their plot over some time, even years, it has been observed that part of their song may converge with that of neighbors. The neighborhood is thus defined by some shared song components that arise dynamically depending on the composition of various plot holders. Clearly, birds cannot learn in advance who they might encounter in the future or where they can secure a territory, meaning that the brain has to remain flexible enough to be able to learn some new sounds.

Finally, there is also a substantial group of lifelong learners that retain the ability to learn new patterns of vocal behavior and even a range of nonvocal cognitive tasks. This flexibility and ongoing learning ability (open-ended learning which is an example of “brain plasticity”) are characteristic of the group that appears to have the greatest potential for complex cognitive abilities; at least one would be led to believe so based on the findings in studies of lifelong learners.

In some cases, as was discovered, vocal communication is refined to a point where individual signals might even be regarded as the beginnings of a lexicon, i.e., the beginnings of what we call “language”: specific sounds that symbolically get earmarked to refer to a specific object or message and are voiced only in the presence of conspecifics. This, in vertebrates generally, is referred to as “referential signaling.” Chickens also use referential signals, so this ability may be more widespread among birds than we currently know, and not just limited to songbirds or passerines in general, or it may be one of the traits gained and lost

over evolutionary time. It was rightly assumed that such avian species had to possess the neural apparatus to process information about referential signals and retain a memory of what had been communicated in a way that humans are known to do.

Song learning in birds recently held a further surprise. In 2008, Prather and colleagues showed that songbirds have mirror neurons that promote learning and long-lasting memory formations in a very special way. A bird can listen to a song and form a memory of it as if it had sung and practiced it itself.

The most convincing aspect of these findings is that these neurons belong to a population of neurons that is not replaced, as other neurons in the song system are (Nottebohm 1980), but is stable across song development. It is this stability in neurons that enables the juvenile to improve its song as the memory trace of the correct version remains intact and can be accessed.

Identifying mirror neurons in birds was such an important discovery because it explained for the first time how songbirds, such as the Australian magpie (Fig. 6), can learn their song without exposure to a tutor. It also explains why songbirds such as Australian magpies can be seen practicing on their own and yet improve the quality of song or mimicry of sounds they have heard. Indeed, magpies (*G. tibicen*) need to hear a particular sequence just once and, after a lag time of about 24–48 h, can produce a good rendition of the complete sound sequence. The same ability has been demonstrated in starlings and mockingbirds and quite a few other species. Even more astonishingly, there is documented evidence that Australian magpies, when trying to mimic a difficult sound sequence (such as level of kHz, speed, etc.), will continue practicing without any further exposure to the original sound sequence while measurably improving the accuracy of its mimicked performance only heard once in the real world. Presumably, this can only happen if there is a memory template of the original against which the singer can practice. Unless we discover other mechanisms, it seems that the mirror neurons are of substantial importance for memory in the passerine brain.



**Passerine Cognition, Fig. 6 The Australian magpie as an alternative model.** The magpie is a representative species at the other end of the spectrum of birdsong learning (the dominant model is the zebra finch – see Fig. 5). Magpies improvise song, have a substantial repertoire, and belong to the group of lifelong learners. Song is never fixed. Magpies, one of the most versatile and melodious songbirds of Australia, are also distinguished from zebra finches in that both males and females sing alike. The bird is not only an excellent mimic but shows cognitive behavior on a par with corvids. Unlike many corvids that are persecuted and culled as vermin, magpies suffer no neophobia and often form lifelong friendships with households in suburban and rural areas. They are strictly territorial and often raise their offspring cooperatively. The magpie is so far only one of two species in which pointing behavior was demonstrated (*Corvus corax* is the other species)

### The Brain

One notable piece of evidence of evolutionary distance was that birds, but not mammals, lack the neocortex, the convoluted area of the brain that was believed to be a prerequisite for complex thought and memory (see Fig. 7). Indeed, it was believed for a long time that meaningful vocal communication was unique to humans. These turned out to be an incorrect assumption. It was thus a major breakthrough to discover that songbirds, despite the evolutionary distance from humans, had the mechanisms to learn

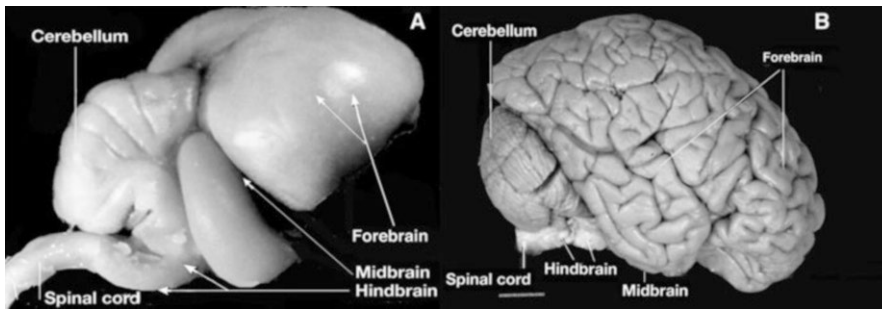
vocalizations (rather than produce sound merely instinctively) and had to rely on forebrain abilities as humans do.

This insight propelled science further to consider what similarities there might be between human and bird brains, admittedly by a process of convergent evolution. In 2004, an international team came together forming the “Avian Brain Nomenclature Forum” to rename the different regions of the avian brain, largely using the small Australian songbird, the zebra finch, as the model species for all passerines. More daringly, in a question which would have been dismissed as fantasy a century earlier, it was asked what can be learned from a bird brain in terms of mechanisms and dynamics of vocal development and retention of sounds that might inform understanding of these processes in humans. All other inquiries into the capacities of the passerine bird brain followed on from the initial interest in trying to understand the development and mechanisms of birdsong.

The second large area of ongoing and intense research is concerned with the perceptual abilities of birds, asking what they see and hear and, importantly, how they navigate in their environment and remember food locations (spatial orientation and spatial memory), also creating a need to look very closely at areas of the brain not directly associated with song learning.

### Brain Weight as a Ratio of Body Weight Versus Neuron and Synaptic Density

In 2009, researchers (Overington et al. 2009) looked for species with documented instances of innovative feeding (be this consuming novel food or using tools to access food) and found examples of this in 800 species worldwide. According to their findings, they argued that it is the brain size (in relation to body size) that made it possible for animals to produce novel behavior patterns. This concerned not only individuals and individual species but also families. Interestingly, they also found that one might predict from behavior alone whether the species was large-brained or not and do so by looking at the diversity of innovations performed and not just the total number of innovations.



**Passerine Cognition, Fig. 7** Rostro-caudal (side-way) view of magpie brain (Panel A) and human brain (Panel B). The human brain is about 150 mm long and has a volume of about 1450 cm<sup>3</sup>. The magpie brain (using the same measures) is about 35 mm long and has a volume of 4.65 cm<sup>3</sup>. The scale bar (gray/stippled) indicates the

relative length of the magpie brain when compared to the human brain. As already indicated, brain size by itself is no indication of relative neuron density. Note that the surface area in all birds is smooth and in the human brain is entirely convoluted. Even so the basic architecture of the brain is similar both in humans and birds

The problem with this approach to passerine cognition is that the argument rests its case on brain volume. Yet brain size may not by itself be able to account for the vast breadth of variations in cognition in passerine birds. Thus, ratios were introduced, relating brain volume with body size. The next logical step was to look at the distribution of neurons and the number and density of neurons.

There are several pitfalls in this reliance on brain/weight ratios alone because it assumes invariability in the architecture and function of the brain and of neurons. One biological fact is that different parts of the brain may have different size allocations according to need, meaning that size can vary from one season to the next or over a lifetime even in one individual. The part of the brain known as the hippocampus, for instance, particularly noted for the ability to form and retrieve spatial memories, is a case in point. It has been shown that in species that store and hide their food, the hippocampus is larger than in those, even in closely related species, that do not scatter-hoarded food. Or, more dramatically, the hippocampus may even shrink in a food-storing bird that stops storing food for a while. The size of the hippocampus varies with seasons and can even vary from one individual to the next, depending on the opportunity to store food, growing larger when such opportunities exist (Krebs et al. 1996). Likewise, the number of neurons in the forebrain

(called the pallium in the avian brain, see Fig. 7) may not be the decisive trigger for cognitive behavior. This important task depends also on the activation or suppression of the links between neurons (synapses), as well as on the number of synapses per neuron and, especially, on the number of synapses that will actually fire in certain circumstances. It is this trigger that will result in action (interneuronal spiking) and, as importantly, may also inhibit actions. It has recently been found that those neuronal synapses that inhibit neural activity may well be equally important for song learning as are synapses that stimulate neural activity. In zebra finch song learning, inhibition works to protect song elements that have already been learned.

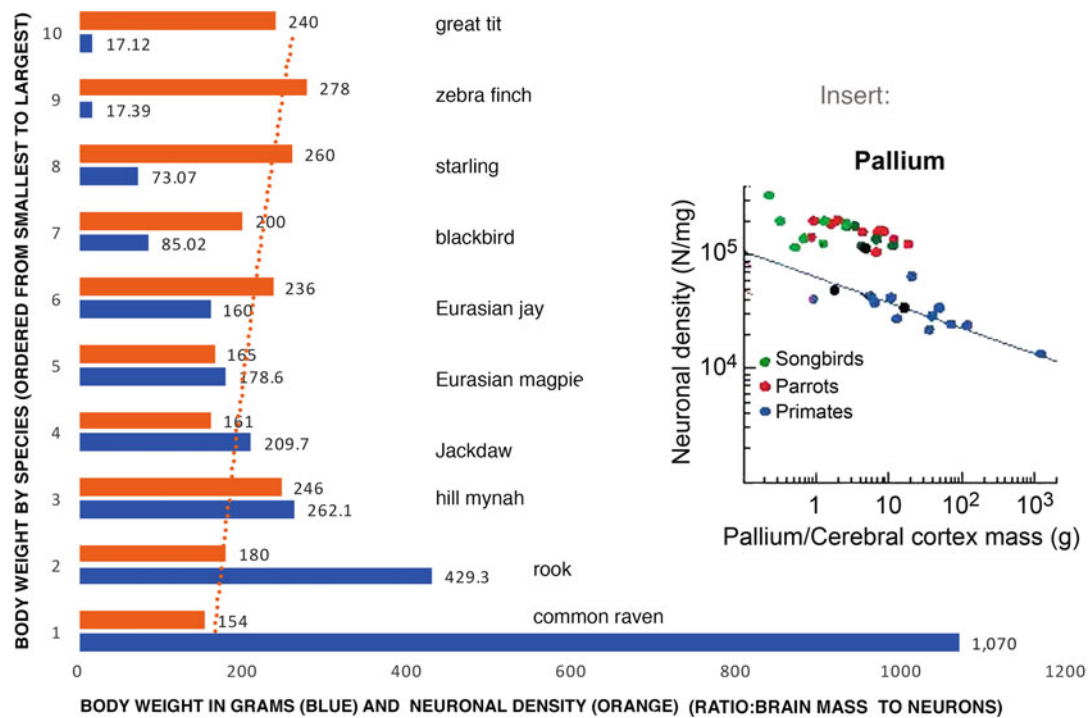
#### Neuron Counts

A final point concerns the neuron counts: there are vast differences in neuron densities between different brains. Recent research has struggled with the idea that it was not the brain size or the brain-to-body weight ratio that is important but that one needed to look in detail at the neuron density in the brain generally, and in the forebrain specifically, in order to arrive at some biological basis for the differences in cognitive abilities among birds and other vertebrates. A paper of 2016 that was quoted all over the world bore the title: “Birds have primate like numbers of neurons in the

forebrain” (Olkowicza et al. 2016). These authors argued that it was not just a matter of volume but a matter of the density of neurons and their location in the forebrain that determined how cognitively enabled and innovative a bird might be. Expressed differently, the researchers had wondered how birds, in this case ravens, were able to do complex tasks on a par with primates when their brains overall are so much smaller, and they concluded that the bird’s neuronal density is much higher than that in primate brains.

Another possibly new and yet untested interpretation, that fits well with the idea of natural constraints on basic brain design, is that biology imposes constraints on minimum and maximum numbers of neurons possible for vertebrate organisms as Fig. 8 may illustrate. Thus, variability remains within certain limits, no matter how small or large the overall body size.

Figure 8 demonstrates a possibly crucial principle that was already shown by Kuhlenbeck across vertebrates (see Table 1 above) and here is demonstrated and consistent also within the class of avian species. Looking at the trend line (stippled line in orange), there seems to be a trend for neuronal density to *increase* as body and overall brain size *decreases*. The sample of species is not large enough to confirm a significant trend. Nevertheless, the current data show at least that very small birds pack in an enormously large number of neurons into a very small space, while large birds have lower neuron density. The number of neurons has remained very similar across species with wide-ranging body weights. Similarly, when primates are compared with songbirds, if this principle is correct, then it ought not to surprise that, despite large differences in body size, there is a similar neuron density in both



**Passerine Cognition, Fig. 8** Ten songbird species – body weight versus neuron density. Blue bar signifies body weight of songbird – actual average body weight of the songbird next to blue bar in grams (e.g., great tit, 17.2); orange bar indicates the ratio of neurons to brain mass, showing that the largest bird, the raven (bottom line), has the lowest neuron density and one of the very smallest

birds, the zebra finch, has the *highest* in this sample. The insert (Adapted from Olkowicza et al. 2016, part of their Fig. 3a, plotted as a log scale) addresses specifically the ratios of forebrain neuron densities (rather than overall neuronal density) and finds that they are specifically high in songbird (green for songbirds) when compared to primates

groups. Expressed differently, biologically a vertebrate brain may require a minimum number of neurons to function efficiently, while beyond a certain maximum number of neurons, it would be wasteful to add more neurons even if the body size increased.

Finally, structure may not always coincide with function, meaning the former may just express a potential of the latter. It is worth remembering that the brain is a dynamic system, capable of responding to environmental factors that may change allocation of neurons or impair or enhance function as the case may be. For example, poor nutrition or high levels of stress during development may contribute to reduced brain growth overall, even to aberrations, or at least to severe limitations of its genetic optimal expression.

#### Laterality and Cognition

Passerines, indeed most avian species, have their eyes positioned laterally (on each side of the head) so that the optic axes are not parallel, as they are in some nightjars, all owls, cats, primates, and humans, but directed outward. The visual field of passerine birds is thus largely monocular with good acuity sideways and with only a small binocular visual field for viewing close objects. To complicate matters further, information from the right eye is received by the left hemisphere of the brain and the information from the left eye in the right hemisphere. It has been shown in the European starling (*Sturnus vulgaris*) that there is an uneven distribution of photoreceptors in the retinas of the left and right eye. Hence, each eye may send quite different inputs to their respective hemispheres. The left-right separation could potentially carry disadvantages or at least constitute unnecessary duplications. Instead, the avian brain, similar to that of other vertebrates, has turned laterality of the brain into a major advantage for survival and general cognitive power – if the left and right hemisphere can do slightly or very different things and/or modify the responses of one side with the inhibition by the other (such as curtailing fear when action is needed), then the cognitive power of and control over the organism's decision-making would be substantially enhanced.

So far, we know of the brain lateralization in passerines in only a few species, such as zebra finches, marsh tits (*Parus palustris*), European starlings, American tree sparrows (*Spizella arborea*), New Caledonia crows (*Corvus moneduloides*), and Australian Magpies. Extensive studies by Rogers (2012) over some years found that in the avian brain, the right hemisphere (use of left eye) is specialized to notice details and respond to novel stimuli. It controls fear, escape, aggression, and sexual behavior and may also be specialized for social behavior, while the left hemisphere (use of right eye) is specialized for categorizing stimuli and hence for learning to distinguish one class of objects from another. Rogers demonstrated this in seed-eating birds, by scattering grain among pebbles. The pebbles looked very similar in size and color to grains: when using both eyes (binocular vision), the birds have no problems in distinguishing food grains from pebbles. Their performance remains the same when using only their right eye but not if they can use only their left eye. When using only the left eye – right hemisphere – birds fail to discriminate between pebbles and seeds.

Research has also shown that birds with laterally placed eyes show responses to predators and conspecific on their left side and to prey on their right side. This has been demonstrated in the Australian magpie showing a clear left-eye preference (right hemisphere) for scanning overhead for an eagle (Kaplan 2017) confirming results also in other avian species that the right hemisphere has broad attention and can attend to unexpected stimuli such as a predator, whereas the left hemisphere may focus on specific tasks. In songbirds, courtship displays are activated by the left hemisphere, controlling right hemisphere-instigated copulation, as can be observed in male zebra finches, for example, that fixate the female with their right eye (left hemisphere) while they perform copulation displays. Overall, given that specific aspects of making sense of the world are controlled by different sides of the brain, lateralization of the brain enhances cognitive capacity and efficiency by retaining the possibility of integrating the information received and the varying capabilities of each side to responding to a



multitude of stimuli. Being able to attend to two tasks at the same time when each task is controlled by a different hemisphere also has clear survival value (i.e., being able to pay attention to ground foraging while remaining vigilant to a predator overhead).

### Ravens and Crows: A Special Case

Before turning to a discussion on specific kinds of the expression of cognitive behavior, ravens and crows need a separate mention because they have taken center stage in research on passerine (oscine) cognition. Indeed, highly productive and substantial research has documented a range of cognitive abilities in corvids that even just 10 years ago would have seemed highly improbable fantasy and are still regarded as exceptional among birds and vertebrates generally. Corvids have emerged as an impressively versatile and cognitively complex group of passerine birds.

Just as zebra finches became the model subject for research on birdsong, corvids have taken center stage in passerine cognition research, and, in both cases, this has had very positive and some unintended negative repercussions.

Ravens and crows as a group (the Corvidae) are useful subjects partly because of their cosmopolitan presence in the world and their easy access. Their Gondwanan origin notwithstanding,

corvids have spread all around the world, consisting of a core group of corvids, which includes crows, rooks, jackdaws, and ravens, making up more than a third of all corvid species worldwide (see Table 3 listing core corvids by distribution below). The core group of “corvus” tends to be rather similar in appearance (Fig. 9). Most of the corvus group are large birds, indeed among the largest songbirds, have strong all-purpose beaks, and have black plumage (some species have some gray plumage as well), and there are generally few, if any, discernible differences between the sexes. When all species are included, the entire family of the Corvidae (e.g., the jays, magpies, tree pies, choughs, and nutcrackers), the number of species rises substantially (to about 120). Especially among the large group of jays, one finds species that are smaller than ravens and crows and also quite often rather colorful (as the Eurasian jay) often bearing no outward resemblance to corvids.

Common ravens and rooks are most often used in cognitive research, while a number of species of jays and nutcrackers have been used in research on episodic memory (recall of past events and accurate retrieval of food taking into account not only where it was stored but also when it was stored) because they scatter-store their food, and hence they are natural choices for study of



**Passerine Cognition, Fig. 9** Cosmopolitan ravens and crows. Left: A common raven (*Corvus corax*) found across much of the northern hemisphere. Right: A Torresian crow (*Corvus orru*) of subtropical Australia and neighboring

islands – slightly smaller beak than *Corvus corax* but similar in size and sleek black feathers but white/light blue iris as against the dark brown eyes of the common raven. Jackdaws have largely dark gray plumage

memory of what and where something was stored and when it was retrieved.

Although song is not one of the most noted abilities in corvids, complex vocal and social communication is. Latest research has identified that Torresian crows use over 200 vocalizations in communication with conspecifics (McCaig et al. 2015). What raven research on cognition is most noted for is the degree of insight and stunning subtleties of social behavior (see entry ► [“Social Behavior”](#)). If one looked for an example of the relationship between cognition and social life, it is amply and well demonstrated in corvids. Ravens distinguish individuals, and it is now even known that ravens will remember individual human faces that have proven to be dangerous.

However, there are several criteria that ought to caution us against drawing the conclusion, as has quite often happened in recent years, that corvids are therefore the smartest birds of all birds and apparently of all passerines. Given our limited state of knowledge overall about individual species and even families, to draw such conclusions might well be premature; and even with the body of evidence that we already have of other birds, this has already been found to be factually incorrect.

There are reasons why corvids have become so prominent in passerine cognition research. First, there is a practical reason. This simply relates to the number of years and the number of researchers who, often over decades now, have studied specific species of corvids in great detail and have developed facilities for the long-term care and housing. Centers of research in Europe, especially in Austria and England, as well as in the United States and New Caledonia, have dedicated excellent facilities or sites to their study. In some cases, birds spend their long lives with well-known human researchers (reducing fear, increasing familiarity) leading to more representative research outcomes.

Increased knowledge derived from studying their behavior has also led to increasingly sophisticated research questions and some brilliant research designs, such as studying behavior that was once considered unobservable (Correia et al. 2007; Bugnyar et al. 2016). The same is true of

Australian magpies whose cognitive behavior has now been studied for 25 years (Kaplan 2019). Hence, the fact that such species have revealed so many astounding abilities and traits may partly be a consequence of the consistency of research making the formulation of hypotheses more sure-footed on a background of reliable and known data.

By contrast, we may possess no more than one or two studies and often quite fleeting observations of many other passerine species and often none at all for possibly thousands of others. If, on the other hand, the same depth of results could be achieved in other passerine birds, at least derived from a few families other than corvids, it is more likely than not that more or new aspects of cognition could be found in such species as well. Comparative work might also lead to questions about phylogeny, the evolution of high levels of cognitive abilities, and how these relate to environmental niches, to family structure, to life histories, to broad social rules, and even to levels of cooperative behavior. These relationships may be important, and some syntheses have been proposed, but we need more studies to be certain as to what they are. One might well also discover that some sophisticated cognitive abilities may be more widespread than can currently be claimed.

Finally, the sheer body of evidence of corvid abilities has also led to statements such as that corvids are the only truly “intelligent” birds. This is factually incorrect. In some instances, it reflects a problem of international communication. Particularly with respect to studies conducted in Africa, South America, or Australia, some findings of avian cognition and extraordinary findings have gone unnoticed or might have been ignored, and some may remain almost entirely unknown, a geopolitical bias that is being increasingly seen as needing to be more fully addressed for the sake of scientific accuracy.

The claim, repeatedly made, that ravens are the only non-hominid animals that have demonstrated planning beyond the current moment, like great apes, is factually incorrect. Anticipatory planning regardless of motivational state had been researched in western scrub jays some years ago (Correia et al. 2007). Negotiations for future

events and roster systems in cooperatively breeding passerines have been studied in other songbirds not even distantly related to ravens. For instance, there has been a fascinating study investigating negotiations in African pied babblers, *Turdoides bicolor*. Indeed, the cooperatively breeding pied babblers have been studied in some considerable detail including demonstrating teaching skills to offspring and routine kleptoparasitism. One particular study of a wild population of pied babblers in South Africa investigated in-group role divisions (Bell et al. 2010). These babblers developed sophisticated levels of negotiations about future sentinel and feeding duties. Indeed, Bell et al. (2010) showed convincingly that individual pied babblers were capable of making anticipatory adjustments to personal investment of helping based on information about the likely future contributions of collaborators. This reciprocity principle (“I will do x if you will do y”) is surely among the most cognitively complex inter-individual interactions so far recorded.

Hence, while the corvid family has become a model family for study of cognition in passerines, it does not follow that this should foreclose research on very different passerines. In doing so, we could well overlook important principles of the evolution of cognition in birds. This, of course, does not invalidate anything we now know about corvid cognition, but it certainly makes it a more urgent task to see how other large families of passerines have fared in their cognitive abilities.

## Studying Behavior: Passerine Cognition as a Graded System

Cognition in passerines has now been studied for long enough to derive the view that passerines are not simply guided by instinct but, to varying degrees, are equipped with the ability to learn, to remember, to solve problems, to innovate, and to communicate in ways that presuppose active decision-making and sometimes innovation and complex problem-solving (ten Cate and Healy 2017). Having said so, however, there are some

skills that are called adaptive because every member of the species can perform them and do so from one generation to another without any evidence of learning. Hence, some of the clever things we might see birds doing have become part of the repertoire of the species suiting their ecological niche.

Part of a basic tool kit also seems to be some basic knowledge that, surprisingly, has been described in terms of disciplines of mathematics (numeracy), geometry (spatial ability), physics (understanding gravity), and even psychology (correctly interpreting the behavior of others or understanding that objects and living things remain complete when half their body may be hidden, called object permanence). It was up to research efforts to establish whether some of the abilities in this basic “tool kit” required active reasoning and to understand whether they were based on some understanding of causality (Vallortigara et al. 2010).

Some cognitive processes are domain-specific, and these are usually referred to as modules. All studies on animal cognition in general have tended to be modular to some extent, i.e., observed skills in one domain followed by testing such particular abilities. Inevitably, research had to concentrate on very specific questions and slowly assemble a picture of the birds’ cognitive world. Some investigations started with natural behavior associated with food acquisition and reproduction, two of the most basic abilities for survival in an individual and the species. Some aspects of spatial abilities, tool use, on causal relationships and now even on matters such as nest and bower building have been explored. The latter have been called physical cognition.

## Nest Building

There are gradations in skill and complexity in nest building. Some very specific examples of nest building may in fact be well explained under the rubric of tool use, innovation, and even creativity.

Building nests in trees was in itself perhaps one of the most important innovations in passerine evolution. Passerines, together with birds of prey, are the main groups of birds that

overwhelmingly build nests in elevated positions, often requiring quite complex processes of tie-downs, observing wind direction, and other structural particulars. Water- and shorebirds, many families other than passerines, and the entire clade of fowl either build ground nests or may hollow out a depression to make a nest, or they may just nest half-hidden in grass or on bare sand or rock. Psittacine species and some other families, such as owls and kingfishers and, unusually, Indian mynas, breed in tree hollows, and yet some others may prefer to find nests others have built. Passerines are the ones consistently adept at using a variety of materials (sticks, spider webs, mud, down feathers, and even manufactured materials such as wires, plastic, clothes, fly-screen wires, and more). They often combine very different materials to satisfy the conditions needed for nestling protection from the elements, and they often camouflage the nest site by the additions of local/natural materials. Recent experimental work has shown that zebra finches are able to learn about nest building from not only their own experiences but also socially, from watching other familiar (but not unfamiliar) birds build (Guillette et al. 2016).

In the northwestern part of Europe, over a 30-year period, astonishingly, in just this one region, there is evidence of as many as 176 nesting innovations spread over a number of passerine species. There have been reports of similar frequency of nesting innovations (be this in location, tie-down, or nest materials used) in Australia (Kaplan 2015), and it would not be far-fetched to proclaim that birds, as architects, have found means of improving their lives or exploited new opportunities. No doubt, innovations, by their very nature, have to rely on forebrain activity, and, if it is a good invention, it can also be copied by others acquiring the skills needed to construct something new. Overington et al. (2009) drew the conclusion from their study that technical innovations drive the relationship between innovativeness and residual brain size.

### **Bower Building**

A peculiar habit of one group of passerines, the bowerbirds, is that all of them build bowers, some

more elaborate than others. Regent bowerbirds build relatively simple structures but dance in addition for their displays, while other species build more elaborate bowers that may involve using “paint” and brushing on color, additional decorations, and design features (Bravery et al. 2006). Some aspects of bower building go beyond mere skill development. Researchers found not only great individual differences and preferences in design but also individual insistence on maintaining their design. If some decoration pieces are removed, males compensate for such loss by increasing bower construction behavior and hastening bower painting. In other words, males are able to assess the quality of their own displays and make decisions about how to augment them. It also seems that females choose bowers not just for their decorations but also for the male’s display at the bower. It seems that the artistic forms of the construction inspire both male and female choice.

The display of the great bowerbird’s court (the areas in front and at the back of the bower) is particularly interesting because it is, in fact, purposely deceptive. Its building strategy is to create a visual illusion. The female is asked to judge the male’s achievement by the visual perspective of the court (Kelley and Endler 2012). The bird arranges the pebbles from large to small from inside to outside in a reverse way (smaller pebbles in front, large in the back) creating a visual illusion known as a forced perspective. The female viewing the male’s display over the court apparently judges the perspective and the quality of the illusion as the most important variable.

### **Use of Sticks and Implements Generally**

The distinction is usually made between proto-tool use and true tool use. Proto-tool use is not in itself a tool but indirectly an aid to achieve something else – for instance, wedging a nut between the fork of a tree steadies the nut and enables the bird to hammer away at the nut until it breaks. Proto-tool use is considered the cognitively simpler form of tool using but can be quite ingenious in helping an individual to obtain food from a source that may be enclosed by a hard shell or, if a caterpillar, has biting or toxic parts. Using an

appropriate substrate (or spear the prey on a thorn) can help to complete the task, remove the shell or the biting parts.

The list of passerines having perfected such techniques is quite long, and such behavior has been observed on every continent. Nearly all ravens and crows worldwide have been observed to use proto-tools and true tools. There is an interim group that has usually been fitted into proto-tool use, but it seems quite remarkable. Quite a number of birds have learned to use bread as a bait for fish. Since such species (observed in herons, Australian ravens, and many others) could readily consume the bread, the birds would have to inhibit their own appetite for the bread for something better (often called deferred gratification). That is, the bird has learned not just what is edible but that it can use the more inferior food if it is willing to risk the loss of this food morsel or something qualitatively better (as a fish) and possibly even larger than the food already in hand (Kaplan 2015). True tool use, by contrast, means that an implement has to be used in order to achieve an outcome that could not be done by the bird without such a tool.

As the tasks get more complicated, the number of passerine species engaging in true tool using behavior dwindles, although the number of ravens and crows (and of the entire widespread corvid family) tends to remain constant. Another, more ingenious way is to drop the prey item onto some substrate. For instance, an egg can be broken easily this way without falling apart, depending on the height chosen of course, enabling the thief (they have to steal it from a breeding species) to keep most or all of the contents inside the shell so that it can be accessed by the bird. Crows in Japan have learned to throw nuts on the road and let car tires crush the nuts for them.

Innovations or spontaneous choices in birds sometimes surprise because of their ingenuity. In England, the great spotted woodpecker (*Dendrocopos major*) has been observed in the wild to peck on a public-address system to amplify its sounds specifically in the direction of a conspecific. In the laboratory, great spotted

woodpeckers have been shown to be capable of cognitive tasks of a complexity matching that found in crows and parrots, so this specific behavior actually fits into a broader scale of cognitively more abstract behavior in this particular species. However, choosing a public-address system to enhance its own impact of an auditory message is a clever trick, but it is used by many animals. For instance, large Australian tree frog males preferentially choose to sit in downpipes of houses where their croaking is substantially amplified and helps to advertise their territoriality or impress a potential partner.

True tool use, for instance, may involve picking up sticks and holding it in the beak to probe for ants, just as do great apes. Birds may use empty shells to prise open a mussel (as white-winged choughs do, *Corcorax melanorhamphus*) or collect and carry sticks to another site as varied sittellas do (*Daphoenositta chrysoptera*) indicating that the bird had a specific goal and has taken the appropriate equipment to the “job site” where retrieval of a wood borer is expected to occur or hoped for. Blackbirds, *Turdus merula*, use tufts of twigs as a broom to remove loose snow cover when trying to find food. Regent bowerbirds are known to use wads of greenish leaves as “paint-brushes” to help change the coloration of the bower, representing a well-known example of tool using by birds. New Caledonian crows and woodpecker finches habitually use and manufacture tools in the wild. New Caledonian crows have also been shown to be capable of tool selection, and modification, and meta-tool use (i.e., using one tool to access another tool to access food).

In a recent set of experiments, the investigators compared two similar-sized (medium) and highly successful passerines in a range of foraging tasks, one an introduced Indian myna, *Acridotheres tristis*, belonging to the starling family, and the noisy miner, *Manorina melanocephala*, a honey-eater (Griffin and Diquelou 2015). They found that, in Australia, Indian mynas were significantly more neophobic than noisy miners, not surprisingly since there are various programs for their culling in place (they are an introduced species). However, in innovative foraging tasks, Indian



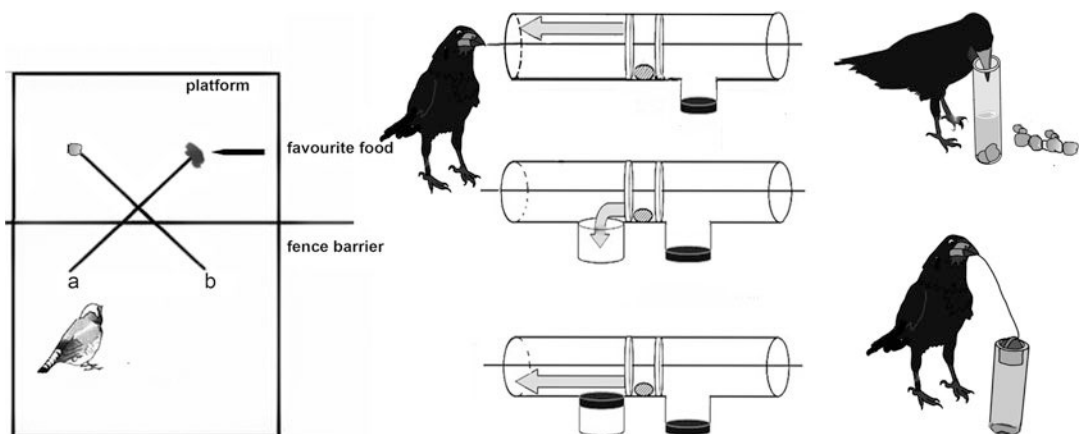
mynas consistently outperformed noisy miners. The ability to use the beak in a greater range of ways, and more flexibly, was highly repeatable in Indian mynas and underpinned their superior problem-solving performance. They also found significant differences in motor diversity and motor flexibility between the two species. Their findings raise an important point about the physical ability of a species and its relationship to cognition. Motor flexibility and even motor diversity proved to be factors that were significantly and negatively correlated with the speed of solving a task. It could be argued then that the differential results between noisy minors and Indian mynas may have nothing to do with more or less complex cognition but with the design and function of the bird's anatomical structure, here the beak (Griffin and Diquelou 2015).

Field observations of tool use in many passerines worldwide have raised the question as to whether passerines can take this tool using a step further by presenting them with a problem that can only be solved when they use reasoning. The most well-known and most frequently used laboratory tests are the tube tests, the means-ends test, and, more complicated, tests that replicate the Aesop's fable of raising the water level in a glass to obtain a floating food item. Equally well tested is tool adaptation or tool selection to obtain a food morsel (see Fig. 10).

### Laboratory Studies – Means-Ends Tests and Others

The means-end test has been used in a number of ways, but the basic principle is the same – a favorite food is affixed to the end of one string, and then another string that overlays it in an angle has a stone or some other inedible item of a similar size as the food morsel attached to it. The two strings are then crossed in such a way that the one end closer to the bird actually has a stone attached and, visually, the favorite food item is in line with the wrong string. If the bird follows just visual markers, it should spontaneously choose the wrong string, but if it had followed the line of the string from the favorite food item back to the end of the string that it can reach, it will choose the right one. Indeed, both seedeaters and insectivorous passerines can do this easily ranging from some of the smallest (zebra finches, sparrows) to the largest passerines (ravens). This test is also rather close to avian natural behavior and is possibly a circumstance seedeaters and even insectivorous birds may encounter periodically.

The tube test, used as another standard piece of testing equipment (Fig. 10), has a favorite food item placed in a transparent tube that is open at both ends. The bird has to use an implement and has to figure out from which end it needs to approach the task because one side will have a hole at the bottom and if the bird chooses this one,



**Passerine Cognition, Fig. 10 Solving problems of access to food. A** Means-ends test – zebra finch needs to pull string and chooses the correct one (a). **B** Tube test in

various configurations with implement; **C** rooks understand how to raise water level or adapt tool to retrieve food (part C adapted from Jelbert et al. PLOS one, 2014)

the food raked in (or pushed out from the other side) with an implement which will drop through the hole and make the food item irretrievably lost. The tests establish whether the subject of the test recognizes which tube is complete and will allow the individual to maneuver the food safely by choosing the right direction for extracting the food. This is a far more difficult test, and many birds fail, possibly for not being able to manipulate the relatively long implement all that well (again – the shape of the beak and its function may be an important factor) or because the hole in the bottom of the tube was not spotted or the consequences of the food falling into the hole were not fully understood.

Cognitively very demanding, and more than just a grade of difficulty harder, is the floating peanut test which presupposes an understanding that rocks can displace water and hence make the water level in the tube rise. A number of recent investigations using the floating peanut test were conducted with rooks and with New Caledonian crows (Fig. 10). The crows solved the physical problem and used the stones to raise the water level to a height where their beaks could reach and retrieve the floating nut. This water displacement principle is an important physics principle but rather beyond comprehension for human children under 6 years of age. It has puzzled researchers for some time why children even as old as 8 years, and with extra help given, have such difficulty in solving a problem at a time when they already use basic implements (Cutting et al. 2014).

Finally, another test involves adapting a tool to fit the purpose. A tube without water has a peanut placed at the bottom of it and several items are placed next to it. When the bird makes the right choice and bends the end of the wire, it can hook up the peanut and lift it out of the tube. Again, this is a task children of 8–9 years old may still find difficult to solve but not ravens. Of course, there is the less elegant but equally effective method that Australian magpies use when confronted with this problem – they simply upend the tube, and the peanut drops out!

There are many simple tests that can be conducted in a laboratory that may suggest how

well a bird has understood and used, or gone beyond, its basic “tool kit” of knowledge of geometry, mathematics, or physics and how well it can predict the outcome of its actions.

## **Behavioral Evidence of Concepts of Past, Present, and Future**

The idea of having a concept of time was thought to be uniquely human. It was believed, almost until the turn from the twentieth to twenty-first century, that the only existence animals knew was in the present. Disproving such a belief scientifically, however, is difficult because time is by its very nature fleeting and abstract. The research that commenced in the 1990s on memory of past events in passerines was ingenious, logical, and scientifically plausible. Researchers picked as their subject birds that were known to hoard food. There are different ways of hoarding food. One is to transport food items to a fixed larder. Hoarding a supply of food for winter months underground or depositing food in a hollow or making holes in the bark of a tree and inserting pine nuts, as woodpeckers do, is a rather widespread phenomenon. This behavior could be triggered simply by changes in temperature and may provide little if any hints as to whether the birds have understood that their present behavior is based on past experience, let alone whether there is any sense of future.

There is another type of food hoarding, however, called scatter-hoarding found in nutcrackers and several species of jays. In those cases, the individual birds take nuts in autumn and hide them in widely dispersed positions across the ground. Researchers rightly assumed that if any species could demonstrate that they have a concrete memory of specific past events, it had to be those species whose survival in the harsh winter months depended entirely on the recovery of food items they had hidden in autumn. Importantly, such hoarding behavior had to include a memory of past actions and events. This process could also be tested experimentally. It is called episodic memory, indicating that a bird may be able to record and remember specific events of the past

and act on that memory in the present. It was possible to measure what the Clark's nutcracker actually did. It was found that it can successfully retrieve as many as 30,000 pine nuts in a season and retrieve more than 90%, a truly remarkable feat. The birds do so by using cognitive spatial maps: that is, using geometry rather than simply remembering the details or landmarks. The latter would not help since snow cover dramatically alters landmark appearances.

Experiments using western scrub jays (*Aphelocoma coerulescens*), part of the larger corvid family, suggested even more strongly that there was more at work than merely memory of geometry. The birds regularly experience conspecific onlookers spying on their activities with the clear intent of stealing the cache. Hence, to hide food in the presence of others is risky and requires re-hiding when a potential competitor has witnessed the caching. Scrub jays, moreover, will cache both perishable and imperishable food, and they retrieve the perishable food first indicating that they remember what they have stored, where they stored it, and when they stored it (Clayton and Dickinson 1998) fulfilling the three important ingredients of episodic memory (what, where, when). The ability to remember the exact and general location of the hidden items for days has also been tested in pinyon jays (*Gymnorhinus cyanocephalus*). The birds watching someone hide a piece of food could remember the location of caches made by the observed bird even 2 days later and even 7 days later searched in the correct general locations. There is a further and specific dimension of time concerning the perishability of food itself.

Similar studies have been conducted with black-capped chickadees (*Parus atricapillus*) and most other tits in the family Paridae, as well as nuthatches (family Sittidae), and magpies, *Pica pica*. They too store food in cache sites scattered through their home range and may create several hundred such sites in a day. They never reuse the same cache site and retrieve their stored food after a few days by remembering the precise spatial locations of their caches. In all the cases recorded,

it was found that the birds used a cognitive spatial map.

One can also argue that by extending the ability to stash valuable resources for the future and not for current consumption, there is a clear extension of the time frame. Hence, episodic memory is associated with future planning which then raises the entire spectrum of time from the past to the future, a fact that finally answered the question whether passerines merely live in the present. They do not (Raby et al. 2007).

There are also passerine species, chiefly but not exclusively the honeyeaters, which do not cache their food but rather rely on a food source that has its own ebbs and flows of availability, and these are all the nectar-producing plants. When a supply has been depleted, it takes some time for the resource to replenish. Birds must remember what they found, where it happened, and even when they found it. They must also learn about the intervals at which this food source replenishes.

The now thoroughly disproved Bischof-Köhler hypothesis that only humans can dissociate themselves from their current context and take action for future needs sounds quite hollow in the twenty-first century because we know that passerines plan for the future in a variety of ways. There are ways of thinking about the future other than food and even in areas that are far more abstract: it has been shown that this is possible but depends on a social context, which will be raised in the next section.

## Social Brain and Memory

What is it about couples and specific groups that may enhance cognitive ability? Swallows and martins have communal activities including nest material collection and social flights in morning and evening, orioles sometimes bathe together, apostle birds and babblers do everything as a group, and finches and many other passerines may have large social gatherings. Superb blue wren males may form "clubs" to support

extramarital activities, and males may help raise offspring not their own, and many avian species engage in social drinking (Kaplan 2015). Yet some of these communal activities remain at the level of aggregation and may neither enhance communication nor social cohesion.

The question occupying researchers is whether activity-based social behavior has an impact on cognition. Indeed, a recent paper showed that, in woodpeckers (Picidae), living in stable social groups is associated with a *reduction* in brain size. The authors explain that multiple and reliable sets of eyes and minds reduce the need for extravagant brain power (Fedorova et al. 2017). Picidae (woodpeckers) are not passerines (two toes forward and two back), and they do not sing. Perhaps this suggests that it is important to consider brain differences and how they have arisen in different orders.

Most passerines live in some kind of social group. Indeed, one of the most remarkable aspects about bird life is that close to 90% of passerines (as against 5% of mammals) raise offspring together as a pair. A fraction of them has opted for a cooperative model, meaning that offspring of previous years provide additional help at feeding the new generations of nestlings. It depends what functions such a group may have and whether such groups can be called “social.” Sociality is an important topic in primatology, but it took some time for ornithology to establish the view that many birds are extremely social and that “social” meant a specialized form of communication that goes well beyond observed incidents of flocking and loose aggregations of nesting colonies.

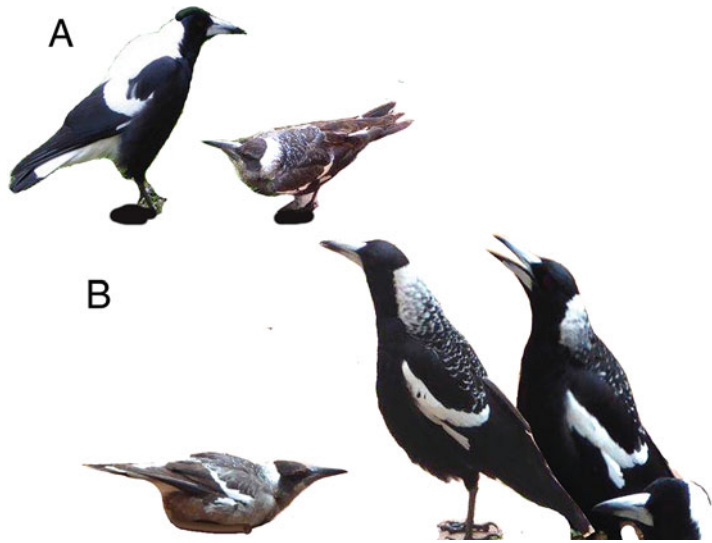
Group living and cooperative passerine species, as well as similar social arrangements in primates, have given rise to the assumption that brain power and cognitive abilities increase with greater and more long-term partner cohesion than in loosely bonded groups or frequently changing partnerships. The social brain hypothesis arose out of these assumptions arguing that the major functional role of the vertebrate telencephalon is the regulation of social interaction.

This hypothesis raises an important question: What does a community of animals gain from being a community? The reasons for colonies of birds nesting together are well documented. There are safety in numbers and the likelihood that more offspring survive if thousands of them hatch at the same time. Equally, large numbers may act as a safeguard against predators generally. It is little more than that.

There are social behaviors that seem to go further and signify communication and information sharing that may benefit everyone in the group and lead to better survival rates and improvements in foraging and other areas. Information sharing can benefit generation after generation of bird groups. Active information sharing with conspecifics may be used to reduce exposure to risk. Sasaki and Biro (2016) investigated such stable communities describing the emergence of a cumulative culture from collective intelligence with the important rider that such group activity tends to increase efficiency over time but not necessarily complexity. Yet what the accumulation of knowledge achieves is that it exceeds the capacities of single individuals and that such a framework in turn may, at times, throw up exceptional innovations or individual innovators.

The social brain hypothesis has fitted well around ravens and crows because they fulfill all criteria – living in close-knit groups, having large brains, and, moreover, showing genuine, sometimes even altruistic ways of dealing with conspecifics, such as bartering, consoling a defeated mate, sharing, and even resorting to reciprocal altruism. If one looked for an example of the relationship between cognition and social life, it is amply and well demonstrated in corvids. Quite a number of birds apart from ravens and Australian magpies, even chicken not belonging to passerines, can distinguish individuals.

Common ravens and rooks have been shown to exchange coalitionary support among bonded friends, which may be expressed by approaching and grooming the other in order for the groomer to secure support later. Of course, such subtle social interactions presume that they know and



**Passerine Cognition, Fig. 11 Interactive postures in Australian magpie families.** This is just one interaction following unacceptable behavior by a juvenile, having snatched some food ahead of the adults. The above panel shows the first consequence: the adult male (the father) shows rising anger not just indicated by the erect body posture but by the feathers rising on his back. The offspring shows submissive behavior by curving its back downward and crouching (just as Charles Darwin had first illustrated in dogs), keeping the head down and tilted and thus putting himself straight into the line of fire by risking a peck, and by doing so, he may, in fact, not get physically punished.

The offspring plays a very different game with the adult females (including his mother). Females usually do not engage in physical punishment. The females, note the three females all face the offending youngster, are also erect in posture, and one even vocalizes in disapproval – the offspring adopts a posture as a nestling and the “cutest” it can possibly manage. In both cases, the strategy succeeded and the adults eventually left. However, a further transgression may, in fact, result in physical punishment. Usually, the juvenile has learned the lesson and won’t repeat the same transgression (but may well commit others)

recognize each other and treat each other not just as individuals but as “significant others,” and we know this because their vocal communication has been studied in detail (Kaplan 2014). Such studies revealed, in common ravens and in Australian magpies, that these vocalizations carry individual characteristics which are recognized by group members (Kaplan 2019). It has recently been discovered that ravens even remember the nature of a single reciprocal interaction sequence over 2 days and even after a month (Müller et al. 2017). In general folklore, one speaks of raven groups as a “parliament” of ravens as if to suggest that they were able to control impulses and make rational and informed decisions, i.e., approaching a quality that is thought to be unique to humans. Indeed, research into passerine cognition has given us an inkling that some passerines may indeed show behavior that approaches rationality.

Often not discussed are the nonvocal forms of communication. Charles Darwin (1904) was fully aware of the complex range of body postures and movements as expression of social dynamics, be this in the context of strict social hierarchies or, perhaps even more so, in rather egalitarian partnerships especially when monogamous or as life-long partnerships. Passerine species with long-term pair or group commitments have often developed a rich range of vocal and nonvocal signals that are clearly understood and can be regulatory or supportive (Fig. 11).

Intimate levels of complex interactions observed in the bird world may well rival those of subtle interactions in troops of chimpanzees, elephant families, wolf packs, and pods of cetaceans, and it suggests that avian cognition in general, and passerine cognition in particular, is an exciting field that has just begun to reveal some of the birds’ cognitive attributes.



The discovery of the broad range of cognitive behavior in passerines has been a beacon for reassessing how evolution works and how even birds, once thought simple mechanistic organisms driven only by instinct, might need a cognitive tool kit to survive. These “tool kits” have been extended into the complex social domain, into long-term memories and knowledge of past events and of a future dimension, and even into the realms of strong allegiances among families and engaging in behavior that suggests empathy and personal conflict resolutions. The results so far available about passerine cognition are very important because they have utterly challenged the idea that evolution has favored the primate line as the only carriers of “intelligence” in the broader sense (called the g factor loading of cognition). The robust findings have undermined the view of *scala naturae* when applied to cognition and finally utterly destroyed the Cartesian notion that animals cannot think, a claim that a philosopher, Rene Descartes, had so brazenly made some 400 years ago. The latter’s dictum which had colored our way of thinking about animals in general well into the twentieth century has been disproven.

## Cross-References

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## Passerine Life History

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## Synonyms

Growth; Perching birds; Reproduction; Survival

## Definition

Passerine life history describes the reproduction, growth, and survival patterns of the avian order Passeriformes, which includes two principal suborders, Tyranni (suboscines) and Passeri (oscines or songbirds), in addition to the basal suborder Acanthisitti (New Zealand wrens).

## Introduction

Perching birds called passerines represent a diverse and species-rich order of mostly small land birds. Defining characteristics of passerines include unique oil glands, spermatozoa, forelimb and hindlimb musculature, and an enlarged flexible hind toe (hallux). Many passerines exhibit unique behaviors and physiologies and possess relatively large brains and superior learning capabilities particularly with respect to vocalization richness and song learning within the suborder Passeri. The behavioral plasticity and learning abilities of passerine birds very likely gave them an advantage over non-passerine competitors that explains their success being the most species-rich order of birds, constituting more than half of all species of birds worldwide. Passerines are generally short-lived and highly social often forming same or mixed-species flocks. Fundamental differences in the anatomy of the syrinx distinguish between suborders of passerines: the suboscines (Tyranni) and the oscines or songbirds (Passeri) (Raikow and Bledsoe 2000). However, recent studies have suggested that New Zealand wrens (family Acanthisittidae) form a third, more ancient, suborder, Acanthisitti, with no living close relatives (Ericson et al. 2002). New Zealand wrens are called “wrens” due to similarities in appearance and behavior to the true wrens (Troglodytidae) of the suborder Passeri but are not members of that family. This chapter addresses key life history traits for passerines, although at times closely related orders are mentioned, focusing primarily on reproduction, growth, and survival. A more thorough account of avian cognition is covered elsewhere within

this encyclopedia and therefore will not be addressed in any depth here.

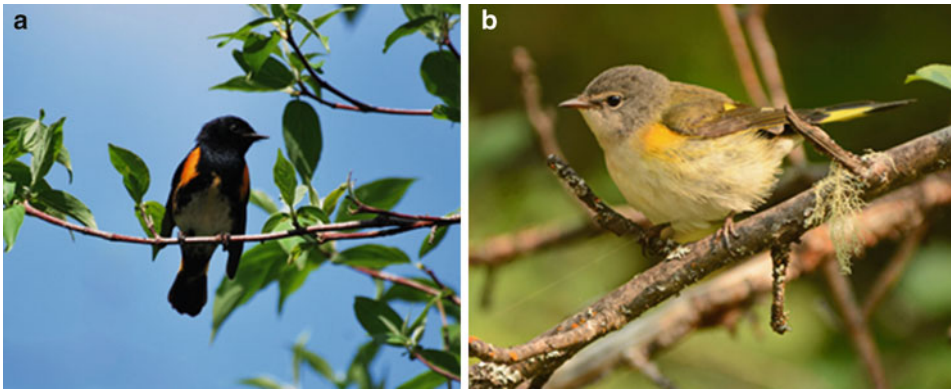
However, a discussion on avian life history would be lacking without a brief mention of the remarkable intelligence of birds. Research over the past 50 years has shown that historical views on bird intelligence, emphasizing that avian behavior is stereotyped, are incorrect. Studies have demonstrated that birds possess considerable behavioral adaptability when foraging, communicating, selecting mates, interacting in social groups, and avoiding predation (see Krebs and Davies 1984). It is clear that using information about the environment to guide behavior can have large effects on biological success or fitness. But to acquire such knowledge, a bird needs to have had suitable experiences and possess the cognitive mechanisms necessary to transfer experiences into knowledge that can then be used in the future (Balda et al. 1996).

## Reproduction

### Mating

Many species of birds are sexually dimorphic in color or color patterns. Sexual dimorphism with respect to plumage color is considered to be a consequence of sexual selection (Hamilton and Zuk 1982). Variation in the extent of sexual dimorphism among passerine species is typically attributed to differences in mating systems. For example, sexual dimorphism in passerines can take on many different forms; male and female corn buntings (*Miliaria calandra*) have nearly identical plumage, but males are typically 40% heavier than females. Male and female American redstarts (*Setophaga ruticilla*) are similar sizes, but the dark black and orange plumage of the males is unlike the drab grey, greens, and yellows of the female (Fig. 1).

Researchers agree that passerines typically conform to social monogamy where individuals pair bond with a single member of the opposite sex. Approximately 92% of all bird species exhibit monogamy. Multiple mating systems have been observed in passerines though polygyny, in which males mate with several females



**Passerine Life History, Fig. 1** Photograph of male (a) and female (b) American redstart (*Setophaga ruticilla*; Photo by D.V. Gesicki)

(but each female mates with only one male), and polyandry, in which females associate with several males, have been observed in passerines. The dunnock (*Prunella modularis*) is unique among all birds because they possess variable mating systems. Female dunnocks are often polyandrous, breeding with two or more males at once. This mating behavior has led to the development of robust sperm competition among males. Males attempt to ensure their paternity by pecking at the cloaca of the female to stimulate ejection of rival male sperm (Davies 1983). Other mating systems also exist within dunnock populations and depend on the sex ratio of individuals in the population and territorial overlap. Based on knowledge of territory quality and sex ratio, dunnocks adjust their mating systems, adopting monogamy, polyandry, or polygyny when each system would seem advantageous (Davies and Houston 1986; Hatchwell and Davies 1992). Individual dunnocks seemingly adjust their social behavior depending on a cognitive assessment of several environmental and social parameters.

Promiscuity and extra-pair copulations have been reported in monogamous species, polygynous species, and polyandrous species. Extra-pair copulations are defined as copulations with an individual(s) other than a mate or social partner. The percent of extra-pair young in avian populations may range from 0% to more than

50%, but in many songbird populations, the percentage of extra-pair young is typically between 10% and 25% suggesting that at least some individuals in a population benefit from extra-pair copulations (Griffith et al. 2002). At one extreme, in the cooperatively breeding superb fairy-wren (*Malurus cyaneus*), it has been shown that other males may father 72% of offspring and that 95% of broods contained extra-pair young (Double et al. 1997; Double and Cockburn 2000). Domestic canaries (*Serinus canaria*), a species known for not having high social cognitive abilities, have been shown to subtly adapt their behavior to the current social environment. In one study, male canaries actively tried to conceal their extra-pair courtships in the presence of their mate and were observed to increase aggression toward other males when their mate was watching (Ung et al. 2011).

### Parental Care

The avian egg is a remarkable structure; it provides not only nourishment for the developing embryo but also proper ventilation, insulation, resistance to temperature fluctuations, and protection. After fertilization, the egg with its embryo pass through the oviduct, where albumen and a hard shell made of calcium carbonate are added to the developing egg, a process that takes from 1 to 7 days. Some birds have fixed clutch sizes; the

clutch size is the number of eggs a bird lays in one set. Variations in clutch size reflect genetic differences between individuals in addition to age, resource availability, geographic region, and season. For example, observed average clutch sizes across populations of passerines show a strong geographic gradient from an average of 4.5 eggs at the high northern latitudes to just over two eggs per brood in the tropics (Jetz et al. 2008). Incubation is the process by which the temperature of eggs is maintained via heat exchange from the brood patch suitable for embryonic development; most birds exhibit biparental care. Nest attentiveness or the percentage of time spent on the nest during incubation is an example of parent-offspring conflict. Incubating birds must balance a trade-off between caring for eggs by staying on the nest versus caring for themselves by getting off the nest to forage. After hatching, parental care involves brooding and feeding nestlings as well as protecting young from predators. All passerines give birth to altricial young. Altricial young are naked, blind, and virtually immobile when they hatch and thus are completely dependent on their parents. Interestingly, it has been suggested that altricial development is only possible because passerines have evolved the ability to construct a nest, which protects chicks from predators and from poor weather. Only a few species, for example, brood parasites, exhibit no post-hatching parental care.

### Brood Parasitism

Avian brood parasitism, or the laying of one's eggs in the nest of another individual, is a reproductive strategy in which one imposes the costs of incubation and rearing of young onto another individual, the host (Davies 2000). Brood parasitism may be either obligate when all the eggs are laid in the nests of other individuals or facultative when some eggs are incubated by the parents and other eggs laid in the nests of other individuals. Facultative brood parasitism is uncommon in altricial birds but is widespread in precocial waterfowl. Brood parasitism may also be intra-specific, with eggs laid in the nests of a parasite's own species, or interspecific, with eggs laid in the

nests of other species. Obligate interspecific brood parasitism has evolved at least seven separate times among various avian clades, including twice within the order Passeriformes (cowbirds (Icteridae) and indigobirds and whydahs (Viduidae)). The benefits for the parasite include increased fecundity as more effort can be directed toward mating and producing eggs rather than building and defending nests, incubating eggs, and feeding young. For hosts the costs include diminished nestling growth rates due to nestling competition with the often-larger parasitic offspring, total abandonment of parasitized broods, eviction of all host eggs by the earlier hatching parasites, or the killing of host hatchlings by parasitic hatchlings (Kilner 2005; Servedio and Hauber 2006). These costs exert selective pressure on hosts to evolve defenses to discriminate against parasitic eggs or hatchlings based on visual and acoustic cues (Cassey et al. 2008).

## Growth

### Hatching and Neonate Size

Hatching, the breaking of the eggshell and emerging from it, is a physical challenge. Postembryonic development before hatching is when the basic systems of life are established, including a skeleton made first of cartilage and then calcified, a digestive system that sets limits on energy intake, a brain that will continue to grow, and a feathered integument. At the time of hatching, the chick barely seems to fit inside the tight confines of the eggshell. To break out of the egg the chick shifts its position within the inner membrane of the egg and begins pipping or pecking regularly at the shell. After 1–2 days, the chick breaks through the eggshell emerging to the outside world. Eggs in a clutch may hatch synchronously or asynchronously at intervals that may range from a few hours to more than a week (Clark and Wilson 1981).

### Patterns of Growth

A typical passerine hatchling's growth of body mass during development follows an S-shaped



logistic curve. At first the young bird grows slowly, then the growth rate accelerates and mass increases rapidly, and, finally, growth decelerates as the bird's weight reaches that of the adult. There are two distinct exceptions to the typical shape of the growth curve. The mass of highly aerial species, such as the American cliff swallow (*Petrochelidon pyrrhonota*), overshoots the adult mass during the final stages of development before juveniles have learned foraging techniques. Body mass then declines as a result of changes in metabolism and water loss as the result of tissue maturation in the skin. The second exception is in ground-feeding birds such as the curve-billed thrasher (*Toxostoma curvirostre*) where chick mass stabilizes below adult mass (Ricklefs 1965). Ground feeding chicks achieve full size after fledging when their plumage and muscle development catch up with their skeletal development. Altricial species, in comparison to semiprecocial or precocial species, generally exhibit faster development and tissue maturation. Individuals of a species can show markedly different growth rates and generally nestling growth rates often decline as brood size increases (Klomp 1970). Perhaps best known in swifts and martins, maturation rate varies with the quality and quantity of food, temporal patterns of feeding, and temperature. For example, maturation of common swifts (order Apodiformes *Apus Apus*) varies from 37 to 56 days, depending on food availability (Koskimies 1948).

### Maximum Size

The maximum size of passerines relates to the costs of flight, which is influenced by the relationship between total wing area and body mass. The relationship between wing area and body mass, called wing loading, is given in grams per square centimeter of wing surface area. Considerable data on the subject of wing loading has been collected from European and North American species. Small passerines have rather large wings and, consequently, low wing loadings. For example, the ruby-crowned kinglet (*Regulus calendula*) has a wing loading of, on average, 0.11 grams per square centimeter. Among North American passerines, the American

crow (*Corvus brachyrhynchos*) has one of the highest wing loading of about 0.41 grams per square centimeter (Poole 1938). Although wing lengths and surface areas increase typically with mass among birds, the increase is less than expected to maintain a constant wing loading. The wing area increases as the product of the length and width of the wing's surface, whereas body mass increases with volume. Therefore, wing area must increase at a rate of 1.5 times for each single unit of increase in mass. The theoretical upper limit therefore for birds is around 2.5 grams per square centimeter. At this point most birds cannot generate sufficient lift with their wings to overcome drag and gravity. Worldwide, the thick-billed raven (*Corvus crassirostris*) has the distinction of being the heaviest passerine weighing approximately 1.15 kg in females and 1.5 kg in males and the smallest being the short-tailed pygmy-tyrant (*Myiornis ecaudatus*) with an average weight of 4.2 grams (g).

### Feathers and Molt

Among passerines, feathers are essential for flight in addition to providing thermal insulation and waterproofing. Feathers play further roles in communication, courtship, and competition for mates and in predator avoidance through camouflage. Although growing feathers are vascularized, mature feathers are dead structures and cannot be repaired. Feathers may become damaged during encounters with rivals, predators or prey, or through normal wear and tear and must be replaced. Molt, the systematic replacement of worn and damaged feathers, is essential to birds. In some species, however, molt serves an additional purpose as it allows birds to change their appearance to suit their needs at a given stage of their life cycle. For example, males of many passerine species annually molt all or some of their feather to shift from a non-breeding plumage to a breeding plumage. Molt strategies are often related to migratory behavior. Among old world warblers (*Sylvia*), species or populations that are relatively sedentary tend to spend a longer time on their molts than species or populations which migrate (Ginn and Melville 1983; Holmgren and Hedenström 1995).

## Survival

### Longevity

Determining aspects of passerine survival can be a challenge given the difficulty in following birds, particularly migratory species, over extended periods of time and considerably large distances. Rates of annual survival change dramatically with age across the first years of life. A young bird's chance of survival to a breeding age is typically about half the rate of adult annual mortality. Once juveniles reach adulthood, their chances of survival increase and stay relatively constant. Annual survival rates of small land birds vary from 30% to 65% per year (Ricklefs 1973). However, survival rates of adults do not remain constant. Carefully controlled studies of mortality among Florida scrub jays (*Aphelocoma coerulescens*) revealed increases in mortality at an average rate of 2% per year because of the degenerative effects of aging (Holmes and Austad 1995). The maximum lifespan of passerine birds can vary significantly. For example, the European goldcrest (*Regulus regulus*), a small member of the kinglet family, has an average lifespan of 3 years while the song thrush (*Turdus philomelos*) has an average lifespan of 13 years in the wild (Payevsky and Shapoval 2000).

### Predation

Predation is often hypothesized to be an important factor shaping the evolution of clutch sizes in birds (Perrins 1977) and is often thought to favor smaller clutch sizes. For example, it takes longer to lay a large clutch than a smaller one, which means that the parent and eggs of larger clutches are at risk for a longer period of time than those of smaller clutches. In the tropics, where most nests are lost to predators, smaller clutches may be advantageous as a mating pair of birds has the opportunity to re-establish nests several times throughout the year. The number of fledged young a parent can attend to or guard against predators may also limit clutch size in some birds (Yom-Tov 1974; Safriel 1975).

Adult birds often form flocks, a behavior that reduces the risk of predation and enables cooperative foraging. Stable food resources and

defensible spaces promote territoriality in birds, but unstable food resources and indefensible spaces will promote flocking behavior. Flocks can range in composition from loose temporary groups of a single species to highly organized foraging groups composed of multiple species. Multi-species flocks of tropical songbirds, which feed together throughout the year, are an example of a closed social system that actively exclude new members. A stable flock membership facilitates individual recognition and the development of dominance hierarchies (Hartzler 1970; Nilsson and Smith 1988). The safety of a large group enables individuals to relax their personal watch for predators, thus enabling them to feed more intensively.

### Movement Patterns

Migration allows for year-round activity. The advantage of migration is that birds can exploit seasonal feeding opportunities while living in favorable habitats and climates throughout the year. Migration clearly involves movement, but not all bird movements can be called migration. Migration is the regular, endogenously controlled, seasonal movement of birds between breeding and non-breeding areas (Salewski and Bruderer 2007). Some birds make less predictable, non-migratory movements in response to proximate environmental factors. Such movements are often referred to as irruptions or nomadic movements rather than migration. For example, whenever spruce seeds are scarce or absent entirely over much of their breeding range in the boreal forests of northern Europe, large numbers of common crossbills (*Loxia curvirostra*) move long distances, often 1000 kms or more, toward southern and western Europe (Newton 1970). Irruptions are irregular, but not infrequent; at least 40 irruptions of common crossbills are known to have occurred between 1881 and 2000 (Newton 2006).

Migratory birds exhibit variation in the distance of their migratory journeys, with some short-distance migrants moving just a few hundred kilometers and some long-distance migrants traveling several thousand kilometers. Many factors can contribute to this variation in migration distance among different populations

and species. For example, among suboscines (Tyranni), migration distance is influenced by feeding behavior, with insectivorous species tending to migrate longer distances than frugivorous or granivorous (seed-eating) species (Boyle and Conway 2007). Because of the differences in the availability of prey, many insectivorous species breed at higher latitudes and migrate relatively long distances to winter at low latitudes.

### Feeding Ecology

Closely linked to migratory movement in many passerines is the location of food resources. Birds expend energy at a high rate and must feed frequently to refuel themselves. Adaptations for feeding are a conspicuous feature of avian evolution. Adaptations not only include those for flight but also anatomical specializations of the bill and tongue, legs and feet, crop, and stomach and intestines. Considerable research interest has been placed on the balance between feeding effort and energy requirements, and the role that learning plays in increasing foraging efficiency. Some bird species are also well known to store food reserves for later use, a behavior known as caching, and the sometimes-spectacular recovery of cached seeds highlights the extraordinary spatial memory ability of some granivorous species (Källander and Smith 1990).

A bird's bill or beak is its key adaptation for feeding. The size, shape, and strength of the bill dictate potential diets. True shrikes (*Laniidae*) are unique among passerines for being carnivorous and having strong, hooked beaks, which tear flesh and sinew. Crossbills (*Loxia*) are specialist feeders on conifer cones, and the unusual crossed-bill shape of their bills is an adaptation that enables them to extract seeds from cones. Seeds sustain a large variety of passerines and most passerines that specialize in seed-eating crack and shuck the seeds with powerful bills. However, birds lack teeth used to chew food before swallowing; therefore, the avian digestive system is specialized to process foods whole. The major parts of the digestive system, the oral cavity, esophagus, crop, stomach (including gizzard), liver, pancreas, intestines, and cloaca are further

specialized to accommodate particular diets and feeding behaviors. Linked with the evolution of flight and high metabolic rate, the digestive system of birds extracts nutrients and energy quickly and with high efficiency from small and quickly handled food (Castro et al. 1989; Afik and Karasov 1995). The avian gizzard is a large, strong, muscular structure primarily used for grinding and digesting tough food. Functionally equivalent to molar teeth in mammals, the gizzards of grain and seed-eating birds are especially large and have powerful muscles.

Unlike the study of the functional feeding anatomy of birds, the study of foraging behavior is more relatively more recent. Hoarding and hiding food for future use is one-way passerines prepare for food shortages (Vander Wall 1990; Källander and Smith 1990). Shrikes are notorious for impaling their prey on thorns for later consumption. Tits, chickadees, and titmice (*Paridae*) depend on autumn caches of seeds for winter feeding. Seed caches are more difficult to relocate than, for example, the impaled prey of shrikes, and the recovery of widely dispersed and concealed seed caches requires a robust spatial memory, which is processed in part by the hippocampus of the avian forebrain. Birds bias their foraging effort to sites where the most profitable feeding may occur, select prey of the size that enhances their energetic profit, and innovate unusual foraging techniques including, in a few species using tools (Hunt 1996; Emery and Clayton 2009).

### Conclusion

Order Passeriformes includes suboscines, oscines also commonly known as songbirds, and New Zealand wrens and represents more than half of all bird species worldwide with representatives on all continents except Antarctica. While all passerines are generally short-lived and highly social, the diversity of species within this order makes it difficult to make generalizations about their life history traits or behavior. However, because of their charismatic nature, high diversity, generally small size, and relative ease of

observation, collection and field study of passerines have historically attracted the attention of a wide range of biologists, including systematists, behavioral ecologists, and evolutionary biologists. Variability in ecological and social conditions contributes greatly to the diversity of passerine species. The diversity of life history traits helps to understand the main selection pressures that passerines are facing in addition to why and how they have become adapted to their environment. The above sections are a board overview of aspects of passerine life history, which conveys the rich species diversity of this avian order.

## Cross-References

- ▶ [Altricial](#)
- ▶ [Biparental Care](#)
- ▶ [Bird Migrations](#)
- ▶ [Clutch](#)
- ▶ [Passerine Cognition](#)
- ▶ [Passerine Morphology](#)
- ▶ [Passerine Sensory Systems](#)
- ▶ [Passerine Vocal Communication](#)
- ▶ [Songbird Learning](#)
- ▶ [Sperm Competition](#)

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## Passerine Locomotion

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## Synonyms

[Perching bird locomotion](#); [Song bird locomotion](#)

## Definition

Movement used by the order Passeriformes (e.g., crows, finches, songbirds, swallow, wren, and bluebirds) to travel throughout their environment.

Passerines make up 60% of all bird species (Barker 2014; Raikow 1982). Passerines can be found on every continent except Antarctica, but are most commonly observed in tropical regions. These birds take a liking to areas filled with trees, as most are arboreal (Raikow 1982). Within the Passeriformes, there are two suborders that further divide these birds by the structure of the vocal apparatus: Oscines and Suboscines. The suboscines are much more limited in species (i.e., flycatchers and the kingbirds) (Ohlson et al. 2013) compared to the much more specious oscines (i.e., “songbirds”) that are divided into 70 families (Barker 2014; Raikow 1982).

There are several characteristics that all passerines share despite the diversity within the order. Passerines are generally small in size, with the exception of the corvids and the lyrebirds, and most have large wings relative to their total body



mass (Polo and Carrascal 1999; Raikow 1982). Additionally, Passeriformes are characterized by having four toes where three are directed forward and one is directed backwards. The hind toe, called the hallux, is continuously pointed backwards and is incumbent, or non-elevated. This arrangement allows them to perch on different slender structures with ease. The anisodactyl foot evolved in arboreal species for the purpose of gripping branches, but passerines have evolved to use them to perch on many different structures. These birds can be observed traversing tree branches, telephone lines, fences and other structures that have narrow places to perch (Botelho et al. 2014; Feduccia 1967).

## Flight Biomechanics

Flight is the most common form of locomotion in the songbirds. All flight begins with the takeoff phase. This is reliant on both wing and leg kinematics. Many species rely on flapping their wings and running simultaneously to begin take off (Dial 2003; Parslew et al. 2018). Most of the velocity that is required for takeoff is provided by the legs. After takeoff is the flight phase. Flight is powered mainly by two proximal wing muscles: *m. pectoralis* and *m. supracoracoideus*. The pectoral muscles functions in depression and pronation of the wing while the *m. supracoracoideus* functions in elevation and supination of the wing. Most wing muscles are proximal within the forelimb to allow for a lighter wing that results in less fatigue when flapping. Distal wing muscles provide more of a functional role in fine tuning of movement rather production of force (Dial 2003).

The flight stroke consists of two main phases: the downstroke and the upstroke. The downstroke is when the wing is pulled downward producing lift. The subsequent upstroke, also known as recovery phase, is when the wing is pulled back up. This resets the position of the wing so that another downstroke can be performed. Downstroke is well conserved among many species. The great variation that occurs during the upstroke provides the basis of gait classification in flight (Tobalske, 2007). There are two main types of flying gait: vortex-ring gait and continuous-vortex

gait. In vortex-ring gait, the lift is provided mainly by the downstroke. During upstroke, the bird tucks back its wings to create less drag which renders the upstroke incapable of producing lift. In continuous-vortex gait there is lift produced in both downstroke and upstroke. Lift is produced in upstroke through the partial extension of the wings (Dial 2003; Tobalske 2007).

Most bird species do not flap continuously; they go through periods of flapping and non-flapping. This alternating pattern of flight is known as intermittent flight. This is effective at conserving energy and allowing the passerine's muscles to relax during a long flight. The non-flapping period of intermittent flight consists of gliding or bounding. Gliding is when the wings are held in the extended position. Bounding is when the wings are tucked against the body. This creates two different types of intermittent flight patterns: flap-bounding and flap-gliding. Flap-bounding is the most common type of intermittent flight that passerines exhibit. Passerines also have the ability to soar. This is a type of gliding that utilizes environmental conditions (e.g., wind currents) to power flight (Dial 2003; Tobalske 2007).

Wing kinematics differ depending on a bird's wing design and flight speed. The orientation of wing forces in birds is facilitated by joints that allow freedom of wing motion around the shoulder as well as wing flexion and extension. The freedom of motion around the shoulder occurs because of the hemi-sellar (or half-saddle) shoulder joint present in most modern birds, which can be modeled as a ball-and-socket joint (Parslew and Crowther 2010). The degrees of freedom are represented as three shoulder rotation angles which are: a stroke-plane angle, wing elevation-depression, and wing pronation-supination (Parslew and Crowther 2010).

Additionally, birds' wings consist of multiple skeletal segments that can be rotated around the respective joints to induce an active shape change, allowing for the flexion and extension of wings, towards and away from the body respectively (Parslew and Crowther 2010). This active shape change, also referred to as active morphing, is one mechanism by which the diversity of bird wings is increased. Changes in the dynamic wing shape

(i.e., wing morphing) can be both passive and active. Passive wing morphing involves transient shape changes during flight that are not a result of muscle activity, rather, they are influenced by the structural properties of the wing's anatomy and feathers (Altshuler et al. 2015). In contrast, active wing morphing occurs within wingbeats as a result of spreadable feathers, intrinsic wing joints, and intrinsic muscles (Altshuler et al. 2015). The spreading and folding of feathers in active morphing generates force, while their structural properties in passive morphing balances aerodynamic and behavioral demands.

In terms of intrinsic wing joints, motion can occur passively through inertial forces during flapping and actively through muscles. Most of the shape variation in wings can be described using three kinematic variables which are: wing folding/expanding, wing twisting, and wrist flexion or extension (Altshuler et al. 2015). In flapping flight, most birds fold the wing during the upstroke by flexing the elbow and adducting the wrist. This shortens the wing-span, lowering the inertial cost of moving the wing, and increases wing safety margins at high speeds or turbulence (Altshuler et al. 2015). Wing twisting is defined as a change in the angle of incidence along the length of the wing, which can occur either passively or actively. Passive twisting involves mechanical forces caused by the structural properties of the wings, while active wing twisting is achieved through pronation and supination of the wrist (Altshuler et al. 2015). Wrist flexion and extension occurs perpendicularly to the plane of the wing, allowing birds to bend their wings. Wing folding and wrist flexion often occur simultaneously and are referred to as wing flexion (Altshuler et al. 2015). Overall, wing flexion reduces exposed wing surface area and wing length decreasing drag and wing-tip velocity, which is useful during upstroke for weight support and propulsion (Parslew and Crowther 2010).

## Migratory Patterns

From a zoogeographical viewpoint, bird migration generally is composed of three elements: the

breeding range of the species, its passage routes, and its winter range (Busse 2001, 2019). For most birds, including many of the order Passeriformes, migration occurs in a seasonal latitudinal movement from north to south and vice versa. In some cases, summer and winter ranges can be separated by thousands of kilometers (Alerstam 1991; Alerstam et al. 2011). However, many bird species have been observed to also migrate relatively locally in an upslope or downslope movement referred to as altitudinal migration. Altitudinal migration is the seasonal movement whereby during the breeding season, there is an upslope movement from lower to higher elevations, and during the non-breeding season, a downslope movement from higher to lower elevations (Pageau et al. 2020). The associated advantages include a decreased risk of predation, avoidance of harsh conditions and tracking of food resources. Within the Passeriformes, 13% are described as altitudinal migrants. However, their migration process is difficult to study due to the variability involved. For example, even within the same species, there is a variation between those that are altitudinal migrants and those that are stationary. Additionally, altitudinal migration may not only occur as a mechanism for birds to reach breeding grounds; birds can also move up or downslope to reach molting grounds (Busse 2001; Pageau et al. 2020).

Pageau et al. (2020) explored the link between passerine migration and diet and observed that foraging guild is evolutionarily associated with altitudinal migration, but this relationship varies across zoogeographical regions. Pageau et al. (2020) demonstrated that passerines in the Nearctic region that were herbivores and omnivores were associated with altitudinal migration. In contrast, only omnivorous species were linked to altitudinal migration the Palearctic region.

## Bio-Inspiration

Avian flight has inspired flying robots used in reconnaissance missions that utilize a perch-and-stare mechanism. Inspired by the

adaptability of songbirds, the design is based on a landing mechanism capable of perching on curved surfaces. This allows the robot (equipped with cameras and other sensors) to land on inconspicuous surfaces involving horizontal or vertical planes. For songbirds, the anatomy of the foot and leg are particularly important in terms of perching. Bird feet are underactuated, allowing them to passively conform to the structure they are attempting to perch on, which also allows them to sleep while perching (Daler et al. 2013; Doyle et al. 2011; Estrada et al. 2014; Pope et al. 2016).

Songbirds also have an unusual locking mechanism whereby the tendon on the rear side of the ankle can automatically cause the toes to grip around a branch when the leg bends, thus allowing the sleeping bird to grip the perch without using any voluntary muscle effort. The more relaxed the bird, the more the leg bends and the tighter the grip. To let go of the perch and take off, the bird must actively straighten up (Parslew et al. 2018). This mechanism and associated anatomy would be key in the development of the flying robots. The design of the gripper is based on the anisodactyl toe arrangement that most songbirds have with three toes facing forward and one backward, and the weight of the rotorcraft is used to enable the grip mechanism. The goal of this avian-inspired approach would be to achieve the passive perching mechanism on drones that can land and remain “perched” on a variety of curved substrates (Daler et al. 2013; Doyle et al. 2011; Estrada et al. 2014; Pope et al. 2016).

## Conclusion

The passerines are a dynamic order of birds that have several different locomotor modes. These birds are known to be able to traverse narrow fences, branches, and phone wires with ease due to their foot structure. They are also able to fly and have distinct take off and flying phases. Further study of passerine locomotion and bird flight can improve the technology of flying robots.

## Cross-References

- ▶ [Activity Budget](#)
- ▶ [Adaptation](#)
- ▶ [Adaptedness of Behavior](#)
- ▶ [Adaptive Radiation](#)
- ▶ [Arboreality](#)
- ▶ [Artificial Selection](#)
- ▶ [Basal Metabolic Rate \(BMR\)](#)
- ▶ [Cognition](#)
- ▶ [Dispersal Ability](#)
- ▶ [Dispersal Patterns](#)
- ▶ [Diurnality](#)
- ▶ [Ecology](#)
- ▶ [Evolution](#)
- ▶ [Extinction in Learning](#)
- ▶ [Gait](#)
- ▶ [Herbivore](#)
- ▶ [Home Range](#)
- ▶ [Homology](#)
- ▶ [Homoplasia](#)
- ▶ [Locomotion](#)
- ▶ [Morphology](#)
- ▶ [Muscular System](#)
- ▶ [Natural Selection](#)
- ▶ [Navigation](#)
- ▶ [Passerine Cognition](#)
- ▶ [Passerine Life History](#)
- ▶ [Passerine Morphology](#)
- ▶ [Passerine Navigation](#)
- ▶ [Passerine Sensory Systems](#)
- ▶ [Phylogeny](#)
- ▶ [Species](#)
- ▶ [Taxa](#)
- ▶ [Terrestrial](#)
- ▶ [Territoriality](#)
- ▶ [Vertebrate Nervous System](#)
- ▶ [Zoo](#)
- ▶ [Zoology](#)

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## Passerine Morphology

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## Synonyms

Passerine anatomy; Perching bird physiology

## Passerines Share Many Traits with Other Types of Birds

In seeking to understand the traits that distinguish passerines from other types of birds, it is useful to consider them in light of the traits that distinguish birds from other groups of animals. Birds are warm-blooded (endothermic) vertebrates, meaning that they generate their own body heat rather than relying on the environment to maintain their body temperature, and their body structure includes a backbone. When we think of birds, features such as wings and eggs may leap to mind, but neither of those features is unique to birds. For example, bats and insects have wings, and egg laying is common across a wide range of animals such as fish and reptiles. When we

consider the adaptations that define birds, many are associated with the demands of flight, such as reduced weight and efficient power. Feathers, pneumatic bones (such as those found in the wing), and a highly efficient respiratory system are all adaptations that facilitate birds' ability to fly (reviewed in Rodewald et al. 2018).

Highly adapted avian structures afford many useful advantages. For example, large flight feathers, such as the primary feathers on the wing, enable birds to generate lift and thrust while also controlling their direction in the air. Other types of feathers are collectively called "plumage" and are a form of ornamentation that plays an important role in courtship and mate choice for many species. Much smaller feathers are collectively called "down" and line the body to provide very efficient insulation to prevent heat loss. Despite their differences in size and appearance, each of these types of feathers is made primarily of a protein called keratin and consists of a hollow shaft with small barbs branching off on either side of that central structure (reviewed in Butler and Rohwer 2018). These highly adapted structures were once thought to be homologous to reptilian scales based on similar composition and development. However, more recent research suggests that feathers evolved through a series of changes in the follicle from which feathers grow (Prum and Brush 2002). The origin of feathers remains a topic of ongoing research, but it is clear that they provide important advantages in terms of flight, ornamentation, and insulation (reviewed in Butler and Rohwer 2018).

Forelimbs are also highly adapted in birds, so much so that they have received the specialized name "wings." At first glance, a bird's wing and a human arm might not appear very similar; however, the skeletal structure is very similar in wings, arms, and forelimbs observed across different species of vertebrates (reviewed in Shubin 2009). The most proximal portion of the wing consists of the humerus (from the Latin for "shoulder"), and the more distal portion is formed by the ulna (from the Latin for "elbow") and radius bones. Proceeding distally from those bones, they are connected to carpal (from the Latin for "wrist") bones that are in turn connected to the bones that compose the

digits (from the Latin for "finger" or "toe"). The names given to these bones by anatomists make clear the parallels between the bones in an avian wing and those in your own arm.

In many species of birds, bones contain hollow spaces that are strengthened by networks of bony filaments called trabeculae (from the Latin for "beam") (reviewed in Voss and Pavia 2018). The hollow structure of these bones not only makes them lighter, it also makes them very resistant to bending and other forces that occur during the downstroke of the wing. This is important, as birds produce forces in excess of their body weight when they fly, and those forces are exerted by large muscles that attach to the bones of the wing. For example, contraction of the pectoralis muscle pulls on the humerus bone and causes the wing to be pulled down in the power stroke of flight. The joints that connect the bones of the wing also permit a wide range of movement, facilitating the power stroke, pulling the wing back up, and folding the wing to rest neatly against the body when the bird is not in flight (reviewed in Voss and Pavia 2018). These structural features of birds' wings – hollow, lightweight, agile, and strong – are ideal specializations for the challenges of flight in which weight is an obstacle and strength is essential.

The avian respiratory system is also highly specialized and adapted to meet the metabolic demands of flight. This system enables the movement of oxygen from air into the blood, and it performs this task very efficiently to enable the vigorous actions of flight. In humans, our lungs operate in a tidal system of air entering and leaving the lungs through inhaling and exhaling. The structure of avian lungs is very different, and air flows in a single direction across the surfaces that permit the exchange of gases (reviewed in Martinez Del Rio et al. 2018). Structures called air sacs and the muscles that control the movement of the rib cage act like bellows to move air through the avian lung, and the unidirectional movement of air across surfaces in the lungs enables birds to exchange nearly all the volume of their lungs in each breath. In contrast, humans and other mammals do not exhale all the volume of our lungs



each time, leading to residual “stale” oxygen-depleted air that then mixes with fresh air in the next inhalation. Complete turnover of air in each breath means that birds have a greater content of oxygen-rich air available to them. The movements of flight further enhance the movements that drive respiration, pumping air through the respiratory system even more forcefully than when the bird is at rest (Jenkins Jr. et al. 1988). This is especially beneficial, as it provides even greater exchange of gases at the time when the metabolic demand for oxygen is greatest.

Together with additional specializations that are not described here (reviewed in Rodewald et al. 2018), the features described above are conserved across nearly all species of birds. These traits distinguish birds from other types of animals, and that is recognized by the taxonomic description of birds as belonging to Class Aves. However, there can be huge differences between different types of birds. For example, ostriches and hummingbirds are both birds, but there are vast differences in their size, shape, ecology, and metabolism. When we parse birds into more finely divided groups, the next level of taxonomic rank beyond Class is Order, and the largest group of birds is the Order Passeriformes. These birds are more commonly called passerines or “perching birds,” and the properties that distinguish passerines from other birds are the focus of the next section.

### Passerine Birds (Order Passeriformes)

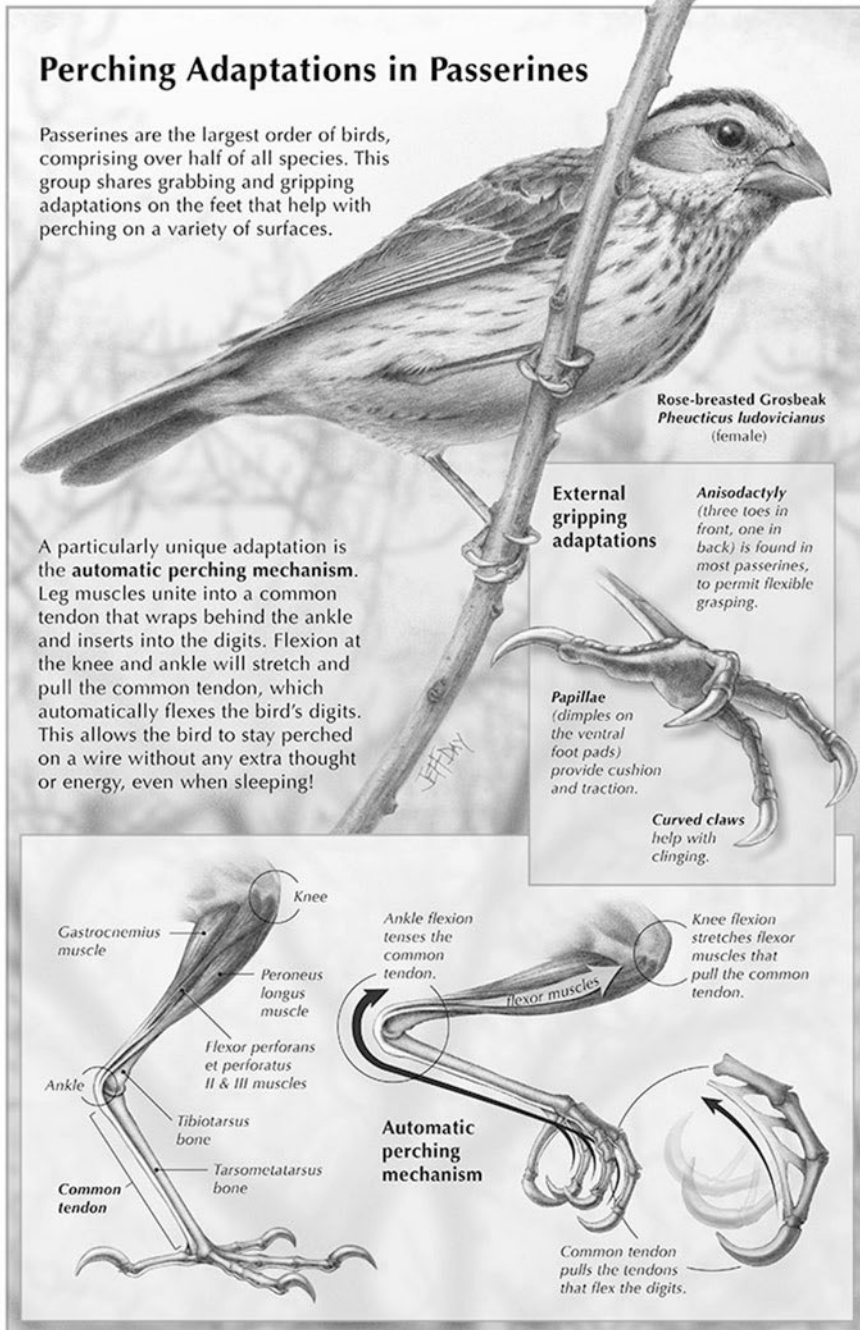
The group of birds called passerines includes approximately 140 families of taxonomic division and 6000 species, comprising approximately half of all species of birds that are alive today (Olalla-Tárraga et al. 2019; Raikow and Bledsoe 2000; Ricklefs 2012). These birds may be very familiar, as they are commonly active during the day and they include songbirds that are commonly seen in the wild, such as sparrows, finches, jays, chickadees, and wrens. Passerines take their name from the Latin name for sparrows and small birds like them (*passer*). They are a very successful group of organisms, flourishing in a very wide range of

habitats and occupying remarkably diverse ecological niches (Olalla-Tárraga et al. 2019; Raikow and Bledsoe 2000). They are typically smaller than members of other orders of birds, with the largest passerines being lyrebirds and ravens (typically around 1.5 kg and 70 cm in height) and the smallest being pygmy tyrants (typically around 4 g and 6 cm in height) (Unwin 2011). Most passerines are small- to medium-sized land-dwelling birds that feed primarily on insects, fruit, seeds, or nectar, and their morphology is generally well suited to a variety of foraging techniques and prey items (Ricklefs 2012).

### Unique Features of Passerine Morphology

Passerines are more commonly known as perching birds because the arrangement of their toes and hindlimb muscles facilitates them perching on twigs and branches. Across all groups of birds, the arrangement of toes on each foot is remarkably diverse (reviewed in Voss and Pavia 2018). Different groups can have not only different numbers of toes on each foot but also different arrangements of those toes. The arrangement in passerine birds includes three toes that point forward on the foot, one toe that points backward, and no webbing between any of the toes (Fig. 1). This arrangement is called *anisodactyl* (literally meaning “unequal digits”), and it facilitates birds grasping either horizontal or more upright perches such as branches and tree trunks.

Passerines are *digitigrade*, meaning that they walk on their toes rather than on the entire foot, so the point of contact with perching surfaces includes only the toes and not the rest of the foot (Fig. 1). The bones in the toes of passerine birds are attached to muscles that work together with the *anisodactyl* arrangement to facilitate the perching reflex. Those muscles include the *flexor digitorum longus*, which flexes the three forward-facing toes, and the *flexor hallucis longus*, which flexes the backward-facing toe (Fig. 1; as detailed in Raikow 1982). The flexor tendons run along the backward-facing (posterior) side of the main bone of the foot (*tibiotarsus*) and insert on the bottom



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**Passerine Morphology, Fig. 1** Perching adaptations in passerines. (Illustration by Jeff Day, copyrighted 2013. Accessed with permission from [jeffdayart.com/illustration-1/#/perching-adaptations/on](http://jeffdayart.com/illustration-1/#/perching-adaptations/on) June 19, 2020)

(plantar) portion of the digits. The tendon from the flexor digitorum longus attaches to each of the three forward-facing toes, and the tendon from the flexor hallucis attaches to the single backward-facing toe (some birds have interconnections between these tendons; detailed in Raikow 1982 and Raikow and Bledsoe 2000). Because of this arrangement, the forward- and backward-facing toes can be controlled separately, but coordinated contraction of the two flexor muscles causes each of the four toes to flex (extension of the toes is controlled by other mechanisms). This is the same sort of action as what occurs when you close your hand around an object in your grasp.

The arrangement of passerine toes and the associated muscles has implications for the way that those birds can use their hindlimbs. Because the toes can be contracted in a grasping motion, passerines can use their feet to hold items such as food or nest-building materials. The wide range of motion in the movements of each toe enables the bird to adapt its grasp to accommodate a wide range of sizes and shapes of different perching sites. Passerines also commonly use their feet and toes in other ways such as aggressive encounters or the precisely controlled movements that occur in preening. Some passerines, such as the Family Corvidae within the Order Passeriformes, are especially adept at these sorts of movements. These birds have been shown to have impressive intellectual abilities, as they are able to solve challenges that require them to employ concepts such as analogy and problem-solving (Smirnova et al. 2015). Corvids have also demonstrated the ability to use the agility afforded by the arrangement of their feet and toes to create rudimentary tools such as hooklike structures to retrieve food from a location that would otherwise be inaccessible to them (Hunt 1996).

The arrangement of the muscles and toes also plays a key role in how the toes function even when the associated muscles are not being actively contracted. When a passerine bird assumes the posture that we refer to as perching, it results in the ankle being bent and the bird's body weight resting on that bent joint (Fig. 1). When the bird bends its ankle (the tibiotarsal

joint), the tendons are pulled along the bottom portion of the foot. This is the same movement of the tendon that occurs when the muscles are contracted, but in this case the tendon moves because of a change in posture rather than an active contraction of the muscle. In either case, movement of the tendon causes the toes to flex. Therefore, when the bird is perched, it can relax its flexor muscles and yet still have the force of its body weight acting to bend the ankle and flex the toes. In that way, the bird is effectively gripping its perch even when it is not actively contracting its muscles. This anatomical arrangement gives rise to a very convenient advantage in that passerines can grip their perch, and this remain safely secured on their branch or other site, even when they are asleep.

## Variability of Passerine Morphology

Just as there is great diversity across all birds (Class Aves), there is also diversity among passerines (Order Passeriformes). That diversity is commonly characterized by comparing specific measurements from each type of bird. For example, these measurements can include beak size and shape, properties of the pectoralis muscle, measurements of the bones in the hindlimb, features of wing shape, and the size of feathers at specific locations on the body. In addition to this anatomical diversity, there are also differences in the behavior and ecology of different kinds of passerines. Those differences are commonly characterized by features of a bird's diet, foraging strategy, and habitat (Kennedy et al. 2020). The following sections describe aspects of the diversity that is found among passerine species and how those differences are thought to have enabled these birds to thrive in a wide range of ecological environments.

## Variability in Beak Morphology

The size and shape of beaks varies widely across passerine species. These differences are correlated with differences in diet and foraging modes, and

they are thought to have played key roles in diversification of species (Mallarino et al. 2012). Differences in beak morphology, such as length or depth of the beak, can enable birds to adapt to diverse and changing ecological niches by enabling them to exploit different sources of a similar type of food. For example, seeds are important food sources for many passerine species, and beaks of different shapes and sizes may provide birds with varying degrees of success in accessing seeds such as those that are large and tough (for which a short and large beak may facilitate cracking those seeds) or that are hidden within the recesses of pinecones or other structures (for which a long and slender beak may facilitate access to those seeds) (Benkman 1993).

Similar patterns are also evident across species that exploit different food sources. Species that feed primarily or exclusively on small fruits (seed dispersers) tend to swallow those fruits whole, and those birds tend to have broader and flatter bills compared to other species (Herrera 2011). In contrast, species that feed on fruits only occasionally and rely on other food sources for most of their diet (seed predators) do not express those characteristics of bill shape (Herrera 2011). It is thought that the traits of beak morphology expressed by seed disperser species are advantageous in allowing them to feed primarily on fruit, whereas seed predator species do not express those specific adaptations and are therefore able to be dietary generalists that can exploit a greater range of dietary options.

Adaptations of bill morphology in association with diet and habitat are apparent even between closely related species. For example, long, flat bills are typical of birds that catch mobile prey, such as flying insects. In contrast, shorter, slightly curved bills are typical of birds that feed on more sedentary prey. In the case of warblers (Genus *Acrocephalus*), mobile prey are more abundant in marsh habitats, and the species of warblers that inhabit those areas tend to have long, flat bills. In contrast, less mobile prey are common in vegetation and undergrowth, and species of warblers that inhabit those areas tend to have shorter, slightly curved bills (Leisler et al. 1989). In perhaps the most compelling evidence in

support of the idea that beak size and ecological opportunities are related, a correlation between changes in beak size and changes in habitat is evident within the seasonal transitions of an individual species. Within honeyeaters (Genus *Meliphagidae*), beak size increases during the summer months, becoming more elongated during a time when those birds also increase their reliance on nectar as a food source (Friedman et al. 2019).

Beak morphology is also related to activities other than feeding, such as thermoregulation, singing, and preening behaviors. Beaks are a primary means through which birds release heat into the environment; thus, smaller or larger beaks have consequences for not only feeding and the acquisition of energy but also thermoregulation and the release of energy (Friedman et al. 2019). A large bill might enable a species to fare better in a very warm climate than if it had a much smaller bill, opening the door to occupying a niche that the species might otherwise not inhabit. In singing, the beak is part of the vocal tract that influences the resonance of specific frequencies in calls or songs. If the beak is wide open, the overall vocal tract is shorter (favoring higher frequencies) than if the beak is more closed (favoring lower frequencies) (Huber and Podos 2006). This is similar to the musical phenomenon in which larger, longer tubes in a pipe organ produce lower notes than smaller, shorter tubes. Finally, beaks can also play an important role in the bird's ability to maintain its health through preening and removal of harmful parasites (Clayton et al. 2005). Thus, beaks can influence many aspects of a species' ability to thrive in different contexts, and demands and advantages such as these are thought to have acted as strong driving forces in shaping the evolution of beak morphology.

## Variability in the Pectoralis Muscle

Flight is a very metabolically expensive behavior, and different species of passerines express different traits in the powerful muscles that enable flight (Welch and Altshuler 2009). The pectoralis muscle is the dominant muscle associated with

powering flight as well as other aspects of survival such as thermoregulation by shivering, and it accounts for the majority of muscle mass in birds. Within the pectoralis, there can be different types of muscle fibers (e.g., DuBay et al. 2020). Some of those fibers can be glycolytic, meaning that they rely on cellular energy reserves such as glycogen that is immediately accessible. Other muscle fibers can be oxidative, meaning that they rely on oxygen obtained through respiration as their energy source. These differences can have functional consequences, as glycolytic fibers are excellent for producing rapid movements but they are more easily exhausted than oxidative fibers. Therefore, different composition of fibers in the pectoralis muscle may be better suited for different types of brief versus sustained behaviors.

Within the pectoralis of small-bodied birds, muscle fibers are often exclusively oxidative, whereas the pectoralis in larger species contain a much greater proportion of glycolytic fibers (Welch and Altshuler 2009). This is thought to reflect the different demands that species of different sizes face in takeoff and continued flapping during sustained flight. For example, large birds may be more dependent on the bursts of power that glycolytic fibers provide to lift them into the air. Interestingly, recent research has revealed that glycolytic fibers may be present in the pectoralis of small birds (DuBay et al. 2020). In most small species, the pectoralis is composed exclusively of oxidative fibers, and these new data suggest that species diversity in the composition of pectoralis fiber types may play important roles in not only powering takeoff but also other aspects of survival such as competitive interactions or predator avoidance (DuBay et al. 2020). In support of that idea, the proportion of glycolytic fibers is greater in socially dominant small birds than in less dominant members of the same species (DuBay et al. 2020). Together, these results reveal that diversity in pectoralis muscle fiber composition is evident not only across but also within passerine species. Those differences have functional consequences, and diversity may be influenced by not only evolutionary history but also experiences that accrue within an individual's lifetime.

## Variability in Hindlimb Morphology

Different habitats place different demands on their inhabitants. For example, flat environments typically require little or no climbing, but habitats with steeper or perhaps even vertical surfaces could require very different patterns of locomotion. These differences in demand may be evident as structural differences between species that have adapted to each type of location. For example, warblers (Genus *Acrocephalus*) that live in environments where they commonly cling to vertical surfaces have long backward-facing toes, while those that live in habitats where they commonly run along the ground have adapted to express a longer version of a different toe (Leisler et al. 1989). In another example, species that are more reliant on hopping behavior for predator avoidance and takeoff tend to have longer foot bones (tarsus) than species who do not rely on those behaviors (Swaddle and Lockwood 1998). Adaptations of the hindlimb are also evident in the muscles that control flexion of the joints in the leg and foot. Anatomical differences associated with greater maximal force of contraction and flexion are evident in species that are more reliant on hanging behavior for their perching and feeding, and it is thought that these adaptations are helpful in counteracting the effects of gravity (Moreno 1990).

## Variability in Wing Shape and Feather Size

Passerine species also vary in the shape and size of their wings, and those differences are thought to be associated with differences in behavior and habitat. In another example from warblers, species that exploit taller vegetation tend to have broader wings than those that move through shorter and more tangled vegetation (Leisler et al. 1989). It is thought that those differences are functionally significant because broader wings may facilitate takeoff from within tall vegetation, whereas more narrow wings may facilitate maneuverability through dense vegetation (Kennedy et al. 2020).



Studies of other passerine species have revealed that species with rounded wingtips as opposed to pointed wingtips are at a lower risk for predation, and it is thought that rounded wingtips may enhance flight performance at slow speeds and thus allow individuals to take off more quickly and at steeper angles than birds with sharper wingtips (Swaddle and Lockwood 1998). The properties of these different types of wingtip are associated with differences in the lengths of the primary and secondary flight feathers on the wings of those species. Thus, passerine species express diversity in the features of the structures that power and control flight, and those anatomical differences are closely correlated with differences in habitat.

### Variability in Behavior

In addition to anatomical differences between species, passerines also vary in their behavior. Some species have been characterized by the ability to learn the sounds they used in vocal communication (Suborder Passeri within the Order Passeriformes). These birds are commonly called “songbirds” or “oscines,” named from the Latin word for singing birds. The ability to learn the sounds used in communication is a feature of human communication through speech, but it is otherwise rare across animal species (reviewed in Martins and Boeckx 2020). Therefore, songbirds have been the focus of research into not only the ways that song is used by those species but also how it may be informative as a means of understanding how we communicate through speech. Vocal learning is associated with the presence of specialized structures in the songbird brain, and a growing body of research is providing insight into how studies of songbirds may help us understand the mechanisms of human communication (reviewed in Mooney et al. 2008). In addition to the songbirds that comprise Suborder Passeri, other passerines (Suborders Tyranni and Acanthisitti) have long been thought to have little or no reliance on learning in their acquisition and performance of the signals they use in

communication (e.g., Kroodsma 1984). That is reflected in the commonly used term “suboscines” to refer to those birds. However, recent research suggests that such a dismissive term may be inappropriate and that the differences between these groups are not as stark as was previously thought (reviewed in Martins and Boeckx 2020). Feedback-dependent effects on vocalizations are a hallmark of the vocal learning process, and suboscine species have been shown to modify their vocalizations based on sensory experience (Kroodsma et al. 2013; Martins and Boeckx 2020). The effects of experience on song performance are much greater in songbirds than the effects seen in suboscines, but research suggests that both groups may be at least somewhat dependent on learning in their vocal communication (Martins and Boeckx 2020). Thus, the difference between these groups may be one of degree rather than a categorical distinction. Ongoing research is seeking to understand these differences and their associated neural circuits more fully as a means of understanding how the brain enables perception and learning in not only these passerine species but also ourselves.

### Passerine Success across Many Different Niches

As noted throughout this entry, passerines comprise a large number of species that are quite diverse in their morphology, life history, and behavior. They have adapted to occupy a broad range of terrestrial habitats and a similarly diverse range of ecological niches. Their characteristics such as relatively small bodies, large brains, arboreal living, reproductive success, behavioral flexibility, and ability to feed on a broad diversity of food sources have apparently provided them with abilities to colonize new areas better than any other group of birds (Olalla-Tárraga et al. 2019). This tolerance and adaptability may also explain how they have been able to thrive across diverse and widespread habitats. Changes throughout Earth’s history may also have played a key role in their success, as global climate changed during

the Tertiary period and adaptive radiation among flowering plants and insects gave rise to a diversity of habitats that may have been especially well suited to support small birds (Oliveros et al. 2019).

Passerines also express many behaviors that are also thought to have helped them thrive throughout their history. For example, passerines have an extraordinary ability to create nests out of a wide range of materials, place them in a variety of areas, and conceal them effectively against threats from predators and the environment (Olson 2001). Those nests provide protection for not only the birds that construct them but also their offspring, and that is especially beneficial in light of how vulnerable hatchlings are during the earliest days of their lives. The ability of passerines to protect their young in this way may also have contributed to their success (Olson 2001). Additional aspects of reproduction such as rapid development to an early age of sexual maturity and the associated short generation times may have also contributed to successful adaptation to novel environments. Passerines are also behaviorally flexible and capable of complex learning, as shown by their mate choice strategies and vocal behavior. In addition, many species are capable of migrating over very long distances, enabling them to disperse over wide ranges and take advantage of resources present across those different locations (Olson 2001). Taken together, these features reveal that passerines express many anatomical and behavioral traits that have likely contributed to their ability to reach new environments, adapt to survive there, and evolve into the diversity of passerine species that we observe today.

## Cross-References

- [Passerine Cognition](#)
- [Passerine Life History](#)
- [Passerine Locomotion](#)
- [Passerine Navigation](#)
- [Passerine Sensory Systems](#)
- [Passerine Vocal Communication](#)
- [Skeletal System](#)

- [Songbird Duets](#)
- [Songbird Learning](#)

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## Passerine Navigation

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## Definition

The methods in which birds of the order Passeriformes are able to orient themselves in regard to their geographic location, and then utilize this information to move toward a geolocational goal.

## Introduction

For thousands of years, humans have borne witness to the incredible navigational abilities of birds. The knowledge and utilization of these birds' abilities goes as far back as ancient Egypt, some 4000 years ago, where sources tell what humans learned about, and proceeded to utilize the homing abilities of domestic pigeons (*Columba livia* v. *domestica*) to carry urgent messages more quickly than human, or other animal couriers (Blechman 2007; Newton 2010). While technology in the past couple centuries has made the use of homing pigeons obsolete, interest in the scientific basis of avian navigation has conversely expanded as questions began to emerge regarding how all types of birds were able to so readily find their way home or successfully migrate across great distances. Considering the popularity of homing pigeons with humans, it was no wonder that early studies on overall avian navigation had focused mainly on members of the *Columbidae* family (Wiltschko and Wiltschko 2003). However, other studies sought to expand upon these early findings to examine navigation in a variety of bird taxonomic groups, most notably, the passerines.

The order of "perching birds" or Passeriformes comprises over half of all bird species diversity (59%, Sibley and Monroe 1990), and the incredibly precise nature and ability of these birds' navigation, particularly in migration, has been observed and analyzed since antiquity (Berthold et al. 2013). In passerines, as with many species of bird, accurate navigation and site fidelity are highly important for accruing fitness benefits – especially in birds that undergo the aforementioned migration as part of their life history (Newton 2010). This importance of navigational ability has made the subject of considerable interest among ornithologists in the past century, with a variety of studies using passerine models to examine different navigational mechanisms and theoretical concepts (Kramer 1952; Able and Able 1993; Cochran et al. 2004; Wiltschko and Wiltschko 2015).

While passerines such as the European Starling (*Sturna vulgaris*), European Robin (*Erithacus rubecula*), and Zebra Finch (*Taeniopygia guttata*)

have been the subject of studies that have provided foundational research into constructing the current understanding of avian navigation, many other important discoveries have used species within different orders – such as homing pigeons and seabirds – to test and form other crucial concepts (Wiltschko and Wiltschko 2003, 2015). However, given the lack of information on potential variation in individual bird species' navigational toolkits, it is generally accepted that most birds navigate by using the same core mechanisms (Wiltschko and Wiltschko 2003). To that end, findings in other avian taxa on the methods and mechanisms of navigation, particularly in regard to earlier, ubiquitous concepts, should be considered and applied when discussing passerine navigational systems.

## Early Studies and Frameworks on Orientation

Pioneering studies in avian, and by extension passerine, navigation utilized an inductive approach which mostly employed large-scale displacement experiments with goals of discovering maximum distances in which birds were able to home, and how various conditions could affect navigational performance (Wiltschko and Wiltschko 2003). While many of these foundational studies occurred in seabirds such as noddies and terns (Watson and Lashley 1915), other studies made use of free-living passerines such as starlings and swallows in their displacement studies (Rüppell 1935; Sargent 1962). Regardless of species, these early studies generally expressed the birds' superb homing abilities over considerably long distances from unfamiliar starting locations. Additionally, another study in seabirds reported that certain seabirds were able to successfully navigate across the open ocean, showing that avian navigation did not necessarily depend on the use of familiar landmarks: a then contemporary viewpoint that had been continually tested in homing pigeons to inconclusive results (Lack and Lockley 1938; Wiltschko and Wiltschko 2003). While these studies were able to further solidify the extent and ability of birds' homing and navigational ability, they were not able to concretely

suggest or show any factors or mechanisms behind this ability only concluding that the birds seemingly had a nebulous “sense of direction” or “sense of space.”

It was not until the middle of the twentieth century that much of the foundational knowledge on the theoretical and mechanistic factors of avian navigation was more thoroughly constructed. One of the most foundational and key concepts developed during this widening in navigational research was the three types of homing orientation first described by Donald Griffin. Having reviewed the literature on past navigational research, his classification, as detailed in Griffin (1952), was characterized by the apparent complexity of the exhibited navigational process. In Griffin’s classification, the most basic form orientation – referred to as Type I or “piloting” – was the birds’ directed search for familiar landmarks or features when displaced. Griffin argued that this was the simplest form of navigation among birds and that most birds in unfamiliar territory would utilize this orientation strategy. Building from piloting, the Type II orientation, later referred to as “one directional orientation,” suggested that birds would use a single directional cue and then proceed to navigate in that direction until a familiar landmark or area could induce piloting orientation (Griffin 1955). Finally, in Type III orientation, the bird would use some sophisticated and undiscovered mechanism to choose the approximate direction and path despite having no precursory direction or familiar landmarks in which to use. As a result, this final type of orientation has been known as “true navigation” and lay the foundation of other proposed mechanisms to thoroughly explain how birds were able to orient themselves (Wiltschko and Wiltschko 2003). Aligning with the “increasing complexity” that Griffin suggested in his three types of orientation, each type was based on an increasing number of references: Type I is largely independent of external references, Type II uses one factor as a reference, and Type III makes use of two external factors to create a more complete navigational compass (Adler 1970). While Griffin’s three types of orientation were criticized among ornithologists for their simplicity and disregard of wild bird motivation and ecology

(Keeton 1974), the descriptions successfully created the first classifications into avian orientation behavior and provided an ample conceptual framework for aligning upcoming discoveries in the mechanisms used in avian navigation.

## Sun Navigation and the “Map and Compass”

During this same period, a series of pioneering in passerines, namely starlings (*Sturgis vulgaris*), were able to determine that the sun is a directional cue used by birds in diurnal navigation (Kramer 1950). In these experiments, researchers trained captive starlings kept in circular cages to feed in a particular compass direction. With only the day-time sky above being visible to the starlings, results showed that the birds were able to maintain their trained feeding directions throughout the day. As the starlings were seemingly allowing for the changing position of the sun in their orientation, the birds must have needed to be keeping track of two different factors: a biological clock, and a knowledge of the sun’s movement (Kramer 1950; Schmidt-Koenig et al. 1991). This discovery was not only key in further unearthing upon the previously nebulous mechanisms of avian navigation, but also importantly allowed for this concept to play a central role in the “Map and Compass” model, a key model in which the current understanding of avian navigation is still largely rooted (Schmidt-Koenig et al. 1991; Wiltschko and Wiltschko 2003).

After discovering the sun compass, Gustav Kramer proposed his “Map and Compass” model in order to provide a theoretical framework to his findings. Kramer described avian navigation or goal orientation in a two-step process: First, the bird determines its goal direction as a compass course, and second, it uses a compass mechanism to locate this course (Kramer 1953). Alternatively stated, the first “map” step allows the bird to find a specific direction – equivalent to humans’ use of cardinal directions – in which its goal is, while in the second “compass” step, this course is converted into a direction of flight. Kramer’s model was able to solidify that compass orientation was a vital aspect of avian goal



orientation, and its subsequent adoption has made navigation researchers compartmentalize their findings in terms of how any experimental manipulation affects either the map or compass step (Wiltschko and Wiltschko 2003).

While Kramer's model had naturally been able to use sun navigation as birds' compass mechanism, it was not able to propose anything for the map step leaving it largely open for future studies. Researchers proceeded to develop two main ideas for maps in order to fill this gap in the model: the grid and the mosaic (Wallraff 1974). The grid map suggested that birds would be able to sense differences in two different kinds of environmental gradients that are in continual change. Using this system as a map, birds would then be able to use a compass mechanism, such as the aforementioned sun compass, to pinpoint differences in scaled values at their present location to remembered values at their goal or home location. While the grid map is highly useful in picking up on more dynamic changes in geolocation, it falters when considering how birds are accurately able to find a target or home within an area of largely similar environmental gradients. As localized navigation has been long known to be predominantly based on visual cues and landmarks, the mosaic model accounts for this by combining mapping mechanisms (Deutschlander and Beason 2014; Wallraff 1974). Thus, in the mosaic model, the map is built as a mental representation of the distribution of known landmarks in the home area combined with the compass-accrued directions from these landmarks to home or other spots of interest (Wiltschko and Wiltschko 2015). Both the grid and mosaic maps indicate the direction to the goal as being a compass course (Wiltschko and Wiltschko 2003).

## Other Compass Mechanisms

While Kramer's work with the sun compass was sufficient in showing how birds were navigating during the day, it left open the question of how birds could navigate in nonclear skies, and nocturnally (Kramer 1950, 1953). This was of particular interest for many species of passerines that migrate nocturnally and thus could not be utilizing

a sun compass (Deutschlander and Beason 2014). One of the first and most widely accepted compass mechanisms to be proposed was a magnetic compass. Through controlled manipulation experiments of birds' magnetic field, researchers were able to show that migratory passerines such as the European Robin (*Erithacus rubecula*) and Savannah Sparrow (*Passerculus sandwichensis*) could have their orientation disrupted, demonstrating a robust ability for magnetic orientation (Wiltschko 1968; Able and Able 1993). To this effect, an inclination for a magnetic compass has been found in all species of bird tested, regardless of order or migratory status (Wiltschko and Wiltschko 2015).

Beyond the magnetic compass, other potential sources of compass information have been proposed and tested in passerines – most of which have been related to celestial aspects for navigation. Multiple species of migratory passerines have been tested to have been able to detect and utilize levels of polarized skylight available in dusk skies (Able 1989). Additionally, stellar patterns have been tested to be an adequate compass for nocturnal migrants such as Indigo Buntings (*Passerina cyanea*) and Blackpoll Warblers (*Dendroica striata*), providing another usable compass mechanism for nocturnal migrants (Emlen 1967; Emlen 1975). With any of these alternate compass mechanisms, birds accrue essentially the same directional information as the sun compass, meaning that any of these mechanisms can be substituted for the compass step in Kramer's model without issue.

## Compass Mechanism Interactions

Given that multiple types of compass mechanisms exist, questions arose regarding the relative importance of these mechanisms to each other. For many years, the role of the magnetic compass was thought of to be just a backup method to be used in unclear or nighttime skies, retaining Kramer's sun compass as the primary mode of gaining directional information (Wiltschko and Wiltschko 2003). After a series "cue-conflict" experiments in which birds were tested in situations where different compasses would provide

contrasting information, it has been generally accepted that birds' compass mechanisms should not be thought of as independent sources of directional information. Rather, the plethora of experiments that have studied the interaction of these magnetic and celestial compasses suggest that these mechanisms should be thought of as different components of a system complex for orientation and navigation (Åkesson 1994; Wiltschko and Wiltschko 2015). While some studies have described this interaction as a compromise between these magnetic and celestial compass systems (Åkesson 1994), others have shown clearer preferences for compass mechanism based on the life history of the bird species. Generally, both nocturnal and diurnal migrant passerines tend to rely more heavily on the magnetic compass with the sun compass playing only a minor role (Åkesson et al. 2006; Bingman and Wiltschko 1988). This contrasts with studies in nonmigratory, diurnal pigeons that seem to have indicated a preference in these birds using the sun compass, only switching to the magnetic compass upon the perceived failure of the sun compass (Wiltschko and Wiltschko 2015). While preferences in compass mechanism may exist between species, these same cue-conflict studies have also readily shown a willingness in birds to adapt by either using a different compass, or by using other compass mechanisms such as polarized light to "recalibrate" their preferred compass (Deutschlander and Beason 2014; Wiltschko and Wiltschko 2015; Cochran et al. 2004). Overall, while the multiple different compass mechanisms used in navigation may be used at different frequencies or may interact with each other, they regardless work together to form a complex, integrative system that allows birds to detect and utilize crucial directional information – even when one particular mechanism is compromised – throughout their course.

## Conclusion

The field of passerine navigation is a continually evolving subfield of avian navigation that is only expected to become more refined and integrative in the future. As the core theoretical framework and mechanisms used in passerine navigation are

highly analogous to that of many other avian species, recent years have seen an increasing number of passerines become focal species in navigational or homing research. And while some of these studies have just sought to better refine concepts in avian navigation collectively, they have also importantly assisted in drawing attention to observed differences in the passerines' navigational behavior and abilities as well. In particular, use of migrant passerines has been and continues to be a major area of study as advances in tracking technology have allowed for less invasive and more comprehensive work on navigation during seasonal migration. Additionally, an interdisciplinary approach to passerine navigation using neurobiological and cognitive techniques has also gained traction to better explain how navigational information is processed in birds' brains, and to gain further insights on passerines' navigational development and ontogeny (Wiltschko and Wiltschko 2015). In utilizing these and other avenues of research, further navigational studies in passerines may not only expand the body of knowledge within this particular taxon, but also importantly continue in contributing to the advancement of avian navigation as a whole.

## Cross-References

- [Bird Migrations](#)
- [Navigation](#)
- [Orientation](#)
- [Passerine Cognition](#)
- [Passerine Life History](#)

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## Passerine Sensory Systems

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### Definition

A passerine is a bird that belongs to the order Passeriformes. This order has over 5,000 identified species, which makes up more than half of all bird species. The order is divided into three suborders: Tyranni (suboscines), Passeri (oscines), and the basal Acanthisitti.

Sensory systems are the peripheral neural structures where sensory transduction and transmission of sensory activity to the central nervous system take place.

### Introduction

Oscines (from Latin *oscen*, “songbird”) are the largest group of passerines, and they owe their name to their complex vocalizations, or songs, which they learn by imitating their conspecifics (in some cases heterospecifics, e.g., mocking birds *Mimus polyglottos*). Songbirds have received a great deal of attention from

neuroethologists and neuroscientists because they are one of the few vertebrate models of vocal learning. However, most studies in avian sensory systems have focused in nonpasserine birds, like pigeons and chickens as general avian models for neuroanatomy and physiology, or in sensory specialists like the barn owl for sound localization. Nonetheless, there is a growing amount of research on the sensory systems of passerines, driven in part by the great ecological and behavioral diversity found in this group, which offers the opportunity to study how sensory system evolves in response to changes in these parameters.

### Vision

Vision has been largely regarded as one of the most important senses in birds. This is likely true in passerines as well. Passerines rely on their visual system to evaluate predation threats, navigate, avoid obstacles, recognize conspecifics, and forage. The first stage of visual processing occurs in the retina, where photoreceptors detect individual photons of the light that make up the image and produce electrical signals that reach the retinal ganglion cells (RGCs) through a complex circuitry involving many other cell types. In turn, the RGCs send their axons to the primary visual centers of the brain. Birds have three kinds of photoreceptors, rods, cones, and double cones, the latter consisting of structurally and functionally integrated pairs of cones. Rods are responsive at low light levels, while cones are responsive at high light levels. Different photoreceptors contain different photopigments called opsins, which are sensitive to different parts of the light spectrum or, more simply put, respond to different wavelengths of light. In passerines, as in other birds, rods contain only one type of photopigment which is most sensitive to light around 500 nm ( $\lambda$ -max of 500 nm), while different cones can contain one of the four types of photopigments, including a short-wavelength, ultraviolet (UV)-violet light-sensitive cone. In contrast, humans have cones with only three types of photopigments, none of which are sensitive to UV-violet light. There is evidence that all four cone types in birds are involved in color vision, and therefore passerines

(and most bird and reptiles) can be considered as having a tetrachromatic visual system, in contrast to a trichromatic in humans and a dichromatic in most mammals. All passerines are sensitive to UV light, but there is a pronounced difference among different clades in the wavelength of peak absorbance ( $\lambda$ -max) of the opsin in the UV-violet cone (first shortwave-sensitive opsin, SWS1). Thus, two types of tetrachromatic vision exist among passerines: a UV-sensitive (UVS), with a SWS1  $\lambda$ -max absorbance of 355–380 nm and a violet-sensitive type (VS), with a SWS1  $\lambda$ -max of 402–426 nm (Ödeen et al. 2011). So far, evidence suggests that all species within the large clade of the Passerida (which includes thrush-, sparrow-, and warbler-like passerines) present a UVS type. Among other passerines, the VS type dominates, although transitions to UVs have occurred many times independently. Some groups show consistency in their color vision type, such as corvids and subocines, which all present VS vision. In contrast, the family Maluridae (fairy wrens and allies) shows several shifts between UV and UVS vision. In all, passerines present at least eight shifts between UV and UVS vision, and the ancestral condition among passerines is unknown. Parrots (Psittaciformes), the sister group of passerines, have UVS-type cones, which suggests that UVS vision might be the ancestral type. The sensitivity of the other cones varies less pronouncedly among passerines although there are some interspecific differences (Hart et al. 2000). The  $\lambda$ -max of the other cone photopigments is around 470 nm for the shortwave type II opsin (SWS2), 505 nm for the rhodopsin type II (RH2), and 565 nm for the long wave-sensitive (LWS) opsin. In addition to the different types of photopigments, passerine cones (as in other birds and reptiles) each have an oil droplet in the proximal part of their outer segment. These oil droplets contain different carotenoid-based pigments and have the function of filtering light before it reaches the photopigments of the cone. This sharpens the spectral tuning of the receptor and thus reduces the overlap with adjacent spectral classes of cone. Further, oil droplets shift the peak sensitivity of each cone toward longer wavelengths (Hart and Vorobyev 2005).

In addition to the variation in spectrum sensitivity of some photopigments between different species, image analysis in the retina is also influenced by variation in the amount and distribution of both photoreceptors and RGCs. Variation on the distribution of different cones in the retina means that different parts of the retina could have different spectral sensitivities. This type of variation has been shown in several groups of birds, including Passeriformes, but has not been studied in many species and is not completely clear what its function is. Many more studies have shown different patterns of distribution of RGCs in the retina of Passeriformes and other birds. These patterns can be, for example, circular, with a very high concentration of RGCs at the center and a gradual decline of RGC density away from the center of the retina. In some species, more than one high-density area occurs, while in others a linear band or streak of high density of RGCs occurs. Areas of very high density of RGCs can be associated with the presence of a fovea, in which the outer layer of the retina is displaced to form a small pit or depression on the surface. The usual interpretation is that these areas of high RGCs density represent areas of enhanced spatial resolution. This means that different parts of the retina, and therefore the visual field, have better or worst visual acuity. The more common explanation for the differences in distribution of RGCs among different species of birds, including Passeriformes, is that they relate to differences in either foraging (the detection of food items in the frontal or lateral field of view) or the detection of predators (Moore et al. 2015).

Finally, there is also variation in the visual field of different Passeriformes. Most passerines have laterally placed eyes; however, the amount of overlap between the visual fields of both eyes and the blind spot behind the head vary between species. It is worth noting that passerines can have wide ranges of eye movements (with both eyes  $>60^\circ$  across all elevations), so visual fields can vary greatly. Variation in the size of binocular overlap, blind spots, and range of eye movements has been proposed to also correlate with foraging strategies and antipredatory behaviors (Moore et al. 2015).

## Hearing

Most passerines, particularly oscines, can be considered auditory specialists, bearing in mind the central role that vocalizations play in their social interactions. Nevertheless, hearing organs and their capabilities differ little from other birds.

Detection of sound waves is achieved in birds, reptiles, and mammals by the ear which consists of three parts: the outer, middle, and inner ear. In birds, the outer ear usually consists of a simple tube with its entrance located behind the eye. In passerines (and other birds), this is usually covered by small feathers. At the end of the outer ear is the ear drum, which separates the outer ear from the middle ear, and consists of the tympanic membrane, a thin membrane that acts as the first step in sound detection as it oscillates with the pressure oscillation produced by sound waves. Birds, like other land vertebrates, cannot respond directly to these vibrations as their inner ear, where the receptor resides, is filled with liquid. The middle ear acts as a transducer between the two mediums, the air in the outer ear and the liquid in the inner, such that it makes the liquid vibrate at the same rate as that of the air. In birds, reptiles, and amphibians, this is accomplished by a single bone, the columella, which at one end connects to the ear drum and in the other to the oval window of the inner ear. In contrast, in mammals this is achieved by three interconnected bones. The receptors that detect the vibrations transmitted into the fluid of the inner ear are called hair cells. Hair cells are located in the basilar papilla. Body size and the length of the basilar papilla are positively correlated, while the most sensitive frequency in a given species is inversely related to the body size and the length of the basilar papilla (Gleich et al. 2005). Unlike mammals, birds (including passerines) can regenerate auditory hair cells in the basilar papilla after loss of original hair cells (Woolley et al. 2001).

The ability of passerines to localize sound in space is rather poor when compared to mammals and specialist birds like owls. In all vertebrates, localization of sound sources depends on interaural comparison of time of arrival and intensity of the sound. These parameters are known as



interaural time difference (ITD) and interaural level difference (ILD). Passerines have been shown to use both of these cues to detect sound sources in the horizontal plane (Klump 2000), although the small size of the head and therefore the small distance between the two ears of most passerines greatly restrict the maximum ITD and ILD that can be attained. These factors result in poor spatial resolution. Passerines can resolve azimuth with acuities of no more than  $20^\circ$  and in many cases worst, up to  $70^\circ$  (Klump et al. 1986; Nelson and Stoddard 1998); this compares to  $1\text{--}2^\circ$  of acuity seen in some species of owls (Knudsen et al. 1979). Passerines, like all other birds with the exception of some owl species, lack pinnae or any other external ear structure. This means that their ears or head offers no cues for detecting sounds in elevation, and therefore passerines have to use behavioral strategies, like tilting their heads or moving to a different location, to localize sounds in three dimensions (Dooling 1992; Klump 2000).

Hearing frequency ranges have been studied for many passerines species. In general, these span from 100 Hz to 10 kHz, although hearing sensitivity rapidly deteriorates above 7 kHz and maximum sensitivity is usually below 4 kHz. Overall, hearing ranges of passerines are higher than those of nonpasserines (excluding owls). For example, a comparison of behaviorally determined audiograms showed that nonpasserines (8 species) have in average a lower maximum audible frequency (7.5 kHz) than passerines (9.7 kHz, 13 species) and also that nonpasserines have a lowest peak frequency sensitivity (2.1 kHz) than passerines (2.9 kHz; Dooling 1992). Among passerines, there is a strong correlation between the frequency of peak hearing sensitivity and specific spectral features of song (Dooling and Fay 2000). Although some species of passerines produce harmonics of their songs into ultrasound frequencies ( $>20$  kHz; Narins et al. 2004), there is no evidence of ultrasound hearing in any passerine (or any other bird). Infrasound detection ( $>25$  kHz) has been shown in pigeons and chickens but not in passerines so far, although it has not been systematically studied.

The clearest role of hearing in Passeriformes, particularly in oscines, is directly related to their complex vocalizations. Both learned and non-learned vocalizations are used in this group for all kinds of social interactions, such as begging, conspecific recognition, courtship, territorial displays, and alarm calls. Hearing in passerines also has been shown to be important in detecting predators. Therefore, hearing plays a central role in the behavior of these birds.

### Somesthetic Senses

The somesthetic senses, which include touch (mechanoreception), temperature, proprioception, and pain, have not been specifically studied in songbirds to a great extent and therefore much has to be drawn from general knowledge in other species, mostly the domestic chicken and pigeons. Passerines are not considered somatosensory specialist as they do not rely heavily on somatosensory information for feeding like other birds, namely, waterfowls, beak-probing birds (e.g., some shorebirds, ibises), and parrots, which use somatosensory information from their beaks and tongues to detect and/or manipulate food (Gutiérrez-Ibáñez et al. 2009). Nonetheless, somatosensation without a doubt plays an important role in many aspects of passerines behavior.

Mechanoreceptors respond to movement of objects or liquids that are in direct contact with them. Different types of mechanoreceptors respond to different properties of movement: vibration, velocity, and amplitude (Gottschaldt 1985). The most common mechanoreceptors in the integument of passerines are the encapsulated Herbst corpuscles, which respond to vibration and are similar to the mammalian Pacinian corpuscles. These sensory endings are located in almost all the body but vary in morphology depending on the location. Herbst corpuscles can be found in the beak, skin, tendons, muscle, joint capsules, and at the base of feather follicles. In grain-feeding Passeriformes, particularly finches, Herbst corpuscles are located in places of the bill which are mechanically involved in seed opening (Martin 2017), as well as in the tongue mechanosensory papillae (Wild 1990). The association of Herbst corpuscles to feather follicles is thought to be

important for providing birds with information about air speed and movements during flight. Some of the first evidence for this comes from studies in Passeriformes (Gewecke and Woike 1978). The bristle feathers, stiff feathers that grow in the face and at the base of the beak of birds (including many passerines), are associated with numerous Herbst corpuscles, suggesting that they constitute tactile specializations (Cunningham et al. 2011). Another type of mechanoreceptor in birds is the Grandry corpuscles, which detect the velocity component of mechanical stimuli and are most common in the beaks of somatosensory specialist birds. However, these receptors have also been found in the beak and skin of Passeriformes, usually near Herbst corpuscles. Little is known about temperature receptors in birds in general and even though these have been detected in a few species (e.g., waterfowls and chickens), they are likely widespread among birds, including passerines. Pain perception has been almost exclusively studied in domestic chickens but is also without a doubt common to all birds. The avian nociceptors are likely very similar to those of mammals.

### Magnetoreception

There is strong evidence that both passerine and nonpasserines birds can sense the earth's geomagnetic field and that this sense is used as a compass for orientation (Wiltschko and Wiltschko 2006). Many behavioral experiments show that strong magnetic fields, which disrupt the weak magnetic field from earth, abolish orientation behavior in birds, including passerines (Wiltschko and Wiltschko 2006). After some controversy, it is now more or less accepted that birds detect magnetic fields through two different mechanisms and that both are likely present in the same individuals. These mechanisms are known as the "radical pair model" and the "magnetite model." The radical pair model proposes a chemical compass based on alterations caused by the magnetic field on a chemical reaction involving special photopigments in the retina and therefore that are detected by the eye. This model is supported

mainly by evidence that in migratory birds, especially passerines, magnetoreception is light-dependent. In classic experiments, passerines kept in captivity orientate themselves toward the direction of migration when the correspondent season arrives but only in the presence of light in the lower end of the spectrum, from blue to green. Birds kept in the dark or under red light do not orientate (Wiltschko et al. 2010). The magnetite model involves crystals of permanently magnetic material in the head. Deposits of iron oxides or magnetite have been found in different parts of the head and beak of birds, including migratory passerines (Beason and Nichols 1984). Also, there is evidence in passerines that changes in magnetic field result in activation of neurons in the brain regions that receive sensory projections from the beak (Heyers et al. 2010). In conclusion, there is good evidence that passerines (and other birds) can detect the earth's magnetic field in at least two different ways and are likely to use it for orientation, although there is still some debate regarding how and when is each system used for navigation and/or orientation.

### Olfaction

The significance of olfaction to ecology and behavior of birds has been historically underplayed to the point that early ornithologists discussed if birds were capable of olfaction at all. It is now clear that not only birds are certainly capable of olfaction but also that it plays an important role in many aspects of avian behavior, including that of Passeriformes. In all vertebrates, olfaction is mediated by sensory cells in the olfactory epithelium. Each of these cells expresses different olfactory receptors (ORs), which constitute the molecular basis of the sense of smell (Gaillard et al. 2004). The total amount of OR genes and the fraction of OR genes that are nonfunctional (i.e., pseudogenes) vary widely between vertebrate genomes, and both have been suggested to correlate positively with olfactory acuity (Niimura and Nei 2006). Birds have between 100 and 650 OR genes, which are lower than reptiles but higher than some species of fish

and comparable to some mammals. Among birds, passerines have some of the lowest amount of OR genes (~150 to 200), although the proportion of pseudogenes is similar to other birds (Steiger et al. 2008). The amount of OR genes correlates positively with the size of the olfactory bulb, the brain region that receives olfactory inputs from the olfactory epithelium. In accordance with the low amount of OR genes, passerines have one of the smallest olfactory bulbs among birds relative to brain size (Corfield et al. 2015). Despite this apparent reduction of the olfactory system in passerines, several species of this group have been shown to have odor detection thresholds comparable to rats and rabbits. More importantly, there is growing evidence for a role of olfaction in different behaviors of passerines. Passerines have been shown to use olfactory cues for the detection of predators, navigation during migration, kin recognition, conspecific recognition, advertisement and mate selection, nest material preference, and foraging by insectivorous passerine birds.

### Taste

Taste has not been studied widely in birds in general, and much less in passerines, but something can be inferred from what is known for nonpasserine birds, mostly the domestic chicken and ducks. It is thought that birds in general have poor taste acuity compared to mammals due to their relative low saliva secretion, number of taste buds, and lack of mastication (Berkhoudt 1985). Nonetheless, it is clear that taste is as important to birds as it is to mammals. In birds, taste is involved in detecting both nutritious compounds, like amino acids, lipids, salts, carbohydrates, and calcium, as well as toxic compounds. Like in all vertebrates, taste signals in birds are generated in the taste buds. These are groups of cells, barrel or flask shaped, embedded in the tongue or oral cavity. In birds, taste buds are found not only in the tongue but also in the palate and other parts of the oral cavity. Unlike most mammals, bird species examined so far have very few or are missing altogether taste papillae and taste buds in the dorsal surface of the tongue. Recent studies

suggest that the number of taste buds in birds is similar to that of mammals in relation to the size of the oral cavity. Both behavioral and genetic evidence show that birds are responsive to several taste categories: sweet, umami, bitter, salt, sour, fat, and calcium. In the case of sweet, omnivorous and granivorous birds do not respond positively to sugars, although nectivorous and frugivorous species do, including the common starling, a passerine (Roura et al. 2013). Genetic analyses have shown that chickens do not possess an ortholog gene (i.e., inherited from a shared ancestor) to the human T1R2 gene (the sweet receptor). On the other hand, in hummingbirds the umami receptor has suffered several changes in its amino acid sequence to allow for the detection of sugars. It is not clear if this is also true for other nectivorous and fructivorous species of birds, including the many passerines with this kind of diet. Umami is generally identified as the taste of monosodium glutamate, and its function is interpreted as being the detection of amino acids or proteins. In birds there is a functional umami receptor gene, and some species of passerines, like the common starling and the red-winged blackbird (*Agelaius phoeniceus*), show preference for amino acids (Werner et al. 2008). Bitter compounds are usually associated with toxic compounds. Bitter receptors are also present in birds, and like in other vertebrates, they produce an aversive response, including in passerines like the common starling and the red-winged blackbird. Although information about other taste categories is scarce, the gene for sourness, that is for the detection of the presence of acids, is present in the genome of the chicken (Roura et al. 2013). Also, birds have the need for intake of salt (sodium chloride, NaCl) and calcium, and therefore it is likely that some receptors are involved in detecting these compounds in passerines and birds in general.

### Conclusion

While passerines can hardly be considered sensory specialist, their great diversity in foraging

strategies, habitat, and ecology provides unique opportunities to study the evolution of sensory systems. A good example of this is the increasing literature on the visual system of passerines. Evidence on the use of olfaction by passerines in different contexts is also ever-increasing and is likely to encourage further research on the physiology and anatomy of the olfactory system of passerines and birds in general. Much of our knowledge about hearing and magnetoreception in birds comes from passerines, but there is still much to be explored, particularly how the different forms of magnetoreception are used. On the other hand, little is known about the somesthetic senses or the sense of taste in passerines and birds in general.

## Cross-References

- [Falconiformes Sensory Systems](#)
- [Passerine Morphology](#)
- [Passerine Navigation](#)
- [Passerine Vocal Communication](#)
- [Sensory Receptors](#)
- [Visual Recognition of Prey and Predators](#)

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## Passerine Vocal Communication

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## Definition

Birds of the order Passeriformes, known as passerines, include over half of the almost 10,000 known bird species (Mayr 1946). In comparison to other orders under the class Aves, passerines have a particular toe arrangement: three toes pointing forward and one pointing back (Proctor and Lynch 1993). This particular arrangement aids in perching, which has lead to the name “perching bird”.

## Introduction

Passerines include many songbirds, a group of more than 5,000 species that engage in vocal learning, similar to how humans, cetaceans, bats, elephants, parrots, and hummingbirds learn their vocalizations (Doupe and Kuhl 1999). Passerines, in general, are commonly referred to as songbirds, but this is not entirely correct. The order can instead be broken down into the Oscines and the Suboscines. Oscines (i.e., songbirds or “true” songbirds) have highly developed song and learn their species-typical vocalizations via a model (e.g., a parent) and have dedicated brain architecture. Suboscines, however, do not require a model to learn their species-typical vocalizations and continue to produce and perceive vocalizations even with damaged auditory brain regions; however, some species do have a rudimentary vocal system, the structure(s) within the brain



associated with production of vocalizations, which appears to act in the same way as in the Oscines (Kroodsma and Konishi 1991). These structures include rudimentary forms of structures like the robust nucleus of the arcopallium, which could indicate an evolutionary predecessor to a true vocal control system (see more details below; Liu et al. 2013). In North America, there is only one family of Suboscines: Tyrannidae, which includes flycatchers, phoebes, and king birds. Passerines primarily communicate using vocalizations, as acoustic signals are difficult to localize (e.g., in the presence of a predator), can travel across greater distances than visual cues, and are advantageous in dense vegetation. Passerines include a wide range of species found in both temperate and tropical climates.

## Passerine Species

### Example Temperate Species

Temperate forests extend north from the Tropic of Cancer to the Arctic Circle and south from the Tropic of Capricorn to the Antarctic Circle. The Paridae family includes the tits, chickadees, and nuthatches. Titmice are widely distributed and can be found in North America (e.g., tufted titmouse, *Baeolophus bicolor*), Africa (e.g., African blue tit, *Cyanistes teneriffae*), Asia and Europe (e.g., Great tit, *Parus major*). Chickadees are a group of North American songbirds including seven different species: black-capped (*Poecile atricapillus*), mountain (*P. gambeli*), Carolina (*P. carolinensis*), Boreal (*P. hudsonicus*), chestnut-backed (*P. rufescens*), Mexican (*P. sclateri*), and gray-headed (or “Siberian tit”; *P. cinctus*). Nuthatches mostly reside in North America (e.g., red-breasted, *Sitta canadensis*), but few species live in Eurasia (e.g., Eurasian nuthatch, *S. europaea*). A few examples of common non-Paridae temperate species include cowbirds (*Molothrus*), jays (*Corvidae*), sparrows (*Passer*), thrush (*Turdidae*), warblers (*Sylvia*), and wrens (*Troglodytidae*; Cornell Lab of Ornithology n.d.).

### Example Tropical Species

Passerines living between the Tropic of Cancer and the Tropic of Capricorn are classified as tropical

species. A few examples of these birds are the Andean cock-of-the-rock (*Rupicola peruvianus*), Wilson’s bird-of-paradise (*Cicinnurus respublica*), Australia’s regent bowerbird (*Sericulus chrysocephalus*), and multiple species of broadbill (*Eurylaimidae*). There are also multiple species of finches, such as the cut throat finch (*Amadina fasciata*), the Gouldian finch (*Erythrura gouldiae*), and the subfamily of Hawaiian honeycreepers (*Carduelinae*; Cornell Lab of Ornithology n.d.).

Zebra finches (*Taeniopygia guttata*) whose range extends from Eastern Indonesia throughout the arid regions of Australia, however, have such a large habitat that they cannot be considered only temperate or tropical. Zebra finches are one of the most widely studied bird species in avian neurobiology because they learn and memorize their song from a tutor bird, and this learning and memory process is similar to how human infants acquire language (Konishi 1985).

### Vocalization Types

Bird calls are often distinguished from song by a variety of characteristics, although in some species this distinction may be somewhat blurred. Songs are usually multipart sounds produced primarily by males during the breeding season as acoustic ornaments (Marler 2004; Smith 1991). Songs are used for the purposes of reproduction and territoriality, are typically produced in a consistent manner, and primarily by males in many species. In comparison, calls are typically simpler (sometimes even monosyllabic), produced by both sexes in all age groups, and used daily for the purposes of communication. Thus, calls serve a variety of functions crucial for survival (Marler 2004).

**Song** Songs are elaborate and complex vocalizations that have two main purposes: (1) to advertise and defend territory from other males and (2) to attract potential females for mating and potentially stimulate female reproductive behavior and physiology (Kroodsma and Miller 1996). The acoustic structure of birdsong is fairly consistent in production, which encompasses the notes, syllables, and phrases, and also dictates the way in which songs and song repertoires are delivered

(Marler 2004). Song repertoires can range in size from one simple song (as seen in the black-capped chickadee) to over a thousand complicated songs (as seen in the brown thrasher) (Kroodsma and Miller 1996). In order for birdsong to be acquired there has to be a predisposition to learning as well as being exposed to song (Brainard and Doupe 2002). Again, the learning process is generally divided into two phases, the sensory phase and the sensorimotor phase, which can overlap. During the sensory period, the songbird is in a sensitive state where the brain is prepared to receive auditory input. The songbird listens to the songs produced by adult songbirds (i.e., tutor birds) and their brain processes this auditory input, forming a memory template of song (Mooney 1999). This input leads to both neural and behavioral changes, which is followed by the sensorimotor phase. In this phase, songbirds start to produce their own song based on the template that was formed or activated during the sensory phase. Initially, this song is fairly inaccurate and variable and is often compared to babbling in human infants (e.g., Marler 1970). The auditory feedback that the songbird receives allows them to assess their performance and make changes until the song they produce matches the song template they developed during the sensory phase (e.g., Konishi 1965).

These early life experiences are crucial for song learning, and this learning can be disrupted in a variety of ways. The length of exposure to a tutor bird can drastically affect birdsong (i.e., shorter exposures lead to less complex song structures; e.g., Thorpe 1958). Acoustically isolating a bird from others during the sensory phase can lead to songs that are simpler, shifted in their frequencies, and extremely variable (e.g., Shackleton and Ratcliffe 1993). Preventing auditory feedback during the sensorimotor phase by deafening birds can also negatively impact song by producing shorter songs, delaying singing behavior, or even eliminating song altogether (e.g., Konishi 1965). However, many species still maintain some of the features of their species typical songs, indicating that there is partial encoding of some song features or an inherent song template that initially directs song learning (e.g., Bolhuis and Gahr 2006).

**Calls** Birds must maintain their social groupings, whether it is in the context of a mated pair, flock, or family group. Most birds have some form of contact call, which allows them to remain in contact with one another during foraging. Separation calls may be a variation of a contact call and are produced when a bird loses contact with its group. Finding food is also crucial for a bird's survival; therefore, some birds emit food calls which announce the presence of a food source enticing other birds in the group to come feed. A subset of these calls, begging calls, is produced by chicks after hatching which coax parents into feeding their offspring. These calls often allow for nest or kin recognition by the parents, or for nest mates to recognize one another (e.g., Beecher 1982).

Aggressive calls are used in antagonistic interactions between individuals, whereas alarm calls are used to announce the presence of a predator or danger in the environment (e.g., distress and mobbing calls). Distress calls are typically produced when the individual is in the grips of a predator (e.g., Zachau and Freeberg 2012). Conversely, when a nearby predator is detected, mobbing calls are used to attract other members of the group to harass or "mob" the predator in order to scare them off. There are also variations of mobbing calls that tend to code for the type of predator or the threat level posed to the individual (e.g., Templeton et al. 2005).

Calls were long believed to be innate; however, this is not the case for all species. Many calls are learned or partially learned (for review see Marler and Slabbekoorn 2004). Learning calls, as with songs, is also accomplished through a process of vocal imitation (Vicario 2004). Unlike songs that are produced primarily during the breeding season, many calls are produced year round and are more easily elicited in laboratory conditions. Again, the male zebra finch distance call, like their song, is learned from a tutor bird, and, as such, the calls vary between individuals (Simpson and Vicario 1990, 1991). Also, many calls are produced by both sexes, unlike song which is primarily produced by males. This allows researchers to examine the learning and development of calls in both males and females. There is

some evidence suggesting that the black-capped chickadee's namesake *chick-a-dee* call is partially learned (e.g., Hughes et al. 1998). Black-capped chickadees raised in social and acoustic isolation produce *chick-a-dee* calls; however, the quality of these vocalizations is poor in comparison to chickadees raised with a tutor (Hughes et al. 1998). Overall, this indicates that there is some evidence for learning calls in songbirds.

Unlike production of the *chick-a-dee* call, the ability to memorize, categorize, and discriminate *chick-a-dee* calls may not be learned. Whether or not birds were raised with their own species, they are able to discriminate between a foreign and familiar species typical *chick-a-dee* calls. Specifically, it appears as though chickadees' internal template for discrimination does not require input from adults within their own species (Bloomfield et al. 2008). Therefore, memorization and discrimination of the *chick-a-dee* call is not learned, but production seems to be partially learned.

## Structures and Perception

Oscines are characterized by a specialized and embellished (compared to Suboscines, see below) sound-producing organ, the syrinx. The syrinx is complex, comprised of five pairs of muscles, and is located at the junction of two bronchi, which allows for each bronchus to act as its own independent sound source. Vocal production is therefore accomplished by a complex interplay between muscle movements in the syrinx, air flow, and beak articulation. Suboscine species also possess a syrinx; however, its role in song production is unclear; song production and frequency modulation do not seem to rely entirely on the syrinx, but primarily on air sac pressure modulation (Amador et al. 2008). Oscines also possess a set of discrete brain nuclei called the vocal control system that are specialized for the acquisition, production, and perception of vocalizations. HVC (proper name, previously referred to as the high vocal center) and the robust nucleus of the arcopallium (RA) are integral components of the vocal control system within the brain of

Oscines, and we know that lesioning these structures can drastically impact song production (Nottebohm et al. 1976). It also appears as though these two structures may be involved in call learning and production. Lesioning HVC and RA in male zebra finches causes one of their vocalizations, the distance call, to become more female-like, and lose their male-typical characteristics (Simpson and Vicario 1990). Certain manipulations can cause females to be able to learn and produce male-like distance calls, such as estrogen treatment during development (Simpson and Vicario 1991). Early life exposure to estradiol causes a masculinization of vocal behavior in zebra finches; estradiol-treated females produce song-like vocalizations in adulthood, as well as being able to produce the male-typical aspects of the distance call. Eastern phoebes (*Sayornis phoebe*), a suboscine species, also possess a rudimentary RA-like structure (Liu et al. 2013). Since suboscine species, like the eastern phoebe, do not learn their song, this suggests that vocal learning may be an evolved trait.

Humans can hear sounds in the range of 20 Hz to 20,000 Hz, but best perceive sounds between 2,000 and 4,000 Hz (Dooling 1982). In comparison, birds have a more restricted hearing range, especially for higher frequencies where they do not detect sounds above 10,000 Hz (Dooling et al. 2000). Similar to humans, birds hear best between 2,000 and 5,000 Hz, with songbirds (i.e., Oscines) typically more sensitive to higher frequencies and non-songbirds typically more sensitive to lower frequencies within this range. Human perception thresholds tend to be lower than birds for all frequencies, meaning that birds can detect quieter sounds, but there are a number of exceptions, including many owl species. Although birds have a more narrow overall frequency perceptual range than humans, birds are more sensitive to absolute frequency, changes in frequency, and timing between sounds, which aid in perceiving and discriminating their own, and other species, complex vocalizations (Dooling 1982).

Even though birds and mammals are not closely related, the ears of both share a number of structural similarities (e.g., they both have inner

and middle ear structures, though the avian ear lacks a pinna or outer ear). In all vertebrate species, the middle ear serves to mediate the transfer of sound from the environment to the inner ear, usually by way of tympanic membrane vibrations and movement of a varying number of small bones. The avian middle ear has little variation among species and takes up a large amount of space relative to head size compared to reptiles and mammals. Avian ears have a single bone, the columella, while mammalian ears have three bones, collectively called ossicles. The mammalian cochlea is longer and coiled, while the avian equivalent, the papilla, is shorter and straight or slightly curved (Dooling et al. 2000). Both cochlea and papilla have specialized hair cells which vibrate in response to sounds of specific frequencies. However, the avian tall and short hair cells serve the same function as, but are not evolutionarily related to, the inner and outer hair cells in the mammalian cochlea. The orientations of these hair cells are fixed across mammalian species, but vary widely in avian species. Vibrations in hair cells are transferred to neurons, and certain hair cells are responsive to certain frequencies. Frequency and intensity are stored and passed into the auditory nerve. The pathway from auditory nuclei through the auditory areas of the brain is conserved across both birds and reptiles. From the auditory nerves, sound information projects to two cochlear nuclei which in turn project onto parallel pathways of auditory nuclei, one of which encodes information about sound loudness and the other which encodes timing. This auditory information eventually reaches Field L, which is involved in auditory processing. In songbirds, Field L projects to HVC and the RA in the vocal control system, allowing for recognition of and response to vocalizations (Dooling et al. 2000).

## Vocal Production

### Vocal Learning

Songbirds acquire some of their species-specific vocalizations through vocal learning; thus,

songbirds must attend to the vocalizations of others and modify their own vocalizations to match these models. Vocal learning is thought to be relatively rare in the animal kingdom, but has been documented in a number of vertebrates (Doupe and Kuhl 1999). However, to our knowledge Suboscines have not shown evidence of vocal learning.

Songbirds can generally be separated into two broad groups based on how they learn their vocalizations: open-ended and closed-ended learners (Brainard and Doupe 2002). Open-ended learners pass through a sensory phase in which they are sensitive to the auditory input they receive and acquire a song template. Open-ended learners then experience a sensorimotor phase during which time they attempt to match their vocal production to that template, which ultimately results in a stable adult song. However, they are still able to continue to learn and modify their song throughout their lifetime. Canaries (*Serinus canaria*) are a good example of an open-ended learner. Canaries learn their songs during the spring, practice throughout the fall, then sing a crystallized song during the following spring (Nottebohm et al. 1986). This process is repeated every year, and thus their song repertoires expand and change annually.

Vocal mimics, a type of open-ended learner (e.g., parrots, *Psittacines*; lyrebirds, *Menura*; etc.), possess highly complex syrinxes which allow for these passerines to produce their species-typical vocalizations. In addition to learning vocalizations produced by other species, including human speech, vocal mimics can also imitate noises from their environment (e.g., chain-saw sounds, camera shutter). These complex vocalizations are integrated into their song resulting in a more complicated repertoire, which many individuals use to attract potential mates (Cocker et al. 2013).

Closed-ended learners only pass through the sensory and sensorimotor phase once, then their songs become relatively fixed for the rest of the birds' lives (Brainard and Doupe 2002). For zebra finches, the sensory and the sensorimotor phases overlap. These birds only produce one

song type, which is crystallized by 90 days post-hatch (Slater et al. 1988). Another developmental path is that of the white-crowned sparrows (*Zonotrichia leucophrys*) which learn their song in the first few months of life, but do not actually sing until the following breeding season (Marler 1970).

## Conclusions

Passerines are the largest order of birds, encompassing more than half of all known avian species. Oscines' ability to learn vocalizations from adults is rare and has only been observed in a limited number of species. This ability contributes to the size of song repertoires, and occasionally calls, observed within this group. Oscines' auditory systems, including their specialized ears and neural pathways, are consistent across songbird species. Oscine and suboscine species differ in the number of vocalizations in their repertoire (i.e., ranging from a few vocalizations to hundreds), the time during which vocalizations are acquired (i.e., during a single acquisition period, annually, or continually), and the underlying neural mechanisms used to produce these vocalizations. Overall, passerine communication is complex and critical for social dynamics, in particular for species that inhabit dense vegetation, communicate over long distances, and cannot rely on visual cues.

## Cross-References

- [Critical Period for Song Learning](#)
- [Contact Calls](#)
- [Countersinging](#)
- [Passerine Cognition](#)
- [Passerine Life History](#)
- [Passerine Morphology](#)
- [Passerine Sensory Systems](#)
- [Signaller](#)
- [Songbird Learning](#)
- [Subsong](#)

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## Passive Avoidance Conditioning

### ► Passive Avoidance Learning

## Passive Avoidance Learning

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## Synonyms

Fear learning; Inhibitory avoidance; Passive avoidance conditioning; Punishment

## Definition

Passive avoidance involves an organism learning to withhold a certain behavior in order to postpone or avoid an aversive event.

## Introduction

Learning to avoid harmful events, stimuli, or places has clear adaptive value and is ubiquitous across the animal kingdom. Experimentally, avoidance involves a subject learning that a specific behavioral response will result in the postponement or avoidance of an undesirable event.

Avoidance behavior is most commonly evaluated using either active or passive avoidance conditioning paradigms. In the active form, the aversive event is avoided by performing a specific response, while in the passive form the aversive event is avoided through the *suppression* of a specific response. The response to be performed or suppressed (the conditioned response [CR]) is typically one that the animal normally performs. In this case, the task is for the animal to learn to suppress a normal response when in a given context, and thus behave contrary to their innate preferences (Bammer 1982).

In both active and passive forms, learning the avoidance contingency results in the postponement or omission of a predictable aversive event (the unconditioned stimulus [US]). Avoidance procedures can be distinguished from escape procedures, in that the former involves behavior causing the omission of a *forthcoming* aversive event, while the latter involves distancing oneself from an *ongoing* aversive event (Bower and Hilgard 1981).

## Passive Avoidance Procedures

Passive avoidance conditioning utilizes one of two procedures: discrete trial or free-operant passive avoidance conditioning. In the discrete trial procedure, a distinctive warning stimulus occurs prior to the aversive event and conveys to the subject that the aversive event is forthcoming. To prevent or postpone the aversive event, the subject must withhold a specific response during the period that the warning stimulus is present (typically 5–60s in duration). In contrast, the free-operant or “punishment” procedure simply pairs a given spontaneous or learnt behavior to an aversive event, with the outcome that the specified behavior is suppressed.

A commonly used form of the free-operant procedure involves training a subject (typically a rat or mouse) in a two-chamber conditioning apparatus that contains both dark and light compartments. As many animals, including rodents, possess an innate tendency toward dark areas, a subject placed in the light compartment will

typically run to the dark compartment where it receives a single or continuous electric shock. The subject thereafter associates the dark compartment with the aversive event (Pavlovian contextual fear conditioning) and withholds entry into this previously punished area (instrumental response) during the subsequent test session. While electric shock is the most commonly used aversive stimulus in passive avoidance tests, puffs of air, loud noises, and extreme temperatures have all been used as well.

Since rodents acquire this task after a single trial, the passive avoidance paradigm is used extensively to study memory, in and of itself, as well as following physiological manipulations or drug delivery. Drug injections, for example, can be precisely timed before training or at different points after training and prior to the retention test, permitting the effects of a given intervention on encoding, consolidation, and retention to be clearly articulated. Likewise, the retention test can be conducted soon or long after training in order to separately assess short-term and long-term memories.

## Experimental Parameters

A wide range of experimental designs have been utilized to evaluate passive avoidance learning, and the procedural differences among these designs have led to significant variability in outcomes. One of the most critical parameters in avoidance paradigms is the intensity and duration of the aversive stimulus. Experiments with electric shock commonly demonstrate a stepwise improvement in avoidance behavior alongside increases in the intensity of the electric shock, up to a certain threshold, above which performance decrements or harm may be observed (Seligman and Campbell 1965). Also important is the relevance of the stimulus and desired response to the organism: stimuli and responses that are evolutionarily relevant to a species will be much more readily acquired than those that are arbitrary (Bolles 1970). For example, associations between taste and induced sickness are more readily acquired than associations between audio-visual

cues and sickness, and running is far more readily acquired by rats in response to an aversive stimulus than trained tail movements. Other factors, such as the temporal nature of stimulus exposure, the experimental context, handling by the experimenter, species-specific differences and differences between individuals may further impact the rate of acquisition and retention.

## Theories of Avoidance Learning

One of the earliest and most influential theories put forward to explain avoidance behavior is Mowrer's two-factor theory (Mowrer 1947), which suggests that avoidance learning is comprised of two processes: predicting a threat and learning to escape from the predictor. This theory asserts that avoidance behavior includes both a Pavlovian and instrumental component. The Pavlovian component occurs when a warning signal previously paired with an aversive stimulus elicits fear, while the instrumental component occurs when the aversive stimulus that was predicted by the warning stimulus is avoided. As a result, avoidance behavior is negatively reinforced through a reduction in fear.

While Mowrer's theory remains an influential explanation of avoidance processes, it has not escaped criticism. One critique concerns the finding that avoidance responses may occur in the absence of experimentally controlled warning stimuli. For example, in *unsignalled* avoidance procedures, animals are exposed to and learn to avoid an aversive stimulus that is delivered at fixed time intervals, and in the absence of a discrete warning signal (Sidman 1962). However, although explicit warning signals are absent in such cases, the "silent" temporal and proprioceptive information inherent within the experimental context may serve as a medium for association with the aversive outcome. Mowrer's theory may therefore still be viable, so long as the definition of what constitutes a warning stimulus is extended to encompass a broader range of contextual cues.

A second critique addresses avoidance behaviors observed in the absence of an initial aversive

experience. Since the two-factor theory assumes that avoidance is based on prior reinforcement learning, avoidance that occurs spontaneously and without exposure to an antecedent stimulus is in conflict with the two-factor theory. For example, avoidance to novel stimuli occurs frequently in naturalistic settings, where an initial encounter with harm can be fatal. In this context, even exposure to the scents of a never-before encountered predator can be sufficient to elicit an avoidance response or other defensive behaviors.

In response to these and other critiques, Seligman and Johnston (1973) put forth an alternative "cognitive" explanation of avoidance learning. Their theory argued that avoidance behavior is driven by expectancies about the response-outcome contingency, rather than stimulus-response associations. During avoidance learning, subjects acquire two response-outcome contingencies: (1) if they perform the appropriate avoidance response (including the omission of some behavior, as with passive avoidance), the aversive stimulus will not occur, and (2) if they do not perform the avoidance response, the aversive stimulus will occur. Subjects perform the avoidance response because they prefer to not experience the aversive stimulus. By including a role for expectancies in avoidance learning and maintenance, Seligman and Johnston's theory accounts for data not easily explained by two-factor theory. For example, many animals continue to perform an avoidance response long after the aversive stimulus has been inactivated. While the two-factor theory assumes that fear and fear-motivated avoidance behavior should gradually diminish once the aversive stimulus has been removed, Seligman and Johnston take an alternative view that deemphasizes the role of fear. According to cognitive theory, an animal that continues to avoid a stimulus that was previously associated with harm does not experience the changed contingency that occurred when the association between the stimulus and harm was removed. As such, the expectancy that harm will follow the previously harmful stimulus is preserved (Krypotos et al. 2015).

## Conclusion

The passive avoidance conditioning test is a well-described paradigm for evaluating the mechanisms involved in cognition. This test allows retention to be examined after a single training session and as such is routinely used in behavioral and neurophysiological research to examine the effects of novel chemical agents on learning and memory.

## Cross-References

- [Avoidance](#)
- [Negative Reinforcement](#)
- [Punishment](#)

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## Paternal Behavior

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## Synonyms

[Father's behavior](#)

## Definition

Set of behavioral patterns exhibited by the male parent.

## Introduction

It is the set of characteristics and patterns associated with the father. The increased concern about the relationship between father and a child is attributable in explaining the belief that fathers can also have a significant influence on the development of their children. Paternal behavior is not common in mammals, but there are much evidences proving paternal behavior being regulated by the same neural circuits that controls maternal behavior. Since the mechanisms are very much similar in paternal and maternal behavior, it leads to an idea that parental circuit is common in mammals. Studies exhibit the vital role of paternal behavior and its influence on increasing the survivorship of offspring (Earls 1976). Testosterone is the most researched hormone which is believed to be affecting the paternal care. However, testosterone is prominently known for its negative effects, but there are facts which show that it can also encourage paternal

behavior in some species (Bredy et al. 2004; Lamb et al. 1985; Snowdon and Suomi 1982).

## Role of Biogenetic Factors in Paternal Behavior

According to many hormonal debates, it is proposed that mothers are more prepared in terms of hormones for the process of pregnancy, parturition, and lactation and other childcare tasks that are important for the survival and development of the offspring as compared to fathers. Therefore, it is believed that men do not have these capacities since they compulsorily need not to participate in childcare. However, there is no reason to consider that these behavioral susceptibilities are in any way deterministic, crediting female involvement in parenting and neglecting the involvement of male. Therefore, fathers can also perform the tasks of parenting as good as the mothers.

Clearly, a biogenetic perspective compels us to consider all the ecological factors explaining the environment in which the potential is displayed along with the physiological susceptibility (Lamb et al. 1985).

## Extent of Paternal Involvement

Psychologists and many researchers consider paternal behavior in a more illustrated way by considering a diverse array of activities where fathers are involved with their children. The amount of time spent by fathers in parenting activities like feeding, provisioning, conceiving, rearing, and protecting plays a very vital role in determining the paternal behavior in their children.

### Components of Paternal Involvement

Components of paternal involvement include various factors responsible for changing behavior in children. These components comprise of:

- Interaction of fathers with their children – It refers to the actual time spent by the fathers with their children through direct contact with

them by participating in caretaking and shared activities.

- Extent of fathers' responsibility toward their children – It refers to the role played by the fathers in ensuring the safety of the children and also making resources available for them.
- Availability of fathers for their children – It refers to the concept that in times of need, they must be potentially available for their children irrespective of the presence of direct or indirect contact (Earls 1976; Lamb et al. 1985).

## Paternal Behavior in Other Taxonomies

Involvement of males in the care of offspring is common in many other species other than mammals. Only 5–10% of mammals exhibit paternal care, of them rodents, primates, and canids are few. In teleost fish species, males play a more vital role than females in nest building and egg attendance.

In birds, around 90% of the species share responsibilities among both the parents including nest building, incubation of eggs, and defending and feeding to the offspring. In bird population, which of the parent will care for the offspring is determined by the available sex ratio. For example, male shorebirds which are more abundant in population as compared to female shorebirds are more likely to take care of the offspring (Cockburn 2006).

A large number of species of anuran amphibians also exhibit paternal behavior like glass frogs. Some species of arthropods also show paternal care like giant water bug, harvestman, etc. Fathers, in many species of crustaceans, play a vital role in building nests or burrows. The most uncommon aspect of paternal care in arthropods includes the investment of males after egg giving, and it exists in only 13 taxa (Brown et al. 2010; Dulac et al. 2014; Smith 1997; Tallamy 2001; Woodroffe and Vincent 1994).

## Sensory Cues in Paternal Interactions

Many researchers and neuroethologists are working to recognize and estimate the stimulating



differences in the nature and complexity of the signals which are responsible for driving paternal behaviors. According to recent studies, it is believed that the vomeronasal organ (VNO) plays a somewhat vital role in determining the infanticidal and paternal behavior. In laboratory mice, infanticide is more common in virgin males.

Recent research in mice also states that the loss of VNO either by surgical or genetic means leads to the significant decrease in the pup-directed aggression and stimulates parental care in virgin males. Virgin rats at first find foreign pups aversive, but their continuous exposure to pups stimulates paternal care. Exposure to pups leads to the stronger activation of the neurons in the vomeronasal pathway in the virgin males as compared to the fathers, and the impairment in the VMO due to its removal leads to decrease in pup-directed aggression and stimulation of paternal care.

In laboratory mice, it is also observed that males after mating with a female stop committing infanticide from the time of birth to the weaning of pups due to the stimulation of the adaptive mechanism that prevents a male mouse from killing its own pups due to the olfactory cues released by the pups (Dulac et al. 2014; Horrell et al. 2018; Marler et al. 2003; Numan 2014).

### Paternal Interactions Underlying Neural Circuits

Neural circuits which are responsible for underlying paternal behaviors come from genetic studies done on mice. Virgin male rats avoid physical contact with foreign pups and then eventually exhibit paternal care after the process of sensitization. Moreover, recent genetic studies have shown that male interaction with the offspring is also influenced by the changes taking place in the hormonal levels. In many species of vertebrates where males participate in paternal care, the levels of testosterone decrease during the fatherhood such as in humans, frogs, etc. (Numan 2014).

Experiments that involve mapping of the brain areas have demonstrated several brain

areas which are responsible for controlling parental behavior like adjacent ventral bed nucleus of stria terminalis (vBNST) and medial preoptic area (MPOA). Lateral septum is also found to be essential in control and regulation of the parental behavior. The electrical stimulation of preoptic area also induces paternal care in males. Further, optogenetic activation of the neurons in the area stimulates pup grooming and paternal care in virgin males.

The regions of brain which are responsible for regulation of the paternal care are highly heterogeneous structures. Many of the newly designed genetic and molecular tools make it easy to identify precise subsets of neurons which allow a deeper understanding of the associated neural behavior circuits (Dulac et al. 2014; Numan 2014).

### Role of Hormones in Paternal Behavior

Prolactin is an important peptide hormone and has many important functions like lactation regulation and sexual gratification and is also involved in proliferation of oligodendrocyte precursor cells. Prolactin is also believed to play a very important role in the onset and maintenance of paternal care in variety of species. According to many studies, the concentration of prolactin increases in fathers during the first weeks after the birth of their first child. High levels of prolactin help fathers to be more alert and respond more positively toward their children (Hashemian et al. 2016).

Cortisol is a stress hormone in humans. Cortisol has a significant role in paternal involvement as it determines the various behaviors like the bonding between the father and the child, experience of paternity, social affiliations, etc. However, the levels of salivary cortisol increases in the expectant fathers in the last week before delivery probably due to the increased anxiety levels in fathers regarding the birth of the offspring. The levels of cortisol

decrease after the delivery and are also found lower in non-fathers.

Testosterone is the principal male sex hormone. Similar to cortisol, testosterone levels also increase before the birth and then gradually decrease after the child is born. It is also observed during many studies that the presence of baby cues can stimulate the production of testosterone in the saliva of fathers. Many studies also show that males tend to have higher levels of vasopressin as compared to females. Vasopressin levels in fathers help in bonding formation and also extend social behavior. The paternal hormonal responses in humans are believed to be dependent on environmental and social stimuli. These variations support paternal behavior and could increase or decrease the quantity and quality of care for the children by the fathers (Marler et al. 2003; Nunes-Costa et al. 2014; Wynne-Edwards and Timonin 2007).

### **Influence of Paternal Behavior on Offspring**

Paternal behaviors can lead to variety of influences on the children. Impacts of paternal involvement on children usually comprise of, in terms of survival, health, cognition, emotional capacity, socioeconomic development, language development, reproductive parameters, etc. The influence of paternal behavior on children can begin before birth. The physiological impacts can be inherited by fathers through genetic and epigenetic mechanisms. These impacts can also influence the maternal investment during the pregnancy (Wynne-Edwards and Timonin 2007).

According to many experimental studies, older fathers tend to transmit more mutations to their children. A variety of research on paternal behavior also suggests that fathers play a very important role in the development of cognition in their children. Paternal involvement tends to reduce negative social behavior in boys and psychological-related problems in girls during the phase of early adulthood (Earls 1976; Lamb et al. 1985).

### **Paternal Inheritance in Cognition**

X chromosome gene inheritance plays a very vital role in the development of intelligence and related cognitive skills. This is due to the fact that X chromosome contains a large number of genes responsible for intelligence and cognition. The male offspring receives the one and only X chromosome from their mothers, but this is not the case for female offsprings who receive their X chromosomes from both the parents. But the X chromosome which daughters receive from their fathers is exactly the same which they have got from his mother (daughter's paternal grandmother). So, the X chromosome inherited by the daughter from her mother is a mix of genes from both of her mother's Xs. Thus, the daughter's maternal X chromosome does not match completely to her mother's X, whereas her paternal X chromosome matches completely to her father's X. Therefore, this makes the relatedness of the daughters to their fathers more similar as compared to the relatedness to their mothers.

This also explains the fact that cognition and intelligence associated with paternal behavior has more influence on the daughters as compared to the sons. So, if the paternal X chromosome is expressed more disproportionately in the brain, then the daughters might be more similar to their fathers in terms of cognition instead of their mothers (Badcock 2011).

### **Conclusion**

Various studies on relationship between a father and child provide a lot of information about the role of fathers in the development of their offspring and the extent of paternal behavior. Many researches explained that the fathers also play a very significant role in parenthood and this is not only true for humans but also observed in many other species (Gubernick and Teferi 2000). In this chapter, various aspects of paternal behavior have been underlined like

the role of biogenetics, sensory cues involved, influence of various hormones, paternal interactions underlying neural circuits, etc. (Snowdon and Suomi 1982).

A large number of studies indicate various molecular mechanisms that are able to regulate paternal behavior in humans. Remarkably, neural circuits that regulate parental interactions with offspring are present in both the male and female brains (Dulac et al. 2014; Lamb et al. 1985; Nunes-Costa et al. 2014). Therefore, more future studies on paternal behavior will unravel the complexity of its interactions and will provide us a better understanding.

## Cross-References

- [Evolution](#)
- [Hormones and Behavior](#)
- [Hormones and Cognition](#)
- [Hormones and Face Preferences](#)
- [Maternal Behavior](#)
- [Neural Control of Behavior](#)
- [Neural Network](#)
- [Parenting](#)
- [Prolactin](#)
- [Sensory Receptors](#)
- [Testosterone](#)

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## Paternity Certainty

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### Synonyms

Cuckold; Cuckolded

### Definitions

Paternity certainty refers to the degree to which a male is certain that his partner's offspring is genetically his own. Alternatively, paternity uncertainty is the degree to which a male is uncertain that his partner's offspring is genetically his own. Cuckoldry occurs when a male invests in offspring that are not genetically his own.

### Introduction

Paternity certainty is a concern primarily for males of species in which females gestate offspring. Whereas females are certain of maternity, males risk the costs of cuckoldry – investing in offspring to whom they are not genetically related. Males are more likely to invest in a partner and offspring when paternity certainty is higher (Propkop et al. 2010). Contrarily, males are more likely to abandon a partner and offspring or to invest less in them when paternity uncertainty is higher (Buss and Abrams 2017; Graham-Kevan and Archer 2011; Pagel 1997). A male's paternity certainty thus has implications for his reproductive success.

### Factors that Influence Paternity Certainty

Paternity certainty is influenced by a female partner's behavior. Females that display sexual faithfulness to their partner thereby increase his

paternity certainty. By abstaining from extrapair copulations, the female is less likely to be inseminated by another male. Females may display sexual exclusivity toward their partner by ignoring other males, living with their partner, and copulating frequently with their partner, especially during times of greater female fertility (Ludwig and Becker 2006; Shackelford et al. 2015). Females experience greater fertility during ovulation or estrus. Although ovulation and estrus are often not accurately detected by either sex, females of some species, including birds, lions, and primates, display greater sexual interest, sperm retention, and conception rates during higher fertility times (Baker and Bellis 2014/1995). Males may display mate guarding behaviors to increase their paternity certainty. Mate guarding behaviors include keeping the female away from other males, discouraging the female from abandoning him, and frequent copulation with the female (Baker and Bellis 2014/1995; Buss and Abrams 2017; Shackelford et al. 2015).

Internal female fertilization can threaten paternity certainty and increase a male partner's risk of cuckoldry. During copulation, the male's sperm travel directly into the female's reproductive tract toward the egg. However, other male's sperm may be in the female's reproductive tract, posing a threat to the current male's paternity. Sperm competition refers to two or more males' sperm competing to fertilize a female's egg. Sperm competition is higher in polygamous species and when two or more males have sexual access to the same female within a sufficiently brief period of time (Baker and Bellis 2014/1995; Shackelford et al. 2015).

Sperm displacement, sperm quality, and copulatory plugs can increase paternity certainty via sperm competition. In some species, such as humans and crabs, the penis acts as a sperm scooping device to remove a previous male's sperm before depositing the male's own sperm – a phenomena known as sperm displacement (Baker and Bellis 2014/1995; Shackelford et al. 2015). In some species, such as bush babies, king cobras, beetles, and moths, the penis can inflict wounds in the female during copulation, allowing sperm to flow directly into the female's

bloodstream, increasing the chance of fertilization (Schilthuizen 2014). Across species, the quality of sperm is higher when sperm competition is more intense. In humans, the first few drops of ejaculate contain more sperm and swim toward the female's reproductive tract with more power, thus increasing the chance of fertilization (Baker and Bellis 2014/1995). These sperm may have a better chance of fertilizing the egg compared to sperm already present in the reproductive tract. Furthermore, females typically retain more sperm for fertilization when the sperm quality is higher and/or the male is more desirable. Males of some species, including snakes, mammals, and insects, produce copulatory plugs after ejaculation which may prevent their sperm from being ejected by the female or block a subsequent male's sperm from reaching the egg (Baker and Bellis 2014/1995; Barker 1994). After conception occurs, the physical appearance, odor, or other cues to genetic relatedness of offspring may provide a last line of defense against cuckoldry in some species such as social insects, fish, birds, and mammals (Dolinska 2019; Pagel 1997). In humans, for example, physical resemblance between the sire and offspring may signal genetic relatedness, providing assurance of paternity.

It is not uncommon for females to change mates, especially in polyandrous species and between breeding seasons. Nonetheless, females that engage in extrapair copulations increase a male's paternity uncertainty. Females may attempt to hide evidence of sexual unfaithfulness to avoid being abandoned due to threatening the male's paternity. However, whether the female was sexually unfaithful, a male's paternity certainty assessment decreases when he perceives sexual infidelity occurred. Strange scents, changes in sexual interactions, unexplained absences, and promiscuity on behalf of the female increase the male's paternity uncertainty (Baker and Bellis 2014/1995; Graham-Kevan and Archer 2011). Females may acquire scents from other males with whom they copulated. Females that engage in extrapair copulations may alter sexual interactions with a primary partner, including

copulating less frequently or for a shorter duration. Unexplained absences may indicate the female left their habitat to copulate with other males. Females that flaunt their attractiveness may be attempting to attract other males.

## Implications for Paternity Certainty

In many species with paternal investment, males that are more certain of paternity invest more in their putative offspring and partner. Males that invest time and resources into genetically related offspring thereby increase their reproductive success. In many species (e.g., humans; Hill and Hurtado 1996), offspring reared by both parents may be more likely to survive and produce offspring. Conversely, in some species such as humans, insects, birds, and mammals, increased paternity uncertainty is associated with greater male sexual coercion, mate guarding, physical abuse, abandonment, and infanticide (Baker and Bellis 2014/1995; Graham-Kevan and Archer 2011; Shackelford et al. 2015). When paternity uncertainty is high, males may force the female to copulate to increase the chance of conception. Males may also keep their female partner in close proximity more frequently to prevent her from copulating with other males. Females are at greater risk for being physically abused by their partner when paternity uncertainty is higher.

## Conclusion

Paternity certainty influences sexual interactions, sperm competition, allocation of resources, and investment in a partner and putative offspring. The degree to which paternity certainty fluctuates depends on the female's sexual behaviors and, in some species, the physical appearance of offspring. Positive outcomes, such as increased paternal investment, are associated with increased paternity certainty, and negative outcomes, such as abandonment, are associated with increased paternity uncertainty.



## Cross-References

- [Cheating](#)
- [Cuckoldry](#)
- [Family Resemblance](#)
- [Forced Copulation](#)
- [Infanticide](#)
- [Mate Guarding](#)
- [Maternal Behavior](#)
- [Parental Investment](#)
- [Paternal Behavior](#)
- [Polyandry](#)
- [Sperm Competition](#)

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## Paternity Uncertainty

- [Cuckoldry](#)

## Pathogen

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## Synonyms

[Disease-causing agent](#); [Infectious agent](#); [Infectious particle](#)

## Definition

Pathogenic microbes, or *pathogens*, have an ability to produce harm in a host organism and exhibit a parasitic or predatory relationship with the host. Pathogens cause infectious diseases such as streptococcal pharyngitis, influenza, botulism, rabies, gastroenteritis, and Creutzfeldt-Jakob disease.

## Introduction

Microorganisms, or microbes, are unicellular or multicellular organisms too small to be seen with the unaided eye (Cowan 2018). Microbes are ubiquitous in the internal and external environments of humans and animals; thus, humans and animals often act as host organisms for microbes. While many microbes in a host's microbiome are harmless or beneficial to the host, the relationship

between a microbe and a host can be a complicated one. Animal hosts can exhibit mutualistic, commensal, cooperative, parasitic, or predatory relationships with microbes. An animal host and microbe that exhibit reciprocal benefits and dependency upon each other share a mutualistic relationship. In the event that a host or microbe benefit from the relationship while the other is unharmed, they are said to share a commensal relationship. Cooperative relationships are beneficial to both the host and microbe, but the relationship is not required for survival. Parasitic and predatory relationships are those in which either the host or microbe will benefit at the expense of the other. The difference between parasitic and predatory relationships is difficult to define. However, parasitic relationships require a coexistence of host and microbe for at least some period of time, while predatory relationships do not (Willey et al. 2017). Parasitic or predatory microorganisms that produce direct or indirect harm to a host are said to be pathogens.

## Classification of Pathogens

Pathogens may be cellular or acellular entities. Cellular pathogens exist across all three domains of life, including *Bacteria*, *Archaea*, and *Eukarya*. However, most cellular pathogenic organisms belong to the domain *Bacteria*. Acellular pathogens include both viruses and prions (infectious proteins). All pathogens are capable of producing harm, disease, or infection in the host. The term *pathogenicity* refers to the ability of a microbe to produce illness in a host, while *virulence* of a pathogen refers to the degree of pathogenicity. Many pathogens are classified by the severity and type of damage it can inflict upon a host, with host-specific considerations such as health of host, taken into account. For instance, some pathogens are able to produce disease in a healthy host and are termed *true (primary) pathogens*. Other pathogens are able to cause disease only in immunocompromised hosts and are termed *opportunistic pathogens* (Talaro and Chess 2012). Pathogens may also be classified by their location within the host. *Extracellular pathogens* remain in the

extracellular fluid surrounding the host cells but do not enter the cells. *Intracellular pathogens* grow and divide inside host cells (Willey et al. 2017). There are also practical classifications for pathogens. The biosafety levels (BLS) are aimed at promoting worker safety when handling infectious microorganisms; the BLS of an infectious agent takes into account virulence and transmission route in safe-handling protocols (Biosafety in Microbiological and Biomedical Laboratories 2019).

## Pathogen-Host Interactions

The cells, tissues, organs, and fluids of animals represent ideal growth conditions for animal pathogens. Yet, the interior of the animal body is generally sterile. This is achieved by use of biological defenses, such as innate and adaptive immune defenses. Innate defenses are composed of anatomical barriers (i.e., skin and mucous membranes), sensor systems recognizing molecular patterns of pathogens or tissue damage, immune surveillance, phagocytosis, and inflammation. Adaptive immunity is a defense mechanism utilized by vertebrates to allow for more sophisticated protection from infection. For instance, adaptive immunity relies on the ability of the immune system to recognize a specific pathogen, mount an immune response to destroy the pathogen, and remember the pathogen. Such a process confers the host *immunity*, or resistance to infection or disease caused by that pathogen. All types of body defenses rely upon distinguishing between self (host) and nonself (pathogen). Antigens are membrane-localized glycoproteins or glycolipids (Nester 2012) utilized by organisms for recognition of self vs. nonself. Additionally, pathogen-associated molecular patterns (PAMPs), such as cell wall components, flagellin molecules, and viral RNA, are expressed by pathogens and can trigger host defenses (Nester 2012). Host immune cells express pattern recognition receptors (PRRs) that bind or detect PAMPs, thereby aiding in the host's detection of a pathogen.

## Characteristics and Strategies of Pathogens

If a pathogen penetrates the first line of defense (i.e., skin or mucous membranes) and gains entry into an animal, the pathogen must rapidly adapt to the host environment. Pathogens express *virulence factors* capable of facilitating infection by evading or outcompeting host defenses. Segments of pathogen DNA coding for virulence factors are called *pathogenicity islands*; *pathogenicity islands* may be transferred between members of a microbial species in a process called horizontal gene transfer (Schmidt and Hensel 2004). Virulence factors can be *adherence factors* that permit physical attachment of the organism to host, *invasion factors* that facilitate spread to other cells, or *toxins* that negatively alter the metabolism of the host cell (Willey et al. 2017). Not all members of a microbial species produce the same virulence factors. In fact, some members of a microbial species may not produce any virulence factors. For instance, most strains of *Escherichia coli* (*E. coli*) are nonpathogenic and relatively harmless to animal hosts. Nonpathogenic *E. coli* are helpful members of the mammalian intestinal microbiota, where they are known to aid in nutrient metabolism. Pathogenic strains of *E. coli* are responsible for bouts of gastroenteritis (inflammation of stomach and intestines) associated with contaminated food sources; pathogenic *E. coli* express virulence factors that nonpathogenic *E. coli* do not. There are six known pathotypes of *E. coli* with each pathotype of *E. coli* expressing different virulence factors. For example, the enterotoxigenic *E. coli* (ETEC) pathotype produces virulence factors called enterotoxins. Heat-stable enterotoxin (ST) and heat-labile enterotoxin (LT) act to increase electrolyte and water content of the intestines, thereby producing symptoms of ETEC gastroenteritis, such as watery diarrhea. The ETEC *E. coli* pathotype is known to cause traveler's diarrhea and is found in contaminated water, as well as raw fruits and vegetables. Conversely, enterohemorrhagic *E. coli* (EHEC) expresses a different toxin, Shiga toxin, which kills vascular endothelial cells and produces severe, bloody diarrhea.

EHEC is found in raw or undercooked ground beef and unpasteurized fruit juices (Croxen et al. 2013). The virulence factors that allow pathogens to penetrate, grow, and thrive cause infection or disease in the host.

## Establishing Infection: Invasion, Adhesion, and Colonization

Pathogens produce a variety of invasion factors which allow for microbial penetration into the host. The microbial penetration process may be active or passive. Active penetration occurs when a pathogen produces and releases lytic substances that alter the host tissue by destroying the host's extracellular matrix or basement membrane underlying epithelial tissue, destroying glycocalyx components, or triggering a rearrangement of the host cell membrane. For example, *Clostridium perfringens* (causative agent in clostridial gas gangrene) produce an invasion factor called collagenase which destroys collagen molecules found in connective tissues (Petit et al. 1999). Destruction of connective tissue by collagenase allows for *C. perfringens* to penetrate and spread into the deep tissues of the body. The invasiveness of pathogens varies, however. Some pathogens utilize passive penetration mechanisms. Passive penetration occurs when the first line of defense is damaged and a pathogen enters the host through a lesion, wound, abrasion, damaged mucous membrane, or otherwise damaged/inflamed tissue (Willey et al. 2017). In passive penetration, the pathogen takes advantage of the weakened host first line of defense.

After a pathogen has gained entry into the host organism, it must adhere to the target cell and colonize. Adherence usually requires the pathogen to have specialized structures, such as *fimbriae* or *pili*, to attach to the host cell. Fimbriae and pili are examples of bacterial adherence virulence factors. Yet, pathogens can express a wide variety of attachment structures; all are well-suited to attach to a designated host cell. For example, influenza virus utilizes a hemagglutinin (HA) spike protein for viral adherence to  $\alpha$ -sialic acid on the membranes of host upper respiratory tract cells (Luo 2012).

After adhesion is complete, the pathogen will colonize (actively reproduce). Pathogens also possess ways to elude the immune system once established, whether it be by hiding inside a host cell (*Shigella*), attacking immune cells (*Streptococcus pyogenes*), or surviving phagocytosis (*Salmonella*) (Willey et al. 2017).

## Damage to Host

Many pathogens enter, adhere, and colonize within a host organism, thereby taking valuable nutrients and resources from the host organism. Yet, there are other ways in which pathogens can inflict damage on a host organism, including the release of toxins. Toxins are substances encoded for by the genetic material of bacteria, fungi, and viruses which change the normal metabolism or activities of a host cell in such a way as to benefit the pathogen while harming the host. The two major classes of toxins are exotoxins and endotoxins. Exotoxins are heat-labile proteins that are released from the microorganism into the surrounding environment; they are inactivated at 60–80 °C. The food-borne disease botulism is caused by products of the bacterium *Clostridium botulinum*; *C. botulinum* produces the exotoxin *botulin* which blocks acetylcholine release at the neuromuscular junction. The botulin toxin prevents neuromuscular communication and produces flaccid muscle paralysis. In the case of food-borne botulism, the individual ingests food contaminated with the heat-stable toxin. Botulism can occur when low-acidity foods are improperly canned (Nester 2012). Ingestion of the botulin toxin causes the symptoms associated with botulism, not the bacterium itself (except in cases of infant botulism). The *E.coli* enterotoxins (Shiga toxin, ST, LT) discussed in the previous section are also examples of exotoxins. Endotoxins, such as lipopolysaccharide (LPS), are found within the cell walls of Gram-negative bacteria. When the animal immune system destroys the Gram-negative bacterial cell, the endotoxin is released into the blood and produces widespread deleterious effects, such as fever, hypotension, organ

failure, and blood coagulation. The net result of LPS activity is often referred to as septic shock (Willey et al.). Fungi are also capable of producing toxins called mycotoxins. *Aspergillus flavus* produces aflatoxins; aflatoxins are known to cause liver disease and liver cancer (Cowan et al.). Viruses are nonliving pathogens capable of utilizing host cell machinery to produce dangerous toxins. Rotaviruses are common causative agents in viral gastroenteritis. Rotaviruses encode an enterotoxin called NSP4 that induces vomiting in a serotonin-dependent mechanism (Hagbom et al. 2011). Thus, the ability of pathogens to produce signs and symptoms associated with infectious disease reaches beyond its ability to invade the body's tissues. Over generations of microevolution, pathogens continue to evolve to become more effective pathogens, whether by finding new ways to elude the host immune system or produce more effective virulence factors.

## Cross-References

- [Archaea](#)
- [Bacteria](#)
- [DNA](#)
- [Eukaryota](#)
- [Fungi](#)
- [Immunity](#)
- [Immunology](#)
- [RNA](#)
- [Woese's Three Domains of Cellular Life](#)

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## Patrick Bateson

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Paul Patrick Gordon Bateson (known as “Pat”) was born on March 31, 1938. Bateson decided from an early age that he would be a biologist, influenced by the legacy of the famous cousin of his grandfather, the geneticist William Bateson. Patrick Bateson was educated at Westminster School before beginning an undergraduate degree in Natural Sciences at Kings College Cambridge University in 1957. In 1963, he married Dusha Matthews and had two daughters, Melissa born 1968 and Anna born 1972. With the exception of a 2-year Harkness postdoctoral fellowship spent working with neuroscientist Karl Pribram at Stanford University, Bateson spent the remainder of his career based in the Zoology department at Cambridge, where he is currently Emeritus Professor of Ethology. His early career was greatly influenced by Niko Tinbergen and Robert Hinde, the latter supervising his PhD on the topic of behavioral imprinting, in the Sub-Department of Animal Behaviour.

Patrick Bateson has made outstanding contributions to the study of animal behavior over a 50-year period, and is now regarded as a world leader in this field, with particular expertise on behavioral development. While Bateson’s research has included investigation of virtually every topic in animal behavior, he is perhaps best known for his research on filial imprinting, involving analyses of the causal mechanisms, development, function, and evolution of this behavioral trait, including work in the laboratory and field. This work, encompassing much experimentation and theory, has included highly intricate and innovative behavioral neuroscience, in collaboration with Prof. Gabriel Horn, which has pioneered new methods, set new standards for behavioral research, shed new light on the interplay of internal and external factors during behavioral development, and become a textbook classic, not just in behavior but adjacent fields. Bateson investigated what ended the sensitive period for imprinting, concluding that it was due to a process of competitive exclusion. Experience with one class of objects made it more difficult for the birds to form attachments to another class and the greater the stimulus value of the first class the more quickly would be the exclusion effect. He later found that once birds had been imprinted, they could use this perceptual experience to help them in discovering new sources of food. This research led to the recognition that imprinting shared many features with perceptual learning and that Konrad Lorenz’s earlier claim that this was a special form of learning was wrong.

Bateson has also made outstanding contributions to the study of mate choice, animal welfare, play, creativity, learning and memory, and the active role of behavior in evolution. He has been a leader in the field of ethology, developing more nuanced understandings of many difficult issues, such as “instinct” and “learning,” and has taught many of us how to think about these topics in the process. He has also shown courage, integrity, sensitivity, and leadership in tackling thorny and emotive issues, such as deer hunting and nonhuman primate research, and standing up against overly simplistic adaptationism and gene-centric accounts.



Bateson has published over 300 scientific articles in leading journals, as well as several influential books, many of which have run to multiple editions. His book *Measuring Behaviour*, with Paul Martin, now in its third edition, has been universally regarded as the definitive methodological introduction for students of animal behavior for decades, and helped turn the field into a rigorous quantitative science. Another book *The Domestic Cat*, with D.C. Turner, is a huge best seller, also in its third edition. Other edited volumes, notably *Growing Points in Ethology* in 1976, and *Mate Choice* in 1983, had massive impact and shaped thinking in these fields. Bateson also edited the influential *Perspectives in Ethology* series for 20 years and was editor of *Animal Behaviour* for 5 years.

Patrick Bateson's contribution to science has been recognized with many honors, notably his election to Fellowship of the Royal Society in 1983. He was knighted in 2003 in recognition of exceptional contributions to behavioral research and British science more generally. He was director of the Sub-Department of Animal Behaviour at Cambridge for 10 years and was also Provost of Kings College, Cambridge, President of the Zoological Society of London, and both Biological Secretary and Vice-President of the Royal Society for many years. He has chaired numerous national committees, in the process bringing a balanced judgment to many difficult issues related to animal behavior, including the use of animals in medical research, dog breeding, and hunting.

In spite of his success and recognition, Patrick Bateson remains an approachable and affectionate scientist and colleague. He is famously dedicated to his students, lab members, and collaborators and always made time for anyone who would like to discuss their research. His commitment to undergraduate teaching is legendary, and he continued to teach for many years postretirement. Students greatly valued the personal touch that he brought to their education – he typically knew them by name and took great interest in their development. He is an exceptional mentor to numerous graduate students, postdocs, and junior collaborators, many of whom have gone on to have very successful careers in animal behavior.

## Cross-References

- ▶ [Animal Welfare](#)
- ▶ [Evolution](#)
- ▶ [Filial Imprinting](#)
- ▶ [Neuroanatomical Plasticity](#)
- ▶ [Nikolaas Tinbergen](#)
- ▶ [Play Behavior](#)
- ▶ [Robert Hinde](#)
- ▶ [Sensitive Periods](#)
- ▶ [Social Learning](#)

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## Patrolling Behavior in Chimpanzees

### ► Chimpanzee Raiding

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## Pattern Learning

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### Synonyms

[Rule learning](#); [Sequence learning](#); [Sequential pattern learning](#); [Serial pattern learning](#)

### Definition

A cognitive operation whereby organisms detect and process repetitive (often rule-based) information from the environment. This subsequently allows the organism to respond more efficiently when the stimuli are next encountered.

### Introduction

Patterned sequences, series of events happening repeatedly and in a predictable way, are ubiquitous. For example, the seasons occur in the same order each year. Detecting and learning about the relationships among events happening recurrently in predictable ways facilitate organisms' survival

by allowing them to respond in a more efficient and appropriate manner. For instance, knowing that spring comes after winter enables humans with limited wardrobe space to cull warmer clothing in favor of cooler clothing during that seasonal transition each year. Thus, recognizing and learning about patterned sequences enable organisms to make predictions about upcoming events and react appropriately.

While some repeatedly occurring events that organisms respond to are organized in a meaningful way, others are not. Whether such organization within the sequence is present impacts how organisms learn about these sequences or patterns as well as their ultimate responses to these events. Researchers continue to investigate organisms' abilities to learn patterns of information and the processes underlying those abilities by studying humans and nonhuman animals across taxa (for review, see Fountain et al. 2012).

### Sequence Organization

Early on, researchers noted that sequences organized in a meaningful way that could be described using a “rule” were learned more quickly and with fewer errors than sequences without such organization. Additionally, such organization led organisms to be able to extend the sequences successfully. For example, Fountain and Hulse (1981) found that rats learned to run more slowly in a runway for decreasing quantities of food pellets when a general “less than” rule (14-7-3-1, where digits represent quantities of food pellets) was present for each successive run within a block of trials compared to a group for which the rule was absent (14-3-7-1). Additionally, when the rule was present, rats were able to better predict a new 0-pellet element added to the end of each sequence.

Meaningful organization likely improves learning, memory, and performance by reducing memory load. When meaningful organization is present, organisms can record or “chunk” the information from the sequence into smaller sets or groups of information, which increases the efficiency of and capacity for learning new

information (e.g., Terrace 1987). Chunks usually are made up of familiar or otherwise significant bits of information that are then recalled together later on. For example, the string WHOFBUIUSA would likely be remembered better than the string WOBUAHFIS, even though the letters in each are the same, because the first string contains three three-letter acronyms familiar to many. This familiarity enables chunking of the information for easier and more accurate later recall.

Additional studies have confirmed the importance of organization to pattern learning and performance by investigating the impact of inconsistencies in the rule or rules governing the sequence's structure. Many of these studies have been conducted with rats or mice using a variation of a Skinner box with eight walls (octagonal chamber) or a computer analogue of this task for humans. This has allowed for exploration of learning longer and more complex patterns across species. In the rodent version of the task, rats learn to make responses on the appropriate wall of the chamber (designated 1–8 clockwise) using a nosepoke or lever in the proper order for reinforcement. Humans complete an analogous two-dimensional version of this task using a computer. In this task, they are presented with eight circles on the screen arranged in a circular fashion (designated 1–8 clockwise) and must learn to make responses to the appropriate circle using either a touchscreen or a mouse.

For example, Fountain and Rowan (1995) investigated the impact of violations of pattern structure on humans' and rats' performance. Humans and rats learned either a pattern with no inconsistencies in pattern structure (123-234-345-456-567-678-781-812...) or a pattern with two inconsistencies in pattern structure (123-234-543-456-567-876-781-812...). Both humans and rats took longer to learn the pattern with inconsistencies and made more errors while learning, reinforcing the notion that meaningful sequence organization facilitates learning and performance and that violations of sequence organization impair learning and performance.

Many recent studies suggest that a variety of species possess the ability to at least minimally abstract rules and chunk information in serial

pattern learning tasks. However, the conditions under which they might do so may vary across species. For example, Garlick et al. (2017) explored pigeons' abilities to learn sequential patterns. While pigeons abstracted the structure of the sequence, they only did so when low-level feature-based information was reduced.

## Pattern Complexity

Sequences of information vary in their level of meaningful organization as well as their complexity. Complexity refers to the number of rules required to represent a pattern. Some patterns can be described using one rule (e.g., 1111111, repeat 1), while others require many rules for complete description. For example, the "runs" pattern 123-234-345-456-567-678-781-812 in the octagonal chamber task described previously requires five rules for representation: (1) start by choosing the receptacle on wall 1, (2) move over one wall in the clockwise direction to choose the next receptacle, (3) repeat rule 2, (4) move over one wall in the counterclockwise direction to choose the next receptacle, and (5) repeat rules 2–5.

A variety of research indicates that patterns that can be described accurately using a fewer number of rules are easier to learn than those requiring greater numbers of rules for complete description (e.g., Fountain and Rowan 1995). For example, Fountain and Rowan (1995) also explored humans' and rats' learning of patterns whose length was constant but whose complexity varied. Humans and rats learned a pattern that could be described using a fewer number of rules (123-234-345-456-567-678-765-654-543-432-321-218) or one that could be described using a greater number of rules (123-234-345-432-321-218-765-654-543-456-567-678). Neither pattern contained any violations of pattern organization. Results indicated that the pattern that required more rules for accurate description took longer to learn and more errors were committed by both rats and humans during learning, suggesting that greater pattern complexity was related to greater learning difficulty.

Pattern complexity is also heightened when two subpatterns (ABCDE, MNOP) are interleaved (AMBNCODPE). This is because organisms must initially recognize the relationships among elements that are not next to one another within the interleaved subpattern before abstracting the subpatterns' individual structures. The relationships among elements within each subpattern must be abstracted over one or more intervening elements from the other subpattern, heightening pattern complexity. That is, a human would need to recognize that A, B, C, D, and E belong to one subpattern and M, N, O, and P belong to another subpattern as well as that for each successive serial position in each subpattern one needs to advance one serial position in the alphabet. A human could then use this information to determine the next likely element in the pattern, in this case "Q."

Studies of organisms' abilities to learn interleaved patterns suggest that they are not just linking one item with the next using pairwise associations. Instead, they appear to be representing the abstract rules describing the subpattern sequences and their relationship to the overall interleaved pattern (Fountain et al. 2012). For example, in Fountain et al. (1999), rats learned either a structured (123-234-345-456-567) or unstructured (153-236-345-426-547) subpattern interleaved with repeating responses on lever 8 (structured 182838-283848-384858-485868-586878; unstructured 185838-283868-384858-482868-584878) in the octagonal chamber task described previously. Results indicated that the rats learned the interleaved pattern with the structured subpattern more quickly and with fewer errors than the interleaved pattern with the unstructured subpattern. The rats showed sensitivity to the relationships between the elements of the structured subpattern even though they were not located next to one another in the interleaved pattern.

The clarity of the relationships among the elements of the subpatterns can also affect pattern learning. The presence of irrelevant relationships among pattern elements can affect the induction of the rules describing a sequence. These relationships can distract from the correct induction of the

rules describing the pattern. For example, in Kundey and Fountain (2011), rats learned a runs subpattern (123-234-345-456-567) interleaved with repeating responses on lever 2 (122232-223242-324252-425262-526272), lever 6 (162636-263646-364656-465666-566676), or lever 8 (182838-283848-384858-485868-586878) in the octagonal chamber task described previously. Interleaving the same runs subpattern with repeating responses on lever 2, 6, or 8 produced differing amounts of potentially confusing irrelevant relationships in the overall interleaved pattern as well as varied the placement of these irrelevant relationships. Interleaving the runs subpattern with repeating responses on lever 8 produced no irrelevant relationships. Interleaving the runs subpattern with repeating responses on lever 2 produced irrelevant relationships at the beginning of the interleaved subpattern, while interleaving the runs subpattern with repeating responses on lever 6 produced irrelevant relationships at the end of the interleaved subpattern. The results indicated that the presence of any irrelevant relationships negatively impacted learning and that irrelevant relationships at the beginning of the interleaved pattern were more detrimental to learning than those at the end of the pattern. These results also support the general relationship between heightened pattern complexity and learning difficulty. Moreover, they hint that rats, like humans, process sequences of information from beginning to end in their search for potential structure within a sequence.

## Conclusion

Beyond understanding the basic cognitive phenomena underlying the ability to learn patterns of information, sequence learning tasks have broad applications to other areas of research. These include sex differences (Kundey et al. 2019), attention concerns (Kundey et al. 2011), and diseases involving motor learning (e.g., Willingham 1998).

For example, Kundey et al. (2019) found that male mice learned serial patterns more quickly as pattern complexity increased. While males and females learned single alternation (right-left-

right-left. . .) and double alternation (right-right-left-left. . .) patterns at similar rates, males learned a runs (123-234-345-456-567-678-781-812) pattern more quickly than females did.

Pattern learning tasks can also be helpful in illuminating the impacts of differences in ability to attend and ways to reduce these impacts. For instance, Kunder et al. (2011) found that college students' learning of serial patterns containing irrelevant information was related to self-reported inattentive and hyperactive concerns. The study also found that differences in pattern learning among those with high and low self-reported inattentive and hyperactive concerns could be reversed by visually enhancing the distinguishing features of the irrelevant stimuli (e.g., making them a different color on the screen).

Finally, sequence learning tasks can also be helpful in elucidating specific impairments in diseases such as Huntington's disease and Parkinson's disease (Willingham 1998). For example, patients affected by Huntington's disease as well as those affected by Parkinson's disease show impairment on a serial response time task when the elements of the non-rule-based sequences to be learned repeat versus appear randomly. In contrast, those affected by Alzheimer's disease do not. Results from patient populations such as these help to identify brain areas critically underpinning pattern learning phenomena.

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## Cross-References

- [Encoding](#)
- [Serial List Learning](#)

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## Biographic Background

Paul L. Vasey was born in Toronto, Canada, on January 30, 1966. He received his B.A. (Honours) from the University of Alberta in Edmonton (1989); his M.A. from Simon Fraser University in Burnaby, British Columbia (1991); and his Ph.D. from the Université de Montréal in Québec (1997). He conducted postdoctoral research at the Université de Montréal and Concordia University in Montréal, and at York University in Toronto.

In 2000, Dr. Vasey accepted a tenure-track position in Psychology at the University of Lethbridge, Alberta, Canada. He was promoted to



Associate Professor in 2005 and to Full Professor in 2010. In 2015, he was awarded a Board of Governors Research Chair in Culture, Organization and Society. Dr. Vasey is one of only a handful of researchers in Canada to receive simultaneous grants from all three federal funding councils (NSERC, SSHRC & CIHR). His Research has also been funded by various other agencies including: NIH, National Geographic and Sigma Xi. He serves as Associate Editor for the *Archives of Sexual Behavior*. His research has been the subject of various television documentaries (National Geographic, Discovery Channel) and has been reported on in hundreds of newspapers and magazines worldwide (*New York Times*, *The Economist*).

Dr. Vasey's research interest focuses on understanding the proximate and ultimate reasons as to why organisms engage in nonconceptive sexuality. For two decades (1992–2012), Dr. Vasey carried out long-term research on the development and evolution of female homosexual behavior in captive and free-ranging Japanese macaques (*Macaca fuscata*). His Japanese macaque fieldsites included Arashiyama (near Kyoto) and Minoo (near Osaka). Vasey's work demonstrated that female homosexual behavior in Japanese macaques is not used to facilitate adaptive social goals (Vasey 1996, 2004; Vasey et al. 1998). This evidence-based claim was a significant departure from most of the animal behavior literature, which typically framed same-sex mounting as a socio-sexual adaptation. Instead, Vasey claimed that in some species, same-sex sexual behavior was a neutral, evolutionary byproduct. He showed that during most same-sex mounts, female Japanese macaques stimulate their genitalia thereby obtaining immediate sexual reward (Vasey and Duckworth 2006). His research group demonstrated that females sometimes choose same-sex sexual partners because they prefer them over the available male alternatives, and in doing so debunked the notion that females engage in this behavior simply because they are unable to obtain a male mate (Vasey 1998; Leca et al. 2015). Vasey demonstrated that male and female Japanese macaques engage in *inter-sexual* competition for female sexual partners – a process of mate

acquisition that had never been explicitly described in the literature (Vasey 1998). Research by Vasey's group revealed that homosexual behavior develops more rapidly in female Japanese macaques than heterosexual behavior, probably because the former involves less risky interactions than the latter (Leca et al. 2015). His group also showed that female Japanese adopt arbitrary mount postures during same-sex mounts and these vary across populations (Leca et al. 2014). This suggests that the expression of female homosexual mounting in Japanese macaques is influenced, in part, by cultural factors (i.e., group specific social processes). Dr. Vasey's long-term research on Japanese macaques is among the most detailed study of homosexual behavior in a non-human species ever conducted.

## Cross-References

- [Homosexual](#)
- [Nonhuman Primates](#)

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## Pavlovian Conditioned Approach

### ► [Autoshaping](#)

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## Pavlovian Conditioning

- [Associative Learning](#)
- [Autoshaping](#)
- [Sign Tracking](#)

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## Pavlovian Inhibition

- [Conditioned Inhibition](#)

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## PD

- [Parkinson's Disease](#)

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## Peak Fertility

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## Synonyms

[Peak reproduction](#); [The peak day](#); [The peak of fertility](#)

## Definition

Peak fertility is broadly defined as the period when both females and males of sexually reproducing organisms are considered most fertile. In the majority of animal species, peak fertility is associated with increased neuroendocrine activity in the brain, as well as with increased secretion of sex hormones in the gonads, and strongly affects sexual behavior and cognition of the individual.

## Introduction

One of the most important processes in the life history of every single organism is reproduction. The ability to produce the next generation of offspring is called **fertility**. Across the animal kingdom, a tremendous variability of life histories, social and breeding systems, different mating strategies, and a great diversity of reproductive behaviors has been documented. All of these factors strongly influence reproductive processes and cycles of particular species including the crucial phase of **peak fertility** (Clutton-Brock 1988). In the vast majority of internal fertilizers, the peak of fertility is commonly considered as a very short period within the female reproductive cycle, usually several days prior to ovulation and the day on which ovulation takes place, when females are most sexually receptive to males. However, in a broader perspective, it can also be understood as a period of life (e.g., several weeks, months, or years, depending on the lifespan of the species) during which both females and males are the most fertile and productive. In this respect, reproductive senescence plays a very important role and generally has a negative effect on reproductive functions after reaching a critical age. Moreover, seasonal changes in the intensity of reproductive activity have been described in various taxa in which seasonal breeding has evolved. For instance, most animals living in a temperate zone reach their fertility peaks in a specific period of time during the year in contrast to tropical species, which usually show no such

pattern and breed rather continuously throughout the year (Chemineau et al. 2008; Willmer et al. 2005).

## The Role of Neuroendocrine Regulation

Reproductive cycles including fertility peaks are under hormonal control. In most animals, two main types of hormones are involved – **gonadotropins**, usually peptides secreted in a specific brain region which control gonadal functions, and **gonadal hormones** (often steroids), produced in female and male gonads, also known as the sex hormones which are, among others, integral for reproduction and development of secondary sexual characters in both sexes. From an evolutionary point of view, this principal regulatory pattern is highly conserved among both invertebrate and vertebrate taxa, although it is strongly modulated by the environment and species' specific life histories (Willmer et al. 2005).

Different phases of the female reproductive cycle with respect to peak fertility have been described mainly in vertebrates, and the most detailed understanding of the reproductive cycle and its hormonal regulation has been achieved in mammals including humans. For instance, in therian mammals (both marsupials and placentals), a recurring female reproductive cycle called **estrous** is present, where a complete reabsorption of the uterine lining takes place in case no conception has happened. On the other hand, in humans and their close relatives among the primates **menstrual cycles** occur, which is associated with shedding of the endometrium and bleeding through the vagina (menstruation) when no ovum has been fertilized. A key role in mammalian cycle control plays the **hypothalamic-pituitary axis**. A specific brain region, the hypothalamus, acts as a “pacemaker,” secreting gonadotropin releasing hormone (GnRH) in pulses, and thereby mediates the link between the individual and the environment (in response to, for example, changes in temperature, photoperiod or the social environment). GnRH stimulates secretion of follicle-stimulating hormone (FSH) and luteinizing hormone

(LH) from the anterior pituitary, which in turn affects ovarian function, oogenesis, and the ovulation process by stimulating the release of sex hormones – estrogens (e.g., estradiol) and progesterone – from ovaries.

In humans, the women's peak of fertility is restricted to the so-called “fertile window” (about 6 days before and during ovulation) and overlaps with a two-day peak of blood estradiol and LH (usually around the 14–15. day of the menstrual cycle called **the peak day**). However, the precise timing of the peak day within the menstrual cycle can be affected by various environmental effects, such as diet, nutrition intake, and stress, and therefore may vary individually. It is supposed that humans and a few other species, for example, orangutans, do not signal their peak receptivity around ovulation by any obvious external signs, a phenomenon called concealed ovulation, which is quite rare in nature (Mihm et al. 2011). More often females express various kinds of signals, such as release of pheromones or expressing the attractivity enhancing signals (for more information see the following subchapter).

Regarding the effect of age, a woman's fertility begins in puberty and peaks around her twenties, starting to decline slowly after this age, and eventually reaching a critical point at around 35 after which women's fertility declines dramatically (Treloar et al. 1967).

Humans as other species which possess menstrual cycles are able to mate during the whole cycle, while in many other species mating activity is restricted only to a specific time period. For example, in mammals undergoing estrous, females are sexually receptive to males (being “in heat”) only during estrous itself. Peak fertility in such species typically comes once per year (monoestrous, e.g., wolves), twice a year (diestrous, e.g., dogs) or several times during the year (polyestrous, e.g., cats). Season may also influence female peak fertility; however, this has been much better documented in males (Willmer et al. 2005).

In contrast to females, many male vertebrates produce sperm rather continuously or in prolonged periods throughout their lifetime, generally being able to reproduce much longer than

females. In mammals, spermatogenesis is initiated by LH secreted from the pituitary gland. LH is then bound to the Leydig cells in the testes and in response starts producing testosterone which plays a key role in the regulation of spermatogenesis. For the normal course of spermatogenesis, FSH is also crucial, for it affects another group of cells in the testes – the Sertoli cells – that makes the testicular cells responsive to testosterone.

The fertility peak in males is also affected by age. The process of reproductive senescence has a negative effect on spermatozoa with substantial evidence of decreased sperm quality (e.g., higher percentage of sperm abnormalities, negative effects of increased oxidative stress, DNA damage, lower sperm motility) in older males across many animal taxa including humans (Harris et al. 2011).

Seasonal changes in male reproductive activity have been demonstrated particularly in seasonal breeders, in which their fertility peaks at the same time when the peak of testosterone secretion occurs. During this time, spermatogenesis reaches its highest intensity and is often associated with increase in ejaculate volume, sperm concentration, and viability and, among others, might be accompanied by an increase in testis size (Chemineau et al. 2008).

## Peak Fertility and Behavior

Beside hormonal changes during peak fertility and its physiological consequences, an individual's behavior is also affected in a substantial way. In that respect, both females and males of many animal species have evolved countless **external sexual signals**, which provide information about reproductive readiness and willingness to mate.

For instance, many nonprimate female mammals, such as rodents or felines, perform so-called **lordosis behavior** when they are in heat, a characteristic posture during estrous and peak fertility that advertises female receptivity to males. In brown rats, which belongs, as other rodent, to the spontaneous ovulators producing ova

regularly, lordosis posture is regulated by the hypothalamic-pituitary system and overlaps with GnRH and LH peaks. Therefore, it allows precise timing of copulation in relation to ovulation. In contrast to this, most felines, for example, domestic cats, are rather reflex ovulators, which means they ovulate immediately in response to mating. This process is regulated by estrogen affecting the brain, particularly the hypothalamus, directly (Beach 1976).

However, in many other mammals, behavioral signals of female peak fertility are not as intense as in previous cases. For example, many female primates react in response to estrogen peak by being only a little more sexually active, but in addition to this, they use various **attractivity enhancing signals**. In many mammals, female signal their peak fertility through swelling often followed by redding of the vulva, and in some primates, an exaggerated form of this signal – **sex skins (sexual swellings)** – has evolved. Several species from the Old World monkeys (including, e.g., mangabeys, mandrills, geladas, baboons or macaques) and the apes (e.g., chimpanzees) possess sex skins, which increase the female attractivity to males. Interestingly, these structures are present more frequently in polyandrous species (i.e., in which females have two or more mates). However, in case species are breeding seasonally, they lack sex skins even if they live in a polyandrous mating system. Moreover, polygynandrous species (i.e., where both males and females have multiple copulation partners) possessing sex skins have longer mating periods and ovarian cycles than those without sex skins. Beside visual signs described above, for example, female rhesus macaques enhance their attractivity also through olfactory signals. During their peak fertility, the increased estrogen stimulates bacteria in the vaginal microbiome to produce odors that attract males (Lee 1999).

Chemical and olfactory signals, particularly **pheromones**, are widespread across the animal kingdom. In many terrestrial invertebrates, such as beetles or moths, pheromones often plays a key role in attraction between mates and are often associated with long-range chemical

communication. During periods of time when females are willing to mate, they release pheromones, in many cases, from abdominal glands, based on which males are supposed to find a way to their potential partner. Such males therefore display various kinds of olfactory structures that are meant to act as detectors, typically various forms of antennae. Pheromones are used as sexual signals also in most vertebrate taxa, from amphibians, through lizards and snakes, birds, to mammals. In more highly derived vertebrate clades (i.e., amniotes), a special male vomeronasal organ system has evolved for the detection of pheromones, sometimes called Jacobson's organ. Some species, such as felids or ungulates (including, e.g., horses, cattle, pigs, camels, or deer – usually both females and males), perform specific sexual behavior associated with pheromonal detection during reproduction – the so-called Flehmen response, during which an individual curls back its upper lip, inhales scents, with the nostrils usually closed, into the vomeronasal organ (Silva and Antunes 2017).

In any case, during phases of reproductive activity and peak fertility, male behavior is obviously also affected extensively and most often is regulated by the primary male sex hormone, testosterone. Males of many animal species display a fascinating range of courtship behavior, usually involving a wide range of sexually selected traits (e.g., colorful patches, various morphological structures) in invertebrates and vertebrates, as well as in both external and internal fertilizers. In addition to this, the increase of testosterone during reproductive phases is also linked to higher aggressiveness of males (towards potential competitors) and the increase in intensity of territorial behavior, which is in turn supposed to increase the probability of mating success of the individual male (Andersson 1994).

## Conclusion

Although peak fertility generally depends upon the genetic program encoded in the animal's reproductive machinery, the environment and its

dynamics also play a very important role. With regard to this, endocrine system and hormones are key in mediating links between genes and environments, strongly affecting animal's reproductive cycles and their behavior. Molecular and some physiological underpinnings of the regulation of reproductive cycles are often evolutionary conserved across animal taxa. However, there are substantial differences, e.g., in the length, frequency, or timing of reproductive cycles including peak fertility between species, as well as in various forms of sexual behaviors associated with it. Moreover, even within species, significant variability can be observed. Beside this, peak fertility might be influenced substantially by age and reproductive senescence of the individual. Furthermore, seasonal changes in peak fertility are very common in many species and often reflect environmental effects, in order to allow the animals the best timing for mating, for example, breeding in optimal temperature, maximizing offspring food availability or minimizing predation risk. Timing of gamete production and mating is therefore crucial for maximizing the offspring's survival and parental fitness and in principal requires a certain level of coordination and synchronization between partners, which is in animals usually mediated through various external signals being involved in various forms of sexual behavior.

## Cross-References

- [Aggression](#)
- [Courtship Rituals](#)
- [Estrous](#)
- [Fertility](#)
- [Hypothalamus](#)
- [Mating](#)
- [Ovaries](#)
- [Pituitary Gland](#)
- [Reproduction](#)
- [Reproductive System](#)
- [Sexual Selection](#)
- [Spermatogenesis](#)
- [Territoriality](#)



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## Peak Procedure

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## Synonyms

Discrete trial fixed-interval schedule; Peak-interval (PI) procedure

## Definition

A technique used to study interval timing in which an event (typically food) becomes available for performance of a target response (operant tasks) or is delivered (Pavlovian tasks) after a fixed duration of time on standard (training) trials and is omitted on randomly interspersed longer duration peak (probe) trials.

## Introduction

Animals live in environments that change with time making their capacity to exploit the temporal aspects of their experiences critical for effective decision-making and survival in the wild. Activities such as foraging for food, avoiding predators, and finding prey all benefit from the ability to anticipate precisely when something will happen and for decisions to be based on estimates of the rate at which these things will be encountered. Studies of interval timing are generally concerned with the ability of animals to measure intervals in the range of seconds to minutes. The peak procedure is one of several methods such as the temporal bisection procedure that have been designed to examine this ability in the laboratory. It has been used to investigate interval timing in birds, fish, and mammals, including black-capped chickadees (*Parus atricapillus*), domestic hens, pigeons, ring doves, goldfish, mice, rats, common brushtail possums (*Trichosurus vulpecula*), and humans. Performance on the peak procedure has been leveraged to develop and evaluate theories of interval timing. Additionally, imaging and pharmacological studies have used the peak procedure to uncover the neural mechanisms of interval timing in normal populations and to understand their dysfunction in clinical populations.

## Procedures and Examples

The basic peak procedure involves two trial types: one to train the subject to anticipate an event once a particular interval has elapsed and one to assess the accuracy and precision of that interval timing.

On standard (training) trials in an operant version of the task using food reinforcement (e.g., Catania 1970; Roberts 1981), a stimulus is turned on and the first response the subject makes after an interval of fixed duration produces a food reward and turns off the stimulus. This trial type is identical to a fixed interval procedure. On peak (probe or extinction) trials, the stimulus is presented for a much longer period of time (typically 2–4 times the length of the fixed interval) and no food is available. Peak trials are intermixed with standard trials. How the rate or probability of responding changes over time is the primary measure used in these studies.

Aside from these two trial types, there is no agreed upon way to implement a peak procedure. External stimuli such as changes in overall illumination, the presentation of sounds (e.g., white noise or tones) or visual cues (e.g., color of response key), and insertion of the response lever have been used as signals to mark the start of the trial. The proportion of standard trials to peak trials has varied widely across studies as have the value of the intertrial interval (ITI) and the total number of trials in a session. Moreover, some studies extend the peak trial for a fixed duration, whereas others have varied its duration; some operant studies require a response to turn off the stimulus on peak trials, whereas others do not.

A study by Sargisson et al. (2016) using the common brushtail possum (*T. vulpecula*) provides an example of an operant peak procedure. On standard trials, a light was turned on and the first lever press after 15 s (or 30 s or 60 s) produced a food reward (3 s access to a mixture of flaked barley and cocoa puffs) and turned off the light. On peak trials, the light was turned on, and the first lever press after 45 s (or 90 s or 180 s) turned off the light. Pressing the lever on the peak trials never earned food reinforcement. Peak trials were pseudorandomly interspersed among standard trials in a ratio of 1:4 and the ITI was 6 s.

Preceding use of the operant peak procedure was a task devised by Bitterman (1964) to study the temporal aspects of Pavlovian conditioning in goldfish. As is the case with the operant version, there are two trial types in a Pavlovian peak

procedure. On standard (training) trials, the conditioned stimulus or CS is turned on, the unconditioned stimulus or US (e.g., food or electric shock) is delivered automatically after a fixed amount of time, and the CS is turned off. On peak (probe or extinction) trials, no US is delivered and the CS remains on for at least 2–4 times the length of the fixed duration. In rodent studies of Pavlovian conditioning, head entries into an aperture where the food US is delivered are often used to index conditioning. The Pavlovian peak procedure may prove useful for testing special populations like transgenic mice because it obviates the need to pretrain a target response such as lever pressing.

Although the majority of studies have used positive reinforcement such as food, a few studies using the Pavlovian peak procedure have employed an aversive stimulus (Bitterman 1964; Drew et al. 2005). In one study using goldfish (Drew et al. 2005), a visual CS (red light) was presented on standard trials for 5 s (or 15 s for some subjects) and terminated with the delivery of a shock US; on peak trials, the CS was presented for 45 s without shock. The ITI was 90 s. General activity was recorded throughout the trials using a mechanical transducer that converted water displacement into discrete pulses.

## Analysis and Interpretation of Response Times

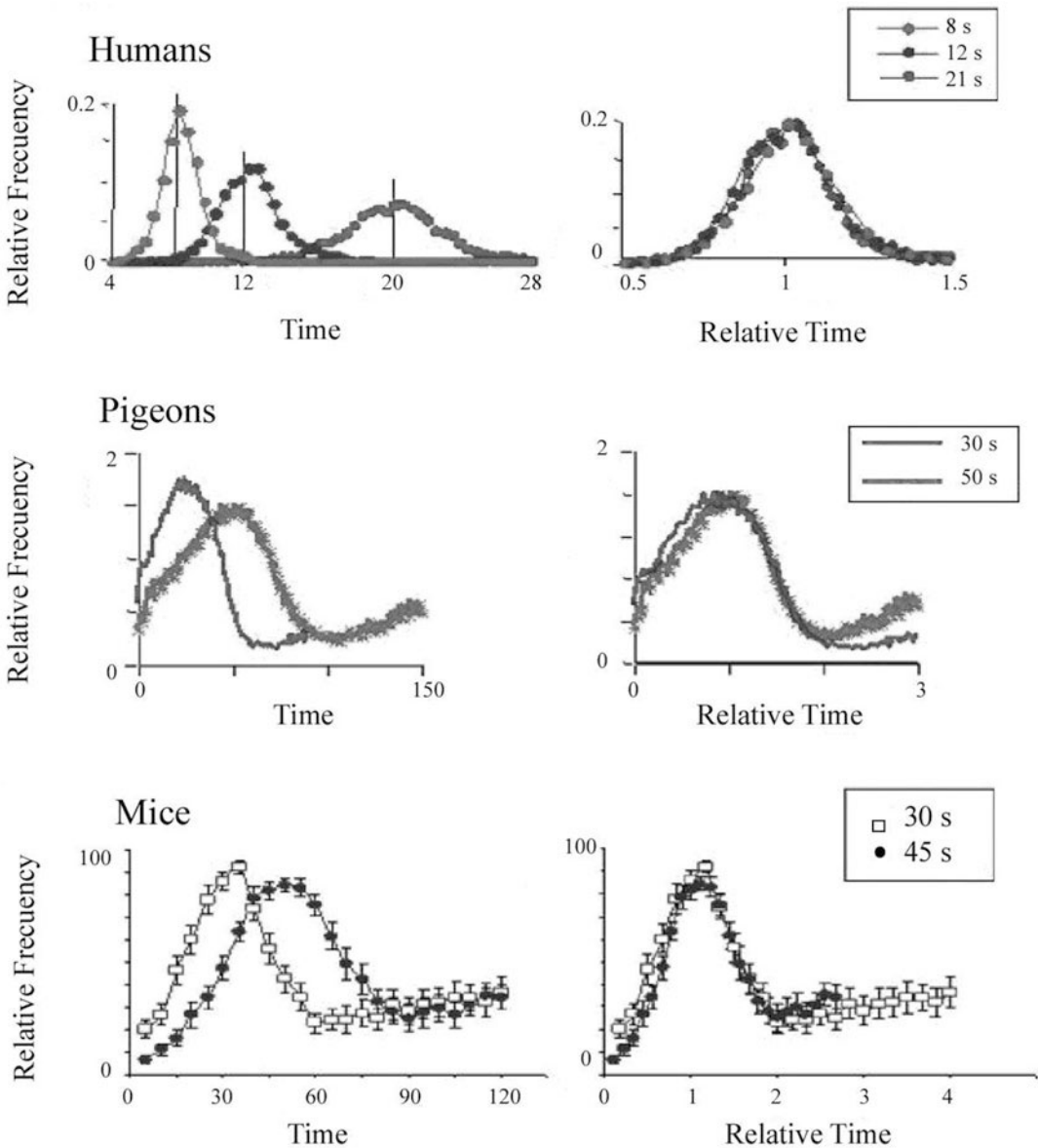
The procedure for analyzing response times on peak trials is the same for both operant and Pavlovian peak procedures. If interval timing were perfect and the only factor contributing to performance, one might expect a single response to be made on peak trials at the time that the expected event became available on the standard trials. In practice, however, even after extensive training, there are still many responses: some occur early (before the fixed interval has elapsed), some occur late (after the fixed interval has elapsed) although the majority of responses occur around the end of that fixed interval and typically within 10% of the FI value (Catania 1970; Roberts 1981). Response data from peak trials are typically plotted in two

ways: by averaging data from many peak trials and by examining data from individual peak trials.

### Averaged Peak Trials

In Fig. 1, the column of left-hand graphs displays response rates plotted as a function of time

averaged across multiple peak trials for a range of FI values for three different species: FI 8 s, 12 s, and 21 s in humans; FI 30 s and 50 s in pigeons; and FI 30 s and 45 s in mice. These graphs show that the rate of responding increases as the time to food availability is approached and then decreases after



**Peak Procedure, Fig. 1** Plots of averaged peak trials for humans, pigeons, and mice (from Balsam et al. 2009, with permission) show the scalar property of interval timing on a peak procedure. The left-hand column shows mean response rate as a function of absolute time in the interval

and the right-hand column shows mean percentage of maximum response rate as a function of relative time in the interval. The superposition of the relative response rate distributions shows the scalar property

that interval is passed. The distribution of response rates is approximately Gaussian. The extent to which the peak rate coincides with the value of the fixed interval provides a measure of timing accuracy. In every graph, the peak rates are close to the fixed interval values. The spread of responding around the peaks, however, is not identical and provides a measure of timing precision.

A ubiquitous characteristic of interval timing is that animals including humans time shorter intervals more precisely than longer intervals. As shown in Fig. 1, after extensive training, the spread of responding around the peak is greater for the longest interval trained than for the shortest interval trained for all three species: humans, pigeons, and mice. Remarkably, when the response rates are expressed as a proportion of their peak rate, the curves superpose, appearing almost identical regardless of the interval being timed (see the column of right-hand graphs of Fig. 1). This superposition feature reveals the scalar property of timing, indicating that the rate of responding is a lawful function of the proportion of the timed interval. This scalar property of interval timing is an example of Weber's law and has been documented in birds, fish, and mammals. For example, in their study with goldfish, Drew et al. (2005) found a peak in conditioned activity at about the time of the expected shock and variability in the activity distribution that was scalar. Sargisson et al. (2016), in their study of interval timing in the possum, also found a peak in responding at the time of expected food reinforcement and support for scalar interval timing.

### Single Peak Trials

When data are aggregated over many peak trials, the variation in the start and stop times of responding gives rise to an approximately Gaussian distribution. However, examination of response times on individual peak trials reveals that their distribution is not, in fact, Gaussian. Sometimes the pattern of responding on individual peak trials is scalloped; but often, the animal switches from a low response rate to a high rate as the time of expected food availability approaches and then back to a low rate of responding after that time has passed. These low-high and high-low transitions do not occur at exactly the same time on each peak trial.

Three measures are commonly extracted from the response patterns on individual trials: the start time (transition from low to high), the stop time (transition from high to low), and the run time (duration of the high rate of responding). Cheng and Miceli (1996) used these statistics to compare scalar and connectionist models of timing performance, with results strongly favoring scalar models.

### Experimental Studies of the Peak Procedure

Research using the peak procedure has uncovered a number of intriguing features about interval timing. For example, studies have shown that rats and pigeons can time multiple intervals in the same session when each interval is signaled by a different stimulus (e.g., Guilhardi and Church 2005; Roberts 1981; Subramaniam and Kyonka 2019). Interestingly, when training occurs in blocks of several consecutive trials with the same interval, temporal performance may be controlled by temporal regularities across trials and not by the discrete stimuli that signal the specific intervals, an effect attributed to overshadowing (Nepomoceno et al. 2020). Several studies using a single interval have reported that multiple peaks may occur when the duration of the peak interval trial is especially long, a pattern suggestive of underlying oscillators.

Early studies found that dopamine agonists such as methamphetamine shifted the peak of responding earlier (leftwards) suggesting an increase in the speed of the internal clock, whereas dopamine antagonists such as haloperidol shifted the peak of responding later (rightwards) suggesting a decrease in clock speed. Such pharmacological findings led researchers to propose a dopamine-driven internal clock. Manipulations of motivational parameters have also been found to affect timing in a similar way. For example, the peak of responding is shifted earlier (leftwards) when food value increases and later (rightwards) when food value decreases (Galtress and Kirkpatrick 2009). Collectively, these and other results have spurred efforts to reconcile the influence of dopamine on interval timing with

mounting evidence that dopamine activity encodes a reward or generalized prediction error (Balci et al. 2008) and to consider more broadly the relationship between temporal cognition and motivational variables.

There is currently no consensus on how animals accomplish interval timing. Behavioral data from the peak procedure have tended to favor Gibbon's (1977) scalar expectancy theory (SET) although they are to a large extent consistent with Machado's (1997) learning to time (LeT) model. fMRI studies support the involvement of fronto-striatal circuitry in human interval timing, and researchers have discovered a previously unknown set of neurons in the medial entorhinal cortex that turn on like a clock when an animal is waiting. The occurrence of commonalities in interval timing across diverse species suggests the potential for a common evolutionary mechanism for temporal processing. So far, the evidence does not point to a central clock for interval timing as there is for circadian timing. This suggests that timing arises from fundamental properties of neurons or networks.

## Conclusion

The peak procedure is a powerful tool that provides two measures of a subject's timing ability: an estimate of the expected time of reinforcement (the peak time) and the accuracy of that estimate (the peak spread). Analysis of individual and averaged response times has yielded evidence that, for a wide variety of species, interval timing is more precise with shorter than longer intervals. Data from the peak procedure have been influential in shaping and evaluating theories of interval timing and have tended to favor SET.

## Cross-References

- [Anticipation of Future Events](#)
- [Associative Learning](#)
- [Circadian Rhythms](#)
- [Classical Conditioning](#)
- [Dopamine Receptor](#)
- [Extinction in Learning](#)

- [Fear Response](#)
- [Food Patch](#)
- [Foraging](#)
- [Internal Clocks](#)
- [Interval Timing](#)
- [Operant Conditioning](#)
- [Overshadowing](#)
- [Predation Risk](#)
- [Schedules of Reinforcement](#)
- [Temporal Bisection Procedure](#)
- [Timing](#)
- [Unconditioned Stimulus](#)

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## Peak Reproduction

### ► Peak Fertility

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## Peak-Interval (PI) Procedure

### ► Peak Procedure

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## Peck Order

### ► Dominance

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## Pecking Order

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## Synonyms

[Dominance hierarchy](#); [Ordinal position](#); [Social hierarchy](#)

## Definition

A hierarchical system of social organization in chickens.

Schjelderup-Ebbe (1922) was the first to recognize chickens have a stable pecking order (i.e., dominance hierarchy). Individual differences (e.g., body weight, comb size, etc.) and social experience play an important role in the establishment and maintenance of the hierarchy (Chase 1980; Cloutier and Newberry 2000). For example, Murchison (1935) assessed the ability of 16 roosters to maintain their hierarchy in a novel social setting. The roosters were ranked using dyadic encounters in which two individuals were simultaneously released from opposite ends of a runway and the distance travelled was used to determine the dominance relationship. The dominance-subordinate relationship determined from these dyadic encounters correlated strongly with the rank established in their natural environment (Murchison 1935).

The consistency of dominance relationships across settings suggests that chickens are able to recognize others. Indeed, individual recognition is crucial to the formation and maintenance of a stable hierarchy (Croney and Newberry 2007). Basic social discrimination has been assessed using a variety of different paradigms. For example, Murchison (1935) placed hens on a runway with a dominant individual caged on one side and a subordinate individual on the other (Murchison 1935). All group members apart from the highest and lowest ranking individuals showed a strong preference for the subordinate hen. To assess the limits of this ability, Ryan and Lea (1994) assessed the ability of chickens to discriminate between slides, video clips, and models of conspecifics. With each stimulus type, the birds were trained to discriminate between pairs of stimuli depicting two different birds. Chickens successfully discriminated between different conspecifics across all stimulus types.

The formation of the hierarchy goes beyond a mere representation of individual conspecifics, as relations between individuals must also be represented. A triad of hens is the smallest social unit in which a hierarchy can be established (Doyen 1987). An important property of linear hierarchies is that all their component triads are transitive such that, given A dominates B ( $A > B$ ) and B dominates C ( $B > C$ ), then A must also

dominate C ( $A > C$ ). Chase (1980) assessed the outcome of groups of three unfamiliar chickens when simultaneously placed in a neutral cage. With three individuals, there are four possible sequences in which the first two dominance relationships may be established. In the first relationship, individual A dominates B, with the bystander C observing the interaction. After this initial relationship is formed, (1) the initial dominant A can dominate the bystander C (double dominance), (2) the bystander C can dominate the initial subordinate B (double submissive), (3) the bystander C can dominate the initial dominant, or (4) the initial subordinate can dominate the bystander. While the first two outcomes guarantee transitive triads irrespective of the direction of the third relationship, the later two can result in either a transitive or intransitive triad.

To assess whether sequences that guarantee transitivity were more common than those that did not, Chase (1980) placed three hens in a neutral pen and observed the establishment of the hierarchy. The double dominance and double submissive patterns that guarantee transitivity were the only patterns observed. This finding is significant as the probability of a transitive triad forming is only 75% in animals meeting for the first time and having an equal chance of winning or losing (Zayan and Vaclair 1998). In a manipulation of his early experiment Chase (1985) and had the three individuals meeting each other in a series of paired encounters. Many of the encounters resulted in the formation of an intransitive or circular triad, for example,  $A > B$ ,  $B > C$ , and  $C > A$  (Chase 1985). This suggests the presence of the bystander (i.e., the bird that observes an aggressive interaction) may influence how the hierarchy is formed.

What information could a bystander gain by watching two birds interact? At a basic level, the bystander could gain information about each individual's fighting ability. More interestingly, the bystander could glean information about the relationship between the two individuals (Barnard and Burk 1979; Cloutier et al. 1996; Cloutier and Newberry 2000). For example, if the bystander watches a bird that is dominant to it being defeated by a stranger, the bystander could

use this information to submit to the stranger and avoiding the potential costs of fighting. This would be a form of social inference, where individuals settle a dominance relationship without conflict (Cloutier et al. 1996; Cloutier and Newberry 2000).

Assessing this experimentally, Hogue et al. (1996) staged a series of encounters in which a bystander (B) observed its former dominant (A) interacting with a stranger (C). Three different encounters were staged with the bystander observing (1) A being defeated by C ( $C > A$ ), (2) C being defeated by A ( $A > C$ ), and (3) two unfamiliar hens settling dominance. Following the observation, the bystander joined the other individuals in the enclosure. If the bystander was able to infer relationships from these observations, then they should respond differently under the first and second scenarios. Fittingly, bystanders that observed their former dominant being defeated by a stranger always submitted to the stranger (Hogue et al. 1996). In contrast, when its former dominant defeated the stranger, the bystander attacked the stranger in 50% of the group interactions (Hogue et al. 1996). In the final condition in which the bystander had no information on the direction of the relationship between A and C, C was avoided on 66% of occasions suggesting indifference toward the stranger (Hogue et al. 1996). The behavior displayed by the bystander under the three conditions demonstrates the hens were able to predict the likely outcome of their interaction with the stranger (Hogue et al. 1996).

## Conclusion

From the early observations by Schjelderup-Ebbe (1922) to the work by Hogue et al. (1996), our understanding of the cognitive operations that underlie the pecking order has grown substantially. More recently, Chase and Lindquist (2016) have argued pecking orders may be dynamic rather than static, suggesting there is still much to learn about how chickens determine who rules the roost and how long they may rule it for.

## Cross-References

### ► Dominance Hierarchy

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## Pederasty

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The term "pederasty" derives from the ancient Greek "paiderastia," meaning "the love of boys." In both Greek and English, it refers to the erotic relations between adult men and pubescent/adolescent boys that were customary in ancient Greek culture. Similar customs have been typical of several other cultures (e.g., ancient Rome, Edo-period Japan). These cultures have generally approved of pederastic relations but disapproved of homosexual relations between adult males. The comparison of ancient Greek pederasty and modern homosexuality led to the development of the theory of social constructionism, now widely accepted in the Humanities and Social Sciences, that views concepts and practices of sexuality as variable over time and culture (Foucault 1985).

Pederasty is distinguished from the modern term/concept "pedophilia," which refers to an individual's tendency to desire sexual relations with children. "Pedophilia" refers to a drive in an individual, without regard for (or contrary to) social convention. The subject of desire can be either male or female, as can the object; conceptually, it refers to desire for prepubescent and pubescent children. "Pederasty" refers instead to a social custom. Participation was very broad and need not have indicated any particular type of desire or psychology, although some speakers (in poetry in particular) represent themselves as habitual and enthusiastic participants. "Pederasty" could only be practiced by males, and it did not include sexual relations with prepubescent children, but only pubescent/adolescent youths. Finally, "pedophilia" is generally thought of as a sexual desire, while the pederastic relationship is often presented in Greek sources of evidence as focused on mentoring and role-modeling more than sex. It was strongly associated with the activities (hunting, athletics, warfare, the symposium) and virtues (courage, loyalty, temperance) comprising the Greek masculine ideal; it was thought

of as the method by which this ideal was passed on from one generation to the next (Lear 2014).

Greek pederasty was regarded by both Greeks and non-Greeks in the ancient world as a defining characteristic of Greek culture (along with the associated practice of nude athletics). It is widely referenced in Greek literature, in particular in lyric poetry, comedy, and philosophy (Hubbard 2003); pederastic courtship is also a common theme in the artistic genre of vase-painting (Lear and Cantarella 2008), and nude male Greek statuary is imbued with the pederastic ethos. This custom does not appear in its developed form in the Homeric epics and seems therefore to have developed later, in the Greek Dark Ages or early Archaic period; from that point on, however, it seems to have been practiced throughout the Greek world (including, e.g., Southern Italy and Sicily, Alexandria, Syria) until the end of pagan Antiquity. It is associated with the elite, as it was associated with ideals, but it seems likely to have been practiced by a broad segment of society.

Greek pederasty (or at least the fact that Greek culture approved of some form of same-sex relations) is well known in the modern world. It is less widely known that erotic relations between adult and pubescent/adolescent males are or were considered acceptable or normative in many other cultures as well. The sexual relations that take place between initiator and initiand during adolescent initiation rituals in certain tribes on/near New Guinea are often compared to Greek pederasty (Herdt 1984), as they too imply a view of pederastic relations as contributing to the younger partner's maturation in a positive way. Several subcultures in premodern Japan were also associated with adult-adolescent male-male erotic relations; those between samurai and their pages had associations with military virtues similar to those of Greek pederasty (Leupp 1995). Other cultures on the other hand have practiced such relations without a marked pedagogical element. In ancient Roman culture, for instance, while pubescent/adolescent male youths were an acceptable sex object for adult males, these relations were not regarded as pedagogical. Thus, these relations are presented differently in Greek and Roman literary sources. Greek sources present the tan, athletic, markedly masculine youth as the ideal

love object and generally present these relations as intralite; they stress the youth's decisional role in the relationship. In Rome, by contrast, sex with a citizen boy would have constituted the crime of *stuprum*; Roman sources present the "effeminate" slave boy as the ideal object of pederastic desire (Williams 2010). The contrast in reported sexual practices underlines this distinction. In both cultures, anal sex was regarded as degrading for the penetrated partner. As a result, in Greek culture, pederastic relations are rarely presented as involving anal sex; even when, in comedy or invective, the possibility of anal sex is alluded to, the allusion is generally oblique. In Rome, pederastic sex is frequently presented as anal. Pederastic relations were also acceptable in earlier periods of Chinese history; the pederastic relations of early, semi-legendary emperors served as examples of this "love of the cut sleeve," but these relations are not presented as pedagogical. Classical Arabic and Ottoman literature and art also present pederastic relations/desires in a positive light, but without any association with pedagogy (El-Rouayheb 2005). The Bacha Bazi dancers of modern Afghanistan represent a related tradition. Pederastic relations were also regarded as acceptable in some milieus in the European Renaissance. Italian court records indicate that such relations were common (Rocke 1996); they are also an important theme in Renaissance Italian art, where many important artists produced works with clear pederastic implications and in several cases are also thought/rumored to have had pederastic relations (Donatello, Boccaccio, Leonardo, Michelangelo, Pontormo, Bronzino, Caravaggio, etc.). Pederastic relations are also an important theme in English Renaissance literature, particularly in Marlowe (*Hero and Leander*, *Edward II*) and in Shakespeare's Sonnets. It is difficult to reconcile this evidence with the strong injunctions against same-sex love in church and state law in both Muslim and Christian countries of this period, but it seems possible that there was a permissive counter-ideology among classically educated elites.

In fact, there is much more evidence in history for pederastic desires and relations than for the same-age homosexual relations among adults considered acceptable in the modern

West. In the cultures in which pederastic relations are practiced, adult-adult male-male relations are generally the objects of social disapproval. In both Greek and Latin, for instance, there are terms of reproach/ridicule for adult males who are penetrated sexually by other males: principally *katapugon* and *kinaidos* in Greek, *cinaedus* and *pathicus* in Latin. *Kinaidos/cinaedus* is etymologically obscure, but *katapugon* (down-the-anus) and *pathicus* (one who habitually submits to abuse) make clear that the disapproved practice of anal intercourse was considered typical of adult-adult male-male relations. Boys of the appropriate age for pederastic relations are generally not referred to with these terms. Pederastic relations were or could be considered an acceptable kind of erotic relations. In both cultures, there were forms of pederastic relation which were considered blameworthy (prostitution in Greek culture, *stuprum* in Roman). They could however be practiced appropriately, and in both cultures, the appropriate kind of pederastic relation was culturally emphasized. On the whole, attractions to women and boys were considered appropriate and normal to any man, rather than to specific types of men. A man could be seen as having a preference for boys over women (or the reverse), but this preference was not considered necessarily exclusive or defining. Adult-adult male-male relations on the other hand were considered inappropriate, and they marked at least the penetrated partner as a type of person subject to blame/ridicule. Interestingly, adulterers (which in these cultures does not mean merely a man who has extra-marital sex, but specifically a man who has sex with the wife of another man) were also seen as effeminate/degenerate. In fact, the *kinaidos/cinaedus* is at times accused of adultery in addition to his same-sex relations. Thus, these cultures did not divide activities or people into categories of heterosexual or homosexual (Halperin 1990). Pederastic relations were of course homosexual, but the people involved in them cannot be considered through an essentialist lens as homosexuals, any more than they can be seen as pedophiles. Instead, they must be seen as participants in a set of sexual customs/concepts different from modern Western ones.

## Cross-References

- [Bisexual](#)
- [Cultural Transmission](#)
- [Essentialism](#)
- [Homosexual](#)

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## Pedigree

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## Introduction

Pedigree is a pictorial representation of the genotype or phenotype of an organism and its family



and ancestors (Griffiths et al. 1999). Pedigree is derived from the French words *pe de grue* which means the crane's foot, because the typical lines and split lines resemble the thin legs of a crane.

To study genetics, researchers trace the relevant characteristic trait in the families that are affected and their multiple generations and analyze it through pedigree chart. Pedigree helps to infer the mode of inheritance of the trait and thus helps in predicting the probability of transmitting the trait to future generation (Schaefer and Thompson 2014; Connor 2001).

### How to Construct a Pedigree?

A pedigree is an orderly presentation of family information. Human nomenclature is followed for pedigree for all species. After collecting information about the trait in the family, a pedigree can be made using standard pedigree symbols (see Table 1). Siblings should be mentioned in the order of birth, oldest to youngest. It is important to take a detailed history of the family including the stillbirths, pregnancy losses, consanguinity, genetic testing results, and cause of death. As this information is drawn based on the information facts given by the family, there is possibility for recollection errors.

Error in data entry or an inconsistent data will affect the downstream genetic analysis. There are tools and software to edit and check for Mendelian inconsistencies when information obtained through pedigree is not consistent with the genotype information.

### Pedigree Patterns

There are different modes of Mendelian inheritance and rarely some disease can have more than one pattern of inheritance. Patterns of inheritance can be autosomal dominant (in which an affected individual has one copy of a mutant gene and one normal gene on a pair of autosomal chromosomes), autosomal recessive (the affected individual has two copies of the mutant gene), X-linked (a mutation in a gene on the X chromosome), Y-linked (mutation

of genes in Y chromosome), and mitochondrial (mutation of and sporadic mode of transmittance).

Figure 2 shows autosomal dominance inheritance pattern. The key points are:

1. There are no skips, i.e., all the generations have the disease.
2. Both males and females have equal chances of having the disease.
3. An affected individual has equal chances of having affected and unaffected offspring.
4. Examples include *Marfan syndrome* and *neurofibromatosis type 1*.

Figure 3 shows autosomal recessive inheritance pattern. The key points are:

1. It might show skipping of generations, i.e., a phenotypically normal individual might have diseased babies.
2. Males and females are equally affected.
3. Both the parents must have the disease trait to transmit disease to the offspring.
4. Examples include sickle cell anemia and cystic fibrosis.

Figure 4 shows X-linked recessive disease. The key points are:

1. Only males are affected (affected females usually die intrauterine because of disease severity).
2. There is no skipping of generations.
3. A heterozygote mother transfers the disease to half the sons.
4. Examples include hemophilia and red-green color blindness.

Figure 5 shows X-linked dominant disease. The key features are:

1. Both males and females are affected.
2. Sons inherit disease only from mothers.
3. Daughters can inherit disease from mother and father.
4. Males are generally more severely affected than heterozygote females.
5. Examples include Rett syndrome and vitamin D-resistant rickets.

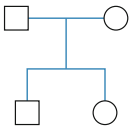
**Pedigree, Table 1** Standard pedigree symbols and terms representation in humans

Male 

Female 

Mating 

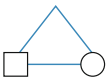
Parents and children (in order of birth), 1 boy and one girl



Dizygotic (nonidentical) twins



Monozygotic (identical) twins



Unspecified sex



Affected individual



Carrier of sex linked recessive



Death



Number of children



Abortion or stillbirth



Propositus



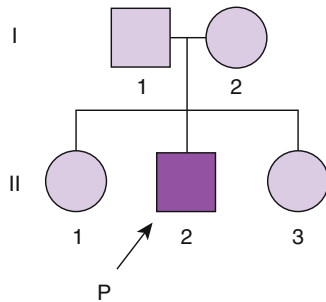
Consanguineous marriage



Proband (P)- First affected member who seeks the physician. Male affected in second generation is shown as P in the model pedigree given in Fig. 1

Figure 6 shows Y-linked disorders. The key points are:

1. Only males are affected.
2. There is no skipping of generations.
3. Example – male pattern baldness.



**Pedigree, Fig. 1** Representation of proband (P) in a pedigree

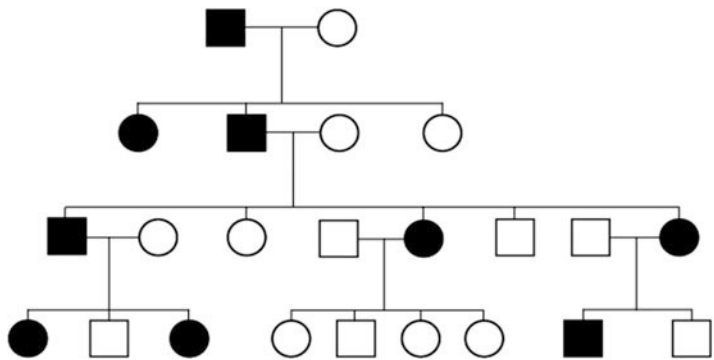
Figure 7 shows mitochondrial inheritance. The key points are:

1. Only mothers transmit the disease.
2. All the offsprings are affected.
3. Examples – Leber’s hereditary optic neuropathy (LHON) and mitochondrial encephalomyopathy, lactic acidosis, and stroke-like episodes (MELAS).

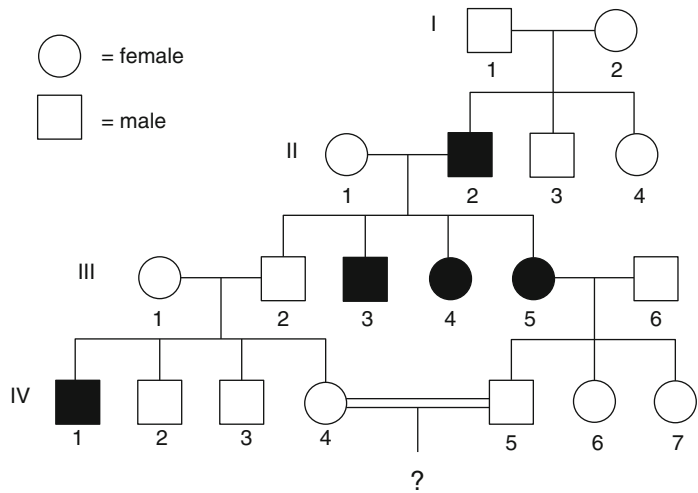
**Sporadic Inheritance**

Some inheritable diseases may involve multiple genes and complex inheritance. Environmental factors and sporadic mutations play a major role in the pathogenesis, e.g., retinitis pigmentosa.

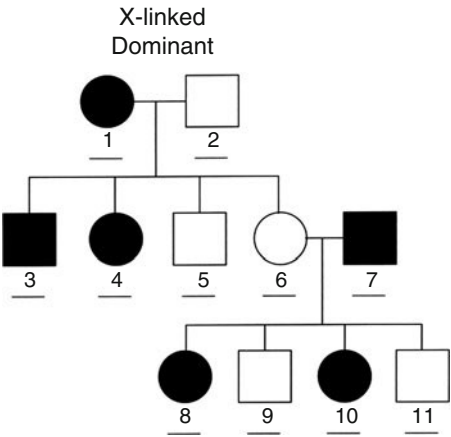
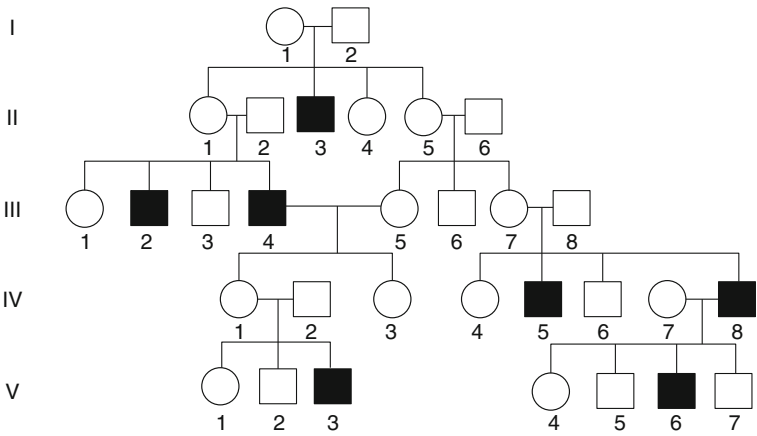
**Pedigree, Fig. 2** Autosomal dominant inheritance



**Pedigree, Fig. 3** Autosomal recessive inheritance

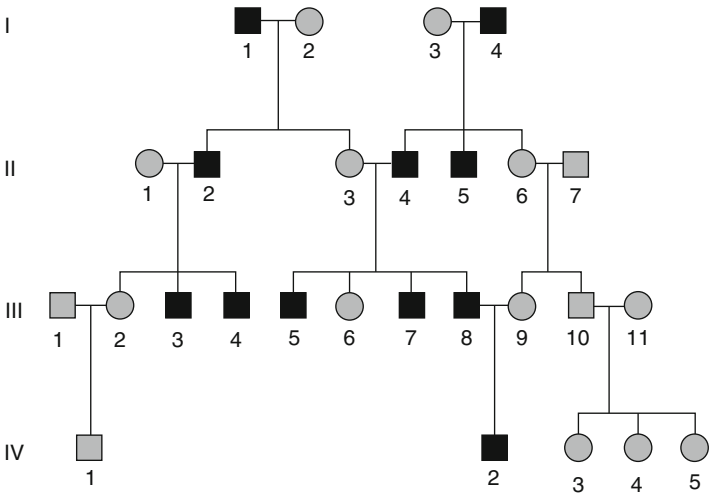


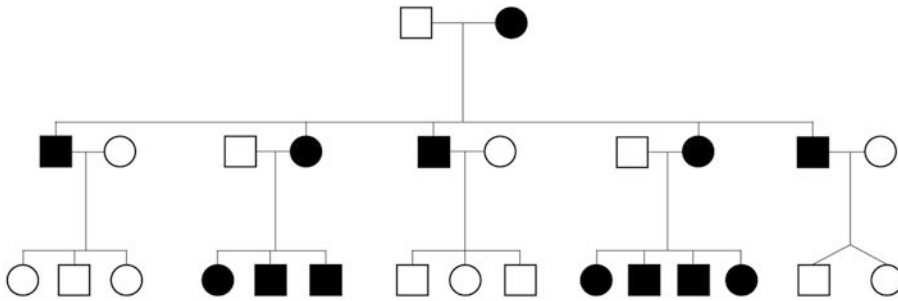
**Pedigree, Fig. 4** X-linked recessive inheritance



**Pedigree, Fig. 5** X-linked dominant inheritance

**Pedigree, Fig. 6** Y-linked inheritance





**Pedigree, Fig. 7** Mitochondrial disorders

## Advantages of Pedigree Chart

Properly constructed pedigree helps us to know the mode of inheritance of a disease in any species where controlled matings are impossible. Using the knowledge of Mendelian inheritance and basic concepts of probability by applying the product and sum rule, geneticists can calculate the probability of the trait among future offspring of the families at risk. It is useful in genetic counseling during prenatal diagnosis and research and in animal breeding (Rubin et al. 1983).

## Summary

Pedigree charts are a systematic, comprehensive representation that summarizes a phenotype/genotype in a family and their ancestors. It is useful in studying the genetics of inherited diseases, including mode of inheritance, and helps in predicting the probability of outcome in future generations.

## Cross-References

► [Phenotype](#)

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- Schaefer, G. B., & Thompson, J. N., Jr. (2014). Chapter 9, Family history and pedigree analysis. In *Medical genetics: An integrated approach*. New York: McGraw-Hill Education.

## Pedigree Mapping

► [QTL Linkage Analysis](#)

## Pedigree Relatedness

► [Coefficient of Relatedness](#)

## Penalty (Not Technical)

► [Punishment](#)



## Penguins: Behavioral Ecology and Vocal Communication

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### Synonyms

[Spheniscidae](#)

### Life History

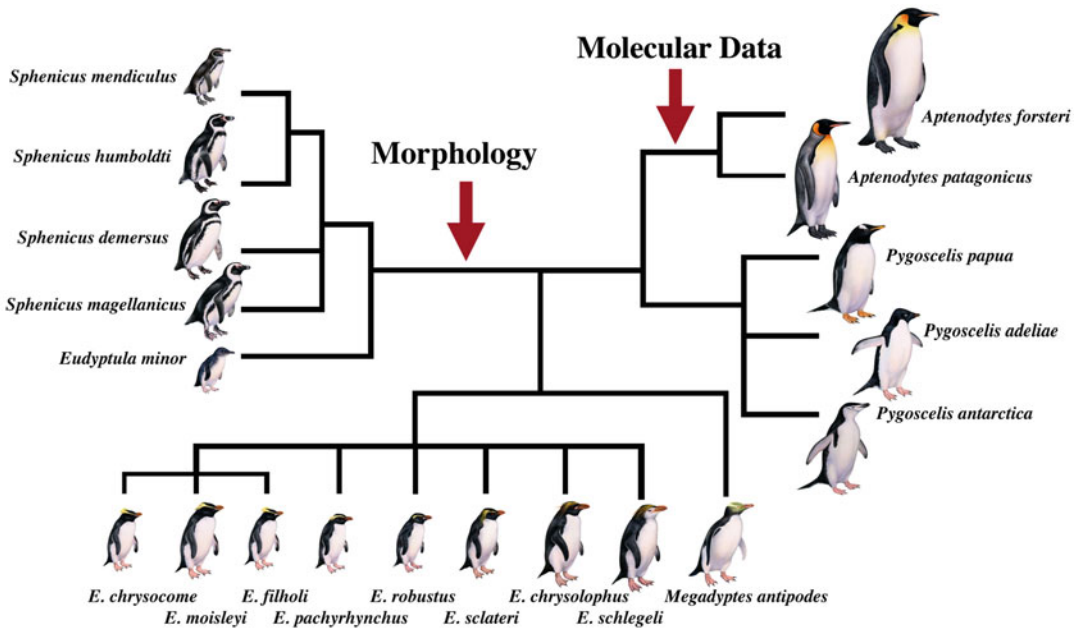
Penguins (Aves, Sphenisciformes, Spheniscidae) are a family of seabirds that have evolved to swim and have lost the ability to fly about 60 million years ago (Williams 1995). Adapted to life underwater, penguins have developed strong hard flippers, with fused bones for fast propulsion when swimming. Their feathers are more abundant, dense, and miniaturized compared to other birds. These feathers are hard and stiff with a flattened shaft that overlaps, to provide insulation and waterproofing. Penguins have heavy, solid bones, as they lost the pneumatization of their bones, which was developed by flying birds to keep as light as possible and would be a disadvantage for penguins, increasing their buoyancy. All penguin species have the classic black-and-white “tuxedo,” a countershading assumed to serve as camouflage and helps disguise them from both prey and predators at sea: their dark back color helps blend in with the dark of the ocean floor, and the white of the belly blends with the light of the sun when seen from below. Their streamlined body is adapted for life in the water but is poorly designed for moving on land, which makes them waddle comically. This stance and gait has, however, generated much fondness from humans to these special birds,

and this charisma makes them excellent ambassadors for marine conservation.

The family is divided into 6 genera and 18 species, all restricted to the Southern Hemisphere (Williams 1995; Fig. 1). The genus *Aptenodytes* includes the largest penguins: the king (*A. patagonicus*) and emperor (*A. forsteri*) penguins. The genus *Pygoscelis*, or brush-tailed penguins, is composed of three species: the Adélie (*P. adeliae*), chinstrap (*P. antarctica*), and Gentoo (*P. papua*) penguins, all of which have a circumpolar distribution. The genus *Megadyptes* has only one species, the yellow-eyed penguin (*M. antipodes*), only found on New Zealand islands. The genus *Eudyptes* consists of crested penguins: the rockhopper penguins, which are divided into two species, the southern *E. chrysocome* and northern rockhopper (*E. moseleyi*); the erect-crested penguin (*E. sclateri*) only found on the Bounty and Antipodes Islands southeast of New Zealand; the Fiordland penguin (*E. pachyrhynchus*) restricted to New Zealand; the Snares penguin (*E. robustus*) breeding only on the Snares archipelago south of New Zealand; and the macaroni penguin (*E. chrysolophus*) closely related to royal penguin (*P. schlegeli*), with a circumpolar distribution. The genus *Spheniscus* includes the banded penguins: the African penguin (*S. demersus*), endemic to Southern Africa; the Magellanic (*S. magellanicus*) and Humboldt (*S. humboldti*) penguins breeding in South America and on the Falklands/Malvinas for the Magellanic penguin; and the Galápagos penguin (*S. mendiculus*) confined to the Galápagos Archipelago. Finally, the genus *Eudyptula* is monotypic, with the little or blue penguin, *E. minor*, found in Australia and New Zealand.

### Breeding Ecology

Penguins are typical K-selected species, characterized by small clutches, intensive parental care, late sexual maturity, and long life expectancy. Beside *Aptenodytes* penguins whom lay a single egg incubated on their feet, all other penguin species lay a clutch of two in a nest. Crested



**Penguins: Behavioral Ecology and Vocal Communication, Fig. 1** Classification of the 18 extant species of penguins (© Barbara Harmon, extracted from Ksepka and Ando 2011)

penguins lay asymmetrical eggs, with the second egg laid, the B-egg, systematically larger than the first laid egg, the A-egg, particularly so in erect-crested penguins where B-eggs are up to 85% larger than A-eggs (García Borboroglu and Boersma 2013). It was long believed that no *Eudyptes* penguins could raise two chicks, but recent evidences showed otherwise for southern rockhoppers in the Falklands/Malvinas (Poisbleau et al. 2008). This asymmetry in egg size favors the survival of the large B-egg and results in facultative brood reduction, a mechanism that increases reproductive output during years of particularly high food abundance (Williams 1995).

Incubation and chick-rearing duties are generally shared between sexes, although not systematically equal and the patterns vary among species. For example, in both *Aptenodytes* species, incubation is a male-only duty, while in crested penguins, females undertake the provisioning of the chicks for the first few weeks after hatching, while males guard the nest. Beside this marked pattern, more detailed analyses revealed a tendency for females to invest more in their current reproduction (e.g., Spelt and Pichegru 2017),

which partially explain the observed tendency for higher mortality of female penguins (Pichegru and Parsons 2014).

The breeding season lasts approximately 3–4 months for most penguin species, although slightly longer for Antarctic breeding birds (4–5 months), and is particularly long for the large penguins (8–9 months for emperors and up to 14 months for kings). The season is fairly synchronized for each species, except for banded penguins, where conditions in more temperate waters vary more widely across years. Therefore, their breeding season is more protracted and pairs sometimes raising two clutches within a year. For example, Galápagos penguins breeding in a relatively unpredictable environment can lay two to three clutches every year, and their success and breeding depend on food availability (i.e., upwelling; García Borboroglu and Boersma 2013).

After the breeding season, all penguins spend time at sea to increase their fat reserves, nearly doubling their weight, before their molt to replace feathers wearing with age. Penguins undergo a “catastrophic molt,” where all feathers are replaced at once, a phenomenon unique in birds.

Molting implies fasting due to total loss of insulation. Therefore, if the birds have not gained enough weight before molting, they will die. This molt period lasts 3–4 weeks, being slightly shorter for adults than for juveniles and slightly longer for large penguin species (García Borboroglu and Boersma 2013). The synchronization in molt is generally greater compared with breeding patterns, strongly associated with seasonality and peak food abundance in the environment. As a consequence, adults of some species like Adélie or African penguins are sometimes forced to desert their chicks to fatten up for molt (e.g., Woolfaardt et al. 2009). These observations suggest that molt could be a key driver of the penguins' annual cycle.

## Foraging Ecology

Penguin's diet varies relatively widely across species, colonies, and years. Antarctic and sub-Antarctic penguins (*Aptenodytes*, *Pygoscelis*), as well as *Eudyptes* penguins, feed predominantly on krill (mostly *Euphausia superba* and *E. crystallorophias* to a lesser extent) and Myctophidae (i.e., lantern fish) or Antarctic silverfish (*Pleuragramma antarcticum*). Warmer-water penguins (*Spheniscus*, *Eudyptula*) and *Megadyptes* feed mostly on small pelagic fish (anchovy, sardine, or sprat). Various species of cephalopods are commonly found in all penguins' diet in smaller proportion, although they can sometimes constitute up to 85% of their diet at some colonies in some years, when preferred prey are absent (García Borboroglu and Boersma 2013).

With the development of animal-borne miniaturized electronic recorders, the understanding of at-sea behavior of penguins greatly improved in recent years. Being flightless, the cost of foraging is much higher for penguins than for flying seabirds, and swimming is slower than flying, so they are bound to forage in a more restricted area. This is particularly true during the breeding season when they are constrained to return regularly to their nests to relieve their partners during incubation or to feed their chicks.

The average swimming speed of penguins is fairly constant across genera (ca 2 m/s). To increase that pace to >3 m/s, penguins are capable of leaping above water (i.e., porpoising), which allows them to reduce the drag of the water while catching a breath. This behavior is more common in penguin species prone to predation when departing their colony, suggesting a predator avoidance benefit. However, traveling at the surface is also energetically costly due to increased drag, and larger penguins are less prone to porpoise than smaller ones.

All penguins are capable to dive at great depth (up to 550 m for emperor penguins), but most dive within the top 70 m of the sea, where the light allows them to catch their prey. Indeed, most penguins are visual diurnal foragers, and their foraging efficiency decreases when feeding at night. They may, however, use their olfactory sense to locate foraging patches (Wright et al. 2011). Dive depths vary with species size and sex, with larger species and males (often slightly larger than females in most penguins) diving deeper, following simple allometric rules. But dive depths also vary with diet, and penguins feeding on myctophids or krill tend to dive deeper (e.g., 40–90 m for large penguins and most crested penguins) than species feeding on pelagic fish (e.g., 20–40 m on average for banded penguins). Some like yellow-eyed penguins are almost exclusively benthic feeders in waters 40–120 m deep, while others like Galápagos penguins foraged mostly within 6 m depth in shallow inshore waters (García Borboroglu and Boersma 2013). Recent deployment of animal-borne video cameras increasingly shows evidences of group foraging in several penguin species, whereby they may improve their foraging efficiency (McInnes et al. [in press](#)).

Generally, foraging distance and trip durations are much larger during the incubation stage compared to chick-rearing (e.g., 100–200 km over up to 2 weeks and 20–50 km during 1–2 days trip for Magellanic penguins, respectively; García Borboroglu and Boersma 2013). Longer foraging trips imply longer fasting periods for the partner guarding the nest and are therefore more common for larger species. But these foraging ranges mostly vary with the location of the species

colonies in respect to the continental shelf or areas of productivity (e.g., polar frontal zone, upwelling cells). For example, Gentoo penguins breeding in Kerguelen on a colony facing the open sea foraged up to 40 km from their colony while incubating diving at 60 m depths on average, while birds breeding in colony located within a gulf foraged only 3–11 km from the shore and at 40 m depths (Lescroël and Bost 2005). These patterns were explained by their diet composed of krill in the gulf and of fish in the open ocean (Lescroël and Bost 2005).

Little is known of their distribution outside the breeding season, with a few species being equipped of satellite transmitters or geo-locator system (GLS), which by recording light at sunrise and sunset indicates the latitude and longitude at which the birds are located. Results suggest relatively large dispersal in species with a circumpolar distribution, although the distance covered may depend on the molting areas.

## Vocal Communication

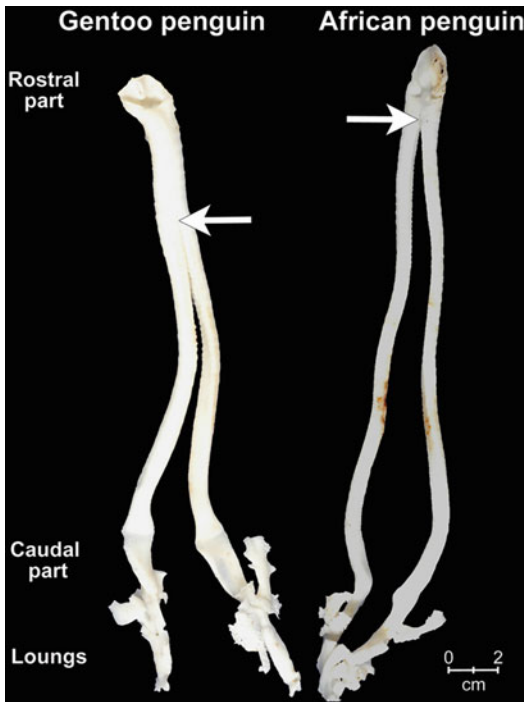
### Vocal Apparatus

Bird calls are produced through the syrinx (King 1989). The syrinx is a two-part organ located at the base of the trachea, formed by modified skeletal elements that provide support for a complex series of vibrating membranes (generating the sound) and muscles (involved in the control of the air flow from the lungs and tension and position of the membranes). The anatomy of the syrinx varies largely across species and orders. Penguins (order: Sphenisciformes) have a rudimentary bronchial syrinx, formed by the flattened first portion of the bronchi and membranous connections to the base of the trachea (Zeek 1951). Vocalizations are generally uttered during exhalation of air (Favaro et al. 2014), although for selected call types, vocal production occurs also during air inhalation. For instance, in the little penguin (Miyazaki and Nakagawa 2015) inhalation and exhalation phases contribute equally to the total duration of mating vocalizations.

Macroscopically, penguin's upper vocal tract consists of the tracheal tube, larynx, glottis (corresponding to the opening of the larynx), oropharyngeal cavity, and beak. The trachea is made of imbricated cartilaginous rings covered anteriorly and laterally by muscles (Zeek 1951), and this anatomical configuration allows the trachea to be voluntarily contracted by the bird, making its length and diameter vary. Overall, the penguin trachea presents a single cavity in the rostral part, while in the caudal portion, it is divided into two pipes, formed by cartilaginous rings connected in the mid-dorsal and mid-ventral area by bone tissue. This particular anatomical configuration is named "double trachea" and has been reported also for other aquatic birds (e.g., some petrels, order: Procellariiformes) and marine mammals (e.g., dugong, *Dugong dugon*, and sea lions, family: Otariidae). However, the functional basis is not yet fully understood. Moreover, it is important to note that the length of the septum varies among penguin species. In the Antarctic penguins of the genus *Pygoscelis* (Lockner et al. 1976) and in other sub-Antarctic or tropical species for which data are available from the literature (i.e., the crested penguins and the yellow-eyed penguin; Hocken 2002), the division of the air pathways is limited to one third or two thirds of the length of the trachea, depending on the species. Figure 2 shows two silicon casts obtained from the vocal tracts of Gentoo and African adult penguins. Silicon impressions show that in the Gentoo penguin, the septum dividing the trachea disappears in the upper portion of the air pathway. By contrast, the trachea of the African penguin is divided by the septum until the laryngeal cavity. Finally, the septum is not present in some penguin species, such as the blue penguin (Hocken 2002). Lockner et al. (1976) also showed that in Antarctic penguins, the number of tracheal rings and percentage of contraction of the windpipe is highly species-specific.

### Vocal Repertoire

Over the last decades, the vocal repertoires of several penguin species have been studied using a variety of methodologies, ranging from basic descriptions of the calls heard in the field to



**Penguins: Behavioral Ecology and Vocal Communication, Fig. 2** Silicon casts of the vocal apparatus of a long-tailed Gentoo penguin (left) and African penguin (right). Arrows indicate where, in the two species, the tracheal bifurcation occurs (© Livio Favaro and Marco Gamba)

detailed acoustic analyses (Jouventin 1982; Favaro et al. 2014). Overall, although different names were given for the same vocalization across studies, adult penguin vocalizations can fit within the following general categorization:

- *Contact calls*, uttered by birds to maintain cohesion with the group or with the partner
- *Agonistic calls*, uttered during fights and in territorial defense
- *Display songs*, complex calls made of sequences of syllables which can be uttered by single birds (*ecstatic display songs*) or by pairs (*mutual display songs*)

Finally, vocalizations interpreted as begging calls (Favaro et al. 2014) have been described for nesting penguin chicks (*begging peep*) and juveniles that had fledged from their nests (*begging moan*).

### Vocal Individuality

Penguins are birds that forage at sea but breed in colonies on land (Williams 1995). Moreover, during the breeding season, penguins form stable pairs where both sex cooperate for several months to rear only one or two chicks (Williams 1995). In large colonies, partners or parents and chicks have to recognize each other when returning from foraging trips at sea, and vocalizations are an essential part of this process (Aubin and Jouventin 2002). The mechanisms used to encode individual identity information in vocalizations vary largely among species and according to their breeding ecology (Aubin and Jouventin 2002). For example, because emperor and king penguins do not build a nest and vocal signals have to propagate through high levels of background noise and obstacles (Aubin et al. 2000), both these species have evolved a very sophisticated vocal recognition system to localize and recognize a parent or a mate in large colonies (Aubin et al. 2000). In particular, because the syrinx of birds is a two-part organ, where independent sounds can be simultaneously produced by different sets of muscles and membranes at the right and left sides (Suthers 1990), non-nesting penguins have evolved the ability to use the beats generated by these two different signals (the two-voice system), together with temporal characteristics of calls (variations in frequency or amplitude with time), to recognize each other. By contrast, the identification of the caller in nesting penguins (e.g., Adélie or Gentoo penguin), which first locate the nest and then use vocalizations as a confirmation of the location cue, mostly occur with relatively simpler mechanisms, such as the pitch of the call and the relative energy content of the harmonics (Jouventin and Aubin 2002). In these latter species, where visual cues assist vocal recognition, penguins have evolved simpler vocal identification systems, mostly based on the frequency analysis of the spectral profile of the call and the temporal pattern of vocalizations (Jouventin and Aubin 2002; Searby et al. 2004).

Recently, the source-filter theory of mammal vocal production (Taylor and Reby 2010 and references therein) has emerged as the dominant theory to explain also the acoustic output of



avian vocalizations. According to this theory, bird calls are generated by vibrations of membranes in the syrinx (source, determining the fundamental frequency, “ $f_0$ ”) and are subsequently filtered by the supra-syringeal vocal tract (filter, resulting in amplified frequencies called “formants”). The most recent literature suggests that the source-filter theory could be used to study vocal individuality in non-nesting penguin calls. In particular, research directed toward the measurement of formant frequencies has shown that individual variation in morphology and size of the vocal apparatus could result in individual acoustic distinctiveness (Favaro et al. 2015, 2016).

### Acoustic Signatures for Species Recognition

In the early 1990s, a study performed by Thumser et al. (1996) attempted to assess taxonomic relationships among captive congeneric *Spheniscus* penguins by analyzing vocalizations uttered during the breeding season. The results showed that these species consistently differ in the acoustical structure of their ecstatic display songs and that African and Magellanic penguins are more similar to each other than the Humboldt penguin. The study also showed that these three species are distinct from the southern rockhopper penguin (*Eudyptes chrysocome*), which was classified as out-group. The relationships found among *Spheniscus* species were consistent with the allozyme phylogenies. Overall, the study by Thumser et al. (1996) was the first to support the hypothesis that penguin vocalizations encode species-specific information, suggesting that the amount of acoustic divergence is proportional to the genetic distance. These findings have been recently confirmed in *Spheniscus* penguins through more detailed acoustic analyses based on the source-filter theory approach (Favaro et al. 2016). However, it is still not clear whether species-specific information encoded in penguin calls can be perceived by heterospecifics. For instance, *Spheniscus* penguins of different species are known to readily hybridize when grouped together in captivity. Moreover, hybrids have been discovered also in wild settings, such as in the Chilean islands of Puñihuil and Metalqui

where *S. magellanicus* and *S. humboldti* overlap their geographical distribution along the coast of the Pacific Ocean.

Recently, the presence of acoustic divergence has been observed also in the little penguins, where the dominant frequency of advertising calls shows a slight shift between the two subspecies (*Eudyptula minor minor* and *E. m. iredalei*), which live in two different regions within New Zealand. In this case, further playback experiments also showed that females recognize and prefer their local male calls (Miyazaki and Nakagawa 2015).

### Hearing Abilities

Hearing in penguins has been investigated by means of evoked cochlear potentials in the African penguin (Wever et al. 1969). Overall, the best auditory sensitivity for this species was identified between 600 and 4000–5000 Hz. Sensitivity beyond 4000 Hz declined approximately 60 dB per octave, and 15,000 Hz was defined as the practical auditory limit. Furthermore, conditioning experiments on the emperor penguin (Jouventin et al. 1979) determined that this species can perceive sounds in a frequency range from 30 to 12,500 Hz, with a temporal resolution of sound perception of 15 ms (i.e., three times more accurate than human abilities). Overall, we can assume that penguins show a hearing sensitivity in air that fits with the values reported for the majority of birds, apart from a slightly higher upper limit compared to the other seabirds.

Penguins can also hear underwater sounds. They are responsive to vocalizations of marine predators, such as killer whale (*Orcinus orca*) calls (Frost et al. 1975), and are particularly sensitive to underwater blasting (Cooper 1983). African penguins also showed avoidance of underwater noises generating by seismic surveys within 100 km of their colony (Pichegru et al. n.d.). However, because hearing sensitivity in diving birds can differ from air to water, detailed measurements about the underwater hearing capabilities of penguins are needed. Results arising from this research would be useful to better understand the potential effects of the anthropogenic

noise on the auditory thresholds and vocal behavior of penguins, which frequently live in populated coastal regions (Thomas and Ksepka 2013), are potentially exposed to disturbance from tourism (Seddon and Ellenberg 2008), and feed at sea in high-traffic naval areas (García Borboroglu and Boersma 2013).

Threats and Conservation

Penguins are among the most threatened seabird families (Trathan et al. 2015), with 60% of the species classified as threatened (five endangered, six vulnerable) and another two as near threatened (Trathan et al. 2015). Most of their populations

**Penguins: Behavioral Ecology and Vocal Communication, Table 1** Penguin species population size, trends, threats and IUCN conservation status. Declining populations and endangered and vulnerable species have

bold red letters. For threats, the boxes are colored to indicate their impacts: red = major, orange = moderate, and yellow = minor

| Species             | Population (PAIRS) | Population Trends              | THREATS:                  |                              |                              | Habitat Degradation          | Introduced predators | Human Disturbance         | Disease                      | IUCN Status |
|---------------------|--------------------|--------------------------------|---------------------------|------------------------------|------------------------------|------------------------------|----------------------|---------------------------|------------------------------|-------------|
|                     |                    |                                | Climate Change            | Fisheries                    | Pollution                    |                              |                      |                           |                              |             |
| King                | 1.6 million        | Stable (Regionally variable)   | Potential                 | Major                        | Minor                        | Minor, increasing            | None                 | Minor                     | Minor                        | LC          |
| Emperor             | 238,000            | Unknown (Decreasing or stable) | Major                     | None                         | Minor                        | Minor                        | None                 | Minor                     | Unknown/None                 | NT          |
| Adélie              | 4-5 million        | Stable (Regionally variable)   | Moderate                  | Minor, potential increase    | Minor                        | Minor                        | None                 | None                      | None, potential              | NT          |
| Chinstrap           | 4 million          | Declining                      | Major                     | Minor, potential increase    | Minor                        | Minor                        | None                 | Minor                     | None, potential              | LC          |
| Gentoo              | 387,000            | Stable/Increasing              | None/Minor                | Minor/Moderate               | Minor                        | Minor                        | Minor                | Minor                     | Minor                        | NT          |
| Yellow-eyed         | 1,700              | Stable/Highly variable         | Minor, potential increase | Minor                        | Minor, potential increase    | Major                        | Major                | Moderate                  | Moderate/Major               | EN          |
| Southern Rockhopper | 1.2 million        | Declining                      | Moderate                  | Minor/Moderate               | Moderate, potential increase | Moderate                     | Minor                | Minor                     | Minor, potential increase    | VU          |
| Northern Rockhopper | 190,000-230,000    | Declining                      | Minor, potential increase | Minor                        | Minor, potential increase    | Moderate                     | Minor                | Minor                     | Minor                        | EN          |
| Erect-crested       | 80,000             | Declining                      | Unknown, potential        | Minor                        | Minor                        | Minor                        | None                 | None                      | None                         | EN          |
| Fiordland           | 2,500-3,000        | Declining/Uncertain            | Minor, potential increase | Minor/Moderate               | Minor, potential increase    | Minor, potential increase    | Major                | Minor                     | Unknown/None                 | VU          |
| Snares              | 26,000-31,000      | Stable                         | Minor, potential increase | Minor, potential increase    | Minor, potential increase    | None                         | None                 | None                      | Unknown/None                 | VU          |
| Macaroni            | 6.3 million        | Declining                      | Moderate                  | Minor, potential increase    | Minor, potential increase    | Minor                        | Moderate/Major       | Minor                     | Moderate, potential increase | VU          |
| Royal               | 500,000            | Declining                      | Moderate                  | Minor, potential increase    | Moderate                     | Minor                        | Moderate/Major       | Minor                     | Minor, potential increase    | VU          |
| African             | 25,000             | Declining                      | Major                     | Major                        | Major                        | Moderate                     | Minor                | Minor                     | Minor, increasing            | EN          |
| Magellanic          | 1.2-1.6 million    | Uncertain (Variable)           | Moderate                  | Moderate, potential increase | Moderate, potential increase | Minor, potential increase    | Minor                | Minor                     | Minor, increasing            | NT          |
| Humboldt            | 15,000-20,000      | Declined/ Slow Recovery        | Moderate                  | Major                        | Minor                        | Moderate, potential increase | Minor                | Minor                     | Minor/unknown                | VU          |
| Galápagos           | 750-2,300          | Declining                      | Major                     | Minor                        | Minor, potential             | Minor                        | Moderate/Major       | Minor, potential increase | Minor, potential increase    | EN          |
| Little blue         | 300,000            | Stable/Declining regionally    | Minor/Variable            | Minor/Unknown                | Moderate, potential          | Moderate, potential increase | Major                | Minor                     | Minor                        | LC          |

have declined since the 1970s, mirroring trends of a wider range of seabird taxa (Palecny et al. 2015). Threats are mainly from anthropogenic origin and shared across most genera (Table 1). Pollution from oil spills (chronic or catastrophic) can strongly affect penguins from temperate areas along tanker routes and alone has the potential to cause the extinction of little and African penguins (García Borboroglu and Boersma 2013). Introduced predators (mustelids, rats, cats) on islands devoid of mammalian predators have caused major damages on some colonies and may still be the most important factor affecting Fiordland penguin population change (García Borboroglu and Boersma 2013). Human disturbance from tourism, coastal development, change in land use, or road accidents can also seriously impact breeding success, increase basal stress levels, and reduce habitat available (e.g., Seddon and Ellenberg 2008). However, the major threats weighing on most penguins are the impact of fishing and climate change. Many penguins are vulnerable to bycatch in trawl or gill nets, in particular the banded penguins. Perhaps even more worrying, however, is the competition with industrial fisheries over the same resources, in particular for penguins targeting predominantly small pelagic fish or krill. Small pelagic fishing is the world largest fishing industry, removing up to 20 million tons of fish annually, mostly from the Benguela and Humboldt Current off the coasts of South Africa and Chile and Peru, respectively (FAO 2016). Krill fishing is also in rapid expansion in response to an increased demand for fish meal by the rapidly developing aquaculture industry (FAO 2016). Impact of resources competition with fisheries can be severe on seabird population (Cury et al. 2011), although clear evidences linking penguin population dynamics to reduced food resources from harvesting are still lacking (Trathan et al. 2015). Finally, climate change reduces breeding habitat and molting sites available for some Antarctic penguins, while heat waves or storms, which frequency is increasing, increase clutch and chick mortality in warmer-water species (García Borboroglu and Boersma 2013). Climate change incurs major ecosystem

shifts worldwide, often with unpredictable consequences on top predators like penguins. Ocean acidification due to increased concentrations of carbon dioxide in the oceans is predicted to reduce availability of calcium carbonate-dependent species, such as krill, on which many population of penguins depend tightly. Marine protected areas are developing across the world, potentially benefiting penguins (Pichegru et al. 2010), and eradication programs are underway on several penguin colonies. But marine pollution such as oil spills, habitat degradation on land, and fisheries impact, either from bycatch of penguins or from competition over the same resources, need to be addressed urgently.

## Cross-References

- [Central Place Foraging](#)
- [Colonial Nesting](#)
- [Communication](#)
- [Contact Calls](#)
- [Ecology](#)
- [Foraging](#)
- [Hatching](#)
- [Parental Investment](#)
- [Passerine Vocal Communication](#)
- [Zoology](#)

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## People for the Ethical Treatment of Animals (PETA)

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## Introduction

People for the Ethical Treatment of Animals (PETA) is the largest animal rights organization in the world, with more than 6.5 million members and supporters. The 501(c)(3) charity works through public education, cruelty investigations, research, animal rescue, legislation, special events, celebrity involvement, and protest campaigns. The group was founded in 1980 by Ingrid Newkirk and a small group of friends.

Headquartered in Norfolk, Virginia, with a West Coast office in Los Angeles, the organization has international affiliates in the United Kingdom, France, the Netherlands, Germany, India, Australia, and the Asia-Pacific region.

PETA focuses its attention on the four areas in which the largest numbers of animals suffer the most intensely for the longest periods of time: the food industry, the clothing trade, laboratories, and the entertainment industry. Its motto: “Animals are not ours to eat, wear, experiment on, use for entertainment, or abuse in any other way.”

In addition to these core issues, PETA campaigns against the cruelty of fishing, the killing of animals regarded as pests, and the keeping of chained backyard dogs, among many other issues.

PETA's Community Animal Project helps cats and dogs near its headquarters, in poorer areas of Virginia and North Carolina. In 2016, more than 15,000 dogs and cats were sterilized – including more than 1300 pit bulls – at low cost or for free.

More than 1000 dogs and cats were transported to and from the clinics, free of charge, for people with no transportation.

PETA's fleet of mobile clinics assists thousands of indigent families by providing free medical services, including repairing prolapsed organs, performing lifesaving surgeries on dogs suffering from dangerous uterine infections, removing tumors and ruptured growths, performing drainage surgery for hematomas and infected wounds, and treating ear, skin, and upper respiratory infections.

PETA also shelters neglected dogs and cats who are ill or injured and pursues justice in cruelty cases.

In 2016, PETA delivered more than 312 sturdy doghouses and more than 1900 bales of straw bedding to neglected "backyard dogs." The organization's program has given away nearly 6500 doghouses since its inception.

## The 1980s

PETA first caught the public's attention in the summer of 1981 during what became known as the "Silver Spring monkeys case," a widely publicized dispute about experiments conducted on 17 macaque monkeys inside the Institute for Behavioral Research in Silver Spring, Maryland. The case lasted 10 years and involved the only police raid on an animal laboratory in the United States. PETA's investigation resulted in the first conviction of an experimenter for animal abuse and the first withdrawal of federal research funds because of cruelty to animals. It was also the first animal-experimentation case ever heard by the US Supreme Court, which gave a unanimous, positive ruling.

PETA's demonstrations led to the closure of Arrow Live Poultry, the last remaining slaughterhouse in Washington, D.C.

PETA distributed an undercover video showing Las Vegas casino "entertainer" Bobby Berosini repeatedly punching, shaking, striking, and slapping the forcibly restrained orangutans he used in his casino act. He subsequently brought suit against PETA, claiming that it had defamed

him and invaded his privacy. In 1995, the Supreme Court of Nevada ruled that Berosini's lawsuit was without merit and ordered him to pay PETA's court costs. The US Department of the Interior revoked his captive-bred wildlife permit, making it illegal for him to buy or sell orangutans, and his animals were sent to sanctuaries.

PETA stopped a plan by Cedars-Sinai, California's largest hospital, to ship stray dogs from Mexico for experiments.

## The 1990s

PETA's "Rather Go Naked Than Wear Fur" campaign was launched on the streets of Tokyo outside a Japanese fur expo in 1992. The protest made headlines around the world and led to PETA's extensive and iconic naked celebrity ad series.

PETA's efforts led to the first-ever cruelty charges filed against a factory farmer for allowing tens of thousands of chickens to starve to death. The president of the company ultimately pleaded guilty.

PETA succeeded in getting Taiwan to pass its first-ever law against cruelty to animals, which prevented countless dogs from being beaten, starved, electrocuted, and drowned in the country's pounds.

PETA's undercover investigations into pig-breeding factory farms in North Carolina and Oklahoma revealed horrific conditions and abuse, including skinning a pig alive, leading to the first-ever felony indictments of farm workers. Three were convicted.

## 2000–2010

After a PETA campaign including more than 400 demonstrations at restaurants in more than 23 countries, as well as advertising and celebrity involvement, McDonald's became the first fast-food company to agree to make basic animal-welfare improvements for farmed animals.

Evidence submitted by PETA led to the mandatory relinquishment of all 16 elephants used by



the Hawthorn Corporation, an elephant-rental company.

PETA's investigation into Aviagen Turkeys, Inc., part of the self-proclaimed "world's leading poultry breeding company," revealed that workers tortured, mutilated, and maliciously killed turkeys. Three former employees were indicted on felony cruelty-to-animals charges – the first felony charges for abusing factory-farmed poultry in US history – and two became the first factory farmers to be convicted of abusing turkeys. One man was sentenced to a year in jail – the strongest penalty levied for abusing a factory-farmed animal in US history – and all three were barred from owning or living with animals for 5 years.

PETA's investigation into animal dealer US Global Exotics prompted the largest animal seizure in history – more than 26,000 animals. The owner fled the country to evade federal charges.

After intense PETA campaigning against horrific combat training exercises conducted by the Bolivian military – a video of which showed live dogs tied down, repeatedly stabbed, and screaming in agony – the country's Ministry of Defense ended the killing by issuing the military's first-ever animal-protection regulation, which "prohibit[s] all acts of violence, exploitation, [and] mistreatment that provokes the death of animals."

The European Chemicals Agency spared up to 4.5 million animals the agony of being used for toxicity testing in a massive EU program after receiving documentation provided by PETA scientists.

Just 1 week after PETA released the results of its shocking eyewitness investigation into Professional Laboratory and Research Services and filed a complaint with the US Department of Agriculture (USDA), the North Carolina-based contract animal-testing facility surrendered nearly 200 dogs and more than 50 cats and closed its doors. This was only the second time in US history that a laboratory was forced to surrender its animals and shut down.

Less than 6 months after PETA released its eyewitness investigation into laboratories at the University of Utah, legislators voted overwhelmingly to amend an archaic state law so that government-run animal shelters would no longer

be forced to sell dogs and cats to laboratories on demand.

In India, the PETA-supported charity Animal Rahat was founded. Its unique mission helps some of the most neglected animals in the world – bullocks, donkeys, and other working animals in India. This lifesaving program now offers services throughout three districts in Maharashtra, one of the largest states in India. Animal Rahat is run by a dedicated staff that includes veterinarians, veterinary assistants, animal caretakers, and a full-time community educator. All Animal Rahat veterinarians are on call for emergencies and advice around the clock, every day of the year.

## 2011–Present

The USDA fined Ringling Bros. and Barnum & Bailey Circus \$270,000 – the largest fine ever paid by an animal exhibitor – for violations of the Animal Welfare Act after PETA presented unequivocal evidence of animal abuse, including beatings, the negligent death of a lion, lame elephants forced to perform despite chronic pain, and a baby elephant who died during a training routine.

PETA blew the lid off Ringling Bros.' animal abuse when a whistleblower shared photographic evidence from the circus's training compound revealing that baby elephants are torn away from their mothers and subjected to violent training sessions so that they will learn how to perform tricks.

Citing a "dramatic drop" in ticket sales, in May 2017, Ringling Bros. and Barnum & Bailey Circus shut down after 146 years.

In the first case of its kind, PETA, three marine-mammal experts, and two former orca trainers filed a lawsuit asking a federal court to declare that five wild-caught orcas forced to perform at SeaWorld were being held as slaves in violation of the 13th Amendment to the US Constitution. The filing – the first ever seeking to apply the amendment to nonhuman animals – named the five orcas as plaintiffs and sought their release into their natural habitats or seaside sanctuaries.

After intensive campaigning by PETA, the US military ended the use of monkeys in the Army's cruel chemical-attack training course.

The US Coast Guard became the first branch of the military to suspend the shooting, stabbing, and killing of animals in trauma training drills. Calling these methods "abhorrent," the military service's commandant said that it would switch to non-animal training methods such as human patient simulators. It confirmed that the shift had come after an official review of its "live tissue training" prompted by a PETA exposé. In 2012, PETA had released disturbing video footage from a secret trauma training course for the service's personnel that showed instructors cutting the legs off semi-conscious goats with tree trimmers, stabbing them with scalpels, and pulling out their internal organs as they moaned and kicked.

The top ten advertising agencies in the United States – McCann Erickson, BBDO, Y&R, DDB, Ogilvy & Mather, TBWA, Draftfcb, Grey, JWT, and Campbell Ewald – all signed PETA's Great Ape Humane Pledge, banning the use of great apes in their advertising.

After PETA donated simulators to Egypt, it ended all use of animals for medical trauma training.

After 2 years of PETA campaigns and a lengthy lawsuit brought by PETA and local residents, the Supreme Court of Puerto Rico nixed a plan by the Bioculture Corporation to set up a primate-breeding facility there and sell monkeys to US laboratories.

Following PETA's investigations and campaign, a sweeping set of reforms – including limitations on whipping, increased drug testing, and mandatory on-site horse ambulances – was introduced and accepted by many horse-racing tracks.

After decades of conducting cruel experiments and just 6 months after PETA purchased stock in the company in order to introduce a shareholder resolution on animal testing, BIOQUAL announced that it would end its use of chimpanzees. Formerly known as SEMA, the facility was first exposed in 1986, when PETA released footage of chimpanzees locked inside tiny isolation chambers there.

After a 2-month PETA eyewitness investigation documented that thousands of animals were being neglected and dying and many more were being cruelly killed, law-enforcement officials raided Global Captive Breeders, a company in Lake Elsinore, California, that bred and sold reptiles and rats for the "pet" trade. This resulted in the largest rescue of neglected rats in US history and the largest seizure of animals, including more than 600 reptiles and 18,000 rats, ever in California. Local authorities charged the owner and manager with a total of 223 felony cruelty-to-animals and related charges.

PETA prevailed in a lawsuit against the US Fish and Wildlife Service for illegally issuing captive-bred wildlife permits, allowing it to keep a closer eye on animals bred in captivity, weigh in on permit applications, and bring legal challenges against permits that are improperly issued to animal-abusing facilities such as SeaWorld, Have Trunk Will Travel, and others.

Following decades of campaigning by PETA, the US Army announced that it would reduce its use of animals in deadly trauma training exercises and restrict training for many military personnel to exclusively nonanimal methods.

After hearing from PETA that many sheep used for their wool endure a painful procedure called "mulesing," in which large chunks of skin and flesh are cut from their backsides without any painkillers, more than 50 national and international clothing retailers, including Abercrombie & Fitch, Liz Claiborne, H&M, Kenneth Cole, Perry Ellis International, and Express, stated that they would use wool that comes only from non-mulesed sheep, as the industry begins to phase out the cruel practice.

PETA's exposé of Taiwan's pigeon-racing industry resulted in a national sweep of pigeon-racing clubs. Police confiscated cash and equipment and froze over \$4.5 million of apparent illegal gambling proceeds in two clubs' bank accounts.

The first-ever eyewitness investigation into the angora wool industry showed workers tying down screaming rabbits and ripping their fur out, leading to a ban on the sale of angora by more than

70 companies around the world including H&M, Calvin Klein, and Tommy Hilfiger.

The scientific and regulatory expertise of PETA and its affiliates was consolidated to form the PETA International Science Consortium Ltd., which, having been accepted as an accredited stakeholder in the agency that oversees the largest chemical-testing program in the world, works with industries, private research facilities, and governments to promote nonanimal tests worldwide.

*I, Chicken*, the first-ever empathy-building virtual reality experience – which allows people to view life from the perspective of a chicken being sent to slaughter – traveled to more than 150 universities across the United States, including Harvard, Stanford, Brown, Dartmouth, the University of Pennsylvania, and Princeton.

After intensive efforts led by PETA India and with scientific support from PETA USA and the PETA International Science Consortium Ltd., India officially banned the importation of animal-tested cosmetics. PETA India rallied support from scientists, ethical companies, celebrities, and leading government officials.

PETA launched a tour of its *I, Orca* empathy project, which uses wireless Google virtual reality goggles to immerse participants in a world in which they are free to swim in the ocean with their orca families. Users also meet an orca mother (voiced by *Nurse Jackie* star Edie Falco) who still mourns the baby who was taken from her decades ago and sent to SeaWorld, where he has been sentenced to a miserable life in captivity. PETA took *I, Orca* on tour to cities near all three SeaWorld parks.

Following a PETA exposé, the National Institutes of Health ended more than 50 years of infant-monkey maternal-separation studies.

PETA secured the first conviction for the production and distribution of disturbing “crush videos” after supplying evidence to law-enforcement officials in Houston and encouraging federal authorities to press charges against Ashley Nicole Richards for violating the Federal Animal Crush Video Prohibition Act of 2010.

PETA filed a groundbreaking lawsuit asking a US federal court to declare Naruto – a free-living crested macaque – the author and owner of the internationally famous “monkey selfie” photograph that he took using a photographer’s unattended camera. The aim is to get the court to declare a nonhuman animal an owner of property (the copyright of the photograph), rather than a piece of property.

After years of intense PETA-led campaigns, SeaWorld announced an end to its orca-breeding program, which means that the current generation of orcas imprisoned in SeaWorld’s tanks will be the last.

Following a PETA campaign that saw the end of year-long pesticide poisoning tests on dogs in 2007 in the United States and in 2013 in the European Union, PETA scientists succeeded in persuading the Canadian government to end this testing, thus preventing hundreds of dogs from being forced to eat pesticide-laced food or inhale pesticide fumes every day for a year before being killed and dissected. This occurred during the same year that PETA scientists’ work with the Environmental Protection Agency (EPA) and industry resulted in an EPA announcement that it intended to reduce and – ultimately – eliminate the use of animals in lethal pesticide toxicity testing.

In a landmark case following the release of a PETA exposé, at least 6 sheep shearers were charged with a minimum of 70 counts of cruelty to animals for the first time in history. The exposé documented that wool industry workers in Australia beat sheep in the face with electric clippers and punched and stomped on their heads and necks. The first five defendants pleaded guilty, and the sixth was found guilty.

## Cross-References

- [Animal Welfare](#)
- [Captivity](#)
- [Ethics](#)

- ▶ [Farrowing Crate](#)
- ▶ [Feather-Plucking](#)
- ▶ [Gestation Stall](#)
- ▶ [Greyhound Racing](#)
- ▶ [Group Living](#)
- ▶ [Harry Harlow](#)
- ▶ [Human-Animal Interaction](#)
- ▶ [Husbandry](#)
- ▶ [IACUC](#)
- ▶ [Pets](#)
- ▶ [Primates](#)
- ▶ [Species-Specific Behavior](#)
- ▶ [Zoo](#)

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## Perceiver

- ▶ [Receiver](#)

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## Perception

- ▶ [Cognition](#)
- ▶ [Equine Sensory Systems](#)
- ▶ [Gestalt](#)
- ▶ [Rodentia Sensory Systems](#)
- ▶ [Sirenia Sensory Systems](#)
- ▶ [Top-Down Processing](#)

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## Perception for Action

- ▶ [Depth Perception](#)

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## Perception-Action Loop

- ▶ [Perception-Action Theory](#)

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## Perception-Action Theory

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## Synonyms

[Affordances](#); [Animal-environment mutuality](#); [Continuous perception-action cycle](#); [Direct perception](#); [Gibsonian approach in ecological psychology](#); [Human motor control](#); [Information-based approach](#); [Perception-action loop](#); [Reflex arc](#); [Relationship between animal and environment](#); [Relationship between perception and action](#); [Sensation and movement](#); [Sensory-motor control](#)

Perception-action theory endeavors to understand and describe the relationship between animal and its environment. The essential question is: How does an animal perceive and interact with the environment it lives in? Right after being born, an animal starts constantly exploring and interacting with its environment via actions, and these behavioral interactions continue until its death. For instance, a human baby looks around his/her environment with deep curiosity and tries to reach and touch the objects that surround him/her to discover and learn about them and turns his/her head to the direction where sounds come from to understand what makes the sound. Likewise, a giraffe reaches to the leaves on the top of a tree to eat; a deer runs away from its predator to survive; you move your eyeballs (even maybe your head) to read this entry on the computer screen or paper that you are holding and slide the screen or turn the page when you reach the end of the screen or page. Actions are an intrinsic part of every animal's daily life. For example, while reading this entry, you may want to enjoy your coffee by taking a sip from it. In order to do this, you need to reach out and take grasp your coffee cup sitting on the table in front

of you. To be able to plan and perform this reaching out action, your brain has to know exact distance and direction of the coffee cup with respect to your position. As if this were not complex enough as it is, your brain also must plan how to grasp the coffee cup. Regarding the grasping plan, for example, your brain must know how the handle of the coffee cup is oriented in order to position your hand appropriately. This simplified example of reaching out to and grabbing a coffee cup to take a sip from your coffee illustrates perceptual requirements of planning and carrying out any task (action). Interestingly, however, not only it is the case that action depends on perception, but it is also true that perception depends on action. Turning back to the coffee cup example, you will need to move your eyes or move your head, or perhaps you may even need to lean in a specific direction to be able to gather the requisite perceptual information in order to assess the location, orientation, and dimensions of the coffee cup. In the words of James Gibson (1979), whose studies and approach give rise to insights of perception-action theory:

Locomotion is guided by visual perception. Not only does it depend on perception but perception depends on locomotion inasmuch as a moving point of observation is necessary for any adequate acquaintance with the environment. So we must perceive in order to move, but we must also move in order to perceive. (Gibson 1979, p. 223)

Perception-action theory came fore with Gibson's information-based approach. Traditional theories of perception treated perception as wholly a matter of sensation and the sensory organs of organisms. Gibson, however, was among the first to recognize that this sensation-based approach fell short of explaining and predicting animal perception and behavior. He asserted that perception is not sensation but information based (Gibson 1979).

The traditional sensation-based approach is rooted in the representational realism of Locke (Lombardo 1987) and Plato (Dotov et al. 2012). According to the sensation-based approach, perception is caused by stimulation on the sense organs and not necessarily requires any action prior to the perception. The registered sensory-

stimulation is processed by the central nervous system in order to simulate a three-dimensional model of the environment, and what we perceive is based on such simulations combined with past memories of our experiences through higher cognitive processes (Gibson 1950, 1966, 1979). For example, if you hear a noise from outside while reading these words, you most likely turn your head and look outside through window. Let's suppose you see a cat in a tree. The cat is only partly projected in your eyes because the branches and leaves of the tree and the frame of the window occlude the rest of the cat. Then, how do you perceive the cat as a cat? The sensation-based approach answers to such question as follows: right after this image is projected onto your retina, in which the cat is partly discernible, thus stimulating your optic nerve, your brain creates a mental image based on the visible parts of the cat and fills out the missing parts by retrieving something like the whole cat image from your past memories of the experiences. As a result, what you perceive is the representation of the cat, which is created in your mind, but not the cat itself. In this sense, we perceive not directly the real world but its representation constructed in our mind; perception is indirect that requires mediation of third parts. However Gibson rejects this sensation-based approach of indirect perception. As in his example, "... [Direct] perception is what one gets from seeing Niagara Falls, say, as distinguished from seeing a picture of it. The latter kind of perception is mediated. So when I assert that perception of the environment is direct, [ mean that it is not mediated by retinal pictures, neural pictures. or mental pictures. Direct perception is the activity of getting information from the ambient array of light" (Gibson 1979, p. 147).

According to the information-based approach, perception does not require any mediation of any constructed representation such as neural image, mental image, nor additional process such as past memories. Instead, perception is itself the activities of perceptual systems. Gibson differentiates the perceptual system from senses; the former one is active, whereas the latter is passive (Gibson 1979). The term perceptual system refers more than just sensation. Vision, for instance, involves



an active system that is not simply dependent on the sensation of a passive sense organ (retinal image). As Gibson indicated, “.. natural vision depends on the eyes in the head on a body supported by the ground...” (Gibson 1979, p. 1). Perception is the product of the actions on the part of the perceptual systems which require that information be gathered directly from the environment by means of looking, listening, touching, testing, and smelling. An animal can continuously act, gathering information throughout its life without reaching any limit and without storing it all in memory (Gibson 1979). Returning to the cat example, Gibson argues that there is no sensation of the occluded parts and perceiving it does not require the past memories attached to the present sense data. The information, which is defining the objects, textures, layouts, and surfaces in the environment and thus the occlusion, is picked up by vision, which is not sense organ but a perceptual system. In the Gibsonian nomenclature, the rich and continuous information source for vision is termed optic array. The structured light (also known as ambient light) reflecting from the environment and reaching the observer’s eyes constitute the optic array. The visual information can be derived from the optic array with respect to point of observation. When the point of observation changes, the visual information which is projecting on the eye also changes as an adjacent order over the time while moving. Yet, some invariants persist in the adjacent order of changing visual information. Such persistent invariants project the information about the continuing surfaces and layouts in the environment. On the other hand, changing the point of observation results in disturbance of the persisting invariants which is projecting the occluded surfaces and layouts; at the edge of any object, surfaces, and layouts that is occluding the background, either accretion of the occluded surface to or deletion of the occluded surface from the visual information occurs over the time in the optic array. Such accretion and deletion indicates the occluded surfaces. In the cat example, when you (the observer) change your perspective (point of observation) by moving or leaning, accretion and deletion series related to cat’s occluded

surface occurs over the time at the edges of the branches and leaves of the tree and the frame of the window; such deletion and accretion series specify the occluded surface of the cat. The optic array is not similar to but specific to the environment. Thus, in the sense of the information-based approach, perception is direct and requires action (Gibson 1979).

Since perception has been regarded as being a relationship between animal and its environment, exploring the “objects of perception” has been essential part of the research relating to perception and action. Then, what are the objects of perception? What is that you perceive when you look at a chair? What are you aware of when you perceive the chair? What is the function of the perception? In the literature perception is considered as it serves two functions: to aid in recognition and to serve as an action-guide. Gibson, however, emphasized that primary function of the perception is “action-guide,” and he introduced the concept of “affordance” to refer to the “objects of perception.” He asserted that looking up nouns and adjectives to express the qualities such as shape or color of the objects (environment) is not the right way to answer the “objects of perception” question (as did Locke 1700):

The psychologists assume that objects are composed of their qualities. But I now suggest that what we perceive when we look at objects are their affordances, not their qualities. . . The differences between [affordances] are not clear-cut, and the arbitrary names by which they are called do not count for perception. If you know what can be done with a graspable detached object, what it can be used for, you can call it whatever you please. . . You do not have to classify and label things in order to perceive what they afford. (Gibson 1979, p. 134.

Gibson coined the notion of “affordances” as the opportunities for the actions, shaped by the layouts and surfaces in the environment, offered to animal. As stated in Gibson’s definition, affordances are action-relevant properties of the environment specified by information that is directly perceptible by an animal. So, for instance, the shape of a standard-size chair affords sitting for an adult human. Although the use of affordances in the planning and performing of

actions requires animal to perceive them, their existence does not depend upon animal's perception – a chair's capability to support an adult human sitting exist whether or not there is someone there to utilize it. Still, affordances are determined in relation to animals' capabilities – the chair has such capacity with respect to an adult human, but not with respect to a child or an elephant (Gibson 1977, 1979/1986).

As pointed out above, existence of affordances is all about how the physical environment is shaped in terms of action possibilities, whereas perceiving affordances is about whether a specific animal is able to actualize relevant actions to those affordances. The environmental property must be relational to an animal's relevant body part in order to actualize affordances, and an animal's perception of the affordance entails such relation (Gibson 1979; Warren 1984). Considering those characteristics of affordances, Gibson emphasized that standard units and scales used in physics are not appropriate to measure the affordances (Gibson 1979). For example, imagine you come upon a hole, which is 60 inches in width and 90 inches in depth on your path while walking on the street. You do not perceive it as 60-inch width and 90-inch depth hole. Instead, you perceive it as wider than your maximum step length or not and deeper than your knee height or not. By perceiving the hole with reference to your own body scales, you simply avoid mathematical calculations in the decision of whether you could jump over or you should walk around it. The information in such a form also serves better in adjusting your step length while jumping over the hole if you decide to do so. Perception of affordances in relation to own body scales requires animal to be aware of his/her own body scales. Animals gain such awareness through proprioception, which is mainly feeded by acquired information from the exploratory actions (Gibson 1979; Warren 1984). You learn about the length of your stride or the size of your foot through proprioceptive information you obtained while walking, jumping, or stretching your legs (Warren 1984). Perception of the environment always involves perception of self, moving in the environment.

When Gibson was talking about the affordances, he had already been admitted a mutual relationship between animal and its environment. An animal is an actor at some degree while perceiving its environment and is a perceiver at some degree while acting in the environment it lives (Gibson 1979). There is no doubt that nobody can think the existence of an animal without an environment it perceives and acts in. Some people, however, may consider that it is true the other way around. Removing the animal from the environment will not change the environment at all; it is still an environment without any single animal that perceives it and acts in it; as an example of their claim, they may state that the environment had already been there millions of years before the first animal (a living creature) developed in it. In response, Gibson stated that it should not be considered as "environment" until the first animal is presented in it; that was just a physical earth, the subject matter of geology but not psychology (Gibson 1979). In psychological approach, especially in the studies of perception and action, the term, "environment," refers to surfaces and layouts and objects that are surrounding an animal who interactively perceive and act in. What the "environment" meant in psychology should not be confused with the physical earth in physics or geology. The physical earth gets the attention in the atomic and cosmic aspects in which it is not available to animal's perception (Gibson 1979). An animal does not perceive the water as two hydrogens and one oxygen; instead it perceives as something to drink, to swim in, and to get drowned in. Therefore, the environment, at least in the sense of psychology, does not exist unless an animal actively lives in it, just like an animal which does not exist without the environment surrounding it. An animal and its environment cannot be isolated from each other; together, they constitute an inseparable animal-environment system.

From Gibson's perspective, the environment is beyond being just a physical earth. It has meanings and values as long as an animal perceives it and acts in it. As being action-relevant properties, which are available into animal perception, affordances carry meanings and values in the

environment. In other words, affordances are functional, and their functions decide the “meanings” and “values.” Gibson (1979) stated, “the perceiving of an affordance is not a process of perceiving a value-free physical object to which meaning is somehow added in a way that no one has been able to agree upon; it is a process of perceiving a value-rich ecological object” (p. 140). A chair, for instance, is functional as it offers sitting, so its meaning or value for us is its being sittable. We do not perceive the chair *per se* but rather its “sittability.” Being aware of the chair’s sittability, in return, guides our sitting behavior. Similarly, the hole, which is 60 inches in width and 90 inches in depth on our path, meant to be an obstacle for us that requires avoiding. So, the hole guides our avoiding behavior, whether we have to walk around it or we can jump over it.

Gibsonian approach implies that, the concept of affordances inherently emphasizes a reciprocal relationship between perception and action. What an animal perceives in the environment is action possibilities, thus affordances. Actualizing affordances requires perception, which guides actions; and the perceptual information that specifies affordances and guides actions is generated by exploratory actions. Hence, perception and action are reciprocally related to each other; cutting off either one will stamp the other one out. They, together, form a continuous perception-action loop. A continuous perception-action loop refers to a close cycle that reflects how an animal action changes its perceptual input on a millisecond timescale. Thus, depending on that, the action planning, required adjustment in action performing, and resulted perceptual information are all updated continuously in time (Neisser 1976). Thinking of a baseball player, how his/her gaze focuses on a flying ball, and how he/she modifies his/her body orientation and position to be able to catch the flying ball may set a good example in order to understand the continuous perception-action loop. Threading a needle might be another example to understand the continuous perception-action loop as it requires intense eye-hand coordination.

The conception of the continuous perception-action loop is developed and evolved from Dewey’s (1896) remarkable critique of the reflex arc concept. Gibsonian approach in perception fulfills the theoretical background when the reflex arc turns into a continuous perception-action loop. The reflex arc is a linear causal linkage between stimuli and motor response, which has its intellectual roots in the sensation-based approach of perception. Dewey states that “[it] is a survival of the metaphysical dualism, first formulated by Plato” (Dewey 1896, p. 365). The reflex arc concept treats the sensory stimulus and motor response as “separate and complete entities in themselves”; one consecutively follows another, but there is no continuity in the reflex arc concept. Dewey argues that “sensory stimulus and motor response shall be viewed, as divisions of labor, functioning factors, within the single concrete whole...in reality they [sensory stimulus and motor response] are always inside a coordination and have their significance purely from the part played in maintaining or reconstituting the coordination” (Dewey 1896, p. 358, p. 360). Thus, the reflex arc idea is deficient in expressing the unity of the activity whereby breaking the integrity and continuity (Dewey 1896). Dewey used a reaching example for his argument: the exact beginning of a reaching action, according to their analysis, is not a sensory stimulus of light, but it is movement of the eye, head, and body muscles, which is a sensory-motor coordination, looking or in other words an act of seeing. Both the sensation and the movement fall within the same act although the sensation is a function of value of the act, whereas the movement is a function of mechanism and control. Then, the act of seeing reciprocally is bound together with the act of reaching within a larger coordination. The act of reaching requires the guide of seeing and, in turn, stimulates the act of seeing for its continuity. What we are having here, according to Dewey (1896), is not a reflex arc, but an organic circuit. Here, the term “organic” is preferred rather than “reflex” because the subordinate members, sensation and movement, of the coordination reinforce and help out

each other to determine each other either directly or indirectly. Sensation and movement cannot be reduced to stimuli and response which are designated as cause and reflex. All in all, rather than a reflex arc, what Dewey's critique suggests is more akin to a continuous cycle, or even a Möbius band (according to Turvey 2004). Besides that, the definition of perception-action loop in Dewey's critique is not predicative, but impredicative (see Turvey's impredicative definition (Turvey 2004, p. 7)). Turvey, together with Shaw, agrees upon Dewey's argument (Shaw and Turvey 1980). Furthermore, Turvey called attention to use of the term "continuous" for the notion of perception-action cycle: "continual seems to be the appropriate adjective for the notion of a perception-action cycle. A *continual* process is one that goes on repeatedly. Applied to perception and action, *continual* means that perception is intermittent and action is intermittent with moments of non-perception and non-action. In contrast, *continuous* means unending and without interruption (Wilson 1993). It seems more appropriate for the perception-action Möbius band" (Turvey 2004, p. 12).

## Conclusion

Animal, which takes place in the core of all studies in psychology, is always present in an environment as an indispensable part of it. A corollary of such animal-environment mutuality is a continuous interaction of animal with its environment. Perception and action is the way of such continuous interaction and communication between animal and its environment. Keeping that in mind, developing a perception-action theory is critical for understanding the complex behaviors of animals in the environment and their functions. It also helps learning and developing animals' capabilities regarding the environment and the beneficial functionalities in the environment. A well-structured perception-action theory is also strong interest of the studies in robotic technology, bionic prosthesis, and artificial intelligence.

As being one of the fundamental and intriguing topics of psychology, the notion of the perception-action is addressed widely but in various ways by different approaches (i.e., embodied view, functional view, ecological view) of psychology. Some approaches consider the action as distinct entity but caused by perception, whereas others claim that perception and action are inseparable and influence each other reciprocally. Even though there is no universal agreement on a single description for a perception-action theory, all approaches agree on that action plays as a critical role as perception and perception and action unify in one way or other. The reason for this could be that the perception-action research has not been developed as a cumulative science in history, as Neumann and Prinz (1990) pointed out. None of the approaches has systematically built its perception-action research upon an earlier one because of the diversity in their goals and methodologies (Fajen 2009; Neumann and Prinz 1990).

In this entry, the perception-action theory is written in the sense of ecological approach as it is in the most favorable light among all approaches.

## Cross-References

- ▶ [Auditory Processing and Perception](#)
- ▶ [Depth Perception](#)
- ▶ [Dynamic Systems Theory](#)
- ▶ [Goal-Directed Behavior](#)
- ▶ [Locomotion](#)
- ▶ [Olfactory Perception](#)
- ▶ [Perception](#)
- ▶ [Social Affordance](#)
- ▶ [Tactile Perception](#)
- ▶ [Visual Perception](#)

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## Perceptual Completion

### ► Amodal Completion

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## Perceptual Decision

### ► Sensory Judgment

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## Perceptual Figures

### ► Gestalt

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## Perceptual Learning

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## Definition

Improvement in the ability to differentiate between similar stimuli following the repeated presentations of such stimuli without reinforcement or feedback.

## Introduction

Human and nonhuman animals learn about stimuli by simply being exposed to them, with the perception of such stimuli changing as a consequence of repeated experience. This type of unsupervised learning is called perceptual learning (PL), and it requires neither reinforcement nor feedback. While PL has been studied within a number of areas in psychology, human PL has, until only relatively recently, been addressed primarily by studies on perception (e.g., Epstein 1967; Fahle et al. 2002; Goldstone 1998). In contrast, in nonhuman animals, this effect has mainly been studied within the field of associative learning (for a review, see, for instance, Hall 2001; Mitchell and Hall 2014). Within this framework, PL is usually defined as an improvement in the ability to differentiate between similar stimuli, an outcome that can be behaviorally assessed in several ways. For nonhuman animals, PL is inferred from the facilitation of performance on a subsequent discrimination task in which one stimulus (e.g., AX) is reinforced and another similar stimulus is not (e.g., BX, where A and B represent the distinctive elements of the stimulus and



X those features shared in common). PL can also be evaluated by a generalization test following pre-exposure to the stimuli and the subsequent conditioning of one of these stimuli. In this case, a PL effect is confirmed if generalization between similar stimuli is reduced after pre-exposure relative to a control condition that received no pre-exposure to the stimuli. In humans, the ability of people to differentiate between similar stimuli after pre-exposure is inferred from the accuracy with which they are able to judge them as same or different or the extent to which they assign similar stimuli to different artificial categories.

PL began as a challenge for the standard associative theory of learning, which traditionally assumed that reinforcement is necessary in order for learning to occur (Spence 1936). One of the earliest theoretical approaches to PL was provided by William James (1890). According to James, discrimination between stimuli improves because, during pre-exposure, associations are formed with other stimuli from the environment. Due to the variability of the stimuli present in a certain situation, each stimulus is associated with different stimuli by chance, with the mental representations of such stimuli becoming increasingly distinct by virtue of their associates. According to this initial account, perception becomes less and less accurate with regard to the sources of stimulation provided by the environment. A subsequent attentional account outlined by Eleanor J. Gibson (1969) adopts exactly the opposite position. According to this theory, during pre-exposure the stimuli are differentiated by the operation of an attentional shift by which attention is selectively and increasingly directed toward the distinctive features of the stimuli (i.e., those that might not be initially perceived, for instance, A and B in our example) at the expense of the common elements. Such common elements are irrelevant for stimulus differentiation, and thus, according to Gibson, the operation of this attentional shift leads to a greater correspondence between perception and the sources of stimulation “because what is learned is not the addition of something but the extraction of something” (Gibson and Levin 1975, p. 23). Moreover, she provided the first experimental reports of both

human and nonhuman PL. In the case of human PL, Gibson and Gibson (1955) presented a target nonsense scribble to children of different ages. Children were then presented a series of similar scribbles and then asked which of these scribbles were exactly the same as the target. They found an improvement in the specificity of the “same” responses with the repetition of the series, an effect that was stronger in older children. According to Gibson and Gibson (1955), the improvement in the ability to differentiate the target from the other scribbles constitutes a PL effect. In the case of nonhuman PL, Gibson and Walk (1956) presented rat pups’ two relatively complex shapes – a circle and a triangle – on the wall of their home cages. The animals and others without experience with the shapes were trained on a discrimination learning task, and it was observed that learning proceeded faster in the former group in comparison to the latter. Unfortunately, Gibson did not offer further details in regard to the operation of the vague attentional shift proposed in her theoretical account. She did, however, specify the pre-exposure conditions under which the attentional shift might occur, that is, the conditions that would be expected to promote stimulus comparison. This hypothesis guided the focus of further research about PL toward the effects of pre-exposure schedules – those that more or less favor stimulus comparison – and, consequently, the more recent associative and nonassociative theoretical models of PL have largely emerged in order to explain such effects.

### Pre-exposure Schedule Effects

The effects of the pre-exposure schedule have been experimentally studied using several procedures and a variety of species (for a review, see Hall 2001; Mitchell and Hall 2014). Currently, most of the evidence in nonhuman animal PL comes from conditioned taste aversion preparations with rats (e.g., Honey et al. 1994; Honey and Hall 1989; Mackintosh et al. 1991; Symonds and Hall 1995). In these preparations, similar stimuli – e.g., similar compounds of flavors, AX and BX – are pre-exposed. One of these

stimuli – e.g., AX – is then paired with toxicosis, and the extent to which the conditioned aversion acquired by AX generalizes to the other stimulus – e.g., BX – is then tested. With human participants, most of the tasks used to assess stimulus differentiation involve same/different judgments of stimuli that are sequentially presented after being pre-exposed or categorization tasks where participants are required to assign similar stimuli to different categories (e.g., Carvalho and Albuquerque 2012; De Zilva and Mitchell 2012; Lavis and Mitchell 2006; Wang et al. 2012; but see also Angulo and Alonso 2012). The so-called *intermixed-blocked effect* has been found in the vast majority of cases using these experimental procedures in both human and nonhuman animals. This effect refers to the greater PL effect observed following intermixed exposure (e.g., AX, BX, AX, BX) in comparison with blocked (e.g., AX, AX, BX, BX) pre-exposures to similar stimuli. Because the intermixed schedule offers better opportunities to compare between stimuli than the blocked schedule, this finding is entirely compatible with the Gibsonian account of PL. However, other more recent accounts could also explain this phenomenon.

McLaren et al. (1989; see also McLaren and Mackintosh 2000), for instance, proposed three associative mechanisms to explain the intermixed-blocked effect as well as the general pre-exposure effect. According to this account, during pre-exposure to similar stimuli (e.g., AX and BX), both the distinctive and common elements undergo latent inhibition (LI). Latent inhibition (e.g., Lubow and Moore 1959) is another well-documented pre-exposure effect that refers to the retardation of conditioning to a stimulus after non-reinforced pre-exposure. During pre-exposure to AX and BX, the common element X (from which generalization is expected to occur) is presented twice as often as the distinctive elements. Therefore, the LI suffered by X is greater than that of the unique elements of the compound, which then is observed as weaker conditioning to X. Given that generalization between AX and BX is expected to occur to the extent that they share features in common (i.e., the X elements), generalization between both stimuli would be reduced following pre-exposure. In fact,

pre-exposure to only the common elements of the stimuli can also reduce the generalization between them (e.g., Bennett et al. 1994).

In addition to this LI mechanism, according to McLaren and colleagues, another associative mechanism known as “unitization” also operates during pre-exposure. This mechanism involves the establishment of bidirectional within-compound associations (e.g., Rescorla and Durlach 1981) during pre-exposure (i.e., between A and X during AX trials as well as between B and X during the BX trials). Such associations would, on the one hand, serve to improve the mental representation of the stimulus, thus enhancing stimulus differentiation. On the other hand, however, these associations might also enhance the generalization between the stimuli. Following pre-exposures to AX and BX and subsequent conditioning to AX, when BX is presented on test, generalization would occur not only through the X elements but also by the X-A-US associative chain (US meaning unconditioned stimulus). This source of mediated generalization would lead to an increase in the generalization between similar stimuli following pre-exposure, i.e., the opposite to what might be expected on the basis of the PL effects just described. However, after intermixed pre-exposures to the stimuli, another mechanism would operate to cancel out this source of mediated generalization. According to McLaren et al. – and in line with the standard associative theory of learning (e.g., Rescorla and Wagner 1972; Wagner 1981) – when the presence of one stimulus element repeatedly retrieves the representation of another absent element, this will lead to the establishment of inhibitory links between them (e.g., Espinet et al. 2004, 2008; Polack and Miller 2019). This should in particular be the case during intermixed pre-exposures to the stimuli (Espinete et al. 1995; see also Artigas et al. 2001; Bennett et al. 1999; Dwyer et al. 2001). After the establishment of these within-compound associations, the X element might associatively activate the mental representation of A on the BX trials, as well as B during AX pre-exposure trials. Therefore, mutually inhibitory links would be established between the distinctive elements of the stimuli – A and B. Thus, although on the test trial the conditioned aversion acquired by AX would still directly generalize to BX on the

basis of the X elements, the mediated generalization source would be canceled because the element B will now inhibit the associative activation of A, breaking the X-A-US chain. During blocked pre-exposures to the stimuli, on the other hand, the establishment of inhibitory links between the distinctive elements of the stimuli would be hindered. On the first block of pre-exposure trials – e.g., with AX – the within-compound B-X associations would not be established, and B cannot be associatively activated. Moreover, during the second block of trials with BX, the within-compound A-X association would gradually be extinguished. Thus, the associative activation of the distinctive elements of the stimuli – as well the subsequent establishment of inhibitory links between them – would be prevented. As a result, the mediated generalization source would operate during the test with BX, with generalization then being stronger in comparison with that observed following intermixed pre-exposure.

The *intermixed-blocked effect* has also been explained from other theoretical approaches that predict changes in the salience or perceptual effectiveness of the stimulus as a consequence of pre-exposure. For instance, Hall (2003) proposed a salience modulation mechanism by which the salience of the distinctive elements of the stimuli increases following intermixed exposure in comparison with blocked pre-exposure. According to this account, during pre-exposure all the elements of the stimuli lose salience due to a process of habituation (e.g., Hall 1991). Given that during pre-exposure to AX and BX the common elements X are pre-exposed twice as often as A and B, the latter elements would maintain more salience than the former, thereby enhancing stimulus differentiation in general after repeated pre-exposure. In addition, Hall (2003) hypothesized that salience might be restored if the stimuli are associatively activated. As outlined previously, the associative activation of the mental representation of the distinctive elements of the stimuli would be facilitated during intermixed pre-exposures relative to blocked exposures. Therefore, the salience of such elements would be expected to be higher after intermixed than blocked pre-exposures (e.g., Blair et al. 2004; Blair and Hall 2003). In animal conditioning

procedures, the greater generalization decrement observed after intermixed than blocked pre-exposures would come from two sources. First, the more salient A element would be more effective in overshadowing X on the AX conditioning trials, and therefore the aversion acquired by the X element (and thus subsequent generalization to BX) would be weaker after intermixed pre-exposure. Second, B would also be more effective at interfering with the aversion to X on the test with BX.

Focusing on the effects of the temporal interval between the stimulus presentations, Mitchell et al. (2008) invoked memory mechanisms to explain why the distinctive elements of the stimuli might be better coded in memory – and thus more effective for stimulus differentiation – after intermixed than blocked pre-exposure. According to the memory theories of the massed-spaced effect (e.g., Ebbinghaus 1885/1964, see also Glenberg 1979; Jacoby 1978; Wickelgren 1972), spaced practice produces better memory of the stimuli than massed practice. During intermixed pre-exposures to AX and BX, the distinctive elements of the stimuli are presented on alternate trials, while during blocked pre-exposures such elements are presented on consecutive trials. The practice with the distinctive elements would then be more spaced in the former than in the latter case, with the result being that the elements would be better encoded in memory and available for stimulus differentiation (e.g., Lavis et al. 2011; De Zilva and Mitchell 2012).

Such theoretical accounts have been tested in various studies, and in general, all seem to generate evidence both for and against their predictions, with all of them being equally able to explain the *intermixed-blocked effect*. Most of these accounts, however, have failed to explain the effect of the another pre-exposure schedule, at least in terms of the same mechanisms proposed to explain the intermixed-blocked effect. This pre-exposure schedule is the controversial *concurrent pre-exposure schedule*. Simultaneous or concurrent pre-exposures to the stimuli might be expected to offer the best opportunities to compare them because they are presented as close in time as possible. The Gibsonian account would predict better stimulus differentiation after

concurrent than blocked pre-exposures to the stimuli, while none of the other theoretical accounts could explain this finding. During concurrent pre-exposure to the stimuli, the distinctive elements of both stimuli would be physically present; therefore, no inhibitory links would be established between them, nor would their salience be restored. Moreover, the temporal interval between their presentations would be the shortest possible, nominally nonexistent. Several studies have addressed this issue and have found different results for human and nonhuman animals. In humans, in particular, concurrent pre-exposure appears to enhance stimulus differentiation to a greater extent than the intermixed or blocked schedules (e.g., Angulo and Alonso 2012; Mundy et al. 2007, 2009). Moreover, evidence for an attentional shift of the sort described by Gibson (1969) has also been found using eye-tracking methodologies, where dwell time for gaze fixations is assumed to represent attentional focus (Angulo et al. 2019). However, most of the studies conducted with animal subjects have found greater generalization between stimuli following simultaneous than with intermixed pre-exposure (e.g., Alonso and Hall 1999; Rodríguez and Alonso 2004; Rodríguez et al. 2008; see, however, Angulo 2018, for different findings). Rapid alternation between the stimuli also appears to increase generalization (e.g., Bennett and Mackintosh 1999; Honey and Bateson 1996). Thus, if the same logic applied to previous findings is applied here, these results would suggest poorer stimulus differentiation following concurrent than intermixed pre-exposures in non-human animals. Because the theoretical accounts of PL make different predictions regarding the effects of a concurrent pre-exposure schedule, this issue has, in recent years, been the focus of much interest for researchers within the field.

### Current Challenges for Perceptual Learning

Verbal instructions are an issue that has attracted increasing attention regarding the effects of the concurrent schedule in humans and nonhumans.

In the majority of these studies, participants were instructed to more or less explicitly search for the differences between the stimuli during pre-exposure (e.g., Angulo and Alonso 2012, 2013; Mundy et al. 2007, 2009). Instructions can be expected to induce processing of the stimuli in a rather different way compared to experiments conducted with animals. For instance, while in humans the stimuli are processed in a top-down manner, other animals process the stimuli in a bottom-up way (Tsushima and Watanabe 2009). This possibility has also been discussed regarding whether instructions could promote a self-supervised form of learning in humans, as opposed to the unsupervised form of learning that is assumed to occur in other animals (Watanabe et al. 2001). Finally, it has also been proposed that an attentional response – in this case focused on the distinctive elements of the stimuli – might be instrumentally conditioned when the instructions ask for stimulus differences, since finding such differences could be a source of reinforcement (Mackintosh 2009).

The findings of some studies seem to confirm an important effect of instructions directing participants toward stimulus differences, both in terms of stimulus differentiation and attentional shift (e.g., Angulo et al. 2019; Navarro et al. 2016). For instance, participants appeared to be more accurate at making same/different judgments after concurrent pre-exposures when they were required to judge the stimuli as same or different, or only as different, compared to participants instructed to judge the stimuli as same or to simply look at the stimuli. Moreover, the instructions asking for same/different or only different judgments also increased the attentional shift toward the distinctive elements of the stimuli compared to nonspecific instructions to only look at the stimuli (Angulo et al. 2019). This pre-exposure condition is more similar to that of animals, and, even in this case, some evidence for an attentional shift was found during concurrent but not during blocked pre-exposures to the stimuli. In light of these findings, instructions directing the participants toward stimulus differences might increase PL as well as an attentional shift akin to that

described by Gibson. Such effects might also arise during concurrent pre-exposure without instructions guiding attention to the distinctive elements of the stimuli. Thus, it is unlikely that differences in the effect of the concurrent pre-exposure schedule in humans and nonhuman subjects animals depend on the instructions, at least exclusively.

Other studies have focused on conditioning procedures using nonhuman animals. As stated before, in this case the ability to discriminate between the target stimuli is inferred from the level of generalization, and the concurrent schedule might increase the generalization between stimuli in at least two ways. First, according to the standard associative theory, when the stimuli are concurrently presented, one would be associated with the other, thereby increasing the generalization between them. Second, stronger conditioning to the common elements of the stimuli has been found following concurrent pre-exposure, these being the elements through which direct generalization occurs (e.g., Rodríguez and Alonso 2008; Rodríguez et al. 2008). To date, it is not clear as to whether or not these factors might operate regardless of the ability of animals to differentiate between the stimuli (for a discussion, see, for instance, Mitchell 2009). But a recent series of experiments seems to indicate that, at least in a situation in which it is assumed that the animals discriminate between stimuli, concurrent pre-exposure does not enhance generalization relative to intermixed pre-exposure (Angulo 2018).

Current discrepancies between the findings of human and nonhuman PL studies remain to be clarified. In this regard, some authors have suggested that PL mechanisms might differ between human and nonhuman animals. However, before accepting this possibility, research should first rule out the possibility that these differences might arise from the procedural differences between the experimental preparations used in humans and nonhumans. This might be an important future line of research, in order to achieve a unified theory of PL able to explain the generality of pre-exposure effects. In this regard, a thorough analysis of the procedures

used to present the stimuli might help reach this objective.

## Cross-References

- [Associative Learning](#)
- [Classical Conditioning](#)
- [Conditioned Inhibition](#)
- [Contingency](#)
- [Ebbinghaus](#)
- [Habituation](#)
- [Latent Inhibition](#)
- [Learning](#)
- [Overshadowing](#)
- [SOP Model](#)
- [Taste Aversions](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Perceptually Driven Processing

### ► Bottom-Up Processing

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## Perching Bird Locomotion

### ► Passerine Locomotion

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## Perching Bird Physiology

### ► Passerine Morphology

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## Perching Birds

### ► Passerine Life History

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## Perfect Pitch

### ► Absolute Pitch

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## Peripheral Nervous System

► Nervous System, The

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### Perirhinal Cortex

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### Synonyms

Mesocortex; Proisocortex

### Definition

Perirhinal cortex is the cortical gray matter found in or around the vicinity of the rhinal sulcus and is of intermediate type between the archicortex and neocortex.

### Introduction

The perirhinal cortex (PC) is a proisocortical area that interconnects the hippocampal formation with other parts of the limbic lobe and with the lateral temporal and occipito-temporal association cortices. It is closely interconnected with divergent unimodal and polymodal association area of the neocortex as well as with the hippocampal formation and the amygdala (Suzuki 1996).

PC is present only in mammals and marsupials and has undergone evolutionary changes. It is just a narrow strip of the cortex in non-human primates, while it is of significant size reaching a length of about 3 cm and a calculated area of about 8cm<sup>2</sup> in humans (Insausti et al. 1998).

### Location

As the name indicates, the perirhinal cortex is found in or around the vicinity of the rhinal sulcus. The PC is located on the ventral surface of the brain in the medial temporal lobe, lateral to the rhinal sulcus running rostrally and dorsally up to the temporal pole from its caudal border. The medial relation of PC is formed by the piriform and periamygdaloid cortices rostrally and by the entorhinal cortex caudally (Suzuki et al. 1993).

### Structure

The perirhinal cortex is composed of two Brodmann areas: area 36 (larger, laterally situated, and dysgranular) and area 35 (smaller, medially situated, and agranular) (Insausti et al. 1998). Area 36 is divided into three subdivisions: 36d, 36r, and 36c. 36d is the most rostral and dorsal and 36c is the caudal extreme of the PC. Between them is 36r. Area 35 can be divided into two divisions: 35d and 35v (dorsal and ventral, respectively) (Suzuki and Amaral 1994).

### Histology

PC does not have a clear columnar organization. It is proisocortex in architecture. Area 36 is characterized with uniformly distributed small neurons in layer II, medium pyramids in layer III, ill-defined thin layer IV, and not differentiated large pyramids in layers V–VI. Area 35 is characterized with accentuated layer II having a mixture of small and slightly larger dark neurons, thin layer III having lack of cellular density, and absent layer IV and contains not well-differentiated very large neurons in layers V and VI (Insausti et al. 1995).

### Connections and Functional Significance

The perirhinal cortex is highly interconnected with many other brain regions including the amygdala, basal ganglia, frontal cortex, etc. and acquires highly refined sensory information of all

modalities from all sensory areas. It forms a crucial gateway for bidirectional transfer of information through the hippocampus and limbic system. When a stimulus may be recognized, the PC processes its association with past history. Thus, it plays an important role in sensory perception and memory associations. In monkeys, the PC receives sensory information predominantly from high-level visual areas, while in rodents, it receives predominantly from olfactory and, to a lesser extent, auditory areas (Meunier et al. 1993).

PC outputs include the following:

1. Medio-dorsal nucleus of the thalamus via the ventral amygdalofugal pathway
2. Anterior thalamic nuclei and mammillary bodies via the fornix
3. Other cortical regions known to be involved in visual recognition memory, such as the ventromedial prefrontal cortex via pathways such as the uncinate fasciculus

Because of these connections, PC is involved in learning and memory (Biagini et al. 2013), visual recognition memory in monkeys (Meunier et al. 1993), object recognition memory in humans (Squire et al. 2007), item-based memory (coding familiarity/recency of items, Gold et al. 2006), and item-context-based memory associations when the stimuli are objects (Graham et al. 2010) and is essential for incidentally learning the order of events in episodic memory (Allen et al. 2020). According to Barbeau et al. (2004), the PC seems to support context-free (non-episodic) knowledge and “item-specific” memories.

## Clinical Disorders

Damage to PC disrupts stimulus-stimulus associations and object recognition abilities finally leading to impairment of visual recognition memory. Any pathological involvement of the monkey PC may impair their ability to identify familiar objects presented in new views (Buckley and Gaffan 1998). Human studies show that any pathological lesions in PC leads

to impairment in discriminating among object concepts having a high degree of visual semantic overlap among choices, such as between a hairdryer and a gun (Douglas et al. 2019). PC may also be implicated in the pathological processes of epileptogenesis and ictogenesis such as the kindling phenomenon and the spread of limbic seizures (Biagini et al. 2013). Recent studies show that PC appears to play an essential role in gustatory neophobia and its attenuation in rats (Ramos 2020).

## Conclusion

The perirhinal cortex has a distinct modular organization in human brains and is strategically located in the medial temporal lobe to influence the flow of information into and out of the hippocampal formation. This region appears to be affected in various diseases like Alzheimer’s, causing alterations in memory. Despite lot of studies on the structural and functional aspects of PC, still there are many unfolded secrets in this small structure that needs to be studied in the future.

## Cross-References

- ▶ Amygdala
- ▶ Entorhinal Cortex
- ▶ Episodic Memory
- ▶ Medial Temporal Lobe
- ▶ Parahippocampal Cortex (PHC)
- ▶ Visual Perception
- ▶ Visual Recognition in Birds

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## Perissodactyla Cognition

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## Synonyms

Cognitive ecology; Equids; Human-horse interaction; Rhinos; Social cognition; Tapirs; Ungulates

## Introduction

Perissodactyla comprise the tapirs (Tapiridae), the rhinos (Rhinocerotidae), and the equids (Equidae). In order to evaluate their cognitive capacities, it is important to consider the species' social and environmental challenges (Griffin et al. 2017). Only by knowing the challenges, to which animals have to adapt, their cognitive capacities can be relativized to other species, for example, if humans are not encountered on regular basis, animals may not need to learn how to read human given cues, even though they may be able to do so in a captive situation.

The Perissodactyla show large variation in their social organization, and in the environments in which they live. All Perissodactyla species are heavily hunted and some species, such as the Asian Baird's tapir (*T. bairdii*), the Malayan tapir (*T. indicus*), the Indian rhino (*Dicerorhinus sumatrensis*), and the Javan rhino (*Rhinoceros sondaicus*) have become nearly extinct as a result. The Przewalski horse was extinct in the wild but was successfully reintroduced into the



Mongolian and Kazak steppe. Some species are exclusively wild while others species have domesticated groups, which are considered to be the same species. All Perissodactyla have to adjust to human-dominated environments (Grzimek et al. 2003).

Below, the particular Perissodactylas' social systems and environments will be briefly described. Thereafter, the state of the art in cognition research will be presented for each species. Cognition research is scarce in the exclusively wild species of tapirs, rhinos, zebras, and horses. This is mostly due to the fact that the species are difficult to observe, because they live in remote areas and because only a few animals are left in the species which are close to extinction.

### The Tapirs (Tapiridae)

#### Habitat and Social Organization

Four extant tapir species are described, the central American lowland tapir (*Tapirus terrestris*) and the mountain tapir (*T. pinchaque*), as well as the Asian Baird's tapir (*T. bairdii*), and the Malayan tapir (*T. indicus*). All species live solitary, avoid contact with humans, live in remote areas of rain forests or mountains, and are facultative nocturnal in areas with high hunting pressures through humans (Grzimek et al. 2003).

#### Social Cognition

Lowland tapirs and Malayan tapirs recognize the voices of their own species (Zenzinger 2010). It was suggested, that they are capable of identifying individual tapirs, i.e., show cognitive capacities of individual recognition, as they live in overlapping territories, mark their territories with urine, and show flehmen behavior when investigating scent marks (Pinho et al. 2014). When animals "flehmen," they lift the upper lip and lay open the efferent duct of the vomero nasal organ, an organ which is used for the investigation of highly volatile odors or even pheromones of, for example, individual animals. Marking behavior and scent mark investigations would be useless if the animal could not infer the donors' species, sex and, maybe the individual identity, from the marks.

### The Rhinos (Rhinocerotidae)

#### Habitat and Social Organization

Rhinos comprise five extant species. All five species are heavily hunted, mostly because their horn is given credit for enhancing human virility, a misconception. The three Asian species, the Asian rhinoceros (*Rhinoceros unicornis*), the Indian rhino (*Dicerorhinus sumatrensis*), and the Javan rhino (*Rhinoceros sondaicus*) live in remote rain forest habitats. The black rhinoceros (*Diceros bicornis*) and the white rhinoceros (*Ceratotherium simum*) inhabit the African savanna. Little is known about the behavior and cognition in the two nearly extinct species, the Indian rhino and the Javan rhino. They avoid contact with humans and live solitary (Grzimek et al. 2003).

Asian rhinoceroses are facultative solitary. Sometimes they form small female groups with offspring, which are hierarchically structured in so-called matriline. In matriline, offspring is usually dominated by their mothers and mothers by the grandmothers. Very seldom, females of the Asian rhino are accompanied by bulls and, seldom, bulls gather in small bachelor groups. Both, females and males mark their home ranges, which can overlap, with feces and urine (Grzimek et al. 2003).

Black rhinoceroses are mostly solitary but have also been described to live in small groups of some females with offspring and sometimes, with a bull close by. Bulls are rarely seen together. They are not strictly territorial, i.e., they do not strictly stay in defined home ranges, but males and females show marking behavior with dung and urine. Feces piles may reach the height of half a meter (Grzimek et al. 2003).

White rhinoceroses are the most social rhinos. However, they appear to need retreat areas for withdrawing from conspecifics, as black and white rhinoceroses, suffer from social stress when several pairs are kept in small zoo enclosures (Carlstead and Brown 2005). In past decades, white rhinos were said to form social networks within their groups of up to eight females and their offspring (Grzimek et al. 2003). Today, animal numbers are reduced through human hunting and group sizes reach

only three females. White rhinos are territorial, i.e., they stay in defined home ranges, and, especially the solitary bulls that mark their overlapping territories with feces and urine.

### Social Cognition

Because marking behavior and intense scent mark investigation are shown frequently in black and white rhinos (Grzimek et al. 2003), it is not surprising that their abilities in social and individual recognition are highly developed. The animals appear to have a strong need to identify group members, mating partners, or rivals in their territory. Black rhinos use olfaction to identify the age, the sex, and the individual identity of conspecifics. White rhinos can identify familiarity and the sex, age, territory, and estrous state of fecal donors (Marneweck et al. 2017). Furthermore, white rhinos discriminate the species and the sex of other rhinos from contact calls (Cinková and Policht 2016; Fig. 1).

### Object Discrimination

Because vision is poorly developed in rhinos, it was said that rhinos have troubles to differentiate between an inanimate person and a tree from a distance. Thus, fast exploratory approaches to humans may have been mistaken for attacks, and some rhinos were shot by mistake (Grzimek et al. 2003). However, vision may not be as poor as expected, because black and

white rhinos are able to learn visual object discriminations. They discriminated black symbols, a triangle and a circle, on white cards (Daniel and Mikulka 1998).

### The Equids (Equidae)

Equids comprise zebras, donkeys, and horses. They can be crossbred and sometimes wild animals crossbreed in overlapping habitats. Equid hybrids are generally called zebroids. They are termed mules when donkeys breed with horses, zebrules, or zedonks when donkeys breed with zebras, and zorse when horses and donkeys breed. The hybrids are usually infertile.

### Zebras

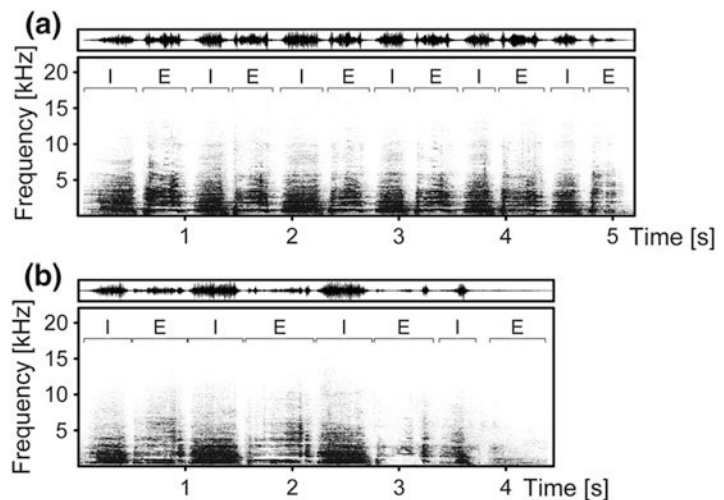
#### Habitat and Social Organization

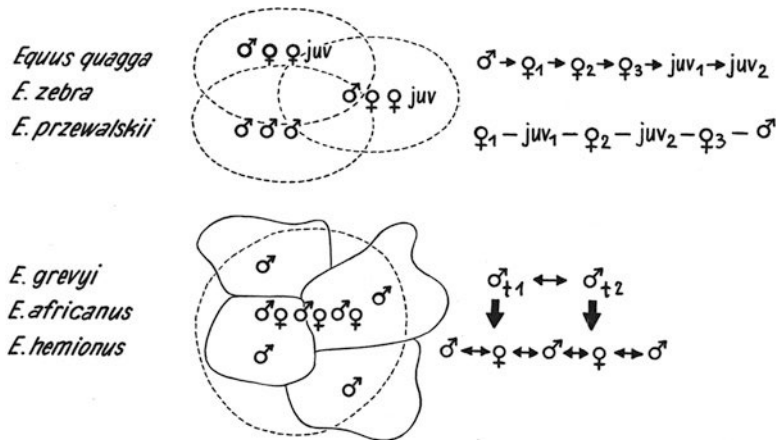
Zebras comprise three, exclusively wild species, Plains zebra (*Equus burchelli*), Cape mountain zebra (*E. zebra zebra*), and Grevy's zebras (*E. grevyi*). Zebra species can be assigned to type I and type II social systems (Klingel 1972; Fig. 2). Plains zebras and Cape mountain zebras live in the African Savanna and form type I social systems. They live in harem groups with several females, their offspring, and one to three mature males. Surplus males gather in bachelor groups. Several of these subgroups may form herds of 200 to 1000 animals (Klingel 1972). Mostly linear hierarchies are formed within and between

### Perissodactyla

#### Cognition, Fig. 1

Contact calls in white rhinos. (a) Depicts the pant call of an adult female and (b) of an adult male. The calls waveform is given above and the spectrogram below of it, time on the X-axis and frequency (kHz) on the y-axis. The Spectrogram parameters are: FFT length 1024, frame size 100% and overlap 87.5%. I = the inhalation and E = the exhalation of the animals (Cinková and Policht 2016)





**Perissodactyla Cognition, Fig. 2** Equid social systems. In type I social organizations, depicted above, females (♀), offspring (juv), and males (♂) live in mostly stable groups with usually one alpha male and several females with their offspring. Whereas, in type II organizations, depicted below, several males protect particular habitats and

dominate loosely bonded females and males that travel through these areas (Klingel 1972). In recent publications *Equus Quagga* is termed *Equus burchellii*, *Equus zebra* is *Equus zebra zebra*, and *Equus africanus* is referred to as *Equus asinus*

subgroups and animals are bonded with group members, they form so-called social bonds. The linearity of the hierarchies and the numbers of social bonds between group members differ between groups (Fischhoff et al. 2007).

Grevy's zebras live in remote African mountains with little vegetation and water. They form type II social systems (Fig. 2). Solitary males defend a territory around a water source and mark the borders with feces. The males claim mating rights over the females within their territory. Whether females form social groups depends on the resource availability. When food and water is scarce, females live solitary with their offspring. In periods with plenty of food and water, they form small groups.

#### Social Cognition

Plains zebras protect their social bonds through intervening in interactions of others (i.e., third party intervention). Foals, yearlings, and adult mares intervene, when bonded group members exchange friendly behaviors (affiliative interventions), yearlings and foals intervene when their mothers are attacked by stallions, and stallions, in multimale groups (agonistic interventions), intervene into courtship behavior (sexual

interventions), especially when bonded females are involved (Schilder 1990).

When Grevy's zebra females have to walk long distances to water sources, they were described to leave their sleeping offspring behind. One or two mature animals stay with the "kinder garden" (Klingel 1972). The report indicates abilities in social and individual recognition in Grevy zebras. Further cognitive abilities were not reported.

#### Spatial Cognition and Movement Decisions

Abilities in spatial cognition allow plains zebras to find distinct paths for short and long distance movements (Brooks and Harris 2008), while the exact mechanism is not known. They use spatial memory for orientating on landmarks, but orientation on the magnetic field may also play a role.

Plains zebra group movements appear to arise out of a mix of low cognitively demanding self-organized movements, in which group members synchronize their movements with group members mostly without making any decisions, and out of decisions on whom to follow. For example, lactating females initiate movements towards water more often, because of their enhanced need for water, but how many group

members will follow depends on the quality and the quantity of their social bonds within their group, i.e., on the number of group members deciding to follow this specific animal (Fischhoff et al. 2007).

## The Donkeys

### Habitat and Social Organization

Donkeys comprise the African wild ass (*Equus asinus*), Asian wild ass (*E. hemionus*), the Kiang (*E. kiang*), and domesticated types. All form type II social organizations (see Fig. 2). Some individuals in donkeys and wild ass appear to mark their territory with urine and feces (Klingel 1972). The wild ass is close to extinction. They avoid contact with humans, and roam in steppe or semidesert habitats, in very remote areas where they can escape heavy hunting. The herds comprised more than 1000 individuals in the past, which went down to few extant herds with less than 200 individuals in recent years.

### Social Cognition

Research on cognition in wild ass is missing but some work has been conducted in domestic donkeys. Anecdotal reports on strong pair bond formation between domestic donkeys were scientifically confirmed. Donkeys identify bonded individuals and prefer to stay close to them (Murray et al. 2013).

### Spatial Cognition

Domestic donkeys appear to have a good short-term memory of between 10 s and 30 s for locations where food disappeared through a barrier (Baragli and Regolin 2008). In a comparative approach, mules (hybrids between donkeys and horses) were superior to donkeys and horses, to learn a path around a barrier. When the gap in the barrier was moved from location A to location B, horses kept returning to the old, now closed gap (A), while mules and donkeys approached the old and the new gap (A and B) on equal terms (Osthaus et al. 2013). Mules and donkeys, therefore, show a higher plasticity in reasoning about

spatial conditions, i.e., in spatial cognition, than horses.

### Object Discrimination

When donkeys, mules, and horses were compared for how many pairs of particular patterns on paper cards they would learn to discriminate within 25 sessions, five out of six mules, but only one horse out of six and no donkey out of six discriminated three different patterns (Proops et al. 2009). The superiority of mules in discrimination learning was discussed to be a matter of hybrid vigor. However, it remains a matter of debate whether the horses gradual and the donkeys' fast decline in performance is rather due to an attention loss than to discrimination learning capacities.

## The Horses

### Habitat and Social Organization

Horses include the domestic horses (*Equus caballus*), the feralized domestic horse (*E. ferus caballus*), and the wild horse (*E. ferus przewalskii*). They prefer steppe habitats but adapt easily to different habitat types. All the horses form type I social organizations (Fig. 2). In contrast to the teaching of some traditional textbooks, harem, and group stability varies considerably between groups of horses (Rubenstein 1986). All-male "bachelor" bands are unstable in feral horse populations with only a few exceptions (see for review: Linklater 2000). While some large harem horse groups show stable smaller core groups, between 90% and 100% of the male offspring and between 80% and 90% of the female offspring disperse from their natal harem groups when they reach maturity. They either join an existing harem or bachelor group or form new groups by themselves. Adult mares sometimes disperse from harems and return.

### Social Cognition

All species build social bonds with up to three animals, form alliances between females for offspring protection, and protect social bonds

through third party intervention similar to plains zebras (see above; Krueger et al. 2015). Horses even show postconflict resolution, by consoling group members, which were object to aggressions from others.

The horses' social system resembles a fission-fusion society, in which animals need to identify the departing and returning group members. In this partially unstable system, horses can stay in contact through distance calls. They identify group members by their whinnies, by their visual appearance, and at the smell of their fecal marks (Krueger and Flauger 2011).

### Horse-Human Recognition and Interaction

The domestication of horses 3000–6000 years ago may have shaped interspecies communication abilities. The skill of horses in responding to human facial and gestural cues is known from the case of Clever Hans in the early twentieth century. Clever Hans was claimed to have the arithmetic skills of a 12-year-old child. Clever Hans presented the solutions for the mathematical tasks by tapping the desired number with his hoof. Although subsequent observations revealed that he could not count, he was, nevertheless, extremely skillful in reading subtle human facial expressions and body movements, which he used for his decision when to begin tapping with his hoof and when to stop. Clever Hans even generalized the cues given by his trainer to unfamiliar persons (Pfungst 1907).

The discovery of Clever Hanses "shortcut" to solving mathematical equations stigmatized cognition research in domestic animals and even more in horses for about 100 years. Nobody dared to approach evaluating whether Clever Hanses skills in reading human given cues were unique or common in horses. Only in the last decade, some research was conducted in this area. Today, we know that horses identify humans individually. Domestic horses are able to use human hand pointing gestures and human head and body orientation to find food. Domestic horses orientate in the direction of human

attention, for example, when humans turn away and stare in particular directions. Domestic horses distinguish between familiar and unfamiliar persons, generalize positive and negative experiences with humans from one human to others and infer emotional states of humans from human photos. Some horses have negative or positive expectations of human behavior, which they acquired in earlier encounters with humans. They may refuse to participate in a test when they expect humans to solve the task for them or when they wait for distinct signals for what they are expected to do (for horse-human interaction see: Hausberger et al. 2008; Schuetz et al. 2016).

### Spatial Cognition and Object Permanence

Interestingly, the horses' short-term spatial memory was said to decline after 10–30 s. Still, in a detour task feral ponies, raised in a semiwild environment, showed an understanding of object permanence, i.e., of the fact that an object which is no longer perceivable still can be regained, even after a delay of 10 s. Nevertheless, Standardbreds which were raised in traditional stabling did not succeed in the task (Baragli and Regolin 2008). Limitations in some horses' spatial reasoning may hamper their performances in simple detour tasks (Baragli and Regolin 2008; Osthaus et al. 2013). However, studies on whether the length of domestication, the aim of the domestication, the management of the horses, or the environment affect the learning capacities or the performance of domestic horses in cognition tests are needed.

### Movement Decisions

As horses have a strong urge to stay with group members for protecting offspring and for fleeing together decisions on moving the group need to be made. Group movements can be initiated by the despotic herding of alpha males. In Przewalski horses and feral horses, however, any group member may initiate movements by departure (Kruger et al. 2014b). Movement initiations by departure are not exclusive to any type of individual, as has been claimed for so-called





**Perissodactyla Cognition, Fig. 3** Horses try to recruit humans by referential communication. Horses (a) gaze to the experimenter or (b) point at a bucket with food for

communicating their interest in the bucket (Malavasi and Huber 2016)

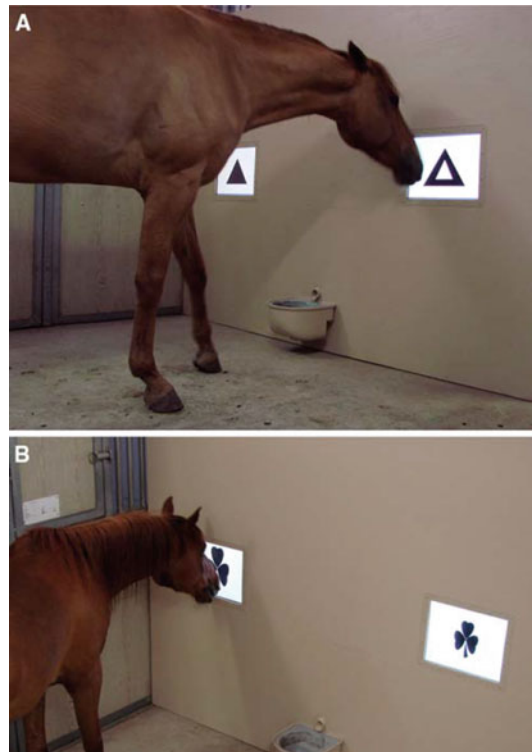
lead mares. Instead horses show a limited form of distributed leadership, with higher ranking animals being followed more often. Most horse movements appear to be self-organized, with little need for cognitive decision-making. However, the fact that social rank affects whether animals are followed or not implies that decision-making on the reliability of the initiating animal takes place. So far, recruitment of group members could not be proven.

However, horses showed distinct recruitment behavior towards humans, when they tried to point humans to opening a gate for getting access to food (Malavasi and Huber 2016; Fig. 3). They even increased their effort when the person in reach was inattentive (Ringhofer and Yamamoto 2017).

### Object Discrimination, Categorization, and Generalization

In individual learning tests, horses discriminate precisely between objects. They learn object categories and concepts and even generalize them to unknown objects (Hanggi 2003; Hanggi and Ingersoll 2009; Fig. 4). For object categories and concepts some horses show an impressive long-term memory of 7 years and 10 years (Hanggi and Ingersoll 2009).

Only lately it was experimentally shown that Shetland Ponies have a number concept which allows them to discriminate between numbers of up to five depicted objects on computer images (Gabor and Gerken 2014).



**Perissodactyla Cognition, Fig. 4** Horses discriminate pictures. Horses were able to understand (a) categories (filled versus open-center stimuli) and (b) concepts (small versus large stimuli; Hanggi 2003; Hanggi and Ingersoll 2009)

### Social Learning

Finally, the Social intelligence hypothesis claims that animals which live in complex social systems face higher cognitive demands. They need to



**Perissodactyla Cognition, Fig. 5** Social learning in horses. (a) Shows the situation in which a demonstrator horse (dem) opens a feeding apparatus by pulling a rope. An observer horse (obs) watches the demonstration. (b)

Shows a successful observer when operating the feeding apparatus. (c) Depicts the feeding apparatus in detail. A rope (1) had to be pulled to open a drawer (2) (Krueger et al. 2014)

identify group members and deal with conflict. Further above, we showed that horses are capable of both. For decades, researchers had difficulties to prove social learning in horses. By now, we know that horses learn from observing other horses (Krueger et al. 2014a) and from observing humans (Schuetz et al. 2016; Fig. 5).

Horses copy the social behavior of other horses, adapt to the expectations of other horses when crossing a carpet, and learn to open a feeding apparatus by observing other horses (Fig. 5) or familiar persons. Interestingly, horses learn from higher ranking, older horses in their social group (Krueger et al. 2014a). Apart from individual trial and error learning, stimulus and local enhancement has been discussed to be the primary social learning mechanism in horses (Krueger et al. 2014a; Schuetz et al. 2016).

## Conclusion

Cognition research has been conducted in the particular Perissodactyla species to quite different amounts. This appears largely to be due to the species visibility and to the importance of the

species to humans. For example, in domestic horses, the interest of the public and the amount of cognition research is huge compared to other Perissodactyla species. Some wild Perissodactyla species are even mostly unknown to the public. Unfortunately, some of these species are close to extinction. If we do not hurry up and bring information on their behavior and cognitive capacities into the open, we may miss the chance of getting to know anything about the species' cognition at all.

## Cross-References

- [Attention](#)
- [Attention-Getting Behaviors](#)
- [Behavioral Variation](#)
- [Categorization](#)
- [Clever Hans](#)
- [Communication](#)
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- ▶ Equine Cognition
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- ▶ Herbivore
- ▶ Home Range
- ▶ Human Approach Test
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- ▶ Social Intelligence Hypothesis
- ▶ Social Learning
- ▶ Social Network Analysis
- ▶ Stimulus and Local Enhancement
- ▶ Ungulate

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## Perissodactyla Communication

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### Horses

#### Vocalizations

##### Neigh

The neigh (or whinny) is a greeting or separation call that appears to be important in maintaining herd cohesion. It is most often heard when adult horses or a mare and foal are separated. Stallion neighs contain lower frequencies

than those of mares or geldings. Horses appear able to discriminate between familiar and unfamiliar horses on the basis of their neighs alone (Lemasson et al. 2009).

A separated mare and foal will neigh repeatedly. These neighs appear to be nonspecific distress calls, which the mare, but not the foal, may recognize individually (Houpt 2017). The neighs of a mare separated from her foal can be distinguished from those anticipating feeding by analysis of their spectral frequencies (Pond et al. 2010).

##### Nicker

The nicker, a low volume call, is a care-giving (epimeletic) or care-soliciting (et-epimeletic) call. It is given by a mare to her foal upon reunion and probably is recognized specifically by each. A horse may also nicker to its caretaker and a stallion to a mare in estrus.

##### Snorts, Squeals, and Roars

Nickers or neighs usually elicit a reply; other equine vocalizations, such as snorts, squeals, and roars, do not. The roar is a high-amplitude vocalization of a stallion and is usually directed to a mare. A sharp snort is an alarm call. More prolonged snorting or sneezing snorts appear to be a frustration call given when horses are restrained from galloping or forced to work. Snorts and nickers are sounds from the nostrils. The mouth is closed. Other calls are given with the mouth open.

When two strange horses meet, or when horses have been separated for some time, they greet each other by putting their muzzles together nostril to nostril. The nostrils are flared, but if any vocal signals are given, they are inaudible to humans. Usually one, the other, or occasionally both of the horses will squeal and strike or jump back, although neither has been bitten or threatened. The squeal is, therefore, a defensive greeting. It is heard frequently when horses are forming a dominance hierarchy and many bites are being exchanged. Mares that are not in estrus squeal and strike when a stallion approaches too closely.



A squeal may also be a response to the sudden onset of pain.

### Postures

The horse's ears are probably the best indicator of its emotions. Ears pointed back indicate aggression, and the flatter the ears are against the head, the more aggressive the horse. The submissive horse holds its ears to the side (Dalla Costa et al. 2014). Horses tend to position their ears in the same direction in which they are looking. Thus, when the horse's ears are pointed straight ahead, it is looking straight ahead. Horses are aware of the other horses' facial expressions so that they will approach a feed bucket toward which a photographic image of a horse is looking or pointing its ears (Walther and McComb 2014).

The posture and bodily actions of the horse are also useful in interpreting its moods. The relaxed horse stands quietly, whereas its nervous counterpart prances and chafes at the least restraint. The aggressive horse, when it is threatening to kick, lashes its tail and may even lift one of its hind legs. The frightened horse tucks its tail tightly against its rump and stands with its feet close together. Muscle guarding is seen, especially if the animal anticipates pain. A few mares will urinate and lash their tails, splattering urine, as they are being chased, and it should not be confused with the frequent urination, but with deviated tail, seen in estrous mares. The stallion moving his mares assumes a unique posture, called herding, driving, or snaking, with head down, nearly touching the ground, and ears flattened.

Horses paw the ground, not in aggression, but rather in frustration when they are eager to gallop or, more commonly, when they want to graze and are restrained by rope or reins. Pawing to eat may be a behavior derived from pawing through snow for grass and might be considered a form of displacement behavior. Tail lashing and pawing can be signs of discomfort (Haupt 2017).

A very detailed description of equine facial expression has been made (Walther et al. 2015). Other facial expressions of the horse are more subtle; nevertheless, they can be used profitably to understand a horse's mood. A submissive horse

turns its ears outward. Young horses (less than 3 years old) have a more dramatic display, snapping, also called champing or tooth-clapping, in which the lips are retracted, exposing the teeth that are sometimes clicked together. This expression is shown by a colt to an approaching stallion or toward an adult who is threatening him. The sexually receptive mare shows a unique expression, the mating face, in which her ears are swiveled back and her lips hang loose. She may also exhibit snapping. A horse that sees but cannot reach food, or is anticipating food, makes chewing movements and sticks out its tongue. This may be a submissive signal indicating that the horse is ambivalent-reluctant but motivated to approach.

The pain grimace in horses is characterized by ears laid stiffly back, orbital tightening, tension above the eye area, prominent strained jaw muscles, mouth strained and pronounced chin, strained nostrils, and flattening of the profile (Dalla Costa et al. 2014).

### Tactile Sense

Horses can detect a fly on their skin and respond either by moving their skin or swishing their tails. Riders make use of the horse's ability to perceive a slight pressure on his flank in order to signal dressage movements.

### Olfactory Signals

#### Scent Marking

Olfactory communication plays an important part in the sexual behavior of horses. Stallions curl their upper lip in the Flehmen position or "lip curl" when they smell the urine of a mare. Estrous urine alone does not stimulate more episodes of Flehmen by stallions than does nonestrous urine, but the frequency of Flehmen by a stallion toward a particular mare in his herd increases as she approaches estrus, perhaps because the mare urinates more frequently (Haupt 2017). After the stallion investigates urine by putting his lips in it, his lips are raised in the Flehmen position, the nostril opening is partially blocked and the horse, by breathing deeply, aspirates the urine into the vomeronasal organ. Although stallions





**Perissodactyla Communication, Fig. 1** Flehmen and urine marking by a stallion

Flehmen most frequently, geldings and mares also exhibit the behavior in response to olfactory or gustatory stimuli. Stallions usually urinate on the urine (scent mark) as they are exhibiting Flehmen (See Fig. 1).

Horses can distinguish the skin odors of one horse from another (Peron et al. 2014). Although they can distinguish their own feces from those of other horses they do not distinguish those of familiar from unfamiliar horses. They sniff most at feces from horses that are aggressive to them (Krueger and Flauger 2011). Mares can discriminate the urine of different individuals (Hothersall et al. 2010).

Wild stallions use manure piles, or stud piles, along well-used pathways, possibly to scent mark. These piles or middens may separate bands of horses both spatially and temporally. Even in a pasture, stallions and some geldings select one place to defecate and then back into the pile to eliminate, so the pile does not grow much wider. On the other hand, mares and most geldings face outward, gradually increasing the diameter of the pile. Because horses do not eat grass contaminated with feces, a pasture containing mares and geldings rapidly becomes “horsed out” or inedible.

Horses are also able to match the neigh of another horse with its picture (Proops et al.

2009). This is an example of cross-modal identification. Horses can learn to recognize human faces and are able to discriminate members of a pair of identical twins. They can transfer recognition from a two-dimensional photograph to a real person (Hothersall et al. 2010). They can match the appearance and smell of a familiar person with his or her voice (Lampe and Andre 2012). Perhaps most interesting is that horses respond differently to happy versus angry faces. They tend to look at the photograph of an angry face with their left eye, indicating right brain lateralization and their heart rate increases faster than it does to a photograph of a happy face (McComb et al. 2016).

## Donkeys

### Vocalizations

Donkey vocalizations are: the bray, grunt, growl, whuffle, and snort. The bray is performed by territorial males in the mornings, upon meeting other male donkeys and at mating. It carries for several kilometers. In agonistic encounters, the bray often begins with a “grunt” or “growl” followed by a very long exhalation and then a series of high-intensity noises. A single bray can last 24 s. In nonantagonistic greeting behavior, the bray is low intensity and ended with a soft atonal “whuffle.” The whuffle is used by mares searching for their foals.

The bray is used as a separation call by foals. The grunt is a short and the grumble a long vocalization, which are produced in antagonistic encounters. A snort is a short explosive sound given by an alert donkey; the sound does not carry (Moehlman 1998).

### Visual Signals

When alert the donkey’s head is raised and turned with ears forward and toward the intruder. When resting in the standing position, the donkey’s neck is almost horizontal, the ears are down and to the side, and the eyes are closed. Threats can vary from the subtle turning of the head by the sender, to adding ears back, head down, approach at a fast

walk, trot, or gallop, to opening the mouth, to actually biting the receiver.

#### Yawing

Donkeys, zebras, and the occasional horse mare exhibit an expression during estrus in which they open their mouths exposing their teeth and turn their ears to the side. Yawing may be an approach/avoidance signal.

#### Olfaction

Male donkeys defecate on fecal piles. These may be at the boundaries of territories, on long trails, and in the vicinity of water sources. In about half the occasions when a donkey encounters a manure pile he will sniff it, paw at it, Flehmen, and then defecate. Urination by one male facilitates urination by another.

#### Zebras

##### Vocalizations

There are species differences in vocalizations. Plains zebra bark whereas Grevy's zebra (*Equus grevyi*) bray like donkeys (King et al. 2016). Mountain zebras' (*Equus zebra zebra*) high-pitched whistling whinnies are given as an appeasement signal. Male Grevy's zebra emit a long "Arrr-Arrr" bray followed by a rising squeak during courtship and copulation (Rubenstein 2011).

##### Postures

When challenging another male zebra, the male will approach, engage, and withdraw. The zebra approaches with its head up and ears erect and at a brisk trot. At the final approach the head may be lowered but the ears are still up. The tail is lashed erratically. Zebras exhibit the arched neck threat at close approach. Once together they exchange olfactory information with naso-nasal and then nasogenital contact. When subordinate male zebras approach a dominant one, they open their mouths without baring their teeth and make chewing motions similar to snapping in foals (Joubert 1972).



**Perissodactyla Communication, Fig. 2** Flehmen by a tapir (2008)

#### Tapir

There are four species of tapir: Baird's (*Tapirus bairdii*), lowland (*T. terrestris*), mountain (*T. pinchaque*), and Malayan (*T. indicus*). The first three are South American and the fourth is Malaysian and remarkable for its distinctive half black, half white coat in comparison to the grey South American tapirs (Fig. 2).

##### Vocalizations

There are three types of call. A snort, a clicking sound made by the tongue and palate, and two shrill/squealing calls. One squealing call is high pitched and made in fear or appeasement and lasts 1.5–5 s. The second squeal is less noisy and is used during exploratory activity and mostly uttered by the dominant tapir. The clicking sound is used for individual identification (Hunsaker and Hahn 1965).

##### Postures

The large, rounded, and thick ears are moved constantly while feeding, whereas they are held upright and slightly forward when frightened (Medici 2011).

##### Olfaction

A tapir moves its proboscis constantly while active, perhaps to locate and identify food by smell and tactile stimuli, for the proboscis always elongates in the direction of food to be consumed.

##### Defecation

Tapirs defecate most frequently in water, but also along trails. Feces are loose and extremely

fibrous, with small squares of undigested leaf parts and pieces of twigs. After defecating the tapir, or specifically the Malaysian tapir, paws, covering the feces with twigs and leaves (Khan 2014).

### Urination

Tapirs, especially males, urinate frequently during the evening. The urine is projected backwards in a spray, which may be several meters long. Urine is often projected when the tapir appears to be annoyed. Urination occurs 3–5 times at interval of 20–50 meters.

## Rhinoceros

There are five species of rhinos: Greater One-horned Rhinoceros (*Rhinoceros unicornis*), the Javan Rhinoceros (*R. sondaicus*), the Sumatran Rhinoceros (*Dicerorhinus sumatrensis*), the White Rhinoceros (*Ceratotherium simum*), and the Black Rhinoceros (*Diceros bicornis*).

The white rhino is a grazer and lives on territories with several females and a dominant male and sometimes with subordinate males. These rhinos are the best studied because of their social structure and visibility on open grasslands.

The social structure of black rhinos is overlapping home ranges (Schenkel and Schenkel 1969). The males are usually solitary and the females live with their calves.

### Vocalizations

In white rhinos the Pant calls provide information about the caller's sex, age, and social situation (Cinkova and Policht 2015). In Indian rhinos the snorting sound (khaawk. . .khwaak) is given when approaching or being approached by another rhino. Honks are given in many agonistic interactions. Groans are emitted during face-to-face confrontations. Bleats and roars occur during courtship chases and fights. Rumbles occur during wallowing. Squeak-pants occur during courtship chases. Moo grunts are contact calls between cow and calf. The breeding call is a whistle-like sound (fleet. . .fleet) that may last for over a minute (Laurie 1982; Hazarika 2015; Table 1).

**Perissodactyla Communication, Table 1** Vocalizations of rhinoceros (Dinerstein 2011; Muggenthalrer et al. 2003)

| Species                  | Function of call                                                        | Name of call      |
|--------------------------|-------------------------------------------------------------------------|-------------------|
| Greater one-horned rhino | Approach of conspecific                                                 | Snort             |
|                          | Head to head aggressive encounters                                      | Honk              |
|                          | Submission and courtship                                                | Bleat             |
|                          | Intense encounters between females either with a male or another female | Roar              |
|                          | Males during courtship chases                                           | Squeal pant       |
|                          | Mother-offspring contact call                                           | Moo grunt         |
| Black rhino              | Confrontations                                                          | Growls            |
|                          | Confrontations                                                          | Trumpet call      |
|                          | Greeting and anger                                                      | Snort             |
|                          | Alarm                                                                   | Sneeze            |
|                          | Fear                                                                    | Wonk high pitched |
|                          | Terror                                                                  | Scream            |
|                          | Mother-offspring contact call                                           | Squeak            |
|                          | Peaceful                                                                | Mmwonk            |
| White rhino              | Contact call                                                            | Panting           |
|                          | Courting male                                                           | Hic-throb         |
|                          | Distress                                                                | Squeal            |
|                          | Agonistic                                                               | Bellow            |
|                          | Agonistic                                                               | Growl             |
|                          | Response to attack                                                      | Shriek            |
|                          | ?                                                                       | Infrasound        |
| Sumatran rhino           | ?                                                                       | Eep               |
|                          | ?                                                                       | Whale             |
|                          | Infrasonic "song"                                                       | Whistle bow       |

### Postures

The vigilance posture is head up, standing still, and ears rotating. The threat posture is an erect stance with erect pinna. The head is carried horizontally. During bull confrontations the animals will walk stiff legged, swing their heads from side to side, and thrash shrubs. They may rub their heads or horns on the shrub. They approach one another with upper lip curled and tail raised while

emitting screaming groans and rolling their eyes (Estes 1993). Baring the lower incisor tusks may serve as a visual display.

Dominance is signaled by a raised head with ears forward and staring. Submission is expressed with the head lowered and the ears back and the tail up.

### Olfaction

Rhinos of both sexes defecate on manure heaps (middening behavior). Before defecating, the rhino sniffs the manure pile then turns to eliminate followed by scraping with the hind limbs, which not only scatters the feces, but also creates two shallow ditches in the manure and the soil beneath, allowing males to spread their scent by means of manure caught in their hooves. Male feces are investigated more than female by both sexes and females investigate sub-adult feces more. Feces and urine can signal age, sex, and identity and reproductive stage to conspecifics and signals may persist for a month (Linklater et al 2013). Rhinos exhibit Flehmen in response to urine (Fig. 3).

### White Rhinos

A territorial male maintains 20–30 dung middens upon which he will always defecate, scattering the feces with slow kicking. Females and nonterritorial males will use the middens, but

not kick. Territorial males will visit a midden site sooner and be vigilant sooner in response to the odor of another territorial male. They will sniff more often and for longer periods in response to estrous female odor (Marneweck et al. 2017).

Only a territorial male sprays urine and does so only on his territory. First he will horn swipe a bush or the ground then scrape with all 4 ft then spray three to five times. Marking is most concentrated along territorial boundaries (Estes 1993).

Scents may be carried in the pedal scent glands. When urinating normally the urine falls down and back, but when squirt urinating the urine is released in four squirts aimed horizontally backwards. Squirt urination and foot-dragging displays are performed by breeding males only. Flehmen occurs during investigation of the cow by the bull.

### Conclusion

The Perissodactyl are a varied order. Some are solitary such as the tapir and black rhino. Most live in small groups in a fusion-fission pattern. Most are grazers, like equids and white rhino, but the black rhino and tapir are browsers. Their means of communication reflect this. The horses use their facial expressions to communicate to their herd mates. Vocal communication is especially important in mother young communication. The tapir appears to use mostly olfactory signs. All the Perissodactyl use feces on middens and urination to communicate, although the rhino do so much more dramatically than the equidae. All exhibit Flehmen See Figs. 1–3.

### Cross-Reference

- [Auditory Signals](#)
- [Dominance](#)
- [Equine Communication](#)
- [Equine Sensory Systems](#)



**Perissodactyla Communication, Fig. 3** Flehmen by a rhinoceros with permission Kees Rockmaaker

- Estrous
- Individual Recognition
- Maternal Behavior
- Olfactory Discrimination
- Olfactory Perception
- Perissodactyla Cognition
- Scent-Marking
- Ungulate

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## Perissodactyla Diet

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Perissodactyla (Schoch 1989) includes tapirs, rhinoceros, wild asses, horses, and zebras. It is the order of hoofed mammals referred to as “odd-toed ungulates” because its members have one to three weight-bearing toes and walk on hoofs or “ungules.” They are herbivores that are specialized to exploit grasslands and brushy habitat (rhinos, horses, asses, zebras) or dense tropical forests (tapirs). All share a common digestive system called hindgut fermentation, or cecal digestion (in the cecum), and can consume relatively tough, coarse forage. Some perissodactyls are “browsers” that forage primarily on woody shrubs and trees, whereas others are “grazers” with a graminoid-dominated diet. They are all predominantly opportunistic feeders and select for quantity over quality of forage; that is, they consume more abundant low-quality forage instead of searching and selecting for higher-quality forage because it gives them the advantage of reducing search effort, which conserves energy.

Vegetation provides herbivores with protein, fiber, small amounts of water, and the nutrients needed to support their metabolism and survive. The minimum protein content required to meet metabolic functions in herbivores is ~6–7% (Owen-Smith 2002). Protein content is generally lower for grasses and sedges than forbs and shrubs, so in fall and winter, forbs and shrubs can potentially meet metabolic requirements better than graminoids. So although many perissodactyls are categorized as “grazers” and therefore consume mostly grass, they are able to subsist on non-graminoids as well. Khur in India have been observed eating seedpods (Shah 1993) and use hooves to break up woody vegetation to obtain succulent forbs at the base of woody plants. Wild

asses feed mostly on *Cyperus capillaris*, *Andropogon* spp., *Dichanthium annulatum*, *Aristida alsicansiouis*, and *Iseilema prostratum* (Jadhav 1979), but they also feed on tree leaves of *Salvadora oleoides* and *Salvadora persica* and leaves and pods of *Prosopis juliflora* (Smielowski and Raval 1988). Feral horse diets in New Mexico contain a lower percentage of grasses (50%) than studies of feral horse diet in other habitat types (Skasta et al. 2016; Hansen 1976), and feral burros are primarily browsers in Death Valley, California (Moehlman 1974). In three of seven annual diet studies, a native annual forb constituted the highest proportion (11%) of feral burro diets (Abella 2008), and shrubs can be the major component (58–84%) of feral burro diets, except in spring when they consume more forbs (Woodward and Ohmart 1976; Moehlman 1974).

Although perissodactyls try to satisfy energy demands (quantity) before quality of vegetation, they do forage selectively when higher-quality forage is easily available. Within a habitat-type, mountain zebras are highly selective, using only 7 of 17 grass species at feeding sites and 26% of plants available (Penzhorn and Novellie 1991). Out of 20 plant communities available in Mountain Zebra National Park, breeding herds preferred 9 in summer, 7 in winter, and 3 in both seasons, although bachelors showed no preference (Penzhorn and Novellie 1991). In Kenya plains zebras eat 6–7 species of grasses on average (Stewart and Stewart 1970), with zebras in South Africa eating 19 (Landman and Kerley 2001) to 27 species (Boyers 2011) displaying a seasonal change in species preference: 6 of 13 species preferred in the early dry season and 9 of 17 in the late dry season (Owen-Smith 2013).

Seasonal differences in perissodactyl diet are due to several factors. First, some plants are exclusively available during the wet season. Second, as more favored plants become less available during dry periods, perissodactyls such as rhinos may shift to less palatable species (Oloo et al. 1994). Third, some species may provide key resources during critical times such as succulents during drought. Finally, plants can differ in their relative palatability between wet and dry seasons, as well as different plant parts. This may be why rhinos

eat different plant parts during different times of the year (Oloo et al. 1994). Seasonal changes in the diet of *Equus* species are more likely due to changes in forage availability across summer and winter seasons (Crane et al. 1997; Hanley and Hanley 1982). In Hustai National Park, Przewalski's horses select a greater variety of vegetation classes in spring and autumn, less in summer, and only few in winter (King and Gurnell 2005). The diet of Asiatic wild asses across their range includes cereals and wormwood in summer, with proportions varying according to locale, conditions, and time of year, whereas in spring they feed on *Ephemerae*, such as *Poa* and *Bromus* (Bannikov 1971). Khulan (Asiatic wild ass) have a shrub-dominated C<sub>4</sub> diet in spring and fall and a grass-dominated C<sub>3</sub> diet in early summer and in midwinter (Horacek et al. 2012). Feral horse diet is generally consistent throughout the year; however, there are seasonal differences in specific grasses consumed or changes in the use of forbs during spring (Schoenecker et al. 2016).

Plants produce tannins and toxins to deter herbivory, called phenolic compounds. Ungulates that are categorized as grazers typically do not have the capacity to break down or detoxify plant phenolic compounds because these compounds are more common in browse species (Janis 1976). Thus, high amounts of phenolics in forbs and shrubs may deter grazing perissodactyls such as white rhinos and *Equus* species from feeding on them. Tannin-binding salivary proteins (TBSPs) that function to block the effect of plant toxins are produced in species that ingest tannins as part of their natural diet, such as black rhinos (Shimada 2006). Black rhinos can even induce production of TBSPs in saliva when they ingest greater amounts of plant toxins (Clauss et al. 2005a) to overcome toxic plant defenses.

Perissodactyls have varying requirements for surface water. White rhinos will drink daily or twice daily during the wet season when water is abundantly available, whereas in the dry season, they can reduce drinking to 2–4-day intervals (Pienaar 1994). Indian rhinos drink daily from streams, rivers, oxbow lakes, small puddles, and wallows, even some heavily contaminated with urine (Laurie 1982). Horses ingest approximately

30–50 mL water/kg body weight/day in both surface water and forage, and Indian rhinos are within the parameters for horses, having a daily water intake from 2.7 kg/day to 5.4 kg/day (Clauss et al. 2005b). In the dry season when standing water and seasonal streams are dry, rhinos feed near man-made reservoirs and in riverine habitat, which retains more water and has longer persistence of palatable herbs (Oloo et al. 1994). Khulan have higher water use efficiency than other equids and can exploit grassland pastures farther from water (Burnik Šturm et al. 2017).

## Tapirs

The family Tapiridae has five extant species which include Baird's tapir (*Tapirus bairdii*), Malayan tapir (*T. indicus*), little black tapir (*T. kabomani*), mountain tapir (*T. pinchaque*), and lowland or South American tapir (*T. terrestris*). Tapirs are browsers that inhabit dense tropical forests of South America and Asia. They feed on leaves, sprouts, stems, fruits and their seeds, aquatic plants, and some grasslike Poaceae and Cyperaceae species (Talamoni and Assis 2009). Tapirs are considered generalist herbivores, and the proportion of dietary items in their diet is closely attributed to what is available in their habitat. Thus, they are typically not "selective" feeders but more opportunistic (Henry et al. 2000), although some preference for certain plants has been observed (Talamoni and Assis 2009; Tobler 2002). The exceptions are the mountain tapir and Malaysian tapir which are more selective and choose certain favored plants regardless of their relative abundance in the habitat (Downer 2001; Meijaard and Strien 2003; Williams and Petrides 1980).

Tapirs have a broad and varied diet. The number of plant species they are known to feed on can be as high as 115 individual plant species (Williams and Petrides 1980; Hilbert et al. 2011) and ranging from between 8 and 50 different plant families depending on the region (Hilbert et al. 2011). In some areas, the diet of lowland tapirs is as high as 33% fruit (Bodmer 1990). Malaysian

tapirs prefer mostly woody plants from the families Euphorbiaceae and Rubiaceae (42%), whereas the recently discovered little black tapir feeds on palm leaves and seeds, but little else is known about its diet (Cozzuol et al. 2013). Baird's tapirs eat a high proportion of fiber from bamboo (40–55%; Tobler 2002). Tapirs are known to engage in geophagy, the deliberate ingestion of soil, as a way to obtain salt and minerals that may be deficient in the diet (Montenegro 1998).

Tapirs are considered important seed dispersers in the tropical forests they inhabit (Downer 2001; Galetti et al. 2001; Henry et al. 2000; Meijaard and Strien 2003). They ingest many seeds without crushing them with their molars, and even unprotected seeds survive passage in the tapir's digestive tract with germination rates of seeds in tapir feces similar to seeds from fresh fruits (Henry et al. 2000). Seeds of  $\geq 122$  different plant species have been identified in tapir feces in the Peruvian Amazon, illustrating the important role and facilitation of seed dispersal by tapirs (Tobler et al. 2010). Particularly for large seeds and palms (Palmae), which play a critical role in maintaining medium and large mammals during the dry season, a reduction or extinction of tapirs would deleteriously affect a substantial portion of native flora that sustains the ecology of the tropical forest.

## Rhinoceros

The family Rhinocerotidae is found in parts of Africa and Asia and is comprised of the black rhinoceros or "rhino" (*Diceros bicornis*), white rhino (*Ceratotherium simum*), Indian rhino (*Rhinoceros unicornis*), Javan rhino (*R. sondaicus*), and Sumatran rhino (*Dicerorhinus sumatrensis*). Rhinos inhabit dry savannas, grassland plains, wetlands, and dense forests in tropical and subtropical regions. The two African species have mouth adaptations to accommodate their feeding strategies: white rhinos are grazers with broad, square lips to facilitate exploiting short grass along the ground, whereas black rhinos are browsers with long, pointed lips for manipulating and gripping foliage

on shrubs and trees. Rhinos supplement their diet by licking or eating soil or rock material to obtain needed minerals, particularly sodium, potassium, calcium, and magnesium (Laurie 1982).

Black and Javan rhinos are exclusive browsers, whereas Sumatran rhinos are intermediate, switching between browse and grass depending on season and availability of plant species in their habitat (Dierenfeld et al. 2006). Black rhinos are selective browsers that forage on plants with low phenolic and alkaloid contents and high fiber, irrespective of protein content (Muya and Ogue 2000), although browse species that are more available in the habitat can be utilized more. However, black rhinos are also reported to select for high-quality forage with high crude protein content in other areas (Ganqa et al. 2005). Rhinos, like other ungulates, are confronted with a "cost" and "benefit" situation in which they have to balance the benefit of selecting for high-quality forage with the cost of search time and energy expended by such effort. For example, three species of plants accounted for more than 65% of the diet of black rhinos in three national parks in Africa, but browse availability only explained 14%, 15%, and 52% of diet selection, respectively (Buk and Knight 2010). Instead of diversifying their diet, black rhinos concentrate their feeding on a few species that have low plant toxins (Buk and Knight 2010). However, in general black rhinos have demonstrated a broad diet wherever they have been studied in Africa. *Acacia* species are important food plants comprising 27% of the diet in the wet period and 36% in the dry season, and the diversity of plants eaten is greater in the wet than the dry season (Oloo et al. 1994).

White rhinos are exclusive grazers of grasslands and even avoid herbaceous patches with too much forb cover. They focus on short-grass grasslands in wet months and shift to medium-tall *Themeda* grasslands as the dry season advances, and by late dry season, they move up to hillslopes to forage on tall-grass grasslands (Pienaar 1994). Indian rhinos, also grazers, feed on up to 183 different species of plants from 57 botanical families, but grass makes up a high percentage of their diet year-round (Pradhan et al. 2008), even as high as 70–89% (Laurie 1982). Indian rhinos will increase

browse intake in dry periods when grass is less available or when graminoids decline substantively in nutrition (Pradhan et al. 2008). Like other perissodactyls, rhinos have smaller ranges in areas with high vegetation diversity (Laurie 1982).

## Horses, Asses, and Zebras

The family Equidae occurs in steppe, semidesert, and desert environments (Schoenecker et al. 2016; Schultz and Kaiser 2013) and includes Grevy's zebra (*Equus grevyi*); plains zebra (*E. quagga*); mountain zebra (*E. zebra*); Asiatic wild ass also called khulan, onager, or khur (*E. hemionus*); Przewalski's horse (*E. ferus*); African wild ass (*E. africanus*); kiang (*E. kiang*); feral horse (*E. caballus*); and feral burro or donkey (*E. africanus asinus*). Equids are primarily grazers and are all very similar in their digestive physiology (Hummel et al. 2017). They are well adapted to low-quality forage (Janis 1976) with a total of 295 graminoid, herbaceous, and woody plant species identified as forage for *Equus* species (Schultz and Kaiser 2013). They select graminoids over other species when available (Schoenecker et al. 2016; see Table 4.1), yet each taxon has a specific spectrum of dietary plants. Przewalski's horse diet consists primarily of grasses, making up 75–83% of the diet even in winter (Siestes et al. 2009); however, when grasses are less available, they can utilize woody plants (Ganbaatar 2003). Feeding strategy of the Przewalski's horse is to satisfy energy demands with high quantity of forage and then secondly satisfy demands for higher-quality forage (Zang et al. 2017). The diet of kiangs is also made up of mostly graminoids, comprising between 84.3% and 100% of the diet (Harris and Miller 1995). Kiangs select for higher plant biomass and percent green foliage relative to random sites in the same habitats. At the plant level, kiangs select grasses over forbs and shrubs, whereas they select sedges in proportion to their availability during all seasons (St-Louis and Côté 2014).

Asiatic wild asses, have seasonally varied diets, foraging on up to 46 different species (Xu et al. 2012). *Stipa* is a major constituent of

khulan diet in spring and summer, with shrubs such as *Haloxylon ammodendron* and *Ceratoides latens* comprising up to 22% of khulan diet in winter (Xu et al. 2012). Khulan show strong seasonality with grazing in summer, mixed feeding in winter, and switching from one mode to the other in spring and autumn; their use of shrubs is more prevalent in winter (Burnik Šturm et al. 2017). Wild asses use water more efficiently (metabolically) than other equids and visit water sources primarily at night (Zhang et al. 2015) instead of during the heat of the day. Many truly desert-adapted species limit activity during the day to reduce heat loading and water loss and can sustain longer intervals between drinking.

The three extant species of zebras subsist predominantly on graminoids. Plains zebra diet consists almost entirely of grasses (Bodenstein et al. 2000; Venter and Kalule-Sabiti 2016), with occasional browse to maintain protein levels (Berry and Louw 1982). During the dry season, plains zebras spend more time foraging (Owen-Smith and Goodall 2014) and graze longer, taller grasses than in the wet season (Stelfox et al. 1986; Kleynhans et al. 2011). They select sites with lower levels of fiber than wildebeest or cattle (Voeten and Prins 1999) and even eat dry leaves (McNaughton 1985). They eat a broader range of species during the dry season than wet season to deal with limitations of reduced nutrition within dry season forage (Owen-Smith 2013). Plains zebra can be more exposed to diseases such as anthrax spores in soil during the wet season when they graze more intensively on short grasses and thus ingest more soil (Havarua et al. 2014). Mountain zebras are also tall-grass grazers, selecting greener grass with a high leaf/stalk ratio (Kraaij and Novellie 2010) and only including browse in their diet as quality and quantity of grass decline in winter (Penzhorn 1982; Novellie et al. 1988; Penzhorn and Novellie 1991; Weel et al. 2015). Grevy's zebras are predominantly grazers, although browse can comprise up to 30% of their diet during drought, and there can be significant variation in diet between individuals (Kleine 2010).

Major constituents of feral horse diets are graminoids, while forbs and shrubs play a more

limited, although sometimes still significant, role particularly in winter (Abaturov et al. 2016; Crane et al. 1997; Hansen 1976; Schoenecker et al. 2016; Skasta 2016). Grass species remain at or above 77% of feral horse diet in all seasons (Skasta et al. 2016) with sedges (*Carex* spp.) being consumed in bogs/meadows and stream sides (Crane et al. 1997) and shrubs making up only ~8% of the diet (Smith et al. 1998).

Donkeys, or feral burros, are the domesticated variety of African wild asses and evolved as a desert dweller able to survive in some of the harshest conditions on the planet. They retain many traits of their ancestors, able to live in areas with sparse vegetation, dispersed water sources, and widely fluctuating temperatures (Burden and Thiemann 2015). Feral burros feed on a wide variety of plant species, up to 39 different species in the Chemehuevi Mountains of California. However, as few as four plant species can comprise as much as 50% of the annual diet of feral burros (*Plantago insularis*, *Cercidium floridum*, *Prosopis* spp., and *Pluchea sericea*; Woodward and Ohmart 1976). They feed on fibrous plants; grasses comprise 66–76% of summer feral burro diets in the Cottonwood Mountains of Death Valley National Park (five times more than predicted based on their availability); however, burros switch to shrubs (50–81% of the diet) from September to April (Ginnett and Douglas 1982). *Muhlenbergia porteri* can be a substantial portion (24%) of July feral burro diets even though it is a very minor component of the plant community (Jordan et al. 1979). Feral burros are better adapted to low-quality diets than feral horses (Hummel et al. 2017) due to their lower energy and nutrient requirements, a greater potential for urea recycling (preserving metabolic water), and longer food particle retention in the digestive tract, which all serves to achieve higher digestibilities in burros (Hummel et al. 2017).

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## Perissodactyla Locomotion

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## Synonyms

Horse gait; Rhinoceros gait; Tapir gait

## Definition

Movements of the Perissodactyla (horses, tapirs, and rhinoceros) to transverse their environment.

The order Perissodactyla is composed of three families of odd-toed ungulates: Equidae, Rhinocerotidae, and Tapiridae (Pitra and Veits 2000). Within the Equidae family, there are eight extant species of horse, donkey, and zebra, whereas there are currently four living species of tapir and five rhinoceros (Wilson and Reeder 2005). The Perissodactyla are fully terrestrial and occupy a range of habitats. The equids inhabit grasslands, semi-desert, and desert-like environments (Schulz and Kaiser 2013), rhinoceros inhabit wet and dry grasslands (Sarma et al. 2011), and the tapirs inhabit various types of habitats ranging from very dry environments to wetlands to rainforests (Nowak 1991). The Perissodactyla are exclusively grass-eating animals classified as either grazers (eating vegetation at ground level) or browsers (eating from trees or bushes). For grazers, certain seasons may necessitate movements to find adequate food. For example, during the rainy season, zebras must migrate large distances in search of proper sustenance. Browsers, such as the rhino, are large and sedentary animals. They can find an adequate food supply year-round and therefore do not

need to migrate considerable distances (Mallet et al. 2019).

A defining characteristic of Perissodactyla is that they bear the brunt of their weight on their middle digit. This led to elongation and thickening of the middle toe and accounts for their mesaxonic symmetry. All present-day Perissodactyla have either one or three hoofed toes. The hoof itself contains wide and flattened bones that bear circular edges and are surrounded by a keratinous layer (comparable to the nails of claws) (Janis and Bernor 2019). The perissodactyls use unguligrade foot postures (walking on the toes) that serve to lengthen the legs, allowing for faster and more energy-efficient running (Janis and Bernor 2019). The tapir is unique in that it retains the structure of the ancestral tetradactyl perissodactyls and presents with four digits on its foreleg (MacLaren and McHorse 2020).

## Gait Sequences

Gait refers to the sequence that the limbs come into contact with the substrate. Within the perissodactyls there are numerous gait types largely driven by gait diversity in the equids (Andersson et al. 2012). To minimize discussion, we will only survey gait sequences observed in undomesticated perissodactyl species. Quadrupedal gaits in perissodactyls are usually categorized as symmetrical or asymmetrical based on kinematics. Symmetrical gaits occur when footfalls of the forelimb and hind limb are evenly spaced in time (e.g., walk, pace, or trot). Asymmetrical gaits (e.g., gallop and bound) occur when the actions of the forelimb or hind limb are unevenly spaced in time. All walking gaits in the perissodactyls are symmetrical and are defined by the sequence and coupling patterns by which animals move their limbs (Alexander 2003; Granatosky 2018). A lateral-sequence gait is one in which each hind limb footfall is followed by an ipsilateral forelimb footfall (i.e., right hind limb, right forelimb, left hind limb, and left forelimb). A diagonal-sequence gait is one in which each hind limb footfall is followed by a contralateral forelimb footfall (i.e., right hind limb, left

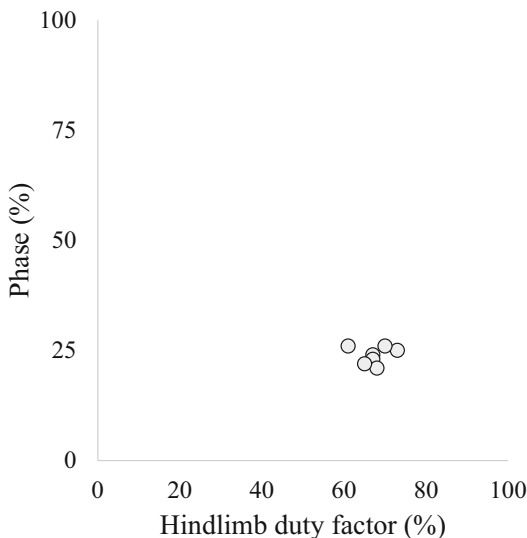
forelimb, left hind limb, and right forelimb). Commonly during walking gaits, the forelimbs and hind limbs are traveling together as a slightly asynchronous couplet. When the ipsilateral forelimbs and hind limbs are traveling together, this is referred to as a lateral-couplet; when the contralateral forelimbs and hind limbs are traveling together, this is referred to as a diagonal-couplet. Very rarely do the limbs move together in perfect synchrony (Granatosky 2018).

Lateral-sequence lateral-couplet footfall patterns tend to be most common in the perissodactyls and are assumed to be the best mechanism to prevent interlimb interference (Hildebrand 1965; Fig. 1). However, this footfall pattern is thought to be inherently unstable because a majority (~66%) of the stride is spent as a unilateral bipod (i.e., only two ipsilateral limbs in contact with the support), which tends to roll the body side to side throughout the stride (Cartmill et al. 2002). Lateral-sequence diagonal-couplet footfall patterns are observed in the tapirs. This footfall sequence is inherently more stable than lateral-sequence lateral-couplet gaits due to the generally low proportion of the stride spent as a unilateral bipod (~22%), and the relatively high proportion of the

stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support). In general, foot positions arranged as diagonal bipods and large tripods are thought to be highly stable (Cartmill et al. 2002; Granatosky 2018).

When it is necessary to increase locomotor speed, animals must transition into running gaits. Although it is commonly believed that the reason for a gait transition is due to maintaining a low-energy cost, it has been noted that other factors, such as reducing bone strain or low interstride variation, may play an important role in these transitions (Granatosky et al. 2018a; Wickler et al. 2003). The trot and pace are symmetrical quadrupedal runs. Running gaits include some period of the cycle in which no feet are touching the ground (i.e., an aerial phase). In trotting, diagonally opposite feet move in phase with each other; in pacing, the two feet on the same side of the body move in phase with each other.

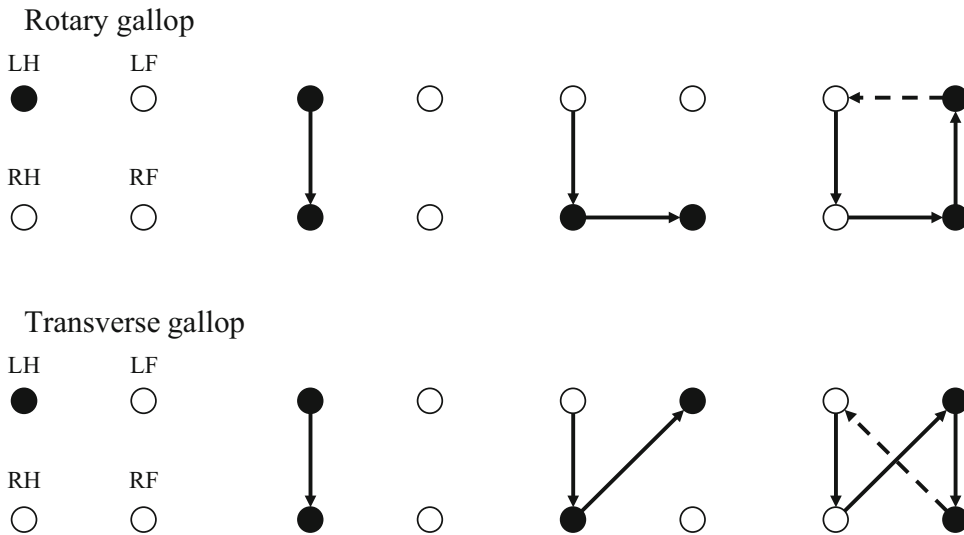
At high locomotor speeds, the perissodactyls adopt asymmetrical galloping gaits. The two types of gallops are known as the rotary and traverse gallops. In horses and rhinoceros, the transverse gallop is most common. The transverse gallop is described as one forefoot being followed forward by the contralateral hindfoot, leading to a single flight phase with the lift off of the two forelimbs. Transverse galloping is mainly utilized by larger animals with longer forelimb segments and is additionally influenced by environmental and biomechanical factors (Biancardi and Minetti 2012). The rotary gallop is utilized most frequently by the tapirs (Hildebrand 1977). The rotary gallop is characterized by one forefoot moving forward followed by the ipsilateral hindfoot. This leads to a flight phase in between the two forefeet hitting the ground and the two hindfeet hitting the ground (Fig. 2).



**Perissodactyla Locomotion, Fig. 1** “Hildebrand” plot displaying phase against hind limb duty factor collected during quadrupedal walking in perissodactyls ( $n =$  seven species)

## Limb Loading

Due to the great size disparity and high-speed locomotion observed within the order, each of the species have developed somewhat differing



**Perissodactyla Locomotion, Fig. 2** Foot fall diagram representing the two types of gallops found in perissodactyls. LH = left hind limb; LF = left forelimb; RH = right hind limb; RF = right forelimb

biomechanical strategies to mitigate the high external loads acting upon their limbs (Mallet et al. 2019). In general, the forelimb of the perissodactyls bears more body weight than the hind limb and serves a net braking function (Dutto et al. 2006). Accordingly, bones of the forelimbs need to be reinforced in all directions to support higher masses in heavier animals. This is especially clear in the Rhinocerotidae. Mallet et al. (2019) explored interspecific variation in long bone morphology in extant rhinos using three-dimensional geometric morphometrics to elucidate how loading, phylogeny, and body mass influence osseous structures. Within the forelimb, the humerus demonstrates the clearest signal associated with loading regime. Across species, the humerus enlarges in the craniocaudal and mediolateral directions proportionally with the increasing mass of the rhinoceros. Furthermore, the lesser tubercle of the humerus has several vital functions in rhino locomotion. Its primary function is to promote greater shoulder stability and prevent hyperextension, which is accomplished by stabilizing shoulder articulation and providing a greater area for the medial end of the *m. supraspinatus* (a primary forelimb extensor and shoulder stabilizer) to insert (Mallet et al. 2019). Additionally, because of its relationship with the *m. supraspinatus*, the lesser

tubercle also acts as a medial lever arm for the extension movements of the forelimb. Moving distally, rhinos demonstrate an enlargement of the epicondyles of the humerus that provides a larger insertion area for the flexor and extensor muscles of the digits and enhances the stability of the elbow articulation (Mallet et al. 2019). Similarly, the distal trochlea of the humerus has an increased articular surface area to diminish the forces of proximodistal compression and mediolateral extension, thus allowing for posture to be maintained at high body masses (Mallet et al. 2019).

In all species of rhinoceros, most of their weight is carried by the proximal articulation surface of the radius, which expands medially and becomes asymmetrical in heavier rhinos (Mallet et al. 2019). Medi lateral weight distribution is enabled through the laterally expanding ulnar shaft. The medial development of the olecranon process of the ulna is related to larger insertions for the flexor muscles, which are essential to prevent wrist hyperextension (Mallet et al. 2019). Several characteristics in the forelimb are present that prevent wrist hyperflexion while enabling the massive rhinoceros to travel sturdily on multiple substrates. For example, there is an increased mediolateral wrist articulation freedom due to a



decrease in the styloid processes of the radius and ulna. Ultimately, this reduces the articular surface for the scaphoid and thus limits craniocaudal wrist flexion (Mallet et al. 2019).

The rhinoceros hind limb carries less weight than the forelimb, yet it has an essential propulsive function. As such, the anatomy of the limb is organized in a fashion to both amplify and resist these forces. The rhinoceros' femur is mediolaterally reinforced under the head and neck that has led to an enlargement of the medial condyle and epicondyle on the distal epiphysis (Mallet et al. 2019). The lesser trochanter is distally located along the femur, which provides the hip flexors have an improved lever arm (Mallet et al. 2019). The rhinos also have a mid-shaft third trochanter that is associated with a more distant and lateral greater trochanter. This anatomical arrangement allows for more vigorous hip flexion and abduction (Mallet et al. 2019). This contrasts sharply with horses and tapirs that have more proximal third and greater trochanters. As the greater trochanter is the insertion site for *m. gluteus medius* (the primary hip extensor), this anatomical arrangement in rhinos indicates that hip extension is less powerful than horses and tapirs (i.e., more cursorial perissodactyls) (Mallet et al. 2019). Finally, there is lateral torsion in the distal femur that results in a more laterally deviated position of the knee. This knee placement may improve weight-bearing by shifting the body mass laterally (Mallet et al. 2019).

In contrast to the massive size of the rhinoceros, the tapirs are smaller and have anatomy more consistent with cursorial locomotion, albeit not as specialized as the equids (MacLaren and McHorse 2020). The tapirs show a general narrowing in the mediolateral aspect of the long bones on the limbs. This reduces bone mass (and limb mass in general), which means that the muscles do not have to overcome as great of an inertial force to accomplish movement (MacLaren and Nauwelaerts 2016). The general musculature in the forelimbs of tapirs is akin to the horse; they differ mainly in their relative size and mass percentage (MacLaren and Nauwelaerts 2016). An

assessment of the physiological cross-sectional area (PCSA) of the muscles shows no notable differences between the *Tapirus* and *Equus* except for two muscles (i.e., *m. flexor carpi ulnaris* and *m. biceps brachii*). These muscles both presented larger in *Equus* are consistent with their high-speed cursorial locomotion (MacLaren and McHorse 2020).

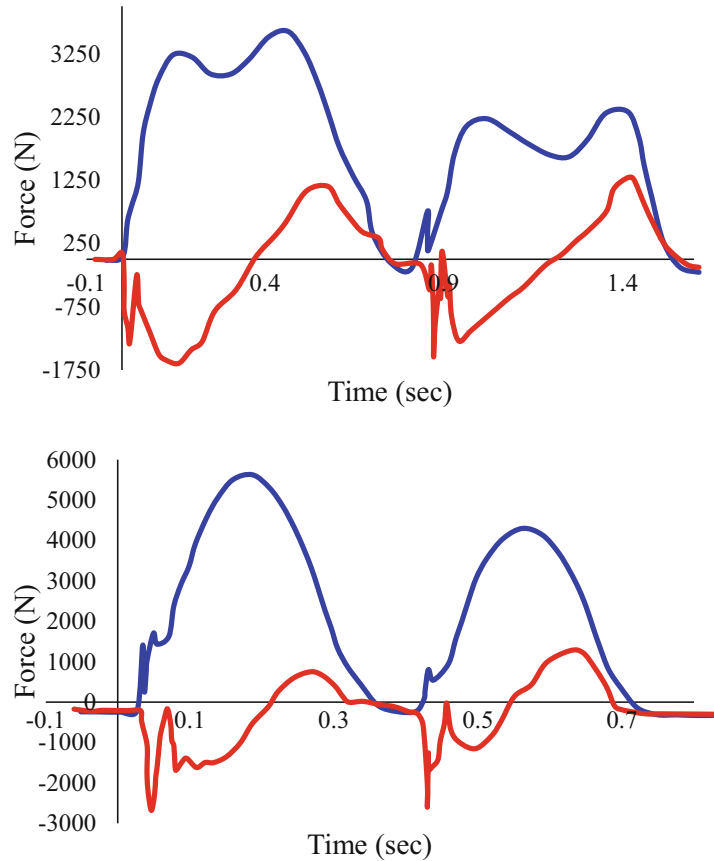
The tapirs display a shallow glenohumeral cavity compared to other perissodactyls, which has been attributed to their use of the rotary gallop (MacLaren and Nauwelaerts 2016). This shallow cavity facilitates a higher degree of shoulder mobility and increases the parasagittal movement of the humeral head within the shoulder joint enabling tapirs to generate greater stride lengths (MacLaren and Nauwelaerts 2016). Together, the combination of a large supraspinous and associated *m. supraspinatus*, a shallow glenoid cavity, and a distal footpad equip the tapir to function well at high speeds (MacLaren and Nauwelaerts 2016). Tapirs also have humeral flexors inserted in a notably proximal manner to the joint center. This proximal muscle insertion results in a shorter lever arm for *m. teres major* and *m. deltoideus* that allows for decreased torque, rapid flexion of the shoulder, and rapid adduction of the humerus (MacLaren and Nauwelaerts 2016).

Merkens and Schamhardt (1994) analyzed kinematics and the ground reaction forces occurring in the fore- and hind limbs of horses during different gait patterns with force plates and kinematic analysis assisted by the presence of photodiodes (tracers) on the limbs. They found that the ground impact occurring during walking and trotting were similar in each limb, but that overall, the forelimbs had a higher ground force reaction than the hind limbs. Forelimbs carry approximately 60% of the body weight at rest and have greater vertical forces when moving (Merkens and Schamhardt 1994) (Fig. 3). However, the hind limbs experience greater horizontal forces during locomotion, as they generate more of the propulsion for the animal (Granatosky et al. 2018b).

During locomotion, high external forces act to hyperextend the fetlock joint in horses.

### Perissodactyla Locomotion,

**Fig. 3** Force plate recording of the horizontal (red) and vertical (blue) ground reaction forces of the right fore- and hind limb at walk (top panel) and trot (bottom panel). Data from Merkens and Schamart (1994)



Hyperextension of the fetlock joint causes high levels of stress in the *m. interosseus medius* (suspensory ligament) and deep digital flexor and superficial digital flexor tendons. The high forces get built up within the tendons as stored potential energy, allowing the limb to act in a spring-like manner, releasing the stored energy as kinetic energy for high-efficiency gaits. However, the high stresses in these tendons increase with speed, and thus, the tendons become more prone to injury with increased speeds (Harrison et al. 2010).

### Perissodactyl Locomotion and Medicine

For millennia, horses have been an essential part of human existence. Their earliest use was for

meat consumption, but they eventually became necessary for transportation and efficient farming (Hausberger et al. 2018). With the onset of modern industrialization, horses transitioned from a necessity into a luxury, as they are now primarily used for entertainment through horse racing and casual enjoyment in horseback riding (Hausberger et al. 2018). One use that has been gaining more traction lately is the use of horses in hippotherapy (Koca 2016). Horses, like humans, have a tri-axial movement pattern of the pelvis and can consequently simulate this movement pattern in patients when they are placed on the horse's back (Koca 2016). The goal of this therapy is to utilize this similar movement to provide motor and sensory input during physical therapy (Koca 2016). The natural gait of horses encourages anterior and posterior swinging movements, the

development of the patient's paraspinal muscles, and affects the bones of the patient's pelvic girdle two times more than the gait of the patient alone (Koca 2016). Hippotherapy has been shown to decrease recovery time in patients, as well as improve their balance, posture, and muscle control (Koca 2016). Clinical trials have demonstrated efficacy in patients with multiple sclerosis, cerebral palsy, autism, and those recovering from a stroke (Koca 2016).

## Conclusion

The Perissodactyla order is composed of the families Equidae, Tapiridae, and Rhinocerotidae. The defining characteristic of Perissodactyla is that they have either one or three hoofed toes and bear the brunt of their weight on their middle digit. All species use symmetrical and asymmetrical gaits and transition through standard mammalian gait patterns as speed increases (i.e., lateral sequence lateral-couplet and lateral-sequence diagonal-couplet gaits during walking, trotting, or pacing during medium speeds, and rotary or transverse gallops during high speeds). The large size disparity within the order has resulted in highly variable limb loading and anatomy across the species. Although the large mass of the rhinoceros is not particularly well suited to speedy gaits, its massive size is an advantage against predators and thus rhinoceroses have developed osteological features to support their large mass. More primitive and significantly smaller than the horse, tapirs have more simplistic anatomy; however, this anatomy has efficiently evolved to enable tapirs to escape predators through their rotary gallop. The horse has evolved several elastic strain adaptations to help facilitate and mitigate the high external loads experienced during cursorial locomotion. The perissodactyls, especially the horse, have had a long history with human. Starting out as a food source, the horse transitioned into a means of transportation and now serves as a medical tool to help patients regain mobility.

## Cross-References

- [Adaptation](#)
- [Adaptive Radiation](#)
- [Basal Metabolic Rate \(BMR\)](#)
- [Dispersal Ability](#)
- [Dispersal Patterns](#)
- [Diurnality](#)
- [Domestication](#)
- [Equine Cognition](#)
- [Equine Communication](#)
- [Equine Diet](#)
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- [Vertebrate Nervous System](#)
- [Zoo](#)
- [Zoology](#)

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## Permanent Teeth

### ► Dental Formula

## Perseveration

### ► A-Not-B Problem

## Perseverative Error

### ► A-Not-B Problem

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## Personality

### ► Temperament

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## Personality in Animals

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### Synonyms

Behavioral syndromes; Individual differences;  
Temperament

### Introduction

What is personality? If asked this question, most people would have an intuitive sense of what the word “personality” means. When describing their pets, or animals at zoos, it would not be uncommon for someone to use terms such as curious, excited, or shy. However, pinning down a clear definition of personality is more challenging. In humans, personality refers to individual differences in patterns of thinking, feeling, and behaving (Gosling 2001). These patterns are thought to be stable across time, meaning that a person who tends to be excitable at one time point will also tend to be excitable a month later, although there are known changes that occur across a person’s life span (Roberts et al. 2006). Individual patterns are also thought to be stable across contexts. For example, someone who is curious about new people will also be curious about new aspects of their environment. It is unfortunately not possible to ask an animal how they are thinking or feeling. As a result, the most commonly used definition of animal personality is individual differences in behavior that are consistent across time and contexts (Gosling 2001). Despite this, researchers have often shied away from labeling individual

differences in behavior as “personality,” for fear of anthropomorphism (Gosling and John 1999). Instead, labels such as behavioral syndromes and temperament have been used interchangeably with personality. However, there must be measures that do not rely on verbal reports of thoughts or feelings, as personality has been repeatedly assessed in young children who are yet to develop language abilities (e.g., Thomas and Chess 1977). So, if we cannot ask an animal, or child, about their personality, what methods can we use?

### Measuring Animal Personality

The methods used to study animal personality can be categorized using two main criteria: the way in which measures are selected or the data collection method. Using the former criterion, methods can be distinguished as either predominantly top-down or bottom-up. Bottom-up procedures involve selecting measures that are specific to the studied species, therefore maximizing the likelihood of including relevant traits (Weiss and Adams 2013). However, this does mean that cross-species comparisons are made more challenging, due to the variation in measures used in different studies. In contrast, top-down approaches adapt an existing model to create a measure for assessing another species (Freeman et al. 2011). This does run the risk of including traits that are irrelevant outside of the original model, but facilitates cross-species comparisons.

When using a top-down approach, a commonly adapted framework is the Five Factor Model (Goldberg 1990). This is a widely accepted model for human personality, and as the name suggests, it consists of five factors: Openness to Experience, Conscientiousness, Extraversion, Agreeableness, and Neuroticism. In this model, an individual with a high score on Openness to Experience tends toward traits such as imagination, creativity, and curiosity, while individuals who are self-disciplined and dutiful score highly on the Conscientiousness factor. The Extraversion factor describes an individual’s tendency to be



sociable, assertive, and active. Agreeableness contains traits such as trust, cooperation, and a lack of aggression, and finally, vulnerability to stress, anxiety, and depression describe the high pole of the Neuroticism factor.

The animal personality literature suggests that factors analogous to all of the human five factors are found in other species (Gosling and John 1999). In the most recent comprehensive review to date, a factor similar to Extraversion was found most frequently, in 90% of studies, across taxa as diverse as chimpanzees and octopuses. Analogues to Neuroticism and Agreeableness were almost as common, with all three of these factors emerging in cats, dogs, rhesus monkeys, gorillas, and chimpanzees. Openness-like dimensions were present in 7 of 12 species, which was at least partially attributed to methodological issues. Finally, although both cats and dogs possessed a factor combining Conscientiousness and Openness, only chimpanzees exhibited a pure Conscientiousness factor. Overall, this suggests that shared, general mechanisms may be responsible for the personality dimensions of Extraversion, Neuroticism, Agreeableness, and potentially Openness, although the specific behavioral manifestations of each differ between species. In contrast, Conscientiousness may be relatively young in evolutionary terms, shared only by humans and our closest phylogenetic relatives.

Although there appears to be a considerable number of personality traits shared across species, there are clear species-specific differences in how these are manifested in behavior. For example, a cuttlefish classed as bold, similar to one facet of human Extraversion, spends more time at the top of the tank and produces a visual threat display in response to a predator (Carere et al. 2015). In contrast, an extraverted bottlenose dolphin may vocalize often and engage in a variety of play behaviors (Highfill and Kuczaj 2007). It is therefore important for specific features of any species to be carefully considered when assessing their personality. For instance, to assess aggressiveness as a personality trait in dolphins, it would be inappropriate to include the skin color threat displays seen in cuttlefish (Carere et al. 2015), but

relevant to measure biting or ramming (Connor et al. 2000).

Instead of top-down versus bottom-up categorization, animal personality methods can be distinguished based on the method of data collection, of which there are two main types: behavioral coding and trait rating. Behavioral coding involves making observations of animals and recording the occurrence of behaviors of interest. Where naturalistic coding is used, animals are observed without any human intervention or manipulation, which can be in a captive or wild setting (Freeman et al. 2011). For example, the behavior of harbor seals and California sea lions has been recorded without experimenter interference (de Vere 2017). Using the frequencies of these behaviors, both species demonstrated two personality factors: boldness and routine activity. Bold seals and sea lions were active, alert, and more likely to move around on land, while highly routine individuals tended to swim in predictable patterns and rest little. In contrast, experimental coding involves making observations during behavioral tests. For example, hermit crabs have been assessed for personality using two tests: predator and open field (Watanabe et al. 2012). The responses of individual crabs were described using two behavioral dimensions. The first, named shy-bold, consisted of the time taken for crabs to emerge versus hide in response to a predator. The second dimension was named exploration-avoidance, as it contained the measurements of exploration in a novel environment, the open field, and the time taken to emerge after the predator was removed.

The main alternative, trait rating, involves people judging individual animals on their tendencies on a number of trait words, such as curious or active. These judgments may be based on a rater's cumulative experience with the focal animal, as in the case of pet owners or zoo keepers (Freeman et al. 2011). An example of this can be seen in a personality assessment of bottlenose dolphins (Highfill and Kuczaj 2007). The dolphin population was housed at a facility where trainers were responsible for their daily care. These people rated the dolphins on traits such as reliable, curious, and

playful, revealing individual scores that paralleled those found in humans (Goldberg 1990). Alternatively, judges may rate animals after having made a certain set of observations. For example, this design has been applied by having judges rate individual horses on traits such as exploration, vigilant, and submissive, after observing 2 hours of their behavior (Lloyd et al. 2007). This revealed six factors that explained the variation in ratings between horses, one of which was named sociability, as it consisted of traits such as sociable, playful, and popular.

## Why Do We Care About Animal Personality?

### Welfare

Now that we know that animals have personality, you may be wondering: why do we care? Well, personality has been linked to several interesting areas of research. One of the most important of these for the animals themselves is welfare. Commonly used indicators of poor animal welfare are stereotypic behaviors, which are defined as those that are repetitive, unvarying, and functionless (Mason and Latham 2004). Given that these behaviors are estimated to be exhibited by more than 85 million animals globally (Mason and Latham 2004), it is important to understand the contributing factors, and growing evidence suggests that one of these is personality.

In one example of this, an interaction was found between rearing conditions and personality. Highly gentle or nervous 4-month-old rhesus macaques who were reared in indoor cages were more likely to exhibit stereotypic behaviors later in life (Vandeleest et al. 2011). The same effect was not seen for nervous or gentle macaques reared outdoors, therefore underscoring the subtle influence that personality can have on welfare outcomes. In another taxon, personality has also been found to mediate the effects of changes in environmental conditions. Parrots rated as highly extraverted developed fewer stereotypic behaviors while living in a barren environment (Cussen 2013). Low extraversion birds also maintained a higher level of stereotypies even after being

reintroduced to a more complex, enriching environment.

However, there are issues associated with using stereotypic behaviors as indicators of poor welfare. One of these is that not all personality types seem to react in the same way to negative environments. A personality dimension along which animals can be characterized is the proactive-reactive axis. Proactive animals respond to stressful stimuli in an active manner, such as by exhibiting stereotypic behaviors. In contrast, those with reactive personalities are more likely to show passive responses, resulting in fewer stereotypic behaviors, despite exhibiting more drastic physiological markers of stress (Ijichi et al. 2013). Therefore, of two animals not exhibiting stereotypic behaviors, one with a reactive personality is more cause for concern than one with a proactive personality. Consequently, knowledge of animal personalities could allow welfare measures to be individualized for maximal well-being.

Personality is also associated with the extent to which animals interact with environmental enrichment. Although definitions of enrichment have changed over the years, a broad definition is increasing the choices available to animals and encouraging species-typical behavior by providing physical, mental, and social stimulation (Kulpa-Eddy et al. 2005). Improving animal welfare is frequently cited as the primary function of providing environmental enrichment, but the needs and preferences of individual animals are often not taken into account.

Most of the evidence suggesting that personality mediates the effectiveness of various types of enrichment comes from studies of chimpanzees, involving research or training participation. In one such study, cognitive tasks involving selecting answers on a screen were thought to be potentially enriching. However, even when these tasks were familiar, chimpanzees characterized as stress sensitive exhibited increased self-directed behaviors, such as scratching, after providing an incorrect answer (Yamanashi and Matsuzawa 2010). High scores on the Openness personality dimension have also been associated with voluntary participation in potentially enriching interactions with humans. For example, high-Openness

chimpanzees chose to spend more time engaged in research activities (Herrelko et al. 2012), as well as successfully completing a voluntary medical sampling procedure in the first session (Reamer et al. 2014).

In a study of a different species, snow leopards, novel objects were provided as a form of environmental enrichment. Leopards who visited these objects more also scored highly on one or both of the personality dimensions of Active/Vigilant and Curious/Playful (Gartner and Powell 2012). This provides two potential implications for using novel objects as enrichment for these animals. Firstly, novel objects may not be effective for providing enrichment for leopards with low scores on Active/Vigilant and Curious/Playful. Secondly, individuals with high scores on these dimensions may visit the objects more and therefore derive greater enrichment value from them. However, they may also become bored faster and require more frequent changes in enrichment provisioning to maintain potential welfare benefits.

Finally, several authors have made suggestions for individualized housing provisions, based on personality assessments. For example, cheetahs with high scores on the tense-fearful dimension were rated as being fearful, insecure, and tense (Wielebnowski 1999). As a result, it was suggested that providing ample access to hiding places, out of reach of disturbances, might disproportionately benefit these individuals. Similarly, shy cuttlefish, who responded most passively and with the least threat behavior toward a predator, may require housing that shelters them from observers (Carere et al. 2015). Lastly, there is emerging empirical evidence to support such suggestions; for example, gorillas with high understanding scores seem to react more negatively to the presence of large crowds of visitors, as they performed more undesirable behaviors under these conditions, including stereotypies (Stoinski et al. 2012). Personality therefore has a large range of potential influences on the welfare animals experience, as well as our measures of it. Expanding our understanding of these effects can help us provide the animals under our care with the best possible welfare.

## Learning and Problem Solving

Personality has also been linked with individual variation in learning performance and problem solving, which is significant for several reasons. First, animal models are often used to inform our knowledge of the general mechanisms underlying learning and cognition. Ruling out any variation caused by confounding factors, such as personality, is therefore important for determining the true effects of experimental manipulations. Secondly, animal in many settings, such as pets, working roles, and veterinary check-ups, often need to be trained on specific behaviors. It is therefore useful to understand the influence of personality on training success, as this can facilitate the use of the most effective techniques for each individual.

The personality trait of exploration has been frequently assessed in relation to learning performance. For example, exploration types in rhesus macaques were associated with training success on a positive reinforcement task (Coleman et al. 2005). This type of training is commonly used in the management of captive populations. In this case, animals learned that a clicker sound was associated with being rewarded with a food treat from the trainer's hand. The monkeys then heard the clicker and received a reward if they touched a target hung outside their cage. Training was considered successful if over three consecutive 10 min sessions, the individual performed the behavior on command at least 3 times. Exploratory monkeys, who approached and investigated novel food, were all successfully trained on the task, whereas only half of the individuals who never investigated the item were successfully trained.

Similar results have been found in other species. Ravens were assessed for their exploratory tendencies by measuring their latency to investigate a novel object, a bottle (Range et al. 2006). First, animals watched the experimenter place food inside a bottle. They were then given access to the bottle, which they had to manipulate to access the reward. More exploratory ravens were fastest at learning to solve this problem, primary due to initially approaching the bottle faster. Parallel results have been found in mice, in which more exploratory individuals were those who

investigated more open areas in a novel environment (Matzel et al. 2003). Mice who exhibited this tendency also demonstrated more efficient learning on several different learning tasks: discriminating between rewarded and unrewarded odors, suppressing movement when exposed to an unpleasant stimulus, accuracy in locating a reward in a maze, and time taken to locate a hidden platform in a pool of water. One possible explanation for such findings is that exploratory individuals are simply more likely to encounter opportunities for learning, as they will be more likely to investigate novel environmental features (Sih et al. 2004).

Emerging evidence implicates other personality dimensions in specific aspects of learning abilities. In one study, rhesus macaques were trained on a serial chaining task, which requires a series of stimuli to be selected in the correct order. Initially, the item list is learnt by trial and error, with a food reward provided for a complete correct response (Altschul et al. 2016). Macaques rated as high on friendliness and openness personality dimensions exhibited lower error rates, and made better progress, meaning that they made it further through the list in the correct order before making an error or completing the sequence. More specifically, friendliness was associated with consistently better performance over time, while high openness was associated with faster rates of learning.

Finally, there is tentative research suggesting that certain personality types are associated with greater innovation and creativity, and therefore more efficient learning. Pigeons were assessed for neophobia, a common measure of the bold-shy axis, by measuring the time taken to feed when a novel object was placed next to their food dish (Bouchard et al. 2007). Birds who exhibited lower neophobia were more innovative in opening a problem box, thus facilitating faster task completion. These individuals also required fewer demonstrations by a conspecific to learn how to remove a stopper from a tube containing food, therefore exhibiting faster social learning. Bottlenose dolphins also show individual differences in the ability to mentally plan their behavior, leading to differences in the extent of trial and error required to solve problems (Kuczaj and

Walker 2006; Kuczaj et al. 2009). Furthermore, the behavior of bold dolphins is more likely to be copied by other individuals (Kuczaj et al. 2006; Kuczaj and Yeater 2006). This is particularly interesting, as it suggests that differences in learning and problem-solving abilities may not only be related to one's own personality but also to that of those around you.

### Friendships

Like humans, members of many other species have friends. Unfortunately, we cannot ask a chimpanzee who they are friends with, but we can measure who they choose to spend time with and what they do during this time (Weinstein and Capitanio 2008). Personality seems to influence who become friends in the first place, and potentially one's satisfaction with these relationships over time. In rhesus macaques, affiliative behaviors tend to be performed most between related individuals of the same age and sex. However, when these factors were taken into account, individuals initiating affiliative behaviors with each other tended to have similar scores on two personality dimensions: adaptability and equitability (Weinstein & Capitanio 2008). Similarly, even when sex and age effects were accounted for, chimpanzee friends tended to have similar sociability scores (Massen and Koski 2014). In this study, the chimpanzee sociability personality dimension contains descriptors such as many animals sitting close by, and the frequency of grooming received and given, both of which are known affiliative behaviors. Chimpanzee sociability has significant parallels with human extraversion (Goldberg 1990), which human friends also tend to score similarly on (Nelson et al. 2011). Another primate study also found support for this extraversion-friendship link, with capuchin pairs demonstrating higher quality relationships if they had similar sociability scores (Morton et al. 2015).

Although research examining links between animal friendships and personality has predominantly focused on primate species, it is likely that similar associations are present in other taxa. For example, recent evidence demonstrated that three personality factors – extraversion,

conscientiousness, and neuroticism – influence the quality of bonds formed between pairs of bottlenose dolphins (Moreno 2017). Dolphins had the most positive bonds when each individual in a pairing scored similarly on the conscientiousness factor. This parallels the role of conscientiousness in human relationships; both teenager friendship quality (Jensen-Campbell and Malcolm 2007) and adult friendship satisfaction (Wilson et al. 2015) are associated with conscientiousness scores. Interestingly, the opposite pattern was true for extraversion and neuroticism. Pairs of dolphins who were dissimilar in their scores on these personality dimensions had the most positive bonds (Moreno 2017). Both similar and dissimilar extraversion scores have been associated with human friendships during college (Nelson et al. 2011), suggesting that bottlenose dolphin friendships may have specific features that facilitate dissimilar scores to a greater extent. The association between dissimilar neuroticism scores and dolphin bond quality (Moreno 2017) contrasts with findings in capuchins, in which relationships were more friendly and affiliative between individuals who were similar in neuroticism (Morton et al. 2015).

The maintenance of friendships over time may also be affected to some extent by personality. For example, not all rhesus macaque friendships are maintained in the long-term. The more similar friends' equitability scores were at 1 year old, the greater the likelihood of those macaques still being friends 1 year later (Weinstein and Capitanio 2012). However, current evidence suggests that personality similarity or dissimilarity may be most important in the forming of friendships and then that other factors may become more important over time. This is consistent with findings in humans, in which personality has a greater effect on the formation of friendships, compared to their maintenance over time (Hartup 1996; Nelson et al. 2011).

### Human Disturbance

Personality may influence the extent to which individual animals are affected by human activities, such as wildlife tourism and urbanization. Firstly, while the former provides the potential

for educating people about the natural environment, the public's high demand for this access to wildlife exposes animals to far greater levels of human disturbance than ever before. It has been suggested that individuals differ in their tolerance of these anthropogenic disturbances (Bejder et al. 2009). Depending on this tolerance level, some animals may suffer more severe consequences than others. For example, more sensitive animals may be immediately displaced upon the onset of human presence, while others may remain in the location. However, even those who remain may have personality characteristics that alter their behavioral reactions. Some animals seem to habituate to human presence, meaning that over time their response to humans decreases, whereas others become sensitized and exhibit more extreme behavior each time they are disturbed (Bejder et al. 2009). Furthermore, once human presence is no longer novel, it is difficult to assess the extent of our impact, as animals with low tolerance levels have already been displaced.

An empirical example of the effects of personality on initial response and subsequent habituation to human disturbance comes from yellow-eyed penguins. This species is endangered and found only in its home country of New Zealand (Ellenberg et al. 2009). Penguins were categorized into three personality types based on their response to a person in close proximity: timid, calm, and aggressive. Each penguin was then assessed for habituation to human disturbance over five days, during which an experimenter approached the nest once per day. On the first day, the heart rates of calm and timid females took the longest time to return to baseline levels after human approach. Over the duration of testing, there was negligible change in the heart rate recovery time of aggressive birds. However, for calm birds, both recovery time and the maximum heart rate induced by the disturbance decreased. This reduction in reaction across repeated exposure indicates that habituation to human disturbance occurred only in birds with calm personalities. Such findings are of great importance for understanding the impact of well-meaning wildlife tourists, particularly for severely threatened species.



Not all sources of potential disturbance by humans come from tourism. Indeed, increased urbanization has the clear side effect of impacting animal populations. This provides the potential for benefits, such as new food sources and warmer temperatures, but also costs, such as increased potential for exposure to urban predators (Sol et al. 2013). Not all animals are equally suited for expanding into these urban environments, and it has been suggested that those of certain personality types, such as exploratory and bold, are most likely to reach more distant habitats and/or arrive first in a new habitat (Sol et al. 2013).

In support of such suggestions, some differences have been found in the personalities of birds inhabiting rural versus urban environments. In one study, personality was assessed in house sparrows from four locations varying in their extent of urbanization (Bokony et al. 2012). The four traits measured – object neophobia, food neophobia, risk taking, and activity – formed one broader personality dimension in birds from the rural locations. In urban sparrows, food neophobia (avoidance of novel food) remained a separate trait. A potential explanation for this finding is that sparrows inhabiting urban locations may have more food sources to choose from, thus relaxing the selection pressure experienced by rural birds. There were also more birds in the urban sample exhibiting very avoidant responses in the predator test. This may represent an advantageous adaptation, due to their increased exposure to one of their predators, the sparrowhawk.

Negative features experienced within urban environments also do not seem to have the same effects on all personality types. In great tits, parents altered their nesting behavior in response to anthropogenic noise differently depending on their personality (Naguib et al. 2013). Parents of both sexes took longer to enter nest-boxes while urban background noise was played, and sex-dependent effects were also found; when noises were played, bold, fast-exploring females and shy, less-exploratory males reduced the frequency of visits to their nest-boxes. Such findings emphasize the complex relationships between anthropogenic impacts, personality, and a range of other factors. As our impact on the natural world

increases, it is important to consider the characteristics of nonhuman animals at each level: species, population, and individual.

## Conclusion

Aside from being an interesting topic of research in its own right, the study of animal personality has far reaching implications and applications. For example, for pet owners, whether a new addition will assimilate well into the existing pack can often be a concern. Perhaps by knowing about the personality of your pets, you could maximize their chances of making friends. On a more serious note, there are millions of animals under human care around the world (Mason and Latham 2004), from pets, to zoo and aquarium animals, to research subjects. We therefore have a responsibility to provide these animals with the best possible level of care. As has been discussed here, personality has been linked with common measures of poor welfare, such as both the presence and absence of stereotypic behaviors (Mason and Latham 2004). Traits such as exploration (Range et al. 2006) and boldness (Bouchard et al. 2007) have also been associated with success in training animals on various learning tasks, which can be used to provide animals with individualized attention. Finally, increasing our knowledge of the differential impacts of human presence on animals with varying personalities can benefit both our own interactions with the natural world and the well-being of the animals we live alongside.

## Cross-References

- [Animal Welfare](#)
- [Temperament](#)

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## Personalized Medicine

### ► Pharmacogenetics

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## PET

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## Introduction

Positron emission tomography (PET) is a medical imaging technique used to visualize and measure physiological processes by administering a radioactive substance, known as a tracer, to living animals. The tracer spreads and accumulates in the body, producing gamma rays that are detected by the PET scanner and used to form an image of the tracer's distribution. PET images are usually combined with other imaging techniques that better visualize anatomical details, such as computed tomography (CT) or magnetic resonance imaging (MRI).

## Physics

The excess protons in the nuclei of some unstable isotopes are released and turned into a *positron*, a neutrino, and a neutron in a process known as  $\beta^+$  decay. Positrons are particles with the same mass as electrons but the opposite (i.e., positive) charge. When released from the nucleus, they travel a short distance (a few millimeters) within the body, colliding with surrounding atoms and rapidly losing kinetic energy. They then combine with an electron to form a positronium that decays through *annihilation*. In this process, the particle's mass disappears and its energy is released as two gamma-ray (short-wavelength, high-energy) photons traveling in opposite directions (at  $180^\circ$  to each other).

The basic function of a PET scanner is to count the number of these released photon pairs. They are absorbed by scintillation crystals arranged like a ring within the PET scanner (collectively known as the “camera”). The crystals convert photons into visible light and then into an amplified electrical signal and are usually made of either bismuth germanate (BGO) or cerium-doped lutetium oxyorthosilicate (LSO).

## Image Production

The detection of two released photons almost simultaneously (within about 4–10 ns of each other) by the scintillation crystals is known as a *coincidence* and is the basis of image formation in PET. Nuclear decay occurs somewhere along the straight line connecting the two scintillation crystals that detected the released photons (the *line of response*). Therefore, the detection of millions of these coincidences allows precise spatial localization and reconstruction of a cross-sectional PET image using the mathematical principles of computed tomography.

When two photons released from the same annihilation event traveling at  $180^\circ$  to each other are detected, a *true coincidence* is said to have occurred. Three other types of events, collectively known as *false coincidences*, degrade both image quality and the accuracy of PET quantification.

These include *random coincidences*, which occur when two photons from separate positron-electron annihilation events are simultaneously detected; *spurious coincidences*, which result from photons produced by mechanisms other than annihilation; and *scatters*, when one of the photons undergoes *Compton scatter* and deviates from its intended path. Compton scatter, caused by interactions between photons and surrounding electrons, changes both the direction and energy of the emitted photons, resulting in coincidences being missed and ultimately reducing signal – a phenomenon known as *attenuation*. In a typical human PET experiment, attenuation affects the vast majority of photons by the time they reach the detectors, and affects photons originating from close to the center of the body more than those released peripherally.

The size of the scintillation crystals determines the spatial resolution of a PET image, which is typically between 2 mm and 5 mm in clinical PET scanners. Other factors include *noncollinearity* of the annihilated protons (the situation where positrons are annihilated before they come to a complete stop, have residual kinetic energy, and thus produce photons that are not emitted at an angle of exactly  $180^\circ$ ) and how far the positrons travel through the tissue before annihilating (*positron range*).

A single scintillation crystal is unable to distinguish two photons resulting from separate coincidences if they occur too close together in time; in this situation, two coincidences may be detected as one. In addition, the electronics of the PET camera can only process and transmit data at a certain maximal rate. These two factors result in some coincidences going undetected, known as *dead-time losses*. These losses can be reduced by using cameras with more scintillation crystals.

## Radiochemistry

*Tracers* are substances that can track biochemical or physiological processes without perturbing them. For this purpose, they are *labeled* using positron-emitting radioisotopes, which are

produced in a particle accelerator (*cyclotron*) by bombarding stable nuclei with a beam of protons that become part of the nuclei. Radioisotopes of elements found in biologically relevant compounds, such as carbon, oxygen, nitrogen, or fluorine, are commonly used in PET studies.

The radioisotopes are then incorporated into another molecule (e.g., water or deoxyglucose) to form the tracer, which is then injected or inhaled by the subject. The molecule to which the radioisotope is incorporated can be a naturally occurring substance, an analogue of a naturally occurring substance or a synthetic substance (e.g., a drug). The tracer is thus composed of both labeled and unlabeled molecules.

Tracers usually have very short half-lives, so they must be used quickly, typically within one or two half-lives after their synthesis. The most commonly used tracers are 2-(18F)fluoro-2-deoxyglucose (FDG), (15O) water, (13 N) ammonia, and (15O) carbon monoxide.

## Quantification

The main advantage of PET is its ability to provide truly quantitative information about physiological processes (blood flow, glucose consumption, etc.). Each spatial unit in a PET image (a three-dimensional volume element or “voxel”) has a value corresponding to the radioactivity concentration in units of nuclear decays per second (*becquerel*) per milliliter. After correcting for physical decay, gamma ray attenuation and scatter, random coincidences, and dead-time, the radioactivity concentration in a voxel is proportional to the mass of the radioactive tracer in that voxel (Meikle and Badawi 2003).

The result is a so-called *diagnostic* PET image, reflecting the tracer’s concentration (and hence distribution/uptake) within each voxel at a certain point in time (this is also known as *static imaging*). Maps can also be obtained by correcting tracer concentration for the subject’s weight and the injected tracer dose. Although not perfect (Thie 2004), these *standardized uptake value* (SUV) maps allow comparisons between subjects,

and within the same subject over time, to be made conveniently.

On the other hand, true quantification in PET relies on what is known as *dynamic imaging*. Radioactivity concentration in a certain region at a certain time depends on the tissue’s blood flow and metabolism, as well as on the availability of the tracer to the target tissue. To calculate the former, information about the latter is required, in terms of the radioactivity concentration in arterial blood over time following the injection of the tracer. This is the *arterial input function*, which is best derived by taking several arterial blood samples from the patient and measuring plasma radioactivity at each time point.

Because this procedure is cumbersome, radioactivity concentration can instead be noninvasively derived from arterial blood within the PET image (an *image-derived input function*). However, this does not work with all tracers, is challenging when the imaged region does not include very large arteries, and only provides whole blood radioactivity concentration instead of that of plasma (Zanotti-Fregonara et al. 2011). Other alternatives include using a *reference tissue* from a region or organ where the tracer is not taken up or *modeling* the input function (i.e., deriving it from the PET image data itself).

Knowing the input function and the regional radioactivity concentration, various physiological parameters such as receptor concentration, blood flow, or glucose metabolism can be extracted using *tracer kinetic models* that mathematically describe the relationship between these factors (Bentourkia and Zaidi 2007).

## Practical Considerations

PET is quite unique in its ability, under appropriate conditions, to provide absolute quantification of many different physiological and metabolic processes. However, despite this, in most clinical and many research situations, PET is often not the first imaging modality of choice because of some notable disadvantages.

Inherent to PET is the exposure to *ionizing gamma radiation*, the extent of which depends



on the body part imaged and the tracer used. Compared to other medical imaging procedures, the amount of radiation a subject is exposed to during a PET scan is generally high, especially when combined with CT (Towson 2003). This is associated with very small increases in exposed individuals' risk of developing cancer (Brenner 2014).

Finally, not only are PET scanners very expensive to purchase and maintain (Berger et al. 2003), but the substantial costs of having an onsite cyclotron (to produce tracers with short half-lives) or of transporting longer half-life tracers from other facilities must also be taken into account. In clinical situations, particularly those in which quick decisions must be made, the benefits of accurately quantifying a disease process must be weighed against these practical drawbacks.

## Applications

The precise application of PET depends on the body part being imaged and the nature of the tracer used. PET tracers have been designed to measure blood flow, gene expression, enzyme activity, cellular metabolism, and receptor binding, finding considerable use in neurology, psychiatry, oncology, and cardiology.

### Neurology and Psychiatry

PET has opened up a myriad of opportunities for researching both normal brain function and the pathophysiology of brain diseases in living subjects. Because it permits the measurement of processes fundamentally linked to brain activity such as blood flow, oxygen consumption, and glucose metabolism, PET has been used in cognitive neuroscience to investigate the brain's functional organization (Raichle 1998). The measurement of cerebral glucose metabolism and blood flow using 18F-FDG and 15O-water, respectively, is also important for studying the pathophysiology of cerebrovascular disorders such as stroke and vascular cognitive impairment (Heiss 2014).

In addition, the communication between brain cells can be quantified and visualized using PET by measuring synaptic density (Finnema et al.

2016) as well as neurotransmitter synthesis and metabolism (Heurling et al. 2017). Pathophysiological processes, such as inflammation and blood-brain barrier disruption, that play an important role in many neurological and psychiatric illnesses can also be imaged using PET (Heurling et al. 2017).

In clinical practice, 18F-6-fluorodopa (18F-DOPA) is often used to investigate the dopaminergic system. In this way, PET helps differentiate Parkinson's disease from similar conditions (*parkinsonian syndromes*), and provides biomarkers for the progression and severity of this disease. In epilepsy, 18F-FDG PET is often used in combination with *electroencephalography* (EEG), a measure of electrical activity in the brain, to localize the focus of partial seizures, particularly when magnetic resonance imaging (MRI) shows no structural abnormalities. Increased blood flow and glucose consumption is seen within the focus during and immediately after a seizure, both of which become low between attacks. 18F-FDG PET also helps in the early diagnosis of different forms of dementia. Low glucose metabolism in the temporal and parietal lobes is characteristic of Alzheimer's disease, interestingly occurring even before symptoms of the illness begin. More specific tracers, such as 11C Pittsburgh compound-B (PIB), are capable of measuring the amount of amyloid- $\beta$  in the brain, a peptide that is closely implicated in the pathogenesis of Alzheimer's disease.

### Oncology

The vast majority of PET studies in clinical practice are done for patients with established or suspected cancer. In these patients, PET is useful for diagnosis, staging, assessing treatment response, detecting disease recurrence, and characterizing the biology of tumors.

The use of 18F-FDG, the main PET tracer used in oncology, as a general tool to detect cancer is based on the *Warburg effect*: the observation that malignant cells get their energy by taking up and metabolizing more glucose than normal cells. However, 18F-FDG is not specific to malignant cells – it accumulates wherever there is high metabolic activity, including in

infected or inflamed tissue. The main routine use of 18F–FDG PET is thus to determine the extent of the disease in patients who have already been diagnosed with malignant tumors, particularly lung cancer, colorectal cancer, lymphoma, and melanoma.

In addition, 18F–FDG PET can be used to monitor patients' responses to chemotherapy, particularly in lymphoma, breast cancer, and gastrointestinal malignancies, where reductions in the SUV of 18F–FDG can be observed after a single treatment cycle and can precede tumor shrinkage. Other PET tracers specifically target tissue hypoxia, new blood vessel formation, programmed cell death, and cellular protein synthesis (Farwell et al. 2014).

### Cardiology

In the heart, PET can be used to assess blood flow to the heart muscle (myocardium), to detect inflammation and new blood vessel formation, as well as cell death.

In clinical practice, 13 N–ammonia or 82-rubidium PET tracers are used to assess myocardial blood flow and, when combined with coronary CT angiography, how narrow the coronary vessels (the arteries supplying the heart muscle) are. Whether improperly functioning heart muscle is viable (i.e., can potentially return to normal function) can also be assessed using an 18F–FDG scan, with viable tissue showing normal tissue metabolism but low blood flow. PET is also used to determine whether atherosclerotic plaques in the coronary arteries are unstable (i.e., likely to rupture and block the artery) because increased 18F–FDG uptake is a marker of inflammation within these plaques.

Special tracers can also be used to assess sympathetic nervous system function in the heart, which is relevant to the diagnosis and prognosis of patients with heart failure. Direct imaging of markers of new blood vessel formation (angiogenesis), which occurs as a result of long-standing low blood flow to the myocardium, can be achieved using tracers targeting pro-angiogenesis factors such as vascular endothelial growth factor (VEGF).

### Hybrid Imaging

Currently, other medical imaging modalities cannot completely replace PET because they are either not truly quantitative (MRI) or have relatively limited range for measuring different processes (CT). However, both MRI and CT are better at revealing tissue anatomy due to their high spatial resolution. Because of this, PET is often combined with either CT or MRI to provide complimentary information about brain function and structure.

Combined PET/CT has the added advantage of improving the accuracy and efficiency of attenuation correction using the information about tissue density provided by CT. However, combining PET and CT has the drawback of exposing subjects to a much higher dose of potentially harmful ionizing radiation than using PET alone.

Combining PET with MRI is less risky as the latter does not produce ionizing radiation. MRI is also far better at distinguishing between different types of soft tissue than CT. However, PET/MRI is logistically complicated as it requires shielding against both radiation and the very strong magnetic field. PET/MRI scanners also have a very narrow bore (the interior part where the subject lies) because of the space occupied by the PET camera, making them uncomfortable, especially for claustrophobic or obese people. Diagnostically, PET/MRI also performs poorly compared to PET/CT in regions such as the lung (Rauscher et al. 2014), where the density of protons is low.

### Small Animal Imaging

Large animals such as pigs, dogs, and nonhuman primates can be scanned on standard clinical PET systems designed for humans. Smaller animals like rodents, on the other hand, need dedicated scanners, also known as *microPET* systems. Commercially available microPET systems have a finer spatial resolution (1–2 mm) than clinical scanners due to their smaller scintillation crystals. However, small animal PET imaging is technically challenging for several reasons, including the overall lower signal sensitivity caused by the small crystals (because fewer coincidences can be detected by each crystal), and the fact that the spatial resolution of PET is fundamentally limited

by gamma rays emitted at angles other than  $180^\circ$  (noncollinearity) causing improper localization of the point of nuclear decay (Moses 2011). However, the numerous potential applications of PET in rodent research are driving steady technological advancement, including the development of small animal scanners that allow imaging with simultaneous PET and high-field MRI (Judenhofer et al. 2008) and small, “wearable” devices for PET imaging of awake animals (Schulz et al. 2011).

## Conclusion

PET is a valuable medical imaging technique that can provide quantitative information about many different physiological processes, and the influence of diseases on them, in a relatively noninvasive manner. It has found considerable use in diagnosing and managing patients, and is also applied extensively in research on both humans and other animals. The benefits of PET in a particular context should always be weighed against its high costs and the risks of exposure to ionizing radiation.

## Cross-References

- EEG
- Neurotransmitters
- Parkinson's Disease

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## Pets

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## Synonyms

[Companion animals](#)

## Definition

Pets can be defined as animals that live with humans or within human social structures where they are provided with some, or all, of their needs. They are considered to play a primarily social role within the household or community and are therefore distinct from working or production animals. Any species can be a pet, as the term is applied based on human perception of the role and value of the animal concerned, and not on an intrinsic quality of the animal per se.

## Introduction

Pet ownership appears to be culturally and historically ubiquitous (Walsh 2009), although research concerning pets in non-European cultures appears

underrepresented. It arises from the historic utility of some, but by no means all, species. However, at least in developed nations, pet ownership is now primarily for the purposes of companionship (e.g., Staats et al. 2008). Despite anecdotal evidence to the contrary (e.g., Shirley 2005), lasting and social interspecies relationships appear to be almost solely the preserve of humans. Numerous species can be sequestered into human environments and ownership with many considered to be exotic pets. Overall, pets are so common that estimates for the USA alone suggest 68% of households contain at least one nonhuman family member (American Pet Products Association 2017). Suitability of species, or sometimes breeds, as pets can be questioned based on their ability to adapt to human environments and the dangers they pose to their owners, others, or the environment (Schluppi and Fraser 2000). Readers are encouraged to consider the implications for the myriad species denoted as pets at their leisure. However, the most popular species are the domestic cat (*Felis catus*) and domestic dog (*Canis familiaris*) which, in the interests of brevity, will be the focus of this work. Current global estimates are difficult to verify with any certainty, given the wide range of lifestyles these animals may have (i.e., from entirely owned to feral). However for dogs it is suggested the population is around 1 billion (Gompper 2014) and, for cats, between 600 million and 1 billion (O'Brien et al. 2012).

Modern day cats and dogs result from the domestication of their wild ancestors: the gray wolf (*Canis lupus*) and wildcat (*Felis silvestris*). This process is estimated to have begun some 20,000–40,000 years ago (Botigué et al. 2017) and 10,000 years ago (Hu et al. 2014), respectively. Domestication is a human-mediated process, which has resulted in both morphological and behavioral changes in these species, making them more suitable for life in anthropocentric environments. How early domestication occurred is still a matter of debate. However, it is now widely considered to have resulted from two main processes. One occurs within the animal population, as individuals learned to scavenge in close proximity to people (referred to as “self-domestication”) (e.g., cats, Bradshaw 2014; dogs,

Coppinger and Coppinger 2001), and the other through selection for desirable traits by humans.

Broadly speaking domestication has functioned to reduce human-associated fearfulness and increase sociability and (in dogs) biddability. Domestication has also resulted in altered vocalizations for both dogs and cats and substantial changes in human-directed, or at least human-mediated, communication behaviors.

## Ownership

The term pet, in and of itself, remains contentious and is largely rejected in favor of the term “companion animal” in much of the literature concerned with welfare and ethics. In part, this is due to the nature of the pet-owner dyad where one individual is in possession of another. Irrespective of the treatment of a pet, it remains possible for an owner to make an entirely legal decision that is not in the animal’s interests (Wykoff 2014). This is because, legally, pets are intrinsically human property and lacking in legal agency, an occurrence that has contentiously been linked, within the animal rights literature, to ideas of slavery (Kymlicka and Donaldson 2014).

## Attachment and Relationships with Pets

### Attachment

There is little argument that most pet owners will report their relationship with their animal as loving, close, and/or familial (Crawford et al. 2006; Farnworth et al. 2012; Meehan et al. 2017) and that these bonds are built on a closeness associated with practical and emotional care, protection, and security. However, our exploration of these relationships can affect our understanding of them. There are two generally applied mechanisms, both with a range of validated tools at their disposal, but neither of which may fully explore the human-animal dynamic (see Crawford et al. 2006).

The first group assess human perceptions of the owner-pet relationship and actions toward pets; these assessments are methodologically “easier” given that they use a human self-report

mechanism. Early tools include the Pet Relationship Scale (PRS) (Lago et al. 1988) and Pet Attitude Scale (PAS) (Templer et al. 1981). More recently, the Monash Dog Owner Relationship Scale (MDORS) (Dwyer et al. 2006) and the derivative Cat-Owner Relationship Scale (CORS) (Howell et al. 2017) have been developed. The latter two, as opposed to the former, allow for the report of both positive and negative perceptions of any relationship. This makes them particularly useful for the exploration of outcomes such as relinquishment.

The second group include attempts to assess human-animal attachment by observing, or asking for recollections of, the interactions between the two parties in the dyad. This often takes the form of an adaptation of “The Ainsworth’s Strange Situation (TASS)” (Ainsworth and Wittig 1969) such as the Lexington Attachment to Pets Scale (LAPS; Johnson et al. 1992; Vanegas-Farfano and González-Ramírez 2016). Use of TASS has focused on the physiological and behavioral responses of pet dogs to separation from the owner, following introduction to an unfamiliar room containing an unfamiliar person. Both Prato-Previde et al. (2003) and Palmer and Custance (2008) identified that a dog’s behavior was indicative of “secure attachment.” This was predicated upon dogs behaving more positively toward a stranger in the owner’s presence than their absence. Similarly, dogs showed behavioral signs of attempting to reunite with the owner in the owner’s absence. Such responses may relate to the distress shown by children when separated from a parent to whom they are securely attached. These findings concur with other evidence that dogs’ heart rates and behavior are negatively affected by separation in the TASS, suggestive of emotional distress (Palestrini et al. 2005). Work applying TASS to cats is relatively sparse and those that do suggest a lack of secure attachment for cats (Potter and Mills 2015). However, behavioral studies do indicate increases in positive behaviors in cats (stretching and purring) following extended owner absences (Eriksson et al. 2017). These contrasting responses of cats and dogs to attachment-based assessments may reflect differences in the processes and purposes



of each species' domestication events (i.e., that dogs were/are primarily used for human-mediated purposes which require greater attachment).

Irrespective of the assessment tool, it is evident that the quality of the pet-owner relationship, both in terms of the human's attitudes and animal's behavior, impacts upon the experiences and outcomes for both parties within the dyad. Research using individuals' assessments of their own confidence as dog owners has been demonstrated to correlate with the attachment style, and behavior, of their dogs during use of TASS. Nonconfident owners had dogs with demonstrably weaker attachment behaviors than confident owners (Siniscalchi et al. 2013). However, contrary evidence arises in research using TASS and MDORS. Rehn et al. (2014) suggest a lack of clear associations between perceived emotional closeness and dog behavior in the TASS. Differences in dog behavior appear to result from direct owner-dog interaction styles, where owners that display more direct interaction have dogs which are less independent in their play and more proximity seeking.

### Changing Owner-Pet Relationships

The roles of pets within society are many and varied as are the relationships that exist between humans and their pets. A number of changes in owner attitudes, circumstances, and behaviors, as well as pet taxonomic grouping, affect owner-pet interactions. At the broadest level, however, there is evidence that pet owners are generally more extroverted and less fearful and report better well-being, than nonowners (McConnell et al. 2011).

When considering pet owners only, the perception of pets as "family members" was weaker in a sample of Japanese cat owners as compared to dog owners, and dogs were considered to have greater emotional capabilities (Arahoru et al. 2017). Interestingly, and with implications for causal factors, choice of pet may be influenced by fundamental aspects of the owner's personality. For example, both Reeve and Delgado (2015) and Gosling et al. (2010) found that those self-reporting as "cat people" were significantly more likely to have a

higher neuroticism and lower extraversion score as opposed to self-confessed "dog people." In turn, this may alter the expression of the owner-pet interaction, where neuroticism may be associated with the potential for greater levels of pet-directed attention. However, Vonk et al. (2016) also found no variation relative to neuroticism. Similarly, increased conscientiousness is identified as a positive pet-owner personality trait and appears not to vary relative to pet type, be that cat, dog, or "other" (Gosling et al. 2010; Reeve and Delgado 2015; Vonk et al. 2016). Whether or not women report higher levels of pet attachment than men appears equivocal; the notion is supported by Vonk et al. (2016) and (in children) Hawkins et al. (2017) but not Bagley and Gonsman (2005). The conflicting findings, even within these limited studies, suggest that an owner's personality and demographic traits have substantial, albeit complex and variable, effects on owner-pet relationships. Indeed, research suggests that, for dogs, owner characteristics have a greater effect on the relationship than dog behavior (Meyer and Forkman 2014), indicating our broadly anthropocentric attitude toward the dyad.

Attitudes toward pets have also been shown to vary relative to life events and stages. It has been proposed that the formation of bonds with pets provides children with social support and opportunities to develop nurturing behaviors (Melson 2003). Recent evidence indicates that younger children, as opposed to older children, have significantly closer bonds with cats and dogs as compared to other animals (e.g., rodents and reptiles), although the disparity is extinguished as they age (Hirschenhauser et al. 2017). Pets (cats and dogs) may provide children with opportunities for social development, increasing their quality of life above and beyond positive relationships with parents and friends (Marsa-Sambola et al. 2017); attachment may be stronger for single children as opposed to those with siblings (Hirschenhauser et al. 2017). Pet ownership may also buffer a child's perception of a stressful event (dogs: Kertes et al. 2017) and positively improve attitudes toward both humans (Paul and Serpell 1993) and other animals (Hawkins et al. 2017).

In adults, feelings of affection toward pets increase until around 54 years of age, but not thereafter (Bagley and Gonsman 2005). In a similar vein, while newly married couples and couples with adult children report strong pet attachments particularly to dogs, those with young children report a decrease in affection (Albert and Bulcroft 1988; Meyer and Forkman 2014), likely indicative of a change in the pet's relative position within the household.

### Euthanasia

As for all animals over which humans have a burden of care, there is a requirement to manage the end of life as much as its beginning. Euthanasia is a complex issue in that an owner is required to make a proxy decision about an animal's state and to weigh up future benefits against future likelihood of suffering. Such decisions are difficult to make objectively, and animals may be subjected to greater or lesser amounts of suffering based on the owner's emotional state, rather than the animal's best interests. Loss of a pet has profound impacts upon the owner akin to the grief experienced by the loss of any attachment figure (Testoni et al. 2017).

## Health Benefits of Pet Ownership

Pet ownership has been linked to a range of health benefits for the owner, or family, within which an animal resides, although such findings are equivocal. Headey (1998) indicated that increased feelings of closeness between the owner and pet resulted in a reduction in visits to the doctor and medication usage. Although this finding was based on self-reports, numerous other studies have provided links between pet ownership and benefits such as increased activity and social integration (see Cutt et al. 2007), especially for aging individuals or those with physical impairments. Following pet acquisition there is some evidence that, in the short term, the owner perceives an improvement in their health (Serpell 1991). However, reviews of the literature suggest that, although pets are important components of such effects, they are not integral to their occurrence

(e.g., a pet may only substantially improve social support where it is otherwise absent).

Improvements in cardiovascular health and postinfarction recovery have also been associated with pet ownership (Chowdhury et al. 2017; Herrald et al. 2002). This dynamic has been reviewed a number of times, focusing on a wide range of factors (e.g., Barker and Wolen 2008). Invariably these reviews conclude that, although some health benefits are evident, results should be treated with caution based on the methodologies employed and the target populations studied. By way of example, a causal link between the demographics of individual women, pet ownership, and health suggests that individuals in better circumstances, where health outcomes may already be improved, are more likely to own pets (Pachana et al. 2005).

The effects of pet ownership on the development of various diseases are likewise difficult to discern. Depending on the community an individual lives in, everyone is likely to be passively exposed to cat and dog allergens, varying in degree, but irrespective of direct cohabitation with an animal. This can make it difficult to extricate causal factors from one another. There is complex evidence as to whether cats and dogs increase or decrease the likelihood that an individual will develop asthma. However, the impacts of cats and dogs on human health are most marked for those people who are already sensitized to pet allergens or suffer from respiratory ill-health (e.g., TePas et al. 2006). Studies of human infants indicate that having a household pet significantly alters the gut biome, increasing the prevalence of *Ruminococcus* and *Oscillospira* bacteria which are, in turn, associated with a reduced incidence of allergies and obesity (Tun et al. 2017). One systematic review concludes that the incidence of asthma development for individuals born into pet-owning households is generally reduced (Lodge et al. 2012), while a wider review, including all childhood ownership studies, indicates the effect is comparatively negligible (Chen et al. 2010). It may therefore be concluded that ownership need not be predicated on a concern about child health outcomes.

## Social Facilitation

There is substantial evidence that pets can provide social support for people and that they have long been considered of similar value to other family members (e.g., Archer 1996). This social effect is of particular relevance to people who may otherwise be isolated or have experiences of social rejection (McConnell et al. 2011). Pet ownership may be particularly beneficial to numerous “at-risk” groups, including the elderly (Raina et al. 1999) and those with physical (e.g., Hart et al. 1987; Lane et al. 1998; White et al. 2017) or psychological impairments (see Beck 2005). The manner by which this occurs may be direct (e.g., the animal is the source of the interaction or companionship) or indirect (e.g., the animal promotes interaction between people).

Social facilitation primarily occurs in the public sphere and so is more likely to be associated with dog ownership. People with their dogs are more likely to interact with strangers or have conversations with others. This is because dogs act as an icebreaker for those seeking interactions, may make an owner appear more approachable, or are a focus of interest. However, the degree of interaction is influenced by the interacting humans’ genders and the breed and age of the accompanying dog (Wells 2004).

## Problems Associated with Pet Ownership

### Welfare Issues

#### Adaptation to the Human Household

Although pets have been domesticated for many thousands of years, the anthropocentric environment presents risks. Both cats and dogs have a critical socialization period (3–9 weeks and 3–14 weeks, respectively) during which exposure to people, and related objects and noises, is important to minimize undesirable responses to novel stimuli. Fear, aggression, and undesirable behaviors (such as poor litter box training in cats) are substantial contributors to erosion of the human-animal bond and substantially increase the likelihood of abandonment or

relinquishment (Salman et al. 2000; Segurson et al. 2005).

People may also misunderstand the needs, or evolutionary histories, of their animals. For example, dogs have evolved to form close social bonds with others and are further selected to bond closely with people. This can lead to the development of separation anxiety where the individual has not been habituated to being left alone for periods of time or where they are “over-bonded” with their owner (Flannigan and Dodman 2001). Likewise, although domestic cats may be considered to be semi-social, with stable aggregations forming based on resource availability (Crowell-Davis et al. 2004), they have also been selected for increased sociability as compared to their wild counterparts. Therefore, they may also suffer from separation-related issues (Schwartz 2002). Cats in multi-cat households do not appear to experience higher levels of stress than single cats as long as resource access is not limited (Ramos et al. 2013). However, for those cats which are not socialized with conspecifics, transferal of human social expectations (e.g., the need for companionship) can result in aggression between unfamiliar individuals, albeit potentially transient (Levine et al. 2005).

### Breed-Related Problems

Anthropomorphic relationships with pets (i.e., the representation of animals in human terms) may have driven selection of cat and dog breeds over time increasing phenotypic (and therefore genotypic) conformation to human expectations (Serpell 2002). These changes are potentially to the detriment of the individual animal, but are even more problematic in that they are “bred into” specific lines, making it hard to improve welfare (Universities Federation for Animal Welfare 2016). This is even more worrying given that breeds with substantial health problems, directly related to their appearance, may continue to be purchased precisely because of that appearance (Packer et al. 2017). The drive to own animals based on their appearance has been shown to be related to owner perceptions of pets as objects, property, or status markers, causing an increase in anthropocentric owner

behaviors (e.g., putting the animal in fancy dress) (Beverland et al. 2008).

Within the companion animal populations, a large proportion of dogs and a substantial but smaller percentage of cats are purebred. The demand for purebred companion animals is not a new phenomenon. However, the pressure placed on breeds to conform to social and aesthetic expectations has resulted in substantial changes to breed morphologies. In turn, the breeding for these features has had two effects: (1) the appearance of features which are exaggerated, breed-related, and in and of themselves deleterious to the individual animal (Asher et al. 2009) and (2) an increase in the prevalence of inherited disorders not related to breed standards but associated with increased homozygosity within a limited breeding pool (Summers et al. 2010).

Morphological and genetic disorders, where sublethal, may substantially reduce the longevity, or quality of life, of individuals within the associated breed (Rooney and Sargan 2010). Although the presence and effects of disorders are not uniform or ubiquitous within any one given pedigree, they are substantial enough to be considered part of the underlying nature of that breed. For example, the prevalence of von Willebrand disease has historically been substantially increased in Doberman Pinschers (and a few other breeds) (e.g., Brooks et al. 2001). Arguably this makes the disease an undesirable characteristic for that breed.

In recent years more attention has focused on brachycephalic (or short-faced) dogs (e.g., the pug and French bulldog) and, to a lesser extent, cats (e.g., Persians and exotics), in part, because they are increasing in popularity (The Kennel Club 2016; The Cat Fanciers Association 2016). This is despite substantial evidence that brachycephalism is associated with an increase in respiratory (Farnworth et al. 2016; Packer et al. 2015), dental, and ocular (Kafarnik et al. 2008) disorders. Owners of brachycephalic dog breeds appear to contribute to the problem by giving greater weight to appearance than health when choosing a breed (Packer et al. 2017) and dismissing some issues (e.g., respiratory distress) as normal breed-related behavior (Packer et al.

2012) without seeking veterinary intervention. Where confirmation-related issues are extreme, surgical interventions are often required to remedy them (e.g., Graham et al. 2017; Trostel and Frankel 2010).

Consideration of the prevalence of genetic and morphological disorders in cats and dogs has resulted in some organizations and professional bodies calling for revisions to the breed standards to promote better welfare (British Veterinary Association 2016). In some cases, there is evidence that veterinary professionals may consider specific breeds too compromised for breeding to continue (Farrow et al. 2014).

### Intensification of Breeding Practices

As with livestock, increased demand for animals drives intensification of production. Companion animals are no exception. Recent decades have seen a substantial rise in puppy and kitten “farms” or “mills” to meet the demands for purebred animals or those designated as “designer breeds” (usually first generation crosses between two pure lines). In addition to increasing the likelihood of recessive and conformational disorders being expressed (see section above), farming of pets for commercial sale can lead to poor socialization (Appleby et al. 2002) and increased behavioral problems (McMillan et al. 2013). Lack of access to the mother, or both parents, of a puppy may be a proxy measure of its origins. Absence of parents, or an inability to meet them, is likely linked to commercial breeding and has been shown to be related to increased behavioral problems (Westgarth et al. 2012). This linkage has resulted in welfare organizations promoting meeting the dam and/or sire as an important component of the purchasing process (Royal Society for the Prevention of Cruelty to Animals 2016). Despite this there is some evidence that the purchaser of popular brachycephalic breeds is less likely to meet the dam as compared to other popular purebred dogs (Packer et al. 2017). Breeding adults often experience restrictive housing environments, poor veterinary care and little hiatus between litters. They are rarely rehomed and those that are often experience

substantial behavioral and health issues related to their history (McMillan et al. 2011).

#### Nonmedical Surgical Alteration

Outside those procedures that are required to manage breed-related conditions (see above) or population (see below), there are a number of surgical procedures to which companion animals are, or have historically been, subjected. In a number of countries and jurisdictions, due to the pain and distress caused and their questionable ethicality, these procedures are no longer legal and so should be considered in light of local legislations. These surgeries are generally applied for two reasons, firstly, to minimize undesirable behaviors (where they are often promoted as a last resort) and, secondly, to improve the aesthetic appeal of an animal.

The first group of interventions include onychectomy and tenectomy in cats which are designed to prevent property damage and/or scratch injuries. The procedures, which are historically common in the USA (Patronek 2001), consist of removal of the third phalanx on each digit or, latterly, severing of the tendon that allows the claws to be unsheathed. Both procedures are considered to cause pain and discomfort, despite non-surgical alternatives being available (Cloutier et al. 2005). For dogs the most common procedures are ventriculocordecotomy or unilateral arytenoid lateralization, colloquially known as “debarking/devocalization.” As for procedures applied to cats, they cause pain and discomfort, but could be considered more invasive. Data suggest that these procedures show substantial levels of postoperative complications, including respiratory distress and pneumonia (Bahr et al. 2014). The latter group of surgical alterations, also known as surgical mutilations, include processes such as ear cropping, tail docking, and dewclaw removal in dogs.

#### Abandonment or Relinquishment

For both cats and dogs, the risks of abandonment or relinquishment are substantial. Abandonment is the act by which cats and dogs are left behind when people move or are actively excluded for the home or property of the owner. This may result in

the development of large population of free-roaming dogs and cats which are reproductively self-sustaining. Free-roaming may lead to a lack of veterinary care and increased risk of injury, human cruelty, continued reproduction, predation, or disease (see Dalla Villa et al. 2010; Finkler et al. 2011). As a result numerous lethal and nonlethal processes can be, and are, implemented to reduce the free-roaming cat and dog populations (e.g., trap-neuter-return, trap-euthanize, poisoning). Population control can be difficult based on social perceptions of control measures (e.g., Farnworth et al. 2014) and the ability to distinguish between unowned and owned free-roaming dogs and cats.

In some countries abandonment is illegal, and erstwhile owners can be prosecuted; however abandonment is only an identifiable phenomenon in countries where free-roaming populations of animals are uncommon. As a result, abandonment of dogs is likely more often identified when compared to that of cats.

Relinquishment is the process by which a cat or dog is transferred into the care of an animal organization. It may be driven by a breakdown in the human-animal bond, often as a result of behavioral problems. Another cause of relinquishment is the inability of the owner to care for the animal in question, often as a result of changing circumstances. Relinquishment may result in the animal being rehomed, although not all rehoming are successful and some result in the animal being re-relinquished. Shelters have “no-kill” policies ensuring all animals that are relinquished are maintained; however this is not the case for all organizations. Relinquishment at a shelter may be considered the better option for the animal; however it causes substantial disruption in the animal’s social bonding and reduces the amount of human-animal interaction that is possible.

#### Conflicts Associated with Pet Ownership

Although pets are commonplace within human societies, they are not universally favored. Differences in the care provided, restrictions placed upon them, and human attitudes toward pets cause numerous conflicts. This section is focused on two such examples of conflict.



## Human-Animal Conflict

### Issues of Nuisance

Dogs and cats may cause substantial public nuisance often through intrusion into the lives of nonowners. Issues identified include excessive noise from dogs barking (Juarbe-Diaz 1997) or the nocturnal activities of cats, disturbance of refuse, fecal contamination of gardens and public sites (Toukhsati et al. 2012), and disruption of traffic when free-roaming (Farnworth et al. 2012).

### Dog Bites

Legislation has been introduced into a number of countries as a result of dog bites and attacks (e.g., UK Dangerous Dogs Act 1991). This legislation is often focused on a number of breeds that are considered as predisposed to biting or aggression. Some breeds can indeed inflict substantial harm based on their size and strength, especially if the victim is a child (de Keuster et al. 2006; King et al. 2009). However, the majority of dog bites are reported to occur in developing nations (Dalla Villa et al. 2010) that appear to be inflicted on people who are familiar with the dog and, more frequently, men than women (Farnworth et al. 2012). In areas where dogs are free-roaming, the likelihood of being bitten appears to rise.

### Zoonotic Diseases and Parasites

Dogs and cats both carry diseases that are zoonotic, (i.e., those that can be passed from the animal to people). These diseases include the following:

Cats: Ringworm infection, toxoplasmosis, salmonellosis, campylobacteriosis, giardiasis, cryptosporidiosis, roundworm and hookworm infection, cat scratch disease, and rabies

Dogs: Ringworm infection, salmonellosis, leptospirosis, Lyme disease, campylobacteriosis, giardiasis, cryptosporidiosis, roundworm and hookworm infection, and rabies

The risk that most zoonotic diseases carry is relatively low, although the larger the population the greater the risks of transmission (Katagiri and Oliveira-Sequeira 2008; Parrado et al. 2011), and

they are most likely to cause harm to people who are already immunologically compromised or naive. One major exception is rabies, where global eradication attempts are already underway (see Morters et al. 2013).

### Animal-Wildlife Conflict

Both dogs and cats cause, or are perceived to cause, substantial predatory (Loss et al. 2013) or competitive (Butler and Toit 2002) impacts upon local wildlife. Dogs may also cause nuisance or harm to domestic livestock. These impacts may be particularly marked when they represent introduced mammals to which endemic species are poorly adapted (e.g., Nogales et al. 2004; Berger et al. 2007). To this end, the domestic cat has been considered one of the most problematic introduced predators, something which is exacerbated by their ability to free-roam. Resolution of the issue of pet-wildlife conflict is complex, directly as a result of the close ties local communities may have with their animals (e.g., Hughes and MacDonald 2013; Loyd and Hernandez 2012).

The literature around these problems is not complete, and it remains unclear as to whether cats and dogs may benefit some native species by controlling other invasive predators (e.g., rats). The impacts of urban pets are also less well understood (see Kikillus et al. 2017; Hughes and MacDonald 2013) than the impacts of feral dogs and cats (i.e., those living outside human control or human environments), leading to a requirement for more systematic exploration of anthropogenic problems arising from pet ownership.

## Conclusion

Pets perform myriad roles within human societies, both providing and deriving substantial benefit. However, the relationship is not one of equal standing for both parties, which results in a number of areas of concern. Improved knowledge about the relationships between owners and their pets, the needs of pets, as well as more focused legislation for their management may be highly beneficial.

## Cross-References

- [Animal Welfare](#)
- [Attachment](#)
- [Canine Cognition](#)
- [Domestication](#)
- [Feline Cognition](#)
- [Human-Animal Interaction](#)
- [Self-domestication Hypothesis](#)
- [Socialization](#)

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## Pharmacogenetics

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## Synonyms

Personalized medicine

## Definition

The branch of research that examines how an individual's genetic code will affect their reaction to drugs.

## Introduction

The field of pharmacogenetics is concerned with improving patient outcomes and response to drug treatment(s). To this end, research efforts in this field have many aims: to identify genetic variants that alter an individual's response to pharmacological agents, to determine the population frequency of identified polymorphisms, and to search for safer or more effective treatments/doses. The ultimate goal of pharmacogenetics is to predict a patient's response to a treatment based on genetic differences, thereby improving success and reducing adverse outcomes (Spear et al. 2001).

Currently available pharmaceutical drugs must go through extensive testing to establish their efficacy in improving outcomes while also minimizing mild or severe adverse outcomes. Despite such testing, there remains a great level of variability in drug responses. These inter-person differences may arise from controllable (e.g., mis-dosing or drug-drug interactions) or uncontrollable (e.g., allelic mutations) factors. The field of pharmacogenetics is most interested in the differences that result from uncontrollable factors, i.e., genetic predispositions.

The genetic code is a highly complex set of rules which regulates the transcription and

translation of genetic material (RNA and DNA) into proteins that, for instance, regulate drug metabolism, absorption, and excretion. Naturally occurring mutations in DNA may alter the composition and structure of proteins and enzymes, ultimately altering drug metabolism and risk of adverse outcomes (e.g., toxicity; Sissung et al. 2014).

## Pharmacogenetics of Membrane Transporters

Membrane transporters are large transmembrane proteins that span the phospholipid bilayer and facilitate the transport of ions, small molecules, drugs, and substrates against their gradient. Humans express many types of membrane transporters; these differ in their direction of molecular transport (influx or efflux), location in the body, and mechanism of action. The ATP-binding cassette (ABC) transporters are a superfamily of efflux proteins that generally draw substrates out of tissues and into the systemic circulation, eventually promoting the clearance of drugs. To date, 49 ABC genes have been identified. The *ABCB1* transporter is commonly found in normal cells of the adrenal gland, kidney, liver, colon, jejunum, pancreas, and in the capillary endothelial cells in the testis and the blood brain barrier (Fung and Gottesman 2009). A total of 66 single-nucleotide polymorphisms (SNP) have been identified in the *ABCB1* gene (24 synonymous, 42 non-synonymous). Some of these SNPs have been implicated in altered mRNA transcription, protein folding, and drug pharmacokinetics. In humans, the functional consequences of polymorphisms have not been fully elucidated; to date, the SNPs that have been studied in vitro have not produced clinically significant effects on protein function (Fung and Gottesman 2009).

Influx transporters mediate the cellular uptake and reabsorption of drugs against a concentration gradient. These membrane proteins also span multiple domains and assume complex structures that allow for the transport of substrates into, and sometimes out of, the cell. Common influx proteins are the organic anion transporters (OATs and OATPs),

organic cation transporters (OCTs), and oligopeptide transporters (PEPTs). Influx proteins are also polymorphic, with some allelic variants affecting drug efficacy and toxicity. One of the more commonly studied influx proteins, the OATP1B1 protein, is a hepatic influx transporter (Niemi et al. 2011) with an identified total 41 non-synonymous SNPs, to date. These polymorphisms are associated with structural and functional changes in the transmembrane protein, some of which have serious implications in the clinical setting. Studies evaluating the pharmacokinetics of *SLCO1B1* (coding for OATP1B1) gene variants have found different clearing rates for pravastatin, a statin that is used to reduce serum LDL levels. Certain allelic variants (*SLCO1B1\*1B*) are associated with a low clearing rate of the drug, which can be associated with a risk of statin-induced myopathy (Pasanen et al. 2006). Fortunately, the targets of the allelic variant are substrate specific; similar statin-reducing drugs (e.g., rosuvastatin) have unaltered pharmacokinetics in individuals with the *SLCO1B1\*1B* allelic variant (Choi et al. 2008).

### Drug Responses: Efficacy and Adverse Outcomes

Aside from the rate of influx into or efflux from a cell, there are several other genetic factors that determine the efficacy or risk of adverse outcomes. Among these are the metabolizing enzymes and drug targets. A prominent example of such effects is highlighted in the variability in dosing guidelines and responses to the commonly prescribed anticoagulant warfarin. Once prescribed, patients are required to visit with the practitioner frequently to ensure that the dose prescribed is safe to use; underdosing and overdosing have serious risks. Patient factors (e.g., age, weight, sex) can account for roughly 20% of warfarin dose variability, and genetic variation accounts for the remaining variability (Gladding et al. 2010). Candidate association studies have found two candidate genes responsible for the differences in dosing: *CYP2C9* and *VKORC1*, coding for the enzyme cytochrome P450 2C9 (metabolizes S-warfarin), and vitamin K epoxide

reductase (warfarin's target), respectively (Limdi et al. 2010). Allelic variation in both of these genes leads to wide differences in dosing guidelines; depending on the type of variant of one or both genes, the individual may be prescribed as low as 3.3 mg/day or as high as 6 mg/day. Because of the high level of variability, pharmacogenetic-guided dosing tools for warfarin administration are now available (<http://www.warfarindosing.org>).

Allelic variations in genes that are not directly involved in the transport or metabolism of a drug may also affect responses to treatment. Several instances of this phenomenon have been documented in, for instance, the risk for deep vein or cerebral vein thrombosis in women taking oral contraceptives or the development of cardiac arrhythmia in patients receiving clarithromycin (antibacterial, antiulcer medication). While adverse drug outcomes such as these are typically noted in the list of potential side effects of a drug treatment, the risk for developing an adverse drug response is highly dependent on genetic factors.

Though not widely studied, the developmental stage also plays an important role. Some metabolic proteins have differential expression depending on stage of development. For example, CYP2E1 (a member of the P 450 family) plays a role in metabolizing xenobiotics. Expression of this enzyme during the third trimester is only 10% of the expression in infants older than 90 days (Krasniak et al. 2014). Further, owing to the differential expression of metabolizing proteins, young children chronically treated with acetaminophen have high rates of hepatotoxicity relative to older children and adults (Krasniak et al. 2014). Unfortunately, the mechanism of action is not fully understood. As such, neonates and young children have different clearance levels of xenobiotics and other drugs, which must be taken into consideration when determining proper dose.

### Pharmacogenetics in the Laboratory

The field of pharmacogenetics originated in the 1950s from observations that genetic differences affected rates of drug clearance (i.e., substrate

levels in plasma and/or urea) and response to treatments (e.g., adverse outcomes, high metabolism). Since then, the systematic study of genetics' role in the physiological response to a pharmacological agent has grown tremendously, with efforts in genomic, transgenic animal models, and in vitro research expanding our ability to diagnose allelic variations and administer safe and effective doses.

A common method to identify candidate genes is through a case-control study. In such studies, patients who have positive reactions to a drug regimen are recruited to a control group, and individuals presenting with either no reaction or an adverse reaction to the drug are recruited to the case group. Then, the researcher looks for genetic variation that may account for the differences in reaction among participants. Though the study of polymorphisms and drug transport/metabolism kinetics are best studied in vivo, it is not always ethical or feasible to conduct such evaluations. Animal models and in vitro studies, then, are an appealing approach. In many cases, it is possible to develop a genetic model or a cell line of a human polymorphism.

In animal models, the researcher can recreate the human phenotype through gene deletion, allelic overexpression, knock-in/-down models, transgenic models, and more. This type of study has the advantage of allowing the researcher to study the effects of the genetic polymorphism on protein formation and function in a controlled setting. Furthermore, animal models also circumvent some of the problems associated with human clinical trials (e.g., requiring large sample sizes) or in vitro studies. In vitro studies are useful when an animal model is not readily available. In an in vitro study, model cells are transfected with cDNAs that represent the polymorph or wild-type gene. While this type of study provides data on the transport kinetics of a drug, it cannot provide a detailed overview of the metabolism or the potential for other adverse drug effects.

While animal models and in vitro studies may paint an incomplete picture of the pharmacogenetics, they may provide additional information that can be used for in vivo studies or inform drug dosing guidelines. As a result of all of the research efforts (animal models, in vitro, and clinical

studies), there have been tremendous advances and discoveries of the genetic associations with drug responses. This has spurred the clinical implementation of pharmacogenetics, wherein the patient is genotyped to determine the likelihood of an adverse reaction or determine sensitivity to treatment. The broadening list of known genetic markers' effects on drug response has also resulted in genetic labeling on new drugs, as well as updating product labels for many existing therapies (e.g., warfarin). Practices such as these allow the clinician to more accurately and safely prescribe a treatment to their patient.

## Cross-References

- ▶ [Alleles](#)
- ▶ [Candidate Gene](#)
- ▶ [Genetic Code](#)
- ▶ [Messenger RNA](#)

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## Phenotype

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## Synonyms

Behavioral qualities; Genotype; Physiological appearance; Visible characteristics

## Definition

Phenotype is attribute or observable appearances/characteristic of an individual organism demonstrating its distinctive morphological, developmental, physiological, biochemical, or behavioral assets.

## Introduction

All the visible characteristics of an organism arise by genotype interaction (complete genetic inheritance) and the impact of environmental aspects. Examples of visible or observable characteristics

comprise color, shape, size, behavior, and biochemical properties. When used to describe a human, this set would contain body weight, hair length, or behavioral qualities such as nervousness (<https://www.investopedia.com/terms/p/phenotype.asp#ixzz5Ty7FsfDM>). In the early twentieth century, Danish botanist and geneticist Wilhelm Ludvig Johannsen introduced the word phenotype to describe the visible and measurable individualities of organisms (he also introduced the word genotype, in reference to the hereditary units of organisms). When two or more conspicuously diverse phenotypes exist in the similar population of a species, the species is called polymorphic. A well-documented example of polymorphism is Labrador Retriever coloring; although the coat color depends on several genes, it is perceptibly seen in the environment as brown, yellow, and black color.

An individual's phenotype may change continuously through their entire life due to changes in environmental conditions and the morphological and physiological changes related with aging. Miscellaneous environments can affect the growth and development of inherited traits (e.g., size is affected by availability of food supply) and alter the expression by identical genotypes (e.g., twins maturing in different families). In nature, the impact of the environment forms the basis of natural selection, which primarily works on individuals, preferring the survival of those individual organisms with phenotypes best suited to their current environments. The existence improvement convened to individuals exhibiting such phenotypes allows those individuals to reproduce with comparatively high degrees of success and thus pass on the efficacious genotypes to next generations (<https://www.investopedia.com/terms/p/phenotype.asp#ixzz5Ty7FsfDM>).

The abilities that contribute to phenotype arise from a combination of congenital genetic traits (genotype) and external or environmental dynamics. However, frontiers between genotype and phenotype are remarkably complex, for instance, all hereditary possibilities in the genotype are not expressed in the phenotype, because certain are the consequence of recessive, latent, or inhibited genes (<https://www.britannica.com/science/phenotype>).

## Phenotypic Variation

Phenotypic variation (due to pivotal inherited genetic change) is an essential requirement for evolution by natural selection. Natural selection interrupts the genetic organization of a population indirectly through the contribution of phenotypes. In natural selection, evolution would be not possible without phenotypic variation (Lewontin 1970).

The communication between genotype and phenotype has been hypothesized by the subsequent relationship:

Genotype (G) + Environment (E) → Phenotype (P)

A more apparent kind of the relationship is:

Genotype (G) + Environment (E) + Genotype  
and Environment Interactions (GE)  
→ Phenotype (P)

Genotypes frequently have ample flexibility in the modification and appearance of phenotypes; in several organisms these phenotypes are very diverse under variable environmental conditions (ecophenotypic variation). For example, the plant *Hieracium umbellatum* is established in two opposite habitats in Sweden. One habitat is rocky, seaside cliffs, where the plants are bushy with broad leaves and prolonged inflorescences; the other is amid sand banks where plants grow prostrate with narrow leaves and dense inflorescences. These habitats alternate along the coast of Sweden and the habitat that the seeds of *Hieracium umbellatum* land in determine the phenotype that grows (Bergfeld et al. 2009). The plants possess their habitat-specific appearance under standardized experimental conditions. An example of arbitrary variation in *Drosophila* flies is the quantity of ommatidia, which may fluctuate (randomly) amid left and right eyes in a single individual as much as they do between altered genotypes overall or between clones raised in miscellaneous environments (Dolph et al. 2011). Another example is *Donax variabilis* shell pattern. The outside of the small shell of this species can have any one of a wide range of possible

colors, from almost white, through yellow, orange, red, purple, pink, to brownish and blueish, with or without the presence of darker rays (<https://www.revolvvy.com/page/Donax-variabilis>; Rosenberg 2009; iLoveShelling 2014; Fig. 1). The notion of phenotype can be extended to variations beneath the level of the gene that disturb an organism's fitness.

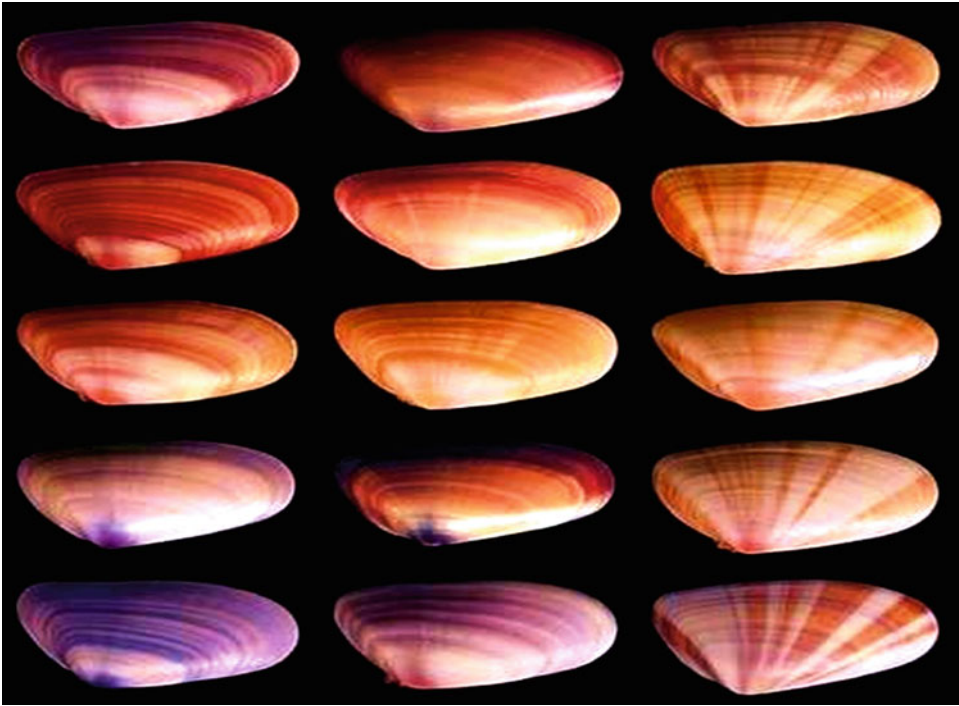
## The Extended Phenotype

Extended phenotype term pronounced by Richard Dawkins. According to Dawkins, a phenotype comprised all response that a gene has on its environments/surroundings, involving other organisms known as an extended phenotype (Dawkins 1978). For example, an organism such as a persist amends its environment by constructing a beaver barrier; this can be contemplated an expression of its genes, such as incisor teeth which uses to alter its environment. Likewise, while a bird feeds a breed parasite, e.g., a cuckoo, it is accidentally spreading its phenotype; and when genes in an orchid interrupt orchid bee behavior to enhance pollination, or genes in a peacock disturbing copulatory verdicts of peahens, once more, the phenotype is being extended. Another example, in the caddis' salivary gland, the caddis house constructed by a silk which is wrapped to prevent against predators and boost the mate selection. According to Dawkins's view, genes are designated by their phenotypic effects (Dawkins 1982). Many of the scientists generally support that extended phenotype concept is significant; however its role is regularly illustrative, instead of supporting in the strategy of experimental tests (Hunter 2009).

## Phenotypic Adaption

Evolutionary adaptations to new environments commonly reverse plastic phenotypic changes. In a new environment, phenotypic adaptation can consist of two phases: plastic change and genetic change (Fig. 2a). In the first phase, the





**Phenotype, Fig. 1** Various coloration and phenotypes pattern in a species of small edible saltwater clam *Donax variabilis* (Coquina)

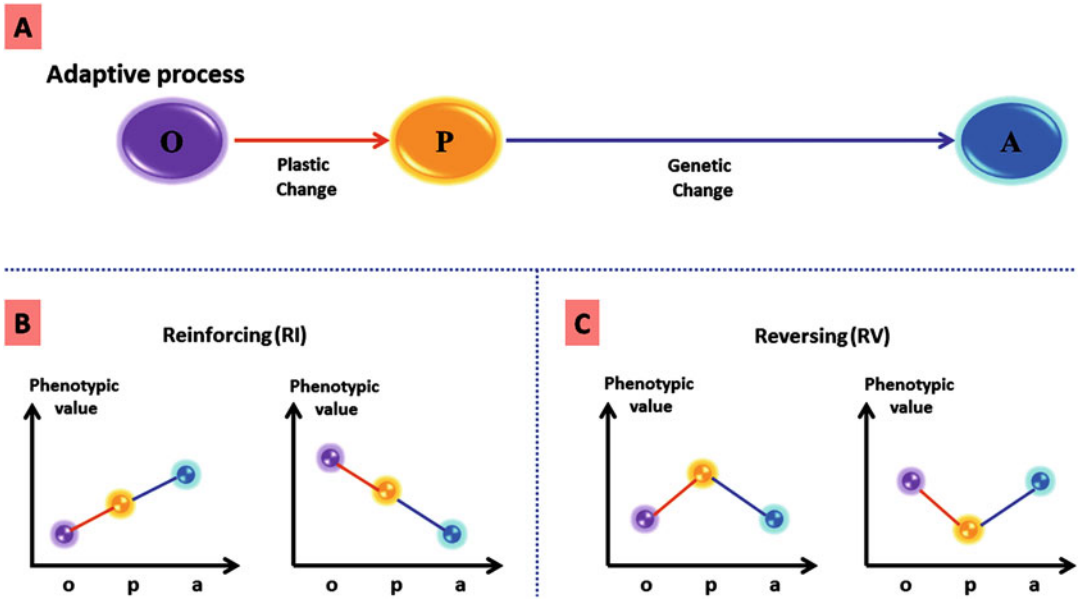
environmental shift activates phenotypic changes without mutation; such types of changes are recognized to as plastic changes (PCs) regardless of their fitness effects. In the second phase, phenotypes are changed by mutations that accrue during adaptive evolution. Although, most of the previous evolutionary studies concentrated on the second phase, but present years have stated a progression in the dispute for the significance of the first phase in adaptation (Laland et al. 2014, 2015; Levis and Pfennig 2016). It is proposed that the plastic phenotypic alterations are frequently required for organism existence in a new environment, which is compulsory because adaptive evolution is not possible, if the environmental adaptation destroys all individuals (Robinson and Dukas 1999). Moreover, it is recommended that genetic adaptations in the second phase are alleviated by the PCs in the first phase (Laland et al. 2014, 2015). For instance, plasticity can change the phenotypic value of an organism closer to the adapted state in the new environment

and provide as a stepping stone to adaptation (Price et al. 2003; Fig. 2b).

For a trait, the plastic phenotypic variation influenced by an environmental shift and the successive genetic change (GC) during the adaptation to the new environment could be in the similar direction toward the ideal phenotypic value in the new environment. Figure 2b indicates that the PC is reinforced by the adaptive GC and thus is deliberated adaptive (Ghalambor et al. 2007, 2015). The PC and the subsequent GC could also be in reverse directions. Figure 2c shows that the PC is reversed by the adaptive GC and is hence usually considered nonadaptive (Ghalambor et al. 2007, 2015; Ho and Zhang 2018).

### Phenotype Matching

Phenotype matching is essential to allow variance of behavior toward earlier unmet animals.



**Phenotype, Fig. 2** Gene expression changes in experimental evolution. (a) Phenotypic adaptation is considered by comprising the phenotypic standards of a trait at three stages: ancestral organisms adapted to the primitive environment controlled in the primitive environment (stage o); ancestral organisms measured in the new environment (stage p); and developed organisms adapted to the new environment distinguished in the new environment (stage a). Plastic alterations refer to alterations from stage o to p,

while genetic alterations refer to alterations from stage p to a. (b) When a pair of plastic and genetic phenotypic alterations of a trait, both are larger than a predetermined cutoff and are in the similar (same) direction known as reinforcing. (c) When a pair of plastic and genetic phenotypic alterations of a trait, both are larger than a predetermined cutoff and are in the dissimilar (opposite) direction known as reversing

Because phenotypic matching almost continuously employs information accomplished from relatives for inequity, these behavioral verdicts are stable with kin selection. Frequently, in phenotype matching the used phenotypes are known as cues, instead of signals. An animal making a more cognitive conclusion links the cues available by the other animal with an internal expectation of what virtual appearances/odors/sounds resemble. This internal expectation is termed a template (Breed 2010).

Phenotype matching is the capability to fascinate the phenotypes of neighboring animals and to expenditure that information to categorize earlier unmet animals. The distinctive arrangement is for phenotypic learning to occur initially in development, when the nearby animals are littermates and parents. On a functional level, this type of phenotype matching is known as kin recognition (Breed 2010).

## Behavioral Genetics and Behavior as a Quantitative Trait

There are numerous behaviors which differ in response to the environmental factors, such as biotic or abiotic, and thus accomplish a significant form of phenotypic plasticity. Behavioral genetics is the inferences amid genetic variances between animals and behavioral changes. Changes among families, subspecies, and species altogether aid to specify how ample variables role genes have in behavior (Renn and Schumer 2013). Behavioral plasticity, similar to more plastic characters, can derive via genetic assimilation or accommodation. The nature of changes in gene expression plasticity that associate with these evolutionary modifications in phenotypic plasticity (Pfennig et al. 2010; Renn and Schumer 2013). The change in gene manifestation level caused by first-order phenotype triggers ample behavioral variation

(Snell-Rood 2013). A number of studies have stated that the genes which show variation in their expression associated with the flexible and developed modifications in behaviour (Snell-Rood 2013).

Animal behavior phenotype is determined by an association of environmental and genetic factors; scientists can evaluate genetic influences by protecting animals in a common environment. For instance, testing to see if variances amid subspecies from diverse environments persist when they are kept together allows comparison of genetic and environmental effects on behavior. Many phenotypes or traits differ constantly, instead of having discrete forms. For example, height in humans, average adult humans range in height over a length of more than 2 ft (more than half a meter). Generally, quantitative traits are typically distributed like in a bell-shaped curve. Behavioral phenotypes frequently differ in this mode. This is mostly accurate of phenotypes for activity levels. Honey bee colony pollen selection rates serve as a typical example of behavioral phenotypes (Johnson and Tsutsui 2011). A normally distributed trait, whether it is physical (height) or behavioral (pollen collection), is normally the result of the involvement of several genes.

## Summary

Phenotypic variations are caused with the result of environmental factors on the expression of genetic potentials. Phenotypic changes do not comprise any inherited variations and are not transferred to upcoming generations; thus, they are not considerable in the progression of evolution. Furthermore, phenotypic changes comprise phases in an organism's life cycle and seasonal changes in an individual.

## Cross-References

- [Environment](#)
- [Evolution](#)
- [Genetic Inheritance](#)

- [Genotype](#)
- [Visible Characteristics](#)

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## Phenotype Matching

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W. D. Hamilton's concept of inclusive fitness is arguably the most significant refinement of Darwin's theory of natural selection, explaining the evolution of costly behaviors that are directed toward close kin (Hamilton 1964). Hamilton also predicted the evolution of mechanisms to facilitate the accurate recognition of kin. Two common mechanisms of kin recognition are familiarity and phenotype matching. With familiarity (also known as "prior association"), animals learn the

cues or labels of related individuals during early development (e.g., siblings) and later discriminate these familiar individuals from unfamiliar ones. Phenotype matching is an extension of familiarity. Here, animals learn their own phenotypes and/or those of their familiar kin and later compare or match the phenotypes of unknown animals to this learned recognition template. For phenotype matching to occur, there must be a correlation between phenotypic and genotypic similarity, so that individuals with traits that most closely match an animal's template are its closest kin. Both mechanisms involve a comparison between templates and unfamiliar or familiar phenotypes, but familiarity leads to recognition only of previously encountered familiar individuals, whereas phenotype matching permits discrimination among various classes of unfamiliar kin and nonkin. That is, unfamiliar kin are "recognized" as belonging to a particular kin class. This recognition occurs through generalization from recognition templates, with the degree of match between an encountered phenotype and an individual's template indicating the degree of genetic relatedness between the two animals (Holmes and Sherman 1982).

Selection will favor the evolution of kin recognition via phenotype matching when novel kin are encountered for the first time after early development because it allows discrimination among individuals without prior association, by comparing strangers' cues to a learned recognition template. This mechanism would be expected in several socio-ecological contexts. These include but are not limited to systems that have multiple mating by males (for recognition of paternal half-siblings), natal or breeding dispersal (for males to recognize their older brothers or fathers), communal nesting (for females to discriminate between related and unrelated young which are both familiar), no parental care (to avoid inbreeding hazards), and overlap of generations, particularly in long-lived species. Phenotype matching would also be favored in cases of intra- or interspecific parasitism (Holmes and Sherman 1982; Mateo 2004).

Self-referent phenotype matching is when animals learn and use their own phenotypes as

referents for kin recognition (dubbed the “armpit effect” by Richard Dawkins in 1982). Self-matching provides the most accurate assessment of relatedness, as an animal’s own cues better reflect its genotype than those of its close kin. That is, an animal’s coefficient of relationship to itself is 1.0, whereas its coefficient of relationship to its nearest kin such as parent, offspring, or full sibling is 0.5. Self-matching would be favored in species with multiple maternity or paternity to discriminate among full and half-siblings or when individuals are likely to encounter older (or younger) siblings after natal dispersal. It would also be favored when there is a risk of learning referents from nonkin such as in communal nesting or brood-parasitic situations. Animals would then not have to learn the cues of familiar (but unrelated) individuals but instead could rely solely or largely on its own cues. Similarly, self-referent phenotype matching would be especially useful in nepotistic situations, when animals need to identify their closest kin, whereas in mate-choice contexts using other referents such as parents and siblings would be sufficient to avoid close inbreeding (Mateo 2004).

Kin-discrimination abilities via phenotype matching have been demonstrated in many taxa, including birds, rodents, primates (including humans), anurans, fish, and insects (Beecher 1988; Mateo 2003; Waldman 1991). Most studies have examined kin labels in the olfactory modality, but others have considered facial and acoustic cues. Cross-fostering, isolation, and natural experiments of animals separated from kin have been used to determine if animals can use phenotype-matching abilities to recognize kin (Mateo and Holmes 2004). However, few studies have examined the context(s) in which such abilities are used (e.g., mate choice, nepotism, nest or offspring identification in a colony, etc.).

## Cross-References

- [Chemical Cues](#)
- [Coefficient of Relatedness](#)
- [Familiarity](#)

- [Family Resemblance](#)
- [Green Beard](#)
- [Kin Selection](#)
- [Richard Dawkins](#)
- [William Donald Hamilton](#)

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## Phenotypic Plasticity

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## Definition

Property of a genotype to generate different phenotypes in response to the environment.

## Introduction

All observable characters of an organism are called ► [phenotype](#), comprising behavioral,



morphological, or physiological traits. Each phenotype is determined by information contained in the DNA – or ► **genotype** – in concert with environmental inputs. Environmentally induced changes in the phenotype, without genotypic variation, are denominated phenotypic plasticity. Although trait variation is a response to environmental cues, plasticity's sensitivity and direction of expression are determined genetically. As phenotypic plasticity exhibits a genetic component, it is under natural selection and can evolve.

The range of all possible phenotypes across an environmental gradient produced by a single genotype is described mathematically by a reaction norm (or ► **norm of reaction**). The specific genotype response to changes in the environment is a result of the genotype-environment interaction, which corresponds to the slope of the reaction norm. A slope different from zero indicates phenotypic plasticity. Parallel curves that differ only in their height demonstrate differences in the trait mean value, but not in plasticity. These two aspects of reaction norms, plasticity (slope) and trait mean value, might be or not interrelated depending on the molecular mechanisms of control of trait expressions. Another important feature of a reaction norm is that it is trait-specific. Organisms are a mosaic of nonplastic and plastic traits, as well as different forms of plasticity.

Plasticity can also be visualized graphically through performance curves. Performance curves show how biological processes (e.g., growth and development rate) vary in response to an environmental variable (Huey and Stevenson 1979). In contrast to reaction norms, performance curves are a property of the individual as a whole, not of the genotype.

Phenotypic variation can be continuous or discrete. The most common form of discrete variation is polyphenisms. Polyphenism is when a genotype produces two or more alternate phenotypes in response to a determined environmental cue, for example, environmental sex determination in fishes and reptiles. In this case of discrete

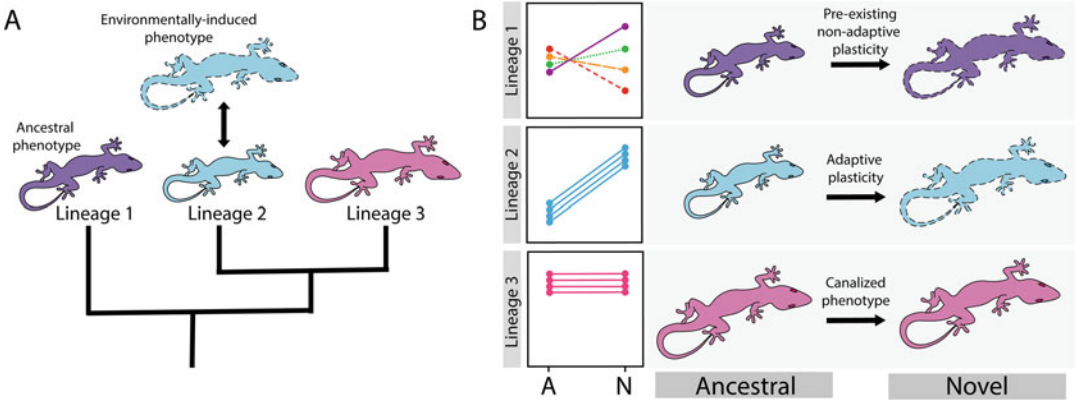
variation, the reaction norm is both plastic and canalized because it generates a single phenotype in a set of environments. ► **Canalization** is a property of the developmental systems that restricts phenotypic variation, enabling the production of the same phenotype, despite changes in environmental conditions. As canalization limits phenotypic variation, it has been often seen in opposition to plasticity; however, they are not mutually exclusive. Homeostasis (i.e., measure of the resilience of developmental systems to environmental changes) is a possible consequence of canalization, and it is negatively related to plasticity.

Phenotypic plasticity is an inevitable outcome when physicochemical processes are disturbed (i.e., breakdown of the homeostasis) during development in stressful conditions. Therefore, organisms are inherently plastic in the absence of buffering mechanisms. Most of these plastic responses to stress will probably be maladaptive. However, some developmental variants might increase chances of survival and reproductive success and fitness.

Phenotypic plasticity is a possible solution for the problem of adaptation to habitats with fluctuating conditions in which selection favors distinct phenotypes in each one. In such instances, plasticity is adaptive, and there might be evolutionary changes in the trait's sensitivity to environmental stimuli. Once plasticity evolves as an adaptation, it can persist in organisms in a latent state under homogenous conditions if there are no costs to its maintenance.

In stressful circumstances, plasticity can generate an explosion of novel phenotypic forms either by the breakdown of homeostasis or by hidden plastic responses resulting from past evolutionary processes. Thus, genetic variations that usually have little or no effect in phenotypic variation (i.e., cryptic genetic variation) are revealed, providing the raw material for natural selection to act.

West-Eberhard (2003) proposed the plasticity-first hypothesis in which she describes a sequence of events by which developmental



**Phenotypic Plasticity, Fig. 1** Evolution of phenotypic plasticity and its role in evolution. (a) Lineage 1 generates only one phenotype during normal development, which corresponds to the ancestral state of the clade; lineage 2, in contrast, produces different phenotypes in response to environmental cues; this phenotypic plasticity is an adaptation to this species habitat; lineage 3 produces a phenotype similar to the environmentally induced phenotype observed in lineage 2. (b) When exposed to novel

environmental conditions, a diverse set of phenotypes are produced in lineage 1 – representing cryptic genetic variation. Most of these novel phenotypes are maladaptive; one (solid purple line), however, is advantageous in the novel environment; the reaction norm responsible for generating the adaptive novel phenotype has been selected and evolved as adaptive phenotypic plasticity in lineage 2; differently, in lineage 3 occurs the genetic assimilation, such that the novel phenotype becomes canalized

plasticity can lead to genetic evolutionary change (Fig. 1). As explained above, when exposed to novel environments, plasticity can generate by chance phenotypes close to the optimal value favored by selection. If there is genetic variability for the form by which individuals produce such variants, selection can refine the trait by altering the regulation of its expression – causing genetic accommodation. In the absence of selective pressures for the maintenance of plasticity, there can be a reduction of the trait's sensitivity to the environmental cue, leading to its constitutive expression – causing genetic assimilation.

Phenotypic plasticity can produce, as well, phenotypes that are in the same direction favored by selection, but with lower values than the optimum. If so, plasticity might enable populations' survival and establishment in the novel environment, allowing natural selection to act in the pre-existing genetic variation or new mutations to arise. Hence, plasticity would act facilitating the movement from one adaptive peak to the other (Price et al. 2003).

## Conceptual History of the Term

The term plasticity was coined by Nilsson-Ehle in 1914 to describe environmental effects on the phenotype, although some studies describing phenotypic variation as the result of environmental changes precede the term. Woltereck (1909), in a seminal study, described mathematically the phenotypic variation in the small crustaceans of the genus *Daphnia*. Woltereck conceived the term of reaction norm, which he suggested as being hereditary. However, the idea of interaction between genotype and environment was not clear at this time. Johannsen (1911), in turn, distinguishes the concepts of phenotype and genotype, demonstrating that even in homozygous lineages with genetic control, he still observed phenotypic variation due to environmental influences.

In 1949, Schmalhausen brought the neo-Darwinian perspective to the conceptualization of the evolution of phenotypic plasticity. According to him, the evolution of a phenotype is mediated by two factors, the external and

internal environments, existing two types of environmentally dependent development: the morphosis, which is nonadaptive, and the dependent autoregulatory morphogenesis, which is adaptive. A few years later, Bradshaw (1965) proposes that plasticity is an alternative mechanism of adaptation of organisms to changes in environmental conditions, counter to the view of most evolutionary biologists at the time, who thought plasticity was a source of error during the ontogenetic development and which should be minimized. From the second half of the twentieth century, plasticity studies have become more recurrent, improving its comprehension. In 2003, West-Eberhard compiled and updated a few concepts and terminologies that had been proposed by other researchers over the previous century. Since then, numerous works have been demonstrating that plasticity has a crucial role in evolution and is a key point in the extended evolutionary synthesis (or ► [modern synthesis](#)).

### Examples of Phenotypic Plasticity

Some works show that phenotypic plasticity can be a mechanism responsible for variations in animal behavior in response to climate changes. A study by Charmantier et al. (2008) done with great tit birds of the species *Parus major* in the United Kingdom demonstrated that the mean egg-laying date advanced by about 14 days in the last 47 years. Their data indicate a relationship between the mean egg-laying date and the environmental temperature over the years, occurring a markedly linear increase in pre-laying temperature since 1970. Concomitantly, there has been a shift in a similar fashion of larval biomass of winter moth larvae, a key food resource for their rapidly growing offspring. Selection thereby favored birds that procreated in time to the peak of food availability, synchronizing birds' egg-laying dates with the timing of caterpillar emergence over the years. The rate of phenotypic changes was too rapid to be explained by

natural selection being more likely the result of individual adaptive plasticity.

Many animal species show considerable geographic variation in body size. Changes in body size can occur due to genetic modifications – possibly through evolutionary adaptation – or by effects of food availability, the latter being, for example, the case of the grass snake, *Natrix natrix*. Madsen and Shine (1993) observed for six years the patterns of body growth of island and continental populations of the grass snake. They found that female grass snakes from the island have smaller body sizes than those from the continent and that the diet of the former is composed of smaller preys. Next, they performed an experiment to test if difference in body size between populations was an effect of distinct food resources. Snakes collected from both populations were raised in captivity with equal food supply and were measured at the same time during the years. Analyses showed that the growth pattern of snakes from different populations did not differ when raised in the same conditions. This suggests that the differences observed between insular and continental snakes are a direct result of influences of food availability in body growth, without any genetic change. Besides, the similar response of the snakes to the treatments indicates that both populations share the same reaction norm.

A specific case of phenotypic plasticity is polyphenism, which can be illustrated by behavioral shifts in the species of locust *Schistocerca gregaria* (Pocco et al. 2019). This locust exhibits two forms according to the population density: a solitary phase with green coloration and a gregarious phase with black spots. This study demonstrates that nymphs living agglomerated are more active and more attracted by conspecifics. Body size is also greatly influenced by population density, with gregarious females being smaller than isolated females, in contrast to males, which are smaller in the isolated phase. These observations show, once again, that besides environmental factors, population density can alter significantly morphology, behavior, metabolism, and reproduction throughout animals' life history.

## Cross-References

- [Canalization](#)
- [Genotype](#)
- [Modern Synthesis](#)
- [Norm of Reaction](#)
- [Phenotype](#)
- [Plantae](#)

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## Phenotypic Reversibility

- [Strategy Reversibility](#)

## Pheromone

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## Synonyms

[Chemical communication](#); [Chemical cues](#); [Chemical signals](#); [Semoiochemicals](#)

## Introduction

In 1959 the chemist Adolf Butenandt and his team identified the first pheromone – the silk moth’s sex pheromone bombykol (Butenandt et al. 1959). This discovery prompted the creation of the word “pheromone” (from the Greek: *pherein*, to carry or transfer, and *hormón*, to excite or stimulate) (Karlson and Lüscher 1959). Butenandt’s discovery (1959) also established that chemical signals between animals exist and can be identified by researchers.

From the outset, Karlson and Lüscher (1959) anticipated that pheromones would be found across the animal kingdom, from insects and crustaceans to fishes and mammals. Actually it is likely that the majority of species across the animal kingdom use pheromones for various kinds of communication in every habitat on land and underwater (Wyatt 2014). To date, only insects, fishes, and mammals have been studied in any depth, while little is known about the pheromones of other taxa.

However, the idea of chemical communication was not new in 1959. For example, the ancient Greeks knew that the secretions of a female dog

attracted males; Charles Darwin included chemical signals as outcomes of sexual selection, describing the strong smells of breeding males in moths, pythons, crocodiles, musk ducks, goats, and elephants; and many scientists in the nineteenth and twentieth centuries, including Niko Tinbergen, had worked on phenomena that we would recognize as involving pheromones (reviewed by Wyatt 2014). However, since the amounts emitted by an individual animal were very small, these scientists could not easily identify the pheromones due to the limitations of the techniques available at that time. Butenandt had the novel idea of using domesticated silk moths, which could be reared in the quantities necessary to collect enough material for analysis using the chemistry of the 1950s.

Since 1959 a great variety of organic molecules has been identified as pheromones (reviewed by Wyatt 2017). This reflects the diversity of the animal kingdom and offers an ongoing challenge for scientists interested in the identification, synthesis, and exploration of natural functions of novel compounds.

## What Are Pheromones? Types and Functions of Pheromones

Pheromones are chemical substances generated by an individual that can affect another individual. The sensing individual will answer by using responses varying from alarm reactions to sexual behavior and to specific types of behavior in lower forms. Pheromones have been very well documented for insects but pheromone compounds vary considerably from species to species.

Pheromones are molecules that have evolved as a signal between conspecifics. The signal elicits a specific reaction, for example a stereotyped behavior (*releaser effect*) and/or a developmental process (*primer effect*), from a conspecific. Responses to pheromones are usually innate, and vary depending on the context and the receiver.

Several pheromones are not single compounds but rather a species-specific combination of molecules in a precise ratio. This combination is

the pheromone itself, although sometimes it is called a *multicomponent pheromone* or *pheromone blend*. The majority of pheromones operate by means of the conventional senses of olfaction and taste, but some pheromones (*allohormone pheromones*) may be ingested and act directly on the brain or other tissues.

Pheromones include numerous compounds or combinations of molecules, and serve a wide variety of functions. Some pheromones are specific to different life stages or castes. One key feature of pheromones is that they are “anonymous”: a given pheromone is the same in all individuals within a species of the same type (e.g., male or female) or physiological state (e.g., fertile or nonfertile), and it conveys a stereotyped message that is independent of the individual producing it. Quantities of pheromone, however, can differ between individuals or in the same individual over time.

The formal definition of a pheromone includes both evolved emission and reception of the signal for that function. Very little is actually known about the evolution of the production and reception of many pheromones. As a consequence, Wyatt (2015) proposed an operational definition of pheromone as “fully identified molecule(s), the same across a species, in all lactating mature females for example, which when synthesized elicit the same characteristic response in the conspecific receiver as the natural stimulus.”

## Pheromones as Intraspecific Semiochemicals

A semiochemical (from the Greek: *semeion*, mark or signal) is a chemical compound involved in the chemical interaction between organisms (reviewed by Wyatt 2014). In the context of semiochemicals, pheromones are molecules that have evolved as signals for communication and used *within* a species. They are emitted by an individual and received by a second individual of the same species, in which they cause a specific reaction, such as a stereotyped behavior or a developmental process.

According to Wyatt (2010), pheromones and so-called *signature mixtures* are two distinct concepts: pheromones can be defined as species-wide signals, while *signature mixtures* may be considered variable cues for identity.



*Signature mixtures* are variable chemical mixtures (subsets of the molecules in the chemical profile of an individual animal) learned by other conspecifics and used to recognize an animal as an individual (e.g., lobsters and mice) or as a member of a social group such as a family, clan, or colony (e.g., bees and badgers).

A pheromone is a molecule (or a specific combination and ratio of molecules for a *multi-component pheromone*) that will be found, for example, in all sexually mature females. Quantities of the pheromone may differ between individuals, which may be important in mate choice, but not in ways that allow a specific female to be recognized as an individual. The pheromone signal is “anonymous”; it could be any female. In contrast, if a phenomenon, such as a male distinguishing his mate from other females, relies on a learned *signature mixture*, it would be fruitless to search for a single combination of molecules eliciting individual mate recognition across the species. It is the great difference between chemical profiles of individual females which makes learning *signature mixtures* by males possible.

### Sex Pheromones

Sex pheromones are chemical compounds, or blends of compounds, emitted by an individual of one sex for the purpose of inducing sexual behaviors by members of the opposite sex; in other words, sex pheromones are pheromones that attract the opposite sex for mating (Teal 2008). Sex pheromones act as *sexual attractants* when they induce the receiving sex to move toward the releasing sex or as *copulatory stimulants*, or *aphrodisiacs*, when released or perceived in close proximity to the receiving sex to induce a receptivity or copulatory behavior (Teal 2008).

Sex pheromones are the only pheromones which are shared by all insect orders. This originates from the universal need to reproduce and the development of chemosensory organs early in the evolutionary history of Hexapoda. In both vertebrates and invertebrates olfactory signals play an important role in synchronizing breeding efforts with social and environmental circumstances. Chemical signals, therefore, support

various aspects of mate discrimination and sexual behavior (Keller et al. 2010).

Pheromones are also important for pre-mating isolation and speciation in both vertebrates and invertebrates (reviewed by Smadja and Butlin 2009). Most animal species have chemosensory barriers at some level or other. Even animals which are well known for courtship songs or visual displays may also use chemosensory cues for pre-mating isolation; for example, this is the case with grasshoppers and brightly colored cichlid fish (reviewed by Wyatt 2014). Behavioral changes are usually the initial triggers for population divergence, and altered recognition and response to chemical cues are expected to be involved in numerous behavioral changes. These can lead to behavioral isolation, reduction of attraction between members of different species, and even the prevention of courtship and copulation (Wyatt 2014).

### Aggregation and Host-Marking Pheromones

As far as cues for aggregation are concerned, chemical cues are very important for animals. In insects, many aggregation pheromones are used for mating, feeding, or oviposition, and may be explained by eavesdropping of sex pheromones intended for the opposite sex. Host-marking pheromones deposited by female insects can also be explained by individual advantage to both the marking and responding females (Wyatt 2014).

Aggregation pheromones lead to the establishment of animal groups near the pheromone source, either by attracting conspecifics from a distance or causing them to stop when they pass by (Wertheim et al. 2005). In contrast to sex-attractant pheromones (which attract only the opposite sex), aggregation pheromones can attract both sexes; in other words, aggregation pheromones are effective where either both sexes respond or the responder is the same sex as the emitter.

Tristram Wyatt (2014) noted that there are three different mechanisms underlying pheromone-mediated aggregations. First, individuals may aggregate in order to benefit from living in a group. For example, pheromone-induced winter aggregations of ladybird beetles facilitate collective success by means of amplification of

aposematic display, survival in harsh winter conditions, and increased mating. Second, aggregation pheromones may be the response of eavesdropping conspecifics. For example, males may respond to sex pheromones, which have been released by other males to attract females in order to mate with those females. By contrast, for instance, host-marking pheromones, deposited on hosts by insects parasitizing fruits or caterpillars, may cause dispersion as they deter other females from laying eggs in that host. Third, the so-called Allee effects may explain the evolution of many aggregation responses to pheromones. Basically, while the negative effects of overcrowding are obvious, the effects of being “undercrowded” (i.e., to have a population density that is too low) are less evident. For example, a lone animal may be more vulnerable to predators or unable to find a mate. Allee effects are often revealed by lower reproductive rates per individual at low numbers or densities of conspecifics.

However, the functional roles of aggregation pheromones differ widely (reviewed by Cardé 2014). For instance, in ladybird beetles, both sexes emit the pheromone, the aggregations persist for several months over winter, and mating only occurs when beetles disperse in the spring; the aggregation pheromone promotes clustering in autumn and does not induce mating. In long horned beetles, male-released pheromone induces attraction of both sexes, resulting in mating and relatively persistent aggregation. In bark beetles, the pheromone promotes mate finding and then mass attack of the host tree.

### Pheromones in Social Organization

Semiochemical signals are also important for kin recognition, mate choice, and other socio-sexual behaviors. A common feature of recognition by conspecifics is the ability to learn odor cues at a certain life stage. Social insects (e.g., ants, bees, wasps and termites) use hydrocarbon odor cues on their cuticles. Colony odors are usually the combination of secretions under genetic control and odors gained from the environment. For instance, the mixture of odors may serve to mask the underlying genetic heterogeneity of a nest of honey bees, which share a mother but have different

fathers. Similarly, social mammals use mixtures of odors that are equally complex. In both insects and mammals, the odor signatures lead to acceptance by the rest of the social group (reviewed by Wyatt 2014).

Recognition of kin or fellow group members is central to social and altruistic behavior toward kin, whether the group is an enormous colony or just a small family. However, recognition phenomena are thought to rely on learning and chemical cues predominately. The signature mixture molecules, learned by receivers as the template for recognition, can be produced by the sender itself or acquired from diet or local environment.

Pheromones are important for social insects, which live in colonies, and for social mammal species, where individuals share and defend the same territory. In some societies of social insects and mammals, cooperation includes reproductive division of labor: some individuals (helpers or workers) do not themselves reproduce but instead help to rear the offspring of other group members (their sisters or mothers). Such altruistic reproductive behavior can persist because of kin selection, which allows the helpers to gain their inclusive fitness indirectly by rearing copies of their genes in their brothers and sisters (Bourke 2011). In social insects pheromones are commonly used to signal queen status or to suppress reproduction in subordinates; however, little is known about how this works in comparable mammal societies (Wyatt 2014).

Nevertheless, even in the most cooperative societies, genetic conflicts of interests are inevitable. In particular, group members can compete over access to reproduction. In those social insect societies in which almost all individuals are potentially able to reproduce, and in the majority of mammalian societies, violent fighting determines who reproduces. In some insect societies, where considerable morphological differences between the queen and workers are apparent, pheromones produced by the dominant female settle the dispute by stopping subordinate females from reproducing. However, it appears that rather than being controlled by chemical manipulation, the queen’s pheromones act as honest signals (Wyatt 2014).

In highly social mammals such as primates, various studies (reviewed by Vaglio et al. 2016) suggest that the role of chemical communication in the regulation of socio-sexual behavior has been underestimated. For instance, chemical signals are known to advertise reproductive state, dominance rank and individual identity in prosimians (ring-tailed lemurs and sifakas) and New World monkeys (marmosets and tamarins); they also advertise sex, age, and family membership in both New World monkeys (owl monkeys) and Old World monkeys (mandrills). Additionally, odor profiles may reflect individual genotype and genetic similarity in ring-tailed lemurs and mandrills, and also mediate reproductive suppression of subordinate individuals by dominants in marmosets and mouse lemurs. However, although chemical signals play an important role in primate communication there is no robust bioassay-led evidence for the claims that pheromones exist in humans (Wyatt 2015).

### Alarm Pheromones

Several animals respond to the threat of predation by producing alarm signals that warn other individuals of the presence of danger or reduce the success of predators. These alarm signals may be visual or auditory, as well as chemical. Alarm pheromones are chemical substances, produced and released by an organism, that warn or alert another individual of the same species of impending danger. They are widespread, especially among insects and aquatic organisms (Verheggen et al. 2010).

Various studies (reviewed by Verheggen et al. 2010) address chemical identification of alarm pheromones and their impact on the behavior of nearby individuals. In order to conclude that a specific chemical compound acts as an alarm pheromone, it is generally considered necessary to demonstrate that (i) the compound is released exclusively under exposure to hazard, (ii) the signal is perceived by conspecifics, and (iii) it induces in the receiving individuals behavioral reactions similar to those induced when directly exposed to the same danger. On the other hand, adaptive responses to the reception of an alarm pheromone may be classified as evasive (i.e.,

receivers flee from the pheromone releaser) or aggressive (i.e., receivers move toward the signal and attack or harass the predator).

Alarm signals offer a great challenge to evolutionary explanations of behavior (Bradbury and Vehrencamp 2011) as animals make alarm signals to warn conspecifics of danger but they do so at risk to themselves. However, several animal species release alarm pheromones for the benefits to kin, which may be direct family members or fellow members of a social insect colony.

In social insects, alarm pheromones are the most commonly produced class of chemical signals after sex pheromones, and have evolved independently within all taxa. They are likely to have evolved as secondary or modified uses of existing compounds. Two common evolutionary routes, both linked to predation, consider alarm pheromones from either chemical compounds used in defense or those released by injury. There is also a third different route, where alarm responses have evolved from cues of injury of unrelated conspecifics or even individuals belonging to other species. These cues, which are also called “*public chemical information*” and can be found in a wide variety of aquatic species, are not considered to be evolved signals and so they are not pheromones (Wyatt 2014).

Alarm pheromones have been found in both invertebrates and vertebrates, with great diversity of alarm signaling systems occurring in presocial (aphids) and social (ants, termites and honeybees) insects; vertebrate animals; and even plants (reviewed by Verheggen et al. 2010). The chemical composition of alarm pheromones is highly variable; some of these pheromones can be composed of a single molecule and some of complicated chemical mixtures, whose activity is determined by their specific composition, the quantitative pattern of the different compounds, and the stereo-isomerism of the most abundant substances.

### Mode of Action of Pheromones

#### Evolution of Pheromones from Chemical Cues

Communicative behavior evolved from functionally different behaviors, and the evolution of

chemical cues into pheromones is no exception from this, although research has mainly focused on visual and acoustic signals (García-Roa et al. 2017). Pheromones are a very diverse group of chemical substances and the use of the olfactory system with its flexibility, using relatively non-specific receptors, makes the evolution of any chemical cue into a pheromone possible (Wyatt 2014). A chemical cue is any chemical compound that is used to the receiver's advantage, but has not evolved for this purpose, for example, how the mosquito finds its host via the detection of CO<sub>2</sub>. A pheromone however is all about communication, where the signal alters the behavior of the receiver, and this response leads to a change in the chemical signal in the originator (Wyatt 2010).

Bradbury and Vehrencamp (2011) discuss the evolution of pheromones following two main theories, sender pre-adaptation (sender precursor model), starting from chemical cues released by the sender, and receiver pre-adaptation, where compounds having other uses originally, for example, host or food odor, evolve to become a pheromone signal. An example of sender pre-adaptation would be chemical compounds leaking from a mature female attracting males for fertilization. A male with a mutation for higher sensitivity to detect these compounds will have more opportunities to mate, which leads to the evolution of increased sensitivity to the female's molecules through increased receptor density or specificity (Bradbury and Vehrencamp 2011). Here the chemical cue has become a pheromone. In an example of receiver pre-adaptation female moths utilize plant odors to localize suitable hosts for egg laying; this sensory bias is used by male moths to attract the females. Wittman (2016) also showed how female parasitic wasps (*Urolepis rufipes*) use the males' substrate-borne pheromones to assess male quality.

The evolution of pheromones plays an important role in species diversification. Recent work by García-Roa and colleagues (2017), using phylogenetic macroevolutionary modeling, gave a deeper insight into the extent and trajectory of diversification of animal communication, which so far had only been investigated for visual and acoustic cues. They found how multiple chemical

signals in lizards have diversified following different evolutionary speeds and directions, with some compounds being subjected to stabilizing selection, while others diversify following the Brownian motion modes of evolution.

### Pheromone Diversity and Specificity

Principally any chemical can be utilized as a pheromone if the compound(s) reliably convey a message against the background noise that can be detected by a receiver and is used to evoke a response (Wyatt 2014). Not surprisingly the chemical diversity of pheromones is large with a second key requirement being that the signal needs to reach the receiver, either directly by diffusion through the environment or indirectly through currents. These currents can be natural flow (of water/air) or even made by the sender organism themselves as described in crayfish. In terrestrial systems most pheromones require a level of volatility for dispersal (Wyatt 2014). There exist structure-activity/function relationships in aquatic systems with volatile distance cues, as well as slow diffusing peptide signals used in pheromone trails. Long-lasting pheromone signals such as territorial markers in mice are volatile but are stabilized in a protein matrix (mouse urinary proteins, MUPS, Hurst et al. 2017) that enables slow release rates and signal exclusivity.

Specificity of pheromones is often essential as predator and competitor "eavesdropping" on pheromones is widespread (Stowe et al. 1995) and can be achieved through a range of strategies such as producing an exclusive molecule usually through de-novo synthesis (Wyatt 2014). Producing exclusive compounds comes at a significant cost as it potentially requires specific synthetic capabilities, coordinated with receptor specificity, and may reduce flexibility and evolutionary change (Wyatt 2014). Utilizing common molecules that can be derived from food uptake or be metabolic by-products (secondary metabolites) is widespread and specificity of these is often achieved by the use of specific blends or bouquets of multiple compounds in specific ratios.

Alternatively animals use environmental timing such as moon cycles, daily rhythms

(zeitgeber) to ensure exclusivity through avoidance in space and time (reviewed by Hardege 1999) as these come with little to no costs. Mating in crustaceans for example is linked to the female molt and pheromones are chitin biosynthesis related, directly reflecting molt stages (Hardege et al. 2011). In polychaete worms environmental timing via moon phases enables a range of species sharing the same pheromone, just as elephants and butterflies share the same pheromones. Specificity is not always required though, coral spawning relies on a variety of species reacting to the same pheromones, thus creating multispecies mass spawning events that increase survival chances of offspring through overwhelming predator effects simply by the huge number of plankton resulting from these.

### Production of Pheromones

Just as diverse as pheromones are as molecules and in their evolutionary pathways, so is their production and secretion. Most animal species synthesize and secrete pheromones via specialized glands, others reuse substances taken up from the environment or even use compounds produced by bacteria for chemical communication.

Honeybees use their mandibular glands to produce diverse fatty acid-derived pheromones. Wu et al. (2017) used comparative transcriptome analysis to find out more about the biosynthetic pathway of these compounds and detected approximately 10,000 genes involved in mandibular glands with caste, queen loss, and maturity status being among factors that influence which of these will be expressed at any one time.

There is a huge diversity of these specialized glands, in ants for example there are more than 40 anatomically different exocrine glands, secreting hundreds of different molecules used for chemical communication (Morgan 2008), with sexual selection being the main driving force for their evolution. Philanthine wasps use their mandibular and postpharyngeal glands for pheromone production and storage. Looking at the morphology of male pheromone glands, Weiss et al. (2017) found a marked interspecific diversity in the type of associated secretory cells, but also in shape and size, concluding that evolution via

sexual selection led to this substantial diversity among these species.

Some moths and butterflies are examples of species that reuse molecules that they take up from the environment and either use unchanged or as a precursor during biosynthesis, emitting them via specialized organs (Wyatt 2014). An example for this are danaine butterflies, where the males use pyrrolizidine alkaloids as precursors to produce dihydropyrrolizines that act as sex pheromones in these species. The production and emission of these substances takes place in their two specialized androconial organs (Honda et al. 2016).

A well-known example of the use of compounds produced by bacteria is the aggregation pheromone of the desert locust, *Schistocerca gregaria*, guaiacol (2-methoxyphenol), causing the congregation of huge swarms. This pheromone is produced by the gut bacterium *Pantoea agglomerans* (Enterobacter) and emitted via fecal pellets (Pener and Simpson 2009 reviewed in Wyatt 2014).

Generally, the metabolic cost of pheromone production is low, compared with for example acoustic signals, where energy for muscular activity is being used. Only small quantities of the compounds are needed and the signal can be spread passively by wind or by current (Wyatt 2014). In chemical communication, the cost of signaling varies between no cost, for example by using body odor for individual recognition, and higher cost by using specifically synthesized compounds, for example the use of proteins in mouse urine (Wyatt 2014).

### Perception and Response to Pheromones/ Releaser and Primer Effects of Pheromones

Chemoreception is working in a similar way throughout the animal kingdom, where the olfactory system is usually playing the main role in the detection of pheromones. The main olfactory system (MOS) in mammals consists of the nasal cavity with the olfactory sensory neurons (OSN), while some terrestrial mammals, as well as amphibians and reptiles, also have an accessory olfactory system (AOS), the vomeronasal organ (VNO) with its own vomeronasal sensory neurons



(VSN) (Munger et al. 2009). Insects have multiple olfactory subsystems, like antennae and maxillary palps, with the olfactory sensory neurons located on sensory hairs (Hanssen and Stensmyr 2011). Structures and connections in these olfactory sensory neurons (OSNs) work in similar ways in arthropods and vertebrates.

In both cases, the odor molecules diffuse through the pores in the cuticle of arthropods' sensory hairs or the mucus protecting the olfactory tissue of vertebrates, and attach to olfactory receptor proteins (ORs). This creates a signal that moves down a single unbranched axon directly to a specific glomerulus in the brain. These glomeruli form a layer on the surface of the olfactory bulb in vertebrates or the main part of the antennal lobe in insects (Whitman and Greer 2009). Enzymes in the insect sensory lymph and the vertebrate mucus constantly break down the odor molecules. Although the structures in vertebrates and insects show a lot of similarities, this is an example of convergent evolution as there are significant developmental differences (Imai et al. 2010).

Chemosensory receptor proteins show a huge diversity with broad, but overlapping specificities (about 1000 in mice, 60 in *Drosophila*). Each OSN expresses only a single receptor type in the “one neuron – one receptor” rule (Imai et al. 2010). Richard Axel and Linda Buck received a Nobel Prize for their work on “odorant receptors and the organization of the olfactory system,” where they first describe this variety of receptors and their genes. All OSNs of the same receptor type come together in one glomerulus. A variety of odor molecules can activate olfactory receptors in different combinations, which creates a characteristic “olfactory picture” (reviewed by Wyatt 2014).

The way animals react to pheromones is innate, but there are various individual differences according to context, for example, time of day, age, sex, hormonal status, etc. The male of the moth (*Agrotis ipsilon*) for example does not react to female sex pheromones for 24 h after mating, although their antennae still detect the molecules (Anton et al. 2007). Males and females of the polychaete (*Platynereis dumerilii*) only react to

the pheromone of the opposite sex once they reach full sexual maturity (Hardege 1999).

The reaction of an animal to pheromones can be described in two ways, the immediate behavioral response (releaser effect) and the longer lasting physiological response, often mediated by hormones (primer effect), as for the first time introduced by Wilson and Bossert in 1963. Primer and releaser effect of pheromones is not mutually exclusive; some pheromones can have both effects. An example for this is how the male mice pheromone attracts females and causes aggression in rival males (releaser effect), but also accelerates puberty in young females and estrus in mature females (Novotny 2003). Villar and Grozinger (2017) hypothesize the queen social pheromone of the honeybee (*Apis mellifera*), 9-ODA (9-oxo-2-decenoic acid), evolved from a sex pheromone of its solitary ancestors. This substance has a primer effect on the physiology of the worker bees, but also attracts males during mating flights.

These few examples show the large variety of perception and response to pheromones within the animal kingdom, but at the same time highlight the similarities and convergent evolutionary pathways in this fast developing field of research.

## Applications of Pheromones

The use of pheromones to control pest species, especially insect pests, and the use of pheromones in breeding programs have been the driving forces in pheromone research from the early stages in this field in the 1960s (Howse et al. 1998). Bombykol, the first identified pheromone in the silkworm moth, *Bombyx mori* (Butenandt et al. 1959), is a good early example of the efforts to use chemicals to enable breeding of the moth to produce silk (Witzgall et al. 2010). Today the use of pheromones is an established technique for pest control combining pheromones with other techniques (trapping, deterrents, crop rotation, sterilization, pathogens, and insecticides) in what is known as integrated pest management (IPM), and they are also used to control invasive species (Wyatt 2014).

In IPM pheromones and chemical signals are employed to either monitor, to reduce the impact of, or to eradicate pest species (Howse et al. 1998). Mass trapping aims to “lure and kill” a pest, such as the removal of palm weevils in Costa Rica, where *Rhynchophorus palmarum* were caught to prevent the spread of a nematode, *Bursaphelenchus cocophilus* for which the weevils are a main vector. While mass trapping has been used successfully in many insect pests, aquatic examples are rare with only the use of migratory pheromones in sea lamprey successfully used at a large scale (reviewed by Witzgall et al. 2010 and by Wyatt 2014).

Mating disruption is a technique designed to prevent the sexual partners to locate each other by simply applying a large density of pheromone-coated pellets with slow release formulations. The many resulting odor trails have so many crossing points that the sex searching (usually males) are becoming confused and eventually stop searching (reviewed by Wyatt 2014). This technique has been applied routinely in vineyards to reduce densities of grapevine moths, and codling moths in orchards (Witzgall et al. 2010).

Push-pull approaches make use of an attractant (either sex pheromone or food signal to pull) and a deterrent (usually predator odor), often using pheromones in combination with other cues to push pests away from crops and concentrate them in areas where attractant traps are located (reviewed by Khan et al. 2012). Attraction of beneficial insects used as natural predators of pests is also achievable via pheromones (Wyatt 2014).

Farming and aquaculture benefit from pheromones through improved breeding programs, control of diseases through removal of vectors, or the development of resistant lines. Recent work includes the production of plants that produce insect pheromones such as aphid cues or moth sex pheromones, all based on the initial discovery that wild potatoes produce the aphid alarm pheromone (E)- $\beta$ -farnesene (reviewed by Wyatt 2014). A wide range of genetically modified crops and animals are expected to arise from our growing understanding of pheromone chemistry (Witzgall et al. 2010), and applications

potentially also include the use of pheromones in humans to, for example, influence mother-child interactions (Vaglio et al. 2009), develop contraception techniques, and influence human psyche (Wyatt 2014) – a field traditionally exploited by the perfume industry.

## Pheromones in a Changing World

Chemical signals are not only released into the environment where they can be impacted upon, but every step of olfactory communication, from production of signals, transfer through the environment, detection, perception, and responses upon pheromones, can potentially be interfered with (Rosenthal and Stuart-Fox 2012). Anthropogenic influences can fundamentally disrupt chemical communication systems with the terms “olfactory disruption” and “infodisruption” describing how human activity interferes with animal signaling systems. Toxic compounds including heavy metals, endocrine disruptors, plasticizers, and pesticides can reduce pheromone production either directly (signal biosynthesis) or by reducing fitness of individuals, which also affect signal reception, processing, and animals’ behavioral responses (Rosenthal and Stuart-Fox 2012).

Disturbing communication systems can have significant impacts upon ecosystem functions impacting not only on animal interactions (Boullis et al. 2016), but all aspects of animals’ utilization of chemical cues such as multi-trophic interactions, leading for example to altered insect pollinator communities. The detection of pathogens through odor profiles is also influenced by the effects of climate change such as increasing temperatures, and noxious gases. Changes to insect chemical communication systems are therefore also regarded as potentially impacting upon their use in Integrated Pest Management programs (IPM), a key practical application of chemical signals (Boullis et al. 2016).

The impacts of climate change especially the increase of atmospheric CO<sub>2</sub> are especially well documented in marine ecosystems, where a recent review by Clements and Hunt (2015) revealed that over 150 studies published between 2010 and

2015 show altered animal behavior upon changes in seawater chemistry with over half of the tested behaviors impacted negatively. In marine fish, changes of responses to olfactory signals seem to be based primarily on altered neurotransmitter function that occurs when animals compensate for the increase in seawater pCO<sub>2</sub>, while in crustaceans a decrease in seawater pH changes the chemical signals themselves (charge distribution and conformation, Roggatz et al. 2016).

To date, it is unclear whether pheromone signaling systems can adapt fast enough to rapidly increasing effects of climate change or whether pheromones possess the plasticity to negate impacts of climate change (Wyatt 2014), and at which costs adaptation may work.

## Conclusion

The use of chemical signals such as pheromones is crucial for the functionality of animal communication systems. These info-chemicals control all types of behavior and physiology in almost all organisms at all trophic levels. There is a significant diversity in the chemistry, and their physiological and biological effects and complex mechanisms of action for pheromones have evolved. Pheromones can be used to manipulate animals and ecosystem functions and services, with insect pest control and invasive species control forming a driving force in research efforts. Almost all pheromones, and with it the biological functions they control, can be affected by human activity and environmental stressors. Climate change represents a challenge for pheromone communication systems, and as such the stability of animal behavior, a key functional trait that controls species interactions.

## Cross-References

- ▶ [Arthropod Cognition](#)
- ▶ [Bear Sensory Systems](#)
- ▶ [Catarrhine Communication](#)

- ▶ [Charles Darwin](#)
- ▶ [Chemical Cues](#)
- ▶ [Chemical Signals](#)
- ▶ [Chemoreception](#)
- ▶ [Communication](#)
- ▶ [Honest Signaling](#)
- ▶ [Insect Communication](#)
- ▶ [Insect Sensory System](#)
- ▶ [Mating](#)
- ▶ [Mating Effort](#)
- ▶ [Nervous System of Invertebrates](#)
- ▶ [Nikolaas Tinbergen](#)
- ▶ [Olfactory Discrimination](#)
- ▶ [Olfactory Perception](#)
- ▶ [Primate Communication](#)
- ▶ [Prosimian Communication](#)
- ▶ [Reproductive Synchrony](#)
- ▶ [Rodentia Communication](#)
- ▶ [Rodentia Sensory Systems](#)
- ▶ [Scent-marking](#)
- ▶ [Sensory Receptors](#)

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## Philopatry

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### Definition

Tendency for an animal to remain or return to their natal site or group.

### Introduction

Philopatry and dispersal are complementary behaviors and as such both will be discussed extensively. Individuals can disperse and leave their natal site or group, or they can stay. Individuals that remain and breed in their natal site or group are referred to as philopatric. This entry will explore examples of philopatry, sex-biases in dispersal, the main reasons for dispersal, and the implications of philopatry for sociality.

### Natal Philopatry

Natal philopatry refers to when an individual remains in their place of birth or returns there after being away for some period of time; the latter is also known as natal homing. The often-cited example is the sea turtle, where females travel great distances to lay their eggs at the location which they had hatched. Loggerhead sea turtles

(*Caretta caretta*) are likely relying on the Earth's geomagnetic field to navigate their way back to their natal site (Brothers and Lohmann 2015). Many migratory species also exhibit natal philopatry, such as fish and birds (Greenwood 1980; Thorrold et al. 2001). Natal homing may be favored due to familiarity with the natal environment and to maintain genetic distinctiveness from other populations or species. Philopatry can also refer to remaining in the natal social group. While some individuals disperse from their natal group around the onset of sexual maturity, others remain in the same group throughout their life (Gandon 1999; Greenwood 1980). Dispersal can be age-biased, where juveniles disperse from the group and adults are philopatric (Jack and Fedigan 2004; Pusey and Packer 1987). Dispersal can also be sex-biased, where females disperse while males remain philopatric or vice-versa (Greenwood 1980; Perrin and Mazalov 2000).

### Reasons for Dispersal

The two main reasons for dispersal are kin competition and inbreeding depression. Since offspring have a high degree of relatedness with parents and kin in their natal group, kin competition decreases inclusive fitness (Gandon 1999). Kin competition includes competition for resources (e.g., food, space) and competition for mating partners. Particularly in species with polygynous or promiscuous mating strategies, males' reproductive success is dependent on securing mating opportunities. Thus, it makes sense for adolescents who are reaching sexual maturity to leave their natal group in order to allow close kin to have more mating opportunities thereby increasing their inclusive fitness (Perrin and Mazalov 2000; Waser and Jones 1983). Due to the high degree of relatedness between an offspring and other members of the group, there is a chance for inbreeding depression if the offspring remains in the natal group (Gandon 1999; Greenwood 1980; Perrin and Mazalov 2000). Inbreeding depression is any detriment to an individual's fitness caused by genetic similarities of the parents. To avoid inbreeding



depression, one or both sexes will leave to prevent mating with close kin.

Dispersal may occur due to other factors besides kin competition and inbreeding depression. For example, infanticide is most likely to occur during male takeovers, whereby the invading male targets unrelated infants. One counterstrategy is for the mother to temporarily or permanently disperse from her group to avoid infanticidal males. In some species, such as ursine colobus monkeys (*Colobus vellerosus*), females can be facultative dispersers, which means that while males always disperse from their natal group, females can either disperse or remain philopatric. In ursine colobus, females were found to be more likely to disperse during slow male takeovers than quick male takeovers, likely due to the social instability and risk of getting caught in agonistic encounters during slow takeovers (Sicotte et al. 2017). Thus, the decision to remain philopatric can be flexible and be dependent on external factors.

It is important to add that sometimes members, usually higher-ranked individuals, will forcibly evict other members to avoid competition. Therefore, dispersal is not always peaceful or voluntary (Pusey and Packer 1987). In fact, dispersal can be extremely costly since the dispersing individual has to explore new and potentially dangerous environments. In addition, individuals attempting to join a new group are often attacked by unwelcoming resident members.

### Sex-Biases in Dispersal

Among social animals, there is usually a tendency for one sex to disperse while the other one remains in the natal group. There is a notable correlation between mating systems and sex biases in dispersal (Greenwood 1980). The majority of bird species are monogamous and have male-philopatry while the majority of mammals are polygynous or promiscuous and have female-philopatry. However, there are also cases of female-philopatry in monogamous species and male-philopatry in polygynous

and promiscuous species, therefore, it is unlikely that mating systems alone determine the sex-bias in dispersal. Other alternative explanations for the sex-bias in dispersal focus on the relative strength of resource defense and mate defense (Greenwood 1980). Strong resource defense (usually by males) will attract females, and since it is very costly for the male to abandon his monopolized physical resources, females are more likely to disperse. Strong mate defense (again usually by males) usually accompanies species where males increase their reproductive success by gaining more access to mates, therefore males will likely disperse according to the distribution of females. Sex-biases can also be influenced by the duration of male tenure (Clutton-Brock and Lukas 2012). If male tenure is shorter than the time it takes for females to reach sexual maturity, then females are likely to be philopatric because they can avoid mating with the resident breeding male who is usually their father. If male tenure is longer than the time it takes for females to reach sexual maturity, then females are more likely to disperse to avoid inbreeding depression and mate with unrelated males.

### Implications for Sociality

Which sex remains philopatric has a strong influence over the social organization of the species. Members of the philopatric sex are more likely to be cooperative with one another, form strong long-term social relationships, and maintain a stable dominance hierarchy. In cercopithecine monkeys, such as vervet monkeys (*Chlorocebus pygerythrus*), females are philopatric and remain in their natal group often from birth until death. Thus, vervet monkey groups are matrilineal and females exhibit strong social bonds. The higher-ranking females are usually older individuals who have been in the group the longest and know the most about the environment and thus represent a valuable source of ecological knowledge. In addition, female members are likely related to one another so altruistic acts such as alloparental care and group

defense against aggressive males are favored to increase inclusive fitness. In contrast, another species of primate, the chimpanzee (*Pan troglodytes*) is male-philopatric and the males, who are usually related to one another, form the core cooperative unit. Therefore, the philopatric sex generally represents the stable, long-term unit, while the sex that disperses represent the transient, short-term addition to the group.

## Conclusion

Dispersal has costs and benefits, but the benefits must outweigh the costs in order for this behavior to persist in so many animal taxa. This entry defines natal philopatry, describes reasons for dispersal, the sex-biases in dispersal, and explores how philopatry influences social relationships. It is apparent that no singular explanation has been able to explain the patterns and reasons for dispersal, so perhaps it is the interaction of multiple factors which accounts for the variability in this behavior.

## Cross-References

- [Dispersal Ability](#)
- [Dispersal Patterns](#)
- [Inbreeding Depression](#)
- [Inclusive Fitness](#)
- [Infanticide](#)
- [Kin Selection](#)
- [Nesting of Sea Turtles](#)
- [Primates](#)
- [Reproductive Fitness](#)
- [Resource Defense](#)

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## Pholidota

- [Pangolin](#)

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## Phonemes

- [Cognition](#)

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## Phonological Loop

- [Cognition](#)

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## Phonology

- [Cognition](#)

## Photoperiod

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Photoperiodism is the ability of plants and animals to measure and respond to duration of light and dark in a day, or length of day and night cycle in a day, season, or year, i.e., photoperiod.

## Photoperiodism in Plants

In plants, the vegetative phase switches over to reproductive phase at particular period of day length known as critical light period or critical day length (Hopkins et al. 2009; Sinha 2004; Taiz et al. 2015). The phenomenon of photoperiodism in plants was first discovered by Somewhere in 1920s (Garner and Allard 1920) while working with Biloxi variety of soybeans and ‘Maryland Mammoth’ variety of tobacco (Hopkins et al. 2009). They discovered that these plants could be made to flower only when the daily exposure to the light was reduced below a certain critical duration.

Depending upon the duration of photoperiod, the plants are classified into three categories:

1. Short-day plants (SDP)
2. Long-day plants (LDP)
3. Day-neutral plants (DNP)

**Short-Day Plants (SDP):** These plants require a relatively short daylight period (usually 8–10 h) and a continuous dark period of about 14–16 h for flowering (Hopkins et al. 2009; Sinha 2004; Taiz et al. 2015). In SDP, the dark period must be longer than a certain critical length in order to flower. If the dark period is interrupted midway by even a single flash of light, flowering is inhibited. Short-day plants even flowers when kept in continuous darkness along with sucrose. Length of day plays insignificant role in flowering. The short-day plants may thus be called long-night plants. Common examples of short-day plants are chrysanthemums, cocklebur (*Xanthium strumarium*), tobacco (mutant ‘Maryland mammoth’, *Nicotiana tabacum*), soybean (*Glycine max*), sugarcane (*Saccharum officinarum*), rice (*Oryza sativa*), etc (Hopkins et al. 2009). They normally flower in the early spring or autumn.

**Long-Day Plants (LDP):** These plants require a photoperiod of more than a critical length, which varies from 4 to over 18 h. They require either a relatively small period of darkness or no darkness at all. In fact it has an inhibitory effect on the flowering of the plants. A long-day plant can be made to flower even under short-day conditions, if a flash of light is given to the plant during long dark period. Examples of long-day plants (LDP) are barley (*Hordeum vulgare*), spinach (*Spinacia oleracea*), radish (*Raphanus sativus*), henbane (*Hyoscyamus niger*), onion (*Allium cepa*), carrot (*Daucus carota*), cabbage (*Brassica oleracea*), etc. They normally flower in late spring or early summer.

**Day-Neutral Plants (DNP):** These plants flower in all possible photoperiods ranging from few hours to 24 h of uninterrupted light exposure. Examples of such plants are bluegrass (*Poa annua*), corn (*Zea mays*), balsam (*Impatiens balsamina*), bean (*Phaseolus* sp.),

cotton (*Gossypium hirsutum*), cucumber (*Cucumis sativus*), potato (*Solanum tuberosum*), strawberry (*Fragaria chiloensis*), and tomato (*Lycopersicon esculentum*).

### Perception of Photoperiodic Stimulus and Presence of a Floral Hormone

Photoperiodic stimulus is perceived by the pigment phytochrome present in the leaves (Hopkins et al. 2009; Taiz et al. 2015). This pigment is present in plants in two interconvertible forms, red-light-absorbing form, Pr ( $P_{660}$ ), and far-red-light-absorbing form, Pfr ( $P_{730}$ ). One form of phytochrome is  $P_{730}$  nm which absorbs light at 730 nm, and other is  $P_{660}$ , which absorbs light at 660 nm. These two forms of the pigment are photochemically interconvertible (Hopkins et al. 2009; Taiz et al. 2015). When  $P_r$  form of the pigment absorbs red light (660–665 nm), it is converted into Pfr form. When  $P_{fr}$  form of the pigment absorbs far-red light (730–735 nm), it is converted into  $P_r$  form. The  $P_{fr}$  form of the pigment gradually changes into  $P_r$  form in dark.

Under long-day photoperiods, Pfr form of pigments accumulates for a longer time and stimulates flowering of long-day plants and inhibits flowering of short-day plants. Under short photoperiods,  $P_{fr}$  gradually changes into  $P_r$  and is retained for a longer time and stimulates flowering of short-day plants. It is believed that phytochrome mediates change in the pattern of metabolism of a flowering hormone called florigen in the leaves (Hopkins et al. 2009; Sinha 2004; Taiz et al. 2015). This substance is synthesized in favorable photoperiodic conditions. Florigens are then translocated through phloem to the apical and lateral bud primordia, subsequently causing initiation of floral primordia. Subsequently the vegetative bud primordia will be converted into floral buds.

### Importance of Photoperiodism in Plants

Knowledge of photoperiodism can be used in agriculture and horticulture. By controlling the photoperiod, some plants where vegetative stage

is important (e.g., many vegetables like spinach, radish, carrot, sugarcane) can be kept in vegetative phase to obtain higher yield of tubers, rhizomes, corms, bulbs, etc. or keep the plant in reproductive phase to yield more flowers and fruits during their off-season. A plant can also be made to flower throughout the year by providing favorable photoperiod, e.g., annuals.

### Photoperiodism in Animals

Animals particularly mammals cope up with seasonal fluctuations in environmental conditions such as temperature and food availability by exhibiting seasonal cycles of physiological, behavioral, and morphological changes (Anderson 2000; Dahl et al. 2000; Vasantha 2016; Walton et al. 2011). They limit the energy demanding processes and activities such as reproduction, preparation for migration, and other extensive activities and instead focus on seasonal fluctuation adaptations. Thus, for an individual to be reproductively successful and subsequent fitness, correct timing of physiology and behavior is crucial.

### Photoperiod and Reproduction

**Mammals:** Many mammals' seasonal photoperiod marks the reproduction successes (Anderson 2000; Dahl et al. 2000; Vasantha 2016; Walton et al. 2011). They detect and respond to environmental cues that indicate the arrival or departure of seasons, and accordingly it can be breeding season or non-breeding season (Anderson 2000; Dahl et al. 2000; Vasantha 2016; Walton et al. 2011). For mammals, spring is the most favorable time of the year to breed, and the length of the gestation period determines when mating occurs. Based on the photoperiodic conditions at the time of the initiation of the mating, seasonally breeding mammals are called "long-day" (i.e., with long or increasing photoperiod) or "short-day" (with short or decreasing photoperiod) breeders (Anderson 2000; Vasantha 2016).

The breeding season of short-day breeders occurs mainly when days are shorter with longer period of darkness. They undergo gestation

lengths of 5–6 months, and their offspring are usually born in spring. Examples of short-day breeders include sheep, goat, and deer. During late winter to spring, they remain in a period of reproductive quiescence because of increased photoperiod. Ewes have relatively long periods of gestation and their breeding season is in autumn and give birth to lambs in the spring season when plenty of food is available and the other environmental conditions are favorable for their growth and development (Walton et al. 2011). Goats' breeding season occurs in autumn and winter. Long-day breeders breed when the period of daylight is longer than darkness. Examples of long-day breeders are horse, rabbit, hamster, mink, etc. They have either short gestation lengths or long gestation lengths and breed in late winter or spring, with their offspring also being born mainly in spring. They remain in anestrus during the short days (Vasanth 2016; Walton et al. 2011). Rabbits are shown to improve the quantity and quality of spermatozoa present in the ejaculates when exposed to long days (16HL:8HD) in comparison with those collected in rabbits exposed to short daylight (8HL:16HD) (Mousa-Balabel and Mohamed 2011).

**Avians:** Birds are not capable of storing nutrients for raising their young as mammals and depend on specific protein-rich food resources, which are often only available during a short period. Abundant food availability triggers a positive stimulus for initiating egg-laying. Birds perceive the temporal seasonal change in day length as an environmental cue required for initiating spring migration and gonadal development before the advancement of favorable breeding seasons. In migratory songbirds, day length acts as a synchronizer, entraining endogenous circannual rhythms of gonadal maturation, molt, and nocturnal migratory activity (Dawson et al. 2001).

## Mechanism of Photoperiodic Stimulation

Most seasonal breeding mammals possess a self-sustained endogenous rhythm of seasonal reproductive activity, which is either synchronized or

entrained by photoperiod (Anderson 2000; Vasanth 2016; Walton et al. 2011). The changing photoperiod acts as a bioregulator of reproductive activity and fertility in mammals (Dahl et al. 2000; Walton et al. 2011). Light is perceived by the eyes and stimulates the photoreceptors present in the retina. Through the optic nerve, neural information is transmitted to the suprachiasmatic nucleus (a group of neurons located in the ventral side of the encephalon). This information is further transmitted to the stellate ganglion (anterior cervical ganglion) and then to the pineal gland (an endocrine gland). Pineal gland translates neural stimuli mediating photoperiod into hormonal stimuli (Walton et al. 2011). It secretes a particular "photoperiodic hormone" called melatonin (*N*-acetyl-5-methoxytryptamine) (Vasanth 2016; Walton et al. 2011).

Melatonin is secreted when the animal is in a dark environment and inhibited by daylight (Clarke et al. 2009; Vasanth 2016). High melatonin concentrations in blood transmit the information that the animal is in a dark environment to the animal's organs and tissues. The critical information is coded by the duration of nocturnal melatonin secretion, which is proportional to the length of the night and decoded by the melatonin-binding sites in the central nervous system. Thus, melatonin can either inhibit ("long-day breeders") or stimulate ("short-day breeders") reproductive activity (Vasanth 2016).

Sexual maturation and reproductive functions in seasonal breeding mammals are dependent on the activation of melatonin receptors and binding sites in the hypothalamic-pituitary-gonadal (HPG) axis. Hypothalamus secretes pulsatile gonadotropin-releasing hormone (GnRH) into the hypophyseal portal system and stimulates the release of gonadotropins (luteinizing hormone (LH), follicle-stimulating hormone (FSH)) from the anterior pituitary (Clarke et al. 2009; Walton et al. 2011). Gonadotropins help in development and maintenance of mature gonads. The seasonal change in sensitivity to estrogen is the major mechanism for shift from breeding to non-breeding. Non-breeding season is characterized by an increase in negative feedback effect of estrogen on GnRH and gonadotrophin secretion. This results in reduced frequency of GnRH



pulses, reducing the secretion of LH and FSH (gonadotrophin), thereby causing the gonadal regression (Clarke et al. 2009; Walton et al. 2011).

In long-day breeders, the inhibitory effect of the pineal gland occurs during the short days of late fall and winter. Once the season changes with increasing photoperiod into long days, the pineal gland becomes less active, and thus the secretion of melatonin is reduced considerably. The inhibitory influence on the hypothalamus is removed. As a result of which, the hypothalamic releasing factors and pituitary hormones are also secreted to initiate the reproductive process for the onset of breeding. The young ones are produced during spring and summer. In short-day breeders, shorter days with more periods of darkness initiate the reproductive activity due to increase in melatonin secretion. The increased melatonin secretion reaching the hypothalamus then stimulates the pulsatile secretion of GnRH which in turn increases production of FSH and LH secretion from the pituitary gland resulting in the onset of ovarian activity and starting of the breeding season.

### Importance of Photoperiodism in Animals

Photoperiod being a constant environmental clue is a very reliable predictor of future environmental conditions (temperature), seasonal changes in climate, and food availability (Dahl et al. 2000; Demas et al. 2009). In animals, by altering the photoperiod artificially, certain activities like migration, reproduction, and changing of coats or plumage can be induced out of season (Dahl et al. 2000). The mating season of a species can be made to occur at an unusual time by manipulating daylight. Goat and sheep mating behavior can be changed by providing long periods of light followed by short periods, while mink's reproductive process can be started when daylight is increased. It also has a huge application in poultry industry as daylight affects egg-laying, mating, and body weight of the fowl. It is a useful tool to improve the lactational performance of cows.

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### Photoreceptors

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### Definition

Photoreceptors are structures in living organisms that respond to incident light and provide signals

that serve to initiate and maintain behaviors as varied as vision, phototropisms, phototaxes, and photoperiodicities.

## Introduction

Life initially evolved by utilizing the energy inherent in light. That same energy now provides the driving force for complex biological processes as diverse as plant photosynthesis, the timing of mating seasons in animals, and the reading of this text. Each of these processes starts with a translation of light to the activation of biological signals. The structures that accomplish that task are the photoreceptors. The focus here is on visual photoreceptors, specifically, on how they evolved and the functions they have come to support.

## Evolution of Photoreceptors

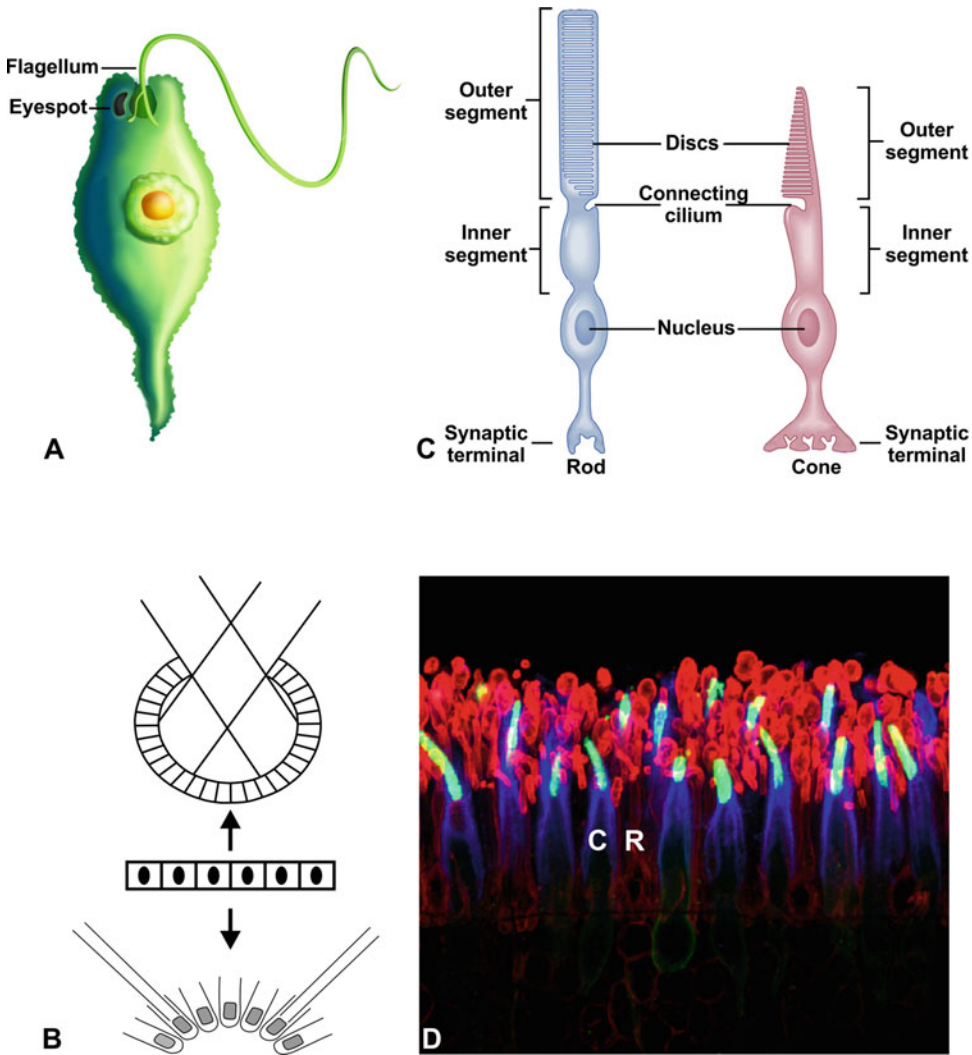
Photosynthetic cyanobacteria utilize organelles (chloroplasts) to convert the energy inherent in sunlight. Having first appeared some 2.7 billion years ago, cyanobacteria are believed to be the earliest organisms to exploit light (Schwab 2012). The capture of light by animal photoreceptors is accomplished through the activation of photopigments, the light-sensitive molecules contained in photoreceptors. Animal photopigments are composed of two conjoined components: a protein, opsin, and a chromophore that, in higher animals, is an aldehyde derivative of the vitamin A obtained from diet. Opsins have a long history, having first appeared around 700 million years ago (Mya) during the very early evolution of animals (Lamb 2013).

Absorption of light energy produces a change in state of the photopigment molecule that leads to the production of a signal used to trigger cellular changes. The signal generated by the activation of an individual photopigment molecule is miniscule. Consequently, concentrating photopigment into package-like structures allows these small signals to be summed together, and this thus serves as a fundamental step toward the goal of increasing the sensitivity of an organism to light.

One such example is the eyespot, an organelle composed of numerous photoreceptive molecules that are densely embedded in supporting structures (Fig. 1a). When activated by light, eyespots can provide a direct drive to a locomotor apparatus – for example, a flagellum of the sort found in some single-cell organisms – so allowing an animal to respond to the presence of light by movements that are either directed toward or away from a light source (positive and negative phototaxis). From similar beginnings complex eyes evolved. Over time, a considerable range of structural and functional adaptations emerged in eyes that served (1) to facilitate increases in sensitivity to light, (2) to provide the ability to detect the direction of a light source, and (3) to yield the means to both analyze and signal subtle changes in the spatial, temporal, and wavelength patterns of light present in the visual environment (Nilsson 2013; Cronin et al. 2014).

The transition from eyespot-like arrangements to complex eyes followed two general pathways (Fig. 1b). In one (top, Fig. 1b), the photosensitive surface cells invaginated to form a cuplike structure that was eventually capped with a small aperture to let in outside light. Subsequent additions to this design included optical elements in the light path to support image formation across the photoreceptive surface and musculature to allow eye positioning and mobility. Camera-type eyes of this sort are predominant in present-day vertebrates. In the other design, the photosensitive sheet was bulged outward to form a convex surface (Fig. 1b, bottom). Addition of accessory optical elements and replication of individual units (ommatidia – “little eyes”), often many times over, led to a variety of different compound eyes. Compound eyes are found in most present-day invertebrates. A detailed discussion of eye formation has been provided by Land and Nilsson (2002).

Contemporary animal eyes come in a bewildering variety of structural configurations, but the photoreceptors they contain appear to have evolved according to two general plans. Visual photoreceptors require considerable amounts of membrane surface to accommodate both the photopigment and the accessory molecules



**Photoreceptors, Fig. 1** Photoreceptors. (a) In some simple organisms, such as the planarian whose outline is sketched here, photoreception is accomplished by the absorption of light by photopigment concentrated in the eyespot; (b) scheme suggested by Land and Nilsson (2002) to illustrate how a sheet of photoreceptors (center) is either invaginated (top) or evaginated (bottom) to form more complex eyes. The lines represent incoming light rays and show how the two designs can be exploited to provide

organisms information about the direction of light sources; (c) schematic drawings of vertebrate rods and cones. Photopigment is densely packed in the discs of the outer segment; (d) picture of a section taken from the monkey retina showing rods (R) and cones (C). The photoreceptors have been labeled such that the outer segments of the cones appear green while those of the rods are red. The orientation of this section is the same as that of the sketch above. Micrograph courtesy of Gabriel Luna

required to transduce signals from the activated photopigment. In one scheme, those membranes were derived from a modified cilium; hence, these are called ciliary photoreceptors. In the other, the required tissue was formed from evaginations of the plasma membrane to form minute projections, microvilli, which are grouped

together in structures called rhabdomeres; photoreceptors of this design are thus called rhabdomeric. Photopigments in the photoreceptors from these two classes generally employ opsins that are products of genes derived from two separate gene families (respectively, **c** and **r** opsins) along with distinctive transduction

machinery. Although there are notable exceptions, ciliary photoreceptors predominate in vertebrates, while invertebrate eyes most frequently contain rhabdomeric photoreceptors. How this division occurred and the functional advantages ascribed to each of the two designs are matters of active debate and discussion (Cronin and Porter 2014; Fain et al. 2010). The remainder of this discussion concentrates on the ciliary photoreceptors of vertebrates, the familiar rods and cones.

## Rods and Cones

1. *Evolution.* The earliest vertebrates and their chordate forebears featured both rhabdomeric and ciliary eyes (Morshedien and Fain 2017). The former eventually faded from the vertebrate line, and by the time jawless and jawed vertebrates diverged (~420 Mya), ciliary eyes were in full ascendance. At the same time, however, rhabdomeric photoreceptors have been retained in vertebrate nervous systems to support some specialized functions. For example, rhabdomeric photoreceptors are found in a small population of retinal ganglion cells in contemporary vertebrates. These cells possess intrinsic light sensitivity and provide signals that are used to drive photic rhythms and control pupillary constriction.

The genes that specify rod and cone photopigment opsins have been intensively studied over the past two decades. The results from that effort suggest that cone photoreceptors appeared at a point in vertebrate evolution prior to the emergence of rods. By one such estimate, rods were added to the retinal complement of photoreceptors by around 400 Mya (Lamb 2016). Although there are the notable exceptions of some vertebrates whose retinas contain exclusively cones or rods, most contemporary vertebrate retinas contain a variable mixture of the two types.

2. *Functional differences.* Nearly 150 years ago, the anatomist Max Schultze discovered that vertebrate retinas contained two structurally distinct types of photoreceptors, rods and cones (Fig. 1c, d). Based on the relative

prevalence of rods and cones in the retinas of different species, these two appeared to be linked to different sets of visual capacities with rods underlying vision in low light-level conditions, while cones supported those aspects of seeing associated with vision under daylight conditions. These functional assignments formed what became known as the duplicity theory of vision.

Over the years, numerous psychophysical studies have documented the ways in which rod- and cone-based vision differs (Lamb 2016). Some of the most prominent differences are: (1) rods support vision under low light-level conditions, whereas cones underlie vision under daylight conditions and, importantly for contemporary humans, in almost all artificially illuminated environments; (2) rod vision operates over a restricted range of intensities while that of cone vision is extremely large; (3) rod vision adapts very slowly to shifts in abrupt changes in light levels, while cone vision adapts rapidly; (4) rod vision supports low spatial and temporal acuity, while cone vision is superior in both domains; (5) color vision is characteristic of cone-based vision only. These differences between rod- and cone-based vision hold true across most vertebrate species.

Signals derived from rod and cone activation are processed through the neural networks of the visual system. Consequently, functional differences between rod and cone vision may arise directly from differences in rod and cone physiology, from differences in the processing of rod and cone signals in the visual system, or from some combination of these two. Recent technical advances have made it possible to better understand how these differences arise.

The basis for the differences in rod- and cone-based vision can be illustrated with a few examples. For instance, direct photoreceptor recordings reveal that rods respond more slowly to the onset and offset of light stimulation than do cones, so some of the difference in temporal resolution of rod and cone vision directly reflect differences in receptor physiology. Similarly, rods cease to respond

(they “saturate”) at rather modest intensities of light, and above those light levels all vision is based on cone signals alone. On the other side of the coin, direct recordings also show that rods have inherently lower electrical noise levels than cones, so they can more reliably signal the presence of very dim lights. The organization of visual systems also impacts differences in rod- and cone-based vision. In vertebrate eyes an image of the visual world is projected across the surface of the retina. Consequently, any differences in rod and cone representations across the retinal extent mean that the relative prominence of rod- and cone-initiated signals will also vary. In the human retina, for example, the image from the point of fixation is projected onto a small central region of the retina, the fovea. At that location there is a dense concentration of cones, but no rods, and thus foveal vision automatically depends on cones not rods. At retinal regions progressively distant from the fovea, rods increase in density and cones decrease and thus objects projected away from the point of fixation can influence rod and cone vision to varying degrees.

3. *Species variations.* Although mixed rod and cone retinas are characteristic of almost all vertebrates, there are striking differences in their relative representations, the organization of their visual systems, and their functional contributions to vision. Across all vertebrates, the greater representation of one or the other type of photoreceptor, the more an animal’s vision is apt to be characterized by the different properties listed above. To take a single mammalian example, the retinas of domestic cats are heavily rod dominated, while those of squirrels have relatively many more cones. In accord with that distinction, plus numerous other features of their eyes and visual systems, cats have superb visual sensitivity under very dim illumination, photic environments in which squirrels are effectively blind.

One of the most investigated cases of the behavioral consequences of photoreceptor

variations is color vision. In vertebrates, color vision is based on cone signals, but its presence requires populations of cones containing different types of photopigment. Two types of photopigment are the minimum, but different vertebrates may possess three or four or in some cases perhaps even more. The acuteness and nature of the derived color vision depends complexly on the number of different types of cone pigments, the relative representation of cones in the retina, as well as other organizational features of the visual system (Jacobs 2018). Such variations can even occur between members of the same species. Variations in human color vision provide a good example of this. Most humans have three types of cone photopigment and enjoy keen color vision, but ~2% of all males have defective photopigment genes that reduce their complement to only two types of cone pigments. Such individuals have correspondingly much more restricted color vision.

## Cross-References

- [Cognition](#)
- [Evolution](#)
- [Evolution of Animal Color Vision](#)
- [Sensory Receptors](#)
- [Visual Perception](#)

## References

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## Phyletic Scale

- [Scala Naturae](#)

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## Phylogenetics

- [Woese's Three Domains of Cellular Life](#)

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## Phylogeny

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### Definition

Phylogeny is the history of evolution of a species or group with respect to its descent and relatedness with other species or groups.

## Introduction

Around 4.5 billion years ago, Earth was formed, but life emerged around a billion years ago (Dodd et al. 2017). Three major phases of evolution have been witnessed since then:

- a) The surfacing of prokaryotic organisms
- b) Followed by the emergence of single-celled eukaryotic organisms
- c) Finally, the evolution of multicellular organisms which occurred in the Precambrian period (Knoll 2003, 2015)

Henceforth, evolution can be understood as an organism's adaptive mechanism in response to the environmental conditions in due time. Evolution broadly can be categorized into three subtypes: (a) chemical evolution which denotes the formation of organic molecules in the period between the formation of earth and the emergence of the first life, (b) molecular evolution which signifies the changes that have brought about the appearance of the unicellular and multicellular organisms on Earth, and (c) Darwinian evolution which focuses on the events of speciation.

## What Is Phylogeny?

After the work of Linnaeus and others in the eighteenth century, the modern hierarchical system of classification came into existence, and the taxonomy stabilized. After Darwin's work and evolution being accepted as the critical factor behind the diversity and variation of life, phylogenies came into existence (Nixon 2001). Phylogeny can be defined as a blueprint of a historical evolutionary relationship amidst species and their higher-level taxa. The proof of this relationship is, in most cases, incomplete because a high number of the species that have ever lived on Earth are extinct, and a minimal number of them have been preserved in the form of fossil records (NAS 1999). This is why most phylogenies have been derived by using indirect evidence and are hypotheses.

However, the present life has descended from earlier ancestors is universally accepted.

## Evidence for Different Phylogenies

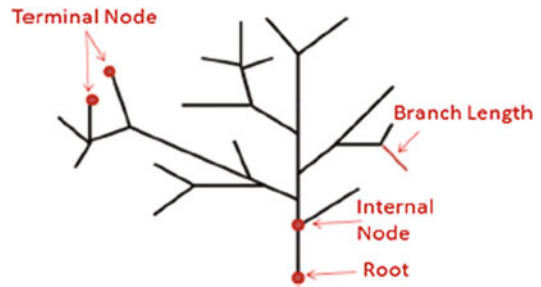
For the postulation of phylogenies, most applicable evidence from the varied fields of molecular genetics, paleontology, comparative embryology, and comparative anatomy are employed. Apart from these, the geographical distribution of flora and fauna along with the fossil records also prove handy in terms of pieces of evidence of phylogenies (NAS 1999; Biology Online 2020). Biochemical evidence has also played a significant role in contributing data to phylogenies. Mitochondrial DNA was found to be more prone to a mutation than the nuclear DNA, which became a valuable tool to ascertain the relationships among the groups that have diverged recently.

## Connection with Taxonomy

Before 1859, the taxonomy had no theoretical basis, and the organisms were classified on the basis of their apparent similarity. However, after the publication of Darwin's book (*On the Origin of Species by Means of Natural Selection*), evolutionary descent and relationship got acceptance for taxonomy (McNulty 2016).

## Phylogenetic Trees

This evolutionary relationship is depicted in the form of a tree diagram or a phylogenetic tree. Earlier, the phylogenetic trees formed were non-reproducible. Furthermore, these trees were constructed by indirect methods, and classification and phylogenetics were difficult to correlate through them. However, modern-day phylogenetics is different and utilizes a cladistic approach wherein molecular and morphological data is used for tree construction. There is a marked difference between cladistics and phylogenetics. Cladistics alludes only to the methods such as maximum likelihood and parsimony, which define the branching patterns; however, phylogenetics



**Phylogeny, Fig. 1** Features of the phylogenetic tree (Adapted from Sarma et al. 2019)

decodes these trees while keeping the historical patterns in mind (Nixon 2001). The essential features of the phylogenetic tree are mentioned in Fig. 1.

A speculatively rooted tree formed by using the rRNA genes, covering the three life domains viz., bacteria, archaea, and eukaryota, is depicted in Fig. 2. In this figure, the black branch connects the universal common ancestor to all the three life forms.

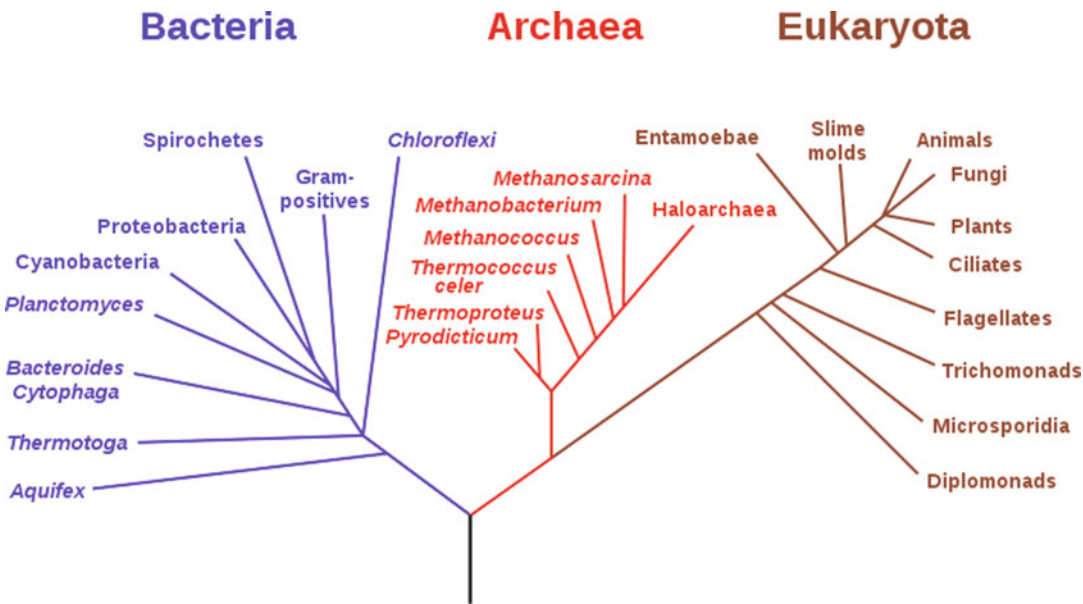
Another example of the phylogenetic tree, for the bacteria, is shown in Fig. 3.

## Applications of Phylogeny

Phylogenetics has its applications in a variety of fields. For instance, in the field of medical science, phylogenies can play a vital role in predicting the source and transmission of infectious diseases like dengue, influenza, and AIDS. An exciting development in phylogenetics is the application of phylogenies to various modern problems. Phylogenies that owe their development from molecular genetics have a huge role to play in the areas of hybridization and inbreeding across species, evolutionary effectiveness of endangered species, and percentage in captive breeding programs (Gittleman 2020).

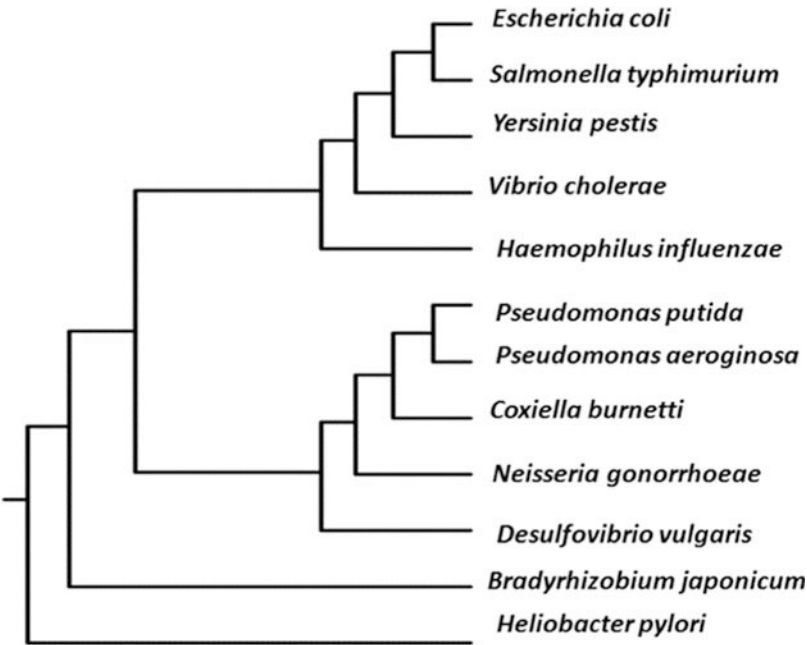
## Conclusion

Phylogeny focuses on the evolutionary relatedness among the various organisms present on the earth. Although, due to the scarcity of the fossil records, it is difficult to predict the features of the extinct organisms, yet other branches like molecular



**Phylogeny, Fig. 2** Phylogenetic tree of bacteria, archaea, and eukaryota

**Phylogeny, Fig. 3** Phylogenetic tree of bacteria (Adapted from Sarma et al. 2019)



genetics are contributing toward a better understanding of the evolutionary relationship among organisms. The development of this field is increasingly important because of its applications in the field of medical science and conservation biology.

**Cross-References**

- [Cladistic Analysis](#)
- [Evolution](#)
- [Selection Study](#)

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## Phylum

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### Keywords

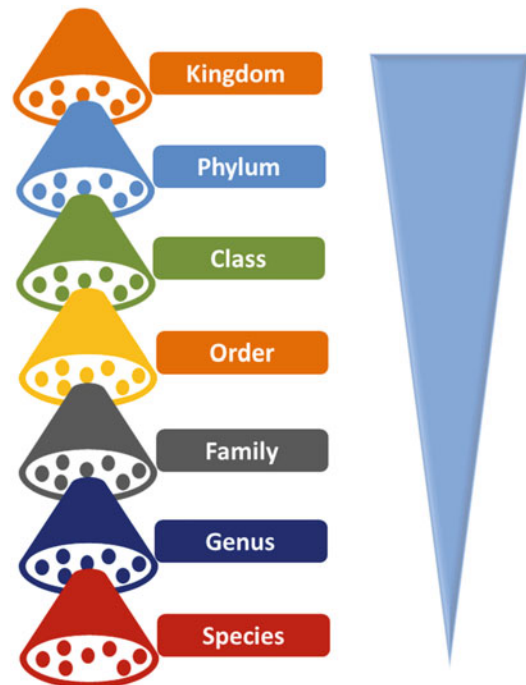
Kingdom · Phylum · Class · Order · Family · Genus · Species · Subspecies

## Definition

A phylum is a scientific term grouping together related organisms on the basis of their fundamental characteristics.

## Introduction

The term phylum was coined by Ernst Haeckel (1866) and is derived from the Greek word “*phylon*,” associated with *phyle* (tribe). A phylum can be defined either by a group of organisms with a certain degree of morphological or developmental similarity or as a group of organisms with an evolutionary relationship. In classification for taxonomic rank, “Phylum” is placed below “Kingdom” and above “Class” (Fig. 1). In botany, the word division has been used instead of phylum, even though the International Code of Nomenclature for algae, fungi, and plants follows the terms as equivalent (Valentine 2004; McNeill et al. 2012a, b). On the basis of definitions, the animal kingdom, plant



**Phylum, Fig. 1** Major taxonomic ranks of biological classification

kingdom, and fungi include 32, 14, and 8 phyla, respectively.

In plant taxonomy, August W. Eichler (1883) classified plants into five groups, known as divisions, for plants, algae, fungi, angiosperms, and gymnosperms. The zoological phyla were classified to six Linnaean classes and the four Georges Cuvier embranchements. It has been estimated that, in 40 phyla, the kingdom Animalia has approximately 1,659,420 species described, which include 133,692 fossil species, and the phylum Arthropoda has the highest number of species (1,302,809 species). Mollusca (the second-largest phylum) contains 118,061 species, with more diverse species than the invertebrate phyla Platyhelminthes, Nematoda, Echinodermata, Annelida, Cnidaria, Bryozoa, and Porifera. The vertebrates (Vertebrata) lie in the subphylum Craniata of the phylum Chordata, with 85,432 species including fossil species (19,974 species), fishes (35,644 species), amphibians (7,171 species), reptiles (15,507 species), birds (11,087 species), and mammals (16,014 species).

A phylum has been also considered as a group of species that contain a similar organization of body plan (Adoutte et al. 1999). Nevertheless, in the surviving fauna, “phyla” give the impression of being the largest grouping of taxa that can readily be believed to be more firmly identified with one another than with some other group. Phyla are typically agreeable and cognizant groupings.

Morphologically, groups of taxa indicate clear affinities to one or other significant phyla. Some groups, such as onychophorans, tardigrades, acanthocephalans, pogonophorans, or echiurans, present an issue for the phylum concept (Budd 1998) and are sometimes alluded to as arthropods, rotifers, or annelids. Phyla show a developmental starting point by their characters and body design in expanded terms and are grouped in a specific order (Valentine and Hamilton 1997; Budd 1996, 1998). There is subsequently an intelligent decoupling between the body plan that the surviving individuals of a phylum share in their phylogenetic affinities to one another, notwithstanding when they are firmly connected with one another in the surviving fauna.

From past events, a clade is the appearance of a group with a specific body plan derived from that in the main branch. The individuals from a sister-

group genealogy of various clades probably were fundamentally the same as one another (Erwin 1993). The differences between that group of organisms most closely related to a particular extant phylum, and the members of that phylum itself, have been formalized into the stem-group and crown-group concepts (Jefferies 1979), which allows a more precise definition to be given to the term “body plan.” A body plan (Valentine and Hamilton 1997) is an attainment of the characteristic developmental programme or morphology or set of features plesiomorphically shared by extant taxa in a monophyletic clade. Body plan conforms precisely to the common sense view as being shared by living groups of animals and does not require any subjective assessment of the “importance” of various body features (Hawkins et al. 1997). This subjectivity has in the past led to such elasticity in the concept that it has become virtually devoid of meaning. Thus, restriction of the body plan to extant taxa enables the concept to be used practically without the problems caused by basal members of the stem groups, which may differ little from members of closely related stem groups. Apart from the origin of the entire clade, the only other objective point that can be seen in a clade is the origin of the crown group. Thus, in the view adopted here, the body plan of the extant members of a phylum can be traced back only to the origin of the crown group. The most basal members of the stem group are virtually identical to basal members of the stem group of the closest living phylum, and as such cannot be said to possess a distinctive “body plan” of one or the other of two phyla (Abele et al. 1989; Arthur 2000).

According to Runnegar (1996), the principal point of this immediate distinction is that divergence of a clade could not be the appearance of a body plan with time. This point creates conceptual difficulties to cope with the origin of phyla, the outcome being consistent over estimation of the time of their origin (Berg 2007). Under stress conditions, stems of phylum groups lead to chief reorganization of the body (Budd 1996, 1997, 1998, 1999; Mooi et al. 1994). Obliviousness of this plausibility leads, in extremis, to the inquisitive view that amid differences, phylum level seems first, trailed by class level, lower arranged level, etc. (Willis 1940; Gellon



and McGinnis 1998; Budd 1999). Stress on the stem group of a phylum is critical because it is a transformative space within which real redesigns of the body can occur, as, for example, in the arthropods (Budd 1996, 1997, 1998, 1999) and echinoderms (Mooi et al. 1994).

There are no specific motivations to believe that the real contrasts in association or advancement happen right off the bat in a clade's history, and in reality, given the level of pre-adaptation most likely required to prepare a clade, a later appearance may be more typical (Erwin 1993). As an individual from stem bunches unavoidably take after one surviving phylum more intensively than another (or perhaps one gathering of phyla more than another), and that sensibly, no fossil life form falls into a surviving phylum. It must be attributed to a stem gathering to a phylum. The presence of creatures resembling individuals from surviving phyla in the Cambrian is not really astonishing.

Notwithstanding, from the foregoing it can quickly be seen that this insignificant acknowledgment is not sufficient to set up the source of the surviving body plan, regardless of whether the creature being referred to appears similar to the surviving structures. Normally, it is the ownership of a solitary character, for example, calcium carbonate (stereostructure) in echinoderms, or division in arthropods, that permits this task (Budd and Jensen 2000). To begin with, it makes the supposition that one character can in truth stand as intermediary for the whole mind-boggling number of characters present in the surviving body plan. This idea may be valid if body designs were certain permanent edifices, so internally obligated that they could not have been procured piecemeal. Yet this supposition does not appear to be correct, and is weakest on the grounds that the fossil record can be utilized to show how this collaboration occurred (Budd 1998).

Further, by demanding a specific character, perceiving stem bunch individuals that presently cannot seem to show it might be neglected. For instance, if the stereostructure was gained inside the echinoderm stem gathering, at that point coherently there must exist a stem mass individual that does not have it: such are subsequently not

likely to be viewed as echinoderms of any kind (David and Mooi 1998). In reality, these sorts of taxa (for example, the stem-assembled arthropods *Opabinia* and *Anomalocaris*) have regularly been allocated to their very own "phylum," in light of the fact that, for this situation, they do not have the assumed key diagnostic characters of the arthropods, for example, the sclerotized exoskeleton. Third, this view neglects to perceive that characters may in actuality have had a more extensive distribution than they do today, and in this way may have been acquired in the stem gatherings of some combination of phyla at any rate, only to be lost in one of them. This probability underlies the "calcichordate" debate, with the hypothesis asserting essentially that the calcite skeleton in echinoderms had a more extensive distribution previously and was in certainty present in the stem heredity to the chordates (Gee and Janvier 1996). In the event that this is not acknowledged, creatures that have a place where it counts in phylogeny will be wrongly allocated to a surviving phylum. The presence of stem bunches, a particularly paleontological idea, implies that the neontological wording of "phyla," particularly when taken to be synonymous with "body plan," should only be connected to the fossil record (Israelsson 1999). Acknowledgment of the significance of stem bunches is accordingly basic, freely alluding to taxa as "arthropods," "annelids," or "priapulids," and ascribing taxa to these elements on deficient grounds can obscure as much as clarify developmental connections and the example of "body plan" rise.

Observation of crown-amass instead of stem-assemble affinities of a species might be troublesome, as it depends on observation of such as one synapomorphy imparted to an individual from a surviving subgathering of the phylum to which we are referring (Zhang 2013). As it were, the taxon being referred to must appear to lie either in a surviving subgathering of a phylum or in the stem gathering of such a gathering. Normally, this possibility frequently depends on a satisfactory comprehension of crown aggregate phylogeny, and particularly on establishing understanding that is occasionally alluded to in discussing body plan development. Equipped

with this understanding, it is conceivable to reexamine the fossil record of key taxa with a view to recognizing clade and crown amass starting points. In the accompanying exchange, we are not planning to display a picture of Cambrian systematics. Or, perhaps, we wish to point to its dubious points, and to take note of how preservationist a perusing of the fossil record is allowed by this vulnerability.

## Evolutionary Role of the Phylum

Evolutionary observation of gene expression can be an approach known as phylostratigraphy (Domazet-Lošo et al. 2007). The EvoDevo method is applicable for observation of developmental gene expression, but it lacks an explicit phylogenetic approach (Hejnal and Dunn 2016). Observations of evolution of development and gene expression must be studied with the same phylogenetic comparative tools used to study other traits and also reveal biological confirmation for phyla (Dunn et al. 2013; Hejnal and Dunn 2016).

According to Levin (1992), there is no clue for specific differences in the origin of phyla. Gene expression in the mid-phase of development is little conserved at evolutionary scales. Only very closely and very distinctly related animal species have been correlated: the main understanding of these changes took place by extension of species sampling to access a higher resolution of which gene expression change might occur in which branch (Fitch and Sudhaus 2002).

## Conclusion

The phylum has a key role in animal evolution and development. At the expense of all ranks, including phyla, organizational tools succeed by the support of many phylogenies, as organizational tools explaining diversity and testing biological hypotheses against the whole tree of life. Considering current animal diversity with phyla, it is difficult to explain a phylum without any evidence, to trace an evolution with the help of phylogenetic approaches. Description and resolution

of any changes that take place in the phylogeny and tree-of-life branches can be useful.

## Cross-References

- [Evolution](#)
- [Species](#)

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## Physical Causality

- [Folk Physics](#)

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## Physical Cognition

- [Folk Physics](#)
- [Swine Cognition](#)
- [Tool Use](#)

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## Physical Composition

- [Karyotype](#)

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## Physiological Adaptations

- [Adaptation](#)

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## Physiological Appearance

- [Phenotype](#)

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## Physiological Reaction

- [Rooting Reflex](#)
- [Step Reflex](#)

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## Physiology

- [Hibernation](#)

## Piagetian Conservation

### ► Conservation

## Pig Gait

### ► Swine Locomotion

## Pig Locomotion

### ► Swine Locomotion

## Pigeon (*Columbidae*)

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### Synonyms

*Columba livia*; Feral pigeon; Rock dove

### Overview

The pigeon is a member of the order Columbidae, which includes both pigeons and doves. The most common member of the order is known as the common pigeon, rock dove, or feral pigeon (*Columba livia*). It is a small- to medium-sized bird with a stocky body, small head, short beak, and short legs. They have excellent color vision, hearing, and olfactory perception. They are strong capable fliers with the ability to return home from long distances. They are monogamous breeders with pair bonds that can last from year-to-year. Within the order, there are 42 genera with 308 wild species. In addition, there are over 700 different breeds of domestic pigeons

including fancy and racing pigeons. Pigeon racing is popular sport worldwide with racing groups on six continents, excluding Antarctica. Pigeons are popular subject in both field research and laboratory investigations of behavior.

### Natural History

#### Breeds, Morphology, and Lifespan

Modern breeds of wild pigeons are divided into four subgroups: (a) typical pigeons found throughout the entire range; (b) fruit pigeons found in Africo-tropical and oriental (sic) regions; (c) large, crowned pigeons from New Guinea; and (d) tooth-billed pigeons of Samoa. Common pigeons are typically medium-sized, stocky birds with short legs, a short neck, a small head, and a straight, thin, black bill with a fleshy cere at the base of the beak. Their wings are broad; tails are wide and rounded. They are variable in color ranging from white to bluish grey to brown. Some can have iridescent patches on the head and the throat; others have dark spots or bands on their wings. The fruit-eating pigeons of the Old World can have very colorful plumage that can include blues, greens, and yellows (Lack 2003) (Fig. 1).

Depending on the species, pigeons (and doves) vary greatly in length from about 15 cm to 75 cm in length and can weigh from 30 to over 2000 g. The smallest, the plain-breasted ground dove (*Columbina passerina*), averages about 35 g; the largest, the Victoria crowned pigeon (*Goura victoria*), weighs between 2000 and 2500 g. The common rock pigeon weighs in at about 350 g. Wild rock pigeons live about 6 years. However, in captivity, rock pigeons can live an average of 15 years and to as long as 35 years (Fig. 2).

#### Distribution and Habitat

As an order, pigeons are likely the most common birds in the world. Wild pigeons are native to Europe, North Africa, and southwestern Asia, but feral pigeons are found on all continents except Antarctica (Fig. 3).

Pigeons do not occur in the driest areas of the world including Antarctica, the Sahara desert, and



**Pigeon (Columbidae), Fig. 1** Common rock pigeon (*Columba livia*). (Photograph of two pigeons by Gwydion M. Williams is licensed under CC BY 2.0)



**Pigeon (Columbidae), Fig. 2** Victoria crowned pigeon of New Guinea (*Goura victoria*) is the largest of the columbids, standing nearly 2.5 feet tall. (Photograph of Victoria crowned pigeon by Magnus Manske is licensed under CC BY- 2.0)

the highest arctic latitudes. They inhabit nearly all habitat regions, including temperate, tropical, and terrestrial environs. They can be found in a variety of terrestrial biomes including deserts, grasslands and savannas, forests, rainforests, scrub forests and mountains, coastal regions, and wetlands.

But they occur most often in areas inhabited by humans, such as suburban and urban areas, either naturally or through human introduction. Wild rock pigeons prefer rocky coastal cliffs or open vegetation; feral birds will roost on buildings with ledges that substitute for cliffs (Lack 2003; Wells and Wells 2001).

### Evolution and Taxonomy

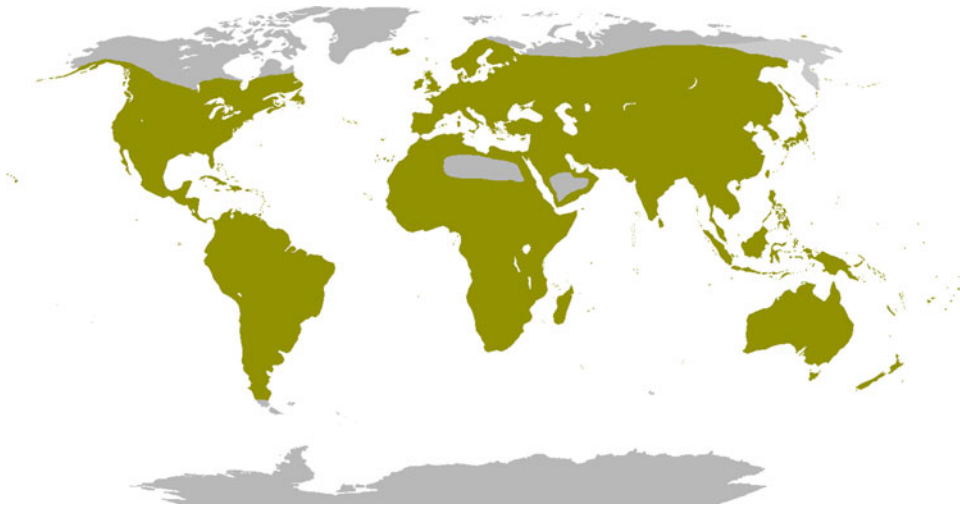
Pigeons are not well represented in the fossil record prior to the Miocene. Fossils of *Columba omnisanctorum* from Gargano Peninsula in Italy are dated to the Miocene (Olson 1985, cited in Pereira et al. 2007). However, more recent DNA sequencing places the origin of columbids over 42 million years ago in the Cretaceous period before subsequent mass extinctions (Pereira et al. 2007). The relationship across modern pigeons and doves and between other families such as the *Pteroclididae* (sand grouses), *Zenaidini* (quail doves), and the extinct *Raphidae* (e.g., the dodo and the Rodrigues solitaire) remains unresolved and tentative due to inconsistencies in DNA sequencing (Pereira et al. 2007) (Fig. 4).

### History of Domestication

Pigeons were one of the first domesticated species of birds. Archeological records document the venerated position of pigeons and doves as far back as 5000 BCE. Ancient Egyptians raised pigeons for ceremonial purposes and for food at least 4000 years ago. Mesopotamian kings gave homing pigeons to their royal couriers to be released in the event that the messenger was attacked to ensure the message would be resent. Kakish (2012) reviewed Iron Age evidence of ancient dovecotes throughout the Middle East, including Jordan, Iraq, Palestine, and Petra (see Fig. 5).

Minimal domestication of pigeons was well established in early Greek and Roman societies to be used for food, and they were used as religious symbols (see Figs. 6 and 7). Their homing





**Pigeon (Columbidae), Fig. 3** Worldwide range of the family: Columbidae. (Photograph of stuffed dodo by Kumpei Shiraishi is licensed under CC BY 2.0)



**Pigeon (Columbidae), Fig. 4** The dodo (*Raphus cucullatus*) from Mauritius is an extinct, flightless bird. It may be most closely related to the Nicobar pigeon, followed by the Victoria crowned pigeon, and the tooth-billed pigeon of Samoa. (Diagram of world-wide range of pigeons by Phoenix\_B\_1of 3, CC0)

abilities soon made them valuable bearers of messages. They were even used to send notifications of the names of Olympic victors.

The use of pigeons as offerings is also mentioned in the Old Testament of the Bible. For example, from Genesis 15:

(9) So the Lord said to [Abram], “Bring Me a three-year-old heifer, a three-year-old female goat, a three-year-old ram, a turtledove, and **a young pigeon.**”  
(10) Then he brought all these to Him and cut them in two, down the middle, and placed each piece opposite the other; **but he did not cut the birds in two.**

### Pigeons in Wartime

In more recent history, pigeons continued to be used to relay messages. During the Siege of Paris (1870–1871), carrier pigeons were used to convey important military successes. Taken out of Paris by balloon, the birds were released once safe passage over Prussian lines was achieved. The birds would return home to the Ministry of War, announcing the troops’ successful arrival to the battlefields. Birds were also used to convey official military dispatches back to Paris. See Fig. 8.

Well into the twentieth century, homing pigeons served both the American and British military forces by carrying important messages, maps, and even cameras across enemy lines during WWI and WWII. Pigeons carried messages on D-Day, June 6, 1944, because the allied troops operated under radio silence. Of the 52 animals that received the PDSA Dickin Medal of Honor in the UK for animal valor in WWII, 32 of them were given to pigeons.



**Pigeon (*Columbidae*), Fig. 5** Ancient dovecote (or columbarium) at Masada, Israel. (Photograph of ancient dovecote at Masada, Israel by pboyd04 is licensed under CC BY-SA 2.0)



**Pigeon (*Columbidae*), Fig. 6** Aphrodite, the Greek goddess of love, is derived from the Babylonian goddess Ishtar. Pigeons were revered as symbols of the goddesses themselves; they also served as sacrificial animals. (Bronze mirror stand from the northern Peloponnese, around 460–50 BCE). (Photograph of Aphrodite with a dove on a bronze mirror stand from the northern Peloponnese, around 460/50 BCE reprinted with permission, Daniel Haag-Wackernagel, artist)

### Pigeons in the Modern World

***Birds in the City.*** Pigeons have a penchant for urban environments. In relatively recent history, cities have commonly attempted to control feral pigeon populations through the process of selective removal of individual birds or through community pigeon shoots. Unfortunately, the consequence of culling flocks is typically the rapid replacement by birds from other areas as long as there are resources to support them (Sol and Senar 1995). Yet, the popularity of pigeon shoots remained popular through the late twentieth century.

Johnston and Janiga (1995) state that one major limiting factor of a city's pigeon colony size is food availability. Food shortages in the city of Perm, Russia, resulted in extreme population declines in two colonies over a 3-year period. According to Angal't (1989, cited in Johnston and Janiga 1995), not only did the two observed populations drop from 161 and 182 birds to 35 and 30 birds, respectively; moreover, the



**Pigeon (*Columbidae*), Fig. 7** Fifth century BCE Cyprian statue of Aphrodite holding a dove. (Fifth century BCE Cyprian statue of Aphrodite holding a dove is in the Public domain (by anonymous); statue found in the Neues Museum, Berlin)

large colonies devolved into multiple small groups of only 5 or 6 pairs of birds. Johnston and Janiga suggest that presence of solitary nesting pairs may reflect poor food resources rather than an anti-colony bias.

In Basel, Switzerland, nine lofts for wild pigeons were constructed between 1988 and 1990 to evaluate and manage the size and health of urban, feral pigeon populations by managing base food supplies. An educational campaign was launched to reduce or eliminate pigeon feeding by residents. Over a 4-year period, Haag-Wackernagel (1993) reported a 50% reduction in the 9 lofts through a combination of feeding management and the removal of 1200 eggs per year, with a corresponding reduction in the Basel pigeon population to 10,000. His data confirm that food resources can be a limiting factor for pigeon populations and an effective intervention tool for cities.

**Pigeon Racing.** The natural ability for pigeons to find their way home over hundreds of miles has interested modern scientists and modern pigeon racing enthusiasts alike. Pigeon racing has



**Pigeon (*Columbidae*), Fig. 8** Pigeon post medal for French military air communications. Bronze medallion, d. = 63 mm. Left panel: A homing pigeon is released by the city goddess Lutetia sitting on a cannon; in the background a hot air balloon is carrying homing pigeons out of the city. Right panel: a homing pigeon flies over an avian

transport basket; the words *Ministere de la Guerre*|*Communications Aériennes* translates as Minister of War|Air Communications. (Pigeon Post Medal for French Military Air Communications. Artist: Charles Jean Marie Degeorge, 1837 Paris-1888 Paris)



become a popular sport across the globe. The American Pigeon Racing Union hosts over 700 affiliated clubs and nearly 150 affiliated breeders in the USA. Racing pigeons will typically fly between 75 and 500 miles but race longer than 1000 miles in a single race (Walcott 1996). Modern racing methods include GPS tracking and electronic monitoring of arrival times.

## Natural Behavior of Pigeons in the Wild

**Courtship and Reproductive Behavior.** Pigeons are generally monogamous birds (Wells and Wells 2001) that form long-lasting pair bonds until one of the pair dies or disappears. They will form new bonds after losing a mate but only slowly. During courtship, several males may solicit an unattached female until she selects a mate. Typical courtship behavior tends to be stereotypic; the male will spread and drag or raise his tail feathers, inflate his neck, and engage in polysyllabic cooing. Males are sensitive to the responses of their mates, and courtship rituals will be persistent as long as the female shows some interest. Bonded pairs may also engage in food sharing.

Nesting is a collaborative process. The unlined nests consists of a loose bundle of twigs, roots, and other materials and are typically placed under an overhang on a relatively flat surface like a building ledge or cave floor. Nest building takes several days, and nests are defended by both partners. Both sexes cooperate to raise the young. Clutches usually consist of two, white eggs; incubation is between 11–30 days depending on the species. Altricial young are fed crop milk – a fluid of sloughed epithelial cells from the parents' crop that is high in fat and protein. The young are cared for continuously until about 25–32 days in the summer or upward of 45 days in winter.

**Social Behavior.** Pigeons can breed year round. Some species are colonial nesters while others are solitary (Wells and Wells 2001). They show no obligatory sign of needing to breed in colonies, and yet, many do when it is advantageous to do so. According to Johnston and Janiga (1995), after the mated pair, the colony is the most social unit. Colony nesting can confer advantages

such as group foraging and communal defense against predators. Neighboring colonies may be characterized by inter-colony exchange of individuals as a result of male-to-male cross-colony interactions, cross-colony courtships, and among females that lack a pair bond.

Johnston and Janiga (1995) state that perhaps the one major limiting factor of a colony's size is food availability. Forage shortages in the city of Perm resulted in extreme population declines in two colonies over a 3-year period. According to Angal't (1989, cited in Johnston and Janiga 1995), not only did the populations drop for 161 and 182 birds to 35 and 30 birds, respectively; moreover, these previously large colonies devolved into multiple small groups of only 5 or 6 pairs of birds.

**Feeding and Foraging.** Worldwide, most pigeons forage on the ground, eating mostly seeds; some eat fruit and will forage in trees and bushes. Few pigeons eat insects. Fruit-eating pigeons do not typically drink water as most of their needs are met with the water in the fruit. However, seed-eating pigeons drink large quantities of water – up to 15% of their body weight daily. Pigeons that drink water have a unique method of drinking. Rather than scooping up water in their beaks, tilting their heads back, and allowing the water to run down their throats, pigeons are the only birds that immerse their beaks and suck in the water.

Rock pigeons are flock foragers, typically traveling less than 20 km (12.5 miles) from the roost to forage. Because foraging is a social behavior in pigeons, observational learning of foraging techniques is an effective way to transmit important skills to young birds. Pigeons are very effective social learners and they learn foraging skills through observation.

**Orientation, Navigation, and Homing.** For wild rock pigeons, daily forays usually cover relatively short distances, up to about 20 km. However, domestic and wild pigeons also have the ability to travel extremely long distances from strange places back to their home lofts or roosts. This ability has baffled breeders, racing enthusiasts, and scientists for decades. In fact, few topics in animal behavior have been studied so

persistently than the orientation, navigation, and homing abilities of pigeons (for an overview, see Johnston and Janiga 1995).

Johnston and Janiga (2001) point out several important limitations to these homing-related abilities. First, pigeons are not migratory birds; they remain in reasonable proximity to their home nests and within their home range all year round. Second, pigeons do not fly at night; they prefer to sleep. As such, they are insensitive to night sky information that is important for the migration of other birds. Instead, the unique orientation and navigational abilities of pigeons appear to be employed in the process of homing long distances and in unfamiliar landscapes. Mehlhorn and Rehkämper (2009) provide an overview of homing in the pigeon.

*Physiology of Homing.* Homing involves good vision, good olfaction, and a biological/neurological compass. In terms of physiology, extensive research has identified several key physiological organs and processes that contribute to successful homing, including iron-sensitive (Fe) magneto receptors in the beak, the trigeminal nerve, and the hippocampus.

*Sources of Homing Information.* Putative sources of homing-relevant information include geomagnetic fields, a sun compass, odors, and landmarks (see Fig. 9). Additionally, individual motivation (e.g., mate separation) and previous homing experience may influence return speed or return success. Furthermore, these systems

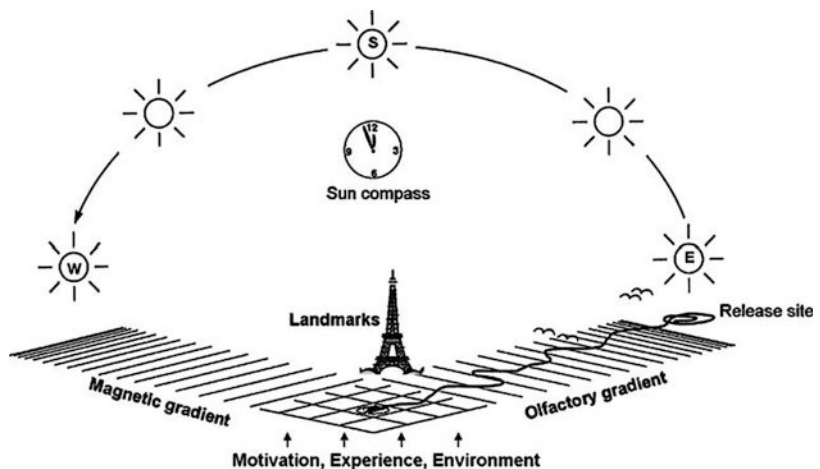
may work together, individually, or in redundant or overlapping subsets to allow birds to return home. Investigations, both laboratory- and field-based, have attempted to isolate and identify the relative contributions of each of these information sources.

*Geomagnetics.* Sensitivity to the earth's magnetic fields is implicated by the presence of magnetite-sensitive structures located in the upper beak of homing pigeons (Wiltschko et al. 2010). Research efforts to test this hypothesis typically attempt to disrupt the magnetic information being received by these structures or rely on naturally occurring anomalies in geomagnetic fields. Keeton (1971, cited in Mehlhorn and Rehkämper 2009) glued bar magnets to the backs of pigeons and then released them up to 50 km from their home roosts on sunny days. The magnets disrupted and slowed the return of the experimental birds (both naïve and experienced homers) compared to controls. Visalberghi and Alleva (1979, cited in Walcott 1996) attached Helmholtz coils to pigeons' heads and released them on sunny days. The result was a disruption in homing behavior suggesting that pigeons cannot (or do not) shift easily between a magnetic compass and a sun-based compass in order to find their way home.

*A Sun Compass.* When homing pigeons use the sun as a reference point, they must take their location and the sun's movement across the sky into consideration. Therefore, any sun-based

#### Pigeon (*Columbidae*),

**Fig. 9** Diagram of the putative contributors to successful homing. (From Lipp 1996, cited in Mehlhorn and Rehkämper 2009). To return from the release site to home (marked with a circle), pigeons may employ the use of a sun compass, a geomagnetic gradient, landmarks, and/or scents. Note also that motivation, experience, and environmental conditions are thought to play a role as well





compass must reflect sensitivity to solar East-West travel, seasonality, and time of day, as well as location. As yet, there is not a thorough understanding of how this is accomplished, but research on the sun compass goes back to the 1960s and 1970s. Most of the sun compass research involves clock-shifting pigeons by several hours, and then releasing them at a distance and watching changes in their compass bearings as they disappear over the horizon. A variety of contributing factors to successful sun compass use have been investigated, including (a) polarized light, (b) hippocampal lesions, and (c) the sun's azimuth. A sample of investigations exemplifies these investigative approaches.

(a) *Polarized Light*. The assumption that excellent vision is necessary for timely and accurate homing is flawed as some pigeons fitted with opaque goggles still find their way back to the loft. So while clear vision may or may not be critical for homing, light does appear to be important – particularly polarized light. Phillips and Waldvogel (1988) described how deflector loft housing redirects light and wind through a pigeon loft in a clockwise or counterclockwise manner. Deflectors are used to increase ventilation, decrease CO<sub>2</sub> buildup, increase light inside the loft, and manage loft temperatures in the summer. Phillips and Waldvogel noted that birds housed in deflector lofts that are released in the summer show a release site departure bias that matches the deflection in the home loft. Although initially used as evidence of olfactory cue effects on homing, they proposed that light deflection from these panels can also influence pigeons' vanishing bearings upon release from a distant site. Using two different deflector panels, the directionality of light and wind could be differentially controlled. Standard deflector panels rotate light and deflect wind such that both enter the loft from the same direction. Their experimental panels reversed light cues relative to wind flow. In this condition, light cues were rotated in a clockwise direction, while wind flow was rotated in a

counterclockwise direction. They also measured light polarization under the two deflector conditions. They found that in the standard deflector arrangement, the "band of maximized polarized light" (BMP) was consistent with natural light across the summer. However, with the experimental deflectors, the BMP is greatly altered relative to natural light. Behaviorally, there were differences too. Results showed that early in the summer, birds from the standard loft with typical deflector panels showed an average + 39° homing deflection upon release, whereas birds from the loft with the experimental panels showed an average – 19° deflection. By the end of August, the two groups' homing deflections had converged. But the findings suggest that an important part of a sun compass system is derived from polarized light, particularly in the early part of summer. The evidence suggests an important role for light polarization in the use of a sun compass for pigeons.

(b) *Hippocampal Lesions*. In a laboratory investigation, Bingman and Jones (1994) provided access to the daytime sky to help pigeons find food. Prior to training, the experimental birds' hippocampus was surgically lesioned. Control pigeons underwent a similar lesioning of the caudal neostriatum (a similar structure not used for orienting or navigating). A 1-meter-diameter, eight-sided, circular, testing arena had a clear top and holes in each of the eight walls for food cups. Cups were blinded to prevent visual cues from outside the arena. The testing apparatus was outdoors. The pigeons could see the sky through the roof of the arena. The birds were trained to eat from these cups. For each pigeon, food was always presented in the cup corresponding to a specific compass direction (East, West, or South). During testing, each bird was released in the center of the arena and allowed to explore the cup holes until it found food. Observers recorded where the birds' sequential choices occurred. Although all birds learned to explore and eat from the cups, the hippocampal-lesioned pigeons never learned

to find the food on the first try. Control pigeons learned the task quickly. Following a 6-h clock-shifting procedure, the control birds showed a 90° shift in their cup choices, as predicted. The hippocampal-lesioned birds were not tested in this condition because they had failed to learn the task initially. Together the hippocampal-lesioned and control birds' data provided strong evidence that (1) pigeons do use a sun compass and (2) the hippocampus plays a critical role in effective sun compass use for food finding.

- (c) *Sun's Azimuth*. Wiltschko et al. (2000) note that homing pigeons that use a sun compass must keep track of the differential movement of the sun throughout the day. This is not a simple task as the sun's path does not follow a simple algorithmic rule. The mathematical relationship between the vertical position of the sun over the horizon (i.e., azimuth) relative to its rate of travel from East to West is not linear. Immediately before sunrise and before sunset, the sun's altitude changes rapidly (but its azimuth does not). Throughout the day that relationship reverses. In the morning, the sun moves *up into the sky* quickly, but *less so across* the sky. Similarly around midday, the azimuth (e.g., travel across the sky) changes rapidly, but the sun's altitude changes little. Interpretation of this information requires sophisticated biology and cognition on the part of the pigeon, if it is to use the sun as a reference point. Wiltschko et al. (2000) clock-shifted birds by keeping them in a light-tight room in which automatic day/night cycles were shift back 4 h for at least 5 days. The shifted photoperiods began 4 h prior to natural sunrise and ended 4 h before natural sunset. Control birds were kept in a similar room with a window allowing for natural sunrise and sunset. The laboratory was approximately 25 km from their home lofts. Birds in both groups were released on sunny days, 1 h after their "sunrise" or 1 h before their "sunset," and vanishing points were recorded within 5°. Deflection of the vanishing points of the experimental birds was compared to that of the control birds. The results showed that the

clock-shifted birds' vanishing points also shifted in a manner consistent with the artificial sun's azimuth and travel rates across the sky. It appears that homing pigeons have sophisticated internal representations of the sun's curvilinear path that makes the use of a sun compass highly effective for homing.

*Landmarks*. Pigeons are remarkably loyal to navigation routes, at least when traveling short to moderate distances. Within familiar local territory, environmental objects and/or scents provide straight-forward sources of information. In the spatial memory literature, these objects are categorized into three groups that provide different kinds of information: beacons, landmarks, and environmental geometry (see Domjan 2015). Beacons are cues located at the goal. In the case of homing pigeons, a beacon might be the sight or scent of the home loft. Once detected, they can fly directly to the goal. A landmark is a distinctive feature that has a reliably fixed, physical relationship to the goal. A tall tree in close proximity to the home loft would be obvious examples of homing landmarks. The geometry of the environment can serve as a cue for narrowing in on a goal. A bird might learn that the home loft is located between a specific road and the highway. But how complex can landmark- > goal relationships become?

Blaisdell and Cook (2005) trained laboratory pigeons to find a food cup that was consistently presented between two landmarks (a red wooden L and a blue wooden T) on a 4 × 4 grid of no-food cups. All cups were filled with gravel; only the target had food buried in the cup. Odor cues were tested and ruled out as a viable cue. Within ten sessions, pigeons were choosing the correct cup on their first attempt. The introduction of distractors (tall PVC tubes painted to match the landmarks) briefly disrupted performance. But the birds' choices quickly came under control of the shapes and locations of the landmarks (and not based on color).

In a second set of training trials, only one reliable landmark, the blue T, was used, and its fixed relationship to the food cup was changed from the first training. Distractors were randomly

placed but never in the positions previous held by landmarks. Performance declined when the landmark- > goal relationship changed, but across trials, performance again improved. By the last session, birds averaged 1.8 choices to find the food.

In final integration tests, the blue T was replaced with the red L. The landmark- > goal relationship was the same as the previous set of trials (which was not consistent with the L's original position). The pigeons responded in a manner that suggests that they were able to integrate information from the two different training sessions to compute a new landmark- > goal spatial relationship. The results imply that pigeons can enlarge their spatial map by cognitively linking common elements with distinctive histories.

**Odors.** It is generally assumed that homing pigeons do utilize odor when homing. Much of the olfaction research had relied on one of two methods: (1) eliminating odors surgically or by blocking the nostrils to create "anosmic pigeons" or (2) experimentally manipulating odors at the home loft, during transport, or at the release site. Evidence from the distant release of anosmic pigeons, and with birds who have either been denied odors, or exposed to experimental odors, shows that their orientation and navigational abilities are compromised by odor manipulations. Despite concerns regarding possible behavioral side effects of the more invasive methods, the evidence remains compelling. However, when releasing at sites close to the home loft, anosmic pigeons simply fly home, suggesting that they are relying on redundant systems for local homing (such as familiar landmarks).

### Multimodal Methods and Redundancy

Throughout the history of homing research, the specter of a system with redundancy became simultaneously compelling and problematic. Homing appears to be part genetics/physiology, part multimodal learning, and part spatial mapping. Numerous theories of multi-system coordination or system redundancy have been proposed (Mehlhorn and Rehkämper 2009; Walcott 1996, 2005; Wallraff 1996). An integrated theory of homing is clearly needed to resolve and

synthesize the evidence from such a broad range of methods and theories (Wiltschko and Wiltschko 1994).

## Pigeons in the Laboratory

Professor B. F. Skinner began working with pigeons in the 1940s and published the first paper that documented the use of pigeons in the psychological laboratory: *Superstition in the Skinner* (1941). Long-lived and well adapted to captivity, pigeons quickly became a popular laboratory subject for the experimental analysis of behavior principles. In 1948, Dr. Skinner opened the Harvard Pigeon Lab (see Fig. 10), which remained in operation, contributing valuable operant conditioning research by exploring and explaining instrumental behavior, until it closed in 1998 (see ► "B.F. Skinner"). Since then, pigeons have become one of the two most common animal subjects in psychological laboratories for over five decades, along with the laboratory rat (*Rattus norvegicus*). Much of the laboratory research with pigeons fits into three main categories: (1) operant conditioning, (2) pigeon cognition, and (3) orientation and navigation.

**Operant Conditioning.** As a method of studying the determinants of behavior, operant conditioning became a dominant force within psychology in the mid-twentieth century. Because of their adaptability to captivity, their excellent perceptual abilities, and their longevity, pigeons quickly became the mainstay species for experimental investigations that focused on the fundamental principles of behavior, including acquisition of behavior, schedules of reinforcement, extinction, stimulus control, discrimination and generalization, and punishment. A truly comprehensive review of the research involving pigeons in the operant laboratory is beyond the scope of this summary. For an overview of the early research and fundamentals of behavior principles, see Domjan (2015). Of particular interest here is the role pigeons have played in the study of highly complex behaviors such as stimulus equivalence (aka derived or emergent relations between stimuli) and response variability as an operant.

**Pigeon (*Columbidae*),**

**Fig. 10** Dr. B. F. Skinner in the pigeon lab located in the basement of Memorial Hall at Harvard University. (Photograph of Dr. B. F. Skinner in the Harvard pigeon lab)



Such studies highlight the noteworthy cognitive ability of pigeons.

***Stimulus Equivalence (Derived Relations).***

Stimulus equivalence is a behavioral phenomenon in which two or more stimuli elicit the same response without having to be trained. It is an emergent phenomenon that was long thought to occur only in humans with language. More specifically, equivalence was said to occur when three specific criteria had been met. These criteria were based on a mathematical definition of equivalence that includes symmetry, reflexivity, and transitivity. Reflexivity (aka sameness) is achieved when a subject can match an item or object to itself (e.g.,  $A = A$ ,  $B = B$ ,  $C = C$ , etc.).

Symmetry is achieved when the relationship between two objects or items is bidirectional (e.g.,  $A = B$  and  $B = A$ ). Transitivity is achieved when relationships exist between several object pairs (e.g., if  $A = B$  and  $B = C$ , then  $A = C$ ). In psychological research, transitivity is often a test of emergent stimulus equivalence, aka a derived relationship. According to Sidman and Tailby (1982, cited in Vaughan 1988), true stimulus equivalence requires all three components.

Over 40 years ago, the formation of functional concepts of trees, bodies of water, and specific people by pigeons was demonstrated when birds were able to generalize their discriminations to never before seen pictures of trees (Herrnstein et al. 1976). But, stimulus equivalence by non-human animals (pigeons) was first claimed by

Vaughan in 1988. Pigeons were reinforced for responding to a set of 20 out of 40 slides of trees over 15 sessions. Responses to the remaining slides were not reinforced. A series of reversals were then repeated for a total of more than 800 sessions. On session 813, a new set of distinct slides of trees were introduced and tested. The results showed that the pigeons had indeed formed equivalence classes. Vaughan referred to a functional similarity to stimulus equivalence because formal tests of the three equivalence requirements were not conducted, raising concerns by equivalence purists. Vaughan (1989) argued for abandonment of the artificial use of mathematical equivalence in favor of a more function definition of equivalence. The idea that nonhuman, nonverbal animals like pigeons could develop equivalence relations provoked controversy and debate (Hayes 1989; Vaughan 1989). Although the debate has not been resolved, limited success with functional equivalence has since been demonstrated in non-human species including pigeons, primates, and sea lions. But strong, reliable experimental evidence of equivalence of any kind across non-human animals continues to prove illusive. However, the original equivalence work with pigeons (Vaughan 1988) rekindled serious interest in avian cognition.

***Response Variability as an Operant.*** Response variability has been viewed conceptually as critically important for processes such as shaping and for schedules of reinforcement. In many ways,

response variability has long been viewed as a key component for Skinner's (1981) selection by consequences explanation of operant conditioning. He considered it an operant/behavioral analog to the individual genetic variation necessary for successful natural selection (Skinner 1981). But for decades, it remained an assumption, and nothing more.

In 1985, Page and Neuringer explicitly asked whether random response patterns could be treated as an operant – whether it was a “reinforceable” (sic) behavior. Pigeons were positively reinforced on every trial if their pattern of 8 left and right key pecks differed from their pattern of responding on previous  $n$  trials. They called this  $n$ -trial requirement a LAG. Over a series of six experiments, Page and Neuringer (1985) systematically increased the LAG requirement to prevent repeated patterns of eight responses over one, two, or three trials, to LAGs of 25 and even LAG 50. In many conditions, (including LAG 25) the birds' response variability approximated a computer random numbers generator. Never before had behavioral randomness come under stimulus control in this way.

Research on response variability has continued for over 30 years (for a review, see de Souza Barba 2012), including evidence from other species. Although not unique to columbids, or even birds, it is important to note the key role pigeons played in the discovery and investigation of the determinants of response variability.

### Pigeon Cognition

In 2001, Robert J. Cook – perhaps the foremost expert on pigeon visual cognition – edited an online volume, *Avian Visual Cognition*, in which he invited 31 of the world's best-known experimental psychologists and animal behaviorists to contribute to a comprehensive summary of the current knowledge of comparative avian cognition. See ► “Visual Perception”. It is important to begin any discussion of pigeon cognition by stating that the pigeon brain is more closely related to the dinosaur brain and it is only about 1/1000th the size of a human brain. As such, comparative research provides insight into both the cognitive abilities of pigeons (and other birds),

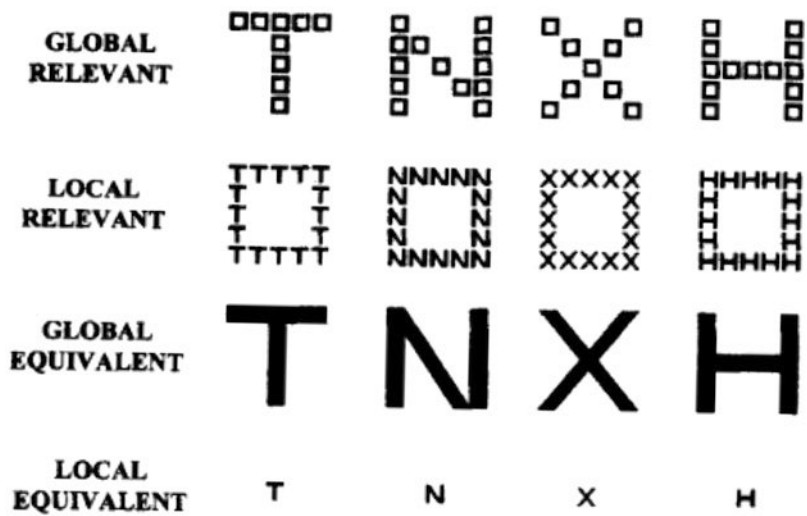
but also into the evolutionary context for the development of bird and mammalian (i.e., human) perceptual cognition.

### Pigeon Visual Perception

Avian perception is highly developed and organized around vision. Flight plays a central role in foraging, predatory avoidance, mate and nest identification, and homing. Therefore, the role of visual information and processing in a bird's life, and how it diverges and converges with human visual cognition, is key to a clear picture of avian cognitive abilities related to texture perception, perceptual organization, and object and motion perception. The method most commonly used is a visual detection task in which an array of images are presented and subjects are timed to see how long it takes to detect a specific image in the array (see ► “Visual Detection Task”).

*Feature perception.* Treisman and Gelade (1980, cited in Cook 2001) showed that humans require several visual passes over a complex stimulus in order to identify a complex target with both color and shape cues. Elements that are inconsistent with the larger array tend to “pop out” from organizationally uniform backgrounds, but this requires simultaneous and pre-attentive processing of the various features (called feature integration theory). Cook, Cavoto, and Cavoto (1996, cited in Cook 2001) tested whether pigeons in operant chambers viewing complex visual displays would exhibit similar visual strategies compared to humans. Using two- and three-dimensional stimuli, Cook et al. highlighted several similarities between the birds and humans. Pigeons and humans vary their search strategies depending on how the stimuli are organized. For example, as the dimensional differences increase, so too did reaction times for both birds and people. Also, distractors similarly hurt performance. Adding irrelevant dimensional information had no effect on avian or human reactions times, and both showed improvements from combining redundant and relevant information. The results suggest that early visual processing for birds and humans converge with regard to globally relevant information. Additional findings suggested important differences. For example, pigeons are



**Pigeon (*Columbidae*),****Fig. 11** Global/local training and testing stimuli from Cavoto and Cook (2001, cited in Cook 2001)

faster at detecting global information differences (100 ms minimal thresholds) compared with humans (150 ms).

*Global/local hierarchical organization.* Humans generally tend to prioritize larger, more global information over local (e.g., component/detailed) information, a phenomenon known as the global precedence effect (Navon 1977, cited in Cook 2001). Early work related to global versus local control of perception (Cook and Tauro 1999, cited in Cook 2001) led to feature-based perceptual models of behavior control (Huber, 2001, cited in Cook 2001). However, additional evidence suggests that it is not just the global or local features that matter but the relationships between global and local features that influence their discriminative abilities. For example, humans attend to words over letters, and entire letters over the shapes used to configure letters. This tendency reflects our acquired reliance on language and reading.

Cavoto and Cook (2001, cited in Cook 2001) provided similar base training for pigeons by presenting them with four letters (TNXH) constructed in four different ways: (a) *global-relevant* (e.g., T, N, X, and H constructed with tiny Os), (b) *local-relevant* (e.g., T constructed with tiny Ts), (c) *global-equivalent* (plain, large font letters), and (d) *local equivalent* (plain, small font letters).

Figure 11 shows the stimuli used in Cavoto and Cook's (2001, cited in Cook 2001) study. For global-relevant stimuli (line 1), only the larger letters were deemed relevant; the smaller "O"s used to construct the larger letters were deemed irrelevant. For local-relevant stimuli (line 2), only the smaller letters used to construct the larger "O"s were deemed relevant; again the "O"s were deemed irrelevant. The larger and small, solid letters presented global and local equivalents of the compound stimuli. Within a trial, birds saw stimuli from one or the other (global or local) organizational arrangement, but across trial both types were presented equally often. Using a simultaneous matching-to-sample procedure, birds were presented with one of the four configurations in random locations on a computer screen. Next, four (solid) letter choices were presented.

Testing to see the order in which the birds matched the global and local stimuli to the eight different equivalents, Cook (2001) highlighted two major findings. First, the birds learned to discriminate the local-relevant stimuli significantly faster than the global-relevant stimuli. Second, accuracy for the local-relevant stimuli was significantly better than for the global-relevant stimuli. These findings were consistent during acquisition and with extended training. They then tested generalization to a new letter S (both globally and locally relevant). The birds

successfully showed transfer of training with the new letter (despite initial difficulty with the global-relevant stimulus). These data contrast with the typically stronger global advantage found in humans. Understanding proximate and ultimate causes of the difference between animals and humans is the next step and should consider possible evolutionary causes as well as neuroanatomical correlates.

### Foraging and Cognition

Pigeons are social animals and flock foragers. They frequently search for food hidden in a background of inedible objects and items; as such, observational learning is a useful way to transmit effective foraging techniques skills to novice foragers (Blough 2001).

*Observation Learning of Foraging Techniques.* Pigeons are effective social learners. They can learn new behaviors through observation and imitation. However, the development of a scrounging approach (e.g., parasitizing other more effective foragers) is a risk. While individual pigeons in a flock use both foraging and scrounging methods, they do so flexibly such that most birds learn the foraging techniques for themselves.

In a laboratory-based investigation of observational learning in pigeons, Giraldeau and Lefebvre (1987) asked if scrounging alone would be sufficient for learning how to forage (see ► [“Imitation”](#)). Tutor birds were trained to obtain food by pecking at a stick that released seeds. Observers were then allowed to watch the tutors work to earn the food. Seeds dropped either toward the observers (aka scroungers) or toward the tutors themselves making the other birds simply observers of the pecking strategy. Observer birds from both conditions were then tested to see whether they had learned to peck at the stick to release the seeds. The simple observers learned to peck at the sticks for themselves, but the scrounger birds (who had received the food) failed to learn the foraging strategy. Giraldeau and Templeton (1991) also note that food producers often consume large shares of the food they find, leaving less for scroungers. So although scrounging may be a valuable strategy

on occasion, it is not effective as the sole foraging strategy because it leaves the learner at risk of food shortage.

*Searching.* In a review of her laboratory investigations, Blough (2001) compared various foraging-related cognitive processes in pigeons to human detection tests. For pigeons and humans, target-to-background contrast facilitates target identification (Treisman and Gelade 1980, cited in Cook 2001). For this reason, evolution has favored crypsis among prey species. Pigeons, like people, search more rapidly for targets that are expected, and when there are fewer distractors, and when there is less similarity between distractors and targets. Target-distractor differences mean a faster search resolution for both species. However, not all features facilitate search efficacy for both humans and pigeons. Humans switch from a serial search to a parallel strategy when changing from distinctly and randomly arranged distractors to distractors that are distinguished by a line or a gap (Treisman and Gormican 1988, cited in Blough 2001). Pigeons did not show that same shift in search patterns – what seem like natural groupings to us don’t help pigeons much at all.

*Memory for Targets.* Memory also plays an important role in the search process, particularly with respect to our memory for acceptable foods or targets. Pigeons (like people) are good at remembering which pictures that they have seen previously or not from a large set (Vaughan and Greene, cited in Blough 2001), and they can learn a “set of targets” which can then be imbedded in a display of previously unseen distractors. Over a series of experiments (Blough 1984, cited in Blough 2001; Vreven and Blough 1998), pigeons were tested with only one target or with several targets in a display of distractors. If a parallel search pattern were being employed, there should be no differences in reaction times. Despite early failures, sizeable differences ultimately emerged during preliminary tests, but performances converged during extended testing, consistent with other changes produced by extended practice. These findings were consistent with other changes produced by extended practice.

## Cross-References

- B.F. Skinner
- Bird Migrations
- Bob Cook
- Cognitive Map
- Colonial Nesting
- Comparative Cognition
- Comparative Psychology
- Compass Orientation
- Group Living
- Insight in Pigeons
- Instrumental Learning
- Landmark
- Passerine Sensory Systems
- Social Learning
- View-based Homing
- Visual Search

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## Pika

- [Lagomorpha Life History](#)
- [Lagomorpha Navigation](#)

## Pika Locomotion

- [Lagomorpha Locomotion](#)

## Pinniped Cognition

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### Introduction

Pinnipeds are amphibious caniform carnivores and can be divided into three families including otariidae (eared seals, including fur seals and sea lions), phocidae (true seals), and odobenidae (walruses; Arnason et al. 2006). Unique physiological and cognitive capabilities have evolved in these species due to their ability to compete in both aquatic and terrestrial environments. For the purposes of this chapter, cognition was considered to include “higher-level processes involved in storing, editing, and integrating sensory information such as memory, perception, and learning” (Deecke 2006, p. 461). This chapter outlines the behavior and cognition of wild

pinnipeds, as well as important laboratory studies. The information presented by these studies has not only provided a window into the pinniped mind, but also revealed new strategies for the management of both wild pinnipeds and those under managed care.

An animal’s ability or inability to perceive specific stimuli, known as an *umwelt*, is limited by species-specific sensory capabilities, thus affecting their behavior and cognition in nearly every context (see Partan and Marler 2002). Because cognition is so greatly affected by an animal’s ability to perceive environmental stimuli, this chapter will focus strongly on pinniped sensory cognition and the implications of pinniped’s sensory capabilities.

### Wild Pinniped Cognition and Communication

With the exception of some phocids, most pinniped species mate and give birth on land. This reliance on land or ice flows for reproduction has allowed scientists to evaluate these species’ reproductive behavior in close detail. For example, many of these species, such as California sea lions (*Zalophus californianus*) and northern elephant seals (*Mirounga angustirostris*), are highly gregarious and congregate in large rookeries (Cassini 1999). In order to facilitate the reunification of mothers and pups within these crowded rookery environments, individual recognition is necessary. Acoustic recognition has been studied extensively in a variety of wild pinnipeds (see Deecke 2006 for a review) and has been observed in otariids (Pitcher et al. 2012), grey seals (*Halichoerus grypus*; McCulloch and Boness 2000), northern elephant seals (Petrinovich 1974), and walrus (*Odobenus rosmarus rosmarus*; Charrier et al. 2013). Playback experiments have been useful in evaluating the function of pinniped vocalizations and their behavioral and psychophysiological responses. This approach has allowed researchers to examine the higher-level processes of pinnipeds in the wild, through employing noninvasive techniques. These capabilities include not only individual



acoustic perception, but also the ability of pinnipeds to account for gradual changes in acoustic stimuli, such as in a pup's vocal signature as it ages (see Deecke 2006 for a discussion). The use of playback experiments has not been limited to behavioral and acoustic assessments alone. Deutsch et al. (1990) utilized recordings of aggressive male vocalizations to lure male northern elephant seals to cross a weighing platform, in order to evaluate changes in body weight throughout the breeding season. In this study, researchers were able to employ an understanding of pinniped cognition to obtain physiological measurements in a noninvasive manner.

Pinnipeds produce a wide range of vocalizations, which has warranted extensive evaluation to determine their structure and function (see Schusterman and Van Parijs 2003 for a brief review). These vocalizations are thought to be social in nature, as they do not use sound for the purposes of navigation or foraging as cetaceans do. Therefore, research aimed at understanding communication has largely focused on the social contexts in which these vocalizations occur (Schusterman 2008). In terrestrially breeding species, where animals congregate in large rookeries, calls are typically both loud and repetitive in nature, making them ideal for information transfer in loud rookery environments (Schusterman and Van Parijs 2003). Alternately aquatic breeding phocids, which mate in less concentrated areas where information transfer is less difficult, produce more elaborate mating vocalizations (Schusterman 2008). When examined through the lens of Information Transfer Theory, it is clear these differences in species' communication styles appear to be adaptive in response to a decrease in competition in less-crowded aquatic environments (Schusterman and Van Parijs 2003).

Both research in the wild and in under controlled laboratory settings has contributed greatly to our understanding of pinniped vocal learning. While these adaptive strategies can be observed in the wild and in laboratory studies, opportunistic studies of animals living in professionally managed care has also been helpful in adding to our understanding of vocal learning in pinnipeds. Experimental evidence has demonstrated vocal

learning in phocids otariids and walrus. In these studies, animals were trained to produce natural vocalizations in response to a discriminative stimulus, regardless of context. However, walrus and phocids have also been demonstrated to have some ability to produce novel vocalizations in response to a discriminative stimulus. While isolation experiments have not been conducted in pinnipeds, for ethical reasons, it has been observed that when raised in the absence of conspecifics, pinnipeds appear not to develop a species-typical vocal repertoire. This is even true in the case of sex-specific vocalizations. That is, males may not develop the full vocal repertoire typical to their wild counterparts, when reared with only female conspecifics (see Reichmuth and Casey 2014 for a review).

## Learning and Long-Term Memory

In addition to vocal learning, capabilities such as discrimination and concept learning have likewise been evaluated. Reichmuth, Kastak, and Schusterman (2002) demonstrated that not only are pinnipeds capable of performing these tasks, but they are also capable of committing these tasks to their long-term memory. In this study, a sea lion who had received long-term exposure to both discrimination and concept-learning tasks was re-tested after a delay. The results of this evaluation demonstrated that the animal (a female California sea lion) showed no reduction in performance on associative concept, equivalence classification, and match-to-sample tasks after a 1-year delay and one matching task after a 10-year delay – even when presented with novel stimuli.

## Pinniped Cognition and Sensory Biology

The field of pinniped cognition and sensory biology has benefited greatly from laboratory-based research. This work examining pinniped cognition under controlled settings has not only increased our understanding of pinniped communication (e.g., Schusterman and Van Parijs 2003), but also our knowledge of brain structure and

function (e.g., Böye et al. 2005; Cook et al. 2015). By extension, this research has led to an understanding of not only the ability of pinnipeds to learn, but also their hearing, visual (see Schusterman 1981), and olfactory capabilities (Laska et al. 2010). Laska et al. (2010) found that South African fur seals (*Arctocephalus pusillus*) can discriminate between 24 of the 25 aliphatic odorants, presumed to be present in the marine environment, which were presented in a simple discrimination task. This ability to discriminate between scents suggests that scent is likely evolutionarily salient for these species. Studies of this nature are critical in that they not only reveal the species' Umwelt, or stimuli which the animals are capable of detecting, but also reveal the animal's cognitive ability to differentiate between these stimuli.

## Threat Perception

Acoustic playbacks have been applied to the management of wild pinnipeds, through the use of aversive stimuli (i.e., killer whale vocalizations) to deter the depredation of managed fisheries (see Deecke 2006 for a review). Unfortunately, these attempts have yielded only temporary behavioral change. The transient effect of these interventions can likely be explained by examining the cognitive mechanisms and evolutionary pressures involved in threat assessments (Schakner and Blumstein 2013). For example, Fanselow and Lester (1988) hypothesized that prey species evaluate threatening environmental stimuli, such as predator vocalizations on a continuum, called the *Predatory Imminence Continuum*. This continuum suggests that if the individual perceives that a stimulus indicates zero threat of predation, they are at the preferred point on the continuum and they will continue engaging in nonaversive behaviors (i.e., foraging, nursing, etc.). However, if the animal perceives that a threat is imminent, they will likely engage in energetically expensive, aversive behaviors (i.e., increase vigilance, decrease foraging, etc.). This theory assumes that evolution would select for an adaptive strategy in which animals would engage in aversive

behaviors until such time as the stimulus, such as killer whale calls, is either evaded entirely or determined to not to be a threat – allowing them to return to the preferred point on the continuum. Drawing on this knowledge and the growing literature on pinniped acoustic thresholds, managers have also introduced intense acoustic stimuli designed to cause pain if the animal approached the signal source, in order to deter depredation (see Würsig and Gailey 2002 for a review). This approach has achieved minimal success due to the ability of pinnipeds to engage in temporary acoustic threshold shifts, or the temporary elevation of auditory thresholds following overstimulation (e.g., Kastak and Schusterman 1996), in which animals are able to cope with loud noises long enough to continue foraging – or permanently, depending upon length of exposure to the stimulus and the intensity of the stimulus. Thus, the animal elects to expose itself to the unpleasant sound stimulus, once it is determined not to be a threat. This cognitive perspective has allowed for researchers and managers to not only evaluate pinniped threat perception, but also to design aversive interventions such as acoustic deterrents.

## Theory of Mind

The ability to recognize oneself in a mirror is considered evidence that one is aware of its own existence. Delfour and Marten (2001) evaluated California sea lion reactions to a mirror in comparison to killer whales (*Orcinus orca*) and false killer whales (*Pseudorca crassidens*). They found that pinnipeds lacked the necessary contingency checking behavior to be considered to possess mirror self-recognition. However, Genty and Roeder (2006) demonstrated that California sea lions performed better than nonhuman primates on a reverse-reward contingency task. In this task, subjects were presented with two options: a selection including one fish and a second selection with five fish. If the individuals selected the first option (one fish), they would receive the second (five fish). Alternately, if they selected the second option (five fish), they would receive the first (one fish). Despite a demonstrated initial impulse

to select the higher quantity of fish, three out of the four animals quickly learned the rules of the trials. The subjects' successful performance on this task is indicative of a higher level of self-control than most nonhuman primates. In humans, only children aged 4 years and older, who present with some theory of mind, show similar self-control capabilities. These enhanced capabilities may have evolved in response to the dynamic foraging environment pinnipeds experience in the wild (see Genty and Roeder 2006 for a discussion).

Alternately Shapiro et al. (2004) evaluated gray seal's ability to follow an experimenter-given point. In this study, the animal was able to follow various points given from central and lateral positions. However, the animal was not able to follow points which indicated an object located behind the animal. Thus, it was concluded that the seal was likely only able to follow points by employing signal generalization as a result of past experience with operant conditioning, rather than a comprehension of the gesture itself. The ability to understand gestures, such as pointing, has been suggested to indicate that the animal is able to engage in visual perspective taking, which is indicative of theory of mind and some level of self-awareness (see Shapiro et al. 2004 for a discussion).

When compared with the literature on cetaceans and nonhuman primates, there have been relatively few studies examining the theory of mind or self-awareness in pinnipeds. More research will need to be done in order to conclusively address questions associated with the abilities of pinnipeds to engage in these concepts.

## Cognitive Abnormalities in the Wild and Under Human Care

Wild pinnipeds are exposed to a variety of threats on an everyday basis, some of which can cause long- and short-term cognitive deficits leading to strandings and possibly death. Domoic acid is an excitatory neurotoxic amino acid produced by the algae *Pseudonitzschia*, which has been shown to cause damage to the hippocampus and hippocampal-thalamic brain networks in animals

that ingest it. This damage ultimately results in deficits in spatial cognition, which can interfere with foraging and navigation, in wild pinnipeds (Cook et al. 2015).

Abnormal behaviors may also arise as a result of insufficient environmental stimulation in animals under human care, requiring the constant evaluation of environmental enrichment protocols used to eliminate or reduce instances of stereotypical behavior. Numerous methods, and a combination of stimuli, have been found to reduce stereotypical behavior. These methods include: allowing animals to have more choice over their environment as well as introducing problem-solving devices and tasks (Clark 2013). Other methods, such as increasing environmental complexity through the introduction of novel stimuli, such as scents, has also been demonstrated to improve the welfare of pinnipeds under human care (Samuelson et al. 2016).

## Summary

Pinniped cognition has been the subject of intensive research for many years. The results of these studies have revealed a wealth of knowledge regarding not only the cognitive capabilities of these marine mammals, but also of their unique Umwelt with which guides their cognition. Advancements in our scientific understanding of pinniped hearing, vision, and scent capabilities have allowed researchers to investigate their communication, conservation, and the welfare of animals in human care.

## Cross-References

► [Pinniped Communication](#)

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## Pinniped Communication

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**Pinniped:** Pinnipeds are semiaquatic, carnivorous mammals comprised of 33 living species in three major families: phocids (true seals), otariids (sea lions and fur seals), and odobenids (walruses; Schusterman 2008).

**Communication:** A signal that provides information from a signaler to a receiver (Tyack and Miller 2002).

## Introduction

Pinnipeds are among the most vocal of all mammals, communicating in both water and air (Miller 1991; Schusterman et al. 2001). The sounds produced by pinnipeds are used almost exclusively for social communication, such as courtship and copulatory signaling, establishing and maintaining territories through agonistic signals, and mother-pup reunification (Winn and Schneider 1977; Van Opzeeland et al. 2008). A majority of the pinniped sounds that have been documented are within the range of human hearing (Dudzinski et al. 2009). Phocid calls are typically between 100 Hz and 15 kHz (Dudzinski et al. 2009). Airborne sounds produced by otariids range from 1 kHz to 4 kHz, while sounds produced in the water are slightly louder (Dudzinski et al. 2009). Odobenids produce low frequency sounds ranging from 500 Hz to 2 kHz (Dudzinski et al. 2009). The amount of vocal communication varies between species. Some pinniped species are almost silent, whereas others have large vocal repertoires consisting of calls characterized

as grunts, rasps, rattles, growls, warbles, trills, chirps, chugs, clicks, and whistles (Dudzinski et al. 2009). The amount and type of calls produced and used varies not only by species but by season, sex, age, and whether the animal is in the air or in the water (Dudzinski et al. 2009). Pinnipeds also communicate through non-acoustic signaling, such as visual displays, tactile communication, and chemical communication (Miller 1991). The following text will review the acoustic behavior of pinnipeds, as well as the forms of non-acoustic signaling used. Gaps of knowledge will be addressed with suggestions for directions of future research.

## Acoustic Behavior and Mating Strategies

The amount of vocalizations produced by pinnipeds is correlated with their mating system and whether mating occurs on land or underwater (Stirling and Thomas 2003). Of the pinnipeds, phocids tend to be more vocal under water, otariids on land, and odobenids in both media (Dudzinski et al. 2009). Pinnipeds that are seasonally monogamous, such as crabeater seals (*Lobodon carcinophagus*) and hooded seals (*Cystophora cristata*) have the least complex mating system, resulting in the simplest repertoire (with the fewest amount of different vocalizations; Stirling and Thomas 2003). In fact, crabeater seals only exhibit a single monotonous call which is thought to be used in short-range male-male competition when guarding a female (Van Opzeeland et al. 2008). Promiscuous pinniped species, in which males are not able to defend exclusive territories and both individual males and females likely mate with more than one seal, have been shown to have an intermediate number of vocalizations (Stirling and Thomas 2003). For example, leopard seals (*Hydrurga leptonyx*) exhibit 9–12 different vocalizations (depending on the region) that they use to establish short term, underwater territories and to attract females to mate with (Dudzinski et al. 2009). Polygamous pinnipeds, in which males defend underwater territories and have access to more than one female at



a time, have the most structured mating systems and, therefore, the greatest number of different vocalizations (Stirling and Thomas 2003). For instance Weddell seals (*Leptonychotes weddellii*) congregate in colonies of up to 100 females and pups, while males establish and defend territories beneath the fast ice and may mate with as many females that enter their territory (Dudzinski et al. 2009). These seals have been found to have an elaborate repertoire consisting of at least 34 distinct sounds, including trills, chugs, chirps, guttural glugs, and knocks (Dudzinski et al. 2009; Van Opzeeland et al. 2008).

When comparing species within each mating system described above, those that form the densest colonies during breeding have broader repertoires with a wider variety of sounds than those at the lowest densities (Van Opzeeland et al. 2008; Stirling and Thomas 2003). Moreover, the high density of animals within breeding colonies seems to favor the production of loud, harsh, repetitious calls (Schusterman 2008). Harp (*Pagophilus groenlandicus*) and Weddell seals, the phocid species that form the densest colonies, are particularly known for the diversity, high rate of occurrence, and amplitude of their calls (Stirling and Thomas 2003). Watkins and Schevill (1979) found that harp seals increase the volume and number of elements per call in response to higher calling rates by conspecifics (i.e., animals of the same species). Additionally, Atlantic walruses (*Odobenus rosmarus rosmarus*), which aggregate in colonies of 30–100 or more, make a large number of distinct vocalizations which are comprised of two main variations on a single-pulsed sound, a sharp relatively low-pitched “knock” and a higher-pitched “tap” given in different combinations (Stirling et al. 1987). In the vicinity of females and calves, male Atlantic walruses vocalize extensively underwater, making repeated, individually stereotyped calls made up of varying combinations of several hundred pulses (Stirling et al. 1987; Van Opzeeland et al. 2008). These vocalizations are loud and can readily be heard by humans standing on the ice (Stirling and Thomas 2003). The increase in volume and number of calls made in high density breeding colonies may help to mask the calls of competitors, while

at the same time, increase the probability of signal detection by others (Stirling and Thomas 2003).

As stated previously, some pinniped species establish and defend territories during mating (Stirling and Thomas 2003). Males of species that maintain territories have intense, complex, inter-male warning calls (Winn and Schneider 1977). Arguably, the most elaborate warning call may be the warbling song of the bearded seal (*Erignathus barbatus*; Winn and Schneider 1977). Additionally, male Weddell seals have 11 types of trills that they use exclusively in agonistic interactions while defending territories (Dudzinski et al. 2009). The territorial calls of otariids are of low frequency, pulsed, and typically accompanied with an elevated posture (Winn and Schneider 1977). The type of male territorial call used is related to motivational state (Winn and Schneider 1977). For instance, the snort produced by northern elephant seals (*Mirounga angustirostris*) is the lowest intensity threat sound produced by this species and is typically the first sound produced in agonistic interactions (Winn and Schneider 1977). The clap threat is of higher intensity and typically signals incipient attack (Winn and Schneider 1977). Similarly, Weddell seals use short, quiet trills as an initial warning to other males and long, loud trills to threaten attack (Dudzinski et al. 2009).

### Acoustic Behavior of Mother-Pup Pairs

In many mammals, including pinnipeds, mother and offspring can identify each other using a variety of sensory modalities (Charrier et al. 2009). Pinnipeds are nearsighted when out of water (Wartzok and Ketten 1999) and can only utilize olfactory cues to confirm recognition once mother and offspring come in contact (Stirling 1971). As visual and olfactory cues are less effective at long range, pinnipeds primarily use acoustic signals for individual recognition (Charrier et al. 2009). Vocal recognition between mothers and offspring is prevalent among pinnipeds; however, it is thought to be better developed in otariids (fur seals and sea lions) than in phocids (true seals; Khan et al. 2006). This difference may be due to

variances in maternal strategy (Insley et al. 2003). Otariids use a “foraging cycle strategy” characterized by a long period of offspring dependence, during which the mother alternates between hunting trips at sea with time on land nursing her pup (Bonner 1984). As a result, mothers must repeatedly relocate their pups throughout the course of lactation (Insley 1992). In contrast, many phocids use a “fasting strategy” in which mothers fast while nursing and continuously care for their pups (Insley 1992). Therefore, mothers and offspring have little need to find one another except when temporarily separated over short distances (Insley 1992). Regardless, females and pups of many phocid species regularly vocalize (Insley 1992).

Vocalizations made by nursing pairs have been termed pup attraction calls (made by mothers) and mother attraction calls (made by pups; Winn and Schneider 1977). Individual stereotypy in these calls is crucial for vocal recognition, as it enables individuals to differentiate between one another (Van Opzeeland et al. 2008). Thus, pup recognition by mothers using acoustic cues is only possible once pups begin to produce unique vocalizations (Khan et al. 2006). Similarly, mother recognition by pups is only possible once pups learn the unique vocalization of their mothers. This can take anywhere from 3 days, in the Steller sea lion (*Eumetopias jubatus*), to 2 months, in the New Zealand sea lion (*Phocarcos hookeri*; Winn and Schneider 1977). To date, the calls used between otariid mothers and pups exhibit individual stereotypy in all species that have been studied (Insley et al. 2003). In phocids, individual stereotypy in calls is much more variable between species. In many phocid species, mothers rarely vocalize to their pups and consequently, do not exhibit call stereotypy (Insley et al. 2003). However, evidence for individual stereotypy in pup calls has been found in colonial breeding phocid species, such as Weddell seals (Collins et al. 2005), grey seals (*Halichoerus grypus*; McCulloch and Boness 2000), harp seals (Van Opzeeland and Van Parijs 2004), and elephant seals (*Mirounga*; Bartholomew & Collias, 1962). Walrus calf vocalizations have also been found to be highly stereotyped

(Charrier et al. 2009). Individual vocal stereotypy has been correlated to individual recognition in many pinniped species, including Weddell seals (Collins et al. 2005), northern fur seals (*Callorhinus ursinus*; Insley 2001), and is well developed in many walrus species (Kibal'chich and Lisitsina 1979; Miller 1985). However, individual stereotypy in vocalizations does not always indicate individual recognition. For instance, McCulloch and Boness (2000) used playback experiments to test individual recognition of pups by mothers in two grey seal colonies in Canada. They found that grey seal females in the Sable Island colony were able to discriminate between the vocalizations of their own and unfamiliar pups, whereas females in the Isle of May grey seal colony were not able to make this discrimination. Additionally, sex differences have been found in some pinniped species in regard to mother-pup vocal recognition. Van Opzeeland et al. (In prep) found that vocalizations of female harp seal pups in the Greenland Sea population were significantly more individually stereotyped than males, biasing maternal recognition towards female pups. The amount of distinct information in both mother and pup calls, combined with visual and olfactory cues, seems to allow mother-pup pairs to recognize each other (Van Opzeeland et al. 2008).

## Non-Acoustic Signaling

Acoustic communication is the best known, and most studied, form of pinniped communication (Miller 1991). However, pinnipeds also use forms of non-acoustic communication, such as displays (i.e., visual signals). Visual displays can be simple, such as body postures, coloration, or sexually dimorphic features, or can be more elaborate, involving sequences of behavior (Dudzinski et al. 2009). Social, land breeding pinnipeds, including otariids and some phocids, have highly stereotyped and ritualized displays (Winn and Schneider 1977). Threat displays are a common part of territorial behavior in pinnipeds and often include acoustic elements (Winn and Schneider 1977). For example, the in water

territorial display of Weddell seals consists of an S-shaped posture with the chest forward and the hind flippers downward paired with loud trill and teeth chatter sounds (Dudzinski et al. 2009). Additionally, when approached on pack ice, Ross seals (*Omatophoca rossii*) assume a head-up posture, showing off the stripes on their chest, and open their mouths, showing their teeth, while making loud sounds (Dudzinski et al. 2009). Flipper waving has also been described as a low-intensity visual warning in grey, harp, and ringed seals (Winn and Schneider 1977). Submissive behavior has also been described in some otariids and in elephant seals (Winn and Schneider 1977). For instance, male southern elephant seals (*Mirounga leonina*) signal submission by deflating their proboscis (i.e., their elongated nose or snout), backing away, and uttering high-pitched whimpers (Winn and Schneider 1977). Visual displays are also used by female pinnipeds to signal estrus and solicit copulation. Female northern fur seals (*Callorhinus ursinus*) display an exaggerated walk when in estrus (Winn and Schneider 1977). Further, displays made by female Steller sea lions when in estrus may be crucial for inducing males to mount (Winn and Schneider 1977).

Visual displays are advantageous in close-range communication among pinnipeds and, because of close proximity, visual displays may turn into tactile signals (Dudzinski et al. 2009). Tactile communication is an important element of pinniped mating (Miller 1991). Males of many pinniped species make extensive contact with females during courtship. For example, male crabeater seals maintain almost constant physical contact when courting a female (Miller 1991). This contact includes resting their head on the female's side, lying with their back touching the female, and lying with their chest over the female's back and their fore flipper extended over her side (Miller 1991). Male and female southern sea lions (*Otaria flavescens*), Australian fur seals (*Arctocephalus pusillus*), and Steller sea lions also use tactile communication during courtship, often caressing one another on the front and sides of the neck and rubbing their mouths together (Miller 1991). Steller sea lions and harbor seals (*Phoca vitulina*) also engage in aquatic

social rolling behavior in which males and females roll around each other while maintaining physical contact (Miller 1991). Additionally, female grey seals may initiate copulation by nuzzling a male and female fur seals that are ready to mate have been shown to rub heads and noses with males, as well as rub and nip at a male's neck and jaws (Winn and Schneider 1977). Tactile communication is also important between mother-pup pairs. Nuzzling, which aids in individual recognition, is common between females and pups of all pinniped species (Miller 1991). Furthermore, many otariid mothers have been shown to mouth and lift their newborn pups (Miller 1991), and female New Zealand fur seals (*Arctocephalus forsteri*) often press themselves on top of their newborn pups (McNab and Crawley 1975). Lastly, tactile communication may be used to solicit play. McNab and Crawley (1975) noted that New Zealand fur seals pups solicited play from their mothers by passing their mother's whiskers through their mouth and over their head and nose and by gently biting their mother's nose, mouth, and upper neck. Mothers responded by gently biting back and ended play by pushing their pup away and moving their head away (McNab and Crawley 1975). Juvenile grey seals also solicit play using tactile communication, often by laying their head over the back of another individual (Miller 1991).

Along with visual displays and tactile communication, pinnipeds often use forms of chemical communication, olfaction in particular. Males of many pinniped species, including ringed seals (*Pusa hispida*) and harp seals, exude strong, musky odors that may be used in territorial marking or to attract a female (Winn and Schneider 1977). Further, olfaction is used by males of many pinnipeds to investigate the reproductive state of females. For example, male New Zealand fur seals smell rocks used by females, as well as the females themselves, to determine if a female is ready to accept a mate (Winn and Schneider 1977). In every pinniped species studied to date, mothers appear to accept or reject pups using olfactory cues (Insley et al. 2003). For instance, female Australian sea lions (*Neophoca cinerea*) are capable of discriminating their own pups from

others using olfaction in the absence of other cues (Pitcher et al. 2011). In an experiment performed by Kaufman et al. (1975), the skin of a dead weddell seal pup was attached to a live pup. The live pup was then accepted by the mother of the dead pup from which the skin had been taken. These observations suggest that olfactory cues play a crucial role in individual recognition and reunion of mothers and pups (Insley et al. 2003).

## Conclusion

Communication plays an important role in the lives of pinnipeds, from mating, to establishing and maintaining territories, to mother-pup reunification (Winn and Schneider 1977; Van Opzeeland et al. 2008). Pinnipeds use a variety of modalities to communicate. The most well-known, and best studied, form of pinniped communication is acoustic communication (Miller 1991). Pinnipeds also use forms of visual, tactile, and chemical communication (Dudzinski et al. 2009; Winn and Schneider 1977). Visual signaling is an important aspect of pinniped communication, yet remains severely under-studied (Miller 1991). Chemical communication also plays an important role in the lives of all pinniped species, with olfaction aiding in the identification of estrous females and the reunification of mother-pup pairs, but little is known about the chemical senses of pinnipeds and further anatomical and experimental research is warranted (Miller 1991; Winn and Schneider 1977). Communication has been studied in a number of pinniped species. However, gaps exist in what is known about the different forms of communication in polar pinniped species (Van Opzeeland et al. 2008). This is due to the fact that studies in polar pinniped species are impeded since many of their behaviors take place in isolated pack-ice areas or in offshore waters (Van Opzeeland et al. 2008). All ice-breeding pinniped species produce underwater vocalizations (Van Opzeeland et al. 2008). Recent developments in recording technologies have allowed researchers to acquire long-term acoustic data in remote areas which may help to improve

our understanding of polar pinniped behavior (Van Opzeeland et al. 2008).

## Cross-References

- [Pinniped Life History](#)
- [Pinniped Morphology and Locomotion](#)

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## Pinniped Life History

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The term pinniped comes from the Latin *pinna* for “fin” or “feather,” and *pedis* for “footed.” The taxonomic grouping Pinnipedia is not its own order, but rather is classified within the order Carnivora and consists of three families of marine mammals: Phocidae which are the true seals (i.e., earless seals), Otariidae, the sea lions and fur seals (i.e., eared seals), and Odobenidae, the walrus. Otariids are most easily distinguished by their external ear or pinnae, their large fore-flippers, and the ability to rotate their pelvis on land and walk quadrupedally. Phocids are distinguished by a lack of pinnae, their short, fur covered fore-flippers which have pronounced claws, and their inability to rotate their pelvis to walk quadrupedally on land. Odobenids are easily recognized by their general lack of fur and their pronounced tusks present on both the male and female walrus. Like the Otariids, they can walk quadrupedally on land (see Fig. 1). Taken together there are 33 extant species of pinnipeds which can be found in almost all marine waters of the globe, though distribution patterns can be seen between groups. Only phocids are found in the Arctic and Antarctic with the exception of the walrus (found in northern circumpolar waters). Most fur seal populations are restricted to the southern hemisphere, yet most other otariids are found in both hemispheres. The Hawaiian (*Monachus schauinslandi*) and Mediterranean monk seals (*Monachus monachus*) are the only tropic species,





**Pinniped Life History, Fig. 1** Photographs of three-species representative of the three pinniped families: (a) Family Phocidae, *Phoca vitulina* (harbor seal); (b) Family Otariidae, *Zalophus californianus* (California sea lion); (c) Family Odobenidae, *Odobenus rosmarus* (walrus)

(Photo credits: Candyce Paparo, Long Island Aquarium & Exhibition Center/Center for the Study of Pinniped Ecology & Cognition (a, b); Center for the Study of Pinniped Ecology & Cognition (c))

and the Baikal seal (*Pusa sibirica*) is the only freshwater species. While pinnipeds inhabit all climate zones, they are not currently in the waters off the coast of Asia or India, and it is suggested that these waters are nutrient poor and therefore do not have a stable food supply for them (Riedman 1990).

## Evolution

Pinnipeds are thought to have evolved from their terrestrial ancestors, a group termed the Canoidea. Since Canoidea consists of multiple groups such as the ursids (bears), mustelids (weasels and otters), and canids (dogs), there has historically been argument within the scientific community as to the specific phylogenetic origins of the three pinniped families (Arnason et al. 2006; Lowenstein 1986; for a recent in-depth review of the debate see Koretsky et al. 2016). There are two views of their ancestry centered around the question of whether pinnipeds evolved from the same, or two different, phylogenetic lines. The diphyletic view states that both otariids and odobenids evolved from a bear-like ancestor around 25 million years ago (MYA) in the early Miocene while the phocids evolved from a mustelid or otter-like ancestor about 20 MYA, mid-Miocene (Koretsky and Holec 2002; Koretsky and Sanders 2002; Koretsky and Barnes 2003; Repenning 1976; Riedman 1990). While this view has been supported by the fossil record, recent molecular

evidence (e.g., DNA and RNA from extant species) suggests a monophyletic view with phocids and otariids descending from a common bear-like ancestor approximately 25 MYA (early Miocene) (Arnason et al. 2006; Dasmahapatra et al. 2009; Higdon et al. 2007, 2008). Despite conflicting evidence between the fossil record and molecular data, the current scientific consensus is the monophyletic view emphasizing a common ancestor; however, there is still some debate as to whether their most recent common terrestrial ancestors are ursids (bears) or mustelids (weasels/otters) (Berta and Churchill 2012; Boness and Bowen 1996).

Currently, of the 33-extant species of pinnipeds, four phocids and one otariid are listed as endangered with five phocid and two otariids listed as threatened (United States Fish and Wildlife (USFW) 2017). The Caribbean (or West Indian) monk seal (*neomonachus tropicalis*) was listed as threatened on March 11, 1967, and officially declared extinct as of October 28, 2008, being removed from the Federal Register after there had been no reported sightings of the seal in 50 years (USFW 2016). The Hawaiian monk seal (*Monachus schauinslandi*) was listed as endangered as of June 2, 1970 (USFW 2017), and critically endangered in 2008 (Karamanlidis and Dendrinos 2015; Littnan et al. 2015) with the recent population estimates at 1,112 individuals (National Oceanic and Atmospheric Administration (NOAA) 2015). While many pinniped populations are thriving, the factors influencing the 12 species listed as threatened or endangered

is the focus of many research and conservation efforts. Data show that the species' populations most in danger are those that inhabit the subtropical/tropical and Arctic/Antarctic regions of the globe (i.e., the more northern and southern latitudes), with more temperate dwelling species having stable and even thriving populations (Ferguson and Higdon 2006). This suggests that the more extreme areas of the globe may be more susceptible to both natural and man-made changes in the ecosystem. The underlying causes of this relationship between latitude and population stability is an area of research with investigations focused on the interactions between ecology and the life history of these varied pinniped species with an emphasis on climate change and prey distribution/availability (Ferguson and Higdon 2006).

The life history of pinnipeds is especially multidimensional because they are amphibious marine mammals that carry out critical life functions both on land and in the water. Their evolutionary ties to their terrestrial ancestors are demonstrated by their dependence on the sea for foraging while often breeding and giving birth on land. While the challenges of individual species vary, there are several generalizations that can be made within the life history of pinnipeds as a group with major differences being drawn between the phylogenetic lines of the phocids and otarioids (both the otariids and odobenids).

## Life Span

The life span of pinniped species ranges from 15 to 30 years with males having a shorter span due to the added biological stressors and potential injuries incurred during male-male aggressive encounters (see Table 1). It has been shown that many northern elephant seals (*Mirounga angustirostris*) die before reaching sexually maturity (age five) and significantly more die before reaching age nine at which time they are considered able to successfully compete for females and reproduce (Le Boeuf 1981; Reiter et al. 1981).

As mentioned above, it should be noted that chronological age of reproductive maturity (age at

which they are physically capable of breeding) is different than the age at which an animal successfully breeds. Typically, females breed once they hit sexual maturity (e.g., age two), but they may not give birth for a few more years (e.g., 4–5 years of age) (Boness et al. 2002; Riedman 1990). This discrepancy in age is more pronounced in male pinnipeds, perhaps because they must be physically capable of breeding, as well as physically large enough and behaviorally mature enough, to compete for territory/females. For example, walrus (*Odobenus rosmarus*) reach sexual maturity at 9–10 years of age but may not breed successfully until 13–16 years old (Fay 1982).

## Reproduction

Overall, both male and female pinnipeds must have sufficient mass and a healthy body condition, as well as the behavioral maturity, to breed successfully and reproduce. Sexually mature pinnipeds typically come ashore to their natal beaches (the site at which they were born) each year to give birth and then mate (Hoffman and Forcada 2012). Most otariids breed and give birth on land (Boness 1991; Franco-Trecu et al. 2015; Giardino et al. 2016), while 15 of the 18 phocid species mate aquatically (for an extensive review of aquatic breeding phocids see Van Parijs 2003). Most exceptions seem to be the ice seals, though data exist for a limited number of species. For example, evidence suggests that weddell seals (*Leptonychotes weddellii*) do not return to breed at the site where they were born (Davis et al. 2008), and they are the only large phocid to breed exclusively on fast-ice (i.e., ice attached to land). This may be due to female movement being restricted to consistent breathing holes in the ice (Cline et al. 1971; Bartsch et al. 1992; Harcourt et al. 1998, 2000).

As amphibious marine mammals, access to land for mating and/or birthing is critical and therefore timing of the annual breeding/pupping season is important. Female estrous cycles (when females are physiologically receptive for breeding) are annually synchronous for all pinnipeds, and mating occurs relatively quickly after the

**Pinniped Life History, Table 1** Information on 26 of the 33 extant species of pinnipeds. The data provide descriptions of general aspects of life history, organized by taxonomic family, including average mass of males and females of a species, existence of sexual dimorphism, life span, breeding strategy, lactation length, and percent milkfat. These data allow one to compare not only across species but across and within the phocid, otariid, and odobenid families. There is not sufficient data reported to provide a valid average of milkfat when “nd” is indicated in the table

| Common name<br><i>Scientific name</i> | Ave female mass | Ave male mass | Sexual<br>dimorphism         | Life span<br>(yrs) | Breeding strategy                             | Ave<br>lactation<br>length | Ave %<br>milkfat | Source <sup>a</sup> |
|---------------------------------------|-----------------|---------------|------------------------------|--------------------|-----------------------------------------------|----------------------------|------------------|---------------------|
| <b>Phocidae</b>                       |                 |               |                              |                    |                                               |                            |                  |                     |
| Baikal seal                           | 130 kg          | 130 kg        | No                           | 50–55              | Monogamy                                      | 2 months                   | nd               | 1, 2, 3             |
| <i>Pusa sibirica</i>                  |                 |               |                              |                    |                                               |                            |                  |                     |
| Bearded seal                          | 260–360 kg      | 260–360 kg    | Slight;<br>females<br>larger | 25                 | Monogamy/Slight polygyny                      | 2–3 weeks                  | 49               | 4, 5, 6             |
| <i>Erignathus<br/>barbatus</i>        |                 |               |                              |                    |                                               |                            |                  |                     |
| Grey seal                             | 250 kg          | 400 kg        | Yes                          | 25–35              | Moderate polygyny/ Ice<br>breeders monogamous | 2–3 weeks                  | 60               | 7, 8, 9,<br>6       |
| <i>Halichoerus<br/>grypus</i>         |                 |               |                              |                    |                                               |                            |                  |                     |
| Harbor seal                           | 110 kg          | 110 kg        | No                           | 25–30              | Slight polygyny                               | 3–4 weeks                  | 50               | 6, 9                |
| <i>Phoca vitulina</i>                 |                 |               |                              |                    |                                               |                            |                  |                     |
| Harp seal                             | 135 kg          | 135 kg        | No                           | Unknown            | Slight polygyny                               | 12 days                    | 57               | 6, 10,<br>11, 12    |
| <i>Pagophilus<br/>groenlandicus</i>   |                 |               |                              |                    |                                               |                            |                  |                     |
| Hawaiian monk<br>seal                 | 170–205 kg      | 170–205 kg    | Slight;<br>females<br>larger | 25–30              | Slight polygyny                               | 4–6 weeks                  | nd               | 3, 6, 13            |
| <i>Monachus<br/>schauinslandi</i>     |                 |               |                              |                    |                                               |                            |                  |                     |
| Hooded seal                           | 200 kg          | 300 kg        | Yes                          | 30–35              | Slight polygyny                               | 3–5 days                   | 61               | 6, 14,<br>15        |
| <i>Cystophora<br/>cristata</i>        |                 |               |                              |                    |                                               |                            |                  |                     |

|                                |                                        |                                        |                      |       |                          |              |    |               |
|--------------------------------|----------------------------------------|----------------------------------------|----------------------|-------|--------------------------|--------------|----|---------------|
| Mediterranean monk seal        | 240–400 kg                             | 240–400 kg                             | Slight; males larger | 20–25 | Slight polygyny          | 4 months     | nd | 3, 6, 16, 17  |
| <i>Monachus monachus</i>       |                                        |                                        |                      |       |                          |              |    |               |
| Northern elephant seal         | 600 kg                                 | 2000 kg                                | Yes                  | 13–19 | Extreme polygyny         | 3–4 weeks    | 54 | 6, 18, 19     |
| <i>Mirounga angustirostris</i> |                                        |                                        |                      |       |                          |              |    |               |
| <b>Phocidae</b>                |                                        |                                        |                      |       |                          |              |    |               |
| Ribbon seal                    | 80 kg                                  | 80 kg                                  | No                   | 20–30 | Slight polygyny          | 3–5 weeks    | nd | 3, 6, 20      |
| <i>Histiophoca fasciata</i>    |                                        |                                        |                      |       |                          |              |    |               |
| Ringed seal                    | 50–70 kg; 110 kg for Saimaa subspecies | 50–70 kg; 110 kg for Saimaa subspecies | No                   | 25–30 | Monogamy/Slight polygyny | 6 weeks      | 42 | 6, 21, 22, 23 |
| <i>Phoca hispida</i>           |                                        |                                        |                      |       |                          |              |    |               |
| Southern elephant seal         | 400–900 kg                             | 1–2 tonnes                             | Yes                  | 10–20 | Extreme polygamy         | 3 weeks      | 40 | 3, 24, 25     |
| <i>Mirounga leonina</i>        |                                        |                                        |                      |       |                          |              |    |               |
| Spotted seal                   | 65–115 kg                              | 65–115 kg                              | No                   | 30–35 | Monogamy/Slight polygyny | 5–6 weeks    | nd | 6, 26         |
| <i>Phoca largha</i>            |                                        |                                        |                      |       |                          |              |    |               |
| Weddell seal                   | 1200 lbs. (544 kg)                     | 544 kg                                 | No                   | 20–30 | Slight/Moderate polygyny | 7 weeks      | 48 | 6, 27         |
| <i>Leptonychotes weddellii</i> |                                        |                                        |                      |       |                          |              |    |               |
| <b>Otariidae</b>               |                                        |                                        |                      |       |                          |              |    |               |
| Antarctic fur seal             | 22–50 kg                               | 130–200 kg                             | Yes                  | 15–25 | Moderate polygyny        | 4 months     | 42 | 3, 28, 29, 30 |
| <i>Arctocephalus gazella</i>   |                                        |                                        |                      |       |                          |              |    |               |
| Australian sea lion            | 61–105 kg                              | 180–250 kg                             | Yes                  | 20–25 | Moderate polygyny        | 11–12 months | nd | 3, 31, 32, 33 |
| <i>Neophoca cinerea</i>        |                                        |                                        |                      |       |                          |              |    |               |
| California Sea Lion            | 110 kg                                 | 315 kg                                 | Yes                  | 20–30 | Moderate polygyny        | 10 months    | 44 | 3, 6, 34      |

(continued)

Pinniped Life History, Table 1 (continued)

| Common name<br><i>Scientific name</i>  | Ave female mass | Ave male mass | Sexual<br>dimorphism | Life span<br>(yrs) | Breeding strategy | Ave<br>lactation<br>length | Ave %<br>milkfat | Source <sup>a</sup> |
|----------------------------------------|-----------------|---------------|----------------------|--------------------|-------------------|----------------------------|------------------|---------------------|
| <i>Zalophus<br/>californianus</i>      |                 |               |                      |                    |                   |                            |                  |                     |
| Galapagos fur<br>seal                  | 27–28 kg        | 60–68 kg      | Yes                  | 20–25              | Moderate polygyny | 18 months                  | 29               | 35, 36              |
| <i>Arctocephalus<br/>galapagoensis</i> |                 |               |                      |                    |                   |                            |                  |                     |
| <b>Otariidae</b>                       |                 |               |                      |                    |                   |                            |                  |                     |
| Guadalupe fur<br>seal                  | 40–50 kg        | 160–180 kg    | Yes                  | 20                 | Moderate polygyny | 9 months                   | nd               | 6, 37               |
| <i>Arctocephalus<br/>townsendi</i>     |                 |               |                      |                    |                   |                            |                  |                     |
| New Zealand sea<br>lion                | 90–165 kg       | 300–450 kg    | Yes                  | ~20                | Extreme polygyny  | 12 months                  | nd               | 3, 38,<br>32        |
| <i>Phocarcos<br/>hookeri</i>           |                 |               |                      |                    |                   |                            |                  |                     |
| Northern fur seal                      | 60 kg           | 270 kg        | Yes                  | 10–27              | Extreme polygyny  | 4–5 months                 | 42               | 6, 39,<br>40        |
| <i>Callorhinus<br/>ursinus</i>         |                 |               |                      |                    |                   |                            |                  |                     |
| Southern sea lion                      | 170 kg          | 300–350 kg    | Yes                  | 15–20              | Moderate polygyny | 11–12<br>months            | 47               | 3, 41,<br>42, 43    |



|                                 |             |             |     |  |       |                   |              |    |              |  |
|---------------------------------|-------------|-------------|-----|--|-------|-------------------|--------------|----|--------------|--|
| <i>Otaria byronia</i>           | 350 kg      |             |     |  |       |                   |              |    |              |  |
| Steller sea lion                |             | 1120 kg     | Yes |  | 20–30 | Extreme polygyny  | 11–12 months | 24 | 3, 6, 44     |  |
| <i>Eumetopias jubatus</i>       |             |             |     |  |       |                   |              |    |              |  |
| Subantarctic fur seal           | 25–67 kg    | 70–165 kg   | Yes |  | 15–20 | Moderate polygyny | 11 months    | 42 | 3, 45, 46    |  |
| <i>Arctocephalus tropicalis</i> |             |             |     |  |       |                   |              |    |              |  |
| <b>Odobenidae</b>               |             |             |     |  |       |                   |              |    |              |  |
| Walrus                          | 580–1039 kg | 880–1557 kg | Yes |  | 30–40 | Polygyny          | 2–3 years    | 30 | 5, 6, 47, 48 |  |
| <i>Odobenus rosmarus</i>        |             |             |     |  |       |                   |              |    |              |  |

<sup>a</sup>1, Nomokonova et al. 2013; 2, Pastukhov 1990; 3, Riedman 1990; 4, Burns 1981a; 5, Fay 1982; 6, NOAA 2016; 7, Amoroso et al. 1950; 8, Boness and James 1979; 9, Fedak and Anderson 1982; 10, Bowen and Sergeant 1983; 11, Kovacs and Lavigne 1986; 12, Oftedal et al. 1993; 13, Alcorn and Buelna 1989; 14, Bowen et al. 1985; 15, Kovacs and Lavigne 1992; 16, Aguilar et al. 2007; 17, Pomeroy 2011; 18, Crocker et al. 2001; 19, Reiter et al. 1978; 20, Burns 1981b; 21, McLaren 1958; 22, Hammill et al. 1991; 23, Zhang et al. 2014; 24, Carrick et al. 1962; 25, Hofmeyr 2015a; 26, Boveng 2016; 27, Kaufman et al. 1975; 28, Payne 1979; 29, Kerley 1985; 30, Doidge et al. 1986; 31, Goldsworthy 2015; 32, Marlow 1975; 33, Ling and Walker 1976; 34, Stewarts and Yochem 1984; 35, Trillmich 1979; 36, Trillmich and Lechner 1986; 37, Gallo-Reynoso and Figueroa-Carranza 1996; 38, Chivers 2015; 39, Peterson 1965; 40, Costa and Gentry 1986; 41, Cárdenas-Alayza et al. 2016; 42, Hamilton 1934; 43, Vaz-Ferreira and Ponce de Leon 1987; 44, Costa 1991; 45, Hofmeyr 2015b; 46, Roux and Hess 1984; 47, Kastelein et al. 2014; 48, Lowry 2016

birthing or parturition process. Though this timeframe between birthing and mating ranges somewhat among species, pinnipeds manage to synchronize in part through embryonic diapause or delayed implantation (Pomeroy 2011). In this way, the egg is fertilized and develops for approximately 7–10 days at which point development pauses at the blastocyst stage. Up to several months later (timing depending on the species), the embryo begins to develop again and implants into the uterus. This delay allows for the gestation period (including the diapause) to last approximately 10–12 months, ensuring that sexually mature males and receptive females arrive at their breeding sites at the same time each year.

Females give birth to one offspring per year of sexual maturity, though this is in part dependent on environmental factors such as food supply. Females may not give birth in a certain year if there are not enough resources available and her body is not in a healthy condition to sustain a pregnancy and lactation period (Boyd 2000; Shero et al. 2015). Twinning is rare, though has been documented (Hoffman and Forcada 2009; Riedman 1990), but research suggests that having twins may be detrimental as it decreases overall survival rates (Schultz et al. 2011). Alloparenting, a system in which individuals in the population other than the mother contribute to the care of the offspring, is rare but has been observed in the pinnipeds (Boness and Bowen 1996; Porter and Trites 2004; Schulz and Bowen 2005). It is most likely to occur when a female has lost her pup and fosters one that has lost its mother. Rarely, females will nurse a stray pup alongside its own. Males do not offer paternal care and, as stated, females do not usually care for offspring that are not their own. In fact, females have been known to behave aggressively toward nonfilial pups attempting to nurse. Infanticide has been observed but is usually caused by a nonfilial pup continuing to approach and attempt to nurse from an aggressive female, or by incidental injury due to proximity of an aggressive male-male interaction, though males have been known to kill pups through directed aggressive contact (Kiyota and Okamura 2005).

## Breeding Strategies

The details of mating strategies vary between species but most are polygynous and fall under either of two categories: harem or lek breeding systems (for a more detailed review see also Boness et al. 2002). In a harem system, the males fight for dominance rankings and access to receptive females on the beach. The most dominant male will spend the breeding season alternating between mating with many females and fighting off male challengers. Due to the physical nature of the male-male competition, many do not mate successfully until they are approximately 10 years old, even though sexual maturity may have been reached at 4 years of age (see “[Life Span](#)”). Males must acquire the size and the experience to win fights with the older, more dominant, males each year to gain access to females. For example, male northern elephant seals herd females inside their territory and keep other males out while male California sea lions (*Zalophus californianus*) compete to control specific locations on the beach. Unlike elephant seals, the female sea lions are free to move between these areas and therefore from male to male. Conversely, male harbor seals (*Phoca vitulina*) demonstrate a lek system and do not tend to have physical altercations with each other during the breeding season, but rather vocalize underwater to claim a territory therefore advertising their presence to females and deterring other males from that area (Van Parijs 2003). This difference in breeding style may be related to resource availability (food and breathing holes for ice seals), mating location (females of species that mate aquatically have more control over their mate choice), and the extent of sexual dimorphism (difference in physical size between males and females) found between various species (Van Paris 2003; González-Suárez and Cassini 2014; Modig 1996). Elephant seals have the largest degree of sexual dimorphism with the female northern elephant seals being an average of 1,300 pounds (600 kg) and males three to five times that at an average of 4,400 pounds (2,000 kg) (see Table 1). Their breeding strategy consisting of males fighting, often violently, to attain dominance and control of females favors

the evolution of a large body size. Harbor seals, on the other hand, demonstrate little to no sexual dimorphism, with males and females both averaging 245 pounds (110 kg), and they demonstrate little to no male-male aggression during the breeding season.

Reproductive success rates are based on number of offspring produced throughout the life span. While this is well defined and relatively easy to quantify for females of a given species, the data is less discernable for males. Regardless of the breeding strategy employed by a species, females give birth to one offspring per year (as noted, twins are rare and most do not survive to maturity), but males mate with multiple females each season making DNA testing the most reliable way to determine paternity and male success rate in a population. Due to the inherent difficulty of DNA testing for male success rates each year, most estimates are based on observed successful copulations and known dominance ranking of individual males. While this seems a reasonable assessment of male success, some data indicate that the most dominant males may not necessarily be providing the DNA for all offspring. For example, in northern elephant seals, “sneaker” males (young juveniles that “sneak” a copulation with a female) have been found to have contributed DNA to the population despite their lower dominance ranking and smaller size (de Bruyn et al. 2011). They have been successful in mating with females on the outer edges of a harem while the dominant male is engaged in a copulation, a fight with another male, or sleeping (hence the term sneaker male). This is interesting to note in relation to the evolution of behavioral/cognitive strategies in pinniped species.

### Maternal Dependency/Lactation

Care of offspring in pinnipeds centers around females and consists of protection from predators but primarily lactation or milk production. The mother-pup bond is strong during the lactation period and decreases significantly, and perhaps completely, after weaning. However, there is evidence that females behave in an affiliative manner with their kin when returning to their natal beaches to breed each year (Insley et al. 2003;

Schusterman et al. 2002), and there is some evidence that a California sea lion and its mother recognized each other for many years (Hanggi and Schusterman 1990).

Length of maternal dependence and lactation is generally divided between pinniped families, though it should be noted that other factors such as body size, ecology, foraging strategy, breeding/birthing location, and substrate all play an integrated role in the lactation strategy displayed by a given species (Bartholomew 1970). The phocids have the shortest lactation period ranging from four days (hooded seal, *Cystophora cristata*) to two and one half months (Baikal seal, *Pusa sibirica*; Pastukhov 1993), with a milk containing 40–50% fat (see Table 1). Otariids have a moderate nursing period between 4 months and 3 years with approximately 20–35% milkfat, while odobenids average a 2–3 year lactation period with about 30% milkfat, making them the pinniped with the longest period of maternal care (see Table 1). In fact, the walrus is the only species to have adopted a strategy of nursing their young in the water and having their young accompany them on foraging trips (Schulz and Bowen 2005). Therefore, three predominant lactation strategies (discussed below) can be seen among female pinnipeds which are generally divided among phylogenetic lines (and will be discussed as such for purposes of generalizing here), though the interactions between species ancestry, maternal mass, breeding substrate, thermoregulation challenges, milk composition, and various other ecological factors must not be overlooked (for a detailed review see Schulz and Bowen 2005).

A *fasting strategy* with little to no feeding is employed by phocids, though the harbor seal and ringed seal (*Phoca hispida*) have been documented to occasionally forage during this time. This may be correlated with their smaller body size, creating an inability to maintain enough energy reserves of their own throughout lactation (Boness and Bowen 1996; Bowden et al. 1992). This foraging during lactation may also be related to the availability of food close to shore, which may entice them to feed later in the lactation period (Boyd 1998). Length of lactation period is correlated with maternal mass and

percent of milk fat. The shorter the lactation period (for all pinnipeds), the more quickly fat reserves must be transferred to pups in the form of milk. Therefore, larger females can handle dumping more fat rich milk into their pups quickly. Of course, longer lactation periods mean more maternal care/time for pup growth and protection from predators; however, if fasting, there will always be an upper limit by which the female must return to sea or risk decreasing her reserves to the point by which she can no longer survive.

Ice-breeding phocids fast and have the shortest lactation periods of all pinnipeds, an advantage in an environment where a mother and pup are together on either fast (attached) or pack (floating) ice. For example, if the ice were to crack, break, and/or float away, a foraging female may not be able to find her pup upon returning to the ice. Breaking ice could crush or drown a pup. Also, in an extremely cold climate, adding blubber to a pup as quickly as possible will help it to thermoregulate appropriately.

Otariids have adopted a *foraging-cycle strategy* meaning that they alternate, or cycle, between nursing and foraging throughout the lactation period. This allows for a longer duration of maternal care, as the females replenish their energy reserves between nursing bouts. Whether this strategy is advantageous because it allows them to care for their pups for longer periods of time while not overly depleting their own reserves, or if it is more energetically demanding in the long run, is an area of continued study (Coltman et al. 1997; see Schulz and Bowen 2005). Perhaps the otariids, being small bodied as compared to most phocids, simply cannot acquire the energy reserves needed for fasting while lactating. These foraging bouts also add another challenge for these mother-pup pairs, as the pups are left alone in the rookery while the mother goes to sea to forage for 2–3 days. When the female returns after a foraging trip of 1–6 days, she and her pup must overcome the challenge of reuniting among hundreds of other mother-pup pairs (see Insley 2000; Trimble and Insley 2010).

A third strategy, the *aquatic nursing strategy*, is only found in the odobenids. The walrus, having the longest period of maternal care (2–3

years), has adopted a strategy of nursing in the water, as opposed to exclusively on land, and pups are known to accompany their mothers on foraging trips (Boness and Bowen 1996; Fay 1982). Walrus pups are born the least precocious of the pinnipeds, and this lengthy dependence on the mother allows for a longer maturation process of the pup prior to survival on its own.

## Foraging

The majority of a pinniped's fresh water supply is extracted from the food they eat and some is acquired through the metabolism of their blubber layer. Pinnipeds have been known to consume salt water in small amounts and metabolize it ending with a freshwater gain, but the process requires a lot of energy and is not an efficient source of hydration (Riedman 1990).

Pinnipeds tend to be generalists with diets consisting primarily of fish, crustaceans, and cephalopods and are typically solitary hunters though they have been documented hunting cooperatively when herding a large school of fish (Gales et al. 2004; Riedman 1990). A few species are specialists and as such have adaptations for feeding on certain prey items. For example, the crabeater seal (*Lobodon carcinophagus*) eats krill, and its teeth are formed in a way that allows them to gulp water and strain it out leaving the krill in their mouths on which to feed. Bearded seals (*Erignathus barbatus*) and walrus feed on mollusks and other bottom dwelling invertebrates. They both have substantial vibrissae, or whiskers, with which they use for rooting through muddy substrates and the walrus' mouth can produce suction strong enough to pull mollusks out of their shells. Ringed seals feed primarily on crustaceans and elephant seals prefer squid. The leopard seal (*Hydrurga leptonyx*), found in Antarctica, eats penguins and is the only pinniped known to prey on other seals (typically young crabeater seals) (Hocking et al. 2013).

Foraging occurs at varying depths and durations based on species, but a notable mention with significant diving abilities is the elephant seal, known to make foraging dives to an average

depth of 1,680 feet (512 m) and 22 min in length (Heerah et al. 2014). The elephant seals' maximum recorded dive depth is 6,562 feet (2,000 m) and for a duration of approximately two hours, rivalling that of the sperm whale, making it one of the deepest diving marine mammals. These long dives are in part possible due to their large size which increases the amount of oxygen they can store and therefore increasing time spent at depth and decreasing the need to come up for air frequently.

As amphibious mammals, pinnipeds must balance the energetic resources needed to leave a terrestrial haul-out location and actively search and hunt for food with the energy gained by the food they consume. Foraging patterns are correlated with, and generally divided by, ancestry with the phocids most likely to employ an *income strategy* and otarioids using a *capital strategy* (Arthur et al. 2016; Stephens et al. 2014). For example, the hooded seal (a phocid) tends to favor a capital strategy based on fewer trips with longer travel distances to and from foraging sites of large density prey (through which they increase reserves in body mass – creating capital reserves), while the California sea lion (an otariid) favors an income strategy with shorter, but more frequent, foraging trips (less reserve and more frequent income replenishment needed). The quality of prey is also important as traveling a long distance for many poor-quality fish will not be energetically advantageous over traveling a shorter distance for fewer fish, if the smaller fish population is a much higher quality. Latitude ranges will, in part, determine prey distribution with colder/temperate waters, and therefore middle latitudes, having higher productivity and prey item availability.

Therefore, factors correlated with a capital versus income foraging strategies (and with the phocid and otarioid groups, respectively) are the species' overall body size, maternal care/lactation strategy (see “[Reproduction](#)”), and global distribution. Whether the driving factors of strategy are ancestry, physical properties of the species (e.g., overall size and depth of blubber layer), water temperature and quality, or habitat ecology including prey availability/distribution is an active area of research. These factors are

inherently interconnected and it is probable that rather than a direct causal link, the best predictor of foraging strategy will be an interactive model of the aforementioned variables.

## Molting

Molting is another event tethering these amphibious marine mammals to land. All species molt, during which time they undergo a relatively drastic shedding of their fur accompanied by the growth of a new coat. The timing of the molt depends on the species as well as the age within species. For example, molting is staggered by age in the northern elephant seal with yearlings hauling out in the fall, adult females in the spring after foraging trips following the breeding season, and adult males molting in the summer (Longstreth 2016; Riedman 1990). Pups of all species go through an initial molt of their lanugo, which is a layer of fur that develops in utero and serves to help newborn pups maintain their core body temperature until their blubber reserves have increased. Some pups (e.g., the harbor seal) shed their lanugo in utero (prior to birth), but most pinnipeds shed it by the end of weaning (Brueimmer 1975; Riedman 1990).

While many terrestrial mammals are known to shed throughout the year with marked changes in this based on seasonality/temperature, the pinniped molt is notably different in large part due to their semiaquatic lifestyle. The growth of new fur requires increased blood flow to the surface of the skin. This is counter to the needs of marine mammals in that they often shunt blood away from the surface to their core (major organs and large muscles) to limit heat loss to the aquatic environment (Erdsack et al. 2012). Therefore, growing new fur and maintaining their core body temperature are essentially at odds. Many pinnipeds compensate for this by not shedding and growing hair continuously throughout the year, but rather by condensing this process into a yearly event or molt. During this time, they remain on land for relatively long periods of time allowing the blood to remain at the surface of the skin providing the nutrients needed for new hair growth.



Among the pinnipeds two main molting strategies emerge: one being to increase body mass (foraging), then fast and remain out of the water (more blood supply to the skin/new fur) allowing for a short molt duration, while the second is to continue to forage throughout the molt, entering the water (interrupted blood supply to the skin/new fur), thus requiring a longer molt duration. Which strategy is employed can be generalized as a division between the phocid and otarioid lines. Harbor seals (a phocid) have relatively short molts lasting on average 1 month while the molt of a California sea lion (an otariid) can last up to a few months with a peak in shedding lasting a month or more. However, it must be noted that there are many interacting variables underlying reliance on these strategies other than ancestry (see “[Foraging](#)”).

An extreme strategy in the phocid line is employed by elephant seal species and the Hawaiian monk seal. They haul out once per year and not only shed their fur but their skin as well. Large patches of their hair and skin peel off to reveal new skin and fur below. This process has been termed a *catastrophic molt* and requires a lot of energy and a large blood supply to the surface of the body (Ling 1970). Therefore, these seals fall under the category of a short duration molt during which time they fast and remain on the beach until its completion.

## Migrations

Pinnipeds have a consistent and annual migratory pattern primarily based on feeding, breeding/birthing, molting, and seasonal ice (for the Arctic/Antarctic species) (see Luschi 2013). They migrate to breed and give birth, traveling to warmer waters for the new pups that lack a thick blubber layer for thermoregulation and then to cooler waters with greater productivity and more prey items. An exception to this are many of the ice seals as they prefer to breed when the ice is most prevalent allowing for larger areas for breeding and pupping and a lowered chance of fast ice breaking off and becoming a moving ice floe. If

this were to happen during the weaning period, females could be separated from their pup (see “[Reproduction](#)”).

The methods by which pinnipeds navigate during these migrations are not completely understood. Researchers believe that it is a combination of their ability to use underwater landmarks, water and wind currents, water temperature, and even celestial bodies. Mauck et al. (2008) found that the harbor seal can utilize the stars in the night sky to navigate, and Ronald and Healey (1981) found that juvenile harp seals (*Pagophilus groenlandicus*) are successful on their annual northern migration (up to about 3,100 miles/5,000 km) on their first trip with no adult seal present. This indicates that, at least in some cases, aspects of these migrations may be innate.

## Conclusion

The life history of a species encompasses a pattern of resource acquisition and utilization in support of the interactions between lifespan, foraging, and reproduction strategies (which may or may not include migratory patterns in relation to prey and/or mate availability and access). This interrelated web of factors is based on the evolutionary history of a species, the past and present environmental pressures, and the ecological systems in place. The above sections are an overview of the basic points of life history within the pinnipeds but, as with any taxonomic group, the physiological and behavioral aspects of these animals are not only influenced by the past and current environments but will continue to be shaped by their environments to come.

## Cross-References

- [Pinniped Cognition](#)
- [Pinniped Communication](#)
- [Pinniped Morphology and Locomotion](#)

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## Pinniped Morphology and Locomotion

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Locomotion enables animals to actively seek food, avoid predators, interact with conspecifics, and respond to diel and seasonal changes in the environment (e.g., seek shade, migrate). However, locomotion can be energetically expensive, so it must enhance survival and fitness. Although animals display a variety of locomotory modes, there is a convergent evolution toward minimizing the energetic cost of terrestrial, aerial, and aquatic locomotion. This is the dominate trend in the form and function of aquatic locomotion in marine mammals including pinnipeds.

Taxonomically, pinnipeds are a diverse clade of carnivorous, semiaquatic marine mammals whose fore and hind limbs are modified into flippers for efficient aquatic locomotion. There are 34 extant species divided into three Families: Phocidae (the earless seals or true seals), Otariidae (the eared seals: sea lions and fur seals), and Odobenidae (walrus). Fossils of the arctoid ancestors of pinnipeds can be traced to the Eocene (45 Mya), although fossil pinnipedimorphs only extend to the late Oligocene (27–25 Mya). Morphological and molecular evidence support a monophyletic origin for the three Families within the taxonomic Order of Carnivora (suborder of Caniformia, infraorder Arctoidea).

This chapter will focus on morphological and physiological adaptations that enable pinnipeds to maximize the acquisition of energy while minimizing the energetic cost. Nowhere is that better demonstrated than in the morphological adaptations for locomotion in water.

### Body Shape and Drag

Perhaps the most obvious adaptation in pinnipeds for an aquatic lifestyle is a streamlined body. The

convergent evolution of a fusiform (spindle-shaped) body shape has occurred in many aquatic vertebrates from fish to mammals, both extant and extinct (e.g., ichthyosaurs), in response to the greater density (820-fold) and viscosity (55-fold) of water compared to air. These two properties of water are responsible for *drag* (the resistive *force* to movement) experienced by a moving body, especially one that is bluff or rounded (i.e., non-hydrodynamic shape). In contrast, the more elongate, streamlined bodies of most marine mammals greatly decrease drag and the energetic cost of locomotion.

### Laminar and Turbulent Flow

Drag is influenced by flow around an object which can be laminar, transitional, or turbulent. When laminar, the fluid is ordered and flows in parallel layers around a body with no disruption like sheets of paper in a stack that slide past each other, with the nearest sheet stuck to the body (due to friction) and the farthest sheet unaffected by the body. However, in turbulent flow, the fluid layers are unsteady and form eddies like marbles that can slide and rotate relative to each other, again with the nearest marble stuck to the body and the farthest marble unaffected by the body.

Flow conditions around a body can be characterized using a *Reynolds number* (*Re*; the ratio of inertial forces to viscous forces used to characterize different flow regimes around an object). A *Re* less than  $2 \times 10^3$  is associated with laminar flow. As the *Re* increases, flow becomes unstable and susceptible to surface texture and disturbance that can cause turbulence. The transition to turbulent flow does not correspond to a single *Re* but may range from  $5 \times 10^5$  to  $10^6$  and depends on body shape and surface roughness. However, at very high *Re* ( $>10^6$ ), even minute disturbances will result in turbulent flow. The *Re* for all pinnipeds is high ( $\geq 10^6$ ) due to their large size, so flow is turbulent over most of the body at routine swim speeds.

### Drag

Drag can be explained by the viscous properties of water and the formation of a *boundary layer*. The viscosity of water results from the cohesive

interactions between water molecules called van der Waals forces and the adhesive molecular interactions of water to the boundary surface (e.g., skin). An ideal fluid without viscosity (inviscid) shows *slip* with respect to solid boundaries, so there is no frictional energy loss. However, when a real fluid moves past a body, it adheres to the surface and has zero velocity (i.e., no slip). Viscous forces create a velocity gradient until the fluid velocity approximates that of the free stream a short distance from the surface of the body.

There are two types of drag that can be explained by the formation of a boundary layer: *pressure drag* and *friction drag*. Pressure drag (also called form drag) is explained by Bernoulli's Principle: that is, for an ideal, inviscid fluid moving around an object, a decrease in velocity results in an increase in pressure and, conversely, an increase in velocity results in a decrease in pressure. For an ideal fluid, the pressures cancel each other and there is no net pressure or drag (d'Alembert's paradox). However, for a real fluid, the viscous forces cause the molecules adjacent to the object to slow. A boundary layer with laminar flow produces the lowest friction drag but is inherently less stable than turbulent flow. If the free stream velocity is fast enough, laminar flow around the rear half of a cylinder will separate causing vortices and a wake. As a result, the dynamic pressure in front of the object is not balanced by a counteractive pressure on the rear. A net force is exerted against the object, and this is what creates pressure drag. Most of the drag on a cylinder or bluff body (not streamlined) at high rates of flow is due to under-pressure that develops in the wake of the body. Pressure drag can be greatly reduced by using a streamlined or fusiform body shape. The optimum streamlined body has a fineness ratio (ratio of body length to maximum body diameter) of approximately 4.5 but can range of 3–7 with only a 10% increase in drag (Fish 1996, 1998).

Body shapes with a fineness ratio larger than 4.5 will have a greater surface-to-volume ratio and experience an increase in *friction drag* (also called viscous drag) which results from shear forces in the boundary layer due to the viscosity of water

and the adhesive molecular interactions of the water to the boundary surface (Vogel 1994). Taken together, pressure drag and friction drag contribute to the total drag on a body, and whether it is dominated by one or the other depends on body shape. The pressure drag on a streamlined body with a fineness ratio of ~4.5 and turbulent flow ( $Re > 10^6$ ), which is typical for pinnipeds, is small (~20% of total drag) relative to friction drag. Total drag is minimized by this ideal hydrodynamic shape which reduces the energetic cost of locomotion in marine mammals.

Total drag ( $D$ , Newtons) on a body can be calculated according to the equation:

$$D = 0.5 \times S \times \rho \times C_d \times U^2$$

where  $S$  is the wetted surface area of the animal ( $m^2$ ),  $\rho$  is the density of seawater ( $\sim 1024 \text{ kg m}^{-3}$ ),  $C_d$  is the nondimensional drag coefficient, and  $U$  is swimming speed ( $m \text{ s}^{-1}$ ). What is immediately apparent from this equation is the exponential increase in drag as a function of swim speed. Hence, the maximum speed will be constrained by drag, but also by mechanical efficiency and thrust production. The other important factor is  $C_d$  which depends on the shape and texture of the body and is less for a hydrodynamic shape than for a bluff body (i.e., more rounded). Pressure drag will be most influenced by  $C_d$ , whereas friction drag will be most influenced by  $S$ . For two animals that differ in size but have the same  $C_d$ , pressure drag will be the same but friction drag will be greater for the larger animal because it has a larger surface area.

This calculation for passive drag does not include the effect of changes in body shape and flipper movement when an animal is actively swimming and maneuvering. Pressure drag will increase because the oscillating, propulsive motions of the body alter body streamlining. Appendages cause induced drag due to the generation of lift and also modify the flow of water around an animal which causes interference drag. Hydromechanical models for actively swimming animals exceed equivalent rigid bodies by three- to seven-fold. Active drag of a free-swimming animal is generally assumed to be

approximately three-fold greater than passive drag (Weihs 1974; Fish et al. 1988).

Drag is further increased when a body moves at the surface (*wave drag*) because it acts like the displacement hull of a ship producing bow and stern waves that radiate energy away from the body. Ultimately, maximum swimming velocity (i.e., hull speed) at the surface is constrained when the wavelength of the bow wave is equal to body length thereby trapping the animal within the bow wave. For some pinnipeds (e.g., sea lions), higher speeds at the surface can be achieved by porpoising (leaping out of the water) which greatly reduces drag while the animal is airborne. As we shall see, the reduction in drag reduces the energetic cost of swimming and increases aerobic dive duration.

### Thrust and Swimming Modes

When an animal is swimming at a constant speed, drag must be countered by a force that is equal and opposite to it – that force is thrust. To generate thrust and overcome drag during aquatic locomotion, pinnipeds have evolved flippers with high (3–9) aspect ratios ( $\text{span}^2 \div \text{projected area}$ ) to improve thrust production and propulsive efficiency (Fish 2000). With their streamlined cross sections, flippers also function as control surfaces that provide maneuverability and stability. Since pinnipeds evolved from quadrupedal land mammals, morphological changes for aquatic locomotion can be traced in the fossil record and include foreshortening of limbs and enlargement of the hands and feet with webbing into high-aspect ratio propulsive surfaces (Fish 1996). These morphological changes in locomotory mode which resulted in pelvic oscillation (seals and walrus) and pectoral oscillation (sea lions and fur seals) also permitted movement on land. The evolution of these modes of swimming were associated with performance changes from drag-based propulsion (paddling) to lift-based that generate thrust throughout the stroke cycle and increase propulsive efficiency (thrust power-to-total mechanical power output  $\sim 0.75\text{--}0.90$ ), power, and speed (Feldkamp 1987a; Fish 1996, 2000).

Pinnipeds exhibit a variety of aquatic modes of locomotion, but they regularly haul out on land or ice to give birth, breed, and rest, often in large groups called rookeries. Seals and walrus swim using pelvic oscillation in which the posterior body is laterally undulated moving the paired hind flippers in the horizontal plane. As they are swept to one side, the leading flipper closes (adduction of the digits) while the trailing flipper maximally expands (abduction of the digits) to generate thrust. At the maximum lateral extent of the undulation, the posterior body sweeps in the opposite direction and the flippers switch their respective open and closed positions. As a result, thrust is generated continuously (by one flipper) through an entire stroke cycle as the flippers alternate opening and closing as the body undulates. The angle of attack of the open flipper is controlled by the ankle analogous to the peduncle in cetaceans.

Sea lions and fur seals use their fore flippers as both lift-based hydrofoils and drag-based paddles. The oscillating fore flippers act as hydrofoils generating thrust and lift as they move vertically through the water over the initial three-quarters of the stroke and as paddles during the final phase of the stroke which lasts about 1 s. Hence, thrust is produced throughout most of the stroke using lift, although the majority is generated during the paddle phase by drag. The hind flippers generate no thrust but contribute to maneuvering. For all pinnipeds, oscillation of high-aspect hind flippers (seals and walrus) and fore flippers (sea lions and fur seals) produces maximum mechanical efficiencies of 0.8 and 0.88, respectively.

Although pinnipeds often appear awkward on land, they are capable of remarkable agility, stamina, and speed. Otariidae can rotate their hind flippers forward, and their fore flippers bend at the wrist, which gives them substantial surface contact for good traction. As a result, they can move rapidly over slippery rocks or ice, much faster than humans in boots. They are also good rock climbers capable of scaling cliffs and fence enclosures. Although walrus can also rotate their hind flipper forward, their large body mass limits agility and speed. However, they have been known to trek inland for substantial distances.

Phocidae move more awkwardly (hitching action) because they cannot rotate their hind flippers forward. However, they also can move remarkably fast (an adult male elephant seal challenging another male on the beach can move as fast as a running human) over short distances or slowly over long distances (the mummified remains of crab eater and leopard seals have been found many kilometers from the sea in the Dry Valleys of Antarctica). Why they make these journeys remains a mystery. Ringed seals have large fore flippers, long claws, and phalanges that bend. This gives them a unique “hauling grip” which they use on the ice when moving forward and for maintaining breathing holes by abrading the ice.

## Energetics

### Power Produced by Contracting Muscles

Animal movement is generated by the contraction of muscles. Muscles act as biological engines that convert *chemical energy* (metabolism) into *power and mechanical work*. Muscles act only as *pulling* engines because they generate force by *actively shortening* and then lengthen by either the contraction of an opposing muscle or by the effect of an elastic structure. Muscles used for locomotion in vertebrates are classified as skeletal muscle (as opposed to cardiac and smooth muscle). The energy for contraction is provided by adenosine triphosphate (ATP), and the energetic cost of locomotion results primarily from the increased energy metabolism of contracting muscles used for propulsion.

The contracting muscles in marine mammals move flippers and flukes to generate thrust to overcome the load created primarily by drag but also viscoelastic forces in the muscles. The power generated by the contracting muscles is translated into the power associated with locomotion (thrust  $\times$  velocity). While drag increases with  $U^2$ , locomotory power increases with  $U^3$  which makes high-speed swimming energetically costly. As a result, routine swim speeds of most pinnipeds remain low at 1–3 m s<sup>-1</sup>, although higher speeds occur during burst swimming when energy economy is not important (e.g., pursuing prey,

avoiding predators). Furthermore, aerobic metabolic efficiency in the muscle is only ~15% and propulsive efficiency (thrust power  $\div$  total mechanical power output) is, at best, ~85% (range 75–90%) in marine mammals that use lift-based propulsion. Hence, the overall aerobic efficiency (the aerobic conversion of food energy into movement) is only ~13%. This means that the aerobic power for submerged swimming actually increases at  $\sim 8 \times U^3$ .

### Cost of Transport (COT)

The COT (J kg<sup>-1</sup> m<sup>-1</sup>) is the energetic cost (J) of moving 1 kg of body mass 1 m and is calculated by dividing locomotory metabolic rate by speed. The COT decreases with speed to a minimum value that has a mass-specific scaling factor that varies with the mode of locomotion (e.g., quadrupedal running mammals [8.46 g<sup>-0.40</sup>], endothermic surface swimming birds and mammals [23.87 kg<sup>-0.15</sup>], marine mammals [7.87 kg<sup>-0.29</sup>], salmon [2.15 kg<sup>-0.25</sup>]) and enables an animal to cover the largest distance for the smallest energy cost (Taylor et al. 1970; Schmidt-Nielsen 1997; Williams et al. 1992). The decrease in minimum COT with increasing body mass results from lower mass-specific metabolic rates during exercise (similar to resting metabolism) and higher optimum speeds for large animals. The mean minimum submerged COT for harbor seals, California sea lions, and southern sea lions is 2.6 J kg<sup>-1</sup> m<sup>-1</sup> for an average mass of 57 kg. For the harbor seals and the California sea lions, minimum COT increases a modest 16% as speed increases to 3.4 m s<sup>-1</sup>.

### Swim Speed

Measuring the swim speed of marine mammals at sea is very difficult. Gauging the speed of an animal swimming at the surface from a boat is inaccurate and impossible for submerged swimming. Transit speeds at the surface determined with Argos satellite locations or GPS do not reflect the animal's three-dimensional movements, so they are a minimum estimates. Vertical descent and ascent speeds alone underestimate actual swim speed, and calculating speed using the rate of depth change and descent or ascent

angle is not accurate for pitch angles less than  $45^\circ$ . The most accurate method is to attach small, animal-borne instruments with calibrated speed sensors, but this approach is expensive and logistically challenging. Even with these instruments, animals need to be monitored over long-time periods to generate an accurate mean value, and this has only been done for a few pinnipeds. However, even a mean value may disguise important and interesting differences in speed associated with changes in behavior, which in itself may be difficult to determine. As a result, the literature is full of values for swim speed that may or may not be accurate or representative of average or routine values and are difficult to place in a behavioral context. Burst speeds are even more suspect because they are often of short duration and generally estimated from a boat or in captivity. Nevertheless, so-called routine and burst speeds are worth considering with the understanding that most are, at best, an estimate. The most striking aspect when comparing the routine swimming speeds of marine mammals ranging in size from the smallest (sea otter) to the largest (blue whale) is the very narrow range. Despite differences in size, feeding ecology and diving behavior, the routine swim speeds of most marine mammals fall in the range of  $1\text{--}3\text{ m s}^{-1}$ .

## Buoyancy

The density of fresh water ( $1\text{ g cm}^{-3}$ ) is 820-fold greater (839 for sea water) than for air ( $1.33 \times 10^{-3}\text{ g cm}^{-3}$ ) but only 1.1-fold greater than for blubber ( $\sim 0.9\text{ g cm}^{-3}$ ). In contrast, lean tissue (e.g., muscle) has a density ( $1.06\text{ g cm}^{-3}$ ) that is slightly greater than for sea water. Hence for marine mammals, net buoyancy (Newtons, N) will be the sum of the positive buoyancy from air in the lungs or trapped in the fur (sea otters and fur seals only) and from blubber and the negative buoyancy from lean tissue. However, air is compressed as the animal descends during a dive resulting in a loss of buoyancy as a function of depth. In contrast, blubber is incompressible so its contribution to buoyancy is independent of depth but may change seasonally. Hence, an animal's

buoyancy will be dynamic and depend on seasonal body composition and the ambient pressure during dives.

During descent, compression of the lungs can result in the transition from positive buoyancy at the surface to negative buoyancy. As a result, pinnipeds can go from active stroking to stroke-and-glide until a depth at which point they are negatively buoyant, stop stroking and glide to the bottom of the dive ( $\sim 300\text{ m}$ ). Gliding is an energy-conserving locomotory strategy that can potentially reduce diving metabolic rate in elephant seals and was later confirmed for other species of marine mammals including bottlenose dolphins, blue whales, and Weddell seals. The effect of negative buoyancy on metabolism was measured for Weddell seals diving from an isolated ice hole. Dives with prolonged gliding during descent had a 27.8% (range 9.2–59.6%) reduction in energetic cost compared with those using stroke and glide or continuous swimming over the same total distance (descent and ascent).

Not all individuals within a population will have the same body composition. On average, the thinner seals glide during descent whereas the fatter seals use stroke-and-glide locomotion. Hence, pinnipeds adopt different stroke patterns according to their individual buoyancies.

Drift dives are an interesting manifestation of changes in buoyancy. They were first described for an adult northern elephant based on time-depth profiles and swim speed during the postbreeding foraging trip and occur in bouts (ca. 2–10 drift dives per day). During drift dives, seals stroke to a depth where they become negatively buoyant (due to lung collapse) and then sink passively in a supine (belly-up) orientation to a depth of 300–400 m for about 23 min, although this varies with body composition. Drift dives have also been observed in southern elephant seals and Weddell seals. However, their function remains uncertain. There has been speculation that they are associated with digestion following bouts of foraging dives. This seems reasonable, but there is no evidence that a suspension of active foraging is necessary for digestion or that it can be postponed until a bout of drift dives. In Weddell seals, digestion and assimilation occur during long foraging



bouts. A more likely explanation is that drift dives are associated with sleep.

## Summary

1. The convergent evolution of a fusiform body shape in aquatic vertebrates decreases drag resulting from the greater density (820-fold) and viscosity (55-fold) of water compared to air.
2. Drag is influenced by flow around an object which can be laminar or turbulent and characterized by a *Reynolds Number* ( $Re$ ). Due their large size ( $>1$  m length), the  $Re$  for all pinnipeds is high ( $\geq 10^6$ ), so flow is turbulent over most of the body at routine swim speeds.
3. There are two types of drag that can be explained by the formation of a boundary layer: *pressure drag* and *friction drag*.
4. Pressure drag is greatly reduced by a streamlined or fusiform body shape with an optimum fineness ratio 4.5 (range of 3–7) which delays boundary layer separation and formation of a wake.
5. Body shapes with a fineness ratio larger than 4.5 will have a greater surface-to-volume ratio and experience an increase in friction drag (also called viscous drag). Taken together, pressure drag and friction drag contribute to the total drag on a body, and whether it is dominated by one or the other depends on body shape.
6. The pressure drag on a streamlined body with a fineness ratio of ca. 4.5 and turbulent flow ( $Re \geq 10^6$ ), which is typical for pinnipeds, is small (~20% of total drag) relative to friction drag.
7. The drag coefficient ( $C_d$ ) depends on the shape of the body and is less for a hydrodynamic shape than for a bluff body. Pressure drag will be most influenced by  $C_d$  whereas friction drag will be most influenced by surface area ( $S$ ). For two animals that differ in size but have the same  $C_d$ , pressure drag will be the same but friction drag will be greater for the larger animal because it has a larger surface area.
8. Active drag of a free-swimming animal is generally assumed to be approximately three-fold greater than passive drag.
9. Swimming submerged at a depth of three body diameters prevents wave drag which can augment total drag 4 to 5-fold.
10. Flippers and flukes with high (3–9) aspect ratios to improve thrust production and propulsive efficiency also function as control surfaces that provide maneuverability and stability.
11. The most derived and efficient modes of aquatic locomotion include pelvic oscillation (seals and walrus) and pectoral oscillation (sea lions and fur seals) with performance changes from drag-based propulsion (paddling) to lift-based that generates thrust throughout the stroke and increases propulsive efficiency (thrust power-to-total mechanical power output ~0.75–0.90), power and speed.
12. Although pinnipeds often appear awkward on land, they are capable of remarkable agility, stamina, and speed.
13. Animal movement is generated by the contraction of muscles which convert *chemical energy* (metabolism) into *power and mechanical work*. The contracting muscles in marine mammals move flippers and flukes to generate thrust to overcome the load created primarily by drag but also viscoelastic forces in the muscles.
14. The power generated by the contracting muscles is translated into the power associated with locomotion (thrust  $\times$  velocity). Since drag increases with  $U^2$ , locomotory power increases with  $U^3$  which makes high-speed swimming energetically costly. As a result, routine swim speeds of most marine mammals are 1–3 m s<sup>-1</sup>. The overall aerobic efficiency (the aerobic conversion of food energy into movement) is only ~13% which means that the aerobic power for submerged swimming actually increases at  $\sim 8 \times U^3$ .
15. There is a convergent evolution toward a minimum COT for running terrestrial mammals and subsurface swimming marine

mammals *of similar size* that optimizes the cost of locomotion.

16. The mean minimum submerged COT for harbor seals, California sea lions, and southern sea lions is  $2.6 \text{ J kg}^{-1} \text{ m}^{-1}$  for an average mass of 57 kg.
17. Despite differences in size, feeding ecology and diving behavior, the routine swim speeds of most marine mammals fall in the range of  $1\text{--}3 \text{ m s}^{-1}$ .
18. Seals adjust their swimming mode (continuous stroking, stroke-and-glide, gliding) during descent and ascent in response to changes in buoyancy.
19. Drift dives are probably associated with sleep at depth. Seals may be negatively or positively buoyant at depth, and this will determine whether they drift downwards or upwards.

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## Pitocin

► [Oxytocin](#)

## Pituitary Gland

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## Synonyms

[Hypophysis](#)

## Definition

The pituitary gland is a pea-shaped endocrine gland hanging from the neural extension of the base of the hypothalamus. It is responsible for regulating and maintaining the normal physiological functions of the body.

## Introduction

The pituitary gland is ubiquitous throughout the vertebrates. It is sometimes referred to as the master gland of the body because it controls the secretion of other glands via its hormones. Hence, most of the pituitary hormones are tropic hormones in nature, that is, they stimulate the other endocrine glands to release their hormones. The pituitary is functionally and anatomically divided into three lobes which secrete their signaling molecules into the bloodstream. The anterior lobe

**Pituitary Gland, Table 1** Hormones of the anterior pituitary gland and their function

| Hormone                                                         | Endocrine cell | Function                                                                                                                 | Stimulated by                                             | Inhibited by                                            |
|-----------------------------------------------------------------|----------------|--------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------|---------------------------------------------------------|
| Thyroid-stimulating hormone (TSH)                               | Thyrotrope     | Stimulates release and synthesis of thyroid hormones T <sub>3</sub> and T <sub>4</sub>                                   | Thyroid-releasing hormone (TRH)                           | T <sub>3</sub> and T <sub>4</sub> (thyroid hormones)    |
| Growth hormone (GH)                                             | Somatotrope    | Stimulates the release of growth factors (IGF-1); cell proliferation; bone elongation; fat breakdown; glycogen breakdown | Growth hormone-releasing hormone (GnRH); ghrelin          | Somatostatin; IGF-1                                     |
| Prolactin (PRL)                                                 | Lactotrope     | Maturation of mammary glands; breast milk production                                                                     | Tactile stimulation of nipples in females (postpregnancy) | Prolactin-inhibiting hormone (dopamine)                 |
| Follicle-stimulating hormone (FSH) and luteinizing hormone (LH) | Gonadotrope    | Sex steroid synthesis; ovulation and follicular development (in females); sperm production (in males)                    | Gonadotropin-releasing hormone (GnRH); activin            | Estrogen (in females); testosterone (in males); inhibin |
| Adrenocorticotrophic hormone (ACTH)                             | Corticotrope   | Stimulates release and synthesis of corticosteroids                                                                      | Corticotropin-releasing hormone (CRH)                     | Glucocorticoids (mainly cortisol)                       |

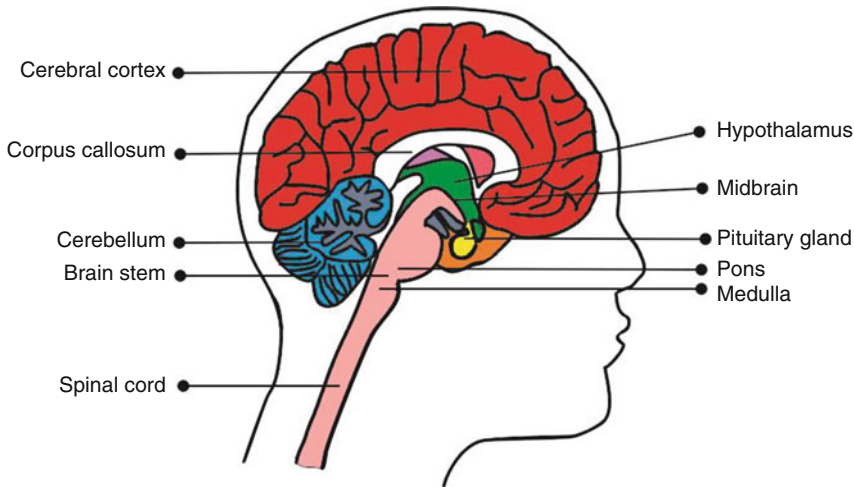
(Table 1) produces growth hormone (GH), adrenocorticotrophic hormone (ACTH), thyroid-stimulating hormone (TSH), follicle-stimulating hormone (FSH), luteinizing hormone (LH), and prolactin (PRL). These hormones are synthesized and stored as vesicles inside the glandular cells of the anterior pituitary and are released via exocytosis when acted upon by the hypothalamic hormones.

The posterior part of the pituitary stores oxytocin and vasopressin. Unlike the anterior pituitary hormones, these are not synthesized in the pituitary but are manufactured by the neurosecretory cells, a special class of neurons that release hormones. These neurons are located in the hypothalamus, the axons of which terminate in the posterior pituitary region. These hormones are shipped down the axon, a long narrow extension of neuronal cells, and are stored as vesicles in the axonal endings (Barrett et al. 2009). The intermediate lobe forms a thin layer of cells that produce melanocyte-stimulating hormone (MSH), which has its role in skin pigmentation. Except PRL and GH, all the anterior pituitary hormones are tropic in nature. The posterior pituitary hormones

along with PRL and GH are nontropic and directly affect the site of action (Barrett et al. 2009).

## Morphology

The pituitary gland sits just behind the nose bridge and is located in the mid-line from a mid-sagittal view, inferior to the optic chiasm (Fig. 1). It rests inside a bowl-shaped depression of the sphenoid bone called the *sella turcica* (named after its resemblance to Turkish horse saddle). The roof of the depression is surrounded by a dura mater (a membranous layer that surrounds the brain and the spinal cord) known as the *diaphragm sella* which covers the hypophyseal fossa (the inferior part of the sella turcica). A hole in this diaphragm allows the vertical entry of pituitary stalk to join the hypothalamus. Hence, another term for the pituitary is the hypophysis (hypo = below; physis = outgrowth) as it appears as a protuberance of the brain hanging from the hypothalamus. The pituitary is richly supplied by the major arteries and dural venous sinuses to transport the released hormones on to its recipient sites.



**Pituitary Gland, Fig. 1** Mid-sagittal view of human head depicting the position of the pituitary gland

## Anatomy and Development

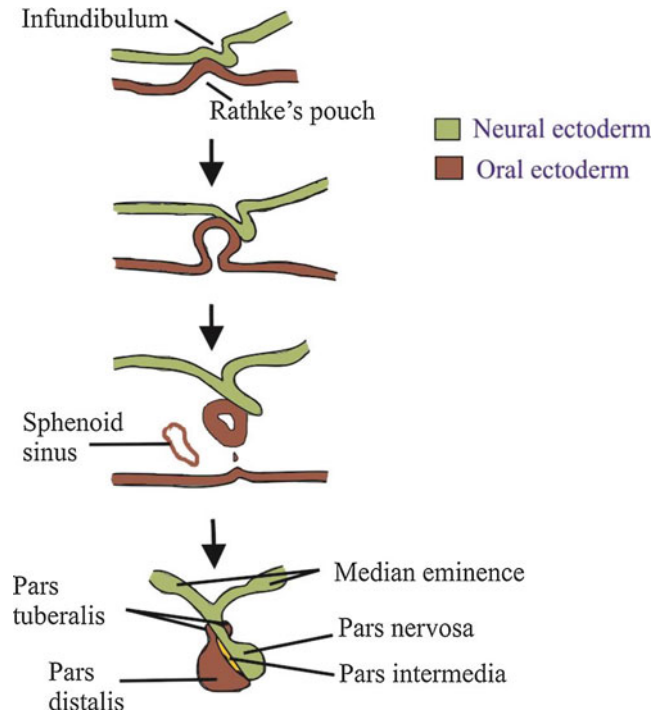
The pituitary is divided into two primary regions. This division of the pituitary is evolutionarily conserved and occurs in almost all vertebrates. The anterior part is called the adenohypophysis or the anterior pituitary lobe. It has abundance of glandular epithelial cells which are responsible for secreting the hormones. The upper portion of this lobe is called *pars tuberalis* while the lower region is called *pars distalis*, which is the site of endocrine secretion (Nussey and Whitehead 2013).

The second major region, called the posterior lobe, is mainly comprised of neural tissues, known as neurohypophysis or *pars nervosa*. The neural tissue is made up of axonal endings carrying the hormonal vesicles. These axonal endings arise from the supraoptic and paraventricular nuclei of the hypothalamus connected by a bundle of axons called the hypothalamo-hypophyseal tract. An extension of the hypothalamus forming a funnel-shaped cavity called pituitary stalk or the infundibulum connects to the posterior pituitary and accommodates the axon bundles and blood capillaries (Barrett et al. 2009). A bulge of the infundibulum forms the interface between the hypothalamus and the pituitary gland called the median

eminence. This is a specialized region where the portal vessels arise and axons from parvocellular neurosecretory cells (small neurons) from various nuclei terminate (Barrett et al. 2009).

In humans, the emergence of the pituitary is seen during the 4th week of gestation period. The embryological genesis of the lobes occurs separately. The anterior lobe is developed from the infolding of oral ectoderm, called *Rathke's pouch* (Fig. 2). The posterior lobe originates from the infolding of the neural ectoderm, specifically the base of the third ventricle (Fig. 2). This explains the differential composition of the cells in posterior and anterior lobes.

A third lobe known as the intermediate lobe is also present; unlike the other two lobes, it is not ubiquitous and it may be completely absent in some vertebrates such as the avians. It lies between the anterior and posterior lobe but is more closely associated with the anterior lobe due its shared embryological origin. This region is not very well defined in mammals such as humans, but it has been attributed to the secretion of melanocyte-stimulating hormone (MSH). Its function is more pronounced in the lower vertebrates such as rodents where this lobe's structure is well developed (Melmed 2010).

**Pituitary Gland,****Fig. 2** Embryological development of the pituitary gland**Vasculature**

A complex network of blood capillaries infiltrates the pituitary and its surrounding structures. The internal carotid artery branches off into several small arterioles that form the portal system of the pituitary. In contrast to the blood vessels that forms the blood–brain barrier, these capillaries are fenestrated (i.e., the tight endothelial junctions harbor multiple pores). This increases the permeability and allows free exchange of large molecules from the surroundings into the circulation (Melmed 2010; Nussey and Whitehead 2013).

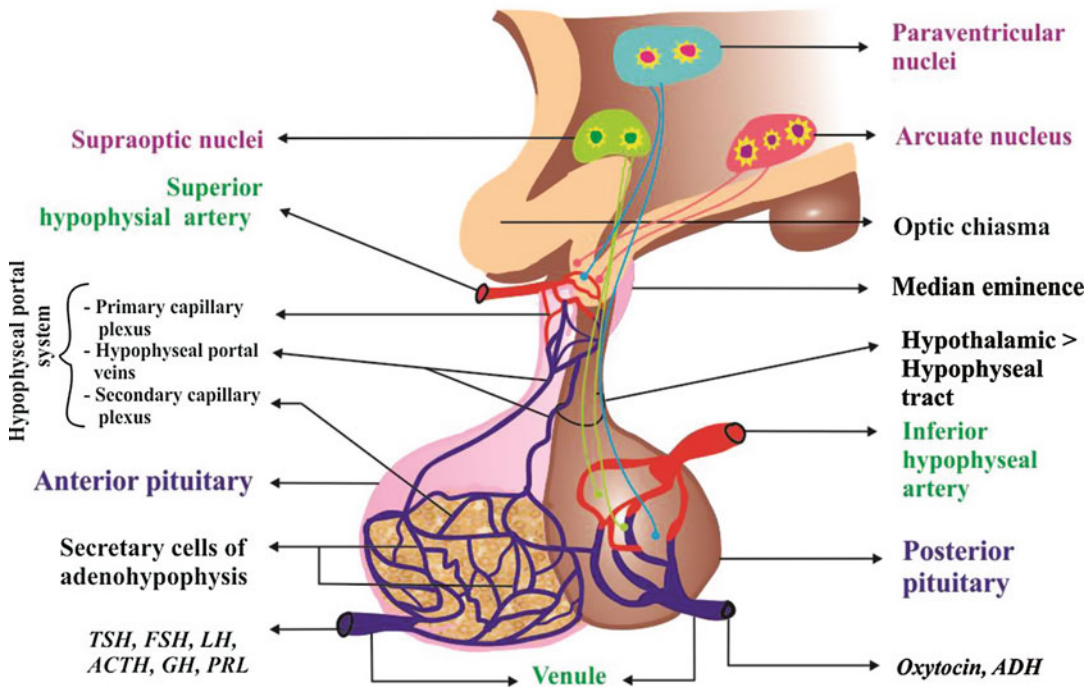
The pars nervosa receives its blood supply from the inferior hypophyseal artery and the infundibular artery. The capillary network surrounding the region receives the neurosecretory hormones which are then drained into the inferior hypophyseal vein and eventually into cavernous sinus (Barrett et al. 2009). The microcirculation inside the anterior pituitary consists of a capillary bed which is linked to a network of capillary near the hypothalamus. This is known as the hypothalamo-hypophyseal portal system (Fig. 3). The superior hypophyseal artery joins a

complex grid of capillary bed known as the primary plexus traversing the median eminence and pars tuberalis. The same blood flows through the pars distalis via another capillary bed known as the secondary plexus which then drains into the cavernous sinus into the systemic circulation. Since the capillary blood drains into another capillary bed without passing through the heart first, this system is known as a portal venous system (Barrett et al. 2009). Hepatic portal system in the liver is another example of such system in the human body. The hypothalamo-hypophyseal portal is responsible for relaying the tropic factors from the hypothalamic nuclei into the anterior pituitary which in turn stimulates the glandular cells to release their respective hormones.

**Function and Site of Action of Different Pituitary Hormones****Anterior Pituitary Hormones**

1. **Thyroid-stimulating hormone (TSH):** It is released in response to hypothalamic thyrotropin-releasing hormone (TRH). TSH





**Pituitary Gland, Fig. 3** Hypothalamo-hypophyseal portal system

travels down the bloodstream and binds to the TSH receptors (a member of G-protein coupled receptors) present on the epithelium of the thyroid gland which increases the production and secretion of the thyroid hormones thyroxine (T4) and triiodothyronine (T3). Thyroid hormones upregulate the transcription of various genes increasing the protein synthesis (Brent 2012). This leads to a wide array of physiological changes such as increase in basal metabolic rate, increased heartbeat, increased number of mitochondria, increased oxygen utilization by the cells, etc. (Brent 2012).

2. **Growth hormone (GH):** It helps in growth and development of body and carries out various anabolic activities as well as aids in cell growth and proliferation, lipid breakdown, protein synthesis, etc. It mediates its effect by activating certain growth factors such as insulin-like growth factor 1 (IGF-1). GH is inhibited by somatostatin released by the hypothalamus as well as IGF-1 (Nussey and

Whitehead 2013). The release of GH is sexually dimorphic in nature, which is evident from the phenotypes of male and females in various species. It works in conjunction with the gonadal hormones such as the testosterone and estrogen to impart the sex-specific characteristics such as a higher cell proliferation and body growth in males.

3. **Adrenocorticotrophic hormone (ACTH):** It primarily functions by increasing the level of cortisol in the bloodstream by binding to its receptors on the *zona fasciculata* layer of adrenal gland cortex. Cortisol is a stress hormone that increases the blood glucose concentration, aids in metabolism of biomolecules, and suppresses the immune system (Nussey and Whitehead 2013).
4. **Prolactin (PRL):** It is physiologically relevant to females where it activates enzymes for lactose synthesis. It is a peptide hormone that acts on the mammary gland and stimulates milk production and its secretion into ducts (Nussey and Whitehead 2013). It also causes

maturation and growth of the mammary gland during pregnancy to prepare for the lactation. PRL has been noted to have suppressive effect on gonadotropin-releasing hormone (GnRH) release resulting in disruptions to normal ovarian cycle in females. This leads to a temporary infertile stage where the females stop menstruating, known as lactational amenorrhea (Nussey and Whitehead 2013).

5. **Luteinizing hormone (LH) and follicle-stimulating hormone (FSH):** These hormones are released by gonadotropes and act on testes (in males) and ovaries (in females). FSH in females induces growth and maturation of ovarian follicles (folliculogenesis) as well as stimulates the biosynthesis of estradiol (estrogen). In males, FSH aids in spermatogenesis by activating the Sertoli cells to synthesize androgen-binding protein (ABP) (Melmed 2010; Nussey and Whitehead 2013). Luteinizing hormone works in synergy with FSH and causes ovulation and formation of corpus luteum in females. In males, it acts on the Leydig cell for the production of testosterone.

### Posterior Pituitary Hormones

1. **Arginine vasopressin (AVP):** It is also called antidiuretic hormone (ADH) and its primary function is to restore the blood osmolarity to its normal physiological value. It increases the production of membrane channels that transport water molecules in the walls of the collecting duct of the kidney nephrons thereby increasing water reabsorption from urine (Melmed 2010). Vasopressin also increases the blood pressure by constricting the blood vessels. Changes to blood osmolality are detected by osmoreceptors in the hypothalamus which results in stimulation of neurosecretory cells in the hypothalamus to secrete AVP (Nussey and Whitehead 2013). The role of AVP has also been implicated in social behavior and bonding, especially male vertebrates (Heinrichs and Domes 2008). Arginine vasotocin (AVT) is a functional homolog to AVP as well as oxytocin and is found in almost all nonmammalian vertebrates including

teleosts, amphibians, and reptiles. It is likely that the vertebrate neurohypophyseal hormones have evolved from AVT (Knobloch and Grinevich 2014).

2. **Oxytocin:** Found in most of the mammalian species, this hormone mandates a diverse range of functions in mammals which include milk ejection reflex, uterine contraction during labor, sperm release, and behavioral responses such as maternal bonding (Jurek and Neumann 2018). It leads to rapid contraction of the uterine smooth muscle layer during parturition. The dilation of the cervix and the uterine during the onset of labor stimulates the hypothalamus to release oxytocin. The act of breastfeeding also activates this hormone where the tactile stimulation of the nipples causes the pituitary to release oxytocin, which in turn acts on the myoepithelial cells of the breast alveoli to release its milk into the ducts and eventually out of the nipples (Jurek and Neumann 2018). In other vertebrates, homologs of oxytocin play a similar role, for example, mesotocin, which is present in marsupials, reptiles, amphibians, and birds (Knobloch and Grinevich 2014).

### Regulation of the Pituitary Gland

**Hypothalamus:** It harbors several clusters of neurosecretory cells that synthesize and release various regulatory tropic and nontropic hormones (Table 2). The axonal endings of the parvocellular neurons terminate at the primary plexus, releasing their factors which travel down the secondary plexus and stimulate the anterior pituitary. In contrast, the magnocellular neurons (large neurons) terminate at the posterior lobe and release their hormones. Thus, hypothalamus directly controls the secretion of pituitary hormones (Nussey and Whitehead 2013). The hypothalamus is susceptible to environmental cues, and thus has a major implication on the tropic effect on the pituitary. Environmental stress can modulate the hormones released by the hypothalamic nuclei; for example, increase in the levels of cortical releasing factor (CRF) stimulates the ACTH and eventually

**Pituitary Gland, Table 2** Hormones synthesized by hypothalamus and their function

| Hypothalamic nuclei                   | Neuroendocrine cell  | Hormone(s) synthesized                                  | Function of the hormone                                      |
|---------------------------------------|----------------------|---------------------------------------------------------|--------------------------------------------------------------|
| Paraventricular nuclei                | Parvocellular neuron | Corticotropin-releasing hormone (CRH)                   | Stimulates the release of CRH                                |
| Preoptic area                         | Parvocellular neuron | Gonadotropin-releasing hormone (GnRH)                   | Stimulates the release of LH and FSH                         |
| Supraoptic and paraventricular nuclei | Magnocellular neuron | Oxytocin                                                | Uterine contraction during parturition; milk ejection reflex |
| Supraoptic and paraventricular nuclei | Magnocellular neuron | Vasopressin                                             | Vasoconstriction; fluid reabsorption                         |
| Arcuate nuclei                        | Parvocellular neuron | Prolactin-inhibiting hormone (PIH)                      | Inhibits the release of prolactin                            |
| Periventricular and arcuate nuclei    | Parvocellular neuron | Growth hormone-releasing hormone (GRH) and somatostatin | Stimulates the release and synthesis of GH                   |
| Paraventricular nuclei                | Parvocellular neuron | Thyrotropin-releasing hormone (TRH)                     | Stimulates the release and synthesis of TSH                  |

increases the blood cortisol levels. These stress cues ensue a differential response in other hormones such as the reduction in the gonadotropin levels and consequently changes to the female sexual cycle (Cameron 1997), increase in VP levels (Aguilera et al. 2008), increase GH levels (Delitala et al. 1987), etc.

## Negative Feedback Control

The hormones of the pituitary are well coordinated and regulated, and any imbalance may lead to severe clinical anomalies. Pituitary tumors are the most prominent cause of the abnormal secretion of the hypophyseal hormones. Depending on the hypo- or hypersecretion, a variety of conditions can develop, for example, *acromegaly* (excess GH), *Cushing's disease* (excess ACTH), hyperthyroidism (excess TSH), etc. Hypophysectomy (surgical removal of the pituitary) in animal studies has also shown several abnormalities, such as infertility, loss of sexual drive, underdeveloped sexual organs and reproductive tract, stunted growth, etc. Thus, the balance of hypophyseal hormones is crucial and is mediated by a complex neuroendocrine system that controls the activation and inhibition of the

endocrine glands. For example, in case of thyroid hormone homeostasis, a drop in T3 and T4 concentration in the blood is detected by the hypothalamus which results in release of TRH, stimulating the pituitary to secrete TSH. This leads to a rise in TSH levels in the blood plasma resulting in upregulation of thyroid hormone synthesis and release. An inhibitory response also works in synergy with the stimulation of TSH to keep the T3 and T4 plasma concentration up to a tolerable limit. This role is played by the thyroid hormone itself, which directly inhibits the release of TSH and indirectly inhibits TRH release from the hypothalamus. As the T3 and T4 levels in plasma elevate, the strength of this inhibitory response would also increase. This is an example of a negative feedback loop which functions almost similarly for other pituitary hormones.

## Cross-References

- [Endocrine System](#)
- [Hormones and Behavior](#)
- [Hypothalamus](#)
- [Oxytocin](#)
- [Testosterone](#)
- [Thyroid and Adrenal Glands](#)

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## Place Versus Response Learning

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### Definition

**Place learning** A form of spatial learning reflecting the acquisition and knowledge of an object/location's actual position in space, relative to a constellation of other visual cues.

**Response learning** A form of spatial learning reflecting the acquisition of a habitual response used to navigate to a location that does not reflect knowledge of a place based on surrounding cues.

### Introduction

Animals use a remarkable variety of methods to navigate their environments. Experimental psychologists have traditionally focused on how spatial relations between visual cues in the environment (landmarks, beacons, etc.) are acquired and whether these relations integrate together or compete for control over an animal's navigation. Early experiments trained animals to navigate a variety of mazes often aided by visual cues that bore a consistent spatial relationship to the goal (i.e., the end of the maze, often baited with food). By varying the position of visual cues surrounding the animal and/or maze, or by changing the animal's start location at critical points during training, three fundamental forms of spatial learning were observed: response learning, directional learning, and place learning. While each form of learning has the potential to support successful navigation, place learning is unique in that it suggests a much deeper understanding of where you are in space. Place learning, moreover, is a far more complex form of spatial learning; animals must process the current position of cues (as well as themselves) and make novel navigational decisions based on the arrangement of cues and/or their starting position in the maze. This behavioral distinction is echoed via investigations of the brain; neurobehavioral studies have found that successful completion of place navigation tasks depends more on the hippocampus region of the brain (a hotbed for learning and memory) compared to directional or response tendencies which tend to rely more on the caudate nucleus (responsible for motivated responding).

### What Fundamental Learning Processes Back Navigation?

For well over a century, researchers have attempted to describe *how* animals (including

our own species) learn. An animal might learn, for instance, that stimuli in the environment (S) are paired with a certain responses (S-R). In S-R learning (Thorndike 1898), a stimulus becomes paired with a response (the rat sees and reaches the choice point in a T maze (S) and turns left (R)). Over time, S-R links are “stamped in” as powerful habits, pending they eventually result in a reinforcing outcome. Another fundamental form of *how* animals learn involves understanding that one stimulus is associated with another stimulus (associative learning). Pavlov (1927) initially observed that if a biologically neutral stimulus (conditioned stimulus, CS, e.g., a metronome) was repeatedly paired with a biologically significant stimulus (unconditioned stimulus, US, e.g., meat), over time, his dogs would learn to associate the two stimuli, eventually salivating to the metronome (CS-US). Both S-R (habit) and CS-US (associative) processes support spatial learning but have varying significance when it comes to supporting response, directional, or place learning.

### Why Is Place Learning Different?

The first form of spatial learning, *response learning*, describes an animal learning to emit a programmed response or chain of responses (e.g., turn left, turn right, turn left) to reach a goal. The aforementioned habit building (S-R) mechanism is fundamental to response learning; either stimuli in the environment (S) or even the animals’ own proprioceptive feedback (i.e., orientation of the body relative to its orientation with respect to gravity) becomes strongly linked to a response (R). An example of response learning would be habitually learning a preset number of turns as you drive to your office building. At each turn point (S), you learn the next appropriate response (R) and chain these learned habits together. An important characteristic of response learning is that it is quite rigid and inflexible. If you’re habitual path to work is interrupted/rerouted by some unexpected construction, you may come to realize you don’t have a precise idea of where to turn next.

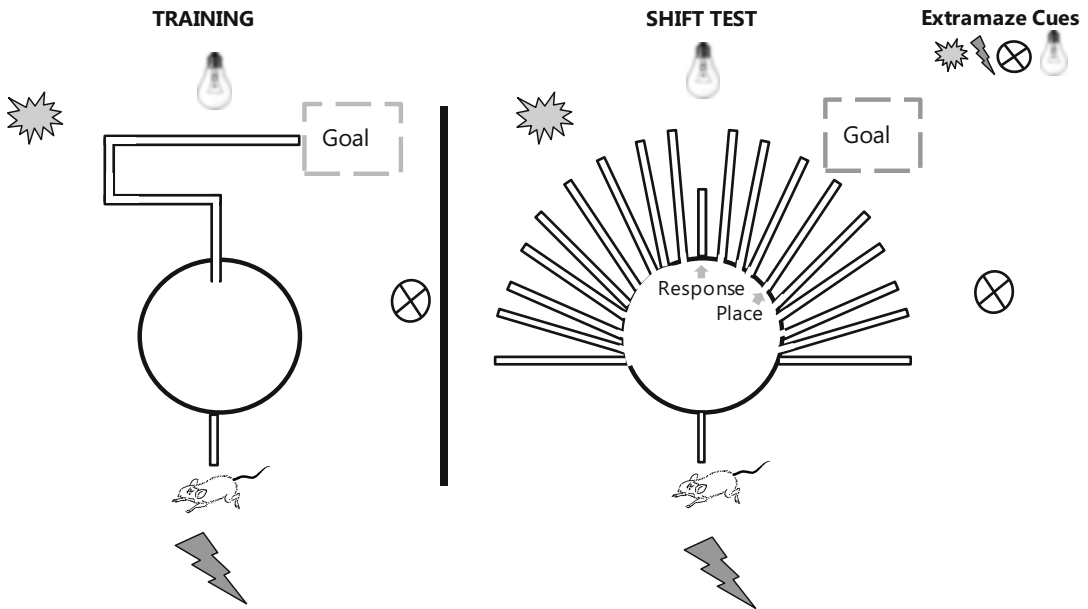
The second form of spatial learning, *directional learning*, describes an animal learning to head or approach a certain direction (e.g., east) in order to reach a goal. Directional learning is thought to work via a similar mechanism as Pavlov’s dogs; the animal is dropped into the maze and might learn to approach (sometimes referred to as sign tracking) the direction (north; CS) that ultimately leads them to the goal (US). This is in some ways more flexible than response learning in that the animal might make varying choices at different turn points but always head toward the direction of the goal.

The third form of spatial learning, *place learning*, describes an animal learning where something is in relation to other cues. Imagine observing that your office is west of a large clock tower and north of a flagpole. Assuming you can see the tower and flagpole, and have some knowledge of spatial relation (associations) between the three points, no matter the direction of your approach, you can successfully navigate to the *place* that your work is located. Place learning is inherently more flexible than either response or directional learning, meaning the animal heads to the correct location even if it’s coming from a different direction or viewing the cues from a novel orientation (see Fig. 1). That isn’t to say that place learning is cue independent; when the entire constellation of cues are shifted around, animals will still tend to head to the “place” in accordance with the current orientation of the cues.

### How Is Place Learning Captured?

The three forms of spatial learning were identified and isolated by observing rats navigating tabletop mazes in search of buried food or swimming to submerged platforms within a water maze (Fig. 2). In both cases, various extramaze (outside of the maze) cues are hung around the maze to serve as navigational landmarks the animal can utilize (or not). A typical spatial learning experiment tends to feature two phases: the training phase and the shift test phase.





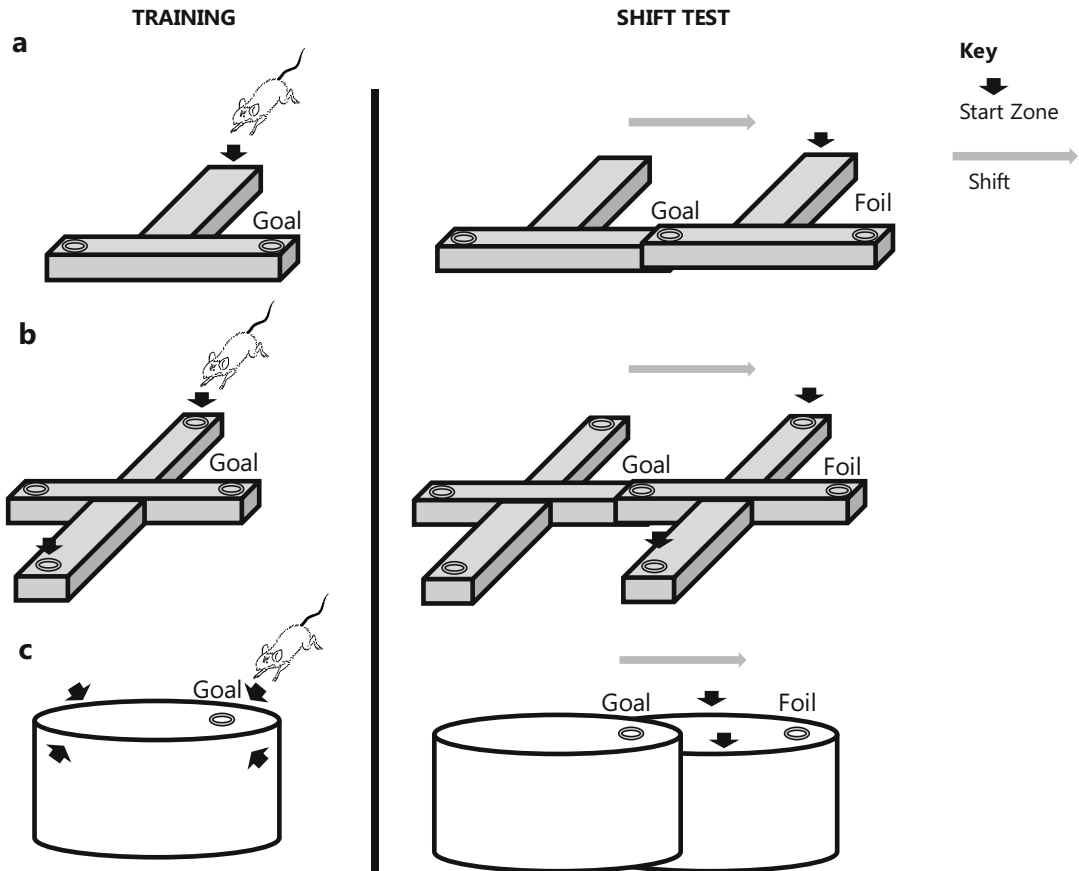
**Place Versus Response Learning, Fig. 1** Tolman et al.'s (1946) famous sunburst maze is illustrated above. During training, the rat was dropped off at the lower start zone. Throughout training, the rat learned to take the same linear path to the goal. Extramaze cues (symbolized by the various icons) surrounded the maze throughout training and test. At test, a sunburst pattern with multiple pathways was introduced. If the animal evidenced response learning (an S-R habit), Tolman predicted it would take the middle route (now blocked) as it did during training. If the animal

evidenced a place tendency, Tolman predicted it would take an alternate route taking it efficiently to the correct "place" where the goal box should have been located, based on the constellation of extramaze cues. Tolmans' rats tended to evidence a place tendency, although some currently debate whether the rats used the rather salient lightbulb as more of a directional cue, simply approaching the signal (leading to a more associative CS-US interpretation)

Animals can be dropped off at a single start zone throughout training (Fig. 2a), dual start zones opposite from one another (Fig. 2b), or four corners of the maze (Fig. 2c) while the location of the buried food (goal) remains at the same location. Following training, the shift test involves experimenters shifting the maze by about 1/3 of its length on a single axis, so that the actual goal (within the maze) has moved, and an alternate "foil" location has taken the original goal's "place." Critically, no extramaze cues are moved; they still share the same spatial relationship with the "place" the goal had been during training. At test, the animal is dropped from one or more start zones. The critical shift trial examines whether the animal heads to the "foil" (more indicative of response/directional learning) or heads to the correct "place" (more indicative of place learning).

## What Parameters Affect Place Learning?

**Type of Navigation Task.** The Morris water maze (Fig. 2c) follows an identical training/shift test format, however, rats are typically dropped from four corners of the maze. These latter variants carry an advantage over path-based mazes such as the T maze (Fig. 2a) or plus maze (Fig. 2b) in that they don't force the animal to make a binary decision at the branch point (i.e., turn right or turn left at the middle of the plus maze). The Morris pool promotes more flexible utilization of visual cues to locate a hidden goal without clear choice points. It isn't surprising that the type of maze favors one form of spatial learning over the other; holding all other variables constant, a classic hedge maze or T maze tends to favor response learning, the plus maze tends to favor (at least initially) place learning followed by directional



**Place Versus Response Learning, Fig. 2** Three common mazes used to study spatial learning are illustrated as well as the “shift test” method used for assessing place learning. The top row (a) shows the T maze; the rat is dropped off at a single start zone and trained to approach the goal (a single arm baited with food). During the shift test, the entire apparatus is shifted 1/3 of its length on a single axis. If the animal turns left and visits the foil, it would evidence response/directional learning; if the animal turns right, and visits the ‘goal,’ it would evidence place learning. The middle row (b) shows the plus maze; the rat is typically dropped off at a two start zones and trained to

approach the goal (a single arm baited with food). During the shift test, if the animal turns and heads toward the foil, it would evidence directional learning; if the animal heads toward the ‘goal,’ it would evidence place learning. The bottom row (c) shows the Morris water maze; the rat is typically dropped off at four corner start zones and trained to swim to the goal (an elevated platform allowing to escape the aversive water). During the shift test, if the animal turns and swims toward the foil, it would evidence directional learning; if the animal heads toward the ‘goal,’ it would evidence place learning

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learning (Skinner et al. 2003), and the Morris pool tends to favor place learning followed by directional learning as training trials increase (Hamilton et al. 2009).

**Amount of Training.** The amount of training on any maze, irrespective of type, has a rather large effect on the type of spatial learning evidenced during the shift test (Hamilton et al. 2009). Perhaps you’ve noticed that when first commuting to work, you paid close attention to

external cues to help better estimate your office’s location only to have this strategy give way (several commutes later) to highly habitual behavioral patterns (driving the same exact way each day). This same pattern generally holds true with rats in mazes: place learning tends to shift to response learning as training trials are increased. However, training effects vary depending on the type of maze, with place learning giving way to directional or response learning much sooner in

the plus maze (e.g., Packard and McGaugh 1996) than the more complex Morris maze (e.g., Hamilton et al. 2009).

**Salience of Intramaze Cues.** Intramaze cues (cues within the maze, including side walls, divots in the floor, etc.) are often kept to a minimum in such navigational studies to feature the effects of extramaze cues in supporting place learning. That being said, intramaze cues are impossible to completely devalue and play a strong role in determining which form of spatial learning is evidenced. Intramaze cues play an even more prominent role near the start zones and goal; start zones highly distinguishable via intramaze cues tend to support directional/response learning, essentially abolishing the early tendency for place early in training (Skinner et al. 2003). As Hamilton et al. (2009) emphasized, even slight scratches surrounding the walls of the Morris pool can abolish place learning preferences early in training (while it may cause a mess, Morris pools should be filled right near the surface to allow for a proper test of place learning!).

**Numerous Additional Factors.** In reality, spatial navigation is enormously complex and multiply determined. By no means an exhaustive list, spatial learning is affected by the organism's current or perceived orientation in space (e.g., Dudchenko et al. 1997), the shape or design of the spatial environment (e.g., Olton and Samuelson 1976), the availability of polarizing visual cues (Rodrigo et al. 1997), the current motivation of the animal (Tolman and Gleitman 1949), and the complexity of the task (Ruprecht et al. 2014).

**Brain (Limbic) Regions.** The distinction between spatial learning strategies is largely behavioral; however, growing evidence supports the notion that place learning and response learning depend on different structure/systems in the brain. Pharmacological agents blocking the hippocampus seem to abolish place learning behavior at the shift test (e.g., Packard and McGaugh 1996; Stringer et al. 2005). Pharmacological agents blocking the nucleus accumbens tend to disrupt S-R (response) processes (e.g., Packard and McGaugh 1996; Annett et al. 1989).

## Conclusions

For nearly all mobile animals, successful spatial navigation is key to the successful acquisition of rewards (food, shelter, mates) and the avoidance of negative outcomes (predators, famine, disease). Animals use a wide variety of interoceptive (signals within the organism's body) cues, such as kinesthetic (repeated muscular movements) and proprioceptive feedback, to support successful navigation while employing a remarkable array of external cues ranging from scents, magnetic fields, to triggers so remote and distant they continue to baffle scientists. Response, directional, and place learning can hardly explain the entirety of these evolved navigational capabilities. Rather, these distinctions try to carefully fit the more fundamental concepts of habit formation and association learning to the more complex phenomenon of spatial awareness and navigation. Our concept of *how* an animal learns about a place will continue to change and evolve. The extent to which a variety of search and navigation behaviors fall under the control of these central learning processes (habit, associative) is worth further investigation.

## Cross-References

- [Cognitive Map](#)
- [Goal-Directed Behavior](#)
- [Hippocampus](#)
- [Navigation](#)
- [Nucleus Accumbens](#)

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## Placoderm Life Histories

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## Synonyms

Armored fish

## Definition

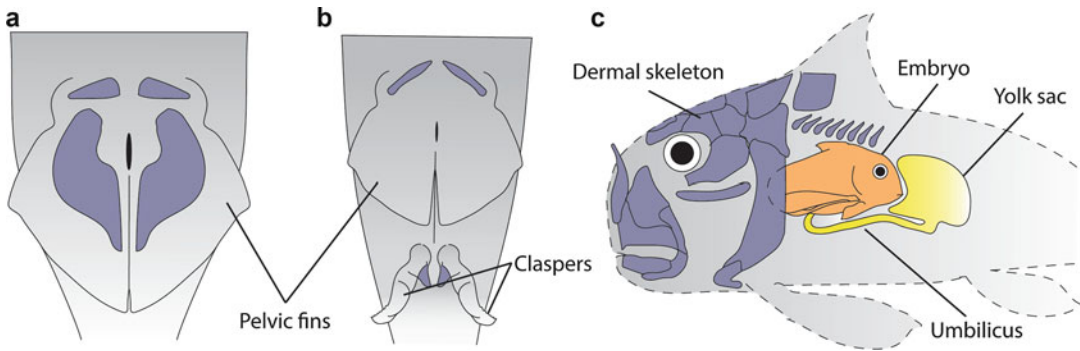
Placoderm life history describes the reproduction and growth for species within the order Placodermi, which includes antiarchs, ptyctodonts, and arthrodires.

## Introduction

Life history strategies are difficult to determine from the fossil record. However, the global distribution and exceptional preservation from some fossil sites has resulted in much being understood about habitat, feeding strategies, reproduction, and growth within placoderms. Studies on the depositional settings in which placoderm fossils have been found, indicate that different species inhabited lacustrine, river, estuarine, and marine habitats. Reproductive strategies varied between the classes of placoderm from egg laying, resulting in a large number of offspring, to live birth with fewer offspring. There is little evidence of resorption and remodeling in the dermal bones that make up the placoderm armor and so lines of arrested growth provide a life record (skeletalochronology). Healed bite marks on the armor indicate that some species survived predations, and the occurrence of placoderms in the stomach of other species indicates the species for which placoderms were prey.

## Reproduction

The presence of intromittent organs in some male antiarchs, ptyctodonts (Fig. 1), and arthrodires indicate that these placoderms reproduced through internal fertilization (Ahlberg et al. 2009). In animals with internal fertilization, reproduction may occur through: oviparity in which fertilized eggs are deposited, ovoviviparity in which fertilized eggs are retained and then hatch within the female, and viviparity whereby the female gives birth to live young. The discovery of placoderm nursery sites (Downs et al. 2011; Olive et al. 2016; Gess and Trinajstić 2017) shows that all three reproductive methods were



**Placoderm Life Histories, Fig. 1** Reconstructed ptactodont reproductive organs and embryo position. (a) Generalised female ptactodont pelvic region. (Adapted from Miles 1967); (b) External morphology

of male ptactodont showing clasper organs. (Adapted from Miles 1967; Janvier 1996). (c) Position of the embryo and yolk sac within the mother. (Adapted from Long et al. 2008)

employed by placoderms. Species which birth live young tend to have longer reproductive cycles and fewer offspring that are born at a more advanced stage of development than species that lay eggs.

Within antiarchs, the reproductive structures include bony claspers in males, which aid in the delivery of sperm, and genital plates in females which protected the genital area from the hooks on the male clasper. These structures are only known for one genus, *Microbrachius*, and represents the earliest evidence of sexual dimorphism in jawed vertebrates (Long et al. 2015). The size of the male claspers differs between individuals, even though the body size of all the fish with claspers is approximately the same. This suggests that the claspers did not fully develop until sexual maturity and that sexual maturity occurred after morphological maturity. To date no embryos or larvae has been recovered associated with *Microbrachius*. However, large numbers of hatchlings are preserved for antiarch species such as *Bothriolepis* and *Asterolepis* and provide evidence that antiarchs were oviparous. In many of the hatchlings there is an opening in the ventral surface of the trunk shield, where a yolk sac could have attached (Downs et al. 2011).

All known examples of reproduction in Ptyctodonts indicate that they were viviparous (Long et al. 2008). Embryos are preserved in the abdominal regions in *Materpiscis*,

*Austroptyctodus*, and *Rhamphodopsis*. There are a number of bone fragments in the abdominal regions of *Ctenurella*, but these are not well enough preserved to be confidently identified as embryos. The maximum number of embryos from an individual ptyctodont (*Austroptyctodus*) is three with all embryos are identical in size, indicating that they were at the same developmental stage. A single embryo has been recovered from *Materpiscis* with an attached umbilical cord indicating that there was considerable maternal investment into the offspring. The ptyctodont embryos recovered were all positioned with the head in an anterior position (Fig. 1c), suggesting the young were born tail first. The young appear to be identical in morphology to the adults in terms of dermal plates and tooth plates. Identical tooth plates indicate that the young most likely fed of similar prey to the adults, only smaller.

Arthrodires, like sharks, utilized both oviparity and viviparity as a reproductive strategy. Some of the best-preserved evidence for reproductive structures comes from arthrodires from the Gogo Formation in the northern part of Western Australia (Long et al. 2009). Both male and female individuals have been recovered with several of the female coccosteomorph arthrodires (*Incisoscutum* and *Compagopiscis*) containing embryos within the abdominal cavity. In one specimen, two embryos of identical size are present; however, in a second individual one embryo is three times larger than a second



embryo. This indicates that the embryos were at different developmental stages and further suggests females had two uteri. One of the smallest embryos has intramittent elements preserved showing that these elements were present prior to sexual maturity (Johanson and Trinajstić 2014).

Intramittent elements are not known for *Eastmanosteus calliaspis*, a large pachyosteoromorph arthrodire from the Gogo Formation in Western Australia. This could be the result of preservation bias, as no specimens with the skeleton preserved posterior to the pelvis have yet been recovered. The smallest individual recovered to date is 25% of the adult size, which is comparable to the size of neonates in other arthrodires. This suggests that *Eastmanosteus* was viviparous. Intramittent structures have also not been recovered from one of the largest predatory placoderms, *Dunkleosteus*. A single egg case, that appears to contain dermal bone with a denticulate ornament, has been recovered and associated with this species (Carr and Jackson 2018).

Numerous very small phyllolepid (*Cowralepis mclachlani*) individuals, whose size is indicative of hatchlings, have been recovered from the same site as adults in Devonian aged rocks from Merriganowry, Australia (Carr et al. 2010). In one female specimen, an ovoid structure has been putatively identified as an egg sac. Other sites such as Red Hill (Daeschler et al. 2003) in North America and Strud in Belgium (Olive et al. 2016) also represent nursery sites, consistent with the phyllolepid arthrodires being egg layers.

The estuarine lagoonal environment of the Witpoort Formation in South Africa represents another location interpreted as the site of a placoderm nursery (Gess and Trinajstić 2017). An ontogenetic series of *Africanapsis*, a phlyctaenid arthrodire, includes individuals whose size is indicative of neonates and combined with the small number of individuals suggests they have been birthed, rather than hatched. No specimens with intramittent elements have been recovered from the site and this could indicate that females entered the estuarine nursery to birth their young, separated from the males of the species. Additional sites such as Red Hill in

USA and Strud Quarry in Belgium also support a viviparous nature for phlyctaenid arthrodires.

It appears that placoderms utilized nurseries in marine estuaries and shallow continental environments to lay eggs or give birth to their young. Within these nursery sites, male specimens are mostly absent suggesting that females separated from males to lay their eggs or give birth.

## Growth

Understanding evolutionary processes and determining the mechanisms that cause them are challenging without developmental and ontogenetic information, which unfortunately is rare in the fossil record. The dermal armor of the head and thoracic region in placoderms has resulted in excellent preservation of ontogenetic changes for placoderms. However, it means that placoderms are effectively growing in an armored box, meaning if one plate proportionally changes then the corresponding plate also needs to change. Placoderms evolved a huge variety of body morphs, which enabled them to occupy many different niche spaces.

The most important cause of variation in placoderms is ontogenetic growth. Juveniles are identified by plates of thin dermal bone, which do not overlap, deeply incised sensory lines and relatively large eyes. Studies done on the antiarch *Bothriolepis* demonstrate allometric growth with the greatest variation seen in those plates which show change through evolution (Werdlein and Long 1986). Heterochrony (changes in the rate and timing of development) plays a pivotal role in evolution and has been linked to changes in orbit size of both antiarch and arthrodires. Large orbits in adults, such as seen in the camuripiscids from Gogo are considered paedomorphic. Both antiarchs and coccosteomorphs show lengthwise growth before an increase in width. In *Bothriolepis* and coccosteomorph arthrodires breadthwise growth of the anterior median ventral plates results in the widening of the trunk shield in adults compared to juveniles and subadults. An evolutionary trend in placoderms, and considered a paedomorphic

characteristic, is a shortening of the trunk shield. Studies on arthrodires from the Gogo Formation show that dissociated heterochrony (Trinajstić and McNamara 1999), where both paedomorphic and perimorphic changes occur simultaneously in the one organism, are important for evolutionary change. Perimorphic changes in the rostral plate, the most anterior plate of the head shield in the camuropiscids, has resulted in an elongation of this plate with the most derived members possessing an anteriorly extending tubular rostral plate. The ancestral condition being a T-shaped rostral flush with the pre-orbital plates at the front of the skull roof. Dissociated heterochrony means that each plate could follow its own ontogenetic trajectory resulting in a wide range of body architectures which natural selection could act on. The diversity and disparity of body shapes suggests that heterochrony had a significant effect in the evolution of placoderm morphologies.

## Habitat

During the Devonian, placoderms were the dominant jawed vertebrates, reaching their maximum diversity in the Frasnian stage with the early Devonian representing the first major radiation of jawed vertebrates. Placoderm fossils are known from all aquatic environments and were the first jawed vertebrates to inhabit freshwater systems and open marine waters.

The majority of arthrodires were marine dwellers, had streamline body forms, and were mostly active predators functioning in the nektonic zone. Like modern ecosystems, where faunal diversity is highest in equatorial regions, the most diverse placoderm faunas are from tropical reefs formed at low palaeolatitudes. Faunas from Burranjuk, New South Wales, and Gogo, Western Australia; Australia represent some of the most diverse faunas known in the Devonian. The smaller arthrodires, such as *Compagopsicis* and *Incisoscutum* are found in large numbers suggesting that they formed schools. Other coccosteomorph arthrodires such as *Tubonasmus* and *Rolfosteus* from the Gogo Reefs in Western Australia had compressiform body, adapted for

quick bursts of speed over short distances between the stromatolites and stromatoporoids which comprised the Gogo Reef margins.

Some of the larger arthrodires such as *Eastmanosteus* and *Dunkleosteus* had an extensive adaptive range across tropical and temperate waters. The fusiform body shape represented an adaptation for fast swimming in open pelagic water. These fish were suited to wide dispersal with fossils from these genera known through North America and across the Middle East and North Africa.

Ptyctodonts were also marine dwellers with a globiform body shape which, coupled with their large eyes and thin scleral plates, are indicative of them being slow moving, deep water inhabitants. Low numbers of ptyctodont fossils compared with arthrodires from the same horizons suggest these were more solitary fishes.

The estuarine Miguasha fauna from Quebec is dominated by *Bothriolepis* with only a single genus of arthrodire recovered (Cloutier et al. 2009). Large numbers of *Bothriolepis* also occur in Canowindra, Australia (Johanson 1998), in association with only two other placoderm genera, *Remingolepis* and *Groenlandaspis*. The environment these fossils were recovered from is interpreted as a shallow, freshwater pool, which had dried up. *Bothriolepis* was interpreted as a fresh water fish; however, its presence in the estuarine sediments such as Miguasha and the cold water Witpoort Formation in South Africa, indicated that *Bothriolepis* was anadromous, living their adult life in marine waters and returning to freshwater habitat to breed. However, ontogenetic series of *Bothriolepis* are known from the fully marine Gogo Formation and a mass mortality nursery site from an estuarine environment in the Catskill Formation of North America (Downs et al. 2011). A high paleolatitude nursery site, also interpreted as estuarine and containing fossils of *Bothriolepis* hatchlings, occurs in the Witpoort Formation in South Africa. The occurrence of both hatchlings and juveniles in marine and estuarine environments does not support an anadromous life history strategy for *Bothriolepis*.

Reference to different body morphologies can permit inferences regarding different

locomotor styles present in placoderms (Young 2010). The dorsoventrally flattened body shape, the terminal mouth and anterodorsal eyes of the antiarchs, rhenanids, phyllolepid and petalichthyids indicated that these were bottom dwellers. The rhenanids had enlarged, semicircular ray-like pectoral fins which, and they either undulated or oscillated to achieve propulsion. Phyllolepid arthrodires are found predominantly in low energy freshwater and/or fluvial systems, although there is evidence of them inhabiting estuarine conditions. Although dorsoventrally flattened, it is thought that these fishes were ambush predators, using their long tail to gain rapid burst of speed to capture and swallow prey whole.

## Conclusion

Placoderms were the dominant jawed vertebrates for over 70 million years. They showed both species diversity and morphological disparity, which indicates a great diversity of ecological niche occupation and life history strategies. Historically most placoderms were considered to be slow moving benthic organisms, but re-evaluation of their biomechanics instead reveals that placoderms had diverse modes of life with the most diverse taxa; the arthrodires interpreted as nektonic inhabiting predators.

## Cross-References

### ► Placoderm Morphology

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## Placoderm Morphology

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### Synonyms

[Armoured fish](#)

### Definition

Extinct jawed fish in which the head and thorax were covered by bony plates.

### Introduction

Placoderms were a diverse class of armoured fishes, which are thought to have had their origin in the Ordovician Period (~485MYA), although the first fossils are from the Silurian Period (~443.8 MYA). Maximum diversity was reached during the Devonian, when they dominated the earth's aquatic habitats (fresh, estuarine, and marine waters). The Devonian mass extinction event resulted in a great reduction in the diversity of placoderms, although there was some diversification in fresh water forms; however, the reprieve was short lived and all placoderms were extinct by the end of the Devonian Period (~358.9MYA) (Janvier 1996; Young 2010).

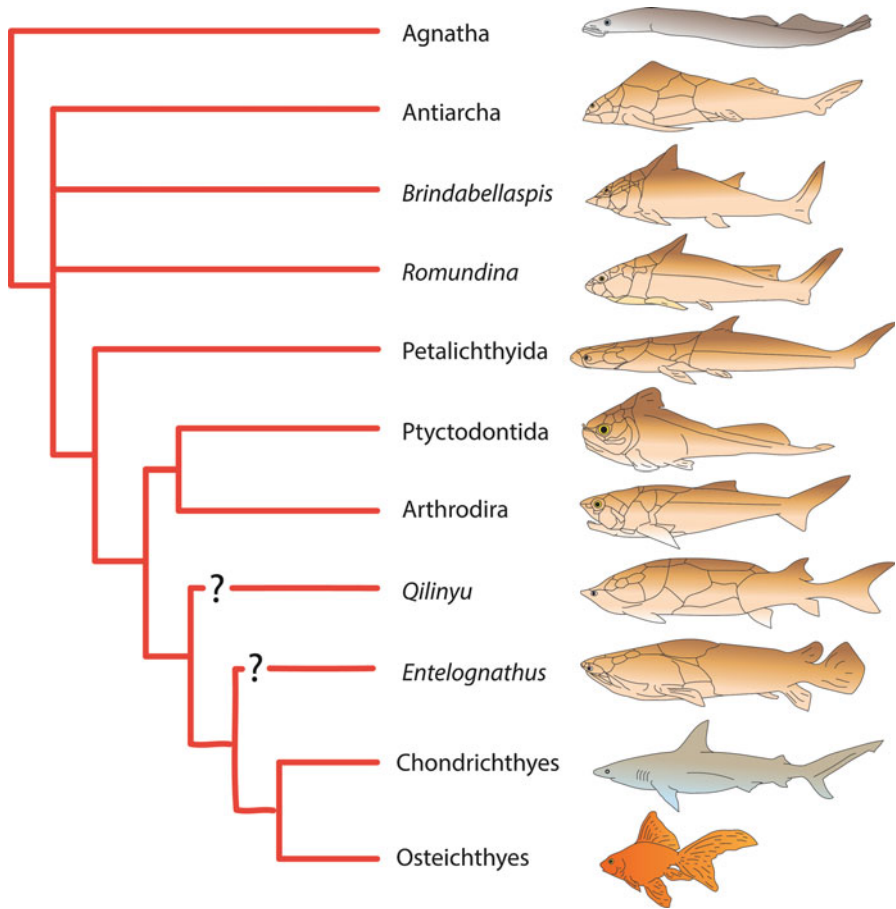
The placoderms are the earliest gnathostomes (jawed vertebrates) and are placed at the top of the gnathostome stem, as the sister group

to all other gnathostomes. However, whether placoderms are monophyletic or paraphyletic remains contentious. The most recent phylogenetic hypothesis support placoderms as a monophyletic class comprising eight established orders: Antiarchi, Petalichthyida, Phyllolepidi, Ptyctodontida, Brindabellaspida, Rhenanida, Acanthostroaci, and Arthrodira (Qiao et al. 2016; Fig. 1). The inclusion of another two orders, Stensioellida and Pseudopetalichthyida, within the class remains problematic. The Silurian placoderms *Entelognathus* and *Qilinyu* from China are classed as order *incertae sedis* having some features of primitive placoderms while possessing an osteichthyan type jaw (Zhu et al. 2013, 2016). Placoderms are informative to the study of jawed vertebrate evolution, showing that extant-jawed vertebrates exhibit a mosaic of primitive and derived characters.

### External Morphology

Placoderms are characterised by having the head and thorax covered by bony plates (Fig. 2) and, in some taxa, the posterior section of the body and tail were covered in scales. The robust nature and excellent preservation of the dermal plates means that the shape of the head and thoracic regions is well known for all placoderm taxa, which show a great diversity of body shapes. The antiarchs, rhenanids, phyllolepidi, and petalichthyids are characterized by being dorsoventrally flattened, whereas the Ptyctodontida have a globiform shape and Brindabellaspida, Acanthostroaci, and Arthrodira species vary between dorsoventrally flattened, compressiform, and fusiform (Young 2010).

Placoderms possess paired pectoral and pelvic fins with girdles, although some taxa have lost their pelvic fins. A short-based fin with narrow articulation appears to be the ancestral condition in placoderms for both the pectoral and pelvic fins. In the more advanced arthrodirids, the fin base has extended and a wide-based fin which is multibasal is present. There is single dorsal fin in antiarchs and arthrodirids and two dorsal fins in ptyctodonts



**Placoderm Morphology, Fig. 1** Placoderm phylogeny showing the relationships between placoderm groups and other gnathostomes. (Adapted from Long et al. 2015; Qiao et al. 2016)

whereas the dorsal fin has been lost in rhenanids. The tail, when known, is epicercal.

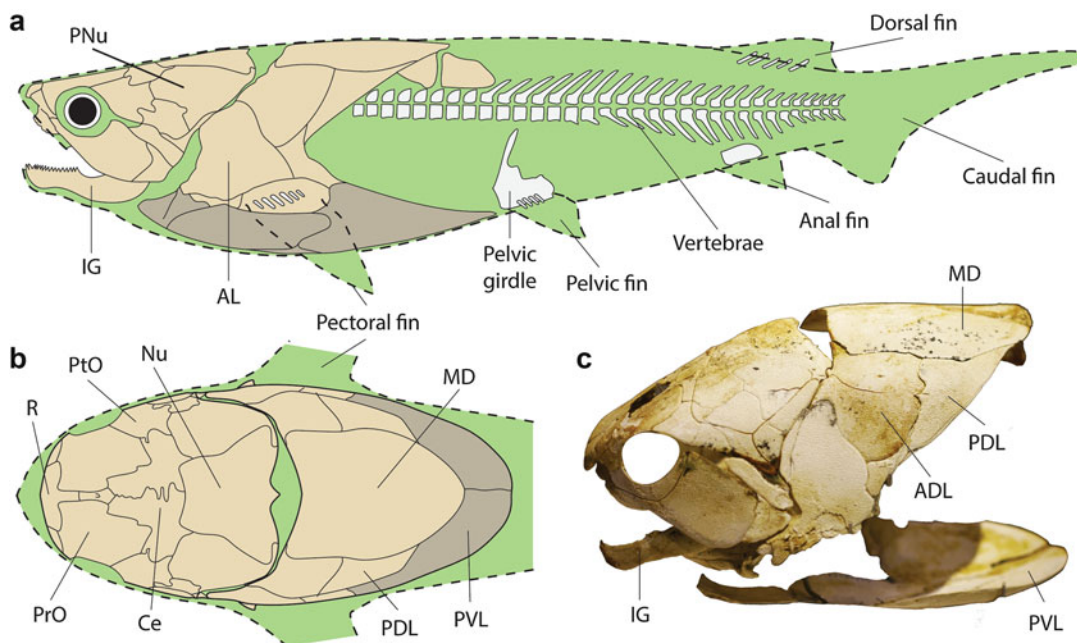
**Dermal Skeleton**

All placoderms have the head and thorax covered in plates of dermal bone (Fig. 2), which in life were thought to be covered in skin (Fig. 3). The dermal plates of the head shield comprise the skull roof, which was fused to the top of the braincase, and the cheek unit, which posteriorly covered the gill chamber and functioned as an operculum. The jaw cartilages attached to the cheek plates. A dermal neck joint connected the head and trunk shields. The trunk shield encircled the anterior portion of the body and in some forms

enclosed the pectoral fin. In more primitive taxa, external dermal plates form part of the pelvic girdle, separate from and posterior to the thoracic armour. In some species, fin spines are present in front of the pectoral and dorsal fins (Young 2010).

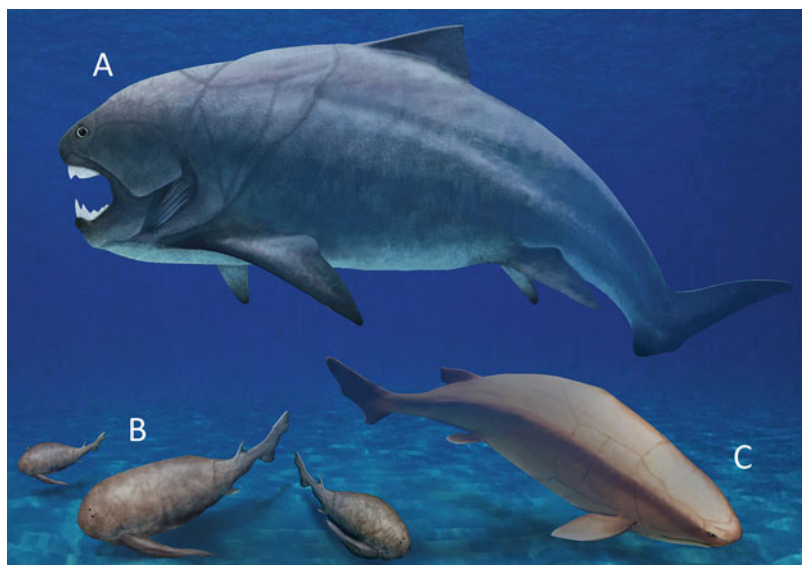
The dermal bone that made up the armour comprised three highly vascularized layers: a superficial lamellar layer, a spongy cancellous layer, and a compact basal layer of lamellar bone (Giles et al. 2013). Embryos show that a base of lamellar bone was laid down first and then an open weave network of spongy bone was deposited over the base. The outer layer is often ornamented, with a series of ridges and/or tubercles made of semidentine. The dermal bone bore the sensory line system housed in open grooves or pits on the surface of the bone.





**Placoderm Morphology, Fig. 2** Simplified placoderm morphology based on Arthrodire placoderms. Arthrodire placoderm in lateral (a) and visteral (b) views highlighting basic internal and external morphology. (Adapted from Dennis-Bryan 1987; Trinajstić et al. 2013); b, photograph of the articulated dermal armor of *Eastmanosteus*

*calliaspis*. Abbreviations: ADL, Anterior dorsolateral plate; Ce, central plate; IG, infragnathal bone; MD, median dorsal plate; Nu, nuchal plate; PDL, posterior dorsolateral plate; PNu, paranuchal plate; PrO, preorbital plate; PtO, postorbital plate; PVL, posterior ventrolateral plate; R, rostral plate



**Placoderm Morphology, Fig. 3** Reconstructions of placoderms including; (a) *Dunkleosteus*; (b) *Bothriolepis*; (c) *Entelognathus*

## Internal Axial Skeleton

The internal skeleton, where known, comprises an external layer of perichondral bone with a cartilaginous core (Janvier 1996). The thinly laminated acellular bone that lines the braincase and nerve canals in primitive placoderms is entirely formed of cartilage in the later placoderms from the Gogo Formation. The placoderm vertebral column comprises separate neural and haemal arches comprising an external layer of perichondral bone surrounding a cartilage core and is the earliest example of a specialized vertebral column in gnathostomes. The anterior portion of the column comprises a series of fused anterior vertebrae, the synarcual, and separate thoracic, abdominal, and caudal vertebrae. The vertebrae under the median dorsal plate do not have neural or haemal spines developed; the haemal spine develops only in more posterior vertebrae; however, neural spines first develop in vertebrae posterior to the median dorsal plate. At the level of the anal fin, the haemal spine is reduced.

## Jaws and Teeth

Within placoderms, the palatoquadrate forms the upper part of the mandibular arch and the Meckels cartilage the lower part (Young 1984). The palatoquadrate is fused to the dermal bones of the cheek, which supports for the jaw articulation along with articulation to the ethmoid ossification of the braincase. In primitive placoderms, the palatoquadrate comprises a single unit, whereas in ptyctodonts, there are three perichondrally ossified elements: the autopalatine, quadrate, and metaterygoid. Placoderms possess two sets of upper tooth plates, the anterior and posterior supragnathals, and a single lower tooth plate, the inferognathal. The anterior supragnathal attaches to ventral surface of the ethmosphenoid regions of the braincase and the posterior supragnathal to the autopalatine. The inferognathal is divided into two sections: the anterior a biting division and the posterior blade. The blade has a groove on the ventral surface where the Meckles cartilage inserts into the inferognathal. The hyoid arch is

less well known as it is rarely preserved. A separate hyomandibular and opercular cartilage has been reported in ptyctodonts and arthrodires (Trinajstić et al. 2012), but the presence of a separate hyomandibular remains contentious. Due to lack of preservation, little is known of the gill arch series posterior to the hyoid arch.

Placoderms have long been considered to lack true teeth; instead, the bony toothplates were considered the wear into shearing blades or grow bony projections that functioned as biting components. The presence of dentine, a dental tissue, has been confirmed in the cusps on the inferognathal in arthrodire placoderms, which also exhibit successional replacement. Further research using synchrotron scanning has revealed, in addition to dentine, the presence of pulp and looped vasculature in teeth of arthrodires thereby confirming the presence of true teeth (Rücklin et al. 2012). The youngest teeth have dentine and an open pulp canal, whereas older teeth are infilled with bone. Placoderm teeth lack a hypermineralized cap common to crown group gnathostome, but it cannot be determined if this is a primitive or derived character state.

## Braincase

All extant vertebrates have a single, fused braincase; however, this is not the case for all placoderms (Young 1986). The braincase in ptyctodonts comprises three (from anterior to posterior) separate units: the ethmoid, orbital, and occipital ossifications, with the ethmoid ossification being the longest of the ossifications (Trinajstić et al. 2012). The general shape of the placoderm braincase is broad and flat. A separate nasal capsule is a primitive character for placoderms and for all jawed vertebrates. A significant reorganization of the head occurs between jawless and jawed fishes. Primitive placoderms such as the antiarchs *Romundina* and *Brindabellaspis* have a short frontal region of the braincase, more similar to the proportions seen in jawless fish, thus placoderms serve to bridge a gap between jawless fishes and crown group gnathostomes in terms of the evolution of the brain anatomy. These early

placoderms also share the character of an upper lip that protrudes well in front of the nasal sacs, also characteristic of the jawless lamprey and osteostracans (Dupret et al. 2014). The early arthrodires provide most of the information known for placoderm braincase morphology as there was extensive perichondral ossification of the braincase, with some of the internal cavities lined with bone, indicating the path of the nerves and vessels. Comparison of the nerve canal lengths between arthrodires and jawless fish shows that arthrodires had much longer nerves suggesting that myelin, a fatty substance used to conduct nerve signals, evolved at the base of the gnathostome stem (Zalc et al. 2007). The optic fissure separates the rostral capsule from the rest of the braincase. The labyrinth cavity of the inner ear is fully enclosed within the braincase and like living jawed vertebrates there are three semicircular canals.

In some placoderms, the sclerotic capsular is perichondrally ossified and muscle scars indicate that the arrangement of the six extraocular eye muscles, which formed antagonistic pairs to move the eyeball (Young 2008; Young et al. 2001). The eyeball is connected to the braincase by a cartilaginous eyestalk, the opening for which is identified behind the optic nerve opening. The orbit is surrounded by five dermal plates, which make up the sclerotic ring.

## Reproductive Structures

Placoderms are sexually dimorphic with many males possessing intromittent elements whereas only the females of more primitive placoderms possessing basal plates. Within the placoderms, the males of three orders (antiarchs, ptyctodonts, and arthrodires) possess an intromittent organ, an external structure used for the transfer of sperm during copulation (Long et al. 2015). These reproductive elements are independent of the pelvic fins (Trinajstić et al. 2015). The presence of intromittent organs indicates that these placoderms reproduced through internal fertilization. In the antiarch *Microbrachus dickii*, as well as all ptyctodonts, the intromittent structures comprise a sheath of external dermal bone with a deep

groove, which may have housed a structure for sperm transfer. The terminal ends of the claspers are often covered in dermal spikes or hooks. Male ptyctodonts also possess paired post-pelvic plates, but these are smaller and flatter than those of females. The intromittent structure of coccosteomorph arthrodires in contrast have an internal support of dermal and perichondral bone, the terminal tip having a small number of dermal denticles.

Within females, external reproductive structures are known for antiarchs and ptyctodonts but not for arthrodires (Long et al. 2015). In female ptyctodonts, paired post pelvic dermal plates curve around the contour of the body; the dermal bone is often ornament with a series of ridges. In one ptyctodont species, *Rhamphodopsis*, females have scales over the pelvic fins, which the males lack. The post pelvic plates were originally thought to have attached to the pelvic fins, but recent work using high resolution microscopy has shown they were separate elements (Trinajstić et al. 2015).

## Musculature

Several regions of life position, three-dimensionally preserved musculature is preserved in some arthrodires is from the Gogo Formation (Trinajstić et al. 2013). The musculature spanning the nuchal gap comprises: large medial paired *capitis* major muscles and smaller lateral *capitis* minor muscles, which functioned as head elevators. The *cucullaris* muscle extends from the base of the skull roof with the origin in the *cucullaris* fossa on the visceral surface of the paranuchal plate and extends onto the upper portion of the anterior dorsolateral plate. Unlike the condition in sharks, where the *cucullaris* muscle functions as a pectoral fin elevator, the *cucullaris* muscle in placoderm functioned as a head depressor. The presence of the *cucullaris* muscle in placoderms represents the phylogenetically oldest occurrence of this muscle, common to all jawed vertebrates. Other cranial muscles that are not as well preserved include the dorsal branchial constrictor muscle, positioned lateral to the *cucullaris* muscle, and the *levator arcus palatini*, a muscle

involved in expanding the mouth cavity for feeding, attached to the postocular process. The preservation of the dermal cheek unit in placoderms, and the perichondral ossification of the quadrate, allow the reconstruction of the adductor muscles, which passed from the lateral side of the Meckels cartilage to the mesial side of the palatoquadrate, a unique condition amongst gnathostomes.

Although the ventral neck musculature is incompletely preserved, synchrotron scans of the shoulder girdle in an arthrodire have revealed the fibers of Sharpey, which indicate where tendons attach muscle to bone. The ventral gill arch depressing muscles in placoderms originate on the interolateral plate (=clavicle). Three separate attachment points on the interolateral plate have been determined to indicate the presence of the *coroacohyoideus*, *coroacoarcularis*, and *coroacomandibularis* muscles between the interolateral plate and lower jaw (Sanchez et al. 2013).

The lateral body musculature is characterized by a metameric arrangement along the length of the long axis of the body, much like in extant fishes. Each vertebra has a short muscle that terminates at the midline of the adjacent vertebra. The architecture of the ventral abdominal muscles, however, is unique for fishes having two anterioposteriorly elongated muscle bands with transversely orientated fibers. The function of these muscles is not fully understood; however the unique presence of claspers, separated from the pelvic fins, and possessing a girdle may have required a unique set of muscles to manipulate them. Another possibility is that these muscles may help resist shear forces between the body armour and the body during swimming.

## Organ Systems

In rare specimens of antiarchs and arthrodires, parts of the soft anatomy are preserved. The infill of the gut indicates that a spiral valve was present and appears to be a primitive characteristic of the vertebrates. Traces of blood vessels can be determined on the trunk armour of *Bothriolepis canadensis*. Although now refuted (Goujet

2011), this vasculature was once interpreted to be associated with lung development.

## Placoderm Classes

### Antiarchs

Antiarchs are second only to arthrodires in terms of species diversity and are perhaps the strangest of the placoderm taxa in terms of body shape. They are also the longest ranging of the placoderms with a continuous record in China from the Silurian to the end Famennian. In east, Gondwana antiarchs range from the Early Devonian and were mostly restricted in Laurussia with the earliest antiarchs not known until the mid-Devonian. This biogeographic difference in the stratigraphic occurrence suggests the origin of the antiarchs is China. Antiarchs are dorsoventrally flattened, the eyes, nares (nasal openings), and pineal opening all occur within the orbital fenestra towards the top of the head. The head shield is closely attached to the trunk shield with the condyles on the paranuchal plate and the fossa on the anterior dorsolateral plate. The body armour comprises two median dorsal plates that extend along the trunk and cover the pectoral fins. The pectoral fins are highly modified; have mid-point ball and socket joint, and a complex specialized joint where the fin joins the pectoral girdle. Primitive antiarchs have short, thick pectoral fins with the body covered in scales whereas in more derived antiarchs the pectoral fins are elongate, and the tail is scaleless. Pelvic fins and a dermal pelvic girdle are known only in the most primitive antiarch *Parayunnanolepis* and are lost in more advanced taxa. Prior to the discovery of *Parayunnanolepis*, it was thought that antiarchs primitively lacked paired pelvic fins. The small eyes and nares occupy a dorsal position in a key-hole shaped opening; the mouth is ventral with highly modified jaws which lack a supragathal and instead the edge of suborbital plate occludes with the inferognathal.

Recent finds of the best-known antiarch, *Bothriolepis*, with the soft anatomy of the tail preserved, show a single, square-shaped dorsal fin, posterior to trunk. Earlier reconstructions

erroneously depict two ovoid-shaped dorsal fins. The shape of the body posterior to the trunk armour is preserved in several specimens. In specimens where the posterior body and tail is covered in scales, the body is stout and tapers to form an epicercal tail whereas in specimens without scales the body tapers to a long whip-like tail.

Males of one species, *Microbrachius dicki*, are known to possess intromittent elements used to introduce sperm into the female (Long et al. 2015). These occur posterior to the thoracic armour and independent of the pelvic fin, which is lost in *Microbrachius*. The intermittent elements vary considerably in size suggesting that they do not appear until sexual maturity has been reached and continue to grow after the body armour has obtained maximum size.

#### **Petalichthyida, Brindabellaspida, and Acanthothoracida**

Outside the antiarchs, the Petalichthyida, Brindabellaspida, Acanthothoracida, Rhenanida, and Ptyctodontida form the non-arthrodire placoderm groups. The relationships of the Brindabellaspida and Acanthothoracida to the antiarchs and other placoderms is not resolved; however, they are considered more primitive than the Rhenanida and Ptyctodontida with the Arthrodire resolved as the most crownward of the Placoderms (King et al. 2016). Petalichthyids have X-shaped sensory line canals on the inner surface of the nuchal plate (also present in ptyctodonts) and two pairs of paranuchal plates (also present in acanthothoracids). They occur in late Silurian rocks in China but have a global range from the early Devonian. The Brindabellaspida are endemic to the early Devonian of eastern Australia. The anterior of the skull is characterized by an elongated rostrum, posteriorly placed orbits, and the unique character of having the nasal capsule housed within the orbit. There is a great deal of intraspecific variation between individuals. The unique morphology of *Brindabellaspis* indicates a specialized ecological niche. The dorsal position of the eye indicates a benthic habitat and the long rostrum with a specialized sensory system, possibly capable of electroreception, could have functioned in the

detection of benthic prey (King et al. 2018). The acanthothoracids are a little-known group due to the generally poor preservation and scarcity of remains. The exception is *Romundina*, which is known from multiple 3D preserved specimens. Re-examination of acanthothoracid collections from the Prague Basin in the Czech Republic have yielded more information, showing them to have a greater diversity than previously thought. The acanthothoracid have a partly tessellated skull-roof and the sensory line canals that run between the plates, rather than through the bone as in other placoderms. They have evolved a flattened body shape, dorsal eyes, and large pectoral fins similar to modern rays and represent the first jawed vertebrates to take up this body morph. The rhenanids differ from other placoderms in that they are covered by unfused platelets with the spaces between the platelets filled by tesserae, which sometime overlay the platelets. The tail and body are covered in scales. The reduction in the size of dermal plates that make up the head and thoracic shields was originally considered to indicate the primitive nature of the rhenanids, but more recently this reduction is considered to be a derived state. The Rhenanida show low species diversity compared with other placoderms and are known from the Early Devonian to the Upper Frasnian.

#### **Ptyctodonts**

The most common fossil remains from ptyctodonts are toothplates, which are known globally throughout Devonian aged rocks. Although body fossils are rare, excellent preservation has yielded a great deal of morphological information. Ptyctodonts are characterized by a reduction in the armour with a number of the dermal plates of the head and trunk shield lost. This frees up the posterior part of the body for increased swimming ability. Ptyctodonts have large eyes, one set of upper (the anterior superognathals are lost) and lower tooth-plates and are the only placoderms known with preserved labial cartilages. Anteriorly Ptyctodonts all have a deep body, one to two dorsal fins, and a long whip like tail. In one taxon, *Campbellodus*, the body and tail are covered in large, oblong scales, which is



considered primitive for this group. The shoulder girdle and pelvic girdle comprise external dermal plates and internal perichondral elements. Both the pectoral and pelvic fins were wide based with two to three basals.

### Arthrodira

The arthrodira are the most speciose and diverse group within the placoderms and are known globally from the early Devonian to the end Famennian. There are reports of earlier (Silurian) occurrences of arthrodira in China but the identification of these taxa as true arthrodira is controversial. Arthrodira are characterized by possessing a specialized moveable neck joint between the head and trunk armours with the condyle present on the anterior dorsolateral plates and the fossa on the paranuchal plate. The excellent preservation of some specimens has provided a wealth of information for both their external and internal morphology. The arthrodira are divided into a number of subgroups.

The Phyllolepidi are characterized by a rounded flat skull with radiating sensory canals. The lack of orbital embayments lead to the suggestion these placoderms were blind (Long 1984). The nuchal plate is elongate and the tail is proportionally long. Their occurrence is restricted to east Gondwana throughout the Devonian. It was only after the Frasnian/Famennian mass extinction event that the phyllolepidi reached their maximum diversity with their biogeographic range extending into Laurussia.

*Groenlandaspis*, so called because it was first found in Greenland, is now found globally and belongs to phlyctaenid subgroup of arthrodira. These arthrodira are characterized by having a high, spine-like median dorsal plate. Specimens of *Africanaspis* have, in addition to the head and thoracic armour preserved, impressions of the body, tail, and fin outlines. This provides an excellent example of the external morphology, showing a short deep body that tapers caudally to form a long whip like tail and a short-wide pectoral fin positioned behind a long serrated spinal plate (Gess and Trinajstić 2017).

Nearly 60% of known arthrodira are eubrachythoracid arthrodira (Young 2004).

They are characterized by shortened body armour connected to the head shield by a lateral ball and socket joint, and in the more derived arthrodira, the pectoral fin is no longer enclosed by the trunk armour and the spinal plate is lost. These modifications are thought to have increased swimming speed and manoeuvrability. The eyes occur further back in the head shield than in earlier groups, where they are set more anteriorly, and the inferognathal comprises an anterior biting division and a posterior blade.

*Coccosteus* from the Old Red Sandstone is often used as the archetypal arthrodire. It is known throughout Europe, North America, and the United Kingdom and is very common in early to mid-Devonian rocks. It has a characteristic arrangement of head shield plates and reduced body armour, the trunk armour encloses the base of the pectoral fin, and there is a spinal plate. The posterior skeleton of *Coccosteus* is known and shows an unrestricted notochord, with paired neural and haemal vertebral elements. *Coccosteus* was an active predator; jaw opening was achieved by moving the head upwards thereby dropping the lower jaws. The distance between the posterior margin of the nuchal plates and the anterior margin of the median dorsal plate, the nuchal gap, determined the gape in the eubrachythoracid arthrodira. Although most arthrodira were between 20 and 50 cm in length, some such as *Titanichthys* are estimated to have reached up to 7 m in length.

### Entelognathus

The position of *Entelognathus* and other maxillate placoderms from the Silurian of China is unresolved. Recent phylogenetic analysis has concluded that most of the uncertainty around relationships at the base of gnathostome tree can be attributed to the maxillate placoderms (King et al. 2016). These placoderms lack the joint between the head and trunk armour and thus the nuchal gap. The trunk armour is elongate, extensively covering the trunk region of the animal. The gnathal plates comprise the maxilla,

premaxilla, and dentary and the adductor muscle both on the lateral and medial side of the palatoquadrate (Zhu et al. 2013). A condition intermediate with crown gnathostome in which the adductor muscle is lateral to the palatoquadrate and other placoderms, the adductor muscle is medial to the jaw.

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## Placodermi Diet

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## Synonyms

[Armored fish](#)

## Definition

Placoderm diet describes the food consumed for species within the order Placodermi, which includes antiarchs, ptyctodonts, and arthrodires.

## Introduction

There are few cases where the diet of placoderms can be observed directly from preserved stomach contents. Most inferences about diet are made from the type of tooth plates present, calculations of gape and bite force, and body morphology. In addition, the fauna associated with the placoderms can provide information of the food sources available.

The antiarch placoderms (Fig. 1a) are interpreted as being benthophagous. Direct evidence from the gut contents of *Bothriolepis canadensis* from the Escuminac Formation, Canada shows that it fed at on the conchostracan *Asmusia membranacea*. Juvenile specimens of actinolepids have been recovered from Lode Quarry in Latvia with stomachs filled with these small crustaceans, supporting them as secondary consumers (Upeniec 2001). This differs from earlier

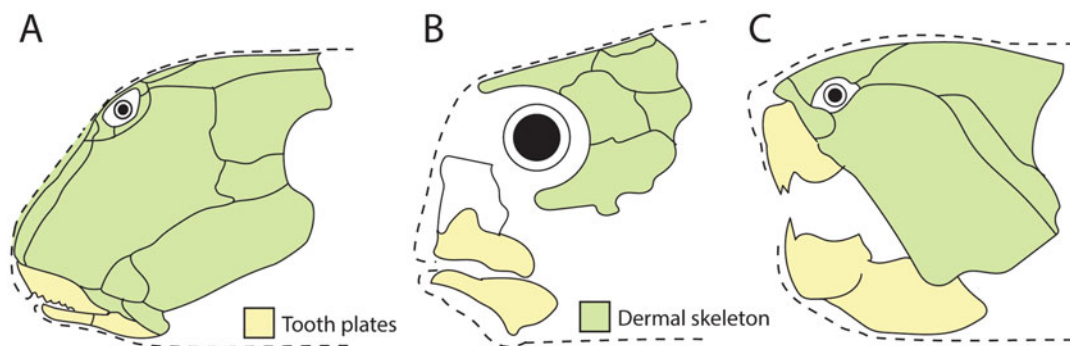
interpretations where sediment infill preserving the gut of *Bothriolepis* was interpreted as indicative of these fishes being detritivores, feeding on the substratum associated with plants.

All known Ptyctodont fishes have either durophagous (crushing) or sectorial tooth plates (Fig. 1b), and so the diet is considered as either hard-shelled organisms for the former and soft organisms for the latter. All complete Ptyctodonts known were around 20 cm in length with a small gape, estimated to be only able to take prey with an upper size range of 2–3 cm. Only one ptyctodont from the Gogo Formation (*Austroptyctodus*) has been recovered with stomach contents and these comprise the carapace of ostracods, small crustaceans that make up a component of the zooplankton. Other prey that durophagous ptyctodonts could have fed on, include brachiopods, crinoids, and ammonoids – all of which are found in the same environment as ptyctodonts.

Arthrodires were the most diverse group of placoderms and as such exhibited diverse feeding strategies and diets (Anderson and Westneat 2009). Studies on the jaw mechanics (Anderson 2009) divided arthrodires into three main feeding groups: crushers/chompers, generalists, as well as biters and graspers. Examination of the tooth plates adds another feeding group, the filter-feeding planktivores.

*Holonema* is one of the more perplexing arthrodire fishes, with strange, ridged tooth plates. *Holonema* may have been a filter feeder using the ridged tooth plates to filter zooplankton from the water. However, one specimen from the Gogo Formation has been recovered with stones in the gut region, possibly gastroliths for breaking up oncoids (Miles 1971). Some large arthrodires such as *Homosteus* and *Titanichthyes*, which reached 10 m in length, are also thought to have been a planktivores based on the long thin inferognathals (lower tooth plates).

The combination of shearing bladed teeth (Fig. 1c) a fast opening action of the jaws and a bite strength calculated as stronger than that of the dinosaur *Tyrannosaurus rex* when closing the jaw, and with an estimated maximum size of 6 m, indicates that *Dunkleosteus* was one of apex



**Placodermi Diet, Fig. 1** Examples of tooth plate morphologies found in antiarch, ptyctodont, and arthrodire placoderms. (a) Reconstruction of *Bothriolepis* (after Young and Zhang 1996); (b) sectorial tooth plates present

in Ptyctodonts such as *Kimbryanodus* (after Trinajstić and Long 2009); (c) large shearing bladed tooth plates of the arthrodire *Dunkleosteus*

predators of the Late Devonian (Anderson 2009). No stomach contents are known, but teeth from a shark *Orodus* have been found associated with *Dunkleosteus*, which have been interpreted as stomach contents (Carr and Jackson 2010). The majority of fishes from the Cleveland shale fit into the choppers and crushers feeding guild. Faunal analyses of the fossils from the Cleveland Shale indicate that most taxa were piscivores, with the prey determined by the gape of the mouth. Fossilized concretions comprising fish bones are thought to have been regurgitated by arthrodire and support this piscivorous diet (Anderson 2008). The placoderm *Holdenius*, from the Cleveland Shale, was found with a ctenacanthid shark spine imbedded in its braincase and has been interpreted that the spine penetrated the skull roof as the placoderm attempted to consume it. Some arthrodire from the Gogo Formation also fit within this feeding guild. *Eastmanosteus*, although smaller in size than *Dunkleosteus*, at a maximum size of approximately 1.5 m is the largest placoderm from the Gogo Formation and with similar shaped teeth and jaw proportions is also interpreted as a piscivore predator. Another arthrodire from Russia has been found with a ptyctodont (*Ctenurella*) within the stomach region supporting the interpretation. Arthrodire within the chopper and crushers feeding guild also include species with a durophagous dentition. The toothplate are broad and the blade of the lower jaw is deep, allowing a strong bite force to penetrate hard outer shells or armor. The dome-shaped

teeth that cover the upper tooth plates and the broad lower toothplate in *Bullerichthyes* would have acted like a mortar and pestle to grind up hard prey items before swallowing.

A large number of arthrodire fall into the biters; these are generally smaller arthrodire, up to 30 cm in length, and have small sharp teeth along the upper and lower tooth plates. Analyses of the jaw mechanics indicates arthrodire jaws acted in a scissor like-cutting fashion (Anderson and Westneat 2009). Bite marks on crinoid ossicles from Poland match the tooth plates of coccosteid arthrodire. Stomach contents of *Coccosteus cuspidatus* contain the remains of acathodians and lungfish bones. These smaller placoderms probably fed on free swimming arthropods, ammonoids, and other fishes including smaller placoderms. Some coccosteid type placoderms were originally thought to have been cannibalistic, with young of the same species found in the abdominal cavities; however, it is now known that these represented embryos, yet to be born (Long et al. 2009).

A final group among the arthrodire was the pickers and graspers. These fish have rather weak jaws with little mechanical advantage; the lower tooth plates are slender and lack teeth. Arthrodire such as *Latocamurus* and *Tubonasus* fit within these groups of small, approximately 10 cm long, predatory rapid biters. Their prey were likely small free-swimming, soft organisms that required little processing, being swallowed whole. Not all dorsoventrally flattened fish are

benthic feeders. The very long tail found in the phyllolepis suggests that *Cowralepis* was an ambush predator. The structure of the gill arches shows that a buccal pump mechanism allowed for forcing whole prey within the mouth, probably to be swallowed whole.

Little is known about the diet of the other classes of placoderms, especially in taxa in which tooth plates are not known. The long snouted brindabellaspids are thought to have used electroreception to find prey in the bottom sediments (King et al. 2018), but it is not known if this was hard or soft infauna. The large number of placoderms living in freshwater environments towards the end of the Devonian Period suggests at least some of these were plant eaters but until further evidence is recovered in terms of well-preserved tooth plates or stomach contents the diets of most placoderms will remain unknown. Despite this, placoderms evolved a number of different tooth types and body types to take advantage of different prey items available and divide their environment into specialized feeding niches (Anderson 2008).

## Cross-References

### ► Placoderm Morphology

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## Placodermi Locomotion

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## Synonyms

Armored fish locomotion

## Definition

Movement used by armored fish to traverse their environment.



Placodermi is comprised of an extinct group of primitive jawed fishes that existed primarily throughout the Devonian Period (416 million–359 million years ago) (Young 2010). As a highly diverse fish group, placoderms were found in many freshwater and marine environments on every continent except South America. The Placodermi receive their name from their characteristic dermal skeleton which formed a head and thoracic shield, allowing them to survive and flourish as into the dominant vertebrates of the time. Over 200 genera of Placoderms evolved between the early Silurian and the end of the Devonian, with the vast majority restricted to the Devonian period. It should be noted that there is considerable debate regarding the phylogenetic relatedness of the placoderms. The earliest were equipped with bony armor plates and adapted to bottom dwelling conditions (Young 2010). Other forms became specialized for fast swimming, traversing open seas. Despite their well-equipped armor and success during the Devonian period, these jawed vertebrates were eliminated during the mass Devonian extinction event.

Nine placoderm subgroups have been identified through observation of skull patterns and morphological features (Young 2010). This chapter will focus on the primary groups and their modes of locomotion. The arthrodires, a major group of the Placodermi, flourished during the Devonian period in various marine environments. They were distinguished by pairs of plates extending from their upper jaw, and a movable joint between the head and body armor (Ferrón et al. 2017). This group produced some of the largest predators of the time such as *Dunkleosteus*, which could measure up to 8 m in length. Most arthrodires were heavily armored and bottom-dwelling with a few evolving into adept swimmers.

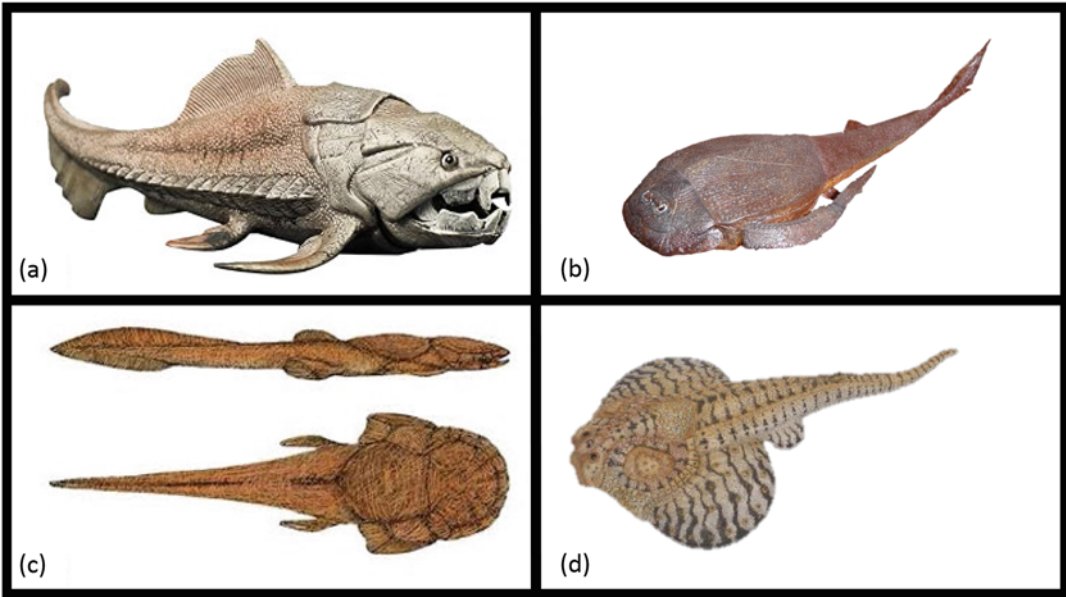
Antiarchi were some of the first discovered Placoderms described in 1839 and originally thought to be the remains of tortoises (Young 2010). *Pteryichthyodes* and *Bothriolepis* are two well-known members of this group. Antiarchs were widely spread during the Middle to Late

Devonian. They are best described by their stout thoracic dermal armor and uniquely jointed pectoral fin, encased in armor. Though the purpose of the armored pectoral fin is not certain, Antiarchi were thought to be bottom-dwelling organisms.

Phyllolepidi were a freshwater benthic group of Placodermi characterized by their flattened body, large bony plates, and small eyes on the lateral surface of the head, these organisms were thought to be blind but had excellent sensory perception allowing them to be effective predators. In contrast to the large bony plates of Phyllolepidi, the Acanthothoraci were a group of placoderms that had large scales and plates. This group is unique from other placoderms due to its unusual dermal plate distribution in the skull roof (Olive et al., 2011). Lastly, Rhenanida consisted of flat, ray-like vertebrates with armor made up of unfused scales and tubercles (Fig. 1). These organisms were bottom dwelling predators whose body plan is well documented through fossils of *Gemuendina stuetzi* (Young 2010).

While the placoderms have been well-studied, much uncertainty remains regarding the placoderms' evolutionary history as well as their relationship to the two major extant groups of gnathostomes (jawed fish) (Young 2010). Our understanding of placoderm diversity and evolution is limited by a rather incomplete fossil record. More specifically, much of the research on placoderms describes arthrodires, the most diverse subgroup that dominated the Middle to Late Devonian period. However, this represents roughly half of the ~70 million-year evolutionary history of the placoderms (Young 2010). Recent evidence of Early Silurian placoderms found in China provide new insight into the complex evolutionary history. Additionally, technological improvements in molecular and developmental biology continue to expand our knowledge of the evolutionary history of placoderm diversity and can help us to better understand changes and discrepancies that occurred in a critical period in earth's history.

Anatomically, placoderms are best distinguished by their dermal armor (interlocking



**Placodermi Locomotion, Fig. 1** Various placoderm exemplars: (a) *Dunkleosteus*, an Arthrodire; (b) *Antiarcha*; (c) *Phyllolepidia*; (d) *Rhenanida*

bony plates). The well-preserved dermal bones greatly contribute to fossil remains; however, these dermal plates were often limited to the cephalo-thoracic (anterior body) region (Ferrón et al. 2017). Consequently, the fossil record provides little information regarding the whole external anatomy of these species. With limited knowledge of post thoracic regions, the size and general body shape of many placoderms remains uncertain. Previous reconstructions of placoderms often focused solely on phylogenetically related taxa and did not consider the functional morphology of biological structures (Ferrón et al. 2017). Both body shape and fin shape heavily influence the mode of life in aquatic species, as functional constraints often play a crucial role in types of locomotion and must be considered when discussing locomotor patterns in placoderms. Advancements in 3D technology and digital manipulation of these novel models lend for a more realistic reconstruction of the whole body of placoderm fish (Bécharé et al. 2014).

### Representative Locomotor Behavior of *Dunkleosteus* and *Bothriolepis*

Placoderm locomotion has largely been believed to be anguilliform, with organisms displaying a similar style of swimming to eels. However, genera from two of the major groups of Placodermi demonstrate differences in swimming modes and niche. This section will examine the two most significant modes of locomotion employed by *Dunkleosteus* and *Bothriolepis*.

*Dunkleosteus* is a genus of the extinct arthrodire that dominated the seas during the Late Devonian period. Approximately 10 species have been documented, with *D. terrelli* being the largest and most well-studied. These vertebrates could grow up to 8 m and possessed sharp bladed jaws that enabled them to thrive as carnivorous predators (Carr 2008). However, the lack of preserved remains of these arthrodire have made complete reconstruction difficult. Previous inferences regarding the size and body plan have been

drawn from fossil records of *Coccosteus*, a separate genus of arthrodire (Ferrón et al. 2017).

Placoderm paleoecology research suggests that most species were benthic, however, an analysis by Carr (2008) suggests that *D. terrelli* was a pelagic organism. This means that *Dunkleosteus* would have traversed the open seas in environments that may have been unfavorable to other Placoderms. The discovery of ceratotrichia, stiff filaments resembling keratin, in a pectoral fin of *Dunkleosteus terrelli* points toward the idea that placoderm fins had a greater range of variability and locomotor capabilities than previously thought (Carr et al. 2010). To further understand its locomotion pattern, we can turn to modern day sharks as models. Both organisms have similarities regarding body plan and function. *Dunkleosteus terrelli* was believed to have been a strong swimmer that employed use of pectoral fins as glide planes for more efficient locomotion (Barron and Etness 1981). Like sharks, *Dunkleosteus* may have swam using body-caudal fin propulsion, thereby generating thrust using lateral tail movements (Ferrón et al. 2017). It has also been proposed that *D. terrelli* used anguilliform propulsion which is normally characteristic of eels. However, this seems unlikely due to limitations in lateral movement of the head and trunk by the cephalic shield (Ferrón et al. 2017).

*Bothriolepis canadensis* was a Late Devonian placoderm species found in eastern Canada. More than 60 species of *Bothriolepis* have been identified, although *Bothriolepis canadensis* is historically considered to be the most well-known (Bécharde et al. 2014). *Bothriolepis* belong to the Antiarchi, which first appeared in China in the Silurian age. Antiarchs remained relatively stable throughout the Early Devonian age and reached their peak diversification in the Middle to Late Devonian ages (Young 2010). Antiarchi are distinguished from other Placoderms through pectoral spines that are covered with dermal plates. While the pectoral fins of early antiarch species were short and thick box-like structures, the pectoral fins of more advanced antiarchs, including the *Bothriolepis*, were long and jointed and loosely resembled the limb of an arthropod

(Liem et al. 2001). The function of these jointed pectoral spines still remains unknown, although numerous hypotheses indicate that they may have been used for swimming maneuverability, to elevate the body, to hold the body stationary in flowing water, or to help pull them across the ocean floor during bottom dwelling walking (Liem et al. 2001).

Locomotion in the aquatic environment is largely dependent upon the underlying functional anatomy of an organism. Despite being considered one of the best-known species, new analysis of the *Bothriolepis canadensis* suggests that prior reconstructions were anatomically inaccurate. As a result, previous hypotheses regarding the mobility of the cephalad armor, submarginal plates, and pectoral fins were based on the misinterpreted external anatomy (Bécharde et al. 2014). This confusion contributed to the idea that some late *Bothriolepis* species may have developed morphological specializations that made swimming an effective mode of locomotion.

*Bothriolepis* is believed to have been a sluggish bottom-dwelling fish that exhibited primitive patterns of locomotion. It is likely that these species remained closely associated with the seabed because they were unable to support themselves in the water, overcome frictional and other forces, maintain stability, or maneuver through the dense water (Bécharde et al. 2014).

Due to the confusion regarding the morphologic features of the *Bothriolepis*, current research on *Bothriolepis* movement focuses on anatomical limitations that suggest that swimming was not a feasible mode of locomotion. There are several requirements that make swimming possible in aquatic organisms. First, a swimming animal must have the ability to support itself in water. An object in fluid displaces a weight of fluid that is equal to its own weight. The fluid that is displaced will exert an upward force on the object (Liem et al. 2001). When an object is placed in water, this upward force is substantial because water is dense when compared with air, resulting in considerable buoyancy. Buoyancy is the major force that supports a fish; however, the weight of a fish slightly exceeds the upward buoyancy force because flesh including bone and muscle have

densities greater than the surrounding water (Liem et al. 2001). Thus, for a fish to swim it must be capable of generating a lift force that can overcome the downward pull of gravity. Heavily armored early fishes including *Bothriolepis* and *Dunkleosteus* exhibit negative buoyancy and consequently swimming would be very costly. Even if the *Bothriolepis* was able to support itself in water, for it to be capable of swimming it would also have to overcome drag forces (i.e., a combination of substantial frictional and pressure forces that provide resistance to movement through a medium) (Liem et al. 2001). Finally, most fish that swim generate propulsive forces using undulatory movements or bends of their bodies that move caudally from trunk to tail. As these undulatory movements travel back, they create lateral and forward thrust forces that propel the fish forward and oppose the drag forces (Liem et al. 2001). Recent analysis showed it is unlikely that the caudal fin of *Bothriolepis* could generate these propulsive forces (Bécharé et al. 2014).

## Evolutionary Implications of the Placoderms

Placoderm are members of the larger group known as gnathostomes, defined as jawed vertebrates. Hinged jaws were a pivotal evolutionary adaptation as they allowed organisms to have a fast, active, and controlled bite. From ancestral gnathostomes evolved two major divisions, the chondrichthyans, or cartilaginous fish that includes modern day sharks and rays, and the osteichthyans, or bony fish which gave rise to all terrestrial vertebrates. Placoderms were always considered a sister group of the gnathostome stem, thus suggesting their bony structure evolved independently of osteichthyans. It was previously hypothesized that the common ancestor of chondrichthyans and osteichthyans resembled a cartilaginous shark and that bony fish were a specialization from this ancestral state (Friedman and Brazeau 2013). However, discovery of a 419 million-year-old fossil in China had rebuked this hypothesis (Zhu et al. 2013). The fossil, *Entelognathus primordialis* resembled a

placoderm, with bony armor and jaws. From this discovery a new hypothesis emerged suggesting that cartilaginous fish were a unique adaptation, losing their bony skull and jaw, the primitive feature.

## Conclusion

In this chapter, we have explored the locomotive patterns of the extinct placoderm vertebrates. There has been some debate regarding swimming behavior and niches with many believing that most placoderms were bottom-dwelling and sluggish in movement. The lack of preserved fossil specimens has made it challenging to reconstruct full body models, requiring inferences to be made based on modern day sharks. However, examination of placoderm anatomy has yielded information pointing to differences among the subgroups, affecting our previous understanding of locomotion within these organisms. This is best evidenced by *Dunkleosteus* and *Bothriolepis*, members of the two most significant subgroups. Further research and exploration is needed to obtain a more in-depth knowledge of Placoderms and their domination of the seas millions of years ago.

## Cross-References

- ▶ [Adaptation](#)
- ▶ [Adaptive Radiation](#)
- ▶ [Chondrichthyes Locomotion](#)
- ▶ [Common Ancestor](#)
- ▶ [Ecology](#)
- ▶ [Evolution](#)
- ▶ [Extinction in Learning](#)
- ▶ [Homology](#)
- ▶ [Homoplasia](#)
- ▶ [Locomotion](#)
- ▶ [Morphology](#)
- ▶ [Muscular System](#)
- ▶ [Natural Selection](#)
- ▶ [Paleontology](#)
- ▶ [Phylogeny](#)

- [Placodermi Diet](#)
- [Species](#)
- [Taxa](#)
- [Vertebrate Nervous System](#)

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## Plane Symmetry

- [Bilateral Symmetry](#)

## Planning

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### What Is Planning? Why Is It Important?

Thinking about the future is a common human behavior. Whether one is anticipating an opponent's move and one's subsequent response in a game of chess, or simply making a plan to pick up milk on the way home from work, the future is something we think about nearly every day. However, the cognitive mechanisms that underlie future-oriented thinking, or prospective cognition, are as complicated as the future itself. Szpunar et al. (2016) have divided prospective cognition into four main modes of future thinking: simulation, prediction, intention, and planning. There is an intersectional relationship between all four modes, but planning is arguably the one that most integrates the other three. One definition of planning is the predetermination of a course of action aimed at achieving a particular goal (Hayes-Roth and Hayes-Roth 1979). Another is that planning requires an individual to predict a future event, simulate the circumstances of and reactions to that event, and set an intention of what to do when the event occurs (Szpunar et al. 2016). A simpler definition comes from Miller et al. (1960): a plan is a hierarchical process that controls the order of sequence of operations. Immediately, one sees that there is not consensus on what we mean by the term planning before we even get to the question of whether animals engage in planning. Our position is that there is extensive evidence of animals engaging in planning as per Miller et al. and Hayes-Roth and Hayes-Roth, and rarer, suggestive evidence of such planning as per Szpunar et al. In the case of “planning as sequencing,” there does not need to be a distant future goal, and planning can involve the structuring of a response or sequence of



responses right before they are made. In the “planning as simulation and prediction” definition, there is greater demand on prospective cognitive faculties that could include so-called mental time travel and the ability to anticipate oneself as being in a different state in the future than one is in at the present.

The question of whether other animals are capable of planning sometimes has been controversial, in part because of these varying definitions of planning. Our goal is to describe some of the forms of planning that have been assessed in nonhuman species and what has been found in those tests. The presentation order is perhaps reflective of a hierarchy of less sophisticated to more sophisticated forms of planning, although we caution the reader that one should not assume that this is a progression through which evolutionary emergence of human planning occurred, or even that this hierarchy could be used to assess a species’ “planning capacity.” Rather, we believe that these are all instances of future-oriented behavior that can be called planning, and that reflect the need for organisms to engage different mechanisms to organize behavior in ways that afford goal attainment.

## Motor Planning and Sequence Planning

Motor planning refers to generated behavior that anticipates how an action will generate an optimal end state for the physical movement that is performed. For example, humans tend to grasp objects based on how they intend to use them rather than on simple convenience with regards to the orientation of the object. Humans will even adopt uncomfortable initial positions that lead to comfortable ultimate positions, as when we reach toward an overturned glass with an inverted hand so that the glass can then be rotated into the orientation we need it to be in to use it as designed. Other species also do this. Capuchin monkeys selectively orient their thumbs and hands in ways that allow them to efficiently retrieve food from an object or use that object as a tool (Zander and Judge 2015). Rhesus macaques select efficient grips when transporting spoons that they

use to gather reward (Nelson et al. 2011). Tamarins (Weiss et al. 2007) and lemurs (Chapman et al. 2010) show the end state comfort effect, grasping objects in a less comfortable first contact so that they can end with those objects in a comfortable and efficient-to-use orientation.

Sequence planning in nonhuman animals has typically been assessed using computerized tasks that afford the subject the necessary information to complete a trial correctly, if it can produce the correct sequence of responses. In some cases, those sequences must be planned in advance or else errors will occur. Computerized maze tasks allow assessments of how far ahead through the maze a subject can determine its moves at choice points, and nonhuman primates sometimes can plan for at least one or two future choice points within a computerized maze (e.g., Frigaszy et al. 2009) or other types of mazes (e.g., Volter and Call 2014). Similarly, pigeons were trained to move a target towards a goal in a plus-shaped maze task (Miyata and Fujita 2008). The goal was then shifted one to four moves away from the intersection of the maze. Pigeons showed more errors when the goal change was done closer to the choice location, suggesting that they had planned the route to take to the goal and had less time to acknowledge and compensate for the change. In a more complicated 2D maze task, capuchin monkeys were trained to move a target to a goal with the addition of correct choices that moved away from the goal, and while those completing the mazes in order of increasing difficulty did better than those completing the mazes in random order, they did not show an overall decrease in errors as time went on. However, it should be noted that the difficulty these animals experienced may have stemmed from a lack of experience with the task, as another study showed that capuchins did better on a similar maze task when given more trials (Pan et al. 2011).

Nonhuman primates and pigeons have been trained to sequence stimuli presented on computer screens in a specific order, and then trials are presented in which the stimuli are occluded or manipulated in other ways so that correct completion of the sequence can only happen if the subject has remembered the rest of the sequence that

needs still to be made. For example, pigeons were trained to select three items in sequential order, with a switch and mask condition introduced after training (Sarf and Colombo 2010). The switch condition involved the location of the second and third items being reversed after the selection of the first item, and in the mask condition, the second and third items were covered by an opaque white square after the subject selected the first item. In the switch condition, the latency in responding between the first and second item was higher than that of baseline trials with no items switching locations, suggesting that the birds needed time to readjust a plan created based on the initial location of the items. The mask condition showed that the pigeons performed significantly better than chance, indicating that they had already spatially mapped out the three items and perhaps planned their selection order before they selected the first item and were thus unhindered by the masking of the items. Other studies showed similar results for latency patterns and difficulty with the switch condition and mask condition, suggesting that sequences were planned at most one item ahead (e.g., Beran et al. 2004; Beran and Parrish 2012; Sarf and Colombo 2009), but in some cases, performance was high even for completing sequences of six or more items that are no longer visibly present (Inoue and Matsuzawa 2007; Kawai and Matsuzawa 2000).

### Anticipation of Future Needs and Planning Accordingly

Although it is not controversial that organisms anticipate needs, there is a debate as to whether they can anticipate needs that they *do not presently have but will have later*. The Bischof-Köhler hypothesis states that animals cannot anticipate future states that differ from current states, and therefore cannot plan for a future that is unlike their present. Instead, animal planning abilities are considered to exist only in cases where immediate needs can be satisfied through the production of a sequence of responses to obtain reward (e.g., Suddendorf and Corballis 2007). However, some research challenges this sharp divide between the planning abilities of humans and other animals.

In multiple studies involving a food caching task, different species have shown the ability to selectively cache food based on the availability of different food sources in the future (e.g., Cheke and Clayton 2012; Raby et al. 2007). Specifically, birds chose to cache foods that they learned would not be available in the future even when they were satiated on that food in the present. In a more applied task involving thirst and water access, squirrel monkeys were given the option to choose a smaller amount of thirst-inducing food with the payoff of their water access being restored quickly, or a larger amount of thirst-inducing food which made the wait time for water much higher. The monkeys came to prefer the smaller amount, presumably because they anticipated a later thirst that could not be quenched (Naqshbandi and Roberts 2006). The choice could not have reflected current thirst since water was available at the time of the choice. This result stood in contrast to the behavior of rats that continued to choose the larger food amount even when water was restricted for longer. It also stood in contrast to the performance of rhesus monkeys (Paxton and Hampton 2009). This difference in the choices made by rhesus and squirrel monkeys could stem from their life histories, as squirrel monkeys naturally consume a more water-rich diet than rhesus monkeys. If a more relevant motivator was used, it is possible that rhesus monkeys would display the same behaviors as their New World counterparts. However, it was also possible that training histories and specific previous experiences played a role in choices, suggesting that outcome contingencies may have been as relevant as anticipation of future states.

Apes tend to provide stronger evidence of planning for future conditions, especially in tasks that require use of tools. Generally, these tasks involve the apes learning to use a tool to retrieve an obstructed reward. They are later given the chance to choose from a selection of multiple tools and keep their choice with them until they need it in the future. Apes consistently choose the correct tool without any cueing for the future task or the current need for the tool, directly opposing the Bischof-Köhler hypothesis (Mulcahy and Call 2006). Osvath and Osvath (2008) also

found that, when presented with a set of novel useful and useless tools, apes consistently chose a useful tool even though it could not be used right away. Sometimes, this choice of a good tool *for a later task* was made over an immediate, lower preference reward. In one particularly illustrative case, a chimpanzee collected stones before the arrival of visitors to his zoo exhibit, and then threw those stones at people. These kinds of behaviors may indicate that chimpanzees at least can anticipate future needs and organize current behavior in a manner that gives them access to future rewards (see Osvath and Martin-Ordas 2014).

More recent work suggests that some birds may show similar capacities for this type of choice behavior for items that can only be used later (e.g., Kabadayi and Osvath 2017). However, it is important to note that these tests afford the possibility of success without need of planning. For example, choosing a tool that is more often associated with food over other tools with no such association could be expected to occur even if an animal had no expectation that it would use that tool later, or want food later, or even still have the tool later (see Hampton 2019). It is important to use conditions in which some trials will have a future possibility to use a tool or exchange a collected token, but others will not, so that the tools or tokens themselves are no longer valuable (or invaluable) in all circumstances, but are differentially valuable *based on what is expected in the future*. Tasks that provide these contrasting trial types have shown that some apes can distinguish between those contexts and selectively anticipate the need to choose and retain items that are only valuable later (e.g., Bourjade et al. 2014).

## Prospective Memory

There is a specific type of planning that has, as its focus, the formation and storage of an intended future action. This is called prospective memory, and it consists of four stages: Anticipating a future need, encoding the necessary response to be made when the relevant cue or appropriate time occurs for that response, retrieving that intention, and

implementing that intention. For example, remembering to add birthday candles to your regular grocery store visit next time you need groceries is an example of a prospective memory. Prospective memory is less frequently studied in nonhuman animals, but there is evidence that some species may engage in such future-oriented forms of planning.

Rats show evidence for prospective memory. Wilson and Crystal (2012) trained rats to classify different tones as short or long in duration. The rats also learned that a large meal would be presented at a future time within each session, and the rats showed anticipatory behavior (e.g., they poked their noses into the food trough) right around the correct time of that meal. This suggested they were monitoring the time in the task to be ready for when it was the appropriate time to go eat the meal. This anticipation and monitoring came with a performance cost in the tone discrimination task (Wilson et al. 2013), a result that aligns with the decrements in performances sometimes seen when humans must engage in active monitoring for cues to evoke prospective memories.

Primates also show evidence of prospective memory. For example, a language-trained chimpanzee was given a choice of two preferred foods, and she received the chosen item immediately (Beran et al. 2012). The other item, that was not preferred at that time, was left indoors, while the chimpanzee was moved outdoors where she found other much more highly preferred foods than either indoor item scattered around a large enclosure. She was allowed to obtain those items and then return indoors at will. The key issue was that she could still get the last item but only if she remembered to bring in a specific token that held the symbol associated with that item. Her behavior indicated that she first retrieved the high preference items, and then moved to find the correct token and complete the retrieval of the least preferred item that was available that day. On control trials, with no other item still indoors, she was less likely to retrieve any token. This pattern could only happen if she encoded the item type she *had not selected*, at the start of the trial, and then later spontaneously decided when to search for and retrieve the token with the symbol matching

that item she had earlier rejected. This performance may also challenge the Bischof–Köhler hypothesis, given that she had to remember the name of a thing she valued less than what she had just selected, although it is difficult to design a task for which a present stimulus could truly have no value to an animal at one point and then become valuable later without training those possible states.

## Planning in the Wild

Laboratory studies always carry with them the limitation of their artificial environment, so it is helpful to also test the planning abilities of animals in the wild. Much of this effort has focused on nonhuman primates. For instance, planning behavior may manifest through communicative signals. One example is in the form of vocalizations seen in wild orangutans (van Schaik et al. 2013). Wild male orangutans use long calls to indicate their travel direction during the day, and they may even travel in the direction of calls they produced the night before. Not only do they seemingly plan their travel routes the night before, but other individuals in the area listen to and use this information, with females moving in the same direction as the calls and subordinate males moving in the opposite direction, suggesting that they too understand that the call indicates where the dominant male will be moving in the future.

Chimpanzees may choose their evening nesting sites based on their likely travel destination the next day, which could suggest that they anticipate and even plan to go in those directions (Janmaat et al. 2014). For example, when preferred and fairly infrequent fruits are ripening, chimpanzees sometimes make their evening nests closer toward the locations where those foods are located compared to where they make evening nests when other, less preferred foods are the items that are eaten the next day. They may even choose to rise earlier or later depending on what fruit was ripe and how far away that food was, and this could involve some form of anticipation and plan for the next day's movements

(also see Ban et al. 2014). Monkeys, too, may do these kinds of things (e.g., Noser and Byrne 2006). Of course, it is not certain that these are plans made the night before in the sense of being intentional series of events toward a specific goal the next day. It could instead be more of a feedback loop where nesting sites are made as the animals are in a state of considering a travel direction in general (because it would lead to food, for example), and there is increased chance that they take that direction of travel the next day because of where the nests are located when they awake, and they are reminded of the food in that direction.

Other possible examples of planning by animals in the wild include tool use. Chimpanzees collect nuts and hammer stones, moving those to areas with a suitable “anvil” against which they can crack those nuts (e.g., Boesch and Boesch 1983), and this sequencing of behavior falls perfectly in line with the idea of planning held by Miller et al. (1960). It also matches in character some studies in captivity. For example, chimpanzees have been reported to save tokens to use them in the near future, indicating that they anticipated a delayed opportunity to exchange them for food (Sousa and Matsuzawa 2001), and they learn to trade tokens or real food items in the present so as to obtain something better (e.g., Dufour et al. 2007). It is even possible that the planned hunts that chimpanzees undertake involve some form of planning (e.g., Stanford et al. 1994), although it is difficult to distinguish this from the coordination of behavior as it unfolds in real time among the group of hunters.

Lest one think that non-primates are non-planners, consider a very different kind of animal. Spiders from the salticid subfamily Sparidae prey on other spiders and have evolved complex strategies for targeting and capturing such prey. In some cases, they take detours away from prey that eventually lead them into more ideal vantage points for a successful capture. Laboratory tests that mimic this natural situation involve presenting the subject spider with a tower from which it can see prey, and see paths to that prey but also paths that would not lead to the prey (Cross and Jackson 2016). These spiders took

the correct path, even though it led to loss of sight of the prey and sometimes involved moving past a more direct (but ineffective) path toward the location where prey had been seen. This suggests a planned motor movement pattern with the goal of reaching the prey animal. Whether spiders or other non-primate species can show evidence contrary to the Bischof–Köhler hypothesis is unclear.

## Summary

It is a fair conclusion that nonhuman animals can engage in planning behavior. The evidence seems conclusive that other species can anticipate things that are about to happen in their environments and adjust behavior to accomplish a goal that is not immediately possible to accomplish. It may be the case that such plans are complex in terms of involving sequences of responses that must be implemented in the correct order, and that order must be determined before the task is begun. In some rarer cases, those planned behaviors may be generated in anticipation of a goal that is not physically present, or even a goal that, at present, is not valued (but it will be in the future for that animal). This is a controversial (and exciting) question that requires more work, especially to ensure that there are not alternate explanations of such behaviors that do not require planning (Hampton 2019). Paxton and Hampton (2009) noted that work on planning behavior, especially for the types of planning that are suggested to involve mental time travel, must allow for assessments without the possibility of trial and error learning (see also Suddendorf and Busby 2005). Those tests also need to avoid species-typical behaviors as those may be more reliant on associative learning rather than planning.

Of course, many of these behaviors we have described as being evidence of planning do not have to involve seeing oneself in a future event. It would be premature to conclude that other species have the “autonoetic” aspect of mental time travel that *sometimes* occurs when humans think about and plan for the future. Of course, much of human planning also occurs without need of autonoesis

or any form of conscious anticipation of the future (e.g., adults rarely think about brushing their teeth even though they engage in a highly routinized plan for doing so). So, the question of mental time travel should not be central to any discussion about whether animals can plan at all for the future, although it is an exciting and important type of planning to study. Foundational future-oriented cognitive processes such as motor planning and the structuring of sequences of responses are not reliant on mental time travel, any more than semantic memories of the past are reliant on autonoetic episodic recall. Not knowing how *it feels* to an animal to think about the future and plan for it does not prevent us from taking the perspective that other species are capable of planning for some aspects of their future so that they can organize behavior in a way that affords accomplishing goals in that future.

## Cross-References

- [Anticipation of Future Events](#)
- [Computerized Testing Paradigm in Primates](#)
- [Prospective Memory](#)

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## Plant Behavior

► [Plantae](#)

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## Plant Cognition

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## Plant Learning

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## Plant Signaling

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## Plant Vision

► [Plantae](#)

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## Plantae

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## Synonyms

[Adaptive behavior](#); [Affordance](#); [Classical conditioning](#); [Communication](#); [Competition](#); [Ecological psychology](#); [Embodied cognition](#); [Foraging](#); [Habituation](#); [Information processing](#); [Movement](#); [Numerosity](#); [Ocelli](#); [Phenotypic plasticity](#); [Plant behavior](#); [Plant cognition](#); [Plant learning](#); [Plant signaling](#); [Plant vision](#); [Predictive processing](#); [Primary consciousness](#); [Sentience](#); [Swarm intelligence](#); [Tropism](#)

## Introduction

### What Is Plant Behavior and Cognition?

A mark of intelligent behavior is the capacity to select actions that allow an organism to achieve its goals. Although there is no universally agreed-upon definition of what behavior is, an operational strategy that applies to both plants and animals is to approach behavior in terms of the “observable consequences of the choices a living entity makes in response to external or internal stimuli” (Cvrčková et al. 2016). Such choices, when performed by animals, usually involve movement. Because plants are sessile, it becomes more difficult to appreciate their behavior. But behavior takes place regardless of the mechanism (e.g., muscle contraction vs. cell elongation) that underlies overt plant and animal responses. Laying the stress upon animal, as opposed to plant behavior, becomes a matter of scale and bias. Compare a plant that grows leaves and orients itself toward the sunlight to a sponge that forages for oxygen and nutrients by pumping water through its body. Plant behavior, understood as phenotypic plasticity in response to environmental contingencies, does take place in the form of growth, for instance (Trewavas 2017). Consider, more dramatically, a climbing plant growing up a

tree clinging with its tendrils, twining, and uncoiling around as it forages for light from one tree to the next (Darwin and Darwin 1880).

With regard to cognition, an encompassing biological perspective calls for the manipulation of the environment in order to enable metabolic functioning. This, however, does not entail that all of plant behavior is cognitive. Inflexible, hard-wired reactions to environmental stimuli are not interesting from a cognitive science perspective. Non-hardwired strategies appear to be needed for a behavioral pattern to become cognitive. It is the degree of flexibility that can be observed in the behavioral repertoire of plants as they assess, say, potential conditions under pressure that grants the ascription of intelligence to them (Trewavas 2014). Among other things, the list of competencies includes the capacity to integrate sources of information into flexible overt responses and the capacity to anticipate future contingencies and make decisions accordingly as to how to alter its traits in the phenotype (Novoplansky 2016). More generally, cognition would encompass plant behavioral patterns that are adaptive, flexible, anticipatory, and goal-directed (Calvo 2016), that is, those overt patterns which are functionally analogous to purposeful and intentional animal behavior, as increasingly exposed under time-lapse photography in many documentaries, David Attenborough's style.

## History

### Early Beginnings

The concepts that gave form to the idea of intelligent behavior in plants were already present in the pioneering work of Charles Darwin (1809–1882), Wilhelm Pfeffer (1845–1920), Gottlieb Haberlandt (1854–1945), and Jagdish Chandra Bose (1858–1937), among others. As Darwin foresaw in *The Power of Movement in Plants*, strictly speaking, if there are no “lower” and “higher” species hierarchically ranked on *Scala Naturae*, then botany is not subordinate to zoology. Darwin suspected that some form of electrochemical communication was behind the responses of carnivorous plants. Lacking appropriate experimental

apparatus, he shared his insights with physiologist Sir John Burdon-Sanderson (1828–1905), at University College London, who, after measuring a voltage difference between the upper and lower surfaces of Venus flytrap leaves, was able to characterize action potentials in plants. Pfeffer had likewise envisioned the similarities with the way plants and animals process information. Haberlandt subsequently proposed the phloem as a nerve-like structure that plays a role analogous to the nervous system of animals for the sake of relaying information.

After the discovery of plant action potentials in the 1870s, Bose investigated the electrophysiology of plants in detail, monitoring electrical activity and the transmission of action potentials. As he urged, there is no doubt about the “nervous character of the impulse transmitted to a distance.” Against conventional wisdom, Bose argued that plants had “a system of nerves that constituted a single organised whole.” In 1926 he published *The Nervous Mechanism of Plants*, challenging the norm by using the expression ‘plant nerves’ in his work. Working on the sensitive plant *Mimosa pudica*, Bose showed that leaf folding was likewise triggered electrically as there is “transmission of excitation” between the petiole and the pulvinus that results in loss of turgor and thereby induces folding. In the 1930s plant action potentials were registered by inserting microelectrodes in the giant cells of freshwater algae *Chara* and *Nitella*. This served to unearth the mechanisms of cellular excitability. All this happened before action potentials were first recorded in the squid giant axon. Some decades later, pioneering research conducted by 1963 Nobel Prize winners Alan Lloyd Hodgkin and Andrew Fielding Huxley revealed the three-fold phase profile of animal cell excitability. It happened to hold equally for plant cells, with electrical transmission being an all-or-nothing action potential. Only in the last decade, plant electrical excitation transmission has been comprehensively linked to plant behavior (Baluška et al. 2006).

### Plant Signaling and Behavior

Plant adaptive behavior requires the coordination of physiological needs among the diverse plant

structures. The environment in which plants eke out a living is highly complex, with many vectors, other than light or gravity, to be appropriately navigated. Fine-tuned integration of information signaling across the root and shoot systems to achieve the plants' overall goals is thus needed (Calvo 2016). Electrical signaling plays a central role in integrating the plant body, as we have learned from plant electrophysiology (Volkov 2006). Despite the lack of neural tissue or synaptic connections, all higher plants regulate physiological processes in part by electrical means. The focus on the electrophysiological properties of plant cellular networks has permitted in the last decade to stress the need of a unified account of integrated signaling and adaptive behavior (Baluška et al. 2006) for the purpose of studying plant behavior and cognition.

In particular, plant anatomy and physiology reveals a highly cross-linked phyto-neurological structure akin to the cellular networks of invertebrate nervous systems. The vascular system of plants, initially thought to mediate exclusively the transport of water and nutrients, allows higher plants to coordinate their behaviors, with electric communication taking place over long distances through vascular bundles (Calvo et al. 2017). Plant science is starting to reveal the analogies in the way sets of behaviors in animals and plants get organized. Animal nervous systems were evolutionarily tailored with the purpose of coordinating free-moving behavior and thereby happen to organize signaling systems differently. Overall, research in plant signaling and behavior aims to unearth the particular way in which plants perceive and act in an integrated and purposeful manner, despite their sessile nature.

## Aspects of Plant Cognition

Stripped of anthropocentric interpretations, many features of cognition traditionally taken to be the sole purview of psychology are present in the *Plantae* kingdom. The list of competencies includes competition and foraging and the capacity to communicate, learn, and memorize, among other aspects of cognition (Trewavas 2017).

## Competition and Foraging

Foraging refers to the type of changes in behavior that permit organisms to procure their life-sustaining supply of energy. The term applies to plants insofar as they actively search for light, water, nitrates, phosphates, and other nutrients (Trewavas 2008), selecting the most convenient direction of growth. Resource foraging takes place in highly dynamic and heterogeneous environments, with resources patchily distributed. This requires precise structural changes at the level of morphology, physiology, and phenotype for the sake of optimal energy intake in a context of Darwinian competition. Red/far-red light ratios, for instance, inform plants as to how to grow out of shade and forage more effectively for light.

Competitive foraging takes place in both shoot and root apparatuses. As a result, shoots and roots typically present a branched morphology that allows plants to scan their surroundings more effectively. Leaves, branches, and root tips make decisions on a regular basis, such as accelerating or decelerating their rate of growth along positive or negative resource gradients, be it gradients of light intensity in the case of shoots or gradients of humidity and nutrient concentration, in the case of roots. Optimal foraging requires that all such local information registered at the sensory periphery of the plant body is integrated for the purpose of delivering a global response (De Kroon et al. 2009). Root territoriality, for instance, exploits the geometric structure of the soil itself. This illustrates the need of integration and the idea that the behavior of plants is not guided locally but rather globally.

## Communication

Plants exchange gases on a regular basis. Over one third of the carbon they assimilate is released back into the atmosphere in the form of volatile organic compounds (VOCs). The release of VOCs is not just a by-product of plant physiology. Plants exude them throughout their whole body to “talk” and “listen” to conspecifics and to members of different species (Dicke et al. 2003). Popularized as “talking trees,” or “eavesdropping,” a tree under stress, for instance, can pass along airborne

warning signals, permitting other plants in the vicinity to trigger defense mechanisms ahead of time. Some plants, like *Cuscuta pentagona* (dodder), unable to photosynthesize carbohydrates, rely on VOCs to twine round host plants and suck their nutrients out of their vascular system. *Cuscuta* can discriminate between volatiles exuded from both tomato plants and wheat plants and choose to grow selectively toward one or the other (Runyon et al. 2006).

Communication also takes place underground courtesy of networks of mycorrhizae that allow trees to remain in contact with one another. Symbiotic growth of these fungi with the root apparatus of trees results in patterns of flexible behavior, delivering ultimately overall fitness (Gorzelak et al. 2015).

There are other forms of sensory input that plants can rely on for the purpose of communication. Research in plant bioacoustics (Gagliano et al. 2012) informs us that plants can benefit from the perception of sound and vibrations. The munching of caterpillars results in specific vibrational patterns that plants can detect. *Arabidopsis thaliana* respond by synthesizing toxins to the vibrations produced by munching caterpillars (Appel and Cocroft 2014). Trichomes (hair cells) located on the leaves and stem of *Arabidopsis* respond to mechanical stimulation, acting as acoustic detectors or “mechanical antennae” (Liu et al. 2017).

### Learning and Memory

Plants enhance their foraging behavior for light and nutrients by modifying their behavioral repertoire through learning and memory processes. Although plant learning and memory may be approached at different levels, the field has benefited particularly from the study of learning as practiced by comparative psychologists. Recent research has focused on overt behavior by applying the methodological toolkit of the animal learning literature under neobehaviorist paradigms (Abramson and Chicas-Mosier 2016).

Both nonassociative and associative forms of learning have been documented to take place in plants. Habituation has been observed in members of the carnivorous *Droseraceae* family (sundew)

and *Passiflora gracilis* (passion flower), with reports dating back to Pfeffer and Darwin. The sensitive plant *Mimosa pudica* is the best-studied model for nonassociative learning. The most detailed study to date has been done using *Mimosa* in the context of light foraging and risk predation (Gagliano et al. 2014), having shown that the leaf-folding reflex of *Mimosa* used for the purpose of defense against herbivory habituates after vertically dropping the plant repeatedly. The learned response lasted up to a month.

Habitation is consistent with an instinctual reading of plant behavior and therefore represents the simplest form of learning. More sophisticated forms of learning include Pavlovian classical conditioning. Classical conditioning has been reported more recently in the garden pea *Pisum sativum* (Gagliano et al. 2016), where the direction of growth was affected by a neutral stimulus against the naturally occurring phototropic behavior. Conditioning evidences the acquisition of new competencies that can enhance foraging behavior and, together with nonassociative forms of learning, constitute adaptive processes that point to a basic form of memory.

### Models of Plant Behavior

Plant behavior could involve the processing of information, depending on whether a computational framework is endorsed or not. Until recently, the study of plant behavior was dominated by information-processing assumptions incorporated from cognitive psychology and artificial intelligence. Alternatively, from an ecological perspective, we may consider the way in which the flexible behavior of plants gets structured as a result of the way internal and environmental factors couple together non-computationally. We can thus explore the guiding role that different models and theoretical frameworks may play.

### Predictive Processing

Anticipatory behavior could rely on estimating the likelihood that one particular state of affairs, and not another, is the source of energy.



According to the “predictive processing” hypothesis (Calvo and Friston 2017), plant perception boils down to a process whereby environmental input is matched to predictions generated endogenously by the system. It is the end result of a process whereby, first, top-down predictions of sensory signals – the conditional probabilities of particular features being the cause of stimulation – propagate backward to the effector organs and, then, predicted inputs are compared with incoming inputs: if predictions fail to match the input signals, the mismatch (a prediction error) is propagated upward. To accomplish it all, plants must embody a model of the causes of the inputs in question, a model whose predictions ensure that prediction error is minimized over time.

Plants may be seen as performing Bayesian model selection. Perception would consist in an active process of probabilistic inference with plants behaving like little statisticians that make tacit inferences about their world through changes in their internal states (Calvo et al. 2016). In order to pass predictions and prediction errors around the plant body and minimize prediction error, a hierarchical organization with reciprocally connected cell populations encoding expectations and prediction error is needed. In the case of plants, there is a functional asymmetry between backward predictive signals from deep vascular cell bundles and forward prediction error signals from mechanoreceptors and chemoreceptors located on the periphery of the plant body that could serve to implement predictive processing.

Prediction error may be minimized in two complementary ways: by updating expectations or by re-sampling. In the former case, a plant may adjust its internal states by updating its expectations so as to furnish better predictions (prediction error is minimized by updating expectations in order to bring them into line with actual states). Such process is called “perceptual inference.” In the latter case, a plant may choose to sample the environment more selectively in order to make new samples match prior expectations. This process is called “active inference.” Probably, prediction error minimization is accomplished through a

combination of both forms of inference. Overall, we may say that plants engage with their surroundings proactively, sampling the local environment in order to elicit information with an adaptive value.

### Ecological Psychology

Contrary to predictive processing, from an ecological point of view, environmental sources of stimulation are not ambiguous, and therefore perception need not be inferentially mediated to enrich an inherently poor landscape. Ecological perception relates to the detection of rich environmental information and is organized around actions. Plants resonate directly with informational invariants that specify opportunities for behavioral interaction whereby an unambiguous environment can be perceived directly (Carello et al. 2012). From the standpoint of ecological psychology, attention is paid to the ecological scale at which interaction takes place. The unit of analysis is the plant-environment system itself. This setting allows ecological psychologists to study plant adaptive behavior in terms of emergence and self-organization.

Consider a coupled system such as a climbing plant and its support or host. According to the ecological psychology framework, a vine would perceive its surroundings in terms of biologically relevant interactions, picking ecological information up as it circumnavigates around and explores its surroundings. Opportunities for interaction are then said to be perceived in the form of affordances, properties of objects that specify ways to interact with them, and guide the climbing maneuver in a continuous and cyclic loop of perception and action. The vine does not infer the support’s availability for twining; it rather perceives *climbability* itself, the possibility to interact with a support that affords climbing.

More generally, a foraging plant growing toward light or a source of nutrients behaves in functionally the same way as an animal that runs toward its prey. The hypothesis is that plants, like animals, resonate to specificational information without cognitive mediation of any sort whatsoever.

## Recent Developments

Many areas of research in plant signaling and behavior are receiving increasing attention in recent years, spanning from numerosity and swarm intelligence to the very possibility of visual guidance and plant sentience, among others.

### Numerosity

Sensitivity to numerosity does not require awareness or symbolic processing. The carnivorous plant *Dionaea muscipula* (Venus flytrap) exhibits numerosity-related abilities, being able to count to five (Böhm et al. 2016). More specifically, *Dionaea* is able to keep count of the number of times it fires action potentials in response to stimulation of the trigger hairs in the snap trap. Mechanical stimulation, such as the touching or bending of the trigger hairs, induces an all-or-nothing action potential. This, in orchestration with hormonal signaling, results in the closing of the trap. But for the snap trap to shut, a second stimulation must be repeated within 20 s of the first. If 20 s elapse with no news, short-term memory decays, and the plant forgets the first stimulation and resets – an adaptation that avoids unintended closure due to, say, raindrops or wind. The first stimulation must be somehow stored in the memory, if the plant is to eventually be able to put a further touch in a meaningful context. Once the trap has been shut, *Dionaea* keeps counting episodes of mechanical stimulation until it reaches five. This is important because after the initial two action potentials, three more are needed before digestive enzymes are synthesized and released.

### Swarm Intelligence

Members in flocks of birds, schools of fish, or swarms of insects responding to sensory input in the vicinity such as the pattern of navigation of the closest mate are the canonical illustration of swarm or collective behavior. But mechanisms that give rise to adaptive forms of collective behavior are widespread, with recent examples of collective behavior coming from the non-animal literature. *Escherichia coli* and *Salmonella typhimurium*, for instance, swarm and spread in

colonies. *Myxococcus xanthus* bacteria exhibit multiple forms of collective behavior. These rod-shaped myxobacteria glide their way through with a smooth continuous motion in swarms known as “wolf packs.” Plants are able to solve problems collectively too (Baluška et al. 2010). Maize roots, for instance, choose direction and rate of growth, reorienting selectively with respect to other roots in the vicinity to respect alignment (Ciszak et al. 2012). They can estimate distance, direction of nutrient gradients, and potential competition and adjust navigation patterns accordingly. By growing together and scanning the soil structure collectively, root systems are able to enhance the detection of nutrient patches.

### Visual Guidance

Recent evidence with the cyanobacterium *Synechocystis* suggests that directional light sensing is mediated by the use of primitive eyespots equipped with microlenses (Schuergers et al. 2016). We find likewise eukaryotic ocelloids in warnowiid dinoflagellates. These algae are equipped with a lens and a retina-like structure with pigments at the back that permit to tell the direction of light. The conjecture that plants have plant-specific eyes or ocelli first appeared in print at the beginning of the last century with Gottlieb Haberlandt's *Die Lichtsinnesorgane der Laubblätter*. As Haberlandt argued, leaf epidermis cells could play the role of sense organs functionally equivalent to animal ones. Commenting on Haberlandt's hypothesis, Francis Darwin subsequently elaborated on the idea that ocelli, in their simplest form, are nothing but an epidermis cell with a dome-like wall. As the cell is illuminated, sunrays effectively get bent, delivering a spot of light on the basal membrane. Plant mimicry in the woody vine *Boquila trifoliolata* provides the latest case for the study of plant vision. *B. trifoliolata* mimics the leaves of the host trees it climbs onto, copying not just the shape and color of host tree leaves but also their size, orientation, petiole length, and vein conspicuousness (Gianoli and Carrasco-Urra 2014).

Two hypotheses as to the mechanism that underlies mimicry are volatile organic compound-based airborne communication and

horizontal gene transfer, with parasites or microbes acting as vectors for gene transfer in between vine and host tree. Considering that mimicry takes place in the absence of touch, a further hypothesis has been advanced: *B. trifoliolata* may perceive their surroundings by forming primitive images courtesy of the visual sensory organs located in their leaves (Baluška and Mancuso 2016). This way, the vine could perceive shapes and colors courtesy of some kind of plant-specific vision akin to the ocelloid-based form of vision documented from research on cyanobacteria and some dinoflagellates. The internal structure of leaves, on top of furthering photosynthesis, could serve to bolster light sensitivity beyond mere photoreception. A transversal cut to a leaf reveals the candidate mechanism that can sustain vision. In particular, three main regions that bear vision-related properties have been identified: a cornea-like cuticle, convex or plano-convex lenslike epidermal cells promoting the convergence of light rays, and the retina-like mesophyll tissue.

### Sentience

The evolution of subjective experience has become a hot topic of research in recent years, with different attempts being made to trace subjectivity at various phylogenetic stages. Evolutionary biology has traditionally put the focus on the Cambrian period to understand the origins of sentience, more specifically, with the explosion of land vertebrate life. But animal sentience may also include invertebrates. The degree of sophistication of the perceptual apparatus of insects and their manifest capacity to learn, memorize, make decisions, and communicate appear to license the quest for the origins of mind beyond vertebrates or mammals in particular. If the mammalian mid-brain plays a key role in sensing and feeling, the central ganglion of insects plays an analogous role. But the origins of subjectivity could date back to the very origins of life itself, as the *cellular basis of consciousness* hypothesis sustains (Reber 2018). According to this hypothesis, the issue boils down to biomechanics, endogenous control, and navigation, and not to neural correlates. If the behavioral repertoire of insects hints at

their mentality, the same may hold for bacteria, whose wide range of competencies are only beginning to be fully appraised. Bacteria would have their own subjective experience, however basic the ascription of consciousness might be.

One way or another, consciousness may have evolved across evolutionary time a number of times. In recent years, the candidacy of plants for sentience has been given due consideration. If, despite the manifest lack of neural correlates of consciousness, bacteria evolved biomechanical structures that underlie their own subjective experiences, there is no reason to exclude the possibility that plants also evolved subjective experience. Plants lack none of the functional structures allegedly needed. Plant anticipatory behavior is goal-directed and soft-wired. Plants make decisions, solve complex problems, learn, memorize, and communicate. All this requires coordination and integration of information signaling across the whole plant body. Plants act as globally organized and coherent systems, supporting in principle their capacity for subjective experience (Calvo et al. 2017).

### Cross-References

- ▶ [Action Potentials](#)
- ▶ [Adaptation](#)
- ▶ [Adaptedness of Behavior](#)
- ▶ [Anthropomorphism](#)
- ▶ [Associative Learning](#)
- ▶ [Bacteria](#)
- ▶ [Behaviorism](#)
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- ▶ Evolution
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- ▶ Goal-Directed Behavior
- ▶ Gregor Mendel
- ▶ Habituation
- ▶ Information Processing
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- ▶ Instinct
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- ▶ Locomotion
- ▶ Numerosity
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- ▶ Perception-Action Theory
- ▶ Phenotype
- ▶ Photoreceptors
- ▶ Roots and Shoots
- ▶ Scala Naturae
- ▶ Territoriality
- ▶ Visual Perception

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## Plasmodial Slime Molds

► [Slime Molds](#)

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## Plathyrrhine Bioacoustics

► [Plathyrrhine Vocal Communication](#)

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## Plathyrrhine Calls

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## Plathyrrhine Vocal Communication

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## Synonyms

[New World monkeys communication](#), [Plathyrrhine bioacoustics](#), [Plathyrrhine calls](#), [Plathyrrhine vocalizations](#)

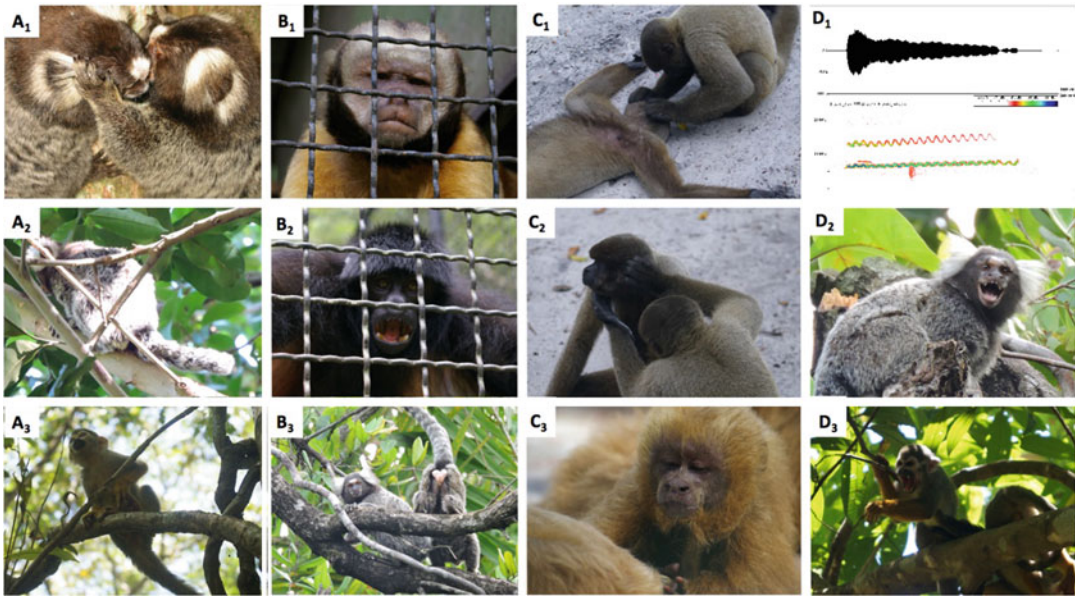
## Definition

Plathyrrhines or New World (Neotropical) monkeys live in South and Central Americas and are mostly arboreal (tree-dwelling) species. Primate communication occurs when one individual influences the behavior of another through the transmission of specific signals (e.g., vocal, chemical, tactile, and visual signals; Fig. 1). Natural selection of a given signal modality will basically depend on the habitat restrictions and social structure of the monkey species in question.

## Introduction

Whatever the definition of communication one adopts, an overriding aspect remains unchanged: the existence of a communication signal. A signal represents the form in which communication is performed and it can be expressed through vocalizations and nonvocal sounds (teeth chattering or trunk drumming, for example), color and facial expressions, postures, movements of the body or body parts, odors, touch, and even changes in the environment (e.g., shaking branches or clearing a path). Besides the signal, there are three other broad interrelated components that explain how communication works: motivation, meaning, and function (Scott-Phillips 2008). The motivation refers to the internal, emotional state of the animal performing the signal, such as, states of fear, aggression, alarm, excitement, and the social interest. Thus, the study of communication in animals may reveal ecological and behavioral aspects of a species. The meaning refers to the message that is received by the receivers of the signals. Recipients of different ages, experience, history, and relationship with the signaler may respond differently to the same signal at the same time. Finally, the function of a signal refers to the evolutionary advantage it confers to senders and/or receivers. In other words, function relates to the survival or reproductive advantages a signal gives to sender(s) and/or receivers. Alternatively, it is the answer to the question: what is the signal for? Thus, for example, when one says that the function of a bird song is to attract a female, such





**Platyrrhine Vocal Communication, Fig. 1** Communication modalities in Platyrrhine monkeys: Chemical, visual, tactile and acoustic. A1: common marmosets, *Callithrix jacchus*, engaged in tactile and chemical communication (Image: Bruna Bezerra); A2: common marmoset scent marking a branch (Image: Karolina Medeiros); A3: squirrel monkey, *Saimiri sciureus*, performing urine washing; B1 and B2: facial expression in buff headed capuchins, *Sapajus xanthosternus*, and black uakari monkeys, *Cacajao melanocephalus* (Images: Bruna Bezerra); B3: common

marmosets showing genitals during an agonistic intergroup encounter (Image: Karolina Medeiros); C1 and C2: woolly monkeys, *Lagothrix cana*, engaged in tactile communication through social grooming; C3 blonde capuchin monkeys, *Sapajus flavius* engaged in tactile communication through social grooming (Image: Bruna Bezerra); D1: spectrogram of a close distance contact call (trill call) made by common marmosets; D2: common marmosets uttering a loud long distance phoe call (Image: Karolina Medeiros); D3: squirrel monkey uttering agonistic calls (Image: Anielise Campelo)

statement implies that attracting a female (and informing species identity and some characteristics of the sender) confers reproductive advantage to the sender.

Animals can use several ways to communicate and, depending on the type of signal employed, communication can be classified as: acoustic (sounds), visual (color or movement patterns), chemical (molecules diffusing in the medium), electrical (production of electric fields), and tactile (contact). Acoustic signals have several advantages over the other signals because of their wide transmission. It is generally possible to know where an acoustic signal comes from, without necessarily looking at or being near the sound source.

This entry will focus on acoustic communication, the modality most widely studied in New World Monkeys. For a better understanding of primate auditory communication, it is fundamental to consider sounds both from a behavioral and

a structural approach. Vocal communication studies can be roughly split into two broad groups: those describing the acoustic repertoire of a species and those dealing with some specific aspect of a given call. In the latter case, it is useful to group calls from different species according to their main function. Another way to group the studies is according to their contribution to a broader theoretical theme. In this entry, both approaches will be adopted, starting with repertoire studies, passing through studies with specific types of calls, and finishing with more theoretical themes.

### Nonacoustic Communication (Tactile–Visual–Olfactory)

Many Neotropical primates have been reported to communicate using olfactory, visual, and tactile cues. Olfactory signals can act as mediators of

intragroup and intergroup interactions. Scent marks through secretion of different glands are the commons marking modes used by most species. Adult males of titi monkeys, *Pleurocebus* and *Callicebus* genera, and common marmosets, *Callithrix jacchus*, for instance, spread some odoriferous secretion when they rub their chest along a branch (Moynihan 1966; Eppe 1970). Some other species, like muriquis (*Brachyteles hypoxanthus*), investigate the reproductive status of females by sniffing or tasting their genitals (Strier 1992). Individuals of both sex of capuchins and muriquis are also known to wash their hands with their urine (urine washing), and pheromones presented on it may convey information about sex, identity, and reproductive status (Milton 1985; Phillips et al. 2008).

Visual signals include facial expressions, postures, and movements of the body or some part of it (including interactions with the environment), and color patterns. For example, muriquis (*Brachyteles hypoxanthus*) have a greeting face, performed between adult males and females, which looks like a grimace, and is accompanied by specific vocalizations (Milton 1984). Many species show pilo-erection (body hair standing up) during agonistic contexts, and some, like titi monkeys (*Pleurocebus moloch*), show a large repertoire of other visual signals during such contexts, including but not limited to, swaying, arch-posture, tail-raising, tail-lashing, and head-down (Moynihan 1966).

Tactile signals have been much less studied than the other modalities. Clear-cut examples are restricted to some behaviors which might have communicative function. Among these, we have the embracement between adult muriquis, which is performed as a friendly gesture or during moment of excitement. Some researchers also consider the time animals spend in contact, while resting, for instance, as a tactile signal, especially because animals may choose who to be in contact with.

## Acoustic Communication

Acoustic communication is the modality which employs sounds as signals. Sound signals have

several advantages: they can be transmitted at a distance, in the absence of visual contact (thus in the dark, in water, or in dense vegetation), they go round obstacles, they show great capabilities of modulation, being thus able to encode a wide variety of information, and they travel fast in the environment. Accordingly, they are employed in a wide variety of situations to perform an equally large range of functions: play, mate attraction, territory demonstration or defense, mate defense, alarm against predators, travel coordination, group cohesion, mother–infant interactions, and several other affiliative and agonistic interactions. Therefore, the ability to produce and hear such an array of sounds is essential to many animals, and Neotropical primates are no exception. All Platyrrhine species employ acoustic communication for a variety of functions, and all species studied so far have been documented to have a relatively large repertoire.

## Acoustic Repertoire

Acoustic repertoire refers to the variety of sounds employed by a given species. Biological sounds can show an impressive range of variation on several different axis: frequency (from infrasound through bass, medium, and treble and up to ultrasounds), duration, frequency modulation (e.g., upsweep, downsweep, and flat, besides more complicated modulations), amplitude (loudness), rhythmic pattern, tone-like aspects (from “pure”, to harsh, hoarse sounds) to name just a few. Furthermore, sounds can be combined into sequences, adding further levels of complexity. Thus, describing the repertoire of a species is usually a basic, necessary first step on which more advanced studies can be built. However, categorizing sounds is not a trivial task, as there is no standard definition for an acoustic unit (see review in Kershenbaum et al. 2014), and defining the boundaries may be seen as arbitrary and subjective. Even with such difficulties, repertoire studies normally categorize the different sounds produced by a species, describe their physical properties, and usually mention the contexts and situations of emission, commonly proposing

hypothesis for their functions. However, despite their importance, we are still short of repertoire studies and, for most New World Monkey species, their repertoire is unknown or poorly studied, resulting in the function and meaning of many different calls remaining unknown.

Despite the differences in categorization, the size of vocal repertoire can also vary widely based on whether the study groups are wild or captive. This is also problematic as captive animals are often limited in their natural vocal repertoire due to the lack of some behavioral and social conditions. Furthermore, some studies usually focus on a particular context instead of a full description of a repertoire, and until very recently, many reports on the vocal repertoire of Platyrrhine species were based on only qualitative observations. The ideal scenario would, thus, be to study the same species both in the wild and in captivity in a variety of contexts to get a thorough representation of their whole acoustic repertoire.

Although there is considerable support for a fixed vocal repertoire for many primate species, other works have also shown some vocal plasticity, based on social interactions or human impact on the environment (e.g., Roy et al. 2011). These abilities are particularly important to help animals deal with some of the disadvantages of acoustic signals, as they may be degraded, or attenuated by factors such as temperature gradients, incidental noise, air currents, or even eavesdropping. For example, to deal with the last issue, woolly monkeys (*Lagothrix poeppigii*) are able to adapt their behavior and avoid calling in areas with high level of human hunters, which would give away their position (Papworth et al. 2013). There is also evidence of regional dialects in some calls of pigmy marmosets (*Cebuella pygmaea*) (De la Torre and Snowdon 2009).

Moreover, the type of calls in a given repertoire (e.g., discrete – calls being clearly distinguished from one another – or graded – calls grade more or less continuously into one another) can impact substantially on the number of calls identified by a given study. Therefore, it is important to consider an acoustic repertoire as a representation of combined distinct calls, variants, gradations, and transitions between them, besides keeping in

mind that is both an arbitrary, albeit useful, concept, and a working hypothesis. Acoustic variation on a call type can signal more information on the category of the external event, motivational or internal state. B-calls (“cheeps”) produced by titi monkeys during encounters with terrestrial predators, for instance, are also given when they are descending or feeding close to the ground. However, significant differences between the calls given in different contexts suggest they may be able to communicate about specific aspects of their environment, by changing some features of the same call.

To more fully understand the function of a sound, or a group of sounds, in different circumstances, we need two complimentary approaches. On one hand, we need detailed comparisons of the sounds in the different circumstances to check if there is significant acoustic variation. Then, either if the sounds are different or not, we need playback studies to see if the animals respond differently to them and/or if they extract meaning from the immediate context (and if the responses make sense in adaptive terms).

### Alarm Calls

Several mammal and bird species produce alarm calls that typically function to signal the presence of predators to conspecifics and/or communicate to the predator that it has been detected (Caro 2005). These call types may show variation in the structure of calls, the number and composition of calls given, and/or the intensity of calls depending on the context in which they are produced (e.g., Seyfarth et al. 1980). Such context-dependent calls can potentially evoke reactions in call receivers that are appropriate for the context in which the calls were given (e.g., Seyfarth et al. 1980). Among those species that produce context dependent alarm calls, two distinct types of call systems have been identified: (1) a “functionally referential” alarm call system, where call structure varies based on threat type (e.g., eagle versus leopard, Seyfarth et al. 1980) and (2) an “urgency-based” alarm call system, that varies based on the degree of threat from a predator perceived by a caller (e.g., high versus low; Blumstein 1999). Moreover, there are also alarm

call systems that combine both functionally referential and urgency-based systems simultaneously (Marler et al. 1992).

Researchers have reported alarm calls as an antipredator behavior for almost all primate species that have been studied in that respect. However, most reports from New World Monkeys come from anecdotal observations and little or no information on type and function of the calls is usually provided (see review in Cäsar and Zuberbühler 2012). In general, alarm calls given to dangerous raptors are usually more specific than alarm calls given to disturbances on the ground, which sometimes are also given during nonpredatory events. Wheeler (2010), for instance, described three different call types given by tufted capuchin, *Sapajus nigritus*, that were regularly produced in response to predator encounters. “Barks” were elicited exclusively by aerial threats, while “hiccups” were produced in response to terrestrial threats but also during nonpredatory contexts. The call rate of hiccups also reflects risk urgency and responses to playback of these calls elicited appropriated antipredator behaviors. A third call, the “peep,” seems to be specific to terrestrial threats (Wheeler 2010).

Some species also appear to be able to create, and understand, specific combination of a limited number of calls, which leads to a variable sum of distinct sequences that differ in distinct contexts. For example, cotton-top tamarins (*Saguinus oedipus*) produce some alarm and alert calls combining other call types, which are given in contexts described as intermediate between the contexts in which each call type is produced alone (Cleveland and Snowdon 1982). Digweed et al. (2005) have also suggested that capuchins’ (*Cebus capucinus*) alarm calls may recruit conspecifics to mob, a behavior well documented in other capuchin monkey species. Mobbing involves one or more prey animals making repeated and aggressive advances on a predator, usually while vocalizing and displaying in a conspicuous manner. These conspicuous and persistent approaches usually distract or repel the predator and are fairly common in New World monkeys. Capuchin monkeys (*Sapajus nigritus*) one of the most studied Neotropical primate genera regarding its vocal

behaviour also use alarm calls deceptively to diminish competition within group during feeding bouts (Wheeler 2009).

### Contact Calls

Animals that live in groups, whose members spread out during their daily activities and who live in habitats of poor visibility (such as in forests or water), need a mechanism to keep track of one another while spread apart and/or to re-gather and/or to coordinate their group movements. Among the communication modalities animals could use to accomplish those tasks, touch is not a possibility, since the animals are separated by definition (often by large distances), visual communication is precluded by the very nature of such habitats, and chemical communication is slow and its directionality is highly unpredictable. Thus, the acoustic mode is the one showing more advantages, and, in fact, this is the modality most widely used in such habitats to perform these contact functions. Accordingly, contact calls is the broad term that encompasses calls that group animals use to maintain contact with one another or regain contact after spreading out (see review in Cunha and Byrne 2009). In the literature, they have been diversely classified as isolation/lost calls, monitoring calls, cohesion calls, and contact calls (or its function is apparent in the description of context of use or the proposed function in repertoire studies). These kind of calls has been mentioned or described in virtually all primate species whose repertoire have been studied so far, and Platyrrhines are no exception. All Platyrrhine genera (apart from *Oreonax*, *Chiropotes*, and *Mico*, whose repertoire have not been studied, and for which only sparse information is available) have been shown to have at least one call of their repertoire which could be labeled as a contact call. Nonetheless, the studies with New World monkeys contact calls are usually restricted to such basic repertoire studies, with just a couple of exceptions dealing exclusively with them or using them to answer a broader theoretical issue (mostly studies looking for individuality in the calls). Nonetheless, as Cunha and Byrne (2009) argue, they have the potential to be used to test hypotheses about intentionality on call emission,



besides begging for more detailed studies, attempting to find these call-specific functions.

### Loud or Long-Distance Calls

Loud or long-distance calls, is a commonly used term in the bioacoustic literature. Although obviously subjective, it usually refers to those calls which are distinctly louder than the other sounds in a species repertoire and/or which seem to be directed to receivers outside the immediate group/sub-group or surroundings of the call emitter. Primate loud calls are typically interpreted as signals of intergroup communication, although they can also function as conspicuous antipredator alarm calls.

Several Neotropical primate species produce loud calls that function for announcing group location, spacing groups, defending mates, and advertising group composition. Howler monkeys (*Alouatta* spp.), for example, whose name comes from their conspicuous loud calls, produce long, loud, and harsh roars and barks, which are amplified by an enlarged hyoid bone present in males. Despite being one of the most studied genera in that respect, no agreement has been found for the calls' function, which have been diversely proposed to work in mutual group avoidance, announcement of group location, marking and defending territorial boundaries, and defending mates, to name some of them. Another well-known loud call is the duet, a long and loud sequence of calls which is uttered by the mated pair, and sometimes their offspring, in a coordinated way. This behavior is an important feature of titi monkey species, genera *Callicebus*, *Cheracebus*, and *Pleuturocebus*, and also seems to be part of a territorial behavior, to define and reinforce territorial boundaries.

### Food Calls

Many New World monkeys produce food-associated calls upon encountering or feeding of specific food items. These calls usually provide information about the type, quality, or quantity of

food, and it may be influenced by the audience. Spider monkeys (*Ateles geoffroyi*), for instance, call more in the presence of dominant animals, and in larger trees, with more availability of food, than in the presence of subordinates and in small trees (Chapman and Lefebvre 1990).

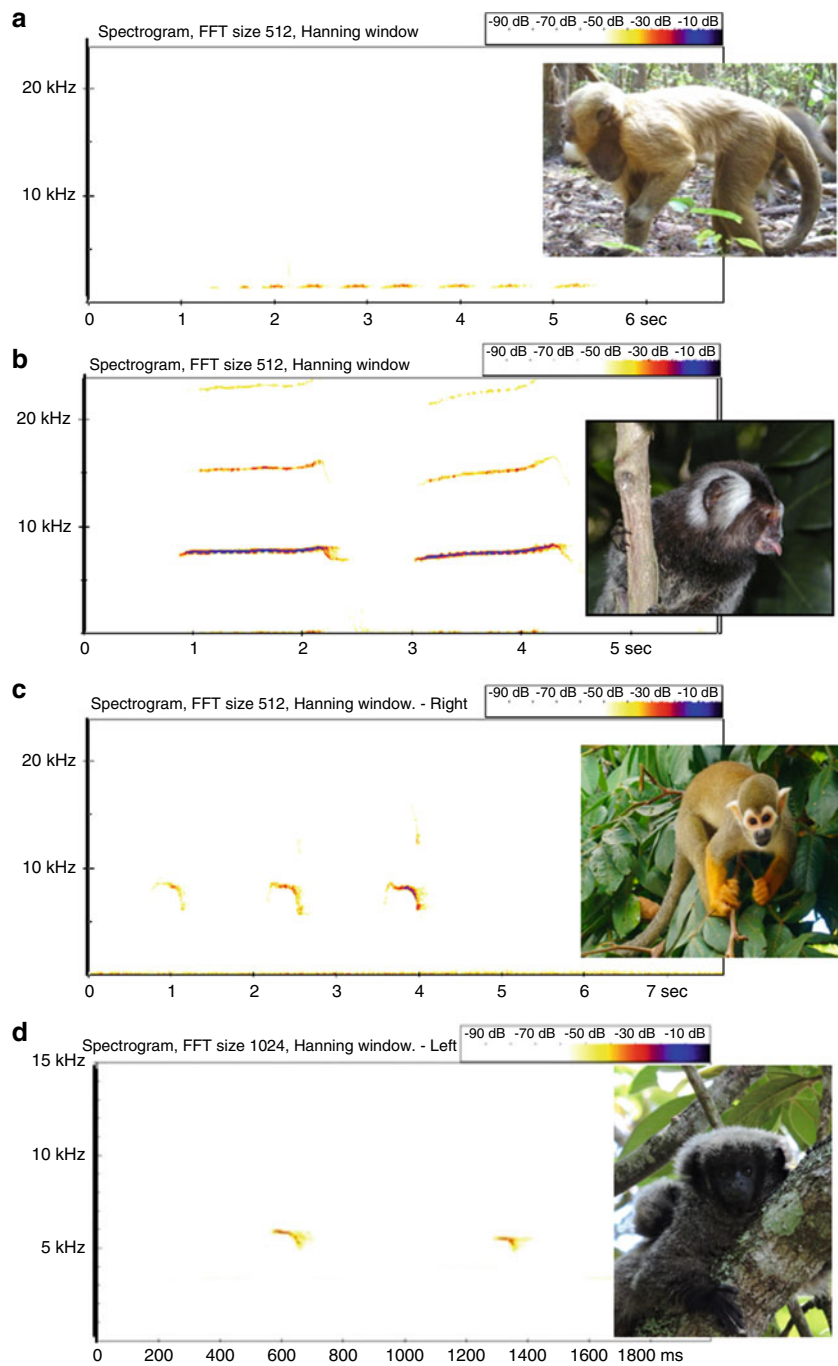
Food calls may function to attract conspecifics to a food source or to announce ownership. Although several Neotropical species have been reported to produced food/feeding associated calls, including *cuxius* and *uacaris*, the function of these calls is still to be tested (Bezerra et al. 2017). Food-associated calls in Neotropical primates have also been reported to happen during food transfer, through infant begging, or the calling of the food possessor to attract group members. Some Neotropical primate infants, especially marmosets, tamarins, and Goeldi's monkey are also known to beg for food, through specific body movements and vocalizations.

### Taxonomy

The use of acoustic signals occurs widely in Primate species, both intra and interspecifically, and such signals are known to vary in their physical structure. Primatologists often use such signals to help locating and surveying their primate species because of the acoustic diversity encountered in these animals. In fact, acoustic diversity has been used as one mean to solve taxonomic uncertainties (Blair et al. 2011). Moreover, loud or long distance calls can be used as a fingerprint to help differentiating among sibling species for taxonomic diagnosis (Hending et al. 2017). Quantitative knowledge of vocal repertoires can help in such tasks, through acting as the basis for comparative analysis (Fischer et al. 2016).

The differentiation between species based on acoustic properties of the calls has already been proved efficient for *Callithrix* species in the Neotropics (e.g., Snowdon et al. 1986). Calls from different primates do sound and look spectrographically different (Fig. 2). Currently, we only know of the vocal repertoire of about 10% of the





**Platyrrhine Vocal Communication, Fig. 2** Structure of vocalizations from four South American monkeys, showing their differences. (a) *Sapajus flavius*, blonde capuchin monkeys (Image: Bezerra – camera trapping);

(b) *Callithrix jacchus*, common marmosets (Image: Bezerra); (c) *Saimiri sciureus*, squirrel monkeys (Image: Campelo); (d) *Callicebus nigrifrons*, black-fronted titi monkeys (Image: Cäsar)

Platyrrhine primates (e.g., Bezerra et al. 2017). As a result, basic research to fully describe the vocal repertoires of Neotropical primates is urged, so that vocalizations can be used as a behavioral character to supplement other taxonomic data to study primate phylogeny and provide taxonomic elucidations.

## Referentiality

Primates communicate about objects and events in their environment in ways that allow recipients to draw inferences about the nature of event experienced by the signaler. This finding has relevance to theory addressing the origins of human language, a system strongly characterized by referential communication (e.g., Fitch 2010). Previous research efforts, however, have been heavily biased toward Old World primates with relatively few studies with New World monkeys, providing limited scope for the development of theories addressing the evolutionary origins of language-relevant capacities. Functionally referential calls must show both context specificity of call production, where the signal is produced in a context-specific way, and perception specificity, where the signal alone is sufficient to evoke an appropriate response to listeners in the absence of the eliciting stimulus (Macedonia and Evans 1993). When studying two sympatric species of tamarins (*Saguinus fuscicollis* and *Saguinus mystax*), Kirchhof and Hammerschmidt (2006) have found that these animals responded with adequate antipredator reaction after hearing playbacks of calls originally given to aerial and terrestrial disturbances. In another study, Wheeler (2010) provided evidence that tufted capuchin monkeys (*Sapajus apella*) also showed appropriate responses after hearing “barks” (aerial predator calls) and “hiccups” (generalized disturbance call), which were produced in the relevant contexts. Recent studies have also shown that black-fronted titi monkeys (*Callicebus nigrifrons*) produce vocalizations in response to natural and experimental predator models. Habituated

groups reliably uttered one of two alarm call types, call A (“chirps”), as a first response to raptors (whether flying, perched or calling) in the canopy and the other alarm call type, call B (“cheeps”), in response to several disturbances on the ground, including to species of predator models (snakes, oncilla, puma, and tayra) and to a control stimulus (deer) on the ground (Cäsar and Zuberbühler 2012). Further evidence suggested that some of these sequences are meaningful to conspecific receivers, by indicating the general predator class and location of threat (Cäsar et al. 2012). Analyses of call order and number of calls per sequence suggested that callers might be able to convey information about predator type and location (Cäsar et al. 2013). However, playback experiments are still needed to investigate if listeners are able to attend to these sequential variants. Although relevant, this selection of studies almost comprises the entirety of researches on referential communication with Neotropical primates alarm calls. The situation is in striking contrast with the research agenda on Old World monkeys and apes, thus begging for an urgent broadening of the research with Platyrrhines. Also, up until now, there are only a few studies with reference calling in feeding, and none in social contexts, which creates a huge gap in our knowledge of referential communication in Neotropical primates.

## Applied approaches

Besides their intrinsic interest, researchers have recently started to use primate calls to pursue more applied objectives outside the behavioral domain, particularly so in surveys and censuses. The first, and most basic, way to do so is to include vocalization as indirect evidence of the presence of a species. With some training, researchers can estimate distance of the caller(s) to their location. Then, alongside data on the direction of the call (with a compass), researchers can then use calls in more systematic surveys, as suggested by Gestich et al. (2017). Whichever the approach, researchers

can further improve study design by playing back calls in their study region through a loudspeaker (usually loud calls, particularly if employed in intergroup agonistic interactions). Such broadcasting is carried out in an attempt to stimulate individuals/groups to counter-call, thus increasing the chance of locating callers. Last, researchers have recently started to employ automatic acoustic recorders, which are devices deployed in the environment which record sounds at a previously determined schedule, being capable to operate for months in a row. Later on, the recordings are scanned (manually or automatically) searching for the sounds of the species of interest.

Future studies should also investigate the vocal behavior of other species, including species that are difficult to study in their natural environments, such as uacaris, cuxius, sakis, and night monkeys. A further way to improve knowledge on those species is to study them in captivity (Bezerra et al. 2017).

## Conclusion

Platyrrhines or New World Monkeys live in Central and South America and are mostly arboreal species. Communication occurs when one individual influences the behavior of another through the transmission of specific signals. Communication in primates can occur through vocal, chemical, tactile, and visual signals. Although many Neotropical primates have been reported to communicate using olfactory, visual, and tactile cues, acoustic communication is the most widely studied modality in this group. All Neotropical primate species employ acoustic communication for a variety of functions – including mate attraction, territory and mate defense, travel coordination, alarm against predators, and several affiliative and agonistic interactions – and all species studied so far have a quiet large repertoire. Although some genera or species have been studied significantly more than others, there is still uncertainty regarding the vocal behavior of even some of the most studied

animals. A major problem with some studies is that little effort was made toward precise quantification of call structures. Despite that, some recent studies have shown the presence of quite complex vocal systems, which have added some important information on the communicative abilities of New World monkeys; an independent radiation within the primate lineage with essential differences in life-history and socio-ecological characteristics from other primates.

## Cross-References

- ▶ [Affiliative Behaviors](#)
- ▶ [Affiliative Bond](#)
- ▶ [Agonistic Behavior](#)
- ▶ [Alarm Calls](#)
- ▶ [Allogrooming](#)
- ▶ [Auditory Signals](#)
- ▶ [Categorization](#)
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- ▶ [Territory Defense](#)

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## Platyrrhine Vocalizations

- [Platyrrhine Vocal Communication](#)

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## Platypus

- [Monotreme Sensory Systems](#)

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## Platyrrhine

- [Haplorhini](#)
- [Primate Sensory Systems](#)

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## Platyrrhine Cognition

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## Synonyms

[Cognitive capacities](#); [Cognitive functions](#); [Cognitive processes](#); [Intellectual abilities](#); [Intellectual capacities](#); [Intellectual functions](#); [Intellectual processes](#); [Intelligence](#); [Mental abilities](#); [Mental](#)

[capacities](#); [Mental functions](#); [Mental processes](#); [Synonyms for cognition](#); [Cognitive abilities](#); [Synonyms for platyrrhines](#); [Neotropical monkeys](#); [New World monkeys](#); [Platyrrhini](#)

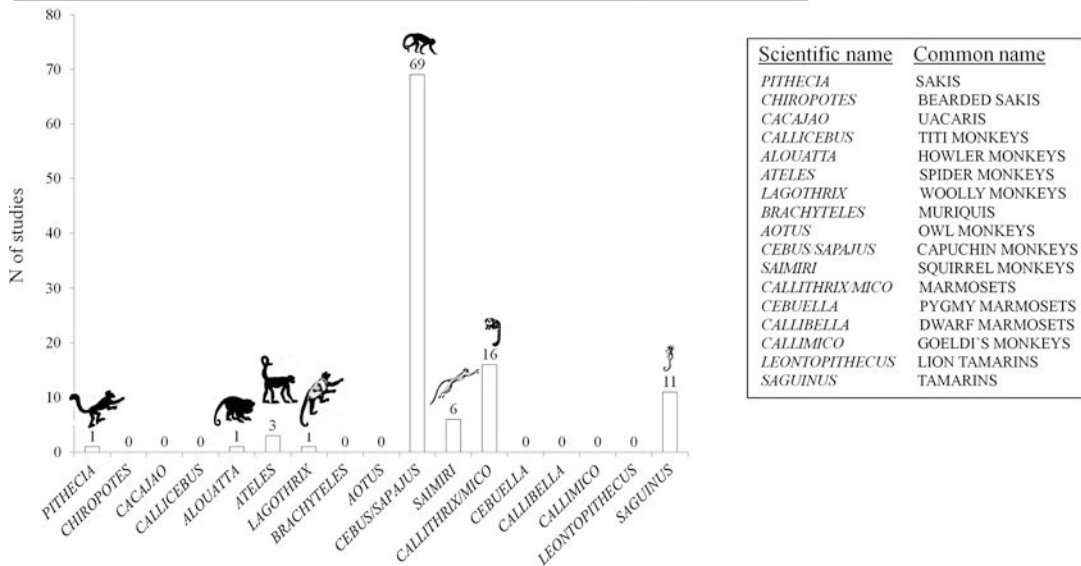
## Definition

*Platyrrhine cognition* (from Latin *cognitio* which means “knowledge”) can be defined as the set of mental functions by means of which New World monkeys acquire and use information – knowledge – to solve the problems they face in their environment.

## Introduction

Platyrrhines, or New World monkeys (NWM), started their independent evolution from catarrhines, or Old World monkeys (OWM), about 30–40 million years ago, when they arrived to the then island continent of South America. Living species include nonhuman primates from South and Central America. They are a very diverse group of small to medium-size species (range, <100 g to ~10 kg in weight) characterized by distinctive ecological and morphological adaptations (Fleagle 2013). First serendipitous observations on platyrrhine cognitive capacities date back some centuries. The most famous one is probably that reported by the British naturalist Erasmus Darwin, the grandfather of Charles Darwin, who observed a capuchin monkey cracking open a nut with a stone in a park in London. Scientists like Erasmus Darwin, George Romanes, Thomas Belt, and Heinrich Klüver were impressed by the abilities of capuchin monkeys, although early prejudices against the intelligence of NWM in comparison to OWM and apes prevented their observations from being highlighted within the scientific community. Systematic research on platyrrhine cognition expanded in the second half of the twentieth century. Since then, the combined efforts of natural observations and controlled laboratory tests have



STUDIES ON PLATYRRHINES PUBLISHED IN *ANIMAL COGNITION* (1998-JUNE 2017)

**Platyrrhine Cognition, Fig. 1** Number of studies on platyrrhine cognition published from 1998 to June 2017 in *Animal Cognition*, an interdisciplinary journal publishing research on all aspects of animal cognition. Search performed on June 21, 2017 using both scientific and

common names of platyrrhine genera in article titles. Although far from being exhaustive, this search is supposed to reflect the relative amount of studies on different taxa published in the overall literature

produced much evidence of cognitive abilities by means of which platyrrhines solve problems both in physical and social contexts. The remainder of this entry touches several research areas on platyrrhine cognition. To date, a limited number of genera have been investigated, typically those widespread in cognitive laboratories, whereas many taxa have been less – or not at all – studied (Fig. 1).

## Platyrrhine Cognition in Physical Contexts

Platyrrhines live in forest environments. They have arboreal habits with little or any propensity to forage or move on the ground, except for some species of *Sapajus*, which can spend a large amount of time feeding on the ground (Fleagle 2013). There are only two genera, *Alouatta* and *Brachyteles*, that specialize on eating leaves, whereas most of the species specialize on fruits, tree gums, or insects. Mastering challenges in the physical environment requires the capacity to

locate and process food resources, avoid predators, and choose safe resting sites. Ultimately, this means to learn how to use information about places, foods, and dangers. To deal with such problems, each species is equipped with its own peculiar anatomical and mental characteristics to perceive, memorize, and categorize external information and to plan and perform appropriate actions.

## Perceiving Objects

Perception allows the integration of information coming from sensory systems into organized stimuli (objects, sounds, tastes, etc.). Primates mainly rely on sight to gather information from the environment; therefore, the way they see the world deeply affects their cognitive abilities. Visual stimuli are identified by means of several perceptual cues such as color and shape. Excellent color vision is a prominent characteristic of primates in comparison with other mammals; therefore, it is one of the best-studied aspects of vision in these species (Jacobs 2012). Color perception is essential for primates to distinguish ripe from

unripe fruit, to identify ripe fruit and young red leaves against a background of green foliage, and to detect the coloration patterns of both preys and predators. All platyrrhines are active during the day and capable of perceiving colors, apart from the nocturnal genus *Aotus*. In most diurnal platyrrhines, heterozygous females have three color receptors (trichromatism), whereas homozygous females and males have two color receptors (dichromatism) and cannot easily distinguish reds and greens, as color-blind humans. In addition to colors, animals use other perceptual cues to group single parts of the perceived field to form an object. A fundamental property of visual scenes is that they are organized hierarchically: scenes are made up of different objects, which themselves are organized into parts and elements. There is evidence of perceptual grouping differences across primate species. Since the pioneering work by David Navon (1977), it has been repeatedly demonstrated that human vision starts from an analysis of the global configuration of the scene and only subsequently proceeds to the analysis of the details. Among platyrrhines, preference for global or local information has been studied extensively in captive capuchins. Capuchins show a mode of processing opposite to the global dominance of humans, despite the similarity of their visual systems. When tested with a variety of tasks presenting figures made of smaller elements that form larger configurations, capuchins detect more accurately local elements than global configuration of visual stimuli. A similar tendency to privilege the local elements has also been found in catarrhines of the genus *Papio* and in birds (Aust 2017; Fagot et al. 2012). It is still unclear whether and to what extent perceptual grouping processes affect object identification strategies of different species.

### Memorizing Objects and Places

Learning and memory allow animals to acquire information at one time and to retrieve them at a later time. Thanks to these abilities, past experiences can be used to adopt more efficient behaviors in the future. Monkeys need to learn and memorize information important for their survival, such as what types of food or objects are

located at particular sites in their territory. For efficiency of movement between feeding sites, animals must be able to memorize topographical features and reference points that are fixed in their location (landmarks) and therefore are reliable indicators of places. They can use cues such as landscape contours, forest margins, and trees of particular shape or size to move from one location to another. Several studies found that NWM as marmosets, squirrel monkeys, tamarins, and capuchins can memorize a landmark and use it as a beacon to find hidden food. However, among these taxa, only tamarins seem to be able to locate hidden food using the spatial relationship between multiple landmarks, which means they can rely on a configuration of multiple landmarks as a single source of information (Dolins and Mitchell 2010). It is still controversial precisely how NWM integrate spatial information and if they use internal representations of the space (*cognitive-like maps*) to reduce travel time and effort.

Along with the ability to memorize places, animals need to bear in mind objects through space and time even when they are currently not perceived. This ability, called “object permanence” (Piaget 1952), develops very early in human ontogeny and is widespread in the animal kingdom (Cacchione and Rakoczy 2017). According to Piaget, cognitive development in infancy proceeds in stages that correspond to different levels of representational abilities, and his theory has proved as a useful framework for developmental and comparative studies. Findings on NWM tested so far (tamarins, marmosets, capuchins, woolly monkeys, spider monkeys, squirrel monkeys) showed that most species can keep track of and search for objects displaced in full view of the subject (*visible displacement*), whereas their ability to track the displacement of hidden objects (*invisible displacement*) is more unclear (Cacchione and Rakoczy 2017). For example, in the *transposition task*, in which the object is placed under one of two/three containers, while the subject is watching and the containers are subsequently shuffled without revealing their content, capuchin and spider monkeys located the baited container significantly less than great apes. So far, only few individuals of marmosets,

tamarins, capuchins, and spider monkeys solved the invisible displacement tests suggesting that the cognitive load imposed by these tasks verges on the upper limit of their representational abilities. Mastering such problems involves the mental reconstruction of an unseen trajectory, rudimentary logical reasoning, as well as the ability to refrain from searching in previously rewarded locations and to retain relevant information for a varying amount of time.

### Motor Planning for Reaching and Grasping Objects

Motor actions, such as reaching for and grasping objects, are often guided by the actor's *anticipation* of upcoming postural and task demands. This ability may provide a scaffold for the development of more sophisticated cognitive abilities such as tool use, long-term planning, and inhibition. For example, in *detour* tasks, individuals have to refrain from reaching directly for a reward they can see, because it is blocked by a clear barrier, but they can access the food by going through a lateral opening. Capuchin and spider monkeys successfully inhibited the tendency to reach directly for food outperforming tamarins, marmosets, and squirrel monkeys (e.g., Rosati 2017). Interestingly, tamarins' performance at detouring improves when the barrier is opaque and food is not visible, probably because it is easier to control the prepotent reach toward food. Other experiments with NWM suggest that the rudimentary motor planning abilities appear to be shared across species (Rosenbaum 2017). Cotton-top tamarins presented with an upside-down transparent cup that had food stuck to its bottom interior grasped the stem of the cup with an uncomfortable hand posture (with the thumb down) in order to easily rotate it and reach a comfortable final hand posture. Recent evidence also suggests that squirrel and capuchin monkeys engage in similar motor planning. Moreover, capuchins show action-selection planning when using tools to interact with distally located targets. These findings suggest that NWM are capable of predicting the likely consequences of future movements and use that information to select proper actions.

### Using Objects as "Tools"

Once having grasped an object, primates can explore and manipulate it, for example, by combining it with another object or a surface. By performing object manipulations and combinations, they acquire information about objects, and the feedback generated from their actions can lead to the acquisition of tool use. Tools – as extensions of the body – allow obtaining goals otherwise difficult or impossible to achieve, for example, giving access to out-of-reach foods. Among NWM, capuchins are the only taxon in which "true" tool use is widely present. True tool use implies that the manipulator is responsible for the proper and effective orientation of the tool and uses it "to alter more efficiently the form, position, or condition of another object, another organism, or the user itself" (Shumaker et al. 2011, p. 5). Advanced perceptuomotor abilities are fundamental to develop manipulations that require the management of at least one allocentric spatial relation, that is, a relationship between the "tool" and a surface or another object (Visalberghi and Fragaszy 2012). Capuchins select and use tools on the basis of functional features and flexibly adapt to the requirements of the task at hand (Visalberghi et al. 2017). For example, they select stones, best suited to crack nuts open, on the basis of weight and/or the sound produced when tapped and not simply on the basis of size. Nut cracking is considered the most relationally complex form of tool use by nonhuman primates routinely found in nature and involves two allocentric spatial relations, one between the nut and the anvil and a second between the stone hammer and the nut. Capuchins typically manage these relations sequentially: the nut is placed and released on the anvil prior to striking it with the stone (Visalberghi and Fragaszy 2012) (Fig. 2).

To study also what other non-tool-using primate species understand about the functional characteristics of tools, researchers use tasks in which the manipulator is not responsible for the position of the "tool" and of other elements of the task (i.e., food and substrate or another object). In these experiments, monkeys are presented with two alternatives prearranged by the experimenter, and they have to pull one of two available "tools"



**Platyrrhine Cognition, Fig. 2** A male capuchin (*Sapajus libidinosus*) uses a stone to crack open a palm nut in Brazil (Photo: N. Spagnoletti)

(e.g., canes, hoes, sticks, strings, clothes) in order to obtain a food reward. In such tasks, cotton-top tamarins recognize that effective pulling tools must be made of rigid materials, but they do not recognize either the relationship between the tool's orientation and the position of the food reward or the relationship between the tool's trajectory and the substrate where it moves on (Ruiz and Santos 2013). Unlike tamarins, capuchins solve this kind of problems involving two and three relations (i.e., food, tool, and one type of hindrance – an obstacle or a trap – which could prevent success). For example, capuchins spontaneously use sticks to retrieve food placed inside a transparent tube. However, they do not seem to understand the relationship between pushing food with the tool and the substrate on which food travels (Visalberghi and Frigaszy 2012). In fact, when they had to push the food outside of the tube avoiding a trap, the only successful subject solved the task using the rule of “inserting the stick into the opening of the tube farthest from the reward.” These tasks are also used to investigate whether

primates understand that the tool must be in contact and connected with the reward in order to be functional. NWM tested (common marmosets, cotton-top tamarins, capuchins) could choose the tool functionally connected to the food after some training. Moreover, when presented with parallel and crossed-string configurations, some NWM seemed to use the strategy of choosing the string closest to the food (Seed and Mayer 2017). However, reliance on proximity is ineffective in other conditions, for example, when one of the strings is broken. In this case, participants have to choose between an intact and a broken string as means to a reward. Capuchins perform better in this standard condition than when nonfunctional perceptual cues are added (i.e., the original strings are covered by ineffective broken and unbroken strings), suggesting that they understand the task's functional properties.

### Quantifying Objects

The ability to deal with quantitative aspects of the world is adaptive in a variety of ecological contexts. During foraging, for example, it allows to evaluate if one fruit is larger than another fruit (nonnumerical quantification of continuous quantities) or if one tree has more fruit than another tree (numerical quantification of discrete quantities). Since the beginning of the twentieth century, research on animal cognition has given special attention to numerical competence because of its potential to shed light on how advanced human numerical cognition and mathematic reasoning emerged through evolution. Studies on discrete quantity judgments demonstrated that marmosets, tamarins, squirrel monkeys, and capuchins are able to discriminate food sets differing in numerosness. The vast majority of these studies have been conducted using two sets including a different number of food items. Similarly to other primates, platyrrhines are able to discriminate food sets differing in numerosness and to choose the larger food amount, although their discrimination ability is mediated by the ratio between the two quantities (Beran 2017). Discrimination becomes more difficult when the to-be-compared sets are more similar in quantity, and this difference approaches a 1:1 ratio. Such a *distance effect*



follows Weber's law, according to which the discriminability of two magnitudes does not depend on their absolute magnitude differences but on their ratio, and has been reported also in catarrhines (including humans) as well as in several nonprimate species. Moreover, some studies indicated that, similarly to other animal species, NWM are better with small than with large item sets, an effect called *size* (or *magnitude*) *effect*. Many authors explain the well-established *distance* and *size effects* with a core processing system, the approximate number system (ANS), in which quantities are represented inexactly, with increasing variance in discriminating or estimating set sizes as the true set sizes increase. The existence of a second system for quantitative judgments in nonhuman primates is still under debate, which is supposed to be a precise but size-limited system that accurately represents small quantities but cannot accommodate sets greater than four items because of limits in memory and attention.

### Understanding Similarities

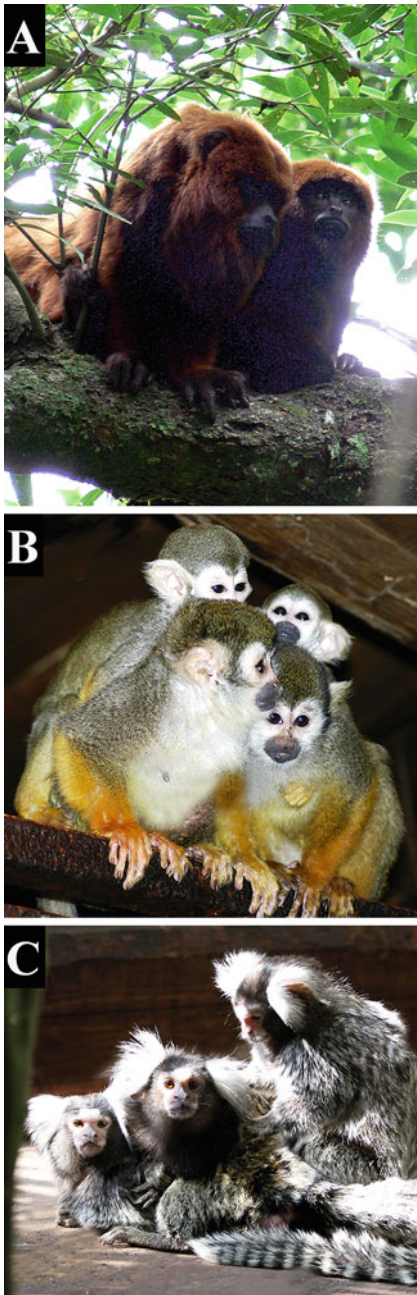
If an appropriate response is known for a familiar object (or problem), it is important to use the same response also with novel objects (or problems) that resemble it. The ability to recognize similarities between objects enables an individual to sort stimuli into equivalence classes and to respond efficiently to novel objects saving cognitive resources. NWM, as other animals, can solve several cognitive problems based on physical similarity between objects. At the simplest level, monkeys can learn to choose objects featured by a certain characteristic such as color or shape when systematically rewarded to do it. Moreover, studies on capuchins found that they can solve more advanced matching-to-sample (MTS) tasks following similarity rules. In the MTS, individuals have to choose which of the two comparison stimuli resembles most closely a target stimulus (sample). Capuchins can solve the MTS with trained stimuli and, after extensive training, can also match stimuli they have never seen before. Dealing repeatedly with problems requiring similar solutions is proven to enhance generalization abilities; such an effect

has been found in many animal species including marmosets, capuchins, spider, and squirrel monkeys. Therefore, NWM are able to use not only similarities among objects but also similarities across sets of problems. According to Harlow (1949), this learning-to-learn pattern (*learning sets*) is a cognitive process indicating that an animal does more than adapt by trial and error to changes in the environment: it learns how to efficiently deal with similar problems it encounters over and over again. In general, the ability to understand and use similarities among objects and among problems emerges clearly in platyrrhines when objects or problems can be judged as similar on the basis of their physical features. On the contrary, in these species, there is still scarce evidence of the ability to manage similarities based on abstract relations which are weakly or, not at all, embedded in the perceptual domain (Thompson and Oden 2000; Wasserman et al. 2017).

### Platyrrhine Cognition in Social Contexts

Platyrrhines show an impressive range of variation in social systems, particularly in view of the comparatively narrow ecological range available to them (Fleagle 2013). Many of them live in monogamous social groups (*Aotus*, *Callicebus*, and *Pithecia*) that are seemingly stable for several years. One genus (*Alouatta*) lives in single-male groups in some environments and in multi-male groups in others or when the population density changes at different sites. *Cebus*, *Sapajus*, and *Saimiri* live in more complex hierarchical multi-male and multi-female groups. *Ateles*, by contrast, typically live in "fission-fusion" societies, in which the individual members of a large community associate on a daily basis in small and flexible parties, frequently changing size and membership. The relatively small marmosets and tamarins (Callitrichinae) show highly flexible patterns of social organization and mating system. These latter species are all communal breeders with many group members aiding in the raising of infants. Such platyrrhine diversity in social systems can thus be highly valuable for better understanding





**Platyrrhine Cognition, Fig. 3** (A) Howler monkeys (genus *Alouatta*), photo: I. Agostini; (B) squirrel monkeys (genus *Saimiri*), photo: A. De Marco; (C) common marmosets (genus *Callithrix*), photo: A. De Marco

the ecological causalities underlying primate social behavior and cognition (Fig. 3).

NWM thus need substantial cognitive skills to deal with intricate relationships and complex

social interactions. Individuals must recognize other group members and continuously track their position, social behavior, and foraging success; classify group members by attributes such as age, sex, and dominance rank; and update this information as circumstances change (Smuts et al. 2008). Even in callitrichines, which live in small groups, there are complex breeding systems that require enhanced socio-cognitive and communicative skills: individuals need to carefully monitor others, to reciprocally coordinate actions spatially and temporally, and to show high levels of responsiveness to others' cues. It is therefore not surprising that social context has been recognized as one of the main driving forces shaping the evolution of problem-solving capacity in primates (Whiten et al. 2011). The following sections will offer an overview of several cognitive skills that allow platyrrhines to successfully deal with their social environment.

### Learning from (with) Others

For many animal species, including NWM, the most pressing problems arise in locating and obtaining food. By living in groups, they can benefit from an increased opportunity for observing the foraging behavior of others and possibly learn about new types of food or new foraging techniques through social facilitation (King 1994). Social facilitation occurs when naïve individuals can learn to eat novel food more readily with others than when alone. For example, infants of both golden lion tamarins and common marmosets are more likely to eat novel food in the presence of adults eating the same food than when alone. Social facilitation occurs in capuchins too but seems to be aspecific: seeing companions eating motivates capuchins to accept novel food items, even when such food does not match with what others are eating. The opportunity to observe a skilled conspecific executing food manipulations can attract the attention of naïve individuals to some salient features in the environment (e.g., tools used to access food, food leftovers, place of food activities) and increase the likelihood of acquiring the observed behavior by individual learning. Such mechanisms, called “local enhancement” or “stimulus enhancement”

(Thorpe 1956), play a fundamental role in the acquisition of foraging techniques in many primates, including NWM. For example, common marmosets that could scrounge the leftovers produced by a model solving an instrumental task learned significantly better to obtain food compared to individuals that could only observe the model or with no social experience. Fragasz et al. (2004) have carried out the most systematic program of research on social learning on capuchins, observing them in several tool-use tasks both in the wild and in captivity. Their findings support the view that stimulus enhancement together with trial-and-error learning (i.e., individual learning) is at the basis of tool-use acquisition in these monkeys.

Evidence of more advanced forms of social learning in NWM are still very scarce (Tomonaga et al. 2012). One of the most debated learning processes is imitation, defined as the ability to learn by copying a novel or improbable behavior performed by others. Imitation is considered highly complex in cognitive terms because it supposedly relies on the capacity to attribute mental states to others (e.g., understanding other's goals or intentions). In general, it is knowingly difficult to experimentally rule out the effect of simpler forms of social learning when testing for imitation. To date, the only evidence of such ability in platyrrhines was found in common marmosets. Marmosets were tested with the *two-action method*: in such task, naïve subjects can watch two demonstrators that use different actions to solve the same task (e.g., opening a box by pushing a door or by sliding it laterally). Some subjects were able to accurately copy the action performed by the demonstrators, suggesting the occurrence of imitation. Such surprising performance is supposedly grounded in the cognitive mechanisms supporting the cooperative breeding systems of callitrichines.

### Understanding What Others Can (or Cannot) See

Often treated as the main cognitive gap between humans and other animals, the ability to

understand what other individuals “see” or “think” has been subject to immense research activity since Premack and Woodruff (1978) first asked: “Does the chimpanzee have a theory of mind?” Despite the effort, evidence for such skills in nonhuman primates (beside great apes) is still controversial and especially fragmentary in NWM. The ability to follow the gaze of others is an adaptive skill that might have been selected as a mean to obtain information about food location, predators, and social interactions among group members. From a cognitive perspective, a low-level explanation considers it an innate response triggered by something shifting individual's attention (like a human's head turn) to an external target, while higher-level explanations rely on the ability to understand what others see up to the more advanced capacity to form a mental representation of the visual knowledge of others. Many paradigms have been used to investigate perspective-taking abilities of NWM. Object-choice tasks, where subjects can use a (human) cue to infer the correct choice of a reward hidden in one of a number of containers, evidenced eye-following skills in marmosets and tamarins. The ability to follow other communicative cues was also found in squirrel and capuchin monkeys. A more difficult task requires subjects to track a looker's gaze that points toward objects hidden behind opaque barriers. In such situations, to identify the interesting object, the individual following the gaze of the looker needs to understand that in order to see what the looker can see, he needs to turn around the barrier. Both spider and capuchin monkeys succeeded in the task, while marmosets did not (Kaminski 2017).

Hare and colleagues (2000) studied perspective taking using a more ecologically valid approach, in which subjects are tested with conspecifics (rather than a human experimenter) and in a competitive context (rather than a cooperative one). This paradigm tests whether a subordinate subject would more likely go for a food item that a dominant individual cannot see than toward one that is in dominant's line of sight.

Such behavior would indicate that subordinate can take the perspective of the dominant subject. When subordinate capuchins were allowed to choose which piece of food to retrieve before the dominant would do so, they did not choose preferentially the hidden food, suggesting that they were not taking into account what the dominant could or could not see. By contrast, subordinate common marmosets showed a preference for the hidden piece of food, but such findings can be possibly explained by simpler cognitive mechanisms than true perspective taking, such as by perceiving conspecific's communicative cues as indicating a possessive relationship between looker and target object. The present state of evidence parsimoniously suggests that NWM do not have a true understanding of others' perspective and that simpler cognitive mechanisms could explain the abilities to exploit others' communicative cues.

### Working Together

Coordination allows the expression of fundamental shared activities in primates' life such as caregiving, vigilance, and group and territory defense. The cognitive functions underlying the ability to coordinate own's action with others stay at the core of social cognition: in coordination actions, individuals have to negotiate a shared goal, monitor the behaviors and the signals of partners, and somehow communicate their respective roles. High degree of tolerance may increase the possibility for individuals to act together, which in turn may set up the conditions for the development of more advanced cognitive skills of shared intentionality and for cooperating in ever more complex ways. Researchers have employed a large variety of methods and of paradigms in the effort to understand how, when, and why primates cooperate. In one of the most common experimental paradigms used in laboratory, two animals need to work together on a task to obtain rewards. For example, animals are required to simultaneously pull two ropes so to successfully reach a platform containing food or

to pull two handles to release some food reward. Although the protocols vary considerably, the logic behind is that if either one does not participate, neither will profit. Variants of this paradigm have been extensively applied to many species, including NWM: common marmosets, cotton-top tamarins, and capuchins all show the ability to coordinate their behaviors to solve the task, with tamarins being the species with higher efficiency rates (Cronin 2017). The success in reward achievement depends of course on many factors, firstly on how (or if) the reward can be shared among partners. Differences in the degree of tolerance across NWM species may play a role in determining the success in such joint tasks. For example, when partners are presented with a single reward to share, highly tolerant species such as cotton-top tamarins cooperate (albeit less than when both partners are rewarded separately), and in both tamarins and marmosets, cooperation is sustained even when the reward is given to only one partner. By contrast, cooperation is drastically reduced in less-tolerant species such as capuchins. The achievement of the reward may well depend upon the social relationship between partners. For example, in capuchins, cooperation levels (and reward sharing) are higher between close kin (e.g., mother-daughter) than non-kin. In a modified version of the string-pulling task in which only one partner is allowed to pull the rope and the other to grasp the food, marmosets cooperated, and the successful dyads were the ones in which the partner obtaining the food did not monopolize it.

Variation in task performance is used to evaluate what monkeys understand about this task and what cognitive abilities are used to solve it. For example, if subjects understand the cooperation task, they should rarely work when alone compared to when a partner is present. Indeed, capuchins are more likely to pull when their partners are present and in reach of the handle, but do not appear to time their pulls with those of their partners. Therefore, capuchins learn to make an association between the task and the location of their partners, although not considering the pulling as a

critical element of the task. Similarly, tamarins are more likely to manipulate levers in the presence of their partners than when alone suggesting some understanding of the role of the partner (Cronin 2017). The opportunity to monitor each other's behavior during the task is important too. It has been shown that if an opaque barrier is placed between the partners, capuchins can't sufficiently coordinate their pulling to reach the food. This suggests that coordination does not simply occur by chance but that some form of intentional cooperation is likely to occur. To sum up, these findings suggest that NWM are able to coordinate their actions in space and time and adjust their own effort in association with the presence, location, and relationship with their partners. The behavioral repertoire associated with the cooperative breeding system of callitrichines may help explaining why cooperation is more common and possibly more efficient in marmosets and tamarins than in species with less egalitarian social systems such as capuchins.

## Conclusions

Cognitive abilities evolved, thanks to the interplay of physical and social environmental forces. The study of platyrrhine cognition is crucial to disclose specific (sometimes unique) adaptations that each species has for its own physical and social environment. Some taxa are highly proficient in combining objects, as exemplified by the case of tool use in capuchin monkeys, whereas other taxa, like marmosets, stand out for their ability to imitate conspecifics. To date, cognitive capacities of the vast majority of NWM still remain poorly, or completely, unknown. Hopefully, future research will provide findings to fill this gap. Contemporary research can exploit increasingly advanced instruments to study animal behavior and cognition. The sad paradox is that most platyrrhines are increasingly endangered by the loss of their habitats and might not survive long enough to be studied.

## Cross-References

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## Platyrrhine Diet

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### Introduction

New World monkeys belong to the primate infra-order Platyrrhini, and they include ca. 152 species (Rylands et al. 2012), 20 genera, 7 subfamilies, and 3 families (Cebidae, Atelidae, and Pitheciidae) (Groves 2017), distributed from southern Mexico to northern Argentina. They range in size from 100 g (pygmy marmosets) to 10 kg (muriquis), and despite being mainly arboreal, they occupy a wide variety of habitats and foraging niches. Fruit is an important component of the diet of most genera; however, they also include leaves, flowers, seeds, nuts, nectar, and invertebrate and vertebrate prey as foods. In addition, some genera show extreme specialization and anatomical and physiological adaptations for feeding on gums (*Cebuella*, *Callithrix*) and fungi (*Callimico*).

Traditional studies of primate feeding ecology describe the diet of different taxa according to the time spent foraging and feeding on different items. Recent frameworks in nutritional ecology recommend collecting and reporting feeding data based on the estimated amount of food and nutrients consumed by the study individuals (Garber et al. 2015), since the quantity of food actually ingested varies greatly depending on food characteristics, food availability, and age/sex of the forager. Obtaining more precise dietary data can be achieved by recording feeding rates (e.g., number of items ingested per minute) and collecting food samples, that later can be dried, weighed, and analyzed for different macronutrients (e.g., protein, lipids, carbohydrates), micronutrients (e.g., minerals), and secondary metabolites (e.g., tannins, alkaloids). Analyzing the nutritional

composition of the selected food items is particularly valuable due to the high variability in the nutritional content of plant parts belonging to different plant genera, species, and even individual trees. As a consequence, it is important to point out that broad characterizations and classifications of feeding strategies, such as folivory, frugivory, and insectivory, are not the best indicators of the nutritional and energetic quality of a diet.

An excellent example of this phenomenon is that primate communities in the Neotropics include more frugivorous taxa than those found in Asia and Africa. This pattern has been attributed to differences in plant species diversity and fruiting patterns as well as nutritional content on the American continent. Specifically, in the Neotropics, young leaves (a good source of protein) tend to be scarce during periods of low fruit availability; there is a high diversity of trees, such as figs, that can be “keystone” resources (i.e., resources that play a critical role in maintaining the structure of an ecological community) during times of general food scarcity; and fruits tend to contain on average more protein than fruits found at other sites (e.g., Madagascar) (Ganzhorn et al. 2009).

Nevertheless, platyrrhines display a wide range of dietary strategies associated with morphological, physiological, and behavioral adaptations. These strategies are generally shared by members of the same subfamily:

### Family Cebidae

#### Subfamily Cebinae (Genera *Cebus*, *Sapajus*, *Saimiri*)

Capuchins (*Cebus* spp. and *Sapajus* spp.) and squirrel monkeys (*Saimiri* spp.) are the two most omnivorous platyrrhines, since their diet can be composed of fruits, flowers, leaves and other plant parts, invertebrates, and vertebrates (such as squirrels, other small mammals, frogs, lizards, and birds). Capuchins are described as opportunistic foragers, whose manipulative abilities and strength help them obtain foods that are unavailable to other species. Their diet, however,

is broadly described as mainly fruit-based, whereas squirrel monkeys rely more heavily on insects. Still, what most characterizes the diet of these taxa is that it can drastically change according to the habitat, the season, or the availability of resources. For example, two neighboring groups of *C. capucinus* in Costa Rica could fit opposite dietary classifications, one being described as frugivorous (82% of their time spent feeding on fruit) and the other as insectivorous (44% of the time spent feeding on invertebrates) (Chapman and Fedigan 1990). Likewise, squirrel monkeys can subsist on a diet composed entirely of insects for short periods during seasons of food scarcity.

### Subfamily Aotinae (Genus *Aotus*)

Owl monkeys (*Aotus* spp.), also called *douroucoulis* or *mirikinás*, concentrate their activity during the night, with peaks at dawn and dusk; only one species, *A. azarae* *azarae*, shows cathemerality (i.e., intervals of activity can occur either during the day or during the night). Quantitative descriptions of feeding patterns for the strictly nocturnal species that range from Panama to Paraguay are scarce; however, studies of cathemeral owl monkeys in Argentina have provided some information on their diurnal diet. They are primarily frugivorous (45–66% of their time devoted to feeding on fruits), but they also can feed on leaves (15–41%), flowers (1–14%), insects, and fungi (Fernández-Duque 2011). However, given the difficulty to observe insect-eating in nocturnal and cathemeral primates, owl monkeys might be more insectivorous than reported.

### Subfamily Callitrichinae (Genera *Callithrix*, *Mico*, *Cebuella*, *Callibella*, *Callimico*, *Saguinus*, *Leontocebus*, *Leontopithecus*)

Marmosets (*Callithrix*, *Mico*, *Cebuella*, and *Callibella*), tamarins (*Saguinus*, *Leontocebus*, and *Leontopithecus*), and callimicos or Goeldi's monkeys (*Callimico*) include ripe fruits, floral nectar, and arthropods in their diet, but are mainly known for harvesting and eating plant exudates (e.g., gums and saps), which may account for up to 67% of yearly feeding time in pygmy

marmosets (*Cebuella pygmaea*) and 83% in buffy-headed marmosets (*Callithrix flaviceps*) (Digby et al. 2011). However, only *Callithrix*, *Mico*, and *Cebuella* have anatomical and dental specializations allowing them to scrap holes in tree bark to stimulate the flow of exudates. This ability to create feeding sites allows marmosets to exploit exudates year-round as a preferred resource. On the contrary, tamarins and callimicos do not possess these morphological features and only feed on exudates opportunistically. *Callimico goeldii* feeds on exudates seasonally, but despite earlier studies reporting only a minor consumption (1% of the annual diet), more recent data show that exudates can account for 20% of this species' feeding time in the dry season (Porter et al. 2009). Callimicos preferred resources, however, are jelly (*Auricularia* spp.) and bamboo (*Ascopolyporous* spp.) fungi, which are consumed year-round but are particularly important during the dry season (up to 63% of the monthly diet) (Porter and Garber 2010). Nonetheless, fungi seem to be a low-quality resource, with small amounts of sugar, fat, starch, calcium, and more than 80% of dry matter constituted by fiber.

Several callitrichines are known for forming mixed-species troops, also described as interspecific associations of two or more species that usually travel together and coordinate activities. *Saguinus fuscicollis* frequently associates with other species of the genus *Saguinus* and with *Callimico* and *Callithrix*. The associated species avoid feeding competition by using different forest strata and foraging techniques. For example, *S. fuscicollis* specializes in manipulative foraging, searching for prey in small and closed microhabitats such as tree holes and epiphytic bromeliads, whereas other *Saguinus* species prefer exploring open microhabitats using visual cues.

## Family Atelidae

### Subfamily Atelinae (Genera *Ateles*, *Lagothrix*, *Brachyteles*)

Spider monkeys (*Ateles* spp.) and woolly spider monkeys (*Lagothrix* spp.) are known as “ripe fruit specialists,” and their diet is very diverse in terms

of fruit morphospecies consumed. However, while fleshy fruits preferred by *Ateles* are generally lipid-rich, those preferentially selected by *Lagothrix* tend to be sugar-rich. Spider monkeys also include other plant parts such as flowers, leaves, petioles, and bark in their diet, and during certain seasons, young leaves can be an important resource in several dry forests or in fragmented landscapes (e.g., ~30% of feeding time in *Ateles geoffroyi* living in forest fragments in the Lacandona region of southern Mexico, Chaves et al. 2012). At several sites, spider monkeys are also observed to visit mineral licks (*salados*) to feed on soil. Instead, *Lagothrix* can complement its diet with insects.

Muriquis (*Brachyteles* spp.) are the largest atelines (males average 9.8 kg). Together with *Alouatta* spp., they are reported to be predominantly folivorous, with 41–93% of their monthly feeding time spent on mature and young leaves. However, the annual diet of *B. arachnoides* in a continuous forest in Southern Brazil comprised >70% fruits, although the consumption of leaves can be high in certain months when fruits are not available (Talebi et al. 2005). As in howler monkeys, the digestion of high amounts of foliage is favored by energy-minimizing behaviors, such as having small day ranges (~600 m), being inactive for many hours (at least 6 h/day), and spending few hours (~1 h) traveling during daytime (Milton 1984a).

#### Subfamily Alouattinae (Genus *Alouatta*)

Howler monkeys (*Alouatta* spp.), which are currently divided into 12 species, have the widest geographical distribution of all New World monkeys, ranging from Mexico to Argentina and inhabiting a variety of seasonal and nonseasonal habitats. They are considered, together with *Brachyteles*, the most folivorous platyrrhines, with a diet composed of leaves, fruits, flowers, and other plant parts. Howler monkeys possess certain anatomical, physiological, and behavioral traits associated to leaf-eating: a capacious colon compared to other members of the Atelidae family, where fiber fermentation occurs; a relatively long food transit time for their body mass (>20.4 h for *A. palliata*); molars with high

shearing crests that favor an efficient processing of fibrous leafy material; and long periods of rest, limited within-group social interactions, and a small day range (Milton 1984b). According to a recent review of the howler monkey diet (Dias and Rangel-Negrín 2015), the degree of frugivory and folivory may depend on rainfall patterns, group size, and forest size. In particular, howler species that live in wetter habitats and in larger forests tend to be more frugivorous and have a more diverse diet than species living in drier forests. An alternative interpretation, based on feeding rates rather than on the proportion of time spent feeding on different food types, has proposed three different dietary syndromes consistent with howler monkey phylogeny and biogeography (Garber et al. 2015). Specifically, howler monkeys from Mesoamerica (*A. palliata* and *A. pigra*) and *A. seniculus* would be characterized by a balanced leaf and fruit diet, Amazonian species (*A. belzebul* and *A. macconnelli*) by a fruit-enriched diet, and Atlantic Forest and southern howler monkeys (*A. guariba* and *A. caraya*) by a leaf-enriched diet.

### Family Pitheciidae

#### Subfamily Pitheciinae (Genera *Pithecia*, *Chiropotes*, *Cacajao*)

Sakis (*Pithecia* spp.) are the smallest pitheciines (1.7–2.4 kg), and fruits, usually unripe and with a hard exocarp, constitute more than 60% of their monthly diet (Norconk 1996). They also consume leaves, flowers, and insects and have been described as the most folivorous of the pitheciines given that leaves can constitute >8% of *P. pithecia* monthly diet (Norconk and Conklin-Brittain 2004). However, their distinguishing characteristic is that they are seed predators, and their dental morphology allows them to open hard fruit. Sakis share with other pitheciines several derived characters associated with their seed predation habits: robust canine teeth and styliiform lower incisors, which help remove the hard pericarp protecting seeds, and very flat molars, which help in the trituration of seeds characterized by a soft and uniform consistency (Garber and Kinzey 1992).

Also bearded sakis (*Chiropotes* spp.) obtain 72–97% of their diet from fruits and consume large amounts of mature and immature seeds. During periods of low food availability, their intake of seeds may diminish and instead shift to fleshy fruits. Their consumption of leaves is much more limited than saki's, but they feed more on arthropods, which occasionally are important constituents of their diet (up to 26% of the feeding records during a given month) (Veiga and Ferrari 2006). As in other pitheciines, the exploitation of structurally challenging items (e.g., seeds, hard fruits) is favored by their dental adaptations, which include flaring canines that aid in opening hard fruits and uneven dental enamel with bands that are useful during chewing and prevent tooth wear. Bearded sakis also have very robust mandibles compared to sakis, confirming their lower degree of folivory, which is correlated with limited jaw robusticity in platyrrhines.

*Cacajao*'s masticatory system is very similar to that of *Chiropotes*, thus allowing feeding on a wide range of hard fruit parts and species. Ripe and unripe fruits and fruit parts, including seeds, comprise more than 85% of the diet of *Cacajao* (Boyle et al. 2016), which can be complemented by leaves (3–4%) and insects (2–5%) (Norconk 2011).

### Subfamily Callicebinae (Genus *Callicebus*)

The diet of titi monkeys (*Callicebus* spp.) includes mainly fleshy fruits (50–82%), leaves (4–66%), and insects (0–20%) (Norconk 2011; Boyle et al. 2016). Compared to the other pitheciids, this genus is considered less of a seed predator, due to the lack of dental adaptations for feeding on hard fruits. However, they are known for feeding opportunistically on immature seeds when they are available.

## Platyrrhine Feeding Ecology

Despite representing a variety of specialized dietary niches, platyrrhines and the study of their diets and nutrition have made important contributions to our general understanding of primate feeding ecology and behavior. For example,

studies of atelines have provided insight into the processes driving food selection. Howler monkeys exhibit strong patterns of fiber and secondary metabolite regulation in which they limit intake of food items with high levels of fiber or secondary metabolites, often switching between food items to minimize the intake of a single secondary metabolite (Milton 1979; Glander 1982). Analogous patterns have subsequently been described in catarrhines. Similarly, the concept of nutrient balance suggests that primates attempt to reach nutritional targets by mixing food items to balance the intake of multiple nutrients as well as fiber and toxins. The first study to directly test for this strategy in a wild primate focused on fruit-specialist spider monkeys (*Ateles chamek*) and demonstrated that they maintain a constant intake of protein, while lipid and carbohydrate intake varies dramatically from day to day (Felton et al. 2009). Evidence for nutrient balancing has also been documented in other primate species around the world, including other platyrrhines.

In addition to nutritional demands, wild primates must also take into account social context when foraging. Experimental work with wild callitrichids has made valuable contributions to this area of the field. Specifically, it has improved our understanding of the extent to which information is shared among individuals in a group of foraging primates and has provided insight into individual foraging decisions within a finder-joiner paradigm (i.e., when to arrive first at a food resource vs. when to follow others) (Bicca-Marques and Garber 2005). Also, these experiments have facilitated the quantitative description of foraging costs and benefits for species participating in mixed-species foraging. Likewise, some of the first studies to focus explicitly on spatial patterns of movement through a habitat were performed on callitrichids (Garber 1989). This research suggested that instead of following sensory cues, wild primates utilize a mental map of their habitats to encounter food resources. However, these mental maps tend to be route-based, with the same routes centered on specific landmarks repeatedly utilized, instead of the shortest, most efficient travel paths from one tree to another.

Furthermore, for decades, tool use was believed to be present only in apes (Family: Hominidae). However, platyrrhines, specifically capuchins (*Cebus* and *Sapajus* spp.), are also adept tool users. In particular *Sapajus* spp. exhibit frequent tool use and are well-known for using stones to crack nuts (Otoni and Izar 2008). This information has broadened our understanding of the environments and contexts within which tool use occurs.

Finally, all mammals, including primates, possess a community of mutualistic microbes in the gastrointestinal tract that contribute to host digestive efficiency. The gut microbiota breaks down structural carbohydrates that are otherwise indigestible by the host, and it produces short-chain fatty acids that can be absorbed by the host and utilized for energy. The gut microbiota also produces vitamins such as B<sub>1</sub> and B<sub>6</sub> and can neutralize secondary plant metabolites (LeBlanc et al. 2013). While our understanding of the primate gut microbiota remains somewhat limited due to the relatively recent development of appropriate analytical techniques, the most comprehensive studies to date have focused on howler monkeys (*Alouatta* spp.) (Amato et al. 2016). These studies have indicated that different host species possess distinct gut microbial communities, and the gut microbiota can shift over time within individuals in response to changes in diet and physiology. Because different microbes utilize different metabolic pathways, these changes in the composition of the gut microbiota have the potential to strongly impact host nutrition, and these studies have incited similar research in a wide range of primate taxa.

## Conclusion

Platyrrhine diets represent a range of niches and specializations that are facilitated by both morphological and behavioral adaptations. Nevertheless, research on diets and foraging strategies of New World monkeys has provided important data from which to build a more

general knowledge of primate feeding and nutritional ecology.

## Cross-References

- [Catarrhine Diet](#)
- [Cathemeral](#)
- [Dorothy Fragaszy](#)
- [Feeding](#)
- [Foraging](#)
- [Insectivore Diet](#)
- [Nutrients](#)
- [Omnivore](#)
- [Platyrrhine Sensory systems](#)
- [Primate Diet](#)
- [Primates](#)

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## Platyrrhine Locomotion

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## Definition

Body displacement relative to physical surroundings in New World monkeys.

## Introduction

Locomotion, i.e., body displacement within space and time, is part of a behavioral continuum with postures, involving minimal to no body displacement, that enables animals to interact with and utilize their environment. As such,

locomotion is an integral part of animal biology, as it provides access to food sources, facilitates social contact and bonding, promotes mate connection and ritual, and enables escape from potential predators. In this way, it feeds back to important biological parameters and contributes significantly to fitness. Locomotion can be seen as the response of morphology (e.g., physiology, anatomy) to the architectural challenges of the environment (substrate availability, size, inclination, texture, stiffness etc.). Thus, terrestrial mammals transfer their body mass on the ground mainly by walking, running, and jumping (but some terrestrial mammals, which live in rocky habitats, can also rock climb). On the other hand, arboreal mammals, having to deal with the irregular three-dimensional environment of forest canopies, tend to display a remarkable diversity of different locomotor modes. In Primates, a well-nested arboreal mammalian order, locomotion has played a fundamental role to the major evolutionary radiations, as well as to the origins of the order itself. The great diversity of locomotor modes encountered in primates (as in other mammalian orders as well) is better termed as locomotor behavior, and its qualitative and quantitative description contributes to the understanding of evolutionary and ecological adaptations of modern and fossil primates. In terms of locomotor behavior, platyrrhines, the monkeys of the New World, exhibit one of the most astounding diversities among primates, from squirrel-like scampering to ape-like arm swinging, involving the evolution of the unique prehensile tail, acting as a fifth limb! The variable ways that platyrrhines have evolved in order to negotiate different habitats also seem to characterize the different evolutionary radiations within the group. In this way, this diversity has contributed to their differentiation into very specific eco-evolutionary niches and has enabled them to exploit a variety of habitats that promoted their expansion across Central and South America.

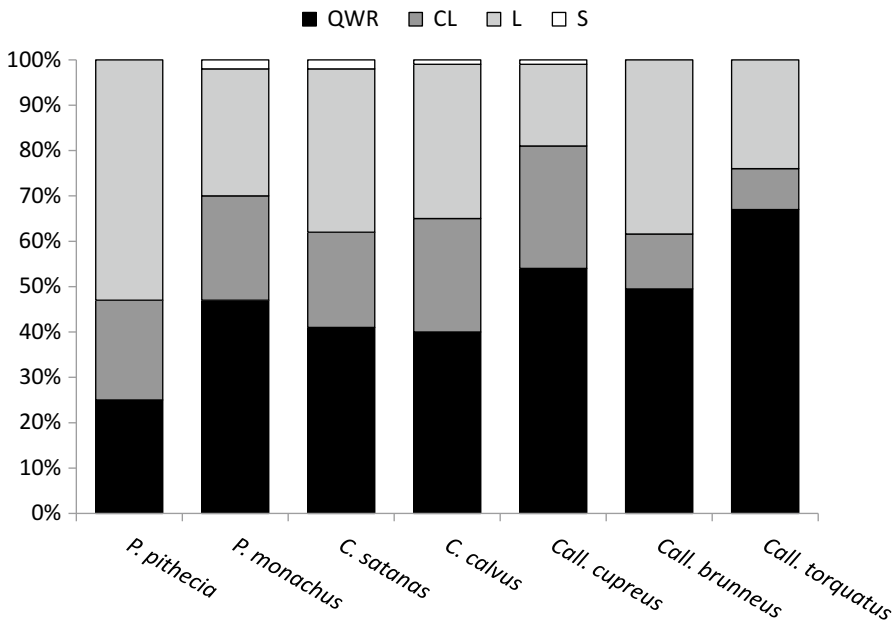
## Setting the Context

As locomotion in primates is basic for elucidating their evolutionary adaptations, it is important to understand the context of this chapter. In this way,

the present chapter explores the locomotor diversity of platyrrhines by surveying the locomotor profiles of the different families, subfamilies, and genera, in cases where substantial diversity is in play. Considering that the platyrrhine phylogeny is still under debate, a fact beyond the scopes of this entry, we shall opt for a rather conservative classification, accepted and used by the experts (Perez and Rosenberger 2014). Thus platyrrhines are divided into three families: (i) Pitheciidae (uakaris, sakis, and titi monkeys), (ii) Atelidae (the prehensile-tailed monkeys), and (iii) Cebidae, composed of the subfamilies Callitrichinae (the clawed marmosets and tamarins) and Cebinae (capuchin, squirrel, and owl monkeys). Moreover, as locomotion is the morphobehavioral response to the mechanical constraints of the environment, we shall only consider those studies that have considered this behavior in the wild, and in case of lack of comparable data, in large enclosures, where the animals can freely move. Fortunately, platyrrhines are relatively well studied in this domain and there are comparable data for many species.

## Pitheciidae

The family Pitheciidae is composed of four genera: *Pithecia* (saki); *Chiropotes* (bearded saki); *Cacajao* (uakari), which are grouped in a single subfamily, the Pitheciinae; and *Callicebus* (titi monkey), representing its own subfamily, the Callicebinae. The locomotor repertoire of these monkeys is rather generalized and is dominated by quadrupedal walking, running, and bounding on top of horizontal and moderately inclined branches, as well as leaping in between tree crown peripheries and hopping across branches (Fig. 1). Among them, sakis appear to be the most saltatory, and more particularly the white-face saki *Pithecia pithecia*, of which, more than half of its locomotor repertoire is represented by different forms of horizontal leaps and hops (Fleagle and Mittermeier 1980; Walker and Ayres 1996). In contrast, the monk saki *P. monachus* differs in being more quadrupedal (Youlatos 1999), underscoring the locomotor flexibility of the



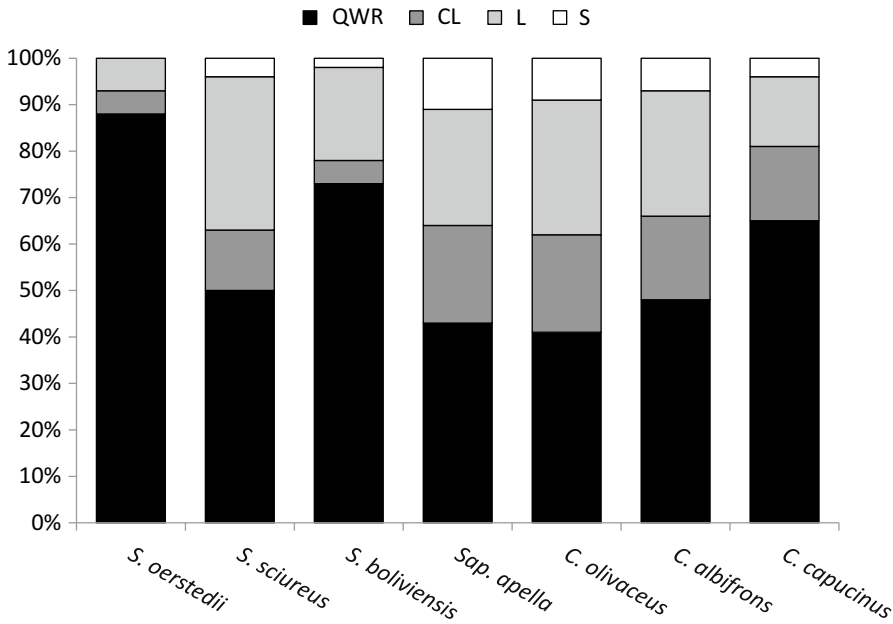
**Platyrrhine Locomotion, Fig. 1** Proportions of major locomotor modes in the Pitheciidae (*QWR* quadrupedal walk and run, *CL* vertical climb and clamber, *L* leap and hop, *S* bridging and suspensory locomotion)

genus (Walker 1993). Quadrupedal activities, involving walking along single horizontal or moderately inclined branches, climbing up and down along vertical or steep branches, and clambering towards all directions across multiple flexible branches also appear to be the dominant locomotor modes for the bold uakaris *Cacajao calvus*, despite the fact that they also use leaping between tree peripheries rather frequently (Walker and Ayres 1996). Bearded sakis *Chiropotes satanas* also rely mainly on quadrupedal walking and running and to a lesser extent on leaping and climbing (Fleagle and Mittermeier 1980; Walker and Ayres 1996). The other member of the family, titis (*Callicebus* spp.), which probably represents the basal member of this clade, is basically quadrupedal (walking, running, bounding) with variable, but generally moderate, rates of leaping behavior (Youlatos 1999; Lawler et al. 2006). What is remarkable about the locomotor repertoire of the family is that it appears to approximate that of the ancestral platyrrhine. In effect, there is a consistent pattern of quadrupedal walking-running-bounding behavior with some variable component of leaping and hopping activities when comparing

the reconstructed locomotor behavior of fossil Pitheciinae with the behaviors of extant forms. All fossil representatives tend to exhibit a repertoire resembling that of *Callicebus* and *Chiropotes*, i.e., quadrupedalism accompanied by leaping. In fact, if *Callicebus* represents in some form the morphological and behavioral prototype of ancestral platyrrhines (Ford 1988), then all these modern monkeys do not appear to have changed much since the inception of the pitheciine radiation. Within this radiation, only *Pithecia*, and more particularly, *P. pithecia* seem to depart far from this blueprint. *Cacajao* also partly differs, as it evolved in Amazonian flooded forests with quite discontinuous canopies that apparently encouraged increased leaping activities (Walker and Ayres 1996).

## Cebinae

The subfamily Cebinae, of the family Cebidae, contains two very widely known monkeys, the squirrel monkeys (*Saimiri*) and the capuchins (genera *Sapajus* and *Cebus*), and one less known,



**Platyrrhine Locomotion, Fig. 2** Proportions of major locomotor modes in the Cebinae (*QWR* quadrupedal walk and run, *CL* vertical climb and clamber, *L* leap and hop, *S* bridging and suspensory locomotion)

the owl monkey (*Aotus* spp.), the only nocturnal monkey. Given this disparity, there appears to be a strong bias in the study of the locomotion of capuchin and squirrel monkeys over owl monkeys. In fact, there are no detailed data on the locomotion of *Aotus*, but anecdotal descriptions and predictions from skeletal traits suggest a mainly quadrupedal monkey with moderate leaping activities (Wright 1989). This behavioral repertoire appears to bear strong similarities to that of titis (*Callicebus*) and is further supported by skeletal similarities between the two monkeys (Ford 1988). On the other hand, there are field data on three different *Saimiri* species and all show that squirrel monkeys are primarily quadrupedal walkers and runners, as well as leapers (Fig. 2). Among them, the common squirrel monkey *S. sciureus* seems to be the more saltatorial, using long acrobatic leaps between the terminal branches of tree crowns (Fleagle and Mittermeier 1980; Youlatos 1999). A comparable locomotor profile is exhibited by the black-capped squirrel monkey *S. boliviensis*, which also uses considerable leaping, but is mainly quadrupedal (Fontaine 1990). On the other hand, the red backed squirrel monkey *S. oerstedii* of Central

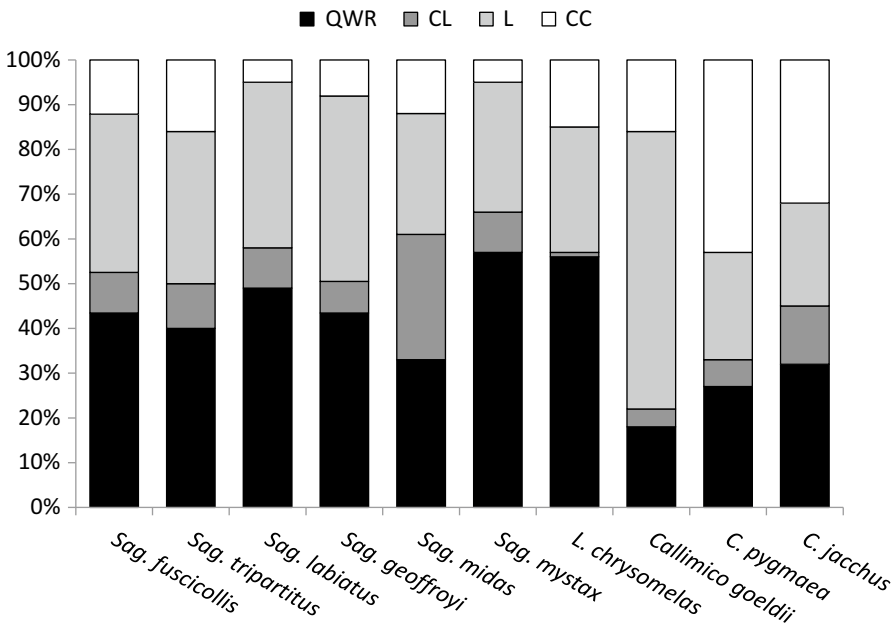
America is the more quadrupedal of all (Boinski 1989). Quadrupedalism along and across branches and horizontal leaping between tree crowns seem to suit the predacious omnivory of squirrel monkeys that travel fast and range in many forest types exploiting all forest strata. The larger representatives of this clade, the gracile capuchins (*Cebus* spp.) and the robust capuchins (*Sapajus* spp.) appear to be rather consistent in their locomotor patterns (Fig. 2). Available field data on three species of gracile capuchins and one species of robust capuchins indicate increased quadrupedal activities, coupled with variably significant rates of leaping and moderate climbing and clambering. In effect, the robust brown capuchin monkey (*Sapajus apella*) appears to mainly walk and run quadrupedally along single branches, to regularly perform acrobatic leaps between tree tops, and to a lesser extent climb along steep and vertical branches and clamber across small intertwined branches (Fig. 2); moreover, these monkeys also use considerable amounts of bridging between tree crown gaps and suspensory quadrupedal locomotion below branches with the aid of the semi-prehensile tail (Youlatos 1998;

Wright 2007). On the other hand, the gracile capuchins seem to rely more on quite high rates of quadrupedal locomotion and slightly less on leaping and climbing and clambering, but show much less below-branch suspensory behaviors (Gebo 1992; Youlatos 1999; Bezanson 2009). These locomotor repertoires seem to suit the adaptive profile of the generalist capuchin, as a particularly agile, inquisitive and destructive omnivore, which exploits all forest strata, ground included, in a remarkable variety of habitats, resulting in nearly one of the most expanded geographical ranges among all New World monkeys (Rosenberger 1992). Unfortunately, there are no relevant fossils with associated skeletal elements in order to directly assess any evolutionary trends within this particularly interesting clade, but it is safe to assume that these medium-sized monkeys have preserved a largely generalized locomotor behavior.

### Callitrichinae

This group of platyrrhine monkeys is unique as they have secondarily developed functional

claws, analogous to those of other clawed mammals, and they are among the smallest New World monkeys. The clade is informally divided into two groups: the tamarins and the marmosets (probably including callimicos). The former group is composed of the highly diversified Amazonian genus *Saguinus* and the less diversified, but very specialized, genus *Leontopithecus* of the Atlantic forests of Brazil. Field observations on several Amazonian tamarin species indicate that they intensively use quadrupedal walking and bounding along single horizontal and moderately inclined branches, coupled with high rates of horizontal leaping between terminal branches of tree crowns (Fig. 3; Garber 1980, 1991; Garber and Leigh 2001; Youlatos 1999; Youlatos and Gasc 2001). On the other hand, they seem to rely less on their clawed extremities, as clawed, squirrel-like, locomotion along medium- and large-sized vertical branches and trunks is variable across species, but less common in general. These locomotor patterns indicate that tamarins still exploit the small-branch milieu of tree peripheries to a great degree. Nevertheless, the use of clawed activities on large vertical supports also demonstrated their



**Platyrrhine Locomotion, Fig. 3** Proportions of major locomotor modes in the Callitrichinae (QWR quadrupedal walk and run, CL vertical climb and clamber, L leap and hop, CC clawed locomotion)



dependence on gums and bark insects, but to a lesser degree compared to that of the marmosets. Unfortunately, there are no detailed field observations on the locomotion of the highly specialized lion tamarins (*Leontopithecus* spp.) of the Brazilian Atlantic forests. The morphology of the genus indicates an adept manipulative forager for non-mobile prey and fruit, as well as seasonal dependence on gum feeding. Studies in large zoo enclosures suggest reliance on quadrupedal activities coupled with leaping behavior (Karantanis 2010). Similar positional patterns would likely facilitate and go well with the intensive manipulative exploitation of the discontinuous canopy of all forest levels that lion tamarins generally exploit.

On the other hand, field data on the locomotion of the radiation comprising the callimico and marmosets are relatively scarce. Callimicos (*Callimico goeldii*) are morphologically very specialized monkeys and this is also reflected on the particularly high rates of leaping, most of which are leaps from and to vertical branches, trunks, or bamboos; quadrupedal walking and bounding locomotion along horizontal and moderately inclined branches and clawed locomotion on large vertical substrates are used in a much lesser degree (Fig. 3; Garber and Leigh 2001). These locomotor patterns appear to be ecologically associated with the exploitation of the lower strata of Amazonian forests, with abundant vertical substrates, where callimicos frequent forage for arthropods and collect fruit and fungi. The marmosets, *Cebuella*, *Mico*, and *Callithrix*, are by far the most ecologically specialized callitrichines, as they exploit large vertical branches in relation to their tree gouging habits and year-round exudate feeding (Garber 1992). The exploitation of this specialized niche has compelled analogous locomotor behaviors. Thus, the Amazonian pygmy marmosets *Cebuella pygmaea*, the smallest representative of the group and of all New World monkeys, appears to use very high rates of claw-climbing on large vertical branches and trunks, as well as frequent leaping, including high rates of leaps in between vertical substrates (Fig. 3; Youlatos 2009). Unfortunately, there are no field locomotor observations on the other highly

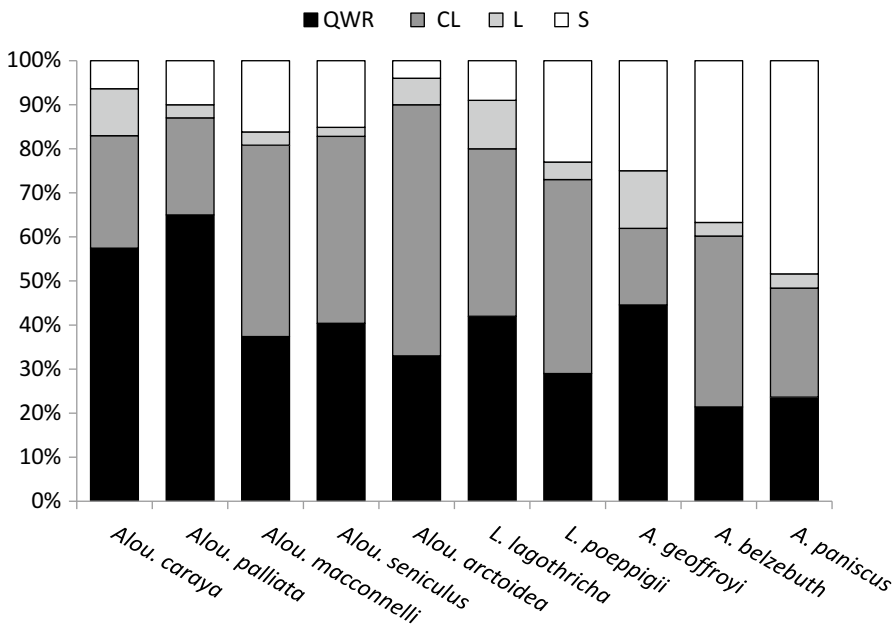
diversified Amazonian marmosets (genus *Mico*). This is also the case for the Atlantic forest marmosets (genus *Callithrix*). The only available data concern the locomotion of common marmoset *Callithrix jacchus*, but not in its natural habitat. These observations indicate that common marmosets emphasized on clawed locomotion on large vertical trunks and branches, and quadrupedal walking and bounding along horizontal and moderately inclined branches, and used a considerable proportion of horizontal leaps between tree peripheries (Fig. 3; Zaluar et al. 2013). These observations suggest different locomotor strategies across the different clades of the Callitrichinae. The prevalent combination of quadrupedalism and leaping implies this pattern as that of the common ancestor of the group and very likely shared by the other members of the Cebidae, as well! In effect, leaping is commonly present in all callitrichine clades but has differentiated into extensive vertical leaps only in callimicos and marmosets. On the other hand, quadrupedal activities have significantly reduced in callimicos and pygmy marmosets, but lack of comparable data on other marmosets provides no clues for further assumptions. Finally, vertical clawed climbing, although used at variable rates, tends to be particularly important for *Callithrix* and *Cebuella*, which are ecologically highly dependent on gum feeding.

## Atelidae

This family comprises the largest and more diversified New World monkeys. All atelids share a fully functional prehensile tail and the variable use of forelimb and hind limb suspensory locomotion. They also represent the group which is best studied in terms of locomotor behavior. The howler monkeys (*Alouatta* spp.) include the smallest, as well as some of the largest, species among the atelids and have been well studied across their range from Central to southern South America. In evolutionary terms, howler monkeys appear to have differentiated earlier than the other genera (they comprise their own subfamily, the Alouattinae) and their locomotion

is characterized by a preponderance of quadrupedalism (Fig. 4). This involves quadrupedal walk along horizontal or inclined single branches, climbing along vertical branches, and clambering across multiple twigs, as well as substantial bridging between tree gaps and suspensory locomotion involving the forelimbs but mainly the hind limbs and the prehensile tail (Youlatos and Guillot 2015). The howler species that inhabit the northern and southern edges of howler range appear to rely more on quadrupedal activities and less on suspensory locomotion. In contrast, Amazonian howler species, of which locomotor observations are available, tend to display a more suspensory and much more clambering and climbing repertoire. The remaining three extant genera (*Lagothrix*, *Ateles*, and *Brachyteles*) compose the other subfamily, Atelinae, and appear to show a gradient of increasing degrees of suspensory locomotion (Fig. 4). Woolly monkeys (*Lagothrix* spp.) are intermediate using significant amounts of quadrupedal walk and vertical climb along single branches and clamber across multiple smaller branches, as well as considerable

rates of forelimb and tail-assisted suspensory locomotion below branches (Cant et al. 2001). During these suspensory bouts, woolly monkeys tend to keep their body in a pronograde (more or less horizontal or slightly inclined) position, which is completely different from the forelimb tail-assisted suspensory locomotion of spider monkeys (Cant et al. 2003). In fact, spider monkeys (*Ateles* spp.) tend to keep their body more or less orthograde (vertical) and rotate it when they travel in a suspensory manner (comparable to the brachiation of gibbons), but they also use suspensory locomotion in higher and significant proportions (Youlatos 2008). Quadrupedal walk, climb, and clamber are represented in much lower rates; however, subtle locomotion differences exist between spider species, with the Central American Geoffroy's spider monkeys (*A. geoffroyi*) being less suspensory than the Amazonian species (e.g., *A. paniscus* and *A. belzebuth*). Unfortunately, there are no detailed locomotor study for the Atlantic forest woolly spider monkeys (*Brachyteles* spp.), although anecdotal observations coupled with morphological analyses



**Platyrrhine Locomotion, Fig. 4** Proportions of major locomotor modes in the Atelidae (*QWR* quadrupedal walk and run, *CL* vertical climb and clamber, *L* leap and hop, *S* bridging and suspensory locomotion)

indicate increased forelimb tail-assisted suspension, similar to that of spider monkeys (Rosenberger and Strier 1989). It appears that as the atelines evolved, they apparently became more suspensory in order to forage more efficiently and cover longer distances in search of sparsely dispersed food sources, and tail-assisted forelimb suspension is a unique locomotor specialization that greatly facilitates canopy travel. The phylogenetic relationships between these three suspensory taxa have not been resolved yet, but it seems that spider monkeys are the sister taxon of both woolly and woolly spider monkeys. If this holds true, this relationship implies that the forelimb-dominated suspensory locomotion evolved in parallel in *Ateles* and *Brachyteles*, whereas *Lagothrix* assumed a different locomotor profile, involving relatively high rates of quadrupedal walk, climb, and clamber in relation to its mixed frugivorous and animalivorous regime (Jones 2008).

## Conclusion

Platyrrhine locomotion is highly diversified. It ranges from arboreal quadrupedal walk and run on top of single horizontal and moderately inclined branches within the tree crown, vertical claw climbing along large trunks or branches in the central parts of tree crowns, to fast forelimb tail-assisted suspensory locomotion below branches within and across tree tops. The proportions of these different modes and the way they are performed have shaped the main platyrrhine radiations that evolved into divergent ecological niches and have contributed to the successful exploitation of the great variety of microhabitats within the different forests across Central and South America.

## Cross-References

- [Clambering](#)
- [Platyrrhine Diet](#)

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## Platyrrhine Sensory Systems

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## Synonyms

Chemosensory; Haptic; Hearing; New World monkeys; Olfaction; Sight; Smell; Tactile; Taste; Touch; Vision

## Definition

*Platyrrhini* – primate suborder that includes all New World or Neotropical monkeys (primates naturally found in the Americas from northern Mexico to southern Brazil and northeastern Argentina). There are 173 species of platyrrhines distributed into 21 genera belonging to five families: Cebidae (capuchin monkeys and squirrel monkeys), Callitrichidae (marmosets, tamarins, and Goeldi's monkeys), Aotidae (owl monkeys), Pitheciidae (titi monkeys, saki monkeys, cuxius, and uakaries), and Atelidae (howler monkeys, spider monkeys, woolly monkeys, and muriquis).

## Introduction

Sensory systems play an essential role in an organism's perception of its surroundings, including the physical and chemical properties of its habitat as well as its conspecifics (individuals of its own species) and those individuals of other interacting species. In the case of primates (prosimians, New World monkeys, Old World monkeys, and apes), the senses of vision, olfaction, and hearing enable individuals to navigate in

their habitats, find their food, avoid predators, and interact with other members of their own species or other species.

## Platyrrhines

Arboreality (tree-living) and frugivory (fruit-eating) characterize all platyrrhines. However, they show large differences in other aspects of their biology. Platyrrhines range in size from the tiny dwarf (*Callibella*) and pygmy (*Cebuella*) marmosets whose adult weight does not exceed 120 g, to the large woolly spider monkeys (*Lagothrix*) and muriquis (*Brachyteles*) that may reach 10 kg. The size of their social units (groups) ranges from the small family groups composed of four to five individuals (an adult couple and their immature offspring) characteristic of the monogamous titi monkeys (*Callicebus*, *Plecturocebus*, and *Cheracebus*) and owl monkeys (*Aotus*) to large multimale-multifemale groups containing up to 100 or more uakaries (*Cacajao*). Whereas pygmy marmoset groups may exploit home ranges of just about 1 ha, spider monkey (*Ateles*) and woolly spider monkey groups may range over about 1,000 ha. Platyrrhines complement their diets mostly with leaves, flowers, animal prey, or exudates (gums).

Platyrrhines show a wide range of within- and between-group communication channels, including complex vocalizations, scent marks, and age-related sexual differences in face or body color. These traits, together with their diet composition and foraging strategies, home range size, and the identity and density of their potential predators, represent important selective pressures that have shaped their sensory systems.

Most platyrrhines live in closed-canopy forests, but some species inhabit more open-canopy woodland habitats in the Cerrado and Caatinga biomes. These structural habitat differences influence the usefulness and range of accuracy of some sensory systems. Whereas a habitat's characteristics do not affect the range of accuracy of the senses of taste and touch, they affect the senses of vision, olfaction, and hearing. For instance, the usefulness of vision is about 20–30 m within a

closed-canopy forest, whereas the usefulness of olfaction may extend to about 200 m and that of hearing probably up to 2,000 m (Dominy et al. 2001). The boundary for vision in the open-canopy habitats of the Cerrado and Caatinga is certainly much wider.

## Platyrrhine Sensory Systems

Little has been investigated about the role of the senses of taste and touch in platyrrhine behavior. Taste may help platyrrhines to select food items and to avoid the ingestion of harming amounts of the same secondary plant metabolites. These toxic or digestion-inhibitor chemicals are mainly found in mature leaves and unripe fruits. The lack of information on whether howler monkeys (*Alouatta*), the most folivorous platyrrhines, are capable of making such discriminations compromises the understanding of the role of taste in their foraging behavior. However, compared to the frugivorous spider monkeys, howlers have less fungiform papillae in their tongues and less taste buds in their oral cavity, suggesting a poorer capacity to detect taste stimuli (Hernández-Salazar et al. 2015).

Touch plays an essential role in all kinds of platyrrhine locomotion. In addition to the importance of this sense in the hands and feet of all platyrrhines, touch is also well developed in the naked skin of the inferior distal third of the prehensile tail of atelids. Touch also contributes to postural behavior, social interactions such as grooming, and food gathering, manipulation, and selection. The role of touch in food selection varies among species. For instance, it is more important for squirrel monkeys (*Saimiri*) than for spider monkeys (Laska et al. 2007). Tactile information is also critical for callitrichids foraging for prey in blind microhabitats (that is, locations where foragers cannot see the content, such as tree holes and the interior of bromeliads). The importance of touch during foraging may have reached its maximum development among platyrrhines in capuchin monkey tool use.



## Vision

Early in primate evolution, a forward rotation of the eyes allowed for stereoscopic vision and a greater reliance on sight. Platyrrhines, like other anthropoid primates, enjoy a high visual acuity. On the other hand, whereas both female and male Old World monkeys and apes are capable of making true color discriminations in the red, green, blue, and yellow spectra (i.e., they are trichromats), platyrrhines present both between- and within-taxa differences in this capacity. While howler monkeys are the only platyrrhines that have evolved a routine trichromacy equivalent to that found in the other anthropoids, all other diurnal New World monkeys present a color vision polymorphism. Most females are also trichromats, but all males and some females are unable to discriminate colors in the red-green axis (that is, they are dichromats). Yet, the nocturnal owl monkeys are monochromats and lost the capacity of seeing colors.

Color vision arises from the neural comparison of the activity produced by different retinal photoreceptors (i.e., rods and cones). Primates have only one type of rod and usually several types of cones. While rods function only under low light conditions, usually during the night, cones are useful at daytime under higher luminosity. The action of cones allows primates to see in colors, and the interaction between rods and cones under intermediate light conditions may improve this ability. Platyrrhines have two genes that encode cone visual pigments. One gene, located in an autosomal chromosome, encodes the short-wavelength (blue) pigment. The other, located in the X chromosome, encodes the medium-wavelength (green) or long-wavelength (red) pigments and has many alleles. Therefore, with the exception of the trichromat howler monkeys and the monochromat owl monkeys, heterozygous platyrrhine females are trichromats, displaying a color vision ability similar to that of normal humans. On the other hand, homozygous females and all males are dichromats and have a color vision roughly equivalent to that of red-green color-blind humans. The frequencies of the alleles of the X gene in a given population affect its

proportion of trichromats and dichromats (Carvalho et al. 2017).

There are two main hypotheses for the evolution of primate color vision. The heterozygote advantage hypothesis suggests that trichromat individuals save time and energy spent in fruit foraging by detecting nutrient- and energy-richers conspicuous ripe fruits at longer distances than do dichromats. This improved detection would favor the fixation of a higher diversity of green-red pigment alleles by increasing the breadth of fruit phenotypes found at the group level (Mollon et al. 1984). The folivory hypothesis also focuses on the advantage of heterozygotes. However, it argues that the discrimination of conspicuous protein-richers, less fibrous, and less toxic younger leaves from the greenish background of protein-poorer, more fibrous, and more toxic mature leaves was the major pressure selecting for the emergence of trichromatic color vision. The fact that the highly folivorous howler monkeys are the only New World primate taxa to show routine trichromacy is compatible with this hypothesis, although the potentially highly folivorous muriquis are also polymorphic. There is also behavioral evidence for the importance of trichromacy especially in the long-range detection of conspicuous fruits (Melin et al. 2017) and predators (Pessoa et al. 2014) and for the advantage of dichromats in the detection of cryptic insect prey (Melin et al. 2007).

A balance between these trichromat and dichromat advantages better accounts for the evolution and maintenance of this poly-allelic platyrrhine visual polymorphism in all diurnal taxa except howler monkeys. The mechanisms of kin selection, mutual benefit of association, or niche divergence may independently or in combination favor this balance (Melin et al. 2008; Mollon et al. 1984). According to the kin selection hypothesis, members of family groups (e.g., marmosets and tamarins) containing dichromats and trichromats enhance their fitness (both direct and inclusive) by taking advantage of the detection of a wider range of predators and food resources. This improved foraging is also at the core of the mutual benefit of association hypothesis, by which the monitoring of kin and nonkin group mates with diverging color vision abilities allows the exploitation of

a richer diet. Finally, the color vision polymorphism may reduce within-group competition for resources if the aforementioned advantages translate into niche divergences between trichromat and dichromat individuals, such as in the preference for different food items or vegetation strata for foraging.

Irrespective of how colorful a platyrrhine sees the world, vision plays a crucial role in foraging, predator avoidance, spatial navigation, and social communication. Although diurnal platyrrhines rely more on visual cues for finding feeding patches and distinguishing food from nonfood items than owl monkeys (Bicca-Marques and Garber 2004), vision is also an important sense for these nocturnal platyrrhines. Owl monkeys travel farther and monitor potential feeding sites more frequently around dusk and dawn, in full or bright moon nights and during periods of stronger moonlight (Wright 1989). The ability to distinguish potential predators from non-predator animals allows platyrrhines to react appropriately and avoid sparing time and energy in unnecessary escape or mobbing strategies. Platyrrhines also use the sense of vision for choosing male and female mates based on physical characteristics, such as body size and color (Moreira et al. 2015). Body displays used in interspecific interactions and in within- or between-group affiliative, sexual, or agonistic contexts also characterize the behavioral repertoire of all platyrrhines.

## Olfaction

The sense of smell is useful for helping to locate rich, out-of-sight sources of odoriferous foods (e.g., flowers and fruits), selecting specific food items to ingest, locating hidden prey, getting information on the reproductive status or social rank of conspecifics, and detecting predators. The reliability of the sense of smell decreases with an increasing distance from the odor source(s). Wind speed and wind direction affect the spatial differences in odor concentration resulting from the diffusion of the odor plumes. In the case of the navigation between feeding patches, the size and

height of the tree crown and the existence of other sources of the same food nearby also influence the effectiveness of the use of the sense of smell (Garber and Hannon 1993).

Captive squirrel monkeys can use the sense of smell to choose objects associated with food and may remember their odors for more than 30 weeks, a memory similar to that of humans (Laska et al. 1996). The highly frugivorous spider monkeys appear to smell unripe fruits at a greater extent than ripe fruits, whereas the senses of touch and taste are more significant in the final, in-hand selection of ripe fruits (Pablo-Rodríguez et al. 2015). However, olfactory cues play a minor role in foraging decision-making when a platyrrhine is within a feeding patch but is not holding a food item. In this respect, owl monkeys are an exception among platyrrhines as they improve their within-patch foraging success by relying on food-related olfactory cues (Bicca-Marques and Garber 2004). In addition to the fact that the low light conditions of the night greatly reduce the usefulness of visual information, odors are stronger, diffuse more slowly, and last longer in the more humid and less windy nighttime atmosphere. Therefore, these nocturnal platyrrhines may also use odor cues to mark and track commonly used travel routes (Wright 1994).

Olfaction is also involved in scent-marking behavior. Platyrrhine scent-marking is believed to function in the transmission of information on the marking individual's quality as a potential mate or as an advertisement of its quality as a competitor to same-sex conspecifics or both (Heymann 2006). Platyrrhines may have odor glands distributed in different body regions. Callitrichids (marmosets and tamarins) are known for their frequent marking behavior with circumgenital (or anogenital), suprapubic, and sternal scent glands (Epple et al. 1993). The highly exudativorous marmosets *Callithrix jacchus* and *C. penicillata*, for example, often leave their individual scents in gouged tree holes by rubbing their circumgenital region.

Platyrrhines may also recognize the smell of predators. Even naïve individuals have been shown to react to the odor of potential predators. For instance, captive-born tamarins (*Saguinus*

*labiatus*) with no experience with encountering predators reacted more strongly to the scent of predator feces than to the scent of feces of non-predators. Specifically, the tamarins sniffed and avoided more predator than non-predator fecal extracts (Caine and Weldon 1989). This ability to discriminate between danger-related and innocuous odors has important implications for the management of captive monkeys. Zoo monkeys may experience higher levels of stress if there are predators in nearby enclosures, as has been found for other mammals (Morgan and Tromborg 2007). On the other hand, if these monkeys become over-habituated to the odor of predators because they do not represent actual dangers in captivity, they may stop to appropriately react to them. Whereas the reduction or elimination of these behavioral responses to predator odors may improve a monkey's well-being in captivity, the survival of over-habituated zoo specimens is likely to be greatly compromised if they are returned to the wild.

## Hearing

Platyrrhines integrate the auditory and visual systems to locate calling or moving prey during foraging. This ability is likely to be particularly important for the omnivorous nocturnal owl monkeys (Wright 1989), although captive individuals have failed to locate hidden food rewards (banana slices) based solely on their association with an artificial auditory stimulus (a 25-dB ticktack) in the unique experimental study testing this ability so far (Costa and Bicca-Marques 2014). The sound of moving and calling predators or other potential sources of danger also elicit escape responses by all platyrrhines. This use of hearing is well known by researchers that are in the process of habituating their study subjects (that is, "training" the monkeys to stop reacting to the observer's presence).

While little is known about the relative importance of auditory cues in platyrrhine prey foraging and predator avoidance compared with information processed by the senses of vision and olfaction, the role of vocalizations in intra- and intergroup communication has long been an

attractive research topic. All platyrrhine taxa emit simple or complex species-specific calls varying in frequency, duration, amplitude, pitch, and composition that influence their likelihood of experiencing attenuation, reverberation, distortion, or other acoustic disturbances caused by the abiotic factors and the biotic noises of their forested habitats (Brown and Waser 2017). The hearing capacity of an individual depends on the distance between its ears (a trait directly related to its body size) and the characteristics of its auditory system. This capacity relates directly with the frequency of species-specific calls, their functions, and the size of the home range (i.e., the space used by a social group during a given time, such as a year).

Platyrrhine vocalizations include food calls; resource, mate, and territorial defense calls; contact and distress calls; and predator alarm calls, among many others. These vocalizations normally change with aging and may vary or not between females and males (Snowdon 2017). Contact calls are important for all platyrrhine individuals and are obviously critical for owl monkeys. Most callitrichids may emit food calls upon the arrival at productive sources. Callitrichids involved in mixed-species associations, such as the tamarins *Saguinus mystax*, *S. labiatus*, or *S. imperator* with *Leontocebus fuscicollis* or *L. weddelli*, give specific predator alarm calls to terrestrial, aerial, or arboreal predators. Regardless of the calling species, the members of both associated taxa recognize and appropriately respond to these calls.

Duetting by the breeding pair is a hallmark of the monogamous titi monkeys, although they also emit solos and group choruses. All these vocalizations are emitted mostly in early morning. Titi monkeys use loud calls for between-group communication aiming the defense of important food sources, mates, or territories (Caselli et al. 2014, 2015). The enlarged hyoid bone of howler monkeys, particularly adult males, enables them to produce their characteristic howl or roar. Howls may promote intergroup space regulation, but may also play a role in maintaining group cohesion, attracting females, avoiding predators, and mediating male-male or intergroup competition

(Kitchen et al. 2015). The vocal repertoire of muriquis include screams emitted by lone individuals, barks emitted during stressful situations, and the amazing neighs (or whinnies), similar to horse ones, used as contact calls especially during travel or lone feeding (Nishimura et al. 1988).

## Cross-References

- ▶ Catarrhine Sensory Systems
- ▶ Hominoidea Sensory Systems
- ▶ Primate Sensory Systems
- ▶ Prosimian Sensory Systems
- ▶ Sensory Receptors

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## Platyrrhini

### ► Platyrrhine Cognition

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## Play

### ► Pretend Play

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## Play Behavior

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### Introduction

The occurrence and value of play in humans, especially as it relates to developmental processes, has been intensively studied (Smith 2010). In contrast, the study of play in nonhumans has had a more checkered history, really only getting serious attention from the 1970s onwards (Burghardt 2005). Moreover, this research has

tended to fall into two broad camps with little or no overlap: experimental studies, mainly on rats, have focused on the neurobehavioral mechanisms involved in producing play (e.g., Siviý 2016), and observational studies, on a broader diversity of species, of captive, semi-captive, and free-living animals have focused on the functions of play that may have been important for its evolution (e.g., Martin and Caro 1985).

Recently, both these strands of research have gained sufficient maturity that major works have appeared integrating these divergent fields while also attempting to unify studies of human and nonhuman animals (e.g., Burghardt 2005; Pellegrini 2011; Pellis and Pellis 2009). Recent special issues of journals devoted to play illustrate the progress that can be achieved when researchers from multiple disciplines talk to one another (e.g., *American Journal of Play*, 7(1), 2014; *Animal Behavior & Cognition*, 1(2), 2014; *Adaptive Behaviour*, 23(6), 2015; *Behaviour*, 153(6/7), 2016; *Current Biology*, 25(1), 2014). Indeed, there are glimmers of a comprehensive model gradually taking shape. Still, for all the progress that is evident in comparative analyses of play, it is important to take stock as to what we know or think we know, identify the key intractable issues, and characterize the questions and methods most likely to be fruitful in the coming decades.

### Defining Play

The first big problem to resolve is that of defining the phenomenon in question. There have been many attempts at defining play (Fagen 1981). These have, to varying degrees, included such distinguishing features as play being autotelic (i.e., done for its own sake), voluntary, and as having no immediate function. As much of the content of play is derived from behavior seen in other functional contexts such as sex, aggression, predation, and antipredator behavior, it is these characteristics that emphasize how the behavior is performed and the context in which it is performed that are critical for distinguishing play from its nonplayful counterparts (Heymer 1977).



These characteristics make actions that are performed during play playful rather than serious, but the application of such criteria tends to be subjective.

The subjectivity inherent in identifying play has led to disputes over what is and is not play. For example, even though the competitive interactions of immature cockroaches appears to be autotelic, with the behavior patterns typical of serious fighting being performed in a way that does not lead to the outcomes typical of aggression, the behavior is not deemed to be play (Fagen 1981). Similar interactions with these properties, involving two puppies or two kittens, would near universally be labeled as play. Indeed, even the mainstay of neurobehavioral research on play, the laboratory rat, had its juvenile play-like social behavior labeled immature aggression by some researchers, until the neurobiological evidence became overwhelming that play involves different behavior and engages distinct, neural mechanisms compared to aggression (Pellis and Pellis 2009). The more animals are like us, the more likely is their autotelic behavior to be labeled as play.

Burghardt (2005) developed a definition of play involving five criteria to lessen the impact of such subjective judgments. To qualify as play, the behavior in question has to (1) be incompletely functional in the context expressed, (2) be voluntary or rewarding, (3) be, in some ways, modified developmentally or structurally compared with when it is used in its normal, functional context, (4) be performed repeatedly, but not necessarily in an invariant form, and (5) be initiated by healthy, relatively unstressed animals in a relaxed context. Two things distinguish this criteria-based definition from earlier definitions. First, it includes all the major criteria that were grouped together in different ways in previous definitions, and it requires that all need to be met before the conclusion is drawn that the behavior in question qualifies as play. This greatly reduces the importance of the observer's "gut feeling" when making this decision. Second, the criteria can be met to varying degrees: one species may just minimally make the grade,

whereas another may greatly exceed that minimum. This latter issue is particularly important to diminish our mammal-centric biases. Indeed, using these criteria, behavioral sequences from a wide range of nonmammalian species, including nonvertebrate ones, have been categorized as play (Burghardt 2005; Pellis et al. 2014).

Another important contribution of this multi-criteria definition is that it has provided a way to distinguish, objectively, play from other behaviors that have often been confounded with play, such as stereotypies and exploration (Burghardt 2005; Pellis and Burghardt 2017). The advent of this definition, however, has not completely solved the problem of unambiguously distinguishing play. Two of the criteria are particularly problematic. While traditionally neglected as a subject of study, play in some species continues into adulthood and adults can use play in a variety of contexts that confer immediate benefits to the players (Palagi 2011). These immediate functions can make applying criterion #2 that "play behavior is incompletely functional in the context expressed," difficult to apply.

Similarly, in some situations, play has been shown to reduce stress. Thus, while severe stress may dampen play, mild to moderate levels of stress may actually facilitate its occurrence (Pellis and Burghardt 2017), making criterion #5, "that play is initiated in healthy, relatively unstressed animals in a relaxed context," difficult to apply in some cases. These limitations are not insurmountable, but to reduce the subjectivity involved in determining how much stress is too much or how small the immediate function needs to be requires more detailed knowledge of the specific case in question. The five criteria are thus a good starting point, but should be applied with the recognition that, to be effective, further research on the behavior and species under investigation may be required to make an objective decision on some of the criteria. Nonetheless, armed with a workable definition, one that can transcend the typically narrow, comparative confines of mammals and a few birds, examination of some of the deeper progress that has been made in the study of play is possible.

## The Many Forms of Play

While in humans play can take many varied forms (Smith 2010), in nonhuman animals three major forms of play are generally recognized (Burghardt 2005). These are locomotor play, involving a lone animal engaging in running, jumping, kicking, and making turns; object play, involving a lone animal engaging in carrying, flinging, ripping, or otherwise manipulating an inanimate object; and social play, involving two or more conspecifics wrestling, chasing, or otherwise manipulating one another. While most cases reported of all these types of play meet the five criteria (Burghardt 2005), there are unresolved issues about the relationship among the types of behaviors encompassed by each kind of play.

When engaged in object play, animals may include a variety of locomotor movements, and social play may involve competition for an object or incorporate locomotor-rotational movements (Burghardt 2005). Consequently, these three types of play may be intermingled in a variety of ways. A further complication is that, often, labeling the three types of play is based on the target of the play (i.e., self, other, object) and not on the actual content of the actions performed, which may be quite varied. For example, the locomotor play of many prey species, such as ungulates, involves the playful execution of the runs, jumps, turns, and other protean movements that are otherwise seen, functionally, in antipredator behavior, whereas, in some species, some of the locomotor behavior may be not only unrelated to antipredator behavior, but are also unique to play, such as the pirouettes done by chimpanzees (Nishida and Inaba 2009). Labeling both as locomotor play may confound behavioral processes that are very different. Conversely, cats may playfully direct predatory behavior patterns to either inanimate objects or to conspecifics. The problem in this case is that even though the same behavior patterns may be used, the differences in target would lead to the behavioral sequences being categorized as different kinds of play. It is not self-evident as to why the behavioral patterns performed have a lower priority in categorizing

play than does the target to which they are directed.

Social play can also be diverse in content. Social interactions involving behavior patterns typical of nurturing young (play mothering), courtship and copulation (sex play), or conspecific aggression (play fighting), have all been categorized as social play (Burghardt 2005; Fagen 1981; Pellis and Pellis 2009). Indeed, even “play fighting” may be an amalgam of behavioral sequences that can involve competitive interactions of diverse origins: the animals may compete for contact with body targets typical of aggression, courtship, greeting, or grooming (Pellis and Pellis 2009).

All this diversity in the content of play raises important questions about both the neurobehavioral mechanisms that produce play and the possible functions that play may serve. One approach has been to view play as being encompassed by a unitary motivational system, whereby behavioral elements from different functional systems can be intermixed (Heymer 1977). Such a view is supported by some studies, convincingly showing that two or more types of play are intermingled, such as object and social play in Japanese macaques (e.g., Shimada 2012). However, contrary to this perspective are accumulating data that suggest that different types of play have different origins and involve different neurobehavioral systems.

First, at a broad phylogenetic level, the three different types of play may appear independently of one another across different lineages (Burghardt 2005). That is, object play can evolve in a lineage independently of either social or locomotor play, and so on. For example, object play is either absent or rudimentary among rodents, whereas locomotor play and social play are quite prevalent. However, even in cases in which locomotor play and the social play are both present and appear to be performed in an intermixed manner, they may not be causally linked. Indeed, when comparing across species, there is a negative correlation between social play and locomotor play – an increase in the complexity of one type of play is accompanied by a decrease in the

complexity of the other (Pellis and Pellis 2009). Such a relationship extends to the subspecies level, with some strains of rats having more locomotor play and some more social play (Schneider et al. 2016). Thus, at a phylogenetic level, different types of play can not only have independent origins, but also follow independent evolutionary changes.

Second, in species which have multiple types of play, different types of play wax and wane at different ages (Burghardt 2005; Pellis and Pellis 2009). That is, the different types of play appear developmentally dissociated. Third, studies of individual differences within species have shown that individuals that exhibit more of one type of play are not more likely to exhibit more of the other types of play (Ahloy Dallaire and Mason 2016; Lampe et al. 2017). Being more playful does not make an individual equally more playful in all ways.

Given that data on phylogenetic trends, developmental changes and individual differences show that different forms of play are independent, how can the cases in which animals seem to intermix behavior patterns from different functional systems be explained? There is an important methodological issue that needs to be resolved before any deeper biological understanding can be gained.

Some reports of mixing are of the following form: a piglet in a crowded pen jumps forward and rotates in the air, striking another piglet on the flank, which leads to a brief tussle between them. Such a sequence has been interpreted as a bout of locomotor play merging into a bout of social play (e.g., Donaldson et al. 2002). That is, locomotor actions are intermixed with socially competitive actions. However, this interpretation may be premature. Consider a young gosling nibbling on grass in a pasture, walking with lowered head while doing so. Periodically, it raises its head and scans its surroundings, and if it has strayed too far from its parents, the gosling will orient and run towards a parent. During this run, the gosling may bump into a sibling, which leads to a brief tussle, before one or both run towards the parents again (Pellis and Pellis 2009). It would seem unlikely that, in such a case, the running and the social

competition resulted from the same motivational substrate. Rather, the most parsimonious explanation would be that the social interaction was an incidental byproduct of one gosling accidentally bumping into another while running towards a parent. Similarly, in animals in close proximity, it cannot be assumed that the running, jumping, and turning are motivated by the same processes that lead to playful competitive interactions when they make contact with a nearby conspecific. Simply scoring the locomotor movements and social actions independently of the context within which they arise can be misleading.

The latter point needs also to be considered when scoring behavior patterns associated with play and then concluding that because some of them occur in functional contexts associated with conspecific aggression and others with anti-predator behavior, sex, etc., that play involves mixing behavior from different functional contexts (Heymer 1977). For example, in grasshopper mice and ground squirrels, play fighting involves two types of competitive interactions – in the mice, they either compete to lick and groom their partner's shoulder area (as in precopulatory behavior) or to bite the nape of their neck (as in predatory behavior), and in ground squirrels, they either compete to mount one another (as in sex) or to bite their partner's shoulder (as in aggression). Individual play bouts last 2–3 s, but over a specific sample period, pairs can engage in dozens of playful interactions. Simply scoring the incidence of mounting, licking and grooming, and biting would suggest that these species mix elements from sexual and aggressive or from sexual and predatory behavior. However, detailed analysis of sequences shows that a play fight that began with a bite directed at the shoulder (squirrels) or to the nape (grasshopper mice) was not countered with counterattacks to lick/groom the shoulder or to mount. Rather, each sequence of attack and defense was appropriate for the target attacked, and only once that sequence was completed would a new sequence start that could involve an attack directed at the opposite target (Pellis and Pellis 2009). That is, at this finer grain time scale, sex and aggression or sex and predation were not mixed.

The conclusion to be drawn is that the apparent intermixing of behavioral elements from multiple functional behavioral systems may be an illusion, and that, in the moment-to-moment context of performing playful actions, behavioral elements from different systems remain distinct. However, there are striking examples of mixing, such as the object-social play of Japanese macaques (Shimada 2012) that cannot be so dismissed. To reconcile such divergent findings, play must be considered with regard to phylogenetic history.

### The Origins and Evolutionary Transformation of Play

Burghardt (2005) developed a model for the independent evolutionary origins and transformation of play across many different lineages of animals that may have important implications for our understanding of both the independence and the combining of types of play. The model asserts that, under certain conditions, such as readily available food, surplus energy, a relatively protected environment, prolonged juvenile development, and with sufficient neural resources to experience boredom, play-like behavior may emerge. This incipient or *primary process play* is the form of play that is most widespread in the animal kingdom, with locomotor, object, or social forms predominating in different lineages (Burghardt 2005). The behavior patterns performed in such play may not differ markedly from their appearance in functional contexts, but the usual functional consequences do not arise. It is possible that under particularly benevolent conditions, such play may be sustained even if it is neutral with regard to fitness benefits (Pellis et al. 2014). An avenue by which such primitive play may begin to gain a fitness advantage has been recently explored in a mathematical model. If the play, at least in its social guise, forces competitors to squander some of their developmental resources, then the cost of inducing that play can be an advantage to the initiator if its cost is smaller than that paid by the competitor (Auerbach et al. 2015).

As noted in the transformational model, if conditions are favorable and primary process play provides players with a fitness enhancing advantage, then the features of the play that are most crucial to that advantage may be subjected to natural selection, so that the critical behavior patterns are either increased in their frequency and/or modified in their form to serve that function better (Burghardt 2005; Pellis et al. 2014). In this way, the play can become even more playful as it is transformed into *secondary process play* and, more strikingly so, as it is further transformed into *tertiary process play*. It should be noted that, in a species with only primary process play, the five criteria in Burghardt's definition of play may only be met to a minimal degree, whereas in a species with secondary or tertiary play, many of the criteria may be fulfilled by a wide margin. This variation, in turn, may account for the marked variation in the complexity of play characterized when researchers contrast cases across a wide comparative range of lineages (Burghardt 2005; Fagen 1981; Pellis and Pellis 2009). The relative fitness gain characterized in the primary process play modeled by Auerbach et al. (2015) also suggests one of the necessary conditions that lead to further transformations of play.

Again, models suggest that once a potential benefit emerges that enhances fitness, play can quickly spread in a population (Durand and Schank 2015). With regard to social play, if playing provides fitness enhancement to one partner at the expense of another, one can imagine a situation arising in which there is a fitness advantage for mechanisms to evolve in competitors to offset that advantage. That is, a kind of arms race develops, with a momentary advantage gained by partners initiating play being neutralized by new actions by the recipients, leading to ever greater levels of complexity in the play performed (Pellis and Pellis 2016). The broad outline of such a transformational process has been characterized for the play of murid (i.e., mouse-like) rodents (Pellis and Pellis 2009; Pellis et al. 2014).

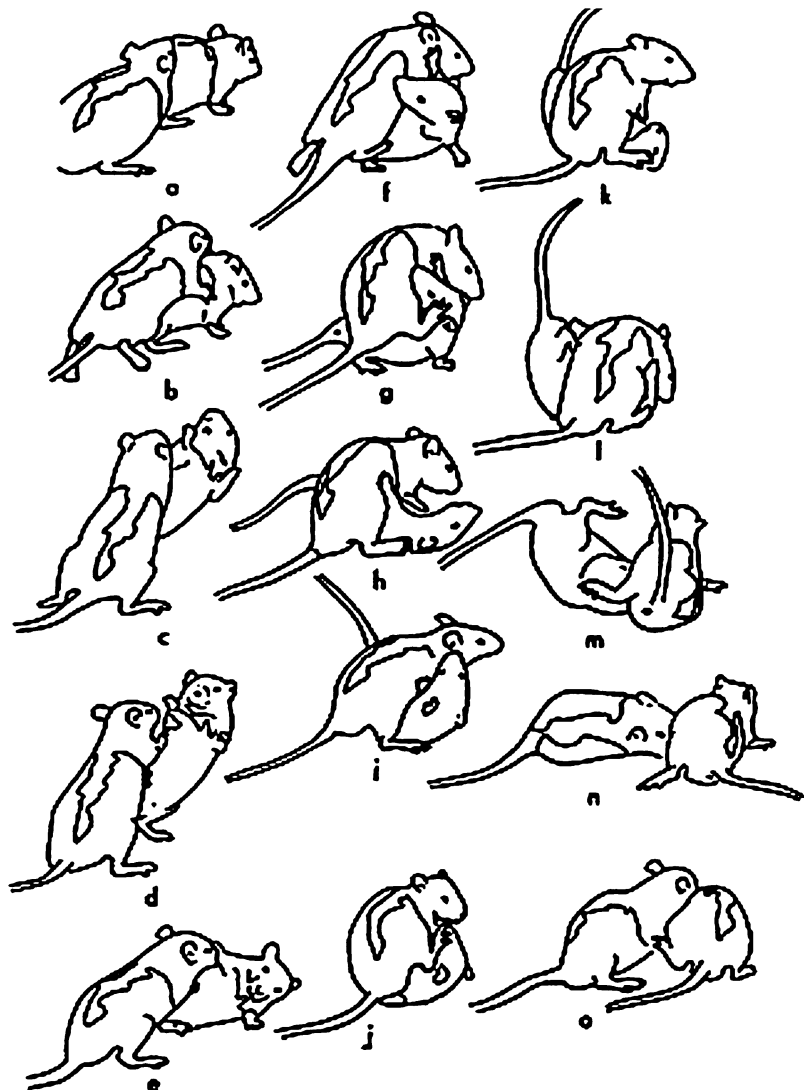
In murid rodents, social play in the form of play fighting involves attack and defense of body targets otherwise contacted during adult pre-copulatory behavior, and across species, this

competition can differ markedly in its complexity. At the simplest levels, there are species that do not engage in any such play and some that attack but do not defend. At a more complex level, defense occurs, but that defense involves evading contact, not wrestling. The addition of tactics that promote the occurrence of playful wrestling makes play even more complex. Finally, high frequencies of counterattack lead to even more complex play fighting, as partners can reverse roles over the course of the encounter. For example, in Fig. 1, play fighting in a pair of juvenile rats is shown, in which attack, defense, and counterattack lead to a

protracted interaction involving close-quarter bodily contact.

From a mechanistic perspective, the greater complexity in the form of the play is accompanied by changes in the neural mechanisms that regulate play (Pellis and Pellis 2009). In the case of murid rodents, these changes in neural organization gradually lead to more and more differentiation from the sexual behavior being performed during play. Other than the precocial expression of emerging behavior patterns, there is little evidence that the simplest forms of play require novel mechanisms to sustain it. In contrast, more

**Play Behavior, Fig. 1** A sequence of play fighting is shown for a pair of juvenile rats. The rat on the left approaches another rat from the rear (a) and pounces towards its partner's nape (b). Before contact is made, the defender rotates around its longitudinal axis (c) to face its attacker (d), but the attacker continues to move forward pushing the defender onto its side (e). The defender then rolls over onto its back as its attacker stands over it, restraining the defender's movements while continuing to reach for its nape (f–h). The supine defender launches a counterattack to its partner's nape (i), which is blocked (j, k). With continued squirming by the supine partner, the rat on top (l) is pushed off by the supine animal (m). The original defender then stands up (n) and lunges towards its partner's nape (o). The sequence involves repeated attack and defense of the nape and role reversals to which partner attacks and which defends (Reprinted from Pellis and Pellis (1987) with permission)





complex forms of play require changes to the regulatory mechanisms that produce sex-related behavior. The most complex forms require novel involvement of cortical systems (Pellis and Pellis 2016). From a functional perspective, there is little evidence for the fitness enhancing effects of the simplest forms of play, but more complex ones appear to have detectable effects on the development of sexual performance and for the most complex ones, additional benefits for the development of more general cognitive and social skills (Pellis et al. 2014).

The transformation of play across lineages and the unique attributes afforded by different lineages begins to provide a solution to the conundrum of different forms of play having originated independently, but clearly, in some species, intermixed in novel ways. First, a lineage must have evolved more than one type of play to afford the opportunity of intermixing behavior from different types of play (Burghardt 2005). Second, the lineage in question must have the resources to combine these different elements effectively when the opportunity presents itself. For example, as noted above, the two most common and elaborate forms of play in rodents – social and locomotor play – are negatively correlated (Pellis and Pellis 2009). That is, increased complexity in one is coupled with a decreased complexity in the other, suggesting that there may be limited neural resources available to allow for the expansion of both types of play. It may, therefore, not be surprising to discover that some of the most convincing cases of intermixing are to be found in primates (e.g., Shimada 2012) – a lineage with a larger brain to body ratio than that in rodents (Eisenberg 1981).

As noted above, while insufficiently fine-scale temporal and contextual analyses may account for many of the presumed reports of intermixing during play, some cases may be true reflections of the composite play possible in some species (Palagi and Norscia 2016). The above transformational model offers a means by which to account for the species differences that may underlie some of this variation in being able to intermix behavioral elements from the different functional systems being mimicked during play. At least one of the

crucial resources needed to make the transition from maintaining independent play systems to novel combinations of such systems is to have a sufficiently large brain. A potential way that such neural resources could make the difference is reflected in the brain-level changes needed to make social play more complex (Pellis and Pellis 2016).

## The Playful Brain

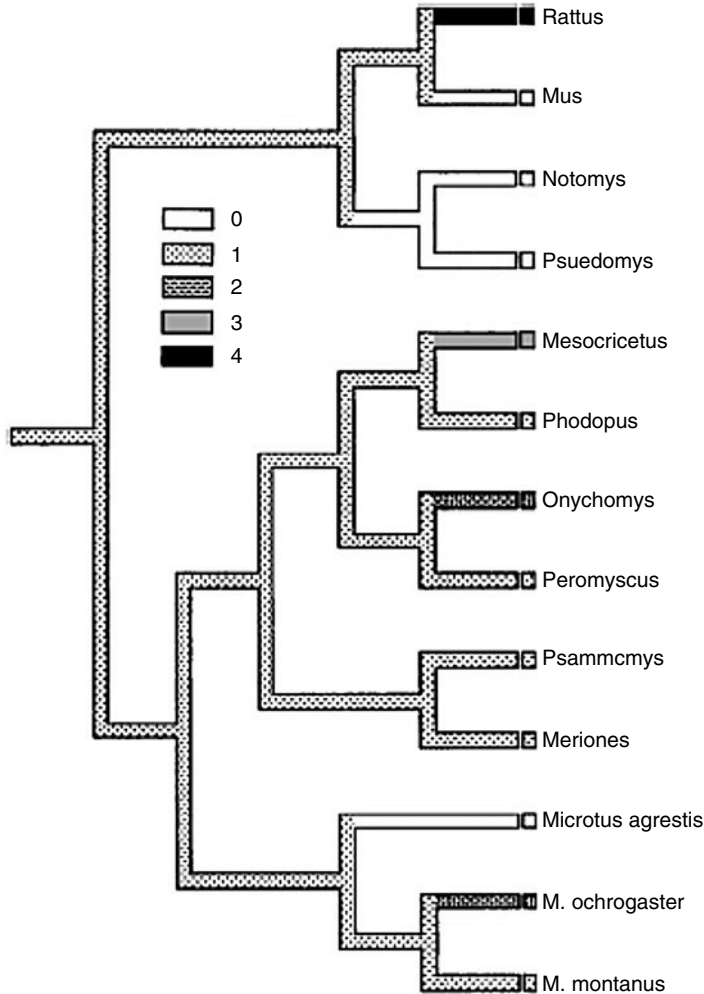
In rats, play has been shown to engage a complex neural circuit of interconnected systems (Siviy 2016). Thus, there are hindbrain systems that generate the appropriate behavior patterns, midbrain systems that motivate and reward the execution of play, lower forebrain systems that regulate the emotions involved and upper forebrain systems that modulate the actions performed to ensure that they are contextually appropriate.

Intriguingly, rats that have had their cortex removed at birth exhibit normal levels of play in the juvenile period, with similar frequencies of attack, defense and counterattack, and exhibit similar levels of reciprocation in their play (Pellis and Pellis 2016). That is, neural circuits below the level of the cortex are sufficient to motivate and execute play and provide the reward necessary to sustain it. This is consistent with the likelihood that the changes needed to transform primary process play into secondary process play in rodents have involved alterations to subcortical circuits (Pellis and Pellis 2009). While not needed to produce or maintain play, cortical circuits, especially those of the prefrontal cortex, are critically involved in modifying the play executed to adapt it, contextually, to both the identity and the actions of the partner (Pellis and Pellis 2016). That is, transforming play from secondary process play to tertiary process play requires higher levels of neural control over the mechanisms regulating it, to make play more complex and adaptable to novel contexts.

Viewed from the knowledge gained thus far about the neural mechanisms involved in producing, maintaining and adaptively modifying social play in rats, a possible way for more complex play

to evolve is for there to be more neural resources engaged, especially by adding more control from neural circuits higher up in the neural hierarchy. Comparatively, even among murid rodents, only

some species have achieved the levels of complexity in social play present in rats, and these have emerged seemingly independently (Fig. 2). These findings lead to two considerations.



**Play Behavior, Fig. 2** The evolution of complexity in play fighting is shown for several species of murid rodents. The species are mapped onto a cladogram, a tree-like diagram that shows the pattern of relatedness among the species, with those sharing a closer node being more closely related than to those from nodes further away. For example, *Rattus* and *Mus* are more closely related to one another than to *Notomys*, but they are both more closely related to *Notomys* than they are to *Mesocricetus*. The insert represents play complexity with the score of 0 indicating little or no play and a score of 4 indicating very complex play. The base of the tree shows that the ancestral state was one of moderate complexity. The species on the terminal branches independently either increased or

decreased the complexity of their play. Note that for most species, only the genus is shown, as only one species is represented for that genus. In the case of voles (*Microtus*), more than one species of the same genus are shown (*M. agrestis* = European vole; *M. ochrogaster* = prairie vole; *M. montanus* = montane vole). For the other genera, *Rattus* represents the Norway rat, *Mus* the house mouse, *Notomys* and *Psuedomys* represent two species of hopping mice, *Mesocricetus* represents the Syrian golden hamster, *Phodopus* the Djungarian hamster, *Onychomys* the Northern grasshopper mouse, *Peromyscus* the deer mouse, *Meriones* the Mongolian gerbil and *Psammomys* the fat sand jird (Reprinted from Whishaw et al. (2001) with permission)

First, while some species of rodents do not play at all and many of those that do have relatively simple forms (Pellis and Pellis 2009), in some other lineages, especially primates, there is not a single species of which we are aware that does not play, with that play probably being at least as complex as that present in rats (Fagen 1981; Palagi and Norscia 2016). That is, lineages with more neural capacity available may be more likely to spawn species with complex play (Pellis and Pellis 2009). Second, the sporadic nature of evolving more complex patterns of play in rodents (Fig. 2) suggests that factors other than increased brain size, such as favorable energy budgets and social systems, may be needed to promote the further evolution of playful complexity (Burghardt 2005). These considerations have a direct impact on why some species may be able to intermix different behavioral elements in their play.

Lineages such as primates, which have, as a group, above average brain size (Eisenberg 1981), have the neural capacity to produce moderate to highly complex play of more than one kind. All species observed have been reported to exhibit complex social play (Fagen 1981; Palagi and Norscia 2016). In addition, some species are noted for their complex locomotor play (e.g., Nishida and Inaba 2009), and others for their complex object play (e.g., Nahallage et al. 2016). Thus, species with the neural resources to evolve complex play of different types, under the right conditions, may also have the incentive, and the requisite level of neural control over play, to be able to intermix behavioral elements from different types of play into novel combinations. If

this model is correct, then the intermixing of behavioral elements in play is not as previously thought, a key characteristic of play (Heymer 1977), but rather, is an evolved feature that arises in the play of particular lineages. At present, there are some major holes in our knowledge that do not make a full evaluation of this model, or any alternative models, possible.

The biggest problem is that the only species for which knowledge of the neural circuitry involved in play is reasonably well developed is for the laboratory rat. In rats, while some play involves locomotor play, the vast majority involves social play, in the form of play fighting (Pellis and Pellis 2009). Consequently, discussions focused on the ‘mammalian play circuit’ (Siviy 2016) are really about the social play circuit of rats. Knowledge of the neural underpinnings of locomotor play and object play is exceedingly sparse. What does seem likely is that all forms of play are likely to tap into the brain’s reward mechanisms, but such a connection is true for most motivated behavior (Berridge and Kringelbach 2013), and so, in itself, is not especially revealing about how different forms of play connect to one another at a neural level. Moreover, as a comparative overview of play reveals, what is labeled as play may have many different grades of complexity (Burghardt 2005; Pellis et al. 2014).

Therefore, if species as model systems are to be selected, they need to be selected within a matrix that compares species with only one type of play and those with multiple types of play in their repertoire on one axis, and the degree of transformation (primary process play, secondary process play, tertiary process play) on the other (Table 1).

**Play Behavior, Table 1** The complexity and evolutionary transformations across different types of play can be mapped in a two-dimensional space, accommodating a wide range of species

| Type/complexity <sup>a</sup> | Absent          | Primary process | Secondary process | Tertiary process |
|------------------------------|-----------------|-----------------|-------------------|------------------|
| <b>Object</b>                |                 | SH, NR, HM, MG  |                   |                  |
| <b>Locomotor</b>             | SH <sup>b</sup> |                 | MG                | NR, HM           |
| <b>Social</b>                |                 | HM              | MG                | SH, NR           |

<sup>a</sup>Play can be either absent, or, if present, can be of varying degrees of complexity using the framework from Burghardt (2005)

<sup>b</sup>Abbreviations represent different species of murid rodents: *SH* Syrian golden hamster, *NR* Norway rat, *HM* house mouse, *MG* Mongolian gerbil. For sources on the primary data on the play of these species, see Pellis and Pellis (2009)

For example, of the four species of murid rodents entered in Table 1 for illustrative purposes, all have, at best, primary process play for object play, but a more diverse distribution for the other two types of play. One has very complex social play (e.g., Syrian golden hamsters) and one has very complex locomotor play (e.g., house mice), and another has social play and locomotor play that are both of moderate complexity. Only in rats does locomotor play involve hops, jumps, rotations, and runs that match that of house mice in complexity (tertiary process play) and have prolonged wrestling in their social play (see Fig. 1) that matches Syrian golden hamsters in complexity (tertiary process play).

While it is unknown whether the neural components involved in social play in rats (Siviy 2016) are the same as those involved in locomotor and object play, there is some degree of confidence that at least the major components of the social play circuit characterized in rats may also be active in the social play of other lineages, such as primates (Graham 2017). For the other dimension, that of level of transformation, if the picture for social play derived from rodents is reflective of the processes involved in other lineages and other forms of play, then it would be predicted that as any type of play increases in complexity, the level of control by cortical circuits would also increase. Therefore, cases of true intermixing of types of play would be expected to be limited to those species that have achieved tertiary process play in two or more kinds of play. For example, in rats, in which both social and locomotor play are very complex (Table 1), hops and other locomotor movements seen in solitary locomotor play are incorporated into their social play, suggesting a degree of intermixing of different types of play that is not present when one or more of the types of play present are at a lower grade of organization (Pellis and Pellis 2009). Much comparative neuroscience remains to be done.

## The Functions of Play

The comparative literature has traditionally been focused on identifying the functions of play

(Martin and Caro 1985). Recent studies with free-living populations of several species have revealed that functionally beneficial outcomes of play are present in some species, but not all (Pellis and Burghardt 2017). In part, these mixed results may arise because of the comparative diversity in both the kinds of play that predominate and the level of complexity that such play may have across the species used for such tests. For example, a common function proposed for play fighting is that it provides training for combat skills (e.g., Fagen 1981). However, play fighting involving competition for an advantageous position typical of sex, as seen in rats or squirrels, may be a poor avenue for training combat skills (Pellis and Pellis 2009).

Furthermore, for play fighting to remain playful, the partners need to curtail their combat to some degree to allow for whatever minimum level of reciprocity is required for the species in question and this may attenuate the fitness benefits derived from the practice afforded. The level of reciprocity varies with species, with age, sex, and dominance relationships, but play cannot be sustained if contests are completely one-sided – in situations in which one individual attempts to dominate the play completely, its partner will refrain from playing further with that individual. Adhering to a mutually agreed level of reciprocity is needed to make play fighting “fair” and so induce the players to keep playing together (Palagi et al. 2016). Different lineages have evolved different rules for ensuring reciprocal exchanges during play fighting. In some, the combat actions themselves are executed in a restrained manner, whereas in others, the restraint is interjected once a combat tactic is used to gain the upper hand. Unlike the former species, in the latter ones, the combat tactics are executed in a way that is seemingly identical to how they are used in serious fighting (Pellis and Pellis 2009). For such species, play fighting may provide an avenue for training combat skills.

These examples illustrate that species differences in how particular kinds of play are performed can greatly influence the development of particular skills. In the above case, a researcher selecting one species may find that there is a

strong correlation between juvenile play fighting and adult fighting skills, whereas another researcher using a different species may find a weak or absent correlation. The situation becomes even more complicated when both type of play and species differ. For example, during the juvenile period, the predominantly social play of rats is executed in such a manner that they experience many instances in which they lose and then regain control over their own bodies and over the movements of their partners (Pellis and Pellis 2009). The executive functions of the prefrontal cortex, such as those involving attention, short-term memory, emotional regulation, and decision making, are improved if rats engage in play with peers as juveniles (Pellis et al. 2014; Vanderschuren and Trezza 2014). That is, the play of rats has the effect of training them to be more resilient (Pellis and Pellis 2009). In contrast, in the house mouse, those individuals that play more appear to be less resilient as adults than those that play less (Richter et al. 2016). But there are two major differences to be considered: first, mice and rats may differ in the complexity of their neural control mechanisms, and second, in mice, unlike rats, the predominant form of play is locomotor play (Pellis and Pellis 2009). That is, the difference between the two species in the relationship between play and resiliency does not negate one another, as different forms of play may differ in their beneficial influences on development. Thus, while locomotor play may improve motor skills in some species, that species may not have the resources to improve executive functions with such play.

Another dimension to consider about the functions of play is whether the play has immediate or delayed benefits. In most examples for which benefits have been demonstrated, it has been for play in the juvenile period having beneficial consequences later in life, but in some cases, play appears to increase survival at that age in which it is performed (Pellis and Burghardt 2017). As already noted, the play of an adult with another adult likely only serves immediate benefits, not delayed ones (Palagi 2011; Pellis and Pellis 2009). It is this complex blend of the types of play present, the complexity

of the play, the species involved, and the age of the players, which makes any test of a functional hypothesis likely to fail. Selecting the most appropriate species for the functional hypothesis to be tested may require consulting a matrix like that in Table 1, in which species with particular types of play and play complexity can be identified. As for understanding the neurobehavioral mechanism of play, much more comparative work needs to be done before functions widely associated with play and those idiosyncratic to particular forms of play in particular species can be identified.

## Conclusions

Even a casual reading of the above review will quickly reveal a major element that is missing in the story – most of the examples, and all those involving detailed analyses of behavioral content, neurobiology, and functional consequences involve mammals. What about all the other species and lineages that have been reported to meet the five point criteria in Burghardt's definition of play? Where do nonmammalian vertebrates fit in, much less the myriad invertebrates that play? We have deliberately focused our review on mammals to show that even within the taxon that has been most intensively studied with regard to play, there are some major gaps in our knowledge. By understanding the problems that need to be resolved so as to have a comprehensive theory of the mechanisms and functions of play in mammals, the difficulties in integrating a broader swathe of species from diverse lineages can be placed in context. Some studies of birds suggest that some of the same considerations outlined above also apply to this lineage. For example, increased brain size in birds increases the likelihood of play, but likely does so as it may in mammals, by lengthening the juvenile period and thus increasing the opportunity to play. Similarly, the complexity of social play can vary in birds in ways similar to that outlined above for mammals (Pellis and Pellis 2009). Further afield, only sporadic examples are available for reptiles, fish, and other nonmammalian/nonavian



vertebrates (Burghardt 2005). The breadth of species becomes even more impoverished as examples are sought among invertebrates (Burghardt 2005; Pellis and Burghardt 2017). At present, the lack of breadth in the literature on the distribution of types and complexity of play makes the development of a comprehensive theory that encompasses the whole animal kingdom highly elusive.

For example, in mammals, play is predominantly a phenomenon of the juvenile period (Fagen 1981), with some forms of play being retained in adults in some species (Palagi 2011; Nahallage et al. 2016). This requires an emphasis on the kinds of factors that have promoted play to emerge in the juvenile period of some species but not others (Burghardt 2005), and an understanding of the factors that have led to play in some of these species being retained in adulthood (Pellis and Pellis 2009). However, several species of cephalopods have been identified to engage in play with objects (Burghardt 2005), but all these octopuses are adults. To our knowledge, no one has reported play in the young of these species. This is perhaps understandable in that most of these species have planktonic young, thus being much smaller and of a different body shape to the adults, so likely do not have the neural wherewithal, the body morphology or the favorable ecological conditions that make play possible. Thus, in contrast to mammals, in cephalopods, play is a phenomenon of adulthood. Such contrasting aspects of behavioral phenomena that meet the conditions set by Burghardt's five criteria have to be taken seriously in developing general theories of play. Clearly, a first step in such an endeavor is to describe the types and complexity of play across a wider range of species from across many different taxa.

## Cross-References

- Behavioral Variation
- Cladistic Analysis
- Heritability of Behavior
- Homoplasy
- Sociosexual Behavior

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## Pleiotropy

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Pleiotropy is the term used to describe the phenomenon where a single mutation affects more than one phenotypic characteristic of the organism (Stearns 2010). Pleiotropy can occur at the allelic level, where a single causal variant is related to multiple phenotypes, or at the gene (or region) level, at which multiple variants in the same gene (or region) are associated with different phenotypes (Solovieff et al. 2013). The term was defined in 1910 by the geneticist Ludwig Plate (Stearns 2010); this trait has implications for genetics, evolution, development, age, disease, and discovery of new drugs (He and Zhang 2006). Before that, in 1866, Mendel reported this type of genetic inheritance in his study with *Pisum* species: he attributed three characteristics (seed coat color, flower color, and axial spots) to a single factor. Although this explanation is not confirmed, it denotes the significance of this mechanism. Many studies have been conducted in different areas of biology using pleiotropy as a target or basis for research. Between them, evolutionary dynamics are influenced by pleiotropic mechanisms in different ways: a single gene product with multiple effects will be strengthened or weakened by processes different from those that will impact a single gene that can produce multiple products. Multiple reading frames and alternative transcripts may be more difficult for evolution to disrupt than a single product incorporated into different pathways (Stearns 2010). According to Reusch and Wood (2007), the effects of pleiotropy on adaptation are important: when they act synergistically, they could allow the population to quickly produce new solutions to environmental problems. An example known as pleiotropy antagonist also operates in evolutionary processes: this phenomenon can be explained by variants that exert different functions according to the period of life, for example,

## Playing Possum

### ► Tonic Immobility

genetic variants that exert beneficial effects in the early stages of life may turn out to be detrimental at older ages and vice versa (Giuliani et al. 2017). Pleiotropy can be caused by a single locus with multiple primary products or by a single product originated from a gene that is incorporated in several different ways (He and Zhang 2006). From this perspective, three categories of pleiotropy can be described: biological pleiotropy where causal variants of different traits fall into the same gene or regulatory unit (e.g., transcription factor binding sites) (Solovieff et al. 2013); mediated pleiotropy refers to the case where a variant directly affects one trait, which in turn affects another (Hackinger and Zeggini 2017); spurious pleiotropy involved encompasses various sources of bias that cause a genetic variant falsely to appear to be associated with multiple phenotypes (Solovieff et al. 2013). In a study of yeast pleiotropic genes, He and Zhang (2006) concluded that “gene pleiotropy is generally achieved by the use of a single molecular function in multiple biological processes, which is realized in part by the distribution of the gene product into multiple cellular components and by participation of the gene in different protein–protein interactions.” Many studies are still being carried out about pleiotropy, demonstrating the importance of this process for several areas of biology and proving that it is more than “artifacts” or “misinterpretations” in genetic research.

## Cross-References

- [Evolution](#)
- [Genetics](#)

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## Plural Marriage

- [Polyandry](#)
- [Polygynandry](#)

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## Point Light Biological Motion

- [Point Light Displays](#)

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## Point Light Displays

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## Synonyms

[Biological motion](#); [Point light biological motion](#); [Single frame lifetime display](#)

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## Definition

A point light display is an experimental paradigm. Instead of presenting the moving body, it only displays the movements of a few landmarks on the body, typically as white points against a dark background.

## Introduction

Point light displays, usually referred to as “point light biological motion” or simply “biological motion” (see also the chapter on ► [“Biological Motion”](#)), have enjoyed a rich research tradition since the 1970s and have been widely applied. Fields of application involve experimental psychology, cognitive development, ► [primate cognition](#), neurology, pain research, and action perception. Using point light displays in research studies is attractive, first because they are easy to generate and manipulate computationally and, second, because they allow the study of the ► [visual perception](#) of biological movement without the rich visual context that is typical of movies.

## History

The point light display was developed by the Swedish Gestalt psychologist Gunnar Johansson, who also coined the term *biological motion* (Johansson 1973). Although the term biological motion is reasonable for visual scientists, it is a misnomer from the biological perspective, because biological motion refers to the movements of biological organisms, rather than just the abstracted visual presentation thereof.

At the time Johansson had formulated Gestalt laws for movements. Gestalt laws are generalized rules for how the visual system structures and organizes the chaotic visual scenes that fall on the retinas. Applied to short sequences of a few moving dots, he found, for example, that observers can recognize a rolling wheel (i.e., the sum of the principles of rotation and translation) from the movements of just two points. When searching for a more complex stimulus to test his

laws, Johansson was completely stunned by the robustness and vividness of the point light display of biological motion. These findings inspired hundreds of scientific studies.

## Technique and Stimulus Types

Originally, an actor dressed in black with bright dots stuck to some major landmarks of the body was filmed against a black background, so just the moving “point lights” showed the movements of the – otherwise invisible – body.

Soon, a simple software program for computing an artificial point light stimulus, simulating a “person walking in-place,” was published (Cutting 1978). Although the resemblance to real walking is really quite superficial, human subjects readily identify this artificial stimulus as a walking person. This feature, and the ease with which this stimulus can be implemented, rapidly popularized the use of point light displays in visual research.

Three-dimensional (3D) kinematic recording techniques and reflective markers attached to whole-body morph suits combined with computer processing power have now replaced the original video technique. Various databases of such recordings are freely available.

Many experimental paradigms have been published, such as visual detection tasks, choice tasks, priming, and so on. Typically, a fixation point is used to control the eye movements. The retinas of primates (and many other animals) have a fovea, a small central field in which vision is greatly enhanced with respect to the visual periphery. Therefore, to control which information exactly enters the brain, it is essential to either keep the eyes fixated or measure the movements of the eyes.

Various paradigms have used masks. Such a (invisible) mask may obscure parts of the stimulus, or it may consist of a large number of moving point lights of the same size and color as the stimulus' point lights.

Point light displays have usually been presented as white points moving on a dark background, but isoluminant points and points of a limited lifetime have been used as well.

Isoluminant stimuli differ from the background by color, but not by brightness. In such stimuli, the points are as bright to the eye as their surroundings. Points of limited lifetime are present only for some time before reappearing on a different location of the body. In the extreme case, the points are presented on one location of the body for just a single display frame. In such a “single frame lifetime” (SFL) display, the observer sees much flicker, but no movement in the direction of the actor’s motion.

Finally, the point lights may have the shape of objects, such as small fruits or tools or even small point light displays.

## Paradigms and Findings

Early studies focused on the robustness of the percept, for example, by embedding the point light movements in a dense field of distracting points. These studies demonstrated the immense ability of the visual processing system for perceptual grouping of biological motion within point light displays. Even if parts of biological motion stimuli are covered or if the point lights are displayed among a large number of distracting point lights, humans can easily recognize the stimulus visually.

Various studies have been performed to establish the richness of information that observers obtain from point light displays. Biological motion conveys rich information to the observer. For example, humans can perceive the gender, weight, and mood from the mere point movements and can reliably identify friends as well as themselves. On the other hand, humans are very tolerant to errors in the stimulus. For example, observers do not notice if the stimulus misses hands and feet. Naive observers readily accept even an artificial stimulus of pendular sine and cosine movements as human walking (see above: Cutting 1978).

The recognition of point light biological motion has been shown to be size-invariant, but not orientation- or location-invariant. That means that human subjects can easily perceive and can even perform decision tasks on point light

displays whose size changes randomly from image frame to image frame.

Counterintuitively, it has been found that point light biological motion is easily recognized even if nothing moves in the display. This has been shown with the SFL display, in which there is a lot of flicker, but no systematic movements of the point lights. On the other hand, biological motion is difficult to recognize if the point lights are replaced by objects (such as tools or fruit). These findings indicate that the visual perception of point light displays is similar to object perception, rather than motion perception.

Other paradigms have used point light biological motion displays to study perceptual effects such as depth perception, biases, bistability, and so on. Since the point lights move in the 2D display, the stimulus conveys ambiguous depth information (Video 1). It is thus impossible to tell if the presented person faces out from the display or into it. However, observers will more frequently report that the presented actor is facing out of the display. This so-called facing the viewer bias has received considerable medial attention. It was thought at first to have an evolutionary origin but in the end turned out to be mainly caused by a geometric perceptual bias for relative point motion.

Further, when looking at it for some time, the two possible percepts will spontaneously alternate. This effect is known as a so-called bistable percept.

## Applications in Animal Research, Patients, and Infants

A number of studies have been performed with rhesus macaques and pigeons as subjects. These have shown that primates and birds perceive biological motion from point light displays. Pigeons may show courtship behavior when presented a point light display of a female pigeon (Troje and Aust 2013). Electrophysiology (electric recording from electrodes stuck into the cortex) in macaques identified neurons in the ► [superior temporal sulcus](#) (STS) that respond to point light displays of biological motion, but not to random



point light displays (Oram and Perrett 1994). This finding has been well established for biological motion. Even neurons in the monkeys' premotor cortex are now known to respond to visually presented actions (Gallese et al. 1996).

Newborns show a clear preference to look at point light displays of biological motion rather than other point light movements (Fox and McDaniel 1982).

A number of studies have investigated patients, suffering, for example, from schizophrenia, autism, and various brain lesions. Some very rare lesion patterns may make a person unable to see motion, whereas they are able to identify visually presented objects. Such patients who are called motion agnosia, were found to perceive point light biological motion displays (Vaina et al. 1990).

## Theory and Modeling

From the beginning, theories and models for the perception of biological motion have focused on mechanisms for visual motion perception. However, many findings indicate that the recognition of biological motion stimuli is driven primarily by the same perceptual mechanisms that underlie the visual perception of objects. As mentioned, motion agnostic patients are not impaired, and healthy persons easily identify SFL displays as biological motion. On the other hand, individuals with facial agnosia (more widely known as prosopagnosia, for severe problems with recognizing faces) are also impaired in recognizing biological motion. Lastly, biological motion is masked effectively if the points are displayed as objects (see above).

A recent theory for biological motion recognition solely depends on visual mechanisms for object recognition (Theusner et al. 2014). The model in addition proposed that the sequential order of recognized body postures is aligned in the brain to more easily recognize the displayed action. The perception of such sequences of configurations is known as higher-order motion detectors, or motion-from-form detectors, and is thought to occur in the ► [superior temporal sulcus](#) (Oram and Perrett 1994; Barraclough et al. 2006).

On the basis of the nineteenth-century theorizing by the pioneer of psychology, William James, it had long been predicted that the motor systems in the brain also play an important role in the understanding of actions. By coincidence such neurons were found in the macaque premotor cortex, which responded only if the monkey performed a specific movement (e.g., a precision grip) but also if the monkey saw another person perform the same specific action (Gallese et al. 1996). This role of the motor system for visual perception of actions is now widely accepted (Rizzolatti and Craighero 2004) and has found various applications with point light displays.

## Conclusion

Point light displays of biological motion have enjoyed a rich and wide field of applications in visual sciences, for humans, monkeys, and pigeons. The stimulus has greatly added to the understanding of visual processes. By virtue of the theoretical framework, the displays have even found their way to neurological applications related to sensorimotor control and action understanding.

## Cross-References

- [Biological Motion](#)
- [Bipedalism](#)
- [Computerized Testing Paradigm in Primates](#)
- [Primate Cognition](#)
- [Primates](#)
- [Superior Temporal Sulcus](#)
- [Visual Detection Task](#)
- [Visual Perception](#)
- [Visual Recognition in Birds](#)

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## Point Mutation

### ► Single Nucleotide Polymorphism (SNP)

## Pointing

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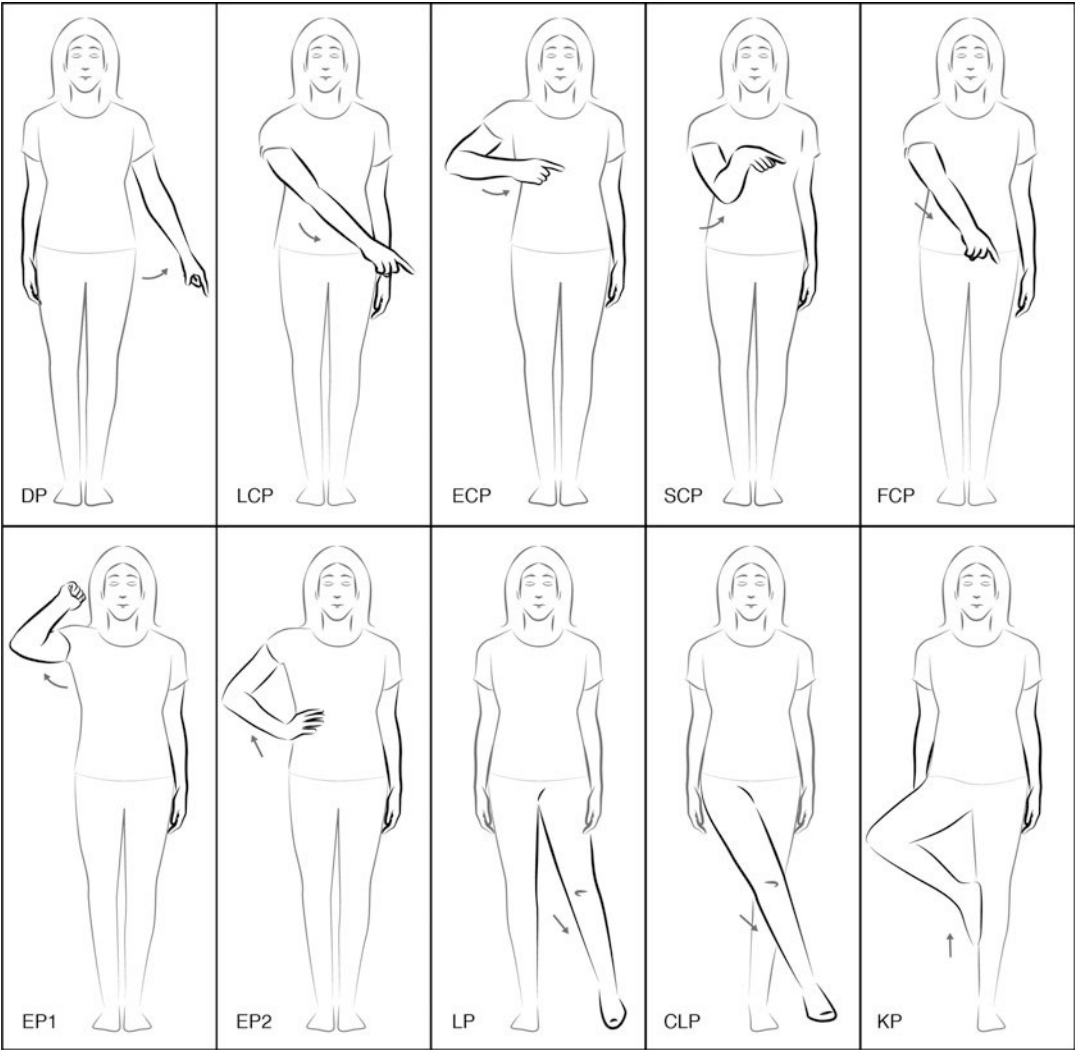
## Introduction

An early developmental hallmark in human social cognition is the ability to understand pointing as a form of referential communication. Referential pointing in humans is a triadic communicative transaction involving the management of joint

attention between an informant, a receiver, and a subject of interest. Pointing is not only adaptive as a form of communication but it can also inform a receiver and an informant about each other’s visual perception, social awareness, and knowledge state. In human infants, the ability to understand the referring function of the pointing cue develops over the first 2 years of life (reviewed in Pfandler et al. 2013). Since the early 1990s, there has been an “explosion” of studies in non-human animals on how they respond to pointing cues, whether they produce pointing cues, and if they appreciate a pointing cues’ referring function (see summaries in Miklosi and Soproni 2006, Pack and Herman 2006; Lyn 2010; Kaminski and Nitzschner 2013; Halina et al. 2018). This entry summarizes key findings on these topics and discusses proposed mechanisms, including domestication, through which some species may have acquired an ability to understand pointing.

## A Classic Approach Used to Investigate Pointing Comprehension in Animals

The “object-choice” task is often used to study pointing comprehension. An informant points at whichever of several containers was previously baited, and the receiver must use the informant’s cue to find the bait. Occasionally, arbitrary objects instead of containers are employed, and the receiver is rewarded for carrying out the informant’s designated action to the indicated object. In both approaches, an animal’s *immediate* success when confronted with novel variations in the type of pointing cue (e.g., “direct pointing” – using the arm ipsilateral to the target or “cross-body pointing” – using the arm contralateral to the target) (see Fig. 1), the spatial relationship between the cue and the target (e.g., proximal or distal), the location of the informant (e.g., equidistant between the objects or asymmetric – either closer to the target or nontarget), temporal aspects of the cue (e.g., “static” – in place already when the receiver views it, or “dynamic” – presented and sustained in view of the receiver, or “momentary” – presented for one or several seconds), the number of objects and their



**Pointing, Fig. 1** Artist's (J. Napurano) rendering of different pointing cues. *DP* direct pointing (pointing with the extended whole arm, hand, and finger on the ipsilateral side of the target), *LCP* long cross-body pointing (pointing with the extended whole arm, hand, and finger on the contralateral side of the target), *ECP* elbow cross-body pointing (pointing with the contralateral arm with the pointing finger kept inside the body silhouette and elbow protruding on the side of the nontarget), *SCP* short cross-body pointing (same as *ECP* except elbow tucked into side of

informant's body), *FCP* forward cross-body pointing (pointing using the contralateral extended whole arm, with hand and finger kept within the body silhouette), *EP* elbow pointing version 1 (pointing using the ipsilateral elbow with fist at shoulder), *EP2* elbow pointing version 2 (pointing using the ipsilateral elbow with fist at waist), *LP* leg pointing (pointing using the extended ipsilateral leg and foot), *CLP* cross leg pointing (pointing using the extended contralateral leg and foot), *KP* knee pointing (pointing using the ipsilateral knee)

arrangement, and any additional cues accompanying pointing (e.g., gazing at the target, hereafter referred to as "target gazing" or gazing at the subject, hereafter referred to as "subject gazing" or gaze alternation between the subject and target) can help reveal how pointing is understood. For

example, pointing comprehension that is limited to conditions in which an informant's pointing finger is either touching or very close to the target may be explained in terms of stimulus or local enhancement (i.e., the pointing cue attracts the receiver to the target or an area where it

encounters the target). Likewise, pointing comprehension with distal objects that is limited to direct dynamic pointing may be influenced by an enhancement-like process inasmuch as the sustained cue provides an asymmetric body image that not only can attract a receiver to a particular area where its chances of encountering the target are increased but also provides a stimulus that the receiver can repeatedly check back against as it moves in the direction of the target.

To guard against such noncommunicative uses of pointing, studies have employed momentary direct pointing and cross-body pointing to distal objects, as well as asymmetric pointing in which the informant's pointing finger is physically closer to the nontarget. In addition, static pointing (described above) and reverse pointing (in which the static pointing arm is lowered in the opposite direction) are useful in revealing if responses are contingent on a receiver perceiving movement in particular direction. Finally, a receiver's accurate responses to an informant's points in novel contexts such as to objects out of its immediate view, to objects aligned with each other on the same side of the informant, and to objects requiring attention but not direct action can collectively provide evidence that the receiver understands the referring function of the pointing cue. Across all of these manipulations, accurate performance on initial trials is essential for eliminating associative learning as an explanation of a receiver's responses to pointing. Below, representative studies of pointing grouped by animal type are presented and assessed for what they reveal about a subject's understanding of the communicative function of the pointing gesture. Unless otherwise specified, an informant's extended index finger aligned with the indicated object and accompanied by variations in the positioning of the arm and hand of the pointing finger constituted the pointing cue. Distances between the informant's pointing finger and the target were considered proximal when  $\leq 40$  cm and distal when  $\geq 50$  cm (see Miklosi and Soproni 2006). Statistically significant performances above what would be expected by chance are referred to as "above chance."

## Pointing Comprehension in Object-Choice Tasks in Human Infants

As noted by Pfandler et al. (2013), many early studies of pointing comprehension in human infants examined the orientation responses of an infant to its mother's pointing cues while seated on her lap. In contrast, most studies with nonhumans employ object-choice tasks in which, after experiencing an informant's pointing cue, the receiver is free to move towards and physically select one of several alternatives. Because the latter method may be more representative of the natural way communicative pointing is achieved, and for comparative purposes, recent studies of human infant pointing comprehension have also employed object choice tasks. For example, some 12-month-olds in an object-choice task understand a dynamic cross-body pointing cue accompanied by dynamic gazing or gaze alternation, and those that can also able to reverse roles (i.e. they can also produce these cues) (Behne et al. 2012). By 18 months, infants can use an informant's dynamic pointing cue alone to find a container positioned  $\leq 60$  cm from the pointing finger (Itakura and Tanaka 1998), and by 24 months, they can understand an informant's static direct and cross-body asymmetric pointing cues to more distally placed objects (Povinelli et al. 1997). To better understand the development of pointing comprehension, Pfandler et al. (2013) investigated how 16 infants responded to pointing at 12, 14, 16, and 18 months of age. On each trial, an informant produced one of the following momentary distal pointing cues: direct pointing, long cross-body pointing, forward cross-body pointing, and far direct pointing (Fig. 1). As infants aged, they responded more accurately to pointing cues. Although a few individually performed well with pointing cues at 12 and 14 months, at the group level, infants performed poorly. For example, in response to far direct pointing, most infants at 12 months tended to select the closer nonindicated object. In contrast, starting at 16 months, a significant number of infants performed above chance on first trials with distal direct pointing, long cross-body pointing, and forward cross-body pointing, and

by 18 months, most infants understood the far pointing cue.

## Domesticated Animals

### Dogs and Cats

Initial studies of pointing comprehension in dogs established their ability to exploit dynamic or momentary pointing cues to distal objects including those out of direct view (reviewed in Miklósi and Soproni 2006). For example, Hare et al. (1998) tested how two dogs (one experienced with human pointing in the context of retrieving distally located objects and the second with no previous human pointing training) responded to human direct dynamic pointing with gaze alternation to whichever of two or three containers placed in front of or behind a dog was baited. Each dog performed above chance in all conditions. In follow-up tests involving static pointing, both dogs performed above chance, one immediately. Next, Hare et al. (1998) used dynamic long cross-body pointing and dynamic “belly” pointing (i.e., elbow cross-body pointing) (Fig. 1), with the informant positioned between two containers as well as behind the unbaited container. Both dogs performed above chance with long cross-body pointing when the informant was positioned between the containers, but only one was correct when the informant pointed distantly to the baited container from behind the unbaited container. Neither dog responded accurately to elbow cross-body pointing from either of these positions.

In another early study, Miklósi et al. (1998) tested 11 family-raised dogs, some of which were highly trained assistant dogs, for their responses to momentary distal pointing cues. Collapsing the data across two tests, 10 of 11 dogs responded above chance to whichever of two containers was indicated by an informant. An analysis of responses across trials revealed that associative learning was not a factor in their performance.

Soproni et al. (2002) expanded on these investigations by examining a dog’s ability to understand different forms of pointing. Of

nine dogs tested, between two and seven performed above chance with momentary direct pointing, reverse pointing, direct pointing using a stick, far pointing, long cross-body pointing, and elbow pointing (Fig. 1), with no evidence that the dogs learned how to perform across trials. Thus, dogs showed good generalization to different forms of pointing including those in which movement was in the opposite direction as the target. Also, as in Hare et al. (1998), the results suggested that the side of the informant’s body on which the arm protruded largely governed the object to which responses were made. That is, when the pointing finger was kept within the informant’s body frame and an elbow protruded on the side of the unbaited container (i.e., elbow cross-body pointing), dogs seemed confused, and in the case of asymmetric elbow cross-body pointing, selected the unbaited container leading to significantly below chance performance. In contrast, when the pointing finger protruded from the side of the informant positioned at the unbaited container (i.e., far pointing), dogs were more successful. In a follow-up study, Lakatos et al. (2009) confirmed the ease of dogs with distal direct and long cross-body pointing cues, as well as their difficulty when an informant’s pointing gesture was kept within their body’s silhouette as occurs in elbow cross-body pointing and forward cross-body pointing. Lakatos et al. (2009) found that comprehension of elbow cross-body pointing was also difficult for 2-year-old children, although by 3 years, they had no difficulty interpreting this cue.

To better understand if dogs understand the referring function of pointing, Lakatos et al. (2012) examined their ability to follow its geometry by arranging two bowls in line with each other on each side of an informant who used a direct momentary pointing cue to indicate the baited bowl. Thus, when distally pointing to the far bowl on either side, the informant’s pointing finger was actually nearer to the proximal bowl. In order for a dog to perform accurately on these critical trials, it had to extrapolate an invisible vector from the angle of the informant’s arm towards the distal bowl. The results did not support an understanding of the referring function of



the pointing cue. When dogs chose the correct side of the informant, they tended to favor the more proximal of the two bowls (i.e., the one closer to the pointing gesture) regardless of which particular bowl was pointed at. Lakatos et al. (2012) also examined whether dogs directed by their owner's pointing cue to one of two informants simultaneously pointing and gazing at one of a pair of containers to their right and left would attend accurately to the cue of the indicated informant. Although dogs accurately chose the informant indicated by their owner, they did not accurately respond to the indicated informant's pointing cue. These findings suggest that dogs do not fully appreciate the declarative nature of pointing (i.e., pointing that directs attention to an entity from which information may be derived).

In a different study of a dog's understanding of the referring function of pointing, Tauzin et al. (2015) examined whether dogs process the identity of the object at the terminal destination of the pointing cue or only the location where they should respond to an object. Dogs were tested in an object-choice task in which two physically different plush toys were positioned left and right of an informant. On each trial, the informant pointed directly and momentarily while target gazing. Following this, the informant picked up both toys, turned 180°, and placed them back on the floor (i.e., opposite from their original locations). Each dog, after watching this procedure, was allowed to make a selection. Half the dogs experienced an ostensive condition in which prior to pointing, the informant called the dog's name and made eye contact, thus showing communicative intent. The other half experienced a non-ostensive condition to gain the dog's attention. Only dogs in the ostensive condition performed above chance. However, they chose whichever toy was at the indicated location more often than the particular toy originally indicated by the informant. These findings suggest that dogs understand the communicative intent of pointing but not that it refers to a particular object that may vary its location.

Finally, Miklosi and colleagues compared dogs and cats in their understanding of momentary direct pointing and dynamic direct pointing

using both proximal and distal pointing cues (summarized in Miklosi and Soproni 2006). Both dogs and cats responded above chance to each cue type, and for cats, but not dogs, performance was better with dynamic than momentary cues. There was no evidence of learning how to respond across trials in either animal.

### Goats, Horses, and Pigs

To examine whether other domesticated species beyond dogs could understand human-directed pointing cues, two early studies employed object-choice tasks with domesticated goats and horses. Summarized in Miklosi and Soproni (2006), McKinley and Sambrook (2000) tested the ability of four horses (*Equus caballus*) to follow human direct dynamic pointing. On each trial, an informant pointed distally to a target while moving her hand up and down. On half the trials, the informant stepped diagonally closer to the target and on the other half further from it. Although one horse performed above chance, this individual first ran his nose down the informant's arm before choosing the target suggesting that local and/or stimulus enhancement played a role in the horse's responses. In the second study, Kaminski et al. (2005) tested how domesticated goats (*Capra hircus*) responded to pointing cues in a two-alternative object-choice task. On each trial, an informant either repeatedly directly pointed at and touched the target while subject gazing or used dynamic distal direct pointing with gaze alternation. Of 23 goats tested, 13 (57%) and 5 (22%) responded above chance to the proximal and distal cues, respectively.

Later studies with horses and pigs appeared to confirm earlier observations that enhancement-type processes are influential in the successful responses of some domesticated species to an informant's pointing cues. Maros et al. (2008) tested 20 horses with various forms of pointing in a two-alternative object-choice task. Each was first tested with distal direct momentary pointing. None performed above chance. Next, the horses were tested on distal dynamic pointing, proximal momentary pointing, and proximal dynamic pointing with dynamic target gazing.

Between 2 and 6 performed above chance across conditions. However, on successful dynamic pointing trials, some of the horses tended to approach the informant's pointing hand before choosing the container on that side. Proops et al. (2010) tested how 28 horses responded to distal dynamic pointing as well as other cues in a two-alternative object-choice task. When responses were grouped together, the horses performed above chance in the pointing condition. However, again some horses that responded correctly to pointing cues first examined the informant's outstretched arm before choosing the correct target.

Recently, Nawroth et al. (2014) examined how 17 pigs (*Sus scrofa domestica*) responded to proximal dynamic pointing with dynamic gazing, proximal momentary pointing, distal dynamic pointing, and distal momentary pointing with the informant positioned between two containers in an object-choice task. Individually, 5 and 14 pigs, respectively performed above chance with proximal dynamic pointing and with proximal momentary pointing. None performed above chance in either of the distal pointing conditions. In a follow-up test, the informant changed locations to either behind the target where they remained without pointing or behind the nontarget where they pointed dynamically while gazing at the target. Nine pigs selected the target in the former condition but only one in the latter. Moreover, with both distal dynamic and proximal dynamic pointing, pigs often approached or touched the informant's pointing finger before choosing a container indicating that as with horses, enhancement-like processes likely influenced their responses.

## Undomesticated Animals

### Monkeys and Bats

Early studies of pointing comprehension in monkeys using object-choice tasks employed proximal direct dynamic pointing cues with results ranging from poor performance with cotton-top tamarins (*Saguinus oedipus*) to highly limited eventual success in rhesus monkeys, to either

eventual or immediate success with capuchin monkeys (*Cebus apella*) (summarized in Miklosi and Soproni 2006). Later studies using these same types of cues with capuchin monkeys (Essler et al. 2017) revealed generalization to novel informants within and across species. Studies with four species of bat (*Pteropus pumilus*, *Pteropus rodricensis*, *Pteropus conspicillatus*, and *Pteropus vampyrus*) were also limited to proximal dynamic pointing with subjects showing immediate success (Hall et al. 2011). Across these studies, findings of eventual success are subject to associative learning mechanisms, and those of immediate success to explanations of stimulus or local enhancement due to the very close proximity of the pointing cue and target.

### Apes

Perhaps not surprisingly, some of the earliest work investigating pointing in species other than humans focused on their closest relatives, apes. Although observational studies at that time suggested that apes in the wild do not readily point indicatively (Call and Tomasello 1994; cf. Halina et al. 2018 for recent positive examples), productive pointing to direct a human's attention to distal objects in conjunction with appropriate use of gazing was observed to emerge in captive enculturated apes with extensive human contact including exposure to pointing. For example, Call and Tomasello (1994) showed how two orangutans, Chantek who was highly enculturated, and Puti who had a more traditional captive upbringing, used pointing differently to direct a receiver. Both orangutans had previously been trained to point in limited contexts. In an initial test, they witnessed food being hidden in one of three containers that they pointed to when a receiver who had not witnessed the baiting entered the room. The receiver either retrieved the food directly if within reach, or, with a tool if out of reach. Next, they observed as both food and tool were hidden in different locations. This time when the receiver entered the room, only Chantek pointed immediately to a possible location of the hidden tool prior to pointing to the baited container and his performance improved over trials. Further tests revealed that both orangutans

pointed more often when the receiver was present than absent or away from the apparatus with their back turned. Chantek, but not Puti, pointed more often when the informant was facing forward with their eyes open than when they were closed. Later, during a test of pointing comprehension, an informant used distal momentary pointing accompanied by subject gazing to indicate which one of three containers had been baited, and then left the testing room. A receiver, ignorant to which container had been baited, entered the room and waited. Only Chantek pointed to the baited container above chance levels.

In another early study, Povinelli et al. (1997) tested seven chimpanzees on their understanding of direct static pointing. On each trial out of a subject's view, one of two boxes was baited and an informant adopted a static pointing position before the subject entered the room and responded. Each of the chimpanzees was first trained to respond to static proximal pointing (without gazing). The chimpanzees were next tested on static distal direct pointing either presented alone or with the informant target gazing or subject gazing. Combining the data from all pointing cue trial types, only one chimpanzee performed above chance. Next, Povinelli et al. (1997) tested the chimpanzees with variations of the pointing cue as well as variations of the informant's position while pointing. With the informant positioned between two containers, subjects could not understand elbow cross-body pointing whether it was accompanied by gazing or not. When the informant was positioned at the unbaited box, performance with elbow cross-body pointing accompanied by gazing was at chance and with elbow-cross-body pointing presented alone fell below chance (i.e., the subject chose the box closest to the pointing cue).

Four follow-up studies summarized by Miklosi and Soproni (2006) focused on ape comprehension of proximal and distal pointing cues with mixed results. Tomasello et al. (1997) found that none of six chimpanzees and only one of three orangutans (Chantek) responded accurately to proximal dynamic direct pointing to whichever of three containers was baited. In contrast, 17 of 24 thirty-month-old children performed

above chance. Using the same pointing cue accompanied by dynamic target gazing, Itakura and Tanaka (1998) showed above-chance performance for children ranging in age from 18 to 27 months, as well as for two chimpanzees and an orangutan. In the absence of gazing cues, Peignot and Anderson (1999) found that all four gorillas tested performed above chance responding to proximal dynamic pointing in a two-alternative object-choice task. Finally, Itakura et al. (1999) examined how four chimpanzees responded to distal dynamic direct pointing accompanied by gazing from either a human or a conspecific informant. No chimpanzee performed above chance with a conspecific informant, and only one was above chance with a human informant. However, this subject likely learned how to respond over the test.

In light of the generally poor performances by chimpanzees with pointing cues, Hare and Tomasello (2004) considered whether the cooperative nature of the traditional object-choice task was confusing to subjects, and whether having the informant act more competitively would yield better results. Using 12 chimpanzees, they compared performance in an object-choice task when an informant acted competitively versus cooperatively. During an introductory phase, chimpanzees attempted to find a baited container in the presence of an experimenter. For half the chimpanzees, the experimenter acted competitively (e.g., reacted negatively if the chimpanzee found the baited container) and for the other half acted cooperatively (e.g., praised the chimpanzee for finding the baited container). A test then ensued. Following a baiting procedure, the competitive informant reached his contralateral hand with fingers spread through a window towards the baited container while staring at it. In contrast, the cooperative informant reached through the window and pointed with gaze alternation at the baited container. Three of six chimpanzees exposed to the competitive informant were successful in finding the bait. None were who experienced the cooperative informant. Furthermore, chimpanzees that initially experienced success with a competitive informant were later successful with proximal pointing from a cooperative informant

with no evidence of associative learning across trials.

Using another strategy, Mulcahy and Call (2009) investigated how the position of the subject, the informant, and the containers might affect an ape's performance in an object-choice task with dynamic distal versus proximal pointing cues. Twelve chimpanzees, four bonobos, and three orangutans participated. The proximal pointing task was presented in the traditional manner used with apes in which a subject was positioned in close proximity to two containers on a single table when a pointing cue was delivered. In contrast, in the distal condition, the distance between the containers was more than four times that in the proximal condition, the informant was positioned between the containers instead of between and behind them, and the receiver was located farther from the informant as well as the containers. On each trial, the informant produced a dynamic long cross-body pointing cue accompanied by dynamic gazing. Performance accuracy collapsed over individuals and species was above chance in the distal condition but no different from chance in the proximal condition. Individually, eight chimpanzees, three bonobos, and one orangutan performed above chance with distal pointing while only one bonobo and three chimpanzees performed above chance with proximal pointing. Why under these conditions was there a marked improvement in ape' responses to an informant's distal pointing cue? Mulcahy and Call (2009) suggested several possibilities including that the position of the informant directly between the containers enhanced their contrast, that the substantial separation of the containers created an additional energetic cost of selecting the unbaited container that motivated the receiver to better focus its attention on the informant's gesture, and that the separation of containers also decoupled them from occurring in the same visual space as the informant's gesture and potentially competing with each other for the receiver's attention.

Using a similar strategy to Mulcahy and Call (2009) with further separation of the informant from the midline of the containers, Lyn (2010) showed that all six bonobos she tested responded

above chance to an informant's distal dynamic pointing cue accompanied by gaze alternation and performed better with distal than proximal pointing. In another study, Lyn et al. (2010) showed that immersing apes in a human-ape sociolinguistic environment significantly enhances their performance in responding to human pointing cues in object-choice tasks.

### Wolves

Studies of pointing comprehension in wolves (*Canis lupus*), the closest wild relative of dogs have been pursued largely to examine whether domestication of dogs lead to their ability to understand pointing cues. Hare et al. (2002) first compared how seven adult wolves and seven adult dogs responded to human dynamic proximal cross-body pointing cues in a two-alternative object-choice task in which pointing was accompanied either by gazing at the target or subject. Five and four dogs performed above chance respectively with each of these cues. No wolf performed above chance with either cue. Next, Miklosi et al. (2003) tested 4-month-old wolves that as puppies were individually raised by humans in homes and subsequently on a farm. Four wolves were tested with proximal and distal momentary direct pointing in an object-choice task. On initial trials, two wolves responded above chance to proximal pointing, but none to distal pointing, although one eventually learned how to perform with this cue. Follow-up tests in problem solving tasks revealed that dogs were much more inclined than wolves to gaze at a human when the task became insolvable. Finally, Viranyi et al. (2008) tested wolves and dogs with comparable human socialization, in the same object-choice tasks. In their initial experiment, three groups consisting of nine 4-month old wolves, eight hand-reared puppies, and nine pet dogs were compared. Each subject was tested with momentary direct distal pointing. The puppy and pet dog group each performed above chance and were not significantly different. In contrast, wolves, despite similar rearing histories and socialization as puppies, performed at chance both as a group and individually.

These studies appear to show uniformly that wolves do not readily understand pointing and perform poorly in object-choice tasks compared with their closest domestic relative, dogs, possibly because they are less prone than dogs to check on the focus of a human's attention. However, Udell et al. (2008) showed that this was not necessarily the case when the degree of human socialization for wolves was intensified (i.e., all wolves from 10 to 14 days old were hand-raised and had daily interactions with humans), the backgrounds of dogs were varied (pet dogs vs. shelter dogs), and the environmental conditions under which testing took place were modified (outdoors vs. indoors with cues from familiar vs. unfamiliar human informants). In their study, 8 wolves and 32 dogs (8 per condition) were tested with momentary direct distal pointing cues in an object-choice task under the following conditions: a familiar informant testing wolves and pet dogs outdoors; and an unfamiliar informant testing pet dogs outdoors, testing pet dogs indoors, and testing shelter dogs indoors. At the group level, only wolves tested outdoors and pet dogs tested indoors performed above chance. Although overall, both of these groups performed at similar levels, individually 75% of wolves performed above chance compared with only 37.5% of pet dogs. In the two conditions in which pet dogs at the group level did not perform above chance (i.e., those tested outdoors by either a familiar or unfamiliar informant), two dogs in each group (25%) performed above chance. Finally, individually, no shelter dog performed above chance. Thus, with intense socialization from an early age and under outdoor testing conditions, wolves not only can perform well with distal momentary pointing cues but outperform pet dogs tested under similar conditions, and do at least as well as pet dogs tested indoors.

### Elephants

Smet and Byrne (2014) reviewed studies of how two species of elephant responded to human-initiated pointing cues. Plotnik and colleagues (2013) tested seven Asian elephants (*Elephas maximus*) on their responses to momentary distal direct pointing in a two-alternative object-choice

task. Only one of the elephants performed above chance. In contrast, Smet and Byrne (2013) tested 11 African Elephants (*Loxodonta africana*) on their responses to dynamic distal direct pointing accompanied by gaze alternation and found that five elephants chose the indicated container above chance levels. Additional tests in which either the location of the informant or the pointing gesture itself was varied revealed that one or more elephants successfully responded to the following dynamic pointing cues: far direct pointing, long cross-body pointing, and forward cross-body pointing. However, all elephants were at chance when the informant produced an elbow cross-body pointing cue. In a follow-up study using a subset of these elephants, Smet and Byrne (2014) showed that at least some could follow momentary direct and cross-body pointing accompanied by gazing at the subject. There was no evidence that specific responses to pointing were learned across trials.

### Seals and Sea Lions

Miklosi and Soproni (2006) reviewed early work examining pointing comprehension in two species of pinniped. Shapiro et al. (2003) trained a gray seal (*Halichoerus grypus*) to respond to dynamic pointing made with an informant's right arm, and then showed that it could generalize to dynamic and momentary direct and cross-body pointing across different spatial configurations between the informant and distally placed land-based objects including with the informant positioned at the nontarget. Novel tests were also conducted with three distally placed objects in a pool, two positioned diagonally to the seal's left and right and the third placed out of view behind it. The seal responded accurately to an informant's points to the left and right objects but not to the object behind it. Shapiro and colleagues concluded that the seal likely did not understand the referential character of pointing but instead used signal generalization and experience from its initial operant training to respond to variations in pointing. In another study, Scheumann and Call (2004) tested how four fur seals (*Arctocephalus pusillus*) responded to different types of dynamic pointing using an informant's right arm in a two alternative



object-choice task. All seals performed above chance with direct pointing, cross-body pointing, and asymmetric pointing, regardless of whether target gazing accompanied or was absent from pointing cues. However, like several other species, performance was poor when the pointing cue was contained within the informant's body frame. An examination of performance across trials suggested that learning was not a factor in the seals' performances.

Recently, Malassis and Delfour (2015) showed in a two-alternative distal object-choice task that four sea lions (*Zalophus californianus*) with previous experience with human pointing responded at or near ceiling levels to direct momentary pointing with and without target gazing, and three of the four responded above chance to long cross-body pointing, elbow pointing, and foot pointing. A second experiment performed with the three more enculturated sea lions tested their understanding of the geometry of human pointing cues using a similar configuration of aligned near and far objects on each side of an informant, as was employed by Lakatos et al. (2012) with dogs. Each sea lion performed above chance with no overall significant difference in responses to the closer and farther targets and no learning effect across trials. In a final experiment, the informant was located at the apex of a triangle with each of two opaque barriers positioned along the legs. One object was placed directly in front of the informant while two others were each located behind the barriers and out of the sea lion's direct sight. On each trial, the informant used direct momentary pointing with target gazing to indicate an object. One sea lion responded accurately on initial trials to points directed at the visible and hidden objects.

### Parrots

Giret et al. (2009) examined how three African grey parrots (*Psittacus erithacus*) interpreted pointing in an object-choice task. Each parrot failed an initial test of distal momentary direct pointing accompanied by subject gazing and showed no evidence of learning how to perform accurately across trials. Subsequently, no parrot was successful with distal dynamic direct pointing

or proximal momentary direct pointing, but two responded above chance to proximal dynamic direct pointing accompanied by target gazing. Eventually, all parrots performed above chance with proximal dynamic pointing alone.

### Dolphins

Pack and Herman (2006) summarized studies of receptive and productive pointing competencies in bottlenose dolphins (*Tursiops truncatus*). Herman et al. (1993, 1999) tested how two enculturated bottlenose dolphins named Phoenix and Akeakamai responded to momentary pointing in several three-alternative object-choice tasks involving novel configurations of distally positioned objects. The dolphins had previously experienced pointing informally from trainers directing them to swim in a specific direction or to retrieve an object. In the earliest test, the objects were placed at the vertices of an equilateral triangle with the informant at the center on a surfboard facing the dolphin Phoenix. On each trial, the informant pointed directly at an object and then signed an action. Phoenix was highly accurate on initial trials in performing the indicated action to the indicated object. In later studies, Phoenix and Akeakamai were tested on their responses to momentary direct pointing with two novel configurations of three objects in which two were positioned diagonally left and right and the third was located behind the dolphin out of its immediate view (distances between the objects and the informant and dolphin were varied between the two configurations). Both dolphins performed above chance on first trials when the informant pointed to the left or right objects. Only Phoenix performed immediately above chance to points to the object behind her. Akeakamai was eventually successful after, for a brief period, the informant exaggerated his points by leaning slightly towards the central object. She also spontaneously understood long cross-body momentary points to the two side objects. In another study, Tschudin et al. (2001) showed that test naïve and relatively less enculturated dolphins spontaneously respond accurately to pointing cues within a two-alternative object choice task. Three of six public-show dolphins with no previous exposure

to human pointing as a signal responded nearly perfectly on tests of dynamic direct and cross-body distal pointing.

Substantial evidence that pointing directs a dolphin's attention and is understood as having a referring function was provided in tests of Akeakamai's immediate interpretation of imperative relational sentences within an artificial language system when one or two pointing cues were substituted for object signs. Within Akeakamai's language system, she understood the 3-item gestural sequence "Object 1"+"Object 2"+"Fetch," that instructed her to create a relationship by transporting the second named object to the first. For example, in response to the sequence Basket+Frisbee+Fetch, Akeakamai located the Frisbee from among numerous named objects in her habitat and transported it to the Basket. Given Akeakamai's high proficiency in carrying out these types of sentences, Herman et al. (1999) tested her responses when momentary direct pointing cues and/or a long cross-body pointing cues were substituted for one or both object gestures within relational sentences with three objects arranged distally to her right, left, and behind. Akeakamai was wholly correct on 28 of 36 novel relational sequences of this type.

Following this pioneering effort, Pack and Herman (2004, 2007) conducted a series of studies to further investigate the dolphin's flexibility in responding to pointing cues and its understanding of their referring function. Aside from showing that Phoenix, like Akeakamai spontaneously understood momentary cross-body pointing cues, Pack and Herman (2004) demonstrated that both dolphins spontaneously understood static direct and cross-body distal pointing within a two-alternative object-choice task. Both dolphins performed errorlessly or nearly so with each cue indicating that movement was not essential for understanding pointing.

In later work, Pack and Herman (2007) tested Akeakamai's ability to understand the geometry of direct momentary pointing using pairs of distal objects aligned on each side of an informant. On each trial, the informant pointed briefly at either the closer or farther object of a pair and then

signed an action to be performed to the indicated object. Akeakamai performed without error demonstrating that she could immediately decode the vertical geometry of pointing from the angle subtended between the informant's arm and his body.

Pack and Herman (2007) also tested Phoenix's ability to jointly attend to whichever of two distally placed objects was being pointed at by an informant and either perform a specified action directly to that object, or if the informant gave a "find-a-match" gesture, not respond directly to the indicated object, but instead determine its identity and find a match for it from among two alternatives at the opposite end of the pool. Momentary direct pointing and cross-body pointing cues were employed in both types of instructions. Phoenix's above-chance performance on initial trials showed that pointing directed her attention to the indicated object.

Bottlenose dolphins have also demonstrated spontaneous productive pointing to direct a human's attention. As reviewed in Pack and Herman (2006), Xitco and colleagues (2001) exposed two dolphins to human divers using an underwater visual/sonic keyboard to label different dolphin foods, toys, tools, and locations, as well as responding to labels by finding the corresponding item within the dolphin's habitat. Objects were regularly placed in transparent containers that the dolphins could see through but not open without either the direct assistance of a human or a tool. After 6 months of observing two divers modeling the use of the keyboard in communicative acts, each dolphin began to spontaneously point at containers using their rostrum and aligned body while alternating gaze between the container and a diver. In response to these cues, the diver opened the container and delivered its contents to the dolphin. Xitco et al. (2001) found that the dolphins were more prone to engage in monitoring a diver through gaze alternation when pointing to objects >2 m away, and when a diver was >2 m from the dolphin. In contrast, they tended to refrain from pointing when a diver was only 1–2 m from the dolphin and container and never pointed when a diver was absent. These findings suggested not only that the dolphins understood

that pointing would only be effective in the presence of a diver but also that a distant diver was more likely to require their attention to be drawn than one close by. In a second study, Xitco et al. (2004) investigated dolphin's pointing behavior as a function of a receiver's attentiveness. They positioned a dolphin on one side of a transparent divider where it viewed a diver on the opposite side bait one of two clear water-filled containers. The dolphin engaged in pointing and gaze alternation more often when the diver faced forward, than when he or she had their back to the apparatus, or swam away from it and hid. These studies suggest that dolphins can spontaneously use referential pointing.

## Discussion

### Who Gets the Point? Receptive Competencies

Based on differences in a receiver's responses to various manipulations in the object-choice task, some researchers have attempted to classify the understanding of pointing as either "low-level" or "high-level" (see Miklosi and Soproni 2006). Responses attributed to associative learning mechanisms and stimulus generalization were considered a "low level" of understanding, while a "high level" was reserved for responses that lent themselves to interpretations of pointing as a communicative tool indicating the informant's attention, terminal focus, and mental state. However, as noted by Miklosi and Soproni (2006), such extremes are likely not representative of the continuum of understanding of pointing, as a receiver might comprehend something of its communicative nature (i.e., an understanding beyond associative learning), but not that it represents the informant's mental state. Likewise, a receiver might understand that pointing is communicative but not fully appreciate its referring function.

As discussed earlier, a receiver's accurate initial responses to distal momentary direct and cross-body pointing presented in novel contexts without prior operant training of how to respond to pointing cues can provide evidence that the receiver understands pointing as a form of communication, and that its responses to pointing

are not the result of associative learning accompanied by generalization and/or some form of stimulus or local enhancement. Furthermore, if dynamic sustained distal pointing cues are employed, cross-body pointing as well as asymmetric pointing can help control for effects related to stimulus or local enhancement inasmuch as the pointing arm is closer to the nontarget than to the target. Evidence that the pointing cue is understood as having a referring function may be shown through accurate first trial performance in novel contexts to points towards objects out of immediate view, and to near and far objects in alignment on a side of the informant. The latter is especially helpful in demonstrating that the pointing cue is understood geometrically as the terminal destination of an informant's attention and not as a directive to move in a particular direction until encountering an object. Evidence that the receiver also attends to information available from an indicated object can strengthen arguments that pointing is understood referentially.

The studies reviewed here reveal animals whose responses to pointing place them along this range of understanding. The eventual rather than immediate success of several monkey species in responding to an informant's proximal pointing cues can be explained in terms of associative learning mechanisms. Because of the close proximity of an informant's pointing finger and the target in proximal pointing along with the absence of tests of distal pointing, the immediate successes with proximal pointing cues found in some studies with capuchin monkeys as well as in bats are confounded by the potential influence of stimulus or local enhancement.

Associative learning mechanisms accompanied by stimulus generalization were also implicated in a gray seal's success in responding to momentary distal pointing across variations in the cue and the informant's position, inasmuch as the seal first received formal operant training in how to respond to an informant's pointing cue and later failed to respond accurately in a novel context in which pointing was directed to an object out of its immediate view. Similarly, despite the success of several fur seals with dynamic pointing and asymmetric pointing, the

researchers remained uncertain whether their performance was due to generalization after earlier instrumental interactions with public show trainers, some form of social learning, or the product of a greater understanding of the pointing cue.

Associative learning and/or stimulus and local enhancement appear to be the most parsimonious explanation of the performance of parrots, horses, and pigs in object-choice tasks. Parrots failed tests with distal momentary pointing and distal dynamic pointing but were eventually successful with proximal pointing. With horses, the poor performance with distal momentary pointing and the behavior of many horses across three studies of first contacting the informant's outstretched arm in dynamic pointing before choosing a target on that side are consistent with an enhancement-like processes. Likewise, enhancement-like processes may also explain similar behavior in pigs.

The accurate initial responses of elephants, dogs, dolphins, and sea lions to an informant's distal momentary direct pointing cues, long cross-body pointing cues, and asymmetric pointing cues with the informant positioned at the nontarget, and data showing that these responses were not learned over the course of testing, suggest that these animals understand something about the communicative function of the pointing cue. Furthermore, additional studies with dogs, dolphins, and sea lions have helped clarify whether they understand the referential character of the pointing cue. With three objects arrayed to the sides and behind a subject, in which the horizontal angle of the informant's pointing cue indicated the object to be responded to, two dogs and a dolphin spontaneously understood such references. Additionally, a sea lion immediately understood points to objects behind opaque barriers. While dolphins and sea lions also understood the vertical geometry of the pointing cue, responding accurately to an informant pointing at either the nearer or farther of two aligned objects, dogs showed no such understanding, favoring the closer object, even when farther one was indicated. Thus, dogs appear more restricted than dolphins or sea lions in their understanding of the referring function of pointing. This

apparent difference seems consistent with the findings of Pack and Herman (2007) that a dolphin derived identity information from the object its attention was directed towards by a pointing cue, either finding a match for this object or responding to it directly depending upon the instruction following the cue (i.e., an understanding of declarative pointing) (reviewed in Pack and Herman 2006), compared to dogs who, when the indicated object in a two-alternative object-choice task switched locations with the nonindicated object, tended to focus attention on the original indicated location rather than on the original indicated object (i.e., failing to focus on the identity of the object being pointed at) (Tauzin et al. 2015).

Regarding ape' understanding of pointing, as described above, early studies seemed to indicate that with some exceptions, chimpanzees, orangutans, and gorillas performed poorly in object-choice tasks unless the tip of the informant's pointing finger was positioned proximally to the baited container and, for chimpanzees, if an informant acted competitively instead of cooperatively. However, in many of these studies, subjects were located proximally to the alternative containers when the informant pointed. In contrast, in object-choice tasks with species such as dogs, elephants, sea lions, and dolphins, subjects were positioned distally to the alternatives when receiving the informant's cue. In light of this, more recent studies by Mulcahy and Call (2009) and Lyn (2010) located subjects and informants distally from alternative objects. In this configuration, bonobos, chimpanzees and orangutans responded successfully to an informant's distal dynamic pointing accompanied by gazing cues. Lyn et al. (2010) also showed that enculturation within a human-ape communicative context can play an important role promoting success in object-choice tasks. It remains to be seen when both of these factors are taken into account whether apes will demonstrate an understanding of the referring function of pointing through accurate responses on initial trials with momentary distal direct and cross-body pointing, distal pointing in novel contexts to objects out of view, and pointing towards a distal object when another distractor object lays along the same path.

### Productive Pointing

Tomasello (1995) noted that for pointing to be considered referential, it should be closely coordinated with the receiver's attention, which can often be inferred from the receiver's face or body orientation (e.g., informant facing the target with eyes open). As noted earlier, other than a few recent observations of pointing by chimpanzees in the wild (Halina et al. 2018), there is currently little evidence that animals in the wild use this cue to direct the attention of others. Nonetheless, in some cases, pointing behaviors have either been explicitly taught to animals, or have spontaneously emerged in enculturated animals during social activities with humans (e.g., Meunier et al. 2013; also see reviews by Call and Tomasello 1994; Pack and Herman 2006). In both cases, a central issue is determining what the animals understand about the pointing cues they employ. That is, does a subject that points appreciate the attention-directing function of that gesture, or is pointing employed solely as performative to produce a particular outcome. To make this distinction, researchers have examined whether animals point in triadic transactions to distal objects, whether pointing is employed flexibly to indicate objects other than food, and whether pointing is coordinated with the receiver's presence and attention. With regard to the latter, a strong indicator of the intentionality of pointing in human infants, and in nonhumans, is when this cue is accompanied by gaze alternation between the target and the intended receiver. Meunier et al. (2013) listed this as well as the use of other attention-getting behaviors such as vocalizations to supplement pointing cues, and the persistence of an informant in pointing when initial attempts fail in defining a child's ability to intentionally attract and direct a receiver's attention through pointing.

As shown above, studies with enculturated apes and bottlenose dolphins have revealed the spontaneous emergence of pointing behaviors that are contingent on the receiver's presence and attentiveness (Call and Tomasello 1994; Pack and Herman (2006), which reviewed these studies, with Xitco et al. 2001, 2004). As with intentional pointing in human infants, pointing

in these animals was often accompanied by gaze alternation between the indicated object and the receiver. For dolphins, gaze alternation occurred most often when the receiver was located distally to the target being indicated, providing additional evidence of its understanding of the contingencies under which pointing as a referential signal is effective. In chimpanzees, evidence suggests that they point intentionally to indicate particular objects. For example, if they point at a specific food item and receive an alternative food, their pointing at the original item persists (Halina et al. 2018). Pointing-like behaviors in dogs, on the other hand, have revealed a sensitivity to the presence of a human receiver, but not necessarily to the receiver having to be face forward during pointing events, although this understanding seems to occur sometimes in nonpointing activities (Hare et al. 1998).

That enculturation is not a requisite for displaying communicative intentionality and referential understanding in pointing was recently shown by Meunier et al. (2013). After nine non-enculturated olive baboons (*Papio anubis*) were trained to display an outstretched arm and whole-hand pointing gesture to obtain a raisin that was distally positioned and out of reach, they each observed as an experimenter baited one of five distally positioned containers. Then, a receiver whose back was turned during the baiting event approached the containers, examined the contents of whichever container a baboon subject pointed to, and if the indication was to the baited container, delivered the bait to the baboon. Meunier et al. found that baboons pointed more often and gazed longer at the receiver and the baited container when the receiver faced them and was within reach of the baited container than either when the receiver was face forward but not yet within reach of the baited container or had their back turned to the containers. Baboons also engaged in more gaze alternation when the informant was face forward and either within or just out of reach of the baited container than when their back was turned.

Regarding the criterion of intentionality in productive pointing that an informant should persist in pointing cues when initial attempts fail,



Halina et al. (2018) examined this using a gestural-persistence paradigm in which the pointing cues of three bonobos and nine chimpanzees towards hidden food in the presence of a human receiver were either successful (the human receiver looked at the object being indicated), or unsuccessful (the human receiver looked at something different than what was being indicated). Halina et al. (2018) predicted that when pointing was initially unsuccessful, subjects would persist in pointing more than if pointing was initially successful. The results indicated that although the apes gestured in a communicative manner (i.e., more time was spent employing points with eye contact than without eye contact), they spent more time pointing at food when they successfully directed the receiver's looking behavior than when they failed. To explain these findings, Halina et al. (2018) proposed that within the context of a task in which subjects point towards food that a receiver cannot see, the pointing of an ape has two goals, first to direct the receiver's attention, and if this is successful to request the indicated food.

### **The Issue of Domestication and Other Biological Foundations for Understanding Pointing**

Based on studies showing relatively superior performance by domesticated dogs in attending to an informant's pointing cue in an object-choice task, compared to apes, our closest relative, or wolves, the closest wild relative of dogs, several researchers have proposed that the ability of dogs to "read" human pointing cues evolved during the process of domestication, either because it had been directly selected for, or as a by-product of selection against aggression and fear toward humans (Hare et al. 2005), or simply as a product of domestication in general (Kaminski et al. 2005). Consistent with the latter view, like dogs, domesticated cats have been shown to be proficient in responding to human momentary distal pointing (Miklosi and Soproni 2006). Also, Kaminski et al. (2005) demonstrated that domesticated goats were capable of accurately following dynamic distal direct pointing cues. However, because no tests of either dynamic distal cross-

body pointing cues or momentary distal pointing cues were conducted, it is difficult to eliminate the possibility that enhancement-like processes may have influenced the goats' performances. As noted earlier, the behavior of both domesticated horses and pigs in first contacting the informant's outstretched arm during dynamic pointing indicated a likely role of stimulus and/or local enhancement in their success. Additionally, horses showed no proficiency with momentary pointing cues, while pigs were only successful at momentary cues accompanied by target gazing. Although no such informant touching was reported for goats, as pointed out by Herman et al. (1999), a sustained pointing cue potentially provides a fixed "trail" that the receiver can follow and continually refer to as it approaches the target (Pack and Herman 2006). Thus, a general effect of domestication on the ability of an animal to follow human pointing cues seems insufficient to capture apparent differences in the proficiency of various domesticated animals in responding to pointing.

Hare and colleagues (2002) concluded that their findings of significant differences in how domesticated dogs and wolves responded to pointing strongly supported the hypothesis that the social-communicative skills between dogs and humans evolved during the process of domestication and represented a case of evolutionary convergence of particular sociocognitive abilities of dogs with those of humans through a phylogenetic process of enculturation. To test whether the receptive pointing competency in domesticated animals like dogs is a result of direct selection for this ability or a by-product of selection against fear and aggression toward humans, Hare et al. (2005) compared pointing comprehension in experimentally domesticated fox kits who had been selectively bred over 45 years to approach humans fearlessly and nonaggressively versus a control group without this deliberate selective breeding background, as well as in dog puppies. Neither fox group were bred for or tested on their ability to use human gestural cues. Among various tests conducted, Hare et al. (2005) compared the responses of 11 experimental foxes and 11 dog puppies to an informant's pointing cue. The informant lay on the floor between two containers and

pointed directly and dynamically at the baited container while gazing at it. There was no significant difference in the choice accuracy of experimental foxes and puppies, both groups performing above chance. Above-chance performance in a subsequent test of dynamic direct pointing accompanied by dynamic gazing was also shown in experimental and control foxes. However, in this case, the experimental foxes used the cue more often than the control foxes. Based on these results and other comparisons of measures of social interaction with humans and objects, Hare et al. (2005) suggested that socio-cognitive evolution allowing for proficiency in understanding pointing cues had occurred in experimental foxes, and possibly domestic dogs, as a correlated by-product of selection on systems mediating fear and aggression.

In addition, more recent studies with wolves showing that when they are reared with substantial human socialization and tested at following momentary distal pointing cues outdoors, they perform better than pet dogs tested under similar conditions and at least as well as pet dogs tested indoors (Udell et al. 2008), and also studies showing that kennel dogs with limited human interaction perform poorly in response to dynamic distal pointing cues compared with pet dogs of similar breed, sex, and age (D’Aniello et al. 2017), indicate that ontogenetic factors and environmental factors also play an important role in the responses of wolves and dogs to human pointing gestures.

The findings of Udell et al. (2008) as well as those with undomesticated species such as elephants, dolphins, and sea lions indicate that domestication itself is not a requisite for understanding an informant’s pointing cue. Kaminski et al. (2005) suggested that considerable interactions with humans promote the ability of undomesticated species to use human-initiated communicative cues such as pointing. However, it may also be that certain natural behaviors within a species’ repertoire provide a cognitive foundation that an animal can build upon to make meaningful responses to an informant’s pointing cue. For example, Herman et al. (1999) suggested that the proficiency with which bottlenose dolphins comprehend and produce

distal pointing cues derive or generalize from their use of echolocation to inspect distal objects including those hidden from view (Pack and Herman 2006). Dolphin echolocation is projected in a narrow directional beam that is often in line with the longitudinal axis of the dolphin’s rostrum and body. Thus, when a dolphin echolocates on an object, its aligned rostrum and body are essentially pointing to that object, although not necessarily with the intent of drawing another’s attention to the object of interest. Nonetheless, because dolphins can eavesdrop on each other’s echolocation signals, an observing dolphin can potentially understand the terminal focus of an echolocating dolphin’s attention.

## Conclusion

From its infancy in the early 1990s to the present time, the study of pointing in nonhumans has become a rich and robust enterprise. Evidence indicates that while some species appear to rely on associative learning, and/or stimulus or local enhancement to respond accurately to pointing, others derive a deeper understanding of that cue’s communicative value including its referring function. Broad-based approaches employing different forms of momentary distal pointing in object-choice tasks, as well as in novel contexts and using different types of tasks have been helpful in distinguishing between these interpretations of an animal’s understanding of pointing. Several species have also been shown capable of producing points to specific objects in accordance with a receiver’s attention state. Although domestication may have influenced pointing comprehension in some species, it is not a requisite inasmuch as there are marked differences in how different domesticated species react to and interpret pointing to distal objects, as well as the fact that several undomesticated species can understand these same cues. Pointing as a unique form of nonlinguistic communication involving joint attention that spatially directs attention in a manner that can benefit both the informant and the receiver remains of broad comparative interest. Future efforts to study pointing in animals should

continue to expand those species under investigation, and employ diverse approaches to examine the degree to which an informant's pointing cue directs a receiver's attention and is understood referentially, the types of information an individual glean from the subject its attention is being directed towards, the biological processes, cognitive mechanisms and social experiences that foster an understanding of pointing, and what a receiver and an informant understand about each other's mental experience during pointing events. Finally, the studies reviewed above varied widely in sample size. Clearly, in those studies highly limited in subjects, if even one demonstrates immediate understanding of momentary pointing to distal objects under novel conditions that suggest referential comprehension, that capability is within the cognitive potential of the species. However, if none demonstrate this ability, it is difficult to arrive at any firm conclusions regarding pointing comprehension at the species level. On the other hand, with larger sample sizes and greater power, the finding that only one or a few subjects out of many tested comprehend the pointing gesture or alternatively that the majority comprehend this cue allows for inferences about the different predispositions of the species. Given this, it would be beneficial for future studies to augment the number of subjects examined for their understanding of pointing. However, in those instances in which generating a large sample size is impractical, in the least studies should diversify the ways in which pointing is examined within individual subjects to allow for converging evidence of their cognitive understanding of this cue.

## Cross-References

- ▶ [Attention-Getting Behaviors](#)
- ▶ [Comparative Cognition](#)
- ▶ [Equine Cognition](#)
- ▶ [Joint Attention](#)
- ▶ [Object-Choice Test](#)
- ▶ [Pinniped Cognition](#)
- ▶ [Pointing](#)
- ▶ [Referential Communication](#)
- ▶ [Stimulus and Local Enhancement](#)

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## Pollex

### ► Opposable Thumb

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## Polluting

### ► Pollution

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## Pollution

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## Synonyms

Deterioration; Greenhouse effect; Polluting

## Definition

Pollution is the introduction of the pollutant or the waste material that deteriorates the quality of environment. It is caused by the pollutants that include chlorofluorocarbons, carbon monoxide, chemical fertilizers, particulate matter,

microplastics, pesticides, herbicides, heavy metals, municipal solid waste, etc.

## Forms of Pollution

There are majorly ten different types of pollution present in an environment along with their pollutants, and those include:

- (a) **Air Pollution** – It is being defined as the presence of particulates and gaseous pollutants in the environment which contaminate the air and deteriorate the air quality. The pollutants include carbon monoxide, sulfur dioxide, chlorofluorocarbons, nitrogen oxide, and particulate matter (PM) that are all produced by motor vehicles and industry. Significant studies are there to support the relationship between the particulate matter and neurodegenerative disorders (Fu et al. 2019). In addition to this, cement plant contributes for approximately 5% of carbon dioxide emission (Hendriks et al. 2004) which results in respiratory disorders and reduction in lung function (Fell and Nordby 2017) if the dust total levels exceed  $4.5 \text{ mg m}^{-3}$ . These pollutants are also associated with high resting blood pressure (Bacardit et al. 2018), chronic obstructive pulmonary disease (Trnjar et al. 2017), and premature deaths (Samorodskaja et al. 2017). Biomass fuels such as animal dungs, coal, charcoal, wood, etc. produce mix of pollutants having more than hundred times particulate matter than outdoor air pollution. This contributes to almost 2.9 million deaths worldwide and also causes tuberculosis among children (Sumpter and Liu 2013). Particulate matter is also being associated with cardiovascular disease including the events like myocardial infarctions (Brook et al. 2010).
- (b) **Light Pollution** – It includes the processes such as over illumination and astronomical interference. Photocatalytic reduction of carbon dioxide to carbon monoxide and organic compounds causes light pollution. The artificial light at night (ALAN) disrupts the



biological clock and suppresses the nocturnal production of melatonin (Reiter et al. 2007). This also results in increased cancer risk (Blask 2009; Davis and Mirick 2006; Kantermann and Roenneberg 2009; Stevens et al. 2007, 2014). Sleep disturbances have also been found due to artificial light and have an impact on aging and metabolic process. Artificial light is also associated with the problems like heart diseases, mood swings, and obesity (Gangwisch 2014; Stevens 2009).

- (c) **Noise Pollution** – This includes the pollution caused by roadway noise, aircraft noise, industrial noise, as well as the sound of SONAR. It is referred to as a kind of unwanted sound. It is a form of pollution that causes threat to health. Highway, rail, and air traffic are major sources of environmental noise pollution. Noise pollution can be natural, or it can be man-made. As population is growing day by day, noise is becoming more numerous and causes more annoyance. Noise is not only harmful but also has adverse health effects. Our body responds or fights with noise resulting in various kinds of changes like hormonal, vascular, etc. The noise of engines, jet engines, radio, television, toys, train horns at crossing are of great concern. The noise of machines and other man-made activities can be tolerated because they serve an important purpose to the society and welfare to mankind. General exposure of sound to levels less than 70 decibels does not cause any impairment. Major effects of noise pollution are hearing impairment, interference with spoken language, sleep disturbances, cardiovascular disturbances, mental health disturbance, annoyance reaction, etc.
- (d) **Plastic Pollution** – It is referred to as the accumulation of plastic bodies over the land and water surface. It is ubiquitous all around the environment. It affects wildlife, nature, and human habitat. Plastic has the property of buoyancy and durability due to which it accumulates in environment and persists endlessly. Plastic degrades as hazardous waste (Rochman et al. 2013) in the environment. Globally it is analyzed that in North Pacific, approximately 21,290 metric tons of floating microplastic was found. Threat of plastic pollution has been ignored for a long time. Small plastic pellet and granules are also equally disastrous. Some plastic particles are found in the stomach of seabirds which have also increased during past 10–15 years. Over past 20 years, polychlorinated biphenyls have polluted marine food webs which result in reproductive disorders, disturbances in hormonal levels, and increased risk of disease. Polythene bags are being used for a long time and are being accumulated in terrestrial as well as marine environment.
- (e) **Soil Pollution** – The presence of pollutants in soil results in contamination of soil. Pollutants like nitrates, phosphate, and other trace elements deteriorate the quality of soil. Nitrogen forms include nitrates, nitrites, and ammonia. Many phosphorous compounds are also present in soil as contaminants. Presence of heavy metals also enhances the soil pollution which results in lowering of the overall density of earthworm and other microfauna. Cadmium compounds are used in rechargeable nickel – cadmium batteries. Cigarette smoking is also one of the major sources of cadmium exposure. Lead contamination is also widespread these days. Various statistical results show that lead content in dust and soil derives from anthropogenic resources. Lead in soil is also being associated with the local traffic. Elevated levels of copper are also being found in some areas.
- (f) **Radioactive Pollution** – It results from the activities such as nuclear power generation and nuclear weapon manufacturing and deployment. It is hazardous because it releases radioactive substances and ionizing radiations like alpha, beta, and gamma rays. Degree of their effectiveness varies with the type of radiation and its concentration. The nuclear reactor and nuclear weapon contaminate air, soil, people, plants, etc. Many radioactive activities are naturally occurring such as elements like uranium and thorium, and their

decay products are present in soil and rock. Naturally detected radon gas is being equally responsible for radioactive pollution. Carbon-14 is continuously created by cosmic rays in humans. Radioactive contamination can affect the body through the processes like ingestion, inhalation, absorption, or injection with a fixed dose of radiation. Radioactive contamination can also occur in our body as the result of eating contaminated plants and animals or drinking contaminated water or milk from animals that are exposed to these kind of radiations.

- (g) **Thermal Pollution** – This pollution occurs as a result of change in temperature of water which is caused by human activities such as use of water as a coolant in power plants by industrial manufacturers. The sudden change in temperature of water affects the oxygen content which directly or indirectly affects the composition of ecosystem. Increase in temperature decreases the level of dissolved oxygen of water. This affects the aquatic animals such as fish, amphibians, and other aquatic organisms. Thermal pollution also increases the metabolic rate of aquatic animals, such as enzyme activity, due to which these organisms consume more food in a shorter time than if their environment were not changed (Goel 2006). A large increase in temperature leads to denaturation of enzymes by breakage of hydrogen and disulfide bonds which decrease the enzyme activity in aquatic organisms and may cause the problems such as the inability to break down lipids, which will lead to the condition of malnutrition. Abrupt change in water temperature will lead to the death of aquatic organisms especially fish (Laws 2000; Chiras 2012).

- (h) **Visual Pollution** – It refers to the presence of municipal debris, motorway billboards, overhead power lines, strip mining, open storage of trash, etc. It is basically the impact of pollution which impairs the visibility to view the things by disturbing the environment. Basically overcrowding of an area causes visual pollution. It can also be defined as the whole of irregular formations, which are

frequently found in nature (Yilmaz 2011; Nagle 2009). Exposure to visual pollution results in distraction, eye fatigue, decreases in diversity, and loss of identity (Yilmaz 2011). High-rise buildings, if made, are not planned properly than it can bring adverse change to the visual and physical characteristics of a city, which may reduce said city's readability (Yilmaz 2011).

- (i) **Water Pollution** – It is the discharge of wastewater from either commercial activity or from industries. It also includes discharge of untreated domestic waste and contaminants like chlorine that releases waste and urban runoff water that contains chemical fertilizers and pesticides including human feces. The prolonged unchecked industrialization and urbanization has polluted the water bodies. Synthetic chemicals disperse into lakes and streams from atmospheric fallout, for example, natural seepage problems of oil and polycyclic aromatic hydrocarbons (PAH) into the continental shelf and beaches pose a health problem. High values of heavy metals are frequently documented in the peri-urban (Singh et al. 2010) and can be extremely toxic to aquatic organisms as well as to humans, where long-term ingestion of water polluted with heavy metals can be devastating, leading to the development of a number of cancers, neurological disorders, and even death.

## Cost of Pollution

Pollution has its own cost (Harvey 2016). Many manufacturing activities cause air pollution that imposes health and cleanup costs on whole of society. A manufacturing activity that causes air pollution is an example because a firm's production reduces the well-being of others which is not compensated by the firm (Gruber 2013). If we take an example of a laundry firm that exists near a polluting steel manufacturing firm, then definitely there will be increased costs for the laundry firm because of the dirt and smoke that are produced by the steel manufacturing firm

(Kolstad 2011). Due to this external costs created by pollution, the manufacturer will produce more and more of the product than would be produced if the manufacturer were required to pay all associated environmental costs. If some external benefits are there such as in public safety, less of the good may be produced and the producer was to receive payment for the external benefits to others. But it was found that goods and services are continuous in production; therefore the products that produce pollution tend to be overproduced and underpriced because the externality is not being priced into the market (Gruber 2013).

Pollution also creates the cost for the firms that produce the pollution. Sometimes these firms are forced by regulation, to decrease the amount of pollution that they are producing. The cost associated with that is called abatement costs or marginal abatement costs if measured by each additional unit (2018). In 2005 it was estimated that pollution abatement capital expenditures and operating costs in the USA amounted to nearly \$27 billion (2018).

## Sources and Causes of Pollution

Pollution has two types of sources, viz., point sources and nonpoint sources. **Point** sources are basically localized and confined identifiable sources of contaminants, for example, power plants, refineries, mining factories, wastewater treatment plants, etc. On the other end, **nonpoint** sources are those which are distributed widely over a geographic area, such as a watershed. Nonpoint sources also cover a wide range of moving sources such as cars, buses, and trains. Though each of these is a point source, they are mobile and thus spread their summative impact over a wide geographic area. Urban runoff can be considered as a typical nonpoint source of pollution, where the contaminant load is considered to be the sum of thousands of small point sources within the watershed.

Types of contaminants are basically classified as follows.

## Anthropogenic Sources

These sources can be broadly divided into two classes: hydrophobic compounds and hydrophilic compounds. As the name suggests, hydrophobic compounds are those that are not at all soluble or very less soluble in water, whereas hydrophilic compounds are largely soluble in water. Hydrophobic organic contaminants (HOCs) are considered to have been class of compounds which are most problematic and the most studied. The hydrophobic contaminants are of great concern because of two reasons. Firstly, due to their hydrophobicity, they have a tendency to accumulate in biota, including humans, and their elevated concentrations show adverse effects (Mackay and Fraser 2000). Secondly, the hydrophobic compounds can be easily extracted and concentrated from environmental media and thus more easily detected, quantified, and studied by various instrumental and analytical methods. In environment these hydrophobic organic contaminants are often stored in sediments. Their storage is present mainly due to hydrophobic interactions of these organic contaminants with humic substances associated with sediment particles (Karickhoff et al. 1979). HOCs adsorb to humic substances due to the presence of natural organic matter in the water column increase HOC solubility (Chiou et al. 1986). Humic substances play a role in mobilizing HOCs from sediment to water column. Thus, it can be explained why the concentration of HOCs is higher in sediments than in the water column (Caron et al. 1985; Suffet et al. 1984).

## Plastic and Marine Debris

The growing amount of plastic in environment and other trash material in the world's oceans and lakes is of immediate concern. Accidentally most of the times, trash is dumped directly into the ocean, mostly from ships and offshore platforms, but more frequently it is carried by rivers and streams or blown in by wind. Safe land filling and trash pickup are important so that they cannot resort to open dumping. Globally we find improper handling of waste in all countries. Circular patterns created by winds and the Coriolis effect from the rotation of the earth rotate millions of tons of plastics, and other marine

debris in the ocean get concentrated in giant gyres. Example of one such giant vortex that accumulates trash is called the Great Pacific garbage patch. It lies in the North Pacific Subtropical Convergence Zone and stretches from California to Japan. At present there are five major garbage patches that are located in different regions including North and South Pacific, North and South Atlantic, and most probably Indian Oceans. More garbage is accumulated below the middle of these gyres rather than elsewhere, but some amount of garbage move in and out, while the rest concentrate at the middle. Plastics can take possibly hundreds of years to break down completely in comparison to natural materials such as cotton that can biodegrade very rapidly. Sunlight and physical stressors can break down plastic trash such as water bottles to the extent that they can be converted into smaller and smaller bits, which form the soup of marine debris that consists of tiny pieces of plastic. Birds and fish sometimes ingest the plastic as food by mistake. One can find more plastic concentrated in certain parts of these gyres than biomass. PCBs and other pollutants are also adsorbed by these gyres. Thus when an organism ingests plastic, it also ingests the contaminants which are present on the plastic. Plastics contain toxins such as bisphenol A which is categorized as endocrine-disrupting chemical, or it may contain phthalates, or vinyl chloride, depending on the type of plastic. These chemicals are persistent in nature, and bioaccumulates will be transferred throughout the food chain. One should be very concerned because it is probable that these chemicals are likely to be found in fish. When these plastic pieces break down into particles of less than 1 mm in diameter, they are called microplastics. Most microplastic is being created from the decomposition of trash and also enters the environment from sewage discharges carrying personal care products. These microplastic beads are being used to make good facial scrubs and in various cosmetics and toothpastes. But zooplanktons ingest microplastics (Cole et al. 2013) which is one of the growing concerns in marine biota, and this all has led to a federal ban of

microplastics. After seeing more trash than fish on a vacation dive the Ocean Cleanup is basically a nonprofit organization out of the Netherlands founded by Boyan Slat, given the design a solution to the problem. After a TED talk and crowd funding campaign, his organization started studying the marine debris problem and is designing technology that will aid in ocean cleanup. This organization believes to have removed half of the plastic in the Great Pacific garbage patch in approximately 10 years. Many other organizations contribute to beach cleanup activities that collect marine debris.

### **Metals and Metalloids**

Most of the water contamination is triggered by anthropogenic factors like industrial effluents leaching into the ground. Groundwater pollution is tough, but once polluted it can be extremely difficult to get rid of. The prolonged unchecked industrialization and urbanization has polluted the two major water bodies. Overexploitation of groundwater resources due to population explosion is also making the problem more tedious in many regions of India as well as in other countries. Heavy metals are likely to rush in from industrial waste dumped untreated into water systems, while nitrates may be distributed on to the surface due to excessive and prolonged use of fertilizers. Arsenic and fluoride are commonly found in groundwater where chemicals have leached from the bedrock due to overexploitation of the source. Fluoride, arsenic, and iron are known to have caused encephalitis, jaundice, and typhoid, mostly among the poor who live in dismal sanitation conditions. High content of heavy metals in water and sediments in river Ganges downstream have been reported (Singh et al. 2005). Arsenic distribution is also affected by anthropogenic activities, such as mining and smelting operations, coal-fired combustion, and use of agricultural herbicides, pesticides, and medicinal and cosmetic products (Orloff et al. 2009), but the major source of As, in general, is chemical weathering of rocks (Bhattacharya et al. 2007). Lead is a contaminant in food and water. The unregulated discharge of

industrial wastes is also seen to pose significant risks to the food system (Marshall et al. 2017). The main contaminants identified within the effluents of these industries include high levels of organic pollutants as well as high concentrations of heavy metals. Human risk was assessed in people exposed to trace metals using exposure risk assessment model indicated. Arsenic was the most important pollutant causing non-carcinogenic and carcinogenic concerns, particularly for sensitive children. As, Sb, and Se were the largest contributors to chronic risks, while Ni, Al, Fe, and Ba were the least contributors in both the dry and rainy seasons (Zhang and Li 2010). The levels of these contaminants in the river and groundwater are consistently above permissible limits, and as a result, the water is considered unfit for recreational activity and the sustenance of aquatic organisms (Rizvi et al. 2015).

### Nutrients

It is basically a form of water pollution that contains contamination by increased input of nutrients. This is being primarily the cause of eutrophication of surface waters, in which overuse of the nutrients like nitrogen and phosphorus stimulates algal growth. There can be various sources of nutrient pollution that include the following:

- (a) Runoff water from farm fields and pastures.
- (b) Various kinds of discharges from septic tanks.
- (c) Emissions caused from combustion.
- (d) Excess nutrients can potentially lead to excess growth of algae known as algal blooms.

Species composition shifts, feed web changes, light limitation, excess organic carbon dissolved oxygen deficits (environmental Hypoxia), toxin production, excess nitrate in drinking water and disinfection by product are the common cause of Nutrient Pollution.

Nitrates and nitrites are naturally occurring, but their increased levels are because of the use of excessive fertilizer that goes into surface and groundwater. Other sources include animal manure or other chemical and factory discharges.

### Radionuclides

They are basically inorganic contaminants which are unstable isotopes that lead to radioactive disintegration to become more stabilized. An isotope of an element has a specific number of nucleons (protons and neutrons). Almost all elements have radionuclide; many of them are naturally occurring, but due to human activity, they become enriched in environment such as elements released from nuclear power plants, mining activity, various medical wastes, or from atmospheric deposition that came from nuclear bomb testing. For example, hydrogen exists in three isotopic forms, viz., hydrogen-1 and hydrogen-2 that contain one and two protons, respectively, and hydrogen-3 also known as tritium which rarely exists and is the result of nuclear power activity. Uranium also exists as a natural radioactive isotope in two forms, that is, uranium-236 and uranium-239. Radium and thorium are also naturally occurring radioisotopes. Groundwater near nuclear power plants have increased levels of several radionuclides, including tritium, radium-228/226, and strontium-90. Some organisms have adapted the ability to repair tissue damage upon exposure to low levels of ionizing radiation due to ubiquity of radionuclides. But when they are enriched in water, they are expected to pose a threat to life.

### Effects of Pollutants on Human Health

Till now in this entry, many pollutants have been described; each of these pollutants has adverse effects on human health. Some effects due to different kinds of pollutants are listed below.

#### Air Pollutants

- Breathing polluted air causes higher risk for asthma and other respiratory diseases.
- Decreased lung function of healthy individual and respiratory inflammation.
- People are at higher risk of cancer as most air pollutants are categorized as carcinogens that include various kinds of gases like CFCs, methane, etc.



- In city crowd coughing and wheezing are most commonly observed.
- Endocrine, reproductive, and immune system are at a great risk.
- Higher incidents of heart problems are being associated with particulate matter.
- Global warming is occurring due to increased level of carbon dioxide in atmosphere which is a result of increased man-made activities.
- Biomagnifications are occurring in food chains due to the accumulation of these toxic elements into plants and water resources because animals eat these contaminated plants that travel up to their body organs.

### **Water Pollutants**

- Many diseases such as amoebiasis, typhoid, and hookworm are associated with polluted drinking water.
- Water is exposed to heavy metals such as lead, arsenic, nickel, and chromium and pesticides (DDT, BHC, etc.), and hydrocarbon causes various hormonal and reproductive problems, leading to the damage of the nervous system, liver, and kidney. Moreover it leads to different types of cancer like bladder cancer, liver cancer, etc. Exposure to mercury may cause Parkinson's disease, Alzheimer's, and heart disease and eventually leads to death.
- If a beach is being polluted, then it may result in diseases like hepatitis, diarrhea, encephalitis, gastroenteritis, stomach aches, and vomiting.
- Pollutants in water affect marine life which can be one of our food sources.

### **Nutrient as Pollutants**

- Infants drinking excess of nutrient-contaminated water may become seriously ill and may go into a coma and can possibly die.
- It can result in complications like shortness of breath and blue baby syndrome, also known as methemoglobinemia, wherein a less percentage of the hemoglobin in the blood is oxidized and unable to carry oxygen.
- The mechanism is not completely clear, but it involves a role of methemoglobin (MetHb) in reducing the binding of nitric oxide

(NO) which allows nitric oxide to readily diffuse to neighboring cells; those results in activation of signaling pathways of vasodilation that leads to hypoxia.

### **Soil Pollutants**

- The presence of pollutants, contaminants, and toxic chemicals in the soil in higher concentration than normal has negative effect on wildlife, plants, humans, and ground water.
- Waste disposal, agricultural activities, acid rain, and accidental oil spill in soil influence health of humans, result in decreased growth of plants, decrease soil fertility, and change the soil structure.
- Soil pollutants mainly lead to the death of plants and complete reduction of the agricultural viability of soil.
- Soil pollutants are equally dangerous to animals because animals ingest plants that are exposed to soil pollution and they may die.
- Human consumption of such plants may lead to heart, kidney, and liver failures as well as cancer.

### **Conclusion**

Environmental pollution is one of the biggest problems that are caused by human activities that should be overcome to see a good tomorrow and to provide our descendants a good future and a healthy life. Many environmental concerns are there for communities and around the world to address. One should always remember that pollution problems are continuously affecting all of us; therefore it is our duty to try our best to help and restore ecological balance to this beautiful world which we call a home. One should recognize the major polluters and must protect the air and water at least of that society. Peoples should be encouraged to stop pollution, create awareness of everything about this problem, and make a protest against the local polluters together. The individual is to be educated on the danger of different types of pollution. People should be aware about all consequences and results of the environmental pollution in order to prevent the worst from

happening. So let's move further to protect the water we drink, the air we breathe, and the soil we use to grow our food and all forms of pollution that are dangerous to the environment.

## Cross-References

### ► Environmental Influences

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## Polyandry

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## Synonyms

Bigamy; Plural marriage; Polygamous marriage; Polygamy

## Definition

Polyandry is one of the forms of polygamy; in sexually reproducing diploid animals, it is the mating system of females having two or more mates, successively or simultaneously.

## Introduction

Historically, according to Bateman's Principle, it has been argued that polyandry provides no fitness benefits to females (Bateman 1948). However, polyandry occurs frequently in nature and later analyses showed that polyandry may provide benefits for females not only in animals (e.g., Arnqvist and Nilsson 2000; Simmons 2005) but also in humans, in particular. Despite some costs, such as increased predation risk, exposure to diseases, energy and time costs, and physical harm, having multiple mates may be beneficial, because it may secure additional male-provisioned resources to the female and her offspring. In addition, paternal uncertainty may decrease a male's willingness to harm offspring produced by the female and increase the male's investment and paternal care. A notable aspect of polyandry is sperm competition between males, which may select for cryptic female choice to thereby secure genetic diversity or higher-quality genes for offspring.

## Polyandry in Nonhuman Animals

In animals, polyandry refers to a female having two or more mates in a breeding season. Polyandry is common in nature and is more prevalent in animals for which having a low-quality male mate is highly costly (Colegrave et al. 2002). It can be observed in various species, such as bees, crickets, honeybees, frogs, fish, birds, tortoises, whales, polecats and other ferrets, house mice, and marmosets. Polyandry is a feature of social organization among Callitrichidae, a family of New World monkeys. Polyandry in primates is often correlated with reduced or reversed sexual dimorphism, such that females are larger than

males. In wattled jacanas, females copulate with many males, which leads to sperm competition, resulting in the most viable sperm fertilizing the eggs and increasing genetic diversity of the offspring (Emlen et al. 1998). In redback spiders, females store the sperm of several mates and can actively affect the paternity of offspring (Snow and Andrade 2005). In addition, in bank voles, monandrous females' offspring have lower survival rates than polyandrous females' offspring, due in part to the decreased risk of infanticide by males (Klemme and Ylönen 2010). There are, however, species in which polyandry occurs but for which there are not clear benefits to the female. In marine turtles, for example, polyandry appears not to generate benefits for the female, but instead appears to be an incidental consequence of intense male sexual aggression (Lee and Hays 2004).

## Polyandry in Humans

In humans, polyandry has been defined in several ways, including having more than one husband or partner at a time, while the husbands or partners are not married or partnered to any other women. It has been argued that the specific shape of the human penis may serve as an adaptation to remove rival male sperm from the reproductive tract of a polyandrous female (Gordon et al. 2003). One of the most common forms of human polyandry is fraternal (adelphic) polyandry, in which a woman marries two or more brothers. Polyandry is much less frequent than polygyny (one male mated to more than one woman) but has been observed in many societies, including in Africa, Asia, Europe, Oceania, and both Americas. Societies with polyandry are usually small, e.g., Indian societies having from several hundred (Toda people) to approximately 80,000 (Khasi people) members. It has been estimated that there are only several hundred modern societies in which polyandry is commonly practiced, but in none of these places is it officially legal. Many sects of most of the major religions (e.g., Christianity, Judaism, Islam) perceive polyandry as unacceptable. In many small societies around the world, the native culture and traditions were

transformed or eradicated and, therefore, it is difficult to estimate the prevalence of polyandry in the past before these transformations or eradication occurred.

## Cross-References

- ▶ [Cryptic Mate Choice](#)
- ▶ [Diploid](#)
- ▶ [Fitness](#)
- ▶ [Genetic Variation](#)
- ▶ [Polygamy](#)
- ▶ [Polygyny](#)
- ▶ [Primates](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Sperm Competition](#)

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## Polyestrous

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## Synonyms

[Estrous, oestrous](#); [Estrus, oestrus, heat](#)

## Definition

Estrus – receptive to mating, sexual activity  
Anestrus – not cycling

## Introduction

Estrus or oestrus is the period of time when a female accepts a male for the purpose of mating. In most placental mammals, this is restricted to hours or a few days. The interval until the next expression of estrus is called an estrous (oestrous) cycle. Polyestrous species including cattle (Sartori and Barros [2011](#)), pigs (Senger [2012](#)), elephants (Hildebrandt et al. [2011](#)), domestic and some non-domestic felids (Brown [2011](#)), water buffalo (Perera [2011](#)), and some rodents (Senger [2012](#)) express an estrus period and estrous cycles that repeat throughout the year.

In contrast, seasonally polyestrous species express multiple estrous cycles in only one period of the year depending on environmental factors such as daylight or feed availability. Examples of seasonally polyestrous species are the horse (Aurich [2011](#)), sheep (Bartlewski et al. [2011](#)), wild domestic and some non-domestic felids (Brown [2011](#)), and hamsters (Henningsen et al. [2016](#)). Species that exhibit only a single estrous cycle and do not return to estrus but exhibit anestrus are said to have a monoestrous cycle. This includes species that have just two estrous cycles in a year separated by an extended anestrus periods. Examples of species with monoestrous cycles include the canine and wolf (Concannon

[2011](#)) and bear (Senger [2012](#)). Interestingly, marine mammals of the orders Pinnipedia, Cetacea, Odontoceti, and Sirenia tend to be monoestrous, but a few may have a second estrus cycle within a year or, like the Pinnipedian sea otter, may be polyestrous until pregnancy (Pomeroy [2011](#)). Marine mammals may be functionally monoestrous because males and females migrate to different locations following mating. There are also examples of captive Cetacea such as the bottlenose dolphin being polyestrous or seasonally polyestrous (Pomeroy [2011](#)).

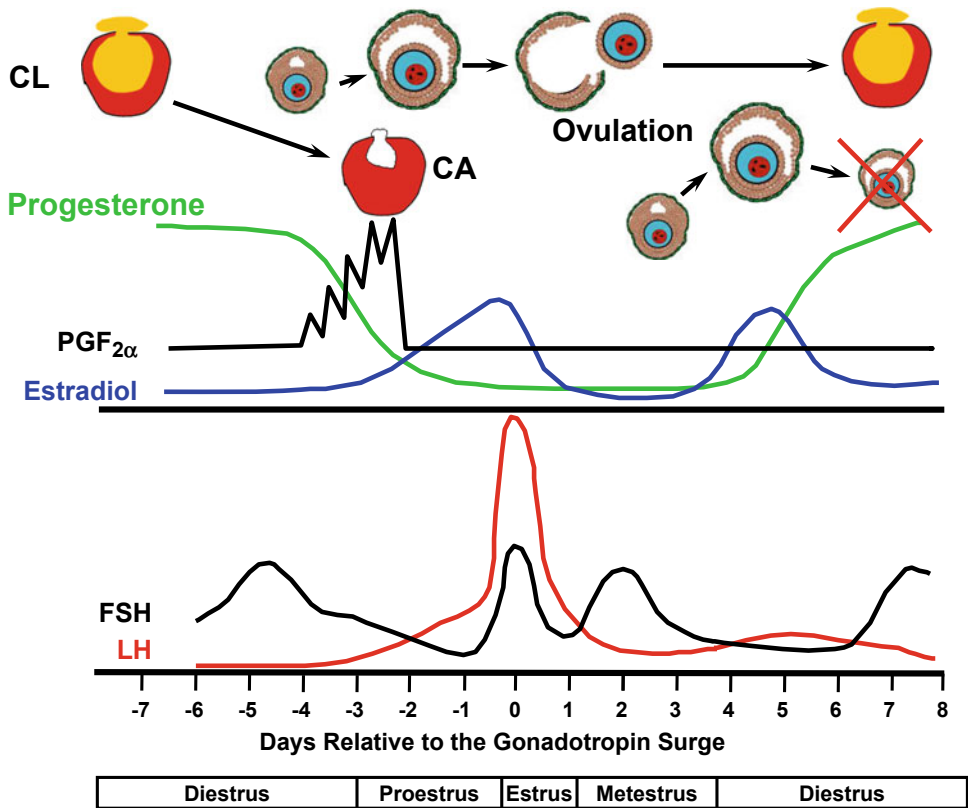
## Length of the Estrous Cycle

The estrous cycle of polyestrous and seasonally polyestrous species varies greatly. The values for various species include (1) 4 days in mice, rats, and hamsters (Senger [2012](#); Henningsen et al. [2016](#)); (2) 17 days in sheep (Bartlewski et al. [2011](#)); (3) 21 days in cattle, horses, pigs, and water buffalo (Perera [2011](#); Sartori and Barros [2011](#); Senger [2012](#)); (4) 21–42 days in captive bottlenose dolphins (Pomeroy [2011](#)); and (6) 91–126 days in the elephant (Hildebrandt et al. [2011](#)). In the felids, most species are induced ovulators, ovulating in response to mating, and have an estrus of a few days to 2 weeks and an interestrus or proestrus period of several weeks that repeats if the female does not become pregnant. The estrous cycle, estrus plus interestrus period, ranges from approximately 14 days in the pallas's cat, 21 days in the domestic cat, 7–21 days in cheetahs, 10–20 days in leopards, 15–40 days in the clouded leopard, and 18–40 days in the tiger (Brown [2011](#)). As monoestrous species cycles do not repeat, a similar comparison is not possible.

## Endocrine Changes of the Polyestrous Cycle

The estrous cycle can be divided by the periods of proestrus, estrus, metestrus, and diestrus. These periods can be seen in relationship to the hormonal changes in Fig. 1. Estrus and the observed





**Polyestrous, Fig. 1** Endocrine changes during an estrous cycle of a polyestrous species. This is an example of the endocrine changes in the bovine. At the top are the ovarian changes with the corpus luteum (CL) undergoing regression to form the corpus albicans (CA). The follicle grows to eventually undergo ovulation and form a new CL. Additional follicles may grow but undergo regression or atresia as indicated by the X through the follicle. In the center are hormonal secretions of the ovary and uterus. The follicle produces estradiol which decreases following

ovulation or regression/atresia. The corpus luteum produces progesterone. Regression of CL is caused by the prostaglandin F<sub>2α</sub> (PGF<sub>2α</sub>) released from the uterus if the female is not pregnant. At the bottom are the changes in the anterior pituitary gonadotropins, luteinizing hormone (LH), and follicle-stimulating hormone (FSH). The FSH triggers development of follicles which are enhanced by LH, and then LH triggers ovulation of a preovulatory follicle (Based on the work of Senger 2012)

receptivity of the female to the male are triggered by an increase in estrogen from follicles on the ovary. The start of estrus is shortly before or after peak estrogen is reached. In some species such as cattle, when males are not available, females will stand to be mounted by other females which indicates the start of the estrus period. In response to the rise in estrogen, gonadotropin-releasing hormone (GnRH) is released from the hypothalamus, which stimulates luteinizing hormone (LH) release from the anterior pituitary. The LH reaches the ovary via the bloodstream, binds to follicular cells, and triggers ovulation of the

follicle. The remnants of the follicle then become the corpus luteum (CL) that releases progesterone or a metabolite of progesterone. In polyestrous species, the corpus luteum regresses if the animal is not pregnant, generally due to release of prostaglandin F<sub>2α</sub> from the uterus. Follicles begin to grow under the influence of follicle-stimulating hormone (FSH), and the estrous cycle is repeated. In a polyestrous species, maternal recognition of pregnancy occurs when a signal from the embryo allows maintenance of the CL and continued progesterone production. This signal can be interferon  $\tau$ , estradiol, or other unidentified

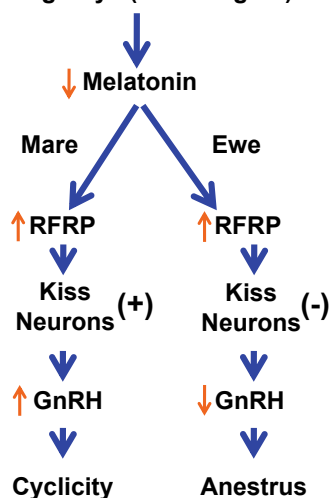
compounds depending on species (Senger 2012). In a pregnant female, progesterone is maintained and estrous cycles stop during pregnancy and lactation as gestational and lactational anestrus.

## The Seasonal Polyestrous Cycle

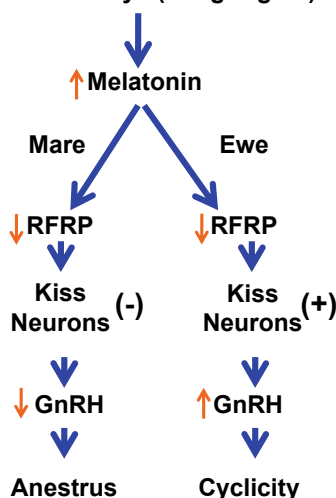
In seasonally polyestrous species, estrous cycles begin during a particular season of the year. Repeated estrous cycles occur until the female gets pregnant or until an environmental signal causes estrous cycles to stop. In most cases this signal changes in length of darkness (Fig. 2). Species such as sheep become polyestrous in the fall (short-day breeders), but horses become polyestrous in the spring (long-day breeders). Melatonin is released from the pineal gland at night so it is higher during the fall with increasing length of darkness and lower in the spring as the dark period decreases. Melatonin binds to receptors on

hypothalamic RFRP neurons (Henningsen et al. 2016) that in turn release RFRP peptides. In general, RFRP peptides bind to kisspeptin neurons modulating the release of kisspeptin. Kisspeptin in turn binds to receptors on GnRH-releasing neurons to trigger release of GnRH. The response of the melatonin-RFRP systems appears to be similar in both short- and long-day breeders in that with increasing melatonin there is decreasing RFRP. Specific species respond to the changing levels of RFRP peptides differently with the apparent goal to have parturition occur during the most optimal time of the year. Sheep have a gestation of 152 days, while horses have a gestation of 330–345 days. In species such as sheep, in the spring when day length increases, there is decreasing melatonin and decreasing RFRP peptides that inhibit kisspeptin neurons, and hence sheep have low GnRH and do not cycle in the spring. In contrast, in the spring horses exhibit a stimulation of kisspeptin neurons by decreasing

### Long Days (Short Nights)



### Short Days (Long Nights)



**Polyestrous, Fig. 2** Impact of seasonal light changes on seasonal polyestrous species. The figure demonstrates the impacts of light changes on the ewe and mare which differ in the impact of seasonal changes in light. Melatonin which is produced during the dark period of a day is low during the shorter nights of the fall as compared to the longer nights of the spring. Melatonin impacts the RFRP neurons to release RFRP peptides. Up to this point in the sequence, there is no difference in the responses of the mare and ewe. The RFRP peptides impact kisspeptin neurons differently

with increasing RFRP peptides stimulating kisspeptin neurons in the mare but inhibiting them in the ewe. The kisspeptin neurons release the kiss protein that stimulates gonadotropin-releasing hormone (GnRH) neurons to release GnRH and thus stimulate cyclicity. Inhibition of kisspeptin neurons results in low GnRH and anestrus. The opposite effect occurs in the mare and ewe when RFRP peptides decrease (Based on the work of Henningsen et al. 2016)

RFRP peptides. Hence in the spring, horses have increasing GnRH that stimulates estrous cycles that become polyestrous. These effects reverse as melatonin levels change. The entering of polyestrous cycles during the breeding season has been described as similar to initiating puberty and the reverse as the species exits the breeding season (Senger 2012). It should be noted that some species may also be seasonally polyestrous due to availability of food resources. This may be true in species that migrate during gestation to a more appropriate environment for parturition and development of young such as seen in marine mammals like whales (Pomeroy 2011).

## The Monoestrous Cycle

In monoestrous species, the endocrine changes in the pregnant and nonpregnant cycle are similar (Concannon 2011). The initial changes of follicular development, ovulation, formation of the CL, and initial progesterone production are similar to what is observed in the polyestrous species. However, there is no maternal recognition of pregnancy signal, and the CL remains present even if the female does not become pregnant. This leads to these species having pseudopregnancy if they do not become pregnant with the development of the mammary gland and lactation around the time when parturition would normally occur.

## Other Environmental Impacts on the Polyestrous Cycle

Many species experience other environmental impacts on the estrous cycle. For example, water buffalo shows decreased cyclicity during dry periods of the year in tropical countries that have relatively constant photoperiods (Perera 2011). There is a decrease in forage availability during this dry period. Following the arrival of the rainy season and increase growth of forages, water buffalo cyclicity returns. Similar effects are seen in cattle due to decreased feed availability (Sartori and Barros 2011). Temperatures also impact estrous cycles with high temperatures triggering

anestrus as is seen in water buffalo in many of the high-heat regions of India (Perera 2011).

## Conclusion

Polyestrous is the presence of repeated estrous cycles. Seasonal polyestrous species respond to environmental signals so that estrous cycles occur during particular seasons depending on how the RFRP peptides indirectly impact GnRH-releasing neurons of the hypothalamus. The basic hormonal changes of the cycles are similar in terms of follicle development, formation of the CL, and need for maternal recognition of pregnancy. A species with a monoestrous cycle is one in which estrus occurs only once or possibly two times per year. A monoestrous species also differs in that maternal recognition of pregnancy does not occur and the CL produces progesterone or a metabolite regardless of whether the animal is pregnant.

## Cross-References

- [Estrogen](#)
- [Estrous](#)
- [FSH](#)
- [Progesterone](#)

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## Polygamous Marriage

### ► Polyandry

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## Polygamy

- Polyandry
- Polygynandry

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## Polygenic Effect

### ► Multigenic Effects

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## Polygenic Inheritance

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## Synonyms

Genetic inheritance; Genetic variation; Multiple gene inheritance

## Definition

Polygenic inheritance refers to any phenotypic trait resulting from the combinatorial effects of two or more genes.

A polygene is any gene that interacts with one or more other genes to influence some aspect of phenotypic expression. Physical characteristics such as height, skin color, and eye color in humans are examples of polygenically controlled phenotypes. However, certain phenotypes, such as height and weight, although partially the result of polygenic inheritance, are also influenced by environmental factors. As a result, it can sometimes be difficult to determine the influence of specific genes and environmental factors on phenotypic expressions.

Much of the existing research concerning polygenes comes from the medical field and typically investigates the extent to which diseases and disorders may be the result of multiple, interacting genes. For example, Antoniou and Easton (2003) presented evidence suggesting that identifying multiple genetic loci associated with breast cancer may be useful for determining whether an individual is more susceptible to developing the disease. Additionally, Antoniou and Easton argued that screening methods that focus on family members may be more likely to identify polygenes associated with breast cancer compared to methods that merely screen the general population.

Other researchers have also detailed the potential benefits of using polygenic information in concert with risk factors for diseases such as age and family history to improve screening procedures (Chowdhury et al. 2013). Specifically, Chowdhury and colleagues noted the potential for polygenic information to inform stratified screening methods, wherein particular demographics within the general population can be identified as high risk for diseases like prostate and breast cancers. However, the researchers contrasted these potential benefits with the risk of failing to identify high-risk populations and subsequently excluding or overlooking these groups during screening procedures.

Khoury et al. (2013) expand on the ideas discussed by Chowdhury et al. (2013), suggesting that, although scientific advances in genome sequencing may enhance the ability to detect monogenic diseases, the capability of this technology to detect polygenic diseases will be comparatively weaker. As a result, Khoury et al. advise caution when considering the use of polygenes to inform stratified screening procedures, especially when these threaten to supplant well-established screening procedures.

Although much of the literature on polygenic inheritance concerns disease in humans, there has been at least some research investigating the polygenic inheritance of behavioral traits in nonhuman animals. In particular, Shaw (1996) provided evidence that genes at several different loci influence differences in songs produced by male crickets. Shaw's research implies that the influence of polygenes is not limited to physical characteristics or disease. Furthermore, research investigating the polygenic inheritance of Tourette's syndrome similarly implies that polygenes affect behavioral traits in humans (Comings et al. 1996).

The existing literature regarding polygenic inheritance, although informative from a medical perspective, is somewhat limited in scope. At this point, there has been little investigation of polygenic influences of behavior in nonhuman animals and few investigations regarding human behavior. These areas are open for future empirical investigation, and indeed, a great deal more research is needed to better understand whether and how various behaviors may be influenced by multiple genes.

## Cross-References

- [Additive Genetic Variance](#)
- [Behavioral Genetics](#)
- [Complementary Genes Hypothesis](#)

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## Polygeny

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## Synonyms

[Cistron](#); [Heritable factors](#); [Multiple gene inheritance](#)

## Definition

Polygenes belong to a group of nonepistatic genes that affect a phenotypic trait by the combined action of numerous similar genes.

## Introduction

A polygene or “multiple gene inheritance” can be defined as a group of nonepistatic genes that act together to influence a phenotypic trait. Traits controlled by polygenes are called polygenic traits, and they display continuous variation in



phenotype. The variation or phenotypic combinations of these traits can be increased by increasing the number of genes. These are quantitative traits, for example, the visible characters like skin color, eyes, height and weight, fingerprint pattern, bristle number, and wing morphology (Mackay 1996). There are nonvisible traits like blood- pressure, intelligence, autism, and longevity. There are adult-onset diseases like Diabetes Mellitus, cancer, glaucoma, hypertension, ischemic heart disease, bipolar disorder, schizophrenia, psoriasis, thyroid diseases, and Alzheimer's disease that are controlled by multiple genes. In the case of skin color, which is governed by numerous genes and two alleles for each gene where one is responsible for pigmentation while other is not, and hence there are so many combinations in skin color (Barsh 2003). Several diseases that have genetic causes in them are polygenic like cancer, diabetes, and numerous others. The frequency of the phenotypes of polygenic traits and pattern of polygenic inheritance follows a bell-shaped curve, which is obtained when the values of polygenic traits are plotted with the mode representing the fit individuals. These traits are influenced by the interaction of a single gene or multiple genes and are controlled by both environment and genes and hence called multifactorial that depends on the interaction of both. The variation in these multifactorial traits also depends on the changeable level of interaction between gene and environment (Complex Trait Consortium 2003). Examples of diseases considered to be the results of many contributing factors are cleft palate, congenital dislocation of the hip, congenital heart defects, neural tube defects, pyloric stenosis, talipes.

Polygenic locus, which is called quantitative trait locus (QTL), is defined as the locus where one or multiple genes are found on the chromosome, and their different allelic substitutions lead to the variation in the quantitative character (Lerner 1968). A mutation that is recessive for a disease but is expressed phenotypically, both the alleles have to be recessive. Similarly, in any polygenic disease, there are more than two alleles, and if anyone of them is normal, then in such a case, the disease cannot be expressed and resemble a normal or Gaussian distribution.

## Mapping of Polygenes

Polygenes are mapped by a technique called QTL mapping. In this procedure, the locus where the genes are present is investigated with the help of other marker genes that belong to traits that are interrelated with that polygenic trait. It is mapped by identifying the molecular markers like SNPs or AFLPS that have the maximum correlation with any observed trait. Sometimes when the genome of an organism is unknown, then the genes of the same function are searched in another organism with known genome, and they are aligned and matched with the help of tools such as BLAST. These genes are then further sequenced and studied to know the degree of change in sequences with the change in the underlying phenotype (Watanabe et al. 2009). The number of loci and their interaction, along with the complexity of genetic architecture affecting the polygenic phenotype, is studied. This can help in knowing how the phenotype is evolving. QTL also helps in knowing about how many genes are involved and the level of expressivity and penetrance of the trait.

QTL mapping is done by the following methods.

- (a) ANOVA: The simplest method to calculate QTL is the application of ANOVA (analysis of variance).
- (b) Interval mapping: Interval mapping technique was first introduced by Lander and Botstein (1989). In it, QTL locus is assumed to be present between the markers that lie in a genetic map.
- (c) Composite interval mapping (CIM): In this type of mapping, various linked markers are taken as covariates for QTL analyses.
- (d) Family-pedigree based mapping: It involves searching genes for the polygenic trait in the organism by analyzing its similarity from other genomes of its own family or related families (Jannink et al. 2001).
- (e) Association studies: Single nucleotide polymorphism (SNP) can be used to link polygenes with the multifactorial trait. They can also reveal the connection between two populations on a disease-causing gene (Gibson and Muse 2009).

## Polygenic Inheritance

Its inheritance is called polygenic inheritance or quantitative inheritance, and it doesn't follow discontinuous variation like Mendelian inheritance, for example, height in pea plant, which is present in two extreme varieties, short and tall. Polygenic traits instead follow continuous variation like human height, that is, it is found in numerous forms. Polygenic genes control both metric and meristic traits.

In polygeny, traits displayed are neither dominant nor recessive where one allele's function does not hinder the effect of another allele as in the case observed in Mendelian genetics, but it exhibits incomplete dominance, and therefore all the alleles contribute in the phenotype by additive effect where different allelic interactions create variation in polygenic traits.

The probability of a progeny to acquire polygenic characteristics from parents cannot be determined by Punnett's square because the total number of genes involved in any polygenic trait is complicated to mark out. It can be determined by the normal distribution of probabilities where offspring displays intermediate phenotype of the trait possessed by the two parents.

## Cross-References

- ▶ [Mendel's Laws](#)
- ▶ [Multigenic Effects](#)
- ▶ [QTL Linkage Analysis](#)

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## Polygynandry

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## Synonyms

[Bigamy](#); [Plural marriage](#); [Polygamy](#)

## Definition

Polygynandry is a form of polygamy; in sexually reproducing animals, it is a multi-male and multi-female mating system. Polygynandry encapsulates both polygyny (males having multiple female mates) and polyandry (females having multiple male mates) within the same species.

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## Introduction

Sexual promiscuity in the form of polygynandry may provide benefits for both females and males. However, the types of benefits females and males gain are different due to differences between the sexes; males have the potential to produce a much higher number of offspring compared to females. Therefore, females more than males typically express quality-based mate preferences and males more than females typically express quantity-based mate preferences. For example, because of sperm competition, females can increase genetic diversity and quality in their offspring and introduce cryptic female choice by mating with multiple males in a sufficiently brief

time period. In addition, having multiple mates may secure additional resources for the female and, due to paternal uncertainty, decrease male infanticide or willingness to harm an offspring and increase their investment and paternal care. In males, fitness is directly increased with multiple female mates because males can fertilize the egg(s) of multiple females and, therefore, increase the number of offspring they produce.

## Polygynandry in Nature

In animals, polygynandry refers to two or more females or males having two or more mates in a breeding season. Polygynandry is common in nature; it can be observed in various species, including cichlid fish, dusky pipefish, European badgers, red foxes, territorial frogs, alpine accentors, sea spiders, collared pikas, and African ground squirrels. In the case of females, the benefits of multiple mating can include increasing the number of offspring produced. Multiple mating partners also may contribute materially to the well-being and safety of offspring, as in Galapagos hawks, dunlocks, and dark-eyed juncos. Multiple mating by females decreases the risk associated with mating with a male with an insufficient quantity or quality of sperm, which decreases the risk of producing unfertilized eggs, e.g., in dark-eyed juncos, in which a female's social partner often has lower genetic quality than the quality of other possible mates (Bellamy and Pomiankowski 2011; Davies et al. 2012). According to Fisher's (1930) sexy son hypothesis, multiple mating by females increases the chances of producing a greater quantity of sons that inherit their father's sexual attractiveness, which could then increase the son's attractiveness as a mate. This appears to occur, for example, in songbirds in which mated females seek extra-pair copulatory partners with more colorful plumage than their social partner. In addition, more colorful plumage and longer tail predict survivability of males. In the case of males, as in fruit flies, reproductive success increases with the number of copulations with different females. Also, if multiple males share paternity in offspring produced by the

same female, a given male may benefit by abandoning the female to search for additional mates (Davies et al. 2012). In humans, polygynandry may refer to a male or female being married or involved in a relationship with more than one male and with more than one female. Polygynandry in humans is relatively rare. One example of polygynandry occurs in peoples of the Indian Himalayas, who mix polyandry and polygyny to thereby form a polygynandry-like social and mating structure (Levine and Silk 1997).

## Cross-References

- ▶ [Cryptic Mate Choice](#)
- ▶ [Genetic Variation](#)
- ▶ [Infanticide](#)
- ▶ [Polyandry](#)
- ▶ [Polygamy](#)
- ▶ [Polygyny](#)
- ▶ [Promiscuity](#)
- ▶ [Sperm Competition](#)

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## Polygyny

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## Definition

A pattern of mating in which the male has more than one female mate.

## Introduction

Darwin theory of organic evolution suggests two forms of mechanisms for evolution: natural selection, wherein a species adapts to its biotic and abiotic environment, and sexual selection which is based upon competition to find the mate. Mating systems describe who mates whom and are dependent upon spatial and time constraints, need of parental care, and genetic compatibility (Kvarnemo 2018). It is classified on the basis of the number of mates acquired by an individual species in a breeding season. In the monogamous mating system, one male mates with one female at a time and is usually prominent in the species in which both the male and female contribute to defend and raise the young or in which males have limited chance of mating more than one female. Polygamous mating system, on the other hand, is either polyandrous (one female mates with more than one male) or polygynous (one male mates with more than one female).

## Polygyny

When one male mates with multiple females, it is termed as polygyny. It is most commonly seen in mammals and is also present in few birds and insects. The system is primarily based on male-male competition for mating a female and helps in increasing their reproductive fitness. It is common in the species where females provide most of the parental care and males offer little or no role in it.

## Resource Defense Polygyny

Its prominent feature is territorial defense by an adult male. It occurs when female groups are attracted to a resource and males defend it and compete for gaining territorial possession (Beletsky and Orians 1994). The territories defended by males have resources required for

successful mating (McCracken and Bradbury 1981), for example, black-winged damselflies males defend a territory containing the aquatic vegetation appropriate for laying eggs and wait for females to come to them.

## Female Defense Polygyny

It is displayed by a harem that is defined as an animal group constituted by a dominant male and a group of females and their offspring. The dominant male mates with the sexually active females in the group and provides them defense. As the juvenile males mature, they leave the harem. The females maturing sexually may continue to be a part of the same harem or move to other.

## Lek Polygyny

This polygyny is displayed by a number of species of insects, birds, and mammals. A lek is defined as an aggregation of males in a location that is not associated with resources. Usually the aggregation is formed in an area that has a significant number of sexually active females or where such females are likely to visit. The group of males attract the females by displaying their sexual features. Females choose the male for copulating and usually don't form lasting association with them. The males provide no parental care to the offspring. Leks are preferred as they provide the choice of finding a mate with better characteristics and at a reduced effort (Kokko 1997).

## Scramble Competition Polygyny

This polygyny is characterized by a competition in mating opportunity by locating females and found in many insects, spiders, and few mammals like squirrel. The mating success is dependent on the repeated location of the

mates, and hence, in addition to social dominance, time management and spatial memory also play a pivotal role in this mating system (Foley et al. 2018). More mobile males show a better success in mating as mobility increases the chance of finding the female mates (Muniz et al. 2018).

## Cross-References

- [Biparental Care](#)
- [Female Choice](#)
- [Mating](#)
- [Monogamy](#)
- [Polyandry](#)
- [Polygamy](#)
- [Polygyny Threshold Model](#)
- [Promiscuity](#)
- [Reproductive Fitness](#)
- [Resource Defense Polygyny](#)
- [Scramble Competition Polygyny](#)
- [Scramble Defense Polygyny](#)

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## Polygyny Threshold Model

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## Synonyms

[The polygamy threshold model](#)

## Definition

The polygyny threshold model is a framework proposed to describe optimal female mate choice in resource defense polygyny systems. The polygyny threshold is defined as the increase in breeding resources required to offset costs of sharing a territory with another female.

## Introduction

Until the 1960s, polygyny was largely considered a result of an excess of female to male breeders (Searcy and Yasukawa 1989). This explanation was found inadequate as it became clear that it is fairly common to see territorial males remaining unmated despite courtship efforts, while neighboring males mate polygynously. In the mid-1960s, the polygyny threshold model (hereafter the PTM) was proposed as an adaptive explanation to this phenomenon (Orians 1969; Verner 1964; Verner and Willson 1966).

Since its inception, the PTM has been applied on a wide range of organisms that exhibit social resource defense polygamy, including birds, mammals, fishes, reptiles, amphibians, and invertebrates. The threshold mechanism in the PTM is identical for polyandrous and polygynous systems, so the “Polygamy Threshold Model” would be a more appropriate term (Gowaty 1981), but because the model initially was proposed for polygynous birds, and because social polygyny is far more common than social



polyandry, the term “Polygyny Threshold Model” has been most widely used.

## How the PTM Works

The PTM describes the mating pattern in resource defense polygyny systems. Unlike in lek polygyny, female defense polygyny, and scramble polygyny, males in resource defense polygyny systems provide breeding resources to the female and offspring. They defend breeding territories which often hold food or other valuable resources, and they often take part in parental activities like food provisioning, incubation, and defense against predators. The breeding territories are typically aggregated in clusters, and females have the opportunity to evaluate several males before making their mate choice.

In the PTM the breeding resources offered by individual males are thought to vary, and to maximize reproductive success (i.e., number of offspring raised), a female should settle with the male breeder that offers the most. Male breeding resources are typically finite (e.g., food resources on the territory, or time spent by male incubating or feeding young), and monogamous females may take advantage of all resources the male offers. Females in polygynous dyads, however, have to share the breeding resources and experience sharing costs in the form of loss of breeding resources to the other female. Therefore, when a female considers settling as a secondary female, she should subtract the expected sharing costs from the overall resources offered by the male. If she finds that the territory still yields more breeding resources than available bachelor-held territories, the polygyny threshold is exceeded and she should prefer polygyny over monogamy (Orians 1969; Verner 1964; Verner and Willson 1966). All females that settle in a breeding cluster are expected to make this calculation for the available breeding territories before making their mate choice, and female settlement should follow an ideal free distribution with the most resourceful males becoming polygynous and

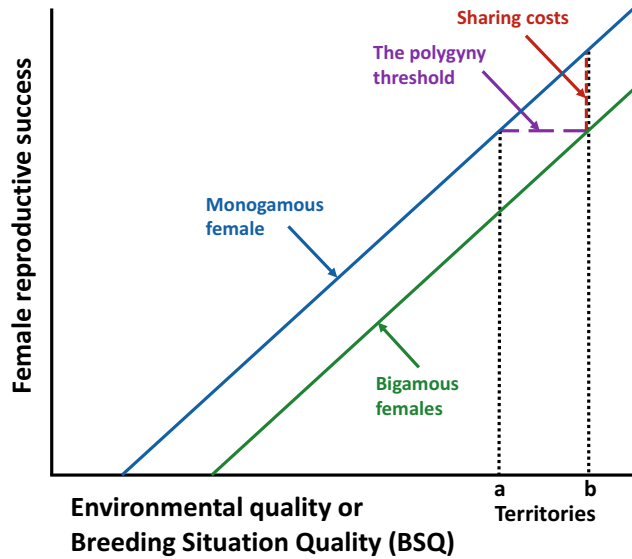
the poorest males either having to settle for monogamy or remaining unmated.

Early variants of the PTM used aspects of territory quality (denoted as environmental quality in Fig. 1) as predictors of female mate choice. In time, it became clear that offspring survival was also affected by male parental effort and male skills (e.g., breeding experience, competitive skills, foraging skills, and skills and resolve to defend against predators) (Davies et al. 2012; Webster 1991). Male attractiveness was also proposed to be a genetic trait that the offspring might benefit from inheriting (Weatherhead and Robertson 1979). This identified the problem of how to decide on which traits mate-prospecting females find most valuable and base their mate choice on – male characteristics, territory characteristics, or a mix of both. Territory quality (or environmental quality) was therefore substituted with the term male “Breeding Situation Quality” (BSQ), which represents the sum of resources offered by males that affect the breeding outcome, and ultimately the reproductive fitness of females (Wittenberger 1981). Instead of trying to pinpoint which cues females use to choose a mate, the assumption is then made that females choose the best males available at the time of their settlement. The first chosen male in a breeding cluster is considered to have the highest BSQ, BSQ then declines over the colonization order, and males that are chosen last or remain unmated are assigned the lowest BSQ (Searcy and Yasukawa 1989).

## Assumptions of the PTM

The PTM rests on the following assumptions:

- Females experience costs associated with sharing a mate.
- There is variation in male BSQ across the breeding population.
- Females can accurately assess BSQ of the males in the system.
- Females value BSQ on a similar scale.
- Females prefer breeding territories that offer the highest amount of BSQ.



**Polygyny Threshold Model, Fig. 1** A graphical representation of the PTM modified from Orians (1969). The *upper diagonal line* gives the expected reproductive success for a monogamous female and the *lower line* for bigamous females. The *dotted lines* denote the environmental quality or Breeding Situation Quality (BSQ) of territories (a) and (b). The *vertical short-dashed line* between the diagonals indicates the sharing costs for bigamous females on the best territory (b) in terms of reduced

reproductive success. The *horizontal long-dashed line* between the diagonals indicates the increase in BSQ needed to offset these costs, i.e., the polygyny threshold. As the threshold balances the costs of sharing, the monogamous female on territory (a) has equal prospects of reproductive success to a bigamous female on territory (b). A larger difference in BSQ favors bigamy, and a smaller difference favors monogamy

- Females are equal in quality and distribute according to offered BSQ in an ideally free fashion (i.e., after settlement, the number of breeders on the territories is proportional to the amount of resources available on the territories).

A critical requirement for the PTM is that females experience a cost associated with sharing a territory with another female breeder. If not, no threshold needs to be compensated and other mechanisms may better explain the dynamics of the mating system (Pribil 2000; Searcy and Yasukawa 1989).

### Predictions Derived from the PTM

A number of predictions may be derived from the PTM, but some of the main ones are related to settlement order, reproductive success for females, and male attractiveness.

**Settlement order:** Using the settlement order as a proxy for BSQ, the first settled territories should have highest BSQ and reach polygynous status first, and:

- Primary polygynous females should precede monogamous females in the settlement order.
- There should be a positive correlation between BSQ and harem size.

**Reproductive success:** If secondary females are compensated for costs associated with sharing a breeding territory, they should on average have access to as much BSQ as simultaneously settling monogamous females, and:

- Secondary females should have similar reproductive success to contemporary monogamous breeders.

**Male attractiveness:** Using harem size as a female preference criterion, polygynous males should be preferred as genetic sires over monogamous males:

- The proportion of genetic paternity loss should be lower for polygynous males than for monogamous males.

## Tests of the PTM Predictions

Species-specific life-history constraints and varying ecological factors have shaped variants of resource defense polygyny which to some extent differ in cost–benefit trade-offs, and over the years modifications have been made to the PTM to tailor it to specific variants (Andersson 1994; Davies et al. 2012; Garson et al. 1981; Grønstøl et al. 2003; Leonard 1990; Searcy and Yasukawa 1989; Slagsvold and Lifjeld 1994). Since the 1960s, numerous studies have tested the predictions of the PTM listed above, and the overall conclusions are: (1) harem size does not overall correlate with settlement order, (2) monogamous females tend to breed earlier in the settlement order than predicted by the PTM, (3) monogamous females perform on average better than secondary females in terms of offspring production, and (4) polygynous males do not suffer less cuckoldry than monogamous males. All of these conclusions are contrary to expectations from the PTM.

There have been many suggestions for how to explain the lacking empirical support of the PTM predictions. These include sexy-son effects, i.e., that reproductive fitness benefits of polygyny may be genetic and manifested as quality rather than quantity of offspring, an excess of breeding females to breeding males, and maladaptive female choice because (1) males deceive females into believing that they are unmated, (2) mate sampling may be costly and the opportunities to engage in mate sampling may be restricted, or (3) the environment is unpredictable and females may be unable to foresee unfortunate changes that may occur after they have made their mate choice. Although some of these explanations may be relevant in some mating populations, neither of them seems likely to provide a general explanation for why predictions are not met (Davies 1989; Grønstøl et al. 2003).

## Revisiting the PTM Assumptions

So, empirical results indicate that the PTM does not accurately describe the settlement dynamics in resource defense polygyny systems. For instance, empirical results place monogamous females earlier in the breeding order than expected. Why so? After all it seems reasonable to assume that the earliest female settlers choose the best available males, and that subsequent settlers also consider these as premium territories, resulting in these earliest settled territories becoming polygynous. Could it be that some early settling females remain monogamous because it is in their interest to do so, and that they are able to enforce monogamy by denying access for subsequent female mate prospectors despite male courtship attempts?

Common for most studies modeling variants of the PTM is the underlying assumption that females are equally resourceful and introduced sequentially to choose a mate in a system with a seasonal decline in reproductive success, in a manner conforming to the ideal free distribution. If females settle with mates in an ideally free fashion, it should in essence be a zero-sum game for the females, but what if it is not? When PTM was proposed and onwards for quite some time, research on mate choice and sexual selection was very much focused on variation in male quality and in the expression of male sexual ornaments considered attractive by females. Female traits and strategies to influence the mating outcome was not so much the focus of attention (Rosenqvist and Berglund 1992). Since then, however, a bulk of studies have shown that females differ individually, much like males do, and that females act in their own interests to maximize their reproductive fitness. This gives reason to question the validity of the equal-female assumption.

## Sexual Conflict and the PTM

What are the female interests in resource defense polygyny? When there is a cost associated with sharing a male, resident females experience a reduction in BSQ with the addition of a secondary

female on the territory. This should motivate resident females to oppose polygyny and try to enforce monogamy. Males, however, are likely to increase the number of offspring they produce if able to attract more mates, so they should strive for polygyny. This highlights a sexual conflict – a conflict of interests between the male and female in a pair-bond over how males should allocate their breeding resources (Davies 1989; Davies et al. 2012; Parker 1979; Trivers 1972).

Some authors realized decades ago that the PTM did not accommodate this sexual conflict. In one of their papers on Dunnocks (*Prunella modularis*), Davies and Houston (1986) commented that: “there is a more general reason for why the [polygyny threshold] model is likely to fail in predicting observed mating systems – namely, it largely ignores conflicts of interests between individuals,” and Krebs and Davies (1993) stated in their textbook on Behavioral Ecology that “The assumptions of the PTM are like those of ‘the ideal free distribution’” . . . [and] . . . “that ideal free conditions rarely hold in nature because dominant individuals attempt to grab more than their fair share of resources.”

### **Division of BSQ on Polygynous Territories**

The original PTM assumes that females sharing a polygynous territory divide the BSQ evenly. This is probably not the case because BSQ appears to be economically defendable units that females compete over (Emlen and Oring 1977). It has been pointed out that different rules for sharing costs between primary and secondary female will yield different PTM-predictions (e.g., secondary females bearing 50% of the sharing costs vs. being forced to bear up to 100% of the costs) (Altmann et al. 1977; Davies 1989). Several factors are likely to contribute to a nonequal sharing of BSQ.

### **Individual Differences in Female Competitive Strength**

It is quite common to see resident females behaving aggressively towards secondary mate prospectors, and many studies have found that females vary in

competitive strength. It seems reasonable to interpret this aggression as attempts to monopolize their male, or to gain more than their fair share of the BSQ (Davies 1989; Slagsvold and Lifjeld 1994; Wittenberger and Tilson 1980).

### **Degree of Synchrony Between Females in Polygynous Dyads**

The competition over the BSQ increases with increasing temporal overlap between the primary and secondary female (Leonard 1990; Slagsvold and Lifjeld 1994). Birds in general seem to have a reproductive fitness premium on breeding early (Perrins 1970), and the optimal timing of breeding is probably determined by a trade-off between costs and reproductive benefits of early breeding. Individuals able to handle the adverse effects of weather and sparse food early in the season generally do better than individuals that breed late. The optimal time of breeding onset is likely to be condition-dependent, and superior individuals may have earlier optima than poorer individuals (Drent and Daan 1980). The early breeders thus enjoy first pick of territory and take advantage of a longer chick growth season, whereas later breeders do the best of a bad job breeding as early as their condition permits. If prospects of reproductive success had not diminished with delayed breeding, secondary females would probably benefit from breeding later relatively to primary females, which would minimize the temporal overlap. But, as it is, females prospecting for secondary mating status probably cannot afford to delay their breeding to reduce the overlap.

### **Division of Paternal Effort Between the Primary and Secondary Female**

In passerine birds, polygynous males often invest more paternal effort in the brood of the primary female than in the brood of the secondary female, and the extent of this inequality often increases with increased asynchrony between primary and secondary females (Slagsvold and Lifjeld 1994; Webster 1991). There are, however, examples of later breeding secondary females not being disfavored by males. It seems sound to assume that males should allocate their paternal effort in a manner that maximizes the return per unit

invested. If early chicks have higher reproductive value and count as greater (reproductive fitness) losses than later chicks, the polygynous males might do best prioritizing their primary female. However, if the male could rely on a resourceful primary female to raise the offspring reasonably successfully without assistance, whereas a less resourceful, less experienced secondary female would face a larger risk of failure without male assistance, the male would probably raise more offspring if contributing more help to his secondary female than to his primary female (Grønstøl 2003). The more paternal care a resident female stands to lose to a secondary female, the higher her motivation should be to try to monopolize the BSQ and behave aggressively towards female mate prospectors.

#### **Male Interference to Mitigate Female Attempts at Monopolizing Breeding Resources**

In cases where resident females attack females prospecting for secondary mating status, males are sometimes seen to attack the aggressor in what looks like efforts to dissuade the resident females from chasing away the newcomers. This behavior has by several researchers been interpreted as male efforts to facilitate settlement of the female mate prospector. If the prospector is able to settle as a secondary female, recurrent skirmishes may occur with the primary females attacking the secondary females in what gives the impression of being attempts to monopolize as much BSQ as possible. How successful males are in facilitating settlement of secondary females probably depends on their strength and tenacity compared to that of their resident females. Females are sometimes successful in enforcing their interests, whereas the males' interests prevail at other times (Davies et al. 2012).

#### **Incorporating Varying Female Competitive Strength in the PTM**

It seems plausible that ability to monopolize BSQ correlates with female competitive strength. It also seems reasonable to expect female

competitive strength to vary individually in a breeding cluster. Therefore, in order to portray the polygynous settlement as accurately as possible, female despotism should be included when modeling resource defense polygyny. Introducing variation in female competitive strength to the PTM requires a revision of the assumptions. One might keep four of the original assumptions:

- Females experience costs of sharing a mate.
- Females can accurately assess BSQ of the males in the system.
- Females value BSQ on a similar scale.
- Females prefer breeding territories that offer the highest amount of BSQ.

And add some new assumptions:

- Females differ in competitive strength.
- Females can assess the competitive strength of other females relative to their own.
- Females benefit from nesting as early as their condition permits.
- Competitive strength decreases from first to last settled female.
- Strong females monopolize resources at the cost of weaker females to a degree determined by the relative difference in competitive strength between the female antagonists.

Running this framework in a simulation where individual differences in female competitive strength are set to approximately match BSQ-differences between males produces a settlement pattern where some of the early females remain monogamous due to successful deterrence of mate prospectors (Grønstøl et al. 2003). From the simulation results, the following can be extracted: (1) harem size does not correlate with settlement order; (2) the settlement order of monogamous females is similar to that of primary females, and monogamous females settle earlier than secondary females; (3) in terms of reproductive success, monogamous females perform equally as well as primary females and better than secondary females; and (4) because some monogamous males are among the earliest breeders, polygynous males should not (by default) be considered more



attractive than monogamous males. All these new predictions match previous empirical findings well: (1) field studies show that monogamous females are found earlier in the settlement order than expected from the original PTM; (2) overall, studies have failed to document that settlement order significantly predicts harem size; (3) monogamous females are in general found to have higher reproductive success than secondary females, instead of similar success which is predicted by the original PTM; and (4) paternity studies reveal that polygynous males are not cuckolded less than monogamous males, which they should according to the original PTM.

## Concluding Remarks

The new predictions generated from a PTM-model that incorporates a variation in female competitive strength match the accumulated empirical results well (Grønstøl et al. 2003), which strengthens the hypothesis that strong females may be able to impose their own interests in the sexual conflict over parental care by enforcing monogamy and monopolizing the breeding resources of their mate.

The simulation results placed monogamous males at both the high and the low end of the BSQ scale. This implies that it is not appropriate to use harem size as a proxy for male attractiveness (or BSQ) in resource defense polygyny systems without accompanying evidence demonstrating that such a link between harem size and male quality does exist. One might speculate that some of the most attractive males perhaps may do better breeding monogamously if they are confident that they will be preferred as extra-pair sires by neighboring females. They would then parasitize the parental effort of neighboring males instead of splitting their own parental care over more females (i.e., a strategy of social monogamy and genetic polygyny for the most attractive males). This might even cause these males to be less resistant to social monogamy and easier to monopolize by their (strong) females.

In natural systems of resource defense polygyny there probably exist additional variables that

play a part in the shaping of polygynous settlement patterns, which so far have not been included in the testing framework. An interesting effect that may alleviate sharing costs (and thereby reduce the polygyny threshold) is relatedness between female breeders that share a territory. If females on a polygynous territory are related, costs associated with sharing a territory may be lessened by indirect reproductive fitness benefits of kin selection, i.e., helping a relative to reproduce returns a reproductive fitness gain proportional to the relatedness (also termed inclusive fitness) (Hamilton 1964). Benefits from mutualistic behavior (or reciprocal helping), such as communal defense, may then increase and the resistance to sharing a territory should be lower than for unrelated females (Grønstøl et al. 2015).

An assumption that all variants of the PTM share is that females agree on how attractive the available males are, and that all females, given the chance, would choose the same male. This assumption might to some extent be challenged by research done on mate choice of complementary genotypes. Results have been presented indicating that females in some species prefer to mate with males with a MHC-genotype that is different from, or complementary to, their own MHC-genotype. This is thought to increase the heterogeneity of MHC in the offspring, which should increase the efficiency of the immune system (Mays and Hill 2004). As females are expected to vary with regard to MHC-genotypes, this effect would introduce an element of disagreement over which males are considered the most attractive. The strength of this objection will depend on how well the males' attractiveness as social mates correlates with their attractiveness as genetic sires. Females might prefer to form social bonds with males that offer the most BSQ and covertly seek out more MHC-compatible males as extra-pair mates. Future research will probably establish how strong the effect of selection for complementary genotypes is compared to the preference for male traits that females agree on.

Theoretical models are not better than the foundation they rest on, and it is necessary to revisit, identify, evaluate, and explicitly state assumptions

when applying them to natural systems. New insights might call for corresponding revisions of the PTM.

## Cross-References

- [Competition](#)
- [Competitive Exclusion](#)
- [Complementary Genes Hypothesis](#)
- [Dominance Hierarchy](#)
- [Female Choice](#)
- [Mating](#)
- [Mating Effort](#)
- [Monogamy](#)
- [Parental Investment](#)
- [Paternal Behavior](#)
- [Polyandry](#)
- [Polygamy](#)
- [Polygyny](#)
- [Reproductive Fitness](#)
- [Resource Defense](#)
- [Resource Defense Polygyny](#)
- [Sexual Selection](#)
- [Territory Defense](#)

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## Polymorbidity

### ► Comorbidity

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## Polymorphic

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## Synonyms

Genetic polymorphism; Genetic variation

## Definition

Polymorphism in biology refers to the discontinuous genetic variations leading to the existence of two or more forms, stages, or phenotypes existing in the same species within the same population.

## Introduction

The literal meaning of “Polymorphic” is “having multiple forms.” In biology, the word “polymorphic” is generally used in terms of genes. A gene

is referred to as polymorphic if more than one allele is present at a specific locus of the gene. Furthermore, for being considered polymorphic, each allele must occur in the population at a minimum of 1%. This phenomenon of occurrence is called polymorphism.

Polymorphism can be subcategorized into two basic types, that is, sexual dimorphism and allelic polymorphism. Sexual dimorphism is when the male and female of a species differ physically or phenotypically like humans, whereas the allelic polymorphism denotes the presence of alternate forms of a gene governing a specific trait.

Owing to the presence of two or more allelic variants, different phenotypes are visible, for instance, flower color. An exciting aspect of polymorphism is that it can be seen in any trait, be it morphological, physiological, or behavioral and that too involving any coding or non-coding segment of DNA (nucleus, chloroplast, or mitochondrion) (<https://www.britannica.com/science/polymorphism-biology>).

## Sources and Effects of Polymorphism

Genetic variations or polymorphism owe their existence to the process of mutations. Mutations occur at different rates in different parts of the genome ranging from  $10^{-7}$  to  $10^{-10}$  nucleotide base per generation (Wright 2001). In addition to this, crossing over, which leads to exchange of the chromosomal segments between non-sister chromatids, also contributes to the genetic diversity (NHGRI 2020).

According to the theory of evolution, evolutionary processes lead to polymorphism. In natural conditions, polymorphism is very common. It not only increases biodiversity but is also linked to the adaptability of an organism.

## Common Misconceptions

There are some general misconceptions associated with the word polymorphism. This term cannot be used for character traits that show continuous variation, such as height, although this may be a heritable aspect. Additionally, this

term is also incorrectly used for the description of different geographical races or variants. Still, polymorphism points out that the alternate forms of a single gene must inhabit the same habitat at the same time (Phillips 2020).

Some examples of polymorphism have been provided here:

### 1. Blood Group

The ABO blood group system exhibits genetic polymorphism. People around the world exhibit different blood group phenotypes A, B, AB, and O. These phenotypes are governed by various forms of a gene, that is, alleles present at a single locus. These different phenotypes never get eliminated by natural selection forces because individuals of a particular blood group would be more susceptible to a distinct disease while remaining less susceptible to the others than individuals with a different blood group (Crow 1993; Meade and Earickson 2005).

### 2. Sickle-Cell Anemia

Sickle-cell anemia is a genetic defect occurring due to the single nucleotide polymorphism, where at the sixth position of the  $\beta$ -globin gene, GAG (Glutamic acid) changes to GTG (Valine). The sickle-celled hemoglobin gene is displayed as HbS in contrast to the normal hemoglobin gene HbA. Under low oxygen conditions, the RBCs change their shapes to sickle, which causes great difficulty in transporting oxygen throughout the body. Additionally, the homozygous recessive condition has a short life expectancy, whereas the homozygous dominant and heterozygous conditions are normal, with the latter suffering from a few problems periodically. It is also essential to know that the heterozygous condition has resistance against the malarial parasite. This denotes genetic polymorphism balanced between the fierce selection against the homozygous recessive patients and selection against the homozygous dominant patients by malaria (Wang et al. 2016).

### 3. Plumage Color in Birds

The pattern, color, and arrangements of the layer of feathers that covers a bird are called its

plumage. A large amount of genetic variations can be seen in the plumage of the birds of same species and subspecies.

In a study conducted by Galeotti and coworkers, birds of different species showing intraspecific variation were studied, and it was observed that among the 334 species of the birds studied Strigiformes, Ciconiiformes, Cuculiformes, and Galliformes showed the highest polymorphism. The study suggested that the color polymorphism was a result of evolution under selective pressures (disruptive selection) with respect to the detectability of the bird (Galeotti et al. 2003).

### 4. Styler Polymorphism in Angiosperms

An important example in case of plants is the styler polymorphism in angiosperms. There are four major classes of styler polymorphism in angiosperms: stigma-height dimorphism, distyly and tristyly, the heterostylous conditions, and enantiostyly. The polymorphism exhibited differs in both the relative position of the sexual organisms and the number of floral morphs occurring within the populations (Barrett et al. 2000).

### 5. Major Histocompatibility Complex

The genes governing the major histocompatibility complex are highly polymorphic, which leads to defense against the pathogens (MHC Sequencing Consortium 1999).

Apart from these, there are many examples of polymorphism, like the genes of glucose-6-phosphate dehydrogenase (Verrelli et al. 2002) and genes involved in human taste polymorphism (Fisher et al. 1939). Polymorphism is also depicted in other organisms apart from humans like hoverflies, drosophila, ants, birds, lizards, fishes, plants, etc.

## Conclusion

Polymorphism means discontinuous genetic variations that lead to several different forms/types of members belonging to the same species. It allows the species to adapt flexibility in the environment. Additionally, this provides the space for natural selection, which will eventually lead

to the change in allele frequencies and then microevolution.

## Cross-References

- [Alleles](#)
- [Genetic Compatibility/Histocompatibility](#)
- [Genetic Variation](#)
- [Mutations](#)
- [Species](#)

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## Polypeptide

- [Protein](#)

## Polyphasic Activity Pattern

- [Cathemeral](#)

## Polyspecific Associations

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## Synonyms

[Heterospecific group](#); [Interspecific group](#); [Mixed species group](#)

## Definition

A temporary or permanent social group consisting of two or more different interacting species in close proximity.

## Introduction

Polyspecific associations, in which two or more species occupy the same space, were noted early on by prolific naturalists like Alfred Russel Wallace (1869) and Henry Walter Bates (1864) in



their descriptions of the mixed flocks of tropical birds in Malaysia and the Amazon (Morse 1977). Since then, nonrandom polyspecific associations have been documented in numerous taxa. It is generally accepted that mixed species groups benefit constituent animals in two primary ways: through predator avoidance and foraging benefits. Mixed species groups therefore aim to achieve an optimal balance between foraging efficiency, given intragroup resource competition, and anti-predator benefits.

### Anti-Predator Benefits

Polyspecific associations provide distinct advantages for avoiding predators, mainly because large group size is an adaptation to predation pressure. There are five mechanisms by which mixed species groups help constituents avoid predation, all of which rely on large group size: the dilution effect, the confusion effect, the selfish herd effect, increased eyes and ears, and defense against predators (Stensland et al. 2003). The dilution effect poses that the likelihood of being attacked decreases with increasing group size. This effect is closely related to the selfish herd effect, in which “selfish” group members (generally more dominant animals) occupy the most central positions in the herd, leaving peripheral members vulnerable to predation. Being in a larger group also confers the advantage of increasing the absolute amount of vigilant eyes and ears. The confusion effect describes the phenomenon in which predators are less successful in capturing individual prey as group size increases (Stensland et al. 2003). All of these mechanisms operate to varying degrees depending on the ecological circumstances in which the mixed species groups form.

Perhaps the most iconic example of polyspecific association as an adaptation to heavy predation is the congregation of ungulate species on the African savannah, in which all of the mechanisms above operate. It has been shown that Thomson’s and Grant’s gazelles (*Gazella thomsoni*; *Gazella granti*) on the Serengeti were less vulnerable to predation by cheetahs (*Acinonyx jubatus*) when in mixed species groups

relative to smaller, conspecific groups. The gazelles shared responsibility for vigilance, thus increasing individual feeding time, providing a significant foraging benefit to individuals in the herd. Cheetahs were detected earlier, and cheetah attacks were less successful and less frequent in mixed groups than alone (Fitzgibbon 1990). Similarly, in a large scale comparative analysis of 66 pairs of terrestrial foraging bird species worldwide, it was found that these bird species increased their feeding rate and decreased vigilance (i.e., scanning behavior) when in mixed species flocks relative to solitary or monospecific foraging flocks (Sridhar et al. 2009).

Heterospecific groups can also facilitate earlier detection of predators. Cowtail stingrays (*Pastinachus sephen*) preferred to rest with whiprays (*Himantura uarnak*) rather than other cowtail conspecifics. In these mixed species groups, whiprays responded to predators earlier than cowtails, thereby alerting cowtails to the presence of predators more effectively than in a monospecific group (Semeniuk and Dill 2006). This same effect was also inferred from studies of monkeys in the Tai rainforest in Ivory Coast. Diana monkeys (*Cercopithecus diana*) responded first to potential predators with loud alarm calls, allowing Campbell’s monkeys (*Cercopithecus campbelli*) to initiate an anti-predator response sooner than if they were among conspecifics only (Buzzard 2010). Lastly, there can be distinct reproductive benefits to polyspecific association, as animals can gain the benefits of increased group size without increasing mating competition (Buchanan-Smith 1999).

### Foraging Benefits

Where shared resources are concerned, intragroup feeding competition will nearly always occur with limited food resources. In most polyspecific associations, the anti-predator benefits of being in a group outweigh the costs of food competition, despite this competition being slightly less due to niche separation and resource switching between species (Chapman and Chapman 2000). Importantly, the ecological factors that contribute

to the formation of polyspecific groups are highly variable, and so it is difficult to generalize about competitive regimes in polyspecific associations throughout the animal kingdom. There are, however, some distinct foraging benefits to be gained by foraging in heterospecific group. Polyspecific associations have been hypothesized to increase food detection and food use. Gautier-Hion et al. (1983) found that within a community of guenons (genus *Cercopithecus*), those groups that consisted of more than one species had a more diversified diet, improved detection and defense of fruit, and exploited resources less intensely. Frugivorous primates whose home ranges differ in size but nonetheless overlap may benefit from associations by obtaining information about the location of patchily distributed fruit resources that fall outside their range. This allows these primates to locate foods that they otherwise would not access (Stensland et al. 2003). Similarly, Avila-Pires saddle-back tamarins (*Saguinus fuscicollis avilapiresi*) in the Amazon capture more insects when in association with red-capped moustached tamarins (*Saguinus mystax pileatus*), because the moustached tamarins flush the arthropod prey from the upper canopy (Peres 1992).

In a striking example of heightened resource exploitation, associations between seabirds, pelagic dolphins, and tuna serve to drive fish to the ocean surface, making them easily exploitable by the dolphins and other members of this heterospecific group (Au and Pitman 1986). In a recent experiment, Freeberg et al. (2017) tested how diversity in interspecific group composition affects foraging success in birds and demonstrated that latency was significantly shorter with increasing species composition diversity and argue that polyspecific association helps wild birds locate and exploit novel food sources more effectively.

## Social Benefits and Other Advantages

There are also distinct social, competitive, and reproductive advantages to participating in a polyspecific association. While most social interactions between heterospecifics are agonistic according to Stensland et al. (2003), immature animals in

polyspecific associations often play with immature individuals of other species, which can help develop social and motor skills for adulthood, as well as cement interspecies bonds as seen among forest monkeys (Struhsaker 1981) and oceanic dolphins (Bearzi 1996). Lastly, there can be distinct reproductive benefits to polyspecific association, as animals can gain the benefits of increased group size without increasing mating competition (Buchanan-Smith 1999).

## Conclusion

In summary, there are two major explanations as to why animals form polyspecific associations: foraging advantages and anti-predator advantages, though there are less studied social, reproductive, and competitive benefits as well. As with the evolution of social groups, the formation of polyspecific association likely has been driven by predation, as different species are able to exploit each other's vigilance, with increased foraging as a side effect of this. The cognitive implications of polyspecific association have yet to be studied, though it is accepted that mixed species groups form nonrandomly. The social cognition of mixed species groups is a matter of ongoing study.

## Cross-References

- [Group Living](#)
- [Optimal Group Size](#)
- [Predator Defense](#)

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## Pongoland

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## Ponzo Illusion

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## Synonyms

[Depth illusion](#); [Geometric illusion](#); [Linear perspective](#)

## Definition

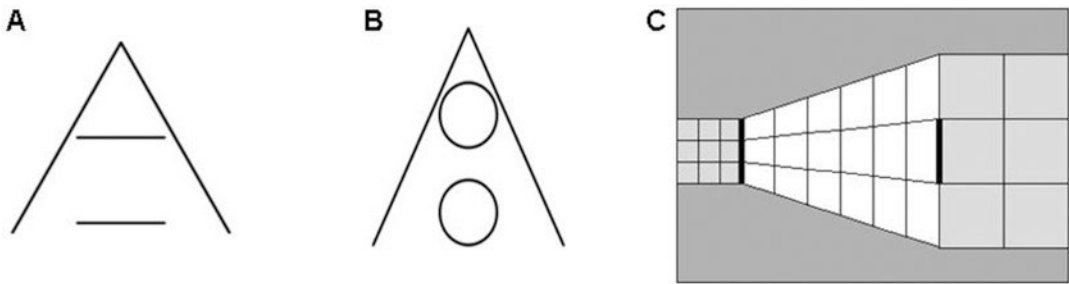
The Ponzo illusion is a geometric visual illusion commonly presented as two horizontal parallel lines, equal in length, above one another, surrounded by a set of converging lines. These converging lines represent an intersecting feature in the display that distort the perception of the equally sized parallel lines such that the upper line (closest to the apex of the converging lines) appears to be longer in length than the lower line. In humans the Ponzo illusion has been well-studied and various theories have been used to explain susceptibility. The Ponzo illusion has also been studied in nonhuman animals (hereafter animals), with most species to date demonstrating human-like susceptibility to the illusion.

## The Ponzo Illusion

Visual illusion susceptibility occurs when visual information is unnecessarily or inappropriately adapted based on preconceptions. More specifically, geometric visual illusions are invoked when

## Polythelia

- [Supernumerary Nipple](#)



**Ponzo Illusion, Fig. 1** Three examples of the Ponzo illusion, where (a) and (c) utilize identically sized vertical lines, and (b) utilizes identically sized circles. (a) and (b) are presentations using a “converging lines” context,

whereas (c) is a presentation of a “grid inducer” context. Here, the object closer to the apex of the converging lines, or in the smaller inducer grid, appears larger than the other object. (Adapted from Byosiére et al. 2017)

the physical characteristics (e.g., size, length, color, brightness, orientation area) of a given stimulus are perceptually distorted. First discovered by the Italian psychologist, Mario Ponzo (1882–1960), the Ponzo illusion, represents a geometric visual illusion in which a size difference between identical stimuli, such as lines or shapes, is invoked due to the presence of other features presented in the display. The stimuli can be distorted by physical features in the background, foreground, or by intersecting shapes that invoke a misperception of length, size, and/or parallelism. Often, the Ponzo illusion is presented as two parallel lines, equal in length, above one another, surrounded by a set of converging lines (Fig. 1a). The parallel line presented atop, closest to the apex of the converging lines, is perceived as being longer than the line presented furthest from the apex, the lower line. Variations of the Ponzo illusion have been created using different stimuli (Fig. 1b) as well as different surrounding features (Fig. 1c). Regardless of the presentation, the theories proposed to explain the emergence of the illusion remain the same.

## Ponzo Illusion in Humans

In the human literature, the Ponzo illusion is well-studied and multiple theories have been proposed to explain susceptibility. Inappropriate size constancy scaling theory (Gregory 1963) posits that

the two identically sized stimuli are perceived to be different in size due to the placement of converging inducer lines, which induce linear perspective cues. Integration field-theory (Pressey and Epp 1992) suggests that converging inducer lines invoke attentional demands to the space in between, which results in misperception of the stimuli. More recently, tilt constancy theory (Prinzmetal and Beck 2001) proposes that perception of size depends on the interpretation of the location of the end points of the converging lines, and this interpretation of the location causes a misperception of size between the two stimuli.

Most humans demonstrate susceptibility when presented with the Ponzo illusion, and research suggests that perception of the illusion requires a high level of visual processing (Song et al. 2011). The illusion emerges after interocular transfer meaning that visual input is processed post-retinally, likely in the primary visual cortex or in higher visual areas (Song et al. 2011). Moreover, the Ponzo illusion is cognitively impenetrable, meaning that humans cannot prevent themselves from visually seeing the illusion even when aware of its presence. Interestingly, human’s visually guided actions may not be affected by the illusory-invoking properties of this illusion, as a double dissociation between vision-for-perception and vision-for-action appears to be present (Ganel et al. 2008). When asked to use an action (a grasping motion using one’s index finger and thumb) to indicate the length of the line

stimuli when presented with the Ponzo illusion, humans appear to scale the opening of their index finger and thumb to the real size of the target line and not the perceived illusory size.

It is also important to note that some variation in Ponzo illusion susceptibility has been observed within humans. Individuals living in non-Western cultures or rural areas are less likely to demonstrate susceptibility to the illusion (e.g., Segall et al. 1963). While these reasons for differences are still debated, it has led to the “carpentered-world” hypothesis. This hypothesis proposes that lines and 90° right angles are more frequently present in Western cultures; therefore, individuals exposed to this environment, especially from a young age, might be more susceptible to the Ponzo illusion (Segall et al. 1963). Interestingly, susceptibility does not appear to be solely dependent on experience. Congenitally blind children demonstrate perception of the Ponzo illusion post-cataract surgery, indicating that even within humans, the underlying mechanisms responsible for perceiving the illusion might not exclusively be learned (Gandhi et al. 2015).

The substantial literature available regarding human illusion susceptibility provides a detailed foundation which can be used to evaluate cognitive and neuropsychological mechanisms of visual processing both within humans and across other animals. As it is possible to evaluate illusion susceptibility nonverbally, this method may serve as an ideal tool to indirectly and comparatively assess perception in humans and animals (Kelley and Kelley 2014). In doing so, similarities and differences underlying psychological and cognitive processes of perception can be compared, furthering current understanding of not only human visual perception, but also animal visual perception (Kelley and Kelley 2014).

## Ponzo Illusion in Animals

To date, susceptibility to the Ponzo illusion has been evaluated across a variety of animal species (Table 1). Typically, susceptibility has been

assessed using experimental testing paradigms in which an animal is trained to make a certain choice (e.g., discrimination task, classification task, same-different task). These findings currently suggest that Ponzo illusion susceptibility in animals is rather unique. Unlike other most other geometric illusions, where inter-specific variability in illusion susceptibility has been observed (e.g., Ebbinghaus-Titchener, Delboeuf, Muller-Lyer), human-like susceptibility to the Ponzo illusion has been found in every species tested to date, except for one. Rhesus macaques (Bayne and Davis 1983; Fujita 1996, 1997), carneau pigeons (Fujita et al. 1991), horses (Timney and Keil 1996), baboons (Barbet and Fagot 2002), Sprague-Dawley rats (Nakagawa 2002), and chimpanzees (Imura et al. 2008) have all demonstrated human-like susceptibility to the illusion. On the other hand, domestic dogs have failed to demonstrate any type of susceptibility to the illusion, indicating they do not fall susceptible to the illusory-invoking properties of the display (Byosiére et al. 2017, 2018).

As the majority of species tested to date have demonstrated human-like susceptibility when presented with the illusion, it is important to note that the results observed in dogs are rather equivocal. In two studies (Byosiére et al. 2017, 2018), canine susceptibility to the Ponzo illusion was evaluated across a variety of different illusory contexts/presentations, including variations of those presented in Fig. 1. Across these presentations and using a two-choice discrimination screen-touching paradigm, dogs as a group generally demonstrated at chance performance, indicative of null susceptibility. These results suggest that unlike all other species tested to date, dogs perceptually viewed the target stimuli as being equal in size. This result appears to be consistent regardless of target stimuli used (i.e., circles or rectangles), the presentational background context (i.e., converging lines or grid inducer contexts), or the orientation in which the stimuli are embedded (i.e., vertical or horizontal). However, it is important to note that like other assessments of illusion susceptibility individual differences were observed. Certain



**Ponzo Illusion, Table 1** Overview of animal susceptibility to the Ponzo illusion

| Species                                                                             | Citation                   | Subjects                                                   | Paradigm                       | Susceptibility?  | Environment | Visual acuity (cycles/degree)                            |
|-------------------------------------------------------------------------------------|----------------------------|------------------------------------------------------------|--------------------------------|------------------|-------------|----------------------------------------------------------|
| Minnows ( <i>Phoxinus laevis</i> )                                                  | Herter (1930) <sup>a</sup> | 2 fish                                                     | Two-choice discrimination task | Yes – Human-like | Aquatic     | 5.45 and 5.56 (Brunner 1935)                             |
| Rhesus monkeys ( <i>Macaca mulatta</i> )                                            | Bayne and Davis (1983)     | 2 male and 2 female                                        | Shape classification task      | Yes – Human-like | Terrestrial | 53 (Covey and Ellis 1967)                                |
| Carneau pigeons ( <i>Columba livia</i> )                                            | Fujita et al. (1991)       | 3 male                                                     | Two-choice discrimination task | Yes – Human-like | Aerial      | 17.17 (Ghim and Hodos 2006)                              |
| Rhesus monkeys ( <i>Macaca mulatta</i> )                                            | Fujita (1996)              | 1 male, 1 female                                           | Size-classification task       | Yes – Human-like | Terrestrial | 53 (Covey and Ellis 1967)                                |
| Horses ( <i>Equus caballus</i> )                                                    | Timney and Keil (1996)     | 2 female                                                   | Two-choice discrimination task | Yes – Human-like |             | 23.3 (Timney and Keil 1992)                              |
| Rhesus monkeys ( <i>Macaca mulatta</i> ) and chimpanzees ( <i>Pan troglodytes</i> ) | Fujita (1997)              | 1 male and 2 female rhesus monkeys and 1 female chimpanzee | Size-classification task       | Yes – Human-like | Terrestrial | 53 and 65 (Covey and Ellis 1967; Spence 1934)            |
| Baboons ( <i>Papio papio</i> )                                                      | Barbet and Fagot (2002)    | 2 male and 2 female                                        | Same or different              | Yes – Human-like | Terrestrial | Unknown                                                  |
| Sprague-Dawley rats ( <i>Rattus norvegicus</i> )                                    | Nakagawa (2002)            | 16 male                                                    | Size-classification task       | Yes – Human-like | Terrestrial | 1.2 (Silveira et al. 1987)                               |
| Chimpanzees ( <i>Pan troglodytes</i> )                                              | Imura et al. (2008)        | 1 male, 2 female                                           | Two-choice discrimination task | Yes – Human-like | Terrestrial | 65 (Spence 1934)                                         |
| Dogs ( <i>Canis familiaris</i> )                                                    | Byosiére et al. (2017)     | 6–8 (2 male, 6 female)                                     | Two-choice discrimination task | No – Null        | Terrestrial | 2.5–10 and 3–19.5 (Graham et al. 2018; Lind et al. 2017) |
| Dogs ( <i>Canis familiaris</i> )                                                    | Byosiére et al. (2018)     | 1 male, 5 female                                           | Two-choice discrimination task | No – Null        | Terrestrial | 2.5–10 and 3–19.5 (Graham et al. 2018; Lind et al. 2017) |

<sup>a</sup>Note: This publication likely represents the first to evaluate animal susceptibility to the Ponzo illusion. While the author suggests minnows experience human-like illusory perception of the Ponzo illusion, the methodology has been suggested to be obsolete and the lack of controls require further investigation before interpreting these results

subjects did demonstrate individual illusion susceptibility, some consistently so across the different variations of the illusion presented (Byosiére et al. 2017, 2018).

Regardless, six out of seven total species evaluated have demonstrated human-like susceptibility to the Ponzo illusion. Taken together, this distinctive interspecific parallel has significant implications for interpreting proposed theoretical mechanisms underlying the Ponzo illusion. As proposed by Feng, Chouinard, Howell, and Bennett (2017), such examples, in which similarities between humans and animals are observed, highlight the importance of visual illusion and perception research in animals as a comparative approach can be used to further test preexisting theories beyond what is possible in a human population (Feng et al. 2017).

Based on theories from the human literature, Ponzo illusion susceptibility is thought to be more prominent in terrestrial species compared to aerial and aquatic species as the systematic judgment of depth and distance across the horizon might invoke stronger linear perspective cues than those observed in three-dimensional space (Feng et al. 2017). As most species evaluated represent those living in terrestrial environments, this explanation may possibly explain why most animals have demonstrated perception of the Ponzo illusion. However, one aquatic (Herter 1930) and one aerial species (Fujita et al. 1991) have been tested and results suggest they are also susceptible to the illusion. Moreover, dogs, a terrestrial species, failed to demonstrate any kind of susceptibility to the illusion. Therefore, environment does not appear to predict susceptibility. Due to the limited species evaluated and the small sample sizes in these studies, it is important that additional assessments of Ponzo illusion susceptibility of animals living within aerial and aquatic environments are conducted to further investigate the relationship between environment and susceptibility.

Physiological differences in visual acuity have also been proposed to affect perception of the illusion (Table 1). The human literature suggests that Ponzo illusion susceptibility emerges as a result of depth perception and advanced visual acuity. As receding images, such as those invoked

by the Ponzo illusion, become smaller in size, retinal information can be more difficult to interpret especially for those animals which may not accurately perceive the scene visually. Thus, animals with poor visual acuity may not fall susceptible when presented with the Ponzo illusion (Feng et al. 2017). To date, the species evaluated range in visual acuity measures of 1.2 cycles/degree (rats)–65 cycles/degree (chimpanzees) (Table 1). Human visual acuity varies, but generally measures of 40 cycles/degree are generally reported (Campbell and Green 1965). Given this extreme variation in visual acuity, and the fact that most animals have demonstrated human-like susceptibility to the Ponzo illusion, it seems unlikely that animals with higher measures of visual acuity are susceptible to the illusion. Then again, many of the visual acuity measures reported stem from studies with extremely small sample sizes that may be obsolete. Therefore, caution should be used when interpreting this relationship.

## Conclusion

In conclusion, it is particularly interesting that most species, regardless of testing paradigm, environment in which they live, and/or visual acuity appear to demonstrate human-like susceptibility when presented with the Ponzo illusion. This suggests that the parallels observed may be due to other shared commonalities, bringing into question whether susceptibility is learned or innate. Practically, this question is impossible to disentangle, and likely, both play a role in the emergence of susceptibility. Regardless, the consistency observed across species suggests that the Ponzo illusion might represent an ideal geometric illusion in which to comparatively assess and develop theories of visual perception in animals.

While it can be exceptionally difficult to evaluate similarities and differences in visual perception across nonverbal animal species, the method of using illusion susceptibility to evaluate perception has been proposed to represent a unique tool in comparatively evaluating various species' perception (Kelley and Kelley 2014). This systematic

and readily generalizable approach (Kelley and Kelley 2014) allows for testing of existing theories beyond what is possible in a human population (Feng et al. 2017). In implementing this comparative framework, the Ponzo illusion is quite unique compared to other geometric visual illusions. While discrepancies in the perception of geometric visual illusions are often present both across and within animal species, most species tested to date have demonstrated human-like susceptibility when presented with the Ponzo illusion. These findings highlight the possibility that visual processing and perception of this visual geometric illusion occurs postretinally in vertebrates. The Ponzo illusion, therefore, represents an ideal illusion in which to continue conducting assessments of geometric illusion susceptibility, in which larger samples are employed, various methodological paradigms are utilized, and more species are tested to begin to further investigate this unique perceptual similarity.

## Cross-References

- [Computerized Testing Paradigm in Primates](#)
- [Corridor Illusion](#)
- [Delboeuf Illusion](#)
- [Depth Perception](#)
- [Ebbinghaus Illusion](#)
- [Gestalt](#)
- [Size Illusion](#)
- [Visual Perception](#)

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## Pop-out

### ► Feature Integration Theory

## Population

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## Synonyms

Area; Community; Individual; Species

## Definition

Group of individuals of same species occupying a particular area at a specific time.

## Introduction

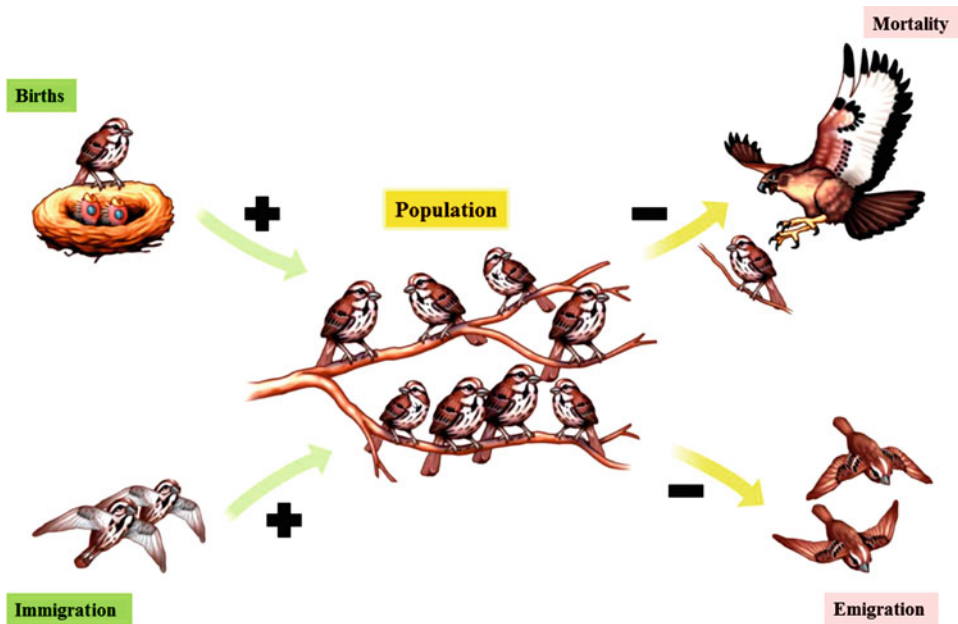
Population refers as a group of potentially interbreeding and interacting individuals of the same species living in the same geographical place and time having common gene pool (Daniel 2007).

The various types of the population are: (a) Monospecific population: It is the population in which individuals are only one species. (b) Poly-specific population: It is referred to the population of more than one species; conversely polyspecific populations are referred to as the community.

## Population Characteristics

### Population Size

Population size is dynamic. It is referred to the total number of individual in a population



**Population, Fig. 1** Effect of natality/or birth rate and immigration as well as mortality/or death rate and emigration on the population size. Births and immigration add

individuals to a population; in other side, deaths and emigration remove individuals from a population

(Husemann et al. 2016). Population size increases by increase natality/birth rate and also immigration of individuals. Population size decreases by mortality/death rate and also emigration of individuals. Figure 1 shows that population size affects via natality and immigration as well as mortality and emigration.

### Determining the Population Size

There are three ways to determining the population size: (a) Direct counts: The most accurate way to determining the population size but seldom feasible. (b) Sample an area and then extrapolate. (c) Capture (mark) – Recapture method is used for mobile species.

### Factors Affecting Population Size

There are three factors which affect the population size. (a) Abiotic factors: sunlight and temperature, precipitation/water, soil/nutrients. (b) Biotic factors: other living organisms: prey (food), competitors, predators, parasites, disease. (c) Intrinsic factors: adaptations.

### Population Density

It represents the number of an individual per unit area/volume (Rosenberg 2011). Crude density: Density per unit total space. Ecological density: Density per unit of habitat. It is also called as economic density or specific density.

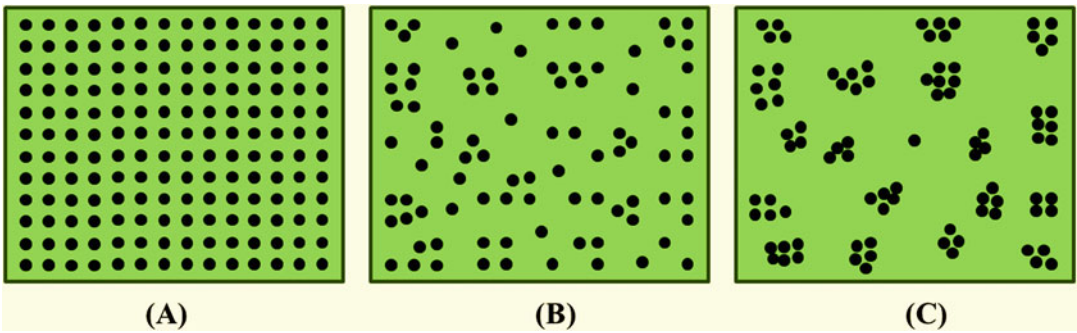
Population density can impact on the health and survival of organisms. In dense populations, pathogens can spread more rapidly (Fig. 1).

### Population Dispersion Pattern

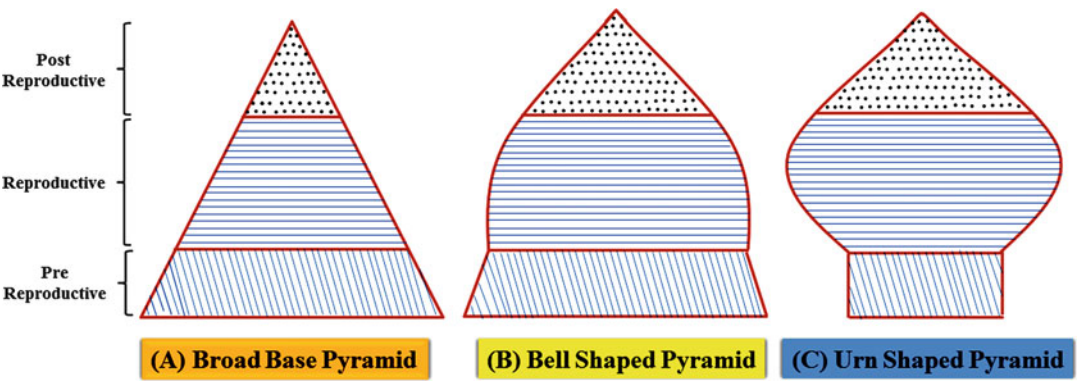
It is the spatial pattern of individuals of a population relative to one another. There may be three types of dispersion patterns (Fig. 2) (Krebs 1928).

**(A) Uniform dispersion:** A uniform dispersion referred as individuals are evenly distributed. Uniform dispersal may be influenced by social interactions such as territoriality. **(B) Random dispersion:** In a random dispersion, the position of all individual is independent of other individuals. It occurs in the absence of strong repulsions or attractions. **(C) Clump dispersion:** Individual which are present in small localized groups or





**Population, Fig. 2** Diagrammatic representation of three types of dispersion patterns. (a) Uniform dispersion; (b) Random dispersion; (c) Clump dispersion



**Population, Fig. 3** Graphical representation of different age groups in a population. Three types of age pyramids showing in the figure which represents: (a) Pyramid with a broad base; (b) Bell-shaped pyramid; (c) Urn-shaped pyramid

patches. It may be influenced by resource availability and behavior.

**Age Structure:** Age structure of the population describes the individual of different age groups. These proportions of individuals in each age group form the age structure of that population. There are three age groups in any population that determine the reproductive status of the population (Cole 1954). These are as follow: (a) Pre-reproductive; (b) Reproductive; (c) Post-reproductive.

**Age Pyramids:** Graphical representation of different age groups in a population. Age pyramids are the best way to describe the age structure of any population. There are three types of pyramids described as follows (Fig. 3) (<http://www.environmentalpollution.in/population/population-features-of-population-explained-with-diagram/>

226). (A) **Pyramid with broad base:** population size increase (Natality is more than mortality); (B) **Bell-shaped pyramid:** population size constant (Natality and mortality approximate similar); (C) **Urn-shaped pyramid:** Population size decrease (Natality is lower than mortality).

**Life History**

The life history of any population includes some features: (a) The total number of reproductive events in the life span; (b) The total number of offspring produced during one reproductive event; (c) Parental care; (d) Generation time: It is a time period between the birth of an individual and production of its own offspring.

## Types of Life History

There are two types of the life history of population (Young 2010).

### Semelparous Type

The characteristic features of semelparous type are: (a) They have only one reproductive event in their complete life span. (b) They produce many offspring during one reproductive event. (c) Parental care is absent. (d) Generation time is very short. For example: small insect.

### Iteroparous Type

The characteristics features of iteroparous type are: (a) They have many reproductive events in their complete life span. (b) They produce very few offspring during one reproductive event. (c) Parental care is extensive. (d) Generation time is large. For example: perennial plants and human.

### Survivorship Curves

These are the plots which explain the numbers of survivors in a population at different age groups, i.e., pre-reproductive, reproductive, and post-reproductive. Three types of curves (Fig. 4) (Pearl 1944; Deevey 1947). (a) Highly concave/Type I: It represents low mortality rate until near

end. Examples: human and perennial plants. (b) Diagonal curve/Type II: Intermediate condition between type I and type II. Examples: rabbit and hydra. (c) Highly convex/Type III: It represents high mortality rate in early young life. Examples: small insects and oyster.

## Biotic Potential and Environmental Resistance

**Biotic potential:** This is the maximum rate at which the populations of a given species can increase when there are no existences of limiting factors. **Environmental resistance:** This is sum total of all environment limiting factors that act together to limit the biotic potential of a population from being attained (Odum 1971).

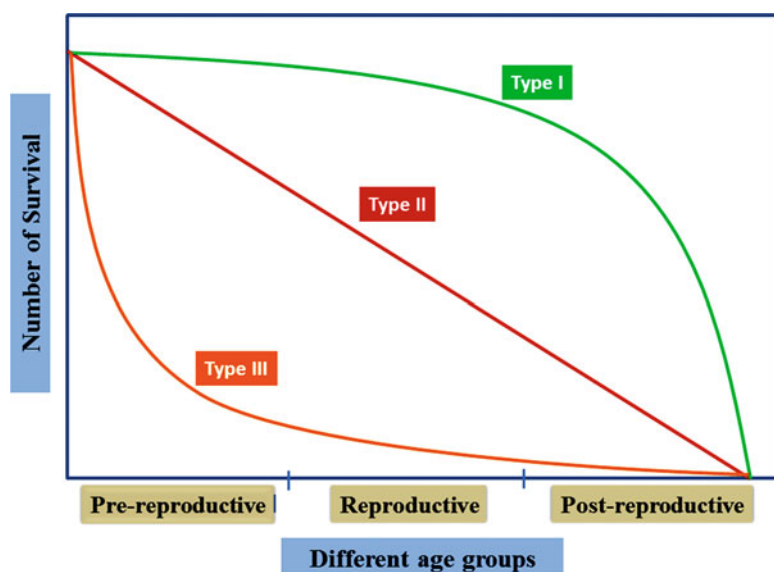
**Note:** Together, biotic potential and environmental resistance decide the carrying capacity (K) of any population.

### Carrying Capacity (K)

It is maximum numbers of individuals of a population which may accommodate by the environment. It fluctuates with environments. Carrying capacity (K) can be different for two different

### Population,

**Fig. 4** Graphical representation of survivorship curves in a population at different age groups



populations of the same species in two different areas because of availability of resources such as food, water, and space.

## Population Dynamics/Population Growth Models

Every population has a characteristic pattern of its growth, i.e., growth form of the population. Such growth forms characterize the interaction of biotic potential and environmental resistance.

There are two types of growth models shown by a population (Snider and Brimlow 2013).

### Exponential Growth Model

It explains the growth of population in ideal condition (no growth limitation and no competition) (Fig. 5a).

The formula of growth model:  $\frac{\Delta N}{\Delta t} = r_{\max} N$

Here,  $N$  = population size;  $t$  = time;  $r$  = growth rate (species-specific)

$\frac{\Delta N}{\Delta t}$  = change in the size of a population

### Logistic Growth Model

It explains the growth of population in real condition (extreme environment and resource limitation) (Fig. 5b).

The formula of growth model:  $\frac{\Delta N}{\Delta t} = rN\left(\frac{K-N}{K}\right)$

Here,  $N$  = population size;  $t$  = time;  $r$  = growth rate (species-specific)

$\frac{\Delta N}{\Delta t}$  = change in the size of a population

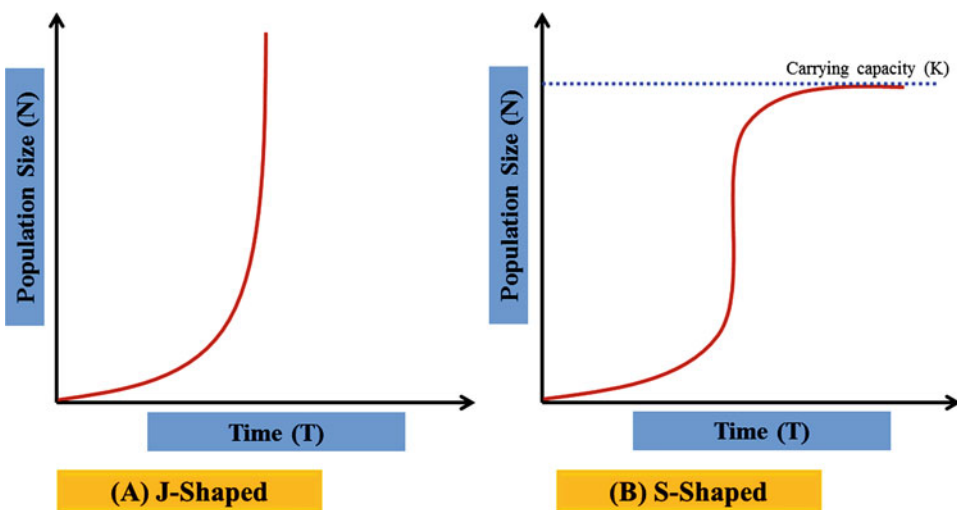
$K$  = carrying capacity

## Population Ecology and Evolution: (r/K Selection Theory)

The two evolutionary “strategies” are termed r-selection, for those species that generate many “cheap” offspring and live in unsteady environments and K-selection for those species that generate few “expensive” offspring and live in steady environments (Table 1). The terminology of r/K-selection was given by the ecologists Robert MacArthur and E. O. Wilson in 1970 (Pianka 1970).

## Population Interactions

In an ecosystem, each species of the different population are connected to each other directly or indirectly. These interactions may be beneficial



**Population, Fig. 5** Population growth models: (a) Exponential growth model; (b) Logistic growth model

**Population, Table 1** Comparative study of r- and K-selection

| r- selection                                                                            | K- selection                                                          |
|-----------------------------------------------------------------------------------------|-----------------------------------------------------------------------|
| Small body size of organism                                                             | Large body size of organism                                           |
| They have only one reproductive event in complete life span                             | They have many reproductive event in complete life span               |
| They produce many offspring during one reproductive event                               | They produce few offspring                                            |
| They allocate most of the energy resources in their in their single reproductive events | They allocate most of the energy resources in their vegetative growth |
| Parental care absent (early maturity)                                                   | Parental care extensive (late maturity)                               |
| Generation time very small                                                              | Generation time is large                                              |
| Show type III survivorship pattern                                                      | Show type I or III survivorship pattern                               |
| Show semelparity                                                                        | Show iteroparity                                                      |
| They show density-independent growth                                                    | They show density-dependent growth                                    |
| Mortality is mainly due to extrinsic factors                                            | Mortality is due to mainly intraspecific or interspecific competition |
| Generally, occupy at seral stages in community succession                               | Generally, occupy at climax stages in community succession            |

**Population, Table 2** Various types of interactions present in the different species of the population

| Name of Interaction | Species A | Species B |
|---------------------|-----------|-----------|
| Mutualism           | +         | +         |
| Commensalism        | +         | 0         |
| Predation           | +         | —         |
| Parasitism          | +         | —         |
| Amensalism          | —         | 0         |
| Competition         | —         | —         |

**Note:** ‘+’ sign for beneficial; ‘—’ sign for harmful (detrimental); ‘0’ sign for neutral

or harmful (National Council of Educational Research and Training 2018). Table 2 shows the various types of interactions present between species of the population.

**Sociobiology/Social Behavior**

Two or more than two individuals of population perform a work together. These are: (a) Agnostic behavior: Agonistic behavior is any Sociobiology related to fighting. The term has a broader meaning than aggressive behavior because it includes threats, retreats, displays, conciliation, and placation. The term was given by Scott and Frederickson in 1951 (Edward 2001). It is performed by an individual of the same species or different species when they compete for common resources. (b) Courtship behavior: It is also called mating behavior. Courtship behavior is the social behavior by which different species are selecting their partners for reproduction. (c) Altruistic behavior: It is a type of social behavior in which the individual who perform altruistic act save the life of other individuals of the population at the risk of its own life (Graham 2008).

**Cross-References**

- Food
- Life History

**References**

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## Position

### ► Ordinality

## Positional Candidate Gene approach

### ► Candidate Gene

## Positive Reinforcement

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## Synonyms

[Instrumental learning](#); [Learning](#); [Operant conditioning](#); [Reinforcement](#)

## Definition

Positive reinforcement is an operant procedure in which the addition of a stimulus increases an aspect of a particular behavior. “A positive reinforcer is

everything that increases the frequency, intensity or duration of a certain behavior when presented either simultaneously or immediately after that behavior takes place.” (Abrantes 2013, p. 12).

## Introduction

Positive reinforcement it is a widely accepted and used term especially in animal training, because of the pleasant connotations it creates. Skinner’s behavioral model analysis shows more efficiency of using several reinforcement models in behavior modification of humans and nohumans species (Skinner, 1966, 1969, 1986).

‘Positive’ does not describe the nature of the consequence; it indicates the addition of a stimulus. ‘Reinforcement’ indicates a strengthening of an aspect of the behavior.

In operant conditioning, reinforcers (and punishers) must have the right quality and intensity to work. Abrantes (2013) mentions their ‘window of opportunity.’ Reinforcers depend on some state of deprivation. For example, food may work as a reinforcer if the individual is hungry and water if it is thirsty. Therefore, the quality of the reinforcer is essential for it to function as envisaged. The intensity of the reinforcer is also fundamental. Too low an intensity does not affect the behavior, and a too high one creates another behavior.

## Positive Reinforcement Versus Rewards

Positive reinforcement is sometimes called rewarding or reward learning. Skinner has rejected this term: “The strengthening effect is missed when reinforcers are called rewards, [...] people are rewarded, but behavior is reinforced” (1986, p. 569).

Although we find the term “reward learning” in the learning, biology and neuroscience literature, the events labeled as rewards often fail to increase or strengthen the following behavior. A stimulus may reinforce a particular behavior in one specific situation but not in another (Sy et al. 2010); “[...] a reinforcer can by definition do nothing but increase an aspect of a behavior (Abrantes 2013, p. 20).



## Positive Reinforcement Versus Negative Reinforcement

Negative reinforcement strengthens a behavior by the removal of a stimulus or a decrease in its intensity.

Both positive and negative reinforcement increase the frequency, intensity or duration of a behavior. The difference is that while positive reinforcement adds, negative reinforcement removes something.

Identifying consequences that strengthen behaviors is a useful strategy for behavior modification but is not always easy to identify whether it is a positive or a negative reinforcer that is working in a particular situation. Iwata (1987, 2006) gives the example of a person in a cold room who turns up the heat. Is the reinforcer an increase (positive reinforcer) or a decrease (negative reinforcer) in the temperature?

## Practical Applications of Positive Reinforcement

Behavior modification depends on several conditions. Both reinforcers and punishers ('inhibitors' according to Abrantes, 2–13, p. 16) are always subject to the individual, the behavior and the occasion.

Some learning procedures to change or strengthen behaviors, e.g., shaping, chaining and differential reinforcement apply positive reinforcers.

Behavioral therapies apply these techniques to both human and non-human behavior, and to behavior management in various environments and situations.

## Reinforcement and Motivation

Mcfarland (2006), defines motivation as “[...] A reversible aspect of the animal's state that plays a causal role in behaviour. Changes in behaviour in an unchanging environment may be due to irreversible processes such as learning, maturation, or injury, or reversible motivational processes. [...] An animal's motivational state changes continually as a result of both external

and internal changes. [...] The dominant motivational tendency is the one that controls the ongoing behaviour. The dominant tendency inhibits the tendencies for other aspects of behaviour.”

Hull (1952) believes that humans and non-humans act because of motivational states called drives, caused by a period of deprivation (such as food). His drive-reduction theory attributes the effectiveness of a reinforcer to the reduction of the drive. It works mainly with primary reinforcers because they alter a physiological state of the individual.

Other motivation theories appear to confirm the efficiency of working with motivational processes though under the constraint of conditions and correct application.

## Cross-References

- [Behaviorism](#)
- [Learning](#)
- [Reinforcement](#)

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## Positive Selection

### ► Directional Selection

## Possessiveness

### ► Jealousy

## Postconflict Affiliation

### ► Reconciliation

## Post-conflict Affiliation

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## Synonyms

Consolation; Reconciliation; Third-party  
affiliation

## Definition

Affiliative behaviors between previous opponents, or between either aggressor or victim and a third-party individual, after an agonistic interaction.

## Introduction

We have all experienced it: two of your colleagues are having an argument over the order of authorship on an impactful new paper, and now your group is in shambles. They fight and scramble to

the detriment of all group members. However, not long thereafter one of the two reaches out to the other; their friendship is restored, perhaps even with an embrace or a handshake, and normalcy, as well as productivity, returns to the group. This form of relationship-mending behavior is not exclusive to humans – not even to primates – but can be found in many species of animals. In fact, conflicts within social groups are common, as individuals benefit from protecting or accessing resources that are threatened or held by others. An individual might behave aggressively over access to food, mates, or social status, as this can benefit fitness. However, aggression also leads to elevated levels of anxiety and distress in both the aggressor and victim (Kutsukake and Castles 2004) and can cause injury. If further aggression is not diminished, it risks destabilizing group dynamics (Katsu et al. 2018). Conflict reduces cooperation and the overall benefit of group living (Aureli et al. 2002; de Waal and Yoshihara 1983). To prevent loss of relationship benefits, several behavioral mechanisms have evolved that mend damage sustained from conflicts (Aureli and de Waal 2000). One such mechanism is post-conflict affiliation. Post-conflict affiliation refers to affiliative behaviors between two previous opponents (reconciliation; Arnold et al. 2010) or between either victims or aggressors and a third party (third-party affiliation; Romero et al. 2011). Post-conflict affiliative behaviors follow at least two criteria: (i) they are exhibited more after an agonistic interaction than when no conflict has happened, and (ii) they have a positive effect on the relationship between previous opponents and/or reduce anxiety levels. Additionally they often involve close proximity and bodily contact (de Waal and van Roosmalen 1979).

Post-conflict affiliation was first observed in chimpanzees (*Pan troglodytes*; de Waal and van Roosmalen 1979) and has since been found in many other primate species (see Aureli et al. 2002 for a review). Similar mechanisms have also been described in, for example, spotted hyenas (*Crocuta crocuta*), domestic goats (*Capra hircus*), wolves (*Canis lupus*), and bottlenose dolphins (*Tursiops truncatus*), as well as in birds such as the common raven (*Corvus*

*corax*) and budgerigars (*Melopsittacus undulatus*) (Cordoni and Palagi 2008; Fraser and Bugnyar 2010, 2011; Lazzaroni et al. 2017; Schino 1998; Wahaj et al. 2002; Weaver 2003; Yamamoto et al. 2020). Interspecific post-conflict reconciliation has also been reported to occur between cleaner fish and their hosts (*Labroides dimidiatus*; Bshary and Würth 2001).

This entry aims to provide a general description of both reconciliation and third-party affiliation, along with a short description of what conditions might lead to the evolution of such behaviors. Additionally, we describe the form and function of post-conflict affiliation in a broad range of species. Later, the methods used in this field, as well variations in analysis, are discussed.

## Reconciliation and Third-Party Affiliation

As social groups often consist of more individuals than the opponents engaged in a conflict, third parties might also get involved. As such, post-conflict affiliation can be divided into two main categories depending on the participation of third parties: reconciliation (also called post-conflict reunions, or post-conflict opponent affiliation) and third-party affiliation (also called consolation). The functions of these two categories can vary slightly depending on situation and species.

*Reconciliation* takes place between individuals that share valuable relationships, as the benefit from repairing such relationships outweighs the risks that come with renewed aggression upon approach (Aureli et al. 2002). Post-conflict reconciliations mend damaged relationships (Fraser and Bugnyar 2011), reduce stress (Aureli et al. 2002), and reduce the chances of more aggression between former opponents (Fraser and Bugnyar 2011; Lazzaroni et al. 2017). Aureli et al. (2002) described a set of conditions for when post-conflict reconciliation would evolve in a species: (i) individual recognition in relationships, (ii) within-group aggression, and (iii) post-conflict hostility between opponents.

Additionally, for post-conflict reconciliation to be advantageous, there must be a loss of fitness due to the now tarnished relationship between opponents. In other words, post-conflict reconciliation is often seen in species where prosocial relationships between individuals are important for survival. In line with this, reconciliation seems to occur with higher frequency the more valuable a relationship is (Fraser and Bugnyar 2011).

*Third-party affiliation* may provide benefits to third parties and opponents alike. Initiation of third-party affiliations by a loser to a bystander might function to protect a loser from further aggression. Conversely, initiation by a bystander to either of the opponents might function as appeasement of a winning opponent, or as protection of a losing opponent affiliated with the bystander (Koski and Sterck 2009; Yamamoto et al. 2015). Sometimes, post-conflict third-party affiliation works as a substitute to reconciliations when these fail between opponents, providing some comfort and stress reduction (Katsu et al. 2018; Romero et al. 2011; Yamamoto et al. 2020).

## Form and Function of Post-conflict Affiliation

As post-conflict affiliation is a widespread phenomenon among different highly social species in the animal kingdom, the behaviors associated may vary between them. Despite that, the behaviors observed often have more similarities than differences, generally involving physical contact and grooming, as will be elaborated upon in this section.

Post-conflict affiliation and its potential function were first described in chimpanzees by de Waal and van Roosmalen (1979). They noted several affiliative behaviors including kissing, embracing, grooming, and holding out the hand toward the former opponent. Now it is clear that post-conflict affiliations are common in all great apes (Cordoni et al. 2006; de Waal and van Roosmalen 1979; Kopp and Liebal 2018) and also present in other primates, such as macaques

(*Macaca mulatta* and *M. sylvanus*), baboons (*Papio hamadryas* and *P. cynocephalus ursinus*), mandrills (*Mandrillus sphinx*), common marmosets (*Callithrix jacchus jacchus*), and black and white guerezas (*Colobus guereza*) (Bjornsdotter et al. 2000; Cheney and Seyfarth 1997; de Waal and Yoshihara 1983; Patzelt et al. 2010; Robertson et al. 2005; Schino and Marini 2012). Affiliative behaviors are similar between primate species and include behaviors such as kissing, grooming, embracing, genital massage, grasping and clasping, grumbling, grunting, and touching (Arnold et al. 2010).

Spotted hyenas also express post-conflict reconciliation. Here, victims of aggression show a higher tendency to reconcile than aggressors, and kin reconcile more often than non-kin. Hyenas, however, do not reconcile as frequently as primates (Wahaj et al. 2002). Affiliative behaviors take the form of non-aggressive approaches after conflicts and ritualized greetings in which two hyenas stand parallel, facing opposite directions, and sniff or lick each other's penis (or pseudo-penis) under a lifted leg (East et al. 1993; Wahaj et al. 2002).

In domestic goats, post-conflict reconciliation is expressed through muzzle-muzzle and muzzle-body contact as well as allogrooming and standing in close proximity. Both aggressors and victims initiate reconciliation, but aggressors tend to do it more. The frequency of behaviors associated with stress and anxiety dropped in victims after reconciliation (Schino 1998).

In wolves, reconciliation appears initiated between aggressors and victims, as well as between sex and hierarchical status. Additionally, the intensity of a conflict does not affect tendency to reconcile (Cordoni and Palagi 2008). However, other findings suggest that victims tend to initiate post-conflict affiliations and that they exhibit more stress-related behaviors than aggressors after a conflict (Lazzaroni et al. 2017). When expressing post-conflict affiliation, wolves allogroom, play, body rub, sniff, or stand with their bodies in contact. Additionally, they might touch the face of another individual with

their nose or lick another's muzzle when exhibiting affiliation (Cordoni and Palagi 2008; Lazzaroni et al. 2017).

Domestic dogs (*Canis familiaris*) show post-conflict affiliation both in terms of reconciliation and third-party affiliations, and familiar individuals reconcile more often than unfamiliar ones. Third-party affiliations are primarily initiated by third parties and not by victims of aggression. Affiliative behaviors include greeting, sitting and lying in close proximity, anogenital sniffing, playing, and licking (Cools et al. 2008).

Post-conflict affiliation, including both reconciliation and third-party affiliation, has been observed in captive bottlenose dolphins. Reconciliations in dolphins have been suggested to decrease renewed aggression between former opponents (Weaver 2003; Yamamoto et al. 2015); however, some results do not support this (Yamamoto et al. 2020). Third-party affiliation seems to serve the purpose of protecting the loser and appeasing opponents affiliated to the third party (Yamamoto et al. 2015). Bystanders are more likely to console the individual they are most affiliated with, presumably to relieve tension or reduce stress (Yamamoto et al. 2020). Affiliative behaviors include contact swimming with pectoral fin touches, flipper rubbing involving touching with a pectoral fin and subsequently rubbing it across the body of another, and synchronous breathing in which individuals swim together and surface for air at the same time (Yamamoto et al. 2020, 2015).

Few non-mammalian species have been studied for post-conflict affiliation, but good evidence exists for birds, especially corvids. A recent study found reconciliation and third-party affiliation in juvenile carrion crows (*Corvus corone corone*), with aggressors affiliating with victims when aggressions were mild and victims affiliating with third parties when aggressions were severe (Sima et al. 2018).

Common ravens reconcile after aggressive conflicts and do so by contact sitting, allopreening or body or beak touching. Reconciliations occur more often when opponents share valuable

relationships, and renewed aggressions are less likely after reconciliation (Fraser and Bugnyar 2011). Furthermore, ravens console other individuals involved in conflicts if they share a valuable relationship and might thus reduce stress and anxiety (Fraser and Bugnyar 2010).

Rooks (*C. frugilegus*) also appear to be selective with whom they choose to console after a conflict and primarily console their monogamous social partners. The initiation in these third-party affiliations is mutual. No reconciliation has been observed between conflicting opponents, likely because aggression was only seen between individuals that do not share valuable relationships (Seed et al. 2007). When present, post-conflict third-party affiliation has been found to reduce the risk of renewed aggression compared to individuals that did not affiliate with third parties after conflicts (Logan et al. 2013b). However, post-conflict affiliation is not universally found in rooks (Benkada et al. 2020), which might be due to different methods being used.

Post-conflict third-party affiliation is found in jackdaws (*C. monedula*) and jays (*Garrulus glandarius*) but does not reduce the risk of renewed aggression (Logan et al. 2013a), suggesting a different function of post-conflict third-party affiliation in these species (Logan et al. 2013a, b).

Regarding parrots, another very social group of birds, very little research exists. One study on budgerigars (*Melopsittacus undulatus*) identified both reconciliation and third-party affiliation, with males engaging in both types more often than females. Third-party affiliations are mainly initiated by winners and bystanding males toward defeated females (Ikkatai et al. 2016).

Lastly, one example in fish exists. Bshary and Würth (2001) found support for interspecific post-conflict affiliative behaviors between cleaner fish and their various clients. Cleaner fish would utilize tactile stimulation in the forms of touching the dorsal fins of clients with their pectoral and pelvic fins. This behavior was used more often on more dangerous clients in addition to occurring more often when a conflict, in the shape of the cleaner

fish taking a bite off a client, had taken place. These behaviors match the criteria needed to be classified as reconciliation, even with the conflict in question being interspecific and different from other examples (de Waal and van Roosmalen 1979).

## Methods for Studying Post-conflict Affiliation

A problem encountered by anyone studying post-conflict affiliation is the issue of comparing a situation in which a conflict takes place with a situation in which a conflict does not take place, as only one of these two scenarios can happen at a given time between the same two individuals. This problem is what the post-conflict-matched-control (PC-MC) paradigm aims to solve. de Waal and van Roosmalen (1979) first used an early version of this method without the MC constituent on chimpanzees, in which the social interactions of opponents were recorded after a conflict only. This was then later expanded by de Waal and Yoshihara (1983) who added a control observation after a given PC observation on the next possible day, at the corresponding time of day, and for the same duration. Having both PC and MC observations allows for comparisons in frequencies and latencies of behavioral interactions between periods after conflicts and periods with none, while controlling for any differences resulting from circadian or seasonal rhythms. The PC-MC method has become standard in post-conflict affiliation research (Arnold et al. 2010), with some variation in how data has been analyzed. A relatively simple way of comparing PC to MC is by comparing the ratio of “attracted” to “dispersed” observations. PC observations with affiliative behaviors between former opponents occurring earlier or later than PC are labelled as attracted or dispersed, respectively, while no difference would be labelled as neutral (Benkada et al. 2020; de Waal and Yoshihara 1983; Kutsukake and Castles 2004). A significantly higher ratio of attracted to dispersed observations



would then indicate a higher tendency to reconcile after a conflict. It is important to be aware that how PC and MC observations are compared can significantly influence the output of an analysis. For example, Logan et al. (2013a) tested three methods of analyzing post-conflict affiliation: latency, frequency, and duration of affiliation in rooks (*Corvus frugilegus*), jackdaws (*C. monedula*), and Eurasian jays (*Garrulus glandarius*). They found no evidence of reconciliation in rooks and jays but did find some evidence in jackdaws when analyzing affiliation duration. Both rooks and jackdaws showed third-party affiliations for affiliation frequencies and duration, but not latency, while jays only did so for duration. Indeed, a later study did not find any post-conflict affiliation in rooks and found no reconciliation between opponents and no third-party affiliations either. These two studies used different measurements (Benkada et al. 2020). As such, one might benefit from analyzing several measurements, or attempt other experimental setups, to achieve more nuanced results. For example, in species that are vocal in their post-conflict behaviors, playback experiments can provide a way to test the effect of vocalizations in a controlled setting. Playback vocalizations related to post-conflict affiliation can be played for individuals after conflicts, and the frequency of reconciliation thereafter can then be compared to controls. Additionally, differences in reconciliatory tendencies in relation to vocalizations may be compared between aggressors, victims and third parties and their respective controls (Cheney and Seyfarth 1997).

## Conclusions

Since its discovery in the late 1970s, it is now generally accepted that post-conflict affiliation is a widespread phenomenon among highly social species in the animal kingdom. Reconciliation is thought to function as stress relief and repair mechanism for valuable social relationships, while third-party affiliations might function as

victim protection, appeasement of winners, or a replacement of non-initiated reconciliations. Different functions are not mutually exclusive and might differ between species, nuances which deserve further attention. Future studies should explore new methods as well as new ways of analysis of PC-MC data to further elucidate the subtle differences in affiliative behaviors between social species with different life histories.

## Cross-References

- [Affiliative Behaviors](#)
- [Affiliative Bond](#)
- [Aggression](#)
- [Agonistic Behavior](#)
- [Post-conflict Resolution](#)
- [Reconciliation](#)

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## Post-conflict Resolution

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### Definition

Aureli and de Waal (2000) defined conflict resolution as the actions necessary to either reduce or eliminate incompatibilities present in goals held by differing parties. The literature mentions at least three mechanisms of conflict resolution, including reconciliation, compromise, and sharing (Aureli and de Waal 2000). Reconciliation entails an amicable post-conflict encounter between conflicting individuals that reestablishes their social relationship's stability (Aureli and de Waal 2000). Alternatively, a compromise is reached when the factions involved agree to align, to some degree, their relatively incompatible goals. Lastly, sharing describes the tolerant distribution of a coveted resource among competing factions.

### Introduction

The study of conflict in social primate species is inevitably followed by the study of its consequences. Post-conflict resolution takes many forms, each of which involves behaviors that achieve strategic objectives surrounding the maintenance and strengthening of cooperative bonds throughout a social group. The necessary degree of cooperation depends on which individuals and groups are involved in the conflict and can impact the extent to which reconciliatory acts are attempted. This entry focuses on the general

principles and mechanisms of post-conflict resolution found across many nonhuman primate species and does not instead discuss unique species-specific behaviors. In doing so, the main focus of this entry is on the unique trade-offs associated with conflict and how they are remedied in acts of subsequent conflict resolution. This also allows for a brief overview of the societal structures that give rise to different forms of post-conflict resolution and the subsequent differences found within and between species.

Multiple literature reviews (e.g., Aureli and de Waal 2000; Cafazzo et al. 2018) suggest that reconciliation occurs in an array of nonhuman species. In nonhuman primates, for example, researchers have documented reconciliatory behaviors in Strepsirhini (*Eulemur fulvus rufus*), Platyrrhini (*Cebus apella*), and Haplorhini (e.g., *Cercocebus torquatus*, *Rhinopithecus roxellana*, *Theropithecus gelada*, *Papio anubis*, *Papio hamadryas*, *Macaca arctoides*, *Macaca fuscata*, *Macaca mulatta*, *Gorilla beringei*, *Pan paniscus*, and *Pan troglodytes*, among others). Additionally, several non-primate species have been observed reconciling after a conflict, including ravens (*Corvus corax*), rooks (*Corvus frugilegus*), goats (*Capra hircus*), bottlenose dolphins (*Tursiops* spp.), spotted hyenas (*Crocuta crocuta*), wolves (*Canis lupus*), and domestic dogs (*Canis lupus familiaris*).

### Relationship's Qualities, Reconciliation, and Consolation

De Waal (1996, 2000) developed a *Relational Model* for understanding conflict and reconciliation. Per this perspective, social partners may adopt one of three behavioral strategies in response to a conflict of interest: (1) tolerate their partner's goal, (2) adopt an aggressive stance, or (3) avoid any physical or social interaction with their peers. The model also claims that reconciliation is possible when individuals manage to align their previously conflicting interests. Furthermore, de Waal's model argued that the outcome of a conflict of

interests is moderated by the social context and the partners' attributes (i.e., social value). Consequently, when two or more individuals compete for resources, the parties involved must evaluate the value of the resource relative to the risk of suffering an injury (i.e., net benefit) and the potential harm this conflict may inflict upon their relationship. It follows then that the resource value must be greater than the more considerable imbalance of power between opponents, or the relationship value, to compensate for the potential costs accrued during the conflict. In contrast, if the opponents can reduce the damage inflicted upon the relationship once the confrontation is over (i.e., *reparability function*), then the likelihood of open conflict between the parties involved increases considerably (de Waal 1996, 2000). De Waal's model postulates that the value of the resource, the relationship's reparability, and the chances of competition all positively predict the frequency of agonistic interactions. In contrast, an individual's inclination toward aggressive exchange decreases with the probability of suffering an injury and the relationship's value.

Other authors have developed similar theoretical models (Aureli et al. 2002; Aureli and Schaffner 2006; Silk 2002). For instance, Cords and Aureli (2000) proposed that the qualitative dimension of a relationship is associated with post-conflict resolution. The authors generated a taxonomy of qualities that included (1) the social partners' value, (2) the relationship's security, and (3) the partners' compatibility. In terms of the notion of value, Cords and Aureli claimed that individuals generally benefit from maintaining social bonds with other group members (goods and services ranging from access to mates and food to social support during agonistic interactions). Consequently, the greater the risk of losing access to relevant goods or services, the greater the willingness to reestablish an affiliate interaction with the afflicted party. It is worth noting that even though subjects are significantly biased toward repairing a high-value relationship, this does not preclude them from reconciling with a less valuable partner. According to Cords and Aureli (2000), post-conflict affiliative interactions with low-value conspecifics decrease the probability of agonistic escalation wherein high-ranking allies are dragged into the conflict. For example, a

mid-value adult may reconcile with a low-value juvenile if the youngling is part of a high-ranking lineage. Such a tactic reduces the probability that the youngling's high-status kin will antagonize the mid-ranking adult in the future.

In addition to limiting the risk of a negative spillover effect, reconciliation with low-value individuals also facilitates the emergence, or consolidation, of bonds with high-value partners. For instance, it is not uncommon for unaffected parties to be drawn near a dyad in the process of reconciliation; hence, under such circumstances, an individual can indirectly benefit from repairing its relationship with a low-value partner by developing new coalitions and alliances with more valuable conspecifics. Besides a partner's value, Cords and Aureli (2000) also argued that the relationship's security influences reconciliation probability. The authors described the notion of security as an individual's confidence concerning its relationship stability over time. Hence, a subject involved in a secure relationship can predict the behavior of a social partner accurately. Security, just like value, is not necessarily symmetrical. For instance, two social partners may differ in their predictability levels. Per Cords and Aureli (2000), individuals are expected to seek reconciliation after a conflict when the relationship is less secure and of considerable value. In addition to value and security, the third and last relationship quality factor, *compatibility*, is based on the shared history of social interactions and the dyad's shared temperament. It is worth noting that partners may differ in the interpretation of their degree of compatibility based on their relationships with other individuals in the group. Thierry and collaborators (2008) collected ethological information on conflict resolution from 15 groups of nine macaque species. In addition to employing traditional statistical procedures, the authors used comparative phylogenetic methods to determine the degree of variation in counteraggression, conciliatory behaviors, and kin bias in macaques. The authors defined counteraggression as the percentage of times the recipient of aggression reacted aggressively. Alternatively, Thierry et al. (2008) operationalized the concept of conciliatory tendencies and the behavioral inclination toward establishing amicable interactions among former opponents. According

to their publication, kin bias was estimated as the proportion of conciliatory tendencies between kin relative to the total number of conciliatory events (equal to the sum of kin and nonkin conciliatory events). A series of ANOVAs identified no significant differences within groups of the same species, whereas the models did detect considerable species differences in counteraggression and conciliatory tendencies.

As part of their study, Thierry et al. (2008) assessed the trait's preservation with two phylogenetic signal metrics, Pagel's  $\lambda$  and Blomberg's  $k$ . These measures indicate whether closely related species feature similar phenotypes due to shared common ancestry (i.e., trait preservation). As expected, the analyses detected that conciliatory tendencies and acts of counteraggression were phylogenetically preserved. Using phylogenetic independent contrasts, a procedure that accounts for underlying phylogenetic effects, Thierry et al. noticed a significant and positive correlation between the species' counteraggression and conciliatory tendencies. The comparative phylogenetic model did not detect a significant relation between counteraggression and kin bias. Overall, these results suggest that frequent agonistic interactions coevolve with nonkin reconciliatory behaviors. Hence, post-conflict resolution reduces the probability of group dissolution due to within-group competition among nonrelatives.

Besides reconciliation, several researchers have claimed that post-conflict consolation also occurs across nonhuman species. De Waal and van Roosmalen (1979) were the first to define the concept of consolation as a rise in the frequency of affiliation between third parties and the target of aggression after the culmination of an agonistic interaction. Although consolation, relative to reconciliation, is less prevalent in nonhuman primates, several publications have reported its occurrence in platyrrhines (*Cebus apella*) and haplorhines (*Papio hamadryas*, *Gorilla beringei*, and *Pan troglodytes*). Given the prosocial nature of consolation, researchers faced challenges in explaining the evolution of this behavior. De Waal and Aureli (1996) generated two evolutionary hypotheses, the Social Cognition Hypothesis (SCGH) and the Social Constraints Hypothesis (SCSH). Under the

SCGH, empathy and metalizing abilities facilitate the rise of consolation among nonhuman primates. Hence, species either lacking or featuring limited empathic abilities will be less prone to consoling others after a confrontation.

In contrast, the SCSH argues that the probability of consolation depends on whether third parties may become the target of aggression if they affiliate with one of the parties involved in a previous conflict. This hypothesis also predicts that consolation will occur between parties if the potential gains are higher than the costs of performing this behavior. De Waal and Aureli (1996) also argued that the risks depended on the power imbalances between the parties involved. Societies that frequently enforce a strict dominance hierarchy and discourage affiliation with low-status individuals generally lack consolation.

## Discussion

Although social groups provide individuals with an array of benefits, from protection against predators to defense against rival groups of conspecifics, gregariousness is also associated with the inevitable competition for finite resources (e.g., including social and mating partners, food patches, and resting spaces). An increased frequency and severity of agonistic interactions pose a threat to societal cohesion. Hence, several social species feature various behavioral tactics destined to repair a social relationship once a conflict culminates, as observed in numerous clades ranging from corvids to eutherian mammals (Cetartiodactyla, carnivorans, and several nonhuman primates). The empirical evidence supports the predicted positive coevolution between counteraggression and post-conflict resolution, suggesting that highly despotic societies also exhibit the necessary social relays to restore group stability.

## Cross-References

- [Affiliative Behaviors](#)
- [Affiliative Bond](#)
- [Post-conflict Affiliation](#)
- [Reconciliation](#)



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## Postcopulatory Intersexual Selection

### ► Cryptic Mate Choice

## Postcopulatory Selection

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## Synonyms

[Cryptic female choice](#); [Sexual selection](#); [Sperm competition](#)

## Definition

Postcopulatory selection is an evolutionary process based on sperm competition and cryptic female choice.

## Sexual Selection

While **natural selection** favors genes that aid survival, **sexual selection** results in the evolution of traits that give individuals an advantage in gaining access to and mating with members of the opposite sex. The process can be intra- or intersexual and occur pre- or postcopulation.

**Intrasexual selection** acts upon members of the same sex who compete for access to the opposite sex. This typically emerges as male-male competition, because of the high reproductive potential associated with producing numerous small gametes (sperm). Consequently, females are the limiting factor for male reproduction.

**Intersexual selection** occurs when individuals of one sex prefer particular members of the opposite sex. This typically emerges as female choice, because of females' comparatively limited number of relatively large gametes (ova) and associated high investment in offspring which, in the case of mammals, includes gestation and lactation. These dynamics create different **reproductive strategies** between the sexes.

Thus, males can maximize reproductive success by mating with many females, while females can maximize reproductive success by choosing high-quality males in terms of genetic makeup

and/or their ability and willingness to invest in offspring.

## Postcopulatory Selection

Within the sexual selection framework, precopulatory selection can be understood as affecting mating opportunity, rather than fertilization – both intrasexually (access to opposite-sex mates) and intersexually (attractiveness to the opposite sex). Similarly, postcopulatory selection reflects intrasexual pressure (typically, via male-male **sperm competition**) and intersexual pressure (typically, via cryptic female choice), but affects fertilization success once mating is achieved.

Fertilization can take place within a female (as in most mammals, reptiles, and birds) or externally (as in many amphibians and fish). Copulation is a form of internal fertilization by which a male introduces sperm directly into a female's reproductive tract. In the case of vertebrates, this is either a vagina or cloaca. Postcopulatory selection is still present in species which do not copulate, such as externally fertilizing species, but happens outside of the female.

Sexual selection after fertilization, for example through abortion or infanticide, tends to reflect competing interests between parents and other individuals, and is therefore not traditionally grouped with postcopulatory selection *sensu stricto*.

## Sperm Competition

Sperm competition is the contest between the sperm of two or more males for the fertilization of a female's ova (Parker 1970). Other things being equal, mating with a greater number of females will increase a male's reproductive success. This not only results in high levels of precopulatory somatic male-male competition, via mechanisms such as weaponry, but also in postcopulatory selection via sperm competition, which influences, among other things, genital morphology and sperm quality and quantity (Birkhead and Pizzari 2002).

The lottery principle suggests that the more sperm a male deposits inside the female reproductive tract, the greater their chances of successful fertilization (Dixson 2012). For instance, male golden hamsters that ejaculate more frequently with a female father more of her offspring (though other factors such as mating order and male genotype can also have an effect). If increased numbers of sperm per ejaculate are advantageous, a corresponding increase in testes size is often found (Harcourt et al. 1981). For example, female chimpanzees tend to mate with multiple males in short succession, whereas female gorillas tend to mate with a single male. Consequently, chimpanzee testes are relatively much larger than those of gorilla males. Similarly, within different species of howler monkey, testes mass increases with group size, while the volume of the hyoid bone (that facilitates the species' typical calls) decreases – illustrating a trade-off between precopulatory (via vocalization) and postcopulatory (via sperm) competition (Dunn et al. 2015). This highlights the potential for strategic allocation of sperm in response to the level of sperm competition. Indeed, male feral fowl increase the number of sperm they allocate to a female when there are more male competitors (Davies et al. 2012).

Sperm morphology and function is likewise affected by sperm competition. For example, increased sperm motility is thought to benefit males in populations where male-male competition is high. Certain molluscs produce a large, nonfertilizing sperm morph called a spermatzeugma that, on its tail, carries hundreds of ordinary spermatozoa up the female's reproductive tract (Dixson 2012). The semen of *Drosophila melanogaster* flies contains proteins from the accessory gland that increase a female's rate of egg laying, decrease her receptivity to remating, and remove or destroy sperm of males she has previously mated with (Davies et al. 2012).

Sperm competition can also act on genital morphology, as exemplified by the complex penile morphologies found in species experiencing high degrees of postcopulatory selection (Dixson 2012). For instance, some primates have exaggerated mushroom-shaped or tapered penises and

keratinized penile spines (thought to compound plugs of coagulated ejaculate, remove the plugs of rival males, and stimulate females, respectively). The baculum (penis bone), a structure that supports the penis and facilitates sperm transport toward the cervix, has coevolved with multi-male/multi-female mating systems across the course of evolution in primates (Brindle and Opie 2016). Moreover, species with high levels of male-male competition tend to have longer bacula than species without.

Genital morphology can also help sabotage the reproductive efforts of competitors. Male ebony jewelwing damselflies have two specialized scoops at the end of their penises, which are used to remove sperm left by previous males before they deposit their own (Davies et al. 2012). Male cave bat bugs “traumatically inseminate” females by injecting sperm directly into their bodies. This sperm then swims around inside the female until it encounters her eggs. Occasionally, males mount and inseminate one another homosexually. In these instances, it is believed that the sperm may then migrate to the victim’s testes, ready to be passed on to the next female they mate with (Davies et al. 2012).

## Cryptic Female Choice

Sperm competition generates potential for females to discriminate between sperm of different males in a process known as cryptic female choice (Birkhead and Pizzari 2002). The associated mechanisms are difficult to establish, since the choice is “cryptic.” It is very subtle, often occurs within the female reproductive tract, and is frequently concealed by male-driven processes; definitive examples, therefore, are hard to come by. However, we expect such choice to be pronounced if a female has only limited pre-copulatory mate choice, such as when macaque females mate with multiple males, or when females are coerced to copulate, as frequently takes place in certain waterfowl.

Various mechanisms of cryptic female choice have been proposed. Examples include differentially rejecting or facilitating the uptake of sperm,

storing sperm before fertilization (to enable selection between males), or altering the chemical environment within the reproductive tract (to be more or less favorable to a given male’s sperm).

Cryptic female choice can be directional, by favoring the sperm of mates with preferred phenotypes, or nondirectional, by preferring the sperm of mates with compatible genotypes, irrespective of their phenotypes. However, in practice, it is difficult to disentangle which type is occurring. Directional choice may occur in feral fowl where females copulate preferentially with high ranking males, yet are sometimes coerced by subordinates (Birkhead and Pizzari 2002). If coerced, females emit a distress call, attracting a dominant male who displaces the subordinate. If calls do not work, females may eject the non-preferred ejaculate via cloacal contractions. Nondirectional choice is illustrated by the comb-jelly Beroë, an oval-shaped marine invertebrate, where numerous sperm may simultaneously penetrate an egg (Birkhead and Pizzari 2002). The egg’s nucleus then travels toward each sperm in turn, apparently assessing them individually before “choosing” which one to fuse with.

As well as enabling unsuitable males to be rejected, cryptic choice can also favor desirable mates. In humans, female orgasm is thought to boost sperm transport, retention, and activation, as well as potentially inducing male ejaculation (Puts and Dawood 2006). Corresponding physiological responses are present in other female primates (Dixson 2012), raising the possibility that female orgasm reflects cryptic choice. Indeed, in Japanese macaques, female orgasm is particularly likely when low-ranking females copulate with high-ranking males, with corresponding low frequency during copulations of high-ranking females with low-ranking males (Troisi and Carosi 1998). In primates, female masturbation before or after copulation with a preferred male may also function as cryptic choice, as the physiological changes to the reproductive tract concurrent with arousal tend to be favorable toward sperm.

Given the differential reproductive strategies of males and females, cryptic choice is likely to provoke counterselection in males, aimed to

influence the outcome of female discrimination. One example of this is antagonistic genital coevolution, a process which may explain why male genitalia diverge faster than other morphological traits (Eberhard 1993). In some waterfowl, for instance, males have elongated, spiny, anticlockwise coiled penises that they evert directly into females. Females have evolved equally morphologically complex vaginas that coil clockwise and contain “dead-end” chambers. If a female does not want to mate with a male, she can contract her muscles in such a way as to block his penis from fully everting or send it down a “dead-end” chamber. If she wants to mate with a male, she can position herself in such a way that he can fully evert his penis, so that the sperm is more likely to reach her cervix.

Thus, sex-differential reproductive strategies and the associated conflicts between the sexes influence not only precopulatory contexts, but also exert their influence after mating has occurred.

## Conclusion

Inter- and intrasexual competition does not stop once copulation begins, as evidenced by adaptations in both males and females on the level of behavior, morphology, and physiology. Sperm competition enables males to continue to compete with one another for fertilization of a female at the cellular level, while cryptic choice gives females a degree of control over which males father their offspring. The interplay between these evolutionary processes has given rise to an extraordinary array of phenotypic diversity, deserving of further investigation.

## Cross-References

- [Intersexual Selection](#)
- [Natural Selection](#)
- [Sexual Selection](#)
- [Sperm Competition](#)

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## Posthumous Fertilization

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## Definition

Act of fertilizing an egg after the death of one of the parents (usually, the male).

## Introduction

While most eggs are fertilized using the sperm of live males, fertilization after the death of the father is known in a variety of animals. This is possible in internally fertilizing species which, to different degrees, present adaptations to enhance the survival of sperm for the period of time between ejaculation and egg fertilization. This period is known to vary from mere hours in common rats *Rattus norvegicus* to more than 10 years in some species of ants (Orr and Brennan 2015). Large periods of sperm survival are possible in many species because females sometimes present natural mechanisms of sperm storage that allow them to fertilize their eggs long after mating with a male and, thus, allow for the possibility that a male can conceive offspring well after death. Posthumous fertilization using stored sperm is commonly observed under laboratory conditions. For example, laboratory-reared fruit flies *Drosophila melanogaster* can store sperm for up to 2 weeks, approximately a third of their lifespan. Many aquarium female poeciliid fish, such as mollies and guppies, can reproduce monthly for up to a year after removing males from the tank; and captive painted turtles *Chrysemys picta* can store sperm for up to 3 years.

In some cases, such as humans and domestic species, technology allows for posthumous fertilization of species without natural mechanisms. This has been thanks to the development of artificial methods of sperm extraction, preservation, and insemination. Posthumous reproduction in humans brings about moral, ethical, and legal implications that remain subject to debate and controversy. In this piece, we focus on describing posthumous fertilization in wild animals.

## Posthumous Fertilization in Natural Populations

Despite the numerous examples in captivity and the ubiquity of sperm storage mechanisms across the animal kingdom, its cryptic nature can make it hard to study in the wild. Therefore, little is known about the importance of sperm storage and posthumous fertilization in natural

populations. Because many species show a clear bias toward the success of younger sperm, it is often assumed that posthumous fertilization is not very common in nature. A handful of examples, however, point out that it may be more important than previously believed.

The most extreme known case of posthumous fertilization through female sperm storage occurs in leaf-cutting ants. Colony-founding queens of the ant *Atta colombica* mate with several males (also known as drones in social insects) during a single flight mating period to obtain their lifetime supply of sperm (Fig. 1). Males die soon after the mating and their sperm is stored in specialized female organs called spermatheca. This sperm will sire all the sexual offspring produced by the queen in that colony, which can be over a period of 10 years or more (Baer et al. 2006). In this example, all males compete simultaneously for matings while alive and then fertilize females after death.

Other examples show a more dynamic interaction between the fertilization success of live and dead males. Such is the case of the Trinidadian guppy *Poecilia reticulata*, a small freshwater fish inhabiting neotropical montane streams (Fig. 1). Female guppies have small receptacles in the ovarian cavity that can store and nourish sperm. A recent demographic analysis of female guppies in the wild shows that this allows males to reproduce for up to a year after their death, and that up to 25% of births are conceived by dead males (López-Sepulcre et al. 2013). In side-blotched lizards *Uta stansburiana* (Fig. 1), this competition for fertilization between live and dead males is associated with alternative mating strategies. Lizards in this species have three different male morphs: orange-, blue-, and yellow-throated. While orange- and blue-throated males specialize in courting and guarding females, yellow-throated males specialize in sneak copulations and invest in postcopulatory sperm competition, thus showing higher levels of posthumous fertilization success (Zamudio and Sinervo 2000).

## Mechanisms of Sperm Storage

There is a large diversity of sperm-storage adaptations, varying in complexity, across the animal





**Posthumous Fertilization, Fig. 1** Three examples of species where the dynamics of posthumous fertilization has been studied in the wild. From top to bottom: the leaf-cutter ant *Atta colombica* (Photo: Christian R Linder), the Trinidadian guppy *Poecilia reticulata* (Photo: Amy Deacon), and the side-blotched lizard *Uta stansburiana* (Photo: Judy Gallagher). All photos were downloaded from Wikimedia Commons and are reproduced under a Creative Common License

world. In most cases, sperm storage is accomplished by the use of a spermatheca: the specialized sperm storage organ in the female reproductive tract present in many taxa including worms, insects, and amphibians. In the absence of specifically derived storage organs, some organisms store sperm in modified tubules or other parts of the female anatomy, initially only used for

other functions of reproduction. Examples of this include the small ovarian pockets in guppies, or the modified epithelial cells, oviduct, or ovarian folds in certain marsupials and skinks. In some cases, these can be combined with nutritious secretions that prolong sperm survival beyond male death. Such is the case of the albumin-secreting glands used in certain species of turtles (Orr and Brennan 2015).

Not all sperm storage adaptations involve morphological changes in the female reproductive anatomy. Females of some species have evolved modified immune systems, which enable them to locally suppress any outside invaders or infection to their body, while at the same time tolerating the presence of invading sperm for long periods of time (Holt and Fazeli 2016). In some organisms, such as ants, however, this immune suppression can also lead to a cost in overall immune function (Baer et al. 2006).

Males can also evolve certain modifications to prolong sperm survival in the female reproductive tract. This includes the presence of antimicrobial agents in their ejaculate, or the production of sperm that reduce their movement during storage, but which can restore activity quickly once the female is ready for egg fertilization (Orr and Brennan 2015).

The above examples highlight an interesting fact: in many cases, the evolution for greater sperm storage capacity in females is coupled with the evolution of sperm modifications in males. For example, in many species of *Drosophila* or diopsid stalk-eyed flies, this coevolution between males and females has led to the evolution of increased sperm length being tightly correlated with the evolution of increased size of the female reproductive tract (especially spermatheca size), or the use of directed female muscular contractions to move the sperm more efficiently into sperm storage locations (Presgraves et al. 1999).

## Evolutionary Causes and Consequences

The evolution of posthumous fertilization needs to be understood as the product of two selective processes: (1) selection on males for sperm longevity, and (2) selection on females for the

development of mechanisms such as sperm-storage organs and sperm nourishment.

The advantages for males of posthumous reproduction through sperm storage are obvious. Sperm storage prolongs the reproductive life while avoiding the maintenance costs of survival (metabolism, antipredatory behavior, etc.). This can be particularly important in seasonal environments where surviving from one reproductive season to the next can be highly costly. In other words, if sperm can survive in the reproductive tract of females, and females have a higher resilience to environmental changes, it may be advantageous to invest in posthumous reproduction rather than adult survival. However, storing sperm incurs costs to females ranging from the allocation of resources to sperm storage (both in terms of the development of structures and the nourishment of sperm), or the previously mentioned potential immune costs due to the need to avoid the recognition of sperm as a foreign entity to eliminate. This means that the evolution of female sperm storage through natural selection requires that the advantages outweigh the costs. Unfortunately, there is little research in this area.

One proposed advantage is that sperm storage allows females to ensure a sperm supply when the access of males is unpredictable. Moreover, this strategy allows for the accumulation of genetically diverse sperm, thus increasing the probability of adapted offspring in a variety of environments, especially the more unpredictable ones. Posthumous fertilization also has important evolutionary and ecological consequences. As the importance of sperm storage increases, so does the strength of postcopulatory selection (i.e., competition among sperm) and the potential for cryptic female choice (Devigili et al. 2016). Moreover, posthumous reproduction may help maintain high effective population sizes despite high male mortality.

## Conclusion

Sperm storage is ubiquitous in species with internal fertilization, allowing for males to reproduce beyond death. While much is known about this potential in captive populations, the study of

posthumous fertilization and reproduction in the wild is difficult, and its evolutionary origins and consequences are poorly understood. Recent developments of genetic and statistical techniques, however, have provided us with examples demonstrating that it can be an important process in the dynamics of animal populations.

## Cross-References

- [Postcopulatory Selection](#)
- [Sperm Competition](#)

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## Postimplantation Delay

- [Developmental Arrest](#)

## Post-transcriptional Modification

### ► Gene Expression

## Posttranslational Modification

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## Introduction

The human genome consists of around 25,000 genes, and the proteins synthesized from these genes are in million. This protein diversity can be explained by the process of PTM, which are not gene-template based (Walsh et al. 2005). The nascent proteins or polypeptides formed as a result of translation from mRNA are biologically inactive. To achieve its biological active form, these proteins undergo certain covalent and enzymatic modifications in the final stage of protein synthesis. These modifications are termed as Post Translational Modifications (PTM). PTM includes folding of newly formed polypeptide chain to its proper three-dimensional conformation, removing of one or more amino acids, addition of certain chemical groups to some individual amino acid residues, and proteolytic cleavage and/or attachment of prosthetic groups to its amino or carboxyl terminals.

## Protein Folding

After translation, newly formed polypeptides with primary structure undergo conformational changes to attain its biological active tertiary/

quarternary structure with the help of Chaperons. Improper folding leads to nonfunctional protein which tends to accumulate in various protein misfolding diseases.

## Biological Functions of PTM

Post translational modifications of proteins can regulate the protein functions, by causing changes in protein activity, their cellular locations, and protein-protein interactions. It also plays a major role in xenobiotics.

These modifications include many mechanisms like glycosylation, prenylation, phosphorylation, acetylation, methylation, SUMOylation, amidation, myristoylation, farnesylation, cysteine oxidation, and ubiquitinylation. Most of these processes are reversible and modulate the protein function significantly. Few types of modifications are explained below.

- A) **Glycosylation:** It plays a major role in many cellular functions, e.g., signal transduction, immune response, cell-cell interaction, and hormone actions. Carbohydrate side chains of glycoproteins are attached covalently to polypeptides. N-linked glycosylation, O-linked glycosylation, C-linked mannosylation, and glypiation are four major type of glycosylation. N-linked and O-linked glycosylation are most common. In some glycoproteins, the carbohydrate side chain is enzymatically attached to Asn residue (N-linked oligosaccharides). O-linked monosaccharide modification of N-acetylglucosamine on Serine, Threonine, or amino acid residue in close proximity to tyrosine phosphorylation sites is frequently observed in many cells.
- B) **Isoprenyl group addition:** A thioether bond forms between isoprenyl group (groups derived from isoprene) and a Cys residue of the protein. Isoprenyl group helps protein to anchor in the membrane, e.g., Ras proteins, trimeric G proteins, and lamins.
- C) **Phosphorylation:** Certain Ser, Thr, and Tyr residues are enzymatically phosphorylated by ATP at their hydroxyl group. This

reversible phosphorylation plays a crucial role in signal transduction pathways (Hunter 2000; Olsen et al. 2010; Chiarugi and Cirri 2003; van Montfort et al. 2003).

- D) **Hydroxylation:** Hydroxyproline and Hydroxylysine in collagen are formed due to hydroxylation of Proline and Lysine, respectively.
- E) **Carboxylation:** Glu residue of some proteins, e.g., blood clotting protein Prothrombin, contains carboxyl groups added enzymatically during PTM.
- F) **Addition of prosthetic group:** Prosthetic Group is a nonprotein organic molecule which is bound covalently to protein for their proper functioning, e.g., biotin molecule of acetyl-CoA carboxylase and heme group of hemoglobin or cytochrome C.
- G) **Proteolytic cleavage:** Many proteins are initially synthesized in their Pre-pro-form, which is larger and inactive precursor protein (zymogens). These undergo cleavage to form smaller and active proteins. Examples of such proteins include Insulin, trypsinogen, and chymotrypsinogen.
- H) **Disulfide bond formation:** Some proteins form disulfide bonds between interchain or intrachain Cys residues. It is common among proteins to be exported from the cells.
- I) **Ubiquitinylation:** Attachment of ubiquitin to certain lysine residues in target proteins marks them for degradation (Wilkinson 1987).

## Techniques to Study PTM

Difference in charges, molecular weight, half-life, and many other physical and chemical properties occur during PTM. These PTMs have been extensively studied and characterized through systemic analysis by mass spectrometer and new analytical techniques (Cantin and Yates 2004).

## Perspectives

PTM plays a major role in various cellular functions. To understand more specifically

about the interface between PTM and its biological functions, significance of altered PTM in disease pathogenesis may be beneficial in developing innovative treatment options.

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## Potto

- [Prosimian Cognition](#)
- [Prosimian Life History](#)

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## Pouched Mammal Locomotion

- [Marsupial Locomotion](#)

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## Pragmatics

### ► Cognition

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## Precedence Effect

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## Synonyms

Law of the first wave front

## Introduction

The precedence effect encompasses several phenomena that influence sound perception and localization when multiple sound sources arrive at the listener in close succession (Brown et al. 2015; Litovsky et al. 1999). For a range of delays between a leading (i.e., first arriving) and lagging (i.e., later arriving) stimulus that arrive from different directions, receivers tend to perceive only a single sound source, a phenomenon known as fusion. When leading and lagging sounds are presented simultaneously or at extremely short delays, a single fused sound is perceived, but the sound's location is perceived to be somewhere in between the actual location of the two sound sources, a phenomenon known as summing localization. At longer delays, receivers tend to perceive this fused sound as originating from the location of the leading sound source, a phenomenon known as localization dominance. Finally, as the delay between leading and lagging sounds increases beyond what is termed the echo threshold, receivers perceive both the leading and lagging sounds as separate images. Leading sounds can not only affect sound localization but also the ability of receivers to discriminate characteristics

of the lagging sound, a phenomenon known as lag discrimination suppression.

## Functional Significance of the Precedence Effect

The precedence effect in humans is generally thought to be a directional hearing mechanism that allows for the perception and localization of sounds in reverberant environments (Wallach et al. 1949). Fusion and localization dominance may reduce the influence of echoes arriving somewhat later and from different directions than sound originating from the source. Psychophysical studies of the various phenomena comprising the precedence effect in humans have shown that the specific time delays at which each phenomenon takes place vary with factors including stimulus duration, frequency, and interstimulus angle, whether stimuli are presented in the azimuthal or median sagittal plane, subject age, previous experience, and hearing capabilities (Litovsky et al. 1999).

The precedence effect also appears to be widespread in animal hearing, although its ecological relevance is less clear. In certain environments, reverberations may be as problematic for animals as they are for humans in buildings. However, in many other cases, reverberation is probably a less serious problem for sound localization than the presence of noise from both abiotic sources such as wind and flowing water and that produced by other signaling animals, as well as general sound attenuation and degradation through the environment. Nevertheless, there is conclusive evidence for one or more of the phenomena associated with the precedence effect in such disparate taxa as crickets, flies, frogs, birds, and mammals (Lee et al. 2009). Furthermore, in many cases, the time delays at which localization dominance and echo thresholds occur are similar in human and nonhuman animals. Precedence effects may be a general adaptation for auditory scene analysis and directional hearing in noisy and complex acoustic environments, which is a fundamental problem in animal communication.



## Methods for Studying the Precedence Effect

In humans, the precedence effect is most often studied by presenting subjects with acoustic stimuli using either headphones or loudspeakers that vary in their relative timing or another relevant characteristic, and having the subjects report on various aspects of their perception of the stimuli (e.g., for fusion and localization dominance, whether one or two stimuli were perceived and where the stimulus was perceived to have originated, respectively). In nonhuman animals, the subject's perception cannot be reported verbally, and most studies rely on either conditioning protocols or on responses that are an important component of the species' natural behavioral repertoire (e.g., phonotaxis toward mate attraction signals, predator-avoidance responses, and orientation toward prey sounds). Animal studies are also used in neurophysiological investigations of the precedence effect. Indeed, correlates of the precedence effect have been found in most areas of the ascending auditory system, although certain precedence effect phenomena may only arise in more central processing centers. The inferior colliculus has been proposed to be a particularly important brain region for the generation of the precedence effect in mammals (Tollin et al. 2004), but the precedence effect is much more taxonomically widespread and may involve different neural mechanisms in other taxa, particularly insects.

## The Precedence Effect and Preferences for Leading Signals in Mate Choice

In behavioral ecology studies, the term "precedence effect" is also used in a somewhat looser manner to refer to the observation that in mate choice, choosing individuals are often attracted to the first arriving of two mate attraction signals (Greenfield 2005). These leader preferences are behaviorally analogous to some aspects of the psychophysical precedence effect because they result in the animal orienting toward the leading of two signals, often with no apparent influence from the lagging signal. However, in only a few

cases has it been demonstrated that the precedence effect (*sensu stricto*, as defined in the Introduction) is the mechanistic basis for such leader preferences (Marshall and Gerhardt 2010). Leader preferences could also arise because leading signals suffer from less masking. Furthermore, even if both signals are equally well-perceived as separate signals, a leader preference could be expressed if leading signalers are of higher quality and are therefore preferred as mates. The delays over which leading signals are preferred to lagging signals in mate choice are often much longer than echo thresholds measured with psychophysical protocols in the laboratory, although these two measurements are rarely carried out on the same species. It is therefore unclear if the precedence effect can account for leader preferences, although neither can it be ruled out because most psychophysical studies use simplified click stimuli, whereas most mate selection involves much more complex signals; echo thresholds depend strongly on stimulus characteristics.

In any event, it has been argued that precedence effects may be a general adaptation to localize an individual signaler among many competing signals, and this is a common situation faced by animals choosing mates. Comparative studies could reveal if the time course of various precedence effect phenomena varies across species and if this relates to the challenges associated with mate localization. Furthermore, regardless of the mechanistic basis, leader preferences appear to be an important mechanism behind the striking temporal patterning observed in many signaling assemblages. Such assemblages are often characterized by highly precise synchrony or alternation of signals and leader preferences, perhaps caused by the precedence effect, selected for competitive signal timing strategies that generate temporally structured choruses as epiphenomena (Greenfield 2005).

## Precedence Effects and Perception in Complex Natural Environments

The precedence effect is just one of many mechanisms facilitating the localization and

discrimination of signals in complex environments, and recent studies suggest that these mechanisms likely interact. Most of these studies have been carried out in humans, but the same phenomena are likely to be found in non-human animals facing similar ecological challenges. First, the precedence effect has recently been demonstrated in humans to be affected by visual input. Cross-modal integration of visual and acoustic stimuli can alter the localization of leading and lagging acoustic signals depending on which of these stimuli is in spatial proximity to the visual stimulus (Bishop et al. 2011). This phenomenon has only been tested in one non-human animal, the gray tree frog *Hyla versicolor*, which experiences the precedence effect but for which there was no evidence of cross-modal integration of visual and acoustic stimuli (Reichert et al. 2016). Interestingly, orientation toward leading signals has also been demonstrated in the visual modality alone: female fiddler crabs evaluate males' claw waving displays and prefer males whose waves lead those of other nearby individuals (Reaney et al. 2008). Many animals evaluate multimodal signaling displays containing both visual and acoustic information, and it would therefore not be surprising if both modalities contributed to localization, potentially via the precedence effect. Second, the precedence effect in humans is strongly affected by recent experience, and the strength of the precedence effect in the perception of any given stimulus can be built up by previous experience with the same stimulus (Litovsky et al. 1999). This buildup, however, can be broken down if the spatial characteristics of the stimuli are suddenly altered. Both effects are likely to be important for animals evaluating signals composed of repetitions of single signal elements. Third, the precedence effect is strongly affected by other characteristics of signals besides their relative timing. Some of these other characteristics, in particular signal duration and frequency, as well as spatial separation, are likely to vary between populations and species, which may result in corresponding variation in the parameters and general importance of the precedence effect.

## Conclusion

The precedence effect is widespread in animals and is an important mechanism for sound localization in complex environments. In humans, this is particularly important in indoor, reverberant environments. In nonhuman animals, echo suppression may also be an important function of the precedence effect, although the adaptive significance of precedence effects and their relative importance in various auditory perception and processing tasks is poorly understood in most species. One potentially important function of the precedence effect is to facilitate localization of a signaler in the midst of multiple other individuals signaling in close temporal proximity. The precedence effect may therefore play an important role in sexual selection resulting in receiver preferences for leading signals, although in only a few cases has it been confirmed that the precedence effect is indeed the mechanism responsible for these preferences.

## Cross-References

► [Auditory Processing and Perception](#)

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## Precision Grip

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## Synonyms

Cattarrhine morphology; Opposable thumb;  
Prosimian morphology

## Definition

A type of grip formally defined as involving the tips of the thumb and finger(s) and used by some primates for precise handling of objects of different size and shape.

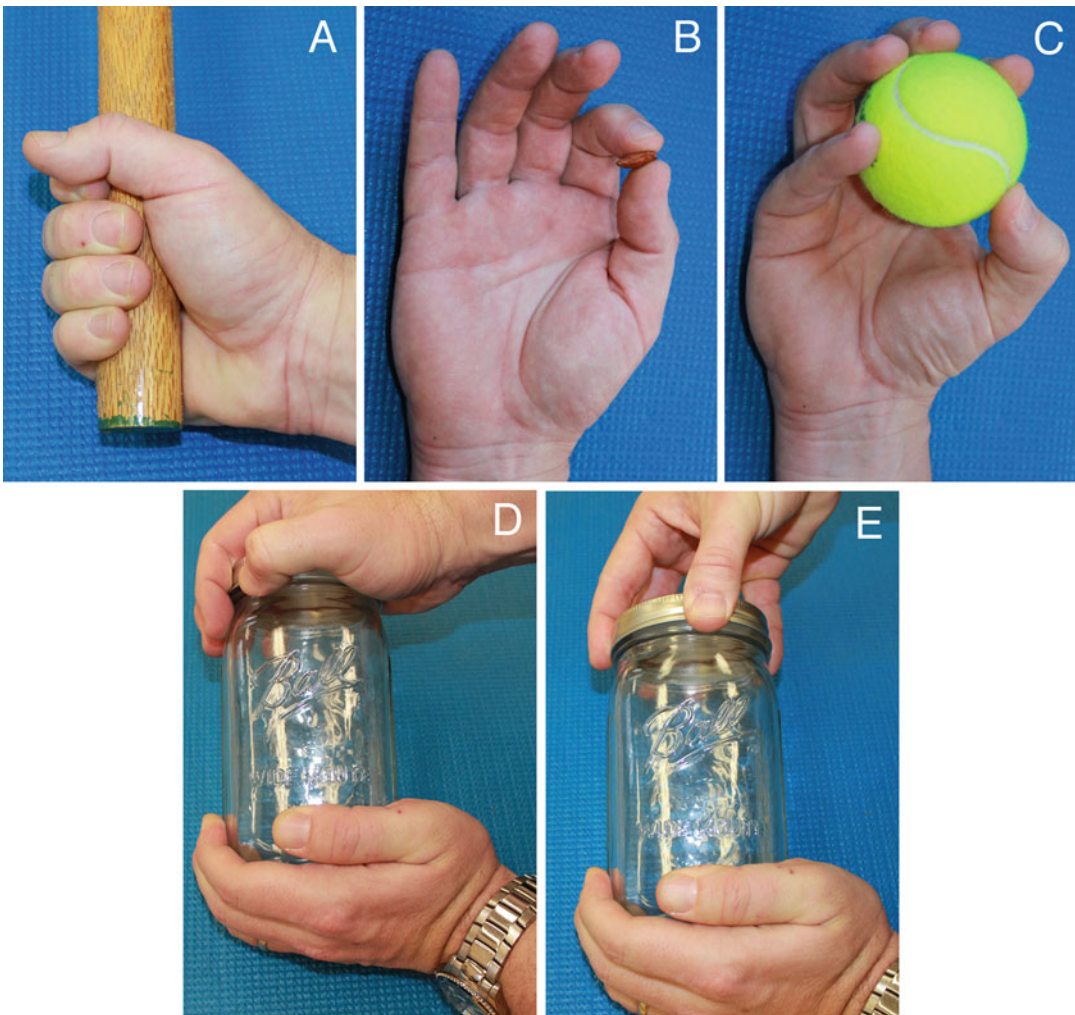
## Anatomical, Mechanical, and Behavioral Definitions of Precision Grip

Hands capable of grasping have been central to our evolutionary success and define the order Primates. More than almost any other mammal, primates engage the world with their hands. Primates explore their environment with their hands.

Gripping branches during movement, collecting food, handling small objects and in some cases tools, and interacting socially with peers are all behaviors that involve the hands. With dexterous hands capable of prehensility and opposability (see ► [“Opposable Thumb”](#) entry), we humans can achieve daily tasks allowing us to make a living, build buildings, and manufacture objects ranging from tools and clothing to fine pieces of art. One feature that makes the hands of at least some, but not all, primates remarkably useful is the ability to manipulate small objects between the tips of the digits, a behavior often referred to as a precision grip. However, the exact definition of a precision grip is elusive, therefore our ability to identify which primates can or cannot use such a grip remains limited. In this entry, we provide a strict definition of a precision grip (while also acknowledging the range of definitions used by others), allowing for what we hope is a clearer, less ambiguous, and more unifying description.

Early descriptions of hand dexterity and grips used by primates were provided by Darwin in 1872 in the *Descent of Man* and then later by prominent anatomists, particularly John Napier whose descriptions and definitions of hand grips are still in use today (see Lemelin and Schmitt (2016) for a review). Napier (1956, 1960) first formally described the range of dexterity, gripping abilities, and behavioral flexibility of the human hand, then turned his attention to those same abilities in nonhuman primates. His observations, particularly in humans, led to the establishment of definitions for two major types of grips: the *power grip* associated with the handling of large objects with the whole hand; gripping the handle of a hammer is a classic example (Fig. 1a), and the *precision grip* associated with the handling of small objects between the fleshy pads or pulp of the digits, especially of the first and second digits (thumb and index finger) (Fig. 1b).

The dichotomy between power and precision grips involves fundamental differences in forces applied to manipulate an object with one hand. According to Napier (1960: 648), “The precision grip is employed where delicacy and precision of movement are required; the application of muscular power being a secondary consideration. In



**Precision Grip, Fig. 1** Examples of power and a precision grips achieved by the human hand: (a) a power grip on a wooden dowel (note that the whole hand, including the palm, is engaged with the object); (b) a precision grip in which a small object is gripped between the fleshy pads of the thumb and index finger; (c) a precision grip on a tennis ball (note the fleshy pads of the fingers facing that of the

thumb, and the palm does not contact the ball); (d) a power grip while opening a jar lid (note that the palm is in contact with the lid); (e) a precision grip used once the lid is loosened and the lid can be easily unscrewed (note the fleshy pads of the fingers facing that of the thumb, and the palm does not contact the lid)

contrast, the dominant characteristic of the power grip is the application of force; with delicacy and precision being of secondary importance.” Landsmeer (1962) picked up on this mechanical definition by classifying power and precision grips by the presence or absence of a “static” phase. While a power grip has a static phase (essentially holding the object tightly on the palm with motion of the whole hand and little

motion of the fingers), a precision grip lacks one (only movement of the fingertips associated with manipulation are involved).

The contrast between “delicacy and power” or “statics and movement” is at the heart of the definitions of precision and power grips. But to observe and classify grips effectively, it is also necessary to define grips by the underlying anatomy and the motions of the digits and at joints of



the hand, especially once an object is grasped. Therefore, Napier (1956: 903) says that the human precision grip is achieved when an “object may be pinched between the flexor aspects of the fingers and the opposing thumb” and the power grip when an “object may be held in a clamp formed by the partly flexed fingers and the palm, counter pressure by the thumb lying more or less in the plane of the palm” (Fig. 1a). Typically, a precision grip is most often illustrated as someone holding a small object between the fleshy pad or pulp at the tips of the thumb and index finger (Fig. 1b). However, as the object gets larger and the distance between thumb and index finger gets wider, the two grips look much more similar to each another, as when we hold a ball (Fig. 1c). This grip is often confused with a power grip but does not involve the palm.

The ways power and precision grips can be used as part of a single task can be illustrated by opening a jar with a lid. As pointed by Napier (1956), the palm is often first pressed against the lid using a power grip hand posture (Fig. 1d). As the lid becomes looser, a precision grip involving the tips of all fingers and the opposed thumb can be used to rotate and remove the lid (Fig. 1e).

Expressed in this way, the precision grip and the ability to rotate the thumb to face the index finger are linked since when holding a small object or rotating a lid, the pulp of the thumb and index finger must face each other. Therefore, it can be argued that only those primates that have a thumb capable of opposability (see ► [“Opposable Thumb”](#) entry for the distinction between an opposable thumb and opposability) should be able to achieve a true precision grip. But is this the case? To answer this, one must examine the abilities of nonhuman primates to achieve precision grips.

Numerous studies have described grip patterns in strepsirrhines (a primate group that includes lemurs, galagos, and lorises), tarsiers (small nocturnal primates from South East Asia), platyrrhines (monkeys from Central and South America), Old World monkeys (monkeys from Africa and Asia), and apes (see Fragarzy and Crast (2016) for a thorough review). Bishop (1964) conducted one of the most exhaustive

studies of strepsirrhine hand use and found little evidence of anything that could be called a proper precision grip. When a lemur grabs a food object, it gathers it up with the palmar surface of the digits, then presses it onto the palm (or sometimes smashes it with the palm first and then gathers it with the digits). Occasionally, galagos use a grip like the one we use on a jar lid, with the thumb opposed to the fingers, to grasp a grape. Bishop acknowledged that “One may apply Napier’s terminology and say these ‘precision grips’ differ from ‘power grips’ of locomotion” (Bishop 1964: 205). However, it is more accurate to say that very few of these grips truly qualify as precision grips, a point Bishop (1964) elaborated on.

There remains considerable debate about whether monkeys and apes can produce precision grips (see Pouydebat et al. 2009 and Marzke and Pouydebat 2009). However, following a strict definition of precision grip, monkeys and non-human apes do not produce true precision grips but rather produce what might be called “precise grips.” Pouydebat et al. (2009) argued that macaques and baboons achieve what might effectively be called precision grips because they can bring the pulp of the thumb and that of the index finger together. This is accomplished in part by virtue of their short index finger relative to the thumb. But to bring those digits together, they must rotate the thumb and generate acute flexion of the thumb and index finger in order to achieve pulp-to-pulp contact (Macfarlane and Graziano 2009). Capuchin monkeys (medium-sized platyrrhines with prehensile tails) also have thumb and index finger lengths that allow for pulp-to-pulp contact but like Old World Monkeys must flex their index finger and thumb to achieve this contact (Spinozzi et al. 2007; Macfarlane and Graziano 2009; Pouydebat et al. 2009). This kind of a grip for handling small objects seen in some New and Old World monkeys is required because their thumbs are incapable of true opposability comparable to that of humans (see ► [“Opposable Thumb”](#) entry). Chimpanzees and other non-human apes use similar contortions to achieve pad-to-pad contact and mostly handle objects between the thumb and the side of the index finger



(Christel 1993 and Frigaszy and Crast 2016 provide an excellent review). Napier (1960) showed that chimpanzees could occasionally handle a small object between the pulp of the thumb and index finger but could not produce a true precision grips because of the relative shortness of their thumbs. Gibbons are similarly incapable of producing precision grips because of their very long index finger relative to the thumb. Most often, gibbons grasp small objects between the pulp of the thumb and the side of the index finger (Christel 1993).

Clearly, only humans and a few monkeys are capable of pulp-to-pulp contact between the thumb and index finger, and they achieve this in different ways. Other primates do handle objects between portions of the thumb and index finger without pulp-to-pulp contact. This raises the question of what to call such grips. Pouydebat et al. (2009), Spinozzi et al. (2007), and Macfarlane and Graziano (2009) examined apes and other primates and classified many grips they observed as precision grips. These include grips that involved the thumb and multiple fingers, grips between the thumb and side of the index finger, and grips between the edges of any adjacent digits. These thumb to lateral edge grips (pad-to-side grips of Macfarlane and Graziano 2009) and “scissor grips” (between fingers grip of Macfarlane and Graziano 2009) may count as “precise” in a mechanical sense, because they allow an animal to hold a small object with delicacy and limited muscle force, thus meeting one of Napier’s (1960) definitions. They are clearly important and effective, but they do not meet a strict definition of precision grip.

## Conclusion

The precision grip, which has its ultimate form in humans, allows the handling of small objects between the pulp (fleshy pad) of the digits. In its strictest sense, a precision grip involves the pulp of the thumb and index finger and is linked with the presence of a thumb capable of true opposability. In that context, this is a type of grip used habitually and effectively only by humans. But a

precision grip may also be achieved in primates with relatively long thumbs or short index fingers (or a combination of both) that are both capable of acute flexion to bring the fleshy pads or pulp together. Broadening further, a “precise” grip can be achieved when an animal holds an object by the tips of its fingers, pinching a small object between the tip of the thumb and side of the index finger, or between two adjacent fingers (scissor grip). Although here we advocate a strict anatomical- and movement-based definition like that first articulated by John Napier (1956, 1960), we acknowledge that the term precision grip has been treated as malleable and readers must examine any work critically to be clear on what definition the authors are using.

## Cross-References

- ▶ [Adaptation](#)
- ▶ [Feeding](#)
- ▶ [Grooming](#)
- ▶ [Mechanoreceptors](#)
- ▶ [Muscular System](#)
- ▶ [Neural Control of Behavior](#)
- ▶ [Nonhuman Primates](#)
- ▶ [Opposable Thumb](#)

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## Precocial

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## Synonyms

Nidifugous

## The Precocial/Altricial Spectrum

At the moment of hatching or birth, animal species differ in their degree of development. While precocial species are able to move in the environment and feed autonomously at the onset of life, altricial species depend on parental care for feeding and cannot navigate the environment. Precocial animals are born with the eyes open and have down, altricial animals are born with eyes closed and little or no down.

Precocial species whose neonates leave the nest soon after hatching are called nidifugous, while species that remain in the nest for much of their development are referred to as nidicolous. Notions based on nest attendance partially dissociate with that of precocial and altricial, for some motor developed birds remain in the nest even if capable of locomotion, when the location of the nest prevents exploration.

Based on maturation of the neonates and behavior, the precocial-altricial spectrum ranges along a continuum that has been particularly well explored in birds (Starck and Ricklefs 1998). Chicks of megapodes (a family of Galliforms) are known as superprecocial, because they are fully independent from their parents and, in some cases, are able to fly from the first day of life. Most galliforms (e.g., chickens, mallards, quails, and pheasants) are precocial and can feed and move independently, leaving the nest 2–3 days after hatching. In these species, though, chicks follow their parents, and parental care is important for thermoregulation and for directing appropriate behavioral responses. Semiprecocial birds, such as the young of many seabirds (e.g., gulls, alcids, and terns), are born with relatively less developed locomotor activity and depend on their parents for feeding. After few days after hatching, chicks leave the nest to hide but return to be fed by their parents. Among mammals, precocial species are found for instance among ungulates (e.g., antelopes, sheep, horses, cows, deer), guinea pigs, and hare. In some of these species, neonates are able to follow the mother few hours after birth (Rosenblatt 2010). Species whose neonates remain in the nest for much or all of their development, such as passerines and psittacines (parrots), are altricial and nidicolous.

## Evolution of Developmental Modes

Precocial and altricial modes of development have important connections with different aspects of the ecology of a species. Precocial animals are typically exposed to high predation rate, such as chicks born in nests located on the ground or

young ungulates that forage in exposed locations. A strategy of altricial species to reduce predation is laying eggs in inaccessible locations. Most of the losses of precocial species are concentrated in the early growth period. This has suggested the hypothesis that the precocial mode of development has evolved as an adaptive response to high predation on relatively vulnerable juveniles (Williams 1966). In line with this idea, many precocial species show filial imprinting, a fast learning mechanism that mediates affiliative responses towards the first conspicuous objects that the neonates experience, and exhibit spontaneous, unlearned behaviors that enable them to effectively respond to the environment even in the absence of specific experience.

### Instinct and Predispositions

At the onset of life, precocious knowledge can help unexperienced individuals in making correct predictions, deciding whether to approach or avoid specific objects and in coping with novel situations (Versace and Vallortigara 2015).

In the first days of life, many precocial species exhibit filial imprinting, a fast and specialized learning mechanism that enables the neonates to learn the features of the first conspicuous, moving objects experienced after a brief exposure. In the wild, filial imprinting produces strong affiliative responses of the young towards their mother. It appears that, in the absence of previous experience, neonates “know” that they will have a *mother*, and they should respond by following her, and that they are equipped to learn the individual details of their mother from the environment. The mechanism of imprinting, made popular by the ethologist Konrad Lorenz (1937), lies hence at the interface between unlearned and learned knowledge. In the fields of ethology, animal and developmental psychology, precocial species have been used to investigate the presence of instincts/innate behavior (see Bateson 2017 for a critical approach to the notion of innate; and Burghardt 1973 for a historical review of this concept that traces back to Darwin), predispositions (Bateson 2017; Johnson and Horn 1988), and core

knowledge systems (Spelke 2000). These notions refer to behaviors and capacities that are not acquired during the ontogenetic development through learning but emerge without specific experience, as *a priori* knowledge. Interspecific differences in spontaneous behaviors provide support of nativist theories of knowledge.

One approach to investigate the presence of spontaneous capabilities is based on deprivation experiments/studies and controlled rearing studies, in which experimenters exclude or manipulate exposure to specific stimuli until the moment of test. If a species shows consistent responses to a stimulus (e.g., a preference for a face configuration vs. a control stimulus) before individuals had any experience that could have influenced their responses (e.g., before having experienced any face-like pattern), then it is possible to argue for the existence of some knowledge on how to respond to that stimulus. This approach has several practical and ethical limitation for altricial species, which have to be nurtured for extended periods before being tested, but is more suitable for precocial species. For instance, it is easy to keep newly hatched domestic chicks in darkness before testing their spontaneous visual preferences (reviewed in Di Giorgio et al. 2016; Versace and Vallortigara 2015), or exposing them to controlled imprinting stimuli to investigate their capacity of learning and memory (Bateson 1966; Bolhuis 1991). In fact, since the late nineteenth century (Andrew 1991; Bateson 2017) many studies on the existence and content of precocious knowledge have been conducted on avian precocial species, such as young domestic chickens, goslings, and ducklings, in different domains and sensory modalities. As for acoustic modality, Gottlieb (1968) showed that, in ducks, embryonic auditory experience with the own calls produces species-specific preferences for acoustic stimuli. In this species, the little experience gained by the embryo is sufficient to orient subsequent approaching responses to calls of conspecific. As for visual stimuli, a wide range of experiments has identified preferences of newly hatched chicks to approach specific colors, size, shapes, as well as configurations of static and dynamic stimuli (reviewed in Di Giorgio et al. 2016;

Versace and Vallortigara 2015), and unlearned knowledge about the properties of objects, number, and geometry has been shown (Vallortigara 2012). The advantages of precocial models is particularly clear for the study of social predispositions, given that altricial species cannot be deprived of social care. Studies on domestic chicks have identified unlearned preferences for static and dynamic stimuli associated with animate, living beings, which have been subsequently observed in altricial species too, including human beings (reviewed in Di Giorgio et al. 2016). The co-occurrence of early preferences for face-like stimuli, biological motion, and self-propelled objects initially investigated in social precocial species has suggested the presence of a core knowledge system dedicated to social responses (Di Giorgio et al. 2016).

## Conclusion

At birth, animal species can be classified along the precocial/altricial continuum, according to their developmental maturity and behavioral independence from parents. Precocial species feed and navigate the environment autonomously, altricial species are immature for locomotion and are fed by the parents. Investigation of the mode of development is important both to clarify the evolutionary pathways that have led to the ecology and adaptation of different species, and as a tool to shed light into the origins of knowledge. Ease of experimental manipulation made precocial birds elective subjects for the study of predisposed behaviors.

## Cross-References

- [Filial Imprinting](#)
- [Instinct](#)

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## Predation

- [Trap Building](#)

## Predation Risk

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## Introduction

Predation is one of the strongest evolutionary forces in the animal kingdom. The need to catch food influences the ecology, morphology, and behavior of predators and prey alike. As a consequence, predation risk has not only a stark effect on the single individual but further shapes food webs and whole ecosystems. Predator-prey interactions can be understood as an arms race: Over evolutionary time spans, predators developed a multitude of hunting strategies to catch prey, which in turn developed better and more sophisticated antipredator strategies. Such arms races are indeed the cause of many extraordinary color patterns and morphological features as well as fascinating behaviors observed in nature. In the following we will elucidate these diverse adaptations of predators and prey, followed by a short overview on the evolutionary consequences of predation risk on shaping complex social organizations of predators and prey at the same time.

## Adaptations of Predators

Predators evolved multifarious morphological and behavioral adaptations that increase their chances to successfully hunt prey. Many predators are active hunters that search for prey animals. Once spotted, these prey items might be chased until they are caught. Such active hunters are characterized by well-developed muscles which support high-speed pursuits, excellent sensory capabilities, and a huge repertoire of stealth and stalking techniques. It is therefore

not surprising that the fastest animals on land, water, and in the air are all highly specialized predators. The peregrine falcon (*Falco peregrinus*), for example, is the fastest animal alive, with a diving speed of up to 389 km/h. But predator's adaptations are not limited to increasing the attacker's speed. Nocturnal predators, such as the African wildcat (*Felis lybica*), have specialist eyesight and large pupils to see even the faintest light during darkness, while sharks are able to sense the electric field of other animals, allowing them to spot prey which is cryptic or hidden in the sand.

By contrast, ambush predators don't rely only on strength or speed; instead they hide and wait until prey is close enough before starting an attack. A common house cat sitting motionless in front of a mousehole is a prominent example of such hunting tactic. To reduce their visibility, many ambush predators, such as the cougar (*Puma concolor*) or the devil scorpionfish (*Inimicus filamentosus*), bear camouflage color patterns that allow them to stay unnoticed by prey until striking the attack. Orchid mantis (*Hymenopus coronatus*), for example, resemble orchid flowers in color. Insects that visit this apparent nectar source are attacked and killed. Ambush hunting is less energy-demanding than active searching for prey. However, the chance to meet a prey item is reduced. To increase such chances, some ambush hunters evolved morphological or behavioral features attracting prey animals, a phenomenon termed "aggressive mimicry" (Jamie 2017). For example, alligator snapping turtles possess a modified tongue, which resembles a worm. Hiding on the muddy bottom of a lake, they open their mouth and move their worm like tongue. Small fishes get attracted by this lure and swim directly into the mouth of the turtle. A further example is Livingston's cichlid fish (*Nimbochromis livingstonii*), a predator showing sophisticated adaptations in behavior and color. To attract its prey items, it feigns death and mimics a rotting fish. Other fishes that approach this potential snack are attacked and eaten. Finally, some ambush hunters like spiders or ant lions evolved sophisticated traps to catch bypassing prey.



Many predators like tigers, sharks, or birds of prey hunt alone. Such solitary hunting has the benefit that the catch does not have to be shared between several individuals. Furthermore, a single hunter is more difficult to be detected when approaching prey animals than a group of predators. However, compared to group hunting species, the success rate of solitary hunters is lower, and they often face difficulties to bring down large prey items. Such problems might be overcome if individuals gather together and hunt as a group (Davies et al. 2012). Indeed, group hunting evolved frequently throughout the animal kingdom, exemplified in packs of wolves or pods of killer whales. While many of such group hunting species did not evolve coordinated hunting strategies, others show highly coordinated behaviors. For example, lions (*Panthera leo*) form hunting coalitions that are more successful than single individual's hunting. Forming such hunting groups requires coordinated behaviors, advanced communication, and very often division of labor between group members. In such highly derived group hunting species, sharing the catch among group members is often based on social hierarchies, which are based on dominance ranks, age, or sex. Sharing the catch is usually neither fair nor equal. Thus, more dominant individuals are often more strongly benefitting from group hunting, while it might pay off for low-ranked individuals to hunt alone.

### Adaptations of Prey

While a predator that is unsuccessful in capturing a prey item usually only loses a meal, a prey animal that fails parrying an attack will lose its life. Consequently, prey animals evolved a fascinating array of morphological, physiological, cognitive, and behavioral features, lowering their predation risk and increasing survival chances. Such antipredator adaptations can be categorized broadly into strategies to (1) avoid encountering and detection, (2) escape an attack, and (3) deter predators (Godin 1999).

### Strategies to Avoid Encountering and Detection

Many prey animals avoid predators spatially or temporally. For example, in the presence of large fish predators, small fishes like guppies (*Poecilia reticulata*) might move to shallow parts of the pond or brook, as large predators are not able to follow them there. Other prey animals might switch their daily activity, hiding during the daytime and foraging during the night. Nocturnal migration to the water column by zooplankton is a fascinating example of such temporal avoidance of predators. However, if the possibilities to avoid predators in space or time are limited, alternative strategies to reduce the risk of being detected and identified as potential prey are needed. A straightforward strategy to reduce the risk of being detected is by seeking a shelter or by reducing body activity to a minimum until the risk is over. Indeed, some prey species reduce their heart rate to cease their activity and remain immobile when being approached by a predator. Detection risk might further be lowered through camouflaging and masquerading. Here, prey coloration and/or morphology resembles the environmental background of the habitat or an uninteresting object such as leaves or twigs to increase the chances of staying unnoticed by predators (Ruxton et al. 2004). Such visual features might be permanent or highly flexible and readily adjusted to the respective environment. Leaf (Phylliidae) or stick insects (Phasmatodea) are prominent examples of permanent camouflage, whereas chameleons (Chamaeleonidae) and octopuses (Octopoda) use a flexible strategy to avoid predators by readily changing skin color to match the surrounding environment. In some cases, harmless and nontoxic species mimic other species that are better able to defend themselves or are poisonous. Harmless hoverflies (Syrphidae) resembling aggressive wasp and bee species (Batesian Hymenoptera) are famous examples for such mimicry (Ruxton et al. 2004).

### Strategies to Escape an Attack

Once being detected by a predator, fleeing is the most common strategy of prey animals to avoid being eaten (Godin 1999). A successful flight by

prey animals consists of an adequate timing to initiate the flight and a high-speed flight trajectory which leads into a safe area. Further, prey species relying on escape often show special adaptations. Many predator fish species, for example, are not able to ascend quickly in the water column, as their swim bladder will burst due to fast changes in pressure. However, physostomous fishes like herring, which are a common prey for many aquatic predators, possess an open swim bladder that is connected to their gut. These fishes can reduce pressure by excreting gas bubbles. This allows them to ascend quickly and thus escape predator attacks (Blaxter 1985).

To successfully escape an attack, it is important to spot the predator as soon as possible. Here, living in a group is highly beneficial. Groups detect predators faster than single individuals do, a phenomenon termed the *many eyes effect*. By joining forces, the overall vigilance time of a group might even increase without compromising time for other behaviors such as feeding and mating (Krause and Ruxton 2002). Furthermore, group living in itself is already a very effective antipredator strategy. Group-living species such as the gigantic flocks of snow geese and the herds of migrating wildebeest in the Serengeti are protected from predators because their sheer numbers confuse and repel predators which are not able to single out lone individuals. Finally, the dilution effect postulates that living in a group simply reduces the risk of each single individual to be the target of the predator (Krause and Ruxton 2002).

### Strategies to Deter Predators

Prey can deter predators using defensive adaptations such as toxicity, spines, or defensive behaviors. Often, toxic prey species evolved signals that are associated with the unprofitability to potential predators. These bright and conspicuous warning colors have been coined “aposematism” (Ruxton et al. 2004). The tropical poison frogs (Dendrobatidae), for example, are brightly colored to advertise their toxicity to potential predators (Santos et al. 2003).

Many prey animals show aggressive defense behaviors toward the predator. These are

especially effective in group-living species which defend the group jointly (Krause and Ruxton 2002). For example, pairs of crows will join together to chase away hawks from their breeding sites, and herds of buffalos will aggressively confront lions together.

### Impact of Predation Risk on Higher Organizational Levels

Predation risk can shape whole populations either indirectly (as explained above in *Adaptions of prey*) or directly through the consumption of prey animals by predators. Direct predation has a negative effect on survival and longevity of individuals and therefore selects individuals which are able to avoid predation risk and thus pass their genes to the next generation. This has a major influence on the way how individuals within a species interact with each other, determining the social structure and mating system of whole populations. For example, predation risk mediates the evolution of highly social societies where individuals cooperate with each other to raise their young (Groenewoud et al. 2016).

Predation risk also affects behaviors and survival of individuals which have not been directly exposed to predators but “inherited” information about predators from their parents. These so-called nongenetic parental effects are widespread in the animal kingdom and enable the transmission of information about local predation risk to the next generation. For example, the common water flea (*Daphnia pulex*) develops a thick armour as a protection from predators. Interestingly, offspring from mothers that experienced predators develop thicker armour irrespective of whether they have experienced predators themselves (Agrawal et al. 1999). In mammals and birds, predation risk as experienced by mothers can alter the stress responsiveness of offspring via maternal hormones through the milk in mammals or through hormones deposited inside eggs in birds (Sheriff and Love 2013).

Ultimately, reproductive barriers between species can be removed or created depending on predation risk. The ability of prey species to

adapt to predators and to expand into habitats containing new predators greatly influences how successful species disperse and thus influences the potential for speciation to occur (Siepielski and Beaulieu 2017).

## Conclusion

The constant struggle to survive is the major evolutionary force in the animal kingdom, leading to an arms race between predators and prey. Predation risk influences individual behaviors, population dynamics, and ultimately the evolution of animal social societies. Certainly, humans are not excluded from this struggle, and human sociality has been shaped just like any other animal sociality by the need to survive and catch food (Hart and Sussman 2008). Only by understanding the evolutionary forces shaped by the struggle to survive we are able to fully appreciate the development of the rich and interesting facets of animal behaviors and animal sociality.

## Cross-References

- ▶ [Aposematism](#)
- ▶ [Cryptic Coloration](#)
- ▶ [Dominance Hierarchy](#)
- ▶ [Escape Response](#)
- ▶ [Group Living](#)
- ▶ [Müllerian Mimicry](#)
- ▶ [Vigilance](#)

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## Predator

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## Definition

An organism that captures and survives by feeding on other organisms is called as predator.

## Introduction

The predator gains energy to sustain life and encourage its reproduction on the cost of an organism being eaten, the prey. Predators sit at the top of the food chain and consume its prey perched one trophic level below, which in return

eats plants, the basis of the ecosystem (Hairston et al. 1960). Predator plays a very crucial role in framing the ecosystem structure and function. Predator-prey interactions change the community structure, arbitrate trophic cascades, and influence biodiversity and species invasions. Moreover, the prey population dynamics can be controlled by predators by affecting features such as survival, behavior, growth, size, structure, and distribution over an area. Besides animals, carnivorous/insectivore plants like the Venus fly trap and pitcher plant which feed on insects also show predation. These plant species grow in nitrogen-deficient soil. Pitcher plants seize their prey in a cavity containing liquid with digestive enzymes; in contrast, the Venus fly trap catches an insect within the leaf lobes, and the insect is sealed inside. The required nutrients are absorbed by the plants from these insects. Microorganisms like protozoa and bacteria also ingest their prey through phagocytosis. These microbes play very crucial role in balancing population size in microbial communities, which in turn stimulate the diversity of microbes and provide a stable community structure. Predators not only involve the fanged animal that consumes primary consumers but also include organism feeding on those organism which are smaller or of the similar size or even larger like grazing animals whether the grazed organisms can be plankton or mats of microbes (Bengtson 2002). Sometimes seed consumption is also considered as predation as seeds are thought as organisms. Under ideal conditions, seeds emerge to become a complete plant, although, consuming a seed terminate the plant before it can originate, making seed consumption an example of predation (Janzen 1971). Seed predators are limited mainly to mammals, birds, and insects and are present in nearly all terrestrial ecosystems (Hulme and Benkman 2002). Likewise, consumption of egg is also considered in the category of predation as it also causes the death of an entire organism before its growth (Nilsson et al. 1985). Egg predators comprise of some snakes, birds, and mammals, for example, red fox as they opportunistically eat the egg (Hanssen and Erikstad 2013). There are some nematophagous fungi that feed on nematodes which use either active traps in

the form of constricting rings or passive traps with adhesive hyphal structures (Primer 1964). There are a number of microbes like bacteria and protozoa that prey on other microorganisms and hence play very significant role in regulating population sizes in these microbial communities promoting diversity of microbes and stable community structure (Velicer and Mendes-Soares 2009; Stevens 2010a).

Adaptations which make predator highly specialized for killing the prey include sharp teeth, claws or jaws to hold the prey, and venom. Moreover, predators are adapted with highly specialized acute senses such as vision, hearing, or smell. Other adaptations include stealth and aggressive mimicry that improve hunting more efficient. Predation has a powerful selective effect on prey, and the prey develops antipredator adaptations such as warning coloration, alarm calls and other signals, camouflage, mimicry of well-defended species, defensive spines, chemicals, etc.

## Classification of Predators

Predators can be classified in two ways: (1) taxonomical classification and (2) functional classification (Begon et al. 2006). Taxonomical classification consists of carnivores consuming plant-eating herbivores. The functional classification includes four types of predators: true predators, grazers, parasites, and parasitoids. True predators more or less kill their prey right after attacking them. Some examples of true predators are most of the carnivorous animals like lion, tiger, eagles, and snake and some carnivorous plants such as pitcher plant and so are seed-eating rodents and ants, plankton-consuming aquatic animal, and so on. Grazers are organisms that partially consume their prey and are hardly lethal. It attacks large number of organism (prey) in their life span. Grazing differs from true predation in the way that the organism being grazed is not killed. The vertebrate herbivores like cattle and sheep are the most common examples of grazers. Parasites feed on parts of their prey (their host) and are rarely lethal in short span of time. Examples of parasites are tapeworm, liver flukes, many

pathogenic bacteria, fungi viruses, etc. Parasitoids are the organism that lives in association with their host bodies where they feed, grow, and ultimately kill their host.

## **Adaptations for Predation**

Predators are key driving factors in structuring ecological communities and processes. A predator's utmost important task is to find or search, chase, and kill its prey to feed. Once predator locates its prey, it must evaluate either to pursue it or to wait for a better option. If the prey organisms are large in number and are mobile, in that case, the sit-and-wait method is the most appropriate method of foraging (Bell 2012). If preys are inactive and scantily distributed, in that case, foraging requires more energy. Predators catch their prey either by pursuing potential prey or by ambushing them. Predation affects the fitness of prey and predators both. To survive and reproduce, organisms must both feed and protect themselves from being eaten. Genetically determined traits that improve an organism's ability to sustain and reproduce will be transferred to next generation. Traits related with improved predation for predators and escaping predation for prey inclined to be positively selected by natural selection. Predators exhibit a variety of adaptations like sharp teeth, claws, speed, and venom that strengthen their capability to catch food. They also own extremely vital sense organs which help them to detect potential prey. To sustain life, predators must be capable to outsmart their prey and use their acute senses, as well as evolved physical adaptations such as sharp teeth and claws, with various hunting tactics.

### **Senses**

Predators have fine sense of smell, vision, and hearing which tend to be very curious regarding their surroundings.

#### **Vision**

Predators have forward-facing eyes placed on the front of their head providing them three-dimensional binocular visions, whereas eyes of the prey are placed on the sides of their head.

Forward-facing eyes allow predator a more restricted view of the surrounding than prey and make it easier to determine distance and see each and every detail from far distance. Apart from binocular vision, predators also have big eyes which help them to pick up light signals easily and are therefore able to spot quick movements.

#### **Smell**

While predators depend greatly on their sight to locate the prey, they also possess a well evolved sense of smell. Almost all animals release some chemicals into the environment, which are by-products of metabolism. Many predators have the capability to detect these chemicals to find the animals releasing them (Conover 2007). There are some animals such as fox, wolves, and coyote that rely on their sense of smell rather than their vision. These animals possess longer snout which has chemically sensitive cells. For example, foxes are very sensitive to smell such that they can smell their prey lying even two feet under the soil or snow. Reptiles also bear acute sense of smell and can detect smells in very different manner. They stick out their tongues to sense smell in the air. A special organ, Jacobson's organ, present on top of the reptiles mouth, allows them to smell chemicals present in the air and detect food present nearby.

#### **Hearing**

Predatory animals have a very sharp sense of hearing. They have a special feature of rotating their ears forward and backward to locate the direction from where the sound is coming. The most common example is the bat, which has very sensitive hearing. They have large ears as their primary means of finding prey. Bats produce high-pitched ultrasonic sound waves which are above the upper limit of human hearing. Whenever these sound waves hit something it produces echo. These echoes are heard by bats and they can locate the object. This process of echolocation is used by bats to find their prey. Dolphins also echolocate their prey.

### **Hunting Strategies**

Predators have developed different methods of locating and killing their prey. Some of these



strategies include stalking, chasing, sit and wait, etc.

### Stalking

Predatory animals that stalk and follow their prey have very well-developed features which assure that they are able to sneak on their prey undetected. For example, soft padded and retractable paws of cats help them to walk silently. Animals stalking for their prey must have quick reflexes to ensure that their prey is caught.

### Sit and Wait

This sit-and-wait strategy requires less energy. The animal that employs this strategy to kill its prey generally has some form of camouflage. They blend in with their surroundings to avoid detection and wait for their prey. The sit-and-wait method of foraging is suitable if preys are densely populated and mobile, and predators require less energy.

### Group Hunting

Some predators hunt their prey in groups. The advantage of group hunting is that the large number of predators kills prey animals much larger than themselves. For example, this type of hunting strategy is often seen in wolf packs which have very systematic way of hunting.

### Physical Adaptation

Apart from various hunting strategies, the predatory animals have adapted different traits such as sharp teeth, jaws, claws, and venom that increase their capability to catch food.

### Teeth and Claws

Predatory animals possess long, sharp claws and teeth particularly for tearing, shearing, and cutting the prey. Predatory birds such as hawks, eagles, and falcons have special long curved claws called talons, which help these birds to grasp their prey easily.

### Jaws

Jaws of predatory animals are very strong which enables them to hold and kill the prey as well as tear them to feed themselves. The jaws move up and down which enables the predator to cut

through flesh. Snake's jaw is adapted in order to swallow whole prey.

### Special Features

Many predatory animals possess some specialized body parts that help them to catch and consume their food. Frogs bear long tongues that help them to capture insects, and long sharp beak of great blue herons helps them to catch fish. Likewise, otters have webbed feet and distinctive oils which make them waterproof and help them swim easily and catch food. These specialized characters have been adapted according to environment and feeding conditions.

### Intelligence

Predatory animals are more intelligent than the prey. Their intelligence helps them to outsmart their prey. Crows and raven are among the most intelligent birds. They can even copy various sound such as cat meows and whistles.

## Antipredator Adaptation

To avoid predation, prey animals must escape from the predators to survive. The aim of feeding is to locate and capture food without being caught by the other animal. Lots of prey animals have developed and adapted to protect themselves from predators: camouflage, senses, warning signals, different types of defensive weapons like chemical defense, behavioral adaptations like bluffing, hiding, and living in groups. In order to survive, prey animals use these kinds of adaptation against predators.

## Coevolution of Predators

Predator-prey interactions are very prevalent in nature. Predator and prey are adapted in such a way that they can counter each other. For example, bats uses echolocation system to detect their prey, and in return, insects have adapted various defenses to counter bats including the capability to hear the echolocation call. Likewise the land predators such as wolves have evolved long limbs to run after prey. These types of adaptation have

been characterized as an evolutionary arms race, an example of the coevolution of two species. When a predator pursues a potential prey, the predator is chasing its food, and the prey is running to save its life. If in any case predators fail to catch the prey, it remains starving, but as a consequence of this interaction, it will not suffer a large decline in fitness. In contrary, if the prey is captured by the predator, the seized animal loses opportunity to reproduce in the future. This “life-dinner principle” arranges an evolutionary arms race between the two species (Dawkins and Krebs 1979). In this evolutionary race, the prey undergoes strong selective pressure to evolve better to prevent predation. At the same time, for survival and reproduction, predators must capture sufficient food, and they are put through selective pressure for traits that allow them to hunt successfully. Because of this arms race, the prey has been capable to avoid capture, and predators become able to catch prey efficiently. In some of the examples explained so far, some of the prey species possess bright coloration. Such aposematic coloration helps prey animals from predation by signalling predators that the brightly colored individual is toxic (Stevens 2010a). All the vivid colorations exhibited by the species are not truly toxic. In some species patterns and colors have evolved to mimic those of toxic species. Batesian mimicry is one of such examples, which includes the exceptional polymorphic *Papilio dardonus* swallowtail butterfly in Southern Africa and Madagascar (Salvato 1997). Female of this species presents in a wide variety of physical appearances among which most of them mimic distasteful species of the *Danaus* and *Amauris* genera with which they co-occur.

## Dynamics of Predation

Population of species is not everlasting. The number of individuals in a population keeps changing from one time period to the next. Such fluctuations are regulated by the resource availability. When the resources are limited, population declined as organism competed for the limited resources. This process of bottom-up control

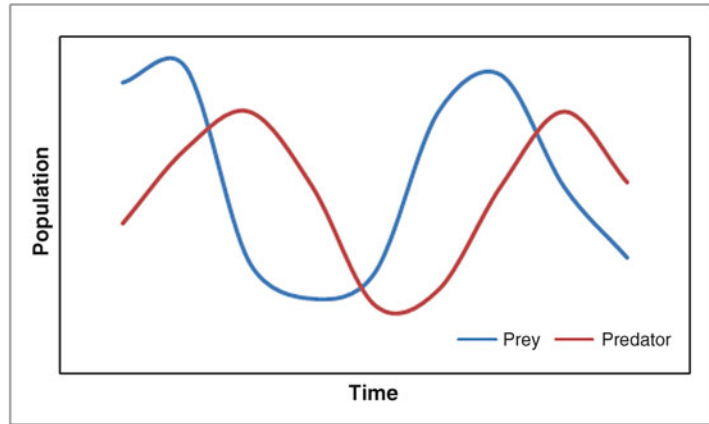
helped to regulate the population about carrying capacity. Recently, scientist has found that predator population can affect the prey population size by acting as top-down control. If predators are not present, the population of species grows exponentially till it reaches the carrying capacity of the environment (Neal and Dick 2004). Predators often control the growth of prey species both by consuming them and by changing their behavior (Nelson et al. 2004). Actually, the interaction between these two patterns of population control efforts together to operate changes in population over the time. Some other factors like parasite and disease can further influence the population dynamics.

Change in population occurs in species that encounter large cyclic swings in the population size. These cycles occur simultaneously with population cycles of other species within the same location. The availability of food resources functions as bottom-up control that affects the size of population. Whenever the food is abundant and easily available, the population size will increase, and when the preferred food is scanty, the organism turns to undesirable food to prevent starvation. As a result, these organisms grow more slowly and reproduce less, and hence, the population declines. As the population of predator organisms increase in number, they put substantial pressure on prey populations and act as top-down control, pushing them to decline. Lotka-Volterra is a simple model that provides a useful tool to help population ecologists understand and determine the factors that affects the population dynamics and to predict population cycle (Stevens 2010). They have been particularly beneficial in understanding and predicting predator-prey population cycles. Although the models greatly simplify actual conditions, it demonstrates that under certain conditions, predator and prey populations can oscillate over time (Fig. 1).

## Role of Predators in Ecosystem

Predators play a very important role in the trophic cascades. They are connecting link between nutrient cycling. They can affect the genetic makeup,

**Predator, Fig. 1** Lotka-Volterra model: Predator and prey population cycle



morphology, physiology, and behavior of prey species. They regulate and control the population of the prey.

### Role in Food Chain

Predators are at the top of the food chain and they play an important role in linking the nutrient cycles in the ecosystem. In the absence of predators, herbivores began to overgraze many plant and grass species, hence, affecting the area's plant population. In a decisive study on the effects of predators on the environment, William Ripple and Robert Beschta (2009) of Oregon State University found that the presence of large predators is important in sustaining native plant communities in both upland and riparian (stream or river) settings because plants contribute to a wide range of "ecosystem services" such as floodplain functioning, soil development, and stream bank/channel stability.

### Selective Impact on Prey

Predators are very selective in choosing the prey species. Predation on larger prey often demands substantial threat to the predator and always demands a significant investment of energy. Accordingly, the predators always select the convenient prey, sick, young, and weak.

### Biodiversity Management by Predators

Biodiversity of different communities may be increased by predators. By preventing single species from becoming dominant, predators manage the biodiversity. Such predators are

called keystone species and can have acute effect in balancing the organisms in a particular ecosystem (Bond 2012). Introducing or removing this predator by changing its population density can result in drastic cascading effects on the equilibrium of many other populations in the ecosystem. For example, in grassland ecosystem, grazers may control the single dominant species from becoming most influential (Botkin and Keller 2003).

### Conclusions

Predators are important in maintaining a healthy ecosystem. Predators are important not only because they create biodiversity but also because they indicate biodiversity. In addition to regulating natural systems as described above, predators (especially large predators) serve as a measure of the health of communities around them. Top predators are associated with high biodiversity value because they are sensitive to ecosystem dysfunctions, such as pollution and habitats.

### Cross-References

- [Adaptation](#)
- [Birds](#)
- [Carnivore \(Diet\)](#)
- [Herbivore](#)
- [Prey](#)
- [Secondary Defenses](#)

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## Predator Defense

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## Synonyms

[Antipredator strategies](#)

## Definition

A set of traits and mechanisms by which prey avoid being detected, recognized, subjugated, or ultimately consumed by their predators.

## Introduction

Most organisms are at risk from predation. For this reason, many species have evolved certain traits or strategies that confer different degrees of protection. Such traits and strategies can be physical (morphological), chemical, or behavioral and can be exhibited by both individuals and groups. As a result, predator defenses are very diverse and are widespread across the animal kingdom. However, several key strategies have evolved separately in multiple groups of animals.

In order to classify and understand these defenses, we must first understand how animals fall prey to others. The process of predation can be thought of as a sequence, beginning with the detection of the prey by a potential predator, followed by its recognition as a suitable prey item, its subjugation and, finally, its consumption (Endler 1991). Animal defenses can intercept and disrupt this sequence at any stage, and many species possess defenses that act on several stages. From the prey's perspective, defenses that interrupt the process at the earliest stages, i.e., before the subjugation stage, may be particularly

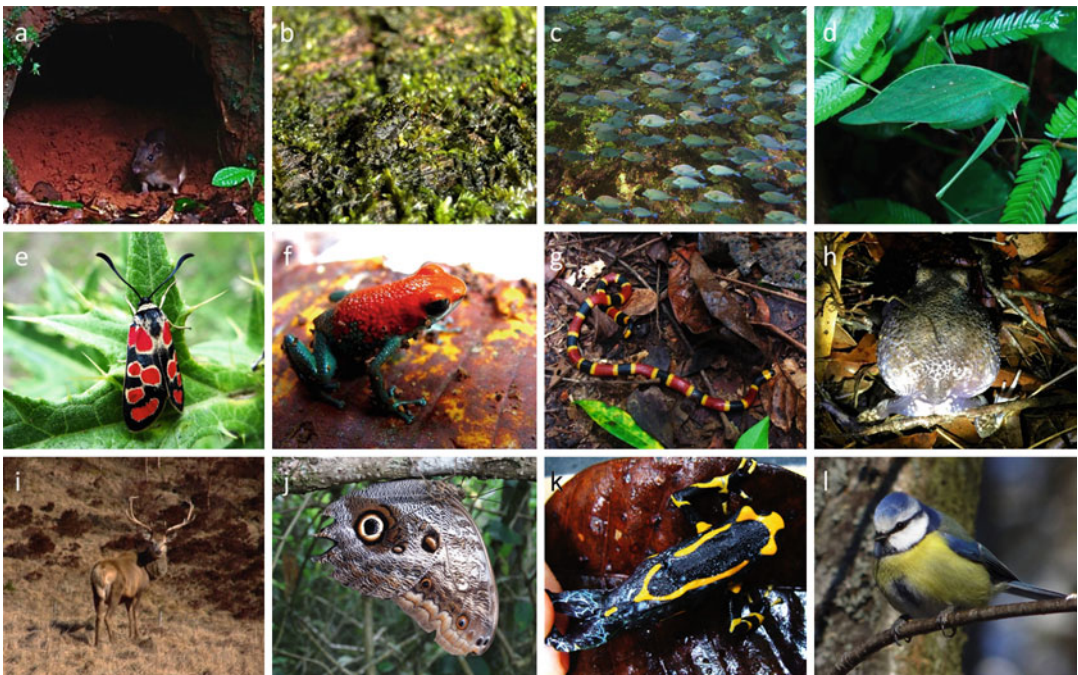


valuable as they reduce the opportunity for injury or energy loss from fighting or escaping.

### Preventing Encounter and Detection: Avoiding the Issue

The first line of animal defenses includes those that prevent encounter or detection. Encounters can be avoided by prey being in low densities, so as to reduce the per capita probability of being found by a predator. Alternatively, prey

may try to create spatiotemporal separation from predators, by either avoiding areas inhabited by potential predators or using those areas at different times than the predators. Prey can also use hiding shelters (Fig. 1a) at known locations within their home ranges and may remember and use set escape routes. One extreme example comes from the Chuckwalla (*Sauromalus obesus*), a lizard that hides in rock crevices when threatened, and then inflates itself with air so it cannot be pulled out (Deban et al. 1994).



**Predator Defense, Fig. 1 Examples of animal defenses against predators.** (a) some animals use shelters or refuges within their home range; (b) many frog species avoid detection by displaying color patterns that match those of their background; (c) fish schools are an example of how some organisms move in groups to minimize the per capita risk of predation; (d) insects such as katydids avoid recognition by resembling inanimate objects, for example, leaves; (e-g), aposematic organisms display distinct color patterns that predators learn to associate with their unprofitability; (e) Burnet moths (family Zygaenidae) sequester cyanide compounds from their food plants, but are also capable to produce them de novo; (f) the granular poison frog (*Oophaga granulifera*) uses its vivid colors to warn predators about its possession of toxic skin secretions; (g)

coral snakes (genus *Micrurus*) serve as models to some harmless colubrid snakes, which gain protection from predators by mimicking the coral snakes' color patterns; (h) body inflation helps animals appear larger than they actually are and discourage attacks from predators, or can make subjugation more difficult; (i) weapons such as deer antlers may be used for purposes other than protection from predators, for example, during male-male competition; (j) eyespots in the wings of butterflies are thought to mimic vertebrate eyes and thus can startle predators, making them hesitate to attack; (k) the defensive secretions of poison frogs contain mostly alkaloids that act as neurotoxins; (l) blue tits (*Cyanistes caeruleus*), among other species of Paridae, produce mobbing calls when predators are nearby (Photos taken by B. Rojas)



Once the prey encounters a predator, then there are behavioral and morphological mechanisms aimed to hinder detection. Rabbits can, for example, “freeze” in response to an unexpected noise. Immobility can also be employed by anuran larvae in the presence of a larger carnivore tadpole, such as an odonate naiad or a water bug. This strategy works because many predators are motion-oriented and, thus, fail to detect static, unmoving, prey. This behavior can be coupled to traits such as cryptic coloration (see below), which act in concert to make it harder for predators to detect prey. Prey can also aggregate, for example, through synchronized hatching (insects, amphibians, reptiles), or the formation of schools (fish; Fig. 1b) or flocks (birds) whereby the per capita risk of predation is very low; this phenomenon is known as the dilution effect. One famous example comes from periodical cicadas: these true bugs, from the genus *Magicicada*, have 13- or 17-year life cycles. They spend the majority of their life feeding underground as larvae, and once every 13 or 17 years emerge simultaneously as adults to mate and lay eggs. The sheer number of cicadas during this emergence means that predators quickly become satiated and cannot eat more than a small proportion of the population (Williams and Simon 1995).

Among the morphological mechanisms to thwart detection, those related to prey coloration are probably the most well known. Cryptic prey, for example, resemble the background on which they rest (Fig. 1c), or exhibit disruptive coloration, which breaks the prey’s body outline (Stevens and Merilaita 2009). This can hide an animal’s distinctive shape and make it harder to distinguish. Because in most cases predators form a search image to look for prey, research has shown that cryptic prey benefit from being polymorphic. That is, from exhibiting variable color patterns within a population to minimize per capita predation risk, as this makes more difficult for predators to create an efficient search image and stick to it. Other forms of color-mediated concealment are *transparency* and *countershading*, both of which are commonly seen in marine organisms.

Transparency is widespread in pelagic (i.e., open water) species, in particular among small, free living organisms such as Ctenophora (or comb jellies), some Cnidaria (a group which includes jellyfish, sea pens, and hydra), and the larval stages of many crustaceans (Johnsen 2001). In countershading, animals have darker coloration on the top side of their bodies and lighter coloration underneath. As light usually hits objects from above, making them appear lighter on top and darker underneath, this form of coloration can mask this effect, making the animal’s body appear less three dimensional, and therefore harder to spot. In particular, countershading has been suggested to function in marine animals such as whales, sharks, and fish, as when viewed from above the darker coloration on the dorsal (top) side of the both will blend into the darker-appearing waters below. In contrast, a lighter ventral (underneath) side will stand out less against the light filtering down through the water when viewed from below. While a great many species show this form of coloration, experimental evidence for its effectiveness against predators is limited, and it has been suggested that other factors, such as protection from harmful UV rays or thermoregulation, may also explain this pattern (Rowland 2009).

### **Preventing or Aiding Recognition: It Is Not What You Think**

Once the prey has been detected, the predator needs to recognize it as an edible item worth attacking. At this stage, animals may benefit from imitating inanimate objects in their surroundings, a phenomenon termed *masquerade*. Stick insects, for instance, get their name from their extraordinary resemblance to sticks and twigs, praying mantises and some katydids also benefit from resembling green leaves (Fig. 1d), whereas some tropical toads look a lot like fallen leaves in the leaf litter, and the larvae of some lepidopterans look like bird droppings. Masquerade is often considered to fall between mimicry and crypsis, as it is often difficult to assess if a

predator has truly misidentified the prey as an object or has simply failed to notice it. However, true masquerade should remain effective across many different backgrounds (Skelhorn et al. 2010). In nature it is likely that many species use a combination of the two, for example, by closely matching the most common items in their environment.

*Aposematism* is another strategy related to prey recognition but, in this case, prey recognition is enhanced rather than hindered. Aposematic animals (Fig. 1e, f, g, k) employ warning signals, often conspicuous color markings, to inform predators about the possession of secondary defenses (chemical, physical, or behavioral), which render the prey unprofitable (Poulton 1890). Predators have an unpleasant experience upon attack, which they will associate with the prey's appearance in future encounters. Thus, predators will learn that this particular type of prey should be avoided. While color polymorphism is favored in cryptic prey (see above), it is thought to be inconvenient for aposematic species. This is because variation in warning signals might make it more difficult for predators to learn their association with prey unprofitability.

Aposematic species may resemble each other, making it easier for predators to learn to avoid them. This is known as *Müllerian mimicry* and leads to so-called "mimicry rings," where multiple defended species in the same area possess similar colors and markings. One example is the prevalence of yellow and black stripes across many wasp and bee species. Such mimicry can also be exploited by prey species without secondary defenses. These undefended species can mimic the appearance of defended ones and take advantage of predators having learned to avoid them. This is known as *Batesian mimicry*. For example, humans, along with many other predators, now associate black and yellow stripes with the stings of wasps and bees, but many harmless hoverfly species also have black and yellow stripes. The hoverflies then benefit, as fewer predators are likely to risk attacking them, for fear of being stung. Likewise, some harmless colubrid snakes mimic the color patterns of the deadly

coral snakes (Fig. 1g) obtaining protection from predators.

Animals can also deter predators through threat, or warning, displays. These can include both honest displays, such as those of tarantulas that draw attention to the animal's defenses (in this example fangs), and dishonest, or bluffing, displays, where an animal attempts to appear more dangerous than it truly is. Many mammal species, for example, erect their fur when threatened in order to appear larger. A similar tactic is used by some frogs, which inflate their bodies with air (Fig. 1h).

Aposematic animals can also make use of behavioral displays to advertise their defenses to would-be predators, and just as the physical marking of these species may be mimicked by other for protection, so too are these behavioral responses. Nonvenomous snakes in the family Colubridae will often perform similar body flattening or inflating displays as venomous ones when threatened. This similarity can be further enhanced by so-called head-triangulation, whereby snakes flatten their head in order to make it appear more triangular, like those of vipers (Valkonen et al. 2011).

Finally, animals may try and convince a predator that they will not make a suitable meal by pretending to be dead. Also known as thanatosis, this strategy relies on the fact that many predators only capture live prey and is found in a wide variety of taxa ranging from insects to frogs and mammals. Indeed, an alternative name for this behavior is "playing possum" after the common opossum (*Didelphis marsupialis*), which has been recorded to feign death for up to an hour following attacks by dogs (Francq 1969).

## Preventing Subjugation: *Fight or Flight*

Before they can be eaten by predators, prey must be subjugated. Perhaps the best-known mechanisms for preventing this are fighting or fleeing. While many animals fight back by whatever means are available to them, for example, by biting or scratching, others have weapons, such

as the antlers of deer or the claws of crabs, that can be used against would-be predators. Notably, most animal weapons are not solely for defense against predators, but often play an important role in feeding or sexual competition. Deer, for example, use their antlers (Fig. 1i) during male-male competition, while male fiddler crabs use their large claws to court females (Pope 2000). Thus the antipredator function of weapons may often be secondary. In contrast, other mechanisms for avoiding subjugation are highly specialized. Physical defenses such as spines can make it difficult for predators to approach or attack. Some of the best-known physical defenses are the quills of porcupines and the spines of hedgehogs. As well as physical, defenses can also be chemical. Bombardier beetles can spray would-be attackers with a mix of toxic chemicals. These beetles store hydroquinone and hydrogen peroxide in specialized glands. When threatened, the compounds are secreted into a chamber near the tip of the abdomen and their oxidation and decomposition creates a powerful chemical reaction which produces a hot jet of fluid. Ejecting noxious chemicals at predators is not only confined to beetles, indeed the most famous animal to use this kind of defense is a mammal, the skunk, which sprays its enemies with foul-smelling volatiles such as sulfides.

Another strategy to escape capture is to startle or scare the attacker. This can be done in a number of ways, from appearing to suddenly change size, to flashing bright colors or making a loud noise. These kinds of defenses differ from aposematism in that they do not rely on predator learning, but instead aim to elicit the predators fear or startle responses, or simply overwhelm their senses momentarily, giving the prey a chance to escape. One example is the mountain katydid (*Acripeza reticulata*), which is a type of bush cricket found in Australia. Mountain katydids appear dull brown until startled, when they lift their wings to flash their brightly colored abdomens (Umbers et al. 2017). Another example is the eyespots displayed by some butterflies (Fig. 1j). These are markings with circular shape that are thought to look like vertebrate eyes and are thus believed to

intimidate or startle predators making them hesitate to attack.

Finally, many, if not all, strategies to avoid subjugation rely on fleeing. Once the predator is startled, injured, or simply distracted, prey must escape to safety. Escape may entail more than simply running away, however. Many lizard species possess tails that detach when pulled, other animals such as crayfish can detach legs, and this ability is widespread across arthropods. This is done through processes known as *autospasy* (when the body part is lost in response to an outside pressure, such as pulling) or *autotomy* (when the part can be detached by the animal itself), which allows animals to sacrifice body parts with minimal blood loss. This enables them to escape, leaving their attacker with only a leg or tail. Fish scale geckos can even shed their skin when grabbed (Scherz et al. 2017). Some lizards take this one step further and have bright markings on their tails to encourage would-be predators to strike there (Castilla et al. 1999). This sort of misdirection is also seen in insects, like the butterfly *Bicyclus anynana* which has conspicuous *eyespot*s along the margins of its wings. These have been shown to draw the attention of attacking preying mantids, which are more likely to strike at the wings, rather than the head or body, of butterflies with these eyespots (Prudic et al. 2014).

Another strategy to avoid attack and subjugation is *motion dazzle*, whereby patterns with high contrast (i.e., stripes, bars, or zigzags) make it difficult for a predator to assess accurately the speed or direction of a moving prey (Thayer 1909). This is because such patterns may create a visual illusion of reduced speed or immobility. Previous correlational work with snakes (Jackson et al. 1976), poison frogs (Rojas et al. 2014), and lizards (Halperin et al. 2016) has suggested the matching between color patterns and movement, such that animals with striped or elongated patterns move linearly and/or at higher speeds, two movement characteristics that may accentuate the visual illusion.

However, animals are often most vulnerable to predators when they are unable to escape, for

example, as eggs or during larval or early development stages. For this reason many species actively protect their young through mobbing or otherwise distracting predators that get too close to their offspring. Other species, such as the red-eyed tree frog (*Agalychnis callidryas*), have embryos that are capable of hatching prematurely when the egg masses are attacked by snakes (Warkentin 1995).

### Preventing Consumption: *The Last Line*

Even once caught and subdued, animals have one last hope of escape if they can prevent their captor from actually consuming them. This can be achieved in one of several ways, by being toxic or poisonous, by tasting bad, or by simply being too difficult to swallow. Many animals use chemicals to render themselves toxic or unpalatable. These can be sequestered from their diet or created by the animals themselves. As they are unable to move away from predators, plants often use chemical defenses (also known as secondary metabolites or allochemicals) to deter herbivores. However, some herbivores have not only evolved strategies to deal with these chemicals, but can also store them in their own bodies for defense. This strategy is particularly widespread in insects and examples include monarch butterflies (*Danaus plexippus*), whose larvae sequester cardenolides from milkweed plants (Brower and Fink 1985), pine sawflies (*Neodiprion sertifer*, *Diprion pini*), who sequester resin acid from pine trees, and bella or rattle box moths (*Utetheisa ornatrix*), which sequester pyrrolizidine alkaloids from the seeds of their host plants (Conner 2009). Burnet moths (family Zygaenidae) (Fig. 1e), on the other hand, are also capable of sequestering cyanide compounds from their food plants and use them as a defense against predators across their different life stages. However, when this source is scarce, they are able to synthesize these compounds *de novo* (Zagrobelyny et al. 2007). Many of these insect species are also aposematic, but predators may “taste-reject” them even if they are not deterred by their warning

signals. But there are examples of toxicity among vertebrates too. Poison frogs, for instance, can sequester toxins from their diet, which consists mostly of ants and mites. These secretions (Fig. 1k) contain mostly alkaloids, several of which are neurotoxins (Saporito et al. 2012); one of them, batrachotoxin, which is also a cardiotoxin, is one of the most potent alkaloids known and the reason why the golden poison frog was given the name *Phyllobates terribilis*. Some species of harlequin toads, California newts (*Taricha torosa*), and puffer fish (family Tetraodontidae) are known to possess another potent neurotoxin called tetrodotoxin (see below). In most cases, its origin is uncertain but, at least in the case of the puffer fish, it has been shown to be produced by symbiotic bacteria (Magarlamov et al. 2017).

### “Social” Defenses: *Safety in Numbers*

Many of the defenses described above work more effectively in groups. For example, aposematism has been shown to be more beneficial when animals aggregate (Riipi et al. 2001). However, there are also strategies that rely on social behavior. The first of these is group *vigilance* behavior, which is widely used in several bird and mammal species. Vigilance simply means that animals are aware of their surroundings in order to detect potential predators; however, remaining vigilant can interfere with other behaviors such as feeding. By foraging for food in groups, animals can reduce their own vigilance while relying on the combined senses of the group in order to remain safe. Some species, such as meerkats (*Suricata suricatta*), take this one step further by having “sentries,” i.e., individuals who keep watch for predators while the rest of the group forages.

In addition, while many species rely simply on sensing their neighbors fleeing to communicate a threat, some also give specific *alarm signals*. Vervet monkeys (*Chlorocebus pygerythrus*) are famous for having three distinctive alarm calls, one for leopards (*Panthera pardus*), one for snakes, and one for eagles. Many small birds,

including tits from the family Paridae (Fig. 11) will produce so-called mobbing calls in response to nearby predators. These calls not only function as alarm signals, communicating the presence of the threat to others, but they also harass the predators and recruit other birds to join the mobbing. Mobbing birds will stay in the area of the predator, performing mobbing calls and displays. These calls can also vary depending on the type of predator and how dangerous it is. Mobbing may also include attacks on the predators, with the aim of preventing them from hunting or driving them out of an area. Notably, these mobbing calls can warn and recruit members of other species, and multi-species mobbing groups are often observed. Despite this, Paridae species vary considerably both in how much information their mobbing calls convey about the threat posed by predators and how this information is encoded in their calls (Carlson et al. 2017).

### **How Do Antipredator Strategies Evolve?: An “Arms Race” Between Predators and Prey**

Predators need to feed, and prey must avoid being eaten. Thus, predators continuously evolve better tactics to ensure they can successfully find, subjugate, and consume prey, while prey improve their defenses to prevent predators from succeeding. This has been likened to an “arms race,” in which an improvement in one side’s abilities results in a corresponding improvement by the opposing side. For example, as predators improve their visual acuity in order to increase prey detection, prey might elaborate their camouflage strategies or adopt different spatial distributions that make it more difficult for predators to find them. Likewise, as prey evolve toxins to avoid being consumed, predators may develop detoxification abilities or toxin resistance mechanisms. Such is the case in garter snakes (*Thamnophis sirtalis*), which have evolved molecular mechanisms to avoid getting intoxicated by the powerful tetrodotoxin from rough-skinned newts. Tetrodotoxin (TTX) is a

neurotoxin that blocks the sodium-potassium channels in nerve cells, leading to paralysis. Garter snakes are capable of avoiding this effect of TTX because they have evolved sodium channels with a different shape, impeding the TTX molecule from binding them. Furthermore, garter snakes from populations co-occurring with the newts have shown to be more resistant to TTX than those from populations without co-occurring newts (Brodie and Brodie 1999).

### **Conclusions**

Predation is undoubtedly one of the greatest forces shaping evolution, and this is reflected in the huge diversity of defense strategies seen in nature. Animals use every possible tool they have available in order to survive. However, no defense is perfect as predators are also constantly adapting to overcome the barriers prey put up against them. As a result many species use multiple defense strategies and may switch between radically different strategies as the predation attempt progresses. Indeed, a single species of frog found in Malaysia has been found to respond to attacks by “fleeing, feigning death, crouching, hiding among leaf litter, diving underwater, inflating the body, body-raising, defensive call(s), and bladder discharge” (Shahrudin 2016). Furthermore, a single strategy can act across more than one stage. A frog that inflates itself may threaten and dissuade predators with its increased size, but if this fails the inflation may also serve to make it too large to swallow. Thus, species can alter their defensive behaviors based on the identity of their attacker, and if one strategy fails to deter them they simply switch to another.

### **Cross-References**

- [Alarm Calls](#)
- [Aposematism](#)
- [Camouflage](#)
- [Mimicry](#)
- [Predation Risk](#)



- **Predator Detection**
- **Primary Defenses**
- **Secondary Defenses**
- **Vigilance**
- **Warning Coloration**

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## Predator Detection

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### Introduction

The chance of prey to escape predation strongly depends on its ability to detect the predator before getting attacked. In order to avoid potential lethal attacks, prey species need to be constantly vigilant. At the same time, they need to engage in other activities such as feeding and mating. This creates trade-offs between the time invested in antipredator vigilance and all other activities. Optimizing the outcome of such trade-offs requires a precise knowledge of the predator appearance in order to minimize false alarms and at the same time maximize correct identification. Predator recognition can be either inherited or learned, for instance, based on own or public information. To recognize the presence of a predator, prey animals may employ various cues, often involving different modalities such as olfactory, visual, or acoustic information. Moreover, the chances to detect a predator will further increase when several individuals are vigilant. In this chapter we will first elucidate the different mechanisms enabling animals to differentiate between non-dangerous animals and predators. We will then introduce the different cues animals use to detect the presence and motivational state of predators. Finally, we show how the presence of group members increases a prey's chance to detect predators and how such information about risk is transferred within the group.

### How to Recognize a Predator?

Many animals, including humans, show inborn fear reactions toward other potentially dangerous

animals (Davey 1995). These prey species do not need to learn respective predator cues but intrinsically react with appropriate behaviors after detecting the predator. In contrast, others need to learn about the potential danger of unknown animals, often through repeated experiences with predators, either by direct contact or by observing others (Brown et al. 2011). Additionally, inborn predator recognition might be fine-tuned by further learning particular predator phenotypes. Whether innate recognition or learning is involved in predator detection often depends on the ecology of the respective species (Brown et al. 2011). Learning to detect predators is more beneficial when the risk of encountering a given predator is variable on a spatial and temporal scale (Brown et al. 2011). On the contrary, genetically determined predator detection is beneficial in species that face always the same predators (Brown et al. 2011). Interestingly, many prey animals are able to generalize learned predator recognition to other predatory species, which are similar in appearance and smell. This enables prey to reduce the costs of learning to detect new predators because potentially dangerous encounters can be reduced (Brown et al. 2011).

### Genetically Determined Recognition

Many animals own an inherent, genetically fixed concept of the phenotypic appearance of a predator. Such concept can be very coarse, following simple rules of thumb (e.g., *avoid all animals that are bigger than you are*). However, such coarse recognition templates will readily lead to false alarms, which might prevent individuals from foraging or mating and which will lead to constantly having acute stress responses. It is thus not surprising that in many cases, more fine-tuned inherent recognition templates have evolved. The cichlid fish *Neolamprologus pulcher*, for example, is able to spontaneously differentiate between predatory and herbivorous cichlids that are of similar size (Fischer et al. 2014). It, thus, does not follow the rule “*all large fish are dangerous*” but rather uses more subtle differences in the respective fish's appearance. Importantly, these behaviors were observed in laboratory-reared fish that had never experienced heterospecifics

before, indicating that the fine-tuned recognition template is inherent and not learned (Fischer et al. 2014).

### Nongenetically Determined Recognition

Information about the predatory environment can also be nongenetically transmitted between generations from parents to offspring. Mothers are the key interface between the current environment and future generations. So-called non-genetic maternal effects are common in many species and lead to responses in offspring, which might not necessarily be adaptive. When offspring responses are adaptive, mothers use cues from the current environment to prepare their offspring for the potential future environment. For example, in yellow-legged gulls (*Larus michahellis*), offspring from mothers that were exposed to predators show an increased antipredator response compared to offspring from mothers that were not exposed to predators (Morales et al. 2018). Adaptive responses are particularly beneficial when environmental conditions of mothers match the environmental conditions experienced by their offspring. However, maternal exposure to predators can also have detrimental effects on offspring behaviors and survival. For example, in three-spined stickleback (*Gasterosteus aculeatus*), offspring from mothers exposed to predators show less efficient antipredator behaviors compared to offspring from mothers that did not experience predators (McGhee et al. 2012). In such cases mothers may experience acute stress while exposed to predators and consequently lay eggs of lower quality, resulting in less developed and less adapted offspring.

### Learned Recognition

Some prey species either don't possess a genetically determined template to recognize predators or do not show appropriate responses. In the first case, animals need to learn to detect predators in order to assess potential danger. For these animals it is crucial to gather information about the identity of potential predators either through personal or social experiences. Gathering personal information can be very costly as animals that misjudge the prevailing danger have the

considerable risk of getting injured or killed while learning. Here, employing the knowledge of other, more experienced individuals can be beneficial. Social information about predators are transmitted from one individual to another, for example, through alarm calls, chemical warning substances, or sentinel behavior. Observing experienced individuals interacting with predators is also an effective way to gain information about successfully interacting or evading predators. For example, juvenile Siberian jays (*Perisoreus infaustus*) start mobbing predators only after observing a knowledgeable individual mobbing the same predator species. This information is crucial for juveniles as it improves the survival during the first winter, when they interact the first time with predators (Griesser and Suzuki 2017).

## Sensory Ecology of Predator Detection

Prey animals use a broad range of different cues to detect predators. The used sensory modality strongly depends on the species ecology. For example, visual cues play an important role in terrestrial, diurnal animals. However, when vision is hampered, for example, in nocturnal or aquatic species, other modalities become more important. Finally, cues from different modalities are usually not used in isolation. Instead, prey animals gather multimodal information to optimize their chances to detect a predator as early as possible. In the following we introduce how animals use different modalities to detect predators.

### Visual Detection

Vision is an accurate and reliable sensory modality to detect predators. Visual cues are transmitted fast and can be perceived over long distances. Accordingly, many diurnal animals rely on visual cues when prospecting potential danger. Here, a large field of view without head movements is beneficial. Therefore, the eyes of most mammal prey species, like antelopes, mice, and rabbits, are located far apart from each other on opposite sides of the head. This increases the field of view and allows them to scan a huge space range on both sides of their body. Similar adaptations occur in

many fishes or birds. Woodcocks (*Scolopax rusticola*), for example, have a nearly panoramic view of 359° in the horizontal plane (Cronin 2005). However, this increase comes at the cost of reduced perception of depth and a hampered ability to see in 3D.

As an adaptation to the good eyesight of many prey species, some predators have evolved cryptic coloration, making it difficult for prey to spot them. Many sharks, for example, show different color patterns on their dorsal and ventral body side. While the dorsal part is dark, the ventral part is often lighter. Seen from above, the dark color camouflages the shark against the dark deeper water below, while from below the pale color conceals the shark against the lighter water surface (*Countershading*, Marshall and Johnsen 2011).

Despite the benefits of vision to transfer information fast and over a long distance, vision is not always the best modality for predator detection, as the transmission of visual cues is easily hampered. For example, visual cues are blocked in highly structured habitats like forests. Furthermore, visual perception is limited during the night. Finally, vision is strongly reduced in aquatic systems due to high turbidity or the lack of light in deeper water bodies. Under such conditions other modalities gain importance.

### Chemical Detection

Prey animals use a variety of chemical cues to detect predators. Such chemical cues can be produced by predators, conspecifics, or other prey animals (Hettyey et al. 2015). Predator-derived cues are mostly released unintentionally. As they reveal the predator's presence to the prey, they are indeed disadvantageous for the producer, though they might have functions, for example, in intra-specific communication. Furthermore, smell might arise from the integument of the predator or from its digestive tract. Finally, feces or urine might contain parts of the predators' gut flora, as well as metabolites of digested prey items (Hettyey et al. 2015). Prey animals readily use such olfactory information to detect the presence of a predator and adjust their behavior accordingly. For example, small freshwater crustaceans

(*Gammarus pulex*) avoid the smell of predatory fishes and form social aggregation, even if the predators were not fed on gammarids before (Baldauf et al. 2007; Kullmann et al. 2008). Similarly, many snake species show characteristic defensive behaviors to the odors of snake-eating snakes, and rats respond with characteristic defense and fear responses toward cat odors (Dielenberg and McGregor 2001). Other predator defense responses might be long-lasting or even irreversible, such as morphological adaptations. For example, many tadpoles develop stronger tails in the presence of a predator's olfactory cues, allowing them to escape faster (Hettyey et al. 2015).

Chemical information about the risk of predation can also be prey-borne and produced when animals are stressed, attacked, captured, or digested (Hettyey et al. 2015). Such chemical cues might be passively released from injured prey tissue and serve others as information. This phenomenon has been already described by Karl von Frisch (1942), one of the founders of modern ethology. He found that European minnows (*Phoxinus phoxinus*) show an intense fear response when exposed to conspecific skin extract imitating a predation event and coined the term *Schreckstoff* for such damage-release cues. While some of these damage-released cues are passive by-products of the predatory act itself, others have evolved to act as active signals for warning other individuals. These signals are costly to produce, and do not directly benefit the sender, which is why they are a puzzle in the evolution of the communication of risk. One solution is that damage-release signals might have evolved mainly in species that live together with close kin. Warning relatives may hence lead to indirect fitness benefits for the sender. For example, sea anemones (*Anthopleura elegantissima*) live in colonies of genetically identical individuals. Injured individuals release a pheromone that induces a typical self-defense response in neighboring individuals, which retract and protect their tentacles (Howe and Sheik 1975). Similarly, honeybee workers (*Apis mellifera*) attack predators threatening their colony by stinging. Stinging is a suicidal act because the sting together with the

whole abdomen stays attached to the intruder. At the same time, the sting continues to simultaneously release venom inside the victim and a pheromone to the outside to attract more worker bees (Breed et al. 2004).

### Acoustic Detection

Acoustic cues are important means to detect predators, especially in habitats with low visibility (Hettena et al. 2014). To discover a predator by acoustic cues, many animals have evolved distinguished hearing abilities to accurately locate sounds. Many herbivore mammals like antelopes, deer, horses, and rabbits are able to move their ears in almost 180°, increasing their acoustic perception and allowing them to accurately locate the origin of sound. Detecting acoustic predatory cues becomes especially important, when predators themselves employ sound waves to find their prey. This is the case in many bats that use echolocation to spot and catch prey insects. These nocturnal hunters emit high-frequency calls and listen to the echoes to determine the size and location of their target (Jones et al. 2016). As a counter adaption, however, many moths and other nocturnal insects can detect the echolocation calls of bats, allowing them to initiate evasive flight maneuvers. A peculiar defense behavior is shown by dogbane tiger moths, *Cycnia tenera*, which produce high-frequency clicks that disturb the echolocation function of the approaching bat (Jones et al. 2016). Finally, acoustic cues also serve as signals that transfer information about an approaching predator from one prey individual to another. Prominent examples are warning calls in many bird species but also in alpine marmots or cooperatively breeding meerkats (Caro 2005).

### Mechanical Detection

Some animals are able to detect approaching predators using mechanical cues. For example, tree-living insects use leaf vibrations to detect the presence of predators (Yack 2016). Thereby, many insects make use of specialized cells arranged in body parts close to the substrate such as legs or antenna (Yack 2016). Furthermore, vibrational signals actively emitted by prey after

detecting a predator also act as an antipredator response to deter the attacker and warn conspecifics.

Fishes, as well as some amphibians and cephalopods, possess a special organ that consists of neuromasts located around the head and along the lateral part of the body. In fishes, these neuromasts are arranged in a long line along the flank, which gives the organ the name *lateral line* (Janssen 2004). The neuromasts are sensitive to pressure changes and hence enable the animal to detect fluctuations in water pressure caused by the movement of con- or heterospecifics. As such, they enable the animal to detect the swimming activity of predators. The lateral line system further plays a crucial role in orientation and shoaling behavior, which is the most common antipredator behavior in fishes and tadpoles (Janssen 2004).

### Multimodal Predator Detection

Each of the previously described sensory systems has its own set of benefits and limitations. For example, chemical cues are particularly useful for gaining information about a predator's presence but are not as reliable for gaining information about the exact location of the predator. Here, visual cues can be more reliable. Still, visual cues have their limits when predators are camouflaged or when light conditions are bad. Acoustic cues might easily be overheard because of other background noises. Thus, in order to gain optimal information about the potential presence of a predator, animals commonly use multiple sensory modalities at the same time (Munoz and Blumstein 2012). For example, mosquitofish (*Gambusia affinis*) uses visual and chemical cues to avoid predators, while each cue in isolation would be sufficient to induce the correct antipredator response. Nevertheless, if both types of cues are available at the same time, these fish show an increased antipredator response where individuals almost double their distance from the predator (Smith and Belk 2001). Cues perceived in different sensory modalities can further transfer different information (Partan and Marler 2005). For example, animals might detect the general presence of a predator by recognizing its smell.



Still, they would lack information about the acute risk, which might be provided by additional visual information about the approaching speed. Thus in this case, olfactory information might lead to an increased level of vigilance, while the visual cue will induce a fast flight response.

The use of multimodal cues in predator detection is not only important to increase detection accuracy but also allows to detect predators under fluctuating environmental conditions. For example, changing weather conditions limits the relative importance of single cues (Caro 2005; Saunders et al. 2013). The need to base decisions on multiple cues is not restricted to terrestrial environments but also of importance to aquatic animals. For example, seasonal rainfall will lead to a temporal reduction in visibility in the African Rift Valley Lake Tanganyika, caused by algae blooms and floating sediment. In this environment, the highly social cichlid fish *N. pulcher* uses olfactory and visual cues to detect predators, and both cues lead to comparable antipredator responses (Fischer et al. 2017).

In recent years, most natural habitats faced drastic human-induced changes, including altered visibility due to algal blooms caused by eutrophication and soil import, increased noise levels, changes in water chemistry, and chemical pollution (Hildebrand 2009; Barber et al. 2010). These changes have strong impacts on predator detection abilities in many species. For example, traffic noise impacts the production and perception of alarm calls in great tits (Templeton et al. 2016) and impacts the use of alarm calls in dwarf mongooses (Morris-Drake et al. 2017). Using different modalities might allow animals to increase their success in predator detection in such modified environments. Still, the relative importance of different sensory modalities governing predator-prey interactions in changing environments is mostly unknown (Hale et al. 2017). Human-induced perturbations might not only influence predator detection in one modality but might influence other sensory systems as well. For example, traffic noise on land and underwater hampers the recognition of chemical cues associated with predation risk in fish and mammals (Morris-Drake et al. 2016; Ferrari et al. 2018).

## Predator Detection as a Driving Force in Social Evolution

Perfect protection from predators requires constant vigilance. However, animals also need to invest time in feeding or mating, and these activities are reduced while being vigilant. Solving the problem of allocating time between being vigilant and other activities is challenging, and diverse strategies exist, which are dependent on the social organization. Most solitary animals increase vigilance only during dangerous situations and decrease vigilance in safe situations. This requires individuals to constantly assess the local predation risk, which has been termed the threat-sensitive assessment of risk (Brown et al. 2011; Fischer et al. 2017) and is an important way to reduce costs of antipredator behaviors. However, this requires animals to possess a reliable estimate of the local predation risk, which might not always be possible. Other animals live in groups, where vigilance can, for instance, be split among group members.

### Predator Detection and Sociality

The risk of predation is probably the strongest force leading to group living in animals. One benefit of living in groups is that the chances of at least one individual detecting the predator and alarm the rest of the group increases with increasing group size (Pulliam 1973). This *many eyes effect* exists in many animal species (Davies et al. 2012). Such detection benefits do not necessarily require more eyes as it is nicely illustrated by a colonial social spider (*Metepheira incrassata*). Here individuals join together and build large communal webs. Individuals within these colonies gain antipredator benefits by detecting mechanical vibrations transmitted through the communal web when other colony members are under risk (Uetz et al. 2002).

An individual in a group might not only benefit from an earlier predator detection but might further share the costs of being vigilant by alternating scanning behaviors between group members. As a consequence, the vigilance of the whole group will be increased, while each individual has to be less vigilant compared to solitary conspecifics

(Beauchamp 2015). Such beneficial effects of group vigilance can be further enhanced, if group members actively warn others, for instance, by alarm calls. The information content of such alarm calls can be highly fine-tuned. For example, meerkats (*Suricata suricatta*) emit different alarm calls depending on whether the predator is a bird of prey or a snake (Manser 2001). Furthermore, the calls might indicate different grades of urgency. This enables other group members to show the respective adequate antipredator behaviors.

While alarm calls are beneficial for recipients, producing such calls is costly in terms of time and energy spent. Furthermore, the caller might increase its risk of being spotted and attacked. Still, emitting alarm calls might lead to direct and indirect benefits for the producer as well as for the receivers within the group, which is why alarm calls are widespread (Caro 2005). For example, alarm calls in the common redshank (*Tringa totanus*) cause the entire flock to fly off together, which might confuse the predator (Will Cresswell 1994), and directly increase the survival chances of the caller. Furthermore, the caller will gain indirect fitness benefits when warning relatives, which therefore are more likely to produce offspring sharing genes with the caller. Belding's ground squirrels (*Urocitellus beldingi*), for example, emit alarm calls more readily when accompanied by relatives (Jill 2010). The most pronounced forms of shared vigilance can be found in highly social species, such as cooperatively breeding meerkats. Here, the sharing of vigilance between group members has evolved into a sentinel system where some individuals entirely stop foraging for a specific period and watch out for predators to alarm the rest of the group. Here, the individual nutritional state is a major predictor of sentinel activity with hungry individuals resuming to forage and saturated individuals acting as sentinels (Clutton-Brock et al. 1999).

Finally, alarm calls are not restricted to within-species communication. Indeed, many birds and mammals react to alarm calls of other species, especially when both species share the same predators (Meise et al. 2018). For example, dwarf

mongooses (*Helogale parvula*) respond to alarm calls of tree squirrels, with which they share predators, but not to alarm calls of baboons, which are vulnerable to different predators (Morris-Drake et al. 2017).

### Reliability and Cheating

In contrast to using own information, obtaining information about predation risk from others poses the risk of being unreliable and inaccurate. This is, for example, the case when predators differ in threat depending on species, size, sex, or age of the prey individual. Consequently, animals that have the choice between different sources of information shall incorporate the reliability of the respective sources in their anti-predator response. For example, zenaida doves (*Zenaida aurita*) show a higher level of vigilance during playback experiments using calls from red-tailed hawk (*Buteo jamaicensis*) compared to playbacks of conspecifics' wing whistles, which serve as alarm cue (Barrera et al. 2011). The reliability of social information is also dependent on the identity of the sender. For example, dwarf mongooses reduce their vigilance more strongly following warnings of experienced dominant individuals compared to subordinate and more inexperienced individuals (Kern et al. 2016).

A further source of unreliability is the probability of deceptive attempts by the caller. Fork-tailed drongos (*Dicrurus adsimilis*), for example, mimic alarm calls of other species when they handle food. Target species like meerkats and pied babblers (*Turdoides bicolor*) readily react with a fleeing response, abandoning their food, which is then taken by the drongo (Flower 2011).

### Conclusion

To survive in risky environments, prey animals need to detect predators before being attacked. Some prey species have a genetic predisposition to detect and recognize predators, whereas others need to learn appropriate responses by direct or indirect experiences. Visual, olfactory, chemical, acoustic, and mechanical cues are used in isolation or in combination to detect predators and to

communicate predation risk to others. Finally, the benefits of increased predator detection and defense are probably one of the main driving forces in the evolution of animal sociality.

## Cross-References

- ▶ [Aposematism](#)
- ▶ [Cryptic Coloration](#)
- ▶ [Escape Response](#)
- ▶ [Group Living](#)
- ▶ [Müllerian Mimicry](#)
- ▶ [Predation Risk](#)
- ▶ [Vigilance](#)

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## Predator Swamping

### ► [Artiodactyla Navigation](#)

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## Predicting Rational Behavior

### ► [Nash Equilibrium](#)

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## Predictive Processing

### ► [Plantae](#)

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## Preening

### ► [Grooming](#)

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## Pregnancy Block

### ► [Bruce Effect](#)

Prehensile Tail

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*Prehensile tail:* The tail of any vertebrate that is adapted for grasping can hold objects or can support some or all of the body weight of animal while stationary (i.e., feeding posture) or during locomotion.

*Anthropoid:* A primate belonging to the suborder Anthropeidea that has a fused mandibular symphysis, fused frontal bone, postorbital closure, a greater reliance on vision than olfaction, and lacking a rhinarium, tapetum lucidum, grooming claws, or dental comb; the group of primates including old and new world monkeys, apes, and humans.

*Platyrrhini:* A radiation of neotropical anthropoids belonging to the infraorder Platyrrhini and defined by their biogeographical distribution (i.e., Central and South America), nasal, auditory and cranial morphology, and dental formula (2133/2133).

Prehensile tails are known for four of the seven classes of vertebrates (Table 1). They are differentiated from nonprehensile tails by being adapted for grasping, holding objects or supporting some or all of the body weight of animal while stationary (i.e., feeding posture) or during locomotion. “Prehensile” is derived from the latin *prehendere* (to take hold of, to grasp). This adaptation has arisen many times and independently in fish, amphibians, reptiles, and mammals. In mammals, this adaptation has evolved independently at least 14 times among 50 genera (representing 14 families) including separate origins in the anthropoid New World primate (Platyrrhini) family Atelidae (woolly, spider, woolly spider, and howler monkeys) and in some members of the family Cebidae (capuchin monkeys) (Emmons and Gentry 1983; Organ et al. 2009; Organ 2010) (Fig. 1). The separate origins of these similar and metabolically

**Prehensile Tail, Table 1** List of prehensile- and semi-prehensile-tailed mammals, reptiles, amphibians and fish

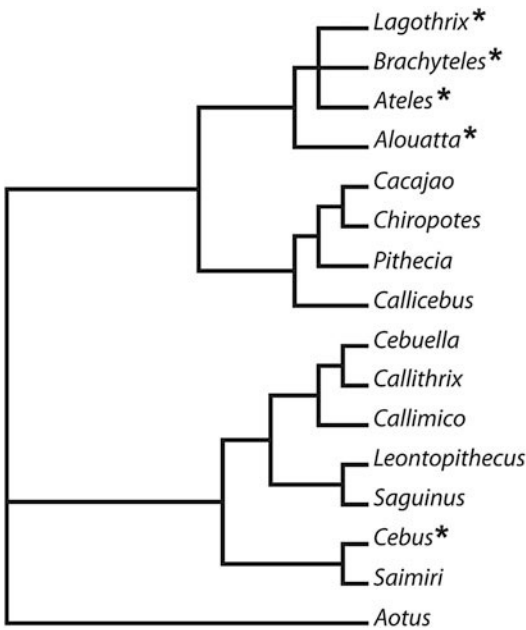
|            |                                                                           |
|------------|---------------------------------------------------------------------------|
| Mammals    | <i>Prehensile</i>                                                         |
|            | Atelidae                                                                  |
|            | i. Spider monkey ( <i>Ateles</i> )                                        |
|            | ii. Woolly monkey ( <i>Lagothrix</i> )                                    |
|            | iii. Woolly spider monkeys ( <i>Brachyteles</i> )                         |
|            | iv. Howler monkeys ( <i>Alouatta</i> )                                    |
|            | Opposum ( <i>Didelphis</i> )                                              |
|            | Anteaters ( <i>Cyclopes</i> , <i>Tamandua</i> )                           |
|            | Binturong ( <i>Arctictis</i> )                                            |
|            | Kinkajou ( <i>Potos</i> )                                                 |
|            | Harvest mouse ( <i>Micromys</i> )                                         |
|            | Porcupines ( <i>Coendou</i> , <i>Chaetomys</i> )                          |
|            | Tree pangolin ( <i>Phatiginus</i> )                                       |
|            | Some possums (suborder Phalangeriformes)                                  |
|            | <i>Semiprehensile</i>                                                     |
|            | Cebidae                                                                   |
|            | i. Gracile capuchin monkeys ( <i>Cebus</i> )                              |
|            | ii. Robust capuchin monkeys ( <i>Sapajus</i> )                            |
|            | Tree porcupines ( <i>Coendou</i> )                                        |
|            | Possums (suborder Phalangeriformes)                                       |
|            | Bettong ( <i>Bettongia</i> )                                              |
|            | Potoroo ( <i>Potorous</i> )                                               |
|            | Monito del monte (Dromiciops)                                             |
|            | Rats ( <i>Rattus</i> )                                                    |
| Reptiles   | Prehensile-tailed skink ( <i>Corucia zebrata</i> )                        |
|            | Chameleons                                                                |
|            | Snakes                                                                    |
|            | Crested gecko ( <i>Rhacodactylus ciliates</i> )                           |
|            | Alligator lizards ( <i>Abronia</i> )                                      |
| Amphibians | Salamanders ( <i>Aneides</i> , <i>Phaeognathus</i> , <i>Blitoglossa</i> ) |
| Fish       | Seahorses ( <i>Hippocampus</i> )                                          |
|            | Pipefish (subfamily Syngnathinae)                                         |

(Emmons and Gentry 1983; Organ 2010)

expensive anatomical structures in diverse lineages of arboreal mammals suggest that prehensile tails are an effective adaptation for negotiating arboreal environments (Emmons and Gentry 1983; Organ et al. 2009; Organ 2010).

Prehensile tails among platyrrhine anthropoids may have arisen as an adaptive accommodation





**Prehensile Tail, Fig. 1** \*Indicates a platyrrhine genus with a prehensile tail. Although species of the genus *Saimiri* are members of the family “Cebidae” they do not retain a functioning prehensile tail into adulthood and are effectively nonprehensile-tailed (Reproduced from Organ (2010))

for larger body sizes in dense tropical canopies (Napier and Napier 1967; Grand 1972, 1977), a postural adaptation for feeding that frees up the forelimbs (Rosenberger 1992; Bergeson 1996, 1998) or else a response to mechanically compliant forest canopy substrates (Emmons and Gentry 1983; Organ 2010). Emmons and Gentry (1983) have suggested that canopy distribution and composition play an important role in the selection for and distribution of mammals with prehensile tails. There are fewer gliding or prehensile-tailed mammals in Africa where the canopy is dense and there is an abundance of lianas yet in Southeast Asia, where the canopy is less dense and there is a scarcity of lianas, there is a relative increase in the number of gliding species. Likewise, in the neotropics of South and Central America, where there is an increased number of palms, more fragile arboreal supports, and an intermediate abundance of lianas, prehensile-tailed mammals are most abundant. However, Australia and New-Guinea are home to a number of mammal

species that are both gliders and that have prehensile tails.

Tails are comprised of caudal vertebrae. Tail length is a direct function of the number of caudal vertebrae. Caudal vertebrae can be identified as either “proximal” or “distal” depending on their specific morphology. Proximal caudal vertebrae are typically shorter craniocaudally and have well-developed neural arches with a single set of transverse processes. Proximal caudal vertebrae articulate via intervertebral disc joints as well as zygapophyseal joints associated with the neural arch. Hemal processes are found on the proximal and ventral surfaces of proximal caudal vertebrae and serve as attachment points for the hemal arches (“chevron bones”) that function as muscle attachment sites. Distal caudal vertebrae are longer craniocaudally and lack a neural arch. They have two sets of transverse processes (one proximal and one distal) and articulate via intervertebral disc joints only. The last vertebra of the proximal caudal region is the “transition vertebra” and is identified by the presence of zygapophyseal joints only at its proximal end. Craniocaudal vertebral length increases throughout the tail from proximal to caudal until the “longest caudal vertebra” (which is always distal to the “transition vertebra”) and then steadily declines to the terminus of the caudal sequence (Organ et al. 2009; Organ 2010, 2016).

Prehensile-tailed platyrrhines differ morphologically from nonprehensile-tailed platyrrhines. Prehensile-tailed taxa have longer proximal regions comprised of a greater number of vertebrae, craniocaudally shorter and transversely wider distal region vertebrae, more expanded transverse and hemal processes (sites of muscle attachment) (Ankel 1962; German 1982; Organ et al. 2009; Organ 2010), and craniocaudally expanded sacroiliac joints (Ankel 1962). The dorsal and ventral caudal musculature in prehensile-tailed platyrrhines crosses fewer joints to permit finer neuromuscular control of individual joints (Lemelin 1995), and the lateral flexor musculature is more developed to generate significantly higher maximum tetanic tension (Organ et al. 2009). Caudal vertebral cross-sectional geometry in prehensile tailed platyrrhines is consistent with

greater resistance to bending and torsion (Organ 2010). Prehensile tailed platyrrhines have larger and more convex intervertebral articular surfaces to permit a greater range of motion (Deane et al. 2014). Morphological differences between prehensile-tailed and nonprehensile-tailed platyrrhine muscle attachments, PCSA, caudal vertebral robusticity, and resistance to bending and torsion are accentuated in the distal caudal region (Organ et al. 2009; Organ 2010). It is presumed that proximal caudal vertebrae of prehensile-tailed and nonprehensile-tailed platyrrhines are less divergent morphologically given the similar functional demands in this region of the tail (i.e., both groups abduct, adduct, flex and extend their tails; German 1982). Regardless, cross-sectional geometry conferring enhanced bending resistance and increased intervertebral articular surface area and surface convexity differentiate the proximal caudal vertebrae of prehensile-tailed and nonprehensile tailed platyrrhines.

The functional capabilities of mammals with prehensile tails are not uniform. Emmons and Gentry (1983, p. 513) define a prehensile tail as “one which can support alone the weight of the suspended body” and a semiprehensile tail as one that “can be wrapped around branches and support a significant part, but not all, of the body weight.” Although there is not universal consensus on the adoption of this terminology (i.e., prehensile vs. semiprehensile), prehensile-tailed platyrrhines do differ in their frequency and mode of tail-use. Cebines use their prehensile tails to brace themselves against a substrate in a tripod posture during feeding and resting, but infrequently use their tails to suspend their entire body weight (Bergeson 1996; Bezanson 2012). Like cebines, atelines use their tails in postural and feeding behaviors, but also use their tails in hindlimb-assisted tail suspension and during tail-only suspensory locomotor behaviors (Bergeson 1996; Bezanson 2012). Despite these behavioral differences, ateline and cebine tails differ morphologically only by the presence of a hairless ventral friction or “volar” pad (Organ 2016) and more well-developed dorsal caudal musculature (Lemelin 1995; Organ et al. 2009) in the former. In contrast, the cebine prehensile tail is

completely covered with hair (Organ 2016) and the dorsal caudal musculature is developed as in nonprehensile-tailed platyrrhines (Lemelin 1995). Likewise, atelines have four distinctive epicritic histologic mechanoreceptors in the skin covering their volar pad (Meissner’s, Pacinian, and Ruffini corpuscles, and Merkel discs). However, the ventrodiscal tail skin of cebines only contains two of these (Ruffini corpuscles and Merkel cells) suggesting that group lacks some of the tactile capabilities of atelines (Organ et al. 2011). Nonetheless, features such as the well-developed ventral caudal musculature, the strong estimated structural mechanical properties of the caudal vertebrae, and the relatively longer proximal tail region in cebines are convergent with those properties of the ateline prehensile tail (Organ et al. 2009; Organ 2010) and cebine prehensile tails appear as a morphological intermediate between the tails of atelines and the tails of nonprehensile-tailed platyrrhines.

## Cross-References

- [Platyrrhine Diet](#)
- [Platyrrhine Locomotion](#)

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## Prehensility

- [Opposable Thumb](#)

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## Prejudice

- [Xenophobia](#)

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## Preparatory Response

- [Appetitive Response](#)

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## Pretence

- [Pretend Play](#)

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## Pretend Play

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## Synonyms

[Object substitution](#); [Play](#); [Pretence](#); [Rough-and-tumble play](#); [Sociodramatic play](#)

## Definition

Play involves exaggerated, “nonserious” versions of functional species-typical behaviors and appears to be more about the behavior itself than the usual function of that behavior when seriously deployed (Pellegrini et al. 2007). Fantasy, or *pretend play*, has the added characteristic that the player/players are knowingly and intentionally applying a mental representation of a real-world object, person, or action to a substitute object, person, or action in service of the play (e.g., Lillard 1993).

## Recognizing Play

In a broad sense of the term, play is observed in humans and across a wide variety of nonhuman animal species. It is observed primarily in mammal and bird species, during immaturity, and in safe or familiar environments (e.g., Burghardt

2005; Fagen 1981). Play is a notoriously difficult behavior to define, and exceptions exist for most attempts. Typically, play involves exaggerated, “nonserious” versions of functional species-typical behaviors, with the play appearing to be more about the behavior itself than the usual function of that behavior when seriously deployed (Burghardt 2005; Pellegrini and Smith 2002; Spinka et al. 2001). More specifically, Burghardt (2005) has suggested that, in order to be considered play, a behavior must simultaneously meet five different criteria (p. 70–78):

1. Performance of the behavior is not fully functional in the form or context in which it is expressed; that is, it includes elements, or is directed toward stimuli, that do not contribute to current survival.
2. Behavior is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic.
3. Behavior differs from the “serious” performance of ethotypic behavior structurally or temporally in at least one respect: it is incomplete, exaggerated, awkward, or precocious; or it involves behavior with modified form, sequencing, or targeting.
4. Behavior is performed repeatedly in a similar, but not rigidly stereotyped, form during at least a portion of the animals ontogeny.
5. Behavior is initiated when an animal is adequately fed, healthy, and free from stress or intense competing systems.

The ways that play manifest and the extent to which engaging in play impacts the development of individuals seems to vary across species. However, the behavior is widely observed; play behavior has been noted in most mammal species, as well as a number of avian and some reptilian species (Burghardt 1998). The high evolutionary conservation of this behavior and the required resources to engage in it suggest that it is a profitable behavior for juveniles, and, as outlined briefly in Section 1, the consequences of being deprived of the opportunity for play can be devastating. Despite the evidence that play is developmentally important for many species, it has

been challenging for researchers to draw strong conclusions about why it exists.

### Types of Play

The type of play most commonly studied within a comparative framework is rough-and-tumble play, or play fighting. This is a broad term, as the specific behaviors that compose this type of play will differ greatly from species to species. Typically, though, rough-and-tumble play has varying degrees of roughness, is entered into voluntarily, and is associated with positive affect (e.g., Pellis and Pellis 2007). Juvenile rats who have been prevented from engaging in this type of play demonstrate deficits in a range of social activities, from the sexual to the competitive, and produce higher levels of stress hormones than socially reared rats (Pellis and Pellis 2007; Von Frijtag et al. 2002).

Object play has also been observed in non-human species. Dogs and cats frequently engage in object play with their human companions, in games of fetch or attacking a ball on the end of a string. It is likely the case that these behaviors represent predatory behavior being elicited by a nonprey object (Pellis and Pellis 1998). Captive gorillas have been observed engaging in play in which the goal appears to be obtaining an object and keeping it from others, alternately playing the roles of possessor and pursuer (Tanner and Byrne 2010). Outside of primates and predatory mammals, however, object play is fairly limited (Pellis and Pellis 1998).

However, there are many other forms of play. One of the most complex of these may be pretend play, the subject of the current entry. Pretend play is a difficult topic to discuss at length from a comparative perspective, for two main reasons. The first among these is, as noted by Lillard et al. (2011), “... pretend play’s purpose is a mystery. The mystery is this: young children need to adapt to the world as it is, yet in pretend play they contrive the world to be as it is not (p. 286).”

The second difficulty of examining pretend play through a comparative lens comes from the nature of pretend play itself. For the purposes of this work, pretend play is a type of play that falls

under the definition of play provided in the first paragraph, with the added characteristic that the player/players are knowingly and intentionally projecting a mental representation on top of their present situation in service of the play (Lillard 1993; Pellegrini et al. 2007). This is a broad definition, which in itself could cover other sorts of play. For example, rough-and-tumble play could qualify as pretend play if the individuals engaged were assuming the role of specific rivals (e.g., in the case of human children, superheroes). Without the benefit of language, it can be extremely difficult to determine with certainty whether any individual from a non-human species is projecting a mental representation on top of the real world.

### Pretend Play in Humans and Nonhumans

Pretend play has been studied extensively in humans. At 15 months of age, human infants are able to track the pretend actions of others and look longer at events in which a pretender violates their pretend scenario, such as pretending to fill one cup and then “drinking” from a different cup (Onishi et al. 2007). The earliest clear example of the production of pretend play is usually object substitution, in which the player uses one object in their play as a representation of some other object (e.g., a banana being treated as a phone); these behaviors emerge around 18 months of age (Leslie 1987; Piaget 1952). Sociodramatic play typically follows, in which more than one pretender engages in a shared pretend situation. This type of play develops sometime between the ages of 3 and 4 years, and even earlier when the player is scaffolded by an older more skilled partner, such as an older sibling or parent (Lillard et al. 2011; Smith 2016).

Pretend play has long been thought to play a crucial role in early human development, scaffolding development in problem solving, creativity, theory of mind, language, and executive functioning. However, a recent review of the literature has placed doubt on a causal role of pretend play, instead casting pretend play as an epiphenomenon of development within these domains (Lillard et al. 2013). Still others have suggested that pretend play forms the basis for counterfactual reasoning; the ability to engage in

pretend scenarios is what underlies the ability to consider possibilities that have not occurred (Gopnik and Walker 2013; Weisberg and Gopnik 2013).

Given the amount of time spent engaging in pretend play by young humans, we might expect to see this behavior in other social species as well, particularly among the great apes. Interest in pretend play in nonhuman animals, primarily apes, began in with the work of Groos (1898), who characterized play as a pleasing way to engage instinctual behavior before having serious need of those behaviors (see also Mitchell 2002). Potential examples of pretend play have been posited most often for “language trained” apes, but these examples are generally anecdotal and occur very infrequently, especially when compared to human children (Gomez 2008). For example, when Kellogg and Kellogg raised Gua, a chimpanzee, with their son Donald, they observed frequent imitative play from Donald, but almost none from Gua (Kellogg and Kellogg 1933, 1967; Mitchell 2002). The chimpanzee Viki was observed performing toy-pulling actions when not in possession of a toy, even acting as though the imaginary toy were stuck. Yet, after a few weeks the behavior stopped and was not observed again (Hayes 1951; Gomez 2008).

As noted, one of the earliest-to-emerge forms of pretend play in humans is object substitution. That this style of pretend play is early emerging is suggestive that it may be one of the least sophisticated forms of pretending and therefore one of the more likely candidates to be observed in non-human species. However, humans typically have a high interest in objects, manufacture artifacts for a wide variety of purposes, and young humans often have access to a number of objects as toys. The absence of these qualities makes object substitution in nonhuman animals harder to be ascertain: the objects used (rocks, sticks, leaves, etc.) are also the most readily available to them in the wild, negating some of the requirement for substitution. For instance, imagine a young chimpanzee observing her mother using a stone to hammer open nuts on a larger rock. Later, that same juvenile is herself observed banging a small stone against a larger rock, without a nut. Is that young



chimpanzee emulating her mother, is she practicing a not-yet developed skill, or is she pretending to open nuts the way her mother does? In contrast, consider a young girl who has observed her mother using a hammer to mend a fence in their backyard. Later, that child is observed swinging her teddy bear against the wall, shouting “bang! bang! bang!”. The child in that example is engaging in pretend play, but our perception of it as such is guided by the fact that the child is using a toy object and because the child is able to speak and make clear that she is considering nonreal world states.

One potential example of a nonhuman species engaging in pretend play is in that described by Kahlenberg and Wrangham (2010), who spent years observing chimpanzees in Kibale National Park in Uganda. They observed individuals engaging in a stick-carrying behavior, in which a chimpanzee would hold a stick, most often tucked between abdomen and thigh, for extended periods of time as they otherwise engaged in regular activity. The stick carrying fulfilled no obvious immediate purpose and was most commonly engaged in by juvenile females, who appeared to be spreading the behavior among each other (adult females rarely engage in the behavior, and it has not been observed in other groups). Kahlenberg and Wrangham hypothesized that this behavior might be a form of pretend-mothering, noting that the chimps occasionally engaged in mothering behaviors toward the sticks, and on the rare occasions this behavior was observed in adult females, it was in the weeks prior to their first birth, and the behavior ceased following that birth.

The stick-carrying example, however, is complicated by the fact that definitions of pretend play are reliant on the underlying mental state and intention of the player. There is no straightforward way to distinguish whether the stick-carrying apes were pretending to mother the sticks themselves, were pretending to be like other older females, or whether their mothering instincts were being co-opted by a “close enough” visual approximation in the way of a cat chasing a toy mouse.

Likewise, while human children frequently pretend to be favorite characters or role models when engaging in play, can we be certain that

juvenile apes are not pretending to be like their older counterparts when engaging in rough-and-tumble play? Not entirely, though Gomez and Martin-Andrade (2005) point out a number of reasons we should be skeptical of this idea: (1) rough-and-tumble play appears in apes without models; (2) if apes are pretending during play fighting they should pretend to engage in other adult behaviors, but do not appear to; (3) rough-and-tumble play is present in virtually all mammalian species; and (4) even in pretend-capable human children, rough-and-tumble play often occurs without the presence of pretend elements.

## Conclusion

Definitions of pretend play posit that a mental representation of a real-world object, person, or action is applied to a substitute object, person, or action. Human children often make explicit (e.g., verbally) their substitutions, and though the role of pretend play in human social-cognitive development is under debate, there is no question that it is a frequent behavior in children between 18 months and 12 years old. In contrast, there is little evidence to date to suggest that pretend play is common in other animal species.

## Cross-References

- [Emulation](#)
- [Imitation](#)
- [Play Behavior](#)

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## Prey

- [Chondrichthyes Diet](#)

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## Primary Consciousness

- [Plantae](#)

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## Primary Defenses

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## Synonyms

[Animal Defense](#); [Anti-predator Defense](#)

## Definition

Primary defenses are behavioral mechanisms or morphological adaptations that allow animals to escape detection or attack from predators. Robinson (1969) defined these as defenses that are in

operation before a predator initiates any predatory behavior, whereas Edmunds (1974) focused on the fact that primary defenses operate regardless of whether predators are in the vicinity.

## Introduction

Primary defenses are adaptations to defend against predation that are typically part of the animal's physiology and are thus genetically determined. They are distinguished from secondary defenses, which involve responses made after detection by a predator. Whereas secondary defenses can be innate or learned responses, primary defenses do not require learning or intentional responses on the part of the prey species. They typically constitute a permanent part of the organism's structure or behavioral repertoire. One possible exception is hiding, a behavior that allows an organism to avoid detection. However, it is likely that hiding is largely involuntary and results from the species adapting to live underground, under rocks, or in crevices – sometimes referred to as anachoresis.

Animals can also hide via morphological adaptations such as camouflage, known as crypsis. In this case, the coat and coloration of the animal is such that it blends into its background, making it undetectable by predators. In contrast, disruptive coloration breaks up the outline of the prey's body, as in giraffe and zebras. Some animals like jellyfish are transparent, which makes it difficult to detect them in their aquatic environments. Others like penguins employ countershading, which is dark coloration on one side of their bodies and lighter coloration on the other, so they are difficult to view from the air when swimming, but also difficult to view from below for underwater predators such as sharks. Some of these traits may serve functions other than protection against predation. For instance, penguins' coloration may also assist with UV protection and thermoregulation. Some species even resemble inanimate objects, like walking stick insects. In a special case of Batesian mimicry, the animal's coloration resembles that of an unpalatable species, causing predators to avoid attempting to

consume it. For example, harmless colubrid snakes mimic the pattern of toxic corn snakes even though they are not themselves toxic. In contrast, in Mullerian mimicry, unpalatable species resemble each other to enhance the effectiveness of their coloration. For example, a predator that has been stung by any species of wasp is more likely to be inhibited from attacking a bee's nest as all species exhibit the same distinctive black and yellow stripes.

Other examples of defensive coloration serve as a legitimate warning that the animal is unpalatable or toxic to consume, as in aposematism, which operates in conjunction with physiological traits such as the production of toxins. For example, the brightly colored poison dart frogs are typically avoided by predators that have learned to associate their appearance with violent illness. Aposematic coloration is most likely to evolve in fairly homogeneous habitats (Merilaita & Tullberg, 2005). Not all warning signals are visual, however. For example, the rattlesnake's rattle provides an auditory signal that warns other organisms to stay away. Other species use noxious odors, such as the spray of the skunk.

Other primary defenses built into an animal's morphology include hard armor such as the shell of the tortoise and armadillo, the spines of a porcupine or hedgehog, and explanate margins in insects. Because of the physical investment in developing such defenses, they are likely to evolve in species that are commonly exposed to predation, such as those in open habitats (Shinohara & Takami, 2020). It is important to note that primary defenses are not mutually exclusive with secondary defenses. For many species, both types of trait are employed, but there can be a functional trade-off. Furthermore, a trait like spines that may appear as a primary defense may actually function to prevent the organism from being swallowed once attacked by a predator (Shinohara & Takami, 2020). All of the primary defenses are widespread within insects with spines being typical (Sherratt & Kang, 2018). Defenses are under extreme selection pressure and will diversify in response to variation among predators in different environments (Shinohara & Takami, 2020).

Although it may seem intuitive that primary defenses would be the most adaptive in the sense that prey should avoid predators as early as possible in the predation sequence (Endler, 1991), researchers have found that prey species vary in terms of when they employ defenses (Bateman et al., 2014). Sherratt and Kang (2018) note that when the primary defense provides adequate protection against predation, the organism often fails to evolve any backup behavioral strategies. Primary defenses are more effective in reducing mortality rates, but predators may be able to overcome these defenses (Ruxton et al., 2018). Bateman et al. (2014) modeled the population dynamics of two prey types and a predator specialized to prey upon them. They found that the mechanism of defense would depend upon the prey species' ratio of population growth rate proportional to costs of predation. The results were similar when modeling a generalist predator. Predator-prey relations are among the most informative for demonstrating evolution in progress as predators must continually evolve mechanisms for thwarting prey defenses and prey, in turn, must continually adapt their defenses to survive.

## Cross-References

- [Aposematism](#)
- [Crypsis](#)
- [Mimicry](#)
- [Predator Defense](#)
- [Predator Detection](#)
- [Secondary Defenses](#)
- [Warning Coloration](#)

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## Primary Dentition

- [Dental Formula](#)

## Primary Memory

- [Short-Term Memory](#)

## Primary Somatosensory Cortex

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In the early twentieth century, eminent scientists like Brodmann and Campbell postulated that the well-developed outer surface of the brain can be viewed as identifiable areas performing discrete functions. They had also observed notable histological differences between areas beholding

motor functions and their sensory counterparts. Out of the various granular cortical areas, the region which lies directly behind the central sulcus in the parietal lobe, i.e., the pre-central gyrus, is the primary somatosensory cortex. *Woolsey C.N.* and his colleagues (*Woosley and Van Der Loos 1970*), after their painstaking endeavors related to this area in Macaque monkeys, found that there is a single large representation of the contralateral body surface area in the anterior parietal cortex. The profoundness of the high density points in this strip of area produced localized sensations upon stimulation. Juxtaposing the previous knowledge, it was evinced that this representation was spanning four distinct cytoarchitectonic fields, Brodmann areas 3a, 3b, 1, and 2. Unlike the lesion studies, which can be successfully applied to study the functional localization of certain areas, studies related to somatosensory cortex had predominantly used electrical stimulation evoked potentials.

### **Gross Connectivity of Primary Somatosensory Cortex (S1)**

The principal function of the area is to receive the inputs which originate from the mechanoreceptors. These information conveyed are relayed in two synapses and modulated in the thalamus. By virtue of processing, it guides the detection of mechanical stimuli such as tactile sensation and proprioception. The stimuli are gauged in terms of magnitude and precise location from body surface. Additionally, in humans, the sensations could also be perceived in cognitive dimensions which help in recognizing the shapes and size (*O'Leary et al. 2007*). In clinical settings, testing of these coherent perceptions is used to discriminate the level of lesion.

Based upon the inputs received, S1 can further be subdivided as areas 3a, 3b, 1 and 2. The afferents from the muscles project predominantly to area 3a and to perform the sensorimotor integration, it retains continuity with primary motor area. This sensorimotor projection, which is more pronounced in rodents, acts as a feed-forward circuit when their whiskers get stimulated and helps in

navigation while moving (*Ferezou et al. 2007*). Few studies (*Sherman and Guillery 2013*) have postulated the trans-thalamic pathway via which the projections from the layer V of the somatosensory cortex travel to the primary motor cortex to serve this function. The proprioceptive inputs are processed mainly in area 3a and 2. From the peripheries, cutaneous afferents project to areas 3b (*Sherman 2016*). The inputs from area 3b are usually projected to areas 1 and 2. Area 1 processes the information for texture and area 2 processes regarding size and shape. Thus, it can be ascertained that the loss of function pertaining to this area depends upon the sub-parcellation of sensory functions (*Kaas et al. 1979*). Furthermore, clusters of neurons are compartmentalized in the form of columns, which are the proprioceptive units of the S1. Each column, spanning across the histological layers receive inputs, process them, and send outputs. Inputs, usually from the thalamus are received by layer IV of the cerebral cortex and outputs, going to various regions of the brain emanate from the pyramidal neurons of layer V (*Welker and Woosley 1974*). The neurons occupying particular column is committed to respond when a particular type of receptor in the stipulated body area is stimulated. Similar to visual processing, if one cluster with larger receptor fields responds to all types of stimulation in a particular area, their counterpart clusters tries to process the complex aspects of stimulation.

### **How Submodalities of Touch Are Segregated in the Sensory Cortex?**

*Mountcastle VB* and colleagues (*Mountcastle 1998*) proposed that the cluster of neurons can be segregated further based on their capability to respond to sustained indentations. His experiments, involving penetrations of vertical micro-electrodes in the S1 of monkeys, found out neurons that were responding to the same sort of mechanical stimulus were aligned perpendicularly to the cortical surface and this paved the way for coining the threshold concept related to columnar organizations (*Mountcastle et al. 1990*). When we receive such stimuli, neurons which



respond throughout the stimuli could be deemed as slowly adapting ones and neurons which respond only to the initiation or caseation of the stimuli could be deemed as rapidly adapting. *Romo* and colleagues (*Romo et al. 1998*) found that when animals are presented with pulses resembling vibratory flutter, only rapidly adapting neurons could sense them. There exists controversy regarding what exactly determines the specifications of the cortical neurons with two school of thoughts. One is grounded on the fact that differential inputs to the cortex deciding the specifications and the other pointing the role of functions related to touch such as texture, intensity, and motion of the stimuli.

### Underpinnings Regarding the Sensory Homunculus

The representation of the various areas is usually organized and this can be represented in the form of a disproportionate and discontinuous caricature of the body, the sensory homunculus. The homunculus is oriented in such a way that regions of the head occupy the inferior part; upper limb occupies superior part of the post central gyrus. The sensations from the lower limb and perineum are represented in the medial portions of the gyrus, near the para-central lobule. The reason for disproportionate representation can be rooted back to evolutionary functionality of the particular species. For example, the vibrissae of the rats play the key function in executing the navigation and thus, they are densely represented in the S1. In fact, the sensory signal from each of the vibrissae goes to the committed collection of neurons and they are arranged in the form of barrels. A typical barrel could be described as the oval shaped dense collection of neuronal cell bodies with a hollow in the centre, made of neuropil. The representation of the rat vibrissae or human digits is determined by the combination of genetic factors and inputs relayed by afferents, which determines the specification within the area.

With evolution, the limbs of primates evolved to act as the tactile sensing organs. This change has increased the representation of the hand and

digits to a remarkable extent. In addition, this helps humans in performing precise, fine motor activities in association with cerebellum and basal ganglia. The rich sensitivity of the lips and vague tactile feelings in back of the body can also be explained by this differential representation. Differences in interpretation of the stimulus also depend upon whether it is active touching, otherwise known as haptics, which usually activates multitude classes of mechanoreceptors or passive touching.

### Implications Regarding Somatosensory Cortex in the Clinics

The above discussed knowledge plays an important role in understanding the wide spectrum of clinical presentations in clinical neurology. Sensory discrimination is a complex phenomenon which requires the multitude processing of the entire somatosensory unit. Lesions resulting in compromised functioning of the S1 present with abnormal sensations and feeling of numbness on the contralateral side of the body. The patient could sense the pain and temperature sensations only in a crude form. This is due to the inability to evaluate the precise form, intensity, and location of the presented stimuli. Higher cortical functions such as stereognosis require assimilation of prior inputs, usually the stored associated memories from other parts of the cortex. For example, when two coins of different weight are placed in the hands of blindfolded person, he tries to associate the texture with the memories and identify the object. *Semmes* and colleagues (*Semmes et al. 1960*) proposed that the effect of lesion differs depending upon the side of lesion and this can be attributed to the cerebral dominance. Left-sided lesions tend to impair the sensations of both sides whereas the right-sided lesions have impairments confined to left side alone. On the other hand, right-sided lesions tend to impair the ability to detect the direction of the provided stimuli and tactile maze learning (*Corkin et al. 1965*). Contrastingly, stimulation of S1 often elicits numbness and tingling sensation in the contralateral body surface which are not accompanied by

pain and temperature sensations. This could be evidenced as a part of “sensory march” during the aura phase of seizures related to this area. *Head and Homes* (Head and Holmes 1911) suggested that dysfunction of parietal sensory cortex leads to minor impairments which are mostly missed out during the clinical examination. For example, in such conditions, sensory perception attains fatigue and often, patients find it difficult to distinguish subsequent contacts at same time. Similarly, patients try to disregard the stimuli presented on the impaired side when two stimuli are given simultaneously on both sides (Carmon and Benton 1969). Presumably, this feature could be used to discriminate the type of lesion during routine neurological examinations.

### **Additional Pearls Regarding S1 from the Laboratories**

An underemphasized role of S1 is related to the precision grip generation which is mediated via its connection with primary motor cortex. Studies (Davare et al. 2011; Hikosaka et al. 1985) involving inactivation of S1 in monkeys have demonstrated impaired prehensile activities such as difficulty in opposition and grip forces. Even though isolated inactivation could not be studied in humans, it has been observed that when the digits are anesthetized, coordination became impaired (Brochier et al. 1999). Zainos and colleagues (Zainos et al. 1997) found that after removal of S1, an animal could detect the stimuli but could not categorize stimulus speed. Few studies also have corroborated abnormalities in S1 in fraction of patients suffering from focal dystonia of hand. Bara-Jimenez and colleagues (Bara-Jimenez et al. 1998) documented degradation of the conserved organization of S1 in these patients along with expansions of finger representations in corresponding cortical centers. Studies (Harrison et al. 2013; Winship and Murphy 2009) in which stroke was experimentally induced in rodents, a shift in the somatosensory map was

observed. This was largely because neurons which were previously involved in integrating motor commands shift their roles and take minor roles in sensory processing (Wolpert et al. 1995).

A significant feature related to the S1 is the visual enhancement of touch, which potentially modulates the visual acuity (Taylor-Clarke et al. 2002). When the subject views the location where stimulus is being provided, then, the tactile acuity tends to improve and this might be due to some under emphasized cross modal interaction between visions and touch (Saal and Bensmaia 2014). The purported reason could be that viewing of the stimuli location improves the degree of representation of tactile space for that prescribed body part and this can be compared to visualizing using magnifying lens (Schaefer et al. 2005a). Thus, we could infer that S1 could function beyond just being a veridical station for peripheral inputs because of its ability to converge tactile perception and bodily representation, modulated by other inputs such as vision. Clubbing the sensorimotor integrative functions of the S1 along with the concept of widening of “body space” purported by the visual enhancement of touch, we could infer that a potential feed-forward model operates over there by combining the sensory consequences of the intended motor command and predicted motor outcomes (Haggard et al. 2003; Schaefer et al. 2005b). Indeed the motor learning, which involves identification of the mismatch between the intended and real sensorimotor states and recalibrating by using necessary motor commands, is facilitated using S1 (Desmurget et al. 2009). Furthermore, integration of somatosensory information from both hands helps the primates to perform coordinated tasks and tactile based explorations. Few studies (Tommerdhal et al. 2006) have shown that finger stimulation of one hand might lead to altered perception of the contralateral side.

Somatosensory cortex also has a role in recognizing emotions. Adolphs and colleagues (Adolphs et al. 2000) documented that patients with lesions involving S1 had impaired ability in categorizing and rating the intensity of emotions.

The role related to somatosensory processing might presumably be due to the connection with amygdala. The empathic responses, which get induced on observing others' states (Straube and Miltner 2011), have associated sensory dimension (Keyesers et al. 2010). Upon recognizing the facial expressions (Adolphs et al. 1996) and self-generated emotions (Damasio et al. 2000), there is an associated activation of somatosensory cortices. In addition to the discriminatory component, the affective component which involves emotional processing involves synchronized action of orbitofrontal and primary somatosensory cortices (McGlone et al. 2007). For example, nociceptive stimuli usually evoke negative reactions such as punishment, whereas pleasant stimuli like caressing touch tend to evoke positive rewarding reactions (Rolls et al. 2003). When the stimuli are given subsequently, we try to preempt the outcome by comparing with previous experience. Sometimes, a mere thought regarding the experience is enough to make us imagine the prior outcome. To sum up, somatosensory cortex, containing conserved representations of the body, maintains the internal and external awareness states (Critchley et al. 2004) and this can be equated with interoceptive attention. Studies (Braun et al. 2005) using functional imaging have documented higher activation of somatosensory cortex when an individual starts bothering about the existing emotional state.

## Plasticity of Somatosensory Cortex

The somatotopic maps, even though being conserved for respective body surfaces, have mutable degrees of plasticity. This can be observed in conditions such as amputation, where the input coming to a restricted area gets lost. In due course of time, the restricted area becomes responsive to neighboring responsive surfaces. Ramachandran VS and colleagues (Ramachandran et al. 2010) did significant amount of research to found the cross activation of neighboring areas after a hand is being amputated. This induces a form of tactile

illusion which is referred as phantom limb (Ramachandran and Hirstein 1998). Amputees in such cases experience the touch to their face as local and referred sensation on the phantom hand which can be deemed as altered reference fields. In one of the models (Flor et al. 2006) developed for pain due to phantom-limb, it was observed that activation of afferents from the face and stump of missing limb elicited sensations in the perceptual areas of missing limb. But these sensations felt in the amputated limb is mostly painful (McCabe et al. 2005), which is plausibly due to the incongruent mismatch happening at different levels of sensorimotor pathway. In addition, expression of genes aiding in synesthesia helps in cross-activation throughout the brain, and in professionals such as pianists the expression is significantly higher.

In addition to the limited cortical reorganization, cortical neurons demonstrate significant degrees of axonal plasticity. After subcortical lesions, it was found that ascending projections from thalamus to sensory cortex were bypassing the lesion areas (Staudt et al. 2006) and reaching their destination in the post-central gyrus. This suggests that the sensory neurons which convey sensations from periphery to specified sensory areas are "committed" much earlier in developmental stages.

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## Primate

- [Hominoidea Morphology](#)
- [Hominoidea Navigation](#)

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## Primate Analogies

- [Primate Perspectives on the Evolution of Human Behavior](#)

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## Primate Behavior

- [Stone Tools](#)

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## Primate Cognition

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## Synonyms

[Simian and prosimian mental processes](#)

## Definition

The study of how primates acquire, process, store, and use information in their environment (Shettleworth 2010).

## Overview

Primate cognition is the study of cognitive processes in nonhuman primates (hereafter, primates). The distinction between cognitive processes and behavioral ones is not easy, but most researchers would likely agree that cognitive processes, as compared to behavioral ones, are characterized by higher flexibility (i.e., individuals flexibly perceive the situation and flexibly react to it, depending on their own goal), and involve some form of mental representation (i.e., individuals mentally assess the situation, by also relying on information sources other than direct perception; Tomasello and Call 1997). Therefore, cognitive skills allow individuals to flexibly respond to a situation according to their goals and based on their mental representation of the situation, thereby making complex decisions. However, disentangling cognitive processes from behavioral ones is not always an easy endeavor, as mental processes cannot be directly observed, and simple noncognitive processes can also lead to complex behavioral patterns (Shettleworth 2010; Tomasello and Call 1997). Moreover, perceptual, motivational, and motor mechanisms may also interplay with mental ones, making it hard to reliably infer mental



processes from the behavioral observation of animals. Therefore, some authors prefer to use a broader definition of cognition, referring to primate cognition as to the study of how primates acquire, process, store, and use information in their environment (Shettleworth 2010). This broader definition implies that cognition may also include perceptual and simple learning processes, as in this view mental representations are not required for a process to be considered cognitive. Given that mental processes are not easily inferred from behavioral observations, other researchers prefer to envision cognition as a distributed process, in which interactions between individuals (rather than mental processes) are the main object of study (see Johnson 2001).

The study of primate cognition dates back at least to Charles Darwin. Darwin was the first scholar known to describe cognitive processes as biological adaptations that humans may share with other primates, and whose evolutionary origins can be traced back by comparing species with each other (see Tomasello and Call 1997). After Darwin, however, the study of primate cognition remained largely unexplored for several decades. Brilliant exceptions include the work by Wolfgang Köhler and Robert Yerkes at the beginning of last century. Köhler was a psychologist who was mainly interested in the primate ability to spontaneously solve novel problems. In a series of seminal studies, for instance, he systematically assessed how captive chimpanzees use tools to access out-of-reach food, setting the agenda for many future studies on primate cognition. Robert Yerkes, in contrast, was more generally interested in the study of primate behavior, and with several of his scholars and associates, he conducted groundbreaking studies on many different topics, like spatial memory, cooperation, communication, and, especially, the effects of enculturation on the development of primate cognition. For a long time afterward, however, most researchers working with nonhuman animals followed a behaviorist or ethological approach, with little interest for cognitive processes and the study of primate cognition. Behaviorists like Harlow, for instance, were mainly concerned with the study of observable behavior and learning processes, while ethologists like Tinbergen and Lorenz were

mostly devoted to the study of innate behavioral patterns, and the evolutionary origins of these behaviors (see Shettleworth 2010; Tomasello and Call 1997). In the 1960s, the situation completely changed, thanks to the first field studies in wild populations and the implementation of new systematic studies, especially in the area of primate communication (see Tomasello and Call 1997). These studies converged in revealing unexpectedly complex behaviors, which were largely suggestive of the existence of mental representations and cognitive processes. Since then, the number of studies on primate cognition has been steadily increasing.

Historically, differences in cognitive skills across primate species have been typically interpreted in line with the existence of a *scala naturae*, with species being phylogenetically close to humans also having more complex cognitive skills. Nowadays, the notion of a *scala naturae* is completely outdated, and it is indisputable that complex cognition repeatedly and independently evolved in different taxa as a result of convergent evolution (see Shettleworth 2010; Tomasello and Call 1997). Therefore, most researchers have turned to a socio-ecological approach when studying primate cognition. The socio-ecological approach mainly views cognition as an evolutionary adaptation to the specific socio-ecological challenges faced by a species. Through an increase in their cognitive abilities, individuals may better deal with the socio-ecological conditions in which they live, and thus be selected for during evolution. However, phylogenetic relationships are still crucial to understand the evolution of cognition. For instance, if two species share a long evolutionary history, it is possible that their cognitive skills will be similar, simply because they share some cognitive traits that emerged in their common ancestor. Therefore, a phylogenetic approach remains crucial to account for the species' evolutionary history when testing other evolutionary hypotheses on the emergence of complex cognition.

According to the socio-ecological approach, ecological challenges have played a crucial role for the evolution of primate cognition. If individuals face complex ecological challenges while

foraging, these challenges may be more efficiently faced through the evolution of complex cognitive skills and thus, larger behavioral flexibility. Several authors have proposed different ecological challenges that might be linked to the emergence of complex cognitive skills. First, primate species feeding on sparsely and patchily distributed food items may require an extra processing capacity to predict when and where to forage (e.g., Milton 1981). Fruits, for instance, are spatially and temporally spread in the environment, and keeping track of them through space and time might require increased spatial memory. Therefore, a high degree of frugivory has been traditionally considered a good predictor of enhanced spatial memory in primates. In the same line, feeding on a highly nutrient diet might allow the evolution of larger brains (as brain tissue is metabolically expensive), which could in turn be linked to enhanced cognitive skills. Second, dietary complexity, as assessed in terms of dietary breadth (i.e., the number of dietary categories consumed by a given species), may be linked to the evolution of complex cognition. Primate species with larger dietary breadth, for example, might be more likely to exploit novel food sources and might have thus evolved enhanced cognitive skills to better cope with this variation. In primates, there is indeed evidence that species with larger dietary breadth also have more complex cognitive skills, at least in some domains (e.g., MacLean et al. 2014). Third, extractive foraging (i.e., the ability to process plants, open nuts, dig insects, and use tools to access embedded food) might be linked to higher hand and hierarchical coordination, better understanding of means–ends relationships and increased propensity for social learning (e.g., Parker and Gibson 1977). Finally, predation may also represent an important selective pressure for the evolution of complex cognitive skills. When facing a higher predation risk, primates may evolve specific strategies to enhance their survival, including better communicative skills and the ability to more quickly classify predators and more effectively warn group members about danger as compared to species facing lower predation risks (e.g., Seyfarth et al. 1980). These skills may be especially enhanced in closed (and mixed)

habitats, where predators may be harder to detect (and cognitive and communicative skills might be especially needed).

Other authors, however, suggest that social challenges may be a stronger selective pressure for the evolution of complex cognitive skills in primates. When social life is complex, individuals need to use flexible cognitive strategies to recognize others; keep track of their relationships; and predict, coordinate, and manipulate their behavior (e.g., Humphrey 1976). In contrast to objects, social partners are reactive, unpredictable, and might respond with different behaviors to individuals' actions. Therefore, social complexity might posit higher cognitive challenges than ecological complexity, and could be a stronger selective pressure for the evolution of cognition. To date, there is yet no consensus on how social complexity should be defined. First, some authors have proposed social group size as an index of social complexity linked to enhanced cognitive skills (Dunbar 1998). However, group size does not necessarily correspond to the number of individuals in a group, and effective group size (i.e., the mean number of partners with whom individuals socially interact) might be a better measure of social complexity. Second, other scholars have argued that both group size and effective group size are a crude measure of social complexity, as social complexity would rather depend on the quality of social interactions. More explicitly, it would not be species living in larger social groups to show enhanced cognition, but rather species living in social groups with a higher frequency of complex social behaviors (Kudo and Dunbar 2001). Third, other researchers have defined social complexity in terms of fission–fusion dynamics. In particular, individuals living in groups that frequently split in subgroups of varying size and composition might need specific cognitive skills to better cope with the specific social challenges they face (e.g., enhanced memory to remember absent individuals, higher analogical skills to deal with fragmentary information about group members that are temporarily absent, higher inhibitory skills to adapt to continuous changes in group size and composition; see Aureli et al. 2008). Fourth, primates engaging in

monogamous pair-bonding might also require higher cognitive skills than primates living in larger cohesive groups, to better establish and coordinate complex behaviors with their partner (Dunbar 2009). Dunbar's original hypothesis mainly referred to monogamy in terms of sexual behavior, but this hypothesis is usually extended to predict that social complexities (and thus cognition) are higher if individuals preferentially interact with one or few partners, as individuals need to complexly coordinate behavior with few valuable partners.

Clearly, the list of evolutionary hypotheses presented here is not exhaustive. Moreover, different hypotheses are not necessarily mutually exclusive, because multiple selective pressures might independently but simultaneously act on different cognitive skills. In line with this, not all evolutionary hypotheses make the same predictions in terms of the cognitive skills involved. While some hypotheses predict an overall enhancement in cognitive skills, others only predict an enhancement in specific cognitive skills, assuming a certain degree of mind brain modularity. Indeed, cognitive skills across different domains are not always correlated with each other (see Shettleworth 2010). Therefore, direct comparisons of multiple primate species are essential not only to test evolutionary hypotheses about cognitive evolution, but also to understand the extent to which different cognitive skills are related to each other across individuals and species. Moreover, the relationship between cognitive skills and brain size is not straightforward. Brain tissue is highly costly in energetic terms, and can thus only be maintained if it provides adaptive advantages (Aiello and Wheeler 1995). In humans, brain size positively correlates with general intelligence, but in other species, there is little experimental evidence confirming this relationship. In primates, for instance, relatively larger brains are associated with a better ability to learn and innovate (e.g., Reader and Laland 2002). However, there is to date no consensus yet on the brain measures that can best serve as proxy for complex cognition. Some authors, for instance, use absolute brain size as a proxy for cognitive skills, while others maintain that

relative brain size, encephalization quotient (i.e., the ratio between observed and expected brain size), or number of neurons are more precise measures of cognition.

Besides differences across species, primate cognition may also be characterized by important intra-specific variation. Intra-specific variation in cognition can happen at different levels, including variation across individuals belonging to the same group, and/or across conspecific groups and populations (Strier 2016). Within the same group, for instance, individuals may show different cognitive skills depending on their age, as some cognitive skills require some time to develop during infancy, and/or may decrease when individuals become older. Across groups, moreover, cognitive differences may result from genetic variation (e.g., if groups belong to different populations) or from differences in the socio-ecological conditions in which individuals grow up, as the socio-ecological challenges experienced through life might also affect the emergence of cognitive skills. Along this line, one central aspect for the study of primate cognition is the possibility that individuals living in captive groups, which are commonly used as study subjects in cognitive studies, may importantly differ in their cognitive skills from their conspecifics living in the wild. Captive primates experience atypical living conditions during their ontogeny and, according to some authors, they might therefore develop unique cognitive skills, thus limiting or even hindering any generalization to wild primates (Boesch 2021). In particular, socio-ecological constraints experienced during life history, continuous exposure to human cultural milieu, lack of predation risk and high exposure to novel objects in captivity might all affect the development of cognition, preventing captive primates from being representative models for the study of cognition. However, studies in captivity provide essential information on the cognitive potential of a species, and allow to systematically control for the effect of several confounding factors in a way that is often not possible in the wild (Tomasello and Call 2008). Therefore, the study of cognition in both wild and captive settings should be viewed as necessary and

complementary for a thorough understanding of primate cognition.

Traditionally, the study of primate cognition has been divided into the study of physical and social cognitive skills (e.g., Shettleworth 2010; Tomasello and Call 1997). At first sight, this division might appear arbitrary, because several cognitive skills used in the physical domain are likely also used in the social domain, and the other way around. However, the traditional distinction between physical and cognitive skills is useful to differentiate between skills that most likely evolved in the foraging context (i.e., physical cognitive skills) and those that probably emerged as a response to the specific social challenges faced by a species (i.e., social cognitive skills). This approach is in line with a modular or partly modular view of cognition, according to which cognitive skills, at least to a certain extent, consist of specialized modules that evolved rather independently from each other, reflecting adaptations to specific socio-ecological problems. Although other scholars emphasize how individual cognitive skills often correlate with each other, with most of the variance across domains being accounted for by a single factor (i.e., G, or general factor of intelligence; see Plomin 2001), it is likely that independent domain-specific modules coexist in the brain with a general factor of intelligence. In particular, while some properties of the brain (e.g., the amount of gray matter) may generally affect multiple areas of the brain, leading to correlations across domains, cognitive processes might be largely localized in discrete regions, so that individuals and species having better cognitive skills in some domains would not necessarily excel in the other domains. Therefore, the distinction between physical and social cognitive skills appears to be both practical and theoretically founded.

Physical cognitive skills include all those cognitive abilities that likely evolved in a foraging context, to more effectively locate, quantify, and process food. Among these skills, researchers usually identify the ability to understand objects and space, understanding of time, quantitative cognition, and causal and inferential reasoning (Shettleworth 2010; Tomasello and Call 1997). First, primates

generally show advanced cognitive skills in terms of object permanence. In particular, primates can successfully locate an object that has moved out of view, and most species have also shown the ability to follow visible and invisible displacements of objects across a variety of conditions (for a review, see Cacchione and Rakoczy 2017). Second, primates can effectively locate resources in their environment. Most species likely do it by using habitual routes that allow them to routinely monitor potential food sources, with little cognitive implications. However, other species might use cognitive maps to flexibly navigate through space, creating mental representations of their environment (Shettleworth 2010; Tomasello and Call 1997). Wild chimpanzees (*Pan troglodytes*), for instance, can approach food sources from multiple directions; they mostly travel in straight lines to reach food, and seem to have expectations about their distance to the food sources (Normand and Boesch 2009). Therefore, they appear to have a mental representation of their home range, relying on cognitive Euclidean maps to navigate through it. Third, primates are known to have relatively good short- and long-term memory. However, much less is known about their understanding of time and, in particular, about their ability to recall individual past events (see Lewis et al. 2019). Similarly, little is known about primate ability to plan future events, although some evidence suggests that at least great apes can plan ahead by, for instance, producing and gathering stones that they require for later use (e.g., Osvath 2009). Fourth, primates are proficient in making relative quantity judgments, reliably selecting the larger amount out of two discrete stimuli (i.e., food items) or even out of two continuous ones (i.e., liquids; for a review, see Beran 2017). Some species are also proficient in “summing” quantities by, for instance, preferring the container in which more food pieces have been inserted, one after the other. Moreover, some studies have tested whether primates show numerical cognition, by exclusively relying on numerical cues (e.g., number of items) rather than using more general nonnumerical cues (e.g., density or size) to select the larger stimuli. These studies have reliably shown that apes and monkeys can also make numerical judgments across a variety of conditions (see Beran 2017). Finally, primates have been tested with

different approaches to assess their understanding of means–ends relationships and causality (for a review, see Völter and Call 2017). A classic setup that has been used to test causality consists in presenting individuals with two strings, only one of which is attached to the food. If primates understand means–ends relationship, they should spontaneously select the string attached to food, regardless of the spatial disposition of the strings – a task that most species can proficiently solve, at least in the easier conditions. In order to assess their understanding of causal relationships, primates have also been tested with trap tasks and tool use tasks. In trap tasks, for instance, a food reward is placed in a Plexiglas tube with a central hole, and the food can be extracted only by moving it in the direction opposite to the hole, where otherwise the food disappears. Primate performance in these tasks is generally poor, unless the cognitive demands of the task are reduced (e.g., without requiring primates to use a tool; see Völter and Call 2017). In tool use tasks, instead, researchers can assess primate ability to flexibly use tools, and/or to select the most effective tools to obtain a reward, based on their functional properties. However, one should note that, when studying causality, it is often not easy to disentangle whether primates really establish causal relationships between stimuli (i.e., inferring the cause from the effect, or predicting the effect from the cause), or whether they simply learn to associate them through time.

Social cognitive skills include those cognitive abilities that likely evolved in a social context, to more effectively interact with others, predict and manipulate their behavior (see Humphrey 1976). One of the most basic social cognitive skills is the ability to acquire, process, store, and use social knowledge (Shettleworth 2010; Tomasello and Call 1997). Abundant evidence shows that primates have complex knowledge about third-party relationships (e.g., kin or rank relationships). For instance, many primate species show redirected aggression, behaving aggressively toward a previous aggressor's kin, thus suggesting that they recognize kin relationships between other individuals. Moreover, primates can classify group members according to different characteristics, simultaneously relying on multiple

information sources. These processes can rely on cognitive mechanisms (e.g., primates learn about third-party relationships through experience, they create mental categories for these relationships, and then generalize them to other contexts/pairs of individuals), although noncognitive explanations may also partly explain these processes (see Shettleworth 2010).

Depending on the species, primates also appear to have second-order intentionality; i.e., they do not only have intentional states (e.g., knowledge, desires, and beliefs; first-order intentionality), but also understand that others have intentional states, which might differ from their own ones (see Shettleworth 2010; Tomasello and Call 1997). Sometimes, researchers also refer to this ability (or to a subset of these abilities) with the term “theory of mind,” or “mental state attribution.” These abilities might be evolutionarily advantageous to more effectively interpret, predict, and manipulate others' behavior, in cooperative and competitive contexts (see Dunbar 1998; Krupenye and Call 2019; Shettleworth 2010; Tomasello and Call 1997). Through the years, several studies have tested whether primates show “theory of mind.” However, it is often hard to disentangle whether primates really understand others' mental states, or whether they are rather inferring them from the observation of others' behavioral cues (for a discussion, see Krupenye and Call 2019). Several studies have shown that primates are sensitive to others' visual (and auditory) perspective, and understand others' attentional state. Apes and monkeys are sensitive to others' gaze, they know what others can and cannot see, and use this knowledge to adjust their behavior. Primates, for instance, follow others' gaze around barriers, more likely use visual gestures when being in the partner's visual field, and/or after entering it, and in a competitive context they prefer to reach for a food that other group members could not see (for a review, see Krupenye and Call 2019).

Moreover, abundant evidence shows that apes and monkeys can understand others' goals and intentions. Primates, for instance, behave differently to humans that failed to share food with them because they were impeded, as compared



to those that did not want to do it. According to some studies, some primate species are also able to understand others' goals and accordingly help them (see Krupenye and Call 2019; Shettleworth 2010; Tomasello and Call 1997). For a long time, however, researchers could not find experimental evidence that primates also understand others' beliefs. In particular, apes failed to use others' false beliefs to maximize their food intake across several studies (see Krupenye and Call 2019; Tomasello and Call 1997). These results were in line with the idea that understanding false beliefs may be especially demanding, by requiring primates to create and maintain two conflicting mental representations: one of their own view of the world, and one of the other individual's view. In the last years, however, the use of novel technologies has allowed researchers to also demonstrate understanding of false beliefs, at least in great apes. By using eye-tracking procedures, researchers could show that apes understand others' false beliefs, anticipating where others would search if they had a false representation of reality (see Krupenye and Call 2019).

Furthermore, the study of social cognition has also included the assessment of primate prosocial skills (i.e., behaviors performed to alleviate the needs of other individuals or to improve their welfare, without the actor necessarily incurring extra costs to provide these benefits). In some primate species, individuals cooperate with each other by hunting in group, rearing infants together, forming coalitions, or sharing food, but these complex behaviors do not necessarily require cognitive skills to unfold. Some of the tasks used to study prosociality in primates have investigated the exact motivations underlying prosocial behavior (e.g., inequity aversion). Other studies, however, have focused on the cognitive underpinnings of cooperation (e.g., understanding each other's role, understanding of others' goals and intentions).

Another area of great interest in primate social cognition is social learning. Social and cultural learning allow the transmission of knowledge and skills across individuals and generations, respectively, and are thought to have played a crucial role for the evolution of human cognition

(see Cacchione and Amici 2020, for a review). To date, social learning is known to be widespread across a variety of taxa, but more complex forms of social learning, like imitation and culture, are likely much less common. In humans, imitation and cultural learning usually rely on complex cognitive underpinnings, like shared intentionality and shared experiences, whereas in other primates these forms of social learning likely unfold in cognitively less complex ways (see Cacchione and Amici 2020). Finally, researchers working on social cognition have also devoted special attention to primate communication. With regard to vocal communication, for example, some species are known to use specific alarm calls depending on the predator approaching, they appear to vocalize intentionally, and can even take other group members' knowledge into account when informing them about the presence of danger (see Cheney and Seyfarth 2018, for a review). Moreover, primates anticipate how listeners will respond to their calls, and may also eavesdrop when others vocalize, suggesting high flexibility in vocal communication and likely complex social cognitive skills.

Despite clear advances in the study of primate cognition, also thanks to the use of new technologies, there are still several problems that affect this research area. First, as we briefly outlined above, it is often hard to exclude alternative lower-level behavioral explanations to seemingly cognitive phenomena (e.g., Povinelli 2020). Well-thought experimental approaches can surely help to address this issue, but gathering conclusive evidence on the cognitive underpinnings of a behavior is often not easy, especially when using an observational approach. Similarly, it is not always easy to disentangle individuals' cognitive performance from other confounding factors (like motivation or perceptual skills; see, e.g., Schubiger et al. 2020). Second, and in line with this, cognitive studies usually include very few individuals. This is often unavoidable due to logistic constraints and low availability of study subjects. However, the inclusion of few individuals clearly poses a serious problem to the study of primate cognition due to the important intra-specific variability that exists in primate behavior

and cognition. Primates, for instance, might show a different performance in cognitive tasks (and/or have different cognitive skills) depending on their sex, age, rank, personality traits, and/or life histories. These differences may be especially relevant across wild conspecific groups (which often experience different ecological challenges), but they may also be present across captive primate groups, depending on the living conditions across study sites. Such a high intra-specific variation has likely contributed to the lack of reproducibility that unfortunately characterizes much cognitive research and general research in psychology (Open Science Collaboration 2012). Third, studies on primate cognition are still often focused on very few species. Clearly, this also largely depends on practical considerations. In captivity, some species are simply not present, and in the wild, it might simply be hard to come up with cognitive tasks that fit with the peculiar socioecology of the species (e.g., nocturnal primates). However, failure to include more primate species might lead researchers to reach wrong conclusions. For instance, it is possible that some cognitive skills are more widespread than actually thought, but that researchers have not yet identified the right target species. Finally, most studies in primate cognition have been conducted in captivity, by isolating individuals from their social groups. This approach has clear benefits, in that it often allows to optimally control for the effect of some confounding factors (e.g., competition in the group). However, some researchers suggest that isolating individuals from their social groups might affect their cognitive performance, and that cognitive tasks should ideally be planned to allow testing in a social setting, thus also increasing their ecological validity (Cronin et al. 2017).

## Cross-References

- Culture
- Episodic Memory
- Inhibition
- Intentionality
- Language Research: Great Apes
- Long-Term Memory

- Nonhuman Primates
- Primate Communication
- Primate Diet
- Primate Perspectives on the Evolution of Human Behavior
- Primate Sensory Systems
- Primate Social Structure
- Short-Term Memory
- Social Learning
- Theory of Mind

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## Primate Communication

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## Introduction

Communication is defined in very many ways. Biological approaches often emphasize that communication is mediated by evolutionary shaped signals (Krebs and Davies 1993), selected for the purpose of communication and the receivers' ability to successfully decode such signals. Some definitions differentiate between non-behavioral and behavioral communication, with the latter not considering invariant displays, such as fur coloration, as means of communication (Smith 1977).

Psychological approaches, on the other hand, focus more on the cognitive mechanisms underlying communication, with central interest in the question whether the actor uses specific signals intentionally to influence others' behavior. Since intentional use is one of the key characteristics of human language, research on primate communication is often motivated by an interest in the origins of human language. By comparing the communicative systems of humans and non-human primates, scientists aim at identifying potential precursors to human language in our closest relatives, the nonhuman primates. As a result, research into primate communication might focus more on cognitive processes than research into other animals' communication.

However, *which* aspects of primate communication are investigated very much depends on

the signal type or “modality.” To communicate, primates use a variety of different sensory channels – olfaction, touch, vision, and audition. Since olfaction has hardly been studied with regard to its cognitive foundations, only facial (visual), vocal (auditory), and gestural signals (tactile, visual, auditory) will be considered for the purpose of this entry. In the next section, the different signal types are defined, followed by a summary of different evolutionary scenarios, each suggesting a different modality as the potential origin human language. Finally, an overview of research into primate communication is provided, to demonstrate which features are studied as potential precursors of human language. However, this overview is not exhaustive, as it can only provide glimpses at the rich body of existing studies. Most importantly, the aim is not to argue in favor or against any theory of language evolution but to highlight that research foci differ in vocal, facial, and gestural research, which hinders systematic comparisons across these modalities, and as a result, impede a multimodal approach to studying the origins of human language.

## Defining Signal Types

The classification of different signal types is often confusing. Most signals are not “pure signals” with regard to their sensory modality, since they can rely on more than one sense. For example, a gesture can convey information via different sensory channels, like the gorillas’ “chest beat,” which produces an audible sound together with a visible movement. Furthermore, the production of one signal type might be inextricably tied to another signal type. For example, producing a “scream” vocalization is linked to the specific “scream face” expression. Finally, gestures comprise signals of different modalities, including visual, tactile, and auditory signals. Thus, different signal types are not always differentiated based on their sensory modality but might be rather categorized based on the different cognitive mechanisms assumed to underlie their usage (Liebal et al. 2013).

Primate **gestures** are considered voluntarily produced, purposeful behaviors, directed at specific individuals to influence their behavior (Leavens et al. 2005). They not only comprise different sensory modalities (visual, tactile, auditory), but they can also be produced with different body parts, such as the limbs (“offer arm”) or the head (“head bob”), and they may involve movements (“slap”) but also postures (“present”). Visual gestures, like “extend arm” or “present,” are distant signals and, in addition to manual gestures, may also include body postures and head movements, but not facial expressions. Tactile gestures, such as “slap” or “gentle touch,” involve the physical contact between two interacting partners. Auditory gestures produce a sound with different body parts, such as “hand clapping” or “chest beat,” but unlike vocalizations, they do not engage the vocal cords in the production of the sound (Call and Tomasello 2007). In contrast to auditory gestures, **vocalizations** (or calls) emerge from the vibration of the vocal folds within the larynx. They should be differentiated from sounds, such as “lipsmacks” or “raspberries,” which are also auditory signals, but they do not engage the vocal cords. Vocalizations are graded signals, which can vary in their structural properties, such as frequency, amplitude, and temporal pattern. **Facial expressions** are also graded signals, and are defined in different ways. While some refer to them as “facial gestures” (Maestripieri 1999), others consider facial expressions a separate signal type than visual gestures, although though both are visual signals. Finally, some specifically focus on orofacial movements to study communicative mouth movements like “teeth chatter” or “lipsmacks.”

## Origins of Human Language

There numerous scenarios suggesting how language might have evolved. While comparative researchers agree that precursors to human language, including neurobiological substrates, anatomical structures, or cognitive skills, are shared

with other primates, they are at odds with regard to the modality from which language might have evolved.

For example, researchers proposing a **gestural origin** of human language suggest that our ancestors initially communicated by using voluntarily produced manual gestures, with spoken language evolving on top of this visual communication system (Hewes 1973). This is supported by the close link between gestures and spoken language, since gestures (in addition to facial expressions or vocalizations) remain to be an integral part of human communication, even if humans possess a fully fledged language (Kendon 2004). Research into developmental pathways of humans shows that before infants start to produce their first words, they already use a variety of gestures, such as showing or pointing to objects (Iverson and Goldin-Meadow 1998). Further support for a gestural origin is provided by the discovery of mirror neurons, which are active both when an individual performs and perceives a specific action, such as manual grasping movements or communicative mouth movements (Rizzolatti and Arbib 1998). Thus, the finding that the corresponding brain area in nonhuman primates seems to be a homologue of Broca's area in humans indicates the evolutionary close link between manual actions and language production.

On the other hand, proponents of a **vocal origin** of human language argue that because speech is using the acoustic channel, language most likely emerged from the vocal abilities of our ancestors (Cheney and Seyfarth 2005; Zuberbühler 2005). In support of a vocal origin, they highlight that there is evidence for both referential (semantical) and syntactical structures in vocalizations of nonhuman primates. Thus, they use functionally referential calls, which seem to refer to specific objects or events, and combine single vocalizations into meaningful, sometimes rule-governed sequences.

Only few theories suggest a **facial origin** of human language. However, orofacial movements receive increasing attention, since one of the major shortcomings of gestural theories is that they are not providing convincing explanations

for the transition from visual, gesture-based communication to vocal, spoken communication (Wacewicz et al. 2016). Thus, orofacial movements may represent the evolutionary link between visual gestures and acoustic utterances, since they convey both visual and auditory information. Furthermore, like manual gestures, orofacial movements are voluntarily produced. Thus, language might have evolved directly as speech from previously non-communicative ingestive mouth movements to a flexible repertoire of syllables in a way that these "...ingestion-related cyclicities of mandibular oscillation (associated with mastication [chewing] sucking and licking) took on communicative significance as lipsmacks, tonguesmacks, and teeth chatters..." (MacNeilage 1998, p. 499).

Together, this section shows that researchers favor different modalities to explain the evolution of language and, consequently, investigate different aspects of primate communication. The following section will summarize the current knowledge for each modality with focus on those findings from comparative research on primate communication relevant for the understanding of language evolution.

## What Do We Know About Primate Communication?

A review of existing studies on primate communication, covering almost 60 years up to the year 2008, impressively demonstrated that our knowledge varies drastically across modalities and primate taxa (Slocombe et al. 2011). For example, two thirds of the total of existing studies ( $N = 553$ ) focused on vocalizations, one fifth on facial expressions, and only 9% on gestures. The majority of vocal research investigated different monkey species, while gesture research almost exclusively focused on great apes, with an apparent lack of gesture research investigating populations in their natural habitats. With regard to the methods used to explore them, experimental approaches are commonly applied to study vocalizations, while observational methods are mostly



used to study gestures and facial expressions. This again shows that there are considerable gaps of knowledge in primate communication and that results are difficult to compare across modalities and species. Most importantly, however, research into primate communication is almost exclusively unimodal, focusing on only one modality at the time. Therefore, with very few exceptions, very little is known about if and how different modalities are combined and how they influence each other.

### Gestures

While classic studies investigated gestures as elements of a species' behavioral repertoire, more recent studies focused more on the psychological aspects and, in this context, the cognitive mechanisms underlying gestural communication (Call and Tomasello 2007). Not only do gesture studies mostly consider great apes, many of them investigate chimpanzees, in both captive and natural settings. Little is known about small apes and monkeys, except for few macaque and baboon species, and there are virtually no studies investigating if New World monkeys or lemurs use any gestures at all. Since most of gesture research is conducted in captive settings, it is currently unclear whether the repertoires found in captive apes are also representative for wild populations. Furthermore, the total number of gestures reported for a given species may vary across studies, because researchers use different methods of data collection or different measures for discriminating between gesture types. For example, the number of gorilla gestures described in several publications varies between 30 and 100, indicating that it is rather difficult to compare findings across different studies.

### Variability of Gestural Repertoires

To highlight the flexibility of the primate gestural communication, much attention has been paid to the variability of gestural repertoires across individuals, age groups, or populations, as well as to different mechanisms of gesture acquisition. Thus, a considerable degree of variability indicates that – unlike in the case of vocalizations or

facial expressions – new gestures can be acquired and/or already used gestures can be modified over an individual's lifetime.

Considering the variability of individual gestural repertoires, most is known about great apes and siamangs, one species of small apes. Across species, gestural repertoires increase with age but decrease again in adults. Thus, many gestures are used during play, but since this context is of less importance for adults, they consequently use fewer gestures. In general, there are only few reports for group-specific gestures, which are used by the majority of individuals of one group, but not in another one. In such cases, it is important to exclude the alternative explanation that specific housing conditions in captivity or ecological factors in natural habitats are responsible for the emergence of group-specific gestures. Some gesture studies report the use of idiosyncratic gestures, which are used by single individuals only, while other researchers point out that such findings might be the result of too short observational periods, which are not sufficient to capture complete gestural repertoires. Together, findings indicate that, while individual repertoires may vary over lifetime, overall, there is only limited variability across different groups and within a species.

Some researchers take this even further and argue that also across great ape species, there is very little variability between their gestural repertoires, suggesting that they are species-specific and most likely genetically determined (Genty et al. 2009). Others suggest that gestures are shaped in repeated social interactions and via this process of ontogenetic ritualization, gestures emerge from previously non-communicative behaviors (Tomasello et al. 1994). This is based on the findings that repertoires vary considerably across individuals and age groups and that specific gestures might be shaped in repeated interactions within dyads, such as initiations of "carries" in bonobo mother-infant dyads. Note that up to date, only very few studies use a longitudinal approach to study gesture acquisition over the first years of life in nonhuman primates. From the little we know, it seems that at least in great apes, both genetic transmission and social factors shaping

communicative behaviors are involved in the acquisition of gestural repertoires.

### Intentional Use

Primate gestures are, by definition, intentionally used signals. A variety of different markers of intentionality are applied across studies, including the social use of a signal in the presence of an audience, accompanying visual orienting behavior or gaze alternation, the adjustment to the recipient's attentional state including the use of attention-getting behaviors, as well as persistent and elaborated gesture in case of the failure of communicative attempts (Leavens et al. 2005). However, there is little agreement with regard to which and how many of these markers should be considered to decide if a given behavior is produced intentionally (Liebal et al. 2013). In the following, some of the main findings regarding each of these criteria are briefly summarized.

The *social use* of gestures has been mostly studied in experimental settings. Great apes or monkeys request food from a human experimenter in varying conditions, with the experimenter present or absent, and/or visually attending or not attending. These studies showed that both monkeys and apes use gestures only in the presence of an audience.

*Visual orienting behavior*, and specifically eye contact or gaze, is a measure used to identify if a gesture is directed toward a specific individual. However, given the lack of a white sclera in most of the nonhuman primate species, for the human observer, it is often impossible to reliably decide if eye contact is established or not. Therefore, some studies use a related measure, *gaze alternation*, with the gesturing individual repeatedly gazing between the recipient and another such entity, such as another individual, an object or a location (Leavens and Hopkins 1998). Note that this measure is only applicable for triadic interactions, which in addition to the gesturer and recipient also involve a third entity. However, this only applies to few of the gestural interactions of non-human primates.

The *adjustment to the recipient's attentional state* is well studied across a variety of ape and monkey species (Call and Tomasello 2007). In

interactions with either conspecifics or a human experimenter, they only use visual gestures if the recipient is visually attending. If the recipient is not attending, however, they rarely use gestures to attract the other's attention, at least in interactions with conspecifics. In experimental studies with humans, results are more mixed, with some studies reporting that great apes use attention-getting behaviors, such as auditory gestures, in case the human is present, but not oriented toward them, while other studies failed to confirm this. Similarly, some experimental studies showed that in more complex settings, with more than one experimenter present confronting the ape with varying attentional states and body orientations, apes were less sensitive to the human's attentional state (Povinelli and Eddy 1996). It seems that different information is conveyed by the orientation of the face and body, respectively, in a way that the face indicates the recipient's attentional state, while body orientation implies whether the human is able to deliver any food or not (Kaminski et al. 2004).

If communicative attempts fail, gesturers may either *persist* and continue to use the same gesture, or they may even *elaborate* their gesture use by using a different, more efficient gesture to elicit the recipient's response. The corresponding studies, mostly conducted with apes, have produced mixed findings. While chimpanzees repeat the same gesture to get the recipient to respond, gorillas and orangutans may also continue to gesture but independently of whether the recipient responded or not. For interactions with humans, there is evidence that both chimpanzees and orangutans elaborate their gesture use in case the human does not respond or not respond appropriately (Cartmill and Byrne 2007), while for interactions with conspecifics, this pattern could not be confirmed.

To summarize, intentional use is a central topic in primate gesture research, as are variable repertoires and their flexible usage. However, definitions of the term "gesture" as well as the type and number of criteria used to identify intentional use may drastically vary across studies. Most studies focus on captive great apes and find substantial evidence for flexible usage of gestures, while

research on the variability between individual repertoires produced mixed results.

### Vocalizations

Since many primate vocalizations are graded signals, it is often difficult to determine the exact number of calls of a species' vocal repertoire. It is therefore difficult to compare the size of vocal repertoires across species. However, the size of vocal repertoires seems to be correlated with group size, indicating that more complex social structures require a more varied communicative repertoire (McComb and Semple 2005).

### Variability and Flexibility in Vocal Repertoires and Their Usage

Isolation studies showed that despite the lack of contact to other conspecifics, monkey infants start to produce their species-specific vocalizations. Similarly, cross-fostering experiments have demonstrated that monkey infants, raised by another species, still produce the species-specific vocalizations of their own species (Owren et al. 1992). This strongly suggests a genetic determination of primate vocalizations, resulting in "closed" repertoires with little potential to acquire novel vocalization. However, there is increasing evidence that the structure of primate vocalizations can be modified, for example, by social factors, indicating more flexibility than previously assumed. For great apes, the acquisition of novel sounds like "whistles" in orangutans or "raspberries" in chimpanzees has been reported (Hopkins et al. 2007). However, it is important to note that unlike vocalizations, these sounds are not produced by using the vocal folds. This indicates that primates have control over articulators such as their lips and tongue, but not their larynx.

Higher degrees of flexibility are reported for the *usage* of vocalizations. Some species only produce food calls if an audience is present or even only in case specific individuals are in close proximity. Similar findings have been reported for other social contexts, such as sexual or territorial behavior, suggesting that primates adjust their call production not only to the presence/absence but also to the composition of the audience.

### Referential Vocalizations and Meaningful Combinations

In human language, many words are referential, because they refer to specific entities in the world. Therefore, comparative researchers are specifically interested in context-specific vocalizations "... to find the animal equivalent to referential words in human language" (Liebal et al. 2013, p. 399). Of particular interest are "functionally referential vocalizations," which are reliably produced in response to a specific stimulus, with recipients responding to this vocalization even in the absence of the eliciting stimulus, in the same way they would respond when the eliciting stimulus would be present. Most of this research was conducted with monkey species, such as vervet monkeys and Diana monkeys, with referential vocalizations reported for different contexts including the discovery of predators or food. One of the first studies describing the use of referential vocalizations found that vervet monkeys in east Africa use specific alarm calls depending on which of their main predators – eagles, pythons, or leopards – they encounter. Playback experiments then demonstrated that these predator-specific calls also elicit a predator-specific response, similar to the response they would show if the predator would be present (Seyfarth et al. 1980). Since then, different alarm call systems have been reported for many primate species, but many of them are less specific. For example, some species differentiate between aerial and terrestrial predators, but not between predator types, and/or they may also consider contextual information in addition to the call itself. In the feeding context, vocalizations refer to the presence of food, in similar ways like alarm calls indicate the presence of a predator. Food calls may also vary in their specificity, and either announce the presence of (large quantities of) food, or may differentiate between different food values. In some cases, calls might even refer to specific food types. Functionally referential vocalizations have also been reported for other social contexts, such as sexual behavior, in different macaque species, bonobos, and chimpanzees. Acoustically different calls during copulations may vary as a function of the females'

reproductive status, the outcome of a copulation (resulting in an ejaculation or not), or the sex and rank of the interacting individuals. However, some of these findings are still debated, since playback experiments are needed to confirm that these acoustically distinct calls are indeed meaningful for the recipients.

The concept of functionally referential vocalizations has been recently criticized, as to successfully understand the information conveyed by some signal, it must be specific to at least some extent. Therefore, it has been suggested that seemingly referential vocalizations are qualitatively not different from other signals (Wheeler and Fischer 2012). However, despite this criticism, functionally referential vocalizations are still intensively studied across different primate species.

Since another key feature of language is the *duality of patterning*, which enables the combination of a finite number of (meaningless) components into a potentially infinite number of meaningful utterances, comparative researchers aim at identifying similar structures in vocal (and also gestural) sequences. Thus, researchers are interested in the question whether nonhuman primates combine vocalizations into longer sequences to create new meanings or at least use these combinations differently than the corresponding component calls.

Some vocalizations, when combined with others, function as modifiers, since they change the meaning of following vocalizations. For example, Campbell's monkeys combine their functionally referential "eagle"- or "leopard"-alarm calls with another, preceding "boom"-call in situations that are less dangerous (Zuberbühler 2002). This species also combines its six distinct loud calls into sequences, which are then used in specific contexts only, and may thus represent instances of combinations which are used for new functions. Putty-nosed monkeys do not use predator-specific alarm calls, but they produce sequences consisting of "hack" and "pyow" vocalizations, which are given in response to many stimuli. They are more likely to use "hack"-sequences in response to eagles and "pyow"-sequences in response to leopards.

Interestingly, they combine these two different calls into a "pyow-hack" sequence in situations when they want to initiate group travels and therefore convey a new message by combining these different vocalizations (Arnold and Zuberbühler 2006).

Together this section shows that while there is limited flexibility in the production of vocalizations regarding the modification of their structural properties and the acquisition of novel vocalizations, there is a considerable degree of flexibility in the usage of vocalizations. Thus, unlike gestural signals, vocalizations are combined into meaningful sequences, which further increase the flexibility of an otherwise "closed" vocal repertoire with only a finite number of elements.

### Facial Expressions

Primates have very mobile faces and can change the appearance of their faces, by moving the jaws and lips, eyelids, and ears. Such facial movements are often referred to as facial expressions. Many facial expressions are commonly used across many primate species, and some are limited to few species only (van Hooff 1967). Facial expressions of nonhuman primates are often considered stereotypical displays and are investigated in an evolutionary framework to study their adaptive function, with focus on the receiver of such displays. On the other hand, very little research considers proximate aspects of facial communication, such as the intentional and flexible usage of facial expressions or the mechanisms underlying their acquisition. To disentangle the evolutionary origins of language, however, comparative researchers dedicate their attention to orofacial movements and specifically the rhythmic patterns of mouth movements during ingestion or communication. Therefore, this entry will focus on these aspects of facial communication.

### Rhythmic Patterns of Primate Mouth Movements

The production of vocalizations is often inextricably linked to facial movements, particularly the lower part of the face. Researchers focus on such communicative mouth movements, since they are interested in the extent of control over such orofacial movements and the interplay of the

vocal and visual modality, specifically how recipients integrate such multisensory information.

Research on communicative mouth movements of monkeys showed that their vocalizations have a similar acoustic rhythmicity like human language, but unlike humans, monkeys lack the concomitant rhythm of the facial movement (Ghazanfar and Takahashi 2014). However, geladas produce lipsmacks together with a “wobble”-vocalization. Interestingly, the rhythm of the mouth movements during these vocalized lipsmacks resembles that of human language (6–9 Hz), which has been interpreted as evidence for the hypothesis that lipsmacking represents a precursor to the emergence of human language (Bergman 2013). Interestingly, the movements of the involved articulators (lips, tongue, hyoid) differ depending on whether monkeys produce a communicative (e.g., lipsmacks) or ingestive (e.g., chewing) mouth movement: only during the production of communicative lipsmacks, the corresponding anatomical structures move with a speech-like rhythm.

Regarding the perception of such orofacial movements, rhesus monkeys seem to prefer lipsmacks produced within the species-typical range of approximately 6 Hz but pay less attention when the rhythm is experimentally perturbed. Concerning the cross-modal identification, both monkeys and great apes recognize the auditory–visual correspondence between their different vocalizations and the corresponding facial movements. Furthermore, crested macaques show an increased probability of affiliative behavior in response to those lipsmacks that consist of both visual and auditory components compared to when lipsmacks only consist of a visual component (Micheletta et al. 2013).

#### Intentional Control

Another major argument for orofacial movements representing the evolutionary origin of language is that primates seem to have voluntary control over their production like found for manual gestures, but not vocalizations (Corballis 2002). Like in humans, the size and structure of the neurobiological substrates innervating facial muscles of great apes indicate the greater differentiation of muscles involved in the production of facial

expressions and the increased voluntary control over the production of orofacial movements (Sherwood et al. 2005). Interestingly, at least in rhesus monkeys, the coordination of facial muscles seems to differ between different types of rhythmic orofacial movements. While a rhythmical coordination of those muscles innervated by the facial nucleus has been found for the production of communicative mouth movements such as lipsmacks, this was not the case for ingestive mouth movements (Shepherd et al. 2012). This finding provides further support for the hypothesis that specific orofacial movements – with a communicative function – might have played an important role in the emergence of human language.

Together these findings suggest that multisensory integration of visual and auditory information is an integral part of primate communication. Furthermore, this close link between auditory and visual information in communicative mouth movements, their speech-like rhythm and their intentional production, seem to provide support for the hypothesis that language might have evolved through the modification of rhythmic facial movements in ancestral primates.

## Conclusion

This chapter demonstrated that in searching for the origins of human language by studying the communication of nonhuman primates, research foci differ across the gestural, vocal, and facial modality. While gestural researchers focus on different markers of intentionality and flexibility in gesture usage, vocal research centers on the referential use of vocalizations and their meaningful combinations. Facial researchers, on the other hand, are mostly interested in the rhythmical patterns of orofacial movements and their interplay with vocal utterances.

In the ongoing debates about language origins, researchers often focus on *one* specific modality only and list the arguments why the corresponding other modalities are not suitable candidates to explain how language might have emerged. Researchers supporting theories of a vocal origin highlight that primate vocalizations refer to



external entities and are combined into meaningful sequences, while these two features seem to be absent in the gestural domain. Gesture researchers, on the other hand, emphasize that unlike vocalizations and facial expressions, gestures are intentionally and flexibly used across several contexts and that repertoires vary across individuals, groups, or age classes. In contrast, primates seem to have little control over the production of their vocalizations and facial expressions, there is very limited variability among individual vocal or facial repertoires, and they do not acquire new signals during ontogeny, resulting in rather constrained or closed repertoires. Gesture researchers therefore argue that because of the lack of intentional use, invariable repertoires, and limited flexibility in the production of both facial expressions and vocalizations, language most likely did not emerge from a vocal or facial but gestural origin.

It is important to highlight that this entry cannot present a comprehensive review of existing research on primate communication. Thus, although each section focused on specific aspects of the corresponding modality, such as intentional use of gestures, there is an increasing number of studies on intentional vocalizations, as well as context-specific, referential gestures, or expressive movements of other parts of the face than the mouth. However, this entry aimed at pointing to some of these current gaps of knowledge about primate communication together with the existing biases toward specific modalities, because they might have very serious consequences for theories of language evolution, since "...many of the assumptions that are currently held about how vocalizations, gestures and facial expressions compare may not be true" and as a result, the "...absence of evidence for a certain trait may not necessarily reflect absence of ability" (Liebal et al. 2013, p. 209).

## Cross-References

- [Catarrhine Communication](#)
- [Language Research: Great Apes](#)
- [Primate Cognition](#)
- [Primate Sensory Systems](#)

- [Primate Social Structure](#)
- [Prosimian Communication](#)
- [Referential Communication](#)

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## Primate Diet

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## Definition

Information related to primate food consumption, nutrition, feeding biology, and digestive strategy

## Introduction

The Order Primates comprises 496 number of species in 16 families, distributed throughout Mexico, Central and South America, Asia, Africa, and Madagascar (Mittermeier et al. 2013). Although the earliest true primates, dating to the late Paleocene – early Eocene epochs – were most abundant in regions of North America and Europe, extant primates are primarily a tropical radiation, found in a diversity of habitat types running the gamut in vegetation types, altitude, latitude, rainfall, and seasonality. Modern primate species exhibit extraordinary diversity in all biological variables, but regardless of dietary specifics of their diet, with a couple of exceptions, all primates are highly flexible feeders, derive the vast majority of their calories from plants, and are indeed one of the modern mammal orders that evolved as primary consumers (Milton 1993).

## Description of Diet: Trophic Feeding Labels

Description of wild primate diet began in earnest in the 1970s (Clutton-Brock 1977) and relied on feeding labels derived from a classic trophic food chain. In this classificatory system, dietary categorization is based on where an organism falls within a system of energy transfer from one trophic level to the next. The ultimate source of energy comes in the form of UV radiation which is fixed into carbohydrate energy by the first trophic level (producers) comprised of plants. Those organisms that consume plants only make up the second level and are labeled primary consumers. Secondary consumers are those organisms in the third trophic level that consume primary consumers and so on. From this system of energy transfer, we gain the terms herbivory (primary consumers), carnivory (secondary and tertiary consumers), and omnivory (herbivory + carnivory). Because many primates augment their plant diet with some percentage of animal foods (primarily invertebrate, but also vertebrate), they are most properly referred to

as omnivores. Nonetheless, among primates, most calories are derived from the producer trophic level, and in many tropical forest habitats, primates can represent a significant percentage – if not majority – of arboreal primary consumer biomass (Janson and Chapman 1999).

From this basic description of diet are an associated set of labels that have been used to describe primate diet in more specific terms related to the form of plant or animal matter consumed, with most species described as being either a frugivore (fruit-eater), folivore (leaf-eater), granivore (seed-eater), gumnivore (gum-eater), insectivore (insect-eater), or faunivore (animal-eater, synonymous with carnivore). These terms linger in the literature and have been the primary means by which to describe primate diet. Moreover, they are often used as a quick index for particular primate taxa. Folivory, for example, is ubiquitous among the Colobinae (leaf-eating monkeys), the genera *Indri* (Indridae) and *Alouatta* (howler monkeys), and *Gorilla beringei beringei* (mountain gorillas). Frugivory is found widely throughout the order but is noted particularly in Atelinae (spider, woolly, and muriqui monkeys), the true lemurs (*Lemur*, *Eulemur*, *Varecia*), and the genus *Pan* (common chimpanzees and bonobos). Seed eating (granivory) is common among Pitheciinae (saki and uakari monkeys) and, to a lesser degree, Colobinae. Gumnivory is observed in the Cheirogalidae (mouse and dwarf lemurs) and Callitrichidae (marmosets and tamarins). Insectivory (a form of carnivory) is seen in particular among the Cheirogalidae, the genus *Saimiri* (squirrel monkeys), and redtail guenons (*Cercopithecus ascanius*). Exclusive faunivory is extremely rare and is found only in the genus *Tarismus* (tarsiers), although some lorises (e.g., *Loris*, *Arctocebus*, *Galagoides*) can be almost 100% in some habitats and in some seasons.

## Description of Diet: Generalist and Specialists

Primate species are also often described in terms of whether they are generalist or specialist

consumers. These terms derive from classic niche theory in which niche width is indicative of whether a species consumes a broad array of food species/parts and thus has a wide dietary niche width or eats a narrow spectrum of food species/parts and thus has a narrow niche dietary space. Overall, primates are generalists, with some taxa particularly so. Extreme dietary generalists also tend to be among the most successful and widespread extant taxa. For example, baboons (*Papio*) and macaques (*Macaca*) are found, respectively, throughout sub-Saharan Africa and regions of Asia and have diet that are marked by extreme eclectic omnivory, with hundreds of species consumed, and high feeding plasticity depending upon food resource availability (Richard et al. 1989; Altmann 1998; Lambert and Rothman 2015).

However, several primate taxa are noteworthy as dietary specialists – it is in these taxa that derived anatomical and behavioral adaptations for procuring and processing food are observed. The Colobinae, for example, are unique among primates in having a modified stomach that facilitates plant fiber (hemicellulose, cellulose, lignin) fermentation and specialized folivory, similar to the digestive strategy of ruminating artiodactyle ungulates. In this system – known as foregut fermentation – the stomach is sacculated into either three or four haustrated chambers that vary in function and pH. The first of these stomach chambers – the forestomach – has a high pH suitable for housing hundreds of bacterial, fungal, and eukaryote symbiont microbe species that ferment dietary plant fiber. The short-chain fatty acids released as a metabolic by-product of this microbial fermentation serve as the primary source of energy for the colobine consumer (Lambert and Fellner 2011). In another example of dietary specialization, the golden bamboo lemur (*Hapalemur aureus*) feeds almost exclusively on grasses, particularly bamboo – some of which are very high in cyanogenic glycosides. In some seasons, *H. aureus* can consume upward of 12 times the lethal dose of cyanide for mammals of their body size (Glander et al. 1989). This strategy is not seen in any other primate taxon, and although the exact mechanism by which

detoxification takes place is unknown, it almost certainly involves specialized microsomal enzyme(s) produced in the endoplasmic reticulum of liver cells (Freeland and Janzen 1974).

## Dietary Flexibility and Nutritionally Explicit Description of Diet

Regardless of which standard trophic label is applied or whether a primate taxon is deemed generalist or specialist, diet is highly variable throughout the course of an animal's lifetime, between individuals and between populations. In some cases, within-species variance in diet can exceed that of interspecific differences (e.g., within and among *Cercopithecus* species; Chapman et al. 2004). Circumscribed terms, such as “frugivore,” “folivore,” etc., fail to capture this plasticity and can obfuscate the underlying reason why a consumer is eating what it is eating and when.

Diet variability is influenced by both *intrinsic* and *extrinsic* factors. *Intrinsic* factors can refer to the inherent features of a plant food (e.g., nutritional, chemical, mechanical attributes of leaves versus insects) or to intrinsic elements of species' particular adaptations and how this varies by age, sex, reproductive, social, and health status. *Extrinsic* factors influence what, when, and how a primate eats and are a function of the current ecological availability of a food and the costs (e.g., competition – a cost of group living) associated with feeding on it as a consequence of that availability; extrinsic challenges to feeding are influenced hugely by habitat and season.

It is important to keep in mind that primates do not eat insects, fruit, and leaves because they are in need of an insect, fruit, or leaf per se – these ecological units are just the packaging for what primates are eating them for: nutrients and energy. Nutrients can be broken down into the energy-yielding macronutrients (carbohydrates, protein, lipids) and micronutrients (vitamins and minerals), which do not provide energy, but instead facilitate the use of the macronutrients and their conversion into energy. Energy is not a nutrient, but an abstraction that references the caloric gain

from converting the macronutrients into their constituent units. In wild primate diet, fruit pulp generally provides simple carbohydrates (sugars, digested autoenzymatically by the consumer), while leaves are the source of more complex structural carbohydrates (fiber) which must be fermented by symbiont microbes. Similarly, saps are high in simple sugars and gums high in structural carbohydrates. Seeds are good sources of protein and also lipids, although they can be high in plant toxins. Protein is provided to the consumer either in the form of insects (more common in smaller – bodied primates because of the constraints of capture rate) or leaves (more common in larger bodied primates because of the constraints of fermenting large amounts of fiber). Insects and other animal prey also provide lipids.

Primate feeding has most recently been described using nutritionally explicit models and not – as has been done most commonly – in terms of the percentage of plant parts or species in the diet. In so-called nutritional geometry models, diet is depicted in multidimensional space representing nutritional targets of protein, carbohydrate, and lipids (Simpson and Raubenheimer 1993). The resulting ratio of macronutrients is a measure of the nutritional decisions an animal makes which, in turn, are indicators of state-dependent nutritional requirements of that animal (Felton et al. 2009). Using this approach, it has been demonstrated that mountain gorillas will overconsume protein in their leafy diet to arrive at a prioritized energy target (an “energy-leveraging” strategy), while spider monkeys (*Ateles chamek*) will overconsume energy to arrive at a protein target (a “protein-leveraging” strategy) (Felton et al. 2009; Rothman et al. 2011).

## Cross-References

- Basal Metabolic Rate (BMR)
- Catarrhine Diet
- Costs of Group Living
- Digestive System
- Energy
- Feeding
- Food Patch

- Foraging
- Herbivore
- Lipid
- Nut-Cracking
- Omnivore
- Platyrrhine Diet
- Primates
- Prosimian Diets

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## Primate Locomotion

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## Synonyms

[Lemur](#), [Tarsier](#), [New World and Old World Monkey](#), and [ape locomotion](#); [Primate movement](#)

## Definition

Patterns of movement observed in members of the order Primates.

Among tetrapods, the locomotor behavior of primates has been the best studied (see Granatosky 2018 for a review). The reason for this bias is twofold. First, *primate locomotion* tends to be fast and highly acrobatic. As such, it is hard for any observer to ignore such feats. Next, as primates ourselves, we have an inherent fascination in the movements of our closest ancestors.

It has often been asserted that primates display the highest locomotor diversity compared to any other mammalian group (Hunt et al. 1996; Vilensky and Larson 1989). This high degree of locomotor diversity observed in primates has been considered an essential adaptation potentially responsible for the evolutionary success of the

order (Schmitt et al. 2016), and it is this assumption that has led to numerous studies documenting locomotor behaviors across a broad phylogenetic spectrum of primate species. These locomotor profiles have provided essential information about behavioral ecology, functional morphology, paleontology, and, by extension, important data concerning primate locomotor evolution (Fabre et al. 2017; Hunt et al. 1996).

There has been extensive speculation as to what factors of primate biology might have led to the considerable diversification of locomotor modes (Cant 1992; Granatosky 2018; Vilensky and Larson 1989). Perhaps the most cited explanation is the link to a long, and potentially restricted, evolutionary history tied to an arboreal environment in early primates (Cartmill 1992; Schmitt et al. 2016; Schmitt and Lemelin 2002). The arboreal milieu is characterized by considerable variation in substrate diameter, orientation, compliance, and continuity. The complexity of this environment is thought to have put strong selective pressures on the ability of primates to rapidly switch between disparate locomotor behaviors to effectively adjust to substrate variation (Schmitt et al. 2016). In contrast, terrestrial environments are commonly considered less complex, and animals within these environments likely must deal with lower substrate variation. The greater substrate homogeneity observed in terrestrial landscapes is thought to relax the need to switch between different forms of locomotion to successfully traverse the environment (Granatosky 2018).

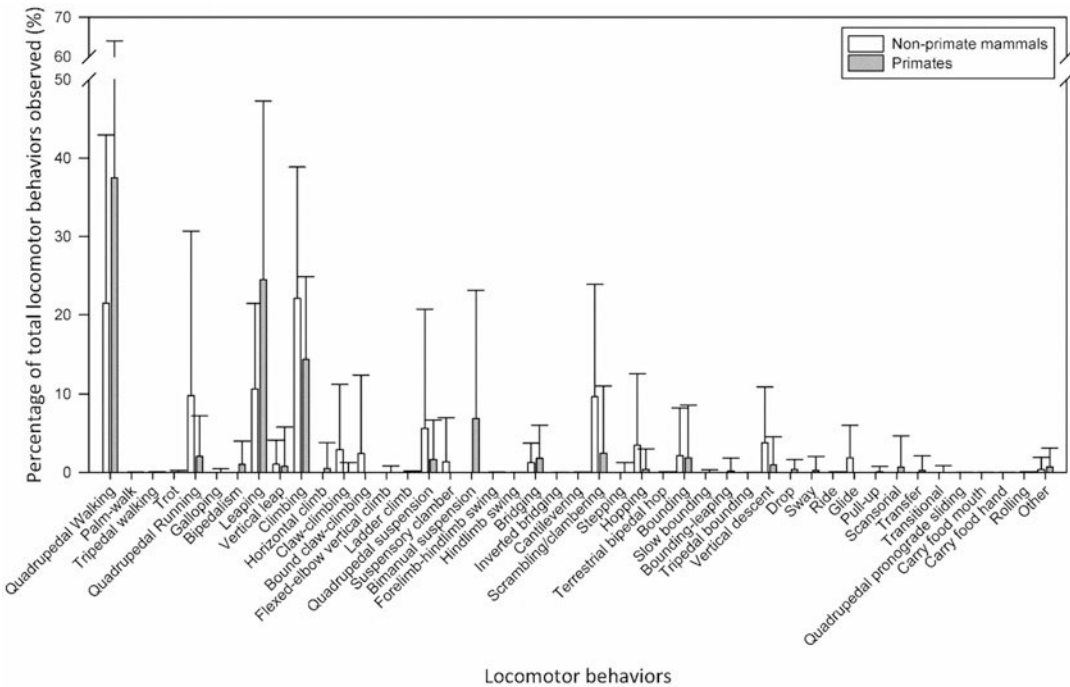
Another explanation for the greater locomotor diversity in primates comes from inherent features of primate anatomy. In general, primates retain a primitive and generalized post-cranial skeleton with grasping hands and feet and highly mobile limb joints (Granatosky et al. 2016; Larson 1998; Schmitt et al. 2016). Together these features allow most primates greater flexibility in overall range of motion, and therefore capable of proficient locomotion in a number of environmental contexts (Schmitt et al. 2016; Vilensky and Larson 1989). However, there are numerous primate species that have evolved anatomical specializations away from the primitive body plan to better fit a

particular form of locomotion (e.g., vertical-clinging and leaping or suspensory behavior) or environmental context (Fleagle 2013; Hunt et al. 1996; Preuschoft 2002). For these species, it has been suggested that overall locomotor diversity is lower when compared to more anatomically generalized species (Fleagle 2013; Granatosky 2018). Body mass also has been argued to influence the locomotor behaviors of primates. Specifically, smaller species/individuals are considered to use a greater range of locomotor behaviors than larger species/individuals that may be restricted in the locomotor modes they are able to adopt due to their larger body mass (Cant 1992; Fleagle 2013; Granatosky 2018).

Major Locomotor Modes

Although *primate locomotion* can be quite diverse, there are five locomotor modes observed most often among the nonhuman primates (Fig. 1). Quadrupedalism remains the most

common form of *primate locomotion* and is often considered the basal locomotor mode for the order (Hunt et al. 1996). Compared to most mammals, primate quadrupedal walking gaits are differentiated by a suite of at least three features (Granatosky et al. 2016; Schmitt and Lemelin 2002). First, primates tend to utilize diagonal-sequence footfall patterns (i.e., each hindlimb footfall is followed by a contralateral forelimb footfall), whereas most other quadrupedal mammals use primarily lateral-sequence footfall patterns (i.e., each hindlimb footfall is followed by an ipsilateral forelimb footfall; Cartmill et al. 2002; Granatosky et al. 2016, 2019). Second, quadrupedal primates exhibit a relatively more protracted position of the humerus at touchdown (Granatosky et al. 2016), whereas other quadrupedal mammals display relatively retracted humeral positions at forelimb touchdown (Larson et al. 2000). Finally, most quadrupedal primates experience higher peak vertical forces on the hindlimbs relative to the forelimbs, resulting in a relatively lower forelimb to

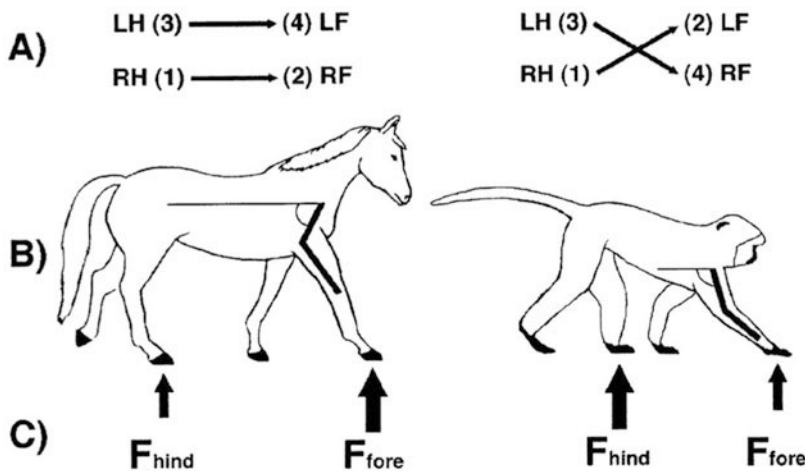


**Primate Locomotion, Fig. 1** The percentages of locomotor behaviors observed for extant mammals. Adapted from Granatosky (2018)

hindlimb peak vertical force ratio (Granatosky and Schmitt 2019; Schmitt and Lemelin 2002). In contrast, most other quadrupedal mammals are characterized by a relatively higher forelimb to hindlimb vertical peak force ratios (Demes et al. 1994; Schmitt and Lemelin 2002) (Fig. 2).

A specialized form of quadrupedal walking called knuckle-walking is seen exclusively in African apes. During knuckle-walking, the palm and proximal phalanges are elevated above the substrate and the hand can be pronated or partially supinated (Fleagle 2013; Schmitt et al. 2016). Flexion at the intermediate phalangeal joints positions the dorsal aspect of the middle phalanges in contact with the substrate as the main weight-bearing elements. The metacarpal phalangeal joints are held in a neutral position (i.e.,  $180^\circ$ ) or slightly hyperextended. It is thought that African apes adopt knuckle-walking postures to reduce bending loads that their fingers would experience in palmigrade or digitigrade postures (Schmitt et al. 2016; Tuttle 1967).

After quadrupedal walking, leaping represents the second most common form of *primate locomotion*, although leaping is quite rare in animals over a certain body size (e.g., orangutans are unlikely to leap; Cant 1992; Granatosky 2018). There are two basic modes of leaping for primates. Most anthropoids utilize an unspecialized form of leaping in which they launch themselves outward along a horizontal plane and then fall downward. This leaping mode is not associated with any notable anatomical specializations. In contrast, vertical-clinging and leaping is a type of *primate locomotion* in which animals adopt orthograde postures at rest on vertically orientated substrates, and movement is initiated through powerful hindlimb extension resulting in animals leaping from one vertical substrate to another (Demes et al. 1999; Fleagle 2013). Vertical clinging and leaping is common among strepsirrhine primates and is also observed in the tarsiids and callithricids (Fleagle 2013; Gebo 1987).



**Primate Locomotion, Fig. 2** Three locomotor characteristics that distinguish primates from other nonprimate mammals. Primates (right) use (a) diagonal-sequence walking gaits (i.e., footfall of right hindfoot is followed by that of left forefoot). In comparison, most nonprimate mammals (left) use lateral-sequence walking gaits (i.e., footfall of right hindfoot is followed by that of right forefoot). Primates also tend to have (b) protracted humeral positions at forelimb touchdown (i.e., humeral angles

greater than  $90^\circ$  relative to horizontal body axis), in comparison to most nonprimate mammals that have more retracted humeral positions at forelimb touchdown (i.e., humeral angle less than  $90^\circ$  relative to horizontal body axis). Finally, when landing on a substrate, (c) forelimbs of primates experience lower peak vertical substrate reaction forces than do hindlimbs. The reverse is true for most other nonprimate mammals. Figure from Schmitt and Lemelin (2002).

The anatomy of vertical-clinging and leaping primates is characterized by relatively long hindlimbs in comparison to the forelimbs (Gebo 2011; Granatosky et al. 2016). These specialized primate leapers generate tremendous forces during takeoff and landing that are orders of magnitude larger than those experienced during typical primate quadrupedal locomotion (Demes et al. 1999). Most arboreal and terrestrial quadrupeds experience peak hindlimb substrate reaction forces that are ~50–100% of body weight (Fabre et al. 2017; Granatosky and Schmitt 2019). In contrast, medium- to large-bodied primates experience forces ~500–1400% of body weight when leaping (Demes et al. 1999; Gebo 2011). Elongated legs help leaping primates generate these incredible external substrate reaction forces, which in turn increases jump height and distance, with relatively little internal muscle force.

Following leaping, climbing is the next most common locomotor mode observed among primates. Climbing, often on vertical supports, is a critical and fundamental form of locomotion for arboreal animals during foraging, travel, escape, or finding a safe resting place (Cartmill 1985; Granatosky et al. 2019; Hanna et al. 2017). In primates, there are two basic types of climbing. The first involves the animal wrapping itself around the substrate. This is observed most among the clawed callitrichid primates and in situations when the diameter of the support is substantially larger than the diameter of the body. In these situations, asymmetrical gaits are most common (Cartmill 1985; Preuschoft 2002).

The second form of climbing is observed most on smaller substrates and involves symmetrical walking gaits [see Granatosky et al. 2019 for a review]. However, unlike quadrupedal walking (see above), lateral sequence gaits are most common (Granatosky et al. 2019). During symmetrical gait climbing, stability and security are paramount. Accordingly, animals usually move more slowly, with longer intervals of grasping the support than what is observed during arboreal quadrupedal walking (Granatosky et al. 2019). As

with arboreal quadrupedal walking, the hindlimb serves as the primary weight support and propulsive limb during climbing (Hanna et al. 2017). This form of climbing is observed across almost all primate species, but has received considerable attention recently in the great apes.

Suspensory positional behaviors are commonly discussed in concert with the hominoids, atelines, and to some extent the Asian colobines, but it should be noted that all primates can, and do, engage in suspensory locomotion, although some groups emphasize these behaviors more effectively, or for longer periods of time (Granatosky and Schmitt 2019; Stern 1975). For most, images of suspensory locomotion are centered on what is commonly referred to as arm-swinging, a form of forward progression in which the animal hangs below the support and the forelimbs bear most of the weight. Arm-swinging may be associated with prehensile tail use in the New World atelines (Byron et al. 2017; Fleagle 2013). The morphology of arm-swinging species has been well studied and is often interpreted as a functional suite of characteristics thought to allow for efficient pendular movement (Bertram 2004; Byron et al. 2017). The fluid, swinging motion observed when brachiators move beneath branches naturally brings to mind the oscillations of a pendulum and the repeated interchange of potential and kinetic energy (Bertram 2004; Byron et al. 2017). It is tempting, then, to assume that arm-swinging primates use natural pendular motions to reduce the muscular investment necessary to travel. Some studies have demonstrated that, under certain conditions, arm-swinging primates do match the expectations of a simple pendulum, but this appears to be the case only for very slow speeds and continuous-contact locomotion. Simple pendular locomotion is restrictive, and to optimize energetic efficiency, animals must limit themselves to a narrow range of stride distance and speed. In most scenarios, the complex three-dimensional arboreal environment that arm-swinging primates live in makes simple pendular locomotion impossible. In these situations, travel pathway adjustments, rather than efficiency,

appears to be the primary concern (Byron et al. 2017; Chang et al. 2000; Fleagle 2013).

It is important to note that many primates utilize below branch quadrupedal locomotion, which is a form of suspensory locomotion in which both the forelimbs and hindlimbs are used in some combination, the torso is pronograde, and the limbs are loaded in tension (Granatosky and Schmitt 2019; Stern 1975). This behavior is like the movement of a sloth, and is common in the lorises, orangutans, and many platyrrhine monkeys. While movements of the limbs are largely similar to what's observed during arboreal quadrupedal locomotion (see above), the forelimb becomes the dominant weight bearing limb. This finding has led some to suggest that below branch quadrupedal locomotion may be a mechanical intermediate transition to arm-swinging (Byron et al. 2017; Granatosky and Schmitt 2019).

Finally, almost all primates demonstrate some bipedal tendencies (Granatosky 2018; Hunt et al. 1996). This is most notable in humans, but also common in great apes, capuchin monkeys, and sifakas. Bipedal walking in humans is often referred to as "striding", which is largely attributable to the smooth means of traveling during which the energy output of the body is reduced to a physiological minimum (Preuschoft 2004; Sockol et al. 2007; Yamazaki et al. 1996). Just as arm-swinging is often equated with a simple pendulum, bipedalism is equated with the interchange of potential and kinetic energy of an inverted pendulum. It is a complex activity involving the joints and muscles of the whole body (Yamazaki et al. 1996), and it is likely that the evolution of the human gait took place gradually over a period of ten million years (Fleagle 2013). The pattern of locomotion of human ancestors immediately preceding the acquisition of bipedalism has long been a matter of controversy. Based on the close phylogenetic position with chimpanzees and gorillas, there is potential that the earliest human ancestors used knuckle-walking (Richmond et al. 2001). However, this has been fiercely debated and other locomotor modes like the slow suspensory progression of the orangutan may be more likely (Stern 1975). Most likely, the earliest hominins

had a wide locomotor diversity, like the orangutans, and found bipedalism to be an acceptable means to traverse a landscape with more open savannahs and less tree cover (Fleagle 2013; Stern 1975).

## Conclusion

This chapter introduces the diversity of primate locomotor behaviors. There has been extensive speculation as to what factors of primate biology might have led to the considerable diversification of locomotor modes. The most cited explanation is the link to a long, and potentially restricted, evolutionary history tied to an arboreal environment and/or maintaining a generalized postcranial anatomy. Compared to other mammals, primates tend to utilize diagonal-sequence foot-fall patterns, exhibit a relatively more protracted position of the humerus at touchdown and experience higher peak vertical forces on the hindlimbs relative to the forelimbs. This odd combination of gait characteristics is likely linked to maintaining stability in an arboreal environment, and may have allowed primates to evolve different locomotor behaviors, such as vertical climbing or bipedalism. Primates are also the only mammalian group to have developed arm-swinging locomotion. There is considerable ongoing research on *primate locomotion* and open questions remain about the origins of primate quadrupedal locomotion, arm-swinging, and bipedalism.

## Cross-References

- [Adaptation](#)
- [Arboreality](#)
- [Catarrhine Locomotion](#)
- [Evolution](#)
- [Hominoidea Locomotion](#)
- [Platyrrhine Locomotion](#)
- [Primates](#)
- [Prosimian Locomotion](#)
- [Quadrumanous](#)
- [Zoology](#)



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## Primate Models

- [Primate Perspectives on the Evolution of Human Behavior](#)

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## Primate Movement

- [Primate Locomotion](#)

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## Primate Orphans

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## Synonyms

[Change of primary caregiver](#); [Loss of care](#);  
[Motherless primate](#)

## Definition

A primate orphan is an immature individual who has lost his or her mother as an infant or a juvenile.

## Introduction

In infancy, all primates require a caregiver who meets their physical needs, such as food and protection (among many others), and their affective, cognitive, and social needs (in some species, this requirement extends until the primate is a juvenile). The caregiver is essential for primate infant survival and social and cognitive development. For that reason, infants are greatly affected if they lose their caregivers; the effects of becoming an orphan range from being unable to survive to behavioral and physiological consequences that last through adulthood. Here the relevant aspects of the study of primate orphans are reviewed.

## Chances of Survival

Primates have a long period of dependency on their mothers. For example, infant chimpanzees require considerable amounts of care during long periods of dependency. Chimpanzee mothers stop carrying and nursing their offspring when the offspring are around 4/5 years old, but for several years thereafter, mother and offspring maintain close spatial proximity. Mothers also defend their offspring against aggression and wait for them during group travel. Young chimpanzees travel almost constantly with their mothers and her other immature offspring (frequently their siblings) until mid-adolescence (<12 years). Orangutans in the wild are dependent on their mothers for food and travel until they are 2.5 years old, and until the age of 7 years, they spend a large amount of time with their mothers, although they are capable of feeding and traveling independently. Gorillas also exhibit this kind of maternal dependency; however, the western lowland gorilla (*G. beringei*) shows greater infant dependence than the mountain gorilla (*G. gorilla*). It is also possible to find this same

kind of dependency in infant and juvenile monkeys; the dependency on mothers (as measured by rates of travel, contact among others) varies, depending on the parenting style of the mother and on environmental conditions. Young primates who lose their mothers are extremely vulnerable; orphaned infants are left without their main source of protection, transportation, food, and comfort, and this loss will likely result in an infant's death. If individuals lose their mothers later in life, despite being capable of finding their own food and traveling independently, they still suffer an enormous loss; they lose their main companion for travel, their main source of comfort, and the most important source for help when navigating the constantly changing social environment of their communities.

Despite the common recognition of the impact of the loss of a mother on a primate orphan, there are conflicting reports of the ability of infants and juveniles to survive after a mother's death (see, e.g., the different rates of survival of orphan chimpanzees reported by Goodall 1986, and Boesch and Boesch-Achermann 2000). Several researchers have attempted to determine the factors that affect an infant's ability to survive after losing their mother. Most researchers agree that the survival of orphans depends upon the timing of a mother's death and the presence of other individuals who might care for the orphaned infant.

Most authors agree that the survival of orphaned infants depends upon whether they lose their mothers after they have been weaned and whether they find another caregiver who can take care of their basic needs. However, there is no agreement regarding the exact age, after being weaned, at which infants are capable of survival. For example, it has been argued that, in chimpanzees, the survival of an orphan before weaning is impossible and that the care provided by siblings usually ensures that orphan's survival, as long as the orphan is at least 4.5 years old. This is because chimpanzees have a very long period of dependence on mother's milk; they are weaned at 4.5–5 years. Moreover, most direct maternal investments, such as maternal transportation of infants and sharing of night shelters (beds or nests), end

when the infant is weaned. Consequently, it has been argued that offspring younger than 4.5–5 years old cannot survive if the mother dies, and it is assumed that a mother's death is no longer critical to the survival of weaned offspring. However, long-term demographic data for a wild chimpanzee population in the Mahale Mountains, Tanzania, show that orphaned chimpanzee sons die younger than expected if they lose their mothers even after weaning (Nakamura et al. 2014). In bonobos (*Pan paniscus*), there have been recorded cases of infants who survived even though they were orphaned before being weaned (De Lathouwers and Van Elsacker 2007).

## Adoption

Despite the disagreement on the age at which independent survival is assured, most authors agree that, for an infant to survive, it is necessary that the infant find another individual who provides care similar to a mother's care. To ensure their survival, infants must be adopted by another individual who provides nursing and/or food-provisioning, carrying, active vigilance during group travel, defense, grooming, and comforting behavior. Boesch et al. (2010) define *adoption* as the provision of species-specific *allomaternal* care (e.g., nurturing behavior normally provided by the biological mother to her dependent offspring, such as carrying, sharing food, defending, or grooming) to an orphan by an adult or mature individual (older than 12 years old) for at least a 2-month period. Boesch also claims that, to be considered an adoption, the adult who adopts the infant must frequently associate with the orphan and exhibit behaviors such as waiting during travel, providing protection in conflicts, and sharing food with the orphan. However, it is important to notice that others have argued that this definition of adoption should be expanded to include reported cases of the adoption of infants by younger individuals.

It is interesting to notice that despite the basic similarities between the behavior of biological mothers and adoptive caretakers (e.g., nursing and/or food-provisioning, carrying, active

vigilance during group travel, defense, grooming, and comforting behavior), researchers have reported differences between the behavior of these two kinds of caregivers. For example, it is common that in species whose infants are typically carried by mothers, biological mothers in monkeys and apes continue traveling and do not wait for their infants. However, both maternal siblings and maternally unrelated adopters are unwilling to leave lagging adoptees behind; instead, they wait for and carry them (see, e.g., in baboons, Hamilton et al. 1982).

### Variables in the Adoption Process

The adoption of orphans has been documented in monkeys and apes (see, e.g., in savanna baboons, Altmann 1980; chimpanzees, Goodall 1986; bonobos, Surbeck and Hohmann 2017; red howler monkeys, Agoramoorthy and Rudran 1992; black and white colobus monkeys, Dunham and Opere 2016; titi monkeys, Cäsar and Young 2008). Researchers have determined the relevant factors that contribute to a successful adoption process.

First, in different captive situations, it has been observed that the experience/age of the adoptive mother is a contributing factor in the successful adoption of an infant. For example, in orangutans (*Pongo pygmaeus*) in captivity, successful introductions of infant orangutans to surrogate mothers have been described (Maple 1980; Sodaro 2007); in most cases, the previous mothering experience of the adult females who adopted the infants contributed to the success of the surrogacy.

Second, variations have been found with regard to the identity of the individual adopting the orphan (e.g., kin, non-kin, sibling, grandmother). Traditionally, it has been argued that female siblings are responsible for most successful adoptions; however, in recent years, it has been found that individuals who are not female siblings can also successfully adopt orphans. In chimpanzees, when mothers die, immature orphans are often adopted by a maternal sibling if they have one. However, the same researchers who observed adoptions by maternal siblings in chimpanzees

also documented several cases of adoption in chimpanzees by both maternal relatives and non-relatives, by siblings, by males or nulliparous females, and even one rare case of adoption, by a grandmother without the death of the biological mother (Wroblewski 2008); all of these different types of adoptive caretakers exhibit remarkable care of the orphans. Hobaiter et al. (2014) reviewed data from four different sites, including their own (i.e., Gombe, Mahale, Tāi, and Sonso), and found that, across all four sites, adopters can be classified into the following groups: immature maternal sibling (<12 years) ( $n = 10$ ); mature maternal sibling (12 + years) ( $n = 4$ ); other kin ( $n = 2$ ); and non-kin ( $n = 20$ ). When considering the variation of the identity of the adopters, Hobaiter and colleagues hypothesize that the social bond, rather than biological relatedness, is the main variable that explains the identity of the adopter of orphaned chimpanzees. However, in most cases, maternal siblings are the ones who have a closer social bond to the orphaned infant. Upon reviewing data from all sites, the authors did not find that the adopter's age nor that the social relationship between the orphan and the adopter predicted the survival of the infant. Only the orphan's age predicted their survival rate: 100% of orphans aged 6 years or older and 95% aged 4 years or older survived. Meanwhile only 42% of orphans under the age of 4 years and 20% of orphans (one case,  $n = 5$ ) under the age of 1 year survived.

Several reports of monkeys have shown that juvenile and infant orphans were fostered by their siblings and non-related adult males (see, e.g., in Japanese macaques (*Macaca fuscata*), Hasegawa and Hiraiwa 1980). Several researchers also have argued that caregiving by grandmothers is rare. However, some exceptions have been recorded (see, e.g., in Japanese macaques, Nozaki 2009).

The adoption of primates by siblings has been explained as a way in which older siblings of individuals gain inclusive fitness benefits from assisting relatives (Hamilton 1964). However, it is not clear why non-siblings adopt orphans. Some have argued that different forms of adoption (i.e., males, females, siblings, non-siblings) can be examined through differences of ecological

and social effects such as seasonality (e.g., birth season, mating season, number of orphans, demographics). Boesch et al. (2010) suggest that adoption by wild chimpanzees should be interpreted as a potential example of altruistic behavior, mainly because of the significant costs that adoption has for the individual who adopts an orphan.

Finally, a third variable in the adoption process is differences among communities; in some cases, it is hypothesized that ecological factors account for these differences. For example, in East African chimpanzee communities (i.e., Gombe and Mahale), cases of older maternal siblings and nulliparous and infertile females adopting orphan chimpanzees have been reported. Most of the reported cases of adoption involve kin-adopters, even if the adopters are still immature and even if mature non-kin adopters are available. Meanwhile in the West African communities (i.e., T   Forest, Ivory Coast) most of the adoptions reported have been done by unrelated (non-kin) mature individuals such as adult males (one father) and parous females who have been allies of the deceased mother with no known kin relationship. However, it is important to clarify that this type of non-kin adoption occurs only if no maternal siblings are available and often only after significant time periods (e.g., weeks or even months; see Hobaiter et al. 2014, for an overview).

It has been argued that ecological pressures, such as the presence of predators and mortality rates, have an influence on the rates of adoption among these different communities (Boesch et al. 2010).

### Effects of Losing Mother

As stated, losing their mother is devastating for primate infants, even when they are subsequently adopted; the lack of a mother can have multiple behavioral and neurophysiological effects throughout the orphan's life. In several species, orphans can experience decrements in growth, reproduction, and longevity and suffer from negative impacts on health, social status, and emotional development such as anxious

behavior and effects on their ability to engage in successful social interactions, with declines in play and other social responses and increases in abnormal behavior, such as lethargy, rocking, and hair plucking (see, e.g., in baboons, Tung et al. 2016; chimpanzees, Nakamura et al. 2014; Walker et al. 2018; bonobos, Clay and de Waal 2013). These effects are much stronger in chimpanzees who become orphans as the result of bushmeat practices and the pet trade (see, e.g., Lopresti-Goodman et al. 2013).

Despite recognizing the effect that losing their mother has for chimpanzees, there is no agreement about what is the minimal age (i.e., time spent with mother) that buffers chimpanzees from serious negative effects. Bloomsmith et al. (2005) performed a review of the existing data on chimpanzees in captivity and concluded that chimpanzees who were separated from their mothers in laboratory settings but lived with their mothers for at least 1 year before the separation exhibited little rocking behavior and four times as much maternal competence as adults (when compared to individuals separated from their mothers before the age of 1 year). They found no behavioral differences in subadulthood between laboratory infants separated from their mothers after age 2 and peer-reared and mother-reared infants. The authors concluded that if chimpanzees spend 2 years with their mothers before separation, they will not exhibit abnormal behaviors. However, these results are in opposition to Botero et al. (2013) who observed the behavior of orphaned chimpanzees who lived in their natal communities when their mother died; they reported anxiety-related behaviors and diminished rates of play in chimpanzees orphaned much later than 2 years of age.

Other researchers have described behaviors of orphaned juveniles changes that do not seem detrimental to the individual such as imitation and other cognitive abilities (see, e.g., in free-ranging rehabilitant orangutans (*Pongo pygmaeus*), Russon and Galdikas 1995). Others have described outcome behaviors that do not seem either detrimental or positive to the individual such as higher levels of social attention (i.e., directing visual attention at conspecifics) and



increases in climbing and object manipulation (see, e.g., in vervet monkey (*Chlorocebus pygerythrus*), Grampp et al. 2019)

Most of the research regarding the effect of the absence of the mother for chimpanzees and infant and juvenile monkeys has been conducted with populations in captivity. Several authors have reported negative behavioral effects for chimpanzees (e.g., anxiety, rocking behavior, lower levels of play, disorganized attachment styles) who had to be separated from their mothers and were reared under limited human interaction or in peer groups. Research in monkeys in captivity has shown that prolonged or repeated maternal separations are associated with lifelong dysregulation of physiological systems and an increased risk of pathological emotional development, including hormonal changes and enlargement in stress-sensitive brain regions, among other effects (see, e.g., in rhesus monkeys (*Macaca mulatta*), Conti et al. 2012).

It is not clear whether these effects are also present in orphaned monkeys in captivity. In opposition to the previous studies, several studies found negligible differences in infancy and post-infancy behaviors (i.e., maternal–infant interactions and neuroendocrine and behavioral responses to separations) between adopted and non-adopted rhesus monkeys in infancy and post-infancy behaviors (see, e.g., in rhesus monkeys, Champoux et al. 1995). Nor it is clear that these effects are present in wild populations, some researchers found no differences in the behavior of orphans (see, e.g., free-ranging male rhesus monkeys, Drickamer and Vessey 1973). Moreover, some research shows positive outcomes of orphans in monkeys (see, e.g., rhesus monkeys, Itoigawa 2001).

Researchers have also focused on the effects of losing a mother on the social relationships of the individual. These effects include an increase in the amount of time they associated, maintained spatial proximity, groomed, reassured, and consoled their siblings (see, e.g., in chimpanzees, Reddy and Mitani 2019). Another kind of effect on the social relationships for orphan chimpanzees is differences in the behavior of foster mothers and group members toward adopted infants. Foster mothers initially tended to be

more possessive and restrictive of their foster infants (e.g., foster mothers take longer before they allow infants to sit at a distance from them and retrieved them faster). Non-related members of the troop approached and sat in proximity more frequently, engaged in contact, touched, groomed, and lipsmacked the foster infants more often than they did with control infants, although this depends on the social ranking of the foster mother (see, e.g., in rhesus monkeys, Holman and Goy 1988)

## Sanctuaries

One final aspect that is important to consider when examining orphaned primates is the outcome for orphaned primates under the care of sanctuaries (see, e.g., gorillas, King et al. 2005; bonobos and chimpanzees, Wobber and Hare 2011; orangutans, Robins et al. 2013). Most wild sanctuaries are different from zoos and other captive environments because apes have access to primary tropical forests every day. Thus, in this dimension, the sanctuary environments may be better able than other captive facilities to meet the “top 10” requirements for the care of apes in captivity based on the daily choices that are available to them. Moreover, as stated earlier, given the violence and neglect that most of these infants endure before coming to the sanctuaries, the effects of losing their mothers are often more severe than the effects of losing a mother for an infant in other kinds of captivity.

Similar to the studies reviewed earlier, the conditions under which the chimpanzees in these sanctuaries are reared by foster mothers have an effect on their behavior later in life. For example, in a recent and novel study, Ortín et al. (2019) evaluated the effects of bushmeat trade outcomes on the personality development of African sanctuary chimpanzees. Mother-reared chimpanzees were rated as lower in restraint than hand-reared chimpanzees. They were also rated as less dominant than hand-reared chimpanzees.

Overall, despite all these difficulties, most orphan chimpanzees from sanctuaries are capable of successfully adapting to life in the wild after a

rehabilitation period in the sanctuaries. After their release, most of them are able to survive; some of the females gave birth to healthy offspring and successfully immigrated into a wild chimpanzee community (see, e.g., Humle et al. 2011). It is important to notice that despite the detrimental effects of being an orphan, for chimpanzees, under the special socio-ecological circumstances provided by some sanctuaries, the release of wild-born adult chimpanzees of both sexes is a viable strategy to remedy the damage caused by the bushmeat and pet industries.

## Conclusion

Young primates who lose their mothers are extremely vulnerable; orphaned infants are left without their main source of protection, transportation, food, and comfort. To ensure their survival, another individual must adopt the orphan. The foster caretaker will provide the infant a similar kind of care as their biological mothers; they will provide nursing and/or food-provisioning, carrying, active vigilance during group travel, defense, grooming, and comforting behavior. However, future studies are necessary to fully understand the complexity and variation of the adoption process among different communities and environmental conditions and the effect that losing their mother and being adopted has for an orphan primate.

## Cross-References

- [Alloparental Care](#)
- [Cooperative Breeding](#)
- [Parental Care](#)
- [Parental Investment](#)
- [Parenting](#)

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## Primate Perspectives on the Evolution of Human Behavior

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### Synonyms

[Primate analogies](#); [Primate models](#); [Primate-human homologies](#)

### Definition

The use of primate behavior studies to reconstruct the evolution of behavior in human ancestors and hypothesize about the persistence of primate behavior components in living humans.

### Introduction

Nonhuman primates (often called simply *primates* for convenience) are the closest living relatives of humans. The main groups are apes, monkeys, tarsiers, lemurs, and lorises. For the sake of space and relative simplicity, the examples in this article are limited to monkeys and apes. The term *hominin* encompasses all members and branches of the evolutionary lineage that separated from other primates and produced the human species (Andrews 2020). Primate behavior has been the basis for many inferences about hominin evolution, especially its earliest stages (King 2016; van Schaik 2016). This information can elaborate on and fill gaps in the archeological record. It can also suggest the presence and form of behaviors that left no direct evidence. Though based on extensive learning, primate behavior also displays innate influences (i.e., relatively specific genetic foundations). The same kind of behavioral complexity must have been true of early hominins, and some of the innate components are probably conserved in living humans.

Thus, comparison with other primates can suggest the existence of such innate components and illuminate their interaction with learning in the behavior of early hominins and living humans.

## Hominin Evolution

Our closest living relatives are chimpanzees and bonobos; both species are assigned to the genus *Pan*. The species ancestral to *Pan* and *Homo* is often called the last common ancestor or LCA (i.e., the last ancestor shared by humans with any other primates). It probably existed between 9 and 6 million years ago (mya). From about 4 mya, hominin species proliferated in a geographic arc from Chad through East Africa to South Africa. These *early hominins* (as the term is used here) have been assigned to several genera, including *Ardipithecus* and *Australopithecus*. Earliest *Homo* (e.g., *H. habilis*) can be included in this category. *Homo* emerged about 2.8 mya with characteristics that can be viewed as continuing trends visible in *Australopithecus*, such as slightly larger body size and a slightly larger brain (Kimbel and Villmoare 2016). The appearance of *Homo erectus* (using the term in its broadest sense) marked the turning point toward human adaptation with a major increase in brain size, nearly modern skeleton, lengthened life history stages, and skilled toolmaking; however, primate comparisons have been applied even at this stage (Swedell and Plummer 2019).

Early hominins combined apelike physical traits, such as long arms, with humanlike characteristics, such as habitual bipedalism (Andrews 2020). Probably most individuals weighed between 30 and 50 kilograms. The degree of sexual dimorphism is disputed, but males in some populations may have been almost twice the size of females. Most early hominins lived in “mosaic environments” that included deciduous tropical woodlands and various more open areas, as well as a substantial body of water (lake, river, or floodplain) (Andrews 2020). The diversity of early hominin environments also included geographic variation, fluctuations across time, and a general drying trend.

Explanations for early hominin adaptations can be sorted into three major categories (Maslin et al. 2015). *Savanna/aridification* hypotheses emphasize the effects of hotter and drier habitats, varying from woodlands to treeless grasslands. *Fluctuating environment* hypotheses focus on the ability to adjust to continuous or recurring changes in environmental conditions. *Social* hypotheses emphasize competition within societies, including status negotiation and sexual selection. Living primates are relevant to all three categories because (1) various living primates have adapted to diverse habitats, from woodlands to savannas; (2) long-term studies have demonstrated primate responses to environmental fluctuation; and (3) primate societies are complex and entail both social and sexual competition.

## Primate Models

The term *model* is usually applied to an aggregation of primate data that is organized to generate hypotheses about hominin behavior (Moore 1996). Definitions vary greatly, and a model can be used in a comprehensive way or as a source of inferences about particular traits.

Basic descriptions and critiques were collected by de Waal (2001) and Kinzey (1987). Primate models have been distinguished from one another in various ways, but the methods and results often overlap (King 2016).

**Referential models** use a real phenomenon to illuminate others that are more difficult to study. In this case, the first phenomenon is one or more species of living primates, and the second is human ancestors. Referential models can show possible behaviors, suggest hypotheses, and provide detailed scenarios as a basis for testable predictions (Moore 1996). These models can suggest both general patterns (e.g., type of diet) and details (e.g., consumption of honey). Referential models use several different premises:

**Phylogenetic models** are based on evolutionary relationships among taxa and postulate that related taxa share some kind of genetic foundation for similar behavioral patterns. These may be homologies derived directly from a common

ancestor or parallel developments based on the common biological heritage. *Pan* referential models are predominant in phylogenetic reconstructions of the LCA and early hominins. Where there are behavioral divergences, *Pan* usually provides a more likely model than *Homo* due to similarities to the probable LCA such as limb proportions and brain size. Where the *Pan* species (chimpanzees and bonobos) differ from one another, the choice of a model is debatable, hence, for instance, a long-running controversy about early hominin aggressiveness. In some cases, the *Pan* species and humans may all differ from the LCA.

A solution to such problems is to expand the comparative sample. Gorillas and/or orangutans may be added to form broader ape models. However, their value for the purpose is limited because there are just three ape genera and there are extreme behavioral differences among them. Broader models can be generated by adding gibbons, Old World monkeys, New World monkeys, and prosimians or using the primates as a whole. These larger samples can provide broadly documented evolutionary similarities but at the cost of fewer relevant traits and less detail.

**Functional models** are based on similarity of effect, emphasizing convergence rather than phylogeny. They can address questions about need (adaptations required by particular conditions) and capability (ability of subjects to perform a postulated behavior). Also based on convergence, *attribute models* (also called *trait models*) start with a particular hominin characteristic and seek an analogous trait in extant primates (e.g., transport of toolmaking materials).

The chimpanzee species (*Pan troglodytes*) is of special significance. The genus *Pan*, as noted, shares the LCA with the hominin lineage. The chimpanzee species also occupies a wide range of environments much like those of early hominins. Chimpanzees can provide trait models for selected features (e.g., tool use) or comprehensive models for a total way of life in woodland or savanna (Muller et al. 2017). Examples include varied tool-using and toolmaking practices distributed across groups and populations in patterns that many scientists characterize as cultural

traditions. Baboons (genus *Papio*) also receive special attention. Unlike most other monkeys, they are large-bodied, largely terrestrial primates that have adapted to a wide variety of environments, including deserts and mountains (Fischer and Zinner 2020). Traits relevant to early hominins include male-female associations and multilevel societies. Chimpanzees and baboons both contribute to discussions of predator defense, social intelligence, and prelinguistic patterns in early hominins.

**Conceptual models** draw on general principles from fields such as behavioral ecology and evolutionary psychology to specify relationships pertinent to a particular situation, such as early hominin environments (De Waal 2001; Kinzey 1987). A comparable mathematical approach used regression equations to produce correlations (e.g., group size with body mass) into which a hominin species can be interpolated. This works only if one variable is already known for the fossil species. *Systems models* avoid this problem by using more complex equations to construct functional models of behavioral ecology. Mathematical models can be powerful, but they require more data than others and apply only to traits that occur in many species. The conceptual and referential approaches overlap; some conceptual analyses have produced sets of traits similar to those of particular living species. Referential models continue to be most prominent in linking hominins with living primates.

**Criticism of Primate Models.** Criticisms of primate models for the LCA and early hominins can be sorted into two major categories: doubts about the relevance of the primates themselves and doubts about the relevance of their environments to prehistoric conditions. Many questions are being resolved as we learn more about primates (e.g., complexity of social life and use of stone tools) and the characteristics of early hominins (e.g., sexual dimorphism and retention of arboreal capabilities). Much the same can be said about environment, as primate studies and paleoecology have demonstrated the ubiquity of mosaic habitats, including dry and open areas. The faunas of prehistoric habitats were different from those of today, but there are also crucial



similarities such as feline predators and small mammals to be hunted.

## Primate Perspectives on Ecology

**Food Preferences.** The inertia hypothesis proposed that humans overindulge in the preferred foods of our ancestors when opportunity allows, resulting in numerous diseases and debilitating conditions (Hamilton 1987). In the evolutionary past, it was adaptive to maximize consumption when fluctuating resources were available. The motivational systems changed little, while access increased for some humans in recent times, resulting in consumption of unhealthy quantities. The hypothesis was formulated for meat and sweets, but it also applies to alcohol (Dudley 2014).

Primate evidence, beginning with a broad phylogenetic perspective, argues for the existence of such motivational systems. Most primates consume insects (as do many human populations), and many monkeys and apes eat vertebrates (Watts 2020). In addition to land animals, some primates exploit fish and other aquatics, which would have been available to early hominins living near substantial bodies of water. Three referential species – chimpanzees, bonobos, and baboons – kill mammals for food. Though meat is a small percentage of the overall chimpanzee diet, cost/benefit analysis of skewed distributions demonstrates significant nutritional value for some individuals. Behavior in both *Pan* species (hunting, begging, and appropriating) indicates strong motivation to consume meat. Some chimpanzees seem to hunt cooperatively, which might be relevant to the appearance of some of the larger prey animals in the archeological record.

Human attraction to sweet taste is probably derived from fruit-eating ancestors. Apes emphasize ripe fruit consumption wherever the environment permits. Chimpanzees endure hard work and pain to obtain honey, which is dense in nutrients. Attraction to fruit has an extra dimension in the form of ethanol, which results naturally from fermentation of fruit sugars. The scent of ethanol may attract primates to sites of ripe fruit and

may also act as a feeding stimulant (Dudley 2014). Genetic analysis indicates that an enzyme for metabolizing ethanol originated in African apes about 10 mya, when some probably started foraging on woodland floors where fallen fruits contained higher quantities of ethanol. Some wild chimpanzees engage in long-term and recurrent ingestion of ethanol from palm trees, often in large quantities. In some locations, monkeys steal alcoholic drinks from tourists.

**Ingestion of Nonfoods.** Early hominins probably ingested nonfoods that had health benefits. Geophagy – the intentional consumption of earthen materials, including soil, chalk, and clay – is widespread among humans and other primates on all continents inhabited by both (Pebsworth et al. 2019). A common feature is the presence of clay minerals such as kaolinite, which humans have long used in antidiarrheal and topical medications. Primate geophagy is also adaptive in providing essential dietary elements, as well as protection against toxins, pathogens, parasites, and gut irritants.

Non-nutritional plant matter also provides health benefits. Sick chimpanzees get chemical relief from intestinal parasites by chewing bitter pith, and several ape species swallow whole leaves that cause the expulsion of parasites. Japanese macaques display some similar patterns. Remains of plants in archeological assemblages include species that are both edible and medicinal along with some that have no value other than medicinal properties. The proportion of medicinal plants at surveyed sites was well above the natural average, so the inclination to self-medication may have been conserved throughout hominin evolution.

**Predator Responses.** Primates are prey to other animals. Snakes eat primates, and poisonous snakes may also strike defensively (Isbell 2009). Primate responses suggest innate visual mechanisms: recognition that distinguishes snakes from other animals and from the immediate environment, followed by close attention. Other behavioral responses vary: flight, avoidance, aggression, and curiosity. Young primates seem to learn agonistic responses from adults by watching them freeze, flee, utter alarm calls, or

mob snakes. Some variation in primate responses may be related to size: constrictors are frequent predators, and many poisonous snakes in primate habitats are large.

Human responses to snakes are comparable to those of other primates and suggest an evolutionary basis beyond the LCA (King 2016). Humans orient strongly to snakes in various experiments, and ontogeny suggests an evolved basis: infants and children orient more rapidly and more often to snakes than to other stimuli. Experiments indicate that the fear component is learned in humans, as in other primates. Cross-cultural evidence shows that humans consistently pay more attention to snakes than to most other animals, while symbolic characterization of snakes varies from dangerous to benevolent.

Early hominins also faced mammalian predators similar to those of recent times, such as big cats and hyenas. Having retained ancestral climbing abilities, they must have escaped into trees when possible and probably slept in trees. However, if trees were not available, they had to flee or fight. Evidence from baboons and chimpanzees, large primates living in large groups, indicates that fighting was a possibility.

## Primate Perspectives on Technology

**Weapons.** One of the most important roles of primate functional models is to demonstrate behaviors possible to small-brained early ancestors. Decreasing size of the canine teeth, combined with increasing exposure to open habitats, suggests a need for nonanatomical weapons to defend against predators. Wild chimpanzees suggest two possibilities. One case is the spontaneous use of sharpened sticks to kill bush babies for food (Pruetz et al. 2015), which indicates that thrusting spears for defense could have been an early invention. Club use is suggested by chimpanzee use of sticks against a mechanical leopard (in an experiment), a real leopard, and a drone that was knocked out of the air (van Hooff and Lukkenaar 2015). Bipedal hominins could have carried spears or clubs as they traveled.

Captive apes throw various objects, sometimes learning great accuracy, and some researchers think that throwing affected the evolution of hominin anatomy and neurology (Lombardo and Deaner 2018). Stone throwing would have been useful to early hominins (against competitors as well as predators) if they accumulated a sufficient quantity at resting or feeding locations (a parallel argument has been made for caching of butchering tools by early hominins). One zoo chimpanzee was said to plan for future weapon use when, on numerous occasions, he collected and cached rocks that he threw at human visitors later in the same day (Osvath 2009). Shettleworth (2010) doubted that the behavior represented foresight. This illustrates the need to distinguish between different types of analogy. Regardless of the underlying cognitive process, the chimpanzee's behavioral sequences (empirically verified on multiple occasions) provide a functional analogy for possible hominin behavior.

**Extraction.** The idea that early hominins might have accumulated stones for throwing is consistent with data on numerous wild primates transporting appropriate tools to subsistence sites. All great ape genera use tools for various purposes in the wild and in captivity. According to phylogenetic models, this makes some tool use by the LCA probable. Several monkey species also use tools, which suggests potential for convergence (Carvalho and Beardmore-Herd 2019). Chimpanzees are especially versatile in making and using tools of perishable materials, such as the termite probes famously reported by Jane Goodall. Such tools would leave no traces in the archeological record but could have been crucial for the survival of the LCA and early hominins. Chimpanzees use sticks to probe nests for various insects and honey, kill bush babies in tree holes for food, excavate plant storage organs from the ground, and get water during dry seasons by digging holes in sandy riverbeds. Digging near standing pools, they obtain water filtered free of algae and detritus – perhaps the conscious purpose of the behavior. Whether reasoning by homology or analogy, these and other cases of primate tool using suggest possible if not probable early hominin behaviors based on mental capability derived from the LCA.

**Stone.** Though long considered characteristic of *Homo*, stone tools were used earlier, perhaps before 3 mya. Primate behavior suggests antecedent developments (Carvalho and Beardmore-Herd 2019). Chimpanzees smash hard-shelled fruits against tree trunks and thick branches. On the ground, they use stone hammers to crack fruits and nuts placed on tree roots or stones as anvils. After use by the apes, these tools resemble remains found at early hominin sites. Capuchin monkeys also crack nuts with stones on stone anvils. Chimpanzees crack tortoise shells, and long-tailed macaques break open shellfish with stones, which suggests how early hominins obtained food from the bodies of water in their habitats.

Eventually, the most important hominin tools were made from stone flakes. The potential for this invention is demonstrated by the residue of stone-on-stone percussion by capuchin monkeys: sharp-edged flakes and cores that resemble early hominin lithics. The capuchin data demonstrate that humanlike cognition, coordination, and manual dexterity are not prerequisites for stone flake production and that attributing intentionality based solely on findings in the archaeological record is questionable for the earliest cases (Carvalho and Beardmore-Herd 2019). In captivity, a few bonobos and an orangutan have learned to use flake tools for cutting, but no such behavior has been seen in wild primates.

**Sequential tool use** and manufacture by primates suggest cognitive abilities that might have characterized early hominins. This is the use of a tool to obtain another object that will then serve as a tool for another goal (usually food). Mental requirements include foresight and planning of hierarchically organized behaviors. All great apes and several monkey species are capable of spontaneously using two tools in sequence, but the *Pan* species and orangutans can use as many as five. The manufacture of bush baby which are spears, for example, requires as many as five steps (Pruetz et al. 2015). Sequential tool use also requires patience, the ability to suppress immediate motivations and defer an action until appropriate preparations have been made. Patience is

required for other natural behaviors such as using a tool to withdraw termites from a nest.

## Primate Perspectives on Social Life

**Societies.** Comparison across the primates demonstrates the social ancestry of humans. A common kind of society, called a troop or community, contains multiple adult females and one or more adult males – numerous males in *Pan*, baboon, and human societies. The *Pan* species and human hunter-gatherer societies display fission-fusion: members form subgroups (“parties”) that are flexible in size and personnel; they can travel independently or coalesce. Fission-fusion organization in the spider monkeys of the New World provides a basis for analogical testing of hypotheses, such as the relationship of fission-fusion processes to food supply and other environmental conditions (Aureli and Schaffner 2010).

**Multilevel Societies.** Some primatologists see better analogies for early hominin organization in more complex primate societies that are characterized by nesting of social units within larger social units, also a characteristic of human societies (Swedell and Plummer 2019). Multilevel societies have been documented in various Old World monkeys and may occur in several New World primates. The constituent groups are one-male units (usually containing several females), which may be embedded in two more higher levels of organization. These social entities (rather than individuals) undergo fission-fusion processes. Terminological confusion has been introduced with regard to the higher levels by the cooption of terms such as “troop” and “community” that were originally coined for single-level societies such as those of baboons and chimpanzees. In addition, these terms are not used consistently across multilevel species.

Related analogies for hominins occur in a few multilevel species. One is dispersal of females from their natal groups, which converges with outmarriage of women among humans. Another is male-male tolerance between constituent units, probably mediated by kinship. These male-male

relationships are also facilitated by elaborate and repeated greeting rituals, which have been compared to certain greetings in human societies.

**Family Antecedents.** Multilevel societies offer one model for the emergence of human families within communities, but there are others. Among baboons and some other Old World monkeys, certain males and females form distinctively close relationships that persist through non-mating periods. In some species, bonding is suggested by the occurrence of affiliative behaviors such as mutual grooming and huddling. In some cases, the males provide some care for the offspring of the female, often their own as well (Fischer and Zinner 2020).

“Pair bonding” is a controversial concept that has been applied to humans and other primates, particularly certain New World monkeys (Fernandez-Duque et al. 2020). The social and sexual arrangements among those primates are diverse. Pair living seems obligatory in some species, common in others, and occasional in still others. Some are sexually monogamous, and some are not. Bonding in the sense of emotional attachment is poorly documented in the wild, but experiments with titis suggest the possibility of analogous insights into human bonds. Owl monkeys and titis show some of the highest levels of paternal care in mammals, and both live in strictly pair-living groups, an association that may provide a functional analogy for early hominin evolution.

**Social Cognition.** Primate models suggest a maximum community size of several hundred individuals for early hominins. Human capacities for social bonding and memory may have evolved in such a context. MRI research suggests that some aspects of social life in humans and other primates are rooted in homologous parts of the brain. A study of captive baboons found that those living in larger social groups had larger brains. The effect was driven mainly by white matter volume and to a lesser extent by gray matter (Meguerditchian et al. 2021). Among captive rhesus monkeys, those housed in larger groups had more gray matter in several regions of the temporal cortex. Other monkey studies demonstrated that one of these regions is involved in

responses to faces, body movements, and probably the direction of attention of other individuals.

The *social intelligence hypothesis* relates enhanced cognition to more complex and intense social life, which entails more than group size. It explains a great deal about monkeys and apes but does not distinguish cognitive features that set apes and humans apart from other primates. The key may be the slow life history associated with larger body size (van Schaik 2016). This permitted greater growth in the metabolically expensive brain over the course of prolonged neural development, resulting in natural selection for cognitive problem-solving. In this case, a single homology may have given rise to multiple parallel developments in social relationships and cognition.

**Prosocial Behavior.** Primates display several of the elements that underlie human morality, including conformity, conflict resolution, reciprocity, reactions to inequity, and empathy (Burkart et al. 2018). These elements are not distributed evenly across primate species, which suggests that they are analogous developments. They are particularly strong in marmosets and tamarins, the small monkeys of the New World. Analogy with these monkeys suggests that elements of morality evolved in the context of shared infant care. Broader comparison indicates that prosociality increases with the amount of cooperative infant care in a species. Chimpanzees score low in tests of prosociality, but they display occasional targeted helping, food sharing, alerting others to danger, and some tendency to conformity. Cognitive abilities like those of chimpanzees may have been the most important phylogenetic factor in the evolution of hominin morality: great apes recognize inequity in the value of rewards, while marmosets and tamarins do not.

**Culture.** Chimpanzees, orangutans, and some monkey species display behavioral variation across populations and societies that many primatologists call “cultural” in the sense that distinctive behaviors are shared among group members, apparently as a result of social learning. This suggests that culture was a mode of adaptation in early hominins, perhaps as far back as the LCA. For example, researchers compared chimpanzee

termite fishing across 17 locations revealing 38 different technical elements, including community-specific combinations of three to seven elements (Boesch et al. 2020). Thirty of those were not ecologically constrained, indicating that variation was cultural. The number and combination of elements shared among individuals were more similar within communities than between them, thus supporting community-majority conformity via social imitation. The researchers asserted that variation in community-specific combinations of elements parallels cultural diversity in human greeting norms or food utensil etiquette.

## Primate Perspectives on Communication

**Tactile.** Social grooming is a vital social interaction in most primate societies and is obviously pleasurable or comforting to the individuals involved. Stimulation of the skin is probably an important stimulus for those being groomed. In humans, with little body hair to groom, other kinds of touching may stimulate a tactile system that is homologous with other primates (Dunbar 2017). Social and emotional components comparable to those of primates are demonstrated by experiments with humans, including neural differentiation between affective contacts and neutral tactile sensations.

Embracing is common among male chimpanzees and between men cross-culturally. Chimpanzees embrace before and during confrontations and in other stressful situations. This is a case where other apes add little to phylogenetic reconstruction because adult male-male relations in gorillas and orangutans are largely hostile. However, embracing is a vital social behavior in spider monkeys, which live in fission-fusion societies analogous to those of chimpanzees (Aureli and Schaffner 2010). Social limitations on this natural behavior in some Western cultures may be psychologically damaging.

**Visual.** Gestures, including facial expressions and postures, are important in communication between primates (Fröhlich et al. 2019). Gestures with the arms and hands are important

components of natural visual communication among the great apes. Many of these gesture types are widely shared and thought to be homologous. Some gesture types used by human children also occur among apes and may be derived from the LCA.

“Smiling” probably conflates two expressions with separate primate origins. One is the “silent bared-teeth display” (less formally, the “grin” or “grimace”). Phylogenetic comparison shows that social submission was its original meaning and function (van Hooff and Preuschoft 2003). The other relevant primate expression is the playface, a relaxed open-mouth expression that occurs mainly in the play of immatures. It signals intent for friendly interaction and is motivated by pleasure. It is probably homologous among the great apes and humans and seems to be convergent in several other primates. An alternative view of smiling is that the two signals actually overlap in humans rather than just being conceptually conflated. They became uncoupled from their original contexts (submission and play) and converged in human evolution to the point of overlapping. Comparable uncoupling of the grimace has occurred in monkeys with relaxed dominance hierarchies that do not require sharply defined social signals.

**Auditory.** In young apes and human children, the playface is associated with laughter, i.e., vocalizations with similar acoustic features that are probably homologous and signal friendly intent even though play may become rough. Some theorists distinguish human laughter from the other primate signals, postulating that it was elaborated by natural selection to cope with short-term fluctuations in danger and hunger. In this view, laughter became a means for rapid communication of safe conditions to all members of a group (Gervais and Wilson 2005). The assumption of stressful conditions for early hominins is supported by analogy with savanna chimpanzees, baboons, and vervet monkeys.

Drumming is a natural display in wild chimpanzees. An individual pounds his hands and feet against a large tree, making a sound that carries over long distances. Captive chimpanzees and gorillas drum on artificial surfaces. Bimanual



drumming may be homologous among great apes and humans, suggesting an early origin for this component of music (Fitch 2006). Analogously, drumming by some captive macaques attracted the attention of other monkeys in a way similar to conspecific vocalizations. It also influenced viewing of conspecifics in a preferential looking experiment, and fMRI showed that drumming activated the same brain areas as vocalizations.

**Intentionality.** Primate communication displays features that are also components of language in the human sense. These have implications for the origins of human cognition. Experiments with chimpanzees demonstrated intentionality in gestural communication by documenting actions that individuals used repeatedly toward a recipient until they got a particular response (Tomasello and Call 2019). Such behavior is motorically ineffective, requires the active participation of a partner to fulfill its purpose, is tailored to the attentional state of the audience, entails waiting for the recipient's response, and often seems directed toward a single social goal. The apes account for the perceptual access of the recipient by using attention-getting gestures such as touching or moving to be in front of the intended recipient. If an initial gesture fails, the sender may persist by repetition or elaborate by sending alternative signals. One example is the use of a string of play gestures, either the same or different, until the other begins playing. Some vocalizations also hint at intentionality. Confronted by a moving snake model, wild chimpanzees called to companions, alternating gaze between the snake and the other chimpanzees, and persisted until all companions were informed.

**Conversation.** Analogy with the small-brained marmosets suggests that elements of conversation could have developed early in hominin evolution, including turn taking and voluntary control of vocalization (Ghazanfar et al. 2019). Marmosets can modulate and interrupt their own ongoing vocalizations and cooperatively modify the amplitude of calls in accord with perceived distance from each other. They take turns in contingent and repeated exchanges over extended periods, an ongoing interaction that differs from simpler call-response patterns. In addition to

facilitating communication between adults, turn taking reinforces learning of vocalizations by young marmosets. They are influenced by contingent parental feedback in much the same way as human infants.

Voluntary control of vocalization requires the involvement of various cortical structures, some of which have been connected to learning and voluntary production of primate vocalizations. A network of frontal regions that could allow such cognitive control seems to be homologous across monkey species and with humans. There is also evidence for neural similarities between humans and monkeys with regard to laryngeal control and to the processing of vocal stimuli from others.

**Multimodal Communication.** Human communication is multimodal. People combine language with nonlinguistic sounds, facial expressions, gestures, and postures, and the capacity to deliver and understand such combinations is apparent in other primates (Fröhlich and van Schaik 2018). This capability can probably be traced back to the LCA and beyond. Primates display flexibility in communication by choosing among modalities depending on circumstances. Chimpanzees and bonobos use gestures when another individual is face-to-face and touch to get the attention of one facing away. Vocalizations may be used in either situation. Making such choices might, for example, have enhanced the safety of early hominins with predators in the vicinity.

Primates also use signals from different modalities simultaneously. Lip smacking during grooming by monkeys and apes, for example, delivers auditory and visual stimuli. African apes, like humans, differ from orangutans in the use of auditory gestures, such as slapping surfaces, stamping on them, drumming, or clapping hands. Simultaneous signals may simply reinforce one another, but they may also deliver more complex meanings with social significance. Bonobos, for instance, emit the same "contest" vocalization in playful and aggressive contexts but add gestures that distinguish their intentions. These and other examples suggest that an important function of multimodal signaling is to reduce ambiguity.

The importance of multimodal combinations is indicated by the fact that chimpanzees often use them even when communication is facilitated by good visibility and familiarity between individuals. The prominence of such communication in our closest relatives suggests that a similar system aided our early ancestors in their expansion across Africa.

## Conclusion/Summary

Many behavioral scientists study nonhuman primates as models or as a source of analogies for a better understanding of our earliest ancestors. The results augment the archeological record and fill gaps where there is no record. Frameworks for such inferences include phylogenetic relationship, convergent evolution, ecological parallels, and functional necessities. Chimpanzees and baboons play leading roles in this approach, but many other primates provide useful information. Rather than result in abandonment of this approach, criticisms have stimulated more cautious and nuanced hypotheses. At the same time, findings in both paleoanthropology and primatology have strengthened the basis for inference. This work has provided insights for a wide range of behaviors, including food preferences, tool use and manufacture, social grouping, male-female relations, nonverbal communication and elements of language, and morality.

## Cross-References

- Affiliative Behaviors
- Allogrooming
- Alloparental Care
- Arboreality
- Attention Bias
- Behavioral Flexibility
- Bipedalism
- Brachiation
- Catarrhine Cognition
- Catarrhine Communication
- Catarrhine Diet
- Catarrhine Life History
- Clambering
- Cognition
- Common Ancestor
- Communication
- Comparative Cognition
- Consort
- Contact Comfort
- Convergent Evolution
- Cooperation
- Cooperative Hunting
- Culture
- Encephalization
- Episodic Memory
- Female Choice
- Fission-Fusion
- Friendships in Animals
- Group Living
- Hominid
- Hominoid
- Hominoidea Locomotion
- *Homo erectus*
- *Homo ergaster*
- *Homo sapiens*
- Hunting
- Innovation
- Intelligence
- Intentionality
- Last Common Ancestor
- Lucy
- Machiavellian Intelligence
- Mate Guarding
- Mating
- Monogamy
- Nut-Cracking
- Pair Bond
- Paternal Behavior
- Philopatry
- Platyrrhine Cognition
- Play Behavior
- Precision Grip
- Primate Communication
- Primate Locomotion
- Primate Social Structure
- Primate Suspensory Behavior
- Primates
- Pro-social Behavior
- Referential Communication
- Sexual Dimorphism

- ▶ Sexual Selection
- ▶ Social Grooming
- ▶ Social Intelligence Hypothesis
- ▶ Social Learning
- ▶ Socialization
- ▶ Sociosexual Behavior
- ▶ Stone Tools
- ▶ Tai Chimpanzees
- ▶ Technical Intelligence Hypothesis
- ▶ Terrestrial
- ▶ Tool Use
- ▶ Troop

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## Primate Research Centers

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## Synonyms

National Primate Research Centers (NPRCs);  
Regional Primate Research Centers (RPRCs)

In 1960, the US Congress passed a legislation that enabled the National Institutes of Health (NIH) to fund and to provide resources for scientists and institutions to conduct research with nonhuman primates (“National Primate Research Centers” 2019; Newbern 2016; “Yerkes National Primate Research Center” 2019) through the National

Center for Research Resources (NCRR; Berns et al. 1996) and now through the Office of Research Infrastructure Programs (ORIP), Division of Comparative Medicine; “U. S. Department of Agriculture, Environmental Enrichment for Nonhuman Primates” 2019. The National Institutes of Health Regional Primate Research Centers program began a network of research facilities for the study of monkeys and apes. Since 2002, the facilities have been known collectively as the National Primate Research Centers (NPRC). Emory, Tulane, and Harvard universities and the universities of California-Davis, Oregon, Washington, and Wisconsin were awarded the grants and the status of Regional (and later, National) Primate Research Centers (Riopelle and Coyle 1971). After the recent closure of the NPRC at Harvard University (2015; Fountain 2013), there are currently seven centers included in this network: the California National Primate Research Center (University of California-Davis, Davis, CA), the Oregon National Primate Research Center (Oregon Health and Science University, Beaverton, OR), the Southwest National Primate Research Center (Texas Biomedical Research Institute, San Antonio, TX), the Tulane National Primate Research Center (Tulane University, Covington, LA), the Washington National Primate Research Center (University of Washington, Seattle, WA), the Wisconsin National Primate Research Center (University of Wisconsin-Madison, Madison, WI), and the Yerkes National Primate Research Center (Emory University, Atlanta, GA) (“National Primate Research Centers” 2019). Scientists at these centers strive to improve the health of humans and other animals worldwide through biomedical research with monkeys (primarily) and apes, including investigations of preventative medicine, treatments, and cures for a wide range of diseases and ailments.

## Yerkes National Primate Research Center (Atlanta, GA)

Two histories of the Yerkes NPRC – originally named the Yale Laboratories for Primate

Biology – have been written: *Yale in Florida*, an unpublished monograph by Ada Yerkes in (1939), which in turn is summarized as part of Donald Dewsbury's (2005) definitive *Monkey Farm: A History of the Yerkes Laboratories of Primate Biology, Orange Park, Florida, 1930–1965*. This history begins well before the NIH began funding the National Primate Research Centers program. In 1916, Dr. Robert M. Yerkes, a psychobiology professor at Yale University, published an article in *Science* calling for the establishment of primate research centers. Dr. Yerkes speculated that by studying nonhuman primates, a wide range of scientists could gain insight about human biology and behavior; further, he argued that this speculation was widely appreciated by others in the field, and that “the neglect by scientists of systematic study of all of the primates excepting man is due, not to lack of appreciation of their scientific value, but instead, to technical difficulties and the costliness of research” (p. 231). He further described the solution to these practical obstacles: a permanent, general-use research station or institute, located in a suitable climate, with particular types of leadership and staffing, that availed and coordinated an interdisciplinary program of research. Subsequently, Dr. Yerkes convinced Yale University as well as the Rockefeller and Carnegie Foundations to provide funding for such an institution. In 1930, Yale Laboratories for Primate Biology opened its doors in Orange Park, Florida (Dewsbury 2005).

Yale University renamed the facility the Yerkes Laboratory of Primate Biology in honor of its founder, following his retirement in 1941. After Dr. Yerkes's death (February 3, 1956), management of the research institute shifted from Yale to Emory University. Around the same time, scientists successfully developed a polio vaccine through the use of a nonhuman primate model. This discovery led to a surge of interest in nonhuman primate research and a federal ruling by the US Congress to allocate two million dollars to the NIH, so that the NIH could establish the first federally funded primate centers (Dukelow and Whitehair 1995; “Yerkes” 2019). In 1961, the NIH granted Emory University with Regional Primate Research Center (RPRC) status and

funds that enabled the move of the Yerkes Center from Orange Park, Florida to Emory's campus in Atlanta (“Yerkes” 2019). Emory also established an affiliated field station in Lawrenceville, Georgia, where behavioral and reproductive research is conducted.

Since the Yerkes NPRC opened nearly 90 years ago, the center has made many important contributions to human health research, including (but certainly not limited to) creating an AIDS vaccine that is now in clinical trials, developing a candidate medication to treat cocaine addiction, and assisting in the development of a drug that preserves kidney function and prevents rejection in organ transplant (“Yerkes” 2019). Yerkes researchers are also dedicated to studying nonhuman primate cognition and behavior. Field-changing discoveries have been reported in the famous ape-language research with Lana chimpanzee by Duane Rumbaugh and his team, which began at Yerkes, and in recent investigations by behavioral scientists like Bill Hopkins, Robert Hampton, and Frans de Waal and his collaborators at the Yerkes-affiliated Living Links Center (“Living Links” 2019). These discoveries include documentation that chimpanzees are as apt as humans at facial recognition; that chimpanzees, like humans, have culture – that is, they adopt social norms and pass down traditions; and chimpanzees are more likely to follow the example of older, higher-status individuals over inexperienced individuals (“Yerkes” 2019) and many more such examples.

Currently, the Yerkes NPRC is home to about 3,000 primates, including rhesus macaques, sooty mangabeys, squirrel monkeys, cynomolgus monkeys, and chimpanzees (“Yerkes” 2019). Since the US Fish and Wildlife Service (FWS) ruled that all chimpanzees – including captive chimps – would be classified as endangered under the Endangered Species Act, primate research centers have effectively ceased all biomedical testing on the animals (Grimm 2015). The Yerkes center continues to conduct noninvasive, behavioral research with their population of chimpanzees. Yerkes researchers often work in collaboration with the Atlanta Zoo to gather behavioral and cognitive data (Dukelow and Whitehair 1995).



## **Oregon National Primate Research Center (Beaverton, OR)**

The Oregon NPRC was the first center to be established using the NIH federal funding from the 1960 US Congressional Action (Dukelow and Whitehair 1995). Construction of the facility began in 1962 (Doughman 2019; Dukelow and Whitehair 1995); however, Oregon's monkeys arrived in the USA well before the research facility was established. In the 1950s, the founding group of rhesus macaques was brought to Brown University from their natural range in Asia, and they were transferred to the Oregon primate research center in 1964. That same year the government of Japan donated 46 Japanese macaques to Oregon, because the species was threatened by deforestation and by farmers who wanted to protect their crops ("Oregon National Primate Research Center" 2019). Shortly thereafter, Oregon became the first of the RPRCs to use outdoor breeding facilities (1970; Doughman 2019), and the university pioneered the social housing of nonhuman primates in the 1970s ("Oregon" 2019) including 81-acre corrals holding up to 250 animals each (Doughman 2019). The ONPRC continues to work toward improving and innovating nonhuman primate housing, for example, by recently developing PENS (Primate Enclosure in a Natural Setting) that give animals indoor-outdoor access, with housing that includes heated floors and misting for seasonal weather fluctuations (Doughman 2019). Since 1998, the ONPRC has been affiliated with Oregon Health and Science University.

The ONPRC have made several important contributions to the scientific community. For example, ONPRC researchers developed mitochondrial replacement therapies that could prevent the transfer of mitochondrial defects from mother to child. They also were able to revert a skin cell back to its embryonic state, demonstrating future potential to use patients' own cells to create new liver, heart, and other cells, greatly reducing risk of transplant rejection. The ONPRC also created monkey models that allow the scientists to explore the effects, complications, and possible prevention of several human afflictions,

such as "high-fat diet-induced obesity" as well as the effects of alcohol- and drug-using mothers on their fetuses' brain and lung development ("Oregon" 2019) and many other contributions.

The ONPRC, located in Beaverton, OR, is currently home to about 5,000 nonhuman primates. Rhesus macaques constitute the largest colony, followed by Japanese and cynomolgus macaques, and a smaller number of baboons and squirrel monkeys ("Oregon" 2019). Most of the macaques were bred on site from the 1964 founding colonies (Doughman 2019).

## **Washington National Primate Research Center (Seattle, WA)**

It was originally planned that the Washington Primate Center would be the first to be established using the NIH federal funding; however, after some maneuvering by the House and Senate Appropriations Committee, the WaNPRC was established at the University of Washington shortly after the Oregon institution's establishment in 1962 (Dukelow and Whitehair 1995). In 1970, the University of Washington founded the Infant Primate Research Laboratory (IPRL) – the only one of its kind in the nation – in collaboration with the WaNPRC (Burbacher et al. 2013). The IPRL employs infant macaque models to investigate questions related to behavioral and biological development (Burbacher et al. 2013).

In the 1980s, the WaNPRC established another important partnership. With the continued use of monkey models on HIV and AIDS-related research, it became clear that there was need for the establishment of a captive virus-free population of monkeys, so as not to deplete natural primate populations. In 1982, Dr. O. A. Smith (a member of the WaNPRC and the World Health Organization) and other members of the World Health Organization met with the Indonesian government to discuss on establishing a monkey breeding facility on Tinjil Island that would eventually become the first Primate Research Center in Indonesia (Kyes et al. 1997). The WaNPRC received their first group of monkeys from Tinjil Island in 1991 for use in AIDS-related research,

and they continue to collaborate with this field station today (Kyes et al. 1997).

The WaNPRC has made several important discoveries that benefit the health of humans and other animals, including, but not limited to, the following examples. For instance, the WaNPRC researchers successfully treated color blindness in two squirrel monkeys with gene therapy. They also created a device that reduces or eliminates vertigo for patients with Meniere's disease, and the device has potential to treat other balance disorders in the future. Scientists at the WaNPRC also researched rewiring of the brain to bypass paralysis and remobilize paralyzed limbs, and in 2008 they developed a neurochip device (currently in use in the Seattle area) that treats patients with cerebral palsy and brain injury ("Washington National Primate Research Center" 2019a). Currently, the WaNPRC is working to develop an animal model to study the genesis of HIV-fighting antibodies. The WaNPRC has also established a Tissue Distribution Program (TDP) that provides nonhuman primate tissues and biological materials to research institutions within and outside the WaNPRC ("Washington National Primate Research Center" 2019b).

The WaNPRC is in Seattle, Washington, and conducts research on approximately 3,500 nonhuman primates. Those primates are located across two UW locations and four off-site locations ("Washington" 2019a), including a recently established (2013) pathogen-free breeding colony of pigtail macaques in Mesa, Arizona ("Washington" 2019b). In addition to pigtail macaques, the WaNPRC also works with long-tailed and rhesus macaques and squirrel monkeys ("Washington" 2019b). The WaNPRC also has a conjoint research program with the Woodland Park Zoo in Seattle ("Primate Info Net" 2019).

### **Wisconsin National Primate Research Center (Madison, WI)**

The Wisconsin NPRC was established in the early 1960s shortly after the ONPRC and the WaNPRC (Dukelow and Whitehair 1995) with the University of Wisconsin-Madison (UWM) as its host institution. However, the University of Wisconsin's history of nonhuman primate

research predates the establishment of the WNPRC. In 1930, Harry Harlow founded the Psychology Primate Laboratory (also known as the Harlow Center for Biological Psychology; "Primate Info Net" 2019; "Harlow Center for Biological Psychology" 2019). In 1958, Harlow conducted his famous Nature of Love experiment at the laboratory, where he demonstrated that maternal comfort and companionship are critical to healthy development in infant macaques (Harlow 1958). Harry Harlow eventually became the first director of the WPRC ("WNPRC" 2019). Today, Harlow's Center for Biological Psychology exists as a separate but affiliated entity to the WNPRC ("Harlow Center for Biological Psychology" 2019).

Scientists at the WNPRC have made several important contributions to human and other animal health research. In 1984, the WNPRC produced the first in vitro-fertilized monkey in the world ("WNPRC" 2019). The WNPRC was also the first to produce pluripotent stem cells from monkeys (1995) and then humans (1998; "Primate Info Net" 2019). This led to the eventual first successful culturing of blood, heart, and brain cells from embryonic stem cells in the early 2000s ("WNPRC" 2019). NPRC researchers also discovered certain developmental origins of insulin resistance and obesity and, relatedly, developed an FDA-approved natural sweetener for those trying to reduce sugar intake in their daily diets ("WNPRC" 2019). The WNPRC also created new and improved drugs to protect patients from transplant rejections and autoimmune diseases ("WNPRC" 2019) along with many other important contributions.

The WNPRC is located in Madison, WI, and houses approximately 1,500 animals, including its own breeding colonies. Presently, the animals include rhesus and cynomolgus macaques and common marmosets. In the past, the center has also conducted research with stump-tailed macaques, cotton-top tamarins, and vervet monkeys ("WNPRC" 2019).

### **California National Primate Research Center (Davis, CA)**

The California NPRC was the original "national center" and was established in the early 1960s

along with the other primate research centers. It was at first designated primarily to be a breeding facility (“UCDavis California National Primate Research Center” 2019). The center was formerly known as the National Primate Conditioning Center (Dukelow and Whitehair 1995), and then the National Center for Primate Biology (“UCDavis” 2019), until its status eventually changed to the California RPRC, corresponding to the other NIH centers, and became a national institution again in 2002 when all of the regional centers were redesignated as NPRCs (“UCDavis” 2019; “Yerkes” 2019). The CNPRC is affiliated with the University of California-Davis.

The CNPRC has made important contributions to biomedical research since its opening in the early 1960s. Scientists at the CNPRC developed tenofovir (PMPA), the most commonly used anti-HIV drug worldwide. This drug leads to large medical advancements for HIV-infected people, allowing them to live longer, healthier lives and enabling HIV-positive mothers to give birth to virus-free infants (“UCDavis” 2019). The CNPRC also discovered that tobacco-smoke exposure and pollution adversely affect organ development and that formula-fed infants are more likely to develop health issues later in life than breast-fed infants (“UCDavis” 2019). The CNPRC has also made advancements in research on Alzheimer’s disease, including the development of therapies currently in clinical use with patients with the disease, among many other contributions.

The CNPRC is located in Davis, CA, and is home to approximately 4,500 monkeys, which are mostly bred on site. The majority of these monkeys are rhesus macaques, but the CNPRC also houses a small population of South American titi monkeys (“UCDavis” 2019).

### **Tulane National Primate Research Center (Covington, LA)**

The Tulane NPRC opened in November of 1964, originally with the name Delta

Regional Primate Research Center, associated with the host institution of Tulane University (“Tulane National Primate Research Center” 2019). The center is situated on a historic 500-acre property known as Alexiusville that was purchased from the Alexius family in 1962. An original building (the “Alexius House,” built in the early 1800s) still exists on the property and will eventually be used as a visitors’ center after restorations (“Tulane” 2019).

Over its history, the TNPRC has made several important contributions to biomedical science. They developed the first macaque model of heterosexual transmission of SIV (simian immunodeficiency virus; the nonhuman primate version of HIV), the first monkey model of malaria in a pregnant female, the first nonhuman primate model of celiac disease, and the first rhesus monkey model of Lyme disease and placental transmission of CMV. Scientists at the TNPRC also made significant discoveries regarding the origin of AIDS: specifically, they found that SIV is evolutionarily much older than originally believed and that the sooty mangabey monkey is the natural host of SIV and the most likely source of HIV-2. They have developed and tested (or are in the process of developing and testing) several vaccines, including a tuberculosis vaccine and an AIDS vaccine. The TNPRC also established an improved diagnostic test for Lyme disease, among many other contributions (“Tulane” 2019).

The TNPRC is located in Covington, LA, and houses nine different species of primates: squirrel monkeys, baboons, vervet monkeys, mangabey monkeys (sooty and white-crowned), patas monkeys, and cynomolgus, pig-tailed, and rhesus macaques (“Tulane” 2019). The TNPRC mostly uses rhesus macaques for their research and has their own breeding colony of rhesus macaques on site (“Tulane” 2019). The current number of nonhuman primates living at the TNPRC is not listed. In 2006, they reportedly housed approximately 4,500 monkeys; however, approximately 50 of the monkeys accounted for in that report are species that are no longer listed on the TNPRC website (“Primate Info Net” 2019; “Tulane” 2019).

## **Southwest National Primate Research Center (San Antonio, TX)**

The Southwest NPRC is the only center open today that was not one of the original institutions established in the 1960s. The SNPRC joined the list of National Primate Research Centers funded by the NIH in 1999 and is affiliated with the Texas Biomedical Research Institute (Texas Biomed; “Southwest National Primate Research Center” 2019). However, Texas Biomed was not new to join in on biomedical primate research. In 1941, Tom Slick, Jr. – a 25-year-old man who strongly believed that scientific research was the key to human progress – established the Foundation of Applied Research (“Texas Biomedical Research Institute” 2019). The foundation’s name was changed to Southwest Foundation for Research and Education in 1952, and then the Southwest Foundation for Biomedical Research in 1984, and, finally, the Texas Biomedical Research Institute in 2011 (“Texas Biomedical Research Institute” 2019). The Texas Biomedical Research Institute brought numerous research strengths, including the world’s largest captive baboon population, to the NPRC program when it joined in 1999 (“Southwest Foundation houses newest NIH primate center” 1999).

Texas Biomed and the SNPRC have had many scientific breakthroughs that have improved human and animal health worldwide. Their scientists produced the high-frequency ventilator, a device that assists premature babies’ breathing and has saved thousands of lives and reduced lung damage in the infants. They also developed surfactant – a natural product now given to all premature infants – which prevents lung damage complications in instances of premature births. Much of the development and testing of the first hepatitis B vaccine (and later, an improved Hep B vaccine) was carried out on Texas Biomed chimpanzees (“Southwest Foundation houses newest NIH primate center” 1999; “Southwest National Primate Research Center” 2019). Researchers at this institute also developed a protein mixture that can greatly reduce the recovery time for broken bones or bone restructuring,

among many other scientific contributions (“Southwest” 2019).

The SNPRC is located in San Antonio, TX, and houses approximately 2,500 nonhuman primates, including baboons, macaques (bred onsite), marmosets, and chimpanzees. The vast majority of the animals at this institute are baboons (approximately 1,100; “Southwest” 2019). In addition to the world’s largest colony of baboons for biomedical research, the SNPRC also has the largest population of aged (>10 years) marmosets in the country, with more than 70 at their center (“Southwest” 2019). Since the FWS ruling in 2015, the population of more than 100 chimpanzees housed at the SNPRC are no longer used for biomedical research. In 2016, SNPRC announced its plan to retire their chimpanzees to Chimp Haven, a national chimpanzee sanctuary in Keithville, LA, as space becomes available (“Southwest” 2019).

## **Controversies and Closures**

Whereas the National Primate Research Centers have made many scientific contributions that have changed the course of human health history, they are also shrouded in controversy. The New England Primate Research Center, hosted at Harvard University in Southborough, MA and one of the original seven institutions funded by the NIH, announced its impending closure in 2013, eventually shutting down in 2015 (Fountain 2013). Harvard cited financial reasons for closing the primate center (Fountain 2013); however, others claimed that violations of the Animal Welfare Act, as cited by the US Department of Agriculture (USDA), contributed to the decision. These issues included a federal investigation into the deaths of 16 primates at the facility between 1999 and 2012 (Fountain 2013; Johnson 2015).

## **Other Primate Research Centers**

Although the seven centers currently funded by the NIH may be the highest-profile primate research centers in the USA, dozens more exist

in both the USA and abroad. The European Union funds its own network of nine primate research institutions, including the Centre Nationale de la Recherche Scientifique (CNRS) in France (“Primate Info Net” 2019). Though not part of the EU network, the Max Planck Institute is a distinguished, well-renowned, and widespread primate research organization located in Germany (“Max-Planck-Gesellschaft” 2019). The Max Planck Institute is a nonprofit organization with 84 institutes and research facilities and more than 23,000 employees (“Max-Planck-Gesellschaft” 2019). Also of note, the Primate Research Institute of Kyoto University (Japan) conducts behavioral, cognitive, biomedical, and other types of research on its primates, including an indigenous species, the Japanese monkey (“Primate Research Institute Kyoto University” 2019).

In the USA, other centers receive funding from the NIH but do not have the NPRC status. One such example is the University of Puerto Rico’s Caribbean Primate Research Center (CPRC), located on the island of Cayo Santiago. Researchers at the CPRC often conduct naturalistic, observational research on their native population of rhesus macaques. Another example is the University of Oklahoma Health Sciences Center in Oklahoma City, OK, and its affiliated baboon breeding facility in El Reno. The Oklahoma centers conducted biomedical research on their non-human primates, such as vaccine development and advancement of neuroprosthetics, until its announcement in 2015 that the program would be shut down by 2019. The university president claimed the closure was due to a shift in the university’s research priorities and a desire to reallocate the university’s funds (Knittle 2015a); however, the announcement came shortly after a high-profile USDA report revealing the death and mistreatment of several monkeys under OU’s care (Knittle 2015b).

Further examples of NIH-funded centers include the Alamogordo Primate Facility (APF), the National Center for Chimpanzee Care (NCCC), and the New Iberia Research Center (NIRC), all of which once housed chimpanzees for use in biomedical research. After the

2015 ruling to list all chimpanzees as endangered under the Endangered Species Act, effectively ending all invasive biomedical research on chimpanzees, the APF, the NCCC, and the NIRC had to either relocate or commit to the husbandry and care of the chimpanzees for the rest of their days.

The Alamogordo Primate Facility houses still over 100 chimpanzees and is located on the Holloman Air Force Base in Alamogordo, New Mexico. The center had been conducted aeronautical and space research with its animals since the 1950s, but in 2001 the NIH assumed ownership of the chimpanzees after the APF repeatedly violated the terms of the Animal Welfare Act. In 2011, after a public outcry when the NIH tried to transfer the chimpanzees to the SPNRC, the APF discontinued all invasive research on their chimpanzees; 126 chimpanzees continue to live out their days at APF but are not involved in any invasive research. Similarly, a colony of over 100 chimpanzees is cared for by the University of Texas MD Anderson Cancer Center’s National Center for Chimpanzee Care, and the animals engage only in noninvasive behavioral studies. The current research goal of the NCCC is to improve welfare and husbandry practices for captive chimpanzees. Likewise, in 2016, the University of Louisiana at Lafayette’s New Iberia Research Center, once the largest chimpanzee research facility in the nation, announced its plan to relocate all of its chimps to a chimp haven (known as Project Chimps) in Blue Haven, GA. The NIRC continues to conduct biomedical and behavioral research with its 6,000 other nonhuman primate residents, including rhesus, pig-tailed, and long-tailed macaques, African green monkeys, and brown-tufted capuchins.

Some primate research centers, such as Georgia State University’s Language Research Center (LRC; “Language Research Center” 2019) in Atlanta, GA, and the Ape Cognition and Conservation Initiative (ACCI; “Ape Cognition and Conservation Initiative” 2019) in Des Moines, IA, have historically conducted exclusively noninvasive research with their animals and have continued that trend to this day. Scientists at the LRC and the ACCI investigate



cognitive and behavioral questions rather than biomedical ones. From the 1970s to 2016, the NIH funded ape-language research and other cognitive studies at the LRC, focused on humans, chimpanzees, bonobos, rhesus macaques, and brown-tufted capuchins. Research on cognition and social behavior in monkeys and continues at the LRC, whereas the language-trained ape Kanzi and his family of bonobos have moved to ACCI where they continue to participate in behavioral research.

## Cross-References

- [Ape Cognition and Conservation Initiative \(ACCI\)](#)
- [Duane Rumbaugh](#)
- [Frans de Waal](#)
- [Language Research: Great Apes](#)
- [William Hopkins](#)
- [Yerkes Primate Research Center](#)

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## Primate Sensory Systems

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## Synonyms

Audition; Catarrhine; Communication; Gustation; Haplorhine; Haplorhini; Hearing; Hominoid; Mammal; Olfaction; Platyrrhine; Prosimian; Seeing; Senses; Sensing; Smell; Sound; Strepsirhine; Strepsirhini; Tactile; Taste; Touch; Vision

## Definition

Primates are mammals with complex and large brains compared to body size and traits including an enhanced sense of touch, increased reliance on vision, and reduced reliance on sense of smell compared to other mammals. Their sensory systems allow them to perceive and interpret the world around them, and include vision (sight), olfaction (smell), gustation (taste), audition (hearing), and tactile systems (touch). Each of these sensory modalities contain adaptations that help primates to survive in a range of habitats including arboreal environments. Through the information provided by their sensory systems, primates can find food, avoid predators, and effectively perceive and interact with other individuals of their species.

## Introduction

The primates are an order of eutherian (placental with advanced development before birth) mammals comprised of strepsirrhines (suborder *Strepsirrhini*: lemurs, lorises, galagos, and pottos) and haplorhines (suborder *Haplorhini*: tarsiers, Old and New World monkeys, apes, and humans). They diverged from other mammals approximately 80–90 million years ago, and today have approximately 504 living species (Estrada et al. 2017). Compared to other mammals, primates are characterized by having larger brains compared to body size, brains with greater complexity, clavicles which allow a broader range of motion, generalized dentition enabling a broader diet, five fingers and toes including opposable thumbs and big toes in many species, power and precision grips, fingerprints, toeprints, and palm prints, nails instead of claws, and forward-facing eyes with binocular vision. These characteristics are thought to be adaptations for arboreal (tree-living) environments, with the earliest primates and many extant primates living primarily in trees (Smith 1924). Many of the traits typifying the primate order reflect differences in sensory adaptations between primates and other mammals. For example, primates have an enhanced sense of touch due

to their fingerprints and nails, while their five digits including opposable thumbs and big toes enable them to grip and manipulate objects in the environment with greater strength and precision (Liman 2006). Primates also rely less on olfaction and more on vision than other mammals. Their front-facing eyes with overlapping fields of vision allow them to see and interpret their surroundings reliably in three dimensions (Liman 2006). These visual and tactile adaptations give primates survival advantages, allowing them to interact with their environments in new ways, while their larger and more complex brains help primates process the additional sensory information received more efficiently. Compared to other mammals, primate brains have particularly enlarged occipital and parietal regions, which are linked to their greater reliance on vision and touch (Liman 2006).

Primates are also uniquely social among mammals, with the majority of primate species living in mixed-sex groups that stay together on a year-round basis (Dunbar 2010). In solitary species, primate sensory systems are adapted to help individuals better navigate diverse habitats and access food resources while avoiding predators. In group-living species, the complexity of primate sensory systems may additionally help facilitate ongoing social contact between conspecifics. Primate vision, olfaction, audition, and sense of touch are especially important for social relationships, with information about other group members obtained through the senses. Visual, olfactory, gustatory, auditory, and tactile senses work together in primates to help them perceive their environments more effectively and to communicate with other members of their species. The complexity of primate sensory systems may be understood as a series of adaptations that enhance primate ability to interact with their environments and with conspecifics.

## Vision

### Primate Stereoscopic Vision

Primates are characterized by their stereoscopic (binocular) vision, with overlapping fields of vision from each forward-facing eye creating a

wide visual field of three-dimensional depth perception (Liman 2006). Stereoscopic vision is a sensory trait that has evolved multiple times, in evolutionary lineages as divergent as cephalopods (Class *Cephalopoda*) and vertebrates (Nityananda and Read 2017). While binocular vision is not unique to primates, having the combination of forward-facing eyes plus stereoscopic vision (stereopsis) is thought to be rare in vertebrates, and is only found in some birds (e.g., birds of prey, Order *Accipitriformes*), mammalian carnivores (Order *Carnivora*), and primates (Nityananda and Read 2017). The combination of forward-facing eyes plus stereopsis allows for a larger stereoscopic visual field than found in animals with side-facing eyes (Nityananda and Read 2017). While a wider stereoscopic visual field helps birds of prey and carnivores be more successful in hunting prey, it also leads to enhanced fitness for primates. As arboreal mammals, primates rely on their binocular vision to travel, find food, and evade predators while remaining in the treetops. The arboreal hypothesis suggests that primate traits including improved stereoscopic vision and increased grasping power evolved as adaptations for life in the trees, allowing primates better ability to perceive distance and therefore to travel between branches without falling (Smith 1924). An alternate hypothesis relates to visual predation and suggests that primate traits including improved binocular vision and fine motor skills evolved to facilitate the hunting of insects, which were likely a key food source for early primates (Cartmill 1992). As small-bodied prey that may move quickly in any direction in three-dimensional space, insects would have been difficult to catch without good depth perception (Cartmill 1992). A third hypothesis relates to angiosperm (flowering plant) evolution and suggests that traits like better vision and improved gripping ability of hands and feet are adaptations that allow primates to more successfully feed on fruit at the end of small branches (Sussman 1991). Regardless of the selective pressures that led to the development of a wider stereoscopic visual field and other derived traits in primates, excellent binocular depth perception is a ubiquitous component of visual systems in living primates.

Stereoscopic vision helps individuals across species travel efficiently through both arboreal and terrestrial (ground-based) environments, find food, avoid predators, and interact with conspecifics.

### Primate Color Vision

Some primates also have color vision. Color vision depends on the ability of retinal photoreceptors (rods and cones) and the brain regions associated with seeing to perceive different wavelengths of light, then to compare them to one another. Retinal rods allow organisms to see their surroundings under low light conditions, such as at night, while cones increase visual perception during brighter conditions, such as during daylight (Bowmaker 1998). Vertebrate eyes have rods and cones with different types of opsin, the photopigment that enables eyes to perceive different types of light wavelength and to see in color. Color vision evolved in fish and reptiles during early vertebrate evolution, but some retinal cones were lost during the evolution of mammals, likely due to the earliest mammals being nocturnal (Bowmaker 1998). As early mammals adapted to using their visual systems primarily at night, their visual acuity in low light levels was enhanced by reducing their color vision to a dichromatic (two light wavelength ranges) system (Liman 2006). This dichromatic system allowed them some color vision but limited their perception to only two light wavelength ranges, short (sensing blue light) and long (sensing red and green light without being able to differentiate between them) (Bowmaker 1998). A dichromatic vision system is still present in most living mammals, but trichromatic (three ranges of light wavelength) color vision evolved again in the primate order. Along with marsupials (Infraclass *Marsupialia*), primates are the only mammals in which some species possess three types of retinal cone (Bowmaker 1998). Trichromacy enables some primates to perceive three different light wavelength ranges in comparison to one another; in addition to short (sensing blue light) and long (sensing red light) wavelengths, trichromats can also perceive medium (sensing green light) wavelengths (Carvalho et al. 2017). This gives

trichromat primates the ability to tell the difference between red and green and therefore to see in full color.

Primates are characterized by this increased ability to see in color compared to other mammals, while still maintaining a wide variation in color perception ability across taxa. Their range of ability to perceive color is thought to be adaptive given the varying light conditions that primates live in, with some primates being nocturnal (active at night), some being diurnal (active during daylight), and some being cathemeral (active across the diel cycle) (Liman 2006). Some extant primates can perceive three different light wavelength ranges (red, green, and blue) and can see in full color (trichromats), others can perceive two different light wavelength ranges (red, plus blue or green) and see in partial color (dichromats), and some can perceive only one light wavelength range (red) and do not see in color (monochromats) (Carvalho et al. 2017). Old World monkeys, apes, and humans (catarrhines, Parvorder *Catarrhini*), and one genus of New World monkey (platyrrhine, Parvorder *Platyrrhini*), the howler monkey (*Alouatta* spp.), are trichromats and consistently able to see in full color (Liman 2006). In most other New World monkeys and some lemur species, females are able to see in full color if they have a specific genetic polymorphism on an X chromosome. However, males and other females in these species lack this gene and are dichromats who cannot differentiate between red and green colors (Liman 2006). Lemur species where females have this trichromat polymorphism include some sifaka and ruffed lemurs (*Propithecus* spp. and *Varecia* spp.) and the red-fronted lemur (*Eulemur rufifrons*), all of which are diurnal or cathemeral (Carvalho et al. 2017). However, most diurnal and cathemeral primate species are consistent dichromats, including nearly all New World monkeys and most lemurs. Monochromat primates can see light, dark, and shades of grey, but no color. Monochromat primates are all nocturnal and include strepsirrhines such as lorises and galagos (*Lorisidae* and *Galagidae* families), lemurs including fork-marked lemurs (*Phaner* spp.), fat-tailed dwarf lemurs (*Cheirogaleus medius*), and

hairy-eared dwarf lemurs (*Allocebus trichotis*), and one genus of New World monkey, the owl monkey (*Aotus* spp.) (Carvalho et al. 2017).

The differences in both activity patterns and dietary preferences among extant primates may explain the persistence of these differences in color perception. Nocturnal primates who are monochromats may be insectivorous (i.e., eat insects as a primary dietary resource) and better able to detect the movement of insects in a low-light environment due to their lack of color perception (Carvalho et al. 2017). In contrast, primate trichromats who are frugivorous or folivorous (i.e., eat fruit or leaves as a primary dietary resource) may be better able to locate red or yellow fruits or young leaves against a background of green vegetation during daylight (Carvalho et al. 2017). Finally, primate dichromats may have a range of dietary adaptations but be better able to find camouflaged or hidden prey than those with full color vision under certain light conditions (Carvalho et al. 2017).

### Other Primate Eye Adaptations

Living primates also show variation in other features associated with visual perception in low- and high-light levels. Like most other vertebrates, nocturnal primates have *tapetum lucidum*, an eye tissue covering which reflects light backwards through the photoreceptor layer and toward retinal cells, causing reflective eye shine and providing greater visual sensitivity in low-light levels (Ollivier et al. 2004). With the exception of a few diurnal brown and ruffed lemur species (*Eulemur* and *Varecia* spp.), living lemurs, lorises, galagos, and pottos have *tapetum lucidum*. However, all haplorhines lack this structure, despite the tarsiers and one New World monkey genus (owl monkey, *Aotus* spp.) being nocturnal (Ollivier et al. 2004). In contrast, haplorhine eyes have fovea, which are small pits in the center of the retina that improve central vision and color perception, particularly during daylight. Lemurs and lorises, which are more likely to be active in low light levels, generally lack retinal foveae (Ross 2004).

### Olfaction

Although primates are characterized by their increased reliance on vision as a sensory modality compared to other mammals, olfaction is still an important mode of perception, especially for strepsirhines. While primate snout length is reduced and primate faces are flattened compared to other mammals, strepsirhines have longer snouts than haplorhines as well as *rhinaria* (wet noses), enabling olfactory organs to get better exposure to potential scent compounds in the environment (Epple 1986). Strepsirhine brains also have larger olfactory bulbs than haplorhines, attesting to the greater importance of this sensory system in lemurs, lorises, galagos, and pottos compared to other living primates. Across taxa, primate olfactory ability is characterized by sensitivity, meaning that all primates can detect odors when at low levels in the environment. Primates are also adept at discriminating between odors, meaning that they can easily tell the difference between different chemical compounds based on scent. In both strepsirhines and haplorhines, smell is enabled by the main and accessory olfactory systems. The main olfactory system allows perception of volatile airborne compounds that might elicit a response from many different animals, such as the esters of ripe fruit. In contrast, the accessory olfactory system perceives more particular nonvolatile compounds emanating from conspecifics, such as pheromones (Liman 2006). The vomeronasal organ (VNO) is the accessory olfactory organ and is located in the nasal septum in vertebrates including some reptiles and mammals including primates. While it is vestigial (nonfunctional) in catarrhines, it is more functional in tarsiers and New World monkeys and is still fully operational and widely used by strepsirhines (Epple 1986).

Primate sense of smell is important for both ecological and social reasons. Across taxa, primates use odor to detect desirable foods (e.g., sugary, fleshy fruit). For example, lemur species including the mouse lemur (*Microcebus murinus*) and diademed sifaka (*Propithecus diadema*) and New World monkeys including the white-faced capuchin (*Cebus capucinus*) and Central American



spider monkey (*Ateles geoffroyi*) use odor to find food items ranging from insects to flowers to ripe fruit for consumption (Nevo and Heymann 2015). Olfaction is also a key component of the social behavior of strepsirhines, tarsiers, and New World monkeys. Urine is used as a type of scent mark in some of these primate groups through urine washing, a behavior where primates direct their urine streams back toward their bodies, then use it to mark substrates like tree branches (Delbarco-Trillo et al. 2011). Urine washing is thought to be especially important in solitary and nocturnal strepsirhines like lorises, galagos, and pottos, while group-living, diurnal lemurs are more dependent on glandular scent secretions (Delbarco-Trillo et al. 2011). Odor is produced by scent glands in various primate body areas, primarily in the genital, sternal, and brachial regions, although scent glands may also be present in palmar, antebrachial, forehead, and chin regions in some species (Epple 1986). Solitary species, like lorises, galagos, pottos, and some lemurs, rub their scent glands on substrates that can retain odor for hours or days, likely lasting until other individuals of the same species pass through the area. These scent marks may signal territory occupancy or sexual receptivity to conspecifics (Delbarco-Trillo et al. 2011). In group-living primate species, scent secretions have myriad social uses. The ring-tailed lemur (*Lemur catta*), for example, uses scent marks for a range of functions, including indicating territorial boundaries, establishing dominance rank (Kappeler 1998), advertising female estrus, and displaying the quality of potential mating partners (Walker-Bolton and Parga 2017). In New World monkeys such as the moustached tamarin (*Saguinus mystax*), scent marks are similarly used for identifying social group members and potentially receptive mating partners (Heymann 1998).

## Gustation

Primates rely on their sense of taste to help them select nutritious food items and reject harmful substances. Taste bud receptor cells convey information to the brain through gustatory nerves, allowing primates to obtain sensory information

about items in their mouths. Through the sensory taste buds, details are provided about the temperature, texture, and composition of potentially edible items. Primates can perceive tastes including sweet, salty, umami (savory), bitter, and sour; they demonstrate general affinities for some tastes (sweet, salty, umami) but aversion for others (bitter, sour) (Liman 2006). Taste preferences show clear fitness benefits, with foods high in nutritive content usually featuring preferred sweet, salty, and/or umami tastes (Liman 2006). Primate avoidance of bitter and sour tastes is adaptive in preventing them from ingesting harmful or poisonous substances, such as spoiled food or plant toxins like tannins and alkaloids (Liman 2006). Across primate taxa, taste receptors show similarities but also some differences, with tasting perceptions more alike in closely related species and less alike in more distantly related groups. For example, Old World monkeys like the olive baboon (*Papio anubis*) and pigtailed macaque (*Macaca nemestrina*) showed greater preference for sour tastes than New World monkeys like the common squirrel monkey (*Saimiri sciureus*) and Central American spider monkey (*Ateles geoffroyi*) (Laska et al. 2003).

## Audition

Primates use hearing to navigate their habitats and to monitor for the presence of predators, prey (e.g., insects), and conspecifics in the area around them. Most natural sounds are made by living organisms as they vocalize or move through their environments, and being able to perceive and interpret these sounds is a key component of primate survival (Heffner 2004). Greater hearing sensitivity is linked to greater social complexity in most mammals, and primates also share this tendency (Ramsier et al. 2012). Similarly to other mammals, all primates have good sound localization ability (i.e., ability to detect where sound is coming from) and can hear low-pitched sounds at and below 125 Hz (Heffner 2004). Although primate species across taxa can generally hear low frequencies, large-bodied primates like Old World monkeys, apes, and humans tend to perceive a

range of frequencies (sound pitches) that is lower than smaller primates. Conversely, smaller-bodied primates such as New World monkeys, tarsiers, and strepsirrhines have hearing ranges that perceive generally higher pitches, with some even perceiving and making ultrasonic vocal sounds (Ramsier et al. 2012). This correlation between relative body size and auditory frequency hearing range is a general pattern seen throughout mammals (Heffner 2004) and may be optimized for perception of species-specific vocalization frequency ranges as well as for sound localization in very small species. The generally strong ability of primates to localize sound is thought to be adaptive given their forward-facing eyes and narrower range of vision compared to other mammals (Heffner 2004). When they hear an unexpected noise, primates need to know the direction in which to turn their head in order to see what is creating the auditory disturbance and to then make the decision to flee if necessary.

Primate auditory systems are well-adapted to respond to potential threats. In addition to perceiving noises that predators make through movement and vocalization, group-living species have also evolved alarm calls, which are used to alert other group members to the presence of a threat in the area (Ramsier et al. 2012). Many social species across taxa have also evolved referential calls, meaning that vocalizations refer to a specific predator type (i.e., snake or eagle) or a predator's direction of approach (i.e., terrestrial vs. aerial). Primates ranging from lemurs (e.g., ring-tailed lemur, *Lemur catta*; Bolt et al. 2015) to New World monkeys (e.g., white-faced capuchin, *Cebus capucinus*; Digweed et al. 2005) to Old World monkeys (e.g., vervet monkey, *Chlorocebus pygerythrus*; Seyfarth et al. 1980) are known to have referential predator vocalizations that conspecifics hear and respond to, even when predators are not visible.

All living primates use vocalizations to communicate, including both solitary and group-living species. Vocalizations allow individuals to stay in touch with conspecifics even when out of visual range, such as in dense forest

environments. Solitary species generally have smaller vocal repertoires than social species, but both use sound to convey information about the occupancy of an area, likely to prevent competition by spacing out individuals and groups (Ramsier et al. 2012). Group-living species have larger repertoires and greater vocal complexity, mirroring the larger range of ecological and social interactions that they engage in with conspecifics (Ramsier et al. 2012). In addition to predatory threat response, primates may vocalize to avoid separation from social groups, to maintain proximity to preferred companions within groups (e.g., contact calls, Bolt and Tennenhouse 2017), to advertise the location of food resources to other group members (e.g., food calls, Heffner 2004), to defend mates, rich food resources, or territories from other groups (e.g., long calls, Bolt et al. 2019), or to establish dominance ranks and attract mates through honest displays (e.g., advertisement calls, Bolt 2013). This reliance of primate social behavior on sound-based communication has shaped primate auditory systems, ensuring that primates can hear each other in addition to environmental stimuli.

## Tactile System

Primates have an enhanced sense of touch and better grip capability compared to other mammals. This impacts their ability to find and ingest food, to make and use tools, to socialize at close range, and to travel, particularly in arboreal environments. In contrast to other mammals, primates have dermatoglyphs (distinctive lines, whorls, and ridges on fingers, toes, and the palms of hands and feet), pentadactyly (five fingers and toes), and nails instead of claws in most species, which work together to give primates greater sensitivity in perceiving the properties of objects and substrates in their environments. Primates also have opposable thumbs, divergent big toes, and power and precision grips, which give them better ability to manipulate their environments through strength and dexterity. Power grips involve simultaneous

grasping by the digits and the palm, thus applying force from the whole hand or foot to manipulate objects. In contrast, precision grips involve fine-motor skill interactions with pressure applied by individual digits to a small area, thus manipulating objects with accuracy and control. All primates have robust power grips, while precision grips are better developed in monkeys, apes, and humans than in strepsirhines. The interaction between these two types of grip capability along with primates' more refined sense of touch enables a broader range of social, locomotory, and foraging behaviors than seen in most other mammals.

Touch is important in primate social behavior, with prolonged tactile contact (e.g., resting while in body contact) and grooming (manipulation of the fur using hands or teeth) being key components in maintaining inter-individual relationships and in reducing individual stress levels (Dunbar 2010). Social grooming (grooming another individual) is important in group-living species, while both group-living and solitary species engage in self-grooming. In monkeys, apes, and humans, greater manual dexterity has led to more grooming using the hands, while strepsirhines use toothcombs (dental structures with outward-facing front teeth) to groom themselves and others (Dunbar 2010).

Their ability to touch and grip enables primates to travel effectively through arboreal environments; for example, by using branches and vines as supports, by leaping between trees, and by balancing at the ends of small branches without falling to the ground (Smith 1924; Sussman 1991). The fingers, toes, and palms of their hands and feet are hairless with textured skin ridges and whorls (dermatoglyphs) to increase friction and gripping power during movement between substrates. Some New World monkeys have additionally evolved prehensile tails, which are arboreal adaptations for dense forest environments. These are also seen in some other mammals, particularly those endemic to South America (e.g., opossums, Order *Didelphimorphia* and anteaters, Suborder *Vermilingua*). Prehensile tails act as extra limbs, providing further gripping power for arboreal

monkeys and increasing their ability to locate and harvest food while suspended in the trees.

Increased sensitivity, dexterity, and strength in hands and feet also mean that primates should be able to make and use more sophisticated tools than other animal species, and tool use is present in living primates ranging from some strepsirhines (e.g., brown lemurs, *Eulemur* spp.) to New World monkeys (e.g., capuchins, *Cebus* spp.) to catarrhines (e.g., macaques, *Macaca* spp.; baboons, *Papio* spp.; great apes, *Gorilla* spp., *Pongo* spp., and *Pan* spp.; Bentley-Condit and Smith 2010). Among other functions, primates use tools to acquire hidden or inaccessible food sources. For example, primates employ hammers and anvils to crack open nuts (e.g., common chimpanzees, *Pan troglodytes*; capuchin monkeys, *Cebus* spp.; macaques, *Macaca* spp.; Bentley-Condit and Smith 2010). They also utilize modified sticks to harvest termites, ants, or bees from inside mounds (e.g., common chimpanzees, *Pan troglodytes*; Sumatran orangutans, *Pongo abelii*; Bentley-Condit and Smith 2010). Primates may also use their hands and feet to harvest foods like insects or small vertebrates that are hidden in tree holes, palm fronds, or under bark. These uses of tools and digits substantially improve primate extractive foraging ability, thus increasing the range of ecological niches that primates can inhabit and demonstrating the strong adaptive function of the enhanced primate tactile system.

## Conclusion

Primates rely on their sensory systems for both environmental and social reasons; they use their senses to perceive food, predators, and their habitats, and to interact with conspecifics. Their large and complex brains with highly developed sensory abilities give them adaptive advantages, with a reduced sense of smell and enhanced vision and touch compared to other mammals allowing them to occupy new roles in their environments. The sophistication of primate sensory systems is

foundational to the behavioral and ecological intelligence of this mammalian order.

## Cross-References

- [Catarrhine Communication](#)
- [Catarrhine Sensory Systems](#)
- [Haplorhini](#)
- [Hominoidea Sensory Systems](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Communication](#)
- [Primates](#)
- [Prosimian Communication](#)
- [Prosimian Sensory Systems](#)
- [Sensory Receptors](#)

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## Primate Social Structure

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### Introduction

Most primates live in social groups and a remarkable variety of social organizations can be observed among species. These different types of organization may constrain the structure of social relationships within groups. For instance, in the primate order, group size range from a few individuals as in some lemur species, tarsiers (*Tarsius*) or gorillas (*Gorilla*), to hundreds of individuals as in mandrills (*Mandrillus sphinx*) or geladas (*Theropithecus gelada*, Mitani et al. 2012). As a consequence of this wide range, communication and interactions between individuals will vary greatly according to the number of available partners and will result in different social structures among species.

There is also a variety in the flow of individuals between groups, defining different dispersal patterns. In some species, males disperse and thus ensure gene flow between groups, such as in macaques (*Macaca*), baboons (*Papio*), or gorillas, while in other species only females will be able to emigrate, as in chimpanzees (*Pan troglodytes*) or bonobos (*Pan paniscus*, Smuts et al. 1987). Social relationships will then not be established in the same way between individuals with a limited interaction time available and others that will be together all their life.

As a result of this variety in group size and dispersal modes, primate species exhibits different grouping patterns and can be classified in five types: solitary, pair, one-male-multifemale group, multimale-multifemale group, and multimale-one-female group. For example, some species will form groups that include several families, such as chimpanzees, bonobos, or many

cercopithecine species, while others will constitute solitary family clans, such as gorillas (Smuts et al. 1987) or callitrichines. However, while most species exhibit uniform social organizations, some others present considerable variations between populations, resulting in different social structure within the same species (Mitani et al. 2012).

Finally, important differences in grouping dynamics can also be noted. Many primate species have stable social groups over time, such as cercopithecines for instance (Smuts et al. 1987). Conversely, some species such as chimpanzees or bonobos have a fission-fusion-like organization characterized by the formation of temporary parties (Aureli et al. 2008). This instability over time may also impact the distribution of social relationships within groups as well as maintenance strategies.

The establishment and maintenance of social relationships within groups will enable individuals to live together and better cope with daily pressures they might experience. The social structure of a population is then shaped by the balance between within-group competition among individuals for the access to food resources or sexual partners, and cooperation needs to answer to environmental pressure (i.e., predation) but also between-group competition.

### Definition

Before looking at the variety of primate social structure and the parameters underlying this variety, it is important to define what is a social structure. Hinde (1976) proposed a hierarchical bottom-up model via dyadic social interactions that determine social relationships whose patterns draw the social structure of a group. The base level of this model is thus dyadic social interactions, defined as the behaviors emitted by two or more individuals toward others at a given time. These interactions have a concrete reality for the animal, since it is the expression of its behavior in the present, and they are observable directly by an external observer. The second level characterizes the social relationships between individuals,



which correspond to repeated and consistent interactions in time observed between these individuals. Finally, the social structure, third level in Hinde's model, gathers all the social relationships existing between group members and thus forms a social network.

Kummer (1968) added a functional dimension to Hinde's model and proposed that social relationships increase the predictability of a dyadic interaction outcome, facilitating social interactions between individuals. Repeated and consistent interactions over time can then lead to stable and valuable relationships between individuals, allowing them to develop social strategies like food sharing, cooperative hunting or agonistic support (Cheney and Seyfarth 2007). Investing in stable relationships may then benefit to individuals as it increase the likelihood that the partners behave in a positive way in return.

Social relationships and social structure are not directly observable but are inferred from the repeated observation of social interactions (Hinde 1976; Kummer 1968). They are often considered as an abstract representation, resulting from the analysis of the distribution of interactions, and the question of the ability of animals to represent these structural levels can then be asked (Barrett and Henzi 2002).

Indeed, to enable understanding and assimilation of social relationships, animals must be able to recognize group members and memorize past interactions, whether they involve them directly or not (Cords 1997). Experiments in primates have revealed knowledge of the relationships that may exist between members of a group in some species (Seyfarth and Cheney 2012). In long-tailed macaques (*Macaca fascicularis*), for example, individuals are able to discriminate pairs of related individuals from unrelated pairs. Macaques have also been shown to be able to differentiate dominant and subordinated individuals in a pair of familiar congeners. Another experiment in chacma baboons (*Papio ursinus*) also showed that females were aware of the dominance link between two individuals, and responded more strongly to inconsistent situations with the group dominance hierarchy. In this same species, the loss of an affiliated individual following a predation event will cause a drastic increase

in the general level of stress in comparison with other individuals not facing the loss of a close social partner (Engh et al. 2006).

Thus, knowledge of these relationships between group members allows individuals to predict the outcome of an encounter or interaction with other individuals (Kummer 1968). This memory gives the animals the ability to develop social strategies based on these social relationships, thus enabling them to acquire survival and/or reproduction advantages (Cheney and Seyfarth 2007).

## Types of Social Relationships

Social relationships are defined as a function of the type, frequency, intensity, and quality of social interactions between individuals. We distinguish three types of interactions: affiliative (indicating a spatial association), affiliative (friendly), and agonistic (including aggressive and submissive behaviors).

Affinitive and affiliative interactions such as body contact, social grooming, and affiliative facial expressions are usually considered together to deduce affiliative relationships. Social grooming in particular is known to be very important for the establishment and maintenance of strong affiliations between two individuals (Dunbar 2010). All these interactions will then define affiliative relationships between individuals, and the distribution of these relationships will depend on the considered behaviors. Indeed, individuals who are strongly affiliated in the context of social grooming may not necessarily be as strongly affiliated when only considering body contact for example. Affiliative relationships are thus made up of a set of interaction networks drawn from different socio-positive behaviors (Dunbar and Schultz 2010). It is thus important to take these different networks into account while studying the social structure of a group.

Affiliative relationships are rarely distributed in a homogeneous way within a group, and privileged relationships between certain pairs of individuals may appear. For instance, yellow baboons (*Papio cynocephalus*) and chacma baboons interact preferentially with a limited

number of preferred partners, and these privileged relationships are stable over time (Seyfarth and Cheney 2012). The quality of the relationship is evaluated on the basis of past interactions between individuals, and a preferred relationship will be reinforced as the interactions continue. Affiliative relationships can also be assymetric, with one partner being primarily responsible for maintaining the bond (Mitani et al. 2012). However, biological market theory suggests that social grooming could be exchanged for itself or for other commodities such as support during conflicts (Noë and Hammerstein 1995). It is thus necessary to consider all the different aspects of affiliative relationships while studying reciprocity.

Group living does not only involve positive interactions between individuals. Indeed, the proximity of individuals sharing similar nutritional needs but also targeting the same sexual partners leads to conflicts between group members (Krause and Ruxton 2002). Thus, individuals will interact agonistically within group, and the sum of these negative interactions enables to distinguish asymmetric relationships of dominance: some group members take the ascendancy more regularly over others during conflicts and are then considered as dominant, while losers being referred to as subordinated (de Waal and Luttrell 1989). In most species, dominance relationships are described using ranking methods, forcing individuals into a linear dominance hierarchy, determined from agonistic interactions (de Waal and Luttrell 1989). Individuals are then ranked in a dominance hierarchy (Appleby 1983) that can be described by its linearity, transitivity, and steepness. More recently, the concept of social power has been used to describe the “degree of implicit agreement or consensus among group members about whether an individual is capable of successfully introducing force into polyadic agonistic situations” (Thierry et al. 2004). This concept seems to be particularly crucial to understand dominance relationships in species such as chimpanzees (*Pan troglodytes*), macaques, and baboons displaying ritualized status signaling outside of agonistic contexts, like submissive behaviors for example. This nonaggressive signaling strategy allows individuals to express their hidden

power or their knowledge of their status, reducing the risk of conflict and injury (Mitani et al. 2012).

Depending on the characteristics of dominance and social power of a species, different dominance style can be described. For example, we can differentiate egalitarian from despotic societies. While in despotic societies, agonistic relationships are clearly defined and dominance hierarchy is highly linear, egalitarian societies displayed absent or poorly defined agonistic relationships and the dominance hierarchy is unclear and non-linear. Dominance relationships will be less important in the social structure of the group in egalitarian species than in despotic ones. It is also possible to distinguish species exhibiting tolerant versus intolerant styles. This degree of tolerance has a direct impact on the frequency of bidirectional conflicts, injuries, or submissive behaviors (Thierry et al. 2004). If egalitarian species are usually tolerant, despotic ones can either display intolerant or tolerant styles. Dominance style has been intensively studied in macaques, and it is possible to rank the different species along a gradient from highly despotic/intolerant to highly egalitarian/tolerant (Thierry et al. 2004).

These dominance relationships are very important for the individuals’ lives as it influence certain behaviors such as social grooming, access and monopolization of food resources, or individuals’ spatial distribution.

## Parameters Underlying Social Structure in Primates

### Kinship

In primates, kinship constrains some of the affiliative and agonistic relationships presented in the previous section (Chapais and Berman 2004). In many species, several families live together within the same group, forming multi-family groups. Depending on the dispersal patterns (male or female philopatry), we observe male or female clans. In some species, kinship accentuates social relationships between individuals who will express stronger affiliative behaviors for their relatives; this is called nepotism. For example, social grooming is more frequent between female relatives in rhesus macaques

(*Macaca mulatta*). Formation of coalitions and/or alliances during conflicts is also more frequent between individuals belonging to the same matriline in this species (Thierry et al. 2004). Kin display more appeasement and reconciliation behaviors after conflicts in many macaque species (Thierry et al. 2008). Finally, this kinship bias may also be observed in the case of food sharing in some species, with males sharing food more often with their relatives in chimpanzees for instance (de Waal and Luttrell 1989).

Concerning dominance relationships, kinship can be a key parameter underlying the dominance hierarchy. Indeed, in some species displaying a female philopatry, an entire maternal lineage can be dominant over the others, and dominance rank is then transmitted from mother to daughter (Thierry et al. 2004). This is observed in a lot of cercopithecines such as vervets (*Chlorocebus pygerythrus*), baboons, rhesus, and Japanese macaques (*Macaca fuscata*).

However, even if genetic kinship is classically used to establish the links between individuals, we usually cannot distinguish genetic link from familiarity that an individual develop with his relatives. Indeed, during his development, a juvenile spends most of his time with his mother and her kin and does not establish relationships with other group members until later (Mitani et al. 2012). The kinship effect could then be the result of the familiarization process of the individual during his development, constrained by the biological needs of the offspring, instead of the recognition of his relatives.

Moreover, it is important to consider kinship not only from the philopatric-sex side but also from the dispersal-sex side. It has been shown in rhesus macaques, baboons, mandrills, and sun-tailed monkeys (*Cercopithecus solatus*), species displaying a female philopatry, that affiliative interactions were significantly higher among paternal siblings than among unrelated dyads (Mitani et al. 2012).

### Age and Sex Composition

In addition to the kinship network, two other parameters are known to influence group social structure: individuals' age and sex. These two

parameters are demographic and represent individuals' intrinsic characteristics. In the majority of social primate species, groups are composed of individuals that vary greatly according to these two parameters, conferring them different needs in terms of nutrition, activity, and experience. These differences can then impact the time that each individual devote to social interactions with the rest of the group but also shape within-group competition for valuable resources, and thus influence the social structure that results from these interactions.

Age has a strong influence on certain social behaviors. For example, age may affect agonistic relationships, with young individuals usually having a lower dominance rank than old ones. However, in classical female philopatric groups such as in macaques or baboons females usually outrank their oldest sisters, model also known as the "youngest sister ascendy rule" (Mitani et al. 2012).

The sex of the individual may also influence the distribution of these relationships between group members since social interactions will be more frequent between individuals of the same sex in most species (Mitani et al. 2012). This sexual segregation can be very extreme: unisex groups are observed outside breeding seasons in some mandrill populations where females may band together to counter male aggression (Abernethy et al. 2002, Setchell et al. 2006). Conversely, in other species such as hamadryas (*Papio hamadryas*), females interact almost exclusively with males, which are at the center of harems, the basic social unit that characterizes this species (Kummer 1968). In chacma baboons, these strong social bonds between males and females allow females to reduce the probability of infanticide when an emigrant male arrives or when changes in the dominance hierarchy occur (Engh et al. 2006).

### Diversity of Social Structures in Primates

Demographic parameters such as age, sex, or kinship can strongly impact the distribution of relationships within primate groups. Depending on

species, group composition according to these parameters is different and will thus constitute a panel of possible combinations, resulting in very different social structures (Kappeler and van Schaik 2002; Mitani et al. 2012). The following section is not exhaustive and will focus on well-documented examples among colobines, cercopithecines, and apes.

### Colobines

Colobine groups vary in size and composition, from pairs and dependent offspring to one-male/multifemale groups to large multimale-multifemale groups. Dispersal patterns vary between species, including male dispersal and female philopatry, female dispersal and male philopatry, and dispersal by both sexes (Mitani et al. 2012). Adult females form stable affiliative relationships, which are stronger between kin. Even in case of female dispersal, it is not rare to find female kin in the same social group as they might join the same group after dispersion (Mitani et al. 2012). Adult females usually form a clear and linear dominance hierarchy, which is not based on kinship but on age: young females are dominant over old ones. Dominance rank can change frequently and females do not form coalitions to maintain their rank. Colobine females are usually tolerant and reconcile very frequently after conflicts, especially with close affiliates (Arnold and Aureli 2007).

Most colobines (African *Colobus*, Asian *Presbytis*, and *Trachypithecus*) live in one-male groups, but multimale groups are found in *Procolobus*, *Nasalis*, *Rhinopithecus*, some *Colobus*, and Hanuman langurs (*Simia entellus*). In these multimale societies, dominance hierarchy among males is linear and high rank gives access to receptive females. Males use policing behaviors to reduce aggression frequency and severity between females when the competition level is high. Very little is known about male-male affiliative relationships in colobines (Mitani et al. 2012).

### Cercopithecines

All cercopithecines live in social groups, ranging from less than 5 individuals in DeBrazza's

monkeys (*Cercopithecus neglectus*) to several hundreds in mandrills and geladas. However, typical group size ranges from 10 to 100 individuals in most species. Cercopithecines societies are characterized by female philopatry and male dispersion, leading to groups structured around matriline: female kin form strong and stable affiliative relationships (Mitani et al. 2012). Coalitions between matriline members are frequent, and depending on the tolerance level between adult females, dominance hierarchy may be matrilineal. However, in extremely tolerant species such as Tonkean macaques (*Macaca tonkeana*) with a weak dominance hierarchy, it is common to observe strong social bonds distributed even between unrelated females (Thierry et al. 2004).

The number of adult males in cercopithecine groups is partly determined by the number of adult females: small groups usually have only one adult male, while groups with more than 5 females become multimale (Andelman 1986). Male-male competition for the access to sexual partner is high, leading to frequent agonistic interactions. Stable affiliative relationships between males are rare. However, male coalitions can be observed between subordinated to gain access to higher ranks or receptive females such as in geladas, baboons, sooty mangabeys (*Cercocebus atys*), and several macaque species (Mitani et al. 2012). Coalitions can also be observed when extra-group competition is intense.

In most cercopithecine species, male-female affiliative interactions are mainly observed during reproduction season, and the level of interactions during the rest of the year is highly variable. In mandrills and talapoins (*Miopithecus talapoin*), males usually join groups only when females are receptive. In guenons (*Cercopithecus*), patas (*Erythrocebus patas*), and vervets, males stay in the group the whole year but are peripheral outside reproduction season. In baboons and macaques, males and females may form cross-sex stable friendships with valuable partners. This strategy ensure mutual agonistic support but also offspring's protection against other males in baboons (Mitani et al. 2012). A more extreme male-female bond type can be observed in gelada societies, exhibiting a multilayered

organization. Indeed, geladas are characterized by strong and stable male-female affiliative relationships as they live in one-male units (OMUs). Several OMUs may group to form bands, which aggregate to a third level of organization called herds. Composition of bands and herds might vary frequently while OMUs are very stable (Swedell 2010).

Finally, hamadryas baboons constitute a remarkable exception to the classical "cercopithecine model" as we observe male philopatry and female dispersal in this species. Hamadryas societies exhibit a multilevel organization in which small OMUs are parts of clans, which may aggregate to form larger bands. In these OMUs, adult males force females into strong and stable affiliative relationships through coercion, even outside breeding seasons. Females within a harem are not related and may develop stable social bonds. Male kin are highly tolerant toward each other within bands (Smuts and Smuts 1993).

## Apes

With only a limited number of species, apes present a wide variety of social organization, resulting in very different social structures. Orangutans (*Pongo pygmaeus*) do not form stable social groups and spend most of their time feeding alone due to a high level of competition over food resources (Wrangham 1979). Individuals' interactions are rare and limited to female-female and male-female contacts. Female-female interactions reflect a certain level of familiarity, while male and female meet only during the reproductive season. Adult males are extremely hostile toward each other, especially flanged males that defend their home range (Smuts et al. 1987).

Adult female gorillas form stable groups with their dependent offspring and one or two adult males, which are usually close relatives (Smuts et al. 1987). Adult males are dominant over adult females and maintain very strong affiliative bonds. Subordinated males may engage frequently in grooming interactions with adult females as it can influence female dispersal in case of group fission. Agonistic interactions are rare between dominant males and females and are frequently followed by reconciliation initiated by

females (Watts 1995). Interactions between males can be aggressive, especially between adults, but coalitions are rarely observed (Smuts et al. 1987). In case of multifemale groups, competition for food access is low and agonistic interactions are rare and usually bidirectional. Adult females may form affiliative relationships, especially between relatives in mountain gorillas (*Gorilla beringei beringei*, Watts 1995). This kinship effect is weaker in western gorillas (*Gorilla gorilla*), due to female dispersal (Mitani et al. 2012).

Chimpanzees live in multimale-multifemale groups with a fission-fusion social organization. As males are philopatric in this species, male-male social bonds are stronger than female-female or male-female relationships (Mitani et al. 2012). The dominance hierarchy in adult males is linear and clear, and competition to access to high ranks is intense, as high-ranking males are more attractive to females and grooming partners, and have privileged access to food resources. Males may form both short-term and long-term alliances to help maintaining their rank (Newton-Fisher 2004). Despite male philopatry, kinship has a weaker influence than age in the distribution of affiliative relationships: males from the same age-cohort maintain stronger bonds than relatives (Mitani et al. 2012). Indeed, as females disperse in this species, adult males may not have a lot of relatives in their group. Adult males interact with adult females mostly during swelling periods, but males may develop stable affiliative relationships with kin-related females, such as mother and son for instance (Goodall 1986). Competition between adult females to get access to food resources and sexual partners is high, and immigrant females will face aggression from resident ones. Except during these immigration events, coalitions between adult females are rare. However, they may form affiliative relationships by frequent grooming interactions and co-participation to parties. Depending on the level of competition for food resources, adult females may form a linear dominance hierarchy, but not in all populations (Mitani et al. 2012).

Bonobos have a very similar social organization and social structure to chimpanzees. However, the level of competition for food resources is lower and adult females develop stronger



affiliative relationships than adult males (Parrish 1996). Females are also less aggressive while new individuals enter the group, protecting them from male harassment. Adult males form a clear and linear dominance hierarchy, but they do not form alliances to maintain their rank (Mitani et al. 2012). Outside of reproductive contexts, male and female kin such as mother and son or sister and brother may form strong social bonds and alliances, helping males to maintain their dominance rank. Unlike chimpanzees, adult females may be dominant over adult males in bonobos, especially when having female coalitions (Mitani et al. 2012).

## Cross-References

- [Affiliative Behaviors](#)
- [Affiliative Bond](#)
- [Agonism and Social Status](#)
- [Dominance](#)
- [Dominance Hierarchy](#)
- [Group Living](#)
- [Kinship](#)
- [Matrilines and Patriline](#)
- [Social Behavior](#)
- [Social Grooming](#)
- [Social Network Analysis](#)

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## Primate Suspensory Behavior

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### Synonyms

Arm-foot hanging; Arm-hanging; Brachiation; Clambering; Quadrumanous locomotion; Transferring; Tree-swaying

As arboreal animals, primates face a locomotor and postural challenge terrestrial animals do not: moving or posturing among small-diameter, irregularly placed, uneven, and unstable supports. Some mammals manage by digging their claws into the surface on which they are climbing, but this strategy only works when the support is large compared to the animal. Some mammals that utilize this strategy, like squirrels, negotiate small branches relying on good balance to compensate for their inability to grip supports, but their “scrambling” locomotion is clumsy compared to primates. Primates have gripping hands and feet that allow them to negotiate small branches by gripping the supporting branch with long,

dexterous fingers and toes. Unlike other mammals, which typically confront compliant branches during travel, primates gather food among smaller branches; thus they both spend more time in this context, and they require a stable positioning that frees a hand to pluck food.

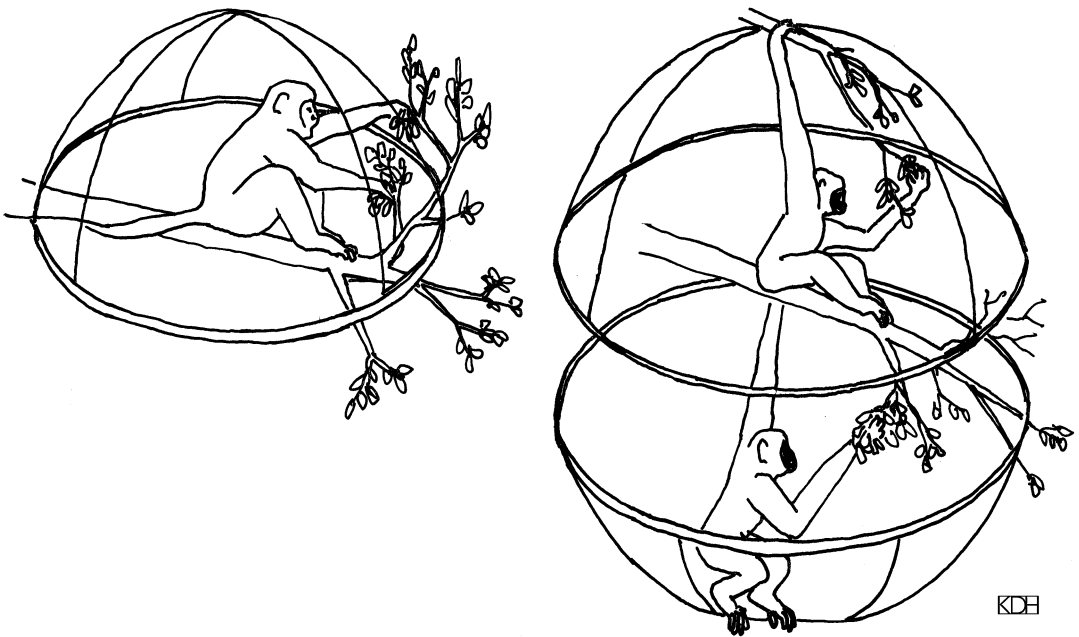
While this strategy works for many small supports, among still smaller-diameter branches, as small as the thickness of their finger, maintaining balance requires extreme muscular exertion or—on extremely compliant branches—walking on top is utterly impossible: such tiny twigs bend under an animal’s weight until they are vertical. Suspensory primates give up on sitting, standing, and walking and instead swing underneath these flexible supports to hang by their arms, their legs, or both. While the body weight of the sitting primate pushes food away from them, it pulls it toward the suspensory primate (Grand 1972; Fig. 1). Suspensory primates have a more flexible gathering scheme because they can feed both on top of branches and below, doubling their feeding space from a hemisphere to a sphere (Fig. 2; after Grand 1972).

A second challenge for arboreal primates is *gap-crossing*. While the large branches, boughs, and boles near the tree center offer firm enough support to allow a stable base for leaping, near the tree edges smaller branches and twigs—the part of the tree specialists refer to as the terminal branches—are too flexible (or compliant) to withstand the forces exerted on them. Here all but the smallest primates face the same limitations as when primates sit to feed among small branches: the branches bend until vertical. As with sitting, hanging underneath these small twigs offers a solution. The primate must then reach out to branches from the neighboring tree while suspending itself and then gradually transfer weight. Orangutans commonly, but other apes seldomly, use their large mass to sway a tree back and forth until they can reach a support in a neighboring tree.

While every species is unique, there are four principal suspensory modes among the primates, an inverted quadrupedalism often referred to as (1) *slow climbing*, (2) *hindlimb suspension* (often assisted by the tail) which is principally postural mode, (3) *clambering* (locomotion only) or



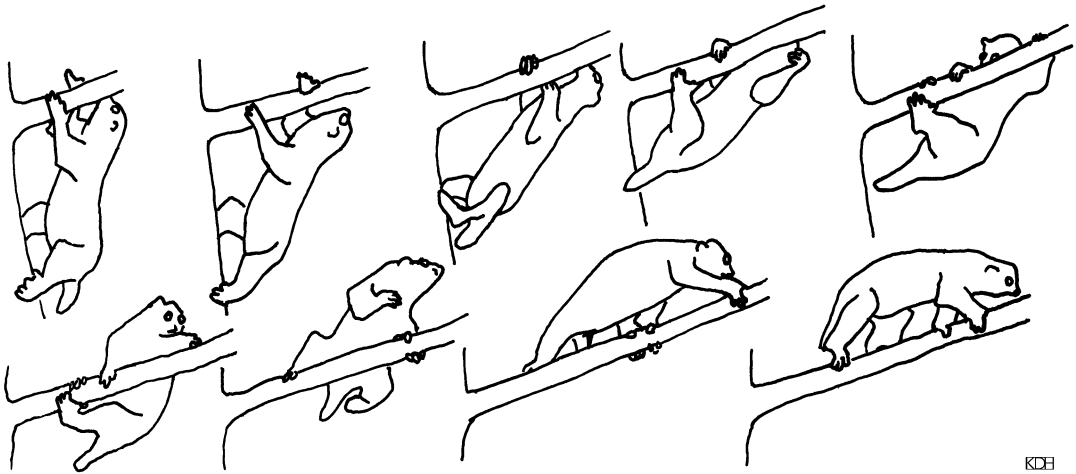
**Primate Suspensory Behavior, Fig. 1** Suspensory behavior precludes the need to balance on top of unstable supports but requires a strong grip



**Primate Suspensory Behavior, Fig. 2** Suspensory behavior doubles their feeding space

*quadrumanous suspension* which is a non-stereotyped combination of arm and leg suspension commonly engaged in only by orangutans, and (4) *unimanual suspension* that, when locomotor, is referred to as *brachiation*.

A third of the members of the superfamily Lorioidea are *slow climbers*. Their inverted walking behavior is slow and deliberate, a stealthy movement that aids their stalk-and-pounce insect-predation adaptation (Fig. 3). All the lorisoids



**Primate Suspensory Behavior, Fig. 3** Pottos often engage in slow-climbing suspensory behavior

move on top of branches in the same slow manner, moving one hand/foot at a time, giving priority to stability and reducing perturbations to their support over speed while reducing perturbations to their support (Walker 1969), the slender loris more so, the potted and slow loris less so. Slow climbers rarely leap and do not run. They progress by shifting one hand or foot at a time, leaving the other three limbs securely gripping the support (Cartmill and Milton 1977). Slow-climbing species have fore- and hindlimbs of approximately equal length. They have rotatable wrists that allow them to orient their hands to any angle a support might offer, an adaptation that allows them to avoid lunges, leaps, and other jerky movements that vibrate supporting branches (Cartmill and Milton 1977).

Howler monkeys and some lemurs, the ruffed lemur in particular (Meldrum et al. 1997), hang from their hindlimbs, often assisted by the tail in howlers and spider monkeys (Fig. 4). Spider monkeys and their relatives may dispense with the feet altogether and hang by the tail alone (Fig. 5). Spider monkeys, but not howlers, often assist forelimb suspension (Fig. 5) with their powerful prehensile tail. Spider monkeys and their close relatives do not have particularly long forelimbs, at least not compared to apes, and they utilize quadrupedal walking more often than do apes (Larson 1998; Fleagle 2013).

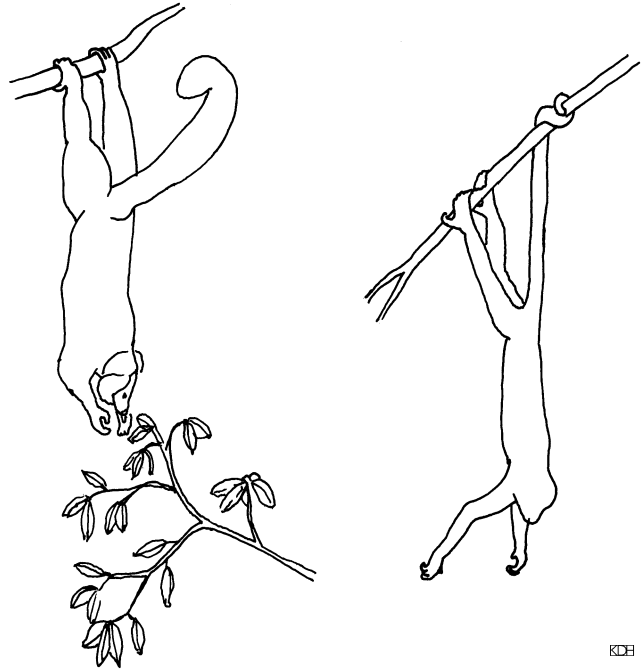
The apes, members of the superfamily Hominoidea, often engage in suspension that involves the forelimbs alone (Fig. 6). Chimpanzees, gibbons, and siamangs feed among small branches using *unimanual suspension*, or one-armed suspensory posture also known as *arm-hanging*. The high frequency of this behavior among these apes requires specialized adaptations, including narrow scapulae and cranially oriented glenoid fossae (tilted-up shoulder joints).

Orangutans have extremely flexible hips, allowing them to engage in suspensory behavior using any combination of hands/feet with the torso held in an upright or vertical orientation (Fig. 7). The locomotor version of this behavior is called *clamber*. Because this behavior involves both hands and feet, it is sometimes called *quadrumanous*, or four-handed, locomotion or posture. Arm-hanging is quite common, but not nearly as common arm-foot hang, a posture in which the body is suspended from an arm and leg on the same side.

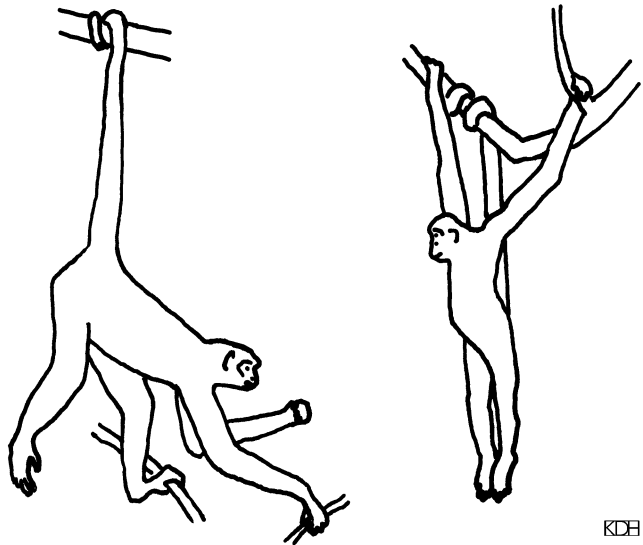
An important locomotor behavior for orangutans is *tree-swaying*, a mode that begins with a clinging posture on a near-vertical support; by oscillating the body back and forth, the orangutan causes the tree bole to sway, bringing a target support in a neighboring tree within reach, after which suspensory or quadrumanous posture and

# Primate Suspensory Behavior,

**Fig. 4** Hindlimb suspension in lemurs (left) and spider monkeys, assisted by the tail



**Primate Suspensory Behavior, Fig. 5** Tail suspension in the spider monkey and tail-assisted forelimb suspension

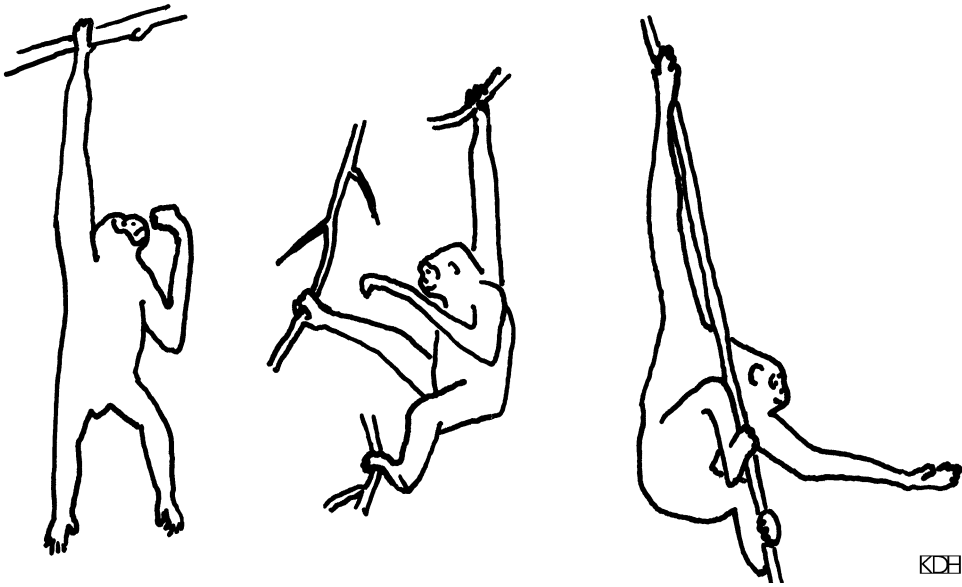


locomotion complete the transfer between canopies.

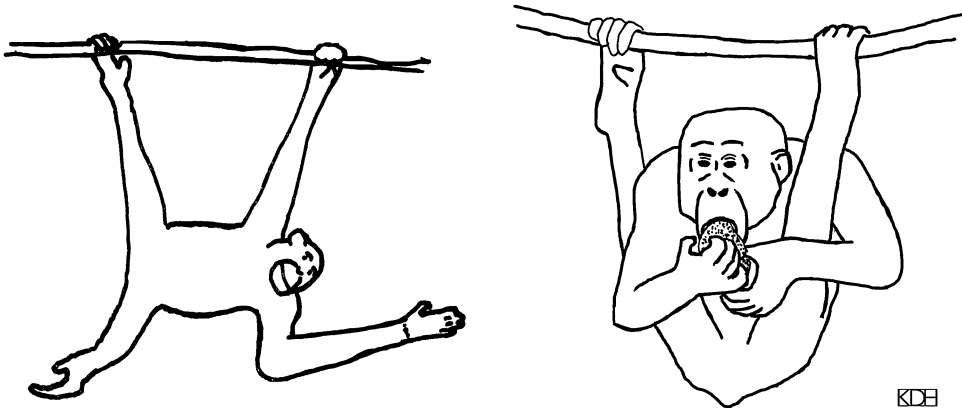
*Brachiation* is a type of rapid and graceful suspensory locomotion that might be considered a locomotor version of arm-hanging in that the body swings forward like a pendulum, suspended first from one arm and then the other (Fig. 8).

Swinging under “monkey bars,” a playground apparatus similar to a horizontal ladder, is the human version of this behavior. This locomotion makes up a large proportion of the locomotor behavior of the lesser apes, the gibbons, siamangs. Their brachiation is so quick and acrobatic that they even propel themselves through the air with a





**Primate Suspensory Behavior, Fig. 6** Unimanual suspension in the gibbon; the forelimb is often assisted by one or more hindlimbs

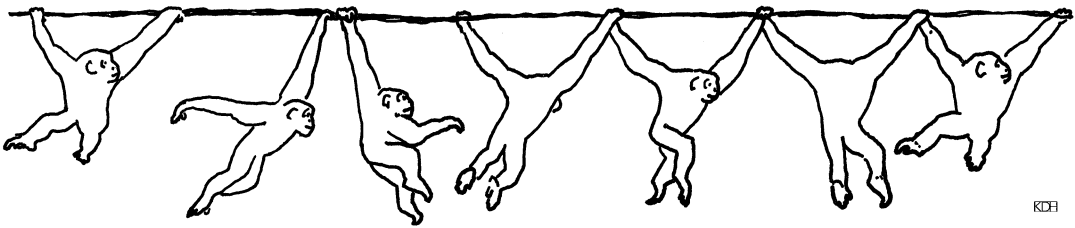


**Primate Suspensory Behavior, Fig. 7** Torso-orthograde (upright) quadrumanous suspensory posture (left) and arm-foot hanging (right) in the orangutan

period of free flight, a behavior so unique that some specialists prefer to limit the term brachiation to the lesser apes alone. While capable of a near-gibbon-like brachiation, the heavier great apes engage in brachiation much less often, and when they do brachiate, it is a slower, more deliberate behavior. A lunging sort of brachiation, in which an individual reaches out to grasp branches

in a neighboring tree, after which it transfers weight onto the new supports, is called *transfer-ring*; this positional mode is the last phase of tree-swaying (see above).

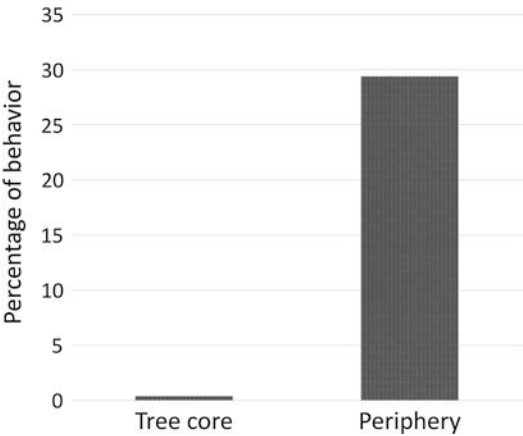
All apes have mobile shoulders, a broad thorax, completely extensible elbows, long fingers, rotatable wrists, arms longer than legs and lack tails.



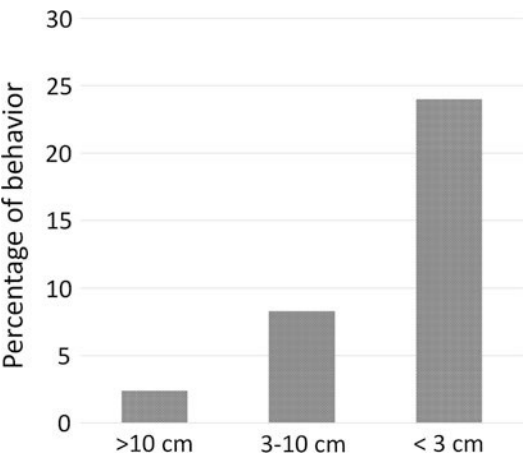
**Primate Suspensory Behavior, Fig. 8** Gibbon brachiation

While all primate locomotion is influenced by the demands of feeding, this is particularly so for the apes. Apes are dependent on ripe fruit, and such fruits are often found in the small, peripheral branches of trees where supports are small and flexible. While supporting branches are small, the great apes have the largest body mass of the primates. The combination of a small-branch feeding regime and great body weight encourages suspension during feeding, rather than sitting or quadrupedal walking, which is the typical monkey feeding behavior. Apes spend so much time among the terminal branches of trees not because they prefer it, but because they must. This is demonstrated by comparing the behavior of high- to low-ranking males. Low-ranking males arm-hang from small-diameter, compliant branches when in the tree periphery; high-ranking males monopolize the few large-diameter branches available in the tree periphery, and they feed while sitting (Figs. 9 and 10) (Hunt 2016).

Because suspensory behavior solves a specific challenge – the need to negotiate small-diameter, flexible (or compliant) supports typically found among the outermost branches of trees – for the larger apes, the size of branches on which they position themselves dictates when suspensory behavior occurs. For example, among chimpanzees, suspensory locomotion makes up only 0.2% of all locomotion, but its frequency rises to 29.4% in the outermost meter of the tree canopy; 8.8% of this suspensory behavior is brachiation and 20.6% is torso-erect transferring. As with locomotion, suspensory posture, too, is more common the smaller the support. Arm-hanging makes up 2.5% of behavior among supports greater than 10 cm, 8.3% of behavior among 3–10 cm supports, and 24% of behavior when supports are less



**Primate Suspensory Behavior, Fig. 9** Among chimpanzees the frequency of suspensory locomotion increases dramatically in the tree periphery, within 1 m of the tree edge, from 0.2% in the tree core to 29.4% in the tree periphery



**Primate Suspensory Behavior, Fig. 10** Among chimpanzees the frequency of suspensory posture increases as support size decreases, from 2.5% of behavior among branches greater than 10 cm to 8.3% among intermediate supports to 24% among branches <3 cm

than 3 cm. Similar trends are seen among the other apes (Hunt 2016).

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Primate-Human Homologies

► Primate Perspectives on the Evolution of Human Behavior

Primates

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Introduction

Primates are a group of eutherian mammals that contain lemurs, lorises, tarsiers, monkeys, apes, and humans. They lack many specialist features and as a result show a wide range of morphological, behavioral, and ecological flexibility. For example, while most primates are arboreal, some taxa are terrestrial. Diet in primates is also quite variable ranging from folivorous to frugivorous to

insectivorous with multiple combinations of each occurring both across and within species. In terms of locomotion, some groups specialize in vertical clinging and leaping to move between trees while some climb on branches slowly on all fours. Still some swing between the branches while others move across the ground using knuckle walking. Morphological variation also exists with the smallest species (mouse lemur) weighing only 30 g with the largest species (male eastern lowland gorilla) weighing up to 250 kg.

With all this variation, it begs the questions, what unifies primates? What features do they have in common that allow for them to be classified under the same order? This is not necessarily easy to answer, but there are a few categories of traits that can be used to distinguish primates from other mammals including: (1) grasping hands and feet, (2) big brains, (3) increased visual system, and (4) generalized skeleton and dentition. Within each of these broad categories, there are distinct features that are seen among primates (Table 1). It is generally accepted that these traits reflect an adaptation to living in the trees, which was the ancestral environment for primates. It is important to note that not all primates have all these features and some of them are shown in variable degrees.

**Primates, Table 1** Features that distinguish primates from other mammalian orders

| Categories of primate traits       | Features within each category                                                                                                                                                                                             |
|------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Grasping hands and feet            | Opposable thumb and big toe, pentadactyly, finger nails instead of claws, power and precision grips                                                                                                                       |
| Big brains                         | Big brains relative to body size, slower rates of development, expanded neocortex                                                                                                                                         |
| Increased visual system            | Forward facing eyes and associated stereoscopic vision, less reliance on smell and associated decrease in olfactory centers in the brain, flatter faces, trichromatic color vision (in catarrhines and some platyrrhines) |
| Generalized skeleton and dentition | Retention of clavicle, retention of two bones in the forelimbs, increase in truncal uprightness, reduction in the number of teeth                                                                                         |

For example, not all primates have fully opposable thumbs with some taxa (i.e., lemurs and lorises) showing a pseudo opposable thumb and some taxa (i.e., tarsiers and marmosets) showing no opposability in their thumb at all.

## Primate Taxonomy

Given the amount of variability in primate characteristics, coming up with a unified system for primate classification has been difficult and there has been considerable revision to primate taxonomies over time. It is generally agreed that all primates arose from a common ancestor roughly 80–90 million years ago and then underwent a proliferation during the Eocene (Martin et al. 2007). This resulted in the formation of many of the current living lineages discussed below. While current taxonomy agrees that primates are divided into two suborders: Strepsirrhini, which is composed of Lorisiformes (galagos, pottos, lorises), and Lemuriformes (Malagasy lemurs); and Haplorrhini, which includes tarsiiiformes (tarsiers), and Simiiformes (further broken down into the parvorders platyrrhines (New World monkeys) and catarrhines (Old World monkeys, apes, and humans)); it took hundreds of years to arrive at this categorization.

### History of Primate Taxonomy

Many iterations of primate taxonomy have been suggested over the years dating back nearly 300 years. In 1735, Carolus Linnaeus published his infamous *Systema Naturae*, and it was in the 10th edition of this book that he recognized primates as one order of mammals including four genera – *Homo*, *Simia*, *Lemur*, and *Vespertilio*; although as the latter included bats, it was removed by future taxonomists who also split *Simia* and *Lemur* into a variety of genera. Work through the remainder of the 1700s included that of Cuvier, Huxley, and Geoffroy Saint Hilaire (just to name a few) who continued to describe new species of lemurs and monkeys. By the mid-1800s, many of the primate species were known and described with a taxonomy that was relatively agreed upon. It was then not until the

1970s that tree shrews were removed from the primate order when genetic evidence revealed them to be less related to primates than to squirrels (order Dermoptera). This left Primates to be divided into two monophyletic groups: Prosimii and Anthropoidea. Prosimians included lemurs, lorises, galagos, and tarsiers, and Anthropoids included monkeys, apes, and humans. The contentious issue with this classification was the placement of the tarsiers, which although share many primitive characteristics in common with lorises and lemurs, including nocturnality, mobile ears, and an enhanced sense of smell, also exhibit Anthropoid characteristics such as a lack of nocturnal eye morphology. While their position within primate taxonomy was left up to debate for many years, it came to rest in the 1980s with the proliferation of genetic methods and techniques that allowed for more testing of individuals and species that revealed despite the morphological and behavioral similarities to lemurs and lorises, tarsiers are more similar genetically to monkeys, apes, and humans. This then led to the development of a new classification system that suggested that primates still be divided into two suborders, however, that these be Strepsirrhini (lemurs and lorises) and Haplorrhini (tarsiers, monkeys, apes, and humans), which is still the classification system used today.

### Current Primate Taxonomy

See Fig. 1

### Strepsirrhini

Strepsirrhine primates, known as the tooth-combed primates, are generally agreed to fall into two infraorders: Lemuriformes (Malagasy lemurs) and Lorisiformes (lorises and galagos). While there has been some suggestion that the lemur family, Cheirogaleidae should in fact be a third infraorder (Chiromyiformes); genetic data does not support this and show that Chiromyiformes fit better within the Lemuriformes (e.g., Chatterjee et al. 2009). Genetic data also suggests that Strepsirrhines

**Primates, Fig. 1** Current taxonomy of living primates

- Order Primates
  - Suborder Strepsirrhini: lemurs and lorises
    - Infraorder Lemuriformes
      - Family Daubentonidae (1 genus)
      - Family Cheirogaleidae (5 genera)
      - Family Lepilemuridae (1 genus)
      - Family Lemuridae (5 genera)
      - Family Indridae (3 genera)
    - Infraorder Lorisiformes
      - Family Lorisidae (4 genera)
      - Family galagidae (5 genera)
  - Suborder Haplorrhini: tarsiers, monkeys, apes and humans
    - Infraorder Tarsiiformes
      - Family Tarsiidae: tarsiers (3 genera)
    - Infraorder Simiiformes
      - Parvorder Platyrrhini
        - Family Pitheciidae (4 genera)
        - Family Atelidae (5 genera)
        - Family Cebidae (7 genera)
        - Family Aotidae (1 genus)
        - Family Callitrichidae (6 genera)
      - Parvorder Catarrhini
        - Superfamily Cercopithecoidea
          - Family Cercopithecidae (23 genera)
            - Subfamily Cercopithecinae
              - Tribe Cercopithecini
              - Tribe papioini
            - Subfamily Colobinae
              - Tribe Colobini
              - Tribe Presbytini
        - Superfamily Hominoidea
          - Family Hylobatidae (3 genera)
          - Family Hominidae (5 genera)

initially split into Lemuriformes and Lorisiformes some 75 million years ago (Perleman et al. 2011). Some of the features which unify Strepsirrhines include a wet nose (rhinarium), a tapetum (reflective lucidum layer in the eye to improve nocturnal vision), large eye orbits including a postorbital bone that runs around the socket, an increased reliance on smell and enlarged olfactory lobes in the forebrain, independently mobile ears and a tooth comb. Behaviorally, while some lemurs are diurnal, the majority of Strepsirrhines (and all lorisiformes) are nocturnal, which is the ancestral condition.

### Lemuriformes

Lemuriformes are endemic to Madagascar and while the fossil record of Madagascar is currently limited to the past 15,000 years, the presence of a

tooth comb like African Strepsirrhines suggests that they have been present on Madagascar since the Eocene. Genetic data also suggests lemurs have been separated from their mainland African counterparts for 75 million years. It is thus proposed they migrated to Madagascar, which has been an island for over 100 million years, during a rafting event at some 50–80 million years ago (Ali and Huber 2010). Due to their isolation on Madagascar, they have evolved many traits that are unusual among primates including torpor in some nocturnal species and female dominance and seasonal breeding in some diurnal species. One unifying trait possessed by most lemurs is the grooming claw on the second toe.

Lemuriformes are divided into five families including Daubentonidae, Cheirogaleidae, Lepilemuridae, Lemuridae, and Indridae. Of



these, it was Daubentoniidae, which includes the genus *Daubentonia* or aye-aye, that split off first at approximately 62–65 Mya (Yoder and Yang 2004), which is why it has posed some problems in terms of its placement in the Strepsirrhines (as described above).

Within the Daubentoniidae, there is only one genus, *Daubentonia* and one species, *Daubentonia madagascariensis*, which include the aye-ayes. Aye-ayes are small (2.3 kg), solitary, nocturnal primates that live in trees. They have elongated fingers and a compressed claw, that when used in conjunction with their long, curved incisors allow them to very effectively capture and feed on tree grubs from underneath tree bark. They also have a reduced dental formula of only 1.0.1.3, which includes rodent-like incisors that continually grow.

The five genera of the Cheirogaleidae (*Phaner*, *Cheirogaleus*, *Allocebus*, *Mirza*, and *Microcebus*) are the smallest of the lemurs with *Cheirogaleus* containing the dwarf and *Microcebus* the mouse lemurs weighing as little as 30 g. They subsist on a diet of mainly fruit and small prey including insects and small lizards. They are solitary and nocturnal and have enhanced hearing to assist with hunting during the night.

Lepilemuridae contains only the genus, *Lepilemur*, or sportive lemur. As the smallest folivorous primates, sportive lemurs weigh just under 1 kg and are around 0.5 m in length. In 2001, it was suggested that *Lepilemur* be combined with the extinct lemur *Megaladapis* in a family named Megaladapidae, largely based on similar dentition where upper incisors are not replaced by permanent dentition in adulthood. This, however, was later rejected, based on genetic evidence that revealed they were not close enough to each other to warrant being combined in one family (Wilson and Reeder 2005).

The family Lemuridae represents the lemur family with the most variation containing five genera including *Lemur* (ring tailed lemur), *Eulemur* (brown lemur), *Varecia* (ruffed lemur), *Hapalemur* (gentle lemur), and *Prolemur* (bamboo lemur). Unlike most other lemurs, these genera primarily move by slow quadrupedal

climbing and live in groups that are either diurnal (*Varecia*) or cathemeral. Their body size ranged from 700 g (*Hapalemur*) to 4.5 kg (*Varecia*) again showing much greater range than the other lemur families. Like with the variation in body size, there is also behavioral variation. Some species are diurnal, in opposition to the majority of Strepsirrhines that are nocturnal. This may be due to a lack of competition from monkeys on Madagascar enabling them to take advantage of the diurnal niche. In addition, some species of *Eulemur* and *Hapalemur* are cathemeral, which means that they are active throughout a 24-h period.

Indriidae includes three sister genera including *Indri* (Indriids), *Propithecus* (Sifakas), and *Avahi* (wooly lemurs). Of these, the Indri is the biggest lemur weighing up to 10 kg, whereas *Propithecus* and *Avahi* weigh substantially less at between 3.5 and 6.5 kg and up to 1.5 kg, respectively. They characteristically move by vertical clinging and leaping between trees or by jumping on the ground due to their long legs and tarsal bones that allow them to jump up to 30 feet. Generally herbivorous, Indriids eat primarily leaves although their diet may be supplemented with fruit and flowers. *Indriids* and *Propithecus* are diurnal, whereas *Avahi* retain the ancestral trait of nocturnality.

### Lorisiformes

Molecular studies, backed up with genetic evidence, suggest that lorises diverged from lemurs some 75 Mya. Currently, lorisiformes are distributed throughout mainland Africa and Asia and show much less variation than lemurs as all species are nocturnal and body size only reaches up to 1.5 kg. There is variation in movement patterns, with African species using slower quadrupedal climbing and Asian species relying on vertical clinging and leaping. Traditionally, lorisiformes are divided into two families: Lorisidae and galagidae; however, due to the monophyly of the lorisidae and a lack of genetic information on the galagidae, some have suggested it is more appropriate to classify them into subfamilies of lorisinae and galaginae.

The Lorisidae (lorises and pottos) are classified into six species in four genera (*Loris*, *Nycticebus*, *Arctocebus*, and *Perodicticus*). Lorises (*Loris* and *Nycticebus*) are distributed throughout Southeast Asia, whereas pottos (*Arctocebus* and *Perodicticus*) are distributed in Central Africa. Lorises and pottos are relatively small (85 g–1.5 kg), arboreal primates with specialized dentition. While they retain the lower tooth-comb, their anterior premolars are more canine than molar-like. They also have extended upper canines. Their postcranial skeleton is also different to other lorisiformes in that the wrist is modified to swinging in the trees and the forelimbs and hindlimbs are of equal length. They are all nocturnal and move slowly through the trees with quadrupedal climbing and avoid predation through cryptic behavior.

Galagidae include the galagos and bushbabies that are all distributed in Africa. It is currently thought there are five genera including: *Galagoides* (dwarf galagos), *Euoticus* (needle-clawed galagos), *Sciurocheirus* (squirrel galagos), *Otolemur* (greater galagos), and *Galago* (lesser galago) in this family. They are smaller and more gracile than the lorisidae and move by leaping through the trees rather than climbing. Unlike the lorisidae, males possess a baculum. Due to a lack of molecular and genetic studies, it is still uncertain if any of these genera are paraphyletic, which has cast doubt on this classification system. For example, there is evidence that *Galagoides* should in fact form two genera (*Galagoides* and *Paragalago*) (Masters et al. 2017).

## Haplorrhini

Haplorrhine primates include two infraorders: tarsiiiformes (tarsiers) and Simiiformes (monkeys, apes and humans; historically known as Anthroipoidea). Simiiformes are then broken down into two parvorders: Platyrrhini (New World monkeys) and Catarrhini (Old World monkeys, apes and humans). Haplorrhines have many distinguishing features from Strepsirrhines that include a flattening of the face that results from a decreased reliance on smell and an increased

reliance on vision. This is also the likely reason why Haplorrhines have dry noses and larger brains with more developed visual centers. Due to differences in diet, Haplorrhines also have different dentition and jaw morphology including fused lower jaws, shovel-like incisors, and the presence of a diastema between the upper lateral incisor and the upper canine tooth and larger, more generalized molars present near the back of the mouth.

## Tarsiiformes

As previously stated, tarsiiformes have a mix of traits associated with Strepsirrhines and Haplorrhines, which has made their taxonomic classification contentious. This has resulted in tarsiers being placed as either a sister taxon to the Strepsirrhines to form Prosimii or placed with the Anthroipoidea to form the Haplorrhines or as its own independent suborder altogether. Given their mix of behavioral and morphological traits (described below), it was not until genetic evidence showed that tarsiers are most likely to be part of the Haplorrhine lineage, that their taxonomy was resolved although they likely split from them nearly 90 Mya (Perleman et al. 2011). Tarsiers also maintain features that they do not share with any other primates including having the largest eye to head size ratio of any mammal, the ability to turn their head nearly 360 degrees, having two or three sets of nipples despite giving birth to single young, and having an unusually long tarsal bone (for which they get their name) that allows them to jump up to 20 feet in length. They are also the most carnivorous of the primates eating primarily insects and small vertebrates. They are currently found on the Islands of Borneo, Sulawesi, Sumatra, and the Philippines. Weighing in at between 80 and 160 g and measuring 85 and 165 mm, they are some of the smallest Haplorrhines. The infraorder contains only one family, Tarsiidae, and while previously thought to contain only the genus, *Tarsius*, it is now believed there are three genera of tarsier. These include *Carlito* (Philippine tarsier), *Cephalopachus* (western tarsier), and *Tarsius* (Eastern Tarsiers). Of these, the latter is thought to be the basal group that diverged first, while the two formers are believed to be sister taxa.

## Simiiformes

### Platyrrhini

The parvorder Platyrrhini includes the New World monkeys (or Neotropical monkeys) found in Central and South America. Like with the lemurs, there remains uncertainty surrounding the origin of the Platyrrhines and how they became distributed in the New World. Genetic studies using nuclear DNA have given variable dates of the divergence between platyrrhines and catarrhines, of between 33 and 70 Mya; studies based on mitochondrial DNA, however, give dates of separation between the parvorders of 35–43 Mya (Ciochon and Fleagle 1987). Regardless of the exact date, it also remains a mystery how this group of primates were able to cross the Atlantic Ocean and get from Africa to South America. It is thought this occurred in the Eocene, possibly through the use of a rafting event across the Atlantic Ocean. As it has been estimated that a small primate could survive up to 2 weeks on a vegetation raft, this is a plausible explanation due to the reduced distance separating Africa from South America at that time. Another hypothesis is that the animals “island hopped” by taking advantage of a lower sea level and the formation of Atlantic Ocean ridges. New World primates are distinguished from Old World primates by some physical characteristics including the positioning of the nostrils on the nose (platyrrhines have sideways oriented nostrils, while catarrhines have downward facing nostrils), body size (platyrrhines are smaller than catarrhines), and a difference in habitat use with all platyrrhines being arboreal. The lack of terrestrial platyrrhines may be due to limited grassland availability in South and Central America or the fact that the smaller body size of New World monkeys compared to Old World monkeys leaves them more vulnerable to terrestrial predators, meaning the arboreal environment may afford more protection from predation.

While initially platyrrhines were divided into just two families, the Callitrichidae that included any New World monkey that had claws and Cebidae that included everything else; this classification has since been rejected due to the fact this would have made Cebids paraphyletic. Currently,

it is agreed there are five families of monophyletic New World monkeys including Pitheciidae, Atelidae, Aotidae, Cebidae, and Callitrichidae. Of these, Pitheciidae diverged first followed by Atelidae and then Aotidae, Cebidae, and Callitrichidae.

Pitheciidae is a family made up of four genera and 40 species. Of these, *Callicebus* split off first followed by *Pithecia* then *Chiropotes* and *Cacajao*. While each of these genera have distinct physical appearances, they all share some features including dentition adapted to eating hard and protected fruit. They are also all found in the rainforests of South America where they move by slow quadrupedal climbing in the trees. Of the pitheciids, *Callicebus* are the smallest weighing up to 2 kg, while *Cacajao* are the largest weighing up to 3.5 kg.

Atelidae are the largest of the New World monkeys and the only group of primates to possess prehensile tails used for grasping. There are five genera within the Atelidae including *Alouatta* (howler monkeys), *Ateles* (Spider monkeys), *Brachyteles* (muriquis), *Lagothrix* (wooly monkeys), and *Oreonax* (yellow-tailed wooly monkeys). While *Oreonax* is commonly accepted as its own genus, this is not supported by genetic data (Rosenberger and Matthews 2008). Atelines are distributed throughout Central and South America with *Alouatta* being the most widely distributed (Mexico to Argentina) followed closely by *Ateles*. *Lagothrix*, on the other hand, are only found in the Amazon while *Brachyteles* are restricted to the Atlantic rainforest of Brazil and *Oreonax* are restricted to the cloud forests of the Peruvian Andes. Body weight among the genera ranges from 4 to 15 kg with the biggest being male *Brachyteles*. Unlike many other primates, some Ateline show male philopatry where males stay in the natal group and females disperse (Strier 1994).

Aotidae are referred to as the night monkeys as they are the only nocturnal monkey. There is only one genus, *Aotus*, that includes eight species. They are small monkeys weighing from 0.45 to 1.25 g and measuring 316–400 mm in length. Males and females of all species are generally the same size

and have the same appearance. All night monkeys are arboreal and share the same large eyes and flat, round faces. They are found throughout Central and South America with a distribution ranging from Panama to Bolivia, Argentina, and Paraguay; only *Alouatta* of the family Atelidae are more widely distributed in the New World.

Cebidae includes two subfamilies (Cebinae and Saimirinae). Cebinae include the capuchin monkeys and contains two genera *Cebus*, which include four species of gracile capuchin and *Sapajus*, which contains five species of robust capuchin. Until 2011, this subfamily only included *Cebus*, but genetic data revealed that there were in fact two groups that diverged from each other approximately 6 Mya, possibly due to the creation of the Amazon River that separated the two groups. In addition to genetic evidence, this split was supported by differences in morphology with gracile capuchins having longer limbs relative to body size and rounder skulls than robust capuchins that are better adapted to heavy chewing and a diet of nuts (Lynch-Alfaro et al. 2012). Robust capuchins also have crests and beards on the males. Capuchins are approximately 30–50-cm long with a tail of equal length. They are omnivorous eating a more diverse diet than other New World monkeys, they are also the most intelligent New World monkeys with the biggest brain to body size ratio of the infraorder. Capuchin monkeys range from Costa Rica down through South America as far south as Argentina.

The subfamily Saimirinae, the squirrel monkeys, contains five species in just one genus (*Saimiri*). Of the five species of Saimirinae, four live in the Amazon, with only one (*S. oerstedii*) found in Central America, Costa Rica and Panama. Until 1984, all squirrel monkeys were placed in the same species; however, this was rejected, and species are distinguished from each other based on the pattern of hair coloration around their eyes (Hershkovitz 1984). Squirrel monkeys measure 25–35 cm in body length with a tail that is at least as long as their body. Males and females are sexually dimorphic with males weighing approximately 0.75–1.1 kg while females weigh only 0.5–0.75 kg.

Callitrichidae includes six genera including *Saguinus* (tamarins), *Leontopithecus* (lion tamarins), *Callimico* (Goeldi's monkeys), *Callithrix* (Atlantic forest marmosets), *Callibella* (black-crowned dwarf marmoset), and *Mico* (Amazonian marmoset). While they were originally placed as a subfamily within Cebidae, this was rejected in 2005 (Wilson and Reeder 2005). They are the smallest of the Haplorrhine primates and unlike other monkeys have claws instead of nails. They also regularly give birth to twins and have a very high level of male parental care where males carry, feed, protect and play with infants in the group. They also show a unique social organization of cooperative polyandry, where only one female is reproductively active with subordinate females showing no ovarian cycling when in their natal group (French et al. 1984). This has been shown to be due to the physiological suppression of these females by the dominant, breeding female through pheromonal control (e.g., Puffer et al. 2004).

#### Catarrhini

Catarrhine primates include Old World monkeys, apes, and humans. As explained above, Catarrhine primates were separated from Platyrrhine primates somewhere between 33 and 70 Mya and can be physically distinguished by the placement of the nostrils on the nose. Catarrhines typically also have bigger body sizes than Platyrrhines and more diversity in habitat exploiting both arboreal and terrestrial niches. This parvorder includes two superfamilies, Cercopithecoidea (Old World monkeys) and Hominoidea (apes and humans).

#### Cercopithecoidea

Cercopithecoidea is a superfamily that contains only one family, Cercopithecidae, which includes all the Old World monkeys and is further broken down into two subfamilies, Cercopithecinae and Colobinae.

Cercopithecinae are the cheek pouched monkeys that are unified by the possession of cheek pouches used to store food. Many species also possess ischial callosities or “sitting pads” that change color in some species to signal sexual

receptivity. Thirteen genera are included in the Cercopithecines: *Allenopithecus* (Allen's swamp monkeys), *Miopithecus* (talapoin), *Cercopithecus* (guenons), *Erythrocebus* (patas monkeys), *Allochrocebus* (L'Hoest's monkey), *Chlorocebus* (vervets), *Macaca* (macaques), *Cercocebus* (collared mangabey), *Lophocebus* (crested mangabeys), *Mandrillus* (mandrills and drills), *Theropithecus* (Geladas), *Rungwecebus* (kipunji), and *Papio* (baboons). This subfamily is further divided into two sister tribes: Cercopithecini and Papionini. Cercopithecini includes the guenons, the patas monkey, vervets, and terrestrial guenons, Allen's swamp monkey, talapoin and arboreal guenons (*Cercopithecus*). Papionini then contains the other genera. Traditionally, there were only two genera in this tribe: *Papio* that contained the bigger species and *Cercocebus* that contained the more gracile ones. Genetic evidence refuted this, which was in fact supported by more detailed morphological studies that revealed there are in fact six genera in this group.

While both tribes exploit both arboreal and terrestrial habitats, most cercopithecine monkeys are limited in distribution to sub-Saharan Africa. This is except for *Macaca* that, aside from humans, have the widest distribution on the globe, ranging from Asia to Africa to Gibraltar. They also range from living in rain forests, savannahs, rocky mountainous areas, and snowy, high altitude locations. Within Cercopithecinae, the arboreal species are smaller and more gracile than the terrestrial ones. Despite differences in body size and habitat, the majority of cercopithecinae are omnivorous, diurnal, and live in large social groups.

Colobinae are the leaf-eating monkeys. They are unique among primates in that they rely on a diet very heavy in leaves that are high in indigestible fiber as well as secondary compounds. The presence of the secondary compounds (generally toxins and tannins) can render up to half of the protein in ingested leaves unusable, which when combined with the high fiber contents makes leaves a relatively low-quality food and hard to digest food item. Colobines have adapted to this, however, by evolving a suite of anatomical

specializations. These include the possession of enlarged salivary glands that produce copious amounts of saliva to help break down fiber before it reaches the stomach. In addition, it has been speculated that, like is seen in ruminants, their saliva includes tannin-binding properties to allow them to remove some tannins and increase the available protein of the food (Clausen 2003). They are also foregut fermenters, which also like ruminants, means that they have a multi-chambered forestomach where food is broken down and fermented (Langer 1988). The four chambers of the stomach are the saccus gastricus, the tubus gastricus, the pars pylorica, and the pyloric mucosa. They also have a large caecum and proximal (Kay et al. 1976; Chivers 1995) in which the presence of volatile fatty acids suggests that bacterial fermentation is also taking place (Kay et al. 1976). The stomach also generally has a pH between 6.5 and 8.0, below which an animal may suffer from acidosis.

While currently Colobinae are divided into two tribes, supported by geographic location and Mitochondrial DNA (Messier and Stewart 1997), there has been some contention around this as when using anatomical forestomach characteristics, it can be argued that the African Colobines may group more closely with some Asian colobines (*Semnopithecus*, *Trachypithecus*, and *Presbytis*), while the African procolobus better group with *Rhinopithecus*, *Pygathrix*, and *Nasalis*. That said, the current phylogeny supports Colobinae being divided into two tribes: Colobini that includes the African Colobines and Presbytini that includes the Asian colobines. The African colobines include the black and white colobus (genus *Colobus*), which is a sister genus to the other two genera of African Colobus: the olive colobus (genus *Procolobus*) and the red colobus (*Ptilocolobus*). The Asian colobines are made up of the odd-nosed monkeys (genera *Rhinopithecus* (snub-nosed monkeys), *Pygathrix* (doucs), *Nasalis* (Proboscis monkeys), and *Simias* (pig-tailed snub-nosed monkeys) as well as the *Semnopithecus* (Indian langurs), *Trachypithecus* (lutungs), and *Presbytis* (surilis). The Asian colobines inhabit a



wider range of habitats than their African counterparts as they live in moist, coniferous, and scrub forests as well as plantations in Indonesia and Malaysia and karst habitat in Southeast Asia. They also live in a wider geographic range from tropical lowland areas to high altitude and temperate montane zones.

#### Hominoidea

The superfamily Hominoidea contains the families Hylobatidae (small apes) and Hominidae (great apes and humans). It is distinguished from the other superfamily of catarrhine by lack of a tail, larger body size, bigger brain to body size ratio, and a slower life history pattern including longer gestation and a longer period of juvenile development. Hominoids also have a shorter spine relative to their body length, along with a broader pelvis that supports more upright posture and better balance than other catarrhines.

Hylobatidae are referred to as lesser apes or small apes and were originally divided into only two genera, *Symphalangus* (the siamang) and *Hylobates* (the gibbons). Due to an increase in genetic and vocalization data, however, there are currently four genera recognized, including: *Symphalangus* (one species of siamang), *Nomascus* (seven species of crested gibbons), *Hoolock* (three species of hoolock gibbons), and *Hylobates* (seven species of “44 chromosome” gibbons). It is believed that the four genera are sister genera that diverged from each other at approximately the same time; however, some mitochondrial DNA evidence suggests *Nomascus* was the first to diverge and *Hylobates* the most recently derived (Takacs et al. 2005). Hylobatidae are distinguished from Hominidae in that they are found only in the forests of Southeast Asia, where as Hominidae are distributed primarily in Africa, except for orangutans and humans. Hylobatidae are also distinguished from Hominidae by their smaller body size (3.9–12.7 kg), ischial callosities, and sexual monomorphism. In addition, they possess elongated forelimbs and shortened hind limbs, long curved fingers and toes, and reduced thumbs, all of which assist in brachiation, which is their primary mode of locomotion. They also live

in smaller social groups that are typically either pair bonded or a small social group of 2–6 individuals. They also tend to show the characteristic behavior of morning duet singing where the male and female in the group sing a unified song, which in some species is facilitated by the presence of a throat sac that acts as a resonating chamber to increase the volume of the vocalization.

Hominidae include the three genera of great apes *Gorilla* (gorillas), *Pongo* (orangutans), and *Pan* (chimpanzees and bonobos) as well as the one genus of humans (*Homo*). The taxonomy of great apes and humans has been heavily debated over the years. Initial classification systems saw all great apes placed together in their own family, Pongidae, with humans left as the only species in Hominidae (Sarich and Wilson 1967). While this was based primarily on morphological evidence, genetic studies have revealed that orangutans diverged first from the other hominids at 18 Mya (Hobolth et al. 2007) followed by gorillas at approximately 8–10 Mya (Sibley and Ahlquist 1984). It also shows that chimpanzees and bonobos are the most closely related species to humans, splitting at roughly 4–6 Mya (Hobolth et al. 2007). This warranted a new classification where all great apes were placed within the same family as humans (Hominidae) and then separated at the subfamily level with orangutans in Ponginae and gorillas, chimpanzees, bonobos, and humans in Homininae.

Hominids are much larger than their hylobatid counterparts weighing between 48 and 270 kg (male *Gorilla*). They also show sexual dimorphism with males being larger than females and typically live in larger social groups, although orangutans live solitary. They also show much longer developmental periods with orangutans not reaching sexual maturity until approximately 10–15 years and having an average interbirth interval of 7–8 years; this is much more than the 2–3 years common in many primate species. Movement patterns tend to be more upright with chimpanzees, bonobos, and gorillas moving by knuckle walking and orangutans moving by quadrupedal climbing. This has resulted in the great apes showing more robustness in their wrist bones than other primates to support a greater weight on

their forelimbs. Hominids also show much shorter forelimbs relative to their hind limbs compared to other primates.

## Conclusion

For the most part, recent phylogenetic assessments and classifications of primates have been done using molecular and genetic data. Thankfully, these have largely agreed with the more traditional classifications that were based on morphology. That said, disagreements do exist in some cases (i.e., the existence of *Oreonax* within the Atelidae and the arguments within galaginae). A bigger issue that has faced primate taxonomy and classification has come from the “lumping vs. splitting” debate. In this approach, lumpers tend to classify groups of taxa together unless there is a proven reason to split them into smaller and distinct groups. Splitters, on the other hand, tend to separate taxa into multiple groups unless there is a very good explanation not to. The argument against lumping is that it may obscure biologically important differences whereas the argument against splitting is that we end up with too many small and fragmented species groups. This has resulted in a varying number of primate species and subspecies being defined over the years, and at any one given time, different numbers of species and subspecies may be presented based on how the particular scientist decides to split or lump species. For example, in 2001, Colin (Groves 2001) split some species resulting in 350 primate species being defined in his seminal work *Primate Taxonomy*. This number was then further increased to 276 in 2005 in the *Mammal species of the world*. Due to recent research that has revealed new species and an increase in the use of genetic and molecular techniques, there are currently approximately 504 known primate species in the genera discussed here (Estrada et al. 2017).

## Cross-References

► [Opposable Thumb](#)

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## Primer

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## Synonyms

Oligonucleotides; Oligos

## Definition

Primers are a short stretch of nucleotides acting as a starting point for DNA synthesis.

## Introduction

A primer is a short strand of nucleotide molecules (generally RNA or DNA of about 18–22 bases) which acts as an initial point for deoxyribonucleic acid (DNA) synthesis. These nucleotide sequences are specific and complementary to their target DNA sequences and allow selective amplification of that specific DNA sequence. Primers bind to denatured DNA template during polymerase chain reaction (PCR) by hybridizing to a complementary region of target DNA and provide a free 3' hydroxyl end. Further, a suitable heat-stable DNA polymerase in the presence of DNA precursors (the four deoxynucleoside triphosphates, dATPs, dCTPs, dGTPs, and dTTPs) initiates the synthesis of new DNA strands complementary to the individual target DNA strands at the 3' hydroxyl end. Similarly, an RNA primer serves as a starting point for DNA polymerase during DNA replication, while in vitro primers are short strand of chemically synthesized nucleotides for complementary DNA synthesis. The design of primers has a major impact on the success of PCR with respect to the specificity and yield of amplified product.

## Characteristics of a Good Primer

Primer designing is a crucial step for the success of PCR amplification. The characteristics of primers can help to evaluate the outcome of PCR experiment. The basic requirements for successful primer designing are considered as length of the primers, the primer length difference, the GC content, nucleotide composition at the 3' end of primer, melting temperature, and melting temperature difference of both the primers. Further, the secondary structures like dimers (including self-dimers and cross-dimers), hairpins, and specificity also affect the efficiency of PCR. The standard PCR primer design characteristics are as follows (Chuang et al. 2013):

1. **Primer length and primer length difference** – Primer length could be variable during PCR amplification. Generally, the optimal

length of primer pairs could vary between 16 and 28 nucleotides with a length difference of around three nucleotides.

2. **GC content** – GC content is a measure of the percentage of the ratio of total G and C nucleotides that appear in the primer. The appropriate GC content of a primer varies in the range of 40–60%. The variation in GC content may directly affect the annealing temperature. Therefore, checking the GC content of forward and reverse primer is a crucial step for PCR primer designing.
3. **Nucleotide composition at the 3' end of primer** – GC base pairing is thermodynamically more stable than AT base pairing. Enzymes selectively add bases to the 3' end of primed double-stranded DNA. Therefore, primers bind more tightly to the template DNA.
4. **Melting temperature** – The melting temperature ( $T_m$ ) is the most critical determinant to perform a successful PCR experiment.  $T_m$  of a primer pair varies between 50 °C and 62 °C. For successful PCR, the  $T_m$  difference of a primer pair should not exceed more than 5 °C. The ideal  $T_m$  difference of a primer pair is zero. The  $T_m$  of a primer could be calculated using mathematical formula given by Wallace, the Bolton and McCarthy, thermodynamic theory, or various other formulas (Wallace et al. 1979; Sambrook et al. 1989; You et al. 2008; Untergasser et al. 2007).
5. **Primer dimers** – The annealing between two primers during PCR results in primer dimer. The presence of dimer negatively affects the efficiency of a PCR. Thereby, hybridization of two primers should be avoided during PCR. Similarly, forward primer and the reverse primer may anneal to each other and may create cross-dimers or self-dimers when the forward primer anneals to another forward primer, or a reverse primer anneals to another reverse primer. Checking for dimers and primers self-complementarity is necessary to ensure the primer can hybridize with the template sequence and a crucial step for success of PCR.
6. **Primer hairpins** – A primer may anneal to itself and thereby it may form a secondary structure called as hairpin. Self-annealing of

primers should also be avoided. Forward and reverse primers should be individually checked for hairpins to allow for the specific hybridization of primers to the template sequence.

7. **Specificity** – Specificity is a crucial component of primer designing. A PCR experiment may be unsuccessful if the primers are not annealed to specific template regions or if they match to more than one position in the DNA template sequence. Therefore, it is important to determine whether a primer pair hybridizes to the target region or whether a primer matches with more than one position in the DNA template sequence or genomic sequence. The specificity ensures that the designed primer can detect a specific sequence to prevent invalid PCR results as well as for a successful PCR.

## Species of Primers

Traditional PCR primers are generally designed to anneal to specific target sequence and thereby act as primer for thermostable DNA-dependent polymerases. However, a wide variety of modified primers have now been developed which greatly broadened the scope of PCR applications (Pelt-Verkuil et al. 2008). These applications may be grouped into three categories:

1. 5' end modified primers
  2. Degenerate modification primers
  3. Miscellaneous primers
1. **5' end modified primers** – These primers are designed to be complementary to specific regions of target DNA sequence similar to traditional PCR but contain additional nucleotides at their 5' ends that are absent in target sequence. These additional 5' sequences are an integral part of the primers and amplify along with the rest of the amplified PCR products. These primers may require the use of lowered annealing temperatures during the first steps of the PCR cycling protocol. Examples of 5' end modified primers include:

- (a) **Restriction sites** – Restriction sites present at the 5' end of an amplified product facilitates cloning of the PCR product into a relevant vector. Different restriction sites could be designed into the 5' end of each of the PCR primer pair and thereby various PCR product cloning strategies could be developed. Further, some terminal nucleotides could be attached immediately upstream of the 5' end of the restriction site sequence for efficient recognition of the site by its restriction enzyme. These terminal nucleotides may be selected at random or adapted according to efficient optimal design of the PCR primer sequence like 50% GC content. These 5' end restriction sites should be chosen with precautions so that these restriction enzymes should not cut within the amplified PCR product itself.
  - (b) **Regulatory sequences** – PCR products could be transcribed into mRNA copies using DNA-dependent RNA polymerase enzymes at the 5' end promoter sequence. It allows the synthesis of a large amount of RNA which could be further used for several applications including RNA probes in hybridization studies and for in vitro protein synthesis studies. Bacteriophage T7 and SP6 promoters are the most frequently used promoters for in vitro RNA and protein synthesis.
  - (c) **Promoters and ribosomal binding sites (RBS)** – A functional 5' end promoter sequence could be designed in association with a ribosomal binding site, and an ATG start codon could be used for optimized in vitro coupled transcription and translation of PCR products. It allows mRNA and protein to be produced in a single “coupled” reaction system.
  - (d) **Capture haptens and fluorophores** – Using PCR protocol and its product, various sequence elements could be added to the 5' end of the primers. Thereby, homonucleotide stretches like poly-dT or poly-dA could be used for purification of the PCR product and RACE-like applications. The sequences of these primer pairs could also be labeled with various haptens such as biotin and digoxigenin as well as a wide variety of fluorophores like fluorescein. These primers labeling facilitates convenient immobilization of the PCR product on to the solid support through the interaction between PCR primer labeled with biotin and streptavidin bound paramagnetic beads and enables amplicon visualization. On the other hand, by attaching a specific monoclonal antibody to the fluorophores could help in the direct detection of the amplified PCR products.
  - (e) **GC clamp** – The 5' end of a primer could be increased by the addition of 20 or more GC bases. The addition of these GC sequence will alter the melting behavior and electrophoretic mobility of the final amplified PCR product. This primer is used for denaturing gradient gel electrophoresis.
2. **Degenerate modification primers** – Degenerate modification primers are designed to introduce target mutations into a specific piece of amplified DNA but are not fully complementary to their intended target sequence. For these purposes, they either do not contain one of the nucleotides of the target sequence or they may differ slightly in their primary sequence. However, these primers may result in incomplete hybridization at the target site which may create a hybrid structure involving bulging or looped-out nucleotides. These bulges or loops destabilize the hybrid structure which requires lowered PCR primer annealing temperatures, especially during the first few PCR cycles. Even more than one mutation located in the 5' half of a 20 nucleotide long primer could be amplified using degenerate PCR primers. However, if mutations are located at or near the 3' end of the primer, PCR amplification may be disrupted because 3' end binding of a PCR primer to its target is crucial in facilitating DNA polymerase mediated amplification. Therefore, degenerate sites should be located nearer to the 5' end of the PCR primer. To



amplify a target with high frequency of mutation, nucleotide inosine (which universally binds to G, C, A, and T nucleotides) could be incorporated into the primer design. Degenerate primers could be used for various PCR protocols, including

- (a) **Site directed mutagenesis** – Mutations present at 5' half of the primer will be found in the final amplified PCR product. Further, post-PCR manipulations, such as cloning/plasmid mediated transformation or transformation using the PCR product itself, allow the introduction and study of this mutated DNA in vivo.
- (b) **Degenerate oligonucleotide primer (DOP) PCR** – DOP PCR can be used to increase the amount of target DNA in a nonspecific manner. For this purpose, a large random mixture of primers is used in a PCR with as a net result the amplification of random genomic sequences. This approach could be useful for the general amplification of bacterial genomic DNA, extremely small amounts of DNA, and DNA from archival anthropological samples. DOP PCR can be combined with downstream methods also such as single nucleotide polymorphism (SNP) detection.
- (c) **Translating amino acid sequences into genomic sequences** – Degenerate primers could also be used to identify the gene sequence from which the original protein was translated and transcribed. These degenerate primers could be designed by using the amino- and carboxyl-terminal protein sequences and its reverse translation when the part of a protein sequence is known (e.g., after sequencing of a protein purified by classical chromatographic methods). Further, sequencing of the PCR products amplified using these pairs of primer will help to know the genomic sequence of the translated proteins.
- (d) **Universal primers** – Universal primers are also known as broad-range or consensus primers. These primers amplify similar target sequences in a variety of different subspecies of organisms. To design these

primers, a limited degree of degeneracy needs to be introduced into the PCR primers in order to account for all of the mutations found in the intended target sequence.

- (e) **Competitor primers** – These primers directly compete with one or more of the primers that have been designed to amplify the specific target DNA when added to the PCR mix. These primers contain dideoxynucleotide analogue at the 3' end and share part of the sequence of the amplifying primer pair. The addition of this dideoxynucleotide analogue effectively inhibits DNA polymerase-mediated replication of the complementary DNA strand to which the competing primer has annealed, and thereby could be useful in preventing the amplification of nonspecific products when PCR amplification is performed using extremely low amounts of target DNA. Competitor primers may also be used during the reverse transcription of mRNA to cDNA for highly specific quantitative RT-PCR protocols.
3. **Miscellaneous primers** – Miscellaneous primers could be used for various PCR protocols, including
- (a) **Repeat sequence primers** – The genomes of organisms consist of a higher percentage of DNA repeat sequence regions. These can be categorized into homopolymeric/heteropolymeric direct repeats, homopolymeric/heteropolymeric inverted repeats, composite heterogeneous repeats, or degenerate repeats and may be scattered throughout the entire genome of an organism. These DNA repetitive sequence regions may be targeted using single repeat sequence primers or multiple repeat sequence primer pairs. As sequence repeats alter with regard to genomic location and number between individual species and isolates, the number of successfully amplified PCR product fragments will differ. Further, this difference in amplified fragments will result in the production of specific DNA fingerprints for each species.

- (b) **Concatemeric primers** – These primers are used to generate a single large PCR amplification product by coupling overlapping PCR products altogether. For this purpose, the PCR protocol is designed to generate overlapping amplimers and the individual strands of these amplimers can partially hybridize. When these amplimers are melted into single strands and then reannealed, some of the amplimers hybridize to each other and act as primers for DNA polymerase. This will lead to the generation of a new and longer DNA product. This concatemer PCR approach has been very important in amplifying significantly large-sized fragments of DNA from and samples that have been subjected to violent extraction protocols resulting in highly sheared and fragmented DNA.
- (c) **Multiplex PCR primers** – Multiplex PCR protocols involve the addition of up to ten different PCR primer pairs within the same PCR reaction mix but they do not overlap like concatemer primers. In order to facilitate this, multiplex PCR normally contains primers which are somewhat extended (28 nucleotides instead of the more customary 18–22 nucleotides) to enhance primer specificity and help prevent unwanted primer/primer annealing interactions.
- (d) **Megaprimers** – Megaprimers consist of primers of around 450–800 bp long which could be used in mutagenesis protocols. After initial hybridization at 37 °C, a limited number of PCR cycles ( $n = 7$ ) are performed and the megaprimers are extended from the 3' end outwards. After limited PCR cycling, a normal PCR protocol is performed using this amplified product from the megaprimer PCR and another pair of specifically designed normal length PCR primers for selective amplification. These normal PCR primers could also be associated with additional site-directed mutations.
- (e) **Molecular beacons** – Molecular beacons are a primer or probe that contains a self-

complementary sequence and forms a hairpin-like secondary structure. This hairpin structure contains a fluorescent reporter molecule and a quencher molecule closely together in the region of folding. If the reporter and quencher molecules are in close proximity, reporter molecule does not give the fluorescence. However, once the molecular beacon primer is incorporated into amplified DNA product during the first PCR cycle, the reporter group and its quencher become separated and reporter molecule gives the fluorescence upon excitation and is recorded with the progress of PCR.

## Cross-References

- ▶ [DNA](#)
- ▶ [Exon](#)
- ▶ [Genes](#)
- ▶ [Microarray](#)
- ▶ [RNA](#)

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## Priming

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### Definition

The presentation of an idea or information that can alter subsequent behavior.

### Introduction

Priming is the presentation of an idea or information that can alter subsequent behavior. It may be presented in the form of a word, image, sound, or a more complex task. For example, presenting a word very briefly may make people faster at responding to that word or a related one in a subsequent task. Priming is an example of implicit memory and does not involve conscious recollection of any previous experience (Tulving and Schacter 1990). Its effects often occur unconsciously, without the observer's knowledge. Priming effects can be short-lived or long-lived (up to 48 weeks; Cave 1997) depending on the nature of the stimuli and tasks used (Bentin and Moscovitch 1988). Priming typically functions both within and across sensory modalities, with the exception of perceptual priming which depends on modality-specific features.

### Types of Priming

Priming can be broken down into many categories depending on the perceptibility of the prime, the nature of the prime and target, the task instructions, and the effect it has on the target stimulus. For instance, priming can impact perception, word choice, speech structure, or preferences, and people may be aware or unaware of the prime they are perceiving. Different types of priming also recruit different neural regions based on the demands of the task.

### Positive and Negative Priming

Primes can be separated into positive and negative primes. Positive primes are those that help a participant's task performance by speeding reaction times and improving accuracy. They do so by priming a word or idea that is the same or related to the target in some way. Negative primes, on the other hand, hinder performance by slowing reaction times and lowering accuracy. Negative priming occurs when the prime is ignored rather than simply perceived.

### Supraliminal and Subliminal Priming

A prime may be presented either supraliminally or subliminally. Supraliminal presentation means the prime is presented at a speed and contrast that can be consciously perceived by the observer, even if they do not realize the impact it produces on their subsequent behavior. A subliminal prime, on the other hand, is one that is presented such that it cannot be perceived by the observer. This may be done using very quick presentation times (less than 500 ms and often only tens of milliseconds) and masking. Masking is the use of symbols immediately after the prime and in the same location, which make it more difficult to perceive by eliminating any afterimage. A mask can also be included immediately before the prime word is presented (e.g., Dehaene et al. 1998).

### Perceptual and Conceptual Priming

Perceptual priming is modality-specific and dependent on the physical features of the prime and target stimuli, while conceptual priming is dependent on the meanings and semantic features of these stimuli (Roediger III and McDermott 1993). Perceptual priming can be demonstrated by the ability to identify the target word more quickly, to perceive words that have been degraded, or to perceive perceptually similar words (e.g., goat and boat). Conceptual priming is demonstrated through tasks that require identifying semantic features. These types of priming can be directly compared by changing the task instructions. For example, participants may be asked to indicate whether a string of characters is written in uppercase or lowercase letters, which would promote perceptual priming, or whether the

word is an object that moves, which would promote conceptual priming. Semantic priming involves priming stimuli with related meanings (e.g., the word “dog” priming the word “wolf”) and may be produced by activation spreading through semantic networks (Collins and Loftus 1975) or through changes in attention (Posner and Snyder 1975). Associative priming involves stimuli that are commonly present in the same contexts (e.g., the word “cat” priming the word “mouse”).

### Structural Priming

Studies have also demonstrated priming of syntactic structure. People read a written clause more quickly if it has a similar syntactic structure to a previously read clause (Elgendi et al. 2018). They are also more likely to use the primed structure in subsequent speech, even in a different language (Loebell and Bock 2003).

### Affective Priming

In addition to behavior on perceptual or language tasks, priming has been shown to affect people’s attitudes toward subsequent objects or stimuli. For example, Murphy and Zajonc (1993) demonstrated that emotional expressions presented through subliminal priming were able to produce more positive or negative judgments toward neutral Chinese ideographs. Similarly, Greenwald et al. (1996) biased participants’ judgments regarding target words based on the positive or negative valence of the prime word.

### Priming Cultures and Social Categories

Not only can priming affect how people perceive objects and stimuli; it can also influence how they perceive those around them and even themselves. For example, Herr (1986) demonstrated that participants described ambiguous target individuals differently based on primed social categories. Priming is thought to play an important role in stereotyping, because trait descriptions of individuals or groups will prime those ideas as interpretations of behavior later on. Furthermore, there is evidence that activation of a specific cultural mindset through priming affects the way individuals behave. For example, some cultures are

perceived as more individualistic, meaning people are perceived as independent and autonomous and the needs and goals of the individual are emphasized more than those of the group. Other cultures are perceived as more collectivistic, meaning they value the needs of the group or community over those of each individual. Many people identify with more than one culture and therefore acquire both individualistic and collectivistic views, which may each be activated depending on the situation. Priming a certain mindset may change the way an individual thinks and behaves toward others, as well as their neural activity (e.g., Knyazev et al. 2018). This demonstrates that cultural priming can lead individuals to perceive themselves and their goals differently and therefore select different behaviors.

### Common Priming Tasks

Some commonly used priming tasks include repetition priming, word-stem completion, and lexical decision tasks. Repetition priming is a common form of priming that simply involves changing a participant’s ability to identify a word or object by showing it beforehand. Repetition priming may be done either supraliminally or subliminally and within or across many sensory modalities. Identification of target words is faster (Dehaene et al. 2001) and more accurate (Bar and Biederman 1998) when they were previously shown as primes compared to when they are first shown. This has also been demonstrated using masked subliminal priming (Dehaene et al. 1998). Word-stem completion involves filling in the remainder of a word based on an initial morpheme that is provided. If participants are provided with a word bank before the task, they are more likely to use these words, compared to if they did not see any word options previously. The lexical decision task is a semantic priming task that involves determining as quickly as possible whether a string of letters is a word or not. Participants are consistently faster at doing so if the trial is preceded by a related prime word. For example, the prime word “doctor” would produce faster responses indicating that the target word “nurse”

is a word, compared to if “nurse” was shown with no prime or an irrelevant prime word.

## Neural Responses Associated with Priming

Many studies have attempted to delineate the neural responses associated with priming effects. A general conclusion is that repeated presentation of stimuli through priming experiments produces a reduction in neural activation (e.g., Schacter and Buckner 1998), which is interpreted as more efficient stimulus processing. The regions exhibiting this reduction vary depending on the type of priming used. A suppression of occipitotemporal areas has occurred in response to priming in word completion tasks (Henson 2003). This has been shown in both visual and auditory modalities but only in unimodal paradigms. A reduction is not typically shown in the early sensory regions or motor areas, demonstrating that not all components of the stimulus processing are altered; however there is some evidence of changes in motor areas in response to masked subliminal priming (Dehaene et al. 1998). Repetition suppression in the left angular gyrus may indicate lexical priming, while in the left inferior frontal regions it likely indicates repeated conceptual processing of words (Poldrack et al. 1998) or reduced competition between possible responses (Thompson-Schill et al. 1999). Several studies have shown an increase in right frontal lobe activation on primed trials, which is thought to indicate an accidental encoding of the stimuli into explicit memory (Badgaiyan et al. 2001). The effect of masked subliminal priming on neural activity is not completely evident, and some researchers have even found enhancement effects rather than suppression (e.g., Schnyer et al. 2002).

## Priming in People with Brain Damage, Alzheimer’s Disease, and Huntington’s Disease

Priming effects occur even without explicit recall of the prime. This can be demonstrated by the presence of priming effects even in people with brain damage to temporal regions that impairs explicit memory (e.g., Warrington and Weiskrantz

1974). However, most of these studies have used perceptual priming techniques, and the results are less clear for conceptual priming. Alzheimer’s patients are more impaired in conceptual priming but show fairly intact perceptual priming effects. Finally, intact perceptual priming has been demonstrated in people with Huntington’s disease (Salmon and Butters 1995), demonstrating that motor learning and priming likely depend on different brain systems.

## Applications of Priming

Priming has implications for everyday human behavior, such as in the cases of advertising, human-computer interactions, and political campaigns (Elgendi et al. 2018). For example, children automatically consumed more food when they were shown food advertising during a television show (Harris et al. 2009), compared to advertising of other items. To facilitate human-computer interactions, priming can be used to enhance certain ideas for the person to increase comprehension. In politics, more positive ideas can be primed in voters through a focus of the media on certain issues. Even in the absence of intentional priming, individuals are constantly perceiving stimuli around them, each of which has an impact on how they behave. However, by being aware of the impact of their surroundings, people can try to select environments that prime positive goal-directed behaviors while avoiding those that prime negative behaviors.

## Doubts Regarding Priming Effects

Despite its long-standing presence in the field of psychology, priming has been criticized as a topic that is especially susceptible to the expectations of experimenters, as well as publication bias. These factors may produce bias in the priming literature that result in an inflated certainty in the robustness of these effects. This doubt has caused many people to worry about the validity of priming studies. One high-profile example of this is a pioneering experiment by Bargh et al. (1996).



The study concluded that university students exposed to words describing elderly people (e.g., wrinkles, Florida) walked more slowly down the hallway following the experiment. A replication attempt used infrared sensors instead of experimenters with stopwatches to time the walking speed and found no difference in the walking speed (Doyen et al. 2012). This study and others have led priming research to become the “poster child for doubts about the integrity of psychological research,” according to psychologist and Nobel Laureate Daniel Kahneman. An increased effort to replicate findings both within and across psychology labs is necessary to confirm these findings and determine confounding variables in priming research.

## Conclusion

Priming is a commonly used method in psychological research for studying implicit memory. Priming may be done through conscious or unconscious means and can affect perception, attitudes, and behaviors. Priming effects have been shown within several different sensory modalities as well as in cross-modal paradigms; however, further replication is needed to confirm the validity of many priming experiments. Priming has real-world effects including determining susceptibility to advertising, improving human-computer interaction, and understanding the influence of ideas used in political campaigns. The objects, words, and concepts that we deal with each day have an influence on our subsequent behavior, and understanding the effects of priming is an important step toward understanding that influence.

## Cross-References

- Cognition
- Declarative Memory
- Interstimulus Interval (ISI)
- Occipital Lobe
- Reaction Time
- Reference Memory

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## Primitive Reflex

- [Rooting Reflex](#)
- [Step Reflex](#)

## Principle of Simplicity

- [Ockham's Razor](#)

## Prisoner's Dilemma

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## Overview

Game theory is a set of ideas developed with the goal of applying analytical rigor to understand decision-making. It includes consideration of key aspects that affect a decision, such as the nature of possible outcomes and the associated incentives (e.g., various degrees of payoff or punishment associated with outcome A versus outcome B). One of the most interesting aspects of game theory is that multiple participants are involved. Each participant can only make their individual choice, but the nature of the global outcome depends on both of their choices. In that way, each participant plays a role in shaping the global outcome, but neither has exclusive control over what happens. Each participant is assumed to be rational and acting in their own best interest, yet an outcome can sometimes emerge in which neither player achieves their optimal outcome. Thus, each participant chooses what is best for them, but that may not always yield the outcome that is best for the group. One of the most well-known ways in which this concept has been framed is the Prisoner's Dilemma in which two prisoners accused of the same crime are interrogated separately and asked whether or not they will confess to the crime. There are costs and benefits associated with their possible choices, and experts have used that scenario as a way to investigate the logical basis of decision-making. Specifically, how do individuals make decisions when risk and reward are involved, and what happens when the outcome that is best for the group is not what is best for each individual? In the following sections, we describe the history and concepts of the Prisoner's Dilemma, and we

discuss ways in which ideas emerging from that analysis have been adopted by organizations such as companies and nations seeking to benefit in their interactions with partners and competitors.

## Historical Background

The foundations of game theory include an assumption of rationality (Davis 1983; Leyton-Brown and Shoham 2008; Myerson 1991). Players in games are assumed to act rationally, meaning that they are expected to choose their actions based on logic and reasoning (Rapoport 1992; Skyrms 1990). This ideal has had to be adapted in the course of research into how mathematical models may account for human behavior, as the behavior of humans and other organisms can be very difficult to characterize and often deviates from a single ideal outcome (Glimcher et al. 2009; Thaler and Sunstein 2008). This is because different choices can each be considered rational despite the fact that they result in very different outcomes. For example, consider a case in which each of the members of a group is dependent on a shared resource in order to survive. If we consider the well-being of the group, we would expect that each member would act in such a way that they would not only benefit from the resource but also preserve it for continued shared use in the future. However, if we consider the well-being of each individual separately, we would expect each member to want to take more for themselves even though that would come at the expense of the group. In each of these possibilities, the members of the group are making rational choices, but the difference lies in whether they are focused on the well-being of the group or themselves as individuals. In this scenario, each individual is incentivized to make choices in a way that is less than optimal for the group. Each individual seeks to protect themselves at the expense of the others, and as a result both end up in a state that is worse than if they had worked together to coordinate their decision-making.

This paradox of decision-making is one of the most well-known ideas associated with game theory, and it lies at the heart of the Prisoner's

Dilemma. These differences between expected and observed behaviors have intrigued experts in economics, psychology, and policymaking, and those researchers have sought to formalize their thinking about that process. In the first consideration of this process, researchers Merrill Flood and Melvin Dresher at the RAND Corporation envisioned a "game" in which two individuals each contributed to choosing an outcome that would affect them both (Flood 1958). Each player was faced with deciding what decision-making process would be best for them individually when the consequences were predictable but the behavior of the other player was not. This challenge of how to make the best decision in a mutually dependent outcome is the essence of what eventually came to be known as the Prisoner's Dilemma, but it awaited contributions from others before it was framed in the way that we consider it today.

## Developing a Formalized Understanding of the Prisoner's Dilemma

When Flood and Dresher first proposed their hypothetical scenario, they and others quickly realized that it is an excellent example of challenges faced by participants in many forms of interaction, from board games to economics to international policymaking. A fundamental advance in the thinking about these scenarios occurred when Princeton mathematician Albert Tucker proposed the context of two people who were each accused of the same crime (Tucker 1950) (Fig. 1). Each person was seeking to minimize their punishment and maximize their benefit, but cooperation was not possible because each was being interrogated separately. In that scenario, each prisoner was told that:

- (1) If one confesses and the other does not, the former will be given a reward of one unit (+1 in the value of the outcome) and the latter will be fined two units (−2 in the value of the outcome).
- (2) If both confess, each will receive a lesser fine (−1 in the value of the outcome for each).

|            |             | Prisoner B  |         |
|------------|-------------|-------------|---------|
|            |             | Not Confess | Confess |
| Prisoner A | Not Confess | 0, 0        | -2, +1  |
|            | Confess     | +1, -2      | -1, -1  |

**Prisoner's Dilemma, Fig. 1** The benefits (positive numbers), punishments (negative numbers), and possibility of going free (zero values) inherent in the decisions faced by each participant in the Prisoner's Dilemma

At the same time, each prisoner has good reason to believe that:

- (3) If neither confesses, both will go free (0 value of the outcome for each).

In subsequent considerations of this scenario, it was further stipulated that both prisoners fully understand the nature of their choices and the associated consequences, neither prisoner has an opportunity for retribution or reward outside of the game, and neither prisoner has any loyalty to the other (Poundstone 1992). In other words, each prisoner acts in their own self-interest and makes their decision independently of the other.

In this scenario, the overall most beneficial result would occur if both players choose to not confess, as both would go free and neither would be fined. Thus, choosing to not confess could yield freedom, but it also exposes each decision-maker to the greatest possible risk if the other prisoner confesses. Therein lies the dilemma – should the prisoner choose the option that could enable them to achieve the best global benefit or the option that could enable them to avoid the worst individual punishment? Should they act in the best interest of the group or of themselves? If the prisoners were able to coordinate their strategies and form a cooperative solution, the safest

and most beneficial option would be for them to each choose to not confess. However, in Tucker's scenario, the participants are not able to work together and form such a coalition. Therefore, each participant lacks the assurance associated with coordinated decision-making.

In the absence of coordinated assurance and collective action, each participant is incentivized to act in their own self-interest. In the case of the prisoners in this scenario, each is incentivized to confess, making confession the dominant strategy for both players. This dominance emerges because neither player is able to improve their individual payoff by altering their strategy (Rapoport 1992). For example, if Player A chooses to confess, Player B is better served to confess (−1 outcome) than to not confess (−2 outcome). Similarly, if Player A chooses to not confess, Player B is still better served to confess (+1 outcome) than to not confess (0 outcome). Regardless of what the other player does, confessing always results in the better payoff. An action profile such as this, where no single player can increase their payoff by deviating from their initial strategy while the other player remains unchanged, is known as Nash equilibrium (Nash 1950). Princeton mathematician John Nash recognized and described this pattern of making choices in the face of uncertainty, and the Nash equilibrium is considered the most rational outcome. In the scenario involving Players A and B, the Nash equilibrium is mutual confession (the bottom-right quadrant in Fig. 1). It results in a small fine, but it also enables them to ensure that they avoid the possibility of a much larger fine. Even though mutual cooperation (both choosing to not confess) would yield the best outcome for both, two players seeking to maximize their own payoff and minimize their own risk would be expected to choose the Nash equilibrium of mutual confession.

The rewards and punishments that drive the emergence of this behavior can be even more easily observed when the game is removed from the familiar context of prisoners and confessions to a more general context in which there are two players with the two options of “cooperate” or “defect” (Fig. 2). If Player A and Player B both

|          |           | Player B             |                          |
|----------|-----------|----------------------|--------------------------|
|          |           | Cooperate            | Defect                   |
| Player A | Cooperate | Reward<br>Reward     | Sucker<br>Temptation     |
|          | Defect    | Temptation<br>Sucker | Punishment<br>Punishment |

**Prisoner's Dilemma, Fig. 2** – The rewards and punishments associated with each player's decision in a generalized form of the Prisoner's Dilemma (adapted from Fig. 1 in Axelrod and Hamilton 1981)

cooperate, they will each receive the “reward” payoff (R). If they both defect, they will each receive the “punishment” payoff (P). If either player is the sole defector, they will receive the “temptation” payoff (T), while the other player who chose to cooperate when their opponent chose to defect will receive “sucker’s” payoff (S). The magnitudes of the rewards or punishments may vary in different scenarios, but a condition like the Prisoner's Dilemma emerges when participants are asked to each engage in an independent choice and the relationships among those outcomes satisfy the condition that  $T > R > P > S$  (Axelrod and Hamilton 1981; Poundstone 1992; Rapoport et al. 1965).

### Iterated Prisoner's Dilemma and the Emergence of Strategies

In the original vision of the Prisoner's Dilemma, the game was only played once (Poundstone 1992). In that context, each player must make their decision based only on the set of actions available to them and the payoffs or consequences associated with each action. Each player must seek the most beneficial outcome even in the face of a completely unknown choice to be made by the other player. This scenario has led to the

emergence of insights about how to make rational decisions in the face of uncertainty, but it fails to allow for the possibility that interactions and the associated choices may occur more than once. When the game is played more than once, players can learn from the previous actions of their opponent and modify their own strategy accordingly. Therefore, the factors influencing each player's decision are not only the payoffs for each action but also their experience and knowledge of their opponent's past behavior as well as their intuition about their opponent's future behavior. This scenario in which each player makes a choice but repeated interactions are possible is referred to as the iterated form of the Prisoner's Dilemma (Poundstone 1992). When the game is played more than once, risks and rewards must be weighed not only in the immediate next step but also in light of past experiences and possible future interactions.

The opportunity for each player to learn from experience and modify their behavior during repeated interactions gives rise to the possibility that each player may develop different types of strategy (Axelrod and Hamilton 1981). In the relatively simple game envisioned in the Prisoner's Dilemma (Fig. 2), both players have two possible actions: they can either cooperate or defect. Strategies can be broadly categorized as those that begin with cooperation (the so-called “nice” strategies) and those that begin with defection (“mean” strategies). When both players are nice, both get an immediate reward. If both players are mean, both players receive the punishment result. The incentive is greatest for a player to be mean when their opponent is nice (temptation payoff goes to the mean player, and the nice player receives the sucker's payoff). The names for each of these strategies reflect the outcome associated with the first choice that each player makes, but much more complex strategies can emerge when we consider how those outcomes may affect subsequent choices.

A player may change their responses based on the opponent's previous actions (a reactionary strategy). For example, a player may change away from cooperation only after their opponent



chooses to defect for the first time. If that player remains in defection, it can be called a “Friedman” or “grudger” strategy because the player’s behavior changed once in response to a mean action and remained fixed thereafter (Axelrod 1980a). Alternatively, a strategy may include an element of “forgiveness” in which behavior may continue to remain variable even after the opponent engages in a mean action. If short-term history dependence is incorporated into that strategy, then a “tit for tat” strategy can emerge in which a player changes their behavior to match that of the previous action made by the other player (Axelrod 1980a). In other forms of strategy, a player may change their response based on some inherent feature of that strategy in which changes are made preemptively in an attempt to gain advantage or to test the reaction of the opponent (a preemptive or testing strategy). For example, if a player detects that their opponent very regularly chooses to cooperate, then the best choice for that player would be to defect, as the player would receive the temptation payoff and the opponent would be stuck with the sucker’s payoff. These types of contingent or preemptive strategies seek to probe the patterns of responses expressed by their opponent and to use that information to exploit other simple strategies to gain advantage.

In seeking to understand which strategies may be most beneficial when games are played more than once, researchers created different kinds of strategies and tested their effectiveness when pitted against one another in simulated competitions. In 1979, a researcher named Robert Axelrod held a simulated tournament in which 14 different types of iterated Prisoner’s Dilemma strategies, as well as 1 random strategy, competed in an attempt to determine which types of strategies were most broadly beneficial (Axelrod 1980a, 1984). In this competition, the iterated version of the Prisoner’s Dilemma still included two possible actions for each player. Those actions were still called “cooperate” and “defect,” but the associated outcomes were considered in the context of earning points rather than avoiding a prison sentence (Axelrod 1980a). If both players defected, then they each gained a small amount of points. On the other hand, if both

players cooperated, both gained a significantly greater amount of points. If one player defected when the opponent cooperated, then the defector received the maximum amount of points, and the player that cooperated received zero points. The value of any strategy relative to others is ultimately dependent on the magnitudes of those point values in the payoff matrix, but this arrangement of  $\text{temptation} > \text{reward} > \text{punishment} > \text{sucker's payoff}$  is the same as described for the generalized form of the Prisoner’s Dilemma.

In Axelrod’s tournament, strategies that began with cooperation (“nice” strategies) tended to fare better than the “mean” strategies that began with defection (Axelrod 1980a). The winning strategy in that competition was the “tit for tat” strategy, created and entered by Anatol Rapoport, in which the player cooperates in the first round and then in each subsequent round simply mimics what the opponent selected in each previous round (Kopelman 2020). In this way, the opponent receives the treatment that they gave in the immediately preceding round, hence the name tit for tat. This strategy is one in which the player retaliates when provoked but otherwise cooperates. The success of this strategy against a wide variety of opponents suggests that there is an advantage in not only behavioral flexibility but also adaptation in the patterning of those behaviors. A similar tournament followed up on that first tournament, this time with an even greater variety of 62 different strategies and 1 random strategy pitted against one another (Axelrod 1980b). Despite the greater variety of opponents, tit for tat again emerged as a broadly beneficial basic strategy. Although tit for tat is not always the overall winner in these types of tournaments, it tends to fare very well across repeated interactions with many different types of strategies, further confirming the value of behavioral flexibility and history-dependent adaptation. A topic of ongoing research is the degree to which different depths of history dependence may be beneficial. For example, what if a player alters their strategy based on not only the previous action of the opponent but also the nature of the collective outcome that it produced (the so-called “win-stay, lose-switch” strategy) (Imhof et al.

2007; Nowak and Sigmund 1993)? What if a player alters their behavior based on not only the most recent action by an opponent but also in response to other actions from the more distant past? In that light, researchers are exploring the degree to which it may be beneficial for strategic algorithms to be “forgetful,” such that only the most recent events matter, or to have some sort of “memory”, in which actions from the more distant past are influential in driving current actions.

### **Relevance of the Insights from the Prisoner's Dilemma for Real-World Applications**

The scenarios and outcomes illustrated by the many forms of the Prisoner's Dilemma reveal the intricacies of decision-making that can arise in those fascinating contexts, but they leave open the question of how insights from the Prisoner's Dilemma may be applicable to decision-making in more practical terms. There are many types of interactions in nature and human society in which choices and consequences can be described using a payoff matrix very similar to those found in the Prisoner's Dilemma (Axelrod and Hamilton 1981). In that way, the choices that participants must make in those contexts can be modeled as a form of the Prisoner's Dilemma, and insights from those scenarios can be applied to develop a better understanding of ourselves and processes in the world around us.

The iterated Prisoner's Dilemma has been used to model interactions in which trust between two participants is essential for their collective success. In the variation known as Rousseau's Stag Hunt, the familiar context of the Prisoner's Dilemma is modified such that the participants are two hunters (Skyrms 2004). Each hunter can pursue either stag or rabbit. The stag would provide a large meal that could feed all of the members of their group, but it is very challenging to hunt and requires the cooperation of both hunters in order to collect it. In contrast, a rabbit is a much smaller meal, sufficient to feed only the hunter, and is much easier to catch, requiring only one

person to collect it. In this scenario, the greater reward of catching a stag requires the cooperative efforts of both hunters, and their success is uncertain. A hunter who chooses to pursue stag runs the risk of their partner choosing to not cooperate, and such a result would leave them with no food. A hunter who chooses to pursue rabbit has a much greater chance of meeting their own needs, but that reduction of risk means that they necessarily forgo the chance to collect the greater reward. The dilemma in this scenario emerges when rational players are drawn toward one option by the possibility of mutual benefit but are pulled towards the other option by the prospect of avoiding individual risk (Skyrms 2004). The most beneficial choice for the group would be to hunt stag, but that cooperative benefit would require cooperative action, and that would require each hunter to trust their partner. In that way, Rousseau's Stag Hunt models situations in which cooperation is difficult but still possible to achieve. Cooperation emerges through communication and experience as a form of social contract that is contingent on each person's belief about what the other person will do. With the accumulation of experience and the development of trust, it becomes more likely that each player can predict the behavior of the other, and they become more comfortable choosing the relatively risky option of cooperation. Thus, insights from the Prisoner's Dilemma reveal how accumulation of knowledge can provide benefits through not only prevailing in adversarial situations but also gradually learning how to work together in cooperative situations (Axelrod and Hamilton 1981; Axelrod 1984; Axelrod and Dion 1988).

The Prisoner's Dilemma can also be used to model the behavior of nations engaged in competition for superiority and security (Jervis 1978). For example, a nation that arms itself is prepared to prevail over an opponent or deter that opponent from attacking, but building those armaments comes at the cost of resources and time. Choosing to disarm would save costs, but that would also make that nation vulnerable to attack. Mutual development of arms by two nations could provide an effective deterrent of conflict, but both

groups would encounter the costs of developing those weapons. Mutual disarmament would reduce the threat that each nation poses to the other, and it would also provide the additional benefit of reducing costs. As in the scenario of the two hunters that were dependent on one another for their well-being, trust is the central factor in this scenario. The least costly outcome would be mutual disarmament, but that would require trust of not only the other nation but also of other nations that may also be able to affect their well-being. Just as it was for the hunters, trust is a rare and precious commodity in any interaction between participants. Lack of trust makes self-interested behavior the only rational choice, and those types of interactions are evident in the relationships between many nations and other groups.

It is tempting to apply the lessons of the Prisoner's Dilemma across a wide range of practical scenarios to devise ways to incentivize specific behaviors or develop ways for participants to resolve conflict and perhaps even cooperate (Rapoport 1962). However, a fundamental challenge to such attempts often lies in the nature of the payoff matrix. In the Prisoner's Dilemma, the rewards or punishments associated with each choice are clear – if the prisoner chooses to cooperate, then there are only two actions that can possibly be performed by the other participant, and only one of two clearly defined outcomes can emerge. In the context of many attempts to apply the Prisoner's Dilemma to practical scenarios, those potential outcomes are not fully known and thus not possible to clearly define. In this way, not all scenarios are amenable to analysis through direct application of the Prisoner's Dilemma, especially those in which there is significant uncertainty regarding possible outcomes.

As evident in the scenario of the Stag Hunt, making rational choices based on the greater good requires trust between participants. This challenge is especially evident in the context of global climate change. As rising levels of atmospheric carbon dioxide appear to be driving correlated changes in climate, those changes are causing instability and undesired events that will continue

if they are not countered by initiatives meant to reduce levels of CO<sub>2</sub> in the atmosphere (Raper and Braithwaite 2006; Solomon et al. 2009). All nations would benefit from reduced levels of CO<sub>2</sub>, but the changes necessary to cause those reductions may be very challenging and costly (Reid et al. 2010). Therefore, each nation is simultaneously incentivized to maintain current behavior or otherwise avoid the expense associated with changing emission behaviors. If trust could be forged between two nations, then they could cooperate in their approach to this challenge, but without trust among all participants, those two cooperators would still be subject to defection and the sucker's payoff if other nations did not join them in their efforts. This challenge further illustrates how valuable trust between participants can be as a means of enabling coordinated action and rational choices that lead to the most broadly beneficial outcomes.

In many real-world scenarios such as each nation's decision of how to take action in response to climate change, there are many more than just two players. The challenge of finding ways to act in the best interest of the group becomes even greater as more players become involved. These types of scenarios in which many individuals share a resource and act independently in their own self-interest are sometimes called the Tragedy of the Commons (Hardin 1968). In those cases, individual users of a resource are incentivized to act in their own interest, but this comes at the expense of the common good. Through their actions, each user experiences short-term benefits, but the resource is adversely affected through their collective actions. Cases such as this in which there are many individual participants all incentivized to act in their own self-interest are especially difficult to analyze and even more difficult to devise solutions that lead to sustainable group well-being. Despite the scale of these daunting challenges, researchers continue to use the ideas inherent in the Prisoner's Dilemma as a context in which to seek generalizable insights into how the members of a population may achieve cooperation and thereby take collective action to provide collective benefits.

## Cross-Reference

- [Coordination Games](#)
- [Decision-Making](#)
- [Dictator Game](#)
- [Game Theory](#)
- [Goal-Directed Behavior](#)
- [Nash Equilibrium](#)
- [Problem-Solving](#)
- [Punishment](#)
- [Rationality](#)
- [Ultimatum Game](#)

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## PRL

- [Prolactin](#)

## Proactive Interference

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### Synonyms

Competing cues; Interference; Memory; Paired-associated learning

### Definition

Proactive interference is the appearing of a problem in a new learning, induced by the recall of previous information. An example would be when two word lists are learned sequentially: first list A and list B after. Proactive interference occurs when it is required to recall list B, but words of the A list are recalled instead.

### Introduction

Proactive interference is a memory phenomenon present in daily life constantly (Baddeley et al. 2009). An example can be seen when the password of your e-mail account changes, but you keep typing the old one instead.

One of the first authors to mention proactive interference was Underwood (1957). In his studies, he asked participants to learn nonsense syllables, observing high levels of forgetting after 24 h. Underwood thought that it could be due to the hard demand of study tasks present in students that used to be the experimental subjects of his studies. The students used to participate in a lot of experiments in the university background, and so much memory stimuli could be interfering in the forgetting general rate.

To sort out this question, Underwood decided to replicate his study but using two different groups: an experimental group with subjects that have participated in several experiments before and a second control group that participated in

the experiment for the first time. Twenty-four hours after the learning of syllables, this author observed that the experimental group forgot a 75% of total stimuli presented, in contrast to control group, which forgot only 25%. Underwood concluded that previous information clearly interfered in new learnings.

At this respect, the concept of interference has been crucial in the mixed field between learning and memory. Interference paradigms in associative learning have been relevant in the way in which behavior scientists try to understand complex situations in the learning of stimuli association (Bouton 1993).

### Experimental Paradigm

In an associated-paired memory paradigm (Fig. 1), the proper design to study proactive interference consists in presenting word pairs in which the first element of the pair (called stimulus) and the second (response) are presented together (e.g., pencil-ring; being pencil the stimulus and ring the response). One group or experimental group is exposed to a set of paired words. After that, experimental subjects are exposed to a second list of word pairs, in which stimuli are the same of the first list, but the associated responses are different (e.g., pencil-window). Control group did not receive anything during the first phase but received the second list in order to compare the level of interference in experimental responses. In the test, the stimuli are presented in order to recover the associate response of the second list. The difference in recall between both groups will set the level of proactive interference (Fig. 2).



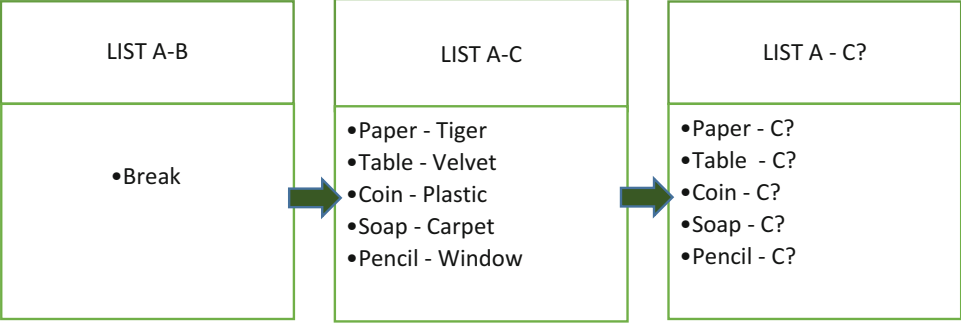
**Proactive Interference, Fig. 1** Proactive interference diagram



EXPERIMENTAL GROUP



CONTROL GROUP



**Proactive Interference, Fig. 2** Example of stimuli for a pair-associated experiment to study proactive interference

**Variables that Modulate the Interference**

- ▶ [Paired-Associated Learning](#)
- ▶ [Retroactive Interference](#)

As it happens in other types of interference phenomena in memory, such as retrospective interference, a few variables are thought to be critical for the appearance of prospective interference. Similarity has been shown as a critical variable to modulate proactive errors. Specifically, the more similarity, the more interference will be observed. Another relevant factor to modify proactive interference is the delay between lists. Delays between stimuli, or between phases, in experimental sets in memory have been very useful to unravel memory processes.

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**Cross-References**

- ▶ [Interference](#)
- ▶ [Memory](#)

**Probability Distributions**

- ▶ [Stochastic Distributions](#)

## Problem-Solving

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### Definition

A broad set of mental processes aimed at overcoming an obstacle to achieve a goal in a context-specific situation.

### Introduction

Animals regularly encounter situations which require problem-solving skills, where trial-and-error learning and spontaneous “insightful” problem-solving lie at the opposite ends of the problem-solving spectrum. The trial-and-error is considered one of the least sophisticated forms of problem-solving and involves learning from the consequences of one’s behavior in a repeated process of trying various attempts until the desired goal is achieved. In contrast, the ability to solve problems from the first presentations is considered one of the most complex mental processes in animals. This so-called “insightful” problem-solving presumes considering possible outcomes before determining the correct solution involves the ability to mentally represent aspects of the environment and to manipulate these representations (Piaget 1954).

The distinction between the two forms has a long history of a comparative study of problem-solving. In his famous experiment, Thorndike (1898) placed a cat in a series of puzzle boxes which were enclosed but contained a release mechanism that, when operated by the cat, would allow the animal to escape and receive the

reward positioned just outside the puzzle box. He recorded how long each animal took to figure out how to escape from the box. Even though the first successful escape occurred simply by accident, the cats became likely to repeat the successful action because they had received an award immediately after performing this action. Thorndike noted that with each trial, the cats became much faster at opening the door suggesting that animals were solving the problem via trial-and-error learning rather than insight.

Since then, the interest in the roles of trial-and-error learning and insight in animal problem-solving have not decreased, and the question of what kind of information animals use when solving problems remains a controversial topic. A variety of tasks has been developed to assess specific types of problem-solving; most of them are based on a tool-use capacity.

### Tool-Use-Related Problem-Solving

Human and nonhuman animals often use tools to solve problems to obtain a visible but inaccessible reward (Köhler 1927). In fact, tool-use-related problem-solving has been found in all sorts of animals (Beck 1980), from a crab attaching anemones to their claws to protect themselves from predators and sea otters using stones as anvils to break mollusc shells to New Caledonian crows and chimpanzees using sticks to extract insects from tree holes or crevices. However, the underlying cognitive processes of tool-related problem-solving may differ.

Early experiments on tool-use-related problem-solving came from the primatologists. Visalberghi and Trinca (1989) designed a task consisting of a long horizontal transparent tube with a peanut in the middle and a stick that fits into the tube. When provided with the stick, the monkeys used them to obtain the food by inserting the stick into one end of the tube and pushing the peanut out. However, the monkeys solved the problem after initially trying to stick their fingers into the tube, detach the tube or break it open, and with increasing speed and efficiency, suggesting that poking

the stick into the tube was acquired through trial and error.

Thus, to test whether the animals understand the actual function of the tool, the task has been modified. In what became a benchmark paradigm to study tool-use-related problem-solving, a trap was introduced on one side of the peanut (Visalberghi and Limongelli 1994) such that if the stick were inserted into the wrong side of the tube, it would push the peanut into this trap making it inaccessible. Most monkeys failed to solve this task and lost the reward in more than 50% of their attempts, using a distance-based associative role and inserting the stick into the side of the tube farthest from the peanut. Since this pioneer work, a variety of species have been tested on the trap-tube task and variants of it, including great apes (Povinelli 2000), other primates (Santos et al. 2006), human children (Horner and Whiten 2007) and adults (Silva et al. 2005), as well as birds (Tebbich and Bshary 2004). Yet there was no conclusive evidence that nonhuman animals can use causal knowledge rather than associative learning to solve complex physical problems.

A more precise method identifying cognitive strategies animals use for problem-solving is presenting a subject with a transfer tasks after it successfully learnt an initial discrimination task. In the transfer tasks, arbitrary stimuli are changed, while the causal structure of the problem remains constant. Successful performance across transfer tasks eliminates the use of associative learning via trial and error and suggests the use of “insight.” In a study using novel trap-tube transfer tasks at least one rook, *Corvus frugilegus*, might have solved the trap-tube problem using causally relevant cues such as “surface continuity”, which means that objects can be moved on continuous surfaces and “object solidity”, which means that objects cannot be moved through each other (Seed et al. 2006).

## Proto-Tool Tasks

Although tool-related problems such as trap-tube task are widely used and accepted paradigms

used to investigate problem-solving strategies in animals, they are less suitable for large-scale comparative studies since the manipulative capacities of the most non-primate species are limited (Santos et al. 2006; Tebbich et al. 2007).

Thus, “proto-tool” tasks, in which the tool is connected to the reward from the beginning, are commonly used for a broader comparative approach (Krasheninnikova et al. 2013). In such tasks, a subject faces a choice between two or more options, one of which is physically connected to an out-of-reach object of desire. One of the most common tasks of this type is the “string-pulling task,” initially applied by Köhler (1927), and the “support problem,” initially introduced by (Piaget 1954). In the string-pulling task, a string is attached to a reward. The reward itself is out of reach of the animal, but the near end of the string is accessible. In the “support problem,” a reward is out of subject’s reach but is placed on a cloth which the subject can pull toward it. Both tasks – the string pulling and the support problem – are based on the assumption that if the animal understands the functional property of the string or the cloth, it will use it as a means to an end, i.e., spontaneously pulls the food into reach on its first exposure to the task. In contrary, subjects who do not understand that pulling the string is the “means” for achieving the desired “ends” of bringing the food within reach will only be able to succeed through repeated exposure and resulting associative learning (Range et al. 2012).

So far, a great variety of animals ranging from primates over dogs, cats, and elephants to birds and even insects have been tested with the string-pulling task and/or support problem. Spontaneous “insightful” solutions were found just in few species, for example, in a number of nonhuman primates (Hauser et al. 1999), large-brained birds such as corvids and psittacids (e.g., Auersperg et al. 2009; Heinrich and Bugnyar 2005; Krasheninnikova and Schneider 2014), and elephants (Irie-Sugimoto et al. 2008). Various cognitive processes have been proposed for different other animals, for example, associative learning (e.g., pigeons, *Columba livia* (Schmidt and Cook 2006) and bumblebee, *Bombus*

*terrestris* (Alem et al. 2016)), relying on perceptual feedback (New Caledonian crows, *Corvus moneduloides* (Taylor et al. 2009)), or attending to perceptual contact rather than connectivity (great apes, Povinelli 2000). Dogs and domestic cats (*Felis catus*), were able to learn to obtain food that was out of reach by means of a string, but failed to understand means-end relationships when tested in various patterned-string tasks (Osthaus et al. 2005; Whitt et al. 2009).

## Cooperative Problem-Solving

Social factors have been suggested to play an important role in problem-solving tasks (Melis et al. 2006). When other conspecifics are present, animals may solve problems through cooperative behavior.

Traditionally, cooperative problem-solving has been assessed in mammals, especially primates. The benchmark test of cooperative problem-solving, the loose-string paradigm (Hirata and Fuwa 2007), requires two subjects pulling the two ends of a string simultaneously to move a platform with reward toward them. A dyad's performance, thus, depends on the subjects' ability to coordinate their pulling action. So far, only chimpanzees, *Pan troglodytes* (e.g., Melis et al. 2006); bonobos, *Pan paniscus* (Hare et al. 2007); orangutans, *Pongo pygmaeus* (Chalmeau et al. 1997); capuchin monkeys, *Cebus apella* (Mendres and De Waal 2000); cotton-top tamarins, *Sanguines oedipus* (Cronin et al. 2005); Asian elephants, *Elephas maximus* (Plotnik et al. 2011); bottlenose dolphins, *Tursiops truncatus* (Kuczaj et al. 2014); wolves, *Canis lupus* (Marshall-Pescini et al. 2017); and spotted hyenas, *Crocuta crocuta* (Drea and Carter 2009) have been reported not only to cooperate to solve a problem but also at least some sensitivity to the need of a cooperative partner to do so. More recently, also several bird species have been tested in the loose-string paradigm with mixed results. While rooks and African gray parrots have so far shown no sensitivity to any task contingencies, ravens and keas were reported to fail additional tests in some studies

(Massen et al. 2015) and to succeed in others (Heaney et al. 2017).

## Future Questions

Many animal species are problem-solvers, but the underlying cognitive processes of the problem-solving may differ. Great apes, corvids, parrots, and some carnivore species appear to excel and show the spontaneous problem-solving in different contexts. Previous findings reveal striking similarities in underlying mechanisms of human and nonhuman problem-solving. Yet understanding taxonomic differences and similarities in cognitive aspects of problem-solving continues to be a significant research challenge. Proto-tool-based counterparts of the tool-use-related task allow us to test a broader range of species with different levels of brain development and manipulative capacities and help to expand our understanding of the problem-solving relevant cognitive abilities across various animal species. Nevertheless, most experimental paradigms described above present animals with specific problems and investigate how the animals solve them in order to examine specific cognitive processes (Auersperg et al. 2012). The majority of these typically started off from a single experiment designed for testing a particular species and some subsequently applied to other species. Consequently, only little attention has been paid to species-specific morphological and perceptual features, in addition to psychological variables such as motivational, emotional, or attentional states, inhibitory control, or neophobia (Auersperg et al. 2012).

A new approach to test animal problem-solving comparatively is the multi-access box (Auersperg et al. 2011). It presents a subject with a novel problem that can be solved in different ways, i.e., it consists of a battery of different tasks that all lead to the same goal. This approach offers a unique possibility to examine how novel problems are perceived, explored, and approached across different species. The multi-access box approach is a helpful tool in establishing behavioral and psychological profiles

of the species to be compared. Future comparative research using this approach may help to identify problem-solving tasks that are equivalently applicable across a broader range of different species and allow a high degree of “comparability” of the data obtained from different taxa (Auersperg et al. 2012).

Along with other cognitive abilities, the problem-solving abilities are most likely determined by the level of taxa-specific brain development rather than the presence of species-specific adaptations in some species. Thus future studies on problem-solving should consider species’ brain anatomy to disentangle the physiological correlates of problem-solving behavior in various taxa. Finally, social influences in problem-solving should be studied more intensively to determine how and when individuals may cooperate to solve problems.

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Comparative Cognition](#)
- ▶ [Edward Thorndike](#)
- ▶ [Insight](#)
- ▶ [String Pulling](#)
- ▶ [Tool Use](#)
- ▶ [Transfer of Learning](#)
- ▶ [Trap-Tube Problem](#)

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## Proboscidea

### ► Elephant Life History

## Proboscidea Cognition

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## Introduction

Proboscidea refers to the order that includes elephant species. The term proboscidea comes from

proboscis, the elephant's trunk or nose being their most distinct feature. The order includes 161 extinct species of proboscideans and the three extant species in the family Elephantidae. The three living elephant species are Asian elephants (*Elephas maximus*) African savanna or bush elephants (*Loxodonta africana*), and African forest elephants (*Loxodonta cyclotis*). Until the beginning of the twenty-first century, the African elephants were considered a single species but have since been determined to be two separate species based on behavior, morphology, and genetics (Shoshani and Tassy 2005). In 2021, the International Union for Conservation of Nature (IUCN) recognized the differences in the two African species, changing their conservation status from "vulnerable" as a combined species to "endangered" for African savanna elephants and "critically endangered" for African forest elephants (IUCN 2021). The IUCN also lists Asian elephants as "endangered."

Animal cognition involves "the mechanisms by which animals acquire, process, store, and act on information from the environment" (Shettleworth 2010, p. 4). Anecdotal tales of elephant cognitive abilities go back centuries. Romanes (1882) tells of an elephant that chased people up a tree and then stacked logs under the tree until it could climb the stack to almost reach them. (Fortunately for the people, there were not enough logs.) However, a 2009 review of peer-reviewed journal articles on elephant cognition going back to 1956 found only 21 papers (Byrne et al.). Since that time, research on elephant cognition has advanced more rapidly.

## The Elephant Brain

As the largest terrestrial mammal, the elephant unsurprisingly has the largest brain of any terrestrial mammal (Shoshani et al. 2006). The elephant brain is roughly three times heavier than the human brain and contains about three times the number of neurons. The elephant brain also shows a more complex gyral structure (more folds in the brain) than the primate brain; however, the cerebral cortex is thinner than a human's. The

elephant's hippocampus (the brain structure associated with learning and memory) is proportionately larger, and the elephant has an extremely large cerebellum, the smaller "brain" behind the cortex. Although the elephant has a greater total number of neurons, the majority of these (97.5%) are in the cerebellum rather than the cerebral cortex. The cerebellum is generally associated with fine motor movement, and its size in the elephant may be due to the complexities of controlling the trunk (Herculano-Houzel et al. 2014).

## Sensation and Perception

The elephant's primary senses are hearing (audition) and smelling (olfaction). Their upper range reaches 10 kHz, compared to 19 kHz in humans. On the lower end, they can hear infrasound as low as 17 Hz (perhaps lower) compared to 29 Hz in humans (Suedemeyer 2006). Elephants are the first terrestrial mammals found to use infrasonic communication (Payne 1998). They also can sense seismic communication from the earth. Massive ossicles (bones in the inner ear) may allow them to hear sound using bone conduction from their feet (O'Connell-Rodwell 2007).

Along with hearing, elephants rely on olfaction. The Asian elephant has seven turbinates, the chemosensory-lined bony plates in the skull. Comparatively, dogs have five turbinates, and humans have three (Shoshani 1997). Rasmussen described the sensitivity of the elephant olfactory system as "awesome" (2006). Elephants have approximately 2000 genes for olfactory receptors, twice as many as any other animal tested (Niimura et al. 2014). Elephants use pheromones to discriminate individuals, relationships, sexual states, and group status (Rasmussen 2006).

The elephant's primary appendage for touch is the tip of the trunk. The concentration of touch receptors in the trunk has been compared to the lip skin of monkeys. There are two types of vibrissae attached to hundreds of sensory neurons. This sensitivity may enable the trunk tip to pick up small objects (Rasmussen 2006; Rasmussen and Munger 1996). The tip is sensitive enough to

grasp items the width of a needle (Shoshani 1997). Rasmussen (2006) called the trunk tip a “refined eating tool.”

Although vision is not the elephant’s primary sense, Pettigrew et al. (2010), estimated that the elephant’s vision is better than previously supposed. Elephants are dichromatic, comparable to human deuteranopes (red-green colorblind). Their vision is thought to be more sensitive in dim rather than bright light (Yokoyama et al. 2005) and good enough to see the many postural gestures of elephant communication (Byrne et al. 2009). Elephants’ visual sensitivity is less than a human being’s but better than a cat’s. Asian elephants may have higher visual acuity than African elephants (Shyan-Norwalt et al. 2010). Taking into consideration the differences between elephant and human sensation and perception is one of the great challenges of research on proboscidea cognition.

## Discrimination

In discrimination tests, animals show that they can tell the difference between different stimuli (symbols, objects, sounds, colors, and odors). They discriminate by classifying and categorizing the stimuli (Shettleworth 2010). In some of the first scientific research on elephant cognition, an Asian elephant learned to discriminate between two visual symbols, a circle and a cross, over 330 trials. The elephant was reinforced with food for touching the cross. Eventually, the elephant could learn this discrimination in 10 trials and also learned to discriminate between 20 different pairs of symbols, different sound frequencies, and orders of notes (Rensch 1957). It was later found that elephants could retain a learned discrimination between light and dark circles for 8 years (Markowitz et al. 1975).

In a series of experiments on wild African savanna elephants, researchers showed that elephants can discriminate between two different tribes, one that threatens elephants (the Maasai) and one that does not (the Kamba). The elephants displayed behavioral fear reactions to visible, olfactory, and auditory stimuli, discriminating

individuals from the two tribes, from the look of their clothing, their odor, and the sound of their languages. The elephants could also distinguish men (a greater threat) from women based on the sound of their voices (McComb et al. 2014).

## Numerosity

An animal can also discriminate between different quantities (usually food in the research studies). This ability is also known as relative quantity judgment. Initial research on Asian elephants was conducted through two experiments on relative quantity judgment. In the first experiment, the elephants were shown different amounts of food in two different buckets and could choose between them. The elephants chose the larger amount at greater than chance levels. In the second experiment, the elephants heard the food dropped into the buckets one piece at a time. In this experiment, the elephants also chose the greater amount. In both experiments, the elephants could also smell the food. The researchers did not see magnitude nor ratio effects, which is typical in relative quantity judgment tasks in animals. In the magnitude effect, success in the task diminishes when using larger numbers of items. In the ratio effect, the success decreases when the difference between the numbers is closer (i.e., 2 to 4 vs. 3 to 4). The study may have found that elephants were the first animals tested that did not show the ratio effect (Irie-Sugimoto et al. 2009).

This research was later replicated by others on African savanna elephants. They had similar results; however, the African elephants showed a ratio effect. They also later tested other Asian elephants on a similar study and, once again, found a ratio effect and no difference in results between the species. Another researcher conducted the experiment using only olfactory cues, and found that elephants chose the larger amount but also showed a ratio effect (Snyder et al. 2021). Finally, the original researchers tested an Asian elephant on purely visual stimuli on a touch screen. Once again, they found that the elephant chose the larger quantity and did not

show a ratio effect. The researchers posited that Asian elephants are better at quantity judgment than African elephants, a result later contradicted by the study that compared the two species (Irie et al. 2019). Further research will be needed to ascertain the elephants' quantity judgment abilities.

## Problem-Solving and Tool-Use

One aspect of intelligence is the ability to solve problems. In animals, the goal is to establish evidence that the animal has a sense of causality, that it understands what it is doing and is not merely repeating previously learned behaviors. One way this has been tested in elephants is through the means-end problem, knowing that when you pull one end of an object that something placed on the opposite end will come with it. The elephant is given a choice of two trays with food. In one condition, the food is on the tray. In another condition the food is next to the tray, or there is a split in the tray. African and Asian elephants have shown an understanding of this relationship in many experiments by primarily pulling the intact tray with the food on it, although not all elephants succeeded at all conditions (Highfill et al. 2018; Irie-Sugimoto et al. 2008).

Tool-use was first thought to be an exclusively human trait until Jane Goodall saw chimpanzees using sticks to "fish" for termites (van Lawick-Goodall 1970). Since then, tool-use has been found in many species. Elephants have shown the broadest use of tools of any animal outside of primates. In a review of elephant tool use in elephants, Chevalier found 21 examples in captive elephants and 9 in wild elephants, including fly swatting, scratching with objects, and throwing water or dirt on the body (Chevalier-Skolnikoff and Liska 1993). Elephants can disable electric fences by dropping logs on them (Poole and Moss 2008) and alter branches to use as fly swatters (Hart et al. 2001). Elephants' primary asset for tool-use is their extraordinarily manipulable trunk.

Problem-solving through tool-use was first studied through a series of experiments on

chimpanzees in the early twentieth century (Köhler 1925). Köhler termed this type of problem-solving as insight because he could see no evidence of trial-and-error learning in the solution. In a series of experiments, three Asian elephants were tested for their ability to solve insight problems with tools. In two different experiments, the elephants were given sticks to obtain food that had been placed out-of-reach. The elephants pulled the sticks into their stalls and manipulated them in many ways but never used them to acquire the food. The researchers decided that the elephants were unlikely to use the sticks because holding the sticks in their trunks blocked the elephants' two primary senses for foraging: touch and smell. The elephants were then given another tool that they did not have to hold with their trunks: a platform that they could move and stand on to reach food that was placed overhead. One elephant, a 7-year-old male, moved a large plastic cube under the food so that he could stand on it and obtain the food. Through a series of experiments, he found the tool in a wide range of places and moved it under the food. He generalized his tool-use to another item, a large truck tire, which he moved and stood on to acquire the food (Foerder et al. 2011).

## Social Cognition

Elephant intelligence may have evolved to deal with the complexities of their fission-fusion social systems. This type of intelligence has become known as social intelligence. Byrne and Whiten (1997) coined the term "Machiavellian intelligence," the theory that intelligence is "linked with social living and the problems of complexity it can pose" (p. 1). African elephants can follow the locations of up to 30 family members, which demonstrates their memory and ability to categorize (Bates et al. 2008).

*Social Learning.* Although there is observational evidence of elephants that appear to be learning from each other in the wild, there has been little experimental evidence of social learning in elephants. In one experiment on six captive African savanna elephants, an elephant was given

a box containing food with two different ways to access the food. Another elephant watched the first elephant use one of the methods to open the box. The researchers wanted to see if the second elephant used the same method. The second elephant did not show mimicry, copying exactly the demonstrator elephant. However, the observer elephant was more likely to investigate the box and acquire the food. This type of social learning is known as stimulus enhancement. The observer's attention was brought to the box by the demonstrator increasing the observer's likelihood of obtaining the food (Greco et al. 2013).

**Cooperative Problem-Solving.** In cooperative problem-solving, two animals are given a food acquisition problem which can only be solved by them working together. The animals are given a sliding tray with food that can only be obtained by the two animals pulling on the rope at the same time. If one pulls on the rope, the rope will come loose and the food will remain out of reach. This problem was given to Asian elephants. The elephants were capable of pulling together to acquire the food. If one elephant approached the apparatus before the second one, the first would wait for the second's arrival before pulling. There was even one elephant who learned how to cheat. She found that if she stood on the rope while the other elephant was pulling she could obtain the food without much effort (Plotnik et al. 2011).

**Mirror Self-Recognition.** The ability to recognize oneself in a mirror is known as mirror self-recognition (MSR). It is thought that MSR may be an indication of consciousness in nonhuman animals. MSR has been shown not only in humans but also great apes, dolphins, and magpies. While some researchers have reported negative results for MSR in elephants, methodological problems may have hampered the elephants showing the ability. The standard test for MSR is the mark test in which a mark is placed on one side of the animal's face. The animal is then observed to determine if it touches the mark upon seeing itself in the mirror indicating that it recognizes itself. Three Asian elephants at the Bronx Zoo were tested and all three showed self-directed behavior in the mirror and one passed the mark test, providing evidence for MSR (Plotnik et al. 2006).

## Conclusion

Elephants have shown a wide range of cognitive abilities. Comparison of cognition between humans and other primates involves divergent evolution. How did human cognitive abilities diverge from other animals? Studying elephant cognition involves convergent evolution. How did an animal so different from humans, and so far from them on the evolutionary scale, evolve similar cognition? Considering that both species have complex societies, and large brains to deal with them, may have led to the cognitive similarities. However, there is still much to learn about proboscidea cognition and many avenues for future research.

## Cross-References

- [Mirror Self-Recognition](#)
- [Numerosity](#)
- [Problem-Solving](#)
- [Proboscidea Communication](#)
- [Proboscidea Diet](#)
- [Proboscidea Locomotion](#)
- [Proboscidea Morphology](#)
- [Proboscidea Navigation](#)
- [Social Learning](#)
- [Tool Use](#)

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## Proboscidea Communication

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### Synonyms

[Elephant communication](#)

### Definition

The order Proboscidea consists of three extant species, the Asian elephant and two subspecies of African elephants. Communication is the exchange of information, accomplished through a variety of modalities, including vocalizations, chemical signals, and behavioral cues.

### Introduction

The order of Proboscidea was historically widespread, consisting of many different species. However, the order has diminished, now comprising only three extant species: the Asian elephant (*Elephas maximus*) and two subspecies of African elephants (*Africana loxodonta*) (Soltis 2010). These two genera are believed to have diverged from one another nearly six million years ago, resulting in slight differences in their ecological niches and social structures (de Silva 2010).

Both African and Asian elephants exhibit complex societies, characterized by matriarchal family groups that periodically overlap with one another within their home ranges (de Silva 2010). This

gives rise to what is known as a fission-fusion society, wherein closely bonded family groups will join together when resources allow and diverge from each other when resources are scarce (Soltis 2010). Such social structures necessitate a well-developed system of communication. It has been suggested that increased social complexity correlates with increased communicative complexity (Meyer et al. 2008). This pattern seems to hold when considering the complexity of the extant Proboscideans.

Elephants have highly developed senses, which are all put to use in intraspecific communication, including their senses of sight, hearing, smell, and touch. Research suggests that many of these senses are often used in concert, lending to the increased complexity of their communicative abilities (Langbauer 2000). Anatomical adaptations have increased their sensitivities to a variety of sensory inputs (O'Connell-Rodwell 2007), enabling elephants to communicate through a multitude of mechanisms including vocal, chemical, and visual. While there is evidence of communication through various modalities, vocal communication is the most widely studied and understood mechanism.

### Vocal Communication

The vocal repertoire of elephants is marked by low frequencies and high pressures (Poole et al. 1988). These characteristics are believed to be adaptive for longer distance communication and coordination, whether it be within a family group or broadcast over a great distance to other groups and individuals (Poole et al. 1988). The production of these distinct calls may be possible due to enlarged anatomical structures, such as their diaphragms and nasal cavities, which are central to noise formation (O'Connell-Rodwell 2007).

A majority of vocalizations made by elephants are inaudible to the human ear (Langbauer 2000), because their fundamental frequencies fall within the infrasonic range of 15–35 Hz (Poole et al. 1988; Langbauer 2000; McComb et al. 2000). Their calls can also reach pressure levels as high as 103 dB at 5 m from the source in one study

(Poole et al. 1988), and 118 dB at 1 m in another (Langbauer et al. 1991). There is much variety in the fundamental frequencies, harmonics, and durations of different types of calls in their repertoire (Stoeger and Baotic 2016). A majority of calls, however, persist for approximately 10–15 s, with frequencies in the range of 14–24 Hz and sound pressures of 85–90 dB (Payne et al. 1986).

Variations in elephants' vocalizations can reflect a variety of features, including individual identity, affect, and reproductive status (Soltis et al. 2005b; Soltis 2010). Increased fundamental frequencies have been linked to increased levels of arousal in numerous species (Stoeger et al. 2012). Calls with higher pitch appear to be correlated with increased levels of arousal; elephants generate more high-frequency calls during periods of high excitement, such as aggression and mating, as compared to calmer contexts (Soltis et al. 2005b).

In addition to increased fundamental frequencies during periods of high arousal, structural features of calls are linked to more adverse contexts, such as dominance interactions (Stoeger et al. 2012). During dominance interactions, the rumbles tend to have lower tonality, less pitch stability, and formants that are closer together than rumbles in calmer circumstances (Soltis et al. 2005b; Stoeger et al. 2012). Moreover, there is a characteristic upward modulation of the second formant in calls that alert others to potential danger (Stoeger et al. 2012).

Although numerous specific calls have been described in the literature, there is a level of disconnect because of incongruity in the naming and descriptions of different vocalizations. This has led to a lack of consensus in the number of vocalizations that have been documented and can be reasonably discerned from other calls. Out of 209 vocalizations, Berg (1983) identified ten unique types of calls. In 1988, Poole outlined seven distinctive types of rumbles that differed in both their acoustic characteristics and their overt social function. More recently, Leong et al. (2003) determined that there were eight types of vocalizations, three of which were distinct rumbles. Other data suggest that there are actually nine types of calls (Soltis 2010). Despite the

inconsistencies in the total number of distinguishable call types, there seems to be greater agreement on the calls in a broader scope; there are six types of calls that can be differentiated from each other. These calls are the rumble, the bark, the grunt, the roar, the snort, and the trumpet (Stoeger et al. 2007).

### Rumble

The most common and varied type of vocalization is the rumble. This laryngeal call is common in both adults and juveniles of both sexes. There are many types of rumbles, classified based on their context in addition to their vocal attributes (de Silva 2010). One such call known as the “let's go” rumble has a fundamental frequency of 15 Hz and sound pressure of up to 63 dB at 25 m (Poole et al. 1988). This call accompanies a series of behaviors used to indicate the intention for the group of individuals to move on from a given location. The call is made by an individual standing toward the edge of the group, with one foot raised and ear flapping. This call signals the other members of the group that they are leaving, and they depart together.

Another common type of rumble is the “greeting” rumble. This call has a fundamental frequency of 18 Hz, which modulates up to 25 Hz and back down to 18 Hz, with a sound pressure of 61 dB at 20 m (Poole et al. 1988). Greeting rumbles, particularly when made after a longer period of separation, spark an impassioned response, including overlapping rumbling and trumpeting from members of the group, physical contact, and defecating and urinating (Poole et al. 1988). This series of behaviors associated with “greeting” rumbles may play an important role in maintaining relationships within and between family groups.

Rumbles accounted for 53% of juvenile calls in one study (Stoeger et al. 2007). Juvenile rumbles have incredible variability in their bandwidths ranging from 70 Hz up to 2000 Hz. Those on the lower end of the spectrum are often produced with their mouths closed and commonly result in a vocal response from their mother, whereas louder calls, commonly produced with the mouth open, often necessitates a more immediate response, as they signal distress or protest (Stoeger et al. 2007).

**Bark**

Barks are specific to juveniles and are non-repetitive, abnormal vocalizations that seem to occur in concert with aggressive behaviors, such as pushing or biting (de Silva 2010). It is often produced when the juvenile is surprised, such as when they are kicked or pushed. It is a rapid, noisy call that results from the expulsion of air from their oral cavity and is produced with the mouth wide open (Stoeger et al. 2007).

**Grunt**

The grunt is a laryngeal call that is specific to juveniles. They are soft calls, often produced with their mouths closed. Their structure is stereotyped with only the first inklings of harmonics (Stoeger et al. 2007).

**Roar**

Roars are used in a variety of settings; commonly, they are heard during group movement, but also during instances of high distress. They are the most common distress call used by all ages, but particularly juveniles (Stoeger et al. 2011). Roars are formulated with the larynx and are uttered with their mouths wide open (Stoeger et al. 2007). In adult elephants, a subtype of roar with an increased duration is known as a longroar. This call is commonly associated with higher levels of distress, particularly when an individual is separated from the group. Longroars often accompany behaviors associated with increased levels of arousal: increased speed, head lifted, and tail erect (de Silva 2010).

Roars produced by juveniles account for the highest pitch of any vocalization in African elephants, reaching fundamental frequencies higher than 390 Hz (Stoeger et al. 2007). In juveniles, there are three subtypes of roars. The most stereotyped roar is the noisy roar, which is a subtype characterized by being noisy and lacking tonality. Noisy roars often coincide with some sort of distress requiring immediate attention. Tonal roars, in contrast, are tonal for the majority of the call and less stereotyped than noisy roars. Mixed roars incorporate elements of both noisy and tonal roars and lack any stereotyped structure. Tonal and mixed roars were often produced in response to

suckle terminations, rather than immediately distressing events (Stoeger et al. 2007).

Chaos is a type of nonlinear phenomena (NLP) in vocalizations that affect the call in such a way as to deviate from the normal vocal pattern. It occurs when both the vocal tract fold tension and air pressure increase, causing abnormalities in the vibrations and subsequent vocalization (Stoeger et al. 2011), when an individual is pushing their vocal capacities past their limits. NLP was observed in 92% of juveniles' roars, suggesting a link between NLP and increased levels of distress (Stoeger et al. 2011). It has been hypothesized that chaos makes juveniles' calls less predictable and harder to become accustomed to, increasing the likelihood that their mother will be able to respond quickly to the distressing situation. The tonality of roars decreases as the severity of the distress increases, meaning that there is more noise and less harmonics during these periods (Stoeger et al. 2011).

**Snort**

Snorts result from a strong blast of air through the trunk and occur in all ages and sexes. Snorts lack any tonality and do not seem to have a specific function in communication. Researchers argue that they serve a cleaning function, rather than a communicative function (Stoeger et al. 2007).

**Trumpet**

Trumpets are quintessentially Proboscidean, described by researchers as having long durations and high sound pressures. Whereas trumpets make up only a small percentage of elephants' vocalizations, they are the call type most readily associated with elephants because they are audible to humans (de Silva 2010). They do not develop until 3 months and are often produced in concert with aggressive interactions. Produced nasally, trumpets are tonal with slight harmonics (Stoeger et al. 2007).

**Growls**

Growls are associated mainly with family groups, as males do not seem to exhibit this type of call. Growls are distinct to the individual caller; thus they are believed to be central in locating

individuals and maintaining group cohesion over distances (de Silva 2010).

### Contact Calls and Answers

Contact calls are important in maintaining cohesion and coordination within family groups. While they are audible to the human ear, they sound relatively soft (Poole et al. 1988); contact calls have an unmodulated frequency of approximately 21 Hz and last 4–5 s (McComb et al. 2000). Contact answers are responses to contact calls, often starting loud and tapering off to a softer sound at the end of the call (Poole et al. 1988). In a playback experiment, contact calls from members of a family group resulted in both contact answers and an inclination to move toward the speaker (Langbauer 2000). Contact calls and answers are crucial in the coordination of group movement as well as the reunion of individuals. When separated from their group, an elephant may engage in contact calling for many hours in an effort to be reunited (Poole et al. 1988).

### Group Coordination

Vocal communication is central to the coordination of elephant herds over great distances. Vocalizations are omnidirectional, spreading in all directions and over great distances (Langbauer 2000). Family groups of African elephants will often vocalize in unison, creating a signal that can propagate nearly three times farther than that of a single elephant (O'Connell-Rodwell 2007). Analysis of the movement of various radio-collared elephants in different family groups revealed that they are able to coordinate their movement within and between family groups over a distance of up to 5 km (Langbauer et al. 1991; Poole et al. 1988).

This coordinative ability is of particular importance to African forest elephants. Their habitat, consisting of thick vegetation, makes it nearly impossible to rely on visual contact in maintaining group cohesion. These groups can grow to be over 100 m in diameter, necessitating a nonvisual mechanism for coordination (Payne et al. 1986).

Vocalizations among conspecifics are not relegated solely to in-group members but are also used in coordinating with other family groups. Separate family groups have been observed assembling prior to their arrival at waterholes (Garstang et al. 1995). While the specific function of this synchrony is unknown, it is hypothesized that it may serve as an antipredatory function.

Such coordination between groups may also serve to alleviate competition over resources (Garstang et al. 1995). Family groups have been observed coordinating their movements over distances of several kilometers without ever converging. This pattern may serve to ensure the groups are sufficiently separated to minimize competition, while maintaining a distance at which they can mutually benefit from predator monitoring (Langbauer 2000). The ability for their low frequency vocalizations to propagate over long distances in every direction allows families to maintain sufficient separation from one another while reaping the benefits of increased numbers (Garstang et al. 1995).

### Vocal Discriminations

#### Familiarity

There are many characteristics that can be discerned from an individual's vocalizations. Formant frequencies are directly related to body size and, more specifically, vocal tract length (Stoeger et al. 2012). Sex, status, and even individual identity can also be garnered from information encoded in elephants' calls. McComb et al. (2000) demonstrated the ability of elephants to discriminate between familiar and unfamiliar elephants. In 2003, McComb outlined the first evidence that certain features of rumbles held the key to discerning individuals' identities.

#### Individual Recognition

Elephants appear to have an extensive vocal recognition network, demonstrating the ability to discriminate between individuals in their family group, bonded group members (individuals in another closely associated family group), less associated group members, and unfamiliar



individuals (McComb et al. 2000). It is likely that this extensive network of vocal recognition is a vestige of their fission-fusion society. It is necessary for individuals to have a working memory of numerous individuals with whom they may associate. In Amboseli National Park, adult females may have familiarity with 14 different families with whom they may come into contact (McComb et al. 2000).

### **Dominance**

Vocal communication is not only important in coordinating behaviors within and between groups, but also maintaining group cohesion and social order. In this vein, it is important for individuals to be able to communicate information about status within their group's hierarchy. A number of vocal tendencies have been observed in the context of dominance interactions. Individuals that are more dominant tended to vocalize when being aggressed upon, whereas those of lowing social standing remain silent. Researchers postulated that higher ranking individuals are more likely to vocalize as a way to assert status, whereas the goal of more subordinate individuals is to deescalate the situation (Leong et al. 2005). Another tendency is for the rumbles of subordinate individuals to have lower tonality and less pitch stability when dominant individuals are present as compared to when they are alone or in the presence of comparable or more subordinate individuals (Soltis et al. 2005b).

### **Antiphonal Calling**

Antiphonal calls are a series of back-and-forth calls between two or more individuals either in response to an initial call or some external stimulus (Soltis et al. 2005a). In a herd of captive elephants at Disney's Animal Kingdom, researchers found that the most common cause of antiphonal calling, at 31.7% of the cases, was the approach of a third-party individual who, most of the time, was dominant to at least one of the participating vocalists. While the response to an approaching dominant conspecific elicited a series of calls, the probability of an individual responding to a call was unrelated to their

dominance ranking; instead it was an individual's affiliation with the caller that predicted their response (Soltis et al. 2005a). Of the calls that were answered, 37.7% were by the individual most closely affiliated with the caller, followed by 31.9% being answered by the second most affiliated individual and 20.5% by the third most affiliated individual (Soltis et al. 2005a). Researchers also examined the conditions under which rumbles were produced. They found that individuals were 1.88 times more likely to vocalize following a rumble from a conspecific than when there were no recent calls (Soltis et al. 2005a). In the wild, it is uncommon for a female's call to go unanswered, as the majority of vocalizations occur in chorus with other group members (Langbauer 2000).

### **Male Communication**

Female elephants are highly social, living in complex matriarchal family groups. Males, on the other hand, exhibit far less social complexity, and their communication seems to reflect this difference. Males produce less varied vocalizations than females (Langbauer 2000). Once males reach sexual maturity, they leave their families and live on their own or in small bachelor herds of similarly aged individuals (Langbauer 2000). When they are not in musth – a period of increased androgen levels and aggression – males form a social structure of closely affiliated companions with a simple dominance hierarchy (Stoeger and Baotic 2016). These groups are relatively fluid, as they disband and reform as they cycle through their periods of musth each year (Meyer et al. 2008).

Although males leave their native family herds when they come of age, they will take up residence in ranges that overlap with a number of family groups (Langbauer 2000). This makes it important for males to be able to discriminate between individuals' vocalizations. As with females, males are able to extract information from conspecific vocalizations (Stoeger and Baotic 2017). This information, however, serves different functions for males (Stoeger and Baotic

2016). One of the most important functions of individual recognition on the part of males is differentiating between related and nonrelated individuals, so as to avoid inbreeding (Stoeger and Baotic 2017).

In a playback experiment, males preferred the rumbles of unfamiliar elephants rather than those from their native herd. This preference was marked by increased attention and orienting responses. In some instances, when presented with a call from an unfamiliar female, the males would entirely cease what they were doing, lift their head and move in the direction of the speaker (Stoeger and Baotic 2017). Males have an incredible ability to pinpoint the location from which a vocalization sourced. In another playback experiment, males passed within 100 m of the speaker following a trek of over 1 km from where they first heard the call (Langbauer et al. 1991).

Musth begins around the age of 25–30 years and recurs annually with increasing duration each year until they reach their peak (Meyer et al. 2008). Musth not only has an effect on males' reproductive success – with 75–80% of all offspring resulting from a musth male – but it also impacts the interactions between males (Stoeger and Baotic 2016). Although bachelor herds have a level of hierarchy, individuals in musth supersede this hierarchy, with musth males having increased access to mates compared to non-musth males (Slade et al. 2003). This ability to jump the hierarchy is rendered moot when they are not the only male in musth. In this situation, musth males have an uncanny ability to avoid one another while in search of a receptive mate, coming into contact only when necessary, often resulting in a fight for dominance in a mating context (Poole et al. 1988).

## Reproduction

Vocalizations specific to the context of courtship and mating impart information about the caller's physiological state and receptiveness, coinciding with musth in males and estrus in females (Langbauer 2000). Musth rumbles are produced by males during their period of musth that can last up to 4 months. They are a pulsated call with a low

frequency of 11–17 Hz and pressures of 78 dB at 5 m up to 108 dB (Meyer et al. 2008; Stoeger and Baotic 2016). They last for an average of 4.4 s and are often accompanied by a loud ear flap (Poole et al. 1988). When in range of a group of females, musth rumbles are often answered by a female chorus (Poole et al. 1988).

The female chorus is characterized by several females vocalizing in unison in response to a male's musth rumbles. They have a fundamental frequency of 15 Hz, which increases to 24 Hz before returning to 15 Hz, and a pressure of 88 dB at 16 m (Poole et al. 1988). Estrus rumbles are produced by females during her short period of estrus, which lasts approximately 5 days. Estrus rumbles have a relatively high-pressure level of 117 dB at 1 m and a fundamental frequency of 15 Hz, modulating up to 35 Hz and then back down to 15 Hz (Langbauer 2000). This call lasts for about 5 s and then repeats. Elephants may repeat this pattern for up to 30 min with progressively decreasing pressure levels. The unique frequency modulation of the estrus rumbles helps it to be differentiated from background noises (Langbauer 2000). Not only do they increase the duration of their calls during estrus, they also increase the frequency with which they make estrus calls, in an effort to increase their chances of attracting a mate (O'Connell-Rodwell 2007). It is crucial for females to find a mate during the incredibly short period of estrus. The uniqueness of the call, coupled with the high-pressure levels, help accomplish this goal. Estrus rumbles can be heard for at least 4 km (Langbauer 2000). While being guarded by a male, estrus females will often produce additional rumbles in an attempt to attract other males. The rationale behind this behavior is that it could induce a competition among the males, ensuring that she is mating with the highest quality mate (Soltis 2010).

In addition to musth and estrus rumbles, there are two additional vocalizations associated with the specific act of mating. Once a female has been mounted, she will produce what is known as a post-copulatory or estrus sequence. This is a series of two or more low-frequency calls that modulate from 18 Hz up to 35 Hz and back down to 18 Hz, with pressure levels of 96 dB at 10 m (Poole et al.

1988). Following this series of vocalizations, a sequence of behaviors known as mating pandemonium occurs. In this, the other females in the herd run to the female who was mounted while trumpeting, rumbling, and screaming, along with urinating, defecating, and secreting temporin from their temporal glands. This pandemonium can reach prolonged pressure levels of 78 dB at 67 m (Poole et al. 1988).

Some research has suggested that female vocalizations may differ based on where they are in their estrus cycle. Clemins and Johnson (2003) found that there were acoustic differences in the calls made by females in their follicular and luteal phases (cited in Leong et al. 2005). Not only is there an increase in the frequency of calls in the weeks leading up to ovulation, but there are specific patterns in their vocalizations in the preovulatory phase that are distinct from other parts of their cycle. In particular, these calls have, overall, lower fundamental frequencies in addition to both lower frequencies and higher amplitudes on their first formants than normal calls (Soltis 2010). These features may play a central role in propagating their calls longer distances during this pivotal time in a female elephant's reproductive cycle.

## Chemical Signaling

Vocal communication in elephants has adapted to suit their environment and carry over long distances; however, there are other mechanisms of communication that are able to serve similar purposes. Chemical communication can be used in both long- and short-distance communication, particularly with respect to signaling different physiological states. Urine and feces are energy-efficient and passive routes of chemical communication (Langbauer 2000; Slade et al. 2003). One of the most common iterations of this method is a hallmark of musth. The urine dribble is characterized by urine continuously flowing from the male's sheathed penis, leaving a trail of strongly scented urine wherever they go (Langbauer 2000). Another characteristically male chemical signal that functions over a much shorter distance

is the ear wave. Simplistically, the male extends their ears to the sides and rapidly brings them forward. This behavior concentrates the chemical signals sourcing from their temporal gland and focuses in a certain direction. This can be agonistic toward other males or an advertisement toward potential mates (Langbauer 2000).

Flehmen is a behavior wherein an elephant touches the tip of their trunk either to another elephant's mouth or urogenital region, or a substance in their environment. Then they deposit some of the sample from the tip of their trunk to the opening of the vomeronasal organ on the roof of their mouth. This organ is able to differentiate between different compounds in the sample, providing the individual with information about the source (Langbauer 2000). Females tend to exhibit this behavior toward urine from males in musth more than those not in musth, with females in estrus performing the most flehmens of musth urine (Langbauer 2000). Urogenital region checks are the most frequency of the many trunk tip behaviors common in elephants (Slade et al. 2003).

## Environmental Factors

A major fault with acoustic communication is its rapid degradation through an environment, experiencing interference from a variety of environmental features (Langbauer 2000). This is a far more pressing issue with higher frequency sounds than low-frequency sounds. Lower frequency sounds, such as those produced by elephants are far less subject to this environmental attenuation and are able to travel greater distances than higher frequency vocalizations at similar pressure levels (Poole et al. 1988). Substrate-borne transmission is also more resilient to air-borne attenuation; the low-frequency, high pressure vocalizations of elephants allow their vibrations to travel seismically over the ground (O'Connell-Rodwell 2007). Additionally, this method of transmission is able to provide information on how far the source is from the recipient, as the level of harmonics in the vibrations decreases over distance at a reliable rate (Langbauer 2000; O'Connell-Rodwell 2007).

There are a number of optimal conditions under which elephants can communicate. These conditions lend evidence to the manifestation of different behavioral patterns. Elephants are able to communicate at night more than twice the distance that they can during the daytime, with the optimal times being 1–2 h after sunset (Garstang et al. 1995). There are temperature inversions during the nighttime that force low-frequency sounds back to the ground, enhancing their communicative abilities (Garstang et al. 1995; Langbauer 2000). Bonded groups converge and travel to waterholes together commonly just before sunrise or just after sunset, suggesting that there is some communicative benefit to these periods of the day (Garstang et al. 1995). There have also been observed increases in elephant vocalizations near and after dusk (Langbauer 2000).

Some climactic conditions actually aid in communication. Clear, dry conditions, typical of dry seasons and droughts, are ideal for producing the temperature inversions during the night that enhance vocal communication. During such periods, enhanced vocal capabilities are crucial in ensuring that elephant herds maintain greater distances between themselves so as to limit resource competition when food and water is scarce (Garstang et al. 1995). The habitat of the African savannah elephant provides ideal conditions for enhanced sound conduction (Garstang et al. 1995). Under optimal conditions – dry, clear, and shortly after dusk – it is believed that vocalizations could travel up to 10 km in any direction (Garstang et al. 1995; Soltis 2010).

## Physiology

Elephants have unique anatomical features that allow them to effectively communicate over great distances (O'Connell-Rodwell 2007). One such feature is associated with their ability to detect seismic signals, either via mechanoreceptors in their skull or through bone conduction leading up from their feet. A series of fatty deposits couples with open sinuses in their skull that are believed to be central in detecting and

interpreting seismic signals. These fatty deposits may function as a way to clarify the signals they are receiving (O'Connell-Rodwell 2007).

Bone conduction is made possible through specific freezing behaviors that elephants demonstrate when they sense seismic cues. They pause and shift their weight toward their forelimbs, which places their front legs directly below their ears (Bouley et al. 2007). This allows the vibrations to travel via their bones up their leg and shoulder, into the middle ear canal (O'Connell-Rodwell 2007). Once they have pinpointed the origin of the signal, they will move to face in that direction, maintaining their weight on their front feet. They will then lift one of their rear feet, placing the front-most part of it back on the ground and rocking it back and forth from the front to the back (Bouley et al. 2007). They will often lift one of their front feet in order to triangulate the source of the signal more accurately (O'Connell-Rodwell 2007).

The pattern of rocking their foot forward and backward on the ground is believed to be associated with the pacinian corpuscles (PCs) that have been found in high densities on the most anterior and posterior regions of their foot (Bouley et al. 2007). PCs are pressure receptors that are incredibly sensitive. They occur in high densities in the fingertips of humans, allowing for the perception of minute sensations (O'Connell-Rodwell 2007). PCs likely play an important role in the interpretation and conduction of seismic signals received by elephants (Bouley et al. 2007).

When producing sound waves, elephants are able to take advantage of two possible vocal paths, each of which creates different sounds signifying different meanings. Vocalizations can be emitted either orally, through the mouth, or nasally, through the trunk (Stoeger et al. 2012). In a study examining these two vocal paths, they found that 115 rumbles were nasally emitted and 52 sources from their mouths. They found that the type of call appeared dependent on the context, with contact calls being mostly nasal and bonding situations eliciting oral calls (Stoeger et al. 2012).

Elephants have vocal tracts that are unique from all other mammals for two reasons: elephants are large animals and they have uniquely

long noses that are external from their skull, allowing for increased flexibility in the production of sound (Soltis 2010). Formant frequency is dependent on the length and shape of the individual's vocal tract. Longer tracts allow for the formation of lower frequencies (Stoeger et al. 2012). Analysis of different vocalizations yielded two approximate tract lengths: 2 m for nasal vocalizations and 0.7 m for those emitted orally (Stoeger et al. 2012). Estimates using measurements of the mandible yielded similar results with the oral tract measuring 0.75 m and the nasal tract totaling to approximately 2.5 m (Soltis 2010). Further analysis of male rumbles placed their vocal tract lengths understandably longer at 3.21 m for individuals older than 25 years (Stoeger and Baotic 2016).

There are a number of physiological adaptations elephants have for producing such low-frequency calls, the first of which is their large diaphragm (O'Connell-Rodwell 2007). Elephants also have a unique hyoid structure that is composed of five bones, rather than the normal nine that is seen in other mammals. Their hyoid structure is also separated into two sections which, combined with the fewer number of bones, allows for greater flexibility of their larynx. This is believed to contribute to their production of low-frequency sounds (Langbauer 2000; Soltis 2010).

Vocalizations result from the vibration of vocal folds in the larynx. The fundamental frequencies of different calls are determined by the rate of vibration. The sound waves are filtered as they propagate through the supra-laryngeal tract, with different vocalizations resulting from those shaped by the oral cavity versus the nasal passage (Soltis 2010; Stoeger and Baotic 2016).

Elephants' ability to successfully propagate low-frequency vocalizations is meaningless without also having the necessary anatomy to receive such signals. Their low-frequency hearing abilities are the best on any animal tested thus far and are at least ten times better than that of humans. It is believed that larger hearing anatomy may lend itself to better low-frequency detection (Soltis 2010). In addition to having large external ears and anatomy scaled to their

size, elephants also have a unique muscle surrounding the external opening of the ear (O'Connell-Rodwell 2007). This muscle functions like a sphincter and can occlude the opening of the ear. This may serve as a type of filter on the information they receive, allowing them to detect more subtle signals in their environment (O'Connell-Rodwell 2007).

## Conclusion

The complexity of elephant communication reflects the social complexity of the species. Specific physiological adaptations have allowed elephants to develop the ability to communicate over several kilometers, coordinating the movements of individuals both within and between family groups. Additionally, specific calls that signal information about the individual's identity and their physiological state have proven to be crucial for the reproductive success of the species. The complexities of the different types of calls, including those specific to males and juveniles, serve important functions that ensure the continued propagation of the species even in the harshest of environments.

## Cross-References

- [Proboscidea Cognition](#)
- [Proboscidea Diet](#)
- [Proboscidea Locomotion](#)
- [Proboscidea Morphology](#)
- [Proboscidea Navigation](#)

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## Proboscidea Diet

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## Introduction

Within the order Proboscidea, there are only two living species, the Asian elephant (*Elephas maximus*) and the African savanna elephant (*Loxodonta africana*). Both species of elephants are intermediate feeders with a preference for woody vegetation (browse), but research has shown that both species were once grazers and are in a transition back to browsing (Cerling et al. 1999). As with many animals, elephants are opportunistic foragers and will eat different foods based on availability. Human encroachment and farming in historical elephant ranges have brought the animals into direct conflict with human – competing for limited natural resources.

## What Wild Elephants Eat

A 7-year study of wild Asian elephants feeding behaviors revealed that the animals in Rajaji National Park consume a diet of 50 plant species

which varied through the year with the season. Tree species comprised nearly 74% of their diet, while grass and shrubs only 14% and 8%, respectively – grass and shrubs are predominantly consumed in the early part of the dry season (Joshi and Singh 2008). Similarly, a 2-year study at the Kuldiha Wildlife Sanctuary in Odisha revealed that the animals in the sanctuary fed on 71 different species of plants, with tree species comprising 56% of the diet, shrubs 20%, herbs 14%, and climbers 10%. Again, what the animals consumed was highly opportunistic and depended on the season (Mohapatra et al. 2013).

In Kruger National Park, African elephants consume ~ 35% of their diet in the form of grasses. A study published in 2006 revealed that the diet of animals in the northern part of the park included more grass during the dry season (~40% of the diet) compared to their southern counterparts who consume only about 10% of their diet in the form of grass during the dry season. However, during the wet season, elephants in both the northern and southern part of the park consume similar amounts of grass (~ 50%). Researchers believe the reason for the high intake of grass during the dry season for the northern animals is the type of browse that grows in that area of the park during the dry season is primarily *Colophospermum mopane* (Codron et al. 2006). This tree generates secondary metabolites which deter herbivory and is likely why the elephants avoid it (Colgan et al. 2015).

## Digestive Morphology

Both species of elephants are monogastric. The digestive tract is similar to that of a horse; elephants do not have a gallbladder, and they rely on hindgut fermentation to extract their nutrients. From mouth to anus, the digestive tract consists of the mouth, pharynx, esophagus, stomach, small and large intestine, cecum, rectum, and anus. The molar teeth, tongue, salivary gland, liver, and pancreas are accessory organs that complete the system. Interestingly, Asian elephants have a longer intestinal tract than their African counterparts. They also have a longer rate of food passage and can extract more nutrients from their food than

African elephants (Clauss et al. 2007). However, both species of elephants differ in their digestive physiology from other ungulate species. In comparison to other herbivores, they have a much shorter digestive tract, and their large and small intestine are almost equal lengths (Clauss et al. 2003b; Loehlein et al. 2003).

All mammalian herbivores depend on the fermentation of plant cell walls by gastrointestinal bacteria. Within the body size range usually studied, the efficacy of this fermentation is directly correlated to fermentation time, i.e., to passage rates. However, elephants deviate from this – they do not have long ingesta passage rates and achieve only comparatively low nutrient extraction compared to foregut fermenters. Clauss and colleagues hypothesize that abdominal space is a limiting factor for body mass; thus herbivores can only achieve great body mass with a gastrointestinal design that allows for a faster rate of ingesta passage and is the reason why elephants are hindgut fermenters and many extinct large herbivores are also believed to have been hindgut fermenters (Clauss et al. 2003a).

## In Captivity

Captive elephants tend to be much heavier than their wild counterparts (Veasey 2006). Historically, this has been largely because they consume foods with a much higher nutrient density and have a lower activity level than wild elephants (Marcus Clauss et al. 2007; Veasey 2006). Captive elephant management has changed dramatically over the past 20 years. Zoos accredited by the American Association of Zoos & Aquariums (AZA) must meet very strict housing and management requirements (“AZA Standards for Elephant Management and Care,” March 2011, April 2012). Exercise, body condition evaluation, as well as diet review and modification are required of all AZA institutions housing elephants.

Zoos and researchers are developing a number of techniques and tools to help better access animal condition, maintain healthy body weights, and ensure gastrointestinal (GI) health. Body condition scores validated through

ultrasound have created a useful tool for captive elephant management (Morfeld et al. 2014). Additionally, studies that evaluate the fecal microflora are helping animal managers better understand how the animals break down food components and identify important “healthy” bacteria within the elephant GI (Güllert et al. 2016; Ilmberger et al. 2014).

The typical captive elephant diet will include a large amount of browse, grass hay, and an elephant supplement pellet designed to ensure the animals receive adequate vitamin and minerals that may be lacking in the browse or hay. Until recently, zoos also offered large amounts of produce – this practice has been abandoned in the daily diet by most zoos as produce is not normally consumed by wild elephants and the gut has not evolved to accommodate it in large amounts.

## Conclusion

Asian elephants are listed as endangered, and their wild populations are continuing to decline (“*Elephas maximus* (Asian elephant, Indian elephant),” n.d.); African elephants are listed as vulnerable (“*Loxodonta africana* (African elephant),” n.d.). Both species live in severely fragmented habitats, are in conflict with humans for land, and poached for their ivory. Understanding their foraging strategies, dietary needs, and nutrient utilization will help identify the resources needed for wild elephants as well as ensure appropriate care in captivity.

## Cross-References

### ► Herbivore

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## Proboscidea Gaits

### ► Proboscidea Locomotion

## Proboscidea Locomotion

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## Synonyms

[Elephant locomotion](#); [Proboscidea gaits](#)

## Definition

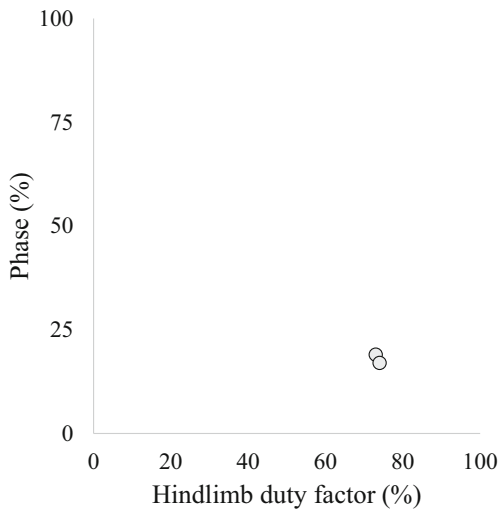
Movement used by elephants (the only extant members of the Order Proboscidea) to traverse the environment.

The elephant and its extinct relatives belong to the Order Proboscidea, a division of Afrotheria (one of the major clades of placental mammals that includes golden moles, elephant shrews,

tenrecs, aardvarks, hyraxes, elephants, and sea cows). At its peak diversity, Proboscidea contained up to 175 species and subspecies, classified into 42 genera and 10 families. After the woolly mammoth (*Mammuthus primigenius*) became extinct, only three living species under the family Elephantidae remain. The three existing species are the African forest elephant (*Loxodonta cyclotis*), the African bush elephant (*Loxodonta africana*), and the Asian elephant (*Elephas maximus*). There are three subspecies of the Asian elephant: *E. m. sumatranus*, *E. m. indicus*, and *E. m. maximus* (Shoshani and Tassy 2005). Of these remaining species, the *Loxodonta* are geographically restricted to Africa, while the *Elephas* has migrated out of Africa and into more temperate regions, such as Asia and Europe. The decline of the Order Proboscidea as well as an increase in the distribution of C4 plants (grasses and hedges), has resulted in the adaptive radiations of elephants (Sanders 2010). Today, elephants are the largest living terrestrial animals. However, their exceptional dimensions come with both advantages, such as a decreased energetic cost of locomotion, and disadvantages, such as a greater fragility as compared to smaller animals (Genin et al. 2010).

## Quadrupedal Gait Mechanics

Elephant locomotion is classified as quadrupedal locomotion, whereby four limbs support and propel the body. Despite this classification, the elephant's gait is somewhat atypical of the classic quadrupedal gait. In most quadrupeds, there is a transition speed between the pendular mechanism of the walking gait and the bouncing mechanism of the running gait, which influences variables such as the footfall pattern, the limb phase (the time interval between two sequential limb touchdowns), and the duty factor (the fraction of a stride in which a limb is in contact with the ground) (Genin et al. 2010). Unlike other quadrupeds, elephants do not demonstrate a defined gait transition. In other words, they do not have a clear shift from a walking phase to a trot or a gallop. As they increase speed, their



**Proboscidea Locomotion, Fig. 1** “Hildebrand” plot displaying phase against hind limb duty factor collected during quadrupedal walking in elephants ( $n = \text{two species}$ )

step length and step frequency also increase. However, an elephant’s gait remains within the boundaries of a lateral sequence footfall pattern (with lateral couplets or single-foot) regardless of their speed. This means, the elephant’s left hind limb is always followed by its left forelimb while its right hind limb is always followed by its right forelimb (Fig. 1). This is why elephants are considered to have a smooth gait transition. Furthermore, as an elephant’s forelimb footfalls increase linearly with speed, the phasing becomes more evenly spaced in time, resulting in lateral couplets at slower speeds and a true single-foot at higher speeds. Because the elephant’s forelimb and hind limb footfalls are evenly spaced in time, its gait can be described as symmetrical (Hutchinson 2006).

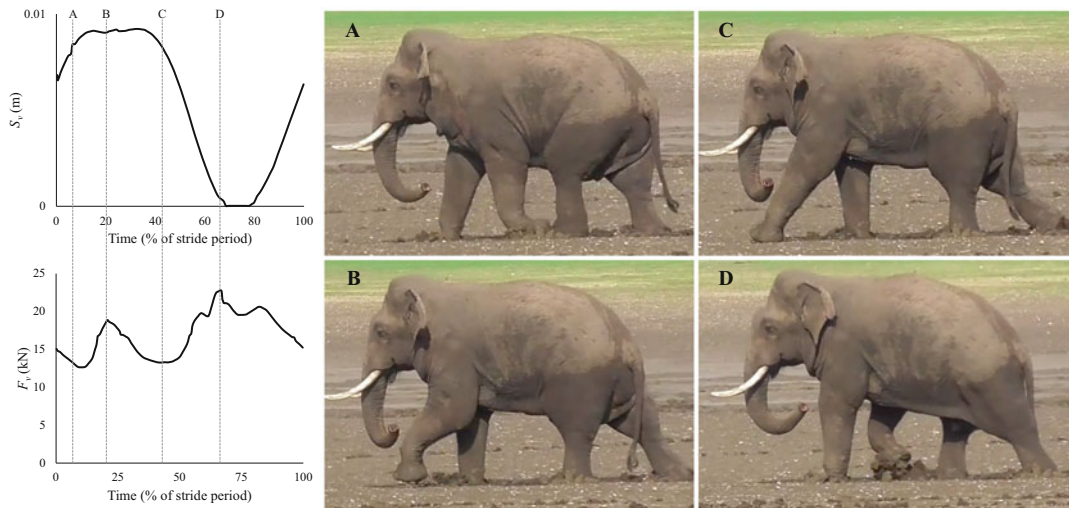
An important question is whether elephants can run? Typically, definitions of running mechanics are based on the interchange between potential energy (PE) and kinetic energy (KE). During running, animals continuously recover the PE stored in tendons and muscles into bouncing KE. During walking, animals convert PE to KE as they step forward (Knight 2010). Furthermore, the transition into the running gait is usually associated with a whole-body aerial phase (period

in which no limbs are in contact with the ground). However, elephants never achieve this full aerial phase. At speeds over  $\sim 2 \text{ m s}^{-1}$ , only the elephant’s hind limbs illustrate an aerial phase with bouncing while the forelimbs maintain a straighter morphology (Ren et al. 2008). Even though elephants may appear to be running at high speeds, Hutchinson (2006) has shown that elephants’ front limbs walk and their hind limbs trot during fast locomotion. Therefore, in a classical sense, elephants do not display a running gait.

Despite the numerous differences, elephants demonstrate some similarities to other quadrupeds. For example, like other quadrupeds, when an elephant increases its speed, it does so by initially increasing its stride frequency as opposed to increasing its stride length. An increased stride frequency results in an increased joint angular velocity (the rate of flexion and extension of a joint). However, when the elephant’s speed begins to reach its near-maximal threshold, the elephant relies on highly increased joint rotation in an attempt to generate longer strides. Therefore as speed approaches near-maximal values ( $> 5\text{--}6 \text{ ms}^{-1}$ ), elephants achieve near-maximal stride frequency, primarily by increasing stride length (Huchinson 2006).

Genin et al. (2010) used a force platform to measure ground reaction forces (forces exerted by the ground on the limbs) under an elephant during its gait cycle. Measurements were taken over a wide speed range ( $0.38 \text{ m s}^{-1}$  to  $4.97 \text{ m s}^{-1}$ ), and it was found that hind limb and forelimb loading were divided into rigid and compliant parts at speeds over  $2.8 \text{ m s}^{-1}$ . During hind limb loading, the elephant’s contralateral forelimb was grounded, and the vertical ground reaction force increased (Fig. 2). However, the elephant’s center of mass (COM) vertical displacement remained relatively constant (Fig. 2). This shows that the hind limb and the contralateral forelimb act as a rigid, noncompliant system. This differs from forelimb loading, where the elephant’s ipsilateral hind limb was grounded, and the vertical ground reaction force increased, while the vertical displacement of the COM decreased. This indicates that the forelimb and the ipsilateral hind limb act





**Proboscidea Locomotion, Fig. 2** Left: Typical curve of vertical ground reaction force ( $F_v$ ) and vertical displacement of the center of mass ( $S_v$ ) over one-step cycle as a function of time. The letters indicate: (a) hind limb

touchdown, (b) hind limb maximal load, (c) forelimb touchdown, and (d) forelimb loading. Hind limb loading (from a to b) and forelimb loading (from c to d). Data from Genin et al. (2010)

as a compliant bouncing system, similar to a spring-mass system (Genin et al. 2010).

### Comparison Between Species

The African and Asian elephants have strong kinematic similarities as they both achieve a maximum speed of slightly less than  $7 \text{ m s}^{-1}$  (Hutchinson 2006). The individual limb bone development is also similar, but the two species differ in their mechanical adaptations, indicating differences in evolutionary adaptations. The limb bones of the Asian elephant are better for adjusting to peak muscular forces than the limb bones of the African elephant. During high speeds, Asian elephants generate muscular forces that exceed their body weight, resulting in a complex bending/torsion and elastic bone stress that allows for large levels of limb compliance. Also, the Asian elephant can maintain higher speeds than that of the African elephant (Kokshenev and Christiansen 2010). On the other hand, the limb bones of African elephants can overcome axial compression through a more energetically

efficient design. Their bones avoid bending/torsion, resulting in a shorter stride length and higher stride frequency than Asian elephants during increased speeds. Regardless of these differences, both are limited in near-maximal stride length and near-maximal speed as compared to other mammals, due to a negative limb bone compliance gradient (Hutchinson 2006).

Another factor that influences locomotion is the size of the elephant. Larger elephants are not capable of reaching the same locomotive intensity as smaller elephants. At increased speeds, larger elephants prefer walking, which relies less on the compliance of bone tissue. Smaller elephants display minimal duty factors and utilize a near-maximal stride length and frequency. The maximum speed of elephants usually peaks at a young age as a result of the environmental pressure to escape predation, a factor that does not have as great of an impact on older elephants. Consequently, older elephants do not have a great need for higher speed capacity. Nevertheless, the gait transition is relatively smooth in all elephants regardless of their size and all have compliant hind limb function at high speeds (Hutchinson 2006).

## Energetics and Migration

Energy consumption, also known as fuel-economy, during animal locomotion are assumed to be driven by the time it takes to apply forces to the ground by each foot and the force that muscles must generate to support the body weight. Movement from rest requires a significant amount of energy, especially as the load increases (Kram and Taylor 1990). Of note for African elephants is their significant body weight (~6000 kg), which is supported by four pillar-like legs. While it was previously theorized that elephants have a low fuel-economy, Langman et al. (1995) has shown that this is not the case. Evolution has favored longer legs in elephants to allow for longer stride length. This allows them to move at slower speeds, while still covering a long distance with each stride. Slower moving muscles help reduce the force generation and thereby increase the fuel-economy. The fuel cost of the African elephant has been estimated to be 1/40 that of a 7 g pygmy mouse due to these biomechanical adaptations. Net cost of transport in elephants, estimated by oxygen consumption during walking, follows a U-shaped curve (Fig. 3). The net cost of transport increases in two conditions: (1) movement from rest (0–0.99 m/sec), to overcome inertia and (2) movement beyond 1 m/sec, in accordance with speed. The lowest net cost of transport ( $0.78 \text{ J kg}^{-1} \text{ m}^{-1}$ ) is at 1 m/sec, which is approximately the walking speed of humans. The consequent high-fuel economy

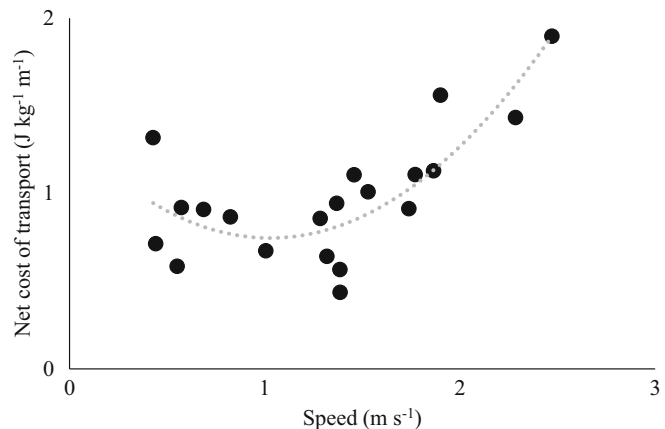
allows the elephant to traverse long distances, especially during seasonal mass migrations. Migrations involve traversing 480–640 km, while maintaining a constant speed for 3–4 h or ~16 km (Langman et al. 1995). The African elephant is known to migrate long distances at a leisurely pace and eventually dwell in open environments. The Asian elephant is found in more heterogeneous, forested environments, and partakes in fewer or no seasonal migrations (Hutchinson 2006).

## Additional Locomotor Activities

In addition to the gait patterns discussed, African elephants can also perform aquatic locomotion to travel from island to island during mainland food shortages. They can travel at a maximum speed of approximately 2.70 km/h and a maximum distance of 48 km. Their locomotion can be described as a “lunging, porpoise-like fashion,” which utilizes a three-step repeating sequence. First, the elephant takes a deep breath by exposing its trunk, top of its head, and half of its body. Second, the elephant submerges its body and begins its first stride. The trunk is kept  $45^\circ$  above water, acting as a snorkel, to assist with breathing. Finally, the elephant sweeps its trunk downward to propel itself forward, and the sequence repeats (Johnson 1980).

### Proboscidea

**Locomotion, Fig. 3** Net energetic cost of transport in African elephants. Data from Langman et al. (1995)



## Influence on Bioinspired Robotics

As described above, the elephant's trunk assists the elephant with moving through aquatic environments. The long and boneless trunk also allows the large terrestrial mammal to grasp and squeeze food particles together, create a pile, and then lift the particles to its mouth. Furthermore, the trunk is capable of curling around nonfood objects and elevating them (Wu et al. 2018). The ability of the trunk to grasp and manipulate objects has proven to be influential for soft robotics. Soft robotics is a field that generates robots using compliant materials inspired by those found in living systems. The dexterity and functionality of these innovative creations make them suitable for use by humans for “wearable, surgical, and collaborative robotics” (Mitchell et al. 2019). One such creation is the Soft Poly-Limb (SPL). The SPL is a fluid-driven and wearable system that is analogous to having an additional limb. Similar to the elephant trunk, the SPL helps the wearer surround, suction, and grasp an object up to 2.35 times greater than its own weight. This bioinspired creation can provide mobile assistance to both healthy and impaired users (Nguyen et al. 2019).

## Conclusion

This entry presents an overview of the elephant's major modes of locomotion. Elephants follow a lateral sequence footfall pattern regardless of speed. To shift to higher speeds, the elephant starts off by increasing its stride frequency and then shifts to increasing its stride length. Elephants are not capable of true running because they never achieve a whole-body aerial phase. Furthermore, despite their large dimensions, elephants can perform aquatic locomotion, a form of locomotion that has not been commonly attributed to them. The distinct locomotive behaviors of elephants make them an interesting class of mammals to study. Further knowledge of their gait sequences and trunk mechanics can continue to produce advances for the scientific community.

## Cross-References

- ▶ Activity Budget
- ▶ Adaptation
- ▶ Adaptedness of Behavior
- ▶ Basal Metabolic Rate (BMR)
- ▶ Common Ancestor
- ▶ Ecology
- ▶ Evolution
- ▶ Extinction in Learning
- ▶ Gait
- ▶ Herbivore
- ▶ Home Range
- ▶ Locomotion
- ▶ Migration
- ▶ Morphology
- ▶ Muscular System
- ▶ Natural Selection
- ▶ Navigation
- ▶ Paleontology
- ▶ Phylogeny
- ▶ Proboscidea Cognition
- ▶ Proboscidea Communication
- ▶ Proboscidea Diet
- ▶ Proboscidea Morphology
- ▶ Proboscidea Navigation
- ▶ Quadrupedal
- ▶ Sirenia Diet
- ▶ Sirenia Locomotion
- ▶ Sirenia Morphology
- ▶ Sirenia Navigation
- ▶ Sirenia Sensory Systems
- ▶ Taxa
- ▶ Terrestrial
- ▶ Woolly Mammoth
- ▶ Zoo
- ▶ Zoology

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## Proboscidea Morphology

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## Synonyms

Anatomy; Elephants; Function; Shape; Structure

## Definition

General structure of elephants, the only extant members of the order Proboscidea.

## Introduction

More than 160 Proboscidean species have existed over time (Sukumar 2003); however, only three remain (Payne 2003). The three extant members of the Proboscidea order are as follows: the Asian Elephant (*Elephas maximus*), the African Savannah Elephant (*Loxodonta africana*), and the African Forest Elephant (*Loxodonta cyclotis*) (de Silva 2010). Elephants are the largest terrestrial animals on the planet, and as such they have adapted a unique morphology to support such size. Elephants' closest relatives are sirenians, hyraxes, and aardvarks, the closest of these being the Sirenians (Sukumar 2003). Proboscidea originated approximately 60 million years ago, during the late Paleocene Epoch; however, only the three extant species remained by the end of the Pleistocene, during which over half of large mammals faced extinction (Sukumar 2003). Proboscideans went through extreme dwarfism and changes of shape before an overall increase in body size around 10,000 years ago (Sukumar 2003). Though Proboscidea fossils have been found on every continent except for Australia and Antarctica (Sukumar 2003), *Loxodonta* and *Elephas* share their origins in Africa during the late Miocene (Todd 2010). It is believed *Elephas*

left Africa during the last ice age in the Northern Hemisphere, roughly 35,000 years ago (Spinage 1994).

## Skeletal

Elephants are the archetype of the graviportal animals, or animals with large body size and long, columnar limbs (Hutchinson et al. 2006). African elephant cows average a height of 2.7 m tall and a weight of 2.5 tons; while African bulls average a height of just over 3 m tall, and a weight of 5.5 tons (Spinage 1994). Asian elephant cows average a height of 2.35 m tall and a weight of up to 2.54 tons; while Asian bulls average a height of 2.7 m and a weight of up to 4.16 tons (Spinage 1994). Elephants may be able to grow throughout the majority of their lives (Smuts and Bezuidenhout 1994). The tails of elephants can measure up to 1.5 m in length (Spinage 1994).

The femur is the longest bone in the elephant skeleton, capable of measuring over 1 m long (Smuts and Bezuidenhout 1994). An elephant's skeleton weighs roughly 16.5% of its total living weight (Spinage 1994). According to Gary West, elephant skeletons consist of over 200 bones, though Asian and African elephants differ slightly in structure; Asian elephants typically have 19 rib pairs and 33 caudal vertebra, whereas African elephants have 21 rib pairs and 26 caudal vertebra (Fowler and Mikota 2006). Elephants support about 60% of their weight on their fore-limbs (Spinage 1994). The bones that make up elephant limbs are very dense and have no bone marrow cavity, which make the bones stronger and more able to carry such great weight (Fowler and Mikota 2006).

## Brain

Animals with large brain size relative to body size exhibit heightened ability process and apply complex inputs (Garstang 2015). With weights ranging from 3.6 to 6.5 kg, elephants have the heaviest brains of any land mammal (Fowler and Mikota 2006). The heaviest elephant brain ever recorded

was 9.0 kg (Garstang 2015). The elephant brain is well-developed, and similarities between human and elephant brains emphasize a capability for higher thinking (Garstang 2015). Within the elephant brain, the cerebellum accounts for 18.6% of the entire brain, a relatively large proportion compared to humans (10.3%); this large cerebellum helps coordinate movements, locomotion, and posture and helps coordinate the complex movements associated with moving the trunk (Garstang 2015).

Elephants have large temporal lobes, associated with memory and learning, and large olfactory lobes, exhibiting a dependence on memory and olfaction (Fowler and Mikota 2006). The large temporal lobe is likely associated with the ability to communicate via infrasonic methods (Garstang 2015). The relative weight of both the temporal lobes and the cerebral cortex are the greatest of all mammals (Garstang 2015).

Elephants also have an abnormally large hippocampus, responsible for memory, emotion, spatial memory (Bohbot 2015), and for identifying individuals by way of social and chemical memory (Garstang 2015). Elephants' well-developed hippocampal structures allow for advanced processing ability, and the experimental evidence of Polansky et al. suggests elephants can recall the locations of other individuals relative to their own locations (Polansky et al. 2015).

## Reproduction

Temporal glands are unique to elephants and are present in all three species and in both males and females (Fowler and Mikota 2006). The female reproductive tract is about 3 m long, making it the longest of all land mammals; the vestibule, or the urogenital canal, accounts for a third of this length at over 1 m (Hildebrandt et al. 2010). The female reproductive tract consists of two ovaries, Fallopian tubes, bicornuate uterus, vagina, and vulva; the most unique features are the 1-m long urogenital canal and the pronounced clitoris (Sukumar 2003). The vagina can measure up to 50 cm in length and is internally marked by longitudinal folds (Hildebrandt et al. 2010).



The hymen ruptures during a cow's first delivery, which separates elephants from most mammals, whose hymens rupture during copulation (Hildebrandt et al. 2010). Birth weights range from 100 kg to 120 kg, and cows carry their calves for 22 months (Spinage 1994).

The bull's penis has an S-shaped structure when erect, allowing it to hook into the forward-directed vagina (Sukumar 2003). Bull elephants lack cooling mechanisms for their testes, unlike other mammals (Spinage 1994). Bull testes are located within the abdomen (Sukumar 2003), and near the kidneys (Spinage 1994). Testes can weigh up to three kilograms each (Spinage 1994).

## Integument System

Elephant skin color is usually gray, but may become brown or reddish depending on the substrate used for bathing (Fowler and Mikota 2006). Skin can be up to 3.2 cm thick on their backs and as thin as 1.8 mm on their ears (Fowler and Mikota 2006). Elephant skin contains complex polygonal columns, which act as studs in a wall, strengthening certain areas of the skin, particularly the forehead (Fowler and Mikota 2006). The skin on the trunk, breast, legs, ears, and groin are the thinnest areas (Spinage 1994). Elephant skin may be the largest sensory organ of the elephant (Fowler and Mikota 2006). Asian elephants are typically hairier than the African species, and fetal and newborn elephants are hairier than adult elephants (Fowler and Mikota 2006).

## Gastrointestinal

The elephant digestive tract begins with the mouth (which includes the trunk), and then continues into the pharynx, esophagus, stomach, small intestine, large intestine, cecum, rectum, and finally, the anus (Greene et al. 2019). Within the mouth, elephant tongues are attached to the floors of their mouths, and though they cannot protrude, they can fold in center; these tongues can weigh as much as 12 kg (Greene et al. 2019). Elephants lack a gallbladder, as do equids (Greene et al.

2019). The gastrointestinal tract of the elephant is approximately three times its body length, which is relatively short when compared to other herbivores; for example, the gastrointestinal tract of the horse is nearly 12 times its body length (Greene et al. 2019).

Similar to rabbits and horses, elephants are hind-gut fermenters, meaning the first significant fermentation site in the digestive tract is the cecum, and the main digestive area is the colon (Fowler and Mikota 2006). This inefficient method of digestion means that elephant must consume large amounts of low-quality forage in short amounts of time; therefore, wild elephants spend between 16 and 20 h eating each day (Fowler and Mikota 2006). The elephant cecum accounts for approximately 12% of its body weight (Greene et al. 2019). This means that the cecum of 10,000 pound elephant would weigh 1,200 pounds! Asian elephants are capable of digesting between 40% and 50% of their diet, whereas African elephants may digest as little as 22% (Greene et al. 2019). Elephants may defecate between 15 and 12 times daily, with average defecation weight of approximately 10 kg (Fowler and Mikota 2006).

## Elephant Trunk Morphology

The elephant trunk has quite the interesting anatomy as it is often perceived as a hand or nose, but on the inside appears as a tongue. One of the most commonly cited elephant facts in literature, media, and elephant outreach is *an elephant trunk has 40,000 muscles, or 150,000 muscle fibers* (Spinage 1997). However, this was only an estimation made by a French Naturalist Georges Cuvier at the beginning of the nineteenth century (Cuvier 1806). There is no current evidence of a proper estimation of the number of muscles inside of a trunk. Elephants have developed trunks to increase bite volume and bite mass. This allows them to increase their food consumption rate (Pretorius et al. 2016). The lack of any bone inside of the elephant trunk makes it very similar to that of octopus arms and tongues; these

three examples are known as muscular hydrostats (Kier and Smith 1985).

Three muscle types are found along the trunk including radial muscles located around the nasal passageways, longitudinal muscles located between the radial muscles and skin, and finally oblique muscles located on the ventral side of the trunk below the radial muscles (Kier and Smith 1985). These muscles allow the trunk to elongate, bend, and twist (Kier and Smith 1985). The two oblique muscles allow the trunk to move to the left or right. The most detailed account of elephant trunk muscle types is shown in the original 1909 monograph on the elephant head by JV Boas and Simon Paulli (Boas 1908). Based on cross-sectional observations of elephant trunks, octopi's arms, and various tongues, Kier (Kier and Smith 1985) posited that muscular hydrostats should satisfy constant volume when moving. It has been approximated these muscles contain a modulus of elasticity of 938 kPa through weight lifting experiments (Wilson et al. 1991).

On the outside of the muscle there is a thick layer of elephant skin that appears to be wrinkled. The wrinkled skin on the elephant functions different than that of the skin on the body, which assists with heat regulation and repelling insects (Martins et al. 2018). The skin of the elephant trunk is comprised of wrinkles near the tip that turn into folds as they approach the base of the elephant trunk. Both the skin on the elephant's body and trunk does not contain sweat glands (Spearman 1970). This is one of the reasons the elephant is constantly spraying itself with water and throwing dirt on their body for aiding thermoregulation.

Underneath the wrinkled skin of the elephant trunk are hairs, specifically vibrissal hairs (Spearman 1970). These vibrissal hairs are commonly referred to as whiskers, and they are sensing or tactile hairs (Prescott et al. 2011). It is unknown currently what the use and function of the whiskers along the elephant trunk are; however, there is a large cluster of the hairs near the tip of the elephant trunk.

Their prehensile trunks can pick up objects as small as a peanut (Onondera and Hicks 1999) and manipulate tools (Hart et al. 2008), demonstrating precise motor control. Anatomically, elephants

have underdeveloped occipital lobes compared to their olfactory and temporal lobes (Shoshani et al. 2006), which may indicate that they rely less on vision to accomplish motor tasks. Elephants can detect TNT with better accuracy than most trained bomb detection dogs (Miller et al. 2015). In fact, their ability to reach for food items may be impaired if the trunk cannot be used to sense olfactory cues (Foerder et al. 2011). However, elephants likely still utilize vision to accomplish reaching. Their retinas have a concentration of retinal ganglion cells in the upper temporal region, which corresponds to the area of the visual field where the trunk moves (Stone and Halasz 1989). Additionally, they can accurately discriminate visual cues that are less than a degree in width of the visual field (Shyan-Norwalt et al. 2010).

## Ears

African elephant ears are large, positioned above the neck, and shaped similarly to the continent of Africa, while Asian elephant ears are significantly smaller, positioned below the neck, and generally trapezoidal in shape (Fowler and Mikota 2006). Ears are supported by "lattice-like" areas of cartilage and they are used for more than just hearing; they are used for thermoregulation, balance, and communication (Fowler and Mikota 2006). Although they struggle with high-frequency sounds, elephants can hear low-frequency sounds more effectively than any other animal (Fowler and Mikota 2006). Utilizing infrasonic sounds, elephants can communicate over great distances (Fowler and Mikota 2006).

In all three elephant species, ears maintain a high surface area to volume ratio (Wright 1984). Elephant ears are important in thermoregulation because by flapping their ears, African elephants can increase up to 20% surface area for heat dissipation, and Asian elephants can increase their surface area by up to 10% (Fowler and Mikota 2006). Ears have a significant and extensive vascular supply, and are fanned often in warm temperatures (Wright 1984). Arteries in elephant ears constrict under cool weather conditions, and elephants tuck their ears against their sides to maintain body temperature (Wright 1984).

## Feet

Elephants are the largest land mammals, and their feet are uniquely fitted to accommodate massive weight (Weissengruber et al. 2006). Movement allows elephants to circulate blood from their feet back to the heart (Fowler and Mikota 2006). The bones of the foot lay on a unique fatty pad, or cushion, that aids in shock absorption and allows elephants to walk without stomping (Spinage 1994). The cushion is composed of sheets and strands of connective tissue that form large and small compartments filled with adipose tissue (Weissengruber et al. 2006). The cushion spreads when weight is upon it, allowing for the hefty load. It also reduces suction when walking through deep mud because the entire circumference of the foot shrinks as the elephant lifts its foot (Spinage 1994). In addition to weight distribution, the elephant foot's cushion may store or absorb mechanical force (Weissengruber et al. 2006).

The bones of an elephant's foot form an arch, similar to a human foot (Weissengruber et al. 2006). Each foot has five digits, though the amount of phalanges and nails vary by individual elephant (Fowler and Mikota 2006). Asian elephants typically have five nails on the front feet, and four on the rear, while African elephants typically have four on the front feet, and three on the rear (Spinage 1994). The sole of the hindfoot is smaller and more oval than the rounder front foot (Weissengruber et al. 2006).

The foot covering is composed of skin, toenails, and a cornified, though flexible sole called the slipper (Fowler and Mikota 2006). Toenails are large, relatively flat, and are embedded against the foot (Spinage 1994). Similar to humans, each elephant toenail has a cuticle, and is not weight bearing like a hoof (Fowler and Mikota 2006).

## Dentition

The enamel loops on the teeth of African Elephants are lozenge-shaped, thus the genus *Loxodonta* was named (Greene et al. 2019).

Elephant molars have a unique system of eruption and replacement (Todd 2010). Elephants go through six sets of four molars throughout their lives (Fowler and Mikota 2006). Molars are degraded and lost in sections, and replaced by new teeth which push from behind the old tooth (Fowler and Mikota 2006). Each new tooth is larger than the previous tooth, and each adult elephant molar may weigh greater than five kilograms (Fowler and Mikota 2006). Because of this unique system of replacing teeth, it is possible to approximate an elephant's age by examining its teeth and determining which set the elephant is on (Lindeque 1990).

All African elephants and male Asian elephants have prominent tusks, and female Asian elephants may have small tushes, or vestigial tusks (Fowler and Mikota 2006). Permanent tusks develop within 6–12 months of age, replacing deciduous tusks with no apparent function (Fowler and Mikota 2006). Tusks emerge from a sulcus on each side of the upper lip and are extensions of the upper second incisors (Fowler and Mikota 2006). Male tusks may grow as much as six times faster than female tusks, and all tusks average a growth rate of roughly 17 cm annually (Fowler and Mikota 2006). Elephant and hyrax tusks differ from other mammalian tusks in that their tusks develop from incisors instead of canines (Greene et al. 2019). Elephants have many functional uses for their tusks. They are used to dig for water, to strip bark from trees, to break branches, to carry heavy objects, and are used as weapons during conflicts (Fowler and Mikota 2006). As a person is right-handed or left-handed, elephants tend to be either right-tusked or left-tusked, and the dominant tusk is usually apparent in the degree of wear on the tusk (Fowler and Mikota 2006).

## Conclusion

Elephants are the largest of all land animals and as such have developed unique morphologies to support such size and intelligence. From a highly

capable brain to heavily adapted trunks and feet, elephants are truly unique.

## Cross-References

### ► Proboscidea Navigation

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## Proboscidea Navigation

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### Synonyms

[Locomotion](#); [Migration](#); [Movement](#)

### Definition

Why and how elephants move from a starting point to a target point.

### Introduction

Approximately 160 proboscidean species have populated the Earth; however, only three remain (Payne 2003). The three extant members of the Proboscidea order are as follows: the Asian Elephant (*Elephas maximus*), the African Savannah Elephant (*Loxodonta africana*), and the African Forest Elephant (*Loxodonta cyclotis*) (de Silva 2010). The demise of Proboscidea is likely due to humanity; in fact, 80% of elephant mortalities take place within a 25-mile radius of people (Roever 2013). Despite this, the three elephant species remain, largely in part due to their ability to navigate and adapt to an evolving world. Though the African species have been observed to walk further and faster than Asian elephants, it is clear that walking is critical to the health of all elephants (Mackey 2014). When moving, the pads of an elephant's foot compress and relax, allowing blood to circulate throughout the central venous system (Mackey 2014). Elephant movement has long been noted in various African and Asian cultures (Garstang et al. 2014).

### Locomotion

The largest of all terrestrial animals, elephants are the archetype of the graviportal animals, or

animals with large body size, columnar limbs, and a vertical posture (Hutchinson et al. 2006). Elephants are known for this vertical posture, which suggests their limbs have very little flexibility and their joint use is limited; however, recent studies have shown that elephant limbs are not usually vertical when supporting weight, especially while moving (Ren et al. 2008). Even while standing, joints maintain degrees of flexion (Ren et al. 2008). As elephants increase speed, they also increase flexion in their limbs, meaning leg posture is significantly different in a fast-moving elephant than in a stationary elephant, most likely because impact on stiff legs could have disastrous consequences in such large animals (Ren et al. 2008).

Elephants are efficient walkers because they are able to convert potential energy into kinetic energy and back via a mechanism similar to a pendulum, meaning muscular work is reduced (Genin et al. 2009). When moving at higher speeds, elephants utilize a bouncing mechanism of energy conversion in order to maximize efficiency (Genin et al. 2009). When moving, elephants move their feet in a lateral sequence, meaning the hind-foot of one side is always followed by the forefoot of the same side (Genin et al. 2009). Even at their highest speeds, elephants never alter their footfall pattern so that all 4 ft are off the ground in what is called an aerial phase, which is why they are unable to run in the classical sense of the word (Hutchinson et al. 2006).

Even though they cannot “run,” the fastest elephants can still move at speeds of up to 25 km/h, though only for short distances (Hutchinson et al. 2003). Elephants are able to gradually increase their speed without significantly changing the way they move their limbs (Ren et al. 2008). To increase speed, elephants increase the frequency of strides, then, when moving at higher speeds, increase stride length (Genin et al. 2009). Although it is maintained that elephants are incapable of running because they exhibit no aerial phase, their hips do exhibit a downward, then upward motion during top speeds, which suggests they are indeed running; however, more evidence is needed on the ground-



force of movement before this matter is resolved (Hutchinson et al. 2003).

## Herd Dynamics and Navigation

Togetherness is a necessity in elephants. Family or herd members spend the majority of their time together, over 80%, and they exhibit coordination in all facets: defense, raising of offspring, and locating resources (Vidya and Sukumar 2005). The matriarch is usually the oldest and most experienced female in the family and is an invaluable source of information for the location of resources (Vidya and Sukumar 2005). Although African elephants typically travel in small family groups, great precipitation events or disasters can lead to aggregations of over 100 individuals (Spinage 1994).

## Sensory Modality of Navigation

Elephants rely heavily on acoustic and olfactory methods of perceiving their environment, rather than vision (Plotnik and de Waal 2014). Elephant vision is limited past 50 m; therefore, they must rely on their other senses when navigating (Garstang 2015).

Often, elephants navigate their way to food sources by smell (Plotnik et al. 2014). Compared to most of the animal kingdom, elephant olfaction is nothing short of amazing. The African elephant genome contains the largest olfactory receptor repertoire of any species ever studied (Nimura et al. 2014). In one study on Asian elephants, individuals were able to discriminate between 24 odor pairs, with each odor only differing by one carbon molecule (Nimura et al. 2014). Elephants may even use olfactory cues from food, water, and other elephants when making migratory decisions, not only for the daily location of foods (Plotnik et al. 2014). Elephants also utilize olfaction to avoid danger. By sniffing out individual mines, Namibian elephants were observed navigating across minefields without injury (Garstang 2015). Elephants also use olfaction for mate-finding (Nimura et al. 2014).

Acoustic ability is equally important to elephant navigation. Elephants can detect low-frequency calls from distances of several kilometers and can even pick up infrasonic signals (de Silva 2010). Separate elephant herds in Namibia exhibited near-simultaneous changes in direction when rainfall occurred over 100 km away, and infrasound created by the rain system is believed to be the trigger for the changes in movement (Garstang et al. 2014). Vocalizations between individuals and herds aid elephants in finding or keeping distance between separate herds. Asian elephants have been observed to vocalize in at least 14 distinct categories that serve various spatial and social functions. Growls and rumbles are unique to individuals and are often used for locating one another or maintaining separation between other herds. Elephants also use acoustic signals for finding mates, especially in African savannah elephants (de Silva 2010).

## Brain, Memory, and Navigation

Since matriarchs lead their herds to food and water by memory, it is logical that herds with more experienced matriarchs, who maintain massive stores of spatial memory, demonstrate higher survival rates during rough periods of drought or famine (Garstang 2015). Because of excellent long-term memory, elephants are able to remember remote areas of food and water and navigate to those areas over great distances of indistinct landscapes; in fact, Namibian elephants have been observed locating oases that had not been visited for over 20 years (Garstang 2015). When switching between watering areas in Namibia, elephants move directly but not always to the closest water source, suggesting memory of resource availability at different times of the year (Polansky et al. 2015). African savannah elephants are believed to utilize spatial memory strategies to navigate their environments, which may be due to their robust hippocampal structures (Bohbot 2015).

Spatial memory is characterized by the ability to straight-line navigate to a target, even from different starting points, and is found to be

dependent on the hippocampus (Bohbot 2015). Elephants take direct trajectories to water holes, which is indicative of the spatial memory strategies used by humans to navigate (Bohbot 2015). Spatial memory may be the major mechanism elephants use to navigate their habitats, especially when locating sources of water (Polansky et al. 2015). This means that elephants can form and follow cognitive maps and then use those maps to take direct routes to specific locations (Bohbot 2015). Cognitive maps are flexible collections of spatial information that can be manipulated so that elephants can discover novel ways to a certain destination, which is different from a rigid, stimulus-driven route that cannot be altered (Bohbot 2015).

Patterns of elephant movement have been detected monthly, seasonally, annually, and over multiyear periods, meaning elephants can pick up on vegetation patterns that span years (Birkett et al. 2012). In India, Asian elephants use well-worn paths in search of food (Spinage 1994). Asian elephants are also capable of adjusting these routes and migration patterns to adapt to human encroachment (Johnsingh and Williams 1999). For example, Asian elephants in India stopped using a centuries-old migration corridor within 10 years of a railroad being built within the corridor (Johnsingh and Williams 1999).

## Home Range

African Savannah elephants inhabit East and Southern African Savannas, and one population exists in the desert region of Namibia; African Forest elephants inhabit equatorial rainforests in Western and Central Africa; and Asian elephants live in forests and forest edges of India, Southeast Asia, and Island Asia (Payne 2003). Though habitats differ across the three species, water, tree cover, slope, and human presence are important factors in habitat selection for all elephants (Roever 2013). Elephant home ranges can stretch anywhere from 200 km<sup>2</sup> to 11,000 km<sup>2</sup> (Mackey 2014). Typical herd behavior involves remaining in one part of the home range for up to 3 days before moving onto another spot (Spinage 1994).

Elephant ranges shrink with increased elevation (Bohrer et al. 2014). Home range changes seasonally in many elephants depending on the availability of water. Most elephants return continually to the same dry season home range in proximity to a permanent water source. These areas become overused in the dry season (Spinage 1994). Desert-dwelling Savannah elephants have significantly larger home ranges during the wet seasons than during dry seasons, due to water availability (Bohrer et al. 2014). Radio-collared elephants have been noted to stray over 40 km away from permanent water sources in the wet season, but no more than 16 km away during the dry season (Spinage 1994). It is important to note that changes in elephant home ranges also occur because of proximity to people. Fifty-eight percent of the Savannah elephant population lives in Southern Africa, and 72% of these elephants' ranges exist beyond protected spaces (Roever 2013).

## Migration

It was once believed that all elephants must partake in long, seasonal migrations to satisfy their feeding needs. There is even one recorded observation of approximately 2000 elephants migrating over 100 km to the coast (Spinage 1994). Though elephants surely have migrated long distances and in large groups, this is not true of all elephants. Asian elephants have not been known to conduct large migrations (de Silva 2010). The movements of African savannah elephants are heavily influenced by precipitation, temperature, and primary productivity in the area (Birkett et al. 2012). In both Asia and Africa, fires influence elephant movement by forcing them to leave burning areas, though they usually return to the area following the flush of green vegetation that occurs after fires (Spinage 1994). Elephants migrate quickly in response to both large-scale and small-scale precipitation events that affect the availability of food and water (Bohrer et al. 2014). These movements are usually performed within family units; however, during large-scale precipitation events, aggregations of up to 1000 individuals have

been observed. Elephants do not migrate as birds do, based on some predetermined signal; instead, they follow foliage and rainfall, which may bring multiple herds to move in the same direction (Spinage 1994).

In favorable conditions, elephants are less likely to leave their home ranges, while elephants in unfavorable year-round climates undergo seasonal migrations. Thus, the average distances traveled by elephants vary greatly (Spinage 1994). Aside from seasonal movements, monthly, annual, and multiyear patterns have been detected in elephants (Birkett et al. 2012). The average straight-line distance of these migrations is roughly 73 km, with a total distance of 90 km. Distance traveled during migration depends on the home range. For example, the Gourma elephants of Mali travel 800 km in a seasonal round trip, crossing up to 80 km daily (Spinage 1994).

### Precipitation and Availability of Food

Elephants spend between 60% and 80% of their day foraging, or searching for food (Mackey 2014). In African savannahs, vegetation changes with seasonal changes in rainfall; thus, rainfall patterns significantly affect the movements of savannah elephants because they shift their patterns to match the availability of food (Birkett et al. 2012). Elephants have been known to abruptly travel between 30 and 50 km in several days to areas of plentiful grazing following large-scale precipitation events (Spinage 1994). In fact, elephants are so sensitive to rainfall that separate elephant herds in Namibia exhibited nearly simultaneous changes in movement when rainfall was occurring over 100 km away (Garstang et al. 2014).

Elephants exhibit seasonal changes in behavior, according to rainfall patterns. African savannah elephants increase their speed of movement during the wet season. Then, they decrease movement at the end of the wet season and the beginning of the dry season, in preparation for the changes in precipitation and availability of foliage (Birkett et al. 2012). In the dry season, movements are restricted to areas within a certain proximity of

a permanent water source. Elephants may not move farther than three kilometers away from a water source during these times (Spinage 1994).

In terms of elevation, elephants tend to move up and down in accordance with the growth and decline of vegetation. When habitats are green and food is plentiful, elephants occupy lower elevations; however, they return to higher areas with evergreen forests when food starts to dry up (Bohrer et al. 2014). Elephants that inhabit flood-plains exhibit not only seasonal but daily patterns of movement, particularly in the dry season. They have been observed to stay in wooded areas in the day, and venture into the flood-plains in the evenings (Spinage 1994).

### Mate-Finding

Movement in elephants, where they are headed, and how fast they move to get there, can also depend on reproductive status, not just on resource availability (Mackey 2014). This is especially true in bulls, which range in search of cows regardless of resource availability (Spinage 1994). Bulls search for cows during the periodic condition of musth, during which they release an oily secretion from their temporal glands, which identifies them to cows (Nimura et al. 2014). Though African Savannah cows cover shorter distances during the drier seasons due to a shortage of foliage, bulls may travel longer distances to find mates (Birkett et al. 2012). Bulls not only find females by olfaction, but through acoustic signals (de Silva 2010). Intense mating can occur during large aggregations, though these incidents seem to be opportunistic as the reason for grouping is thought to be the availability of food (Spinage 1994).

### Conclusion

Elephants are often associated with grandiose ideas of navigation and migration; however, elephant movements are not always so simple. Elephants rely heavily on their senses to get where they are going, especially acoustics and olfaction.

Typically, African elephants are led by a matriarch, which relies heavily on memory to navigate, even following a cognitive map. Elephants move following the availability of food and water, which both depend on rainfall events. Specifically, bull elephant movements are influenced by the need to reproduce, while cow movement usually follows vegetation. Proboscidea navigation is a fascinating topic and one that will undoubtedly be studied for generations to come.

## Cross-References

### ► Proboscidea Morphology

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## Procavia capensis

### ► Hyracoidea

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## Procedural Memories

- [Cognition](#)

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## Process

- [Coding](#)

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## Process of Elimination

- [Reasoning by Exclusion](#)

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## Productiveness

- [Fertility](#)

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## Productivity

- [Cognition](#)

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## Progesterone

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## Synonyms

[4-Pregnene-3,20-dione](#)

## Definition

An endogenous steroid hormone, derived from cholesterol.

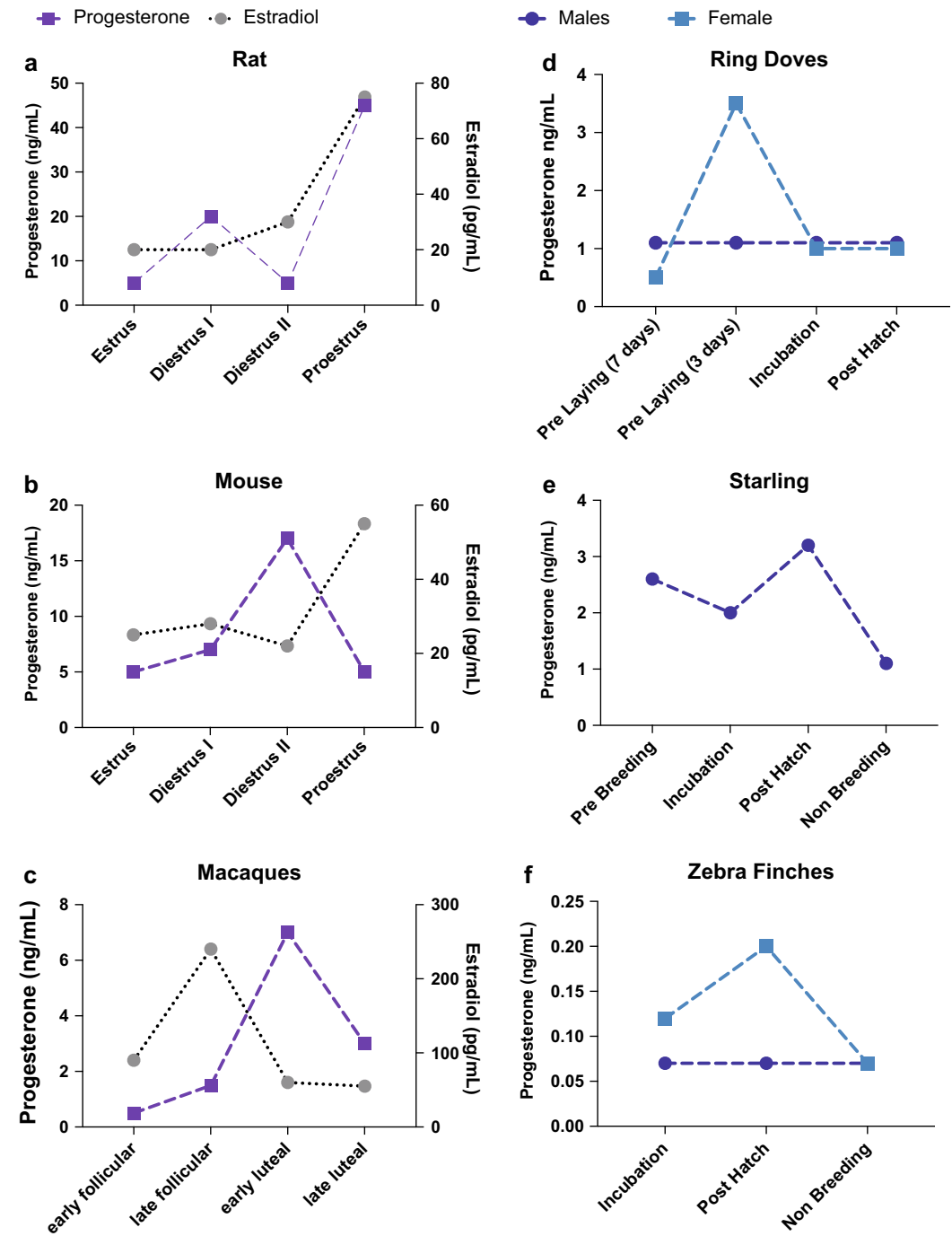
## Summary

The effects of progesterone on the brain and behavior have been studied since the early 1900s. Across vertebrate taxa progesterone has been linked to the regulation of reproduction (Adkins-Regan 2005) (Fig. 1). Beyond reproduction, researchers in the fields of animal behavior, behavioral endocrinology, and neuroendocrinology have utilized a variety of techniques and methods to investigate the role of progesterone in a range of behaviors across contexts. Some of the long-standing methods used include the measurement of steroids via enzyme and radioimmunoassays, pharmacological manipulations (e.g., progesterone and progesterone receptor (PR) antagonists) both globally and locally in the brain, and autoradiography to describe the distribution of PRs. To further elucidate PR function, those techniques have recently been complemented by the integration of genomic methods and technologies such as targeted disruption of PR action via administration of antisense oligonucleotides and mutant strains of mice with PR deficiencies. Interdisciplinary research on progesterone has revealed interesting differences in the effects of progesterone across species and has led to many new discoveries in the molecular mechanisms by which steroids act in the brain to affect behavior.

## A Classical Endocrinology Perspective: Where Is Progesterone Made and How Does It Act?

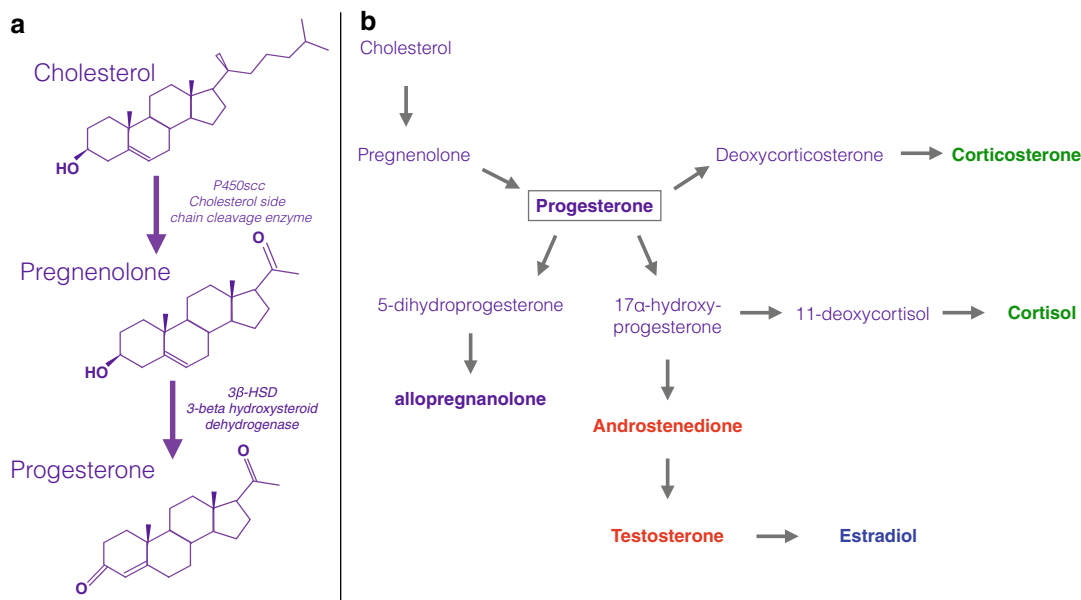
Progesterone is a steroid hormone that is produced in the gonads and adrenal glands. Unlike some hormones, such as oxytocin and prolactin, steroid hormones are not encoded within the genome, but rather are derived from cholesterol via the activities of steroidogenic enzymes (Fig. 2). Progesterone occurs relatively early in the steroidogenic pathway (Fig. 2); thus in addition to effects via its own receptor, it can also function as a pro-hormone and be converted into other behaviorally relevant steroids (e.g., corticosteroids, androgens, and/or estrogens) in target tissues.





**Progesterone, Fig. 1** Endogenous cycles of progesterone across species. Panels (a–c) show circulating estradiol and progesterone in female mammals: (a) and (b) depict changes in female rats and mice across the estrus cycle (Redrawn from Walmer et al. 1992 mouse; Butcher et al. 1974 rat); (c) depicts changes in macaques across the menstrual cycle (Redrawn

from Kromrey et al. 2015). Panels (d–f) show circulating progesterone levels in female and/or male birds. (d) Ring doves, *Streptopelia capicola* (Redrawn from Silver 1978). (e) Starlings, Sturnidae (Redrawn from Ball and Wingfield 1987). (f) Wild zebra finches, *Taeniopygia guttata* (Redrawn from Prior et al. 2016).



**Progesterone, Fig. 2** A simplified schematic of the steroidogenic pathway. Panel (a) shows cholesterol conversion into progesterone by two steroidogenic enzymes (cholesterol side-chain cleavage enzyme and *3β-HSD* 3-beta hydroxysteroid dehydrogenase). Panel (b) shows the

downstream modifications that progesterone goes through as it is metabolized into glucocorticoids (depicted in green), androgens (depicted in red), and estrogens (depicted in blue)

Progesterone's effects on behavior are largely mediated by its action in the brain. As with other steroid hormones, progesterone is membrane permeable and thus can easily cross the cell membrane and bind the cytosolic PR. Ligand-bound PRs then form dimers that bind DNA and function as transcription factors, affecting physiology and behavior through modification of gene transcription (Fig. 3).

### Distribution of the PR in the Vertebrate Brain

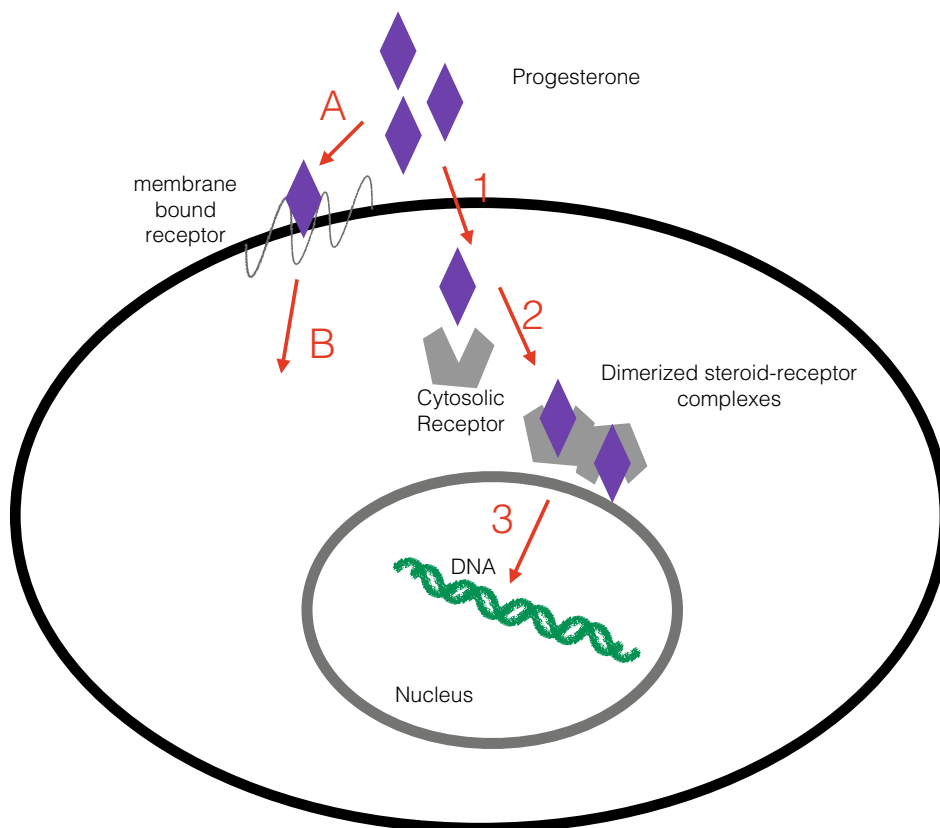
The distribution of PRs has been described across several vertebrate taxa, including some species of lizards, frogs, and fish as well as several bird and mammal species. Most of the behavioral effects described here have been associated with PR action in key brain regions within the hypothalamus, the amygdala, and the striatum. Variation in the expression of PR within these brain regions has been related to

variation in social behavior. There are two primary progesterone receptors (PR-A and PR-B), which affect transcriptional activity of PR-responsive genes to differing extents. Generally these receptors co-occur in specific brain regions. However, the ratio of PR-A and PR-B in these regions is hormone-, region-, and sex-dependent (Becker et al. 2007).

### Beyond the Classical Perspective

There exist many nuances and complexities at each level of progesterone action described above in the classical perspective (Mani and Oyola 2012). Importantly, such complexities likely reflect the potential for subtle and context-dependent effects of progesterone on the brain and behavior:

- Steroidogenic enzymes have been found throughout the vertebrate brain, and evidence that the brain can synthesize steroids de novo



**Progesterone, Fig. 3** Schematic illustration of the two predominate modes of action of progesterone. One pathway, steps 1–3, shows progesterone binding to intracellular cytosolic progesterone receptor (PR), dimerizing and

affecting gene transcription. A second pathway, steps A and B, shows progesterone binding to a transmembrane protein receptor, having subsequent effects in the signal transduction pathway

from cholesterol has been confirmed in numerous species. This means the brain itself can synthesize progesterone during periods when circulating levels are low.

- Allopregnanolone, a predominately brain-derived metabolite of progesterone (Fig. 2), is a potent ligand for the GABA<sub>A</sub> receptor (the receptor for GABA, the primary inhibitory neurotransmitter). This discovery in the 1980s explained why large doses of progesterone had anesthetic and barbiturate effects.
- Progesterone can bind to transmembrane receptors (Fig. 3), which can activate rapid nonclassical signal transduction pathways (via activation of second messenger signaling or kinase cascades) and could impact behavior within minutes.

- The PR can have genomic effects in the absence of progesterone binding, through ligand-independent activation by coregulators or through binding of alternate steroids such as estradiol or neurotransmitters.

### Differential Effects of Progesterone on Sexual and Receptive Behavior in Rodents

Extensive research has been conducted on progesterone and female sexual behavior in rats, guinea pigs, and mice (Blaustein and Mani 2007). Some of the earliest research used ovariectomized rodents to identify the dose and timing of steroids necessary in order to activate reproductive and

sexual behaviors. The generalizable pattern that has emerged is that several “priming” doses of estradiol followed by progesterone exposure are required to elicit an optimal behavioral response. This relationship is largely due to the fact that estradiol is a potent regulator of the PR gene. Following estradiol priming, lordosis, the paracopulatory behavior associated with female receptivity in rodents, can be observed within 1 h of progesterone treatment and is maximal 2 h after treatment (Glaser et al. 1983).

The primary mechanism through which progesterone regulates female sexual behavior appears to be through genomic PR action. For example, female PR-deficient mutant mice are sexually unresponsive to progesterone administration following appropriate priming of estradiol. However, a general caveat with mutant mice strains is that the targeted gene disruptions are present throughout development; thus, it is not possible to distinguish between the effects of hormones on the organization of the brain during development versus acute effects of treatment in adulthood.

### **Role of Progesterone in Courtship Parental Behavior and Pair Bonding in Birds**

Identification of progesterone as a regulator of avian reproductive behavior dates to the 1940s. Research on poultry demonstrated that progesterone inhibits egg laying and identified the female oviduct as a key target of progesterone action. Some of the earliest behavioral research examined the role of progesterone in the regulation of courtship and parental behavior in male and female ring doves. Like the majority of bird species, ring doves form monogamous pair bonds and engage in biparental care. Komisaruk (1967) chronically implanted progesterone into different brain areas in both males and females in order to determine where progesterone was acting in the brain to influence behavior. Progesterone implants in the preoptic nuclei and lateral forebrain were found to induce parental behavior (incubation) in both males and females but inhibited male courtship behavior.

A more recent study by Smiley et al. (2012) investigated the role of progesterone on pairing behavior in another monogamous bird species, the Australian zebra finch. Here the authors focused on comparing the effects of progesterone administration on pairing behavior during courtship and bond formation versus pairing behavior after bond formation (pair bond maintenance). Interestingly, they found that while injections of progesterone increased pairing behavior (e.g., clumping) during pair bond formation, they saw no effect of progesterone administration on pairing behavior in couples that already had established pair bonds.

### **Progesterone in the Avian Sex Role Reversed**

Although progesterone has been widely implicated in the regulation of reproductive behaviors, there are many interesting species-specific differences in how this occurs. One great example of such variation can be seen in free-living female African black coucals, *Centropus grillii* (Goymann et al. 2008). In this species females are polyandrous (having several male mates) and defend territories. Whereas for many temperate breeding songbirds testosterone is implicated in the regulation of territorial aggression, in this species research suggests that progesterone is a key hormone regulating the timing of territorial aggression by attenuating female aggressive displays. Further research could clarify whether progesterone is affecting behavior via action on its own receptor or whether it is functioning as a prohormone.

### **Progesterone in Whiptail Lizards**

Another stunning example of the variation that exists is the role of progesterone in sexual behavior of whiptail lizards. *Cnemidophorus uniparens* is a unisexual (all-female) species of whiptail lizard. In this species, like closely related species of whiptail lizards, females become sexually receptive when preovulatory estradiol is high. However, *C. uniparens* females have increased

fecundity if they have copulated (sperm is not necessary). During the postovulatory phase, when progesterone levels are high, *C. uniparens* females will mount other females and thus facilitate reproduction of other individuals (Crews et al. 1986). Interestingly, although it is not as effective as testosterone, progesterone also stimulates mounting in castrated males of another closely related species, *C. inornatus*.

### Progesterone and Social Dominance in the African Cichlids

African cichlids are model species for research on the physiological basis of social behavior. In the species *Astatotilapia burtoni*, males can be dominant (brightly colored and aggressive defenders of territories) or subordinate (dull in coloration and reproductively suppressed). Interestingly, PRs have different effects on dominant and subordinate males. In dominant males, PRs facilitate courtship behavior, whereas in subordinate males it appears to modulate their perception of social threats (O'Connell and Hofmann 2012). This is a good illustration of the context-dependent effects of progesterone.

### Progesterone and Cognition in Animal Models

The majority of research focused on the effects of progesterone on cognition is motivated by a desire to understand the side effects of contraceptives and hormone replacement for women. There are several lines of research in rodents and nonhuman primates testing the effect of combinations of progesterone- and estradiol-like hormones paralleling the human pharmaceutical options on various aspects of cognition (Lacreuse 2006).

For example, Kromrey et al. (2015) related circulating progesterone levels in female cynomolgus monkeys to the acquisition and maintenance of a discrimination operant task. Consistent with the patterns described in humans, they found relationships between progesterone levels and performance during the acquisition

but not maintenance phase. Specifically, females with higher progesterone levels took more trials to acquire the discrimination task and made more errors.

In general, although the effects of progesterone appear to depend on the task, the general pattern that has been described is that progesterone is detrimental to female cognition. From human research, progesterone seems to predominately have negative effects on cognitive tasks involving spatial reasoning, target direct motor tasks, and mathematical reasoning, whereas progesterone seems to have no effect and may even improve performance on tasks involving verbal fluency and fine motor skills.

### Conclusion

This article provides an introduction to the basic endocrinology of progesterone, the methodologies researchers use to study the effects of progesterone on animal behavior and cognition, as well as a brief overview of some of the key findings from both classical and recent research. While progesterone has fundamental and essential functions as a female reproductive hormone, it also has context-specific effects on a wide range of behaviors and cognition in both males and females. Future research is likely to expand on our current knowledge by further describing the environmental factors influencing complex signaling pathways of progesterone and linking these neuroendocrine mechanisms to progesterone's context-dependent regulation of behavior.

### Cross-References

- [Endocrine System](#)
- [Estrogen](#)
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- **Reproductive System**
- **Sex Differences**
- **Testosterone**

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## Progressive Deterioration

- **Senescence**

## Proisocortex

- **Perirhinal Cortex**

## Prolactin

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## Synonyms

Galactin; Lactogen; Lactogenic hormone; Luteotropic hormone; Luteotropin; Mammotropin; PRL

## Definition

A polypeptide hormone associated with parental care, lactation, osmoregulation, reproduction, and immune function in vertebrates.

## Introduction

Prolactin (PRL) is a 23 kDa single-chain polypeptide hormone most notable for being associated with parental care in vertebrates and lactation in mammals and some bird species. While named for its role in lactation, prolactin is also important for osmoregulation in fish and acts both directly and via interaction with other hormones in functions throughout the body.

## Overview

Evolution of prolactin is hypothesized to be the result of gene duplication, which also produced growth hormone (GH) and somatolactin (SL) (Ocampo Daza et al. 2009). Prolactin was named by Oscar Riddle who purified it and developed its original bioassay. However, prolactin is an extremely versatile hormone that is associated with over 300 biological functions (Bole-Feysot et al. 1998; Freeman et al. 2000; Whittingham and Wilson 2013). Prolactin is a conserved hormone across the vertebrate clade. With reference to behavior and cognition, it is associated with reproduction and parental care in some species. However, it also plays roles in osmoregulation, growth and development, metabolism, angiogenesis, integument regulation, and immune function (Freeman et al. 2000; Marano and Ben-Jonathan 2014; Horseman and Gregerson 2014). Both circadian and circannual rhythms in prolactin secretion have been observed (Freeman et al. 2000).

Prolactin is mainly secreted from lactotroph cells in the anterior lobe of the pituitary. Studies of radiolabeled prolactin indicate that it can cross the blood-brain barrier (Freeman et al. 2000; Marano and Ben-Jonathan 2014). Extrapituitary prolactin has been found in various regions of the

brain, spinal cord, ovaries, decidua, tonsils, thymus, lymph nodes, spleen, lacrimal gland, sweat glands, hair follicles, skin, endothelial cells, mammary glands and their adipose deposits, cochlea, and male gonads (Bole-Feysot et al. 1998; Freeman et al. 2000; Marano and Ben-Jonathan 2014). Prolactin can act as a regulator of immune function and is associated with lymphocytes; extrapituitary prolactin expression has been observed throughout the immune system (Marano and Ben-Jonathan 2014). Prolactin receptors (PRLR) are members of the class I cytokine receptors and have been found in many tissues throughout the body including the mammary glands, brain, pituitary, uterus, ovaries, thymus, spleen, liver, pancreas, adrenal glands, heart, integument, gills, intestine, kidney, fertilized eggs (fish), bones, skeletal muscle, central nervous system, and in immune cells (including monocytes, macrophages, lymphocytes, natural killer cells, and granulocytes) (Freeman et al. 2000; Bole-Feysot et al. 1998; Whittingham and Wilson 2013).

The prolactin signaling mechanism is known as the JAK-STAT pathway. This involves phosphorylation of tyrosine kinase Jak2 and consequent phosphorylation of several STAT transcription factors (Freeman et al. 2000). Prolactin may influence the MAP kinase pathway (Whittington and Wilson 2013). It may occur in multiple isoforms within a species and is highly similar in structure to another hormone of the anterior pituitary, growth hormone (GH). The prolactin receptor also occurs in multiple isoforms with variable function (Freeman et al. 2000). Human GH is a functional ligand for human PRLR, though it binds differently from PRL suggesting flexibility on the part of the receptor in ligand activation (Langenheim et al. 2006). Additional prolactin-like proteins can also function as auto- or paracrine ligands for PRLR. Similarity to GH can complicate the study of prolactin in nonmodel organisms, particularly where animals are treated with exogenous hormone derived from a different species. Prolactin and prolactin receptor genes have been cloned in mammals, birds, reptiles, amphibians, and fish (Kato et al. 2005).

## Function in Vertebrates

### Fish, Amphibians, and Reptiles

In fish, prolactin has been implicated in osmoregulation, reproductive development and cycling, migration, pigmentation, immune function, growth, and parental care (e.g., mouth brooding, nest building/pit-digging, nest fanning, nest defense, nutrient provisioning) though specific function varies across species (Whittingham and Wilson 2013). It is likely important for development in anadromous fish where prolactin appears to mediate the osmoregulatory changes required for acclimating to changes in water salinity, with specific implication in adaptation to freshwater (Whittingham and Wilson 2013). Increased prolactin, both circulating and mRNA expression, has been associated with changes in water salinity, with implications that it may influence migratory behavior; however, its role here is not well understood (Whittingham and Wilson 2013). In amphibians, prolactin secretion has been observed in association with developmental metamorphosis; while several relevant actions have been documented, the details of its role remain controversial (Denver 2013). Prolactin purification has not been confirmed through development of a bioassay in reptiles, and study of its effects in this clade is limited (Norris and Carr 2013). Molecular study of prolactin gene expression has been conducted in at least one reptile species (Kato et al. 2005).

### Birds and Mammals

In birds, prolactin is associated with parental care (i.e., contact incubation, broodiness, chick-feeding, and alloparenting) in both sexes and lactation in several species that produce crop-milk (Buntin 1996). Prolactin increases with the duration of incubation period in birds and, while generally attributed to incubation behavior, must act in concert with sex steroid hormones to induce and maintain contact incubation in adults (Buntin 1996; Angelier et al. 2016). In Columbiformes (i.e., pigeons and doves) circulating prolactin levels are delayed, not rising until 5–7 days into incubation, which has been attributed to the production of crop-milk that parents of this group

feed their young (Buntin 1996). The induction of crop-milk in pigeons was significant as an early quantitative bioassay used to measure hormone levels in mammalian samples (Horseman and Gregerson 2014). Prolactin also mediates parental response to chick food demand with parents responding to increased begging of food-deprived chicks with higher feeding rates, increased prolactin secretion, and higher crop-milk production (Buntin 1996); however, species differences in circulating prolactin vary during the chick-rearing period (Buntin 1996). This variation during the chick-rearing period is associated with altriciality, meaning precocial birds tend to decrease prolactin, while altricial birds maintain higher levels (Buntin 1996; Angelier et al. 2016). Prolactin has also been implicated in premigratory fattening in some avian species (Wingfield et al. 1990).

In mammals, it is associated with reproductive development and cycling, lactation, and maternal behavior though the influence of prolactin differs between groups (e.g., prolactin is associated with maternal behavior in rodents but does not seem to be important in nonhuman primates, Freeman et al. 2000). It is also generally associated with paternal behavior in mammals though, again, this is not universal (Nelson and Kriegsfeld 2016). During lactation, circulating prolactin acts in concert with other hormones to stimulate the mammary glands to produce milk (Freeman et al. 2000). Some prolactin makes its way into milk where it is ingested by the young and plays a role in the maturation of several key systems (i.e., immune and neuroendocrine, Freeman et al. 2000).

### Common Promoters and Inhibitors

Prolactin is stimulated by nursing young in mammals and inhibited by stressors. The presence of young stimulates secretion of prolactin (Buntin 1996). In both birds and mammals, stress (and associated glucocorticoid hormones) is associated with reduced circulating prolactin levels (Freeman et al. 2000; Angelier et al. 2009; Angelier et al. 2016). This inhibition is primarily controlled by the hypothalamus through prolactin-releasing factors and prolactin-

inhibiting factors. In birds, increased circulating corticosterone and lower prolactin levels are correlated with lower levels of parental investment (Angelier et al. 2009; Angelier et al. 2016).

Hormones that generally promote increases in prolactin in mammals include vasoactive intestinal peptide (VIP), thyroid-releasing hormone (TRH), oxytocin, vasopressin, cytokines, galanin, neurotensin, serotonin, gonadotropin-releasing hormone, estradiol, ghrelin, and growth hormone secretagogue (Freeman et al. 2000). Common inhibitors of prolactin include dopamine, GABA, somatostatin, prolactin, acetylcholine, glucocorticoids, and cannabinoids (Freeman et al. 2000). Opioids, by blocking dopamine, may increase PRL. A hypothalamic inhibitory regulator, presumptively referred to as “prolactin release inhibitory hormone” (PRIH), is most likely dopamine (Freeman et al. 2000, Norris and Carr 2013). Other hormones (e.g., estrogen, progesterone) may also influence tissue responsiveness to prolactin, resulting in synergistic or antagonistic effects (Norris and Carr 2013).

## Cross-References

- [Hypothalamus](#)
- [Immunity](#)
- [Incubation](#)
- [Pituitary Gland](#)
- [Stress](#)
- [Thyroid and Adrenal Glands](#)

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## Promiscuity

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## Definition

Indiscriminate mating with multiple partners

## What Is Promiscuity?

Promiscuity means mating with multiple partners in an indiscriminate way, that is, without any selection-based process or quality-based discrimination of mating partners. Contrary to popular belief, promiscuity does not merely mean mating or engaging in sexual activities profusely with different partners. The misuse of the term “promiscuity” in behavioral sciences and evolutionary biology has been pointed out before (Elgar et al. 2013), and the improper use of the term extends to other areas including evolutionary psychology.

The “without choice” qualifier of the term is important because in spite of the fact that males and females mate with multiple partners in most sexually reproducing animal species, in the majority of these species sexual interactions are governed by mate selection criteria. Thus, applying the strict and correct definition of promiscuity would render very few animals promiscuous indeed. Conversely, if a broader definition of promiscuity was used (e.g., as in “to mate with multiple partners”), then most sexually reproducing species would exhibit promiscuity.

## Promiscuity and Mating Systems

Mating systems are defined by whether individuals associate with one or more sexual partners, and by the sex that engages in multiple sexual interactions with members of the opposite sex. Polyandry occurs when females mate with several males within the same reproductive cycle, polygyny defines the system where males mate with multiple females, and polygynandry takes places when both sexes engage in sexual interactions with multiple partners. These three mating systems are polygamous systems, meaning that either sex or both of them mate with multiple individuals of the opposite sex. They differ from a monogamous mating system in that in such a system each individual of a given sex mates just with one individual of the opposite sex (at least during each discrete reproductive cycle). Promiscuous behavior is possible within polygamous mating systems. It may also occur under social

monogamy if individuals engage in copulations outside the social pair-bond (extra-pair copulations).

The terms to define the different mating systems are also used to define behaviors. For instance, polyandry is generally used in the scientific literature to denote the multiple-mates mating behavior of females, even if this behavior occurs outside a formal polyandrous mating system in which females monopolize males. Henceforth, polyandry and polygyny terms will be used in this broad sense, that is, referring to the behavior of multiple mating of females and males respectively.

Interestingly, it has become apparent that many so-called monogamous species are monogamous from a social, but not from a genetic, perspective. The application of modern DNA fingerprinting technology has revealed overwhelming evidence that female multiple mating, the ensuing sperm competition (competition among the sperm from two or more males for the fertilization of a female's ova), and multiple paternity are much more widespread phenomena than it was previously thought (Birkhead and Møller 1998; Birkhead 2000; Barash and Lipton 2001). As an example, the male-female pair bonds established by the great majority (90%) of bird species have proven to be not so tightly bonded. Paternity analyses of broods have uncovered that females in over 70% of these “monogamous” species engage in extrapair copulations (Birkhead 2000; Griffith et al. 2002). In other words, most bird species are socially monogamous but they exhibit genetic polyandry (and genetic polygyny). And this is just a small representation of the extent of multiple mating in nature.

## Is Multiple Mating Widespread? Is Promiscuity Widespread?

When it comes to sex, males are often seen as willing, indiscriminate, eager, rampant, sexually demanding, or predisposed for multiple sexual partners. Indeed, in most sexually reproducing species, there is selection on males to mate multiply for well-known reasons rooted in biology, as



discussed below. As for females, they have traditionally been seen as reluctant to engage in sexual interactions with multiple partners, and they have been often defined as acquiescent, coy, or sexually reticent. There is, nonetheless, increasing evidence that this is a simplistic assumption.

Female multiple mating can be found in innumerable species of fish, a great deal of mammal species, many primates including chimps and bonobos, crickets, beetles, numerous fly species, butterflies, damselflies, and many other insect species including members of social insects groups (e.g., some bees, such as honeybees, and several species of ants and wasps), dolphins, most (over 90%) species of birds including socially monogamous species, horseshoes crabs, snails, arachnids, many reptiles, a great deal of amphibians, octopuses and other cephalopods, crustaceans, sharks, and the list continues on and on. By contrast, monogamy (or monandry) is much less frequent. Monogamy occurs in some species of blowflies, several species of social insects including termites, some fish including the majority of seahorses, a handful of species of birds (e.g., geese, some woodpeckers and passerines, swans, kittiwakes, some raptors including owls, etc.), beavers, and a few other species in other groups. Monogamy is the rule in less than 10% of all mammal species, and this includes genetic monogamy and species that form pair-bonds (which are not necessarily sexually monogamous, although unlike birds social monogamy in mammals is generally associated with genetic monogamy) (Lukas and Clutton-Brock 2013). Social monogamy occurs in around 30% of all primate species (e.g., hamadryas baboons), and monogamy has also been documented in some species of bats (6%) and rodents (6%), around 15% of carnivores (notably foxes and coyotes), and less than 3% of ungulates. True monogamy of course occurs less frequently than the percentages shown previously because social monogamy does not always translate into genetic monogamy. Overall, monogamy is not so common or ubiquitous as multiple mating across the animal kingdom.

As for humans, anthropological studies have indicated that strict social monogamy is rare (less

than 20% of human cultures). It has been estimated that around 80% of human societies were preferentially polygynous before their contact with Western cultures. Polyandry as a formal or accepted mating system is exceedingly uncommon, but nonetheless female multiple mating still has some incidence in monogamous or polygynous societies due to extrapair copulations (Simmons et al. 2004; Barash and Lipton 2001; Barash 2016). Female multiple mating is quite common in some cultures (e.g., 70% of Amazonian cultures (Walker et al. 2010)), but genetic analyses indicate that rates of extrapair paternity due to female multiple mating in contemporary Western societies, and through historical times, is low (between 1% and 2%) (Larmuseau et al. 2016). It is important to note, however, that rates of extrapair paternity are a lower limit for rates of female multiple mating since not all matings result in fertilizations (e.g., due to the coitus taking place outside the female's peak fertile period, or to other traditional or modern contraceptive methods).

In summary, most animals exhibit polygamous mating systems or socially monogamous mating systems with varying rates of extra-pair copulations. This does not imply that promiscuity is a ubiquitous behavior. Despite the taxonomic spread of polygamous behavior, research into sexual selection over the last decades has proved that mating preferences are prevalent in all mating systems (Jennions and Petrie 1997). In most primates, as in most other groups, mating preferences for particular males or females are well known. Bonobos are reportedly claimed to behave "promiscuously" to resolve conflicts, and some human groups or individuals are labeled by some people as "promiscuous," but in the majority of cases (perhaps not all) this is the result of a frivolous use of the term.

Mate choice implies that promiscuity *sensu stricto* is infrequent. Some of the best candidates for truly promiscuous animals could be encountered among external fertilizers and in particular broadcast spawners. In these species, multiple individuals of both sexes release their sex cells into the water and so any individual may mate quite indiscriminately with a large number of individuals from the opposite sex. However,

recent discoveries are starting to reveal that even in broadcast spawners such as in some species of sea urchins and mussels, reproduction includes a component of choice at the level of gamete interactions (Evans and Sherman 2013; Evans et al. 2012; Levitan and Ferrell 2006). As for other external fertilizers such as fishes and amphibians mate choice is well documented.

### **Differences Between the Sexes, Sex Roles, Sexual Stereotypes, and Promiscuity**

Typically males and females have different strategies to maximize fitness through sexual reproduction. Many of the disparities between the two sexes in regard to reproduction can be rooted to baseline differences in gamete size between males and females (Trivers 1972). In fact, the size dissimilarity in the sex cells is essentially what defines the sexes: within any given sexually reproducing species the kind of individuals that manufactures relatively smaller (but abundant) gametes are called males, whereas individuals from the sex producing relatively larger (and fewer) gametes are called females. This asymmetry in gamete size (anisogamy) has far-reaching implications for sex roles. For a start, the disparity in gamete size implies that from conception there are differences between the sexes when it comes to the investment they make in the offspring. The female ovum provides the nutrients for the embryo, and females generally provide the environment for embryo development. Males, on the other hand, typically contribute little more than the DNA contained in a minuscule cell. This initial asymmetry in parental investment generally deepens as the offspring develops, especially in vertebrates, with females making a much greater effort protecting or nurturing the embryos and even the young after birth. For instance, pregnancy in a typical mammal lasts several months (e.g., 12 months for horses, 22 months in the case of elephants), and this is followed by lactation. Thus, maternal investment is substantial compared to paternal investment. In other groups, the difference in

parental investment between the sexes is not so large but it is still apparent.

The asymmetry in gamete size also means that the sex producing smaller sex cells produces many more gametes (and at a lower energetic and physiological cost per gamete) than the opposite sex: males typically produce astronomical numbers of gametes, and at a much higher production rates than females. An outcome of this is that males generally compete for access to the limiting resource that allows them to maximize their biological fitness: females, or from a reductionist's point of view, their ova.

Anisogamy and all its direct and indirect implications mean that males can theoretically father hundreds or thousands of offspring with different partners (at the expense of other males). This is well known, and in fact, put into practice, by animal breeders. In contrast, females typically have lower potential reproductive rates (measured in terms of number of offspring) due to them producing fewer gametes (sometimes a fixed low number of ova in a lifetime) and investing a great deal of time and effort into the offspring. In short, sexual differences in gamete size has created reproductive competition among males and asymmetries between the sexes over parental investment and reproduction, with the consequence that male reproductive success is usually limited by the number of mates while female reproductive success is limited by gamete production (Trivers 1972; Bateman 1948; Kokko et al. 2006; Kokko and Jennions 2008; Janicke et al. 2016).

As a consequence of these biological underpinnings, males are expected to be comparatively indiscriminate and females comparatively choosy, and males are expected to be keener than females to engage in multiple matings. Females are expected to maximize their reproductive success with only one or a few matings, and would benefit to a larger extent from careful mate discrimination to ensure their energetically and time-expensive parental efforts go into highly viable or attractive offspring. In humans, for instance, cross-cultural sex differences in sex drive and sociosexuality are well documented, with men typically having more sociosexually unrestricted attitudes and behaviors

than women (Schmitt 2005; Lippa 2009). Anisogamy and parental investment disparities are therefore at the core of many morphological, physiological, and behavioral differences between the sexes in regard to sexual interactions. In the context of the evolutionary drivers of promiscuity, males would thus be expected to benefit more from promiscuous behavior than females, but evidence shows that mate choice underlies, in general, male mating decisions too (Edward and Chapman 2011; Shackelford et al. 2005).

### **Why Do Animals Mate Multiply? And Why Do They Engage in Promiscuous Matings?**

As discussed in the previous section, it is easy to envisage the benefits of multiple mating for males. Sperm is generally produced on a continuous basis, the cost of producing a single sperm, compared to an ovum, is much lower, and male parental investment is low. Thus, males can ultimately maximize fitness (in terms of number of offspring sired) in a more or less proportional way as they increase the number of mating partners. Indeed, polygyny is very common in the animal kingdom. As for females, as a result of anisogamy and a high parental investment they are expected to maximize reproductive success with only one or a few matings. Moreover, the sperm from a single copulation are usually enough to ensure fertilization of the complete set of a female's ova. Finally, mating generally entails costs (for instance, increases in the risk of contracting sexually transmitted diseases), and mating outside the pair bond may entail important costs such as mate desertion in species with biparental care. Consequently, female multiple mating would not be expected to be a common and widespread behavior. Nonetheless, as indicated above polyandry is virtually ubiquitous among sexually reproducing species. Explaining this discrepancy between observation and theory has received considerable attention in recent times (though it is also possible that monandry rather than polyandry is what requires an adaptive explanation; see Kokko and Mappes 2013).

Female mating frequency may be explained, at least in some species, by selection on males to

maximize their reproductive success, that is, by sexual conflict leading to higher-than-optimal mating rates for females (Arnqvist and Rowe 2005). In some other cases, it may be less costly for females to accept copulations than to suffer male sexual harassment (convenience polyandry). In other situations, notably in mammals, female multiple mating may have evolved to create paternity uncertainty so as to deter infanticide. Notwithstanding, from a broader point of view, the evolutionary maintenance of polyandrous behavior is more easily understood when polyandry entails benefits. Indeed, females in some species obtain direct (also known as "material") benefits from males at copulation. For instance, females can obtain nutrients in the form of food items or substances transferred in the ejaculate during copulation, or by mating multiple females can generate slight confusion regarding paternity and in this way increase the number of partners willing to share care duties, or they may gain access to better territories, or females may mate multiply to ensure fertilization of the ova (fertility insurance).

Regardless of the presence of material benefits, polyandrous females can also obtain genetic benefits from mating multiply. These are benefits that are manifested in the offspring. For instance, females may "trade-up" to obtain good genes for their offspring when a male is considered of superior genetic quality than the female's previous mate. The traditional "good genes" and "sexy sons" hypotheses hold that females that mate with additional males may increase their fitness indirectly through their offspring because of the inheritance of "good genes" or "attractive genes" (Garcia-Gonzalez and Simmons 2005; Neff and Pitcher 2005).

In addition, one of the most frequently invoked genetic benefits from polyandry in recent years is based on processes that allow females to avoid the negative effects that arise from mating with genetically incompatible males (Neff and Pitcher 2005; Evans et al. 2007). Alternatively, females may engage in copulations with several males to increase the diversity of paternal genotypes in their offspring so that the likelihood that at least some offspring will survive in a changing environment is higher than when offspring genotypes are less diverse (that is, when the females mate monogamously). Finally, females may behave

polyandrously if by mating with multiple males they reduce the risk of having all their offspring sired by a male of low genetic quality (henceforth reducing the risk of potentially losing entire clutches because of low offspring viability). Such risk spreading strategies of the kind “don’t put all your eggs in one basket” are known as bet-hedging polyandry (Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016).

### **Promiscuity, Direct Benefits, and Bet-Hedging**

Studies have found evidence that females frequently obtain one or several of the benefits above mentioned when they mate with multiple males. However, as it has been pointed out repeatedly in this article, some form or another of female (and male) mate choice is the norm across human and nonhumans, in which case there is no room for talking about promiscuous (indiscriminate) sexual behavior. Nevertheless, promiscuity is compatible with the accrument of direct, and in some circumstances, indirect benefits of mating. Promiscuous behavior is more likely to occur when mating entails direct or material benefits because individuals would obtain the resource (access to food, for instance, in nuptial feeding species) as long as they mate, even though there might be variation in the quality of resources held by potential mates. Indirect benefits are unlikely to explain the evolution of promiscuous behavior in general, because the magnitude of indirect benefits accrued increases following mate quality discrimination and mate choice. For example, high-quality individuals are expected to express traits that indicate their higher reproductive value, and individuals of the opposite sex would be selected to discriminate these signals insofar mating with high-quality individuals gives rise, due to inheritance, to high-quality offspring. Most hypotheses to explain the maintenance of polyandry are based on the existence of mate choice, and the vast majority of indirect (genetic)-based pay-offs from multiple mating are not expected to be responsible for the evolutionary maintenance of promiscuity, because if individuals can discriminate mate quality they will do so.

There are nonetheless, a few exceptions. For example, if males that attain higher fertilization success via sperm competition sire offspring with higher viability or higher attractiveness, females that mate multiply will increase their fitness simply by facilitating sperm competition among their mates because they will produce attractive, competitive, or viable offspring sired by the most successful mate. This benefit can be obtained in the absence of mate choice, though some sort of female choice either before mating or after mating (e.g., via female-driven paternity biases known collectively as cryptic female choice) is normally in place.

Bet-hedging multiple mating is another hypothesis compatible with promiscuous behavior because a bet-hedging mechanism is based precisely on a lack of sire selection criteria. In some species, or under some circumstances, mate choice is unreliable, imperfect, or absent. In such cases, it may pay to mate multiply and indiscriminately rather than monogamously because, by doing so, individuals may reduce the risk of mating with an unsuitable (low quality, infertile, etc.) partner, or they may reduce the risk of having offspring sired by a single genetic background in a changing and unpredictable environment. In other words, by mating indiscriminately individuals may reduce the consequences of assessment errors when choosing a mate, or they may increase the genetic diversity of their offspring (Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016). The hypothesis of bet-hedging multiple mating is compatible with promiscuity because it just requires multiple mating, regardless of the phenotypic traits of the potential mates. Empirical tests of this hypothesis are, however, scant.

### **Conclusions**

It is important not to confuse promiscuity with polyandry, polygyny, or polygynandry (i.e., any form of polygamy). All these terms mean sexual encounters with multiple partners, but promiscuity is a restrictive term that in reality implies indiscriminate sexual behavior. There cannot be promiscuity without polygamy but there can be

polygamy without promiscuity, and in fact this is the most common case in nature. The advent of molecular tools applied to paternity analyses has revealed that multiple paternity within a single brood is commonplace. Multiple mating, either from the perspective of males (polygyny) or females (polyandry), is extremely common in the animal kingdom. In fact, true (genetic) monogamous mating systems have turned out to be exceedingly rare in nature. But, even though we currently know that mating with multiple partners is a common and ubiquitous behavior across animals and occurs with some frequency even in socially monogamous species, promiscuity is extremely rare because when it comes to sexual interactions some form or another of mate choice is the norm. Mate choice is also prevalent in the majority of the diverse range of traditional or modern nonmonogamous relationships or practices exhibited by humans.

## Cross-References

- ▶ [Bateman Gradient](#)
- ▶ [Cryptic Mate Choice](#)
- ▶ [Extra-Pair Copulation](#)
- ▶ [Female Choice](#)
- ▶ [Female Defense Polygyny](#)
- ▶ [Intersexual Selection](#)
- ▶ [Polyandry](#)
- ▶ [Polygamy](#)
- ▶ [Polygyny Threshold Model](#)
- ▶ [Scramble Competition Polygyny](#)
- ▶ [Sexual Selection](#)
- ▶ [Sperm Competition](#)

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## Pronucleus

- [Nucleus](#)

## Properties of Human Language

- [Cognition](#)

## Prosimian

- [Haplorhini](#)
- [Primate Sensory Systems](#)

## Prosimian Cognition

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## Synonyms

[Galago](#); [Lemur](#); [Loris](#); [Potto](#); [Strepsirrhine](#); [Tarsier](#)

## Introduction

Prosimians are a diverse group of primate species including the infraorders Tarsiiformes, Lorisiformes, and Lemuriformes. Primate cognition has interested researchers from varying disciplines ranging from psychology to anthropology. Primates are regularly expected to solve problems and scenarios that require a level of cognitive competence can be classified into two categories, physical and social cognition. Primates are unique among mammals in that they have a larger brain to body size ratio (Isler and van Schaik 2009). The corresponding cognitive capacity varies disproportionately across the order Primates (Dunbar 1992). Lemuriformes are by far the most studied infraorder relative to the other prosimians, but pale in comparison to the number of studies focused on New World primates, Old World primates, and Apes. In order to better understand cognitive abilities in primates, research on cognition in basal extant primates can contribute to our greater understanding of cognition in all primates including humans.

## Tarsiiformes

Few studies have examined tarsier cognition in the same ways that lemurs, lorises, and galagos have been tested both in captivity and in the wild. There have been some field experiments focused on predator response, where Gursky (2003) tested the response calls of mother and infant spectral

tarsiers in Sulawesi. She found that infants used specific alarm calls for terrestrial predators and another for aerial predators. These findings suggest that tarsiers use complex communication and some form of social learning to pass this information from mother to offspring.

## Lemuriformes

To survive in the wild, physical cognition aids in the ability to efficiently search for key resources (i.e., food and shelter). Orientation and efficient travel while using spatial cognition is seen in mouse lemurs, ring-tailed lemurs, mongoose lemurs, ruffed lemurs, and Coquerel's sifakas. Rosati et al. (2014) showed that frugivory elicited a stronger use of spatial memory, compared to folivory. Several diurnal lemur species were able to successfully complete object permanence tasks, including visible but not invisible displacements scenarios. Ring-tailed lemurs can implicitly learn spatial sequences picking up information from the environment without explicit instruction or conscious awareness of the learning process (Drucker et al. 2016).

Lemurs are able to understand numerical ascension; this is specifically seen in ring-tailed lemurs, who can apply these principles to numerosities, and in brown, mongoose, and ruffed lemurs, who can comprehend simple arithmetic. Furthermore, their sensitivity to numerical discrimination and accuracy in sequential memory are comparable to rhesus monkeys, and their order sequences tests are comparable to other haplorhines (Jones et al. 2014). Inhibitory control test are commonly used to measure behavioral self-control. MacLean et al. (2014) found that ring-tailed lemurs did not outperform other lemur species in inhibitory control studies whereas other researchers had different results when testing ring-tailed lemurs alongside, ruffed lemurs, mongoose lemurs, black lemurs, and Coquerel's sifakas. Though there are no reports from the wild or captivity, of unsolicited lemur tool use, it is also reported that they may have an understanding of tool functionality. Ring-tailed

lemurs were able perform equally to capuchins, tamarins, and vervet monkeys, when choosing between two tools, where one was functional for retrieving a reward and the other was not. A common cognitive trait seen in black, brown, red-fronted and ring-tailed lemurs are the ability to be trained in new skills and behaviors to complete puzzle boxes.

Ring-tailed lemurs live in large multi-male, multi-female groups and maintain dominance hierarchies, which are not acquired through matrilineal kinship (Kappeler 2012). Black, brown, mongoose, and ring-tailed lemurs use transitive interference at varying levels, which is a form of deductive reasoning (Tromp et al. 2015). Ring-tailed lemurs performed better than mongoose lemurs, suggesting that their varying group size influences the cognitive capacity for this mechanism (Kittler et al. 2015). Reconciliation after conflict, which is regularly seen and measured in higher primate taxa, has also been seen in ring-tailed, black, brown, and red-fronted lemurs, as well as Verreaux's sifakas. Coalitions are only formed in specific situations and tend to be female based and is only observed in ring-tailed lemurs, though red-fronted lemurs reportedly form partnerships while migrating (Gould 1997). Gaze follow, which is used to measure conspecific attention, is reported in ring-tailed, black and brown lemurs, as well as the ability to coordinate attention (Ruiz et al. 2009). Brown and ring-tailed lemurs are also able to follow human gaze (Botting et al. 2011; Sandel et al. 2011).

Various lemur species use social learning while transmitting information from one individual to another. O'Mara and Hickey (2012) found that infant and juvenile ring-tailed lemurs used generalized stimulus enhancement with older conspecifics to gain ecological knowledge; Hosey et al. (1997) also reported evidence of stimuli enhancement in ring-tailed lemurs. According to Fichtel and van Schaik (2006), the Verreaux's and Coquerel's sifakas and possibly the red-fronted display behavioral traditions. Regarding social intelligence, ring-tailed lemurs appear to be more skilled than other lemurs in using social cues during food competition tasks. They use specific

alarm calls for specific threats both aerial and terrestrial (Pereira and Macedonia 1991), whereas sifakas and red-fronted lemurs used specific alarm calls for aerial threats only (Fichtel and van Schaik 2006). These findings suggest that ring-tailed lemurs have a more complex communicative repertoire compared to other lemurs.

## Lorisiformes

Physical cognition in Lorisiformes is limited to a few studies in bushbabies and lorises; pottos and angwantibos are rarely considered in these tests. In object permanence and displacement testing, Jolly (1964) reported that one slender loris did not search for hidden food once it left its direct line of sight, but simply struck at the object covering the food item, which was later perceived as an inconclusive result accounting for the varying adaptation lorises may have for quickly grasping an item. Simply because they were unable to displace the obstructing object does not mean they do not have some concept of the food item once out of sight. Since Jolly's early work and following increased interest in basal primate cognition, researchers have provided evidence for a right-hand preference in wild-born *Nycticebus* spp. and a complex understanding of their physical environment.

During object manipulation tasks, Jolly (1964) found that the lesser bushbaby only struck at the objects, while the greater and thick-tailed bushbabies and the potto were more exploratory as they poked and pushed the food-baited novel objects. A similar study looked at novel object interaction in the greater bushbaby and found that they were interested in novel non-food baited objects, but preferred larger, more maneuverable objects. In numerical discriminate tasks, thick-tailed greater galagos were slower and less accurate in discrimination learning tasks but performed similarly to other primates in set-learning tasks. Researchers studying Garnett's greater bushbaby reported that they took longer to search for items that resulted in smaller rewards, suggesting that they could distinguish

between less and more. Garnett's bushbabies were also tested in regards to the approach-avoidance paradigm, where Hanbury et al. (2013) reported that they displayed a left hemisphere specialization during approach-related behaviors.

## Conclusion

Despite the perceived variation in cognitive ability across primate taxa, when it comes to basic cognitive abilities prosimians are not qualitatively different than other primates. Regardless of their smaller relative brain size, they display comparable and complex cognitive function, with regards to physical and social cognition. Though extensive research has been conducted on various lemur species, there is still much to learn among prosimians.

## Cross-References

- [Prosimian Communication](#)
- [Prosimian Navigation](#)
- [Prosimian Sensory Systems](#)

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## Prosimian Communication

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## Synonyms

Galago; Lemur; Loris; Olfaction; Scent mark; Strepsirrhine; Tarsier; Vocalization

## Introduction

Prosimians are a group of primates which include lemurs, galagos, lorises, and tarsiers. They are diverse in their social systems, activity periods, and habitats. They may live in groups or forage solitarily, be diurnal or nocturnal, and live in diverse environments. They have complex, multimodal communication systems which rely heavily on auditory (vocalizations), olfactory (scent marks), and visual signals (movements and fur markings). These signaling modalities enable prosimians to communicate at various distances during both day and night and through different types of habitat. Both vocalizations and scent can be used to communicate between individuals that are near or far. Soft vocalizations are used for close range, and loud calls are used for distant individuals. Similarly, scent can be perceived by nearby individuals, or scent marks can be deposited to be detected by others long after the individual that produced it has moved away. Movement and fur color patterns are used to communicate at distances that are close enough for visual contact. These various communication modalities combine to enable prosimians discern information about an individual, potentially including species, individual identity, sex, reproductive status, and kinship relationships. Prosimians communicate while engaging in complex social interactions including maintaining ranges, attracting and searching for mates, and raising young.

## Vocalizations

The auditory channel is an important part of prosimian communication and the primary method of signaling is through vocalizations. Prosimian vocalizations vary greatly across species in acoustic range and usage. Most species vocalize in the range that is audible to humans (up to ~20,000 Hz), but a few species also have vocalizations which are either partially (mouse lemurs) or entirely (tarsiers) in the ultrasonic range (Ramsier et al. 2012; Zimmermann 1995). Because such ranges are above the hearing range of predatory birds, this is thought to be an adaptation for avoiding eavesdropping by predators (Ramsier et al. 2012; Zimmermann 1995).

Vocalizations have been shown to convey a great deal of information about the caller including species, sex, individual identity, and even kin group (citations below). Source-filter theory (Fant 1960) explains how such information is detectable in vocalizations. The source of the sound is air passing through the animal's vocal folds. The rate at which the vocal folds vibrate determines how high or low the sound is. Then as the sound waves pass through the vocal tract and out the mouth, different frequencies are amplified or dampened due to the morphology of the vocal tract. Because an individual's vocal tract morphology may vary according to its species, sex, individual identity, and kin group, this can produce voices that are distinctive by species, sex, individual identity, and kin group.

Of the prosimians, the lemurs are probably the most intensively studied. This research has shown that various lemur species have calls that are distinctive by species (sportive lemurs: (Méndez-Cárdenas et al. 2008), true lemurs: (Gamba et al. 2012b)), sex (sifakas: (Patel and Owren 2012)), individual identity (sifakas: (Patel and Owren 2012), red-bellied lemurs: (Gamba et al. 2012a), mouse lemurs: (Leliveld et al. 2011)), and kin group (mouse lemurs: (Kessler et al. 2014; Kessler et al. 2012)). Similarly, galago calls have been argued to be distinctive by individual (Kessler et al. 2015) and species (Anderson et al. 2000). In comparison, much less research has been done on the vocalizations of the lorises and

tarsiers, though vocalizations are increasingly used in species identification among the tarsiers (Burton and Nietsch 2010).

Research into the acoustic variations between individuals, populations, and species is currently under intense interest for its potential applications to conservation as a tool for identifying species and developing acoustic monitoring programs (Burton and Nietsch 2010). Such programs would enable conservationists to obtain a great deal of information about how these species – many of which are small, cryptic, nocturnal, and difficult to follow – use the forest without trapping them or disturbing them.

However, from the perspective of animal communication, it is important to distinguish between when the variability exists to statistically distinguish between species, individuals, sexes, or kin groups and whether the animals actually detect and use this information. This requires the use of playback experiments. During playback experiments, recordings of vocalizations are played, and the subjects' behavioral responses, like whether they look toward the loudspeaker, are measured. Playback studies have been used to show that prosimians may detect when vocalizations vary by species (mouse lemurs: (Braune et al. 2008)), individual identity (Kulahci et al. 2014), and kin group (mouse lemurs: (Kessler et al. 2012), ring-tailed lemurs: (Nunn 2000)).

Prosimians use vocalizations to communicate in many different social contexts. This includes both species that live in cohesive social groups and solitary foraging species. Vocalizations can be given as coordinated vocal displays, like the duets of sportive lemurs (Méndez-Cárdenas and Zimmermann 2009) and tarsiers (Burton and Nietsch 2010) or the loud group choruses given by Indri groups when engaging in territorial displays (Torti et al. 2012). Alternatively, vocalizations may be given without being part of a coordinated display but may still have important roles in social bonding (ring-tailed lemurs (Kulahci et al. 2015)), defense against predators (mouse lemurs (Eberle and Kappeler 2008), sifaka and red-fronted lemurs (Fichtel 2004), tarsiers (Gursky 2006)), maintaining spacing between individuals and group coordination (mouse lemurs (Braune et al.



2005), red-fronted lemurs (Pflueger and Fichtel 2012)), mate advertisement and territory defense (sportive lemurs (Seiler et al. 2015)), and rearing young (bush babies (Becker et al. 2003), mouse lemurs (Scheumann et al. 2007)).

## Scent Marking

Prosimians rely more on olfactory communication than do other primates. They are believed to have functional vomeronasal organs that help them to detect olfactory cues (Smith et al. 2015). Prosimians use several types of scent marks including latrines, fecal marking, urine marking, and/or urine washing (when the animal urinates on its own hands and feet, and then deposits the urine from the hands and feet as it travels), as well as marking using scent from the chin, forehead, palms, genitals, or specialized scent glands (Delbarco-Trillo et al. 2011). Sources of the scent may include feces, urine, saliva, sweat, skin, or secretions from glands in the genital, perianal, gular, sternal, brachial, or antebrachial regions (Delbarco-Trillo et al. 2011; delBarco-Trillo et al. 2012). Some species also mix scents from more than one source before depositing it (Greene et al. 2016).

Because much less is known about olfactory communication than vocal communication, studies comparing olfactory communication across prosimian species are still relatively rare. However, there have been a few studies which have begun to illuminate how olfactory communication has evolved in prosimians. Urine marking has been reconstructed as one of the oldest forms and is the main form of scent marking used by nocturnal, solitary foraging species such as the galagos, lorises, and several nocturnal lemurs (Delbarco-Trillo et al. 2011). Such urine marking may also take the form of urine washing. In general, these predominantly urine-marking species have more chemically complex urine, meaning that the urine contains more different compounds, than species which do not mark with urine (Delbarco-Trillo et al. 2011). The evolutionary shift from urine marking in nocturnal, solitary foragers to depositing scent from scent glands in

cathemeral and diurnal species is believed to have evolved due to the increasing social complexity in these species (Delbarco-Trillo et al. 2011). These species forage in cohesive social groups; thus, these marks may be important for both intragroup and intergroup communication (Delbarco-Trillo et al. 2011). Glandular scent marks can be highly complex relative to urine (Delbarco-Trillo et al. 2011). For example, the number of compounds found in urine ranged from 2 to 33, while ring-tailed lemurs may express 200 to 300 different compounds in their glandular secretions (Delbarco-Trillo et al. 2011).

This relationship between social complexity and chemical complexity in scent marks was also supported in a study comparing scent-mark chemistry and degree of sociality between eight *Eulemur* species (delBarco-Trillo et al. 2012). These species live in cohesive social groups with differing social organizations (pair-bonded or multi-male multi-female) and differing dominance relations between the sexes (female dominant or codominant). Interestingly, differences associated with social system and dominance relationships between the sexes were found (delBarco-Trillo et al. 2012). Female scent marks were chemically more complex in species that live in multi-male, multi-female groups relative to the marks of females of pair-bonded species (delBarco-Trillo et al. 2012). Similarly, male scent marks were more complex in species where males are codominant with females relative to the marks of males in female-dominant species (delBarco-Trillo et al. 2012). When the sexes were compared, males in codominant species had more complex scent marks relative to females in the same species (delBarco-Trillo et al. 2012). However, in female-dominant species, the females had more complex signals relative to the males (delBarco-Trillo et al. 2012).

Much less is known about the signal content of scent marks relative to vocalizations, but it is an area that is receiving a lot of research. So far, scent marks appear to have the potential to reveal a lot of information about the individual that placed the mark. Lemurs have received the most research with studies showing that sifaka secretions signal sex, season, and genetic relatedness, meaning that

the signals of closely related individuals are more similar than those of more distantly related individuals (Morelli et al. 2014). Similarly, ring-tailed lemurs secrete scents which vary by individual (Scordato et al. 2007), season (Scordato et al. 2007), and genetic relatedness (Boulet et al. 2009). Scent signals appear to be important for mate choice. Male ring-tailed lemur scent marks have been shown to convey information on genome-wide heterozygosity of the signaler, which itself correlates with health and survivorship, making it a useful signal for mate choice (Charpentier et al. 2008). Female signals also provide important information, varying according to whether they are pregnant (Crawford and Drea 2015) or on hormonal contraception (Crawford et al. 2011). Relative to the lemurs, much less work has been done on the other prosimians species. Early work on greater galagos showed that thick-tailed galagos use scent marks to discriminate between the sexes, evaluate reproductive state (Clark 1982a), and differentiate between individuals (Clark 1982b). Both thick-tailed galagos and Garnett's greater bush baby discriminated between their own and the other species (Clark 1988).

While the above studies largely focused on the information content of scent marks, either through examining whether the chemical composition varies by individual, species, etc. or by examining whether the animals respond differently to scents from different individuals, species, etc., another subset of studies has begun to investigate the how scent marks are used. For example, recent work has shown that wild spectral tarsiers scent mark primarily for territory defense, not to monitor the reproductive state of females (Gursky-Doyen 2010). Tarsiers marked most often along territory borders, more frequently on nights with territory disputes, and more often during the dry season when resources were scarcer than in the wet season (Gursky-Doyen 2010). They did not mark more often during the mating season than the non-mating season (Gursky-Doyen 2010) as would be expected if scent marks were used to monitor female reproductive state. Similarly, mouse lemurs are more likely to scent mark when leaving a sleeping site than when reuniting at a sleeping site suggesting that the marks were important for maintaining

spacing between sleeping groups and access to sleeping sites (Braune et al. 2005).

Interestingly, the slow lorises also secrete chemicals, but these secretions are specialized for defense (Nekaris et al. 2013). The loris mixes oil from its brachial arm glands with saliva to produce venom which it rubs on its own fur (Nekaris et al. 2013). This venom is strong enough to induce shock and death in small mammals (Nekaris et al. 2013). The main functions are thought to be for defense against parasites and other lorises (Nekaris et al. 2013).

## Multimodal Communication

While most work on prosimians communication has focused on vocalizations and scent marks individually, recent work has emphasized that these modalities work together. For example, ring-tailed lemurs were shown to be able to match the scents and vocalizations of individuals (Kulahci et al. 2014). Similarly, not only do species using glandular scent marks emit olfactory signals, but these signals are also multimodal (Scordato et al. 2007). The individual depositing them often does so with conspicuous visual or auditory cues (Scordato et al. 2007). Visual cues include handstands to deposit anogenital marks or elaborate movements such as the ring-tailed "stink fights" in which males anoint their tails with brachial and antebrachial secretions and then wave their tails at each other (Scordato et al. 2007). Auditory cues include scratching tree bark with an antebrachial spur during deposition (Scordato et al. 2007). Other group-mates may respond to this multimodal signal by investigating and adding marks of their own. Similar opportunities for combining sensor modalities occur when vocalizations or scent marks are paired with individually or species specific face markings, such as those occurring in several species of loris (Nekaris and Munds 2010) and galago (Bearder 1999).

## Conclusion

Prosimians have multimodal communication systems in which they combine auditory, olfactory,

and visual signals to convey information about who they are and to navigate social interactions. These communication systems are complex enough to communicate information about their species, sex, individual identity, kin group, and reproductive status during interactions relating to dominance, territorial displays, mate choice, and raising young. These signals are also flexible to enable communication during day or night, through dense forest, and to individuals both within a cohesive social group and to others in a dispersed social network.

## Cross-References

- [Primate Cognition](#)
- [Primate Communication](#)
- [Primate Sensory Systems](#)
- [Primate Social Structure](#)

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## Prosimian Diets

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Due to their smaller size, lower metabolic rates compared to haplorhines, and adaptation to vertical strata, prosimian diets are highly specialized and range between purely insectivorous and purely leaf

eating. Sympatric *Cheirogaleus medius* and *C. major* have a diet of mostly fruits, followed by flowers, insects, and tree gums. Their foods are high in fiber, averaging 45.2% nitrogen detergent fiber (Lahann 2007). They reduce competition with other species by foraging at different heights with *C. medius* lower down and *C. major* higher up. Their diets are seasonal and select fruit during the weight gain season, to last through the following periods of hibernation. *Microcebus murinus* also has a varied diet of fruits, flowers, insects, and gums, which is highly seasonal and quite different depending on the field site (Dammhahn and Kappeler 2010; Lahann 2007). Gum is a major food source during particular seasons (Thoren et al. 2011). *Microcebus rufus*, being smaller in size, supports itself with fruits and insects and specifically the fruit of *Bakerella* spp. (Atsalis 1999). This is typical of many small-sized prosimians. The smaller *Microcebus berthae* ingests a larger proportion of insects and also ingests insect secretions which reduce the seasonal fluctuation in diet (Dammhahn and Kappeler 2008). This technique is also employed by *Microcebus ravelobensis* which also ingests insects, gum, and fruit (Thoren et al. 2011). *Mirza* spp. are omnivorous and eat fruits, leaf buds, insects and their secretions, tree gums, and also some small vertebrates when available. *Allocebus* spp. are mostly insectivorous but were also observed licking twigs or bark which may have contained some sap, secretions, or exudates such as gum (Biebouw 2013). *Phaner* spp. are an extreme, ingesting mostly gum with a small compliments of insects (Charles-Dominique 1977). At another extreme is *Daubentoniidae madagascariensis* which ingests largely insects, specifically grubs, which it can find burrowed in tree trunks (Pollock et al. 1985). They also ingest some plant matter such as the fruit and seeds of *Canarium* spp.

The larger bodied lemurs also have varying and seasonal diets. *Indri indri* are folivorous; however, they have been observed ingesting some other plant parts depending upon their location and probably have an important amount of seed ingestion (Powzyk and Mowry 2003). Young leaves are around 73–80% of feeding time, 7% mature leaves, and 5–8% fruits and a combination

of bark and petioles (Britt et al. 2002). Other leaf eaters include *Avahi laniger* and *A. meridionalis* which eat a mix of young and old leaves. *A. meridionalis* are also able to diversify their diets to flowers during the growing season. Naturally, their diets are quite high in fiber which is similar throughout the prosimians (Norscica et al. 2012). *Avahi occidentalis* have a broader diet, feeding from 25 trees and 5 lianas, feeding on mostly leaves (77% of feeding time) with fruits and flowers also being eaten (Thalmann 2001). *Propithecus* spp. are similar, with *Propithecus diadema* being entirely plant eaters ingesting flowers (3–25%), fruits and seeds (22–65%), and young leaves (28–53%) (Overdorff and Strait 1998; Powzyk and Mowry 2003). *Propithecus verreauxi* and *Propithecus tattersalli* ingest between 25% and 46% leaves, 33% and 65% fruit, and 9–10% flowers based on feeding time (Richard 1978). The well-known *Lemur catta* are extensive generalists and opportunistic omnivores which spend equal time on fruits and leaves (Sauther et al. 1999). Specifically spending 25–58% of feeding time on leaves, 34–70% on fruits, and 2–8% of flowers with animal matter being ingested from time to time (Sussman 1974). *Eulemur* spp. are also generalists but supposedly described as frugivores. *Eulemur fulvus* ingests a diet of mostly leaves or fruits depending on the season (Sussman 1974). *Eulemur rubriventer* and *Eulemur coronatus* are much more frugivorous and only ingest up to 13.6% leaves with fruits sometimes being 100% of their foraging time (Overdorff and Strait 1998). *Eulemur macaco* and *Eulemur mongoz* have similar diets; however, only *E. mongoz* has been reported to ingest nectar more prominently (Colquhoun 1993). Similarly, *Varecia* spp. are largely fruit eaters with 70–90% of their diets being fruit, with leaves, flowers, and nectar being a seasonal part of their diet based upon availability (Ratsimbazafy 2002). The *Hapalemur* (*Hapalemur griseus*, *Hapalemur simus*, and *Hapalemur aureus*) are specialized on ingesting bamboo leaves, except for *H. aureus* which also enjoys foraging in reed beds (Eppley et al. 2011; Glander et al. 1989). Each species prefers different parts of the bamboo and some are specific for particular species. *H. griseus*



ingests 88% bamboo and minor other grasses, preferring young leaf bases. *H. aureus* is similar, however prefers giant bamboo which is 78% of its feeding time and some other bamboo species and fruits. The strictest diet is that of *H. simus*, with giant bamboo being 95% of the diet, eating both mature and immature leaves (Grassi 2001). *H. griseus* has been known to also ingest soil and fungi, with the diet being quite seasonal (Grassi 2001). Only *H. griseus alaotrensis* is described as eating 100% leaves (Randrianarisoa 1999). Other leaf eaters include the *Lepilemur* spp. which are less catholic in their choices of food than the previous Hapalemurs. *Lepilemurs* select their food based on the nutrient concentrations, allowing for a large variety of food items throughout the seasons (Thalmann 2001). *Lepilemur ruficaudatus* and *Lepilemur edwardsi* spend 75% of their foraging time on leaves and 25% on fruits, buds, and flowers, with coprophagy also having been observed (Thalmann 2001). Leaves were the main food of *Lepilemur leucopus*, spending 91% of its foraging time eating them and the rest on fruits, tree gum, and some bark.

The Lorisiform prosimians are generally smaller bodied and nocturnal. This allows for a specialized feeding of insects and tree gums, more so than any other mammalian group. With diets varying between insects, fruits, and gums, body size is generally able to dictate their general diet. Medium-sized *Perodicticus potto* are largely fruit eaters, while the smaller *Arctocebus calabarensis* are described as more insectivorous (Charles-Dominique 1977). This trend continues with the small-bodied *Loris* spp. who are either entirely insectivore (*Loris tardigradus*) or mostly insectivorous with minor amounts of gum and legume pods (*Loris lydekkerianus*) (Nekaris and Bearder 2007). This is to the contrary of the Asian slow lorises (*Nycticebus* spp.), which are largely exudativorous. The smallest *Nycticebus pygmaeus* has a diet of approximately 30% gum, 30% nectar, and 40% insects (Starr and Nekaris 2013). Their smaller size does not allow for sufficient fermentation of gums for their energy, insects and nectar are necessary for denser energy. The larger *Nycticebus coucang* has a more varied diet of fruits, insects, and tree gum in larger

proportions than its smaller cousin (Wiens et al. 2006). The larger *Nycticebus javanicus* has a diet mostly of gum and insects, but also ingests a small amount of fruits, nectar, flowers, and leaves which is a transition based on their larger body size (Cabana et al. 2017). The largest of the Asian slow lorises is *Nycticebus bengalensis*, which has a highly fermenting diet of 96% gum and some insects and leaves (Das et al. 2014).

The bushbabies are a group of nocturnal primates varied morphologically but also in size and ecology. The smaller *Galago zanzibaricus* and *Galago senegalensis* are largely insectivorous, ingesting up to 70% insects, with some fruit and gum (Harcourt and Nash 1986). Gum is particularly important to the diet of *G. senegalensis* which can feed on it for up to 30% of its feeding time. This is similar to *G. moholi* which spends up to 48% of their time on gum and 50% on insects (Nekaris and Bearder 2007). The larger *Otolemur garnettii* and *Otolemur crassicaudatus* are able to ingest more gum (40%) and insects (40%) due to their size, with *O. garnettii* also relying on seasonal fruits (Harcourt and Nash 1986; Nekaris and Bearder 2007). Depending on the field site, *O. garnettii* was also described as highly insectivorous, having a diet 50–55% of animal matter, specifically insects and molluscs (Masters et al. 1988). The *Galagoides demodivii* and *cocos* have a highly insectivorous diet of 70% insects and 30% fruits (Charles-Dominique 1977; Nekaris and Bearder 2007). *Galagoides alleni* spent its time equally on animal matter and fruit. *Euoticus elegantulus* is the most exudativorous of the bushbabies, with only 20% of time spent on animal matter.

All of the diet information reported in this chapter is based on the percentage of time spent on foraging or feeding, therefore the percentages reported do not directly reflect the intake. Especially for insects and nectar, the ingested amount is often much lower than the feeding percentage and fruits tends to be higher (Cabana et al. 2017).

## Cross-References

- [Dentition](#)
- [Digestive System](#)

- ▶ Feeding
- ▶ Platyrrhine Diet
- ▶ Primate Diet
- ▶ Prosimian Life History
- ▶ Prosimian Morphology
- ▶ Protein

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## Prosimian Life History

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### Synonyms

Galago; Lemur; Loris; Potto; Strepsirrhine; Tarsier

### Definition

Life history characteristics include gestation period, size and number of offspring, lactation period, size at birth and age at weaning, pattern of postnatal growth, size and age at sexual maturity, interbirth interval, and lifespan (Martin 2008).

## Introduction

The Order Primates is made up of two unique suborders, the Haplorhini and Strepsirrhini, characterized by life history (including gestation, birthing patterns, weaning, and dispersal) patterns that are among the slowest of the mammals (Campbell et al. 2011). The prosimians comprise a polyphyletic clade including the haplorhine Tarsiiformes and the strepsirrhine Lemuriformes and Lorisiformes. Although the Tarsiiformes are more closely related to monkeys and apes, their nocturnal life style, habitat selection, and communication systems mean that aspects of their life history allows for interesting comparison with other Strepsirrhini, and for discussion of the evolution of these traits within the Order Primates. Because primates are long-lived, data for these traits often come from more common species in captive populations as collecting accurate data in the wild can take up to 50 years of study to understand these parameters even in a single population (Martin 2008; Fleagle 2013). In this entry, I summarize current knowledge of key life history traits across the three infraorders comprising the prosimians.

### Infraorder Tarsiiformes

Tarsiiformes (hereafter tarsiers) are comprised of three genera and 13 species. They are restricted to Borneo, Sumatra, Sulawesi, and surrounding smaller islands. *Cephalopachus bancanus* from Borneo and Sumatra seems to exhibit a noyau (solitary) social organization; little is known about *Carlito*, although they may be similar to *Cephalopachus*. In the better-studied genus *Tarsius*, uni-male, uni-female social units are common, characterized by duetting; within these units, however, more than one adult of either sex can occasionally occur. Ranging in size from 98 to 135 g, tarsiers have a gestation period of about 180 days. Tarsiers give birth to singletons; despite having three pairs of mammae, no multiple births of tarsiers have been recorded. Infants are large, typically 20–33% of the adult body weight. The

mother carries her young in her mouth and parks it for about half an hour at a time as she forages. Development of the young is rapid, and within 100 days they can forage self-sufficiently. The lactation period is on average 78–120 days. Adult weight tends to be reached at 8–10 months. Dispersal data are only available for *Tarsius spectrum*; both males and females disperse from their natal range, settling within 500 m of their original range. Captive individuals have been known to live for 17 years (Gursky 2004).

### Infraorder Lemuriformes

Lemuriformes comprises five families, the Cheirogaleidae, Lepilemuridae, Lemuridae, Indriidae, and Daubentoniidae. The Cheirogaleidae (hereafter cheirogaleids) include six genera and 19 species, the Lepilemuridae (hereafter sportive lemurs) include four genera and 13 species, the Lemuridae (hereafter lemurids) include four genera and 13 species, the Indriidae (hereafter indriids) include four genera and 13 species, and the Daubentoniidae (hereafter aye ayes) include four genera and 13 species. This radiation of primates is restricted to Madagascar and some small surrounding islands (Cavallini 2009).

Cheirogaleids comprise five genera and 31 species. Most species studied until now exhibit promiscuous mating systems. Ranging in size from 30 to 460 g, cheirogaleids have a gestation period ranging from 54 to 70 days. Perhaps due to their small size and high predation pressure, cheirogaleids give birth to litters of 2–3 young up to twice a year. Infants are kept in a nest or in tree tangles. They are carried in the mouth when they are young, but as they grow older they are able to cling to or follow the mother. The lactation period is on average 42 days. Members of the genus *Microcebus* can reach full sexual maturity at 8–10 months. Social patterns are diverse within this speciose family, with dispersal possible in either sex or being biased to one sex. Captive individuals have been known to live for 18 years (Fietz 1999).

Sportive lemurs comprise one genus and 26 species. Most of these species remain unstudied in the wild, with most data coming from

*Lepilemur ruficaudatus* and *L. sahamalazensis*. Although they are often described as solitary, there is evidence for multiple types of social units within this genus ranging from noyau to uni-male uni-female to dispersed family groups. Ranging in size from 700 g to 1.0 kg, sportive lemurs have a gestation period ranging from 120 to 150 days. Breeding tends to be seasonal depending on the region of Madagascar; the genus typically gives birth to singletons. Infants are kept in a tree hole or in tree tangles. When moved, the mother carries the infant in her mouth and keeps it in a tree nearby to where she is foraging. There is no evidence for paternal care in the genus. The lactation period is on average 75–120 days. Sexual maturity occurs at about 1.5–2 years. No evidence is available on longevity of this taxon.

Lemurids comprise five genera and 21 species. Social organization is diverse and include uni-male, uni-female groups; multi-male, multi-female groups; and single-male multiple-female groups. Ranging in size from the 800 g to 3.8 kg, lemurids have a gestation period ranging from 99 to 150 days; young of a size of 60 g have been reported. Most lemurids give birth to singletons, although twins can occur (Gould et al. 2003). The major exception is the genus *Varecia*, which can give birth to up to five infants. In the case of *Varecia*, infants are kept in a nest, whereas all other lemurids sleep in groups, and infants are huddled among the adults. Although *Varecia* may carry infants in the mouth, all other taxa exhibit fur grasping and riding on the dorsum or ventrum. The lactation period is consistently reported at about 6–7 months for all genera. In the best-studied *Lemur catta*, infants reach complete independence at 6 months, whereas in *Eulemur flavifrons*, sexual maturity does not occur until 20 months. A number of taxa are reported to reach 30–35 years in captivity; wild data from *L. catta* report one individual reaching 20 years.

Indriids comprise three genera and 19 species. The smaller indriids range from 1 to 6.8 kg, with *Indri* being the largest living lemur, reaching up to 9 kg. Group sizes range from small cohesive family units to large multi-male multi-female groups. Sexual maturity is reached at about 2.5 years in

*Propithecus* but not until 7–9 years in *Indri*. Indriids have a gestation period ranging from 120 to 176 days; breeding appears to be highly seasonal, with some species only able to mate on one day per year. Indriids typically give birth to one young, and in some cases inter-birth intervals are as long as 1.7 years. Infants are carried by the mother on her back or on her belly and become independent at about 4 months. All group members associate with and play with infants. The lactation period averages 240–300 days. Infants of *Indri* are born black and change to adult color at 4–5 months. Among *Propithecus*, infant mortality is described as high, including heavy predation from the fossa (Carnivora: *Cryptoprocta ferox*). In the case of *Propithecus diadema*, wild individuals of 20 years have been observed, and in the case of *P. edwardsi*, one wild individual obtained the age of 27 (Pochron et al. 2004).

Aye ayes comprise one genus and one extant species. Its social organization is multi-male, multi-female, and during estrous a female can mate with up to six males. Ranging in size from 2.4 to 2.6 kg, aye ayes have a gestation period ranging from 164 to 172 days. Single offspring are born any time of the year; unlike most other lemurs aye ayes are not seasonal breeders. Infants are typically born at 90–140 g. Infants remain near the nest until they are about 3 months old. The mother carries young in her mouth for about the first 3 months, until locomotor independence is achieved. The lactation period is on average 170 days. The young become independent at 18–24 months. Interbirth interval is long, with one young being produced every 2–3 years. In captivity, individuals have reached 24 years of age (Kappeler 1998).

### Infraorder Lorisiformes

Lorisiformes comprises two families, the Galagidae and the Lorisidae. The Galagidae (hereafter galagos) include six genera and at least 19 species, whereas the Lorisidae (hereafter lorises) include four genera and at least 13 species.

Galagos are distributed throughout Sub-Saharan Africa. Most species studied until now live in multi-male, multi-female social units, although several taxa also exhibit uni-male, uni-

female social units. Ranging in size from 35 g to 1.8 kg, galagos have a gestation period ranging from 110 to 135 days. With the known exception of *Otolemur crassicaudatus*, which regularly gives birth to twins, galagos typically give birth to one young; although twinning occurs in other taxa, data from the wild suggest that survivorship is low (Bearder and Doyle 1974). Infants are typically born less than 8% of the parent's body weight. Infants are kept in a nest or in tree tangles. When moved, the mother carries them in her mouth and parks them in a tree nearby to where she is feeding. The lactation period is on average 70–150 days. Adult weight tends to be reached at 8–10 months. In some taxa such as *Galago moholi* and *G. senegalensis*, females are philopatric and stay with their mother or establish a neighboring range, whereas in uni-male, uni-female genera like *Euoticus* and *Otolemur*, both sexes tend to disperse from their natal range at about 10–14 months. No wild data are available for the life span of galagos, but captive individuals have been known to live for 12–16 years.

Lorises include a Sub-Saharan African subfamily (the pottos of the Perodicticinae) and the slow and slender lorises of south and south-east (Lorisinae). Until now, all species studied exhibit uni-male, uni-female social units, although variability can occur within a single population (e.g., *Loris* – uni-female, multiple male; *Nycticebus pygmaeus*, uni-male, multiple female). Ranging in size from 110 g to 2.5 kg, lorises have a gestation period ranging from 157 to 205 days. With the exception of *N. pygmaeus*, where twinning is the norm, and *L. lydekkerianus*, where twinning comprises about half of births, lorises typically give birth to one offspring; although twinning occurs in other taxa, data from the wild suggest that survivorship is low (Weisenseel et al. 1998). Infants are typically born less than 5% (lorises) to 20% (pottos) of adult body weight (Charles-Dominique 1977). Lorises do not use tree holes, and the mother regularly carries infants after birth, clinging to her fur. When they are a few weeks old, the mother parks them near her foraging site or at the sleeping site. Adult males and older siblings regularly visit, feed with, and play with parked infants. The lactation period is on average



120–200 days. Adult weight tends to be reached at 8–10 months. In all taxa studied so far, both males and females disperse from their natal range at about 18–20 months (Nekaris 2003). No wild data are available for the life span of lorises, but captive individuals have been known to live for 18–26 years.

Overall, prosimians comprise a diverse group of primates. Despite their relatively small body sizes, they are characterized by slow life histories. Across all taxa that have been studied, there is evidence for social learning in regards to food and habitat selection and social behavior between offspring and parents over their relatively long period of development. It is the long lives of these animals that still means much more is to be learned about the very basics of life history of more than two third of the described taxa.

## Cross-References

- ▶ [Basal Metabolic Rate \(BMR\)](#)
- ▶ [Cetacean Life History](#)
- ▶ [Interbirth Interval](#)
- ▶ [Life History](#)
- ▶ [Marsupial Life History](#)
- ▶ [Prosimian Locomotion](#)
- ▶ [Prosimian Sensory Systems](#)
- ▶ [Weaning](#)

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## Prosimian Locomotion

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## Definition

Anthropoid

Primate group including Old World monkeys, New World monkeys, and apes. Largely diurnal, arboreal (but many species are terrestrial), and larger-bodied.

|                |                                                                                                                          |
|----------------|--------------------------------------------------------------------------------------------------------------------------|
| Cantilever     | A method of locomotion where the hind limbs are fixed to a tree branch to support the upper body in reaching activities. |
| Locomotion     | The movements and postures used by any animal.                                                                           |
| Prosimian      | Primate group including lorises, galagos, lemurs, sifakas, and tarsiers. Largely nocturnal, arboreal, and small-bodied.  |
| Quadrupedalism | A form of locomotion where all four limbs are used to move horizontally across a substrate.                              |

## Introduction

Locomotion encompasses the movements and postures that vertebrates use in day-to-day activities, especially in obtaining food, avoiding predators, and finding mates. Primates are specialists at arboreal locomotion and specifically at navigating life in the trees among small branches (Sussman 1999; Ankel-Simons 2007; Fleagle 2013). Among mammals, primates are remarkable in having an unusually high range of locomotor behaviors. They leap, walk quadrupedally, suspend from branches using their tail or feet, brachiate, climb, cling, and cantilever (Fleagle 2013). Despite this large range of locomotor behaviors, primates have relatively few postcranial morphological specializations that reflect these locomotor niches.

Grasping hands and feet with a divergent first digit (the first digit being called the “pollex” in the hand and the “hallux” in the foot) are one of the defining morphological adaptations in primates linked to the arboreal lifestyle (Cachel 2015). Unlike other mammals primates have nails instead of claws which support the soft tissue tactile ridges (dermatoglyphics) present on the digits. All primates (humans included) possess these dermatoglyphic patterns on the palms of their hands and soles of their feet (including at the end of the digits, i.e., fingerprints). The papillary ridges of

the hands and feet provide a source of friction during locomotion and object manipulation. Some primates also possess dermatoglyphic patterns on the skin of other organs. The distal third of the ventral surface of the prehensile tail of ateline monkeys is marked by a friction pad replete with papillary ridges (Organ 2017; Organ et al. 2011), which functions to provide sufficient friction during tail-assisted locomotion. The tarsier *Tarsius bancanus* also possesses a friction pad on the tail, although in this case it is located on the ventroproximal aspect of the tail and is used to prop the body during vertical clinging and resting activities (Sprankel 1965).

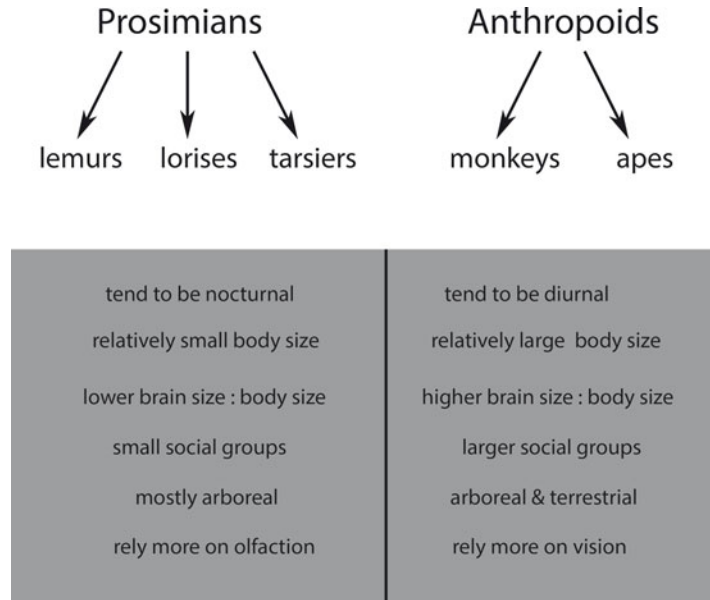
Lastly, primates are unique among mammals in the structure of the eyes and the bony components of the skull that holds the eyes. Non-primate arboreal mammals, such as squirrels, have eyes located on the sides of the head. Primates have both eyes situated at the front of the skull in an arrangement called “orbital convergence” (Ankel-Simons 2007; Fleagle 2013). This allows for overlapping visual fields and binocular (stereoscopic) vision. Living a successful arboreal lifestyle high in the forest canopy with thick vegetation is tied to accurate three-dimensional vision, which is necessary for locomotor planning (think about leaping from branch to branch high off the ground) as well as catching insects. Binocular vision allows for this three-dimensional vision.

Primates can be broadly organized into two groups (Fig. 1). The prosimians (“pre-monkeys”) consist of lorisiforms, lemuriforms, and tarsiers. They are considered to be the more “primitive” group of primates and more representative of what the earliest primates may have looked like. They also are considered good models of how the earliest primates may behaved because the fossil record indicates that the earliest primates were morphologically similar to tarsiers or galagos, thus likely arboreal (Sussman 1999; Covert 2002; Cachel 2015). Anthropoids (Old World monkeys, New World monkeys, and apes) are considered to be more “derived” than prosimians.

This entry provides first a summary of the prosimians, who they are, what they look like, how they live, and how they behave, and then moves

**Prosimian Locomotion,**

**Fig. 1** The classification of the order Primate into prosimians and anthropoids, with major defining characteristics of each group



into the factors that influence development of particular locomotor styles. Lastly, this entry provides a summary of the types of locomotion within the prosimians with illustrations of each type.

### Prosimian Lifestyles

Prosimians include the lorisiforms, lemuriforms, and tarsiers (see Fig. 2). Lorisiforms include the Asian lorises (slow lorises and slender lorises), African lorises (pottos and angwantibos), and galagos (bush babies). Slow lorises (*Nycticebus* spp.) and slender lorises (*Loris* spp.) are widely distributed in southern India, Sri Lanka, and throughout much of Southeast Asia (Nekaris and Bearder 2007). Pottos (*Perodicticus* spp.) and angwantibos (*Arctocebus* spp.) are found through much of central Africa (Nekaris and Bearder 2007). Galagos (*Euticus* spp., *Galago* spp., *Galagoides* spp., *Otolemur* spp., and *Sciurocheirus* spp.) are scattered throughout eastern, southern, and central Africa (Nekaris and Bearder 2007).

Lemuriforms are found only on the island of Madagascar and include the aye-aye (*Daubentonia* spp.), indriids (*Avahi* spp., *Indri*

spp., and *Propithecus* spp.), bamboo lemurs and lemurs (*Eulemur* spp., *Hapalemur* spp., *Lemur catta*, *Phaner furcifer*, *Varecia* spp.), mouse lemurs and dwarf lemurs (*Allocebus* spp., *Cheirogaleus* spp., *Microcebus* spp., and *Mirza* spp.), and sportive lemurs (*Lepilemur* spp.) (Gould and Sauther 2007). The tarsiers (*Carlito* spp., *Cephalopachus* spp., and *Tarsius* spp.) are found in the Philippines and the islands of Southeast Asia (Shekelle et al. 2010). While their phylogenetic affinities are debated (Hartig et al. 2013; Kumar et al. 2013), they are grouped here with the lorisiforms and lemuriforms on the basis of their behavior, ecology, and some morphological features.

While there is great diversity within the prosimians, they can be described as sharing several fundamental behavioral and morphological characteristics to the exclusion of anthropoids (Fig. 1). Prosimians are almost exclusively nocturnal and arboreal (Sussman 1999); ring-tailed lemurs (Fig. 3) and sifakas (Fig. 4) are the only prosimians that spend any regular time on the ground (ring-tailed lemurs spend up to 30% of waking time on the ground but sifakas come to the ground with less frequency), and, as shown in Fig. 2, they are two of the very few diurnal prosimians (Fleagle 2013).

| Infraorder                                  | Lorisiformes                                                                                                                                 |                                                                                                                                                                     | Lemuriformes                                                                                                                         |                                                                                                                          |                                      |                                                                                                        |                                         | Tarsiiformes     |
|---------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------|--------------------------------------|--------------------------------------------------------------------------------------------------------|-----------------------------------------|------------------|
|                                             | Loridae                                                                                                                                      | Galagonidae                                                                                                                                                         | Lemuridae                                                                                                                            | Cheirogaleidae                                                                                                           | Lepilmuridae                         | Indridae                                                                                               | Daubentonidae                           |                  |
| Species (common name)                       | slow lorises ( <i>Nycticebus</i> )<br>slender lorises ( <i>Loris</i> )<br>potto ( <i>Perodicticus</i> )<br>angwantibos ( <i>Arctocebus</i> ) | galagos ( <i>Galago</i> ,<br><i>Galagoides</i> , <i>Eutotius</i> ,<br><i>Sciuroides</i> , &<br><i>Otolemur</i> )                                                    | ring-tailed ( <i>Lemur catta</i> )<br>ruffed ( <i>Varecia</i> )<br>eulemurs ( <i>Eulemur</i> )<br>bamboo lemurs ( <i>Hapalemur</i> ) | mouse lemurs ( <i>Microcebus</i> )<br>dwarf lemurs ( <i>Allocebus</i> , <i>Cheirogaleus</i> , & <i>Mirza</i> )           | sportive lemurs ( <i>Lepilemur</i> ) | sifakas ( <i>Propithecus</i> )<br>indrids ( <i>Indri</i> )<br>avahis ( <i>Avahi</i> )                  | aye-ayes ( <i>Daubentonia</i> )         | tarsiers         |
| Body Size (mouse = 20g, house cat = 4,500g) | 370g-1400g ( <i>Nycticebus</i> )<br>103g-322g ( <i>Loris</i> )<br>847g-1858g ( <i>Perodicticus</i> )<br>150g-325g ( <i>Arctocebus</i> )      | 162g-360g ( <i>Galago</i> )<br>45g-183g ( <i>Galagoides</i> )<br>182g-360g ( <i>Eutotius</i> )<br>258g-502g ( <i>Sciuroides</i> )<br>604g-1258g ( <i>Otolemur</i> ) | ~2.2kg ( <i>L. catta</i> )<br>3kg-4kg ( <i>Varecia</i> )<br>1.5kg-2.5kg ( <i>Eulemur</i> )<br>700g-2400g ( <i>Hapalemur</i> )        | 30g-90g ( <i>Microcebus</i> )<br>75-80g ( <i>Allocebus</i> )<br>75-200g ( <i>Cheirogaleus</i> )<br>300g ( <i>Mirza</i> ) | 700g - 900g                          | 2.8kg-6.9kg ( <i>Propithecus</i> )<br>6.5kg-6.9kg ( <i>Indri</i> )<br>600g-1200g ( <i>Avahi</i> )      | 2,000g                                  | 100g-150g        |
| Locomotion                                  | "slow climbers"<br>AQ, C ( <i>Nycticebus</i> & <i>Loris</i> )<br>AQ ( <i>Perodicticus</i> & <i>Arctocebus</i> )                              | VCL or "hoppers"<br>( <i>Galago</i> , <i>Galagoides</i> ,<br><i>Eutotius</i> , <i>Sciuroides</i> )<br>AQ ( <i>Otolemur</i> )                                        | AQ ( <i>Varecia</i> & <i>Eulemur</i> )<br>AQ & TO ( <i>L. catta</i> )<br>VCL & AQ ( <i>Hapalemur</i> )                               | AQ                                                                                                                       | VCL                                  | VCL, TBH, AQ, TQ<br>( <i>Propithecus</i> )<br>VCL, AQ, TQ ( <i>Indri</i> )<br>VCL, AQ ( <i>Avahi</i> ) | AQ                                      | VCL              |
| Predation Pressure                          | for <i>Loris</i> : relatively high; unclear for others                                                                                       | relatively high for most                                                                                                                                            | relatively low                                                                                                                       | high                                                                                                                     | high                                 | relatively low                                                                                         | relatively low (except for humans)      | high             |
| Diet                                        | <i>Nycticebus</i> : gums & fruit; <i>Loris</i> : animal prey; <i>Perodicticus</i> & <i>Arctocebus</i> : animal prey & fruit                  | <i>Galago</i> & <i>Eutotius</i> : gums & animal prey; <i>Galagoides</i> & <i>Sciuroides</i> : fruit & animal prey; <i>Otolemur</i> : gums, fruit, & animal prey     | <i>L. catta</i> & <i>Eulemur</i> : leaves, fruit, bark, sap, & flowers; <i>Varecia</i> : fruit; <i>Hapalemur</i> : bamboo & fruit    | <i>Microcebus</i> : gums, fruit, insects<br><i>Allocebus</i> , <i>Cheirogaleus</i> , & <i>Mirza</i> : nectar & fruit     | fruit & leaves                       | <i>Propithecus</i> & <i>Indri</i> : leaves with some fruit; <i>Avahi</i> : leaves                      | larvae, insects, seeds, fruit, & nectar | insects, lizards |

**Prosimian Locomotion, Fig. 2** The major groups within the Prosimii, characteristics linked to their lifestyle, and major locomotor categories of each group. *AQ* arboreal quadrupedalism, *C* cantilever, *VCL* vertical clinging and leaping, *TQ* terrestrial quadrupedalism, *TBH* terrestrial bipedal hopping

**Prosimian Locomotion,**

**Fig. 3** Ring-tailed lemurs (*Lemur catta*) in a terrestrial quadrupedal stance. Ring-tailed lemurs are the only prosimian group that routinely spend lengths of time on the ground. Note the divergent first digit on the hand and foot, helpful in maintaining a grasp on small tree branches (Photo credit Hajarimanitra Rambeloarivony)



Life in an arboreal environment does not typically support large social groups (see Liebal et al. 2013). Correspondingly, most prosimian species live in groups where sizes range from 2 to 3 individuals up to 12 individuals. The terrestrial ring-tailed lemurs (*L. catta*) are noted for consistently having large groups, sometimes in excess of 25 individuals, with a relatively complex social hierarchy system and a heavy reliance on stink bomb warfare (Gould and Sauter 2007; Liebal et al. 2013).

Prosimians have a smaller brain size: body size ratio than anthropoids, which may be related to their heavier dependence on olfaction and less dependence on vision in social communication. They also tend to have a smaller body size relative to anthropoids, which is likely related to development of locomotor styles (Ankel-Simons 2007; Liebal et al. 2013).

### Body Size and Locomotion

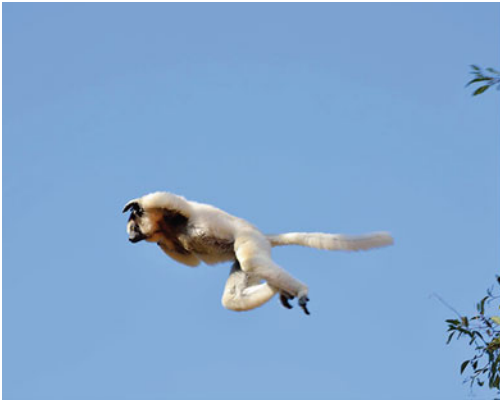
Locomotor behavior is influenced by numerous factors such as diet, social behavior, and skeletal morphology. However, body size is perhaps the most influential factor in locomotor style (Merritt 2010). Small mammals tend to be prey more often than predator. This in turn may push some small mammals to be nocturnal rather than diurnal, a mechanism for “hiding” from some predators. Being an arboreal mammal can also be a means of hiding from predators, with some

notable exceptions such as snakes (Merritt 2010).

Small mammals, weighing less, can often inhabit arboreal environments that would only support a relatively low body weight, such as thin, narrow branches (the so-called fine branch arboreal niche). Combined with increased avoidance of predators, a small body size is typically associated with arboreality in primates, many of whom are found within Prosimii (Fleagle 2013). Only the larger prosimians, such as the ring-tailed lemurs (Figs. 2 and 3) and sifakas (Figs. 2 and 4), routinely spend time on the ground out of the trees. While still subject to some predation, these larger prosimians are not subject to predation pressure as intensely as the smaller prosimians (Sussman 1999).

Lastly, body size has an important influence on dietary requirements in mammals. Smaller mammals have higher metabolisms than larger mammals and tend to need a higher quality diet with greater percentages of protein relative to larger mammals (Merritt 2010). Protein is typically represented in the form of other animals such as insects, young birds/eggs, and small reptiles. These food sources may be rare in any given arboreal environment and typically are not eager to be prey items so they may have to be chased and captured. Within primates this type of food is often associated with fast styles of locomotion such as leaping, hopping, or running. Larger mammals have slower metabolisms than small mammals and can afford to subsist on relatively





**Prosimian Locomotion, Fig. 4** *Left Image:* sifaka (*Propithecus* spp.) performing a spectacular aerial leap across the forest canopy. These vertical clinging and leaping prosimians push off of the tree limb with their powerful

hind limbs and fly through the air. *Right Image:* group of sifakas hopping bipedally on the ground with upper limbs extended to the side (Photo credit Hajarimanitra Rambeloarivony)

low quality but plentiful foods such as leaves, which don't need to be caught. Within primates this type of diet is often associated with slower styles of locomotion such as arboreal quadrupedalism or slow climbing (Ankel-Simons 2007; Fleagle 2013).

### Ways to Get Around as a Prosimian, or Locomotor Styles

Locomotion among prosimians takes widely divergent forms (see Fig. 2). With increasing body size, the amount of climbing in prosimians increases and the amount of leaping decreases (with the vexing and obvious exception of sifakas, who make spectacular leaps at their large body size – Fig. 4). Among primates in general, locomotion can be classified into four major types: vertical clinging and leaping (VCL), quadrupedalism (both arboreal and terrestrial varieties), brachiation, and bipedalism. Many primates adopt a mix of these locomotor styles throughout their activity cycle, depending upon which substrate they are using at any given time and what the goal of their movement is (gathering food, agonistic encounters, predator avoidance, etc.). Within these four major types of locomotion, there are a number of subtypes, such as arboreal versus terrestrial quadrupedalism, and the differences between the categories lie primarily

in the degree to which the forelimbs versus hind limbs are used to climb, swing, jump, and run.

Small-bodied prosimians tend to be arborealists and exploit quadrupedalism and/or vertical clinging and leaping. The smallest prosimians tend to be committed vertical clingers/leapers and are the small galagos, weighing in at 50 g–450 g (*Galago*, *Galagoides*, *Sciurocheirus*), and the tarsiers, weighing in at 60 g–150 g (*Carlito*, *Cephalopachus*, and *Tarsius*), as shown in Fig. 5. The tiniest lemuriforms of Madagascar are the mouse lemurs weighing in around 50 g (see Fig. 2). These diminutive prosimians use both arboreal quadrupedal running and vertical clinging and leaping (Fig. 6), all occurring along the smallest branches of trees. This is a rare locomotion style for large prosimians. Sifakas (*Propithecus* spp.) are enormous among the prosimians, weighing in around 6 kg, well above the average house cat. These diurnal prosimians are vertical clingers and spectacular leapers (see Fig. 4). No doubt due in part to their large body size, sifakas spend time on the ground and employ a unique style of locomotion, bipedal hopping (Fig. 6).

### Vertical Clinging and Leaping (VCL)

This locomotor mode involves, as its name suggests, clinging to a relatively narrow vertical tree branch with both forelimb and hind limbs (e.g.,



**Prosimian Locomotion, Fig. 5** Tarsier (*Tarsius* spp.) clinging onto a tree branch in a typical posture. Tarsiers are categorized as vertical clingers and leapers. Note the characteristic large eyes in this nocturnal prosimian as well as the flattened nails on the hands and feet (Photo credit Sharon Gursky)



**Prosimian Locomotion, Fig. 6** A mouse lemur (*Microcebus* spp.) clinging onto a spiny tree in the spiny forest of Madagascar. These lemuriforms are among the smallest of the prosimians and use both vertical clinging and leaping and arboreal quadrupedalism (Photo credit Hajarimanitra Rambeloarivony)

see Fig. 5). Vertical clingers and leapers – typically small-bodied prosimians – largely avoid going to the ground by using long-distance, ricochet leaps to get from tree to tree. Using the hind limbs and powerful hamstring muscles, these primates push off of the vertical substrate and reach for the upcoming substrate with their forelimbs. VCL is a fast way of moving that can be helpful in avoiding predators and catching animal prey.

### Arboreal Quadrupedalism

The vast majority of primate species are arboreal (Fleagle 2013) and most prosimians adhere to this general rule (see Fig. 2). The conservation of quadrupedalism in primates is evident in examinations of the primate fossil record as well, with indications that the earliest primates included some quadrupedalism in their

locomotor repertoire as well (Larson 1998). Arboreal quadrupedalism is the preferred mode of locomotion for the larger galagos (*Otolemur* spp., Fig. 7), lorises (Fig. 8) and pottos and all lemuriforms except sifakas and sportive lemurs. Among the arboreal quadrupeds, slow lorises and slender lorises (*Nycticebus* and *Loris*) stand out for their remarkably slow method of advancement. While most of the small galagos and the tarsiers are rapid VCLs, lorises take an opposite approach.

Quadrupedalism in primates is somewhat different than in most other quadrupedal mammals. While many mammals move quadrupedally, primates do so using a high degree of forelimb protraction with a diagonal, couplet gait. This diagonal gait allows only one limb to be off the substrate at any one time, increasing contact on curved, narrow branches and proffering added

**Prosimian Locomotion,**

**Fig. 7** One of the larger galago species, *Otolemur crassicaudatus*, using arboreal quadrupedalism on a small branch. Note the grasping hands and feet in this galago as it moves along the branch (Photo credit Simon Bearder, Nocturnal Primate Research Group, Oxford Brookes University)

**Prosimian Locomotion,**

**Fig. 8** Upper image: slow loris (*Nycticebus coucang*) in preparation for a cantilever stance. Note the widely divergent lower limbs grasping onto small branches to support the rest of the body as the cantilever begins. Lower image: same slow loris from below in a full cantilever body. Note the fixed hind limbs and the forelimbs reaching ahead (Photo credit Andrew Walmsley, Little Fireface Project)



stability in the canopy (Larson and Stern 2006; Schmitt 1998; Schmitt et al. 2006).

Whether done in the trees or on the ground, primate quadrupeds tend to protract their upper limbs to a higher extent than other mammalian quadrupeds (Schmitt 1998; Schmitt et al. 2006).

Protracting the forelimbs may produce a longer stride, reducing the frequency of gait. This sort of gait pattern may be useful in reducing the branch sway during quadrupedal walking, thereby reducing the danger of falling off the branch and alerting potential prey. Primate quadrupeds also



use a diagonal gait or diagonal couplet where opposite forelimbs and hind limbs move together.

Lorises are among the most carnivorous of all primate species (feeding on insects and small reptiles). Instead of rapidly approaching their prey like carnivorous galagos and tarsiers, lorises tend to take a slow, stealthy approach. Lorises, especially slow lorises, are also remarkable in their use of cantilevering in moving through small branches. Cantilevering is a mechanism by which the hind limbs are fixed in grasping a small branch, while the rest of the body projects forward, not unlike a cantilevered beam (see Fig. 8).

### Terrestrial Quadrupedalism

Very few prosimian species come down from the trees to move quadrupedally on the ground, with the notable exception of *L. catta* (Fig. 3). The very small prosimians, such as tarsiers, mouse lemurs, and some galagos, prefer to stay in the trees which may provide some protection against predation. The larger *L. catta* spends almost a third of its waking time on the ground in a variety of activities. While there are no definitive explanations for why ring-tailed lemurs spend so much time on the ground, it may be associated with their highly complex social behavior and relatively large social groups. Ring-tailed lemurs are indeed preyed upon by fossae, raptors, boas, and civets but predation pressure varies from site to site. Functionally, terrestrial quadrupedalism is similar to arboreal quadrupedalism with the main difference being differences in substrate compliance.

### Bipedalism

The only prosimian that engages in any sort of routine bipedal locomotion is the sifaka (*Propithecus* spp.). Figure 4 shows a typical bipedal hopping bout in an adult sifaka. While these large-bodied primates are usually a VCL when in an arboreal setting, they come to the ground with varying frequency. Instead of using quadrupedal locomotion when terrestrial, they engage in a hopping behavior with their hind

limbs. Tails are typically extended along with the upper limbs at their sides.

## Conclusion

The focus of this entry was to provide a summary of prosimian diversity, including basic taxonomy, preferred habitats, and unique modes of locomotion employed to navigate those habitats. In brief, prosimians employ a wide range of locomotor repertoires including vertical clinging and leaping, arboreal and terrestrial quadrupedalism, and bipedalism. The preferences for locomotor style are directly tied to issues of body size, with smaller species occupying more arboreal habitats and employing more leaping and quadrupedal walking/running, whereas larger species occupy more terrestrial habitats and use combinations of quadrupedal and bipedal locomotion to negotiate their environments.

## Cross-References

- [Prosimian Cognition](#)
- [Prosimian Diets](#)
- [Prosimian Life History](#)
- [Prosimian Morphology](#)
- [Prosimian Navigation](#)

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## Prosimian Morphology

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## Synonyms

Galago; Lemur; Loris; Potto; Strepsirrhine; Tarsier

## Introduction

There is a wide range of unique morphological features present across prosimians. Some features are seen in each species, though others are seen only in a few. As the majority of nocturnal primates are prosimians, features such as the tapetum lucidum, which aids their vision during the night, a grooming claw on the foot, and a wet nose are universally present. Though, as in most cases there are exceptions to these generalized rules. Each prosimian is unique and distinguishable, giving way to their identification as separate families, genera, and species. Presented here are general morphological features grouped by the three infraorders included in the classification prosimian (Tarsiiformes, Lemuriformes, and Lorisiformes).

## Tarsiiformes

Tarsiiformes (tarsiers) classify of three genera and 11 species. Tarsiers are morphologically unique in that they display many features associated with both strepsirrhines and haplorrhines. They have a short trunk and a large head; they also lack a wet rhinarium, which places them among the haplorrhines. Their ears are hairless, round, mobile, and membranous; it is well understood that they have very acute hearing, and the terminal nuclei of the cochlear nerve is particularly large.



Tarsiers have the ability to rotate their heads almost 360°. They have large eyes, where a single eyeball is the same size as their brain and their eye sockets are only partially closed, compared to the fully closed sockets seen across primates. Unlike other nocturnal primates, this genus is exceptional, as they seem to lack a tapetum. Compared with other prosimians, it is clear that tarsiers are morphologically specialized for predatory functions; their auditory acuity and their comparatively reduced olfactory region support this theory. Regarding dentition, tarsiers are identified by the dental formula 2-1-3-3/1-1-3-3. Their postcranial morphology focuses on their vertical clinging and leaping locomotor specialization. Their intermembral index is about 56, the lowest among all primate species, which means that their hindlimbs are longer than their forelimbs, most notably they have an elongated tarsus, which is reflected in their name. While resting in vertical postures, tarsiers can use their tails, which has a friction pad, to provide additional support. On their hands, the fingertips are enlarged and disc-shaped; they are also the only primates that have two grooming claws.

## Lemuriformes

Five families make up the infraorder Lemuriforme, Cheirogaleidae, Lepilemuridae, Lemuridae, Indridae, and Daubentoniidae. Cheirogaleidae (cheirogaleids) include six genera and 19 species, Lepilemuridae (lepilemur) include four genera and 13 species, Lemuridae (lemurids) include four genera and 13 species, Indridae (indriids) include four genera and 13 species, and Daubentoniidae (aye-ayes) include four genera and 13 species.

Cheirogaleids, which include both dwarf and mouse lemurs, range in body size from 19 to 27 cm and are among the smallest known primates. Compared to other Lemuriformes, they have a globular head, hairless ears, and a more elongated muzzle. Their postcranial morphology reflects their locomotor behavior and diet. In cheirogaleids, their hindlimbs are somewhat longer than their forelimbs but not as elongated as in vertical clingers and leapers. Their intermembral index averages at 71. They grasp substrates and

items using their second and third digit, instead of the more typical thumb and index finger grasp. They have keeled nails, which facilitates their ability to access saps and gums on vertical substrates. An extreme specialization within this group is the fat tailed dwarf lemur and its use of their tail to store fat during periods of torpor.

Lemuridae range in size between 28 and 60 cm, this includes the larger ruffed lemur to the smaller bamboo lemur. Morphologically lemurids possess specialization that facilitates a specific ecological or behavioral function. The bamboo lemur is able to consume levels of cyanide that would otherwise kill any other mammal (Glander et al. 1989). Wright and Randriamanantena (1989) suggested this specialization enabled multispecies sympatry in a single environment. *Lemur*, *Eulemur*, *Hapalemur*, and *Varecia* all have scent marking glands on their wrists, inside their elbow, and in the genital area, which are used as a form of communication, between individuals and different animals. Most Lemuriformes are arboreal and have hair covering their heels, except for *Lemur catta*, a terrestrial species that have hairless heels. All lemurs have a dental formula of 2-1-3-3/2-1-3-3 except for lepilemur who have a dental formula of 0-1-3-3/2-1-3-3 and aye-ayes who have a dental formula of 1-0-1-3/1-0-0-3.

Indridae is comprised of the largest extant lemurs, indris have a body length of about 70 cm; sifakas are about 45–54 cm long. Indriids have a specialized postcranial morphology; their hindlimbs are longer than their forelimbs with an intermembral index of 62. Indris are distinguished from all other genera of Madagascan prosimians by having very short tails and limbs designed for vertical clinging and leaping. Between the leaping indri and quadrupedal ruffed lemurs, their vertebral morphology is distinct, which highlights the importance of varying spine morphology as well as limb morphology in identifying locomotor specializations (Shapiro 1995).

Daubentoniidae is a highly specialized lemur species, known for its rodent like teeth and elongated third digit. Aye-ayes have a body length of about 40 cm and a tail that exceeds the length of their body. They have large eyes, large membranous ears, and a narrow muzzle. A series of

complex ridges on the inner ear allow the aye-aye to have an acute auditory sense, to hear insects and respond to their movement while series tree cavities. The cranial morphology of the aye-aye is easily identified by their reduced dentition and relatively large brain case. All four limbs are comparatively short, though the hind limbs are relatively shorter than the forelimbs. They have an intermembral index of 70 and unlike other lemurs, the aye-aye has claws on its hands and feet except on the big toe, they also have an elongated third digit used to tap along branches and trunks, which aid them as they feed on structurally defended resources (Sterling 1994).

### Lorisiformes

Two families make up the infraorder Lorisiformes, Galagidae (galagids), and Lorisidae (Lorisids). Galagidae include six genera and about 19 species and Lorisidae include four genera and about 13 species.

Lorisids, including all lorises, angwantibos, and pottos, all have a vice-like grip. They also possess a specialized vascular supply, which allow lorisids to maintain static positions for extended periods of time, called the *retia mirabilia*. Slender lorises range in body length between 18 and 27 cm. They have a round head, round ears, and large eyes. They have a narrow muzzle, especially in comparison to other prosimians. They have long thin limbs, which give them a slender appearance. The slow loris on the other hand is more robust; they have large limbs and a less elongated muzzle. They have a reduced tail and a reduced second digit on their hands. This digit morphology aids in the previously mentioned vice-like grip. *Nycticebus* not only has powerful hands but especially powerful grasping feet compared with the hands and feet of the slender loris. In the slow loris, the limbs are essentially equal lengths; thus, their intermembral index is about 89. Pottos range in length between 33 and 42 cm; much like the slow loris they have a reduced tail, though it is the longest among all Lorisids. Pottos have large eyes reflecting their nocturnality, but relative to other Lorisids they are somewhat small. They have an intermembral

index of about 88, where their hindlimbs and forelimbs are the same length, similar to the slow loris. Regarding their postcranial morphology, they have strong hands and feet specialized in grasping. Their second digit is extremely reduced enabling a more secure grasp between the thumb and third digit. On the foot the second toe has a grooming claw, which is not uncommon among prosimians. Perhaps the most fascinating morphological feature in this primate is the use of a scapular shield, as a defense mechanism. Their dorsal spine protrudes above the surface of the skin and when threatened an individual will curl its head under its shoulders and quickly throw their bodies forward in a punching motion. Angwantibos range in body length between 22 and 27 cm. Their head is quite similar to slender lorises in that they are globular with a narrow muzzle, though their ears are smaller and flatter in comparison. A trend among Lorisids they also do not have a tail, but Angwantibos are extremely unique in regards to their hand and foot morphology. Their index finger is reduced and is positioned opposite digits three to five in the hand. Digits four and five are webbed and the third digit is much shorter than both digits four and five. They also have webbed toes; digits three to five are webbed, similar to their hands.

Galagids, also known as bushbabies, range in body length between 29 and 47 cm and have large eyes, a globular head, and large membranous ears, which can move independent of each other. Bushbaby ears are relatively the largest ears of all primates. Galago skulls resemble those of lorises but differ slightly. They have a wider interorbital distance and a more rounded cranium. All bushbabies are vertical leapers and have been observed resting in upright position. Their hindlimbs are considerably longer than their forelimbs, as expected for a vertical leaper. Among galagos, their intermembral indices vary between 57 and 64. A unique feature among three species of bushbaby is their hand and foot morphology. The needle claw bushbabies have needle-like nails on the ends of most of their fingers and toes, to facilitate access to tree trunks as they eat gums and saps. As is the case in most prosimians, they have a grooming claw on the second toe, and the remaining digits just have nails.

## Conclusion

Prosimians are a large and diverse group of primates, which makes it difficult to succinctly describe all of the morphological characteristics that make them unique across the Order Primates and among each other. The characteristics discussed above are generalized across the families, within the three infraorders: Tarsiiformes, Lemuriformes, and Lorisiformes. Each family, genus, and species has a number of specific features that distinguish one from another. These features are seen in their pelage variation, genetic variation, and anatomical differences. This entry focused on general anatomical differences and their behavioral and ecological function. Many researchers have extensively studied morphological differences in living individual and preserved specimen. Thus, this entry can be supplemented by a number of historical and recent research articles and books that further detail the differences seen in prosimians.

## Cross-References

- [Cattarrhine Morphology](#)
- [Precision Grip](#)
- [Prosimian Diets](#)
- [Prosimian Life History](#)
- [Prosimian Sensory Systems](#)

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## Prosimian Navigation

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## Definition

Navigation – the intentional act of determining and maintaining a route from one place to another (Gallistel 1990).

## Introduction

Prosimians are comprised of three infraorders: Tarsiiformes, Lorisiformes, and Lemuriformes. Few studies focus on prosimian navigation to the same extent as it is studied in other animals; instead aspects of navigation are incorporated into analyses of foraging and dispersal patterns. Call and Tomosello (1997) noted the limited amount of information on spatial cognition in prosimians, emphasizing that further research was needed to discover their capacity for negotiating their environment. Knowledge on this topic is continuously expanding and with an increase in dedicated research, new findings will shed light on the navigational capacity of these primates. Here I summarize findings on navigational behavior in prosimians including directed searches, such as, foraging patterns.

## Tarsiiformes

Researchers working on habitat utilization and behaviors clearly show that *Tarsus* species travel to goal locations and engage in exploratory movement and nonrandom use of their homeranges.

Path lengths in *Tarsius diana* of Kamarora fluctuated based on habitat disturbance compared to those in more pristine forests (Merker 2006), suggesting that these individuals are in search of specific resources lacking in the disturbed areas. *Tarsius syrichta* males frequently move along the periphery of their homerange and traveled from one end to the other, presumably to survey their territory. Females regularly followed the same path for several nights and then changed to a new travel path (Neri-Arboleda et al. 2002). Minimum nightly travel varies between species, where *T. syrichta* (260–556 m) travel less than *Tarsius bancanus* (Crompton and Andau 1987) and *Tarsius spectrum* (Gursky 1997; Dagosto et al. 2001). No studies on more complex navigational skills, including mental map use, are reported for tarsiers.

### Lorisiformes

Traveling and foraging make up as much as 50% of nightly activity in *Loris* species, where traveling is defined as directed movement (Nekaris 2001). Lorises traveled along the perimeter of their home ranges, for territorial purposes, similar to tarsier species. Males were also observed traveling in a direct line for more than 50 meters to reach female conspecifics (Nekaris 2001, 2003). *Nycticebus* species also display goal-oriented travel. The Javan slow loris likely uses route-based mental maps to navigate their environment. Other species of slow lorises possess many of the same feeding and behavioral characteristics as the Javan slow loris, thus likely use some form of mental representation, as well, to return to immobile resources, including parked infants (Fitch-Snyder and Ehrlich 2003). *Galago* species utilize gum, another immobile food resource, which requires nonrandom use of their homerange and directed travel to regularly find gum-producing tree and return to its location.

### Lemuriformes

Following a number of studies including Lemuriformes, all consistently report that they do not randomly move within their environment, a preliminary indicator of higher navigational skills. *Propithecus edwardsi*, *Eulemur fulvus rufus*, *Microcebus murinus*, *Eulemur rubriventer*,

*Eulemur rufifrons*, and *Varecia variegata editorum* all display nonrandom use of their environment, leading researchers to acknowledge that they utilized distinct routes when traveling from point A to point B (Everhart and Overdorff 2008; Lührs et al. 2009; Razafindratsima et al. 2014; Joly and Zimmerman 2011; Schliehe-Diecks et al. 2012). *P. edwardsi* and *E. f. rufus* uses “traditional” travel routes to get from one food patch to the next. Through the use of “traditional” travel routes, animals are able to check the status of various resources along the way as they move from one important food source to another (Milton 2000), particularly resources that are out of sight from their current location. Similar to *P. edwardsi* and *E. f. rufus*, *M. murinus*, *E. rubriventer*, *E. rufifrons*, and *V. v. editorum* all reused particular routes to travel between feeding resources (Lührs et al. 2009; Razafindratsima et al. 2014), where *E. rufifrons* displayed frequent backtracking behavior. Reusing the same routes and feeding locations suggests that these animals have some form of mental representation of their environment. How complex these representations are is a point of debate among those studying spatial cognition and can be difficult to determine outside of controlled experiments. *M. murinus* uses cues to successfully travel along routes and route overlap than compared to that of larger more social diurnal primates (Joly and Zimmerman 2011). While dispersing, this species moved in a straight line and covered many areas than during normal ranging patterns. Schliehe-Diecks et al. (2012) concluded that these unusual patterns were the result of a standardized exploration/dispersal strategy. Lemuriformes have been the focus of both basic and complex navigational research, providing a much more complete picture of how these species negotiates their environment.

### Conclusion

Navigation, or the act of using an intentional route to move from one location to the next, is seen across a number of animal species. In prosimians, basic navigational skills including foraging patterns and seeking conspecific are seen in all three infraorders. Research focused on more complex

navigation like mental mapping is limited to *Nycticebus* species and some Lemuriformes. Though spatial cognition is not a new topic and there is no limit to the amount of research focused on navigation in other animals, there is an emerging interest in expanding this research to include prosimians.

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## Prosimian Sensory Systems

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## Introduction

To successfully negotiate the challenges of living in a dynamic environment, animals generally can receive and interpret sensory information. This information includes visual, olfactory, auditory, tactile, and gustatory cues. Using their sensory system, they can discern dangerous situation, identify conspecifics, and locate food resources. Prosimians are a taxonomic group comprised of lemurs, lorises, galagos (strepsirrhines), and tarsiers. Unlike other primate taxonomic groups, the majority of nocturnal primates fall within the classification of prosimian. As such, there are varying ways that sensory cues inform these primates. Here I will focus on vision, olfaction, and auditory cues, as our understanding of the prosimian sense of touch and taste is limited.



## Vision

Vision plays an essential role in small-scale prey detection in nocturnal strepsirrhines (Bearder et al. 2002; Nekaris 2005). Experimental research suggests that there is little difference between nocturnal visual detection and that of sympatric diurnal species (Bicca-Marques and Garber 2004). Veilleux and Kirk (2014) measured the visual acuity of six strepsirrhine primates (*Cheirogaleus medius*, *Eulemur macaco*, *Galago senegalensis*, *Lemur catta*, *Microcebus murinus*, *Otolemur crassicaudatus*) concluding that both diet and diel patterns influenced the evolution of optical resolution in strepsirrhines.

Strepsirrhine eye morphology shares certain features that make them distinct from other primate taxa. Their retinas lack foveae (a small pit in the back of the retina) and have a lower cone/rod ratio, and their eyes often contain reflective tapeta. The tarsier (Tarsiidae) deviates from this pattern as a haplorrhine, despite being included as a prosimian. Tarsiers have incredibly large eyes relative to their body size and lack the tapetum lucidum that is typical in other nocturnal primates. The retinal foveae in tarsiers are variably reported, some report that they are universally present while others say it is absent in some individuals. Another point of departure from the strepsirrhine standard is the report of underdeveloped foveae occasionally seen in galagos (DeBruyn et al. 1980).

Generally speaking, strepsirrhine tend to be monochromatic or dichromatic, but some species show a population level polymorphism where some females are trichromatic. Dichromatic versus trichromatic color vision in primates is the result of variations in opsin genes that code for different classes of cone photopigments in the eye (Jacobs et al. 1996). Strepsirrhines have two types of retinal cones S (short wavelength-sensitive) and M/L (medium/long wavelength-sensitive), as is true in most mammals. This dual system facilitates dichromatic color vision between shorter (blues) and longer (greens/yellows/reds) wavelengths of light (Jacobs 2009).

Whereas dichromacy is retained in many lemurs, all loriforms (lorisids and galagos) have lost S cones due to deleterious mutations in specific opsin genes (Jacobs 2013). Species of lemurs exhibit variability in the peak spectral sensitivities of their M/L and S cones (Veilleux and Kirk 2009). In contrast, all loriforms seem to share the same M/L peak spectral sensitivities (Tan and Li 1999).

Polymorphism may be linked to behavioral trichromacy in heterozygous ruffed lemurs but there is no evidence of behavioral trichromacy in heterozygous sifaka (Leonhardt et al. 2008). They reported a modest effect of opsin polymorphism on behavioral trichromacy, mirroring the small shift in spectral sensitivity further suggesting that trichromacy may be only one of several routes toward increased foraging efficiency in visually complex environments.

## Olfaction

Many prosimian species use glandular secretions to engage in scent-marking. Through scent-marking behaviors, these species can use olfaction to communicate information about themselves including their health, reproductive stage, relatedness, and age.

The pygmy slow lorises (*Nycticebus pygmaeus*) during peak estrus showed a significant preference for counter marking males (Fisher et al. 2003). They suggested that the act of countermarking could signal continued competition and the counter marker could be perceived as the “winner.” In this situation, olfaction leads females to perceive counter markers preferentially; it also highlights how olfaction is used to delineate individuals. This research also supports the “competitive countermarking hypothesis,” and demonstrate that chemosignals play a profound role in governing female reproductive behavior in prosimians. In ring-tailed lemurs (*Lemur catta*), semiochemical profiles within and between males provided two types of genetic information (individual heterozygosity and genetic distance).

During the breeding season, male ring-tailed lemurs use their scrotal secretions to convey olfactory cues indicating their genetic distance and genetic quality. This represents another instance where valuable information about an individual during a time when male competition and female choice can have long-term consequences on fitness. Ring-tailed lemur females dampened their expression of volatile chemicals during pregnancy, and the compound richness is notably reduced in females bearing sons. Such olfactory signatures of pregnancy may help guide social interactions, potentially reducing intragroup conflict; cues that also advertise fetal sex may additionally facilitate differential energetic allocations based on sex. In an analysis of urine and nonurine chemical composition in a broad range of prosimians, urine markers expressed the most chemically complex and distinctive urine. More distantly related species had more variation in urinary profiles, suggesting gradual signal evolution (Delbarco-Trillo et al. 2011). It was further suggested that urine marking is an ancestral behavior related to solitary, nocturnal living and that parallel evolutionary shifts toward greater reliance on glandular marking, a derived trait occurred in diurnal and more social lemur genera.

Red-ruffed lemurs (*Varecia rubra*) use scent-marking to convey information about sex and female age, with male neck marking behavior serving a defensive territorial function and anogenital marking is used in sociosexual communication (Janda et al. 2019). There is also evidence to support that lemur species use olfactory indicators to signify naturally occurring injury. This is beneficial given the social and physical costs of injury; it is possible that lemurs are aware of the health status of conspecifics and are selective in who they engage in aggressive behaviors (Harris et al. 2018). In addition to communicating sociosexual information, olfaction plays an important role in interpreting environmental cues. Across the Order Primates, there is a variation in the number of functional olfactory receptor (OR) genes, which is associated with processing ecological olfactory cues. In haplorhines, there are 300–400 functional

genes, and in strepsirrhines, there are approximately 640 functional genes (Matsui et al. 2010; Niimura et al. 2014). Research on how prosimians use olfaction in an ecological context is emerging, including the following examples.

Lemur olfactory foraging behavior was negatively associated with fruit volatile organic compound (VOC) sums, whereas higher VOC sums showed a marginally significant negative association with how much an individual was observed sniffing a food item (Valenta et al. 2016). The authors concluded that items with a higher VOC did not require individuals to use olfaction as much as they would for items with a low VOC sum. The relationship between the olfactory cues emitted by fruits, insects, and other vegetation can act as another signal in which prosimians can use their sensory system to utilize their environment successfully. The authors also noted that it is likely that the overall smell signal is not the only predictor of olfactory foraging behavior.

Wooly lemurs (*Avahi*), a nocturnal folivore, engaged in more olfactory-based foraging when the visual signals of a leaf species were not conspicuous enough to discern young and mature leaves (Sawyer et al. 2019). This report in a nocturnal folivore emphasizes that the traditional notion of a trade-off between olfaction and vision is not a linear path by which nocturnal prosimians only use olfaction, and trichromatic haplorhines do not. As we dig further into the mutual and antagonistic relationship between vegetation and the species that feed on them, we will gain a better understanding of the role olfaction plays in the prosimian sensory system.

## Auditory

Across prosimian species, there is an extensive repertoire of audible vocalizations ranging from contact calls to alarm calls, used to communicate with conspecifics, as well as, high frequency and ultrasonic vocalizations which can be used to evade predators. Along with the ability to produce high-frequency vocalizations comes the

ability to hear at a higher frequency compared to other primates.

Primate auditory morphology varies along phylogenetic lines; in extant strepsirrhines, most lemurs have an unfused tympanic ring surrounded by a large, single-chambered middle ear cavity, whereas lorises have a tympanic ring that is fused to the lateral tympanic wall and exhibit a multi-chambered middle ear cavity (Cartmill 1975); the latter is also the case in haplorrhines. The shape of the pinna in strepsirrhines is generally relatively tall and narrow compared with that in haplorrhines (Coleman and Ross 2004).

Following an auditory brainstem response (ABR) analysis of 11 prosimian species (*Daubentonia madagascariensis*, *Eulemur coronatus*, *Eulemur fulvus collaris*, collared lemur *Eulemur fulvus rufus*, *Eulemur mongoz*, *Eulemur rubriventer*, *Lemur catta*, *Nycticebus coucang*, *Nycticebus pygmaeus*, *Propithecus coquereli*, *Varecia rubra*), Ramsier et al. (2012) found that social complexity and enhanced hearing sensitivity coevolved, and this relationship is a general biological pattern in other mammals. Given that larger social groups form in part to act as a deterrent for predation and that predator-specific alarm calls often have a high-frequency, it is reasonable that sociality is linked to the evolution of high frequency calls. This relationship between group size and high-frequency vocal sensitivity is a natural progression to what we see in some of the smaller bodied nocturnal prosimians. Tarsiers are the most notable case as a strictly insectivorous primate and are one of the only known primates that use pure ultrasound to communicate. Mouse lemurs also utilize ultrasonic communication (Zimmermann 2018). Reportedly, the Javan slow loris also used pure ultrasonic vocalizations. It is suggested that they use it as a form of contact call as they are solitary foragers (Nekaris and Geerah 2018).

## Touch and Taste

Relative to vision, olfaction, and auditory senses, tactile and gustatory sensory cues are

understudied. In regards to tongue morphology, there is little variation across primate species, though some prosimian species display a serrated sublingual. In addition, many prosimians appear to lack foliate papillae and have fewer circumvallate papillae. Strepsirrhines also have fewer taste buds in their circumvallate papillae compared to haplorrhines.

In humans, fungiform papillae density (FPD) is positively correlated with taste sensitivity; in strepsirrhine, sucrose sensitivity was negatively correlated with FPD, but positively correlated with the size of papillae among primates (Alport 2009). In addition, FPD was negatively correlated, and the papilla area was positively correlated, with the percent of fruit and flowers in a species' diet. These results suggest that strepsirrhines use their taste buds to discern different sugar levels and that there is a link between taste sensitivity and diet.

Black-and-white ruffed lemur individuals showed a marked preference for different sugars, where sucrose > fructose > glucose ≥ maltose ≥ lactose (Wielbass et al. 2015). The pattern of relative preferences for various sugars was similar in platyrrhine primates and humans, but differed from catarrhine primates. They concluded that their results support the idea that relative preferences for food-associated sugars in primates, but not necessarily their sweet-taste sensitivity, may correlate with diet.

Regarding prosimian touch, Erickson (1991) noted that in Aye-Ayes, the sense of touch likely played a role in foraging. They were observed to tap their third digit in an unexpectedly gentle fashion, suggesting that it serves a function in sensing surface vibrations. More research on this sense is needed to fully understand the role it plays in ecological and sociosexual success in prosimian species.

## Cross-References

- [Catarrhine Sensory Systems](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Sensory Systems](#)

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## Pro-social Behavior

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### Definition

*Pro-social behavior* is any voluntary action or set of actions performed by an individual that serves to benefit another individual or individuals, whether that action has a direct or indirect benefit to the actor.

### Introduction

Pro-social behavior, or behavior that benefits another individual, is of interest to researchers studying both humans and other animals. Perhaps because it is of widespread interest, there are a variety of different usages across disciplines. For our purposes, pro-social behavior encompasses all acts that benefit another individual, including altruism and reciprocity (the former being differentiated by a cost to the actor and the latter by the alternation of benefits between the individuals involved; see entries in this encyclopedia for more detail). Importantly, pro-social behavior does not necessarily imply pro-social *intent*; animals may act in a way that is functionally pro-social without any intention of doing so (see discussion of function versus mechanism, below). For instance, an individual may provide a benefit to another as a side effect of an action that benefits himself or herself, and there is no assumption that animals understand their actions as pro-social. Thus, it is more appropriate to discuss whether

an animal engages in pro-social behavior, which is agnostic to intent, rather than whether they behave pro-socially, which is often assumed to imply active intent on the part of the actor.

The hypothesized function of pro-social behavior is to strengthen affiliative bonds, which are critical for group-living species that must work together in at least some contexts. Pro-social behavior includes behaviors such as grooming, support, or food sharing that are widespread across species, as well as behaviors seen in a more limited number of species, such as alarm calls given to alert conspecifics to a predator's presence. Despite the hypothesized importance of pro-social behavior, it has proven remarkably difficult to demonstrate this behavior in experimental contexts. This could be because pro-social behavior is rare, of course, but this runs counter to evidence from the field, which in some species indicates fairly frequent pro-social behavior across a variety of contexts. Some authors have argued that this apparent contradiction is more likely due to subjects not understanding the purpose or mechanics of the tasks designed to elicit pro-social behavior than to pro-social behavior being rare in reality. Moreover, despite their challenges, due to the ability to manipulate factors one by one, experiments are key for understanding the contexts in which pro-social behavior occurs and determining what, if anything, subjects understand about their behavior.

Because of the breadth of potentially pro-social behaviors, for this entry we narrow to focus to a recent body of work considering the degree to which animals make decisions that benefit others. Although such decisions typically involve a small cost (the opportunity cost of making the decision), in order to maximize the chances of finding pro-social behavior, most do not entail any other costs to the actor making the choice and are therefore not altruistic. Moreover, most experiments explicitly avoid the possibility of reciprocity. Nonetheless, such work is important to consider within the contexts of both altruism and reciprocity, which we do briefly at the end of this entry. Finally, unless otherwise specified, we throughout refer to pro-social behavior in the functional sense of behavior that provides a benefit to another but remains agnostic as to the intent of the actors.



## Pro-social Behavior in Naturalistic Settings

Although recent work has focused on experimental contexts designed to understand the mechanisms underpinning pro-social behavior, original work on the topic derives from field observations or from observations made in naturalistic captive populations. Perhaps the most commonly reported pro-social behavior is grooming. Although grooming serves a biological function (i.e., removing parasites, which helps maintain health), many animals, including primates, engage in far more grooming than is necessary for health purposes and subjectively appear to enjoy being groomed. In addition, endocrine changes have been observed in conjunction with social grooming, indicating that social grooming has a physiological effect. As mentioned above, there is evidence that grooming strengthens social bonds, which can be critical for fitness. Recent work in baboons shows that females with more friends both live longer and have more surviving offspring than those with fewer friends (Silk et al. 2003). Grooming is not particularly costly nor is it zero sum (i.e., grooming one animal does not remove the possibility of grooming another, the way that food shared with one individual cannot then be shared with another), which may contribute to why it is such a widespread pro-social behavior.

Food sharing, a costlier pro-social behavior, has been seen in several primate species; however, food sharing occurs in much more limited contexts than grooming. For example, chimpanzee food sharing is generally limited to sharing with infants, excepting situations in which individuals work together to acquire food. Chimpanzees show coordinated hunting, or at least simultaneous hunting with allies, and often share the spoils of a hunt with others that participated in the hunt, even those that are not related to them (Boesch and Boesch 1989). Importantly, forest-dwelling chimpanzee populations, such as those in the Tai forest in the Ivory Coast, where tree cover is contiguous, are much more likely to meat-share than populations that live in more open grounds, such as the Gombe populations. This is presumably because the smaller, lighter monkeys they

hunt can more easily escape in contiguous forest, where they can more easily run between trees than the heavier chimpanzees, than in isolated trees, where they can be treed by individual chimpanzees. This may make coordination more essential, and meat-sharing based on hunt participation has been suggested to be a key feature in maintaining cooperative hunts. While other species engage in cooperative hunting and prey-sharing based on hunt participation (i.e., lions), this type of active meat-sharing post-hunt is more rare.

Food sharing in the form of allonursing is also seen in some species. Although uncommon, it does occur in primates; golden snub-nosed monkey and capuchin monkey females have been reported to nurse each other's offspring. Allonursing has been most often observed in species that typically reproduce in litters, such as rodent and canid species. This is hypothesized to be because a mother nursing a litter is already expending a lot of energy producing a large amount of milk, so it may be that nursing additional young incurs a low additional cost relative to the overall cost already incurred (MacLeod and Lukas 2014). However, allonursing in these primates, who produce only a single offspring at a time, is more costly. It is possible that this occurs in species in which females form very long-term relationships, changing the cost-benefit ratio, similar to what is seen with cooperative breeding.

Perhaps the most costly pro-social behavior seen in natural contexts is adoption of non-offspring, which incurs an individual cost of energy, time, and a potential loss of reproductive fitness. Both male and female wild chimpanzees have been observed adopting non-kin orphaned infants in their group upon the death of the infant's biological mother (i.e., Boesch et al. 2010). Such adoptions generally involve multiple pro-social behaviors; for example, male adopters have been observed sharing food with their adoptees, as well as providing support in aggressive conflicts with other group members, and female adopters may allonurse. Although most (but not all) cases of primate adoption occur on the death of the mother, other mammals adopt non-kin offspring following separation from their own infants (i.e., northern elephant seals). Such adoption is unlikely to be

due to a lack of recognition, because playback experiments have shown that elephant seal mothers can acoustically distinguish their pups from unknown pups, suggesting that they are actively accepting non-kin offspring.

Of course, adoption may sometimes benefit the adopters, emphasizing the fact that lines can blur between pro-social and self-beneficial behavior. Brood size in the lesser snow goose can fluctuate post-hatch and past the stage where goslings would be expected to recognize their parent, including *increasing* brood sizes, which suggests emigration of new chicks (Williams 1994). These increases in brood size appear to increase the “social rank” and viability of the group as a whole and appear to have little extra cost to the parent of the brood. Such alloparenting occurs in other birds, and aside from the social rank hypothesis, others have suggested that tolerance of added non-kin to a brood may also increase the reproductive fitness of the parent by providing their biological offspring with proximate non-kin that become potential mates.

Finally, there are numerous anecdotes about pro-social behavior, particularly in species such as primates, dolphins, elephants, and dogs. This list, not surprisingly, correlates with species that are both most often observed and are among the largest brained species; it is likely that similar behaviors observed in a species with a smaller brain would be interpreted very differently. Aside from this reporting bias, anecdotes are not typically used in animal behavior because of the risks of false positives (i.e., one pro-social-looking behavior is reported and thousands of cases in which the animals are not pro-social are not) and the risk of over-interpreting the animals’ actions, not to mention it is impossible to determine the subjects’ motivations. In many cases, purported pro-social behavior could be explained in another way, and the two interpretations cannot be disambiguated. For instance, in a famous case in which a gorilla female carried a young human child who fell into the exhibit to the keepers waiting at the enclosure’s door, there was a debate over whether her behavior represented a recognition of the young boy’s predicament and an idea for how to solve it or whether she was following

the behavior pattern she had been rewarded for previously by the keepers.

Despite these challenges, however, anecdotes can provide key insight into rarer forms of pro-social behavior. Although they cannot replace careful experiments, they can provide suggestions as to what is worth considering. For instance, there are numerous anecdotes of apes helping others who need assistance with no apparent gain on their part. This includes reports of acquiring hard-to-reach foods for older individuals or rescuing youngsters from the moat. There is some evidence of cross-species pro-social concern, such as a female bonobo who found a stunned, but otherwise unharmed, bird on the ground in her enclosure, carried it high into a tree, and, attempting to orient its wings correctly, set it loose into the air (de Waal 2009). While we can debate the weight we should put on these anecdotes, one can test them by developing experiments that replicate some aspect of the context. Indeed, given the preponderance of cooperative or pro-social interactions now documented in the literature, including across different species, anecdotes like this are useful for developing new lines of inquiry.

## Experimental Evidence of Pro-social Behavior

Despite the substantial body of field literature implying pro-social behavior, most of this fieldwork is observational, limiting our ability to determine subjects’ motivations and the underlying mechanisms. As a result, recent work has moved to the lab, where conditions can be tightly controlled. Somewhat surprisingly, however, finding evidence of pro-social behavior in experimental tests has proven to be difficult. While this could indicate that the supposedly pro-social behavior witnessed in observational contexts has other explanations, it is also possible that the subjects either failed to understand the purpose or mechanisms of the tasks (i.e., did not understand the contingencies of an apparatus), or that the experiments did not involve a context that would typically elicit pro-social responses. The majority of

the work in this area has been in primates, although it will be important to see how other species respond as well.

The most commonly used paradigm is the *pro-social choice task*. The basic task involves giving the subject a choice between an option that rewards both subject and a conspecific (the “pro-social” option) and an option that rewards only the subject. Subjects are said to behave pro-socially if they choose the pro-social option more frequently when in the presence of a conspecific – that is, when there is someone to benefit – than when alone (called the partner absent condition). This partner absent control is critical for useful interpretation of results, because without it, it is difficult to assess if subjects are making choices based on some criterion irrelevant for pro-social choice (for instance, the total amount of food that is present or a mistaken belief that they will be able to access the food). A benefit of this task is that, aside from testing pro-social behavior, it is easy to include variations that alter the benefit to the actor or the action required to benefit the recipient (effectively changing the “cost”).

This task has been used in a variety of species that have shown naturally occurring pro-social behavior, but nonetheless, results are quite mixed. The history of pro-social studies in chimpanzees nicely illustrates the challenges of designing a task for complex social behaviors. Early studies in chimpanzees, all based on the pro-social choice design, yielded no evidence of pro-social decision-making. In one early task, chimpanzee subjects were given a choice between two platforms, each of which contained a reward for the subject and one of which also contained a reward for the conspecific (if present). Rewards were obtained by pulling in a “sweeper” that brought the foods within reach. Chimpanzees were no more likely to choose the option that delivered food to both themselves and their partner when the partner was present than when they were absent, which they hypothesized meant that the chimpanzees were not choosing to be pro-social (Silk et al. 2005). Another study, completed independently but at the same time, used a slightly different design and found the same results (Jensen et al. 2006). In addition to the pro-social

option, this latter study included both an altruism condition (subjects could reward partners, but not themselves) and a spite condition (subjects could actively block partners from receiving food), yet the chimpanzees never responded in a way that indicated that they were sensitive to anything but their own outcomes. This study also included an additional control that was not possible in the first study but that suggested that the subjects understood which foods were available in the different conditions.

One hypothesis for why the chimpanzees were not pro-social was that they were so focused on their own rewards that they failed to pay any attention to their partners. This could have explained their apparent understanding of the task, yet their failure to behave pro-socially. Thus, in a subsequent design, chimpanzees were given the option to acquire their own reward followed by their partner’s. The prediction was that if the challenge for the chimpanzees was that they were too focused on their own outcomes to pay attention to their partner’s needs, this would allow them to do so. Nonetheless, subjects again failed to choose the option that helped their partner at any higher rate when their partner was present than absent (although they always obtained their own food; Vonk et al. 2008). Another hypothesis was that the chimpanzees may not have behaved differently because there was no reason to do so; after all, one key hypothesis for the evolution of helping behavior is reciprocity, and in these studies the partner was never in a position to reciprocate. To test whether reciprocity played a role, pairs received the same pro-social choice task as in Silk et al. (2005) but alternated access to the apparatus on a trial-by-trial basis. The prediction was that they would behave more pro-socially in this reciprocal condition, but yet again, they did not make pro-social choices (Brosnan et al. 2009).

Another possibility was that chimpanzees were simply not pro-social in such tasks. To address this, experimenters tested bonobos, a great ape species that is closely related to chimpanzees but is considered a more peaceful and affiliative species than chimpanzees (who are generally considered more competitive). Therefore, the

expectation might be that bonobo subjects are more likely to act pro-socially. However, bonobos were not more likely to choose pro-socially in an analogue of the pro-social choice task (Tan et al. 2015), and evidence for food sharing differences between chimpanzees and bonobos has been inconsistent. This supports the hypothesis that it may be something about the task that is challenging, and indeed, even human children have failed to exhibit pro-sociality in the no-cost primate version of the task due to the attentional demands required, so the failure of other primates to do so is not necessarily surprising.

Of course, all of the above studies shared in common a reliance on food sharing as the expression of pro-social choice, and in most cases in the wild, pro-social behavior is elicited in non-food contexts, such as providing grooming or support. Thus, experimenters also began testing pro-social behavior in a more naturalistic way using a helping task, in which the subject gives aid to another individual to help the recipient achieve some goal or reward. As many primates have been observed helping in-group conspecifics in the wild, it may also be more ecologically relevant. In a series of early tests, a small sample of young chimpanzees helped both a human experimenter and each other acquire out of reach objects, even if doing so required extra effort (Warneken and Tomasello 2006), although they failed to do the same when the experimenter's goal was less obvious (as in avoiding a physical barrier). Subsequent studies by this group indicated that chimpanzees were sensitive to whether assistance was actually needed by a conspecific. Further, in a flexible helping task, chimpanzees were able to assess what tool would best benefit a conspecific, and spontaneously provided that tool (Yamamoto et al. 2009).

Because of the success of the helping tasks, researchers again questioned why chimpanzees – who do share food in at least some contexts – were not doing so in the pro-social choice tasks. New methods focused on altering the methods of the task to be more relevant to the chimpanzees. For example, one possibility was that the barpull task was too complicated, and indeed, when subjects chose between two tokens (rather than

pulling in one of two options), they more often chose the pro-social option (Horner et al. 2011). This study was criticized for not including a partner absent condition, and this result failed to be replicated in subsequent study (Amici et al. 2014); however, a key point was that in this task, the food rewards were not visible to the subject throughout a trial. In helping tasks, too, the occlusion of the recipient food reward or using symbols to represent food quantities was more likely to produce pro-social results. These results indicated that the presence or absence of visible food could be a crucial task feature in both the pro-social and the helping tasks.

Two more recent studies strongly suggest that the chimpanzees either did not understand or were not motivated by the pro-social choice task in its original form. In the first, the researchers replicated the original Silk et al. (2005) pro-social task with the same subjects and apparatus, with one tweak; after subjects had experience as the actor making the choice, they were given experience as the *recipient* to another chimpanzee who had been trained to always make the pro-social choice. Following this, the subject was put back with their original partner and given another pro-social choice test. Initially, no subject showed evidence of pro-social behavior but, after experience as the recipient, they began to choose the pro-social option more frequently when with their partner, indicating that they may have learned something about either the goals of the task or the experience of their partner (these are not mutually exclusive; Claidiere et al. 2015). In the second study, chimpanzee subjects only got the option to make a pro-social choice after their partner (who would be the recipient of a pro-social choice) gave up food in order to unlock the apparatus. Subjects were far more pro-social subsequent to this than in control conditions in which the partner's initial unlocking was unnecessary, or a human experimenter unlocked the apparatus (Schmelz et al. 2017). Indeed, they even chose the pro-social option when the partner got more than they did, to a limit. This indicates that chimpanzees may only be motivated to provide pro-social rewards when there is a reason to do so, something that was not present in earlier studies.

Other species have showed far more evidence of pro-social behavior even with the original pro-social choice task, although there remains variability. Capuchin monkeys, a species that, like chimpanzees, are highly cooperative and has a large brain-to-body ratio (a purported measure of cognitive ability), made other-regarding choices on both a version of the pro-social choice task (Lakshminarayanan and Santos 2008) and the token-based task (de Waal et al. 2008), as well as the helping task (Drayton and Santos 2014). As in the chimpanzees, however, the response is not consistent. Capuchins in another study were only pro-social when the disparity between their reward and their conspecific's was relatively low (Brosnan et al. 2010), and the same monkeys who succeed on the token-based task showed no evidence of pro-social behavior on several alternatives, such as a touch screen version of the task or an alternate helping task in which they could provide rewards to a conspecific partner. In addition, the abovementioned replication of both the pro-social choice tasks and the token study not only found no evidence of pro-social behavior in chimpanzees, but no evidence in either capuchins or spider monkeys, either (Amici et al. 2014). It's not clear why capuchins would make pro-social decisions in more contexts than did chimpanzees, but it may relate to either their social system or a different interpretation of the experimental context.

Finally, some of the best evidence of pro-social behavior in the primates comes from callitrichids, a cooperatively breeding species of New World monkey. In cooperatively breeding species, many individuals in a group help to raise offspring within the group, and both parents provide equal amounts of investment in offspring rearing. One hypothesis in the literature is that a cooperative breeding system may encourage pro-social decision-making, due to this interdependence. Consistent with this, common marmosets given the choice to donate to an unrelated recipient are more likely to behave pro-socially to a bonded pair-mate than to an empty cage; interestingly, only male and female "breeder" individuals showed this pattern, while female "helper" marmosets were no more likely

to choose pro-socially than without a recipient present (Burkart et al. 2007). However, this pattern isn't always consistent; marmosets are *less* likely to donate altruistically to a groupmate than to a stranger, although when given oxytocin, a hormone related to bonding, marmosets now prefer to behave pro-socially toward a familiar pair-mate rather than a conspecific stranger (Mustoe et al. 2015; see discussion of the endocrinology of pro-social behavior below). This hypothesis is supported outside the primate literature as well. Although not all corvids make pro-social choices, cooperative breeding azure-winged magpies do (Horn et al. 2016).

Some of the best evidence of pro-social behavior comes from rodents. Rats will spontaneously free a trapped cagemate, even before they open container of chocolate, and often even shared the chocolate with the freed cagemate. Rats also provide evidence as to what factors influence pro-social behavior. For instance, rats help familiar cagemates and strangers of familiar strains more than conspecifics of unfamiliar strains (Bartal et al. 2014). One key distinction between the rodent tasks and the version presented to other species is that the rodent tasks all feature a salient negative stimulus, in the form of a distressed conspecific, whereas the pro-social choice task both has less emotional valence and involves providing a positive benefit rather than taking away a stressor. It may be that pro-social behavior is simply more likely in such negative, high valence contexts, although rats appear to be pro-social in more positively valenced contexts as well. In addition, the partner's distress may be an aversive stimulus, which may increase the chances of subjects acting to help (this has been ruled out in several tasks). Overall, this series of studies reiterates the importance of context and the subjects' understanding and interpretation of the paradigm in studying pro-social behavior.

## Factors Influencing Pro-social Behavior

In order to understand when and under what conditions pro-social behavior occurs, and to understand its evolution, it is important to understand



the social and contextual factors that affect pro-social behavior.

### **Dominance**

Because pro-social behavior involves an interaction between two or more individuals, it's unsurprising that these behaviors would be influenced by the social relationship. Indeed, as dominants typically obtain more resources, and lower-cost services such as grooming are typically directed up the hierarchy, a reasonable hypothesis is that dominant individuals would receive more benefits from lower-ranking individuals than the reverse. However, in a modified pro-social task, dominant rhesus macaques were more likely to deliver the food to a subordinate monkey than vice versa (Massen et al. 2010). The authors hypothesize that dominants were using generosity to maintain alliances with subordinates and preserve their status, a result supported in other primate species: dominant chimpanzees are more often involved in food transfer than more subordinate individuals. Observations of avian species, such as rooks, indicates that seemingly altruistic food sharing may be used as a costly symbol by dominants that wish to broadcast their high-ranking status.

### **Existing Social Bonds**

There is a large body of evidence suggesting that individuals act more pro-socially toward a recipient with whom they have an existing affiliative relationship. This intuitively makes sense; an existing affiliative relationship by definition indicates recurring interactions with the same individual, presumably increasing the benefit of pro-social behavior for the actor (or the cost of failing to be nice). Indeed, capuchin monkeys are more likely to choose a pro-social option when paired with a close social partner (de Waal et al. 2008), and, as discussed above, rats help members of familiar strains, but not unfamiliar ones. Similarly, female mice (but not male mice) will approach a trapped and suffering same-sex familiar conspecific to initiate social contact, and they do so significantly more than they approach an unfamiliar conspecific in the same situation (Langford et al. 2010). This isn't always the case. Black-tufted marmosets were less inclined

to share with groupmates than they were with strangers (Mustoe et al. 2015). The authors posit, however, that this is because in this cooperatively breeding species, a stranger is a potential new group member and thus may be a high priority for establishing social bonds.

### **Communicated Intent**

It has also been hypothesized that pro-social behavior should be influenced by the partner's need and that, in particular, pro-social behavior may be more common when the recipient has expressed need. There has been virtually no evidence for this in primates; however, in corvids, a recipient's approach to a reward area increased the likelihood that an actor would choose to reward both them self and the recipient rather than just themselves. However, the researchers that conducted the study posit that this effect was due to the attention directing to the reward rather than to the recipient's inherent desire for the reward (Schwab et al. 2012). Indeed, despite these being species with complex communicative repertoires, it is unclear whether the recipients even indicate desire in this way.

### **Hormonal Influences**

Differences in endogenous (i.e., naturally occurring) hormones may influence the likelihood of an actor behaving pro-socially. Perhaps the most researched is oxytocin, a neuropeptide hormone that has a variety of effects on social bonding in mammals, often in mother-infant interactions or sexual behaviors. Evidence from multiple primate species supports an association between urinary oxytocin levels and rates of affiliative behaviors and strength of social relationships among individuals (Crockford et al. 2013). Supporting the hypothesis that oxytocin plays a causal role in pro-social behavior, oxytocin treatment appeared to shift the preferences to behave pro-socially to an in-group member in marmosets, a cooperative breeding species (Mustoe et al. 2015). However, there has been very little evidence of oxytocin influencing pro-social or cooperative behavior in other studies, suggesting that while endogenous oxytocin rates may vary with pro-social behavior, there is not a causal link such that increasing

oxytocin increases pro-social behavior or, if there is, it is quite a bit more complicated. For instance, oxytocin interacts with another hormone, cortisol, to produce anxiolytic effects in humans and, it is hypothesized, other species. Such a physiological interaction might inform the emergence of social contact behaviors in response to a conspecific's pain, as observed in mice. The differing levels of these endogenous hormones and their interaction are all factors that play a key role in determining an individual's behavior in a given context, especially in species that exhibit complex social cognition, and more research in this area is clearly warranted.

### Cognitive Factors

There has been some debate about which socio-cognitive abilities are necessary for pro-social behavior to emerge. On the one hand, functional pro-social behavior may be based on positive social reinforcement of certain types of behavior, which requires little in the way of cognition. On the other hand, understanding others' needs or the effect of one's behaviors on others could lead to more complex or directed forms of pro-social behavior. Theory of mind, or the ability to attribute mental states to or take the perspective of others, would allow individuals to make inferences about another's needs or desires using those behavior cues and has been hypothesized to be integral to altruism and helping behavior. For instance, subjects could predict what a conspecific might want, which would be useful in tailoring specific pro-social behaviors (Barnes et al. 2008). However, there is not a lot of evidence for perspective taking in other species, which may indicate that it is not an essential component of pro-social behavior, however useful it might be. Indeed, many species that display pro-social behaviors both in experimental paradigms and in wild observations do not show evidence of theory of mind; even the great apes species show only limited abilities to take the perspective of others, and predicting conspecifics' future actions is complicated no matter what level of social cognition a species possesses.

Another hypothesized mechanism is empathy, the phenomenon in which one individual's

emotional or mental state is affected by the emotional state of another (de Waal 2009). While this can be quite complex, it can also be as simple as mirroring of another's emotional state, which may be sufficient to induce pro-social behavior in many species. This would allow pro-social behavior without complex social cognition; if another's distress or desire causes discomfort to an actor, that actor is likely to act in a way that alleviates that discomfort. For instance, when rats act altruistically to help a conspecific, it may be that the recipient's distress causes cognitive discomfort in the actor, who then acts to alleviate that discomfort (Bartal et al. 2014). Therefore, pro-social behavior does not seem to require such complex social cognition, but instead may use a much simpler mechanism to achieve the same end of group cohesion.

### Future Directions

Pro-social behavior is hypothesized to be important in animal social groups, but more work is needed to determine the degree to which it is seen across species and contexts, as well as the underlying mechanisms. For instance, one prominent hypothesis for the evolution of pro-social behavior is the cooperative breeding hypothesis, but to date it is based on evidence from only primates and corvids. Future work should expand to other cooperatively breeding species. In addition, an area that needs more exploration is how pro-social behavior differs toward individuals who are new immigrants to the group, or strangers versus a long-term groupmates. This is likely to vary depending on whether the new individual is seen as a threat or a potential mate and will presumably also differ depending on the residents' status in the group. In particular, it would be interesting to see how pro-social behavior changes in pair bonded species across the course of their relationship, from pair bond formation through reproduction.

Finally, more work is needed to clarify underlying mechanisms of pro-social behavior. It is not clear in which contexts perspective taking is useful, nor do we know much about the underlying

hormonal correlates. It would also be useful to determine how pro-social behavior changes depending on whether the context is to provide help, to provide a good (i.e., food), or to help an individual avoid or escape a negative reinforcer. As the current literature consists of a mix of methods, it can be challenging to compare results from different species or contexts to one another. Understanding this complexity and the subtleties of context will be critical in further exploring pro-social behavior.

## Cross-References

- Cooperation
- Cooperative Breeding
- Cooperative Hunting
- Empathy
- Helping Behavior
- Reciprocity
- Social Behavior
- Social Grooming

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## Prosocial Choice Test

### ► Dictator Game

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## Prosociality

- Self-Domestication Hypothesis
- Xenophilia

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## Prosopagnosia

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## Introduction

Animals and human beings tend to recognize others by seeing their face, and this constitutes one of the cornerstones for determining the type of relationship and degree of interaction between individuals. Primates in the apex of evolutionary pyramid could even recognize the emotional expressions showed upon the face and could identify the internal milieu of the confronting counterparts and their amicability. The face, either as a complete image or in parts, gets registered in the areas of brain, and upon subsequent encounter, the reactivation of the stored image helps in recognition of the person as such. The ability to recognize and recollect the person upon seeing their face differs from one individual to other. This ability is strongly dependent upon visual expertise pathways and extent of memory representation. However, some subjects tend to fail in recognizing even the faces which are well-known to them, and such impairment is termed as “prosopagnosia.” The terminology was coined by Bodamer (1947) who had witnessed three patients with evident brain damage suffering from selective impairment in recollecting whether they have seen the face before or not. It is essential to keep in mind that not all subjects, with or without brain lesion, who could not recognize persons by face, should be labelled under this condition. Either a subject with visual impairment or a subject with generalized impairment in object recognition or a subject with diminishing memory or a subject with cognitive disturbances might harbor similar complaints (Corrow et al. 2016). But, to deem as the purest form of prosopagnosia, the subject should have difficulty in identifying the face as such and rely upon cues

such as hairstyle or voice to embark their identification process (Corrow et al. 2016; Duchaine and Nakayama 2005). They could name the parts of the face or sometimes even identify the emotions in it, but connection between a particular face and a particular identity is absent in them.

Prosopagnosia could be either developmental, where the presentation is there without any overt brain lesion, or acquired, where the presentation is the resultant of structural brain damage. Acquired brain lesion could be due to the result of different pathologies including injury, ischemic infarcts, infections, tumors, degeneration, or surgical resection of selected areas (Barton 2008). Developmental prosopagnosia usually runs in families and is more frequent compared to acquired form (Susilo and Duchaine 2013).

### Cognitive Perspectives of Prosopagnosia

To understand it better, we shall reiterate the cognitive basis behind processing of faces. Bruce and Young (1986) proposed a model for face processing which is a sequential structural encoding neural schema. When we see a person's face, the pictorial code gets generated in an abstract form, and upon seeing the same or different photograph of the corresponding person, matching takes place leading to identification. Familiarity gained out of repeated exposure leads to generation of face recognition units which can activate personal identity-specific semantic codes (Eimer and McCarthy 1999). Thus, the code generation pattern differs depending upon familiarity, and unfamiliar faces are predominantly recognized by their distinct physical properties which culminate in generalized identity such as race and country. Stronger personal identity nodes lead to unified access to other semantic information regarding the individual such as their profession, past experiences, recalling names, etc. According to Damasio et al. (1982), prosopagnosia is the clinical resultant of one of the three mechanisms: (a) destruction of templates archived in the

cortical areas, (b) inaccessibility of the templates, and (c) inactivation of the templates after access. Even normal individuals tend to misrecognize faces, and this happens when there is lack of inactivation of templates. But prosopagnosia should only be considered when there is a failure in transference and matching of the pictorial code with the identity-specific semantic codes upon stimulus. In other words, it is the result of damage to a cognitive system specific to visual processing of facial identity.

Yet another hypothesis proposed is "configural processing hypothesis" which states that subjects with prosopagnosia could not get the overview of the face at a single glance, and this results in the failure of recognition (Levine and Calvanio 1989). This hypothesis is supported by the fact that these patients could match and compare several features of the face in a sequential manner as in face matching tests. However, this hypothesis is not supported by strong evidence because face identification cannot be considered as a set of discernible objects and the visual processing stream required for objects is different from the one required for face identification (Moscovitch et al. 1997). McNeil and Warrington (1993) observed that subject with prosopagnosia had difficulty in recognizing human face, and this ability to recognize sheep was unimpaired. Farah (1996) postulated the concept of two-shape representation systems, whereby one construct is broken down into numerous sub-components. Face recognition systems are holistic when compared to other recognition systems such as words which are handled by part-based system and objects which are handled by combination of both. When part-based systems become defective, it results in alexia and damage to holistic system results in prosopagnosia. The clinical spectrum of presentations result even when there is slight decomposition of shape, and this could be attributed to the different degree of malfunctioning of processing systems. This could also be explained based on the difference in visual processing streams, and thus a comprehensive knowledge regarding the cortical areas involved in face recognition is essential.



## Cortical Areas Involved in Face Recognition

Neurons involved in facial recognition are distributed as clusters in the superior temporal sulcus of humans and also in nonhuman primates such as macaque monkeys (Moeller et al. 2008; Tsao and Livingstone 2008). Functional neuroimaging studies have showed that some areas of the brain are highly involved in recognizing the face when compared to other objects (Haxby et al. 2002; Kanwisher and Barton 2011). Three principal areas responsible for synchronized processing the face are inferior occipital gyrus, middle lateral fusiform gyrus, and posterior part of superior temporal sulcus (Kanwisher and Barton 2011). Electrical stimulation of occipital face area made the subjects to temporarily lack their ability to recognize the faces of celebrities (Jonas et al. 2012), and when the same stimulus was given in fusiform face area, perceptions of facial structures got distorted when compared to control objects (Rangarajan et al. 2014). Rossion et al. (2003) documented that the loss of right inferior lateral occipital lobe and left medial temporal lobe (where fusiform gyrus is located) would present with prosopagnosia.

Studies (Wachsmuth et al. 1994; Logothetis et al. 1999) have shown that humans have a category-specific and segregated modular organization related to different stimuli. Similarly, in macaque monkeys, neurons which respond maximally to face images are predominantly located around superior temporal sulcus and inferior temporal cortex (Allison et al. 1999; Chao et al. 1999). These neurons are usually clustered either as patches or columns (Allison et al. 1999). Another study based on neurophysiological recordings in the macaque visual cortex observed that anterior temporal area acts as the storehouse of image-invariant representations of facial identity irrespective of rotations (Meyers et al. 2015). When compared with non-face objects, cells in the superior temporal sulcus show 20-fold increased selectivity for face selection (Pinsk et al. 2005). Especially, the posterior most region of the temporal lobe, located 6 mm anterior to the interaural canal, was the most

selective region. In macaque monkeys, there exists functional specialization such that along the occipitotemporal direction, face selectivity increases (Bell et al. 2009). Similarly, confusion of mirror symmetry emerges, and facial identity increases in strength (Axelrod and Yovel 2012).

The extent of activation of face area differs according to the dominance of the cerebral hemisphere, and in majority of human and non-human primates, right hemisphere is superior compared to left counterpart (Tsao et al. 2003). The chances of developing prosopagnosia are more when the dominant hemisphere gets damaged. Another interesting mechanism which has been proposed for developmental prosopagnosia is the defect in the subcortical mechanisms. De Gelder and Stekelenburg (de Gelder et al. 1999) proposed that infants tend to attend to faces because of their subcortical mechanism and, if it is defective, they would neither attend to the faces nor process it for further storage. In cases with congenital prosopagnosia, it has been found that the volume of anterior fusiform gyrus is reduced (Behrmann et al. 2005). Diffuse tensor imaging and tractography also showed impaired structural connectivity in the ventral occipitotemporal cortex (Behrmann et al. 2005). Thus, compromise in the core region of ventral occipitotemporal cortex and its peripheral processing units in anterior temporal and frontal cortices would be the plausible hypothesis for congenital prosopagnosia. Recent works have used unique functional signature to facial processing, namely, N170 which is a form of event-related potential for understanding the mechanism of prosopagnosia (Bentin et al. 1996). The results of these works showed that developmental prosopagnosia is highly heterogeneous and presentation can be from subtler to severe forms.

Leaving behind the acquired causes which overtly lead to the disruption in connectivity and result in clinical presentation, the etiology for developmental and congenital prosopagnosia might be either due to transmissible mutations of the gene or significant events during infancy. Another model which has been proposed is the neurodevelopmental disorder due to the defective migration of neurons which ultimately result in

compromised cognitive abilities (Ramus 2004). Applying the hypothesis, neural migration errors in the fusiform gyrus and superior temporal sulcus could be the plausible hypothesis for developmental prosopagnosia which is a highly circumscribed dysplasia (Duchaine et al. 2006). With respect to therapeutics, even though many regimens have been tried including oxytocin which has given feeble benefits in increasing the social interactivity in developmental prosopagnosia patients, none could yield significant proof of benefits (Bate et al. 2014).

## Conclusion

Prosopagnosia is characterized by heterogeneity of clinical presentations which differs across developmental and acquired forms. The extent and nature of structural damage is the significant determinant for clinical outcome. Even though laboratory findings and neuroimaging studies have shown the processing stream related to face recognition and genetic factors with significant clarity, there are still questions regarding the interaction of face recognition processing streams with other object recognition streams. This can be attributed to the small patient sample in which the disease has been studied along with inconsistency in experimental models. Further studies involving large patient sample, accurate definition criteria, and advanced imaging tests would yield better knowledge regarding prosopagnosia.

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## Prospective Memory

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Prospective memory (PM) is defined as the ability to complete a planned action at a specified time in the future (Einstein and McDaniel 1990). There are many situations in which an individual needs to do something, but cannot accomplish the goal at the present moment, so the intention must be retained and remembered at an appropriate time. For instance, a student may think about needing to call her mother while taking an exam, but cannot do so until the test is complete and the student is out of the classroom. But will she remember to do so? Is she more likely to forget if distracting events occur right after the test? The study of these processes and the potentially influencing factors is the focus of PM research. In a traditional PM task – which has been primarily conducted with human adults in laboratory settings – the participant is engaged in an ongoing task with the stipulation that when a particular event occurs (i.e., the PM target), the participant should make a unique response to that event which is distinct from their response to the ongoing task. A common variant of this paradigm is to have participants complete a lexical decision task with the PM instructions to press a particular key when a target word (e.g., *history*) appears on the screen. This is thought to mimic the key dual-task components of how PM might occur in non-laboratory

settings (e.g., remembering to stop and mail a package on the drive home from work).

Researchers have broadly classified PM tasks into two varieties. Event-based PM refers to situations in which the intended action should be performed when a particular external event is encountered. Time-based PM refers to scenarios where an individual must remember to perform the action after a particular amount of time has elapsed (e.g., 15 min) or at a particular time (e.g., 3:00 PM). At a general level, time-based tasks are typically associated with worse performance than event-based tasks (e.g., Sellen et al. 1997). No matter the task, theorists have noted that successful PM retrieval relies on several sub-processes including, intention formation or planning, retention of the planned intention over a delay interval, recognition of cues that signal the appropriate time to perform the action, and the ability to remember and execute the planned action (Ellis 1996). Importantly, in PM tasks, there are no explicit retrieval cues that signal to the individual to initiate the retrieval, as is the case with retrospective memory tasks.

Prospective memory research expands our understanding of memory in general. Further, research suggests that PM accuracy is sensitive to a variety of factors, including the characteristics of the remembering environment. For example, highly salient cues (McDaniel and Einstein 2000), instructions that stress the importance of PM success (Walter and Meier 2014), and situations in which noticing of the PM target happens naturally as a part of completing the ongoing task (i.e., focality; Einstein et al. 2005) have all been shown to promote highly accurate remembering. In the case of focal tasks, these high levels of PM are obtained while incurring no costs to the ongoing task, suggesting to some researchers that retrieval of PM intentions in certain situations is spontaneous or automatic (McDaniel and Einstein 2000; Scullin et al. 2010). In contrast, when noticing of the PM target does not overlap with the ongoing task (i.e., nonfocal tasks), PM performance has been shown to rely on controlled attentional monitoring processes dedicated to noticing and responding to the target events (e.g., Smith 2003).

Another important reason for research into PM in humans is that increased PM failures are associated with cognitive decline in normal aging (Crystal 2013). Recent meta-analyses on the effects of aging demonstrated PM impairments in laboratory tasks for older adults relative to younger adults, and these effects were present even when retrieval was thought to be mediated by spontaneous processes (Henry et al. 2004; Kliegel et al. 2008). These age-related effects of declining PM ability can be devastating, such as forgetting to take critical medication at the appropriate time, and efforts are underway to develop interventions or treatments to aid PM performance. The establishment of a validated animal model of PM opens up opportunities to study these interventions in a controlled manner. Of course, one important question in this pursuit is the extent to which PM abilities are exhibited in nonhumans. One can imagine many scenarios in which PM would be advantageous for a number of animal species. For example, some species must remember the location of a particular fruiting-tree and, critical to PM, they also must remember to move to this foraging location at the appropriate future time in order to reap its benefits. Animals have also shown evidence of future-oriented cognition (e.g., Bräuer and Call 2015), which overlaps with PM ability. The study of these processes offers insight into the nature of PM and may also allow for carefully controlled studies on interventions or PM training if animal models can be validated.

Early work suggested that animals might exhibit prospective coding or prospective memory like behaviors as well as retrospective memory (e.g., Cook et al. 1985; Murray and Gaffan 2006; Rainer et al. 1999). More recent work has continued to support this possibility and expanded the species under investigation. Jon Crystal and colleagues have provided a compelling line of support for PM in rats. Initially, rats were trained to classify a tone as either short or long, also known as a temporal bisection task. After performing this task for a certain period of time, rats were given free access to a food source. They found that the rats would engage in anticipatory behaviors (e.g., begin poking their noses into the

food trough), which required a break from the bisection task, as the time to the end of the session grew near (Wilson and Crystal 2012). These findings align with the time-based prospective memory tasks used in humans and suggest continuity across species. In addition to the time-based PM work, these researchers have created an event-based PM paradigm for rats. The rats learned that a tone would signal when extra food would be freely available. At the sound of the tone, performance on the ongoing task declined (Wilson et al. 2013). These findings suggested that rats may respond similarly to an event cuing that a different response may now be appropriate.

In addition to the work with rodents, there has been an increasing focus on investigating non-human primate PM. Primates offer a model which affords many similarities and overlaps with the features of human PM and further suggests evolutionary continuity in the ability. Evans and Beran (2012) trained capuchin and rhesus monkeys on a computerized task designed to test PM ability. On some test sessions of an ongoing computer game, a visual stimulus would signal that an additional reward could be earned by making a particular response at the end of that block of trials (but not immediately). Monkeys successfully performed both aspects of the task (the ongoing task and the PM task), and they even initiated the response (i.e., began moving the cursor with the joystick) in the PM blocks before the stimuli were visible on the screen, suggesting that subjects were anticipating the opportunity to make this special response.

In another study addressing the possibility of PM in chimpanzees, a single language-trained chimpanzee was given the choice between two food items (Beran et al. 2012). The chosen item was immediately scattered around an adjacent outdoor yard and the unselected item remained in a container indoors. The subject was given access to the outdoor yard and allowed to forage for food for 30 min. In addition to the scattered food, there also were lexigram tokens (images representing various food types) in the same space. One of these tokens matched the identity of the item that remained inside. If the subject chose to, she could find the correct token and

bring it back inside to exchange for the food hidden in the container. This reflected many critical parts of PM tasks because the subject had to form an intention that could not be fulfilled immediately. If, at the appropriate time (i.e., once the preferred item had been consumed), the subject could successfully fulfill the intention (i.e., remember and find the correct token to trade indoors), then the PM intention could be executed and the additional food items would be given to the subject. The subject returned the correct token successfully on the majority of test trials and significantly more often than on control trials in which no additional food was hidden indoors.

Finally, a more general task was designed to test PM using a similar methodology in children and chimpanzees (Perdue et al. 2014). Human and nonhuman subjects were again given a choice between two items (food for chimpanzees, toys for children). The unchosen item was hidden in a container. Subjects then had to complete an ongoing quantity judgment task. At the end of that task, a request to the hidden container (via pointing or gesturing from the chimpanzees or asking from the children) would allow the subject to obtain the contents of the container. The chimpanzees and the children – sometimes given additional prompts – performed fairly well on the task, suggesting that they were retaining the intention to retrieve the hidden item even during the ongoing task.

All of the animal tasks described thus far vary somewhat from the human literature in that the new response should occur at the end of an ongoing task (Beran et al. 2015). This is a subtle but potentially important distinction from the human work in which the participants must self-initiate disengagement from the ongoing task at an appropriate time. One recent study attempted to test this ability in chimpanzees with a task that required active disengagement from an ongoing task to complete the PM intention (Evans et al. 2014). The chimpanzees were trained to sort tokens representing various food types into one of two trays. On some trials, an actual food item that would later be shown on the picture cards was placed in a hidden container in the back of the enclosure at the beginning of the test session. The



chimpanzee could retrieve that item if it traded the matching token out when it was later presented. The subject was shown the contents of the container at the beginning of the trial, but the experimenter engaged in the sorting task did not know if food was hidden or not, nor did they know the identity of the food. When the token for the hidden food was given to the chimpanzee later in the test session, the chimpanzee could either sort it into one of the piles for a small food reward, or, if the chimpanzee remembered the intention to get that real food item, he or she could disengage from the sorting task and use the token to retrieve the hidden item. Thus, the chimpanzees had to successfully recall the information in addition to remembering to act at the appropriate time. The pattern of performance on this task closely matches human performance on a PM task. Subjects had to retain an intention that could not be acted on immediately, and disengage from an ongoing task at an appropriate time to fulfill the intention.

All of the comparative research suggests substantial overlap between human and nonhuman animal prospective memory and great potential for future work in this domain (Crystal and Wilson 2015).

## Cross-References

- [Episodic Memory](#)
- [Long-term Memory](#)

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## Prospective Processing

### ► Matching-to-Sample: Comparative Overview

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## Protandric Hermaphroditism

### ► Protandrous Hermaphroditism

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## Protandrous Hermaphroditism

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## Synonyms

Protandric hermaphroditism; Protandry

## Definition

A reproductive system where individuals mature as males, but may reproduce as females later in life.

## Introduction

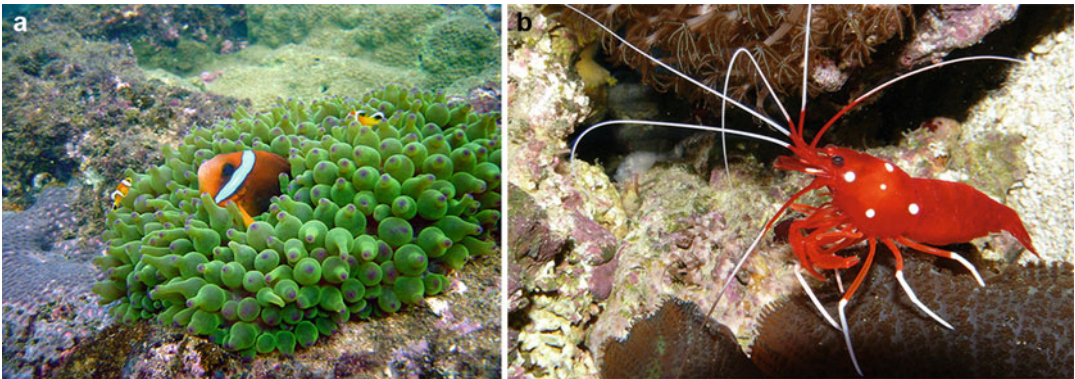
In most animals, “males” and “females” are distinct classes of individuals that specialize in the production of sperm and eggs, respectively. However, a substantial minority of species are hermaphrodites, meaning that a single individual can produce both eggs and sperm, either simultaneously or at different stages of its life. “Protandrous” hermaphrodites begin their reproductive lives as males, but reproduce as females later in life.

Two examples help to illustrate (Fig. 1). Anemonefish live in small territorial groups, where reproduction and sex change are determined by a strict dominance hierarchy (Munday et al. 2006). The largest individual in the group is a breeding female, the second-largest is a breeding male, and all smaller individuals are non-breeding males. If the female dies or is removed, then the largest male changes sex and takes her place. Protandrous hermaphroditism is also found in several species of “cleaner” shrimp that feed on the parasites and dead tissue of their fish clients. In shrimps of the genus *Lyssmata*, individuals begin their reproductive lives as males, but can reproduce as both sexes later in life (Bauer 2006).

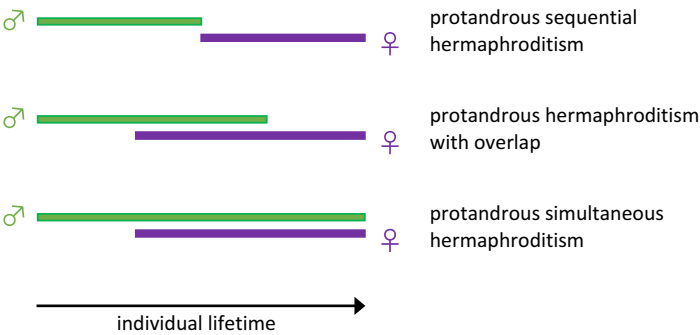
## Terminology

Protandrous hermaphroditism encompasses a continuum of life histories, distinguished by the degree of temporal overlap between male and female reproduction (Collin 2013; Fig. 2):

1. *Protandrous sequential hermaphroditism*: Reproduce early as a pure male, and later as a pure female.
2. *Protandrous hermaphroditism with overlap*: Reproduce early as a pure male, and later as a pure female, with an intervening period of reproduction as both sexes.
3. *Protandrous simultaneous hermaphroditism*: Reproduce early as a pure male, and later as both sexes.



**Protandrous Hermaphroditism, Fig. 1** (a) An adult and juveniles of the Oman anemonefish *Amphiprion omanensis*, a protandrous sequential hermaphrodite, shown with the host anemone *Entacmaea quadricolor* (Photo taken from Simpson et al. (2014)) (b) The fire shrimp *Lyssmata debelius*, a protandrous simultaneous hermaphrodite (Photo by User:Haplochromis, CC BY-SA 3.0 (<http://creativecommons.org/licenses/by-sa/3.0/>), via Wikimedia Commons)



**Protandrous Hermaphroditism, Fig. 2** Schematic showing different forms of protandrous hermaphroditism, distinguished by the degree of temporal overlap between male function (green lines) and female function (purple lines) over an individual's lifetime (cf. Collin 2013)

Still further along this continuum are species that reproduce as both sexes over their whole reproductive lifespans (i.e., life-long simultaneous hermaphrodites), but shift their relative allocation of resources from male to female reproduction over time (Leonard 2013). There are also species that start out as simultaneous hermaphrodites, but later reproduce as pure females. Neither of these latter life histories is commonly referred to as “protandrous.”

Sex change is usually unidirectional. In a few taxa, however, the gonad degenerates between reproductive seasons, and sex is redetermined at the start of the next season (Collin 2013). Protandry may then occur within each reproductive

season. A very small number of species exhibit flexible bidirectional sex change (Munday et al. 2006). These species are sometimes called “protandrous” if the initial sex is invariably male.

These definitions emphasize reproduction (i.e., functional sex) rather than morphological criteria, because the adaptive significance of protandry is best understood by looking at reproductive success via each sex (Policansky 1982). The distinction matters because an individual may reproduce consistently as one sex (i.e., produce only one gamete type) and yet contain reproductive tissues typical of the other sex (Sadovy de Mitcheson and Liu 2008). Particular care should be taken in comparisons with the botanical literature, where

“protandry” is often defined according to purely morphological criteria (Policansky 1982). In defining *when* an organism acts as a male or female, the timing of fertilization is the most useable criterion. For instance, in some species sperm mature earlier than eggs, even though both types of gamete are used in the same reproductive episode; these species should be classified as simultaneous hermaphrodites rather than sequential (Policansky 1982). This convention can lead to curious consequences when there is a long delay between the production and fertilization of gametes (e.g., due to storage of received sperm). For instance, a protandrous individual may act as a male (i.e., achieve fertilization) long after it ceases producing sperm.

## Diagnosis and Detection

Protandrous hermaphroditism should ideally be diagnosed using (1) histological series of the gonads or other gametogenic tissues showing the stages of transition (e.g., from functioning testis to functioning ovary for protandrous sequential hermaphrodites), and/or (2) field or laboratory observations of sex change in individual animals, based on unambiguous behaviors such as spawning (Sadovy de Mitcheson and Liu 2008). External sex characteristics and behaviors are not always reliable indicators of functional sex. Even when assessing the gonads, care must be taken to distinguish functional tissues from immature, vestigial, or otherwise nonfunctional tissues that do not produce mature gametes (Sadovy de Mitcheson and Liu 2008).

Differences in age or size distributions between males and females (or simultaneous hermaphrodites) can be suggestive of protandry, but should not be relied on as the only line of evidence. This is because (1) these patterns can equally be caused by sex differences in maturation or mortality, and (2) protandrous species may in any case show substantial overlap between the sexes, which may not be detected in low-powered studies (Charnov 1982; Sadovy de Mitcheson and Liu 2008).

These relatively stringent diagnostic requirements probably lead to under-detection of protandrous hermaphroditism (Policansky 1982; Collin 2013). In practice, separate sexes are usually assumed if no simultaneously hermaphroditic individuals are found; simultaneous hermaphroditism may similarly be diagnosed based on a small sample of individuals with both gonad types. Some species that are currently classified as separate-sexed may consequently be protandrous sequential hermaphrodites, whereas some supposedly simultaneous hermaphrodites may have an undiscovered protandrous phase (Leonard 2013).

## Occurrence

Protandrous hermaphroditism is rare but taxonomically widespread, occurring in a diverse range of animal phyla (Policansky 1982). In vertebrates, protandrous sequential hermaphroditism is known in the clownfish (subfamily Amphiprionina of the Pomacentridae), porgies (Sparidae), and flatheads (Platycephalidae), with isolated examples in several other fish families (Sadovy de Mitcheson and Liu 2008). All three forms of protandry are well-represented in the mollusks, including both gastropods (e.g., true limpets, Patellogastropoda; slipper limpets, Calyptraeidae) and bivalves (e.g., oysters, Ostidae; scallops, Pectinidae) (Collin 2013). Protandrous hermaphroditism is rare in crustaceans, but occurs in many decapod shrimp (Charnov 1982; Bauer 2006). Protandry is notably very rare in freshwater fish and entirely absent in land vertebrates and insects. Most protandrous species have close relatives that are separate-sexed or simultaneous hermaphrodites, indicating that protandry has evolved many times independently (Charnov 1982; Collin 2013).

## Mechanisms and Cues of Sex Change

Protandrous sex change is underpinned by a wide variety of mechanisms, consistent with its taxonomic diversity. Some taxa have clearly separated

ovaries and testes, whereas others combine ovarian and testicular tissue inside a single organ, called an ovotestis (Policansky 1982). Germ cells may specialize as one sex early in development or remain sexually bipotent for extended periods (Sadovy de Mitcheson and Liu 2008). In teleost fish, the endocrinal cues of sex change are highly species-specific, most likely reflecting the multiple independent origins of protandry, although gonadal steroids appear to play a key role in all studied species (Frisch 2004).

In protandrous sequential hermaphrodites, sex change is almost always sensitive to social cues such as the sex and size of nearby individuals (Munday et al. 2006; Leonard 2013). For instance, the largest individual in a pair or group may be female, while smaller individuals are male. Even when sex change is more gradual, it may respond to environmental or social indicators of the potential for reproduction via each sex (Charnov 1982; Leonard 2013).

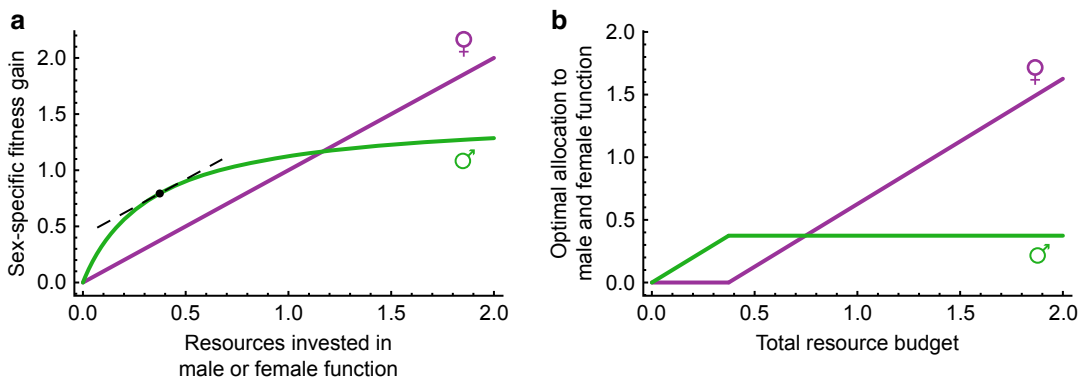
## Evolution and Adaptive Significance

To explain the evolution of protandrous hermaphroditism, theorists have explored how the

potential for reproductive success changes with size (or sometimes age) for each sex. Two kinds of size effects are commonly studied: (1) “budget” effects, in which the benefits of size are due simply to greater resource availability, and (2) “direct” effects, which are benefits of size per se (e.g., the dominance hierarchies of anemonefish) (Leonard 2013).

For protandrous simultaneous hermaphroditism, the most prevalent explanations rely on budget effects. For instance, suppose reproductive success is primarily determined by investment into gametes. If there is limited competition among the sperm of different individuals, then sperm production may bring diminishing fitness returns with increasing investment, while egg production shows more linear returns (Charnov 1982; see Fig. 3). Smaller individuals, with fewer resources at their disposal, should then invest only in sperm production, to make use of the higher initial returns. Larger individuals should invest more heavily in egg production, while continuing to produce a small amount of sperm (Fig. 3).

For protandrous sequential hermaphroditism, the most influential explanation is the size advantage model, which is based on direct effects of size



**Protandrous Hermaphroditism, Fig. 3** (a) Hypothetical relationship between gamete investment and the rate of fitness gain for male function (green) and female function (purple). For female function, fitness increases linearly with investment, whereas for male function, fitness increases steeply at first but then levels off. (b) The optimal investment of resources into male and female reproduction, shown as the total resources available to an individual varies, assuming the fitness gain curves from panel (a). If

the individual has a small resource budget, it is optimal to invest only in male function. As the resource level increases, the marginal gains from female function eventually equal those from male function (marked as a black dot with dotted tangent line). After this point, all additional resources should be invested in female function. If access to resources increases with age, this selects for protandrous simultaneous hermaphroditism



on reproduction. It predicts that when reproductive success increases more rapidly with size in females than males, that individuals should begin their lives as females and then change sex (Warner 1975; Charnov 1982; see Fig. 4). Faster growth or lower mortality in males than females may similarly select for protandrous sequential hermaphroditism (Kazancıoğlu and Alonzo 2009). The model implicitly assumes that it is optimal to reproduce as only one sex at a time (i.e., no simultaneous hermaphroditism).

The size advantage model has been successful in predicting the direction and even the timing of sex change (e.g., Charnov 1982), but less effective at predicting its taxonomic distribution. Indeed, given the near-ubiquity of sex differences in growth, mortality and size-specific fecundity, many authors have questioned why sequential hermaphroditism is not more common (Warner 1975; Charnov 1982; Kazancıoğlu and Alonzo 2009; Leonard 2013). Sex change may be selected against if there are large costs associated with changing sex (e.g., due to the need to restructure the reproductive organs or secondary sexual traits: Kazancıoğlu and Alonzo 2009). Evolutionary transitions from separate sexes to protandry may also face developmental or morphological

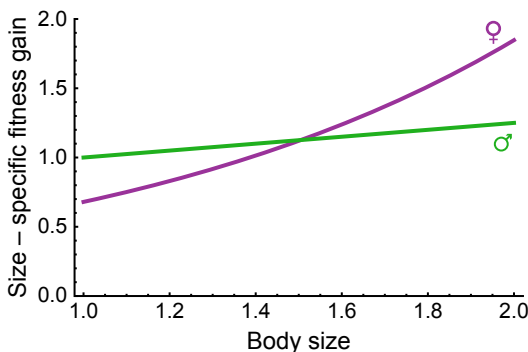
constraints associated with combining two previously separate sex functions in a single individual (Charnov 1982). Even considering these factors, our ability to explain the distribution of protandrous hermaphroditism in any of its forms remains very limited (Leonard 2013).

## Cross-References

- [Anisogamy](#)
- [Fecundity](#)
- [Gametes](#)
- [Gonochorism](#)
- [Hermaphrodite](#)
- [Ova](#)
- [Ovaries](#)
- [Protogynous Hermaphroditism](#)
- [Sperm Competition](#)

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**Protandrous Hermaphroditism, Fig. 4** Hypothetical relationship between body size and the rate of fitness gain for individuals of each sex. In the size advantage model, protandrous sequential hermaphroditism is adaptive if the female curve increases more steeply than the male curve, as shown here. The optimal timing of sex change occurs when the male and female curves cross

Simpson, S.D., Harrison, H.B., Claereboudt, M.R., & Planes, S. (2014). Long-distance dispersal via ocean currents connects Omani clownfish populations throughout entire species range. *PLoS ONE* 9(9), e107610.

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Protandry

► Protandrous Hermaphroditism

Protein

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Synonyms

Amino acid; Polypeptide

Definition

Protein is a biomolecule consist of carbon, hydrogen, oxygen, nitrogen, and a small amount of sulfur with a chain of amino acids forming a complex folded and functional structure. Protein performs several crucial functions in the living entity, such as maintenance and growth of body, transcription factor, chemical messenger, immunogenic substance, energy provider.

Introduction

Protein is considered as one of the major important biomolecules included in our daily diet because of its nutritional and caloric value. The

term protein, derived from the Greek word “Proteois,” means primary. The term protein was coined by Swedish chemist Jacob Berzelius in 1839. The structural and functional unit of protein is an amino acid that was unknown even after its discovery in 1830. The 20 standard amino acids are either nutritionally essential or not depending on its synthesis in our body (McCoy et al. 1935). They are coded either in single letter or in three digits which is easy and more comprehensive in sequencing and Bioinformatics (Lehninger et al. 2000; Voet et al. 2008) (Table 1).

Protein, Table 1 List of amino acids in alphabetical order

| 1-digit code | Amino acid     | Code (3-digit) | Nutritionally essential |
|--------------|----------------|----------------|-------------------------|
| A            | Alanine        | Ala            | NE                      |
| B            | –              |                |                         |
| C            | Cysteine       | Cys            | NE                      |
| D            | Glutamate      | Glu            | NE                      |
| E            | Aspartate      | Asp            | NE                      |
| F            | Phenyl alanine | Phe            | E                       |
| G            | Glycine        | Gly            | NE                      |
| H            | Histidine      | His            | E                       |
| I            | Isoleucine     | Ile            | E                       |
| J            | –              |                |                         |
| K            | Lysine         | Lys            | E                       |
| L            | Leucine        | Leu            | E                       |
| M            | Methionine     | Met            | E                       |
| N            | Asparagine     | Asn            | NE                      |
| O            | –              |                |                         |
| P            | Proline        | Pro            | NE                      |
| Q            | Glutamine      | Gln            | NE                      |
| R            | Arginine       | Arg            | E                       |
| S            | Serine         | Ser            | NE                      |
| T            | Threonine      | Thr            | E                       |
| U            | –              |                |                         |
| V            | Valine         | Val            | E                       |
| W            | Tryptophane    | Trp            | E                       |
| X            | –              |                |                         |
| Y            | Tyrosine       | Tyr            | NE                      |
| Z            | –              |                |                         |

NE nonessential (can synthesize), E essential (can't synthesize)

## Protein Evolution

The genetic information of an individual stored in DNA transcribes into mRNA and thereafter translates into amino acids which polymerize and folded to form functional protein. Over long periods of time, protein randomly mutate and the survive individuals with mutated form brings the evolutionary change in the process of natural selection. The protein sequences are conserved mostly among species due to divergent evolution or common ancestry. The amino acids sequences in proteins among the inter- and intra-species are present in a conserved manner. These evolutionarily conserved sequences in the proteins are named as domains which can be grouped into different families. Domains with >40% similarities have a similar function and <25% similarities differ in their function. Nonidentical protein performing the same function in different species is considered as homologue. Homologous proteins with similar function in different species are named as orthologues (e.g., Cyt C or hemoglobin in different species), whereas in a similar species due to gene duplication the same protein varies in their sequences and roles are called paralogues (e.g., Hemoglobin and myoglobin in globin family in same species). Amino acid sequences comparison of homologous protein in different species helps to draw the phylogenetic tree. Different proteins have different evolutionary rates except histone proteins which are highly conserved in evolutionary history.

## Structural Organization of Protein

Proteins are unbranched polymers constructed from 20 standard  $\alpha$ -amino acids. They have four levels of structural organization. Genetic information specifies the amino acid sequences of the primary structure. As the polypeptide chain folds, it forms certain localized arrangements of adjacent amino acids that constitute the secondary structure. The overall three-dimensional shape that a polypeptide assumes is called tertiary structure. Proteins that consist of two or more polypeptide chains are said to have a quaternary structure.

## Protein Metabolism

Protein is the final product of a gene. Genes are present in the specific loci of DNA in the chromosome. mRNA is synthesized from DNA by the process of transcription in the nucleus which undergoes translation in the cytoplasm to form proteins. Co-transcription-translation occurs in prokaryotes. Three nucleotide sequence presents in mRNA (codon) specifies the amino acid. Specific t-RNA with the corresponding anticodon sequence bears the specific amino acid and helps in the formation of a polypeptide by reading the mRNA sequence.

## Amino Acid Synthesis

The capacity to synthesize amino acid differs for protein synthesis in living organisms. Plants and many microorganisms can synthesize all 20 standard amino acids from readily available precursors (such as glutamate and glutamine from  $\alpha$ -keto glutarate, serine, glycine and cysteine from 3-phosphoglycerate, alanine, valine, and leucine from pyruvate; These are all intermediates of glycolysis or Krebs cycle).

**Some of the important functions of proteins**  
(<https://www.healthline.com/nutrition/functions-of-protein>)

- (i) General growth and maintenance of tissues in body
- (ii) Participate in biochemical reactions
- (iii) Acting as a messenger
- (iv) Structural backbone
- (v) pH maintenance
- (vi) Fluid balance
- (vii) Provide immunity
- (viii) Transport and storage of nutrients
- (ix) Energy provider (4.1 Kcal)

## Ailment Due to Protein Misfolding or Deregulation in Metabolism and Energy Malnutrition

The following table (Table 2) is the list of diseases due to misfolding, deregulation, and energy malnutrition of protein.

**Protein, Table 2** List of diseases

| Disease type                 | Diseases                                        | Cause                                                                                | Comment                                                           |
|------------------------------|-------------------------------------------------|--------------------------------------------------------------------------------------|-------------------------------------------------------------------|
| Protein metabolism disorders | Gout                                            | Uric acid overproduction and deposition in synovial fluid                            | Excessive intake of red meat                                      |
|                              | PKU (phenyl ketonuria)                          | Defect in enzyme (phenyl alanine hydroxylase) for phenylalanine/tyrosine degradation | Accumulation of phenyl alanine                                    |
|                              | Alkaptonuria                                    | Absence of homogentisate oxidase, failure of homogentisic acid breakdown             | Dark black urine                                                  |
|                              | Albinism                                        | Tyrosinase enzyme deficiency                                                         | Lack of synthesis of melanin pigment                              |
|                              | Tyrosinemia                                     | Tyrosine transaminase loss                                                           | Tyrosine degradation hampered                                     |
|                              | Cystinuria                                      | Increased excretion of cystine                                                       | Cystine stone in kidney                                           |
|                              | Homocystinuria                                  | Homocystine accumulation                                                             |                                                                   |
|                              | Cystinosis                                      | Cysteine crystals deposition in tissues and organs                                   | Lysosomal dysfunction                                             |
|                              | Glycinuria                                      | Excess glycine excreted in urine                                                     |                                                                   |
|                              | Hartnup disease                                 | Low level of plasma tryptophan                                                       | Elevated level of tryptophan in urine                             |
|                              | Maple syrup urine disease                       | Disorder of branch chain amino acid                                                  | Urine smell like maple syrup                                      |
|                              | Isovaleric acedemia                             | Defect due to enzyme isovaleric Co-A dehydrogenase                                   | Abnormal leucine metabolism                                       |
| Protein misfolding disorders | Amyloidosis                                     | Extracellular deposition of misfolded amyloid fibril protein                         | Cognitive decline and dementia                                    |
|                              | Amyotrophic lateral sclerosis                   | SOD1 (superoxide dismutase) misfolded and deposited                                  | Loss of motor neuron, muscular atrophy                            |
|                              | Huntington disease                              | Huntingtin with polyglutamate expansion                                              | Movement, thinking (cognitive) and psychiatric disorders          |
|                              | Parkinsons disease                              | Lewy body deposition due to misfolding of $\alpha$ -synuclein                        | Cognitive decline, bradykinesia, akinesia                         |
|                              | Transmissible spongiform encephalopathies (TSE) | Prion protein misfolding                                                             | The tiny hole gives a sponge-like appearance to the brain         |
| Protein-energy malnutrition  | Kwashiorkor                                     | Insufficient intake of protein (carbohydrate diet)                                   | Large belly, diarrhea, pigmented skin                             |
|                              | Marasmus                                        | Calories deficiency (starvation)                                                     | Muscle wasting, skin folding, prominent ribcage, shrunken abdomen |

Courtesy Voet et al. (2008) and <https://www.slideshare.net/lubaz/disorders-86416256>

## Conclusion

Proteins are one of the major and most important nutritional biomolecules. They consist of a polymer of amino acids, which helps in the maintenance of bone, muscle, and the entire framework of the body, acts as an enzyme, hormone, transcription factors and when not properly folded or

functionally anomalous causes severe ailments in the body.

## Cross-References

- [Carnivore \(Diet\)](#)
- [Catarrhine Diet](#)
- [Feline Diet](#)

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## Proteome

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## Definition

The set of proteins encoded by the genome. This includes the added changes that are made to proteins by a posttranslational modification (PTM) (Adams 2008). The proteome is dynamic and is constantly changing depending on the needs of a cell. Proteomics refers to the study of the proteome.

## Introduction: What Is the Proteome and Why Study It

To better understand how cells function and where cells get their defining characteristics from, scientists have taken a keen interest in elucidating the composition of proteins within an organism. This has spurred the field of proteomics.

The proteome is the set of proteins that is encoded by an organism's genome. In the broadest sense, the proteome could refer to all the proteins that are encoded by an organism's genome. However, the various cellular subsets

within an organism have different functions and subsequently have different protein compositions. Despite having the same genome, these different cellular subsets will have different protein makeups. Therefore, one can study the proteome of an organ such as the liver, a tissue type such as vasculature, or a lineage of cells such as hematopoietic cells. In fact, one could even go as small as an individual cell's proteome.

Biologists have known for decades that the human genome encodes the information needed to create all the proteins of an organism. Through scrupulous genomic control mechanisms, the proteins that are required for each cell to function are meticulously expressed and regulated. It is the unique genetic expression profile of each cell – and the proteins that stem from this expression pattern – that gives a cell its identity and ultimately its function.

## The Proteome: A Dynamic System

When studying the proteome, it is important to remember that the proteins that a cell requires, and produces, are constantly changing (Adams 2008). When a cell responds to a signal from a neighboring cell or conditions in the extracellular environment, there will be an accompanying change in the intracellular protein composition (Adams 2008). Cell cycle stage, cellular needs, genomic regulation, developmental stage, and much more will also affect the expression level of proteins in a cell (Larance and Lamond 2015). These changes in protein concentration ensure that a cell is best suited to fulfill its function and thrive in its environment.

Thus, the unique complement of proteins contained by each cell in an organism, and the constant flux of protein concentration that occurs in response to the ever-changing cellular milieu, makes the proteome a transmutable entity. The dynamic nature of the proteome is in direct contrast with an organism's genome, whose sequence of nucleotides is the same in every cell of an organism (Adams 2008).



## Posttranslational Modifications as an Important Source of Dynamism and Diversity

Certain biochemical processes play vital roles in the dynamism of the proteome. One such process is PTMs. There are over 200 types of PTMs (Brett et al. 2002), which allows for a vast array of protein modifications. These PTMs add even more complexity to a protein and allows one gene to generate unique protein products in different cells. A PTM is a change made to a protein after it has been translated from RNA. After a protein has been synthesized, sugars, lipids, phosphates, and even other proteins can be added to alter a protein (Adams 2008). In some cases, a protein may not be functional until a PTM has been made. The location of these modifications on a protein also affects the protein's structure and function. Sometimes a protein is cleaved to regulate its activity, either activating or inactivating it (Jensen 2006). A PTM does not need to occur to every protein of a given type to have an effect. For example, 5% of a protein population being phosphorylated may be enough to activate a signaling pathway in a cell even though the other 95% of the protein population is unmodified and inactive (Jensen 2006). PTMs help make the proteome a complex, changing network. PTMs are tightly regulated, which enables a cell to have access to the specific protein it needs to function. Depending on the requirements of a cell at a given time, a PTM will or will not be made.

## Alternative Splicing and Its Role in the Proteome

Another contributing source of dynamism in the proteome is alternative splicing. When RNA is transcribed in the nucleus, it is made from coding exons and noncoding introns. The final mRNA product is made by splicing exons together to make a unique mRNA transcript. Alternative splicing is the cell's ability to make multiple splice variants at the RNA level. Some of these RNA variants can encode distinct protein isoforms (Kim et al. 2014). Because one gene has many

coding exons, the way alternative splicing arranges these exons will produce unique mRNA transcripts (Kim et al. 2014). Even though these mRNA transcripts arise from the same gene, their unique exon arrangement will allow them to be made into different proteins.

Intron retention is another type of alternative splicing, but intron retention is used to down-regulate the expression of a protein (Liu et al. 2017). In intron retention, at least one intron is spliced into the mRNA transcript. When this occurs, the mRNA transcript's ability to exit the nucleus is altered since mRNA transcripts with introns may not be competent to exit the nucleus (Liu et al. 2017). Intron retention may also insert a premature stop codon into the mRNA transcript causing protein degradation by the nonsense-mediated decay pathway (Liu et al. 2017). Recent studies show that around a third of genes can make unique protein isoforms from alternative splicing (Kim et al. 2014). Again, through stringent regulation, alternative splicing allows an organism to alter its protein composition in real time to satisfy its immediate biological needs.

## Conclusions

As researchers further attempt to understand cell biology, interest in proteomics will only intensify. The proteome itself is a wide-ranging term, which could refer to the study of an entire organism's, or a single cell's, protein composition. When studying the proteome, it is important to remember that it is a dynamic system. An organism's proteome will vary from day to day and even hour to hour as an organism responds to the specific stimuli it is presented with.

PTMs and alternative splicing are important sources of dynamism and diversity in a cell's proteome. A common theme in the proteome is the tight regulation of the processes that make it dynamic and diverse. It is a cell's precise control over the expression of its genome that gives each cell its unique function, and allows a cell to rapidly change its intracellular protein makeup.

With technologies such as mass spectrometry improving every day, researchers will be able to

glean even more information from the proteome. This will continue to give scientists invaluable insights into biology and will bring us closer to understanding the fundamental biochemistry of life.

## Cross-References

- [Alternative Splicing](#)
- [Exon](#)
- [Genes](#)
- [Intron](#)
- [Messenger RNA](#)
- [Protein](#)
- [RNA](#)
- [Transcription](#)

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## Protocooperation

- [Mutualism](#)

## Proto-counting

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Studies of the quantitative and numerical abilities of nonhuman animals extend back to the earliest days of comparative psychology. A variety of terms have been applied to the different kinds of abilities that animals show when given tests that require them to quantify stimuli. This encyclopedia contains many of these terms, and the present article introduces one of the more controversial terms – proto-counting. This term was championed most successfully in the highly influential *Behavioral and Brain Sciences* paper by Davis and Perusse (1988). In that article, they made a distinction between true counting behavior and performances that lack the essential features of true counting but also cannot be ascribed to processes such as subitizing, relative numerosness judgments, or absolute numerosness judgments. In essence, proto-counting has come to refer to instances of counting-like behavior of animals where not all of the defining principles are met, perhaps because of methodological constraints or perhaps because some principles were not assessed.

To illustrate this idea, one must first understand the widely accepted criteria for true counting

behavior. These criteria were first offered by Gelman and Gallistel (1978) and basically consist of five principles:

1. The one-to-one principle states that during a counting event each item in a to-be-counted set should be given a unique tag so that there is an exact correspondence between all items and their unique tags. In other words, an individual who is counting must tag each thing once and only once.
2. The stable-order principle underlies the idea of ordinality, and it basically says that the tags that are used are always applied in the same order. For example, “3” is always the third tag applied, always comes after “2” and is always followed by “4.”
3. The cardinality principle says that the final tag is special: it represents not only the tag of the individually last tallied item, but also of the sum total of the counted set. Thus, last tags represent totals, and when presented with that tag, it represents a specific number as well as a specific ordinal position within a counting sequence.
4. The order irrelevance principle says that the tagging of stimuli can occur in any order, as long as that tagging satisfies the one-to-one principle, and the resulting cardinal value will still be accurate. In other words, counting pennies from left to right, right to left, or in terms of shininess will still produce the same cardinal knowledge.
5. The abstraction principle says that the above three principles can be applied to any set of stimuli to generate ordinal and cardinal knowledge, including highly abstract things such as jumps, remembered birthdays, and other such things. Those principles also can be applied to highly varied stimuli, such as counting the number of electronic devices in a home, or the number of species in a zoo.

These principles have guided some of the research into the numerical abilities of non-human animals. Various tasks to assess counting-like behavior have been designed and used with species ranging from insects to great

apes and those tasks are too numerous to describe or document in this article. The key issue for this article is the idea that in nearly all of those cases, the term proto-counting would be applied as defined above because of limitations in what those studies could show. For example, a chimpanzee named Sheba learned to label sets of items with an Arabic numeral, including in cases where multiple subsets had to be combined. She also showed evidence of tagging those items with touches to them, and so there was evidence of one-to-one correspondence, ordinality, and cardinality, but there was no indication that she could be given a numeral and collect items equivalent in number to that symbol (see Boysen 1993). Other chimpanzees used Arabic numerals to guide their responses of collecting sets of items on a computer screen equal in number to that numeral value, but they were never asked to do a labeling task (e.g., Beran and Rumbaugh 2001). So, full evidence of the counting principles was not present in those cases. In another impressive project, the parrot Alex was able to label sets according to their numerosity and announce subsets of a specific quantity, and Alex also showed the ability to do this with all kinds of stimulus types, including heterogeneous sets of things (see Pepperberg 2006). However, it was not clear that Alex engaged in tagging of items in any way, allowing again the claim that this would be proto-counting.

What is compelling is the breadth of proto-counting in the animal kingdom. Although primates, parrots, and other large-brained animals have shown strong evidence of proto-counting, so too have other more diverse species. For example, rats have been shown to enumerate the number of tunnel runs they encountered to find a specific cardinal value that predicted food reward (e.g., food is in the fourth tunnel; Capaldi and Miller 1988). Similar designs have shown that honeybees can enumerate specific numbers of tunnels or landmarks to pass by to find the correct site that predicts reward (e.g., Chittka and Geiger 1995; Dacke and Srinivasan 2008) and ants perform various foraging tasks that also rely on numerical cues and some of the counting

principles (e.g., Reznikova and Ryabko 2011). Pigeons also show cardinality and ordinality in their use of symbols representing labels for enumerated sets and also as cues to how many items need to be collected (e.g., Xia et al. 2000, 2001), but this was in only one testing context. Thus, in many of these cases, proto-counting would be the claimed mechanism solely because of lack of transfer tests of the ability to apply counting routines to completely new types of stimuli. Of course, this is a high bar given that transfer tests given to human children are scaffolded by language, and clear verbal instructions can be given in new contexts, whereas this cannot be done with animals. So, it is very difficult to show such transfer for methodological reasons. In other cases, real behavioral limitations are evident in nicely designed transfer tests, or tests where numerical symbols must be used flexibly for ordinal and cardinal relations. For example, honeybees can learn associations between quantities and arbitrary signs, but not in a bi-directional manner necessary for counting. This means that honeybees that learned to match a sign to a number of elements were not able to use that sign to indicate which numerosity to choose as a match (Howard et al. 2019).

Ultimately, most researchers working in this area today concern themselves less with the question of whether these behaviors are *counting* or *proto-counting* and instead the focus is on the degree to which numerosity is the defining stimulus feature of the representation that drives responding. Although there are still claims of counting by animals, no cases present as comparable to what the average 5-year-old human child can do fairly easily. But, that should not be the goal of this comparative research, to confirm that counting is “real” or that some new experiment definitely moves an animal’s performance from proto-counting to “true” counting. Our goal in this comparative research is to understand what numbers mean to animals, how they can (or cannot) enumerate different types of stimuli, and how accurately they can represent quantitative information in symbolic form. Ultimately, what one calls

these performances is less valuable than how well one understands them.

## Cross-References

- ▶ [Absolute Number Discrimination](#)
- ▶ [Alex the Parrot](#)
- ▶ [Approximate Number System \(ANS\)](#)
- ▶ [Counting](#)
- ▶ [Irene M. Pepperberg, PhD](#)
- ▶ [Relative Numerousness](#)
- ▶ [Sarah “Sally” Boysen](#)

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## Protogynous Hermaphroditism

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The sexual ontogeny and developmental patterns of organisms are incredibly diverse. Much of this diversity is rooted in interspecific variability in sex allocation, which is the provision of resources to either female or male reproduction in order to optimize reproductive success for individuals and populations. *Protogynous hermaphroditism* refers to a life-history characteristic, whereby individuals in a population change sex from functional females to functional males at some point during their life span. Hence, resource investment is more heavily allocated to female reproduction early in the life span, and later this investment switches to male reproduction. Hermaphroditism has been documented in a range of taxa, including both terrestrial and marine invertebrates and vertebrates, but is highly common and very well studied in many families of teleost fishes, particularly coral reef fishes with complex social systems, as is evidenced by the high volume of scientific literature examining protogyny in coral reef fishes. Because younger individuals are generally female and older individuals are generally male, protogynous populations are often sexually dimorphic (i.e., males, on average, are larger than females) and in some cases sexually dichromatic (i.e., sex change is concomitant with a change in body coloration or other morphological characteristics).

Protogyny is a form of sequential hermaphroditism, which is a trait where individuals function as both sexes at different times in their life spans, necessitating a transition from one sex to the other. The theory behind sex allocation (Charnov 1982)

provides a framework for understanding the advantages of variable distribution of resources among males and females in a population. The central tenet regarding the evolutionary cause of sequential hermaphroditism is the “size-advantage hypothesis” (Ghiselin 1969), which predicts that sequential hermaphroditism will be favored when reproductive fitness increases with size (and therefore age) at a greater rate in one sex than the other. Hence, for protogynous species, optimal resource allocation would be exhibited by a predominance of females at smaller body sizes and a switch to males at larger body sizes (Warner 1975). Protogynous hermaphroditism is common in species with complex mating systems. Mating strategies, such as harem territoriality where large males defend territories and harems of smaller females, influence the fertility rates of both males and females across different body sizes. This suggests that the optimal timing of sex change for individuals is strongly determined by the extant social system, such that an individual will change sex if and when it increases their reproductive value (Munday et al. 2006a).

Protogynous hermaphrodites can display either monandry or diandry. Monandric species are those in which all males in the population are derived secondarily from functional females, termed secondary males. Diandric species have two pathways of male development and, thus, two types of males. Primary males become functional males at the onset of maturation; secondary males are derived only through sex change from functional females. In sexually dichromatic (i.e., different colorations broadly associated with females and males) species, primary males often display initial phase coloration, which is generally associated with females, but some of these individuals will later undergo metamorphosis to terminal phase coloration. This change is generally concomitant with a behavioral change in reproductive strategy. The sexual patterns described here are common in the well-studied Labridae (wrasses and parrotfishes), but the nuances of sexual ontogeny can be much more complex and variable across other taxa.

Factors controlling the onset of sex change or the development as a primary male in individuals



have been clearly linked to social organization and mating system (Ross 1990). Warner and Swearer (1991), using the oft-studied bluehead wrasse (*Thalassoma bifasciatum*), demonstrated one-to-one replacement of terminal phase males that were removed from local populations. Replacement occurred via sex change in the largest remaining initial phase females. Munday et al. (2006b), using the same model species, showed that development of primary males was determined by the resident population size, whereby primary males are more prevalent within larger resident populations. These strategies relate to reproductive success rates of different sexes and phenotypes under different mating systems, which vary with local population size. In fact, among the teleost fishes, the evolutionary history of functional hermaphroditism appears highly associated with the structure of mating systems (Erisman et al. 2013).

Previously, the wide range of studies examining factors controlling sex change were conducted at very small spatial scales, often in controlled experimental settings. However, because social systems, population size, and resource availability can vary across space and time, there is tremendous spatial and temporal variability in life-history strategies within species. Warner (1991) proposed utilizing the vast levels of intraspecific variability across space and time to test hypotheses in evolutionary ecology. He states, "[...] phenotypic plasticity of a trait within a species represents a set of functional adaptive responses to short-term variation in the environment. A study of phenotypic plasticity can identify just which aspects of the environment appear important in eliciting a functional response. [...] Given a particular trait, the environmental factors to which a particular species responds in the short term should be the same as those that shape differences between species over evolutionary time." The length at sex change in protogynous hermaphrodites is among the more labile life-history traits, and, in some dichromatic species, can be accurately and rapidly estimated by relating lengths of individuals with body color phases. Expanding observations up to scales stretching

across diverse ecosystems or across species ranges represents a new frontier in studying protogynous hermaphroditism and should facilitate a greater understanding of the extent of local adaptation in populations (Petersen and Warner 2002).

## Cross-References

- [Gonochorism](#)
- [Hermaphrodite](#)
- [Operational Sex Ratio \(OSR\)](#)
- [Protandrous Hermaphroditism](#)
- [Sexual Dimorphism](#)

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## Protolanguage

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### Definition

The term “protolanguage” occurs in the linguistics literature with two different meanings. One meaning of the term refers to a language (in general extinct) from which a family of modern languages is descended. An example is Latin, which gave rise to the Romance family of languages. Whereas Latin is an attested language (known to us through preserved documents), in other cases the progenitor language is unattested, known only by reconstruction from the attested languages that descend from it. An example is the hypothetical language of Proto-Indo-European, from which all modern Indo-European languages have developed.

The other meaning of the term, which will be emphasized here, is a hypothetical stage in the biological evolution of language in the hominin lineage. According to the theory of language origins proposed by linguist Derek Bickerton (1990, 1995), hominins in the protolanguage stage (which Bickerton associates with *Homo erectus*) communicated with words that were not organized by syntactic rules. At a later point in evolution, genetic mutation gave rise to an innate “language bioprogram” (which some, although not Bickerton, would describe as a “module”) that enabled syntactically organized language to emerge (Bickerton 1984, 1990). Protolanguage, on this view, was a stepping stone toward true language.

Bickerton’s notion of protolanguage actually has broader scope than suggested above, however, as it can be observed in certain populations in the world today. These populations include children younger than 2 years, feral and closet children (those raised in social isolation and hence deprived of early exposure to language), and apes that have been taught language-like

communication systems (such as rudimentary sign language). But the modern-day form of protolanguage that plays the most central role in Bickerton’s theory of language origins is the crude system of communication known as a pidgin language.

### Introduction

During the era of European colonialism, from the sixteenth to nineteenth century, laborers from various language communities (e.g., Chinese, Koreans, Japanese, Africans, and Filipinos) were brought together in places like Haiti, Jamaica, Belize, Surinam, Mauritius, and Hawaii, in many cases, to work on sugar plantations (Bickerton 1990). Since the workers possessed no common language in this polyglot situation, there existed a need for a lingua franca to make communication possible. Uniform adoption of the superstrate language (that spoken by the master class) was inhibited, however, by the minimal opportunities for interaction between the workers and their masters in the rigidly stratified social structure. Instead, the potpourri of words known as a pidgin language emerged as the workers cobbled together lexical items originating in the superstrate language, with additional borrowings from the various substrate languages (the native languages of the workers).

A pidgin language in its early stages is a bare-bones form of communication that lacks several major features of natural languages like English or Japanese. First, function words are rare or non-existent. These are words, such as articles, conjunctions, and prepositions, that lack inherent meaning and instead play a grammatical role. They are to be contrasted with the inherently meaningful content words, which include nouns, verbs, adjectives, and adverbs, and which refer to objects, actions, and properties. A typical utterance in a pidgin language (and other forms of protolanguage) will consist almost entirely of such items. Also lacking are grammatical items such as auxiliary verbs, as well as noun and verb inflections, which mark number and tense.

A second feature that is lacking in early-stage pidgin languages is the use of word order to express differences in meaning. A simple example from English is the contrast in meaning between *John kissed Mary* versus *Mary kissed John*; these contain the same words, but due to the difference in word order, the roles of agent and patient are reversed. Pidgin languages do not sequence words in a principled manner; instead word order is highly inconsistent, with different speakers of the language tending to order words in a manner that carries over from their native language. Nor are differences in word order used to convey differences in meaning.

Framing the issue in terms of word order is a bit simplistic, however, for it seems to suggest that language consists of words strung together like beads on a string. While such a linear pattern may adequately characterize pidgin and other forms of protolanguage, the organization of true language is hierarchical rather than linear. That is because natural languages like English provide rules by which words can be built up into phrases, which can in turn be built up into still-larger phrases. For example, a noun like *dog* can be expanded into a larger noun phrase by adjoining it to the adjective *black*, resulting in *black dog*. Applying this rule recursively, we can add another adjective, yielding a still-larger noun phrase like *big black dog*. English and many other languages permit still further expansion by adjoining a specifier like *the* to a noun phrase, which in the present case would result in *the big black dog*.

Similar possibilities for expansion are also available to verbs. Thus, a transitive verb like *chase* requires an obligatory object such as *cats*, which can be combined to form a verb phrase like *chase cats*. The noun *cats* might in turn be expanded into *the small gray cats*, resulting in the larger verb phrase *chased the small gray cats*. This hierarchically structured verb phrase can now be adjoined to a subject noun phrase, itself hierarchically structured, adding yet another level to the hierarchy, resulting in a sentence like *the big black dog chased the small gray cats*. The resulting conglomerate can be diagrammed as an inverted treelike structure, where each phrase is hierarchically embedded in the next-larger

phrase, the complete assembly hanging from an overarching *S* (sentence) node.

At least, this is the case in natural languages like English. Pidgins and other forms of protolanguage lack rules for the assembly of words into more expansive phrases, resulting in a linear, rather than hierarchical, structure. This in turn limits the expressiveness of protolanguage, for example making it difficult to ascertain which of two nouns in a word string is the agent and which is the patient. We can gain deeper insight into this shortcoming of protolanguage by taking a closer look at the grammar of verbs.

As noted above, the verb *chase* requires an obligatory object such as *cats*. Other verbs sharing this property include *hit* and *kiss*. Thus, you cannot say *John hit* or *Mary kissed*, as the grammar of English requires you to state who received the hit or the kiss (as in *Mary kissed John*).

Linguists call the thing affected by an action the *patient* (typically expressed as the object of the verb), whereas the actor that performed the action plays the role of *agent* (usually expressed as the subject of the verb). These “thematic roles” and the nouns that express them are said to be *arguments* of the verb, meaning that they are role-players or participants in the action named by the verb. In contrast to transitive verbs like *chase* or *kiss*, an intransitive verb like *sleep* or *arrive* takes only a single argument (ordinarily expressed in English as the subject of the verb). Such a verb cannot take an object, and indeed it sounds strange if you try to give it one. Thus, we can say *Mary slept* but not *Mary slept the dog*. Still other verbs, such as *give*, *lend*, *send*, and *hand*, take three arguments, as in *Mary sent John a letter*.

These particularities of a given verb are said to comprise the verb’s *argument structure*. Typically, in natural languages like English, the arguments of a verb must occur obligatorily and in canonical position in the sentence structure. Thus, if Mary kissed John, we can say *Mary gave John a kiss*, but we cannot say *Mary gave a kiss John*.

The requirement for obligatory verb arguments may seem to be violated, however, by an utterance such as *What did Mary give John?* Here the supposedly obligatory object of the verb (let’s suppose it was a kiss that Mary gave to John),

which would canonically occur after *John* (as in *Mary gave John a kiss*), seems to be missing. In the transformational grammar of Chomsky (1957), this is explained as the result of so-called movement rules. If we suppose that the sentence starts out as *Mary gave John what?*, a movement rule would relocate the question word *what* to the beginning of the sentence, while also inserting a form of the auxiliary verb *do*, resulting in *What did Mary give John?*

While these phenomena are pervasive in the natural languages of the world, they are absent in protolanguage. For example, in a pidgin language, the arguments of a verb are not obligatory but rather can be omitted freely. This means that word strings like *John hit* or *Mary kiss* would be permissible. True, in natural languages a constituent may be missing from its canonical position, but when this happens, the empty slot is linked in a principled manner to an antecedent that is related to it. If we use *e* to represent such an empty slot, then in a question like *What did Mary give John e?*, the *e* is related to the question word *what*, helping us to understand that this word refers to the object of the verb *give*. As Bickerton notes, such grammatical devices permit us to interpret the language we hear in an automatic and effortless way, making it easy for us to understand who did what to whom. Protolanguage, lacking such devices, fails to provide such clarity.

It is the lack of these features in pidgin languages that relegate them to the status of protolanguage (along with the language of children before their second birthday and language-trained apes, of which more below). Bickerton sees these features of protolanguage as relevant to the evolutionary origins of language in the hominin lineage.

### Protolanguage and Bickerton's Theory of Language Origins

The relevance of protolanguage to the problem of language origins lies in the changes that occur in a pidgin language as it is passed from the first generation of pidgin speakers to their children.

In the span of one generation, a pidgin language is transformed into a much more expressive form of language called a creole. A creole language possesses all of the features that are lacking in pidgin languages (and other forms of protolanguage), including function words and hierarchical organization that is governed by phrase-formation rules.

But how does this transformation from pidgin into creole occur? Starting with function words, these do not emerge *ex nihilo* but rather consist of content words from the pidgin language that are called into service for a new purpose (Calvin and Bickerton 2000). For example, in the creole that emerged in Hawaii (known as Hawaiian Creole English), auxiliary verbs are derived from content words like *go* and *stay* (which, when used as content words, have roughly the same meanings as in English). When used as auxiliary verbs, *go* is used to mark the main verb for irrealis modality (subsuming future tense and conditional and subjunctive moods), *stay* to mark nonpunctual aspect (roughly equivalent to English progressive), and *bin* to mark anterior tense (roughly equivalent to English pluperfect) (Bickerton 1981, 1983a).

As noted above, a creole language emerges not among the first-generation immigrants but rather among their children. We know this because the adult pidgin speakers, unlike their children, seldom achieve proficiency in the creole. Rather, they continue to speak pidgin (while retaining fluency in the native language of their home country). Bickerton draws the conclusion that it is the children who created the creole language. (For alternative views on the origin of creoles, see the commentary on Bickerton's 1984 target paper.)

But why is this act of language creation possible for the children and not for their parents? Bickerton's answer is that the parental generation cannot achieve proficiency in the creole (let alone *create* such a language) because they have matured beyond the critical period for language acquisition (perhaps better described as a "sensitive" period). Their children, however, achieve full fluency in the language that they themselves have created, presumably in the course of their verbal interactions with each other.

It appears, then, that there is a discontinuity, or quantum leap, in the sophistication of language from one generation to the next. According to Bickerton a similar discontinuity occurred in the evolutionary history of language in the hominin lineage. On this view, the pidgin-to-creole transition constitutes a recapitulation of the evolutionary history of language in the hominin lineage. In the latter case, however, it was genetic mutation that accounted for the transition from protolanguage to true language, by giving rise to an innate language bioprogram containing the fundamental principles that underpin all human languages.

These are the essentials of Bickerton's (1984) language bioprogram hypothesis. Readers familiar with the linguistics literature will note the clear similarity of this theory to Noam Chomsky's (1975) theory of an innate "language organ," or "language acquisition device", embodying the principles of universal grammar (as elucidated in popular form by Pinker 1994). This notion was proposed by Chomsky to account, among other things, for how the complexities of natural languages like English, Japanese, or Swahili can be acquired in a relatively effortless manner by children. Going beyond that, Bickerton's theory proposes to explain not only how children can learn a language but can actually *create* one *de novo* when they are deprived of an even remotely adequate model, as in the pidgin situation.

Going still further, Bickerton's hypothesis provides a coherent account of certain universals that occur in the structure of all creole languages. An example is the placement of auxiliary verbs in relation to the main verb of a clause. Creole languages that have sprung up independently of each other invariably place auxiliaries before the main verb and in a uniform sequence (Bickerton 1983a, 1990). In every creole language, the anterior marker (when present in a particular utterance) precedes the irreal marker (when present), which precedes the nonpunctual marker (when present), which in turn precedes the main verb. This uniformity, on Bickerton's (1983b) account, can be seen as the default setting of innately specified parameters of the sort postulated by Chomsky's (1981) theory of principles

and parameters. (For an accessible account of Chomsky's parametric theory, see Baker 2001).

## The Diverse Forms of Protolanguage

As noted above, pidgin is not the only form that protolanguage can take but rather, according to Bickerton, is a part of the human biological endowment for language that manifests itself in additional ways, including the language of children under 2 years old. The earliest language outputs of children consist of single words, which first appear at around the age of 1 year. Children first start putting words together at around the age of 20 months. While utterance length at this stage is at most two words, children learning English evince regularities of word order that reflect the canonical SVO (subject-verb-object) pattern of this language. For example, while a three-word utterance like *Mommy throw ball* is beyond a 2-year-old's reach, two-word fragments respecting English word order such as *Mommy throw* (SV), *throw ball* (VO), or *Mommy ball* (SO) are likely to occur.

As noted by Bickerton (1990), these word-order patterns in early child language are not universal but rather reflect the syntactic pattern of the language the child is learning. For example, a child learning Japanese will produce two-word utterances reflecting the OV pattern of that language (contrasting with English VO), whereas children learning Tagalog will produce outputs conforming to the VS pattern of that language (contrasting with English SV).

While these regularities suggest that an incipient syntax is starting to emerge, this appearance is illusory according to Bickerton (1990). Even in the cases where the two-word combinations are novel (as opposed to memorized idiom-like units), the appearance of syntactic organization is superficial only. While the child may grasp the fact that nouns are different from verbs and order them in a language-appropriate way, this understanding is based on semantic rather than syntactic criteria. Thus, for a child at this age, what makes a word a noun is that it denotes a concrete object (*bed*, *toy*, *mommy*), and what makes a word a verb is that it



denotes a physical action (*run, play, eat*). Syntactically organized language will not emerge until the child recognizes that word classes are based on formal rather than semantic criteria. The language learner will then be able to talk about such things as *lack* and *absence*, which play the grammatical role of nouns but do not refer to anything concrete or perceptible to the senses.

According to Bickerton, this breakthrough occurs when the child's language module comes on-line at around the age of two, marking the transition from protolanguage to true language. While this presumably results from biologically programmed maturation, the normal development of the module requires at least minimal language input from the child's environment (although, as we have seen, even the highly impoverished input afforded by a pidgin language is sufficient). If such input is not available during the child's sensitive period, then normal language development cannot occur. We know this from the case of children who have been deprived of exposure to language during their early years.

Probably the best-known case of this is the "closet child" known as Genie, who was rescued from extreme social isolation at the age of 13. Her language at the time of her rescue was virtually nonexistent. Over the course of several months, she began to utter, at first, single words and then, later, two-word combinations (Fromkin et al. 1974). Examples include the following:

*Want milk.*  
*Paint picture.*  
*Mike paint.*

Like a normally developing child, she eventually came to produce longer utterances:

*Applesauce buy store.*  
*Father take piece wood. Hurt. Cry.*

While the second example may look like English SVO word order, according to Bickerton this ordering is based on functional rather than grammatical factors. In particular, in Genie's speech the topic of an utterance (what the utterance is "about") would always come first, meaning that it is not serving the formal role of grammatical subject, which in turn means that

we can relegate such structuring to the level of protolanguage rather than true language.

Another example suggestive of grammatical sophistication is Genie's apparent use of the grammatical device of subordination, as in the following:

*I want Curtiss play piano.*

Here we appear to have the subordinate clause *Curtiss play piano* embedded in a matrix clause that begins with *I want* – a seemingly clear example of hierarchical embedding of the sort that cannot exist in protolanguage. Bickerton discounts this, however, on the grounds that every putative example of grammatical subordination in Genie's speech began with *I want* followed by what would ordinarily be a complete utterance in itself. More to the point, there is no use of complementizers like *that* or *to*, which would mark the beginning of a subordinate clause in English (as in *I want Curtiss to play [the] piano*). What we have here, then, is better understood as the juxtaposition of clauses rather than the grammatical embedding of one clause within another (Bickerton 1990).

Although Genie made progress in her language development, and in fact this development paralleled in many ways the language development of normally developing children, this progress came to a halt when she reached roughly the level of a normal 2-year-old. This is the point where, according to Bickerton, protolanguage gives way to true language in the language development of normally developing children. This is the limit for closet children, like Genie, who cannot avail themselves of their language module, which has gone off-line by the time of their first exposure to language, bringing to a close the sensitive period for language acquisition, leaving the child stuck at the protolanguage stage.

While exposure to at least a crude form of language is necessary for normal language development to occur, it is not in itself sufficient. According to Bickerton and other language nativists, it also requires that the language learner be equipped with an innate language module. As this adaptation is unique to humans, it follows that syntactically organized language should not

be accessible to any nonhuman species. There remains the possibility, however, that with appropriate tutelage, a nonhuman might be capable of acquiring protolanguage. That such is the case has been demonstrated, in Bickerton's view, by the efforts to teach apes a form of language. Indeed, while apes have been proven capable of acquiring a lexicon of a hundred "words" or more (be they manual signs, plastic chips, or lexigrams on a computer console), according to Bickerton (1990) their quasi-linguistic outputs fail to evince a command of syntactic organization.

Such a command might seem to be demonstrated by certain regularities that appear in language-trained apes' ordering of "words" (e.g., hints of SV word order, as in *Roger tickle* or *you drink*). Moreover, in their language comprehension (as opposed to production), there is even some recognition that meaning changes when word order changes (e.g., *Roger tickle Washoe* versus *Washoe tickle Roger*). But as we saw in the case of child language acquisition, mere regularity of word order does not suffice to demonstrate a command of syntax. A more compelling indicator would be evidence of hierarchical structure, and this, according to Bickerton, is lacking in the quasi-language of apes (see also Anderson 2004). For instance, there is no embedding of one clause within another. Indeed, in this respect apes fall short of even the meager accomplishments of Genie, who at least produced a semblance of embedding in the case of outputs like *I want Curtiss play piano*.

Equally telling is the lack of function words in apes' quasi-linguistic outputs. This might be attributed to the fact that such words, unlike content words, cannot be defined ostensively, making them difficult to learn (Bickerton 1990). But this difficulty does not stop human children from learning them, where this, arguably, is made possible by a language module that exists in humans but not in apes. With regard to the comprehension (as opposed to production) of function words, apes fare no better. For example, even the high-performing bonobo Kanzi cannot distinguish between putting something on, in, or next to another thing (Anderson 2004).

The evidence reviewed to this point seems consistent with the suggestion that a non-syntactic form of language, called protolanguage, characterizes the linguistic (or quasi-linguistic) outputs of children younger than 2, closet children, and apes. The question remains, however, whether this form of communication is discontinuous from true language or whether the former can grade gradually into the latter.

## Evaluating the Theory of Protolanguage

A key feature of Bickerton's argument is that protolanguage and true language are distinct modes of behavior, each of which is an inherent part of humanity's biological endowment (and in the case of protolanguage is within the reach of apes). A corollary of this assumption is that when, in the course of ontogeny or phylogeny, protolanguage is replaced by true language, the transition is not smooth or gradual but rather involves a discontinuity. In the case of child language acquisition, the transition can be explained by the maturation of a language module that comes on-line at around the age of 2. In the biological evolution of human language, the transition was caused by a genetic mutation that gave rise to the language module in the first place. This notion of a discontinuity in language development has been questioned in at least two different ways.

First, even if such a discontinuity occurs in child language development, it does not follow that a comparable discontinuity occurred in the biological evolution of language. The reason, as noted by Pinker (1992), is that a genetic capability for forms of language intermediate between protolanguage and true language might once have existed in the hominin lineage but were selected out in the course of evolution. (Jackendoff 1999, has in fact outlined a plausible sequence of stages by which grammatical language might have evolved. And Bickerton himself in later works allowed for the incremental elaboration of the language faculty after its initial appearance in evolution (Calvin and Bickerton 2000). Consideration of these refinements in

Bickerton's theory would take us too far afield, however.)

A second and possibly more serious objection to Bickerton's notion of protolanguage as discontinuous from true language is that stages intermediate between the two can, and evidently do, exist in child language development. The existence of these stages suggests that syntax develops incrementally and not in one fell swoop. One way to see this is by examining the child's acquisition of verb argument structure. This is evidently accomplished in a piecemeal manner, one verb at a time. A verb like *cut*, for example, may initially appear only in a simple construction with one argument, for example, *cut*\_\_\_ (as in *cut paper* or *cut finger*). More-complex constructions with more than one argument, such as *daddy cut paper*, do not occur with this verb. But at the same point in development, other verbs may occur in frames that accommodate multiple slots for multiple arguments, resulting in constructions like *draw*\_\_\_ *on*\_\_\_, *draw*\_\_\_ *for*\_\_\_, \_\_\_*draw on*\_\_\_ (Tomasello 2003, 2011).

Thus, it seems that a given child's growing command of argument structure is verb-specific (for which reason these are called item-based constructions). And even within a given verb, the various constructions do not appear all at once. Rather, change occurs in a stepwise manner, with the child successively adding additional arguments to a particular verb (Tomasello 2003, 2011). It seems, therefore, that rather than acquiring abstract rules that apply generally to all verbs, the child initially learns the various constructions possible for each verb one at a time, and these are based on how the child has heard that particular verb being used (Tomasello 2003, 2011). This poses a challenge to the "words-and-rules" approach to language development of the sort advocated by Pinker (1999), where this process is seen as depending on a Chomsky-type language module. If that were the case, and if this module comes on-line at around the age of 2 years, as Bickerton suggests, then one might expect, contrary to fact, that the child would acquire a particular argument structure, applying across the board to many verbs, all at once. The fact that this kind of sweeping

change does not occur seems more consistent with operation of general-purpose learning mechanisms than with the sudden awakening of a dedicated rule-learning mechanism.

Indeed, the very notion of an innate language module, or language "instinct," has been called into question (Tomasello 1995). Instead, general-purpose learning and cognitive mechanisms may be adequate to account for language acquisition (Tomasello 2003). And if a language module does not exist, this undercuts the rationale for positing two distinct kinds of language, one of which (true language) depends on such a module, while the other (protolanguage) does not.

## Cross-References

- [Critical Periods](#)
- [Kanzi](#)
- [Language](#)
- [Language Research: Great Apes](#)
- [Lexigrams](#)
- [Sensitive Periods](#)
- [Syntax](#)
- [Washoe](#)

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## Proto-social Behavior

- [Coalition Enforcement](#)

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## Prototheria

- [Monotreme Sensory Systems](#)

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## Proxy Species

- [Indicator Species](#)

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## Prudence

- [Parsimony](#)

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## Psittaciformes Locomotion

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## Synonyms

[Cocaktiel locomotion](#); [Cockatoo locomotion](#);  
[Parrot locomotion](#)

## Definition

Movement used by members of order Psittaciformes to traverse their environment. The order is subdivided into 3 superfamilies—Psittacoidea, or true parrots, Strigopoidea, or New Zealand parrots, and Cacacuoidea, or cockatoos and cockatiels (Luescher 2006).

Parrots, cockatoos, and cockatiels are skillful foragers within tropical and sub-tropical rainforests, in part due to their unique limb morphology. Their zygodactyl feet, in which the first and fourth digits face backward while the second and third digits face forward, assist in both perching and climbing. The tarsus, which lies between the heel and toes, is characteristically short and stout, allowing parrots to climb and manipulate objects easily (Parr and Juniper 2010; Toft and Wright 2015). Sedentary parrots invest a significant amount of time and energy into building strong, well-protected nests to incubate eggs and raise their young. Due to their migrant lifestyle, nomadic parrots opt for large clutches and spend less time incubating and rearing their young (Luescher 2006).

## Flight Biomechanics

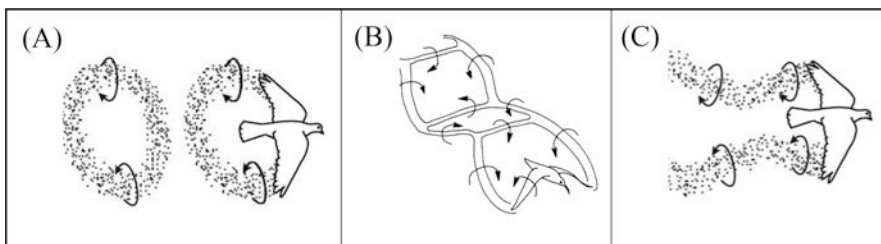
There is debate within the field of avian flight biomechanics on classifying gait during flight, since birds mostly stray from typical terrestrial locomotion. Historically, studies have utilized two-dimensional models to understand flight aerodynamics and to classify gait. Others have proposed that instead of discrete gait classification, kinematics should be quantified through a Strouhal number (wingbeat frequency \* wingbeat amplitude/forward flight speed). Tobalske (2007) explains that all birds seek to maintain their Strouhal number through flight by accordingly modifying aerodynamic variables. Recent technological advancements, including high speed cameras and turbulence-simulating wind tunnels, have allowed for a three-dimensional study of avian locomotion. These studies have revealed that gait patterns largely overlap between members of the same order. Psittaciformes primarily rely on flapping flight as a main gait pattern, as opposed to gliding, soaring, hovering, or short-flight. In addition to flapping flight, each family within the order has adapted unique characteristics to their gait, to optimize energy cost based on body composition (Deetjen et al. 2017; Hedrick et al. 2002; Nespolo et al. 2018).

Cockatiels (*Nymphicus hollandicus*) of the superfamily, Cacatuoidea, will be used as the archetype for discussing general flight patterns of Psittaciformes. At slow speed flight (<7 m/sec), cockatiels primarily use downstrokes, or downward directed flapping, resulting in a vortex-ring gait (Fig. 1). At slower flight speeds, cockatiels use downstrokes to forcefully push air downward. This

maneuver helps to either maintain the bird's flight altitude or assist in climbing to higher altitudes, known as lift. Forceful downstrokes cause the air trailing behind each distal wingtip to swirl and form a vortex at each wingtip. At slow speeds, these vortices connect in the cockatiel's wake, forming a single vortex ring. During the slow-speed upstroke, cockatiels and other Psittaciformes utilize a "tip reversal upstroke" or "upstroke flick," whereby their wings remain extended, but their feathers are supinated to allow air flow. However, the upstroke provides little to no vortex shedding or lift. This mechanism is characteristic of parrots, but the true aerodynamic purpose remains unknown (Hedrick et al. 2002).

At 7 m/sec, cockatiels transition from vortex-ring gait to continuous vortex gait by accelerating upward and forward. This transition occurs through several high-amplitude wingbeats followed by several low-amplitude wingbeats. Vortex-ring gait and ladder-wake gait are used for brief periods of acceleration, while continuous vortex gait is used for brief periods of deceleration during gait transition. Ladder-wake gaits occurs when downstroke air circulation is greater than the upstroke (Hedrick et al. 2002; Pennycuik 1988).

At high speed flight (>7 m/sec), cockatiels use both upstrokes and downstrokes, resulting in two separate trailing vortices—one from each wingtip, known as continuous vortex gait. The vortices are formed via equivalent air circulation from the proximal wingtip during the upstroke and the distal wingtip during the downstroke. The continuous upstroke–downstroke cycle produces lift with forward velocity, providing most of the air



**Psittaciformes Locomotion, Fig. 1** During flight Psittaciformes transition between different “gaits,” such as (a) vortex-ring gait, (b) ladder-wake gait, and (c) continuous vortex gait. (Figure adapted from Hedrick et al. (2002))



flow. The “upstroke flick” is not commonly used at high speed flight. At maximum speed flight (~15 m/sec), cockatiels utilize ladder-wake gait to minimize drag (or the aerodynamic force opposing forward velocity) and to produce forward thrust (Hedrick et al. 2002).

Pacific parrotlets (*Forpus coelestis*) are a small species (~26 g) of parrot that can serve as a useful model to understand psittacine wing morphing during flight. Psittacines refer to the sub-family, Psittacinae, in the family, Psittacidae, in the super-family, Psittacoidea. After takeoff, parrotlets and other parrots morph their wings to become aerodynamically favorable throughout flight. Upon takeoff, parrotlets push off horizontally using their legs to accelerate forward. During the first downstroke, parrotlets then rotate their tail downward, while simultaneously twisting and rotating their wings downward relative to their body. This allows an aerodynamically favorable lift upon takeoff. During experimental short 20 cm flights, parrotlets primarily used partial downstroke wingbeats to reach their destination. During longer 75 cm flights, parrotlets folded their wings mid-flight to produce flexed-wing bounds (Chin and Lentink 2017). Producing bounds necessitates high energy expenditure, and therefore is only used by birds <300 g (Tobalske 2007). While landing, parrotlets direct leg impulses horizontally against the air, with few winged upstrokes to assist in smooth deceleration (Chin and Lentink 2017).

Wing loading, typically measured as body mass (kg) / wing area (m<sup>2</sup>), is useful in understanding how different species within the Psittaciformes order adapt their flight to optimize aerodynamic variables and minimize energetic costs. For example, though both cockatiels (~70–120 g) and African grey parrots (~400 g) have a wingspan of ~33 cm, and likely similar wing areas, wing load varies significantly due to large differences in body mass (Holman 2008; Newmyer 2011). Assuming wing area remains constant, aerodynamic theory suggests that as body mass increases, wing load increases. Within the psittacines, there is significant variation in body mass and resultant wing load. For example, some birds of the *Poicephalus* genus can weigh ~120 g (comparable to the cockatiel), while others

can weigh as much as ~400 g (comparable to their relatives, *Psittacus* birds). By this principle, the African grey parrot (*Psittacus erithacus*) should have a higher wing load as compared to cockatiels. To compensate for their large mass, African grey parrots utilize vertical flight at slow speeds during foraging to travel between the ground and treetops. During the upstroke, wing elevators, such as *m. supracoracoideus*, forcefully contract to produce an upward aerodynamic force. Powerful wing retractors are needed to maintain this position, since the energetic cost of vertical flight is high. Muscle weight analysis across Psittaciformes and non-Psittaciformes has revealed that parrots have significantly bulkier *m. deltoideus pars propatagialis* to assist in vertical take-off and to maintain a negative angle of attack, or vertical body position (Razmadze et al. 2018).

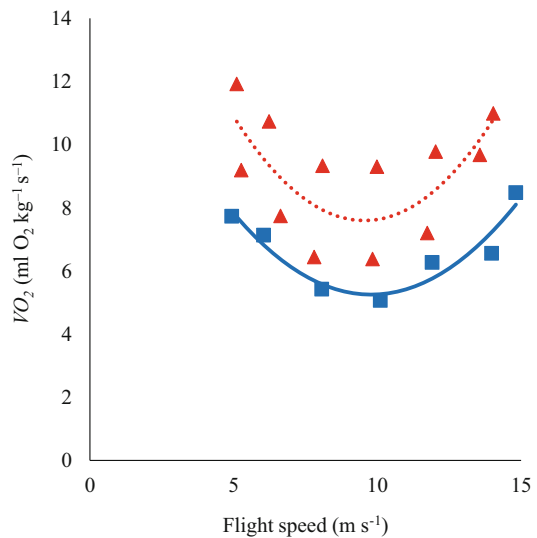
In many regards, the flight mechanics of the parrots closely match those observed in pigeons (*Columba livia*), which have a mass (~370 g) more comparable to *Psittacus* and some *Poicephalus* birds (~400 g). In between flapping phases, pigeons and two species of Psittaciformes, including cockatiels, use intermittent extended-wing glides to reduce the aerodynamic power ( $P_{aero}$ ) required for flight. During slow flight, both pigeons and cockatiels utilize rolls during the downstroke to maneuver through turns. For example, a left turn is accomplished by asymmetric contraction of both pectoralis muscles. The result is higher velocity on the outer wing of the turn (right) during the initial downstroke. Termination of the roll involves switching the side of greater pectoralis force, causing higher velocity on the inner wing (left) midway through the downstroke (Tobalske 2007).

## Flight Energetics

Locomotor energetics can be best understood by comparing basal metabolic rate (BMR) to oxygen consumption during activity. Basal metabolic rate represents the oxygen consumption of an animal's tissues and organs at rest, and is proportional to total energy expenditure. A species' BMR is also significantly influenced by the environment it

inhabits and is adapted to. For example, red-tailed black cockatoos can exist in either arid or cool environments. Those adapted to arid environments have lower BMRs than those adapted to cooler forested habitats (Cooper et al. 2002). Disturbances to environmental temperatures, such as extreme heat or cold, force animals to exert energy to maintain thermal homeostasis. Psittacines in particular are adapted to living in warm tropical climates, and as such have low BMRs. Low resting energy expenditure assists in energy conservation by allowing more energy to be spent in foraging or flying, especially when resources are limited. The energetics of psittacines can therefore also be affected by a seasonally variable environment. For example, the burrowing parrot (*Cyanoliseus patagonus*) resides in the Patagonian region of Argentina, which tends to have an unpredictable climate with mild winters. Due to significant temperature variance, the burrowing parrot must exert extra energy to maintain thermogenic homeostasis. As a result, these psittacines have been shown to have variable BMRs depending on the season. During the winter, psittacine BMRs tend to decrease (on average 45%) as an energy conservatory mechanism. Reducing winter energetic costs is vital for the survival of such species, especially since food is scarce during colder months (Zungu et al. 2013). These adaptations are crucial for the survival of Psittaciformes, and ultimately dictate the energy expenditure allowed for locomotion.

Parrot flight demands high energy expenditure, and is therefore primarily reserved for travel between neighboring nesting sites. Anatomically, the pectoral muscles provide most of the mechanical power needed for flight, through multiple sustained contractions (Morris et al. 2010). Energy consumption in relation to flight speed for cockatiels and budgerigars (*Melopsittacus undulatus*) follows a U-shaped curve, in accordance with aerodynamic theory [i.e., the greatest energy consumption occurs at low and high speeds, while intermediate speeds require the least amount of energy (Bundle et al. 2007) (Fig. 2)]. Study of metabolic consumption during budgerigar flight has revealed that energy cost is also highest in ascending flight, followed by descending flight, and least in level flight. Oxygen



**Psittaciformes Locomotion, Fig. 2** Oxygen consumption ( $\dot{V}O_2$ ) in budgerigars (red triangles) versus cockatiels (blue squares) at varying flight speeds. (Data reproduced from Bundle et al. (2007) and Tucker (1968))

consumption, during level flight, was most economical at ~35 km/h. Researchers found that maintaining a speed of 42 m/s optimized energy consumption, while maximizing the distance covered (Tucker 1968).

As flight is an energetically expensive mechanism of travel, Psittaciformes have adopted several mechanisms to reduce this cost. As mentioned earlier, Pacific parrotlets push off using their legs during takeoff and accelerate up to ~80–100% of average flight speeds. Energetic studies have revealed that it is more efficient to use leg muscles during takeoff and landing, than to use multiple contractions of the pectoral muscles, as in flapping flight (Chin and Lentink 2017). Parrots, in particular, also conserve energy by incorporating gliding into their flight. A flap-glide pattern takes advantage of the bird's inertia to minimize the amount of power the pectoral muscles produce to maintain flight. When flapping, the pectoral musculature must use multiple concentric muscle contractions to produce flight, which requires more energy than the sustained isometric contractions used in gliding. Using this method, parrots are able to reduce the high energetic cost of flight (Bundle et al. 2007).

## Additional Locomotion Modes

In addition to flight, Psittaciformes utilize other locomotor modes such as hopping, walking, and climbing to travel short distances. These modes assist in energy preservation when foraging from the ground to the treetops. During foraging, Pacific parrotlets use similar energy conservation strategies as during flight takeoff and landing. To hop and walk, parrotlets rely on small horizontally directed leg impulses to travel across branches. Doing so reduces energetic cost as it relies on short infrequent bursts of energy, rather than alternating between many forceful and sustained contractions of the pectoralis muscle (Chin and Lentink 2017).

Climbing is another energetically favorable form of locomotion that parrots use for play, foraging, and exploratory behaviors. Unique to the parrots during climbing is the use of their hook-like maxilla, or beak, and zygodactyl feet to climb and manipulate objects (Demery et al. 2011). To accomplish this, they primarily use *m. ethmomandibularis*, which is derived from *m. pterygoideus*. *M. ethmomandibularis* is a dual-bellied adductor muscle that when contracted, causes powerful elevation of the lower jaw, resulting in a strong grip. This tight grip is essential for anchoring parrots to branches as they climb upward against gravity.

Parrots also use their zygodactyl feet to assist in climbing and hanging off of tree branches. Each zygodactyl foot contains intrinsic foot muscles (mostly flexors) to accomplish this. Toe orientation allows for dexterity, allowing handling of food by one foot and support of hanging body weight by the other. Muscle analysis studies of zygodactyl feet have shown that birds which rely on climbing for travel, such as psittacines and monk parakeets, have hindlimb muscles greater in mass than birds which rely on flight for travel. These studies once again support the theory that Psittaciformes prefer to use hopping, climbing, or walking to optimize

their locomotor energy consumption (Carril et al. 2014).

## Migration

The majority of Psittaciformes do not undergo typical large-scale seasonal migration, but rather are nomadic within a fixed geographical area, between nesting and feeding areas. Some examples of nomads include budgerigars, scarlet-chested parrots, night parrots, African grey parrots, blue-headed parrots, and Eclectus parrots. African grey parrots often travel daily between neighboring woodlands and prefer roosting in trees over water or on islands with rivers. Parrots rely on pine nuts as a main food source. Unpredictable food shortages can force migration from core areas of food distribution to surrounding areas with more favorable foraging conditions, as seen with the thick-billed parrot. Some rose-ringed parakeets (*Psittacula krameri*) reside in mountainous areas and move to lower altitudes during winter months to escape the harsh coldness. Few parrot species, such as the orange-bellied parrot and blue-winged parrot (*Neophema* genus), are inherently migratory birds. Both birds seasonally migrate between Tasmania and the Australian continent across the Bass Strait (Parr and Juniper 2010).

## Bioinspiration

Aircraft design and human flight has been greatly influenced by Psittaciformes locomotion. Researchers have found that at low speeds, cockatiels reorient their bodies and change their bank angle, or the angle of their wing relative to the horizon, to execute a turn (Hedrick and Biewener 2007). Experimentally to make a 90° turn, cockatiels established a bank angle of 60° and flapped through the turn. Aircrafts mimic this flight strategy of body reorientation and increasing bank angle to make quick or tight turns (Hedrick and Biewener 2007).

To efficiently move through the air, both birds and aircrafts must modify their structure to reduce drag. Both aircrafts and cockatiels at high speeds produce continuous vortices, and thereby significant drag from each wingtip. In cockatiels, vortices are a result of flapping flight, whereas in aircrafts, they are a result of fixed wing length. To reduce drag while flying, cockatiels will lay their crest, or the feathers on top of their head, flat against the skull. Although aircrafts do not have crests, engineers have installed winglets at the tips of aircraft wings to assist in both producing lift and reducing drag produced by the continuous vortices. These winglets parallel the function of winglets in soaring birds and cockatiels flattening their crest during flight to decrease drag and improve energy efficiency (Hedrick et al. 2002; Newmyer 2011).

Current commercial aircraft wings are manufactured as immobilized entities, which are unable to flap or change orientation in the same manner that birds' wings can. Avian biomechanists have sought to improve current aircraft technology by creating biohybrid robotic wings, which can morph shape, as occurs during Psittacine flight. Morphing of the wing requires overlapping feathers and the presence of three primary positions—flexed, mid-tucked, and extended. Wing morphing includes movement of discrete wing elements to change the overall shape of the wing. This maneuver has been shown to increase efficiency and agility during flight, while also allowing for faster and tighter turns. Using kinematic data from parrotlets and lovebirds, researchers have since created PigeonBot, 280 g biohybrid robot modeling pigeons. PigeonBot can mimic pigeon and psittacine gait patterns including rolling, turning, flapping, and morphing, even in turbulent winds (Chang et al. 2020).

Study of Pacific parrotlet flight adaptations have also been used to advance biohybrid wing morphing technology. During flapping flight, parrotlets use wing muscles and energy stored in tendons to fold their wings. Wing unfolding, on the other hand, occurs passively as a result of

centrifugal acceleration. Scientists have sought to model this phenomenon in biohybrid wings, by using tuned springs to mimic energy storage in tendons during wing folding. Wing morphing thereby reduces drag during the upstroke of forward flight (Stowers and Lentink 2015). Improvements to such bioinspired projects may in the future help transform the field of aircraft engineering to improve maneuverability and fuel efficiency.

## Conclusion

During flight, Psittaciformes gait is mostly classified by speed—vortex-ring gait is used at slow speeds ( $<7$  m/sec) and continuous vortex gait at high speeds ( $>7$  m/sec). Psittaciformes are foragers and rely on stable food availability within a relatively fixed geographical location. Given that many Psittaciformes are relatively heavy birds, they have adapted their locomotor preferences to fit energetic constraints. For example, to minimize energy expenditure, psittacines especially prefer to climb, hop, and walk when traveling short distances. Vertical flight, which allows birds to briefly pause mid-flight, is used for foraging between the ground and treetops. Study of Psittaciformes gait has also helped inform the development of new technologies, such as PigeonBot. Ultimately, by understanding avian locomotion and creating biohybrid robotic models to mimic their patterns, avian biomechanists could help transform and optimize current aircraft technology.

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Radiation](#)
- [Alex the Parrot](#)
- [Arboreality](#)
- [Basal Metabolic Rate \(BMR\)](#)

- ▶ Canopy
- ▶ Captivity
- ▶ Cognition
- ▶ Dispersal Ability
- ▶ Dispersal Patterns
- ▶ Diurnality
- ▶ Ecology
- ▶ Evolution
- ▶ Extinction in Learning
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- ▶ Muscular System
- ▶ Natural Selection
- ▶ Navigation
- ▶ Pets
- ▶ Phylogeny
- ▶ Pigeon (*Columbidae*)
- ▶ Psittacine Cognition
- ▶ Species
- ▶ Swine Cognition
- ▶ Taxa
- ▶ Vertebrate Nervous System
- ▶ Zoo
- ▶ Zoology

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## Psittaciformes Sensory Systems

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## Introduction

Parrots have a number of behavioral attributes that make them stand out from other bird taxa. In particular, they have a high level of manipulative skills, a life-long curiosity about new objects, and highly developed cognitive abilities. In addition, most parrot species are highly social, often coming together in large aggregations to roost and feed and fly in compact formations. In many species, long-term social bonds are formed, and some species are long-lived, even on a human scale.

These features, as well as their often colorful plumages, have made parrots a focus of fascination to humans, and they have been favored as pets since at least the time of the early Roman Empire.

About 400 species of parrots (Order Psittaciformes) are recognized currently. They are divided into three or four families depending upon the approach to systematics adopted. Parrots occupy a wide range of habitats, from rain forests to arid savannahs. Despite this diversity of environments, several aspects of their ecology are common to most taxa. The majority of species feed predominantly on the reproductive structures of plants (i.e., seeds, fruit, nectar), although some species can be considered omnivorous, due to their consumption of invertebrates.

Fruits and seeds tend to be highly clumped in time and space, and many aspects of the behavior of parrots, such as forming large social groups and long daily and seasonal movements, are likely linked to the need to track these ephemeral resources (Lopes et al. 2018). Nearly all parrots nest in cavities, often making use of naturally occurring holes in trees and cliffs, while some species excavate burrows or parasitize the nests of other species. Most species are primarily diurnally active although there are a few species (notably Kākāpō *Strigops habroptila*, night parrots *Pezoporus occidentalis*) that are primarily nocturnal.

The dextrous manipulatory abilities of parrots are typically based around extracting embedded food items (Fig. 1), but they also readily explore nonfood items. These skills are made possible by distinctive morphological adaptations of their feet, bills, and tongues. Their feet are zygodactyl (two toes face forward and two back), an arrangement that allows objects to be grasped securely. All parrots have a highly curved upper bill and a thick muscular tongue. The maxilla (bone of the upper mandible) is joined to the skull by a synovial hinge joint and this allows movement of the upper as well as the lower jaw. The ability to articulate the maxilla is unique to parrots as in all other birds the maxilla is fused to the skull.



**Psittaciformes Sensory Systems, Fig. 1** A grey parrot *Psittacus erithacus* extracting seed from a palm fruit. The fruit is held in the zygodactyl foot and manipulated by the bill and tongue. The eyes are placed high in the skull and on the sides of the head. This gives the bird extensive visual coverage of the world about it, and two areas of high visual resolution occur on each side of the head. However, the bird can only just see what is held in its bill. Manipulation of the food item is controlled by a touch-sensitive bill-tip organ. (Photograph R. O. Martin/World Parrot Trust)

A particularly notable feature of parrots is their ability to use the bill as a “third limb.” They do this while climbing both up and downward through complex vegetation or across solid surfaces, such as tree bark, rock, and soil.

To express their full range of manipulative and climbing skills, and their complex social behaviors, parrots require a constant stream of accurate information about their environment. This includes information on the positions of close and remote objects, information about objects held in the bill and mouth, and information about the positions of others in a flock.

Information is extracted from the environment by the senses, and it is now clearly understood that all animal species have a “sensory ecology” that describes the specific and general relationships between an animal’s behavior and the information used to control it (Martin 2017a). Furthermore, it is now evident that an animal’s senses are as much subject to fine tuning through natural selection as

are its morphological features. While morphology is tuned to the physical challenges posed by the conduct of different tasks in different environments, the senses are tuned to the sensory challenges that these tasks and environments pose. In essence, morphological features can be regarded as the tools with which animals interact with their environment, while the senses provide information for the efficient guidance of those tools. Senses also provide information that ensures individual safety. These include the screening of food items, the detection of predators, and the detection of damage to the body.

One result of this natural selection of sensory information is that senses can vary between species just as much as morphology. Even closely related species can differ in their senses and in the information that they extract from the environment. No species is “all-seeing” or “all-hearing” any more than it can have a bill or a foot that allows it to do all manner of physical tasks. However, while morphology can be readily described and measured, information on senses is less accessible and so the diversity of senses within a taxon is usually less well cataloged and understood. Fortunately, broad descriptions of sensory capacity, and of the information that they provide, are available for most animal groups. In many taxa, some aspects are known in more detail than others, and this is the case among parrots.

### The Senses of Parrots

The telereceptive senses function primarily to gather information about objects remote from the animal. They provide the bulk of information used to orient an animal within its physical and social environments. The intimate senses provide information about objects and substances that are in physical contact with the animal.

In parrots, as in other birds, two telereceptive senses are key: vision and hearing, and it is possible to describe them in broad terms that will apply to most species. Vision is, however, a multifaceted sense and impossible to describe succinctly. Furthermore, it is probably true that vision is not exactly the same in any two species of birds and there are likely to be subtle specializations between parrot species as well as

differences between parrots and other bird taxa. Hearing in parrots is perhaps less specialized, showing characteristics shared among many other bird species.

The sense of smell is also telereceptive, and in parrots, it may be similar to that of other birds. It is likely to provide important information in some, if not all, species of parrots. Magnetoreception, the extraction of information from the Earth's magnetic field, is perhaps best regarded as telereceptive. It does not, however, provide information about distant objects. Rather it provides information about the magnetic environment in which an animal is situated, and this is used to help orient the animal at various spatial scales. Magnetoreception has not been directly demonstrated in parrots but it may well be widely distributed among birds of various orders and could play a role in guiding both long and short distance travel in parrots.

Among the intimate senses, the sense of touch is highly specialized in parrots. From one perspective touch could be considered a key sense of parrots. This is because it is crucial in the control of some of parrots' most distinctive and intriguing behaviors, especially object manipulation and climbing using the bill. Taste provides information on substances within an animal's mouth and gut and is therefore the ultimate intimate sense. Little is specifically known about taste in parrots but, as in other birds, it probably plays a crucial role in the selection of food items.

## Vision

The primary reliance of parrots on vision is easily asserted. It can be based upon casual observation of parrots completing their everyday behaviors, and it is supported by evidence that relatively large portions of parrot brains are devoted to the analysis of information from vision (Iwaniuk and Hurd 2005).

Vision is a difficult sense to investigate because there are many aspects to the information that vision provides. These include the breadth of the visible spectrum, the presence and subtlety of color vision, the accuracy of spatial resolution at different light levels, differences in the directions about the head in which vision is most acute, and

the total volume about the head from which information can be extracted at any moment.

## Spatial Resolution

Spatial resolution (the ability to resolve detail in a scene) varies markedly across animal species. Acuity is often used as a benchmark of spatial resolution in a species. However, acuity captures only one specific attribute of visual performance. It is a measure of the highest resolution possible by an eye and refers to the situation when the stimulus is a high contrast (black and white) regular pattern of stripes, viewed under light levels equivalent to bright sunlight. Acuity defines the upper limit of the detail that can be detected in a scene. It is best determined using behavioral training methods, but it can be estimated from knowledge of the focal length of the eye's optical system, and the spacing of photoreceptors, or retinal ganglion cells, in the region of the retina where they occur at their highest density.

The highest acuity recorded in any animal species is that found in eagles (Accipitriformes) and equals 0.2 min of arc (142 cycles/degree) (Table 1). This is about twice that of the best acuity recorded in young humans and five times better than the acuity of an older person (Martin 2017a). This means that an eagle could detect a given target at twice the distance at which it first becomes visible to a young human, or five times the distance of an older person. Acuity in parrots is considerably below the performance of eagles or humans. Behaviorally measured acuity was found to be about 2.6 min in Budgerigars *Melopsittacus undulatus* and 3.2 min in Bourke's Parrots *Neopsephotus bourkii* (Lind et al. 2012). Thus, spatial resolution in these parrots is 13–16 times lower than in eagles and perhaps 3 times lower than an average mature human. The spatial resolution of these parrots is, however, not exceptionally low among birds and is, for example, similar to that found in species of doves, passerines, ducks, and geese (Martin 2017a).

A useful context in which to view this difference in spatial resolution between parrots and eagles is to consider that in eagles, vision is primarily used for detecting larger objects at great distances when hunting. This is a visual task that

**Psittaciformes Sensory Systems, Table 1** The highest spatial resolution reported in a sample of bird species, and in young humans. Resolution is shown as both cycles/degree and minutes of arc. The two measures are interchangeable; older studies tended to use acuity while more recent studies prefer to express resolution in cycles per degree. In some species the highest resolution has been estimated from knowledge of the eye’s size and the spacing of retinal ganglion cells at their highest density (see Fig. 3). Behavioural measures were determined by training birds to

make discriminations which indicate the finest spatial detail that can be resolved using high contrast patterns viewed under high, day-time light levels. To compare between species simply divide their acuity values. Thus, the eagle’s spatial resolution is about 8 times higher than that of a dove, 13 times higher than a budgerigar, and 30 times higher than a sparrow. Expressed another way, an eagle should be able to detect a given object eight times further away than a dove, and 13 times further away than a budgerigar

| Species                                     | Spatial resolution<br>Cycles/degree | Acuity<br>Minutes of arc |
|---------------------------------------------|-------------------------------------|--------------------------|
| Wedge-tailed Eagle <i>Aquila audax</i>      | 142                                 | 0.2                      |
| Brown Falcon <i>Falco berigora</i>          | 73                                  | 0.4                      |
| Rock Dove <i>Columba livia</i>              | 18                                  | 1.7                      |
| Budgerigar <i>Melopsittacus undulatus</i>   | 11.7                                | 2.6                      |
| Canada Goose <i>Branta canadensis</i>       | 9.6                                 | 3.1                      |
| Bourke’s Parrot <i>Neopsephotus bourkii</i> | 9.4                                 | 3.2                      |
| Great Horned Owl <i>Bubo virginianus</i>    | 7.5                                 | 4                        |
| House Sparrow <i>Passer domesticus</i>      | 4.8                                 | 6.3                      |
| Human (young)                               | 72                                  | 0.4                      |
| Human (mature/with spectacles)              | 30                                  | 1.0                      |

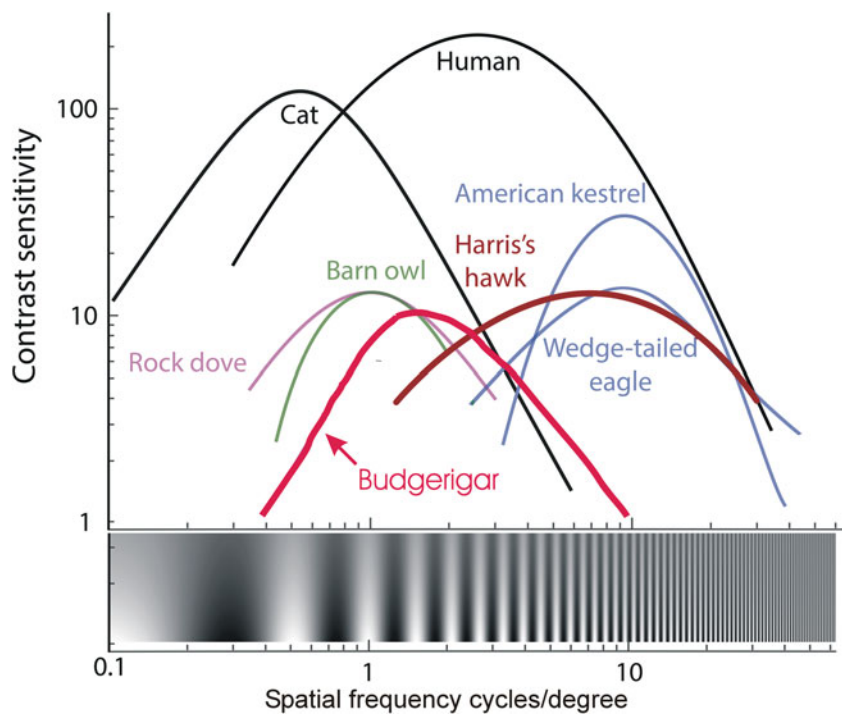
parrots are not interested in. Parrots are primarily interested in relatively large objects that are nearby and so it seems likely that their acuity matches the visual challenges of such tasks. Basically, there would be no selective pressure to evolve higher spatial resolution.

Although acuity can be readily compared across species, spatial resolution is not a fixed value. It is highly dependent on light level, the position at which it is measured within the visual field, the color, and the contrast within stimulus patterns. Natural stimuli are often of low contrast and may be colored, furthermore visual tasks are commonly undertaken at low light levels. In birds, spatial resolution has been shown to decline markedly with light level in a range of species, and this is true of parrots (Lind et al. 2012). Contrast sensitivity in Budgerigars is lower than in hawks, eagles, and falcons but similar to that of doves and owls (Fig. 2). Even under high light levels, acuity measured with colored stimulus patterns is lower than with black and white patterns (Potier et al. 2018). Although this has not been investigated in parrots this is likely to be the case in these birds. It means that color vision is best suited for discriminating between relatively large

patches at close range rather than detecting fine spatial detail at a distance.

Spatial resolution varies markedly within the field of view of an eye. Typically, in bird eyes, there is a region within the retina where photoreceptor and ganglion cell densities are highest, with density falling away from those regions. The result is that spatial resolution is much lower in the peripheral region of each eye’s field. This is certainly the case in Budgerigar eyes; retinal ganglion cell density is highest in a central region of the retina (Mitkus et al. 2014) (Fig. 3). Some Budgerigars have been shown to have a second region within their retinas in which the density of ganglion cells is elevated (Mitkus et al. 2014). These regions project backward within the field of view and the elevated acuity associated with them may play an important role in the detection of predators and conspecifics.

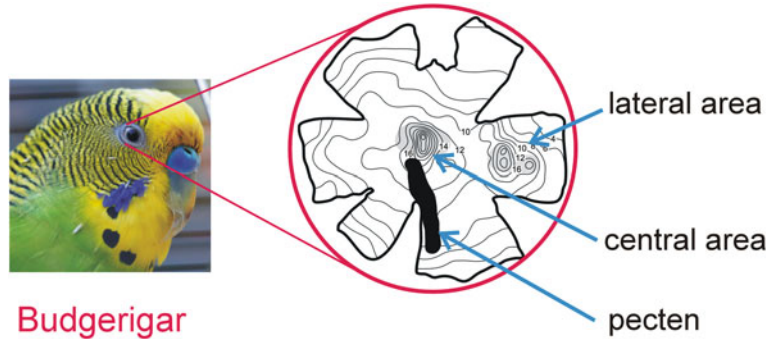
Spatial resolution has also been found to differ between the two eyes in some species of parrots. While the pattern of distributions of retinal ganglion cells in the left and right eyes are similar their densities have been found to differ significantly, with much higher densities in the left eye (Fig. 4). Such asymmetry between the eyes has



**Psittaciformes Sensory Systems, Fig. 2** Contrast sensitivity functions of birds, cats, and humans. All functions show the same general shape. However, differences in the positions and height of each of these curves indicate that each species can extract information from a different range of spatial frequencies and contrasts. Humans and cats are more sensitive to contrast than any of the birds, and they

can extract information over a broader range of spatial frequencies than any of the birds. Budgerigars can detect information only from a range of lower spatial frequencies compared with diurnal raptors, but their spatial vision is similar to that of doves and owls. (Redrawn from an original figure by Simon Potier of the Lund University Vision Group)

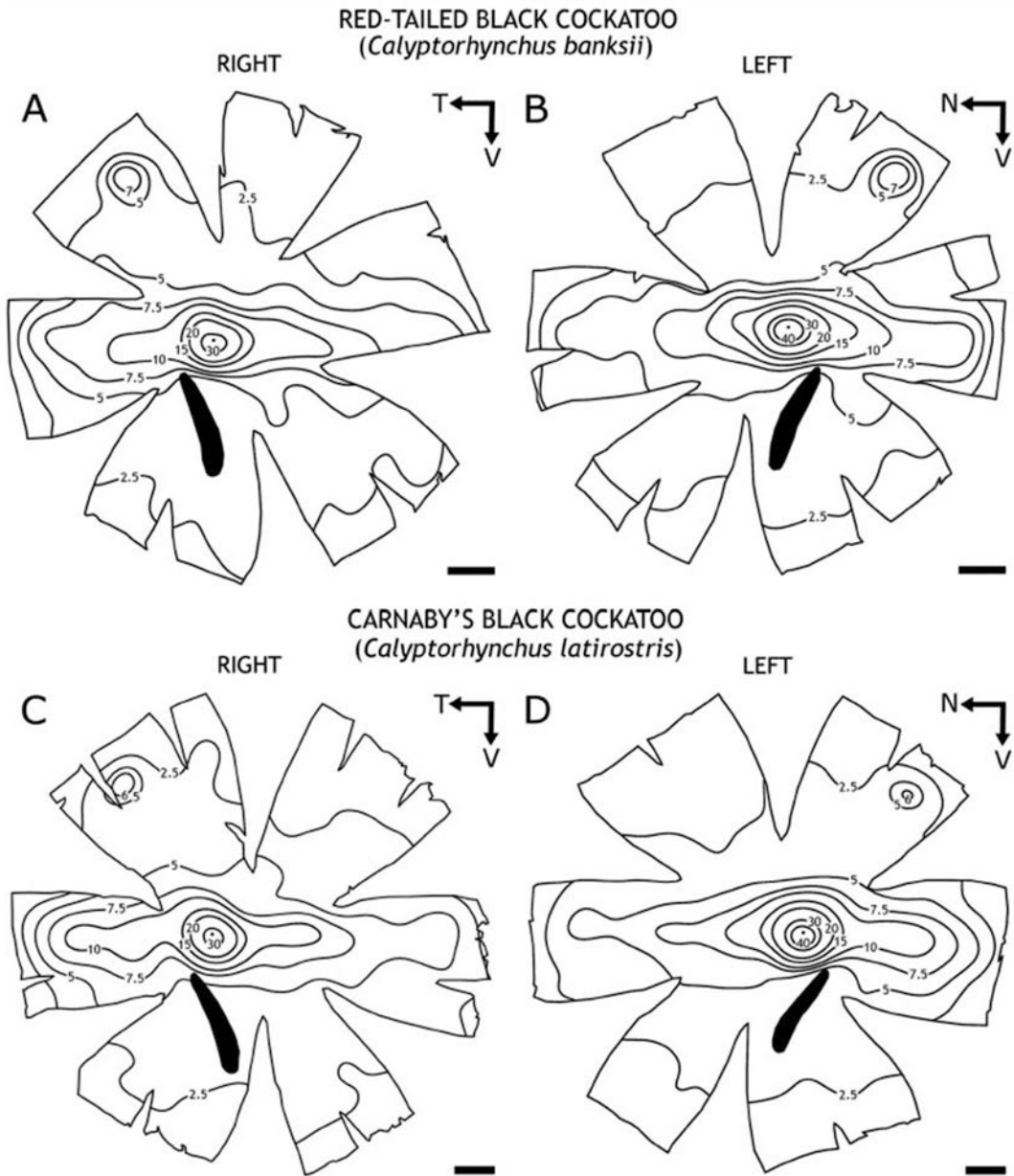
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**Psittaciformes Sensory Systems, Fig. 3** The pattern of ganglion cells' distribution in the retina of a Budgerigar. This is an isodensity contour map, and numbers indicate the density of ganglion cells in 1000s per mm<sup>2</sup>. In this Budgerigar's retina, there are two areas of high cell density. Each provides a region of enhanced visual acuity in the

bird's visual field. The central area looks out toward the viewer from the eye of the Budgerigar as shown in the photograph. The lateral area lies toward the bird's bill and looks backward within its visual field. (Redrawn from original diagrams by Mindaugas Mitkus, Lund University Vision Group and from Martin 2017a)





**Psittaciformes Sensory Systems, Fig. 4** Left-right eye asymmetry in the patterns of ganglion cell distributions in the retinas of red-tailed black Cockatoos and Carnaby's

black cockatoos. Numbers on the isodensity lines indicate the density of ganglion cells in 1000s per  $\text{mm}^2$ . (From Coimbra et al. 2014)

been found in Carnaby's Black Cockatoos *Zanda latirostris*, Red-tailed Black Cockatoos *Calyptorhynchus banksia*, Long-billed Corellas *Cacatua tenuirostris*, and Little Corella (*C. sanguinea*). This asymmetry indicates that spatial resolution in the left eye is higher than in the right eye. These

differences have been functionally linked to the preference in these birds of using the left foot to hold, and the left eye to inspect, objects. Such asymmetry between the eyes is not found in all parrot species. The same study showed no left-eye right-eye asymmetry in Galahs *Eolophus*

*roseicapillus* or Cockatiels *Nymphicus hollandicus*, species which do not show strong eye preferences (Coimbra et al. 2014).

### Color Vision and Ultraviolet

It is highly likely that parrots have color vision and can discern small differences within the spectrum. Like most birds, parrot retinas have six photoreceptor types (rods, double cones, and four types of single cones) (Martin and Osorio 2008). Rods function at lower light levels and do not provide color discrimination, double cones probably function to provide luminance information, and the four types of single cones underlie color vision. Each type of cone contains a specific photopigment and oil droplet combination (Fig. 5). Although each receptor type covers a relatively narrow part of the visible spectrum, together they give parrots vision across a broad spectrum of light frequencies. Definitive color vision tests have not been done in parrots, but the similarity of their suite of photoreceptors to those of birds in which such tests have been conducted suggests strongly that parrots can make fine discriminations. Given what is known of the physiology, ecology, and behavior of parrots it is unlikely that parrots are exceptional among birds in their fine color discrimination, but they are likely to be better than most mammals, including humans.

The visible spectrum of parrots shows a strong parallel with those of the songbirds (Passeriformes) (Hunt et al. 2009). Parrots and passerines are considered sister taxa, that is, they are more closely related to each other than they are to other birds and share a common ancestor. Both parrots and passerines are exceptional among birds, apart from gulls (Laridae, Charadriiformes) and ostriches (Struthionidae, Struthioniformes), for having a type of cone photoreceptor which has maximum sensitivity in the ultraviolet (UV) part of the spectrum. This means that parrots can potentially gain information from UV patterns in plumage, foliage, and fruits that other nonpasserine birds (and humans) are unaware of. In some parrot species, there are plumage patterns that show up in the UV part of the spectrum, patterns that human eyes cannot detect and which can

convey important information about species, sex, and possibly health (Berg and Bennett 2010).

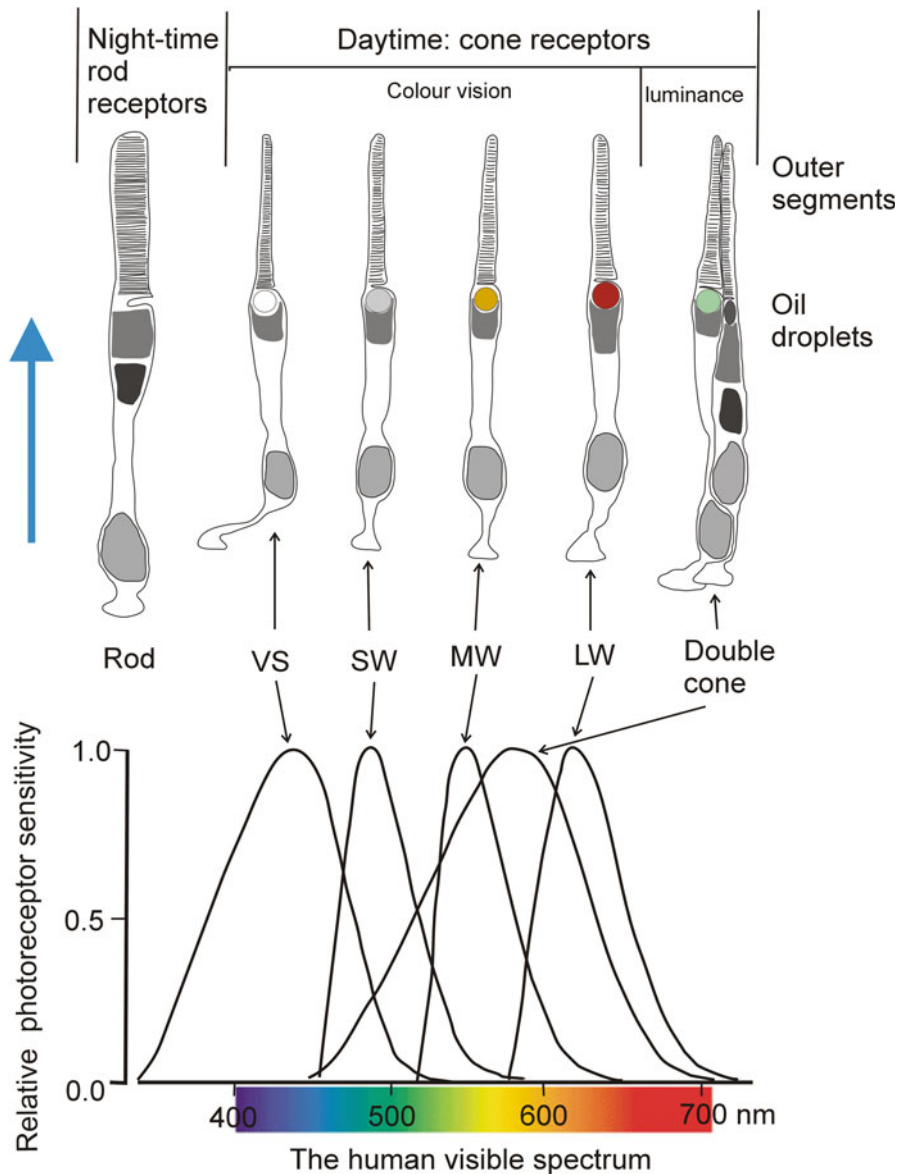
### Visual Fields

In parrots, as in all birds, the eyes are positioned on the side of the head. Each eye looks in a different direction with little overlap in their fields of view. This arrangement results in a much more comprehensive view of the world at any moment than is the case in humans. The result of the lateral placement of eyes is that birds in effect flow through their visual world; objects are seen in front, and they flow past and disappear slowly from the view behind (Martin 2017b).

Another important consequence of birds' laterally placed eyes is that the direction of best resolution lies not in front (as in ourselves), but to the sides of the head. This means that parrots have two separate areas of high resolution, to the left and to the right of the head. For parrots, as in many other birds, examination of an object in detail involves looking laterally with one eye only, not examining it with frontal vision. Parrots are frequently seen to turn their heads to peer at something laterally, apparently taking a "sideways look" at an object, but they are in fact examining it with their highest resolution vision.

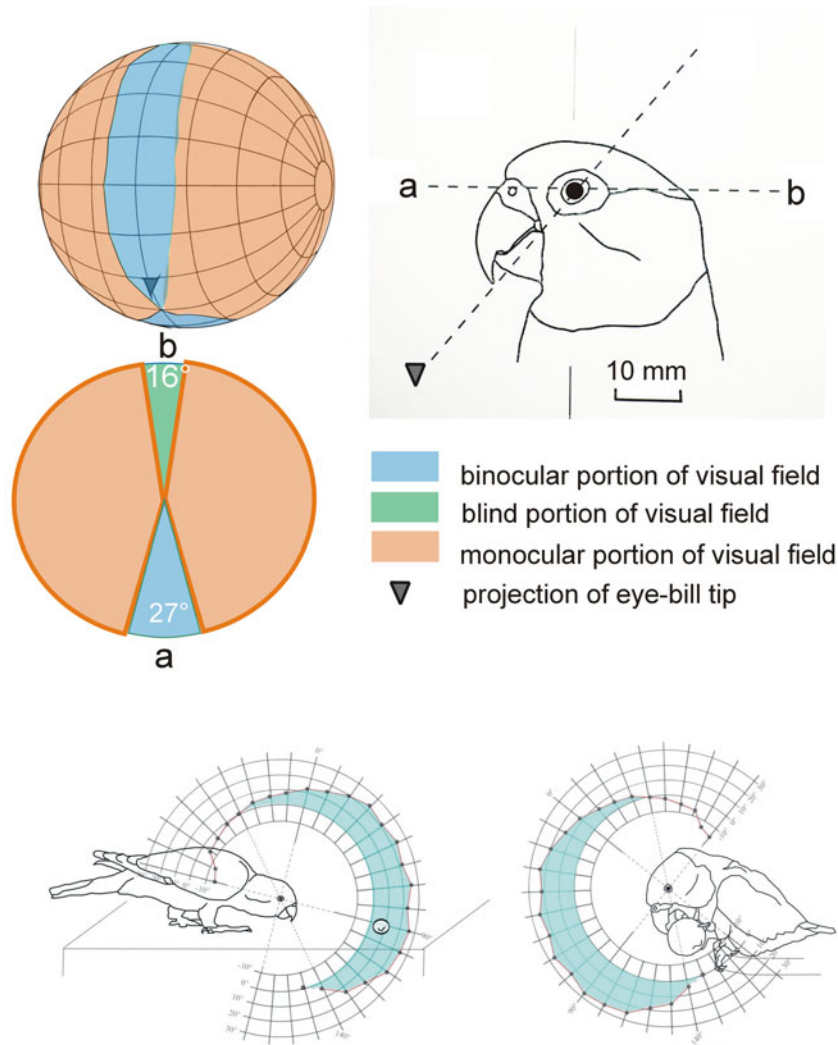
In Senegal parrots *Poicephalus senegalus*, it has been possible to show that they have a vertically long and horizontally narrow binocular field (Fig. 6) (Demery et al. 2011). Its maximum width is 27° in the horizontal plane, but it extends vertically through 180° (there is binocular vision directly above the head) and there is a blind sector only 16° wide directly behind the head. This means that only small head rotations are necessary to achieve comprehensive scanning of the scene above and behind the head. Because the eyes are positioned high on the sides of the head, a bird can only just see its bill tip.

It seems likely that the arrangement of the visual field in Senegal parrots is typical of most other parrot species. It means that parrots can be continually vigilant for approaching predators and also be aware of others in their social group, even when they are foraging or manipulating objects with their bill and feet.



**Psittaciformes Sensory Systems, Fig. 5** The different types of photoreceptors found in the eyes of parrots (and passerines). The sensitivity in the spectrum of each cone type is shown in the lower part of the diagram. Parrots have four types of single cones whereas most mammals, including humans, have three. The lower part of the diagram indicates that the visible spectrum in parrots is broader than in humans. This is due to the presence in parrots of a cone type which has sensitivity that extends into the ultra-violet. However, in both humans and parrots, visual sensitivity is similar at the red end of the spectrum. The rod

receptors in parrots, and in most animal species, have a very similar sensitivity centered upon the green part of the visible spectrum. The four types of single cones underlie color vision and are each sensitive to a narrow part of the spectrum. The double cones, which underlie the detection of luminance (brightness), have a broad range of sensitivity extending from the blue to red portions of the spectrum. (Based upon illustrations by Peter Olsson (Lund University Vision Group) and Daniel Osorio (University of Sussex, UK) and from Martin 2017a)



**Psittaciformes Sensory Systems, Fig. 6** The visual field of a Senegal parrot. The top left diagram shows the field as seen projected onto the surface of a sphere surrounding the bird's head. The lower diagram shows a horizontal section through the visual field along the line a–b indicated in the sketch of the bird's head. The projection from the eye to the bill-tip is depicted. The diagram indicates that parrots have a narrow and vertically long binocular field and a very extensive monocular field to each side of the head. The extent of the binocular field in the vertical (median sagittal) plane of the head is also depicted in the two lower diagrams. On the lower left, a

bird is shown walking across a flat surface approaching an object. Even with the head lowered, so that the object lies in the broadest section of the binocular field, the birds can see almost the whole of the sphere surrounding its head, just a small rotation of the head is necessary to scan the world behind. When holding an object in the bill, a parrot – shown perching in the lower right diagram – can still see extensively above and behind, but it can only just see the object held in the bill. Also see Fig. 1 showing a photograph of a parrot manipulating an object. (Redrawn from illustrations in Demery et al. 2011)

Parrots' ability to only just see the tip of their bill is quite different to the situation in many other birds. In many species, the bill projects more or less centrally in the region of binocular vision

(Martin 2017b). This arrangement is used to direct the bill with high accuracy toward a target and to time its arrival there with precision. This arrangement is the key to accurate pecking and lunging

with the bill and is also used for catching prey with the feet which are brought up into the binocular field when pouncing on prey (e.g., in raptors). Parrots do not feed by pecking or lunging at items guided by vision. Like other birds which have near comprehensive vision about their heads, such as some shorebirds and ibises (Martin 2017b), the foraging of parrots is aided by touch sensitivity at their bill tips (see section on “Touch” sensitivity below). Having near comprehensive vision may also be important in the flock behaviors of parrots, allowing accurate spacing and coordinated flight movements.

### Temporal Resolution

Temporal resolution of vision is usually investigated by determining the flicker fusion frequency (FFF). This is the frequency of a flashing light, at which the eye can no longer distinguish a flickering light from a constant light of equal intensity. It has been determined both behaviorally and physiologically. High temporal resolution, well in excess of that of humans, has been described in some species of small songbirds. Such high FFFs have been interpreted as associated with the need to detect detail when moving rapidly in complex environments. Like spatial resolution, temporal resolution is a function of light levels with highest FFFs occurring at higher, daytime, light levels. The flicker fusion frequency of Budgerigars has not been found to equal those of small songbirds. At typical daytime light levels, the FFF of Budgerigars is similar to those of humans, with a flicker fusion frequency of 82 Hz (Bostrom et al. 2017). Based upon this it has been concluded that Budgerigars, and possibly other parrot species, are unable to detect the flicker of artificial lights that use fluorescent tubes or lamps with incandescent filaments.

### Hearing

Hearing has been investigated in detail in some parrot species and most extensively in Budgerigars (Dooling et al. 2000). The frequency range of hearing and the hearing sensitivity of parrots is similar to those of other birds, there being only relatively small differences in hearing across a wide range of bird species (Dooling et al. 2000;

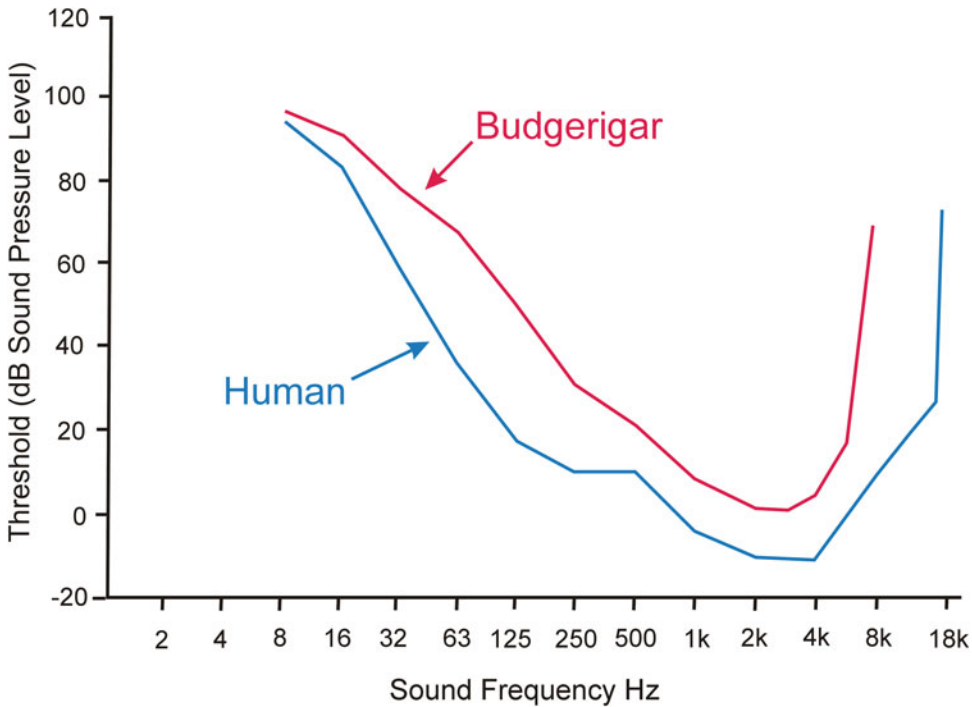
Fay 1992). The frequency range of parrot hearing is narrower than that of humans and it seems that the hearing of nearly all birds sits within the overall envelope of the hearing of young humans (Fig. 7). This indicates that whatever sounds a parrot can hear, a young human will be able to detect. Parrots can hear sounds within a frequency range of about 200 Hz–8 kHz (Heffner et al. 2016), this compares with the young human frequency range of 20 Hz–20 kHz. In both humans and parrots, the maximum sensitivity to sounds occurs in the 1–4 kHz range, which is roughly the frequency range of the notes on the upper half of a piano keyboard. The hearing range of humans narrows with age, with hearing loss primarily in the higher frequency ranges. This suggests that the frequency range of hearing in aging humans may become more similar to that of a parrot. Whether the longer lived parrots also suffer hearing loss with age is not known.

### Sound Location

The ability to locate sounds in both direction and distance (sound range) is important in determining just how useful sound can be as a means of gaining information from the remote environment. While the simple detection of a sound may be useful, knowing the direction from which it came and how far away the source is adds considerably to the utility of that sound information. Evidence shows that in most birds these abilities are rather poor, especially compared with humans who can determine the direction of a nearby sound source, to within one or two degrees (Klump 2000). Humans are also able to learn to determine the range of nearby familiar sounds within a few meters, but this is a learned cognitive ability and requires repeated exposure to similar sounds under a range of acoustic conditions.

The poor sound location found in the majority of birds is attributable primarily to physics. Ear openings in parrots are hidden by a small group of feathers (ear coverts) and are situated just behind and below the eyes. Because of the relatively narrow heads of parrots, the ear openings are separated laterally by only a small distance. The consequence of this is that there are only very small differences in the timing and intensity of





**Psittaciformes Sensory Systems, Fig. 7** Audiograms of a young human and a Budgerigar. Hearing sensitivity in both species shows the typical U-shape of audiograms found in most animal species. Sensitivity falls gradually as sound frequency decreases but there is a more rapid decrease in sensitivity as sound frequency increases. Both

species are most sensitive to sounds between 2 and 4 kHz. The audiogram of the parrot sits wholly within the human audiogram indicating that all sounds that a young human can hear can also be heard by the Budgerigar, and that there are sounds which humans can hear that parrots are unable to detect. (Redrawn from Heffner et al. 2016)

sounds arriving at each ear. It is these differences that are used to determine sound direction in the horizontal plane. The larger these differences, the more accurately sound can theoretically be located. It is the large solid head, widely separated ears, and the elaborations of the outer ears that give humans the advantage over parrots and other birds when trying to locate a sound.

Owls (Strigiformes) are the only group of birds which can match human sound localization accuracy, and they use this ability to locate hidden prey from a static location (Knudsen and Konishi 1979). This ability is primarily attributed to the elaborate outer ear structures that among birds are unique to owls. It seems that most birds, including parrots, would receive no selective advantage from such high accuracy of sound localization or sound ranging. This is because parrots do not use sound for prey location and because they are also highly mobile. Parrots can move rapidly in the

general direction of a sound that they find interesting and home in on it through successive approximations. There is no need to have a highly accurate fix upon the sound source before deciding to investigate it.

There have not, however, been any direct investigations of sound location or ranging in parrots, but it seems unlikely that they will have accuracy that is higher than in passerines. For example, Common Starlings *Sturnus vulgaris* can locate sound direction to within only 20 degrees (Feinkohl and Klump 2013), and Common Chaffinches *Fringilla coelebs*, seem to range sounds only into broad near (closer than 40 m), far (further than 80 m), and intermediate distance categories. The flightless nocturnal parrot Kākāpō *Strigops habroptila* uses sound to locate mates at long distances, and then approach them slowly on foot. Whether Kākāpō are able to determine the direction and

range of these calls with high accuracy is not known, but it is worth noting that the birds tend to move around their home ranges using pre-defined trackways, and this may obviate the need for accurate location and range.

### Smell

The sense of smell is often overlooked in birds. Like vision and hearing, smell is a telereceptive sense providing information about properties of the environment that are remote from the animal. There is increasing evidence that smell plays a vital role in the behavior of many bird species, especially in the location of potential food sources. Well-studied examples include petrels *Procellariidae*, Turkey vultures *Cathartes aura*, Oilbirds *Steatornis caripensis*, and kiwi *Apterygidae* (Martin 2017a). It is now becoming clear that smell is also used by a wide range of birds to mediate social interactions based primarily upon secretions from the uropygial gland. Species in which this has been demonstrated include chickens *Gallus gallus*, auks *Alcidae*, some passerines, and Budgerigars (Zhang et al. 2010).

That smell may function in the location of food sources has been demonstrated in some species of passerines (Amo et al. 2013). In view of the relatively close phylogenetic relationship between passerines and parrots, it is possible that the sense of smell could play an equally important role in parrots. Many parrot species rely on locating ephemeral food sources, such as fruiting trees, which can be highly variable in time and space, and the ability to detect food patches using smell would bring clear advantages. However, experimental investigations of the role of smell in food location in parrots do not seem to have been conducted. One intriguing example of a parrot using smell in the location of food comes from the observation of a Kākāpō which was shown able to use odor cues to locate hidden food (Hagelin 2004). Whether using smell in this way is part of Kākāpō natural behavior is not clear, but the fact that they can latch onto and exploit odor cues does suggest that smell is important to these birds, and possibly to other parrots.

### Taste

The taste system of birds can be viewed as a group of nutrient sensors which have evolved to evaluate the quality and nutritional content of foods, primarily at the point of ingestion, but also at various points within the gut (Berkhoudt 1985). Nothing is known specifically about taste in parrots, but it is probable that, like other birds, parrots use taste information to assess each item of potential food taken into the mouth cavity. Thus, taste functions as a sampling or screening process that detects the presence of specific groups of chemical compounds. Much of what is known about taste in birds comes from studies of domesticated breeds, notably chickens, ducks, and turkeys (Berkhoudt 1985).

The receptors of taste in birds are of relatively few types, but they can be numerous and occur in different concentrations in different locations within the body. The distribution of taste receptors in the mouths of birds follows the ingestion pathway. This allows items taken into the mouth to be rapidly screened for a range of chemical properties before entering the gastrointestinal tract.

In all vertebrates, taste signals are generated in taste buds. These are flask-shaped pits embedded mainly within the skin of the tongue but also in other structures within the mouth. Each taste bud contains groups of receptor types that detect the presence of specific chemical compounds. Like other sensory receptors, taste receptors have a long evolutionary history and show basic uniformity of structure and function across diverse animal groups. Taste receptors in the gut are probably involved in many aspects of sensing foods as they are digested and may trigger vomiting following the ingestion of a noxious substance.

In all birds so far investigated, taste receptors occur on the tongue, particularly toward the back, but they do not occur widely over the upper surface of the tongue, as is typical in mammals. It is highly likely that a similar distribution of taste receptors in the mouth cavity occurs in parrots (Berkhoudt 1985).

It seems likely that birds have at least seven distinct tastes (Martin 2017a). Five tastes function primarily in driving appetites for particular nutrients, and two tastes function primarily to provide

warning signals about items that are likely to be detrimental to health. The well-established “appetite tastes” of birds are sweet, umami (or amino acids), and salt, and these seem to drive the acquisition of foodstuffs. Less well-established appetite tastes are calcium and fat. Calcium may function particularly during breeding when calcium intake in females may need to increase to ensure the development of eggshells. Evidence for a specific fat taste, or fat detector mechanism, in birds is not well established but may be a feature of bird species. Bitter and sour receptors are regarded as providing “warning tastes,” which indicate substances that are likely to be harmful and should be rejected before or post ingestion.

### Touch

The configuration of the visual field in parrots precludes them from guiding the bill with high accuracy using visual information (see section on “Visual Fields”). Parrots are, however, noted for their manipulation of objects using their bill and for their use of the bill as a third limb when climbing. This control of the bill relies upon the sense of touch, specifically from a specialized collection of touch receptors positioned within the keratin of the rhamphotheca in the curved tip of the upper bill.

This collection of touch receptors is known as a “bill-tip organ” and is one of three types of bill-tip organs that occur in birds (du Toit et al. 2020). In ibises (Threskiornithidae), shorebirds (Scolopacidae), and kiwi (Apterygidae), the bill-tip organ consists of groups of touch/mechanoreceptors (Herbst corpuscles) that are embedded within densely clustered pits in the bone at the tip of the bill and are beneath the soft keratin that covers the bill tip. In ducks and geese (Anseriformes), a different type of bill-tip organ also employs Herbst corpuscles but they are grouped in “touch papillae” which extend through the hardened rhamphotheca which occurs around the bill tips in these birds (du Toit et al. 2020). Both of these types of bill-tip organs function primarily in the detection of food items hidden in leaf litter and soil, or in water-filled substrates, such as mud and sand.

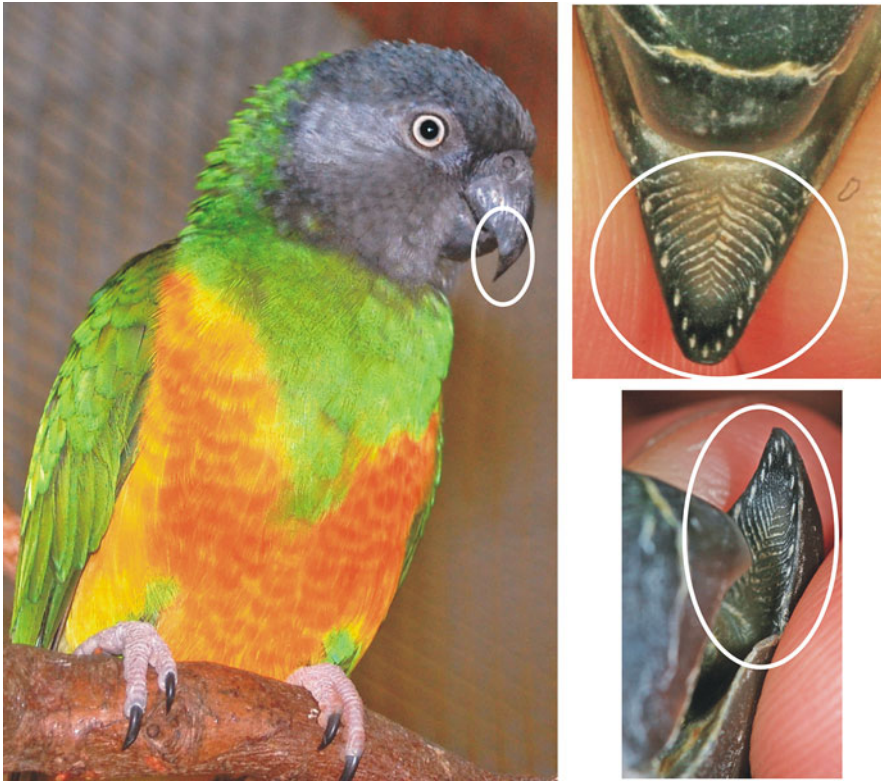
In the bill-tip organs of parrots, the mechanoreceptors are arranged in discrete clusters around

the edge of the rhamphotheca of the upper bill. The parrots’ bill-tip organ is not used for the detection of hidden food items, but rather to guide the manipulation of food items. The bill-tip organ of parrots was first described in 1896 (Goujon 1896) but has only recently received further investigation, and is yet to be fully understood (Demery et al. 2011).

Figure 8 shows the bill-tip organ in a Senegal parrot. The touch receptors are clusters of primarily Herbst Corpuscles housed in pits in the keratin of the bill. The clusters are arranged symmetrically in seven pairs situated just inside the edges of the bill. There is a further single cluster of touch receptors at the bill tip. This arrangement gives a parrot detailed touch information about objects grasped between the bill tips. This information allows a parrot to manipulate and position an object without seeing it. The bill-tip organ provides information on the position, mechanical and surface properties of the grasped object. Many parrots are primarily seed predators and have powerful bills that enable them to feed on large hard-shelled seeds. For example, Great Green Macaws *Ara ambiguus* are highly dependent upon the seeds of Mountain almonds *Dipteryx oleifera*, which are large (60–80 mm × 40 mm) and very hard. Opening the seed case depends upon accurate positioning of the seeds in the bill, and this must be achieved using touch sensitivity since once in the mouth the seed cannot be seen.

This ability to open seed cases and examine food items using their bill-tip organ probably enables parrots to exploit food sources unavailable to other bird species. It is also possible that touch sensitivity plays a role in the transfer of regurgitated food from males to females during the incubating and brooding periods.

Another important function of the bill-tip organ in parrots may be that it provides touch information which allows parrots to use their hooked bill as a “third limb” when climbing about. Many parrots nest inside deep cavities and will use their bill to climb in and out of these cavities as well as for maneuvering around other environments such as within branches. Touch information from the bill-tip probably allows a parrot to assess the mechanical



**Psittaciformes Sensory Systems, Fig. 8** The bill-tip organ in a Senegal parrot. The touch-sensitive receptors are arranged in clearly visible discrete clusters along the

edges of the upper bill within the curved section of its tip. (From Martin 2017a)

characteristics of a grasped object, and thus allows the bird to confidently rely on what it is grasping when climbing.

As in other birds (Gottschaldt 1985), touch receptors (Herbst and Grandry corpuscles) in parrots are likely to be found distributed across much of the body surface, and around skeletal joints. They probably function to provide information on the position of limbs and feathers, as well as information about objects in contact with the body surface. However, the distribution of touch receptors across the body has not been investigated in detail in parrots.

### Magnetoreception

Magnetoreception is the ability to detect properties of a magnetic field. Magnetic fields vary in both strength and direction with respect to the

object that generates the field. The magnetic field of the Earth (the geomagnetic field) varies continuously and variations in strength and direction are potentially a rich source of information about position on the Earth and direction toward other positions. A large body of research indicates that birds are among the animal groups that can detect the geomagnetic field and potentially use it to determine position and guide travel. However, the actual mechanisms employed by birds to detect magnetic fields remain elusive.

It seems possible that in birds more than one mechanism is involved, providing magnetic information separately on direction and strength. The mechanisms also appear to be tuned to detect magnetic fields of the strengths that occur at the Earth's surface. One detection system may be

based in the eyes and provides information on field direction; the other mechanism is associated with the nostrils and the nerves that lead from them and provides information on field strength (Beason and Wiltschko 2015; Munro et al. 2014; Wiltschko and Wiltschko 2013).

Although the sample is small, the range of bird species in which detection of the geomagnetic field has been shown to exist is drawn from a wide taxonomic sample and includes pigeons, chickens, and songbirds. It has also been shown that detection of these fields can influence the orientation behavior of these birds. This suggests that magnetoreception may be widely distributed across bird species and may provide a source of information used to guide movements at different spatial scales. It is possible, therefore, that parrots could be counted among the species that can use geomagnetic information, but experimental evidence is lacking. However, some parrot species migrate and many species range over large areas (Collar 1997). To do this, individuals need to know where they are and the direction toward where they want to go. Magnetoreception may provide a source of information that helps parrots to do this, but definitive evidence is lacking, although it has not been sought.

## Cross-References

- ▶ [Accipitriformes Sensory Systems](#)
- ▶ [Bear Sensory Systems](#)
- ▶ [Cephalopod Sensory Systems](#)
- ▶ [Cetacean Sensory Systems](#)
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- ▶ [Psittacine Cognition](#)
- ▶ [Rodentia Sensory Systems](#)
- ▶ [Visual Recognition in Birds](#)

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## Psittacine Cognition

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## Introduction

The parrots of the world have always delighted humans for their stunning plumage, their playful nature, and their ability to mimic human speech and form friendships with people. Importantly, many, not all of them, belong to a group of birds with the largest brain to body weight ratio, and some are even on a par with primates. Brain weight or size is measured relative to body weight or size.

The order of Psittaciformes is the third largest group of birds. According to the International Ornithology List of Birds (Gill et al. 2021), the order Psittaciformes consists of 398 extant species belonging to 87 genera, and within it, one might distinguish three super families: the Psittacidae (“true” parrots), about 350 species worldwide, 40 of which are in Australia; the Cacatuidae (cockatoos), 22 species (14 within Australia); and the Strigopidae (New Zealand parrots) with five species, all endemic to New Zealand. Neotropical (South and Central American) species include the subfamily of Neotropical Arinae, which includes macaws, aras, and Amazon species. Further, across the entire range of southern continents, there are a large number of diverse parrots, the true parrots, and finally the groups of parakeets, lorikeets, and lories. In a recent resurgence in systematic studies of parrots, Joseph and colleagues (2012) proposed a revised nomenclature and classification for family-group taxa of parrots, and they have

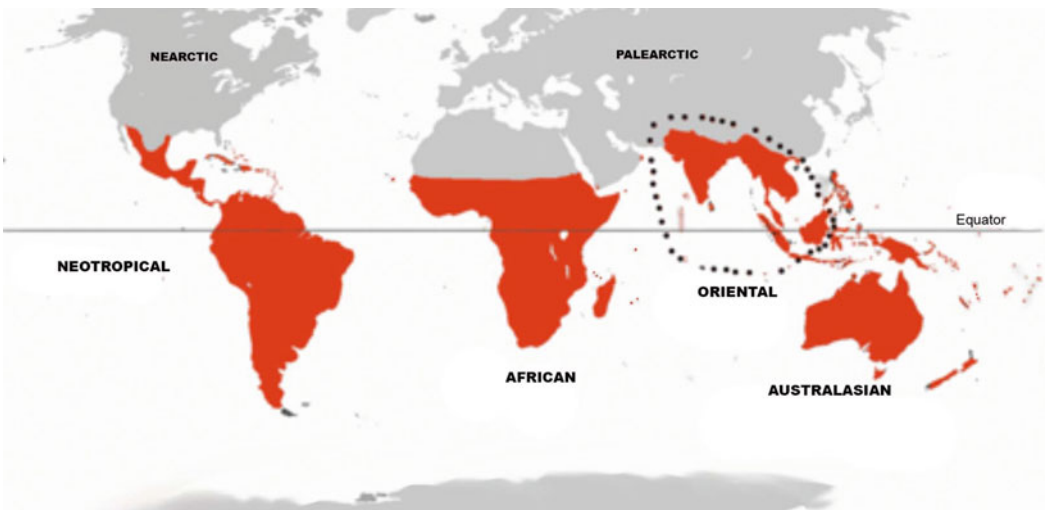
advocated that all the various groups be subdivided into three superfamilies: Strigopoidea (New Zealand) Cacaoidea (all cockatoos), and Psittacoidea (for all remaining parrots).

Parrots are species of the southern hemisphere, or they are equatorial, meaning that most of the equatorial species extend 23.5° latitude to the north (the Tropic of Cancer) and 23.5° south (to the Tropic of Capricorn) which, however, does not imply that parrots are restricted to tropical or subtropical regions or to forests. They also live in the temperate zones of the southern continents, and some, such as the ringneck, *Barnardius zonarius*, and princess, *Polytelis alexandrae*, parrots of Australia or the burrowing conure, *Cyanoliseus patagonus*, of southeastern Patagonia, are even desert dwellers, but only two psittacines are cold-climate specialists – one is the austral or emerald parakeet, *Enicognathus ferrugineus*, of southern Patagonia (South America) and the other the kea, *Nestor notabilis*, of New Zealand, the only mountain parrot in the world (Fig. 1).

In 2008, a molecular study was published in support of a Gondwanan origin of parrots during the Cretaceous Period (Wright et al. 2008). Gondwana is the name of the continent that contained Africa, Australia, Antarctica, and South America. Some psittacine species, such as the Australian

cockatoos, are thought to have an evolutionary history of 95 mya (Wright et al. 2008), of importance in so far as these time frames go together with a number of considerable climate changes and ice ages, eventually leading to a drying out of the Australian continent. Over millions of years, these changes demanded substantial adaptations from flora and fauna.

The 22 species of cockatoos are split into the black cockatoos (*Calyptorhynchus* spp.) and the white cockatoos (*Cacatua* spp.). The species of cockatoos outside Australia are distributed on island populations northeast of Australia (Papua New Guinea and the Solomon Islands) and also north/northwest (indigenous to Tanimbar Island), such as the Goffin cockatoo or, more appropriately called, the Tanimbar corella (*Cacatua goffiniana*). Today, many species of parrot are on the endangered list either because of ongoing and large-scale habitat destruction (largely of forests) or because such species are being poached and traded as valuable export items. The result has been an accelerating slide toward extinction. Indeed, almost half of all parrots are listed on the list of endangered species, of which nearly 100 species are either critically endangered or in the highly endangered category (IUCN Red List of Threatened Species) – as compared to 13% of



**Psittacine Cognition, Fig. 1** Distribution of parrots throughout the world (marked red). The areas include tropical, subtropical, temperate, desert, and mountain

climates. The “oriental” bird region is delimited in the north by the mountain range of the Himalayas

birds worldwide. This is despite their long evolutionary history, their adaptability, and the discovery of the relatively large brains of many families within this order.

### Definition/Identity

The term “psittacine” is an umbrella term for all birds that form the order Psittaciformes. The name for the order “psittacine” is derived from psittacine or, more correctly, psittacofulvin. This is a red feather pigment unique to parrots worldwide, responsible for the bright red, orange, and yellow colors, and is produced in the parrots’ bodies. Puzzlingly, these unique psittacofulvin pigments occupy an essentially identical red/orange/yellow region of color space as the carotenoid pigments found in the passerines (Passeriformes). Parrots have ample concentrations of carotenoids in their blood to color their feathers (McGraw and Nogare 2005) but still evolved this distinct alternative color palette into the long wavelength regions of color space (Stoddard and Prum 2011). Parrots from any group use the same set of five lipochromes to color their feathers in reds (McGraw and Nogare 2005). They can also produce yellow that can fluoresce under UV light.

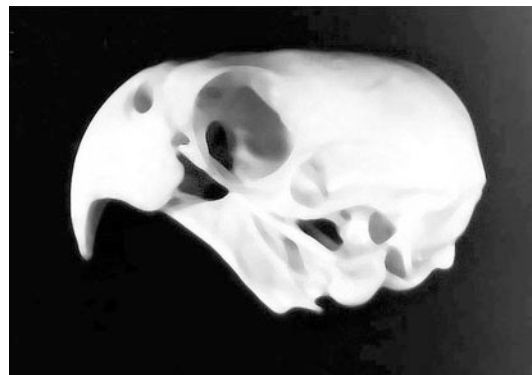
Feathers with high levels of psittacofulvin are said to resist feather-degrading bacilli. Indeed, in certain species, plumage patch sizes have been linked to health and positive social attributes, but such studies have usually been confined to males. Many psittacines, especially cockatoos, exhibit little or no sexual dimorphism in the visual spectrum, while other parrots are vividly colored, and some are multicolored. Notable in parrots is the lack of sexual dimorphism in plumage. Many are monomorphic, i.e., males and females have the same or very similar plumage. The eclectus parrot, *Eclectus roratus*, shows among the most extreme sexual dimorphism in males, and there is a reversal of the more common dimorphism in male/female coloration: the male has plain green plumage, and the eclectus female has stunning and conspicuous reds and blue.

### Physical Features and Habits of Relevance to Cognition

The finding that parrots, especially macaws (South America/Neotropical), cockatoos (Australia/Oceania), and keas (New Zealand), have extra-large brains relative to body size is now an established fact. Some corvids, often hailed as the “most intelligent birds worldwide,” are just on par with these psittacine species. These factors are based on a raft of biological adaptations to specific and demanding environments.

Although there are substantial size differences between species and families, there are physical commonalities. Even for the least uninitiated in bird identification, it is easy to identify a parrot as distinct from songbirds, fowl, or waterbirds, and this is due to the hooked beak (Fig. 2). One hastens to add that especially the similarities in the feeding apparatus among parrots are usually the result of convergent evolution. They have evolved in unrelated species as adaptations to particular environmental demands (Homberger 1980). The beak is the tool with which parrots and cockatoos can rip, turn, chew, bite, and excavate. Many of the psittacines use their feet for grasping, manipulating, or holding of food.

The beak’s upper mandible (maxilla) is curved and extends over the lower mandible. Its design is thought to point to a common ancestor adapted for forest living. The shape of the beak is already well pronounced in hatchlings (Fig. 3).



**Psittacine Cognition, Fig. 2** The psittacine beak

The largest psittacines, such as macaws and the large cockatoos, have very robust heads with high and massive beaks, while some species, such as the South American slender-billed parakeet, *Enicognathus leptorhynchus*; the Australian long-billed corella, *Cacatua tenuirostris*; and New Zealand's keas, *Nestor notabilis*, have long and slender beaks, suggesting that they can use the

upper mandible as an excavation or ripping tool (Fig. 4).

Psittacines are exceptional for their high levels of exploratory behavior and manipulatory abilities. These manipulative abilities are made possible by distinctive morphological adaptations of the feet, bill, and tongue. The zygodactyl feet of psittacines are distinct from the anisodactyl feet of songbirds (see ► “[Passerine Cognition](#)” entry) in that the second and third toes point forward and oppose the first and fourth toes which point caudally. Such feet are not only useful for a firm grip during roosting. In parrots, the feet are used for grasping and manipulating items.

Beak shape, tongue morphology, musculature of the tongue and jaw apparatus, and skull morphology have been the subject of many investigations because by doing so one can study feeding adaptations as well as vocal performance and signal diversity. The upper jaw and skull evolution in parrots and cockatoos are quite complex (Homberger 1980, Bright et al. 2019). The bill tip organ further provides tactile information and acts like an additional mechanism to assess the quality of food or the nature of objects (Demery et al. 2011).

The tongue of parrots is also unique to parrots, very fleshy and equipped with an internal bone that gives the tongue maneuverability for manipulating food. But this may not be its only function. The tongue, its extrinsic musculature, and the hyoid apparatus generally are referred to as the lingual apparatus, and it has been investigated in



**Psittacine Cognition, Fig. 3** Eastern rosella hatchling 2 days old. (Photo credit: G. Kaplan)



**Psittacine Cognition, Fig. 4** Long upper mandibles (maxilla). Left: Chile's slender-billed parakeet, *Enicognathus leptorhynchus*; right: the Australian long-billed corella, *Cacatua tenuirostris*. In addition to the

specialized beak structures, note that all cockatoos have crests, some far more elaborate and even colorful, used extensively in communication. Insert: New Zealand's kea, *Nestor notabilis*. (Photo credit: G. Kaplan)



detail in African gray parrots, *Psittacus erithacus* (Homberger 1986), and in the orange-winged amazon parrot, *Amazona amazonica* (Nottebohm 1976). Nottebohm (1976) suggested that parrots may use their tongues to modify the shape and thus the resonant properties of the vocal tract. Tongue movements observed in parrot vocalizations independently modulate formant characteristics from the vocal source. This may be an important factor in the production of their natural vocalizations (Beckers et al. 2004) as well as in their remarkable ability to articulate and mimic human words and sounds which they can do with surprising accuracy (see section “Vocal behavior” below).

## Social and Environmental Conditions

For many years, it has been asked what circumstances drove the evolution of this particular order, and of specific families within this order, to evolve into the large-brained and long-lived species as we know them today. Research had uncovered that brain size was related to a confluence of various environmental and social circumstances. Many psittacine species, especially conures, macaws or cockatoos, and also many other parrots, exhibit a high degree of fission-fusion behavior. A fission-fusion society indicates a fluidity of size and composition, i.e., the social group may vary in size and membership throughout a season. Several family groups may merge into one group (fusion) when roosting together or at times of external threats (stationary or in the air), or they may separate (fission) when foraging in small groups during the day or splitting into pairs for exploratory flights or at breeding time. Further, pairs tend to form long-term pair bonds (Kaplan 2019; Torres-Ortiz et al. 2019), and their offspring have substantial adult guidance for periods well exceeding that of most songbirds and other avian species (Kaplan 2019). Apart from developmental and experiential advantages of a slow maturation process, they also have the advantage of being able to socialize with same-age and older members of their species and also unrelated individuals of a larger flock. Further, as

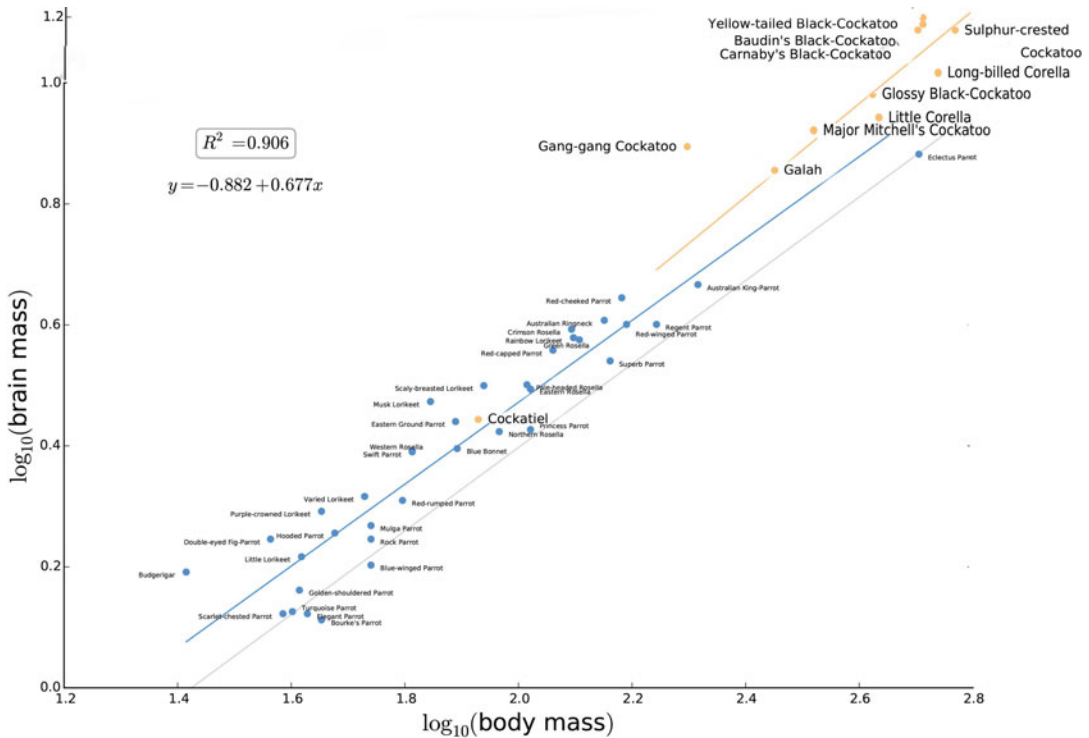
parrots are largely forest species relying on fruits, nuts, and/or seeds, they (a) require a good memory for geographical location of available foods and (b) understand seasonal timetables for foods ready to harvest. Long-distance flying and searching while keeping family members safe and retaining contact with them further require communication often over long distances. It is generally agreed that the foraging habits of parrots are cognitively demanding and given their complex social system (a construct most likely to have evolved because of their foraging habits) in turn suggest the need for a complex communication system (Torres-Ortiz 2019), which in turn may signify social cooperation and supportive traits of sharing knowledge of new food sources.

These social and environmental conditions combined are thought to have primarily contributed to larger brain sizes (Bradbury and Balsby 2016). Subsequently, researchers who wanted to learn more about the cognitive abilities of parrots and cockatoos tended to choose species in which all these characteristics described here are present (long-lived, complex social system; slow maturational development) such as keas, peach- and orange-fronted conures, or Amazons as well as African gray parrots and Goffin cockatoos (see laboratory studies below). Sol and colleagues (2007) concluded in their study on mortality versus brains that the larger the brain, the lower was the mortality rate. Hence, they appeared to have established in their study a clear and identifiable benefit in having a large brain.

## The Psittacine Brain

The reason for a predilection with brain size in relation to cognition was stated bluntly in 2005: “advanced cognition can only occur where there is sufficient neural tissue to perform complex cognitive tasks” (Iwaniuk et al. 2005). Hence, measurements of parrot brains have been extensive. The most common and relatively simple one is to compare relative brain weight with relative body weight. It can reveal unusually large brains compared to the mean of avian species. For instance, the budgerigar is the smallest of all





**Psittacine Cognition, Fig. 5** Mean weight/mass of the brain versus relative body mass in Australian parrots and some cockatoos. The gray line: mean of songbirds; blue, mean of parrots; yellow: mean of cockatoos. The mean of

relative brain versus body size is substantially higher than that of songbirds generally. Species with larger brains within their own group are located above the line (Source: Franklin et al. (2014) and Kaplan (2015))

psittacine species, and the kea is medium size, but the brain size relative to body size of both these species much exceeds the mean of psittacines and is well above the mean for songbirds generally, while the brain of the large eclectus parrot is exceptionally small relative to body size (Franklin et al. 2014).

Among Australian psittacine species, such measures offer a few surprises. Budgerigars (the smallest) and palm cockatoos (the largest) stand out as having exceptionally large brain to body weight ratios, while that of the eclectus parrot is exceptionally small (Fig. 5).

Next came the measurement of the size of the telencephalon (forebrain) against the total brain volume. It generally covaries with the size of the brain, but the percentage of the brain given over to those parts of the brain for cognitive tasks may show variations by as much as ten percent and

even more just within the superfamily of the psittacines.

Measurements of neural density particularly in the forebrain (once called the telencephalon, now the pallium) were also conducted using an isotopic refractometer. The surprising result was that some parrots in similar weight ranges as primates have the same or higher number of neurons (Olkowicz et al. 2016) (Fig. 6 and Table 1).

Gutierrez-Ibanez et al. (2018) argued that evolution of complex cognitive abilities would have required (a) the enlargement of some brain areas and (b) the establishment on additional brain circuits. They found that, indeed, parrots have evolved brain circuits (telencephalic-midbrain-cerebellar circuit) similar to those in primates, which may be of some importance in the way information is processed (Gutierrez-Ibanez et al. 2018).



**Psittacine Cognition, Fig. 6** Position of the eyes. Left: male red-tailed black cockatoo, *Calyptorhynchus banksii* (family: Cacatuidae) – direct upward viewing is blocked by the substantial number of crest feathers, but of course, they can see overhead by tilting the head. Centre: king parrot, *Alisterus scapularis* (family: Psittaculidae) (taken at mid-north coast, NSW, Australia) – very large eyes with clear

views above. King parrots, although quite large, are prey items for most Australian birds of prey. Right: hyacinth macaw, *Anodorhynchus hyacinthinus* (family: Psittacidae) (image taken in the Pantanal, Brazil) – the eyes permit views behind and above, suggesting that, despite their size and beak, they have enemies. (Photo credits: G. Kaplan)

**Psittacine Cognition, Table 1** Body size versus brain mass and brain areas in primates and birds. Extracted from Olkowitz et al. (2016); marked with X: monkeys of similar

body weight and their brain sizes and brain and forebrain neuron numbers compared to parrots/cockatoos of similar weight range

| Species                | Brain mass (g) | Brain neurons ( $\times 10^6$ ) | Pallium neurons ( $\times 10^6$ ) | Body mass (g) |
|------------------------|----------------|---------------------------------|-----------------------------------|---------------|
| Blue+yellow macaw      | 20.7           | 3136                            | 1917                              | 1008          |
| X Squirrel monkey      | 30.2           | 3246                            | 1340                              | 858.8         |
| Kea                    | 13.6           | 2149                            | 1281                              | 708           |
| X Galago               | 10.2           | 936                             | 226                               | 946.7         |
| Sulphur-cr. cockatoo   | 10.1           | 2122                            | 1135                              | 430           |
| African gray parrot    | 8.83           | 1566                            | 850                               | 453.5         |
| Goffin cockatoo        | 8.27           | 1161                            | 599                               | 244.8         |
| X Marmosets            | 7.79           | 638                             | 245                               | 361           |
| Eastern rosella        | 2.72           | 642                             | 333                               | 102           |
| Cockatiel              | 2.21           | 453                             | 258                               | 101           |
| X Mouse lemur          | 1.83           | 262                             | 22.3                              | 60            |
| Budgerigar             | 1.32           | 322                             | 149                               | 35.3          |
| Green-rumped parrotlet | 1.15           | 227                             | 103                               | 23.23         |

### Explanations for Growing a Larger Brain

An argument has been made that climatic variabilities and pressures brought to bear on species by the environment fostered the growth of larger brains. This was confirmed in a study on Neotropical parrots, arguing that differences in relative brain size were particularly tied to an increased dependence on more open and climatically unstable habitats (Schuck-Paim et al. 2008). One would expect that such large-brained species should then tolerate a higher degree of environmental

uncertainty and be more adaptable than species without such adaptations. Yet, about the greatest proportion of species currently on the endangered list are parrots. The latter is not an indication of their inability to adapt (although the time span for such adaptations to human-induced climate change is generally considered far too short in evolutionary terms) but a sign that the human predilection for colorful parrots has encouraged and supported a growing and thriving poaching subculture that continues to this day, plus, of course, ever-accelerating habitat destruction.

Other explanations for evolving large-brained species have been far sparser than descriptions of the consequences of advanced cognitive abilities. Many studies were quick to point out that having a large brain offered many distinct advantages. Relative brain size in birds has been correlated with greater flexibility of behavior, shown in abilities to colonize new areas, including urban environments, and to adjust the time of breeding to a changing climate. Larger-brained species should tolerate a higher degree of environmental uncertainty. Parrots are known for their highly inquisitive nature, sharing this quality with corvids, primates, and some other vertebrates. Many of the features believed to be associated with advanced cognitive processing, such as high levels of sociality and life history traits, are marked by high longevity, slow development, and a long period of parental investment.

## Brain Lateralization

Brain lateralization refers to the specialization of the brain to carry out different types of processing on each side of the brain and hence to control different behavioral responses. To consider the importance of brain lateralization, one first has to consider the visual field of birds and of parrots. In cockatoos and macaws and in most parrots, the eyes are positioned such that their binocular visual field is relatively small while the monocular field is large. This is so because the eyes are placed laterally on each side of the head in such a way that each eye's field of vision faces in a different direction. In other words, most of their visual field is monocular. There are also species differences as to whether the eyes limit overhead vision or whether the above field is visually accessible. Smaller parrots and macaws have eyes set well back on the head to enable overhead vision, while cockatoo species all have crests that may partially or totally block overhead vision (Fig. 6).

Viewing the world monocularly means seeing very different things on the left and on the right side of the head. Moreover, as in all avian species, the information transmitted by the right eye crosses over in the brain to the left side of the

brain and is processed in the left hemisphere. Likewise, information from the left eye crosses over to the right hemisphere and is processed there. Processing information in different brain hemispheres can also mean that each brain hemisphere can become specialized for processing different things (many birds view an object first with one eye and then the other); specialization not only avoids duplications but also enables the brain to perform many different and nuanced tasks and therefore also increase the amount of information and processing (Rogers 2012).

The right hemisphere is responsible for intense emotions (such as fear of attack), and these are largely controlled by the amygdala: a structure just beneath the forebrain. Hence, the right hemisphere expresses intense emotions, and the left hemisphere may inhibit some of these strong responses (Rogers et al. 2013). The right hemisphere is largely responsible for detecting fine details which includes the ability to recognize conspecific individuals, mates, and partners. While the right hemisphere is responsible for strong negative emotions, it also regulates some strong positive emotions and social attachments. Importantly, the right hemisphere responds when there is danger (such as a predator), and it is generally capable of strong and instant action. As in other vertebrates, fear and escape are controlled by the right hemisphere.

The left hemisphere (right eye), by contrast, largely takes care of learned behavior and routine functions. It discriminates between objects (food from nonfood) and processes geographical markers. However, the left hemisphere can only process classes of objects and organisms as categories, and thus, the left hemisphere does not distinguish between individuals or finer points. That is accomplished by the right hemisphere (left eye).

If certain tasks are largely performed by the left hemisphere and others consistently by the right hemisphere, we speak of a lateralized brain, meaning the division of tasks is stable at the population level for that species (Rogers 2012). It can be inferred that the stronger lateralization is, the swifter and more focused the ability to respond (Rogers et al. 2004).



**Psittacine Cognition, Fig. 7** Footedness shown in food manipulation and feeding. From left to right: left-footed sulphur-crested cockatoo, little corella, yellow-tailed black cockatoo, right-footed rainbow lorikeet, and hyacinth macaw

The question arises whether lateralization is of some importance in cognition. This has been tested in parrots by simple behavioral tasks of scoring which foot they use for manipulating food (Fig. 7).

### Footedness

The researchers (Magat and Brown 2009) tested lateralization (and its strength) of foot and eye use and then conducted cognitive tasks (means-end test; see below) to see whether the lateralization index corresponded with cognitive performance levels. They used eight Australian parrot species; first, cockatiels and budgerigars – two Australian species known not to use their feet for feeding and not to have a foot preference on other tasks (i.e., they have no “footedness” but may otherwise be weakly or strongly lateralized) – and, further, six other species that do use their feet. Four of them were cockatoos (galah, gang-gang cockatoo, red-tailed black cockatoo, and sulphur-crested cockatoo), and two were parrots (Australian king parrot and superb parrot). Note that foot preference correlates with eye preference (Brown and Magat 2011). They found in their experiments that performance was better in species with stronger foot preferences. This was true of the results in a food discrimination task: red-tailed and sulphur-crested cockatoos outperformed every other parrot species, followed by galahs, gang-gangs, and cockatiels, and the least well-performing group (budgerigars, the king and superb parrots), among which there were no significant differences, was also the group with the weakest

lateralization. In a cognitive task (means-ends test), budgerigars and cockatiels could not do it all, while the cockatoos outshone all others. The important finding was that the most strongly lateralized, mostly left-footed (Fig. 7) individuals were also the most successful ones in solving the means-end test.

### Studies of Cognition

Much of what we know about parrot cognition stems from captive studies and from birds bred and held in laboratories in Western Europe and also the USA (Auersperg and von Bayern 2019). Except for some keas, very few of the major cognitive studies were conducted in their place of origin (southern hemisphere) but in the northern hemisphere, i.e., under very different climatic and seasonal conditions. Inevitably, research has tended to concentrate on relatively few species. As Cussen recorded in 2017, in 30 years of research effort, 462 unique individual parrots (incl. 28 African grays, 55 orange-winged Amazons, and 128 keas) were used as subjects in cognition research. In most cases, results have been achieved in laboratories that could not be matched by observations in the wild, either because it would be too difficult or because such behavior, for instance, tool using, rarely occurs in wild psittacines (O’Hara et al. 2019) (see details below). As Piaget first described it in children, the world is first understood through their motor abilities such as touch, vision, taste, and movement. Goffin cockatoos (*Cacatua goffiniana*) have been described as a species with pronounced

behavioral plasticity and practical memory and have special characteristics such as intense curiosity, tactile exploration techniques, and persistence: cockatoos explore surrounding objects with their bill, tongue, and feet (Auersperg et al. 2013). Indeed, this characterization of children and Goffin cockatoos might well hold for all psittacines. Intense curiosity can be a dangerous thing in the natural environment, but if they also retain the memory of their exploits, they may turn them into an advantage.

The question is what cognitive abilities parrots have and why they have them. More broadly, what is it that an animal needs to understand (or know) about the world around it so that it can function, and how can it improve its survival chances – is it by adding knowledge (via experience or associative learning) or, if need be, by adding more brain capacity? Some cognitive scientists have argued convincingly that all vertebrates, including birds, need to come with several core knowledge systems as adaptations in order to function at all. These are not abilities that need to be learned but are basic survival necessities involving basic concepts of numeracy, gravity, geometry, and psychology. The debate was very well summarized in a review by Vallortigara et al. (2010). Concepts such as cause and effect in physical tasks, gravity, and visual cognition, including object permanence (explained below), may be part of the core requirements of knowledge.

The now established fact that many psittacines have large brains relative to body size has usually been associated with a “package” of other life history criteria shared also by primates, cetaceans, and corvids. These include traits such as slow development, long period of parental investment as well as high degrees of social interactions (sociality), and natural inquisitiveness. Some have even pointed to the individuality and capriciousness of behavior characteristic of explorative and playful birds that employ their own idiosyncratic methods when manipulating attractive objects (Huber and Gaydon 2006). Remarkably, psittacine species have in common that they are very long-lived by comparison with other birds in similar weight ranges (in the largest parrots ranging from 40 to 100 years), and this life history

criterion has been related to cognition (Wirthlin et al. 2018).

Among standard experimentally tested technical cognitive tasks are the string-pulling task and the trap tube, which are benchmark tests to comparatively study causal understanding in animals (O'Neill et al. 2019), but there are many variations such as opening boxes and inserting sticks, and all of them test some causality in reasoning in order to choose the right action that leads to a desired outcome. Motivation is usually created by providing a favorite piece of food put in a position where it can be accessed only by removing some obstacles (Gajdon et al. 2013). Keas have been tested on similar sets of tasks and, without hesitation, solved the problem on each occasion and also solved the problem of retrieving food from a box with locks and complicated mechanisms, performing just about as well as chimpanzees (Auersperg et al. 2011; Miyata et al. 2011).

### Means-End Tests

A “means-end test” is a general term applied to tests that typically present a problem in the sense that a desired item that is potentially reachable would remain out of reach unless a number of steps are taken to overcome the problem (which may be an obstacle or simply distance). Hence, as Huber and Gajdon defined it, the exercise “involves the deliberate and planned execution of a sequence of steps to achieve a goal.”

### String-Pulling Task

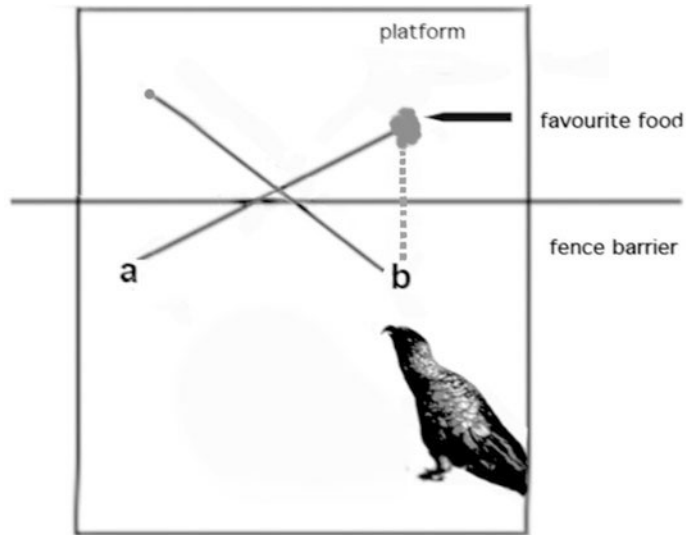
The string-pulling task is a very well-established test and easy to set up (Fig. 8). It can be used in testing individuals (Krashennnikova et al. 2013), but also be set up in ways that can test the willingness of two birds to pull food toward them, if the experimental design demands two birds to overcome the problem.

One can make this test more complicated or even test cooperation between two parties. One interesting study by Pepperberg (2004) showed how even such a simple test can get cognitively complex and go in unexpected directions. For instance, some of the African gray parrots had learned human referential signals such as “come here” and “pick this up” and expected the



**Psittacine Cognition,**

**Fig. 8** String pulling: the kea faces two strings. One end (b) seems closer in distance to the favorite food item (dotted line) and could be chosen intuitively unless the bird assesses the relationship of the string to the favorite food item and then chooses the one to which the favorite food item is attached (a). Most parrots and many songbirds can do this correctly and spontaneously



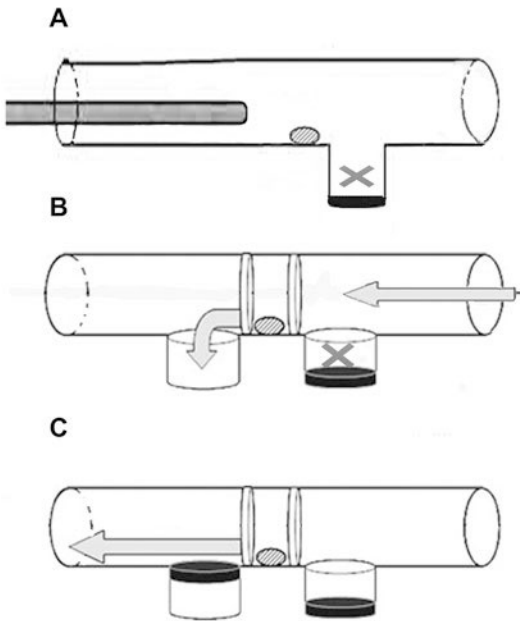
appropriate action from the human trainer. The parrots that had not learned the human commands solved the problem of string pulling very quickly by themselves, while those who knew the commands called impatiently to their human trainer and tried to manipulate the trainer with words like “pick it up” and then behaving badly when the trainer did not respond (Pepperberg 2004).

Schuck-Paim and colleagues (2009) offered an interesting hypothesis. They proposed that problem-solving ability (as the means-end test represents) is related to social complexity. In order to prove their idea, they selected species with varying degrees of social complexity (i.e., specific traits of social organization). The first two they chose were highly social, living in large fluid groups, as is true of the South American spectacled parrotlet, *Forpus conspicillatus*, and of the Australian galah, *Cacatua roseicapilla* (more below). As the second variant, they chose the Australian rainbow lorikeet, *Trichoglossus moluccanus*, which also lives in highly social and fluid groups but without a crèche system. Finally, they selected two species characterized by small and stable group composition with one stable (dominant) breeding pair: the South American green-winged macaw, *Ara chloropterus*, and the Australian sulfur-crested cockatoo, *Cacatua galerita*.

The researchers then presented all four species with the same experimental design, asking of them not simply to do an individual means-ends test but to do so via observation, designating an observer and a demonstrator. Their hypothesis was confirmed: the parrotlets performed best, followed by the rainbow lorikeets, both of which followed exactly what the demonstrator had done, while the macaw and the cockatoo made more errors. In other words, the more complex the social system, the more likely it was that the bird could solve the problems and learn from demonstrators (Schuck-Paim et al. 2013).

**Trap-Tube Task**

The trap tube is one of the benchmark tests to comparatively study causal understanding, in this case, grasping physical causality (gravity), in animals (O'Neill et al. 2019). The task demands manipulating a food item past a trap (Fig. 9). Noticeably, parrots do not perform well in this test, including keas and cockatoos, while apes and corvids succeed (Liedtke et al. 2011). As we already know, cockatoos and keas are masters in dissecting and solving complex problems, so their poor performance raises many questions, one of them on experimental design. Parrots are usually not nest builders, except for the ground parrot, and thus do not routinely manipulate sticks. Many of them, as was already shown, use their feet for



**Psittacine Cognition, Fig. 9** Variants of the trap-tube task. Food item: gray. (a) Pushing a stick would result in losing the treat into a trap; hence, the stick has to be removed and inserted on the other side. (b) Two downward traps but one of them is open and releases the treat. (c) Downward trap tubes but one of them is closed off at the top. Each task, while similar, requires an examination of where the treat might drop into something irretrievable

manipulation and ought to have been given alternative ways (via the feet) to retrieve the food (Fig. 9).

Hence, one cannot tell from the results of such a test whether the failed outcome was the result of physical limitation rather than a lack of understanding of the problem. In the very least, the results should caution us to rethink what we term tests of cognition (or intelligence).

### Object Permanence

The concept of object permanence plays a significant role in the theory of cognitive development in children, first developed by psychologist Jean Piaget and later adapted as an important concept in animal behavior. According to Piaget, there are four stages of cognitive development in children. Object permanence belongs to the first stage. Briefly, it means that the individual needs to know or

learn that things continue to exist even though they go out of sight and cannot be seen.

Object permanence has been tested in many birds be they songbirds, non-songbirds, or parrots. African gray parrots, as well as budgerigars and Australian cockatiels, have also been tested on various tasks relating to object permanence. On a number of occasions, they solved the tasks that were assumed to be more difficult before they attended to the easier ones (Pepperberg and Funk 1990). However, the number of bird species tested other than parrots, pigeons, chickens, and corvids remains very small and does not compare to the wealth of papers on the subject in primates. In precocial birds (fully feathered, walking, and self-feeding very soon after hatching), this ability is an essential adaptation, i.e., it is the ability to follow a parent immediately post-hatching even when going out of sight. In altricial species, as all parrots are (helpless, nest-bound, and underdeveloped at hatching), object permanence is an ability that has to be learned, as is also the case in humans.

### Numeracy/Assessing Volumes

Numerosity has been tested a number of times in African gray parrots (Pepperberg 2006). The same abilities have been tested in primates and dolphins (Kilian et al. 2003) but, to my knowledge, not in any other psittacine species. Some birds (chicks and Clark's nutcrackers) have also been tested on ordinal positioning, and it has been found that they can not only order objects from lower to higher but also do so from left to right (Rugani et al. 2010a). This leftward bias assumes that the lower number is on the left side.

African gray parrots have also been asked to select the largest amount of food between two sets, either discrete food items (experiment 1) or as volume of a food substance (experiment 2) (Al Ain et al. 2009). No matter what combinations and conditions the experimenters used (volumes of fluid or seeds), subjects performed above chance for almost all combinations. Accuracy was negatively correlated with the ratio, that is, performance improved with greater differences between amounts.

A more abstract knowledge of volume is provided in experiments requiring insight into the

fact that stones can displace water and make the level of the water rise, finding such solutions to a problem that demands knowledge of physical causation. Experiments have shown that rooks, Eurasian jays, and New Caledonian crows managed to solve Aesop's fable paradigm, using stones to raise a water level to get a previously out of reach reward. When keas were tested by Schwing et al. (2019), however, it seems that they managed to bypass the problem without showing any evidence of understanding the physical causation of water displacement, highlighting either that such an understanding is not required for solving Aesop's fable or that circumventing problems may also be a remarkable cognitive feat.

### Food Searching/Memory

In 2014, Cussen and Mench were among the very few and first researchers that investigated cognitive abilities in a Neotropical parrot species (the orange-winged Amazon parrot, *Amazona amazonica*) by using a food-searching task. The test used was a standardized test, called the Hamilton search task which has been widely used in primates and is considered a cognitively complex task. Their results showed that almost all (92%) of the parrots acquired the task and were able to alter their search strategies when reward contingencies changed, demonstrating cognitive flexibility. Their findings also showed that lateralization (of foot use) had a significant influence on learning set acquisition and, just as impressively, the parrots were able to remember the task for 6 months, demonstrating long-term memory. More strongly lateralized parrots performed better on the initial search task, but did not show more cognitive flexibility.

### Inferential Reasoning

Inferential reasoning refers to the ability of an individual organism to infer something from a context. For instance, shake a closed container, and if it rattles, the listener can infer that there is something inside the container and by the type of rattling sound created may even guess at the contents. If it is known that this type of container holds kernels of food and there are two containers and the first one does not make a sound when

shaken, it could be inferred that the food might be in the second container. An experiment with African gray parrots did exactly that using noise created during the shaking of containers to detect hidden food. Even from the very first trial, the parrots inferred correctly that the absence of noise in a shaken container meant that the food must be in the other, non-shaken container (Schloegel et al. 2012). Such immediate understanding has been shown in dogs and great apes, in other birds (pigeons, Clark's nutcrackers, and corvids), and in children from an age of 3 to 4 years (Pepperberg et al. 2013).

### Nonverbal Signals (Gestures, Body Postures, Facial Expressions)

One advantage of living in a social group is having access to information provided by conspecifics, to locate predators and food sources. Social animals can also use social cues provided intentionally or unintentionally. Even nonverbal cues can become meaningful signals that are understood by the entire group. Most parrots have an elaborate system of communicating their state or intention by feathers alone. In cockatoos, the position of the crest can indicate play readiness (fully forward), alarm (half-mast), or anger (erect) and be accompanied by body movements such as head bobbing or wing flapping (play readiness) and arching of the neck (anger) and also by simultaneous vocalizations (for an extensive coverage of these issues, see Kaplan (2015)).

Facial expression is achieved by movements of the beak; by independent positioning of feathers below or above the beak, on the ear coverts, on top of the head (the crown), and at the nape of the neck; and, in some species, also by moving the feathers above or below the eyes independently of other feathers. In recent research, the role of colors in the communication of emotions between birds has led to surprising discoveries. Changes in facial coloration are well-known in the human context (blushing, paling), but this has never been observed until recently. For instance, blue and yellow macaws (*Ara ararauna*) have been found not only to have facial displays but even spontaneous color changes

in their face, both at the bare skin patch (“blushing” turning a hue of pink) and changed feather positions (Bertin et al. 2018). For learning more about social and emotional cognition, it would seem well worth investigating the potential importance of facial expressions in close range communication in birds. Birds also have open mouth displays or, rather, open beak displays, which, together with other body signals, are usually used in fear or threat displays or during hyperventilation.

Eye and head movements can also be informative and shared. A stare in one direction, say down at some branch, and wings extended may alert others that there may be a snake hiding in the foliage. Even if this was an affective and spontaneous act, it will be understood by others who might immediately retreat from the area.

Looking (eye gazing) and pointing may also be intentional, and the direction of eye/head movement and the body may lead others to look in the same direction. Pointing and gazing (human cues) were tested in three African gray parrots in an object-choice task (Giret et al. 2009). They found that one subject spontaneously used the most salient pointing gesture (looking and steady pointing with hand at about 20 cm from the baited box). The two others were also able to use this cue after 15 trials. None of the parrots spontaneously used the steady gaze cues (combined head and eye orientation), but one learned to do so effectively after only 15 trials when the distance between the head and the baited box was about 1 m.

## Play Behavior

Play behavior has rarely been discussed specifically under the rubric of cognition, but latest research has confirmed that playing may be an important variable to consider in cognitive performance. Play behavior tends to be discussed in three distinct categories of play, single (or locomotory) play, object play, and social play, and these categorizations have continued to be applied as meaningful categories in describing structure, and often context, of play behavior (Ortega and Bekoff 1987).

The first category, called solo, solitary, or locomotory play, includes a very wide range of behaviors such as running, skipping, jumping, ducking, rolling, hanging, swinging, dancing, and even sliding and snow romping. In the second category, object play, activities involve objects of any kind ranging from sticks, to stones, to small household objects. Such object play in birds can also lead to social play as a chasing game or even play fighting. The third category is social play and involves the playing together of any two or more individuals. Such interactions have been documented in far fewer species than solo or object play. Published cases of social play so far are largely limited to psittacines and corvids. Social play may include aggressive and play fighting on the ground and in the air (Diamond and Bond 2003; Skeate 1985).

It is clear from the evidence that, at least among Australian psittacine species, there is a powerful association between brain size and play behavior. The largest brains relative to body size belong to species that play socially, but even in species that play non-socially, brain size is larger than that nonplaying species but smaller than that of social players. This was the finding of a research paper that compared brain size with play behavior and also with tool using. The surprising results showed that tool using seemed to count for little in overall brain size while play behavior was significant, positively correlating with brain sizes of any form of active play (Kaplan 2020a), future research might well want to explore the capacity for social play in many psittacine species as a frontier of cognitive research (Pellis and Pellis 2016).

## Cooperation, Prosocial Behavior, and Cognition

Social organization of any species is important, and evidence of results in any vertebrates and even in invertebrates demonstrates convincingly that cooperative behavior in general (not as a specialized behavior as helpers at the nest) can lead to particularly good outcomes. As explained before, many parrots and cockatoos live in fission-

fusion societies, and their main unit of sociality is the long-term pair bond, i.e., they have stable pair units that may last a lifetime but also have associations with other family groups that may be mutually supportive. These arrangements permit two different levels of sociality – the intimate and close coexistence with one partner and offspring and the carefully maintained broader social contacts, very similar to some social arrangements in primates, cetaceans, and elephants (Heaney et al. 2017). Whether these are peach-fronted conures, *Eupsittula aurea* (Torres-Ortiz et al. 2020); keas; galahs or sulphur-crested cockatoos; African gray parrots (Péron et al. 2011); or blue-throated macaws, *Ara glaucogularis* (Tassin de Montaigu et al. 2020) which have all been tested, we find that they not only cooperate well but also can solve problems cooperatively.

Cooperation can occur between individuals of the same and different species. Several studies have examined the intentionality of this behavior and tested the birds' understanding of the need for a partner when working in pairs or even family groups. There is now increasing evidence that cooperation is advantageous to animals, and in some parrot species, it has been shown that cognition is implicated and leads to sharing and cooperation (Schwing et al. 2016).

Kaplan (2020a) argued recently that pairs with juvenile history of bonding will also be likely to form bonds early and be more successful in parenting and in producing surviving offspring. Indeed, a presexual bonding may become a training ground for learning mutual responsiveness between the pair partners even including voluntary sharing and mutual support. The latter is related to qualities such as empathy (as perspective taking) and thus an increasing awareness of interests and needs of others. Guo et al. (2019) argued that the higher the cognitive ability, the more likely is the expression of prosocial behavior. It seems that some species are other-directed, and that is often expressed in their social system. The social organization of galahs, *Cacatua roseicapilla*, may serve as an example here. Galahs hatch asynchronously and also fledge asynchronously which presents a

problem of location of feeding. Galahs have found an ingenious solution by establishing a crèche in which newly fledged and young juveniles congregate, being supervised by one or two adults while the parents can fly off feeding elsewhere, then feed their nestlings not ready to fledge in the nest hole, and eventually fly back to feed those supervised in the crèche. Such crèche arrangements last for several weeks in which time the youngsters from different families get to know each other and may form close affiliations, i.e., have opportunities to develop prosocial tendencies, and they may also begin playing with each other (Rowley 1980). Teitelbaum et al. (2017) found bonding behavior in a case of totally unrelated order of birds, the migratory whooping cranes, *Grus americana*. They had tagged a multitude of birds before sexual maturity and then analyzed 58 breeding pairs of the ones that had been tagged. Results showed that the majority of the breeding pairs had started associating at least 12 months before first breeding, and some breeding pairs had associated with their future partner for over 2 years before first breeding. These pair bondings happened before either one of the future partners had reached sexual maturity. Having such data in hand makes it all the more plausible to hypothesize that species, such as parrots, known to be gregarious, large-brained, and capable of long-term bonding, have the social and cognitive prerequisites for empathy and many of the qualities, such as patience, self-control, and perspective taking. In research on humans, it has been asked and apparently confirmed that smarter individuals are also more prosocial and more attuned to the possibilities of cooperation (Guo et al. 2019). There are many open questions that have only begun to be raised in the late 2010s and are just beginning to be addressed.

## Vocal Behavior

### General Calls

Psittacines, even though they are not songbirds, are vocal learners, and thus, their cerebral architecture includes unique vocal and auditory nuclei,



which are not present in non-songbirds. More importantly, the psittacines share a capacity for open-ended learning, meaning that they can learn new sounds throughout life, an ability that not all songbirds possess (they may have a sensitive period in which they can learn and then their song or songs crystallize and take on the final form) (see ► [“Passerine Vocal Communication”](#)). Usually, parrot communication has been described as complex although this requires further clarification. In Neotropical and New Zealand parrots, in which vocal repertoire in the wild has so far been described, the repertoire varies between five and ten major call types for long and mid-distances and some short-range calls, such as sentinel call, flight contact call, and feeding appeal. In close encounter, some species may use gestural communication and low-intensity calls (Martins and de Araújo 2020).

All of these factors combined generally suggest that such call types, when mixed and matched according to context, may add up to substantial vocal complexity, and such complexity, largely speculative so far, may reflect high cognitive capacity (Martins and de Araújo 2020).

### Recognition Calls

Some calls need to be learned and remembered by newly hatched nestlings. Galah parents, for instance, devote considerable time in getting their youngsters to be vocally responsive. They simply do not feed their young until the young emits a special vocal signal first, training them to do so and making them listen to their parents' low-intensity calls (Rowley 1980). The reasons for such detailed preparation become obvious when the social context of their crèche system is considered containing a small or large number of newly fledged or older fledglings looking very similar to each other. As also in colonially nesting species, making sure that one picks up one's own offspring is achieved by voice check. It is so personal and so specific that, even in large and noisy groups, parents and offspring successfully recognize each other, but unlike shore bird and colonial nesters, in galahs, such recognition needs to be learnt.

### Referential Signals

Meaningful communication, as we understand language in human terms, can also be found in signals, referred to as “referential signals.” These are vocal signals that impart unambiguous and stable meanings, as has been studied in alarm and food calls in some songbirds (see ► [“Passerine Cognition”](#)). A referential signal has a semantic content rather than being generalist, i.e., a call that indicates a specific item be this a food source to lead the group to that source or contain a warning to conspecifics that a predator is near. It is other-directed and designed to inform others. Since parrots are lifelong learners, they can add new words or sounds throughout life, and those species with sentinels emit specific calls that inform all others (Martins and de Araújo 2020). Whether or not parrots have specific calls for aerial or terrestrial predators and how widespread this is has as yet to be examined in their natural environment.

### Vocal Mimicry

Vocal mimicry is defined as the imitation by birds of sounds outside their species-characteristic vocalizations. Far from elucidating important links between the ability of vocal learning and cognitive capacity, vocal mimicry has been regarded by some as an impressive motor skill but little else. Mimicry, particularly by various psittacine species, such as budgerigars, cockatiels, galahs, corellas, and sulfur-crested cockatoos, has been discredited as an artifact of captivity and hence as being of no further scientific interest.

However, there are several contexts and circumstances in which mimicry is part of a fundamental process of survival. For instance, birds may mimic (or copy) their own parents or members of their group. Such copying and being absolutely accurate about a specific sound profile are important for individual or group recognition and can facilitate and enhance communication within groups (Wheatcroft and Price 2013). In addition, birds may copy sounds of neighbors of the same species often as a concession to peaceful coexistence between same-species neighbors and closely related species. Full mimicry from other

species may be in snippets or segments or contain copies of key sounds of mammals (or the sounds of inanimate objects). In captivity, parrots mimic human speech, sometimes whole sentences, and, as one cockatiel in our neighborhood annoyingly did most of the day, were to have copied the sound of a phone ringing so accurately and loudly (the old-type landline phone ringing) that the neighborhood kept running to check their own phones.

Vocal mimicry has generally been considered marginal to science in that it seemed to have no particular function. But do birds merely “parrot,” and is it just an artifact of captivity? Irene Pepperberg tried to convince us otherwise by engaging in meaningful vocal exchanges with her African gray parrot, Alex (Pepperberg 2007). And indeed, vocal imitation cannot be so easily dismissed, because it is a widespread behavior, especially so in Australian birds. Vocal mimicry is a rather special ability performed by psittacine species, songbirds, cetaceans, some seals, and humans (Moore 1996).

Parrots, particularly birds growing up in captivity, usually have a focal human partner and learn to adopt parts of their language, just as they may initially mimic their own parents. Mimicry may thus not just be mindless copying but, in some important instances, need to be regarded as a first stage in vocal learning. As experiments with Alex, the African gray parrot, have shown, there was evidence that the sounds he uttered had outgrown mimicry because the words were now applied in new but correct contexts (Pepperberg 2007), i.e., the bird had learned and understood their meaning and used them only in contexts in which they were meaningful. This is indeed evidence of cognitive capabilities for meaningful communication.

In summary, the extent of cognitive abilities in psittacine species has been thoroughly investigated but has been undertaken in very few species. Still, this research has so far revealed remarkable abilities, but whether these observations hold for the vast majority of psittacine species that have not been tested is not clear. One would expect substantial variations in specific abilities in different species and in accordance with taxonomic relationships. The evolution of extra-large-

brained cockatoos, macaws, and keas cannot be truly understood until we begin to understand the mechanisms and specific relationships of psittacine birds among each other and in their specific environments. Given the extraordinary abilities that have already been discovered, this will be a fertile field for future research.

## Cross-References

- [Alex the Parrot](#)
- [Comparative Cognition](#)
- [Means-End Reasoning](#)
- [Passerine Cognition](#)
- [Trap-Tube Problem](#)

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## ***Psittacus erithacus***

### ► [Language Research: Parrots](#)

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## **Psychomotor Test System (PTS)**

### ► [Computerized Testing Paradigm in Primates](#)

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## **Psychopharmacology of Sex Steroids**

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### **Synonyms**

[Aggression](#); [Anabolic steroids](#); [Androgen](#); [Estrogen](#); [Hypothalamic pituitary axis](#); [Libido](#); [Mating](#); [Parenting](#); [Progesterone](#); [Testosterone](#)

### **Definition**

The psychopharmacology of sex steroids is the study of how sex steroids, which are cholesterol-derived lipid hormones produced by the testes and ovaries (the gonads), affect mind and behavior.

### **Introduction**

Gonadal steroids – also known as sex steroids or gonadocorticoids – are powerful hormones that are released by the gonads and travel in the bloodstream to reach target receptors (Balthazart et al. 2018). Activation of steroid receptors induces numerous biological and behavioral responses. The primary sex or gonadal steroid families are

androgens (19 carbons), estrogens (18 carbons), and progestagens (21 carbons) (Kamrath et al. 2014). In humans, the most active forms from each family are testosterone, estradiol, and progesterone, respectively. The largest producer of sex steroids are the reproductive organs, i.e., the testes and ovaries. The brain and adrenal glands can also produce these hormones, occasionally contributing to disease states (Turcu and Auchus 2015). Because of their lipid nature, sex steroids easily diffuse across the blood-brain barrier to reach their target cells in the brain to alter behavior. Steroids can act by binding to receptors found in the cytosol, in the nucleus or on the plasma membrane. Steroids have been shown to have long-lasting effects through actions on the genome that regulate the production of peptides and proteins to affect cell structure and function.

Gonadal steroids have been implicated in many different behaviors including aggressive behavior, sexual behavior, depression, and parenting. Their role in behavior was first described in 1889, by Charles Brown-Séquard, who injected himself with fluids extracted from the testicles of animals and experienced a number of astonishing health improvements including a pronounced increase in physical strength and mental stamina (Brown-Séquard 1889). His publication created international interest and by the end of the year over 12,000 physicians had prescribed the “Elixir of Life” for a variety of conditions including epilepsy and hysteria. Most of these treatments had no scientific merit and little if any effects on patients.

### **The Hypothalamic Pituitary Gonadal Axis (HPG)**

The production and release of gonadal steroids is regulated by the hypothalamic – pituitary- gonadal axis. This group of glands is connected by feedforward and feedback loops that assure steroid production within a functional range (Fink et al. 1991).

The hypothalamus is a region in the brain that sits just above the optic chiasm and regulates a



wide variety of functions including, aggression, circadian rhythms, drinking, feeding, parenting, temperature, and mating. The hypothalamus communicates with the pituitary gland by releasing chemical (anterior pituitary) and neural (posterior pituitary) signals.

The pituitary is actually two glands. The anterior pituitary is a group of cells that release hormones when stimulated by releasing factors or hormones produced by the hypothalamus. Releasing hormones are produced in neurons, and then released into the portal veins that surround the hypothalamus and anterior pituitary. Releasing hormones bind to receptors on “trophs” or cells that produce “trophins” or hormones that travel through the bloodstream to their receptors on target organs. The target organs, in turn, release hormones that travel through the bloodstream to affect the brain and body. In contrast to the anterior pituitary, the posterior pituitary is actually a neural structure – it contains nerve endings and axons of neurons whose cell bodies lie in the hypothalamus and produce vasopressin and oxytocin.

The hypothalamic pituitary-gonadal-axis has the following components. The hypothalamus produces Gonadotropin Releasing Hormone (GnRH) which stimulates the gonadotrophs in the anterior pituitary to release Luteinizing Hormone (LH) and Follicle Stimulating Hormone (FSH). More recently, gonadotropin inhibitory hormone (GnIH) – a peptide that inhibits gonadotropin release – has been identified (Bédécarrats 2015). In females, LH and FSH stimulate the ovaries to produce estradiol and progesterone. In males, LH stimulates the testes to produce testosterone whereas FSH supports spermatogenesis (the production and maturation of spermatozoa). Testosterone and estrogen feed back on the hypothalamus and pituitary to inhibit the release of GnRH, LH, and FSH. It should be noted that all of the hormones in the HPG are released in a pulsatile manner which is important for normal function. Many receptors “downregulate.” That is – the number of receptors available to accept a hormone decreases after exposure to the hormone. The phasic release of hormones allows the number of receptors to return to previous level (and the organ

or cell to the initial responsiveness) before the next wave of hormone is released (Constantin 2017).

## Steroid Synthesis

The gonadal steroids are synthesized from cholesterol. In humans, the rate-limiting step in creating gonadal steroids is the conversion of cholesterol to pregnenolone within the mitochondria. While steroids are mainly produced in the gonads (the ovary and testis), gonadal steroids are also produced by the adrenal cortex and synthesized by neurons in the brain in mammals and birds. Steroids are lipophilic and hydrophobic – they do not dissolve well in water. They are carried through the bloodstream by globulins such as sex hormone-binding globulin.

## Brain Areas

The key brain regions involved steroid regulation of behavior include the amygdaloid nuclei, preoptic area/hypothalamus, and periaqueductal gray (PAG) (Sokolowski and Corbin 2012).

The amygdaloid nuclei – primarily the medial and cortical nuclei and the bed nucleus of the stria terminalis – receive and integrate signals from each of the senses and many of the internal organs. These nuclei play important roles in behavior by providing salience or emotional content to the information received. The amygdaloid complex then relays this information to the preoptic area and hypothalamus, which play critical roles in the expression of motivated behaviors.

Several nuclei in the preoptic area and hypothalamus have been identified for their roles in specific behaviors (Chen and Hong 2018). For example, the destruction of the medial preoptic area disrupts male mating and parenting while those of the ventromedial hypothalamic nucleus (VMN) disrupt female sexual behavior. Aggression is regulated by the lateral preoptic area. Interestingly, recent studies using optogenetic techniques suggest additional roles for the VMN in male mating and aggression.

The PAG, a large region in the center of the brainstem, receives information from the hypothalamic and preoptic nuclei and projects to motor regions in the spinal cord to effect synchronized movements required for each behavior. The PAG controls respiration and heart rate and has been implicated in the expression of fear and anxiety. Moreover, the PAG projects to the frontal cortex and the accumbens areas involved in decision-making and reward, respectively. Taken together, the connections of the PAG suggest it adds emotional valence to reflexive behaviors (Motta et al. 2017).

## Aggressive Behavior

In humans, aggressive behavior has been studied in relation to sports competition, criminal violence in prison inmates, self-reporting of aggressive behavior after anabolic steroid use, and in laboratory tests of aggressive behavior. Overall, it remains controversial whether or not steroids, mainly androgens, play a role in human aggression.

In nonhuman animals, there is direct experimental evidence that in some species, androgens, and possibly estrogens (which are synthesized from androgens), play a role in mediating aggressive behavior in males. In females, the number of studies studying the role of steroids on aggressive behavior is limited. Aggressive behavior can be subdivided into several categories that include but are not limited to territorial, maternal, fear-induced, predatory, parental, and self-defense.

### Territorial Aggression

Aggression related to territorial encounters has been extensively examined in non-human animals. Evidence suggests that androgens, estrogens, and progesterone play a role in mediating aggressive behavior in some species. The role of steroids is usually species specific, sex-dependent, and seasonally dependent (breeding vs. nonbreeding seasons).

### Maternal Aggression

In some rodent species, the increase in progesterone is correlated with maternal aggression. Non-sex steroids such as oxytocin, and its receptor, are

known to affect maternal behavior in rodents. The hormonal basis of maternal aggression in humans is not well-studied.

## Sexual Behavior

Gonadal steroids play an essential role in the expression of sexual behavior in mammals. Removal of the gonads which produce the steroids reduces or eliminates mating in males and females and treatment with gonadal steroids restores sexual behavior in both sexes. Sex steroids play gender-specific roles. Systemic treatment with testosterone restores male sexual behavior in castrated males by activating neural areas required for copulation and the musculature required for penile reflexes. Testosterone is readily metabolized to estrogen and treatment with estrogen is sufficient to restore many aspects of mating behavior in male rodents primarily through actions on the brain. Estrogen fails to restore penile reflexes; androgens, which regulate the peripheral structures in males, are required for the full expression of the behavior.

Circulating estrogen and progesterone are required for female sexual behavior. These steroids also act on the brain. Estrogen induces the expression of progesterone receptors, thus estrogen treatment must precede that of progesterone to induce receptivity in gonadectomized females. Testosterone has been shown to influence female sexual behavior in rodents primarily through its conversion to estrogen. While there has been considerable interest in the role of testosterone in the regulation of female sexual behavior in humans, clinical studies fail to support a role for testosterone or non-aromatizable androgens in the regulation of libido in women.

## Parental Behavior

Steroids are also important in parenting behavior—castrated rodents do not parent. Gonadal steroids play sex-specific roles (Peter 2017). Estrogen is critical for maternal (mother) bonding after parturition and may work by increasing levels of

oxytocin and its receptors in the brain. Estrogen's role in paternal (father) behavior is still under investigation. Testosterone has been linked to maternal behavior in rodents primarily through its conversion to estradiol. In contrast, testosterone levels are inversely associated with parenting in males. Lower levels of testosterone are found in high caring primate fathers and mothers (including humans) than their counterparts. Interestingly corticosterone, an adrenal steroid, has been shown to be positively related to maternal and paternal responsiveness and can facilitate parental behavior in inexperienced animals. Progesterone levels have been both positively and negatively associated with parental behavior depending on the species and the method of measurement.

## Other Behaviors

### Depression

Testosterone has been shown to improve depressive symptoms in both men and women (Akerman et al. 2017). While the neural basis for this is poorly understood, it may be mediated by receptors for both androgens and estrogens which are high in the "emotional brain" including the amygdala and BST.

### Alcohol Consumption

Gonadal steroids are positively correlated with alcohol consumption. Surprisingly, this effect is sex specific. High levels of testosterone are associated with increased alcohol consumption in men but not women whereas high levels of estrogen are associated with alcohol consumption in women but not in men (Erol et al. 2017).

### Sleep

The quality of sleep differs in men and women (Lord et al. 2014). While women report poorer quality of sleep than men, objective sleep measures suggest the opposite. The quality of sleep differs over the menstrual cycle and is disrupted during periods of hormonal functions such as puberty, pregnancy, and menopause. Nonetheless, hormone replacement therapy is associated with

more restful sleep states. As men age, circulating levels of testosterone decrease and so does the quality of their sleep suggesting a positive effect of androgens on sleep in males. Thus as in other behaviors, the effects of steroids are sex specific.

## Conclusion

Gonadal steroids have profound effects on a number of behaviors. The nature of these effects is tempered by gender and the nature of the steroid. Steroid actions are long lasting, and long-term treatment can have cumulative effects on behavior. To date, much of the work has been conducted on a variety of animal models. To draw proper conclusions, we must continue to find ways to extend this work to humans.

## Cross-References

- [Aggression](#)
- [Amygdala](#)
- [Androgens](#)
- [Estrogen](#)
- [Estrous](#)
- [Hypothalamus](#)
- [Oxytocin](#)
- [Parenting](#)
- [Progesterone](#)
- [Testosterone](#)

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## Psychophysical Threshold

- [Sensory Judgment](#)

## Psychophysiological Responses

- [Cognition](#)

## Pterotillomania

- [Feather-Plucking](#)

## Ptilonorhynchidae

- [Bowerbird Aesthetics and Cognition](#)

## Puberty

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## Synonyms

[Adolescence](#); [Adulthood](#); [Juvenescence](#); [Pubescence](#); [Sexual maturity](#); [Youth](#)

## Definition

The condition of being or the period of becoming first capable of reproducing sexually that is brought on by the production of sex hormones and the maturing of the reproductive organs (such as the testes and ovaries), development of secondary sex characteristics (such as male facial hair growth and female breast development), and in humans and the higher primates by the first occurrence of menstruation in the female.

## Some Definitions Related to Puberty

**Adrenarche** which is the activation of the adrenal cortex to produce adrenal androgens (typically occurs before the onset of puberty)

**Gonadarche** mainly involves activation of the gonads by the pituitary hormones follicle-

stimulating hormone (FSH) and luteinizing hormone (LH)

**Pubarche** is the first appearance of pubic hair

**Thelarche** is defined by the appearance of breast tissue

**Menarche** defines the age of onset of the first menstrual period

**Spermarche** is the first ejaculation (heralded by nocturnal sperm emissions and appearance of sperm in the urine)

## Introduction

Adolescence is increasingly recognized as a critical period in the life course, a time when rapid development of the brain, body, and behaviors opens a window of opportunity for interventions that may affect health throughout life. Puberty results in very rapid somatic growth, brain development, sexual maturation, and attainment of reproductive capacity. It is accompanied by final maturation of multiple organ systems and major changes in the central nervous system and in psychosocial behavior (Patton and Viner 2007). The discovery of continued brain development through adolescence is one of the great advances of neuroscience in the past 20 years. A dramatic spurt in brain development begins during adolescence and continues until the mid-20s, with marked development of both cortical and subcortical structures (Goddings et al. 2012).

## Physiology of Puberty

There have been remarkable advances in the field of neuroendocrinology to understand the basics of pubertal development during the last few decades. The major areas of focus in this discussion are summarized below.

### Pulsatile Secretion and Release of Gonadotropin

The main reason behind the pulsatile secretion of gonadotropins is due to the pulsatile stimulation of pituitary gonadotrophs by hypothalamic gonadotropin-releasing hormone (GnRH). The

background of pulsatile secretion was experimentally proved by some scientists working on immortalized hypothalamic cells *in vitro* to occur much faster than those of GnRH release *in vivo*, suggesting that the central nervous system influences the rhythmicity of such release patterns. The pulsatile release of GnRH and gonadotrope stimulation is particularly important physiologically. The reason lies in the fact that when the pulsatile release is altered to continuous exposure to GnRH, the receptors for GnRH decrease and ultimately produce a post-receptor defect (Fig. 1).

### Negative Feedback

There are evidences that show that children with normal reproductive organs express increased gonadotrophic secretion during the first few years after their birth; however, it is followed by a period of quiescence, which is also commonly called as juvenile pause, and then finally characteristic display of puberty occurs where there is increased gonadotrophic secretion. Subjects with Turner's syndrome, classical example of patients without gonads, have increased gonadotropin secretions even without the development of secondary sexual characters mainly because of non-functional gonadal system. Thus, juvenile pause is necessary for proper timely occurrence of puberty in early childhood displaying a negative feedback control by sex steroids.

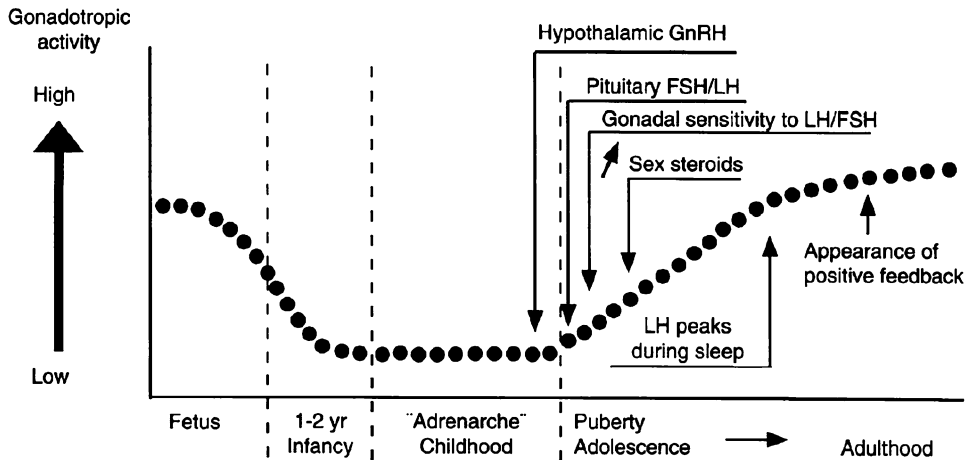
### Control by Higher Centers

The major inhibitory mechanism of the central nervous system (CNS) demonstrated by juvenile pause lasts mainly from the age of 1–4 years up to 10–12 years in the maximum number of children, resulting in low or decreased gonadotrophic secretion. The exact mechanism by which CNS exerts its effect is poorly understood; however, certain disorders like Turner's syndrome explain the plausible role.

### Stages of Puberty

Professor James M. Tanner, a child development expert, was the first to identify the visible stages of puberty. At present, these stages are known as the Tanner stages or, more appropriately, sexual maturity ratings. They serve as a general guide





**Puberty, Fig. 1** Activation of hypothalamo-pituitary gonadal axis. Figure taken from Rosenfield R. *Pediatric Endocrinology*. Sperling 3rd edition, 2008

to physical development, although each person has a different puberty timetable.

### Pubertal Stages (Tanner) in Females

The five stages of breast development in females are as follows:

P1: Prepubertal

P2: Early development of subareolar breast bud +/- small amounts of pubic hair and axillary hair

P3: Increase in size of palpable breast tissue and areolae, increased amount of dark pubic hair and of axillary hair

P4: Further increase in breast size and areolae that protrude above breast level adult pubic hair

P5: Adult stage, pubic hair with extension to upper thigh (Fig. 2)

### Uterine Development

The prepubertal uterus is tear-drop shaped, with the neck and isthmus accounting for up to two-thirds of the uterine volume; then, with the production of estrogens, it becomes pear shaped, with the uterine body increasing in length and thickness proportionately more than the cervix (Fig. 2).

### Ovarian Development: Stage 1

The rising levels of plasma gonadotropins stimulate the ovary to produce increasing amounts of

estradiol. Estradiol is responsible for the development of secondary sexual characteristics, that is, growth and development of the breasts and reproductive organs, fat redistribution (hips, breasts), and bone maturation. The maturation of the ovary at adolescence correlates well with estradiol secretion and the stages of puberty.

### Ovarian Development: Stage 2

In prepuberty, the ovarian size volume extends from 0.3 to 0.9 cm<sup>3</sup>. More than 1.0 cm<sup>3</sup> indicates that puberty has begun. During puberty, the ovarian size increases rapidly to a mean postpubertal volume of 4.0 cm<sup>3</sup> (1.8–5.3 cm<sup>3</sup>).

### Ovulation

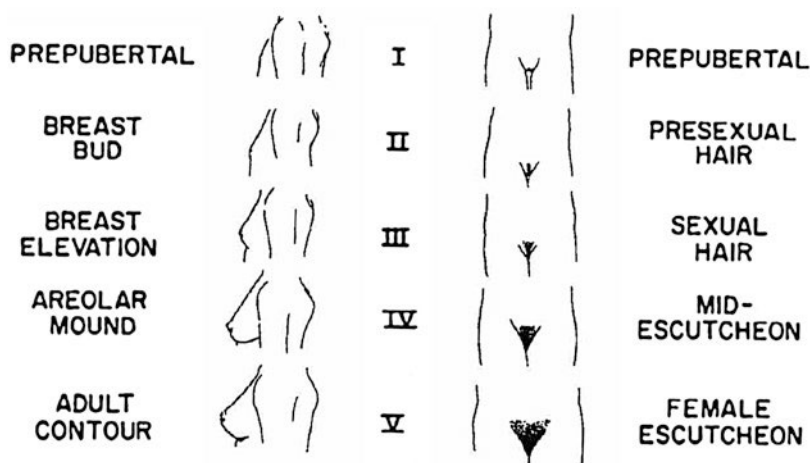
Plasma testosterone levels also increase at puberty although not as markedly as in males. Plasma progesterone remains at low levels even if secondary sexual characteristics have appeared. A rise in progesterone after menarche is, in general, indicative that ovulation has occurred. The first ovulation does not take place until 6–9 months after menarche because the positive feedback mechanism of estrogen is not developed (Chakraborty 2019).

### Female Secondary Sexual Characteristics

If breast development, pubic and/or axillary hair, and menses occur earlier than normal variations

**Puberty, Fig. 2**

Different pubertal stages in female. Figure taken from Rosenfield R. Pediatric Endocrinology. Sperling 3rd edition, 2008



from the mean, the terms premature thelarche, pubarche and/or adrenarche, and menarche are used.

**Pubertal Stages (Tanner) in Males (Fig. 3)**

- P1: Prepubertal, testicular length less than 2.5 cm  
 P2: Early increase in testicular size, scrotum slightly pigmented, few long and dark pubic hair  
 P3: Testicular length 3.3–4 cm, lengthening of the penis, increase in pubic hair  
 P4: Testicular length 4.1–4.5 cm, increase in length and thickening of the penis, adult amount of pubic hair  
 P5: Testicular length greater than 4.5 cm, full spermatogenesis

**Secondary Sexual Development in Boys**

Growth kinetics are enhanced from early puberty, and maximal velocity is attained only around 14–15 years of age. Testis increases in size, mainly at the expense of the seminiferous tubules, and the interstitial (Leydig) cells develop and ensure synthesis and secretion of testosterone. A testicular volume of 4 ml or a longitudinal diameter greater than or equal to 2.5 cm and a slight progressive increase in scrotal folds and pigmentation constitute the first signs of puberty.

**Testes Development: Stage 1**

The increase in testicular size observed during prepuberty and puberty results essentially from

the development of the seminiferous tubules under the stimulating effect of FSH. The testicular volume increases throughout puberty up to Tanner stage P4 when a longitudinal diameter of  $5.0 \pm 0.5$  cm or a volume of  $17.6 \pm 4.0$  ml is reached.

**Testes Development: Stage 2**

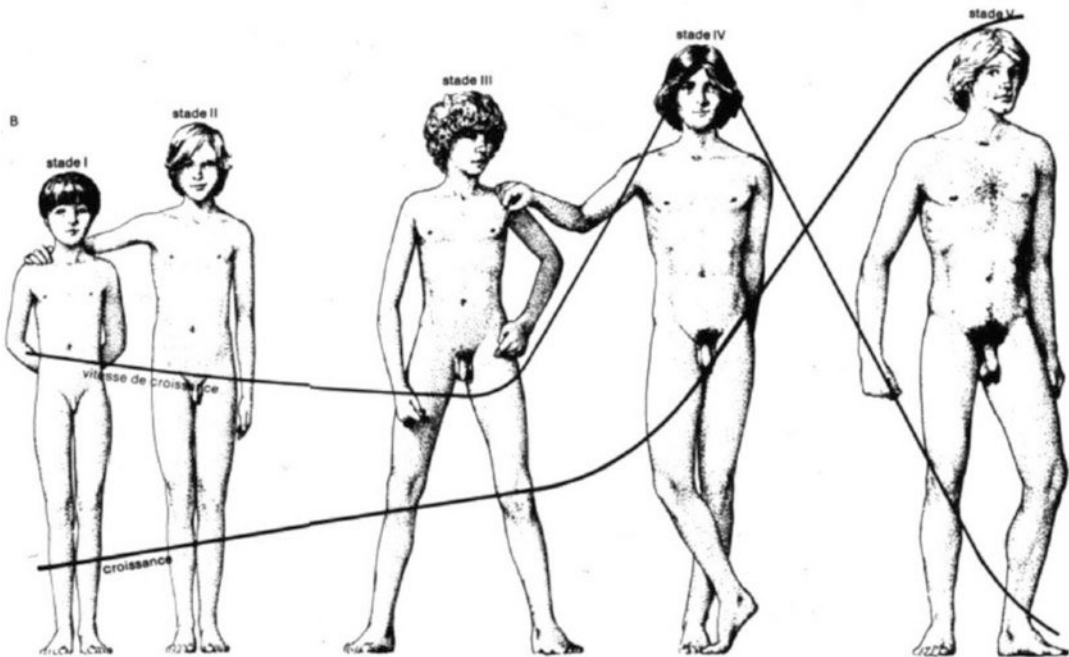
Long-standing pulsatile LH secretion induces the differentiation of interstitial cells into testosterone-secreting Leydig cells, which, in turn, exert a negative feedback control on LH secretion. As puberty progresses, spermatogenesis is initiated and then sustained by FSH and by testosterone produced by the Leydig cells under LH control.

**Testes Development: Stage 3**

A significant increase of plasma testosterone is found only between Tanner pubertal stages P3 and P4. Dihydrotestosterone shows a pattern similar to that of testosterone, and the proportion of dihydrotestosterone to testosterone decreases gradually until adulthood, when dihydrotestosterone levels are approximately 10% of those of testosterone.

**Bone Age**

Puberty is completed usually within 3–4 years of its onset, and the final height resulting from complete fusion of the epiphyses occurs within approximately 2 years after menarche.



**Puberty, Fig. 3** Different pubertal stages in male. Figure taken from Sizonenko 1987

### Precocious/Delayed Puberty

Puberty is considered precocious if these changes are noted prior to 8 years of age in girls and 9 years of age in boys and is considered delayed when such changes do not occur prior to 13 years of age in girls and 14 years of age in boys (Europe).

### Hormonal Changes in Puberty

**Gonadotropin-Releasing Hormone 1:** In prepubertal children, no significant luteinizing hormone (LH) or follicle-stimulating hormone (FSH) response to intravenous or subcutaneous administration of GnRH is observed. During adolescence, the LH response to GnRH increases progressively in both sexes. The increase of FSH is much less marked than that of LH. The primary triggering mechanism that initiates the activation of the hypothalamic-pituitary-gonadal axis at puberty is still hypothetical.

**Gonadotropin-Releasing Hormone 2:** One of the important neuroendocrine mechanisms that control the onset of puberty is probably an increase in the frequency of GnRH pulse stimulation of the pituitary. Whatever the mechanism, the process is not abrupt but develops over several years, as evidenced by slowly rising plasma

concentrations of the gonadotropins and testosterone or estrogens.

**Gonadotropin-Releasing Hormone 3:** One of the factors involved in triggering GnRH secretion is the GPR54 gene, encoding a G protein-coupled receptor. Human mutations of this gene are found in hypogonadotropic hypogonadism. Defect in migration and/or final differentiation of the neurons is found in the hypothalamus. They modulate the activity of GnRH in various ways, leading to appropriate timely occurrence of GnRH release during puberty. GPR54 also regulates the release of GnRH at hypothalamic level.

**Gonadotropins 1:** The first demonstrable biological change of puberty is the appearance of pulsatile LH release during sleep. As puberty progresses, the frequency and amplitude of LH secretory peaks increase, although peaks are also found during the wake period. At the end of puberty, the difference between sleep and wake LH secretory patterns disappears.

**Gonadotropins 2:** In girls, circulating FSH levels increase progressively from 10 to 11 years of age (stage P2), approximately 1 year prior to those of LH. Thereafter, gonadotropins continue

to increase throughout puberty, but important fluctuations are observed in relation to the menstrual cycle.

*Gonadotropins 3:* In boys, a significant increase in both plasma FSH and LH is also found from the onset of puberty (stage P2), closely linked to the rapid increase in testicular size characteristic of this pubertal stage. A further significant increase in circulating gonadotropins is also observed at late puberty (stages P4 and P5).

*Adrenal Steroids 1:* Adrenal androgens vary from infancy through adolescence. This phenomenon is called adrenarche. In girls, dehydroepiandrosterone (DHEA) and dehydroepiandrosterone sulfate (DHEAS) increase as early as 6–7 years of age, followed within 1–2 years by a concomitant increase in androstenedione.

*Adrenal Steroids 2:* In boys, DHEA and DHEAS increase as early as 8–9 years of age, followed by androstenedione 1–2 years later. Adrenarche begins before the rise in gonadotropin secretion. The adrenal androgens are responsible for the appearance of axillary hair and, in part, for the appearance of pubic hair in the adolescent; however, they do not appear to play a decisive role in determining the initiation of puberty.

*GH, IGF-I, and Insulin in Puberty:* There is accumulating evidence that GH plays a role in pubertal development. In experimental animals, GH seems to stimulate FSH-induced differentiation of granulosa cells directly, increase ovarian levels of IGF-I, and amplify the ovarian response to gonadotropins.

IGF-I, in turn, enhances the gonadotropin effect on the granulosa cell, and GH seems to act synergistically with a still-developing pattern of gonadotropin secretion to facilitate ovarian maturation postmenarche. It also appears that the local production or accumulation of GH and IGF-I exerts an intraovarian paracrine control on steroidogenesis.

Puberty of patients with isolated GH deficiency is frequently delayed, Leydig cell function is diminished, and the response to chorionic gonadotropins is decreased. GH administration can restore testicular responsiveness to LH and Leydig cell steroidogenesis.

Growth hormone-releasing factor (GRF) levels and GH secretion increase considerably during

puberty, mainly at night. The amplitude of GH peaks increases early in puberty. IGF-I is an important modulator of growth during childhood and adolescence. Adrenal androgens seem to have no physiological role in normal growth. The characteristic pubertal growth spurt results mainly from the synergetic effect of gonadal sex steroids, growth hormone, and IGF-I production, with all showing a significant increase at the time of pubertal growth acceleration.

Insulin is also important for normal growth. Plasma insulin levels increase throughout childhood, but the rise is particularly pronounced during puberty with a strong positive correlation with IGF-I.

*Leptin in Puberty:* Leptin a peptide hormone is very essential for food intake pattern and regulates food intake and energy expenditure at the hypothalamic level (satiety factor). It is expressed predominantly in adipocytes. Leptin is regulated by body weight and nutrition. Recently, it has been found to be involved in the regulation of GnRH secretion. It interacts with insulin, IGF1, GH, and glucocorticoids, thereby playing a vital role in the regulation and occurrence of puberty in both sexes.

*Puberty and Neurosecretions:* Gamma-aminobutyric acid (GABA) neurons inhibit prepubertal GnRH release and secretion. It has been experimentally demonstrated in monkeys that puberty advances by pharmacological blockade of GABA A receptors. GABA inhibits excitatory neuronal systems synaptically connected to GnRH neurons, thereby blocking GnRH secretion and release. Therefore, during puberty, there occurs an active inhibition of GABA neurons, thereby consequential occurrence of puberty.

## Conclusion

The stage of puberty can be challenging for kids and parents. In addition to causing many physical changes, hormones are also causing emotional changes making the person moody or rage. Children's experiencing puberty might feel insecure about their changing body, including their acne. It is particularly important to understand the physiological reasons and deal accordingly.

## Cross-References

- [Adolescence](#)
- [Diploid](#)
- [Embryo](#)
- [Fetus](#)
- [Reproduction](#)

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## Pubescence

- [Adolescence](#)
- [Insect Locomotion](#)
- [Puberty](#)

## Punishment

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## Synonyms

[Differential reinforcement of other behavior](#); [Omission training](#); [Penalty \(not technical\)](#);

[Response-dependent aversive stimulation](#); [Response-initiated delays in reinforcement](#); [Time-out from reinforcement](#)

## Definition

According to the American Psychological Association Dictionary of Psychology, punishment is a noun that refers to (1) a physically or psychologically painful, unwanted, or undesirable event or circumstance imposed as a penalty on an actual or perceived wrongdoer; (2) in operant conditioning, the process in which the relationship, or contingency, between a response and some stimulus or circumstance results in the response becoming less probable. The punishing stimulus is called a punisher.

The characterization of events or circumstances as “physically or psychologically painful” is not useful unless the observational basis for these terms is spelled out. Therefore, the standard and most widespread definition of punishment in the behavior-analytic literature refers only to a response – stimulus change contingency and a resulting reduction in response frequency. Thus, Azrin and Holz (1966) defined punishment as a procedure that results in a decreased frequency of specific responses when these responses have produced certain immediate stimulus changes. Thus, in the same way that reinforcement requires that the response rate is increased or maintained as a result of the response – stimulus-change contingency, punishment requires that the response rate decreases or remains lowered as the result of the response – stimulus-change contingency.

## History

In the vernacular, punishment and reward are closely related terms. Whereas rewards are generally considered as something pleasant, punishment is considered as unpleasant. However, the terms “pleasant” and “unpleasant” are not well defined. The observational basis for characterizing an event as “pleasant” or “unpleasant” for a particular organism is not obvious.



In an early statement of “The Law of Effect,” E. L. Thorndike (1911) wrote that,

Of several responses made to the same situation, those which are accompanied or closely followed by satisfaction to the animal will, other things being equal, be more firmly connected with the situation, so that, when it recurs, they will be more likely to recur; those which are accompanied or closely followed by discomfort to the animal will, other things being equal, have their connections with that situation weakened, so that, when it recurs, they will be less likely to occur. (p. 244)

As with the term “painful” mentioned above, it is not helpful to define reward as “a satisfying state of affairs,” and punishment as “a discomforting state of affairs,” without clarifying the observational basis for saying that something is satisfying or discomforting, and so on. Thorndike realized this problem and added that,

By a satisfying state of affairs is meant one which the animal does nothing to avoid, often doing such things as attain and preserve it. By discomforting or annoying state of affairs is meant one which the animal commonly avoids and abandons. (p. 245)

When these definitions were put back into the law of effect, however, another problem was soon realized: the law became circular. The concept of “reward” had other problems as well. In colloquial speech, rewards are defined as much by their intended affect as by their actual effects. Thus, people are rewarded, and whether behavior is actually strengthened is secondary. In modern behavior analysis, the term “reward” is abandoned in favor of “reinforcement.” Reinforcement is defined by its effect – in strengthening behavior. There have been a few efforts to abandon the term punishment in a similar way, and to promote the concept of “reduction procedures.” Yet, the concept of punishment has survived in the behavioral literature.

## Two Types of Punishment Procedures

It is common practice to distinguish between two types of punishment procedures as well as two types of reinforcement procedures: In *positive punishment*, as in *positive reinforcement*, the

response-contingent stimulus change consists of the presentation, or the increased intensity, of a stimulus, whereas in *negative punishment*, as in *negative reinforcement*, the response-contingent stimulus change consists of the removal or reduced intensity of a stimulus. The stimuli that are presented or intensified are designated positive (reinforcers or punishers in the respective procedures), and the stimuli that are removed or decreased in intensity are designated negative (reinforcers or punishers in the respective procedures). Sometimes, both positive and negative punishments are involved simultaneously.

## An Alternative Definition of Punishment

In his classic textbook, *Science and Human Behavior*, B. F. Skinner (1953) had suggested a different definition of punishment than the standard one. He concluded that punishment is not simply the opposite of reward, that punishment did not simply subtract responses where reinforcement added them, and therefore,

We must first define punishment without presupposing any effect. [Then,] what course is open to us? The answer is as follows. We first define a positive reinforcer as any stimulus the *presentation* of which strengthens the behavior upon which it is made contingent. We define a negative reinforcer (an aversive stimulus) as any stimulus the *withdrawal* of which strengthens behavior. . . In solving the problem of punishment we simply ask: What is the effect of *withdrawing* a *positive* reinforcer or *presenting* a *negative*? . . . We do not presuppose any effect; we simply raise a question to be answered by appropriate experiments. (pp. 184–185)

Although Skinner doubted a permanent or lasting reduction in response strength as a result of punishment, the immediate effect on response probability was clear enough. He went on to describe three ways in which punishment may work “indirectly.” First, aversive stimuli may function as elicitors of behavior that is incompatible with behavior upon which those aversive stimuli are contingent. Second, behavior that is previously punished may become (or become a source of) conditioned stimuli that evoke behavior

that is incompatible with the punished behavior. Third, certain responses may be reinforced by reducing conditioned aversive stimulation arising from the punished behavior or from associated circumstances. This effect may be most clearly observed when, as a result of punishment, the organism not only does refrain from repeating the punished behavior, but also shows a marked resistance if manually prompted to engage in that behavior.

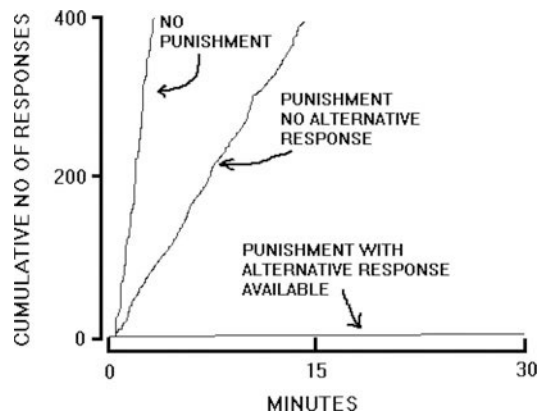
### Variables that Influence the Effectiveness of Punishment

When we use the standard (Azrin and Holz 1966) definition, punishment always works – because it is defined that way. If we use the alternative definition (Skinner 1953), the question of whether punishment works is more meaningful. However, with either definition a more useful question concerns the extent to which the rate of specific responses will be reduced when specific stimulus changes are contingent upon those responses. Can we formulate some general rules regarding the circumstances under which punishment is most effective? The central variables that influence the effectiveness of punishment procedures have been identified by Azrin and others in basic research since the early 1960s and their findings have been supported by later work in applied behavior analysis (see Lerman and Vorndran 2002). Some of the most important variables are the following:

1. *Immediacy.* Punishment is most effective when administered immediately after the target response.
2. *Intensity.* Punishment is more effective when introduced at high intensity rather than introduced at low intensity and later increased.
3. *Schedule of punishment.* Behavior is more effectively reduced when punishment is administered contingent upon every response rather than intermittently.
4. *Reinforcement of target behavior eliminated or reduced.* Punishment works more effectively when target responses are not simultaneously

reinforced than when reinforcement remains contingent upon those responses.

5. *Reinforcement of alternative behavior.* Punishment reduces the occurrence of target responses most effectively when reinforcers are accessible through alternative responses. Representative cumulative records of responding under no punishment, straight punishment, and punishment combined with alternative reinforcement is shown in Fig. 1. The steeper the record, the higher rate of responding, thus simple punishment was effective in reducing behavior (compared to no punishment), but it was most effective when accompanied by reinforcement of alternative responding.
6. *Minimized motivation for reinforcers that maintain target behavior.* The effectiveness of punishment increases when motivational variables are changed so as to reduce the effectiveness of reinforcers that otherwise maintains the punished behavior.
7. *No pairing of punishment with reinforcement.* Punishment may lose its effect entirely and even begin to have the opposite effect if consistently paired with reinforcement.



**Punishment, Fig. 1** Cumulative response records of the punished responses of human participants under an intermittent reinforcement schedule. The punishment was an annoying buzzing sound that was delivered for each response. (After Azrin, N. H., & Holz, W. C. (1966). Punishment. In W. K. Honig (Ed.), *Operant behavior: areas of research and application* (pp. 213–270). New York: Appleton-Century-Crofts)

## Theories of Punishment

The two definitions of punishment described above largely coincide with two different theories of how punishment works. According to the first theory, reinforcement and punishment are symmetrical processes. Fantino and Logan (1979) suggested that this symmetrical theory was directly inspired by the symmetrical definitions of reinforcement and punishment. Moreover, the theory was also inspired by the fact that when punishment is shown to reduce response rates, observable competing responses are not likely to be reported (Fantino and Logan 1979).

According to the second theory, punishment is not considered as the opposite of reinforcement. An early, clear statement of this view was made by Thorndike (1932) in his revision of “The Law of Effect,” where he wrote that “the wrong tendencies are not reduced in strength one jot or tittle by the punishment.” Additional support for this view came from Skinner’s (1938) early experiments and from Estes (1944). Skinner (1938) punished rats’ lever presses during a limited time period and found that when punishment was terminated, response rates increased, and the total number of responses was not affected by the punishment. Estes (1944) compared the effect of response-dependent and response-independent electric shocks and found that they were equally effective in suppressing responses. The results suggested a two-factor theory of punishment. According to this theory, punishment works by eliciting responses that are incompatible with punished behavior or by generating conditioned aversive stimuli that are terminated by behavior that is incompatible with punished behavior and, hence reinforce such incompatible behavior.

## Commonly Listed Problems with the Use of Punishment

A series of important side effects of punishment are typically listed in textbook chapters. These include the following:

1. Elicitation of challenging emotional behavior.
2. Weakening of other (wanted) behavior in addition to that which is being punished.
3. Avoidance or escape from those who punish.
4. Aggression toward those who punish as well as toward others.
5. Weakening of behavior only in the presence of persons or situations paired with punishment and as long as the procedure is implemented.
6. Reinforcement of punishing behavior whenever punishment works.

## Effects of Negative Punishment on Behavior

The reinforcement of alternative/incompatible responses to the punished one is at the base of negative punishment. In most negative punishment procedures, a positive reinforcer is cancelled or postponed if the target behavior occurs, and reinforcers occur if the behavior is not emitted during a specified time period, or an alternative response is directly reinforced. But even in the absence of explicit alternative reinforcement, some behavior should coincide with reinforcer occurrence, thus setting the occasion for the operation of reinforcement to occur. As can be seen, negative punishment is an alternative way to reduce target behavior, which complements (and perhaps contrasts) the more traditional positive punishment seen in previous sections.

A consequence of weakening behavior through negative punishment instead of positive punishment is the low, or even lack of, negative emotional side effects, as can be seen, for example, by the failure of anxiolytic drugs to increase behavior reduced by negative punishment in contrast to the clear antipunishment effect observed when the behavior has been reduced by means of positive punishment (Pérez-Padilla and Pellón 2007).

There are different ways to implement negative punishment:

1. *Time-out from positive reinforcement* consists of removing the individual from the reinforcing situation for a defined time period contingent upon execution of a target behavior,

thus resulting in the reduction of such behavior. This technique originated in applied behavior analysis and is commonly used by school teachers or parents. In the laboratory, time-out also refers to a time interval during which a behavior is not possible to occur, breaking trains of behaviors by eliminating their stimulus effects or acting as a marker in a series of events.

2. *Differential reinforcement of other behavior*, or *omission training*, is a procedure in which reinforcement occurs if a particular response does not occur for a specified time period, thus decreasing the rate of the target behavior. If some specific other behavior is identified, then the procedure is better named *differential reinforcement of alternative behavior*. This negative punishment procedure combines extinction of a particular target behavior and reinforcement of a competitor one, even if is not explicitly identified.
3. *Response-initiated delays in reinforcement*, based on the knowledge that response rate decreases as the interval between target behavior and reinforcer delivery increases (known as the delay-of-reinforcement gradient), due to the breaking of the response-reinforcer contiguity.

To exemplify how omission training works coupled with response-initiated delays, consider the procedure where an established response by means of reinforcer delivery is now punished by delays to the reinforcer initiated by each of those responses. This is the case of spout-licking when food is intermittently delivered to moderately food-deprived rats, as shown in Fig. 2. Rats developed a fair number of licks per reinforcer delivery during the first experimental phase (identified as Stage A), then behavior was reduced by negative punishment for master rats (filled circles) during Stage B, and when the delay contingency was removed in the final Stage A behavior resumed. In that particular experiment, delays were signaled by houselight off, but they could be unsignaled (similarly effective), and they were resetting (initiated by each response), but they could be non-resetting (just initiated by the first response, normally not as effective).

A similar lick-contingent delay procedure can be used to reduce initial acquisition of behavior, as shown in Fig. 3, in which individual rats submitted to such negative punishment (filled circles) reduced or abolished acquisition of spout-licking behavior depending on the length of the contingent unsignaled delays. When delays were removed during a second experimental phase, licking developed further in most of the master rats. Thus, negative punishment is an effective procedure not only to reduce already acquired behavior but to impede the establishment of new behavior.

## Ethical Punishment and Societal Issues

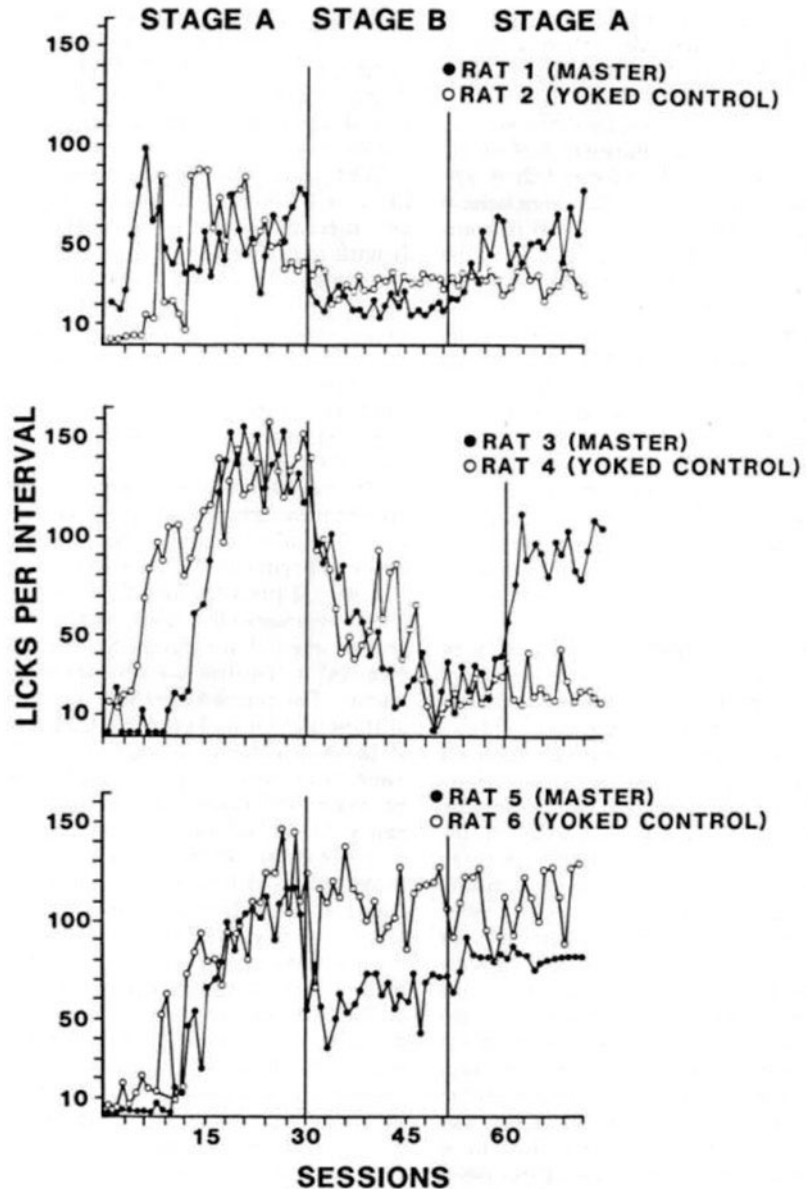
For punishment to be effective it should be contingent upon behavior, be consistently applied and be sufficiently intense, as seen before, therefore its application in cases of aversive stimulation cast some doubts in terms of its potential side effects, its potential misuse, and the ethical issues related to the application of aversive treatments to change behavior.

The undesirable consequences in the application of positive punishment, along its lack of long-term suppressive effects, led B. F. Skinner to question the application of punishment in favor of reinforcement as the way behavioral interventions should follow. In *Science and Human Behavior*, he wrote:

Severe punishment unquestionably has an immediate effect in reducing a tendency to act in a given way. This result is no doubt responsible for its widespread use. We ‘instinctively’ attack anyone whose behavior displeases us – perhaps not in physical assault, but with criticism, disapproval, blame, or ridicule. Whether or not there is an inherited tendency to do this, the immediate effect of the practice is reinforcing enough to explain its currency. In the long run, however, punishment does not actually eliminate behavior from a repertoire, and its temporary achievement is obtained at tremendous cost in reducing the over-all efficiency and happiness of the group. (p. 190)

Furthermore, in *Beyond Freedom and Dignity* (Skinner 1971, p. 83), he wrote: “A person who has been punished is not thereby simply less

**Punishment, Fig. 2** Daily mean licks per food pellet for individual rats. Stage A: food pellets were delivered at regular 60 s intervals [a fixed time (FT) schedule]. Stage B: FT 60 s, but with each lick made by a master rat initiating a 10-s delay in food delivery, accompanied by blackout. A yoked rat received food at the same time as its master, but no blackout. During final Stage A there were reinstated the original conditions of the experiment. (Reprinted with permission from Pellón, R., & Blackman, D. E. (1987). Punishment of schedule-induced drinking in rats by signaled and unsignaled delays in food presentation. *Journal of the Experimental Analysis of Behavior*, 48(3), 417–434. <https://doi.org/10.1901/jeab.1987.48-417>)



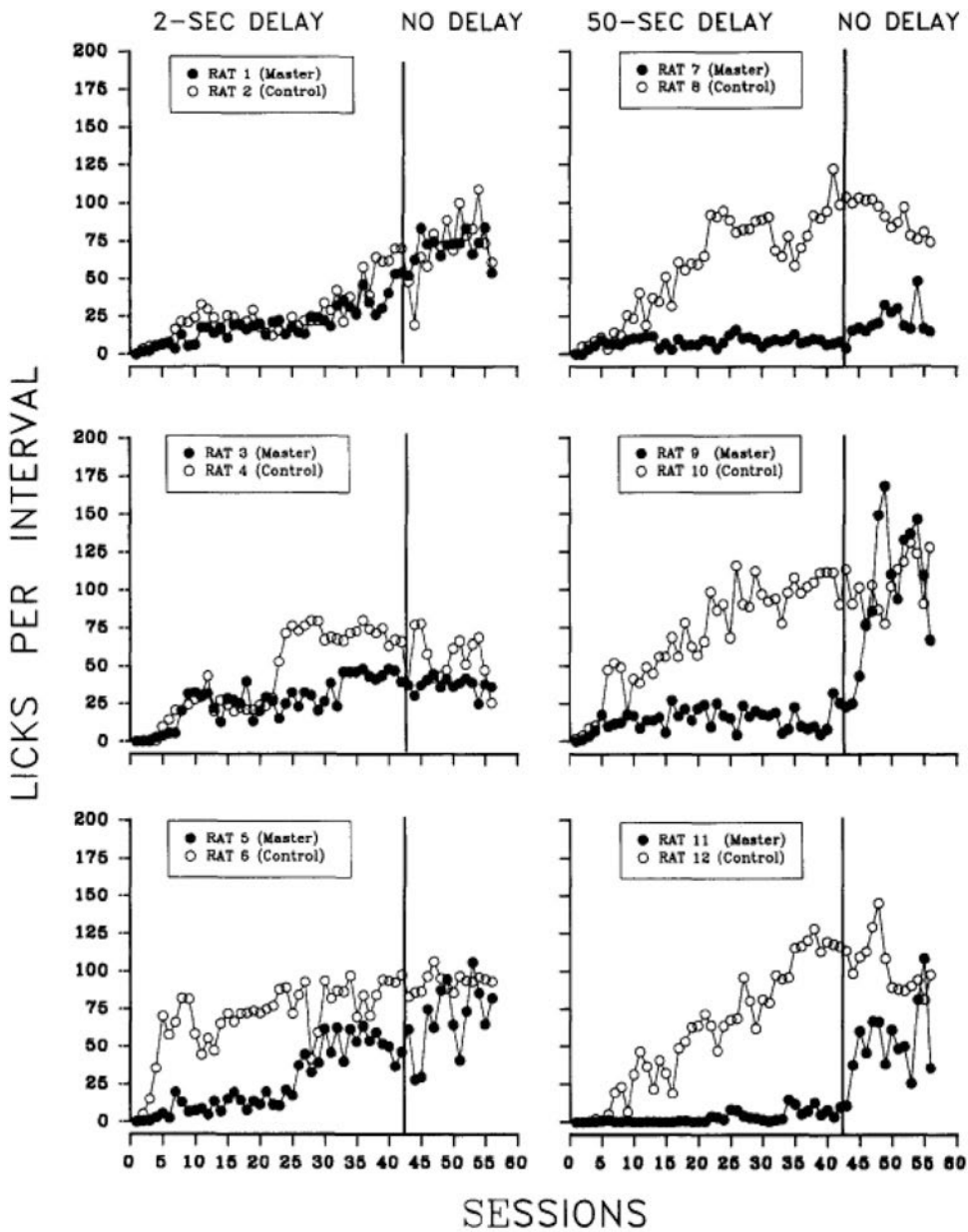
inclined to behave in a given way; at best, he learns how to avoid punishment,” thus emphasizing the role of negative reinforcement to account for the suppressive effect of positive punishment.

Thus, punishment (positive) often does not seem to outcompete reinforcement at a behavioral level, nor does it appear to do so at a neurobiological level. For example, there seems to be a longer-lasting neural activity after reinforcement than after non-reinforcement or punishment

(Histed et al. 2009). Therefore, the use of explicit reinforcement for alternative responses in combination with extinction of target behavior is advised with negative punishment procedures.

Behavioral recommendations for societal applications of punishment should promote a move from positive punishment to negative punishment and reinforcement of alternative behavior as interventions to reduce undesired behavior. Good contexts can be offered by psychiatric





**Punishment, Fig. 3** Daily mean licks per food pellet for individual rats. Food pellets were delivered at regular 60 s intervals [a fixed time (FT) schedule], and during the first experimental phase each lick made by a master rat initiated a 2- or 50-s unsignaled delay in food delivery. Yoked rats received food at the same time as their masters, but there was no contingency imposed on their licking. During the

second phase of the experiment, food was simply delivered according to the FT 60-s schedule to all rats. (Reprinted with permission from Lamas, E., & Pellón, R. (1995). Food-delay duration and the development of schedule-induced polydipsia in rats. *Physiology and Behavior*, 57(6), 1221–1224. [https://doi.org/10.1016/0031-9384\(94\)00371-B](https://doi.org/10.1016/0031-9384(94)00371-B))

settings or prisons. In the latter case, incarceration normally combines positive and negative punishment, and with the efficacy of positive

punishment being questioned (Apel and Diller 2017), there is room to explore a major role of prisons as places for removal of positive

reinforcement for challenging behavior in combination with the opportunity for reinforcement of alternative behaviors.

## Punishment in Other Disciplines

It may be useful to note that certain disciplines have their own definitions of punishment, which may be closer to the vernacular. In criminology, for example, punishment is typically defined by its purposes (to physically prevent the criminal offender from hurting society, to rehabilitate the offender, to deter the offender and others from further crime, and to get retribution). Such definitions do not require that the purpose to reduce the probability of target behavior is met.

## Conclusion

Punishment is an effective procedure to reduce behavior. However, the application of contingent aversive stimuli upon behavior has cast some ethical doubts and many have questioned its net efficacy. The use of alternative negative punishment procedures, which effectively reinforces alternative behavior, provides techniques capable of reducing undesired behavior without the implication that the use of aversive stimulation might have, thus providing a good alternative for parents, teachers, and applicants of behavioral techniques.

## Cross-References

- [Animal Models](#)
- [Animal Psychopathology](#)
- [Anticipation of Future Events](#)
- [Approach/Withdrawal Theory](#)
- [Avoidance](#)
- [B.F. Skinner](#)
- [Behavior Systems](#)
- [Behaviorism](#)
- [Comparative Psychology](#)
- [Contingency](#)
- [Delay of Reinforcement](#)
- [Delayed Gratification](#)
- [Edward Thorndike](#)
- [Environmental Influences](#)
- [Escape Response](#)
- [Extinction in Learning](#)
- [Foraging](#)
- [Free Operant Response](#)
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- [Passive Avoidance Learning](#)
- [Positive Reinforcement](#)
- [Reinforcement](#)
- [Schedule-Induced Behavior](#)
- [Schedules of Reinforcement](#)
- [Self-Injurious Behavior](#)
- [Species-Specific Behavior](#)
- [Stimulus Control](#)

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## Purpose

► [Goal](#)

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## Putative Candidate Gene

► [Candidate Gene](#)

# Q

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## QTL

### ► QTL Linkage Analysis

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## QTL Linkage Analysis

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## Synonyms

Pedigree mapping; QTL; QTL mapping

## Definition

Quantitative trait locus (QTL) linkage analysis is a statistical tool which is used to correlate the genotype of a polygenic trait using molecular markers at different genomic locations and the complex phenotype that underlie a quantitative variation.

## Introduction

The quantitative genetics is aimed at anatomization of complex traits. There have been several

advancements in this field, e.g., increased availability of molecular markers combined with enhanced statistical analysis has given many new tools to quantitative geneticists. One such tool is to use quantitative trait locus (QTL) detection methods which utilizes phenotypic and molecular marker data collected in designed biparental mapping populations of large size (Boer et al. 2007 ; Bink et al. 2012).

In order to dissect the QTL detection methods, let us first understand what is quantitative trait and what is quantitative trait locus (QTL). A trait that has measurable phenotypic variation due to interaction of multiple genetic and environmental factors is referred to as a quantitative trait. This variation can display discrete values, e.g., neural tube defects (NTD), or can be continuous such as measurement of height, weight, and blood pressure. The QTL is referred as genetic loci, the alleles of which contribute to the phenotypic variation. QTLs represent a fascinating biological phenomenon that is fundamental to our understanding of human phenotypic variation (e.g., height, weight, skin color). They are also responsible for diversity in human disease susceptibility and severity. Quantitative genetics is largely influenced by allelic frequencies and allelic effects.

Mapping genes associated with various traits and diseases has been one of the most important research areas in human genetics. The process of mapping genes has several steps, but the most critical step is the use of statistical methods for

identifying areas of genome where the target genes are likely to lie. These statistical methods can be broadly divided into two categories: linkage methods and association methods. Linkage methods use family data and try to detect cosegregation of traits and shared genetic material within families. Linkage analysis allows mapping of genes, including genes associated with diseases which are detectable as phenotypic traits only. It is based on measuring the frequency with which two genes remain together through meiosis as they are passed from one generation to the next. Genetic linkage analysis utilizes the frequency of recombination to measure how close genetically different loci are to each other.

The resolution of mapping in QTL linkage studies is dependent on the number of meiosis events. Hence, accounting the meiosis events that have occurred in the ancestors of the parents of the mapping population should be beneficial in the detection of QTL and locating these QTL precisely on the genetic map. A Bayesian approach to combine parental identity by descent (PIBD) information into a QTL linkage analysis was proposed in 2012 by Bink and his coworkers. The parental identity by descent (PIBD) information corresponds to the parents of the connected populations that form the analysis dataset. However, it is assumed that this information is in the form of an identity by descent (IBD) matrix which is specific to a particular marker. QTL linkage analysis is based on the principle that genes and markers segregate via chromosome recombination (crossing over) during meiosis (i.e., sexual reproduction), thus allowing their analysis in the progeny (Patterson 1996). Genes or markers that are close together will be transmitted together from parent to progeny more frequently than genes or markers that are located farther apart.

## What Do We Need for QTL Analysis?

For QTL analysis, we need:

1. A large population of individuals that can be scored for variation in phenotype

2. Markers all over the genome to pinpoint QTL location
3. A way for identifying which markers from each parent have been inherited to the progeny
4. Map of the genome

## QTL Mapping

A detailed genome-wide analysis of the link between genotype at different genomic locations and phenotype for a set of quantitative traits with respect to number, genomic positions, effects, and interaction of quantitative trait loci is referred to as QTL mapping (Zeng 2006). With the help of QTL mapping, we can analyze whether phenotypic differences are due to few loci with greater effect or due to many loci, each having some additive effect.

### Analysis of Variance (Crosses 2001)

The simplest method for QTL mapping is analysis of variance at the marker loci (Soller et al. 1976). This method is also known as ANOVA or marker regression. In this method in a backcross, a t-statistics can be applied to compare the averages of the groups of two marker genotypes. In some other types of crosses (e.g., intercrosses), there is a possibility of getting more than two genotypes, in such cases a more general form of ANOVA is used, which provides F-statistics. There are mainly three shortcomings of this mapping method:

1. A separate estimate of QTL location and QTL effect is very hard to obtain.
2. Individuals whose genotypes are missing at the marker site cannot be taken into account.
3. QTL may be very far from all the markers if markers are widely spaced and hence the extent to which QTL may be detected will decrease.

### Interval Mapping

Interval mapping is popularly used for QTL mapping in experimental crosses. Interval mapping takes into account the use of a genetic map of the typed markers and assumes the presence of a single QTL. In this method, each locus is



considered one at a time, and the **logarithm of the odds ratio** (LOD score) is calculated. The odds ratio is related to the phenotype and the genotype of the marker for every individual in the cross, through Pearson correlation coefficient (Lynch and Walsh 1998). It is used to estimate the position of a QTL within two markers and was originally based on the maximum likelihood.

### Composite Interval Mapping (CIM)

In this method, interval mapping is performed, where marker loci are used as covariates. These markers act as surrogate for other QTLs to improve resolution of interval mapping by accounting for linked QTLs and minimizing the residual variation. One of the major disadvantages with this method is the selection of suitable marker loci which can serve as covariates.

### Family-Based QTL Mapping/Family Pedigree-Based QTL Mapping

Family-based QTL mapping involves multiple families instead of a single family. This type of mapping is the only way to map genes where

experimental crosses are difficult to make. It may include linkage and association mapping.

Linkage analysis is the primary tool for gene discovery, localization, and functional analysis and is the phenomenon whereby alleles at different loci cosegregate in families. Linkage between markers is calculated by odds ratios. Odds ratio is the ratio of linkage versus no linkage. This ratio is expressed as the logarithm of the ratio and is called a logarithm of odds (LOD) value or LOD score (Risch 1992). LOD values of  $>3$  are generally used for constructing linkage maps. A LOD value of 3 between two markers indicates that linkage is 1000 times more likely (i.e., 1000:1) than no linkage (null hypothesis). LOD values can be lowered for detecting a greater level of linkage or for including additional markers within maps that have been constructed at higher LOD values. The odds ratio provides a valid statistical method for using the family data to estimate the recombination frequency. The LOD score is represented as “Z.” Positive value of Z suggests that two loci are linked, whereas negative value indicates that linkage is less likely than the possibility that loci are unlinked. LOD score is calculated as under:

$$\text{LOD score} = Z = \log_{10} \left\{ \frac{\theta^{(\text{frequency of recombinants})} \times (1 - \theta)^{(\text{frequency of non recombinants})}}{1/2^{(\text{frequency of recombinants})} \times \frac{1}{2}^{(\text{frequency of non recombinants})}} \right\}$$

$\theta$  = probability of recombination

$1 - \theta$  = probability of non-recombination

The estimation of identity by descent (IBD) matrix is a very important component in mapping of QTL using variance component model. Alleles are identical by type (IBT) when they are producing the same phenotypic effect. There are two groups of allele which are identical by type:

- (i) Identical by descent (IBD) since they originated from same allele in previous generation
- (ii) Nonidentical by descent (NIBD) or identical by state (IBS) as they originated from separate mutations

Parent-offspring pairs have 50% of their genes that are identical by descent, and monozygotic twins have 100% genes that are identical among themselves by descent. In linkage analysis, inheritance of alleles at adjacent loci is important; therefore, it is critical to identify whether the alleles are identical by descent or only identical by state. Three categories of family-based linkage analysis are there; they have been summed up as under:

- (i) Strongly modeled (the LOD score model)
- (ii) Weakly modeled (variance components methods)
- (iii) Model-free

Lander and Kruglyak (1995) proposed certain criteria for reporting the significance of a linkage

relationship on the basis of standard genome scans in intercross and backcross populations. These criteria for statistical significance have now become standard practice: “highly significant” refers to  $p < 0.001$ , “significant” refers to  $p < 0.05$ , and “suggestive” refers to  $p < 0.63$  after correcting for multiple testing in a genome-wide scan. Permutation analysis is a more common approach that is likely to yield QTLs without affecting statistical significance. While reporting QTL map positions, the LOD score, the peak position, and an estimate of the confidence interval should be given. This allows to compare the map position with that for other QTLs that control potentially related traits. It may be possible that a QTL might fall outside a calculated confidence interval region owing to problems in marker order, genotyping errors, and/or model misspecification (Complex Trait Consortium 2003). In such cases, QTLs are difficult to identify, and overlaps between QTLs are difficult to determine. Any significant linkage should be confirmed before moving ahead for fine mapping.

### Construction of Linkage Map (Collard et al. 2005)

Linkage maps have been widely used in identification of chromosomal locations with genes and QTLs that are associated with traits of interest; such maps are referred to as “genetic” or QTL maps. There are three main steps of linkage map construction:

- (i) Production of mapping population
- (ii) Identification of polymorphism
- (iii) Linkage analysis of markers

The construction of linkage map requires a segregating population. Population size generally ranges from 50 to 250 individuals (Mohan et al. 1997). For linkage maps, which will be used for QTL mapping, it is important to note that mapping population must be phenotypically evaluated before proceeding for QTL mapping.

After production of mapping population, the next step is to identify polymorphic markers.

Once polymorphic markers have been identified, they must be checked across the entire mapping population including the parents. This process is known as marker genotyping of the population. Significant deviations from expected ratios can be analyzed using chi-square test. In general, markers will segregate in a Mendelian fashion; however, distorted segregation may also be encountered (Sayed et al. 2002; Xu et al. 1997). The final step in the construction of a linkage map involves coding data for each DNA marker on each individual of a population and conducting linkage analysis using computer programs. Though linkage analysis can be performed manually for a few markers, it is not feasible to manually analyze and determine linkages between large numbers of markers that are used to construct maps.

Software programs that are widely used are Mapmaker/EXP and MapManager QTX, which are freely available. “JoinMap” is also a commonly used software for constructing linkage maps (Stam 1993).

### Softwares for QTL Linkage Analysis

#### MapQTL

MapQTL is a program for the analysis of quantitative trait loci (QTL) in experimental populations of diploid species. MapQTL is a MS Windows program. This program can analyze QTL experiments with interval mapping, with MQM mapping, and with a nonparametric method. <https://www.kyazma.nl/index.php/MapQTL/>

#### QTL IciMapping (Meng et al. 2015)

QTL IciMapping is a software that is freely available, generally used for generating high-density linkage maps and mapping of QTL in biparental populations. Eight functionalities have been integrated in this software package. They are:

1. BIN: binning of redundant markers
2. MAP: construction of linkage maps in biparental populations
3. CMP: consensus map construction that is generated from multiple linkage maps which share common markers

4. SDL: mapping of segregation distortion loci
5. BIP : mapping of additive, dominant, and digenic epistasis genes
6. MET : QTL by environment interaction analysis
7. CSL : mapping of additive and digenic epistatic genes which have chromosome segment substitution lines
8. NAM : QTL mapping in NAM (nested association mapping) population

Input files are usually plain text, MS Excel 2003, or MS Excel 2007 formats. The prefix name is similar for output and input files but with different extensions.

## Conclusion

The genomic regions that contain genes which are associated with a particular quantitative trait are known as quantitative trait loci. Multiple genes control the expression of quantitative traits. The use of DNA markers with construction of linkage maps is vital for identifying chromosomal regions that contain genes controlling simple traits and quantitative traits using QTL analysis. Application of QTL linkage analysis is an important tool for identifying genomic regions associated with traits. Once QTL has been identified, molecular techniques can be employed to narrow down QTL to candidate gene. One of the major drawbacks in QTL analysis is at the level of phenotyping.

Genome-wide association studies (GWAS) have been a popular tool in genetic research, and they are an excellent complement to QTL mapping. Whereas QTL contain many linked genes, GWAS produce many unlinked individual genes and sometimes even nucleotides. Though GWAS remain limited to organisms with genomic resources, combining GWAS, the two techniques can utilize most of both approaches. Although GWAS, next-generation sequencing, and many other high-throughput robust techniques came into picture during the past few years, the use of linkage analysis is still a very precise classical technique for identifying novel candidate genes and potential candidate genes.

QTL studies have a long and rich history and have played important roles in gene cloning and characterization; however, there is still a great amount of work to be done. The available data on model organisms should be expanded to the point where meta-analysis is practically possible in order to account for robust trends with regard to genetic architecture. Moreover, QTL studies can be an important tool for studying functional genomics as well, where allelic variation is characterized. The correlation between genotype and phenotype is still difficult to evaluate, but QTL analysis will likely continue to provide key advancements in functional genomics.

## Cross-References

- ▶ [Linkage Analysis](#)
- ▶ [Quantitative Genetics](#)
- ▶ [Quantitative Trait Loci \(QTL\)](#)

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## QTL Mapping

### ► QTL Linkage Analysis

## Quadrumanous

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## Synonyms

Grasping hands and feet

## Definition

Having both hands and feet that are capable of grasping

In the most basic sense, *quadrumanous* represents the anatomical and neuromuscular modification of the *hands and feet* that allows them similar functional roles of grasping onto supports or other objects (Boyer et al. 2013; Gebo 1985; Napier 2009). Traditionally the term *quadrumanous* has been applied only to the nonhuman primates, but it is important to note that such an anatomical configuration has evolved in other tetrapod lineages, albeit rarely (Sustaita et al. 2013; Fig. 1). The most notable are the highly arboreal lizards of the family Chamaeleonidae. In these animals, the digits of the feet and hands are organized into bundles (i.e., group of two and a group of three digits) which oppose one another to grasp branches in a pincer-like arrangement (Sustaita et al. 2013). The *quadrumanous* configuration of the hand and foot is also observed in the arboreal anteaters (*Tamandua* and *Cyclopes*) and sloths (*Choloepus* and *Bradypus*) (Godfrey et al. 2016; Granatosky 2016). In these animals, a reduction of the digits has essentially modified the hands and feet into large hooks. A similar condition, albeit without the digital reduction, is observed in the colugos. These animals are able to utilize these hooks as grapples to maintain security during arboreal locomotion (Granatosky 2016).

In the nonhuman primates, a different pattern of grasping has evolved where the first digit (i.e., pollex in the hand; hallux in the foot) is divergent from the rest of the digits (Boyer et al. 2013; Gebo 1985; Napier 2009). This configuration allows for opposition of the pollex and hallux against the other digits, therefore allowing the generation of grasping forces (Cartmill 1985; Napier 2009). Interestingly, the grasping ability of the hand and foot did not evolve in synchrony. Early primates appeared to have evolved grasping abilities first in the foot, while the hand retained a claw-clinging grasp (Boyer et al. 2013). This configuration is typical of many of the living arboreal didelphids (Cartmill 1985). Only at the origins of Euprimates did the “typical” *quadrumanous* configuration of





**Quadrumanous, Fig. 1** Examples of quadrumanous grasping in tetrapods

the hands and feet arise (Boyer et al. 2013). Anatomical evidence for grasping extremities in primates are usually characterized by a lack of nails, elongated digits, and a divergent pollex and hallux (Boyer et al. 2013; Cartmill 1985; Gebo 1985).

The functional and evolutionary origins of the *quadrumanous* condition have invariably been linked to the challenges of moving on thin arboreal supports (Cartmill 1985). The terminal ends of branches provide important foraging locations for animals, as they are often the site of young leaves, fruit, blooming flowers, and insect prey. Access to these branches, however, is difficult for animals of relatively large body and presents these animals with novel mechanical challenges compared to movement on larger diameter supports (Granatosky et al. 2016). As the body size to support size ratio increases, the tendency to topple off the support also increases (Cartmill 1985; Grand 1972). One solution to this balance problem may be for arboreal animals to move their center of mass below branch, thereby adopting suspensory behaviors (Cartmill 1985; Granatosky 2016; Grand 1972). This is the condition for orangutans,

colugos, and sloths. In these animals, the hands and feet are modified into *quadrumanous* hooks that prevent the animal from falling off the support (Godfrey et al. 2016; Granatosky 2016).

In contrast, non-suspensory arboreal quadrupeds (e.g., primates and chameleons) use powerful grasping musculature to overcome the toppling torques imposed upon the body (Boyer et al. 2013; Cartmill 1985; Gebo 1985). While the presence of grasping feet alone seems to be enough to overcome these toppling torques (e.g., arboreal didelphids) (Cartmill 1992; Sustaita et al. 2013), it is likely that the *quadrumanous* condition observed in primates and chameleons has allowed for the invasion of the fine branch niche and exploitation of the resources available within this environment (Boyer et al. 2013; Cartmill 1985; Grand 1972).

## Cross-References

- [Adaptation](#)
- [Arboreality](#)



- [Catarrhine Locomotion](#)
- [Catarrhine Morphology](#)
- [Evolution](#)
- [Haplorhini](#)
- [Hominid](#)
- [Hominoid](#)
- [Hominoidea Locomotion](#)
- [Marsupial Locomotion](#)
- [Marsupial Morphology](#)
- [Platyrrhine Locomotion](#)
- [Primate Locomotion](#)
- [Primates](#)
- [Prosimian Locomotion](#)
- [Prosimian Morphology](#)
- [Quadrupedal](#)
- [Skeletal System](#)
- [Zoology](#)

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## Quadrumanous Locomotion

- [Primate Suspensory Behavior](#)

## Quadrupedal

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## Synonyms

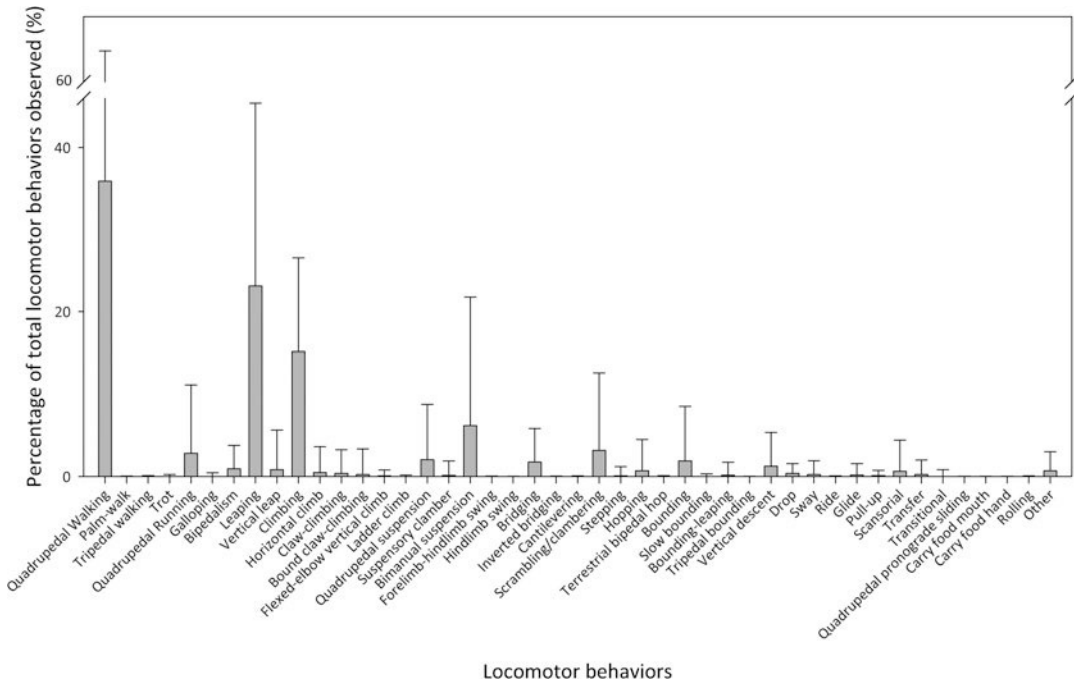
[Quadrupedalism](#)

## Definition

Movement using a combination of four limbs.

**Quadrupedal** locomotion encapsulates any form of progression in which four limbs support and propel the body. **Quadrupedal** movement represents the basal condition for all tetrapods and as such remains the most commonly utilized form of locomotion (see Fig. 1 and Granatosky 2018 for data on mammals). Interestingly, the origins of **quadrupedal** locomotion appear to predate the invasion onto land by tetrapods. Experimental studies on living sarcopterygians (i.e., lungfish and coelacanths) demonstrate that the neuromuscular patterns and functional subdivisions of the “limbs” required for effective **quadrupedal** locomotion were likely present in fully aquatic tetrapod ancestors prior to the invasion onto land (Aiello et al. 2014; Décamps et al. 2017; Fricke and Hissmann 1992).

**Quadrupedal** locomotion is usually categorized as symmetrical or asymmetrical based on kinematics and then further subdivided into walking and running on the basis of either kinematics or kinetics (Fig. 2; Alexander 2003; Cavagna et al. 1977). Symmetrical gaits occur when footfalls of the forelimb and hindlimb are evenly spaced in



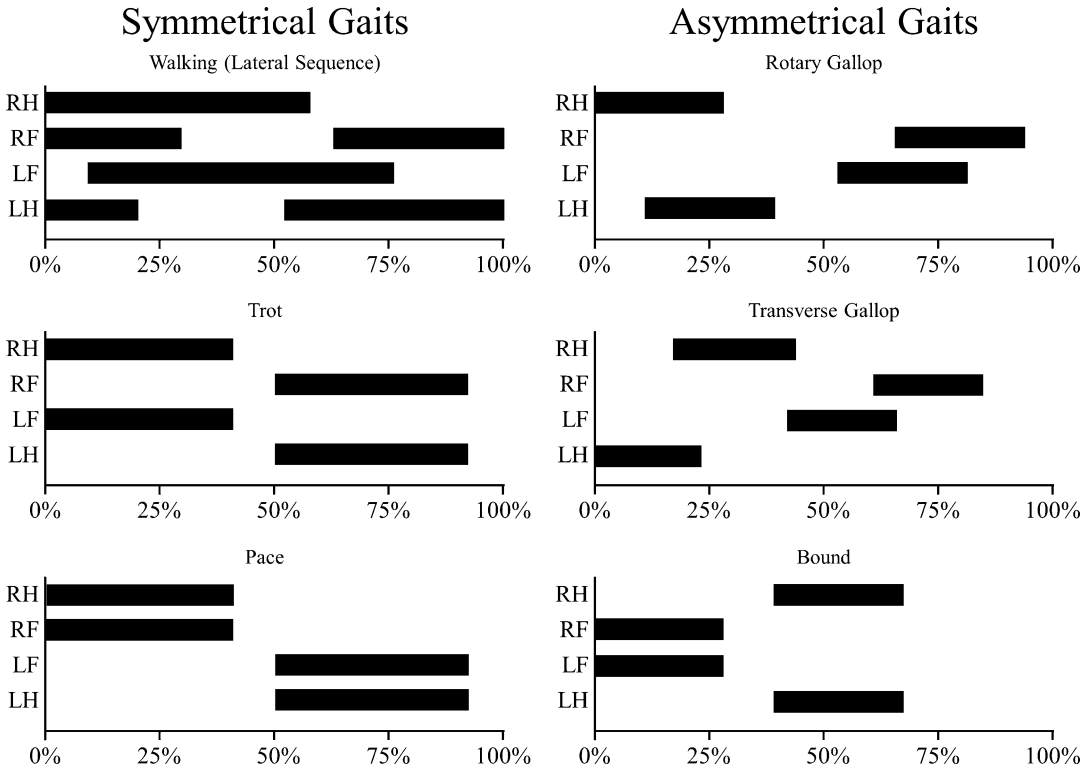
**Quadrupedal, Fig. 1** The percentages of locomotor behaviors observed for extant mammals. (Adapted from Granatosky (2018))

time (e.g., walk, pace, or trot). Asymmetrical gaits (e.g., gallop and bound) occur when the actions of the forelimb or hindlimb are unevenly spaced in time. A kinematic definition of a walking gait is one with a duty factor over 50%, while gaits with duty factors less than 50% are considered a run. A duty factor is simply the percent of the total cycle which a given foot is on the ground. Alternatively, it is possible to divide walking and running based on center of mass mechanics (Cavagna et al. 1977). During walking, the center of mass is analogous to a swinging inverted pendulum. With this mechanism, kinetic and potential energy are exchanged out of phase with each other as the animal's center of mass rises and falls throughout a stride. During running gaits (e.g., hopping, trotting, or galloping), center of mass movements move in phase with one another, analogous to a spring or bouncing ball. In mammals, the kinematic and kinetic definition of walking and running tend to describe the same behavior. However, recent work looking at the center of mass mechanics in reptiles and amphibians demonstrates the relationship is less clear (Reilly

et al. 2006). As such, further discussion in this chapter will be reserved to kinematic patterns.

## Walking Gaits

All walking gaits are symmetrical and involve two general patterns at which animals move their limbs (Alexander 2003). A lateral-sequence gait is one in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb). A diagonal-sequence gait is one in which each hindlimb footfall is followed by a contralateral forelimb footfall (i.e., right hindlimb, left forelimb, left hindlimb, right forelimb). Commonly, during walking gaits the forelimbs and hindlimbs are traveling together as a slightly asynchronous couplet. When the ipsilateral forelimbs and hindlimbs are traveling together, this is referred to as a lateral couplet; when the contralateral forelimbs and hindlimbs are traveling together, this is referred to as a diagonal couplet. Very rarely do the limbs move together in perfect synchrony.



**Quadrupedal, Fig. 2** Gait graphs. Dark areas indicate times of contact; bottom axis is % of cycle. RH = right hindlimb; LH = left hindlimb; RF = right forelimb; LF = left forelimb

Lateral-sequence lateral-couplet footfall patterns tend to be present in long-legged terrestrial animals and are assumed to be the best mechanism to prevent interlimb interference. However, this footfall pattern is thought to be inherently unstable because a majority (~66%) of the stride is spent as a unilateral bipod (i.e., only two ipsilateral limbs in contact with the support), which tends to roll the body side-to-side throughout the stride. This instability is argued to be negligible for long-legged animals but can be devastating for short-limbed broad-chested quadrupeds. For these species, lateral-sequence diagonal-couplet footfall patterns tend to be more common. This footfall sequence is inherently more stable than lateral-sequence lateral-couplet gaits due to the generally low proportion of the stride spent as a unilateral bipod (~22%) and the relatively high proportion of the stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed

limbs in contact with the support). In general, foot positions arranged as diagonal bipods and large tripods are thought to be highly stable (Cartmill et al. 2002).

Primates and other highly arboreal mammals tend to use diagonal-sequence diagonal-couplet footfall patterns when moving along relatively thin arboreal supports (Cartmill et al. 2002; Granatosky et al. 2016; Hildebrand 1967). This gait pattern maximizes the proportion of the stride in which the limbs are arranged as a widely splayed diagonal bipod and ensures that one of the grasping hindfeet is placed in a protracted position (and thus lies roughly underneath the animal's center of mass) on a tested support at the moment when the contralateral forefoot strikes down on an untested support during arboreal locomotion (Cartmill et al. 2002; Lemelin and Cartmill 2010). The legitimacy of this adaptive scenario for diagonal-sequence diagonal-couplet gaits has received considerable debate (see

Shapiro and Raichlen 2005). Diagonal-sequence lateral-couplet gaits are rarely observed in nature and are considered highly unstable.

## Running Gaits

The trot, pace, and amble are symmetrical *quadrupedal* runs. All running gaits include some period of the cycle in which no feet are touching the ground (i.e., an aerial phase). In trotting, diagonally opposite feet move in phase with each other; in pacing, the two feet on the same side of the body move in phase with each other; and in ambling, the four feet move at roughly equal intervals, in the same order as in walking. Most quadrupeds trot when traveling at moderate speeds, but camels' pace and elephants sometimes amble (Alexander 2003; Hildebrand 1976).

At high speeds, *quadrupedal* mammals use asymmetrical gaits, generally making the change from a trot or pace to a gallop. Early studies (Muybridge 1887) identified two fundamental types of gallop variously called the diagonal or transverse gallop and the lateral or rotary gallop. These were fully described in detail in the classic paper by Hildebrand (1959), where the transverse gallop is epitomized by the horse and the rotary gallop by the cheetah (Fig. 3). The canter, which is recognized by horse riders as a distinct gait, is a form of galloping used at low speeds. Galloping mammals arch their backs during the part of

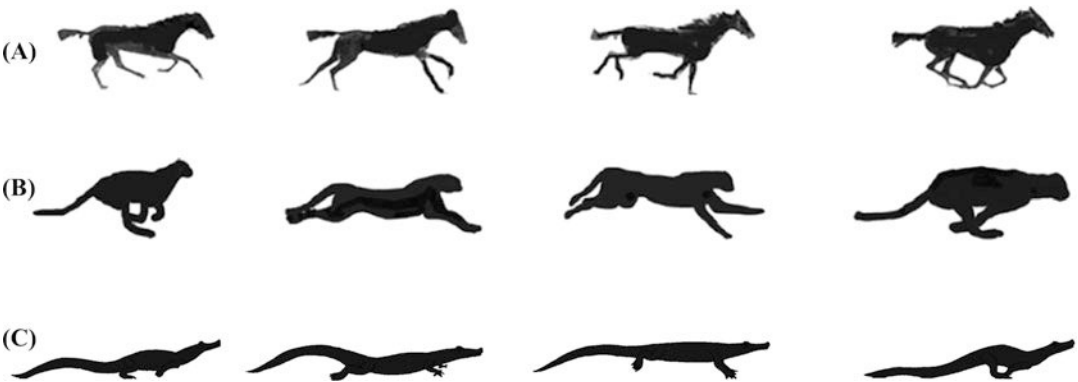
the stride when the fore feet are on the ground and straighten them while the hind feet are on the ground (Alexander 2003).

In general, running gaits in reptiles are usually constrained to trotting. However, some crocodilian species are capable of adopting asymmetrical galloping gaits. This is exemplified in the Australian freshwater crocodile (*Crocodylus johnstoni*). The crocodilian gallop has been described as the fore- and hindlimbs working in serial pairs similar to that of a bounding gait (Fig. 3). However, these movements are highly variable, and animals have been recorded using a transverse or rotary gallop, a half bound, or a bound (Renous et al. 2002; Zug 1974). This diversity of asymmetrical gaits in *C. johnstoni* is not overly surprising considering patterns of rhythmicity in bradymetabolic (poikilothermic) tetrapod lineages (Ross et al. 2013).

## Gait Transitions

A general feature of *quadrupedal* locomotion by mammals is that, as they increase speed, they switch between gaits (e.g., walk, run, trot, gallop) (Griffin et al. 2004; Hoyt and Taylor 1981). While numerous studies have characterized gait transitions from kinematic, kinetic, and metabolic perspectives, the mechanism triggering gait transitions remains unclear.

The most commonly cited function of gait transitions is to minimize energetic expenditure



**Quadrupedal, Fig. 3** Examples of a transverse gallop in a horse (a) and a rotary gallop in a cheetah (b) and crocodile (c)

(Griffin et al. 2004; Hoyt and Taylor 1981). In an idealized situation, plots of energetic cost of transport per unit distance (COT;  $\text{J kg}^{-1} \text{m}^{-1}$ ) against locomotor speed reveal intersecting curvilinear relationships for different gaits (e.g., walking, trotting, galloping) (Griffin et al. 2004; Hoyt and Taylor 1981). The peaks of the lines are locomotor speeds with a high COT, and the valleys are speeds with lower energetic costs. For the most part, when animals are allowed to move at self-selected speeds, they select the most economical speeds within a given gait type and avoid speeds that are more energetically costly (Griffin et al. 2004; O'Connor et al. 2012). However, as animals adopt speeds near the peaks of their gait-specific COT curves, energy costs increase rapidly. This makes it energetically costly to maintain those gaits, and gait transitions become critical for energy conservation (Griffin et al. 2004; Hoyt and Taylor 1981).

This energy minimization hypothesis for gait transitions is not without its critics (Brisswalter and Mottet 1996; Farley and Taylor 1991). In light of limitations to the energetic minimization hypothesis, a number of studies have proposed that animals use mechanical triggers to make gait transitions to preemptively limit high stresses on the bone (Biewener and Taylor 1986; Farley and Taylor 1991). As first observed by Farley and Taylor (1991), at the transition from a trot to a gallop, peak forces on the muscles, tendons, and bones, and presumably the chance of injury, are significantly reduced. Furthermore, when animals move with added weight, they switch from a trot to a gallop at a lower speed but at the same critical level of force. However, no such effect is observed during the transition from a walk to a trot or during the trot to gallop transition in small mammals (Iriarte-Díaz et al. 2006). Taken together, this evidence suggests that the forces applied to the musculoskeletal system likely do not trigger gait transitions, at least at the walk-trot transition.

An alternative approach to understanding gait transitions emerges from considering stability. When animals adopt speeds close to the optimal stride length and frequency for a particular gait type (e.g., walking or trotting), locomotion is

stable, highly rhythmic, and energetically efficient (Diedrich and Warren 1995; Granatosky et al. 2018; O'Connor et al. 2012). However, when an animal is forced to speed up or slow down, it enters more variable, potentially unstable locomotor conditions (Brisswalter and Mottet 1996; Diedrich and Warren 1995; Jordan et al. 2007). This suggests that unstable, highly variable locomotor states, like those preceding a gait transition, are noisier and less predictable than steady-state movement (Brisswalter and Mottet 1996; Granatosky et al. 2018; O'Connor et al. 2012). Sensorimotor feedback about these unstable conditions could help guide the animal to a new stable locomotor state (Granatosky et al. 2018). In this stability context, it has been suggested that gait transitions serve to reduce locomotor variability and avoid unstable states that might lead to injury or unnecessary energy expenditure (Brisswalter and Mottet 1996; Diedrich and Warren 1995; Granatosky et al. 2018).

## Cross-References

- [Adaptation](#)
- [Arboreality](#)
- [Artiodactyla Locomotion](#)
- [Bovine Locomotion](#)
- [Canine Locomotion](#)
- [Catarrhine Locomotion](#)
- [Caudata Locomotion](#)
- [Crocodilia Locomotion](#)
- [Equine Locomotion](#)
- [Evolution](#)
- [Feline Locomotion](#)
- [Greyhound Racing](#)
- [Hominoidea Locomotion](#)
- [Insectivore Locomotion](#)
- [Lagomorpha Locomotion](#)
- [Marsupial Locomotion](#)
- [Megachiroptera Locomotion](#)
- [Perissodactyla Locomotion](#)
- [Platyrrhine Locomotion](#)
- [Primate Locomotion](#)
- [Primates](#)
- [Proboscidea Locomotion](#)



- [Prosimian Locomotion](#)
- [Quadrumanous](#)
- [Rodentia Locomotion](#)
- [Salientia Locomotion](#)
- [Squamate Locomotion](#)
- [Swine Locomotion](#)
- [Zoology](#)

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## Quadrupedalism

### ► Quadrupedal

## Qualitative Disorders

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### Definition

Qualitative disorders are the type of genetic disorders that arise from change(s) in a single gene leading to suppression or abnormal expression of a gene causing corresponding phenotype with no intermediate form. The phenotypic representations are qualitatively accessible and not quantitatively.

### History

The linking of medical conditions with the concept of genetics was first done by Archibald Garrod in 1902 when he studied the recessive nature of inheritance of the disorder alkaptonuria, a rare genetic disorder which is characterized by the accumulation of homogentisic acid in the body due to mutation of the homogentisate 1,2-dioxygenase (HGD) gene. Later in 1911, E. B. Wilson then mapped the gene for color blindness to the X chromosome, and since then, about 36 X-linked disorders were mapped within the next 40 years (Kennedy 2005). According to the Online Mendelian Inheritance in Man (OMIM), approximately 4000 qualitative disorders have been identified.

## Autosomal Recessive Qualitative Disorders

The qualitative disorders that arise from mutation of the recessive allele of autosomes are called as autosomal recessive qualitative disorders. Being recessive, only homozygous condition will cause the disorder to manifest, i.e., both copies of the mutated recessive alleles need to be present. For a child to be affected, both the defective alleles must be inherited from both the parents, i.e., both the parents must be either carrier or affected individuals. With two carriers, there is 25% of having an unaffected normal child, 25% of having an affected child, and 50% of having an unaffected carrier child.

## Autosomal Dominant Qualitative Disorders

This type of qualitative disorders arise when there is a mutation of a dominant allele of a gene that will cause the manifestation of the disorder in both homozygous and heterozygous states. Individuals with such disorder have 50% chance of transmitting the disorder to their children. Examples of such disorder are Huntington disease, polycystic kidney diseases, neurofibromatosis, etc.

### Huntington Disease

Huntington disease is an autosomal dominant qualitative disorder that arises when there is a mutation in the huntingtin (HTT) gene located on the short arm of chromosome 4 that causes neuronal degeneration in the brain (National Institute of Neurological Disorder and Strokes 2019). The HTT gene has a trinucleotide repeat (CAG) that shows variations in length from individual to individuals. Dynamic mutation often results in increase in the number of trinucleotide counts resulting in a defective gene producing an altered mutant protein (mHTT), thereby causing different pathological changes in the body such as increased rate of neuronal death. Normally, the HTT gene is highly expressed in neurons, and its absence was found to induce embryonic death in mice (Nasir et al. 1995);

however, its primary function in human remains unclear. The physical symptoms of this disorder, collectively called as chorea, are first observed between the ages of 35 and 40. Chorea includes jerky and random movements. However, the cognitive and behavioral symptoms are not easily recognizable. Since the penetrance of the mHTT is high, even a single copy of the mutated allele is enough for the disorder to manifest.

### Phenylketonuria

Phenylketonuria (PKU) is an autosomal recessive qualitative disease that arises due to mutations in the PAH gene on chromosome 12 that encode the phenylalanine (Phe)-hydroxylating enzyme called phenylalanine hydroxylase (PAH; EC 1.14.16.1) that results in a production of a non-functional PAH enzyme. If untreated, blood level of Phe concentration is elevated and causes severe mental retardation with reduced levels of dopamine, catecholamine, and serotonin apart from other symptoms (Groot et al. 2010). Being a recessive condition, for this disorder to manifest, both the copies of the mutated alleles are required to be present. If both parents are carriers, the chance of a child being born with PKU is 25%. PKU remains incurable. However, upon early diagnosis, a child can be treated to minimize neurological damages through the management of the level of Phe in the system either through diet or medications or both.

### Sex-Linked Qualitative Disorder

Certain qualitative disorders are caused due to mutation of genes that are located on the sex chromosomes, usually the X chromosome. Such disorders are called as sex-linked qualitative disorders. The mutated/deleted allele may be either recessive or dominant. For X-linked disorders, in recessive form, a homozygous condition is also required for the disorder to occur. An affected female will always transmit the disorder to her son, while her daughter will simply be a carrier, unless both parents are affected. In dominant form, only a single allelic copy is sufficient, and an affected male will always transmit the disorder to

his daughter but never to his son. The common sex-linked qualitative disorders are hemophilia, X-linked hypophosphatemia, thalassemia, red-green color blindness, Duchenne muscular dystrophy, glucose-6 phosphatase deficiency disorder, etc.

### Hemophilia

Hemophilia is an X-linked recessive disorder that arises due to mutation in the gene for the clotting factors VIII (hemophilia “A”) and IX (hemophilia “B”) that compromises the activation of factor X during the process of blood coagulation and result in failure of blood to clot even in minor injuries. Point mutation in these gene is the most common mutation and accounts for 90% of all hemophilia. Such point mutations are usually missense, nonsense, or splice site point mutations (Bowen 2002). Deletion of the whole gene occurs in 5–10% of hemophilia. X-linked recessive disorders, including hemophilia, affect male more than female since female have two copies of X chromosome in which the one that carries the normal allele may compensate for the mutated genes. However, such female remains a carrier and has a 50% chance of transmitting the mutated genes to her offspring. The major problem associated with the treatment of hemophilia is the synthesis of antibodies against the infused clotting factors administered to the patient via replacement therapy. Researches have been going for the application of gene therapy for the treatment of hemophilia; however, this remains an unapproved strategy (National Heart, Lung, and Blood Institute 2013).

### X-Linked Hypophosphatemia

X-linked hypophosphatemia is an X-linked dominant disorder which exhibits ricket/osteomalacia-like symptoms that arise due to the mutation of the PHEX gene which is involved in the mineralization of bone and dentin. One important function of PHEX is the regulation of renal phosphate reabsorption by inhibiting the activity of fibroblast growth factor 23 (FGF-23) that promotes renal reabsorption of phosphate. Mutation of PHEX results in overactivity of FGF-23 and thus causes an excessive reabsorption of phosphate, thereby leading to

hypophosphatemia in the bloodstream (Farzana et al. 2007). In 2018, the FDA approved immunotherapy with the monoclonal antibody “Burosumab” for the treatment of X-linked hypophosphatemia (Carpenter et al. 2018).

## Symptoms of Qualitative Disorders May Be Pleiotropic Effect

Pleiotropy is the phenomenon where a single gene may have more than one phenotypic effect. This pleiotropic effect of a single gene may give rise to the different phenotypic representations of a qualitative disorder. For example, the monogenic disease Marfan syndrome is caused by either an inherited or sporadic mutation in the FBN1 gene located on chromosome 15. The FBN1 gene primarily encode for the microfibril Fibrillin-1 which forms part of the microfibrils in the heart valves and aorta along with Fibrillin-2 (Quondamatteo et al. 2002). The mutation in the FBN1 not only cause impairment in the structure of the heart valves but also exhibit other phenotypic symptoms such as thoracic scoliosis, thin and long limbs and digits, etc.

## Conclusion

Qualitative disorders are responsible for a heavy loss of life globally. The global prevalence of all single gene diseases at birth is approximately 10/1000 (Scriver 1995). Complete cure of qualitative disorders seems a far-fetched achievement as of now, although medications and replacement therapy are successfully employed for symptomatic treatment. Gene therapy, where the defective gene is replaced by a normal gene, has become promising for the definite cure of such disorders and is still a huge area of biomedical research.

## Cross-References

- Alleles
- Allele Sharing
- Candidate Gene

- Functional Genomics
- Quantitative Genetics

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## Quality

- Nature Versus Nurture

## Quantitative Genetics

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## Introduction

Most traits have a continuous spectrum and cannot be classified in discrete, qualitative categories such as height, weight, blood pressure, etc. Quantitative genetics is the field of genetics which deals with the study of continuously varying characters such as height, weight, blood pressure, etc. Continuous variation that is observed is usually because the traits are polygenic (when more than two genes control a particular type of trait or traits) and also there are environmental effects that has their own effect on the phenotypic state of each individual (Anderberg 1973; Mendel and Bateson 1891a, b; Steel and Torrie 1980; Hill 2010). To explain the effect of environmental factors on gene expression, let's understand it by this example, temperature is an environmental factor. Himalayan rabbits carry C gene which is temperature sensitive and is responsible for different coat colors of rabbits. This gene is active below 30 °C and inactive above 30 °C. Thus the rabbits that stay at cold temperature have pigmented body.

Traits which are controlled at single gene locus are called as Mendelian traits. These traits have two alleles dominant and recessive, inherited one from each parent. Dominant allele is expressed in both homozygous and heterozygous conditions, while recessive allele is expressed only in homozygous condition. One of the major differences between quantitative and Mendelian (qualitative) traits is the number of genes controlling them.

Each participating gene follows the Mendelian trait rules with each of them having some effect on the trait; this is called as polygeny. Another important difference between quantitative and qualitative traits is their sensitivity to environmental factors. Suppose our genes have the potential of gaining weight up to 75 kg, but if we don't have good nutrition and food while growing up, we might not reach this weight. So, in the case of quantitative traits, phenotypic variation (designated VP) is primarily the combination of variation resulting from different sources: variation from genetic effects (designated VG) + variation resulting from environmental effects (designated VE) (Hill 2010; Goddard et al. 2016). Understanding it with an example, in a herd of sheep, each and every sheep has different body weight and woollen fleece thickness. This phenotypic variation (VP) is because of the different (VG) and the type of condition, i.e., water intake, food intake, and sleep pattern (environmental factor) (VE) they had.

$$VP = VG + VE$$

Other factors, such as variation resulting from interactions between genetic and environmental effects (designated VGE), are also important in quantitative genetics. In contrast to qualitative traits, there is no simple relationship between genotype and phenotype, so in order to study them, different approaches are used.

**Additive genetic variance (VA):** Each participating allele has a specific effect on the phenotype. Potentially or in other words we can say this is one of the most important variance wrt the dominance and interaction variance. For example diabetes is a polygenic disorder. Multiple genes are involved in the pathogenesis of diabetes mellitus.

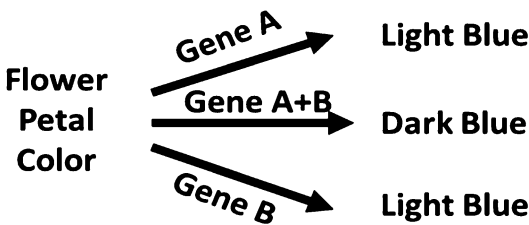
**Dominance genetic variance (VD):** This is similar to the Mendelian inheritance. In this case, we have the same relationship between alleles at a single locus as we discussed in classical Mendelian inheritance. Since presence of one dominant copy is enough, homozygous dominant and heterozygous genotypes contribute equally to the phenotype (effect of HH = effect of Hh). Recessive allele will not be able to show its effect



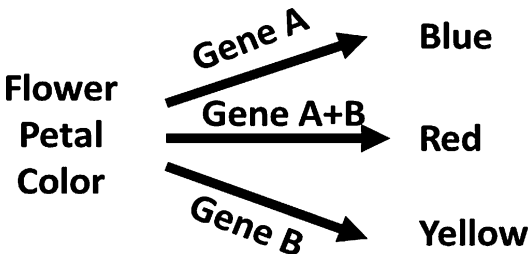
in heterozygous condition (Hh) and can only show its effect when present as homozygous copies (hh). For example, in sickle cell disease presence, one defective gene copy doesn't have serious effect on the person carrying it, while if mutant gene is present in two copies, then the person will have adverse outcomes.

**Epistatic variance or interaction genetic variance (VI):** in this type of variance, different loci interact to affect the trait. By "interaction" we mean usually an effect on the phenotype beyond additive. In additive effect, multiple genes culminate to produce a particular type of effect, while in interaction effect, for example, in epistatic variance, one gene masks the effect of other gene, and this way the variation thus observed is because of interaction of multiple genes.

Example of additive variance:



Example of interaction variance:



Thus the genetic variance can be partitioned into additive (VA) and dominance (VD) components:  $VG = VA + VD + VI$ . (VI = Interactive Variance).

The total phenotypic variance is thus partitioned:  $VP = VA + VD + VI + VE$ . (VE = Environmental Variance).

## Heritability

The general term that describes the proportion of the genetic variance to the total variance is

heritability. Two specific types of heritability can be estimated. Heritability denotes the proportion of phenotypic variance that is due to genotype.

The broad-sense heritability is the ratio of total genetic variance to total phenotypic variance (Hill 2010). We can understand few important things from the mentioned definition: it's entirely open in the respect that how specific genetic effects contribute to VG. Broad-sense heritability isn't affected irrespective of whether VG is the outcome of one gene's single Mendelian variant, or the small additive effects from variants in 100 different genes, or complex interactions between every variant in the whole genome.

$$H^2 = VG/VP$$

The narrow-sense heritability is the ratio of additive genetic variance to the total phenotypic variance (Hill 2010). In other words, what proportion of phenotypic variation in the given population is due to the genetic effects which can be inherited in offspring from their parents  $h^2 = VA/VP$

The narrow-sense and broad-sense heritability are the same under the condition when there are no dominant, recessive interaction, and also it is to be noted that narrow-sense heritability will be smaller since it excludes (i.e., VG) these other types of genetic effects.

## Cross-References

- [Epistasis](#)
- [Genotype](#)
- [Heritability](#)
- [Phenotype](#)
- [Polygeny](#)
- [Traits](#)

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effects, as was the case for Gregor Mendel's pea plant seeds being smooth or wrinkled, yellow or green. Instead, many complex traits, diseases, and disease susceptibilities are influenced by interactions between alleles at multiple genetic loci that each exerts quantitative effects on a phenotype, commonly producing a continuous phenotypic distribution. These traits are polygenic (i.e., influenced by multiple genes) and often multifactorial (i.e., can be further influenced by environmental factors). When polygenic or multifactorial traits present with numerical phenotypic variation, they are additionally termed “quantitative traits” (Consortium 2003).

## Quantitative Trait Loci (QTL)

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### Definition

Quantitative Trait Loci (QTL) are genetic segments containing one or more genes that correlate with phenotypic variation in a quantitative trait.

### Introduction

Advances in DNA sequencing over the last 25 years have reduced the cost to generate a high-quality draft of the human genome from hundreds of millions to less than \$1,500 (Wetterstrand 2018). The ease of access to sequence data has led to remarkable growth and demand for sequence analysis – how changes in genes and gene expression contribute to morphology and disease. For scientists, the process of connecting a phenotype to a gene can be complex. Many human traits and diseases are not solely determined by alleles at a single genetic locus that produce discrete “all-or-none” phenotypic

## Quantitative Trait Loci (QTL)

Quantitative Trait Loci (QTL) are physical chromosomal segments containing one or more genes that contribute to variation in a quantitative trait. QTLs are identified by observing the inheritance of variation in a quantitative trait and then linking that variation to the inheritance of molecular markers (e.g., sequence variation, usually in noncoding DNA) across several generations of plants, experimental lab animals, or human families. Passage of the molecular markers with a change in degree of a quantitative trait may suggest that the sequence between these two inherited markers contains at least one gene contributing to the phenotype. QTL mapping is useful for identifying genomic regions that can be further analyzed for candidate genes or alleles underlying a change in a multifactorial trait or disease.

Quantitative traits typically present with continuous variation that forms a normal distribution due to the contributions of multiple additive genetic loci. Height, blood pressure, skin color, and body mass all form bell-shaped distributions in large populations (Jorde et al. 2016). This is the result of Mendelian inheritance at multiple loci, also termed polygenic or quantitative inheritance. This is distinguished from pure Mendelian inheritance in that multiple loci allow for combinations of alleles and polymorphisms that may each exert varying effects on the phenotype. These loci are often unlinked, possibly on

separate chromosomes, allowing for independent assortment of contributing loci to offspring.

Human height, for example, is estimated to be 90% determined by inheritable factors spread over 180 identified genetic loci (He et al. 2015). At each locus, alleles may exist in a population that exert relative height decreasing (aa), or height increasing (AA) influences. Assuming non-dominance, the three possible phenotypic effects at any loci are decrease height (aa), maintain height (Aa), or increase height (AA). If we assume that the alleles functioning to increase and decrease height are present in equal frequencies, then at any single loci 50% of offspring will have a height increasing or maintaining influence (Aa), 25% will contain height decreasing influence (aa), and 25% will contain height increasing influence (AA). Alleles at any locus may be recessive, dominant, or co-dominant. This process repeated at many additive loci will typically result in a bell-shaped curve, a normal distribution (Fig. 1).

The phenotypic effects of individual QTL may be dependent on complex interactions between other factors and have variable impact on the phenotype of their associated trait. Gene-gene and gene-environment interactions are common and can impede QTL identification, particularly when a phenotype is controlled by numerous loci that produce relatively small effects, termed

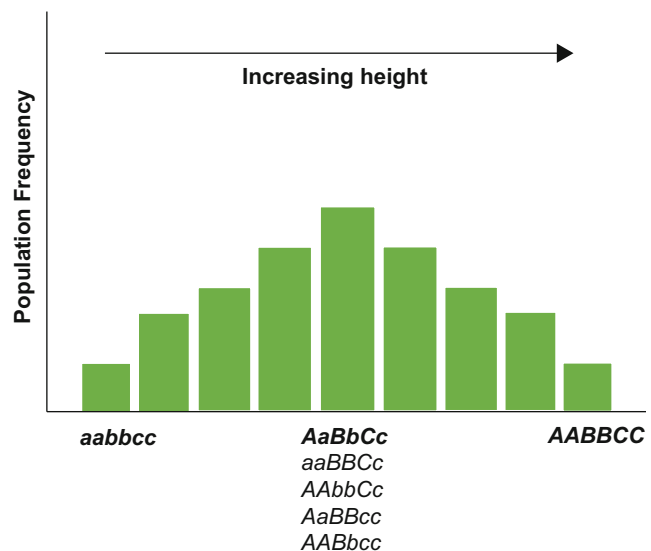
modifier loci. Notably, quantitative traits may be influenced by other loci that seem to produce significant discrete effects that are indistinguishable from Mendelian traits. (Miles and Wayne 2008). Returning to human height, the majority of loci exert minute effects, otherwise we would not see a normal distribution in populations, yet a few generate significant changes in phenotype. For example, a mutation in a transmembrane domain of the fibroblast growth factor receptor *FGFR3* produces a significant reduction in height diagnosed as achondroplasia, the most common form of dwarfism. This type of control is common in quantitative traits, with a typical phenotype affected by a few loci producing discrete or Mendelian effects and numerous modifier loci of minute effect (Remington and Purugganan 2003).

### Quantitative Trait Loci in Multifactorial Disease

The majority of the human disease burden has a genetic component – disease or disease risk is inheritable by offspring (Jorde et al. 2016, p. 239). Genetic conditions can be broadly sorted into two types: disease induced by mutation at a single loci (e.g., cystic fibrosis, Duchenne

#### Quantitative Trait Loci (QTL),

**Fig. 1** Quantitative trait alleles forming a normal distribution



muscular dystrophy) or disease that is attributable to multiple genetic and environmental influences. Multifactorial disease, the latter category, represents the majority of human conditions and includes cancer, diabetes, dementia, and heart disease (Stolk et al. 2008). Since these ailments are influenced by interactions of multiple loci, and the environment, they follow polygenic or quantitative inheritance. Yet, instead of a phenotypic bell curve, multifactorial diseases often appear to be either present or absent. For many diseases, a threshold of risk must be passed before a disease is expressed. Commonly, alleles circulating in populations may predispose individuals to a disease, exert no effect on disease risk, or be protective. Thereby, multifactorial disease risk in populations forms a bell curve similar to quantitative traits, termed a liability distribution. Individuals with higher numbers of disease-causing alleles will be more likely to develop disease, while individuals with noncausative or protective alleles will be at lower risk (Fig. 2).

Quantitative trait locus analysis conducted on multifactorial disease can yield biomarkers correlating to disease risk, progression, and lethality. One example is the discovery of mutations in the well-known homologous DNA repair proteins *BRCA1* and *BRCA2* that lead to 69–72% risk of developing breast cancer by age 80, in addition to

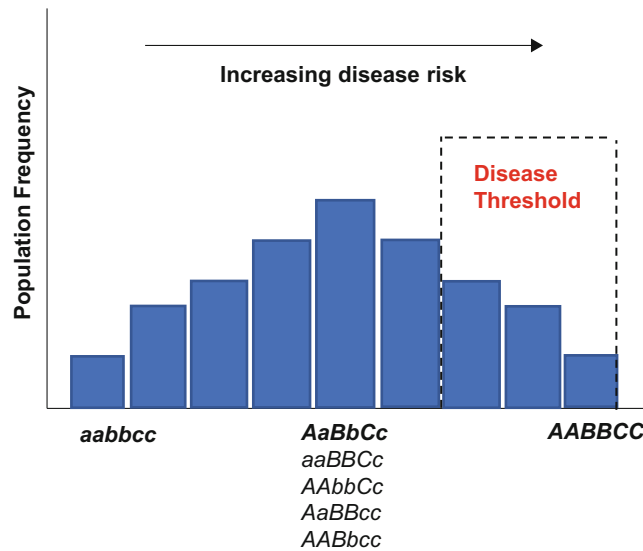
an increased risk of stomach, pancreatic, and colon cancer (Kuchenbaecker et al. 2017). Following the discovery of these markers, the US Preventive Services Task Force (USPSTF) issued a recommendation for *BRCA1/2* screening for women with a family history of breast, ovarian, fallopian, or peritoneal cancer (Moyer 2014). However, it is estimated that *BRCA1/2* mutations account for only up to 30% of the total inherited cases of breast cancer, implying that rare or less penetrant mutations in other loci compose the majority of genetic risk (Economopoulou et al. 2015).

Conclusion

Intensive efforts have already identified diverse QTL that contribute to the development of many diseases and brought multigene panels into clinical use that screen for common and rare mutations in patients with familial risk. Further research into novel gene-gene and gene-environment interactions that underlie human traits, disease risk, and progression is of continuing scientific interest. The ease of access to genome sequencing will allow researchers and clinicians to increasingly personalize care and better target high risk individuals for screening and preventative treatments.

Quantitative Trait Loci (QTL),

**Fig. 2** Multifactorial disease liability distribution. Disease may be absent until a genetic and/or environmental threshold in risk has been passed



## Cross-References

- Alleles
- Autosome
- Chromosomes
- Crossover
- DNA
- DNA Marker
- Frequency Distribution of Phenotypes
- Genetic Variation
- Genotype
- Locus
- Mendel's Laws
- Phenotype

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## Quantity Judgments

- Conservation

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## Quiescence

- Developmental Arrest



# R

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## Rabbit

- [Lagomorpha Life History](#)
- [Lagomorpha Navigation](#)

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## Rabbit and Hare Locomotion

- [Lagomorpha Locomotion](#)

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## Racing

- [Horseback Riding](#)

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## Radial Arm Maze

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## Synonyms

[Apparatus to measure spatial learning and memory](#)

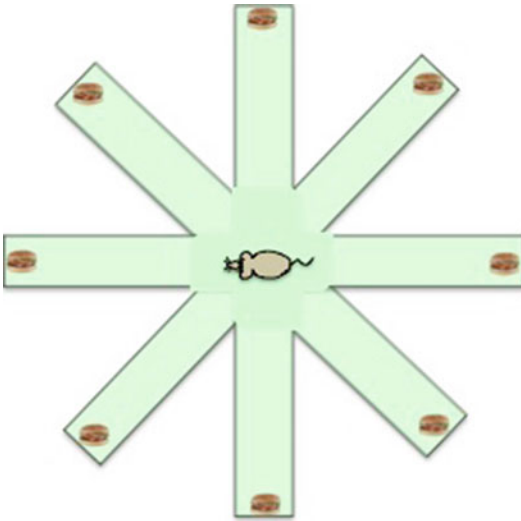
## Definition

A radial arm maze is an apparatus with multiple equidistant arms connected to a central platform, which is used to study spatial learning and memory in animals, primarily rodents.

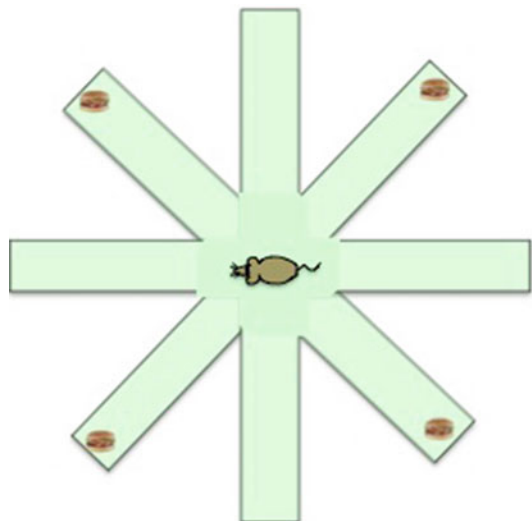
## Introduction

The original eight-arm radial arm maze (RAM) was designed by David S. Olton and Robert J. Samuelson in 1975 at The Johns Hopkins University. The maze was designed to assess cognitive functions like spatial learning and memory in rodents and other animals (Olton and Samuelson 1976). As shown in Fig. 1, an individual animal is placed in the central platform and allowed to freely explore the maze. Typically, the ends of each maze arm are baited with food rewards, which the animal can retrieve. If the animal remembers where it has been, it should avoid revisiting arms in which it has already retrieved the food rewards.

The RAM is a noninvasive technique, which has been well validated all across the globe (Kandel et al. 2014; Olton et al. 1977; Saxe et al. 2007) and thus can be easily modified to assess the effects of environmental, pharmacological, or surgical interventions on behavior (Samuelson et al. 2016). In addition, the number, size, and substrate of the arms can be modified to suit the foraging techniques used by different species, including insects, birds, and even humans (Mennenga et al. 2014; Samuelson et al. 2016).



**Radial Arm Maze, Fig. 1** Schematic diagram showing the structure of a typical radial arm maze (RAM)



**Radial Arm Maze, Fig. 2** Schematic diagram showing the usage of radial arm maze (RAM) for testing **Reference memory**

## Types of RAM

Using the RAM task, researchers can assess different types of memory:

1. **Working Memory:** In the standard RAM task, all the arms are baited with a food reward, as shown in Fig. 1. To perform perfectly, an animal should visit each arm only once. If the animal visits one or more arms more than once or visits non-baited arm, it is counted as a working memory error.
2. **Reference Memory:** In this test a subset of the arms of the maze are baited with a food reward, and these arms remain constant throughout testing. As shown in Fig. 2, an animal should visit only the baited arms. Visiting the same baited arm more than once or visiting non-baited arm is considered as reference memory error.

## Conclusion

To summarize, the RAM is used for the assessment of spatial working and reference learning and memory in animals. The radial arm maze can be easily modified to investigate different aspects of behavior and cognition.

## Cross-References

- [Cognition](#)
- [Memory](#)
- [Reference Memory](#)
- [Working Memory](#)

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## Radial Symmetry

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### Definition

Radial symmetry can be defined as the body plan of those animals, which can be divided into two equal halves if they are cut through any of the radial planes.

### Introduction

Body symmetry stands for the characterization of body plan and can be defined as the similarity of parts in different regions and directions of the body. Based on symmetry, the animals can be divided into asymmetrical, radially symmetrical, and bilaterally symmetrical animals. Animals that cannot be divided into two equivalent halves through any plane are described as asymmetrical animals, e.g., sponges, adult snails, etc. Animals that can be divided into two equivalent halves if they are cut through any of the radial planes are described as radially symmetrical animals, e.g., jellyfish, corals, sea anemones, etc. Animals which can be divided into two equal right and left halves only if they are cut in the vertical plane passing through their median longitudinal body axis, e.g., flatworms, earthworms, and humans, are known as bilaterally symmetric

(Playfair and McMurrich 1896). Exact spherical symmetry is not found in the animal body plans.

## Radial Symmetry

A radially symmetrical animal can be divided into equal portions from its center, much like that of cutting a pizza into slices. These animals do not possess head (anterior) and tail (posterior) or left and right regions. Such symmetry allows animals to reach out in all directions from one central point, though at a much slower speed as compared to the bilaterally symmetrical animals. Moreover, their sensory organs are generally scattered over the body, unlike the central nervous system of other symmetrical animals (Fig. 1). In case of amputations or injury to the peripheral parts, but with intact central part, these animals have the unique property of self-repair to maintain their radial symmetry. This biological process is known as symmetrization (Michael et al. 2015).

Historically, the taxonomic classification of animals was based on their symmetry. For instance, French naturalist Georges Cuvier grouped animals with radial symmetry in the taxon Radiata (Zoophytes) (Cuvier et al. 1834). Today, this taxon is believed to be a polyphyletic group of distinct phyla of the Animalia (Hadzi 1963). Most radially symmetric animals are symmetrical about an axis extending from the center of the oral surface (which contains the mouth) to the center of the opposite, aboral end.

### Different Forms of Radial Symmetry

Radial symmetry can be modified evolutionarily by the arrangement of some paired structures or other combinations around the central axis, which gives rise to some unique forms of radial symmetry. Depending upon the number of axis of symmetry, the radial symmetry can be categorized as follows:

- (a) **Biradial symmetry** (e.g., ctenophores and some anthozoans) due to presence of only



**Radial Symmetry, Fig. 1** Pentaradial symmetry in *Asterias arenicola*. (Taken from Playfair and McMurrich 1896)

two planes of symmetry, i.e. the transverse or tentacular plane through the tentacle sheaths and the vertical sagittal or pharyngeal plane at right angles to the tentacular plane

- (b) **Tetramerous symmetry** (e.g., in most of the jellyfish) due to four canals in radial body plan
- (c) **Pentaradial symmetry** (in all the echinoderms like sea stars, sea urchins, and sea lilies) due to branching of body parts into five distinct compartments
- (d) **Hexamerous symmetry** (e.g., corals and sea anemones of subclass Hexacorallia) due to the arrangement of mesenteries and tentacles in the multiple of six
- (e) **Octamerism symmetry** (in Octocorallia and octopus) due to presence of eight appendages and octameric radial symmetry

### Phylum in Animal Kingdom Showing Radial Symmetry

Phylum Coelenterata or Cnidaria is the only phylum in the animal kingdom, showing a good example of radial symmetry. A few examples of this symmetry are also found in phylum Echinodermata.

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### Raffle Principle

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Within polyandrous mating systems, females mate with multiple males over their lifetimes, sometimes within quick succession. In internally fertilizing species this can lead to the ejaculates of multiple males being simultaneously present within the female's reproductive tract (or in the case of external fertilizers, ejaculates being simultaneously present at the site where eggs have been laid), and therefore competition between the ejaculates to fertilize the female's eggs. This is known as "sperm competition," and is recognized as a major force of sexual selection (Parker 1970). It is thought that the selection pressure of sperm competition combined with the cost of producing sperm has led to the evolution of numerous, small sperm, a phenomenon known as anisogamy.

Parker (1990) compared sperm competition to a "raffle" (lottery); a game of chance in which people buy tickets bearing numbers. All of the tickets are mixed together, and then a small subset is drawn at random. The purchasers of the tickets from this subset win prizes. The more tickets a person buys, the greater their probability of winning. Sperm can be thought of as raffle tickets, and the prizes as fertilization of ova – the more sperm

with which a male inseminates a female, the greater his chance of siring offspring.

In a “fair raffle,” each ticket has an equal chance of winning, and so the number of sperm a male inseminates into a female is directly proportional to his fertilization success. In these cases, there is no loss of sperm by any of the competing males during or after mating, all sperm enter the fertilization set, and are equally likely to be used for fertilization. This can occur when sperm storage organs allow free mixing of sperm, for example, in cricket species (Simmons 1986).

Conversely, in a “loaded raffle” tickets do not all count equally. While a male’s success in fertilizing offspring may still increase with increased investment of sperm, the relationship is not directly proportional. The skew in fertilization success among males may be determined by a number of factors, for example, in certain species females may choose not to uptake (Simmons 1986), or to actively eject (Pizzari and Birkhead 2000), the ejaculate of less favored males. Males may use specialized genitalia to remove competing ejaculates from a female’s reproductive tract (Waage 1979). Sperm may be stored in specialized storage organs within the female reproductive tract. If the physiology of these stores leads to stratified rather than freely mixed storage of sperm (Walker 1980), the order in which sperm enter storage will greatly affect the order in which they leave, thus restricting access to the ova. There may be differences among males in some inherent quality of their sperm, which confer greater success in their ability to traverse and survive the rigors of the female reproductive tract, and to fertilize ova (Snook 2005). Factors such as these mean that, even if a competitor buys copious tickets, they do not necessarily have a better chance of winning the raffle.

## Cross-References

- [Anisogamy](#)
- [Cryptic Mate Choice](#)
- [External Fertilization](#)
- [Gametes](#)

- [Internal Fertilization](#)
- [Ova](#)
- [Polyandry](#)
- [Reproduction](#)
- [Reproductive System](#)
- [Sexual Selection](#)
- [Sperm Competition](#)

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## Raiding

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## Synonyms

[Intergroup Violence](#); [Tribal Warfare](#)

## Definition

A sudden, often violent, display of force by members of a group against one or more individuals



from another group, with the goal of inflicting injury, taking resources, or capturing females.

In anthropology and biology, raiding commonly refers to a spontaneous display of force, enacted by one group against a separate group or individual. Raids may be violent, resulting in injury or death for the targeted individuals, and are often biased in favor of the attacking group. The goal of a raid might be to inflict injury or death on members of the target group, to kidnap females or to steal resources such as food.

## Nonhuman Primates

Raiding is present in both chimpanzees and humans, but not in bonobos (Pandit et al. 2016). Watts et al. (2006) provided anecdotal examples of lethal intergroup aggression in chimpanzees and argue that these observations are consistent with an evolved function of lethal, intergroup aggression in chimpanzees. (The proposed fitness benefits of chimpanzee raids include that killing rival group members reduces competition for limited resources). This hypothesis is further supported by Mitani et al.' (2010) study which observed territorial expansion of chimpanzees who fatally wounded rival group members. In an investigation of patrolling behavior (which typically precedes intergroup attacks), Watts and Mitani (2001) observed that chimpanzees who patrolled more frequently and who were more likely to join an existing patrol experience greater mating success. Taken together, the literature on chimpanzee raiding behavior evidences strong empirical support for the fitness benefit of lethal, intergroup aggression.

## Humans

Raiding has also been observed in human tribal societies. In these contexts, tribal warfare is often used interchangeably with raiding and is characterized by highly organized sneak attacks by the men of one tribe against a rival tribe. Often, these raids involve taking resources or capturing women from the rival group; however, raiding may have

reproductive benefits, even when women are not captured and taken as wives. Glowacki and Wrangham (2015) observed that men from a tribe of nomadic pastoralists who participated in more raids during their youth have more wives and children later in life. The authors suggest that, because Nyangatom men trade livestock in exchange for wives, and because raids often involve the taking of livestock, Nyangatom men may enhance their reproductive success as an indirect result of performing raids.

In a meta-analysis comparing patterns of raiding behaviors across species, Manson et al. (1991) noted several similarities and differences between chimpanzees and tribal humans. Manson et al. noted that human and chimpanzee raiding are similar in that intergroup aggression is largely displayed by males, with females rarely taking an active role in the hostilities. The authors suggest that this sex difference may be due to males being the philopatric sex, meaning that, as opposed to females, males do not leave the group into which they are born. As a result, males are unlikely to injure or kill genetically related kin during a raid. The authors also provide evidence that, for humans in particular, raids are likely intended to capture females from rival groups when there are few material resources (e.g., food, land) that can be taken instead. Additionally, Manson and colleagues found that accumulation of material resources was associated with polygyny, which suggests that raiding to take material resources and raiding to kidnap women may both have consequences for men's reproductive success.

Overall, empirical data on raiding in tribal societies of humans suggests that, for them raiding does and for ancestral humans, raiding did generate reproductive benefits. Further, the apparent similarities in raiding behaviors between humans and chimpanzees suggests the possibility that raiding has been a feature of hominid life since the most recent common ancestor between humans and chimpanzees, 5–6 million years ago. Still, further investigation is needed to determine whether raiding in humans is best understood as a phylogenetically conserved behavior whether human raiding might reflect specialized adaptation in humans that is not present in chimpanzees.

## Cross-References

- [Aggression](#)
- [Chimpanzee Raiding](#)
- [Hunting](#)

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## Ralph Miller

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## Education and Early Influences

Ralph R. Miller (1940–) grew up on the south side of Chicago, near Hyde Park, in the shadow of the University of Chicago, and near a lot of great

bookstores. Miller entered MIT in 1958, and in 1962 he earned a BS in Physics with a thesis titled, “Considerations of Precision Nuclear Spectroscopy Utilizing Fiber Optics Detection Systems.” Miller went on to earn a Master’s degree in High Energy Physics from Rutgers University (1964) with a thesis titled, “An Automated System for the Detection of Elementary Particles.” While at Rutgers, his interests shifted to psychology, and under the supervision of William Pavlik, Miller went on to earn a Master’s degree in Social Psychology from Rutgers (1966) with a thesis titled “No Play: A Means of Conflict Resolution.” While working on his Masters, Miller became interested in the social learning theory of Neal Miller and John Dollard and was greatly influenced by his interactions with those focused on learning and conditioning processes, such as Norman Spear, George Collier, Michel D’Amato, and Carolyn Rovee Collier. With his focus being now the study of learning and memory in rodents and humans, Miller joined the laboratory of Donald Lewis at Rutgers. He went on to earn a Ph.D. in Physiological Psychology (1969) with a thesis titled “Effects of Environmental Complexity on Amnesia Induced by Electroconvulsive Shock,” which investigated amnesia and recovery of memories after amnesic insult. Miller’s work was extremely timely, as there was extensive debate at the time regarding whether amnesia-inducing trauma disrupted memory consolidation or retrieval. In Miller 1973, he published a landmark paper on *Psychological Review* (“Amnesia, consolidation, and retrieval”), which is still considered a citation classic in this area. As a graduate student, Miller was one of the original investigators to observe that cued reactivation of an old memory renders it briefly vulnerable to experimental amnesia (Misanin et al. 1968). Today, that brief window of vulnerability is presumed to represent retrieval-induced destabilization during which memories are labile and subject to change prior to entering a period of “reconsolidation.” Notably, Miller has always strongly disagreed with the “reconsolidation interpretation” of the phenomenon because recovery from the performance deficit induced during the vulnerability period is sometimes observed.

## Academic Career

After obtaining his Ph.D., Miller joined the Psychology Department faculty at Brooklyn College of the City University of New York (1969) and rose through the ranks to become a tenured Associate Professor (1973) and Professor (1978). During this time, he spent a year as a visiting Fellow in Experimental Psychology at the University of Cambridge (Kings College, UK, 1975–1976). In 1979, Miller joined the faculty at the State University of New York at Binghamton (today, Binghamton University), where he has spent the rest of his career. In 2003, Binghamton University awarded him the rank of Distinguished Professor of Psychology. Throughout his academic career, Miller has served as Editor of *Journal of Experimental Psychology: Animal Learning & Cognition* (2014–2019) as well as *Learning & Behavior* (1997–2002). He has also served as President of the Eastern Psychological Association, the Pavlovian Society, and Division 3 of the American Psychological Association. He was named Fulbright Scholar on two occasions. At the time this entry was written, Miller's work had resulted in 345 publications and continuous federal funding for a 43-year period. Since becoming a professor, 22 students earned their Ph.D. and 13 individuals received Postdoctoral training under Miller's supervision.

## Major Contributions to the Study of Animal Cognition and Behavior

Although Miller is arguably one of the most recognized researchers in the field of animal learning, conditioning, and cognition, throughout his career he has made significant contributions to the theoretical and empirical advancement of neuroscience, cognitive processes, social processes, animal behavior, and psychopathology. Much of Miller's work has used Pavlovian associative conditioning procedures with rats; however, he has also made significant contributions using contingency judgment and evaluative conditioning with human participants. Miller's contributions have been significant to the understanding of memory retention through metamorphosis in frogs,

Machiavellianism, causal reasoning in human and nonhuman animals, source monitoring in Korsakoff's syndrome, preference for signaled shock, neophobia, electroconvulsive shock (ECS)-induced amnesia, occasion-setting, treatment of fear of public speaking, associative interference, experimental extinction, fear relapse, artificial intelligence, processing information as a member of a group, altruism and selfishness, opioid analgesia, conditioned inhibition, coding of temporal intervals, tail shock methodology, biological significance, context and habituation, treatment for smoking cessation, infantile amnesia, cue-competition phenomena (e.g., blocking, inhibition, overshadowing, and relative stimulus validity), associative learning as a model of schizophrenia, and adaptive memory.

## The Learning-Performance Distinction

If Miller's work were to be summarized in one sentence, it would be *the systematic investigation of the difference between what has been learned and how that learning is expressed in performance*. His view is that performance (e.g., conditioned responding) does not always reflect what a subject has encoded; thus, there are complex processes that determine whether or not a given environmental situation results in the elicitation of a conditioned response. The learning-performance distinction is a long-standing debate in the history of the study of learning and conditioning. For example, in his classic studies of *latent learning*, Tolman (1948) observed that rats allowed to navigate a maze did not express learning of the layout of the maze until they were under a motivational state that facilitated expression of that learning. That is, what they knew (learning) was not necessarily expressed in their behavior (performance). Another example of the learning-performance distinction is the phenomenon of *spontaneous recovery*, first reported by Pavlov (1927). Pavlov presented dogs with a sound (the conditioned stimulus or CS) that was paired with food (the unconditioned stimulus or US), resulting in a salivation conditioned response when the CS was presented. Repeated presentations of the CS alone resulted in low levels of conditioned responding (extinction). Pavlov observed that

the response recovered without further training if time was allowed to elapse between extinction and assessment. This observation suggested that extinction involves some kind of masking of the acquired CS-US association that remained intact through extinction.

Miller's interest in the learning/performance distinction stems from his work as a graduate student at Rutgers. In a series of seminal studies, Miller and colleagues trained rats with a passive avoidance conditioning procedure followed by ECS. With this treatment, rats showed amnesia for the passive avoidance conditioning experience. If rats received a single "reminder" shock (Miller and Springer 1972a, b) between ECS treatment and assessment, however, the avoidance response was expressed. This showed that the association *was* formed during training and that the amnesia-inducing ECS did not destroy it or keep it from being consolidated and retained; it merely prevented its expression. Indeed, they observed that the memory was formed in 0.5 s or less since the amnestic treatment presumably disrupted all relevant ongoing neural processing in the brain 500 ms after training (Miller et al. 1969). Miller's findings in this area, along with the work of others such as David Riccio, Norman Spear, and Mark Bouton, have helped shape our understanding that many instances in which performance is not consistent with the conditions of training may reflect not a failure to acquire and retain a memory, but a difficulty in retrieval of acquired memories that remain intact even after treatments intended to disrupt them.

### **Acquired Information Expression is Relative to the Situation: The Comparator Hypothesis**

In Miller's view, responding based on an acquired association does not only depend on the strength of the memory of the association, but also on the context in which the memory was acquired and retrieved. According to this view, CS-US pairings will control behavior not only as a direct function of the strength of the CS-US association, but as a relative comparison of the strength of this association and the strength of association between the background cues and the US. These background cues (the environment or "context" as well as

other stimuli that were present in the learning situation) are presumed to serve as "comparator stimuli" for the CS that is being assessed (the "target" CS). The degree to which the target CS produces a conditioned response will be determined by the extent to which the target CS can retrieve the memory of the US (the associative strength of the target CS-US association) *relative* to the extent to which other cues that were present in the situation during learning can retrieve the memory of the US; this latter retrieval of the memory of the US is indirectly triggered by the target CS because presentation of the target CS retrieves a memory of the comparator stimuli, which in turn retrieve a memory of the US. Thus, the comparison is between a memory of the US directly retrieved by the target CS (with a strength that equals that of the associative strength of the CS-US association) and a memory of the US indirectly retrieved by the target CS (with a strength that equals the product of the strength of association between the target CS and its comparator stimuli *and* the comparator stimuli and the US). Hence, if the memory of the US activated directly by the target CS is stronger than that activated indirectly by the target CS, responding will be robust; in contrast, if the memory of the US activated directly by the target CS is weaker than that activated indirectly by the target CS, responding will be attenuated. Thus, failures in performance are expected not because the association between the target CS and the US is weak, but because associations to the comparator stimuli prevent full expression of the CS-US association. Since the mid-1980s, Miller's *Comparator Hypothesis* (cf. Miller and Matzel 1988) has been supported by hundreds of studies and has sparked novel research showing that responding can be modulated through training of the comparator stimuli (e.g., Blaisdell et al. 1999), with new theories being developed to explain these phenomena (for reviews, see Denniston et al. 2001; Stout and Miller 2007). The Comparator Hypothesis has undergone significant evolution since its first formulation, with an extended version, the development of which was prompted by the empirical discovery that overshadowing and latent inhibition treatments mutually counteract

their response-attenuating effects other (Blaisdell et al. 1998), that incorporated rules for dealing with multiple comparator stimuli (ECH; Denniston et al. 2001), and a mathematical formalization of the ECH (Sometimes Competing Retrieval [SOCR]; Stout and Miller 2007).

### Temporal Coding as an Essential Component of the Formation and Expression of Associations

Temporal contiguity (the extent that two events occur in close temporal proximity) was described by Aristotle as one of the basic laws of association between ideas. Not surprisingly, contiguity is essential for the formation of associations between the CS and US; however, sometimes contiguous events (e.g., a CS and US that are presented simultaneously) do not lead to robust behavior. Miller has suggested that the temporal relationship between paired events is encoded as part of the “association” that links their representation in memory. This temporal information includes synchronous versus asynchronous onset, order of presentation, and duration. In this strict contiguity view, an association is formed as long as the two events are presented fairly close together. This temporal information is not just incidental; rather, it is a critical determinant of how the association will later be expressed in behavior. Miller’s *Temporal Coding Hypothesis* (e.g., Arcediano and Miller 2002; Miller and Barnet 1993) incorporates the extent to which the CS predicts the US and how this predictability is modulated by their temporal relationship. The most commonly held view of classical conditioning is that pairings of a CS and a US lead to the CS predicting the US, and that conditioned responding is determined by this predictive relationship; functionally, the CS prepares the subject for the impending occurrence of the US. Various observations support this view: if the CS and US occur simultaneously (simultaneous conditioning) or the US precedes the CS (backward conditioning), little conditioned responding is observed because the CS has little predictive value. According to Miller’s Temporal Coding Hypothesis, however, prediction only determines whether performance, not learning, is to occur. In this view, if the CS and US are presented together, an

association is formed between them. Performance depends on the temporal arrangement of the CS and US and is determined by the extent to which the CS predicts the US. Miller has presented extensive evidence that these latent associations can be uncovered through the use of second-order associations. For example, if a CS1 receives backward pairings with the US (i.e., US-CS1), CS1 elicits little responding (CS1 is not predictive of US occurrence). If a second CS (CS2) is paired with CS1 (CS2-CS1), however, CS2 comes to be predictive of CS1’s occurrence. If CS1 has developed an association to the US, then CS2 should come to elicit a response because CS2 holds a predictive relationship to the time at which US occurrence should be expected. Such integration of multiple experiences with temporal components has been demonstrated in human and non-human subjects (e.g., Arcediano et al. 2003).

### Conclusion

R.R. Miller has been one of the greatest contributors to the advancement of animal learning, memory, and cognition. His theoretical contributions, including the Comparator Hypothesis and Temporal Coding Hypothesis, have not only served to provide a framework of understanding the complex dynamics of acquired behavior, but have sparked novel research and theoretical developments that have advanced our understanding of the complex relationships between what is learned and what is expressed in behavior. Miller’s prolific experimental contributions have spanned multiple fields beyond learning and memory, including social, abnormal, and physiological processes, and have had broad impact beyond psychology. With a career that spans over 50 years, Miller’s work is still considered to be current, with even his graduate student research continues to shape our understanding of learning and memory, such as the reconsolidation debate.

### Cross-References

- [Altruism](#)
- [Associative Learning](#)



- [Avoidance](#)
- [Classical Conditioning](#)
- [Conditioned Inhibition](#)
- [Extinction in Learning](#)
- [Habituation](#)
- [Ivan Pavlov](#)
- [Learning](#)
- [Long-Term Memory](#)
- [Machiavellian Intelligence](#)
- [Neophobia](#)

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## Randy Thornhill

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## Early Life and Educational Background

Thornhill was born on December 7, 1944 in Decatur, Alabama, USA. He obtained a B.S. in Zoology at Auburn University in 1968, an M.S. in Entomology at Auburn in 1970, and a Ph.D. in Zoology at the University of Michigan in 1974. His 633-page Ph.D. dissertation, *The Evolutionary Ecology of the Mecoptera (Insecta)*, reported on his original research on the behavior and ecology of mecopterous insects and included the first study of female mate choice in an animal under field conditions.

## Professional Career

After receiving his Ph.D., Thornhill was a research entomologist for a year in the Department of Entomology and Nematology of the University of Florida in Gainesville, FL. In 1975, he accepted a faculty position in the Department of Biology at The University of New Mexico, Albuquerque, New Mexico, where, as of 2016, he is still on the faculty. His position in 2016 at the University of New Mexico is Distinguished Professor Emeritus. Since 1975 until present, he has taught courses in evolutionary biology, ecology, and animal behavior at The University of New Mexico. He has had temporary appointments with numerous universities, including the University of Helsinki, the University of Colorado, the University of Melbourne, Kyoto University,

Nagoya University, University of Bielefeld, University of Michigan, and Colorado State University.

Thornhill has authored approximately 200 publications, including four research monographs/books. As of 2016, his publications have been cited about 25,000 times.

Thornhill has received various awards for research contributions, including the Senior Distinguished Scientist Award of the Alexander Von Humboldt Foundation, a Guggenheim Fellowship, a Japan Society for Promotion of Science Fellowship, Fellow of the Animal Behavior Society, and Distinguished Entomologist Award from the Department of Entomology, University of Georgia.

Thornhill has served on editorial boards of several scientific journals. He has served as president elect, president, and past president of the Human Behavior and Evolution Society.

## Research Interests

The evolution of human behavior and psychology is the topic of the majority of Thornhill's publications, including three of his books—one with Craig Palmer, *A Natural History of Rape: Biological Bases of Sexual Coercion*, one with Steve Gangestad, *The Evolutionary Biology of Human Female Sexuality*, and one with Corey Fincher, *The Parasite-stress Theory of Values and Sociality: Infectious Disease, History and Human Values Worldwide*. Judging from the citation record of his papers and books, his research has contributed to a range of disciplines, including ecology, evolutionary ecology, behavioral ecology, evolutionary biology, entomology, ornithology, and human psychology and behavior. His main interest continues to be sexual selection processes, especially female choice.

## Cross-References

- [Bilateral Symmetry](#)
- [Comparative Psychology](#)
- [Cryptic Mate Choice](#)

- [Estrous](#)
- [Evolution](#)
- [Evolutionary Psychology](#)
- [Extra-Pair Copulation](#)
- [Female Choice](#)
- [Good Genes Hypothesis](#)
- [Hormones and Behavior](#)
- [Orgasm](#)
- [Ornamentation](#)
- [Sexual Selection](#)

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## Range

- [Sirenia Navigation](#)

## Rank

- [Basic Rank](#)
- [Ordinality](#)

## Rank Order

- [Dominance Hierarchy](#)

## Rape

- [Forced Copulation](#)

## Rare-Type Advantage

- [Frequency-Dependent Selection](#)

## Rational Imitation

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## Definitions

### Imitation

Imitation is a behavior where an individual observes a conspecific's (or even an individual's

belonging to another species) movements or actions and consequently replicates it. This copying behavior – be it blind or insightful with respect to understanding of means-end relations of the action – occurs in most of the cases for novel behavior, previously unknown to or out of the repertoire of the observer (cf. Want and Harris 2002; and see also Call et al. 2005, for alternative definitions on imitation). As such, imitation is seen as a tool for learning novel behavior, that is, as a form of social learning that can lead to the transfer of information between individuals and also between groups of people. This form of information transfer allows the transmission of behaviors, such as tool use, customs, and rituals as well – behavioral patterns that are generally considered as cultural knowledge (Boyd and Richerson 1985). Though imitation as a process is accepted as an important tool of information transfer in social sciences in general, the nature of this skill is still disputed – whether it is a conscious cognitive mechanism or a basic low-level mechanism (Gergely et al. 2002; Paulus et al. 2011a).

### Rational(ity)

The principle of rationality was introduced as a fundamental factor governing action selection on the bases of background knowledge. According to Newell (1982) “if an agent has knowledge that one of its actions will lead to one of its goals, then the agent will select that action” (p. 102). In that sense, rationality is an inferential principle-guiding selection of behavior in accordance with one's knowledge: humans will choose actions to execute that seem the best option based on the knowledge the individual possesses. The rationality principle has also been proposed to be the central inferential principle for humans' – even infants' – action interpretation mechanism (Gergely and Csibra 2003): humans interpret behavior in terms of actions executed to attain goals as efficiently as possible in a given environment.

### Rational Imitation

Rational imitation refers to the phenomenon that agents apply the *rationality principle* in the process

of social learning: they take into account the efficiency of observed actions to achieve a specific goal or outcome when deciding whether to reenact a specific behavior or not, in other words whether to imitate or not. The approach of rational imitation as a selection process presupposes imitation to be a conscious, inference-based, insightful mechanism (Gergely et al. 2002).

## Introduction

Rational imitation as a theoretical construct emerged from experimental research. In this entry, therefore, the phenomenon and relatedly the formation of its explanations will be introduced through empirical examples.

### The Birth of Rational Imitation

The principle of rationality has been introduced as an inferential principle to the cognitive machinery as a component of humans' so-called teleological action interpretation mechanism. The teleological action interpretation system – teleological reasoning – relates three aspects of action interpretation in a systematic manner by the assumption of rationality: *goals, actions, and situational constraints*. Given information about any two of the three elements, one can infer and predict what the third element ought to be if the agent behaves in a rational manner (see Csibra et al. 2003). Within this frame, teleological reasoning operates with the help of two main assumptions: (a) actions serve to bring about future goal states and (b) goal states are realized by the most efficient action available to the actor within the constraints of the situation (Gergely and Csibra 2003).

Empirical evidence supports that already young human infants (henceforth “infants”) – from the age of 6 months – are able to use the above naïve theory of rational action: they represent actions as efficient means to bring about specific goal states in the world, so teleological action interpretation is supposed to be a core, early available mechanism (Gergely and Csibra 2003). This naïve theory for action interpretation, capacity to infer rational, goal-directed action, has

been shown to be part of the cognitive machinery of nonhuman primates as well (Wood and Hauser 2008).

Interestingly, the availability of teleological reasoning has been demonstrated only for action perception and understanding, both in human infants and nonhuman primates. Indeed, if teleological reasoning as a naïve theory is available already for infants, and based on this, they expect agents to act rationally, it is reasonable to assume that infants themselves would also rely on the same principle of rationality to guide their own choices of instrumental actions. This prediction, however, was apparently contradicted by the results of *imitation studies*. As an illustrative example, in Meltzoff's (1988) seminal imitation study, 14-month-old infants chose to reenact a model's unusual and sub-efficient action: after infants witnessed a model use their head to illuminate a light box instead of just using their hands to induce the same effect, most of the children chose to perform the same unusual action when given the opportunity to operate the box. Such a behavior is difficult to interpret as the rationality principle would dictate to choose a solution that leads to the goal state with the least amount of effort – in this case, operating the light box by touching it with one's hand seems more efficient (and hence more rational) than bending forward from the waist to use one's forehead to achieve the same end.

In order to test whether imitation as a form of learning also exploits the naïve theory of rational action, Gergely et al. (2002) developed a modified version of Meltzoff's (1988) imitation paradigm. The aim of the study was to investigate whether efficiency evaluations could modify infants' action choice and production. In the example study of Meltzoff, infants watched an adult place her hands on the table and then use an unusual action to illuminate a light box: she bent over and pressed the box with her forehead. Note that the model's hands were obviously free and she could have easily used them to achieve the goal. In addition to this original version, a new context condition was introduced in which the demonstrator's hands were occupied when she performed the unfamiliar head action to operate the touch

lamp (hands-occupied condition): infants were shown the adult performing the same unusual action but with the difference that her hands were unavailable during the demonstration (she was holding a blanket around her shoulders). In this hands-occupied condition, thus, the situational constraints *justified* the use of the novel means, while this was not true for the original (hands-free) condition. When these infants were given the chance to play with the box a week later, in the hands-free condition, most of them (69%) also used their head to illuminate the light, replicating Meltzoff's results. However, in the hands-occupied condition, only a small proportion of infants (21%) later used their head to illuminate the light box; the majority of them just used the more normal (but undemonstrated) method of pressing the box with their hands.

Gergely et al. (2002) referred to this phenomenon as *rational imitation*, which is a context-sensitive, selective learning mechanism of novel means actions. In a situation where the contextual constraints justified the use of a non-efficient novel means, infants did not imitate it but turned to a familiar action: manipulating the box with their hand. However, high-fidelity imitation – that is, performing the novel means – was induced when goal attainment was realized intentionally by the novel means despite the obvious availability of the most efficient action to the actor within the constraints of the situation.

### Replications

Since the original demonstration, the finding of selective rational imitation has been replicated several times and shown to generalize across a range of different task contexts with 12- and 14-month-old infants.

In a close replication attempt, Zmyj et al. (2009) investigated whether 9- and 12-month-olds detect voluntary as well as nonvoluntary constraints in the head-touch task. In this study, infants watched *video sequences*, which displayed a person illuminating a lamp using the head. The hands of the model were either free (like in the hands-free condition above), or occupied by voluntarily holding a blanket (like in the hands-occupied condition above), or non-voluntarily

restrained by being tied to the table. This study yielded further evidence for rational imitation in 12-month-old infants who chose to use their hand but only in the condition where the model's hands were tied down. Nine-month-olds did not differentiate between the conditions. Thus, these results suggest that by 12 months of age, infants can take into account constraints that the actors do not have the power to change when interpreting behavior and choosing a learning strategy. Yet, comparing the results with those of the original study, it seems that it is not until the age of 14 months that children also consider constraints that are deliberately chosen.

Among the conceptual replications, Schwier et al. (2006) developed a different new task and investigated whether 12-month-olds understand that actors choose action plans rationally based on an assessment of current reality. In this study, infants were presented with a toy house and a toy dog. During the demonstration, an adult took the dog and made it enter the house by going down the chimney. In the condition that was analogous to the hands-occupied condition in the original study (see above), the demonstrator first attempted to use the door instead of the chimney, but as it turned out, it was locked, which justified the use of the chimney as an entrance. In the other condition (analogous to the hands-free condition, see above), the door was visibly open but the demonstrator voluntarily chose the chimney. In both conditions, the door was always open during infants' turn to manipulate the toys. Infants made the dog enter the house through the door more often in the condition in which the door was closed during the demonstration, arguably because the use of the chimney could be attributed to the door being locked. On the other hand, in the condition in which the door was open during the demonstration, infants faithfully imitated the unusual action of putting the dog through the chimney. These results highlight that young children not only learn how to attain goals in the form of imitation but also how to plan the attainment of the goal in the given situation.

The pattern of selective imitation was also shown for complex tool-use behavior (Király 2009). In the experimental condition of this



study, the model first demonstrated that the hand is not efficient to attain a given goal (to take a little box out of a bigger one) and then used a novel tool (a string with a magnet) successfully. In the other condition, only the tool-use action was demonstrated. Infants were more likely to reenact the demonstrated rather complex tool-use procedure to attain the goal when they were shown negative evidence with respect to the efficiency of the hand action (93%), than in the condition where only the tool-use behavior itself was shown (54% attempted tool use). Infants inhibited their prepotent response, the hand action, when the demonstration highlighted and justified the use and efficiency of the novel means.

The above-introduced studies are examples of a growing body of research that revealed the capability of preverbal infants to imitate selectively; however, the flexibility of this capacity has only been recently targeted. The objective of the study of Gellén and Buttelmann (2017) was to test whether 14-month-old infants can flexibly alternate between faithful copying and introducing novel solutions in an imitation paradigm. Participants were presented with two novel actions in a sequence. In one of the situations, the model illuminated a light box; in the other situation, she turned on a sound box. The model alternated the way of attaining her goal in these situations, either she used her forehead (head touch) or sat on the apparatus (sit touch). Importantly, each participant observed one of these actions where the model's hands were occupied, while during the demonstration of the other, the model's hands were free. The results revealed more faithful imitation when no physical constraint provided justification for the unusual action. The study also provided evidence that preverbal infants can adapt their behavior to the changing circumstances. These results point to the flexible, adaptive nature of action interpretation and imitative behavior on an individual level.

Action interpretation with the help of the rationality principle seems to guide the selection of the to-be-learned novel action sequences, at least in the case of human infants. The question is: is this capability present in other species as well?

## The Evolution of Rational Imitation: Evidence in Nonhuman Animals

The phenomenon of rational imitation highlights that infants' action interpretation takes into consideration the situational constraints and relatedly the supposed adaptability of action choice in order to attain a certain goal.

In order to investigate whether rational imitation as a competence is specific to humans or not, Buttelmann et al. (2007) tested enculturated chimpanzees (*Pan troglodytes*) with a paradigm following closely the procedure of Gergely et al.' (2002). Chimpanzees watched a human demonstrator act on six different apparatuses, showing how to operate them using an unusual body part (e.g., by pressing it with foot). Like in the original study, participants were either tested in a hands-free or a hands-occupied condition. The results of the study revealed that like human infants, chimpanzees imitated the modeled action more often in the hands-free than in the hands-occupied condition. Thus, enculturated chimpanzees, who could have profited from the gradual acquisition of behavioral expectations revealed and reinforced by human keepers raising them, seem to have some understanding of the rational planning and execution of others' intentional actions.

However, it is an open question whether this intention reading capacity is only present in enculturated individuals or it is part of apes' cognitive capacity repertoire in general. The above-modified paradigm of Buttelmann, Carpenter, Call, and Tomasello was tested with chimpanzees, orangutans, gorillas, and bonobos and also with a comparison group of 14-month-olds (Buttelmann et al. 2008). While infants used a tool more often when a demonstrator freely chose to use it, in contrast to situations when she was forced to use it, among the ape species, orangutans were the only ones that showed this pattern.

Range et al. (2007) showed an analog capacity in the domestic dog. In their experiment, subjects watched as a demonstrator dog used her paw to pull a rod closer instead of taking it into her mouth (which would be more natural to the species). In the first group, the demonstrator dog was holding a ball in her mouth, thereby providing a justification for the paw action. In the second group,

however, no such constraint was visible. In the first trial after observation, dogs only imitated the unusual means if the demonstrator dog had been carrying a ball in her mouth during the modeling of the behavior. Consequently, domestic dogs, like children, demonstrated inferential selective imitation. However, this finding has been criticized by Kaminski et al. (2011), since the results of their replication attempt suggest that dogs do not distinguish rational from irrational acts and instead simply show a capability of monitoring humans and “predicting” their behavior on the basis of past experience or to follow certain communicative commands.

Overall, the above results suggest that among animal species, only some apes (orangutans) show clearly an understanding of the rationality principle.

### **Challenges and Reconsiderations: Problems with the Original Interpretation of the Rational Imitation Phenomenon**

The explanation of rational imitation as a context-sensitive and selective reenactment of novel actions has been challenged on several grounds. Both alternative interpretations described below were raised based on empirical data questioning the inferential nature of the phenomenon and theoretical challenges brought a need for theory refinement.

#### **The Dispute on Rational Imitation as an Inference-Based Process**

In their alternative account, Paulus et al. (2011a, b) suggested that the phenomenon is rather attributable to a low-level copying process, and it is not inferential. In their view, imitation – rather than being rational – emerges due to the interaction between an automatic motor resonance elicited by the observed actions and the limited motor capabilities of infants. Automatic motor resonance means that observing the behavior of another individual evokes similar brain activity in the observer to what is necessary to bring about the action in reality. The motor resonance

account thus claims that young children show less imitation in the hands-occupied condition because the observed action is not part of their motor repertoire, whereas the one performed in the hands-free condition is. This is due to the fact that in the latter case, the hands of the demonstrator rest on the table and thus provide support for the bending actions, whereas in the hands-occupied condition, the hands provide no such support.

Modifying the paradigm by varying whether the actions in the hands-free and hands-occupied conditions are realized with leaning on the table seems to have an impact on the results. For example, when the model’s hands were occupied by two foam balls on the table, infants imitated the head action arguably because the hands resting on the table (on top of the balls) provided support and thus evoked motor resonance despite the fact they were actually used for a different purpose.

The underlying supportive mechanism of action selection and the role of context in action understanding have been studied in human adults by functional brain imaging. In the study of Brass et al. (2007), participants observed an unusual action in non-justificatory or implausible (pushing a button by elbow while the hands are free) versus justificatory or plausible contexts (pushing a button by elbow while the hands are occupied with holding books). The results of this study showed that those brain areas that are part of a network involved in inferential interpretive processes of rationalization and reasoning about the mental states of others are found to be distinctively active when the action occurs in an implausible context. However, no differential activation was found in the primary motor and mirror network, so in regions that are supposed to be active in blind imitative contexts. These findings support the assumption that action understanding and preparation to act in novel situations is primarily mediated by an inferential interpretive system, involving rationalization induced by contextual factors, rather than simply by the motor mirror system.

With respect to the competences of infants, importantly, the motor resonance model can explain the findings of the original head-touch

paradigm but cannot account for selective imitation in the conceptual replication paradigms (see also above in section “[Replications](#),” Schwier et al. 2006; Király 2009) where the demonstrated actions are identical, and thus the induced motor resonance should be equal, and consequently no difference in imitative behavior is predicted by the motor resonance account.

Another contrasting view was proposed by Beisert et al. (2012), who argued that the selectivity of infants’ action imitations is due to differences in attentional factors. According to their account, the head action receives less attention in the hands-occupied condition – in contrast to the hands-free context – as the hidden hands are unusual and therefore more salient and attract more attention.

The validity of this perceptual distraction model has been tested with the help of tracking gaze directions – as a cue for attention focus – in infants and adults as well (Buttelmann et al. 2017). The looking behavior was analyzed when participants observed the head-touch demonstration in the two original (hands-free and hands-occupied) conditions. The results of the eye-tracking data do not support the perceptual distraction account: both infants and adults predominantly observed the relevant head action in each condition. The amount of looking at the modeled head-touch action did not statistically differ in the empirical conditions. Consequently, infants and adults do not seem to attend differently to constrained and unconstrained modeled actions.

Overall, the suggested alternative accounts questioned the inferential interpretation of the phenomenon of selective imitation based on empirical data, yet their approach cannot fully account for the controversial findings in the field.

### **Challenges for Rational Imitation as a Coherent Theoretical Construct**

The description of rational imitation emphasized that action interpretation emerges from the observation of the overt behavior within a given context: in the head-touch procedure, when the experimenter’s hands were occupied, touching the light with her head was the only available means for turning on the light, so its use was

justified. Consequently, based on the observation of behavior and context, infants could have interpreted her head touch as not essential to accomplishing her goal. Infants thus used their hands to light up the lamp. But one might raise the question of why the majority of infants reenacted the novel head action in the hands-free condition? Here both the model’s and infant’s own hands were free, so infants could have (rationally) opted for accomplishing the goal by performing the more efficient “hand action.” A possible interpretation would be that in this situation, where the experimenter’s hands were free, and she could have used her hand to turn on the light, infants may have made the inference that using her head was indeed essential to accomplishing her goal.

However, this apparently paradoxical behavior highlights the need for a broader explanation framework that goes beyond the rationality account. These accounts build on infants’ proneness to interpret action demonstrations as social communication. Let us revisit from this angle the rational imitation proposal (Gergely et al. 2002; and see also Buttelmann et al. 2008 for a similar argument) which suggests that the reproduction of this apparently irrational action reflected infants’ interpretation that using the novel head action was possibly essential to attain the goal, so the novel action was a manifestation of some unknown reason that must justify the action as rational. The imitation of this new head action can be seen as a way of learning what the agent’s (rational) reason for his action might have been. The main problem with this proposal is that it essentially makes the idea of appealing to the rationality principle unfalsifiable; when infants did not reproduce the demonstrated action (in the hands-occupied condition), it was treated as evidence of the application of the rationality principle, and when they did reproduce it (in the hands-free condition), it was also interpreted as evidence for the operation of the same inference. Overall, the original explanation of selective head-touch imitation purely in terms of the application of the rationality principle fails to capture all of the relevant aspects of the selective imitation phenomenon.

## Introducing a New Approach to the Selective Imitation

A new approach to the selective imitation phenomenon attempts to explain not only why infants refrained from imitating the novel action when it seemed rational but also why they reproduced it when it was obviously not efficient. Király et al. (2013) proposed that this strange behavior is explained by infants' interpretation of action demonstrations as communicative manifestations of novel and culturally relevant means actions to be acquired. According to this theoretical framework, in their endeavor to master the often arbitrary customs of a given society, young children are prepared to learn behaviors of which the function is not apparent at first glance. In doing this, in the absence of the possibility to apply the rationality principle, they rely on the communicative signals of experienced others. Király and colleagues found that 14-month-olds reenacted the novel arbitrary means action, the head touch, only following a communicative demonstration, and not in an incidental observation context. Additionally, results revealed that infants' tendency to reproduce communicatively manifested novel actions is restricted to behaviors where the model obviously accomplished a change of state in the environment, so the goal could have been identified, and infants could construe goal-directed instrumental act.

In details, (following the argument of Király et al. 2013) because of the communicative signals that accompany the action demonstration, infants construe of it as a communicative action rather than a purely instrumental action (Csibra and Gergely 2011; Gergely and Jacob 2012). They take the situation as a teaching context where the demonstrated action and the communicative context together make them learn a functional action. In the hands-occupied condition, the rationality principle is sufficient to form a coherent interpretation of the situation; however, this is not the case in the hands-free condition. Thus, observers will search for alternative explanations. The communicative nature of the demonstration will induce the expectation that there is some relevance of the specific behavior presented. Because of this, besides construing of the final goal as "lighting

the lamp," infants will also construe of a subgoal, which is to achieve this by making contact between the lamp and their forehead. Rationality is interpreted in terms of this subgoal: if the goal is to touch the lamp with the forehead, then the demonstrated action no longer violates the rationality principle. Since the function of this subgoal is not apparent, but the demonstrator has expressed the intention to pass this behavior on, the action itself will be interpreted as normative.

## Conclusions

The phenomenon of selective imitation highlights that humans, and in some cases other species as well, do expect to learn from actions performed communicatively. In that angle, they are rational in the evolutionary sense; they learn efficiently from their environment observing and analyzing the attempts of their conspecifics. Nevertheless, as the current results indicate, the mechanisms of such learning cannot be explained solely by reliance on the principle of rationality of instrumental actions alone.

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## Rationality

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## Definitions

### Rational

To be *rational* means to reason based on logic (see [Logic](#)). This definition of rationality is agnostic with respect to physical mechanism, and as a result allows for descriptions of both biological organisms and computing machines as being rational, if their behavior is governed by logic. For an excellent discussion of reasoning in both humans and animals, see the edited volumes by Hurley and Nudds (2006) and Watanabe et al. (2009) from which this work heavily draws. Rational behavior can also be considered to be *optimal* or *ideal*. The behavior of a living organism can therefore be compared to a model designed according to principles of rationality, such as optimal foraging theory (Stephens and Krebs 1986), ideal observer models of perception (Liu et al. 1995), rational accounts of causality (Cheng 1997; Waldmann et al. 2006, 2008), and Bayesian approaches to decision-making (Holyoak and Cheng 2011; Lu et al. 2008; Oaksford and Chater 2007). The remainder of this entry will focus exclusively on psychological rationality (i.e., reasoning and logic) and not rationality by functional rationality.

### Logic

*Logic* describes the rules or principles by which a conclusion is validly derived from its premises.



A logical inference involves the use of logical rules or principles by which a conclusion is validly derived from premises. A hallmark of a logical inference is that it allows new knowledge to be inferred rather than acquired through direct experience (Watanabe and Huber 2006).

### Top-Down

Rational processes are often characterized as being top-down, in contrast to bottom-up processes such as associative learning and conditioning. Top-down processes are rational because they involve the individual going beyond prior experience to derive knowledge or base decisions on the principles of logic. Some examples to be covered below involve rats or pigeons making inferences about the temporal, spatial, or causal relations between events that had never been directly experienced together. These types of inference can be derived from coherent and connected representations (aka cognitive maps, Blaisdell 2009; Tolman 1948) that integrate prior direct experiences, such as prior learning of an A–B and a B–C relationship. The integrated A–B–C map provides the structure upon which A–C relationships may be logically computed (further details below).

Related to the concept of top-down processing is the concept of an informational approach to learning and behavior. These approaches range from early work conceptualizing animal behavior as hypothesis testing (Krechevsky 1932), to recent accounts in terms of propositional knowledge (De Houwer 2009) and information theory (Gallistel and Gibbon 2000; Gallistel et al. 2001).

### Reasoning

*Reasoning* is the process of behaving following principles of logic and rationality. Most descriptions and discussions of reasoning involve behavior that goes “beyond the information given” (Waldmann et al. 2006), in that the behavior was not previously directly learned through principles of reinforcement or reward, nor through other means of direct experience or observation, but instead through an extrapolation beyond the scope of prior learning.

## Categories of Rationality

The following section catalogs the types of reasoning processes that reflect rationality in animals. Many of these concepts are derived from their use in the study of human rationality and reasoning and are necessarily anthropocentric in their origin. Nevertheless, there is no *a priori* basis for defining rationality as a strictly human behavioral trait, and the origins of many human-type cognitive processes often have deep evolutionary roots. Thus, homologous, or at least analogous, reasoning processes that lend themselves to rational analysis can be found in nonhuman animals (Blaisdell 2016).

### Logical or Deductive Inference

The following section presents the six most common types of deductive logical inferences studied in animals. Such inferences are also called *deductive* because the conclusion is deduced from its premises. For example, if all swans are white, and you are told there is a swan in the pond, you can deduce that it is white (cf. *inductive* inference in section [Induction](#)).

### Stimulus Equivalence

Equivalence is a property that defines the relationship between stimuli. Stimulus equivalence was originally defined by Sidman (1990) and involves three types of relations between three stimuli (A, B, and C) that have appeared together in pairwise fashion (i.e., AB, and BC), such as during operant or Pavlovian conditioning, or through mere exposure. These relations are *reflexivity*, *symmetry*, and *transitivity*. In an operant matching procedure, for example, if the subject is reinforced for choosing B after A and C after B, called A–B and B–C matching, respectively, subjects will often match each stimulus to itself (A–A matching), which is called reflexivity. If subjects do the reverse of what was explicitly learned, choosing B after A or C after B, this is called symmetry. Finally, if the subject matches C to A, despite C and A never having appeared together before, this is called transitivity. Urcuioli (2008) has provided a theoretical account for these types of matching behavior in pigeons (see also Urcuioli 2015). Equivalence

learning is thought to serve as the basis for equivalence class formation, by which multiple stimuli are grouped into the same category through sharing a common outcome or an equivalence relationship (Honey and Hall 1989).

The stimulus relation of transitivity deserves special mention due to its role in studying logical deductive inference in animals. A transitive relation need not involve equivalence. Rather, a transitive relationship could involve the ordinal relations between sets of paired stimuli. For example, when presented a choice between A and B, if choosing A but not B is always rewarded, and when presented with a choice between B and C, if choosing B but not C is always rewarded, then, when faced with a novel choice between A and C, a transitive inference would involve the choice of A over C. While A and C never had a history of comparison or differential reward with respect to each other directly, a transitive relationship of  $A > B > C$  would result in a logical deduction that, if  $A > B$  and  $B > C$ , therefore  $A > C$ . This would be a highly useful behavior for an individual living in a social group with a dominance hierarchy. For example, if Individual C has previously observed Individual A always (or usually) win in competitions for a resource (food, mating opportunities, etc.) against Individual B, and Individual B always (or usually) win in competitions with the observing Individual C, Individual C would benefit from inferring that it would also lose in competition with Individual A despite having no previous competitive experience with A. This inference could certainly save Individual C the danger (or embarrassment) of losing a competition.

There has been much debate over the psychological mechanisms that underlie the transitive inference. While some have claimed evidence for a representational account in terms of encoding ordinal relations between stimuli (Bunsey and Eichenbaum 1996), others have found support for simpler associative accounts based on concepts such as value transfer (Frank et al. 2003; Zentall et al. 1996).

#### Spatial Deductive Inferences

Deductive inferences have been shown in the spatial domain. Perhaps the most primitive type

of spatial inference is *dead reckoning* (short for deductive reckoning). Dead reckoning is the process of calculating one's current position by using a previously determined position and advancing that position based upon a known or estimated rate of movement through space over elapsed time. Many vertebrate and invertebrate species show evidence of using a *path integration* process to navigate by dead reckoning (Collett et al. 1998; Etienne et al. 1986). After making an outward journey from a home nest, with many twists and turns, the animal is able to navigate in more or less a direct line back to the home nest after encountering a food item. The spatial vector encoding the distance and direction from the animal's current location to its home nest is computed by integrating each segment of the journey and computing a vector between the current location and the starting point (home nest).

A second kind of deductive inference involves the calculation of the allocentric spatial relationship, or vector, between two external points in space that have never previously been observed together, nor for which the animal has traveled directly from one to the other. According to the spatial integration hypothesis of *cognitive map* formation (Blaisdell 2009), complex spatial representations can be built by linking together simpler representations that share common elements. A spatial representation containing three events (A, B, and C) can be built in one of two ways. On the one hand, all three events could be presented simultaneously, in which case the animal could construct a spatial representation containing all three elements. For example, presenting landmarks (LMs) A and B together with a food goal could establish a spatial map containing all three elements. On the other hand, the same three-element spatial map could be constructed in a piecemeal fashion by joining together two simpler representations, each containing two of the three elements. This process would allow subjects to construct the same three-element map without experiencing all three elements at the same time. An integrated map allows the subject to compute novel relationships among map elements beyond direct experience; a hallmark of the cognitive map.

In Phase 1 of an experiment with pigeons (Sawa et al. 2005; see also Blaisdell and Cook 2005a), subjects received presentations of two visual landmarks consisting of colored geometric shapes (A and B) on a touchscreen in an operant chamber in Phase 1. The screen location of the pair of landmarks varied across trials, but they always bore the same spatial relationship to each other. Pigeons then received training in Phase 2 consisting of  $A \rightarrow \text{Goal}$  pairings. The screen location of the goal was randomly determined from trial to trial. LM A maintained a stable spatial relationship to the goal, thereby signaling the goal location. After pigeons were reliably finding the goal in the presence of LM A, they received nonreinforced test trials with LM B alone. If pigeons had acquired the  $B \rightarrow A$  map during Phase 1 and the  $A \rightarrow \text{Goal}$  map during Phase 2, then they would be able to compute the  $B \rightarrow \text{Goal}$  spatial relationship or map. Evidence for the  $B \rightarrow \text{Goal}$  spatial inference was found in the highest density of screen pecks being clustered at the inferred Goal location. Similar findings have been reported by Chamizo et al. 2006 and Leising et al. 2012.

#### Temporal Deductive Inferences

There is an equivalent type of inference in the temporal domain as to that involving spatial integration. According to the temporal coding hypothesis (Arcediano et al. 2003; Savastano and Miller 1998), the subject forms temporal maps between events experienced such as during a Pavlovian or instrumental conditioning procedure. Moreover, separately acquired temporal maps can be superimposed when they contain common elements, thereby forming an integrated map. This integrated map can be used to compute temporal relationships between events that had never been physically paired. Temporal integration has been shown using a variety of Pavlovian tasks such as second-order conditioning and sensory preconditioning (Barnet et al. 1997; Leising et al. 2007). In second-order conditioning, the CS1-US association is learned prior to the CS2-CS1 association. In sensory preconditioning, the CS2-CS1 association is learned prior to the CS1-US association.

#### Causal Deductive Inferences

Similar to cognitive maps involving spatial and temporal information, causal information can be encoded as a cognitive map. Such causal-based cognitive maps are typically referred to as causal models (Griffiths and Tenenbaum 2009; Waldmann et al. 2006). Once formed, a causal model can be used to deduce cause-effect relationships that have not previously been observed or experienced. One special type of causal inference involves the distinction between observing versus intervening on an effect (Sloman and Lagnado 2005; Waldmann and Hagmayer 2005). For example, observing that the window outside is wet might lead to the diagnostic inference that it has recently rained, which would be a cause for alarm to someone who hung up the wash to dry outside. On the other hand, if the individual knew that they had just watered the garden and that therefore they had caused the window to get wet, they would discount the plausibility of it having recently rained and would therefore not be worried about the state of their laundry. Some evidence that animals can similarly make different causal inferences when presented with an effect that they merely observe versus with an effect that resulted from their own intervention comes from experiments in rats (Blaisdell et al. 2006). Rats in a conditioning chamber first observed a light followed by a tone ( $\text{Light} \rightarrow \text{Tone}$ ). Next, they observe the same light followed by presentations of a food reward ( $\text{Light} \rightarrow \text{Food}$ ). If the rat forms a causal map between each pair of events, then they should form a causal model consisting of light as a common cause of both tone and food. Causal model theory would then make specific predictions about what inferences about food the rat should make when the rat hears the tone at test. If the rat merely observes the tone, then the rat should diagnostically reason that the light must have occurred, and therefore should make the predictive inference that food should also be present. In this case, the rat should look in the feeder for food. If, on the other hand, the tone only occurred whenever the rat pressed a new lever that was placed in the chamber for the first time in the test session, the rat should infer that it, and not the light, had caused the tone, and therefore

should not diagnostically infer the presence of the light. Because the rat does not expect that the light had just occurred, then it also should not expect food, which is an effect of the light (and not the tone or the lever). In this case, the rat should not look in the feeder. This was indeed what has been found in a number of experiments (Blaisdell 2016; Blaisdell et al. 2006; Blaisdell and Waldmann 2012; Leising et al. 2008).

### Inference by Exclusion

Another type of decision-making that can occur under conditions of ambiguity involves inference by exclusion. Oftentimes, an individual is faced with the prospect of making a choice when the correct option that was available in the past is not immediately apparent. In these situations, evidence of absence can signal the likely correct choice. This is called *inference by exclusion*. A simple example of an inference by exclusion is the popular childhood game of asking “In which hand am I holding it?”, where “it” is some small item – such as a coin – that can be enclosed in the hand without revealing its presence. If the decider chooses a hand and the questioner opens their hand to reveal an empty palm, the decider infers that the item must, by logical exclusion, be in the other hand.

Variations on this child’s game have been used as a procedure to study inference by exclusion in animals. At its most advanced level, it is of interest because human children likely learn the meaning of many words by way of an inference by exclusion – a form of word learning termed *fast mapping*. Inference by exclusion has been found in a variety of nonhuman animals, including dolphins (Herman et al. 1984), dogs (Kaminski et al. 2004), and rats (Blaisdell 2016), though the evidence for pigeons has been mixed (Aust et al. 2008; Lauffer et al. 2017).

### Inference in Ambiguous Situations

Because they typically involve drawing an inference beyond prior direct experience or the information previously given, rational inferences are useful when information about a relevant aspect of the world is obscured from perception. Such situations create ambiguity about which of many

possible states of the world is currently present. If a decision to respond or not respond depends on knowing about which of the two (or more) states the world is currently in, the individual may have to make an inference about the true state of the world. Recent experiments that investigate how rats deal with ambiguous states of the world during decision-making utilize a technique by which possible world states are first learned, and then at test, information about a cue necessary to discriminate between states is withheld (Blaisdell et al. 2009). For example, a rat may first be trained to make an instrumental discrimination based on a set of visual discriminative stimuli. After learning the visual discrimination, one of the visual cues, such as a light, can be covered by an opaque metal shield. Thus, the state of the light is ambiguous; it may be on or it may be off. There is no way for the rat to be certain. The rat might act as if it reasons that the light could be on, despite not being able to see it. If this is the case, the rat might base its response by entertaining the possibility that the light, though covered, is actually on. Variations of this procedure have provided evidence that rats indeed are able to make hypothetical inferences about which are the likely states of the world under ambiguous conditions (Fast and Blaisdell 2011; Fast et al. 2016a; Waldmann et al. 2012), and this ability seems to be dependent on a functioning hippocampus (Fast et al. 2016b).

### Induction

An inductive inference involves inducing a general rule, principle, or property by extrapolation from prior examples and evidence. For example, if you’ve seen hundreds of swans during your lifetime, and all of them were white, you might draw the inductive inference that all swans are white (cf. *deductive* inference in section [Logical or Deductive Inference](#)). Inductive inferences are generally more difficult to make given the uncertainty in (a) the accumulated evidence, and (b) the scope of the inference. For example, how many white swans must one observe before one can be certain to draw the inductive inference that all swans are white? And how broadly can you generalize this inductive inference, to all swans in England, all swans in Europe, all swans in the

world, all water fowl closely related to swans, etc.? Furthermore, it only takes one counterexample (e.g., a black swan) to completely undermine the inductive inference. Even for humans, such black swan events can show the fragility of relying too heavily on inductive reasoning (Taleb 1997, 2012).

#### Causal Power

The topic of deductive causal inference has been discussed. Such deductions may require the acquisition of causal representations. Cause-Effect relationships cannot be directly observed, nevertheless, they may be induced through observation of the statistical and temporal relationships between events (Young 1995). Models that account for causal induction include causal model theory (Waldmann et al. 2006), models of causal power (Cheng 1997), and causal Bayes nets (Gopnik et al. 2004; Griffiths and Tenenbaum 2009). Indirect evidence for causal induction in animals comes from the same rat experiments that were used to study deductive inferences from causal maps (Blaisdell et al. 2006). When a rat makes different deductive inferences about the likely presence or absence of food based on whether it had intervened to cause a tone or the tone was merely observed in the absence of an intervention, this implies that the rat had represented the light-tone and light-food relationships as causal, and not merely associative. That is, the rat must have formed a causal model linking light as a common cause of both tone and food. If these relationships were merely associative, then the rat should have expected food every time it heard the tone at test, regardless of whether the tone was merely observed or the result of the rat's intervention (see Leising et al. 2008, for further analysis of the special role of causal agency in deductive causal inferences).

A more direct test for causal induction in the rat comes from a study by Polack et al. (2013). Rats first learned to press a lever for water reinforcement. They then learned that lever pressing produced a tone. Following this, some rats learned that the tone is followed by a footshock (importantly, the levers were not present in the chamber during this training). At test, the thirsty

rats were placed in the chamber with free access to the lever (that had previously earned water when pressed). Rats for which the tone had previously been followed by shock made significantly fewer lever presses than did rats for which the tone had not been paired with shock. If the pairings between tone and shock had established merely a tone-shock association, then the rats should not avoid pressing the lever (for water) because, even though they might have learned that pressing the lever is associated with the tone, *the tone merely predicts but does not cause the shock*. If, on the other hand, the rat encodes the tone-shock relationship as causal, then the rat should avoid pressing the lever, which in the past had also led to the presentation of the tone because the tone itself is perceived as a cause of shock, which is to be avoided. This experiment provides perhaps the best direct evidence for causal induction of a cause-effect representation in a nonhuman animal.

#### Concept Learning

The ability to discriminate stimuli based on category membership exemplifies conceptual behavior. Concept learning involves the process of stimulus classification based on a generalizable rule or property. There are three types of concept that animals have been shown capable of learning: perceptual, functional/equivalence, and abstract/relational. Category membership in a perceptual concept is defined by perceptual features of the item, as illustrated by the classic experiments by Herrnstein et al. (1976). Pigeons were reinforced with food for responding to photographs that contained pictures of people or parts of a person (e.g., a face) but were not reinforced for responding to photographs that did not contain pictures of people. Pigeons were able to learn this person/no-person discrimination. Pigeons were not merely learning the correct responses to each picture of the training set. Instead, they showed true concept learning in that their discrimination performance transferred quite accurately to novel pictures that did or did not contain humans in them. Much evidence has accumulated as to the general ability of nonhumans to acquire perceptual concepts (Lea et al. 1993; Wasserman et al. 1988) and include not only discrimination of



objects but also of actions and movement (Cook et al. 2001; Dittrich et al. 1998).

A functional concept involves the classification of items based on their functional similarity, such as furniture, tools, etc. While the individual members of the category might be perceptually different from each other – such as a saw, sledgehammer, and miniature screw driver – they all share the same functional property, such as all being tools. Like a functional concept, an equivalence class is also defined by perceptually disparate items being grouped together based on sharing a common relation, such as an association with an outcome. By sharing a common associate, the items within the equivalence class become functionally equivalent. There is quite a bit of evidence that animals are capable of forming equivalence classes (see section [Stimulus Equivalence](#)). For example, after learning A–B and C–B associations (where A and C are sample stimuli presented on a center response key and B is a comparison stimulus presented on a side response key), pigeons that then learn a new A–D association will automatically have an increased probability of choosing D following C, despite never having been explicitly trained on a C–D relation (Urcuioli and Lionello-Denolf 2001). Equivalence category learning has received extensive attention in the animal learning and cognition literature (Bovet and Vauclair 1998; Hall 1996; Honey and Hall 1989; Zentall 1998).

Perhaps the most abstract form of concept learning involves categorizing stimuli based on their relational properties. Most of this work involves training subjects on a Same/Different discrimination, by which responding to a set of items is reinforced if the items are all the same as each other (“Same” category) or not (“Different” category). After successfully learning the discrimination, Same-Different concept learning is demonstrated by above chance transfer to novel items that also belong to Same and Different categories (Blaisdell and Cook 2005b; Wasserman et al. 1995; Wright et al. 1984). Chimpanzees (Gillan et al. 1981; Oden et al. 1988), and perhaps baboons (Fagot et al. 2001), macaques (Flemming et al. 2011), and pigeons (Cook and Wasserman 2007), may also have the capacity for

encoding higher-order relations (e.g., relational match to sample), such as those that underlie analogical mapping.

### Rule Learning

Another form of inductive learning involves the abstraction of a rule that defines the underlying structure or regularity among a set or sets of stimuli. Rule learning is typically studied by presenting the structured input to the subject and rewarding the subject for choice responses that conform to the rule. Evidence for rule learning must come from tests involving novel stimuli to see whether the subject has abstracted the rule. The subject should be able to apply the abstracted rule to novel stimuli. If not, then the subject may have simply memorized correct responses from the training set of stimuli.

One of the simplest rules, and with the longest history of study in animal cognition, involves the matching-to-sample (MTS) and non-matching-to-sample (NMTS) procedures. In these procedures, the subject is first presented with a sample stimulus (e.g., showing a red key light to a pigeon). Next two comparison stimuli are presented, one that matches and one that does not match the sample (e.g., a second red key light and a green key light). In a MTS procedure, the subject receives a reward (e.g., food) for choosing the comparison that matches the sample (red in this example); while in a NMTS procedure, the subject is rewarded for choosing the non-matching comparison (green in this example). While early work failed to find evidence for transfer to novel stimuli, therefore showing that such a procedure did not lead to true rule learning (Cumming and Berryman 1965), it has been subsequently shown that increases in the training set size led to increases in accuracy of transfer performance (Bodily et al. 2008), providing evidence for learning and applying an abstract rule of “choose same.”

More complex and sophisticated rule learning involves sequence information (Fountain 2008; Murphy et al. 2008), spatial patterns (Brown et al. 2000), number (Brannon and Terrace 2000; Scarf et al. 2011), syntax (Kako 1999), and artificial grammar (Herbranson and Shimp 2008;

van Heijningen et al. 2013). Dissociations between bottom-up associative accounts and top-down rule induction accounts of serial pattern learning have been reported in rats (Wallace and Fountain 2002) and pigeons (Garlick et al. 2017).

### Tool Use, Physical Cognition, and Theory of Mind

There are numerous reports of tool use in the animal kingdom. While many such instances likely involve noncognitive processes such as innate mechanisms (e.g., bird nests, spider webs, etc.), some examples have attracted the attention of more cognitive accounts. Some of the most likely candidates for rational processes in tool use involve apes and birds, and utilize physical traps (Mulcahy and Call 2006; Logan et al. 2014; Tebbich et al. 2007), string pulling (Taylor et al. 2010; Werdenich and Uber 2006), and even optimal tool construction or modification (Weir and Kacelnik 2006).

Some of the abilities that underlie rational tool use and construction involve more general processes that are collectively referred to as *physical cognition*. Physical cognition includes object permanence (Mendes and Huber 2004), causal effects of physical properties of objects (Call 2007; Helme et al. 2006), and means-ends relations (Krasheninnikova et al. 2013). A related domain of rational behavior involves predicting the behavior of, and communicating with, other agents. This domain is referred to as theory of mind and involves holding beliefs about one's own or other's beliefs and knowledge. Evidence for true theory of mind (i.e., mindreading) versus a theory of behavior (i.e., behavior reading) in nonhumans is contentious (Call and Tomasello 2008; Heyes 2015).

### Conclusions

I have reviewed evidence for rational processes in animals. Many animals show evidence for rational processes falling into two domains: deductive inference and inductive inference. These types of rational processes have been the direct focus of empirical study. Furthermore, there is a large and growing literature on physical cognition and theory of mind in animals, which touch on both domains of inference.

Given the extensive evidence for a variety of rational processes in animals, the question should be asked, are there any rational processes that seem beyond the capacities of nonhuman animals? Actually, there are. Abductive reasoning has yet to receive serious attention in the animal literature. An abductive inference involves the process of seeking and assessing explanations (Johnson et al. 2015; Turrisi 1997). Unlike deductive reasoning, in abductive reasoning the premises do not guarantee the conclusion. Instead, an abductive inference is derived from the strength of the premises and can be thought of as a likely (or best) explanation for the state of the world that brought about the conclusion. The few studies that have investigated whether nonhumans seek explanations have compared human children to chimpanzees. In contrast to human children, who have the natural proclivity to seek explanations for anomalous or unexpected events, chimpanzees fail to display this capacity (Povinelli and Dunphy-Jelii 2001).

Another rational process for which there is extensive evidence of absence in animals is true language. As opposed to many forms of communication found throughout the animal kingdom, true language is recursive and open-ended such that any meaning may (in theory) be communicated symbolically (e.g., through spoken or written word, signs, tokens, etc.). Even great apes, parrots, and dolphins that have received extensive symbolic training – such as with lexigrams, signs, or vocalizations – acquire only rudimentary properties of language, including syntax and vocabulary (Kako 1999; Pepperberg 2017). Some have taken this, and the poor quality of evidence for true theory of mind, to argue that there exists a deep divide between human and nonhuman minds (Penn and Povinelli 2007; Penn et al. 2008). This may be the case, but for now it is still an open, empirical issue that awaits further testing.

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## Ray Locomotion

- [Chondrichthyes Locomotion](#)

## Ray-Finned Fishes

- [Actinopterygii \(Bony Fish\)](#)

## Reaching

- [Parieto-occipital Sulcus \(POS\)](#)

## Reaction Norm

- [Norm of Reaction](#)

## Reaction Time

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## Historical Background

Reaction Time (RT) data have been used as a measure of human behavior throughout the history of psychology. The Dutch physiologist Franciscus Donders (1969) believed that RTs were a window into *mental chronometry* or the duration of various mental operations that included perceiving a stimulus, recognizing it, and making a choice. His methodology heavily relied on a subtraction method in which tasks purportedly with and without various mental components were compared. The difference in reaction time between two tasks that varied in one task component was assumed to measure the duration of that component. For example, the two tasks could require deciding whether to push a button when a stimulus appeared versus pressing any button when it appeared. Trials involving a button press for the former task might produce RTs that average 65 ms longer. Using Donders' logic, this suggests that the mental process of deciding is 65 ms in duration. The basic assumptions of the subtraction method were questioned (Kulpe 1909) largely because the addition of a new task requirement could fundamentally alter the way in which ongoing task components were processed by the brain. In the button press example, it is possible that requiring the participant to decide whether to press the button may also alter the way that the stimulus properties are perceived or the attention directed to the task.

In studies of human cognition and perception, reaction time is a critical variable in the study of choice. A choice that is made more quickly is assumed to be easier. When discriminating between two very similar stimuli, RTs will be longer than when the two stimuli are very different. If there is a “correct” choice, the error rate will

also be higher for harder discriminations. Although this relationship between reaction time and difficulty can be weakened by either encouraging fast RTs on every trial or giving people an unlimited amount of time to make a choice (thus producing the speed-accuracy trade-off, Henmon 1911), long RTs and high error rates are usually coupled for tasks in which at least one choice is designated as correct.

The utility of RTs for human experiments is rooted in their continuous nature that allows the experimenter to know whether a particular choice was easier or harder than other choices even when the categorical response (chose the “left” button or the “correct” button) was identical. For example, a person categorizing stimuli as “red” or “violet” may have chosen the same response for a deep red stimulus and a reddish-purple stimulus, but the reaction time for the first choice is likely to be much shorter than that for the second. In sum, reaction time has proven a useful metric of choice difficulty in human experiments.

In comparative psychology, however, reaction time has played a much smaller role than it has in human experiments. The key variable for most experiments involving the nonhuman animal is the choice – did the animal choose the left lever or the right? One of the reasons that reaction time is rarely utilized in studies of nonhuman species is that there are so many uninteresting factors that influence the speed at which an animal will choose. Unlike humans in a laboratory that sit in front of a display with their fingers poised on the response keys, rats, pigeons, and mice in an experimental chamber can spend an inordinate amount of time grooming themselves, not looking at the stimulus, and performing other nontask behaviors. This additional variability makes reaction time data especially noisy in animal studies.

For example, Fig. 1 shows a frequency histogram of a subset of 57,098 RTs for a study of object recognition by pigeons. The raw RTs are extremely skewed and highly variable, varying from 0.02 s to 186 s (i.e., over 3 min; the 42 responses longer than 15 s were omitted from Fig. 1). Using the most powerful tools currently at our disposal (multilevel modeling after RT transformation) without aggregating the data, the only

effect of any importance was all too obvious – when the stimuli were randomly assigned to choice keys rather than assigning all objects of the same class to the same response key, the pigeons took longer to respond (2.2 s vs. 1.1 s). So, despite the extremely large sample size, it was difficult to assess reaction time differences for any but the largest and most obvious effect.

To appreciate the problem with reaction time in the typical animal experiment, consider a study in which a pigeon performs a series of trials in which a stimulus is centrally displayed and two response keys are presented. In the typical design, the pigeon is required to peck at the stimulus one or more times (the orienting response) thus acknowledging that the pigeon has seen the stimulus. After fulfilling this peck requirement, the response keys are then made available. Given the amount of time required to peck the stimulus, the neural processes supporting a decision may have occurred long before the response keys were even displayed. Indeed, the location of the last orienting response will affect the speed at which an animal can move to each of the response keys.

Another complicating factor in animal studies is that animals differ in key preference (e.g., showing a side bias). In human studies, this is readily addressed by either switching the stimulus-response assignment during the experiment (within-subject counterbalancing) or having each subject assigned to a different stimulus-response mapping (between-subject counterbalancing). This type of counterbalancing is less common in animal work because the slow learning of a new mapping can complicate within-subject counterbalancing, and the small sample size of the typical animal study may be insufficient to be confident that between-subject counterbalancing will increase the validity of RTs.

There are some preparations using nonhuman animals that have produced much cleaner reaction time data. Some primate studies use designs in which the subject holds a joystick that is moved from side to side, thus eliminating many of the inattentive nontask behaviors that might be produced between stimulus onset and the response (Heimbauer et al. 2012; Hopkins et al. 1989). Another design successfully used with primates

simply registers the onset of an eye movement to a location (Roitman and Shadlen 2002). For rats, designs that require the subject to be located at the lever can produce more useful reaction time data. This requirement has been implemented by requiring a rat to hold down the lever and to only release it when a response is necessary (Baunez et al. 1995; Laubach et al. 2000). Although the resulting RTs are much less variable, this design is not easily translated into studies requiring a subject to choose between multiple options.

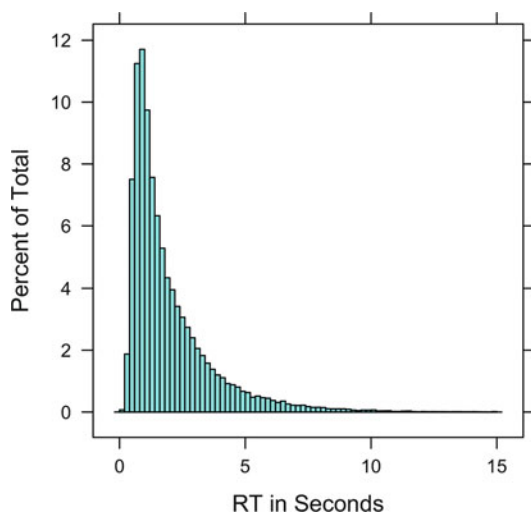
Donald Blough and colleagues have had some success in eliciting reliable RTs from pigeons. Blough and Blough (1978) projected small stimuli on a response key approximately once every 20 s and measured the elapsed time between the presentation of the stimulus and a pigeon's peck. Like the design involving a rat holding down the response key, the strength of this design relies on the subject being poised over the response key thus eliminating the variability created due to nontask behaviors. A different design used in Blough (2002) served a similar purpose and likewise produced useful RT data. In this task, a cue occurred immediately before the target stimuli, but in the same location as the stimulus that was contingently reinforced. The cue was a valid cue for some target stimuli but not for others, so it was possible to use the RT duration as an assessment of the pigeon's expectation regarding what would follow.

For rats and pigeons, each of the designs that generated valid and reliable RT data are, in essence, go/no-go designs in which the subject either responded to a stimulus (released the lever or pecked the key) or did not. There is one reported use of RTs for a choice task in the pigeon that overcame the problems typically present in nonhuman studies of choice. Blough (2009) required pigeons to discriminate between 5 mm spots of light separated by 6 cm, and the selection of one or the other stimulus was registered if a peck occurred within 0.5 cm to the left or right of it. Given the small size of the stimuli, it was possible to place them in close enough proximity to the ready cue that nontask behaviors between stimulus presentation and the response were

greatly reduced. Of course, this type of design places significant constraints on the size (and thus complexity) of the stimuli to be discriminated. Consequently, producing useful RT data for choice tasks is likely to continue to prove problematic for many species.

### Other Time-Based Measures Used in Studying Animal Cognition

Two measures related to reaction time that have been regularly used in comparative psychology are the time to complete a task (e.g., latency to finish a maze, or when finding a stimulus among many which is not the latency of a reaction but rather the duration of a search) and the rate of responding (e.g., how quickly a pigeon is pecking at a stimulus, often assessed by interresponse time but also indirectly assessed by the number of responses that occurred during a constant time interval). Although these are not RTs, the analysis of these time-based measures present many of the same analysis challenges raised in the next section due to the skewed nature of temporal variables. Subjects have a floor on how quickly they can respond but often no ceiling on how slowly, and this asymmetry can create a skew in the dependent variable that should be considered in statistical analyses (see Fig. 1).



**Reaction Time, Fig. 1** Skewed distribution of RTs

## Current Uses and Theory

Because of the issues raised earlier, RTs are not common in contemporary studies of nonanimal behavior. As a result, many researchers who do examine reaction time and other latency measures are not familiar with the challenges that these data present. Thus, this treatment will draw heavily from what has been learned in human reaction time studies to help the comparative psychologist confront these challenges.

First and foremost, RTs and other latency measures are heavily skewed. A subject can only respond just so fast to a stimulus (limited by the speed of neural processing) thus placing a floor on RTs, but very long RTs are not unusual, especially when nontask behaviors occur. There are multiple approaches that can be and have been used to deal with this skew, although some researchers rely on the ill-informed assumption that their favorite analysis technique is robust to violations of normality (Bradley 1978; Harwell et al. 1992). Interestingly, the principal problem is not non-normality per se but rather the heterogeneity of variance that inevitably occurs in the presence of nonnormal distributions of residuals. Current approaches include: (a) analyzing the median reaction time, (b) truncating the upper tail of the distribution, (c) transforming the RTs, (d) use of generalized linear modeling to fit an alternative distribution, and (e) fitting mixtures of multiple distributions. The following paragraphs will describe each of these in turn along with recommendations regarding their use.

### Analyzing Median RTs

The mean is not the appropriate measure of central tendency for reaction time data because it is affected by extreme observations and possible outliers in the right tail. The median is commonly used as an alternative measure of center for skewed data (Miller 1988) because it is more robust to extreme outliers than the mean. However, several issues arise when analyzing median RTs. This estimator varies more than other sample statistics leading to a significant decrease in power (Ratcliff 1993). Still, if it can be assumed that the probability of outliers is not consistent across

conditions, the median may be the most stable estimator. Another concern with using median RTs in analyses is their effect on linearity. Linear trends in the mean are not necessarily linear trends in the median (Ratcliff 1993). Generally, unless the specific location of the true center of the distribution is of interest, the median is not a particularly good sample statistic. Finally, any form of aggregation before analysis loses information about the uncertainty in that summary statistic as well as the sample size on which it was based.

### Truncating the Upper Tail

An outlier is an observation produced by a mental process other than the one of interest (e.g., experimenter error, loss of attention, fatigue, etc.). These observations interfere with the analysis and obscure the effects of legitimate responses and thus should be eliminated. However, valid yet extreme values should be retained and properly accounted for in the analysis. The distinction between extraneous and valid RTs is important for drawing accurate conclusions, but the proper classification is challenging because they coexist in the tails of the distribution. In reaction time data, most outliers will occur in the upper tail of the distribution, hidden among the other very long but valid RTs (Baayen and Milin 2010; Ratcliff 1993).

This long right tail is problematic for a conventional analysis, and researchers often resort to truncating, or omitting, these “outliers” in order to increase statistical power. The problem with truncating very long RTs is that researchers are often truncating valid responses. Common truncation methods involve using an a priori range of acceptable RTs (Ulrich and Miller 1994). The most common technique is eliminating data that are two to three standard deviations beyond the mean. However, because the mean is not a good measure of central tendency for skewed data, it is also not a good measure for identifying outlying responses. Because of the skew in reaction time data, this method of truncation will cause more observations in the upper tail to become eliminated than from the lower tail. This creates a downward bias when estimating parameters and fitting models to the data (Ulrich and Miller

1994). Because of the difficulty in distinguishing outliers from valid responses, truncating observations in the tails may lead to failing to exclude some illegitimate and very influential data values or to excluding legitimate responses (Baayen and Milin 2010; Ratcliff 1993). Although including outliers does add unwanted variability to the data, the bias caused by significant truncation is much more harmful and should be avoided (Ulrich and Miller 1994).

In spite of the danger in truncating valid responses, truncating obvious errors is necessary for obtaining accurate results. Some RTs may simply be impossible. For example, negative or extremely small RTs are not physically possible. Any reaction time less than 150 ms is measuring an anticipatory response and not an actual reaction time. Likewise, a decision reaction time involving minutes (which is quite possible in animal experiments) is arguably the result of inattention, grooming, and other nondecision behaviors.

### Transforming RTs

Transforming the original data can help minimize the effects of outliers and reduce heteroscedasticity (Bartlett 1947; Van Breukelen 2005). Transformation creates a dependent variable that can be analyzed using familiar linear methods of statistical analysis (e.g., regression and ANOVA). Commonly used reaction time transformations are logarithmic, inverse, and square root transforms (Bartlett 1947).

There are three known issues with transformations, (a) some transformations may not reestablish normality (Baayen and Milin 2010), (b) transformations can make it difficult to interpret the results within the transformed space, and (c) they can create complications when trying to convert back to the original scale (Bartlett 1947; Erceg-Hurn and Miroseovich 2008). To be maximally useful, researchers should consistently use the same transformation so that the results of one study can be readily compared to those of other studies. It is possible, however, that similar designs may produce RT distributions that are differentially affected by the same transformation. The transformation could actually introduce skew where none exists or undercorrect the existing

skew. Furthermore, applying nonlinear transformations (i.e., log, inverse, etc.) changes the original ratio scale. For example, a multiplicative effect in the raw data becomes an additive effect once a logarithmic transformation is used. This issue becomes problematic when trying to back-transform the results into the original units and when trying to assess interactive effects. When RTs are transformed, the direct connection with the mental processes can be lost (Lo and Andrews 2015). Lo and Andrews (2015) demonstrated an additive to overadditive effect in raw lexical data, but an underadditive effect when an inverse transformation was applied. This difference is notable because an additive to overadditive model suggests independent, serial processing between predictor variables whereas an under-additive model suggests interactions between predictors.

An additional issue when transforming RT data is ensuring that basic summary statistics like the mean are properly reported. Generally, researchers are only familiar with the arithmetic mean which is computed by adding the values and dividing by the sample size. However, a geometric or harmonic mean is a better measure of central tendency for heavily right skewed data (Sauro and Lewis 2010; Wainer 1977). The harmonic mean is based on the speed of a response and is less affected by the long right tail, but the geometric mean is based on log-transformed values and generally fits RT data better (Sauro and Lewis 2010). The harmonic mean is also more sensitive to outliers.

While transforming data to permit the application of general linear models is simpler than determining the underlying distribution and applying a generalized model (discussed below) and is certainly superior to aggregating the data before analysis, transformation should be done with awareness of the consequences for interpretation.

### Generalized Linear Modeling

A more complex but more accurate approach is to apply generalized linear models to RT data. Research on the benefits of generalized linear modeling is limited but suggests a greater ability to model the more nuanced nature of RT data. The generalized linear modeling approach



encompasses general linear models, such as linear regression and ANOVA, as a special case in which the assumed distribution of the residuals is normal. The advantage of generalized linear modeling is that it allows the analyst to specify alternative assumptions about the distributions of the data.

Historically, these models have not been attractive for researchers due to their complexity, limited development (e.g., a lack of repeated measures versions), and necessary computational power. Applying a generalized linear model required mastery of the specific model to be used and extensive mathematics that was beyond the area of expertise of nonmathematical researchers. In addition, each nonnormally distributed dataset required a unique, nonlinear model. Accordingly, linear modeling became the gold standard in most research.

However, with the advent of statistical modeling computer packages, generalized linear modeling has become more accessible. Currently, major statistical packages include options that allow researchers to select from numerous distributions with just as much ease as selecting a linear model. Given that RT data has skew that may be best modeled using alternative distributions like the Gamma or Weibull (Van Zandt 2000), future analysis of RTs may be best accomplished by using a model that uses a more appropriate distribution than the normal without requiring a transformation to normality. At this point in history, only a few researchers are adopting this approach, but it is expected to grow as researchers obtain training in generalized linear modeling.

### Mixtures of Distributions

Some data analysts have posited that RTs may be arising from multiple independent sources thus producing multiple superimposed distributions (e.g., Dolan et al. 2002). This approach is rarely utilized due to limitations in software for fitting mixture models, but it rests on the assumption that there are multiple sources driving recorded RTs. Reaction time distributions are considered the result of the superimposition of multiple distributions, one for each task component. For example, the ex-Gaussian approach combines an

exponential distribution with a Gaussian (or normal) distribution (Dawson 1988; Ratcliff and Murdock 1976). The exponential is assumed to arise from decision processes that are superimposed on a Gaussian reaction time distribution.

More generally, reaction time distributions could arise from combining multiple processes like reactions to the stimulus and nontask behaviors (Blough 2011; Ratcliff et al. 1999). Thus, a distribution could have two or more modes depending on which behaviors are evidenced on a particular trial. Mixture-based approaches attempt to estimate the parameters of each distribution along with the likelihood that a particular measure was drawn from one distribution rather than another.

### Other Issues Arising in the Analysis of RTs

*Practice Effects.* A ubiquitous source of variance in RTs is due to practice effects. Not surprisingly, the more practiced a subject, the faster the RTs. In human studies, the effects of practice are often the strongest source of RT variability in a study. Thus, isolating this source by including trial (or its logarithmic transformation) as a predictor in a statistical model can significantly increase the power of a data analysis. It can also be important to include predictors like trial or session in interactions with each independent variable in order to assess whether the effect of that IV is increasing or decreasing over time. For example, a subject's RTs may be insensitive to a variable like stimulus size early in training but show increased sensitivity with practice. Some comparative psychologists, however, train an animal to asymptote before introducing an intervention thus precluding the study of RT changes across time. Furthermore, temporal predictors are often blocked so that the data can be subjected to an analysis of variance (ANOVA) rather than identifying the functional relationship between a time-based level like trial and reaction time (Young 2016).

*Censored Data.* A common problem with animal studies involving any type of latency to a response is the possibility that the subject will simply not respond in a timely manner. Some designs may have a response deadline before a trial terminates and the next trial begins. This

raises the question of how to treat these missing RTs. Two approaches are common although a third is optimal.

First, the value could be replaced with the maximum possible that could be observed (i.e., equal to the deadline latency). For example, if a rat is given 90 s to find a hidden platform in a water maze, then a failure to find the platform is treated as a latency of 90 s. In his treatment of search times, Blough (2002) treated trials on which a pigeon had not responded by the end of the 10 s display of a search display as having a 10 s RT. This approach can be problematic because it can distort the RT distribution and create bimodal residuals when there is significant censoring. It also assumes that all failures to respond should be treated equally as being at the minimum possible RT for response failures, thus decreasing the RT variance.

Second, the trial may be treated as having a missing value. This approach acknowledges that the actual RT is unknown. However, these missing values are not missing at random which is a prerequisite for the optimal statistical treatment of missing data. It is not that the subject has an unknown RT (any value between zero and infinity) but rather that the RT is greater than a particular threshold (it can be any value between the deadline and infinity).

Third, the values are replaced with the maximum possible as in the first method, but these data are subjected to a censored regression that explicitly attempts to fit a distribution that acknowledges that this maximum value represents a value beyond the censoring threshold, but the value is treated as being in an unknown range.

To compare and contrast these approaches, Fig. 2 shows three illustrations of the consequences of different treatments of an RT distribution. The distribution on the upper left assumes that every trial generated a known RT. For the middle distribution, there was a deadline to respond, and any trial without a response occurring by that deadline was treated as having a value at the deadline. For the distribution on the upper right, RTs greater than the deadline are simply treated as missing. Both of the approaches illustrated on the upper right and bottom produce a

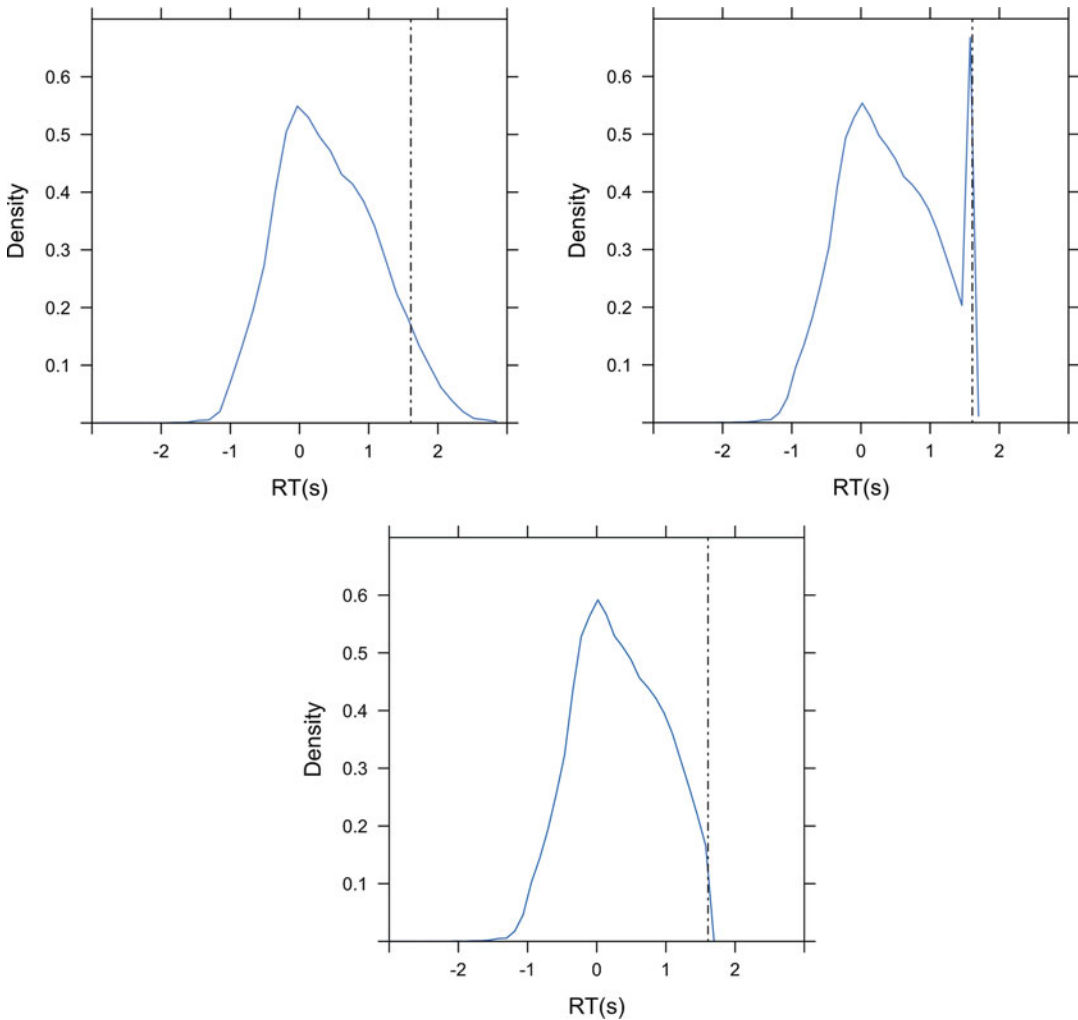
mean RT and standard deviation RT that were lower than the complete (ideal) distribution on the upper left (5% and 5% lower for the replacement method, 25% and 14% for the missing value method; of course, these values would be different for different distributions but should always be smaller). Thus, both approaches distort common statistical summaries of the data.

Censored regression is the proper analysis technique for fitting censored data and would be conducted on the data in the upper right panel. Unfortunately, scientists are often unfamiliar with the consequences of censoring, and repeated measures versions of censored regression are not broadly accessible. The effects of response deadlines on an analysis will depend on the response threshold and the amount of data that is censored. A response deadline may result in a large degree of censoring early in an experiment but, as subjects adapt to the deadline, the censoring may be rare later in an experiment. Regardless, it is recommended that researchers avoid the use of response deadlines that will result in a level of censoring that is obvious to the eye.

*The Speed/Accuracy Tradeoff and the Analysis of Errors.* A common observation in experiments in which one response is correct whereas others are incorrect is that subjects will show a speed/accuracy tradeoff: the faster that a subject responds, the greater the likelihood of making an error. This self-evident fact has consequences for the treatment and interpretation of RT data. To handle the potentially different meanings of correct RTs and incorrect RTs, researchers have either only analyzed correct RTs, used accuracy as an additional predictor in the analysis, or treated all of these RTs similarly.

The first approach sidesteps the speed/accuracy tradeoff by ensuring that all of the analyzed RTs are from correct trials. This approach is usually taken when errors are generally rare because otherwise it can result in a significant loss of data for analysis. The approach also makes the untenable assumption that all correct trials are equal, whereas some correct responses may be the result of guessing and only inadvertently correct.

The second approach has the advantage of not losing any data, and it isolates a potentially large



**Reaction Time, Fig. 2** RT distributions when not truncating at a deadline (left), truncating at a deadline (middle), and omitting data beyond the deadline (right)

source of variance in RTs (correct vs. incorrect). It has two drawbacks, however. First, if the independent variables covary with accuracy, as they often do, then adding accuracy as a predictor will result in accuracy competing to account for the same variance as the independent variables. Second, if some conditions produce few or no errors, then many analysis techniques will fail due to the design imbalance created.

The third approach must be coupled with a separate analysis of accuracy. For example, an analysis may show that the independent variables have no effect on accuracy but a significant effect

on RTs or vice versa. It is also common to observe that one or more variables increase accuracy while also decreasing reaction time, an indication that performance is improving in multiple ways.

*RT Validity with More than two Response Options.* Even in humans, the validity of RTs decreases as the number of response options increases because choosing among more than two responses is less automatized and may require searching for the right option among many. This search process thus contaminates RTs with additional nontask behaviors. For humans, the use of voice as a response can overcome this problem,

but so can other highly automatized multiple-response behaviors like typing on a standard keyboard for a skilled typist or using a gaming console for expert video game players. For nonhuman animals, this same benefit might be achieved by using eye tracking or direct assessment of neural behavior that precedes a response. In general, however, most researchers would be well-served with an initial focus on two-alternative choice tasks when RTs are to be collected and analyzed.

Unresolved Issues

Are Different Distributions Expected to Occur for Specific Paradigms or Species?

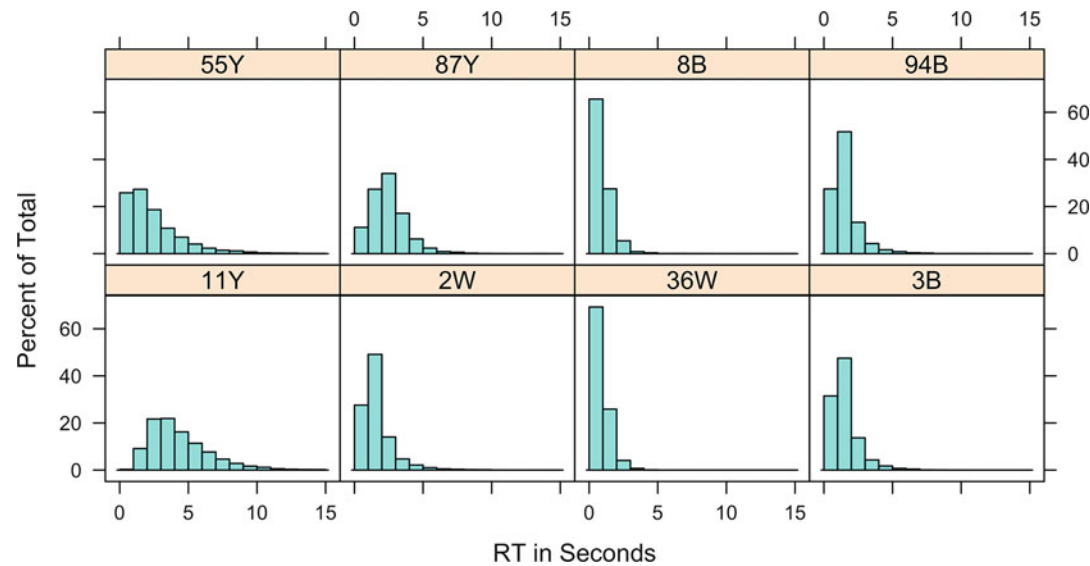
In human experiments involving RTs, nontask influences on RTs are typically much rarer than those occurring in nonhuman animals. Different paradigms have been shown to be more or less likely to produce nontask behaviors that influence the measured RTs, and different individual members of a species may be more or less likely to do so. Figure 3 shows plots for eight pigeons in an object recognition choice task. It is evident that some pigeons predominately made their choices soon after the choice keys were displayed (e.g., the four on the right of Fig. 3) whereas others

(notably, 11Y) showed more variable and delayed choices. Are some subjects producing few if any nontask behaviors whereas others are much more likely to spend time grooming, exploring, or resting? If so, distributions for the latter subjects may not only be more variable but may actually include multiple RT modes that complicate interpretation.

A related issue arises when comparing RTs across species or behaviors. Given that a response to a visually presented stimulus requires orientation toward the stimulus, species for which hearing is dominant might show different RT profiles if the stimuli were auditory because auditory stimuli do not require orientation to a specific location to identify the stimulus before responding. Finally, species or behaviors that tend to have long RTs or latencies are less likely to be skewed and may produce normal RT distributions.

Can Neural RTs Realize Donders’s Goals?

Donders (1969) originally set out to measure the duration of neural processes. Given that technological advances are providing the opportunity to measure the brain’s response to stimuli and the time at which a neural region changes activity, assessing the reaction time of multiple neural



Reaction Time, Fig. 3 RT distributions for eight pigeons

regions may provide the tool to address concerns like Kulpe's (1909). However, the original concerns about the subtraction method have arisen in brain imaging when making comparisons across tasks (Friston et al. 1996). Although the goal of mental chronometry is laudable, realizing this goal will not be easy.

## Cross-References

### ► Decision-Making

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## Reafference Principle, The

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### Definition

The principle of reafference is a theory proposed by von Holst and Mittelstaedt in 1950. This theory proposes that the brain distinguishes reafferent (self-generated) sensory stimuli from exafferent (externally generated) sensory stimuli based on an internal copy of an outflowing (efferent), movement-producing signal generated by the motor system.

### Introduction

Our sensory systems gather information in order to build an accurate estimate of the outside world. In turn, this information is used to guide our behavior. In everyday life our sensory systems are stimulated not only as a result of events in the external world (termed sensory “exafference”) but also as a result of our own voluntary actions (termed sensory “reafference”). In order to

achieve accurate perception and motor control, it is critical for the brain to distinguish between these two broad categories of sensory stimulation.

**Functional significance:** This ability to distinguish between sensory exafference and reafference is vital at multiple levels of sensory processing. For example, at the most basic level, it is essential in the context of reflex generation that the sensory stimulus is correctly assigned as originating from an actively generated movement rather than an externally applied stimulus. Consider the example of slipping on ice. In this situation, the corrective movements generated by vestibulospinal reflexes are essential for maintaining balance. In contrast, if a similar movement was actively generated as a voluntary movement, vestibulospinal reflexes would be counterproductive since they would counteract the intended movement. Likewise, the ability to distinguish between sensory exafference and reafference is a hallmark of higher-level cognitive functions; it is essential to know whether the origin of sensory stimulation is externally or self-generated. Indeed, a misinterpretation of “self-generated” versus “external world” has been implicated in psychiatric disorders such as schizophrenia.

**Original formulation:** Our ability to distinguish between sensory exafference and reafference has long been appreciated. Notably, in the nineteenth century, Helmholtz observed that we do not sense the visual world moving across our retina when we make voluntary fast eye movements. Yet tapping on the canthus of our eye – an external event that causes the eye to move at comparable velocity – creates the illusion that the world is moving (Helmholtz 1925). To help explain this, Sperry coined the term corollary discharge, to refer to information originating from a motor area sent to a sensory area in order to modulate the response of this sensory area to sensory inputs that are the result of voluntary actions (Sperry 1950). In the same year, von Holst and Mittelstaedt proposed a more specific formulation of this idea termed the principle of reafference. This principle states that, during active movements, a copy of the motor command is sent to sensory areas to cancel sensory

information that is the result of active behavior (von Holst and Mittelstaedt 1950). In turn this framework has subsequently been used to explain the result of perceptual studies. For example, the principle of reafference has been used to explain why we cannot tickle ourselves. Specifically, it has been proposed that a copy of the motor command that generated your voluntary movement is used to suppress the tactile sensory information (Blakemore et al. 1998).

*Evidence from sensory systems in model organisms:* Since the 1950s, electrophysiological studies in model systems have provided evidence for principle of reafference. These include experiments in the auditory system of the cricket and mechanosensory system of the crayfish. In each of these systems, the reafferent sensory stimulation is removed from further processing in order to correctly interpret and emphasize external stimuli (reviewed in Cullen (2004) and Crapse and Sommer (2008)), providing support for the reafference principle. Insight into the reafference principle has also been provided from experiments in the weakly electric mormyrid fish, where movement of the fish's body during its electric organ discharges alters incoming sensory input (reafference). A series of elegant studies revealed that efference copy signals are sent directly to the second-order principle cells to cancel reafferent sensory information regardless of whether the actively generated electric discharge is actually allowed to occur. Specifically, when the animal is prevented from generating an electric discharge, the investigators observed a "negative image" (or cancellation signal) in second-order principal cells that would have cancelled the self-generated sensory information if it had been allowed to occur (Requarth and Sawtell 2011).

*More sophisticated computations occur in mammalian systems:* More recently electrophysiological studies have tested the principle of reafference in mammals for the processing of vestibular information during self-generated motion. Reafferent vestibular information is indeed substantially suppressed in rodents and primates at the first central stage of processing in the vestibular nuclei (reviewed in Cullen 2012), as well as at the next stages of sensory processing in the vestibular cerebellum (Brooks and Cullen

2013) and vestibular thalamus (Dale and Cullen 2017). However, the mechanism operating in the vestibular system appears to differ in a significant way from the classically stated formulation of the reafference principle. Specifically, in contrast, to what is observed in the electric fish, the mechanism underlying the suppression of vestibular reafference is more sophisticated. Neurons in the vestibular nuclei, deep cerebellar nuclei, and thalamus do not receive direct efference copy information, such that a negative image is never observed when head movements are prevented. Instead, a cancellation signal is only present in behavioral conditions where the actual sensory feedback matches the brain's estimate of the sensory consequence of a voluntary movement. This more sophisticated mechanism allows the brain to emphasize unexpected sensory inputs that occur either because of inaccurate motor control (expected sensory feedback doesn't match actual sensory feedback) or because of unexpected externally imposed motion (exafference).

## Conclusions

Despite long-standing interest in the computations required for accurate motor control, the neural mechanism underlying the computation of sensory exafference in mammals remains unknown. In particular, to date, where and how the cancellation signal is generated is still an open question. There are many reasons to believe that the cerebellum plays a critical role in the implementation of the reafference principle. Studies in the electrosensory system of fish have shown that their cerebellum-like circuitry computes predictions about the sensory consequences of the animals' own behavior, brain imaging studies in humans show increases in cerebellar activity when sensory tactile feedback does not match what is expected (Jenmalm et al. 2006), and finally, neurons in the primate cerebellum, more specifically the rostral fastigial nucleus, one of the deep cerebellar nuclei, have been shown to encode unexpected vestibular signals (i.e., vestibular exafference; Brooks and Cullen 2013). Although these results support the idea that the cerebellum is part of the circuitry underlying the implementation of the principle of reafference,

ultimately, further studies in the cerebellar cortex and deep nuclei are required to provide a better understanding of the mechanism and neural circuitry underlying the suppression of sensory reafference.

## Cross-References

- [Cerebellum](#)
- [Cetacean Sensory Systems](#)
- [Comparator, The](#)
- [Insect Sensory System](#)
- [Primate Sensory Systems](#)
- [Reflex](#)
- [Tactile Perception](#)

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## Rearing

- [Parenting](#)

## Reasoning

- [Catarrhine Cognition](#)
- [Insight in Rats](#)

## Reasoning by Exclusion

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## Synonyms

[Inference by exclusion](#); [Process of elimination](#); [Reasoning by the disjunctive syllogism](#)

## Definition

Representing mutually exclusive alternatives (“A or B”), ruling out one or multiple alternatives (“not A”), and thereby concluding that the remaining alternative must be true (“therefore B”).

## Introduction

Reasoning has long been regarded as an exceptional ability that makes humans unique, but this notion has been heavily challenged in the past century. A growing body of evidence suggests that many animals are capable of reasoning, even at levels comparable to young children. However, reasoning is a broad concept that encompasses various abilities. One of the most widely studied reasoning abilities in animals is reasoning by exclusion, which is often defined

using the logical definition of disjunctive syllogism: “A or B, not A, therefore B” – in other words, reasoning that given options A and B and the knowledge that option A is incorrect, option B must then be correct. Although “reasoning by exclusion” and “process of elimination” are often used interchangeably with “disjunctive syllogism,” some researchers argue that these terms lack the deductive certainty of the disjunctive syllogism, meaning that we cannot know whether option B was represented as the *necessary* conclusion (Mody and Carey 2016; Pepperberg et al. 2019). Such conceptual and methodological issues are highlighted in this review of reasoning by exclusion in animals, which has become an area of growing interest in the last two decades.

The ability to reason by exclusion may provide animals with many benefits. A capuchin monkey may knock on a branch to listen whether something edible is hidden inside. The ability to exclude locations based on this feedback can save him both time and trouble attempting to extract a non-existing treat. A hungry house cat chasing a mouse may find one possible hiding spot empty and then reason that her prey must be hiding in the other location. Various selective pressures may have given rise to this ability (De Petrillo and Rosati 2020; Petit et al. 2015). However, such behavior can arise through numerous cognitive processes, with reasoning by exclusion being only one explanation. Is the capuchin monkey actually considering the contents of the branch, or has he learned to avoid certain cues after previous failures? Did the cat perhaps smell the mouse near the second location? Excluding such alternative explanations is an important reason for investigating reasoning by exclusion in controlled experiments.

The earliest study on reasoning by exclusion dates back to that of Grether and Maslow (1937), in which several monkey species were presented with two cups, of which one held a reward. The monkeys were allowed to choose after observing that one cup was empty. They chose the correct cup more often than expected by chance. This experiment presented the basic idea on which almost all future methodologies would be based, but the topic received little attention until the

influential studies by Premack and Premack (1994) and Call (2004). While Call’s study built further on the methodology of Grether and Maslow (1937), Premack and Premack (1994) took a slightly different approach. Their chimpanzees witnessed an experimenter hiding two different but equally desirable treats (A and B) under two cups. The cups and experimenter were then briefly blocked from sight of the subjects, after which the experimenter could be seen eating one of the two food items. The rationale behind this method was that the chimpanzees would first need to infer that the cup where treat A was hidden should be empty if the experimenter was eating A. By excluding that cup, the chimpanzees can conclude that the remaining cup must be the only rewarded option left, containing food item B. While such a task may seem easy to us, only one of the four chimpanzees succeeded consistently.

The methodologies used to test for reasoning by exclusion are subject of heavy debate. Successful performance in these experiments is often attributed to mechanisms other than reasoning by exclusion, such as learned solutions, behavioral biases, or avoidance of empty locations. Unsuccessful performance is often ascribed to the detrimental effect of interfering factors – such as poor attention, motivation, memory, or inhibition – which may mask the extent of reasoning abilities. Various methods have been developed to offer more conclusive tests of reasoning by exclusion in animals.

## Two Cups Task

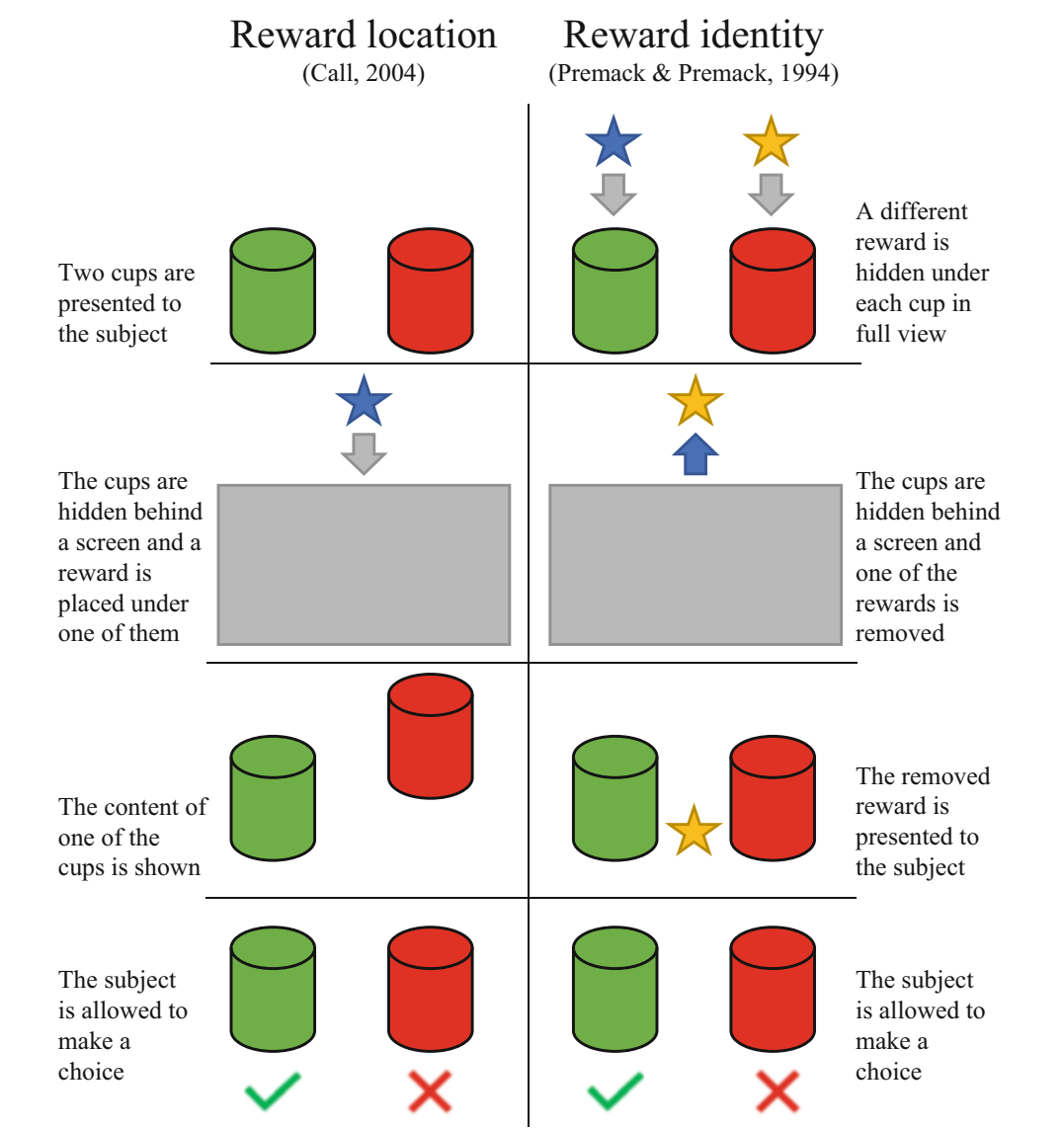
The two cups task was the first method used to test for reasoning by exclusion (Grether and Maslow 1937) and is the most common method to date. The diverse methods all involve two cups (or similar opaque containers) and incomplete information on the location of one or multiple food items, followed by the opportunity to choose one of the cups. The tasks can generally be considered as either more similar to that of Call (2004), with only one cup being baited and the empty one shown to the subject, or more like that

of Premack and Premack (1994), with each cup having a different reward type and one type shown to the subject (Fig. 1).

**Reward Location**

Call’s version is the most common version of the two cups task. The original study involved great apes that observed two cups hidden from view

behind a screen. A reward, usually in the form of a favorite treat, is shown to the subject and then placed under one of the cups. The screen is removed, and the experimenter provides information on the content of one or both of the cups to the subject, which is then allowed to make a choice (Fig. 1). This information is given acoustically by shaking the cup or visibly by lifting the cup and



**Reasoning by Exclusion, Fig. 1** Schematic overview of the two cups task in the most common visual variations: reward location (left) and reward identity (right). Rewards are represented by stars, and arrows indicate whether a

reward is placed (pointing downward) or removed (pointing upward). Correct and incorrect choices are shown by check marks and crosses, respectively



revealing its content. The information given depends on the trial type and is generally one of four: information on both cups, baited cup only, empty cup only, or no information at all. The reasoning behind giving full information and only information on the baited cup is to ensure subjects can use visual or auditory information to locate the reward in this task. Trials where subjects receive information on only the empty cup are the ones that test for reasoning by exclusion. Trials with no information are carried out as a control, to ensure subjects are not using alternative solutions such as olfaction or experimenter cues.

Most great apes and monkeys tested on the visual version performed above chance level, but the prosimians tested thus far did not (Call 2004; De Petrillo and Rosati 2020; Hill et al. 2011; Petit et al. 2015; Völter and Call 2017). Other species that passed this task include dogs, dwarf goats, ravens, Clark's nutcrackers, and African gray parrots, whereas performance at chance level was found in sheep, pigs, Eurasian jays, jackdaws, and kea (Nawroth et al. 2014; Pepperberg et al. 2013; Plotnik et al. 2014; Schloegl et al. 2009; Tornick and Gibson 2013; Völter and Call 2017). Thus, there is a mixed phylogenetic distribution of this ability, even though apes, corvids, and parrots often reach similar performance on the same tasks (Lambert et al. 2019; Völter and Call 2017), which to a large degree may be due to differences in testing procedures (see below).

A strength of the two cups task is the possibility to adapt the testing modality to best suit a species. Most paradigms in animal cognition are vision based, but many animals are more reliant on other senses. Compared to the visual version, fewer species have been tested on the auditory task, and performance is generally poorer. The great apes in Call's (2004) study nearly always selected the correct cup when seeing the location of the food but less so when hearing a rattling noise of a shaken cup with food within. Those that passed the full information condition were then tested on the exclusion condition in which only the empty cup was shaken or shown. These individuals performed near ceiling level in the visual version but performed significantly poorer

yet still above chance in the auditory version. Controls of the auditory version involve noiseless rotations, tapping the baited cup, and a tape recorder playing sounds of a shaken cup. The apes failed to choose correctly in these controls, which suggests they relied on the causal connection between the presence of food and non-arbitrary sounds in the auditory exclusion task (Call 2004). However, other explanations for these results have been proposed, such as the recording not being a perfect replication of the actual sound and that subject may have associatively learned to use the combination of shaking and sound (Hill et al. 2011).

Most animals tested on similar conditions perform poorer on the auditory than visual version (De Petrillo and Rosati 2020; Hill et al. 2011; Plotnik et al. 2014; Völter and Call 2017). The importance of audition under natural circumstances does not easily translate into outstanding performance in the auditory task because the presence or absence of food has to be inferred through its interaction with the cup. In other words, the food itself does not produce sound, whereas it can directly be seen in the visual version. Interestingly, Asian elephants were unable to locate food by following an auditory cue, even though sound is an important modality for them. They could locate food by using olfactory cues and performed well on the olfactory version of the two cups task; they chose a baited container when smelling an empty one (Plotnik et al. 2014). In contrast to the auditory version, the olfactory and visual versions are more naturalistic and less arbitrary because the presence of the food item can be perceived directly, which likely aids reasoning based on the absence of such cues.

Most versions of the cups task require an experimenter to reveal the content of one of the cups. Touching and moving one of the cups, and not the other, is picked up as a social cue by some animals. They may subsequently choose the cup handled by the experimenter due to stimulus or local enhancement, which would result in poor performance when an empty cup is revealed or shaken. An efficient solution is to use inner cups that are placed over the reward but are never handled by the experimenter (Nawroth et al.

2014). The opaque outer cups are lifted simultaneously to reveal the inner cups, which are transparent or opaque depending on the experimental condition: two transparent cups for full information, two opaque cups for no information, and one of each for partial information.

Failure to succeed in these tasks can often be attributed to factors other than inability to reason by exclusion. False-negative results occur as animals may follow inadvertent social cues, become distracted, or rely more strongly on a modality not central to the test. On the other hand, success in these tasks cannot unequivocally show the use of reasoning. Animals may quickly pick up on the association between a cup being lifted or shaken and it never being rewarded, thereby learning to always choose the other option. Researchers should check whether there is an improvement in performance over trials, which is suggestive of learning. It has often been pointed out that the two cups task does not convincingly rule out a strategy based on avoidance of the empty cup. Before the content of any cup is known, an animal may represent both options as “maybe A, maybe B.” After learning that one cup is empty (“not A”), an animal can still be successful by looking in the only other location while still representing it as a possibility (“maybe B”). True disjunctive syllogism required deductive certainty (“therefore B”). Other methods are typically regarded as more conclusive (Mody and Carey 2016; Pepperberg et al. 2019).

### Reward Identity

In Premack and Premack’s (1994) reward identity version, two different food items are hidden under two cups in view of the subject. Then, the cups are hidden from view, and the food item is removed from one of the cups. The removed item is presented to the subject by the experimenter eating it, visibly discarding it, or placing it between the cups. Through reasoning by exclusion, one can conclude that the cup previously containing this item is now empty and that the other cup contains the other kind of reward (Fig. 1). Because two different food types are used, it is crucial that a preference test is also performed to confirm that both rewards are similarly preferred.

This version has provided evidence for reasoning by exclusion in some gorillas, bonobos, chimpanzees, orangutans, and gray parrots, though performance is notably poorer than in the reward location version (Call 2006; Pepperberg et al. 2013; Premack and Premack 1994). For instance, Clark’s nutcrackers excel in the location version, but only one of the six birds was successful in the identity version (Tornick and Gibson 2013). Older great apes performed markedly better than younger ones (Call 2006).

Similar to the location task, the subject may understand that one cup is empty, but is not required to reason about the contents of the remaining cup to be successful. There are two notable attempts at controlling for this weakness. Call (2006) gave gorillas, bonobos, chimpanzees, and orangutans additional association trials using colored chips to test whether subjects can solve the task by learning a conditional discrimination. Subjects first learned an association between the color of a chip and a particular food type. Then, instead of presenting the removed food item to the subjects, the colored chip corresponding with the remaining reward was placed in the middle between the two cups. Thus, the color of the presented chip indicated which of the two hidden food items still remained. Subjects failed to perform above chance in these association trials and also in further experiments where the chips were replaced with two new food items – different from those hidden under the cups – to increase salience of the stimuli. Subjects also failed when a copy of the food type that would be removed was present in the middle throughout the entire trial. Call (2006) reasoned that the consistent failure of the subjects to learn to use a conditional discrimination, compared with their success in the classic inferential task, meant that subjects were likely solving the task through reasoning by exclusion.

A different set of control experiments was designed by Pepperberg et al. (2013) to determine whether African gray parrots used the rule “pick the food item which was not shown.” In these trials, food was placed under the cups as before, but neither was removed. Instead, the experimenter produced another piece of food, identical to one of the hidden items; showed it; and then

removed it again. The birds did not prefer to choose the cup containing the non-displayed food type, which shows their choices were not guided by this conditional rule.

Pepperberg et al. (2013) also introduced trials in which a more and a less preferred food item was used. Instead of a single item, two pieces were hidden under each cup, and only one piece was then removed. Thus, one cup contains two pieces of either the more or less preferable reward, and the other cup contains only one piece of the other type. The reasoning behind this experiment was that the subject would always choose the preferred food item, even in a lower quantity. The task was similar to the regular reward identity task if a piece of the less favorable food item was removed, but subjects should pick the cup containing the revealed item if the more preferable food item was removed. This was assumed to be more likely if the subjects were actively reasoning about the content of both cups, rather than avoiding the empty one. Although all four gray parrots in this experiment passed, their success may be explained by mechanisms other than reasoning by exclusion. Critically, because subjects are shown both food items being hidden, they can simply choose the side where the preferable rewards were hidden and ignore all experimenter manipulations.

## Three Cups Task

### Evenly Spaced

Studies on metacognition often involve a reward hidden under one of three evenly spaced cups (Call and Carpenter 2001; Lambert and Osvath 2020). In an adaptation to investigate reasoning by exclusion, several monkey species were tested with three opaque cups in four conditions (Marsh et al. 2015). Subjects were given either partial negative information (revealing one empty cup), complete negative information (revealing both empty cups), or two types of complete positive information (revealing the baited cup or revealing the baited cup and an empty cup). The complete negative information condition serves as the test for exclusion, as subjects can exclude both empty

options and choose the remainder. The partial negative condition is a control for extraneous cues and discourages the subjects from using avoidance of the empty cup as choosing mechanism. The condition where the baited and an empty cup are revealed is implemented to see whether subjects learned the incorrect rule to “choose the other cup when two cups are lifted.” This study showed that the lion-tailed macaques and hamadryas baboons were able to use exclusion, as well as two out of eight capuchin monkeys.

This evenly spaced three cups task is similar to the reward location two cups task, except that the probability of guessing correctly is lower. For the subject to deduce the location of the reward, both empty cups must in some way be revealed. This results in a similar situation where alternative strategies can be used to obtain the reward. Comparable control conditions are required to narrow down which mechanisms a subject uses to pass these tasks.

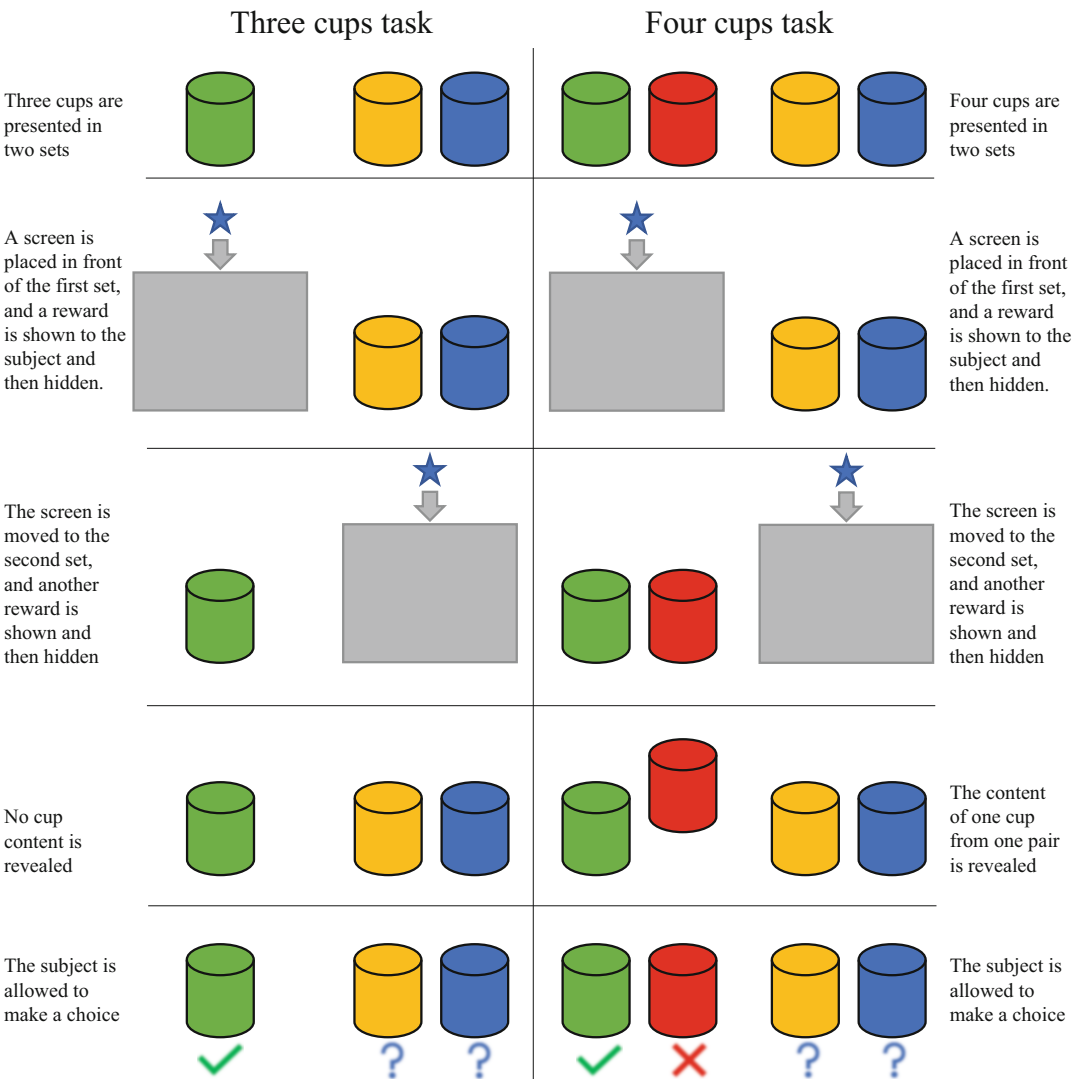
### Two Sets

Recently, Pepperberg et al. (2019) used a new method with one of their gray parrots. This method, designed originally for testing children (Mody and Carey 2016), aims to be a more robust test of reasoning by the disjunctive syllogism rather than reasoning by exclusion. The critical difference is that implementing a disjunctive syllogism requires representation of the concepts *or* and *not* – “A or B,” “not A” – as well as deducing the conclusion, “therefore B,” as a *necessity*. This stands in stark contrast with avoiding empty locations, as discussed above, and the strategy where both options are considered independently, as “maybe A, maybe B,” which does not contain this notion of necessity. In this latter non-updating strategy, acquiring new information on the content of one option (“not A”) does not affect the representation of the other option (“maybe B”). In other words, both locations are first seen to possibly contain the reward, and one location is excluded after it is revealed to be empty. The likelihood of the second location being baited does not get updated, yet this second location is still chosen since it is the only *likely* alternative in the two cups

task. Using the disjunctive syllogism means regarding this second location as the *necessary* alternative.

To tease apart these explanations, subjects are first tested on a three cups task (see Fig. 2). Unlike the evenly spaced cups from the previous section, these cups are arranged in two sets: a pair on one side and a single cup on the other side. A small screen covers the view, and a reward is placed in a cup on one side, and the same procedure is

repeated on the other side. The screen covers only one side at a time, making it clearer that a reward is hidden under a non-visible cup rather than in a cup on the visible side. No cup content is revealed in any way. This procedure avoids the aforementioned factors of stimulus enhancement and avoidance of empty cups, but does not require an updating strategy. The reward is guaranteed to be in the single cup, whereas each cup in the other set has a 50% chance of containing a reward.



**Reasoning by Exclusion, Fig. 2** An overview of the three cups (left) and four cups (right) procedure. The star indicates the hiding of the reward, X indicates the cup is shown to be empty, check mark indicates the certain

location of the reward, and question marks indicate uncertainty. Rewards are represented by stars and the downward-pointing arrows show their placement. Image modeled after Mody and Carey (2016)

Similar to 2.5-year-old children, the gray parrot Griffin was able to pass this task (Mody and Carey 2016; Pepperberg et al. 2019).

Additional conditions can be run to further tease apart alternative strategies. For instance, by hiding a reward in the paired cups only, mock-baiting the singleton cup (i.e., showing empty hands and performing the typical baiting procedure), and then revealing the other cup in the pair to be empty, the *avoid empty strategy* would predict that the unrevealed cups will be chosen equally. The *non-updating strategy* leads to always choosing correctly because the probability of the singleton cup being baited was zero from the beginning, and hence, no updating is required upon acquiring new information. Another control test is to bait only the singleton cup and mock-bait one of the paired cups and then again show a paired cup to be empty. This condition can reveal the *empty adjacency strategy* (i.e., choosing the cup next to the one shown to be empty), which is an ineffective strategy here but effective in the two and four cups conditions.

## Four Cups Task

In the four cups task, the cups are again split into two sets, but now, each set consists of two cups (Fig. 2). A reward is hidden under one of the cups in one pair behind a small screen, and the same procedure is repeated on the other side. The screen again covers only one side. Then, the content of one of the empty cups on one side is revealed. Thus, a subject using the disjunctive syllogism now knows that the revealed cup is certainly empty and the paired cup *must* hold a reward, whereas each cup in the other pair *may* hold a reward. In contrast, the three non-revealed cups will be chosen equally often if the subject avoids empty cups or does not update its representation after learning which cup is empty. Not only did Griffin perform above chance in this condition, but also he outperformed 5-year-old children (Mody and Carey 2016; Pepperberg et al. 2019).

The authors point out that Griffin's success could be achieved by picking the cup next to the one that was shown – the *empty adjacency*

*strategy*. They designed two control conditions to circumvent use of this strategy. In the first, called *type 1 gambling* trials, they baited only one pair of cups, mock-baited the other pair, and revealed the content of one of the cups from the non-baited pair. If Griffin was using the previously mentioned rule to decide, he would now incorrectly choose an empty cup. In *type 2 gambling* trials, a more desirable reward was placed in one of the pairs, with the standard reward placed in the other pair from which the empty cup would be revealed. As a result, the desirable reward is a gamble of 50%, whereas the standard reward is guaranteed. Griffin passed the type 1 gambling trials, which shows he did not choose the cup next to an empty one, and his willingness to gamble in the type 2 trials seemed to rely partially on whether he previously gambled correctly – a very recognizable response.

However, the increased diagnostic robustness of the four cups task comes at a cost. First, subjects must have some understanding of underlying probabilities, which has been studied relatively little. For example, while chimpanzees perform well when choosing between two options with large discrepancies in probability, they performed around chance level when these probabilities were 1 and 0.5 for each option – the same ratio as the three cups task with both sets baited (Hanus and Call 2014).

Second, as also pointed out in the initial study of Mody and Carey (2016), the task may have high memory demands because it involves two rewards, four cups and two cups pairs. Pepperberg et al. (2019) proposed this as an explanation for the differences in performance between 2.5- and 5-year-old children and why all performed poorer than Griffin did. According to this hypothesis, the usefulness of this task is limited to animal species that have comparable short-term memory to 3-year-olds, which were the youngest to pass the four cups task.

Third, there remains a risk of obtaining false-positive results. Most notably, the subject's mental representation of the task may resemble that of the two cups task, in which case it would suffer from the same issues. In the initial experiment by Pepperberg et al. (2019), Griffin may only focus



on the cups which are handled by the experimenter and ignore the other set. The type 1 gambling to a degree controls for this. However, the issue with these is that contrary to the standard trials, the subject is shown that only one of the two sets is baited. In these cases, the subject's focus may be on the baited set from the start and would ignore the experimenter's manipulations of the other set.

The four cups task is best suited to reveal the non-updating strategy, for which the other tasks are poorly equipped. It is designed specifically to test for disjunctive syllogism, which requires an updating strategy and then coming to a necessary conclusion of where the reward *must* – rather than *might* – be hidden. It follows that using this stricter definition leads to more conclusive results. Interpretation of the results depends on whether the subject considers there to be four viable choices (every cup) or only two (only the cups on the side that is handled). Various control conditions should be performed to rule out these alternative explanations. To date, Griffin is the only animal that has been tested on the four cups task with controls. However, performance on the four cups task may be limited due to additional cognitive demands – especially short-term memory and probabilistic reasoning. Nonetheless, the four cups task offers an elegant approach that should be further explored in more species.

Table 1 summarizes the various designs of the cups tasks and performance per strategy. The expected performance for each solution per task can be used to determine with what strategy a subject's performance is most consistent. Actual performance is likely lower due to limiting factors such as motivation, attention, inhibitory control, memory, and efficiency. There can be large variation of duration, waiting time, and other aspects of the procedure. Within the same task, subjects may learn or employ multiple strategies; across tasks, their learning may transfer or strategy use can be flexibly adjusted. The most rigorous task would only be solvable by reasoning through a disjunctive syllogism and would predict significantly lower scores when using alternative strategies. Only a combination of multiple tasks has the power to do so, and there are clearly more possible

strategies than the ones discussed here. Furthermore, increasing the complexity of a task carries a higher risk of false negatives. The larger numbers of cups, rewards, sets, and actions of the four cups task demand more attention and better memory than the various versions of the three cups tasks. Thus, these trade-offs need to be considered when planning empirical studies.

## Invisible Displacement

The invisible displacement task is usually not specified as a test for reasoning by exclusion, even though it is. It was originally designed as a test for the concept of object permanence – understanding that objects continue to exist when not perceived – during development in children. This task has since been tested in numerous species, including chimpanzees, bonobos, gorillas, orangutans, dogs, dolphins, Goffin's cockatoos, and gray parrots (see Zewald and Jacobs 2021).

The general setup of invisible displacement tasks consists of multiple opaque hiding locations (e.g., cups or screens) and a smaller opaque displacement device (e.g., a small cup or the experimenter's hand) that is used for moving the reward between locations without being visible to the subject. The experimenter places a reward in the displacement device in full view of the subject. The device is moved behind a hiding location, and the reward may or may not be secretly deposited there. After the reward has been deposited and before moving to the next location, the displacement device is shown to be empty. The observer should choose this location because the reward has been invisibly displaced there. The identity version of the two cups task also involves invisible displacement.

Great apes generally pass invisible displacement tasks (Barth and Call 2006). This does not only attest to their representation of object permanence but also their inference by exclusion, because upon seeing that the displacement device is empty after visiting a hiding location subjects should infer that the reward has been moved from the device to this particular hiding location. In other words, they should represent that the reward

**Reasoning by Exclusion, Table 1** Task properties of key variations of the cups tasks in the visual domain and prevalent solution strategies. Expected performance is shown as a probability of choosing correctly for each solution per task. Task design reflects memory and attention loads as quantified by number of cups, sets, rewards, reward types (preference differences shown in parentheses), baiting actions (placing real or mock rewards and moving or removing the screen), and updating actions (revealing a cup to be empty after screen is removed, except in the reward identity task where the updating action is removal of a reward before the screen is removed). Type 2 gamble

shows the probability of choosing the preferred reward when it is the subject's specific goal; the corresponding probability for the non-preferred reward is shown in parentheses. When a strategy does not apply in a task, the expected probability equals chance level. Not shown are control tasks such as reveal all cups, baited cup, or no cups. An avoid empty and empty adjacency strategies have identical predictions within sets. An empty adjacency strategy across sets would have different predictions depending on the location of the baited cup

| Number of              | Two cups                            |                 | Three cups               |                   | Four cups              |                    |                        |                        |                        |
|------------------------|-------------------------------------|-----------------|--------------------------|-------------------|------------------------|--------------------|------------------------|------------------------|------------------------|
|                        | Reward location                     | Reward identity | Evenly spaced            | Both sets baited  | Only pair baited       | Only single baited | Regular                | Type 1 gamble          | Type 2 gamble          |
|                        |                                     |                 |                          |                   |                        |                    |                        |                        |                        |
| Probability of success | Sets                                | 1               | 1                        | 2                 | 2                      | 2                  | 2                      | 2                      | 2                      |
|                        | Rewards                             | 1               | 2                        | 2                 | 1                      | 1                  | 2                      | 1                      | 2                      |
|                        | Reward types                        | 1               | 2 (equal)                | 1                 | 1                      | 1                  | 1                      | 1                      | 2 (different)          |
|                        | Baiting actions                     | 3               | 4                        | 3                 | 5                      | 5                  | 5                      | 5                      | 5                      |
|                        | Updating actions                    | 1               | 1                        | 1-2               | 0                      | 1                  | 1                      | 1                      | 1                      |
|                        | Chance level                        | 0.5             | 0.5                      | 0.33              | 0.67                   | 0.33               | 0.33                   | 0.25                   | 0.25 (0.25)            |
| Example references     | Stimulus enhancement (lifted cup)   | 0               | 0.5                      | 0                 | 0.67                   | 0                  | 0                      | 0                      | 0 (0)                  |
|                        | Avoid empty (across sets)           | 1               | 0.5                      | 1                 | 0.67                   | 0.5                | 0.5                    | 0.33                   | 0.33 (0.33)            |
|                        | Empty adjacency (within set)        | 1               | 0.5                      | 1                 | 0.67                   | 1                  | 0                      | 0                      | 0 (1)                  |
|                        | Non-updating ("maybe B")            | 1               | 1                        | 1                 | 1                      | 1                  | 0.67                   | 0.5                    | 0.5 (1)                |
|                        | Disjunctive syllogism ("therefore") | 1               | 1                        | 1                 | 1                      | 1                  | 1                      | 0.5                    | 0.5 (1)                |
|                        |                                     | Call 2004       | Premack and Premack 1994 | Marsh et al. 2015 | Pepperberg et al. 2019 | Current entry      | Pepperberg et al. 2019 | Pepperberg et al. 2019 | Pepperberg et al. 2019 |

is either in the device or the hiding location; the reward is not in the device; therefore, the reward is in the hiding location. Because subjects do not see any of the locations being empty, avoidance is not a viable strategy (Völter and Call 2017). However, subjects may instead choose the last or first visited location, depending on the experimental procedure. Moreover, this task cannot test for disjunctive syllogism because subjects are not required to update the possible contents of locations and the device in terms of certainty and uncertainty. Thus, this task suffers from similar weaknesses as the two and three cups tasks.

To explore this issue, Watson et al. (2001) allowed children (4–6 years old) and dogs to search all locations and used search speed as a measure for reasoning. They reasoned that if subjects updated their understanding of the potential contents of the remaining locations after each visit, they should increase the speed at which they check each subsequent location. Instead, if subjects use a general search strategy, each unsuccessful visit would act as an extinction trial – weakening the association between container and reward – which would result in slower visits to subsequent containers. The children showed an increase in speed as predicted by the updating strategy, whereas the dogs slowed down and were thus likely using a general search strategy.

## Bent Tube Task

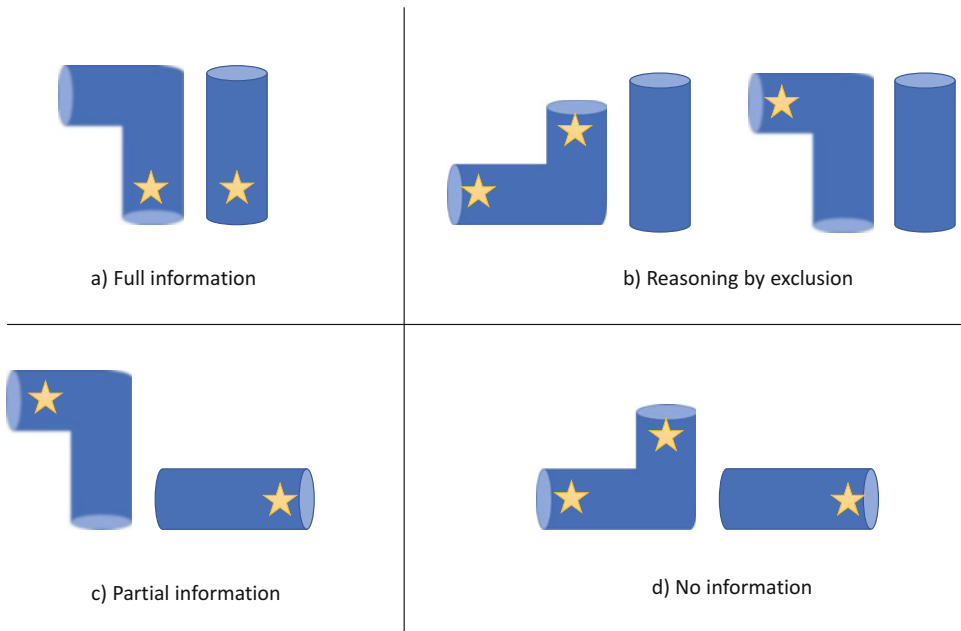
Instead of cups, bent tubes have also been used to test for reasoning by exclusion. This task was originally used for studies on metacognition, much like the three cups task (Call and Carpenter 2001; Lambert and Osvath 2020). The subject is presented with two tubes, one straight and one bent in an L shape. The tubes are presented in different orientations, which means subjects may or may not be able to look into them from their starting position. This creates three possible locations for the food: in the straight tube, the close end of the bent tube, or the far end of the bent tube (see Fig. 3). Subjects either have full information from the start (3a), can see the straight tube is empty and should therefore be able to reason by exclusion about the location of

the reward (3b), have only partial information but cannot exclude either tube as an option (3c), or have no information at all (3d). This method has been tested with taxa such as great apes, capuchin monkeys, kea, New Caledonian crows, and ravens (Call and Carpenter 2001; Jelbert et al. 2015; Lambert and Osvath 2020; Schloegl et al. 2009; Völter and Call 2017).

In one study, ravens and kea were allowed to freely move around the tubes, so they could inspect them from all sides (Schloegl et al. 2009). The researchers argued that the amount of explorative behavior would depend on the amount of information the animals get from their starting position. For example, with full information, the birds were not expected to explore the tubes. If they were unable to see the reward, they were expected to either explore until they find it or exclude other options to infer the reward's location. Choosing the bent tube after seeing the empty straight tube in the “reasoning” condition is suggestive of reasoning by exclusion. In the no information condition, subjects should choose the baited tube after inspecting only the empty tube. Using these criteria, the authors concluded that the ravens used reasoning by exclusion, whereas the kea did not because of their high number of redundant inspections.

False negatives can arise because searching for the reward may present a less demanding solution than reasoning by exclusion. While more time-consuming, it may be a more natural strategy that will still result in a food reward eventually. This may explain the low prevalence of the “reasoning” strategy in the study of Schloegl et al. (2009), where out of all situations where inference was possible it was only shown between 10% and 25% of trials for ravens (see also Lambert and Osvath 2020). This issue is even more obvious for the kea, which generally opted to investigate all locations. As the authors point out, this is likely a result of the kea being more explorative by nature compared to ravens. It may also be difficult to discern whether a subject moving for a tube has reasoned there must be a reward in it or is heading over to inspect it and happens upon the reward.

A similar setup was used with New Caledonian crows, but here, subjects were not allowed to



**Reasoning by Exclusion, Fig. 3** Schematic overview of common orientations of the bent tube task. The stars indicate the possible locations for food to be hidden for every orientation (note that only one piece of food is hidden per trial). (a) The food is visible. (b) The subject can see the straight tube is empty and should be able to reason that the

reward is in the bent tube (two possible orientations for the bent tube shown). (c) One end of the bent tube is visibly empty, so the reward can be present in either tube. (d) The subject cannot look into any of the openings. All orientations shown are also performed mirrored (i.e., bent tube on the right). (Image modeled after Jelbert et al. 2015)

explore the tubes (Jelbert et al. 2015). Thus, the crows only had the information available from the orientation of the tubes relevant to their starting location. The authors predicted no difference in performance on the first orientation shown in Fig. 3b, but in the second orientation with an end of both tubes visible, they anticipated subjects to perform at chance when using avoidance. They argued that both tubes would appear empty, so the subject would guess or adopt a side bias. If they instead had a mental representation of the whole setup, they could reason the reward is in the third unrevealed location of the bent tube. In the incomplete condition (Fig. 3c), if birds were applying avoidance, they would be expected to avoid the seemingly empty bent tube, while if they were using reasoning by exclusion, they would understand the reward may be in either tube.

Jelbert et al. (2015) acknowledged a potential concern with their setup. The subjects may view the two ends of the bent tube as two different locations, thus essentially turning the task into a

three cups task. This would mean that subjects could be avoiding all visibly empty ends and still reach the performance predicted by reasoning. In the first orientation of Fig. 3b, subjects can then avoid the empty straight tube (“Not A, maybe B and maybe C”), and in the second orientation of Fig. 3b, subjects can avoid the two empty options (“Not A, not B, maybe C”). Moreover, as the bent tube is considered one choice, subjects would succeed even if they can only exclude only one option (“maybe B, maybe C,” with both seen as correct choices). As such, the bent tube task appears to be less conclusive than the three cups task. Jelbert et al. (2015) argued that if subjects viewed the bent tube as two different locations, the birds would approach the bent tube by avoiding the visibly empty side. Instead, they observed that both successful birds approached each side of the tube equally, which they took as supporting evidence that their subjects were indeed using exclusion. This reasoning, however, depends on whether the birds would indeed avoid

passing the visibly empty side on their way to the reward.

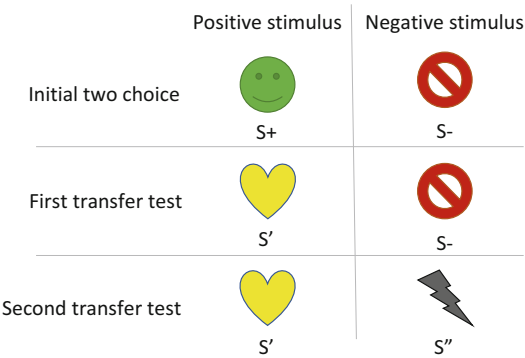
Although the bent tube task offers an ecologically relevant approach because it involves various knowledge states when searching for food, it does not provide conclusive evidence for reasoning by exclusion. False positives may arise from avoidance of empty locations. Much like in the two cups task, subjects perceive which of two locations is not baited and can subsequently choose the other option. False negatives are likely caused by inefficient rather than erroneous search behavior. The only cost of looking in all locations is the small delay and extra effort compared to reasoning by exclusion because the reward can always be obtained. Humans fully capable of reasoning by exclusion still behave sub-optimally. This is illustrated by the “passport effect” – repeatedly checking whether one has packed a passport when embarking on international travel. This may seem irrational when one remembers that it is already packed, yet the costs of checking are low, and the potential benefit is high if it was actually forgotten, which makes double-checking a reasonable strategy (Call and Carpenter 2001).

Two-Choice Transfer Tasks

The methods discussed so far involve hidden rewards. In contrast, matching-to-sample (MTS) tasks take a more abstract approach. One example comes from a study with chimpanzees, which were initially taught an association between a symbol and a picture of an item in their environment (Beran and Washburn 2002). They were then presented with the picture and several symbols, of which one matched the picture. The chimpanzees were allowed to choose one of the symbols and were rewarded if they chose the one that matched the picture through their initial association. In some trials, a novel picture (i.e., a picture the subject had not yet learned to associate a symbol with) was presented, followed by a novel symbol among a selection of already associated symbols. To choose correctly, the subjects must exclude all familiar symbols (“not A”) and match the novel option to the novel sample

(“maybe B”). MTS tasks have been done with many species, such as chimpanzees, dogs, seals, sea lions, and pigeons (Völter and Call 2017). However, they are inconclusive because subjects can solve the task by choosing the novel option. MTS tasks have been further adjusted in some studies where subjects are required to assign a property (positive or negative) to a novel stimulus in a forced-choice design. These tasks may in the literature still be referred to as (delayed) MTS or two-choice tasks but lack the presentation of a sample. Similar tasks in word learning are called fast mapping, but this term does not exclude avoidance or reliance on novelty (Völter and Call 2017). Therefore, these tasks are called two-choice transfer tasks here. They have been successfully tested with Goffin’s cockatoos, dogs, kea, and rats (Felipe de Souza and Schmidt 2014; O’Hara et al. 2015, 2016; Zaine et al. 2014).

In an extension of the MTS paradigm, Aust et al. (2008) trained pigeons, dogs, human adults, and children with four positive (S+) and four negative (S−) stimuli using a touch screen. In each trial, an S+ and an S− were presented, and the subject had to choose between them, where only choosing the S+ was rewarded (Fig. 4). Upon having learned this discrimination, some unrewarded transfer trials were intertwined with these training trials, in which the S− stimuli were presented in combination with one of four novel



**Reasoning by Exclusion, Fig. 4** Schematic of the two-choice transfer tasks. Subjects are taught to discriminate between a positive and negative stimulus. In the first transfer task, the known negative is displayed together with a novel stimulus S'. In the second transfer task, the novel S' is displayed together with a more novel S''



stimuli, dubbed  $S'$ . The underlying mechanism for choosing  $S'$  here can be either (1) preference for novelty (neophilia), (2) aversion to the  $S-$  stimuli (avoidance), or (3) reasoning that if  $S-$  is negative,  $S'$  must be positive (reasoning by exclusion). To tease apart which mechanism is used, the experimenters introduced four novel  $S''$  stimuli in a second test series. During these test trials, subjects were presented with the  $S'$  stimuli against the novel  $S''$  stimuli. If subjects passed test 1 due to neophilia, they would likely show a high preference for  $S''$ . If subjects initially chose by avoidance of  $S-$ , it is unlikely that enough aversion for  $S'$  has formed during the previous test trials. Thus, subjects using this technique might be expected to follow no coherent strategy and therefore gamble. Finally, if subjects chose by ascribing a positive value to  $S'$ , they would be expected to continue picking  $S'$ , either through a preference of  $S'$  due to previous inference or through a second instance of ascribing a negative meaning to  $S''$ . Regardless of a second inference, subjects that picked the  $S'$  consistently in test 2 were argued to have used inference in the first test. Here, evidence was found for reasoning by exclusion in dogs and humans, but not pigeons.

The first concern with this task is the possibility of an alternative explanation that combines avoidance and other motivations. Subjects that chose  $S'$  by avoiding  $S-$  in test 1 would likely not have formed a strong preference for  $S'$  as these trials were unrewarded. Choice in the second test may then have been guided by secondary weaker motivations or be chosen at random, because neither stimulus has a value yet. For example, through mild neophobia – not strong enough to overcome aversion of  $S-$  in test 1 – the subjects might choose  $S'$  in test 2, thus appearing to choose based on reasoning by exclusion. Moreover, the incoherent strategy in test 2 predicted by avoidance in test 1 may not only result in gambling but also in adoption of a bias, for example, for the  $S'$  stimuli.

A notable limitation of this method is that it is unsuitable for neophobic and neophilic species, which would avoid or prefer the more novel stimuli regardless of inference capacities. This is comparable to the potential influence of local

enhancement in the cups tasks, where subjects often choose the cup last handled by the experimenter. Exploring and controlling for alternative strategies are crucial in all task variations, even when they appear unlikely at first. For example, Aust et al. (2008) found that their most successful pigeon seemed to choose novel stimuli, despite previous research indicating that pigeons are generally more neophobic.

Finally, each  $S'$  was presented a total of only eight times by the end of test 1, at which point subjects were expected to have remembered each stimulus and applied a positive meaning onto it. Some children expressed difficulty in remembering stimuli and pairings (Aust et al. 2008), which puts into question how well the nonhuman subjects were able to remember the  $S'$  stimuli. Regardless of reasoning by exclusion, subjects might not be capable of remembering previous choices, especially when they are continuously distracted by the training trials given in between. Increasing the amount of test trials, however, increases the risk of creating simple preference or avoidance of  $S'$  as the choosing strategy.

O'Hara et al. (2015) made substantial changes in their experiment with Goffin's cockatoos. Also using a touch screen, subjects were first taught to discriminate between two arbitrary stimuli defined as  $S+$  and  $S-$ . Then, novelty trials were mixed in with these training trials in which the  $S+$  stimulus was shown together with a novel  $S-*$  stimulus, where only the  $S+$  was rewarded. The aim here was to train the subjects to not choose based on neophilia (see Fig. 5). Contrary to Aust et al. (2008), the test trials in this experiment were rewarded if the subject chose correctly. The test trials were (1)  $S+1$  vs  $S-$ , (2)  $S+$  vs  $S-1$ , (3)  $S+1$  vs  $S-2$ , and (4)  $S+2$  vs  $S-1$ , where  $+/-n$  indicates a novel stimulus. Thus, while tests 1 and 2 can be solved through trained avoidance and preference, respectively, tests 3 and 4 would require some form of inference as two novel items are compared. Only correct choices on each of these tasks would imply inference by exclusion. Moreover, they argued that the first attempt at test 2 must also be correct, in order to exclude one-trial learning as the mechanism for test 4. The main response types shown by the

| Test 1                                                                                                                                                                                           | Test 2                                                                                                                                                                                           | Test 3                                                                                                                                                                                            | Test 4                                                                                                                                                                                            |                                       |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------|
| <div> S+1</div> <div> S-</div> | <div> S+</div> <div> S-1</div> | <div> S+1</div> <div> S-2</div> | <div> S+2</div> <div> S-1</div> |                                       |
| ✓                                                                                                                                                                                                | ✓                                                                                                                                                                                                | ✓                                                                                                                                                                                                 | ✓                                                                                                                                                                                                 | Reasoning by exclusion                |
| ✓                                                                                                                                                                                                | ✓                                                                                                                                                                                                | ✓                                                                                                                                                                                                 | ✗                                                                                                                                                                                                 | One trial learning                    |
| ✓                                                                                                                                                                                                | ✗                                                                                                                                                                                                | ✓                                                                                                                                                                                                 | ✓                                                                                                                                                                                                 |                                       |
| ✗                                                                                                                                                                                                | ✓/✗                                                                                                                                                                                              | ✓                                                                                                                                                                                                 | ✓                                                                                                                                                                                                 | Novelty rule abolishment/<br>reversal |
| ✗                                                                                                                                                                                                | ✓                                                                                                                                                                                                | ✓                                                                                                                                                                                                 | ✗                                                                                                                                                                                                 | Novelty aversion                      |
| ✓                                                                                                                                                                                                | ✗                                                                                                                                                                                                | ✗                                                                                                                                                                                                 | ✓                                                                                                                                                                                                 | Novelty preference                    |
| ✓                                                                                                                                                                                                | ✓/✗                                                                                                                                                                                              | ✗                                                                                                                                                                                                 | ✗                                                                                                                                                                                                 | S-avoidance                           |

**Reasoning by Exclusion, Fig. 5** Schematic of the two-choice task by O’Hara et al. (2015). The top row presents the type of stimuli which were presented to the subjects in each test. Their performance on each test was categorized as one of the processes shown on the right side, i.e., scoring correct on each test (✓) meant the subjects were likely using reasoning by exclusion. Errors (✗) on each test were noted as “bad day,” and every other combination of

errors/correct tests was attributed to preference and/or avoidance to certain stimuli or novelty. “Novelty rule abolishment/reversal” means the subjects initially chose by novelty avoidance but changed their strategy after not being rewarded. Additional strategies were explored in the original study, but not included here. Image modeled after O’Hara et al. (2015)

cockatoos were reasoning by exclusion, one-trial learning, and S–2 avoidance. In a similar study with kea (O’Hara et al. 2016), some subjects received these conditions in the order 1-3-2-4 to test whether reduction in the amount of time between the first and second time S+1 and S–1 were presented improves the performance. This would indicate the subjects had trouble remembering the stimuli, but performance did not differ.

However, it is difficult to distinguish between one-trial learning and reasoning by exclusion in this task. The authors mention one-trial learning after an error only, but subjects may learn to avoid S–1 from guessing correctly in test 2 and thereby succeed in test 4. This would not be distinguishable from reasoning by exclusion. Thus, the strictness of these criteria may cause the performance to be incorrectly classified. Birds that were using reasoning may have fallen into any of the other

categories they proposed, including one-trial learning, simply by making a single mistake.

The two-choice transfer task has also been carried out without a touch screen. In dogs, the stimuli consisted of toys which the subjects had to fetch (Zaine et al. 2014). In an experiment for reasoning by exclusion in rodents, rats were shown different shapes as stimuli, which were projected onto a surface with a hole which they could poke their nose into to get a reward (Felipe de Souza and Schmidt 2014). However, none of these experiments contained a second transfer task. Instead, they implemented only a novelty (S+ vs novel S–) and exclusion test (S– vs novel S+). Thus, these studies lack some of the strength of the previously discussed methods.

In the end, the MTS and two-choice transfer tasks can provide robust evidence of reasoning by exclusion. However, the task requires significant

memory capacity, involving numerous abstract stimuli with initially arbitrary reinforcement values and presented in a single trial with several “distracting” trials in between – which is already difficult for children aged 7.5–10 (Aust et al. 2008). The further alteration of the task by O’Hara et al. (2015) provides a more refined approach but is in turn less forgiving for single errors (i.e., choosing the wrong option within the strategy used by the subject). This strictness may also be a major strength that allows for analysis of strategy per session, which is reasonable given that subjects may use a variety of mechanisms for solving the task throughout testing. The kea’s performance was best predicted by inference by exclusion, which stands in stark contrast with their poor performance in the two cups task (Schloegl et al. 2009). This illustrates how different methods aimed to examine the same ability can lead to highly divergent results in the same species, which highlights the importance of employing multiple methods to reach firmer conclusions.

## Conclusion

A variety of methods have been developed to test whether animals are capable of reasoning by exclusion. The two cups task is the first and most common but is unable to discern whether the results are due to reasoning by exclusion or some other process, such as avoidance of empty cups. The bent tubes and three cups tasks are similar to the two cups task but instead provide a third potential hiding location. These tasks are mainly used in the context of metacognition but have seen some adaptations to test for reasoning by exclusion as well. The three cups task may also be used as a prerequisite for the four cups task. The four cups task is designed to test for the stricter definition of the disjunctive syllogism, which requires *certainty* when choosing. This promising task has to date only been tested in a single animal – the gray parrot Griffin – and it remains to be seen how other species perform in this paradigm. It is likely suited for apes and capuchins, which perform well on the two cups task (Call 2004, 2006; Hill et al. 2011; Premack

and Premack 1994; Völter and Call 2017). Finally, the MTS-like two-choice transfer tasks have provided evidence for reasoning by exclusion in parrots, rats, and dogs (Felipe de Souza and Schmidt 2014; O’Hara et al. 2015, 2016; Zaine et al. 2014). This task has different cognitive demands than the cups tasks, which may explain why results differ strongly even within species. Inferring the cognitive mechanisms in any given task requires mapping the predicted outcomes of prevalent strategies and within-subject testing on multiple variations (Table 1, Fig. 5).

These tasks have to date provided some evidence for reasoning by exclusion in several species. The species tested most are chimpanzees, orangutans, gorillas, capuchin monkeys, dogs, gray parrots, kea, and ravens. While a wider spread of taxa tested in cognitive research is an important step to better understand the evolution of cognition (Lambert et al. 2019), the diversity of methods yielding divergent results makes it more difficult to draw strong conclusions. Instead of asking which species can reason by exclusion, we should clarify the definitions and concepts at the core of this question and refine the methods with suitable controls that reduce the probability of both false negatives and false positives, until we can ask the more productive question to what degree a species can reason by exclusion and work through disjunctive syllogisms.

## Cross-References

- ▶ [A-not-B Problem](#)
- ▶ [Attention](#)
- ▶ [Cognition](#)
- ▶ [Inductive Reasoning](#)
- ▶ [Intelligence](#)
- ▶ [Invisible Displacement](#)
- ▶ [Memory](#)
- ▶ [Object Permanence](#)
- ▶ [Short-term Memory](#)

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## Reasoning by the Disjunctive Syllogism

### ► Reasoning by Exclusion

## Recall

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## Synonyms

### Memory; Recollection

Recall is the act of reproducing information from memory. In psychology, recall often refers specifically to the type of test that requires subjects to reproduce remembered information. Recall is usually characterized as relying primarily on the memory process of recollection, or the detailed retrieval of information from memory. For example, when

you complete a fill-in-the-blank question, you recollect information on a recall test. Although recall and recollection are often used interchangeably, most literature suggests that multiple cognitive processes contribute to performance on recall tests and that recollection contributes to performance on non-recall tests. Recall is most often contrasted with recognition, the act of indicating whether a currently-experienced stimulus was experienced previously. Recognition is usually characterized as relying on a combination of recollection and familiarity, the vague sense of having experienced something before. For example, when you complete a multiple-choice question, you use recollection and the familiarity of each possible answer on a recognition test. The key difference between recall and recognition is whether the possible answers are present when the subject is making their decision.

In humans, recall is usually studied using language. This is primarily because speaking or writing is an easy way for subjects to reproduce word stimuli. For example, a common recall test might have a subject read a list of words, wait through a retention interval, and then be asked to say all words they recollect. Nonverbal recall tests also exist, and these usually require subjects to reproduce a remembered shape by drawing it. For example, tests using the Rey–Osterrieth complex figure require subjects to study a figure composed of various lines, dots, and circles and then draw it on a blank sheet of paper after a delay period (Rey 1941). The defining feature of these recall tests is that they require a generative response.

Because recall tests rely on generative responses such as speaking or drawing, they are rarely used with nonhuman animals. In 1971, Eugene Winograd wrote, “Given the traditional distinctions made between findings based on recall and recognition data, it is intriguing that the question is so inappropriate with animals. . . . Animals, to my knowledge, have not yet been accorded the privilege of having an executive editor rummaging around in a mnemonic file cabinet. They are still denied the power of recollection”. Partially due to our inability to ask nonhuman animals if they recall past information, some researchers have proposed that nonhuman



animals are “stuck in time” and only respond to the needs of the present moment (Suddendorf and Corballis 1997).

Nonetheless, a small body of evidence demonstrates that some nonhuman species can complete generative recall tests, and a larger body of evidence suggests that the ability to recollect information is phylogenetically widespread. For example, rhesus monkeys can reproduce simple shapes on a touchscreen after short retention intervals (Basile and Hampton 2011). Although much simpler, this test parallels human recall tests such as the Rey-Osterrieth complex figure. Similarly, great apes and dogs can reenact observed behaviors after delays (Bjorklund et al. 2002; Fugazza and Miklósi 2014). Outside of these demonstrations of generative recall, there is good evidence from non-recall tests that a variety of species, such as scrub jays, rats, monkeys, and great apes, can recollect information (e.g., Clayton et al. 2003; Eacott and Easton 2007; Guderian et al. 2011). One of the more impressive demonstrations comes from Panzee, a lexigram-trained chimpanzee (Menzel 2005). After seeing food being hidden in an outside forest, Panzee would later spontaneously recruit a caretaker from inside, touch the lexigram corresponding to the hidden food, go outside, and direct the caretaker to the food by pointing to the correct location. Although “Panzee did not literally draw a lexigram or a map of the forest” (Menzel 2005, p. 214), her performance certainly indicates that she would have if she could.

In summary, recall is the act of reproducing information from memory, or the type of memory test that requires a reproductive response. Recall is thought to rely primarily on the memory process of recollection, and it is most often contrasted with recognition. Comparatively, nonhuman animals are rarely given recall tests, but there is decent evidence that many species can recollect information.

## Cross-References

- Delayed Match-to-Sample
- Familiarity
- Memory
- Recollection

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## Receiver

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## Synonyms

Accessor; Mind reader; Perceiver

## Definition

Any individual who obtains a signal during the communication process.

There are many definitions of a receiver in the communication literature, which vary from a passive individual receiving a signal to one that is more active in obtaining and using that signal. Krebs and Dawkins (1984) provided a more manipulative view of the communicative process. They felt that receivers were “mind readers.” For example, in order for a communicative signal to persist in the environment, it must coevolve with a signaller and a receiver; therefore the mind reader role is that of anticipation and reading of the signaller’s behavior through the signal (Krebs and Dawkins 1984). Zahavi (1975) had a greater focus on the receiver’s side of communication. The handicap principle, which focused on the relative cost of a signal, meant that receivers could not just passively accept or read a signal. Instead, selection required that receivers differentially act on the reliability or honesty of a signal (Zahavi 1975).

The handicap principle is not the only theory to emphasize a more active role of receivers. Morton (1982), in his motivational-structural rules theory, also felt that receivers played a more active role in the communicative process. Morton emphasized that selection cannot, and does not, favor information sharing. Singallers and receivers have very different interests, and thus selection must act on the selfish behavior of each independently in order to a communicative signal to continue. This idea is similar to that of Zahavi’s but places further emphasis on the active role of a receiver. Henessey et al. (1981) further suggested that although manipulation was a good starting point for understanding the communicative process, the receiver (perceiver) faces a different problem than the signaller and as a result will act differently to each signal as it applies to them. The idea of a perceiver, or a more active participant in the communicative process, was further expanded upon by Owings and Morton (1998) and again by Morton (2017). Here the receiver (perceiver) is defined as an individual who is actively perceiving a signal and

differentially acting on it based solely on self-interest. Moreover, perceivers were assessing the signal, in a sense adjusting their behavior to the differing circumstances that the signal communicated (Henessey et al. 1981; Owings and Morton 1998). Expanding on this active role of assessment further Rendall and Owren (2001) expanded on the active role of assessment by receivers, in their affect induction theory. Here receivers are initially affected by the acoustic structure of a signal; in other words certain acoustic features tend to induce attention and arousal and thus initially affect a receiver by garnering their attention. Rendall and Owren (2001) suggest that these types of signals directly affect receiver’s behavior due to their structure and thus result in an appropriate behavioral response for the receiver. They go on to suggest that more indirect effects of signal structure require more learning and assessment on the part of the receiver and that through multiple interactions with particular signals, receivers will come to learn (through basic conditioning) the type of useful behavioral response (Rendall and Owren 2001).

Although these definitions focus on the contributions of acoustic communication to the understanding of receivers, the diversity of the term is portrayed by the research. Further research on the interaction of signaller and receiver in all communicative process will tease apart further the divergent interests of these individuals and broaden our understanding of the receiver’s role.

## Cross-References

► [Signaller](#)

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## Receptivity

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## Introduction

Receptivity can be defined as the female response necessary to result in successful fertilization by a male. In most species the acceptance that comes from a receptive female is essential to mating; a female has control over sperm transfer and whether it occurs, and nonconsensual mating is generally rare. The onset of sexual receptivity in females is often coordinated with ovarian development and is fundamentally mediated by the production of estrogen in vertebrates (Rissman et al. 1997) and juvenile hormone in insects (Ringo 1996). Receptivity in females is often affected by the quality and persistence of courting males. In many species males will attempt to court the female with nuptial gifts, pheromones and behaviors designed to illicit a sexual response. It is generally accepted that males have constant potential sexual receptivity.

## Receptive Period

The period for which an individual is receptive varies greatly between even closely related species. Some species remain receptive indefinitely whereas some experience very short windows of receptivity, or may only mate once in a lifetime (Beach 1976; Ringo 1996). Receptivity follows a predictable, cyclic, path in many vertebrates (Beach 1976), whereas female invertebrates can be continuously receptive, very briefly receptive, or cyclically receptive and are frequently reluctant to mate (Ringo 1996). Continuous receptivity is generally limited to the invertebrate orders Orthoptera, Hymenoptera, and Heteroptera (Ringo 1996). Receptivity is often highest in virgin individuals and declines rapidly after copulation.

## Signs of Receptivity

Sexually receptive individuals often produce signals that alert potential mates to their reproductive state. Signals of receptivity can be very loosely grouped into two categories: behavioral and non-behavioral cues. These two categories are by no means mutually exclusive and behavioral cues may often be overlooked if they are too subtle for human observers. Nonbehavioral cues can include chemical stimuli such as pheromones, enlargement of sexual features, and color change. For example, chemical stimuli are important in rodents, carnivores, and primates (Reviewed in Beach 1976). Female chimpanzees develop swollen skin to indicate receptivity (Deschner et al. 2004) and females of some fish species change color as an indication of being ready to spawn (Svensson et al. 2009).

Behavioral cues can be much harder to detect. Some, more conspicuous, behavioral displays of female receptivity can be found in female non-human primates and include postures of the body and facial expression such as eye contact (Dixon 1990). Combinations of nonbehavioral and behavioral cues are common where behavior enhances the efficacy of nonbehavioral cues, for example, female Norway rats leave their burrows

at night in order to leave chemical trails for males (reviewed in Beach 1976).

Female signs of receptivity are readily detectable by males. For example, male dogs approach females injected with estrogen more frequently than control bitches (Beach and Merari 1970). Male wolf spiders are able to assess reproductive status and potential receptivity of females using cues from their silk (Roberts and Uetz 2005).

### Male Control of Female Receptivity

Female receptivity is often the key to successful sperm transfer and males can influence the receptivity of females. For example, male mice are able to regulate female reproductive behavior through a specific male pheromone (ESP1) contained in tear fluid (Haga et al. 2010); upon mounting the females, the males are able to enhance female reception allowing for copulation. In some moth species female egg maturation is stimulated by juvenile hormone derived from the accessory gland of the male. In other systems, males are able to influence the receptivity of potential mates through the presentation of nuptial gifts. These “gifts” are frequently used by arthropods with the intention of persuading the female to mate and are made up of food or male secretions that the female consumes.

Reduced female receptivity can also be triggered by males following copulation. Often, the deposition of sperm in the reproductive tract of the female initiates a process that quickly renders the female unreceptive. In some insect species, such as mosquitoes and fruit flies, individuals experience a sudden shift in receptivity termed “post-mating switch” that is mediated by transfer of molecules present in the male’s seminal fluid (Yapici et al. 2008); in extreme cases this unreceptivity is permanent (Ringo 1996). In *Drosophila* species, receptivity can be reduced via the neural stimulus caused by mating, the paragonial gland secretion and the transfer of sperm.

### Cross-References

- Estrogen
- Reproduction
- Sex Differences
- Testosterone

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## Recessive

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## Synonyms

[Dormant](#)

## Introduction

The term “recessive” in genetics is most often used with the alleles. An allele is a form or variation of the gene which can be either dominant or recessive. Each individual, for a particular gene, attains two alleles, one from the mother and the other one from the father. Therefore, in other words for a particular gene, each individual has two alleles. If the effect of one allele is masked by the other one, then the former allele is called as the recessive allele, whereas the latter one is called as the dominant allele (Mimi Biology 2017; The American Heritage® Science Dictionary 2017). In case of a dominant trait, the presence of only one dominant allele can also ensure the phenotype to be dominant and the related genotype to be heterozygous. In order for recessive trait to be expressed, both the alleles for the corresponding trait should be homozygous recessive (The American Heritage® Science Dictionary 2017). It is necessary to understand the recessive and the dominant genes on the molecular level. Broadly, a gene is responsible for coding a protein and this protein can be an enzyme which will catalyze some reaction. In the simplest of the cases, the dominant gene would code for the protein/enzyme that would further catalyze the reaction (Wanjin and Morigen 2015, Genetics/

Reproduction. ScienceNet – Life Science 2017). For example, in case of cystic fibrosis transmembrane conductance regulator gene (CFTR gene), the dominant allele encodes a channel that can efficiently let chloride into and out of the cells contrary to the recessive allele that cannot encode the mentioned protein. As the recessive allele loses its function therefore, this event is also called as loss of function mutation. Therefore, in case of cystic fibrosis, only if an individual gets both the altered copies of the alleles, he would suffer from the disease otherwise even one normal copy of the allele would be enough to do the job.

Sometimes, at the molecular level, a gene can also encode a dominant-negative variant of the protein which would inhibit the functional version of the protein to do its job too. In a different case, sometimes, a gene encoding a protein acquires a mutation which adds up to its function the event thus called as gain of functional mutation. For example, in case of Huntington’s disease, the protein gains a function of clumping together in plaques which can prove disastrous in the brain tissue. A single copy of the mutant protein can perform this function; therefore, this gain of function is a dominant one (Biology stack exchange 2017; Wanjin and Morigen 2015).

## Depiction of Dominant and Recessive Alleles

There are said ways in order to depict the dominant and the recessive alleles. The dominant allele is depicted by the capital letter say “B” and the recessive allele is depicted by a lower case letter say “b.” The following examples of the genetics in different human traits will help in a clear understanding of the topic.

## Ear Lobe Trait in Humans (Cruz-Gonzalez and Lisker 1981; Krampf n.d.)

It is among few traits in human beings which are still unclear in being Mendelian traits or following



polygenic inheritance (Dutta and Ganguly 1965). But for a clear understanding, we would take it as a Mendelian trait in this example. In case of the ear lobe trait, free earlobes are dominant and attached earlobes are recessive. In this example, the dominant allele for the ear lobe trait is being depicted by “E” and the recessive allele is being depicted by “e.” There can be three possibilities for an individual to have a genotype of “EE,” “Ee,” or “ee.”

1. In the first case, if an individual obtains both the dominant alleles for the ear lobe trait from both parents, then that individual will have a free ear lobe phenotypically and the genotype would be “EE.”
2. In the second case, if an individual obtains one dominant allele from either of the parents and other recessive allele from the other parent, the individual although would be carrier for this condition, phenotypically would have free ear lobes. The genotypic condition of the individual will be “Ee.” It can be seen that the presence of one dominant allele (E) has masked the effect of the other recessive allele “e.”
3. In the third case, if an individual obtains both the recessive alleles from both of the parents, then the individual will have attached ear lobes and the genotypic condition would be “ee.” Here, as there is no dominant allele to mask the effect of the recessive allele and it is present in the homozygous condition therefore, the individual has attached ear lobes.

### Lactase Persistence Trait

This is a different condition following the Mendelian Inheritance pattern. Hypolactasia or lactase nonpersistence or lactase deficiency is a condition that is known to be associated with the deficiency of an enzyme called lactase. This deficiency leads to lactose intolerance and primary lactose malabsorption. This condition follows autosomal recessive inheritance pattern. In other words, it can be stated that the individuals having nonpersistent phenotype are homozygous for the recessive

allele and would have received the two copies of a low lactase-activity allele from both their parents, who may be homozygous or at least heterozygous for the allele (Troelsen 2005). This condition can be normalized by the presence of only one dominant allele since lactase persistence behaves as a dominant trait because half levels of lactase activity are sufficient to show significant digestion of lactose (Troelsen 2005; Wang et al. 1998).

### Eye Color

It is a trait that was previously considered to be Mendelian, but new research has shown that it does not follow Mendelian inheritance but follows the polygenic inheritance pattern. In addition to the extent of melanin found in ones iris, the white collagen fibers are responsible for producing different shades of grey, green, and hazel. In general, the most common eye color is brown, followed by blue, grey, and then green. Eye color is a trait that is influenced by multiple genes. As said earlier that a form or variation of gene is an allele. In normal condition, one form of this gene or an allele can lead to brown eyes, whereas the other form can lead to blue eyes. And if both the forms of this gene are present in the genotype of the individual, the resultant would be brown eyes. But as the eye color trait follows polygenic inheritance, the scenario is different than the normal Mendelian type inheritance. In the current case, the dominant allele of brown color has been represented with “B” and the recessive allele with “b.” Each individual carries 2 copies of alleles; therefore, the genotype of that person can be either “BB,” “Bb,” or “bb.” Due to the polygenic inheritance, the “BB” and “Bb” genotype would not solely lead to the brown eyes, but there are chances that green and blue eyes can also occur. Similarly, the recessive genotype “bb” would mostly form the blue-eyed individuals, but there are possibilities of green and brown eyed individuals as well (Liu et al. 2009; Sturm and Larsson 2009).

Some common recessive and dominant traits have been mentioned in Table 1 (Obtained from

**Recessive, Table 1** Table depicting some human traits and their corresponding dominant and recessive variants

| Trait          | Dominant   | Recessive         |
|----------------|------------|-------------------|
| Chin cleft     | No cleft   | Cleft             |
| Hairline       | Widow peak | Straight hairline |
| Eyebrow size   | Broad      | Slender           |
| Eyebrow shape  | Separated  | Joint             |
| Eyelash length | Long       | Short             |
| Dimples        | Dimples    | No dimples        |
| Eye shape      | Almond     | Round             |
| Freckles       | Freckles   | No freckles       |
| Tongue rolling | Roller     | Nonroller         |

[http://faculty.southwest.tn.edu/jiwilliams/human\\_traits.htm](http://faculty.southwest.tn.edu/jiwilliams/human_traits.htm)).

## Recessive Inheritance Pattern

If a trait is recessive, then in order to express the trait both the copies of the allele should be recessive, i.e., the offspring must receive one recessive allele from the mother and the other one from the father. This genotype would be called as homozygous recessive. The recessive inheritance pattern can be explained with the example of Chin cleft which is a Mendelian trait in humans. Here the dominant trait is the cleft chin in contrast to the recessive trait which is the smooth chin. The dominant allele has been mentioned with “S” and the recessive allele has been mentioned with “s.” Individuals having a genotype of “SS” would have a cleft chin, whereas the “ss” genotype individuals will have a smooth chin. The individuals having “Ss” genotype would also show the cleft chin phenotype, but they would be carriers of the recessive allele (Genetics Generations 2015). In order to determine the probability of the inheritance of the smooth chin (or any other recessive trait), the genotypes of the parents must be taken into account. If one parent is heterozygous and has “Ss” genotype and the other is homozygous recessive having “ss” genotype, then the probability of their offspring having recessive genotype or the smooth chin trait can be shown by a Punnett square as shown in Fig. 1.

|   |    |    |
|---|----|----|
|   | S  | S  |
| S | Ss | Ss |
| s | Ss | Ss |

**Recessive, Fig. 1** Figure depicting that with parents having genotypes of “Ss” and “ss,” the chances that the offspring will have a smooth chin is 50%

## Some Common Myths Explained (Learn. Genetics. Genetic Science and Learning Center (n.d.))

### 1. Dominant phenotypes are not always common than the recessive phenotypes

It is well known that two dominant alleles will lead to a dominant phenotype, one dominant and one recessive allele will also lead to a dominant phenotype and two recessive alleles will lead to a recessive phenotype. Therefore, it is a common myth that the possibility of a dominant phenotype in a population is twice that of the recessive phenotype. This is not always correct. In case of eye color, brown color is the dominant phenotype, whereas the blue color is the recessive phenotype. In Scandinavia, blue eyed people (light color) are higher in number than the brown eyed people (dark color). Therefore, the recessive alleles for the eye color in Scandinavia are higher than the dominant alleles.

### 2. Dominant alleles are not better than recessive alleles

It is a common myth that the dominant alleles are better than the recessive alleles. But the truth is that the mode of inheritance has nothing to do with the beneficiary effects of the allele on an individual. For example, rock pocket mice has a gene that controls the fur color. The fur can be of two different colors,

one is dark and the other one is light. The dark fur color is the dominant trait, whereas the light fur color is the recessive trait. When these mice thrive in the habitat where the dark rocks are abundant, then the dominant allele becomes advantageous as it allows the mice to have a dark fur and it can easily mix into the surroundings and escape the predators. Contrary to the above situation if the dark fur mice thrive in the regions of the light colored rocks, they would be easily identified and killed by their predators. Hence, in this kind of environment, the light fur color proves to be advantageous. Therefore, it can be concluded that it is not the inheritance pattern that determines that an allele can be advantageous or disadvantageous for a particular individual, but the environment plays a major role in it.

### 3. A “broken” allele can have a dominant inheritance pattern

Broken alleles/genes here mean those genes that do not perform their normal function. Many genetic disorders involve such kind of genes that produce altered proteins, but the other copy of the protein produced by the normal gene comes to rescue and masks the effect of the broken allele/gene. Henceforth, these kind of genetic disorders follow the recessive inheritance pattern. But the myth that all genetic diseases are recessive in nature is not correct. Keratin proteins are fibrous proteins that have the role in strengthening the hair, fingernails, skin, and other tissues of the body. It is surprising, but the genetic disorders involving the keratin proteins follow mostly dominant inheritance patterns, an example of the same is pachyonychia congenita. This disease is characterized by dystrophic, thickened nails, and painful palmoplantar keratoderma and occurs due to the mutation in one of the four keratin genes (George 2016).

## Conclusion

Each individual possesses genes that encodes proteins and these proteins are involved in some or the other reaction in the body. These genes are

governed by the alleles that an individual acquires from parents. If both the obtained alleles are dominant or if even one of them is dominant in nature, then the gene shows a dominant phenotype and the relevant protein is expressed. But in case both the alleles obtained from the parents are recessive, then the gene would show a recessive phenotype and the relevant protein would not be produced. In other words, it can be said that the recessive traits follow an inheritance pattern in which an individual should be homozygous recessive in order to depict the recessive phenotype. Many examples of the Mendelian traits which have one gene encoding for one trait are available in nature such as chin cleft, dimples, lactase persistence trait, hairline. Many other traits that follow the polygenic mode of inheritance such as eye color give us an understanding that apart from the dominant and the recessive phenotype multiple other intermediate phenotypes can also be available. Furthermore, many myths regarding the genetics of the dominant and the recessive alleles have been discussed in detail so as to provide the readers a clear understanding of the topic.

## Cross-References

- [Carrier](#)
- [Dominance](#)
- [Polygenic inheritance](#)

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## Reciprocal Altruism

- [Mutualism](#)

## Reciprocity

- [Exchange Behavior](#)

## Recoding

- [Chunking](#)

## Recollection

- [Recall](#)

## Recombinant Inbred Lines

- [Recombinant Inbred Strain](#)

## Recombinant Inbred Strain

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## Synonyms

- [Recombinant inbred lines](#)

## Definition

A recombinant inbred strain is a strain formed by crossing two inbred strain, which is continued to be crossed or say repeated for the next 20 generations.

## Introduction

Recombinant inbred strains (RIS) are the offspring developed from the two foremost inbred lines, which contains approximately the same ratio of genetic contributions of their ancestors. The repeated crossing is strictly done between brother x sister to form a new inbred line; this leads to the construction of a genome which is mosaic of the genome of the parents.

In this way production of a line is done which has unique property but is related to one another. It can also be understood as when different parents which were inbred meant as members of a set.

These organisms undergo important recombination events in their chromosomes, which they inherit from more than two inbred lines.

Recombinant inbred strains are produced by combination of selfing progeny of individual members of an F2 generation until complete homozygous achieved.

It also equalizes marker type like double haploids; the genetic segregation ratio for both dominant and codominant marker would be 1:1.

They are also crucial and useful in identifying tightly linked markers when obtained after several cycles of meiosis (Adamová et al. 2018).

## Discovery

Mainly, recombinant inbred strains of mouse produced during the 1950s. Dr. Donald Bailey made other scientists understand the importance of these genetic constructs. He conceptualized its usage for linkage analysis. As these recombinant strains provided a promising alternative to the lengthy procedure of classical breeding analysis which was required generally to map the uncovered locus.

Dr. Bailey first made eight recombinant inbred strain set – the original CXB set – and moved it to Jackson Laboratory in 1967. In the year 1969, along with Dr. B. Taylor, he took up the cause of the recombinant inbred approach and set about, developing from several pairs of progenitor parents, large sets of recombinant strain that are now standards for mouse genetics communities including BXD, BXH, ARXL, and AKXD.

The recombinant inbred strain is used to map mouse genes and helps in the study of other experimental organisms such as the plant *Arabidopsis thaliana* (Bailey 1981).

## Taxonomy

Recombinant inbred strain should be designated by uppercase one- or two-letter abbreviation of both parental names, with the female strain written first and separated by an uppercase letter X with no intervening spaces (e.g., HXB1,

HXB2, HXB3; members of the HXB set of recombinant inbred strains consequent from a cross of SHR/OlaIpcv x BN-Lx/Cub) (Pollard 2012).

## Usage

Rat and mouse recombinant inbred strains (RIS) provide powerful tools for genetic mapping. These include the following: genotyping of each strain is required only once; multiple individuals from each strain may be phenotyped to reduce individual, environmental, and measurement variability; multiple phenotypes can be assessed on the same genetic background. Also, as recombination events are denser in RIS than those occurring in any one meiosis, higher mapping resolution can be achieved (Silver 2001).

## Advantages

1. Each strain is an everlasting resource as the study of multiple phenotypes is possible with the same genotype.
2. For any study, a strain is needed to be genotyped only once.
3. Individual variations are reduced, utilizing phenotyping several individuals from each strain.
4. These recombinant strains are immortal lines. They are replicated over years and years at several locations and hence are of prime importance in producing quantitative trait loci.

## Conclusion

Recombinant inbred strains are a vital resource for intricate mapping traits in various species. Inbred lines are already made majorly for experimental species like *Arabidopsis*, mouse, *Drosophila*, and *C. elegans*. It serves excellently for the analysis of epistatic interaction. It is also a powerful mechanism for analysis of gene function and quantitative traits, which is useful in studying proteome data sets under a variety of environments.



## Cross-References

- [Epigenesis](#)
- [Mating](#)
- [Phenotype](#)
- [Quantitative Genetics](#)
- [Recombination](#)

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## Recombination

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## Synonyms

[Alteration](#); [Combination](#); [Modification](#)

## Definition

Genetic recombination is a process which recombines the alleles of two parental DNA molecules or different segments of same DNA molecule and produces new combinations of alleles in the recombined DNA with features not present in either of the parents. Recombination can be observed when sequences are homologous region of chromosomes or when some extent of sequence similarity is present. This process is performed by both prokaryotic cells and eukaryotic cells.

## Functions of Genetic Recombination

Each organism has remarkable potential to sustain in the environment over an extent of time. Genetic variation or genetic diversity allows organisms to evolve in this changing environment and in addition maintain a vast quantity of genetic information. The rearrangement of genetic information is performed by the genetic recombination. Apart from genetic diversity, recombination is also required in double-stranded DNA breaks repairing and during DNA replication for gaps filling and for preventing replication fork stalling (Li and Heyer 2008).

## Models of Recombination

On the basis of type of initial DNA break (single stranded or double stranded), the recombination model can follow two pathways, but important steps involved in homologous recombination model are similar in both pathways like homologous DNA strands alignment, breakage of strands, exchange between the strands, and final sealing of the recombined strands (West 1992).

## Holiday Model (Single Strand Break Model)

The holiday model is also known as hetroduplex model as the final recombined double stranded DNA molecule is derived from two homologous chromosomes. Recombination event starts with the alignment of homologous chromosomes. Then a nick is introduced in one of the DNA strand of both the homologous chromosomes at same position. The produced nicked strands invade the opposite complimentary strands by the process called strand invasion resulting in hetroduplex formation followed by sealing of gaps by DNA ligase forming a crossover structure called Holiday junction. Holliday junction is dynamic in nature and migrate laterally resulting in the formation of recombined DNA strands by exchange of DNA strands between homologous chromosomes. Subsequently, the resolution of the

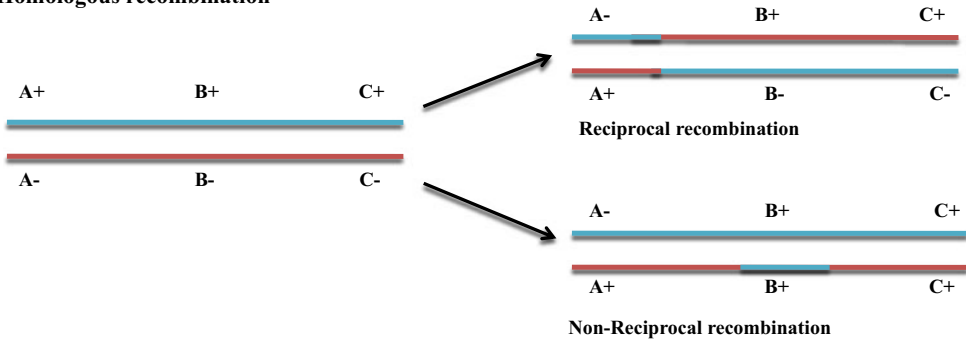
recombined DNA molecules is performed by cleavage across the branch point in two ways producing two different results. If invading strands were cleaved and rejoined then the separated products will be two nonrecombinant molecules. On the other hand, if noninvading strands were cleaved and joined then the products will be reciprocally recombined DNA molecules. Holliday model does not explain how single strand nicks are produced at equivalent positions in each helix. Hence, Meselson-Radding modification proposes the initiation of recombination by

single strand break in DNA strand of only one of the homologous chromosomes (West 1992) (Fig. 1).

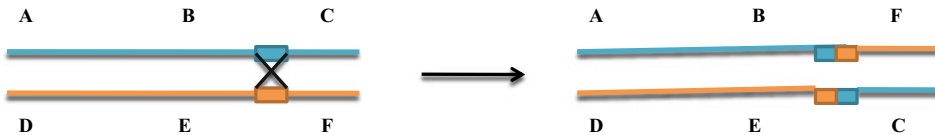
**Double strand break model:**

This model is similar to the Holliday model except that the initial break is a double strand nick in one of the two homologous chromosomes. Exonuclease trims from the 5' end of the nicked region producing 3'-OH overhangs. Only one overhang then invades the opposite duplex and this procedure is called single strand invasion. Elongation of the strands from the 3' ends using opposite homologous chromosome as a template result in the formation of two Holliday junctions (Haber et al. 2004).

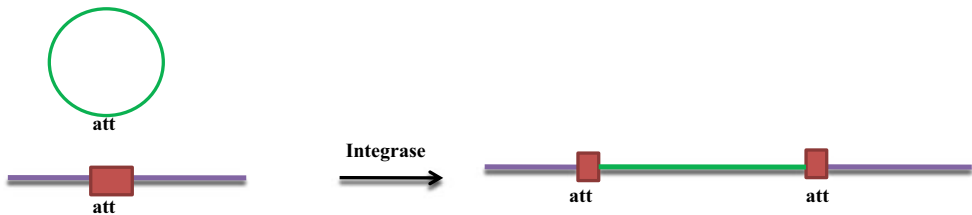
**A. Homologous recombination**



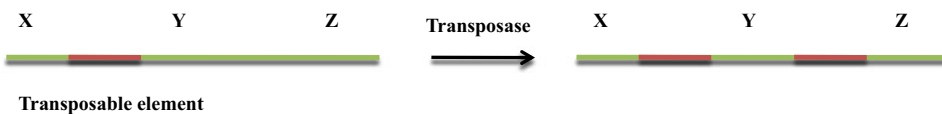
**B. Non-Homologous recombination**



**C. Site specific recombination**



**D. Replicative recombination**



**Recombination, Fig. 1** Types of natural recombination. Single line represents double stranded DNA. (a) Homologous or general recombination. (b) Nonhomologous

(or illegitimate) recombination (c) Site-specific recombination and (d) Replicative recombination

## Enzymes Involved in Recombination

The steps involved in homologous recombination were first described in bacterial system (Clark 1973) and the well-identified recombination system is RecBCD. RecBCD enzyme is also known as exonuclease V and is a protein complex of three different subunits called RecB, RecC, and RecD.

The RecB subunit has nuclease and 3′–5′ helicase activity and RecD has 5′–3′ helicase activity. RecC is involved in chi site recognition while RecA has property to coat DNA fragment and invade the double helix. Branch migration is performed by RuvA and RuvB protein complex and lastly RuvC protein catalyzes the cleavage step that resolves the Holliday structure. In eukaryotic system, the recombination event has been explored in the budding yeast *Saccharomyces cerevisiae*.

## Types of Recombination

Recombination has been classified into four types in different organisms.

### 1. General or homologous Recombination

Homologous recombination is performed during meiosis in eukaryotes and involves alignment of homologous chromosomes with similar DNA sequence. Chiasma is the site of crossing over between the two chromatids of the homologous chromosomes which allows recombination of the genes between the homologous chromosomes (Sung and Klein 2006).

General recombination can be further classified into reciprocal recombination and non-reciprocal recombination (gene conversion).

- (a) Reciprocal recombination involves even exchange of genetic material between the homologous chromosomes. For example, homologous recombination between A and B genes of two homologous chromosomes A+B+C+ and A–B–C– results in recombined products A–B+C+ and A+B–C–.

- (b) Nonreciprocal recombination is also known as gene conversion. Nonreciprocal recombination occurs when genes are transferred from one sister chromatid to the other chromatid, but no reciprocal exchange of genetic information occurs. For example, homologous recombination between two homologous chromosomes A+B+C+ and A–B–C– will produce new recombined products A+B+C+ and A–B+C– with one of the parental chromosome remained unchanged.

### 2. Illegitimate or nonhomologous recombination:

Nonhomologous recombination requires only little sequence similarity between the DNA segments. Joining the broken DNA ends and DNA replication errors are the main sources for the occurrence of nonhomologous recombination event. Examples for non-homologous recombination are deletions and translocations of the DNA segments.

### 3. Site specific recombination:

Unlike homologous recombination, site specific recombination does not require extensive DNA homology sequence for recombination. Site specific recombination occurs between short (about 12–24 bp) and specific region DNA. It also requires specific recombination enzymes. Site specific recombination is performed using two types of mechanisms (Grindley et al. 2006).

- (a). Transpositional site-specific recombination: Transpositional site-specific recombination does not require specific sequence homology and thus no heteroduplex formation occurs.
- (b). Conservative site-specific recombination: Conservative site-specific recombination requires short sequence similar between the two DNA molecules and also involves formation of a short heteroduplex.

### 4. Replicative recombination:

Replicative recombination is a process performed by many transposable elements in which a new copy of a DNA segment is generated at a new location.

### 5. Mitotic recombination:

Mitotic recombination takes place during interphase i.e. the resting phase between mitotic divisions. Mitotic

recombination is a rare phenomenon and is similar to the meiotic recombination.

Most of the prokaryotic organisms have asexual reproduction and possess only one set of chromosomes while organisms participating in sexual reproduction have two sets of chromosomes which increases the genetic diversity in them. However, prokaryotic organisms also increase genetic diversity by different molecular mechanisms like conjugation, transduction and transformation (Carpa 2010). Recombination has similar functions in prokaryotic cells like DNA repair and replication as observed in eukaryotic cells.

1. **Conjugation:** Conjugation based recombination involves physical contact between donor and recipient cells. Donor cell transfers the single strand of DNA from F-plasmid (not present in recipient cells) to the recipient cell via a bridge-like structure called pilus.
2. **Transduction:** The transfer of genetic material between the cells occurs through virus or bacteriophage. When virus infects the bacteria, it exploits the host machinery for its replication and breaks down host DNA. Host DNA gets packaged into few of the phages envelop forming transducing phages. After lysis of the donor cells, both normal phages and the host DNA containing transducing phages release out. If transducing phage infects recipient cells, it will introduce donor DNA inside the recipient cell which can get incorporated in the genome of recipient cells via recombination.
3. **Transformation:** Some species of bacteria can take up the naked DNA from the surrounding and incorporate them into their genome. This process is called natural transformation. Many bacteria are not competent in nature and therefore many methods are used (electrophoresis, calcium chloride treatment) to increase their competency for transformation.

## Conclusion

Genetic recombination is a well-studied mechanism responsible for providing genetic diversity in

eukaryotic and prokaryotic cells. It has other functions like in DNA repair and replication. The mechanism of homologous recombination is well known in both eukaryotic and prokaryotic cells. Prokaryotic cells also perform recombination mechanisms via conjugation, transduction, and transformation.

## Cross-References

- [Conjugation](#)
- [Mutations](#)

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## Reconciliation

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## Synonyms

[Postconflict affiliation](#)

## Definition

Postconflict friendly reunions between former opponents soon after the end of an agonistic conflict.

## Introduction

Although aggression is not an inevitable outcome of conflict of interest, and social animals have a number of possible options to manage it (e.g., avoidance or increasing tolerance, de Waal 1996), individuals may use aggression as a negotiation tool (Aureli et al. 2002). For instance, animals may threat and attack group mates to gain access to a contested resource or to establish or reinforce dominance relationships. However, aggression is energetically costly and can result in injury, which can entail tremendous costs through infection and disability. For gregarious animals, aggression may also entail other less obvious costs. Observational and experimental data from various primate and nonprimate species show that opponents who have just fought are less tolerant to one another and are also more likely to be involved in renewed attacks after the original conflict has ended (Romero and Aureli 2017). Not being able to approach and interact with a former opponent may compromise the cooperative aspects of the relationship, which in turn may have important fitness consequences for social animals, since the maintenance of stable social bonds positively affect individuals' competitive success and reproductive performance (Seyfarth and Cheney 2012). Once aggression erupts, one or more of these costs are inevitable.

Accumulated evidence from studies on wild and captive populations shows that social animals use an array of behavioral mechanism to mitigate the costs of aggression, generally labeled as conflict resolution mechanisms (Arnold et al. 2010; Aureli and de Waal 2000). Among them, reconciliation – i.e., a friendly reunion of former opponents shortly after the end of a conflict – is probably the most efficient one, since it involves direct communication between involved individuals.

## Occurrence of Reconciliation

Reconciliation was first described by de Waal and Roosmalen (1979) in a zoo colony of chimpanzees (*Pan troglodytes*) in the Netherlands. Since this pioneering study (see de Waal 2000 for a historical review on earlier descriptive accounts), systematic studies in more than 30 species of primates and a number of nonprimate species have shown that affiliative interactions between former opponents occur sooner after the cease of aggression than during control periods, suggesting that reconciliation is a widespread phenomenon among social species (reviewed in Arnold et al. 2010; Aureli et al. 2002; Romero and Aureli 2017). Furthermore, the fact that reconciliation is present in phylogenetically distant species, such as primates, carnivores, cetaceans, birds, or fish, also suggest that this conflict resolution mechanism must have evolved independently several times due to selection pressures associated with living in groups (Schino 2000). The scarce relevant data on nonprimate species, though, does not allow us to know whether reconciliation is a general phenomenon in group living species or, on the contrary, whether it has evolved in only a fraction of social species (Schino 2000).

The majority of research on reconciliation has been conducted in captive populations (76% of all studies), where space is often limited and the avoidance of a former opponent may not be possible. However, a number of studies have demonstrated that reconciliation is not an artefact of captivity, since this postconflict behavior has been observed in populations living in large enclosures (de Waal and van Roosmalen 1979) where prolonged avoidance was possible, and in wild populations, where the option to leave the group, at least temporarily, was available (Silk et al. 1996; Watts 1995).

In most species, reconciliation occurs soon after the end of the aggressive conflict, typically within the first few minutes of the postconflict period (Arnold et al. 2010). However, the type of affiliative behavior that opponents exchange is highly variable. While for some species merely staying in physical contact or in close proximity to



a former opponent may be sufficient to reconcile, other species may use highly differentiated behavioral signals, such as kissing and embracing in chimpanzees (de Waal and van Roosmalen 1979; Fraser and Aureli 2008; Romero et al. 2010), that are rarely observed outside the conciliatory context (i.e., explicit reconciliation, de Waal 1993). This interspecific variation in reconciliation style has been attributed to variation in the average quality of social relationships among species, with high levels of affiliation or tolerance being associated with the occurrence of explicit conciliatory behaviors (Aureli et al. 2002; Thierry et al. 2008).

Variation in conciliatory patterns has also been observed within species. For instance, not all chimpanzee populations use explicit gestures to reconcile, and when they have used these highly differentiated behavioral signals they only represent a proportion of all friendly reunions observed during the postconflict period (Fraser and Aureli 2008). Thus, it is possible that individuals use different behaviors to reconcile depending on their relationship with the opponent or the characteristics of the previous conflict. For instance, individuals may use noncontact behaviors, certain types of vocalizations or facial expression as a less risky conciliatory strategy than directly approaching a former opponent (Schino and Marini 2011). It is also possible that variation on conciliatory patterns is associated with individual behavioral plasticity. However, too few studies are available to draw conclusions about the sources of variation in conciliatory patterns.

Some studies have examined whether aggressors or recipients of aggression are more likely to initiate the affiliative reunion (Arnold et al. 2010). Individual's motivation to initiate the reconciliation should depend on a number of factors. Because of the asymmetric nature of aggressive interactions, the cost of aggression is likely to differ between the recipient of aggression and the aggressor. Also, most relationships are asymmetrical to some extent, and one party may have more to gain from the postconflict contact than the other (Cords and Aureli 2000). In addition, there are methodological difficulties in detecting genuine attempts to reconcile, or subtle conciliatory

signals, such as changes in body posture or facial expression (e.g. Silk et al. 1996). Thus, it is not surprising that findings are inconsistent across studies examining whether aggressors or recipient of aggression are more likely to initiate reconciliation (Arnold et al. 2010). However, the majority of studies that have considered the identities of the initiator of reconciliation regardless of their role during the previous conflict have found that individuals that tend to take the initiative to reconcile are also primarily responsible for friendly contacts outside the postconflict period (Arnold et al. 2010).

## Function of Reconciliation

Reconciliation is a heuristic term that implies the specific function of relationship repair, that is, the restoration of the usual pattern of interactions among former opponents (Arnold et al. 2010; Romero and Aureli 2017, see Aureli et al. 2012 for discussion on alternative interpretations). It should be noted that despite the widely use of the functionally loaded term reconciliation, very few studies have investigated the consequences of these postconflict friendly reunions. The functional analysis of these interactions is extremely important since the occurrence of similar behaviors under similar contexts does not necessarily warrant that the function of such behaviors is the same. In other words, although reconciliation may be a phenomenon common to many social species, its proximate mechanisms and short-term consequences may differ widely.

Studies that have investigated the function of reconciliation show that these friendly reunions serve to reduce the cost of aggression and to restore opponents' relationship. For instance, the occurrence of an affiliative interaction between contestants reduces their probability of receiving postconflict attacks from both former opponents and other group members, which otherwise are higher than baseline rates (Arnold et al. 2010; Romero and Aureli 2017). Furthermore, the usual interaction patterns between former opponents, measured by approaches, time spent in proximity, and affiliation, are lower than baseline

after a conflict, and restored to usual levels once reconciliation takes place (Arnold et al. 2010; Romero and Aureli 2017).

By reducing the risk of renewed aggression and restoring the opponents' tolerance levels, the occurrence of reconciliation also reduces the uncertainty about the postconflict situation, which in turn alleviates the postconflict distress experienced by both opponents. Using self-directed behaviors, such as self-grooming in mammals or self-preening in birds, as noninvasive indicators of anxiety and distress responses (Aureli and Smucny 2000) a number of studies have shown that both opponents may experience high levels of anxiety following agonistic conflicts (e.g. victims: Aureli and van Schaik 1991; aggressors: Romero et al. 2009). Rates of self-directed behaviors in one or both opponents are lower if they reconcile than when they do not (Romero and Aureli 2017). Moreover, the few studies examining physiological responses during the postconflict period bring further support to the behavioral evidence. Cortisol levels in children (Butovskaya 2008) and heart rate in rhesus macaques (Aureli and Smucny 2000) decrease to baseline levels after reconciliation compared to unaffiliated postconflict periods.

Given that reconciliation repairs the relationship between opponents, this conflict resolution mechanism is not only functionally relevant for animals that maintain long-term relationships with conspecifics, but it is also relevant for any species relying on cooperative relationships. The only reported case of interspecific reconciliation between cleaner fish (*Labroides dimidiatus*) and client fish supports this idea (Bshary and Würth 2001).

Despite the widespread occurrence of reconciliation among social animals and its beneficial consequences, reconciliation does not occur after every conflict. Characteristics of the previous conflict, opponents' age-sex class, or matting seasonality can affect the occurrence of reconciliation, at least in some species (e.g. Palagi et al. 2005). However, the factor that most consistently has been reported to determine the occurrence of reconciliation across studies is the quality of the relationship between former opponents (Arnold

et al. 2010). The valuable relationship hypothesis (de Waal and Aureli 1997) predicts that if reconciliation restores the relationship between opponents it should occur more frequently after aggression between individuals that maintain more valuable relationships since they have more to lose if they do not repair the relationship. Supporting this hypothesis, high baseline levels of positive social interactions in primates, canids, or corvids – such as grooming, agonistic support, close spatial association, or food sharing – are typically associated with higher rates of reconciliation (Arnold et al. 2010; Romero and Aureli 2017). Although the name of the hypothesis refers to the value of the relationship, other components of the relationship, such as compatibility (i.e., the general tenor of social interactions in a dyad) or security (i.e., the perceived probability that the relationship with the partner will change; Cords and Aureli 2000) are also expected to determine whether contestants reconcile their conflicts. These latter components of the relationship, however, have received much less attention.

Although the valuable relationship hypothesis relates the variation in reconciliation to the benefits associated with the occurrence of the postconflict reunion – and therefore proposes a possible ultimate explanation – it does not imply that opponents are motivated to reconcile by anticipated benefits or that they are conscious of the long-term outcome of their actions. Such assessments require memory and computational skills that may exceed the cognitive capacities of nonhuman animals, including primates (Aureli et al. 2012). It has been proposed that animals may be able to assess the postconflict situation and modify their behavior according to the quality of the relationship with their opponents by using a much lower cognitively demanding mechanism, such as emotional mediation in the form of postconflict anxiety. The Integrated Hypothesis (Aureli 1997) suggests that the higher the value of the relationship between opponents, the higher the postconflict anxiety should be, as the loss of benefits is greater. This hypothesis thus provides a link between the function and the possible proximate mechanism of reconciliation. Supporting this hypothesis, in some species of primates, the

recipients of aggression and aggressors show both increased postconflict anxiety and higher conciliatory tendencies after conflicts with individuals with which they shared strong affiliative bonds than after conflicts with other individuals (Aureli 1997; Kutsukake and Castles 2001; Romero et al. 2009); but see McFarland and Majolo 2011). Importantly, in none of these studies, the risk of renewed aggression varies with the quality of opponent's relationship (Aureli 1997; Kutsukake and Castles 2001), Romero, *unpubl. data*) suggesting that higher levels of anxiety are due mainly to the damage that the conflict causes more valuable relationships.

An additional, yet largely unexplored, factor that may also explain part of the observed variation in the occurrence of reconciliation is the presence of stable individual differences in behavior, also referred as personality traits (e.g., Sih et al. 2004). Although often less intuitive to approach the study of sociality from the individual level of analysis, cumulative evidence shows that individual differences significantly influence how social processes themselves unfold (Seyfarth and Cheney 2012). Recent work on chimpanzees shows that beyond relationship value, stable individual differences represent a meaningful source of variation in conciliatory tendency, with subjects' conciliatory tendency being consistent across years and situations (Webb et al. 2014).

## Conclusions

More than three decades ago, a pioneering work described how two chimpanzees kissed and embraced to reconcile a conflict. There is now substantial evidence that reconciliation is a widespread conflict resolution mechanism among social species, and that animals reconcile their conflicts in a flexible way. Only a minority of studies, however, have examined the function of reconciliation. This is certainly a shortcoming, as reconciliation may function differently in different species under different conditions. Therefore, the next generation of studies on reconciliation should focus on the functional aspects of reconciliation in a wide range of primate and non-primate species. Another aspect that should

receive more attention is the role of individual differences in reconciliation, since these studies could help us gain a complete understanding of the adaptive consequences of conflict resolution behaviors. Also, we know very little about the development of conciliatory skills. A parallel development of social competence and conflict resolution skills is likely, although no previous research has addressed this topic. Future studies focusing on these topics will help us to develop a more comprehensive framework for reconciliation in animals.

## Cross-References

- [Aggression](#)
- [Agonism and social status](#)
- [Costs of Group Living](#)
- [Group living](#)
- [Post-conflict Affiliation](#)
- [Post-conflict resolution](#)
- [Social Behavior](#)
- [Social grooming](#)
- [Species-specific behavior](#)

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## Recreation

### ► Horseback Riding

## Red Queen Effect, The

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The Red Queen Effect or Red Queen Hypothesis is a term coined by Leigh Van Valen (1973) to explain the ever-changing nature of evolution by natural selection. The hypothesis states that the likelihood of extinction for any given species remains relatively constant over time. Although a species in a given environment may have an

advantage at one point in time, this places selective pressure on neighboring species who are themselves constantly evolving. Over evolutionary time, no one species maintains a long-term net advantage because other species that inhabit the same environment will evolve counteradaptations. The term is a reference to Lewis Carroll's *Through the Looking-Glass*:

"Now, here, you see, it takes all the running you can do to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!" (Carroll 1982, p. 104).

## Interspecies Competition

Red Queen effects are exemplified in competition between species, such as the relationships between predators and prey. At any one point in time, predators in a given environment seem well-adapted to catch their preferred prey species, whereas prey seem to be similarly well-adapted to avoid being captured and eaten (Angerbjorn et al. 1999). Over evolutionary time, predator species evolve adaptations that improve their ability to capture prey, whereas prey species evolve adaptations to better avoid capture. A similar dynamic exists in parasitic relationships, wherein parasites are adapted to infect their preferred host species, and host species are adapted to defend against parasites (Brun et al. 1992). A less direct form of interspecies competition exists when two species compete to fill a single ecological niche. For example, if two species occupied the same environment and had similar diets, one species might evolve adaptations either to consume a more diverse range of foods or to outcompete the rival species for the contested food.

## Intersexual Competition

The Red Queen Hypothesis can also be applied to opposite-sex members of the same species, as males and females of the same species often have conflicting interests. For example, males have a lower minimum obligatory parental investment required relative to females (Trivers 1972). As a result, males are less discriminating when selecting

sexual partners and have adaptations that facilitate maximizing the number of sexual partners. Females, in contrast, are more selective when choosing sexual partners, prioritize mate quality over quantity, and often evolve preferences for physical cues to fitness. Males also sometimes have adaptations that increase their ability to circumvent female mate choice by gaining sexual access via force or coercion (Bisazza et al. 2001). In response, females evolve adaptations that guard against coercive sexual advances.

## Intraspecies Competition

The Red Queen Hypothesis can also be useful for understanding individual competition between same-sex members of a species. Same-sex individuals of a given species often compete with one another for access to food and mating opportunities. Individuals of some species may even be said to have different strategies, whereby some individuals possess more vibrant physical characteristics that confer an advantage in sexual competition, but a disadvantage in terms of survival. Intrasexual competition over evolutionary time may also result in more exaggerated physical characteristics used to attract mates (Loyau et al. 2005) or better weaponry for competing with same-sex rivals (Robinson et al. 2006). An individual member of a species born with a genetic mutation resulting in a comparative advantage in attracting sexual partners may have an edge in his or her generation. However, such a mutation would be passed down to subsequent generations, eventually becoming a characteristic feature of the species, at which point the mutation could no longer be said to confer an advantage to any one member of the species. Over time, intraspecies competition for resources and mating partners drives the evolution of adaptations to outcompete conspecifics in much the same way that adaptations result from interspecies and intersexual competition.

## Cross-References

- [Cuckoo Brood Parasitism](#)
- [Intra-sexual Selection](#)



- [Predator](#)
- [Runaway Selection](#)
- [Sexual Selection](#)

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## Reduced Penetrance

- [Incomplete Penetrance](#)

## Reductionism

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## Synonyms

[Mind-body problem](#); [Mind-brain problem](#)

## Introduction

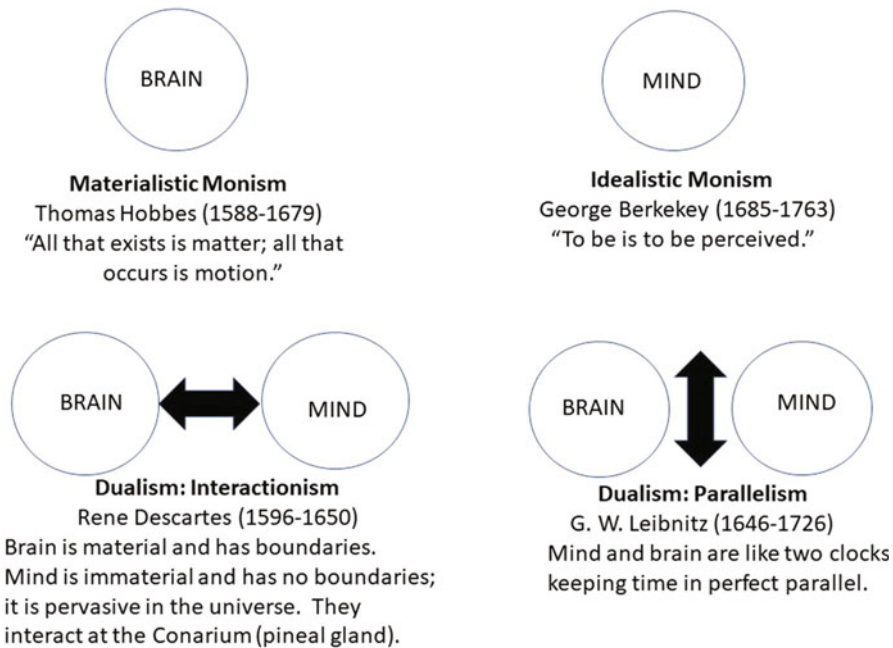
To set the stage for writing about reductionism, it may help first to review briefly the history of philosophy associated with, as it was known historically, the mind-body problem. However, mind-brain will be used here instead of mind-body. The four basic views are diagrammatically summarized in Fig. 1.

As may be seen in Fig. 1, there are two forms of monism, namely, either the brain alone exists (Thomas Hobbes's Materialistic Monism) or the mind alone exists (George Berkeley's idealistic monism, where *idea* not *ideal* is the root word). There are also two forms of dualism where both the mind and the brain exist. With dualism the question becomes that of how they relate to each other. Descartes believed that both the mind and brain exist, and they interact at the conarium (pineal gland). He also believed that the brain was material and had a boundary and that the mind was immaterial and had no boundaries; it permeated the universe. This form of dualism was known as interactionism. Gottfried Wilhelm Leibnitz believed that the mind and brain both existed independently and that they functioned in perfect parallel, a view known as parallelism.

There is no way to prove the truth or falsity of any of these positions regarding the mind and the brain. All that one can do is choose the one that is most useful or most comfortable personally. Many behavioral scientists are clearly materialistic monists, but many others write in ways that indicate that they are mind-brain dualists. This writer believes that science functions best with materialistic monism, and he cannot in good conscience write about any of the other viewpoints.

Returning to reductionism, two sources were examined for contemporary definitions of reductionism, *The Oxford Guide: Philosophy* (T. Honderich, Editor, 2005) and Turner's (1967) *Philosophy and the Science of Behavior*. The *Oxford Guide* included five definitions pertaining to reductionism by three authors, and Turner provided four definitions. One of the five in the *Oxford Guide* had minimal, if any, relevance for animal cognition and behavior, and it will not be considered further here.

Explicitly or implicitly, the eight definitions emphasized material reductionism. The following



**Reductionism, Fig. 1** Diagrammatic representation of the mind-brain relationship problem

selected portions of the eight definitions are quoted to validate this conclusion.

**Ontological reductionism** (Ruse 2005, p. 793):  
*"All organisms are reducible ultimately to molecules," but often the claim is meant in the more metaphysical sense that there is but one substance or "world stuff" and that this is material.*

**Methodological reductionism** (Ruse 2005, p. 793): *The best scientific strategy is always to attempt explanation in terms of ever more minute entities. It has undoubtedly been the mark of some of science's greatest successes and not just in physics.*

**Theory reductionism** (Ruse 2005, p. 793): *Theory reductionism raises the question of the relationship between theories in a field, as between Newton's theory and that of Einstein. [Given the examples from physics, material reductionism is implicit.]*

**Reductionism, mental** (Kim 2005, p. 794): *Reductionism in philosophy of mind is the claim that facts about mentality are reducible to physical facts, i.e., facts about matter and material processes.*

**Constructual reduction** (Turner 1967, p. 302):  
*The existential status of an object derives from it being empirically real and not inferred.*

**Theoretic reductionism** (Turner 1967, p. 304): *The laws of the reduced science are hereby explained by the laws of the reducing science [e.g., behavioral science is reduced to physiology].*

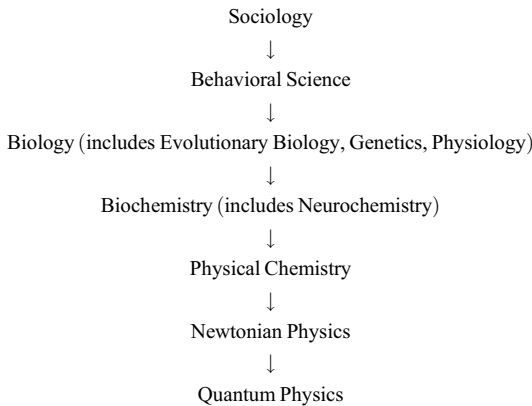
**Methodological reductionism** (Turner 1967, p. 309): *For psychology, this would mean restricting its theoretical constructs to terms in principle to the language of physiology.*

**Metaphysical reductionism** (Turner 1967, p. 309): *It asserts that for psychology ultimately all questions of theory are to be resolved by physiological reductionism.... This compares with a metaphysical behaviorism which assumes all sentences in the mental language are really translatable into sentences in the physicalistic language; the language presumably of pure mental content is meaningless.*

Of course, there are those who may accept material reduction in principle but who believe one can be a good scientist and work, for example, only at the behavioral level. B. F. Skinner was a

good example of this type of behavioral scientist, and he will be considered further below.

In a material reduction scheme, where is behavioral science among the social, biological, and physical sciences? To illustrate the answer, the down arrow symbol “↓” means “reduces to”:



## Limitations of Measurement that Affect All Sciences

It is important to recognize that, regardless of reductionism, all sciences are affected by limitations of measurement and that reductionism itself can contribute to such limitations (see Figure Legend and discussion associated with Fig. 4 later in this entry). Werner Heisenberg (1901–1976) is well remembered for showing that precise measurement of the position *and* momentum of atomic particles cannot be done. This became known as the uncertainty or indeterminacy principle. Later, Heisenberg (2007) was clear in his *Physics and Philosophy: The Revolution in Modern Science* that the uncertainty/indeterminacy principle was not limited to quantum physics; see, especially, chapter “The Relation of Quantum Theory to Other Parts of Natural Science.” He mentioned psychology but was less clear how his principle applied to “psychological phenomena” except with reference to the brain. However, 13 years before Heisenberg (2007), London (1945, p. 162) had written:

It is the purpose of this paper to demonstrate that the principle of indeterminacy as formulated for quantum theory is grossly inapplicable for psychology and that, in consequence, no matter what may be the

arguments in defense of the statistical approach to psychological problems, Heisenberg’s principle of indeterminacy may *not* be one of them.<sup>2</sup>

In part of footnote 2, London (p. 162) quoted Russell (1943, p. 249) who noted Max Born’s preference for the concept of a “principle of limited measurability” over the concept of the uncertainty principle. Max Born was a Nobel Laureate in quantum physics.

Here, the “principle of limited measurability” is also deemed more useful, although its roots in the uncertainty/indeterminacy principle remain relevant. Applying Heisenberg’s principle to behavioral science, one cannot know completely how the acts of observing and measuring influence the behavior or physiology of the human or nonhuman animals who are being observed and measured. Particularly applicable to animal cognition and behavior is the “Rosenthal effect.”

## The Rosenthal Effect

Based on previous research conducted by Rosenthal and colleagues, Rosenthal (1963) provided a general account in *American Scientist* of what came to be known as the *Rosenthal effect*. The following quotation summarizes the essence of the *Rosenthal effect*:

For many of the sciences there seems to be little danger that the act of observation itself may change the object of study. . . . [Rosenthal did not cite and may have been unaware of Heisenberg (2007).] For the behavioral sciences, however, where humans or animals may be the object of study, the act of observation may very well change the object of study. (Rosenthal 1963, p. 268)

Further, Rosenthal and colleagues had shown that *observer expectations* may affect the behavior of the observed; it is this aspect of observer effects that most think of when they refer to the *Rosenthal effect*.

**The Rosenthal effect in animal cognition research.** The classic example of the *Rosenthal effect* in animal cognition research is that of Clever Hans. Interestingly, Rosenthal wrote the Introduction to the 1965 republication of the classic, *Clever Hans (The Horse of Mr. von Osten)* by Oskar Pfungst (1911); Pfungst was an early German psychologist. Rosenthal’s Introduction

should be required reading for anyone who studies animal cognition and, especially, those who work in the presence of the animals being studied. It will be instructive to recall some of the more relevant details about Clever Hans. All information here about Clever Hans comes from Rosenthal's Introduction, except for the comment below about marginal cue detection.

Clever Hans was best known for foot tapping (see below) the answer required in response to "questions" usually in the form of visual cues (see photo of Clever Hans and Mr. von Osten, (Fig. 2)). Presumably, Hans could add, subtract, read, spell, and identify musical tones as long as the question could be answered with foot tapping. Mr. von Osten sincerely believed that Hans's performances were genuine, and he invited critics to observe as Hans performed.

According to Rosenthal in Pfungst (1965, p. x):

...on September 4, 1904, thirteen men risked their professional reputations by certifying that Hans was receiving no intentional cues from his owner of any other questioner...these men, included in their number, a psychologist, a physiologist, a veterinarian, the Director of the Berlin Zoo, and a circus manager...

To jump ahead in the Clever Hans story, psychologist Oskar Pfungst conducted extensive studies that failed to reveal the basis of Hans's performance. Only when he put a visual barrier between Mr. von Osten and Hans did Hans's performances fail. Mr. von Osten was emitting inadvertent cues

that informed Hans when to begin tapping his foot and when to stop tapping. Cues might be such as a slight forward lean of the head or body or other inadvertent slight movements, cues that were undetected by the 13 motivated human observers. There was never any basis to believe that Mr. von Osten was aware that he was cueing Hans. Furthermore, Pfungst found that 23 of 25 questioners in the place of Mr. von Osten also engaged in inadvertent cueing of which they were unaware.

Somewhat lost in this story is the amazing ability of Hans to detect such marginal cues that went undetected by human observers who were deliberately looking for them. Whether other horses or other animals possess such marginal cue detection skill is a question worthy of further investigation.

Given that the questioners were unaware that they were emitting inadvertent cues, one should question whether this applies to contemporary investigators whose research occurs in the presence of their animal subjects. Perhaps all who study animal cognition today are aware of the lessons of Clever Hans, but it is doubtful whether any investigator who works in the presence of the animals can avoid inadvertent cues. Beran (2012) provided a commendable commentary intended to remind contemporary researchers in animal cognition of the hazards of inadvertent cues.

**An effort to avoid Clever Hans cues in animal research.** Harry Harlow invented the Wisconsin General Testing Apparatus (WGTA; see

## Reductionism,

**Fig. 2** Clever Hans and Mr. von Osten



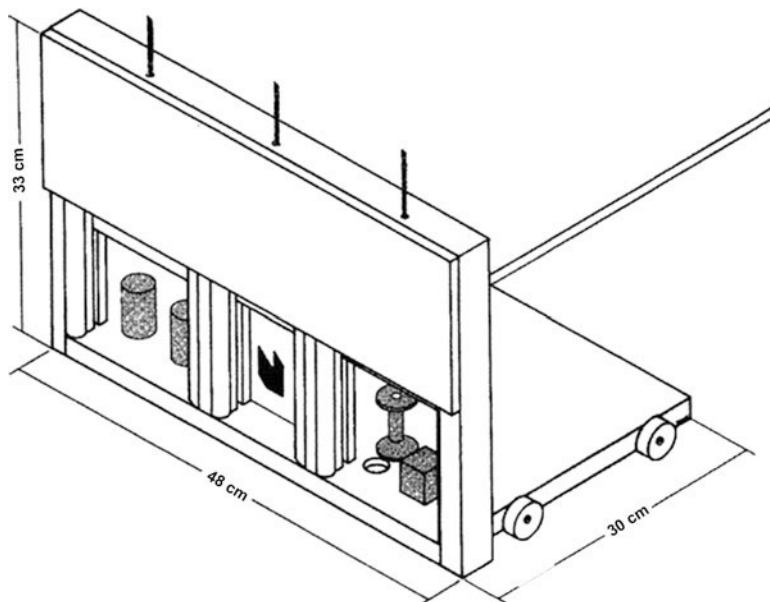
separate entry about the “► [Wisconsin General Test Apparatus](#)” in this encyclopedia) as a way to avoid Clever Hans cues. The WGTA is essentially an enclosed box, illuminated inside, and with guillotine doors at the front and back. With the front door closed to prevent the animal seeing the experimenter set up a problem involving discriminanda and food reinforcers, the experimenter sits behind the WGTA and raises the back door to set up the problem. After setting up the problem, the experimenter closes her/his door and raises the front door so the animal can see the discriminanda and make its response. Correct responses typically are reinforced with a bit of food that is typically located in a food well beneath the discriminanda, and responses are observed by the experimenter usually through a one-way mirror and, historically at least, recorded by hand. With nonhuman primates who are micro-nosmic, it seems unlikely they would smell the food and make their responses on that basis, but with macronosmic animals, such as rats, it is best to have food beneath all discriminanda while also

using some means to prevent access to the food beneath incorrect discriminanda (see Bailey and Thomas 1998; Thomas and Noble 1988).

Often the WGTAs will have a tray or cart on wheels on which discriminanda are presented that can be pushed toward the animal in order to place the tray with the discriminanda within reach of the animal. Consider the apparatus below (from Thomas 1993) where the cart was designed with three guillotine doors (Fig. 3).

For example, as the cart moved forward toward the subject, strings and pulleys might raise all three doors as shown here; there were other possibilities (see Thomas 1993 for further details). In the trial shown here, when a heptagon appeared in the center door, the “difference” pair of objects was correct, and the subject needed to move the difference-object nearest the center door to reveal the food well and its food reinforcer. Had a triangle appeared in the center door, the correct response was to the sameness pair of trial-unique discriminanda.

The main point is that Thomas was concerned that one might hesitate in pushing the cart forward if



**Reductionism, Fig. 3** Apparatus and representative discriminanda. Here a heptagon in the center door is the cue to choose the member of the difference-pair of objects nearest the center door where a food reinforcer is in the exposed food well. Had the center door revealed a triangle,

the triangle would be the cue to choose the member of the sameness-pair nearest the center door. Unique, sameness-difference pairs of objects were used on each trial, and their left-right positions were determined quasi-randomly. Other options were tested; see Thomas (1993)



the animal appeared to be moving toward the incorrect choice. This suggests that even the WGTA can be fallible to experimenter bias, and other examples, even inadvertent and unrecognized, might be cited to show how experimenter bias might occur using the WGTA. All that Thomas could do was to encourage his examiners to be consistent in how they advanced the cart on each trial.

## Reductionism and Explanation

Reductionism does not mean that a person cannot be a good scientist and also limit her/his research to a given level. For example, B. F. Skinner forcefully and effectively advocated throughout his career that behavioral science can be done meaningfully and well without reduction to, say, physiology, as long as it fulfills two of the defining goals of science, namely, prediction and control.

Most behavioral scientists conduct their research with little concern about what happens inside the organism. They are interested only in controlling the stimuli presented to the organism and measuring its responses with the goal of achieving the greatest degree of prediction and control that their research enables them to achieve.

A brief digression may be useful to distinguish between “stimuli” and “discriminanda.” Those who use “discriminanda,” such as objects or

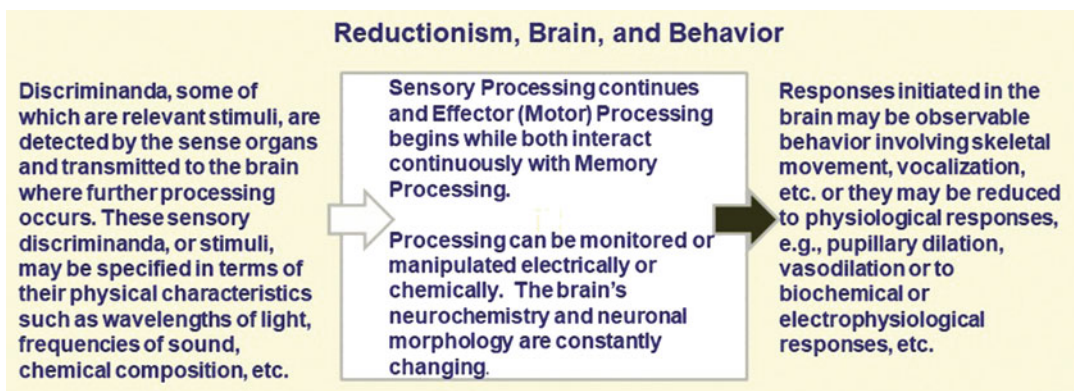
two-dimensional pictures or other representations, prefer “discriminanda” because a discriminandum may have several properties or features, and one may not always know to which feature a subject is responding. However, when one reduces the discriminanda to specific properties, such as, a 2,000 Hz versus a 5,000 Hz tone of equal loudness and duration, then it is appropriate to use the term “stimuli.”

The reductionist approach may be represented with a diagram such as Fig. 4. In Fig. 4, the focus is on the brain, but it is realized that other parts of the body are involved in behavior.

## Skinner’s View of Explanation Compared to a Reductionist’s Explanation

In Thomas’s commentary on Skinner’s article “Behaviorism at Fifty” (1963), Thomas (1988) quoted Skinner as follows:

An explanation is the demonstration of a functional relationship between behavior [responses] and manipulable or controllable variables [stimuli]. [Paragraph break] A different kind of explanation will arise when a physiology of behavior becomes available. It will fill the gaps between terminal events. ... It must be arrived at by independent observations and not by inference, or not by mentalistic constructions. (Thomas 1988, p. 650. Thomas’s commentary and Skinner’s response



**Reductionism, Fig. 4** Box representing and organism’s brain. Not shown here, but responses at one moment in time likely become part of the discriminanda in the next moment in time. Therefore, (a) the bases for inferences from observing discriminanda and responses as indicated

in the diagram are always changing, and (b) the exact meaning of behavioral concepts based on observations as indicated in the diagram also change, perhaps undetectably, from moment to moment

were reprinted in Catania & Harnad, 1988, with different page numbers, viz., 367–369)

Writing as a reductionist, the best explanation is equivalent to the best description together with conclusions related to prediction and control, and the more complete the description (e.g., via reductionism from behavior to physiology to neurochemistry, etc.), the better the explanation. The reductionist approach represented in Fig. 4 accomplishes the most complete description; therefore, the reductionist approach provides the best explanations. This author agrees with Skinner that, “It [explanation] must be arrived at by independent observations and not by inference, or not by mentalistic constructions.”

## Closing Remarks

Finally, Fig. 4, especially its Figure Legend, takes us back to earlier discussion here regarding limits on measurability as well as the involvement of uncertainty/indeterminacy. As indicated in the diagram and its legend, the neuronal morphology and the neurochemistry of the brain are continuously changing; therefore, what one observes, measures, and interprets at the behavioral level at one moment will change from moment to moment, even if unnoticeable or undetectable.

Such continuous changes in the organism and its behavior, together with the Rosenthal and Clever Hans effects, may appear to create a pessimistic perception of the future of behavioral science. However, all sciences are afflicted with uncertainties in observation and measurement, but most, including behavioral science, find sufficient constancy to obtain useful knowledge. This writer has sufficient confidence in the rabies vaccine that if he were to be bitten by a rabid animal, he would rely on the extremely high probability of the effectiveness of the rabies vaccine. This author is impressed by the high probabilities among the various sciences including behavioral science that enabled a human to walk on the moon, to place the Hubble telescope in outer space and enable it to send back observations and measurements that Galileo could only have dreamed, and to place to date (April 2019) the four rovers

*Sojourner, Opportunity, Spirit, and Curiosity* on Mars and design them to send back a wealth of information about Mars as well as to position themselves for optimal recharging of their batteries by the sun.

## Cross-References

- [B.F. Skinner](#)
- [Cognitivism](#)
- [Equine Sensory Systems](#)
- [Hermann von Helmholtz](#)
- [Johannes Müller](#)
- [Morgan's Canon](#)
- [Stimulus Control](#)
- [Wisconsin General Test Apparatus](#)

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## Reference Memory

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The term *reference memory* was originally introduced by Werner K. Honig (1978). He defined reference memory as long-term memory for associations between two or more stimuli or between responses and the stimuli that follow them. Reference memories were often formed by repeated trials using the same stimuli and ending in reinforcement. Thus, memory for a path through a maze or for a conditioned habit, behaviors long studied by comparative psychologists, were forms of reference memory. Reference memory was distinguished from *working memory*, memory for events that occurred once on a single trial and had to be remembered only for the duration of the trial.

In a highly cited article, Olton and Papas (1979) showed that both reference and working memory could be studied on the radial maze. Using a 17-arm maze, eight of the arms contained food on every trial, but the remaining nine arms were always empty. The rat's task was to enter all the baited arms and avoid entering the empty arms. Avoiding the empty arms required reference memory because the same arms were empty on every trial. Visits to the baited arms, however, required working memory. Once a rat visited a baited arm and consumed its reward, the rat had to remember for the duration of the trial that it had already visited that arm. Thus, revisits to working

memory arms were working memory errors, and visits to reference memory arms were reference memory errors. Olton and Papas found that fimbria-fornix lesions to the rat's hippocampus impaired working memory but had no effect on reference memory. This study sparked a number of subsequent experiments that examined the role of brain structures and pharmacological manipulations in reference and working memory on the radial maze.

The interaction of reference and working memory has also been examined in another popular procedure used to study memory in pigeons, delayed matching-to-sample. On each trial of a session, a pigeon is initially presented with a red or green sample stimulus on the center key of a three-key panel. The sample then disappears and after a few seconds, red and green stimuli appear on the side keys. Choice of the side key that matches the sample yields reinforcement, but choice of the nonmatching side key does not. Working memory for the sample is high at 90% or better accuracy immediately after seeing the sample but declines as the retention interval increases. Roberts, Strang, and Macpherson examined pigeons' performance in this delayed matching task after pigeons had learned a reference memory. Pigeons were initially given visual discrimination training in which they saw red and green side keys on each trial but were only reinforced for choosing the red key. After pigeons learned to always choose the red key (reference memory), they were tested on delayed matching with red and green sample stimuli. When working and reference memory were congruent (red sample stimulus), matching accuracy remained high over a 10-s retention interval. When working and reference memory were incongruent (green sample stimulus), the retention curve dropped rapidly from 90% matching on an immediate test to chance (50% matching) at a 10-s retention interval. This pattern of performance with the green sample was quite important because it showed that working memory initially controlled choice behavior. As working memory faded, however, reference memory emerged as the dominant memory system controlling choice behavior. A human analog of this effect is remembering a friend's new

phone number immediately after hearing it (working memory) but later calling the friend's old phone number (reference memory). Roberts et al. (2015) further showed that this interaction of memory systems can be strengthened or weakened by manipulations that vary the strength of reference or working memory.

Reference memory may also be distinguished from a more recently discovered form of long-term memory called *episodic memory*. Although reference memories are well-learned habits based on repeated reinforcement, episodic memory is the memory for specific past events experienced by an individual animal. Experiments with scrub jays (Clayton and Dickinson 1998), rats (Babb and Crystal 2005), and other species now indicate that animals remember the details of specific prior experiences. Specifically, they remember what event occurred, where it occurred, and when in time it occurred. As memory research in animals has proceeded, we have learned that the reference memory habits studied for many years are only one of several memory systems and that reference memory may influence and be influenced by these other memory systems.

## Cross-References

- ▶ [Delayed Match-to-Sample](#)
- ▶ [Episodic Memory](#)
- ▶ [Memory](#)
- ▶ [Radial Arm Maze](#)
- ▶ [Reinforcement](#)
- ▶ [Working Memory](#)

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## Referential Communication

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## Synonyms

[Arguments](#); [Conflicts](#); [Discussions](#)

Referential communication is defined as the interaction between signaler and receiver using referential signals that denote information about objects or events in the external environment. In humans, this typically corresponds to a mental representation in both parties and has been highlighted as an important element in the evolution of human language (Fitch 2010). In nonhuman animals (thereafter referred to as animals), the term of referential communication is used in a different way, as evidence for the relevant psychological states of mental representations is lacking, though the behavioral outcome appears to be comparable (Marler et al. 1992). To emphasize that while animal signals may function referential, but do not underlie the cognitive processes as in human communication, these signals have been called functionally referential (Macedonia and Evans 1993).

The prevailing text book example for functionally referential signals in animals are the different alarm call types used by vervet monkeys (*Chlorocebus aethiops*) that were described to show a distinct relationship to the appearance of specific types of predator types (Struhsaker 1967). Vervet monkeys produce structurally different alarm call types to terrestrial predators such as

leopards than to eagles in the air or snakes. Playbacks in the natural habitat of the monkeys were used to demonstrate that these different alarm call types elicit different predator-specific escape responses as if the real predator was approaching (Seyfarth et al. 1980a, b). The playback of a terrestrial alarm call results in receivers running into the tree, while an aerial alarm call drives them either into the next bush or the center of the tree if already sitting up, and the snake alarm call induces them to stand up bipedally and monitor the ground next to them. These findings of the production of predator-specific alarm calls have been confirmed in several other species, including nonprimate mammal and bird species (for recent reviews on mammals, see Townsend and Manser 2013, on birds Gill and Bierema 2013; Smith 2017). These studies all indicate that the structural variation between these alarm call types seem meaningful, as they are emitted in highly specific contexts to a certain predator type and enable the receivers to show the appropriate predator-specific escape response.

Highly context-specific signaling referring to external events have also been described in the context of animals encountering food (Clay et al. 2012). The first functionally referential signal described is the honeybee waggle dance (von Frisch 1974), which refers to the direction and in some species also the distance to the foraging patch. Chimpanzees (*Pan troglodytes*) (Slocombe and Zuberbühler 2006) and bonobos (*Pan paniscus*), as well as rhesus macaques (*Macaca mulatta*) (Hauser and Marler 1993), capuchin monkeys (*Cebus capucinus*) (Gros-Louis 2002) produce calls when finding food that are acoustically distinct depending on food quality or desirability. The description of the specific context showed that the likelihood to produce one food call type and not another in apes also varied between groups (Clay et al. 2012), and in capuchin monkeys, it depends very much on which individuals are close by as potential receivers (Gros-Louis 2002). Food calls are also described for ravens (*Corvus corax*), where they increased in their number of “haa” calls depending on their food preferences (Bugnyar et al. 2001). However, whether the receivers relate the variation in vocalizations to

the signaler’s perceived food quality has not been experimentally shown, although based on natural observations, these calls recruit other ravens to the location of the calling individual (Heinrich and Marzluff 1991).

## Defining Functional Referentiality

The model put forward by Macedonia and Evans (1993) defining functionally referential communication requires a high production specificity and a high perception specificity of the different alarm call types within a species. Call types can only be regarded as functionally referential, if two specific conditions are met: the call type must be produced in close association to a specific external event or object and the receivers must respond to the call type as if the stimuli was present. However, this does not imply what aspect of the external stimuli is responsible to induce the specific call type. For example, studies on referential alarm calls suggest that in some species, call types are associated with specific predator species (Gunnison’s prairie dogs (*Cynomys gunnisoni*) Slobodchikoff and Placer 2006), while in others they seem to refer to behavior of the predator (Siberian jay (Griesser 2008), and in most cases, it is not clear whether it is the spatial location (air versus ground) or aerial versus terrestrial approach (fast versus slow) the call refers to (e.g., meerkats, *Suricata suricatta*) (Manser 2001).

Recent studies provide evidence for the combination of meaningful, highly specific call types put into a sequence, whereby the combinations of the calls carry the meaning of the single call types. Thereby different types of sequences have been described depending on the combination of the two call types (recent review Collier et al. 2014). A first type is the use of an affixation system by Campbell monkeys (*Cercopithecus campbelli campbelli*) (Ouattara et al. 2009). They add an affix to both of their predator-type specific calls to produce new calls with a different meaning. The terrestrial alarm call with the additional suffix is given to any disturbance, while the aerial alarm call with the affix is given to any disturbance in the canopy. It seems the addition of the affix modifies the meaning of the predator type specific



calls into a less specific disturbance call in the according physical space indicated by the specificity of the predator type. The second type of meaningful sequences is the use of two predator-type specific calls, terrestrial and aerial calls, in combination, as described for putty-nosed monkeys (*Cercopithecus nictitans*) (Arnold and Zuberbühler 2006). The combination of the calls elicit movement of the calls, rather than the predator-type specific response given to each of the call types themselves. Different to the Campbell monkey combinations, here the meaning of the sequence seems not to derive from the meaning of the components. Recent studies on call sequences in animals have described the combinations of two meaningful call types; however, these are typically not based on functionally referential calls that seem to refer to an external event or object. Many call combinations have been described in the context of mobbing predators to recruit other group members to the caller (Suzuki et al. 2016), or in social context where calls are related to the behavior or the general context the caller experiences (Collier et al. 2014).

### The Level of Specificity on the Production and Perception Side

A recurrent pattern described is that typically the alarm calls to aerial predators are more specific to a narrow range of predators, and therefore more functionally referential, than alarm calls to terrestrial predators. For example, in lemurs (*Eulemur fulvus*), a distinct aerial call type refers specifically to hawks while terrestrial alarm calls given in response to fossa, dog, and baboon calls are also given to other disturbances (Fitchel and Kappeler 2002). A similar pattern is found in blue monkeys (*Cercopithecus mitis*) who emit pyows to an even broader array of stimuli including dog, snakes, motorcycle, civet, and baboons (Fuller 2014). There are at least three possible explanations for this recurring pattern. First, aerial alarm calls are typically of high urgency and require immediate responses. Receivers cannot afford the time to attend to any contextual information before responding. In contrast, terrestrial predators

typically approach at slower speeds which gives receivers more opportunities to gather additional contextual information and then respond. Second, animals may categorize the threat differently than us humans, and therefore we perceive the stimuli they respond to on a variation of terrestrial stimuli as broad, versus raptors to approach as a very clear defined narrow category. None of the studies so far published on functionally referential calls has thoroughly addressed this question, as it is a huge effort to determine how a species categorizes its environment (Townsend and Manser 2013; Zuberbühler and Neuman 2017).

We also find variation in the perception specificity of the receiver's response to the functional referential signals. Recent studies on different vervet monkey populations have shown that the response of receivers to the originally described functionally referential call types elicit qualitatively different responses for the same predator type call. Ducheminsky et al. (2014) showed in response to playbacks of alarm calls that receivers often looked first towards the speaker and either did not show escape behavior or delayed. This variation in receiver response across populations could indicate a lack of perception specificity, or it may reflect the fact that we find variation in the recipients depending on their own situation. If they are close to shelter, they may not have to run immediately but can take additional cues into account for their appropriate response. Diana monkeys respond to guinea fowl alarm calls with leopard alarm calls themselves, as if a leopard were present, but they remain silent when they seem to have a situation indicating that the guinea fowls calls were given to chimpanzee or humans, potentially hunting for the monkeys (Zuberbühler 2000). This has also been demonstrated in dwarf mongoose, where receivers take their own situation into account whether to respond and how fast and intense (Kern et al. 2017).

### Limitations of the Theoretical Framework

This variation in production and perception has recently brought up some criticism on the concept

of functional referentiality and its current definition (Wheeler and Fischer 2012). The basic argument is that any call type, whether highly context specific to the external environment of the signaler or referring to the signaler's behavioral state, conveys some referential information to the receiver. From this argument, the observed signals should be seen along a continuum rather than be divided into discrete categories, functionally referential versus other call types, in the past usually referred to as motivational signals expressing the behavioral context of the caller. Yet, the theoretical framework has hold up and seems to be helpful in stimulating new research (Scarantino and Clay 2015). Also, besides the specific information to the external event, it is likely any vocalization shows some variation relating to traits of the caller, such as indexical information or the intrinsic (motivational) state of the caller (Manser et al. 2002). One could then argue we should go along a multidimensional characterization of the signal structure, where referentiality could be identified for each of these different types of traits. For example, the individual signature conveying unique information on the identity of the caller, the expression of the motivational state reflecting the behavior of the caller, etc... (Manser 2016). The obvious difference here is that it is not referring to a stimuli in the external environment of the caller.

### **Selective Pressures on Evolving Functionally Referential Signals**

The evolution of referential signals in animals seems to vary depending on the context, whereby in all cases the need to provide accurate information on the external stimuli to enable the receiver to make the appropriate decision how to respond seems the driving factor. This is very obvious in the situation of the alarm call types in vervet monkeys and some other species, where different escape responses to the different predator types in a three-dimensional space are of benefit (Macedonia and Evans 1993). However, e.g., in meerkats, this seems not the full explanation, as the ground squirrel living in the same habitat do not use predator type specific

calls. Rather, the argument has been that social aspects to keep cohesion with the group may explain the need for functional referential calls (Furrer and Manser 2009). Even less clear are the selective pressures underlying food calls (Clay et al. 2012). While in alarm calls, the urgency aspect which does not allow to monitor for additional contextual cue due to time constraints seems logical, this does not apply on food calls. Here, rather social reasons, in particular the social structure of the group has been put forward as explanation, where finding high quality food and share it with group members may be linked to social rank and enhance the establishment of the reputation of the caller.

### **Nonvocal Functionally Referential Signals**

Referential signals in animals other than vocalizations include visual signals, such as the bee dance or gestures described for primates, birds, and potentially also fish (Smith 2017). Most research has been done on the acoustic modality, likely due to the difficulties in identifying and manipulating visual signals, and convincingly test whether the criteria for production and perception specificity apply. In the gesture studies in primates, the production of single gestures and also combinations of them is highly specific to an external stimuli (Hobaiter and Byrne 2014). In birds, they point with their body and head towards the predator and the other group members apply the same pointing position. This behavior has been suggested to meet the criteria for referential gestures, as the signal is directed towards the eliciting referent and seems ineffective for other purposes (Pika and Bugynar 2011). Whether the body vibration signal of the fish to recruit an eel to join the cooperative hunt (Vail et al. 2013) also fits the criteria of a functional referential signal is something to discuss (Smith 2017). Similar to the vocal recruitment calls in the bird studies, it may just represent the social recruitment for hunting together from the signaler side, while for the receiver it may refer to prey. These would then only be object specific on the receiver side but not on the production side (Seyfarth and Cheney 2003).

## Functionally Referential Signals and the Evolution of Human Language

An obvious approach, when trying to understand the evolution of human language, is the comparison to animal communication, and in particular identify and compare the underlying cognitive mechanisms. Zuberbühler and Neuman (2017) suggest that in humans at least three levels of information processes for the referential nature of human language need to be considered: (a) fulfill the criteria of functional referentiality with the production of distinct signals to specific external events or objects; (b) the signaler taking the nature and the composition of the audience into account; and (c) the ability of the signaler to take the knowledge of the audience into account. Over the last decades, empirical evidence in several animal species for the first aspect on the production of functionally referential signals has been convincingly accumulated, and in several circumstances, the signalers also seem to be aware of the nature of the audience and adjust their signaling accordingly. In contrast, only for chimpanzees, empirical evidence exists that animals are also able to take into account the knowledge state of the receiver (Crockford et al. 2012), while in human communication, all of the three cognitive processes seem to be present, often at the same time.

## Conclusions

The study of referential signals in animals still seems to be a useful theoretical framework for the understanding of the evolution of animal communication and human language. It has stimulated much research in identifying the underlying cognitive mechanisms involved in animal communication. The critical evaluation of the theoretical framework of referentiality in animals has helped to rethink and potentially in the future also to extend it in aspects that may advance the understanding of information processes involved in communication. The application of linguistic concepts can help to formulate new hypotheses but also needs to be applied with caution and any

conclusion need an objective evaluation of the existing empirical evidence in animal communication. To produce such evidence is challenging, as the according experiments in animals are difficult, in particular also to perform the correct control situations. We are still far away in understanding how animals categorize their environment, and therefore it is difficult to make unbiased interpretations of what information affects the signaler in the production of signals, and what information is of importance in the response of the receivers.

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## Reflection Symmetry

### ► Bilateral Symmetry

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## Reflex

### ► Unconditioned Response

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## Reflex Action

### ► Rooting Reflex

### ► Step Reflex

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## Reflex Arc

### ► Perception-Action Theory

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## Reflexes

### ► Innate Behaviors

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## Reform Darwinism

### ► Social Darwinism

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## Regional Primate Research Centers (RPRCs)

### ► Primate Research Centers

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## Regurgitation

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## Introduction

The upper part of the digestive system serves as the conduit for the passage of food from the area of ingestion to the stomach. There are two sphincters, in the upper and lower part of the esophagus, that regulate the entry of gastric contents. The opening of the lower esophageal sphincter (LES) is mediated by the vagal impulses. The sphincter, in routine conditions, is taut enough to prevent the reflux of digested contents into the esophagus. The absence of tautness leads to esophagitis, resulting in the “heartburn” sensation. In contrast to humans, in whom abnormal regurgitation leads

to disturbing symptoms, ruminants regularly present with the discharge of food into the esophagus (Dirksen 2002). In many cases, regurgitation is misdiagnosed as vomiting. But it should be taken into account that vomiting will always present with a period of restlessness and forceful exit of food from mouth or nose. Regurgitation is defined as the reflux of gastric contents into the esophagus for a defined period of 30 s or longer and associated with a decrease in esophageal pH to <4 (reflux of gastric acid). In many cases, regurgitation is misdiagnosed as vomiting. But it should be taken into account that vomiting will always present with a period of restlessness and forceful exit of food from mouth or nose.

## Mechanism for Regurgitation

There are several plausible mechanisms for regurgitation. First, regurgitated contents enter the esophagus because of phasic elevations in pressure developing as a result of contractions in the rumen (Colin 1871). This is found to increase with inspiration, which suggests that diaphragmatic contractions have a small role to play. Second, regurgitation may manifest as a result of decrease in intrathoracic pressure during inspiration against a closed glottis. This happens usually just before the forward passage of a food bolus (Touissant 1875). Finally, it may be that alternate shortening and contraction of longitudinal and circular muscles results in the fall of intraesophageal pressure. Subsequently, the esophagus becomes a cone-shaped infundibulum projecting to the cardia and the aspiration of contents (Wester 1926).

Carr et al. (1983) performed manometer-based recordings of the esophagus in sheep and observed variable patterns of contractile activity during eructation, regurgitation, and peristalsis. Eructation had small spurts of passive increase in pressure of 7–15 mmHg which caused the entry of gas into the esophagus. During regurgitation, contractions moved cranially and compared to the contractions observed during eructation, those observed during regurgitation were more intense and regular. While contractions of eructation terminated in the caudal part of the thoracic esophagus, regurgitation could be



documented in all parts of the esophagus. The differential pattern of contraction during eructation, regurgitation, and peristalsis could be attributed to the variations in the stimuli producing these. Thus, it could be hypothesized that regurgitation can be differentiated from other types of movements because the food contents travel in reverse direction in contrast to others.

The proportion of esophagus disposed in the abdominal cavity is one of the crucial factors in determining the chances of regurgitation in a particular species. In species where the esophagus is completely within the thoracic cavity, the chances of gastroesophageal reflux are comparatively higher (Pratschke et al. 2001). This can be attributed to the fact that the portion of esophagus in the abdominal cavity, by virtue of its shorter radius, develops greater pressure in accordance with Laplace law. Differential pressure generated over gastroesophageal junction helps in preventing the regurgitation (Pratschke et al. 2001). In support of this hypothesis, rats having two distinct elevated pressure regions in the upper gastrointestinal system along with a distinct abdominal part of esophagus lack the ability to vomit and seldom have chances of developing reflux (Soto et al. 1997). Thus, it can be postulated that distension of esophagus when food contents propel in a retrograde direction and in the absence of swallowing could initiate minimal propulsive esophageal contractions as well as relaxation of LES. These peristaltic contractions primarily serve to clear the esophagus of its refluxed contents and are referred as secondary peristalsis. These do not involve the conventional pathway encompassing the medullary swallowing center and are mostly mediated by localized nervous plexuses within the muscles comprising of non-adrenergic and non-cholinergic (NANC) nerve endings. Inhibition of NANC nerve endings causes sphincter relaxation. This can be observed when drugs such as ketamine and midazolam are administered for anaesthetizing dogs during surgical procedures (Kohjitani et al. 2005). It is interesting to note that the regurgitation phase of rumination in adult herbivorous animals shares the mechanism of vomiting (Watson 1941). Similarly, the resoesophageal groove reflex takes place in young

ruminants which helps them to bypass the primitive rumen. Thus, it is difficult to differentiate the regurgitation phase of rumination and vomiting which could plausibly be due to the shared neural coordination pathways for both acts.

Titchen (1979) observed the esophageal and diaphragmatic activity during regurgitation using electromyography and found the contraction of the lower esophagus developed about 2 s before the regurgitation act. Regurgitation was associated with inspiration which ceased the esophageal contraction. The inspiration was due to the contraction of the costal fibers of the diaphragm. The same hypothesis could be extended to understand why heavier dogs have higher risk of regurgitation. These dogs often have distorted proportion of thoracic cavities which could influence gastric pressure and the contractile activity of their diaphragms (Anand and Katz 2010). Yet another closely related condition with regurgitation is mega-esophagus which might either be congenital or acquired (Smith 2009). Here, the dilated part of esophagus is dysfunctional and gets filled with ingested contents, resulting in regurgitation (Smith 2009). Szczesniak et al. (2011) conducted a landmark study to decode esophagus-pharyngeal regurgitation in humans and found that a few salient features underlie the condition. First, most of the regurgitation episodes took place when subjects were upright. Second, a certain degree of upper esophageal relaxation preceded the regurgitation episodes, and these brief episodes of non-swallow-related relaxation could be considered as the pathognomonic mechanism of regurgitation. Finally, unless the relaxation happened, even significant amount of abdominal strain could not precipitate regurgitation.

## Regurgitation and Veterinary Practice

Regurgitation constitutes a significant issue during the surgical procedures in veterinary medical practice especially while administering anesthetic medication which would potentially relax the lower esophageal sphincter (Vlasin et al. 2004). In such situations, external compression offered

by diaphragmatic fibers fails in addition to the internal factor constituted by lower esophageal musculature. Acepromazine in particular is one of the pre-anesthetic medications that is associated with a 29% increased risk of gastroesophageal reflux because of the reduction in lower esophageal sphincter pressure (Wilson et al. 2005). However, these effects haven't been significantly documented in studies involving larger sample sizes and therefore the risk of developing reflux alone need not be taken as a stand-alone determinant while choosing the anesthetic agent.

To conclude, regurgitation is a normal phenomenon in ruminants and this might be coordinated by pathways in the medullary region, similar the pathways used to stimulate vomiting. However, there are also abnormal causes of regurgitation, stemming from anatomical obstruction in the esophagus. In such cases, a detailed examination along with possible diagnostics might help in planning the required management protocol.

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## Rehearsal

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## Synonyms

Central executive; Cognitive control; Working memory

Rehearsal is the effortful maintenance of information in working memory. For example, you

rehearse when you mentally repeat to yourself the name of somebody you just met, or the six items your spouse asked you to pick up at the market. Rehearsal, along with mental manipulation, is a characteristic process of working memory. Active working memory is most often contrasted with passive short-term memory, in which information continues to be available over short delays, but is not effortfully maintained.

In humans, rehearsal is most often studied using verbal or verbalizable stimuli and then takes the form of vocal or subvocal repetition. This vocal repetition is often called a “phonological loop” (Baddeley et al. 1998). Some of the many findings from research into human rehearsal are: Rehearsal allows the maintenance of information across an extended time, when otherwise that information would be rapidly lost. Rehearsal is cognitively effortful, in that cognitive distraction interrupts rehearsal and results in the loss of information from memory. Rehearsal is limited to a capacity of four to seven unrelated items. Rehearsal is domain dependent, in that distractors from the same domain will interfere with rehearsal more than distractors from another domain (e.g., rehearsal of numbers is more impaired by a numerical distraction task than an image distraction task).

In nonhuman animals, evidence for rehearsal is surprisingly mixed. First, it is difficult to infer rehearsal from nonhuman studies of working memory because the comparative literature has historically used the term working memory differently than in the human literature. In the human literature, working memory necessarily includes some type of effortful maintenance, such as rehearsal. In the comparative literature, working memory often refers to the operational definition of whatever memory the subject needs to remember for the current trial or session, such as a rat knowing which locations in a radial maze have already been searched today. This definition of working memory is contrasted with reference memory, which is the information the animal needs to apply to all sessions, such as a rat knowing the rule that food is sometimes hidden at the end of radial maze arms. Notably, the historical comparative definition does not specify any

psychological properties of working memory other than that it is used in the current session, meaning that many reports of working memory in nonhuman animals can be attributed to memory systems that do not rely on effortful rehearsal.

Outside of the comparative psychology literature, neuroscientific studies have a long history of attempting to measure the neural bases of rehearsal in nonhuman animals, usually monkeys, remembering items over short periods of time. In most of these studies, monkeys must remember an image or a spatial location over a short retention interval, sometimes while ignoring other images. Researchers then record electrical activity from different brain areas, such as the prefrontal cortex. The assumption of many of these studies is that monkeys are rehearsing. Consistent with this, researchers have found neurons in the brains of both monkeys and corvids that show persistent elevated activity over the retention interval, which has been interpreted as the neural signature of the animal effortfully keeping this information in working memory via rehearsal (Goldman-Rakic 1995; Hartmann et al. 2017). However, later behavioral investigations with monkeys revealed that humans and monkeys solved these tasks in different ways (Wittig et al. 2016). Humans overwhelmingly differentiated between to-be-remembered images from the current trial and those from previous trials, suggesting targeted rehearsal of specific items. Whereas monkeys indiscriminately remembered items from all trials, suggesting that monkeys were primarily judging items based on a decaying passive familiarity trace rather than using targeted rehearsal. Thus, persistent neural firing per se is not necessarily evidence of working memory and is difficult to interpret without behavioral validation.

A surprising number of behavioral studies have concluded that nonhuman animals either do not actively rehearse, or only rehearse under limited circumstances. Humans’ performance increases when they have more time to rehearse between items in a to-be-remembered list, but monkeys’ performance does not (Cook et al. 1991). Humans’ memory accuracy is decreased by a distractor task such that more involved distractor tasks decrease accuracy more, but

monkeys' accuracy is decreased by a set amount regardless of how involved the distractor task is (Washburn and Astur 1998). In pigeons, many of the putative demonstrations of directed forgetting, in which targeted rehearsal is inferred due to an accuracy increase for items that subjects are instructed to remember, were later shown to be task artifacts due to reward availability or surprise (Zentall et al. 1995). Furthermore, studies of single-neuron activity in pigeons performing these directed forgetting tasks were originally interpreted as reflecting sustained rehearsal activity, as in similar monkey studies, but later studies showed that the persistent neural activity over the retention interval was related to reward availability rather than stimulus maintenance (Browning et al. 2011).

Some studies have provided good evidence for rehearsal in nonhuman animals, but even these suggest that it is probably not the predominant strategy and likely occurs only under limited circumstances. In directed forgetting paradigms, pigeons and monkeys showed evidence of rehearsal that was not subject to the previous criticisms, but the narrow task parameters necessary to prevent subjects from using alternative strategies perhaps speak to how readily these species use working memory when not required (Tu and Hampton 2014; Zentall et al. 1995). In dual-task paradigms that present a second task during the retention interval, monkeys' decrement in memory accuracy scaled to the difficulty of the distraction task, but only if the to-be-remembered items were from a small set of familiar images (Basile and Hampton 2013). Similarly, monkeys showed robust primacy, the increased memory for initial list items that is sometimes due to rehearsal in humans, with small sets of familiar items but not large sets of unfamiliar items (Basile and Hampton 2010). In a direct comparison with humans, evidence of rehearsal in monkeys was limited to task conditions with small sets of stimuli or frequent distractor images, whereas humans showed evidence of rehearsal across most tests, even those for which active rehearsal was likely unnecessary (Wittig et al. 2016). In all these cases, when the task parameters did not pressure monkeys to rely on rehearsal, monkeys seemed to use

a passively decaying familiarity trace. Taken together, these studies indicate that some non-human species can rehearse under some circumstances; however, rehearsal appears to be the dominant memory strategy only in humans.

In summary, rehearsal is the effortful maintenance of information in working memory. It is often contrasted to passive short-term memory. Comparatively, the most-noticeable species difference appears to be that humans, but not non-humans, are predisposed to rehearse even when unnecessary, which may point to the unique utility of language in rehearsal. Surprisingly, much evidence suggests that nonhuman animals rarely rehearse. Nonetheless, there is good evidence that nonhuman animals do rehearse, but likely only in limited circumstances.

## Cross-References

- [Attention](#)
- [Delayed Match-to-Sample](#)
- [Divided Attention](#)
- [Familiarity](#)
- [Interference](#)
- [List Memory Effects \(Primacy and Recency\)](#)
- [Memory](#)
- [Recall](#)
- [Reference Memory](#)
- [Short-Term Memory](#)
- [Working Memory](#)

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## Reichstein's Substance H

### ► Corticosterone

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## Reinforcement

- Law of Effect
- Positive Reinforcement
- Schedules of Reinforcement

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## Related: Visual Senses

### ► Visual Perception

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## Relational Concepts and Symbolic Logic

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### Introduction

“Relational concepts” means different things to various investigators. Fortunately, any experimental task and procedure used by any animal research investigator can be reduced to the fundamental ways that Bourne (1970) and Thomas (1980) defined relational concepts. Bourne based all concepts on five basic logical operations and their complements, and he used tasks that were constructed consistently with the truth table that defined each of the five primary and complementary logical operations. Bourne referred to the five primary and complementary truth-table-based operations as “rules,” and that term will be used here as Bourne used it. In order from most basic to most complex and with the primary listed first and the complementary listed second here, the five basic pairs of rules are (a) affirmation and negation, (b) conjunctive and alternative denial, (c) inclusive disjunction and joint denial, (d) conditional and exclusion, and (e) biconditional and exclusive disjunctive.

Thomas (1980) drew heavily from Bourne (1970) and Gagné (1970), to construct a hierarchy of eight fundamental types of learning. Any and all learning tasks and procedures, no matter how complex, can be reduced to one of or combinations of the eight types in the hierarchy Thomas (1980) constructed; see Thomas (1996) and Bailey et al. (2007) for slight modifications to the 1980 hierarchy. The eight types and their levels in Thomas's hierarchy (1980) are (a) Level 1: Habituation and its opposite, Sensitization, (b) Level 2: Classical or Pavlovian Conditioning, (c) Level 3: S-R Learning also known as Operant Conditioning, (d) Level 4: Chaining of S-R units, (e) Level 5: Concurrent Discrimination Learning, (f) Level 6: Class Concepts, (g) Level 7: Relational Concepts I, and



(h) Level 8: Relational Concepts II. Following Gagné (1970), that the types of learning are hierarchical is based on lower levels being prerequisites for higher levels, although Thomas believes Levels 2 and 3 may be parallel levels.

Thomas (1980) mostly followed Gagné (1970) for the first five levels, but Gagné, an educational psychologist, focused his highest three levels on tasks (mostly verbal tasks) that were primarily used to study human learning and that were *mostly not usable* with animals. Thomas realized that he could base his highest three levels on Bourne's (1970) approach to concepts and that all of the tasks at Gagné's highest levels could be reduced to Bourne's three levels. Thus, Thomas identified Level 6: Class Concepts as based on Affirmation and Negation. Agreeing with Bourne that concepts based on Conjunctive, Disjunctive, and Conditional rules involved parallel operations, Thomas used them for Level 7: Relational Concepts I. Again, agreeing with Bourne, that Conditionals are prerequisites for Biconditionals, Thomas identified Level 8 as Relational Concepts II based on Biconditionals. *One or more Level 6: Class Concepts must be involved to construct tasks that assess Relational Concept use at Levels 7 and 8.* In most instances of problem-solving by an animal, whether in the laboratory or in its natural habitat, an animal might use several types of learning from Thomas's hierarchy serially and/or concurrently as the task solution requires.

## Class Concepts

To affirm a discriminandum as being an exemplar of a Class Concept, tasks must use trial-unique discriminanda, or if discriminanda are used more than once, evidence of concept learning must be limited to first-trial performances; otherwise, the animal might perform the tasks successfully by rote learning based on trial and error. Thomas (1980) distinguished between Absolute and Relative Class Concept use based on the operational difference that (a) to affirm a discriminandum as being an exemplar of an absolute class concept, the animal *need not compare discriminanda* but

(b) to affirm a discriminandum as being an exemplar of a relative class concept, the animal *must compare discriminanda*.

For example, if the concept of interest is "tree," and, among two or more discriminanda presented to the animal, one is obviously a tree and, if the animal *knows or learns* the concept (see quotation from Hayes and Nissen (1971, in the next paragraph) of "tree," *it need not compare other discriminanda* to affirm that each new exemplar of a tree is an example of the absolute class concept "tree." The most used example of a relative class concept in the animal learning/cognition literature has been the Oddity task. The most common method to study oddity is to present three discriminanda, two of which, the nonodd discriminanda, are identical, and the other discriminandum, the odd one, differs in color form and size from the nonodd discriminanda. To affirm the odd discriminandum, the animal *must compare* all discriminanda.

Before leaving this section, this is a good place to remind all who study use of class concepts by animals of what Hayes and Nissen's wrote in 1971.

We cannot imagine any set of operations, applied to any subject, that could detect a concept without at the same time operating to induce its formation. (Hayes and Nissen, 1971, p. 79)

After quoting Hayes and Nissen, Thomas and Ingram (1979, p. 42) added,

In other words, the acquisition of new concepts and the detection of existing concepts are hopelessly confounded with the subject's acquisition of the reinforcement contingencies, thus the distinction between newly learned and existing concept use is scientifically meaningless.

Most animal cognition investigators, including this writer, have tended to write about animals "learning" concepts when, as just shown, that cannot be known. However, that is not likely to be an easy habit to break. Hayes and Nissen's statement and Thomas and Ingram's addition *do not apply* to learning to use relational concepts. Relational concept learning requires using class concepts in relation to other discriminanda which may or may not be conceptual and then determining via experience (learning) over trials what that relationship is. One cannot imagine an animal

approaching such a task with a prior knowledge of the relationship being investigated. In other words, an animal cannot preemptively know that there is a relationship between, for example, “triangularity *and* sameness” or “*if* triangle, *then* sameness,” because the relationship contingency in a given test is determined arbitrarily by the experimenter, and it is the animal’s task to determine what it is.

**Uses of Some Relational Concepts Are So Far Unknown**

The complementary rules identified above and the biconditional apparently have never been investigated using nonhuman animals, so these six will not be considered further here. However, these are equally valid and may become relational concepts to be investigated by future animal researchers. Furthermore, it is doubtful whether any animal investigator using animals has determined whether disjunctive relational concepts that conform to the truth table has been determined conclusively; this will be discussed in the next section. Conjunctive and conditional concepts will be considered extensively in later sections.

**Disjunctive Relational Concepts**

Wells and Deffenbacher (1967) investigated the use of conjunctive and disjunctive concepts by squirrel monkeys, and there may be others unknown to this writer, but it is doubtful if any experiments have conformed to either of the two truth tables for the disjunctive (see below). Wells and Deffenbacher (1967) will be used to examine the issues. Wells and Deffenbacher used 81 discriminanda that varied in size (large, medium, small), shape (triangle, circle, square), color (green, yellow, blue), and patterns within a figure (cross, vertical stripes, cross-hatching). Apparently, these were two-dimensional figures pasted on “the face of” 2" × 2" wooden blocks. Their chosen attributes for the disjunctive were large-square and yellow-cross. There are two

types of Disjunctive; one is known as the Inclusive Disjunction (sometimes symbolized in a truth table as  $\vee$ ) and the other is known as the Exclusive Disjunctive (sometimes symbolized  $\neq$ ). Wells and Deffenbacher did not specify which they studied, but one can infer reasonably that they meant the Exclusive Disjunction, and that will be the one diagrammed below. Wells and Deffenbacher’s Exclusive Disjunction might be verbalized as “all patterns that are large-square or yellow-cross are correct exemplars.”

**Exclusive Disjunctive Truth Table Illustrated with Discriminanda**

| p                  | q                  | $p \neq q$  |
|--------------------|--------------------|-------------|
| T large square     | T yellow cross     | T correct   |
| T large square     | F not-yellow cross | T correct   |
| F not-large square | T yellow cross     | T correct   |
| F not large square | F not-yellow cross | F incorrect |

“ $\neq$ ” is the symbol for the exclusive disjunctive

Row 1 shows that any large-square discriminandum or any yellow-cross discriminandum when chosen by the monkeys is correct, while any other discriminanda are not. Row 2 shows that any large-square is correct, yellow-cross is not to be presented, and any other discriminandum there is incorrect. Row 3 shows that any yellow-cross is correct, red-square is not to be presented, and any other discriminandum is incorrect. It is not clear whether Wells and Deffenbacher’s procedures included trials that corresponded to row 4, namely to present discriminanda to the monkeys that are not a red-square or a yellow-cross to assess whether the monkeys made no choices on such trials. Assuming that was the case, their research regarding the Disjunctive is regarded here as inconclusive. Although it is unknown whether the truth table for the conjunctive was considered by Wells and Deffenbacher, their demonstration of monkeys’ use of a conjunctive rule might be valid. However, the way they reported the results leaves this writer unable to determine whether their squirrel monkeys might have learned the reinforcement contingencies for either or both the conjunctive or the disjunctive by rote.

## Misuse of the “Conditional Discrimination” Task

There is a long history of animals being tested on “conditional discrimination” problems and being misinterpreted as providing evidence of the use of a conditional rule. Paraphrasing French (1965), the basic conditional discrimination task involves a set of simultaneously presented discriminanda and a set of successively presented discriminanda; typically, two or more simultaneous discriminanda are used on each trial but only one successive discriminandum is used on each trial. Dozens or more experiments referred to as learning a conditional discrimination as French defined it have been used with animals and humans, but most successful performances can be attributed to rote learning based on trial and error.

An easy example might be to use a red block and a blue pyramid as the simultaneous discriminanda and white or black trays on which the simultaneous discriminanda are presented as the successive discriminanda. The experimenter determines the reinforcement contingencies and, for example, when the objects appear on the white tray, responses to the block might be correct, and when they are presented on the black tray, responses to the pyramid might be correct. There have been too many investigators to reference here (including this author earlier in his career) who interpreted the results of conditional discrimination testing as providing evidence for their subjects having used conditional rules such as “if the tray is white, then the red block is correct” or “if the tray is black, then the blue pyramid is correct” when the task was not constructed to meet the conditions of the truth table for use of a conditional rule and when the task might have been learned by rote.

Maier and Maier (1970) described conditional discrimination as a measure of concept learning. That might be correct in some cases (see two examples below), but most conditional discrimination tasks used with animals do not provide evidence of conceptual conditional discrimination; rather, they likely involved learning by rote. Interpreting such results as reflecting an animal’s use of a conditional rule is at best inconclusive and is most likely incorrect.

An early study using rhesus monkeys and a conditional discrimination task as French (1965) defined it was by Spaet and Harlow (1943). They did not use the term “conditional discrimination”; rather, they referred to their investigation as involving “multiple sign problems.” They administered two tasks. The simultaneous discriminanda in both tasks were the same three identical brass doorbell buttons (hereafter “button” for short) and same three identical T-shaped objects. The successive discriminanda were yellow or black trays on which the simultaneous discriminanda were presented. Spaet and Harlow’s (1943) first task involved oddity problems where a button or a T might be odd and two buttons or two Ts might be nonodd simultaneous discriminanda. If the oddity problem was presented on the yellow tray, the odd object, either the button or the T, was correct, and if the tray was black, either of the nonodd discriminanda, either of two buttons or two Ts, was correct. Food reinforcers were used for correct responses.

Spaet and Harlow were not clear whether the odd object might appear in the left (L), center (C), or right (R) positions versus only on the L or R right positions. If the L-C-R positions were used and, given that the same six simultaneous discriminanda were used, only six specific configurations of object presentations were possible. If only the L-R positions were used, only four specific configurations of object presentations were possible. With only four or six specific configurations, it is possible the monkeys learned the specific configurations by rote. For the second task, when three buttons appeared on the yellow tray, the correct choice was to the left-most button. When three Ts were presented on the yellow tray, the right-most T was correct. These contingencies were reversed on the black tray. With this task, only four specific configurations were possible. That the monkeys required from 4320 to 6840 trials to learn both tasks suggest that they learned the different configurations by rote. Nissen (1951) trained a chimpanzee on 16 concurrently presented conditional discrimination problems, and it took 15,796 trials to learn them. Nissen was unsure how the animal performed the task, but the following appear in his

discussion of how the chimpanzee, Frank, might have performed.

... it might be that each of the ... [discriminanda] ... was learned more or less independently (p. 14) [four paragraphs later]. It still remains possible, however, that Frank did become responsive to ... a principle but that its expression in overt behavior was obscured by prepotent effects on a "lower level." (p. 15)

Thomas and Kerr (1976) tested three squirrel monkeys on a task involving trial-unique oddity problems as the simultaneous discriminanda, and black or white trays on which to present the oddity problems as the successive discriminanda. Responses to the odd object were correct when an oddity problem was presented on a white tray and responses to either of the nonodd objects were correct when presented on a black tray. Given the use of trial-unique discriminanda, specific configuration learning was not possible. Correct responses resulted in a food reinforcer that was accessible from a food well beneath the correctly chosen discriminandum. Object positions and color of tray used on each trial were varied quasi-randomly. All three monkeys met a criterion of 90% correct responses in 20 successive trials. Thomas and Kerr concluded that the monkeys had demonstrated "conceptual conditional discrimination," which would be accurate if only "conditional discrimination" as defined by French (1965) was intended. However, Thomas and Kerr (1976) then made the mistake, as many others have done, when they interpreted their monkeys as having used a biconditional rule analogous to Bourne's (1970) humans subjects' use of a biconditional rule. Unrealized by them, Thomas and Kerr's task did not conform to the truth table for the biconditional or for the conditional.

### The Conjunctive-Conditional Conundrum

Thomas eventually realized that Thomas and Kerr's (1976) findings might be explained best by their monkeys using a conjunctive rule, as

their task was consistent with the truth table for the conjunctive. Nevertheless, even though their task did not conform to the truth table for the conditional, it remained possible that the monkeys were responding according to using a conditional rule; see more on this below.

Thomas's first opportunity to correct the record was in the discussion section of a study by Burdyn and Thomas (1984) who investigated "conditional discrimination" as French (1965) defined it. Burdyn and Thomas tested squirrel monkeys and conceptual simultaneous and conceptual successive discriminanda. Trial-unique exemplars of objects manifesting "sameness" or "difference" were used as the simultaneous discriminanda. The successive discriminanda were exemplars of "triangularity" and "heptagonality" (solid triangles and heptagons drawn on white cards); they used a sufficient number of these discriminanda to render rote memorization of specific triangles and heptagons unlikely. However, again like Thomas and Kerr (1976), while Burdyn's and Thomas's monkeys might have used a conditional rule, the experimental design conformed only to the truth table for a conjunctive rule.

Other investigators have reasoned erroneously that animals performed conditional discrimination tasks by means of propositional reasoning such as a conditional rule [e.g., chapter by Jerre Levy (pp. 157–173) and Terrence Deacon's first of two chapters (pp. 363–381) in Jerison and Jerison (1988)]. Levy and Deacon suggested the significant role that conditional discrimination had in the evolution of language. Levy (p. 164) cited animals' abilities for conditional discrimination as possibly representing "a preadaptation of the simian brain for the evolution of human propositional reasoning," and Deacon (p. 408) referred to the role of conditional discrimination learning in the evolutionary selection for "symbolic communication." Levy based her hypothesis on research by Dewson (e.g., 1977) and Deacon based his on research by Petrides (1987). However, the conditional discrimination experiments by Dewson and Petrides were amenable to rote learning. Dewson made no claims regarding propositional reasoning, but Petrides was clear in his belief that his experiments showed use of a conditional rule; specifically, he referred

to “if-then” reasoning when his task did not conform to the truth table for a conditional rule.

Bourne’s (1970) Fig. 1 (please see Bourne 1970, p. 548 for his Fig. 1) shows how human or animals (Bourne only studied humans) might partition nine discriminanda into correct and incorrect examples using conjunctive, disjunctive, conditional, or biconditional rules. In Bourne’s Fig. 1, there were nine discriminanda based on three colors and three shapes (square, triangle, and circle) where all shapes might be presented in one each of three colors. As his article was in a black and white print journal, “redness” (Bourne’s characterization) was represented when the square, circle, and triangle were drawn with stripes. The other two colors not named in Fig. 1 were represented as black-filled or white-filled squares, circles, and triangles. To illustrate correct versus incorrect partitioning according to conjunctive, disjunctive, conditional, and biconditional truth tables, Bourne used red and square as his focal attributes. These attributes will be the illustrative discriminanda in the truth tables for the conjunctive and the conditional below. The “&” symbol or the word “and” symbolize the conjunctive rule, so  $p \text{ \& } q$  is equivalent to saying “p and q.”

Conjunctive truth table illustrated with discriminanda

| p         | q            | p & q       |
|-----------|--------------|-------------|
| T red     | T square     | T correct   |
| T red     | F not-square | F incorrect |
| F not-red | T square     | F incorrect |
| F not-red | F not-square | F incorrect |

In partitioning, row 1 indicates a discriminandum must be red and square to be a correct exemplar. All other discriminanda are exemplars of incorrect discriminanda.

With the conditional, the “>” symbol or the words “if-then” symbolize the conjunctive rule, so  $p > q$  is equivalent to saying “if p, then q.”

Conditional truth table illustrated with discriminanda

| p         | q            | p > q       |
|-----------|--------------|-------------|
| T red     | T square     | T correct   |
| T red     | F not-square | F incorrect |
| F not-red | T square     | T correct   |
| F not-red | F not-square | T correct   |

In partitioning correct and incorrect discriminanda according to the conditional rule, row 1 shows discriminandum p must be red and discriminandum q must be square to be correct. Row 2 shows that if discriminandum p is red and discriminandum q is not-square, by implication the red triangle and the red circle are incorrect exemplars. Rows 3 and 4 where p is not-red shows there is no constraint against any not-red discriminanda being correct. This writer is unaware of any animal research purporting to study use of the conditional rule that has incorporated into its experimental design ways to test the contingencies in rows 3 and 4. This writer is not confident that a conditional-rule-use-experiment can be designed that could be used successfully with animals, but that is an open question.

Bourne’s (1970) Fig. 1 was for demonstration. His actual testing discriminanda included three colors (red, green, blue), three shapes (square, triangle, circle), three sizes (small, medium, large), and three variations in number; that is, 1, 2, or 3 discriminanda of a given color, shape, and size might be used. For each rule being tested (viz., conjunctive, disjunctive, conditional, or biconditional), the subject was handed a card specifying the pair of relevant attributes being used to partition whether each discriminandum was correct or incorrect. The subject had a two-button device, one for “Correct” and one for “Incorrect” discriminanda according to the rule being used. A light above each button would illuminate if the answer was correct. The subject had to infer the rule over several to many trials based on feedback from the lights whether her/his choice on each trial was correct or incorrect. The criterion for mastery of a given rule was 16 successive correct responses. Based on the number of trials needed to meet criterion, Bourne’s subjects revealed the following order of difficulty where < symbolizes fewer trials

$$\text{Conjunctive} < \text{Disjunctive} < \text{Conditional} < \text{Biconditional}$$

An important part of Bourne’s evidence was the subject’s explanation of the rule that was correctly inferred. Such evidence is not available to animal research investigators.



## Natural or Mental Logic Versus Symbolic or Standard Logic

It would be remiss to fail to consider the long-standing interest by many cognitive scientists in “natural logic” or “mental logic” as opposed to standard truth-table-based logic such as that used in Bourne’s research. Martin D. S. Braine (1926–1996) was among the best-known advocates for “natural” or “mental” logic. Earlier he used the phrase “natural logic” (Braine 1978), and later he preferred the phrase “mental logic” (Braine and O’Brien 1998; this was an edited volume published after Braine’s death in which Braine, O’Brien, and others contributed chapters. This literature is too vast and too complicated to summarize here, but relevant points pertaining to animal research are that (a) Braine and others used only human subjects and verbal tasks, usually in the form of providing the premise of a syllogism where the subjects provided the predicate that they conceived to be appropriate and (b) critical to the evidence were the subjects’ verbal explanations. Neither of those are possible with animals. Perhaps, the most important result of this research for animal researchers is that Braine and others concluded that humans can reason correctly, for example, according to a conditional rule without necessarily using tasks that conformed fully to truth table requirements for a conditional rule.

An important implication for animal research is that it is *possible* that when “conditional discrimination” tasks as defined by French (1965) that involve class concept discriminanda are performed successfully by animals, the animals *might* have used a conditional rule. However, it seems unlikely that tasks to confirm such with animals can ever be constructed. Therefore, unless someone can design an experiment using class concept discriminanda and procedures that conform to either disjunctive or conditional truth-table-based rules, the only conclusive evidence of relational concept learning by animals appears to be limited to using conjunctive rules.

Finally, one can do nothing more than speculate about what neural processes an animal might employ to use conjunctive rules successfully. Referring back to Burdyn’s and Thomas’s (1984)

evidence of squirrel monkeys using conceptual conjunctive rules, a human might verbalize externally or internally that “triangle *and* sameness” go together and that “heptagon *and* difference” go together. One can easily imagine a human verbalizing externally or internally the solution to the same task as “*if* triangle, *then* same” and “*if* heptagon, *then* difference.” A human can explain her/his conceptualization of the task, but unfortunately a monkey cannot. It is baffling to think how a monkey is able to perform a conjunctive task without having language to express it, even if only internally. Dr. Doolittle, we need you!

## Cross-References

- [Categorization](#)
- [Harry Harlow](#)
- [Intelligence](#)
- [Learning](#)
- [Oddity](#)
- [Problem-Solving](#)

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## Relational Learning

- [Transposition](#)

## Relational Matching

- [Analogical Reasoning](#)

## Relational Thinking

- [Analogical Reasoning](#)

## Relational Understanding

- [Oddity Learning in the Rat](#)

## Relationship Between Animal and environment

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## Relationship Between Perception and Action

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## Relationship Quality

- [Friendships in Animals](#)

## Relative Numerousness

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## Introduction

Stevens (1951, p. 22) distinguished between numerosity and numerousness. Numerosity referred to the determination of the cardinal number of a set of objects by counting, and numerousness referred to the determination of the cardinal number for a set of objects by a method other than counting. Stevens' distinction is used here, although many investigators do not, and they often use numerosity in instances where numerousness should be used.

## What is Counting?

Counting research involving children and non-human animals usually relies on whether the child or animal has met the requisite number of Gelman and Gallistel's (1978) five principles of counting. In order as listed, the five principles are:

1. Stable Order – say you have five apples, you must always count them in the same order (e.g., 1–2–3–4–5).
2. One-to One Correspondence – each object receives one and only one count. Gelman and Gallistel also wrote that “tagging” each object with a unique tag was a part of this principle (again, e.g., “1,” “2,” “3,” “4,” “5”).
3. Cardinality – the last tag correctly applied represents the quantity for that set of objects.
4. Abstraction – the ability to count any set of objects, e.g., apples, oranges, cows.
5. Order Irrelevance – using the example of five apples side by side. You may start at either end, in the middle, etc. but you must count each apple only once and end with the correct cardinal number of apples.

Most investigators, including Gelman and Gallistel, consider that if the first three principles are met, one has provided evidence that the child or animal can count.

In most animal research, it is questionable whether an animal has learned the necessary tags to be able to count. Perhaps, research from the laboratories of Sarah Boysen, Duane Rumbaugh, and Tetsuro Matsuzawa has come the closest; all studied chimpanzees. Most animal research associated with animals' use of number has not involved counting as no tagging system is used. An alternative process to counting that most animals likely use will be described below.

Interest in animals' use of number achieved prominence in the early twentieth century with well-known research on “Clever Hans,” the counting horse. Eventually, it was determined that Hans's apparently successful performances were based on inadvertent cues by his owner

and that gave birth to the need to prevent “Clever Hans cues” in animal learning and cognition research.

## Ecological Salience of Numerousness

James Lipton (1991) is a modern authority on nouns of assembly (e.g., a gaggle of geese, a colony of ants, a flock of sheep). Lipton reported that the earliest known list was *The Edgerton Manuscript* (circa 1450), and the best known of the early compilations was the *Book of Saint Albans* (1486). Most nouns of assembly were associated with game and domestic animals, but humans as well (e.g., a den of thieves). The history of nouns of assembly shows the long-time interest in the uncounted numerousness of animals. In some cases, a noun of assembly was shared by several species, such as “herd” or “flock.”

Numerousness has ecological salience for many animals. For example, the monkey in a group of monkeys feeding competitively that first detects several bushes of edible fruit is likely to go first to the bush perceived to hold the most fruit and, with clusters of fruit on a single bush, is likely to go for the cluster with the most fruit. A predator, such as a lion, that feeds on prey that depend on escape for defense such as wildebeests, will be more successful by attacking a large group, as it will be more likely to yield a young, weak, or lame wildebeest. Leopards that prey upon baboons will seek a smaller group to attack, as baboons in significant numbers are more likely to fend off the predator. The numbers of eggs and hatchlings for most nesting birds or the number of offspring for other animals giving multiparous birth likely find numerousness salient. Imagine the mother with multiple altricial offspring trying to keep an account of the proximity of her young. Of course, it seems unlikely that any of these animals meet Gelman and Gallistel's (1978) prerequisites for counting, especially that of having a “tagging system.” So what might they use to process number?

## Processes Used to Determine Numerousness

Davis and Perussé (1988) presented an ambitious glossary of numerical processes. In the following order, Davis and Perussé's glossary included (a) Relative numerousness judgments, (b) Subitizing, (c) Estimation, and (d) Counting, which they further divided into (e) Protocounting and (f) Concept of number.

Thomas and Lorden (1993) countered that only three types of numerical processes were necessary: (a) absolute numerousness judgments, (b) relative numerousness judgments, and (c) counting. See Thomas and Lorden (1993) for reasons why they disagreed with Davis and Perussé's glossary.

Absolute numerous judgments by squirrel monkeys were investigated by Thomas et al. (1980). They used cards with black-filled circles (hereafter "dots") and all the appropriate controls. After lengthy, intermingled stepwise training and testing, their two squirrel monkeys learned to discriminate seven from eight dots; one monkey discriminated eight from nine dots. Thus, both monkeys learned that "sevenness" was different from "eightness." The monkeys could not count the dots as they had no opportunity to learn a "tagging system" (see "[What is Counting?](#)" above).

With practice, humans may become adept at accurately and immediately perceiving as many as seven or eight dots. Thomas et al. (1999) showed that most humans tested could identify sevenness and eightness under conditions that prevented counting. A few were accurate with higher numbers. The upper limit may be related to G. A. Miller's well-known "magical number seven, plus or minus two," which Miller said specified the limits of unidimensional information processing; see discussion in Thomas et al. (1999).

Children and adults, especially in Western cultures, have considerable experience recognizing numerousness accurately without counting. Consider the number of dots on the six faces of dice used in many board games. Most will recognize the number of dots (1 – 6) on the top

face without counting, and if two dice are used, most will immediately perceive the sum of the dots on the two top faces. This ability can be acquired with less fixed patterns. For example, if you approach a bus stop with three people waiting, you will likely perceive "three" without counting them. If a group of four birds flew overhead, you will likely perceive "four" without counting. If you saw five sheep grazing, in a cluster, you will likely perceive "five" without counting, and when in doubt, one may easily count them. Go out and see for yourself whether you can immediately perceive low numbers of objects, animals, people in clusters, etc. without counting and whether with practice, as in the Thomas et al. (1999) study, you can learn to perceive as many as eight objects without counting.

Making relative numerous judgments without counting is usually easier if you do not need to know the exact numbers. For example, if driving along a country road, you see a small pasture on the left with 20 cows and, on the right, you see a similarly small pasture with 50 cows, you likely perceive immediately that there are more cows on the right. Smaller differences might be perceived immediately, say 20 versus 30 cows, but 20 versus 23 cows might require counting. Later, an experiment that investigated relative numerous judgments by squirrel monkeys will be described.

## Prototype Matching

Inspired by Rosch (1975), Thomas and Lorden (1993) proposed that accurate perception of numerousness is done by prototype matching. Among other semantic categories, Rosch used 53 species of birds (and the mammal, bat; see page 232) as examples of the category "Bird." For her American students, the best prototype of a bird was the American robin; the penguin and the bat were deemed to be farthest from the prototypical robin. Based on research by Thomas et al. (1980), Thomas and Lorden concluded that squirrel monkeys acquired prototypes

for as many as eight discriminanda. Thomas et al. (1999) extended that conclusion to humans.

## Conceptual Relative Numerousness Judgments

Apparently, the first published study using animals (three squirrel monkeys) to demonstrate the ability to make conceptual relative numerosness judgments was by Thomas and Chase (1980). Like Thomas et al. (1980), they also used “dot” cards as discriminanda, and they used all the appropriate controls. Three cards were presented on a platform. The monkey responded by pushing aside a card holder that exposed a food well. If it was correct, a food reinforcer (a currant) was easily accessible from the food well. On the front of the platform was a row of three 25-watt, neon panel lamps. If all lamps were illuminated, the correct response was to choose the card with the highest number of dots. If the two end lamps were illuminated, the correct response was to choose the card with the intermediate number of dots, and if only the single center lamp was illuminated, the correct response was to choose the card with the fewest dots. Position (left, center or right) of the card bearing the correct numerosness card was randomized.

Sixteen intermingled training and testing steps were used. In order, the most definitive steps were to learn to (a) choose the highest number when three lamps were on, (b) choose the intermediate number when two lamps were on, (c) choose between random presentations of highest and intermediate numbers according to the cue lights, (d) choose the lowest number when one lamp was on, and (f) choose among the highest, intermediate, and lowest dot-number cards presented in random order and consistent with the cue lights. One monkey succeeded on the final step; that is, it could choose correctly the card with the highest, intermediate, or lowest number of dots as cued by the lights. Another monkey was able to choose correctly between highest and intermediate numbers of dots presented randomly, but the third monkey learned only to choose the most dots. Nevertheless, all monkeys showed some

ability to respond to relative numerosness conceptually, and the best monkey’s performance indicated that it made ordinal judgments involving relative numerosness.

## Concluding Remarks

Animals including humans accurately identify as many as eight discriminanda without counting. They do this by acquiring prototypes (“fourness,” “eightness,” etc.) and applying them accurately. Relative numerosness is judged easily when two or more sets of discriminanda are sufficiently different in number and are distinctly clustered.

Because at least two squirrel monkeys in Thomas and Chase’s (1980) study learned to choose the intermediate-in-numerosness set of discriminanda when three sets (most, intermediate, and fewest) were presented concurrently, Thomas and Chase (1980) also concluded that squirrel monkeys learned “ordinal numerosness judgments,” a higher-order example of relative numerosness judgments.

However, subsequent researchers have not followed Thomas and Chase’s condition that ordinal judgments should be based on a minimum of three sets of numerosness discriminanda being presented concurrently, and some investigators refer to their animals having made “ordinal judgments” when only two sets of discriminanda were presented (e.g., Olthof et al. 1997, who tested squirrel monkeys; Washburn and Rumbaugh 1991, who tested rhesus monkeys).

However, Beran et al. (2005) conducted a clever experiment testing two chimpanzees and a rhesus monkey. They began their article by quoting Brannon’s (2002) definition of “ordinality.”

*Ordinality* refers to the relative position of one entity with respect to other entities in a sequence. . . an understanding of ordinality implies not only differentiating two sets of objects or symbols from each other but also knowing what set or symbol is numerically larger or smaller (Brannon 2002; Beran et al. 2005, p. 351).

However, Beran et al. went beyond Brannon’s definition and used five differently colored plastic



eggs, each covering a different number of identical food items. Initially, only two eggs were presented at a time, but eventually trials were presented with three, four or five eggs, and the primates were able to choose the eggs in the order that covered the most food items, the next-most, etc., which indicates that the primates had learned the optimal order of the egg-color, food-items relationship.

## Cross-References

- [Absolute Number Discrimination](#)
- [Cardinality](#)
- [Comparative Cognition](#)
- [Numerosity](#)
- [Predator Defense](#)
- [Prey](#)

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## Releaser Stimulus

- [Innate Releasing Mechanism](#)

## Remnant

- [Vestigial Organ](#)

## Remorse

- [Shame and Guilt](#)

## Repeat Sequences

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## Synonyms

[Endogenous retroviruses](#); [Long interspersed nuclear elements](#); [Repetitive elements](#); [Short](#)

interspersed nuclear elements; Transposable elements; Transposons

## Introduction

Nearly half of the human genome is comprised of repeat sequences. Once thought to be parasitic “junk” DNA, decades of research have revealed some of this repetitive sequence is under selection, and much of it is involved in biochemical activities (ENCODE 2012). Genomic repeat sequences can be divided into two large categories: noncoding tandem repeats (interstitial TTAGGG sequences or ITSs, and satellite DNAs) and transposable elements (including short interspersed nuclear elements or SINEs, long interspersed nuclear elements or LINES, long terminal repeats or LTRs, and DNA transposons) (Tomilin 2008).

There are numerous nuclear mechanisms in place to silence the mobility of transposable elements (TEs), and via genetic drift the majority of TEs have lost the ability to mobilize. However, there is growing evidence for exaptation of TEs as promoters/enhancers that drive expression of endogenous host genes. Some of these TE derived regulatory sequences are bound by tissue-specific transcription factors and are therefore likely to contribute to cell differentiation in embryo development.

Despite the many evolutionary adapted advantages, TEs still pose a threat for inducing or contributing to disease phenotypes. TEs can cause mutations from new insertions and lead to rearrangements of chromosomes. This in turn can lead to cancers, autoimmune disorders, and other diseases, many of which have been shown to have upregulated levels of TEs – the mechanisms that lead to this phenomenon are not well understood.

## Long Interspersed Nuclear Elements (LINES)

LINES are a class of retrotransposons that make up ~21% of the human genome. Full-length LINES are around 6000–7000 base pairs long, and functional LINES work by generating an mRNA that can be translated into a reverse

transcriptase (RT) protein. This protein then converts its RNA into DNA and integrates it into the genome at a new site; however, most LINES are now functionally inactive, at least in terms of the conventional RT pathway. There are three main classes – LINE1, LINE2, and LINE3 – of human LINES. A nontruncated LINE1 element contains two flanking untranslated regions (UTRs) and two open reading frames (ORFs). One of these ORFs contains the RT protein as well as an endonuclease able to cut open DNA (which is necessary for integration) (Rodić and Burns 2013).

Most genomic copies of LINES are inactive due to a 5' DNA truncation that cause a loss of the RNA polymerase II promoter located in LINES. In humans, however, LINES are still retrotranspositionally active in the germ line, with estimates of 1 new LINE insertion per 95 live births (Huang et al. 2012). Thus, there is a large amount of LINE1 polymorphism in the human population. LINES are also active in somatic cells, most notably in neural stem cells, which contributes to genetic mosaicism in the human brain. To prevent mobility, LINE1 elements are therefore silenced by various transcription factors, which in turn silences nearby genes and promote methylation in these areas. Subsequently, LINE1 elements are typically found in gene poor sections of the genome and are thought to contribute to the compartmentalization of the genome via the segregation of these silenced domains of genes. Other proposed functions of LINE1 elements include establishing a chromatin state for Xist to induce X chromosome inactivation (Chow et al. 2010), a binding site for various transcription factors that have both positive and negative regulatory effects, and acting as the nuclear machinery (the RT and endonuclease protein) for propagating short interspersed nuclear elements. LINE1 expression is also shown to be upregulated in human cancers and may be a useful marker for detecting cancers in the future (Rodić et al. 2014).

## Short Interspersed Nuclear Elements (SINEs)

SINEs are another type of retrotransposon – they make up around 13% of the genome. They are under 600 base pairs in size. As SINEs do not

translate into protein (they are only transcribed into RNA), they do not encode for RT or any endonuclease activity. SINEs are dependent on other TEs (usually LINE1 elements) to reintegrate into the genome. The Alu family of SINE elements is the most abundant retroelement in the human genome. Alu elements contain a 5' sense facing RNA polymerase III promoter, which is followed by an adenine rich region that is surrounded by repeats derived from initial insertion events. The 3' end of the sequence has a stretch of adenines and is variable in length (Batzer and Deininger 2002).

SINEs are derived from genes transcribed by RNA polymerase III (like transfer RNA). This, however, is not sufficient for initiating transcription – other neighboring sequences are necessary. SINEs have also been potentially linked as a mechanism for increasing genetic diversity as they act as sites for homologous recombination – this occurs due to their repeat regions.

Some SINEs contain binding sequences for transcription factors associated with higher order genomic organization, such as CTCF (Chuong et al. 2017). SINEs are highly enriched around “active” areas in the genome. Alu elements, like many SINEs, are found in gene-rich sections of the genome and specifically near promoters of active genes. Alu elements protect these active regions from the spread of DNA methylation; this phenomenon is tissue-specific, allowing for a mechanism to turn genes on and off (Batzer and Deininger 2002; Tomilin 2008).

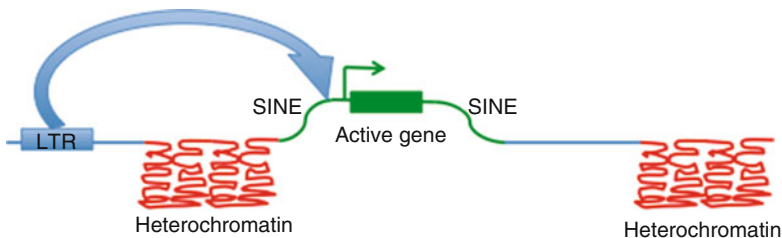
The role of SINEs is varied; from being boundaries for areas of active genes, to tissue-specific gene regulatory function, to hot spots for

recombination events, SINE elements have evolved to help organize genomic content.

## Long Terminal Repeats

Long terminal repeats (LTRs) are repetitive sequences found in the genome. They are derived from endogenous retroviruses (ERVs) although their modern structure is different. Together, ERVs and their remnant parts make up 8% of the genome. The traditional sequence of an integrated retrovirus, called a provirus, is a coding region comprised of the *Gag*, *Pol*, and *Env* genes (Yu et al. 2013). These are responsible for encoding the capsid (the protein structure that holds the genetic content), replicating the viral genetic content and integrating it into the host's genome, and the protein able to enter the host cell, respectively. Those genes are flanked by LTRs on either side, which contain promoter, enhancer, and polyA signals, and also help integrate the viral content into the genome. Most ERVs have undergone recombination between 5' and 3' LTRs during the course of evolution and lost the coding region, leaving primarily “solo” LTRs throughout the genome (Chuong et al. 2017).

These LTRs now act as promoters, enhancers, and poly adenylation sites for other genes. Many LTRs function in a tissue-specific capacity (via acting as transcription factor binding sites) and are most highly active during embryogenesis. Finally, LTRs can play a role in disease phenotypes (such as tumors) by regulating oncogenes or through recombination events (Yu et al. 2013) (Fig. 1).



**Repeat Sequences, Fig. 1** An example of repeat elements acting in a cis-regulatory fashion. Short interspersed nuclear elements (SINEs) are making boundaries around

an active gene, while a long terminal repeat (LTR) is acting as an enhancer

## DNA Transposons

DNA transposons are a type of repeat element that mobilize via a cut-and-paste mechanism, with only a DNA intermediate. DNA transposons encode a transposase protein, which is responsible for the movement of the gene (the cut-and-paste activity); some DNA transposons also are known for encoding genes not related to transposition. This protein coding sequence is flanked by terminal inverted repeats, which are needed for the insertion function of the transposase protein. The number of transposition events among members of a species can vary greatly. Over the course of time, this can lead to numerous evolutionary events. Thought to be drivers of evolution throughout different species, DNA transposons can undergo partial transposition events, which can cause large chromosomal rearrangements (Feschotte and Pritham 2007).

DNA transposons can alter the host genome in a number of ways, some unique from other retrotransposons. Obviously they can cause mutations by inserting into a gene, but they can also insert in promoters, introns, enhancers, and other genomic regions causing a myriad of epigenetic outcomes. Unlike other retrotransposons, DNA transposons can excise themselves and jump to nearby sites; therefore, some phenotypes are reversible. Due to the association of repressive histone marks, DNA transposons have also been linked as moveable pieces in silencing heterochromatin. Finally, DNA transposons have also been domesticated for a number of critical host functions, including the recombination-activating genes (RAGs), which mediate VDJ recombination, a process that increases the diversity in the immune system (Feschotte and Pritham 2007).

## Conclusion

At least 16% of conserved noncoding regions across mammalian genomes are found in transposable elements, indicating a key role in the evolution of gene regulation (Tomilin 2008). With nearly 48% of the genome made up of these repeat elements, it is unsurprising that they

have become a necessity to the genome. Many act as tissue-specific regulatory elements, either as promoters, enhancers, or boundary elements. Often they act in unison – LTRs and SINEs can contribute to a similar developmental gene networks, such as HPAT5 (an essential gene for inner cell mass development), a transcript made from an Alu SINE and an ERV (Chuong et al. 2017). While there is still much to learn about the role that repeat elements play in the genome, their generalized function as genomic organizers has become accepted by the larger scientific community.

## Cross-References

- [Centromere](#)
- [Chromatid](#)
- [DNA](#)
- [Embryo](#)
- [Exon](#)
- [Gene expression](#)
- [Genetic drift](#)
- [Protein](#)
- [RNA](#)
- [Simple sequence repeats](#)

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## Repeating Puzzle Box

► [Skinner Box](#)

## Repentance

► [Shame and Guilt](#)

## Repetitive Elements

► [Repeat Sequences](#)

## Replicating

► [Reproduction](#)

## Replication

► [Reproduction](#)

## Represent

► [Coding](#)

## Representation

► [Top-Down Processing](#)

## Reproduction

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## Synonyms

[Cloning](#); [Duplicating](#); [Duplication](#); [Replicating](#);  
[Replication](#)

## Definition

Reproduction is a process by which organisms replicate themselves. In a general sense, reproduction is one of the most important concepts in biology: it means making a copy, a likeness, and thereby providing for the continued existence of species. Although reproduction is often considered solely in terms of the production of offspring in animals and plants, the more general meaning has far greater significance to living organisms. To appreciate this fact, the origin of life and the evolution of organisms must be considered. One of the first characteristics of life that emerged in primeval times must have been the ability of some primitive chemical system to make copies of itself. At its lowest level, therefore, reproduction is chemical replication. As evolution progressed, cells of successively higher levels of complexity must have arisen, and it was



absolutely essential that they had the ability to make likenesses of themselves. In unicellular organisms, the ability of one cell to reproduce itself means the reproduction of a new individual; in multicellular organisms, however, it means growth and regeneration. Multicellular organisms also reproduce in the strict sense of the term – that is, they make copies of themselves in the form of offspring – but they do so in a variety of ways, many involving complex organs and elaborate hormonal mechanisms.

## Introduction

Reproduction is important for the survival of all living things. Without a mechanism for reproduction, life would come to an end. There are basically two types of reproduction in a broad sense, asexual and sexual reproduction. The term asexual reproduction refers to simple cell division that produces an exact duplicate of an organism (Billing et al. 1995). There are many different types of asexual reproduction which can be discussed to show students the variability of modes of reproduction. Some single-celled organisms reproduce by simple cell division – this is called binary fission. In this manner, the mother cell simply splits in half producing two daughter cells. Some cells reproduce by unequal division of the cells – this is called budding. In this process the bud forms as a knob on the mother cell. The nucleus divides, and identical parts go to the mother cell and the bud. The bud may grow until it is as large as the mother cell and can form buds of its own. In some cases buds remain attached to the mother cell. In others, they break away and live as separate organisms. On the other hand, sexual reproduction involves the joining of male and female sex cells. The sperm refers to the male sex cell, and the egg refers to the female sex cell.

## Reproduction Types

Living organisms reproduce in two ways – asexual and sexual reproduction.

### Asexual Reproduction

Asexual reproduction involves the production of an offspring from body parts other than the reproductive organs. It is a common process of reproduction in lower plants and animals.

The following are the basic features of asexual reproduction:

- (i) It involves only one organism, i.e., different sexes are not involved.
- (ii) The cell divisions during this type of reproduction are either mitotic or amitotic.
- (iii) New individuals produced are genetically identical to the single parent.
- (iv) It is a fast mode of multiplication.

There are different types.

#### Fission

Fission is of two types: binary fission and multiple fission. In binary fission, two individuals are formed from a single parent. This type of reproduction is found in organisms like bacteria, yeast, and amoeba.

#### Multiple Fission

In multiple fission, many individuals are formed from a single parent. This type of reproduction by multiple fission occurs during unfavorable conditions.

#### Budding

In this type of reproduction, a bulb-like projection or outgrowth arises from the parent body known as bud, which detaches and forms a new organism.

**Regeneration or Fragmentation** In this type of reproduction, the body of an individual breaks up into two or more parts, and each part develops into a complete individual, for example, *Spirogyra* and *Planaria*.

**Spore Formation** In lower forms of life like the alga, *Chlamydomonas*, the protoplast of the cell divides to form 4–8 spores. These being motile are termed as zoospores. When spores are released

in the surrounding medium, they develop into new plants.

**Vegetative Propagation or Vegetative Reproduction** Vegetative reproduction (or vegetative propagation) is a form of asexual reproduction in plants in which a bud grows and develops into a new plant. In this type of reproduction, any vegetative part of the plant body like leaf, stem, or root develops into a complete new plant. Vegetative reproduction can take place by two methods – natural and artificial.

### **Sexual Reproduction in Plants**

In flowering plants, the flower is the reproductive part of a plant. Most flowers have both male and female reproductive organs. They include pollination and fertilization.

## **Animal Reproduction**

### **Female Reproductive System**

The ovary, or female gonad, is the primary organ of reproduction in the female and is responsible for two basic functions: production of the female gamete and production of two primary reproductive hormones, estrogen and progesterone. For example, a cow has two bean-shaped ovaries that are around 3 cm long and are suspended from the broad ligament near the end of the oviducts. The size of the ovaries varies with the stage of the reproductive cycle and age of the female. The ovary consists of an inner part, the medulla, and an outer part, the cortex. The medulla part contains blood vessels, nerves, and connective tissue. The cortex part contains the germinal epithelium and produces the ovum by a cyclic process called oogenesis (Valerie 2006).

#### **The Ovary**

The ovary contains several thousand tiny structures called primary follicles. Each primary follicle consists of a germ cell surrounded by a layer of cells. This germ cell has the potential to mature into an ovum if the follicle completes development (known as the Graafian follicle). However,

most of the primary follicles never develop. Rather, they die and are absorbed by the ovary and replaced by newly formed primary follicles. So a cow will generally ovulate less than 100 since only one ovum is released at each cycle. By the injection of hormones, a cow can be induced to release more than one ovum at each estrous cycle. This technical is used in embryo transfer. After puberty a Graafian follicle is generally produced every 21 days until the cow becomes pregnant. The Graafian follicle can be palpated through the rectal wall. At maturity the ovum and follicular fluid are released from the ovary in the process called ovulation. After ovulation the wall of the follicle collapses and forms the corpus luteum, commonly referred to as CL or yellow body. The yellow body gets its name from its deep yellow color in the cow due to the presence of  $\beta$ -carotene.

#### **The Oviduct**

The oviduct begins as a funnel-shaped tube that engulfs the ovary. This funnel portion of the oviduct is called the infundibulum. When ovulation occurs, the ovum is picked up by the infundibulum and channeled into the oviduct (also called Fallopian tube), where fertilization takes place if viable sperm were present. The infundibulum has a fringed border, the fimbria, which helps to pick up the ovum from the ovary. Into the oviduct the ovum remains capable of fertilization for only a short time. Thus it is essential that sperm be present in the oviduct near the time of ovulation. The ovum moves through the oviduct into the uterine horn within the next three to four days. If the ovum is fertilized, it then begins embryological development; if not, it degenerates and disappears, and the next estrous cycle ensues.

#### **The Uterus**

The uterus consists of two parts, the body and horns. The uterus is suspended from the broad ligaments. The body of the uterus of the cow is short and poorly developed, while the uterine horns are relatively long and well developed. The developing of the fetus takes place in the

uterine horns. During most artificial insemination procedures, semen is placed in the body of the uterus. If semen is placed in the horn opposite the ovary from which the ovum was released, the chances of fertilization are very low.

### The Embryo

The fertilized embryo moves from the oviduct into the uterine horn, where fetal and maternal membrane development begins. This newly developing fetus grows within a layer of membranes called the placenta. There is no direct blood connection between the fetus and the dam but rather a complex system that selectively allows certain molecules to pass from the maternal side of the placenta to the fetal side and vice versa. It also provides nutrients and carries waste products from the fetus. The endometrium (lining) of the uterus becomes very vascular after fertilization, in preparation for the implantation of the fertilized ovum. The uterus develops the maternal side of the placenta to protect and nourish the developing fetus. The caruncles (about 100) of the uterine endometrium interlock with the cotyledons of the fetal placenta and provide a passageway for the nutrients from the cow to the fetus and for the waste products to be removed from the fetus. Villi of the embryonic cotyledons fit into crypts of the maternal caruncles to form placentomes, the functional units of exchange. The developing embryo sets up its own placental membranes, which consist of the chorion (outer membrane), the amnion, the yolk sac, and the allantois. The amnion contains a cavity that surrounds the embryo and becomes filled with liquid that serves as a protective cushion to the fetus. The yolk sac supplies nutrients to the fetus during early development but functions for only a short period of time. The chorion contains a rich source of blood vessels and gives rise to the cotyledons. The allantois is an outpouching of the hind gut of the fetus and serves as a urinary receptacle for the fetus.

### The Cervix

The cervix is a thick-walled structure about 10–11 cm long and 2.5–5 cm in diameter located between the uterine body and the vagina. In effect

the cervix is the neck of the uterus. The cervix contains ridges called annular folds. These folds must be manipulated through the wall of the rectum during artificial insemination in order to pass the insemination rod into the uterus. An opening in the cervix, through the annular folds, allows a passageway for sperm at mating (or insemination rod) and expulsion of the fetus at the time of birth. The cervix produces a mucus secretion that is usually thick; however this secretion is fluidized at the time of estrus to facilitate the movement of sperm to the uterus. This fluid can be seen as part of the discharge from the vulva at estrus. During pregnancy, the thick mucus secretion is called cervical plug, which protects the uterus from infections entering from the vagina. The cervical plug is expelled, and the cervical opening begins to dilate in the days prior to calving. So the major function of the cervix is to restrict access to the uterus. The cervix and its secretions thus form a physical barrier and protect the uterus against microorganisms (bacteria, virus) and other foreign material.

### The Vagina

The vagina, which is about 18 cm long and located between the cervix and the vulva, serves as a receptacle for the penis during service. In the cow, the semen is deposited in the vagina near the cervix during natural mating with the bull. When artificial insemination is used, the insemination rod is threaded through the vagina and cervix, and semen is deposited at the uterine side of the cervix. In addition, the vagina serves as a birth canal during parturition. The vaginal epithelium secretes fluids, which, along with the fluids of the cervix, inhibit growth of bacteria and thus provide a line of defense against bacteria invasion of the uterus. Urine is discharged from the urinary bladder through the urethra, which opens into the base of the vagina. The region behind the urethral opening is called the vestibule and is a common passageway for both the urinary and reproductive systems. Care must be taken during artificial insemination because the insemination rod can be introduced into the urethral opening. The vulva forms the external opening of the reproductive tract and consists of thickened folds of skin

(vaginal lips). The vulva is sensitive to changes in blood estrogen, which causes an increase in blood flow to the vulva and results in redness and swelling. These signs can be a help in estrus detection.

### Male Reproductive System

The primary organ of reproduction in the male is the testicles, of which the bull has two, as is the case in most animals. Secondary sex organs and three accessory sex glands are part of reproductive male tracts. All reproductive organs work in concert for formation, maturation, and transport of spermatozoa, which are eventually deposited in the female reproductive tract. The secondary sex organs are the epididymis, vas deferens, and penis. The three accessory sex glands include the seminal vesicles, prostate, and bulbourethral gland (Chakraborty et al. 2016).

#### The Testicles

The testicles are located outside the body cavity in the scrotum (external oval sac) and have two vital functions: producing the spermatozoa and producing the testosterone (male hormone). Location of the testicles exterior to the body cavity is essential for normal sperm formation, which occurs only at 1–4 °C cooler than body temperature. The scrotum provides physical protection to the testicle and helps regulate the temperature for optimum spermatozoa development. This regulation is done by coordination of three structures: a temperature-sensitive layer of muscle (tunica dartos) located in the walls of the scrotum, which relaxes when hot and contracts when cold; the external cremaster muscle within the spermatic cord, which controls the proximity of the testicle to the body by lengthening or shortening depending on environmental temperature; and a counter-current temperature exchange regulated by a blood flow process known as the pampiniform plexus, which is a coil of testicular veins that provide an effective mechanism for cooling arterial blood entering the testicle and transferring its heat to the venous blood leaving the testicle. One or both testicles occasionally fail to descend into the scrotum during embryological development and are retained in the body cavity.

This condition is known as cryptorchidism. Hormone production by cryptorchid males is near normal, and the male develops and behaves like a normal male however will generally be subfertile. This condition is genetically inherited; therefore such males should not be used for breeding. The seminiferous tubules are lined with germinal epithelium, the spermatogonia. The seminiferous tubes are formed by many long, tiny, coiled tubes, within which the sperm are produced and begin to mature. Specialized cells, known as Sertoli cells, localized in the seminiferous tubes are responsible to provide nutrients to the spermatozoa. Scattered throughout the loose connective tissue surrounding the seminiferous tubules are other kind of specialized cells, the interstitial cells of Leydig, which produce testosterone. There are hundreds of individual seminiferous tubules in the body of the testicle which unite with one another to form a few dozen tubules that exit from the testicle and pass into the epididymis (Guraya 1987).

#### The Epididymis

The epididymis is a compact, flat, elongated structure closely attached to one side of the testicle. It is divided into three regions, the head, body, and tail. The many tubules enter the head of the epididymis from the testicle and unite to form a single tubule. An epididymis bull has approximately 35 meters long, and this tubule is convoluted and packed into 18 cm. Four major functions occur in the epididymis, including the transport of the developing sperm cells from the testicle to the vas deferens; the concentration of the sperm by absorption of surplus fluids; the maturation of the developing spermatozoa; and the storage of viable sperm cells in the epididymis tail. If sexual activity is slowed, resorption of sperm cells from the epididymis tail occurs. The epididymis serves as an outlet for all the sperm produced in the testicle, and any blockage of this tube will cause sterility. Temporary blockage due to swelling following an injury or infection (epididymitis) will result in short-term infertility. If the swelling or infection results in formation of scar tissue in the tubule, it may permanently block the passage of sperm. If blockage occurs in both epididymides, the

bull will no longer be useful as a breeder. Surgical removal of the tail of the epididymis (epididymectomy) is frequently used as a means of sterilization for teaser (Gomer) bulls for estrus detection. Epididymectomized bulls will mate cows in the usual manner, because they still produce testosterone from cells of Leydig, however will not deposit sperm in the female reproductive tract.

#### The vas Deferens

The vas deferens, also known as ductus deferens, emerges from the tail of the epididymis as a straight tubule and passes as part of the spermatic cord through the inguinal ring into the body cavity. Spermatozoa are transported further along the reproductive tract to the pelvic region through the vas deferens by contraction of the smooth muscle tissue surrounding this tubule during ejaculation. Bulls may also be sterilized by vasectomy in which a section of the vas deferens is removed so that sperm cannot pass to urethra and go outside of the body. The urethra is a single tube that communicates with two vasa deferentia. Anatomically the urethra is the channel passing through the penis. The urethra serves as a common passageway for semen from the reproductive tract and urine from the urinary tract. As mentioned above, the bull has three sets of accessory glands. Semen is made up of fluids from the accessory glands and the sperm (mature spermatozoa). The volume of ejaculate is very variable, 1–15 ml. The concentration will also vary considerably; however the usual is 1–1.8 billion sperm per ml. Since only one sperm is required to fertilize an ovum, considerable dilution of the semen can be done.

Two of the accessory glands, the seminal vesicles and prostate, are located in the region where the vasa deferentia unite to become the urethra. Secretions from these glands make up most of the liquid portion of the semen. In addition, the secretions activate the sperm to become motile. The seminal vesicles consist of two lobes about 10 cm long in the bull, each connected to the urethra by a duct, which the main role is the production of nutrients for spermatozoa. The prostate gland is located at the neck of the urinary

bladder where it empties into the urethra. The prostate is relatively small in the bull, as compared to other species, and does not produce a very large volume secretion, which is rich in enzymes for spermatozoa metabolism.

The third accessory gland, the Cowper's glands, is small, firm glands located on either side of the urethra. The clear and buffered secretion that often drips from the penis during sexual excitement prior to service is largely produced by these glands and serves to flush and cleanse the urethra of any urine residue that may be harmful to spermatozoa. The secretion from Cowper's glands assures an optimizer pH for the semen. This is a protection against an eventual low pH of female reproductive tracts and pH decrease due the spermatozoa metabolism. One of the accessory glands may occasionally become infected, resulting in semen samples that are yellow and cloudy and which contain puss cells. It is not uncommon in bulls for the seminal vesicles to be so affected (seminal vesiculitis). Antibiotic treatment is sometimes necessary, but time will generally correct the problem.

#### The Penis

The penis of bulls has sigmoid flexure. This is an anatomical structure that provides a means by which the penis is held inside the sheath except during time of mate. Strong retractor muscles hold the penis in the "S"-shaped configuration. Occasionally these muscles are too weak to function properly, and a portion of the penis and sheath lining protrude at all times. This exposes the male to the danger of injury, and this characteristic should be avoided when selecting a herd bull. The penis is the organ of insemination. Spongy-type material within the penis is filled with blood during sexual arousal, resulting in erection of the organ. The end of the penis is the glans penis and is richly supplied nerves, which are stimulated during copulation to induce ejaculation. The normal functions of male reproduction are largely controlled by hormones that are secreted from the endocrine glands. The testicle functions as an endocrine gland because of its production of the male hormone, testosterone, by the interstitial cells (cells of Leydig). The



major functions of testosterone are as follows: It is largely responsible for development and maintenance of the male reproductive tract; it causes the development and maintenance of the secondary sex characteristics associated with masculinity, such as the crest and heavily muscled shoulders of a bull; it is a major factor in the normal sex drive and behavior of the male; it increases muscular and skeletal growth; and it is essential for normal sperm formation. The same gonadotropic hormones that regulate ovarian functions in the cow also regulate testicular functions in the bull. LH and FSH are released from the pituitary gland and cause the testicle to secrete testosterone, which then acts on the germ cell lining of the seminiferous tubules to stimulate formation of primordial sperm cells (Chandra and Chakraborty 2017). The maturation of spermatids into fully developed sperm cells requires the presence of FSH. Normal functioning of the male accessory glands requires testosterone. Not only is hormone production of the testicle regulated by hormones released by the anterior pituitary, but the reverse is also true. The level of testosterone in the blood regulates the secretion of gonadotropic hormones from the anterior pituitary via a feedback system. A proper balance of all hormones is vital to successful reproductive functions.

## Conclusion

Reproduction is the basis of life, and this chapter provides a thorough understanding of all the basic and applied aspects of reproductive physiology ranging from plants to higher mammals.

## Cross-References

- [Bear Life History](#)
- [Catarrhine Life History](#)
- [Feline Life History](#)
- [Lagomorpha Life History](#)
- [Orgasm](#)
- [Ovaries](#)
- [Passerine Life History](#)

- [Puberty](#)
- [Reproduction](#)
- [Sex Differences](#)
- [Spawning](#)
- [Zygote](#)

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## Reproductive Cell

- [Gametes](#)

## Reproductive Fitness

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## Synonyms

Reproductive success

## Definition

Reproductive fitness reflects the ability of an individual to pass on its genes to the subsequent generations (Kosova et al. 2010).

## Survival of the Fittest

Every species has two major aims: food and reproduction. Food availability and reproduction are so intricately linked that a number of species chose their breeding season according to the food availability. As soon as food is secured, reproduction is the next aim to ensure survival of the species. The term **survival of the fittest** is one of the most prophetic ideas, originally coined by Herbert Spencer after reading Charles Darwin's work. It gained more popularity when Darwin used it in the fifth edition (published in 1869) of the book, *On the Origin of Species*. Survival of the fittest is basically an interchangeable expression to Darwin's "natural selection." The phrase suggested that the organisms that are best acclimatized to their environment are most efficacious in survival and reproduction. However, this glib term often obscures a more precise explanation of evolution. In terms of evolution, "fitness" simply corresponds to the **reproductive success** and reflects how well an organism is adapted to its environment. In other words, it also describes the genetic contribution of an individual to the future generations (Zietsch et al. 2014). Thus, in the evolutionary theory, fitness is a shorthand for "ability to survive and reproduce" (Hansen 2018). The reproductive fitness reflects the potential of an individual to pass on its genes to the subsequent generations. Fitness traits, also referred to as the life-history traits, integrate measures of fertility and mortality and are intricate phenotypes that are direct targets of Darwinian selection (Kosova et al. 2010).

## Absolute and Relative Fitness

There are different ways in which fitness can be measured; for example, **absolute fitness** basically

measures the number of offsprings contributed to the next generation. Absolute fitness is ascribed to a genotype's expected total fitness. Relative fitness is rather a comparative term and is an indication of an allele's or genotype's fitness compared to the maximum fitness. Therefore, **relative fitness** measures differential reproductive success. The term "differential reproductive success" often in statistical terms refers to the comparison of successful reproduction rates between various individual members or groups within generations of a species. If there are two groups, with each group having different variations of the same trait, then determining the differential reproductive success rate will provide an indication of the "fittest" group among them.

Let us understand it with the help of an example; suppose, there are two variants, X and Y, of the same trait. Variation X of a trait reaches the reproductive age more frequently and produces more number of offsprings than variation Y, then estimation of differential reproductive success rate means that variation X is able to dispense more of the genetic material to the next generation and has a greater potential to preserve and deliver it to the future generations. Quite the reverse, variation Y will be more liable to gradually disappear.

Here, it is important to note that the natural selection operates by differential reproductive success of individuals and if the characters that affect reproductive success are not heritable, evolution will no longer occur. Besides, the process of natural selection entails that genotypes must differ in fitness. Without variances in fitness, natural selection cannot act and adaptation cannot ensue (Orr 2009). Furthermore, a longer life span is favored by the natural selection, only if it brings higher reproductive success rate. For example, if a short-lived cat leaves more descendants than a long-lived cat, its genes will spread faster and will be favored by the natural selection. Since reproduction is at the core of propagation and vertical transmission of the genetic material, fitness generally refers to the reproductive fitness and every other fitness has no meaning in the evolutionary terms if it does not correlate with the reproductive fitness.

## Cross-References

- [Fitness](#)
- [Natural Selection](#)

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## Reproductive Output

- [Fecundity](#)

## Reproductive Potential

- [Fecundity](#)

## Reproductive Strategies

- [Mustelidae Life History](#)

## Reproductive Success

- [Reproductive Fitness](#)

## Reproductive Suppression

- [Bruce Effect](#)

## Reproductive Synchrony

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## Synonyms

[Synchronized reproduction](#)

## Definition

The temporal clustering of reproductive events (mating, spawning, and/or births) among individuals in a population, colony, or social group.

## Description

Reproductive synchrony is widespread in plant and animal populations, encompassing phenomena as varied as the mass emergence of periodical cicadas, the colonial nesting of seabirds, and the synchronized menstrual cycles of female roommates. In its most straightforward form, synchrony may arise simply as an adaptive consequence of seasonality in climate or resources, since selection should favor individuals that produce young during advantageous conditions. Changes in photoperiod are thought to be the primary trigger for seasonal reproduction in terrestrial environments, often in combination with shorter-term cues such as food availability, rainfall, and temperature. However, as Ims (1990a, b) pointed out in a pair of seminal reviews, many instances of reproductive synchrony cannot be explained by seasonality alone, and these have inspired several alternative (and non-mutually exclusive) hypotheses for the selective pressures favoring reproductive synchrony, as well as its underlying proximate cues and physiological mechanisms.

One of the earliest and most powerful hypotheses for the evolution of reproductive synchrony

was proposed by Fraser Darling (1938), who found that the degree of nesting synchrony increased with colony size in herring gulls (*Larus argentatus*) and posited that synchronous nesting might increase individual offspring survival by reducing the per capita predation rate (the *predator swamping* or *predator satiation* hypothesis). There is widespread support for this hypothesis in the literature, and predation is now thought to be an important driver of reproductive synchrony in (for example) swarm emergences of aquatic insects, larval release of crabs and other marine organisms, and nesting aggregations of female ridley sea turtles (*Lepidochelys* spp.; Sweeney and Vannote 1982). In these examples, the selective advantage of predator satiation likely occurs at short timescales (within a single breeding season) and local spatial scales (within a single swarm or colony), simply as a consequence of safety in numbers. However, predator satiation has also been proposed as a potential driver of reproductive synchrony over larger spatial and temporal scales, as in the multi-year periodical emergences of cicadas (*Magicicada* spp.) and, in plants, the synchronized seed crops of masting trees and the mass flowering of bamboos (Kelly 1994). These examples are striking because cycles occur at the landscape scale – among geographically dispersed individuals in the population – and over remarkably long timescales (up to 17 years in cicadas, <10 years in most mast-seeding tree species, and up to 120 years in some bamboos). Clearly, predator satiation is only one of several factors influencing the evolution of these unusual life histories, and the selective pressures driving community-level synchrony are still under debate.

For species that defend their young, a secondary advantage to reproductive synchrony is efficient collective defense of spatially clumped broods (the *predator defense* hypothesis, Robinson 1985). Predator defense and predator satiation both predict that asynchronously produced offspring should suffer higher rates of predation, so it has been difficult to empirically distinguish between these two hypotheses. However, the coordinated defensive behaviors of many group-living animals – such as the remarkable

protective circles of female muskoxen around their calves and the collective mobbing behavior of colonially nesting seabirds – suggest that predator defense can be an important benefit of synchrony in some taxa.

*Mate availability* has also been proposed to influence the evolution of reproductive synchrony, but the direction of the correlation is conditional on the life history, population sex ratio, and mating system of the species in question. Emlen and Oring (1977) proposed that if mating opportunities are limited – for example, due to a biased sex ratio or widely dispersed individuals of the opposite sex – this should favor asynchronous reproduction. However, this prediction assumes that courtship and mating are time-consuming and is most relevant for species with some degree of biparental investment in the offspring. Most of the support for this hypothesis comes from studies of birds and mammals examining the covariation of synchrony and sex ratio within the same species. In promiscuous species lacking paternal care, by contrast, limited mate availability has been proposed to favor synchronized reproduction, particularly when individuals are short-lived and have few opportunities for reproduction. This pattern is best illustrated in the mass mating flights of ants (Hymenoptera), mayflies (Ephemeroptera), and other insects, in which locally high densities of receptive mates are thought to increase the odds of reproduction for individuals of both sexes. The hypothesis that simultaneous flowering in mast-seeding trees has evolved in order to maximize the chances of successful wind pollination is essentially the same concept applied to plants. In mast-seeding trees and swarming insects, both predator satiation and increased reproductive opportunities (via mating flights or wind pollination) likely favor synchrony, but the relative importance of the two factors is much debated (Kelly 1994).

Finally, *communal breeding* in animals also imposes strong selection for reproductive synchrony within social groups, albeit at smaller scales than the selective pressures discussed above. Since communally breeding females produce offspring together and provide cooperative care to the mixed brood of young, reproductive

synchrony is favored both by selection for group-level traits that increase the individual fitness of all breeders, such as efficient care of the communal brood, but also by competition between offspring in the brood. Young that are born after the majority of the brood may be at a competitive disadvantage, whereas young that are born early may be the target of aggression by group members that have not yet bred, favoring offspring that are produced synchronously (Riehl 2016). Reproductive synchrony is required for successful reproduction when the offspring must be gestated simultaneously (e.g., in communally nesting birds that produce a joint clutch) and enables alloparental lactation in socially breeding mammals. In many animals, including group-living birds, primates, felids, equids, and pinnipeds, synchronous reproduction has also been proposed as an adaptive strategy by females to avoid infanticide by males or by non-reproductive females within the social group, or as a nonadaptive consequence of cyclical takeovers by extra-group males (Gilchrist 2006).

*Proximate mechanisms* coordinating synchronized reproduction include both environmental and social cues. Seasonality in climate, leading to relatively predictable fluctuations in resources, synchronizes reproduction on broad scales in most animal populations. These physiological rhythms are largely under endogenous control, entrained by proximate environmental cues like photoperiod and temperature. In marine animals, including polychaetes, crustaceans, echinoderms, corals, and sponges (among others), synchronized gamete and larval release are also thought to be under endogenous control, with proximate entrainment by lunar, tidal, and light-dark cycles (Morgan and Christy 1995). By contrast, water temperature appears to be the salient trigger for mass emergences in freshwater aquatic insects in temperate regions, sometimes in concert with lunar cycling (Corbet 1964). Synchrony over multi-season timescales, such as the supra-annual reproduction of periodical cicadas and bamboos discussed above, is thought to be almost wholly dependent on endogenous rhythms, but little is known about the genetic or physiological underpinnings of these rhythms.

In social and colonial animals, local reproductive synchrony within the breeding season is often coordinated by behavioral cues, mediated through neuroendocrine pathways. Fraser Darling (1938) hypothesized that the positive correlation between colony size and reproductive synchrony in herring gulls was due to the visual and auditory stimulation of individuals coming into reproductive condition in close proximity, a type of social stimulation often referred to as the Darling or Fraser Darling effect.

## Cross-References

- Colonial Nesting
- Communal Behavior
- Predator Defense
- Predation Risk
- Reproduction
- Reproductive Fitness

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## Reproductive System

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## Synonyms

Genital system

## Definition

Reproductive system is the system of organs and its parts which are helping in reproduction and production of live offspring.

## Introduction

Reproductive system consists of male and female reproductive system. The male reproductive system consists of testes, vas deferens, seminal vesicles, ejaculatory ducts, prostate, and external genitalia. The female reproductive system comprises ovaries, uterine tubes, uterus, vagina, and external genitalia.

## Male Reproductive System

### Testis and Epididymis

The testes are a pair of ovoid organ which are suspended in the scrotum by the corresponding spermatic cord. In adult, their length = 4–5 cm, breadth = 2–3 cm, anteroposterior diameter = 3–4 cm, weight 12–20 g, and their average testicular volume = 15–25 ml (Standring 2016).

The testicular volume gradually increases in age 11–30 years and then remains constant between ages 30 and 60 years. But later, beyond 60 years of age, the testicular volume decreases slowly. The volume of the testis was found 31% smaller in men >75 years in comparison to those between 18 and 40 years of age (Gunes et al. 2016). These age-related changes in testes cause decrease in number of Leydig cells which is responsible for the increase of the follicle-stimulating hormone concentration and lower serum free testosterone (Mahmoud et al. 2003).

Left testis usually lies about 1 cm below the right testis. Each testis is covered by three layer from outer to inner side: (1) visceral layer of tunica vaginalis, (2) tunica albuginea, and (3) Tunica vasculosa (Datta 2010). Normally, there is a potential space between the visceral and parietal layer of tunica vaginalis which is filled by capillary straw coloured fluid. But, in certain conditions like inflammation, trauma, and tumour of testes, this thin film fluid can increase due to obstruction in lymphatic drainage and this condition is known as hydrocele (Standring 2016). Tunica albuginea forms mediastinum of testes interiorly which give rise to fibrous septa and divides the interior of testis into 250 lobules. Each lobule of testis contains one to four seminiferous tubules which is the site of spermatogenesis (Pawlina 2016). Normal spermatogenesis requires 3–4 °C lower temperature than abdominal cavity temperature. This lower temperature maintained by counter-current heat exchange system between pampiniform plexus and testicular arteries branches (Snell 2017).

The seminiferous tubules open into rete testis and rete testes communicates with upper end of epididymis through efferent ductules. The epididymis is comma-shaped structure overlying the superior posterolateral surface of the testis. Laterally, the visceral layer is tucked between the testis and epididymis which forms the sinus of epididymis. It consists of expanded head, body, and a pointed tail (Romanes 1998). The tail of epididymis further proceeds as continuation with the vas deferens. The main function of epididymis is absorption of fluid. It also helps in maturation of the sperm and secretion of substances in seminal fluid for nutrition of sperms (Snell 2017).

### Blood supply of testis and epididymis

1. Testicular artery which arises from abdominal aorta and it is a part of approximately two-thirds of the testicular blood supply.
2. Artery to vas deferens arises from superior vesical artery and cremasteric arteries arise from inferior epigastric artery, together they form approximately one-third of the testicular blood supply (Raman and Goldstein 2004).

**Venous drainage:** About 15–20 veins, after draining the testis and the epididymis, approximate to each other to form the pampiniform plexus which ascends anterior to the vas deferens, and at superficial inguinal ring this plexus joins and form four veins. At deep inguinal ring, they again join and form two veins. Finally single vein is formed in posterior abdominal wall that drains into the inferior vena cava on the right side at an acute angle, and into the renal vein on the left side at a right angle (Datta 2010).

**Lymphatic drainage:** The testes drain into pre-aortic and para-aortic lymph nodes.

**Nerve supply:** The testis is supplied either by nerve fibres that arise from the tenth and eleventh thoracic segments of spinal cord, through the renal and aortic plexuses, or by nerve fibres that arise from the pelvic plexus (Rauchenwald et al. 1995).

The ampulla of the vas deferens unites with the duct of seminal vesicle and form ejaculatory duct. It opens on the verumontanum of prostatic urethra. The seminal vesicle secretes viscid, yellowish-white alkaline fluid and form bulk of semen which is rich in fructose, prostaglandin, and coagulating enzyme vesiculase for nourishing spermatozoa. Ejaculatory duct obstruction due to congenital cysts or urethral injury can cause oligospermia or azoospermia (Standring 2016).

**Vasectomy:** This is the most common method of male sterilization. In this procedure, a small segment of the ductus deferens is ligated and/ or cut out in the upper part of the scrotum (Moore et al. 2014).

### Prostate

The prostate is a conical fibro-muscular glandular organ that encloses prostatic urethra. It is around 20–25 gm in young adult and 30 gm in

old parson. The prostate provides about 30% of the volume of seminal fluid. Its secretion is slightly acidic with a pH around 6.4 which consists of acidic phosphatase, citric acid, fibrinolysin, prostaglandins, prostate specific antigen (PSA), and zinc. PSA liquefies semen, helping in sperm motility and also dissolving cervical mucus (Arneth 2009).

The normal level of serum PSA is 0–4 µg/L. PSA is commonly elevated in prostate carcinoma but in BPH, inflammation, and infarction, PSA level may be increased (Arneth 2009). Zinc protects sperms in female reproductive system. Fibrinolysin liquefies semen. The prostate lies in the lesser pelvis behind the lower part of pubic symphysis and pubic arch. The Prostate is covered by inner true and outer false capsule. The space between these capsules is filled with prostatic venous plexus. The prostatic venous plexus communicates with the internal vertebral venous plexus (para-vertebral vein of Batson), due to this communication prostatic carcinoma can spread to the brain.

### Zonal Anatomy of Prostate

On the basis of the glandular tissue, prostate may be divided into three distinct zones.

1. Transition zone (5% by volume of total glandular tissue) lies around distal part of pre-prostatic urethra. Ducts of transition zone open on verumontanum, just above where the ducts of peripheral zone open into prostatic sinuses. Benign prostatic hypertrophy (BPH) affects transition zone. As transition zone grows, it compresses preprostatic and prostatic part of urethra which leads to anatomical bladder outlet obstruction. It may present as lower urinary tract symptoms, infections, and retention of urine (Patel and Parsons 2014).
2. Central zone (25% by volume) is wedge-shaped and forms base of gland with its apex at verumontanum. It surrounds ejaculatory ducts as they course through the gland. Central zone is rarely involved in any disease process.
3. Peripheral zone (70% by volume) surrounds central zone from behind and below, but does not reach up base; it extends downwards to

form lower part of gland, except anteriorly. Peripheral zone is solely involved in carcinoma of prostate.

#### Age Changes in the Prostate

At birth, prostate mainly consists of system of duct embedded in fibro-muscular stroma. At puberty, the prostate exhibits maturation phase mainly due to follicular development and achieves more than two times of its infant size. During 40–50 years, epithelial folding tends to vanish and follicles contain corpora amylacea (prostatic concretions). After 50 years, the prostate tends to develop BPH.

#### Arterial Supply

The Prostate is supplied by branches of the inferior vesical and middle rectal arteries and internal pudendal arteries.

**Venous drainage:** The veins form the prostatic venous plexus, which lies between the true and false capsule of the prostate. The prostatic plexus receives the deep dorsal vein of the penis and vesical venous plexus and drains into the internal iliac veins. A few vein drain posteriorly into internal vertebral venous plexus which is also known as para-vertebral veins of Batson. This route helps in metastasis of tumour cells from prostate to the vertebrae and brain (Datta 2010).

**Lymphatic drainage:** The lymphatics of prostate drain into internal iliac, external iliac, sacral, and obturator lymph nodes (Standring 2016).

#### Spermatic Cord

It is a tubular sheath-like structure, which begins at the deep inguinal ring and exits at the superficial inguinal ring. The spermatic cord contains vas deferens, testicular artery, pampiniform plexus of veins, and lymphatics and nerve supplying the testes, all these structures lie within the internal spermatic fascia. Besides these, the spermatic cord includes ilioinguinal nerve, genital branch of the genitofemoral nerve, the cremasteric artery, veins and lymphatics, and artery to vas deferens, veins, and lymphatics which are confined within the external spermatic fascia.

#### Penis

The penis is the male organ of copulation. It consists of a root or attached portion or radix and a body (shaft) or free portion.

The root consists of two crura and median bulb of penis. The body of penis is composed of three elongated masses of erectile tissue: a pair of corpora cavernosa on the dorsum and unpaired corpus spongiosum containing the urethra on the ventral surface. Each corpus cavernosa consists of cavernous spaces which are lined by the endothelium. During erection, blood flow increases and these spaces are filled with blood, leading to penile engorgement and compression of venous outflow channels.

**Arterial supply:** The penis is supplied by the bulbourethral artery, the dorsal penile artery, and the cavernous (deep, cavernosal) artery which are terminal branches of internal pudendal artery (Standring 2016).

**Venous drainage:** The penis is drained by the superficial and deep dorsal vein. The superficial receives blood from the prepuce and skin and drains into great saphenous vein. The deep dorsal vein ultimately drains into the prostatic venous plexus.

**Lymphatic drainage:** The penile and perineal skin is drained into the superficial inguinal lymph nodes. Lymphatics from the glans penis drained into the deep inguinal and sometimes into external iliac nodes and those from the erectile tissue and penile urethra drain to the internal iliac nodes.

The erection of penis is vascular phenomenon which is controlled by parasympathetic nerves (nervi erigentes, S<sub>2-4</sub>). In emission process, semen is transported to the prostatic urethra by the ejaculatory ducts, which is under control of the sympathetic nerve (L<sub>1-2</sub> nerves). Ejaculation is discharge of seminal fluid from the prostatic urethra to outside of body which depends on both autonomic and somatic nerve and includes closure of the internal urethral sphincter under sympathetic effect (L<sub>1-2</sub> nerves), contraction of the urethral muscle by the parasympathetic response (S<sub>2-4</sub> nerves), and contraction of the bulbospongiosus muscles with the help of pudendal nerves (S<sub>2-4</sub> nerves) (Moore et al. 2014).

Developmental anomalies:

1. **Phimosis:** It is a condition in which the prepuce is elongated and covers partially the external urethral opening. Surgical circumcision is the treatment.
2. **Epispadias:** In this condition, urethral meatus is found on the dorsum of the penis (Sadler 2015).
3. **Hypospadias:** In this condition, there are abnormal openings of the urethra along the ventral side of the penis (Sadler 2015).
4. **Micropenis:** It occurs due to insufficient androgen stimulation.
5. **Bifid penis:** It occurs due to splitting of the genital tubercle (Sadler 2015).

## Female Reproductive System

The female reproductive system comprises uterus, uterine tubes, and ovaries (the upper genital tract) and the vulva and vagina (lower genital tract).

### Uterus

The uterus is thick walled, hollow, muscular, and inverted pear-shaped structure. It is situated in the lesser pelvis between the urinary bladder and the rectum. Superiorly, it opens into the uterine tube and inferiorly opens into vagina.

### Subdivisions

The uterus is subdivided into two parts from superior to inferior: muscular body (corpus uteri) and fibrous cervix (cervix uteri). The ratio of body: cervix length is 2:1 in adult, whereas, 1:2 in infant. The body extends from the fundus to a constriction which is called isthmus (internal os of cervix). The part of the body which lies above the opening of uterine tube is called fundus.

### Axes of Uterus

In the adult nulliparous state, uterus lies in anteversion and antelexion. Anteversion is forward tilting between the axis of cervix and the axis of vagina which is around  $90^\circ$ . Antelexion is forward tilting between the axis of cervix and the axis

of body which is around  $125^\circ$ . In 10–15% of women, the uterus is retroverted in which uterus leans backwards at an angle to the vagina and is called retroverted. When the body of uterus leans backwards at an angle to the cervix, it is called retroflexed (Standring 2016).

### Body of Uterus

Body is flattened antero-posteriorly, so it has two surfaces – anterior and posterior, and right and left lateral borders, and a uterine cavity. Anterior surface is flat which is lined by peritoneum up to isthmus and after covering up to isthmus it goes on to the superior surface of the bladder, creating a space between uterus and bladder which is known as utero-vesical pouch. Posterior surface is convex and covered by peritoneum up to posterior fornix of vagina, after that it reflected on rectum and forming rectouterine pouch (pouch of Douglas). Each lateral border is rounded and non-peritoneal and gives attachment to the broad ligament. The uterine artery enters in broad ligament through the lateral border and supplies the uterus. The lateral angle of this border gives attachment to three structures: uterine tube, round ligament, and ligament of the ovary. The round ligament of uterus is attached antero-inferior to the tube, whereas the ligament of ovary postero-inferior to the tube. The cavity of the uterine body is triangular in coronal section, base of which is formed by an imaginary line between the opening of uterine tubes and apex is formed by internal os of the cervix. The implantation commonly occurs in the upper and posterior wall of uterine cavity in the midsagittal plane (Kim and Kim 2017).

### Cervix of Uterus

In nulliparous woman, cervix is more cylindrical and narrower than body of uterus. The cervix is a fibrous structure which consists of mainly collagen and small amount of smooth muscle and elastin (Snell 2017). Its lower part continues into the upper part of the vagina at the external os. Thus, the cervix is divided into two parts: (a) upper supravaginal (b) lower vaginal part. The cavity of the cervix is fusiform on coronal

section, communicating with the body of uterus through the internal os and that of the vagina through the external os. In nulliparous women, the external os is circular aperture, whereas in multiparous it looks like transverse aperture with anterior and posterior lips (Standing 2016).

The wall of the body of the uterus consists of three coats or layers:

- Perimetrium: It is outer serous coat or visceral peritoneum and consists of a mesothelium and a thin layer of connective tissue.
- Myometrium: It is thick muscular layer in which branches of the blood vessels and nerves, supplying uterus are present. It is continuous with muscular layer of fallopian tube, vagina, and true ligaments. It acts as the “living ligature of the uterus” because this layer helps in halting bleeding during menstruation and placental separation by muscular contraction (Datta 2010). During the menses, myometrial contractions may produce cramping.
- Endometrium: It is inner mucous coat and consists of epithelium and lamina propria. During reproductive life, it consists of outer basal layer or stratum basale and inner functional layer or stratum functionale (Pawlina 2016). The stratum basale is retained during menstruation and helps in regeneration of stratum functionale. The stratum functionale is sloughed off in each month with uterine bleeding.

#### Ligaments of Uterus

There are two types of ligament: false and true ligaments. False ligaments are made up of peritoneal folds whereas the true ligaments consist of fibrous and muscular component which mainly provide support to the uterus.

False ligaments are: (1) Broad ligament, (2) Uterovesical fold, and (3) Rectovaginal fold.

True ligaments are: (1) Round ligament, (2) Uterosacral ligament, (3) Transverse cervical, and (4) Pubocervical ligaments.

**Broad Ligament:** These are the folds of peritoneum that extend from the lateral border of the uterus to the lateral pelvic wall on each side. The broad ligament is subdivided into mesosalpinx, mesovarium, mesometrium, and suspensory

ligament of the ovary. Mesosalpinx is the upper part of broad ligament which is attached between the uterine tube and the ovary with the ligament of the ovary. Mesometrium is the inferior part of broad ligament which lies below ovary and the ligament of ovary. Mesovarium is the fold of posterior (or upper) layer of broad ligament. It acts as hilum of the ovary. Infundibulo-pelvic ligament is (suspensory ligament of the ovary) attached between the infundibulum of the tube and the upper pole of the ovary and the pelvic brim.

**Contents of the broad ligament:** The broad ligament contains the following structures:

1. The uterine tube except the intra-mural part.
2. The round ligament of the uterus (proximal part).
3. The ligament of the ovary.
4. Two vessels: the uterine and ovarian vessels.
5. Two plexuses of nerve: uterovaginal plexus and ovarian plexus.
6. Three embryological remnants: epoophoron and its duct (Gartner's duct), paroophoron. Vesicular appendices.
7. Other structures: lymphatics and fibroareolar tissue.

#### True ligaments

1. Cardinal ligaments (transverse cervical or ligaments of Mackenrodt) extend from the lateral part of cervix and the fornix of the vagina to the lateral pelvic walls. The ureter and uterine artery traverse the cardinal ligament.
2. Utero-sacral ligaments pass from the sides of the cervix to the third sacral vertebra. They are palpable during per rectal examination.
3. Round ligament- Each round ligament extends from the lateral cornu of the uterus through the broad ligament to enter the deep inguinal ring lateral to the inferior epigastric artery and attaches distally in the ipsilateral labia majora conventionally. But in a cadaveric dissection study, some researchers found three types of distal attachments: in the first type, the round ligament ended just outside the superficial inguinal ring in more than half cases; in the



second type, before the deep inguinal ring; and, in the third type, under the pubic bone. They didn't observe distal attachment of it at labia majora in any cases (Bellier et al. 2018).

4. Pubocervical ligament passes forward and lies between cervix and posterior surface of the pubic bones.

#### Support of Uterus

##### A. Primary Support

1. Muscular or active: (a) pelvic diaphragm, (b) urogenital diaphragm, and (c) perineal body.
2. Fibromuscular or mechanical: (a) uterine axis, (b) round ligament of the uterus, (c) pubocervical ligament, (d) uterosacral ligament, and (e) cardinal ligament.
3. Visceral: (a) Urinary bladder (upper surface) and (b) Vagina (posterior wall).

##### B. Secondary Support

- (a) Broad ligaments, (b) Uterovesical fold of peritoneum, and (c) Rectovaginal fold of peritoneum.

#### Arterial Supply and Venous Drainage of Uterus

The uterus is mostly supplied by the uterine arteries and partly by the ovarian arteries. The uterine veins form a uterine venous plexus on lateral side of cervix which mainly drain into the internal iliac veins.

#### Lymphatic Drainage

The lymphatic drainage of the uterus is very important because uterine tumour metastases occur through lymphatics.

1. From fundus and upper part of the body: Majority of the lymphatic vessels drain into pre- and para-aortic lymph nodes. But a few lymphatic vessels from the lateral angle of the uterus drain into superficial inguinal lymph nodes.
2. From the lower part of the body: The lymph vessels drain into external iliac nodes.
3. From cervix: On each side, the lymph vessels drain in three directions:
  - a) Laterally, the lymph vessels drain into external iliac and obturator nodes, few of

these vessels drained by para-cervical lymph nodes.

- b) Postero-laterally, the lymph vessels drain into internal iliac nodes.
- c) Posteriorly, the lymph vessels drain into sacral nodes.

#### Nerve Supply

The uterus is supplied by both sympathetic and parasympathetic nerve. The sympathetic fibres are derived from neurones in the T<sub>12</sub>–L<sub>1</sub> spinal segments. The sympathetic fibres cause contraction of uterus and vasoconstriction. Pain fibre from body of uterus is carried by sympathetic sensory fibres. The parasympathetic fibres are derived from neurones in S<sub>2–4</sub> spinal segments. The parasympathetic fibres inhibit the uterine muscles contraction and cause vasodilatation. Pain fibres from cervix are carried by parasympathetic sensory fibres. But all these uterine activities are mostly under hormonal control.

#### Clinical Correlation

1. Cervical carcinoma: It is the most common cause of death among cancerous women in developing countries. It is the second most common cancer effecting women of age group 15–44 years (Sreedevi et al. 2015). It is uncommon in early 20 years of age (Sreedevi et al. 2015). In 70% of patients, Human papilloma virus (HPV-16, HPV-18) is associated with cervical carcinoma. In about 80% cases, cervical cancers are squamous cell carcinoma and related to sexual activity (Shrestha et al. 2018).
2. Fibroids/leiomyomas of uterus: These are the most common benign tumours in women which arise from the uterine smooth muscle tissue (Sohn et al. 2018).
3. Endometriosis: It is defined as the presence and proliferation of ectopic endometrial glands and stroma-like lesions outside the endometrial cavity of the uterus. The most common sites of pelvic endometriosis are the ovaries, fallopian tube, uterine ligament, and rectouterine pouch (Alimi et al. 2018).
4. Prolapse of uterus: In this condition, the uterus herniates into or beyond the vaginal cavity due

to weakness or injury of fibromuscular supports of the uterus. Major risk factors for prolapse are old age, multiparity, high body mass index, constipation, family history, etc. (Doshani et al. 2007).

### **Uterine (Fallopian) Tube**

The uterine tubes are a pair of ducts in which medial end are attached to superior angle of lateral border of the uterus and lateral end communicates with the uterine cavity through its ostium. Main function of fallopian tube is to transmit ova to the uterine cavity after collecting from the ovaries. The two uterine tubes are each about 4 inch. (10 cm) long and lie in the upper free border of the broad ligament of the uterus. The tubes extend laterally from the superior angle of the uterine cavity and open into the peritoneal cavity near the ovaries. Each tube consists of four main parts: intramural, isthmus, ampulla, and fimbria. Intramural (Interstitial) part (1 cm long and 0.7 mm wide) lies within the wall of the uterus. It traverses the uterine wall at the junction of fundus and body. Isthmus (2.5–3 cm long and 1–5 mm wide) is round and cord-like due to thick muscular wall and continuous laterally with ampulla which is the widest part with 1 cm diameter. Ampulla (5 cm long) is the longest, thin walled, and tortuous part of the uterine tube. It is usually the site of fertilization of ovum. The ampulla opens into a trumpet-shaped infundibulum (1 cm long) at the abdominal os. Fimbriae, numerous mucosal finger-like folds 1 mm wide, are attached to the circumference of the infundibulum. One fimbria longer and more deeply grooved than the others is closely applied to the tubal extremity of the ovary and is called an ovarian fimbria. At the time of ovulation, the fimbriae swell and dilated due to engorgement of the vessels in the lamina propria, which helps in capture of the released oocyte.

**Arterial supply:** The fallopian tube is supplied by two arteries – ovarian and uterine arteries. Usually the medial two-third of the tube is supplied by the uterine artery and lateral one-third by the ovarian artery.

**Venous drainage:** The veins correspond to arteries, thus venous blood is drained by the ovarian and uterine veins.

**Lymphatic drainage:** The lymph vessels follow the uterine vein drain into internal iliac lymph nodes and the lymph vessels follow ovarian vessels drain into the para-aortic lymph nodes.

**Nerve supply:** The tubes are supplied by both sympathetic and parasympathetic fibres. The sympathetic fibres are derived from ovarian and superior hypogastric plexuses. The preganglionic sympathetic fibres are derived from the T<sub>10</sub>–L<sub>2</sub> spinal segments. The preganglionic parasympathetic fibres to the lateral part of the tube are derived from the vagus nerve and to the medial part from the pelvic splanchnic nerves (S<sub>2-4</sub> spinal segments).

### **Clinical Correlation**

**Salpingitis:** It is an infection and inflammation of the uterine tubes which is mainly caused by sexually transmitted micro-organism. It is the most common cause of tubal block leading to subfertility and infertility in female (Owhor et al. 2019). The patency of tubal block is tested by the Hysterosalpingography in which radiopaque substance (e.g., Lipiodol) is injected into the uterus by a suitable canula. If tubes are patent, the contrast medium spills into the peritoneal cavity.

**Tubectomy:** This is the ideal method of family planning in female. In this procedure, each fallopian tube is ligated at two points and between the ligatures, the segment is resected.

### **Ovaries**

The ovaries are paired gonads which are homologous of testes in the male. The main function of ovaries is to produce female gametes (oocytes). The ovaries are like almond in shape with dull white colour. In nulliparous, each ovary located in the ovarian fossa which lies on the lateral pelvic wall. They are suspended in the pelvic cavity with the help of the mesovarium. Initially, the ovaries have smooth surface, but post-puberty they become nodular.

**Peritoneal and ligamentous supports of the ovary**

1. Infundibulopelvic (suspensory) ligament: It connects upper part of lateral surface of the

ovary to the lateral pelvic wall. The ovarian vessels and nerves pass through it to reach the hilum of ovary.

2. Ovarian ligament (ligament of the ovary): It lies between uterine end of the ovary and the lateral angle of uterus.
3. Mesovarium: It helps in attachment of the ovary to posterior surface of the broad ligament.

**Arterial supply:** The ovarian artery, which arises from the abdominal aorta, supplies the ovary.

**Venous drainage:** The right ovarian vein drains directly into the inferior vena cava, whereas the left ovarian vein drains into the left renal vein.

**Lymphatic drainage:** The lymphatics from the ovary drain into the pre-aortic and para-aortic lymph nodes.

**Innervation:** Ovaries are predominately supplied by the sympathetic fibres. The preganglionic sympathetic fibres are derived from T<sub>10-11</sub> spinal segments.

#### Clinical Correlation

**Ovarian cancer:** It is the sixth most common cancer worldwide affecting women in developed countries. It is the most fatal of all gynecological carcinomas (Modugno and Edwards 2012). Majority of ovarian cancers arise from neoplastic changes in the surface epithelium. Sometimes tumour cells from the abdominal organs undergo transcoelomic migration and produce secondary ovarian tumour, this type of metastatic ovarian tumour is known as Krukenburg's tumour.

#### Vagina

The vagina is a female organ of copulation. In front, it is bounded by the bladder and urethra while behind it is related with rectum and anal canal. The anterior wall is shorter than the posterior wall. The length of anterior wall is 7.5 cm, whereas length of posterior wall is 9 cm.

**Fornices of vagina:** The circular area of vaginal lumen around the cervix is called fornix of the vagina. The fornix of vagina is divided into four parts: a) anterior fornix, b) posterior fornix, and c)

two lateral fornices. The posterior fornix is about 2 cm deeper than the anterior fornix.

**Arterial supply:** The vagina is supplied by (1) vaginal artery which is a branch of the internal iliac artery, (2) Vaginal branch of uterine artery, (3) Internal pudendal artery, (4) Middle rectal artery, and (5) Inferior vesical artery.

**Venous drainage:** The veins of the vagina drain into the internal iliac veins through the vaginal veins.

**Lymphatic drainage:**

The lymphatics of vagina are divided into three groups:

1. From upper third of vagina: lymphatic vessels drain into internal and external iliac nodes.
2. From middle third of vagina: lymphatic vessels drain into internal iliac nodes.
3. From lower one-third (below the hymen): lymphatic vessels drain into the medial group of superficial inguinal nodes.

#### External Female Genital Organs

The female external genitalia (or vulva/pudendum) consists of mons pubis, labia majora, labia minora, clitoris, vestibule of the vagina, bulb of the vestibule, female urethra, and ducts of the paraurethral and greater vestibular glands.

**Mons Pubis:** It is a round, conspicuous, adipose tissue over the pubic symphysis and pubic bone. Before puberty, the mons pubis is relatively flat and hairless. In adult, it becomes prominent with coarse pubic hair and atrophies slightly after menopause. It is commonly absent in the male.

**Labia Majora:** These are broad, prominent, longitudinal fold of skin filled with subcutaneous fat and loose connective tissue which extend back from the mons pubis to the perineum. Two labia majora join anteriorly and form anterior commissure. Posterior commissure does not join, but merges into neighboring skin and forms ridge which overlies the perineal body. They form posterior limit of vulva. They are homologues of the two halves of the scrotal sac. Subcutaneous smooth muscle in them is homologue of the dartos muscle. The round ligament of the uterus may end in adipose tissue and skin in the anterior part of labium majora.

**Labia Minora:** These are thin elongated cutaneous folds and situated medially to labia majora. There are no fat and hair within these folds. The cavity between the medial surfaces of the labia minora is called Vestibule of vagina. The fold formed by union of labia minora behind is known as Frenulum of the labia (Fourchette). Prepuce or hood of the clitoris is formed by the upper folds of the labia minora over the clitoris. Frenulum of the clitoris is formed by the lower folds of the labia minora under the clitoris.

**Clitoris:** It is homologous of the penis in male. It is not traversed by the urethra. It has a root, a body, and a glans. It consists of two erectile bodies called Corpora cavernosa. Corpora cavernosa is attached to the ischiopubic ramus by a crus that extends from root of clitoris. They unite in midline to form the body of the clitoris. Glans or Tip of the clitoris is a small, round tubercle of spongy erectile tissue at end of body and connected to bulbs of vestibules by thin band of erectile tissue. It is richly supplied with sensory nerve endings.

**Vestibule of Vagina:** It is a cavity between the medial surfaces of the labia minora. It contains urethral orifice anteriorly and vaginal orifice posteriorly. The vaginal orifice is incompletely covered by hymen. In addition to the above openings, it also contains the openings of greater vestibular glands (of Bartholin), lesser vestibular glands, and paraurethral glands (of Skene).

**Bulbs of Vestibule:** These are pair of elongated mass of erectile tissue which are located on each side of vestibule. Each bulb is a homologue of half of the bulb of the penis. Anterior end joined by a commissure and to clitoris by slender band of erectile tissue. Posterior end are expanded and are in contact with greater vestibular gland. They are covered superficially by bulbo-spongiosus muscle posteriorly. They do not surround the urethra. Their deep surfaces contact the inferior aspect of perineal membrane.

**Greater Vestibular Glands (Bartholin's Gland):** They are small, round, reddish-yellow bodies, mucous secreting gland. They are located at the posterior pole of the bulbs of the vestibule. They are homologues of male bulbo-urethral glands. Their duct open into vestibule by a 2-cm long duct, situated between hymen and labia minora (5 and 7 o'clock).

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## Reputation

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## Synonyms

Image score; Social impression; Standing; Status

## Introduction

Reputation is based on two things: behavior plus an audience. In its most basic definition, “reputation” is an information source (Russell 2016). Any episode of animal behavior is a potential signal to another animal (Danchin et al. 2004), even if that signal was not a deliberate intention to communicate.

Consider the example of territorial urine marking in mice. When a mouse urinates in your house, that urine deposit is a meaningful signal for other mice (Hurst 2005). In many animals, scent marks have an important role in social communication, allowing “recognition of group members and kin, the advertisement of territory ownership and social dominance, assessment of the quality of competitors and potential mates, and the advertisement and control of reproductive status” (Hurst 2005, p. 220). After a mouse deposits urine, the scent stays behind in the absence of the signaler, detectable by other mice passing near.

The scent mark is more than two-way communication. It is a form of “broadcast signal” or “advertisement” (Hurst 2005). In territorial scent marking, the dominant male repeatedly urinates at a high rate (which keeps the scent strong) within a given spatial area (Hurst 2005). The urine provides information about the identity of the absent depositor and pins that identity to a geographic location. The scent marks provide information for females (which helps them to assess the quality of the territory holder as a potential mate) and for other males (which helps them assess the dominance of that male and therefore whether he should be challenged or avoided).

Social information is abundant in the lives of most animals. Whenever they flock, herd, swim or fly together, or merely coexist within the same area, they have ample opportunity to witness the behavior of others (Danchin et al. 2004). The field of “public information” is the source material for reputation. For example, in territorial bird species (see McGregor 1993), males monopolize a finite territory, bordering territories occupied by other males. In this setting, vision is useful in direct encounters with other males at close range – but there is also auditory communication which allows “learning at a distance” about the activities of other birds. Thus, a male might hear a fight between two unseen males, the outcome of which allows the male to gain “inadvertent social information,” such as the identities of winners and losers of a fight (Danchin et al. 2004; McGregor 1993; Mennill and Ratcliffe 2004). In everyday language, we often hear the word “reputation” as a human-only concept, referring to information conveyed through language-based gossip: where people tell stories about other people (Haviland 1977). To understand reputation in animals, we can approach the topic in two ways: (1) looking from the *human* concept or (2) looking from studies of social eavesdropping in animals. There are three sections below. The first will cover the human concept of gossip and reputation and then compare it to animal capabilities. The second section is on social eavesdropping research. The final section is on the role of reputation in the evolution of cooperation in humans and animals.



## The Human Concept of Reputation

Human definitions put emphasis on morality and character (Morris 1999), with a main focus on gossip (Dunbar 2004). Consider the classic ethnographic work of Haviland (1977), a detailed examination of human reputation. Haviland studied gossip networks in a rural area of Mexico (Zinacantán region), consisting of people living in dispersed hamlets and making a living through agricultural and other types of work. Here, the flow of gossip was highly clustered within local neighborhoods (geographically separated clusters of hamlets). Most people stayed in their own neighborhoods and therefore gossiped mostly on local people and events. However, some people had reason to travel, either for work (seasonal jobs), for political reasons (attending meetings), or for trade (e.g., farmers selling corn at market). This allowed opportunities to gossip with people from other neighborhoods and to learn gossip from faraway. Zinacantán was thus a mix of people with many different sizes of gossip network, depending on residence, livelihood, and travel opportunities. Haviland (1977) also made a detailed analysis of the *content* of gossip, which always took the form of “A tells B about an absent C” (p. 28). There were three stages: (1) *identifying* the person being gossiped about (e.g., if not known personally, then that person’s position on a family tree was discussed: e.g., “he’s the son of . . . who lives in . . .”), (2) telling a *story* about an event (e.g., “[he] went to borrow money from him,” p. 117) and that person’s behavior in the event (e.g., “they say he got angry right away,” p. 117), and (3) *evaluation* of personality (e.g., “He is foolishly ill-tempered,” p. 128). These three stages (identification, story, evaluation) were recurrent over all gossip; but sometimes the stories were heavy on interpretation. For example, one bit of gossip was: “I can tell from the way he slammed the door that he fought with his wife and is now probably going out to get drunk” (p. 175) – a statement that provides not only a description but an interpretation, a conjecture on why it occurred, and a prediction of what that person will do next.

As illustrated in the slamming door example, human gossip is often focused on behavior which deviates from societal rules. How do you define “rules”? According to philosophers (see Haviland 1977, pp. 148–170), rules are socially agreed-upon guidelines for future behavior, assessment of behavior, and role expectations. Haviland (1977, p. 74) provided a catalogue of the most common gossip themes in Zinacantán, and topping the list are (sometimes grim) stories of sexual transgression, drunkenness, divorce, fighting, illegal activities, and various other conflict. The observed rule-breaking focus of gossip led Haviland (1977) to characterize gossip as an essential component of being a citizen in a society: being able to gossip shows knowledgeability not only of the language but of cultural rules. Furthermore, Haviland (1977) proffered that gossip not only consists of reports of rules but helps to define the rules themselves: when gossipers gossip, the evaluative stage of the conversation can be an elaborate shared analysis of a focal person’s behavior and how that behavior compares against acceptable social norms/rules – which, if necessary, leads to a redefinition of the range of acceptable behavior (e.g., if someone broke a rule but had a perceived justification for doing so). Haviland (1977) defined reputation as the accumulated knowledge, shared by many, of a person’s behavior, and how that behavior is judgeable against cultural rules. Seemingly, the human definition of gossip and reputation – as illustrated by Haviland (1977) – is incompatible with the abilities of animals. There are two main barriers.

The first barrier is the lack of explicit cultural rules. As illustrated by Haviland (1977), gossip is often a “report of rule breaking.” Lacking language, animals cannot discuss the rules, communicate the rules, redefine the rules, come to agreements about rules, nor morally evaluate others with respect to these rules. This does not mean that animal societies lack rules (think of the “rules” of dominance hierarchies in primates), but in animals, the rules are nonverbal, and in humans, the nonverbal rules are overlaid with language-based codification and organized justice (Tennie et al. 2010). We can ask whether animals have an innate sense of justice – that which would

allow animals to understand “rule breaking” in the first place. Human justice systems are predicated on *fairness* (Rawls 1958): the notion that an individual should benefit only to the extent that others do not suffer a reduction of benefit. Nonhuman animals do seem to have notions of fairness (see Brosnan and de Waal 2012), particularly as shown in “inequity aversion” experiments where a focal animal A has been shown to react negatively to disadvantageous inequity (“A observed that B received more than A; therefore, A reacts negatively”) and, to a lesser extent, to advantageous inequity (“A observed that A received more than B”). This implies that animals can understand rule breaking to some extent.

Another important part of human justice is the punishment of unfairness. Some animal studies appear to show some form of proto-justice. Aureli et al. (1992) investigated apparent “revenge” incidents in the aftermath of aggressive incidents among Japanese macaques, with two important results. One was that losers in a fight (the victims), being negatively aroused, subsequently engaged in “kin-oriented redirection”: having lost the fight against an aggressor, the victim attacked a more vulnerable member of that aggressor’s family. Their second important result is that these redirections occurred in contexts where the original aggressor was unlikely to intervene. For example, the victim would attack the kin member as part of a group. In that situation, the original aggressor would avoid intervening to defend its kin because of the high probability of injury in fighting a group. This kin-targeted “revenge” often happened in full view of the original aggressor. Observability played a key role in these events: “public information” allowed the macaques to accumulate knowledge about the kin relationships of others (which parallels with our above example from Haviland 1977: “he’s the son of. . . who lives in. . .”) and furthermore allowed the macaques to observe aggressive incidents between others. Thinking about this case of kin-oriented redirection, we can attempt to draw parallels to the three stages of gossip as identified by Haviland (1977): “identification, story, evaluation” (occurring in some nonverbal form among the macaques).

The second barrier is language. Although animals have complex communication systems, their systems are missing features of language (Fitch 2010) which would enable gossip. As Haviland (1977) described it in Zinacantán, information flowed according to human patterns of geography and mobility. Animals also have geography and mobility constraints. We can think back to the examples of territorial urine marking in mice (Hurst 2005) and social eavesdropping in territorial birds (McGregor 1993). In each example, detection of a broadcast signal depended on travel. A mouse needed to be inside a territory to smell its local urine. A bird needed to be within earshot of an aggressive encounter to learn the identities of winners and losers. A signal can reach only so far. Compare this to human reputational signaling. Thinking back to the slamming door example of Haviland (1977), the door slammer’s action is a signal whereupon gossip was a mechanism of broadcast. Even though it probably occurred in front of only one person, the door slamming was “broadcast” in the sense that a gossip verbally reported this event to a wider audience. It is unlikely that the door slammer intended his behavior to be widely known. Instead, his behavior was a symptom of his emotional state (negatively aroused after quarreling). In the internet age, the reach of a reputational signal can be global, enduring, and limitless (Tennie et al. 2010).

In animals, the lack of language ability is a major constraint on the reach of the signal. Mouse B might sniff a urine deposit and learn about the dominance of mouse A (the territory holder), but mouse B cannot subsequently convey that precise message to mouse C who is outside the territory and cannot smell the signal firsthand. The message ends at the perceiver and travels no further. Maynard Smith and Harper (2003, pp. 121-122) partitioned reputation into three “channels” of reputational information:

1. Direct reputation
2. Indirect reputation
3. Reported reputation

Humans have access to all three – but animals only have two (Russell 2016). Direct reputation refers to information gained from any type of one-on-one encounter. Reported reputation refers to gossip. The middle channel – indirect reputation – refers to information gained through pure observation.

## The Social Eavesdropping Paradigm

The basic design of an eavesdropping paradigm has two parts: (1) the study animal is allowed an opportunity to witness playacted or simulated events (“public information”) and (2) the animal’s behavior is measured as an assessment of whether the animal was influenced by the witnessed events. There have been many social eavesdropping studies in recent years (see Abdai and Miklósi 2016; Anderson et al. 2017, Herrmann et al. 2013; Tennie et al. 2010) – but, in fact, the basic design has deep historical roots. Going back decades to studies of animal learning, there are numerous experiments on “observational conditioning” and “observational learning” (Heyes 1994), where a focal animal is allowed an opportunity to view an interaction between another animal and some stimulus; and then the focal animal’s behavior is measured. Classic examples of this paradigm (reviewed in Heyes 1994) are observational conditioning where monkeys learned to fear a snake by observing the fearful interaction between another monkey and the snake and observational learning where a budgerigar learns how to open a covered food dish by observing another budgerigar successfully open the food dish. In observational learning, the focal animal observes the model engage in “action-upon-an-object.” In the chimpanzee study of Hirata and Morimura (2000), the object was a “honey bottle” located within a room with a scattered selection of 20 tools, only some of which were usable for extracting honey from the bottle. They first trained chimpanzee models to use the tools correctly. Then, they allowed other chimpanzees (who were naïve to the task) to observe the models. They found that observer chimpanzees did pay close attention to the model

chimpanzees as a guide for extracting the honey, using tools that models had used – and they paid particularly close attention to the model after their own previous efforts had failed. This study showed that animals are very observant when watching a model perform “action-upon-an-object” (watching the chimpanzee model extract honey). The social eavesdropping paradigm is much the same, except that, in contrast, it involves “action-upon-an-agent.”

Mennill and Ratcliffe (2004) conducted a social eavesdropping experiment modeled closely on the example of eavesdropping territorial birds (cf. McGregor 1993). They studied black-capped chickadees, testing actual territorial males in the wild. They determined the dominance of each male within each flock, using a variety of measures involving males chasing or supplanting other males, or showing resistance, or avoidance, or being observed to adopt a submissive posture. The male’s position in the dominance hierarchy was a key variable. The procedure involved a playback experiment. The investigators obtained recordings of chickadees from a sound library, altered them slightly for uniformity, and then set up a series of opportunities for focal birds to hear the recordings. They began the procedure by luring the focal male to within 5 m of the speaker by playing a chickadee “flock-rallying call.” Then, when the focal male was close enough, they introduced a completely new set of calls that simulated the sounds of territorial males. In the recording, the investigators made one male sound dominant over the other by simulating an episode of “countersinging,” which refers to a situation where one male overlaps his call over another male. Countersinging is a sign of aggression, with the overlapping male perceived as dominant. The investigators gave each focal male the opportunity to learn which of the two male “intruders” was dominant. The final phase of each trial was an assessment of the focal male’s approach behavior after hearing these playbacks. Results differed according to the focal male’s position in the dominance hierarchy. High-ranking males almost all approached the overlapping (dominant) speaker, whereas the low-ranking males approached the overlapping speaker less often, sometimes

approaching the overlapped (subordinate) speaker or not approaching at all. This study showed that some focal males used reputation to learn the dominance of previously unknown (in this case, fictional) males.

Another bird study is from Ophir and Galef (2003), who used the social eavesdropping paradigm on Japanese quail. They allowed female quail to observe aggressive interactions between pairs of males. The procedure consisted of two phases. The first was the fight phase, where females observed males pecking at each other across a transparent partition. The winner of the fight was determined as the male that pecked more often. The second phase was a choice phase, where a barrier was lifted, allowing the female the opportunity to approach either the winner or the loser (although these males were still behind a transparent partition). The dependent variable was the amount of time that the female spent near a given male. The female was recorded as “preferring” a male when it spent more than half of the testing period near that male. The investigators compared this result against a control group (females who had not viewed a fight). The main result is that females “preferred” the loser. The authors conjectured that females might prefer to avoid the danger of injury and hence avoided the more aggressive winner. This study showed that female quail used reputation to learn the dominance of males.

Primates, too, have been the subject of social eavesdropping experiments (Abdai and Miklósi 2016; Anderson et al. 2017; Tennie et al. 2010). Russell et al. (2008) studied indirect reputation on four great ape species (chimpanzees, orangutans, gorillas, and bonobos). Here, apes were given the opportunity to observe playacted incidents between human actors. In every incident, one actor played the “beggar” who observed another human eating green grapes out of a transparent container and then extended his hand outward in front of the eater in a begging gesture. There were two types of incident: (1) a “nice” person gave grapes to the human who begged for it and (2) a “nasty” person ignored the begging gesture; then the beggar reached into the container to obtain a grape; then the

nasty person slapped him on the hand, preventing him from obtaining grapes. Subjects observed both nice and nasty incidents in every trial as uninvolved bystander. Next was the choice phase, where a barrier was lifted, allowing the subject into a different compartment where both nice and nasty actors were sitting side by side at adjacent windows. Each window had holes through which food could pass. The dependent variable was the amount of time (in seconds) that the subject spent near a given person (with neither person giving any food). The main result was that chimpanzees and bonobos together (but not other species) spent significantly more time near the “nice” window than the “nasty” window. Furthermore, over four trials, they collectively reduced the amount of time at the nasty window but did not reduce their time at the nice window. This study showed that *Pan* species used indirect reputation to gauge which of the two human actors were more likely to give food. A number of other studies subsequently used the same paradigm (reviews in Abdai and Miklósi 2016; Anderson et al. 2017; Tennie et al. 2010). One example was from Herrmann et al. (2013), who tested all four great ape species plus human children aged 2.5 years. They used the same basic design, but with a larger sample size, using a more diverse range of food for the animals, and, for children, they used toys instead of food. Their “direct” playacted incidents involved a “nice” person who attempted to give food to the apes or use toys to play with the children and a “nasty” person who tried to interrupt the food giving or play. The “indirect” incidents were the same except that the subject observed the incidents among third parties as an uninvolved bystander. The dependent variable was the subjects’ willingness to approach either the nice or nasty person. Overall, they found that orangutans and children preferred the nice person in both the direct and indirect situation. Chimpanzees also showed a preference for the nice person in the indirect reputation condition.

Anderson et al. (2013a) used a similar social eavesdropping paradigm on capuchin monkeys. Again, subjects were shown a playacted incident between two humans. In each trial, the monkey

observed either a “helpful” incident, or a “non-helpful” incident, and then was able to choose which of two people to approach for food. In the first part, every incident had an “attempter,” a person attempting to retrieve a toy from a transparent plastic container. The toy inside the container was clearly visible to all, and the subjects observed the attempter attempt to lift the lid from the container with no success. In each incident, there was another human sitting beside the attempter. The identity of the other person depended on the type of incident. In the “helpful” incident, the other person was the “helper.” After unsuccessfully trying to open the container, the attempter looked at the helper and held the container toward the helper. The helper then co-handled the container, and then the attempter was able to lift the lid and obtain the toy. In the “non-helper” incident, the attempter playacted the same thing: trying to remove the lid with no success and then looked at the helper and held the container toward the helper. Here, the non-helper turned away from the attempter and did not help. Subsequently, the attempter continued attempting to lift the lid with no success. In the second part of the trial, an opaque screen was lowered, blocking the previously observed area. Then the screen was lifted, revealing both helpful and non-helpful actors sitting side by side with a piece of food (monkey pellet) resting on the fingers of their open palms. The monkey had the choice to approach either the helpful or non-helpful person for food. Once the monkey had made its choice (by putting its hand through the 3-inch gap in front of the person’s hand), the selected person extended her hand to allow the monkey to take the food. Their main result was that the monkeys accepted food less frequently from the non-helpful person than the helpful person.

There are many other social eavesdropping studies beyond that mentioned above. Anderson et al. (2013b) did another study of capuchin monkeys, showing them incidents of humans in either a reciprocating (human A gives human B a set of balls and then B returns them) or a non-reciprocating condition (B does not return them). After giving the monkeys an opportunity to approach either the reciprocator or non-reciprocator for food, the monkeys chose the reciprocator. There has also been a burgeoning literature

on social eavesdropping in dogs (Abdai and Miklósi 2016; Anderson et al. 2017). One interesting study by Chijiwa et al. (2015) found that, when dogs were given a chance to observe their owners interacting with either a helper or non-helper for trying to retrieve an object from a container. When dogs were given an opportunity to approach the helper or non-helper, they approached the helper.

## Benefits and Evolution

Gossip and reputation are thought to have played an important role in our cognitive evolution and ability to thrive within cooperative groups (Dunbar 2004; Milinski 2016; Tennie et al. 2010). Reputation is beneficial in at least three ways: (1) benefit-to-approacher, (2) benefit-to-winner, or (3) benefit-to-group. The first benefit is that reputation provides opportunities for low-risk, low-cost, information gathering (McGregor 1993): in territorial birds, for example, eavesdropping helps animals to avoid injury by avoiding the winners of fights. The second benefit involves the winner (Adams 2001): when an animal has gained a reputation for winning fights, it saves that animal from needing to expend energy in further fights (because other animals will hesitate to attack). A third type of benefit relates to the “tragedy of the commons” (Hardin 1968; cf. Binmore 2007, pp. 27–29), whereupon a negative outcome (e.g., depletion of a resource) occurs because individuals are independently pursuing their own desires/needs without doing anything to avert the negative outcome. In various human-focused empirical and theoretical studies (see Milinski 2016), it has been shown that reputation actualizes better cooperative outcomes on a group level – based on the bottom-up explanation that individuals with good reputations tend to prosper and those with bad reputations do not.

Reputation can also be studied game-theoretically (e.g., Morris 1999). Game theory is a mathematical approach to investigating the costs and benefits of behavioral strategies, specifically focused on the dynamics arising from interactions between actors (Binmore 2007). Game theory is well-suited to analyzing conflicts/contests between animals (Adams 2001;



Maynard Smith and Harper 2003). One early game-theoretic study is the simulation study of Van Rhijn and Vodegel (1980), which quantitatively compared the success of various fighting strategies where a contestant (player) was facing an opponent whose fighting ability was either dominant, submissive, or unknown. The player had three options: make a threat display, engage in actual fight, or retreat. Their results showed that, out of four possible strategies, the most successful one was where the player starts off with caution, showing a threat display if the opponent was subordinate/unknown, never initiating with dominants (and retreating if encountering one), and then escalating into an actual physical fight if the opponent continued to appear subordinate/unknown. Key to success was that the player adopted a strategy contingent on updateable knowledge about the opponent's fighting ability.

On the topic of *indirect* reputation, one way to infer its adaptiveness in evolution is through mathematical modeling. Pollock and Dugatkin (1992) modeled the tit-for-tat (TFT) strategy: player 1 cooperates in the first encounter with player 2 and, if encountering player 2 again, copies player 2's previous action (cooperate if player 2 cooperated, defect if player 2 defected). Their aim was to compare the success of TFT to another strategy called "observer tit-for-tat" (OTFT), the same as TFT except that player 1 paid attention to player 2's previous behavior toward others (e.g., if player 2 defected on someone else, then OTFT would defect on player 2 even on a first encounter). Using the criterion of evolutionary stability (a strategy is successful if it can outcompete rival strategies in a survival-and-reproduction game), the result was that OTFT was more successful than TFT, but only in models that set a low probability of repeated encounter. The implication of their model was that indirect reputation is particularly adaptive in large, mixed, and dispersed populations.

## Cross-References

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- [Triadic Awareness](#)

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## Requesting Paradigm

### ► Bucket Experiment

## Rescue Behavior

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## Definition

To define an action as *Rescue behavior*, Hollis and Nowbahari (2013; Nowbahari and Hollis 2010) proposed that four conditions should be met. Firstly, there is a victim endangered. The victim is in a situation that implies imminent direct physical harm and/or indirect harm through severe fitness decrease (e.g., releasing humans from a stressful situation that is harming dramatically their mental health and indirectly their fitness). Secondly, the behavior of the rescuer is suited to the circumstances of the victim's distress. This condition creates a connection between the rescuer's behavior and the victim's situation while, simultaneously, avoids referring to the rescuer's intentionality. This last element allows the inclusion of rescue behaviors actions performed by human and nonhuman animals. Thirdly, the rescuer places itself at risk by engaging in rescue behavior. This condition is linked to the classification of rescue behavior as an extreme case of altruism, which will be analyzed later. The fourth condition is that the act of rescuing is not inherently rewarding or beneficial to the rescuer. The only exceptions are the benefits associated with kin selection or reciprocal altruism, concepts that are explained later in this entry. This fourth

condition is difficult to evaluate in humans because rescue behavior could be inherently rewarding at a psychological level, for example, strengthening the perception of oneself as a good individual, which is less likely to occur in other animals.

The definition of rescue behavior does not require a successful rescue, nor necessarily implies prosocial motivation aimed to reduce other individuals' suffering. The existence of this motivation has been questioned in nonhuman animals. Therefore, the wide definition of rescue behavior includes acts performed by human and nonhuman animals (Hollis and Nowbahari 2013).

The third and fourth conditions of rescue behavior allow classification as an extreme case of altruism, a behavior that benefits another subject with a cost for the helper. The rescuers perform a behavior highly risky for themselves which is, nonetheless, not inherently rewarding for themselves (except for the cases explained by the two mentioned theories, kin selection and reciprocal altruism).

## Explanations of Rescue Behavior

Altruism implies a cost for the altruistic individual and, according to natural selection, it should be eliminated because it reduces the individual relative fitness (i.e., reproductive success in comparison with other subjects). This argument is especially problematic for an extreme case of altruism, such as rescue behavior, because the rescuer could die or be severely damaged by rescuing. Therefore, researchers ponder the ultimate causes of rescue behavior; that is, explanations of how this behavior has been selected through the species' evolutionary history. Those explanations address how rescue behavior contributes to the rescuer's gene propagation. Three theories have been proposed in this respect: kin selection, reciprocal altruism, and multilevel selection theory.

### Kin Selection

This theory was developed by Hamilton (1964), and as its name indicates, kin selection explains altruistic behavior toward genetically related subjects. Hamilton, studying the behavior of insects

like ants, bees, and wasps, proposed that altruistic behavior could imply an indirect fitness (i.e., the transmission of one's genes through other bodies). He synthesized this proposal in an equation: an altruistic behavior is more likely to be selected naturally when the relatedness degree between the altruistic individual and the recipient, weighted by the reproduction benefits for the recipient, is higher than the reproduction cost for the altruistic individual. If kin selection explains altruism toward a related individual, how to understand why this behavior is sometimes directed to a non-kin? Reciprocal altruism addresses this question.

### Reciprocal Altruism

This theory, proposed by Trivers (1971), explains that a subject might help unrelated recipients because they would return the help in the future, which increases the helper's survival probability and therefore, the natural selection of this altruistic trait. Reciprocal altruism is more probable when there are frequent interactions between a helper and the recipients, which can be found in these conditions: (1) low dispersal rate, then there would be more interactions between a subject and the same others, (2) interdependence of members, so they need to be closer to each other, and in consequence, there would be more interactions among them, and (3) long lifetime for helper and recipients, because then there are more opportunities for the interaction.

Whereas in kin selection theory, the selection operates at the genetic level, in reciprocal altruism theory the selection works at the individual level. A third selection mechanism, occurring at group level, is offered by the following model.

### Multilevel Selection Theory

This theory extends the selection from genes or individuals to a group level (Wilson and Sober 1994). According to within group selection, altruistic subjects would have a relative fitness disadvantage compared to selfish individuals, because altruists help selfish subjects, who receive help without returning it. However, according to between groups selection, those groups with a higher proportion of altruistic individuals would

have more chances of survival than groups with more selfish subjects. This is because the former groups are more prepared to defend themselves from external threats and maintain a feeding system than the latter ones. Hence, multilevel selection theory proposes that altruistic traits are selected at the group level when between groups selection prevails over within group selection.

### Rescue Behavior in Humans and Nonhuman Animals

In humans and nonhuman animals, rescue behavior has been addressed in field and laboratory studies. Rescue behaviors are rare, especially in nonhuman animals. However, there is evidence of rescue behavior in social species of ants, dolphins, birds, and primates (including humans).

In *Ants*, this behavior has been informed in field and laboratory studies with few ant species, as *Tetramorium* sp. *E* (Taylor et al. 2013), *Cataglyphis cursor* (Andras et al. 2020; Nowbahari et al. 2009, 2012), *Formica sanguinea* Latr., *F. fusca* L., and *F. cinerea* Mayr (Czechowski et al. 2002), *F. cinerea* (Miler 2016), and *Veromessor pergandei* (Kwapich and Hölldobler 2019). The evidence shows that ants only rescue homocolonial individuals. For example, in a laboratory study two American *Tetramorium* sp. *E* ants were chosen as the victim and potential rescuer in different trials. The victim was put in an antlion's (the predator) pit in such a way that it was stunned and with injured legs. The antlion captured the victim, and then the other ant (potential rescuer) was put in the sand. The rescue behavior was displayed in 36% of trials approximately, and the most common was pulling the victim's limbs (less sensitive ant area) and, in a few cases, the rescuer attacked the antlion or transported sand away from the victim's body. The risk for the rescuer was the possibility of being grabbed by the antlion, which actually happened in some trials (Taylor et al. 2013).

In *Nonhuman primates*, rescue behavior has been reported in white-faced capuchins (Jack et al. 2020; Perry et al. 2003; Vogel and Fuentes-Jiménez 2006), and chimpanzees (*Pan troglodytes*; Boesch 1991). Those field studies show rescue behaviors among conspecifics, but there is

no evidence about the extension toward other species. An example of rescue behavior was described in a field study in Costa Rica with white-faced capuchin monkeys (*Cebus capucinus*). In a behavioral observation, a female was rescued from a threatening situation. In the situation, monkeys were organized in two groups (Vogel and Fuentes-Jiménez 2006). Individuals from Group A left the resting area and were chased by subjects from Group B. Behind all of them, an adult female and her infant from Group A were in a pool. Males from Group B came back and surrounded her and her infant. Those males made threatening vocalizations toward the female and tried to grab her infant. The female made alarm calls and submerged herself and her infant into the water, only keeping both heads above. A male from Group A came back to the pool and made threatening vocalizations against males in Group B, who then left the female and her infant.

In *Dolphins*, there is also some evidence of rescue behavior among conspecifics, specifically in *Tursiops truncatus* dolphins (Siebenaler and Caldwell 1956). For example, in an American school of dolphins, one adult, partially stunned by a dynamite explosion detonated by a fishing boat, was helped by two other adult dolphins. The rescuers placed themselves below and on either side of the injured dolphin, and then carried the victim to the surface where it could breathe. The position of the rescuers implied risk for themselves: they were near the explosion source and could not breathe because they were submerged. After a moment, the rescuers moved away from the stunned dolphin and went to the surface and blew. Two dolphins (there is no clarity whether they were the same original rescuers) then appeared and displayed continuous help for the stunned dolphin. This conduct, detailed by Siebenaler and Caldwell (1956), shows a possible coordination in helping among dolphins.

In *Birds*, a field study presented the first evidence of rescue behavior in social birds: Seychelles warblers (*Acrocephalus sechellensis*) from Cousin Island (Hammers and Brouwer 2017). Those birds are most of the time foraging in the tree's canopy but when they are on the

ground, they can get entangled in the sticky seeds of the *Pisonia grandis* tree, the most common tree in the study area. In this situation, the Seychelles warblers' lives are at risk because they have problems to fly and the seeds are hard to remove. The victims made alarm calls and received help from conspecifics, which took off the seeds by pulling or picking them. Rescuers put their lives at risk because they can also get entangled in the seeds.

Finally, other studies in *nonhuman species* refer to rescue behaviors that would not meet the conditions proposed by Hollis and Nowbahari (2013). For example, there are reports of rodents or dogs rescuing other trapped rats or dogs in a tube, and people in a cubicle, but it is questionable if those individuals put themselves at risk (e.g., Carballo et al. 2020).

In *Humans*, there is evidence of rescue behavior displayed toward other human and nonhuman animals in different contexts, for example, wars, natural disasters, daily life, etc. This behavior has been performed by firemen, first responders, soldiers, and general population, among others (Atran 2010; Fredman et al. 2015; Thompson 2013; Whitehouse 2018). Most reports come from field studies, probably because putting a victim in danger in a laboratory would be against ethical standards in human research. Thus, most laboratory studies tend to evaluate willingness to perform rescue behavior but not the action itself. An example of rescue behavior was performed by owners of pets (cats and/or dogs) in Wisconsin, United States, when cars of a train carrying propane derailed, and caught fire (Heath et al. 2001). Officials from the Emergency Operations Center asked people living around this area to evacuate the place because there was a risk of a major explosion. Some people, whose pets were not evacuated in the first days after the derailment, illegally entered the dangerous zone, putting themselves at risk, and rescued their pets.

## Conclusion

This entry reviewed the ultimate causes of rescue behavior and the different types of this behavior

displayed by human and nonhuman animals. Rescuing a genetically related subject can be explained by kin selection, multilevel selection, or reciprocal altruism theories, while rescuing a non-related individual can be explained only by the latter theory. Specifically, when rescuing related individuals, rescuers would (a) propagate their own genes in the rescued animals (kin selection), (b) receive help in the future from the victim (reciprocal altruism), and/or (c) contribute to their group survival of genetically related members (multilevel selection). On the other hand, rescue behavior toward a non-kin can be explained by reciprocal altruism theory: rescuers would increase their survival likelihood by eventually receiving help from the rescued animal.

Evidence of rescue behavior is available for some social species. This social dimension has promoted interest in moral variables associated with rescue behavior, such as empathy, intentionality, and consciousness of other individuals' needs. Nevertheless, the evidence is not sufficient and unequivocal to conclude that those moral variables are present in nonhuman rescuers, mainly because an operational definition of such constructs is a complex task. The exploration of these and other related variables is one of the main challenges for animal cognition and behavior research agendas.

## Cross-References

- [Altruism](#)
- [Cooperation](#)
- [Helping Behavior](#)
- [Karen Hollis](#)
- [Kin Selection](#)
- [Pro-social Behavior](#)
- [Reciprocity](#)

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## Resistance to Extinction

### ► Partial Reinforcement Extinction Effect

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## Resource Defense

### ► Territoriality

## Resource Defense Polygyny

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### Synonyms

Polygyny

### Definition

Resource defense polygyny is a mating system, whereby males of a species control a resource or territory necessary for successful female reproduction, and in which the male will mate with more than one female during a breeding season.

### Introduction

Resource defense polygyny is one of several different types of mating systems often observed in habitats with variation in the quality and distribution of resources. Different species will require different types of resources when determining habitat quality during the reproductive period. Factors that may increase the likelihood of polygynous behavior include the dependence by the animal on certain features in the habitat and time and resource requirements for male parental care (Emlen and Oring 1977). Polygyny often occurs in habitats with scarce resources. Females may have the capacity to assess resource quality within a male's territory and tolerate male polygynous behavior if her chance of reproduction within the high-resource quality territory is increased. The fitness benefits for the female under this system may be greater than if mating monogamously with a male who had secured poor resources.

When a female is selecting a mate, her decision is likely heavily based on two factors: the quality of the resources the male is defending and the quality of the male himself. If there is a cluster of resources that is appealing to a female, males of the species fight for control of those resources, thus indirectly controlling the female's ability to mate. In species that exhibit biparental care of offspring, the benefit of the male-defended resources and/or the genetic contribution of the male must outweigh the risk of extra-pair copulations or polygynous behavior where the male secures alternative mates (Emlen and Oring 1977). In polygynous relationships, males must balance perceived fitness tradeoffs in decisions to seek multiple mates. However, males that are polygynous typically exhibit greater fitness, provided costs of mate acquisition do not outweigh fitness gains. Males exhibiting polygynous behavior must also decide if the genetic benefit of mating with multiple females outweighs the fitness benefits associated with male parental care. For monogamy and parental care to be advantageous to a male, the cost of mating with multiple females must be greater than the cost of parental care. There are two groups of factors that impact fitness tradeoffs. First, there are factors that balance the costs/benefits of parental care in terms of survival rate of the offspring. Second, there are factors that impact the cost/benefit of multiple copulations (Westneat et al. 1990).

### Examples of Resource Defense Polygyny

An example of resource defense polygyny can be found in the yellow-bellied marmot (*Marmota flaviventris*), in which males guard caves that are valuable for shelter and hibernation. A group of females will co-occupy a specific cave with a male at a given time. Often these female groups are called harems and linked to harem defense polygyny; however, the male marmot is not forcing the female marmot into the cave. Instead, males are dominating the desirable cave resource, which is valuable enough that the females will tolerate male polygynous behavior.

Hummingbirds also exhibit resource defense polygyny associated with resources provided by their primary food source, nectar. Males will defend areas with substantial production of nectar flowers in a cluster. Female hummingbirds have substantial nectar requirements for effective parental care, and resource-defending males will allow select females access to the resource while excluding other individuals. In this example, the amount of resources (i.e., number of nectar producing flowers) the male controls will dictate the number of females he will secure as mates (Emlen and Oring 1977).

The Colombian cranainae (*Phareicranus pff. spinulatus*) is an Arthropoda species that also demonstrates resource defense polygyny. Males of this species use their long legs in direct conflict with other males to secure optimum habitat for female egg laying (García-Hernández and Machado 2018). Individuals either use a set of secondary legs to whip and momentarily immobilize other males, or use their first set of legs to strike the other secondary leg of competing males.

## Conclusion

Animals displaying resource defense polygyny have adapted to this mating system due to myriad factors including changes in male parental care, increasing variation or restriction of key resources in the environment, or other factors. Researchers suspect that resource defense polygyny can evolve to be an optimum strategy in resource or space-limited environments and will likely be evident in more species when studied extensively. The more likely that resources and parental care are the limiting factors, the more likely it is for a species to exhibit resource defense polygyny.

## Cross-References

- ▶ Aggression
- ▶ Competition
- ▶ Cuckoldry
- ▶ Extra-Pair Copulation
- ▶ Female Choice
- ▶ Female Defense Polygyny

- ▶ Mating Effort
- ▶ Pair Bond
- ▶ Parental Investment
- ▶ Paternal Behavior
- ▶ Polygamy
- ▶ Reproduction
- ▶ Resource Defense
- ▶ Scramble Competition Polygyny
- ▶ Scramble Defense Polygyny
- ▶ Sneaky Copulator
- ▶ Territory Defense

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## Resource Holding Potential

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## Synonyms

Fighting Ability; Resource holding power

## Definition

Morphological and physiological traits affecting the ability to win a direct competitive contest over a limited resource.

## Summary

Animals use contests, with displays and/or fighting, as direct competition to resolve disputes over finite resources (Parker, 1974; Rudin and Briffa, 2012). The resources fought over can affect their fitness either directly (e.g., mating opportunities) or indirectly (e.g., food) (Palaoro and Briffa, 2017). The contests are frequently decided when one of the individuals withdraws from a fight or refuses to engage, and less frequently by one individual killing another. Morphological and physiological traits determining the potential to win these contests are defined as an individual's resource holding potential (RHP). The concept was initially proposed by Parker (1974) who referred to it as the 'resource holding power'. Traits typically considered to determine RHP include body mass, body size, weapons, contest experience, and physiological state (Batchelor et al., 2012; Hsu and Wolf, 2001; Parker, 1974). More recently some authors have suggested that also certain behavioral traits, such as daring or boldness, should be considered a RHP trait (Rudin and Briffa, 2012).

Physical RHP traits can be either offensive or defensive. Offensive traits include body size and strength, and defensive traits include stamina and the ability to endure damage and attacks (Palaoro and Briffa, 2017). These traits form the individual's fighting ability, which often determines the outcome of contests (Hsu and Wolf, 2001; Palaoro and Briffa, 2017). In social species the outcome also depends on the group size. Group RHP depends primarily on the number of group members and the RHPs of individuals within each group (Batchelor et al., 2012), although in some cases presence of an individual with very high RHP (e.g., a mature male) can offset any advantage in numbers (Cooper, 1991). The traits that determine RHP in contests can be a complex combination depending on the environment and resources being fought over.

Accurate assessment of RHP, both one's own (absolute RHP) and in comparison to their opponent's (relative RHP), is a key factor in determining the outcome of contests. Many intraspecific contest displays and initial fighting are ritualized in order to assess the opponent's RHP and reduce injuries (Keeley and Grant, 1993; Parker, 1974).

Prior visual assessment allows for assessment of size which can decrease contest duration, while initial fighting allows for assessment of strength and other traits (Keeley and Grant, 1993). If assessments of RHP are accurate it allows animals to avoid conflict, engage, or disengage from conflicts and therefore increase or limit the time and energy lost during contests as well as the potential for risk of injury (Arnott and Elwood, 2008; Parker, 1974). Variation occurs in individual's abilities to accurately assess RHP, and prior experience increase self-assessment of RHP, but does not necessarily affect fighting ability itself (Hsu and Wolf, 2001; Keeley and Grant, 1993). Many species have evolved behaviors or morphological traits that exaggerate the cues used for RHP assessment, such as displays of large teeth, horns, claws and other weapons, or ornamentation such as luxuriant hairs, feathers and fins. Such 'evolutionary cheating signals' are attempts to increase the apparent RHP, although such features are often good indications of an individual's fitness and absolute RHP (Parker, 1974).

Although RHP is a critical factor in determining the outcome of contests for a resource, empirical test have repeatedly demonstrated that individuals with higher RHP do not necessary always win a contest. Instead the outcome can also be influenced by other factors, including motivation (the subjective value individuals place on the resource), aggressiveness and ownership status (Allen et al., 2016; Arnott and Elwood, 2008; Batchelor et al., 2012; Parker, 1974). The initial owner of a resource is often more likely to win a contest, potentially due to either their experience or investment in the resource (Arnott and Elwood, 2008) or due to the benefits gained from the tenure of the resource itself (Parker, 1974). Rarity of a resource increases its value and therefore the motivation to obtain and investment in the resource, and also makes resource guarding more likely (Keeley and Grant, 1993; Parker, 1974).

Most studies to date have focused on intraspecific contests over resources. Although RHP in interspecific contests are understudied to date, they have the potential for increasing our understanding of RHP with future study. The ability to

assess RHP varies by species (Arnott and Elwood, 2008), as does size, strength, and other morphological traits that determine RHP. As with intraspecific contests, size and stamina are likely critical to RHP and determining the winner of interspecific contests. Initial research shows that species-specific weapons are also important in these contests (Allen et al., 2016; Martin and Ghalambor, 2014), as well as social behavior since group-living species are clearly advantaged as greater numbers can outweigh body-size differences (Cooper, 1991). Species-specific traits create advantages and mismatches in RHP (Allen et al., 2016; Martin and Ghalambor, 2014), that make assessment important. Most interspecific bouts are over food and other resources, indirect sources of fitness that can hold less value than direct sources of fitness. However, interspecific contests also more often result in death of one or both of the contestants than in intraspecific contests, thus directly affecting fitness.

## Cross-References

- Aggression
- Agonistic Behavior
- Competition
- Dominance
- Mate Guarding
- Motivation
- Resource Defense
- Resource Holding Potential

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## Resource Holding Power

- Resource Holding Potential

## Resource Provisioning

- Mate Provisioning

## Respiratory System

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## Synonyms

Breathing; Lung



## Definition

System that allows animals to breathe and exchange oxygen and carbon dioxide throughout the body; it is composed of nose, pharynx, larynx, tracheobronchial tree, and lungs.

## Introduction

The respiratory system can be divided into the upper respiratory system, which is composed of the nose and pharynx, and the lower respiratory system which is generally composed of the larynx, tracheobronchial tree, and the lungs. This vital system of the body has many functions including olfaction detection, vocalization production, behavioral cues, filtration and humidification of inhaled breaths, and of course gas exchange. This text will discuss the anatomy and function of the respiratory system as well as domestic animal differences that may be important in a clinical setting.

## Upper Respiratory System

The upper respiratory system is composed of the nose and pharynx (Tortora and Derrickson 2009).

### Nose

The nose allows entrance of an inhaled breath to be carried towards the lungs or the olfactory center, warms and humidifies incoming air, and contributes to animal behavior. For example, a horse exhibits “flared nostrils” when angry. The form of the nares is altered by raising the ala via facial musculature or by breathing deeply/sniffing. The nose consists of the external nose, the nares, paired nasal cavities, and the paranasal sinuses. Unlike humans, animals’ noses are generally contoured within the muzzle. In most domestic animals, the external nose is composed of cartilaginous material covered by thick keratinized epithelium. The left and right nasal cavities are separated by a nasal septum cranially which is mostly cartilaginous but is ossified caudally.

The hard palate forms the floor of the nasal cavities separating them from the oral cavity. Nasolacrimal ducts and serous lateral nasal glands empty into the nose which aids in humidification of the air. The right and left nasal cavities join caudally and are filled with nasal conchae (usually dorsal, middle, and ventral conchae). The nasal conchae are composed of tissue with extensive vasculature whose purpose is to warm the incoming air. The conchae mucosa thickness depends on the health of the vasculature. For example, if the vessels are swollen from inflammation/congestion, this leads to decreased airflow and decreased sense of smell which is often associated with the common cold in humans. These conchae are separated by ethmoidal meatuses. The dorsal meatus carries inhaled air to the olfactory mucosa. The middle meatus allows the sinuses to drain. The ventral and common meatuses carry air to the pharynx on its way to the lungs (Dyce et al. 2002).

### Pharynx

The pharynx is a passageway for air and food. It serves as a resonating chamber for vocalization and also contains the tonsils. It is divided into three portions – the nasopharynx, the oropharynx, and the laryngopharynx. The soft palate separates the nasopharynx (which lies dorsal to the soft palate) and the oropharynx (which lies ventral to the soft palate).

The nasopharynx is lined by pseudostratified ciliated columnar epithelium which works to move debris collected from the incoming air towards the laryngopharynx where it can be swallowed into the esophagus. The nasopharynx also communicates with the middle ear to equalize air pressure during changing altitudes. The oropharynx is a passageway for food or air entering through the mouth and is lined by nonkeratinized stratified squamous epithelium which is able to better sustain damage from abrasive food particles compared to the pseudostratified ciliated columnar epithelium of the nasopharynx. The palatine tonsils are located in the oropharynx. The laryngopharynx lies caudal to the nasopharynx and oropharynx. It enters directly into the esophagus and larynx. The larynx, or “voicebox,”

then leads into the trachea (Tortora and Derrickson 2009).

## Lower Respiratory System

The lower respiratory system includes the larynx, tracheobronchial tree, and lungs (Tortora and Derrickson 2009).

### Larynx

Commonly known as the voice box, the larynx connects the laryngopharynx to the trachea. The function of the larynx is to prevent aspiration of food/liquids, produce sound, and capture dust that escaped the upper airways (Tortora and Derrickson 2009). The larynx is composed of cartilages which vary from species to species. The major laryngeal cartilages present in most species include the epiglottis, thyroid cartilage, cricoid cartilage, and the paired arytenoid cartilages. When at rest, the epiglottis allows air into the trachea. When swallowing, the epiglottis covers the entrance to the larynx directing food into the esophagus and preventing food from entering the trachea. The thyroid cartilage is the largest of these cartilages and forms the majority of the laryngeal floor. The most rostral part is thickened and corresponds with the “Adam’s apple” in humans (Dyce et al. 2002). The cricoid cartilage usually has the appearance of a “signet ring” which articulates rostrally with the thyroid cartilage and dorsally with the arytenoid cartilages (Dyce et al. 2002). The arytenoid cartilages are mobile and influence changes in position and tension of the vocal folds (Tortora and Derrickson 2009). The arytenoid cartilages and the vocals folds are collectively referred to as the glottis. The vocal folds of the glottis are appropriately named as they produce sound as air flows over them. The pitch is controlled by thickness, length, and tension of the folds, and the sound is altered in the resonating chamber of the pharynx (Dyce et al. 2002). The lining of the larynx rostral to the vocal folds is composed of nonkeratinized stratified squamous epithelium. Caudal to the vocal folds, the lining is composed of pseudostratified ciliated columnar epithelium that moves up towards the

pharynx to prevent debris from entering the trachea and traveling into the lungs. This epithelium contains goblet cells that produce sticky mucus to trap dust which can then be transported up the mucociliary elevator (Tortora and Derrickson 2009). In addition to preventing aspiration of food/liquids, phonating, and capturing debris, the larynx also plays a role in strenuous breathing and coughing. During vigorous breathing, the arytenoids are actively abducted to allow for larger breathes to be taken. During coughing, large expiratory forces build up against the closed glottis and allow for a forceful expulsion of air when opened. The glottis will also close with increased thoracic pressure/straining such as during defecation, forceful micturition, and parturition (Dyce et al. 2002).

### Tracheobronchial Tree

The trachea is a tubular passageway composed of cartilage which may form complete or incomplete rings, depending on the species (Dyce et al. 2002). Animals with complete tracheal rings are usually more difficult to intubate for procedures. Incomplete tracheal rings are connected by the trachealis muscle which allows the diameter of the trachea to change. The trachea is lined by pseudostratified ciliated columnar epithelium which functions similar to the ciliated epithelium of the larynx (Tortora and Derrickson 2009). In most animals, the trachea travels from the larynx, through the thoracic inlet, and bifurcates into bronchi. However, in ruminants and pigs, another bronchus arises proximal to the tracheal bifurcation to supply the cranial lobe of the right lung (Dyce et al. 2002). The right bronchus is slightly shorter than the left, making aspiration into the right lung more common than into the left. The primary bronchi (main bronchi) continue down into the lungs and become the secondary bronchi, tertiary bronchi, bronchioles, and terminal bronchioles. The secondary bronchi are also referred to as lobar bronchi as there is one for each lung lobe. Tertiary bronchi (segmental bronchi) mark the transition from pseudostratified ciliated columnar epithelium to ciliated simple columnar epithelium in the bronchioles. The larger bronchioles contain goblet cells, but the smaller bronchioles do not.

In the terminal bronchioles, the epithelium transitions to simple non-ciliated cuboidal epithelium with debris being removed by macrophages rather than carried orally by the mucociliary elevator. The tracheobronchial cartilage structure continues to the level of the bronchioles, with gradual replacement of cartilage by smooth muscle. The terminal bronchioles are only supported by smooth muscle which can be a problem during asthma attacks. During an asthma attack, the smooth muscle in the terminal bronchioles constricts, closing off the airways (Tortora and Derrickson 2009).

## Lungs

The main function of the lungs is to facilitate gas exchange. The lungs are free-floating structures within the thorax suspended from the mediastinum. They change in size depending on respiration, although the right lung is always larger than the left due to the natural position of the heart. The left and right lungs are subdivided into different lobes which vary depending on the species. Most animals have an accessory lung lobe that is associated with the right lung and lies over the caudal vena cava (Dyce et al. 2002). The apex of the lungs lies cranially with the base of the lungs contacting the diaphragm caudally. The costal surface lies against the ribs and the mediastinal surface lies against the mediastinum. The lungs are covered by a pleural membrane which is composed of the parietal pleura and the visceral pleura. The parietal pleura lines the wall of the thoracic cavity and the visceral pleura lies over the lungs. Between the pleurae, there is a pleural cavity that contains fluid that allows the lungs to easily slide against the pleura during expansion upon inhalation (Tortora and Derrickson 2009). The inner portion of the lungs includes the tracheobronchial tree as discussed above. The terminal bronchioles give way to alveolar ducts, alveolar sacs, and alveoli as continued branching occurs (Dyce et al. 2002). Alveolar sacs consist of two or more alveoli that share a common alveolar duct opening (Tortora and Derrickson 2009). Gas exchange takes place within alveoli. Alveoli are small spaces that consist of thin epithelium closely opposed to pulmonary capillaries (Dyce

et al. 2002). Gas exchange occurs by diffusion, with oxygen diffusing into the capillaries and waste gases such as carbon dioxide diffusing from the capillaries into the alveolus. Inhalation is an active process involving contraction of the diaphragm and external intercostal muscles. The lungs are pulled down and expanded allowing for air intake. Exhalation is normally a passive process that results from elastic recoil of the chest wall. However, during strenuous exercise or disease, exhalation can become an active process with forceful contraction of the abdominal muscles and internal intercostal muscles (Tortora and Derrickson 2009).

## Domestic Animal Differences

### Dogs and Cats

Dogs' skull conformation widely varies compared to cats'. Dogs may be referred to as dolichocephalic, mesaticephalic, or brachycephalic. These dogs have long, medium, or short noses respectively. In many brachycephalic dogs, the nasal conchae are contained in such a small space that it causes breathing through the nose almost impossible. These dogs also usually have a soft palate that is disproportionately long and lies over the entrance to the larynx, causing respiratory difficulties. Dogs' ethmoidal conchae, which allow for sense of smell, are actually larger and more extensive than their nasal conchae. Cats have a unique adaptation to their larynx which allows them to purr. Purring is produced by fast twitching of the muscles in the larynx and diaphragm. The laryngeal muscles cause the glottis to rapidly widen and narrow leading to the vibration of air which we know as purring. Dogs and cats have incomplete tracheal rings. Both have the same lung lobe anatomy – the right lung being divided into the cranial, middle, caudal, and accessory lung lobes, and the left lung being composed of a divided cranial lung lobe and a single caudal lung lobe (Dyce et al. 2002).

### Horses

The nostrils of horses are especially large and are supported by alar cartilages which allow them to

actively flare the nostrils during certain behaviors. The alar cartilages are also important because horses are obligate nasal breathers. During strenuous exercise, the horse is able to actively widen the nostril to allow for a bigger breath. Within the nose, there is a blind nasal diverticulum dorsal to the actual nasal cavity. When passing a nasogastric tube, it is important to pass the tube central and ventral to avoid the nasal diverticulum. The nasopharynx contains flaps that overlie the entrance to the auditory tubes. These flaps open during swallowing, so the horse is only able to equalize pressure during swallowing. Horses have incomplete tracheal rings. The lungs are more equal in size than in any other species and are elongate. Because of this, the left and right lungs are both only divided into cranial and caudal lung lobes, with the right lung also having the accessory lung lobe (Dyce et al. 2002).

### Ruminants

The oropharynx in ruminants is particularly small, restricting the size of food boluses that these animals can ingest. During eructation, the pharynx directs most of the eructated gas into the lungs. The reason for this is unknown, but animals on certain rations may have lung pathology associated with this phenomenon. Ruminant intubation may be limited by the small size of the glottis cleft and the slight caudal deflection of the entrance to the larynx. Ruminants have incomplete tracheal rings and a bronchus arises proximal to the tracheal bifurcation to supply the cranial lobe of the right lung. The right lung is composed of cranial, caudal, middle, and accessory lung lobes. The left lung is composed of divided cranial lobes and a single caudal lobe. As other animals, the diaphragm predominates normal breathing activity for ruminants. However, cattle have been known to survive diaphragmatic paralysis. Unlike horses, which have a large reserve capacity, ruminants have a small total alveolar surface area, of which a large portion is required for basal needs. Therefore, during stressful circumstances, there is not much more gas exchange area that can be utilized (Dyce et al. 2002).

### Pigs

Unlike noses of other animals, pigs have a snout that has a rounded moveable tip that incorporates the upper lip. Pigs use their snouts for rooting behavior. Some farmers prevent rooting behavior by placing rings through the dorsal border of the snout rather than the nostrils as seen in bulls. Pigs have a very good sense of smell which the French exploit by having pigs search for truffle mushrooms. Pigs have a unique feature within the pharynx called the pharyngeal diverticulum, which arises from the pharyngeal wall dorsal to the entrance to the esophagus. This structure is important to locate and avoid when dosing pigs with syringes, because injections into the pharyngeal diverticulum can cause serious injury to underlying tissues. The larynx has lateral ventricles and forms an obtuse angle with the trachea, both of which cause intubation to be difficult. Pigs have incomplete tracheal rings. The right lung is composed of cranial, middle, caudal, and accessory lobes. The left lung has a divided cranial lobe and a caudal lobe. Like in ruminants, the cranial lobe of the right lung is ventilated by a separate tracheal bronchus that arises before the tracheal bifurcation (Dyce et al. 2002).

### Ferrets

Ferrets are obligate nasal breathers. The trachea has incomplete rings and is 2–3 times the length compared to dogs and cats. The left lung is divided into cranial and caudal lobes while the right lung is divided into cranial, middle, caudal, and accessory lobes. Ferrets have extremely large lung capacities, having the second largest lung capacity of all mammals behind the sea otter. Their large lung capacity allows for successful underground hunting. Ferrets also have very compliant chest walls, which allow them to turn in tight spaces. Like humans, ferrets vasoconstrict pulmonary vessels under hypoxic conditions such as changes in atmospheric pressure (Johnson-Delaney and Orosz 2011a).

### Guinea Pigs and Chinchillas

Guinea pigs and chinchillas are obligate nasal breathers. Guinea pigs have small vocal folds compared to other animals but are still able to

vocalize loudly. For both guinea pigs and chinchillas, the right lung is divided into cranial, caudal, and accessory lobes, and the left lung is divided into cranial, middle, caudal, and accessory lobes. Compared to other animals, guinea pigs and chinchillas have small lungs because the heart occupies most of the thoracic cavity. It is interesting to note that on radiographs, bony spicules may appear in the lungs of guinea pigs which are a normal radiographic finding. These spicules are often asymmetric throughout the lungs and may be mistaken for foreign bodies (Yarto-Jaramillo 2011).

### Hedgehogs and Sugar Gliders

Hedgehogs rely heavily on sense of smell to navigate, detect predators, and communicate. An interesting behavior that hedgehogs possess is known as “self-anointing” which occurs during an intense olfactory stimulation such as anesthetic gases, perfumes, cat food, etc. The hedgehog will hypersalivate and slather the saliva over its spines on its flank and back with its tongue. This behavior is thought to be used to mark the individual or the surrounding territory. Hedgehogs usually have a silent respiration; however, when frightened, they may exhale forcefully. This hissing sound should not be confused with respiratory distress. Another important fact is that hedgehogs undergo hibernation when the temperature drops to a certain degree or estivation when the temperature rises to a certain degree. The degree at which this occurs depends on the breed of hedgehog. Captive hedgehogs do not undergo hibernation unless there is a temperature discrepancy or a nutritional issue. Normal respiratory rate during hibernation may drop to 1–8 breathes per minute. Hibernation actually increases the blood oxygen affinity and blood-to-tissue diffusion of oxygen so this lower respiratory rate still adequately supplies the entire body with oxygen. Sugar gliders also rely on sense of smell for communication via multiple scent glands and make a variety of odd vocalizations that should not be confused with respiratory disease. While sugar gliders do not undergo hibernation, they may exhibit torpor (a shortened hibernation that lasts anywhere from 2 to 23 h) and huddling behavior. Oxygen

consumption is decreased at this time. Torpor is triggered by starvation or lack of foraging rather than temperature changes, so if a client presents a sugar glider with this issue, husbandry and nutrition are the key issues to focus on (Johnson 2011).

### Mice, Rats, Hamsters, and Gerbils

All rodents are obligate nasal breathers. Mice, rats, and guinea pigs have high chest wall compliances. Mice, rats, hamsters, and gerbils have incomplete tracheal rings. Rats possess a special nasal gland called the Steno’s gland that is located in the rostral maxillary sinus and produces watery secretions to humidify inspired air and regulate mucus viscosity. Newborn rats have no alveoli or alveolar ducts, and gas exchange occurs in sacculi until about 4 days of age. By day 7, the rat lung is mature. Rat lungs do not contain bronchioles. Rats also have unique serous cells within their respiratory epithelium that secrete serous material to decrease viscosity in the airways. The rat’s lung surfactant is high in polyunsaturated phospholipids rather than monounsaturated phospholipids compared to other mammals. Like rats, hamsters also possess a Steno gland along with 13 other nasal serous glands and do not have bronchioles. In mice, rats, hamsters, and gerbils, the left lung is composed of a single lobe. In mice, rats, and gerbils, the right lung is divided into cranial, middle, caudal, and accessory lung lobes. The hamster has an extra right lung lobe known as the intermediate lung lobe (King 2011).

### Rabbits

Rabbits are obligate nasal breathers with incomplete tracheal rings. They have sensory pads on their nostrils which makes the nose a sensitive area. When breathing normally, the nose is still, but rabbits’ noses may twitch up to 150 times per minute. Both the left and right lungs have cranial, middle, and caudal lobes, with the right lung also possessing an accessory lobe. The diaphragm is the sole muscle responsible for inhalation (Johnson-Delaney and Orosz 2011b).

### Chelonians (Turtles, Tortoises)

Chelonians have significant differences in their respiratory system. Their trachea is short



and flexible which allows for retraction of the head into the shell and is composed of complete tracheal rings. Chelonians do not have a tracheo-bronchial tree, but it instead possess unbranched interpulmonary bronchi with ediculi and faveoli as the gas exchange sites rather than alveoli. Their lungs have limited room to expand due to their bony shell. They also do not have a diaphragm. Ventilation is achieved by contraction and relaxation of the inguinal, axial, and shoulder muscles, so it is normal for the limbs to move slightly during respiration. Unlike other animals that rely on negative pressure ventilation to breathe, chelonians rely on positive pressure ventilation which allows them to ventilate normally even with a compromised shell. In general, open mouth breathing in these animals is a sign of respiratory distress. However, they may exhibit movement of the ventral mandibular area called “gular pumping” which may be mistaken for open mouth breathing. Gular pumping in chelonians is a behavior used to assist in olfaction contrary to gular pumping in amphibians which is part of normal respiration (Bennett 2011).

### Birds

Like chelonians, birds have major differences in their respiratory system compared to domestic mammals. The nostrils of birds are located at the base of the beak. In some species of birds such as psittacines, pigeons, and raptors, the nostrils are covered by a cere which is a membrane that may be a different color depending on the sex of the bird. For example, male budgerigars have a blue cere and females have a light brown cere. The nostrils lead into a divided nasal cavity that, through the choana, communicate with the oropharynx. Birds have a nasal gland within the nasal cavity similar to the Steno gland in rats and hamsters. The larynx of birds does not contain vocal folds. Instead, vocalization is produced by the syrinx, a specialized structure that lies at the tracheal bifurcation. In male ducks and swans, an osseous bulla is present on the left side of the syrinx, believed to be a resonator. Song birds have complex syringeal muscles that allow for a variety of sounds to be produced. The trachea in birds is composed of

complete tracheal rings and, in long-necked birds, can be so extensive that it folds back on itself. The true lungs in birds are small and lie craniodorsally to the heart, but do not contact the heart. The lungs have an extensive cartilage make-up and are non-expansile. Birds do not have a diaphragm, and instead rely on rib cage movements to breathe. At the tracheal bifurcation, primary bronchi give way to secondary bronchi which communicate with air sacs. Air sacs are actually enlargements of the bronchial system that have diverticula that extend to enter various bones and skeletal muscles. The secondary bronchi give off 400–500 parabronchi in the lungs where counter-current gas exchange takes place. The complete respiratory cycle of the bird requires two breath cycles. On the first inhalation, air is moved into the caudal air sacs. On the first exhalation, air is moved into lungs. The second inhalation moves air into the cranial air sacs. The second exhalation moves the air out of the bird. Inspiration draws air through the lungs and into the air sacs – the caudal air sacs receive fresh air and the cranial air sacs receive relatively de-oxygenated air. During expiration, the air sacs are compressed and air from the caudal air sacs flows through the lungs and air from the cranial air sacs is expelled. In this way, the bird respiratory system is extremely efficient as there is always oxygen-rich air moving through the lungs, which is especially important during flight when the bird is using massive amount of oxygen at high altitudes (Dyce et al. 2002).

### Conclusion

While there are many species variations in the anatomy of the respiratory system, the function remains cohesive across all species. The respiratory system enables animals to smell, vocalize, communicate, filtrate, and humidify incoming air and exchange gas to provide the body with oxygen and rid the body of waste gases. A compromised respiratory system may be life-threatening to any animal. However, understanding normal respiratory behaviors in some animals may be necessary to differentiate behavior from disease.

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## Response Bias

- [Judgment Bias](#)

## Response-Dependent Aversive Stimulation

- [Punishment](#)

## Response-Initiated Delays in Reinforcement

- [Punishment](#)

## Restraint

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## Synonyms

[Control](#); [Deprivation of liberty](#); [Dispassionate](#); [Immobilization](#); [Moderate behavior](#); [Restriction](#); [Self-control](#); [Understatements](#); [Unemotional](#)

Restraint is a condition of being inhibited or controlled (Merriam-Webster Dictionary online 2019). Restraint can be physical, chemical, and psychological (Sheldon et al. 2006; Browning 2012; Lawson 2004). In reference to animals, it is necessary to use restraint in order to perform medical procedures, give medications, to collect samples for diagnostic tests and to complete husbandry needs. In some cases animals serve a valuable use and some form of restraint is necessary for them to complete the task. Over the past three decades, there has been a definitive shift from acting from the standpoint of completing tasks as quickly as possible despite the struggle or stress from the animal to spending time calming and reducing the stress placed upon the animal in order to complete the task. Studies have found that each time an animal is stressed during handling it not only can impact the animal's health but also adversely affect future handling (Hammerle et al. 2015).

## Physical Restraint Can Be Manual or Mechanical

Manual restraint is the forced restriction of movement of all or part of an animal's body by an individual. There is a large variety of manual restraint techniques that those in the professions of research, veterinary medicine, and farming are trained extensively in to stay safe and keep the animal safe. How the animal is held depends on the species, the ethology of the animal, and how

that species can cause damage to the handler(s). Specifically, the animal's most dangerous body part is controlled first, and then through the use of pressure points, the animal is kept from moving. For example, the head of a dog would be the primary body part to keep from moving, as the teeth and mouth are the most dangerous.

Mechanical restraint is using a device to immobilize the animal. There are many restraint devices but some of the more common are: leashes, slip leads, muzzles, stanchions, squeeze chutes, cat bags, towel wraps, head collars, hip clamps, head halters, body harnesses, fences, invisible fences, cattle prods, hog snares, bridles, rabbit boxes, and face masks. Physical restraint has evolved over the last two decades from forceful immobilization to using mechanical devices to calm animals while also immobilizing them. These accommodations both keep staff members safe as well as calm the animal (Rudolph 2015).

Chemical restraint is the use of compounds to either sedate or anesthetize an animal to a point of immobility or compliance. Chemical restraint is used when physical restraint is not possible or the animal's stress or physiological state would make it dangerous to physically restrain. Over the past two decades chemical restraint is being used more often as a means of causing less stress to animals along with being more efficient (Hammerle et al. 2015). There is inherent risk using chemical restraint, especially if the animal's health status is not well known. However, in the professional animal fields, it is found that the risk of chemical restraint is preferable to the risk of the animal becoming overly stressed and the subsequent physiological and psychological consequences due to the excessive stress, (Hammerle et al. 2015). Recommended medications to relieve stress and at times immobilize patients in veterinary clinics are: BZD's (benzodiazepines), TCA's (tricyclic antidepressants), SARI's, (selective serotonin reuptake inhibitors), SARI's (dual serotonin 2A agonist/serotonin reuptake inhibitors), MAOI's (monamine oxidase inhibitors), Buspirones, centrally acting 2A agonists, and local anesthetics (Hammerle et al. 2015). The use of these anxiolytics are to relieve fear, anxiety, and stress (FAS), in the animal along with low stress handling to make medical exams and procedures more efficient and smooth.

Psychological restraint is the use of an animal's ethology, body language, and learning theory to gain compliancy (Browning 2012). Learning theory is the combination of classical conditioning and operant conditioning. Classical conditioning is the associations made between an external stimuli and internal physiological response. Operant conditioning is associations made between an act or nonaction on the environment and the subsequent consequence. Within operant conditioning, there are four possible consequences: positive reinforcement, positive punishment, negative reinforcement, and negative punishment (Pryor 1999). Positive reinforcement is when the consequence is added (positive) to increase the probability of the preceding behavior to be repeated (reinforcement). Positive punishment is when the consequence is added (positive) to decrease the probability of the preceding behavior to be repeated (punishment). Negative reinforcement is when the consequence is removed (negative) to increase the probability of the preceding behavior to be repeated (reinforcement), where negative punishment is the consequence removed (negative), to decrease the probability of the preceding behavior being repeated (punishment). The four possible outcomes of an individual's actions are what are known as the learning theory quadrant (Pryor 1999).

Psychological restraint is becoming a focal point of animal restraint over the last 30 years (Browning 2012; Wyatt 2013; Reiche 2016; Moffett 2015). Historically, the use of negative reinforcement has been the primary psychological restraint used along with manual and mechanical physical restraint. For example, when working with horses, a person will apply pressure on to the horse through a physical restraint until the animal complies slightly at which point the pressure is taken away; thus the animal "learns" that by not fighting the pressure is removed. There has been a strong history of positive punishment used in past decades when it came to controlling an animal that has dropped in popularity in the animal professions. Devices such as cattle prods and whips are now considered last resort measures in most professions as a means of controlling animals (Hammerle et al. 2015). Studies have shown that the use of cattle prods used in the beef industry is at 5.5%, which is well below the 10%

accepted limit placed by the Beef Quality Assurance, BQA (Woiwode and Grandin 2014).

A pioneer in psychological restraint is Dr. Temple Grandin, a professor from Colorado State University, with her use of chute and squeeze chute designs for large moving large animals. Through strategically placed curves and blind spots, she has improved the efficiency of the meat industry as well as decreased stress and anxiety for animals (Grandin 1995). By viewing a facility with an animal's ethology in mind, Grandin has succeeded in making the environment less threatening and thus reducing the stress and sympathetic nervous system response of the animal, making the whole system more efficient. Her work was groundbreaking in the field of farming and agriculture. Several facilities have taken to implementing Dr. Grandin's chute designs and auditing system to make production more efficient (North American Meat Institute 2017).

Another pioneer in psychological restraint is Dr. Sophia Yin, a veterinarian and animal behaviorist. Dr. Yin began a movement of stress free handling and restraint in the field of veterinary medicine. Dr. Yin developed a series of books, videos, and workshops on the use of negative reinforcement and positive reinforcement as a means of desensitizing and counter condition animals to medical restraint and procedures. Her work has been eye opening in the field of veterinary medicine.

Dr. Marty Becker, a veterinarian and popular radio personality, recently developed a certification program for veterinary professionals in the art of fear-free veterinary visits. Through the fear-free certification process, veterinary and animal professionals are taught to work with companion animals in as fear free manner as possible. First, the individual is taught the normal ethology of the animal, deciphering their body language, and understanding the basics of learning theory, an individual is taught how to approach and measure an animal's FAS: Fear, Anxiety, and Stress. If an animal's FAS is measured as high chemical restraint is used early on so as to not worsen the animal's FAS for future visits (Browning 2012).

Many research facilities are training animals to take an active role in their husbandry and medical procedures. Ken Ramirez, the head curator and

trainer at the Shedd Aquarium in Chicago, Illinois, is a forerunner in educating professionals in how to train exotic and wildlife species in cooperating in their own husbandry and medical care (Ramirez 1999).

An example of active compliancy is primates, being trained to place their limb outside their cage and hold it there until the caregiver has taken a blood sample. The animal is then rewarded with a treat of some kind (positive reinforcement). This use of positive reinforcement has been implemented across species of wildlife and domestic species in research and conservation facilities such as zoos and aquariums (Grandin 1997; Phillips et al. 1998). This means of acquiring active compliance is becoming more common place in the veterinary field as well.

Restraint is an integral part of managing and caring for animals. What used to be a means of obtaining control via force and coercion has begun to shift toward a more cooperative endeavor.

## Cross-References

- Classical Conditioning
- Ethogram
- Feline Cognition
- Feline Communication
- Husbandry
- Learning Theory
- Negative Reinforcement
- Operant Conditioning
- Pets
- Reinforcement

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## Restriction

### ► Restraint

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## Restriction Endonucleases

### ► Restriction Enzyme

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## Restriction Enzyme

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## Synonyms

Molecular scissors; Restriction endonucleases

## Definition

A restriction enzyme is a site-specific endonuclease encoded by bacteria and archaea that recognizes a specific, short nucleotide sequence and cuts the DNA only at that specific site, i.e., restriction site.

It provides a defense mechanism to bacterial host against invading viruses, i.e., bacteriophages (Arber and Linn 1969; Krüger and Bickle 1983). Basically, restriction enzymes were named for their ability to restrict the growth of bacteriophages in a host bacterial cell by selective cleavage of the invading foreign DNA. This process is called restriction digestion. Interestingly, the host DNA is protected from their own restriction enzymes by the activity of



a modification enzyme (methyltransferase or methylase), which detects the same restriction site as the restriction enzyme and methylates a specific nucleotide (e.g., 4-methylcytosine, 5-methylcytosine, 5-hydroxymethylcytosine, or 6-methyladenine) on each strand within this restriction site. Methylation of only one strand, i.e., hemi-methylated state of restriction site, is also protected from restriction enzyme. Together, these two processes constitute the restriction modification (RM) system.

## Restriction Site

Each restriction enzyme identifies a specific sequence of nucleotides (between four and eight bases) and makes cut in both strands of the double-stranded DNA (Kessler and Manta 1990). Many of the restriction sites are palindromic in nature, i.e., reads same forward and backward. These palindromes could be mirrorlike (viz., GTAATG) or inverted repeat (viz., GGATCC being complimentary to CCTAGG). Inverted repeat palindromes are more common with greater biological importance than mirrorlike palindromes.

Once restriction enzyme recognizes restriction site, it can generate either sticky ends (e.g., *EcoRI*, *BamHI*, *HindIII*, etc.) or blunt ends (e.g., *SmaI*, *EcoRV*, etc.) depending upon type of restriction enzyme (Fig. 1).

Different restriction enzymes that recognize the same restriction sequences but cleave at different location are called neoschizomers (e.g., *ApaI* and *Bsp120I* are neoschizomer pair). On

the other hand, when recognize and cut in the same site or location they are called isoschizomers (*SmaI* and *XmaI* are isoschizomer pair).

## Types of Restriction Enzymes

Based on enzyme subunit composition, cofactor requirements, nature of their target sequence, and position of restriction site relative to the target sequence, restriction enzymes are of four types (Types I, II, III, and IV):

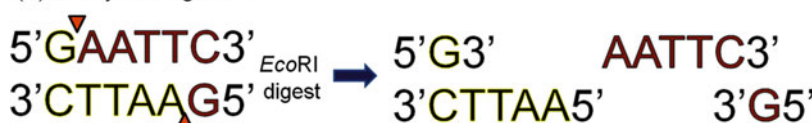
1. *Type I restriction enzyme* – It cuts at sites far from a recognition site (asymmetrical in nature) and requires both ATP and S-adenosyl-L-methionine (AdoMet) as cofactor to function. It has a feature of both restriction digestion and methylase.
2. *Type II restriction enzymes* – It cleaves within or at short-specific distances from a recognition site (palindromic in nature) and mostly requires magnesium to function. It has only feature of restriction digestion independent of methylase.
3. *Type III restriction enzymes* – It recognizes two separate non-palindromic and inversely oriented sequences and cleaves at 20–30 base pairs away from a recognition site. It contains more than one subunit and requires ATP for restriction digestion and S-adenosyl-L-methionine for DNA methylation.
4. *Type IV restriction enzymes* – It recognizes modified DNA (methylated, hydroxymethylated, and glucosyl-hydroxymethylated). Examples are McrBC and Mrr systems of *E. coli* (Table 1).

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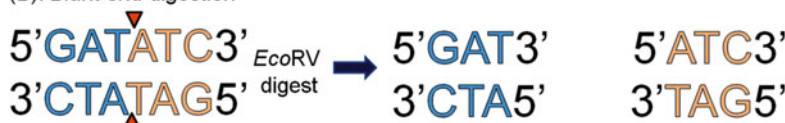
## Restriction Enzyme,

**Fig. 1** Restriction enzymes produce either sticky ends (viz., *EcoRI*) or blunt ends (viz., *EcoRV*) at restriction site

### (A). Sticky end digestion



### (B). Blunt end digestion



**Restriction Enzyme, Table 1** Types of restriction enzymes and their features

| Types                    | Type I                                            | Type II                                                        | Type III                                                                               | Type IV                                                                      |
|--------------------------|---------------------------------------------------|----------------------------------------------------------------|----------------------------------------------------------------------------------------|------------------------------------------------------------------------------|
| Examples                 | <i>EcoKI</i> , <i>EcoAI</i> , <i>CfrAI</i> , etc. | <i>EcoRI</i> , <i>EcoRV</i> , <i>KpnI</i> , <i>NotI</i> , etc. | <i>EcoP15I</i> , <i>EcoPI</i> , <i>HinIII</i> , etc.                                   | <i>BcgI</i> , <i>BaeI</i> , <i>CjeI</i> , etc.                               |
| Cofactors and activators | Mg <sup>2+</sup> , AdoMet, ATP (hydrolyzed)       | Mg <sup>2+</sup>                                               | Mg <sup>2+</sup> , AdoMet (stimulates activity but not required), ATP (not hydrolyzed) | Mg <sup>2+</sup> , AdoMet                                                    |
| Recognition site         | Interrupted bipartite                             | Palindromic or interrupted palindrome                          | Non-palindromic                                                                        | Interrupted bipartite                                                        |
| Cleavage site            | Cleave far from recognition site                  | Defined, within restriction site, give sticky or blunt ends    | Cleaves ~25 bases away from restriction site                                           | Cuts both strands on both sides of restriction sites and leaves 3' overhangs |
| Subunits and structure   | Pentameric complex (2R, 2M and 1S)                | Homodimer (2R-S)                                               | Both R and M-S required                                                                | Heterotrimer (2 R-M, 1S)                                                     |
| Methylase features       | Heterodimer (1M, 1S) or heterotrimer (2M, 1S)     | Separate, single, monomeric (M-S)                              | Methylates adenines, only one strand independently                                     | Same heterotrimer (2 R-M, 1S)                                                |

More than 3000 restriction enzymes have been studied in detail till now, and more than 600 of them are available commercially (Roberts et al. 2007). These enzymes are key tools in molecular cloning.

## Application of Restriction Enzymes

### (A) Gene cloning and protein expression

Restriction enzymes in combination with DNA ligase help in insertion of genes into plasmid vectors during gene cloning and protein expression. For this, both plasmid DNA containing multiple cloning sites and gene insert are treated with the same restriction enzymes and then glued together with the help of DNA ligase (Fig. 2; Russell and Sambrook 2001). Restriction enzymes are also used after cloning to confirm that insertion of gene has taken place correctly.

### (B) DNA mapping

A DNA map generated by restriction digestion can be used to find the relative positions of the genes. The restriction digestion generates different lengths of DNA which gives a specific pattern of bands after gel electrophoresis. This can be used for DNA fingerprinting.

Additionally, it helps in diagnosis of single nucleotide polymorphisms (SNP) and insertions/deletions (Indels) (Kudva et al. 2004), identification of genetic disorder loci, assessment of the genetic diversity of populations, and parental testing.

### (C) Restriction fragment length polymorphism (RFLP)

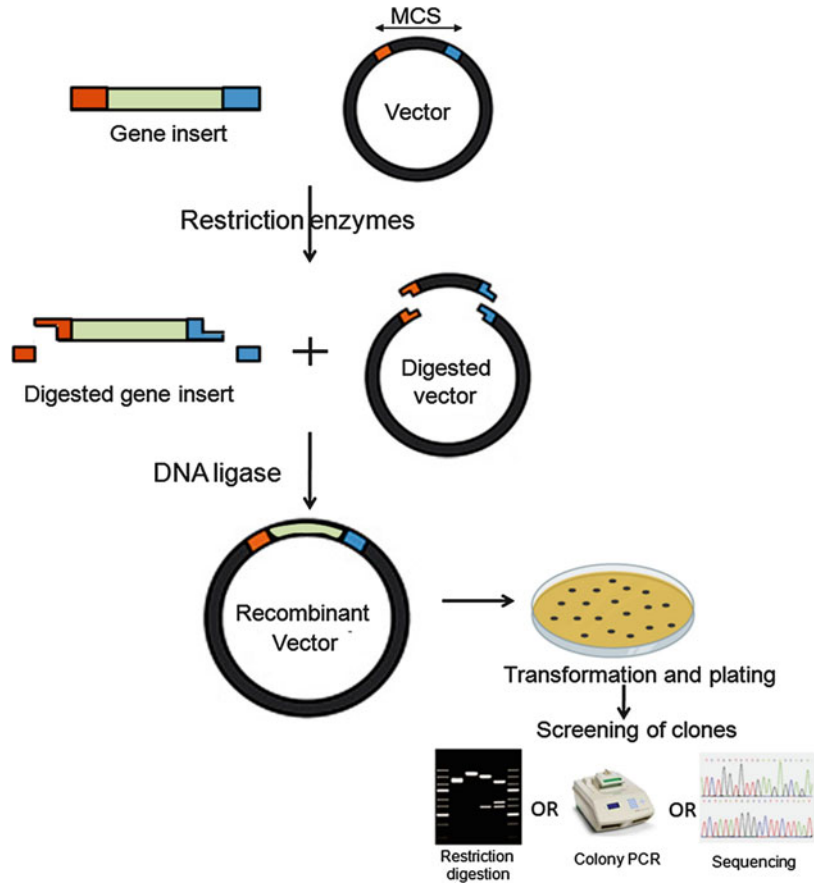
Restriction enzymes are used to digest genomic DNA for gene analysis using Southern blot. With the help of this technique, researchers can find copy number of a gene present in the genome of one individual as well as number of gene mutations (i.e., polymorphisms) within a population. The latter is called restriction fragment length polymorphism (RFLP) (Botstein et al. 1980).

### (D) Studying epigenetic modifications

The sensitivity of restriction endonucleases toward methylated bases has been used to map modified bases within genomes. In brief, restriction landmark genome scanning (RLGS) is a 2-D gel electrophoresis-based mapping technique that utilizes *NotI* (GC<sup>^</sup>GGCCGC), *AscI* (GG<sup>^</sup>CGCGCC), *EagI* (C<sup>^</sup>GGCCG), or *BssHII* (G<sup>^</sup>CGCGC) to identify changes in the methylation patterns of the genome of normal and cancer cells.

**Restriction Enzyme,**

**Fig. 2 Workflow of molecular cloning using restriction digestion.** Both gene insert and vector were digested with same restriction enzymes and purified. The insert and vector were joined using DNA ligase and transformed in competent bacteria cell (e.g., *E. coli* DH5a). Colonies were screened for positive clones using restriction digestion with same enzymes or colony PCR or sequencing



**(E) Preparation of DNA libraries**

Restriction enzymes are used in SAGE (serial analysis of gene expression) for identification and quantification of a large number of mRNA transcripts in cancer research to diagnose mutations and study gene expression. Few restriction enzymes including *ApeKI* used to construct the DNA library for a genotyping-by-sequencing technology to study the sequence diversity in genome of organisms (Elshire et al. 2011).

biotechnological approaches have resulted in new face of restriction enzymes with high fidelity and efficiency in their activity. This ultimately eases the work of researcher. Innovative applications of restriction endonucleases have accelerated the development of biotechnology and insight us with new opportunities and challenges.

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**Cross-References**

- [Restriction Fragment Length Polymorphism](#)
- [Single Nucleotide Polymorphism \(SNP\)](#)

**Conclusions**

Restriction enzymes are a vital tool of recombinant DNA technology. It is one of the major driving forces that enabled the cloning of genes and transformed molecular biology. Advanced

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DNA sample is digested by specific restriction enzymes, and the resulting restriction fragments are resolved according to their size using gel electrophoresis. RFLP was discovered in 1984 by the English scientist “Alec Jeffreys” while working on area of hereditary diseases.

- RFLP acts as a molecular marker and is specific to a single clone or combination of restriction enzyme.
- Majority of RFLP markers are codominant (i.e., both alleles are detected in heterozygous sample).
- It is highly locus-specific.

## Principle of RFLP

RFLP employs the use of restriction enzymes which cut at specific sites on DNA. With the help of a specific restriction enzyme, fragments of DNA are generated which is detected with the help of restriction probes. In RFLP, the length of restriction fragments of a certain type of restriction enzyme differs between individual organisms and species which help to identify and study genetic polymorphism as well as inter- and intraspecific variations.

## Restriction Fragment Length Polymorphism

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### Synonyms

[DNA typing](#); [Genetic fingerprinting](#)

### Definition

Restriction fragment length polymorphism (RFLP) is a molecular biology tool that reveals the difference between samples of homologous DNA molecules from differing locations of restriction enzyme sites. In this method, the

### How Does RFLP work?

The procedure of RFLP is a multistep process which has been detailed below:

#### 1. Extraction of DNA

RFLP starts with extraction of DNA from different origin like blood, saliva, semen, etc. and purified.

#### 2. Restriction digestion of DNA

In this step purified DNA is digested with a specific restriction enzyme, which will cut DNA into fragments of different sizes along with the specific desired fragments.

#### 3. Separation of DNA fragments using gel electrophoresis

The digested fragments are separated using gel electrophoresis composed of either polyacrylamide or agarose, on the basis of length or

molecular weight. Different size of fragments gives different bands across the length of gel.

#### 4. Denaturation

Once the run is complete, gel is placed in denaturation solution (1.5 M NaCl/0.5 M NaOH) to get single-stranded DNA (ssDNA) which is required for Southern blotting.

#### 5. Blotting

The denatured gel containing ssDNA is placed over charged nitrocellulose or nylon membrane to transfer ssDNA over membrane by capillary blotting or electro-blotting.

#### 6. Cross-linking and blocking

The transferred ssDNA is cross-linked in order to fix in membrane either by baking in vacuum at 80 °C for 2 h (in case of nitrocellulose) or exposure to UV radiation (for nylon membrane). The nitrocellulose paper transferred with DNA is fixed by autoclaving. Further, membrane is blocked with the use of bovine serum albumin or casein to prevent non-specific binding of the radiolabeled probe to the charged membrane.

#### 7. Hybridization and visualization

The radiolabeled RFLP probe which is complementary in nature is hybridized with DNA

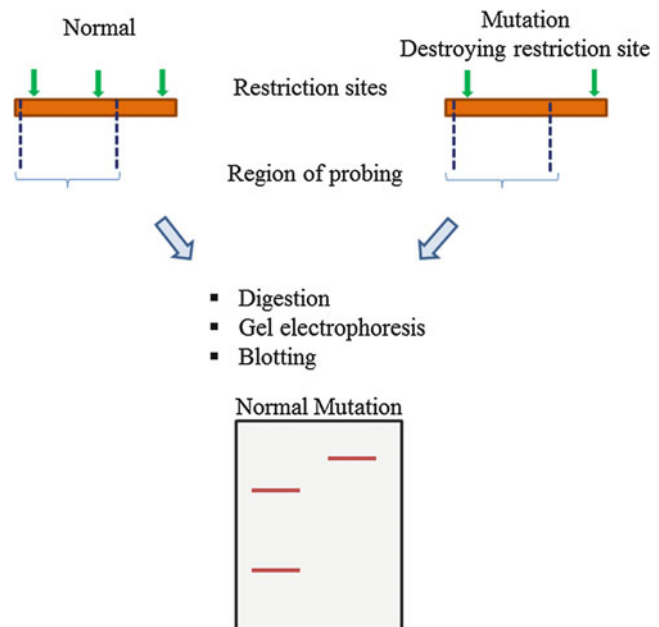
present on the nitrocellulose membrane. The membrane is washed several times to remove unbound probes and then processed for autoradiography for visualization of DNA band.

### Applications of RFLP

1. **Genome mapping** – As RFLP gives unique band pattern of genome after restriction digestion, it is used in identification and differentiation of organisms. In addition, it helps to calculate recombination rate which ultimately provides genetic distance between the loci (Menz et al. 2002).
2. **DNA finger printing (forensic test)** – DNA finger printing uses the principle of RFLP which is useful in paternity test, identification of rape victims or other criminals, etc. (Cousins et al. 2000).
3. **Analysis of genetic diseases** – RFLP helps in analysis of genes involved in genetic or hereditary diseases (e.g., cystic fibrosis) among family members.
4. Detection of mutated gene (Fig. 1; Liu et al. 2004).

### Restriction Fragment Length Polymorphism,

**Fig. 1** Schematic representation of steps involved in RFLP for diagnosis of mutation





5. RFLP can be used in analysis of genetic diversity or breeding patterns in plant or animal populations (Wei et al. 2007).

### Demerits of RFLP

1. Being widely used in forensic science, medicine, and genetic studies, RFLP is no longer evident in front of relatively simple and less expensive DNA-profiling techniques like polymerase chain reaction (PCR).
2. The RFLP is a multistep, time-consuming process unlike PCR which can amplify target DNA sequences in few hours.
3. RFLP needs a large amount of DNA sample for analysis whose extraction or isolation is laborious and time-consuming. On the other hand, PCR can amplify very small amounts of DNA in fraction of hour.
4. PCR has replaced RFLP in application requiring DNA sequencing like paternity testing or forensic analysis.
5. The identification of single-nucleotide polymorphisms (SNPs) for analysis of disease status in Human genome project has no more required RFLP.

### Conclusion

Restriction fragment length polymorphism uses specificity of restriction endonucleases to generate different fragment of variable length of DNA samples across different individuals or organisms. Analysis by RFLP played a vital role in genome mapping and genetic disease analysis. With the recent advances in molecular biology and genomics, the use of RFLP has reduced due to slow, costlier, and cumbersome features.

### Cross-References

- [Mutations](#)
- [Restriction Enzyme](#)
- [Single Nucleotide Polymorphism \(SNP\)](#)

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### Retroactive Interference

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### Synonyms

[Competing cues](#); [Memory](#); [Paired-associated learning](#); [Retrospective evaluation](#)

### Definition

Retroactive interference arises when a new learning affects a previous recall. For instance, in an experimental procedure, a list of words, A, is presented. After that, a new list, B, is shown. Retroactive interference comes when the learning of the new list (B) affects the recall of the list first presented (A).

### Introduction

A common and annoying effect in learning is when new data modify previous information.

For example, a pregraduate student is sometimes confused when he/she needs to study two lessons, one after the other. When the student tries to remember the first lesson, it is possible that the information of the second lesson interrupts the learning of the first lesson. This situation is clearly stated and summarized in Fig. 1.

**Forgetting: Time Passing or Interference?**

This interference effect is related with the nature of forgetting (Baddeley et al. 2009). The first author interested in the dynamic of forgetfulness was Hermann Ebbinghaus. This scientist, crucial in the study of the roots of memory, drew the forgetting curve (Ebbinghaus 1885) to try to explain how memories vanish along time. Ebbinghaus proposed that to forget is due to the decline of the information by the passing of time.

After Ebbinghaus, theories based in association started to claim the concept of interference as the motor of forgetting (Ruiz-Vargas 2010). According to interference theory, the loss of information is not only due to the passing of time, but could also be caused by different situations and competing cues in the learning process and subsequent memories.

To unravel if forgetting is due to time passing or mediated by other experience interferences, the paradigm of dream and wakefulness was used by memory topic researches. In this procedure, the dream phases are used to induce time lapses without interferences or physiological changes due to learning in wakefulness.

Jenkins and Dallenbach (1924) were pioneers in the use of this paradigm. In their study, students

from Cornell University had to learn series of 10 meaningless syllables. Series were repeated until they were totally learned by participants. When they were able to correctly repeat all the stimuli, the series were later recovered in a 1, 2, 4, and 8 h delay. This recall test could be in a dream condition or in a wakefulness condition. Results showed that forgetfulness was higher in wakefulness than in the dream condition. These data suggested that forgetting was not only caused by the passing of time, but was also influenced by experiences in the wakefulness phase.

Anyway, this procedure has problems because of different levels of processing occurring during sleep, and it is not equivalent to not having experiences on processing. On the other hand, another hypothesis considers that consolidation during dream phase could enhance the recall (Mercer 2015).

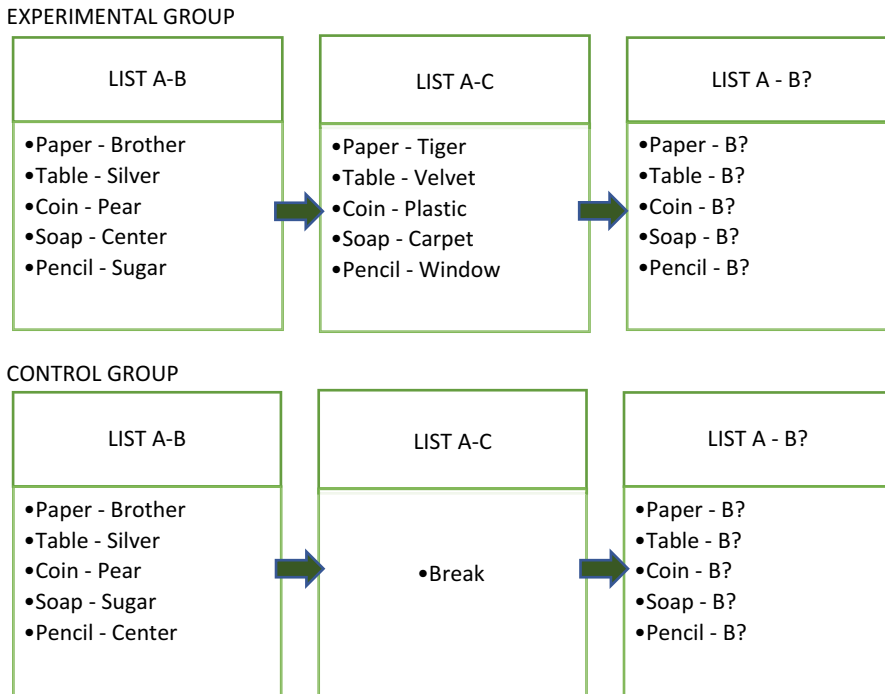
**Experimental Paradigm**

If we want to induce an experimental retrospective interference effect in memory, the classic paradigm of the paired-associate learning can be used. In this procedure, a control and an experimental group learn a list of paired words. The first of the pair is the stimulus and the second is called response (for instance, in table-girl, table is the stimulus and girl the response). After the list of associate-paired words was presented, the experimental group is exposed to a second list, in which the stimulus is the same, but the response changes (table-picture, for example). On the contrary, the control group only receives the first list. Both groups are tested at the end of the training. In this test, the stimuli are presented, and the

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**Retroactive Interference,**  
**Fig. 1** Retroactive interference diagram





**Retroactive Interference, Fig. 2** Example of stimuli for a pair-associated experiment to study retrospective interference

participants have to give the response of the first list. This experimental set reproduces precisely the conditions of retroactive interference (see Fig. 2 for details); therefore, the difference in correct recalls between both groups will measure the effect of retroactive interference.

## Variables that Modulate the Interference

Within the variables implicated in the modulation of interference theory, time interval between the first and the second list presentation can influence interference. Another relevant factor that modulates the strength of information overlap is the similarity of the information. The more similarity in stimuli to recall, the more interference. For example, McGeoch and McDonald (1931) asked their participants to learn a list of adjectives. One group learnt a list and took a rest after for 10 min. The other group learnt the list and another list of different adjectives immediately afterward.

Both groups were tested and asked for the first list. They also manipulated the similarity of the list in the last group and found that the highest forgetting rate was observed when the second list presented synonymous of the first list. This study and others showed that the more similar the material to learn is, the most marked retroactive interference effects are found.

## Cross-References

- [Interference](#)
- [Proactive Interference](#)
- [Retrospective Revaluation](#)

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## Retrospective Evaluation

### ► Retroactive Interference

## Retrospective Revaluation

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John Stuart Mill's well-known *Method of Agreement* proposes that if in all cases in which an effect occurs, there is a single prior factor that is common to all of those cases, then it is deemed to be the cause of the effect rather than other rival factors (Mill 1843). So, if on one occasion, a child has an allergic reaction to eating a chocolate bar containing peanuts as well as on a second, later occasion to eating only a package of peanuts, then peanuts would be deemed to be the cause of the allergic reaction; chocolate would be discounted as the cause of the allergic reaction.

To the logician, there is nothing special about the order of causal episodes. The above case of pairing a compound cue (e.g., two foods, let's call them AX, such as peanuts and chocolate) with an outcome (e.g., let's call it "+", an allergic reaction) and then presenting one of the single cues (e.g., peanuts, A) paired with the outcome as well (i.e., AX+ followed by A+), should be equivalent to the case of A+ followed by AX+. In both cases, pairings of one of the cues alone with the outcome (e.g., A+) should lead to weakened causal attribution to the other cue (e.g., X).

However, the leading theory of associative learning during the final decades of the last century – Rescorla and Wagner's (1972) model – makes a striking prediction as to the causal strength of the distinctive factor: namely, X will acquire little strength in the case of A+ followed by AX+, whereas X will acquire and maintain substantial causal strength in the case of AX+ followed by A+. Why? In the case of A+ followed by AX+ (Kamin 1968), according to the Rescorla-Wagner model, A will acquire most of the available causal strength following the A+ experience, leaving little causal strength for X to acquire during the AX+ experience. In the case of AX+ followed by A+, both A and X will acquire substantial causal strength after the initial AX+ experience, and X will maintain that strength because it can neither gain nor lose strength during the later A+ experience, because it is not presented.

But contrary to the Rescorla-Wagner model, considerable empirical evidence suggests that X does indeed lose causal strength when A+ is presented after the initial AX+ pairings (see Chapman 1991; Dickinson and Burke 1996; Shanks 1985; Wasserman and Berglan 1998, for results with humans; see Harris and Westbrook 1998; Kaufman and Bolles 1981; Miller and Matute 1996, for results with animals). The change in the causal strength of absent cue X during A+ training represents a case of *discounting* – a fall in the causal strength of X that is not attributable to experience with X, but rather to experience with A after initial training with AX. In other words, because A is later proven to be the common causal factor, X is retrospectively discounted after having previously been as plausible a causal candidate as A.

Conversely, if the presented cue loses strength in the light of evidence (e.g., presentations of A without the occurrence of the allergic reaction), then nonpresented cue X correspondingly gains strength as well. In other words, subsequent presentations of A alone *without* the outcome lead to strengthened causal attribution to the absent cue – *augmentation*.

These effects – both discounting and augmentation – are instances of the so-called *retrospective revaluation*. People change their causal

evaluations of the cues that are *presented* on an informational trial; however, in the light of new evidence, they also change their causal evaluations of prior cues that are *not* presented on that given trial. The nonoccurrence of an event, as well as its occurrence, can indeed be informative.

Various different theories try to explain retrospective revaluation effects such as discounting and augmentation. We can divide these theories into associative accounts (e.g., Dickinson and Burke 1996; Van Hamme and Wasserman 1994) and normative accounts (e.g., Cheng 1997): associative theories focus on the automatic and mechanistic nature of causal judgments, whereas normative theories focus on their rational and deliberative nature.

As mentioned above, the Rescorla-Wagner model cannot explain those cases in which the value of *absent* cues is modified, as occurs in discounting and augmentation. Each of these effects entails the apparent retrospective revaluation of a cue, something that is not predicted by the original model. Van Hamme and Wasserman (1994) observed that the Rescorla-Wagner model does not consider both the occurrence and non-occurrence of a cue. Only a cue that is actually presented is assigned a learning rate parameter; a nonpresented cue is not entered into any associative process and therefore is assigned a zero value. Instead, Van Hamme and Wasserman suggested assigning different learning rate parameters to presented and nonpresented cues, so that the learning parameter for a present cue is *positive*, but the learning parameter for an absent (but expected) cue is *negative*. This simple modification allows the Rescorla-Wagner model to explain those problematic findings regarding non-presented cues (also see Dickinson and Burke (1996) for a revision of Wagner's (1981) SOP model that can also explain retrospective revaluation effects, and Ghirlanda (2005)).

Normative models explain the different phenomena observed in causality judgments as the result of an inductive reasoning process. For example, Cheng's (1997) theory embraces the following precepts: (a) causes are not merely followed by their effects, but they *generate* those effects; (b) people do not infer a causal relation

between a cue and an outcome unless they know of a specific causal mechanism that connects the cue to the outcome; and (c) people have to determine to what extent the cue influences the probability of the occurrence of the outcome (when all other events are kept constant), taking into account the base rate of the outcome.

Critically, according to Van Hamme and Wasserman's revised Rescorla-Wagner model, in retrospective revaluation situations like the ones described above, both discounting and augmentation should be observed. According to Cheng's theory, only augmentation should be observed; according to Cheng, discounting is not a true effect; people cannot make a judgment in this case, because they lack information about the cues in the absence of the outcome.

Most of the studies that have previously reported discounting and/or augmentation have compared judgments in the discounting condition to judgments in the augmentation condition (e.g., Chapman 1991; Chapman and Robbins 1990; Dickinson and Burke 1996). This experimental design lacks an appropriate control condition; so, it is unclear whether the difference between conditions is due to discounting, to augmentation, or to both effects.

Wasserman and Berglan (1998) included a critical control condition, in which none of the cues initially trained in compound were later presented in the second stage of training. This improvement to the standard retrospective revaluation experimental design allowed them to observe that *both* effects, discounting and augmentation, take place (see also Castro and Matute 2010). Later, Wasserman and Castro (2005) showed that explicit information about the absence of non-presented cues increased their salience, leading to stronger retrospective revaluation effects than when no explicit mention is made about the absence of nonpresented cues, a prediction that follows directly from the revised Rescorla-Wagner model. Cheng's (1997) theory cannot explain either why both discounting and augmentation are observed or why informed absence enhanced the magnitude of both discounting and augmentation. Thus, the empirical observations in relation to retrospective revaluation effects may



be better explained by an associative than by a normative model.

Finally, we should note that retrospective revaluation effects, and cue competition effects in general, have stimulated a fruitful theoretical and empirical exchange between associative learning in nonhuman animals and human causality judgments (Allan 1993; Alloy and Tabachnik 1984; Dickinson et al. 1984; Gluck and Bower 1988; Shanks 1995; Wasserman 1990), an exchange from which both research areas have greatly profited. This productive interchange ought to have hearted David Hume (1777/1951), who deemed the mechanics of causal judgment to apply with equal force to humans and our animal kin.

## Cross-References

- [Associative Learning](#)
- [Blocking](#)
- [Comparative Cognition](#)
- [David Hume](#)

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## Return of Fear

### ► Spontaneous Recovery

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## Reversal Learning

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## Introduction

Reversal learning has been a widely used procedural paradigm in the field of animal behavior and comparative cognition since its inception in the early twentieth century (Williams 1942). This is, in part, due to reversal learning's relatively simple procedural design, which allows it to be implemented in almost any context, using a variety of apparatuses, and with a potentially limitless array of stimuli. In terms of its efficacy as a research tool, it can be used to measure differences, both within and across species, in the "...adaptation of behavior according to changes in stimulus–reward contingencies" (Clark et al. 2004). This type of overt behavioral change that is evoked by environmental feedback is called behavioral flexibility, which appears to be closely tied to, or an outward expression of, internal levels of cognitive flexibility (Gonzalez et al. 1966). Cognitive flexibility is the ability to shift attention to relevant discriminative stimuli, depending on their effectiveness in optimizing environmental outcomes. In turn, cognitive and behavioral flexibility are believed to be essential components of intelligent and adaptive behavior. The reversal learning paradigm has functioned to advance our understanding of how organisms discriminate between stimuli, as well as how they learn to attend to relevant vs. irrelevant information. It illuminates how organisms utilize environmental

information to predict the probability of future reinforcement, as well as to produce a different behavior or learn new associations when environmental consequences change.

There are numerous iterations of the reversal learning procedure, each of which illuminate important findings on the differences in performance obtained within and across species. Various theories have been proposed as to why these differences occur. These include differences in external pressures, such as an organism's ecology, as well as internal differences in cognitive mechanisms thought to underlie levels of cognitive flexibility, such as impulsivity, inhibition, memory for previous associations, and the learning of new ones. Finally, some possible neurological correlates that may underlie these differences in behavioral change have been identified. Below is a summary of this information.

## Reversal Learning Procedures

The topic of reversal learning can be conceptualized both from a procedural and behavioral viewpoint. This is similar to the idea of extinction, which can be defined procedurally as when responses to a previously reinforced stimulus are no longer reinforced, but behaviorally when the animal stops performing the previously reinforced operant response (Sidman 1988). From the procedural viewpoint, the reversal learning paradigm can be characterized as presenting an organism with an initial phase of simple discrimination learning, where reinforcement is repeatedly paired with a response to one stimulus (e.g., red circle, S1+) and not another (e.g., green circle, S–). At some point, the reward values associated with the two stimuli are reversed (S1–, S2+). Now responses to the previously incorrect stimulus (e.g., green) are reinforced, while responses to the previously correct stimulus are extinguished. Although the procedural transition point is clearly marked by the change in contingencies, from a behavioral point, this transition point is less clear. From the animal's point of view, the feedback associated with the first reversal trial comes after the animal responds. Therefore, the animal will most likely respond

incorrectly on this trial if it is still under the control of the previous contingency. Only after this feedback can the animal adjust to the change. That is, the animal must cease responding to the previous, but no longer reinforcing, stimulus while learning to reliably respond to the previously incorrect stimulus which is now reinforced. The specific point at which the contingencies are reversed typically occur after the subject has achieved some predetermined criterion level of performance; however, researchers have also assigned reversals to occur after a specific number of trials or sessions. Both of these designs have yielded interesting results.

## **Trials to Criterion**

**Simple Comparison Group Design** In a simple comparison group (AB) design using trials to criterion as a marker for reversals, an initial phase of simple discrimination learning is followed by a single reversal phase once the subject begins to reliably respond to the initial S+ while also withholding responses to the initial S-. Reliability of this type is typically operationalized as some criterion level of performance (e.g., 90%) within a block of trials or sessions. At this point, the contingencies are reversed and the number of trials to the same criterion as in the initial phase is plotted as the dependent measure. Rates of reversal learning are measured by the rapidity with which the animal is able to adjust these two behaviors to the appropriate stimuli (withholding responses to S-, responding to S+). Many early, simple comparison group studies focused on the effect of various methodological parameters, such as the number of relevant cues in a discrimination, the complexity of the task, the amount and type of food reward provided to the S+ responses, and the effect of various levels of training on subsequent learning of the reversal problem. In these initial studies, the goal was to theorize about how an animal comes to learn about the relevant cues in the experimental context as well as how the animal learns the appropriate responses to the stimuli attached to those cues.

One major area that attracted attention in the early 1950s was the counterintuitive finding of the overtraining reversal effect (ORE). This effect was discovered by Reid (1953) using a Y-maze apparatus and a black/white visual discrimination in rats. Reid (1953) found that ORE rats given an additional 150 trials on the initial discrimination after reaching criterion learned to switch in about half the time as compared with rats who were given a reversal as soon as they reached criterion. Traditional theories of learning predicted that this overtraining should attenuate reversal learning. The major contribution of the ORE was that it lent support to the attentional theory proposed by Sutherland and Mackintosh (1971), which states, "...reversal learning will be rapid to the extent to which the relevant analyzer is maintained during reversal" (p. 252). Therefore, in order to learn the reversal of any discrimination, the subject must continue to attend to the originally relevant stimulus dimension or cue. This follows that overtraining should be more likely to facilitate reversal learning the more there are irrelevant cues present in the environment. Overtraining results in relevant cues (e.g., brightness) appearing as more salient to the subject while irrelevant cues (e.g., spatial cues) are less likely to be attended (Lovejoy 1965; Schade and Bitterman 1966).

An additional point of interest lies in the behavioral stages of transition often seen in many animals and of interest to theories of flexibility and learning. As Sutherland and Mackintosh (1971) state "Reversal learning can, in effect, be regarded as consisting of two parts: first, the extinction of the original discrimination, and second, the acquisition of the reversal discrimination" (p. 258). These two processes may very well tap into different cognitive mechanisms of learning, with the former dealing with inhibition and extinction learning, and the latter dealing with the learning of new associations. One aspect of the theory that is important is that the cessation of responses to the previously relevant stimulus and the initiation of responses on the previously irrelevant stimulus might be driven by two separate processes. The former being controlled by inhibition to an excitatory response, while the latter could be characterized by exploration for new relationships. The first process appears to deal with the

strength of working-memory for previously learned relationships, while the second process appears to deal with the ability for the animal to learn and seek out new relationships. Both of these processes contribute to the levels of behavioral flexibility that will be demonstrated by a given subject.

Another important aspect to reversal learning is that the animal has to also be able to behaviorally inhibit responses to the previously correct stimulus, which may differ in time from, or be expressed at a different time than, having learned to attend to the relevant dimension. Mackintosh (1975) further added insight to how animals learn to change behavior in the reversal task. His theory centered around attention to relevant “analyzers” or relevant stimulus dimensions (Sutherland and Mackintosh 1971). If the animal was attending to brightness when spatial location was the relevant dimension being manipulated, for example, it would not be able to learn how to maximize reinforcement because it would not be able to discover the functional relationship between spatial location and reinforcement. After repeated trials, of random reinforcement, the animal might shift attention to, or from a more behavioral account, respond based on the spatial dimension (go left, regardless of brightness), wherein it would come in contact with the functional relationship and learning would ensue.

**Serial Reversal Learning Design** One variation in the procedure of the initial reversal learning (AB) design called the serial reversal procedure has been to repeatedly reverse the contingencies over training. In this procedure, specific contingencies remain constant until the animal reaches some criterion level of discrimination performance. Usually this criterion involves choosing the correct stimulus 85–90% over a specified unit, such as a block of trials or sessions (e.g., the last ten trials, two consecutive sessions). Each time the animal reaches this criterion, contingencies reverse. This process (ABABAB...) is typically repeated a handful of times. The dependent measure is usually plotted as the number of errors or number of trials to criterion across reversal blocks. Additionally, a relative measure of reversal learning determines a ratio of errors, for

example, for the initial acquisition divided by the errors demonstrated on subsequent reversal phases. In this respect, the length of time it takes for an animal to initially learn the discrimination can be compared to the errors on the subsequent reversal phases to get a measure of the overall rate of reduction in errors over time. That is, if it takes a pigeon 15 trials to reach criterion and only 5 trials during one of the reversal phases, then the animal has reduced its errors to 33% of its initial error rate, which is the same as if it had taken 30 trials initially and 10 on a subsequent reversal phase.

What is often found is that the first reversal phase shows the greatest number of errors, due to the fact that the history of reinforcement at this point is 100% for S1 and 0% for S2. As reversals recur, the overall percentage shifts to 50%/50%, then 75%/25%, and so on, constantly evening out the long-term values of the two stimuli. What ends up becoming important, or what provides the most information about the functional relationship, is the most recent experience with reinforcement and the associated response (Rayburn-Reeves et al. 2013). The more an animal can both detect and react to this event, while ignoring the overall value of the stimuli, the more efficient they will be in maximizing reinforcement.

The reversal learning paradigm began to grow in popularity around the middle of the twentieth century, when it appeared that this paradigm could be used to classify different species according to their level of improvement across reversals as an indication of their level of general intelligence. This was, in part, due to the work of Harry Harlow (1949), who studied a variety of species on a similar procedure to reversal learning, called an object quality discrimination task. In this task, the animal is presented with two novel stimuli, such as a star and a circle, where the values of these stimuli are randomly assigned as S+ and S−. In this respect, the animal could not predict which stimulus would be rewarding on Trial 1, but regardless of which stimulus the animal chose, the outcome of the response should provide all the information the animal would need in order to choose optimally on subsequent trials. The animal would be presented with six trials of this same

object-pair contingency and would then be presented with a novel pair of images, randomly assigned in value. What Harlow found was that species differed over learning in their ability to choose optimally on Trial 2 of each new problem, with some primate species performing above 90% on Trial 2, while other species, such as squirrels, cats, and rats, showing poorer performance on these trials. Harlow discussed these differences in performance as differences in the ability to develop a *learning set*, which he defined as "...learning to learn from a situation an animal frequently encounters" (Harlow 1949). It appeared that some animals could learn a general rule based on reinforcement contingencies that could be applied to all objects, regardless of their novelty (Harlow 1949; Schrier 1984). Based on this finding, the serial reversal learning task became a popular paradigm for studying the relative changes in behavior over reversals which served as a measure of behavioral flexibility across species.

Since the initial experiments in the early twentieth century, beginning with Buytendijk (1930) using a position/spatial discrimination and Krechevsky (1932b) using a brightness discrimination, the main finding in serial reversal learning tasks is that, over repeated reversals of the discrimination, the animal learns to switch responses to the presently reinforced stimulus with increasing rapidity, sometimes resulting in a single trial needed to show the reversed behavioral responses (Dufort et al. 1954; Mackintosh et al. 1968). This behavioral pattern has been termed rapid reversal learning, where the animal only has to be exposed to a few instances of the reversed contingency to shift to the appropriate strategy (Lionello-Denolf 2013). Like Harlow (1949), researchers began studying a variety of species on the SRL task, noting differences in the ability of certain species to reduce the number of errors before reaching criterion across reversals (Behrend et al. 1965; Bitterman 1965; Gonzalez et al. 1966; Mackintosh 1963, 1971; Mackintosh and Holgate 1969; Mackintosh et al. 1968; Schade and Bitterman 1966). Bitterman's (1965) research led him to conclude that there were qualitative differences in the way certain species solved the

task, while Sutherland and Mackintosh (1971), Mackintosh (1975) argued that the differences in learning rate were not qualitative, but quantitative, suggesting the same mechanism for learning was involved, but some species were quicker to change behavior than others.

Other researchers, such as Warren (1964), however, began pointing out the issues in procedural differences that could account for the performance differences seen. When trained under optimal conditions, many species that had previously shown no improvement across reversals now showed significant improvement. A number of factors, such as sensitivity to the dimension being tested, discriminability of the dimension being tested, relationship of discriminative stimuli to complexity in the environment, the relevance of the stimuli to survival, and other competing sources of information present during learning, could influence the rate of learning in reversal tasks as measured by sensitivity to changing reinforcement contingencies. These findings complicated the interpretation of prior results, leading researchers to move away from the reversal paradigm as a way of assessing general intelligence levels across species.

Due to the reversal event being contingent on the animal's performance, the varying point of reversal that occurs when using trials to criterion as a marker for the reversal event appears to create a situation where the recent response-reinforcement contingency provides the most relevant information about future reinforcement. Reversals occurring in consistent, fixed, units result in the increase in value of other sources of predictive information.

### Fixed Time or Trial Number

Another way to present reversals is by fixing or actively manipulating the number of trials before a reversal occurs. Here, the reversals occur independently of the animal's performance. One benefit of this procedure, therefore, is that the experimenter has control over when and how many reversals to which the animal is exposed. The potential drawback is that the animal's performance, then, may



vary widely before each reversal. Low accuracy (or high numbers of errors) would indicate a lack of control by relevant discriminative cues, which could complicate the interpretation of error rate over time. However, if the reversals are on a fixed schedule of time, animals learn to anticipate the reversal and are better able to discriminate the time at which a given response will result in reward (Rayburn-Reeves and Cook 2016). If reversals are on a variable time (or number) schedule, the value of using time as a source of information is weakened, and often eliminated, while the recent history of reinforcement is strengthened. Depending on how salient temporal cues are, as well as their effectiveness in contrast to other cues, such as working memory for most recent response-reinforcement contingency, the animal may show control by one cue or the other.

**Serial Reversal Learning: Reversing Mid-session** Some of the first studies using fixed reversal locations presented reversals across sessions, such as every other day or every few sessions (Gonzalez and Bitterman 1968). These studies showed that pigeons eventually began sessions at chance, quickly learning the relevant discrimination within the session. Very few reversal tasks were conducted with fixed trial number in the mid-twentieth century; however, more recent research has used highly predictive reversal events to compare relative strengths of various discriminative cues on optimizing behavior. For example, in a midsession reversal procedure using a simple simultaneous discrimination task, two stimuli are presented at the same time, such as a red (S1) and a green (S2) key light. In this scenario, one stimulus is correct for the first half of a session (S1+, S2−) while the other stimulus is correct for the last half (S1−, S2+).

In the initial experiments on midsession reversal learning (Cook and Rosen 2010; Rayburn-Reeves et al. 2011), every session began with S1+ and ended with S2+ and the reversal always occurred in the middle of the session (e.g., Trial 41 of 80). This procedure produces consistent patterns of behavior both within and across sessions, where animals, such as pigeons, rats, dogs,

rhesus macaque monkeys, and humans, learn to respond at a high rate to the S1 and S2 stimulus at the beginning and end of every session (McMillan et al. 2014; Laude et al. 2014; Rayburn-Reeves et al. 2013; Rayburn-Reeves et al. 2017). What is interesting is the pattern of behavior that occurs near the reversal location, which has been shown to differ both between and within species under various experimental methods.

For example, pigeons have been shown to produce systematic increases in responses to the S2 stimulus before the reversal occurs, as well as continuing to maintain responses, although at a decreasing rate, to the S1 stimulus after the reversal occurs. This pattern of data suggests that the predictability of the reversal location increased attention to, or made more salient, the temporal cues associated with the reversal event. A series of studies confirmed that pigeons were basing responses on the passage of time within each session based on a reference memory for the reversal event over sessions (ref).

Other recent research has shown that reversal learning performance can be affected by the stimulus modality, such as the use of visual or spatial discriminations, the apparatus (McMillan et al. 2014), the addition of external visual cues, such as colored screens or houselights (Rayburn-Reeves et al. 2016) during the intertrial interval, the presentation of the stimuli (i.e., simultaneous or successive), and the length of the intertrial interval. This research has illuminated how various cues come to exert control over behavioral choice depending on their predictive value for future reinforcement, as well as their level of salience as compared to other available, relevant cues. In pigeons, it appears that time as a cue is quite salient and persistently acquires control over behavior, unless other external cues eliminate the need for timing. Even then, studies have shown that time is still attended to by pigeons, as when the external context cues are removed, pigeons revert to making time-based errors around the reversal location, as if they had been timing throughout the session. Other species such as rats (McMillan et al. 2014) and dogs (Laude et al. 2016) have also been shown to produce marked anticipation and perseveration errors, similar to pigeons.

Although time maintains control over reversal performance in pigeons, dogs, and rats under some conditions, in others it appears to take a back seat to recent response-reinforcement contingencies. One commonality about reversal learning tasks in general is that the recent history of reinforcement provides, almost exclusively, the most predictive and effective information about what response will be reinforced on the following trial than any other cue (with the exception of context cues). If an animal is able to utilize the recent history of reinforcement as a cue, it will receive reinforcement on every trial except the reversal trial. Behavioral patterns that are generated by reinforcement cues sometimes vary in the number of perseverative errors demonstrated by different species, but they typically do not show the anticipation errors, which are indicative of time-based control.

In an initial study by Rayburn-Reeves et al. (2013), rats were shown to display highly adaptive behavior after being trained on a spatial midsession reversal task using lever presses in an operant setup. They also showed consistently high accuracy when reversals occurred in unpredictable locations across sessions, and when multiple reversals were presented in individual sessions. Smith et al. (2016) also found highly accurate performance by rats using nose-poke or lever pressing responses in spatial discrimination tasks. Pigeons have shown similar performance when both visual and spatial discriminations are confounded (McMillan et al. 2014), as well as when the ITI is very short (i.e., 1.5 s) and the discrimination is spatial (Laude et al. 2014). Finally, pigeons have been shown to utilize color cues presented during the ITI that signal which stimulus will be rewarded on the following trial, which result in a lack of anticipation errors and a significant reduction in perseverative errors.

By far, the most efficient behavior has been shown by humans (Rayburn-Reeves et al. 2011), who almost always show a pattern of win-stay, lose-shift responding (Levine 1975). This pattern, where responses to a stimulus that were reinforced on the preceding trial are repeated, while unrewarded responses are not repeated, has been argued to be dependent on the development of a higher-order cognitive process of rule-based learning.

## Neuroscientific Evidence for Reversal Learning

Reversal learning has moved into the psychopharmacological and neuroscience fields where researchers study the effects of various NTs, such as dopamine and 5-HT (serotonin), on errors in the reversal task (Costa et al. 2015; Grandy and Kruzich 2004; Murray et al. 2008). Studies have implicated that these two NTs are critical to reversal learning performance. Both serotonin and dopamine have been shown to have dissociative and selective roles in the reversal learning process (den Ouden et al. 2013). Dopamine has also been shown to be specific to reward-related learning and behavioral flexibility. Too much or too little dopamine can be detrimental to performance on the reversal learning task (Clark et al. 2004).

The reversal learning task has been studied in human subjects to ascertain its relationship to neurobiological mechanisms and underlying neural correlates of behavior. Findings suggest that neural coding has much to do with performance pertaining to the reversal learning task, especially in the frontal lobe (Dargis et al. 2017; Izquierdo and Jentsch 2012). More specifically, it has been suggested that the lateral orbitofrontal cortex (OFC), as well as the ventromedial and lateral prefrontal cortex (PFC) play a critical role in decision-making, inhibitory control, affective responding, and stimulus-reward learning; all of which are processes affecting reversal learning performance (Fellows and Farah 2003; Hampshire et al. 2012; Xue et al. 2013).

The cognitive ability to learn a reversal is also contingent upon age. Younger subjects consistently perform better on the task when compared to older animals (Kovalchik and Allman 2006). Studies have implicated other brain regions in reversal learning as well, and headway has been made in attempts to identify the purpose of these regions in the learning process. More research is needed to further corroborate these findings, but they reflect a shift in reversal learning toward a neuroscientific focus.

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## Reversible Plasticity

### ► Strategy Reversibility

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## Rhinoceros Gait

### ► Perissodactyla Locomotion

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## Rhinos

### ► Perissodactyla Cognition

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## Rhombencephalon (Hindbrain) Without Brain Stem

### ► Cerebellum

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## Ribonucleic Acid

### ► RNA

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## Ribosome

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### Definition

“Ribosome is a tiny granular cellular organelle that floats freely in cytoplasm as well as attached with the endoplasmic reticulum and performs translation (Protein synthesis).”

# Introduction

The word “ribosome” originates from ribonucleic acid and Greek word soma, which means body (Bakowska-Zywicka and Tyczewska 2009). Albert Claude gave the term “microsome” after his excellent work of cell fractionation in the 1930s. Later, his two students – Philip Siekevitz and George Palade worked on the morphological and biochemical analysis of the secretory process related to the “microsome.” Further, Zamecnik’s group correlated microsome with protein biosynthesis and finally, Richard Brooke Robert in 1958 gave the term “ribosome” (Bakowska-Zywicka and Tyczewska 2009).

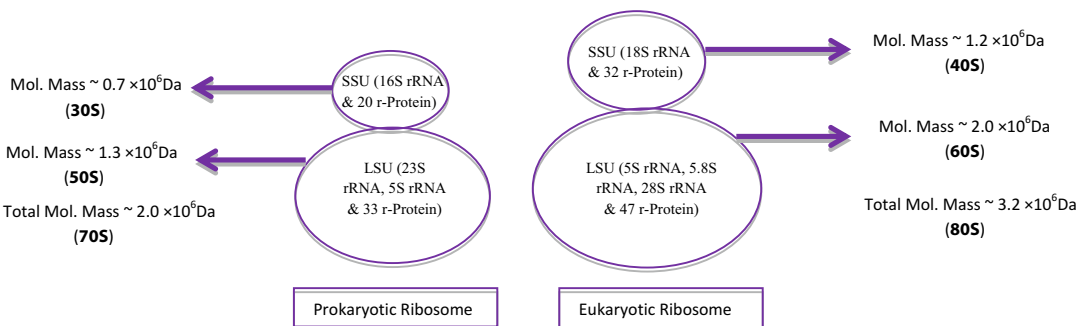
The ribosome is a cellular structure which helps in protein synthesis. The mystery of life is stored in the genome sequence of their deoxyribonucleic acid (DNA). The genetic information of DNA is made available by transcription of genes to messenger ribonucleic acid (mRNA) that are subsequently translated into the various amino acid sequences, which are the building block of proteins. The ribosome plays a central role in the biogenesis of proteins from mRNA. The biogenesis of ribosome occurs in nucleoli. The nucleoli are nuclear domains, which are specialized in the production of ribosomal subunits (Stepinski 2014).

# Structure of Ribosome

Thomas Steitz started the work on the structure and functions of the ribosome in 1990s and finally,

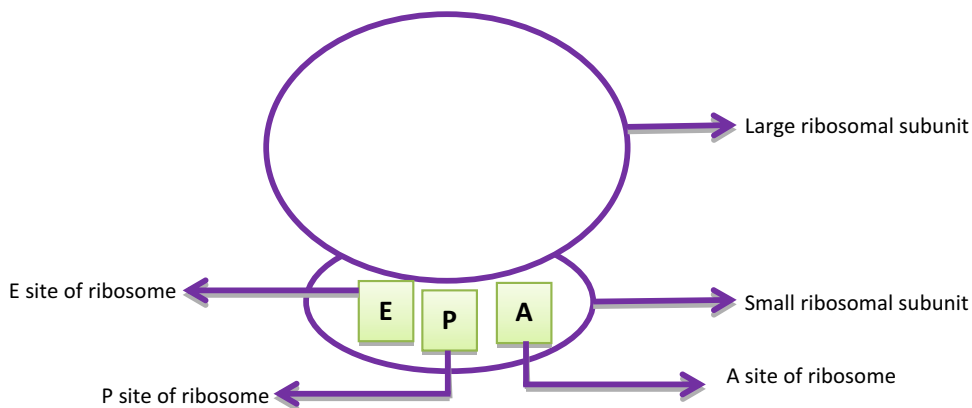
in 2000 obtained a high-resolution structure of ribosome. Afterwards, other researchers were able to study the structure of the different subunits of ribosome as well as molecular interaction between them (Zhao 2011).

Ribosomes are composed of RNA and protein. It has two subunits consisting of approximately two-third RNA and one-third protein. Ribosomes from mammalian mitochondria are exception, in which the ratio of protein and RNA is reversed (Sharma et al. 2003). Prokaryotic ribosome (70S) contains a smaller subunit (SSU) 30S and a larger subunit (LSU) 50S. The SSU (30S) is composed of one 16S ribosomal RNA (rRNA) containing around 1600 nucleotides and 20 ribosomal proteins (r-proteins), while the LSU (50S) contains 23S rRNA sequence of 2900 nucleotides, 5S rRNA sequence with about 120 nucleotide and 33 r-proteins (sum total ~4620 nucleotides of rRNA and 53 r-proteins of the bacterial 70S ribosome), where S stands for the Svedberg unit for sedimentation velocity. Compared with the prokaryotes, eukaryotic 80S ribosomes also contain a SSU (40S) and a LSU (60S). The SSU (40S) is composed of one 18S ribosomal rRNA containing about 1753 nucleotides and 32 ribosomal proteins (r-proteins), while a LSU (60S) has 5S rRNA containing sequence with about 120 nucleotides, 5.8S with about 154 nucleotides, and 28S r RNAs with about 3354 nucleotide along with 47 r-protein (sum total ~5381 nucleotides of rRNA and 79 r-proteins of the yeast 80S ribosome) (Fig. 1) (Wilson and Daudna Cate 2012; Ramakrishnan 2009).



**Ribosome, Fig. 1** The simplified structure of prokaryotic and eukaryotic ribosome





**Ribosome, Fig. 2** All three RNA- binding sites on a ribosome

### Function of Ribosome

The ultrastructure of prokaryotic ribosome revealed that it has three tRNA binding sites namely Aminoacyl-tRNA binding site (A site), Peptidyl-tRNA binding site (P site), and Exit site (E site). In the biosynthesis of protein, aminoacyl-tRNA bind to A site during elongation process, whereas at P site the tRNA linked to the growing polypeptide chain is bound. Further, E site provides the binding site for tRNA (Fig. 2).

In prokaryotes, biosynthesis of protein begins by the establishment of a 30S complex between the 30S subunit, mRNA, initiation factors, and aminoacylated tRNA. The 30S subunit binds to specific sequence of mRNA (Shine-Dalgarno sequence) which is situated upstream to the AUG start codon and its complementary sequence is present on the 16S rRNA of the small subunit. The ribosome then changes its own position in a 3' direction with the mRNA till meeting with the start codon. After that large subunit (50S) binds to the 30S initiation complex to form the 70S initiation complex. In this complex, anticodon of AUG is paired in the P site, and further this initiation complex encounters again with other codons and protein synthesis takes place unless the stop codon is encountered.

In eukaryotes the assembly and the protein synthesis process is complex than prokaryotes. Initiation of protein synthesis is basically similar in prokaryotes and eukaryotes except the involvement of initiation factors. Some

important differences between the protein biosynthesis of prokaryotes and eukaryotes are the initiating amino acid is methionine in eukaryotes while *N*-formylmethionine in prokaryotes, eukaryotic mRNA is monocistronic while polycistronic mRNA in prokaryotes. Eukaryotic mRNA does not contain Shine-Dalgarno sequence like prokaryotes therefore initiation codon is recognized by ribosomal scanning of mRNA. Initiation of protein biosynthesis in eukaryotes involves the formation of 48S pre-initiation complex between the small subunit (40S), mRNA, initiation factors, and start codon. The ribosome then scans the mRNA to locate the start codon. Further, the large subunit (60S) binds to form complete 80S initiation complex. Further, this initiation complex encounters again with other codons and protein synthesis takes place unless the stop codon encounters like prokaryotes.

### Summary

The ribosome is a cellular structure which involves in protein synthesis. The transcribed mRNA associate with ribosome and protein synthesis occurs according to the codon of mRNA with the help of tRNA and accessory factors. Thus, in prokaryote, 70S ribosomes and in eukaryotes 80S ribosome play role like protein-making machines.

## Cross-References

- [Gene Expression](#)
- [RNA](#)
- [Transcription](#)

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## Richard Byrne

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## Early Life and Educational Background

Richard “Dick” Byrne was born on 13 August 1950 in London, UK. He attended Hampton Grammar School and went on to St. Johns College, University of Cambridge, to read physics within a Natural Sciences degree. Discovering the excitement of psychology, he switched focus and specialized in cognitive psychology, completing

an undergraduate research project under supervision of Donald Broadbent. Another strong influence was John Morton, who supervised Byrne for his PhD (*Memory in Complex Tasks*, 1976) at the Medical Research Council’s *Applied Psychology Unit*, Cambridge.

## Professional Career

Byrne gained a lectureship at University of St Andrews in 1976 and has remained there all of his career. He has authored more than 150 journal papers and 70 book chapters, in addition to writing *The Thinking Ape* (Oxford University Press 1995; Japanese translations 1998; Chinese translation 2006) and *Evolving Insight* (Oxford University Press 2016; Japanese translation forthcoming) and co-authoring the two *Machiavellian Intelligence* volumes with A. Whiten (Oxford University Press 1988, Cambridge University Press 1997; Japanese translations of both, 2004).

Byrne’s work has been cited more than 17000 times, and he has an h-index of 58. His first book, *The Thinking Ape*, was awarded the Book Prize of the British Psychological Society in 1997. Byrne was awarded the Wright and Hughes Prizes of St Johns College, Cambridge, a Medical Research Council Postgraduate Scholarship, a Development Fellowship of the Association of Commonwealth Universities (held at Auckland University, NZ), and leadership of a Focus Group at the Collegium Budapest, Hungary. He was elected Fellow of the Royal Society of Edinburgh in 2002.

## Research Interests

Byrne’s PhD work developed methods for studying the use of memory in everyday planning tasks. At that time, most cognitive psychology was based on a set of heavily used laboratory paradigms and tended to ignore ordinary human behavior. But when Byrne came to St Andrews, he joined a psychology department with an unusual number of researchers studying animal behavior and discovered that ethology already

had a well-developed approach that meshed natural behavior with controlled experiments.

That led to a move into primate behavior: William McGrew, then at Stirling University, invited him to work on baboons at a site in Niokolo-Koba National Park, Senegal, where he studied how long-range vocalizations are used to coordinate the frequent fission and fusion of ranging baboon parties, thus minimizing predation risk. A collaboration with Andrew Whiten at St Andrews followed in the early 1980s, setting up a field site to study baboon behavioral ecology in the Drakensberg Mountains, South Africa. The project showed how the food constraints of high altitude caused baboons to switch social organization from multi-male groups to small harems. Unexpected observations of baboon tactical deception there led to a data-mining and survey study of primate deception in general: when analyzed in the early 1990s, these data pointed to primate abilities that were not matched in the laboratory until 20 years later, including evidence of theory of mind understanding in (all) great ape species, and geometric perspective-taking ability in Old World monkeys and apes. Byrne's research on monkeys continued through supervision of PhD students, working on spider, howler, and titi monkeys in Central and South America, and vervet monkeys and baboons in Africa. A particular focus was on primate spatial navigation and ranging, leading to the development of a new method of analyzing ranging routes of animals, the "change point test." With Rahel Noser, Byrne showed that the mental maps of baboons, just like those of people, were non-Euclidian, and well described by the concept of a "network-map" – a cognitive model which Byrne had originally developed on the basis of human error patterns he had studied in the 1970s!

The major focus of Byrne's work, on the cognition of African great apes, began fortuitously. Getting to know Professor Toshisada Nishida, who was then visiting McGrew in Scotland, led to an invitation to study chimpanzees in Tanzania; and getting to know Dr Dian Fossey led to her encouragement to work on the famous mountain gorillas in Rwanda. Working on apes allowed Byrne to benefit from his early training in human

cognition, in particular recognizing the hierarchical organization of their complex skills – such as chimpanzee tool-use and the elaborate multistage plant processing that Byrne discovered in gorillas. He found that individual apes were able to construct new routines of skilled manual behavior, using observational as well as individual learning, just as humans do. Byrne developed a cognitive model of how such imitation would be possible, without involving the intentional capacity to read the mental states of the demonstrator – "Behavior Parsing" – a theory that meshes well with the Rizzolatti/Arbib account of mirror neurons as an automatic system of action-understanding which was being developed at the same time. The complexity of the natural plant-processing of mountain gorillas also allowed Byrne to recognize that while strong laterality (hand preferences) developed in individuals as a result of task complexity, population laterality (handedness) was elicited more by the need for bimanual, asymmetric processing – as shown, for instance, when we grip a jar and twist the lid with the other hand. As with theory of mind, these findings from observational data have subsequently been corroborated in the laboratory.

Working with a number of PhD and postdoctoral students, Byrne has studied the natural gestural communication of great apes since the 1990s, a project that now includes orangutans, gorillas, bonobos, and chimpanzees. Their findings confirmed the highly intentional nature of gestures and their careful targeting of gesture modality to the intended audience's attentional focus – and went beyond earlier work in showing that apes take account even of the audience's degree of understanding in selecting their gestures. All species studied have proved to use very large repertoires of gesture types, and these "lexicons" are extensively shared, not only between different populations of the same species but also between different ape species; specific intended meanings as well as gesture forms are shared across species. Byrne's group interprets these patterns to be a result of an innate potential in each ape species to develop the set of gestures used under species-typical natural circumstances (a potential that was "phylogenetically

ritualized” during evolution within the great apes). Young apes explore their innate potential repertoire and its uses, rapidly increasing their active set of gestures and often using whole sequences of gestures with similar meanings, before this repertoire is finally pruned to a smaller number of gestures in the final adult state. Other gestures, in the adult’s potential or passive repertoire, are not totally lost but can be “primed” by seeing another use them. This gives rise to the phenomenon of gestural imitation, in which the copies often vary from the original model – because they are in fact not imitations, but evocations of pre-existing gestures seldom or never used by the adult.

Byrne has long believed that an exclusive focus of comparative and evolutionary psychology on species most closely related to the human – that is, the primates – would be unfortunate, as it is through convergences in distantly related species that we can learn the original adaptive function of cognitive capacities. He has taken several opportunities to turn this idea into concrete results. He worked with Mike Mendl and Susanne Held on the cognition of the domestic pig, modifying experiments first used with apes; they showed that pigs have the ability to take account of some of the knowledge as well as the likely reactions of others in competitive situations. He and Lucy Bates worked with members of the Amboseli Trust for Elephants, analyzing existing narrative records of elephant abilities and devising field experiments to test hypotheses generated from that analysis. They found that elephants possess high levels of empathy for others; that they subcategorize humans into types, reacting distinctively even to indirect cues of a particular human “tribe”; and that they show powerful working memory abilities, perhaps in excess of human working memory capacity, when they keep track of out-of-sight individuals in wide-ranging family groups, picking up cues from identifying individual scents among other cues. Most recently Byrne has collaborated with Martin Whiting and colleagues in studying the cognition of social Australian lizards of the *Egernia* group. Selected publications that illustrate each research topic are shown in Table 1.

**Richard Byrne, Table 1** Selected References

| Topic                                                    | References                                                                                                           |
|----------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------|
| <i>Synthesis</i>                                         | Byrne (2016)                                                                                                         |
| <i>Primate cognitive evolution</i>                       | Byrne and Whiten (1992); Byrne (1997); Byrne and Bates (2006, 2010)                                                  |
| <i>Manual skill and imitation in cognitive evolution</i> | Byrne and Byrne (1993); Byrne and Russon (1998); Byrne (2003, 2006)                                                  |
| <i>Animal culture</i>                                    | Byrne (2007); Byrne et al. (2011)                                                                                    |
| <i>Mental maps and navigation</i>                        | Byrne (1982, 2000); Noser and Byrne (2007); Byrne et al. (2009)                                                      |
| <i>Elephant cognition</i>                                | Bates et al. (2008a, b); Smet and Byrne (2013, 2014)                                                                 |
| <i>Great ape gestural communication</i>                  | Cartmill and Byrne (2007); Genty et al. (2009); Hobaiter and Byrne (2014); Graham et al. (2016); Byrne et al. (2017) |

**Cross-References**

- [Cognition](#)
- [Cognitive Imitation](#)
- [Cognitive Map](#)
- [Comparative Cognition](#)
- [Imitation](#)
- [Intelligence](#)
- [Intentionality](#)
- [Laterality \(Handedness\)](#)
- [Machiavellian Intelligence](#)
- [Primate Cognition](#)
- [Primate Communication](#)
- [Primates](#)
- [Social Intelligence Hypothesis](#)
- [Teaching](#)
- [Technical Intelligence Hypothesis](#)
- [Theory of Mind](#)

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**Richard W. Byrne** is Emeritus Professor at the University of St Andrews, Scotland. He is best known for his work on primate cognition in the wild, especially in gorillas and chimpanzees, but has also carried out research on baboons, domestic pigs, and African elephants.

## Richard Dawkins

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## Main Text

Richard Dawkins (born March 26, 1941, in Nairobi, Kenya, as Clinton Richard Dawkins) is a British evolutionary biologist, ethologist, and author. He is an Emeritus Fellow of New College, University of Oxford. Since 1997, he has been a fellow of the Royal Society of Literature (FSRL). In 2001, he was elected fellow of the Royal Society (FRS).



## Education

Dawkins attended Oundle School in Northamptonshire from 1954 to 1959. In 1962, he graduated Zoology at Balliol College, University of Oxford. Under the supervision of Nikolaas Tinbergen, one of the pioneers of animal behavior research and a Nobel Prize winner (Burkhardt 2010), he continued his study, receiving a PhD in 1966. He stayed as Tinbergen's research assistant until 1967. At the time, his own research interests focused on animal decision-making, on which he has published several papers (Dawkins 1969a, b, c; Dawkins and Impekoven 1969).

## Academic Career

Richard Dawkins began his teaching career in 1967 as an assistant professor of Zoology at the University of California, Berkeley. He stayed at this position until 1969, when he returned to University of Oxford as a senior research officer at the Department of Zoology. In 1970, he became a lecturer in Animal Behavior and a fellow of New College, University of Oxford. He became a reader in Zoology in 1990. In 1995, he was appointed the Simonyi Professorship for the Public Understanding of Science, the chairmanship created specifically for him by a donation from Dr. Charles Simonyi. The aim of the professorship is "to contribute to the understanding of science by the public" (Simonyi 1995). Dawkins held this position until 2008 (Richard Dawkins Foundation for Reason and Science 2015).

Dawkins has edited several peer-reviewed journals. From 1972 to 1973, he was the European editor of "Animal Behaviour Monographs." Between 1974 and 1978, he was the European editor of "Animal Behaviour." In 1983, he became an executive editor of "Oxford Surveys in Evolutionary Biology," which he remained until 1986. In 2002, he founded the "Episteme Journal." He edited "The Oxford Book of Modern Science Writing," an anthology of scientific writings from a variety of authors on diverse of topics, published in 2008. Dawkins has been a member of over 15 committees and has

given over 60 invited lectures across the world. In 1997, he presided the Biology section of the "British Association for the Advancement of Science".

In 1999, Dawkins set up "The Simonyi Lectures." This annual event open to everyone aims "to promote the public understanding of science" (The Oxford Simonyi Professor for the Public Understanding of Science 1999). Over the years, many influential scientists were invited to present on a topic of their choice: Daniel Dennett (1999), Richard Gregory (2000), Jared Diamond (2001), Steven Pinker (2002), Martin Rees (2003), Richard Leakey (2004), Carolyn Porco (2005), Sir Harry Kroto (2006), and Sir Paul Nurse (2007). After Dawkins retired from the position in 2008, the lectures continued under the organization of the new Simonyi professor, Marcus Du Sautoy. Richard Dawkins gave a talk in 2008 and was followed by Timothy Gowers (2009), Christoph Koch (2010), David Spiegelhalter (2011), Luc Steels (2012), Eric Weinstein (2013), David McKay (2014), Melissa Franklin (2015), and Simon Baron-Cohen (2016).

## Publications

Dawkins has authored and co-authored more than 80 small books and peer-reviewed articles. His work has been published in highly cited international journals, such as *Animal Behaviour*, *Behaviour*, *Evolution*, *Nature*, *Science*, and many others. But despite his long-lasting academic career, Richard Dawkins is best known to the general public for his books on evolutionary biology, many of which have been translated in multiple languages and have become bestsellers.

In 1976, he published "The Selfish Gene" (Dawkins 1976). In this book, Dawkins explores the biology of selfishness and altruism, explaining a gene-centered view of evolution, which is in contrast to the organism- or group-centered views developed by scientists such as William D. Hamilton in the 1960s. According to this view, the more the two organisms are genetically related, the more beneficial will it be for them to behave selflessly toward each other, as this will maximize their inclusive fitness. Dawkins

explains that genes' selfishness is a metaphor, as genes that are replicated are those whose evolutionary consequences serve their own implicit interest, and not necessarily the interest of the organism that carries them. This book is also known for the first mention of the term "meme," coined by Dawkins to mean a unit of human cultural evolution, analogous to the gene. This book became a bestseller and has been translated into over twenty-five languages.

In 1982, Dawkins published "The Extended Phenotype." This book, which he considers his principal contribution to evolutionary theory, discusses the idea that phenotype is not limited to biological processes but should be extended to encompass all effects that a gene has on its environment, both inside and outside of the individual organism that contains it (Dawkins 1982). Dawkins explains three types of extended phenotypes. The first type refers to animals' capacity to modify their environment through the use of architectural constructions and by that increase their fitness. The second type is the so-called parasite manipulation, and it involves parasites' manipulation of hosts' behavior, for the purpose of creating distinct advantages for their own fitness. The third type is the parasitic manipulation of host behavior without being physically associated with the host (e.g., as with the chicks of cuckoo birds). In this book, Dawkins also introduced the "Central Theorem of the Extended Phenotype," which postulates that animal's behavior tends to maximize the survival of the genes "for" that behavior, whether or not they happen to be in the body of the animal performing said behavior.

Dawkins's next book, "The Blind Watchmaker," was published in 1986. Herein, Dawkins presents the argument for the theory of evolution by natural selection. He explains the unintentional nature of evolution by making a reference to William Paley's "watchmaker analogy," made famous in Paley's 1802 book "Natural Theology." Also known as "the watchmaker argument," this teleological argument states that design implies a creator. Dawkins, however, contrasts the planning potential of human design to the accumulation of random mutations, likening the evolutionary processes of natural selection to a blind watchmaker

(Dawkins 1986). In 1987, Dawkins was awarded the "Royal Society of Literature Award" and the "Los Angeles Times Literary Prize" for this publication. The same year, a documentary carrying the same name was released. Written by Jeremy Taylor and presented by Dawkins, it won the "Sci-Tech Award for Best Science Documentary" of the year.

In 1995, Dawkins published "River out of Eden: A Darwinian View of Life." In this book, Dawkins uses a metaphor of a river flowing through time (instead of space) to discuss descent, heredity, and speciation (Dawkins 1995). He debates about the last common ancestor of all living humans – the "Mitochondrial Eve." Moreover, he asserts that the key feature of evolution is its gradualness.

The following year, Dawkins published "Climbing Mount Improbable." This book, in which he discusses the applications of probability on evolution, was developed from the ideas Dawkins discussed in his series of lectures entitled "Growing Up in the Universe," written and recorded in 1991 as a part of "Royal Institution Christmas Lectures." Designed to debunk creationists' claims about natural selection, the main metaphor used in "Climbing Mount Improbable" is that of a geographical landscape, which Dawkins uses to explain how seemingly complex mechanisms develop from many gradual steps (and not from "climbing cliffs") (Dawkins 1996). This visualization of the relationship between genotypes and reproductive success is also known as an adaptive or fitness landscape. In this metaphor, fitness is represented as landscape's "height," and genotypes that are similar are visualized as "close" to each other. This idea is also used to explain flawed forms in evolution by natural selection, such as animals' reactions to supernormal stimuli.

In 1998, Dawkins published "Unweaving the Rainbow," subtitled "Science, Delusion and the Appetite for Wonder." In this book, he battles the stereotype that scientists such as himself deprive life of meaning and argues that they see it as full of wonders and pleasures that arise from the understandable laws of nature (Dawkins 1998). He discusses the relationship between

science and the arts from a scientist's perspective, using different examples to illustrate how artists and scientists are motivated by the same spirit of wonder. He argues that unfolding mysteries leads to even more exciting ones. Throughout the book, Dawkins exemplifies how scientific methods can be used to detect and correct the fallacies that can arise from a lack of statistical reasoning, such as over-interpretation of coincidence. Dawkins also discusses the selfishness of cooperation. Bringing it down to a genetic level, he explains coadaptation and coevolution as two contexts of collaboration through which genes compete.

In 2003, Dawkins published a book of selected essays and other writings entitled "A Devil's Chaplain" (subtitled "Reflections of Hope, Lies, Science, and Love"). The title is a reference to Charles Darwin's quotation on his lack of belief in "a perfect world" designed by God: "What a book a devil's chaplain might write on the clumsy, wasteful, blundering low and horridly cruel works of nature!" (The Guardian 2003). The topics he discusses in this publication range from evolutionary biology, scientific methods, memes, ethics, and religion. The book also includes chapters on some of Dawkins's "heroes," such as Douglas Adams, W.D. Hamilton, John Diamond, Richard Leakey, and Stephen Jay Gould. The book ends with a letter Dawkins wrote for his then 10-year old daughter, Juliet. In this letter, he spells out the importance of evidence as basis of knowledge, encouraging her to always look for and value evidence over "tradition, authority or revelation" (Dawkins 2003).

Dawkins published his longest book to date, "The Ancestor's Tale: A pilgrimage to the Dawn of Life," in 2004. This book, nominated for the 2005 Aventis Prize for Science Books, follows a backward path of human evolutionary history, meeting humanity's cousins and their last common ancestors (or "Concestors," as Dawkins calls them, using the term coined by Nicky Warren). Making a notion that patterns recur and evolution rhymes (in reference to a quote on history, attributed to Mark Twain, which says that history does not repeat itself, but it rhymes), Dawkins discusses the predictability of evolution. Using a backward chronology all the way to the grand

ancestor of all surviving life forms on Earth, Dawkins celebrates equality of all species and unity of life (Dawkins 2004).

Richard Dawkins is broadly known for his openly antireligious views. Although often regarded as the most famous atheist in the world, he declared himself as agnostic in his 2006 book "The God Delusion." In this book, which sold in over one million copies, Dawkins uses multiple examples to explain the nonnecessity of religion for morality. He asserts the near certainty of non-existence of a supernatural creator and declares a persistent belief in a personal god to be a delusion, due to its stronghold against the rich contradictory evidence (Dawkins 2006). This book has been translated into 35 languages, and many books have been written in its response (Dawkins 2015).

In 2009, Dawkins published "The Greatest Show on Earth: The Evidence for Evolution." The title of this book comes from a T-shirt quote, anonymously sent to Dawkins, which read "Evolution, the Greatest Show on Earth, the Only Game in Town" (Dawkins 2009). This publication contains succinct discussions of multiple explicitly set out evidence for biological evolution, from the artificial selection to the fossil record. Despite previously having written numerous publications on this topic, Dawkins considers this book to be his "missing link," and a "personal summary of the evidence that the 'theory' of evolutions is actually a fact – as incontrovertible a fact as any in science" (Dawkins 2009, p. vii).

Dawkins has also written books for children and young adults. In 2011, he published "The Magic of Reality: How We Know What's Really True" (Dawkins 2011). This graphic book, illustrated by Dave McKean, comprises retellings of multiple creation myths from all over the world, both traditional and contemporary. It also includes Dawkins's recollections of his own childhood thoughts on various phenomena. Some of the topics include atomic theory, planetary motion, gravitation, stellar evolution, spectroscopy, plate tectonics, exobiology, and human psychology.

In 2013, Dawkins published an autobiographical memoir entitled "An Appetite for Wonder: The Making of a Scientist" (Dawkins 2013). In this book, Dawkins talks about his first 35 years,

his life before “The Selfish Gene.” The second volume of his autobiography, “Brief Candle in the Dark: My Life in Science,” was published in 2015 (Dawkins 2015). In this publication, he discusses his ideas, inspirations, and “heroes,” from Charles Darwin to Peter Medawar, Nikolaas Tinbergen, William D. Hamilton, John Maynard Smith, Douglas Adams, Carl Sagan, and David Attenborough.

### Television Documentaries and Other Appearances

Dawkins has devoted much of his time and effort to the popularization of science. In addition to his numerous publications, this is well evidenced by his many appearances in television productions. In 1986, he released “Nice Guys Finish First,” a documentary in which he discusses selfishness and cooperation, arguing that the evolution favors the latter. In 1996, “Break the Science Barrier” was released, a documentary in which Dawkins promotes the perspective that scientific endeavor is not only useful but also intellectually stimulating and exciting. In 2004, Dawkins was interviewed in an episode of “The Atheism Tapes,” a BBC documentary series presented by Jonathan Miller. He discussed how he became an atheist and explained the fallacy of the “God of the gaps” argument, which uses gaps in scientific knowledge as evidence of God’s existence (Stanford Encyclopedia of Philosophy 2005). In 2005, Dawkins presented an episode of a British documentary series entitled “The Big Question.” This five-part series featured renowned scientists examining provocative questions about the universe and life. Dawkins’s episode answered the questions “Why are we here?” In 2006, “The Root of All Evil?” later retitled “The God Delusion” was released. Here, Dawkins argues that humanity would be better off without religion and belief in God. In “The Enemies of Reason,” a two-part documentary released in 2007, Dawkins aims to expose the “areas of belief that exist without scientific proof, yet manage to hold the nation under their spell” (National Secular Society 2007), such as the mediums, acupuncture, and psychokinesis.

In 2008, he wrote and presented a three-part television documentary “The Genius of Charles Darwin,” which won the “Best TV Documentary Series 2008” at the British Broadcast Awards. In “Faith School Menace?,” released in 2010, Dawkins exposes the effects of faith schools on both their students and the society. In 2012, “Sex, Death and the Meaning of Life” was released. In this three-part documentary, Dawkins explores the benefits that reason and science might offer in major events of human life, challenging the ideas about the soul, sin, and afterlife offered by religion. The same year, he starred in the second series of BBC’s “Beautiful Minds” documentary, which featured significant British scientists describing their big moments or discoveries. In the final episode of the season, Dawkins discussed “The Selfish Gene” and how this book made him a spokesman for atheism. In 2013, Dawkins starred in “The Unbelievers,” a documentary following him and Lawrence Krauss on their public lectures on the importance of science and reason in the modern world. He also gave two TED Talks, “Militant Atheism” (2002), and “Why the Universe Seems So Strange” (2005).

Dawkins has been featured in numerous television and radio programs, providing his political opinions and debating many religious figures. Additionally, he has made 70 appearances as himself in television shows and movies (Internet Movie Database 2017), such as “Doctor Who” – “The Stolen Earth” (2008) and “The Simpsons” – “Black Eyed, Please” (2013). He also appeared on The Colbert Report (2006) and The Late Late Show (2009).

Dawkins was featured as a narrator on the album of a Finnish symphonic metal band Nightwish, called “Endless Forms Most Beautiful,” which was released in 2015. He was a guest on two songs – “Shudder Before the Beautiful” and “The Greatest Show on Earth” (Richard Dawkins Foundation for Reason and Science 2015).

### Honors and Awards

During his career, Dawkins received many awards and honors. They include the Zoological Society

of London's Silver Medal (1989), the Finlay Innovation Award (1990), the Royal Society of London's Michael Faraday Award (1990), the Committee for Skeptical Inquiry's In Praise of Reason Award (1992), the Nakayama Prize for Achievement in Human Science (1994), the American Humanist Association's Humanist of the Year Award (1996), the International Cosmos Prize (1997), the Kistler Prize (2001), the Medal of Presidency of the Italian Republic (2001), the Freedom From Religion Foundation's Emperor Has No Clothes Award (2001, 2012), the Royal Philosophical Society of Glasgow's Bicentennial Kelvin Medal (2002), the Shakespeare Prize for Contribution to British Culture (2005), the Lewis Thomas Prize for Writing about Science (2006), the Galaxy British Book Award's Author of the year (2007), the Deschner Award (2007), and the Nierenberg Prize for Science in the Public Interest (2009).

### The Richard Dawkins Foundation for Reason and Science

In 2006, Dawkins founded a nonprofit organization called the "Richard Dawkins Foundation for Reason and Science" (RDFRS), with the mission to promote scientific literacy and a secular worldview and remove the influence of religion in science education and public policy (Richard Dawkins Foundation for Reason and Science 2017). Dawkins stated his belief that critical thinking is the real savior of humankind and that welcoming secular views in policy-making will "advance human safety, security, health, achievement, prosperity, and most of all, science" (Richard Dawkins Foundation for Reason and Science 2017).

In 2016, RDFRS merged with the "Center for Inquiry" (CFI), a nonprofit educational organization with a mission "to foster a secular society based on science, reason, freedom of inquiry, and humanist values" (Center for Inquiry 2017). Richard Dawkins is on the board of directors of this new, unified organization, and RDFRS continues to operate as its division.

### Cross-References

- Artificial Selection
- Charles Darwin
- Common Ancestor
- David Attenborough
- Evolution
- Genotype
- Inclusive Fitness
- Natural Selection
- Nikolaas Tinbergen
- Species
- William Donald Hamilton

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## Richard Wrangham

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## Words

Richard Wrangham (born Leeds, Yorkshire, United Kingdom; 1948–) is a British primatologist and evolutionary anthropologist. He is an internationally renowned expert on wild chimpanzees who has made significant theoretical and empirical contributions across a wide range of

topics related to primate socioecology and human behavioral evolution. Wrangham has authored over 250 scientific articles and has written 3 books and co-edited 7 others. He married Dr. Elizabeth Ross in 1980 and has three adult sons.

Wrangham received his BA from Oxford University and subsequently received a PhD in Animal Behavior in 1975 from Cambridge University under the advisement of noted ethologist Robert Hinde. He received postdoctoral training from John Crook in the Bristol University Department of Psychology and from David Hamburg in the Stanford University Department of Psychiatry. Wrangham spent most of his early career at the University of Michigan, where he held a joint appointment in Biology and Anthropology. He joined the faculty of Biological Anthropology (now Human Evolutionary Biology) at Harvard University in 1989. He is currently the Ruth B. Moore Professor of Biological Anthropology. Wrangham received a prestigious MacArthur Foundation Fellowship in 1987 and was awarded the Rivers Medal from the Royal Anthropological Institute in 1993. He is a fellow in the American Academy of Arts and Sciences (1993) and the British Academy (2013) and received an honorary Doctor of Sciences degree from Oglethorpe University in 2011.

During his doctoral studies, Wrangham was one of the earliest students to conduct fieldwork on wild chimpanzees in collaboration with Jane Goodall at the Gombe Stream Research Center. His thesis, entitled “The Behavioural Ecology of Chimpanzees in Gombe National Park, Tanzania” focused on the chimpanzee diet and its influences on ranging and social behavior (Wrangham 1975). This work spurred a career-long emphasis on the fundamental role of nutrition and ecological variability in shaping the evolution and behavioral diversity of primates. In 1987, Wrangham established his own field site for the study of wild chimpanzees in Kibale National Park, Uganda. This study of the Kanyawara community, comprising 50–60 chimpanzees, is one of the longest-running naturalistic studies of wild primates and has yielded important scientific contributions on chimpanzee nutritional ecology, social



relationships, sexual and aggressive behaviors, hormone-behavior interactions, disease, culture, and communication.

In 1980, Wrangham published a seminal paper in primatology entitled, “An Ecological Model of Female-Bonded Primate Groups” (Wrangham 1980). Building on models of resource competition developed for birds and bats, Wrangham argues that the structure of primate groups depends primarily on female responses to the distribution of food resources in the environment. The common pattern of female-bonded social organization in primates results from the competitive advantages that females gain by forming cooperative alliances with other (mostly related) females to the exclusion of rivals. This contributed to a broader theoretical revolution in socioecology, coalescing in a volume Wrangham co-edited entitled, *Ecological Aspects of Social Evolution: Birds and Mammals* (Rubenstein and Wrangham 1986). While Wrangham’s original model has received numerous revisions and critiques, it remains an essential framework for understanding primate socioecology and has been a driving force behind inquiry into primate nutritional ecology. To this end, Wrangham directed a nutritional ecology laboratory at Harvard, partnering with Nancy Lou Conklin-Brittain to perform pioneering analyses of the nutritional composition of primate foods. Wrangham has

also published several influential papers on the use by primates of plants with medicinal properties and (with phytochemist Eloy Rodriguez) coined the term “zoopharmacognosy” to describe intentional use of such plants (Rodriguez and Wrangham 1993).

Wrangham has been a leader in the field of primatology for four decades. He co-edited *Primate Societies*, one of the first and most widely used textbooks in primatology (Smuts et al. 1987), along with an edited volume on chimpanzee behavioral biology: *Chimpanzee Cultures* (Wrangham et al. 1994). He served as president of the International Primatological Society from 2004 to 2008. Throughout his career, Wrangham’s work has been distinguished by an enduring focus on using primates to inform models of human evolution. In a 2000 article entitled “African Apes as Time Machines,” Wrangham joined paleoanthropologist David Pilbeam in laying out the argument for positioning chimpanzees (as opposed to gorillas or bonobos) as the most apt living model for the last common ancestor of *Homo* and *Pan* (Wrangham and Pilbeam 2000). Supported by nearly two decades of additional evidence, this argument forms the basis for a recent volume on *Chimpanzees and Human Evolution*, co-edited by Wrangham, Pilbeam, and Martin Muller (Muller et al. 2017). This text compiles evidence from diverse aspects

of hominid biology to probe the evolutionary roots of human traits.

In 1996, Wrangham published (with co-author Dale Peterson) the book, *Demonic Males: Apes and the Origins of Human Violence* (Wrangham and Peterson 1996). Once viewed as aberrant behaviors, infanticide, lethal intergroup raids, and sexual aggression have each proven to be habitual behaviors in one or more of human's great ape relatives. *Demonic Males* critically examines the functional significance of these behaviors within the apes, arguing for fundamental evolutionary continuities with violent behavior in human societies. Rather than merely portraying violence as biologically predisposed, Wrangham and Peterson emphasize its context dependence, using examples from humans and from the relatively peaceful bonobo to suggest ways to promote the better angels of our nature. Wrangham, in collaboration with Michael Wilson, Luke Glowacki, and others, authored numerous subsequent works examining empirical data on chimpanzee and human aggression and developing evolutionary models for collective violence in the contexts of gangs, warfare, and raiding in small-scale societies. He also co-edited, with Martin Muller, a volume using data on male-female aggression in humans, primates, and other mammals to position sexual coercion within the conceptual framework of sexual selection (*Sexual Coercion in Primates: An Evolutionary Perspective on Male Aggression Against Females*: Muller and Wrangham 2009).

In 1999, Wrangham collaborated with colleagues at Harvard University to propose a bold, new hypothesis that the innovation of cooking food would have fundamentally changed the course of human evolution. The paper "The Raw and the Stolen: Cooking and the Ecology of Human Origins" (Wrangham et al. 2000), later elaborated in Wrangham's book *Catching Fire* (Wrangham 2009), argues that a diet comprised primarily of cooked foods would not only have substantially increased energetic gains from foraging effort, resulting in the large body and brains and smaller dentition and digestive systems first observed in *Homo erectus*, but would have motivated changes in social behavior, including pair bonding, as a response to the increased demands

of defending stored foods. This has been one of the first significant challenges to the long-held model for meat-eating as the prime mover shifting hominid diets and lifestyles. With Rachel Carmody and others, Wrangham has generated numerous lines of metabolic, behavioral, and genetic evidence for the biological significance of cooking. This work has also stimulated renewed enthusiasm in the search for archaeological evidence for the control of fire.

In recent years, Wrangham has been instrumental in developing new theories for how evolutionary processes resembling domestication may have shaped behavioral diversity among hominids. Reduced aggressive behavior in bonobos compared with chimpanzees coincides with morphological and developmental differences that resemble the correlated changes that occur when species (e.g., dogs vs. wolves) have been artificially selected for reduced aggression (Hare et al. 2012). This suggests that selection against aggression may have been one of the major evolutionary forces promoting the divergence of chimpanzees and bonobos. Wrangham further argues that humans exhibit derived features that are suggestive of an analogous selection process. Such "self-domestication" to reduce reactive aggression may have been instrumental in the development of the complex, highly cooperative societies characteristic of our species. This argument will form the basis for Wrangham's forthcoming book, tentatively titled *The Virtue Paradox*.

Throughout his career, Wrangham has been an advocate for great ape conservation. In conjunction with his work in Kibale National Park, Wrangham initiated the Kibale Snare Removal Program in 1997 to reduce illegal poaching activities in the Park. The same year, he co-founded the Kasiisi Project with Elizabeth Ross to promote conservation via programs in the community that support education and health of children and families. Wrangham was also instrumental in partnering with the Uganda Wildlife Authority to develop the Kanyanchu chimpanzee ecotourism site in Kibale. In 2008, Wrangham and Ross co-edited *Science and Conservation in African Forests: The Benefits of Long-term Research*, which outlines strategies for creating synergy

between scientific research and conservation goals, citing tangible success stories from the teams working in and around Kibale National Park (Wrangham and Ross 2008). Wrangham is an ambassador for the Great Apes Survival Partnership (GRASP), an alliance between the United Nations and international government entities, conservation organizations, corporations, and scientists devoted to the protection of great apes. Wrangham also serves on the board of directors of the Pan African Sanctuary Alliance (PASA), a partnership among wildlife centers that coordinates the rescue and rehabilitation of primates impacted by habitat destruction and the pet and bushmeat trades. He is a member of the International Union of the Conservation of Nature (IUCN) Species Survival Commission Primate Specialist Group. He has previously served as a trustee or board member for several international conservation organizations, including the Jane Goodall Institute, Dian Fossey Gorilla Foundation, Wild Chimpanzee Foundation, WildAid, and the Great Ape World Heritage Species Project.

Wrangham has a rich academic lineage. Past PhD or postdoctoral advisees in faculty positions include Adam Clark Arcadi, Rachel Carmody, Colin Chapman, Richard Connor, Margaret Crofoot, Melissa Emery Thompson, Alexander Georgiev, Ian Gilby, Luke Glowacki, Tony Goldberg, Anne Goldizen, Brian Hare, Kevin Hunt, Dominic Johnson, James H. Jones, Cheryl Knott, Zarin Machanda, Andrew Marshall, Katie McAuliffe, Bethan Morgan, Martin Muller, Herman Pontzer, Lars Rodseth, Adrian Treves, Michael Wilson, and Brian Wood.

## Cross-References

- [Aggression](#)
- [Conservation](#)
- [Ecology](#)
- [Group Living](#)
- [Homo sapiens](#)
- [Jane Goodall](#)
- [Last Common Ancestor](#)
- [Primate](#)

- [Primate Diet](#)
- [Primate Social Structure](#)
- [Self-Domestication Hypothesis](#)
- [Social Behavior](#)
- [Territory Defense](#)

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## Riding

### ► [Horseback Riding](#)

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## Ritualization

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### Definition

Ritualization is a process by which non-signaling behavior patterns evolve to become communicative signals.

### Introduction

By signaling, an animal can influence the behavior of other animals and, consequently, change their own environment. Signals and displays are designed in the course of evolution for use in communication. They are shaped by natural selection to effectively convey information from the signaler to the recipient, i.e., to enhance the clarity of a signal and to reduce confusion (Endler 1993; Laidre and Johnstone 2013). The evolutionary process where activities, movements, and structures primarily not associated with communication obtained signaling function is called ritualization (Krebs and Davies 2006).

### History

The process of ritualization was first described by Edmund Selous in 1901 and later by Julian Huxley, who named it ritualization in 1914 (Dissanayake 2006; Lorenz 1966). Later it was used by Konrad Lorenz and other ethologists to describe ceremonial acts in social animals (Erikson 1966).

## Process of Ritualization

During evolution, signals may have derived from cues, incidental movements, or responses like those that can be seen during the motivational conflict (Krebs and Davies 2006; Laidre and Johnstone 2013). During the ritualization process, these behaviors become stereotyped, repetitive and conspicuous, or precise and gain the function of a signal to decrease misunderstanding (Krebs and Davies 2006; Hickman et al. 2008). The origins of signals can be found in different everyday activities, and some of them already are a source of information to other animals (McFarland 2006). The signal may incorporate some attractive or aversive cues, e.g., food or predatory cues (Pascoal et al. 2016).

Cues can provide information to others, although they are not evolutionarily shaped for the purpose of communication. They are conveying information unintentionally and passively, and they can be a by-product of some other animal activities (Biernaskie et al. 2018; Laidre and Johnstone 2013). On the other hand, signals are actively used in communication, and they are designed in the course of evolution to change the behavior of another individual. Usually, signals convey one information, and that can be the chemical, visual, auditory, tactile, seismic, or electric message. Similarly, displays are behaviors or series of behaviors that are highly stereotyped and used in communication to show specific physical characteristics (e.g., colors, patterns, and weapons) that are important for mate attraction, social (pair) bonding, coordination of group activities, intimidating rivals, predator deterring, etc. (Hickman et al. 2008; Laidre and Johnstone 2013; McFarland 2006).

If there is an evolutionary advantage, natural selection enhances the transformation of certain behaviors to become reliable and conspicuous signals. By the ritualization, signals become less ambiguous, easily distinguishable from some activities and other signals. From an evolutionary point of view, it is important to prevent hybridization, so different species need to have different signals that are used in courtship. Furthermore,



signal differentiation may play an important role in the prevention of aggression between related species that share habitat but differ in ecology (e.g., food). This is also important for the separation within species, such as between age groups or sexes, and consequently, interspecific signals were also under selection pressures that favored unambiguous recognition. Finally, some species signals may differ between individuals, giving possibility that individual animal is recognized by the other individuals in their social group, their mate, or by agonistic neighbors in territorial species. On the other hand, the process of ritualization is limited by signal-generating structures and sense organs available to a species, by habitat characteristics, the vulnerability of the species to predation, as well as some other factors (Cullen 1966).

Some locomotory movements, feeding behaviors, breathing, or body secretions can be ritualized to create new communication signals. Darwin was the first to point out that vocal signals may have originated from altered breathing patterns that were originally cues associated with the types of physical activity the breathing animal was preparing to undertake (Laidre and Johnstone 2013) and they are further developed by signaling environment (Endler 1993; Krebs and Davies 2006).

Ritualized behaviors have rigorously regulated speed and amplitude, so-called “typical intensity” (Morris 1957). They are also characterized by repetitions and invariable elements which are linked into a single obligatory sequence. By ritualization, motor patterns that are producing visual and auditory stimulation in communication channel become exaggerated, and those with mechanical function are reduced or even disappear (Dissanayake 2006; Lorenz 1966). Furthermore, behavior patterns become incomplete in execution, such as typical grooming which becomes restricted to certain parts of the body and movements become shortened (McFarland 2006). Therefore, by ritualization, new independent behaviors are developed, each with its own releasing mechanisms, spontaneity, and appetitive behavior (Lorenz 1966).

Behavioral changes are followed by morphological modifications that boost the

visibility and distinctiveness of the behavior, i.e., movements can be emphasized by skin, fur, or feather coloration (Wilson 1980). For example, in wild *Canidae*, the coloration of the coat is adjusted to enhance visual communication. Therefore, in wolves, coyotes, and red and gray foxes, the sides of the face or cheeks are white, and the lips are black. In that way, black lips and their horizontal retraction are enhanced, giving facial expressions that can be seen in fear or aggression (Fox 1971).

Finally, the motivation for some primary behavior may be different from the signal that evolved from it, for example, when female birds are begging for food during courtship ritual, even though they may not be hungry (McFarland 2006). However, some signals maintain the function of the behavior from which they developed. For example, threatening display may evolve through the ritualization of aggressive movements, i.e., real preparation for the fight, and the animal with clear signaling behavior could be preferred by evolution because it is disadvantageous to engage in actual fighting. Fights over mates, food, and territory may become ritualized to avoid bloody battles, in which even the winner can sustain dangerous injuries (Hickman et al. 2008; Wilson 1980).

Ritualization processes cannot be observed directly, but are instead researched by comparative studies of closely related species, wherein some species certain behaviors can be observed in their primary function while in other species, they become signals (Krebs and Davies 2006).

## Examples

Ritualization has been described in birds; mammals, including humans (Erikson 1966; Lorenz 1966); as well as fishes (Lorenz 1966) and invertebrates (e.g., marine *Crustacea*, Hazzlet 1972; caterpillar *Drepana arcuata*, Scott et al. 2010).

Bartoš et al. (2007) researched the agonistic behavior of fallow deer bucks (*Dama dama*) during the rut. Agonistic displays in deer are considered a ritualized behavior, where signals are obtained from a real fight, including the

display of vigor and strength. In this research, vocalizations and parallel walk increased the probability that one of the opponents will leave without an actual fight, while increased symmetry of the contestants' behavior was correlated with a higher likelihood of a fight. Therefore, fallow deer bucks efficiently use ritualized displays in the breeding season which minimizes the chance of injury that may be the consequence of real fighting.

Ground pecking of *Phasianidae* birds is another example of ritualization. To attract female a male domestic fowl (*Gallus*) and ring-necked pheasant (*Phasianus colchicus*) scratch the ground and peck food or pebbles – and this is the least ritualized form of display. In impeyan pheasant (*Lophophorus impejanus*) and peacock pheasant (*Polyplectron bicalcaratum*), the signal becomes more formalized and elaborated, so displays include slow rhythmical up and down movements of the head and tail (bobbing). Finally, male peacock (*Pavo*) starts with scratches and bows to attract a hen but then shows the tail spreading and pointing toward the ground with his beak (Dissanayake 2006; Krebs and Davies 2006).

Scott et al. (2010) show that a ritualized vibratory signal in caterpillars (anal scraping) originated from walking (locomotory behavior) and from physical fighting behaviors. In this way, competitors signal to each other to avoid the cost of fighting.

## Conclusion

Ritualization is one of the fastest evolutionary processes recognized in undomesticated animals (Lorenz 1966). This emphasizes the evolutionary flexibility of animal communication, as well as their importance in maintaining animal social life and reproduction.

## Cross-References

- [Communication](#)
- [Display](#)
- [Evolution](#)

- [Signal](#)
- [Signaling](#)
- [Sociobiology](#)

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## RNA

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## Synonyms

Ribonucleic acid

## Definition

RNA is a single stranded nucleic acid which is a polymer of ribose sugar, phosphate group, and nitrogen bases (Adenine, Uracil, Guanine, and Cytosine). The main function of RNA is the regulation of gene expression and synthesis of cellular proteins, and it serves as a genetic material in some viruses.

## Introduction

Nucleic acids were first seen and isolated by Johann Friedrich Miescher in 1868, from the nucleus of the white blood cells who named them as nuclein. Later it was found that nucleic acids are also present in prokaryotic cells which are devoid of any nucleus. There are two types of nucleic acids present in the cell: DNA (Deoxyribonucleic acid) (Nucleotides and Nucleic Acid, UCLA) and RNA (Ribonucleic acid). Unlike DNA, RNA is single stranded nucleic acid which differs from the DNA in the presence of ribose sugar instead of deoxyribose sugar and uridine in place of thymidine. Moreover, RNA is less stable than DNA due to the

presence of an additional hydroxyl (–OH) group at the 2' position in the ribose sugar which can attack nucleophilically the phosphate group of next nucleotide making RNA highly reactive in alkaline conditions (Alberts et al. 2015; Watson et al. 2014). RNA can be grouped into two broad categories: genetic and nongenetic. In most plant viruses, some animal viruses and bacteriophage, RNA acts as genetic material. While the nongenetic RNA (mRNA, tRNA, and rRNA) are polymers of ribonucleotides, synthesized from the DNA. The main function of the nongenetic RNA is protein synthesis from the active genes (the process called as translation). Besides these two main categories some other forms of RNAs like snRNA (small nuclear RNA), snoRNA (small nucleolar RNA), miRNA (micro RNA), siRNA (small-interfering RNA), piRNA (piwi-interacting RNA), lncRNA (long noncoding RNA) also exist which serve primarily to regulate gene expression by binding to the complementary sequence on the mRNA. Sometimes RNA forms short-term double stranded helices by unusual non Watson-Crick pairing; G (Guanine): U (Uracil), this is because it can also act as an enzyme (Ribozyme) (Clancy 2008; Karp 2013). RNA also has a role in cell division, differentiation, and aging. Deregulation in the expression level and localization of RNA is associated with many human diseases like heart disease, Alzheimer's disease, cancer, etc (Cooper et al. 2009).

## Structure of RNA

Ribonucleic acid is a high molecular weight molecule which is a polymer of ribonucleotides. Each ribonucleotide unit is made up of D-ribose sugar (pentose sugar), a phosphate group, and a nitrogen base. Like DNA, RNA also consists of four types of nitrogen bases, the only difference being the replacement of thymine with uracil. These ribonucleotides in RNA are termed as adenylic, guanylic, cytidylic, and uridylic acids. Ribonucleotides are linked with phosphodiester bond in a polymer chain. Besides these four types of nitrogen bases RNA also has some methylated forms and pseudouridine. Generally RNAs are

single stranded molecules but can also occur in double stranded form as in reovirus, rotavirus, etc (Alberts et al. 2015; Watson et al. 2014) (Fig. 1).

## Types of RNA

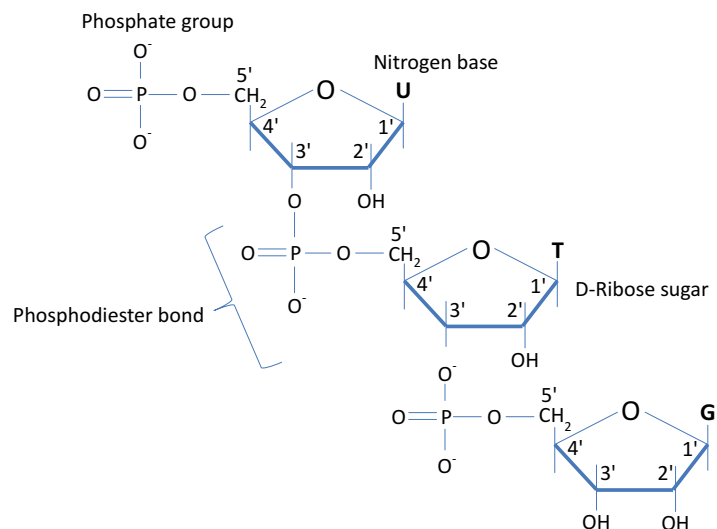
RNA can be grouped as genetic and nongenetic RNA on the basis of the functions they perform (Berg et al. 2002; Watson et al. 2014)

- (A) Genetic RNA: In all plant viruses, some animal viruses (Influenza, Rous sarcoma) and bacteriophage (MS2) RNA is the genetic material, as DNA is absent in them. It can be either single or double stranded. The genetic RNA in viruses can self-replicate in a RNA-dependent RNA synthesis manner. The genetic RNA also codes for genetic information like mRNA for protein synthesis.
- (B) Nongenetic RNA: In the organisms where DNA carries the genetic information, RNAs constitute the nongenetic material. Nongenetic RNAs are synthesized as a complementary sequence on the DNA in the nucleus by the process called transcription and transferred to the cytoplasm to perform various cellular functions like protein

synthesis, gene expression, regulation, etc. Nongenetic RNAs are of three types which have specific functions in the process of protein synthesis:

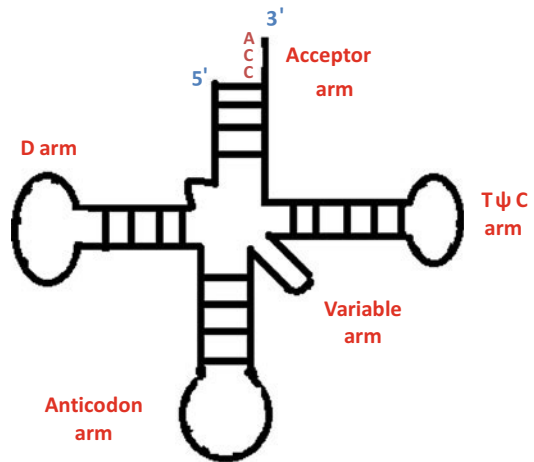
1. Ribosomal RNA (rRNA): rRNAs are the structural part of the ribosome, which along with the ribosomal proteins constitutes around 80% of the total RNA. Ribosomes in the eukaryotic cells is 80s with 60s (large subunit) and 40s (small subunit). The large subunit is composed of three types of rRNAs viz. 28s RNA, 5.8s RNA, and 5s RNA, while the smaller subunit have 18s RNA. In prokaryotic cells, only three types of rRNAs are present, viz. 23s, 5s, and 16s. Except 5s all forms of rRNAs are synthesized by the RNA polymerase I in the nucleolar organizer region of the chromosome which is present inside the nucleolus.
2. Messenger RNA (mRNA): The term mRNA or information RNA was coined by the Jacob and Monad in 1961. mRNA is also termed as photocopy RNA as it carries the genetic information as a complementary sequence of DNA from the nucleus to the cytoplasm. It is synthesized in the nucleus by RNA polymerase II and

**RNA, Fig. 1** Structure of RNA. Ribonucleoside (D-ribose sugar + Nitrogen base) linked by phosphodiester bond



transported to the site of protein synthesis, i.e., ribosome. mRNA contains the genetic information in the form of triplet genetic code (codon) which are being translated into polypeptide chain on the ribosome. The primary transcript synthesized in the nucleus is termed as heterogeneous nuclear RNA (hnRNA), which further undergoes posttranscriptional modifications as 5' capping (addition of 7-methylguanosine), splicing (removal of noncoding intron and joining of coding exons), and polyadenylation (addition of poly A tail at the 3' end) to become functionally active and stable. Average life span of mRNA is 1–4 h. The mRNA is relatively less stable as it gets degraded by the cytoplasmic ribonuclease enzymes. Certain mRNAs with delayed translation are not released in naked forms but covered in a protein complex which is termed as informosome (Spirin 1979). Like rRNA, mRNA sometimes form loop or coiled structure by the base pairing between A: U and G: C.

3. tRNA: Soluble or transfer RNA is the smallest RNA among the three. It constitutes around 10–15% of the total RNAs and is synthesized by RNA polymerase III in the nucleus. They function as adaptor molecules for mRNA and amino acids during translation. A single tRNA carries a specific amino acid according to the codon on the mRNA to the site of protein synthesis. Each tRNA is specified by its 3' base anticodon to carry a particular amino acid. Alanine tRNA was first sequenced by Holley and colleagues in 1965 who also proposed the two-dimensional clover leaf model of tRNA structure. tRNAs are generally 70–80 nucleotides long containing five arms or regions viz. 3' acceptor arm (where amino acid attaches), D arm (recognize and aminoacylate tRNA), T $\psi$ C arm (possess recognition site for ribosome), anticodon arm (read and bind codon of mRNA), and variable arm (Fig. 2). Later Kim and Klug in 1974



**RNA, Fig. 2** Structure of tRNA with five arms as T $\psi$ C arm, D loop, anticodon arm, acceptor site for amino acid and a variable arm

gave the 3D model of tRNA which is L shaped. The tRNAs are relatively stable and transcribed continuously than the other types of RNA (Watson et al. 2014).

## RNA World Hypothesis

The RNA world hypothesis was proposed in 1960s independently by Carl Woese, Francis Crick, and Leslie Orgel. These three scientists first gave the idea that RNA can act as a catalyst. The “RNA world” phrase was first used by the Walter Gilbert in 1986. The RNA world hypothesis proposes that RNA is the precursor of all the existing forms of life (Watson et al. 2014). Before DNA and proteins came into existence, RNA was functioning both as a genetic material and as a biocatalyst/enzyme and in due course of evolution due to its instability and poor catalytic activity; it got replaced by DNA and proteins. In 1980s, two independent groups Thomas Cech and Sidney Altman discovered the catalytic activity of the RNAs and named them ribozymes, which provides strong supporting evidence of the RNA world hypothesis. 23s rRNA as a structural component in the larger subunit of ribosome have the catalytic activity for the peptide bond formation (peptidyl transferase). Similarly during RNA



processing, RNA component of the RNase is involved in the cleavage of the pre-mRNA and splicing (Higgs and Lehman 2015; Watson et al. 2014). Thus in the earlier life forms RNA was performing the enzymatic activity which was later taken over by proteins due to their increased stability and versatility.

## Conclusion

According to the central dogma theory by Francis Crick, DNA is duplicated into DNA by the process of replication; DNA is transcribed to synthesize RNA, which along with the ribosome synthesizes the proteins according to the coding information provided on the mRNA by the process of translation. The process of formation of DNA using RNA as a template by the RNA-dependent DNA polymerase is termed as reverse transcription and was discovered by Howard Temin and David Baltimore in 1970. Transcription occurs during the interphase of cell cycle. DNA transfers its genetic information as a complementary single stranded molecules, i.e., mRNA which along with other types of non-genetic RNAs (tRNA and rRNA) translate the information into specified polypeptide chain. The RNA world hypothesis explains that RNA evolved before DNA and proteins and was performing both the functions as genetic material as well as biocatalyst. Further research is needed to decode the RNA's involvement in various functions other than role in protein synthesis.

## Cross-References

- [Ribosome](#)
- [Transcription](#)

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## RNA Sequencing

- [Gene Expression Profiling](#)

## Robert Hinde

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## Introduction

Robert Hinde was a British ethologist from the mid-twentieth to the early twenty-first century. He worked on a multitude of topics during his career, including bird migration, courtship in birds, mobbing behavior, social learning, parent-offspring relationships in primates, human social relationships, religion, morality, and war. He is well known for discounting Lorenz's drive model of behavior, developing a framework for animal social behavior, and campaigning for nuclear disarmament.

## Life and Work

Robert Hinde was born in Norwich in 1923, the youngest of four children, with one brother and two sisters. He was an avid naturalist from an early age, encouraged by his parents and an uncle. This passion for nature was nurtured while attending boarding school at Oundle, where he went on bird-watching expeditions with the headmaster and his son (Hinde 2010).

Following school, Robert joined the Air Ministry, serving as a pilot and navigator on Coastal Command. Kenneth Fisher, the headmaster of Oundle, arranged a closed exhibition (a scholarship based on personal recommendation) for Robert in St. John's College at Cambridge. This allowed him to leave the Air Ministry at the end of 1945, before the end of his original term of service, and start at Cambridge in January of 1946. Robert described himself at this time as working too hard and in a rush to get on with life (Hinde 2010).

Still an avid bird-watcher, Robert found the Cambridge sewage farm to be an excellent place for his hobby and visited about one to two times a week. Through the British trust for ornithology, he connected with bird-watchers across the country, a collaboration which led to several publications on the migrations of waders and terns (Hinde 2010). He also conducted an observational study on birds that had learned to open milk bottles, which was one of the earliest reports of observational learning in animals (Bateson 2017). Additionally, a chance spotting of a bird he did not recognize led to a consultation with local ornithologists, who excitedly determined it to be a moustached warbler, a rare bird that had not been recorded breeding in Britain. Recently, on a fifth review, the conclusion that this sighting was truly a moustached warbler was called into question (Hinde 2010); regardless, it was a major break in Robert's career.

One of the individuals who had consulted on the moustached warbler sighting was David Lack, who offered Robert a research assistant position following his graduation from Cambridge. Originally, Lack had intended to have Hinde work on the feeding habits of Jackdaws and Rooks as a test

of Gause's hypothesis, which is that two closely related species living in the same area don't compete (Hinde 2010). Robert, however, wanted to do behavioral research, and so with Lack's assistance, he began a naturalistic observational study of the behavior of great tits and closely related species, which became his graduate work at the University of Oxford. Incredibly, the population he began observing in 1948 has been studied every year since, providing a detailed long-term record on this model species in behavioral research. During Hinde's 2nd year as a graduate student, Niko Tinbergen, one of the developers of the field of ethology, joined the faculty at Oxford. Due to their similar research interests, Tinbergen effectively became a second mentor and taught Hinde how to analyze behavior, which was complementary to Lack's focus on using an ecological perspective (Hinde 2010).

In 1950, Bill Thorpe was in the process of establishing an ornithological field station in a four-acre field at Madingley. Thorpe was searching for a researcher to help develop and run the station; he knew Hinde from consulting on the moustached warbler sighting and so offered him the position (Hinde 1985). Together, they and the researchers and students they brought in developed the site and studied a variety of aspects of bird behavior. Robert particularly appreciated that he was able to do whatever research he wanted there (Hinde 2010).

His early research at Madingley focused on courtship and conflict in birds, particularly finches. For his courtship studies, he used hybrid birds to parse genetic and environmental influences on courtship postures between finch species. Furthermore, he found links between the social environment, hormones, and behavior patterns. His other main study with finches was an effort to use the mobbing responses of chaffinches to large predators, such as owls, to measure the action-specific energy reservoirs and releasing stimuli thresholds integral to Lorenz's model of motivation. However, in attempting to do this, he found that the model's components were not fixed and thus could not be measured. This led him to the conclusion that this drive model was not useful as it is too vague and lacks unitary definitions and

mechanisms. Instead, he argued that our ability to analyze chains of behavior patterns makes the concept of drive unnecessary, a stance which did not endear him to Konrad Lorenz. Additionally, this work demonstrated habituation of chaffinches to owls, indicating learning was taking place (Klopfer 1974; Hinde 2010).

Around the same time, Hinde was also assisting Thorpe with his research on imprinting. Thorpe was particularly interested in understanding the roles of instinct and learning for birdsong. Robert described his mentor as ahead of his time, for he heavily favored cognitive explanations which were not yet widely accepted (Hinde 2010). This research also sparked an interest in studying the parent-offspring relationship, which would prove to be the foundation of Robert's next research direction.

Furthering the development of Robert's new interest in parent-offspring relationships was John Bowlby's invitation to his weekly seminar on child development. Bowlby was a psychoanalyst interested in the early relationships of mothers and children and the impact of separation events on that relationship and later behavior. His seminar brought together scientists from a range of perspectives to weigh in on this topic; meetings typically included Bowlby, a Freudian, a Kleinian, a Piagetian, a Hullian leaning theorist, a Skinnerian, an anti-psychiatrist, two to three psychiatric social workers, and Hinde as an animal ethologist (Hinde 1985).

Additionally, Bowlby wanted to find experimental evidence of the negative impact of separation events and so worked with Hinde to set up a rhesus monkey colony, as they were one of the few nonhuman primates for which any knowledge existed at the time. To test the impacts of separation on parent-offspring bonds, they constructed housing had six large pens with inside areas for each, all connected to a large central area, with each large pen eventually housing a group of one male and three or four females with dependent offspring. This allowed control of the features of separations to mimic different hospitalization scenarios. Astonishingly, separations of just 10 days had long-term negative effects, results which helped change hospital regulations

to minimize patient separation from their families (Hinde 2010).

With the establishment of the monkey colony in the early 1960s, the Ornithological Field Station at Madingley became the sub-department of animal behavior. Additionally, Hinde was awarded a Royal Society Research Professorship in 1963, a very prestigious position which ensured job security and allowed him to focus on research and mentorship. The addition of primates to Madingley led to Robert becoming the mentor for students focusing on primate behavior, notably Jane Goodall and Dian Fossey, who worked with chimpanzees and gorillas, respectively (Bateson 2017; Hinde 2010). Both women had started in their research through Louis Leakey and needed a formal Ph.D. advisor. Notable students of Robert came to include Richard Wrangham, Tim Clutton-Brock, Dorothy Seyfarth, Phyllis Lee, Joyce Poole, and Judy Dunn. Robert felt that his role as supervisor was to teach his students to think critically and record behavior systematically. He also maintained that research students learn more from each other than their supervisor, and the supervisor learns at least as much from his or her students as the students do from the supervisor. For example, Jane and Dian both influenced his research by demonstrating the importance of individual differences in animals (Hinde 2010).

Robert's work with primates led, in the early 1970s, to an interest in the nature and dynamics of human social relationships, an interest he shared with his second wife, Joan. Together, they brought ethological methods to studies on children in pre-schools and in the home. Along with Robert's postdocs, they also conducted a cross-cultural comparison of family relationships between Britain and Hungary. Joan later became a leader in attachment theory (Hinde 2010).

As he became more active in studying interpersonal relationships in animals and humans, Robert noticed there was little research on the level which lies between group behavior and brief interactions. Thus, he set about describing what would be needed to study long-term dyadic relationships and developed a framework for understanding the connections between different levels of social behavior (interactions,

relationships, and social structure) which is widely used today. The model's greatest contributions were describing how each level is built from the content, quality, and patterning of the level below it, resulting in different properties for each (Hinde 1976).

Robert Hinde officially retired in 1989, though he remained academically active until his passing in 2016 (Anderson 2017). Upon his official retirement, he became headmaster of St. John's College, where he helmed the building of a new library. His academic focus shifted to matters of war, morality, and religion. He wrote multiple books on the topics, including *Defended to Death*, *Why Gods Persist*, and *Why Good is Good*. His books on religion examine the universal elements of religious belief, as well as how each is tied to human nature and how religion likely came about. While Hinde himself was atheist, he strongly believed that we have no right to take away the comfort of religion from someone else, especially if we have nothing to offer in its place. In order to have an acceptable alternative, he felt we should develop an outline of how to have morality without religion. His stance on war was that it is a stupid way of solving disputes and extracts vast amounts of resources which could be put to much better use. He was influenced by his own experiences in the military, his brother's death in WWII, and his research on behavior. This strong conviction motivated his active involvement in multiple anti-war organizations, including the Ex-servicemen Campaign for Nuclear Disarmament, the Movement for the Abolition of War, and the British Pugwash Group, for which he served as chairman for several years in the 2000s (Anderson 2017; Hinde 2010).

Throughout his life, Robert aimed to make the world a better place, a guiding principle which influenced him from his early work with birds to his later work against war. He made many contributions to science and society and was particularly influential in promoting cross-disciplinary perspectives. He recognized ethology's strengths and greatest achievements were in its links to other disciplines and played a

key role in integrating its principles and techniques with many other fields, including comparative psychology, physiology, learning, and many other biological and social science perspectives (Hinde 1982, 2010). He was also instrumental in moving ethology away from Lorenz's model building and instead promoted understanding behavior in a manner compatible with physiological processes. In a 2010 interview, he said that he was very lucky in his life in many ways, from the places he worked to the timing of his career, which enabled him to follow his interests wherever they led and work in new, exciting fields.

## Cross-References

- Dian Fossey
- Jane Goodall
- John Bowlby
- Konrad Lorenz
- Louis Leakey
- Nikolaas Tinbergen
- Richard Wrangham
- Social Behavior

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## Robert Mearns Yerkes

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Robert Mearns Yerkes (May 26, 1876 – February 3, 1956) was an American comparative psychologist best known for initiating the intelligence testing movement and establishing the first American primate laboratory. His namesake, the Yerkes National Primate Research Center, is now located at Emory University in Atlanta, Georgia. The Yerkes-Dodson Law that describes the parabola-shaped relationship between performance and arousal is well known and used in a multitude of disciplines (Hilgard 1965).

Growing up on a rural farm in Bucks County, Pennsylvania, Robert M. Yerkes, in his 1930 autobiography, recalled a happy childhood that inspired curiosity and allowed for a young scientist's mind to flourish. In his early years, however, Robert and his eldest sister both contracted scarlet fever. She passed away but Robert survived (Yerkes 1930) although he was plagued with chronic fatigue for many years following (Hilgard 1965). He had three other siblings, all quite a bit younger than Robert. Although Robert Yerkes' mother and father never attended college, he had an uncle and cousin who practiced medicine. They encouraged the young Yerkes to study medicine in order to attain an education that would provide an easier lifestyle, a doctor's lifestyle, rather than the difficult and labor-intensive livelihood of his father, a farmer (Yerkes 1930).

At the age of sixteen, Yerkes' uncle, Dr. Edward Atkinson Krusen, provided him room and board along with a small compensation for schooling at Ursinus College in exchange for household chores. Five years later, in 1892, he graduated with an Atrium Baccalaures (A.B.) degree, or more commonly known as a Bachelor of Arts. Yerkes was then offered a one-thousand-dollar loan from Harvard University to pursue graduate work in zoology. Needing the money,

Yerkes abandoned medicine and began as a provisional undergraduate for 1 year beginning in 1897. Yerkes proved worthy of graduate status and gained another A.B. degree along the way. His first paper, *Reaction of Entomostraca to Stimulation by Light* (Yerkes 1899), was published under the supervision of Charles B. Davenport in the Laboratory of Comparative Zoology in 1899 at Harvard University (Yerkes 1930).

It was Josiah Royce, an American philosopher, who suggested comparative psychology to Yerkes that began his study of animal behavior and cognition and how it relates to that of different animals or humans, thus pairing his main interests, zoology and psychology. Hugo Münsterberg, shortly thereafter, extended a position to Yerkes in his laboratory to study comparative psychology and subsequently became a mentor and dear friend. Over the course of his graduate career, Yerkes lectured in courses on genetic and comparative psychology as well as conducted what he referred to as psychobiological research. His dissertation, *The Psychic Process of the Frog* that examined learning in the frog while in a labyrinth, was completed in 1902 for which he earned a Doctorate of Philosophy in Psychology from Harvard University (Yerkes 1930).

Yerkes' research interests first included various aspects of organic receptivity and its relation to behavior. Using subjects such as amphibians and reptiles, he frequently published on these topics between 1905 and 1912 (Dewsbury 1996). He was also dedicated to the advancement of comparative psychobiological methods and, therefore, devoted much of his research and time to the development of tasks that could reliably measure phenomenon across different species (Yerkes 1930). Soon his subject choice evolved from amphibians and reptiles to lower mammals. *The Dancing Mouse* (1907), his first book, helped establish the use of mice and rats as standard laboratory subjects in psychological testing (Dewsbury 1996). His goal ultimately became to establish a comparative psychobiological research center that would house anthropoid subjects (Yerkes 1930).



After graduation, Yerkes attained a position at Harvard and remained there for the next 15 years (1902–1917). As an instructor and later as assistant professor of comparative psychology, his colleagues included eminent scholars such as William James, Hugo Münsterberg, Francis Peabody, George Santayana, Dickinson Miller, Robert MacDougall, Edwin B. Holt, Ralph B. Perry, and John D. Dodson (Yerkes 1930). In 1908, Yerkes and Dodson formulated the famous Yerkes-Dodson Law describing the parabola-shaped relationship between arousal and performance (Dewsbury 1996).

With Yerkes marriage to biologist Ada Waterson in 1909, his home and professional life flourished as she participated with him in numerous research projects and cowrote one of his classics (Yerkes 1930), *The Great Apes: A Study of Anthropoid Life* (Yerkes and Yerkes 1929).

Although Yerkes studied observable phenomenon, he believed psychologists should also study mental processes (Hilgard 1965). He thought it was possible to empirically investigate the phenomena of experience in relation to the environment in which it occurred. Therefore, he rejected John B. Watson's radical behaviorism, but as a participant in the developmental phase of the theory with Watson, he found merit in parts of behavior theories (Yerkes 1930). Records of correspondence between the two provide evidence of close collaboration and sharing of ideas (Hilgard 1965). Watson and Yerkes, through their collaborations, also contributed to the improvement and standardization of methods for the comparative study of vision (Yerkes 1930).

Edward B. Titchener, a British psychologist who worked with Wilhelm Wundt, often exchanged letters with Yerkes in which they discussed the psychology of the self. Yerkes was intrigued with the use and measurement of introspection and wrote his first and only textbook, *An Introduction to Psychology* (1911), to explore the topic thoroughly and gain a clearer conceptual understanding of introspection and the psychology of the self (Yerkes 1930). Furthermore, Yerkes was responsible for the first American scientific journal devoted to the study of animal

behavior in 1911, the *Journal of Animal Behavior* (Burkhardt 1987).

Beginning in 1913, Yerkes became a hospital psychologist at Boston Psychopathic Hospital while continuing his Harvard obligations. During the next 5 years at the hospital, he discovered a need for improved techniques and measurement regarding psychobiological issues. In 1915, Yerkes helped to create the Yerkes-Bridges Point Scale of Intelligence which measured aspects of intellectual activity and the multiple-choice method for the study of ideational behavior (Yerkes 1930).

In 1917, The University of Minnesota asked Yerkes to reorganize the psychology department and establish a new laboratory. After much consideration, Yerkes reluctantly accepted the position and left Harvard and the Boston Psychopathic Hospital in the spring of 1917 for Minnesota. Yerkes did manage to set the proper motions in place for the psychology department and secure a location for a new laboratory, but his stay at Minnesota was cut short with America's entry into the First World War (Yerkes 1930).

One year prior, in 1916, Yerkes had become president of the American Psychological Association (APA), Psychology's flagship organization. As such, he found himself at the forefront of Psychology when America entered World War I in April of 1917. A group of psychologists, including Yerkes, happened to be at Harvard the time. They felt compelled to aid in the war efforts and recognized an application of Psychology was needed (Yerkes 1930). Thus, the intelligence testing movement began, and the Army Alpha and Beta tests were born out of the Committee on the Psychological Examination of Recruits that Yerkes chaired. The Army Alpha test allowed matching of recruits to skills required by appropriate positions in the army. The Beta test served the same function but was administered to foreigners and those who were illiterate. As president of APA, Yerkes' role was to take the initiative in organizing the testing effort. He established the appropriate relations with the Medical Department of the Army despite several obstacles and, through this arm of service, became personally responsible for the psychological examination of

recruits. For the first time, intelligence tests were administered to a group of people instead of individually allowing 1,726,000 United States soldiers to be tested during the movement (Hilgard 1965).

Psychology received positive public acknowledgment for the success of the intelligence testing movement allowing Yerkes and other psychologists to begin testing the general population with ease. The tests used have been called the forerunners of standardized tests such as the scholastic aptitude test (SAT), which measures college readiness. Yerkes also published two books that continue to serve as models for the advancement of intelligence testing, *Army Mental Tests* (1920) and *Psychological Examining in the US Army* (1921) (Hilgard 1965).

The intelligence-testing movement also demonstrated Psychology's usefulness as a profession. Given Yerkes' vital role, he is often credited for aiding in the application of psychology in a professional capacity (Hilgard 1965). This is important because the role of American psychologists at the time was to conduct research exclusively.

Psychology accumulated massive accumulation of data after the completion of the first mass-scale-testing movement. Yerkes's personal analyses led him to controversial conclusions about the origins of racial and ethnic differences in intelligence that coincided with the eugenics movement in the US and abroad. Along with racial and ethnic differences, he also found generational differences in IQ which led him to conclude that IQ was declining in the US. His interpretation of the findings about race and ethnicity resulted in more restrictive immigration laws. Eventually, his conclusions were refuted, but the data remain a psychometrist's treasure trove (Hilgard 1965).

Shortly after the 1918 Armistice, Yerkes had to choose between continuing his work with mental testing to aid the war efforts or following his academic pursuits and returning to the position at the University of Minnesota that was interrupted by the war. He ultimately decided to abandon his post at Minnesota to complete a large report of Psychology's effort during the war and to

begin securing financial support for the systematic study of anthropoid apes (Yerkes 1930).

Yerkes joined the faculty at Yale University in 1924 where he remained for the next 20 years. He began pursuing his initial goals of opening a primate facility and renewed his investigations of the great apes. He soon was the top researcher in the field. Previously, he had published a plan of action to open a primate facility (Yerkes 1916), but the proposal lacked financial support. His professorship at Yale provided him with the time necessary to acquire the finances and complete his plan. In the summer of 1924, he traveled to Havana, Cuba to observe a large colony of primates (Yerkes 1930). Upon returning, he moved to New Haven, Florida and purchased two chimpanzees, Chim and Panzee, from a zoo. He brought the two chimps home, where they lived in a bedroom and were taught to behave much like small, human children. Yerkes documented this experience in his paper *Almost Human* (Yerkes 1925; Hilgard 1965).

In 1929, he reached his long-time goal and established the Yale Laboratories of Primate Biology in Orange Park, Florida. It was the first center for the study of the neural and physiological bases of behavior and the first primate laboratory of comparative psychology (Yerkes 1930). After Yerkes resignation as director in 1941, the center was renamed Yerkes Laboratories of Primate Biology. Ninety chimpanzees were studied under his direction. Yerkes' publication, *Chimpanzees: A Laboratory Colony* (1943), established the significance of studying primate behavior to gain understanding about human behavior and was his last work. Yerkes retired from Yale University in 1944 (Hilgard 1965).

After retirement, Yerkes continued to serve as chairman of the National Research Council Committee for Research on Problems of Sex (1921–1947). During this time, he was fundamental in the sponsorship of projects that led to such studies as the Kinsey report which focused on human sexual behavior (Hilgard 1965).

On February 3, 1956, at age 79, Yerkes passed away in New Haven, Connecticut, from coronary thrombosis after spending 2 years as an invalid (Hilgard 1965). Near Yale University, he is buried

in Evergreen Cemetery in New Haven, Connecticut, with his wife who died in 1965. After his death, the Yerkes National Primate Research Center was relocated to Atlanta, Georgia, at Emory University where anthropoid subjects are still studied today (Hilgard 1965).

## Cross-References

- [Comparative Psychology](#)
- [IQ](#)
- [Primate Research Centers](#)
- [Yerkes Primate Research Center](#)

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## Robert Seyfarth

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## Introduction

Based on their novel combination of mechanistic and functional questions in a natural setting, Robert Seyfarth and collaborator Dorothy Cheney inspired cross-disciplinary scholars of animal behavior for decades. Seyfarth and Cheney are not only pioneers in ASKING questions about the social lives and minds of animals, they also revolutionized the methods we use to investigate these questions.

## Background

Robert M. Seyfarth was born February 16, 1948, in Illinois to Robert and Mary (Moo) Seyfarth. After graduating from Exeter in 1966 (leaving behind a promising cheerleading career), Seyfarth received his Bachelor's degree in Biological Anthropology from Harvard in 1970, earned his PhD in Animal Behaviour from Cambridge in 1976, and completed a postdoctoral position at Rockefeller University in 1979. After tenure-track positions at Rockefeller University and UCLA, he joined the Department of Psychology at the University of Pennsylvania in 1985 until his retirement in 2016. Seyfarth is an elected fellow of the American Psychological Association (Division: 3 1996; Division 6: 2002), Animal Behavior Society (1997), Association for Psychological Science (2007), and American Academy of Arts & Sciences (2012). Seyfarth holds an honorary PhD from University of Neuchâtel, Switzerland (2013), received the Distinguished Primatologist Award from the American Society of Primatologists (2016), and was elected into the US National Academy of Sciences (2017).

Seyfarth married Dorothy L. Cheney in 1971, having two children, Caroline (Keena) and Lucia (Lucy). Seyfarth and Cheney conducted joint field research together throughout their careers (frequently joined by their daughters), focusing on communication, cognition, and social behavior of wild monkeys. Their award-winning book *How Monkeys See the World: Inside the Mind of Another Species* (Cheney and Seyfarth 1990a) is an engaging summary of their 11 years spent studying vervet monkeys in Amboseli National Park, Kenya. Their second book *Baboon Metaphysics: The Evolution of a Social Mind* (Cheney and Seyfarth 2007) describes their 16 years of research on baboons in the Okavango Delta of Botswana. Counted among its many accolades, *Baboon Metaphysics* was runner up in the *Diagram Prize for Oddest Book Title of the Year* (narrowly losing to *The 2009–2014 World Outlook for 60-milligram Containers of Fromage Frais*, but soundly beating *Curbside Consultation of the Colon*). Through both hard-hitting science and a clever writing style, Seyfarth and Cheney develop an argument in both their books for the adaptive value of social cognition. They encourage the reader to look behind the curtain to explore the many surprising ways that animals are similar to ourselves and, perhaps more importantly, where they fall short in their cognitive and communication abilities.

Seyfarth and Cheney have published over 200 articles, commentaries, and book chapters – 90% of these written together – on their original empirical work (many alongside colleagues and students) or that review the implications of such work. Their major contributions are in vocal communication and social cognition. We summarize the former here, but to understand Seyfarth's impact on the field of social cognition see “► [Dorothy Cheney](#)” entry in this series. Harrowing tales of encounters with hippos, lions, and other assorted megafauna are best communicated by Seyfarth and Cheney themselves.

## Contributions to Social Behavior and Communication

Under the guidance of their dissertation advisor, the eminent ethologist Robert Hinde, Seyfarth,

and Cheney were among the first major wave of primatologists that focused on social behaviors and relationships from the standpoint of the individual. For example, Seyfarth wrote a seminal paper (1977) demonstrating that simple, individual-level rules could predictably produce the grooming networks seen in various different primate social systems. Given their interest in the adaptive value of social bonds (see “► [Dorothy Cheney](#)” entry), grooming remains an important measure of affiliation in Seyfarth and Cheney's long-term research.

After completing dissertations on the social behavior of chacma baboons in Mt. Zebra National Park, South Africa, Seyfarth and Cheney began a long-term study of vervet monkeys in Kenya. The impetus for this project was their postdoctoral collaboration with Peter Marler, an ethologist well known for his groundbreaking work on bird song learning and for his interdisciplinary, big-picture ideas. Public notoriety for this research program was launched with a now famous publication in *Science* (Seyfarth et al. 1980). In it, Seyfarth and colleagues confirmed a previous finding, by Thomas Struhsaker, that leopards, raptors, and snakes elicited distinct calls from the monkeys as well as predator-specific escape responses from listeners. However, it remained unclear if the jarring nature of the loud alarm calls simply alerted the monkeys, who then gathered information by looking at the caller or by spotting the predators themselves. To determine if, from the listener's point of view, the three alarm calls mean roughly “there is a leopard in that bush,” “there is a raptor diving at my head,” or “there is a poisonous snake-like object crawling between my legs,” Seyfarth and colleagues adopted methods from wild bird vocal studies – playback experiments. In 88 carefully designed trials, they played examples of each call type from a hidden speaker to unsuspecting subjects. Seyfarth and colleagues found that based on acoustic features alone, alarm calls produced the appropriate, predator-specific escape response in listeners; for example, subjects ran up trees following the sound of leopard calls, dove into bushes following the sound of raptor calls, or stood and looked into tall grass following snake calls. Thus, alarm calls functioned as

though they were semantic to the listener; the call seemed to signify objects or events external to the signaler, much like words function in human language.

This experiment inspired decades of research into the potential semantic properties of non-human primate vocalizations and ushered in an era of playback experiments in primatology. Although such experiments had been conducted on birds, amphibians, and insects prior to 1980, the method had only crossed into primatology a few times. Rather than using the age-old approach of simple observation to study primates, playbacks added a level of rigor and control not previously available. However, the logistics of conducting these experiments with social mammals was far more complicated than with frogs or birds. Seyfarth and Cheney have continually conceived new ways to incorporate this technique in a systematic way, creating a tool that is now a mainstay in behavioral ecology.

Seyfarth and Cheney's future studies would occasionally revisit alarm calls and predation, finding that listeners can glean information about predators from a variety of dissimilar sounding calls (e.g., Diana monkeys: Zuberbühler et al. 1999), and that listeners can differentiate alarm from nonalarm calls even when the call types grade together along an acoustic continuum (e.g., baboons: Fischer et al. 2001). However, the emphasis of their future work combined playbacks with their first interest – social relationships. With this new tool, they could not only ask about the functional significance of a call during dyadic interactions, they could also use it to ask their subjects, in the animal's own tongue, "*What do they know – and do they know they know it?*" (Cheney and Seyfarth 1990b, p. 38).

To probe the minds of monkeys, Seyfarth and Cheney used unremarkable vocalizations to provide remarkable insight. Their study of grunt vocalizations, first with vervets and later with chacma baboons in Botswana, is a perfect illustration of this elegant approach. Grunts are ubiquitous primate vocalizations, produced by many species, and the most commonly uttered calls of vervets and baboons. Seyfarth and Cheney found that vervets utter four acoustically distinct grunts

in four different social situations and that subjects in playback experiments responded appropriately based on acoustics alone (Cheney and Seyfarth 1982). Whereas they also found that baboons have at least two acoustically different types of grunts and respond appropriately to these calls during playback experiments (Rendall et al. 1999), baboons also appear to consider context. Grunts appear to mediate social interactions, mollifying subordinate animals and facilitating reconciliation after aggression. For example, female baboons are more likely to have an affiliative interaction (e.g., groom) if a dominant individual grunts either following an aggressive encounter with or an approach of a subordinate female. However, grunt exchanges do not simply correlate with social bonds. For example, mothers and daughters are much less likely to grunt at each other during an approach than other dyads, and high-ranking animals are more likely to grunt at low-ranking than the reverse, suggesting these calls signal benign intent (Silk et al. 2016).

Using the same model, Seyfarth, Cheney, and colleagues have uncovered the function of other vocalizations. For example, the loud wahoo vocalizations of male chacma baboons are given in several contexts and although these calls intergrade – making it difficult for human observers to differentiate them in the field – female baboons respond differently to “alarm” wahoos (produced when encountering predators) than “contest” wahoos (given during male-male competitive displays). Using behavioral observations and acoustic analysis, Seyfarth and colleagues determined that contest wahoos and the displays that accompany them are honest indicators of male condition, and during playback experiments, subjects were more attentive to exaggerated calls that simulated a superior opponent. In another experiment that simulated male-male contests, subjects were more interested in anomalous interactions between males of disparate ranks – which typically indicate a major resource is being disputed – but only when the subject outranked both callers (Kitchen et al. 2013 and citations therein). This experiment demonstrated that males were assessing not just call meaning but also caller identities and their own relative rank.



Using playbacks of various vocalizations to simulate social situations, Seyfarth, Cheney, and colleagues have also uncovered details about the social lives of these animals. For example, lactating female baboons form “friendships” with some resident males – dyadic relationships that are quantifiably distinguishable from others based on frequency of affiliative behaviors (approaches, infant handling, grooming). Using playback experiments to simulate attacks on females in various scenarios, Palombit et al. (1997) demonstrated that these friendships actually serve to protect small infants, likely the male’s offspring, from infanticide by immigrant males.

In another experimental set-up designed to mimic a social interaction, Seyfarth and colleagues found that both vervet and baboon females were more likely to attend to another female’s threat grunts (a vocalizations used to solicit aid) if the dyad had recently shared a grooming bout (Cheney et al. 2010 and references therein). This is empirical evidence that grooming vs. cooperation during aggressive interactions are different “currencies” reciprocally exchanged among nonkin in a social group. Despite experimental tests on several species, researchers have only rarely demonstrated reciprocal altruism/contingent cooperation in the lab. Thus, Seyfarth and Cheney’s work suggests that, by providing both external and internal validity, experimental studies in the wild are the most useful for uncovering “emotional bookkeeping” in socially complex species (Cheney et al. 2010).

## Conclusion

Using innovative field techniques (and consummate parlor game skills), Seyfarth, Cheney, and their various collaborators have dispelled many of the false dichotomies traditionally believed to separate primate vocalizations from human speech (Seyfarth and Cheney 2017). For example, they clarified that although nonhuman primates have intergraded vocalizations, conspecific listeners can parse these calls as though they are discrete (e.g., Fischer et al. 2001). They

demonstrated that alarm call production is innate in young vervet monkeys, but they learn over time which stimuli should elicit calling (e.g., producing raptor alarm calls to eagles, not to falling leaves) and how to appropriately respond to the alarm calls of others without needing visual cues (Seyfarth et al. 1980). Thus, restrictions in production are not necessarily limitations in usage and comprehension. Finally, they have shown that meaning and emotion are not mutually exclusive ends of a vocal spectrum – rather, nonhuman primates can actively respond to vocalizations based on call meaning, caller identity, their own identity, and context.

By breaking down these false dichotomies, Seyfarth and Cheney not only uncover the ways we are similar, they also focus our attention on what is truly different between human speech and nonhuman vocalizations – namely, intentionality and theory of mind. However, they point out that the social mind of the monkey can interpret combinations of signals in a variety of sensory modalities, holds representational information on social interactions, and can contend with multiple discrete categories simultaneously in a hierarchically structured, rule-governed, and open-ended fashion (Seyfarth et al. 2005). In their words, “*Baboons – like dogs, chimpanzees, and many other species – understand much more than they can say. Their language of thought is impressive; their ability to articulate their thoughts much less so.*” (Cheney and Seyfarth 2007, p. 276). Despite limitations in vocal communication, they hypothesize that the ability of nonhuman primates to grapple with social knowledge provides a lattice-work on which human language could have been built (Seyfarth and Cheney 2017).

## Cross-References

- ▶ [Dorothy Cheney](#)
- ▶ [Friendships in Animals](#)
- ▶ [Post-conflict Resolution](#)
- ▶ [Primate Cognition](#)
- ▶ [Primate Communication](#)
- ▶ [Primate Social Structure](#)
- ▶ [Reconciliation](#)

- ▶ [Robert Hinde](#)
- ▶ [Social Behavior](#)
- ▶ [Social Intelligence Hypothesis](#)
- ▶ [Theory of Mind](#)

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## Robert Trivers

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Robert Trivers is an American evolutionary biologist who has made a number of significant contributions to evolutionary theory, including parental investment theory and parent-offspring conflict.

## Parental Investment Theory

Parental investment theory was developed by Trivers (1972) and predicts that, in sexually reproducing species, the sex that invests more resources in its offspring will also be more selective when choosing a mating partner. As a result, the sex that invests less parental resources will experience greater intrasexual competition for mating partners and will exert greater mating effort to gain sexual access. Differences in minimum obligatory parental investment have also informed predictions regarding sex differences in sexual strategies. For example, women rate financial resources as more important in a potential mate than do men (Buss 1989) and are less interested in casual sex than are men (Buss and Schmitt 1993). Parental investment theory has led to numerous hypotheses regarding animal behavior and cognition as it relates to offspring investment and mating strategies.

## Parent-Offspring Conflict

Parent-offspring conflict (Trivers 1974) refers to the differing levels of desired investment from the perspectives of a parent and his or her offspring. Although parents may increase their genetic success by investing resources in offsprings to a certain extent, there is a point at which the costs of offspring investment outweigh the potential benefits to the

parent. For example, a parent who invests too heavily in a single child may reduce the likelihood of their own survival and, as a result, the likelihood that they will produce more children. Additionally, a parent with two or more offspring may maximize their reproductive success by investing equally in each offspring or by investing more heavily in the offspring with better prospects for survival and reproduction. However, from an offspring's perspective, they can maximize their reproductive success by extracting as many parental resources as possible, regardless of what the parent desires to invest. Further, because any individual shares 100% of its genes with itself and approximately 50% of its genes with a full sibling, an offspring may attempt to extract a disproportionate amount of investment from their parent, thereby increasing his or her survival or reproduction but to the detriment of siblings.

## Reciprocal Altruism

Reciprocal altruism (Trivers 1971) refers to any behavior performed by an organism that temporarily reduces its own genetic success but increases the genetic success of another organism. Kin altruism proposes that, by engaging in behavior that increases the fitness of a genetic relative, even at the temporary expense of one's own fitness, an organism may enhance its overall genetic success by promoting the success of shared genes in another organism (Hamilton 1964). Reciprocal altruism, in contrast, suggests that an organism may improve its own fitness in the long-term by incurring a temporary cost to help a genetically unrelated organism, who may return the favor at some point in the future. Altruistic behavior may also generate long-term benefits for an individual by improving social reputation with fellow group members.

## Trivers-Willard Hypothesis (Facultative Sex Ratio Determination)

The Trivers-Willard hypothesis (Trivers and Willard 1973) suggests that female mammals

may alter the sex ratio of their offspring in response to environmental cues. The hypothesis suggests that, although selective pressures often promote the production of an equal sex ratio among offspring, environmental pressures may facilitate the reproduction of one sex more than the other. For sexually reproducing species in which males compete with for sexual access to females, parents will invest in sons when environmental conditions are more favorable and daughters when conditions are less favorable. Because males have lower obligate parental investment than females, they also have the potential to sire more offspring. Well-provisioned sons may be especially likely to sire offspring if, as a result of receiving increased parental resources, they are better able to compete with other males for sexual access to females. Therefore, investing in sons when conditions are more favorable has the potential consequence of greater long-term genetic success than would investing in daughters. However, when conditions are less favorable, the potential reproductive benefits of investing in daughters will outweigh the investment costs, as daughters are likely to reproduce, even if they have been poorly provisioned. In these scenarios, it is preferable to produce and invest in daughters, who are likely to produce even a few offspring, rather than attempt to invest in sons, who, if poorly provisioned, may fail to attract a mate, thus producing no offspring.

The evolutionary theories developed by Robert Trivers have greatly benefitted the scientific understanding of animal behavior and cognition. His theoretical contributions to evolutionary biology have informed numerous hypotheses regarding the behaviors of sexually reproducing species, which have in turn produced substantial empirical knowledge.

## Cross-References

- [Altruism](#)
- [Parental Investment](#)
- [Richard Dawkins](#)
- [Sex Ratio](#)

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Rock Dove

► [Pigeon \(Columbidae\)](#)

Rock Hyrax

► [Hyracoidea](#)

Rock Rabbit

► [Hyracoidea](#)

Rodent Gaits

► [Rodentia Locomotion](#)

Rodent Locomotion

► [Rodentia Locomotion](#)

Rodentia Cognition

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Definitions

|           |                                                                                                                                                        |
|-----------|--------------------------------------------------------------------------------------------------------------------------------------------------------|
| Abundance | Frequency of occurrence of a species within an environment or ecosystem.                                                                               |
| Cognition | The neural process of acquiring, remembering, and using information.                                                                                   |
| Genotype  | The genetic makeup of an organism.                                                                                                                     |
| Ontogeny  | The development of a trait over an organism’s lifetime.                                                                                                |
| Mechanism | Systems within an organism that control and regulate the expression of a trait.                                                                        |
| Phenotype | The physical expression of the genotype.                                                                                                               |
| Proximate | Factors (ontogeny or mechanism) affecting an organism’s phenotype throughout its lifetime.                                                             |
| Rodent    | A mammal belonging to the order Rodentia, characterized by a single pair of continuously growing (unrooted) incisors on both the upper and lower jaws. |

|          |                                                                                      |
|----------|--------------------------------------------------------------------------------------|
| Trait    | A character or feature of an organism.                                               |
| Ultimate | The function and/or evolution (particularly natural selection) of phenotypic traits. |

## Introduction

Rodents (from the Latin *rodere*, meaning “to gnaw”) are the largest mammalian order (40%), comprising nearly 2300 species. They are diverse and abundant, occurring in nearly every terrestrial environment on Earth, apart from Antarctica. Their habits extend from burrowing, hopping, and climbing to swimming, and they show great diversity in diet, ranging from strictly herbivorous (e.g., capybaras *Hydrochoerus hydrochaeris*) to strictly carnivorous (e.g., grasshopper mice *Onychomys torridus*).

Rodents, like other animals, engage in costly behaviors, such as foraging, mating, territory selection, and defense, to access resources. To successfully access resources and avoid predation, rodents must be able to rapidly adjust their behavior based on the information they receive from their environment. Rodents rely extensively on olfactory cues to respond to environmental stimuli (Moriceau et al. 2010). Rodents then use their cognitive abilities to decode and use this information.

The word *cognition* (from the Latin *cognoscere*, meaning “to come to know”) covers a wide array of mental functions that relate to the acquisition, processing, remembering, and using of information (Dukas 2004). Until the 1950s, scientists generally avoided or dismissed animal behavior as having an underlying mental process. However, the Canadian psychologist Donald Olding Hebb was instrumental in recognizing that much of animal behavior is governed by underlying cognitive processes, laying down the foundations for understanding how behavior and cognition are related in animals and demonstrating that central processes operate in response to external stimuli (stimulus response).

Cognitive processes are essential for perceiving, recognizing, and discriminating between stimuli, for learning and decision-making, and for solving

problems, all of which are crucial for survival. However, while different types of cognition allow rodents to adjust their behaviors in response to different environmental stimuli (Dukas 2004), the approaches to studying and understanding rodent cognition are varied. To understand the ultimate (evolutionary history and adaptive significance) factors of cognition, it is useful to first gain an understanding of proximate (ontogeny and mechanisms) factors affecting cognition. The underlying neural machinery that supports cognitive processes is complex, and much of a rodent’s cognitive capacity is governed by underlying neuroendocrine mechanisms (Gilbert and Kesner 2002; Green and McCormick 2013). Specifically, these mechanisms and their influences may differ depending on the sex of the individual and may also change as the individual ages, resulting in fundamental changes in cognitive abilities occurring throughout the animal’s lifetime.

## Types of Cognition

### Perception, Recognition, and Discrimination

Rodents must be able to perceive stimuli. Perception is the process of interpreting and assessing environmental signals (Dukas 2004). Principally, rodents must perceive signals relating to food resources; otherwise they will starve, and they must perceive signals relating to predator presence; otherwise they will be predated. Recognition follows perception and can be defined as the repeatable and predictable response to environmental stimuli (Mendelson 2015). Even if the rodent encounters novel stimuli, it should respond in a predictable manner to a comparable, similar, stimulus that it has experienced previously. Recognition can be either innate (fixed in the genotype or acquired during early development) or learnt over time by associating the cue with its relative level of risk (Mendelson 2015). If a rodent cannot successfully perceive and recognize stimuli, it cannot learn the association between stimuli and outcome, leading to decreased fitness.



While perception and recognition are critical, discrimination between stimuli is not always essential. Discrimination is the ability to differentiate between stimuli (e.g., Object A is different from Object B) based on different memories that the rodent has associated with each stimulus. Discrimination is likely to be more common in situations relating to resource acquisition (i.e., knowing that food A has a higher nutrient content than food B), whereas it is likely to be less common in situations relating to predator avoidance, where generalized responses could be more effective in ensuring survival (Paulling et al. 2019).

### Learning

To improve the accuracy and/or success of the behavioral response, rodents should learn from each encounter with the stimulus. Learning refers to the acquisition of new information, including associations between stimulus (state of the immediate environment) and outcome, or behavior and stimulus (Dukas 2004). Rodents can learn in different ways. Individuals can learn by “trial-and-error” learning through reward and punishment (Sherwood et al. 2005), but they take a risk because of naivety (e.g., tasting new food runs the risk of it being noxious or unpalatable).

Alternatively, individuals in groups may learn via social learning, which involves observing the behavior or products of behavior of conspecifics or directly interacting with them (Heyes 1994). This reduces the costs associated with individual learning. Types of social learning include local enhancement, where individuals are drawn to an area by the activity and behavior of others; imitation, which is a process that involves accurately replicating behaviors shown by others; and observational learning, where individuals observe conspecifics, but do not directly duplicate their behaviors (Heyes 1994). Individuals in social groups have the opportunity to learn from demonstrators throughout their lifetimes (Heyes 1994).

### Memory

To learn, a rodent must remember the information or association for later reference. Memory can be categorized based on how information is stored

(episodic vs. semantic) or how long information is stored for (short-term vs. long-term). Episodic memory refers to the storage of episodes of contextual information. For example, episodic memory is related to what was happening when the information was learnt, where the information was learnt, who else was present at the time, and when the information was learnt (Templer and Hampton 2013). Semantic memory, on the other hand, is the storage of information without contextual detail (Templer and Hampton 2013).

Regardless of how the information is stored, information can be retained for either a short or a long period of time (Sherwood et al. 2005). Short-term memory is maintained only for short periods of time (seconds to hours). When new information is acquired, it is stored as short-term memory and accessed to avoid incorrect, repetitive behavior (Dudchenko 2004). For example, remembering which resource sites have been visited reduces repeated visits to empty sites, minimizing time spent foraging and reducing potential exposure to predators. However, short-term memory cannot store large amounts of information and is quickly forgotten if unnecessary for survival (Sherwood et al. 2005). In contrast to short-term memory, long-term (also known as reference memory or the memory of associations) is an association between stimuli and response that is maintained over longer periods of time (days to months/years; Dudchenko 2004). If information is important, and is actively recalled multiple times, it is consolidated into long-term memory, which can store large amounts of information (Sherwood et al. 2005). Long-term memory is activated through repeated exposure to a stimulus (i.e., Behavior/Stimulus A leads to Response B; Dudchenko 2004). The ability to remember information over long periods of time minimizes the costs of continually learning stable/constant associations, allowing more energy to be diverted to short-term memory acquisition.

### Decision-Making

Decision-making is the cognitive ability to evaluate stimuli or behaviors against the value of their outcome and then prioritize and choose the most appropriate action (Lee et al. 2012). Rodents

rarely obtain complete information about the value of different outcomes. Instead, they learn how to predict outcomes (Lee et al. 2012). Learning these relationships is easier in consistent, stable environments but becomes more difficult in unpredictable or dynamic ones (Lee et al. 2012). Decision-making leads to trade-offs between behaviors that could influence fitness (McFarland 1977). For example, if a rodent is hungry, it will evaluate the benefits of foraging against the cost of predation (McFarland 1977). The motivational state of the individual affects its decision to continue executing a current behavior or to change to a new behavior, with the final choice being determined by the current most demanding motivational state (McFarland 1977).

### Spatial Cognition

Spatial cognition is the process of using localization, sensory imagery, and decision-making to successfully navigate through environments (Arleo and Gerstner 2000). Successful navigation is necessary for any rodent that moves between fixed points in the environment, such as between nesting and foraging locations. To begin navigating, rodents must be able to generate and use a spatial representation of the relationship between their position and environmental landmarks, which requires the individual to regularly update its positional information as it moves through its environment (Gallistel 1989). This is initially done through dead reckoning, where the individual uses velocity as a function of time to determine a change in position, which allows for continuous feedback about location, even though it is a form of estimation that is prone to error accumulating over time (Gallistel 1989). Therefore, to correct this error, the rodent will use landmarks at known positions to recalibrate the spatial representation (Arleo and Gerstner 2000). Repeated navigation through the environment generates a cognitive map, which involves mentally configuring external stimuli (e.g., visual cues) into distinct environmental regions in the brain. This map is then stored as long-term memory to be accessed in the future (Arleo and Gerstner 2000).

### Social Cognition

Broadly speaking, social cognition is knowledge about conspecifics (Seyfarth and Cheney 2015) and includes those cognitive processes that are used to understand and interpret the social environment (Beer and Ochsner 2006). For example, social cognitive abilities are used to process social interactions and networks, and to engage in appropriate sexual behavior and mate choice, ultimately allowing the individual to determine who to interact with and how to interact with them (i.e., avoid or mate with; Kavaliers and Choleris 2017).

Social cognition is initiated by perception and social motivation, which is an individual's willingness to approach and interact with a social target, and then social recognition, learning, and memory allow for the formation of long-term attachments and hierarchies that are crucial for social functioning (Bicks et al. 2015). Importantly, social cognition involves a component of self-recognition, as the individual's understanding of "self" as a social object (Beer and Ochsner 2006) plays a critical role in the establishment and recognition of alliances and partnerships, which could function to reduce competition or aggression (Seyfarth and Cheney 2015). Conceptually, social cognition, therefore, consists of a suite of skills, ordered according to cognitive demand, which allow rodents to observe, perceive, and recognize other individuals, to remember past interactions and social relationships, and to attribute mental states (e.g., feel empathy) to other individuals (Seyfarth and Cheney 2015).

### Problem-Solving and Innovation

Accessing resources (e.g., food and mates) and avoiding predation require problem-solving. Problem-solving is the ability (acquisition of behavior or information) of an individual to access a reward (i.e., resources or goals) by either moving itself or manipulating an object. The ability to solve problems does not depend on higher-order cognitive ability (e.g., insight; Griffin and Guez 2014). Instead, to successfully problem-solve, the individual must (a) be motivated to engage with the task, (b) be flexible in its behavior to try different tactics if one strategy is not successful, and (c) learn and remember what

behavior successfully solved the task (Griffin and Guez 2014). While successful problem-solving generally occurs through either trial-and-error or social learning, rodents, such as guinea pigs *Cavia aperea f. porcellus*, can solve problems through innovation, which is the use of new behaviors or using existing behaviors in a new context.

## Cognitive Neuroendocrine Mechanisms

### Sensory Integration

The external environment provides an array of sensory cues that are perceived by the sensory organs (e.g., eyes, ears, and nose). Once received, this information is processed in associated regions of the brain. For example, the somatosensory cortex processes tactile (touch) signals, and the optic tectum and thalamus process visual information. The brain then stimulates appropriate neuroendocrine responses that drive the expression of specific behaviors (e.g., flee from a predator). Similar to the external environment, changes in the internal environment (e.g., hunger) stimulate a cascade of neuroendocrine responses that drive appropriate behaviors (e.g., foraging). All types of cognition rely on sensory integration.

### The Brain

**Hippocampus** The mammalian hippocampus is responsible for navigation and spatial cognition. Hippocampal grid cells are triggered when a rodent moves into a specific location within an environment, while head direction cells are triggered when the animal moves its head in a particular direction (Foster and Knierim 2012). These cell types work in tandem to generate a cognitive map via learning and remembering the stimuli associated with locations, which is used for navigation (Foster and Knierim 2012). The hippocampus is also associated with decision-making, as it organizes and retrieves information from short- or long-term memory storage (Dudchenko 2004), forms associations, and separates patterns (Gilbert and Kesner 2002). While hippocampal cells respond to visual, olfactory, auditory, and somatosensory information, they can only

process spatial associations, which means that other cognitive abilities are not affected by disruption to hippocampal functioning (Gilbert and Kesner 2002).

**Prefrontal Cortex** The prefrontal cortex also plays a crucial role in multiple aspects of cognition. Firstly, it is involved in executive functioning, including error detection, motor control, goal-directed learning, evaluating risk and reward, decision-making, and maintaining attention (Euston et al. 2012). Secondly, the prefrontal cortex is neurally connected to the hippocampus and works in association with the hippocampus to form short- and long-term memories (Wang et al. 2009; Euston et al. 2012). The prefrontal cortex first organizes information about the relationship between stimulus and response/consequence, which is then replayed repeatedly to consolidate the memory (Euston et al. 2012). If necessary, the hippocampus also gathers spatial information to associate this memory with a location (Wang et al. 2009). The prefrontal cortex then organizes behavioral plans and goal-directed behaviors to act on this information (Wang et al. 2009) and plays a role in recalling information when required (Euston et al. 2012). Thirdly, the prefrontal cortex is also used to maintain social interactions and behavior in rodents, due to its involvement in memory formation, and damage to this region is known to disturb social memory and motivation and can disrupt social learning in mice (Bicks et al. 2015).

### Hormones and Neurotransmitters

**Dopamine** Dopamine is a neurotransmitter (a chemical messenger that transmits signals across a chemical synapse) that influences many aspects of rodent behavior and cognition. Dopamine receptors are present throughout the entire forebrain, especially the basal ganglia, regulating motor and limbic processes and contributing to the coordination of different behavioral and cognitive processes (Nieoullon and Coquerel 2003). Different cognitive processes require different levels of dopamine receptor activity, which could result in dopamine

receptor stimulation impairing performance in one task, while enhancing cognition in another (Chudasarma and Robbins 2004). Furthermore, different concentrations of dopamine can also affect cognitive processes involved in the same task (Chudasarma and Robbins 2004). Consequently, dopamine acts as a neuromodulator by, for example, impairing the memory of stimuli that have already been investigated (Chudasarma and Robbins 2004).

Dopamine controls motivation, attention, and alternating between behaviors (Nieoullon and Coquerel 2003). For example, lesions to the nucleus accumbens and prefrontal cortex, with high dopamine receptor abundance, result in a lack of motor inhibition and disruption to behavior sequence organization, spatial orientation, and social interaction (Nieoullon and Coquerel 2003). Dopamine also contributes to the detection of novel stimuli (Nieoullon and Coquerel 2003) and assists with decision-making by relaying error signals to update reward prediction values (Lee et al. 2012). Dopamine also plays a role in learning and memory, mediating reward-related learning (Nieoullon and Coquerel 2003), and impacting spatial and working memory performance (Chudasarma and Robbins 2004).

**Corticosterone** Stress can affect behavior and cognition (Green and McCormick 2013). Once a stressor is detected, the hypothalamic-pituitary-adrenocortical (HPA) axis in the brain stimulates the release of corticosterone from the adrenal gland (Green and McCormick 2013). Stress can be acute, where corticosterone concentrations peak for short periods of time, or chronic, where corticosterone peaks for sustained, or frequently repeated, periods of time. In the rodent brain, the hippocampus, prefrontal cortex, and amygdala have the highest densities of corticosterone receptors (Green and McCormick 2013). Therefore, corticosterone affects spatial cognition, goal-directed behavior, working memory, emotional learning, and memory functions (Green and McCormick 2013). However, while acute stress can improve memory performance, as it is beneficial to remember aversive events, chronic corticosterone exposure may have a negative impact

on brain morphology, reducing the number of synapses and impairing signal cascades in the hippocampus and prefrontal cortex (Green and McCormick 2013).

**Oxytocin** Oxytocin is an oligopeptide (a small protein that contains only a small number of amino acids) that is produced in the hypothalamus and transported to different brain regions associated with social cognition, including the amygdala, olfactory regions, thalamus, hypothalamus, and hippocampus (Kavaliers and Choleris 2017). As a result, oxytocin controls and processes the response to social information, allowing for social recognition, learning, and memory to occur (Kavaliers and Choleris 2017). A disruption in oxytocin production, therefore, interferes with how rodents interact with conspecifics. Rodents without proper oxytocin function make poorer social choices (e.g., mice with low oxytocin do not avoid parasitized individuals, Kavaliers and Choleris 2017). Oxytocin is also involved in sexual, affiliative, and parental care behaviors, leading to individuals with impaired oxytocin expression showing poor mate choice discrimination or copying (Kavaliers and Choleris 2017).

## Developmental Effects: Age and Sex

### Age Effects

#### Physical Changes

As rodents age, they undergo developmental changes in their brain physiology and morphology, affecting their cognitive abilities. The most dramatic developmental changes are generally experienced during the first three weeks of a rodent's life, where the pup becomes a mature, independent individual (Moriceau et al. 2010). During these early stages, pups need to acquire the necessary information required for survival, and they experience changes in their learning preferences and abilities, for example, by quickly forming positive or negative associations with unfamiliar cues (Moriceau et al. 2010). Due to low corticosterone concentrations present at this stage, the amygdala is not yet involved in learning,

As the individual ages, corticosterone concentrations may rise, and the amygdala becomes more actively involved in the formation of associations (Moriceau et al. 2010). Despite not undergoing such drastic changes as juveniles, the cognitive abilities of mature individuals are still affected by the aging process. Some of these changes are due to changes in the vascular morphology and physiology of the brain. Aging brains experience an increase in capillary length and volume, thinning of capillary walls, and a reduction in blood vessel growth (Goldman et al. 1992). These physical changes, coupled with changes in secretion of the hormone vasopressin, affect learning and retrieving learnt responses as they reduce the amount of blood flow and nutrient movement in the brain (Goldman et al. 1992).

#### Stress Effects

Stress during early life stages can have long-lasting impacts on rodent cognition. Even in the womb, pups can be exposed to stress via the maternal environment. Corticosterone can cross the placental barrier, affecting the brains of fetal pups, and this stress experienced during the prenatal period can have a knock-on effect on hippocampal function during adulthood, leading to decreased learning abilities (Lupien et al. 2009). Early postnatal stress can also lead to changes in brain physiology and morphology. Prolonged periods of early postnatal maternal separation in pups affect corticosterone production pathways later in the adult hypothalamus, amygdala, prefrontal cortex, and hippocampus, leading to overstimulation of the HPA axis and cognitive deficits, such as an inability to recognize new objects (Lupien et al. 2009).

Adolescence is also a period of significant brain development. The HPA axis is more active during adolescence, and juvenile rodent brains, therefore, experience higher concentrations of corticosterone than adult brains (Lupien et al. 2009). Juveniles do not habituate to a stress like adults, taking longer to form negative feedback systems (Lupien et al. 2009). Consequently, chronic, unpredictable stress experienced during adolescence can result in lower hippocampal volume in adulthood (Lupien et al. 2009) and deficits

in hippocampal-dependent cognitive performance (Green and McCormick 2013), including performance in spatial tasks, such as the Morris water maze, and avoidance learning. However, environmental effects can, to a degree, mitigate the negative effects of stress experienced during this sensitive period. For example, housing young rats in social groups can reduce the effects of a social deprivation stress on hippocampal-dependent and prefrontal cortical cognitive tasks (Green and McCormick 2013).

Finally, chronic stress in adulthood may also have a negative influence on brain morphology and cognition of rodents. Chronic stress in adulthood results in the death of hippocampal neurons and prevents the production of new neurons in the dentate gyrus, thereby reducing hippocampal volume, which then negatively impacts learning and memory (Lupien et al. 2009). Unlike juveniles, however, adults may be more plastic in their response, showing a recovery and reverse of effects just a few weeks after the stressor has ceased (Lupien et al. 2009).

#### Sex Effects

Sex-specific patterns of gonadal steroid secretion, namely, testosterone (predominantly in males) and estrogens (predominantly in females), during specific periods in ontogeny may accompany the development of different brain regions associated with cognitive processes, such as the hippocampus. For example, infusing estrogen into the hippocampus improves memory in the object recognition task in female rats (Chisholm and Juraska 2013). Long-term increases in estrogen concentrations also improved performances in object recognition, spontaneous alteration, and matching to position tasks in female mice (Chisholm and Juraska 2013). Furthermore, hippocampal dendritic spine density is also increased in male rats in response to testosterone, which can have a corresponding enhancing effect on spatial learning and memory (Spritzer et al. 2011).

But sex differences in hormonal expression also vary with age and reproductive cycles or events. The expression of estrogen receptors in the hippocampus is dynamic, and estrogen concentrations change with both the estrous cycle and



with age. Synaptic remodeling of the hippocampus occurs repeatedly during the estrous cycle in response to ovarian steroids (Spritzer et al. 2011). Furthermore, birthing and raising pups enhance spatial cognition in female rats, most likely due to the action of estrogens on brain structure (Macbeth and Luine 2010). Age-related decreases in gonadal hormone concentrations are common to both males and females; however, testosterone in males can potentially better modulate the effects of cognitive decline via aromatization of testosterone to estrogen, leading to increased working memory (Spritzer et al. 2011).

Finally, stress affects cognition of males and females differently. Estrogen is known to alter or interact with the HPA axis, influencing the production of glucocorticoid hormones, with females generally having higher circulating concentrations of corticosterone as a consequence (Macbeth and Luine 2010). Interestingly, females may experience positive cognitive effects from increased corticosterone concentrations, showing heightened spatial working memory (Green and McCormick 2013), because oxytocin release is mediated by estrogen and can induce hippocampal plasticity over long periods (Macbeth and Luine 2010). Interestingly, highly sexually differentiated neurochemical changes are also observed in the dopaminergic system of the prefrontal cortex, the part of the brain critical for delete memory in rodents (Bowman et al. 2003). Male rats that experienced significant restraint stress showed decreased dopamine activity in the prefrontal cortex and amygdala that, combined with elevated corticosterone, resulted in impaired object recognition and spatial memory, whereas females stressed for a similar period of time in the same test showed no changes in dopamine activity and no impairment in cognitive tasks (Bowman et al. 2003).

## Conclusions

Rodent cognition is multifaceted, consisting of processes that identify, store, access, evaluate, and remember environmental information. Brain morphology and physiology, in particular, are the

underlying regulators of cognition, with some brain regions and hormones controlling a variety of cognitive functions. Cognitive processes naturally change with age due to changes in brain morphology and physiology, especially indirectly through stress effects. Finally, rodent cognitive abilities can differ between the sexes due to the differing effects of reproductive hormones on brain structure and physiological function. There is, therefore, a strong link between cognition and the neuroendocrine system, highlighting the importance of considering the physiological processes of rodents when studying their cognitive abilities.

## Cross-References

- ▶ [Corticosterone](#)
- ▶ [Dopamine Receptor](#)
- ▶ [Endocrine system](#)
- ▶ [Episodic memory](#)
- ▶ [Estrogen](#)
- ▶ [Hormones and Behavior](#)
- ▶ [Learning](#)
- ▶ [Ontogeny](#)
- ▶ [Oxytocin](#)
- ▶ [Problem-solving](#)
- ▶ [Rodentia Navigation](#)
- ▶ [Sensitive Periods](#)
- ▶ [Social Learning](#)
- ▶ [Testosterone](#)

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## Rodentia Communication

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## Synonyms

[Signaling](#); [Vocalization](#)

## Definition

Communication is the exchange of information between a sender and a receiver that the receiver can both perceive and decode, as well as the use of that information by the receiver to make a decision.

## Introduction

Rodents are a diverse group of mammals that belong to the order Rodentia which are characterized by a pair of continuously growing incisors in the upper and lower jaws. There are over 2000 known species of rodents that are found across the globe in a variety of aboveground and subterranean habitats. Rodents vary in size, from the Baluchistan pygmy jerboa (*Salpingotulus michaelis*) weighing in at 5 g to the capybara (*Hydrochoerus hydrochaeris*), which weighs over 50 kg. Rodents also range in their sociability, with eusocial naked mole-rats (*Heterocephalus glaber*) living in large colonies and woodchucks (*Marmota monax*) living solitarily. In addition, mating systems range from monogamy in prairie voles (*Microtus ochrogaster*) to promiscuity in black-tailed prairie dogs (*Cynomys ludovicianus*). The diversity of living conditions in rodents led to the evolution of highly adaptable sensory systems used in communication (see “► [Rodentia Sensory Systems](#)”).

Rodents communicate information about identity, fitness, willingness to mate, location, food availability, and danger. This communication takes place during different social and asocial events, such as foraging, play, mating, aggression, or predation. Information can be relayed through touch, such as nose touching in yellow-bellied marmots (*Marmota flaviventris*), scent (scent marking in wild house mice (*Mus musculus*)), or another sensory modality. Modes of communication, or the dominant sensory modalities that an animal employs, are critical for understanding the evolution of an animal's behavior and the signal used during communication (see “► [Rodentia Sensory Systems](#)”). In this entry we will focus on different behavioral venues during which communication occurs in wild and laboratory rodents.

## What Is Communication?

Communication is a process in which one animal, the sender, transmits information to another animal, the receiver, subsequently causing a change in the receiver's behavior. There are two

requirements that must be met for an interaction to be defined as communication. First, the sender must be supplying information on purpose, and not by accident. In other words, communication is a transfer of information between two active parties. The second criterion is that the receiver must benefit from the information being received (Bradbury and Vehrencamp 1998). During communication, senders may present accurate and reliable information or try to deceive the receiver.

The basic unit of communication between a sender and a receiver is a signal. The signal is any visual, auditory, chemical, tactile, or mixed stimulus that leads to a change in the behavior of a receiver. This process usually occurs within a species, benefiting the sender and the receiver. One can assume that the sender and the receiver in this exchange likely have the same goals. However, signals can also be used by other species. For example, the great gray shrike (*Lanius excubitor*) uses scent marks left by prairie voles (*Microtus agrestis*) to find suitable hunting grounds (Probst et al. 2002). In this example, it is clear that prairie voles left scent-mark communication signals for their conspecifics, yet predators used these signals for their own benefit. Signals that are used to another species' detriment are known as cues. Receivers of the same or of a different species can exploit these cues through eavesdropping.

In some cases a signal may be “honest,” meaning that the sender is displaying reliable information. It has been suggested that rodents use scent marks as an honest form of communication, revealing information about an individual's identity, health, and reproductive condition. Wild house mice can modulate their scent marking based on factors such as health, diet, and mating opportunities. Zala et al. (2004) showed that female mice can reliably assess whether a male had a bacterial infection based on scent marks. In this study, reproductively active males left more scent marks than juveniles and consequently left more honest signals for female mice. Another example of honest signaling occurs between pups and mothers. Mouse pups emit isolation calls in the ultrasonic range prior to the onset of hearing in this species, suggesting that pup calls function to evoke a response. These calls are easy

to detect and lead to a retrieval response from the mother (Ehret 2005).

A “dishonest” signal, or misinformation, is when the sender is sending out false information to a receiver, likely to improve their own fitness. The most obvious area of deceit in the animal world is in mating behavior. One example of a dishonest signal occurs in Columbian male squirrels (*Spermophilus columbianus*) that produce a mating call post copulation that is acoustically similar to their predator alarm call (Manno et al. 2007). Male squirrels increase their reproductive success by monopolizing females and preventing their partner from copulating with other males. A mating call that is acoustically similar to an alarm call may occupy a rival’s attention and delay the female’s future encounters. Both male and female squirrels habituate to mating calls during the mating season, but they react by seeking cover and becoming more vigilant when they hear the same mating call during the non-mating season. This suggests that signals that are acoustically similar may convey different information during the mating season.

## Venues of Communication

### Foraging

Foraging for food is directly related to the survival of an animal in the wild. Thus, animals spend a significant amount of time looking for food. Early on, rodents must learn the location, identity, potential benefit, or danger of different food sources through olfactory, gustatory, and social cues (see “► [Rodentia Sensory Systems](#)” in this volume for more details). Rodent foraging choices vary based on interactions between factors such as nutritional value, water content of food, soil density and texture, ability to cache and recover food, and others (Randall 1993). It is commonly believed that rodents are prey species and thus consume grains and grasses. Nonetheless, many rodent species are omnivorous and will feed opportunistically (Wang et al. 2003), and some are predatory and will hunt other rodents and venomous arthropods (e.g., grasshopper mice, *Onychomys arenicola*) (Egoscue 1960).

Communication about food sources has evolved in a variety of social species. Perhaps the most famous example in communication is the dance of the honeybees, although social rodents are also capable of exchanging information about food through olfactory and auditory signals. For example, mice (*Mus domesticus*) and rats (*Rattus norvegicus*) have been shown to use olfactory cues from partners to obtain information about the food they are eating and its location (Galef 1994). This information aids in future foraging and feeding behaviors. In addition to olfactory communication, mice also utilize auditory information to understand the nutritional satiety state of a conspecific. In mice, ultrasonic vocalizations (USVs) have been observed during interactions between a food-deprived observer and a non-deprived demonstrator. Mice that were food-deprived vocalized extensively to non-deprived demonstrators, suggesting that auditory communication and satiety play a critical role during foraging (Moles and D’amato 2000).

Nonetheless, not all rodents want to reveal the location of food they found or collected; therefore special precautions have to be taken to prevent visual or auditory communication of food sources. Rodents that cache, or rodents that store food in locations hidden from members of the same or different species, spend a lot of time trying to conceal the location of their caches. Eastern gray squirrels (*Sciurus carolinensis*) forage and hide their food in small clusters during mid to late autumn. These animals show sensitivity to the presence of a conspecific audience during caching, visually concealing whether they are hiding food or digging, by turning their back to the observer (Leaver et al. 2007). In other words, gray squirrels try to intentionally throw their competitors off by concealing their true actions.

Foraging is an important activity for the survival of rodents. The choice to communicate or to conceal food locations varies within Rodentia based on the social structure and evolutionary adaptation of these mammals.

### Play

Social play, or play directed toward others, is a critical element of mammalian development and

is associated with social and emotional skills in humans and animals. Deficits in social play during critical developmental periods are correlated with childhood onset of neurodevelopmental disorders (e.g., autism, schizophrenia, and attention-deficit/hyperactivity disorder) and difficulties in communication. Social play is especially important for establishing social bonds and learning proper communication skills in rodents. Similar to humans, rodents engage in a variety of play behaviors, including playing with inanimate objects, solitary locomotor-rotational play, and social play. Competitive rough-and-tumble (RT) play, or play fighting, is a form of social play in which two animals compete physically for some sort of advantage, without physically harming one another. It is important to note that there is no universal standard for what level of roughness distinguishes play fighting from aggression (see “► [Play Behavior](#)” in this volume for more details). Communication during play is critical for understanding the social context and intention of the opponent.

Play communication may be one of the most complex communication systems seen in rodents. The prolonged reciprocal interactions that occur during play involve a situation in which the players are, often simultaneously, both signalers and receivers. Touch, scent, and auditory cues are emitted during RT play. In juvenile laboratory rats, the location of nipping can communicate the competitor's intention (Pellis and Pellis 1987). During play fighting, rats will touch/nip on their playmates nape of the neck, whereas a serious confrontation includes biting of the rump and other areas. Rats also communicate play through auditory cues. During play, rats of both sexes use high-frequency calls to communicate their intention and emotional arousal. These vocalizations are in contrast to low-frequency calls that are associated with aversive interactions and fighting (Burgdorf et al. 2008).

There are sex differences in play behavior and communication in rodents. Pellis and Pellis (1990) showed that male rats initiate more play-fighting encounters than female rats. Males also initiate more physical attacks and defenses with a male than a female. In contrast to rats,

juvenile male and female golden hamsters (*Mesocricetus auratus*) engage in rough-and-tumble-play approximately the same amount of time. Hamsters, however, are more likely to engage in play behavior with the same sex (Guerra et al. 1992). Male-female dyads spent a significant amount of time engaging in physical contact but very infrequently engage in play behavior (Guerra et al. 1992). In addition, female hamsters experience an earlier onset of aggression than males, suggesting that hormonal development may play an active role in absence of play behavior in heterosexual dyads (Taravosh-Lahn and Delville 2004). Together these findings suggest that play is critical for communication development in social rodents and may serve different functions in males and females.

### Mating

All species of animals that reproduce sexually must search for suitable mates. Communicating sexual receptivity and fitness is an efficient way to identify a potential mate and to avoid aggression. Rodentia mating systems range from monogamy to polyandry and require complex communication venues while searching for and/or maintaining a mate.

Olfactory signals are frequently used by rodents to communicate reproductive condition to conspecifics. Specifically, females that are approaching estrus (an active reproductive state) are more likely to leave scent marks than females in a non-estrus state. In addition, female scent marks are more attractive to conspecific males while females are in estrus. Females may also change who they communicate with during estrus. For example, female golden hamsters leave more scent marks in dominant male territories and create scent trails leading the dominant male to her burrow. Scent marks can also provide an honest signal to a potential mate. As previously mentioned in the *Introduction*, female mice can assess whether a male had a bacterial infection based on scent marks. In addition, females can determine whether the male has had a high-quality diet and what their present nutritional status is. Meadow voles (*Microtus pennsylvanicus*) show a preference for scent marks left by high-quality



diet-consuming conspecifics of opposite sex (reviewed by Ferkin 2018).

Olfactory cues are long-lasting forms of communication. However, visual and auditory modes of communication contribute to mate choices. In guinea pigs (*Cavia porcellus*), there is a pre-copulatory visual “rumba” display in which the male shifts his weight from one hindleg to the other to produce a rhythmic swaying in front of the female. The execution of this mating display is critical during mate choice, although males perform this dance for both familiar and novel females (Cohn et al. 2004). The effectiveness of this presentation is important during the female’s choice. In addition, many rodents engage in tactile (grooming, sniffing, licking) and auditory communication prior to, and during, mating. Rats emit high-frequency USVs associated with positive affect and reward prior to and during mating. The mating is usually concluded by a low-frequency ultrasonic vocalization associated with aggression. This aggressive auditory signal may function as a deterrent for other males (Burgdorf et al. 2008). In naked mole-rat colonies, queens are the only females that mate within the colony. Queens mate with a few males in order to increase genetic diversity in a subterranean population. Mole-rat queens produce a variety of vocalizations that function to attract males and solicit mating with the fittest males (Pepper et al. 1991).

Rodents use a combination of modalities to communicate reproductive fitness and to attract potential mates. The effectiveness of these signals is reflected in the reproductive success of rodents throughout their evolutionary history.

## Aggression

Aggression is a complex overt behavior that evolved in the context of animal’s survival and fitness. Aggressive interactions involve auditory, visual, olfactory, and tactile communication signals. Aggressive behavior is characterized by physical damage whenever two or more animals are in conflict over access to a mate or food, defending a territory, or their position within a social hierarchy. Aggression can be categorized into two distinct classes: offensive and defensive. Offensive behavior is initiated by the aggressor

intending to cause physical and social damage to the opponent. Defensive aggression is the counterpart to the abovementioned interaction, in which an animal doesn’t approach the opponents or inflict intentional damage but could cause harm defending oneself (reviewed by Takahashi and Miczek 2014).

There are broad similarities in features of aggressive behavior across Rodentia, related to maternal or territorial defenses or the establishment and maintenance of social status within a group. There are also notable sex differences in the contexts during which aggressive behavior occurs. Males tend to show aggression during territorial and social dominance encounters, while females may establish territories but tend not to defend them with aggressive behavior. Females also express offensive and defensive aggression during maternal periods, in which the mothers defend their young against intruders (Takahashi and Miczek 2014).

Communicating aggression ahead of time can minimize the physical damage, loss of resources, and can provide long-term survival advantages to rodents and other animals. For example, laboratory mice (and numerous other rodents) of both sexes scent mark territorial boundaries with urine, thus avoiding unnecessary aggression and its consequences. In some non-laboratory rodents, communication of aggressive behavior is activated hormonally and is correlated with pair-bonding. Adult prairie voles (*Microtus ochrogaster*) are monogamous rodents that communicate aggression and dominance similarly to mice through scent marking, visual displays, and vocalizations. In contrast to mice, aggression in prairie voles is influenced by social experience, with sexually naïve male voles choosing to nonaggressively interact with a male intruder through sniffing and vocalizing, rather than attacking them. However, following a mating-induced pair bonding, males display high levels of offensive and defensive aggression and communicate aggression reliably toward conspecifics other than their mate (Winslow et al. 1993).

Another example of aggression communication in rodents occurs in fox squirrels (*Sciurus niger*). Adult fox squirrels continuously compete

for food and other resources in their overlapping home ranges, making it critical to communicate aggression without engaging in potentially dangerous or deadly interactions with their neighbors. Squirrels communicate aggression using a variety of modalities. For example, squirrels can use a combination of visual signals, such as tail fluffing and foot stomping, vocalizations (audible vocalizations and tooth chattering), and olfactory cues to deter an opponent or warn others of an intruder or a predator. Interestingly, tail motion has been used extensively to assess communication of aggression and irritation in squirrels in both field and laboratory settings. Rapid tail jerking and fluffing has been observed in irritating but nonaggressive interactions between a squirrel and a conspecific or heterospecific intruder. This tail motion may be a visual warning signal. More serious aggressive interactions and disturbances are associated with flexible waving or flagging of the tail. In the laboratory setting, tail motion has been used to measure aggression, irritation, and frustration in a squirrel during an operant task. If a squirrel performed a task, such as pressing a lever, they learned to expect a reward of high nutritional value over time. In a task where reward value was changed unexpectedly, squirrels expressed frustration and irritation. Animals would use tail flagging during trials in which they received a reward of lesser nutritional value or no reward at all (Delgado and Jacobs 2016). Together studies of the communication of aggression suggest that signals of aggression can be used to gain insight into emotional and cognitive states of rodents.

### Predation

Predation (or predatory aggression) is an interaction between two animals in which one or multiple animals (predators) kill and eat another animal or animals (prey). Predatory aggression is primarily driven by appetite mechanisms. Generally, rodents fall into the category of prey species that have evolved specific adaptations necessary for survival in the presence of predators. These adaptations enable them to recognize when predators are present, avoid and defend themselves against predators, and communicate the presence of such danger to their conspecifics.

Social rodents have evolved various anti-predator adaptations which allow an individual animal to reduce the time necessary for “lookout” or vigilance behaviors. One way to reduce individual vigilance is through sharing “lookout” duties with others and communicating about possible dangers using signals that all conspecifics, and some heterospecifics, can understand. Perhaps the most famous form of communication about predators is alarm calling. Alarm calls are auditory signals in response to danger produced by social rodents and other animals. Over 20 diurnal rodent species have been observed producing alarm calls, although some nocturnal species engage in alarm calling as well (e.g., the plains viscacha, *Lagostomus maximus*). These vocalizations are loud warning calls, varying in duration from several utterances to prolonged bouts, that create an escape opportunity for conspecifics (reviewed by Blumstein 2007).

Alarm calls may also function to deter predators from attacking since they have been exposed. Banner-tailed kangaroo rats (*Dipodomys spectabilis*) are desert-dwelling rodents that engage in foot drumming (e.g., the repeated striking of a hind foot or feet on the ground) as a form of alarm communication. Male and female rats of all ages have been observed engaging in foot drumming in response to snakes. In addition to foot drumming, rats responded to snakes with alert postures, kicking sand and jumping back. Kangaroo rats engage in a different anti-predator behavior upon detecting aerial predators, emitting a single-note alarm call and escaping into their mound. These different communication signals likely convey the identity of the predator but also alert the predator that they have been detected. Snakes are sensitive to low-frequency vibrations caused by foot drumming and often retreat when exposed to low-frequency vibrations (Randall and Stevens 1987). Similarly, rattlesnakes (*Crotalus horridus*) leave their ambush sites and move to a more distant location if they detect a visual anti-predator display from rodents or birds (Clark 2005).

Rodents can also utilize olfactory cues to communicate the presence of a predator and other dangers to their conspecifics through the release

of alarm pheromones (APs). Alarm pheromones are chemo-signals present in scent marks that warn conspecifics about possible dangers. Experiments in mice showed that individual mice can identify conspecifics that experienced a stressful event based on the presence of AP in their urine. The receivers of this olfactory signal exhibit increase in vigilance behaviors similar to predator-response behaviors (Rottman and Snowden 1972).

Studies on predatory communication give insight into how rodents have adapted over time in order to avoid predation.

## Conclusion

Communication is defined as a transfer of information from a sender to a receiver. This entry has examined some of the mechanisms of and contexts in which rodents communicate. In general, rodents utilize auditory, visual, olfactory, tactile, and mixed sensory modalities to exchange honest and dishonest signals with conspecific and heterospecific receivers. The preferred channel of communication varies with context (e.g., foraging) and species (e.g., domestic mice vs. prairie dogs). Different communication strategies reflect evolutionary adaptation and natural history of an individual rodent species and the whole Rodentia order.

## Cross-References

- ▶ [Arthropod Cognition](#)
- ▶ [Auditory Signals](#)
- ▶ [Bear Communication](#)
- ▶ [Canine Communication](#)
- ▶ [Catarrhine Communication](#)
- ▶ [Categorization](#)
- ▶ [Cephalopod Communication](#)
- ▶ [Cetacean Communication](#)
- ▶ [Chemical Cues](#)
- ▶ [Chemoreception](#)
- ▶ [Chorus](#)
- ▶ [Communication](#)
- ▶ [Contact Calls](#)

- ▶ [Countersinging](#)
- ▶ [Critical Period for Song Learning](#)
- ▶ [Dawn Solo/Chorus](#)
- ▶ [Echolocation](#)
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- ▶ [Food Calls](#)
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- ▶ [Passerine Vocal Communication](#)
- ▶ [Perissodactyla Communication](#)
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- ▶ [Sex Differences](#)
- ▶ [Social Behavior](#)
- ▶ [Songbird Duets](#)
- ▶ [Visual Recognition of Prey and Predators](#)

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## Rodentia Diet

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Rodents are the most diverse mammal group and are found in nearly every terrestrial ecosystem on the planet. Thus, it is not surprising to find that rodent diets are as diverse as the Rodentia family itself, evidenced by their unique foraging

behaviors, dentition, and other unique qualities (Hunter and Jernvall 1995).

Optimal Foraging Theory holds that animals should prefer food items which are high in protein, and low in fiber. To account for the large number of mammalian herbivores, this approach to studying animal nutrition would also suggest that herbivores would have to develop behavioral and/or physiological strategies designed to compensate for the lack of protein in their primarily fiber-focused diets. This could include, but is not limited to, higher energetic costs for digestion, lower metabolisms which would preserve energy expenditure, and an increased need for food intake in order to maintain adequate energy levels. Herbivorous rodents have similarly altered their locomotor strategies to compensate for their decreased metabolisms (Zhang et al. 2016).

Maternal fiber intake during pregnancy and lactation is directly related to offsprings' energy intake and body mass in adulthood. Additionally, rodents whose mothers consumed a low-fiber diet experienced an improved glucose tolerance, but also suppressed fat accumulation (Zhang et al. 2016). While this may sound appealing to the modern human, for many species of wild mammal, the reduced inability to accumulate fat may be the difference between surviving and not surviving a long winter, for example. Thus, it is unknown whether the impact of decreased maternal fiber intake is practically for the evolutionary fitness of offspring.

Sex differences in diet can not only be attributed both to the energetic challenges associated with parturition and lactation, but also with the ranging habits common to each sex in most species of rodent. Specifically, males are likely to exhibit increased dietary diversity as a result of their broad ranges and associated travel. Alternately, females typically exhibit high site fidelity as a result of the needs of rearing young. Thus, females are likely to utilize familiar territory and known food sources to provide for herself and young (Ferrando et al. 2019).

Diet not only shapes the ethology of rodent species, but also impacts – and is impacted by – physiology. This is most evident when one considers dental morphology; particularly the morphology of the first upper molar has been

demonstrated to differ significantly in shape as a result of the target species' diet in murine rodents. This knowledge assists researchers in studying the evolution of murine diets and by extension assists also in forming inferences regarding their behavior and role in the ecosystem. Similarly, other physiological features such as ear size and olfactory ability may differ between carnivorous and herbivorous rodents as a result of their unique foraging tactics (Gómez Cano et al. 2013).

Carnivorous rodents can be further divided into vermivores, insectivores, and the amphibious rats. Carnivorous rodents share unpigmented tooth enamel particularly on the anterior surface of the incisors, a smoothing of the occlusal surface of molars, and typically exhibit fewer molars than do their herbivorous relatives (Rowe et al. 2016). These evolutionary adaptations indicate a decreased need for the breakdown of hardened plant materials through gnawing and mastication.

Rodent foraging strategies frequently bring them into conflict with humans, resulting in an ever-expanding pest-control industry designed to exterminate unwanted rodents. In order to deter depredation on crops and/or unwanted cohabitation with rodents, reducing attractants is key. To deter herbivorous rodents, the planting of vegetation high in terpenes is likely to deter foraging behaviors and habitation in most herbivorous rodent species (Skopec et al. 2019). Similarly, omnivorous and carnivorous rodents can be deterred by determining the likely prey items attracting the unwanted rodents and reducing the key attractants for those prey species.

As one would expect, dietary preferences, and the related evolutionary adaptations, are directly related to the overall fitness of a species – impacting behavior, habitat preference, and other key factors. Developmental growth rates, and by extension survival rates as well as fecundity, are directly related to adequate nutrition. Rodents living within the same ecosystem often have different nutritional needs which result in species-specific preferences allowing for variation across species within an ecosystem. For example, in Alaskan microtine rodents such as brown lemmings, collared lemmings, and voles, each has developed a dietary preference which yields



optimal growth rates for that particular species. Brown lemmings tend to exhibit a preference for sedges, while collared lemmings tend to exhibit a preference for willows, and voles for both sedges and willows. However, all three species avoid those food items which, although not necessarily considered poisonous, do not yield an optimal growth rate such as ericaceous evergreen shrubs. These developed preferences appear to be unrelated to the availability or taste of the deleterious food item(s) (Jung and Batzli 1981). Similarly, dietary preferences do change seasonally, depending upon both the changing availability of various food items, and the changing nutritional needs of a species throughout the year and breeding seasons (Gasperini et al. 2018).

## Cross-References

- [Rodentia Diet](#)
- [Rodentia Morphology](#)

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## Rodentia Life History

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## Definition

Set of traits that are important to the life of rodents.

## Introduction

The order Rodentia is the most diverse among mammals and is divided from four up to seven main groups depending on the authority, but Wilson et al. (2016) separated it into five groups; namely, Anomaluromorpha, Castorimorpha, Hystricomorpha, Myomorpha, and Sciuromorpha that, altogether, comprise nearly half of the mammalian species. The majority of species are small-bodied (<5 kg) Myomorpha rodents, although some are as large as capybaras, which may reach up to 66 kg (Caviomorpha group).

The small-bodied rodents show a similar set of life history traits, such as high metabolic rate, short gestation length, weaning, and sexual maturity attained at early age, large litters produced at short intervals with brief parental care, fast growth, short life span, and high mortality (Promislow and Harvey 1990). Although some traits are fairly conserved, others vary widely. Variation across taxa will be presented first (Section “[Life History Variation Across Taxa](#)”), followed by variation within taxa, i.e., non-phylogenetic sources of variation (Section “[Life History Variation Within Taxa](#)”). Most of

the information regarding Section “[Life History Variation Across Taxa](#)” can be found in Wolf and Sherman (2007), Patton et al. (2015), and Wilson et al. (2016). Additional information that was not found in these books will be presented with its respective reference accordingly.

## Life History Variation Across Taxa

### Anomaluromorpha

*Size, Habit, and Habitat.* Sometimes included in the Hystricomorpha group depending on the authority, this is an African clade, composed by the rare anomalure flying rodents (not closely related to the flying squirrel from Sciuromorpha group) and the springhares, *Pedetes* spp. They may reach 90 cm and weight 1.8 kg. All anomalures are primarily herbivorous and feed on fruits, seeds, and leaves, but some colonial species may ingest insects. As for springhares, they are large, bipedal, and saltatorial rodents, reaching 50 cm and weighing 4 kg, considered as the third largest African rodent (surpassed by the porcupine *Hystrix* and the cane rat *Thryonomys*).

*Breeding Period.* With scarce information, anomalures seem to be seasonal breeders. They give birth in tree hollows, and there is not much else known regarding other reproductive biology aspects. As for springhares, females are polyestrous (fertile at multiple times in a year), and pregnancies have been recorded throughout the year, although depending on rainfall and grass production.

*Litter Size, Gestation Length, and Weaning.* Females are more frequently found with only one young, but there are records of up to four pups in *Anomalurus pelii*. Gestation of springhares is long, around 3 months, with an interbirth interval of 101 days. Gestation of springhares is long, around 3 months, and interbirth interval is of 101 days, and thus they are able to produce 3 to 4 litters a year.

*Sexual Maturity and Longevity.* Springhares reach sexual maturity around 2 years of age, reproducing 7 years in the wild, and living for 19 years in captivity.

*Mating System.* The matings for springhares are unique: two males chase a female, and the fastest male has the chance to mate with her, forming a vaginal plug and preventing the second male to mate.

*Parental Care.* The *Anomalurus beecrofti* mother carries the young with her, but if in the nest, *A. derbianus* parents regurgitate food for the young. Birth occurs in chambers, and offspring is considered precocial, covered in fur, and able to move within a few hours after birth.

### Castorimorpha

*Size, Habit, and Habitat.* Castorimorpha is composed of unique rodents, such as pocket gophers, kangaroo rats, pocket mice, and beavers. The pocket mice and kangaroo rats can be tiny, measuring up to 35 cm, but many other representatives are large, robust and semi-aquatic rodents, such as the beaver, weighing about 20 kg and measuring 120 cm. The pocket gopher (*Thomomys* spp.) is a solitary subterranean rodent, hard to observe and study in the wild, and the other Castorimorpha members are solitary too, with a few exceptions. Conversely, beavers are highly social, build large dams in which they rest, breed, and interact socially with family members. Beavers are active mostly at night and only observed outside the dam while foraging or obtaining wood for dam construction. Therefore, there is little information on these elusive species. They occur from the temperate grasslands to the deserts and tropical forests.

*Breeding Period.* Some species are highly seasonal breeders, such as the pocket mouse *Heteromys anomalus*, where males present testicular recrudescence and both sexes are sexually active at the same time. Beavers reproduce only once a year and females come into oestrus for a very brief period (12–24 h).

*Litter Size, Gestation Length, and Weaning.* When compared to other similar-sized relatives (e.g., Myomorpha rodents), litter size of this group is smaller, with 2–4 young as the most common litter sizes. Additionally, gestation is longer, maturation is slow, and the number of litter per year is also smaller (around one). Tinier Castorimorpha species tend to have larger litters

(up to 7 in *Thomomys*), while larger species have smaller litters (up to 2 in *Orthogeomys* or up to 3 pups in *Geomys*). Beavers have a long gestation length of about 100 days, and the nutria *Myocastor coypus* may delay birth in the face of a threat.

**Sexual Maturity and Longevity.** Beavers attain sexual maturity at about 2 years of age, when they disperse from their natal group. Tropical and subtropical pocket and kangaroo rats may live short lives and reproduce only once, while others breed several times. Gophers are roughly unknown, but it is estimated that larger species might live for 3 years or more. Beavers can live up to 24 years in captivity.

**Mating System.** Beavers seem to express genetic monogamy (exclusive monogamy) as they mate exclusively with only one partner (not confirmed by DNA analyses). Pairs remain together for up to 6 years, with dissolution resulting from death of partner rather than desertion. Although monogamy is the main pattern, density may influence mating system. In low densities, individuals mate with a single partner, while at higher densities, they mate with multiple partners. This strategy is called facultative monogamy. Spiny pocket mice exhibit the highest secondary sexual dimorphism in which males are 40% heavier than females that possibly results from intrasexual competition for females.

**Parental Care.** Beavers show high degree of biparental care and extensive paternal investment in young. They are highly territorial, and older family members live together in a group. During parturition, fathers and older offspring may help protect newborns and lick them. Afterwards, young individuals may beg for food from older individuals. In other representatives of this group, such as gophers and kangaroo rats, the most common pattern is lack of male paternal care.

### **Hystricomorpha**

**Size, Habit, and Habitat.** This group comprises some unique rodents, such as the largest living one, the capybara (*Hydrochaerus hydrochaeris*); second largest, Patagonian maras (*Dolichotis patagonum*), the only eusocial mammal; naked mole-rat (*Heterocephalus glaber*); porcupines;

and a wide range of other South American rodents. Their biology also varies greatly, from being aquatic to rock dwellers and from nocturnal to diurnal. One almost ubiquitous aspect of this group is their high propensity to group living (up to 300 individuals in the naked mole-rat), although some may be solitary (*Cavia magna*). One of the Hystricomorpha representatives, *C. intermedia*, is considered as one of the rarest mammalian species on Earth, while the Guinea pig (*C. porcellus*) is commonly domesticated as a pet and laboratory animal.

**Breeding Period.** The most common pattern is to reproduce year-round. Gestation is around 2 months, and some females may produce three litters per year. Reproductive inactive females (e.g., *Cavia gundi*) present a vaginal closure membrane, being sexually inactive most of the year, but females are able to store spermatozoa in their genital tracts for 2 months. A very unusual behavior for rodents but present in this group is the exhibition of sexual activity outside of the oestrus period, as seen in porcupine species (Cape porcupine *Hytrix africaeausstralis* and Indian crested porcupine *H. indica*). In cane rats, *Thryonomys* spp., oestrus cycles seem erratic, and thus, researchers think that their ovulation is induced (i.e., it requires an extra stimulus for ovulation, such as male presence or the physical act of copulation).

**Litter Size, Gestation Length, and Weaning.** Like Sciuromorpha, this group has a smaller litter size. Singletons are reasonably common, with litter size ranging from one to four pups per female (but exceptions occur, as in nutria *Myocastor coypus*, which may give birth to 12 pups). Unlike its small-litter-size relative, Hystricomorpha has only two pairs of mamma. Naked mole-rats are the exception. Queens raise litters equal to the number of mammae (12), and litters of 28 offspring have been reported in both field and lab colonies. Such extremely large litters are possible because pups take turns at nipples, and colony members share food with them to protect the queen. Gestation is generally long (around 5 months in Cane rats *Thryonomys*, 4 months in the porcupine *Hystrix*, and 7 months in the North American Porcupine *Erethizon*

*dorsatum*) and suckling continues for another 2 months in porcupines, 1 month in cane rats, or 54 days in New World hystricomorphans. In smaller species, gestation is generally shorter, except for ashy chinchilla rat (*Abrocoma cinerea*), which is exceptionally long for a rodent this size, lasting 4 months.

**Sexual Maturity and Longevity.** Sexual maturity is reached as early as 60 days in *Cavia intermedia*, or around 1 year of age in *Hystrix*. If born in the beginning of the breeding season, some females may breed at an earlier age (30 days in *C. magna*), and some may stay reproductively active until 16 years of age (e.g., naked mole-rat). Some hystricomorphans are long-lived in captivity; for instance, 14 years in Maras (*Dolichotis patagonum*), and 20 years in Old World porcupines (*Hystrix*). In gregarious or social porcupines, there might be reproductive suppression of subadult/subordinate individuals, such as the Cape porcupine (*Hy. africae australis*) and the naked mole-rat (*He. glaber*).

**Mating System.** Mating systems can be polygynous, with one male accompanying one or two females. Thus, strong sexual dimorphism has been observed in this group (e.g., *Cavia aperea*) with males 15% heavier than nonpregnant females. Another common mating system is monogamy, as observed in some Old World porcupine (*Hystrix*) species. Interestingly, in naked mole-rats, the queen solicits copulation with one to three males (the older, heavier, and less familiar ones), instead of intrasexual competition (male-male combat), so that multiple paternity is common. An unusual pattern for mammals is present in North American porcupines *Erethizon dorsatum*, in which males are the philopatric sex, while females disperse.

**Parental Care.** Hystricomorpha rodents have particularly precocial neonates (covered in fur, eyes open, and fairly developed locomotion). Young may complement milk with solid food almost immediately after birth. Despite that, nursing can occur for weeks or months, but parental care is intense and long in porcupines, with males caring for the young as much as the mother. With mainly precocial young, some mothers allow offspring to feed from their mouths, as seen in green

acouchi, *Myoprocta pratti*. Interestingly, in naked mole-rats *Heterocephalus glaber*, parents shove infants around the nest in order to teach pups to respond to a threat by fleeing. A characteristic of precocial young is their high mobility. Therefore, maternal contact calls may be frequent in this group. Yet, despite being highly social/gregarious, some Hystricomorpha species may present no paternal care at all (e.g., *Galea spixii*).

## Myomorpha

**Size, Habit, and Habitat.** Myomorpha is one of the most diverse rodent groups, including nearly a fourth of all **Mammalian** species. It includes rats, mice, gerbils, lemmings, voles, and hamsters. Despite, or due to, its diversity, many species lack proper life history information. They are generally small (less than 5 kg) and nocturnal and may feed on seeds, leaves, fruits, invertebrates, and fungi. Their habits vary greatly with respect to locomotor habit, such as arboreal, semi-fossorial, semi-aquatic, and saltatorial. They can be found from sea level up to 3,000 m high in the Andes. Those that live in cold places and/or in high elevations may show activity during the warm periods of the day. They are cosmopolitan, inhabiting all continents, except Antarctica, and many can live close to human settlements, influencing – and being influenced by – human activities.

**Breeding Period.** Their reproduction is closely related to rainfall and primary production, breeding seasonally, and somewhat after a rainfall peak, but some may breed year-round. Young individuals appear later on, when the primary production is still high after the rainy season. Voles and lemmings are known for their marked population fluctuation, while some are mostly in high densities (e.g., *Necromys lasiurus*) and others seem to be always in low densities (e.g., *Andinomys edax* and *Irenomys tarsalis*).

**Litter Size, Gestation Length, and Weaning.** Litter size generally ranges from 2 to 6, but a litter of 13 young has been registered in the wild, and one of 20 young has been recorded in captive colonies of rats. Gestation period is similar across taxa, lasting around 21 or 22 days. Weaning occurs around 20 days of pup age, and nipple

fidelity has been observed in prairie and pine voles. Some species present postpartum oestrus, breeding again right after giving birth (e.g., *Necromys lasiurus* Almeida et al. 1981). Some females may show several infertile ovulation cycles before becoming pregnant.

**Sexual Maturity and Longevity.** Young individuals may reach sexual maturity soon after weaning (~20 days). Their life span is possibly no longer than two winters, or of a couple of years in the wild, but some may live up to 5 years in captivity.

**Mating System.** Myomorpha presents some famous monogamy examples, such as the vole *Microtus ochrogaster*, the gerbil *Meriones unguiculatus*, and a couple of deer mice species *Peromyscus* spp. Yet, recent findings show that none of these males were able to fully monopolize a female, as multiple paternity has been detected in litters of both *Microtus* and *Meriones*, but not in *Peromyscus*, in which genetic monogamy was detected with certainty (Solomon et al. 2004).

**Parental Care.** Despite being rare in this group, some species have direct male parental care. Male muskrats *Ondatra zibethicus* are famous for constructing and maintaining burrow structures in the wild. Males of this species and of pine voles *Microtus pinetorum* feed juveniles. In white-footed mice, *Peromyscus leucopus*, fathers accompany weaned young on foraging trips. Some fathers may perform grooming of young at the anogenital region to stimulate urination and defecation, a critical behavior for newborns, a behavior observed in spiny mouse *Acomys cahirinus*, Djungarian hamster *Phodopus campbelli*, Siberian hamster *Ph. sungorus*, and prairie vole *Microtus ochrogaster*. Biparental care has been seen in prairie voles, where a mated pair may be quite aggressive to intruders, despite their small size, and both mothers and fathers coordinate nest visitation so that pups are often not left alone. One interesting behavior observed in social voles *M. socialis guentheri* is the so-called forced babysitting. The father (mainly) drags the mother to the nest to stay with the pups, while he leaves the nest.

Because nest building before parturition is frequent in this group, this feature deserves more attention. When babies try to venture out of the

nest, mothers tend to retrieve them, a common maternal behavior. Mothers with large litters spend less time in the nest, a reality of Myomorpha mothers with their up to 13 young per litter. Some explanations converge to the need that they have to acquire more food for nursing so many young, in order to meet their nutritional demands. Another hypothesis, however, is related to the maintenance of body temperature. Larger litters require less help to maintain individual body temperature as they can huddle to each other. In addition, huddling with large litters may lead to hyperthermia in mothers.

### Sciuromorpha

**Size, Habit, and Habitat.** Sciuromorpha is composed of all the world's squirrels, as well as prairie dogs, marmots, and dormice. Squirrels are mainly diurnal and adapted for life in trees, but prairie dogs and marmots are burrow dwellers. Body size varies from 115 mm (BL) and 45 g to 340 mm BL and 5 kg. Sciuromorpha inhabits a wide range of environments, such as the temperate zones in North America and Europe, to the tropical forests in South America, and the savannahs in Africa. Yet, the life history of this group is still poorly known. Some species may be solitary, highly communal/social, or both (depending on ecological factors), but marmots and prairie dogs are mostly gregarious.

**Breeding Period.** Difficult to collect and observe for long periods, everything else regarding Sciuromorpha life history is based on scattered observations. These observations suggest that breeding period can occur throughout the year in some tropical species, once a year in temperate environments or bimodally in some Amazonian species. No breeding was observed when food availability was low, which suggests that reproductive failure is closely related to food availability, as in many other groups.

**Litter Size, Gestation Length, and Weaning.** Litter size ranges from 2 to 4 in most species, despite that some may present up to 12 mammae. The largest litter has been observed in the antelope ground squirrel *Ammospermophilus* and dormice (14 pups). Gestation lasts less than 60 days, and some females breed up to three times in their lifetime. Length of gestation and lactation period



together is of 15–16 weeks in some species. This group presents typical altricial young (the opposite of precocial pups from Hystricomorpha, see above). Altricial young is characterized by pups that are born with eyes closed, naked, low locomotor development, and highly dependent on parents. Therefore, the degree of parental care in this group is higher as altricial pups need intense care and for a longer period.

**Sexual Maturity and Longevity.** Most species mature during the first year of life, but some colony-living species (prairie dogs and marmots) delay their maturity, extending until the 4th year of life. Longevity is not known for most of the species, but one squirrel species (*Notosciurus granatensis*) was recaptured for 6 years, with approximately 7 years of age, and marmots may live up to 15 years (very rare).

**Mating System.** Within this group exists one of the most iconic reproductive strategies observed among rodents. Cape ground squirrel *Xerus inauris* males have one of the largest penis/testicle ratios within Mammalia, related to a promiscuous mating system and high sperm competition. As for other species, males may experience testicular recrudescence (testicles reduced in size and positioned inside the abdomen, with diminished or absence of spermatogenesis). As for other representatives, such as prairie dogs, there are many polygynous species, in which females mate usually with only one male, even though living in groups with other males.

**Parental Care.** Biparental care is not common, even in gregarious species like prairie dogs and marmots, in which male care is restricted to defense of territory. Conversely, maternal care is intense and complex in this group. Sometimes a mother may bring food to the nest, such as groundhog *Marmota monax*, and there are species (e.g., Belding's ground squirrel *Urocitellus beldingi*) with complex communication skills, with mothers warning their young with specific calls to advise that a predator is close.

## Life History Variation Within Taxa

Although life history traits deal with important parameters, they are quite plastic, varying among

species, among individuals of the same species, and in the same individual through time. Rodents are known for displaying great plasticity in their life history traits, presenting great population fluctuation and responding quickly to a wide range of environmental changes.

## Age and Size-Related Variation

The life history of individuals is not fixed throughout their lifetime, so that age, size, and experience are the most important sources of variation. Since age is closely related to experience and size, the three are interconnected, and it is difficult to separate each. For instance, the more litters a mother has, the more experienced she gets and some presents a higher success in rearing larger or subsequent litters. More litters also means the female is getting older. Regardless of which specific effect rules, it has been observed that reproductive success is correlated with the age of the mother in beavers (Wilson et al. 2016).

Age is not the only way of acquiring experience. Another way is through alloparental care, in which an individual helps caring for the young that are not its own. The extent to which alloparenting occurs in some species is still under discussion. Adult prairie voles did not show higher survival success in pups that were raised with alloparental care, but they developed faster (Stone et al. 2010; Wilson et al. 2016). However, few studies have addressed the paternal experience in relation to parity, as in experienced males having or not having more offspring. Apparently, it had little effect in prairie voles, white-footed mice, deer mice, and Norway rats (Wolff and Sherman 2007).

Age influences growth, and association between size and life history traits is widespread among animals. Larger females show a higher degree of maternal care (Ralls 1976), while larger males are better at mate acquisition when compared to young smaller males, relating to a better reproductive success (Isaac 2005). Therefore, reproductive success of males is dictated not only by the effective production of semen but also by its physical dominance over other males and the ability to attract females benefited by an increased body size, leading to a high energetic cost (Bronson 1985). Thus, competition is

avored by size in many species, particularly among males.

### Silver Spoon and Maternal Effects

Each individual has its own life history trajectory that starts during his or her development. Thus, variation between individuals is expected. For instance, when a favorable environment during development brings positive traits in the adulthood, it is called the silver spoon effect (Grafen 1988). Such an effect has been detected in tree squirrels *Sciurus vulgaris*, operating by means of younglings growing during good seed-crops seasons presenting an advantage when compared to others (Wauters and Dhont 1995). However, when analyzed in a different species, the root vole *Microtus oeconomus*, this effect was not as pronounced, perhaps because there is a very specific and sensitive period for this effect to be important, for example, during lactation (Rémy et al. 2011).

Another and a more familiar effect is a trans-generational one called the maternal effect (Kempthorne 1969). The phenotype of the mother or the environment she experienced affects the phenotype of her offspring, as in larger mothers give birth to larger babies. Degus *Octodon degus* present an interesting example. Degus mothers that had increased androgens (testosterone) levels during the prenatal period had masculinized offspring. Masculinized females, although more aggressive and sometimes less attractive to males, produce larger litters and heavier individual pups (Correa et al. 2016). It is important to note that the uterine environment is decisive for the development and changes of many life history traits.

### Geographic Variation

Abiotic and biotic variables are closely related to geographic locality. Thus, when considering geographic variation, it is difficult to separate variation related to climate/resource from variation related to geographic locality. The parameters that vary across regions are photoperiod, food, rainfall, and temperature.

Regardless, an important requirement for studying geographic variation is a wide distribution, similar to the genus *Peromyscus* in North America (Bronson 1985). At higher latitudes, *Peromyscus* exhibit short breeding seasons (2 or 3 months), and

they produce only one litter per year. At mid-latitudes, their breeding season is longer, from 5 to 7 months, and several litters are produced in the same year. At low latitudes, they breed mostly year-round, except for the highly seasonal habitats regarding rainfall patterns.

Altitude also influences life history traits. Alpine yellow-bellied marmot (*Marmota flaviventris*) females do not breed in successive years at 3,400 m high, while females at 2,900 m breed every year (Johns and Armitage 1979).

Differences in parental care related to geography have been identified in prairie voles and meadow voles (Wolff and Sherman 2007). Prairie vole populations located at two different places (Illinois and Kansas, USA) had different levels of parental responsiveness. Differences in parental care were considered to be a result of resource abundance (Illinois is richer). As for meadow voles, males of different origins also had different levels of paternal care. Males from Canada, with harsher environmental conditions, cared more for the pups when compared to males from the United States.

### Yearly Variation

General yearly fluctuation is expected for rodents. Some populations will show periods of high abundance alternating with periods with near-zero abundance. Lemmings are known for presenting cyclic and fluctuating populations (Boonstra 1994). In the Neotropics, many rodents go population booms/bursts, what has been called “ratada,” a more intense but less rhythmic population fluctuation.

Booms/bursts and “ratadas” are commonly reported throughout the world. Abnormal rainfall or higher primary production may trigger these population outbreaks by facilitating out-of-phase breeding periods. Ratadas have been described for *Oligoryzomys longicaudatus*, *Abrothrix longipilis*, *Rattus argentiventer*, and *Wiedomys pyrrhorhinos* in South America and in Indonesia (Singleton et al. 2001; Pearson 2002; Sobral and Oliveira 2014). The mast seeding of bamboo is a common explanation for many of the ratada events, especially because some bamboo species breed every dozens of years, augmenting the environment capacity support.

### Iteroparity Versus Semelparity

Other interesting strategies regard how many breeding opportunities an animal has throughout its lifetime. Iteroparity can be defined as the ability to reproduce more than once in your lifetime, while semelparity is like salmon, in which they breed only once and then die (Barry et al. 2001). The arctic ground squirrel *Urocitellus parryii* presents a drastic life history strategy, considered as “partially semelparous.” By hibernating necessarily for 8 months, breeding opportunities are restricted to a short period of the year. Competition for mating opportunities is high so that the energetic requirements of breeding lead to the disappearance of 48% of males after their first (and only) breeding season (Edwards et al. 2016).

Because multiple matings are commonly observed in rodents, amusing strategies exist to cope with this competition. As seen in Cape ground squirrels, males are exposed to a high sperm competition because females copulate with various males. However, prairie dog species (*Cynomys* spp.) present a distinct behavior in which males sequester a fertile female, blocking the entrance and preventing her from leaving as well as other males from entering. Interestingly, male maras urinate on fertile females, which researchers have proposed to act as a repellent to other males.

### The r-K and the Fast-Slow Continuums

Mammalian life history strategy is frequently visualized as an r-K continuum (Pianka 1970). In theory, at the r-endpoint animals experience environments with no competition, so that the optimal strategy is to focus on producing as much offspring as possible, even at the expense of caring less for each individual young. Thus, r-selected organisms are marked by high productivity. As for the K-endpoint, animals experience environments with high competition. Therefore, the optimal strategy is to produce fewer young but focus on caring more for each one – a young of high quality. Unlike the r-selected organisms, the K-selected mothers and fathers direct energy on producing just enough offspring to replace them.

There is body literature relating the r-K continuum with adult body mass among mammals.

However, when the influence of body size is removed (statistically speaking), life history traits continuum is termed as fast-slow continuum (Promislow and Harvey 1990). This continuum reflects mainly the fertility related to age at maturity, but also high reproductive rate, early maturity, and low survival. Both the r-K and the fast-slow continuums are commonly known as “mouse-elephant” differences.

Rodents are usually considered as r-selected organisms that produce large litters with brief parental care. They usually live shorter lives, and, when compared to other mammalian species, they are placed at the fast end. However, when comparison comprises only Rodentia, representatives we can still observe differences (Dobson and Oli 2007). For instance, the capybara attains sexual maturity at an early age, gives birth to a small litter with precocial young after a long gestation. This strategy is very different than that of elephants (1 young produced every few years and sexual maturity reached at 15 years), so capybaras can be considered as r-selected and fast-living if the other endpoint is an elephant. However, when compared to a smaller relative, the house mouse, capybaras can be considered as a K-selected slow-living animal. Hence, both r-K and fast-slow continuums are not universal and depends on the scale we are dealing with.

### Conclusions

Rodents comprise nearly half of the mammalian species and inhabit all continents and environments (except Antarctica). Although the vast majority is small-bodied (<5 kg) species, there are exceptions to the rule, such as the capybaras, the largest rodent that may reach up to 66 kg. One almost universal trait among rodents is their early maturation, but they generally share other life history traits, like high metabolic rate, short gestation length, weaning and sexual maturity attained at early age, large litters produced at short intervals with brief parental care, fast growth, high mortality, and short life span, characteristics that identify them as r-selected or fast-living creatures. However species deviate from

this pattern. For instance, Sciuromorpha group representatives are mainly solitary, but marmots and prairie dogs, included in the same group, are not. As for litter size, most groups have large litters, such as the lab rat (Myomorpha) that can give birth up to 20 pups. However, other groups, like the Caviomorpha, do not have such large litters. Moreover, although many rodents display brief maternal care and lack male parental care, muskrats do have direct male parental care, and naked mole-rats rely on the colony for taking care of newborns. Despite these differences, life history variation follows similar trends. The most common sources of variation are age and size (endogenous) and environment (exogenous), and rodents are particularly sensitive to environmental variation. Finally, rodents are generally considered as r-selected organisms with fast life history strategies when compared with other mammalian orders. Yet, there are differences within the order Rodentia, with large and long-lived rodents producing small litter with precocial young after a long gestation placed at the slow end and the small short-lived ones at the fast endpoint.

## Cross-References

- [Extra-Pair Copulation](#)
- [Mate Guarding](#)
- [Rodentia Cognition](#)
- [Rodentia Communication](#)
- [Rodentia Diet](#)
- [Rodentia Locomotion](#)

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## Rodentia Locomotion

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## Synonyms

Rodent locomotion; Rodent gaits

## Definition:

Movement used by members of the order Rodentia to transverse their environment.

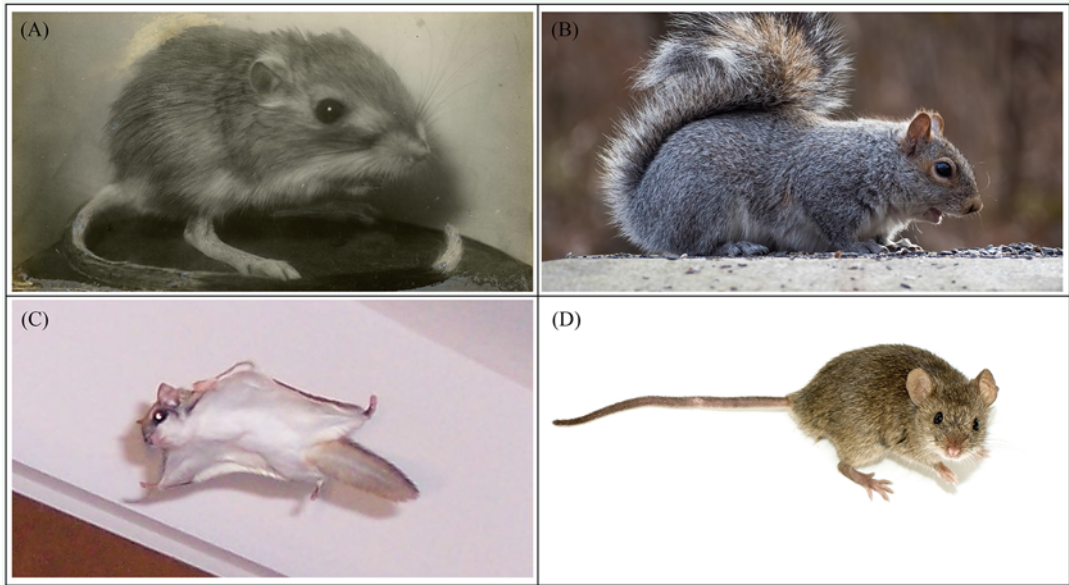
The Rodentia encompasses a diverse family of species; by size, the order ranges from the Baluchistan pygmy jerboa at 3.75 grams and 4.4 centimeter body length to the capybara at 66 kilograms and 134 centimeter body length. Accordingly, species have ranging habitat preferences from deserts to urban environments. While Rodentia

includes many common pests, many of these species play important ecological roles including being keystone species in some ecosystems (Martínez-Estévez et al. 2013). For example, the prairie dog maintains soil properties, creates new islands of habitat, and improves nutritional quality of forage (Martínez-Estévez et al. 2013). Species such as the squirrel, scaly-tailed squirrel, woodrat, and chipmunk inhabit arboreal environments (Essner 2007; Karantanis et al. 2017), while gophers, mole rats, groundhogs, and prairie dogs spend most of their time underground in tunnel systems (Martínez-Estévez et al. 2013). The earless water rat, beaver, and muskrat are semi-aquatic (Casanovas-Vilar et al. 2008). The house mouse and brown rat are commonly found cohabitating with humans in urban centers including cities, towns, and farms (Langton et al. 2001). The ecological diversity of the order has resulted in a range of locomotor adaptations and species are known to utilize terrestrial quadrupedal and hopping gaits, arboreal locomotion, gliding, and even swimming (Fig. 1). This chapter introduces the varying locomotor modes observed within the Rodentia.

## Terrestrial Locomotion

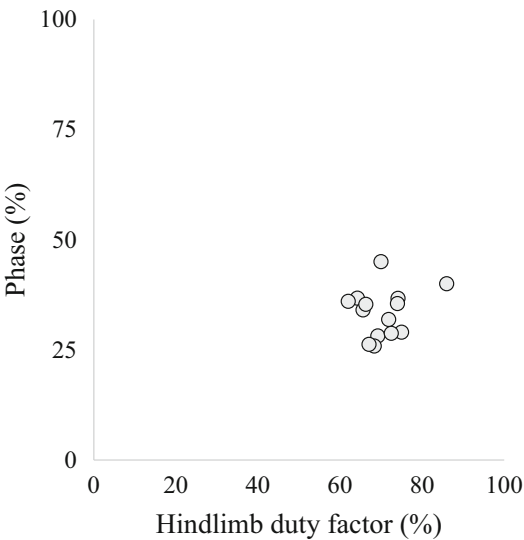
Quadrupedal walking and running represent the most common form of terrestrial locomotion in rodents. At moderate paces, rodents tend to have symmetrical gaits. However, at higher velocities, their gaits can be asymmetrical (Karananis et al. 2017). Lateral sequence diagonal couplet gaits tend to be the most common limb sequence observed in terrestrial rodents (Fig. 2). A lateral-sequence gait is one in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb). Commonly, during walking gaits, the forelimbs and hindlimbs are traveling together as a slightly asynchronous couplet. When the ipsilateral forelimbs and hindlimbs are traveling together, this is referred to as a lateral couplet; when the contralateral forelimbs and hindlimbs are traveling together, this is referred to as a diagonal couplet. Very rarely do the limbs move





**Rodentia Locomotion, Fig. 1** Rodents show a range of locomotor modes, such as (a) hopping in kangaroo rats (*Dipodomys sp.*), (b) arboreal climbing in gray squirrels (*Sciurus carolinensis*), (c) gliding in flying squirrels (*Glaucomys sp.*), and (d) quadrupedal walking in mice (*Mus musculus*). Photo credit for panel A: Smithsonian Institution - <https://www.flickr.com/photos/25053835@N03/13537163983/>, No restrictions, <https://commons.wikimedia.org/w/index.php?curid=57192070>.

Photo credit for panel B: Rhododendrites - Own work, CC BY-SA 4.0, <https://commons.wikimedia.org/w/index.php?curid=76103045>. Photo credit for panel C: Bluedustmite at English Wikipedia, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=2132835>. Photo credit for panel D: George Shuklin (talk) - Own work, CC BY-SA 1.0, <https://commons.wikimedia.org/w/index.php?curid=5521043>



**Rodentia Locomotion, Fig. 2** Hildebrand plot showing the relationship between hindlimb duty factor (%) and Phase (%) for fourteen species of rodent

together in perfect synchrony. The lateral sequence diagonal couplet gait is argued to be quite stable due to the generally low proportion of the stride spent as a unilateral bipod (~22%), and the relatively high proportion of the stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support).

While the above definitions of gait are useful for classifying rodents compared to mammals, the utility of such definitions is questionable in species that primarily rely on intermittent locomotion (also known as stop-and-go locomotion). Intermittent locomotion is when the force an animal exerts to move itself through space is applied discontinuously and the pauses last longer than a single cycle of limb movement (Gleeson and Hancock 2001). A terrestrial organism engaged in intermittent locomotion typically comes to a

complete stop during the nonpowered phase. Intermittent locomotion in the rodents is most common during foraging and habitat assessment, but the reader should be aware that rodents can adopt longer cyclical locomotor bouts during certain behaviors (e.g., predator escape). Studies on intermittent locomotion have been limited due to the noncyclical nature of the behavior and high variability between locomotor bouts. For example, gray squirrels approaching a food source away from forest cover made 22 pauses per minute and spent 35% of their time paused, while those carrying a nut to a site for hoarding in forest cover made 10 pauses per minute with 14% of their time paused (Gleeson and Hancock 2001; Kramer and McLaughlin 2001).

One major concern for rodents, and small-sized animals in general, is energetic expenditure during locomotion (Reilly et al. 2007). In fact, some of the highest daily locomotor costs have been observed in rodents [i.e., the golden-mantled ground squirrels (*Spermophilus saturates*) expend ~13% of total daily energy expenditure devoted to movement; Kenagy and Hoyt 1989]. Intermittent locomotion of rodents may amplify these concerns as this stop-and-start movement pattern entails more acceleration, more deceleration, and a higher speed. Both acceleration and active deceleration require energy expenditure. Moving at higher speeds may also require more energy expenditure per unit distance. Therefore, intermittent locomotion is expected to increase the energetic costs of moving over those of continuous locomotion under many circumstances (Gleeson and Hancock 2001). However, intermittent locomotion may permit some recovery from fatigue and pausing may result in an overall greater distance travelled (Kramer and McLaughlin 2001).

Bipedal hopping is a specialized form of terrestrial locomotion described as a sustained saltatory motion in which the hindlimbs contact the ground simultaneously without the use of the forelimbs (McGowan and Collins 2018). Bipedal hopping is commonly noted to have originated from desert regions. It has been hypothesized that bipedal hopping is advantageous for animals in desert environments because it confers locomotor efficiency for access to scarce water resources

(McGowan and Collins 2018). Other hypothesized advantages of bipedal hopping include greater forelimb availability for use in activities like foraging (McGowan and Collins 2018).

Hopping has been shown to be energetically favorable in Fawn hopping mice (*Notomys cervinus*) (Dawson 1976). Energy consumption increases with stride frequency until faster gaits are achieved. In faster gaits, energy consumption continues to rise despite little changes in stride frequency (Dawson 1976). This energy expenditure is observed as locomotion changes from normal gait to hopping, with increased hopping strides at higher speeds (Dawson 1976). Consequently, Fawn hopping mice have markedly lower energy costs at faster locomotor speeds than quadrupeds of similar size (Dawson 1976).

Hopping rodent locomotor capabilities have directly influenced research into tissue engineering. Kangaroo rat (*Dipodomys sp.*) tendon properties are unexpectedly strong and tough. Accordingly, Javidi et al. (2019) proposed that these tissues could serve as a model for improving engineered tendon replacements. Javidi et al. (2019) observed that the tendons of kangaroo rat locomotor muscles have failure loads (a marker for how much deformity a material can bear before breaking) 45–49% larger than those of red kangaroos. Despite their small size, kangaroo rats can generate significant muscle stresses typically observed in much larger animals like red kangaroos.

## Arboreal Locomotion

The exploitation of an arboreal environment provides access to additional resources and minimizes risk from terrestrial predators. However, the diversity of available arboreal substrates (i.e., variable size, inclination, length, fragility, etc.) presents a demanding, discontinuous, and unpredictable three-dimensional environment that imposes a range of biomechanical challenges to arboreal rodents. As such, arboreal mammals have evolved a range of anatomical and biomechanical adaptations that have allowed them to navigate in trees safely and effectively (Granatosky et al. 2019; Karantanis et al. 2017).

In an arboreal context, gait patterns may serve as a behavioral mechanism to enhance stability and safety (Granatosky et al. 2019). These gaits can be either symmetrical, when the left and right limbs of a pair alternate, or asymmetrical, when the left and right limbs move more synchronously. Diagonal-sequence gaits [hindlimb footfall is followed by a contralateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb)] contribute to dynamic stability in arboreal substrate navigation and reduce the periods of the stride where the limbs are arranged as unilateral bipod. In contrast, lateral sequence gaits may be functionally linked to static stability in substrate navigation and maximize the proportion of the stride where the limbs are positioned as a wide polygon of support. During arboreal locomotion, duty factor usually decreases on larger substrates (i.e., longer swing phase) along with an increase in the frequency of asymmetrical gaits (Granatosky et al. 2019; Karantanis et al. 2017).

Asymmetrical gaits, including gallops, half-bounds, and bounds, are commonly used by mammals at high speeds and frequently include a whole-body aerial phase (Granatosky 2018; Hildebrand 1980). It has been proposed that asymmetrical gaits may be preferable over symmetrical gaits during faster locomotion as they confer a reduction in the peak reaction forces, decrease the strain on the musculoskeletal system, and may optimize metabolic costs, at least at the trot-gallop transition (Hoyt and Taylor 1981). For small arboreal rodents, asymmetrical gaits further confer advantages in stability by limiting center of mass oscillations. However, data on the use of asymmetrical gaits during arboreal locomotion in rodents is limited (Karananis et al. 2017).

Beyond categorical gait sequences, arboreal stability is also influenced by speed, which is a function of stride frequency and stride length (Granatosky et al. 2019; Karantanis et al. 2017). Arboreal neotropical rodents exhibit overall higher velocities than terrestrial species as a mechanism to maintain dynamic stability (Karananis et al. 2017). Increased velocity during arboreal locomotion can be achieved either by

increasing stride frequency, and decreasing stride length, by increasing primarily stride frequency and, at a lesser rate, stride length, or by reducing stride frequency while increasing stride length. Increasing velocity through increased stride length is often encountered in medium-sized and larger arboreal mammals. This enhances safety during arboreal locomotion as the longer reach of the forelimbs minimizes branch sway. In contrast, increasing velocity by stride frequency may be better suited for smaller arboreal mammals, which are subject to insignificant branch sway, as it decreases body oscillations at limb touch-downs (Granatosky et al. 2019; Karantanis et al. 2017).

Forelimb and hindlimb kinematics of arboreal locomotion have been primarily limited to studies of medium/large-bodied primates using symmetrical gaits. Thus, the applicability of “general kinematic patterns” gleaned from these previous works may be limited regarding joint movements of the rodents. However, research on the arboreal locomotion of *Rattus norvegicus* by Schmidt and Fischer (2010) did reveal some commonalities with primates that might indicate shared behavioral adaptations caused by the biomechanical constraints of arboreal locomotion. Specifically, arboreal animals tend to show increased elbow and knee flexion throughout stance phase compared to terrestrial counterparts. Increased flexion at these joints is thought to lower peak vertical forces during arboreal locomotion, which in turn reduces joint reaction forces at mobile, but unstable, limb joints. Furthermore, shoulder and hip excursion tends to be greater in species that commonly utilize arboreal locomotion. Greater excursion at these joints arguably increases stride length, which in turn reduces stride frequency and therefore substrate oscillations. These joint movements tend to become exaggerated as substrate size becomes smaller relative to the body size of the animal. However, such generalities are not without criticism. Schmidt (2005), using a comparative approach across a range of small mammals, demonstrated that hindlimb kinematics change little in response to substrate (i.e., arboreal versus terrestrial), but instead are size dependent. As such, it may be the case that forelimb

kinematics are affected more by moving on thin arboreal substrates compared to hindlimb movements. It should be noted that these patterns may apply only to symmetrical gaits and are not relevant when animals use asymmetrical gaits, including gallops, half-bounds, and bounds.

Gliding is another mode of arboreal locomotion used by some rodents [e.g., the northern flying squirrel (*Glaucomys sabrinus*), common giant flying squirrel (*Petaurista petaurista*), and the Anomaluridae]. During gliding, animals increase their body surface area to enhance drag as they parachute down from elevated arboreal substrates. Anatomically, *Glaucomys* species exhibit elongated lumbar vertebrae and forearms (Granatosky et al. 2014; Thorington and Santana 2007). These anatomical features allow for enhanced drag as the body's surface area is increasingly in contact with air. In gliding animals, the energetic cost of quadrupedal locomotion increased as their morphology evolved to better align with gliding arboreal locomotion (Flaherty et al. 2010). However, gliding results in significant energy savings and reduced total travel time as the animal is moving in-between foraging sites (Flaherty et al. 2010).

## Aquatic Locomotion

There are Rodentia species, such as the members of *Castoridae*, that exhibit mixed terrestrial and aquatic locomotion, but with preference towards aquatic environments (Casanovas-Vilar et al. 2008). Morphological features specific to this genus include externally rotated femurs with a broad diaphysis and tibiae with lateral curvature that result in lateral deviation of the feet. In contrast to other Rodentia species, members of the *Castoridae* family also have knee and hip joints that contain more connective tissue, thus making these joints more fixed. These features, combined with the presence of large adductor muscles and intrinsic foot muscles, make the rapid alternating sequence of foot dorsiflexion and plantarflexion more suitable for propulsion in aquatic environments (Carlson and Welker 1976).

## Conclusion

Rodentia consists of a wide range of species occupying varied habitats and disparate locomotor behaviors. These locomotor modes developed based on survival needs, lifestyle, and energetic favorability. Modes of locomotion in Rodentia include terrestrial and arboreal quadrupedalism, gliding, hopping, and swimming. Studying these different locomotor styles in rodents provides further insight into evolutionary characteristics that allow these species to survive in their environments and enlightens future innovations.

## Cross-References

- ▶ [Activity budget](#)
- ▶ [Adaptation](#)
- ▶ [Adaptedness of behavior](#)
- ▶ [Adaptive radiation](#)
- ▶ [Arboreality](#)
- ▶ [Basal Metabolic Rate \(BMR\)](#)
- ▶ [Canopy](#)
- ▶ [Captivity](#)
- ▶ [Common ancestor](#)
- ▶ [Dispersal ability](#)
- ▶ [Dispersal patterns](#)
- ▶ [Diurnality](#)
- ▶ [Ecology](#)
- ▶ [Evolution](#)
- ▶ [Extinction in Learning](#)
- ▶ [Gait](#)
- ▶ [Herbivore](#)
- ▶ [Home range](#)
- ▶ [Homology](#)
- ▶ [Homoplasy](#)
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- ▶ [Species](#)
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- ▶ [Vertebrate nervous system](#)
- ▶ [Zoo](#)
- ▶ [Zoology](#)

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## Rodentia Morphology

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### Introduction

The order *Rodentia* includes over half of all modern mammals including over 2,200 species divided into 33 families (Yarto-Jaramillo 2015). This entry will discuss, generally, the unique morphological adaptations of rodents, with a particular focus on rats and mice due to their common usage in psychological and biomedical research.

### Cardiovascular System

As mammals, rodents possess a four-chambered heart, a dominant left ventricle, and thinner right ventricle. Heart rate varies depending upon species (e.g., mouse ~350–700 beats/min and rats ~300–400 beats/min). The rodent heart is spherical to oval in shape and lacks a distinct intraventricular groove (Beutow and Laflamme 2018).

### Dentition

Mammalian dental morphology provides clues for the animals' diets and habitat, thus providing insight into the species' behavioral ecology (Helder Gomes et al. 2013; Renaud et al. 2005). One notable morphological adaptation present in all rodents is the characteristic open-rooted and rapidly growing incisors – which require individuals to constantly chew on dense material to prevent overgrowth (Grant 2014; Yarto-Jaramillo 2015). All rodents have monophyodont dentition, meaning that all teeth are permanent and will not be replaced if extracted. Rodents also possess a large diastema between the incisors and molars (Yarto-Jaramillo 2015). In guinea pigs and

chinchillas, however, all teeth are open-rooted and grow throughout the lifespan. Like the incisors, the animals' natural diet of dense vegetation controls this growth, preventing malocclusion. If unchecked, malocclusions can be both painful and deadly, leading to starvation as well as bone and soft tissue damage (Grant 2014). Rodent enamel is unevenly distributed along the labial surface of teeth (Yarto-Jaramillo 2015) and is typically yellow due to iron deposits in the enamel (Treuting et al. 2018).

### Excretory and Gastrointestinal Systems

All rodents are monogastric, possessing a simple stomach with glandular portions. Structural deviations in the structure and function of the rodent gastrointestinal system directly reflect the animals' diet. Strict herbivores, such as muskrats, have glandular tissue throughout the entire stomach, a large cecum, and an elongated colon to maximize nutrient absorption. However, in carnivorous species such as the water rat, approximately 70% of the stomach is covered in glandular tissue. Rats are unique in that they do not possess a gall bladder (Yarto-Jaramillo 2015). However, the rat common bile duct demonstrates ciliary adaptations which allow it to function in a manner similar to the rabbit gall bladder in terms of permeability (Smith and Boyer 1982). The presence of a gallbladder, in rodents, appears to be reliant on the presence of only one or two mutations. This, coupled with varying selection pressure in the wild, has resulted in considerable variation across rodentia. That is, many species present with, and without, a gallbladder (Geise et al. 2004; Kruepunga et al. 2019).

Unlike humans, rodents possess a lobated liver which contains four lobes: the ventromedial lobe, right and left dorsolateral lobes, and the caudate lobe. Additional lobes tend to develop in order to form a proportionately larger liver, increasing the general number of lobes rather than the overall lobular size. Regardless of the number of lobes present, the internal architecture of the liver remains the same (Kruepunga et al. 2019).

## Reproductive System

Famous for their ability to procreate, the rodent reproductive system is efficient and well-studied. Many small rodents are spontaneous ovulators. However, in many species the vagina is opened only when the animal is in heat, during parturition, or has an infection in the reproductive tract (Yarto-Jaramillo 2015). Male murine rodents have been found to have a near isometric relationship between body size and testes size, although the size of spermatozoa was not found to be related to either body or testes size (Breed and Taylor 2000).

## Respiratory System

The rodent trachea is C-shaped and contains between 15 and 25 (depending upon species) incomplete cartilaginous rings. In rodents, the right lung contains four lobes (cranial, caudal, middle, and accessory) while the left contains only one. Mice and rats both have two extrapulmonary bronchi (conducting airways with cartilage). These extrapulmonary bronchi subdivide to form the intrapulmonary bronchi, supplying air throughout the lungs. These intrapulmonary bronchioles lack both cartilage and submucosal glands. Instead, nonciliated cells are predominantly responsible for rodent airway secretions. Rodent airways branch in what is known as an asynchronous, monopodial branching pattern, meaning that smaller branches project from larger branches of the airway. Unlike humans, rodents lack well-defined bronchioles (Meyerholz et al. 2018).

## Neurological System

The structure and function of the rodent brain reflects their unique sensory and cognitive capabilities, and by extension their Umwelt. The rodent brain lacks the sulci and gyri known to human brain anatomists to provide external landmarks. Unsurprisingly, the rodent olfactory bulb is quite large in comparison to humans and thus

reflects their advanced sense of smell. The parafloccular lobule of the cerebellum is much larger in comparison to humans, while the cranial lobule has less lateral spread than humans. Similarly, the human middle lobe is proportionately larger in humans. These differences in cerebellar structure reflect the rodent's need to establish and maintain balance, processing visual and vestibular information to achieve this aim (Snyder et al. 2018).

## Inbred Rodent Strains

Understanding the biology and behavior of the order Rodentia can be a daunting undertaking due to the size of the order and the inter- and intraspecies variation represented therein. However, this endeavor is further complicated by the development of inbred rodent strains used in biomedical research. For example, the structure of mouse strains C57BL/6 and BALB/c present with vastly different tracheal structures (Meyerholz et al. 2018). Thus, laboratory studies must include a thorough evaluation of the baseline anatomy, morphology, and behavior of rodent strains prior to experimental manipulation.

## Discussion

The morphological characteristics described here are critical for the proper phylogeny and anatomical evaluation of the many rodent species (Stein 2000). Rodents, of course, are not only found throughout nearly all terrestrial ecosystems, but are also employed as a model in a great number of biomedical tests, and thus, a detailed understanding of their anatomy, ethology, morphology, and evolutionary history is critical to the development of proper experimental design and scientific advancement.

## Cross-References

- [Rodentia Cognition](#)
- [Rodentia Diet](#)

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## Rodentia Navigation

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## Synonyms

Acquisition of knowledge about spatial location; Spatial learning

## Definition

Rodentia navigation refers to how rodents find their way about (i.e., to find food or water, or to return home), to the many strategies and mechanisms underlying spatially guided behavior. Rodents have a varied range of strategies, some innate and others learned, that help them to navigate, and when faced with a specific spatial task, the one they choose will depend both on their sensorial capacities and on the nature of the stimuli that are available (for reviews see Rodrigo 2002; Tommasi et al. 2012).

## Background

Rodents can use different navigational strategies to locate a goal. Moreover, they can use a given strategy in a specific situation and under different conditions, use another one. The ability to find their way round their world is seen as of critical adaptive significance. Rodents can navigate using

information based on conspecifics (social influences), on their own movement (i.e., dead reckoning or path integration), on a single beacon or landmark, on multiple landmarks (which includes geometric encoding), or they can navigate using information based on the relationship of multiple landmarks (i.e., which is often called “a cognitive map”). Rodents can also use a visual matching strategy. In the last decades, there has been a great interest in discovering the navigational strategies they use, the conditions for using each strategy, as well as understanding the neural mechanisms of navigation. The most interesting results have been obtained with gerbils and with rats. Rodents are usually considered to be burrowing animals. They use their burrows for different purposes (e.g., to store food and to escape from perceived threats). A number of behavioral examples will be reviewed below.

### **Social Influences on Navigation while Foraging. A Case of Episodic Memory?**

Learning from other conspecifics is important for many animals and the spatial domain is not an exception. Rats begin their search for food from a central point, their burrow. This characteristic makes the exchange of information with their conspecifics crucial in order to determine where food is located.

In social interaction, the information is transmitted through olfactory cues. Moreover, rats have the ability to detect if their conspecifics have eaten recently as well as what they have eaten, which can lead to a preference for a particular food in a specific spatial location. Therefore, social interaction can facilitate where food is located (Galef 1988).

Social influences while searching for hidden food has been much studied recently using different arenas as well as the radial maze, where choices are determined by spatial location (Brown 2011). For example, a recent study by Bisbing et al. (2015) examined the conditions under which the spatial choices of rats searching for food were influenced by the choices made by other model rats. The results showed that the social influence could be very strong under at least some conditions; they support the claim

that the information that an animal acquires directly from its own experience with the environment (personal information) as well as the information provided by model rats (social information) are important. However, social information about the food location could influence spatial choices only when the social cues provided information that was not redundant with the information provided by other nonsocial cues. The clear implication is that the social cues and other kinds of stimuli seem to share the same or similar conditions, basic effects, and mechanisms. Both sources of information can be used in a flexible and adaptive way to guide choice decisions.

Are the previous examples a case of episodic memory, of memory based on conscious recollection? Could the rats remember the integrated “what,” “where,” and “when” information from specific past events? A very interesting approach to understand episodic memory in rats involves what is referred to as “source” memory (also called source monitoring). Source memory refers to memories about the conditions under which a memory was acquired (see Jonathon Crystal in the present issue).

### **Dead Reckoning or Path Integration**

Dead reckoning or path integration refers to the process by which animals keep track of their current position in relation to a known position by using internal vestibular and kinaesthetic information, that is, information based on their own movement. To do so, they continuously process information about changes in distance and direction at the different points of their path. For example, Mittelstaedt and Mittelstaedt (1982) placed mother gerbils and their pups inside a nest that was at the edge of a large circular arena. The pups were then caught and displaced to a hole in another part of the arena. They observed that the mother soon began to search for the pups and that as soon as she found them, picked each one up in her mouth, and went straight back to the nest. The gerbils performed equally well in conditions of total darkness and when the outward path had zigzags and detours. The best demonstration accomplished by dead reckoning comes from experiments on displacements. Mittelstaedt and

Mittelstaedt (1982) rotated the edge of the arena while the mother gerbil was in the hole, so that the nest was displaced. They observed that the mother gerbil returned to the place where the nest had been previously, demonstrating that the homing performance was not based on a cue present in the nest, but rather one based on path integration. They also observed that if the hole was rotated strongly while the mother and their pups were inside, the mother compensated for the rotation and headed straight back to the nest. However, if they rotated it or displaced it slowly sideways, the gerbil did not compensate and was disoriented. Similar results have also been obtained with golden hamsters. Although path integration can often be a very effective homing mechanism, it also has limitations. Both random and systematic errors often occur.

#### **Navigation Using a Single Beacon or Landmark**

Path integration tends to accumulate errors. Therefore, most rodents tend to use external landmarks to locate themselves or their goals. Preferably, they use proximal cues or beacons. Beacons are objects situated so near the goal that the animal simply has to perceive them in order to locate the goal. For example, Morris (1981) trained rats in a circular pool full of opaque water. Some of the rats could escape from the water by climbing up onto a black platform which was a centimeter above the level of the water. Under these conditions, the platform functioned as a beacon. The rats, good swimmers but not very fond of water, quickly learned to escape from the water by climbing onto the platform from different points of the pool. In the presence of a beacon, all the animals have to do is orient themselves and approach. For this kind of navigation, rodents only need to associate the stimulus-goal (or a stimulus that is close to the goal) with the reinforcer.

But landmarks are normally far away. Distal landmarks are fixed singular objects situated further away from a goal than a beacon is, but which are still close enough to provide some information about the distance to the goal. If they are asymmetrical, they can also provide directional information. Finding a goal (i.e., determining both

direction and distance) on the basis of landmarks is called “piloting” (Cheng and Spetch 1998). A very influential study was carried out by Collett et al. (1986), with female gerbils. The animals learned to dig for a sunflower seed buried in bedding, with a cylinder landmark placed at a fixed distance away. The gerbils learned to search in the correct location based on the landmark. To locate a goal based on a landmark, an animal has to perceive the distance and the direction of their position with respect to the landmark, to remember the distance between the landmark and the goal and its direction, and then to calculate the distance and direction from its position to the goal. The authors used a single symmetrical landmark in these experiments, which is not enough to pinpoint the location of a goal. Such a landmark only indicates the distance to the goal, but not the direction. Thus, the animals must have obtained directional information from another source. Given that the landmark was moved from trial to trial, but always at the same orientation with respect to the experimental enclosure, possibly the gerbils were able to obtain directional information from some other cues (like a door or a window). Moreover, Collett et al. (1986) carried out different tests in which they changed the size of a landmark and observed that these changes did not affect the place in which the gerbils searched for food. These results showed that gerbils do take into account the distance between the landmark and the goal, regardless of the landmark’s size.

#### **Navigation Using Information Based on Multiple Landmarks (Which Includes Geometric Encoding)**

In another experiment by Collett et al. (1986), it was shown that gerbils can use information about the relative position of several landmarks that maintained a constant relationship to a goal. Gerbils were trained in an arena, a sort of open field, to find hidden food in a place that maintained a fixed relationship with the position of two distinct and equidistant from the food landmarks. Following training (i.e., once they had learned to locate the food), a series of test trials were conducted. When one of the landmarks was removed, the gerbils searched in two locations whose directions



and distances corresponded to those between each of the landmarks and the goal during training. This suggests that the animals knew the direction and distance of the food from the landmarks, but that they did not know the identity of the landmarks. Each landmark was treated as if it could have been either of the two training landmarks. In another test, the distance between landmarks was doubled and the gerbils searched in two places defined by the direction and distance of the goal from each of the two training landmarks. These results show that the gerbils, at least the females, calculated the distance and direction of the food from each cue independently.

Cheng (1986) was the first author to present evidence that rats can use geometric information to locate a hidden goal. He trained male rats in a rectangular arena, where the two short walls of the box and one of the long walls were black, while the other long wall was white. In addition, distinctive visual patterns were placed in each of the box's corners, as well as other nongeometric cues, like different odors. Food was buried in one corner of the box, and the rats had to search for it. Although rats learned to search in the correct location for the food, they made frequent rotational errors searching in the corner diagonally across from the one where the food was hidden. The only characteristic that the target corner and the corner diagonal from it shared in common was having one long wall to the left and one short wall to the right, which implies that the information provided by the nongeometric sources of information to find the food location did not seem to be important. Cheng (see also Gallistel 1990) concluded that the rats used the geometrical framework of the box itself. Thus, what the rats learned was to search for food in the corner that had the long arm to the left and the short arm to the right. This would explain why the animals made rotational errors, since the corner diagonally opposite had the same properties. This experiment clearly shows that rats are sensitive to the geometrical relationships of a test environment. According to Cheng (1986) and Gallistel (1990), learning about geometric information (i.e., like the metric relations of distances and angles between a target place and the shape of an

apparatus) occurs in a specialized module, which is impenetrable to nongeometric information. However, Miller and Shettleworth (2007) have claimed that changes in the associative properties of the geometric cues are governed by the same principles that apply to more traditional stimuli. Following these authors, geometric and featural cues (or landmarks) are separate elements, so that, for example, each corner in a specific apparatus has its own combination of the two kinds of cues, which are learned simultaneously and can interact (i.e., therefore, blocking and overshadowing, cue competition designs, are expected to occur). Well-designed experiments and different authors have confirmed the two previous outcomes with male rats (for a review see Pearce 2009).

Interestingly, in a pioneering study by Williams et al. (1990) with geometric and nongeometric cues, in which males and females were employed, a surprising result was found. Williams et al. (1990) trained rats in a radial maze. After they had reached asymptotic performance, the rats were tested following various manipulations to the geometry of the room or to the landmarks. Provided the geometry of the room was unchanged, males' performance was unaffected by any change to the landmarks, but alteration of the geometry of the testing room disrupted their performance, even when the landmarks were still available for navigation. In contrast, females' performance was disrupted by rearrangement of the landmarks whether the geometry of the room was changed or not, although they were unaffected by the removal of the landmarks provided the geometry of the room was unchanged. A more recent study by Rodríguez et al. (2010) employed a different procedure to demonstrate rather similar effects. These results imply that a geometrical cue is more salient for males, while a landmark cue is more salient for females. A subsequent study by Rodríguez et al. (2011), where cue competition designs were used, confirmed this claim by showing that overshadowing is asymmetrical, both in males and in females. In males, geometry learning tends to overshadow landmark learning, but not vice versa; while in females, landmark learning tends to overshadow geometry learning, but not vice

versa. Moreover, these effects were not influenced by the females' estrus cycle.

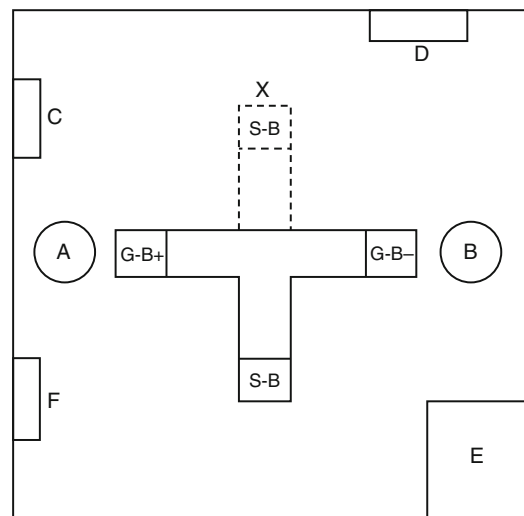
Subsequent work with male rats suggests that the relative salience of both cues (geometry and landmark) seems to be able to completely reverse the previous results (Kosaki et al. 2013; Mesa et al. 2017). Taken together, the clear implication of the previous studies is that the rules that govern learning about the shape of the environment (Cheng 1986; Gallistel 1990), or its boundaries (Doeller and Burgess 2008), are not necessarily different to those that govern learning about landmarks. Moreover, the study by Williams et al. (1990) was the first to show that the failure to consider sex as a variable while studying spatial learning can undermine the reproducibility of research findings. Hopefully this should be corrected in the future.

The distribution of two or more landmarks in space also has geometrical properties. There is evidence that rats can learn both the geometrical properties defined by a configuration of landmarks as well as the landmarks' identity (Greene and Cook 1997). Greene and Cook (1997) trained male rats in a modified open field in which a fixed configuration formed by six different objects was presented to the animals. The rats searched for food, which was hidden in the upper part of several poles. Following acquisition, several test trials were conducted: with the same objects but in different positions, with different objects although occupying the same positions of the training objects, and with the training objects in their normal position. The results revealed that the number as well as the identity and the geometrical configuration formed by the objects were important factors when searching for food. Greene and Cook (1997) claimed that the animals learned the geometry formed by the objects and such learning included the objects identity as well as their specific position within the configuration they formed.

### Navigation Using Information Based on the Relationship of Multiple Landmarks. The Cognitive Map.

Tolman (1948) was the first author to propose that animals form sophisticated representations of

their environment and called this a cognitive map. Tolman conducted many maze experiments. We know that rats typically solve maze problems by learning to approach the place where the goal is. But how is this place defined? For example, how does a rat solve a T-maze problem? (see Fig. 1). Usually, food is placed in one of the two goal-boxes (GB+) and not in the other one (GB–), and the subject has to choose between one arm and the other at the choice point. This is a spatial discrimination task, and traditionally it has had two alternative explanations (i.e., place vs. response learning — classical conditioning vs. instrumental or operant conditioning). According to Tolman (1948), the rat learns to associate the correct goal-box, GB+, with food and the incorrect one, GB–, with its absence, so that after a certain number of trials it chooses the correct goal-box and avoids the incorrect one. On the other hand, according to Hull (1943), what the rat learns is to execute a certain response instead of another at the choice point, because the first one is followed by food while the second one is not. In both cases, it can be said that the animal has been



**Rodentia Navigation, Fig. 1** A schematic diagram of a T-maze. S-B = start-box, G-B+ and G-B– the rewarded and unrewarded goal-boxes. A, B, represent distinctive objects immediately adjacent to the goal-boxes, and C, D, E, and F are various landmarks (doors, windows, tables) in the room. The dotted start-box and arm at X represent a new location for the start of a test trial. (After Mackintosh 1983 –with permission)

conditioned, although for Tolman it is a case of classical conditioning, “place” conditioning (the rats learn associations between places and rewards), and for Hull it is a case of instrumental or operant conditioning, “response” conditioning (one could say that the rats learn associations between responses and rewards).

The results have been generally in favor of place learning (classical conditioning), even when the maze is rotated 180°. Tolman regarded conditioning as the acquisition of new knowledge about the world, instead of the acquisition of new responses or new reflexes. For him, the rats arrived at the correct goal-arm by using a cognitive map of the experimental room. But Tolman never explained the specific properties of the cognitive maps and gradually his theory lost credibility (O’Keefe and Nadel 1978).

In their very influential book, O’Keefe and Nadel (1978) claimed that rats can learn the correct trajectory to reach a goal in a maze in two ways. The main one, “true spatial learning,” they label locale learning (or the “hypothesis of the cognitive map”). A rat solving a problem by locale learning would form a cognitive map of the environment where the maze is located, and of the specific location of the rewarded goal-arm within that environment. A crucial feature of their account was that O’Keefe and Nadel (1978) consider that such learning is nonassociative, that it happens in an all-or-nothing way, and that it implies the formation and readjustment of a complete, global, representation of the environment in response to novelty. They also claimed that this kind of learning is highly flexible and that the hippocampus is the responsible cerebral structure. The second way to approach a goal they termed guidance learning. Learning by guidance implies approaching one specific cue or set of cues (a particular color, shape, odor or texture in the rewarded goal arm, for example, or a particular landmark or configuration of landmarks just behind the correct arm). Guidance learning was regarded as one form of taxon learning, the other being orientation learning, which is basically the same as Hull’s response learning. Guidance learning is associative and can be regarded as a form of Pavlovian conditioning that does not depend on the hippocampus. It is also

less flexible than true locale learning. These two strategies, locale and guidance, proposed by these authors to solve spatial tasks were traditionally understood as only one form of learning, place learning. However, O’Keefe and Nadel (1978) emphasized that locale and guidance strategies are two fundamentally different and independent forms of learning, each of them controlled by a different cerebral structure, and that only the taxon strategy, the guidance one, is controlled by associative laws. However, the following decades have demonstrated that their claims were not always correct. The two main ways of learning (locale and guidance strategies) are not independent, they interact. The clear implication is that knowledge about spatial location can be acquired in the same way as knowledge about other relations between events (for reviews see Chamizo 2003; Leising and Blaisdell 2009).

A critical test of a cognitive map (according to O’Keefe and Nadel’s proposal) would imply that experience of the route A-B-C-D not only would give knowledge of the direction and distance between A and B, B and C, and C and D, but would also be sufficient to allow deduction of the distance and direction from A to D in the absence of any experience of the direct route from one to the other. Very few experiments have shown this with rodents, although one by Roberts et al. (2007) is worth mentioning. In the study by Roberts et al. (2007), male rats were allowed to travel selected routes along the internal alleys of a cross-maze that led from one distinctive end box to another. A critical feature of this set of experiments was that only the internal geometry of the maze could be learned and used to travel between one end box and another. After an initial exploration phase, rats were given novel routes and shortcut tests that involved unknown peripheral alleys, that the rats had not used before. The animals chose the correct novel path or shortcut significantly above chance. These findings suggest that rats were able to compute novel routes and shortcuts within the maze on the basis of limited experience with the internal geometry of the maze. This study further shows that rats could link a place with a number of other locations when allowed to travel a single linking pathway.

### Navigation Using a Visual Matching Strategy.

An alternative account to the cognitive map hypothesis has shown that geometry can be less important than initially thought in rats. It refers to a snapshot (mental image) account of rat navigation, which is most important when animals are at a goal or near it (Cheung et al. 2008). According to Cheung et al. (2008), search behavior can be explained by assuming that the animals take a snapshot at the goal or near the goal. Then, on subsequent journeys to the goal, they will move in a way to minimize the difference between the memorized image and its current view. Cheung et al. (2008) proposed that mental snapshots are global in nature and involve a panoramic view of the entire environment; they include information about the spatial relationships between the different elements (i.e., distant from the goal landmarks or other featural cues) they contain. All that is required for an animal to be able to find a goal is that it can see at least a portion of the elements contained within a specific snapshot. This procedure based on the coincidence of images does not require an explicit learning of the landmarks or of the spatial geometry of the environment in which the goal is located. These cues are implicitly contained in the panoramic images taken by the animal and their relative salience will determine if the differences between the images perceived by an animal will be dominated by geometry or by features or landmarks. Subsequent research has revealed that mental snapshots can also refer to local cues (Gilroy and Pearce 2014).

The term “cognitive map” is nowadays used in many ways, so that depending on the author it can mean very different things. Following Mackintosh (2002) this term has lost explanatory value. What is needed instead is to ask what are the mechanisms underlying any particular example of spatially guided behavior. Many questions remain to be answered.

### Cross-References

- ▶ [Bennett G. Galef](#)
- ▶ [Blocking](#)
- ▶ [Classical Conditioning](#)

- ▶ [Cognitive Map](#)
- ▶ [Dead Reckoning](#)
- ▶ [Discrimination Learning](#)
- ▶ [Episodic Memory](#)
- ▶ [Foraging](#)
- ▶ [Geometric Encoding](#)
- ▶ [Hippocampus](#)
- ▶ [Jonathon Crystal](#)
- ▶ [Landmark](#)
- ▶ [Learning](#)
- ▶ [Morris Water Maze](#)
- ▶ [Open-Field Test](#)
- ▶ [Operant Conditioning](#)
- ▶ [Overshadowing](#)
- ▶ [Place Versus Response Learning](#)

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## Rodentia Sensory Systems

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## Synonyms

[Perception](#); [Sensation](#); [Stimulus response](#)

## Definition

Sensory systems are the physiological modalities by which individuals engage with the world. The major systems include audition, vestibular, gustation, olfaction, touch, and vision.

## Introduction

Across the order Rodentia are a variety of different mammals which use their sensory systems to interact with the world. These sensory systems vary in complexity and importance depending on the evolution and lifestyle of the animal. Rodents are diverse in both physical size and the environment in which they live. They are dependent on highly specialized and adapted sensory systems to engage with their environments and to survive.

Rodents live in wet and dry, hot and cold, aboveground and subterranean, and light and



dark environments. Across these environments, they live in either solitary conditions or large social groups (Feldhamer et al. 2015). In each of these contrasting environments and climates, different sensory systems assume the dominant role in environment navigation and survival, rendering others lesser or completely unused. A vast majority of research on physiology and function of sensory systems has been conducted on rodents due to this diversity, their small body sizes, short lifespans, and links between sensory systems and survival.

One relatively universal feature of the major sensory systems is the topographical organization of information in the environment being maintained within the sensory pathway. This is maintained by areas of higher and lower resolution on one feature of sensory objects that are being maintained within the system. For example, in the tactile system, touch for different parts of the body is relayed to adjacent locations in the brain. In the auditory system, frequency content is organized from low to high frequency in the cortex. In each sensory system, this cortical gradation starts at the receptor cells and is maintained along the entire pathway from receptor, to neurons, to the brain. The relationship between objects in the real world is maintained in stimulation of receptors and activation of the animal's cortex.

Each of the five major sensory systems (hearing, taste, smell, touch, and vision), as well as the vestibular system, will be discussed in this chapter. The range of acuity (or sensitivity) of these sensory systems differs systematically across different evolutionary contexts within the order Rodentia. The systems that prove the most biologically adaptive for each rodent species will have heightened acuity relative to other sensory systems. Some of the functional roles of the sensory systems include mate attraction, courtship, territory defense, and threat signals. These will also be discussed within the contexts of different major systems and in further detail in the Rodentia Communication chapter in this edition.

### **Audition**

The auditory system is the sensory system that is responsible for hearing. The auditory system in

all mammals, including rodents, is comprised of several different hearing structures located in the outer, middle, and inner ear. These structures function to receive sounds from the environment, amplify or suppress their intensity, and convert them into neural signals that can be interpreted in the brain. These major structures include the tympanic membrane, ossicles (malleus, incus, stapes), and the cochlea. The cochlea is a structure containing outer and inner hair cells and the basilar and tectorial membranes, which together convert sound into an electrical signals (action potentials) through mechanical movement. Action potentials are then transferred to the central auditory system, allowing for perception of frequency, duration, location, and meaning of sounds. Along the entire central auditory pathway, this information is coded tonotopically and organized in a low to high gradient, with low-frequency information in a different spatial location along the pathway than high-frequency information.

Methods of studying auditory function in rodents include observational studies of animals in the wild responding to sounds, as well as laboratory studies of the fine auditory resolution abilities of individual subjects. Skinner boxes, a behavioral apparatus used to study animal perception, can be used to train awake and behaving animals to respond only in the presence of a sound. Physiological tests, such as the auditory brainstem encephalographic response and distortion product otoacoustic emissions, can be conducted in anesthetized animals to estimate hearing abilities. These tasks measure the responses of the auditory system to sounds but are less sensitive than behavioral methods (Dent et al. 2018).

Audition is an important sensory system for rodents because signal transduction, such as in the case of communication signals, and receipt are not dependent on the presence of light in the environment. Across rodents, production of acoustic signals is diverse because individual animals are able to modulate the frequency range, duration, and/or temporal characteristics to change the meaning of their vocalizations. The auditory system needs to be tuned to these

changes for the system to be effective in communicative settings. The range of hearing sensitivity is represented by an audiogram, showing acuity in absolute thresholds across frequencies (see Dent et al. 2018 Fig. 4.1 Pg 74). In rodents, this range is highly variable, with some having much better high-frequency acuity (e.g., laboratory mice (*Mus musculus*) hearing spans between 1 and 100 kHz), while other rodents are more sensitive to lower frequencies (e.g., prairie dogs (*Cynomys*) hearing spans from 46 Hz to 26 kHz). The peak sensitivity of the species can also reflect the physical factors in the environment in which an animal lives and how that environment (e.g., high vegetation) affects signal propagation.

The auditory systems of rodents are tuned for detection of communication signals important for survival and reproduction. One classic example in rodents is the ability to detect an alarm call. California ground squirrels (*Otospermophilus beecheyi*) and Belding's ground squirrels (*Urociellus beldingi*) produce categorically distinct flee vocalizations for aerial predators and alerting vocalizations for terrestrial predators and conspecific intruders (Mateo 2010). The vocalizations that are emitted by squirrels must have specific features that make them easily discriminated from non-alarm signals and must also be able to be heard and understood by conspecifics in order to be effective. However, complex sound perception in rodents is not limited to interpreting alarm signals. Similar to categorical speech perception in humans, chinchillas (*Chinchilla chinchilla*) can be taught to discriminate a /d/ from a /b/ from a /g/ sound. Auditory signals also play an important role in rodent foraging behavior. Eastern gray squirrels (*Sciurus carolinensis*) eavesdrop on the non-alarm calls of nearby birds to know when to engage in food-seeking behaviors or to know when to engage in vigilance behaviors to a predator (Lilly et al. 2019). For a more complete review of Rodentia Communication, see *Kobrina and Burke* in this volume.

The auditory systems of rodents are highly tuned sensory systems that are important for communication, mate selection, play behavior, foraging, and survival. Loss of effective utility in this system, as in the case of anthropogenic

(human-caused) noise, can lead to detrimental consequences in any of these functional roles of this system.

## Vestibular

The vestibular system is the fundamental sixth sense that provides information about linear motion, acceleration, equilibrium, and balance (Bradbury and Vehrencamp 2011). Major organs of the vestibular system are the semicircular canals, the utricle, and the saccule. The three semicircular canals are important for detecting angular accelerations of the head, while the utricle and saccule are important for detection of linear velocity. Rodents utilize this system primarily for navigating their environment by integrating information about their own anatomy with the mode of locomotion and agility. This sensory system is crucial to maintaining normal function, but it is often ignored in humans until it becomes dysfunctional.

The vestibular system is evaluated in the laboratory based on a variety of different behavioral phenotypes. For example, animals with vestibular problems often engage in stereotypical circling behaviors, have difficulty correcting their body position when dropped, and struggle when being suspended in the air by their tail. The vestibular system can also be evaluated by studying the anatomical structures of several different species and comparing them to see whether there are evolutionary differences in the development of this system.

The vestibular system structurally has not changed much over evolutionary time, but slight differences in the conformation of the organs do occur across species. In several rodents the semicircular canals show evidence of differences in anatomical structure that is based on the primary mode of locomotion of the subject. For example, northern flying squirrels (*Glaucomys sabrinus*) glide for long distances in the air, which requires an intact, functional equilibrium system and involves balancing body weight at a constant velocity (Pfaff et al. 2015). Across *sciurids*, one of the major families of squirrels that is characterized by different types of locomotion, arboreal living tree squirrels (*Sciurinae*),

terrestrial living ground squirrels (*Xerinae*), and gliding squirrels (*Pteromyinae*) all show differences in the angle of the semicircular canals. These canals are typically located orthogonally, or in 90 degree angles to each other, so the width between them, diameter and lengths of the canals, and the angles of the planes can be characterized. Ground, flying, and gliding squirrels all have slightly different semicircular canal positioning and sensitivities, likely linked to the difference in major mode of locomotion and to avoid overstimulation.

The vestibulo-ocular pathway is an open-loop system in which a vestibular signal triggers compensatory eye movements (or a spontaneous nystagmus) to stabilize gaze in the absence of sensory feedback. Eye movements can be traced as a proxy to evaluate the efficiency of the vestibular system by characterizing the vestibulo-ocular reflex (VOR). In laboratory mice, the VORs have been measured in response to a vestibular sensory cue (e.g., being tilted into different angular planes corresponding to the semicircular canals). Often the compensatory mechanisms of the VOR are quantified to try to understand the level of vestibular impairment.

Vestibular functioning has been evaluated in laboratory rats as it relates to their gravity perception (Jamon 2014). A tail-lift reflex and an air-righting reflex are two types of antigravity reflexes regularly assessed in lab rats, as well as lab mice. The tail-lift reflex is where rodents are lifted by their tail, and the amount of time it takes to right their body position, as well as the angle of their body in space, can be measured. The air-righting reflex involves dropping the rodent from a suspended height in the air and seeing if it can correct its body position before landing on a padded platform. In subjects that experience a vestibulo-spinal deficit, there are usually gross alterations in spontaneous motor activity and motor reflexes that facilitate the identification of animals suffering from vestibular problems. These problems can then be quantified by measures like the amount of time it takes an animal to correct its body position in space.

The vestibular system is very important to avoiding predation. Because rodents are prey

species, small changes in their vestibular function could be the difference between effectively fleeing a dangerous situation and being captured and killed by a predator.

## Gustation

The gustatory sensory system is responsible for the perception of taste. Rodent gustation has been studied in the context of their food acquisition and to understand the specifics of how mammalian taste receptors work. The major sensory organs of the gustatory system include the tongue, papillae, and salivary proteins. The process of digestion begins in the animal's mouth, where food is pushed around by the tongue, crushed with teeth, and moistened with saliva. Salivary proteins begin the process of digestion of food within the animal's mouth. The salivary proteins differ based on the main dietary choices that animal makes and can play a critical role in future food preferences. On the surface of the tongue are papillae, which are special structures, most of which contain taste buds. Taste buds are sensory organs responsible for sending information about the taste and type of food an animal consumes to the cortex. In rats (*Rattus norvegicus*), the gustatory cortex has been mapped out indicating that there are distinctive spatial patterns with some overlap in the four classic taste qualities of salty, sweet, bitter, and sour foods (Accolla et al. 2007).

Taste is an important sense because discrimination between nutritious and toxic sources of food can be the difference between life and death. Wild rodents living in highly populous urban environments often face this type of risk and need to be sensitive to gustatory, olfactory, and visual cues in potential food sources to survive. For reproduction, the ability to pick out nutritious foods is correlated with larger body sizes and a better ability to produce strong vocalizations, leading to an increased likelihood to be selected for mating (Bradbury and Vehrencamp 2011). Whether all rodents' taste receptors can discriminate between all of the different major types of tastes is unclear, yet there does appear to be spatially separate cortical representation for these different tastes in some rodents (Accolla et al. 2007). One way to examine this

behaviorally is using a flavor avoidance learning task. Norway rats (*Rattus norvegicus*) and golden hamsters (*Mesocricetus auratus*) categorize different tastants into the four major groups of sweet, sour, salty, and bitter. Their inherent preference for, or avoidance of, particular tastants can be exploited to encourage them to ingest particular food sources based on their nutritional value. This is also a useful cue for them to attend to in order to avoid potential chemicals. For example, differences in dietary choices are one factor responsible for why pocket gophers (*Thomomys umbrinus*) are more tolerant of bitter-tasting foods than squirrels, chipmunks, and most laboratory mice and rats (Hani et al. 1998).

Taste has been studied in the lab using behavioral and physiological methods. In an operant task, rodent feeding behavior can be assessed by quantifying the number, preference, and size of feeding events for different types of diets (e.g., bitter versus sweet) (Tordoff 2007). In the wild, bitterness is usually a cue to toxicity, but this association must be learned. Saliva can also be collected and evaluated to see whether a physiological change occurs in response to dietary choices. Preference studies can reveal how a subject may respond to different dietary options and whether there are specific food choices a subject would rather consume than others (or whether one food choice is particularly aversive). Flavor avoidance learning is one type of behavioral test that has been conducted to show how rodents are able to behaviorally categorize different types of tastes (Parker 2014).

In the laboratory, taste preferences have been explored in rats to show that they prefer sweet sucrose solutions to bitter quinine solutions (Torregrossa et al. 2015). This preference has also been shown in golden hamsters (*Mesocricetus auratus*), with differences across the sexes linked to progesterone levels (Zucker et al. 1972). The preference for sweet solutions is strong in laboratory mice (CBA/CaJ) that are more motivated to engage in a behavioral task when given a chocolate Ensure<sup>®</sup> protein shake as reinforcement than any other flavor of Ensure<sup>®</sup> or water (Radziwon et al. 2009).

Taste is one of the most crucial sensory systems for survival because finding appetitive food sources and discriminating them from aversive food sources can be the difference between ingesting poisonous/toxic or nutritious sources of food.

## Olfaction

The olfactory system is the sensory system that is responsible for the sense of smell. In rodents, the olfactory system is composed of two separate systems: the main olfactory system and the vomeronasal system (VNS; also known as the accessory olfactory system). The main olfactory system processes chemosignals in a variety of behaviors such as mating, feeding, predation, and aggression, while the VNS is used for pheromone-based communication with conspecifics. Arguably, the olfactory system is the most critical sensory system for survival in rodents because olfactory cues can have effects on mood, behavior, hormonal status, or sexual arousal of the recipient. In addition to these effects, rodents are obligate nasal breathers, where the upper air passage meets the slightly elevated epiglottis in the nasopharyngeal areas, thereby not sharing a common pathway with food in the oropharynx (Negus 1927). The biological advantage to the rodents then is that the animal may continue to eat or swallow without pausing to sniff for potential predators (Gautam and Verhagen 2012).

Chemical signals have advantages over other types of signals because they remain in the air or on the surface for prolonged periods of time, even after the signaler has left. This allows a rodent to depart from a potentially dangerous situation and enables them to communicate with others (Bradbury and Vehrencamp 2011). Rodents use chemical signals to mark territories and for sexual selection. These signals remain in the environment for prolonged periods of time which allows animals to be cryptic when signaling to avoid predation. The olfactory sensory system is characterized by the detection of a chemosignal (odor or scent), or any combination of chemicals emitted, that is detected by the olfactory receptors (i.e., odorant receptors) located at the olfactory

epithelium. The information obtained from the environment is received by the olfactory receptors and transmitted through the sensory neurons to the olfactory cortex. The olfactory system is highly related to taste perception due to the role of retronasal olfaction in taste. Substances released from food and drinks inside of the mouth form the retronasal odor as they travel to the olfactory epithelium.

Olfaction has been studied *in vivo* by using odorants to stimulate olfactory receptor neurons. Behaviorally, discrimination studies have been conducted to evaluate whether rats can tell different odorants apart (Gautam and Verhagen 2012). Aside from laboratory discrimination studies, wild rodents can be examined for their behavioral or physiological response to different types of odorants such as urine from a conspecific.

Studies on golden hamsters and meadow voles (*Microtus pennsylvanicus*) have reported on the responses of individuals to olfactory cues from conspecifics and heterospecifics (Ferkin et al. 2010). These chemosignals help rodents respond to the social context, age, and conditions of senders and receivers. Just like in other modes of communication, olfactory signals are most effective if they are able to be sent by a signaler and then detected and interpreted by a receiver. The behavioral responses of rodents to chemosignals have revealed that scent-marking signals convey information to the receiver about the sender's state, phenotype, and genotype. These signals are often individually distinct. The subsequent response of the receiver is dependent on their cognitive abilities as well as a desire to increase their survival and fitness.

One example of a rodent that uses olfactory cues to avoid predation is the California ground squirrel (*Otospermophilus beecheyi*). These squirrels have a specific, innate, defensive odor response to avoid the scent of their natural predator, the Pacific rattlesnake (*Crotalus oreganus*). This odor is specific to the predator species and does not generalize to all snakes (such as the Pacific gopher snake, *Pituophis catenifer catenifer*, another snake that they may encounter but is not their natural predator). Rats also use a combination of olfactory cues and social learning

to learn about the location and identity of food sources and to distinguish between potentially dangerous and bountiful new sources of food. Rats will sniff a conspecific and modify their food choice behavior in response to the olfactory cues present on another rat.

Olfactory cues can also be important for individual recognition. In mice, major histocompatibility complex (MHC) proteins contain hundreds of alleles which reflect chemical individual identity. These MHCs are in sweat, urine, and other secretions which enable individuals to use their olfactory system to avoid inbreeding with close relatives, abort pregnancies when threatened by strange males, identify kin with which to cooperate, or learn to identify specific individuals in groups (Bradbury and Vehrencamp 2011). As such, in house mice (*Mus domesticus*), intruders are met with aggression if they do not have the proper olfactory marks.

Lifestyle choices play a role in how rodents respond to different chemosignals. For example, prairie voles (*Microtus ochrogaster*), a socially monogamous species, can detect and discriminate between different individuals' chemosignals and show partner preferences for familiar opposite-sex conspecifics over novel opposite-sex conspecifics (Blocker and Ophir 2016). In contrast, montane voles (*Microtus montanus*) and meadow voles (*Microtus pennsylvanicus*), two polygamous species, showed partner preferences for novel opposite-sex conspecifics over familiar opposite-sex conspecifics (Gobrogge and Wang 2016).

The olfactory system's far-reaching implications in mating, individual recognition, communication of defense signals, and foraging push it to the top of the list as one of the most important sensory systems across the order Rodentia.

## Tactile

Touch is a universal sensory system that is important for social grooming, communication, and bonding. Tactile information in humans has the largest sensory receptor sites in the hands; however, in rodents, information received anywhere on the body can convey crucial information as to the location of a potential threat, or social cues,



such as play or aggression. In rats, the somatosensory cortical areas devoted to the representation of the nose, whiskers, mouth, forepaw skin, and whisker-like hairs under the rat's wrists have the greatest sensory representation of all other body parts with more sharply defined receptive fields (Hermer-Vazquez et al. 2004).

Whiskers are one type of a specialized touch organ that, when deflected, give information about the direction, velocity, and duration of vibrational movement, giving an animal information about the location, size, texture, and other tactile features of objects. In mice, the quantity of the cortex dedicated to the whiskers is greater than that of the paws, with each whisker sending about 100 myelinated fibers via the trigeminal nerve to the somatosensory cortex. The mapping of the mouse whisker barrels in layer IV of the cortex has 1500–2500 neurons, and each barrel corresponds precisely to the number and arrangement of whiskers on the face.

One way touch is measured in rodents in the laboratory is through physiological studies that measure cortical responses to tactile stimulation. For example, in rats evoked response latencies in the cortex can be measured in response to whisker stimulation (Shuler et al. 2001). Cells responsible for touch sensation in the forelimbs of squirrels have been mapped in the cortex using histological analyses (Thorington Jr. et al. 1997). Observational studies in several species of rodents have studied the behavioral responses of animals to tactile stimulation from a conspecific. For example, individual rats attempting to engage in play will provide a categorically different sequence of tactile stimulation to a receiver in order to signal their intentions (e.g., huddling and rump biting).

Rats and mice also have specialized tactile neural mechanisms for tickles and itches. In laboratory mice whose itch neurons in their spinal cord were eliminated, the injection of a chemical that makes them scratch led to no itching behavior. In rats, cells in the trunk area of the somatosensory cortex of their brains fire at higher rates when they are being tickled. Tickling also leads to higher instances of play behavior in rats, suggesting that tactile stimulation similar to this by

conspecifics may be important for communicating intentions to play in rats.

Mating signals are also usually visual, olfactory, and tactile in rodents. Olfactory signals can be slow, and auditory signals can be too conspicuous; therefore, tactile stimulation can provide the quickest and most effective means of communication of intention to mate. For example, in mice and rats, prior to mating, the animals will engage in active genital sniffing, climb on top of a potential mate, and brush up against them.

The tactile sensory system in rodents has widespread implications for navigating social situations and environments. Effectively interpreting these signals can be the difference between engaging in social play or a potentially aggressive social situation and shutting away from a predator that is nearby.

## Vision

The visual system is one of the most largely studied sensory systems, from simple perception of things like spots and stripes, or discrimination of lines of different orientations, to color perception. The major sensory organs involved in the visual system include the eye, the optic nerve, and the primary olfactory cortex. Within the eye are highly complex layers of cells that reflect, refract, and detect light from the environment which is then translated into neural signals to be interpreted in the brain. The small body size of many rodent species limits the visual resolution at long distances, and their color vision is often less precise than black and white detection. This, coupled with the need for a direct line of signal transmission, makes visual stimulation a closer range sensory system for rodents.

In the laboratory, several aspects of vision have been studied in rodent models. For example, depth perception has been evaluated in golden hamsters using visual cliff paradigm, similar to what is used in human infants, where subjects are faced with what appears to be the edge of a cliff with a patterned floor and if they can perceive depth differences, they will not go past the edge (Keselica and Rosinski 1976). Object identification can be tested in a visual open field test where food items are scattered around a grid and subjects

are tasked with locating the food objects. Lesion studies have been conducted to evaluate the role of different visual associated areas in the brain in specifying the location and distance of an object.

The acuity of the visual system in rodents varies widely. For example, visual acuity in the naked mole rat (*Heterocephalus glaber*) is considered poor because of their degenerated eye and optic nerve (Crish et al. 2006). Naked mole rats typically reside in subterranean burrows that have poor visual cues due to being underground, making vision a less crucial sensory system for navigating their environment and survival. However, anatomical studies in naked mole rats have revealed that there are intact neural connections to major visual subcortical regions in the brain similar to seeing rodents. This suggests that, while blind to tasks like identifying whole objects, naked mole rats may still be able to detect differences between light and darkness (Crish et al. 2006).

Rats are nocturnal, which means that they are more active at night. Cones, the sensory cells in the eye responsible for color vision, are less active in the dark. Rods, responsible for black and white detection, are more active in the dark. The retina in rats is rod-dominated, but rats also have two types of cones corresponding to different wavelengths along the electromagnetic spectrum (Walls 1934; Jacobs et al. 2001). The characterization of rats as dichromats means that they can see only two wavelengths (blue and green), but not red. Some research suggests that a small proportion of cones is also sensitive to ultraviolet light (Jacobs et al. 2001). Rats also use environmental geometry and patterns as a cue to the location of food sources. Lab rats searching for food that is located on top of a vertical pole are able to use a painted pattern on the pole as a cue, but can also use the geographic spatial location as a cue to reliably determine the source of food (Vorhees and Williams 2014).

The visual system plays a crucial role in food acquisition, mating, and navigation in rodents. This system needs to be intact, especially in terrestrial environments, to effectively evaluate whether a situation is safe or dangerous.

## Conclusion

Rodents are highly social creatures that rely on complex integrated sensory systems for survival. They are often prey species, which makes it essential for them to utilize information that is obtained from several of their senses to safely engage with their environment, conspecifics, and heterospecifics. The biological advantages of highly specialized sensory systems enable rodents to utilize the auditory, gustatory, tactile, olfactory, visual, and vestibular information to engage with their environment, other conspecifics and heterospecifics, and to avoid predation. These systems are highly variable in sensitivity across species but are highly adaptive to the primary living and social environment of the species.

## Cross-References

- ▶ [Adaptedness of Behavior](#)
- ▶ [Affiliative Behaviors](#)
- ▶ [Agonism and Social Status](#)
- ▶ [Agonistic Behavior](#)
- ▶ [Alarm Calls](#)
- ▶ [Alternative Reproductive Tactics](#)
- ▶ [Associative Learning](#)
- ▶ [Auditory Processing and Perception](#)
- ▶ [B.F. Skinner](#)
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- ▶ Female Defense Polygyny
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- ▶ Genetic Compatibility/Histocompatibility
- ▶ Grooming
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- ▶ Hormones and Behavior
- ▶ Huddling
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- ▶ Taste Aversions

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## Roger K. Thomas

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Roger K. Thomas, Age 69 in 2008

## Birth to High School Graduation

Thomas was born on September 14, 1939, in Americus, Georgia, Sumter County. Sumter County is also the lifelong home of USA

President Jimmy Carter. Due to the relative brevity of this bio sketch, family history will be omitted except to note (a) should they live until October 14, 2020, he and Anne Easley Thomas will have been married 60 years and (b) that his ancestors include several Patriot soldiers who served in the American Revolutionary War.

Thomas changed schools nine times from grades 1 through 8. However, he attended all high school years at Glynn Academy, a public high school founded in 1788 in Georgia's Glynn County. Glynn Academy is notable (a) for its original charter that provided for the education of girls and boys and (b) for being the second oldest, continuously operating public high school in Georgia and the fifth oldest in the USA.

Thomas enrolled at Georgia Southwestern College (GSC) a 2-year college in Americus, GA in 1957. He earned an Associate of Arts degree in 1959 with the highest-grade average among male students. During the two years at GSC, he worked from September 1957 until June 1958 for a funeral home that also provided ambulance services. Among his experiences were seating attendees at memorial services, driving a hearse, driving a family car, witnessing the closing of graves as required by law, and occasionally assisting the mortician. His most exciting ambulance run was a full emergency run from Americus, GA to Emory University Hospital in Atlanta, GA, a distance of 125 miles. Thomas' role was limited to helping to load and unload the patient; a cardiologist and a nurse attended the patient during the run.

From June 1958–May 1959, Thomas was radio announcer for a station that operated from official sunrise to sunset. He worked from mid-morning Saturday to sunset and all-day Sunday. After noon on Saturdays, he was alone unless an engineer was needed. Thomas read the news, weather, etc. from Associated Press, read commercials or played tape-recorded commercials, and played records. On Sundays, one of the local African-American funeral homes sponsored live music from a studio, which Thomas could observe from his broadcasting booth. The music was mostly a *capella* singing with infrequent piano or guitar accompaniment. These were amateur

musicians chosen by the funeral home, rarely the same from one week to the next. Thomas expressed regret that he lacked the foresight to record and preserve that truly authentic, African-American gospel music.

In the summer of 1959, Thomas enrolled at the University of Georgia (UGA). UGA is the oldest chartered state university in the USA (1785); however, the University of North Carolina enrolled students first. UGA was on the quarter system when Thomas arrived, and Thomas completed all requirements for the B. S. degree in Psychology Winter Quarter, 1961, which coincidentally was the quarter when UGA's first two African-American students, Hamilton Holmes and Charlayne Hunter, were enrolled under a federal court order. They had transferred as Juniors and both graduated in May 1963.

Holmes was Emory University's first African-American medical student. He became an orthopedic surgeon in Atlanta and Associate Dean of the Emory University Medical School. Hunter's degree was in Journalism. Her employment began with *The New Yorker* and later as CNN's correspondent in South Africa. Calvin Trillin (1964) chronicled some turbulent events associated with UGA's integration. Later, Hunter-Gault (1992) described her experiences. First Hunter-Gault and later Hamilton Holmes reconciled with UGA. In 2001, UGA renamed an historic campus building, the Holmes-Hunter-Gault Building.

## Graduate Education

Thomas's enrollment in Graduate School was unplanned and fortuitous. One of his teachers in his next-to-last undergraduate quarter, Robert Travis Osborne, did not post grades. Osborne told the class that if one wanted her/his grade, she/he would have to come to his office or wait to receive it in the mail. Osborne was Director of UGA's Guidance and Counseling Center where his office was located. Almost by chance, and while his wife waited in their car to go home for Christmas, Thomas went to get his grade. When Thomas returned to the car, Osborne had assured him he would be accepted

to Graduate School and he would immediately have part-time employment equivalent to a graduate assistantship in the Guidance Center.

Osborne supervised Thomas's M.S. thesis, *Intelligence and Socioeconomic Status: A Longitudinal Study with the Wechsler Intelligence Scale for Children* (WISC). Osborne had a grant from the Educational Testing Service to conduct a longitudinal study of IQ test scores, and Thomas was one of the field test examiners pre- and post-first grade.

Informally, Thomas saw evidence suggesting that attending first grade reduced IQ test score differences among socioeconomic classes. David Wechsler visited Osborne, and Osborne asked Thomas to describe his research to Wechsler. Wechsler told Thomas he would not find anything, because their standardization procedures were too good. Wechsler was wrong; Thomas did find reduced differences among socioeconomic classes on some subtests of the WISC. Thomas's M. S. degree was conferred in 1963.

Thomas's interest turned to the study of brain and behavior, and his new Major Professor was Lelon J. Peacock. Osborne was gracious about Thomas's change, and they remained friends until Osborne died in 2013, 5 months short of age 100. Thomas was Executor for Osborne's Estate, which was gifted entirely to UGA (\$5,375,000.00).

Word limits prevent describing Peacock adequately as a mentor, but he challenged his students unrelentingly and compelled them to be self-sufficient. Peacock hired Thomas as research assistant on his NSF grant. Peacock and a UGA electronics shop partner invented a complex electronic apparatus to measure the activity of rats (see Peacock and Williams 1962). On Thomas's first day as research assistant, Peacock handed him an electronics diagram scrawled on butcher paper and told Thomas to "build it." Thomas knew nothing about electronics. Peacock told him to buy the *Radio Amateur's Handbook* and learn chapter 1. That was the only help Peacock gave. Daily when Peacock checked on Thomas laboring away, he would mutter "it won't work." It worked well enough, although Peacock had to give it a few tweaks. Thomas's



Ph.D. dissertation was *Immediate and Subsequent Effects of Brain Damage in Rats*, and the Ph.D. degree was conferred in 1965.

### Postdoctoral Fellowship

In September 1965, Thomas began a postdoctoral fellowship in the interdisciplinary Center for Neurobiological Sciences in the University of Florida's Medical School. Thomas's home department was Neurosurgery. His primary mentor was Frederick A. King, a physiological psychologist, and his secondary mentor was Lamar Roberts, Chief of Neurosurgery. Thomas's main research compared squirrel monkeys with frontal lobe lesions to control monkeys. Performances were similar for all of the lesioned monkeys but differed from the control monkeys in nearly identical classical and instrumental conditioning tasks. A tone signaled the possibility of a mild foot-shock. In the classical task, the experimenter determined when shock was delivered. In instrumental conditioning, leg flexion as soon as the tone was presented enabled the monkey to avoid foot-shock. With both tasks, the lesioned monkeys responded significantly faster than the control monkeys, suggesting that frontal lobe lesions resulted in release of inhibition.

In 1966, Thomas was chosen one of 10 "outstanding young psychologists" by the American Psychological Association. The award was a trip to Moscow to attend the International Congress of Psychology. Seven of the 10 were Ivy Leaguers; one was from Stanford, and one was from Canada. Thomas guessed that it likely helped his receiving the award that he had passed a proficiency examination in Russian translation as one of his Ph.D. degree requirements.

### Career at the University of Georgia (UGA)

The award might have helped gain Thomas an invitation to apply for a tenure-track position at UGA in 1967. He was hired in September 1967, retired in 2002 as Professor Emeritus, and

remained at UGA until he vacated his office in July 2018.

### Teaching

Including 19 years as administrator, Thomas rarely taught more than one class per quarter or semester. He enjoyed teaching and received teaching awards, especially for his graduate classes, "Neuroanatomy for Behavioral Scientists" and "History of Psychology." More information about the range of classes taught as well as the names of mentored graduate students (27 M.S. and 21 Ph.D. degree students) may be seen on Thomas's UGA website: <http://psyc.franklin.uga.edu/directory/people/roger-k-thomas>.

### Research

Thomas's UGA website also shows that currently (January 2019), he has 120 publications and 120 regional, national, and international presentations; many are downloadable as PDFs. His research began mainly in brain and behavior, transitioned to animal cognition, and finished mostly with research in history of psychology. What Thomas believes to be his two most important articles (Thomas 1980, 1996) were theoretical-methodological.

In the context of assessing the evolution of intelligence, Thomas (1980) proposed that fundamental to intelligence was learning ability. He presented an eight-level hierarchy of learning abilities ranging from sensitization to high-level relational concepts. In Tables III and IV, he showed how relational concepts can be expanded logically to challenge even the most intelligent humans. Thomas also proposed that any and all learning tasks used with human or nonhuman animals in the past or future could be reduced to levels or combinations of levels in his eight-level hierarchy. Finally, he proposed that tasks be adapted to each species so that failure can be less likely attributed to contextual variables such as sensory, motor, and motivational variable differences as well as environmental variables (such as light, temperature, humidity, etc.) that might differentially affect the *performances* of different species and misrepresent their learning abilities.

Thomas (1996), "Investigating cognitive abilities in animals: Unrealized potential" was in a

special issue of *Cognitive Brain Research*. The cover was adapted from an illustration in his article, his article was first in the issue, and the editors singled it out in the introductory editorial as follows.

Roger Thomas describes how the various animal models of cognition function relate to each other, thereby providing a framework in which most of the following papers can be discussed. (T. Steckler & C. D. D'Mello, p. ix)

Thomas believes his best laboratory research involved tasks involving concepts such as oddity in conditional discrimination contexts. Thomas and Kerr (1976) tested squirrel monkeys using trial-unique oddity discriminanda (also known in this case as the *simultaneous discriminanda*). When oddity problems were presented on a white tray (one of two *successive discriminanda*), white signaled that the odd discriminandum was the correct choice, but on a black tray (the other successive discriminandum), black signaled that either of the nonodd discriminanda were correct choices. Burdyn and Thomas (1984) went further and successfully tested squirrel monkeys using concepts as both the simultaneous discriminanda (trial-unique exemplars of "sameness" and "difference") and the successive discriminanda (exemplars of "triangularity" and "heptagonality"). Reasoning erroneously, Thomas and Kerr (1976) concluded that the monkeys were using biconditional reasoning (e.g., *if white, then odd* and *if black, then nonodd*). Burdyn and Thomas (1984) corrected that error. In this *Encyclopedia* (see "Relational concepts and symbolic logic") Thomas examined the issues associated with determining conditional reasoning in animals.

Thomas and colleagues have also contributed importantly to the literature on animals' use of numerosness. See Thomas's entry "Relative numerosness" in this *Encyclopedia* for references and discussion.

Since 1993, Thomas began making noteworthy contributions to research in the history of psychology. For example, Thomas (2007) examined five recurring and important errors among recent history of psychology textbooks, and he discussed some of the reasons for that. Thomas

(2011) described the curious circumstances associated with the fact that the first African-American to earn a Ph.D. degree in psychology, Francis Cecil Sumner (Ph.D., 1920; G. Stanley Hall, Supervisor, at Clark University) was a member of the Southern Society for Philosophy and Psychology.

Thomas's website (<http://psyc.franklin.uga.edu/directory/people/roger-k-thomas>) shows his research-related honors, including being a Fellow in the AAAS and having served as President of the Southern Society for Philosophy and Psychology (SSPP) in 2000.

### Administration

Thomas rose through the ranks, and in Fall, 1983, his department head told the Dean he was "burned out" and wanted to be replaced as soon as convenient. Thomas felt he could endure 6 months (January to July 1), so he accepted the Acting Headship beginning January 1984. His first task was to prepare faculty evaluations for 40+ tenured or tenure-track faculty members, and it was required that the evaluations justify recommendations for salary increases.

With zero-based budgeting, that meant that, if someone got an above average raise, someone else had to get a below average raise. Thomas set out to use as much data as he could, and he created a system to turn those data into ratings on a 10-point scale in the categories of teaching, research, and professional services.

Previous Heads had used data but had not developed a standard system for processing it. Thomas discovered that psychologists, who believe in measurement in their teaching and research, do not like to be measured. One senior faculty member wrote Thomas a note saying his approach reminded him of the 5th grade. Presumably, he was referring to receiving a report card. Thomas also learned that no one was happy. Those receiving the larger raises never thought them to be large enough and those receiving lower raises were naturally unhappy.

When Spring came and it was time to appoint a regular Head, Thomas decided he could make a difference and became a candidate. At UGA, the Dean appoints the Heads for 3-year terms. The

Dean consults the faculty which votes, but the Dean is not bound by the vote. Thomas always received favorable votes.

After two, 3-year terms, Thomas sincerely informed his Dean that he too was “burned out” and did not want a third term. The Dean asked Thomas what could he do to change his mind. With little thought Thomas replied, “a \$12,000.00 raise. The Dean said, “What else?” Thomas knew he could not decline such a raise as it would thereafter be a permanent part of his salary.

Upon leaving the Headship, in 1993, after 9.5 years, he was appointed 1/3 time to be Director of the College of Arts and Sciences’ Public Service and Outreach Program. He served as Director until retirement in 2002. After retirement, he continued to teach History of Psychology once/year at the graduate level until 2010, and as this is written (January 2019) he continues to publish.

### Avocational Interests

Due to working from age 12, Thomas had no opportunity for organized sports. However, in 1970, he had the highest batting average on a softball team that won the Athens City Championship (among 68 teams). He has been a whitewater canoeist since 1974 and has canoe-camped in the Okefenokee Swamp about 10 times. Finally, he owns Gibson J-45 and a Martin D-28 acoustic guitars with which, to quote a female picker – singer friend, “we make a joyful noise.”

### Cross-References

- [Learning to Learn](#)
- [Morgan’s Canon](#)
- [Oddity](#)
- [Reductionism](#)
- [Relational Concepts and Symbolic Logic](#)
- [Relative Numerousness](#)

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### Role-Reversal Experiment

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### Definition

The role-reversal experiment is a social cognition paradigm in which two animals first work together on a cooperation task requiring complementary roles and then switch roles to test the degree to which they take the perspective of their partner.

## Introduction

Cooperation, a widespread phenomenon across animal species, ranges from simple actions that incidentally benefit another to complex behavior coordinated in time and space. One of the most complex forms of cooperation involves complementary roles, in which animals perform different actions that contribute to achieving a joint goal. Such complementary roles have been observed in the wild, particularly in the context of group hunting, in such distantly related species as chimpanzees, lions, and hawks (Dugatkin 1997), and have recently been shown even *between* species of fish (Vail et al. 2013). However, it is unclear whether individuals performing one role learn about the complementary role of their partner by working with and observing their partner or whether they must perform the role themselves in order to understand their partner's contribution. Role-reversal experiments try to address this question using novel collaborative tasks to ensure that subjects are initially naïve to both roles.

## Procedure

The basic role-reversal experiment tests pairs of subjects, which may include a subject and a conspecific or a subject and a human experimenter, and consists of two phases. Subjects first learn to perform one of the roles in the cooperative task (*training*). For example, in the classic “communication apparatus,” partners sit on opposite sides of a platform with pairs of food cups (Mason and Hollis 1962; Povinelli et al. 1992a, b). One partner (the informant) can see the rewards but cannot access them; the other partner (the operator) cannot see the rewards but can pull a handle to make one pair of cups accessible, one to the operator and one to the informant. Thus, to be successful, the informant has to indicate the food location (by pointing or positioning themselves in front of the food), and the operator has to pull the corresponding handle. In another task by Fletcher and colleagues (2012), one partner has to push a ball down a ramp and the other has to direct it

down to the next level in order to release rewards to both partners.

After pairs are proficient at the task, they switch roles so that they now have to perform the action that their partner did during training (*role reversal*). Some studies include a third phase, in which roles are returned to the original setup. The ability to reverse roles is then measured as successful transfer (i.e., no drop in performance) when first switching roles or increased performance (e.g., higher percentage correct, decreased latency, fewer trials to criterion) either compared to the first subject in that role or to their own baseline training performance. Using the communication apparatus, rhesus monkeys showed a significant drop in performance from the last training session to the first role-reversal session (Povinelli et al. 1992b) and did not perform better in their original role after having experienced the other role (Mason and Hollis 1962). Chimpanzees have been found to transfer immediately from training to role reversal using the same apparatus (Povinelli et al. 1992a) but did not, in a different task, outperform a partner who had completed the role previously, despite their experience with the complimentary role (Fletcher et al. 2012).

## What Do Role-Reversal Experiments Measure?

Povinelli and colleagues (1992a, b) interpreted successful performance in role-reversal experiments, i.e., the ability to profit from experiences in one role when later switching to the role their partner had performed previously, as evidence of role- or perspective-taking. They argued that successful subjects must have used social attribution to infer the mental states of their partner, which facilitated their own performance when roles were reversed; thus, successful performance is taken as evidence of a theory of mind or “a simple form of cognitive empathy” (Povinelli et al. 1992a).

However, others have pointed out that subjects can learn about the second role while performing the first without having to know the partner's

mental states. For example, Fletcher and colleagues (2012) suggest that successful performance instead provides evidence that subjects form a single mental representation of the collaborative task by integrating their understanding of the complementary roles. It is this “bird’s eye view,” they argue, that then facilitates performance when the roles are reversed.

Of course, the extent to which subjects are able to understand their partner’s role while completing their own is limited by their ability to learn through observation. For example, if subjects learn about and copy not the partner’s precise *actions* (imitation, e.g., pulling the proper handle) but rather the *outcome* of the partner’s actions (emulation, e.g., food cups delivered to both partners), then observing the partner during training may not aid performance during role reversal. Indeed, the outcomes in these tasks were straightforward and had been demonstrated, so subjects could be successful without learning the partner’s specific actions. If so, differences in ability in the experiment across species may simply reflect differences in social learning strategies (see Tennie et al. 2009). In fact, emulation or imitation may not be required at all; successful performance in this task may simply be due to local enhancement effects, in which the partner’s action directs the subject’s attention to the relevant part of the apparatus. In such a case, it might not even be necessary that the subjects understand the necessity of their partner, which would indicate that these tasks are not measuring role reversal so much as how they understand the apparatus. Indeed, understanding their partner’s complementary role was not necessary for subjects to successfully complete the tasks used to date.

Finally, failure to reverse roles in this paradigm may be the result of experimental factors, many of which are common problems in comparative cognition research. One issue with the studies to date is that subjects have had vastly different rearing and testing histories (e.g., juvenile rhesus monkeys that had been separated from their mothers at birth, to chimpanzees with extensive human contact and experience with numerous cognitive experiments), which limits the extent to which we can make cross-species comparisons. This is

further complicated by the small sample sizes (a common problem in animal studies) and because researchers have used different criteria for successful role reversal (see above), which may measure different aspects of cognition. Further, one might assume that in a cooperation task such as this, the subjects’ relationship with the partners would influence their behavior. Indeed, partners during training include everything from reliable human experimenters to trained conspecifics to conspecifics who learn their role at the same time (and are therefore presumably much less reliably good at the task), making it difficult to disentangle the role of the subjects’ knowledge and skill.

There are also methodological differences. Aside from differences in procedure, even when an identical apparatus is used, the different dimensions and test setups can make it more difficult for subjects of some species pairs to see (and therefore presumably understand) what their partner is doing. Similarly, some required actions, such as pointing, may be frequently observed in one species (such as chimpanzees) but may need to be shaped through extensive training in another (such as rhesus, Povinelli et al. 1992a, b). Actions that require extensive training may not be fully understood by the partner based solely on observation, either, because rather than just apply a known behavior, the subjects must first learn the behavior and then apply it correctly.

## Conclusion

The role-reversal paradigm offers an interesting experimental approach to studying complex forms of collaboration in which animals complete different, complementary roles to achieve a joint goal. However, there is currently little consistency in the criteria used to measure successful role reversal or agreement on what success at the task (or lack thereof) actually means. Whether subjects understand that they need a partner in the first place (e.g., will they wait for or recruit a partner?), and how their relationship with the partner (e.g., is the partner a conspecific or a human? Are only socially tolerant pairs successful?) and their rearing and



testing histories affect their performance in this task have not been addressed in depth. Further, it is not even clear whether animals' behavior would change if an understanding of the partner's complementary role was necessary to complete the task successfully, because it is not known whether they can solve the task without this knowledge. Although studies using this paradigm have thus far focused on primates, wide arrays of other species are known to collaborate by performing complementary roles. Thus, a comparative approach will be key in order to better understand whether and how perspective taking is required for the evolution of complex coordination.

## Cross-References

- [Cooperation](#)
- [Empathy](#)
- [Emulation](#)
- [Imitation](#)
- [Theory of Mind](#)

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## Roles of Medial Prefrontal Cortex Activity in Human and Animal Social Learning

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## Established Functions of the Medial Prefrontal Cortex in Human and Nonhuman Animal Cognition

Research over the last two decades has seen advancements in neuroimaging techniques that reveal functional specialization within the prefrontal cortex (PFC) of the brain. Evidence thus far has implicated the PFC as the brain region responsible for high-level behavioral regulation via inhibition, executive function, and facilitation of complex social behaviors. Activation in subregions of the PFC, such as the medial prefrontal cortex (mPFC), is found to correspond with measurements of higher-order cognitive processes critical for learning, including attentional processes, decision making, and working memory (Hoover and Vertes 2007). The mPFC has been studied predominantly in rodents and rhesus monkeys. Derived analogue models of the brain suggest that mPFC is both anatomically and functionally similar to the human dorsolateral PFC (Goodell et al. 2017).

While literature has thus far focused on the mPFC as a site associated with perceptual functioning, including attention and memory (Siddiqui et al. 2008), few discussions have explicated its role across social-cognitive development. Recently, emerging interests have led to the discovery of the mPFC's importance in social processing and learning. Both animal and human studies indicate that the mPFC is involved in moral reasoning, mentalizing, monitoring, and predicting others' behaviors as well as person perception. This review attempts to elucidate the role of the mPFC in guiding social learning and

predicting positive and negative outcomes of others' actions (e.g., Apps and Sallett 2017) through examination and discussion of extant neuroimaging and neuropsychological findings across animal and human research. Directions for future research will also be presented, such as those that investigate the mPFC and related circuitry underlying emotional and social processing in both human and animals.

### **Initial Evidence for mPFC Role in Memory and Higher Cognitive Processes**

Interest in the mPFC region was previously limited to its relationship with the anterior cingulate cortex (ACC) in facilitating purely cognitive processes such as memory and attention, having little to no involvement with emotion processing or social behavior in both humans and animals. For example, studies have shown involvement of the mPFC in short-term and long-term memory and more complex cognitive processing to aid in guiding behavior and decision making. Due to differences in methodology, research has produced inconsistent findings on the mPFC's contribution to cognition (Alexander and Brown 2011). These discrepancies in results impose challenges for theoretical models to explain the purpose of the ACC/mPFC relationship in higher-order functions. Some results show significant involvement of the mPFC in the motivational aspects of attention, error detection, learning from aversive outcomes, and executive functions (Apps and Sallett 2017).

Past studies have highlighted the role of mPFC in memory function through consistent results showing decreased performance on recall tasks when the mPFC was inhibited during learning (Euston et al. 2012). Results have suggested that the mPFC tracks "remote" memories consisting of information learned more than one week before the date of attempted retrieval (Takashima et al. 2006). Additionally, mPFC inactivation has been associated with impaired retention of fear-related memories when tested one day after exposure to fear stimuli, suggesting its role in "recent memory" formation. Still more studies show that

mPFC interference immediately following a learning period inhibits later recall ability, pointing to the role of the mPFC in memory consolidation, i.e., long-term memory. In short-term memory, mPFC lesions lead to recall deficits for location-specific reward associations over delays of 30 min (Seamans et al. 1995). These results demonstrate the importance of mPFC activation in long- and short-term memory and recent and remote memory. However, more functional specializations in the mPFC have been found in recent studies, adding to the variety of functions carried out by this area.

Despite its overlap with memory functions, what differentiates the mPFC from other brain areas is its critical role in directing adaptive behavior (Euston et al. 2012). Evidence suggests that the mPFC uses the aforementioned memory systems to store and process contextual information to produce an adaptive response. Specifically, combined electrophysiological and anatomical findings in rat studies indicate that the mPFC takes current contextual information to predict the most adaptive response in particular situations, based on remembered experiences (Euston et al. 2012). This forms a kind of behavioral feedback loop where the organism learns new adaptive behavioral responses based on the alignment of previous responses with environmental expectations and conditions (i.e., context).

Electrophysiological studies show divergent specializations pertaining to specific subregions of the mPFC, where the internal structure of this system can be divided on a dorsal-ventral gradient: Activity in the dorsal mPFC (including the infralimbic and ventral prelimbic cortex) appears to be strongly associated with musculoskeletal action, whereas activity in the ventral mPFC (including the dorsal prelimbic and anterior cingulate cortex) is more associated with reward-dependent outcomes, i.e., emotional control (Euston et al. 2012). Dorsal mPFC regions thus receive input from motor areas of the brain to produce adaptive action, and the ventral mPFC receives input from emotion-related brain regions, producing adaptive emotional responses based on reward contingencies. As such, the input/output differences occurring between the subdivisions of

the dorsal/ventral mPFC gradient account for the processing of motivational stimuli on the one hand and control motor activity on the other.

To learn adaptive behavioral skills, the mPFC's feedback mechanism initially tracks contextually relevant environmental information that is motivationally salient with help from the hippocampus. The mPFC relies on the rapid associative functions of the hippocampus to learn from spatial and emotional cues quickly, as it binds associations between contexts, events, and responses (Hirel et al. 2013), helping the mPFC obtain maps of its inputs and outputs based on associations of motivationally salient cues. As associations become routine, the mPFC begins to store feedback information locally – independent of the hippocampus – in the form of schemata (Euston et al. 2012). This transition is largely due to memory consolidation, where memory is consolidated in the mPFC during periods of reactivation, mirroring hippocampal “sharp waves” with high-density field potential oscillations (Euston et al. 2012; Johnson et al. 2010). Again, this is suggestive of the role long-term memory plays in mPFC functioning.

The learning of adaptive behavior as a result of mPFC functionality also extends to emotion regulation. For instance, the relationship between the mPFC and ACC is implicated in negative and positive emotion appraisal and expression (Etkin et al. 2011). mPFC connectivity with regions of the limbic system such as the amygdala, periaqueductal gray, and hypothalamus supports complex processing of emotional information via top-down processing. These connections form a network that supports working memory (Etkin et al. 2011) and serve as a basis for integrating emotional information into memory processing. Further studies demonstrate that greater activation in the ACC and mPFC is associated with the regulation and sensitivity of negative emotions (i.e., disgust), as well as the expression of negative emotions such as pain and empathic concern (Ochsner and Gross 2008). Extinction of fear and appetitive learning, as well as processing anger, activates the ventral and dorsal regions of the mPFC, respectively. These findings provide further support for the idea that intact mPFC

connectivity to subcortical regions is fundamental to processing and responding to emotional stimuli in social contexts.

Prior studies on mPFC functionality provide evidence for a division of labor in emotion processing, where mPFC subregions work independently to regulate fear. Similar to the aforementioned anatomical division between motor- and reward-based input/output configurations, these emotion-oriented subregions include dorsal areas (prelimbic/dACC) which regulate fear expression and ventral areas (infralimbic/vmPFC) which regulate fear suppression (Giustino and Maren 2015). The body of research presented here demonstrates the importance of an intact mPFC in learning, memory, and emotion regulation, the latter being crucial for adaptive social behavior. It is thus important to understand how the mPFC is involved in different types of social learning, cognition, and behavior.

## mPFC Role in Social Cognition and Learning

Here, we refer to social learning as (a) the formation of emotional responses to others' behaviors, facial expressions, and speech, (b) formation and maintenance of expectations about social environments, and (c) decision making processes related to social interactions. Recent studies have shown that the mPFC has been implicated in “processing, representing and integrating social and affective information” (Grossman 2013, p. 1). Additional studies demonstrating social learning processes in the mPFC involve self-reflection, person perception, and theory of mind/mentalizing (Amodio and Frith 2006), understanding self and others, decision making in adults (Heekeren et al. 2008), predicting others' preferences (Kang et al. 2013), and learning and predicting the likely outcomes of actions of the self and others (Alexander and Brown 2011). Additionally, it has been demonstrated that the mPFC is implicated in facilitating coordination between animals, regulating social interactions, and carrying out complex defensive behaviors (Goodell et al. 2017).

In fact, functionality of the mPFC is implicated in social learning very early on in development. According to a review of infant studies on the PFC by Grossman (2013), mPFC lesions lead to anti-social behaviors such as interpersonal violence, vandalism, and stealing. In terms of moral reasoning, mPFC lesions lead to more utilitarian, ego-centric responses to moral dilemmas, decreased willingness to resolve interpersonal conflicts, and consideration of the consequences that behavior has on others and dysregulated autonomic responses to punishment (Grossman 2013). This pattern of results suggests that damage to the mPFC has severe consequences for social functioning; in terms of development, the mPFC seems to be less plastic than other areas of the brain (Thomas and Johnson 2008).

The formation of expectations in social situations is an important aspect for successful interpersonal attachments and relationships. In a speed-dating experiment with human participants, Cooper and colleagues (2014) found that expressions of interest in potential partners, as well as feelings of rejection, were associated with increased activation in the posterior superior temporal sulcus and the rostromedial PFC. The mPFC specifically responded to prediction errors from the reinforcement-learning model of personal desirability, suggesting that predicting and expressing both desirability and rejection involve a quantitative calculation in neural networks responsible for processing social rewards (Cooper et al. 2014). This study provides further evidence for the role of the mPFC in forming social expectations that are informed by emotions.

The mPFC promotes the ability to monitor others' actions and detect errors in others' actions, an important factor in successfully responding to others in interpersonal interactions. In a study of two monkeys, Isoda (2017) found that when monitoring both the individual and the others' actions, differing neuronal populations in the mPFC coded divergently for actions pertaining to the individual versus actions pertaining to the other. When another monkey committed errors in its actions, mPFC neurons demonstrated a phasic increase in activity, suggesting that the mPFC is biased toward social information that would inform future expectations.

Neuroimaging findings in humans show that a newborn's mPFC activity significantly increases in response to a mother reading a book using infant-directed speech, as opposed to a mother reading in adult-directed speech. This suggests that the mPFC aids in motivating attention toward cues that are socially interactive (Saito et al. 2007). The mPFC might thus be involved in learning from others by detecting the relevance of others' actions with reference to the self.

Recent evidence highlights the mPFC's direct involvement in regulating aggressive behaviors. According to Goodell et al. (2017), aggression observed in rodents may be directly associated with changes in mPFC function due to post-weaning social isolation (PSI) may be directly related to aggression in rodents that were previously exposed to PSI. Intuitively this would make sense, as emotion regulation and executive functioning are both strongly related to mPFC functionality (Goodell et al. 2017). In addition, a decrease in executive functioning has previously been linked to an increase in physical aggression, supporting the notion that mPFC functionality would be involved. Other studies linking mPFC abnormalities to PSI provide evidence for atypical changes in structure and function, including a dampened expression of early genes (Wall et al. 2012), dendritic spine morphology (Ferdman et al. 2007), and synaptic-related proteins such as PSD-95, a protein involved in synaptic plasticity, (Hermes et al. 2011). In a study using optogenetic stimulation, increased stimulation of the mPFC demonstrated a decrease in aggression in mice; optogenetic silencing, on the other hand, showed a marked increase of aggressive behaviors (Takahashi et al. 2014). Demonstrating increases of FOS (a family of genes responsible for regulating cell proliferation, transformation, and differentiation) in the prelimbic area (PL), results from Goodell et al. (2017) support previous findings that socially dominant mice expressed higher levels of the c-FOS gene in the PL subregion of the mPFC (Wang et al. 2011). Their results indicate an elevation in social rank when rodents interact with other nonaggressive rats, revealing mPFC functional sensitivity to the behavioral characteristics of stimulus rats. Finally,

changes in PSD-95 punctae in the ventral mPFC of isolated rats with social learning differences indicated more time spent with aggressive stimulus rats. Their results insinuate that social isolation may play a causal role in the maintenance of abusive social behavior.

A few theoretical orientations have arisen from these results. According to the somatic marker hypothesis (Damasio 1996), information from the ventromedial PFC and orbitofrontal cortex contains somatic markers that allows learning by experience by linking experiential contingencies with previous emotional experience. For individuals with vmPFC damage or dysregulation, effectively utilizing context-appropriate somatic markers becomes difficult, resulting in behavior and cognition that appears similar to sociopathy (Siddiqui et al. 2008). mPFC dysfunction has also been implicated in other clinical disorders including schizophrenia, bipolar disorder, and autism spectrum disorder in which social impairment is a main characteristic (Goodell et al. 2017).

Both human and monkey fMRI studies demonstrate that learning to anticipate the value of actions and forming expectations about actions, as well as detecting unexpected outcomes, seem to be important processes aided by the mPFC. Alexander and Brown's (2011) theory and model of mPFC function referred to as the predicted response-outcome (PRO) model suggests that: "individual neurons generate signals reflecting a learned prediction of the probability and timing of the various possible outcomes of an action. These prediction signals are inhibited when the corresponding predicted outcome actually occurs. The resulting activity is therefore maximal when an expected outcome fails to occur, which suggests that mPFC signals in part the unexpected non-occurrence of a predicted outcome" (p. 2). Instead, it maps existing action plans in a stimulus context to predictions of the responses and outcomes that are likely to result, i.e., response-outcome learning. It allows multiple possible action outcomes to be predicted simultaneously, each with a corresponding probability (Alexander and Brown 2011).

As previously stated, the majority of research relating the mPFC to social cognition is based on

studies examining the sulcus of the ACC – specifically, the sulcus of the ACC (ACCs) – and pertains to the ACCs's influence on reinforcement learning (Kolling et al. 2016). To recapitulate, reinforcement learning theory (RLT) states that the ACCs anticipate and monitor the value of behaviors by evaluating the differences between behavioral outcomes and expectations, yielding a prediction error (PE) (Apps and Sallet 2017). Impaired PE coding is strongly associated with impaired social cognition (Hill et al. 2016), as PEs inform future-oriented decision making, learning, and adaptive behavior. These recent findings mark the beginning of a social learning-focused model for mPFC function in which the avoidance and anticipation of social errors influence social behaviors. However, not much is known regarding more complex and specific social behaviors in humans.

A study conducted by Kumaran et al. (2016) provides new evidence for how social hierarchies, defined by status inference, are learned. The study suggests that the degree of change in an individual's perception of social hierarchies fluctuate depending on whether they are self-relevant or not. In their study, participants were asked to differentiate the social status of individuals based on whether they belonged to either a "self-hierarchy" – the one to which individual participants themselves belonged to – or an "other-hierarchy," which included strangers, as well as acquaintances and close friends (Cikara and Gershman 2016). How much the participants' belief about social status changed due to feedback was associated with increased activation in the mPFC, amygdala, and hippocampus. According to Kumaran et al. (2016), these brain regions thus form the basis of a "social status inference engine," in which the mPFC pertained specifically to changes in belief regarding the self-hierarchy condition, i.e., when participants demonstrated a bias toward their own social status. This is corroborated by mPFC regions (including the pregenual anterior cingulate) that are correlated with thoughts about one's own personal traits, mental status, and characteristics (Jenkins and Mitchell 2011). The role of the mPFC is further supported by its designation for representing others who are



characteristically similar to one's own traits. Kumaran et al.'s (2016) results highlight a condition where the mPFC is only able to make representations of others when the "self" is used as a diagnostic template (Cikara and Gershman 2016). In other words, the mPFC uses information that is self-referential when making judgments about others who exhibit similar traits. Self-referencing is not relevant when beliefs about a hierarchy pertain to another hierarchy; thus the mPFC only seems to code for the behavior of others when they are similar to one's own behavior (Cikara and Gershman 2016). These results support Festinger (1954), who established the idea that evaluations of self-referential behaviors are acquired via social comparisons with others that exude behavioral characteristics similar to one's own.

In sum, experimental data on human and non-human animals demonstrate the crucial role of the mPFC in social learning and cognition. We have established that the mPFC, due to its functional connectivity to subcortical regions of the brain, informs social learning processes via emotional and motor inputs, error detection and predictions, and self-relevant information. The present review has demonstrated that the mPFC is important for far more complex social and emotional behaviors than purely higher-level cognitive/perceptual functions, as previously thought.

## Future Directions

The current review of the literature on the role of the mPFC in social learning suggests that more research focused on specifying the preference for varying types of social information in the mPFC is needed. In addition, there is a lack of research on mood and anxiety disorder-related effects on mPFC activation during social learning tasks. This type of research would help identify which components of social learning processes are affected by mPFC dysregulation caused by psychopathology. More research looking at the developmental pattern of mPFC activation during social cognition tasks would determine whether the role of the mPFC changes over time. In

addition, continued mPFC neuroimaging research in clinical samples could inform treatment methods for patients diagnosed with various communication disorders and psychopathology. For example, transcranial magnetic stimulation of the mPFC modulates the processing of facial expressions in a priming task. Additional research in this vein, especially with clinical samples, could further our understanding of how social information, such as faces, are processed in clinical disorders and how TMS techniques can be applied to remediate dysfunctional information processing in the brain and positively affect emotional experiences of others.

In addition, several studies have been limited by possible confounding results stemming from overlapping brain areas. In some cases, it is unclear whether a lesion-based finding is the result of one distinct brain area or due to the effects of another overlapping area. Furthermore, it has been found that surrounding brain regions are able to compensate for loss in a proximally related region. Hence, more studies involving single unit recordings and neuropsychological studies showing double dissociations that measure causal factors responsible for functional deficits due to neural abnormalities are needed.

## Cross-References

- ▶ [Amygdala](#)
- ▶ [Decision-Making](#)
- ▶ [Hippocampus](#)
- ▶ [Hypothalamus](#)
- ▶ [Long-Term Memory](#)
- ▶ [Short-Term Memory](#)
- ▶ [Social Learning](#)
- ▶ [Theory of Mind](#)
- ▶ [Top-Down Processing](#)
- ▶ [Working Memory](#)

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## Ronald Schusterman

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Ronald Jay Schusterman (1932–2010) was an American comparative psychologist that contributed innovative experimental and behavioral research with humans, primates, and marine mammals from the late 1950s to the end of his life in 2010. He had a long and productive career in the biological and behavioral sciences, and his research intersected many diverse fields. He considered himself an eclectic scientist, borrowing the most useful ideas from every discipline that he encountered and blending them into a practical and synergistic approach to his studies of animal learning and behavior. Schusterman was best known for the meticulous experimental methods that he developed, refined, and applied to the research problems he explored, as well as for his dedication to searching for the most parsimonious explanations for the behaviors he observed and analyzed (Nachtigall et al. 2010).

Schusterman began his career in the 1950s working with human subjects, and also the behavior of non-human primates, including chimpanzees, gibbons, and monkeys at the original Yerkes Laboratory of Primate Biology in Orange Park, Florida (Schusterman 2010). He credited his training as a psychologist to Mortimer Fienberg at Brooklyn College, where he completed his Bachelor's degree, and Joel Greenspoon and Winthrop Kellogg at Florida State University, where he earned his Master's and Doctorate degrees. He

also credited his success to lucky timing and the support of the National Science Foundation following massive American investment in young scientists – starting in 1958 – in response to the shocking successful Soviet launch of *Sputnik I*.

Schusterman shifted his focus from primates to marine mammals during a time when little was known about these animals and their behavioral and sensory capabilities. His subsequent experimental work with dolphins, seals, sea lions, and walruses spanned nearly 50 years, a period over which understanding of these animals changed dramatically. Schusterman's early studies with sea lions were spurred by his former professor Winthrop Kellogg, who had recently reported the discovery that dolphins used specialized ultrasonic sonar to orient and to detect objects under water (e.g., Kellogg 1958). Schusterman sought to determine whether sea lions similarly used echolocation to gain information about the environment. By observing sea lions in controlled environments and training them to cooperate in a variety of behavioral procedures, he eventually found that they did not echolocate (see Schusterman et al. 2000a; Rice 2010; Schusterman 2010). Ultimately, Schusterman combined sensory and cognitive assessments to understand how sea lions and other marine mammals acquired and used information from a variety of modalities to modify their own behavior.

Schusterman's research with primates and marine mammals covered a broad range of topics that addressed fundamental topics in animal learning, including those related to the themes of *efficiency in learning*, *decision-making in uncertainty*, and *emergent behavior*. Schusterman's research in these areas relied on the basic tenants of conditioning and learning theory, which he used to develop innovative and effective methods for training animals which he studied mostly in the controlled conditions of the laboratory (see e.g., Schusterman 1980). He correlated what he learned through rigorous experimentation with observations of animals in the wild to better understand how learning and sensory capabilities might be used by individuals to solve complex social and ecological problems (e.g., Schusterman et al. 2003). Especially later in his career,

Schusterman worked to connect knowledge of species-typical behavior to understanding of proximal mechanisms that support cognition and communication (e.g., Schusterman et al. 2000b, 2002).

## Efficiency in Learning

Schusterman was intrigued by Herb Terrace's research on *errorless learning* in pigeons (Terrace 1963), which described examples of discrimination learning that occur with few or no responses to negative stimuli. Terrace was the first to show that errors are not required for successful discrimination performance to occur, but rather that gradual fading methods can dramatically reduce (or eliminate) the number of errors needed to learn new discriminations.

Schusterman immediately followed Terrace's thread by showing that similar methods could be used to accomplish complete reversals of well-established visual discriminations in sea lions, virtually without error (Schusterman 1966; Schusterman and Thomas 1966). He found that reversals of stimulus form preferences could be accomplished by progressive dimensional changes in shapes. Importantly, Schusterman measured subtle behavioral responses as well as trial outcomes, and thus, was able to determine the transition points at which the subject's attention shifted from one stimulus dimension to the other. Like Terrace, Schusterman found that learning in these optimal conditions could occur efficiently and without errors, and that subjects could learn without frustration or other emotional responses that might bias later responses to stimuli. Schusterman used variants of errorless learning procedures in a variety of different experimental contexts over the next decades (e.g., Schusterman 1980).

In the 1980s, Schusterman and colleagues discovered that sea lions were capable of *learning by exclusion*. Exclusion learning refers to behavioral control by familiar negative stimuli, or in layman's terms, decision-making by process of elimination. This type of learning has been called by many names in the

psychological literature, including "emergent mapping," "psycholinguistic inference," "disambiguation," "mutual exclusivity," and most recently "fast-mapping" (Reichmuth Kastak and Schusterman 2002a). At the time, this learning process was not well identified or described in the comparative literature, but became evident to Schusterman during his studies of complex learning and artificial language learning in sea lions (Schusterman and Krieger 1984).

During learning of conditional discriminations, or *if . . . then* associative rules, Schusterman found that sea lions could immediately relate two new items when they were paired with a familiar or incorrect alternative (Kastak and Schusterman 1992; Schusterman et al. 1993). He further saw, as did others working independently in the fields of human behavior analysis and psycholinguistics, that this type of problem solving strategy generated "learning outcomes"; that is, that after exposure to problems that could be solved by an exclusion strategy, new associations were eventually established that could be performed in the absence of familiar alternatives. In this way, new conditional discriminations could be acquired virtually without error. This was an important and effective training procedure, but also, critical to interpretations of relational learning in animals (Kastak and Schusterman 1992). The principle of exclusion improves our understanding of what individuals know about what is *not* correct, and how that knowledge can induce new stimulus relationships. The exclusion principle was evident in Schusterman's studies of artificial language learning by sea lions, enabling him to argue that linguistic competence was not a prerequisite for apparent object labeling.

Efficient learning and teaching strategies for animals were also evident in Schusterman's research with learning sets. Learning sets refer to the process of learning to learn, as described originally by Harlow (1949) – where independent but similar problems are learned faster with experience. Demonstration of learning sets relies on transfer between similar successive problems. Schusterman used visual shapes to train simple two-choice discriminations with sea lions and found a decrease in the number of errors required

to learn each successive problem, until eventually one trial or a few trial learning occurred when novel stimulus sets were introduced (Schusterman and Thomas 1966). Evidence of the learning-to-learn phenomenon in animals leading to nearly errorless learning of new relationships strongly influenced Schusterman's view that that learning benefited from exemplar training. As a result, he tended to use large stimulus sets and large numbers of training and testing problems in many of his experiments (e.g., Kastak and Schusterman 1994). In doing so, Schusterman prepared his animals for the types of test problems they would encounter later on, thus dampening responding influenced by trial novelty and enabling the use of trial-one (first exposure) measures of performance on transfer problems.

### Decision-Making in Uncertainty

Efficiency in learning and learning without errors or frustration were recurrent themes in Schusterman's work; however, errors tell us a great deal about what animals can do, and sometimes what they cannot do. This is certainly true in assessment of sensory performance, where errors reveal the limits of sensory capabilities.

Schusterman was interested in how animals made decisions in conditions of uncertainty. Throughout many of his experiments, he used behavioral observations and performance metrics to evaluate attention, motivation, and strategy during problem solving. Due to his interest in sensory biology, he was among the early psychobiologists to conduct empirical work on signal detection theory (Schusterman 1974). His rigorous work in this area revealed a great deal about learning and behavior during difficult tasks. Over the years, he and his collaborators conducted detailed and systematic experiments to explore the role of response bias in animal psychophysics (e.g., Schusterman and Johnson 1975; Schusterman et al. 1975; Schusterman 1976).

The experiments revealed that strategies and decision making during difficult discriminations are influenced by a variety of factors, including reinforcement ratios, trial ratios, conditional probabilities within trial sequences, and response

generalization. Schusterman's work helped shape our understanding of how prior experience influences decision-making in humans and other animals, and has relevance to many modern applications of signal detection theory.

### Emergent Behavior

Schusterman's most important contributions to comparative cognition come from research on what some have called emergent learning or concept learning. This refers to the emergence of new or untrained behavior from logical inferences about previously learned relationships. Schusterman considered these emergent performances examples of new knowledge arising from old knowledge, or synergistic problem solving.

Schusterman's efforts, starting in the late 1970s, to teach sea lions to comprehend an artificial gestural language led him to a rigorous experimental analysis of syntax and semantics (Schusterman and Krieger 1984, 1986; Schusterman and Gisiner 1988; Gisiner and Schusterman 1992). Following training with four *modifiers* (e.g., small, white), 14 different *objects* (e.g., ring, cone), and seven *actions* (e.g., flipper touch, tail touch), Schusterman showed that a sea lion could respond appropriately to over 7000 unique instructional sequences. Furthermore, the sea lion could answer questions about the presence or absence of particular objects in her pool, perform relational trials which required her to take one object to another, and indicate the relative size of objects. The sea lion's performance in this paradigm rivaled or exceeded that of language-trained dolphins and chimpanzees, indicating that large brains and extreme sociality were not prerequisites for highly complex associative behavior.

The results of the artificial language study clearly showed the emergence of a "slot" grammar supporting novel behavior, with apparent functional equivalences arising between signs of a given type. However, whether or not the gestural signs were truly symbols, or referential signals was difficult for Schusterman to demonstrate in this linguistic task, as the sea lions could not



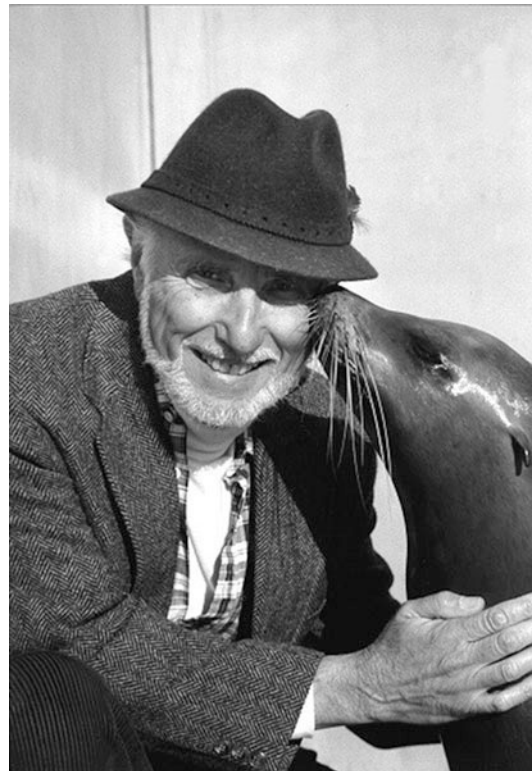
“name” the objects by producing the gestures used by their trainers. Schusterman suspected that general learning processes, rather than specialized cognitive abilities like language, were involved. Instead of comprehending the instructional sequences within a linguistic framework, he believed that the sea lions, and maybe other animals trained on similar tasks, were using structured sets of problem-solving rules to succeed in the comprehension tasks.

To further explore the basis of emergent behavior in animals, he and his students began a detailed series of studies on symbolic behavior, concept formation, and memory which allowed for a deeper experimental analysis of component behavior and contextual control (for review see Schusterman et al. 2002). Strongly influenced by the behavior analyst Murray Sidman, Schusterman turned to complex discrimination learning procedures to examine the conditions which promoted emergent learning. Schusterman used highly specific training procedures with sea lions to demonstrate that these animals were capable forming an assortment of abstract concepts. These included generalized *identity* matching, symbolic matching or *symmetry*, *associative transitivity*, *stimulus equivalence*, and *functional equivalence* (Schusterman and Kastak 1993, 1998; Kastak and Schusterman 1994; Kastak et al. 2001). These concepts, once formed, proved to be highly durable, lasting as many ten years (Reichmuth Kastak and Schusterman 2002b).

The sea lions’ successful performances in these procedures, which are notoriously difficult for nonhuman animals, were attributed in part to Schusterman’s use of large stimulus sets during training. Multiple exemplars also afforded the sea lions practice with similar problems prior to testing, and enabled “trial-one” performance measures of transfer. The sea lions’ success with novel transfer problems demonstrating specific cognitive abilities provided some of the first convincing evidence that nonhuman mammals could use “rules of logic” to solve complex problems. In this sense, Schusterman was a true pioneer in the field of comparative cognition. Many of his systematic teaching methods for animals have been adopted to improve learning outcomes for language-disabled people.

## Legacy

Ronald Schusterman’s careful work in the laboratory to document the conditions under which animals gather and process information, and use it to solve a variety of synthetic and natural problems, leaves a strong empirical framework for the study of animal cognition. During his lifetime, he published more than 100 professional papers which continue to influence many studies in contemporary comparative psychology. Schusterman was a Fellow of the American Association for the Advancement of Science (1967), the American Psychological Association (1984), the Animal Behavior Society (1996), the Acoustical Society of America (1998), and a founding member of the Society for Marine Mammalogy (1981). His laboratory, which Frans de Waal has called “*the strangest and most delightful animal laboratory he ever set a slippery foot in*” (de Waal 2016, p. 181) has remained at the University of California’s Long Marine Laboratory since 1985.



Ron Schusterman and California sea lion Rocky, taken at the University of California Santa Cruz in 2003 (photo: C. Reichmuth)

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Comparative Cognition](#)
- ▶ [Discrimination Learning](#)
- ▶ [Echolocation](#)
- ▶ [Frans de Waal](#)
- ▶ [Harry Harlow](#)
- ▶ [Intelligence](#)
- ▶ [Language Research: Parrots](#)
- ▶ [Matching-to-Sample](#)
- ▶ [Neophobia](#)
- ▶ [Pinniped Cognition](#)
- ▶ [Reasoning by Exclusion](#)
- ▶ [Same/Different Learning](#)
- ▶ [Semantics](#)
- ▶ [Syntax](#)
- ▶ [Transfer of Learning](#)

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## Ronald Weisman

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Ronald G. Weisman made major contributions to the field of Comparative Cognition for over 50 years. Ron finished his career as Professor Emeritus in the Departments of Psychology and Biology at Queen's University located in Kingston, Ontario. Ron was born in Detroit, Michigan, in 1937 and died in Kingston, Ontario, in 2015. Ron earned a B.A. (1960), M.A. (1961), and Ph.

D. (1964) from Michigan State University. Ron's first research publications came from work that employed principles of learning in an educational setting (e.g., Krumboltz and Weisman 1962). Ultimately, Ron completed his graduate work with Jack King and M. Ray Denny studying animal behavior with a focus on learning processes in mice (e.g., Denny and Weisman 1964; King and Weisman 1964).

Following his graduate work at MSU, Ron was a National Science Foundation (NSF) postdoctoral fellow with David Premack at the University of California, Santa Barbara from 1965 to 1966. Ron was hired as Assistant Professor of Psychology at Queen's University in 1964. He was promoted to Associate Professor in 1970, again to Professor in 1977, cross appointed to the Department of Biology in 1993, and finally promoted to Professor Emeritus in 2000. In sum, Ron was a professor at Queen's for over 50 years. During his time at Queen's, Ron took up many visiting appointments at other universities, including at Duke University, Florida Tech, Johns Hopkins University, Sussex University, King's College at Cambridge University, and the University of California, San Diego.

Ron made numerous significant contributions to our understanding of animal learning, cognition, and behavior. In his early career as an independent scientist, much of his work focused on investigating the determinants of behavior, using what can be considered a traditional approach to understanding behavior: experiments conducted in conditioning chambers, using rats and pigeons as subjects (e.g., Weisman 1975). In these studies he made many contributions to understanding basic learning processes such as discrimination, inhibition, and avoidance learning. This work, although important and well regarded, is not what most people will remember as Ron's main scientific contributions. The work from the "second act" of his career is the work for which Ron will be most remembered.

In the 1980s, Ron embarked on a new career, studying all aspects of songbird vocal perception and production. Being a newcomer to the empirical study of songbirds, Ron started almost from scratch. The genesis of this new career was

Ronald G. Weisman. Ph.D., Professor Emeritus of Psychology and Biology (14 September 1937–27 January 2015)

characterized by a series of happy coincidences, a real life evolution of a research program, if you will. Around the time of his trip to San Diego, Ron had become interested in understanding how animals process information and wanted to apply *information integration theory* as a conceptual framework to do so. Up to this point, Ron had tested his ideas with pigeons as subjects but felt that studying a natural system was a better way to proceed. It was around this same time that he met Laurene Ratcliffe, who had recently started working at Queen's University, and asked her, as an expert in songbird behavioral ecology who had experience working with great tits (*Parus major*) at Oxford University, whether birdsong would be a good system to approach these questions. Ratcliffe suggested black-capped chickadees (*Poecile atricapillus*) as a potential model system because they had a two-note song that seemed relatively simple acoustically. One of the first set of studies involved conducting operant-type procedures in the field and the laboratory that showed chickadees were sensitive to the number, note type, and order of the notes in their song (Ratcliffe and Weisman 1986; Weisman and Ratcliffe 1987; Ratcliffe and Weisman 1988). Thus the simple song seemed to be not so simple upon closer experimentation. The happy coincidences continued when Stuart Hulse and Jeffery Cynx, who were already studying pitch perception in starlings (*Sturnus vulgaris*; Hulse and Cynx 1986), performed calculations on black-capped chickadee songs that Ratcliffe and Weisman reported in their 1985 Condor paper and pointed out to Ron and Laurene that chickadees produced their two-note songs with a consistent relative pitch relationship between the two notes. Once again, the "simple" song turned out to be paradoxical in its complexity embedded in seeming simplicity.

Ron forged a truly integrative research program that combined elements of learning, cognition, ethology, and neuroscience using a variety of songbird species as his study subjects (for reviews of some of this work, see Weisman and Ratcliffe 2004 and Weisman et al. 2012). Following the early success of this work with songbird perception, Ron also began to

compare the auditory perceptual abilities of songbirds with those of humans. Ron and his colleagues (notably Laurene M. Ratcliffe, T. Andrew Hurly, Daniel M. Weary, Scott A. MacDougall-Shackleton, Douglas J.K. Mewhort, Leslie S. Phillmore, Milan G. Njegovan, Marisa Hoeschele, Laurie L. Bloomfield, and Christopher B. Sturdy) uncovered aspects of songbird production and perception that were largely unknown before Ron embarked on this new research area. Among the most notable of his research findings, Ron and his colleagues described black-capped chickadee singing behavior in detail and, among other findings, showed that chickadees produce the frequency interval in their two-note *fee-bee* song with remarkable fidelity (Horn et al. 1992; Ratcliffe and Weisman 1985; Weisman et al. 1990). Moreover, Ron showed that birds could perceive this interval with a high degree of accuracy (Weisman and Ratcliffe 1989; Weary and Weisman 1991). Importantly, Ron showed that this perceptual ability and other auditory perceptual abilities and neurobiological correlates (Njegovan and Weisman 1997, Phillmore et al. 2003) were impacted if the birds were reared in conditions that resulted in abnormal vocal production. Further studies, both with chickadees and zebra finches (*Taeniopygia guttata*), revealed that songbirds far outperformed humans, even trained musicians, at frequency-based discrimination tasks (e.g., Weisman et al. 1998; for a review see Weisman et al. 2012). Later work showed that zebra finches, like chickadees, had perceptual and production deficits following manipulations of the social, acoustic environment during development (Sturdy et al. 2001). A constant theme throughout his career was the encouragement and support he provided his collaborators and trainees, imploring them and others to conduct research aimed at "explaining nature" (Weisman 2008).

Ron's career was impressive by any measure, but his impact extends beyond that accounted by metrics like number of publications, H indices, and other such measures often used for assessment. Some of the most lasting contributions



that Ron made to the scientific communities to which he was utterly devoted throughout his career defy such routine enumeration. After his death in 2015, many colleagues offered descriptions of Ron's influence using phrases such as "force of nature," "intellectually challenging," "passionate," and "inspiring." All of these things he surely was. Among Ron's many important contributions to the scientific community was his creation of an international conference designed to bring together researchers from Psychology and Biology to share their findings and insights about behavior, learning, and cognition across species. This conference, called the Conference on Comparative Cognition (CO3), started in 1994 with an attendance of approximately three dozen scientists and rapidly grew into a popular annual conference with a stable attendance at well over 100 presenters from all over the world. Over the years, there have been talks about numerous aspects of behavior and cognition on over 100 species.

In response to the growth and overwhelming success of the CO3 conference, and the recognition that a more formal organizational structure was needed, Ron founded the Comparative Cognition Society (CCS) in 1997 and was the first president of CCS. This society has grown and thrived since its founding, and Ron was awarded the CCS Research Award for his substantial contributions to the field in 2007. Ron also initiated and was the first editor and publisher of the online and open-access journal, *Comparative Cognition & Behavior Reviews*, which has published important reviews and critical commentaries on a wide range of topics in Comparative Cognition since 2006.

## Cross-References

- [Auditory Signals](#)
- [B.F. Skinner](#)
- [Charles Darwin](#)
- [Communication](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Countersinging](#)

- [Discrimination Learning](#)
- [Passerine Cognition](#)
- [Passerine Sensory Systems](#)
- [Perception](#)

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## Rooting Reflex

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## Synonyms

Inborn reflex; Innate reflex; Instinctive reflex; Physiological reaction; Primitive reflex; Reflex action; Unconditioned reflex

## Definition

The rooting reflex is the automatic head turning response to the stimulus of face, mouth, or cheek touching.

The rooting reflex is the automatic head turning response to the stimulus of face, mouth, or cheek

touching. Infant apes will involuntarily orient their face toward the stimulation, often the mother's nipple, searching for the stimulating object with an open mouth. During development, the rooting reflex appears in utero, is present at birth, and disappears in early development. It is a primitive reflex present in newborn apes to facilitate feeding via maternal milk secretion. The rooting reflex is related to the suckling reflex, the automatic sucking response to any pressure to the newborn mammal's mouth. The rooting reflex has primarily been studied in humans, although it is evident in other apes including chimpanzees (Salloway 2011).

Primitive reflexes in humans include the step reflex, tonic neck, Palmar grasp, Plantar reflex, Babkin reflex, Galant reflex, the suckling reflex, and the rooting reflex. The rooting reflex in humans normally appears around 28 weeks gestation, is fully developed at 34 weeks gestation, becomes less prominent 1 month after birth, and disappears around 4 months after birth (Sosa et al. 2004). Absence of the rooting reflex in newborns indicates brain stem dysfunction, whereas persistence of the rooting reflex beyond early infancy indicates cortical dysfunction (Sosa et al. 2004). Frontal lobe disorders sometimes produce the reappearance of the rooting reflex in humans later in development (Salloway 2011). The rooting reflex coincides with altriciality, or the inability of young to attain food independently via locomotion. Altricial animals require more parental care for survival than do precocial animals. Precocial mammals are able to root and nurse voluntarily at birth and do not require reflexive responses to secure nutrients.

Primates are a relatively altricial mammalian order, with humans representing a highly altricial species, which can be explained by the metabolic limit hypothesis (Dunsworth et al. 2012). According to this hypothesis, labor and delivery occur when the mother can no longer continue to supply the fetus with metabolic and nutritional requirements in utero. The large brain of the fetus becomes too energetically costly for the mother to continue to supply nutrients in utero and external feeding is more efficient for the mother, creating a tradeoff between prenatal

brain development and maternal energetic expenditure. Birth canal size produces another constraint on gestation duration for a large-brained, metabolically demanding fetus, resulting in earlier labor and delivery than is optimal for brain growth (Ruff 2017). As a result of the increasing metabolic demands of a large-brained fetus, birth occurs when the brain is not fully developed and, therefore, the newborn human is altricial. The rooting reflex, combined with the suckling reflex, solves the adaptive problem of altricial infants having insufficient cerebral capacity to locate and secure nutrients and feed. The rooting reflex is mediated by the brainstem, and as the cerebral cortex develops, the rooting reflex is replaced by voluntary motor functions (Yoo and Mihaila 2020).

Nursing is normally necessary for mammalian infant survival. Maternal milk is dynamic and uniquely suited to the growth and developmental requirements of offspring. Maternal milk contains a high proportion of fats relative to proteins, facilitating newborn brain development (Belfort et al. 2016; Jenness 1979). Operant conditioning facilitates the disappearance of the rooting reflex. Rooting, suckling, and crying serve as infant hunger cues and motivate caregivers to feed newborns. Mothers or caregivers respond to the rooting reflex by nursing, causing the infant to cease display of hunger cues, creating negative reinforcement for the caregiver, and, therefore, motivating feeding as a response to rooting. Nursing in response to the rooting reflex provides positive reinforcement for rooting behavior as an indication of hunger in infants. As infant cerebral cortex development progresses and the rooting reflex disappears, infants continue to root for a period of time as a voluntary indication of hunger (Glodowski et al. 2019).

## Cross-References

- ▶ Altricial
- ▶ Feeding
- ▶ Fetus

- ▶ Grasping Reflex
- ▶ Hominid
- ▶ *Homo sapiens*
- ▶ Innate Behaviors
- ▶ Natural Selection
- ▶ Nutrients
- ▶ Operant Conditioning
- ▶ Parenting
- ▶ Positive Reinforcement
- ▶ Precocial
- ▶ Reflex
- ▶ Reinforcement
- ▶ Species
- ▶ Suckling/Nursing

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## Roots and Shoots

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Jane Goodall's Roots & Shoots is the global humanitarian and environmental education and youth engagement program of the Jane Goodall Institute. It was founded in 1991 by renowned primatologist and conservationist, Dame of the British Empire and United Nations Messenger of Peace, Dr. Jane Goodall, with the mission to:

Foster respect and compassion for all living things, to promote understanding of all cultures and beliefs and to inspire each individual to take action to make the world a better place for people, other animals and our environment.

Roots & Shoots began with 12 Tanzanian high school students who approached Goodall with concerns about local sustainability issues, such as the destruction of the coral reef by illegal dynamiting, poaching in the wildlife parks and reserves, lack of assistance for street children, ill treatment of animals in markets, lack of environmental education, river pollution, and draining the wetlands. Upon Goodall's suggestion and with her support, they formed student groups to raise awareness and take action on these issues. The program now comprises a global network, engaging hundreds of thousands of young people (and the young at heart) in nearly 100 countries on 6 continents.

The central tenet of Roots & Shoots is that every individual matters, makes a difference, and has a role to play in making this world a better place for people, other animals, and the environment we all share. The program asks individuals to choose what kind of difference they want to make and, through the programmatic pillars of knowledge-compassion-action, provides them with opportunities and support to develop and lead local actions that address issues they are

passionate about. Participant outcomes include an increase in awareness, compassion, connection to nature, empowerment, confidence, leadership skills, and understanding of sustainability and volunteerism. Long-term goals include building the knowledge, attitudes, and practices for participants to live and lead more sustainable lifestyles.

The program is adaptable to both formal education systems and nonformal learning settings and has a specific goal of engaging underserved and socioeconomically vulnerable young people. Participants often include individuals, family groups, community groups, homeschools, classrooms, student clubs, whole schools and universities, as well as unique situations such as the group in Boulder County Jail (Holland 2015).

Recent youth-led actions include local projects such as constructing greenhouses with plastic bottles in Argentina, planting a new woodland in the UK, raising awareness about chimpanzee poaching in Tanzania and the Republic of Congo, planting pollinator sanctuaries in the USA, flying giant peace doves in Israel and the Democratic Republic of Congo, building a Medicine Wheel outdoor learning space in Canada, organizing an annual Animal Parade in Taiwan, and assisting refugees in Germany and Greece and global campaigns such as Roots & Shoots Peace Day (Jane Goodall Institute 2017), a September celebration of living in harmony with each other and with nature in honor of the United Nations International Day of Peace, and International Mobile Recycling Day on January 24 to raise awareness about the detrimental effects of conflict minerals such as coltan and encourage recycling of devices that contain them.

In the words of Dr. Goodall, the name Roots & Shoots is symbolic. "Think of a big tree. It starts as a little seed. Pick it up when the first tiny shoot and roots appear. It seems so small, so weak. Yet there is a life force in the seed so powerful that the shoot, to reach the sun, can work through cracks in a brick wall and eventually knock it down. And the roots, to reach the water, can work through rocks and eventually push them aside. See the rocks and walls as all the problems we humans have inflicted on the planet, environmental and social. And you realize Roots & Shoots is about

HOPE. Hundreds and thousands of Roots & Shoots around the world can break through and make this a better world for all” (Jane Goodall Institute 2015 and personal communication).

For more information on Jane Goodall’s Roots & Shoots, please visit [www.rootsandshoots.global](http://www.rootsandshoots.global).

## Cross-References

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## Roughage

► [Equine Diet](#)

## Rough-and-Tumble Play

► [Pretend Play](#)

## Route Following

► [Mustelidae Navigation](#)

## r-Reproductive Strategists

► [r-Reproductive Strategy](#)

## r-Reproductive Strategy

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## Definition

r-Reproductive strategy is adopted by r-selected species which is characterized by smaller body size, rapid developmental rate, high reproductive rate or fecundity, early reproduction, smaller offspring, semelparity, and short life span.

## Synonyms

[r-selection](#); [r-Reproductive strategists](#)

## Introduction

Dobzhansky (1950) studied the natural selection in tropical and temperate zones and found a fundamental difference in between. He found that the mortality in temperate zones is independent of density as well as genotype and phenotypes of organisms. It rather depends on the environmental condition. So, selection favors the organisms with high reproduction and growth rate. On the contrary, in tropics where climate is stable, selection favors the organisms with higher competitive ability. Therefore, in tropics organisms tend to produce fewer offspring with slower developmental rate which ultimately leads to improving competitive ability.

Later on MacArthur and Wilson (1967) came up with the idea of r-selected and K-selected species in their book entitled *The Theory of Island Biogeography*. The K denotes the carrying capacity, and r represents the maximal intrinsic growth rate ( $r_{max}$ ). MacArthur and Wilson originally gave their hypothesis with respect to island where the early colonizers are tend to r-selected with higher intrinsic growth rate, while the late colonizers are K-selected with higher competitive ability.

Further, they elaborate their findings to populations other than islands. Fisher, Haldane, and Wright's work already shown that *r* is suitable for the measurement of fitness at low and increasing population densities. MacArthur and Wilson introduced the *K* for measurement of fitness at higher population densities. They further concluded that in unpredictable environment, populations are rapidly decline, so *r*-selected organisms prevails, while in stable environments, the populations will grow to their carrying capacity where *K*-selected organisms will prevail. They also suggest that *r*-selection will lead to "a shorter developmental time, a longer reproductive life, and greater fecundity, in that order of probability." It means fast and high productivity is the outcome of *r*-selection, while efficiency (especially in resource utilization) is the outcome of *K*-selection.

Pianka (1970) published a short note on "*r*- and *K*-selection." He elaborated the *r*/*K* concept in detail and described the connection between *r*- and *K*-selection. In his words "However, it is clear that there are two opposing kinds of selection, which usually have to be compromised. Certainly, no organism is completely "*r*-selected" or completely "*K*-selected," but all must reach some compromise between the two extreme" (p. 592 in Pianka 1970). He further suggests that an *r*-*K* continuum exists in nature and organisms may present at any point in between two end points (*r* and *K*). In his words "The *r*-endpoint represents the quantitative extreme—a perfect ecologic vacuum, with no density effects and no competition. Under this situation, the optimal strategy is to put all possible matter and energy into reproduction, with the smallest practicable amount into each individual offspring, and to produce as many total progeny as possible. Hence *r*-selection leads to high productivity. The *K*-endpoint represents the qualitative extreme—density effects are maximal and the environment is saturated with organism. Competition is keen and the optimal strategy is to channel all available matter and energy into maintenance and the production of a few extremely fit offspring. Replacement is the keynote here. *K*-selection leads to increasing efficiency of utilization of environmental resources" (pp. 592–593 in Pianka 1970).

## Life History of r-Reproductive Strategists

*r*-Reproductive strategists are characterized by several life history attributes such as high reproductive rate (higher fecundity), rapid development, short life span, early reproduction, and semelparity. These life history attributes help the *r*-Reproductive strategists in successful utilization of environmental conditions in their favor. *r*-Reproductive strategy is successfully employed by the organisms present at lower trophic level, e.g., invertebrates (insects and other invertebrates), small rodents, herbaceous plants, small fishes, phytoplanktons, zooplanktons, some amphibians, etc. These organisms are having very short life span and high reproductive rate, and they attain sexual maturity quickly. The characteristics of *r*-Reproductive strategists are listed in Table 1.

## High Reproductive Rate

*r*-Reproductive strategists have higher intrinsic rate of reproduction. Mostly smaller organisms adopt *r*-Reproductive strategy and tend to produce large numbers of offspring. Most of the invertebrate and some vertebrates (amphibians) tend to produce large quantity of eggs. *r*-Reproductive strategists tend to follow exponential growth.

$$\frac{dN}{dT} = r_{\max} N$$

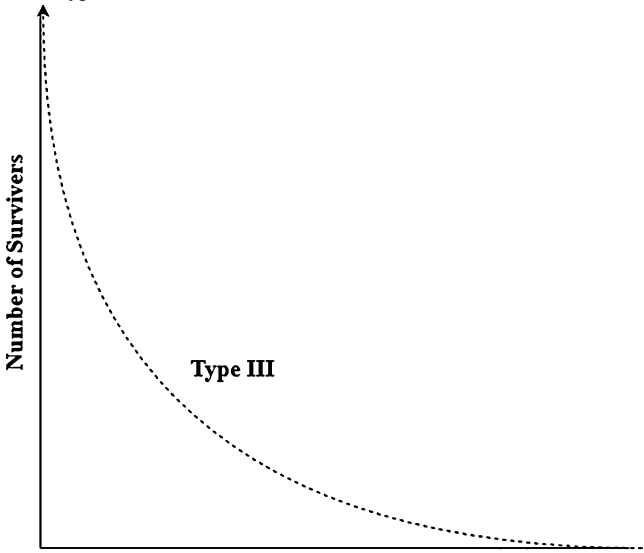
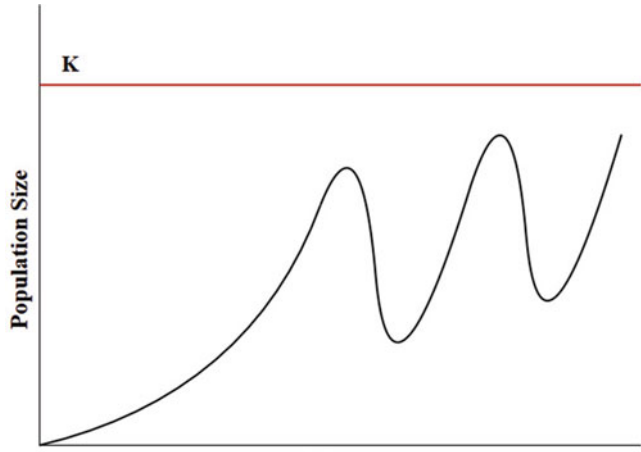
Per capita/individual growth rate in exponential growth remains unchanged, irrespective of the population size. This allows the populations to grow at faster rate as it becomes larger in favorable environmental conditions. When environmental conditions fluctuate, there is a rapid decrease in population observed but onset of favorable environmental conditions; the population grows exponentially (Fig. 1).

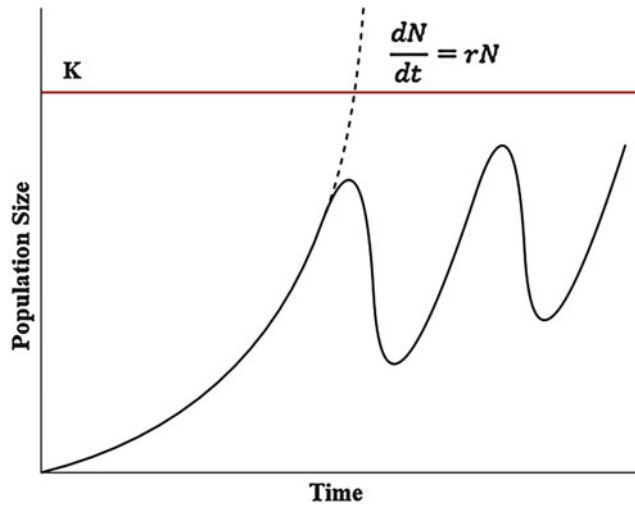
## Rapid Development

*r*-Reproductive strategists tend to grow at faster rate to fully utilize the window of favorable



**r-Reproductive Strategy, Table 1** Characteristics of r-Reproductive strategists. (Adopted from Pianka 1970)

|                                        |                                                                                                                                                                                                         |
|----------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Attribute                              | Characteristics                                                                                                                                                                                         |
| Climate                                | Variable and/or unpredictable                                                                                                                                                                           |
| Mortality                              | Often catastrophic and unpredictable, nondirected, density-independent                                                                                                                                  |
| Survivorship curve                     | <div>Often type III</div> <div></div>                                                                                 |
| Population size                        | <div>Variable in time, nonequilibrium, usually well below the carrying capacity of the environment</div> <div></div> |
| Competition (intra- and interspecific) | Variable, often lax                                                                                                                                                                                     |
| Life history                           | <div>Rapid development</div> <div>High <math>r_{max}</math></div> <div>Early reproduction</div> <div>Small body size</div> <div>Semelparity: single reproduction</div> <div>Short life span</div>       |



**r-Reproductive Strategy, Fig. 1** Growth curve of **r-Reproductive strategists:** r-Reproductive strategists follow exponential growth model at greater extent. The population of r-selected species grows rapidly with maximum growth rate ( $r_{\max}$ ). However, the population size

never reaches to carrying capacity (K) of the environment. Population size varies in time and shows density-independent fluctuation in population size due to change in environmental conditions

environmental conditions, e.g., several species of insects and herbaceous plants grow quickly during monsoon period. The seeds/propagules of ephemeral plants remain dormant during winter and summer season but onset of brief monsoon period, and dormant seeds/propagules germinate and quickly attain sexual maturity. Similar strategy is also adopted by insects, they came out from their hideouts during monsoon and reproduce to give rise a large number of offspring which take advantage of favorable conditions and complete their life cycle.

### Small Body Size

Smaller body size is a recognizable feature of r-Reproductive strategists. Due to lack of competition, r-Reproductive strategists do not need a robust or big body size, so they tend to be smaller. The unpredictable environmental conditions often cause mass mortality, so smaller body size is preferred over larger body size among r-Reproductive strategists.

### Early Reproduction

The r-Reproductive strategists attain sexual maturity early in their life history in order to quickly utilize the environmental opportunity. Due to availability of abundant resources, lack of density-dependent selection, and being opportunistic, r-Reproductive strategists tend to early in their life cycle, e.g., several ephemeral species (mostly insects and plants).

### Semelparity

Most of the r-Reproductive strategists are semelparous in nature, i.e., they reproduce only once in their life time, e.g., several species of r-Reproductive strategists such as many invertebrates including majority of insects, herbaceous plants, etc. However, there are some exceptions like some insects and most r-Reproductive strategists like mammals which are iteroparous (reproduce multiple times in their life history).

## Short Life Span

Since the r-Reproductive strategists have to utilize a brief window of opportunity of favorable environmental conditions, hence, its successful strategy to grow and reproduce quickly. The uncertainty of environmental conditions is a major issue among r-Reproductive strategists as it causes density independent mass mortality which leads to shorter life span. The life span of r-Reproductive strategists varied from few hours to few months.

## Ecological Significance of r-Reproductive Strategy

r-Reproductive strategists are generally opportunistic in terms of resource utilization. In favorable environmental condition, they grow rapidly and tend to utilize maximum resources. However, any fluctuation in favorable environmental conditions (in the form of drought, flood, fire, and thunderstorms) often leads to density-independent mass mortality. Such calamities reduce the population density significantly below the maximum sustainable level of the ecosystem, e.g., sudden burst in populations of herbaceous plants (annual) and insects during spring and summer but rapid decline during winter season. Since, such populations are subjected to regular explosive growth episodes, hence known as opportunistic population. Catastrophic mass mortality in r-Reproductive strategists due to sudden variation in environmental conditions has no/little relation with genotype, phenotype, and population size of the related organisms.

r-Reproductive strategy is generally adopted by the early colonizers during ecological succession of newly formed habitat (Gadgil and Solbrig 1972; Abrahamson and Gadgil 1973; Gaines et al. 1974). Since, pioneer communities inhabiting the newly formed habitat are reach to carrying capacity of the environment. Hence, they rarely deplete their resources to low level as do the organisms present in climax communities. Due to the presence of plentiful resources, the pioneer communities (r-Reproductive strategists) face little or no

competition as compared to intense competition among climax communities (K-reproductive strategists). In the absence of competition, the pioneer communities are able to invest maximal amount of their energy in reproduction and tend to produce large number of offspring. Smaller offspring are energetically efficient to be produced in such environments as the absence of competition allows the growth of even smaller progeny. Hence, the early colonizers are characterized by rapid growth, early maturation, high reproductive rate, and smaller offspring. Such qualities in early colonizers enable to occupy and spread quickly in newly formed habitat.

However, as succession proceeds, the pioneer communities are replaced by more stable seral and climax communities, and the environment becomes more stable. The stable environmental conditions lead to density-dependent selection and thus support the more competitive organisms (r-Reproductive strategists) over less competitive one (K-reproductive strategists).

Although an organism may be either r-strategist or a K-strategist only in comparison with other organisms, e.g., if we compare small rodent mammals such as mouse with insects or microbes, then, ofcourse, it will be a K-strategist, but when we compare it with large mammals such as whales and elephants, then it would be considered as r-strategist. Hence, the determination of r- and K-selection is purely comparative. In nature no organism is completely r-selected or K-selected; rather an r-K continuum exists as earlier suggested by Pianka (1970). The organisms modulate their reproductive strategy according to environmental conditions. Several r-Reproductive strategists shift their habit from r- to K-selection at some extant during the change in environmental conditions. For example, Mueller and coworkers generate r- and K-selected lines of fruit flies (*Drosophila melanogaster*) by breeding the duplicate populations at high and low densities. At lower population densities, r-selected lines developed a high capacity to increase population size while a lower capacity for increase in population size at higher population densities (Mueller and Ayala 1981; Mueller et al. 1991).

Fugitive species are an interesting example of opportunistic species, as they are considered as poor competitor because their dominance is reduced significantly due to interspecific competition, but they tend to dominate in newly formed habitat due to their high dispersal rate (Pianka 2008). Such abilities in a species allow them to persist in patchy environment by continually changing their position despite the presence of highly competitive species. In the case of planktonic species, several species of planktons can coexist in diverse planktonic communities under comparatively uniform physical condition without any apparent ecological separation, also known as “paradox of the plankton” (Hutchinson 1961). This can be explained by the fact that temporal change in environmental conditions may lead to increase in diversity of related planktonic species by changing their competitive ability, thus promoting their coexistence.

## Conclusion

The r-Reproductive strategy is commonly adopted by the opportunistic species. r-Reproductive strategists exploit the resources of newly formed habitat due to their life history characteristics such as rapid development, high  $r_{\max}$ , early reproduction, small body size, semelparity, and short life span. However, any fluctuation in favorable environmental conditions leads to catastrophic density-independent mass mortality among r-selected organisms. During ecological succession, the early colonizers are r-selected, but as the succession proceeds, r-selection organisms are replaced by K-selected. In nature, there is no organism which is completely “r-selected” or “K-selected”; rather an r-K continuum is present. The term r-strategists or K-strategists are relative; it means that if we compare two r-Reproductive strategists, then one will be more r-selected than the other and vice versa for K-reproductive strategists.

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## r-Selection

► [r-Reproductive Strategy](#)

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## Rudiment

► [Vestigial Organ](#)

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## Rudimentary Organ

► [Vestigial Organ](#)

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## Rule Learning

► [Pattern Learning](#)

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## Rumbaughx

### ► Computerized Testing Paradigm in Primates

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## Runaway Selection

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## Synonyms

Fisherian selection

## Definition

Runaway selection is a mechanism whereby a secondary sexual trait expressed in one sex becomes genetically correlated with a preference for the trait in the other sex. The genetic coupling of the trait and the preference leads to self-reinforcing loops of coevolution between the trait and preference for the trait. This process is known as runaway selection and can lead to accelerated evolution of exaggerated traits and preferences.

## Introduction

One of the greatest challenges to Darwin's theory of evolution by natural selection was the presence of exaggerated male traits (Darwin 1859). Such traits encompass a wide variety of elaborate visual, acoustic, chemical, and behavioral characteristics (e.g., tail of the peacock or courtship song in birds). These traits appear to contradict Darwin's idea that selection acts on traits that increase survival. Elaborate ornaments and displays seem maladaptive to their bearer as they are costly to maintain (Grafen 1990; Zahavi 1975); they can trade off against investment in other important life history traits such as immune function (Folstad and Karter 1992) and can make

an individual more conspicuous to predators. Why would selection favor traits that incur fitness costs with no obvious fitness benefits? Darwin himself suggested that these traits might evolve through sexual selection, where the bearers benefit from higher reproductive success (Darwin 1871). He proposed that male ornaments could evolve through female choice if females prefer to mate with males sporting exaggerated traits. Thus, the benefit to males gained through sexual selection would offset the costs incurred through natural selection. Since Darwin, female preference and the benefits females accrue from exhibiting preferences have been studied across many taxa. The idea that elaborate male traits evolve via female choice is now widely accepted (Andersson 1994).

Females can increase their reproductive success by mating with males that provide direct and indirect benefits. The expression of a male trait may indicate a male's ability to provide resources. If so, females can increase their fitness directly by mating with males that provide, for instance, bigger nuptial gifts or more paternal care (Arnqvist and Nilsson 2000). In species where males provide no direct benefits, the most commonly invoked mechanism for female preference for exaggerated male traits is indirect (i.e., genetic) benefits (Jennions and Petrie 2000). In this scenario, traits are indicative of male genetic quality, rather than of the ability to provide resources. Therefore, by mating with particular males, females can increase their fitness indirectly because their offspring will inherit genes that increase their fitness (Kirkpatrick and Barton 1997). However, much debate still surrounds the selective mechanisms underlying the origin and maintenance of female preference.

## Fisher's Theory

One mechanism to explain the evolution of female preference was proposed by Ronald A. Fisher. Fisher proposed that a female's preference for a particular male trait could benefit that female indirectly through the production of more attractive offspring (Fisher 1930). According to Fisher's theory, females with a preference for ornamented males will produce sons with higher mating



success due to their inheritance of the extravagant trait from their father. Hence, increased mating success of sons characterizes the indirect benefit of female preference. In addition to sons inheriting the male trait from their fathers, daughters will also inherit the preference for the trait from their mothers. Consequently, genes responsible for the male trait and genes responsible for female preference for the trait become genetically coupled in the offspring. The higher mating success of the ornamented male helps carry the allele for the male trait to higher frequencies. Importantly, it also increases the allele frequency of female preference for the exaggerated trait due to the genetic correlation brought about by assortative mating.

Fisher originally hypothesized that the preferred male trait would initially confer some naturally selected advantage. For example, if tail length in males increases survival, females with the preference for long tails will benefit from producing sons with both a natural and a sexual selection advantage because they are preferred by females (Fisher 1930). However, when the genetic coupling of the trait and preference in the offspring is established, the male trait will eventually become so extreme due to the positive feedback loop between trait and preference that it will no longer carry any naturally selected advantage. At this point, the trait may even be deleterious to survival, so the fitness advantage of the trait exists only because of its covariance with the preference, providing sons with higher mating success.

However, mate preference resulting in the genetic coupling of trait and preference can originate in ways different from natural selection (e.g., sensory bias). Regardless of the initial reason for female preference, a positive feedback mechanism will result in more exaggerated sons and choosier daughters being produced with each successive generation, leading to self-reinforcing loops of coevolution. This will lead to the spread of both the preference and the trait throughout the population. Female preference for more exaggerated male traits is predicted to continue until the cost of carrying the ornament outweighs the benefit of possessing it in terms of mating success.

Note that while in most species females are the choosier sex because of their more substantial reproductive investment, the principles of runaway selection can equally apply to female secondary sexual traits and male preference in sex role-reversed species.

### Postcopulatory Runaway Selection

Until a few decades ago, females were viewed as being fundamentally monogamous. Thus, it was generally assumed that female mate choice only occurred prior to mating. It has since been realized that females in most species mate with multiple partners, which extends sexual selection into the postcopulatory arena. When females' mate multiply (polyandry), sperm from several males can compete for access to the female's ova (sperm competition; Parker 1970). By mating polyandrously, females can exert selection on male traits that increase a male's fertilization success (Simmons 2001). In analogy to precopulatory female preference for exaggerated male secondary sexual traits, females can act as agents of selection on male postcopulatory traits by mating multiply. Hence, Fisherian selection may act on male postcopulatory traits. For instance, the sexy sperm hypothesis posits that female multiple mating can drive the coevolution of polyandry and sperm competition (Keller and Reeve 1995). By inciting sperm competition, polyandrous females will be fertilized by competitively superior males. Thus, sons of polyandrous females will inherit genes for enhanced sperm competitiveness from their fathers, and daughters will inherit polyandry genes from their mothers. This is predicted to generate the coevolution of sperm competitiveness and polyandry through Fisherian runaway selection (Curtisinger 1991; Keller and Reeve 1995).

### Testing Fisher's Model of Runaway Selection

Fisher's theory assumes the presence of heritable variation both in the male trait and female preference for it. It also predicts a genetic correlation between trait and preference through linkage disequilibrium that builds up by assortative mating. However, persistent directional female choice on a male trait should exhaust genetic variation in the

trait and eventually drive the trait to fixation. Once at fixation, there is no genetic variation in males, and female choosiness will no longer be associated with increased mating success in sons. This can create the conundrum where female choice persists despite that choice providing no benefit, the lek paradox (Kirkpatrick and Ryan 1991; Taylor and Williams 1982). Given this paradox, there has been much focus on investigating what maintains heritable variation in male traits despite directional selection from female preference.

Genetic models have examined Fisher's theory (Andersson 1994; Kirkpatrick 1982; Lande 1981; Mead and Arnold 2004), and much empirical work has addressed the assumptions underlying Fisher's mechanism. For the trait and preference to be correlated, a key assumption is the presence of heritable genetic variation in both traits. Empirical evidence supports the existence of ample additive genetic variation in both male attractiveness and female preference (Bakker 1999; Bakker and Pomiankowski 1995; Taylor et al. 2007).

Several studies have found support for the runaway process. In a wild population of three-spined sticklebacks, Bakker (1993) found genetic variation for male redness intensity and female preference for redness in males. He also found a genetic correlation between the red pigmentation in sons and preference for the red coloration in daughters as predicted by Fisher's theory. Other studies have investigated evidence for Fisherian selection in the postcopulatory arena (Lüpold et al. 2016; Simmons and Kotiaho 2007). In the dung beetle, *Onthophagus taurus*, males with short sperm have a fertilization advantage when mating with females that have large sperm storage organs (spermathecae; Simmons and Kotiaho 2007). The authors found heritable variation in both male sperm size and female spermathecae size and a negative genetic correlation between the two (Simmons and Kotiaho 2007). This finding supports Fisherian selection, whereby postcopulatory female choice can shape the evolution of male traits (in this case, sperm size), similar to precopulatory female preference driving the evolution of male secondary sexual traits.

If there is genetic covariation between female preference and secondary sexual male traits, then

artificial selection for an increase or decrease in the male trait should lead to a corresponding shift in female preference. Houde (1994) diverged guppy selection lines by selecting for high and low levels of coloration, respectively. In line with Fisher's prediction, females from lines in which males were selected for increased coloration showed stronger preference for coloration than females from lines selected for decreased coloration.

In contrast to these positive findings, several studies have failed to find support for Fisher's theory. For example, a large-scale quantitative genetic analysis of over 8500 collared flycatchers revealed significant heritable genetic variation in a male ornament and in female mate choice for this ornament but negligible evidence for a genetic correlation between the two (Qvarnström et al. 2006). This suggests that alleles for mate choice had not coevolved with alleles for the ornament as predicted by the runaway theory. Similarly, in a study of a wild-derived population of *Drosophila montana*, Ritchie et al. (2005) found genetic variation in male courtship song and female preference for the song but no covariance across families between the preference and the trait. Moreover, Travers et al. (2016) examined the genetic basis of polyandry and sperm competitiveness in *Drosophila melanogaster* and found little heritability in sperm competitiveness, indicating that Fisherian selection did not drive the coevolution of sperm competitiveness and female multiple mating.

In conclusion, investigation into covariation between male traits and female preference has yielded mixed findings, with many studies finding weak or no genetic correlations between trait and preference (Kirkpatrick and Ryan 1991; Andersson 1994; Bakker and Pomiankowski 1995; Greenfield et al. 2014). A review on within-population preference and trait coevolution found overall weak levels of covariance (Greenfield et al. 2014), which suggests either that runaway selection plays a marginal role in the evolution of female preference and/or that measuring the strength of runaway selection is empirically challenging.

## Challenges and Future Directions

Given the contradictory findings thus far, the role of runaway selection in promoting the coevolution of male traits and female preferences remains unclear. A number of factors may have contributed to producing conflicting findings.

In Fisher's theory, linkage disequilibrium, the genetic covariation between male trait and female preference, accumulates by assortative mating; females with preferences for exaggerated traits mate and produce offspring with males bearing those traits (Fisher 1930; Lande 1981). Because the genetic covariance by linkage disequilibrium is established and maintained by assortative mating rather than physical linkage, linkage disequilibrium can break down rapidly (by 50% per generation) when assortative mating ceases (Bakker 1999; Bakker and Pomiankowski 1995). Thus, the genetic covariation can be lost in just a few generations. Many have highlighted that experimental conditions in the laboratory have the potential to disrupt assortative mating and hence break down the genetic correlation between female preference and male traits. For example, many quantitative genetic studies impose random mating in the parental generation to uncouple maternal and environmental effects from genetic parameters. This can break down linkage disequilibrium and result in the failure to detect the genetic correlation between trait and preference (Bakker and Pomiankowski 1995). Studies in wild populations could overcome this limitation, as could experiments performed within the first generations of laboratory breeding.

A second issue is whether studies that have investigated Fisher's theory had sufficient statistical power to detect the genetic covariance. Simulations by Sharma et al. (2016) indicate that the sample size needed to confidently detect trait-preference genetic correlations is much larger than those reported in studies thus far. Therefore, it may not be possible to appropriately gauge the importance of runaway selection in natural populations until more studies with large sample sizes are conducted.

Finally, little is known about the nature of female mating preference. Most studies that have investigated trait-preference coevolution have focused on measuring the relationship between

the expression of a single trait in males and female preference for that trait in isolation. However, several traits contribute to a male's overall attractiveness, and females are likely to choose males based on multiple traits (Prokop and Drobniak 2016). The heritability of overall attractiveness will typically be lower than the heritability of any individual trait. Thus, to assess the strength of Fisherian selection, one must quantify the benefit to the female through her sons' mating success, rather than the value of a single trait. Explicit measures of male mating success will prove useful for understanding the fitness consequences of female choice.

## Conclusion

Darwin first proposed mate choice as an explanation for the evolution of elaborate behavioral displays and morphological traits in males. Fisher's runaway process has become a central theory to the investigation of the evolution and maintenance of mate choice and exaggerated male traits. Its theoretical importance has led to intense theoretical and empirical testing of the theory's assumptions. Yet, our understanding of mate choice and the role of Fisherian selection in driving male traits beyond their naturally selected optima remains limited. Much interest remains in this potentially pervasive explanation of how selection on males and females leads to the stunning and often bizarre traits we observe in nature.

## Cross-References

- [Assortative Mating](#)
- [Fisher](#)
- [Genetic Variation](#)
- [Ornamentation](#)
- [Promiscuity](#)
- [Sperm Competition](#)

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## Rutting

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## Synonyms

Musth; Rutting period; Tugging

## Definition

The periodically recurring sexual excitement of mammalian species including cervids (e.g., deer, sheep, goats), elephants, and other mammals.

## Introduction

The term rutting (i.e., the behavior of mammals during the rut) is derived from the Latin word “*rugire*,” meaning to roar. This phenomenon occurs in deer, goats, sheep, camels, bison, moose, elephants, and several other mammals and is particularly evident in species of the Cervidae family. Due to changes in photoperiod, hormones in animals fluctuate, resulting in increased testosterone levels in males and triggering onset of rutting behavior. Similarly, increases in estrogen and other hormones in females triggers onset of estrous in many species. Increased testosterone levels increases male aggression during peak rutting times, which coincides and sometimes releases estrous in females of rutting species.

During non-breeding periods males of some rutting species can be found in bachelor groups, which consist of several males that travel and live together. Prior to and during onset of rut, levels of aggression rise and bachelor groups separate. Males of many rutting species become intolerant of other males and often engage in direct conflict or make displays of dominance toward other males. Some species of mammals have intense displays of aggression which reduces the amount of direct conflict in these species. Fighting in males during the rut is a tradeoff (Geist 1964). The animals risk injury and death for the opportunity to pass on their genes. Some males practice conflict avoidance to reduce the risk of injury. In some species, such as white-tailed deer (*Odocoileus virginianus*), necks of males will swell to increase apparent body size. White-tailed deer bucks will also lock antlers and spar with one another until one of the males submits to the more dominant individual.

Vocalizations are another indicator of rutting behavior in several different species, and are used during the rut to demonstrate dominance among

males and to attract females into an area. Male elk (*Cervus canadensis*) are often observed and heard bugling during rut – this behavior is best described as a low growl that turns almost into a whistle. Hangul deer (*Cervus elaphus*) males are also often observed roaring during the rut (Bhat et al. 2009).

Male African elephants (*Loxodonta africana*) exhibit two indicative signs that they are in musth (i.e., a period of surging testosterone levels in elephants akin to rut in cervids). Temporal gland secretion can be seen on the side of the forehead of elephants in musth and is distinguished by a wet line that is running down their face. The second sign is urine dribbling. A rise in aggression also accompanies these two visual signs when elephants are in musth (Ganswindt et al. 2004). Males will also utilize scent-marking as a means to attract females and display dominance in an area.

White-tailed deer bucks make scrapes in the dirt with their hooves, and then eliminate to leave their scent in an area (Pruitt 1954). They also frequently make rubs that coincide with scrapes by peeling bark from small diameter trees and limbs with their antlers. Moose (*Alces alces*) also exhibit rubbing during rut. They can extensively damage small trees by removing the bark up to 7 f. high on the trunk. Rubbing is thought to leave scent on marked trees as well as provide a visual sign to females and other males.

The initiation of the rut is commonly triggered by photoperiod during the season. Photoperiod, or daylength, is the period of time each day that illumination, or solar light, is available to an organism. When the days shorten, changes to circadian rhythms in the body trigger hormone release and/or suppression, causing behavioral and physiological changes that prepare the individual for breeding. Female deer, commonly referred to as does, come into estrous due to a combination of photoperiod-linked releases and other factors (Murphy et al. 1994). Does remain in estrous for only about 24 h, and if not bred will go out of estrous. They then begin a 21–27 day cycle to return into estrous, which is repeated up to four times during a breeding season (Knox et al. 1988). This recurring estrous cycle in females can contribute to the late breeding reports that are sometimes received. This



is important because the estrous cycle can determine how long males rut. Males will continue to breed until they cannot find any females that are in estrous or until they are too exhausted energetically to breed.

## Conclusion

Onset of rutting is triggered by photoperiod in white-tailed deer, elk, moose, and several other species. During these times, males become more aggressive and start to show strange behaviors related to pursuit of females in estrous. During the rut, male deer, moose, elk, elephants, and other species will also expand their home range to increase opportunities for breeding with a greater number of females. They may also pursue females to great lengths and expend a tremendous amount of energy while in pursuit.

## Cross-References

- [Agonistic Behavior](#)
- [Competition](#)
- [Estrous](#)
- [Mating](#)
- [Mating Effort](#)
- [Reproduction](#)

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## Rutting Period

- [Rutting](#)

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## Saccades

### ► Cognition

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## Saccadic Eye Movement

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### Introduction

Animal vision is incomplete without the ability to change the gaze that involves coordinated control of eyes, head, and body movements (McCluskey and Cullen 2007). Saccadic eye movement is one of the mechanisms by which an animal redirects the gaze. As opposed to smooth pursuit movement that helps in tracking a moving object, saccades consist of a rapid ballistic movement of both the eyes from one point of fixation to another. Thus saccades require rapid movement of eyes to new location followed by fixation and inhibition of further eye movement. The orienting eye movement is achieved by the oculomotor system in the brain (Enderle 2002). However, saccadic gaze can be

achieved even in a case of congenital eye muscle paralysis by similar saccadic movements of the head (Gilchrist et al. 1997). Thus, saccadic gaze is an integral part of the visual system. The term “saccade” (jerk) was first used by a French ophthalmologist Louis Émile Javal. However, research on saccadic eye movements was initiated even before the popularity of this terminology. The first appearance of saccade-like movement in animal kingdom is seen in fish where the role of these eye movements was to re-center eye direction whenever the animal turns. However, with evolution the main function of saccades became to position the fovea (part of the retina with where vision is most precise) onto the object/s of interest. In humans, the direction, duration, and destination of the saccades are selected by the cognitive brain processes that often occur without conscious awareness (Walker et al. 2000). Thus, study of saccadic eye movements can help us in understanding the brain processes during cognitive tasks.

### Neural Substrate of Saccadic Eye Movement

As mentioned earlier saccadic eye movements are mediated by the neurons in the oculomotor system that includes nuclei of III, IV, and VI cranial nerves. Moreover, neurons of brainstem, superior colliculus, frontal eye field, supplementary eye field, basal ganglia, cerebellum, and frontal and

parietal association areas are involved in saccadic eye movement (Enderle 2002). High-frequency burst of the oculomotor neurons innervating the extraocular muscles overcomes the inertial forces to initiate the saccades. The direction of the eye movement is controlled by two gaze centers, viz., paramedian pontine reticular formation for horizontal gaze and rostral interstitial nucleus for vertical gaze. Frontal eye field (FEF) receives input from the extrastriate cortex for initiating stimulus-driven saccades. The sequential planning, execution, and learning of saccades are done by FEF via coordination with the basal ganglia and cerebellar neuronal circuitry. Higher-level planning of saccades is done by prefrontal cortex, while information related to the spatial coordinates provided by the associative parietal areas. Visual stability during saccades that prevents blurring of vision even though there is movement of the image on the retina is known as saccadic suppression. Saccadic suppression is possible at high-contrast visual conditions with the help of visual masking which involves neuronal suppression of primary visual cortical neurons (Bremmer et al. 2009), while saccadic suppression in low-contrast conditions is mainly by corollary discharge that suppresses the magnocellular pathway in lateral geniculate nucleus and motion-related areas in middle temporal and medial superior temporal cortices (Bremmer et al. 2009).

## Recording Paradigms and Types of Saccades

One of the earliest methods of recording saccades was using contact lens optical lever that could record eye movement in seconds arc (Kowler 2011). Later studies were done using magnetic-field/search-coil method that was more precise and could record three-dimensional eye movements (Eggert 2007). However, both the techniques were invasive. Electrooculography (EOG) is one of the commonest techniques used in present day to record eye movements (Eggert 2007). The principle behind this technique is that each eye acts as a dipole with retina relatively

negative as compared to the cornea. The direction of this dipole is almost the same as the direction of the visual axis. Moreover, the dipole moves along with the movement of the eyes. Using surface electrodes, the movement of the dipole can be tracked to record horizontal or vertical eye movements. Another common technique used to record eye movement is using infrared reflective devices that track the eyes by measuring the intensity of infrared light reflected from the eye at fixed locations close to the eye. These devices require regular calibration in order to maintain the accuracy and cannot record torsional eye movements. With the recent advances in digital processing, video-oculography (VOG) has gained popularity in recording eye movements (Larrazabal et al. 2019). This technique uses pupil, iris, and other head-fixed markers to track the movement of the eyes and can even record torsional eye movements.

Saccades can be classified based on the type of stimulus that initiates them. Reflexive saccades are peripheral stimulus-driven bottom-up responses, while voluntary saccades are endogenous stimulus-driven top-down responses (Walker et al. 2000). The prefrontal lobe dysfunction seen in schizophrenia leads to decreased ability to inhibit reflexive saccades and decreased ability to produce voluntary saccades when required (Enderle 2002). Saccades are typically stereotypic ballistic movements, and thus each saccade shows similar patterns. Nevertheless, various parameters are used to study saccadic eyes movement. Saccadic latency is the time taken for saccade initiation from the presentation of the stimulus. This latency depends on the time taken for the impulse to travel along the afferent and efferent pathway including central processing time. Saccade amplitude or size and saccadic duration are nonlinearly related to each other, while saccadic velocity linearly correlates with saccadic size. Slow (decreased velocity) hypometric (decreased size) saccades are seen in spinocerebellar degeneration (Geiner et al. 2008). Probable cause of slow saccades seen in spinocerebellar ataxia type 2 is degeneration of excitatory burst neurons of the brainstem (Geiner et al. 2008). A type of voluntary saccades in which

the timing and position of the stimulus can be predicted is called anticipatory saccade (Pfeuffer et al. 2016). Anticipatory saccades are markers of learning during sequential procedural cognitive task (Pfeuffer et al. 2016). A task in which the participant is instructed to delay the saccade by increasing the duration of fixation stimulus produces delayed saccades which can help in understanding the mechanism involved in inhibition of saccades. Frontal eye field inhibition that diminishes the superior colliculus activity forms one of the mechanisms by which delay in saccades is produced (Enderle 2002). Even during eye fixation tasks, small dynamically continuous miniature eye movements are seen called microsaccades. The function of microsaccades is to maintain a continuous visual perception and prevent perceptual fading (Rolfs 2009).

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## Sacred Cats

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## Synonyms

Feline cult; Felines in religious ritual; Temple cats

## Introduction

Through their appearance and behavior, animals have always provided visual imagery, metaphors, and materiel through which a culture may express its ideas about – and interact with – the “divine” (Wilkinson 2003; Guthrie 2005; Counts and Arnold 2010; Allen 2016). In religious and other cultural contexts, animals are not only sources but also recipients; the often complex and contradictory symbolic functions assigned by a human society to a nonhuman species shape human interactions with these other animals (Engels 1999; Lawrence 2003). Felines have played simultaneously conflicting roles as antagonist and as guardian probably since Paleolithic times, if not earlier (Saunders 1991; Allsen 2006). Early humans (genus *Homo*) and their ancestors competed with big cats (subfamily Pantherinae) for living space and for prey, such as deer, tapir, and

cattle (Saunders 1998). Big cats posed a predatory threat to hominins, but also served as providers of kills that could be scavenged.

The oldest surviving evidence of a feline in a culturally meaningful role is the figural art of *Homo sapiens* during the Upper Paleolithic (beginning about 38,000 BCE), a period when animals dominated the visual repertoire (Guthrie 2005; Fig. 1). Relative to images of herbivorous prey species, images of cats and other carnivores are uncommon for this period (Saunders 1991). The lions of European Upper Paleolithic art are *Felis leo* or a close relative. The lack of manes in most representations suggests that the artists were portraying lionesses, but even those that do have manes sport only scanty ones, so male lions in these times and places might not have grown the magnificent manes that characterize the animals at later periods (Guthrie 2005). Short strokes protruding from the nose of one of the Lascaux lions have been interpreted as either blood pouring from a wounded animal or the animal's breath, either as an indication of fury or the power of its life (Guthrie 2005).

Necessity may have driven early humans to become keen and close observers of these predators (Guthrie 2005). Still, some scholars attribute the relatively crude rendering of cats in some Paleolithic cave art (such as at Lascaux, France),

which contrasts with sensitive, well-observed renderings of bison and other prey animals, to the danger of viewing the predators up close (Saunders 1991). Chauvet Cave, also in France (c. 35,000–29,500 BCE), features surprisingly abundant and realistic heads of lions. That the Chauvet lions include the detail of whisker spots on the muzzles suggests that the differences between these lions and those at Lascaux may result from “inexperienced drawers” rather than inexperienced observers (Guthrie 2005), but greater realism does not lead to greater understanding of the meaning or motive of the artists.

### Big Cats (Pantherinae)

Symbolisms that later cultures assigned to big felines are better understood. While varied, these share some common themes. Through image, word, and/or parts of the animal, powers of dangerous animals – scorpions and snakes, for example – are commonly coopted for use in apotropaic (protective) rituals performed either by individuals or by the state. Big cats (particularly the lion [*Panthera leo*], leopard [*P. pardus*], tiger, [*P. tigris*], jaguar [*P. onca*], and puma [*P. concolor*]) have commonly been adopted as emblems of the governing class and other powerful social strata (McCall 1973–1974; Zuidema 1983; Malek 1993; Saunders 1991, 1998; Counts and Arnold 2010; Sugiyama et al. 2013). Through the use of feline skins, fur, claws, teeth, bones, and flesh, kings, warriors, and shamans have sought to acquire ferocity, strength, vision, and other feline traits deemed desirable (McCall 1973–1974; Zuidema 1983; Saunders 1998; Sugiyama et al. 2013).

Despite their generally nocturnal habits, members of the subfamily Pantherinae commonly acquire solar associations. This might be due to the tapetum lucidum, a brightly reflective layer of cells behind the retina of the eye that gives cats their superb night vision (Saunders 1988). In some cultures, the yellow color of a cat's coat might be specifically cited as a reason to affiliate the animal with the sun (Saunders 1998). The ancient Egyptians had several solar lion deities.



**Sacred Cats, Fig. 1** Felines of uncertain symbolic significance to Paleolithic humans: Drawings of lions in Chauvet-Pont-d’Arc Cave, France, c. 35,000–29,500 BCE



Most of the leonine goddesses (Sekhmet, Bastet, Tefnut, and Mut, among others) were viewed as the dangerous and vengeful Eye of the sun god, Re, who was depicted most often as a falcon (typically the peregrine falcon, *Falco peregrinus*) but also on occasion as a smaller cat species (see Felinae, below). Another Egyptian goddess often shown as a large feline, Mafdet, guarded the sun from the divine serpents that attempted to thwart the sunrise. Perhaps inspired by the care lionesses give their cubs, ancient Egyptian religious texts refer to these fierce goddesses in maternal roles. They conceived, birthed, and nursed the king, who was called the “son of the sun” (Delvaux and Warembo 1991; Wilkinson 2003).

The Egyptians symbolized distant regions with lions, which inhabited the arid regions beyond the fertile agricultural land of the Nile Valley. In their temples, the leonine goddesses were appeased with waterways (*isheru*) intended to mimic the natural pools that formed at the edge of the desert as the groundwater rose with the Nile River’s annual inundation, believed to herald the return of the Eye of Re (Delvaux and Warembo 1991). The Egyptians visualized the eastern and western horizons, where the sun rose from and set into the underworld, as two lions either seated or joined

back to back (Wilkinson 2003). Liminal associations, dusk/dawn and the interface between the world of the living and the realm of the dead, appear in Mesoamerican sources as well. The crepuscular and nocturnal habits of jaguars, and their spotted coats, identified these cats with the morning and evening stars (Venus), nighttime aspects of the sky, and the chthonic “Night Sun” of the underworld (Saunders 1998; Latsanopoulos 2008; Sugiyama et al. 2013, 2015).

The arboreal hunting habits of the jaguar further linked it in Mesoamerican symbolism with the sky and high places, such as the tops of buildings. Its affinity for water – unusual for a felid – gave rise to the Water Lily Jaguar (Fig. 2), one of several jaguar deities of the Maya underworld, which, it was believed, could be reached through cenotes (sinkholes filled with groundwater). Among the Shipibo, Waiwai, and Wayana of South America, although the Yellow Jaguar is a solar animal, the Black Jaguar (i.e., melanistic) is a creature of earthquakes, rain, and dangerous manifestations of water (Saunders 1998).

As wild animals, and particularly as predators perceived as threatening human life and livelihood, big cats were also appointed as embodiments of the more generalized natural world



**Sacred Cats, Fig. 2** Feline signifying liminal regions: The Maya god Water Lily Jaguar, dancing in an aquatic environment, with a scarf around his neck that

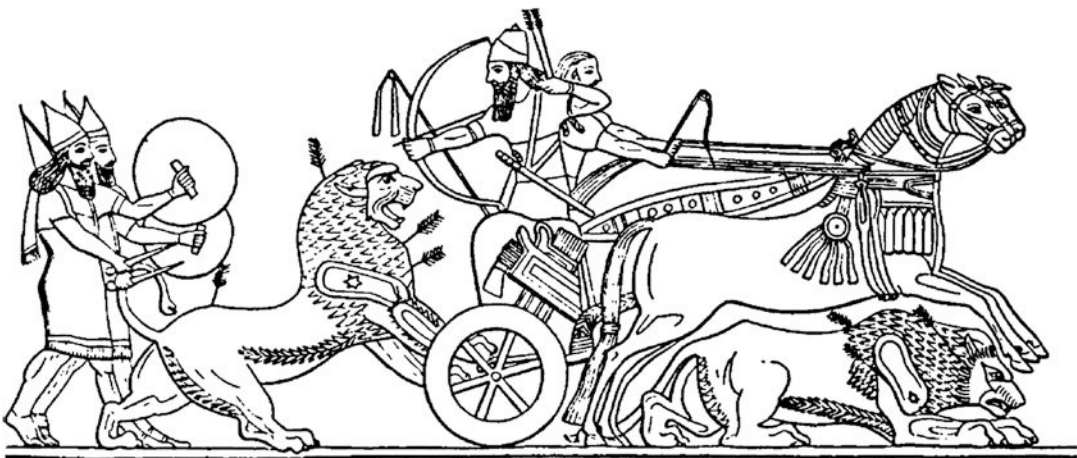
indicates his impending sacrifice. Maya codex-style vase, Calakmul, Campeche, Mexico. Classic Maya period, c. 1001–251 BCE (After Coe 1978)

that existed beyond the boundaries of human settlements and agricultural land. Lions and other Pantherinae appear occasionally in the “master/mistress of animals” motif found in the art of cultures throughout the Old World, although herbivores are far more common (Childs-Johnson 1998; Counts and Arnold 2010). This motif features a human figure grasping or otherwise dominating one or more wild animals to visually express conceptual divisions in religion, politics, and other systems within the culture that created it. Typical examples are dualities of order and chaos, mortal and divine, and life and death. Viewed through such cultural lenses, predatory felines become aggressors that threaten not only livestock but also human social order and wellbeing (Counts and Arnold 2010).

This metaphor was not merely an artistic motif. Ritualized hunts for big cats and other dangerous game allowed rulers to display their dominance over the natural world for political and ceremonial ends; in many cultures, these became royal obligations above and beyond mere sport (Allsen 2006; Weissert 1997). Shang Dynasty kings of China (c. sixteenth to mid-eleventh centuries BCE) hunted tigers for sacrifice. This was an act of legitimation, demonstrating the king’s physical prowess as “master of the hunt” and his ability to propitiate the spirits of the royal ancestors. Oracle bones (bovine scapulae or underparts of turtle

shells, heated to produce cracks that were then interpreted to answer questions) might determine the time, place, and purpose of the hunt and subsequent sacrifice. Most often, the tiger (or other religiously significant animal) was captured alive, to be later shot with an arrow near the ancestral temple (Childs-Johnson 1998).

Assyrian sources (seventh century BCE) present a similar duality of field and urban lion kills with a different overt symbolism (Fig. 3). Field hunts were undertaken under the pretext that an incursion of lions had begun to prey upon even penned livestock. At sunrise, the king mounted a chariot and, within a conventionalized span of “forty minutes,” shot all of the lions. One urban hunt was undertaken at Nineveh (modern Mosul, Iraq) in a place dedicated to the goddess Ishtar. Overlooked by a hill where spectators could gather to witness the spectacle performed specifically for their benefit, the area was cordoned off by armed men. Eighteen lions – one for each gate of the city – were released from cages for the king to shoot from his chariot. When necessary and/or to emphasize the king’s heroism, during these confined hunts some lions were killed with sword or spear. Slain lions were accorded the same treatment as defeated human enemies in a public ceremony of triumph, being presented with food offerings as the king poured a libation of wine upon their heads. Evidence suggests that



**Sacred Cats, Fig. 3** Felines representing forces of chaos: Assyrian royal lion hunt. Nimrud, ninth century BCE. Original in the British Museum, WA 124534 (Line drawing after: Morey 1903)

lion hunts took place near the end of the year to ritually secure the safety of the herds during the coming year. By defeating lions that embodied divine forces of chaos and evil, which made them allies of the primordial goddess Tiamat, the king played the part of a war deity, either Ishtar or her father, Ashur (Weissert 1997).

One text stressed that each caged lion was “of its plain,” that is, wild, although whether this is true remains open to question (Weissert 1997). Ashurbanipal boasted of having captured fifteen full-grown lions and fifty cubs, which he brought to Nimrud (near Mosul, Iraq) and bred. His zoological collection in this city also included tigers and leopards, among other wild animals, as elements of political propaganda demonstrating his mastery of the world (Allsen 2006).

The Egyptians maintained lions in captivity as well, including in specifically religious contexts. In the first century BCE, the Greek historian Diodorus Siculus recorded that Leontopolis (“Lion City”) in the Nile Delta (modern Tell el-Yehudiya) kept a lion in its sacred enclosure, well cared for and fed with great number of live birds (Book I.84.4–5). This animal served as an embodiment of one of Egypt’s leonine deities, Bastet’s son Mahes (Wilkinson 2003).

Particularly in Egypt and Mesoamerica, archeological sites have revealed physical details regarding the capture and keeping of wild felines, both Pantherinae and Felinae. Animal burials dating to the Egyptian Predynastic Period (specifically Naqada IC–IIB; c. c. 3750–3550 BCE) excavated in cemetery HK6 at Hierakonopolis in southern Egypt included the remains of a single large cat – a large male leopard (*F. pardus*) – dated likely to Naqada IIA–B. Placement of its burial and those of other wild species found thus far at this site (e.g., aurochs, *Bos primigenius*; hippopotamus, *Hippopotamus amphibius*; crocodiles, *Crocodylus niloticus*) suggest that they functioned as guardians for the elite human burials in HK6 or as expressions of human mastery over the forces of chaos. While young, the leopard had experienced a pelvic injury, perhaps from a fall. This had healed. Because the animal was elderly at the time of its death, the injury had likely happened long before its capture. The discovery of bones of a

newborn piglet with evidence of digestion suggest that this was its last meal. The manner of the leopard’s death is unknown, but its body was treated with care, being covered with a woven textile and mat before the grave was filled (Van Neer et al. 2013, 2017). Seven or more young leopards – until recently identified as lions – between the ages of six to 12 months, were found at the tomb complex of Aha, one of Egypt’s earliest kings (c. 3100 BCE), at Abydos, also in southern Egypt. Their scattered and incomplete skeletal remains evidenced deformities (rickets-like curvature; missing dentition) indicating that these animals had lived most of their lives in captivity and may have even been born there, perhaps in a royal menagerie (Flores 2003; Van Neer et al. 2013).

Another large feline that had spent considerable time in captivity in Egypt was a very large adult male lion found in a Ptolemaic/Roman-era context (333 BCE–fifth century CE) at Saqqara. It had, however, evidently been taken as an adult or nearly adult, a conclusion drawn from the generally good health of its bones. This animal, too, had evidently suffered a fall with resulting injuries to its vertebrae and ribs. These healed, and the animal appears to have been cared for thereafter, presumably in a temple context, but its diet may have been based on bread that had a heavy inclusion of sand (which was typical of Egyptian bread in antiquity). This resulted in considerable wearing of the teeth, a condition initial examination had attributed to gnawing. The lion lived to the age of about nine, died a natural death, and was mummified and placed in a human tomb that had been repurposed as a Bubastaeion (or Bubasteum), a burial place for mummified sacred cats (Callou et al. 2011; Zivie and Lichtenberg 2003; Ikram 2005).

An incident of Pantherinae burial at Teotihuacan, Mexico, was quite different. There, as elsewhere in Mesoamerica, creation or expansion of architectural monuments occasioned the depositing of offerings selected and arranged with symbolic significance related to the state and its ruling elite. In the third century CE, one of the episodes of enlargement of the Moon Pyramid occasioned an elaborate burial that included

an array of mammals, birds, and a reptile. Two Pantherinae species were represented, puma and jaguar. Some of the deposited felines were merely skulls from animals that had been skinned and defleshed. Others, with their legs bound, had been buried alive. Analyses of bones and stomach contents of some of the complete individuals indicate a varied history. Some had evidently been captured from the wild not long before their sacrifice. One of the pumas, a female approximately a year and a half old, was evidently held in captivity for a much longer period of time than the others. Perhaps during its capture in the wild, it had suffered several injuries, including one to the pelvic region that would have been fatal without human intervention. The state of the animal's teeth indicates that it had chewed on something, perhaps the wooden bars of a cage, for a prolonged time. Its last meal was a pair of young desert cottontails, one of which had signs of having been cooked, indicating that the cat had been fed by humans before being buried alive (Sugiyama et al. 2013). While rabbits (and similar animals) were the typical last meal for these captive cats, chemical analysis of the bones revealed that two of the pumas had also been fed omnivores, perhaps the flesh of domestic dogs or even humans. Mesoamerican art and Spanish accounts of the Aztecs more than a 1000 years later attest to the practice of feeding human flesh to captive carnivores (Sugiyama et al. 2015).

### Small Cats (Felinae)

Smaller feline species also acquired significance in human symbolic systems, although during antiquity only in Egypt did any Felinae achieve the prominence of the lion, jaguar, and other Pantherinae. Posing no threat to livestock, the presence of smaller cat species – for example, the wildcat, *F. sylvestris*, in Africa, Asia, and Europe, and the ocelot, *Leopardus pardalis*, in South and Central America – may have been encouraged by humans for control of commensal undesired species: the rodents attracted by stored food or waste, and the snakes attracted by the rodents. By the eighth millennium BCE, humans

had deliberately introduced the wildcat to the island of Cyprus, perhaps to control the house mouse (*Mus musculus*) that had also arrived with humans. The Neolithic site at Shillourokambos, Cyprus, has yielded the earliest known human burial of a feline, an 8-month-old male African wildcat (*Felis sylvestris lybica*) deposited in its own grave beside that of a young man. The excavators concluded that the wildcat served no religious purpose but had been, nonetheless, very likely killed in order to be included in the human burial (Le Mort et al. 2008).

An unidentified small cat (*Felis* sp.), presumably not domestic because of the age of the grave (Badarian, fifth millennium BCE), was found interred with a human and gazelle at Mostagedda, Egypt (Flores 2003). At cemetery HK6 at Hierakonpolis, in the early Naqada II period (c. 3700–3600 BCE), a young jungle cat (*Felis chaus*) was included in a grave with several anubis baboons (*Papio anubis*) and a very young hippopotamus (*Hippopotamus amphibius*). Between six to 8 months of age at the time of its death, the cat had already suffered at least one, and possibly two, episodes of trauma, likely during or after capture. Its survival for a period of 4–6 weeks, during which the bones healed, is attributed to human care. Its burial may have served the same function as that of the leopard interred at the site at a much later date, as a guardian and/or as an expression of subjugated chaos/nature. At about this same time, also in cemetery HK6, six young wildcats (*F. sylvestris*) were buried together. Their remains showed no sign of trauma or other pathology. The ages of the individual cats (two 7–12 months; four 4–5 months), which were buried simultaneously, suggest that the Egyptians may have been keeping and rearing tamed wildcats for pest control. These may even have been fully domesticated (Flores 2003; Van Neer et al. 2014, 2017).

Although a number of small cat species in both the Old and New Worlds are tamable, whether they possess other traits (exaptations) that would make each seemingly amenable to domestication (Cameron-Beaumont et al. 2002) or not (Ottoni et al. 2017) remains an open question. Among felines, only the commensal relationship between



*F. sylvestris*, the wildcat, and human developed into domestication, resulting in *F. catus* (or *F. sylvestris catus*) (Ottoni et al. 2017). This is the species most frequently thought of as a “sacred cat.” Paleogenetic analysis has demonstrated that domestic cats from Egypt contributed significantly to the populations elsewhere in the world of late antiquity (1st millennium CE), perhaps because it possessed behavioral traits that were exceptionally suitable for its interactions with humans (Ottoni et al. 2017).

By the Middle Kingdom (c. 2030–1640 BCE), and possibly earlier, domestic cats had acquired symbolic value as protective predators, as had their Pantherinae relatives. Cat deities were among the many protectors of the sun god Re as he traveled through the underworld at night (Delvaux and Warembo 1991; Malek 1993). Re himself was sometimes described as the “Great Cat” who slew his own foes. Re’s chief opponent was the great serpent of chaos, Apep, and in vignettes of spell 17 of the Egyptian Book of the Dead, a small cat – sometimes identifiable by its spotted coat as a serval, *Felis serval* – beheads the snake with a knife (Fig. 4; Delvaux and Warembo 1991; Malek 1993). These texts are of New Kingdom date (c. 1550–1070 BCE) and, in this same

period, plays on words led to equations between a female cat (in Egyptian, *miit*) and the goddesses Mut (“mother”) and Maat (“cosmic/social order”).

The strongest and best known of such leonine goddess/domestic cat associations was that of Bastet. This probably transpired sometime in the Twenty-second Dynasty (c. 945–712 BCE), but may have begun earlier. The Egyptians had long viewed Bastet as a less ferocious counterpart of Sekhmet, the goddess of war, disease, and healing (Delvaux and Warembo 1991; Malek 1993; Wilkinson 2003). The fertility of the domestic cat may have inspired the appearance of cat motifs on ritual objects and other contexts related to with Hathor, a goddess of human sexuality (Delvaux and Warembo 1991; Malek 1993). Human fertility and the survival of children was a concern in ancient times, and the nurturing, prolific domestic cat provided an attractive image of a divine force that might render aid in these matters (Fig. 5; Engels 1999).

Since the beginning of the pharaonic era (c. 3100 BCE), the Egyptians had singled out individual animals to serve as manifestations of particular gods. Not viewed as gods themselves, these animals functioned as living counterparts of



**Sacred Cats, Fig. 4** Feline predatory skills against snakes used to symbolize the defeat of chaos: The sun god Re as a cat slaying the serpent Apep. Facsimile drawing by Charles K. Wilkinson of a scene from the tomb of Sennedjem, Thebes (Theban Tomb 1). Original: Nineteenth Dynasty, reign of Ramesses II, c. 1295–1213 BCE. The Metropolitan Museum of Art, Rogers Fund, 1930, accession no. 30.4.1



**Sacred Cats, Fig. 5** An image of feline fertility used to ritually promote human fertility and good fortune: The Egyptian goddess Bastet as a cat suckling kittens. Lid probably from a box containing a cat mummy. Late Period–Ptolemaic Period (c. 664–30 BCE). The Metropolitan Museum of Art, gift of Abby Aldrich Rockefeller, 1929, accession no. 29.5a, b



the inanimate cult statues kept by every temple. Animal or image provided a medium through which to reach the divine, not only for oracles but to satisfy and appease the gods by means of regular cultic attention. The lion of Leontopolis reported by Diodorus Siculus would have been such a divine representative on earth, but otherwise virtually nothing is known of specific sacred felines. The most ancient sacred animal, and one of the best attested, was the Apis bull, which embodied the divine power of the creator god Ptah in the city of Memphis. Evidence for the Mnevis bull, sacred to the sun god, and ram of Mendes (a sheep, *Ovis aries longipes*, dedicated to the sun and to Osiris, god of the dead) is nearly as old. There was a series of each of these animals, a new one being chosen upon the death of the old, which was mummified and entombed. The Apis bulls were identified by special markings, the particulars of which changed with time. The selected animal was brought to the sacred precinct of the god with great fanfare and lived out its life in luxury (Ikram 2005).

The popularity of this kind of animal cult escalated in the late phases of ancient Egyptian history. From the Late Period (c. 712–332 BCE) until Christian times, Egypt experienced lengthy episodes of foreign rule, culminating with that of the Greeks and, eventually, the Romans. The distinctively Egyptian animal cults, which were viewed with varying degrees of negativity by neighboring contemporaries, may have been attempts to solidify an “Egyptian” cultural identity (Ikram 2005; Bleiberg et al. 2013). They may have also been attempts to return to what was perceived as the traditional cults of earlier, “better” periods. This would, it was hoped, appease the gods who would consequently restore Egypt’s former glory (Ikram 2005). The Greeks who ruled Egypt after its conquest by Alexander the Great sponsored the animal cults as part of their own attempt to legitimize themselves as successors of the native Egyptian pharaohs (Bleiberg et al. 2013).

Sacred cats may have existed earlier in the pharaonic period. At Abydos, during the Twelfth Dynasty (c. 1981–1802 BCE), seventeen cats and ceramic pots that the excavator presumed had contained milk were placed in a small pyramidal

tomb (Malek 1993). Whether these were sacred animals is unknown. Stelae (monumental slabs) from the workman’s village Deir el-Medina (near Luxor, Egypt), dating to the Nineteenth and Twentieth Dynasties (1295–1070 BCE), show individuals venerating divine cats called “peaceful,” “perfect,” or “great.” Whether these were sacred – that is, living – cats or simply depictions of deities in feline form is likewise unknown (Malek 1993).

Whatever motivated the animal cults in later times, they resulted in the keeping and breeding of vast numbers of sacred animals of many taxa until the fourth and fifth centuries CE, when the Christian Roman emperors abolished pagan worship. Among them were crocodiles, birds (especially ibises and raptors), primates (especially baboons), domestic dogs, and a variety of small felines (Ikram 2005; McKnight 2010; Bleiberg et al. 2013). The cats served as the sacred animals of Bastet above all, but, in the symbolic entanglement of big and small cats, they also functioned for other goddesses whose primary association remained the lion, which was not so readily manageable in captivity. In the fourth century BCE, a man named Padikem was “prophet of the living cat of the temple of (the lion goddess) Pakhet” at Hermopolis, in Middle Egypt, site of a large animal mummy necropolis (Malek 1993). Such cult centers existed throughout the country, including major ones at Bubastis in the Nile Delta, at Saqqara (near modern Cairo), and, in Middle Egypt, at Tuna el-Gebel and Speos Artemidos (Delvaux and Waremboel 1991; Ikram 2005). At such places, devout individuals came to make offerings to the god or goddess or to solicit an oracle in which the sacred animal may have played some role (Ikram 2005).

Foreign and Egyptian textual sources, as well as the excavated remains of the animals, offer hints regarding the management of the sacred cats. Temple slaves (*hierodouloi*) with the title “cat-feeder” (*ailouroboskos*) are known (Engels 1999). According to Diodorus Siculus, cats were given raw fish, or milk with pieces of bread (I.83.2). Feedings were done publicly (I.83.4), and to call the cats for their meal, the caretakers made a clucking sound (I.83.2). Temple cats were

fed lavishly, bathed regularly, anointed with oils, censured with aromatics, and adorned with jewelry (I.84.5–6). In this respect, they were treated very much like the temple's cult images. For male animals, especially fine females were provided as “concubines” and treated with equal splendor (I.84.6). Upon its death, a cat was mummified and awarded a lavish burial (I.83.5, I.84.7–8).

This resulted in vast necropolises of animal burials (Ikram 2005; Bleiberg et al. 2013). Study of the cat mummies from the Bubasteion at Saqqara revealed that the overwhelming majority of cats were domestic, although wild species were also treated in this manner (Ikram 2005; McKnight 2010). Those provided with wooden coffins or stone sarcophagi may have been individual animals singled out and maintained as manifestations of the goddess (Ikram 2005; McKnight 2010).

The vast majority of mummified cats had been desiccated intact (without evisceration) and

wrapped in linen, commonly with an indication of the face provided by shaping of the linen and/or painted details. Some two-thirds of the mummies were immature animals that had died either by strangulation or by a blow to the head (Ikram 2005; McKnight 2010). The temples were evidently breeding cats expressly to be killed in order to create votive mummies, which were sold to worshippers. The devout individual would then offer the mummified cat to the goddess: the souls of the dead animals would serve as intermediaries between human and the divine realm and intercede on behalf of the supplicant (Bleiberg et al. 2013). To this end, literally millions of cats (and comparable numbers of other taxa) were sacrificed, mummified, and interred (Figs. 6 and 7). As fertile as domestic cats are, demand outstripped supply. Examination with X-rays has revealed that the priests also created fake votive mummies with a little or no remains



**Sacred Cats, Fig. 6** Votive cat mummy and radiograph. University of Pennsylvania Museum of Archaeology and Anthropology accession no. L-55-13. Courtesy of Penn Museum, image # L-55-13



**Sacred Cats, Fig. 7** Votive “cat” mummy and radiograph revealing it to be “fake.” University of Pennsylvania Museum of Archaeology and Anthropology accession no. 50-17-1. Courtesy of Penn Museum, image #45479

of an animal (Fig. 7) (Ikram 2005; McKnight 2010).

Because of their utility as controllers of pests, domestic cats from Egypt and elsewhere spread throughout the Roman Empire (Engels 1999; Ottoni et al. 2017). The worship of Egyptian and Egyptian-influenced deities (such as the Greek and Roman goddesses of the hunt, Artemis and Diana, who were identified with Bastet) spread as well. Although the early Christians adopted the motherly cat as a symbol of the Virgin Mary, an artistic motif that continued to appear into the Renaissance (1300–1700 CE), the deep pagan associations of felines might have resulted in their later identification as animals of witchcraft and consequent episodes of persecution of the cat in Europe (Engels 1999; Lawrence 2003).

## Conclusions

The historical reality of the sacred cat – a binary of reverence and sacrifice – is largely at odds with modern imagination and popular culture. Being

identified with gods and other divine forces on account of their appearance, behavior, and “super-human” abilities did not spare cats or other animals from exploitation. On the contrary, religious associations encourage their use not merely as metaphoric imagery and foci of worship but also, first and foremost, as consumables in cult ritual. Culture-specific human perception of specific taxa (either species or higher ranks) and the natural world at large has important implications for conservation efforts, animal welfare, and other human-animal interactions.

## Cross-References

- ▶ [Animal Welfare](#)
- ▶ [Anthropomorphism](#)
- ▶ [Captivity](#)
- ▶ [Carnivora](#)
- ▶ [Carnivore \(Diet\)](#)
- ▶ [Domestication](#)
- ▶ [Feline Diet](#)
- ▶ [Feline Life History](#)

- [Feline Morphology](#)
- [Feline Sensory Systems](#)
- [Human-Animal Interaction](#)
- [Pets](#)
- [Zoo](#)

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## Safari

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## Synonyms

Biodiversity; Hunt; Journey; Outfit; Tourism; Wildlife

The term “safari” originates from the East African language Swahili, meaning expedition or outfit for a journey, while utilizing state, communal, and/or private land and currently lacks a specific definition (Roth and Merz 1997; Chardonnet et al. 2002). Historically the term safari was associated with big-game hunting (also known as “safari hunting”) in East Africa that started in the 1800s (Mbaiwa 2008). Safari hunting for tourism purposes, only deemed as tourism since the 1960s, still occurs within many African countries today resulting in various benefits (e.g., employment opportunities, economic benefits) and challenges (e.g., reliance on foreign companies, controversy surrounding its use) (Mbaiwa 2004, 2008).

In the modern day, the term also refers to traveling, most commonly associated with the African savannah, for the purposes of tourism (i.e., viewing and appreciating natural landscape and unique wildlife such as the “Big Five” including lions, giraffe, elephant, rhino, and hippos)

and/or for film/photography and research purposes (Eastman 1995; Roth and Merz 1997). Forms of safari transport vary and may include, but are not limited to, guided vehicles, self-drive vehicles, walking/hiking, hot air ballooning, and horseback. This form of wildlife tourism is well established in many African countries and has been noted to attract large numbers of foreign tourists. Furthermore, safaris have been found to be one of the most popular tourist attractions in Africa as provided by 96% of 145 tour operators surveyed selling trips to Africa from 31 countries, and it has become an economic driver in a range of African countries (Chardonnet et al. 2002; World Tourism Organization 2014). Safaris also take place within other countries, which may be conducted in order for tourists to view specific endangered species, such as the endangered arctic fox (*Vulpes lagopus*) in Sweden (see Larm et al. 2017).

More recently, the term safari has also been incorporated into captive zoological collections, such as drive-through wildlife parks (e.g., Woburn Safari Park, UK), while the term has also been used within zoos to highlight resembling themes and species of the African savannah and/or for events such as “Safari in the City” held by ZSL London Zoo in 2017 which raised over £375,000 in order to help tackle poaching and illegal wildlife trade (ZSL London Zoo 2017). The safari theme has also been incorporated in other commercial aspects and has influenced areas ranging from films to fashion (e.g., safari chic). More research is required to help to further understand the definition and perceptions of the term and its use in relation commercial settings and within popular culture.

In summary, despite the popularity of safaris, both in terms of tourism and use of the term in popular culture, more evidence-based research is needed on safari hunting, tourism, and how it affects wildlife and the environment in which it occurs. This would help inform safari stakeholders about future planning, monitoring, and governance of such activities especially in areas which hold small groups of endangered species. Further research could also investigate alternative



avenues (e.g., virtual tourism) that may ensure endangered species are protected while ensuring minimal environmental disturbance.

## Cross-References

- [Conservation](#)
- [Hunting](#)
- [Savannah](#)

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## Salamander

- [Caudata Cognition](#)

## Salamander or Newt Locomotion

- [Caudata Locomotion](#)

## Saliency

- [Feature Integration Theory](#)

## Salientia Communication

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## Introduction

Animal communication occurs when a sender exchanges information, through a codified signal, with a receiver to the benefit of both. In anurans, communication is notorious during courtship and male-male agonistic interactions. Usually, males advertise their presence and readiness to mate while keeping rival males at bay, whereas females scrutinize chants in order to assess males' qualities and choose preferable partners (see Vallejos et al. 2017 for an exception). Thus, in most species, signals are primarily produced by males, placing them as senders and receivers, while females act mainly as receivers (Gerhardt and Huber 2002). In this section, we synthesize studies on anuran senders and receivers, what sort of information they exchange, what are the signals, and how they are produced and transmitted in anuran interactions. Moreover, we examine potential communication modalities

based on observed sensory cues perception by conspecifics.

Because anurans communicate primarily via acoustic signals, other sensory modalities seem to have been neglected for a long time and have only recently received more attention (Starnberger et al. 2014a, b; Woodley 2015). Recent studies have reported alternative modalities such as chemical and tactile communication. Additionally, for most vertebrate groups, communication has been shown to occur through complex signaling, composed of multi-sensory modalities. These signals are frequently referred to as “multimodal.” Possible causes and functions of multimodal signaling in anurans are based on behavioral field observations and experimental tests.

## Acoustic Communication

Calling activity is the primary communication mechanism for anuran amphibians (Gerhardt and Huber 2002). Each anuran species can have distinct vocalization patterns, and individual frogs produce a variety of calls, for which several distinct categories are recognized (Toledo et al. 2015). Several authors have proposed classifications and categories for the calls emitted by anurans (e.g., Duellman and Trueb 1994; Wells 2007). Recently, Toledo et al. (2015) standardized the anuran call classification, with 13 distinct call types, which can be divided into 3 categories according to social context: (1) reproductive, (2) aggressive, and (3) defensive.

Reproductive calls are the most commonly heard and with the highest value for systematics due to its function as an important premating isolation mechanism. Advertisement calls are long-range signals emitted usually by males during breeding season to attract conspecific females for reproduction. A single male's call usually reveals its species, sex, reproductive state, and location. This call can also attract males at a long distance to join the chorus and might be used to establish territorial limits for conspecifics (Toledo et al. 2015; Köhler et al. 2017). More than five types of

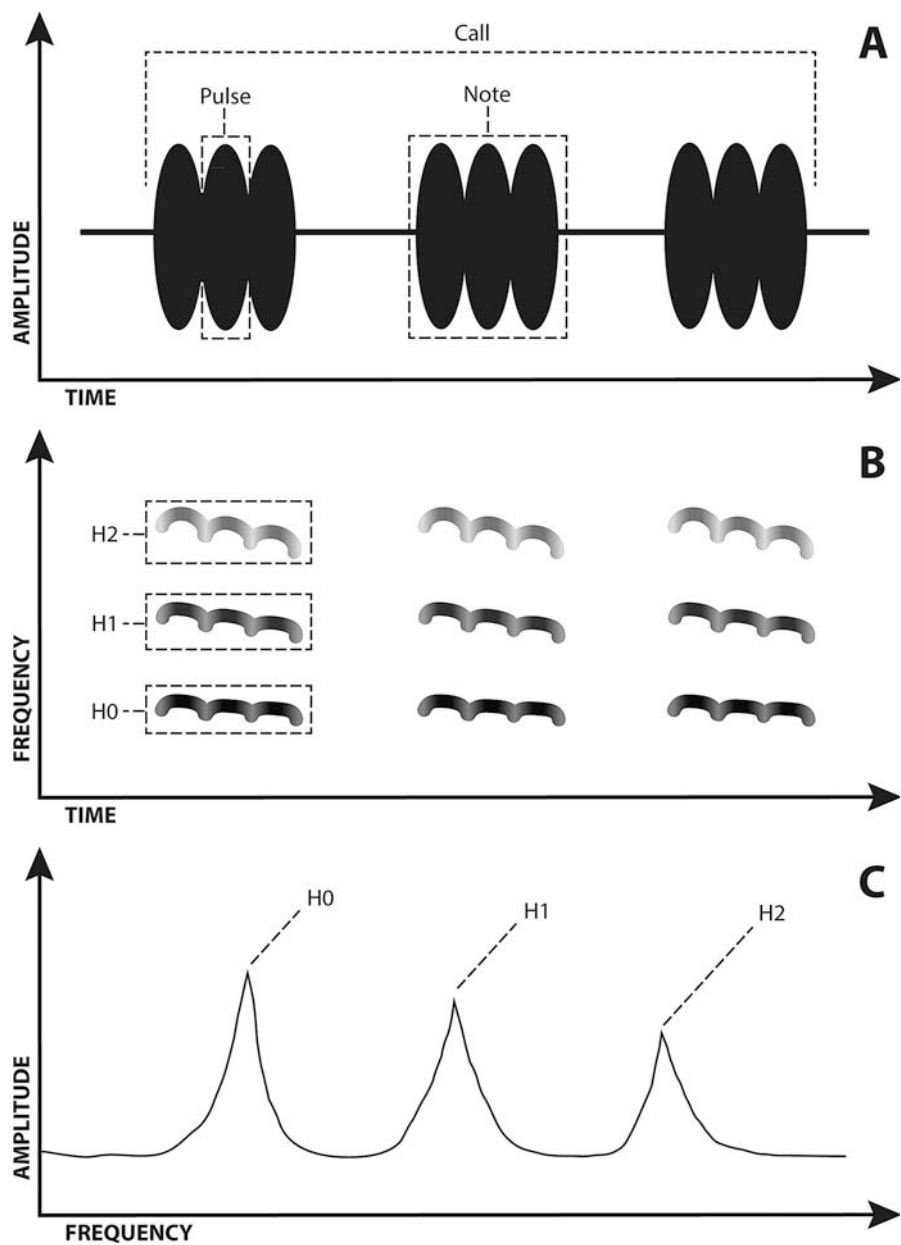
reproductive calls have been proposed for anurans: courtship, amplexant, release, post-oviposition male release, and rain calls (see Toledo et al. 2015 for further definitions).

Aggressive calls are emitted by male frogs to defend their calling sites against conspecific competitors. Territorial call, the most common of this category, is emitted by males defending specific resources inside a territory like the calling, egg laying, retreat, or feeding sites. Consequently, this call acts by setting boundaries between males in a reproductive chorus. There are another three types of aggressive calls described for anuran species: encounter, fighting, and displacement (see Toledo et al. 2015 for further definitions). Besides the aforementioned categories, three sub-categories (alarm, distress, and warning calls) of defensive calls are interpreted as adaptations to prevent predation (see Toledo et al. 2015 for further definitions).

## Structures of Bioacoustic Signals

Sound is a pattern of transmitted energy through pressure waves. Wave components can be depicted in sound graphs, illustrating changes in amplitude over time (oscillogram) or transformed into frequency domains through a fast Fourier transformation, which decomposes the complex waveform into sine waves for analysis, producing spectrograms and power spectra (Fig. 1). Many sounds concentrate energy in several separate, evenly spaced frequency bands, called harmonics, which are multiples of the lowest harmonic (i.e., first or fundamental; see Fig. 1). The dominant frequency is the one that contains the greatest amount of energy. This can be either the fundamental frequency or one of its harmonics (Ryan 2001; Vitt and Caldwell 2013; Köhler et al. 2017).

Bioacoustic signals are divided into units (call) and subunits (notes and pulses). The term pulse applies to short signals, with a single unbroken wave train delimited in time by significant amplitude reduction. Notes are usually groups of pulses and the main subunit of a call, with short intervals, relative to total call length, of 100% amplitude modulation (i.e., silence) between them. Calls are the primary structure of an anuran



**Salientia Communication, Fig. 1** Oscillogram (a), spectrogram (b), and power spectrum (c) of a single hypothetical call composed of three notes with three pulses

each. Note the first three harmonics indicated in b and c. The fundamental frequency (lowest band in b) corresponds to the dominant frequency (highest peak in c)

acoustic signal and are separated from other calls by periods of silence (typically much longer than the call). Calls may be composed of one or several notes of the same type (simple call) or different types (complex call) (Köhler et al. 2017). The waveform shape of a call, note, or pulse is called

envelope. A period is the duration of a call structure, unit or subunit, plus the interval between consecutive structures. Repetition rates are the number of such call structures emitted per period of time, usually per one second or minute (Ryan 2001; Köhler et al. 2017).

## Mechanisms of Sound Production and Reception

The basic mechanism of sound production in most anurans is activated while exhaling. A positive pressure, created by the contraction of muscles in the buccal cavity, pumps air into the lungs. Then, contraction of trunk muscles forces the air from the lungs into the buccal cavity, through the larynx, where it causes the vocal cords to vibrate and produce sounds. These sounds are further modified by muscles of the larynx and associated cartilages, between the lungs and the buccal cavity. Then, such morphological structures are more developed in males. Exceptions to this sound production process can be seen in *Bombina* (during inspiration) and in *Discoglossus* (during both inspiration and expiration) (Wells 2007).

The anuran laryngeal apparatus lies between the lungs and the buccal cavity and therefore is involved in both respiration and sound production. In most anurans, the larynx is composed of a pair of arytenoid cartilages, which houses the vocal cords. These moveable cartilages are supported by the cricoid cartilage, which attaches the larynx to the hyoid apparatus and serves as a point of attachment for various muscles. The vocal cords can only be stimulated when the arytenoid cartilages are apart, allowing air flow through the larynx. In the family Pipidae, however, males lack vocal cords and use a modified laryngeal skeleton to produce sound. Calls consist of sharp clicking sounds produced when the arytenoid cartilages are suddenly pulled apart. Sounds are amplified by an enormous boxlike cricoid cartilage. Hence, sound production in pipids requires contraction of the laryngeal muscles, but does not involve contraction of the trunk muscles or the production of vibrations in an air stream (Duellman and Trueb 1994; Wells 2007).

In males of many frog species, vocal sacs are connected to the buccal cavity, typically via slit-like openings, and are inflated during vocalization. The vocal sac is not an acoustic cavity resonator as it was previously suggested, although it may serve to direct the call toward the receiver or as a reservoir of mechanical energy during

calling. Morphology varies from a median single subgular sac to bilobate and paired subgular sacs or paired lateral sacs. Anuran vocal sacs can be slightly or highly distensible and are defined as either internal or external vocal sacs. Their form and color might also have a role in visual signaling (Wells 2007; Köhler et al. 2017).

Anurans have a large tympanic membrane of thin, nonglandular skin, which receives airborne sound waves and transfers sound pressure-induced vibrations to the columella in the middle ear. These vibrations disturb the fluids in the inner ear through the oval window between the columella and the inner ear. Within the anuran inner ear, two sensory organs are largely responsible for the perception of airborne sounds: the amphibian papilla, sensitive to low and mid-frequencies (typically 50 Hz to 1 kHz), and the basilar papilla, sensitive to higher frequencies (above 1 kHz). Some anurans species, however, lack tympanic membranes, columella, or even middle ear cavities and might communicate effectively with airborne sounds throughout the *opercularis* system, which detects vibrations from the substrate. However, recently, two anuran species (*Brachycephalus ephippium* and *B. pitanga*) lacking tympanic membrane, extrastapes, stapes, and middle ear cavity – hence considered “earless” – are deaf to high-frequency signals, suggesting that these species are unable to perceive their own produced calls (Goutte et al. 2017).

## Morphological and Environmental Effects on Acoustic Signals

Noise is any unwanted sound that interferes with the detection of a signal and the information transmission, being a combination of non-biological or environmental noise (e.g., wind and turbulence) and biological noise (sounds from other animals) (Forrest 1994).

Many individuals of a different number of species using the same breeding sites could generate noise and become a potential problem (Stebbins and Cohen 1995). Heterospecific acoustic interference have diverged due to temporal characteristics of their calls (calling rate, call duration, call complexity, or the number of notes), spatial

separation at breeding sites, and spawning and in other ways. Vocal divergence helps to ensure species recognition and reduces the chances of mismatings between closely related species and wasted reproductive effort serving as an efficient premating isolating mechanism (Forrest 1994; Ryan 2001; Gerhardt and Huber 2002).

Naturally, the sound's pressure, intensity, and fidelity decrease the longer the distance it travels. The call can be attenuated and degraded, and the surrounding environment might impose a strong constraint on it by means of sound refraction, reflection, and absorption along the transmission path. Sound scattering and reflection also play a role in call degradation, defined as the decreasing of call integrity by losing definition in temporal traits and amplitude patterns. So, long-range communication must be efficient in order to overcome these issues. For effective mate attraction, the call should not only have sufficient intensity when it reaches the receiver to be detected, but it must also be discernible as a conspecific call (Ryan 1988; Forrest 1994; Wells 2007).

Habitat can differentially affect aspects of the calls. For instance, reverberations are almost completely absent in open habitats. On the other hand, signals in open habitats are prone to degeneration from different sorts of temporal interferences, like the wind (Ryan 1988).

The speed of a sound depends on air density and temperature. Sound travels faster in warmer air; thus temperature can influence spectral properties of calls. Temperature can be especially important when it affects properties of calls used by females to discriminate among sympatric species (Ryan 1988). Furthermore, anurans are ectotherms, and temperature influences those attributes of acoustic signals that are controlled by neuromuscular system (e.g., call, note, and pulse rates and durations) (Gerhardt and Huber 2002; Wells 2007; Köhler et al. 2017). Usually, researchers evaluate the strength of the association between environmental temperature at the time of recording and acoustic features by means of correlation tests or linear regression (Köhler et al. 2017).

The body size is usually strongly correlated with spectral traits, suggesting that fundamental

and dominant frequencies are under morphological constraints. Since larger vocal cords are able to vibrate at lower frequencies and larger frogs usually produce calls at lower frequencies, vocal cord mass and length seems to be directly proportional to the frog's size. However, temporal traits have only rarely been suggested to be influenced by body size (see Bee and Gerhardt 2001). Besides the body size, call frequency can also be actively modified by changing the tension of the vocal cords associated with the contraction or relaxation of various muscles associated to the larynx (Gerhardt and Huber 2002).

### Social Interactions

Choruses are aggregations of acoustically signaling animals, formed by individuals of different species in areas where physical resources (within or along the margins of standing water in anurans) required by females to lay their eggs are present. Such behavior can reduce individual risks of predation making harder to find signaling individuals or by increasing the chances of predators being detected by some individual who then alerts the rest of the group. Chorusing increases the range of female's attraction since a group of signalers can be heard louder than single individuals at great distances. On the other hand, these aggregations intensify the competition among males to attract mates, to acquire and defend resources needed by female, or both (Gerhardt and Huber 2002).

Satellite behavior is a tactic in which males do not call while situated near a calling male, parasitizing the calling efforts of other males. This behavior usually depends on the individual's age, size, energy reserves, physical condition, signaling ability, and density of calling males. This tactic may be the only chance to mate for small, young, or weak individuals in species in which larger, established males hold territories and attack other males within or near their territories. Satellite males can intercept females that are attracted to the calling male, wait for the calling male to vacate its territory or calling site, or both (Gerhardt and Huber 2002; Wells 2007).

To avoid interference of overlapping conspecific calls, males commonly alternate their



calls when close to one another, a behavior essential to preserve energy when high calling rates are emitted, particularly in those species that have prolonged breeding period and in which males are territorial.

### Honest and Dishonest Signals

Sexual selection encompasses the array of behavioral tactics used by individuals to acquire mates. Females select males as mates and represent a limiting resource and object of competition among males. Thus, males are subject to more intense sexual selection than females, and traits that enhance the ability of males to locate, attract, capture, or retain possession of females will be favored by sexual selection, as will traits that reduce the amount of time between successive matings (Wells 2007).

Honest signs transmit reliable information from sender to receiver. There is a general assumption of sexual selection that signals given by males to attract females tend to be energetically expensive to produce. Females often are attracted to males that emit long, loud, or high-rate signals, traits that are positively correlated with levels of energy expenditure (Ryan 2001). The energy cost usually keeps the signal traits honest and then reliable to receivers while assessing senders' information (Searcy and Nowicki 2005).

Besides the signal costs, constraints can influence in keeping signals honest. Given the physical body-size constraint of frequency in anuran calls, females and male competitors can interpret frequency traits as an honest signal portraying body size of the sender and, thus, its strength and quality. The fundamental frequency of calls is partially determined by the shape and size of laryngeal apparatus, which in turn is constrained by the body size (Bee et al. 2000; Wells 2007; Köhler et al. 2017). Thus, females and males rely on spectral properties of acoustic signals to assess male's quality and opponent's size during courtship and aggressive encounters, respectively (Bee et al. 2000; Köhler et al. 2017).

There are a few reported cases of dishonest signaling in anurans. In some species, males can alter call properties in order to emit a dishonest signal and be perceived as being bigger than they

really are. For instance, in *Lithobates clamitans*, small male frogs can alter spectral properties during intraspecific interactions, emitting a dishonest low-frequency call when confronted by larger opponents (Bee et al. 2000).

### Visual Communication

Visual signaling is an alternative or complementary form of communication. This communication can be transmitted over relatively short distance and are often hindered by obstacles in the environment. This means distance (usually individuals need to be less than 50 cm apart) and light are restrictions for the communication process. This behavior may occur in both intra- and inter-specific levels and is associated with reproduction (e.g., for female attraction), aggressive interactions related to territoriality, or predation and might be seen in males only or both males and females.

Species that breed at sites with high ambient noise levels, such as near waterfalls or torrential streams, might favor communication through visual display that either supplement or replace acoustic signals. Background noise might also be produced by other frogs and insects' vocalizations in species that breed in lentic water bodies (e.g., *Boana albomarginata*) and reduces the female's ability to discriminate among conspecific calls. The usual explanation is that the background noise makes vocal communication difficult; thereby close-range communication (visual and acoustical) is favored.

Foot-flagging or arm-waving displays might indicate agonistic contexts. Such displays are usually performed after conspecific males' approach or vocalize close a signaling individual. Once the first visual displays are performed, the outcome of interactions depends on the potential intruder. If the intruder calls, approaches further, or displays visually, the initial display is usually followed by further displays or physical combats. Initial displays or combats usually end when the intruder retreats. However, in some cases, the male starts to emit advertisement calls, and, when close to the female, he starts foot-flagging displays that

presumably increase the female's excitation. The female may respond to the visual signal with the same display or with a different one (Ryan 2001).

Anuran vocal sacs are quite diverse in coloration and shape and have an important role in visual signaling. The change of vocal sac color during the courtship, known for some anuran species, suggests that it could play a role in visual communication. Gular inflation is synchronic with the call emission and may facilitate female localization of individual males in an aggregation. Even in species without distinctly colored vocal sacs, movements of the vocal sac may serve as a visual signal to other males or to females searching for mates (Rosenthal et al. 2004).

Visual communication can also be used in interspecific interactions. Aposematic signals as well as deimatic behavior are important and well-known anti-predator defenses. Deimatic behavior consists of intimidating postures or actions taken when caught by pursuing predators. It is usually associated with aposematic colors or a mimetic behavior. The *unken* reflex is a type of deimatic behavior in which the frog lifts all four legs and arches its back, drawing attention to the bright ventral surface. Such defensive behavior is effective in species with ventral warning coloration (e.g., *Bombina* and *Melanophryniscus*) (Ryan 2001). On the other hand, the eyespot display used by *Physalaemus nattereri* might be a tactic to mimic a bigger animal's body part such as a snake's head (Sazima and Caramaschi 1986).

## Chemical Communication

Chemical signal is the primary source of communication in salamanders (Caudata) and probably in caecilians (Gymnophiona). Historically, chemical communication has been presumed for many anuran species considering their skin permeability and the occurrence of physical contact during the amplexus (Rödel et al. 2003; Willaert et al. 2013). The first evidences suggesting the occurrence of this communication modality in anurans came from experimental studies on chemical perception (e.g., Rabb and Rabb 1963).

Tadpoles of many species are known to be able to detect chemical cues from predators (and injured conspecifics), conspecifics (to avoid intraspecific competition), heterospecifics, and relatives (kin recognition), which may active or passively release chemical compounds (reviewed in Belanger and Corkum 2009). In *Anaxyrus cognatus*, for example, post-metamorphic individuals aggregate possibly guiding each other by using chemosignals (Graves et al. 1993).

Part of the expectation for perception of chemosignals underwater is related to the known complex dual olfactory system of amphibians. Besides the main olfactory epithelium, which is more sensitive to airborne molecules, anurans have a vomeronasal organ (VNO; Belanger and Corkum 2009), which is more sensitive to waterborne molecules (Starnberger et al. 2014b). Apparently, the VNO develops and achieves early significant maturation in tadpoles in order to detect chemical cues in the water (Jungblut et al. 2012). For instance, tadpoles of *Kurixalus eiffingeri*, a Taiwanese rhacophorid tree frog, increase their activity in water conditioned by adult female or male, suggesting chemical perception of conspecifics (Kam and Yang 2002).

Chemical mate recognition and/or attraction based on waterborne substances has also been demonstrated for adults of some species. In the tailed frogs, *Ascaphus truei*, reproductive individuals show a preference for chemical cues from the opposite sex than those from the same sex (Asay et al. 2005). Females of *Ranoidea splendida* are attracted by "splendipherin," a waterborne pheromone produced in males' cephalic glands (parotid and rostral glands; Wabnitz et al. 1999).

Sexually dimorphic skin glands (SDSG; dermal macroglands often called "breeding glands"; e.g., Pearl et al. 2000; Willaert et al. 2013) have been reported for several anuran species (e.g., Brizzi et al. 2003) and recently their intra- and intersexual functions have been observed and/or tested (e.g., Pearl et al. 2000; Starnberger et al. 2013; Brunetti et al. 2014). Taxonomists have described and used presence and shape of conspicuous glands as a taxonomic

feature for many anuran groups (e.g., Vences et al. 2007). Studies on reproductive biology of *Boana punctata* species group (i.e., *B. atlantica* and *B. punctata*), both in field and laboratory, described female contacting her snout to the flanks and gular regions of the male, where lateral and mental glands are located, respectively (Brunetti et al. 2014 and references within). Based on these observations and on the structure of the glands, it is suggested that the mental and lateral glands might produce substances used during courtship communication, as in many plethodontid salamanders (see Wells 2007).

In an experimental study, females of a dwarf African clawed frog, species of the genus *Hymenochirus*, show a positive chemotaxis to water with males or male's homogenized post-axillary breeding glands, whereas males of this species show no response to either water housing males or females, indicating a production of mate-attractant chemosignal (Pearl et al. 2000). On the other hand, the odorous mucus of both sexes functions as a sexual attractant in the terrestrial Australian toadlet *Pseudophryne bibronii* (Byrne and Keogh 2007).

In many anurans (e.g., *Leptodactylus* spp. and *Rana* spp.), males develop, as secondary sexual trait, keratinized spiny nuptial pads on the bases of the first fingers (i.e., thumbs) during the breeding season (reviewed in Brizzi et al. 2003). These nuptial pads usually have associated glands that would presumably produce glue-like substances to enhance the amplexus (Brizzi et al. 2003). Nonetheless, in *Rana temporaria*, these glands produce proteins structurally similar to those found in plethodontid salamanders, called "amplexins," that might stimulate females to lay eggs. Apparently, these proteins could be delivered directly into female's circulatory system through wounds on the female's ventral surface, which result from abrasion between the male's spiny pads and female's skin during amplexus (Willaert et al. 2013).

Although rarer, some studies have reported male-male interactions stimulated by chemosignals (see Woodley 2015). For instance, males of *Leptodactylus fallax* produce a substance

(*Leptodactylus* aggression-stimulating peptide; LASP) in their skin glands induced by intrasexual aggression (King et al. 2005). Males exposed to LASP become more aggressive, displaying behaviors such as jumping and rearing, whereas females had no response to LASP. Males of *Pseudophryne bibronii* avoid substrate marked by other males and react to this, switching from emitting advertisement calls to territorial calls after being exposed to other males' chemosignals (Byrne and Keogh 2007).

Chemicals reported in aforementioned cases are peptides or proteins and then limited to be spread in water or through direct contact (Starnberger et al. 2013; Starnberger et al. 2014a; Willaert et al. 2013). Yet, a few studies also indicate communication via airborne chemical cues (see examples in Woodley 2015). Experiments with the American toad, *Anaxyrus americanus*, show male orientation toward volatile chemical cues obtained from females (Forester and Thompson 1998). Individuals of the poison frog, *Dendrobates auratus*, are attracted to the opposite sex based on olfactory communication (Korbeck and McRobert 2005). More recently, Brunetti et al. (2018) found that the sex-specific volatile components of the Neotropical tree frog, *Boana prasina*, are produced by bacteria of the genus *Pseudomonas* present in the frog's skin. Biochemical and histological analyses of the gular glands of 11 species of 4 hyperoliid genera demonstrated males as capable to produce volatile compounds (Starnberger et al. 2013; reviewed in Starnberger et al. 2014a, b). These glands are located at the gular region of the tree frog males, forming a distinct patch on the inflated vocal sac during calling activity. Moreover, there is a huge compound diversity (65 different types) in species-specific chemical combinations (Starnberger et al. 2013). It has been suggested that these compounds might be actively fanned out and spread into the air by vocal sac pulsations, while males are calling, functioning as a chemosignal in a multimodal communication to species recognition and mate choice (Starnberger et al. 2013, 2014a, b). Species-specific communication via volatile chemosignals is also likely in mantellid

frogs from Madagascar (Poth et al. 2013). Males of many mantellid species have distinct femoral glands (Vences et al. 2007), which produce airborne chemicals capable of increasing individual activity in both sexes (Poth et al. 2013).

## Tactile Communication

Pre-mating touching between male and female has been reported for some species, such as *Aplastodiscus* spp., *Hylodes* spp., *Bokermannohyla ibitiguara*, *Boana atlantica*, *B. punctata*, *B. faber*, and *B. rosenbergi* (Brunetti et al. 2014, de Sá et al. 2016; and references within). For many of these taxa, the amplexus only occurs after female physically contacts the male (see Brunetti et al. 2014; de Sá et al. 2016). Females of *Hylodes japi* can repeatedly touch the posterior part of male's body out of his sight during the courtship behavior, inducing him to emit courtship calls, which suggests the tactile signal as the single stimulus in this case (de Sá et al. 2016). However, for most cases, occurrence of chemical or visual communication during the physical contacts cannot be excluded, making the presence and extension of mechanical stimulus not clear (Brunetti et al. 2014). Moreover, tactile communication studies have failed to fully explain how information can be coded into and assessed from the signals. For instance, in *Boana rosenbergi*, female choice seems to be likely based on differences of male's physical contact. However, how exactly females assess a male's quality through physical contact and what are the preferable signal traits are not known (Kluge 1981).

Tactile stimuli are also frequently observed when tadpoles beg for unfertilized eggs in species with maternal egg provisioning (e.g., Kam and Yang 2002; and references within). Tadpoles of dendrobatid strawberry poison frog, *Oophaga pumilio*, stop swimming and start vibrating their bodies when close to the parents (reviewed in Dugas 2018), while tadpoles of the rhacophorid tree frog *Kurixalus eiffingeri* also nip the skin of mother's cloaca and thighs (Kam and Yang 2002).

## Multimodal Communication

Multimodal communication refers to the cases where the signals are produced and received using two or more sensory modalities. Although anurans have, as well as for most animal taxa, their predominant modality (i.e., acoustic communication), a growing amount of evidences has demonstrated the occurrence of multimodal signals (usually composed of an acoustic signal plus a visual or chemical one; see above). Four information content hypotheses have been proposed for additional components in anuran communication. They may be (1) useless such as in signals produced by-product (epiphenomenon), (2) redundant in relation to that present in the primary modality (i.e., components possess similar information but only one is necessary), (3) complementary as a reinforcement for signal perception by receivers (they make the whole signal more conspicuous to receivers but are still not necessary), or (4) essential as subcomponents of a complex signal, which, if decomposed, would not be perceived by receivers during communication (de Luna et al. 2010).

The different components of the apparent trimodal communication (chemical, visual, and acoustic) of the hyperoliid species might function as redundant stimuli for females (Starnberger et al. 2013). Since these tree frogs usually breed in a multi-species context (i.e., several species communicating and breeding at the same time and space), redundant signals emitted through different channels and sensory systems might facilitate recognition and locating of conspecific males (Starnberger et al. 2014b). In *Engystomops pustulosus*, extra sensory modalities are not necessary for female attraction but may be beneficial for sender while increasing efficacy and conspicuousness of the signal and for the receiver as acting as additional cues to assess male's quality during mate choice (Taylor et al. 2011). Although female tactile stimuli only stimulate males during courtship interactions, a combined bimodal (visual + tactile) signal can be threefold more stimulating than separated ones (de Sá et al. 2016).

Evidences of whether each signal component is important as stimulus come from experimental studies. For example, territorial and aggressive *Allobates femoralis* males only attack other males if a bimodal signal (acoustic + visual) is produced, i.e., there is no reaction in cases with a single modality only (either visual or acoustic; Narins et al. 2003; de Luna et al. 2010). In this species, both sensory modalities seem to act as nonredundant components (de Luna et al. 2010). Initially, the required visual component was attributed to the pulsation of the vocal sac during calling (Narins et al. 2003). However, de Luna et al. (2010) found that body movement can instigate the same aggressive behavior, suggesting that any individual movement can function as an additional component to the acoustic one.

## Conclusion

Anurans primarily communicate intra- and interspecifically through acoustic signals. Males inform their position, readiness, and status to rival males and females. The assessment of male's quality by female is particularly important to species-specific recognition and sexual selection, since females of many species choose mate mainly based on acoustic signals (Gerhardt and Huber 2002; Köhler et al. 2017). Although these signals are the most conspicuous, other communication modalities have received more attention from researchers who have demonstrated them as being more widespread and important within the order than originally thought (Starnberger et al. 2014a, b).

As well as in the acoustic modality, visual and chemical communications occur in both male-male agonistic interaction and male-female mate choice (review in Ryan 2001; Woodley 2015). However, in species with repertoires composed of different signal modalities, regardless of whether the signals are obligatorily synchronized or not, each sensory channel seems to be used in a different phase of the behavioral event. According to field observations, initial phases of the courtship and aggressive interactions usually occur at significantly long inter-individual

distances and, therefore, are similarly dependent on long-range signals such as sounds, whereas final phases of these interactions tend to occur at closer distances, allowing the use of typical close-range signals such as in chemical, visual, and tactile communication (see Pearl et al. 2000; e.g., Starnberger et al. 2013; Brunetti et al. 2014; de Sá et al. 2016).

Even in synchronous multimodal signals, each of them may play a different role and be used for a slightly different purpose in intraspecific communication. In most species with acoustic, visual, chemical, and tactile signals, the former and the latter occur in a long- and close-range communication, while the rest tend to occur at intermediate distances, in short-range interactions (Starnberger et al. 2014a).

Although non-acoustic communications have been historically neglected in the order, the number of reports of chemical, seismic, visual, and tactile signal, during intra- and interspecific interactions, has been growing in the past three decades (Ryan 2001; Starnberger et al. 2014b; Woodley 2015; Köhler et al. 2017). Therefore, we expect to see a significant number of new cases related to all these modalities in the anuran communication literature in the next decades.

## Cross-References

- [Auditory Signals](#)
- [Behavior Systems](#)
- [Chemical Signals](#)
- [Communication](#)
- [Honest Signaling](#)
- [Reproduction](#)
- [Reproductive System](#)
- [Salientia Communication](#)
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- Sexual Selection
- Social Behavior
- Sociobiology
- Sociosexual Behavior
- Species-specific Behavior
- Visual Recognition in Birds
- Visual Recognition of Prey and Predators

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## Salientia Gaits

### ► Salientia Locomotion

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## Salientia Life History

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The Salientia is a branch of the Amphibia that includes all extinct and living taxa of frogs. The Order Anura encompasses the 6,400+ known and extant species. Frogs occur on all continents except Antarctica and in all of the major biomes of the world. The many life history strategies in these animals evolved in response to the extremely variable niches created by interactions among environments, habitats, and other organisms. About 30% of the world's anurans are

threatened with extinction primarily due to habitat loss and disease (Pechmann et al. 1991).

A life history is a suite of coevolved traits that affect individual survival and lifetime reproductive potential and are studied at the population level. They include age-specific survival, brood or clutch size, size of offspring at birth or hatching, growth rates, interaction of reproductive effort with adult mortality, and variation among these traits in offspring (Vitt and Caldwell 2014). Genetics and environmental conditions such as temperature, rainfall, food availability, predation, and competition influence life history traits. Biologists categorize frog life histories into reproductive modes defined by where the larvae (tadpoles) develop and the primary habitats used by adults. Reproductive modes vary from direct development in the egg out of water resulting in emergence of a miniature adult form (froglet) to eggs deposited in water with embryos hatching into free-swimming tadpoles which remain in water for variable lengths of time then change body form during emergence to the adult form. Species with direct development do not need water for reproduction, whereas those with aquatic tadpoles require water. Species with complex life cycles have gill-breathing, aquatic tadpoles with a body form adapted for swimming, and adults with lungs that have a body form adapted for jumping or leaping on land.

There are 40 recognized reproductive modes for anurans, far more than any other group of animals (Table 1). Except for the handful of species with eggs that develop inside the female, eggs are deposited and fertilized externally. Aquatic eggs are deposited in water often attached to vegetation, in bubble or foam nests on top of the water, or embedded in the backs of aquatic females. Eggs not deposited in water can be on or under the ground, on rocks, in burrows, attached to arboreal sites, in terrestrial foam nests, and carried by adult females or, in some cases, carried by males. Most frog life histories are termed bi-phasic because the aquatic stage (tadpoles) differs dramatically from the terrestrial stage (juveniles and adults). During metamorphosis, tadpoles grow forelimbs (they develop rear legs early in larval development), absorb the tail,

and turn into terrestrial froglets without tails. The wide range of reproductive modes illustrate the many ways frogs accomplish that critical event.

The two ends of the variable life history spectrum for frogs are completely aquatic with all life stages remaining in water and completely terrestrial with some or all of larval development taking place in the egg and within the female (Salthe and Duellman 1973). There are many variations between these two ends. Reproductive modes include egg deposition site (aquatic or terrestrial), larval growth, egg and clutch size, and degree of parental care, if any. These modes affect size at metamorphosis, diet structure, predator escape, individual development, survival, and population growth. These traits are in turn affected by various aspects of behavior, ecology, and physiology, as well as many environmental factors (Wilbur and Collins 1973). The time it takes to progress from egg to sexual maturity is determined by synergistic interactions among all these factors. Individuals that enter the breeding population have survived a highly variable and complex gauntlet.

The most common life history strategy is eggs and gill-breathing, feeding tadpoles in still water, followed by metamorphosis, and lung-breathing juveniles and adults on land. This strategy is the most widespread reproductive mode in anurans. Once deposited in water following mating, frog eggs and resulting tadpoles face many challenges as they develop and grow. The primary challenge is how long water, the hydroperiod, is present. If the pond dries completely before tadpoles complete their development, then mortality is high. Developmental periods of some frogs are short and growth is rapid. This life history trait allows them to be successful in shallow ponds and water-filled depressions with short hydroperiods. Frogs with relatively long larval periods must reproduce in permanent ponds or depressions that do not dry for 1–2+ years, if ever. One benefit to living in ponds and puddles that frequently dry out is that predatory fish cannot establish populations. Larval periods of 15–33 days for Eastern Spadefoot Toads (Fig. 1; *Scaphiopus holbrookii*) in eastern North America and 7–20 days for Couch's Spadefoots (*Scaphiopus couchi*) in southwestern

**Salientia Life History, Table 1** Reproductive modes in anurans; from Vitt and Caldwell (2014).

|                                                                                                                                          |
|------------------------------------------------------------------------------------------------------------------------------------------|
| Eggs aquatic                                                                                                                             |
| Eggs deposited in water                                                                                                                  |
| Eggs and feeding tadpoles in lentic water                                                                                                |
| Eggs and feeding tadpoles in lotic water                                                                                                 |
| Eggs and feeding tadpoles in constructed subaquatic chambers, tadpoles in streams                                                        |
| Eggs and feeding tadpoles in natural or constructed basins after flooding, tadpoles in ponds or streams                                  |
| Eggs and feeding tadpoles in subterranean constructed nests after flooding, tadpoles in ponds or streams                                 |
| Eggs and feeding tadpoles in water in tree holes or axils in aerial plants                                                               |
| Eggs and nonfeeding tadpoles in water-filled depressions                                                                                 |
| Eggs and nonfeeding tadpoles in water in tree holes or aerial plants                                                                     |
| Egg deposited in streams and swallowed by female, eggs and tadpoles complete development in stomach                                      |
| Eggs in bubble nest                                                                                                                      |
| Bubble nests floating in pond, feeding tadpole in pond                                                                                   |
| Eggs in foam nest (aquatic)                                                                                                              |
| Foam nest floating on pond, feeding tadpole in pond                                                                                      |
| Foam nest floating on pond, feeding tadpole in streams                                                                                   |
| Foam nest floating on water in constructed basins, feeding tadpoles in ponds                                                             |
| Foam nest floating on water in axils of bromeliads, feeding tadpoles in water                                                            |
| Eggs deposited in dorsum of aquatic female                                                                                               |
| Eggs hatch into feeding tadpoles                                                                                                         |
| Eggs hatch into froglets                                                                                                                 |
| Eggs terrestrial or arboreal (not in water)                                                                                              |
| Eggs on ground, on rocks, or in burrows                                                                                                  |
| Eggs and early tadpoles in excavated nests, subsequent to flooding, feeding tadpoles in streams or ponds                                 |
| Eggs on ground or rock above water, hatchlings move to water                                                                             |
| Eggs on humid rocks, in rock crevices, or on tree roots above water, feeding tadpoles semiterrestrial on rocks or crevices in water film |
| Eggs hatch into feeding tadpoles, carried to water by adults                                                                             |
| Eggs hatch into nonfeeding tadpoles that complete development in nests                                                                   |
| Eggs hatch into nonfeeding tadpoles that complete development in dorsum or pouches of adult                                              |
| Terrestrial eggs hatch into froglets by direct development                                                                               |
| Eggs arboreal                                                                                                                            |
| Eggs hatch into feeding tadpoles that drop into lentic water                                                                             |
| Eggs hatch into feeding tadpoles that drop into lotic water                                                                              |
| Eggs hatch into feeding tadpoles that develop in water-filled cavities in trees                                                          |
| Eggs hatch into froglets by direct development                                                                                           |
| Eggs in foam nest (arboreal or terrestrial)                                                                                              |
| Foam nest on humid forest floor, subsequent to flooding, feeding tadpoles in ponds                                                       |
| Foam nest with eggs and tadpoles in basins subsequent to flooding, feeding tadpoles in ponds or streams                                  |
| Foam nest with eggs and tadpoles in subterranean constructed nests, subsequent to flooding, feeding tadpoles in ponds                    |
| Foam nest with eggs and tadpoles in subterranean constructed nests, subsequent to flooding, feeding tadpoles in streams                  |
| Foam nest in subterranean constructed chambers, nonfeeding tadpoles complete development in nest                                         |
| Foam nest arboreal, tadpoles drop into ponds or streams                                                                                  |
| Eggs carried by adult                                                                                                                    |
| Eggs carried on legs of male, feeding tadpole in ponds                                                                                   |
| Eggs carried on dorsal pouch of female, feeding tadpoles in ponds                                                                        |
| Eggs carried on dorsum or in pouch of female, nonfeeding tadpoles in bromeliads or bamboo internodes                                     |

(continued)

Salientia Life History, Table 1 (continued)

|                                                                                       |
|---------------------------------------------------------------------------------------|
| Eggs carried on dorsum or in dorsal pouch of female, direct development into froglets |
| Eggs retained in oviducts                                                             |
| Ovoviviparity, larva feeds on yolk                                                    |
| Viviparity, larva feeds on oviductal secretions                                       |



Salientia Life History, Fig. 1 Eastern Spadefoot Toad from eastern North America, an example of the most common life history strategy of eggs and tadpoles in water and adults on land. Photo by J.C. Mitchell

North America allow these species to be successful in ephemeral pools created by unpredictable rainfall events (Dodd 2013). These frogs can speed up development in response to the rate of pool drying and reduce the lengths of their larval periods. In contrast, the larval period for American Bullfrogs (*Lithobates americanus*; 3–25 months) is much longer and highly variable, which means tadpole survival requires permanent ponds and the ability to survive one and sometimes two winters (Wells 2007).

Complex challenges to individual survival in water begin as soon as eggs are deposited. Those deposited singly or in small groups are more vulnerable to predators than those deposited in aggregations or within thick jelly masses. Egg predators in ponds and pools include a variety of invertebrates such as crayfish, leeches, fish, some turtles, and adult Red-spotted Newts (*Notophthalmus viridescens*). Survival of free-swimming tadpoles is often determined by aquatic predators such as dragonfly naiads, giant water bugs, aquatic beetles and their larvae, fishing spiders, fish, predatory

salamander larvae, and water snakes. Tadpoles hide in vegetation, reduce their activity, and develop colors and patterns on tails in response to the presence of predators. The decorated tails direct predators away from the important part of the tadpole, their bodies. Gray Treefrogs (*Hyla versicolor*) respond to the presence of larval dragonflies by increasing the height and length of their tails and by developing red color near the margins (Relyea 2002). Wood Frog (*Lithobates sylvaticus*) tadpoles increase lengths of forelimbs and legs and lengthen the larval period in response to larval dragonflies (Relyea 2001). Such changes usually occur in ponds that have predatory invertebrates. Such changes do not occur if there are no predators.

Size at metamorphosis is a key life history trait in frogs because it influences adult fecundity. Large metamorphs have a higher probability of survival in terrestrial environments than small metamorphs. The size achieved at metamorphosis depends on interactions among plasticity in growth rates, environmental conditions, food availability, larval density, and abundance and types of predators (Pough et al. 2016).

Reproductive characteristics of frogs vary substantially with elevation and latitude. In general, high elevation anuran populations have shorter breeding seasons, longer larval periods, are larger at all larval stages, larger as adults, reach reproductive maturity at older ages, and produce larger eggs and clutches than populations at low elevations (Morrison and Hero 2003). There are exceptions, however. Temperature is a key factor that influences development rates and growth. In a low-elevation population of Common Toads (*Bufo bufo*) in Europe, age at first reproduction for breeding males and females is 2–3 years, respectively, but increase to 6 and 8 years, respectively, in high-elevation populations (Hemelaar



1988). The timing of male vocalizations and egg deposition in populations of Sauter's Frogs (*Rana sauteri*) in Taiwan shifts from October to December in low elevations to May in high elevations, thus decreasing length of the breeding period and increasing length of the larval period (Su-Ju et al. 2003). Adult females at high elevations are larger and have smaller clutch sizes, but larger eggs and tadpoles, compared to low elevations.

All of these factors affect the number of metamorphs that leave the pond and enter the terrestrial environment. Long-term studies in a South Carolina pond clearly show that the number of newly produced juveniles is significantly impacted by predation, competition among species, and hydroperiod irrespective of the number of breeding females. During one 16-year study, recruitment of juvenile frogs into the population varied from zero to thousands depending on species and years. Female Eastern Narrow-mouthed Toads (*Gastrophryne carolinensis*) bred in abundance in each year, but produced large numbers of juveniles in only one year (Semlitsch et al. 1996). A nearly identical pattern occurred for the Southern Leopard Frog (*Lithobates sphenoccephalus*).

Once juveniles have entered the population and grow to adulthood, their survival is impacted by a host of terrestrial predators (e.g., snakes, raccoons), avian predators (e.g., crows, herons), invertebrates (centipedes, spiders), and environmental factors such as drought and rainfall patterns. In Central America, the calls of male Tungara Frogs (*Physalaemus pustulosus*) attract Fringe-lipped Bats (*Trachops cirrhosis*) that eat them (Ryan 1985). Marine Toads (*Rhinella marina*) also eat calling males of this species (Wells 2007). Semi-aquatic snakes around the world prey on adults that are breeding in water. Herons have been seen catching males of the Southern Toad (*Anaxyrus terrestris*) in Florida while they were calling next to a small pond under a canopy (Mitchell et al. 2017). Adult behavior associated with life histories is an important factor in individual survival and lifetime reproductive success.

Many other frog species have life history strategies that consist of aquatic eggs, free swimming

tadpoles, and terrestrial froglets and adults. Widespread examples include Fire-bellied Toads (*Bombina bombina*) in Central and Eastern Europe (Kuzmin 1999), Marine Toads in Latin America (Savage 2002), Frogs (*Tomopterna* sp.) in sub-Saharan Africa (Channing and Howell 2006), Paradise Toads (*Vandijkophrynus robinsoni*) in southwestern Africa (Du Preez and Carruthers 2009), and Siberian Wood Frogs (*Rana amurensis*) in China, Korea, Mongolia, and Siberia (Kuzmin 1999).

Other reproductive modes that include aquatic eggs and tadpoles also face similar suites of challenges, albeit at smaller scales. Several species in the tropics have taken advantage of water in tree holes and in the axils of bromeliads. Female Coronated Treefrogs (*Anothea spinosa*) in Central America deposit eggs directly into these small bodies of water (Duellman and Trueb 1986). Tadpoles feed on aquatic insects or plant matter and emerge as froglets. The tadpoles of several neotropical frogs, such as Strawberry Poison Dart Frogs (*Dendrobates pumilio*), cannibalize conspecific eggs and increase their own probability of survival (Crump 1983). In some species of *Dendrobates*, females provide food by laying unfertilized eggs along with fertilized eggs. Climbing Frogs in the genus *Anodonthyla* in Madagascar lay eggs in tree holes or axils in vegetation that develop into nonfeeding tadpoles which use their yolks as food to complete development (Glaw and Vences 1994). In this species, males stay with the tadpoles until the larvae are washed out by rain. Some treefrogs in Africa and Central and South America attach their eggs to leaves over water so that once they hatch, the newly formed tadpoles drop into the water where they complete development.

Adults of several species in three Families of frogs in Africa, Asia, and Central and South America construct foam nests (Duellman and Trueb 1986). Secretions from the female's oviduct are churned by rapid movement of her rear legs to create a gray to white foam on the water's surface. Eggs and sperm are distributed throughout the foam as it is being built. In about a week, developing embryos drop into the water where they will grow and complete development. Nests can also



**Salientia Life History, Fig. 2** Sumaco Horned Treefrog from Peru, an example of the life history strategy of eggs deposited on the back of the female where they imbed in her skin and develop directly into froglets. Photo by J.C. Mitchell

be small terrestrial depressions adjacent to water where the eggs hatch when the depression is flooded. Some frogs in Africa and Asia construct foam nests in vegetation over ponds or streams. Early stage tadpoles drop into the water where they will complete larval development. Foam nests protect the eggs and are guarded by males and females in some species.

Eggs of the aquatic Sumaco Horned Treefrog (Fig. 2; *Hemiphractus proboscideus*), a marsupial frog in South America, are deposited on the dorsum of females where they adhere to her skin by gelatinous substances, sink into her skin, and develop directly into froglets (Duellman 2015). All 90+ marsupial frogs in Central and South America carry their eggs attached to their backs or in pouches in which eggs develop and hatch as advanced tadpoles or froglets (Duellman 2015).

Males and females of the fully aquatic Surinam Toad (*Pipa pipa*) from tropical South America undergo a series of somersaults during mating (Duellman and Trueb 1986). When the male and female are on their backs at the top of the loop, the female lays several eggs on the male's belly where he fertilizes them and roll the eggs onto the female's spongy back where they adhere. Her skin envelops each egg separately creating a brooding pouch. All development occurs in the pouch, and at metamorphosis 3–4 months later, the toadlets hatch by breaking through the female's skin.

Some species avoid the aquatic gauntlet altogether. Frogs in the speciose genus *Eleutherodactylus* (Rain Frogs) in Central and South America lay terrestrial eggs in moist soil or in leaves on the ground or vegetation over water that develop directly into froglets (Wells 2007). Female Mozambique Rain Frogs (*Breviceps mossambicus*) in east Africa lay about 20 eggs in jelly in a small chamber she makes under a rock (Channing and Howell 2006). Tadpoles do not swim or feed in the soft jelly; metamorphosis into froglets occurs about 6–8 weeks later.

The role of the male is not always to fertilize eggs. Midwife Toads (*Alytes obstetricans*) in Europe mate on land and males wrap strings of 20–50 fertilized eggs around their hind legs (Spellerberg 2002). Fifteen to 45 days later, they carry the eggs to a pool or pond where the eggs hatch into free-swimming tadpoles. Males of many South American poison dart frogs stand guard near their eggs and tadpoles. Some, such as Common Rocket Frogs (*Colostethus panamensis*) in Central America, carry tadpoles to water on their backs (Wells 2007). Others simply sit on the eggs to guard them (e.g., Green Poison Frog [*Dendrobates auratus*]).

A few frogs have internal fertilization and the eggs develop into late-stage tadpoles or froglets inside the female's body cavity. Critically endangered Kihansi Spray Toads (*Nectophrynoides asperginis*) in Tanzania accomplish internal fertilization by males depositing sperm into females by pressing his cloaca tightly to hers (Channing and Howell 2006). There is no intromittent organ in this or any other species of frogs. Fertilization and complete development occur in the oviducts; toadlets emerge through the cloaca at metamorphosis. The Golden Coqui (*Eleutherodactylus jasperii*), now extinct in Puerto Rico, combined internal fertilization with egg retention in the oviducts and subsequent birth of froglets (Wells 2007). Tadpoles of two species of *Nimbaphrynoides* (Liberia Nimba Toad [*N. liberiensis*] and Western Nimba Toad [*N. occidentalis*]) in West Africa complete development in the female's oviducts while they subsist on their yolk (Wells 2007). A new species of

Fanged Frog (*Limnonectes larvaepartus*) on the island of Sulawesi has internal fertilization, complete development of eggs within the oviducts, and live birth of late-stage tadpoles and occasionally froglets (Iskandar et al. 2014). Tadpoles initially feed on their yolk reserves, but then feed on secretions (“uterine milk”) from glands inside the oviduct. The froglets emerge following internal metamorphosis.

Female Gastric Brooding Frogs (*Rheobatrachus silus* and *R. vitessinus*) in rainforests of eastern Australia picked up the eggs after fertilization and swallowed them (Tyler 1994). All of the tadpoles developed into froglets in their stomachs and emerged as toadlets through their mouths. Birth was rapid with females disgorging all the froglets at the same time, called propulsive vomiting, in water. The many unanswered questions about how they accomplished this extreme behavior will have to remain so because both species are now extinct.

Questions about and scientific studies on frog life histories began in the 1800s and expanded in the 1900s. Since then, ecologists have discovered most of the life histories that deviate from the biphasic tadpole-in-water and adult-on-land strategy and most of these species occur in the New World tropics. The extraordinary variation in frog biology means that the 40 life histories we know of today will likely not be the whole story. New species and strategies continue to be discovered in the twenty-first century. Unfortunately, we may miss some of them because frogs are going extinct at a frightening rate. Loss of the Gastric Brooding Frogs is only the start. Additional information on frog life histories can be found in the references cited here and in a recent review by Crump (2015).

## Cross-References

- [Brooding](#)
- [Clutch](#)
- [Communal Behavior](#)
- [Fecundity](#)
- [Fecundity](#)
- [Ova](#)

- [Ovaries](#)
- [Reproductive Synchrony](#)
- [Sex Role Reversal](#)
- [Species](#)

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## Salientia Locomotion

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## Synonyms

Anuran gaits; Anuran locomotion; Frog locomotion; Salientia gaits; Toad locomotion

## Definition

Movement used by anurans (i.e., frogs and toads) to traverse their environment.

The Salientia, or the anurans, is an order within Amphibia. This order includes all extinct and living species of frogs and toads (Mitchell 2017). Frogs are inhabitants of all major ecosystems in the world where water is present, except in areas where there are less-than-ideal temperature conditions (i.e., Antarctica). Anurans possess a diverse set of locomotor modes that allow them to function in varying environments, such as swimming, jumping, hopping, walking, and in some instances burrowing. Current and extinct species of Salientia also provide researchers crucial insight regarding the evolution of modern-day amphibians.

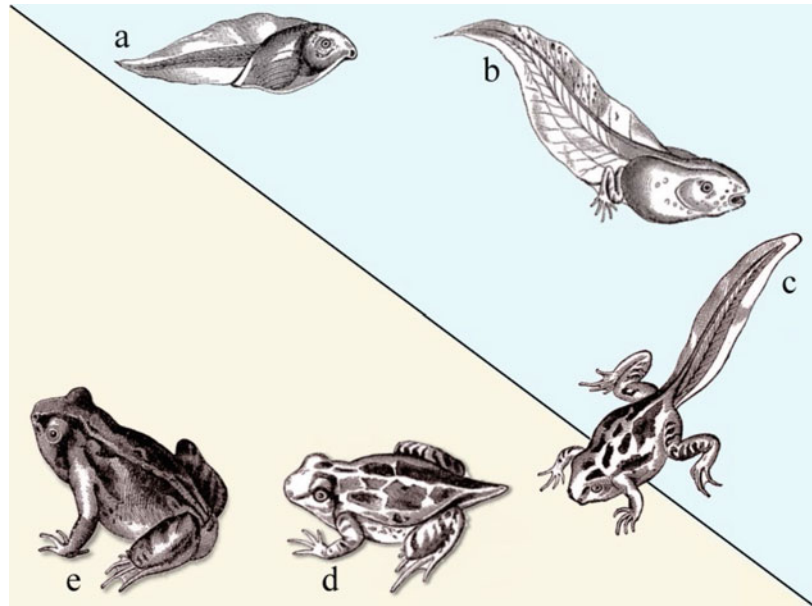
## Metamorphosis

A proper analysis of anuran locomotion cannot be conducted without analyzing basic development, anatomy, and life cycle (Fig. 1). Most anurans follow a common life cycle that includes a tadpole stage followed by a metamorphosis that transforms them into an adult form. Some anurans can completely bypass the tadpole stage and develop into their adult form in a process called “direct development” (Elinson 2001). Despite this unusual transition within some species, the great majority of anurans undergo a standard metamorphosis in which they transform from their freshwater form (tadpole) into a terrestrial form (frog or toad) (Herner and Frieden 1960).

The anatomy of the tadpole does not resemble the typical adult or other larval vertebrates. Anatomically, tadpoles are characterized by a bulbous head attached to a relatively small body and tail (Elinson 2001). The tadpole's sole locomotor mode is swimming since it lacks both fins and functional limbs. Propulsion during locomotion is provided by the tail (Elinson 2001). All larvae possess gills for respiration, which serve as their main modality of gathering oxygen from their environment. Anurans can remain in their larval stage for varying periods of time dependent on

**Salientia Locomotion,**  
**Fig. 1** Anuran

metamorphosis involves a locomotor transition from fully aquatic undulatory swimming tadpoles (**a** and **b**) to limb-powered quadrupedal walking, hopping, and swimming (**c–e**)



their specific species. Some species remain in their larval stage for only a few days while some others can remain in their larval stage for anywhere from 3–5 years (Dodd 2013). Despite this varying time frame, all tadpoles eventually mature until the point where they undergo metamorphosis.

The tadpole-to-adult metamorphosis involves a complex set of morphological and physiological changes that radically alter the body plan of the larvae. Once the metamorphosis is complete, they transform into a form they will carry through adulthood. In the adult stage, all frogs are quadrupeds. They all share a common body structure consisting of a short head, bulging eyes, little or no neck, a short compact body, and paired forelimbs and hindlimbs. Another important distinct feature is that frogs, unlike their tadpole stage, lack a tail (Dodd 2013). Despite the lack of a tail, adult anurans still possess the ability to swim.

### Major Locomotor Modes

Anura is a specious order and the methods of their locomotion mirror this diversity. The main methods of anuran locomotion are jumping,

hopping, walking, swimming, and in some cases burrowing. The percentage of utilization of each mode might vary interspecies, but all species still use these modes to some degree.

The most common method of locomotion among terrestrial anurans is jumping. Jumping is defined as a catapult mechanism. This is when muscle contraction is used to store energy in elastic structures such as tendons/ligaments (the loading stage). The stored energy in these structures then recoils releasing a large amount of energy in a short amount of time (the recoil stage). Jumping involves a synchronous extension of the hindlimbs. This extension starts proximally and moves more distally, starting at the hip joint followed by the knee and then by the ankle. Most of the power is generated in the flexion–extension axis. There is very minimal adduction/abduction that occurs during jumping. Strain energy is primarily stored in the large Achilles tendon. Hopping involves this same mechanism of movement but has some slight differences. The difference is the distance covered during one leap. A jump is a leap greater than ten snout–vent lengths. A hop is a leap less than ten snout–vent lengths. Jumping anurans tend to have long hindlimbs, while hopping anurans have shorter hindlimbs. Hopping is characteristic of toads



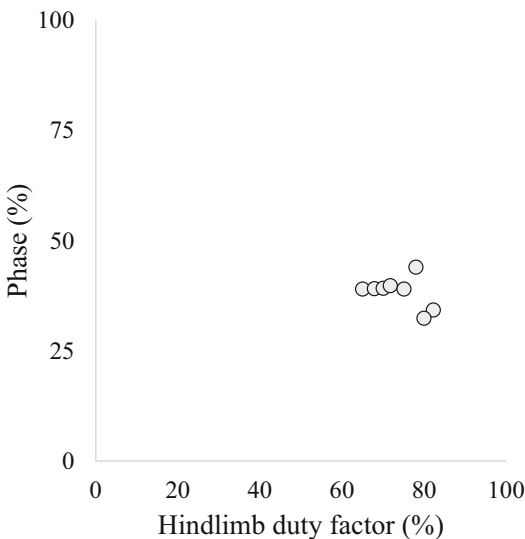
while jumping is characteristic of frogs (Simons 2008).

Additional terrestrial modes of locomotion exhibited by anurans are walking and running. This involves the asynchronous motion of the hindlimbs to produce force. Walking is defined as a gait in which each foot is in the stance phase for at least 50% of the stride. Anuran walking consists of a sequence in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, and left forelimb) (Fig. 2). The movement during walking is modeled by an inverse pendulum because the leg during the stance phase is rigid and the body rotates around it. The body's center of mass is highest at mid-stance. Then the body arcs downward and forward over the stance foot. This drop in the center of mass is utilized to produce kinetic energy. Running is characterized as a spring-like gait. During the beginning of stance phase the leg is compressed and stores potential energy within the tendons and muscles. At mid-stance, the center of mass is at its lowest. After mid-stance, the tendons and muscles recoil releasing their energy propelling the center of mass up and forward. Increased speed in walking or running is achieved by increasing stride

length and stride frequency. Stride length is modulated by further extending the leg at the end of stance phase. Increasing stride frequency is achieved by decreasing the time in stance phase. There are also increased energy demands on the muscle when moving faster. Speed is related to the type of movement that the salientian exhibits. At lower speeds a walking mechanism is utilized. At intermediate speeds a combination of walking and running gaits is exhibited, this motion is also known as a "trot-like gait." At high speeds only a running gait is seen. Most speeds involve the use of this trot-like gait. This shows that there is no clear transition between walking and running. There is a gradual transition period from the walking gait to running gait. This is not typical in most quadrupeds which have a clear transition speed (Ahn et al. 2004; Granatosky et al. 2018).

Tadpoles possess a unique gait compared to that of adult anurans because they utilize an undulatory motion to swim. This is characterized by a wave-like pattern of movement. The tadpole performs lateral undulations that move from head to tail. This is accomplished by waves of muscle contraction moving caudally. These motions produce linear motion. Some of this thrust is also produced by oscillations at the tadpole's snout. The tadpole also can turn using two distinct methods. They can make very tight turns in response to a mechanical stimulus, such as when the tadpole is at rest and employs this method as a defense mechanism to avoid predators. This motion is characterized by ipsilateral muscle contraction only. They also possess the ability to make wide turns which they naturally do during linear motion. This wide turning motion is characterized by muscle contraction on both sides of the body. Additionally, tadpoles do not have the ability to stop their velocity on their own, rather they rely on the drag from the water to glide to a stop. Tadpole motion is dominated by constant turning after linear motion. They rarely move in a linear path for long periods of time (Hoff and Wassersug 2000).

In adults, the mechanism of swimming is characterized as "kick and glide" motion. This motion involves an extension of the hindlimbs that produces a rapid acceleration. This extension is done



**Salientia Locomotion, Fig. 2** "Hildebrand" plot displaying phase against hindlimb duty factor collected during quadrupedal walking in anurans (n = 8 species)

in a specific pattern starting at the knee, followed by the hip and then ankle. The timing and angle of extension at these different joints vary among species. What remains constant is the qualitative increase in joint angle throughout this kick phase over time. This increase in joint angle over time shows a sinusoidal relationship between the two which is conserved among many species. During the glide phase the hindlimbs are kept in this extended manner as the organism glides losing velocity due to the drag on the body. After this glide, the hindlimbs flex and retract to prepare for the next stroke. The length of this glide phase greatly affects the average swimming velocity of the organism. These kicking leg motions are synchronous which allows for greater thrust and faster swimming when compared to asynchronous motion. This kicking motion can be achieved by either rotational or translational motion of the hind foot. Many species utilize both means of producing foot velocity. The hip, knee, and ankle joints all contribute to translational movement of the foot. Only the hip and ankle contribute to the rotational movement of the foot. Due to the anatomical structure of the knee joint, which points medially, knee extension contributes negatively to the rotational movement of the foot. The hip is the major contributor to translational movement as well as rotational movement of the foot. There is no apparent correlation between speed and the method of producing foot velocity. Both rotational and translational movement are effective methods in producing thrust during swimming. Anurans can increase swimming speed in subsequent strokes by increasing foot velocity, thus increasing thrust. The mechanism of swimming does not differ significantly based on the swimming speed (Nauwelaerts et al. 2001; Richards 2010).

## Bioinspiration

Salientian locomotion may prove to be an excellent model for bioinspired robots. Frogs can adapt to many environments due to their vast locomotive capabilities. Remarkably, the bull frog can jump up to 15x its body length (Reddy et al.

2011). In fact, the jumping mechanism requires so much power that it has been shown that jumping frogs need to deliver a peak power up to 7x higher than the maximum muscle power (Scarfogliero et al. 2007). This powerful jumping mechanism is unique to anurans and has been the basis for several robots designed that simulate frog locomotion. These robots can be used for real-world applications including efficient fast locomotion in unstructured terrains. Robots can be adapted in hopes of environmental monitoring and exploration (Scarfogliero et al. 2007). One proposed robot has quite a simple structure: two degrees of freedom for jump powering and steering, passive forelegs, and feed-forward control (Scarfogliero et al. 2007). This robot has springs in its rear limbs that allow for a powerful jump through a small motor mechanism. In addition, passive, compliant forelegs were developed allowing for soft ground contact which would subsequently allow for preserving stored energy for the next jump. The final robot weighed about 15 g and was expected to run 1.5 m/s, which would correspond to 30 body length per seconds. The most impressive finding of this study was the possibility that a commercial battery could make the robot run for two hours which would in turn cover a distance of several kilometers (Scarfogliero et al. 2007). Innovations such as these have the potential to lead to long-term advances in bioinspired robotics.

Multimodal function has become significant for robots to work in a variety of environments. Robots that can not only jump like frogs but can also swim like frogs have become an active area of research. One research model aims at analyzing frog locomotion in water using cine film recordings and finally implementing those designs in a robotic frog-like system (Pandey et al. 2013). Another research model came up with a model that consisted of a three-dimensional printed robotic body and two legs and feet actuated by dielectric elastomer actuators (Tang et al. 2017). Researching frog locomotion has proven to be useful in creating robots with extraordinary swimming and jumping capabilities. In the future, innovations such as these can prove to be very helpful in a variety of

aspects such as in improving transportation modalities in various terrains.

## Conclusion

Anurans are a diverse order of amphibians that span vast regions near bodies of water. Anurans have a broad variety of locomotor modes that allow them to be successful inhabitants of nearly every ecosystem on earth. These methods of anuran locomotion include jumping, hopping, walking, swimming, and in some cases burrowing. Larval anurans in their tadpole state are quite different than their adult form and are only capable of undulatory swimming. Bioinspired robotics based on the biomechanics of anuran locomotion has proven quite fruitful and the field can benefit greatly from further research into multimodal locomotor abilities of these species.

## Cross-References

- Activity Budget
- Adaptation
- Adaptedness of Behavior
- Adaptive Radiation
- Arboreality
- Basal Metabolic Rate (BMR)
- Canopy
- Caudata Cognition
- Caudata Locomotion
- Caudata Sensory Systems
- Common Ancestor
- Dispersal Ability
- Dispersal Patterns
- Ecology
- Evolution
- Extinction in Learning
- Gait
- Home Range
- Homology
- Homoplasy
- Locomotion
- Morphology
- Muscular System
- Natural Selection
- Navigation
- Paleontology
- Phylogeny
- Quadrupedal
- Species
- Taxa
- Terrestrial
- Territoriality
- Vertebrate Nervous System
- Zoo
- Zoology

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## Salientia Morphology

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## Introduction

Salientia is a superorder of lissamphibians, which includes frogs and toads (order Anura) and the Early Triassic Proanura *Triadobatrachus* and *Czatkobatrachus* (Benton 2015). This is the major extant order of the class Amphibia, encompassing more than 7000 species (Frost 2019) with a high morphological diversity. They are distributed all around the globe, except for the poles and most oceanic islands. Salientia

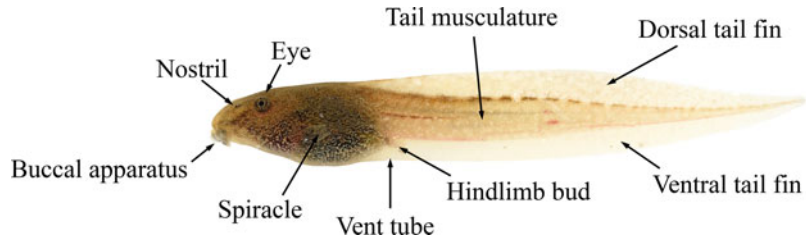
synapomorphies (characteristics that are shared by the group, derived from a common ancestral) include: lack of a tail in the adult stage; five to nine presacral vertebrae; postsacral vertebrae (posterior to the pelvis) fused into a bony coccyx; and hind limbs elongated, modified for jumping. Other characteristics of Salientia include: fertilization, often external; eggs laid in water or humid places; aquatic larval stage present in most species; males usually with vocal cords, vocal sac, and a voice (Hickman et al. 2014; Kardong 2015). In this section, we synthesize the main knowledge about larval and adult morphologies, and also include changes during metamorphosis, adult sexual dimorphism, and evolution.

## Larval Morphology

Most Salientia species have an aquatic, free-swimming larval stage (tadpole). Tadpoles are typically found in ponds and streams, but some species grow in puddles, roadside ditches, or even in the ground litter. They mainly feed by scraping off the substrate or capturing particles suspended in the water, though there are some predator species. These specialized habits require an entirely different morphology from the adult. Anuran adults have short bodies with long limbs and are tailless, while tadpoles have a tail with fins and are limbless during early stages of development (Fig. 1). Skin, mouthparts, digestive (usually herbivore larvae and predator adult), and respiratory systems (aquatic larvae and air breathing adult) are also dramatically different.

The mouthparts are composed of an oral disk, usually covered with papillae (small dermal projections), several corneous denticles (toothlike projections) arranged in rows, and two strong, highly keratinized, corneous beaks. This arrangement is highly variable according the food habits of the species: tadpoles that scrape stones and other hard substrates usually have more corneous denticles, while predators have reduced oral discs without denticles, but stronger corneous beaks. The position of the mouthparts also reflects food habits: species that feed on deposited particles have anteroventrally oriented mouthparts; species

**Salientia Morphology,**  
**Fig. 1** General  
 morphology of a tadpole



that feed on suspended particles or that are predators have anteriorly oriented mouthparts; species that feed on particles in the water surface have a dorsally oriented funnel-shaped oral disk. Recent studies have also shown a large diversity of internal oral morphology across species.

Besides the variation on mouthparts, the overall morphology varies according to species habits. The tadpoles of pond breeders characteristically have large bodies and deep caudal (tail) fins, which in some species might have a terminal tail extension, like the familiar swordtail fishes (*Xiphophorus*). The mouth is relatively small, located anteriorly, on the underside or upperside of the snout and usually contains weak denticles. These tadpoles swim easily in quiet waters and feed on attached and free-floating vegetation, including algae. In contrast, the stream tadpoles have depressed bodies, long muscular tails, and shallow caudal fins. The mouth is relatively large and usually contains many rows of strong denticles. In highly modified stream tadpoles, the mouth is ventral and modified as an oral sucker, with which the tadpole anchors itself to stones. These tadpoles swim slowly, grazing on the coating of bacteria and algae as they move.

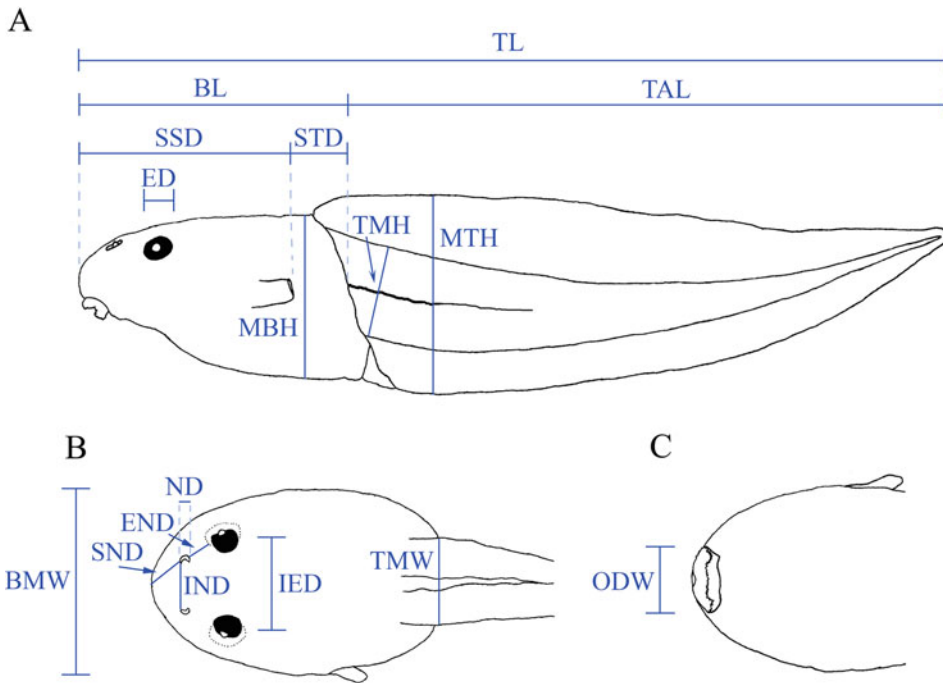
As underwater breathers, tadpoles are lungless and perform branchial respiration. The gills are external in the early stages of development, eventually becoming internalized in branchial chambers or gill cavities due the development of the opercula (gill covering). The water is pumped through the mouth and pharynx to the gill cavity by muscular contractions. After irrigating the gills, the water is expelled through one or two spiracles (small slit- or tube-like openings), depending on the species. Most species have a single spiracle located on the left side of the body. Others possess a single

ventrally positioned spiracle, or two spiracles, one on each side of the body.

In taxonomic studies, tadpole descriptions usually address all of these external features plus others, like eye color and position, nostrils shape and position, vent-tube position (the opening of the cloaca), tail and fin sizes and proportions, body and tail coloration, and presence or absence of neuromasts (mechanical sensors that compose the lateral line). Morphometrically, the following measurements are usually present (Fig. 2): total length (TL), body length (BL), body width (BW), body height (BH), oral disc width (ODW), snout–spiracle distance (SSD), snout–nostril distance (SND), nostril diameter (ND), inter–nostril distance (IND), eye–nostril distance (END), eye diameter (ED), inter–eye distance (IED), spiracle–tail distance (STD), tail length (TL), tail muscle height (TMH), tail muscle width (TMW), and maximum tail height (MTH). In order to enable comparisons between tadpoles with similar development, Gosner (1960) established a table for classifying the development from the one-cell egg (stage 1) to a completely metamorphosed anuran (stage 46).

Tadpoles have a cartilaginous skeleton, divided in a chondrocranium and hyobranchial, axial, and appendicular skeletons. The chondrocranium is a case that houses and protects the brain and main sensory organs, besides supporting the feeding system. The hyobranchial skeleton provides support and directs current water to the gills. The axial skeleton is composed by the vertebral column and is responsible for sustaining tail muscles, playing a fundamental role on under the water mobility. The appendicular skeletons are absent through most of the tadpole's development, appearing only during metamorphosis (Altig and McDiarmid 1999).





**Salientia Morphology, Fig. 2** Schematic drawing of measurements usually presented in tadpole descriptions. (a) lateral view; (b) dorsal view; (c) ventral view. See text for abbreviations

## Metamorphosis

After a variable period of growth, the tadpole undergoes metamorphosis, in which limbs become well developed, and the tail is lost, two of the most obvious morphological changes that take place. Such changes occur gradually throughout tadpole development, the tail loss being one of the last morphological changes. Among the first changes is the appearance of hind limb buds, which grow and develop until completely differentiating into hind limbs with toes, webbing, and tubercles (small, round nodules). Larval mouth parts begin to change; the corneous denticles and papillae, if present, disappear, while the jaws and true teeth develop. A tongue (except in pipids) and associated hyolaryngeal structures develop. The eyes are enlarged and undergo structural modifications; eyelids develop. Later on, the forelimbs emerge through the operculum skin; the tail begins to shrink, being resorbed by the body and the skin thickens following development of dermal glands. The vertebral column and limb bones ossify

(a process that continues during the entire adult life of the anuran), and the adult digestive system differentiates as the long coiled intestine shrinks into a short, thick-walled, folded intestine. The lungs develop, and, for a short period of time, tadpoles have both lungs and gills, before the latter disappear.

How, when and where the changes from larva to adult take place varies greatly across species – a fascinating aspect of studying frogs. The time it takes before metamorphosis depends on the species but also on environmental conditions like temperature and food availability. Most tadpoles complete their development in 2 or 3 months, but there are notable exceptions. Tadpoles of spadefoot toads, genus *Scaphiopus*, develop in temporary rain pools in arid parts of North America, where it is imperative for the tadpoles to complete their development before the pools dry up. Some *Scaphiopus* tadpoles metamorphose about 2 weeks after hatching. In its turn, tadpoles of the neotropical tree frog *Flectonotus pygmaeus* have the intestines filled with yolk and do not feed until the metamorphosis

is complete. They are carried in a female dorsal pouch and metamorphosis is completed in 11–17 days after being released from the pouch and 34–43 days after mating (Duellman et al. 2011). Contrastingly, in the northern part of its range in North America, the tadpoles of the bullfrog *Lithobates catesbeianus* require 3 years to undergo their development.

## Adult Morphology

The name “Salientia” means “leapers.” Not surprisingly, anurans are animals built for jumping, and many of their body features are adapted for this type of locomotion. The short, flattened body provides mid-air stability. Jumping relies on simultaneous movement of hind legs, which are much larger than the front legs, acting as a spring together with the pelvic girdle. The muscles of the hind legs act as a power output generated during a frog’s jump and is enhanced by elastic energy stored in tendons and muscle fibers. The relative size of each toe ensures that all of them will be in contact with the ground during the impulse, increasing friction. Anurans have completely lost their tail and the vertebral column is greatly shortened through reduction in number of vertebrae. The scapular girdle is strongly attached to the column by cartilage ligaments, absorbing the impact on the arms during landing. Bony elements and teeth are reduced in most species, which presumably serves

to reduce the mass of the skull, thereby enhancing jumping performance (Vitt and Caldwell 2013).

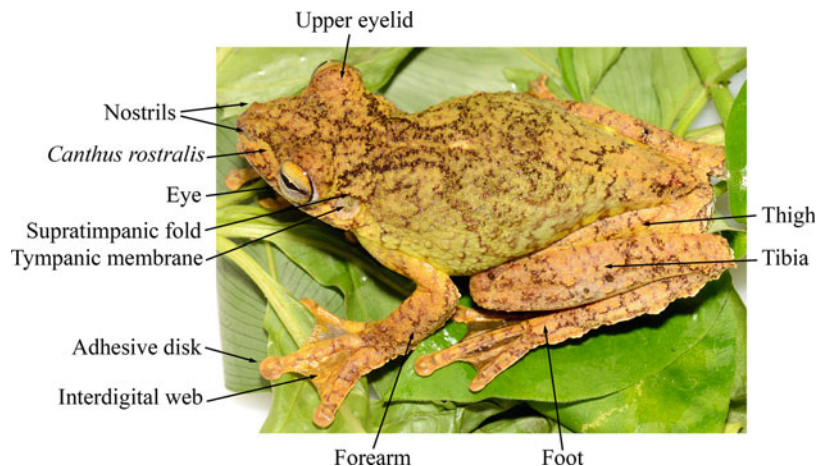
Besides jump, anurans might have other modes of locomotion. A few frogs have become almost entirely aquatic and typically have streamlined bodies, large, muscular hind legs, and hind feet with webbing extending to the tips of the toes. Often anurans can burrow in loose soil or sand to escape cold winters, hot summers, or long dry seasons. Such frogs dig with the hind feet, which are often equipped with special tubercles. Their hind legs are relatively short, with the tibio-fibula especially shortened. Tree frogs have adhesive discs on the fingertips, allowing them to adhere to some suspended surface during the jump. Gliding frogs typically have very large toe pads and extensive webbing on both the front and hind feet, and some have skin flaps on the sides of the body and legs. These frogs spread their toes and hold their limbs bent to the sides of the body while gliding, reducing the landing speed and allowing for a longer jump.

## External Morphology

Although most Salientia species are readily recognizable by their external morphology (Fig. 3), there is a great variety of sizes and structural modifications. Many frogs are tiny animals; perhaps one of the smallest adults is the Brazilian *Brachycephalus sulfuratus*, with 8.0 mm or less in

### Salientia Morphology,

**Fig. 3** General morphology of an adult amphibian



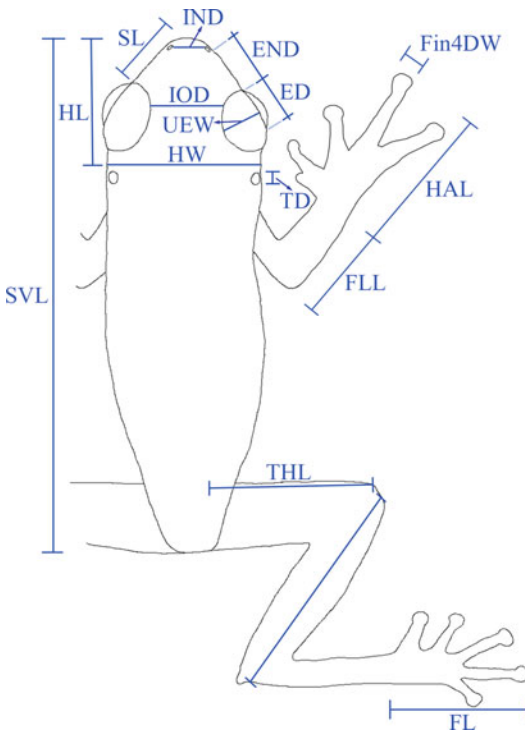
total body length, whereas the West African goliath frog, *Conraua goliath*, has a body length of nearly 300 mm. Morphometric measurements are necessary for species delineation, phylogenetic analyses, and even our understanding of evolutionary change in an organism's physical characteristics. In a recent review of morphometric measurements for anurans (Watters et al. 2016), a subset of 16 measurements were recommended as relevant to frogs' descriptions (Fig. 4). These are: head width (HW), snout-vent length (SVL), tibia length (TL), interorbital distance (IOD), head length (HL), eye diameter (ED), internarial distance (IND), eye-nostril distance (EN), foot length (FL), tympanum diameter (TD), thigh length (THL), snout length (SL), hand length (HAL), forearm length (FLL), upper eyelid width (UEW), and Finger IV disk width (Fin4DW). However, frogs continue to grow throughout their life. Thus proportions, rather than actual measurements, are better for comparing samples and species and can

be expressed as ratios of between a specific measurement and the SVL.

The shape of the snout is a reliable and easily discernible taxonomic feature. In dorsal view, the snout can be semicircular, nearly rounded, rounded, subovoid, subelliptical, pointed, truncate, or mucronate; these same shapes are evident in lateral views, although laterally, the snouts of some species are rounded, vertical, obtuse, acute, strongly acute, acuminate or protruding (see Heyer et al. 1990 for more information). Still on the anterior part of the head, two highly subjective characters are present: *canthus rostralis*, the angle of the head from the anterior corner of the eye to the nostrils or to the tip of the snout; and, loreal region, the side of the face between the *canthus rostralis* and the lips. A tympanum and usually a tympanic ring are evident in most species. Commonly, a supratympanic (dermal) fold extends posteriorly from the corner of the eye and passes just above the tympanum and continues onto the flank, sloping downward to a point above the insertion of the arm.

Some characters are found in anuran eyes, such as pupil orientation and presence of pigment on the palpebral membrane. Although the most common orientation is horizontal, some species have vertical pupils. The palpebral membrane is usually transparent (unpigmented) or only slightly pigmented in most species, with rare cases of pigmented reticulation. Also, palpebral and rostral (on the tip of the snout) fleshy appendages might be present in some species, as some of the genus *Proceratophrys* and *Hemiphractus*. In males of many species of frogs, vocal sacs connect to the buccal cavity, typically via slit-like openings, and are inflated during vocalization. Their morphology varies from a median single subgular sac, to bilobate and paired subgular sacs, or to paired lateral sacs.

Structural characters of the hands and feet are of immense taxonomic importance. Alberch and Gale (1985) recognized anuran fingers as homologous to vertebrate digits II–V. The relative lengths of the digits and toes, from shortest to longest, are usually represented in scientific works. Some fighting males have a curved, sharp prepollical spine on each hand, anteriorly to Digit II. This structure



**Salientia Morphology, Fig. 4** Schematic drawing of measurements recommended for anuran descriptions. See text for abbreviations

was thought to be homologous of Digit I, but this idea is no longer accepted. On its ventral surface, both hands and feet might have tubercles, which are classified according to their position, shape, and quantity. Subarticular tubercles are those below the articulations of the phalanges. Supernumerary tubercles are the small ones on the ventral surfaces of the digits, adjacent to the larger subarticular tubercles. Inner metacarpal or metatarsal tubercles are the large tubercles on the ventral surface of the hand or foot, at the base of the shortest finger or toe, respectively. Outer metacarpal or metatarsal tubercles are the small tubercles on the ventral surface of the hand or foot at the base longest finger or toe, respectively. Tubercles might be absent in many species.

Fingers and toes might have an interdigital webbing: a membranous skin that connects them with each other. The presence and extent of webbing on fingers and toes has been emphasized by many authors as a feature for recognition of different species, but it might exhibit considerable intraspecific variation, reducing its reliability for diagnosis. The degree of webbing is expressed in terms of how many segments of the digits (phalanges), hand (distal metacarpal), or foot (distal metatarsal) are free of webbing (see Myers and Duellman 1982; Savage and Heyer 1997 for more explanation).

The skin is the cellular boundary between animal and external environment. It serves as a protective barrier, preventing the invasion of microbes and inhibiting access by potential parasites, resists mechanical invasion and abrasion, and buffers the internal environment from extreme external conditions. The skin also acts in physiological regulation, sensory detection, respiration, and coloration. Several types of epidermal glands are widespread on the head, body, and limbs (mucous and poison glands are always present). The secretions produced by these glands include numerous polypeptides with several activities reported, including antibiotic, antitumor, and insulin-releasing activities. The skin is shed in a cyclic pattern of several days to a few weeks. Using its limbs, the frog emerges from the old skin, which is often consumed.

The color of amphibians is affected by the presence of pigmented cells (chromatophores) in the dermal layer of the skin. The three classes of chromatophores (melanophores, iridophores, and xanthophores) are arranged as a unit and produce the external coloration. Different classes can be combined and arranged to produce a wide range of colors and patterns. In some species, skin color can be quickly altered, in less than a minute, through dispersal or reduction of the eumelanin within the melanophores' processes.

## Internal Morphology

When the first tetrapods colonized the earth, new demands affected their bodily systems. Supporting body weight and moving on the ground, capturing and ingesting food, breathing and mating were challenges to overcome. The musculoskeletal system was, perhaps, the most affected in this transition. The Salientia, of course, inherited morphological solutions for these challenges and adapted them for their own specialized way of life.

The anuran skeleton is highly specialized. The cranium, much different from other vertebrates, is light, flattened, scarcely ossified and with a small number of bones. Nevertheless, it is resilient enough to withstand the impact of the landing after a jump. The teeth are bicuspid and pedicellate (supported on a pedicel). The vertebral column is very short, with only five to nine presacral vertebrae, without ribs but with overlapping processes that reduce lateral movement. The post-sacral vertebrae are fused in a long, single bone, the urostyle. Both scapular and pelvic girdles are firmly attached to the vertebral column, a characteristic inherited from the first tetrapods but enhanced by the jumper habit. The posterior limbs are longer than the anterior ones. Both fingers and toes have long and numerous articulated elements (with up to four phalanges), enhancing ability to grab and climb while helping with their ability to jump.

The cranial musculature contains one functional group for jaw movement and another for breathing and swallowing. The jaw muscles are attached to

the dorsal, lateral, and ventral surfaces of the mandible to open and close the mouth. The muscles that function in respiration and swallowing move and support the gills and/or the hyoid and the tongue. The tongue is strong, muscular, retractile, and has a free posterior end. This end is highly glandular and produces a mucus that adheres to the prey, pulling it into the mouth. Thanks to *retractor bulbi* and *levator bulbi* muscles (the latter, a synapomorphy of Lissamphibia) and to the lack of a hard palate, the eyeballs can be pulled into the oral cavity, helping to swallow. The musculature of the vertebral column consists of epaxial (dorsal trunk) muscles and hypaxial (flank or ventral trunk) muscles providing rigidity and strength to the vertebral column and supporting the viscera, respectively. The pectoral girdle is anchored to the trunk vertebrae by axial muscles and absorbs the jump impact. The pelvic girdle has a less extensive muscular system. The limb muscles are divided into a dorsal extensor and a ventral flexor unit, both strong and robust.

Other systems differ less from the basic patterns found in vertebrates. The central nervous system includes the brain and the spinal cord. The brain is divided during development by a flexure into the forebrain and hindbrain, which are further partitioned, structurally and functionally. The forebrain consists of the telencephalon and the diencephalon and the midbrain consists of the mesencephalon and the hindbrain. Twelve pairs of cranial nerves arise from the brain. The spinal cord is a flattened cylinder of nerve cells that extends caudal through the vertebrae. Regarding the sensory system, two characteristics need to be mentioned: the presence of green rods on the eyes and the presence of a second distinct auditory patch, the *papilla amphibiorum* (both are unique to amphibians). The digestive system is simple. The digestive tube includes a large stomach and short intestines, typical of predators. Fat bodies (also called yellow bodies) store fat and are associated with the gonads in all amphibians. In anurans, the fat bodies form numerous finger-like projections which are larger and more pointed in males. These bodies serve as a source of nutrients for the gonads during the breeding period, after which they are in the smallest size. In males of the family Bufonidae, a growth of embryonic

ovarian tissue, called Bidder's organ, is located between the fat bodies and the testicles. It is thought that it can develop in a functional ovary under certain conditions (Pancak-Roessler and Norris 1991).

After metamorphosed, anurans perform cutaneous (through the skin) and pulmonary respiration. The skin is highly vascularized and contributes significantly, but the lungs are always present. These are paired, conical sacs with a pulmonary membrane folded to form internal septa. The lung of anurans is structurally simple when compared to those from other tetrapods, lacking bronchiole, alveolus (like in mammals) and many reptiles) or air capillaries (like in birds). In the absence of ribs and a diaphragm, lung aeration is performed by buccal pumping. Amphibians have double circulation, but the hearth is divided into three chambers: two atriums and one ventricle.

## Sexual Dimorphism

Sexual dimorphism is defined as phenotypic differences between conspecific males and females (Shine 1989). In anurans, it might be observed for many traits, such as coloration, skin texture and skin glands, vocalization, dermal ornamentations, vocal sacs (males), and breeding behavior, body size, and shape (Mesquita et al. 2004). Some differences persist throughout adult life, but others develop in response to gonadotropic hormones and therefore are present only during the active reproductive cycle. Some structures are used in courtship and others for holding the couple in an embrace during mating or oviposition (Duellman and Trueb 1994).

Sexual dimorphism description is very important in taxonomic studies, including body-size measurements, mainly because the female is usually larger than the male. However, interspecific variation in mean body size among closely related species is not clear unless sexual size dimorphism is taken into consideration. Larger body sizes in females might be an advantage for increased fecundity. Nevertheless, competition between males, female choice, parental care, and vocalization are

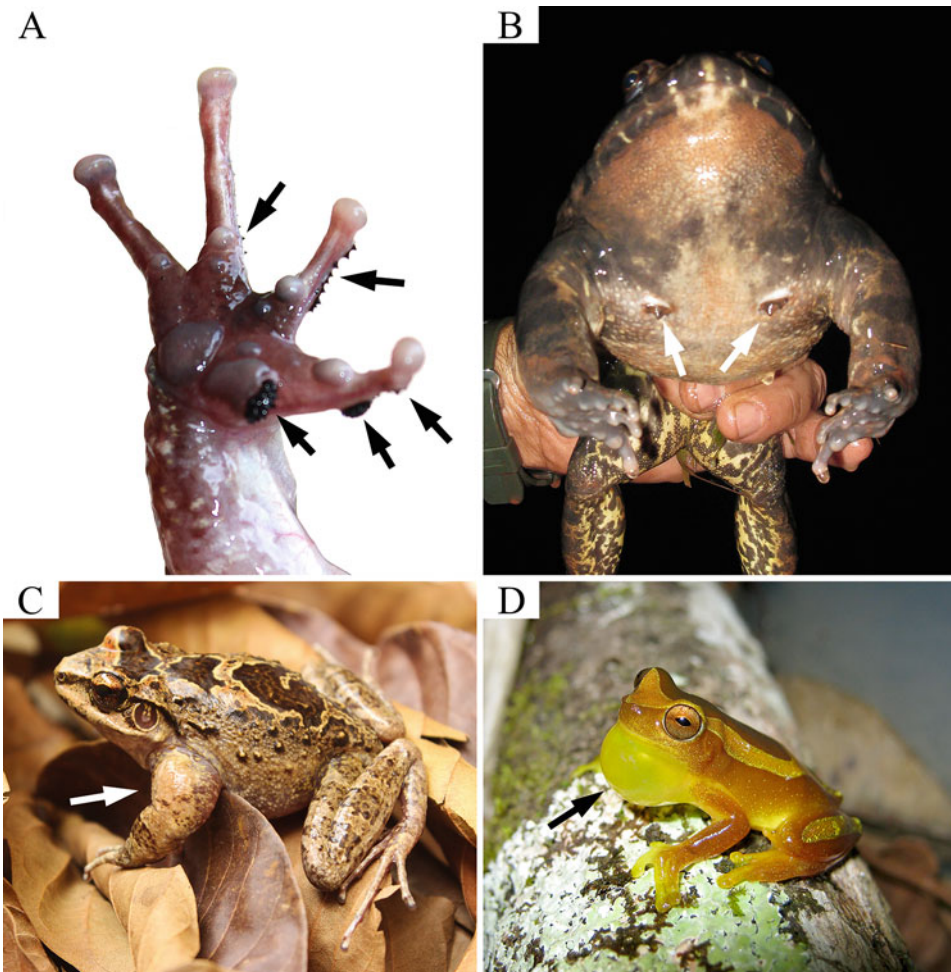


the main drivers for equal or slightly larger individuals among males in species with aggressive behavior (Kupfer 2007; Han and Fu 2013).

In addition to body size, it is possible to distinguish between sexes externally by the nuptial excrescences (Fig. 5a, b) or hypertrophied forelimbs (Fig. 5c). Nuptial excrescences are associated with male-male combat or with amplexus. Hypertrophied forelimbs can be associated of holding the pair during in an embrace during mating or oviposition. Sometimes, the mature oocytes of adult females can be visually perceptible through the transparent tegument of the venter. Many other anurans exhibit sexual differences in skin texture, with either the male or

female having rough or spiny skin that is not found in the other sex. These differences might function as tactile cues for sex recognition. The same is true for sexual differences in coloration, which is especially common in toads that are diurnally active.

Some frogs have glands of unknown function on various parts of the skin, and in many cases, these are sexually dimorphic or found only in one sex. Ventral glands are known to produce mucus secretions that glue the male to the female during amplexus in some rotund microhylids. In other frogs, these glands can either have the same function or produce pheromones that are transferred to the female during courtship or amplexus.



**Salientia Morphology, Fig. 5** Examples of sexual dimorphic characters present in males (pointed by arrows). (a) and (b) nuptial excrescences. (c) hypertrophied forelimb. (d) vocal sac

Calling is energetically expensive and requires suitable metabolic machinery to supply the muscles with large amounts of energy and oxygen. Vocalizations are usually emitted by males during the breeding season and the machinery necessary for its functions are: strong trunk muscles and large laryngeal apparatus in males than those of females; and vocal slits and sacs developed in males for most species (Fig. 5d).

When external sexual characters are absent or not visible, it is possible to determine sex and reproductive conditions through direct observation of the gonads. The bilaterally paired ovaries are ventromedial to the kidneys and suspended from the body wall by a pair of mesenteries. When enlarged with mature oocytes, the ovaries occupy much of the body cavity and may envelop other abdominal organs. Anurans oviducts are bilaterally paired and lie firmly held by peritoneum along the dorsal surface of the body cavity, extending from an adjacent position (usually ventral) to the lungs, posteriorly to the cloaca, lateral to each ovary. Reproductive males have testis that increase in size and become pigmented in some species during the breeding season. Such structures are attached ventrally to the kidneys by a membrane and usually are spheroid or ovoid small structures.

## Evolution

Whether the Lissamphibia originated from the Lepospondyls or the Temnospondyls remains controversial, though a stronger case for the latter can be found in the literature. Likewise, the relationship between lissamphibian groups is also shrouded in controversy. Recent studies indicate a close relationship between Salientia and salamanders, with caecilians placed as an external group (Benton 2015). Perhaps the discovery of new salientian fossils will shed light on the emergence and evolution of this group.

The oldest known Salientia date from about 247 million years ago, in the lower Triassic: *Triadobatrachus* from Madagascar and *Czatkobatrachus* from Poland. Despite some obvious differences, these fossils closely resemble an

extant anuran, especially regarding the flattened shape of the cranium. The first Salientia had a short tail, unlike the anuran fused postsacral vertebrae (urostyle). They also had a longer body, with up to 14 presacral vertebrae, and the limbs were shorter than that of extant anurans. In general, the overall skeletal morphology of extinct salientian shows an evolutionary path to the jumping habits found in anurans. After a large gap of about 60 million years since the occurrence of these two taxa in the fossil record, the Early Jurassic *Prosalirus* is the oldest known anuran, discovered in Arizona. This species had a vertebral column that resembles the one in modern anurans, though the exact number of presacral vertebrae is unknown. Nevertheless, the jumping habit is clearly already present. During the Jurassic period, anurans had a massive irradiation, and, by the end of this period, fossils attributed to several of the modern families are known. More on the evolution of the amphibians, including the Salientia, can be found in Carroll (2009) and Benton (2015).

## Cross-References

- [Adaptation](#)
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- [Color Change](#)
- [Digestive System](#)
- [Evolution](#)
- [Excretory System](#)
- [Integumental System](#)
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- [Skeletal System](#)

- Taxa
- Vertebrate Nervous System
- Vertebrates (Chordata)

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## Salientia Movement

- Salientia Navigation

## Salientia Navigation

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## Synonyms

Anuran movement; Anuran navigation; Salientia movement

## Definition

The over 5000 species in the taxonomic superorder Salientia (Latin for “to jump”) represent a group of amphibians in the order Anura – frogs and toads. Anura translates from Latin to “without tail,” meaning that species in this order physically change to a tailless state when transitioning from larval stages to juveniles and adults. Navigation (goal-directed) is movement of an individual

toward a destination, which incorporates information about current location and knowledge of a goal location during movement.

## Introduction

Frogs and toads of the superorder Salientia, also called anurans, are small-bodied, short-distance dispersers who rely on movement and navigation to reach important habitats during their biphasic (i.e., two distinct morphological stages) life cycle. Anurans are sensitive to many stressors because of their limited movement capacity and inherent ties to water for hydration and breeding. Therefore, proximity to aquatic habitats and moist environments are a major driver of juvenile dispersal distances, adult distributions, and migratory strategies. Factors that eliminate or fragment preferred habitats, or limit the ability of individuals to disperse from their natal sites can be problematic to anuran populations. Roads, in particular, can cause both a loss of direct connectivity and a disruption of water flow to breeding/natal sites (Andrews et al. 2008). However, other disturbances risk fragmenting and/or altering microsite conditions, particularly those related to soil moisture. In translocated northern green frogs (*Rana clamitans melanota*) and northern leopard frogs (*Rana pipiens*) Mazerolle and Desrochers (2005) found strong avoidance of disturbed sites as well as disruption in abilities to home back to capture ponds when traversing disturbed areas. Soil moisture has been found to be a key environmental condition that drives habitat preference for ground-dwelling anurans and has been shown to impact movement in bullfrogs (*Lithobates catesbeianus*) and Blanchard's cricket frogs (*Acris blanchardi*) (Youngquist and Boone 2014). Fragmentation of habitats can also have long-term implications for the genetic structure of populations. A study of European tree frogs (*Hyla arborea*) suggested inbreeding effects, as well as evidence of a genetic bottleneck among fragmented breeding ponds in Denmark (Andersen et al. 2004). Connectivity of populations in fragmented habitats is therefore a primary concern for many Salientia species, to maintain gene flow and maximize

opportunities for survival and reproduction among populations.

## Navigation and Orientation Strategies in Salientia

Orientation and navigation mechanisms in Salientia have been a topic of study since the 1960s because of limited movement capacity and high vulnerability to environmental conditions across many species. Adult anurans have been shown to have strong site fidelity (i.e., loyalty) and experiments with translocations of individuals show evidence of navigation ability back to their home site in many anuran species. Oldham (1967) suggested translocated green frogs (*Rana clamitans*) used olfactory cues to navigate back to their breeding site if moved within a reasonable distance; however, when moved at a further distance such that olfactory cues were disrupted, individuals of this species tended to move downhill (presumably toward water) or toward conspecific (i.e., other individuals of the same species) calls. In similar work with leopard frogs Dole (1968) suggested individuals displaced <1 km from their home site were able to successfully navigate a return, but those capabilities diminished at greater distances. He also found that visual impairment did not disrupt homing ability within the 1 km range, providing further support for an alternative cuing ability such as olfaction. Grubb (1970) also found displaced post-reproductive Mexican toads (*Bufo valliceps*) in the fall were capable of orienting back to their initial site of capture, even after a month removed (Grubb 1973). Impairing either the visual or olfactory capabilities of individuals in this species did not impact their homing behavior; however, impairing both senses simultaneously disrupted their ability to orient and navigate back to the capture site. This suggests toads may rely on multiple sensory mechanisms for orienting and navigating in the environment.

Other orientation mechanisms have been suggested, including solar compass orientation in a line perpendicular to the home site shoreline in Fowler's toads (*Bufo fowleri*) (Landreth and Ferguson 1966). This solar compass persisted

into darkness, suggesting either some kind of internal clock mechanism, or a switch to lunar orientation. However, solar compass orientation was disrupted when individuals were displaced at noon, after sunset, under dense cloud cover, or when playing a chorus of conspecific calls away from their home site. Sinsch (1989) later suggested there was redundancy and hierarchical ordering in orientation mechanisms in anuran species, and cueing depended on the degree of displacement and site familiarity. Orientation using a dual-cue system (e.g., olfactory and auditory cues), combined with use of landmarks and piloting (i.e., use of landmarks to drive navigation) in familiar landscapes are the most likely mechanisms for navigation in this group of species.

### Physiological and Behavioral Adaptations for Movement

As anurans transition from aquatic larval stages to terrestrial adults, physiological adaptations for survival shift as well. Once terrestrial, they are vulnerable to a host of predators and require quick movements to escape. They also shift diets and have developed adaptations for rapid capture of prey (primarily insects) in the environment. Adaptations for jumping are therefore paramount for the persistence of these species. Some species (e.g., the striped rocket frog (*Litoria nasuta*)) can leap up to 50 times their body length (James and Wilson 2008). In their terrestrial stage, frogs are physiologically and morphologically designed for jumping. Unlike humans their forearm contains a fused radioulna, and their leg bones contain a fused tibiofibular to provide structural integrity for jumping. Frog ankle bones (tibiale and fibulare) are long, providing leverage (more surface area to push off from) in jumping. The ilium is also long and jointed with the sacrum to provide greater force during leaping, which is also supported by fusion of tail vertebrae into a retracted urostyle. Similar to bone adaptations, a host of muscular adaptations, including enlarged leg muscle mass, have developed to facilitate jumping. Frog leg muscles are astoundingly powerful, capable of exerting more power during a

jump than physiologically possible due to the transfer of energy to an adjacent plantaris tendon, which functions in a catapult capacity to amplify acceleration beyond what is capable by muscle acceleration alone (Astley and Roberts 2011).

Adaptations for navigation in frogs and toads also vary with habitat needs – with different size, shape, and structure of legs and feet found in ground- vs. water- vs. tree-dwelling anuran species. Frogs may have partially or completely webbed feet if the species is primarily an aquatic-dweller, although some arboreal frog species maintain webbed feet for gliding. Tree-dwelling, or arboreal, frog species have mucous-lined padded toes to maintain grip in vertical conditions through adherence to surfaces via surface tension. Many frogs are also capable of walking instead of hopping, which may aid in prey acquisition. Burrowing and other ground-dwelling frogs also often have adaptations called “spades” on their hind feet to aid in digging burrows.

Of utmost importance at all life stages are behavioral mechanisms to aid in the regulation of temperature and water in their environment. Many frogs and toads seek thermal and moisture shelters called refugia underground, under structures (e.g., logs), and/or by shifting to nocturnal periods of activity. All anurans are ectotherms (i.e., rely on external temperatures for function), thus moist skin can help maintain thermoregulation, such as aiding in cooling body temperatures during extreme heat conditions. In temperate zones that experience seasonally freezing conditions, anurans will also undergo a state of torpor (i.e., temperature-induced reduction of activity similar to hibernation in mammals) until external temperatures warm to levels that allow for activity. All of these behavioral and physiological adaptations aid in individual survival and facilitate movement toward preferred refugia areas or away from environmental conditions that would lead to thermal or water stress.

### Dispersal Movements in Salientia

Dispersal in Salientia species primarily (but not exclusively) involves movement of juveniles in a



single direction away from the natal site (where metamorphosis from the aquatic larval phase to terrestrial phase takes place). For anurans breeding in ponds or other standing water bodies dispersal predominantly occurs in juveniles as they transition to the terrestrial life stage. Dispersal typically only occurs once during an individual's life, and generally covers a longer distance than movements of adults during migration, though distance covered is still limited in scope (Semlitsch 2007). Unfortunately, little is known about dispersal mechanisms in juvenile frogs and toads, though there is wide-ranging evidence that individuals are particularly vulnerable while dispersing across unfamiliar terrain (Pittman et al. 2014).

Studies on movement mechanisms in anuran species have become more prevalent in the last decade as the discipline of movement ecology has developed. Individuals at different life stages display different forms of movement for different reasons. Movement may therefore be characterized into “modes,” or phases, based on life stage and behavior in anuran species. Pittman et al. (2014) characterized these phases under a movement ecology framework (see Nathan et al. 2008). In the predeparture phase, newly metamorphosed juveniles initiate movements away from their natal site, often in large numbers of same-aged individuals called cohorts. The predeparture phase can be broken into two distinct substages – preemergence (individuals undergoing recent metamorphosis move to the water's edge and begin to orient themselves for departure) and wait stage (individuals assess timing regarding when conditions are appropriate to depart). Individuals during the predeparture phase may also engage in foray loops where small, temporary exploratory movements are made into surrounding terrestrial habitat with return to the natal site. However, drivers behind decisions to initiate the predeparture phase are still not understood, particularly how individuals assess environmental conditions that suggest greater risk to departure at certain times compared to others (Pittman et al. 2014).

From the predeparture phase, individuals will then move into the initial juvenile movement phase, where it is thought that individuals move

relatively quickly initially from the natal site then slow movement and begin seeking appropriate habitat as they move further away (Pittman et al. 2014). During the movement phase, individuals will decide what distance to and direction to move during each “step” or single movement interval, which may result in a complex movement pattern if turning occurs frequently. Oriented nonrandom movement occurs with greater propensity during the final stages of the initial movement phase as the individual becomes increasingly responsive to habitat in the vicinity – this is termed the directed mode of the initial movement phase (Pittman et al. 2014). This leads to a settlement state within the initial movement phase whereby individuals are searching for specific environmental conditions with greater intentionality (e.g., refugia locations). During settlement dispersing juveniles will begin to establish a small home range where the suite of resource needs can be met in a given area. For anurans, this may include areas centered on moist terrestrial locations (e.g., under logs, rocks etc.), or inundated or flowing water areas for aquatic species. Once settled into a home range, movements tend to shift toward short foraging forays until breeding migration occurs (Pittman et al. 2014). Home range size varies by species and habitat affinity and can range from 1–2 m<sup>2</sup> to 60 m<sup>2</sup> (as shown in green frogs; Martof 1953) or more. Semlitsch (2007) proposed an alternative take on stages of juvenile dispersal for smaller or slow to mature amphibian species, suggesting in the first year recent metamorphs will remain close to natal sites, then as body size and locomotor skills grow, disperse increasingly further distances each subsequent year into adulthood. However, dispersal distances are still generally limited (e.g., <1 km) under this framework.

## Migration in Salientia

Following initial juvenile dispersal from natal sites, many anuran species will undergo seasonal migration as they mature into adult stages. Migratory movements likely evolved as the need to locate and navigate to spatially dispersed resources arose over time. Migration is

differentiated from juvenile dispersal in that navigation and orientation takes place with a known destination in mind. However, the destination is largely constrained by exothermic temperature regulation and moisture/water needs. Migration toward aquatic breeding sites is the most common form of migratory movement in anurans. Breeding anurans show evidence of philopatry (fidelity to breeding sites) and many will return to the same aquatic breeding site for the duration of their life (Semlitsch 2007). Breeding site fidelity has been shown to be preferential in common toads (*Bufo bufo*; Reading et al. 1991) as well as wood frogs (*Rana sylvatica*; Kupfer and Kneitz 2000). Site fidelity may reduce risks of mortality relative to open exploration for better breeding sites. However, many species are also willing to relocate to newer, better sites when made available in close proximity, as shown in Natterjack toad (*Bufo calamita*), gray treefrog (*Hyla versicolor*), chorus frog (*Pseudacris triseriata*), and others (Semlitsch 2007).

Species are known to use a variety of homing and orientation mechanisms (e.g., olfaction, visuo-spatial memory, conspecific attraction) to navigate during migration. Migration movements have been shown to vary among species and between sexes within the same species. Rittenhouse and Semlitsch (2007) showed frogs and toads tend to move further than their salamander relatives, with toads moving at greater distances than terrestrial or tree frog species. In most amphibian species migrating males tend to migrate earlier than females, allowing for ample opportunity for mate choice when females arrive at breeding sites (Douglas 1979). Timing of migration depends on geographic location and thus climate factors that drive local environmental conditions. Often migration movements are closely linked to seasonal rainfall, which provides ephemeral (i.e., temporary) aquatic breeding sites such as pools, ponds, and wet depressions. However, migration movements are also tied to seasonal temperatures as these species need milder temperatures to avoid effects of water or thermal stress during movement. There has even been some evidence of nonbreeding migration between spatially disjunct home ranges, foraging sites, and microsite refugia, or to access important

overwintering locations (Semlitsch 2007; Pittman et al. 2014).

The degree of permeability (or, alternatively, resistance) in the landscape has direct influence on migration of individuals (Sinsch 2014). Some estimates suggest maximum migratory distances in adults of 0.5–15 km from their settlement location. Osawa and Katsuno (2001) found maximum migration distances of 500 m in two species of brown frogs (*Rana japonica* and *R. ornativentris*). If aquatic habitats are clustered, such as a cluster of ponds within a single home range, then frogs and toads may use the entirety of the cluster as breeding centers (Semlitsch 2007). Some evidence points to clustered wetland or pond networks allowing anuran populations to function as metapopulations, or connected subpopulations functioning as a super-population through local extinctions and colonizations among habitat patches (Marsh and Trenham 2001; Heard et al. 2012).

Ensuring that management for dispersal and migration are treated as separate processes can prevent mismanagement as movements associated with dispersal (e.g., departure from the natal site) can be very different than movements associated with migration (e.g., goal-directed seasonal navigation to breeding sites) (Semlitsch 2007). Indeed, the cumulative resources needed to facilitate both dispersal and migration should be a focus of comprehensive management for anuran species. Movements during dispersal and seasonal migration are particularly vulnerable times for individuals (Pittman et al. 2014). Changes in environmental conditions that make habitats and migration corridors less hospitable can have severe fitness consequences for individuals. Fragmentation of habitats may dramatically alter the permeability of landscapes; whereas loss of key habitat features (e.g., aquatic breeding sites) may render an area unusable for the population.

## Conclusion

Much effort is presently focused on conservation behavior approaches to developing creative ways to connect and restore populations of declining amphibian species. Management actions that

restore connectivity to habitats fragmented by roads and that attract adults to restored breeding sites have been promising thus far. Green frogs and leopard frogs have been shown to use substrate-lined PVC tunnels >0.5 m in diameter as an alternative to road crossings (Woltz et al. 2008). Recent research has also shown individuals can be attracted to restored breeding sites using conspecific call playbacks, as found in the endangered green and golden bell frog (*Litoria aurea*) (James et al. 2015). A comprehensive understanding of the ecology of movement, its behavioral mechanisms, as well as the scale at which processes are occurring is critical for conservation of anuran populations (Semlitsch 2007).

## Cross-References

- Behavioral Flexibility
- Behavioral Variation
- Compass Orientation
- Conservation
- Conspecifics
- Dispersal Ability
- Dispersal Patterns
- Ecology
- Fidelity
- Fitness
- Foraging
- Home Range
- Homing
- Learning
- Life History
- Locomotion
- Migration
- Navigation
- Orientation
- Philopatry
- Population
- Predation Risk
- Salientia Communication
- Salientia Life History
- Salientia Locomotion
- Salientia Morphology
- Salientia Sensory Systems
- Species
- Taxa
- Thermoregulation

- Torpor
- Translocation

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terrestrial habitats, and on all continents, with the exception of Antarctica. Their highest diversity is in the New World tropics, with approximately half of known species inhabiting this environment (Vitt and Caldwell 2009).

Members of Salientia undergo dramatic metamorphosis from larva to adult life stages. The fully aquatic larva is physiologically, ecologically, and behaviorally unique from, mostly terrestrial, juveniles and adults. As such, frogs and toads require a variety of mechanisms for sensing both terrestrial and aquatic environments. The most prevalent sensory systems of Salientia include: (1) cutaneous sense organs for mechanoreception, (2) auditory sense organs, (3) well-developed eyes, (4) chemoreception through olfaction and taste, and (5) internal sense organs for proprioception.

## Cutaneous Sense Organs

The skin of toads and frogs contains a number of receptors that inventory environmental cues outside of the animal's body. These receptors include those that register pain, temperature, and pressure. These mechanoreceptors are comprised of free and encapsulated nerve endings in the dermis, with a several spreading into the epidermis (Catton 1958).

The most conspicuous of the cutaneous sense organs is the lateral line system, which is present in the larval stage, and in a few species, through adult stages as well. These mechanoreceptor organs are organized singly or in linear arrangements called “stitches.” Most commonly, these organs are arranged in lines on both sides of the animal's body, behind the head and around the eyes (Elepfandt 1982). In all amphibians, the lateral line organs are superficially located and free standing on the skin so that water directly impinges upon them. The lateral line organs are sensors for water velocity, as the frictional force of the water running alongside the system is proportional to velocity. From each organ, 4–12 cupulae, jelly-like cups surrounding the hair cells, extend up to a millimeter in the water. They are oriented perpendicularly to the organ's axis to allow passing water to deflect the cupulae. Each cupulae contains approximately 40–80 sensory hair cells

## Salientia Sensory Systems

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## Introduction

Salientia, the group of amphibians that includes frogs and toads, is a widely diverse clade, with more than 5,450 species documented. Frogs and toads can be found in most freshwater and

(cilia), which respond to deflection from water. The cilia respond to changes in water pressure by bending in only one axis (Tinsley and Kobel 1996). Retention of the lateral line system after metamorphosis is well-documented in all pipids and a few discoglossids, but has also been found in various other families, all of which are characterized by an aquatic lifestyle. Therefore, the retention of the lateral line system throughout ontogeny appears to be related to the ecology of the animal, and not systematics (Tinsley and Kobel 1996).

The response of the lateral line organs to wave stimuli has been studied in aquatic species, *Xenopus*, and through electrophysiological recordings, it was determined that wave amplitude of 0.2  $\mu\text{m}$  can be detected (Elepfandt and Wiedemer 1987). Lateral line organs are innervated by both afferent neurons to locate water flow, as well as inhibitory efferent neurons. Inhibitory efferent neurons are only activated when the animal is swimming, to reduce sensory “noise” that would reduce sensitivity (Russell 1971). The lateral line system is ecologically useful by allowing the animals to detect wave stimuli created by prey and predators (Elepfandt 1984), and orient themselves in their aquatic environment (Elepfandt 1982; Elepfandt 1984).

## Auditory Sense Organs

The ears of frogs and toad are paired sensory structures on each side of the head. The frog’s auditory system has three components: (1) a low-frequency vibration detector (sacculus), (2) a low to mid frequency sound detector (the amphibian papilla), and (3) a high frequency sound detector (the basilar papilla) (Smotherman and Narins 2000). Each ear is comprised of an inner, middle, and outer part. The inner ear is a fluid-filled membranous sac which contains the sensory receptors (neuromasts). The ears of frogs and toads provide two unique functions: (1) the reception of sound waves, or hearing, and (2) balance and the detection of the movement of the body. Neuromasts serve as the receptors for both

of these functions. Similarly to the neuromasts of the lateral line system, the neuromasts record fluid movement along a single axis through deflection of cilia (Smotherman and Narins 2000).

The middle ear contains the bone and muscle that transfers vibrations from the eardrum to the inner ear. The middle ear of frogs and toads has two auditory paths: (1) the tympanum-stapes option for airborne sounds, and (2) the forelimb-opercular option for seismic sounds. The stapes, a single bony rod that extends between the external eardrum and the inner ear, often lies in an air-filled cavity. The limb-opercular option is unique to frogs and salamanders, where sound waves are propagated from the ground through the skeletal system and onto the opercular muscle within the shoulder.

The inner ear consists of two sac-like structures joined by a wide passage. The dorsal structure projects three semicircular canals, which provide sensory information for the animal to properly balance. Each of these canals lies in a different orientation (one lies horizontally, two are vertical, and all three are perpendicular to each other), allowing movement to be documented in three different planes and provide a sense of balance. In frogs and toads, outer ear is minimal, or may be entirely absent (Lombard et al. 1981).

## Photoreception

The structure of the Salientia eye is similar in structure to other vertebrates. The eye consists of a hollow sphere, lined by the retina, the sensory lining of the structure. The sclera, dense connective tissue on the external structure of the eyeball, supports the retina. The transparent part of the outer sheath, which allows light to enter the eye, is the cornea. In postmetamorphic frogs and toads, eyelids and a nictitating membrane provide protection to the cornea. Behind the cornea lies a spherical lens, and the amount of light passing through the lens is regulated by the iris. The opening of the iris, the pupil, is opened or closed by musculature surrounding the iris. The shape of the eye is maintained by the presence of fluid in



the cavity behind and in front of the lens (Vitt and Caldwell 2009).

After light enters the eye, it is focused onto the retina through the lens. The receptor surfaces of the sensory cells face inward, away from the light source. Most members of Salientia have four types of sensory receptors, including red and green rods as well as single and double cones. The cones are responsible for color reception and possess specialized pigments that register a small range of wavelengths. The chemical state of the receptors is changed when light strikes the pigments. The green rods are unique to amphibians, and they are the only vertebrates with double rods. In species with degenerate eyes, these rods become absent. The visual pigment of rods detects all wavelengths of light and therefore only registers the presence or absence of light (Maturana et al. 1960).

The metamorphosis of frogs and toads from aquatic larva to terrestrial adults requires a change in the morphology of the eye. In aquatic conditions, there is no refraction of the light at the cornea; therefore, in tadpoles, all refraction is achieved through the lens alone. During metamorphosis, the lens flattens in to adapt the refraction of the eye for air conditions. In some aquatic species, such as *Xenopus*, the lens remains roughly spherical (Chung et al. 1975).

## Chemoreception

Olfaction is a chemosensory processes performed in paired nasal organs, as well as the vomeronasal organ (Jacobson's organ). Each organ opens to the environment through the external opening of the nostril, and internally into the buccal cavity. In terrestrial frogs, metamorphosis from tadpole to adult requires a shift in chemical detection from water to air. Between the internal and external openings is a large olfactory cavity, with several additional chambers that extend sideways and downward. The surface of these chambers contains mucous cells lined with ciliated epithelium. There are three major patches of ciliated epithelium. The largest patch is found on the roof,

medial wall, and anterior end of the principle cavity. Two small patches occur on the middle of the floor, and another in the vomeronasal organ. Innervation of the principle cavity occurs from the olfactory bulb of the brain, whereas the vomeronasal organ is innervated by a separate olfactory branch (Scalia 1976).

Taste buds are found in all amphibians and are present in two varieties: (1) papillary organs, which are located on the outer surface of the tongue, and (2) nonpapillary organs located throughout the buccal cavity, with the exception of the tongue. Taste buds have been shown to be highly sensitive to salts, acids, and bitter chemicals (Tinsley and Kobel 1996; Vitt and Caldwell 2009).

## Internal Sense Organs

Proprioceptors organs, found in muscles, tendons, ligaments, and joints, are the major internal sensor organs in clade Salientia. These organs provide information on the tension and stress within the musculoskeletal system, allowing the brain to coordinate the movements of the body during locomotion. These organs show structural diversity from simple nerve endings to netlike endings (Vitt and Caldwell 2009).

## Conclusions

Clade Salientia is comprised of a wide variety of frogs and toads, each occupying a range of ecological niches. To navigate life from tadpole to adult, these animals require a number of sophisticated senses to avoid predators, find prey, and maximize their environment, both in the water and on land. While sensory abilities vary by species, frogs and toads largely sense their world through a combination cutaneous sense organs for mechanoreception, a complex sense of hearing, specialized vision, and chemoreception through olfaction and taste, which has led to an extremely successful group of animals around the world (Vitt and Caldwell 2009).

## Cross-References

- [Chemoreception](#)
- [Evolution of Animal Color Vision](#)
- [Mechanoreceptors](#)
- [Salientia Communication](#)
- [Salientia Life History](#)
- [Salientia Navigation](#)
- [Sensory Receptors](#)
- [Visual Perception](#)

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## Same/Different Concept

- [Matching-to-Sample: Comparative Overview](#)

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## Same/Different Learning

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## Introduction

The major goal of comparative cognition is to compare cognition across species. For many years, a species' cognition was rated (compared) on a hierarchy of cognitive-task difficulty with ability to learn abstract concepts typically at the top. Abstract concepts transcend individual features of the stimuli and depend instead on the relationship between stimuli, for example, judging two pictures as being the *same* or *different*. Such judgments can become an abstract concept when they are accurately made to novel stimuli.

*Same/different* abstract-concept learning has a special role in abstract cognitive learning during human development (e.g., learning equivalence and conservation relationships) and provides the basis for more complex strings of equivalent operations involved in novel sentence construction and novel sequences of mathematical operations (e.g., Chen and Mo 2004; Smith et al. 1992). This generalization of equivalence carries forward into adult years, apparently forming the “very keel and backbone of our thinking” as the famous psychologist William James proclaimed 128 years ago (1890/1950, p.459).

Related to human abstract-concept learning is the issue in comparative cognition of which non-human animal species can learn a *same/different* abstract concept. This issue was brought into focus 40 years ago when David Premack (1978) asserted that only humans and language-trained animals (i.e., chimpanzees) had the ability to learn *same/different* concepts. But considerable progress in testing animal cognition and concept learning has been made since Premack’s claim suggesting that a variety of other animal species (baboons, rhesus monkeys, capuchin monkeys, parrots, crows, Clark’s nutcrackers, black-billed magpies, pigeons, and possibly even bumblebees) might have the ability to learn at least a partial *same/different* concept (e.g., Bhatt and Wright 1992; Bovet and Vauclair 2001; Brown and Sayde 2013; Katz and Wright 2006; Katz et al. 2002; Magnotti et al. 2015, 2016; Pepperberg 1987; Wasserman et al. 2001; Wasserman and Young 2010; Wright et al. 1984a, b, 1990, 2003, 2016, 2017).

Nevertheless, obtaining convincing evidence that these animals actually do have the cognitive ability to fully learn a bona fide *same/different* abstract concept can be tricky and likely depends upon: (i) the nature of the relational comparisons being made and (ii) the level of abstractness learned from those relational comparisons. Some tests of relational comparisons used multiple-item visual stimulus arrays where animals (e.g., pigeons) detected differences among items (vs. no item differences) or texture variations from an imbedded item block. Although manipulations of the texture-block size or number of

different items in the array were shown to produce orderly changes, when those arrays were reduced to just two stimuli, accuracy often approached chance performance (e.g., Cook et al. 1997; Young et al. 1997). But bona fide *same/different* abstract-concept learning should also be supported by judgments of two stimuli, the simplest case of relational comparisons. The gold standard for evaluating abstractness and the level of abstractness necessary for claiming bona fide *same/different* abstract-concept learning is full transfer to novel stimuli (i.e., equivalent to the level of training accuracy). In principle, full transfer could be produced by training with a limited (small) set of training stimuli (i.e., small number of exemplar pairs of the *same/different* rule), although this rarely occurs (but see Oden et al. 1988; Smirnova et al. 2015). Some earlier tests of animal *same/different* concept learning used pairs of stimuli, but were too limited in the number of training stimuli (e.g., colored geometric shapes) which resulted in too few exemplars of the rule to obtain full abstract-concept learning (e.g., Blaisdell and Cook 2005; Robinson 1960; Wright et al. 1984; Zentall and Hogan 1974). Humans too require variation in the exemplars to adequately learn rules (e.g., Chen and Mo 2004). Finding partial concept learning tends to be inconclusive and difficult to interpret *vis-à-vis* the cognitive ability to learn the bona fide *same/different* abstract concept.

To overcome issues of (i) interpreting the nature of the relational comparisons being made, and (ii) evaluating abstractness of the relational comparisons, a new approach seemed necessary. Related to the first issue, it seemed necessary to use simple pairs of stimuli for training and testing. Related to the second issue, it seemed necessary to use novel stimuli on all transfer trials and not reuse transfer stimuli to avoid confounding learning and transfer. Also related to the second issue was the level of transfer for establishing abstract *same/different* concept learning. As logic would have it, no transfer would indicate an absence of abstract-concept learning, whereas transfer equivalent to the highest level of training performance would indicate full abstract-concept learning. Having

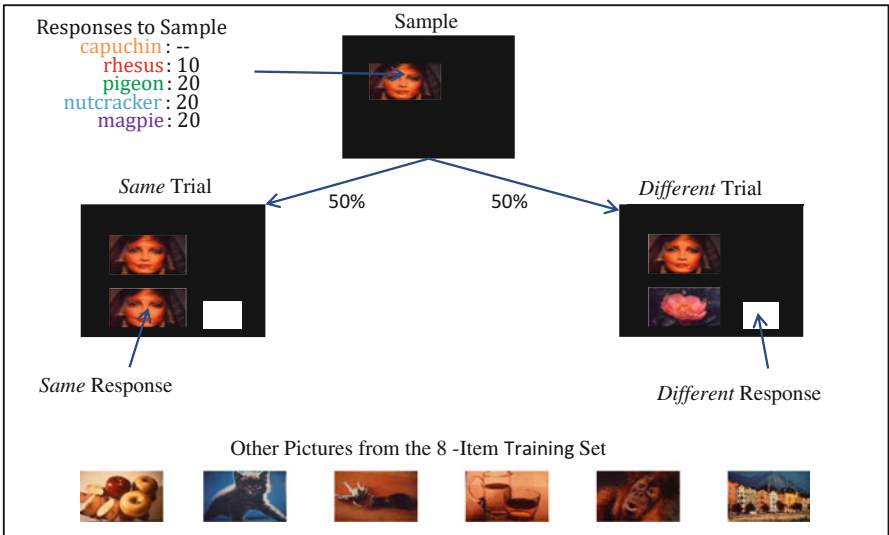
said this, it follows that interpretation of intermediate levels of transfer (i.e., partial concept learning) would be unclear about whether the animal being tested could or could not learn the bona fide *same/different* abstract concept. Therefore, a manipulation was necessary that would likely affect the degree of transfer and provide a continuum of transfer between little or no transfer to that of full concept learning. The manipulation chosen was the size of the training-stimulus set; small training sets would result in fewer exemplars of the rule and likely less transfer, whereas large training sets would result in more exemplars of the rule and likely more transfer. Accordingly, if partial concept learning was initially obtained, then some larger training set might produce full concept learning. Said otherwise, if a species is truly capable of abstract-concept learning, then there should be some conditions where those individuals can perform as accurately with novel stimuli as they do with the training stimuli. Moreover, there should be a whole function relating the size of the training set to the degree of transfer, which would then provide more powerful comparisons across species than any single level of transfer from an arbitrary selected training set size. To insure that training set sizes would likely reach a sufficiently large set size for any realistic evaluation of full concept learning, training set sizes were successively doubled (logarithmic scale) with training and transfer testing following. This approach required a much larger number of stimuli than earlier approaches using limited numbers of colored geometrical shapes. To make the stimuli as distinctly different as possible, so-called travel-slide pictures (e.g., scenes, objects, animals, buildings, people) were used (see Wright and Katz 2006 for the stimuli used for training in each set size and stimulus pairs used for testing transfer after learning at each set size). This approach of expanding the training set size to generate concept-learning functions was used to obtain full transfer (i.e., abstract-concept learning) and make direct comparisons among capuchin monkeys, rhesus monkeys, pigeons, Clark's nutcrackers, and black-billed magpies.

### **Same/Different Abstract-Concept Learning by Capuchin Monkeys**

The first concept-learning test using these procedures was with three (experimentally naïve) capuchin monkeys (Wright et al. 2003). Trials began with the simultaneous presentation of two pictures, one above the other, plus a white rectangle in the lower right-hand corner (Fig. 1).

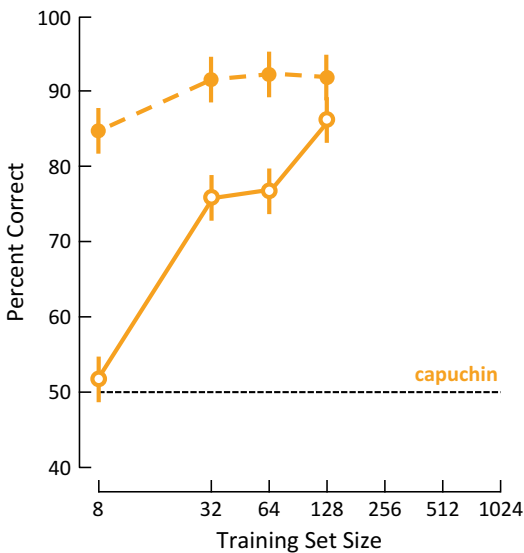
If the two pictures were the same, then a touch (choice) to the lower picture was correct; if the pictures were different, then a touch to the white rectangle in the lower right-hand corner was correct. Correct responses were reinforced with a banana pellet. Daily sessions contained 100 trials (50 *same* trials and 50 *different* trials). Monkeys were trained until overall performance was 80% correct or better on three consecutive sessions and were then tested for concept learning. On transfer sessions there were 90 training (baseline) trials and 10 transfer trials (5 *same* trials and 5 *different* trials). Picture stimuli on transfer trials were novel, and six transfer test sessions were conducted consecutively. Correct responses on transfer trials were reinforced similar to correct responses on baseline trials. Transfer trials were intermixed with training trials and trial sequences varied daily. Following transfer testing, the 8-item training set was doubled. Doubling the training set was repeated four times. Transfer testing was conducted following training with 32-, 64-, and 128-item set sizes when performance accuracy was 85% correct (or greater) on a single training session.

As the size of the training set was expanded, there was a dramatic decrease in the number of training trials (from more than 3500 trials to the minimum of 100 trials) necessary to meet the performance criterion relative to the number required with the initial 8-item training set (3533 trials). All three monkeys met the performance criterion in their first 100-trial session with one or both of the two largest set sizes containing 64 and 128 items, respectively. Mean transfer and baseline performances are shown in Fig. 2. Initially (8-item training set) transfer performance with the novel pictures was not significant (51.7% correct) relative to chance performance (50%



**Same/Different Learning, Fig. 1** Examples of *same* and *different* trials. Capuchins were not presented with the sample stimulus alone and instead were presented with both pictures and white rectangle simultaneously. Rhesus touched the sample picture 10 times to get the lower picture and white rectangle. Pigeons, nutcrackers,

and magpies pecked the sample picture 20 times to get the lower picture and white rectangle. A response to the bottom picture was correct on *same* trials and a response to the white rectangle was correct on *different* trials. The other six pictures of the initial 8-item training set are shown at the bottom



**Same/Different Learning, Fig. 2** Mean percent correct performance from three capuchin monkeys on training (baseline) trials (bold broken lines, filled symbols) and novel (transfer) trials (bold lines, unfilled symbols) with successively expanded training sets from 8 to 128 picture stimuli in the *same/different* task. The dotted line at 50% correct is chance performance. Error bars are  $\pm$  one standard error of the mean

correct), a result showing no evidence of any (partial) abstract *same/different* concept learning. As the set size was increased, transfer performance increased to 76.1%, 77.2%, and 86.7% with increases in set size of 32, 64, and 128 stimuli, respectively. Importantly, transfer performance accuracy following training with the 128-stimulus set was equivalent to baseline performance accuracy revealing that these capuchin monkeys had fully learned the *same/different* abstract concept.

### Same/Different Abstract-Concept Learning by Rhesus Monkeys

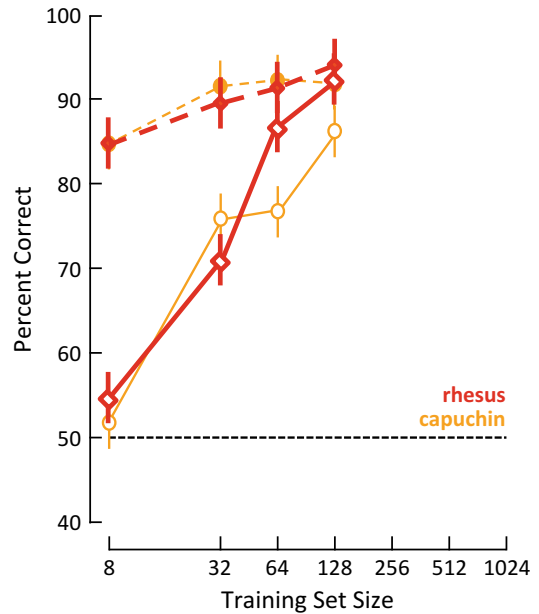
A group of three rhesus monkeys was trained similar to capuchin monkeys, including the use of the same picture set, simultaneous presentation of two pictures, and the white rectangle, a touch (choice) to the lower picture was correct on *same* trials, a touch to the white rectangle was correct on *different* trials, and daily sessions of 100 trials (50 *same*, 50 *different* trials) (Katz et al.



2002). Surprisingly, only one of the three rhesus monkeys ever learned the task with the initial 8-item training set and that monkey required 200 training sessions to do so; the other two monkeys never showed any learning despite a year (250 sessions) of training. By comparison, all three capuchin monkeys had learned the same initial *same/different* task to the criterion of three sessions of 80% or better in just 34 to 38 training sessions. In order to encourage task learning, this group of rhesus monkeys plus another group of three experimentally naïve rhesus monkeys were required to make 10 touches to the top item prior to being presented with the lower (test) item and the white rectangle (Fig. 1); only then could they make their choice response (*same* response to the lower item, or *different* response to the white rectangle). With this response requirement to the sample stimulus, all monkeys rapidly learned the *same/different* task, at about the same rate (40 training sessions) as did the capuchin monkeys. Importantly, the rhesus group initially trained with 10 responses to the sample stimulus showed novel-stimulus transfer increasing from near chance with the 8-item training set to better than 85% correct with the 128-item set which was equivalent to their respective baseline (training stimuli) performance accuracies (Fig. 3).

Thus, the 10-response group of rhesus monkeys demonstrated full concept learning, similar to that shown for capuchin monkeys. The requirement that rhesus monkeys of the 10-response group respond to the upper picture had a profound effect on their ability to learn the *same/different* task relative to the group not required to respond to the upper picture. This observing response requirement was apparently necessary for the rhesus monkeys, but not capuchin monkeys, to fully learn the abstract concept (see also chapter ► [Primate Cognition](#)). Such fine-tuning of procedures for learning the abstract concept of *same* vs. *different* would be useful later in training and testing avian species (e.g., pigeons, nutcrackers, magpies) for *same/different* abstract-concept learning.

Despite this procedural difference between these monkey species, once the concept was



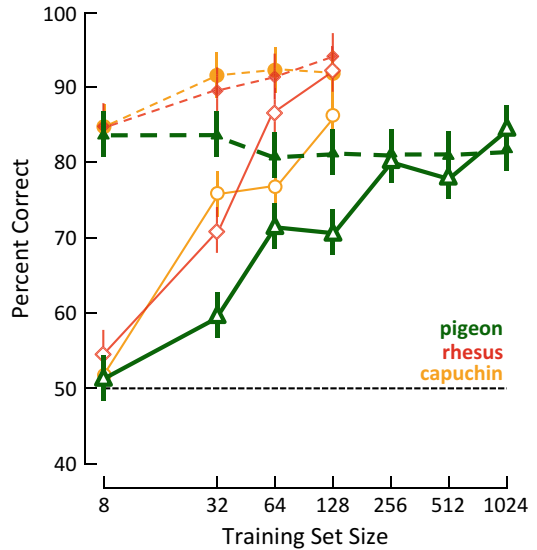
**Same/Different Learning, Fig. 3** Mean percent correct performance of three rhesus monkeys on training (baseline) trials (bold broken red lines, filled symbols) and novel (transfer) trials (bold red lines, unfilled symbols) with successively expanded training sets from 8 to 128 picture stimuli in the *same/different* task and are compared to capuchin monkeys (thin orange lines, Fig. 2). The dotted line at 50% correct is chance performance. Error bars are  $\pm$  one standard error of the mean

learned by the rhesus monkeys they then could accurately perform the *same/different* task without having to make any observing responses to sample stimuli, a requirement for accurately performing list-memory tasks [see chapter ► [List Memory Effects \(Primacy and Recency\)](#)]. Control tests with other rhesus monkeys included a group where the set size was not expanded, but the numbers of training sessions and transfer-testing sessions were otherwise matched to the experimental group. Transfer by this control group did not improve despite the same amount of training and transfer testing, thereby demonstrating that the manipulation of progressively expanding the training set and exponentially expanding the number of exemplars was the key to learning the *same/different* abstract concept.

### Same/Different Abstract-Concept Learning by Pigeons

Four pigeons were trained and tested with procedures similar to those previously described for rhesus monkeys (Katz and Wright 2006). The successful training and testing of rhesus monkeys that depended upon the monkey touching the sample stimulus 10 times before being presented with the test stimulus and white rectangle prompted the use of a similar response requirement for studies with pigeons. Since pigeons tend to peck stimuli more rapidly than monkeys touch stimuli, the pigeons were trained to peck the sample stimulus 20 times before being presented with the test stimulus and white rectangle (see also chapter ► [Pigeon \(Columbidae\)](#)). Otherwise, the trials and sessions were virtually identical to those used with the rhesus monkeys including, 100 trials (50 *same*, 50 *different*), selected from the same 8-item picture set used to test monkeys. Training continued until performance was 80% or better for three consecutive sessions. Transfer testing was conducted for six consecutive sessions each with the same baseline trials and the same 5 novel *same* and 5 novel *different* transfer trials as used with monkeys. After the first transfer test, the picture set size was progressively doubled to 16, 32, 64, and 128 picture items, like with the monkeys. Because of some uncertainty whether the pigeons would attain full *same/different* concept with 128 items, the training set was also further doubled to 256, 512, and 1024 pictures. Training was conducted with all expanded training sets for a minimum of 3 sessions along with a performance criterion of 85% correct on a single session prior to transfer testing. The transfer stimuli were novel on all transfer tests (see Wright and Katz 2006 for novel testing pairs used for transfer testing after learning with each training set size).

Pigeons initially learned the task in about 30 sessions (range 19–45) similar to rhesus (40) and capuchin monkeys (35). Novel-stimulus transfer increased from 51.3% after learning the task with the initial set of 8 items to 59.6%, 71.7%, 70.8%, 80.4%, 78.5%, and 84.6% for set sizes 32, 64, 128, 256, 512, and 1024, respectively (Fig. 4). For the 256, 512, and 1024 set sizes, the



**Same/Different Learning, Fig. 4** Mean percent correct performance of four pigeons on training (baseline) trials (bold broken green lines, filled symbols) and novel (transfer) trials (bold green lines, unfilled symbols) with successively expanded training sets from 8 to 1024 picture stimuli in the *same/different* task and are compared to rhesus monkeys (thin red lines, Fig. 3) and capuchin monkeys (thin orange lines, Fig. 2). Dotted line at 50% correct is chance performance. Error bars are  $\pm$  one standard error of the mean

levels of transfer were equivalent to their respective baseline levels, thereby producing compelling evidence that pigeons can indeed fully learn the *same/different* abstract concept. Such a conclusion was further supported by two control groups, like with rhesus monkeys, where the numbers of training sessions were matched to the experimental group's training but only the initial 8-item training set was used. One control group was matched in transfer testing to the experimental (expanding training set) group, and another control group was only transfer tested at the very end of the experiment. Neither group showed any evidence of transfer. This is compelling evidence, like that from rhesus monkeys, that pigeons can indeed fully learn the bona fide *same/different* abstract concept and also that this abstract-concept learning depends on expansion of the set of training stimuli.

Notwithstanding the compelling evidence that pigeons can fully learn the *same/different* abstract

concept, the smallest set size for which pigeons attained full concept learning is larger than that for capuchin and rhesus monkeys. This finding means that pigeons need to experience and learn more exemplars of the abstract-concept rule to fully learn the abstract concept than do monkeys. Moreover, the whole set-size transfer function for pigeons is primarily below those for monkeys, showing that the rate of transfer growth occurs more slowly and requires more exemplars of the *same/different* rule than required by monkeys. Such a conclusion highlights the importance of comparing entire training set-size functions, particularly for an important cognitive function like abstract-concept learning that can be compared across a number of different animal species, like Clark's nutcrackers that store thousands of seeds in the autumn, and rely on excellent spatial memory to recover cached seeds to survive winter and spring (Vander Wall and Balda 1977).

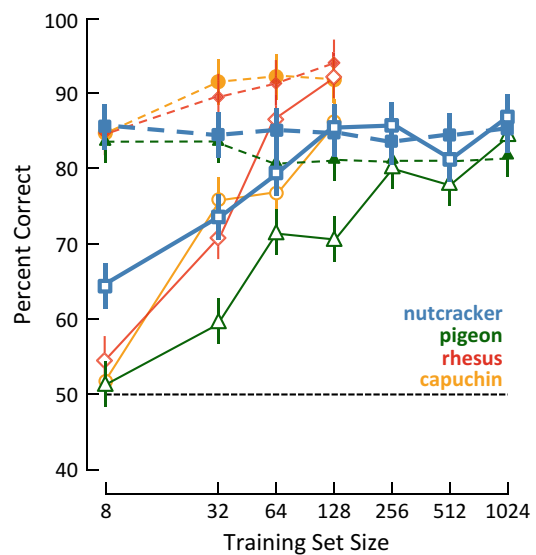
### Same/Different Abstract-Concept Learning by Clark's Nutcrackers

Seven wild-caught Clark's nutcrackers were tested for their *same/different* abstract-concept learning with procedures very similar to those used to test pigeons including the same: stimuli, stimulus pairs, sequences of stimulus pairs used in training and transfer testing, display size, and 20 pecks to sample stimuli (Magnotti et al. 2015; Wright et al. 2016). Nutcrackers made their pecks from a perch in front of the stimulus display. Like pigeons and monkeys, a response to the comparison picture was correct when it matched the sample picture. A response to the white rectangle to the right of the comparison picture was correct when the comparison picture did not match the sample picture. Correct choice responses were reinforced with mealworms delivered below the monitor via a rotating wheel.

Like pigeons and monkeys, nutcrackers were trained on 100-trial sessions (50 *same*, 50 *different* trials) until they achieved 80% accuracy (or above) for three consecutive sessions with the same initial 8-item picture set (Magnotti et al. 2015). Following acquisition, abstract-

concept learning was assessed in six consecutive transfer sessions, each session contained 90 baseline (training) trials and 10 novel (5 *same*, 5 *different*) transfer trials. Correct responses on transfer trials were reinforced identically to baseline trials. The training set was then expanded to 16-items, and they were trained until accuracy was equal or greater than 85% correct. The cycle of set-size expansion, training for a minimum of three sessions, obtaining 85% correct or better, and novel-stimulus transfer testing was repeated six times for training sets of 32, 64, 128, 256, 512, and 1024 picture items (see Wright and Katz 2006 for training and testing stimuli).

Nutcrackers maintained a high level of baseline accuracy (85% correct) throughout expansions of the training set size (Fig. 5). Their mean transfer increased from 65% correct with the 8-item training set, to 74% correct with the 8-item training set, to 74% correct with the 32-item training set, 80% correct with the 64-item



**Same/Different Learning, Fig. 5** Mean percent correct performance of seven Clark's nutcrackers on training (baseline) trials (bold broken blue lines, filled symbols) and novel (transfer) trials (bold blue lines, unfilled symbols) with successively expanded training sets from 8 to 1024 picture stimuli in the *same/different* task and are compared to pigeons (thin green lines, Fig. 4), rhesus monkeys (thin red lines, Fig. 3), and capuchin monkeys (thin orange lines, Fig. 2). Dotted line at 50% correct is chance performance. Error bars are  $\pm$  one standard error of the mean

training set, and 86% correct with the 128-item training set. Moreover, this high accuracy level was maintained across larger training set sizes of 256, 512, and 1024 items. The same critical parameter of training set size that was responsible for full concept learning with the other species was also effective with nutcrackers, allowing direct comparisons to pigeons, rhesus monkeys, and capuchin monkeys. Nutcrackers showed superior initial transfer compared to the other species, despite requiring a similar number of trials as the other species to learn the initial task: 3300, 4000, 3500, 3000 trials, for nutcrackers, rhesus, capuchins, and pigeons, respectively. As the training set was expanded to 32 items and then to 64 item set sizes, the monkeys' transfer closed the gap with the nutcrackers, resulting in all three species achieving full concept learning (i.e., transfer statistically equivalent to baseline performance) at the 128-item set size. Pigeon transfer and concept learning was slower, but nevertheless pigeons achieved full concept learning at the next larger set-size of 256 items. Together, these functional relationships provide much more information about each of the species' concept learning than would be from any single point of comparison. Most remarkable is the qualitative similarity of abstract-concept learning across these different and diverse species, where all species eventually achieved full concept learning, despite the best partial 8-item concept learning by nutcrackers, increasing baseline performance by monkeys, and the larger set size required for pigeons to attain full concept learning.

What might have been responsible for separating the nutcrackers' better initial concept learning from the other species possibly could have been their amazing memory for locations of cached seeds. They bury as many as 30,000 pine seeds in as many as 3000 cache sites, often in new locations yearly, to be recovered when the alpine forest is covered in many feet of snow. Such highly developed location memory depends upon precise relational memory and executive decision making. Those are traits typically associated with episodic memory, folded neocortex, and human primates. So how could such a

differently evolved neural architecture of an avian possibly end up – by chance – producing abstract-concept learning that equals, and initially surpasses, that of nonhuman primates which are more closely related to humans?

### **Same/Different Abstract-Concept Learning by Black-Billed Magpies**

Black-billed magpies provide a test of the nutcrackers' abstract-concept learning skills being based on their amazing seed-cache memory and recovery. Magpies cache much less than nutcrackers, are much more omnivorous, and winter at lower altitudes. Several possible outcomes of such a test can be considered at the outset. If nutcrackers' extensive caching and retrieval was based on their proficient *same/different* abstract-concept learning, then the magpies' *same/different* abstract-concept learning might appear more like that of pigeons. Alternatively, if some other relational-processing skill (e.g., social) were very highly developed in magpies, then their *same/different* abstract-concept learning might even surpass that of nutcrackers. Finally, if *same/different* abstract-concept learning is “baked” into the evolved neural architecture of these two corvid species, then magpies and nutcrackers might be expected to show equivalence in their *same/different* abstract-concept learning.

Ten wild-caught black-billed magpies were tested with the same procedures used to test nutcrackers (Magnotti et al. 2016; Wright et al. 2017). As with the other species, they were trained on 100-trial sessions (50 *same*, 50 *different* trials) until they achieved performance criterion accuracy of 85% (or above) and a minimum of three training sessions. Following acquisition, abstract-concept learning was assessed in six consecutive transfer sessions, each session containing 90 baseline (training) trials and 10 novel (5 *same*, 5 *different*) transfer trials. The cycle of set-size expansion, training for three or more sessions, obtaining 85% correct or better, and novel-stimulus transfer testing was repeated six times for 32, 64, 128, 256, 512, and 1024 item training sets.

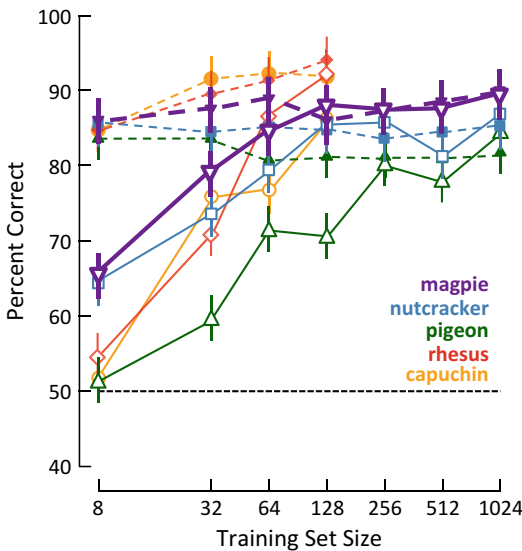
Abstract-concept learning, as measured by transfer to novel picture pairs, was 67% correct (chance 50% correct) following initial learning with the initial 8-item training set and increased regularly and monotonically with the training set-size expansions until transfer performance was indistinguishable from baseline (Fig. 6). Magpies and nutcrackers were identical in their substantial transfer following training with the initial 8-item set. Both of these corvid species clearly outperformed pigeons. Magpies, like the nutcrackers, outperformed the monkeys in their initial transfer (partial concept learning) following training with the initial 8-item set. Like monkeys and nutcrackers, magpies attained full *same/different* abstract-concept learning with the 128-item training set size. Comparing learning rates on the initial acquisition, magpies learned in 3500 trials, very similar to the other species (nutcrackers 3300, rhesus 4000, capuchins 3500, and pigeons

3000 trials). Magpie learning rates actually declined as the training set size was expanded from 16 to 1024 items (570, 480, 340, 320, 330, 340, 300 trials) similar to the other species, demonstrating the benefit of progressively better partial concept learning (see also Wright and Katz 2007).

## Concluding Remarks

The functional relationships in Figs. 2, 3, 4, 5, and 6 for these different species embody many of the most important mechanisms and processes of *same/different* abstract-concept learning. As these animals (subjects) experienced more and different items in greater numbers of combinations, they learned to focus on the abstract relationship (*same/different*) between items, ultimately doing so with novel items. By training and testing these different species with the same stimuli and procedures allowed direct species comparisons of how novel-stimulus transfer develops and systematically changes with training set size, including initial transfer with a small 8-item training set and the size of training set where transfer reaches its asymptotic level of full concept learning in the vicinity of 128 training items and more than 4000 exemplars of the *same/different* rule.

These comparisons establish that the magpies' initial transfer (partial concept learning) and full concept learning were not different from nutcrackers, and therefore do not point to the caching and recovery skills of nutcrackers being an advantage in *same/different* abstract-concept learning. The same can be said for the highly developed social skills of magpies. It appears that *same/different* abstract-concept learning is likely "baked" into the evolved neural architecture of nutcrackers and magpies. Mammals, particularly primates, evolved large brains (compared to body weight) with folded neocortex, including the prefrontal cortex, and elaborate temporal lobe structures (e.g., hippocampus plus adjoining parahippocampal cortex), key structures for primate relational processing, abstract-concept learning, and episodic memory (see also chapter



**Same/Different Learning, Fig. 6** Mean percent correct performance of ten black-billed magpies on training (baseline) trials (bold broken purple lines, filled symbols) and novel (transfer) trials (bold purple lines, unfilled symbols) with successively expanded training sets from 8 to 1024 picture stimuli in the *same/different* task and are compared to nutcrackers (thin blue lines, Fig. 5), pigeons (thin green lines, Fig. 4), rhesus monkeys (thin red lines, Fig. 3), and capuchin monkeys (thin orange lines, Fig. 2). Dotted line at 50% correct is chance performance. Error bars are  $\pm$  one standard error of the mean



► **Episodic Memory**). The “bird brain” by contrast has, until only recently, been thought to be primitive. Because most birds fly, light weight is required (hollow and trussed bones, lack of bladder, etc.). Nevertheless, many bird brains (particularly corvid brains) are substantial in size and weight compared to their body weight. Birds have a hippocampus and a caudolateral nidopallium that functions similar to the primate’s prefrontal cortex. Although birds have no folded neocortex, their nodal/nuclear structures have connectivity and speed advantages over folded six-layered neocortex of primates.

How did the so-called primitive “bird brains” become competitive with the more elaborately evolved primate brain to perform thoughts and processes considered of the highest cognitive order, *same/different* abstract-concept learning? (See also chapter ► **Intelligence**) The answer most certainly lies in evolution itself, a multi-million year process. (See also chapter ► **Evolution**) Environmental pressures undoubtedly selected for and shaped these different neural architectures to successfully accomplish many of the same essential and intelligent behaviors for survival, an example of *convergent evolution* where organisms not closely related (not monophyletic) independently evolved similar traits or functions as a result of having to adapt to similar environments or ecological niches (see also chapter ► **Convergent Evolution**). But this example of convergent evolution is comparatively unique because its identification required developing special tests of the cognitive ability (trait) to fully learn a *same/different* abstract concept for this cognitive function to be revealed, unlike other examples where there is a fossil record of an obvious physical trait like wings that provides an obvious function of flying by some insects, birds, and bats.

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## Sara Shettleworth

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Sara J. Shettleworth is Professor Emerita at the University of Toronto. Born in Maine, she completed her undergraduate degree in psychology at Swarthmore College (1965) – where she had her first experiences studying operant conditioning with John Nevin – and her MA at the University of Pennsylvania (1966). She then moved to Canada to complete her PhD at the University of Toronto (1970), where she worked with Jerry Hogan. She remained in Toronto as a professor in the departments of Psychology and Ecology and Evolutionary Biology from 1970 until her retirement in 2009.

In the 1970s, Shettleworth was one of the leading proponents of what became known as “constraints on learning.” In contrast to earlier approaches to associative learning, which assumed that any response an animal was capable of performing could be made to depend on any stimulus it could perceive, Shettleworth and others showed that innate predispositions often limited the associability of particular stimuli and responses. For example, in a series of studies on golden hamsters, Shettleworth showed that the hamsters could be taught to dig or rear up on their hind legs for a food reward, but could not learn to wash their faces for the same reward (even when “encouraged” by being sprayed with water; Shettleworth 1978a). Hamsters could, however, learn to suppress washing their faces in order to avoid a mild shock (Shettleworth 1978b). Findings such as these, which demonstrated that the nature of the stimuli used and the behaviors targeted mattered for learning, suggested to researchers that learning had to be contextualized within the ecology of their subjects. In an influential paper, Shettleworth (1972) argued that such species-specific variation in the “laws of learning” reflects the adaptive significance of various behaviors in the animal's natural environment. The ways in which animals learn, the relationships

they form between stimuli, reinforcers, and responses, depend on the functions of different types of learning in their natural lives.

Closely related to this work, Shettleworth began to push for a closer integration of experimental psychology with ecology, which has been a constant theme of her career. She emphasized the idea that studies of cognitive processes should be tied to the natural behaviors they serve – sometimes referred to as the synthetic approach (Kamil 1987; Shettleworth 1993) – and, conversely, that questions in the emerging field of behavioral ecology could benefit from an exploration of their underlying mechanisms (Shettleworth 2001). These concerns led her to interact and collaborate extensively with both ecologists and psychologists and to show, in numerous publications, how the two fields could gain from a better understanding of each other's methodologies and concerns.

A sabbatical year spent at Oxford University (in 1980) led to a long-lasting collaboration with John Krebs on optimal foraging and to a series of studies on memory and spatial cognition in food-storing birds. Shettleworth, Krebs, and others brought questions on foraging choices into the lab and began to delve into the neural mechanisms that drive them. For example, Shettleworth and others showed that hippocampus size differs between food-storing birds and closely related but nonstoring species (Hampton et al. 1995).

In 1998, Shettleworth published *Cognition Evolution, and Behavior* (an updated second edition was published in 2010). This uniquely comprehensive book has been widely praised for its integration of the ecological and psychological approaches and has become the standard citation for introducing the argument for their closer collaboration. Shettleworth promotes a broad approach to comparative cognition, encompassing everything from perception to communication, together with a suggestion that a detailed study of the elementary mechanisms of behavior can help explain even the most complex of cognitive feats.

Shettleworth has received numerous honors for her contributions to the field of comparative psychology, including a Guggenheim Fellowship (1980), the American Psychological Association

Distinguished Scientist Lecturer Award (1996), a visiting fellowship at the Berlin Institute for Advanced Study (2004), the Comparative Cognition Society Research Award (2008), the Canadian Society for Brain, Behavior and Cognitive Science's Donald O. Hebb Distinguished Contribution Award (2012), and her election to the Royal Society of Canada (2008).

Shettleworth has published over 100 peer-reviewed papers and dozens of popular reports on every aspect of animal cognition. Her experimental studies span the range from pigeons in operant boxes and rats running through mazes to chickadees foraging in artificial indoor forests. Together with her husband Nicholas Mrosovsky, she conducted field studies on sea turtle spatial behavior and migration. In addition to the contributions noted above on foraging, food-storing birds, and constraints on learning, her work has addressed – amongst others – questions of cognitive mapping and spatial learning more generally, episodic-like memory, and geometry learning.

Throughout her career, Shettleworth has thought and written extensively and searchingly on the enterprise of comparative cognition. She has enriched the debates on how different forms of spatial learning may combine to form a cognitive map, on what we can (and cannot) infer about brain processes from comparative studies of behavior, on the importance of studying a wide range of questions and species, and, over and over again, has emphasized the need for a closer connection between the ecological, evolutionary, and psychological approaches to animal behavior. The emergence, over the past 25 years or so, of fields such as neuroethology, cognitive ethology, and cognitive ecology is due in no small part to her influence.

## Cross-References

- ▶ [Cognitive map](#)
- ▶ [Comparative cognition](#)
- ▶ [Constraints on learning](#)
- ▶ [Ecology](#)
- ▶ [Geometric module](#)

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## Sarah "Sally" Boysen

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Sarah (Sally) Boysen's scientific contributions began early in her career when, after obtaining a masters degree in psychology from the University of Oklahoma, she worked as a researcher at the Yerkes Regional Primate Research Center in Georgia. There, along with Sue Savage-Rumbaugh and Duane Rumbaugh, she published a paper in the journal *Science* that suggested that two chimpanzees who were trained to associate symbols with objects in their environment could use these symbols to request items from each other (Savage-Rumbaugh et al. 1978). At the time, the ability of chimpanzees to learn a symbolic language system was a topic of great interest

to many psychologists in the growing field of cognitive psychology. The paper, detailing a novel approach to this topic, provided an opportunity for critical thinking about the cognitive requirements and possible human-uniqueness of language (e.g., Epstein et al. 1980; Savage-Rumbaugh et al. 1980; Terrace 1985).

Sally returned to Ohio, her state of birth (b. 1949), after leaving Yerkes. She received a PhD in Psychology in 1984 at The Ohio State University under the supervision of David Hothersall. Subsequently, as a faculty member of the Department of Psychology at OSU, she directed the Chimpanzee Center until it closed in 2006.

It was at the Chimpanzee Center that Sally and her colleagues conducted groundbreaking research examining numerical abilities in chimpanzees. Sally taught chimpanzees to recognize Arabic numerals by initially training one-to-one correspondence between food pieces and non-edible small objects (e.g., two food pieces on a plate would be matched to a plate that contained two small cotton balls). Over time, the objects were replaced with Arabic numerals, and ultimately the chimpanzees could touch a corresponding numeral for arrays of 0–8 objects (Boysen 1993). This research program also provided one of the first examinations of arithmetic in a nonhuman animal. When one of the chimpanzees, Sheba, was allowed to search a room for hidden food items or numerals in various locations, she was able to return to the starting location and report, by touching a numeral, the summed amount (Boysen and Berntson 1989).

One particularly seminal finding from this work has been the role of numeral use in a reversed contingency task. Boysen and Berntson (1995; Boysen et al. 1996) created a task in which the chimpanzees had to choose the smaller of two piles of candies to receive the larger amount. However, the chimpanzees could not inhibit choosing the larger amount of candy, even though that choice consistently led to a smaller reward. In contrast, when Arabic numerals were used in place of the candy arrays, chimpanzees readily chose the smaller number and subsequently gained the larger amount. The numerals seemed



to represent magnitude symbolically and aided the inhibition of prepotent responses to actual food quantities. This work has proven informative to the study of executive functioning in young children (Carlson et al. 2005) and other ape species (Vlamings et al. 2006).

Other work at the Chimpanzee Center focused on the ability of chimpanzees to recognize the correspondence between a three-dimensional symbol of space (e.g., a scale model) and its real-world referent. Across a series of three studies modeled after seminal work by DeLoache with human children (e.g., DeLoache 1987), Boysen demonstrated that chimpanzees could correctly navigate an enclosure to find a hidden treat after observing a miniature treat being hidden in the analogous location in a scale model. Further, the chimpanzees appeared to recognize the correspondences between individual landmarks in the model and enclosure as well as the spatial relationships of the landmarks (Kuhlmeier and Boysen 2001, 2002; Kuhlmeier et al. 1999). Similar to Sally's research with symbols for quantity, this work has been informative to the study of human cognitive development (e.g., Kuhlmeier 2005; Marsh et al. 2013).

Sally Boysen's role as a leader in field of Comparative Cognition is also apparent in less quantifiable outcomes than number of publications and citations. She was one of the founding members of the Comparative Cognition Society, an international group of psychologists and biologists studying animal behavior and cognition. She has authored a book on animal cognition, written not for other researchers but designed through clear text and graphics to translate science to a broad readership (Boysen and Custance 2009). Earlier in her career, she developed a children's book to introduce chimpanzee behavior to young readers (Boysen 1991).

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## Sarah Brosnan

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### Early Life and Education

Sarah Frances Brosnan was born in La Grange, Illinois, although she grew up in Alexandria, Virginia, and later Baltimore County, Maryland. Throughout her childhood, she was enthralled with exploring the nearby creek and forest. Brosnan always enjoyed sharing her discoveries with others, often bringing critters home for show and tell (much to her parent's chagrin!). Although she had always been fascinated with biology, David Phoebus, her high school biology teacher, was particularly influential in deepening her interests. He structured his classes around experiential learning, focusing on labs and conducting many classes outside the classroom. He encouraged students to write papers on topics that they found interesting. When Brosnan wrote a paper on Dian Fossey, he handed her a few extra books, granted her an extension, and told her to dig deeper – so she did.

Brosnan had the opportunity to further explore various branches of biology when she attended Baylor University in Waco, Texas, where she graduated magna cum laude. She spent 2 years in a limnology lab, studying inland waters, and 3 years in a mammalogy and ecology lab. In the latter, she participated in a number of mark and recapture studies, tracking small mammals across a gradient of old wood forest to an annually mowed field. This experience also led her to working with captive prairie voles, which was

the focus of her undergraduate research. Brosnan received two research grants for her honors thesis in which she compared the reproductive behavior of unrelated females and sisters when they had access to a single male. Her work with prairie voles is what piqued Brosnan's interest in cooperation, as this species is a monogamous, cooperatively breeding species.

These formative experiences inspired Brosnan to apply to graduate programs that studied cooperation. She was much more interested in the mechanisms underlying cooperation than the species per se, but ultimately, she realized that primates were the best model for understanding how individuals decide when to cooperate and with whom. Therefore, when Frans de Waal offered her a position at Emory, she accepted. Brosnan's dissertation research, published in *Nature* (Brosnan and de Waal 2003), was the first to document negative responses to inequity in capuchin monkeys, a behavior hypothesized to support long-term cooperation.

The video demonstrating her experiment quickly became a YouTube sensation and was recently featured on Last Week Tonight with John Oliver (Avery and Perota 2014). The video depicts two capuchin monkeys separated by a clear partition, sitting side by side in front of a human experimenter (Fig. 1). The first monkey exchanges a token (in this case, a rock) with the experimenter. The experimenter rewards the monkey with a cucumber, a food they happily eat in any other context. The experimenter then offers the token to the second monkey, who exchanges the token and receives a grape (a grape!), a highly preferred food among many primates. The first monkey observes this, exchanges the token, and once again receives a cucumber, but this time, she throws it right back at the experimenter! These responses, rejecting the token and refusing to exchange the token or eat the reward (which takes a good amount of self-control), are considered refusals. Capuchin monkeys refuse the token or the reward more often when their partner receives a better reward than themselves but will continue to accept cucumber as "payment" when they both receive a cucumber for their efforts in the control condition.



**Sarah Brosnan, Fig. 1** A monkey in the test chamber returns a token to the experimenter with her right hand while steadying the human hand with her left hand. Her partner looks on (Drawing by Gwen Bragg and Frans de Waal after a video still)

Responding negatively to getting less than a partner has received for the same amount of work has been hypothesized to support long-term cooperation as a means to compare your own efforts and outcomes with that of a partner. Therefore, when you are not getting your fair share, it may be in your best interest to find a new, more equitable partner or work alone. This inspired further research and continues to be the main foci of Brosnan's research.

## Research Interests

Currently, Dr. Brosnan is a professor in the Departments of Psychology and Philosophy and the Neuroscience Institute at Georgia State University. She conducts her research at the Georgia State Language Research Center and the Keeling Center for Comparative Research, where she holds an

adjunct faculty position. By taking a comparative approach to her research, Brosnan is better able to deduce the evolutionary function of particular trait. She examines behavior across the phylogenetic distribution of species, which have evolved in various ecological contexts, to help elucidate whether the behavioral trait in question evolved due to common descent or due to shared selective pressures. In the case of inequity, for instance, several primate species have since been shown to respond negatively to inequity. However, the trait is not universal within primates. This appears to be true even within smaller clades. Within the great apes, for example, chimpanzees (Brosnan et al. 2005, 2010; but see Bräuer et al. 2009) and possibly bonobos (Bräuer et al. 2009) react negatively to inequity, but orangutans do not (Bräuer et al. 2009; Brosnan et al. 2011). Moreover, while Brosnan demonstrated that capuchin monkeys respond to inequity, closely related squirrel monkeys do not (Talbot et al. 2011). Therefore, negative responses to inequity appear to be a convergent trait that evolved due to shared selective pressures. Thus far, about a dozen species have been tested on the inequity paradigm, within and outside the primate order (reviewed in Talbot et al. 2016b). Although several alternative hypotheses have been posited, all of the species that respond to inequity routinely cooperate with non-kin in a variety of contexts such as in group hunts, food sharing, and coalitions and alliances. Thus, the current data suggest that responding negatively to inequity is a convergent trait that evolved in tandem with cooperation.

The comparative approach also lends insight into some of our own, more complex, behaviors not only through understanding their evolution but also the contexts in which they may occur and whether the trait is still beneficial today. The foci of Brosnan's research lie within some of these more complex behaviors generally considered to be quintessentially "human," including fairness and morality. Although she does not expect to observe equivalently complex behaviors in the nonhuman primates she studies, she does expect to observe precursor behaviors, those from which more complex behaviors may have evolved.

Responding negatively to getting less reward than a partner may be a precursor to humans'

sense of fairness. Of course, “fairness” also implies knowing when *others* are treated unfairly as well. Therefore, another line of inquiry for Brosnan is prosocial behavior. That is, behavior that helps another, including situations in which the actor directly benefits themselves (e.g., reciprocity/cooperation) and situations in which the actor does not (e.g., altruism; Brosnan and Bshary 2010). Many primates are seemingly indifferent to helping others even with little to no cost themselves (e.g., Vonk et al. 2008), although there is some evidence that chimpanzees were likely to refuse when they are rewarded more than a partner (Brosnan et al. 2010). This suggests foresight of their partner’s behavior and requires individuals to give up an immediate benefit (e.g., food), in order to stabilize a long-term cooperative relationship. At the very least, it shows that they notice when their partner is rewarded less than themselves.

Fundamentally, morality is a suite of behaviors that help maintain social norms necessary for regulating social life (Brosnan 2017). Precursors to a moral code may include respect for possessions, which several species of primates demonstrate for items such as food, toys, and mates (reviewed in Brosnan 2011). Similar to humans, Brosnan has evidenced the endowment effect in several great apes, in which individuals (somewhat irrationally) prefer to maintain property they currently possess to trading it for something they typically value more in a free-choice context. In contrast to humans, who tend to exhibit this effect in a wide variety of contexts, however, studies in nonhuman primates indicate the effect is limited to food items and tools that can access immediate food rewards, meaning that it is only triggered in evolutionarily relevant contexts (Brosnan et al. 2007, 2012; Drayton et al. 2013; Flemming et al. 2012). Cognitive and behavioral biases, such as the endowment effect, are important to study as they affect decision-making and, at times, contrast the traditional economic view that humans make rational decisions.

Much of Brosnan’s research is rooted in experimental economics, which utilizes game theory to model complex decision-making behavior. Experimental economic games break down strategic

interactions based on other individuals (e.g., cooperation) into simple choices (e.g., accept or reject). This is particularly useful for comparative researchers as it helps standardize methodology across multiple species, including humans. For instance, human reactions to reward distribution in a cooperative interaction are often examined through the ultimatum game in which two players, a proposer and a respondent, must agree on a reward distribution in order to receive a payout. In humans, proposers usually offer a generous portion of the reward to the respondent so that they accept the offer, rewarding both participants. To examine sensitivity to reward distribution across phylogeny, children and chimpanzees were tested in a modified version of the ultimatum game in which proposers could choose between two tokens representing either an equitable or inequitable offer favoring the proposer. Respondents could either accept the offer by exchanging the token for rewards or reject the token/offer. Despite initial preferences for the selfish token, both apes and children made more equitable offers when cooperation of the respondent was required, suggesting continuity between humans and apes in their sensitivity to reward distribution (Proctor et al. 2013).

Brosnan’s Laboratory for Comparative Economics and Behavioral Studies (CEBUS lab) has examined coordination and decision-making through several other experimental economic games across the primate order, such as the assurance game (e.g., Brosnan et al. 2011) and the Iowa gambling task (e.g., Proctor et al. 2014). The CEBUS lab is currently expanding this line of research to include other facets of decision-making including social and ecological influences on decision-making behavior and cognition, more generally. For instance, individual recognition likely impacts decision-making as many species alter their behavior depending on with whom they are interacting. Although several primate species discriminate unfamiliar conspecific faces, little is known about the underlying mechanisms and the role of familiarity (Talbot 2016). Capuchin monkeys tested on a computerized testing paradigm were better able to recognize familiar faces compared to unfamiliar faces, suggesting that

familiarity (or experience with individuals) impacts capuchins' face perception, as it does humans and apes. Still, capuchins performed equally well on familiar in-group and familiar out-group members. Ecologically, this makes sense as capuchins regularly come into visual and physical contact with neighboring groups, which are in competition for food and mates. Quick and accurate recognition of individuals living in neighboring groups may help predict their behavior, potentially avoiding dangerous interactions (Talbot et al. 2016a).

In fact, ecology can dramatically shape cognition. In collaboration with Redouan Bshary at the University of Neuchâtel, Brosnan and colleagues have recently demonstrated that small-brained species, cooperative cleaner fish, can outperform large-brained species (i.e., primates) on a decision-making task. The task was derived from cleaner fish ecology. In the wild, cleaner fish work together to obtain food by removing ectoparasites and dead skin from larger fish that visit their "cleaning station," or territory. Cleaner fish preferentially service visiting clients, those with larger home ranges and access to multiple cleaning stations, over resident clients, those that have smaller home ranges and access to one station. Therefore, the task presented subjects with two choices, one representing an ephemeral food source (i.e., the visiting client) and one representing a permanent food source (i.e., the resident client). As in their natural environment, cleaner fish quickly adapted a maximizing strategy, first choosing the ephemeral food and then the permanent food, permitting access to both rewards. Chimpanzees, orangutans, and capuchin monkeys, however, took much longer to acquire the task, but once they did, they performed equally well in a reversal learning test in which in the opposite choice yielded the largest payoff (Salwiczek et al. 2012). Moreover, adjusting the parameters of the task to be more ecologically relevant to primates improved their performance, matching the performance of the fish in the original study, demonstrating the importance of an ecologically relevant approach to the study of cognition (Prétôt et al. 2016a, b).

Through national and international collaborations and within her own CEBUS lab, Dr. Brosnan

fosters a highly collaborative work environment. Throughout her career, she has demonstrated an incredible ability to approach scientific questions from a number of perspectives (e.g., psychology, philosophy, anthropology, neuroscience, and biology to name a few!), which has ultimately led to her successful and encompassing research program. Dr. Brosnan's contributions to the field of behavior, experimental economics, and animal cognition have thus far evidenced similarities and differences among primates that provide insight into the evolution of decision-making, which may ultimately help us develop interventions and promote better decision-making in ourselves.

## Cross-References

- ▶ Altruism
- ▶ Cognition
- ▶ Cognitive Bias
- ▶ Computerized Testing Paradigm in Primates
- ▶ Conspecifics
- ▶ Convergent Evolution
- ▶ Cooperation
- ▶ Cooperative Breeding
- ▶ Cooperative Hunting
- ▶ Coordination Games
- ▶ Decision-making
- ▶ Dian Fossey
- ▶ Frans de Waal
- ▶ Game Theory
- ▶ Georgia State University's Language Research Center
- ▶ Helping Behavior
- ▶ Reciprocity
- ▶ Ultimatum Game

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## Sarah, Lana, Sherman, and Austin

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Some of the most important contributors in the history of comparative psychology were not themselves comparative psychologists. In fact,



some were not even humans! Four of the most significant contributors to comparative psychology were chimpanzees (*Pan troglodytes*): Sarah, Lana, Sherman, and Austin. These animals served as participants in many behavioral studies, and their data made seminal contributions to a wide range of topics but particularly to the understanding of symbol use and comprehension, both in the communicative domain and also with respect to numerical cognition. The great impact of the four apes on these cognitive competencies, and the relation of symbol-knowledge and numerical judgments to other aspects of cognition, merits special attention.

## Sarah

Fundamental questions about great ape minds were addressed by David Premack and other researchers over the course of their work with a chimpanzee named Sarah. Sarah was wild-born in Africa around 1962 and was brought to the United States when she was less than 1 year old to participate in laboratory-based cognitive testing. She wore diapers, was fed with a bottle, and received an elementary education into the world of psychology in the mid-1960s by testing 5 days a week on matching-to-sample tasks and other paradigms (Premack and Premack 1994; Premack and Woodruff 1978).

At about 4 years of age, Sarah was trained on a series of tasks engineered to teach her a visual language (Premack and Premack 1972). She learned to associate plastic chips of various size, shapes, and colors with nouns, verbs, adjectives, and concepts like “same” and “different.” The training procedure was designed to build on knowledge that the ape might have naturally, for example, about the differences between various foods and about the activity of giving and receiving. Initially, Sarah was simply given pieces of food by an experimenter. Next, a plastic piece (e.g., a pink plastic square, with a thin piece of metal mounted to the back, representing banana) was placed near Sarah with the fruit reward out of her reach. When Sarah moved the plastic piece to a nearby magnetic board – in effect,

communicating “give” the food – Sarah was rewarded with the corresponding fruit. After Sarah had learned this sequence, a different type of fruit morsel and a different plastic piece (e.g., blue triangle, meaning “apple”) were introduced. After this association was formed, another fruit/plastic-piece pair was introduced, and so forth, as new symbol-referent associations were established. This training formed the backbone of Sarah’s vocabulary. Subsequently, additional layers of complexity were added. Presenting the correct plastic piece was made insufficient for reward unless an additional plastic piece (glossed as “give”) was presented as well. When other names were introduced, rewards could only be received by adding more pieces to the magnetic board (e.g., “[Experimenter] Give Apple Sarah”). Conversely, Sarah was also asked to “read sentences” on the magnetic board and respond appropriately. Premack and Premack (1972) described the example “Sarah Insert Apple Pail Banana Dish” to which Sarah responded by placing the apple in the pail and the banana on the dish. Complex sequences such as these required Sarah to know the objects or actions associated with each plastic chip and also to be sensitive to the relation between symbols. With the introduction of relational-concept symbols – plastic pieces that meant “name of,” “not name of,” “same,” or “different,” for example – training and testing of meanings could be done outside the context of social exchange.

These experiments demonstrated flexible learning by Sarah of about 130 “words” as well as impressive performance on tests of relational concepts. Premack and Premack (1972) compared Sarah’s “language ability” to that of a 2-year-old child. However, the extent to which Sarah’s performance should be understood as language learning is in question. Savage-Rumbaugh et al. (1980a) described Sarah’s performance in strictly associative terms and identified a number of components of experimental design that challenged what Sarah was really learning. For example, when Sarah needed to name multiple nouns to receive reward (“[Experimenter] Give Apple Sarah”), many components of the required sequence (“[Experimenter],” “Give,” “Sarah”) were

remained constant within each session. This and other design issues make Sarah's actual "vocabulary" difficult to quantify and interpretations of her actions as revealing language learning as tenuous.

Premack and Woodruff (1978) attempted to test Sarah's awareness of other minds. Sarah viewed video clips of an actor struggling with a relatable (to a chimpanzee) problem. For example, the actor might be unable to reach a banana when the space between actor and banana was obstructed or if the banana was suspended over the actor's head. Sarah's task was to choose between a photograph that showed the correct solution to the actor's problem (e.g., climbing on top of boxes to reach the overhead banana) and one that would not solve the actor's problem. Sarah was highly accurate on this task and on a second task with problems not applicable to a chimpanzee's ecology (e.g., plugging in a phonograph or connecting faucet and hose). This and other early studies of how one primate perceives the behavioral and cognitive capabilities of another (Menzel 1974; Menzel and Johnson 1976) helped to initiate an entire field of psychological and philosophical scholarship on the study of nonhuman animal "theory of mind" – as well as an enduring fascination with what the minimum cognitive mechanisms are that could account for Sarah's performance (see Call and Tomasello 2008; de Waal 2011).

Sarah continued to participate in laboratory-based cognitive studies including those on numerical ability (Woodruff and Premack 1981), spontaneous categorization (Matsuzawa 1994), responding to other individuals' knowledge states (Povinelli et al. 1990), the reverse-reward contingency paradigm (Boysen and Berntson 1995), conceptual matching to sample (Thompson et al. 1997), and many more. Some of these findings serve to illustrate a critical but underappreciated value of research with chimpanzees like Sarah, Lana, Sherman, and Austin: Their "failures" (e.g., Limongelli et al. 1995) are as important and informative as their successes, in that they help to reveal cognitive limitations of nonhuman animals – even the most highly educated apes on the planet. Sarah's contributions to the emerging field of comparative cognition in the 1960s–1980s

were extensive, long-lasting, and critical to the now well-established understanding of the sophistication of the chimpanzee mind.

## Lana

Lana was born on October 7, 1970, at the Yerkes Regional Primate Research Center, Emory University, Atlanta, GA. She was assigned (along with a young orangutan named Biji) to a new behavioral research program under the direction of Duane Rumbaugh to determine whether apes could learn and use a human-like language. Rumbaugh named the initiative the Language ANalog (LANA) Project after its focal 2-year-old participant.

A computer-based keyboard was designed that held visuographic symbols called "lexigrams" – each representing a word. Pressing a key caused the corresponding symbol to appear on a series of projectors and to be recorded on the data transcript, and a grammar for combining these symbols into stock "sentences" was established. Grammatical sentences led to computer responses (e.g., delivery of juice to the utterance "PLEASE MACHINE GIVE JUICE PERIOD," where "PLEASE" and "PERIOD" were stock lexigrams used to start and end such utterances). This so-called "Yerkish" language was also used by Lana to interact with human researchers (particularly Dr. Timothy Gill, then a graduate student and Lana's primary teacher) when they communicated with her.

Lana was initially shaped to touch the keys and to string them together into two- and three-symbol responses, after which she began to learn the referents of symbols that represented objects (e.g., juice, apple, movie), actions (e.g., give, tickle, put), and actors (e.g., machine, Tim, Shelly). She used the keyboard to make requests, to ask questions, to name objects, and to comment on her surroundings. After the first year, Lana's keyboard had expanded to 75 symbols, of which about 50 were typically backlit and active at any point (Rumbaugh et al. 1974). The positions of the lexigrams were changed frequently to ensure that Lana was attending to the symbols rather than the

locations. Lana was reported to make few errors in lexigram use, and she even came to innovate a way of aborting sentences in which the wrong key had been pressed, by immediately using the PERIOD lexigram to terminate the utterance. She was greater than 90% accurate, both in completing sentences that were started validly and also in aborting sentences with errors at the beginning (Rumbaugh 1977).

Lana's remarkable performance garnered considerable attention, both complimentary and critical, in the scholarly literature and the popular media. Lana learned the meanings of at least 140 symbols. Although many of her stock-sentence utterances were formulaic requests (as indeed is true in human language) criticized as chains of conditioned responses, she also innovated novel lexigram combinations to describe new objects and used legal variations in sentence structure to make the same requests. Sentence length increased as the number of available symbols increased. Project scientists concluded that the frequency of utterances that were purely imitations was low (Hillix and Rumbaugh 2004) and that Lana was generally using the lexigrams meaningfully. Beran et al. (2000) tested Lana's long-term memory for lexigrams and found that Lana showed excellent retention of symbol meanings for lexigrams she has not seen for two decades! Despite the debate that surrounded the question of whether Lana "had language," with the publication of *Language Learning by a Chimpanzee: The LANA Project* (Rumbaugh 1977), her pioneering contributions to the understanding of symbol acquisition through keyboard use received full discussion, as did the potential led to widespread application of the computer-based communication system for nonspeaking human children with profound language impairments (see also Ronski et al. 1985).

In 1981, Lana moved to Georgia State University's Language Research Center (LRC), where she continued to be the focus of noninvasive cognitive and behavioral research. Lana's contributions were not limited to the language domain. She was also taught to enumerate and to indicate quantities using Arabic numerals. Using the computerized test system (also called the

"Rumbaughx" to parallel other classic apparatus like the Skinner box, Thorndike problem box, and so forth; see Washburn et al. 2013), Lana manipulated a joystick so as to move a cursor on a computer screen, "counting out" stimuli corresponding to the number of items represented by a target numeral (Beran and Rumbaugh 2001; Rumbaugh et al. 1989). She remained active and productive in research until her death at the age of 46 years, participating voluntarily in many other computerized and manual research studies, including investigations of learning, perception, attention, memory, cognitive control, metacognition, language, numerical cognition, and other topics. By current estimates, Lana produced data for more than 200 journal articles and chapters and has been studied by more than 100 scientists from various fields. Because her performance with lexigrams was critical in the formation of the LRC and the resources it has provided to scholars interested in primate cognition, Lana has also contributed indirectly to countless research areas with monkeys, human adults, and children (both typically developing and developmentally delayed).

## Sherman and Austin

Inspired by the success with Lana, but seeking to address some limitations of the LANA Project, Sue Savage-Rumbaugh and her research team (including Duane Rumbaugh, Sally Boysen, and others) initiated a new ape-language project in 1976. Project scientists were increasingly convinced of the importance of the social functions of language. Lana had been trained to communicate with a computer and with human researcher. To encourage social communication between conspecifics, the new project obtained four chimpanzees (Austin, Erika, Kenton, and Sherman) from the Yerkes Center. Ultimately, the demands of raising four apes in language training proved too demanding for the research team, and so the effort was focused on just two of the chimpanzees. Sherman (1973–present) was 2.5 years old when symbol training began; Austin (1974–1996) was 14 months younger.

The computer-based keyboard and lexigrams developed for the LANA Project were introduced to Sherman and Austin (S&A), including many new lexigrams to represent the many indoor and outdoor areas available to these apes at the LRC. Whereas Lana had been trained to produce strings of lexigrams, defined by the rules of Yerkish, to obtain desired outcomes, the foci of the Animal Model Project with S&A were interindividual communication and comprehension or understanding of the symbols (Savage-Rumbaugh et al. 1980a). Tests were developed in which S&A might solve problems using the lexigram keyboard that could not be solved without symbol-based communication (Savage-Rumbaugh et al. 1978). For example, Austin might see food locked in a box but have no key; Sherman might have access to the key, among many other objects, but not the box. Using the lexigram keyboard (but not without it), Austin could request the key from Sherman, who in turn would receive a portion of the reward from Austin for his assistance.

The focus on what the chimpanzees understood about the symbols is illustrated by an important categorization study (Savage-Rumbaugh et al. 1980b). S&A were trained to sort six specific items into two bins: foods versus tools. The animals were then tested for generalization to new items and passed this transfer test successfully. The apes were then shown photograph of exemplars, which they were able to sort into the food or tool categories (even though the photographs themselves were all inedible). The apes were then tested with lexigrams and were able to pass novel transfer tests by sorting symbols that represented foods into one bin and lexigrams representing nonfoods into the tool bin. Combined, S&A responded correctly on 32 of 33 trial-1 generalization tests, showing that they understood the lexigrams to represent specific referents that were not present at that time and place.

Like Lana, S&A moved to the LRC in 1981 and continued to participate in studies of language and new research on numerical cognition. For example, they were the focal animals in a series of studies on summation (e.g., Rumbaugh et al. 1987). Using a modified Wisconsin General Test Apparatus, the

apes were presented with pairs of wells, with each well containing some number of chocolates. The apes could select either pair of wells, but to optimize their choices, they needed to determine which pair had the greater total number of candies. S&A selected the greater sum on more than 90% of the trials, and their accuracy could not be explained by lower-level strategies like “choose the pair with the largest single number” or “avoid the pair with the smallest single number.”

S&A demonstrated many other competencies in the domain of numerical cognition, learning, memory, and problem-solving. Sherman remains highly motivated to participate in behavioral research and has been a star performer in tests of memory, delay of gratification, metacognition, and visual perception (e.g., Beran et al. 2015 for a review). His ongoing contributions to science illustrate the irreplaceable value of longitudinal cognitive research with nonhuman animals, in which new abilities may emerge on the scaffolding of previous training and competencies. Sherman’s lifetime of research participation provides unique opportunities to understand what language training allows an organism to do cognitively that it could not do otherwise and what behavioral competencies do not benefit from experience with symbols. The contributions of all of these chimpanzees serve to remind us that although their rearing histories are unique, and the efforts to work with them for so many decades were massive, the results were transformative for understanding more about chimpanzee minds and more about our own.

## Cross-References

- ▶ [Categorization](#)
- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)
- ▶ [Counting](#)
- ▶ [David Premack](#)
- ▶ [David Washburn](#)
- ▶ [Duane Rumbaugh](#)
- ▶ [Episodic Memory](#)
- ▶ [Georgia State University’s Language Research Center](#)

- ▶ [Kanzi](#)
- ▶ [Language Research: Great Apes](#)
- ▶ [Lexigrams](#)
- ▶ [Matching-to-Sample](#)
- ▶ [Meta-cognition](#)
- ▶ [Michael J. Beran](#)
- ▶ [Panbanisha and Panzee](#)
- ▶ [Primate Cognition](#)
- ▶ [Primate Communication](#)
- ▶ [Prospective Memory](#)
- ▶ [Sarah “Sally” Boysen](#)
- ▶ [Sue Savage-Rumbaugh](#)
- ▶ [Theory of Mind](#)
- ▶ [Wisconsin General Test Apparatus](#)
- ▶ [Yerkes Primate Research Center](#)

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## Satiation

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## Definition

Maintenance of energy balance is a critical feature for species survival and elegant physiological mechanisms have evolved throughout the years in order to maintain homeostasis (Woods and D'Alessio 2008). One of these mechanisms is satiation, defined as the process that leads to the termination of eating, thus plays an important role in the system of appetite control. As a physiological component of humans, satiation acts as an energy regulator, manifested as a sensation during food consumption, the main roles of which are to signal when enough energy has been consumed and consequently, leads to the cessation of eating.

Normally, satiation is accompanied by satiety, which is the persistent sensation of fullness post ingestion. Satiety has the important role of signaling that no further energy intake is necessary until feeling hunger again (Benelam 2009; Blundell 1999). Satiation primarily depends on the volume of food ingested and is not always dependent on caloric value. Foods that are rich in fibers and fat and/or fibers and protein are greater in volume and deliver the “fullness” sensation faster than foods rich in fat, other carbohydrates, and protein only.

## Physiological Mechanisms of Satiation

Maintenance of energy balance and a healthy body weight has been critical to human survival, and sophisticated physiological mechanisms exist in the body to maintain homeostasis (the maintenance of a constant internal environment in the body) (Woods and D'Alessio 2008). The control of energy intake is vital to energy balance, and satiation and satiety are part of a complex system of appetite control, which regulates how much we consume. The process leads to the termination of eating, which may be accompanied by a feeling of satisfaction, satiety – the feeling of fullness that persists after eating, potentially suppressing further energy intake until hunger returns.

## Gastric and Intestinal Mechanisms

Satiation is influenced by a great number of body mechanisms, including gastric distension and hormone action. Once food or drink is ingested, a cascade of physiological events is triggered as a response and a series of inhibitory signals are released to stop food consumption and prevent further ingestion until another meal is needed. These signals are part of the satiety cascade and act together with satiation processes to regulate energy balance.

When food reaches the gastrointestinal tract, stomach distension is signaled to the brain through the afferent fibers of the vagus nerve which project to the nucleus of the solitary tract (NTS). From the NTS, these short-term signals are integrated in the hypothalamic area, along with other information related to ingestion sent from different regions of the body, such as from the adipose tissue. As digestion continues, the food is released to the small intestine for nutrient absorption. The intestine also communicates with the brain regarding the amount of nutrients consumed which contributes, in part, to satiation and satiety (Blundell et al. 1987). During this process, hormones such as cholecystokinin (CCK), glucagon-like peptide-1 (GLP-1), peptide YY, and pancreatic polypeptide (PP) are released. CCK is the main hormone responsible for meal termination and satiation, whereas the others previously listed play a role in satiety, by

sensing fullness and communicating to the brain that no further ingestion is necessary (Wynne et al. 2005).

In a postingestion state, the adipose tissue and pancreas release leptin and insulin, respectively, and they both act in the long-term modulation of satiety and satiation based on the amount of fat obtained from the food and the amount that is stored in the body. All signals are integrated in the brain to affect energy intake and expenditure, and a reciprocity between the adipose tissue, the gut, and the brain is necessary for appetite regulation.

## Brain Mechanisms

The brain is responsible for integrating the information received from the gut regarding satiation and satiety, and the arcuate nucleus of the hypothalamus is the region that was identified to play a role in homeostatic balance over six decades ago. Such integration is carried out by anorexigenic (appetite suppressing) and orexigenic (appetite stimulating) neuronal populations within the hypothalamic area, which translate signals of satiation and satiety to modulate energy intake thereby maintaining energy balance (Morgane and Jacobs 1969). Regarding the orexigenic pathways in the hypothalamus, these are comprised by agouti-related peptide (AgRP) and Neuropeptide Y (NPY) expressing neurons, which are known to increase appetite and consumption, whereas the anorexigenic pathway is comprised of pro-opiomelanocortin (POMC) neurons, the main neuronal population involved with appetite suppression in the arcuate nucleus of the hypothalamus (Balthasar et al. 2004; Sohn 2015). This brain region also contains the neurotransmitters glutamate and GABA, which have been shown to modulate feeding behavior and can influence, in part, the functioning of other neuronal populations in the hypothalamus. The function of the specific neuronal populations in the arcuate is tightly regulated and is essential for energy balance; any disturbances can lead to obesity or starvation. Furthermore, the brain also receives information from the substances being digested, which can directly affect neurotransmitter synthesis and, therefore, strongly influence circuits that play a role in homeostasis.

## The Impact of External Factors on Satiation

Satiation can be primarily influenced by many sensory and cognitive factors, such as the expectation prior consumption, cues and contexts associated with food, the smell, taste and texture of the food, and once the food is ingested, a series of postingestive mechanisms. Although everyone has internal mechanisms to control appetite, in some cases people ingest food when they are sated and not in a negative energy balance, and that can be attributed in part to external factors. Both satiation and satiety can be strongly influenced by environmental factors, such as the variety of food available and portion size, physical activity, sleep, stress, eating in the presence of a television, social situations, eating along with alcohol consumption, and palatability. The effect of palatability has been widely studied in eating disorders and obesity. The intake of highly palatable foods is typically pleasurable and activates reward pathways in the brain. The activation of these hedonic systems can override the effect of satiation and long-lasting signaling of satiety, which is a key driver of eating beyond energy requirements, i.e., overeating (Bellisle 2003; Read 1992).

The consumption of food and drink to provide energy is a voluntary behavior, and, despite the existence of sophisticated physiological mechanisms to match intake to requirements, humans often eat when sated and sometimes refrain from eating when hungry. Thus, there are numerous influences on eating behavior beyond satiation and satiety. These include: the portion size, appeal, palatability, and variety of foods and drinks available; the physiological impact on the body of physical activity and sleep; and other external influences such as television viewing and the effect of social situations.

## Cross-References

- ▶ [Appetitive Response](#)
- ▶ [Endocrine System](#)
- ▶ [Homeostasis](#)
- ▶ [Hormones and Behavior](#)
- ▶ [Hypothalamus](#)

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## Savannah

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## Definition

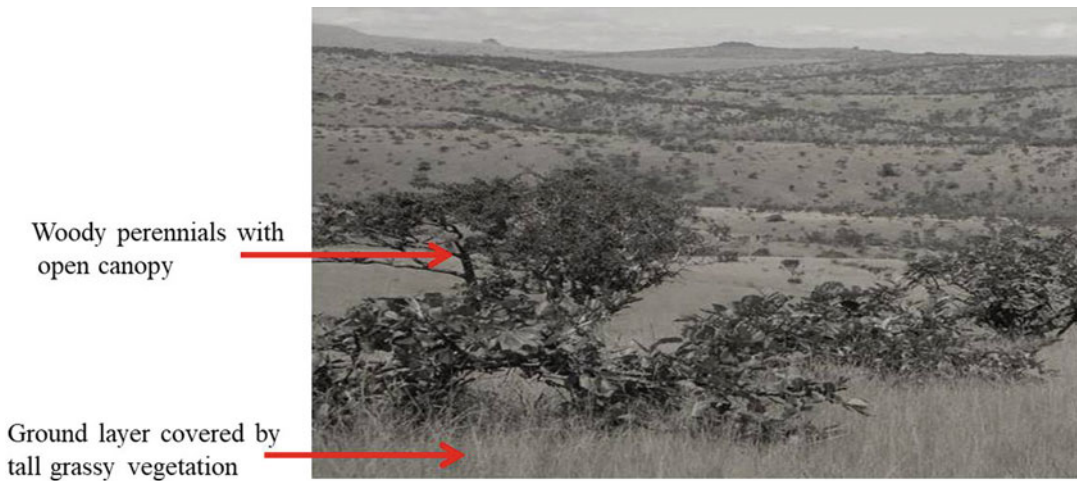
Savanna is defined as a tropical or subtropical vegetation type that has a continuous grass cover occasionally interrupted by trees and shrubs.

## Introduction

Savanna represents a vegetation type that grows under hot, seasonally dry climatic conditions

and is characterized by an open tree canopy (i.e., scattered trees) above a continuous tall grass understory (the vegetation layer between the forest canopy and the ground) (Fig. 1). The coexistence of trees and grasses is common to savanna ecosystems, with the ground layer dominated by shade-intolerant C<sub>4</sub> grasses. This layer persists because woody perennial plant species growth is limited below its rainfall-based potential by disturbance, including periodic grass fires and browsing (Bond 2008; Sankaran et al. 2005). The equilibrium between these two life forms (woody tree layer and grasses) influences both plants and livestock production and has profound impacts on several aspects of ecosystem functioning, including carbon (C), nutrient, and hydrological cycles.

Tropical savannas are very common and cover approximately 20% of the total terrestrial surfaces. The importance of the savanna can be understood by the fact that these are the home for one-fifth of the world's total population. But unfortunately, these ecosystems are continuously subject to intense human exploitation by conversion to agricultural and grazing land (Hoffmann et al. 2002). They are the most frequently and extensively burnt ecosystem on Earth, accounting for around 44% of global C emissions by fires (van der Werf et al. 2010). Dry-season fires, fuelled by dried grasses, may kill some trees, especially the more-vulnerable young saplings, and therefore, their severity also greatly influences the nature of savanna vegetation. Savannas are of different types and occur under a wide range of bioclimatic conditions, and it is likely that the importance of different processes in regulating woody cover may vary in different savanna regions. Ecosystems with these characteristics are found throughout the tropics in all continents particularly in the Americas (North and South), Africa, Australia, India, the Myanmar-Thailand region in Asia, and Madagascar. Tropical savannas occupy the greater area of the southern continents – some 65% of Africa, 60% of Australia, and 45% of South America. Despite their vast area, wide distribution, and potential importance in terms of livestock and crop production, savanna has not enjoyed the intensity of research interest



**Savannah, Fig. 1** A typical savanna vegetation with scattered tree in continuous grassland (photo credit: Gretchen Walters/IUCN)

devoted during the last several decades to the deserts, rainforests, and mediterranean regions. In fact they are probably the least understood of the world's major terrestrial ecosystems. This chapter will provide the information about the savanna ecosystem, their advantages in terms of ecosystem services, and current threats to this diverse and one of the most successful ecosystems.

## Origin and Spread of Savanna

Explaining the geologically rapid appearance and spread of  $C_4$  savanna ecosystems onto the ecological stage remains a major scientific challenge. During the late Miocene (Miocene is an epoch of Neogene period during the Cenozoic era) around 6–8 million years ago, savannas and  $C_4$  grasslands became prominent features of tropical landscapes as a result of a rapid global increase in the dominance of  $C_4$  grasses (Edwards et al. 2010). The leading hypothesis states that atmospheric  $CO_2$  concentration fell below a critical threshold during the Miocene, where the photosynthetic efficiency of  $C_3$  plants dropped below that of their  $C_4$  counterparts (Cerling et al. 1997). However, subsequent evaluation of this “ $CO_2$  starvation hypothesis” with multiple atmospheric  $CO_2$  proxy records (Royer et al. 2001) has

consistently failed to show the anticipated decrease at any time during the entire 18 Ma duration of the Miocene. In fact, declining  $CO_2$  had already breached a critical threshold some 20 Ma earlier in the Oligocene, an event linked with the evolution of the  $C_4$  pathway. Declining atmospheric  $CO_2$  concentration is, therefore, unlikely to be the sole driver of worldwide  $C_4$  savanna expansion. Consequently, the well-documented rise of this extraordinarily successful terrestrial biome continues to demand explanation (Beerling and Osborne 2006).

The second hypothesis found climate change as an important factor for the expansion of savanna. Increased aridity in the late Miocene has been shown to cause the retreat of forests in North America and Eurasia, allowing grasslands to spread in their place. The South American fossil record provides evidence of well-developed vegetation, rich in grass and thought to be equivalent to modern savanna, being established by the early Miocene Epoch, about 20 million years ago. Climate across the world became steadily cooler during that period. This drop in atmospheric temperature leads to decrease in ocean surface temperature and therefore reduced water evaporation, which ultimately slowed the water cycle, with less cloud formation and precipitation. This climatic condition significantly affected the vegetation of mid-latitude

regions, lying between the wet equatorial areas and the moist cool temperate zones. The main areas in which savannas originated in response to that long-term climatic change include tropical America, Africa, South Asia, and Australia which were already separated from each other by ocean barriers by that time. Plant migration across those barriers was stopped, and the details of the emergence of savannas on each continent varied. In each area different plant and animal species evolved and adapt to occupy the new seasonally dry habitats. In temperate region, savannas became much more frequent, at the expense of forests, during the long, cool, dry intervals – contemporaneous with the ice ages – or glacial intervals, of the Pleistocene Epoch (2.6 million to 11,700 years ago). Studies based on fossilized pollen in sediments from sites in South America, Africa, and Australia enable strong support for this view.

Apart from atmospheric CO<sub>2</sub> decline and climate change, there is another hypothesis that explains the role of mammalian herbivores in creating open canopy. Many experimental and observational studies have shown that mammals have the capacity to create open canopy by reducing tree biomass whether in the tropics or temperate or boreal regions. Browsing animals either of megaherbivores (>1000 kg) or mesobrowsers (4–450 kg) such as deer, antelope, and caprids are primarily responsible for open habitats and are very effective at preventing woody plant species from crossing the “browse trap” line and growing into larger size classes. They have also been implicated as agents maintaining open ecosystems and preventing forest development. Today, large number of research is still required to connect the exiting information and to explain the origin and spread of the savanna ecosystem.

### Climatic Condition that Support Savanna

The climatic conditions are warm to hot in all seasons, but significant rainfall occurs only for few months each year and about October to

March in the Southern Hemisphere and April to September in the Northern Hemisphere. Mean annual precipitation is generally 80–150 cm, although in some central continental locations it may be as low as 50 cm. The dry seasons are typically longer than the wet season, but it varies considerably, from 2 to 11 months. Savanna climate is similar to equatorial climate as regards temperature, but the annual range of temperature ranging between 3 °C and 8 °C is greater than in the equatorial climate. The dry season in savanna grasslands is cooler than the wet season by few degrees, and mean monthly temperatures are about 10–20 °C in the dry season and 20–30 °C in the wet season. The prevailing winds in tropical grasslands are the trade winds. They are easterlies, blowing from east to west. These winds have an enormous impact on the rains in this climate zone. For instance, rainfall in the savanna decreases from east to west. They are also the cause of the alternating dry and wet seasons. During summer, onshore winds bring rain, and in winter, offshore winds keep the savanna region dry. The trade winds are strongest in summer.

### Types of Savanna

Savanna can be subdivided into different categories depending on length of dry period or the physiognomy of the landscape. Depending on the dry period length, it may be dry (dry period last for 5–7 months), wet (dry period last for 3–5 months), or semiarid savanna (Table 1).

On the physiognomy basis, savanna can be subdivided as woodland, tree, shrub, or grass savanna as it is dominated by trees and shrubs, scattered tree, shrub, and grasses, respectively.

**Savannah, Table 1** Classification of savannas according to amount of rainfall received per year, length of dry season

| Types of savanna | Mean annual rainfall (mm) | Length of dry season (month) |
|------------------|---------------------------|------------------------------|
| Moist savanna    | 1000–2000                 | 3–5                          |
| Dry savanna      | 500–1000                  | 5–7                          |
| Semiarid savanna | 250–500                   | 7–10                         |



## Biological Diversity of Savanna

### Flora

Tropical savannas have high species diversity, especially when compared with temperate grasslands and dry tropical woodlands. Different groups of plants are prominent in the savannas of different regions. In the drier regions of East Africa, acacias (*Acacia*) and bush willows (*Combretum erythrophyllum*) are the most common savanna trees, with thick-trunked baobabs (*Adansonia digitata*), sturdy palms (*Borassus* sp.), or succulent species of spurge (*Euphorbia*) being conspicuous in some areas. In the drier savannas in particular, there is often a wide diversity of spiny shrubs. Among the most prevalent grasses are species of bluestem (*Andropogon*), thatching grass (*Hyparrhenia*), and kangaroo grass (*Themeda* sp.). In wetter savannas, *Brachystegia* trees grow above a 3-m-tall understory of elephant grass (*Pennisetum purpureum*). The most-common West African savanna trees are in the genera *Anogeissus*, *Combretum*, and *Strychnos*.

At temperate latitudes in Australia, the flora of the savanna resembles that of other types of sclerophyllous vegetation. Sclerophyllous characteristics like thickened cuticle, rolled margins, dense indumentum, high specific leaf weight, and increase in volatile oils are common to savanna genera. Most Australian savanna trees are evergreen, surviving the dry season not by dropping their leaves but by reducing water loss from them. The dominant trees of savannas in Australia and southern New Guinea are various species of *Eucalyptus*, *Acacia*, *Albizia*, *Cassia*, *Bauhinia*, *Casuarina*, screwpine (*Pandanus*), and other tall shrubs also common. Baobabs (*Adansonia gregorii*) are the most common, and conspicuous savanna trees in parts of northwest Australia indicate its Gondwana link. Tall spear grass (*Heteropogon*), annually growing *Sorghum*, or the shorter kangaroo grass (*Themeda*) dominates the understory of large areas of moist savanna. The prickly spinifex grasses (*Plectrachne*, *Triodia*) are prominent in more arid regions. Most trees and shrubs of the Australian savanna are markedly sclerophyllous.

Small patches of monsoon rainforest and other types of vegetation occur locally within mainly savanna regions, surviving in places that have some degree of protection from the dry-season fires.

Across large parts of the tropical American savannas, the most common broad-leaved trees are *Curatella americana*, locust berries (*Maricao cimarrons*), and *Bowdichia* sp., their place being taken in some seasonally waterlogged sites by the palms *Copernicia* sp. and *Mauritia* sp. Grasses include species of cutgrass (*Leersia*) and bahia grass (*Paspalum notatum*). In Argentina the most common woody plant is the bean relative *Prosopis* tree.

In India the savanna vegetation of most areas has been extensively altered by human activities, which also have expanded its range. Where least altered, Indian savannas commonly consist of thorny trees of *Acacia*, *Mimosa*, and *Ziziphus* growing over a grass cover consisting mainly of *Sehima* and *Dichanthium*, the latter also referred to as bluestem. The savannas of Asia and tropical America, unlike those of Africa and Australia, are best considered as attenuated rainforests, their natural biotas having strong affinities with those of the wetter environments nearer the equator in the same regions. Trees in those savannas are usually deciduous, their leaves falling during the dry season.

### Fauna

Savannas provide habitats for a large number of wild animal species, some of which help the vegetation through grazing, browsing, pollinating, nutrient cycling, or seed dispersal. Many regions of savanna are managed today to maintain large grazing mammals, such as the native fauna of Africa or the cattle used for commercial production in large areas of Australia and South and Central America. Less spectacular but nevertheless very important are the small invertebrates, for instance, grasshoppers and caterpillars are among the keen consumers of the understory foliage, and termites are significant consumers of dead plant material, including wood. The role and importance of termites in savanna as ecosystem engineers in tropical ecosystems are functionally

similar to earthworms in temperate areas. Termites are important for soil turnover, and in symbiosis with *Termitomyces* sp. belonging to fungi, *Macrotermes* termites transform organic material into plant-available inorganic forms, creating favorable sites for tree and forb (broad leave herbaceous plant species) establishment (Van der Plas et al. 2013). Thus termite mounds behave as nutrient hot spots changing the spatial distribution of resources on a landscape scale (Jouquet et al. 2011). Animals of savanna ecosystems have adapted to surviving the seasonal variations in their food supply. Many bird species (especially in Africa) and many mammals are seasonal migrants, occupying savannas during and immediately after the wet season when vegetation is lush and food abundant. They move elsewhere for food as the green parts of the plants disappear later in the dry season. This seasonal migration benefit birds by moving between environments where breeding is successful and environments where survival during the non-breeding season is relatively easy. The significant seasonal contrast in availability of plant food is less marked belowground where roots, tubers, and other subterranean organs commonly make up a large proportion of the total plant biomass. For example, up to four times of aboveground component has been found belowground in some West African study sites, especially in the dry season. It is not surprising, therefore, that most savanna invertebrates not only termites but also many other arthropods and earthworms spend most of their life span below the ground. The large mammals basically are part of a grassland community, despite the presence of low trees in their environment. Most animals depend on the grass component of the vegetation for their food either directly, as do the herbivorous buffalo, zebra, gnu, hippopotamus, rhinoceros, antelope, etc., or indirectly as is true of the carnivores like lions, leopards, etc. and scavengers such as vultures and marabou stork (*Leptoptilos crumenifer*) that feed primarily on those herbivores. Only a small number, including the giraffe (*Giraffa* sp.) and elephant (*Loxodonta* sp.), rely on foliage or fruit from the often thorny woody tree species. Large animals are relatively uncommon in savannas of Australia

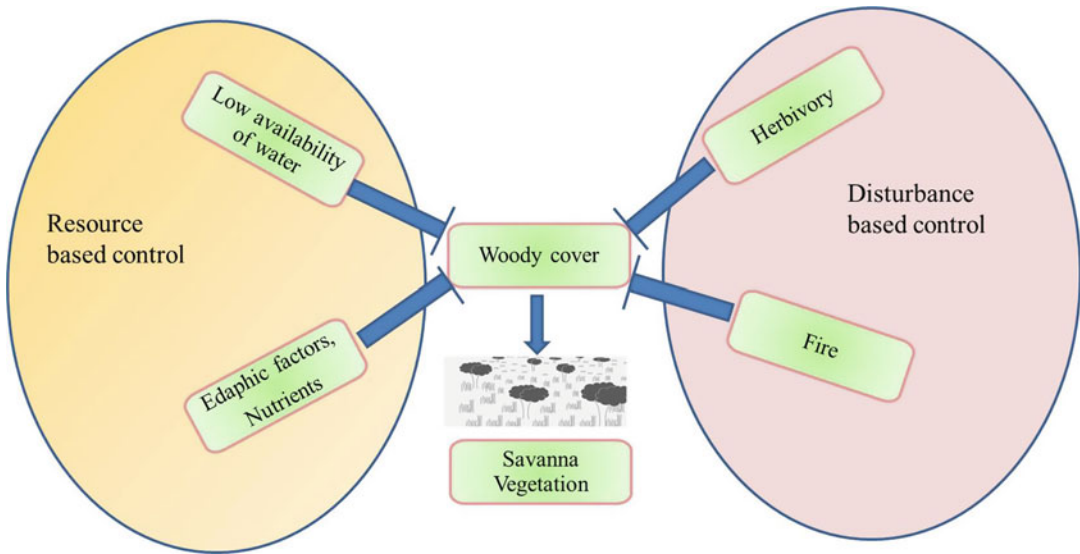
and are represented mainly by several species of the family Macropodidae, such as kangaroos and wallabies. However, in that area, a wide variety of very large mammals and reptiles became extinct million years ago. Their place today is taken by animals, both domesticated and wild, which have been introduced by humans including mainly cattle but also horses and, more locally, camels, donkeys, Asian water buffalo (*Bubalus bubalis*), etc.

## Factors Regulating Savanna Ecosystem

The structure of the savanna ecosystem is maintained and regulated by the environmental factors such as moisture, nutrient level (resource-based factor), herbivory, and fire (disturbance-based factor) (Fig. 2). These factors restrict the growth of the woody cover in a different way (detail given later on) and maintain one of the most successful ecosystems. Further the physiognomy of savanna at given site is influenced by the edaphic and climatic determinants which control the potential growth and survival of trees as well as grasses.

### Fire

Fire is an inevitable consequence of the annual cycle of profuse herbaceous production during the wet season followed by burning of this material in the dry season. Savanna fires are virtually all surface fires, consuming the highly flammable herbaceous layer. Crown fires rarely occur as the fuel loads are dominated by fine fuels (grass and leaf litter) and the foliage of savanna trees and shrubs tend to be of low flammability. In several studies it has been found that fire restricts the perennial woody tree species to establish by burning the young saplings. Perhaps the most compelling evidence that fire controls the distribution of forest is the results of fire-exclusion experiments that have shown forest species invading fire-protected savanna, especially in high rainfall areas with a complete biome shift from grassy to closed canopy sometimes occurring within a few decades (Woinarski et al. 2004). Some plants survive over fire, for example, those buds located



**Savannah, Fig. 2** Schematic diagram showing the regulation of savanna vegetation through resource- (bottom-up effect) and disturbance (top-down effect)-based control

underground or beneath thick bark that provides fire protection; regeneration quickly takes place from those shielded structures when condition becomes favorable. Other plants can reproduce effectively from seeds shed onto the scorched ground in the wake of wildfire. Such plants benefit from burning and become more abundant than the fire-sensitive plants that occur in areas of frequent burning. Among those plants, *Eucalyptus* trees, which dominate most areas of Australian savanna, are important. Other trees in Australian savannas, for instance, cypress pine (*Callitris*), are highly drought-tolerant, though fire-sensitive. Today *Callitris* is restricted to sites such as gorges and rocky outcrops where there is some protection from fire. Similar patterns are recognizable in other regions. For example, in northern Nigeria, thickets comprising a few fire-sensitive rainforest trees such as *Diospyros*, figs (*Ficus*), and *Tamarindus* grow on rocky knolls lacking grass. Those rocky “islands,” protected from fire and cattle, are surrounded by expanses of grazed and frequently burned savanna. Where plots of African savanna vegetation are protected from being burned, they tend to revert quickly to deciduous forest.

### Herbivory

The grazing animals also can alter the balance between woody plants and grasses in a savanna – in either direction, depending on their feeding habits. For example, grass-eating mammals may overgraze and push the grass toward local extinction. However, even high populations of those grazers cannot eliminate tall woody plant species, whose upper branches are out of their reach. Subsequent regeneration will favor the woody plants, which will become denser and shift the profile of the vegetation from savanna to forest. Megaherbivores can have the reverse effect if their populations increase. For instance, a steady rise in the elephant population between 1934 and 1959 in Virunga National Park, Congo (Kinshasa), led to an increase in the destruction of woody plants and transformed a heavily wooded savanna into a grass savanna with very few trees. Grazing (consumption of grass) can favor woody vegetation by reducing grass biomass, thereby reducing both tree grass competition and fire frequency and intensity, which have been shown to increase tree recruitment and growth. Such a grazing effect explains bush encroachment following heavy overgrazing by

domestic stock (van Langevelde et al. 2003). Bush encroachment is the suppression of palatable grasses and herbs by encroaching woody species often unpalatable to domestic livestock. Therefore, bush encroachment reduces the carrying capacity for livestock. Conversely, browsing (consumption of woody plants) can limit woody plants, maintaining open, grassy systems. Indeed, browsing has been shown experimentally to reduce woody plant abundance in savannas (Augustine and McNaughton 2004), largely due to its strong negative effect on height growth, especially in conjunction with fire.

### Edaphic Factor

Soil fertility is generally rather low in savannas but may show significant small-scale variations. It has been studied in Belize and elsewhere that trees can play a significant role in drawing mineral nutrients up from deeper soil. The leaves and other tree litter drop to the soil surface near the tree, where they decompose and release nutrients. Soil fertility is thereby greater near trees than in areas between trees. An unusually large proportion of dead organic matter approximately 30% is decomposed through the feeding activities of termites. Thus, a significant proportion of released mineral nutrients may be stored for long periods in termite mounds where they are not readily available to plant roots. In savannas of Thailand, it has been shown that soil fertility can be markedly improved by mechanically breaking up termite mounds and spreading the material across the soil surface. In Kenya, old termite mounds, which are raised above the general soil surface, also provide flood-proof sites where trees and shrubs can grow, with grassland between them, forming the so-called termite savanna. The biota of savannas reflects their derivation from regional biotas; therefore, species vary between regions.

Savanna plants annually experience a long period in which moisture is inadequate for continued growth. Although the aboveground parts of the shallow-rooted grasses quickly dry out and die, the more deeply rooted trees can tap moisture lying further beneath the surface longer into the dry season. Grasses grow rapidly when moisture is available but die back when it is not, surviving long dry periods as dormant buds close to the soil

surface. The sandy soils, which supply abundant moisture during rainy periods but which dry out almost completely in the absence of rain, favor the grassy component of savannas. Trees, on the other hand, require water in at least small amounts at all seasons even if they drop their leaves; deep soil layers supply that need. Trees in savannas are favored by stony soils, which allow deep penetration by roots but which are less favorable to grasses. Nevertheless, especially toward the end of the dry season, many trees may lose their leaves to reduce transpirational loss of water, even though the leafless branches of some species carry open flowers. Soil, therefore, exerts some control over the nature of savanna vegetation, particularly in the drier parts of its distribution where sandy soils support grass-rich savanna with few trees and coarser, deeper soils support more tree-rich savanna with less grass.

### Effect of Anthropogenic Activity

Anthropogenic activities also disrupt fire and mammalian herbivory regimes, two of the key spatial processes maintaining open savanna ecosystems (Sankaran et al. 2005). In particular, changes in land management, commercial agriculture, and fragmentation by road networks alter the size, season, frequency, and intensity of fires, thereby altering natural fire regimes. The tree component of savannas generally becomes more important as rainfall increases, but other factors such as topography, soil, and grazing intensity all exert influences in complex and variable ways. Because grazing and fire are strongly affected by human activities and have been for thousands of years, humans continue to have a controlling influence on the nature, dynamics, development, structure, and distribution of savannas in many parts of their global range. The effect is especially pronounced when economic development and increased population densities cause cropland expansion (Andela et al. 2017). Indeed, much of the 25% decline in global fire can be attributed to increasing human influence in savannas. People have similarly impacted herbivory regimes with a continent-wide switch occurring across Africa from free-roaming

native herbivores to largely sedentary grazing livestock. These changes in herbivory regimes are further worsening by the continent-wide poaching (illegal hunting) of iconic African megaherbivores, like elephant and rhinoceros. The culling of wild mammals to prevent disease transfer to livestock has also drastically reduced population sizes, while fences and roads hinder migration and restrict range sizes. Smaller and more fragmented populations, in turn, diminish the ecosystem-engineering effects of megaherbivores on vegetation openness and nutrient distribution. Such engineering has likely influenced savanna structure and function since the Miocene (Charles-Dominique et al. 2016). Savannas are also affected by the overuse of woody plants for fuel. Together with grazing and cultivation, this depletes both the grassy and woody components of the vegetative cover. Often a subsequent acceleration of soil erosion occurs. Such processes are associated, in densely settled savanna areas such as Africa north of the equator, with the type of land degradation called desertification. Human impacts on one or more of the determinants of savanna structure and function. Clearly increased knowledge of their interactions will provide improved understanding of savanna processes and enable better management in a rapidly changing world. Savannas may be ideal ecosystems for agroforestry applications, rather than traditional cropping systems. Small shifts in fire regime may dramatically increase productivity; thus savanna systems could be used for carbon sequestration and greenhouse gas mitigation schemes, providing alternative livelihoods and aiding in the maintenance of biodiversity. Anthropogenic activity impacts the determinants of savanna structure and function. Increased knowledge of their interactions will provide improved understanding of savanna processes and enable better management in a rapidly changing world.

## Conclusion and Future Prospective

The impact of ecosystem services provided by savanna on human population is large, since one-fifth of the world population depends

on it. Anthropogenic activity impacts the determinants of savanna structure and function. Currently, savannas are undergoing rapid changes at the continental scale but unlike in forested biomes. The ongoing woody plant encroachment in savannas is detrimental to the ecosystem services provided to local people. Efforts to avert a crisis in savannas are impeded by inadequate understanding of the ecological mechanisms, driving observed changes, and of the diversity among savanna types in their resistance and resilience to change. These knowledge gaps hamper the development of sound management strategies at the local and regional scales. It is clear that increased knowledge of savanna processes and factor regulating it enables better management in a rapidly changing world. Savannas may be ideal ecosystems for agroforestry applications, rather than traditional cropping systems. Small shifts in fire regime may dramatically increase productivity; thus savanna systems could be used for carbon sequestration and greenhouse gas mitigation schemes, providing alternative livelihoods and aiding in the maintenance of biodiversity.

## Cross-References

- Biomass
- Canopy
- Population
- Tropics

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## Savings

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## Definition

Savings are the proactive influence of prior learning on later learning or behavior even when the originally learned behavior appears to have been eliminated.

## Introduction

In Pavlovian conditioning, the pairing of a neutral conditioned stimulus (CS: such as a tone) with an unconditioned stimulus (US: such as a puff of air to the eye) results in the acquisition of a conditioned response (CR: blink response to the tone). Following acquisition of the CR, presentations of

the CS alone result in the progressive elimination of the CR, known as extinction. In operant conditioning, following a response with reinforcement increases the frequency of the reinforced response which extinguishes when reinforcement is omitted. Superficially, the elimination of the CR in Pavlovian conditioning and the response in operant conditioning appears to be the reversal of the original learning. However, even after complete elimination of the CR or response, a substantial residual of the original learning is saved and, as will be detailed below, can be recovered in a variety of ways. That is, there are savings of the original learning which can be evidenced by the recovery of the CR or response and which proactively interfere with later learning even when the originally learned behavior has been abolished.

### **Spontaneous Recovery, Renewal, and Reinstatement**

Following the extinction of a CR in classical and a response in operant conditioning, the CR and response can spontaneously reappear, following a period without exposure to the cues, when the CS or antecedent cues are reintroduced (Pavlov 1927, p.58; Skinner 1938, p.78). This spontaneous recovery is transient and responding quickly disappears unless the CS is followed by the US or the operant response is reinforced. Responding is also renewed when the CS or antecedent cues are presented in a context other than the context in which extinction occurred and is strongest when returned to the context in which conditioning occurred (Bouton and Ricker 1994; Bouton et al. 2011). Also if the reinforcer is delivered independently of the response or the US is delivered independently of the CS then responding can be reinstated (Rescorla and Skucy 1969; Rescorla and Heth 1975). Spontaneous recovery, renewal, and reinstatement all indicate that the original learning remains in long-term memory following extinction and can re-emerge in performance of the original CR or response.

### **Rapid Reacquisition, Learning to Learn and Concurrent Recovery**

Additional to the re-emergence of the CR or response, savings can also be demonstrated in altered learning curves following the acquisition and extinction of Pavlovian and operant conditioning. In Pavlovian conditioning, spontaneous recovery and reinstatement can largely be abolished by conducting extinction across numerous days with delays between extinction sessions and by presenting the US during extinction but explicitly unpaired from the CS (Napier et al. 1992). Following this type of extinction procedure when the CS and US are paired again in reacquisition, reacquisition is much faster and shows a much steeper learning curve than either original learning in the same participants or compared to a control group that have received an equivalent amount of exposure to the learning context in the absence of the CS and US (Napier et al. 1992; Weidemann and Kehoe 2003). This faster rate of learning also transfers to a new stimulus, from a different sensory modality to the originally trained and extinguished CS, when it is paired with the same US (Kehoe et al. 1995; Weidemann and Kehoe 2003). This form of transfer has been labeled learning to learn, general transfer and nonspecific transfer. The training of the new stimulus also results in concurrent recovery of the original trained and extinguished CS without any additional pairings of the CS with the US. The amount of extinction training influences the magnitude of rapid reacquisition and learning to learn but has no effect on the degree of concurrent recovery (Weidemann and Kehoe 2003).

### **Theories of Savings**

Evidence for savings suggests that extinction does not eliminate the original learning but either results in new learning which retroactively interferes with the original learning to silence responding (Bouton and Ricker 1994; Bouton et al. 2011) or results in diminution of the original

learning which silences responding while some portion of the original learning remains protected (Napier et al. 1992; Weidemann and Kehoe 2003). Inhibitory theories of extinction and savings can successfully explain spontaneous recovery, renewal, reinstatement, and rapid reacquisition but have a great deal of difficulty explaining learning to learn and some aspects of concurrent recovery. Whereas, Kehoe's (1988) connectionist model of learning and extinction which incorporates a "hidden" unit layer which is common to all CSs paired with the same US and includes an attenuation and protection mechanism can explain rapid reacquisition and learning to learn but cannot explain spontaneous recovery, renewal, reinstatement, and concurrent recovery without some additional mechanisms (Weidemann and Kehoe 2003). A model which combines both layered connectionist architecture with inhibitory connections that are gated by features of the extinction context is able to explain most savings phenomena (Weidemann and Kehoe 2003).

### Implications of Savings for Therapeutic Procedures

Practically, extinction is the foundation of most exposure centered therapies for anxiety and addiction. Such therapies are highly effective, but, like laboratory based extinction, savings are commonly seen in the high rates of relapse. Hence understanding savings after extinction has widespread significance for improving the efficacy of clinical treatments for both anxiety and addiction. Both preclinical and clinical research on anxiety has shown evidence of savings following exposure based interventions and treatment. Current research is examining ways to strengthen the extinction memory and weakening the original conditioning memory in order to reduce savings (Vervliet et al. 2013).

### Conclusion

Evidence for savings following the acquisition and extinction of Pavlovian and operant

conditioning is seen in the form of the re-emergence of the CR or response such as during spontaneous recovery, renewal, reinstatement, and concurrent recovery. Alterations to the learning curve of Pavlovian and operant conditioning, as shown in rapid reacquisition and learning to learn, also indicate that there are savings of the original learning. No single theory of extinction learning is able to explain all of the different savings phenomena but a hybrid model that includes the formation of inhibitory connections during extinction that are gated by the extinction context and other forms of protection of the original learning can explain most savings phenomena. Therapeutic interventions that include exposure to either a source of anxiety or cues and situations that elicit craving can benefit from understanding savings phenomena to understand sources of relapse and to maintain and extend therapeutic outcomes in the client's ordinary environment.

### Cross-References

- Acquisition
- Classical Conditioning
- Extinction in Learning
- Learning to Learn
- Operant Conditioning
- Reinforcement
- Spontaneous Recovery
- Unconditioned Stimulus
- Unconditioned Response

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## Scala Naturae

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## Synonyms

Evolutionary ladder; Great chain of being; Ladder of being; Phyletic scale

## Definition

A view of life from ancient Greece placing different kinds of natural objects on ascending levels of a fixed hierarchy with inanimate objects, that is, rocks, on the bottom and humans at the top level.

## Introduction

### History

The *Scala Naturae*, also known as the *Great Chain of Being*, is a model or view of life

formalized in ancient Greece first by Plato and then Aristotle (1910, 1912, for translations; Lovejoy 2011) and maintaining prevalence into modern times. It orders nature on a hierarchical scale of complexity, “advancement,” and value starting with inanimate objects, for example, rocks, on the bottom and ascending to “simpler” life forms, for example, plants, then invertebrates, and “up” to mammals, then primates, then humans. In versions of the *Scala Naturae* adopted in Medieval times, supernatural beings, for example, angels, occupy levels just above humans, with god at the peak.

According to Aristotle, the “principle of form” is more “advanced” in organisms higher on the scale than those lower. Describing the life forms as one moves up the *Scala Naturae*, Aristotle stated that “one after another shows more possession of life and movement.” The levels on the scale are static classes which, while linked, are fixed for eternity. Therefore, the *Scala Naturae* engendered a world view that, within a Medieval European religious context, saw god as perfect and all other creatures, including humans, as progressively less perfect semblances of god. Humans, however, occupied a special status in the hierarchy as the most “advanced” species and therefore closer to god than any others. Even a secular adoption of the *Scala Naturae*, however, views humans as “higher” than other animals, whose positions on the scale are determined by resemblance, not to god, but to humans.

Needless to say, the *Scala Naturae* is not supported by modern empirical evidence. Yet, it has held sway over scientific thinking for thousands of years. It was championed by Thomas Aquinas, who saw the levels as reflections of “divine order,” attaching great religious and value-laden significance to each. In the thirteenth and fourteenth centuries it found expression in the writings of such thinkers as St. Albertus Magnus and the medieval schoolman Nicholas of Cusa.

The *Scala Naturae* represents an idiosyncratic blend of two seemingly incompatible ideas: one that all organisms on the ascending levels are connected and, at the same time, remain fixed in their positions as distinct “kinds.” For instance, Leibniz (1646–1716) promoted the notion of

connection across levels which formed a single chain in his *Law of Continuity* based on the *Scala Naturae* all the while upholding the categorical distinctions across organisms.

Despite the more sophisticated later classification schemes of Linnaeus and Cuvier (<http://www.macroevolution.net/scala-naturae.html>), *Scala Naturae* thinking remained entrenched in “tree of life” depictions of nature. The idea of branching lineages of organisms was laid upon an overall view of “lower” to “higher” branches. Just before the emergence of Charles Darwin’s theory of natural selection, Jean Lamarck put forth the idea that nature represented progressive levels of “perfection” in nervous system organization and that as one moves up the hierarchy new psychological capacities emerge as nervous systems become more “perfect.” Although Lamarck may be best known for his abandoned theory of “inheritance of acquired traits,” his *Scala Naturae* notions about the brain and intelligence remain influential in modern thinking. Charles Darwin brought temporality and dynamism to our view of life but despite his revolutionary work *Scala Naturae* was not completely abandoned so much as superimposed upon his ideas.

In post-Darwinian times the *Scala Naturae* found new life in notions of phylogeny and teleology. Implicit in the *Scala Naturae* are teleological notions, that is, that there is a progression in cosmic and biological evolution toward better or more advanced organisms. This idea, or, rather, misconception, of evolution remains a “thorn in the side” of Darwinian theorists to this day. The modern “phyletic scale,” which reflects evolutionary relationships among species, is still a hierarchical scheme that promotes the idea that “higher” organisms are more “evolutionarily developed” than “lower” organisms. And while the phyletic or phylogenetic scale is based upon comparisons across current species, it is often interpreted as a linear scale of progression. For example, a linear scale would classify modern teleost fish “below” modern mammals despite the fact that modern fish and modern mammals do not have an ancestor-descendent relationship.

By the mid-to-late twentieth century scientists possessed a sophisticated understanding of

evolution and molecular genetics. Evolution came to be known as a change in gene (allele) frequencies over generations. Yet the notion of the phyletic scale continued to have a profound influence in many scientific fields and, in particular, those fields, like comparative psychology, that are focused explicitly on describing and explicating similarities and differences across species. Influential psychologist Harry Harlow wrote in 1958:

[S]imple as well as complex learning problems might be arranged into an orderly classification in terms of difficulty, and that the capabilities of animals on these tasks would correspond roughly to their positions on the phylogenetic scale. (p. 283)

As late as the 1970s the *Scala Naturae* was re-energized by the wildly popular book and television series *The Ascent of Man* by Bronowski (1974). In addition to the main title, his chapter titles, such as “Lower Than Angels” and “Ladder of Creation,” were clear affirmations of *Scala Naturae* thinking. The great poet Ralph Waldo Emerson wrote (<https://quotes.yourdictionary.com/author/ralph-waldo-emerson/49009>):

Striving to be man, the worm  
Mounts through all the spires of form.

Although this was written in the nineteenth century it very much reflects a current perspective on life originating in the *Scala Naturae*. “Lower” forms of life strive to gain ascendancy up nature’s ladder to reach the pinnacle of nature’s creation – humanity. Other animals are viewed as simpler and lesser versions of life than humans.

In the twenty-first century our understanding of the nature of life and its evolution completely rejects the validity of the *Scala Naturae*. And, indeed, it would be rare to find explicit advocacy for the *Scala Naturae* or Great Chain of Being sensu stricto in today’s world. Nevertheless, implicit notions connected to *Scala Naturae* remain firmly ensconced in both our public discourse and scientific language and thinking. It influences not only what kinds of questions are asked in science but how data are interpreted and explained. And this ancient model continues to have a profound influence on how we relate to and treat other animals.



## Impact and Implications in the Twenty-First Century

### Scientific Thinking

A cursory review of modern college-level textbooks, lesson plans, presentations, and scientific articles and webinars reveals that *Scala Naturae* thinking still strongly shapes our views and our language in the twenty-first century. One finds, in these sources, “scientific” phrases such as “lower versus higher animals,” “advanced versus primitive,” “subhuman,” “humans and animals,” and depictions of humans at the pinnacle of evolution above other modern species (Nee 2005), to name a few. All are evidence that, despite our scientific knowledge, we retain the ancient perspectives of linear and hierarchical thinking and assumptions about evolutionary “progress.” For instance, as recently as 2004, Lenton et al. described life through the ages with a ladder whose rungs “progress” from microbes to plants and, at the top, megafauna (i.e., large animals).

In the area of comparative psychology and other related scientific disciplines that involve comparisons across species the *Scala Naturae* shapes the directionality of scientific inquiry (Marino 2003). That is, most of comparative psychology is an exercise in identifying capacities that humans possess and a search for those same abilities in other species. Examples include the study of language, arithmetic ability, tool making and use, mirror self-recognition, and numerous other forms of cognition. Less often do we change the direction of inquiry, asking whether humans possess a characteristic known to exist in other animals. One might argue that it is more difficult to probe the existence of a cognitive or mental trait in another species that is absent in our species. However, the vast majority of questions about cognition, intelligence, communication in other species defaults to an exercise in determining “how low can you go” on the phyletic scale and still find that human characteristic. The influence of *Scala Naturae* thinking does not end there, however.

A longstanding stricture in science is the principle of parsimony (also known as Ockam’s Razor), that is, the requirement to give the

simplest explanation possible that explains the greatest number of observations. In the study of animal behavior and comparative psychology, neuroscience, and other related fields, it takes the form of Morgan’s Canon, which says that no activity or ability found in nonhumans should be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes or mechanisms that are lower in the scale of psychological evolution and development. While rules of parsimony are important guidelines in science the very definition of Morgan’s Canon presupposes a *Scala Naturae*-based view of life. It imposes a unidirectional restriction on scientific explanations that assumes other species are not as “advanced” as humans. And while we may assert that modern scientific thinking is free of these kinds of ancient biases, the very language used to define Morgan’s Canon belies this claim. As such, *Scala Naturae* thinking often pushes scientific explanation away from parsimony. An increasing number of cognitive abilities previously thought to be unique to humans are found in species distantly related to our species, that is, cephalopods, insects, fish. These include observational learning, numerosity, various short-term and long-term memory capacities, reasoning, and problem solving. Some of these capacities may only appear to be similar to those in humans but are based on different neurocognitive mechanisms. Yet, a summary application of Morgan’s Canon without considering all possibilities can lead away from parsimony and imposes the equally unwieldy formation of multiple explanations for the same phenomenon – a “complex” one for humans and “simpler” ones for members of other species. In response to this tendency toward linear hierarchical thinking, many contemporary scientists and philosophers have pointed out that the most parsimonious explanation can be one that recognizes continuity and functional convergence across humans and nonhumans.

### Human-Nonhuman Relationships

In addition to how we reason about scientific findings across species, *Scala Naturae* has had longstanding relevance to how humans treat other animals, resulting in global animal

exploitation, abuse, and extinction. *Scala Naturae* thinking has its origins in views that place different beings, including demographically different human beings, on different levels of the hierarchy with the implicit notion that as one goes “down” the hierarchy the value of those lives decreases. The viewing of humans as superior to all other life on earth is tantamount to speciesism, that is, viewing other animals’ lives as of lesser value and import than our own. Speciesism, and thus *Scala Naturae* thinking, is the core justification for vivisection and invasive research, factory farming, poaching, sport hunting, religious sacrifice, fur-wearing, confinement for entertainment, and other forms of aggression visited upon other animals by humans.

Even within the domain of animal welfare, *Scala Naturae* thinking allows for gerrymandered proscriptions about how to treat other animals in such formalized schemes as Utilitarian philosophies and the 3R’s. For instance, Russell and Burch’s (1959) 3R’s (Replacement, Reduction, and Refinement) are meant to guide research practice so as to mitigate as much suffering as possible. The principle of Replacement (replacing one species with another or, ideally, with non-animal methods) is often invoked to conduct invasive research on species “lower” on the evolutionary scale than others. Replacement would proscribe replacing dogs with mice and mice with frogs, for instance, working “down” the scale of presumed ability to suffer. This is similar to notions of eating “down” the food chain. But these principles are based more on presumed attributes of various species than evidence and are, in the end, merely reflections of our own longstanding biases.

## Conclusion

It is not possible, at this time in history, to determine whether the *Scala Naturae* is an expression of our species’ innate bias against other animals or whether it has been employed through the ages as a convenient proscription for mistreatment of other animals. Although both are likely to be the case, it is inarguable that these ancient views

continue to fuel some of the worst forms of violence against other animals throughout history to this day.

## Cross-References

- [Animal Welfare](#)
- [C. Lloyd Morgan](#)
- [Charles Robert Darwin](#)
- [Comparative Psychology](#)
- [Evolution](#)
- [Harry Harlow](#)
- [Jean Baptiste Lamarck](#)
- [Morgan’s Canon](#)
- [Ockham’s Razor](#)
- [Parsimony](#)
- [Phylogeny](#)

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## Scaly Anteater

- [Pangolin](#)

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## Scavenger

- [Omnivore](#)

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## Scent

- [Bear Communication](#)
- [Mustelid Communication](#)

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## Scent Mark

- [Prosimian Communication](#)

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## Scent-Marking

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## Synonyms

[Territorial marking](#)

## Definition

Scent marking is a form of olfactory communication used by an animal that deposits its odor in specific places to transmit a signal to other animal.

Scent marking is mainly defined as a behavior displayed to mark territory ownership (Gosling 1982). However, nonterritorial species can also scent mark to communicate with conspecifics. So not all marking is territorial, and the meaning of the scent can vary according with the species, its social system, and ecological factors.

Because the scent remains in the environment for some time, it represents a way of olfactory communication and allows the owner to be identified by a rival even in its absence, reducing the costs of physical conflicts (Gosling 1982). The

scent may signal a threat and a fitness cost to the receiver that must evaluate the risk of being detected by the signaler, accounting for its competitive ability and the value of the marked resource to both individuals (Gosling and Roberts 2001). Therefore, the responses of competitors to scent marks are variable.

In intraspecific communication, scent marking can function for individual or group recognition, age and social status recognition, site familiarity, as sex attractant or stimulant, and even for intrasexual competition (Johnson 1973; Müller and Manser 2008). With interspecific communication, scents can be used to recognize a species, which can represent a prey or a predator, or even to signal warning and defense (Johnson 1973).

Because the scent remains in the environment, other individuals can also detect the signal and take advantage on it, which is called eavesdropping (Gosling and Roberts 2001). Scents used by males to chase rivals from an area, for example, can attract potential mates or even predators.

## Behavior

Scent marks can be eliminated by urination, defecation, or by the secretion of scent glands, which can be located in different parts of the body. Therefore, it is important to distinguish scent marking behavior from the elimination of urine and feces just for excretory finality. During the scent marking behavior, the individual leaves its odor by distinct movements at selected sites that are visited repeatedly. In some species, such as Ethiopian wolves (*Canis simensis*, Sillero-Zubiri and Macdonald 1998) and giant otters (*Pteronura brasiliensis*, Leuchtenberger and Mourao 2009), individuals may use specific postures during scent marking behavior. Ethiopian wolves scent mark raising a hind leg and by scratching the ground when urinating a scent post (Sillero-Zubiri and Macdonald 1998). Giant otters scent mark rubbing their legs on the ground and the front legs on the vegetation, spreading the secretions that are left on communal latrines or at campsites along the banks (Leuchtenberger and Mourao 2009).

The posture used during scent marking and also the frequency that an animal scent marks are commonly related with its sex and dominance rank (Leuchtenberger and Mourao 2009; Müller and Manser 2008; Sillero-Zubiri and Macdonald 1998). Dominant males tend to mark more often, and it is also common that the dominant overmark the scent of other members of its group (Leuchtenberger and Mourao 2009; Sillero-Zubiri and Macdonald 1998). Overmarking may be a strategy of reproductive suppression, especially when the dominant individual has reproductive priority within the group (Palagi et al. 2004).

Some species may also associate other marking behaviors to the scent marking ritual, as for example, giant otters rub their fore paws on the vegetation soon after they emerge from the water (Leuchtenberger and Mourao 2009). Associate-behaviors may produce a visual signal that reinforces the detectability of scent marks enlarging the distance that these marks can be found by receivers (Gosling and Roberts 2001).

Once the receiver has matched the scent, the response can vary, according with the function of the scent, the identity of the owner, the competition ability of the receiver, and the behavioral context. Because scents can transmit the identity of the owner, receivers can memorize the smell and react to a known scent differently than to a stranger one. Some hypotheses, as the dear enemy effect and the familiarity hypothesis, try to explain the reaction of animals to known signs. The dear enemy effect, for example, suggests that territorial animals respond more aggressively to neighbors than to strangers, which is common in social mammals that live under intense competition (Müller and Manser 2007).

## Location of Scent Marks

The range of scents is usually low, so the location of scent marks is relative to the level of threat from opponents (Gosling and Roberts 2001). Therefore, it is expected that the density of scent marks is higher at places that are more visited by rivals. Within a territory, usually scent marks are more concentrated at the boundaries, where

invasions are more eminent, or even toward the center (Gosling and Roberts 2001). But some species, like some primates and otters, deposit scents near food resources (Kruuk 1992; Miller et al. 2003). However, within the same species, the distribution of scents can change according to ecological constraints and population density.

## Composition

The chemical composition of scents is controlled by endogenous and exogenous factors, including hormones (Setchell et al. 2010), and is still unknown for many species. Scent marks contain a mixture of compounds, especially pheromones (a chemical compound that causes a behavioral and/or a physiological reaction on a receiver; Johnston 2003), and proteins, such as the major urinary proteins that stabilize the odors and maintain them for longer in the environment (Hurst et al. 1998). Because most of the chemical compounds of scents are genetically regulated, they can encode the identity of the sender.

Some species may present different scent glands that secrete different kind of secretions and scents, which may display different functions. In ring-tailed lemurs (*Lemur catta*), for example, both sexes present apocrine and sebaceous gland fields in their genital regions, while males have two additional glands at the labial and brachial regions (Scordato et al. 2007). Seasonal differences in the chemical composition of the secretion eliminated by labial, brachial, and scrotal glands suggest that scent marking functions for reproductive advertisement and intrasexual competition in this species. While the secretions of genital glands of both sexes present individual identity.

Although scents are used by other taxa, like insects and reptiles, those of mammals present a more complex range of components (Johnston 2003). The variety of components, their combination, and concentration lead to a range of complex olfactory signs that can be transmitted by scents. In Old World Monkeys (*Mandrillus sphinx*), for example, approximately 97 volatile components were identified in samples of scent-glands secretion, which may inform variable

(age, dominance rank in males) and fixed (sex, individual identity) cues of the signaler (Setchell et al. 2010). In Marmoset monkeys, females' (*Callithrix jacchus*) scent marks were composed by 162 identical components, but the concentration of highly volatile chemicals varied among individuals, suggesting that the quantity of these components allow individual identification (Smith et al. 2001).

## Conclusion

Scent marking is a way to communicate with conspecifics and also with other species. Scent marks are left at specific sites and transmit a signal even in the absence of the owner. Therefore, scent marks must be deposited at sites where they are easily found by intruders, maximizing the chance to be detected and reducing physical conflicts. The function of scent marking varies among and within species and may induce different reactions on the receivers. Scents are composed by a variety of chemicals that may transmit information of the sender as well as the age of the scent. The variety of messages that can be transmitted by these chemicals and their persistence in the environment make scent marking one of the most efficient and important communication system for many species.

## Cross-References

- Agonistic Behavior
- Alpha
- Chemical Signals
- Dear Enemy Effect
- Individual Recognition
- Kin Selection
- Pheromone
- Social Behavior
- Territoriality
- Territory Defense
- Testosterone
- Vigilance
- Warning

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## Schedule-Induced Behavior

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## Synonyms

Adjunctive behavior; Collateral behavior; Superstitious behavior

## Definition

Schedule induction refers to the process of behavior being developed during inter-reinforcement intervals without explicit arranged contingency between its occurrence and the delivery of reinforcement but only by the repeated occurrence of intermittent scheduled reinforcers.

## Introduction

Schedule-induced behavior occurs at significant high rates as a result of exposure to intermittent reinforcement, having, in general, a post-reinforcement temporal location with an inverted U-shaped distribution along inter-reinforcement intervals. These behaviors were initially called adjunctive (Falk 1971) because it was thought that they occurred as adjuncts to target behaviors that were explicitly reinforced and that they had no apparent functionality on their own.

The first reported example of schedule-induced behavior was psychogenic polydipsia (i.e., excessive drinking), observed in laboratory rats when they were exposed to intermittent food reinforcement while being moderately hungry (but not thirsty), and did not have to drink in order to obtain the food reinforcer. The understanding of schedule-induced behavior as adjunctive behavior

has been challenged since its inception (Segal 1972), and recently two theoretical alternatives to account for their occurrence have been proposed (Baum 2012; Killeen and Pellón 2013; see below).

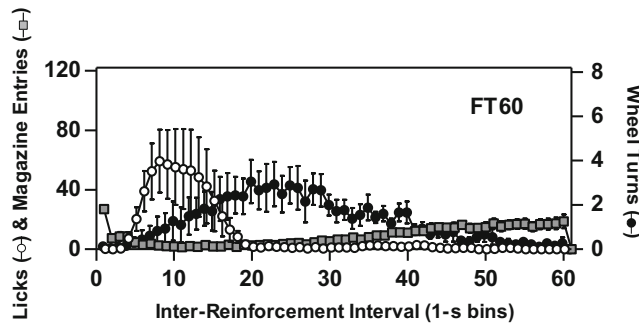
Staddon (1977) proposed a motivational explanation of induction based on competition for expression as a function of proximity to reinforcement: interim activities occur immediately after reinforcer delivery, while terminal activities occur before or just at the time of the presentation of the reinforcer. Schedule-induced drinking would be an example of interim activity, while magazine entering will be an example of a terminal one.

## Generality of Schedule Induction

Among the behaviors that have been described as schedule-induced are drinking (polydipsia), wheel running, pica, attack, air licking, wood chewing, escape, defecation, or smoking, and they have been observed in such diverse animal species as pigeons, rats, mice, hamsters, gerbils, pigs, monkeys, and humans.

When various schedule-induced behaviors are available simultaneously, they tend to organize within inter-reinforcement intervals in a sequential and orderly manner. For example, if rats can drink, run, and get into the food magazine, the typical distribution of behavior is as shown in Fig. 1, where drinking (licking) antecedes running (wheel turning), and they finalize by entering into the magazine.

Schedule-induced behavior has been observed to occur under a wide range of reinforcement schedules, including fixed interval, variable interval, fixed time, variable time, fixed ratio, differential reinforcement of low response rates, and in the extinction components of some multiple schedules. Different types of reinforcers/events have been used as inducers, mostly food, but also water, condensed milk, access to an activity wheel, brain electrical stimulation, and money. Details on how motivational variables related to reinforcement affect schedule induction will be described later.



**Schedule-Induced Behavior, Fig. 1** Mean ( $\pm$  SEM) of number of licks, wheel turns, and magazine entries recorded every second (bin) during inter-reinforcement intervals of a fixed time (FT) 60 s schedule. The FT 60 s schedule

delivered a single pellet of food every 1 min regardless of rats' behavior, i.e., animals did not have to lick, turn the wheel, or enter into the magazine for food pellets to be delivered. (Data taken from Gutiérrez-Ferre (2019))

### Motivational Variables that Influence Schedule-Induced Behavior

This is central in order to characterize the nature of schedule-induced behavior, and their study has been limited almost exclusively to schedule-induced drinking. The amount of licking and drinking depends on the level of hunger and is influenced by most variables related to food delivery, such as its frequency, magnitude, quality, or delay in its procurement, with more schedule-induced drinking as those parameters of food delivery are more favorable (Reid and Staddon 1990). However, schedule-induced drinking is not so dependent on characteristics of the liquid available, nor on the level of thirst. Even more, schedule-induced drinking is not observed when wet instead of dry food is used as reinforcer, and the use of intermittent water reinforcement does not induce food consumption. Water accessibility, however, has been shown to add value to the situation of food reinforcement, thus making it quite resistant to reduce or eliminate.

Figure 2 shows ideal inverted U-shaped or linear functions of schedule-induced drinking in terms of behavior being measured as units per reinforcer occurrence or per time elapsed and as a function of inter-reinforcement interval length. Behavior is controlled both by frequency of reinforcement (15–120 s) and by the magnitude of the reinforcer (1 versus 4 food pellets). Typically, in order to assess the effects of both rate and magnitude of reinforcement, it should be taken into

account that reinforcers also induce other patterns of behavior (see Fig. 1) that compete with each other for expression.

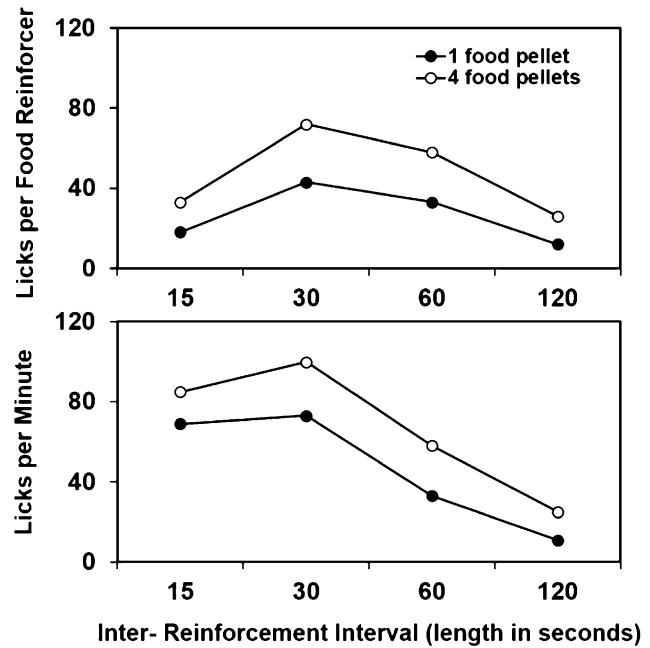
### Induction and Reinforcement as Behavioral Mechanisms

The study of schedule-induced behavior has led to the development of two theoretical accounts describing the mechanisms responsible for its acquisition and maintenance: reinforcement and induction. We will describe them as separate approaches even though there have been attempts for their integration (Ruiz et al. 2016).

Since the beginning of the study of schedule-induced behavior, some authors claimed that it was adventitiously reinforced. Although the proposal did not prosper until recent years, there are a few studies that evaluated the effect of consequences on schedule-induced behavior by, for example, introducing delays contingent to behavior emission. Killeen and Pellón (2013) extensively analyzed such literature and developed a model of competing traces to explain both schedule-induced and operant behavior. They proposed that different classes of behaviors have different temporal windows during which they can be reinforced; those temporal windows would be the exponential traces of proximity that determine the time that can elapse between the behavior and the delivery of the reinforcer for the behavior to be reinforced. More recently it was

### Schedule-Induced Behavior, Fig. 2

Ideal licks per reinforcer or licks per minute as a function of duration of the inter-reinforcement interval and of magnitude of reinforcer, expressing respectively bitonic or linear functions. (Data adapted from original transformations reported in Pellón (2012))



also proposed that behaviors are not just reinforced individually but that they collaborate and compete (Pellón and Killeen 2015).

On the other hand, Baum (2012) proposed a new paradigm in which he redefines the concept of operant behavior, replacing it with induction. He proposes that induction implies that some events in the environment increase the occurrence of a behavior, or the time spent doing that behavior, more closely related to the traditional definition of discriminative stimulus. Those events are called phylogenetically important events, and when they occur consistently with a behavior, a contingency in correlational terms is formed between them, resulting in the increase of that behavior when that event occurs. He also suggests that behaviors compete among them and distribute in a hierarchical way throughout the inter-reinforcement interval, similarly to what Staddon (1977) and Pellón and Killeen (2015) proposed.

### Implication of Neurobiological Circuits on Schedule Induction

Schedule induction has been related to two lines of neurobiological involvement: mesolimbic

dopaminergic pathways, focused on the motivational features of the incentive involved in the release of a reinforcer, and hypothalamic-pituitary-adrenal axis that proposes an adaptive function of schedule-induced behaviors as a response strategy to stressful situations. Several studies have evaluated the effects of pharmacological and lesion treatments/interventions on mesolimbic pathways and found that the amount of schedule-induced behavior was affected. On the other hand, animals that developed excessive-induced drinking showed decreased plasma levels of corticosterone. A further approach suggests that structural plasticity of cortical-striatal regions associated with goal-directed actions and habit formation could mediate the persistence and excessiveness developed during induction (Íbias et al. 2015).

Pharmacological studies have also evaluated if schedule-induced drinking can serve as an animal model of compulsivity and have suggested that induced behaviors may have common features with compulsive behavior in humans. This approach has tested the efficacy of drugs normally used to treat compulsive symptoms that involve the serotonergic system. Thereby, the use of antidepressants (i.e., selective serotonin reuptake

inhibitors and serotonin receptor agonists) decreases the amount/frequency of schedule-induced drinking (see Moreno and Flores 2012).

## Conclusion

Schedule-induced behavior refers to behavior that is induced by schedules of reinforcement in which there is not experimentally arranged contingency between occurrence of behavior and occurrence of reinforcer. This is why it was initially called adjunctive behavior, or even collateral behavior, but today schedule-induced behavior refers to the process by which schedules of reinforcement induce behavior that is evolutionary relevant to its obtention, thus setting the conditions for its subsequent strength by (correlation with) reinforcement.

## Cross-References

- Acquisition
- Activity-Based Anorexia
- Animal Models
- B.F. Skinner
- Behavior Systems
- Classical Conditioning
- Comparative Psychology
- Competition
- Contingency
- Corticosterone
- Dopamine Receptor
- Environmental Influences
- Goal-Directed Behavior
- Hypothalamus
- J.E.R. Staddon
- Laboratory Research
- Learning
- Motivation
- Negative Reinforcement
- Neuroanatomical Plasticity
- Neurotransmitters
- Operant Conditioning
- Parsimony
- Pituitary Gland
- Positive Reinforcement

- Reinforcement
- Schedules of Reinforcement
- Serotonin
- Species-Specific Behavior
- Stress
- Thyroid and Adrenal Glands

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## Schedules of Reinforcement

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### Synonyms

[Instrumental conditioning](#); [Operant conditioning](#);  
[Reinforcement](#)

### Definition

A reinforcer is a stimulus that serves to maintain or increase the future probability of the behavior on which it is contingent. The term *schedule of reinforcement* denotes a particular method of reinforcing behavior. A variety of schedules of reinforcement exist, and each has unique effects on behavior.

### Introduction

In 1930, B. F. Skinner, then a graduate student at Harvard University, devised an experimental chamber to study conditioning in rats. Rats placed in this chamber learned to depress a lever which caused a food pellet to be delivered from an external magazine. The apparatus, known formerly as an operant chamber and colloquially as a Skinner box, helped launch a new era of behavioral research (Bjork 1993). An advantage of the method was that it permitted an extended sequence of behavior to be observed that was free of outside interference (Skinner termed this free-operant behavior). By comparison, most experiments on learning at the time consisted of a series of discrete trials, and the researcher was

required to reset conditions between each trial. Most importantly, Skinner found that the acquisition and subsequent patterning of the response to be orderly, which meant that the apparatus could be used to carry out a systematic examination of the factors controlling operant conditioning.

Initially, the effect of schedules of reinforcement did not concern Skinner. He first used an intermittent schedule of reinforcement as a way of conserving food pellets when his supply was low. He discovered not only that responding persisted but that the cumulative records obtained during partial reinforcement differed from those obtained under continuous reinforcement. Skinner soon realized that a variety of intermittent reinforcement schedules were possible and that each might shed light on response-reinforcement relations. Therefore, he began to make schedules of reinforcement a major focus of his research (Morgan 2010; Skinner 1956). The first major publication describing schedules of reinforcement was *The Behavior of Organisms* (1938), which was followed by Charles Ferster's and B. F. Skinner's seminal *Schedules of Reinforcement* (1957). Much of the work conducted by Skinner and colleagues involved defining various types of intermittent schedules of reinforcement, describing the performance each schedule characteristically produced, and manipulating different aspects of the task so as to reveal the key factors controlling performance. The discovery of the variables controlling schedule performance led eventually to the development of formal theories of schedule of reinforcement.

### Methods Used in Schedule Research

The operant chamber used in schedule research includes, at a minimum, a means by which multiple responses can be emitted, and multiple reinforcers obtained, without researcher assistance. Data collection commonly occurs under conditions that minimize external stimulation. For example, the chamber may be placed inside a sound-attenuating chest, and/or a white-noise generator may be used to help mask external sounds. To further create a high degree of



experimental control, the timing of feedings and the amount of food provided to subjects outside of the experiment are carefully controlled so as to keep constant the efficacy of the reinforcer. Each successive reinforcer obtained during data collection may reduce somewhat the efficacy of the next available reinforcer; therefore each reinforcer is typically small, and the number of reinforcers which subjects can obtain during a session is limited.

In Skinner's original research, the sound made by the mechanical operation of the pellet dispenser signaled to subjects that reinforcement was being delivered. Since then it has become commonplace to include lights and/or speakers in an operant chamber, so as to allow the researcher to signal in other ways the moment when a response produces reinforcement. Lights and tones are also commonly used to signal changes in the conditions of reinforcement (e.g., a transition from reinforcement to extinction or a transition from one schedule to another).

A majority of research on schedules of reinforcement has been conducted with pigeons and rats. For pigeons, it is typical for the response to be a key peck and the reinforcer to be brief access to a tray of birdseed. For rats, it is typical for the response to be a lever press and the reinforcer to be a food pellet. However, other responses and reinforcers have been used with rats and pigeons, and schedule research has also been conducted with humans and many other species of non-humans (e.g., fish, octopi, horses, and insects). Skinner (1956) famously presented nearly identical cumulative records obtained from several species and asked, "Pigeon, rat, monkey, which is which?" before suggesting "It doesn't matter" owing to the similar ways in which the environment acts on the behavior of different organisms. Since then a more nuanced view of the importance of general learning processes has been adopted by schedule researchers (e.g., Timberlake 2001).

The analysis of performances under schedules of reinforcement typically focuses on steady-state behavior, which emerges when subjects have fully adapted to the conditions of reinforcement. In

other words, a point is reached in subjects' training when additional observations will not reveal additional changes in behavior.

The results of early research on schedules of reinforcement were examined primarily through a visual analysis of the cumulative records created during data collection (cf. Lattal 2004). A cumulative record is a real-time, graphical representation of the responses and reinforcers generated during an experimental session. The records are made by a cumulative recorder, which includes a paper scroll that slowly unwinds with the passage of time, and a pen which moves each time a response is emitted and which also marks each time reinforcement is delivered. It was from cumulative records that Skinner was able to demonstrate that different response patterns typify each schedule of reinforcement, how those patterns first emerge in naïve subjects, and what transitional responding looks like when the contingencies are altered.

Cumulative records were long mainstays of research on schedules of reinforcement, but their use has become less common. One reason for the change is that researchers began using computers to precisely time and record each response emitted during the session, which allowed for a more precise and more molecular examination of schedule performances than permitted by cumulative records. Another reason is that behavior analysts have come to be less reliant on visual analyses of data; instead, group-statistical designs and inferential statistical tests are increasingly in use.

## Basic Types of Schedules

Because a schedule of reinforcement describes any rule by which reinforcers correspond to behavior, the number of potential schedules of reinforcement is very large. However, Skinner and colleagues devised a relatively restricted set of terminology for describing schedules as a way to simplify the discussion. The terminology they used also helped call attention to those variations in the environment that may be most helpful in understanding how reinforcement changes behavior.

## Continuous vs. Intermittent Reinforcement

A **continuous schedule of reinforcement** is one in which every response is followed by reinforcement; for this reason, it is arguably the simplest possible schedule. An **intermittent (or partial) schedule of reinforcement** is one in which only some responses are reinforced. Many different factors can make a schedule of reinforcement “intermittent,” and this gave rise to the distinctions among schedules of reinforcement described below.

Continuous schedules of reinforcement are known to create a high rate of responding and rapid behavioral change, and they are often used in at least the early stages of behavioral change interventions. (However, it is commonplace to later transition to an increasingly intermittent schedule so as to help shift control over the behavior from the intervention to other, naturally occurring reinforcement contingencies.) Intermittent schedules are also capable of producing a high rate of responding, but this often does not occur when the schedule is first introduced.

Extinction of responding is more rapid after reinforcement is withdrawn from subjects trained on a continuous basis than on an intermittent basis. The discovery that the persistence of responding during extinction should be inversely related to the frequency of reinforcement obtained during training seems counterintuitive. A common explanation for this finding is that it is easier for subjects to discriminate conditions of reinforcement from conditions of extinction when reinforcement is provided on a continuous schedule than when it is provided on an intermittent schedule (Mowrer and Jones 1945).

## The Four Basic Schedules of Reinforcement

B. F. Skinner made four intermittent schedules of reinforcement a particular focus of his research, and they are regarded today as the four basic schedules of reinforcement. They are the fixed-ratio (FR), the variable-ratio (VR), the fixed-interval (FI), and the variable-interval (VI) schedules of reinforcement.

A **fixed-ratio schedule of reinforcement** is one in which reinforcement is obtained by completing a certain number of responses, and the number of responses necessary to obtain a reinforcer is kept constant. The term “ratio” specifically refers to the ratio of responses to reinforcers. For example, under a FR 10 schedule of reinforcement, the ratio of responses to reinforcers would be 10:1, meaning that subjects would obtain reinforcement every time they emit 10 responses.

Performances under fixed-ratio schedules are characterized by what has been termed a “break-and-run” pattern of behavior. That is, subjects often do not initiate responding at the first opportunity; instead, there is first a period of time without responses that is then followed by a relatively rapid and sustained period of responding that culminates in the delivery of reinforcement. The initial period without responding has been referred to as a postreinforcement pause or as a preratio pause. The initial pause is not required by the contingencies and is of questionable benefit to subjects; therefore some researchers have suggested that pausing on fixed-ratio schedules of reinforcement may serve as an animal model of procrastination (Schlinger et al. 2008).

The duration of the pause is sensitive to the exact contingencies of reinforcement. Under relatively favorable conditions (e.g., the ratio is low), a pause before responding may be difficult to discern. However, when the ratio of responding to reinforcement is high, or the magnitude of the reinforcer is small, pauses may be of considerable duration. When subjects transition from a lower ratio to a higher ratio, or are maintained on a very high ratio of reinforcement, breaks in responding may repeatedly occur after responding on a given ratio has been initiated, creating a pattern known as “ratio strain.”

A **variable-ratio schedule of reinforcement** is one in which reinforcement is obtained by completing a certain number of responses, but the number of responses necessary to obtain reinforcement varies from reinforcer to reinforcer. The exact ratios used in each session are preplanned so that the researcher can control the mean response-reinforcement ratio (e.g., VR 10).

Performances under variable-ratio schedules are similar to those of fixed-ratio schedules in that a break-and-run response pattern may be observed. However, it's more frequently the case that the pause on a variable-ratio cumulative record is difficult to discern, and pause durations at a given variable ratio are usually shorter than those under an equivalent fixed ratio. Variable-ratio schedules are similar to fixed-ratio schedules in that pause durations increase when the ratio size is raised or the magnitude of the reinforcer is lowered. Additionally, however, variable-ratio pause durations are sensitive to the lowest ratio used during the session. For example, pause durations tend to be quite brief if sometimes a single response suffices to produce reinforcement (Blakely and Schlinger 1988).

A **fixed-interval schedule of reinforcement** is one in which reinforcement is obtained by emitting a response after a certain interval of time has elapsed. For example, under a FI 30 s schedule of reinforcement, a response emitted at least 30 s after the start of the interval would produce reinforcement; any earlier responses have no effect.

Performances under fixed-interval schedules are traditionally characterized as following a “scallop”-shaped pattern in that the rate of responding is low during the first part of the interval, but it begins to accelerate with the passage of time. However, scalloping is not evitable, and on many individual intervals, a break-and-run pattern appears instead (Dews 1978). Although fixed-ratio and fixed-interval schedules may share a tendency to create a break-and-run response pattern, in the former case the initial pause confers no obvious benefit, while in the latter case, the pause appears to reduce the number of unreinforced responses. Pause durations under fixed-interval schedules increase as a function of the interval duration. Pause durations are especially pronounced when the schedule is accompanied by a “clock” that signals the passage of time during the interval (Ferster and Skinner 1957).

One of the most striking findings from research with fixed-interval schedules is the propensity for subjects to repeatedly perform, in a stereotyped manner, some nonscheduled behavior during the interreinforcement interval. For example, if water

is made freely available during the session, then subjects may drink excessive amounts (polydipsia), or if another subject is present during the session, then it may be subjected to repeated attacks. Collectively, these corollaries of periodic reinforcement are known as adjunctive behavior (Falk 1971). Adjunctive behavior is more pronounced under fixed-interval schedules than on the other three basic schedules of reinforcement, but it has been observed to sometimes occur under fixed-ratio and variable-interval schedules.

A **variable-interval schedule of reinforcement** is one in which reinforcement is obtained by emitting a response after a certain interval of time has elapsed, but the period of time that must elapse before reinforcement can be obtained varies from interval to interval. As is the case with variable-ratio schedules, the duration of each of the intervals used during a session is preplanned so that the researcher can control the exact mean interval (e.g., VI 30 s).

Performances under variable-interval schedules are characterized by a relatively slow rate of responding that is maintained fairly evenly during the interval. The exact rate of responding is negatively correlated with the mean duration of the interval.

Fixed- and variable-interval schedules are sometimes combined with a “limited hold” requirement; under this arrangement, subjects have a limited period of time to emit a response after the interval ends before the opportunity to obtain reinforcement is lost. If the limited hold period ends without reinforcement, a new interval begins.

## Variables Affecting Schedule Performance

Performances under a given schedule of reinforcement are affected not only by the reinforcement contingency defined by the schedule but also by a host of other factors. Some of the variables affecting schedule performance pertain to manipulations that precede data collection on a given schedule. For example, when food is used as a reinforcer, performances vary with the level of

food deprivation used before data collection begins. Performances on one schedule of reinforcement may also depend on subjects' prior history with other schedules of reinforcement (e.g., Wanchisen et al. 1998). The performances of human participants are sensitive to how the schedule is described. For example, if participants are told that one schedule of reinforcement is in effect, when in actuality reinforcement is provided on a different basis, then the verbal description may gain ascendancy over the pattern of responding (Baron and Galizio 1983).

Researchers have considerable latitude over how a given schedule of reinforcement is carried out, and the specific parameters they set may have a considerable influence on behavior. For instance, performances vary with the specific ratio size or interval duration, with the quality and magnitude of the reinforcer, and with the amount of effort required to emit the response. Researchers may also choose to adjust the schedule by imposing a delay to reinforcement after the schedule is completed or by providing reinforcement on only a percentage of schedules. Performances are also affected by the addition of stimuli that accompany each response on a ratio schedule or that mark the passage of time on an interval schedule (Ferster and Skinner 1957).

Variations in the use of a given schedule of reinforcement allow researchers to more fully characterize how the schedule controls behavior, aids in the development of mathematical models of schedule performance, and better enables researchers to relate basic research to the variety of reinforcing contingencies that are present in the natural environment. However, some of the variables controlling schedule performances are difficult to deduce from manipulating schedule parameters and examining schedule performances. For example, fixed ratio and fixed interval produce different patterns of responding, but it is difficult to disentangle the roles that the contingency of reinforcement and the frequency of reinforcement have in creating this difference. Sometimes a more substantial departure from the usual methods is required; one solution is to use a **yoked schedule of reinforcement** in which performances on one schedule of reinforcement are

used to set conditions on a second schedule. In this instance, the interreinforcement interval obtained by one set of subjects on a fixed-ratio schedule may be used to select the duration of the fixed-interval schedule for a second set of subjects; in this way, the frequency of reinforcement is held constant, while the reinforcement contingency is allowed to vary (Killeen 1969).

## Other Simple Schedules of Reinforcement

The four simple schedules of reinforcement provide researchers with a mean of examining the effects of two basic distinctions involving the contingencies of reinforcement: whether reinforcement principally relates to work (ratio schedules) or time (interval schedules) and whether the exact work or time requirement is predictable (fixed schedules) or unpredictable (variable schedules). In addition to the four basic schedules of reinforcement, several other "simple" schedules of reinforcement may be recognized in that they feature a single rule that determines how reinforcement is obtained. (In other respects, such as how quickly steady-state behavior is obtained, "simple" schedules may differ considerably from each other.)

A variant to the ratio schedules described above is a **progressive-ratio schedule of reinforcement**. In this case, each ratio the subject completes is followed by a higher ratio. For example, each ratio might increase in steps of 5, beginning with a ratio of 5. Subjects therefore would be required to emit 5 responses for the first reinforcer, 10 responses for the second reinforcer, 15 responses for the third, etc. Progressive-ratio schedule sessions eventually end when the ratio becomes too high to support further responding; the final ratio subjects complete is known as the break point (or breaking point). Subjects are expected to be more persistent in responding (i.e., complete more ratios and reach a higher break point) when the reinforcer is particularly efficacious. For this reason, progressive-ratio schedules have been used widely in behavioral pharmacology as a way of measuring subjects'

motivation to obtain a particular drug, both under ordinary conditions of reinforcement and when a method of curbing the reinforcing properties of a drug is tested (Stafford et al. 1998). A related procedure is a **progressive-interval schedule of reinforcement**, in which the duration of the interval increases after every reinforcer.

Another ratio schedule is the **random-ratio schedule of reinforcement**. In this case, every response has a certain probability of reinforcement. For example, under a random-ratio 20 schedule, each response has a 5% probability of producing reinforcement). Like variable-ratio schedules, random-ratio schedules are both work-based and unpredictable. As a result, performances under the two schedules can be similar (Crossman et al. 1987). However, reinforcement under a random-ratio schedule is more truly unpredictable, and it has therefore been used repeatedly in research concerned with behavior under gambling-like conditions (e.g., Haw 2008). A related procedure is a **random-interval schedule of reinforcement**, in which the interval has a certain probability of ending every time a certain duration of time passes. For example, under a random-interval 4-min schedule, there may be after every 4 s a 1/60 probability that the interval will elapse, allowing a response to be reinforced (Millenson 1963).

A duration-based schedule of reinforcement is one in which reinforcement is based on the duration of a response (or responses) rather than on the number of responses. For example, rats might be required to hold down a lever for 10 s to obtain reinforcement. Reinforcement might be obtained after the subject emits several responses that have a collective duration of 10 s or after a single response that lasts 10 s. (In some versions of the procedure, responses shorter than the scheduled duration do not contribute to reinforcement and instead cause the criterion to reset.) In line with other basic schedules, the reinforcement contingency may involve a **fixed-duration schedule**, a **variable-duration schedule**, a **random-duration schedule**, or a **progressive-duration schedule** (cf. Valois et al. 2017).

Under a **fixed-time schedule of reinforcement**, reinforcement is delivered after a certain

period of time has elapsed. Unlike a fixed-interval schedule, subjects obtain reinforcement without emitting a response. In other words, reinforcement is not contingent on behavior. A **variable-time schedule of reinforcement** is similar, except in this case the period of time between reinforcement deliveries is not constant. B. F. Skinner (1948) demonstrated that subjects placed on a fixed-time schedule of reinforcement may begin to exhibit stereotyped response patterns during the interreinforcement interval that appear to be consistent with superstitious behavior in people; however, this interpretation has been challenged, and it has been suggested that the appearance of stereotyped response patterns under a fixed-time schedule is better understood from the standpoint of adjunctive behavior (cf. Staddon and Simmelhag 1971).

Certain patterns of behavior are associated with each schedule of reinforcement because those patterns tend to maximize reinforcement gain while minimizing the effort expended. However, subjects are still able to obtain reinforcement when a nonoptimal pattern of responding occurs, which allows performances under a given schedule to be variable. Two schedules make reinforcement directly dependent upon the rate of responding. Under a **differential reinforcement of low rate of responding (DRL) schedule**, the first response emitted after a certain period of time has elapsed is reinforced, but, unlike an interval schedule of reinforcement, responses emitted before the period has elapsed cause the timer to reset. In other words, DRL schedules require subjects to respond at a slow, steady rate. DRL schedules are most commonly used in applications designed to reduce, but not eliminate the frequency of a behavior. Alternatively, a **differential reinforcement of high rate of responding (DRH) schedule** may be used to create rapid responding. In this case, reinforcement depends on subjects emitting a response that satisfies a criterion for short interresponse times (e.g., to obtain reinforcement, one response must be emitted within .5 s of the previous response). In some cases, the criterion is extended to include the interresponse times for multiple responses (i.e., a



series of responses must be emitted within a specified period).

Other differential reinforcement schedules have been used most prominently in applied research (cf. Miltenberger 2015). In the case of a **differential reinforcement of alternative behavior (DRA) schedule**, a target behavior is placed on extinction, while an alternative, but normally less probable, response is made to produce reinforcement. In the case of a **differential reinforcement of other behavior (DRO) schedule**, the target behavior is again placed on extinction, and any other behavior produces reinforcement.

A **lag schedule of reinforcement** is used to promote response variability. In this case, the apparatus must permit more than one response to be made. Reinforcement depends on emitting a response, or in some cases, a response sequence, which differs from previous responses or response sequences (e.g., Lee et al. 2002).

## Combining Schedules of Reinforcement

Simple schedules of reinforcement can be regarded as representations of how basic contingencies of reinforcement alter behavior. Behavior analytic researchers have likened the contingencies present in simple schedules to “building blocks,” which, when combined with each other, give rise to the more complex contingencies found in conjunction with many natural forms of behavior (Zeiler 1984). As a step toward understanding how complex contingencies of reinforcement operate, researchers have examined the effects on behavior of combining two or more simple schedules of reinforcement in some manner. The different schedules might be presented to subjects at different times, or they might be presented simultaneously to subjects. The different schedules might operate independently of each other, or responses on one schedule may affect how reinforcement is obtained on the other. The different schedules may share a single response, or each might be associated with a different response. Finally, the different schedules might be accompanied by distinct discriminative stimuli, or variations in the contingencies might be unsignaled.

There is no single framework for classifying complex arrangements of schedules. Combinations of schedules are grouped below into three categories: cases in which simple schedules alternate, cases in which subjects can choose between simultaneously available schedules, and cases in which a compound schedule is created from two simple schedules.

## Alternating Simple Schedules

One way of combining schedules of reinforcement is to alternate which schedule of reinforcement is in effect throughout the session. Under a **mixed schedule of reinforcement**, two or more schedules of reinforcement are presented at different times, such that when one schedule of reinforcement is completed, another, different schedule of reinforcement may be introduced. For example, a session may be composed of a mixture of FR 20 and FR 40 schedules (i.e., a mixed FR 20 FR 40 schedule). This specific instance creates an intermediary between a FR and VR schedule of reinforcement in that the response requirement is not constant, but the variation is limited. A **multiple schedule of reinforcement** is similar to a mixed schedule, but in this case each of the two or more schedules used during the session is accompanied by a distinct stimulus. Performances under multiple schedules of reinforcement have shown that performances under one schedule of reinforcement depend on how relatively favorable the conditions of reinforcement are compared to another schedule of reinforcement. For example, pause durations are longer when a subject switches during a session from a low to high fixed ratio than when subjects complete two consecutive high fixed ratios (e.g., Baron and Herpolsheimer 1999).

A **tandem schedule of reinforcement** also involves an alternation of simple schedules during a session, but in this case two or more schedules are consistently presented in a regular sequence, and reinforcement is delivered only after the final schedule in the sequence is completed. For example, under a tandem FI 10 s, FI 30 s schedule of reinforcement, completion of the first (FI 10 s)

schedule causes the second (FI 30 s) schedule to begin, and completion of the second schedule leads to food reinforcement. Under tandem schedules of reinforcement, the change from one schedule of reinforcement to another is unsignaled. By comparison, under a **chained schedule of reinforcement**, each of the two or more schedules comprising the sequence is accompanied by a separate discriminative stimulus.

## Schedules of Reinforcement Used to Study Choice

A **concurrent schedule of reinforcement** is one in which two or more schedules of reinforcement are available simultaneously to subjects, and each schedule is associated with a different response. For example, a pigeon may be placed in an operant chamber that includes one key for which responses are reinforced according to a FR 10 schedule of reinforcement and another for which responses are reinforced according to a FI 30 s schedule. Subjects are not required to respond on both schedules, but there is an opportunity to maximize reinforcement by responding on the FR 10 schedule during the first part of the 30 s interval and then respond on the fixed-interval schedule when the interval nears completion.

Research with concurrent schedules of reinforcement most commonly employs concurrent VI VI schedules. Under this arrangement responding on either schedule may be reinforced at any time, but reinforcement is maximized by matching the choice for a given schedule to the relative frequency with which those responses are reinforced (this relation is formally encapsulated in the matching law; Herrnstein 1961). For example, under a concurrent VI 30 s VI 60 s schedule of reinforcement, subjects are able to obtain twice as many reinforcers from the VI 30 s schedule as they are from the VI 60 s schedule; therefore reinforcement is maximized by making twice as many VI 30 s schedule responses as VI 60 s schedule responses. Research with concurrent VI VI schedules has shown that humans and non-humans are adept at matching and that matching

is a characteristic of naturally occurring human behavior (e.g., Vollmer and Bourret 2000).

A **concurrent chains schedule of reinforcement** is one in which two chained schedules of reinforcement are available simultaneously to subjects. That is, a discriminative stimulus associated with the initial link in each chain is presented in conjunction with each simultaneously available response. Once subjects begin to respond on one chain, the other becomes inoperable, forcing the selected chained schedule to be completed. In this way, a concurrent chains schedule of reinforcement extends the study of choice to a more complex and temporally extended reinforcement contingency than (simple) concurrent schedules – one which includes both immediately present conditioned reinforcers and delayed primary reinforcers.

## Compound Schedules of Reinforcement

Compound schedules of reinforcement include two or more schedules that are simultaneously in operation and which share a single response.

In the case of a **conjoint (or superimposed) schedule of reinforcement**, subjects' responses simultaneously contribute to reinforcement on two separate schedules. For example, if a FR 5 schedule were to be superimposed on a FI 20 s schedule, then reinforcement would be obtained both for every fifth response and for every response emitted after 20 s have elapsed. If a fixed-time schedule were to be superimposed on a fixed-interval schedule, then subjects would have access to both response-dependent and response-independent reinforcers. A similar method is an **alternative schedule of reinforcement**. In this case, two or more schedules are again simultaneously in effect with a single response, but once reinforcement is obtained on one schedule, progress toward the other schedule is reset. Thus, under an alternative FR 5 FI 20 s schedule of reinforcement, subjects might obtain all reinforcement from the FR 5 schedule, all reinforcement from the FI 20 s schedule, or a mixture of reinforcement from the two schedules,

depending on how frequently each contingency is met.

Under a **conjunctive schedule of reinforcement**, two separate schedule requirements must be met before a response is reinforced. For example, when a conjunctive FR 5 FI 20 s schedule is in effect, reinforcement depends both on emitting five responses and on making a response after 20 s have elapsed. The two components to the conjunctive schedule may be satisfied in any order. An **interlocking schedule of reinforcement** combines a response-based criterion with a time-based criterion in a variable manner. Specifically, a certain number of responses must be emitted to obtain reinforcement, but the response requirement decreases with the passage of time. For example, under a conjunctive FR 10 FI 30 s schedule, subjects are required to emit 10 responses to obtain reinforcement at the beginning of the schedule, but as time passes, the number of responses required for reinforcement decreases until after 30 s have passed a single response suffices to produce reinforcement. How the response requirement changes over time can be varied. When the response requirement decreases slowly over time, performances on an interlocking schedule more closely resemble those typically obtained with a ratio schedule of reinforcement; when the response requirement decreases rapidly, performances more closely resemble those of an interval schedule.

Under a **higher-order (or second-order) schedule of reinforcement**, the completion of one schedule is treated as a response that is reinforced according to a second schedule. A stimulus change occurs each time the first schedule is completed, which serves as a conditioned reinforcer in that it marks progress toward completion of the second (higher-order) schedule. Primary reinforcement is obtained only after the second schedule is complete. For example, if the first schedule is FI 5 min, and the second schedule is FR 10, then subjects obtain reinforcement after every tenth FI 5 min schedule (Kelleher and Goldberg 1977). Higher-order schedules are designed to allow an extended observation of behavior to occur while subjects receive few reinforcements; they are used especially in the study

of behavioral pharmacology to help separate the reinforcing effects of drugs from other behavioral effects drugs may induce (cf. Di Ciano and Everitt 2005).

## Uses of Schedules of Reinforcement in Research

Schedules of reinforcement are an enduring and pervasive feature of research in the field of behavior analysis because schedule research serves a variety of purposes. Schedules of reinforcement shed light on how reinforcement affects learning and behavior and has provided researchers with a way to examine the effects of variations in reinforcement (e.g., positive reinforcement vs. negative reinforcement, primary reinforcement vs. conditioned reinforcement, immediate reinforcement vs. delayed reinforcement). Schedules of reinforcement are also essential tools in research on other behavioral phenomena, including extinction, stimulus generalization, contrast effects, verbal behavior and rule-governed learning, foraging, choice, gambling, addiction, self-control, animal cognition, behavioral economics, creativity, avoidance, and learned helplessness, to name some examples. Although a schedule of reinforcement is normally thought of as a rule that determines how responses are reinforced, schedules may also be used to help researchers conceptualize and describe the ways in which behavior leads to reinforcement in the natural environment. For example, the behavior of checking an inbox for new email messages may be likened to a variable-interval schedule of reinforcement, or complex behavior that involves a series of steps may be likened to a chained schedule of reinforcement.

Outside of basic research on learning, schedules of reinforcement are used in applied research on behavioral change interventions. Because schedules of reinforcement have predictable behavioral effects, schedule research provides guidance as to how a particular form of behavioral change can be accomplished. Other common uses of schedules of reinforcement in research include the use of schedules of reinforcement as

behavioral baselines for assessing drug effects in studies of behavioral pharmacology and the use of schedules of reinforcement to assess gene effects in studies of behavioral genetics.

## Cross-References

- [B.F. Skinner](#)
- [Behavioral Genetics](#)
- [Behaviorism](#)
- [Contingency](#)
- [Delay of Reinforcement](#)
- [Discrimination Learning](#)
- [Extinction in Learning](#)
- [Instrumental Learning](#)
- [Learning](#)
- [Negative Reinforcement](#)
- [Operant Conditioning](#)
- [Positive Reinforcement](#)
- [Skinner Box](#)
- [Timing](#)

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## Schooling

### ► Learning

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## Scramble Competition Polygyny

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### Definitions

Scramble competition polygyny is a form of competition among males of species that occurs when resources or mates are not defensible (i.e., not able to be monopolized), thus individual males compete for access to females in a population.

### Introduction

Species must be flexible in their reproductive strategies to persist and maximize fitness contributions in resource-restricted environments. Thus, a wide variety of mating systems have evolved, including polygynous behavior where males obtain multiple female mates. When resources or female mates are not defensible, males of some species will compete for direct access to females in a form of scramble competition. When males compete for access to

multiple females, scramble competition polygyny occurs.

## Scramble Competition Polygyny Life History Strategy

Polygyny is a mating system in which a male will mate with multiple females to maximize his reproductive potential. Scramble competition polygyny is a variation of polygynous behavior that arises in environments where resources or mates are limited and/or distributed in a manner that prevents securing or defending a territory or individual female mates during the breeding period. Sexual selection in the form of mate choice is a component of this particular mating system, which includes a “scramble” among males to search for and gain access to female mates, and a preference by females for males with greater mate searching capacity.

Scramble competition can take many forms, including variation in home range size, short-term guarding of mates, as well as energetic expenditure as males move around to gain access to females. The wide variety of behaviors that can be characterized by scramble competition have therefore been the focus of several studies in an effort to understand behavioral mechanisms, as well as the net fitness outcomes in different species (Kappeler 1997). For example, male gray mouse lemurs (*Microcebus murinus*) have been shown to increase home range size over time during the mating season, indicating the occurrence of scramble competition as males search for available female mates (Radespiel 2000). Energetic costs of male North American red squirrels (*Tamiasciurus hudsonicus*) have also been shown to be very high as a result of scramble competition. Thus, food and resource availability during the breeding period may limit reproductive success in males of this species, if energetic demands cannot be met (Lane et al. 2010). However, these energetic demands were only shown to occur during circumstances of intensified investment in males and did not persist throughout the year. These particular studies assist researchers in understanding the complexity of how resource



availability can determine the effects of scramble competition polygyny.

Researchers have also assessed scramble competition polygynous mating systems in gopher tortoises (*Gopherus polyphemus*; Johnson et al. 2009), some amphibian and fish species (e.g., Miranda et al. 2008), fiddler crabs (*Uca paradossumieri*), and many mammals and insects (e.g., Dickinson 1992). In one study by Murai et al. (2002), researchers observed scramble competition polygynous behavior in fiddler crabs during the mating season. Upon finding an ovulating female, the male fiddler crab quickly mate with the female, then guard her for a period of time before departing in search of another female. In this case, the sequence of events that included searching, guarding, and searching again for a mate represents scramble competition, and males may fertilize multiple females during this time. Throughout the courtship period, the male crabs became quite aggressive toward other males. Females will lay a clutch of eggs inseminated by the guarding male but have also been shown to mate with multiple males – potentially reflecting an ambisexual polygamous mating strategy across both sexes in addition to scramble competition.

Some desert tarantula (*Aphonopelma spp.*) species also display discrete courtship strategies associated with scramble competition polygyny but limited instances of male-male aggression or mate guarding (Shillington and Verrell 1997). Courtship can occur in rapid succession in these tarantula species, with multiple males in a “scramble” to reproduce with as many receptive females as plausible. Sphecids wasps (*Palmodes praestans*) also show evidence of nonterritorial patrolling and scramble-competition to seek out isolated nests of females (Alcock and Kemp 2005). Thus, reproductive success in these invertebrate species depends wholly on the male’s ability to search for, locate, and reproduce with as many females as energetically possible.

## Conclusion

Many species engage in some form of competition to enable them to survive and reproduce, with the

intent of maximizing the passing of genes to their offspring. Scramble competition polygyny is studied in various animal populations to understand the interactions of how this mating system may maximize fitness in both males and females. For researchers, scramble competition polygyny is an important component of some species’ life history and can aid in understanding of the complexities of competition and resource availability.

## Cross-References

- [Competition](#)
- [Fitness](#)
- [Home Range](#)
- [Mating](#)
- [Mating Effort](#)
- [Polygamy](#)
- [Polygyny](#)
- [Reproduction](#)
- [Reproductive Fitness](#)
- [Scramble Defense Polygyny](#)
- [Sexual Selection](#)

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## Scramble Defense Polygyny

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## Synonyms

Defense polygyny; Scramble competition polygyny; Scramble polygyny

## Definition

Polygyny is a mating strategy through which a single male secures or attempts to mate with more than one female during a breeding period to optimize reproductive success. Scramble polygyny is one tactic taken by males whereby an individual attempts to secure as many female mates in a given area at a given time through a competitive searching approach. Defense polygyny involves behaviors that attempt to control access to females or resources required by females through territoriality. Thus scramble defense polygyny, though ill-defined as a concept, may represent a combination of nondefense scramble behavior and defense behavior in males to obtain a maximum number of female mates.

## Introduction

Males and females of many species exhibit flexible mating strategies to optimize reproduction under a variety of conditions. These strategies taken together comprise a species' mating system. Polygyny occurs when a male of a species mates with multiple females during a breeding season. Polygyny is thought to be the most common mating strategy in mammals (Clutton-Brock 1989) but is prevalent in many other taxa as well. Within the scope of polygynous behavior, males may exhibit a suite of tactics to mate with as many females as biologically reasonable given availability of receptive females in the area. However, ability to mate with multiple females may be constrained by factors of resource availability, energy requirements, and competition with other males. The polygynous mating strategy is thus a trade-off among the benefits of securing multiple female mates with little to no parental care required vs. the costs of competition and defense. One strategy involves either direct defense of females by males or, more commonly, defense of resources required by females through territoriality to secure successful copulations with multiple mates – hence the term “defense polygyny.” On the contrary, scramble polygyny is a form of non-defense polygyny whereby males partake in competitive searching for a maximum of female mates. There is no definitive defense of resources or mates in scramble competition, and this reproductive success is determined by which male can cover the greatest area and has the greatest skill in locating receptive females prior to other males. Success, in the case of scramble competition, is directly related to movement and search behavior, as well as economics of energetics required to win access to females through exhaustive search efforts.

## Scramble Defense Strategy

Scramble defense polygyny is a largely ill-defined concept that likely reflects a flexible mating strategy where nondefense tactics, such as scramble competition behavior may be

combined with temporary defense tactics. The term “scramble defense polygyny” is rarely used and ambiguous, though mentioned in Lombardi (1998) where seemingly defined as synonymous with scramble competition polygyny. Thus, the term is in need of clarity in definition. The utility of this strategy, as defined here, is determined by the distribution of females, density of competing males, and plausibility of short-term defense tactics in an area during a given time. It is reasonable to assume that scramble defense polygyny will occur as a strategy when density of males, and thus competitors, is great enough that territorial or direct female defense is not economical. However, some level of defense, likely intermittent and sequential in nature, must take place as males temporarily defend females or territories to allow enough time for fertilization. Similar to Dobson’s (1984) “density-male hypothesis,” if male density is high in populations that are restricted in spatial distribution, nondefense polygynous behavior, plausibly scramble competition, will be the dominant strategy. When densities of males in this same population are relatively low, males will switch to defense polygyny and exhibit territorial behavior. Dobson tested this hypothesis in ground squirrel species and found it is not simply density of males dictating this behavior, but that female density and clumping (or dispersion) of female distributions and timing of receptivity also play an important role in mating tactics.

Male rodents, in particular, exhibit flexible mating strategies to secure female fertilization. This includes defense strategies as reviewed in Waterman (2007), including black-tailed prairie dog (*Cynomys ludovicianus*), yellow-bellied marmot (*Marmota flaviventris*), American porcupine (*Erethizon dorsatum*) several species of ground squirrel (*Spermophilus* spp.), and others. Some aspects of behavior in thirteen-lined ground squirrels (*ICTIDOMYS TRIDECIMLINEATUS*) have been linked to scramble defense polygyny whereby individuals will actively search for broadly distributed females and reproductive success is dependent on ability to access female mates,

which was influenced by spatial-memory of sites where female interaction had previously occurred (Schwagmeyer 1994).

## Conclusion

The optimum strategy for mating in most species is intricately tied to energetics and likelihood of reproductive success. Success in polygynous mating strategies is related to availability, distribution, and receptivity of females in a given area, as well as competition among other males for mates, and female or resource defense tactics. Scramble defense polygyny by definition should demonstrate elements of scramble, or competitive search behavior. However, it is unclear due to the mixed-use of the term in the literature whether it is synonymous with scramble competition, or a separate strategy that incorporates short-term or sequential defense tactics while engaging in competitive search behaviors. Scramble defense polygyny, as a discernable mating strategy, is in need of improved definition and differentiation from other strategies.

## Cross-References

- [Female Defense Polygyny](#)
- [Mating](#)
- [Resource Defense](#)
- [Resource Defense Polygyny](#)
- [Scramble Competition Polygyny](#)
- [Territory Defense](#)

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## Scramble Polygyny

### ► Scramble Defense Polygyny

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## Screamers

### ► Waterfowl

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## Sea Cow

### ► Sirenia Morphology

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## Sea Cow Ambulation

### ► Sirenia Locomotion

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## Search Image

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## Introduction

The expression “specific searching image,” usually shortened nowadays to “search image,” was popularized first by Jakob von Uexküll (1934) and later by Lukas Tinbergen (1960). It is typically used in the context of a predator deploying

selective attention for finding cryptic prey. “Searching” in front of “image” specifies that an individual is making a concentrated effort to detect and identify something in particular, and “effort” pertains to selective attention. Being a particularly demanding cognitive process, selective attention is subject to severe limitations (Dukas 2004), implying that selective attention will be deployed only after being primed in some fashion (Blough 1989) and also implying that, after priming, selective attention will be sustained for only a short time.

However, while “search image” may be a convenient, casual expression to use in the context of discussing selective attention, it has a history of being discussed in inconsistent and often confusing ways. Early on, Marian Dawkins (1971) suggested that the term had become too imprecise to be useful, but her advice went unheeded. The expression “search image” is still used and often it is still imprecise.

## von Uexküll and Tinbergen

In 1934, von Uexküll wrote of how, at dinner time, he was accustomed to finding a clay pitcher of water on the table in front of where he sat. However, when he went to pour himself a glass of water one day, he became flustered by not seeing the expected clay water pitcher. When he asked the butler where the water was, the butler confessed to breaking the clay pitcher, but pointed out that the water was there in plain sight where it should be, only now in a glass carafe. Reflecting on this experience, von Uexküll proposed that nonhuman animals use search images in ways that are similar to his water-pitcher anecdote. A core meaning that may have been behind his use of this expression is that “image” in “specific searching image” corresponds to what is now more often referred to as a “representation.” More specifically, this means that an individual has become selectively attentive to a stimulus corresponding to a particular representation.

With his search-image hypothesis, von Uexküll was being provocative because he appeared to be talking about animal cognition. In

his time, such talk would have been widely regarded as scientifically disreputable because, in those days, “animal cognition” was often automatically associated with the notion of animals having subjective experiences (Kennedy 1992). However, there is no obligation to take that step. It may be easy to imagine what it was like for von Uexküll in the water-pitcher story, and intuition derived from anecdotes can be useful as the rationale for hypotheses, but intuitions about subjective states are not themselves hypotheses that can explain anything.

It was primarily with Tinbergen (1960), rather than von Uexküll, that the expression “search image” became widely used in biology and especially in ecology (Bond 2007). Tinbergen’s field-based research, which took place in the Netherlands, began in 1946 and ended abruptly in 1955 with his untimely death at the age of 39 (Baerends and de Ruiter 1960). Five years later, his work was published posthumously (Tinbergen 1960) in a monograph that included his search-image hypothesis. Unlike von Uexküll, Tinbergen mobilized a massive amount of data as the rationale for his proposed hypothesis. These data came from meticulously recording the different types of insects that the birds he studied (tits) took back to their nests and fed to their chicks. He also estimated the relative abundance of the different types of insects in the field. Tinbergen’s data revealed that tits did not prey on the available salient insects in the environment at a rate corresponding to the relative abundance of the different prey. Instead, Tinbergen found a trend toward rarer prey being neglected and more common prey being over-selected.

On the basis of his field-sampling data, Tinbergen proposed that the birds in his field site were using specific searching images, and he also proposed that his birds, and predators in general, may use search images in a flexible manner. More specifically, Tinbergen proposed that a prey type more abundant at a given time becomes the predator’s search-image target and then, when this prey becomes less abundant, the predator switches to using a search image for targeting a different salient prey that has now become more abundant. This particular hypothesis has become especially

influential in ecology, where it is closely associated with a particular category of natural selection known as “negative frequency-dependent,” or “apostatic,” selection (i.e., owing to the predator, rare forms of the prey have greater fitness and more common forms have lesser fitness). Apostatic selection (rare-form advantage) is of particular interest because it may account for the maintenance of prey diversity and also explain the evolutionary origin of polymorphism within single populations of single prey species.

This is an impressive legacy, but some important distinctions need to be clear when discussing Tinbergen’s work. Tinbergen presented field-sampling data in support of a conclusion concerning negative frequency-dependent predation, and then he used this conclusion as the rationale for proposing a hypothesis, not a conclusion, that his birds were using specific searching images flexibly (i.e., he proposed, but did not demonstrate, search-image use combined with switching). Later, the distinction between negative frequency-dependent predation and search-image use was often overlooked. This is a nontrivial problem because search-image use is not the only viable explanation for the occurrence of negative frequency-dependent predation. Alternative explanations include reliance on an acquired preference (i.e., preference for familiar targets) and non-selective adjustment of searching effort (referred to as the “search-rate hypothesis” by Guilford and Dawkins 1987). Effects derived from search-image use and effects derived from other mechanisms can be distinguished from each other, but only with appropriately designed experiments (Zentall 2005).

### Experimental Evidence of Search-Image Use

When the goal is determining whether individuals are using specific searching images, experiments should include priming events followed by trials in which an individual’s capacity to detect and identify objects is tested (Kamil and Bond 2006; Langley 1996; Reid and Shettleworth 1992). The priming stimulus is often called a “cue” and the object to be identified during a trial is often called



a “target.” During experiments, it is important to vary the difficulty the subject will have (i.e., the required attentional effort) when attempting to detect and identify a target, with the expression “cryptic” being used when the target is more difficult to detect and identify and “conspicuous” being used when targets are easier to detect and identify. The rationale for the cryptic-conspicuous comparison is a prediction that the benefit the subject will derive from deploying selective attention will be especially pronounced when the target is cryptic (Dukas and Kamil 2000).

Some of the most elegant evidence of animals adopting specific searching images has come from experiments based on using photographic images of prey (Pietrewicz and Kamil 1979) and computer-generated digital (virtual) prey (Bond and Kamil 1999) as surrogates for living prey. As a major milestone, Bond and Kamil (2002) demonstrated experimentally that flexible search-image use by a predator can result in an initially monomorphic prey population becoming polymorphic. In these experiments, living predators (blue jays) searched for digital moths displayed on computer monitors and the prey populations evolved via a genetic algorithm. These were true evolutionary experiments happening in real time, not simulations.

## Learning to See

Tinbergen (1960) also found some especially evocative ways of characterizing what he meant by search-image use. For example, he called using a specific searching image “a highly selective sieving operation” (p. 332), which appears to be his way of acknowledging the role of selective attention (Broadbent 1958). He also proposed that, after discovering a particular type of prey, a predator can “learn to see” it. By “learn,” Tinbergen probably meant that a bird gradually assembles a template or prototype which is then deployed in the service of detecting and identifying a stimulus matching this prototype (Shettleworth 2010; Watanabe and Sasaki 2015).

Perhaps it is unsurprising that, after Tinbergen, it became conventional in search-image experiments to expose test subjects to a stimulus corresponding to a specific target not once but repeatedly. After all, this would appear to simulate the manner in which Tinbergen proposed that his birds gradually acquired representations (images) by learning. However, research using jumping spiders (family Salticidae), instead of birds, illustrates the importance of maintaining a sharp distinction between first demonstrating the use of search images by animals and then explaining the manner in which search images (representations) are acquired.

## Search-Image Use by Salticid Spiders

Being predators with exceptional proficiency at detecting and identifying prey by sight, salticids may be the spiders which most closely resemble birds, but with important practical differences. For example, ensuring that prior experience has been standardized tends to be a lot easier when salticids are used as experimental subjects. This is illustrated in experiments pertaining to search-image use by *Evarcha culicivora*, a salticid with an active innate preference for mosquitoes as prey. However, the details of these experiments (Cross and Jackson 2010a) differ strikingly from more familiar experiments on birds. Each test spider, for example, experienced only one exposure to a priming stimulus, and this single exposure was its only prior experience with this stimulus. Moreover, this single exposure was not accompanied by anything corresponding to conventional reinforcement.

The priming stimuli and the targets were lures made either from the preferred prey (mosquitoes) or from mates (opposite sex conspecific individuals). During the priming period, the test spider was inside a glass chamber from which it could see prey lures or mate lures (no lures were present during control trials). At the end of the priming period, the test spider was transferred to an arena where its task was to detect and identify a lure made from prey or a lure made from a mate, with

the lure being outside the transparent glass arena. This meant that, during experiments, *E. culicivora* could see, but not contact or smell, these priming stimuli and targets.

No priming effects were evident when the lures were conspicuous. However, when the lures were made “cryptic” by being covered with nylon netting and by adding distractors (cork discs) to the scene, more spiders found prey after being primed by seeing prey, and more spiders found mates after being primed by seeing mates.

### Using Specific Olfactory Searching Images

Tinbergen’s expression “learning to see,” along with “image” in “specific searching image,” may suggest that search-image use pertains solely to selective visual attention. However, this restriction is unwarranted because selective attention and representation are relevant irrespective of sensory modality (Spence and Driver 2004). For example, mammals (dogs and skunks) have been used in experimental studies aimed at detecting the use of olfactory search images (Gazit et al. 2005; Nams 1991, 1997), but, as no cryptic-conspicuous comparisons were included in these experiments, reliance on acquired preferences is a credible alternative explanation for the findings. Nams (1991) made the interesting suggestion that the cryptic-conspicuous distinction is clearly applicable only when the sensory modality is vision, but this is misleading because, in the context of selective-attention experiments, the cryptic-conspicuous distinction pertains to how attentionally challenging a task is to the animal irrespective of the sensory modality.

In an olfactory search-image study using *E. culicivora* (Cross and Jackson 2010b), target odor was made cryptic by using a masking odor from *Lantana camara*, a highly aromatic plant which *E. culicivora* is known to detect and respond to (Carvell et al. 2017). During priming, the test spider could smell, but not see or contact, mosquitoes or a mate (no odor source was

present in control trials). After priming, the test spider’s task was to find the source of the target odor (mosquito or mate), again with no opportunity to see or touch the odor source. Depending on the experiment, the target odor was either cryptic or conspicuous. Besides the presence of a masking odor in cryptic trials, the test spider had to pass through a “transition chamber” before it could get close to an odor source, the rationale being to make the source of the test odor even more difficult to find. In conspicuous trials, the transition chamber and masking odor were absent.

No priming effects were detected during conspicuous trials. However, in cryptic trials, more spiders found the source of mosquito odor after being primed by mosquito odor and more spiders found the source of mate odor after being primed by mate odor. The close similarity between these findings and the findings from the visual search-image study illustrates that the sensory modality is secondary: search images are fundamentally about selective attention.

### Trade-Offs

Tinbergen (1960) suggested that birds might make use of more than one search image at a time, but subsequent research has given very little support to this particular hypothesis. Instead, it is now widely accepted that, even for big animals such as birds and mammals, selective attention is subject to severe capacity limitations (Dukas 2004) and that these limitations will lead to impaired performance when an animal’s task is to find more than one kind of target in any given session (Langley 1996; Pietrewicz and Kamil 1979; Shettleworth 2010). These trade-off effects, in turn, are the basis for predictions which can be used for distinguishing between search-image use and either acquired preferences or nonselective increase in searching effort.

When considering these predictions, the distinction between congruent and incongruent priming is important. This is illustrated in the

search-image experiments using *E. culicivora* (Cross and Jackson 2010a, b). In these studies, the priming stimulus was either the same as the target during experimental trials (congruent) or different (incongruent), with no priming stimulus being used in control trials.

When targets were conspicuous during experimental trials, performance at detecting and identifying them was much the same regardless of whether there had been congruent, incongruent or no priming beforehand. This is contrary to what the acquired-preference hypothesis would predict: if the spiders were simply expressing a preference for familiar targets, then strong evidence of preference would be expected when the target is especially easy to detect and identify. On the other hand, when targets were cryptic, performance was better after congruent priming than after incongruent priming or after no priming (control), as predicted by the hypothesis that priming triggers selective attention to the primed-for target. Also, when targets were cryptic, performance after no priming was better than after incongruent priming: compared with performance after no priming, *E. culicivora* individuals that had been primed by seeing or smelling mosquitoes became less successful at detecting and identifying mates and individuals primed by seeing or smelling mates became less successful at detecting and identifying mosquitoes (Cross and Jackson 2010a, b). This combination of findings was expected on the basis of selective attention being accompanied by trade-off effects (also see Langley 1996) but not expected on the basis of effects from nonselective adjustment of searching effort (i.e., the “search-rate hypothesis”: Guilford and Dawkins 1987). When nonselective adjustment of searching effort is all that is occurring, the subject is predicted to detect and identify both target types at least as well as in control trials. Impaired performance in both of the two kinds of incongruent trials (mosquito as target after priming with mates and mate as target after priming with mosquitoes) is expected when selective attention is deployed and unexpected when only nonselective increase in attentional effort is deployed.

## Cross-modality Priming of Selective Attention

Cross-modality priming of selective attention occurs when a priming stimulus in one sensory modality prepares an individual to detect and identify a target stimulus in a different modality (Spence and Driver 2004). Although search-image use is most often discussed in the context of same-modality priming (e.g., visual stimuli priming selective attention to corresponding visual targets), it can also be considered in the context of cross-modality priming and this may be especially useful as a warning not to assume that search-image use must be tightly linked to perceptual learning.

When *E. culicivora* was used in same-modality (vision or olfaction) search-image studies (Cross and Jackson 2010a, b), the only reinforcement individual test spiders might have received was from a single instance of simply seeing or smelling a prey individual or a mate. One-trial perceptual learning in the absence of conventional reinforcement may be conceivable, but unlikely. However, even this remote possibility was ruled out in a study (Cross and Jackson 2009) in which there was no conventional reinforcement and yet cross-modality priming occurred in two directions (visual priming triggering olfactory search-image use and olfactory priming triggering visual search-image use).

The methods used in these cross-modality priming experiments had basic similarities to the methods used in same-modality priming experiments, including lures being either cryptic or conspicuous and including priming being either congruent or incongruent. The findings were also similar: seeing mosquitoes made test spiders more proficient at locating a source of cryptic mosquito odor and smelling mosquitoes made test spiders more proficient at locating cryptic mosquitoes by sight. However, in these cross-modality experiments, one-trial perceptual learning was irrelevant. The spiders had no experience with mosquitoes before being used in experiments and yet odor priming made test spiders more proficient at finding mosquitoes by sight and visual priming made test spiders more proficient at finding mosquitoes by olfaction.

## Conclusion

Tinbergen played a major role in generating interest in search-image use by animals, but it would be artificial and counterproductive to restrict discussing search images solely to the contexts of predators responding to prey, individuals relying on a single sensory modality (vision), or representations being acquired by perceptual learning. The expression “specific searching image” needs to be aligned clearly with selective attention and representation (Zentall 2005), with search-image use as a phenomenon being kept conceptually distinct from issues related to, but not defining, search-image use. Related issues include the manner in which the “image” (representation) is acquired, the consequences of trade-off effects and the role of search-image use in the evolutionary origin and maintenance of prey polymorphism. Of course, it might be argued that, for a mechanistic understanding of search-image use, the goal should be an understanding of underlying neural processes and that acquiring an understanding at a neural level will remove the need for talking about “specific searching image,” along with “representation,” “priming,” and “selective attention” (Anderson 2011; Mandler 2013); however, while striving for this ultimate goal, clear conceptual distinctions and consistent use of terms have an important role in indicating what needs to be explained.

## Cross-References

- [Arthropod Cognition](#)
- [Attention](#)
- [Bear Sensory Systems](#)
- [Cross-Modal Transfer](#)
- [Innate Behaviors](#)
- [Learning](#)
- [Modality](#)
- [Predator](#)
- [Prey](#)
- [Priming](#)

- [Representation](#)
- [Sara Shettleworth](#)
- [Visual Search](#)
- [Working Memory](#)

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## Searching

### ► Learning

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## Secondary Defense

### ► Secondary Defenses

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## Secondary Defenses

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## Synonyms

Deimatic behavior; Predator; Secondary defense; Signals

## Definition

Strategies used by prey to defend them from predator when they are singled out by them.

## Introduction

For sustaining life, energy is necessary, and it is gained by eating other organisms, either wholly or partly. All organisms are a predator in a certain way and at the same time prey for other organisms. For example, if the lion is the predator for impala, then in certain cases, they become prey for hyenas as they are their natural enemies. So, predation acts as the selective force leading to coevolutionary arms race between them and prey and thus driving the ecology and evolution of



both of them (Abrams 2000; Wang et al. 2018). To avoid predation, prey organisms have evolved morphological, physiological, and behavioral adaptations.

Antipredator defense mechanism can be categorized into two types depending upon when they are used. These types are primary defense mechanism and secondary defense mechanism (Barnard 2004). Primary defense mechanisms are those which are used by organisms to avoid getting detected by the predators, while the secondary defenses are used by prey after detection from the predator and thus used to increase the chance of survival from predator's attack (Robinson 1969; Edmunds 1974). Once picked up, preys use different strategies to protect themselves from getting hunted. The secondary defenses may be of various types like stings, horns, hard shell, physical or chemical deterrence, etc. which protect prey from predators in a different way.

## Types of Secondary Defenses

Different animals possess different types of secondary defenses. Some animals may have only one type of defense, while some may have a combination of it. Intraspecific variation in the level of defense has also been seen. For example, some prey in a population may not have any of the defenses (Brower et al. 1970; Broom et al. 2005), while in the other population, there is the presence of defense up to some extent. At the individual level in prey population with defenses, there is considerable variation in the level of defense and also in the precise types of the toxins (Bowers 1992; Holloway et al. 1991; Broom et al. 2005). Different animals use different strategies as secondary defenses against predators. The following are some of the different types of secondary defense mechanisms deployed by prey against predators, once singled out by them.

### Withdraw to Retreat

Many animals prepare a shelter place like crevices and burrows and live within it. They are called anachoretetes. This place is helpful during the

situation of attack from a predator. During the attack, the animals retreat to these hiding places. Some of the retreats are constructed by animals themselves but sometimes natural retreats like hollow tree, vegetation, etc. can be used by animals.

For carrying out important activities like foraging, the animals have to come out from seclusion. Sometimes they come partially out of their retreat, as in case of *Sabella*, or even many times, emergence will be complete. But in both the cases, their activity is limited nearby to their hiding place (Barnard 2004). One example is of hermit crabs (*Pagurus bernhardus*) in which the crabs select the shells very carefully. Generally, two larger crabs initiate the fight to gain access of the shell of smaller crabs (Briffa and Elwood 2001). During the cheliped display, the relative size of crabs is assessed (Neil 1985). It has been shown the contest for shells is started when a crab found its own shell as well as the opponent shell (Dowds and Elwood 1983). During the contest, the attacker raps up the shell by running its walking leg and cheliped over it while the defender withdraws himself within the shell (Briffa and Elwood 2001). Therefore, the assessment and proper selection of retreat site is important as it affects survival rate of prey from attacker.

### Flying Behavior

In animals like an impala (*Aepyceros melampus*), wildebeest (*Connochaetes* sp.), etc., flight behavior is one of the common defense mechanism after getting detected by prey. Between herbivores and carnivores, speed and agility seem to be most obvious and coevolved adaptation.

Fast and sustained speed comes with a cost and various sacrifices like body mass. The flight behavior can be enhanced in two ways.

### Protean Behavior

In this type of flying behavior, the animals run in an uncertain and unpredictable way. For example, the rabbits and gazelles run in zigzag manner. The unpredictable and random changes in direction of running confuse the predator and make it difficult for the predator to keep track of the prey.

### Flash Behavior

In this type of flight behavior, the prey runs for a short distance and suddenly stops and freezes. Immobile animals discourage certain animals, and they don't tend to attack them, and also sudden activity and then complete freezing of prey animals confuse predators (Barnard 2004). The flash behavior is accompanied by bright markings or conspicuous coloration in some organism. For example, the scales of fish produce flash when they turn. Exhibiting conspicuous colors and noise during fleeing is postulated to hinder the location of prey (Loeffler-Henry et al. 2018).

### Diversions

Sometimes, prey has features which divert the attention of their predators from them or their young ones or their vital organs like heads or wings. Autotomy is also one of the ways by which prey divert the attention of the predating animal. Autotomy is the process in which the organism sheds one of its organs voluntarily. The most common example for autotomy is a common lizard. When attacked, they shed their tail which can show movement for around 30 min for which they use anaerobic metabolism (Sanggaard et al. 2012; Dial and Fitzpatrick 1983). As in the case of sustained high speed, the autotomy also has some cost. The organs shedded by the organism may play a vital role as in the case of some lizard species. In the lizard, the tail acts as a fat storing organ and thus is important for them. So, the lizard visits back to place where it shedded the tail and eat its own autotomized tail (Clark Jr 1971; Sanggaard et al. 2012).

Many organisms, to save themselves from predation, have developed eye-like spots (Stevens 2005; Smith 2014; Osterloff 2018), for example, peacock pansy butterflies (*Junonia almana*) which have eyespots on their wings (Fig. 1). It diverts the attention of predators. For the evolution of eyespots, two hypotheses are given, which are as follows (Stevens 2005): **(i) Intimidation hypothesis**, the butterflies intimidate predator by their own enemy which gives them time to flee away. **(ii) Deflection hypothesis**, according to this hypothesis, eyespots are evolved to divert the attack of predators to non-vital organs.

Similar to eyespots, some butterflies have evolved false head. It is hypothesized that the evolution of the false head is an anti-predation adaptation in butterflies as it serves the function of diverting the attention of predators (Robbins 1981; López-Palafox and Cordero 2017). But the role of the false head as anti-predation adaptation is still doubtful as some recent work shows that butterflies are still predated by their natural enemies, mantis (López-Palafox and Cordero 2017).

Many ground-nesting birds perform feigning behavior like broken wing display to distract the predators away from their nest or chicks. The broken wing display is predominantly found in shorebirds like sandpipers. The birds showing broken wing display runs with half-spread wings and drags fanned tail on the ground (Gómez-Serrano and Valenciana-VAERSA 2018). The broken wing display is sometimes combined with other behaviors like injury calls, false feeding, or incubation like displays (Gochfeld 1984; Gómez-Serrano and Valenciana-VAERSA 2018). The intensity of display generally increases from the time of egg-laying to egg-hatching date (Byrkjedal 1989). So, these behaviors and displays of birds increase the breeding success and thus increase the chances of hatching of eggs (Gómez-Serrano and López-López 2016).

Another antipredator strategy used by animals is death feigning or thanatosis. When the predator come very close to the prey or when both come in physical contact to each other, the prey freezes and enters the immobile state and plays dead. Thanatosis reaction was measured using the tonic immobility (Toledo et al. 2010; Humphreys and Ruxton 2018). The tonic immobility state can last from a few seconds to hours and even after the predator threat has been removed. In thanatosis, the animal attains dead-like posture as in the case of the hognose snake (*Heterodon platirhinos*) or *Virginia opossum* (*Didelphis virginiana*), and this posture diverts or may inhibit the attack from the predator (Toledo et al. 2010).

### Deimatic Displays

Deimatic displays serve as surprise element for the potent predators and is used to scare or startle the predators. Generally, the element of

**Secondary Defenses,****Fig. 1** Eyespots on wings of *Junonia almana* (a, b, c)

surprise is some visual component which is hidden (Holmes et al. 2018) and is revealed only when the prey is approached by the predator. For example, when leaf mantis is touched or approached by any predator, it attains the defensive deimatic posture exposing its eye spots, bright colors, and rasping sound (Umbers et al. 2015). Sometimes prey mimics other organisms to produce startle response in their predators (Barnard 2004; Umbers et al. 2015). For example, elephant hawk-moth caterpillar (*Deilephila elpenor*) mimics the head of young pit viper.

**Aposematism**

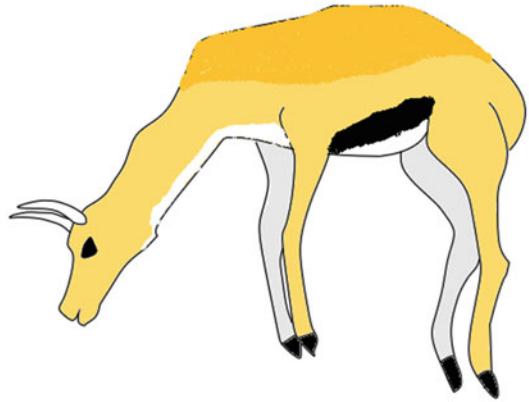
Many times, the prey possesses both the effective defense mechanism (like sting, toxin, horn, or tough shells) and a warning display depicting

that mechanism (Speed et al. 2006; Wang et al. 2018). Such types of preys are referred to as aposematic prey. Warning displays are used by prey to display the presence of toxins or some other defense weapons with them and thus their unpalatability and unprofitability to the predators. Many aposematic preys prefer olfactory aposematism as warning display where they use noxious odors (Eisner and Grant 1981; Gohli and Högstädt 2009). These odors act both as a warning signal and noxious defense.

Some organisms like poison frog, wood tiger moths, and plain tiger butterflies (Fig. 2) use the bright color display as a warning signal for their toxicity and thus unpalatability (Rojas et al. 2015). Productions of secondary defenses are costly, and thus “cheaters” are found among the aposematic population. Some mutants of a



**Secondary Defenses, Fig. 2** Aposematism in *Danaus chrysippus*. These butterflies contain toxic in them and thus are unpalatable. They display their toxicity by bright coloration



**Secondary Defenses, Fig. 3** Stotting in Thomson's gazelle (*Eudorcas thomsonii*)

population without any defense mimic those organisms of the same population which have an effective defense mechanism for protection from the predator. Such mimicry is called auto-mimicry (Speed et al. 2006; Rojas et al. 2015). In certain cases, the organism mimics another organism which already has some defense mechanism. Such type of mimicry is called Batesian mimicry (Barnard 2004).

Some other strategies used by animals for their defense against predator animals are “mobbing” and displaying “alarm signals.” Mobbing is a cooperative behavior in which individuals of a group attack or harass a predator altogether. It can simply be defined as assemblage or formation around potential predator. This kind of behavior is usually seen for protection of offspring. Alarm signals refer to strategies used for alerting the members of same species, which may be exploited by others in certain cases. Alarm signals can be visual, chemical, auditory, tactile and even electrical channels. Stotting is one type of alarm display used generally by ungulates like gazelles, deer, etc. This is a display in which animals under attack or when is alarmed by the presence of the predator start to jump with stiff leg where all feet leave the ground simultaneously (Fig. 3). Stotting is also used by animals to draw the attention of predators away from their fawn and to attract them toward themselves or used by fawn to alert its mother when it is disturbed while hiding.

## Conclusion

There is always arms race between predator and prey. To sustain in nature, predators need to hunt on prey, while for sustaining, the prey needs strategies to protect themselves from predators. So, both are always coevolving and under pressure of arms race. Prey has evolved adaptation and different types of secondary defenses to protect them from predation when the first line of defense fails. They have evolved aposematism to warn the predators for the presence of toxins; some insects like *Pachyrhynchus* weevils have evolved hard shells to protect themselves from getting hunted.

## Cross-References

► [Aposematism](#)

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## Secondary Dentition

### ► Dental Formula

## Secondary Sex Characteristics

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## Definition and Introduction

Secondary sex characteristics (SSC) in animals are traits that develop after sexual maturity. Unlike



primary sex characteristics such as sexual structures or organs that are directly related to sexual reproduction, secondary sex characteristics seem to be indirectly related and likely increase mating opportunities. Increased mating opportunities often result from individuals being chosen because they appear more attractive to the opposite sex, have better courtship behaviors, and/or are able to out-compete competitors.

## Sexual Dimorphism

Many SSC are also sexually dimorphic. Sexually dimorphic traits are those that differ between the sexes. Secondary sex characteristics and sexually dimorphic traits are highly variable in animals and encompass differences in size, coloration, mass, and behavior.

Sexually dimorphic characteristics that pertain to the body are categorized as sexual size dimorphism. Frequently, one sex is larger than the other (body mass dimorphism). This type of dimorphism can be seen in many taxa. Females are larger 86% of the time when body mass dimorphism is present, which is known as reverse size dimorphism (RSD) (Fairbairn 2013). Throughout most of the animal kingdom – including insects, amphibians, reptiles, and fishes – the females are larger (Fairbairn 2013).

Reverse size dimorphism is less common in mammals and birds, but exceptions exist. Examples of avian and mammalian RSD can be seen in spotted hyenas (*Crocuta crocuta*), baleen whales (Mysticeti), and birds of prey (Falconiformes). Alternately, males are larger 14% of the time. An extreme example is the cichlid fish (*Lamprologus callipterus*). In this species, males are almost three times longer than females.

According to Rensch's rule, male-biased size dimorphism increases with the size of a species, and female-biased size dimorphism (i.e., reverse size dimorphism) decreases. Although this rule does not apply to many lineages, it is present in even-toed ungulates, pinnipeds (seals), and primates. To illustrate, small primates such as tarsiers and galagos exhibit less size dimorphism than monkeys and apes.

SSC may also be expressed as skeletal sexual dimorphisms, such as the elongated tusks seen in male narwhals (*Monodon monoceros*) and Asian elephants (*Elephas maximus*). A subtler example of skeletal dimorphism occurs in the gorilla, skull that facilitate temporal (near the temples) and nuchal muscular (back of the neck) development.

## Biological Ornamentation and Color

One obvious way that secondary sex characteristics vary is via ornamentation and color. Species in which males and females differ by color are said to exhibit sexual dichromatism. Most male birds (Aves) are more ornamented and colorful than females. For example, male red junglefowl (*Gallus gallus*) have long and arching feathers in their tails that appear black but have shiny blue, green, and purple colors compared to the lackluster females.

Many male mammals are also more ornamented and colorful than females. Male bearded pigs (*Sus barbatus*) and Nubian ibex (*Capra nubiana*) have more distinctive beards than females. Male elephant seals (*Mirounga spp.*) and proboscis monkeys (*Nasalis spp.*) have enlarged noses, while male baboons (*Papio hamadryas*, *Papio papio*) and geladas (*Theropithecus gelada*) have thick manes that females do not possess.

Some SSC appear to be influenced by different selection pressures (factors that drive evolution) on the different sexes, and as a result, often vary within a single species. Male eclectus parrots (*Eclectus roratus*) are green, which helps them blend-in with foliage, and appear less detectable to predators when they forage alone for up to 11 months, while females defend nest hollows (Heinsohn 2008). The males' green plumage is shiny and has ultraviolet (UV) pigmentation, which is less visible to predators, but obvious to other parrots. Female eclectus parrots are brightly colored too, but instead of being green, they are red-and-blue. This coloring can be seen by parrots from a distance, letting others know that a nest hole is occupied (Heinsohn 2008).

Colorful females seem to be a pattern in some bird species. Nonmigratory female birds are more

likely to engage in conflicts over territories and resources, and face more intrasexual competition. As a result, they tend to be as colorful as males of the same species. The color serves as a signal to other females that the territory can be defended (Simpson et al. 2015). In contrast, migratory female birds face less intrasexual competition over territory and resources and tend to be less colorful than males. This is likely because they no longer experience selective pressure to signal their status (Simpson et al. 2015).

## Female Choice

In general, females choose to spend time and/or mate with more ornamental and brightly colored males, which is called female choice. Female common roaches (*Rutilus rutilus*) choose the males with the most elaborate breeding tubercles (Kortet et al. 2004). Also, female stalk-eyed flies (*Diasemopsis meigenii*) are more likely to consort with males that have enlarged accessory glands and preferentially mate with males that have exaggerated eye-spans (Chapman et al. 2017). Female wolf spiders (Lycosidae) choose males with ornamental tufts, which are used in leg-waving displays during courtship (Hebets and Uetz 2000).

Among fish, female yellowhammer (*Emberiza citronella*) spend more time in front of, and perch more, beside the most colorful males (Sundberg 1995). Female guppies (*Poecilia reticulata*) have demonstrated choice for males with complex color components and patterns including iridescent blues, violets, greens, and silver; orange, red, and yellow spots; and black and brown spots, bars, and fuzzy markings (Brooks and Endler 2001).

Female pied flycatchers (*Ficedula hypoleuca*) mate preferentially with more brightly coloured males, while female birds of paradise (Paradisaeidae) choose males with elongated and elaborate feathers that extend from the beak, wings, tail, or head. Blandly-colored female quetzal birds (Trogonidae) mate with males that are the most iridescent green and that grow the longest colorful train of tail feathers during the mating season.

Upon closer inspection, even bird species that humans perceive as mostly monochromatic (one main color) may have color differences that appeal to the opposite sex. European starling (*Sturnus vulgaris*) males have feathers with UV colors that humans cannot see. Female birds in these species can see the UV colors, and select males that have the brightest ones (Bennett et al. 1997).

Although most male lions (*Panthera leo*) live in the sweltering heat of Sub-Saharan Africa, they have thick manes akin to humans wearing winter scarves. One reason may be that females mate with the darkest and most decadently maned males (West and Packer 2002).

Female selection of secondary sex characteristics in males is also common in primates. For instance, during the breeding season, male squirrel monkeys (*Saimiri*) use water and fat to increase their body mass approximately 25%. Females choose the largest male squirrel monkeys. In addition, adult male mandrills (*Mandrillus sphinx*) exhibit more colorful red, white, and blue faces and ano-genital regions than females. Likewise, mature male drills (*Mandrillus leucophaeus*) have a pink lower lip, red and lilac genitals, and blue, purple, and lilac bottoms. In both species, the males with the brightest colors have the highest rank in the dominance hierarchy, and the females choose them over subordinate males. However, because dominant males usually can control whether or not lower-ranked males have access to females, it is difficult to tell whether females are actively choosing dominant males or mating with them because they are the only males with whom they are “allowed” to mate. This situation is clear in orangutans (*Pongo*) where females have been observed actively guiding the penises of males that have well-developed face flanges (cheek pads) into their vaginas, and rejecting matings with subadult males and males with undeveloped flanges.

Moreover, females choose males with exaggerated traits that do not exist in nature. For instance, female vinegar flies (*Drosophila serrata*) show preferences for male cuticular hydrocarbons (specialized exoskeletons) and combinations of

traits that do not occur in natural males (Van Homrigh et al. 2007). Also, female long-tailed widowbirds (*Euplectes progne*) choose males with tails that have been artificially lengthened by researchers (Andersson 1982).

Behavior can also be considered a secondary sex characteristic. Female field crickets (Gryllinae) select males that call for longer periods (Hedrick 1986), while túngara frogs (*Engystomops pustulosus*) prefer males with elaborate “chucks” in their mating calls (Ron 2008). Also, male warblers with larger song repertoires mate earlier than those with smaller repertoires (Catchpole 1980).

## Males Can Be Choosy Too

Reproduction, gestation, lactation, and other offspring care are so energetically expensive for females that females should only invest in growing elaborate secondary sex characteristics when they outweigh the energy it costs to produce those traits. Males may select females with these enhanced traits. For example, in some fly species (Empididae), the females’ dark wings, inflatable abdominals sacs, and feather-like scaly legs may make them more attractive to males. Males choose one of the swarming females to be the recipient of his nutritious silk-wrapped prey item “nuptial gift.”

Female slender-necked shorebirds (*Phalaropus spp.*) are larger and more brightly colored than males. After males choose a female with which to mate, they then incubate the clutch of eggs and care for the hatchlings. Male Gulf pipefish (*Syngnathus scovelli*) invest in offspring care as well, which is a hot commodity. Correspondingly, female pipefish have brighter abdomens than males. Males choose to mate with, and provide offspring care to, the females with the most and/or largest silvery blue iridescent abdomen bands.

## Bright Male Hypothesis

It is overwhelmingly clear that females, and in some cases males, select the most exaggerated

ornaments and colors, but why? The “Bright Male” hypothesis proposes that ornaments and bright colors advertise a healthy condition free of disease and parasites (Hamilton and Zuk 1982). The idea is that if an individual was sickly, it would have to expend energy healing rather than growing extra-large and/or colorful traits. Healthy individuals would then pass on the beneficial and desirable traits to their progeny.

Most female animals should be picky and select males with advantageous traits so their offspring inherit them. Because reproduction and offspring care are so draining for females, it is even more important that they choose to reproduce with males that possess characteristics indicative of the highest genetic fitness. When individuals choose to mate with those that possess the traits they most desire, it is called sexual selection. Sexual selection was first proposed by Charles Darwin (1871) to explain the exaggerated and colorful characteristics of male peacocks (*Pavo cristatus*). Darwin (1871) discussed how a combination of female mate choice (females choosing to mate with the most colorful males) and intrasexual competition between males for mating opportunities with females were likely responsible for the peacock’s ornaments and colors.

Sometimes it is difficult to tell if sexual selection is at work or some other mechanism. For example, during peak fertility, female brown capuchins (*Sapajus apella*) only solicit matings with the dominant male. If the dominant male is replaced by another male, the females will no longer mate with him, even though the previous dominant male still possesses the same genes, but a different rank. This makes it likely that females are not selecting the dominant male for his genetic fitness, but rather for his ability to protect the offspring he likely fathered.

Male northern cardinals (*Cardinalis cardinalis*) are a vibrant crimson red, while the females are a duller red-olive. Female cardinals practice assortative mating, which means that they mate with individuals that resemble themselves. Females with red bills choose to mate with males that have the reddest bills (Jawor et al. 2003). These males also have better body conditions than males

with lighter red bills. House finches (*Haemorrhous mexicanus*) have orange-reddish coloring in their crowns and plumage related to carotenoid pigments in high quality foods like seeds. Female house finches choose to mate with brighter males, and these males appear to be better food providers for the females and hatchlings (Hill 1990).

For months every spring, male sage grouse (*Centrocercus minimus*, *C. urophasianus*) perform an elaborate courtship ritual on leks (groups of males competing to mate) for several hours. They expand white air sacks on their chests, make soft drumming noises, extend their tail feathers, and strut around in front of drabber-colored females. The females tend to choose males that strut more and vocalize in a specific manner, and these males end-up having the greatest reproductive success that season (Gibson and Bradbury 1985).

A demonstrative example of biological ornamentation serving a primarily decorative function instead of a utilitarian one is the previously mentioned Indian peafowl's (*P. cristatus*) grand plumage. Male peacocks have bright plumage and long tail feathers decorated with eye-spots. Female peahens are duller in color and choose to mate with the peacocks that have the largest eye-spots. Eye-spots serve as signals of the owner's health and vitality because peacocks with larger eye-spots have progeny that weigh more and live longer than the offspring of peacocks with smaller eye-spots (Petrie 1994).

Along with intersexual (between the sexes) selection for attractive traits, body size and armaments used as weapons may result from intrasexual (within a sex) selection to win battles for access to females. For example, male hissing cockroaches (*Gromphadorhinini*) have pronounced horns (chitinous protrusions) on top of the pronotum (plate-like thoracic structure) that are used during fights. Also, the largest male teiid lizards (Teiidae) win more fights, mate with more females, and produce more offspring than smaller males (Anderson and Vitt 1990). The antlers of deer bucks, many antelopes and goats (Bovidae), as well as the horns of male dung beetles (Scarabidae) and Hercules beetles

(*Dynastes hercules*) are used in male-to-male competition for females. Female deer select males with larger antlers, and the larger the antler, the more likely a male is to fight off other males and control a harem (group) of females.

## Immunocompetence Handicap Hypothesis

The Bright Male hypothesis makes sense, except when one considers that many of the traits that are being selected for could increase the likelihood that the owner dies and/or gets sick. For example, shiny colors could make an individual stand-out to predators, while heavy appendages could slow down an individual trying to escape danger. This means that the individual's genes could be removed from the gene pool quicker than those that do not possess the "sexy" traits. Thus, secondary sex characteristics can be energetically costly and leave organisms vulnerable to predation, illness, and parasitism.

Although male peacocks with larger eye-spots and longer/heavier trains enjoy higher reproductive success, they also expend more energy growing those feathers and have weaker immune systems. Likewise, although female great tits (*Parus major*) choose males with larger breast-stripes because they are more dominant and potentially show greater parental investment, those males have worse body conditions and suffer greater mortality during periods of cold weather (Moore et al. 2015). How then do secondary sex characteristics that increase mortality persist in a population?

There seems to be a trade-off between sexual ornamentation, bright coloration, and the negative consequences resulting from them. The "Handicap Principle" (Zahavi 1975) offers an alternate explanation as to how seemingly disadvantageous traits and behaviors can be maintained – and selected for – within a population. Crucial to this hypothesis is the idea that the handicaps are signals of health, as only the fittest individuals could afford to squander resources to grow and maintain the traits (Roberts et al. 2004). For instance, the antlers of male deer (Cervidae)

grow fast and are energetically and nutritionally demanding because deer regrow antlers every year. This means that antlers can be considered an “honest signal” of food-gathering ability and health, conveying information that would increase a female and her offspring’s fitness, should she choose to mate with a male with a strong signal.

In males, androgens stimulate the development of SSC, but also impair the immune system. Under the “Immunocompetence Handicap” hypothesis (Folstad and Karter 1992), the immunosuppressive effects of testosterone indirectly signal an animal’s capacity to withstand sickness, as only the healthiest individuals maintain the high levels of androgens required for sexual signalling. Accordingly, in reptiles and birds, there is a negative correlation between testosterone and immunity. For example, male European starlings (*S. vulgaris*) implanted with testosterone showed lowered immune responses (Duffy et al. 2000). However, this hypothesis does not seem to hold for all taxa. For example, there is not a strong correlation between testosterone and lowered immunity in mammals (Roberts et al. 2004).

### Fisher’s Runaway Hypothesis

Furthermore, according to Fisher’s Runaway Hypothesis or Runaway Selection (Fisher 1915), extreme secondary sex characteristics/sexual dimorphism can occur because: (1) females preferentially mate with males that have certain characteristics, and (2) offspring inherit their father’s characteristics, as well as their mother’s preferences for them. Together, this leads to a “runaway” effect through which increasingly exaggerated traits evolve in one direction (directional selection). An example is Wilson’s bird-of-paradise (*Diphyllodes respublica*). Males of this species have evolved extreme ornamentation and coloration that includes bare blue headskin, a velvet green breast, a scarlet back, and two curved violet tail feathers. Male Wilson’s birds of paradise clear an area and perform a complex dance ritual that females use to determine with whom to mate.

### Primary Hormonal Controls

In most vertebrates, secondary sexual characteristics (SSC) are mediated by the hypothalamic–pituitary–gonadal (HPG) axis. The hypothalamus secretes gonadotropin-releasing hormone (GnRH), which stimulates gonadotropic cells within the anterior pituitary to secrete luteinizing hormone (LH) and follicle-stimulating hormone (FSH). In response, LH and FSH act on the gonads (ovaries or testicles) to produce sex hormones (estrogen, testosterone, progesterone, etc.) that trigger either follicle growth or spermatogenesis. In females, LH causes the ovaries to secrete estradiol and progesterone, while in males, LH causes the testicles to secrete testosterone. It is through this hormonal cascade that sexual maturity occurs and SSC develop.

### Secondary Hormonal Controls

Some hormones peripheral to the HPG axis also influence SSC. For instance, in mice, GnRH-1 (the mammalian variant of human GnRH) is upregulated by the neuropeptide kisspeptin. The hormone leptin, produced by adipose (fat) cells, also appears to upregulate GnRH. For this reason, increased body fat can indirectly modulate SSC through the actions of leptin. GnRH can also be downregulated by the hormone inhibin. Upregulation refers to an increase in receptors for a particular type of hormone, while downregulation refers to a decrease.

### Species-Specific Hormonal Controls

To reach sexual maturity, most insects, unlike vertebrates, undergo metamorphosis. The process of metamorphosis is under endocrine control. In the brain, prothoracicotropic hormone (PTTH) is released, stimulating the prothoracic glands to secrete ecdysone, a hormone that induces molting. In females, juvenile hormone (JH) stimulates egg production. Relatively little is known about what hormonal factors control SSC in imagoes (adult insects). Nevertheless,



insects exhibit some of the most vivid SSC that are sexually dimorphic in the animal kingdom. Notably, male honeybees (*Apis*) lack stingers and do not partake in resource collection, while male fruit flies (*Drosophila*) have evolved sex combs (chitinous bristles on the forelimbs) that facilitate successful courtship.

In fish, SSC are mediated by the HPG axis. In addition, many species of fish are capable of sequential hermaphroditism (switching sex). This process has been linked to the enzyme aromatase, which catalyzes estrogen from androgens.

A distinguishing feature of nonmammalian sexual behavior is the nonapeptide arginine vasotocin (Maney 2010). In male túngara frogs (*Engystomops pustulosus*), vasotocin injection leads to increased calling behavior and sexual advertisement (Kime et al. 2007), suggesting that vasotocin is an important modulator of SSC in amphibians. Generally, in reptiles, SSC are either reduced or limited to differences in size. One prominent exception is male Carolina anoles (*Anolis carolinensis*) that have bright red dewlaps that females lack.

Like mammals, birds achieve sexual maturity and develop SSC through the HPG axis. However, birds rely heavily on visual cues to signal fitness. As a result, raised testosterone levels in males correlate positively with raised levels of carotenoids, which includes most of the pigments involved in feather and beak coloration (Blas et al. 2006). Also, the peptide hormone prolactin (PRL) directs parental care in many passerines.

### Chemical Controls and Endocrine Disruption

The endocrine system is vulnerable to a class of exogenous compounds (produced outside cells, tissues, organisms) known broadly as endocrine disruptors. These compounds can be natural or synthetic and include phthalates, oxybenzone, tributyltin (TBT), dichlorodiphenyltrichloroethane (DDT), and xenoestrogens such as polychlorinated biphenyl (PCB) and bisphenol A (BPA), among others. These compounds affect the endocrine system by either mimicking natural

hormones and/or binding to receptors and blocking the actions of natural hormones.

Industrial advances in production and use of plastic has led to increased accumulation of endocrine disruptors in the environment. As a result, adverse effects have been observed in insects, fish, reptiles, birds, and mammals, including humans. The extent to which endocrine disruptors affect wildlife remains unclear, but there is an increasingly large body of evidence demonstrating that endocrine disruptors cause deformities, alter neurological function, shorten pubescent timelines (in humans), change sexual behavior, reduce fertility, and lead to masculinization and/or feminization. Inducing masculinization or feminization affects the expression of SSC.

For example, fathead minnows (*Pimephales promelas*) exposed to bleached sulfite mill (BSM) experience profound changes in sexual development, including increased size and masculinization (Parrott et al. 2004). Likewise, the use of TBT on boats causes female common periwinkle sea snails (*Littorina littorea*) and related taxa to develop male sex organs, a condition known as imposex. TBT has also been shown to cause estrogenic activity in mice (Penza et al. 2011). Further regulation is necessary, as endocrine disruptors not only affect SSC but pose health risks to both wildlife and humans.

### Environmental Controls

Maintenance of SSC is sensitive to environmental cues. Because the hypothalamic–pituitary–adrenal (HPA) axis works in tandem with the HPG axis, factors that influence the stress response can in turn affect sexual function. For instance, chronic stress may lead to cessation of the menstrual cycle in human females. Other important cues are seasons, light, and food availability, which regulate HPG activity in many species of vertebrates. Food availability also regulates the SSC of invertebrates. This has been demonstrated in male wolf spiders (*Schizocosa ocreata*). When given access to more food, they develop larger forelimb tufts, a trait selected for by females (Hebets and Uetz 2000).

Similarly, intersexual and intrasexual interactions can cause hormonal fluctuations, leading to changes in SSC. When male song sparrows (*Melospiza melodia*) are exposed to other males, their testosterone levels increase (Moser-Purdy et al. 2017). Similar occurrences have been observed in mammals. Subordinate female marmoset monkeys (Callitrichidae) have low levels of GnRH and do not ovulate. Thus, gene-environment interactions underlie the development and maintenance of SSC.

## Sex Differentiation and the Environment

Chromosomal sex is determined at conception. The XY sex-determination system is found in most mammals, while the ZW sex-determination system works in birds, as well as some insects, reptiles, and fish. Conversely, sex differentiation is under hormonal control and can be modulated by environmental factors. Thus, different developmental environments can lead to functionally significant differences in the size and shape of male sexual traits, such as cryptorchidism (failure of the testes to descend). Developmental responses to different ecological conditions produce trait variation and can lead to selection and subsequent genetic accommodation of the plastic phenotypes (an individual's physical traits). For example, male and female water fleas (*Daphnia magna*) reared in the presence of diethylstilbestrol and methoprene show rapid sexual development (Olmstead and LeBlanc 2000).

## Conclusion

In humans, secondary sex characteristics develop at the onset of puberty (the stage at which a person becomes capable of sexually reproducing). Classic examples of human SSC are differences in fat distribution and voice pitch. In nonhuman animals, secondary sex characteristics (SSC) develop after individuals reach sexual maturity and can take many forms. SSC may manifest as differences in body sizes/masses, shapes, ornamentations, colors, and

behaviors, and most seem to be subjected to sexual selection by females on male traits. SSC are also mediated by various hormones and can be affected by environmental factors. Of particular concern are xenoestrogens, which cause endocrine disruption in a variety of taxa. Endocrine disruption can lead to feminization/masculinization, changes in sexual behavior, reduced fertility, etc., which can affect the expression of secondary sex characteristics, as well as the health of the individual.

## Cross-References

- ▶ [Charles Darwin](#)
- ▶ [Environmental Influences](#)
- ▶ [Estrogen](#)
- ▶ [Fisher](#)
- ▶ [Handicap Hypothesis](#)
- ▶ [Honest Signaling](#)
- ▶ [Intersexual Selection](#)
- ▶ [Puberty](#)
- ▶ [Runaway Selection](#)
- ▶ [Sex Differences](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Sexual Selection](#)
- ▶ [Testosterone](#)
- ▶ [William Donald Hamilton](#)

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## Seeing

### ► Primate Sensory Systems

## Selection Pressures

### ► Adaptive Memory

## Selection Study

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## Synonyms

[Adaptation studies](#); [Biological evolution](#); [Phylogeny](#); [Social evolution studies](#); [Survival studies](#)

## Definition

The selection study is the study of the basic mechanism by which nature ensures better adaptation, survival, and selective reproduction of some animals as compared to other animals. Natural selection plays an important role in the development, maintenance, inheritance, and variability of simplified algorithms for decision-making in animals, that are otherwise capable of only limited computational power and memory (Bach and Dayan 2017). It is frequently observed that selectively bred domesticated animals behave very differently from their wild counterparts. It implies that behavioral changes in animals are occurring in response to their surrounding environment. The cognitive system helps animals to adapt and alter their behavior according to the demands of the environment. They can also be at certain times under positive

or negative selection depending on the extent of variability in the environment.

To understand the extreme variability of behaviors within and among species, selection has been studied with the help of two different yet complementary perspectives: ultimate and proximate studies (Bateson and Laland 2013). Ultimate studies examine ecological or social determinants of natural selection that lead to the evolution of a specific behavior without considering the cognitive mechanisms underlying these behaviors. Darwin in his famous book “Origin of Species” proposed the famous theory “Survival of the fittest,” which emphasized the role of behavior adaptation to complex social and ecological situations for better survival.

On the other hand, proximate studies establish the correlation between behaviors that have been favored by natural selection and mechanisms underlying the evolution of key biological structures including neural and developmental aspects. In a way, proximate studies report that the cognitive functions or neural structures evolve along with the evolution of species; collectively known as phylogenetic studies. Phylogenetic studies can reveal constraining factors that limit the evolution of a more complex form of cognition. Evolutionary psychologists believe that like any other biological trait, animal behavior too undergoes the process of natural selection and this evolutionary approach should be used to understand the evolution of animal mind. Furthermore, studying the role of natural selection on cognition and neural structures can help shed light on why specific abilities or mechanisms arose in some species but not others.

Alfred Lotka (1926) believed that there were mechanisms within a body that enable the organism to make evolutionarily good decisions: He pointed at an evolved neurological basis and an ability to predict that controls decisions. However, behavioral ecologists argue that the animals use emotional motivation, and learning to process and implement in the decision-making process (Frankenhuis et al. 2018; Higginson et al. 2018).

## Conclusion

Thus, it can be inferred that natural changes in the environment as well as evolutionary changes within the organism itself determine animal decision-making ability, which plays a major role in the natural selection of animals (Mobbs et al. 2018).

## Cross-References

- [Biological Evolution](#)
- [Social Evolution Studies](#)
- [Ultimate Causation](#)

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## Selective Attention

- [Cognition](#)

## Self-Administration

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## Definition

Self-administration is a technique used in animal behavior, which relies on operant conditioning processes. Self-administration involves a process whereby an animal performs a particular behavior to receive a rewarding stimulus of some kind – generally a drug, food, or liquid such as water or alcohol but can also include stimulation of brain reward areas. The learning of this behavior is termed instrumental learning and is an operant conditioning process whereby an action becomes associated with an outcome (delivery of rewarding stimulus). Self-administration has many applications and is considered the gold standard test for assessing the potential abuse liability of new pharmaceutical compounds in a preclinical setting. The substance is considered to be of high abuse potential if the animal will self-administer it readily. Self-administration in a laboratory setting is typically performed by rats but can also be performed by any species capable of operant learning, e.g., humans, nonhuman primates, pigeons, mice, and even honey-bees.

## History and Apparatus

Self-administration originated in the laboratory of eminent psychologist B. F. Skinner and is



inextricably linked to his theory of learning called operant conditioning, a theory which focuses on the linking of behavior with rewards/consequences (Skinner 1938). B. F. Skinner created the first self-administration chamber (colloquially referred to as a “Skinner Box”). The apparatus typically consists of an enclosed chamber, which contains, at its simplest, a lever or nose-poking device and a receptacle where liquid or pellet rewards can be delivered. Performance of the reward-paired operant response results in reward delivery. Many permutations and applications of this paradigm now exist and the self-administration apparatus is tailored to each application, route of administration, and species.

### **Motivation and Reinforcement: Central Tenants of Self-Administration**

According to operant conditioning theory, reinforcement occurs when after a particular operant response the outcome results in an increase in the probability of another response being performed. Reinforcement can be positive, i.e., involve the consumption of a rewarding stimulus, or negative, i.e., involve the removal of an aversive stimulus. Both types of reinforcement increase the probability of another response being performed. In this context, a rewarding stimulus is termed a positive reinforcer and an aversive stimulus is termed a negative reinforcer. When an aversive stimulus or removal of a rewarding stimulus is paired with the behavioral response, the process is termed punishment, as the behavioral response is less likely to occur as a result of the stimulus.

Though the work of Skinner does not focus on the internal states and drives that result in an operant response, it should be acknowledged that the concept of appetitive motivation is a fundamental aspect of positive reinforcement and therefore self-administration. The stimulus is considered to have primary (or unconditioned) reinforcing properties, which elicit approach behavior towards the reward-paired operandum (e.g., lever). Reinforcers are also referred to as goals, incentives, or rewards and these terms embody this concept of appetitive motivation.

It is useful to distinguish between the appetitive and consummatory aspects of the behavior involved in self-administration. An animal self-administers because they have a drive to obtain the reward (e.g., a sugar pellet). Appetitive behavior is that which increases the likelihood of obtaining this reward, e.g., increased approach behavior towards the reward-paired operandum, increased performance of the operant response. By contrast, consummatory behavior is that which is involved in the consumption of the reward (i.e., satisfaction of the need), for example, licking, chewing and swallowing are considered consummatory behaviors.

Operant learning in the initial stages of self-administration is driven by action-outcome contingencies, where an animal learns to perform a particular behavior based on the value of the outcome. For example, if pressing on a lever results in delivery of palatable food, an animal will generally readily learn this response. As a result the operant response to obtain the palatable food is considered goal-directed (the rewarding stimulus is the goal towards which the animal is directing their behavior). However, if the food is devalued, through satiety or conditioned aversion, the animal will reduce or cease responding. It should be noted that extended periods of self-administration can eventually lead to habitual responding that is resistant to devaluation.

### **Free Access**

Though self-administration typically involves engaging in an operant response (e.g., lever press) to obtain a specified amount of a rewarding substance, the simplest form of self-administration involves giving free access to a particular substance and monitoring intake. Obviously the manipulations possible in this sort of experiment are more limited and there is no appetitive component to the self-administration behavior; however, basic consummatory information can be obtained which can be useful when working with lower order species such as invertebrates. Examples include experiments using *drosophila* or ants, which measure the amount of sucrose or ethanol the insects consume. It is also possible to give a choice between two substances, e.g., the

two bottle free choice paradigm in alcohol research will give the subject free access to both ethanol and water in the home cage and the preference of the subject for ethanol as compared to water is measured. It should be noted that these basic consumption experiments, though sometimes referred to as self-administration, are not generally considered “operant self-administration” as there is no distinction between the operant response and the consumption of the reward.

### **Operant Self-Administration (Skinner Box)**

The type of self-administration that everyone is most familiar with is that performed in an operant conditioning “Skinner box” and generally involves pressing a lever, the pecking of a response key, or the breaking of an infrared beam with a nose poke. Though one operandum is sufficient, there is usually the choice of two and one will be paired with reward delivery. Responding on the other will result in no programmed response or the delivery of a control substance (nonrewarding) such as saline or water. The inclusion of a 2nd operandum allows the experimenter to determine that the animal is responding for the reward and not just engaging with the operandum per se.

The operanda used in various self-administration setups are tailored to the abilities of the species in question and the type of experiment being performed. Ideally it is something that the animal will readily engage with when exploring their environment because this is how the first operant response occurs. Operanda are typically levers or nose-poking devices, although modern versions of Skinner boxes can also have touchscreens with digital displays. Skinner boxes for pigeons will have a response key, which detects mechanical pressure and the pigeon learns to peck this key. Nonhuman primates given their high levels of dexterity can learn to press buttons or perform sophisticated tasks to self-administer rewards such as drugs or orange juice. In the runway task, the operant response is actually the movement of the animal (usually a rat) towards the goal box. Once the animal reaches the goal box, it will receive an administration of drug.

The reward can be in the form of a food pellet (delivered by a dispenser) or a small amount of liquid delivered into the receptacle (e.g., liquid sucrose or ethanol) or straight into the mouth. If the reward is a drug, this is usually delivered intravenously through a catheter (often a jugular vein or tail vein catheter). Animals can also learn to perform an operant response to receive intracranial stimulation of reward areas in the brain. This stimulation can be electrical or optical (using light to activate channels that have been inserted into the brain using a viral vector). Cues (e.g., lights or tones) are often paired with reward delivery and these act as a discrete cue which can then be used to precipitate reward-seeking behavior. When discriminative stimuli (denoted S+), otherwise known as occasion setters, are present in the chamber, it is indicating that the operant behavior will be reinforced. Responding usually increases in the presence of these cues.

### **Typical Self-Administration Procedure**

Self-administration typically involves daily sessions for a period of time until the behavior is considered acquired. Once acquired manipulations can be performed, e.g., interventions that are hypothesized to reduce responding for the reward. Sessions can be as short or as long as experimentally required and in some instances the animals are even housed in the self-administration chamber.

### **Schedules of Reinforcement**

Self-administration experiments can adopt different reinforcement schedules to examine different aspects of motivated behavior. A schedule of reinforcement describes the relationship between the response and the reinforcer. Reinforcement schedules can vary both in the number of operant responses required to obtain the reinforcer (ratio) and in how much time must pass before the next reinforcer can be obtained (interval). Stimuli are also often presented to signal reward availability or to coincide with reward delivery. Different schedules of reinforcement produce characteristic rates and temporal patterns of responding that are reasonably consistent across species.

### Fixed Ratio

For fixed ratio (FR) schedules, a fixed number of operant responses are required to obtain a reward. For example, on a fixed ratio of 3 (FR3), every 3rd response would result in reinforcer delivery. The most simple schedule of reinforcement is FR1, whereby every operant response is reinforced (this is also referred to as continuous reinforcement). This type of schedule provides the most direct relationship between operant responding and reinforcer delivery. Increasing the response requirement (ratio) is useful when examining a substance that does not support a high rate of self-administration, such as a high dose of a drug. This means that the rate of self-administration can be low while still maintaining a high level of responding. In general, animals learn more readily on FR schedules than other schedules, especially FR1. While FR schedules are useful for examining patterns and rates of self-administration, they are limited in some respects. For example, a decrease in the rate of responding for a substance is ambiguous and could be interpreted as either an increase or a decrease in its reinforcing efficacy. For this reason, simple FR schedules are not recommended when attempting to assess changes in the strength of the reinforcer (Arnold and Roberts 1997).

### Variable and Random Ratios

For variable ratio schedules, the number of required operant responses varies around an average. For example, a variable ratio of 3 (VR3) might require 1, then 3, then 2, then 5, then 4 responses – an average response requirement of 3. Random ratios are built on a similar principle, except that rather than varying around an average there is an equal probability of any ratio within a range being selected, resulting in an unpredictable average. Both variable and random ratios generally support a steady rate of responding and are particularly resistant to extinction, a phenomenon known as the “partial reinforcement extinction effect” (Lewis 1960).

### Progressive Ratio

For progressive ratio (PR) schedules, the response requirement to obtain a reinforcer systematically

increases. The ratio increase usually follows each reinforcer delivery, but can also occur at the beginning of each self-administration session (Richardson and Roberts 1996). The purpose of the PR schedule is to increase the response ratio up to a point where the animal no longer responds. The highest ratio that the animal achieves in order to obtain one reinforcer is termed the break point, or breaking point. The break point is typically used as a measure of an animal's motivation to acquire a particular reinforcer.

Many different formulas can be used to determine the pattern of ratio increases in PR schedules. The earliest PR schedule, developed by William Hodos to examine the reinforcing efficacy of sweet milk solutions, followed a simple formula where the ratio increased by 2 following each delivery (e.g., 2, 4, 6, 8, 10, 12...) (Hodos 1961). Other PR schedules double the response requirement each time (e.g., 2, 4, 8, 16...) and others follow an exponential function (e.g., 1, 2, 4, 6, 9, 12...) (Richardson and Roberts 1996). The best choice of schedule depends upon many factors including the species of animal, the type of reinforcer, and the session length.

PR schedules have some advantages over FR schedules, in that interpretation of behavior is generally less ambiguous. For example, a decrease in break point suggests a decrease in the reinforcing efficacy of a substance, whereas a decrease in the rate of responding under an FR schedule could indicate either an increase or decrease in reinforcing efficacy. However, it has also been questioned as to whether PR schedules always provide an effective measure of reinforcing efficacy (Arnold and Roberts 1997). For instance, some self-administered drugs can increase locomotor activity which can facilitate operant responding and increase break point, an effect that is independent of the value of the substance (Cantin et al. 2010).

### Fixed and Variable Interval Schedules

For fixed interval (FI) schedules of reinforcement, the first response following a designated period of time results in reinforcer delivery. For example, an FI20 min schedule would mean that the first response following a 20-min interval would be

reinforced. Responses emitted during the interval are not reinforced. The timing of the interval can either begin from the end of the preceding interval, or from the time of the last reinforcer delivery. The former can result in reinforcers being delivered within a shorter time frame than that specified by the interval. It is common for drug self-administration experiments to incorporate a fixed interval between drug deliveries, known as a time out period, to mitigate the risk of overdose. It is also common for some operant tasks, such as touch screen tasks, to incorporate a time out period after an error is made as a form of punishment. FI schedules can also be useful for minimizing the impact of behavioral effects of a drug on responding (Balster and Schuster 1973). Variable interval (VI) schedules of reinforcement work according to a similar principle to FI schedules except that the duration of each interval varies around an average length of time.

#### Tandem, Multiple, and Mixed Schedules

Ratio and interval schedules can be combined to form *tandem* schedules. For example, the tandem schedule FI 20 FR 10 would result in every 10th response after a 20-min interval being reinforced. Mixed schedules are where two or more different schedules alternate (either successively or randomly), and each schedule is signaled by a distinct stimulus. Mixed schedules are the same as multiple schedules except that the schedule change is not indicated by a stimulus.

#### Second-Order Schedules

Under second-order schedules, reinforcer delivery occurs infrequently, following an extended sequence of responses that are maintained by intermittent conditioned stimulus presentations. Second-order schedules are built from two schedules – one schedule dictates the response requirement for conditioned stimulus presentation (often referred to as the component or unit schedule) and another schedule dictates the conditions for reinforcer delivery. Second-order schedules are generally either composed of two FR schedules or a combination of ratio and interval schedules. For example, FI 20 min (FR 10:S) describes a second-order schedule where every 10th response results

in conditioned stimulus (S) presentation, and reinforcer delivery occurs after the 10th response following the fixed interval of 20 min. FR 100 (FR 10:S) describes a second-order schedule where every 10th response results in S presentation and reinforcer delivery occurs after every 100th response. Whether it is best to adopt an FR/FR or combined FI/FR schedule depends upon the purpose of the experiment. FI/FR schedules tend to promote the development of habitual responding that is less sensitive to changes in reinforcer value, whereas FR/FR schedules exert less temporal control over reinforcer delivery (Everitt and Robbins 2000).

Prior to animals being tested on a second-order schedule, they are first trained on a basic FR schedule where reinforcer delivery is paired with presentation of a stimulus. With repeated reinforcer-stimulus pairings, the stimulus itself becomes a conditioned reinforcer, capable of maintaining operant responding. Once stable responding has been acquired, the frequency of reinforcer delivery is gradually reduced. This is followed by a gradual reduction in stimulus presentation until the desired FR or FI is achieved. Omission of the primary reinforcer, conditioned stimulus, or substitution with an unpaired stimulus results in a gradual reduction in response rate (Schindler et al. 2002).

It has been demonstrated that responding under second-order schedules can be maintained with as little as one reinforcer delivery per session (Goldberg and Tang 1977). For this reason, second-order schedules have a major advantage when used in drug self-administration studies, in that a large amount of behavioral data can be obtained while animals are in a drug-free state. This is in contrast to low FR and PR schedules where almost all responding occurs under the influence of drug. This is an important issue to consider given that many self-administered drugs can have behavioral effects that either increase or decrease rates of operant responding. Examination of responding prior to the first drug delivery under a second-order schedule can therefore provide a more accurate measure of a drug's reinforcing efficacy (Arroyo et al. 1998).

The main disadvantage of the use of second-order schedules is the extended training that is required compared to more simple schedules. This is an issue for intravenous drug self-administration studies that are constrained by the length of time that intravenous catheters maintain their patency. Responding under second-order schedules also tends to exhibit more day to day variability compared to low FR schedules (Schindler et al. 2002).

### Chained Schedules

Chained schedules require the completion of a series of linked component schedules that eventually culminate in reinforcer delivery. It is common for each component schedule to be associated with a unique discriminative stimulus. Theoretically, chained schedules can be comprised of any number of components; however, the more components, the less likely it is that the animal will complete the terminal link to obtain the reinforcer. With homogenous-chained schedules, each component schedule requires a similar topographic response, whereas heterogeneous chains require different topographic responses for each link.

Chained schedules are often used in drug self-administration studies to loosely model the sequences of behavior that precede drug self-administration, such as procuring money, purchasing and preparing the drug. Chained schedules can also be used to separate drug “seeking” from drug “taking” behaviors, which are usually represented by the same response in intravenous drug self-administration experiments (Roberts et al. 2013). This is because self-administration of intravenous drug does not require an additional consummatory response like self-administration of food or alcohol (e.g., chewing, licking, swallowing). This separation of drug “seeking” versus drug “taking” is usually achieved by implementing a chained schedule where responding on a “seeking” operandum eventually provides access to a “taking” operandum which then provides reinforcer delivery.

### Concurrent Schedules

A concurrent schedule is where more than one schedule is available for an animal to choose.

The different schedules usually have different response requirements (e.g., FR1 vs. FR10), but can also be combined with different reinforcers (e.g., different types of food, different drugs, food vs. drug), different reinforcer magnitudes (e.g., high vs. low dose of drug), or different reinforcement probabilities (e.g., 100% vs. 25%). The purpose of concurrent schedules is usually to examine an animal’s preference for a particular schedule, and/or how preference can be affected by variables such as changes in unit price.

### Extinction and Reinstatement

Once operant responding for a reinforcer has been acquired it can be extinguished by removal of the reinforcer. Extinction describes a gradual reduction in responding that results from new learning about the action-outcome relationship (i.e., learning that the operant response no longer produces reinforcement). How quickly responding is extinguished depends upon many factors including the value of the reinforcer, the period of self-administration, the schedule of reinforcement and cognitive factors. Extinguished responding can be reinstated by re-exposure to the reinforcer (known as “priming”) or presentation of stimuli previously associated with reinforcer delivery. Extinction-reinstatement paradigms are commonly used in drug self-administration studies to model relapse to drug seeking.

### Applications

Self-administration can be applied to a multitude of research questions and is easily manipulated to experimental needs. It is an ideal technique to study food and drug reinforcement and is therefore commonly used in preclinical drug discovery research to assess whether or not a drug has abuse potential. If an animal will readily self-administer a drug then, it is generally considered to have abuse potential. Self-administration is also widely used in the addiction neuroscience field as a technique to investigate the neurobiology underlying addictive behavior, as inherent to addiction is the administration of the drug being abused. Self-administration is equally as applicable to studies of cognition given that it is based on operant learning processes. This is particularly the case



for touchscreen chambers where a wide array of cognitive tests can be used to screen potential therapeutic compounds for the treatment of conditions such as dementia.

## Cross-References

- Acquisition
- Appetitive Response
- Extinction in Learning
- Free Operant Response
- Goal
- Goal-Directed Behavior
- Instrumental Learning
- Learning
- Motivation
- Operant Chamber
- Operant Conditioning
- Partial Reinforcement Extinction Effect
- Positive Reinforcement
- Priming
- Reinforcement
- Schedules of Reinforcement
- Skinner Box
- Unconditioned Stimulus

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## Self-Awareness

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## Synonyms

Awareness; Consciousness; Introspection

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## Introduction

Think of yourself. Now, try to imagine what it would feel like to *not* be self-aware. You probably find it difficult. Arguably, it would not feel like anything. Self-awareness infuses human experience. Because human self-awareness is so conspicuous to us personally, it is natural to wonder if it, or any related cognitive process, occurs in nonhuman animals. At the same time, because self-awareness is so private and personal, the role it plays in behavior is difficult to articulate, much less study scientifically. The difficulty in studying subjective conscious awareness has long troubled psychology and especially comparative psychology. In 1932, Edward Tolman highlighted the problem by saying:

And, if psychology could only be content with the lower animals, and preferably with rats, and not try to mess around with human beings, this whole question of consciousness and ideas might well have been omitted. But human beings insist upon being included in any psychological purview. And they insist that they are conscious and do have ideas – however improbable this latter may often appear. The shameful necessity, therefore, devolves upon us of having to invent some sort of an hypothesis as to these matters. Our attempts, however, will be but mere guesses. (p. 204)

Here, we address the broad concept of self-awareness and how it has been defined. We next address the challenges that scientists have faced in operationalizing that definition in a way that would be testable in nonhuman animals. We then describe three major areas of study that have each been described as informing our knowledge of self-awareness in nonhuman animals: metacognition, theory of mind, and mirror-guided behavior. For each, we attempt to bracket what we do know, and can know about nonhuman self-awareness, by presenting both liberal and skeptical interpretations. We end by returning to Tolman's conclusion, updating it to reflect that, although there will probably never be consensus about the question of nonhuman self-awareness, the efforts to answer it have not been wasted, as they have revealed a wealth of knowledge about more-tractable issues of comparative cognition and behavior.

## Defining Self-Awareness

Self-awareness is both subjectively obvious to us and objectively obscure. Ask your colleagues, and they will all likely tell you that they “have” self-awareness. However, ask them to provide a definition of self-awareness, and most will stumble and hedge. Further, ask them to provide a set of objective behaviors that would unambiguously indicate self-awareness in another human, animal, or machine, and few of them will be able to agree on the criteria.

Self-awareness is one of the oldest subjects of philosophical and psychological study and thus has been assigned several broad definitions. It is alternatively the ability to introspect about one's emotions and thoughts, the ability to distinguish oneself from others, and the representation of oneself as a being. Operationalizing these definitions into objective measures that can be tested scientifically is tricky, and it has not been clear that efforts to do so even converge on the same topic. Nevertheless, the desire to understand self-awareness is strong enough that researchers have made a variety of attempts.

## The Evidence We Would Need

The inherently subjective quality of self-awareness creates barriers to objective study. You likely experience self-awareness based on your apparently direct introspection about the activities in your own mind. But you cannot introspect into others' minds and thus cannot know firsthand if others are self-aware. The inherent difficulty in knowing what others experience has aptly been called the “problem of other minds.” Because we cannot know other minds by the same apparently direct means by which we know our own minds, we must rely on several types of indirect evidence. First, neurotypical adults will say they are self-aware. Absent converging supportive evidence, such a report is weaker evidence than it might appear to be at first. We can readily write a computer program that would declare itself self-aware, but we know that would be a fabrication. A drunk or a sleeping person might declare

that they “know what they are doing” even when they clearly do not. Second, one might infer similar cognition from shared phylogeny. Other humans have the same evolutionary history and share the neural mechanisms that produce your cognition and behavior. Thus, they might also share your self-awareness. If another species behaves like it might be self-aware and they are closely related to us, then perhaps the most parsimonious explanation is that they are. However, this assumption ignores the fact that closely related species, and even individuals within a species, can differ dramatically in their cognitive abilities. Third, one may infer the thoughts of others from shared behavior. For example, you eat when you feel hungry, so you may infer that another person who eats is experiencing a subjective state of hunger. But we know that eating also occurs in the absence of feeling hungry. We also know that even complex behavior can often occur without self-awareness. The beginning driver must attend carefully to every use of the blinker and every rule of the road, but an expert driver can arrive safely at the destination without any apparent awareness of the trip.

Because nonhuman animals cannot give verbal self-report, we are left to use a combination of shared behavior and phylogeny to evaluate hypotheses about the degree to which different species are self-aware. To do this, researchers use a constellation of behaviorally testable traits that seem to correspond to self-awareness in humans. The benefits of this approach are that it allows assessment of self-awareness in nonverbal species and that it is solidly based on behaviors from a verbal species, humans, that professes self-awareness. The weaknesses of this approach are that we must assume that nonhuman animals and humans rely on the same cognitive or neural mechanisms to accomplish behavior. Many testing conventions routinely vary between human and nonhuman tasks, such as verbal instructions versus trial-and-error learning, being tested in mother’s arms versus a cage, or having years of explicit schooling versus being naïve. Different species tested in different ways often use different mechanisms to perform the same feat, and researchers must always seriously consider the

degree to which apparent behavioral similarity between humans and nonhumans could be superficial.

## The Evidence We Have

Comparative psychologists have developed several notable approaches with nonhumans to test behaviors that imply self-awareness in humans. Here, we give an overview of the performance of multiple species on tests for three notable capacities related to self-awareness: metacognition, theory of mind, and mirror self-recognition.

### Metacognition

If you have ever second-guessed how you spelled a word and looked it up to double-check yourself, you have engaged in metacognition. Metacognition is colloquially described as thinking about thinking. It encompasses a broad spectrum of cognitive processes involved in the monitoring and control of thinking. Metacognitive behavior can be controlled by multiple cues, both public and private (e.g., Basile et al. 2015; Brown et al. 2017; Hampton 2009). Public cues are those that others can monitor, such as knowing that the person sleeping in class will need to restudy the material later, whereas private cues are those that only the thinker can monitor, such as knowing that you should restudy the class material later because you have forgotten it. Both public and private cues are useful for efficient cognition; however, the ability to metacognitively monitor private cues may uniquely inform our knowledge of self-awareness because self-reflective thought has been proposed to be a key component of self-awareness.

### Basic Metacognition Paradigms

Metacognition paradigms in nonhuman animals rely on a primary task that requires a cognitive judgment and a secondary metacognitive judgment based on the subject’s perceived likelihood of success on the primary task. To elicit metacognitive responding, the primary task usually involves a range of difficulty levels: easy trials on which the subject is likely to answer correctly

and difficult trials on which the subject is likely to answer incorrectly. Secondary metacognitive judgments allow the subject to take some form of adaptive action, such as allowing subjects to opt out of difficult trials, return to difficult trials later, make wagers based on past choices, or seek information when ignorant. Metacognitive responses can occur prospectively before tests, concurrently at the same time as the test, or retrospectively after the primary cognitive test has been completed.

Primary cognitive tests typically require one of two types of judgments: perceptual or mnemonic. Because it is relatively simple for experimenters to manipulate the objective difficulty of psychophysical stimuli, metacognition tasks have often relied on perceptual discriminations. A psychophysical discrimination requires animals to discriminate stimuli that differ along a continuum, with some difficult trials that fall close to the boundary of the just noticeable difference between two anchor stimuli. For example, subjects might discriminate between sparse or dense dot displays (e.g., Smith et al. 2014) or need to identify a target of a specific size or brightness from among distractors (Brown et al. 2017). The second major type of judgment used in metacognitive tests is mnemonic. Memory tests depend on the persistence of a mental representation for a previously seen stimulus through a retention interval. The quality of the memory either varies stochastically or can be experimentally manipulated, so subjects sometimes remember and sometimes forget (e.g., Basile et al. 2015; Hampton 2001). With memory paradigms, subjects make metacognitive judgments about whether they remember or have forgotten the answer.

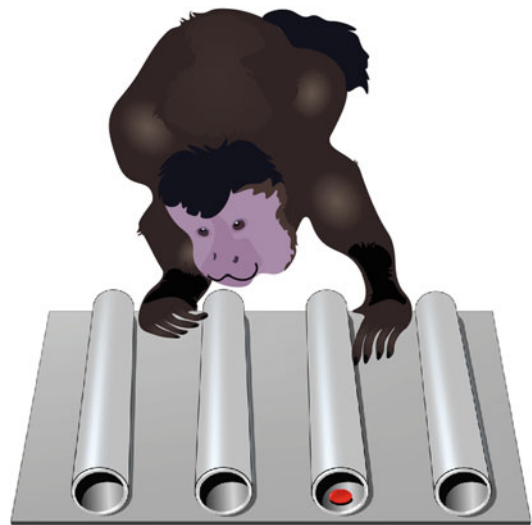
Different tasks rely differentially on public and private cues. Metacognitive judgments about perceptual stimuli may rely on public cues because the difficulty of the stimuli is externally observable by all, whereas judgments about memory are more likely to be controlled by private cues because the state of your memory is something only you can access. Similarly, prospective judgments may rely more on private cues because the subject must make their judgment without seeing

the choice stimuli and therefore are more likely to rely on internal representations. Thus, in the evidence we describe below, we cover perceptual judgments briefly and concentrate on prospective tests of metamemory.

### Evidence About Metacognition

Most species that have been tested have succeeded at making adaptive metacognitive responses about perceptual tests. These include insects, cetaceans, rodents, birds, old- and new-world nonhuman primates, and humans (the success of this field has yielded more good comparative studies than our citation limit allows; for two good reviews, see Hampton 2009; Smith et al. 2014). Because these perceptual tests can often be based on externally observable public cues, it is difficult to unambiguously interpret them as evidence for a private, introspective self-awareness (Fig. 1).

Compared to metacognitive tests that use perceptual tasks, those that rely on memory for their primary discrimination have given more mixed



**Self-Awareness, Fig. 1** A capuchin crouches to look down a tube in search of hidden food. According to the premise of several metacognition experiments, an introspective animal will search when ignorant but select a tube immediately when knowledgeable. One interpretation of this introspective access is that it is only possible if the animal is self-aware. (Adapted with permission from a photo by Benjamin Basile)

results across different species. Humans, other great apes, and old-world monkeys reliably opt out, seek information, or wager small amounts when their memory is weak (for a recent review, see Smith et al. 2014). Similar evidence from new-world monkeys is equivocal (e.g., Basile et al. 2009; Fujita 2009). A recent paper suggests that rats can opt out of difficult odor memory tests (Templer et al. 2017). Evidence from dogs and pigeons shows that they generally do not behave metacognitively in memory tests (Brauer et al. 2004; Sutton and Shettleworth 2008). The most robust conclusion from these results is that humans, apes, and old-world monkeys seem able to explicitly monitor some aspect of their memories.

One reason memory tests are important is because they provide the unique opportunity to present the metacognitive judgment prospectively, before the test stimuli are seen. Placing the metacognitive discrimination before the test stimuli are visible limits the availability of public cues to control metacognitive judgments, which increases the likelihood that metacognitive judgments are controlled by private cues like introspection of an internal memory state. Large-billed crows have made successful metamemory judgments in retrospective but not prospective paradigms (Goto and Watanabe 2012). In new-world capuchin monkeys, at least one individual was able to make prospective judgments, but the other tested individual could not (Fujita 2009). The recent report of rat metamemory used a “pseudo-prospective” response that is promising and justifies more investigation (Templer et al. 2017). However, only old-world primates, including humans, apes, and old-world monkeys, robustly and repeatedly pass prospective metamemory tests (for a review, see Hampton 2009).

#### Does Metacognition Test Self-Awareness?

The liberal interpretation of observed species differences in metacognitive performance is that they reveal the degree to which different species introspect about their own cognition and thus the degree to which they are self-aware. Specifically, humans, other great apes, and old-world monkeys robustly “succeed” on prospective metamemory

tests and thus are most likely to share an introspective self-awareness. The successes and failures in perceptual or non-prospective metacognitive tests are harder to interpret with respect to introspection, but even they could possibly indicate some level of self-awareness. Humans and nonhumans alike use a variety of cues to make metacognitive judgments, based on what information is salient and available under given testing conditions. For example, although public cues are available in perceptual tests, multiple studies have shown that some species, such as rhesus monkeys, generalize performance across a variety of metacognitive tasks (e.g., Brown et al. 2017). Generalization suggests that their metacognitive judgments may be controlled by a domain-general cue, such as private introspection about uncertainty, even on perceptual tests.

The skeptical interpretation of these metacognitive tests is that the ability to make metacognitive judgments does not necessitate self-awareness. If a metacognitive task relies on judgments about public cues, then it is difficult to strongly infer any introspection. For example, a pigeon completing a psychophysical brightness discrimination could learn that certain brightness levels, those near a perceptual threshold, are rarely rewarded. The pigeons might then naturally avoid these low-reward trials if given the option. Importantly for any interpretation relating to self-awareness, this behavior would be a cognitive judgment of the reward contingencies in the external environment and would not involve any introspection involving a subjective sense of self. Thus, the skeptical interpretation of perceptual metacognitive tests is that they measure learning about the relations between reward probabilities and environmental cues.

Even tests of metacognition that likely preclude the use of public cues, such as prospective memory judgments, may not test self-awareness. Although introspection may involve self-awareness, it does not always need to do so. For example, a vending machine monitors what is inside itself and will opt out of transactions it cannot complete, but it does not have human-like self-awareness. Researchers of human



metacognition make the distinction between noetic metacognition, judgments based on an explicit cognitive representation, and autonoetic metacognition, judgments based on a self-referential state that would relate to self-awareness (Metcalfé and Son 2012). Thus, a monkey faced with a prospective metamemory judgment may noetically know “the answer is stimulus X” but still not autonoetically think “I am certain that the answer is stimulus X.” Metamemory judgments may reveal which cognitive processes are subject to explicit monitoring in a given species without necessitating that the subject is thinking about itself.

#### Metacognition Summary

Many species make metacognitive judgments, but the interpretation of that performance changes substantially depending on specific task parameters. Prospective judgments of memory provide the strongest evidence for explicit introspection and thus hold the most relevance for self-awareness. Most species are able to make judgments about public cues, such as with concurrent perceptual discriminations, but generally only old-world primates show robust evidence for making decisions about private cues, as with prospective mnemonic judgments. The liberal interpretation of this evidence is that old-world primates, including humans, other great apes, and old-world monkeys, all possess an introspective self-awareness. The skeptical interpretation of this evidence is that metamemory tests indicate which cognitive processes are explicitly monitorable, but such monitoring does not necessitate self-awareness. Nevertheless, these studies provide information about what cognitive processes are explicit or implicit in different species.

#### Theory of Mind

In poker, you might bluff by betting a lot even though your cards are terrible. Bluffing relies on a player’s ability to know that different players know different things, to predict another’s behavior based on their unique knowledge, and to influence that behavior by deceptively giving incorrect information. This ability to know that knowledge states control behavior and that your knowledge

states are different from those of others is called theory of mind.

#### Basic Theory of Mind Paradigms

Most theory of mind tests are variations on a false belief task. In human developmental work, the most well-known false belief task is the Sally-Anne test (Baron-Cohen et al. 1985). In the Sally-Anne test, an experimenter shows the child subject that a desired object is in one of two hiding places. Then, the first experimenter leaves the room, and a second experimenter arrives to move the object to the other location. The child is then asked where the object is and where the first experimenter will look for the object when they return. The first question tests whether the child understands that the object has been displaced. The second question tests whether the child understands that the behavior of the first experimenter will be controlled by their now out-of-date knowledge about the location of the object. If the child expects the experimenter to search where the experimenter saw the object previously, it is taken as evidence that the child attributes a “false belief” to the experimenter and thus that the child has theory of mind.

Most paradigms used with nonhuman animals have borrowed their logic from the Sally-Anne test. In general, the subject is presented with a desired and hidden object, usually food, and another individual that is either ignorant or knowledgeable of the hiding location. Different studies have used either a conspecific or a human experimenter as the other individual. If the subject behaves differently in the presence of a knowledgeable partner than in the presence of an ignorant partner, then an argument can be made that the subject attributes the respective knowledge state to their partner.

Additional evidence for theory of mind comes from anecdotal observations that might be attributable to deception or audience effects. Deception involves the act of hiding information, or giving incorrect information, to others. For example, a poker player may act nonchalant after receiving a good hand, or a chimpanzee might not give its usual food call upon finding desired food. Audience effects refer to when an individual behaves

differently when in the presence of other individuals than when alone. For example, a poker player may bluff only when playing against another individual and not when playing on a poker machine, or a monkey may give a predator alarm call only in the presence of other monkeys. Both deception and audience effects have been taken as implying that subjects attribute mental states to others.

### Evidence About Theory of Mind

Many species produce natural behaviors that seem deceptive or vary as a function of audience presence. Chimpanzees have been observed to walk in the opposite direction of highly prized food when in the presence of other chimpanzees (Hirata and Matsuzawa 2001). This could be interpreted as reflecting intentional deception. Marsh harriers have been reported to begin courtship routines but then terminate those routines when they had gained access to the mate's food cache (Simmons 1992). Similar behaviors have been observed in a variety of species.

In studies based on human false belief tests, a variety of evidence has been gathered in great apes. Chimpanzees will attempt to retrieve food if a dominant conspecific is ignorant of the food's location but will avoid retrieving the food if the conspecific knows the food's location (Hare et al. 2001). This might indicate that they attribute a knowledge state to the conspecific. In a recent study using eye tracking, chimpanzees, bonobos, and orangutans watched a human chase a costumed human into a straw pile but then watched the costumed human dart to the opposite straw pile while the first human wasn't watching (Krupenye et al. 2016). When the first human returned to search the two piles, the apes looked at the first pile in anticipation, as if predicting that the human would search in the wrong location because he held a false belief.

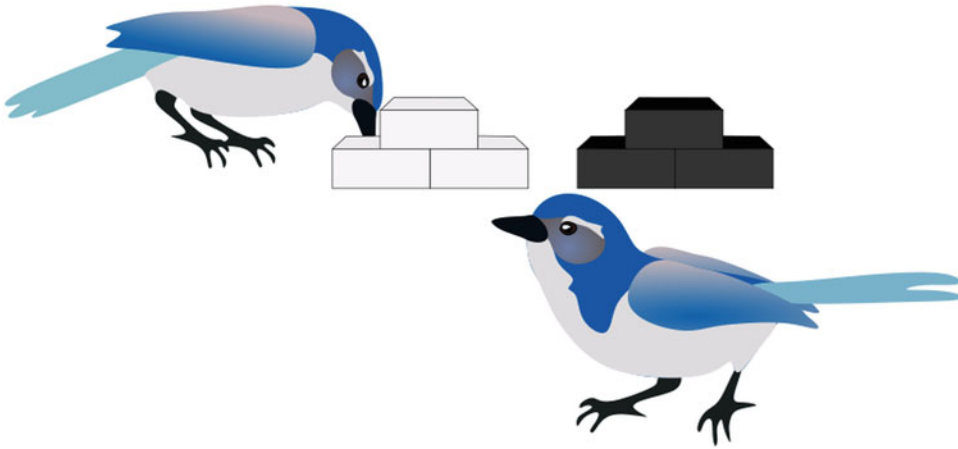
Related studies have looked at the ability of subjects to retrieve food based on the indications of knowledgeable or ignorant partners. In some studies, chimpanzees spontaneously use human or conspecific signals to choose among potential locations of hidden food (Itakura et al. 1999). In contrast, monkeys such as capuchins generally learn to follow similar signals only after trial-

and-error training (Essler et al. 2017). These species differences suggest that some species, like chimpanzees, spontaneously attribute knowledge states to others, whereas other species, like capuchin monkeys, may only do so under limited circumstances. Similar studies have been done with food-caching birds. Jays will preferentially cache food behind opaque barriers compared to transparent barriers when in the presence of conspecifics (reviewed in Clayton and Emery 2015). In addition, if they were observed by another bird, they would later re-cache the food in a different location. Importantly, this re-caching was dependent on whether they had previously pilfered another bird's cache. This suggests that they infer the knowledge state of other birds by simulating what their own knowledge state would be in that situation (i.e., I would pilfer this site if I were him, so I'll re-hide it somewhere he hasn't seen) (Fig. 2).

### Does Theory of Mind Test Self-Awareness?

The liberal interpretation of theory of mind tests is that "passing" them is only possible if the subject is self-aware. If you attribute a mind to me and know that I believe something different than you, then you must also be attributing a mind to yourself, one that believes something different from me. This knowledge of your mind as a unique mind among many is, for some, the very definition of self-awareness.

There are several skeptical interpretations of theory of mind tests. The most lasting criticism of theory of mind tests is that they are non-mentalistic "theory of behavior" tests (e.g., Heyes 1998). You can probably predict with some accuracy the behavior of a poker machine, but you likely don't attribute a mind to that machine. Further, your ability to predict a poker machine's behavior says nothing about your own self-awareness. Similarly, it is possible that a chimpanzee who predicts that a conspecific will retrieve visible food or a bird that re-hides its food cache may be predicting another's behavior without representing another's mind or another's false belief. Thus, a plausible explanation for putative theory of mind studies in chimpanzees, for example, may be that they have learned to predict the



**Self-Awareness, Fig. 2** A western scrub jay caches food while a conspecific watches. According to the premise of several theory of mind experiments, an animal that attributes mental states to others will avoid thievery by changing the location of its caches when the conspecific

is no longer present. One interpretation of attributing minds to others is that it requires being self-aware of one's own mind. Illustration based on description of experiments reviewed in Clayton and Emery 2015

behavior of conspecifics under given circumstances, without necessarily attributing a mind to them. One intermediate explanation, proposed specifically for chimpanzees, is that they attribute limited mental capacities to others, such as intentions and knowledge states, but not other mental capacities, such as false beliefs (Call and Tomasello 2008). Whether a limited but present theory of mind implies a limited but present self-awareness is unclear.

Even in studies of humans, for whom we generally assume self-awareness, the discriminative validity of theory of mind paradigms has been questioned. In studies of human children, there are country-to-country differences in the age at which human children begin to “pass” the false belief test. For example, at 44 months of age, roughly 40% of Japanese children “pass,” whereas nearly 70% of Australian children “pass” (Wellman et al. 2001). These differences are better explained by other factors, such as variability in inhibitory control due to cultural differences in parenting style, rather than by positing that Australian children are more self-aware than Japanese children. Consistent with this, a wide variety of relatively minor task parameters, such as how the question is asked or if the actors are live humans or puppets, significantly change

whether children “succeed.” The susceptibility of theory of mind tests to changes in relatively minor task parameters, even in a species to which we regularly attribute theory of mind, makes the success or failure of an individual subject or even an entire group in an individual study difficult to interpret.

Much of the evidence relying on anecdotal observations cannot be unambiguously attributed to theory of mind. Seemingly deceptive behavior can be exhibited as a result of operant learning of external behavior-reward contingencies (omitting food calls in the presence of others results in more food and is thus repeated), happenstance (a potentially deceptive behavior of initiating mating to gain access to the mate's food could result from a legitimate mating display being abandoned once desired food is visible), or species-typical behavioral patterns. For example, clear demonstrations of deception and audience effects are exemplified by behaviors that are sometimes considered fixed action patterns. Fixed action patterns are highly stereotyped reflexive behavior sequences. Consider the broken-wing display given by several bird species (see also similar behaviors in fish), in which a parent bird will walk away from its nest in a hobbling fashion that resembles a bird with a broken wing. The

behavior has the outward appearance of being intended to deceive a predator and is only performed when a predator is present. Nonetheless, the behavior is highly stereotyped, reliably elicited by the correct stimuli and circumstances, and exhibited without training in several species. The varying explanations for such observations make it difficult to attribute them to intentional deception or theory of mind.

### Theory of Mind Summary

Studies of theory of mind in nonhuman animals come primarily from observational anecdotes of seemingly deceptive behavior or from experiments based on human false belief tests. Several species, such as chimpanzees and some bird species, seem to engage in deceptive or audience-dependent behaviors in the wild and discriminate between knowledgeable and ignorant partners in false belief-like tests. The generous interpretation of these tests is that these species attribute independent minds to others and thus are likely aware of others' minds and their own minds. The skeptical interpretation of these studies is that the observational anecdotes can be attributed to a variety of non-theory of mind causes, that theory of mind tests are poor at actually discriminating those who have theory of mind from those who do not because "failure" can be attributed to other causes, and that the behavioral prediction seen in nonhuman tests does not necessitate the attribution of minds.

Regardless of the ability of these studies to address questions about self-awareness, they have revealed a variety of interesting behaviors and cognitive capacities. Several species behave in seemingly deceptive ways, and these behaviors may be elicited via different mechanisms. Some species seem to reliably predict others' behaviors. It is likely that similar future studies will produce interesting insights into comparative cognition.

### Mirror-Guided Behavior

Look in a mirror and you're probably reflecting on yourself both literally and figuratively. Because we so often react to mirrors with self-reflection, researchers who are interested in self-awareness in animals have long wondered: What do they see

in the mirror? If they see themselves, then maybe they're self-aware.

### Basic Mirror-Guided Behavior Paradigms

The basic paradigms of studying mirror-guided behavior in nonhuman animals generally fall into three broad categories: (1) studies of the ability to understand the optics of mirrors, as evidenced by the ability to use them as tools, (2) qualitative observations of self-directed behavior elicited by the presence of a mirror, and (3) evaluating whether individuals "pass" the mark test by touching a visual mark on their body that they could not have seen without the mirror.

Studies of the ability to understand the optics of mirrors usually involve requiring individuals to use the mirror as a tool to interact with the world. For example, imagine a rhesus monkey wants to retrieve a piece of food but cannot see the food's location due to a visual barrier. Using the sight of its arm in a mirror, it can correctly find the food. Using a mirror as a tool to see around corners does not in itself test any aspect of self-awareness. However, understanding that mirrors reflect the world is a prerequisite for recognizing oneself in the mirror. Most animals do not live in environments with access to mirrors, or with access only to surfaces that provide blurry reflections, so we cannot assume they would even be able to learn or understand the visual properties of mirrors. The ability to use a mirror as a tool suggests that they do.

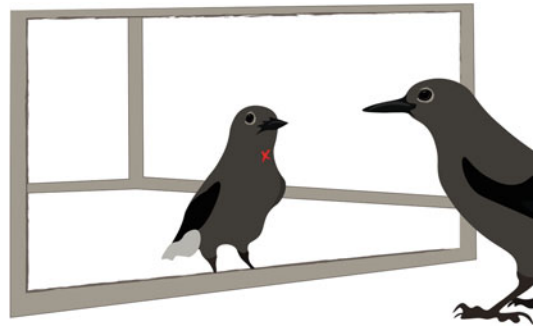
Qualitative observations of mirror-guided behavior encompass a broad array of possible types of evidence. In these observations, there is no universally agreed upon litmus test for what "counts" as evidence in favor of self-awareness. Put an individual in front of a mirror and describe its reaction. If that reaction seems largely self-directed, such as using the mirror to look at parts of the body that are usually visually inaccessible, then perhaps the individual recognizes itself in the mirror. If the individual behaves as though its reflection is a conspecific, such as trying to fight it, or if it ignores its own reflection, then perhaps the individual does not see itself.

The mark test is a special type of experiment in which the experimenter imposes a strict pass/fail criterion for self-directed behavior. Typically, a mark is placed somewhere in the individual's body where it cannot be seen without the help of a mirror, such as a dab of dye on the ear. The critical test is whether the individual touches or tried to remove that mark. To "pass" the mark test, individuals should touch the mark more in the presence of the mirror than in the absence of the mirror. This controls for non-mirror-related touching due to the mark being itchy or the individual naturally liking to scratch its ear. For many years, the mark test has been the de facto pass/fail test of mirror self-recognition.

#### Evidence About Mirror-Guided Behavior

What makes studies using mirrors particularly fascinating to researchers of comparative cognition is that species display a wide variety of different patterns of behavior in front of mirrors. Betta fish will "fight," and anole lizards will perform dominance displays to scare off their mirror image. For these species, these displays stay fairly consistent across exposures. The animals seem to never learn that their reflection is not an enemy and thus treat what they see in the mirror as another individual, rather than a reflection of themselves.

Some species, like most species of monkeys, show a different pattern. They do not fight with their reflections, or if they do, they quickly learn that it is not another monkey (de Waal et al. 2005). They can learn to use mirrors as tools to locate and retrieve food (Anderson and Gallup 2011). Mirrors are also routinely used as enrichment devices, and monkeys will use them to peer around corners. Thus, they likely understand the optics of the mirror to some degree. Nonetheless, monkeys do not spontaneously engage in much self-directed behavior, such as using mirrors to examine their mouths or perineae (Anderson and Gallup 2011). Despite numerous investigations, most monkeys "fail" the mark test (but see Chang et al. 2017). Similar results, being able to use a mirror but not engaging in mirror-guided self-exploration, have been reported in parrots (Pepperberg et al. 1995). In one interesting example that combines theory



**Self-Awareness, Fig. 3** A Clark's nutcracker looks in the mirror after an experimenter has surreptitiously placed a mark on its chest. According to the premise of the mirror mark test, an animal that recognizes itself in a mirror will use its reflection to examine the mark on its own body. One interpretation of mirror self-recognition is that it requires self-awareness. (Adapted from Clary and Kelly 2016, distributed under the terms of the Creative Commons CC BY license)

of mind tests with mirror tests, Clark's nutcrackers treated blurry reflections as themselves, pecking a mark and caching normally, but treated clear reflections like another bird, avoiding caching and not pecking the mark (Clary and Kelly 2016). This may represent a limited mirror self-recognition based on broad contingent motion but not extending to fine-grained visual features (Fig. 3).

Finally, a select group of species, most notably chimpanzees, produces a pattern of behaviors that is strikingly similar to that of humans (Anderson and Gallup 2011). They do not treat the mirror as another animal. They can use the mirror as a tool. They often spontaneously use the mirror to explore difficult-to-see body areas. They often "pass" the mark test.

This variety in how different species react to mirrors suggests a possible continuum of mirror self-recognition. On one end, species like fighting fish appear to not understand mirrors or recognize themselves. In the middle, species like monkeys appear to not recognize themselves in mirrors, despite understanding how mirrors work and not treating the mirror image as a stranger. On the other end, species like chimpanzees appear to fully recognize themselves in the mirror. However, species that "pass" the mark test do not



cluster along only a single phylogenetic branch. In addition to humans and chimpanzees, dolphins, elephants, and magpies have been reported to “pass” the mark test. These cases may result from convergent evolution of cognitive processes.

#### Does Mirror-Guided Behavior Test Self-Awareness?

The liberal interpretation of mirror-related studies, especially the mark test, is that they assess self-awareness. Further, that they demonstrate a species continuum revealing both the evolutionary origins of human self-awareness, as seen in chimpanzees, and cases of convergent cognitive evolution, as seen in dolphins. Perhaps more than any other paradigm, the link between recognizing oneself in the mirror and self-awareness is intuitive. A person who looks in the mirror and says “That’s me!” is explicitly self-aware. It is parsimonious to assume that a chimpanzee who looks in the mirror and touches its own face may be thinking something similar.

The skeptical interpretation of mirror studies is that many “failures” reflect less about self-awareness and more about motivation. There is little doubt that species do differ in their reaction to mirrors. However, it is not always clear how to interpret these differences. For example, pigeons and monkeys typically “fail” the mark test. But if they are trained that touching a visible mark results in food, then they will indeed transfer to touching that mark when they need a mirror to do so (Chang et al. 2017; Epstein et al. 1981). In addition, without any such training, monkeys often fail to show any interest in touching marks on themselves even when those marks are plainly visible without a mirror (Roberts 2011). These types of studies suggest that at least some of the “failures” in the mark test are due to motivation.

In humans, there are cultural differences in the age at which children “pass” the mark test. This is similar to studies of theory of mind (see previous section). For example, at 3 to 4 years old, almost 90% of children from the United States “pass,” whereas roughly 50% of children from Peru and 0% of children from Fiji “pass” (Broesch et al. 2011). These cultural differences are better explained by other factors, such as cultural

norms, rather than by positing that Peruvian children are partially self-aware and Fijian children are not.

In chimpanzees, the nonhuman species that most often and clearly passes the mark test, there are also inconsistencies in the data. Roughly half of chimpanzees “pass” the mark test. In longitudinal data, with the same individuals tested year after year, sometimes individuals that “pass” one year will “fail” the next year (de Veer et al. 2003). It seems unlikely that only half of the individuals in a given species would be self-aware, or that self-awareness takes the occasional year off. It is more reasonable to assume that this variability is due to other factors, such as differences in motivation between individuals or days. If true, then the mark test does not discriminate self-aware species from nonself-aware species but rather the combination of an individual’s ability to understand mirrors and their motivation to touch marks.

#### Mirror-Guided Behavior Summary

Tests of mirror-guided behavior generally test whether species understand the optics of mirrors, whether they spontaneously use mirrors to explore their own bodies, and whether they “pass” the mark test by touching an otherwise out-of-view mark on their body. Results show wide spectrum of interesting species differences from complete non-understanding of mirrors to apparent self-recognition. The generous interpretation of mirror tests is that they assess which individuals or species can recognize themselves and thus are self-awareness. The skeptical interpretation is that they assess understanding of mirrors and motivation to touch marks. Regardless of their applicability to self-awareness, the obvious species differences seen in these studies will likely continue to motivate informative research.

### Unresolved Issues and Future Directions

This entry only scratches the surface of what we know about metacognition, theory of mind, and mirror-guided behavior. In addition, these are only three of the major paradigms that researchers

have used to approach the comparative study of self-awareness. With this in mind, it is worth addressing some of the major unresolved issues and future directions.

First, there is the question of whether self-awareness has any utility or if it is an epiphenomenon. There is no question that some of the paradigms described here tap specific abilities that could be useful. Predicting the behavior of others would be useful for social animals because it allows one to anticipate the actions and reactions of conspecifics that help determine foraging and mating opportunities. Introspection and memory monitoring have utility in cognitive control – the ability to actively change thinking to improve learning and remembering. However, in none of these candidate sub-cases is an organism necessarily any better served by being truly self-aware rather than having the component features. It may be that self-awareness is not a unitary process but the complex interplay of multiple processes, with self-awareness arising epiphenomenally from some combination of them.

It is unclear how to interpret the different patterns of species differences seen in the different paradigms that researchers often use to inform questions of self-awareness. For example, rhesus monkeys robustly “pass” metacognitive tasks, even those relying on the introspective private cues, but generally “fail” or show equivocal evidence on theory of mind and mirror tasks. Complicating interpretation, some species “pass” one version of a paradigm and “fail” another, or “pass” the same study 1 year and “fail” it the next. The possible interpretations of these discrepancies broadly fall into one of these variants: (1) These paradigms test self-awareness but have not yet been sufficiently refined to give valid and robust measures. (2) These paradigms test different aspects of self-awareness and not all species display all aspects. (3) These paradigms do not test self-awareness but rather test other aspects of cognition that vary among species and individuals. One explanation for the cross- and within-species difference is that while self-awareness is a categorical binary, it depends on a range of sub-processes. Self-awareness probably did not emerge as a unitary process fully formed for the

first time in humans. Self-awareness emerges gradually via intermediate stages along a developmental trajectory in humans, and it is likely that this was also the case during evolution. If this is the case, many nonhumans may possess a smattering of cognitive capacities that are prerequisite to self-awareness without a fully formed and human-like subjective sense of self-awareness. Future research will benefit from combining the often-abstract laboratory tests with more naturalistic studies that respect a given species’ ethology. Self-awareness is a human concept, and so it is natural that comparative researchers started by borrowing methods from human psychology. However, this leaves open the possibility that species will “pass” or “fail” these tests as a function of how similar they are to humans in ways that are irrelevant to the question of interest. For example, it makes little sense to test a naked mole rat with a mirror, because they have such poor vision. Similarly, it may make little sense to test a monkey in a mirror-guided mark test, because they often do not care about marks. One of the major challenges for researchers who want to expand the comparative study of self-awareness, or related cognitive capacities, to other species will be to devise tests that make sense for a given species.

One recurring issue that hinders progress in research on self-awareness and related cognitive capacities is finding the proper balance between anthropomorphism, attributing human qualities to nonhumans, and anthropodenial, denying human qualities to nonhumans. It is tempting to think that one’s cat recognizes itself in the mirror but also to dismiss the possibility of pigeon self-awareness as inherently silly. This balance is continually threatened by our human biases and by the reinforcement contingencies of academia that reward demonstrations of “smart animals” with high-profile publications. As with many balances, the truth is likely somewhere in the middle, and continued progress in the comparative psychology of self-awareness will probably rely on not tipping too far in either direction. To the extent that we can formulate clear hypotheses that can be tested objectively, we can avoid both anthropomorphism and anthropodenial.

A challenge for future researchers is to identify factors that can alter these processes. Some of these factors will probably be tied strongly to a species evolutionary niche. For example, we might reasonably expect highly social species to be better than solitary species at predicting the behavior of others. Other factors will probably reflect individual experience. For example, most human children experience years of daily mirror exposure and explicit instruction (e.g., “Who’s that in the mirror? That’s you!”), and much of this difference might produce the observed cultural differences. Similarly, reliable differences are present between chimpanzees that are enculturated and those that are not, and results from monkeys and pigeons indicate that they can reliably be trained to engage in mirror-guided behavior, both using mirrors as tools and passing the mark test, if motivated by food. Thus, just as identifying the factors that influence performance on these tests in humans has been a major research focus, identifying the factors that influence similar performance in different species will be a major challenge moving forward.

Behavior necessarily depends on the brain, so it is natural to examine the neural correlates of self-awareness to better understand the degree to which nonhumans possess the same capacities. However, using neural evidence to assess the presence or absence of self-awareness in other species is problematic. First, it is unclear, even in adult humans, how best to arrive at a neural signature of self-awareness. Imaging studies usually require a comparison of two conditions, and self-awareness is so automatic in humans that it is unclear how best to compare a self-aware human to a non-self-aware human. Second, even if we had an unambiguous neural signature of self-awareness in humans, it would be unclear how to interpret the presence or absence of a similar signature in nonhumans. Although neural homology should inform theories of comparative cognition, it is not necessary or sufficient to assume shared function. For example, if we use the liberal interpretation of theory of mind studies in food-caching birds, then bird brains are so different from primate brains that they likely perform the same cognitive function using different neural

hardware. Interpreting the lack of a neural signature as a lack of self-awareness would be ignoring convergent brain evolution, and interpreting the presence of such a signature as proof of self-awareness would be modern phrenology. Ultimately, these are psychological phenomena, and we need to understand them on a psychological level before we attempt to identify their neural substrates. Nonetheless, outside of self-awareness, studying the brain bases of metacognition, mirror-guided behavior, and prediction of social actions holds promise for our understanding the neural correlates of those cognitive capacities.

Comparative psychologists have made many clever efforts to understand processes in nonhumans commonly associated with self-awareness in humans. However, self-awareness continues to be a subjective individual experience. Our best evidence for self-awareness in humans is verbal self-report. We will never be able to “ask” nonhumans if they are self-aware in the same way that we can ask other humans. Our challenge is to better state what animals with self-awareness can do that animals without it cannot and design experiments that test whether animals can or cannot do the behaviors that depend on self-awareness.

## Conclusion

Eighty five years ago, Tolman stated that the very question of self-awareness in nonhumans could produce only guesses (1932). Today, there is still no consensus about self-awareness in nonhumans, and there probably will never be.

Researchers have attempted to answer the question by studying a variety of cognitive capacities that seem intuitively related to self-awareness. Three of the most notable are metacognition, theory of mind, and mirror self-recognition. The liberal interpretation of these studies is that some species think about their own minds, attribute minds to others, and recognize themselves in a mirror. Together, these behaviors paint a rich picture of self-awareness in some nonhuman species such as chimpanzees. The skeptical interpretation of these fields is that

some species can use some aspects of their own cognitive states as discriminative cues, can predict the behavior of others in their environment, and understand that mirrors reflect the world and have the motivation to touch marks. Together, these behaviors demonstrate a variety of interesting cognitive capacities, but none that could not be carried out by a non-self-aware robot. The primary impediment to reaching consensus between the liberal and skeptical views of self-awareness is the classic philosophy “problem of other minds,” which describes the fact that we must take the existence of others’ self-awareness on their word. Because nonhumans cannot give us their word, it is likely that the comparative “problem of other species’ minds” is unsolvable.

Regardless of our ability to answer the big question of whether nonhumans possess human-like self-awareness, the pursuit of this question has produced a wealth of answers to smaller, more-tractable questions. Some nonhumans can monitor some aspects of their cognitive states, can predict what others might do, and can use mirrors in self-guided behaviors. Some cannot. This has been useful research and will continue to inform comparative psychology for years to come.

## Cross-References

- Alarm Calls
- Anthropomorphism
- Broken Wing Display
- Bucket Experiment
- Consciousness
- Deception
- Fixed Action Patterns
- Mark Test, The
- Metamemory
- Meta-Cognition
- Mirror Self-Recognition
- Role-Reversal Experiment
- Self-Directed Behavior
- Sparse/Dense Discrimination
- Swine Cognition
- Theory of Mind
- Uncertainty Paradigm
- Visual Self-Recognition

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## Self-Control

- Inhibition
- Restraint

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## Self-Decoration

- Self-Decoration in Dolphins

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## Self-Decoration in Dolphins

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## Synonyms

Animal kingdom; Body decoration; Bottlenose dolphins; Object handing; Ornamentation; Self-decoration; Social behavior



## Self-Decoration in Humans

Decorating the body with objects or pigments is so routine in every contemporary human culture that most people take it for granted (Kuhn et al. 2001). Yet contemporary jewelry, cosmetics, and tattoos have a long history. Body decoration probably began with colors and expanded to objects. To decorate objects or themselves, ancestral humans in Africa used a red-brown pigment called ochre 200,000–300,000 years ago (Barham 2002) and European Neanderthals used another red pigment called hematite 200,000–250,000 years ago (Roebroeks et al. 2012). Thus, body decoration with color is not unique to *Homo sapiens*. Early decorative objects were pendants and necklaces made by piercing and stringing teeth, shells, or bones. The oldest beads used in human self-decoration, found in Skhūl, Israel, are dated to at least 100,000 years old (Vanhaeren et al. 2006). Fossil beads are among the earliest unambiguous evidence that objects were worn to communicate (Kuhn et al. 2001), broadcasting such information as ethnic, social, and personal identity (Hynes 2006). Self-decoration was pivotal in human evolution because it represented the earliest human attempts at art (Morriss-Kay 2010) and new vehicles of communication (Kuhn et al. 2001). An important prerequisite for self-decoration was the loss or great reduction of body hair (Morriss-Kay 2010).

## Object Handling in Animals

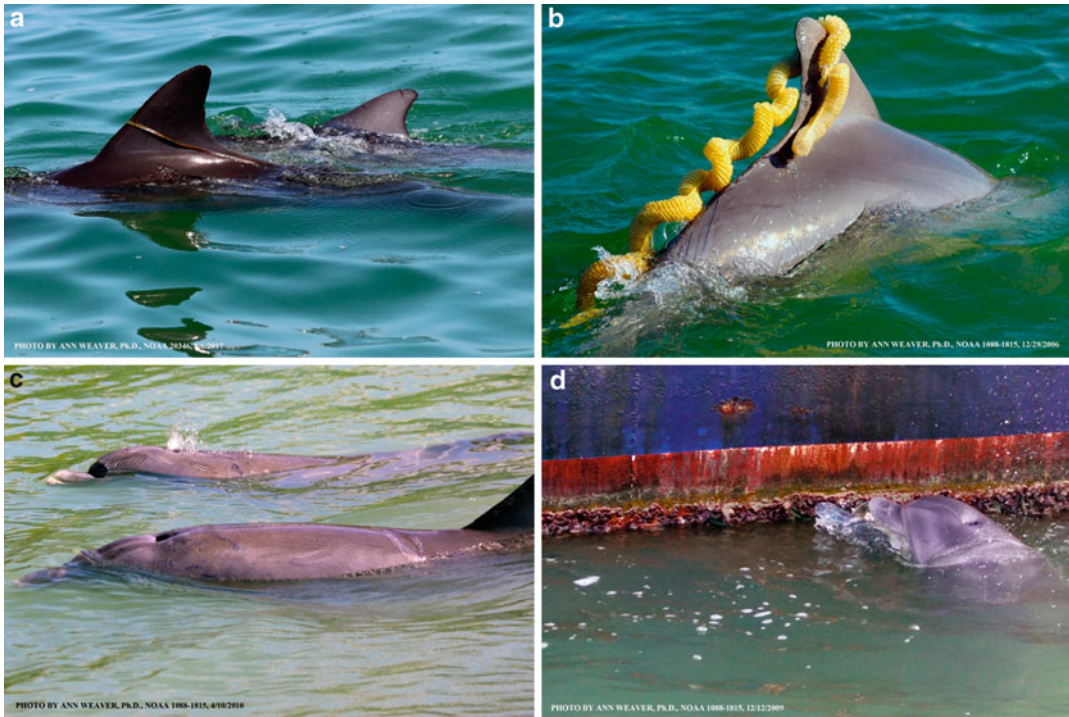
Birds and mammals also routinely handle objects to eat, play, groom, defend, or hide themselves (Beck 1980; Bentley-Condit and Smith 2010; Shumaker et al. 2011; Mann and Patterson 2013), yet rarely self-decorate with them. The best example of self-decoration is a free-ranging female chimpanzee who wore a strip of skin from a fresh monkey kill like a necklace for a day, albeit a one-time observation (McGrew and Marchant 1998). Captive elephants twisted vegetation into ropes and rings that they placed on their bodies, behavior that suggested self-decoration but which Chevalier-Skolnikoff and Liska (1993) classified

as ambiguous. Most examples of animals wearing objects are typically interpreted as protection, play, or display. Crabs ward off predators by shielding themselves with stinging anemones (Griffin 1992). Urchins, caddis fly larvae, and decorator crabs camouflage themselves with broken shells (Bekoff 2004). Apes play and protect themselves from rain by draping themselves with plant material (Beck 1980; Weaver pers obs, San Diego Zoo). Adult male hoofstock, such as rutting elk and moose, amplify their antlers with tattered vegetation in intimidation displays (Walther 1980).

## Self-Decoration in Bottlenose Dolphins

Free-ranging bottlenose dolphins, *Tursiops truncatus*, in Florida have a potential form of self-decoration, grass worn splayed across their dorsal fins (Fig. 1a), in their suite of object handling behaviors (Weaver 2012; Fig. 1b–d). Theoretically, this behavior should not occur because dolphins dislike anything touching their bodies they did not attach themselves (Kuczaj et al. 2012), and accidental contact with plant materials in the author's study area (Weaver 2015) elicits immediate shuddering and diving to remove it. Finally, swimming creates vortices on leading edges of fins that immediately remove objects caught there (Fish et al. 2011). Yet grass-wearing does not elicit shuddering, grass is worn across multiple dives, and some episodes are deliberate. These facts suggest that at least some of the 200+ grass-wearing episodes were intentional. Why do it? Weaver and Kuczaj (2016) investigated grass wearing from 965 surveys of Weaver's 6-mile estuarine study area (2006–2013) that yielded 9,551 dolphin sightings and 190 observations of grass wearing among 79 dolphins. Three years of subsequent grass-wearing data (2014–2016 Weaver, unpub. data) reinforced the following findings, which do not establish but do imply that some social situations encourage bottlenose dolphins to wear grass as self-decoration.

Dolphins primarily wear grass when new dolphins join the group, making it object use in a social setting (Weaver and Kuczaj 2016). Grass



**Self-Decoration in Dolphins, Fig. 1** Suite of object handling maneuvers among Boca Ciega bottlenose dolphins (a) grass-wearing behavior; (b) wearing a whelk

egg case on the dorsal fin; (c) wearing a discarded sunglass lens on the melon; (d) rubbing a catfish along shells growing on ship's hull to remove spines

wearing is five times more likely when dolphins are socializing in affiliative and sexual contexts than when traveling, feeding, or resting. Two-thirds of the grass-wearing dolphins have been seen wearing grass up to eight different times. Yet grass-wearing dolphins do not play with grass as toys or use it as tools to feed, protect, or camouflage themselves, and grass wearing is not an obvious consequence of activities near seagrass meadows. Males and females wear grass at comparable rates, contraindicating a gender bias. Females wear grass across reproductive phases, suggesting it is not limited to social receptivity associated with estrus. For example, the mother of a 4-day-old calf wore grass twice as her group tripled in size with new dolphins.

Grass wearing occurs across various social groups: mating pairs, heterosexual and homosexual groups, and during recreational sex. One example in an affiliative context involved four females and a male who wore grass during a protracted convergence that eventually totaled

32 dolphins. One example in an explicitly sexual context involved frequent changes in sexual pairings between one female and six males, during which the female wore grass four different times and four males each wore grass once.

The common thread across all the varied contexts was that dolphins wore grass when forming a new group, the social process of fusion. During fusion events, a new group member wore grass as it converged on an existing group or a dolphin in the existing group wore grass as new group members joined it.

A fusion event changes the social environment. It can increase existing competition for attention from group members. It can certainly change the social dynamics of sexual interaction by intensifying competition over social partners. Fusions may also introduce ambiguity about subsequent interactions that could benefit from communication that clarifies intentions.

Fusion itself is common. But wearing grass is rare and therefore novel. Novelty attracts attention.

Bottlenose dolphins are attracted to novelty (Kuczaj et al. 2006, 2012), selective about who they observe (Kuczaj et al. 2006; Bender et al. 2009), and modify their own behavior to keep it interesting (Kuczaj et al. 2012). As familiar but moderately discrepant behavior, grass wearing potentially functions as stimulus enhancement that increases conspecific interest in the grass-wearing dolphin. This is consistent with dolphins self-decorating with grass to enhance greetings and bids for attention, or to communicate interest in further social intercourse (Weaver and Kuczaj 2016).

The association of fusion, novelty, and potential bids for attention suggests that grass wearing is related to two fundamental bottlenose dolphin features: loss of body hair and kaleidoscopic social shifting created by fission-fusion behavior. But bottlenose dolphins also practice recreational sex. The combination of fission-fusion and recreational sex may have created unique social pressures that selected for an unusual vehicle of communication involving self-decoration as an occasional social lubricant.

Alternatively, increasing evidence argues that chimpanzees, elephants, parrots, corvids, and cetaceans have culture (McGrew 1992; Boesch 1996; Rendell and Whitehead 2001; Kuczaj and Highfill 2005; Whitehead and Rendell 2015). Further research is needed to establish if grass-wearing behavior is specific to bottlenose dolphins in this geographical location that persists over generations and thus constitutes a cultural component of this dolphin community.

## Cross-References

- Attention-Getting Behaviors
- Cetacean Cognition
- Cetacean Communication
- Ormentation

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## Self-Directed Behavior

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Self-directed behavior can be defined broadly as any behavior directed toward the self, such as scratching, grooming, etc. Self-directed behavior has also been studied specifically within the context of identifying the capacity for self-recognition in nonhuman species. The theoretical interest in self-recognition is motivated by the idea that this cognitive ability could imply self-

awareness, which is a higher cognitive function that has been argued to be unique to humans.

In 1970, Gordon Gallup published an influential paper in which he introduced the mark test. Four chimpanzees (*Pan troglodytes*) were surreptitiously “marked” with an odorless red dye on a point on the body that could be seen only with the aid of a mirror (e.g., on the brow). Researchers subsequently observed the chimpanzees’ behavior both in the presence and absence of the mirror. Individuals that “passed” the mark test increased their mirror-directed exploratory behavior, touching the mark on themselves rather than in the mirror. In contrast, in control situations (in the absence of the mirror and when individuals were sham marked such that the mark did not appear in the mirror), individuals did not show self-directed behavior to the mark area (Gallup 1970). Thus, examining differences in self-directed behavior in the presence versus absence of the mirror (or the mark) was pivotal in demonstrating that chimpanzees were capable of mirror-self-recognition.

## Evidence of Self-Recognition in Studied Species

The mark test has been used to examine self-recognition ability in many species, both invertebrates and vertebrates (see below). When individuals are confronted with their mirror reflection, five different results (or a combination of them) can be obtained: (1) Many of them ignore their mirror-image; (2) many respond to the self-image with social behavior, i.e., treating the mirror-image as if it were a conspecific; (3) some show self-directed behavior; (4) some show self-contingency behavior, i.e., the individual moves in front of the mirror as if assessing the relationship between the mirror-image and its own movements; and (5) a few are able to pass the mark test. Mirror-image exploration and self-contingency behaviors are important requirements in order to pass the mark test, but these behaviors do not imply self-recognition. In fact monkeys and three species of corvids (jungle crows (*Corvus macrorhynchos*), jackdaws (*Corvus monedula*), and new Caledonian crows (*Corvus moneduloides*)) present high levels of



interest for the mirror showing both self-directed and self-contingency behaviors, but crucially, they do not use self-directed behaviors for mark inspection or removal to pass the mark test (Soler et al. 2014). Strong evidence of self-recognition would need touching the mark on themselves (i.e., self-directed behaviors) rather than in the mirror, and/or self-directed exploratory behavior to areas of their body that are otherwise invisible in absence of the mirror. However, often the requirements for the acceptance of self-recognition have been relaxed with less importance attached to the occurrence of self-directed behaviors and, even when individuals are deemed capable of recognizing themselves in a mirror based on their performance in the mark tests, conclusions are often contradictory and/or contentious.

By the end of the twentieth century, it was well known that monkeys did not demonstrate the capacity for self-recognition, although they could use a mirror to locate a hidden object (Anderson and Gallup 2015). Therefore, it was thought that self-recognition was restricted to humans, great apes, and some other mammals with relatively large brains and highly evolved social cognition (Prior et al. 2008). However, during the twenty-first century, numerous papers have claimed that many different species even including insects and other invertebrates are able to recognize themselves in the mirror (see below). Nevertheless, solid compelling experimental evidence involving self-directed behaviors has only rarely been provided. Frequently, there are important problems with these studies. For instance, in many cases, they are based on informal observations showing little more than interest and curiosity by mirror reflections like many non-self-recognizing species. In others, the methodology is too rudimentary to conclude anything, the conclusions are based on evidence provided by a single animal, or the study has failed to be replicated (Soler et al. 2014; Gallup and Anderson 2018).

In invertebrates, the possibility of self-recognition has been suggested in two different groups: squids and ants. Cephalopods such as octopus and squids have relatively large brains and highly developed intelligence; thus, it is

worth testing them for self-recognition. Oval squids (*Sepioteuthis lessoniana*) were subjected to the mark test and marked individuals tended to observe and touch the mirror for longer periods of time than sham-marked individuals (Ikeda and Matsumoto 2007). These cases of interest for the mirror and touching the mirror cannot be considered evidence of self-recognition without direct evidence of self-directed, and not mirror-directed, mark touching (Gallup and Anderson 2018). With respect to ants, recently, Cammaerts and Cammaerts (2015) performed the mark test in several individuals of three different species of the genus *Myrmica*. The authors claim that they passed the mark test given that blue-marked ants in front of a mirror started self-cleaning behavior sooner than in control conditions (absence of the mirror or marked with brown paint, which matches natural coloration). These are seemingly clear results showing self-recognition in ants, but they are very surprising in these small-brained insects. However, given the impoverished vision of ants, the initiation of these self-directed behaviors was likely mediated by the different chemical cues provided by the blue and brown dyes used as marks. In fishes, although some previously published papers suggest that some fish species are able to recognize themselves in the mirror, the provided evidence is very weak, because in studies of manta rays and cichlids, the mark test was not always conducted and, when it was made, self-directed behaviors toward the mark were not observed, which means absence of mirror self-recognition (Hotta et al. 2018).

Mark-test experiments have been performed in several species of birds, including parrots and corvids; two groups that have large brains and complex cognitive abilities. In most of these experiments, the subjects did not pass the mark test by showing self-directed behaviours to the mark. However, in two species of corvids (magpies (*Pica pica*) and Clark's nutcrackers (*Nucifraga columbiana*)), apparently strong evidence of self-recognition behavior has been provided, especially in the magpie. Magpies performed self-directed preening behaviors when in front of the mirror to remove the stickers used in the mark test in two cases. In addition, the



individual that showed clearer evidence for mirror use removed the mark in the four additional tests, (each with a different colored mark), including the control black mark (Prior et al. 2008). However, it has been suggested that the use of tactilely perceivable self-adhesive stickers and the impossibility of producing a true sham mark control could have generated these self-directed behaviors to the mark, leading to false-positive results within a small sample size (Soler et al. 2014; Gallup and Anderson 2018).

In addition, there is a characteristic that could be considered typical of self-recognizing species (elephants (*Elephas maximus*), dolphins, and chimpanzees; see below) that does not occur in corvids: habituation. That is, they lose interest in the mark when they realize that it is their behavior that they are observing in the mirror. When this occurs, they stop self-contingent behavior (i.e., rapid left and right or back and forth movements of the head or the whole body in front of the mirror) and begin to explore normally unseen body parts. However, the two corvid species considered to pass the mark test continuously persisted in responding toward their reflection in the mirror, which indicates social behavior paralleling the behavior of corvids (jackdaws and jungle crows) and all other bird species that fail to pass the mark test (Gallup and Anderson 2018). This point is indicative of lack of self-recognition in corvids.

A convincing demonstration of self-recognition in one bird species would have enormous biological and cognitive implications because it would mean that this capacity has evolved independently in birds and hominoids (i.e., humans and apes), which diverged 300 million years ago. However, the problems mentioned above cast doubts about the validity of previous results and, therefore, more replication experimental studies with improved methodology and larger sample sizes will be needed before the existence of self-recognition in one bird species can be widely accepted.

Most studies of mirror-induced self-directed behavior involve mammals, both aquatic and terrestrial. Among aquatic mammals, different species of the family delphinidae could be predicted

to recognize themselves in mirrors because they possess high degrees of encephalization, sophisticated memory, and a complex social life. Indeed, the bottlenose dolphin (*Tursiops truncatus*) is frequently cited as the non-primate species most clearly showing self-recognition based on Reiss and Marino (2001) who reported evidence that two dolphins used mirror reflection to investigate directly unobservable parts of their bodies that had previously been experimentally marked. Based on these results, it was later suggested that two other species of the family delphinidae possess the capacity for self-recognition because experimental subjects displayed contingency checking behaviors in front of the mirror. However, self-directed actions to the mark could not be detected and quantified as dolphins cannot touch the mark. Therefore, conclusions are based only on contingency checking behaviors and what seems to be prolonged observation of marked parts (Reiss and Marino 2001). In the absence of self-directed behaviors, these results are ambiguous and based on subjective interpretations of results, which “fail to rise to the level of definitive evidence” (Gallup and Anderson 2018; p. 17).

Self-recognition has been attributed to several terrestrial mammal species. In some of them, such as dogs, horses, Rhesus monkeys, and siamangs, provided evidence is very weak (Anderson and Gallup 2015; Gallup and Anderson 2018). However, elephants and great apes are usually cited as species that have shown convincing evidence of mirror self-recognition. The elephant study (Plotnik et al. 2006) had the advantage that an unequivocal mark test could be performed given that these animals can make self-directed behaviors by touching their head with their trunks. It was found that one out of three subjects passed the mark test, i.e., this elephant touched with its trunk the visible mark significantly more than the invisible sham-mark located at the other side of its head. However, the fact that two elephants did not pass the mark test and, mainly, that subsequent repetitions of the test in the successful elephant did not reach the same positive results, cast doubts about the existence of self-recognition capacity in elephants (Gallup and Anderson 2018).

With respect to great apes, it is clear that chimpanzees pass the mark test (see above; Gallup 1970) because the pioneering work by Gallup has been replicated several times with similar results (Calhoun and Thompson 1988; Lin et al. 1992). This is also the case for orangutans (*Pongo pygmaeus*), although studies have included smaller sample sizes and fewer replication studies have been performed (Anderson and Gallup 2015). However, like other species, only a subset of tested apes makes self-directed behaviors to the mark. With respect to bonobos (*Pan paniscus*), it has been reported that, in response to mirror images, they use the reflection to investigate normally unseen body parts, and that their behavior is very similar to that exhibited by chimpanzees (Westergaard and Hyatt 1994). Based on these observations it is broadly accepted that bonobos, as well as chimpanzees, are able to recognize themselves in front of the mirror. However, the mark test has not been conducted in this species, which is considered the indispensable requisite for self-recognition to be demonstrated (see above).

Gorillas (*Gorilla gorilla*) deserve special mention because of the mixed and contradictory results with respect to self-recognition capacities (Patterson and Cohn 2006). In several studies, convincing experimental evidence of some individual gorillas passing the mark test has been reported, whereas, in most cases, no signs of self-recognition were observed. However, in some of the individuals that passed the mark test, different types of training were used. These cases should not be considered as positive evidence of self-recognition in gorillas because it is well known that after training of self-directed actions in front of the mirror, not only monkeys, but also pigeons are able to display self-directed behaviors to the mark (Epstein et al. 1981; Uchino and Watanabe 2014; Chang et al. 2017)). Then, in contrast with compelling evidence found in chimpanzees and orangutans, the findings from gorillas are contradictory. However, in their review of self-recognition in primates, Anderson and Gallup (2015) concluded that, given gorillas' phylogenetic closeness to chimpanzees and humans, the basic capacity of self-recognition may be present in some individuals.

## Conclusions

Self-recognition has been unambiguously demonstrated only in chimpanzees and orangutans. This consensus has been established due to these species consistently making self-directed behaviors to the mark when in the presence of a mirror. Despite claims to the contrary, compelling evidence for self-recognition has not been provided for any other species. These claims have been the consequence of a lack of rigor in two ways. First, claims of self-recognition have at times been made without compelling evidence of self-directed behaviors to the mark in the presence of a mirror during the mark test; and second, in the general scientific basis that confidence in scientific conclusions can be reached only after rigorous replication of previously published studies (Forstmeier et al. 2017). In self-recognition studies, replication is extremely rare and sometimes evidence based on a single individual has been accepted as definitive. Clearly, further well-designed experimental studies are needed to replicate previous findings, particularly studies with a renewed emphasis on evaluating self-directed behaviors to the mark, which have the potential to further elucidate self-recognition capacity in these animals.

## Cross-References

- [Gordon Gallup](#)
- [Mirror Self-Recognition](#)
- [Self-Awareness](#)
- [Visual Self-Recognition](#)

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## Self-Domestication Hypothesis

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## Synonyms

Artificial selection; Domestication; Prosociality

## Definition

Self-domestication is a process by which organisms become domesticated as a product or by-product of natural selection. It is a multi-generational process by which animals become tame, but without human direction. Evidence suggests that self-domestication emerges as a result of selection against aggression, which, in theory, can occur in myriad ways. Like domestication, self-domestication results in a relatively consistent set of phenotypic changes that emerge across species and manifest morphologically, physiologically, behaviorally, and cognitively. This set of phenotypic changes is known as “the domestication syndrome.”

## Introduction

Throughout human history, animals have mostly been domesticated for the purpose of food production and replacing human labor (McHugo et al. 2019). These needs arose with the scaling-up of human societies from smaller hunter-gatherer bands and horticulturist societies to agricultural societies during the Holocene and likely due to environmental and climatic changes associated with warming in this period (Bettinger et al. 2009; Ferrio et al. 2011). The first evidence of domestication appears in the archeological record around 15,000 years ago with the domestication of the wolf, *Canis lupus*, to create “man’s

best friend,” *Canis familiaris*, the domestic dog (Freedman and Wayne 2017).

Since then, humans have domesticated a number of animal species. Pairs of the wild progenitor species and their domesticated variant include: the bezoar ibex, *Capra aegagrus* and the domestic goat, *Capra hircus*; aurochs, *Bos primigenius* and the domestic taurine bull, *Bos taurus*; the wild boar, *Sus scrofa* and the domestic pig, *Sus domesticus*; and the red jungle fowl, *Gallus gallus* and the domestic chicken, *Gallus gallus domesticus* (McHugo et al. 2019).

In the above cases, the domestication process is directed. In other words, humans picked animals with favorable physical characteristics and mated them together to produce offspring that have a greater chance of possessing the desirable parental traits themselves, while selectively eliminating from the breeding pool animals with less desirable traits. This is known as artificial selection. Artificial selection hijacks the power of natural selection, but directs the selection of phenotypic traits that possess heritable variation towards a different end – namely, increasing the probability of animals with traits that are favorable to humans.

However, *self-domestication* is the process of domestication in wildlife but without human direction, resulting from natural changes such as ecological factors (Hare et al. 2012).

For instance, an animal population might experience a change to their feeding ecology that pushes them towards a different mode of foraging that has downstream consequences to their patterns of intergroup conflict. Such a process as this is part of the explanation for the unique evolutionary history of one of humans’ closest great ape relatives, the bonobo (more on this below).

Self-domestication tends to result in a consistent set of phenotypic changes that are seen in other domesticates, which is known as the domestication syndrome (Hare et al. 2012). This is because both self-domestication and domestication likely share many of the same underlying mechanisms, and therefore phenotypic changes that are the result of these mechanisms. Researchers have argued that selection for tameness, friendliness, or prosociality, which can alternatively be understood as selection against aggression, is the primary initiator of

domestication and gives rise to the domestication syndrome (Hare et al. 2012). This is because such a reduction in aggression and fear and greater prosocial feelings towards humans is necessary for successfully breeding animals in captivity (Wilkins et al. 2014). In addition to the animals becoming more tame, friendly, prosocial, and less aggressive through the generations, they also exhibit a host of phenotypic changes that are a by-product of the selection process (Hare et al. 2012). These phenotypic changes serve as a means to identify self-domesticated species in the wild.

Additionally, it is possible for organisms to undergo both self-domestication in the wild and domestication from humans. Hare et al. (2012) describe a two-step process of self-domestication followed by more human-directed domestication in the domestication of wolves to dogs, which serves as a model of how self-domestication might occur more generally in the wild. Because of the relative lack of research on self-domestication per se, this entry will also discuss domestication more broadly, since the former process falls within the latter.

## The Role of Aggression

Researchers have proposed that the constellation of phenotypic changes characteristic of domestication and self-domestication – the domestication syndrome – is a by-product of selection against aggression (Hare et al. 2012). The fact that the main behavioral trait that is consistent across all domesticated animals is reduction in aggression compared to their wild ancestors supports this hypothesis. Domesticated animals have less intra-specific, interspecific, offensive, and defensive aggression compared to their wild ancestors (Hare et al. 2012).

Some of the most convincing work on the connection between domestication and selection against aggression has come from the famous “Siberian fox study” that was initiated by Russian geneticist, Dmitry Belyaev, in 1959 (Belyaev 1979). For this study, Belyaev and colleagues choose as their subjects a species that is

taxonomically close to dogs, but has never been domesticated, the silver fox, *Vulpes vulpes*.

Since the start of this study and up until the present day these foxes have been selectively bred for generations based on a single behavioral criterion – less aggressiveness towards humans. The researchers have also maintained a control group of foxes that are kept in identical conditions as the experimental group except for one difference, they are bred randomly with respect to their aggressiveness towards humans (Belyaev 1979; Hare and Tomasello 2005). In this way the experiment can isolate the effect of one variable – selection against aggression – on the changes they observe.

The researchers have found that by simply selecting less aggressive behavior in foxes and breeding them, over generations the experimental foxes have exhibited a host of phenotypic changes that mirror those of dogs and other domesticated species (Belyaev 1979; Trut 1999). For example, the experimental foxes exhibited tail wagging, floppy ears, barking, and whimpering, along with greater prosociality and tameness (Belyaev 1979; Hare 2018; Trut 1999). This suggests that selection against aggressive behavior specifically is at the basis of the domestication syndrome.

## The Domestication Syndrome

The consistent set of phenotypic changes that is the result of domestication can be put into a few different categories: changes to morphological traits like fur color and patterning, teeth and skull size, and muscularity; changes to physiological traits including the hypothalamic pituitary adrenal (HPA) axis, which regulates the stress response, as well as hormones involved in the stress response like glucocorticoids and adrenocorticotrophic hormone (ACTH); and cognitive and behavioral traits like docility, less aggression, greater social cognition, and prosociality (Hare and Tomasello 2005; Trut 1999; Wilkins et al. 2014; Wilkins 2020). For example, many domesticated animals are piebald, lacking pigmentation on certain parts of their fur, giving rise to the familiar black-and-white-spotted cow commonly

seen in America's Midwest. Additionally, many pig and dog breeds have curly tails and floppy ears, the latter being a trait not seen anywhere else in nature except in elephants (Trut 1999).

Hare et al. (2012) describe other consistent characteristics that are associated with domestication. Domesticates have greater sexual receptivity for more periods of the sexual cycle; morphologically domesticates show reduced sexual dimorphisms, reduced cranial capacity, depigmentation, feminization of skull; and cognitively, domesticates tend to be more sensitive to human social and communicative cues, and show greater skill on cooperative, social tolerance tasks (Hare et al. 2012; Tan and Hare 2013; Trut 1999).

Paedomorphosis, or the retention of juvenile characteristics into adulthood, is one of the most common phenotypic changes characteristic of domestication (Hare et al. 2012). These include changes that are morphological, such as reduced skull size and altered skull shape, and behavioral, such as whining and submissiveness. And they are traits that are present in juvenile wolves but not adult wolves while being maintained in adult dogs (Trut 1999).

What explains the emergence of this common and consistent set of changes that contains very different phenotypic traits across domesticated species? One hypothesis that potentially accounts for most of the phenotypic changes in the domestication syndrome is the neural crest hypothesis (Wilkins et al. 2014; Wilkins 2020). According to this hypothesis, the domestication syndrome is a product of changes to the developmental pathways of an organism. Specifically, domestication acts on the gene regulatory network that gives rise to neural crest cells in embryonic development (Wilkins et al. 2014).

Neural crest cells are a class of stem cells that first appear during early embryogenesis on the dorsal edge of the neural tube, which is the embryonic precursor to the central nervous system. During early development, neural crest cells migrate throughout the body giving rise to the cellular precursors to many different cell and tissue types. Wilkins et al. (2014) explain that the developmental trajectories of the phenotypic traits seen in the domestication syndrome are linked to these



different cell and tissue types that neural crest cells give rise to. Tissues derived from the neural crest cells include much of the skull, peripheral neurons involved in the sympathetic nervous system, the adrenal medulla, which secretes hormones involved in responding to stressful events, pigment-related precursor cells to melanin containing cells, and cells that are precursors to teeth (Wilkins et al. 2014). These characteristics are all altered in domesticated animals and are linked to neural crest cell development.

Specifically, Wilkins et al. (2014) posits that the varied traits involved in the domestication syndrome are products of a reduction in neural cell migration to those specific cellular and tissue areas of the body. For example, many domesticated animals are piebald, depigmented, or possess pigmentation changes on certain parts of their fur. It is known that pigmentation cells (i.e., melanocytes) are derived from neural crest cells, in which case irregular pigmentation is due to the lack of melanocytes in certain areas of vertebrate fur. In this case, it is likely that the irregular pigmentation is a result of reduced neural crest cell migration to these areas (Wilkins et al. 2014). Another example is floppy ears which are a product of insufficient cartilage – a neural crest-derived tissue – in the outer ear (Pendleton et al. 2018). Data from genetic analysis also corroborate the neural crest cell connection to depigmentation and the other traits involved in the domestication syndrome (Pendleton et al. 2018; Qiu et al. 2015; Wilkins et al. 2014).

## Domestication in Dogs

Dogs were the first domesticated animal species (Freedman and Wayne 2017). Before humans played any intentional role in the domestication process, dogs were likely being self-domesticated in response to exploiting the novel ecological niches that humans created. In the two-step model of self-domestication of dogs, Hare et al. (2012) explain that the first step consisted of dogs being self-domesticated in the absence of intentional breeding by humans. In this step, less aggressive dogs likely had a selective advantage compared to more aggressive dogs in hanging around human

settlements, eating their food, and gaining some degree of protection and security compared to being completely in the wild. The first step made possible the second step, which consisted of directed, intentional breeding of dogs by humans to be less aggressive and more prosocial.

Studies show that dogs possess a range of features characteristic of domestication including morphological, physiological, behavioral, and cognitive features (Freedman and Wayne 2017; Hare et al. 2002; Hare and Tomasello 2005). For instance, evidence suggests that dogs possess social-cognitive and social-communicative abilities that are the result of domestication by humans, even relative to animal species with similar cognitive ability (Hare et al. 2002; Hare and Tomasello 2005).

Hare et al. (2002) compared the ability of dogs to use human social cues to identify the location of food to chimpanzees and wolves. Their study design allowed them to assess competing hypotheses for these social cognitive skills in dogs, including that dogs obtained their social-cognitive abilities to make use of human social cues from wolves (i.e., the canid generalization hypothesis), from living with and learning from humans over their life span (i.e., the human exposure hypothesis), or from selection pressure on dogs to acquire social cognitive skills that understand and make use of human communicative cues (i.e., the human domestication hypothesis).

Under different experimental conditions that allowed for the testing of these three competing hypotheses, the researchers only found support for the human domestication hypothesis. Dogs were significantly more skilled than chimpanzees and wolves at following human visual social cues to identify the location of food. Most importantly, their ability to do so did not vary depending on their age or their level of exposure to humans, indicating the role of selection for these social cognitive skills rather than learning over the life span (Hare et al. 2002).

## Domestication in Bonobos

Because of the relative consistency of the correlated phenotypic traits that emerge in species that

underwent selection against aggression, it is possible to infer which species were self-domesticated. This is exactly what Wrangham and Pilbeam (2001) did and Hare et al. (2012) developed more thoroughly to argue that bonobos, our most closely related great ape relative along with chimpanzees, have undergone self-domestication.

Bonobos, *pan paniscus*, are a good animal model to assess self-domestication since more precise comparisons can be made to its undomesticated great ape sister, the chimpanzee, *Pan troglodytes*. Evidence indicates that bonobos speciated from chimpanzees due at least in part to allopatric speciation as a result of the physical barrier of the Congo River, where there is little genetic admixture between the bonobos south of the river and chimpanzees north of the river (Hare and Wrangham 2017).

One of the most striking behavioral differences between bonobos and chimps is their levels of aggression. Chimps are known to be highly aggressive compared to bonobos where encounters of chimps from different tribes are almost always hostile (Hare et al. 2012). While levels of violence and hostility between chimpanzee groups are much higher than within chimpanzee groups, there is still plenty of aggression within chimpanzee groups almost all of which is mediated by males (Wrangham and Peterson 1996).

Chimpanzee societies are organized by dominance hierarchies, which provide a stable albeit somewhat totalitarian social structure that drives many of the incentives for violence (Hare and Wrangham 2017). Dominant chimps bully subordinates and subordinate male chimps bully others below them, who in turn bully female chimps. Additionally chimpanzee males often form coalitions of adolescents that attempt to and often successfully aggress against other chimps especially the dominant chimps in an attempt to oust them from power (Hare et al. 2012; Hare and Wrangham 2017; Wrangham and Peterson 1996).

In contrast to chimpanzees, bonobos are far less aggressive and far more prosocial, which provides initial evidence that bonobos are domesticated relative to chimpanzees (Hare et al. 2012). Field experiments and laboratory experiments

testify to this fact. Laboratory experiments have shown that like humans but unlike chimpanzees, bonobos will share food with other bonobos they do not know (Tan and Hare 2013).

Across four experiments researchers found out the following regarding bonobo prosocial behavior: (1) more times than not the bonobos chose to share food when they could monopolized it, and especially with a stranger, even more so than a groupmate; (2) bonobos will not give up food in their possession if a desirable social interaction is not possible; (3) however, bonobos will also act outside of their self-interest to help another, by exerting effort to help strangers or groupmates acquire out-of-reach food (Tan and Hare 2013). Therefore, this evidence corroborates the self-domestication hypothesis of bonobos since relative to chimpanzees they are much more prosocial and exhibit enhanced social cognition, similar to the difference between domesticated dogs and wolves.

Unlike chimpanzees, bonobos show very little to no aggression towards females, in large part because males do not form coalitions while females do, and they often do so to fight off aggressive males (Hare and Wrangham 2017; Surbeck and Hohmann 2013). Females form the highest ranking members of bonobo society, where no bonobo society has been recorded to have a male or a coalition of males as its highest ranking members (Hare et al. 2012; Hare and Wrangham 2017).

These are striking differences compared to chimpanzee groups in which females bond little with other females and are commonly aggressed against by males. Additionally, chimpanzee groups are ruled by males who violently attack other males in contests for social status in their dominance hierarchy (Hare and Wrangham 2017; Wrangham and Peterson 1996).

Additionally, if bonobos are domesticated via reduction in aggression, they should show developmental delays in their behavior and cognition relative to chimpanzees. In a set of experiments, Wobber et al. (2010) showed that indeed evolution appears to have affected bonobo prosocial behavior and cognition through shaping ontogeny to delay development when it comes to social cognitive and behavioral skills. They assessed

this by looking at behaviors related to food competition, showing that (1) as chimpanzees reached adulthood they became increasingly intolerant of sharing food with another, whereas bonobos retained high levels of juvenile food sharing into adulthood; and (2) relative to chimpanzees, bonobos showed developmental delays in the acquisition of social inhibition (Wobber et al. 2010). Therefore, this research supports the hypothesis that bonobos show developmental delays in cognitive and behavioral traits relative to chimpanzees that are consistent with domestication.

## Conclusion

Self-domestication is a very interesting and still under-researched phenomenon. It is a topic that highlights the need for more evolutionary researchers to assess and specifically look for by-products rather than just targets of selection. If something that results in as complicated of a set of phenotypic changes as selection against aggression does, one really begins to wonder what other similar processes have and are continuing to occur in nature unbeknownst to many researchers. This especially could be the case when considering animal populations that have experienced habitat destruction, shifts in feeding ecology, natural disasters, and maybe even climate change. Such fundamental changes to animal populations would likely result in new selection pressures that give rise – either directly as a product or as by-products of selection – to phenotypic changes that come to characterize the population.

Additionally, these changes can result in very different behaviors and patterns of social structure from the ancestral population that cannot be understood without accounting for these ecological factors. Recently, researchers have begun analyzing human evolution in the light of self-domestication, finding evidence that like bonobos, humans have a number of phenotypic traits that are evidence of *Homo sapiens* being domesticated variants of earlier human species (Hare 2017; Wrangham 2019). These traits include reduced skull, brain, and teeth size, reduced sexual dimorphism, greater prosociality, and less

reactive aggression, among others (Hare 2017; Wrangham 2019). Therefore, in addition to providing a powerful lens through which we can understand behavior and cognition in nonhuman animals, self-domestication might also provide a crucial piece to the puzzle of the evolution of modern humans.

## Cross-References

- Aggression
- Chimpanzee
- Development
- Genetics

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## Self-Injurious Behavior

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## Synonyms

Deliberate self-harm; Self-injury; Self-mutilation

## Definition

Self-injurious behavior (SIB) encompasses the act of intentional harm to one's body that can result in or have the capacity to cause organ or tissue damage (Sigafos et al. 2014). Self-injurious behavior consists of a series of repetitive responses that often has no obvious reinforcer (Tate and Baroff 1966). Self-injurious behavior does not account for various ritualized cultural practices like ear piercing. SIB can vary in severity and can be put in a spectrum depending on the extent of injury (House and Cercone-Keeney 2004). SIB is utilized by individuals to temporarily alleviate intense negative emotions. They may also express self-directed anger or may be a notion to seek help from others. Such behaviors may also help avoid suicidal ideation (Klonsky and Muehlenkamp 2007).

## Common Forms of SIB

Examples of SIB can include behaviors like skin picking, head punching/slapping, pica (eating inedible objects), teeth grinding, eye poking, trichotillomania (pulling out hair), self-cutting, self-pinching, lip chewing, nail removal, air swallowing, and self-poking in body openings like the anus and vagina. Among these, head banging is the most commonly found self-injurious behavior (Sigafos et al. 2014). It is imperative to bear in mind that other behaviors may be more common among various subpopulations.

## SIB Classification

SIB can be classified within four categories: stereotypic, major, compulsive, and impulsive.

### Stereotypic SIB

Stereotypic SIB consists of behavior that is highly repetitive, fixed, rhythmic, and monotonous. It is often seen in individuals with autism and various congenital and developmental disorders. SIB behavior in these individuals is often exhibited as head banging, self-hitting, skin

picking, self-biting, and hair pulling (House and Cercone-Keeney 2004). Although pharmacologic treatment is slightly therapeutic for these individuals, behavioral interventions are much more effective in eliminating such behaviors.

### Major SIB

Major SIB includes single episodes of severe or life-threatening SIB. Examples include castration, eye gouging, and limb amputation. Such behaviors often times have significant meaning to the individual. Psychosis due to schizophrenia or a severe mood disorder are often related to major SIB (House and Cercone-Keeney 2004). The most common form of major SIB is genital mutilation; it is found at higher rates in men than in women. Antipsychotics are the recommended therapeutic pharmacologic treatment for major SIB (House and Cercone-Keeney 2004).

### Compulsive SIB

Compulsive SIB consists of repetitive, high-frequency behaviors that can be mild to moderately severe. These behaviors include trichotillomania, skin picking, and nail biting. Individuals find it difficult to resist such behaviors because they decrease tension or anxiety. Nail biting is the most common behavior in the general population and often times decreases in frequency over time. Behavioral treatments are effective in treating compulsive SIB. Medications can be taken simultaneously to therapeutically treat SIB (House and Cercone-Keeney 2004).

### Impulsive SIB

Impulsive SIB includes skin cutting, skin burning, and self-hitting. These behaviors temporarily relieve unbearable distress among individuals. Impulsive SIB is most commonly seen in those with borderline personality disorder. It is also seen in individuals with antisocial personality disorder, eating disorders, dissociative disorders, and post-traumatic stress disorder. Traumatic experiences can also trigger impulsive SIB. Data suggests that women are more likely to engage in impulsive SIB than men. Treatment includes adaptive strategies that replace the impulsive behavior to help cope with pain and emotions associated with

trauma. Dialectical behavior therapy is effective in treating impulsive SIB in those who have borderline personality disorder. There is little data supporting effective pharmacological treatments at this time. (House and Cercone-Keeney 2004).

### SIB in Development

SIB is most commonly seen in adolescence and early adulthood. The age of onset is usually between ages 13 and 14. (Klonsky and Muehlenkamp 2007). SIB can also occur in early development between 2 and 3 years of age (Schroeder et al. 1997). Without proper treatment early in development, improvement of SIB is unlikely. SIB will often increase in severity during childhood and adolescence and will level out in adulthood (Emerson et al. 2001). Treatments for SIB will be likely throughout an individual's life.

### SIB Risk Factors

#### Disabilities

SIB is prevalent among individuals who have intellectual disabilities (Sigafos et al. 2014). Certain intellectual disabilities may increase the risk of SIB, further explaining its prevalence among this population (Holden and Gitlesen 2006; Lowe et al. 2007). SIB is even more prevalent in those individuals with intellectual disabilities as well as in those with autism or a psychological disorder like depression (Matson and LoVullo 2008). The prevalence of SIB increases with severe intellectual disabilities (Schroeder et al. 1997). SIB is seen more frequently in individuals who have severe disabilities in performing activities of daily living, socializing, and communicating (Emerson et al. 2001; Matson et al. 2000; Schroeder et al. 1997).

#### SIB Prevalence

Approximately 4% of adults report a past history of self-injury with up to 1% reporting a severe past history (Klonsky and Muehlenkamp 2007). Higher rates have been found in adolescents and in young adults, with even greater rates amongst



those individuals receiving mental health treatment (Klonsky and Muehlenkamp 2007).

### Gender and Ethnicity

SIB is found at similar rates amongst men and women. The methods of SIB vary between genders. Women are more likely to self-cut whereas men are more likely to self-burn. Caucasian individuals are more likely to have SIB than its non-Caucasian counterparts (Whitlock et al. 2006).

### Why Individuals Engage in SIB

Affect regulation: SIB aid in alleviating intense negative emotion. Anger, anxiety, and frustration are present before initiating SIB, and a sense of calm immediately follows after injury. Self-punishment can also motivate SIB when the individual has low self-esteem. Although not as common, the urge to influence others may motivate SIB. Those engaging in SIB may feel antidissociation. These individuals explain that they often feel very little or nothing at all. By engaging in SIB, they are able to regain their sense of self (Klonsky and Muehlenkamp 2007). Some may use SIB to avoid attempting suicide. Other individuals may use SIB to seek excitement or exhilaration similar to those experienced during sky-diving or bungee jumping. Some individuals may use SIB to create physical boundaries, differentiating the individual from its environment and other people around him or her (Klonsky and Muehlenkamp 2007).

### Impacts of SIB

Treatment is imperative for individuals with SIB due to high risk of injury and health complications. Long-term health consequences can develop by accumulating damaged tissue over time. These individuals also will have increased medication use, isolation, and use of restraints to prevent SIB. Treatment can also be very expensive due to repetitive hospitalizations and medical care. (National Institutes of Health 1989). Negative social implications of SIB include isolation, difficulty assimilating into society, and

maintaining employment. Likewise, there is a considerable strain in relationships between the individual with SIB and his or her parents, educators, and members of the community. This may significantly decrease overall quality of life for the individual with SIB (Rojahn et al. 2008).

### Treatment Options

Effective treatment includes those based on principles of applied behavior analysis (ABA) as well as those based on principles of behavior modification through environment manipulation. ABA treatment involves a two-step approach that uses assessments to identify the operant function of SIB and then implementing a treatment that will directly reduce SIB. Examples of ABA-based treatments include functional communication training (FCT), non-contingent reinforcement (NCR), and function-based extinction (FBE). Behavior modification treatments involve manipulation of the environment through reinforcement and/or punishment schedules without prior identification of SIB variables. Examples of behavior modification treatments include differential reinforcement schedules, punishment procedures, and contingent use of restraints (Scotti et al. 1991). Other treatment options include cognitive behavioral therapy, auditory integration training, sensory integrative therapy, weighted vests, gentle teaching, electroconvulsive therapy, and exercise. Although these treatment options are available, further research is required to determine their effectiveness. A combination of ABA and behavior modification is often recommended for SIB (Sigafos et al. 2014).

Currently, there is no research that supports the use of pharmacologic treatment as an effective treatment independently. However, the use of pharmacologic agents can effectively treat symptoms of mental disorders that are often experienced in those individuals with SIB.

### Cross-References

- [Avoidance](#)
- [Behaviorism](#)

- [Conditioned Inhibition](#)
- [Extinction in Learning](#)
- [Goal-Directed Behavior](#)
- [Negative Reinforcement](#)
- [Operant Conditioning](#)
- [Positive Reinforcement](#)
- [Punishment](#)
- [Reinforcement](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Self-Injury

- [Self-Injurious Behavior](#)

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## Self-Mutilation

- [Self-Injurious Behavior](#)

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## Self-Recognition

- [Mirror Self-Recognition](#)
- [Visual Self-Recognition](#)

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## Self-Reproach

- [Shame and Guilt](#)

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## Self-Serving Attribution

- [Self-Serving Bias](#)

## Self-Serving Bias

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## Synonyms

Benefectance; Egotistical attributions; Self-serving attribution

## Definition

Self-serving bias is a psychological strategy referring to the tendency of people to make internal attributions for positive outcomes and external attributions for negative outcomes.

Heider (1958) first enunciated self-serving bias in his explanation of attributions for ambiguous situations. He claimed that attributions are shaped by “a person’s own needs or wishes” (Heider 1958, p. 118). Thus, self-serving bias refers to somewhat distorted explanations and inaccurate interpretations of the given situation as compared to an objective standard. Two accounts have been defined to explain biases in the service of the self: the cognitive account and the motivational account.

The cognitive account states that self-serving bias is a result of limited cognitive capacity rather than a motivated strategy (Miller and Ross 1975). Accordingly, individuals as naïve scientists strive to use the available information to make accurate attributions, yet the bounds of cognitive functioning lead to erroneous attributions, and somehow those errors are in favor of the self. Specifically, individuals set goals with the expectation to achieve. Thus, a positive outcome fits well with the previous expectation and results in an internal attribution in favor of the self. However, feedback indicating failure is inconsistent with the prior expectation which leads to search for explanations most, if not all, of the time outside of the self. The

reason behind this process is the asymmetry in memory in which positive experiences are much more salient and easier to retrieve compared to negative outcomes (Taylor 1991). As a result, individuals take action with the expectation to succeed based on the biased retrieval of past experience and make an internal attribution when the expectation is met. A similar explanation states that negative outcomes are inconsistent with the self-view or schemas about oneself (Tetlock and Levi 1982). Since individuals perceive themselves as skillful (i.e., decent, moral, and intelligent), explanations for positive outcomes result in internal attributions while negative outcomes lead to external attributions.

Another explanation derived from the cognitive account for self-serving attribution, in line with the previous one, is biased hypothesis testing, especially for negative outcomes. Though individuals behave like scientists to find explanations for their experiences, they are inclined to collect and rely on information that verifies their previous expectations (i.e., confirmation bias). Therefore, any information supporting the previous expectation regarding the self and positive outcomes is weighted more as compared to inconsistent information (Sheppard et al. 2008).

The motivation-driven account states that individuals engage in self-serving attributions to preserve and protect their self-esteem. Thus, self-serving bias is a motivated action that aims to increase global self-worth by taking responsibility for positive outcomes and externalize responsibility for negative ones (Blaine and Crocker 1993). Various explanations have been provided for the relationship between self-esteem and self-serving bias. Wills (1981) asserted that low self-esteem drives individuals to engage in self-serving attributions while Alloy and Abramson (1979) claimed that low self-esteem is associated with the lack of motivation to enhance self-esteem. Campbell and Sedikides (1999) in their meta-analysis defined 14 moderators including self-esteem and outcome expectation. Accordingly, the common theme underlying those moderator variables, which are associated with self-serving attributions, is a threat to the self. Self-threat is defined as any kind of failure experience, and the link between self-threat

and self-serving bias is stable even after controlling for errors in information processing. Furthermore, findings suggest that self-serving bias is universal rather than being exclusively Western (see Mezulis et al. 2004).

Another motivation defined in the motivation-driven account is self-presentation. According to the self-presentation explanation, individuals try to manage impressions about them formed by others. To be liked and approved by social surroundings, individuals claim responsibility for success and disclaim responsibility for failure (Forsyth and Schlenker 1977).

Overall, individuals engage in biased explanations for their success as a result of imperfect cognitive functioning and motivations to bolster self-worth. A body of research supports both explanations, implying that they are operating in tandem.

## Cross-References

► [Cognitive Bias](#)

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## Self-Starvation

► [Activity-Based Anorexia](#)

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## Semantic Coding

► [Cognition](#)

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## Semantic Memory

► [Cognition](#)  
 ► [Long-Term Memory](#)

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## Semanticity

► [Cognition](#)

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## Semantics

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## Introduction

Semantics, the study of meaning and its communication, has been a perennial focus of linguists and philosophers. Traditionally, interest in

semantics was restricted to meaning in natural human language, although recent decades have seen the emergence of the fields of biosemiotics and zoosemiotics, which investigate the possibility of semantic content in the behaviors of non-human plants and animals. Given the nature of this encyclopedia, the present entry provides a brief overview of traditional semantics before describing biosemiotics and zoosemiotics in some detail, using the honeybee waggle dance as a case study.

## Approaches to Semantics Across Disciplines

Among Western philosophers, interest in semantics can be traced at least to Plato, who expressed concern about the arbitrary nature between words and their meanings in his dialogue *Cratylus*. Throughout the late nineteenth and early twentieth centuries, philosophical semantics was closely related to logic, concerned with the disconnect between what a sentence appeared to mean and what it should mean following logical analysis. (Mathematically, for instance, “ $3 + 2 = 3 + 2$ ” means the same thing as “ $3 + 2 = 5$ ,” but “Clark Kent is Clark Kent” has a different cognitive significance from “Clark Kent is Superman.”) In recent decades, this logical approach to semantics has been extended to computer science, where the semantics of programming languages is an active subfield.

The modern field of linguistics has been concerned with semantics since its inception in the nineteenth century (and soon gave rise to the separate field of semiotics, concerned with the relationship between sign, signified, and signifier outside of linguistic contexts). Although academic linguistics was dominated from the mid-twentieth century onward by meaning-independent universal grammar, linguists throughout this period considered (and continue to consider) how meaning is related to grammar (i.e., syntax) and how lexical items map onto concepts and events. Meanwhile, it is the semantic implications of many well-known linguistic theories that have captured the popular imagination. The Sapir-Whorf hypothesis, for

instance, continues to fascinate because it suggests that translation is a fool’s errand: no word in Japanese means exactly the same thing that “green” means in English. The notion of embodied cognition strikes us as incredible because it asserts that a word’s meaning, at base, is equivalent to the activation of a group of motor neurons.

In psychology, interest in semantics centers around how meaning is implemented in the minds and brains of human beings and has spanned several subfields of the discipline. Developmentalists, for instance, have investigated how children map spoken words to referents in their environment; psycholinguists have sought to describe the mental lexicon and how it interfaces with concepts; and neurolinguists have investigated how meaning is neurally instantiated, using lesion studies and neuroimaging. Moreover, some cognitive psychologists have endeavored to simulate the neural organization of meaning through the construction of computational models.

Notably, scholarship on semantics has been largely preoccupied with meaning and its communication in humans, but forays into nonhuman semantics were made in the mid-twentieth century. Linguist Charles Hockett, a critic of Chomsky and his universal grammar, identified 13 design features of language; all were found in human language, but most were found in at least one other animal communication system (Hockett 1960). For instance, the arbitrariness that concerned Plato is also present in the song of the western meadowlark and gibbon calls, and semanticity is present in the western meadowlark, gibbons, and the waggle dance of the honeybee. Recognition by the linguistic establishment of semanticity in nonhuman animals came early in the twenty-first century, with Hauser, Chomsky, and Fitch’s (2002) concession that, among the components of language, only the capacity for recursion (i.e., linguistic nesting) is unique to humans.

## Biosemiotics and Zoosemiotics

Animals across a broad range of species convey meaning through their communicative behavior.



Some scholars believe that each “animal provides the stimulus for its partner’s response, which in turn provides the stimulus for the next response in the chain, and so on” (Shettleworth 2009). One way to examine humans’ language specialization is to ask how far another species could progress toward language. Without question, animals communicate. Chimpanzees “clutter” to warn of snakes, “rraup” to warn of an eagle, and “chirp” to let the others know that a leopard is nearby. Even insects have complex communication systems. For example, honeybees perform a “dance” to report information about the distance, location, and quality of a pollen source to their hive’s mate. Clearly animals communicate with one another, but are they capable of mastering language? It is fairly obvious that we can withhold the designation “language” from the informational exchanges of genes and bacteria, but scholars are more interested to see nonhuman animals as having languages of their own. Animal communication is likely to be less complex and elaborated than ours, perhaps, but includes the same general class of systems.

Much discussion on animal communicative behavior has sought to analyze it by attributing semantic content to particular signals: such an approach, for instance, characterizes the treatment of vervet monkey alarm calls as “functionally referential.” Some scholars have offered a formal semantics for the signaling behavior of other monkeys. In contrast, a growing trend in the animal behavior literature rejects the attribution of properly semantic content to such signals, arguing that the meaning they convey should be attributed to their pragmatic value in particular contexts.

When we look at the communicative behavior of other species, all of the systems that we find display a somewhat similar character, based on a number of shared properties. A primary feature is that all (nonhuman) animals have limited, fixed sets of discrete messages to convey. These messages constitute a fixed list and one that cannot be expanded by combining elements to form new and different messages to respond to new and different communicative needs. Even in those

cases where the system is learned, of which bird-song is by far the most robust example, the actual system acquired does not go beyond the character of an essentially fixed inventory. Each message in these systems is limited to the here and now, driven by the immediate circumstances of production. The messages reflect the immediate internal state of the organism, and their production is often triggered by measurable internal factors such as hormone levels. For example, in most temperate species of oscine birds, it is the male that defends territory, and thus only male birds sing. When injected with appropriate levels of testosterone, however, female birds can be induced to sing as well.

In general, when we examine the ecologically significant communicative signals of any animal species, we find that evolution has shaped the animal’s biology so as to be particularly effective in the relevant domain. There has long been a tendency to try to treat animal signals as information-bearing symbols like the words of our language, but it seems more productive to see communication as relying on the ability of one animal to interpret the behavior of another in its observed context. Animal signals do not have the character of symbols, comparable to words in a human language, but observers can still derive information from them by taking into account the context in which they are produced.

When animal language research began in the 1960s and 1970s, some critics contended that primates were simply producing learned responses to their trainers’ nonverbal cues rather than demonstrating true language skills (Terrace 1985). Von Uexküll (1992) gives an extended analysis on the science of signs and meaning in living systems and organisms, “We no longer regard animals as mere machines, but as subjects whose essential activity consists of perceiving and acting. We thus unlock the gates that lead to other realms, for all that a subject perceives becomes his perceptual world and all that he does, his effector world. Perceptual and effector worlds together form a closed unit, the *Umwelt*.” In this context, from a semiotics perspective,

Jakob's idea of cognition is based on semiosis, and a biological understanding of living organisms reveals that *body* plays an essential role to conceptualize and visualize the object and event in the environment of the living system. One of the main points of biosemiotics – the semiotics of all living systems – is that semiosis constitutes a basic structure for the functioning of living systems, semiosis is a basic part of the way living systems function, and it is the element of *interpretants* that creates, affects, and constructs the perceptual world of the organism. Hence, the living systems operate and function in signification spheres (Brier 1999), so seen from the lens of biosemiotics it is an essential prerequisite for all cognition and signification in living systems.

### Case Study: The Honeybee Waggle Dance

The movement patterns of honeybee have been intensively studied as a communication system, and waggle dance activity is associated with nest site selection and probability of nectar sources from the hive. Yet, little is known if neurobiological mechanisms support to analyze how dances are “produced” and “interpreted” (Barron and Plath 2017). In European honeybees (*Apis mellifera*), for example, dances are performed in the contexts of foraging and nest site selection, and on a successful return to the hive, they perform highly stereotyped dance movements. For resources more than a few hundred meters away from the nest, the dance can be described as a repeating figure-of-eight movement, typically performed on the “vertical wax frames” within the dark cavity of the comb hanging inside the hive. European honeybees also dance on the “horizontal board” and perform the most lauded and remarkable “waggle run” of the dance, typically at the “junction between the two loops of the figure of eight”; the bee strides and leans forward, vibrates her wings, and rapidly waggles her abdomen. While

“wagging,” the successful forager also makes a sound by “buzzing” her wings, which results into her realigning and encircling by other 1–6 bees, and after several wagging runs, they leave the nest (Dyer 2002). Waggle dance also guides and escorts a “novice forager” to find her first food source either by using the dance “information” or by “following” the waggle dance (Biesmeijer and Seeley 2005). For an experienced forager, a waggle dance serves as a source to *reactivate* and resume her foraging interrupted by either rainstorm or nightfall or a daytime dip in her flowers' nectar (Frisch 1967; Gil and Farina 2002). Finally, an experienced and engaged forager may need to “find a new food source when her old one fades, and when this happens, she can do so either by following a dance (being a recruit) or searching independently, being a scout” (Biesmeijer and Seeley 2005).

Such an amazing organization of colonies and effectively structured coordination of their activities confirms the belief of Benveniste (1953) that the bees possess the means of communicating with one another. Their capacity to tackle collectively with the unforeseen circumstances, waggle run, and their waggle dance to signal the probability of available food resources lead us to suppose that they have a fascinating capacity of exchanging real messages and evoke a certain behavior as a response.

### Conclusion

Semantics is undergoing a paradigm shift. Scholars across disciplines increasingly recognize that, while nonhuman animals are generally not adept at conveying meaning using human codes, other codes exist that are more appropriate to the creatures that use them. Ongoing research in biosemiotics and zoosemiotics will likely continue to reveal meaning in places where it has not been previously perceived, and the definition of semantics may need to be expanded accordingly.

## Cross-References

- [Cognition](#)
- [Communication](#)
- [Foraging](#)
- [Syntax](#)

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## Semen

- [Ejaculate](#)

## Semi-aquatic

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## Synonyms

[Adaptations](#); [Amphibious](#); [Life history trade-offs](#); [Semiterrestrial lifestyle](#)

## Definition

Lifestyle enclosing living (or life stages) both in water and on land.

## Origin of Life and Transition from Water to Land

Animal life developed in water and later invaded the land. Primitive land organisms were mostly myriapod-like forms occupying cryptozoic (i.e., low light, stable and cool temperature, high humidity) habitats. Providing complementary oxygen supply to water respiration during periods of oxygen shortage, air-breathing likely evolved in response to the insurgence of large areas of shallow waters provoked by the shift of the continents in the Silurian period, global decline in oxygen levels during the Middle Devonian, and higher metabolic costs due to greater mobility, competition, and predation pressures. In the end of the Devonian period, the so-called tetrapods (modern amphibians, reptiles, birds, and mammals), animals with limbs, supporting the skeleton, and lungs, slowly evolved into walking terrestrial vertebrates from aquatic ancestors, most likely lobe-finned fish. Tetrapods' later explosive radiation involved major structural and

functional innovations, including new locomotion, respiration, and hearing modalities, making tetrapods one of the most successful groups invading land, together with arthropods and mollusks.

## Extant Semi-aquatic Organisms

The definition of purely aquatic or purely terrestrial – and consequently semi-aquatic – species is arduous. Several small organisms, like nematodes, tardigrades, and rotifers, in fact, live in a film of water, and others, like flatworms, ribbon worms, velvet worms, annelids, centipedes, and millipedes, strictly depend on moist habitats and could be therefore considered freshwater organisms. Many insects (e.g., mosquitos, several aquatic macroinvertebrates) lay eggs and hatch in water and may live in water after hatching, as either nymph or larva, before metamorphosing in flying adults. Penguins and pinnipeds, often considered terrestrial, rest on land but feed in the sea. Also, many phyla are highly variable in their water dependence. Crabs exemplifies this particularly well, varying from species more associated to water, such as the interesting bromeliad crab, which raises its young in water-filled bromeliad leaf axils, where it may form family groups and even change the water quality, to terrestrial species that invaded the land in a late adaptive radiation from marine ancestors. Mollusks also include more terrestrial gastropods with lungs and more aquatic ones with gills.

Several extant fish are capable of prolonged periods of activity on land, either to feed, lay eggs, or escape exsiccation, turbulence, or predators, burrowing and even holding territories, like the mudskippers *Periophthalmus*, which spend enough amount of time on land to be victims of mosquitos and even react negatively to submersion (Graham 1997). Amphibians have several morphological, behavioral, and hormonal adaptations to semiterrestrial life. They have permeable skin and need water to lay eggs and to grow in the first stages of their life cycle as larvae with gills, before becoming air-breathing adults with lungs, except some salamanders and frogs that lack lungs

and rely only on their skin. Land poses a problem for gamete transfer and storing, often overcome by internal fertilization, waterproof eggs, and viviparity. Many of these modifications were obtained with the amniotes (reptiles, birds, and mammals), which, contrary to amphibians, do not require water to lay eggs. Amniotes' remarkable adaptations to survive on land include the "amnios," a bubble with fluid and membranes protecting the embryo, and a skin covered with keratin, a waterproof protein minimizing water loss through evaporation. Several reptiles are extremely adapted to aquatic living, including virtually all turtles but Testudinidae, which are aquatic or semi-aquatic and probably descend from an aquatic ancestor, crocodilians, especially *Gavialis*, which rarely leave the water, and many highly aquatic snakes. Like amphibians, the most specialized forms (e.g., aquatic turtles and some snakes) may extract oxygen from water through their skin. Semi-aquatic birds (e.g., penguins, gulls, geese, ducks) and mammals (e.g., beavers, otters, seals, Pyrenean desman, water shrews, water opossum, minks, hippopotami) have varied degrees of water dependence, from species that almost never leave the water, such as penguins and sea otters, to species that are highly comfortable on land, such as minks and river otters. Humans have also been historically tethered to aquatic habitats, for daily drinking needs, and relying heavily on aquatic and semi-aquatic resources (Erlandson 2001).

## Adaptations to Semi-aquatic Living

Air's and water's physical properties are rather different. Thus, organisms regularly moving between aqueous and terrestrial environments (hereafter "semi-aquatic animals") had to evolve several morphological, physiological, ecological, and behavioral adaptations to perform efficiently both on land and in water (see below).

### Anatomy

Semi-aquatic animals had to evolve special morphological adaptations to regularly move in water and on land. They often have streamlined,

hydrodynamic bodies for increased aquatic locomotion. The forelimbs of Phocidae, for instance, are specialized for locomotion on land while during swimming are retracted into axillary hollows, whereas their hind flippers are specialized for swimming. Otters have a less elongate shape than most other mustelids, as well as shortened limbs and webbed toes, and feet muscles regulating interdigital web tension, supporting their underwater propulsion, providing advantages in water, but less on land, where otters are less mobile than most terrestrial mustelids (Estes 1989). The globally threatened, yet poorly researched, Pyrenean desman (*Galemys pyrenaicus*) presents similar anatomical adaptations to semi-aquatic living, like its comparatively large and webbed feet, fringed with rigid hairs augmenting their surface (Fig. 1). The more aquatic sirenians even lost hind limbs, obtaining propulsion mostly through a laterally expanded tail, and penguins have elongate bodies and reduced limbs modified as paddles. Animals foraging underwater also need to avoid water inflow while swallowing and to cope with mechanical pressure, which increases with depth, and thus developed modifications to close ears and nostrils and to swallow under water (e.g., otters and the Pyrenean desman) and structural bone modifications in the ears to protect from pressure changes (e.g., pinnipeds).

The higher density of water compared to air provides significantly more buoyancy and physical support for the skeleton, in turn facilitating animals' locomotory capacity, while on land animals must compensate the lower physical support to their body provided by the air relying on endo- or exoskeleton, limbs, and tucker muscles. Taking advantage of the positive buoyancy provided by the water, aquatic living often led to the evolution of larger body sizes. Pinnipeds and sirenians, for instance, are large, the largest rodents and shrews are aquatic, otters are the largest mustelids, and polar bears evolved larger body mass than terrestrial bears after their secondary invasion of the marine environment. Increasing body size usually enhances diving capacity, particularly in endotherms (Brischoux et al. 2008). On the other side, however, water's higher viscosity provides more resistance to movement. Semi-aquatic mammals provide a particularly interesting example of morphological adaptations to secondary aquatic life balancing trade-offs between buoyancy and diving. They are denser than water, mostly due to air and high lipid content in their lungs and bodies, respectively, which provides considerable buoyancy (a sea otter remains above water even when using stones to open sea urchins), reducing energetic costs of surface swimming and aiding resurfacing, but is disadvantageous for diving.



**Semi-aquatic, Fig. 1** Some of the anatomical adaptations of the Pyrenean desman (*Galemys pyrenaicus*), a globally threatened semi-aquatic mammal restricted to some part of Spain, France, and Portugal, to semi-aquatic

living: webbed feet with fringed hairs (left) and nasal trompe provided with hypertrophic vibrissae and chemo-/mechanosensitive Eimer's organs helping prey detection (right). (Pictures credits by Lorenzo Quaglietta)



To compensate positive buoyancy and reduce diving costs, they evolved increased bone density, similarly to human divers using counterweights and various birds, like penguins, using gastroliths (Fish and Stein 1991). Foraging strategies and variation in water density between marine and freshwater environments (higher in the former) also influence this trade-off. Within the Lutrinae, for example, the more deep forager and marine sea otter have larger lungs and denser bones than the shallower foragers and mostly freshwater river otters (op. cit.).

Light rarefaction and sound transmission also differ in water and on land. Vision and hearing underwater thus required special adaptations, such as mechanisms for aerial and submerged emmetropia (refraction of light to focus on the retina). A unique example of visual adaptation is represented by the duplicated eye of the four-eyed fish (*Anableps anableps*), allowing it to simultaneously see both over- and underwater. Adaptations aiding vision are particularly relevant for semi-aquatic mammals, as one of their most fundamental senses, the olfaction, is intensively used on land but does not function underwater, being often reduced in semi-aquatic organisms. The Pyrenean desman and *Neomys* sp., for instance, have reduced sense of smell (Stephan and Bauchot 1959), and aquatic carnivores have decreased olfactory turbinate areas compared to terrestrial carnivores (Valkenburgh et al. 2011), possibly reflecting adaptations to secondary aquatic living. Vibrissae, hairs specialized for tactile sensing, help animals with prey detection, especially when vision underwater is limited. They are generally more developed in semi-aquatic (e.g., otters, Phocidae, and semi-aquatic insectivores like the aquatic tenrec *Limnogale mergulus*, the Potamogalinae, and the Pyrenean desman) than terrestrial mammals, particularly in species foraging by vibrations detection (e.g., *Aonyx*) than by vision (*Lutra*) (Estes 1989). The Pyrenean desman perceives vibrations also thanks to chemo-/mechanosensitive Eimer's organs present on its stunning nasal trompe (Fig. 1), and the Platypus and several amphibians even developed electrical senses to locate prey under water.

## Physiology

Animals foraging underwater make prolonged apneas and thus have to solve the problem of breath-holding. To cope with aerobic metabolism constraints during diving, semi-aquatic animals developed several strategies, including reduction in heart rate, diversion of oxygenated blood to the heart and brain, elevation of muscle myoglobin concentration, and anaerobic metabolism of glucose providing the energy for diving and tissue maintenance (Scholander 1940). Lowering physiologic consumption, providing high anaerobic capacity, is common in ectotherms, such as reptiles, which, differently to endotherms, are capable of impressive dives independently of their size – even a nonspecialized green iguana may dive for 4.5 h – and may be a preadaptation to aquatic life (Pough 1980).

Osmosis is another major trade-off regulating animal life in water and on land. Freshwater animals are usually subject to osmotic inward water flow and have to excrete water in excess, while several marine organisms tend to lose water and therefore drink water, which leads them to excrete the excess of salts. A classical example of notable osmoregulatory capacity is provided by the nasal gland of the marine iguana (*Amblyrhynchus cristatus*), which is physiologically adapted to excrete salt, being thus able to survive while feeding almost exclusively on intertidal and subtidal marine algae. Similarly, sea otters are able to maintain water balance despite feeding mostly on invertebrates, which are isotonic to the sea, thanks to their larger kidneys compared with other mammals, which allow them processing large amounts of electrolytes.

## Thermoregulation

Maintenance of body temperature different than environment, i.e., thermoregulation, heavily conditions animal life history strategies in water and on land. As water thermal conductivity is higher than that of air, water absorbs more heat from an organism and more rapidly than air. Thermoregulation is therefore easier in air than water, i.e., the latter is a poorer insulant medium, exposing its inhabitants to thermal stress (heat loss). On the other side, however, temperature absolute values

and fluctuations are generally higher on land, and therefore heat loss is also crucial on land. Semi-aquatic endotherms cope with heat loss by increasing their insulation or metabolic heat production and decreasing surface/volume ratio (Scholander et al. 1950). Dense underfur and air layer trapped within it insulate mammals by preventing water penetration to the skin. Although all mammals have fur, semi-aquatic mustelids (e.g., mink and freshwater otters) and more aquatic-obliged mammals (e.g., platypuses and rodents) and carnivores (e.g., pinnipeds, sea otters, and polar bears) have higher underfur densities than terrestrial or less aquatic forms, revealing potential convergence among poorly related taxa in evolutionary fur modifications due to the transition to aquatic living (Estes 1989; Liwanag et al. 2012). Semi-aquatic carnivores, rodents, and insectivorous also have milk with higher content of fat and lower of lactose, compared to terrestrial taxa, possibly reflecting another adaptation to aquatic living (Estes 1989).

On land, on the other hand, semi-aquatic animals must cope with the risk of desiccation. Most invertebrates and amphibians are strictly dependent from water or humidity and evolved various mechanisms to track the best moment of emergence, usually synchronized with water temperature and light conditions, or of active migration from drying waterbodies. Organisms living in more hot climates show even more extreme adaptations to survive desiccation, including resistant eggs/stages, physiological dormancy, burying underground, shifting to shaded habitats or permanent waters, and other behavioral strategies. Particularly interesting is the behavior of some tree and desert frogs, which secrete and wipe lipids over the body and form cocoons of old epidermis, respectively, to increase skin resistance and maintain their water balance at high temperatures. Organisms living in Mediterranean or dammed rivers also evolved strategies to adapt to regular alternations between dry and wet phases, or floods and droughts, like many insects' life history strategies synchronized to avoid floods or droughts and fish behaviors to avoid displacement by floods (Lytle and Poff 2004). The dense fur of semi-aquatic mammals, while providing insulation in water, imposes a cost on land,

potentially leading to heating, especially during intense physical activity. Strictly aquatic sea otters use their enlarged rear flippers to dissipate heat (Estes 1989), while Eurasian otters may recur to behavioral thermoregulation to either limit heat loss or heating, by foraging more intensely in colder waters (Kruuk 2006) or by reducing their activity at higher temperatures in Mediterranean climates (Quaglietta et al. 2018). Penguins, among the most aquatic birds, also have to deal with opposite pressures resulting from semi-aquatic living. Namely, to facilitate energy conservation in water and resistance to heat stress on land, they evolved several morphological adaptations, including thick subdermal fat, dense, waterproof, and streamlined plumage and extensive arteriovenous associations facilitating countercurrent heat exchange and resistance to heat stress, as well as behaviors, including burrow nesting, body-orientation, and evaporative cooling (Frost et al. 1976). Other examples of behavioral thermoregulation in semi-aquatic vertebrates are changes in body postures or huddling, to drop resting metabolic rate at temperatures below the thermoneutral zone (e.g., pinnipeds, marine iguanas, and the *Myocastor coypus*).

## Cross-References

- [Homeostasis](#)
- [Mustelidae Cognition](#)
- [Mustelidae Locomotion](#)
- [Mustelidae Navigation](#)
- [Pinniped Life History](#)
- [Thermoregulation](#)
- [Water Balance](#)

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## Semiochemicals

- [Pheromone](#)

## Semi-Starvation-Induced Hyperactivity (SIH)

- [Activity-Based Anorexia](#)

## Semiterrestrial Lifestyle

- [Semi-aquatic](#)

## Sender

- [Signaller](#)

## Senescence

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## Synonyms

[Age-related decline](#); [Aging](#); [Progressive deterioration](#)

## Definition

Senescence refers to the progressive deterioration of function with increasing age, observable in various traits related to behavior, physiological functions, survival, and reproduction. The process is detectable both on the cellular and organismal level, and involves every major organ systems.

The term senescence is often used interchangeably with aging, although according to some authors, aging refers to the time-dependent accumulative changes (part of the underlying cause), while senescence is either the observable outcome (consequence) of aging or it refers to cellular senescence.

## Introduction

Cellular senescence underlies organismal senescence. In general, cells cease to divide after a finite number of times and may or may not die. The number of senescent cells in tissues rises during

aging. However, certain cell lines can divide infinitely. “Immortal” cells include most cell lines derived from tumors and embryonic germ cells. Senescent cells are characterized by bigger size, more diverse morphotypes, increase in b-galactosidase activity (a lysosomal hydrolase), increase copies of chromosomes (i.e., three or more in humans instead of two), change in several genes’ expression levels, and shortened telomeres (non-coding regions at the tips of chromosomes). Several factors can trigger cell senescence such as O<sub>2</sub>, H<sub>2</sub>O<sub>2</sub>, ethanol, and ionizing radiations. Senescent cells in tissue may impair renewal and homeostasis and decrease organ function.

Organismal senescence is a complex process which is mainly characterized by increased homeostatic imbalance, declining ability to respond to stress and recover, adapt to changes, and the increased risk of aging-associated diseases. While almost every organism age, the rate and onset of aging shows large variation between and within species. During the last century, several theories attempted to explain the phenomenon, with some of them viewing it as a random error, while others ascribing it to being part of a developmental program. Current data supports that senescence is not simply a random accumulation of detrimental mutations across time but an inherent part of the lifespan connected to the development and life history of the organism (Monaghan et al. 2008). Phylogenetically, senescence is a surprisingly ancient process (Warner et al. 2016), already present in the single cell bacteria *Escheria coli* (Nyström 2007).

In general, longer-lived species have a lower resting metabolism per gram body weight than shorter-lived species do, but there are several exceptions, for example, birds live considerably longer than expected for their metabolic rate. Rodents (mouse and rats) have a short lifespan relative to humans (2–3 years), although the naked mole rat (*Heterocephalus glaber*) live up to five times longer (up to 30 years) than expected by size, due to several factors such as enhanced antioxidant defense, lower insulin levels, and fewer aberrant proteins (Azpurua et al. 2013).

## Background

Senescence can refer to numerous processes, usually categorized based on branches of biology. Physiological senescence covers a variety of changes in behavior, survival rates, and reproduction. For example, muscular senescence (atrophy), immunosenescence, and neurodegenerative processes in the sensory and central nervous system all belong to physiological senescence, affect behavior and cognition, and are widely reported to occur in animals.

Behavioral senescence occurs when the age-related changes are detectable via behavioral characteristics. The primary cause behind most of these changes is physiological senescence (i.e., brain aging), as behavior and cognition is tightly connected to the sensorimotor and central nervous system. For example, physiological deterioration is suspected to be the underlying cause of declining predatory performance in case of aging wolves (MacNulty et al. 2009), while decreased memory and learning abilities are related to brain atrophy. In humans, cognitive decline begins in the mid-twenties. Mild changes in orientation might be a normal part of aging, but deficits in orientation is a sign of pathology. Attentional abilities, memory functions, performance on verbal tasks (i.e., word retrieving) also decline with age. Nearly half of people over 85 years of age have dementia, caused by brain diseases or injuries, which impairs daily functioning. Behavioral changes can also influence survival and reproduction.

Actuarial senescence stands for the increase in mortality rate with advancing age. It is characterized by the age at the onset of senescence and the rate of senescence. A large diversity of actuarial senescence patterns can be observed among species. Zoo animals generally outlive their wild counterparts. In some populations, mortality rates cease to increase at late ages, resulting in a mortality plateau. Fast growth, larger early investment in growth, as well as harsh environmental conditions in early life has been correlated with more pronounced actuarial senescence.

Reproductive senescence means decreasing fecundity with increasing age. Sex difference

in reproductive senescence, if present, usually equal to faster senescence in males. Additionally, females of certain species live considerably longer than they can produce offspring, a stage referred to as the post reproductive lifespan. This occurs, for instance, in cetaceans, elephants, and great apes and is thought to be linked to living in social groups with resident females, but the exact evolutionary mechanisms leading to its emergence is still debated (Bonduriansky et al. 2008).

Different phenotypic traits showed asynchronous changes during senescence in wild mammals (Hayward et al. 2015), leading to uncoupling them, for instance, in case of actuarial and reproductive senescence it can lead to the emergence of a long post-reproductive lifespan such as in humans. This idiosyncratic pattern highlights the complexity of senescence, where the unique pattern of a given individual's aging phenotype is the result of the interplay between different (epi) genetic and environmental factors.

As it has been established during the last decade, senescence is common in wild and captive populations living in their natural or restricted environment, across every taxon, within the life expectancies of the species (Nussey et al. 2013). Its widespread presence is explained by life history theories of aging, based on the concepts of antagonistic pleiotropy (certain alleles which are beneficial on early survival or reproduction are favored by natural selection even if they have negative effects on fitness later in life); and the disposable soma (as resources and energy are limited, allocation and distribution between somatic maintenance and reproduction will be adjusted based on the organism's ecological context). In this sense, senescence is the consequence of sexual reproduction and natural selection favoring investment in early reproduction over long-term somatic maintenance (Gaillard and Lemaître 2017).

Senescence can be delayed. Calorie restriction, specific diet, enough sleep, avoidance of chronic stress, and physical exercise increases lifespan in many animal species. Medical intervention is also available for both humans and animals.

## Conclusion

Senescence is currently viewed as the consequence of natural selection, an evolutionary adaptive trait. The adaptation seems to be a tradeoff between early life gains and late life disadvantages. Its nature as an inherent strategy instead of random error is supported by both experimental laboratory and long-term observation data across various taxa. Linked to the organism's life-history, this interconnected system results in mosaic aging, where different phenotypic traits can show different onset and rate of senescence, with overlapping divisions of actuarial, behavioral, physiological, and reproductive senescence.

## Cross-References

- [Fitness](#)
- [Life History](#)
- [Natural Selection](#)
- [Reproductive Fitness](#)

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## Sensation

- [Hominoidea Sensory Systems](#)
- [Rodentia Sensory Systems](#)

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## Sensation and Movement

- [Perception-Action Theory](#)

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## Sensations

- [Cognition](#)

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## Senses

- [Cognition](#)
- [Primate Sensory Systems](#)
- [Sirenia Sensory Systems](#)

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## Sensing

- [Primate Sensory Systems](#)

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## Sensitive Period for Song Learning

- [Critical Period for Song Learning](#)

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## Sensitive Periods

- [Critical Periods](#)

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## Sensitization

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## Synonyms

[Dishabituation](#); [Habituation effect](#); [Sensitization effect](#); [Sensitization process](#); [The Dual-Process theory](#)

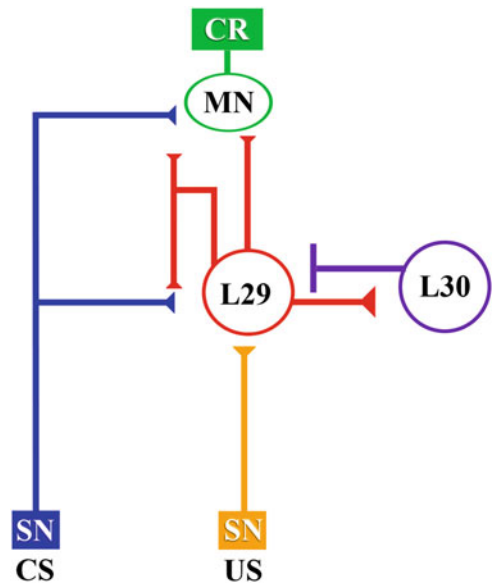
## Definition

*Sensitization* is a term that applies to both an effect and a process. The sensitization effect is observed when repeated exposures to an environmental stimulus elicit an increase in behavioral response. For example, a child visiting the hospital to receive an injection might exhibit sensitization through an increased behavioral response after each pinch of the needle. In contrast, the habituation effect is a decrease in the level of response after repeated stimuli. The sensitization process deals with the underlying neurological mechanisms that drive response increases in the face of repeated stimulation. The effect (either habituation or sensitization) will be the net result of both habituation and sensitization processes, with arousing stimuli more likely to tilt the overall balance toward sensitization. Organisms use

habituation and sensitization to focus priorities by filtering environmental stimuli such as sights, sounds, smells, etc. (Domjan 2015).

According to the Dual-Process Theory of Habituation and Sensitization, sensitization processes occur in the state system, which is the compilation of an organism's nervous system that determines the general propensity to respond to particularly arousing stimuli (Groves and Thompson 1970). This is analogous but not identical to the Dual-Process Theory that involves thoughts derived by implicit and explicit means (Petty and Cacioppo 1986). In the case of the Dual-Process Theory of Habituation and Sensitization, habituation serves to decrease conscious reflection of a stimuli, while sensitization acts to increase conscious awareness of a stimulus (Domjan 2015; Groves and Thompson 1970). In the Dual-Process Theory of thought, the implicit is always unconscious, while explicit thought is fundamentally conscious (Petty and Cacioppo 1986). Although sensitization is an independent process that can occur in relative isolation, both habituation and sensitization processes interact to produce behavioral responses (Groves and Thompson 1970). The state system cannot function as a simple reflex, as habituation can; therefore for sensitization to take place, arousal must be triggered (in some animals this can take the form of an emotional response). Once prompted, any environment or situation with repeated eliciting stimuli can yield the sensitization effect, even the same stimuli that the individual was habituated to previously but occurs now with arousing background "noise" (Shettleworth 2010).

In all cases, the sensitization effect is understood as an increased facilitation of neural impulses in response to repeated exposures of an arousing stimulus (Domjan 2015). In the relatively simple invertebrate system *Aplysia* (Fig. 1), this can manifest as the result of mediation of interneurons that cause increased action potentials to reflex motor neurons in response to repeated stimulation (Hawkins et al. 2006). Sensitization can be divided further into subcategories, such as incentive sensitization and behavioral sensitization (Temple 2016).



**Sensitization, Fig. 1** *Aplysia sp.* Neural circuit implicated in conditioned response (CR). There are multiple pathways that facilitate action potentials by stimuli. Unconditioned stimulus (US) cause a sensory neuron (SN) to fire and travel to the L29 pathway before the motor neuron (MN) finally causing a conditioned response. Sensitization by a conditioned stimuli (CS) fires action potentials directly to motor neurons causing a heightened response. This pathway has a direct route to the motor neuron (MN)

## Incentive Sensitization

The dopaminergic system is responsible for incentive sensitization due to its response to a broad range of stimuli (Leyton and Vezina 2014). Behavioral incentives range from food to preference of sexual partners to drugs. In humans, the sensitization of the dopaminergic system explains the progressive nature of addiction (Temple 2016). Although drug users need higher doses of psychoactive substances to reach the same level of effect due to habituation, the neural system for drug cravings has been shown to become sensitized. In one study, rats preexposed to amphetamine and nicotine self-dosed cocaine at lower levels than rats without preexposure to psychoactive stimulants suggesting dopaminergic release in anticipation of substance effect (Hogger et al. 1992). There is a form of locomotor sensitization that manifests behaviorally in more active

and responsive subjects. This will occur when dopaminergic pathways become more sensitive to excitatory pharmacological stimuli after repeated presentations (Kalivas and Stewart 1991; Temple 2016).

## Behavioral Sensitization (Sensitization Effect)

Sensitization effects are observed as increases in behavioral responses to repeated stimuli that are substantial enough to elicit arousal or fear. While habituation must maintain stimulus consistency for an effect to ensue, sensitization can occur across a broad range of stimuli due to the activation of arousal systems (Domjan 2015). Multiple studies of rodent species demonstrate that subjects presented with unconditioned foot shocks associated with an auditory stimulus show significant sensitization to that sound (Dirks et al. 2001; Sasaki and Hanamoto 2007; Sheets et al. 1988).

Through sensitization, past experiences can shape behavioral or incentive response levels to future invoking stimuli. Post-traumatic stress disorder, PTSD, is a human condition that has been modeled in animals. The condition results from exposure to chronic stressful events or a single traumatic event. PTSD patients exhibit persistent physiological and behavioral symptoms including increased levels of corticosteroids indicative of stress and a sensitized startle response to triggering stimuli. These associations can manifest as a result of a sensitization process. In one study, rats exposed to tail shocks for a longer period of time developed an exaggerated startle response and increased stress hormone levels even after 10 days. Control rats that received fewer shocks did not show this same persistence of startle responses. The authors propose that this is a model of both sensitization and PTSD (Servatius et al. 1995).

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## Cross-References

- Desensitization
- Habituation

## Sensitization Effect

- Sensitization

Sensitization Process

- Sensitization

Sensorimotor Striatum

- Dorsolateral Striatum

Sensory Acquisition Phase

- Critical Period for Song Learning

Sensory and Motor Impulses

- Afferent and Efferent Impulses

Sensory Channel

- Catarrhine Communication
- Mustelid Communication

Sensory Discrimination

- Sensory Judgment

Sensory Drive

- Chemoreception

Sensory Judgment

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Synonyms

Perceptual decision; Psychophysical threshold; Sensory discrimination

Definition

A decision made by a human or nonhuman animal on the basis of incoming sense data processed by perceptual/cognitive systems of the brain.

Introduction

Humans and nonhuman animals alike are able to behave adaptively in their environment in part because their behavior is based on incoming sense data and prior knowledge of the world. Research on sensory judgment in both cases generally falls under the purview of *psychophysics*, which focuses on how changes in a physical stimulus map onto changes in perception. The simplest case occurs when a stimulus changes from “absent” to “present” (or vice versa), but stimulus changes can also occur across any dimension available to the perceptual system of the observing animal. For example, changes to a physical object may be spatial (e.g., length, color), temporal (e.g., duration, tempo), or constitutional (e.g., weight, volume). Animals – human or otherwise – will vary in their ability to detect these changes, and research on sensory judgment is primarily concerned with discovering the critical factors influencing this process.

A *sensory judgment* is made when an observer decides between competing interpretations of a

stimulus and alters their behavior accordingly, either by responding to an experimental probe (e.g., “same” or “different”) or by acting differently in a real-world environment. Sensory data (e.g., light) physically impinges on a sensory apparatus (e.g., cells of the retina) and is transduced from a physical signal into an electrochemical patterns of neuronal firing. These patterns increase in their abstraction away from the sensory signal that further up the nervous system’s hierarchy. In this sense, all sensory judgment is *perceptual and cognitive* rather than purely sensory; that is, judgments about the nature of stimuli occur only after some neural processing beyond the original sensory trace that has occurred. For this reason, research in this field is generally concerned with the relationship between qualities (and quantities) of a physical stimulus (such as light, which changes in *intensity*) and its perceptual analogue (for light, this is perceived *brightness*).

Some stimulus changes are modality-specific; that is, they operate in only one sensory domain. Color is an example of a modality-specific dimension, as it is an emergent property of several physical properties (hue, saturation, intensity) operating only in the visual domain. Other properties on which sensory judgments may be based are shared across modalities. Frequency is an example of a dimension coded in multiple sensory domains. In vision, spatial frequency is a critical variable coded by the primate visual system, as it is useful for representing certain properties of objects and textures. Auditory frequency is similarly important for primate hearing, as it corresponds with the perceptual property of pitch.

Since sensory judgments depend on the nature of the sensory and cognitive system processing incoming sense data, and animals vary significantly in how their brains and minds are organized, a great deal of diversity exists in the animal kingdom. Certain animal models will be more useful for certain questions. For example, cats and primates are often used in visual perception experiments, as they share certain visual capacities with humans.

Animal psychophysics also requires special consideration of how responses will be elicited and measured by the experimenter (Stebbins

2013). In human experiments, subjects can be asked to produce responses. In animal experiments, of course, no such instructions may be given. Instead, animals are typically conditioned to produce responses to easy cases of the experimental stimuli in question, with the difficulty ratcheting up slowly as the animal acquires the conditioned response. For example, take a hypothetical experiment in which primates must estimate line length and decide which of the two lines is longer. One approach to ensuring that the animals respond appropriately would be to condition them over many trials to associate choosing a longer line with a treat or some other unconditioned stimulus. Over time the primate will learn the rule that choosing the longer line will be rewarded. Once this rule is learned, more difficult trials can be slowly introduced, until the line-length discriminations begin approaching the animal threshold for line-length discrimination.

## Theoretical Foundations

As stated above, the research into sensory judgment is centrally concerned with understanding the effects of changes in stimulus quantity, or intensity, on the perceptual system, as well as the decision-making process guiding responses. This concern motivated much research into the concept of thresholds, both *absolute* (the smallest intensity of a stimulus that can be detected against a neutral background) and *change* (the smallest difference that can be detected). Subsequent theory introduced a pivotal role for decision-making processes as well, which is inherent to the signal detection approach to sensory judgment research. Several complementary approaches, described more fully below, are employed toward achieving a fuller understanding of how sensory judgment changes depending on both physical stimulus characteristics and decision-related variables.

## Thresholds and the Just Noticeable Difference

Sensory judgment becomes more difficult as the difference to be detected approaches a subject’s



absolute threshold for that stimulus type. In this context, as noted above, a sensory threshold refers to the least intense stimulus detectable by an observer. Ernst Weber formalized this concept by discussing thresholds in terms of a *just noticeable difference (JND)* or the minimum amount a stimulus must be changed from some baseline level so that it will be detectable by an observer. This “change” can either take the form of a difference between two or more stimuli or may be simply the onset of the stimulus against a blank, neutral background, in which case the absolute threshold is typically being assessed. Calculation of this difference was formally described in a ratio formula that is now called Weber’s law. This formula encapsulates the fact that as the starting intensity of a stimulus increases, the amount of change needed to achieve a JND also increases. It was noted that Weber’s law did not work well near threshold, and so Fechner (Weber’s student) derived his own law from Weber’s, demonstrating that there is a logarithmic relation describing change in perceived and actual stimulus changes. Stevens (1957) later noted that the relationship between physical intensity and perceived magnitude appears to conform to a log-log function and proposed a new formula, now called Steven’s power law that more accurately describes the relationship for most, if not all, stimuli. Note that there is a stimulus-specific exponent term in this formula; each stimulus is thus somewhat unique in how it is coded. Consequently, the mathematical mapping from physical intensity changes to perceptual changes depends on the stimulus change in question and can be expressed by an exponent the value of which depends on the nature of the relation between the two (exponential, logarithmic, linear).

Take again our example of line-length estimation. What controls whether an observer detects the difference in line length is not the absolute size of the difference in length between the lines but rather the ratio of the line’s length to the length of the difference. That is to say, smaller absolute length differences are more detectable when lines are shorter. This ratio in length judgment is essentially linear; that is, the exponent is one. The perception of brightness changes, however, and is described by an exponent less than one, meaning

that as light intensity increases, perceived brightness initially increases rapidly, but as intensity is increased still more, perceived brightness increases much more slowly.

## Estimating Classical Thresholds: Methods

### Threshold Estimation

#### Method of Adjustment

This simple threshold estimation procedure entails having subjects manually adjust stimulus intensity to its minimum detectable level. Often this procedure is performed many times for the same observer, with the difference between the adjusted intensity values corresponding to the answer given on the previous trial. Once an observer has adjusted the value up and down around a specific value for more than a preset criterion number of times, that value is taken as the threshold.

#### Method of Limits

This method is characterized by estimating a subject’s threshold twice and then averaging the two estimates. Subjects are presented with intense (i.e., easily detectable) stimuli or stimulus differences at first, with subsequent stimulus presentations becoming less and less detectable. Once a minimum intensity at which the subject can detect the stimulus is reached, the reverse procedure is performed; subjects are then presented with very weak stimuli or stimulus differences incrementally increasing in intensity until the detection threshold is reached again. Once both of these have been performed, the average of the two intensity thresholds is calculated and deemed the detection threshold.

#### Method of Constant Stimuli

Another way of indexing an observer’s threshold for a given detection task is to randomly present stimuli of varying intensities over a number of trials. Multiple trials at each intensity level must be tested, and these stimulus intensities must span the range from clearly above to clearly below the observer’s threshold. According to this method,

an observer’s detection threshold is the minimum intensity at which the observer’s detection accuracy falls above chance.

Adaptive Staircasing

Modern computing has proffered dynamic solutions to the problem of threshold estimation, including the use of adaptive testing methods capable of dynamically adjusting stimulus intensity based on prior subject responses. The simplest version of this procedure is called “adaptive staircasing.” Staircasing essentially entails presenting the observer with easily detectable, high-intensity stimulus on the first trial and reducing stimulus intensity by some regular intensity increment every time an accurate detection occurs. Once the subject begins encountering trials near their threshold, they begin making errors. Each error committed leads to an increase in intensity, typically by a multiple of the absolute value of the decreases (i.e., the so-called 1-up-N-down procedure). This is now a common means of obtaining a classical threshold in the vision literature.

Signal Detection and the Role of the Observer

The study of sensory judgments soon was made to go beyond simple characterizations of observer accuracy and instead characterizes the interaction between observers’ judgments and the presence of the stimulus (i.e., the signal). Central to this refinement was the transition from casting sensory judgment as a fixed perceptual process to a mutable decision process based both on the nature of the stimulus and the cognitive state of the observer.

In any detection task, a 2 × 2 matrix can be created fully describing the potential interactions between the observer’s belief about the stimulus and the true nature of the stimulus. Each of the four cells of this matrix represents hits, misses, false alarms, and correct rejections.

- Hit** A subject detects the signal, and the signal occurred.
- Miss** A subject does not detect the signal, and the signal occurred.
- False alarm** A subject detects the signal, and the signal is absent.

**Correct rejection** A subject does not detect the signal, and the signal is absent.

|           | Subject’s<br>Yes | Response<br>No    |
|-----------|------------------|-------------------|
| Signal    | Hit              | Miss              |
| No signal | False alarm      | Correct rejection |

The concept of a classical threshold, while less meaningful in signal detection theory (SDT), is similar to the signal detection concept of *sensitivity*. Sensitivity refers to the ability of the observer to detect a given stimulus, but in signal detection theory, this is only one influence. In fact, the threshold concept in SDT would be incomplete if it only included sensitivity; it must also include *response bias*. Bias reflects a set of influences present in an observer at a given time. These influences affect the extent to which an observer is prepared (or willing) to respond “yes” to the question “was the signal present?”, independent of the presence of the signal itself. An example would be a situation in which a driver is operating a vehicle on a foggy road. The driver is aware that there are other cars on the road, and the danger of colliding with one is high. Consequently, the driver is much more likely to begin braking (say “yes”) if anything that might resemble a car appears (e.g., a swirl of fog). Indeed, the driver’s internal state of increased anxiety might cause them to brake for no external reason. Both of these would constitute false alarms, as noted in the table above. This demonstrates the issue; signal detection and signal reporting are separate but related parts of the process, and can be influenced by different things, but both matter in measuring the ability to detect a change. SDT allows the experimenter to measure sensitivity under different bias conditions and to see that sensitivity does not change when an observer’s level of bias is altered. The fact that classical threshold theories cannot account for the effect of bias on threshold measures led theorists to argue that the concept of sensitivity is a better measure of detection than that of a threshold, which in essence assumes that bias is always controlled across experiments so that it does not

change. Regardless, classical threshold measurements, which are described next, are still regarded as highly informative under controlled conditions and are used routinely in many experimental tests. Note, however, that the classical methods generally assume that bias is well-controlled; therefore, thresholds obtained using classical methods may not generalize well to situations where this is not the case.

## Threshold Estimation in Vision

Sensory judgment – like perception more generally – has been studied most extensively in visual processing. The emphasis on vision is due to both the relative importance of this modality and to the ease of studying it; audition, for example, presents problems in terms of stimulus creation and presentation that until recently have been difficult to overcome. Some sensory modalities (touch, olfaction, gustatory) are still quite difficult to test, and relatively few researchers have attempted to address these modalities.

**Line-Length Estimation:** Tests of this ability use a starting standard line length and examine the ability of observers to detect a change in the length of the line. This can be done by providing both the standard line and the changed (or unchanged) line at the same time or by presenting the standard first, removing it, and then presenting either the same line or a line of a different length. This approach requires that the observer remembers the actual line length for a short amount of time.

## Animal Research

### Rodents

Rodents are often used as animal models of human behavior for several reasons, including their relative ease of use and shared mammalian biology (i.e., a highly developed neocortex). Despite their ubiquity as an animal model, they are less suitable for modeling human perception than they are in other domains. This is largely because rodents use very different aspects of the environment to guide their behavior. While

rodents do use vision to navigate their environment (Chen et al. 2013), their spatial vision is weaker than humans by several orders of magnitude (Huberman and Niell 2011) and is oriented toward nocturnal environments, at least in the wild.

However, that is not to say that rodents are incapable of serving as experimental subjects in research about sensory judgment. In fact, owing to their complex neocortex, including parietal (Kolb and Walkey 1987) and frontal (Uylings et al. 2003; Clark et al. 2004) regions that integrate multimodal sensory data to contribute to decision-making, rodents are increasingly used as animal models for processes once thought too complex for probing with rodents (Carandini and Churchland 2013).

### Primates

Research on primates is more difficult and expensive to carry out but provides a deeper and more direct mapping between the animal model and humans. Hubel and Wiesel famously won the 1981 Nobel Prize in physiology and medicine by mapping the neural basis of visual processing in monkeys. They showed convincingly that visual neurons were selective for basic properties such as orientation, contrast, and spatial frequency (see Wurtz 2009 for a modern retelling of the long-term influence of this research). An early analysis of contemporary research by De Valois et al. (1974) reviewed the basic characteristics of macaque vision and established their fit for use as models of human visual processing.

Primate research is often used as the tip of the spear; findings revealed with the more invasive methods are followed by less-invasive probing into human perception. A modern review emphasizes this: Horwitz (2015) notes the strength of macaque models of vision in reviewing his own work on color perception.

## Human Development

As useful as animal models are, they are mainly intended to facilitate greater understanding of human sensation and perception. It is also worth

noting that there is a great deal of overlap between the behavioral experimental methods used with primates and those used with human infants. Both monkeys and infants are nonlinguistic primates incapable of receiving and complying with simple experimental instructions and are otherwise difficult to work with. Human infants, like primates, require the use of either implicit indices of sensory judgment or conditioning paradigms to elicit responses. For example, one might measure differences in looking time at two stimuli to see if infants can tell them apart (e.g., Teller 1979) or condition infants to kick at mobiles when they see a certain stimulus and then switching the stimulus and measuring kicking (Hartshorn and Rovee-Collier 1997).

Children are born with poor visual capabilities and show substantial development across the first few months of life as input from the eyes and maturation of the brain help to shape perception. The use of threshold detection tasks has been useful in characterizing infant and child maturation levels (compared to adult thresholds) in multiple visual stimulus dimensions. Visual acuity (pattern vision) is tested using multiple methods. Braddick, Atkinson, and colleagues have studied multiple aspects of visual development, including contrast sensitivity (the ability to detect the difference between dark and light areas of a stimulus) and visual acuity. This group and others have developed means of testing these abilities using both behavioral and electrophysiological methods. An example of this type of test is from Braddick et al. (2005). They used visually evoked potentials (an EEG signal temporally tied to the presentation of a stimulus) to examine the emergence of orientation sensitivity in infants between 4 and 18 weeks and found that infants showed a detectable response to orientation changes (e.g., flipping between a diagonal left and a diagonal right grating) even at the youngest ages tested. Braddick et al. (2005) also tested directional motion, using an essentially random pattern that moved rapidly from side to side. Here, infants showed essentially no response until about 11 weeks for faster motion and about 9 weeks for slower motion. Note that the stimulus parameters used were such that adults would have found

both types of change extremely easy to detect; this is a demonstration of the first onset of these abilities. For an overview of multiple such studies, see Braddick and Atkinson (2011).

## Experimental Validity

Most research on sensory judgments has occurred in a laboratory setting. Likewise, and deriving both from the nature of this topic and the experimental method itself, most research on sensory judgment also attempts to isolate single perceptual processes or variables rather than study them in realistic or emotion-laden scenarios. Of course, the real-world processing these experiments are meant to index does not occur in this context. Real-world processing is highly integrative, and multiple internal and external cues may be used to guide adaptive behavior.

The more general concern of experimental external validity, or the extent to which a given experimental method is capable of indexing a real-world process, can be raised regarding research on sensory judgment. Take an example from a task about auditory pitch discrimination. A typical human experiment would be conducted in a soundproof room using flat-frequency headphones and a response box. Such a task would be meant to index how “pitch is processed” generally, but by isolating pitch from other auditory variables, the experimenter limits the extent to which those other variables can influence pitch perception in a normative way.

The concern is magnified in comparative research. Take the case of a highly cited study by Beecher et al. (1979), who investigated Japanese macaque’s perception of other monkeys’ vocalizations. Low- and high-pitched versions of two distinct monkey vocalizations (smooth early high coos and smooth late high coos) were presented to listener monkeys over headphones. With some clever experimental manipulations, the researchers were able to make quite strong conclusions about how monkeys represent acoustic and semantic properties of vocalizations. However, those conclusions were drawn from a highly contrived experimental scenario in which monkeys were wearing headphones and vocalizations

otherwise lacked their normative social context. These caveats limit the extent to which the results can be considered ecologically valid.

## Application

Research on sensory judgment has deeply impacted a number of design fields concerned with how humans interface with machines and computers. One such area is human factors' research and human-computer interaction [HCI], respectively. Heads-up displays (HUD), which are typically translucent displays that allow an operator to receive information without moving their head, have been around in military applications for some time and in nonmilitary applications from at least the 1980s. Tests of the ability of an observer to detect and use this information without being distracted from an external focal point (such as through a vehicle window, with the information being displayed on the window) have been examined using the types of judgment/decision-making testing described above, and there is a strong assertion in the literature that attention capture by the display can have both positive and negative (distracting) effects. This is a demonstration of the role that attention plays in sensory judgments and decision-making in ecologically valid (nonexperimental) settings.

## Conclusion

Sensory judgment is a fundamental topic in psychology, both human and comparative. Adaptive behavior is guided by perception, and perception fundamentally depends on judgments (implicit or explicit) made on the basis of sensory data. The field of psychophysics, aimed as it is at unpacking how physical changes map onto perceptual ones, is quite old and methodologically robust. By characterizing sensory judgments in terms of thresholds, and later in terms of both sensitivity and bias, rich mathematical models of various perceptual processes have been produced.

Human psychophysics is quite developed as a field, and animal psychophysical studies are

increasing in their sophistication, despite requiring extra experimental work to elicit meaningful responses. Rodents are easy-to-use but imperfect models, at least for visual psychophysics. Primates are better models but are more difficult to work with. There also exists a great deal of similarity between primate studies and studies of human infancy. Concerns do exist regarding external validity – experiments in sensory judgment require rigorous control of the experimental scenario, which entails a low degree of overlap between real-world sensory and perceptual processing and that which occurs in the laboratory. Despite this, sensory judgment research, and psychophysics in general, has been applied a great deal in industrial and technological application to improve how humans interact with technology.

## Cross-References

- ▶ [Auditory Processing and Perception](#)
- ▶ [Evolution of Animal Color Vision](#)
- ▶ [Olfactory Perception](#)
- ▶ [Primate Sensory Systems](#)
- ▶ [Prosimian Sensory Systems](#)
- ▶ [Saccadic Eye Movement](#)
- ▶ [Sensory Receptors](#)
- ▶ [Size Constancy](#)
- ▶ [Stereoscopic Vision](#)
- ▶ [Visual Cliff, The](#)
- ▶ [Visual Detection Task](#)
- ▶ [Visual Perception](#)
- ▶ [Visual Recognition in Birds](#)
- ▶ [Visuospatial Memory](#)

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## Sensory Receptors

- [Cognition](#)

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## Sensory Systems

- [Caudata Cognition](#)

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## Sensory-Motor Control

- [Perception-Action Theory](#)

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## Sentience

- [Plantae](#)

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## Sentinel Species

- [Indicator Species](#)

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## Sequence Analysis

- [Bioinformatics](#)

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## Sequence Learning

- [Pattern Learning](#)

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## Sequential Pattern Learning

- [Pattern Learning](#)

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## Serendipity

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## Synonyms

[Eureka effect](#); [Insight](#); [Lucky finding](#); [Sporadic discovery](#)

## Definition

Serendipity is an epistemological term created to design the occurrence of a fortuitous and fortunate discover.

## Introduction

Serendipity is a term that suggests that accidental discoveries could lead to valuable and relevant results. Serendipity moments are usually those in which the outcome of the research has no relation with the path followed to obtain it. This type of accidental discoveries has sometimes led to huge changes in the course of history. For instance, the erroneous trajectory followed by Columbus that eventually brought him to America.

## Origins of Serendipity

Serendipity is a neologism. The word was generated to denominate the unexpected resolution for an unsolved problem. The origin of the term comes from a traditional Persian story called *The Three Princes of Serendip*. It was proposed by the politician Horace Walpole in 1751 (Cannon 1940). In the tale, the three main characters move forward their adventures using their sagacity over accidental discoveries, taking advantage of fortuitous information (Cammann 1967).

## Scientific Serendipities

Several historic examples of serendipity are well known in the scientific field. Archimedes discovered his famous principle when he took a bath and observed how his body moved an equivalent volume of liquid. His “eureka” expression passed to history as an exclamation of discovery.

In psychology, an example of serendipity was the determination of classical conditioning by Ivan Pavlov. From digestive system to learning, Pavlov was a physiologist interested in the digestive system. While investigating the dog’s salivation reaction, Pavlov accidentally observed that dogs salivated without direct stimulation of their glands (Boakes 1984). He realized that dogs

salivated in the presence of a sound that was involuntarily paired with the food that was used to induce salivation. Progressively, the dog associated the innocuous sound with feeding time, and the salivation response was also observed in the presence of sound alone. Later, Pavlov derived his scientific interest to this curious phenomenon founding the basis of classical conditioning, also called Pavlovian conditioning.

## Serendipity: Chance or Reasoning

Serendipity’s phenomena could seem sporadic. However, it has been proposed (Arfini et al. 2018) that the scientific ability to recognize an unexpected event is a relevant piece to solve a problem. Hence, how the researcher fits accidental observations in the general frame of a problem is crucial for a serendipity to become a scientific discovery.

Through this idea, there is a key concept necessary for a fortuitous observation to become a solid discovery. This is the “insight” concept. To have an insight is to experience a sudden reorganization of information that supports a brief resolution of an issue. Wolfgang Köhler was the one who coined insight as this quick reorganization of reasoning in the middle of a difficult problem. Köhler investigated to what extent primates could solve complex problems (Köhler 1925). This author observed that, in the previous seconds before solving a problem, animals seemed absorbed looking at the situation and later solved it quickly and confidently. Köhler called this lucid moment as “insight.”

Following this argument, some authors have tried to explain the factors that arise from the lucky nature of serendipities. Arfini et al. (2018) explained three factors that involve serendipity discoveries: first, it is a fortunate coincidence usually related with the luck stereotype. Secondly, serendipity has a surprising nature, as it is a non-expected event. Finally, serendipities encourage revolutions in the path of science. In that sense, several serendipities have modified paradigms of knowledge in a Kuhn’s point of view (Kuhn 1970). For example, the discovery of penicillin by Fleming was an accidental chance that dramatically changed the medical field forever.

Serendipity is also possible as far as the researchers are able to fit an accidental observation into a general schema of explanations, thus providing the ability to reorganize a solution in a new qualitative level. So, serendipity acts could be described as keys that led to scientific discoveries.

## Cross-References

- ▶ [Eureka Effect](#)
- ▶ [Insight](#)
- ▶ [Ivan Pavlov](#)
- ▶ [Problem-Solving](#)

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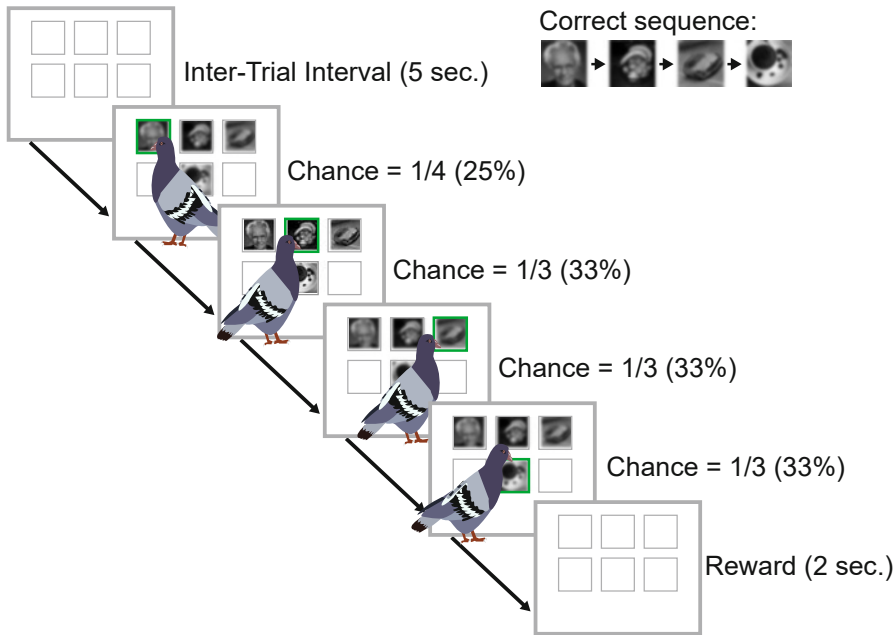
## Serial List Learning

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On the week of September 20, 1948, a symposium titled “Cerebral Mechanisms in Behavior” was held at the California Institute of Technology. The symposium focused on the question of how the nervous system controls behavior and was attended by a number of eminent scientists, such

as John von Neumann, Wolfgang Köhler, Karl Lashley, and Heinrich Klüver. Of the papers presented at the symposium, Lashley’s (1951) paper is likely the most influential and enduring (Bruce 1994). Lashley (1951) focused on the problem of explaining how serially organized behaviors are represented and executed. At the time of his address, the dominant theory postulated that all serially organized behaviors were composed of a chain of stimulus-response (S-R) associations. That is, the functional stimulus for a response ( $R_n$ ) is the response to the preceding stimulus ( $R_{n-1}$ ). Lashley (1951) rejected the chaining theory of serial-organized behavior, especially as an explanation for language, and noted that many errors of speech and writing provide evidence that entire sentences are prepared before they are produced. For example, spoonerisms, the transposition of word sounds such as saying “the Lord is a shoving leopard” rather than “the Lord is a loving shepherd,” are common in speech; if the chaining theory of language was correct, spoonerisms would not occur because only a single word in the sentence would be activated at any given time.

Unfortunately, Lashley’s (1951) focus on examples of human behavior meant that his criticisms of chaining theory had relatively little impact on theories of animal behavior. In the late 1970s, however, a novel paradigm was developed that allowed the chaining theory of animal behavior to be tested (Terrace et al. 1977). Terrace et al.’s (1977) simultaneous-chaining paradigm involves presenting subjects with a list consisting of  $n$  number of simultaneously displayed items (Fig. 1). The subject’s task is to respond to each item of the sequence in a prescribed order learnt during training. Several aspects of the paradigm make it difficult for a subject to rely on an S-R chain. First, all of the stimuli are encountered at the same time, making it difficult for a single item to be the discriminative stimulus for a response. Second, the on-screen positions of the items are changed on each trial, thereby preventing the subject from learning a rote motor sequence. Third, beyond responding to the last item correctly, which results in reward, or committing an error, which results in a punishment, a response to the  $n$ th item of a sequence provides no information as



**Serial List Learning, Fig. 1** The typical flow of a correct trial on the 4-item list. Following the inter-trial interval (5 sec), all four items A (B. F. Skinner), B (fruit bowl), C (car), and D (cup of coffee) were presented simultaneously and subjects were rewarded for responding to them in the order  $A \rightarrow B \rightarrow C \rightarrow D$ . With four items on screen, the chance of a correct response to A is 1 in 4 (25%). Given repeat pecks to a correct item were not classed as an error (e.g.,  $A \rightarrow A \rightarrow A \rightarrow A \rightarrow A \rightarrow B$ ), unless the list order was violated (e.g.,

$A \rightarrow A \rightarrow A \rightarrow A \rightarrow A \rightarrow B \rightarrow A$ ), the chance of a correct response for items B, C, and D is 1 in 3 (33%). Thus, the chance of completing a trial correct was 0.9% ( $0.25 \times 0.33 \times 0.33 \times 0.33$ ). Reinforcement was only provided when all list items had been responded to in the correct order. Any violation of the order immediately terminated the trial and subjects entered a time-out period. A green boarding appearing around the stimulus reflects a correct response

to the identity of item  $n + 1$ , because the feedback following each response is identical. We note that the name “simultaneous-chaining paradigm” is an unfortunate choice of words for a paradigm that was developed, in part, to debunk chaining theory. Therefore, in the current paper, we will refer to the paradigm as the serial-order task.

The serial-order task is unique in the sense that it has been utilized with an extremely wide variety of species and adapted to assess multiple aspects of how serial-order behaviors are represented and executed. With respect to the diversity of species, the serial-order task has been utilized in work with adult humans (Colombo and Frost 2001), chimpanzees (Ohshiba 1997), a gorilla (Ross 2009), capuchin monkeys (D'Amato and Colombo 1988), crab-eating monkeys (Scarf and Colombo 2009), snow monkeys (Ohshiba 1997), rhesus

monkeys (Brannon and Terrace 1998; Terrace et al. 2003), marmosets (Koba et al. 2012), lemurs (Merritt et al. 2007, 2011), chickens (Scarf 2011), and pigeons (Scarf and Colombo 2010b, 2011; Straub and Terrace 1981; Terrace et al. 1977). This diversity provides a unique opportunity to compare the serial learning abilities of a range of species. In the current paper, we not only provided a comparative analysis of the measures that are traditionally derived from the serial-order task, we also compare species on some of the more recent adaptations of the original paradigm.

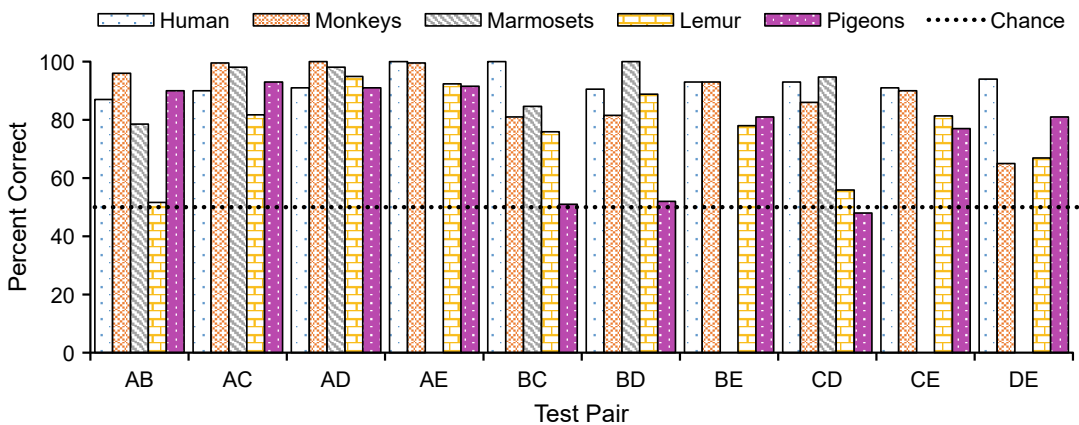
## Representation of a List

The most common performance measure derived from the serial-order task is the pairwise test. The

aim of the test is to determine what knowledge a subject acquires when learning a list. A list containing  $n$  items gives  $(n)(n-1)/2$  possible pairs. For example, on a 5-item list, ten pairs can be generated (AB, AC, AD, AE, BC, BD, BE, CD, CE, and DE). On the pairwise test, the subject is presented with each pair and must respond to the items in the pair true to the order in which they appeared in the original sequence. If presented with pair BD, for example, the subject must respond to the items in the order  $B \rightarrow D$  to obtain a reward. It is important to clarify that when we say that the subject is presented with pair BD we do not mean to imply that item B is presented on the left and item D on the right. In fact, the items of each test pair have an equal chance of being presented to the left or right of one another irrespective of their order in the original list. The performance of adult humans (Colombo and Frost 2001), monkeys (D'Amato and Colombo 1988), marmosets (Koba et al. 2012), lemurs (Merritt et al. 2007), and pigeons (Terrace 1987) on the pairwise test is shown in Fig. 2. Adults perform between 84% and 100% correct across the ten test pairs. Although the performance of monkeys and marmosets is not as good as that of adult humans, they generally perform above chance on all pairs. Similarly, the lemurs perform above chance on all pairs with the exceptions of pairs AB and CD. Finally, the performance of pigeons on the

pairwise test is as good as that of adult humans, monkeys, and marmosets, but only for test pairs that contain either item A or E. For these pairs (AB, AC, AD, AE, BE, CE, and DE), the pigeons performance ranged from 80% to 95% correct. In contrast, performance on test pairs that did not contain an end item (BC, BD, and CD) was no better than chance (50% correct). Thus, in the absence of item A or E, pigeons seem at a loss as to how to respond to the items of a pair.

With respect to the performance of adult humans (Colombo and Frost 2001), monkeys (D'Amato and Colombo 1988), marmosets (Koba et al. 2012), and lemurs (Merritt et al. 2007), the accuracy with which they respond suggests that over the course of learning the serial-order task they formed a representation of the list and use that representation to guide their behavior. By “guide their behavior” we simply mean that when a pair is displayed, the subject accesses their representation of item A and then searches for item A in the display. If they do not find item A displayed, they access their representation of item B and then search for item B in the display. If subjects are progressing in an orderly fashion through their representation and examining whether the current item in their representation is displayed, then we would expect the latency to respond to the first item of a pair to be a function of the position of that item in the list. In other



**Serial List Learning, Fig. 2** The performance of adult humans (Colombo and Frost 2001), monkeys (D'Amato and Colombo 1988), marmosets (Koba et al. 2012), lemurs (Merritt et al. 2007), and pigeons (Terrace 1987) on the

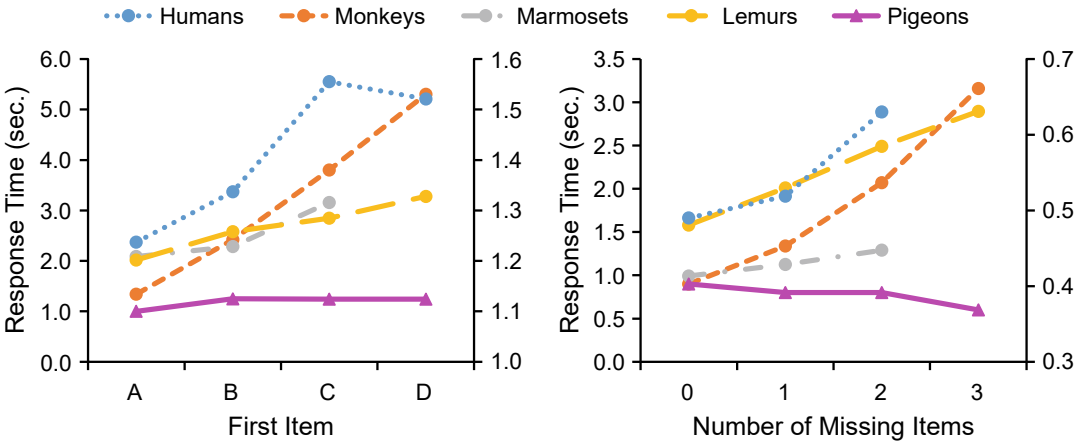
pairwise test. Data for marmosets are limited to pairs AB, AC, AD, BC, BD, and CD due to the fact they were trained on a 4-item, rather than a 5-item, list



words, they should take longer to respond to item D in pair DE than item C in pair CE, because in the case of pair DE the animal has to access three items in their representation (A, B, and C), whereas in the case of pair CE they only have to access two (A and B). A linear relationship between the latency to respond to the first item of a pair and the position of that item in the series is called the *first-item effect*. Figure 3 shows the latency to respond to the first item of a pair as a function of its position in the sequence for adult humans, monkeys, marmosets, lemurs, and pigeons. Adults, monkeys, marmosets, and lemurs all show a *first-item effect* in that the latency to respond to the first item of a pair increases as a function of the position of that item in the sequence. In contrast to these subjects, pigeons show no *first-item effect*.

If adults, monkeys, marmosets, and lemurs are solving the serial-order task by progressing through the sequence in an orderly fashion, as described above, a second prediction would be that the latency to respond to the second item of a pair should be a function of the number of items missing between the first and second item. For example, after responding to item C in pair CE, the subject would next access their representation and search for item D, and upon not finding it

displayed they would then access their representation and search for item E in the display and, upon seeing it, respond to it. In other words, the animal should take longer to respond to item E in pair CE than to item E in pair DE, because in the case of pair CE the subject has to access an additional item in their representation (D) before coming to item E, whereas in the case of pair DE there are no additional items to access. A linear relationship between the latency to respond to the second item of a pair as a function of the number of missing items is called the *missing-item effect*. Figure 3 shows the latency to respond to the second item of a pair as a function of whether the first and second items were separated by 0, 1, 2, or 3 missing items. Monkeys, marmosets, and lemurs show a *missing-item effect* (D'Amato and Colombo 1988; Koba et al. 2012; Merritt et al. 2007). Interestingly, adults do not show a *missing-item effect* when tested on the pairwise test (not shown in Fig. 3). Colombo and Frost (2001) suggested this may be due to the fact that adults realize that once a response is made to the first item of a pair, the second item can be responded to by default. Accordingly, when adults are tested with triplets that prevent them from being able to simply make a default response to the second item, they too show a *missing-item effect* (see Fig. 3).



**Serial List Learning, Fig. 3** Data for adult humans (Colombo and Frost 2001), monkeys (D'Amato and Colombo 1988), marmosets (Koba et al. 2012), lemurs (Merritt et al. 2007), and pigeons (Terrace 1987) derived from the pairwise test. The left panel depicts the *first-item*

*effect* and the right panel depicts the *missing-item effect*. Data for marmosets are limited to items A, B, and C for the *first-item effect* and 0 to 2 missing items for the *missing-item effect* due to the fact they were trained on a 4-item, rather than a 5-item, list

Overall then, adults, monkeys, marmosets, and lemurs perform at a high level on the pairwise test and display a *first-item effect* and a *missing-item effect*. These findings are consistent with the view that in the process of learning a 5-item serial-order task, subjects form an associative representation of the order  $A \rightarrow B \rightarrow C \rightarrow D \rightarrow E$ . It is important to note that this representation differs from an S-R chain in a couple of important ways. First, an associative representation provides a subject with an internal representation of the entire sequence of items, while an S-R chain does not. Second, even when only pairs of items are presented, an associative representation can be worked through successively in order to work out which item of a pair comes first. A chain of responses, however, makes it impossible for a subject to work out the order of pairs that do not contain item A, as the chain cannot be activated in the absence of this initial physical stimulus.

As noted above, in contrast to adults, monkeys, marmosets, and lemurs, pigeons perform poorly on the internal pairs of the pairwise test and show no *first-item effect* or *missing-item effect*. These findings have led several investigators to suggest that pigeons cannot form a representation on the serial-order task (D'Amato and Colombo 1988; Terrace 1993, 2006). How then, in the absence of forming a representation, do pigeons learn to respond to the items of a list in the correct order? One possibility is that, in contrast to adult humans and nonhuman primates, pigeons adopt an approach consistent with chaining theory. That is, the onset of the stimulus display (i.e., the five items appearing on the screen) may serve as a discriminative cue to respond to item A. In turn, responding to item A serves as a discriminative cue to respond to item B, and so on. In addition, pigeons learn to respond to item A first and avoid item E until last, allowing them to perform well on pairs that contain either item A or item E (Terrace 1993). Until relatively recently, this line of reason was used by several authors to conclude that pigeons acquire a qualitatively different representation than adult humans and nonhuman primates (D'Amato and Colombo 1988; Terrace 1993, 2006).

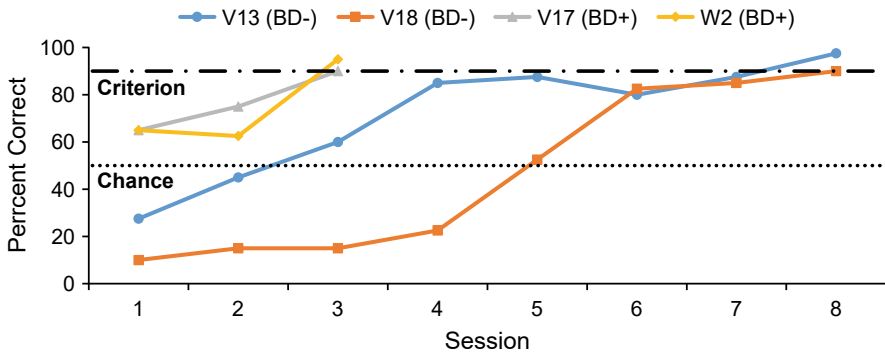
Rather than reflecting a qualitative difference, Scarf and Colombo (2010b) suggested pigeons'

failure on the internal pairs may be due to the sudden contextual change that a pigeon experiences when transferred from a 4- or 5-item list to the pairwise test. Indeed, when an internal pair (i.e., BC, BD, and CD) is presented, the context for responding to each item has changed. Take the case of pair BD. Responding to item B is no longer preceded by a response to item A, and responding to item D is no longer preceded by a response to item C. The result of this sudden contextual change is that pigeons perform poorly on the internal pairs.

To test the possibility that the poor performance of the pigeons on the internal pairs was the result of this contextual change, Scarf and Colombo (2010b) trained two groups of pigeons on a 5-item list and, after reaching criterion, simply trained them on just the BD pair. To control for learning effects, half of the birds were trained on the BD+ pair (in which reinforcement was provided when the items were responded to in the order true to that of the original sequence), and the other half were trained on the BD- pair (in which subjects were reinforced for responding to the items in the order opposite to that learned in the original sequence). If subjects have no knowledge of the order of the items in an internal pair, then subjects learning the positive pair and the negative pair should acquire them in a comparable amount of time. Consistent with the view that pigeons form a representation of the sequence, rather than rely on a simple response chain, subjects trained on the BD+ pair achieved the 90% criterion in significantly fewer trials than did subjects trained on the BD- pair (Fig. 4).

## Knowledge of Ordinal Position

Of course, a representation of a list can come in many forms. One possibility is that adult humans (Colombo and Frost 2001), monkeys (D'Amato and Colombo 1988; Harris et al. 2007), marmosets (Koba et al. 2012), lemurs (Merritt et al. 2007), and pigeons (Terrace 1987) acquire simple item-item associations on the serial-order task. Alternatively, they may acquire knowledge of each item's ordinal position (e.g., associating



**Serial List Learning, Fig. 4** The performance of pigeons on the BD+ and BD- pairs (Scarf and Colombo 2010b)

item A with the 1st position, item B with the 2nd second position). In the early work on serial learning in humans, derived lists were a popular method to distinguish between these possibilities. For example, Ebenholtz (1963) trained two groups of subjects on a 10-item list composed of nonsense syllables. Once the subjects acquired the list, one group was trained on a derived list in which the even or odd items from the first list maintained their ordinal position, and the other group was trained on a derived list in which the ordinal position of the even or odd items from the first list were changed. Ebenholtz (1963) found that the group trained on the maintained list learned their list faster than participants learning the changed list, suggesting that subjects encoded the ordinal positions of the list items and used that information to guide responding on the derived lists.

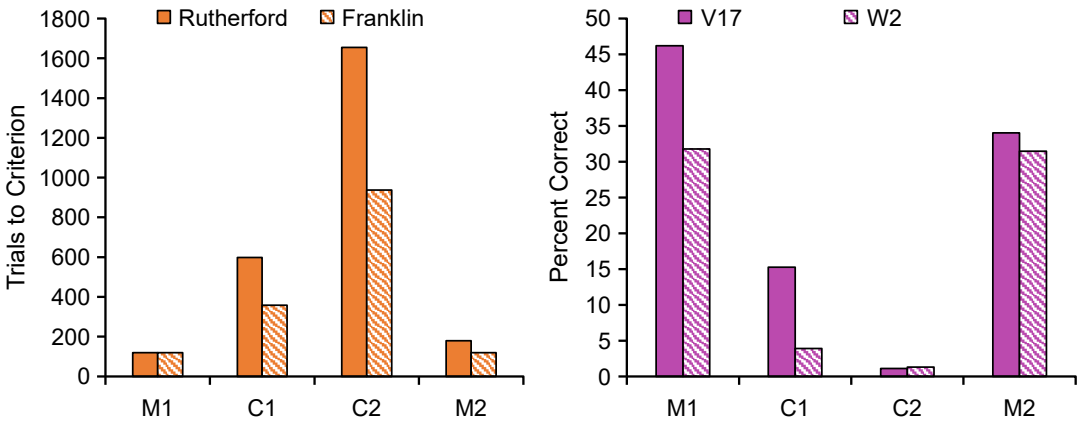
Relative to the large number of species that have been tested on the pairwise test, only monkeys and pigeons have been trained on derived lists (Chen et al. 1997; Scarf and Colombo 2011). In the first of these studies, Chen et al. (1997) trained two monkeys on four 4-item lists (List 1: A1 → B1 → C1 → D1, List 2: A2 → B2 → C2 → D2, List 3: A3 → B3 → C3 → D3, and List 4: A4 → B4 → C4 → D4). Following training, subjects learnt four derived lists. In two of the derived lists, items maintained their ordinal position (Maintained 1: A2 → B4 → C1 → D3; Maintained 2: A3 → B1 → C4 → D2), while in the other two the ordinal position of the items was

changed (Changed 1: B3 → A1 → D4 → C2; Changed 2: D1 → C3 → B2 → A4). Both subjects acquired the two maintained lists much faster than the two changed lists, indicating that both relied on their knowledge of ordinal position to guide responding on the derived lists (Fig. 5).

Following Chen et al. (1997), Scarf and Colombo (2011) trained three pigeons on three 4-item lists (List 1: A1 → B1 → C1 → D1, List 2: A2 → B2 → C2 → D2, and List 3: A3 → B3 → C3 → D3) and then presented them with maintained and changed lists. In contrast to Chen et al. (1997), only the ordinal position of the interior items was maintained (e.g., A1 → B2 → C3 → D1) or changed (e.g., A1 → C2 → B3 → D1). Scarf and Colombo (2011) argued that derived lists constructed in this manner provide a more precise test of subjects coding of ordinal position because the first and last items can be discriminated on the basis of factors other than their ordinal position. The data for two of Scarf and Colombo's (2011) pigeons are shown in Fig. 5. Both subjects got significantly more trials correct on the maintained lists than the changed lists, suggesting pigeons, similar to monkeys, used their knowledge of ordinal position to guide responding.

## Planning List Responses

Recently, variations of the serial-order task have been used to investigate the planning abilities of chimpanzees (Biro and Matsuzawa 1999),



**Serial List Learning, Fig. 5** The performance of monkeys (left panel) (Chen et al. 1997) and pigeons (right panel) (Sarf and Colombo 2011) on maintained (M1 and M2) and changed (C1 and C2) derived lists. It is important to highlight the fact the monkey data report trials to

criterion, with higher values reflecting a slower rate of learning. In contrast, the pigeon data report percentage correct over the first six sessions of training; thus, lower values reflect a slower learning rate

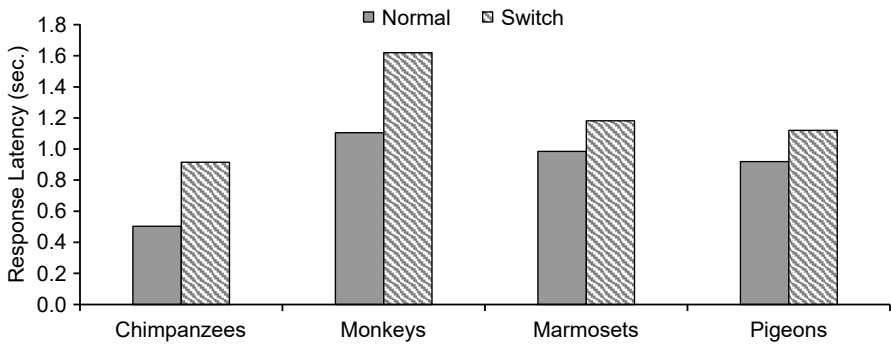
monkeys (Beran et al. 2004; Sarf et al. 2011a), marmosets (Koba et al. 2012), and pigeons (Sarf and Colombo 2010a). With respect to the representation of sequences, the ability to plan is of interest because it provides an additional way of distinguishing between animals that rely on a chain of responses and those that form a representation. Indeed, Lashley (1951) suggested spoonerism demonstrate that sequences are planned in advance and that they would not occur if a chain of responses was the mechanism underlying language. Further, Miller, Galanter, and Pribram (1960) noted in their influential book, *Plans and the Structure of Behavior*, “Therein resides the crucial difference between a chain of actions and a Plan of action. When a chain is initiated with no internal representation of the complete course of action, the later parts of the chain are not intended. When a Plan is initiated, the intent to execute the later parts of it is clear.” (pp. 62). It follows that an animal that relied on a chain of responses would display no evidence of planning at all.

In the first study to investigate planning using the simultaneous chaining paradigm, the chimpanzee Ai was trained to respond to three Arabic numerals, drawn from the range 0 to 9, in ascending order (Biro and Matsuzawa 1999). In addition to these baseline trials, “switch” probe trials were introduced. On switch trials, after Ai responded to

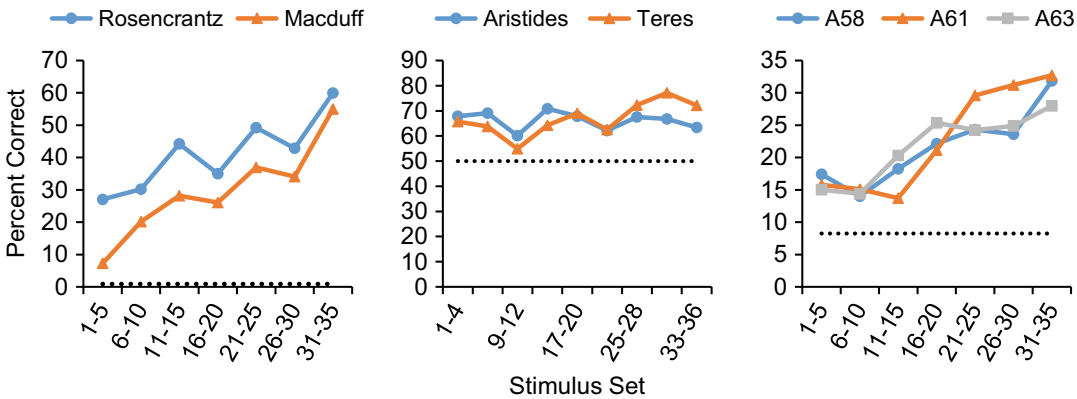
the first item, the on-screen positions of the second and third items were exchanged. When switch trials were responded to correctly, Ai’s response latencies to the second item were longer than on baseline trials (Fig. 6). Biro and Matsuzawa (1999) suggested that the increased response time on switch trials reflected Ai’s updating of the motor response plan formed at the outset of the trial. Similar findings have now been observed with monkeys (Sarf et al. 2011a), marmosets (Koba et al. 2012), and pigeons (Sarf and Colombo 2010a) (Fig. 6).

## Numerical Lists

Thus far, we have only considered lists in which the order of items is arbitrarily defined by the experimenter. For a wide range of behaviors, however, the relation between items or behaviors is defined by a rule. Two prototypical human examples are language and numerical concepts. With respect to language, in the comparative literature, there are a growing number of studies investigating animal grammatical abilities (ten Cate 2017). With respect to numerical concepts, modifications of the serial-order task have been used to assess whether monkeys (Brannon and Terrace 1998), lemurs (Merritt



**Serial List Learning, Fig. 6** The response latency of chimpanzees (Biro and Matsuzawa 1999), monkeys (Scarf et al. 2011a), marmosets (Koba et al. 2012), and pigeons (Scarf and Colombo 2010a) on normal and switch trials



**Serial List Learning, Fig. 7** Performance over the stimulus sets used during training for monkeys (left panel) (Brannon and Terrace 1998), lemurs (middle panel) (Merritt et al. 2011), and pigeons (right panel) (Scarf et al. 2011b). The dashed line represents chance. The

chance line differs for each species due to the fact monkeys were trained on 4-item lists (Chance = 0.9%), lemurs were trained on pairs of items (Chance = 50%), and pigeons were trained on 3-item lists (Chance = 8.33%)

et al. 2011), and pigeons (Scarf et al. 2011b) can form abstract numerical rules. For example, Brannon and Terrace (1998) trained two monkeys on 35 4-item numerical lists, with each list item containing 1, 2, 3, or 4 elements. Consistent with the view that monkeys were deriving a numerical rule (i.e.,  $1 \rightarrow 2 \rightarrow 3 \rightarrow 4$ ), over the course of learning the 35 lists, the monkeys performance on the first session of training steadily increased (Fig. 7). To determine whether the numerical rule was specific to the training numerosities (e.g., nominal categories) or more abstract, subjects were tested on pairs of numerosities drawn from the range of 1 to 9. The pairs were one of three types: familiar-

familiar (F-F) pairs contained two numerosities drawn from the training range (e.g., 1 vs. 2, 1 vs. 3, etc.), familiar-novel (F-N) pairs contained one trained numerosity (i.e., 1, 2, or 3), one novel numerosity drawn from the values 4 to 9 (e.g., 1 vs. 4, 2 vs. 9), and novel-novel (N-N) pairs contained two novel numerosities drawn from the values 4 to 9 (e.g., 5 vs. 6, 7 vs. 9). Not only did the monkeys perform above chance on F-F and F-N pairs, they also performed above chance on N-N pairs. Given N-N pairs contained numerosities the monkeys had not seen before, their performance on N-N pairs suggests they developed an abstract numerical rule that was not tied to the training numerosities.



More recently, both lemurs (Merritt et al. 2011) and pigeons (Scarf et al. 2011b) have been trained using comparable procedures to those employed by Brannon and Terrace (1998) with monkeys. Rather than training subjects on 4-item lists, the lemurs were trained on pairs of items drawn from the range 1 to 4 (e.g.,  $1 \rightarrow 2$ ,  $3 \rightarrow 4$ ,  $1 \rightarrow 3$ ), while the pigeons were trained on 3-item lists (i.e.,  $1 \rightarrow 2 \rightarrow 3$ ). In contrast to monkeys, the lemurs failed to show any clear improvement in performance over the stimulus sets during training, while pigeons displayed increasing performance over the 35 3-item lists during training (Fig. 7). Even in the case of pigeons, however, their performance on the training lists was markedly below the proficiency displayed by Brannon and Terrace's (1998) monkeys. Despite differences in performance during training, the lemurs and pigeons performed above chance on the F-F, F-N, and N-N pairs (Merritt et al. 2011; Scarf et al. 2011b). In addition, several other aspects of the lemurs' and pigeons' performance suggest they extracted a similar to numerical rule to Brannon and Terrace's (1998) monkeys. For example, their discrimination performance was dependent on the ratio of the paired items. In other words, both 1 versus 3 and 6 versus 8 are separated by one item, but the 1 versus 3 discrimination (ratio = 0.33) is easier to discriminate than the 6 versus 8 discrimination (ratio = 0.75), and this was true for both monkeys and pigeons.

## Conclusion

Sequences lie at the heart of everything humans do. From reciting the alphabet to writing a novel, from playing chopsticks on a piano to performing Beethoven's 5th Symphony, from planning what is for dinner to planning one's career path, behaviors must be performed in a specific sequence in order for success. The serial-order task has proven a versatile tool with which to explore the foundations of sequence learning across a variety of different species, from how serial-order information is represented to planning. Although it was initially thought some of these abilities were unique to certain orders (e.g., primates but not

pigeons), it is now clear that the ability to process serial-order information is conserved across a wide range of species. This view is bolstered by findings employing other serial-order paradigms. For example, Fagot and Cook (2006) demonstrated that both monkeys and pigeons display one of the hallmarks of serial memory, the serial position curve.

With the advent of recent computational models of serial-order learning (Enquist et al. 2016) and work on the neural representation of sequences (Dehaene et al. 2015), we are moving ever closer to solving Lashley's (1951) problem of serial-order behavior and providing a window into some of the most complex aspects of human thought (e.g., language). Much like the behavioral data we have reviewed, however, solving the problem will require us to take a comparative neuroscience approach, moving beyond a sole focus on primate models, and providing an answer that has the power to explain serial-order behavior across a diverse range of species and behaviors.

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## Serial Pattern Learning

### ► Pattern Learning

## Serotonin

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## Abbreviations

|       |                                        |
|-------|----------------------------------------|
| 5-HT  | Serotonin                              |
| 5-HTR | Serotonin receptors                    |
| CNS   | Central nervous system                 |
| SERT  | Serotonin transporter                  |
| SSRI  | Selective serotonin reuptake inhibitor |

## Synonyms

[Adaptation](#); [Nervous system function](#); [Neurosciences](#); [Neurotransmitter](#)

## Definition

Serotonin is a molecule with no informative value on its own. It acquires biological properties through the organization of the neurons producing and releasing it, and through its numerous receptors. A system of neurotransmission like serotonin can modulate the activity of nervous tissues in animals, and ultimately impact cognition and behavior.

## Introduction

Serotonin (5-hydroxytryptamin, 5-HT) is a small molecule playing the role of neuromodulator in virtually all complex organisms of the animal kingdom but its overall function is still not well understood. As quoted by Azmitia and Jacobs in 1992, “although 5-HT has been implicated in a vast array of physiological and behavioral processes in vertebrates, it appears to be essential for none of them” (Jacobs and Azmitia 1992, p. 165). This would be a perfect definition of a neuromodulatory role upon central nervous

system (CNS) functions, reaching its quintessence in case of 5-HT systems over other neuromodulatory systems like catecholamines, acetylcholine, histamine, or neuropeptides.

It has been reported for several years that the 5-HT systems can modify cognition and behavior, and this property has been shown at many occasions in invertebrates as well. Often considered as a neurotransmitter positively involved in well-being, in part due to the positive effects of selective 5-HT reuptake inhibitors (SSRI) in some patients suffering from mood disorders, the situation is much more complex as 5-HT participates in stress responses and mood disorders, irrespective of its levels. In several cognitive tasks and behavioral responses, 5-HT can mediate opposite outcomes. This is related to (1) the diversity of its receptors having different affinities for 5-HT and intracellular signaling pathways and localization, and (2) the widespread presence of 5-HT in the CNS capable of acting on several neurobiological targets at the same time. Thus, 5-HT is intimately linked to fine-tuning adaptive behaviors, perhaps by delaying responses for appropriate behaviors and by inhibiting learned responses that are not currently adaptive (Bari and Robbins 2013; Soubrié 1986).

In this chapter, the organization of the 5-HT systems in numerous vertebrates and invertebrate species is briefly mentioned. Thereafter, the influence of 5-HT in cognition and some behaviors has been illustrated with the motor activity and arousal, feeding behavior, circadian rhythm, sleep, social status and aggressiveness, anxiety, mood, learning and memory, and cognitive flexibility.

## Organization of 5-HT Systems in Animals

The organization of the 5-HT systems is completely different between species ranging from a limited number of cells in *Aplysia*, *Drosophila* (100 immunoreactive cells) to several thousand neurons in vertebrates localized in the midbrain raphe nuclei. The variety and the heterogeneity of 5-HT neurons have been highlighted in vertebrates and invertebrates. In general, the 5-HT

systems in animals comprise 5-HT neurons which share a particular shape made of thousands of varicosities, leading to the concept of volume transmission (De-Miguel and Trueta 2005), and several 5-HT receptors (5-HTRs). The specificity of 5-HT transmission comes also from reuptake sites, which are specific (serotonin transporter, SERT) and less specific including catecholaminergic transporters. The distribution of these transporters around the synapses permits the regulation of the extracellular concentrations of 5-HT extrasynaptically. Thus various modalities of neurotransmission have been reported in the case of 5-HT including classical synapses, neurohumoral, and/or paracrine influences (De-Miguel and Trueta 2005). The latter has been well shown in insects (female cricket *Acheta domestica*) where 5-HT innervates the genital chamber muscles without identified synapses. These modalities are more or less present across the animal kingdom.

5-HT acts on a variety of receptors. In mammals, 5-HTRs are organized in seven families (5-HT<sub>1-7</sub>R) and more than 16 subtypes have been described. They have been characterized for several years regarding cloning, pharmacology, and brain expression (Saudou and Hen 1994). Conversely, 5-HTRs in some invertebrates are less known (Saudou and Hen 1994) despite the prediction that it could be almost similar. Briefly, four 5-HT receptors named 5-HT<sub>1Adro</sub> (or d5-HT<sub>1A</sub>), 5-HT<sub>1Bdro</sub>, 5-HT<sub>2dro</sub>, and 5-HT<sub>7dro</sub> have been discovered in drosophila, and two in crustaceans (5-HT<sub>1ACrust</sub> and 5-HT<sub>2BCrust</sub>). In molluscs, two 5-HT receptors were cloned belonging to 5-HT<sub>1</sub> and 5-HT<sub>2</sub> families in *Lymnaea stagnalis* whereas five were cloned in Aplysia. In a pond snail (*Helisoma trivolvis*) two receptors types (5-HT<sub>1Hel</sub> and 5-HT<sub>7Hel</sub>) have been cloned and characterized.

## Motor Activity and Locomotion

5-HT directly acts on all motor centers and even in muscles. Indeed, 5-HT has been reported to act directly in neuromuscular junction in insects, crustacean, annelids, or gastropods (see review

Wu and Cooper 2012). In crustacean or gastropods' neuromuscular junction, 5-HT enhances synaptic transmission by a presynaptic action. Such an action has been well described in Aplysia where the contraction of the buccal muscle is facilitated by 5-HT. In leech neuromuscular junction, Retzius cells innervate muscles and release 5-HT leading to a reduction of muscle contraction.

5-HT can also increase the motor activity by acting on motoneurons or central pattern generators (CPGs) in insects, crustaceans, annelids, and vertebrates. In mammals, it is well known that the application of 5-HT on isolated preparations of spinal cord from a newborn rat initiates a fictive locomotion corresponding to alternating patterns of neuronal activity normally controlled right and left paws. In insects, 5-HT enhances the motoneuron drive in drosophila larvae and in leeches, 5-HT depletion or 5-HTR blockade impaired swimming activity. It is noteworthy that several mechanisms triggered by 5-HT are often combined and these mechanisms refer to specific actions of 5-HT at the level of the motoneurons. For instance, in Crustacean motoneurons, 5-HT increases tonic discharge at 10  $\mu$ M and decreases it at 100  $\mu$ M. These two responses involve different types of receptors: the excitatory effect involves 5-HTR localized in the neurites that acts by closing a K<sup>+</sup> conductance; the inhibitory response involves 5-HTR receptors located on the axon close to the action potential initiation segment acting by opening a K<sup>+</sup> conductance.

Acute activation of 5-HT neurons disrupts normal locomotion activity in adult flies (Majeed et al. 2016). 5-HT being apparently absent in the fly's neuromuscular junction (Wu and Cooper 2012), such an effect could correspond to an important regulatory role of motor programs by 5-HT systems. This has been further evaluated by using mutations in the 5-HT biosynthetic enzymes and by knock-down 5-HTRs expressed in mushroom bodies (d5-HT<sub>1AR</sub>, d5-HT<sub>1BR</sub>, d5-HT<sub>2R</sub>, and d5-HT<sub>7R</sub>) using RNAi strategy. Animals expressing an RNAi for d5-HT<sub>1BR</sub>, d5-HT<sub>2R</sub>, and d5-HT<sub>7R</sub>, but not d5-HT<sub>1AR</sub> in mushroom bodies show increased motor behavior. Thus, d5-HTRs expressed in mushroom bodies differentially modulate motor programs in fly larvae.

## Arousal

The link between arousal/activity and 5-HT system has been proposed for several years (Jacobs and Azmitia 1992; Soubrié 1986). This idea comes in part from studies performed in mammals including cats, rodents, or humans. During the rapid eye movement (REM) phase of sleep, 5-HT neurons stop firing coinciding with the atonia of skeletal muscle groups during REM. Conversely, oral activity, grooming, biting, or chewing are associated with a marked activation of a group of 5-HT neurons. These neurons are also activated by stimuli applied to the head and the face. It has been suggested that 5-HT neurons, like CPGs, are activated by repetitive motor activities (Jacobs and Fornal 1999). While stressful situations are not necessarily associated with a change of firing rate of 5-HT neurons, acidosis can increase the activity of a subset of 5-HT neurons (chemosensitive) in various raphe nuclei.

The roles of 5-HT in arousal have been studied in gastropods and notably in *Aplysia*. Two major classes of arousal elements exist: localized versus general (Jing et al. 2009). Actions of localized arousal elements are often limited to one class of behavior. They may mediate specific effects of arousal. General arousal elements may influence multiple classes of behaviors, and mediate both specific and nonspecific effects of arousal. 5-HT can act as either localized or general arousal elements. Prominent roles of 5-HT systems in arousal are conserved in gastropod molluscs. The role of 5-HT in arousal is unclear in *Drosophila* where dopamine could promote arousal (Nall and Sehgal 2014).

## Sleep and Circadian Rhythm

As already mentioned, 5-HT has a role in sleep in mammals. The activity of 5-HT neurons is lower during slow wave sleep and almost null during REM. It probably contributes to the circadian rhythm because a substantial projection of the 5-HT neurons of the raphe nuclei has been identified in the suprachiasmatic nucleus, a hypothalamic nucleus involved in the regulation of the

wake-sleep cycle (Monti 2011). 5-HT is involved in the synchronization of the circadian clock located in the suprachiasmatic nucleus in pigeons, and a positive correlation between the circadian rhythms of activity and serum 5-HT levels has been reported in ringdove. In addition, 5-HT is the metabolic precursor of melatonin, known for its regulatory role on the circadian system.

Multiple 5-HT receptors participate in the regulation of sleep in mice. 5-HT<sub>1A</sub>R and 5-HT<sub>1B</sub>R reduce REM sleep whereas 5-HT<sub>2A</sub>R, 5-HT<sub>2C</sub>R, or 5-HT<sub>7</sub>R do the opposite. The mechanisms contributing to these effects are different for all the receptors (Monti 2011).

5-HT could play an inhibitory role on the effects of light on circadian rhythmicity as proposed in vertebrates (Jacobs and Fornal 1999). Interestingly, entrainment of the *Drosophila* circadian clock to light involves the light-induced degradation of the clock protein *timeless*. This mechanism is inhibited by 5-HT via d5-HT<sub>1B</sub>R. Additionally, d5-HT<sub>2</sub>R in the third instar larvae would play a role in the circadian activity by controlling the anticipatory behavior. Sleep was demonstrated to be different from circadian rhythm. Elevating 5-HT promotes sleep in *Drosophila* likely via d5-HT<sub>1A</sub>R. For instance, RNAi knockdown of tryptophan hydroxylase caused a loss of night-time sleep (Artiushin and Sehgal 2017). *Drosophila* with suppressed d5-HT<sub>1A</sub>R exhibit reduced and fragmented sleep, whereas d5-HT<sub>1A</sub>R expression in mushroom bodies rescues the normal phenotype (Nall and Sehgal 2014).

In Crustaceans, the situation is much less known compared to *Drosophila*. Regulation of circadian rhythm is mainly operated via the Eye-stalk X-organ-sinus gland system where 5-HT and melatonin have been largely found.

## Feeding

The involvement of 5-HT in feeding behavior is an important topic in 5-HT research (Voigt and Fink 2015). In humans 5-HT-based pharmacological agents have been used as anti-obesity agents such as D-fenfluramine. The anorectic effect of



D-fenfluramine has been associated with its property to enhance 5-HT release in laboratory animals, indirectly leading to the stimulation of 5-HT<sub>2C</sub> receptors. Due to noxious cardiac effects, D-fenfluramine has been withdrawn while the 5-HT<sub>2C</sub> agonist lorcaserin has reached the market. The influences of 5-HT in feeding behavior are probably numerous as several receptors have been implicated (5-HT<sub>1A</sub>R, 5-HT<sub>1B</sub>R, 5-HT<sub>2C</sub>R) and brain regions including subregions of the hypothalamus. 5-HT, through its different receptors, would prolong the satiety signals and limit the size of the meal.

Parallels have been done with the situation in invertebrates and notably, in *C. elegans* feeding (Luedtke et al. 2010). 5HT via the 5-HTR SER-7 activates the pumping behavior required to take bacteria from the environment into the gut. 5-HT is also required for food-dependent induction of bursts as well as for maintaining their high rate of pumping through two distinct mechanisms, one via SER-1 for food-induced pumping, the other triggered by exogenous 5HT via SER-7.

5-HT also participates in insect feeding behavior. In *Rhodnius prolixus* after blood meal, the Malpighian tubules increase their secretion 1000-fold to preserve salt and water balance. This activity is controlled by neuropeptides and 5-HT. In drosophila, the alteration of the 5-HT system by feeding larvae with 5-HT, 5-HT precursor or inhibitor of tryptophan hydroxylase impaired locomotion and feeding in the larvae (Majeed et al. 2016). Blocking or enhancing 5-HT transmission in larvae or adult also resulted in impairment of locomotion and feeding behavior.

## Social Status and/or Aggressiveness

A number of studies in invertebrates and vertebrates have reported that 5-HT participates in social interactions including sexual behavior or the social status (Edwards and Spitzer 2006; Jacobs and Azmitia 1992). The social status is usually addressed through fights leading the animals to establish the status of dominant (winner) and subordinate (loser) (Edwards and Spitzer

2006; Miczek et al. 2002; Stevenson and Rillich 2012). Pairing two crayfish for 15 days leads to fights. During this period, the sensitivity to 5-HT application of giant fibers encompassing escape behavior circuit evolves. Whereas in isolate and dominant crayfish, 5-HT enhances the response to mechanosensory inputs, 5-HT has little or no effect in the subordinate. The change of sensitivity to 5-HT is progressive during the 15 days and is associated with modifications of body posture and the neurobiological network underlying escape behavior (Edwards and Spitzer 2006). In addition, the 5-HT system could have an acute role on the issue of the fight. Injection of 5-HT can considerably increase the aggressiveness of the crayfish having a slightly lower physical size (usually detrimental for the issue of the fight). Yet, it is difficult to argue for a permissive role of 5-HT on aggressiveness. Indeed, the 5-HT precursor attenuated aggression in pigeons without affecting feeding in dominant members, and decreased the time spent running away by subordinates. It is noteworthy that in the reptile *Anolis carolinensis*, the chronic exposure to the SSRI sertraline, likely via an enhancement extracellular 5-HT levels, reverses the social dominant status.

The studies performed in insects give similar uncertainty as regards the serene side of 5-HT. 5-HT would depress escape responses in aggressive crickets and oppose the action of octopamine which is required for aggressive responses (Stevenson and Rillich 2012). Nonetheless, 5-HT depletion leads to hyperactivity without affecting the level of aggressiveness. After a fight, losers exhibit escape behavior and have lower 5-HT levels. The findings are similar in the fruit flies drosophila. On one hand, the increase or decrease in 5-HT synthesis does not alter aggression in drosophila. On the other hand, increase in 5-HT synthesis or activity of 5-HT neurons elicits aggression whereas the disruption of 5-HT transmission led to reduced fighting ability. The 5-HT aggressive drive in drosophila would be due to a single 5-HT neuron expressing a d5-HT<sub>1A</sub>R (Alekseyenko et al. 2014).

The connection between 5-HT and social status and aggression has been the object of several studies in mammals and notably mice (Miczek

et al. 2002). This is a complex field of research as there are many ways and parameters to experimentally address aggressive behaviors and social interaction that are dependent on the strain as well. Lower tissue levels of 5-HT coincide with higher level of aggressiveness, but, again, it is not always the case. In macaques, the antisocial behavior marked by violence and aggression is associated with low levels of the metabolite of 5-HT in the CSF. It has been reported in mice or healthy volunteers that a diet without tryptophan, an essential amino acid only found in diet and necessary for the production of 5-HT, increases the level of aggressiveness under specific circumstances.

Different 5-HTRs have been shown to be involved in aggressive responses. Mice lacking 5-HT<sub>1B</sub>R exhibit higher rates of aggressive episodes, whereas 5-HT<sub>1A/1B</sub>R agonists such as eltopazine reduce several aspects of aggressiveness in mice and/or rats (de Boer and Koolhaas 2005; Miczek et al. 2002). The efficacy of these compounds is unclear as it could be related to the reduction of 5-HT neuron activity inherent to the stimulation of 5-HT<sub>1A</sub> and 5-HT<sub>1B</sub> autoreceptors and/or the direct stimulation of these receptors on neurobiological networks. In drosophila, the 5-HT<sub>1A</sub>R agonist 8-OHDPAT increases the level of aggression, mainly wing threats and fencing components, whereas the 5-HT<sub>2R</sub> agonist DOI decreases overall aggression, mainly lunging and boxing components (Johnson et al. 2009).

Beyond the intrinsic complexity of aggressive behaviors, the definite proof that the above-mentioned mechanisms engaged by the 5-HT system are specific of aggressive behavior is uncertain. While an indirect action of 5-HT on motor activity can be tested, an action of 5-HT on other behaviors indirectly modulating the decision to fight or to flee with an opponent cannot always be discarded. For instance, the apparent anti-aggressive effect of eltopazine in mice could be implemented by its anxiogenic effect.

## Anxiety

Anxiety is indeed a complex dimension with several forms in animal behavior (Millan 2003). Anxiety

has been recently acknowledged in invertebrates (Fossat et al. 2014) and it has been the object of numerous clinical and preclinical studies in mammals. Anxiety is considered a secondary emotion because it occurs when the stressor is absent or not clearly identified.

In drosophila, anxiety-like behavior resulting from stress is sensitive to the benzodiazepine and anxiolytic drug diazepam and share similarities with rodent anxiety-like behavior (Mohammad et al. 2016). The anxiety-like behavior is altered when acting on d5-HT<sub>1B</sub>R, d5-HT<sub>2B</sub>R, and SERT but not 5-HT<sub>1A</sub>R and d5-HT<sub>2A</sub>R. Specifically, knockdown and overexpression of d5-HT<sub>1B</sub>R and dSERT increased and decreased anxiety-like parameters, respectively; knockdown or impairment of d5-HT<sub>2B</sub>R reduced anxiety-like behavior (Mohammad et al. 2016). Using an aquatic dark/light plus-shaped maze, it has been shown in crayfish that repetitive electric shocks produced behaviors compatible with anxiety (Fossat et al. 2014). The anxiety-like behavior, associated with an increase in tissue 5-HT in brains, can be triggered by the administration of exogenous 5-HT, reduced by a cocktail of 5-HTR antagonists and by the potent anxiolytic chlordiazepoxide.

In rodents, extensive researches indicate that several 5-HTR can be targeted with agonists or antagonists depending on the subtype considered to modulate anxiety-like behaviors. It has to be kept in mind that the multiple circuits involved in different forms of anxiety complicate the choice of one specific target (Millan 2003). The 5-HT agents being used in clinic have widespread effects on 5-HT neuron activity and are either SSRI or partial 5-HT<sub>1A</sub>R agonist.

## Mood

A crayfish regularly defeated by a stronger congener during fights and then harassed by the winner presents an increase of anxiety-like behavior directly related to the harassment period duration (Bacque-Cazenave et al. 2017). If this social stress is prolonged for 2 weeks, the loser will progressively present a subordinate behavior, while the winner will become the dominant. This change in

social status is accompanied by a loss of 5-HT modulatory effects not only on the giant fiber escape circuit but also on the locomotor network. In both cases, a depression of neural activity is observed. Although it is difficult to evoke a depression-like behavior for the subordinate crayfish, the loss of 5-HT modulation resulting from chronic stress was recently demonstrated in another invertebrate, the drosophila, and clearly associated with a depression-like state. In drosophila, a depression-like state can be induced by vibration stress over 3 days (Ries et al. 2017). This state, which is controlled by 5-HT signaling in alpha and gamma lobes of the mushroom bodies, is ameliorated by lithium chloride. The behavioral changes correlate with reduced 5-HT release at the mushroom body. These changes can be relieved by feeding the metabolic precursor 5-hydroxytryptophan or sucrose, which results in elevated 5-HT levels in the brain acting at d5-HT<sub>1A</sub>R.

These recent findings in drosophila remind the reported role of 5-HT in depression symptoms observed in mammals and humans, in particular. Modification of 5-HT levels in CSF or the brain has been occasionally found in case of major depression associated with suicidal tendencies. Moreover, it has been reported that a diet without tryptophan could promote depression in individuals vulnerable to mood disorders. However, a strict relationship between depressive symptoms and 5-HT content does not exist in mammals. The 5-HT systems seem to play an important role in the mechanism of action of antidepressant drugs whatever their pharmacological action in interaction with the other monoaminergic systems (Hamon and Blier 2013).

## Learning and Memory

5-HT system has been known to be involved for a long time in learning and memory. It was originally described in an elementary behavioral response in Aplysia at the level of neuromuscular synapses in buccal motoneurons. The persistent facilitation of the withdrawal reflex is related in part to 5-HT producing an increase in release of

glutamate at sensory-motor neuron synapses. This involves a 5-HTR coupled to adenylate cyclase (Lee et al. 2009). Other data in invertebrates have also reported short- and long-term plasticities notably in drosophila and honeybee *Apis mellifera* (Blenau and Thamm 2011). The long-lasting plasticity occurs in vertebrates with some analogy with what has been described in invertebrates. The 5-HT system appears to play a role in behaviors that involve a high cognitive demand and in memory improvement. Multiple 5-HTR subtypes are involved, sometimes in opposite manner, often in different manner, in memory processes (Meneses 2015).

## Impulsive/Compulsive Dimension and Behavioral Flexibility

Impulsive and compulsive behaviors have been reported in invertebrates including Aplysia, honeybee, and drosophila, but the role of 5-HT in these nonadapted responses has never been studied in those species as far as we know. In humans, maladaptive decision-making is a common core symptom of diseases like obsessional compulsive disorders, Tourette's syndrome, attention deficit disorder, pathological gambling, or addiction. Numerous laboratory tests have been created in order to address these dimensions and it has been shown that 5-HT plays an important role.

The impulsive/compulsive trait involves complex interactions between prefrontal and orbital cortices, the basal ganglia, a group of subcortical structures involved in the control of motor behavior, and monoaminergic systems of the midbrain including 5-HT neurons (Dalley et al. 2011). Reduction of 5-HT has been proposed to result in premature responses in numerous behavioral tests. Behavioral (cognitive) flexibility means that the animal can modify its behavior in response to modifications of the environment. 5-HT depletion in rodents and primates causes perseverative errors in behavioral tasks such as extinction and reversal learning paradigms. This suggests that the animals without 5-HT have difficulties in stopping responses to previously

rewarded stimuli which are no longer reinforced. The actions of 5-HT involve at least 5-HT<sub>2A</sub>R and 5-HT<sub>2C</sub>R.

## Conclusion

This chapter briefly reports the widespread influence of 5-HT in adaptive behaviors and cognition in both vertebrates and invertebrates. It is a modulatory system capable of mediating opposite effects on cognition and behaviors. It is thus challenging to attribute a specific role to 5-HT in animals except a neuromodulatory role. The neuromodulatory influence of the 5-HT system is evolutionarily well conserved.

## Cross-References

- Adaptation
- Adaptedness of Behavior
- Attention
- Cognition
- Day/Night Cycle
- Decision-Making
- Dominance
- Escape Response
- Executive Function
- Nervous System of Invertebrates
- Neuron
- Short-Term Memory
- Social Behavior

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## Service Dogs

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## Synonyms

Assistance dogs; Working dogs

## Definition

A dog that has received specific training to perform specialized tasks that aid people with disabilities, including visual impairment, reduced mobility, and psychiatric and neurological disorders.

## What is a Service Dog?

All service dogs are united by the fact that they have undergone a specialized training regimen, which has provided them with a behavioral repertoire not normally found in other dog populations that enables them to assist (or serve) people with physical or mental disabilities. Service dogs come in many different and varied forms. Some are well known and long established, such as guide dogs, which aid people with visual impairments, while others such as seizure alert dogs are relatively new. Another type of dog often confused with service dogs is the therapy or support dog. Support or therapy dogs are used to provide companionship and sometimes to help with treatment of psychiatric disorders such as depression or post-traumatic stress disorder. However, therapy and support dogs do not undergo specialist training and do not perform tasks to assist people, so under US and UK law, they are not considered to be service dogs (Bennett and Desai 2016; Brennan 2014).



## Types of Service Dog

Service dogs are differentiated by the tasks they are trained to perform and the people whom they serve. The tasks that a service dog can be trained to perform are varied and can be quite complex.

Guide dogs for the blind undergo perhaps the most complex training regimen of all service dogs, as they are specifically responsible for their owner's safety in all environments outside of the home. These dogs are trained very carefully to be able to walk to a straight line until instructed to turn left or right, ignore distractions, identify and indicate obstacles in the owners path (including those that would not be an obstacle to a dog, such as a pen on the floor or branches hanging at human head height), find safe alternative routes around obstacles, sit at curbs until instructed to move forward, and, perhaps most advanced of all, disobey a command to walk forward if they determine that there is an oncoming danger such as a car coming toward them (Audrestch et al. 2015). Contrary to many lay views of guide dogs, however, the dog does not choose the route nor make the decisions but instead works in partnership with their visually impaired owner through a series of interactions characterized by complementary cooperation (Naderi et al. 2001).

Hearing dogs are trained to signal their owners when a sound occurs, such as the ring of the doorbell, but they are also trained to retrieve their owner when another person in the household calls them. In this capacity, hearing dogs act as valuable safety aids as well as aids to communication between people.

Seizure response dogs assist people with disorders such as epilepsy. These dogs can be trained to retrieve help when their owner has a seizure or to stand guard over them as they do. Some, such as seizure alert dogs, are specifically trained to warn their owners of an imminent seizure before it begins, enabling the person to get to a safe place in advance (Dalziel et al. 2003).

Disability assistance dogs are specifically trained to help with everyday tasks that can be impeded for a person with mobility issues. The training each dog receives is often specifically tailored to the needs of the individual client and

can include tasks such as picking up and retrieving objects, opening and closing doors, pressing buttons, loading and unloading washing machines, and assisting with dressing/undressing (Lane et al. 1998).

Autism assistance dogs (also known as sensory signal dogs or social signal dogs) are trained to interrupt repetitive movements made by those with autism. When working with children with autism, they can also serve a role in road safety, as they are trained to sit at a curb and not move forward until instructed to; if the child pulls away toward the road before it is meant to, the dog sits and prevents them from moving via an attached dog-child harness (Anon 2016).

## Why Dogs?

People often ask whether any animal could be trained as a service animal and what makes the dog so suited to the task. Other types of animals have been trained to perform tasks for people with disabilities such as monkeys and miniature horses; however the dog is by far the main species utilized. Not only are dogs more practical than other animals, as they take less time to train and can accompany their owners wherever they go, but dogs have a unique set of cognitive abilities that make them exceptionally well suited to working as a service animal. Dogs have been domesticated for longer than any other species (at least 15,000 years (Frantz et al. 2016)) and have been artificially selected over thousands of years to work cooperatively with humans in various working roles from hunting to guarding (Clutton-Brock 1995). Further, dogs can be habituated during the sensitive period of development (at 3–12 weeks of age) to the anthropogenic environment, which may prove stressful for other species that lack this habituation window.

Domestication of the dog involved processes that increased their sociality, communication ability, and co-cooperativeness, and while we cannot say dogs have the same cognitive capacity as humans, it has been suggested that these behavioral facets are functionally analogous to those of the Human Behavior Complex which involves sociality, behavioral synchronization, and constructive skills (Topál et al. 2009). Topál and

colleagues suggest that there is a suite of functional behavior they referred to as the Dog Behavior Complex that they argue contributed to the success of dogs in the human environment. The first of these skills is *sociality*, which is evidenced by a predisposition to form close bonds with humans (Gácsi et al. 2005) and the predisposition of dogs to be attracted toward humans, which wolves are lacking (Frank and Frank 1982). Additionally, dogs have been shown to exhibit various types of *behavioral synchronization*, which promotes interspecies relationships, including rule following (Kubinyi et al. 2003), social learning (Range et al. 2007), emotional synchronization (Vas et al. 2005), and complementary cooperation (Naderi et al. 2001). The role of a guide dog, in particular, has a strong requirement for the dogs to be able to synchronize their behavior to that of their human companion.

Another aspect of the Dog Behavior Complex is the dog's ability not only to learn and follow rules but also to anticipate the behavior of another individual (Kubinyi et al. 2003), which aids synchronized behavioral interactions (Topál et al. 2009). While dogs do not have human linguistic skills, they have demonstrated the ability to be able to *constructively communicate* with humans, initiating communication via direct gaze, gaze alternation, vocalization, and physical contact, traits which are more prevalent in dogs than wolves (Miklósi et al. 2003). The predisposition of dogs to gaze at the human face may have also led to the ability of dogs to, at least partially, read human facial expressions to enable better perception of our emotions (Racca et al. 2012). Dogs have also been shown to be able to adapt their behavior in order to "request" help by providing information to people whose knowledge is lacking, to help the dog achieve a goal (Virányi et al. 2006). Such skills allow for interspecific information sharing and complex cooperation, which are necessary prerequisites for forming successful human-animal working relationships. Indeed, the dog's ability to read human behavioral cues and alert humans to an oncoming event is precisely what enables seizure alert dogs to perform their duties, a role which was originally

untrained and performed innately by a small number of pet dogs (Dalziel et al. 2003).

### Selecting Suitable Dogs

When considering which dogs are suitable to be a service dog, the most important factor is individual differences in behavior (referred to from hereon as personality). Animal personalities develop based upon interactions between an animal's genetics and its social and nonsocial environment (Saetre et al. 2006). Studies reporting heritability of personality traits in dogs suggest that 0–46% of behavioral variation is heritable, with differences between traits (Goddard and Beilharz 1983; Saetre et al. 2006; Wiener et al. 2015). Thus, experiential or epigenetic processes mediate a large proportion of behavioral variation between individuals. Recent evidence from a study of juvenile guide dogs suggests that the dog's social environment and how it interacts with its social partners may be most salient in shaping its adult personality (Harvey et al. 2016).

Traditionally, service dogs tend to be medium-sized breeds such as Labradors, golden retrievers, German shepherd dogs, and their crosses, with hearing dogs tending to be smaller sized such as spaniels. However, not every dog of these breeds will be suitable as a service animal due to considerable within-breed differences in personality, and many other breeds of suitable size to perform the required tasks have been successfully trained. Evidence from guide dog breeding programs demonstrate that dogs bred by guiding organizations are more successful as guide dogs than those of the same breeds sourced from other breeders (Pfaffenberger et al. 1976). While some of this difference may undoubtedly be caused by breeding selection toward dogs with more suitable traits, a large part is also due to the organizations having control over the early-life experiences of the puppies and the ability to begin socialization habituation early on (Pfaffenberger et al. 1976).

Service dog organizations need to routinely evaluate the behavior of the dogs they train in order to decide upon the most suitable training regimen for each dog and to determine their suitability to the training program. The vast majority of published studies on service dog behavior

assessments have been conducted with the aim of selecting guide dogs, with at least one study investigating the potential of utilizing shelter dogs as a source of dogs for training as assistance dogs such as hearing dogs or dogs that aid people with mobility issues (Lucidi et al. 2005). While there may be overlap in the basic traits required to be a successful service dog, for example, to be highly trainable, eager to work with humans as a cooperative unit and not be fearful, aggressive, or defensive, different organizations often have slightly differing requirements depending on the exact circumstances the dog is expected to work under and tasks they are expected to perform. Hearing and disability assistance dogs, for example, tend to need high energy levels and enthusiasm to work at any time, whereas guide dogs need to be able to be calm and steady in a variety of circumstances and are often expected to sit or lie quietly under desks and tables or on buses for extended periods of time. Successful guide dogs are typically low on fearfulness, not easily distracted/impulsive, nonaggressive, and highly trainable and adaptable (Duffy and Serpell 2012; Goddard and Beilharz 1983; Harvey et al. 2017).

### Evidence for Cognitive Differences in Service Dogs

While service dogs undergo a strong selection pressure so that only those with suitable traits should undergo training, there is evidence that the level of training itself and the experience of being a service dog impact upon the dog's cognitive capabilities. Dogs that have been intensively trained using positive reinforcement methods have been found to exhibit a more proactive response in problem-solving tests, improving their problem-solving capabilities (Marshall-Pescini et al. 2008), and are more reliant upon their own judgments when humans provide them with misleading information in food choice tasks than untrained dogs (Prato-Previde et al. 2008). However, a recent study on adolescent guide dogs found that juveniles (as yet untrained for service work) that performed better in certain problem-solving tasks were more likely to be selected for work as a guide dog later in life (Bray et al. 2017), so the exact cause and effect of the relationship between a dog being highly trained and exhibiting

improved problem-solving ability has yet to be established.

Gaunet 2008 sought to investigate whether guide dogs differed from pet dogs in their ability to constructively communicate with their owners in an unsolvable task paradigm, specifically whether they adapted their behavior to the visual status of their owners. Gaunet concluded that while the guide dogs exhibited incidental learning, adding an additional method of communicating with their visually impaired owners to their repertoire via sonorous mouth licking in the presence of food, there were no differences between guide dogs and pet dogs in the use of other methods of communication such as gaze alternation between the food and the owner, vocalization, and contact with the owner.

While aspects of cognition have undoubtedly impacted upon the success of dogs in service roles, the role played by individual differences in cognition toward service dog suitability has yet to be fully evaluated.

### Cross-References

- Artificial Selection
- Canine Cognition
- Canine Communication
- Classical Conditioning
- Human-Animal Interaction
- Operant Conditioning
- Personality in Animals

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## Set

► [Assemblage](#)

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## Sex Changer

► [Hermaphrodite](#)

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## Sex Characteristics

► [Sex Differences](#)

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## Sex Check

► [Sexual Identification](#)

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## Sex Differences

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## Synonyms

[Gender differences](#); [Sex characteristics](#); [Sex hormones](#); [Sexual dimorphism](#)

## Sex Determination

Sex differences refer to the numerous qualities and characteristics that vary between the sexes. There are different sexes in most animals, as well as some insects, and even plants. In humans, an individual's sex is determined by their chromosomes. Humans are born with 46 chromosomes in 26 pairs. On the 23rd pair, the chromosomes are known as either X or Y chromosomes. If someone is born with two X chromosomes, they are female. If there is one X and one Y in the pair, then they are male. These are the most common outcomes; however, in rare cases, there can be other variants. One in every thousand humans will be born with only one sex chromosome, and at a similar rate, some individuals are born with three sex chromosomes (Aydin et al. 2019). Additionally, some people are born with some cells containing an XY pair, while other cells contain XX; this is known as intersex. Hormonal variation during fetus gestation can also contribute to sex determination. When a Y chromosome is present, around the tenth week of pregnancy, a gene called *SRY* acts upon the embryonic gonads to cause differentiation into male testes (Becker et al. 2005). In an absence of the Y chromosome, the embryonic gonads will become ovaries. Embryonic testes secrete hormones that act on cells in the body and brain to make them male-typical (Nef and Parada 2000). Testosterone is one of these hormones, and in the presence of testosterone, neuronal connections in the brain will begin to form that are more commonly found in males than females and that are responsible for certain behavioral and functional traits (Becker et al. 2005). Read Arnold (2016) for more information.

## Hormones

One key difference between male and female humans is the level of hormones throughout an individual's life cycle. Three main hormones are present in both sexes – estrogen, progesterone, and testosterone – but to different extents. On average, higher levels of testosterone are commonly found in males as compared to females,



higher levels of estrogen are commonly found in females as compared to males, and equal levels of progesterone are found in both males and females. An exception to this would be during the luteal phase of the female menstrual cycle, during which progesterone levels are elevated (Oettel and Mukhopadhyay 2004).

Estrogen is synthesized in all vertebrates, as well as some insects, and has a variety of functions in both male and female humans. In females it helps with memory, cholesterol regulation, heart and muscle health, maturation and maintenance of bone density, blood clotting, and regulation of sugar and insulin sensitivity and increases fat storage (Barakat et al. 2016). In addition, in the female reproductive system, estrogen helps stimulate the growth of the egg follicle and enhances and maintains the membrane that lines the uterus (Hampson 2019). In males, it is primarily responsible for bone density maintenance and liver function, helping to metabolize fats and sugars (Wibowo and Wassersug 1999). In the male reproductive system, estrogen aids in the maintenance of libido, erectile function, and the creation of sperm (Schulster et al. 2016).

Progesterone is a hormone that is only present in birds and mammals, but aids in several important functions within these animals. In humans of both sexes, progesterone has been proven to improve sleep and stimulate weight gain and appetite, as well as playing a role in the immune system, cardiovascular system, respiratory system, and kidney function (Oettel and Mukhopadhyay 2004). In males, progesterone is responsible for creating testosterone and aiding in the creation of sperm. In females, progesterone helps thicken the lining of the uterus to prepare for a fertilized egg (Patel et al. 2015). In humans, testosterone is responsible for several important processes, including encouraging bone growth and density, stimulating the production of red blood cells, promoting muscle development, and improving mood and libido (Rothman and Wierman 2009; Smith et al. 2013). In males, specifically, testosterone aids in erectile function and prostate growth and function (Smith et al. 2013).

Males and females both go through regular cycles of hormonal change. Male testosterone levels

fluctuate throughout the day, whereby they are highest in the morning and lowest at night (Brambilla et al. 2009). In contrast, female estrogen and progesterone fluctuate monthly. The female hormone cycle is part of the menstrual cycle, which is composed of three parts: the follicular phase, the ovulatory phase, and the luteal phase. The follicular phase begins on the first day of menstrual bleeding, prior to the release of the egg, and lasts about 14 days. In this phase levels of estrogen (20–50 pg/mL; (Hampson 2019) and testosterone (200–300 pg/mL; Abraham 1975) start out at their lowest and gradually rise, until they reach their highest peak of the cycle (130–200 pg/mL is typical for estrogen, 500 pg/mL for testosterone). Production of progesterone by the ovaries is negligible during this time. Behaviorally, females display high energy, high positive affect, and low anxiety. Working memory tends to be improved during this time, as estrogen enhances working memory. The ovulatory phase, which lasts approximately 16–32 h, occurs when the egg is released into the uterus. During this phase estrogen increases, causing the luteinizing hormone to peak. The Luteinizing hormone is responsible for ultimately triggering the release of the egg. Libido tends to be highest during this phase. The luteal phase is the period of time after the egg has been released, which lasts about 14 days, unless fertilization occurs. Progesterone is at its highest concentration at 100–200 pg/mL, estrogen plateaus at 100–150 pg/mL, and testosterone falls to 300 pg/mL (Hampson, 2019). Cortisol levels also rise during this time due to higher progesterone levels, and as a result, females tend to experience low energy, increased negative affect, and heightened reactivity to stress. If fertilization does not occur, then this phase will end in a sudden drop in estrogen and progesterone. This results in the shedding of the uterine lining, causing menstrual bleeding and the beginning of the next cycle.

Levels of hormones also fluctuate dramatically depending upon the stage of life. For females, hormone levels rise as puberty is reached, but by 18 the hormonal levels are still only ~50% of levels reached at full reproductive maturity. The highest levels of hormones can be measured during ages 25–35, before they begin to slowly

decrease (Hampson, 2019). Once menopause is reached, around age 50, hormone levels decrease more dramatically. As males reach puberty, testosterone levels increase. They continue to increase until they peak in their 20s. After approximately age 30, testosterone begins to slowly decline by about 2% per year (Smith et al. 2013). Some men will experience a significant decrease in testosterone after the age of 60.

## Aggression

Though males tend to be seen as the more aggressive sex, both males and females usually display an equal amount of aggression, with females in some species displaying more aggression than males (Choleris et al. 2017). The difference largely comes in the types of aggression displayed. Males tend to express physical and direct aggression, whereas female aggression is usually indirect. This can be seen in mice, with males exhibiting territorial aggression through attacking, biting, and lock fighting, in contrast to females who aggress through pushing and chasing (Choleris et al. 2017). This can also be seen in humans, as males are more likely to assert dominance with direct physical confrontation, while females are more likely to manipulate social relationships (group exclusion, rumors, etc.) as a form of indirect aggression.

Testosterone is often characterized as a hormone that causes aggression. This is often true in many species; however in humans there seems to be a more complex relationship between aggression and testosterone. Testosterone in humans seems to induce social status supporting behaviors, through both prosocial and antisocial behaviors. For those who are higher in status, testosterone increases displays of more dominant aggression. Conversely, an increase in testosterone in those with a lower social status is associated with a reduction in aggression to those above them in the social hierarchy and an increase of aggression to those below them (Rejeski et al. 1988). One study found that females who received testosterone before playing a bargaining game actually increased the amount of money offered to their partner, when compared to those given a

placebo (Eisenegger et al. 2010), which displays prosocial behavior in an act to maintain their social status and avoid negative social consequences.

## Cognition

Hormonal influence on embryonic neural networks causes some cognitive differences to be seen between the sexes. For example, testosterone has an organizational effect on the orbitofrontal cortex (OFC), which is responsible for decision-making. Potentially as a result, males tend to be better at tasks that engage the OFC (Evans and Hampson 2015). A meta-analysis of regions of activation in response to emotion-eliciting tasks showed differences in areas of activation between the sexes. For males compared to females, these areas include the medial prefrontal cortex, anterior cingulate cortex, frontal pole, and mediodorsal nucleus of the thalamus. Females show distinct activation in the bilateral amygdala, hippocampus, and regions of the dorsal midbrain including the periaqueductal gray/superior colliculus and locus coeruleus (Filkowski et al. 2017). This supports research that has found that the difference in working memory lies not in performance quality but instead in differing networks utilized. Females tend to activate more limbic (e.g., amygdala and hippocampus) and prefrontal structures (e.g., right inferior frontal gyrus), whereas males tend to activate a broader network that includes more parietal regions (Hill et al. 2014).

On average, males have been shown to have improved ability on spatial tasks compared to females, and females have been shown to have improved abilities on verbal and perceptual speed tasks compared to males (Hyde et al. 2016). These different proclivities have been postulated to be the reason behind further differences, such as an enhanced visual episodic memory performance in males and enhanced auditory episodic memory in females (Pauls et al. 2013). One theory that may explain the spatial differences from an evolutionary perspective posits that species which require males to travel greater distances to gain access to mates leads to a spatial advantage over females

who did not face the same pressure (Gaulin et al. 1990). This was shown in a study which compared a monogamous strain of voles to a strain that did not pair bond. It found that males in the nonmonogamous strain covered significantly more distance than females and that the sexes in the monogamous strain were equally well-traveled. Better spatial ability was indeed found in the males compared to females in the non-monogamous strain, whereas the difference did not exist in the pair bonding strain (Galea et al. 1996; Gaulin et al. 1990).

Sex differences are also frequently found in social learning, which is the process of acquiring new knowledge through observing and mimicking others. In humans as well as rodents and birds, females tend to show superior social learning when compared to males (Brodin and Utku Urhan 2014; Wang et al. 2014). Estrogen may play a role in this, as mice, rats, and gerbils have been found to have increased social learning during times of estrogen flux (e.g., pregnancy, parturition; Choleris et al. 2017).

A distinct difference in cognition between the sexes also arises in self-assessment. When asked to assess their intellectual abilities, males consistently overestimate their abilities, whereas females significantly underestimate their abilities. This is termed the male hubris, female humility effect, or simply the hubris-humility effect (HHE; Storek and Furnham 2012). This can have societal implications, as well as affect results in research, and thus should be noted in any study assessing cognitive differences between the sexes.

## Mating and Attraction

In general, the sex that must invest the most into offspring tends to be the most selective in choosing a mate. For mammals, this is most often the female. Males, consequently, must invest significant energy into being the best candidate for females to choose from. As a result, mating displays can be seen from males across many species, and intra-sex competition is highest in males. Some ways in which males have evolved to increase their chances of mating are often through

being brightly colored or displaying loud calls, in an effort to show that they can still evade predators effectively even when blatantly visible and heard. One interesting reversal in these roles is in the poison arrow frog. Males of this species care for and raise offspring from the time of fertilization of the eggs and thus invest significantly more time and energy into offspring than females do. In this case, it is the males who are the choosiest, and the females must compete with each other to win the favor of male poison arrow frogs (Wells 1978).

Hormones continue to play a role in sex differences when it comes to attracting and choosing a mate. The menstruation cycle dictates what kind of mate females prefer at certain times, in addition to their attractiveness to males. During the short window of time during which females are ovulating, their preference switches from mates that would be beneficial as long-term partners to those who would have the greatest genetic advantage. While ovulating, females tend to be more attracted to mates that have symmetrical faces and masculine features, as this signals a potential mate's heritable fitness. At other times in the cycle, different male characteristics are valued more highly, such as conscientiousness, loyalty, and good parenting qualities. This switch is most readily seen in females who are assessing short-term mates and is less apparent in those who are searching for long-term partners. In a similar fashion, females tend to be rated as more attractive by males while they are ovulating as opposed to other times during their cycle.

Menstruation dictates mating in many mammals outside of humans as well. In rodents, females will only pursue a mate when estrogen and progesterone are both at peak levels (Choleris et al. 2017).

## Health

Some significant differences between the sexes that are often overlooked are the differences in mental and physical health. In humans, females are much more vulnerable to developing Alzheimer's disease, depression, and anxiety and suffering strokes. Males have a greater risk of

developing Parkinson's disease and are more likely to be afflicted with schizophrenia than females, as well as experience earlier onset and display more severe cognitive symptoms (Choleris et al. 2017). Additionally, disorders of social behavior such as autism spectrum disorders and violence and impulsive aggression have a higher incidence rate in males compared to females (Choleris et al. 2017).

Many of these issues can be attributed to the differences between the structural organization of neural networks, or to the different evolutionary challenges faced by each sex. For example, females' higher rates of diseases associated with activation of the stress response system may be due to the evolutionary benefit of being more risk averse than males. With a greater investment in offspring comes a greater loss in losing them; thus, threats are a greater risk to females compared to males. As such, females experience enhanced defensive behaviors and stress responses, which prepare them to be more responsive to potential threats. This may be what makes them more vulnerable to a disorder of this system, causing increased instances of anxieties, phobias, depression, and post-traumatic stress disorders (Choleris et al. 2017). Similarly, males have been more involved in territorial defense and must engage in more intra-sex competition for resources and access to mates. This engagement in aggressive activities may be one cause of the higher rates of social behavior disorders in males.

Other biological differences between the sexes may further exacerbate differences in health. The sex differences in hormone levels have led to distinctions in disease presentation. Estrogen provides a protective role in the immune system, whereas testosterone has toxic effects, and this can partially account for the higher incidence rates of Parkinson's disease in males compared to females (Invernizzi et al. 2009). Differences in mitochondria lead to a difference in incidence rates for multiple diseases and may be one of the causes of higher incidence rates of Alzheimer's disease in females. A key factor in the development of Alzheimer's is mitochondrial dysfunction. In healthy individuals, female mitochondria produce only half the amount of hydrogen peroxide that the mitochondria of males do (Silaidos

et al. 2018). This difference may therefore have significant consequences for female vulnerability to the development of Alzheimer's disease. For a variety of reasons, males tend to be more vulnerable to infections than females. The immune response is different between males and females, with females demonstrating a stronger cellular and humoral immune response (Invernizzi et al. 2009). This may be due to estrogen having an enhancing effect on the immune system, or the X chromosome carrying more genes that relate to the immune system. Whatever the case, a side effect appears to be a significant increase in autoimmune diseases. Of those who suffer from autoimmune diseases, 80% are female.

There is a significant sex difference in the treatment of diseases as well, correlating to the overall mortality rates of these diseases. Females are more likely to have a stroke, with symptoms that often differ significantly from males. The outcomes of females suffering a stroke tend to be much worse than for males, with females facing longer hospitalization times, double the likelihood of being transferred to long-term care, and a higher chance of mortality (Choleris et al. 2017). Similarly, heart disease is the leading cause of death in females; however, cases of heart disease are often not recognized by medical professionals due to atypical presentation and deviation from "classic" male symptoms. As such, mortality and morbidity rates in female patients are frequently higher when compared to males (Campo 2016).

## Cross-References

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- [Androgens](#)
- [Chromosomes](#)
- [Cognition](#)
- [Dominance](#)
- [Dominance Hierarchy](#)
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- Gametes
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- Sex Role Reversal
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- Spermatogenesis
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- Ultimatum Game
- Working Memory

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## Sex Differences in Cognitive Abilities

► Susan D Healy

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## Sex Hormone

► Androgens

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## Sex Hormones

► Sex Differences

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## Sex Ratio

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## Synonyms

Fisher's principle; Gender balance

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## Definition

In sexually reproducing species, sex ratio is the proportion of males to females in a given population. It is usually expressed as the number of males per 100 females.

## Introduction

Depending on the context, sex ratio might be measured in a particular life stage, e.g., ratio at the time of fertilization (also called primary sex ratio), ratio at birth (secondary sex ratio), ratio in organisms that have reached sexual maturity or adulthood (tertiary sex ratio), ratio of sexually active and fertile organisms (operational sex ratio), or ratio in organisms past reproductive stage (quaternary sex ratio). The ratio tends to be approximately 1:1, which is explained by Fisher's principle (see below). However, a significant deviation from that rule is observed in many species, either permanently or periodically. In humans, sex ratio at birth is sometimes skewed because of factors such as infanticide, sex-selective abortions, age of mother at birth, or environmental factors (Davis et al. 1998).

In 1982, Eric L. Charnov, an American evolutionary ecologist, published a book on the prediction of sex ratios based on a species' natural history. He attempted to identify the equilibrium when allocating resources to female versus male function in simultaneous hermaphrodites, equilibrium of time of sex change and sex order in sequential hermaphrodites, and equilibrium in the ratio maintained by natural selection in dioecious species (having both male and female reproductive organs). He also analyzed when natural selection favors an individual's ability to adjust its allocation to female versus male function, as a reaction to particular life history or environmental variables. He analyzed the conditions favoring evolutionary stability for various states of dioecy or hermaphroditism and when mixtures of various sexual types are stable (Charnov 1982).

## Fisher's Principle

Fisher's principle is an evolutionary model outlined by Sir Ronald Fisher, British geneticist and statistician, in his book *The Genetical Theory of Natural Selection*, published in 1930. It explains why the sex ratio in sexually reproducing species is close to the so-called "Fisherian" ratio of 1:1, which is considered

evolutionarily stable (Fisher 1930). Fisher argued that the process of natural selection leads to sex ratio adjustment. If the total parental investment (such as resources, energy, or time) in the offspring of both sexes is equal, then the birth ratio of sexes should be 1:1.

An important addition to Fisher's theoretical discussion of sex ratio was provided by Trivers and Willard (1973) that stated that, in mammals, females are able to adjust sex ratio of their offspring in response to the maternal condition. Despite the fact that Fisher's principle secures the 1:1 sex ratio, evolution will favor deviations from this rule if one sex has a probability of achieving greater reproductive payoff than the other. The findings of Trivers and Willard suggest that the reason for promoting such disproportion is that, in good condition, mothers should invest more in producing males, because sons of a high quality are expected to out-reproduce daughters of high quality. Consequently, mothers who are in poor condition should invest more in producing females, because daughters of low-quality are expected to out-reproduce sons of low quality. The implication is that parental ability to adjust offspring sex ratio depending on the quality of conditions should be favored by natural selection. Data on sex ratio of mammals supports this hypothesis: as maternal condition increases, females tend to produce more males than females.

## Sex Ratio in Nonhumans

Most animals maintain a relatively stable operational sex ratio, but some are known for having their sex determined not just by genes but also by, e.g., environmental factors or hormonal changes (e.g., Ferguson and Joanen 1982; Pike and Petrie 2005). Proper assessment of a sex ratio is neither easy nor straightforward. It has been observed that deviation from the 1:1 ratio is widespread in marine crustacea; there are male-female relationships of discrete patterns, so instead of overall sex ratio, calculation of different within-size-class ratios should be taken into consideration (Wenner 1972).

Temperature-dependent species have a higher within-species variance in sex ratios than

chromosome-determined species (Bókonyi et al. 2019). For example, in American alligators, sex of the individual is dependent on incubation temperature of the egg. Females are hatched from eggs incubated at a lower temperature than males, who require higher temperatures (Ferguson and Joanen 1982). Temperature-based sex determination is also found in turtles. However, a study performed on eggs incubated in the same temperature shows evidence that some heritable differences in sex determination exist as well (Bull et al. 1982). Temperature can also influence sex in fish, such as in Nile tilapia (Abucay et al. 1999), and the effect for interaction of genotype and temperature is observed in species such as the Atlantic silverside (Conover and Kynard 1981).

Environmental determination of sex ratio is also observed in the potato root eelworm, a parasite. In eelworms, the ratio can differ depending on primary and lateral roots, and on the intensity of their parasitic infection (Ellenby 1954). Environmental influence on primary sex is also observed in dioecious plants. Maternal parents in close proximity to males produce female-biased progeny sex ratios (Stehlik et al. 2008). In copepods, sex ratio differs between families depending on whether females produce eggs continuously after just one mating, or they require several matings (Kiørboe 2006). In fig wasps, females adjust offspring's sex ratio in response to the level of inbreeding and the intensity of mate competition in the local population (Herre 1985). Parasitic wasp females adjust offspring sex ratio depending on whether they are the first or second wasp parasitizing the host. The first one biases strongly towards daughters, and the second one varies sex ratio depending on local mate competition level (Werren 1980). In collared flycatchers, females manipulate offspring sex ratio depending on the male partner's genetic quality (Ellegren et al. 1996). To summarize, not all species of flora and fauna follow the strict Fisherian ratio rule; in some species, sex is moderated by various environmental factors. In short, the sex ratio tends to be that which is most likely to propagate copies of the parents' genes in that environment.

In mammals, one way of increasing eventual offspring production is to vary the sex ratio of offspring as a function of the benefits and costs of producing daughters versus sons. There are at least three factors that may affect sex ratio in mammalian offspring: cooperation or competition between siblings or between parents and siblings; differences in the relative fitness of female and male offspring; and sex differences in viability during early growth or in energy requirement. There is growing evidence that in many species there remains significant variation in mammalian birth sex ratio, which suggests continued adaptive manipulation of sex ratio. However, there are also other mechanisms affecting sex ratio at birth, and they are not likely to reflect adaptive manipulation, because the distribution of observed trends in sex ratio does not conform to the assumptions of any adaptive theory in a significant way. Some studies, however, argue that such trends might be adaptive within a particular population if the sex ratio differs with the benefits or costs of producing female and male offspring, such as a hypothetical population finding a very good and stable source of food, and therefore being able to afford the more costly sex of offspring (Clutton-Brock and Iason 1986).

Potentially adaptive significance of sex ratio variation caused by parental and environmental conditions is reported not only in mammals but also in birds. Findings suggest that sex ratio at birth could have been interfered with by steroid hormones and gonadotropins; however, whether it is an adaptive sex ratio adjustment or merely a consequence of physiological constrain is a subject of debate (Krackow 1995; Navara 2018).

There are, however, exceptions to the expectations of the Trivers-Willard theory. For example, in American kestrels, the sex ratio of offspring is correlated with female body size. Parents can adjust the sex of their offspring depending on the amount of resources available and as the food supply declines, the proportion of males hatching increases. Also, parents in poorer health produce more male-biased offspring and smaller females produce more males (Wiebe and Bortolotti 1992). In Seychelles warblers, biased sex production, not embryo mortality, is the cause of a bias in hatching

sex ratios. Pairs on bad-quality territories produced 77% sons, and pairs on good-quality territories produced 13% sons. Pairs that transferred from a poor to a high quality territory subsequently produced significantly more females (Komdeur et al. 1997). These exceptions may be caused by, for example, reversed sex characteristics in the species, such as females being physically larger in order to compete for mates.

## Sex Ratio in Humans

In humans, sex ratio at birth is approximately 1:1, and research measuring sex ratio has been conducted all around the globe, producing over 100 years of data. Sex ratio varies across age groups and geographical locations, and several factors can influence sex ratio, including race, birth order, plural birth, duration of gestation, and parental age, psychological stress, and health history. The sex ratio produced in relation to these factors, however, is not consistent over time for a given country, or across countries at a given time. It has been observed that in the USA, between 1950 and 1972, fetal and neonatal death more frequently occurs in females, which biases the birth sex ratio slightly towards males (McMillen 1979); however, proper estimation of this bias is difficult and affected by factors such as sex-selective abortions. In infancy, boys have higher mortality rates because they are more susceptible to disease (Pongou 2013). For the USA, sex ratio at birth for Hispanic and African-American ethnic groups is lower than for white ethnic groups. Also, in a white ethnic group, sex ratio at birth was 1.04 if the gestational age was 33–36 weeks, but if the age was shorter (<28–32 weeks) or longer (37 weeks or more), the sex ratio was 1.15 (Branum et al. 2009). Women tend to live several years longer than men, which biases sex ratio in older generations towards women.

In 1990, economist Amartya Sen analyzed whether birth sex ratios are affected by sex-selection, e.g., aborting female fetuses, or natural causes, such as greater vulnerability of male fetuses. Sen argued that strong socioeconomic factors, e.g., one-child policy in China or India's

dowry system, affect prenatal sex-selection. Some disagree with this argument; however, for example, Garenne (2004), who observed that, in many African nations, e.g., Nombia, Botswana, and Angola, there are fewer boys born than girls, which is not the case for other nations.

Sex ratio imbalance differs across the globe as a consequence of various factors, such as environmental stressors in the form of, e.g., cold weather; women exposed to colder temperatures tend to spontaneously abort (i.e., miscarry) male fetuses more frequently, and therefore, more females are born. It has also been shown that males living in colder temperatures tend to live longer, thus raising sex ratio in later life stages (Catalano et al. 2008). Helle et al. (2009) found the reverse effect; they documented that environmental stress, such as war or warmer temperatures, skew human birth sex ratio towards more frequent male births in Northern Europe. In females, experiencing stress during pregnancy, such as malnutrition, increases fetal deaths among males, in particular, leading to a female-biased sex ratio (Catalano et al. 2008). Due to the contradictory results regarding stress experienced by mothers during pregnancy on survivability of fetuses, more studies are needed to fully understand the effect. It has been found that some types of environmental pollution leading to exposure to persistent organochlorine pollutants, which are endocrine disruptors, increases the amount of ejaculated spermatozoa carrying the Y-chromosome, which might alter the sex ratio of offspring (Tiido et al. 2005). A longitudinal study on a Finnish population reported changes in sex ratio caused by environmental chemicals and showed that the birth sex ratio of males to females has decreased. It was found that the peak of male birth dominance occurred before the introduction of hormonal drugs and pesticides and the period of industrialization; after that, the sex ratio decreased. The researchers excluded the possibility that the change occurred because of other factors, such as birth order, age difference of parents, or parental age (Vartiainen et al. 1999). Finally, there has been identified an effect of father's age on sex ratio of offspring. Younger fathers had significantly more sons than older fathers. Mother's age did not affect a child's sex

(Jacobsen et al. 1999). To sum up, sex ratio in humans is a subject to various pressures, and the final sex ratio observable in a given population is a resultant of all of them.

## Cross-References

- ▶ [Chromosomes](#)
- ▶ [Ejaculate](#)
- ▶ [Environmental Influences](#)
- ▶ [Evolutionarily Stable Strategies](#)
- ▶ [Fetus](#)
- ▶ [Genotype](#)
- ▶ [Hermaphrodite](#)
- ▶ [Incubation](#)
- ▶ [Infanticide](#)
- ▶ [Operational Sex Ratio \(OSR\)](#)
- ▶ [Parental Investment](#)
- ▶ [Pollution](#)
- ▶ [Population](#)
- ▶ [Stress](#)

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## Sex Role Reversal

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## Introduction

In sexually reproducing animals, males usually search and compete for mates more actively than females do, whereas females are choosier than males when selecting mates (conventional sex roles). Accordingly, in sexually dimorphic animals, males often develop elaborate weapons or ornaments (Trivers 1972). Female-only care of offspring is much more ubiquitous than male-only care in many animal taxa. Moreover, in species with biparental care, females generally invest more in caring for their offspring. As the parental investment to offspring is a trade-off with the investment to mate acquisition, the evolution of these two life history traits are intimately linked (Fromhage and Jennions 2016). Therefore, sex differences in brooding behaviors are often treated as sex roles. Sex role reversal denotes reversion in one or more of these gender roles in reproduction, that is, masculine females or feminine males.

## Evolution of Conventional Sex Roles

The reasons for the evolution of conventional sex roles are still being debated. By definition, males

produce smaller gametes (spermatozoa), which are usually produced in much higher numbers than the ova in a population (anisogamy). Therefore, a male who secures multiple mating opportunities can pass many more gene copies to the next generation than a female can. Historically, this difference in the potential reproductive rate, or the resultant male bias in a pool of sexually mature adults at a given point in time (operational sex ratio), has been considered as the major determinant of conventional sex roles (Trivers 1972).

However, the sum of male reproductive success is equal to that of females in a population (Fisher's condition), and the “mean” reproductive success should be equal between the sexes in a population with an adult sex ratio of 0.5. Hence, anisogamy itself cannot explain the evolutionary maintenance of conventional sex roles.

Recent theoretical and comparative studies (Kokko and Johnstone 2002; Fromhage and Jennions 2016; Fromhage et al. 2016; Janicke et al. 2016) demonstrate that the following factors, which are associated with anisogamy (but not anisogamy itself), are important for determining sex roles: (1) sexual selection is usually stronger in males (not all, but some males can produce many more offspring than most females, resulting in a larger variance in reproductive success); (2) females usually have a “time-lag” between insemination and fertilization of eggs (in animals with internal fertilization) during which they are no longer available for mating in a population of adults; (3) females can mate with several males, resulting in uncertainty of paternity compared with maternity. Consequently, males usually invest more energy in mate acquisition and less in brooding than females do.

## Evolution of Reversed Sex Roles and Examples

Reversed sex roles are considered to evolve when one or more of the aforementioned conditions are violated. Fishes of the infraorder Teleostei are well known for their sex role reversal in parental care (Janicke et al. 2016). In contrast to many other animal groups, male-only care is more common than female-only or biparental care in teleost

fishes. In some species, females use sex-specific ornaments to attract males (potential care givers) and engage in female-female competition for territories (including potential nest sites for males). Because eggs are fertilized externally, male fish experience lower uncertainty of paternity. Additionally, the primary tasks associated with male parental care are supplying oxygen (fanning) and defending against predators, both of which enable males to simultaneously care for multiple clutches from multiple females. Therefore, parental investments by male fish are less likely to be paid at a cost to mate searching. Moreover, in some species, eggs cared for by males attract additional mates, resulting in the reinforcement of parental investment by sexual selection (Ah-King et al. 2005).

Similar phenomena are reported for some insects. In the assassin bug *Rhinocoris tristis* (Insecta: Hemiptera: Reduviidae), males can simultaneously care for eggs from up to seven different females. Interestingly, although male-only care is the norm of the species, females care for their own eggs when males are not available (reviewed in Shuker and Simmons 2014).

Male waterbugs of the family Belostomatidae (Insecta: Hemiptera) also care for eggs. Females lay dozens of eggs on a substrate (such as a plant stem) or on the back of the male mate, during which time the pair will repeatedly copulate. This behavior is considered to be a male adaptation to avoid taking care of unrelated eggs. Females actively search and compete for male caregivers. Moreover, since males do not mate during paternal care periods, females sometimes destroy an egg batch already cared for by a male to take over the mate. For this group of insects, in which males can care for only one egg batch from a single female at a time, it is presently unclear why males, not females, are the sole caregivers (Shuker and Simmons 2014).

Female-only or biparental care of broods is the norm for birds (Cockburn 2006). However, male-only care is reported for some unique species that represent only 1% of class Aves. Male-only care predominates in ratites (Infraclass Palaeognathae: ostriches, kiwi, emu, etc.). As in fishes, ratite males can care for eggs from multiple females

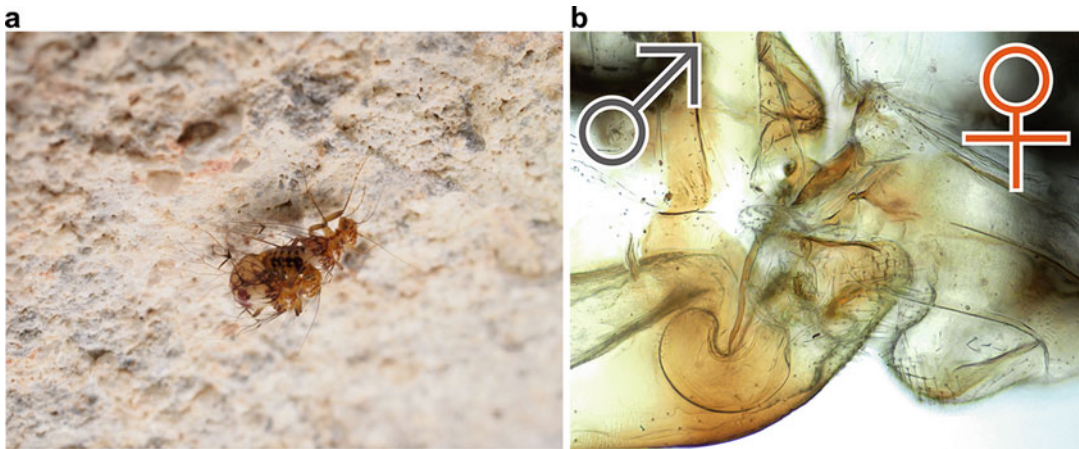
simultaneously. Additionally, the young are relatively mature and mobile upon hatching (i.e., precocial) and do not require biparental provisioning efforts.

The suborder Charadrii (waders) is another bird taxon with many representatives exhibiting male-only care. For example, female spotted sandpipers (*Actitis macularius*) compete for territories, in which several males provide care for her clutches. Like waterbugs, male sandpipers cannot care for multiple clutches at a time, so there is continuing debate on why males are the predominant caregivers. One possible explanation is that the cost of care is higher for females than males. In this group of birds, paternal care is relatively common in species that migrate to high latitudes, where it seems to be difficult for females to produce more than one clutch if they engage in brooding.

As illustrated in the aforementioned examples, the evolution of parental care is intimately related to the evolution of other sex roles, i.e., mate attraction, mate searching, intrasexual competition, and mate choice. These numerous aspects of sex roles are considered to coevolve under a complex set of natural and sexual selective pressures (Fromhage and Jennions 2016).

Strongly female-biased adult sex ratio can also make males (and their sperm) a limited resource for female reproductive success, and thus can result in sex role reversals, as paternal care of offspring does. In the butterfly species *Acraea encedon* (Insecta: Lepidoptera: Nymphalidae), females form aggregates (leks), presumably, to attract males in populations where male-killing bacteria (*Wolbachia*) persists, making males rare. Only males of this species engage in lekking behavior in populations that have nearly equal sex ratios (reviewed in Shuker and Simmons 2014).

Nutritional contributions from males to females also may cause reversed sex roles (reviewed in Yoshizawa et al. 2014). Males of dance flies (Insecta: Diptera: Empididae) donate prey items to females as nuptial gifts. Because larger gifts prolong copulation, nuptial gifts are considered to be a sexually selected male trait for enhancing paternity. Females of some



**Sex Role Reversal, Fig. 1** (a) *Neotrogla* sp. in copula. The female mounted on the male (the mating occurred on the roof of a cave). (b) Terminal abdomens of *N. curvata* in

copula, lateral view. U-shaped structure observed through the male's abdomen is the sclerotized part of the gynosome

*Rhamphomyia* species have fringed legs and/or inflated abdomens. These structures function as size-enhancing devices used to deceive males that would otherwise prefer to donate large-sized prey items to more fecund, large-sized females. Similarly, males of many bush cricket species (Insecta: Orthoptera: Ensifera) provide a large gelatinous mass (termed spermatophylax) attached to a spermatophore (sperm ampulla). The primary function of the spermatophylax is to protect the ejaculate. Sperm will evacuate the ampulla and move to the female sperm storage organ during the female's consumption of the spermatophylax. Females of *Hemianthus pallitarsus*, a species of ground weta, use an elbow-shaped structure to obtain this nuptial gift from males.

As illustrated above, sex role reversals are sometimes accompanied with drastic evolutionary changes in male and female morphologies. Male seahorses and pipefishes (Teleostei: Syngnathiformes: Syngnathidae) have a specialized pouch on the ventral side of the abdomen wherein females oviposit eggs using a specialized ovipositor. In these groups of fishes, only males care for eggs until they hatch. In some species, females are much more ornamental than their male conspecifics and compete with other females for access to males (Wilson et al. 2003).

Females of the cave insect genus *Neotrogla* (Psocodea: Prinoglarididae) use their

evolutionary novel penis-like structure, termed gynosome, for mating with males (Yoshizawa et al. 2014, Fig. 1). This “female penis” is ornamented with species-specific lobes and/or spine bundles, which are accommodated in specialized pouches of the vagina-like male genitalia. During copulation, which lasts 40–70 hours, voluminous and potentially nutritional seminal substances are passed from the male to the female through the gynosome. Since they live in dry, nutritionally poor caves in Brazil, gynosomes likely represent elaborate ways for females to exploit seminal foods from males. In accordance with this view, females of a related species with similar nuptial gifts (Psocodea: Trogiidae) compete for access to males. Moreover, *Neotrogla* females have also developed a specialized, evolutionary novel structure in their sperm storage organ that enables retention of two gifts simultaneously.

## Cross-References

- [Anisogamy](#)
- [Nuptial Gift](#)
- [Operational Sex Ratio \(OSR\)](#)
- [Parental Investment](#)
- [Precocial](#)
- [Sexual Selection](#)

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## Sexing

### ► Sexual Identification

## Sex-Linked

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## Synonyms

Gender-based; Gender-related; Sex-related

## Definition

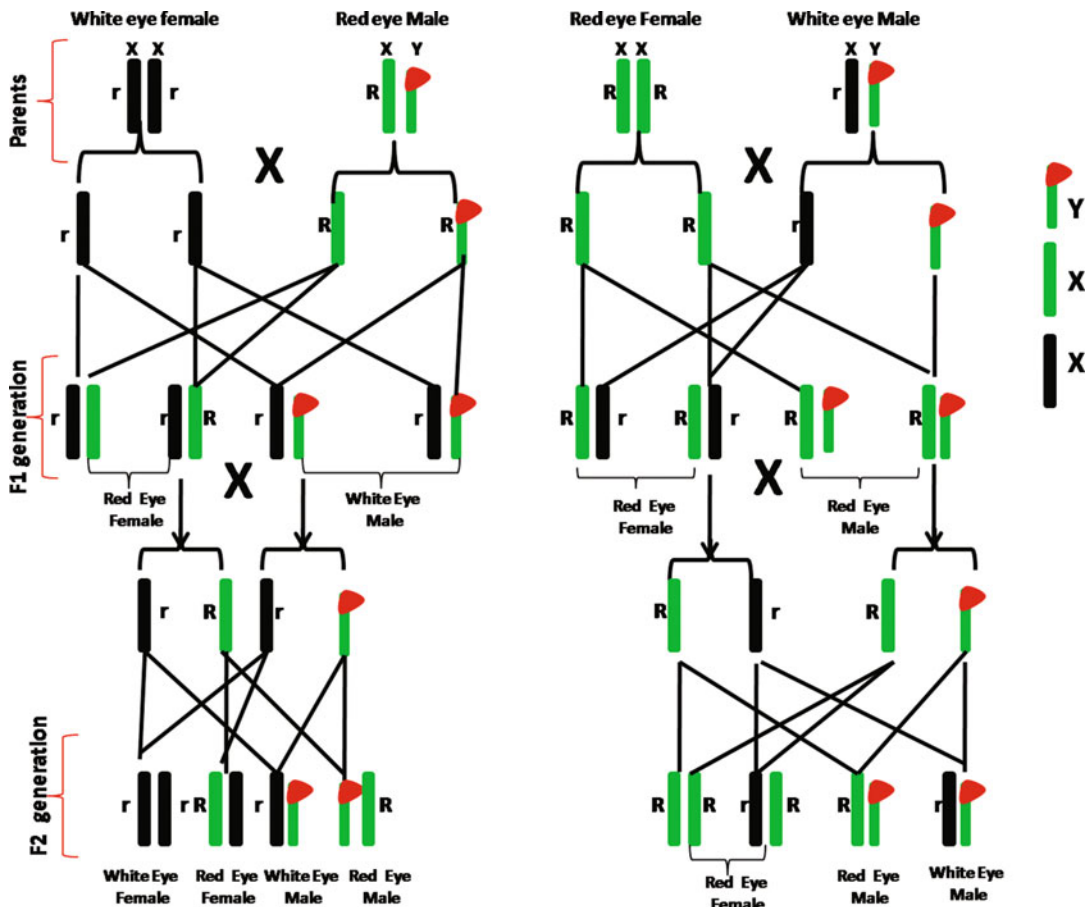
Any phenotype is said to be sex-linked if the triggering gene for that phenotype is located on a sex chromosome (Morgan et al. 1915). Sex-linkage is the pattern of the allele expression and inheritance in association with the sex chromosomes of the individuals (Charlesworth 2017). For example, in humans, the term sex-linked phenotype generally refers to the characters that are influenced by the genes that are located on either X or Y chromosomes (Snell and Turner 2018).

## Introduction

Sex-linked phenotypes were discovered in the year 1910 by Thomas Hunt Morgan (an American geneticist) as white-eyed mutations in the “male” fruit fly (*Drosophila melanogaster*). Morgan was awarded a Noble Prize in Physiology or Medicine in 1933 for this discovery. He performed a series of experiments on fruit flies and reported that the gene that controls the color of the eyes in these flies is located on the X chromosome. He did a cross between a white-eye (mutant) male with a red eye (wild-type) female fly. In the first generation, all flies obtained were of red eye color as the white eye trait was recessive. The next cross between F1 generation males and females produced an F2 generation that was comprised of 3470 red eyed (both male and female) and 782 white eyed (only male) flies (Fig. 1). Sex-linked traits or genes are located on the sex chromosome, that is, X chromosome and Y chromosome in humans. The genes located on the X chromosome are called X-linked genes and, on the Y chromosome, Y-linked genes. In humans, Y-linked genes are transmitted only by males and have genotype XY. Contrarily, X-linked genes are transmitted by both males and females (Morgan et al. 1915).

## Characteristic Features of the Sex-Linked Phenotypes

- Mendel’s law does not apply to those genes that are completely located on either X or Y chromosomes.



**Sex-Linked, Fig. 1** Experiments/cross performed by TH Morgan

- Sex-linked inheritance is the inheritance of traits that are determined by the expression of genes located on the sex chromosomes (Raznahan et al. 2018).
- Sex-linked inheritance mostly occurs due to the X chromosome as compared to the Y chromosome.
- The genes located on the X chromosome are known as diandric and on the Y chromosome as holandric genes.
- The inheritance of X-linked genes and Y-linked genes from parents is called sex-linked inheritance.

### Sex-Linked Inheritance

Sex-linked inheritance is the passing of characters/alleles that are located on either of the sex

chromosomes (X and Y chromosome) from parents to the progenies. Therefore, the inheritance of X-linked traits is generally from mother to daughter, but Y-linked inheritance is from father to son only.

### Sex-Linked Disorder

Like autosomes, sex chromosomes are comprised of different genes that are required for the normal function. Functional alteration in these genes due to mutations leads to sex-linked disorders (Schurz et al. 2019). Mutations in Y chromosomes (Y-linked inheritance) are characterized by an alteration in male sexual functions and secondary male characters. For example, Y-linked inheritance disorder is comprised of



hypertrichosis that is characterized by growth of hair at the outside rim of the ear and Webbed toes that is characterized by web-like connection between second and third toes. Y-linked inheritance is carried out by the Y chromosome from father to his son only (Pavone et al. 2015). Similarly, the mutation in the X chromosome is defined as the X-linked inheritance. Some common sex-linked disorders are hemophilia (Lewis et al. 1963), red green color blindness (Wale et al. 2018), congenital night blindness (Le Pichon et al. 2013), Duchenne muscular dystrophy (Ward and Weber 2019), and Fragile X syndrome (Bagni and Zukin 2019).

In humans, sex-linked disorders can be categorized into X-linked and Y-linked disorders. X-linked disorders can be further divided into X-linked recessive and X-linked dominant disorders.

1. **X-linked recessive disorder:** X-linked recessive disorder is a mode of inheritance in which mutation in a gene located on the X chromosome that causes the phenotype is always expressed in males and females that are homozygous for gene mutation. The most common X-linked recessive disorders found in humans are Hemophilia (Hemophilia A and B) (Lewis et al. 1963) and color blindness (Le Pichon et al. 2013).
2. **X-linked dominant disorder:** X-linked dominance disorder is a mode of genetic inheritance, in which a dominant gene is carried on the X chromosome. X-linked dominant disorder is uncommon as compared to other Mendelian disorders, and females are mostly affected as compared to males. Females have two X chromosomes and do not show the transmission from father to son, and affected males are more severely affected than females. The X-linked dominant disorder is rare as compared to X-linked recessive disorder. The examples of X-linked dominant disorder are Fragile X syndrome, oral-facial syndrome type 1, and hypophosphatemic ricketsm (Bagni and Zukin 2019).
3. **Y-linked disorder:** Mutations in the genes that are located on the nonhomologous region of

the Y chromosome and directly pass from male to male may cause Y-linked disorder.

The list of some of the sex-linked disorders is as following:

| S. no. | Disorder                        | Symptoms                                                                                                                           | Sex-linked status                                                    |
|--------|---------------------------------|------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------|
| 1.     | Color blindness                 | The person is not able to distinguish between red or green or both color                                                           | Due to X-linked recessive genes (Yatsenko et al. 2016)               |
| 2.     | Hemophilia (Bleeder's disorder) | Pain, swelling, or tightness in joint and blood in urine or stool                                                                  | Due to X-linked recessive genes (Lewis et al. 1963)                  |
| 3.     | Rett syndrome                   | Leading to cognitive impairment in female                                                                                          | Due to X-linked dominant genes (Feldman et al. 2016)                 |
| 4.     | Double-cortex syndrome          | Intellectual disability, seizures, and behavioral problems                                                                         | Due to X-linked dominant genes (Sprugnoli et al. 2018)               |
| 5.     | Incontinentia pigment type 1    | Characterized by dermatological, ocular, dental, and neurological abnormalities                                                    | Due to X-linked dominant genes (Roberts 1958)                        |
| 6.     | Hypophosphatemia                | Electrolyte disorder in which there is a low level of phosphate in the blood                                                       | Due to X linked dominant genes (Cubillos Celis and Mena Nannig 2018) |
| 7      | Y-chromosome infertility        | Adult male produce immature sperm cells, fewer sperm cells, or sperm cells that are abnormally shaped or that do not move properly | Due to Y-linked disorder (Dhanoa et al. 2016)                        |

Cross-References

- Mendel's Law
- Phenotype

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## Sex-Related

### ► Sex-Linked

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## Sexual Adaption

### ► DNA Repair Hypothesis

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## Sexual Antagonism Hypothesis

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## Synonyms

### Sexual conflict

## Definition

Sexual antagonism (or sexual conflict) arises between the sexes when the evolutionary interests of males and females differ. Conflict can arise over the expression of a trait shared by both sexes, or over the outcome of reproductive interactions between males and females.

## Introduction

Sexual antagonism (or sexual conflict) arises between the sexes when the evolutionary interests of males and females differ (Parker 1979; Chapman et al. 2003; Arnqvist and Rowe 2005). It can be separated into two main forms, known as intralocus and interlocus sexual conflict, which differ in whether the target of selection is a single trait shared by both sexes, or different traits in either sex that interact to influence fitness, respectively. Conflict is the result of selective processes acting differently between the sexes, and may arise due to differences in the strength or direction of sexual selection, natural selection, or both. Sexual conflict ultimately arises when there are fundamental differences in reproductive roles between the sexes (Parker 1979). For example, female mammals carry young during pregnancy, and then suckle infants with milk until they are able to fend for themselves. Male mammals do none of this, and so have a much higher potential reproductive rate than females. Therefore, the best reproductive strategy for females is to focus on rearing healthy offspring, whereas for males it may be to contribute little to parental care, and instead father offspring with as many females as possible. These biological differences thus lead to very different optimal reproductive strategies. Recognition of these evolutionary conflicts of interest between the sexes allows us to explain a variety of adaptations in males and females, especially those relating to reproduction and parental care (Arnqvist and Rowe 2005).

### Intralocus Sexual Conflict

Intralocus sexual conflict arises when the optimal expression of a trait that is shared by both sexes differs (Arnqvist and Rowe 2005; Bonduriansky and Chenoweth 2009). For example, male elephant seals compete with each other for access to females, and so benefit from having a very large body size, whereas females do not. In other words, sexual selection acts to increase body size in males but not in females. This means that

selection on body size will act in opposite directions in either sex. This form of conflict is likely to be widespread, given that males and females have many shared traits with a common genetic basis. The outcome of such divergent selection depends on the extent to which gene expression is constrained between the sexes. If plasticity in gene expression is limited in some way, then the trait may be expressed at an intermediate, and thus suboptimal, level in both sexes (Bonduriansky and Chenoweth 2009). Alternatively, gene expression may become decoupled between the sexes, leading to sexual dimorphism. The fact that males and females are dimorphic in most species suggests that such differential expression is achieved often, and indeed we should expect it to evolve quickly when selection is strong. Therefore the evolutionary importance of intralocus sexual conflict remains unclear, and will ultimately depend on the importance of genetic constraints on trait evolution.

### Interlocus Sexual Conflict

Most theoretical and empirical work has instead focused on interlocus sexual conflict, which arises over the outcomes of interactions between males and females (Arnqvist and Rowe 2005). This form of conflict is most relevant when studying animal behavior, given that it arises primarily due to behavioral interactions between the sexes. Interlocus sexual conflict can arise in two ways (Arnqvist and Rowe 2005). First, conflict will arise for any sexual interaction for which the optimal outcome differs between the sexes. This includes conflict over aspects of the mating system such as mating rate, remating behavior, and parental roles. Second, conflict may arise whenever males and females need to cooperate during reproduction. This occurs for example in birds, in which both males and females provision young. Though both parents may benefit from sharing provisioning (as this should result in the greatest chance of offspring survival), each parent will also benefit if its partner does more work. This means that tasks previously seen as cooperative are more appropriately viewed as a form of negotiation,

with each parent trying to exploit the efforts of the other (Trivers 1972).

Interlocus sexual conflict is most commonly studied in relation to reproductive traits, and can occur before, during, and after mating. This includes conflict over mating frequency, fertilization, female remating behavior, and female reproductive rate. For example, in many species there is conflict between the sexes over whether females should be monogamous or polygamous (Arnqvist and Rowe 2005). For a male, the optimal outcome is for each female to mate only with him, as this will ensure that he fertilizes all of her eggs. However, females can often benefit by mating with multiple males during each breeding bout, for a variety of reasons. Therefore the optimal level of polyandry may be higher for females than for males. This conflict has led to the evolution of male adaptations in many species that prevent females from remating. These include behavioral adaptations such as mate guarding, anatomical adaptations such as mating plugs that block the female reproductive tract, and physiological adaptations such as male seminal fluid compounds which delay female remating (Arnqvist and Rowe 2005).

Another common form of sexual conflict arises over mating itself. Given that sperm are relatively cheap to produce, males can generally benefit most by mating with every female they encounter. In contrast, female reproductive rate is more restricted, and so females benefit most by mating with only the highest-quality males, either in terms of resource-holding potential or genetic quality. This has led to the evolution of female choice based on the assessment of male phenotype. However, sexual conflict means that selection on males will favor any adaptation that allows a male to circumvent female choice, either before or after mating. This conflict can explain a variety of antagonistic male mating behaviors, such as forced matings (Clutton-Brock and Parker 1995).

In some cases, sexual conflict may lead to one sex being directly harmed by adaptations in the other sex. For example, harassment and coercion by males may lead to the drowning of female waterfowl (Clutton-Brock and Parker 1995). Females may also be physically harmed by male

grasping structures, or by sharp spines found on the male genitalia (Arnqvist and Rowe 2005), and in some species this harm may significantly reduce female fitness and fecundity (e.g., Dougherty et al. 2017). In these cases harming of females does not seem to benefit males directly, but rather arises as a by-product of selection on male traits that increase male mating or fertilization success (Morrow et al. 2003). In such species, selection on females to evolve counter-adaptations to reduce harm is particularly strong. Examples of such counter-adaptations include the thickened reproductive tracts and increased immune activity seen in female seed beetles (Dougherty et al. 2017).

Males and females also have to interact when raising offspring, and this leads to a variety of conflicts between the sexes over parental care strategies and behaviors (Trivers 1972; Arnqvist and Rowe 2005). Though both parents have equal relatedness to the offspring, and so would benefit equally from offspring survival, parents are generally unrelated to each other. This means that each parent can gain by allowing the other to contribute more to care: the “cheating” parent will then have more resources available to allocate to future breeding attempts (Trivers 1972). Conflict can thus arise over the amount of care each sex provides in monogamous species. Theory predicts that biparental care is evolutionarily stable when reduced care by one parent leads to increased care in the other, but not so much that it completely compensates for the reduction, a pattern which is supported by experimental data (Harrison et al. 2009). There is also conflict over the optimal reproductive strategy of each sex in relation to parental care. This is because males usually benefit from mating with many females, and getting someone else (either the female or another male) to rear his offspring. In contrast, females usually gain most from the male staying and exclusively helping her with caring. This conflict has for example led to the evolution of female behaviors that prevent males from soliciting extra-pair matings, such as showing high levels of aggression to rival females, or to males when they exhibit display behaviors (Arnqvist and Rowe 2005).

## Sexually Antagonistic Coevolution

One important consequence of sexual conflict is that any adaptation that moves a shared trait or outcome closer to the fitness optima of one sex necessarily moves it away from the fitness optima of the other. This leads to strong selection on the other sex to resist or counteract such change. This results in a process called sexually antagonistic coevolution (SAC), whereby males and females are locked in an evolutionary “arms race,” with adaptations which increase fitness in one sex being countered by adaptations in the other (Parker 1979; Arnqvist and Rowe 2005). SAC can be distinguished from other forms of coevolution (such as the Fisher runaway process) by the fact that it is driven directly by a reduction in fitness in the opposite sex. However, SAC has been historically difficult to detect. This is because during conflict selection will strongly favor counter-adaptations, which should therefore evolve rapidly. This means that in most species, even those characterized by strong sexual antagonism, males and females should be at a fitness equilibrium, with the fitness costs of conflict essentially hidden from view (Arnqvist and Rowe 2002, 2005). However, this problem can be overcome by considering male and female traits simultaneously, allowing signs of SAC to be detected when there is a relative imbalance in male and female trait expression (Arnqvist and Rowe 2002; Dougherty et al. 2017). SAC has the potential to generate rapid phenotypic divergence, and has been suggested to have driven the evolution of elaborate behavioral and anatomical traits in a range of species.

## Conclusion

The development of the theory of sexual conflict in the 1970s revolutionized our understanding of how males and females interact with each other, and how reproductive behavior and anatomy may evolve. It is now clear that male and female interests are rarely exactly aligned, and that there may be conflict between the sexes at almost all stages of reproduction. Only by recognizing the presence

of conflict can we understand the evolution of a variety of male and female behaviors, including mate choice, polyandry, and parental care. More broadly, this recognition of the importance of conflict has required a change in perspective when thinking about sexual interactions. Reproduction is now more rightly seen as a careful negotiation between two independent and self-interested parties, rather than as a completely cooperative endeavor.

## Cross-References

- [Promiscuity](#)
- [Sneaky Copulator](#)

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## Sexual Cannibalism

- [Mate Provisioning](#)

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## Sexual Classification

- [Sexual Identification](#)

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## Sexual Climax

- [Upsuck Hypothesis](#)

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## Sexual Coercion

- [Forced Copulation](#)

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## Sexual Conflict

- [Sexual Antagonism Hypothesis](#)

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## Sexual Dimorphism

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## Synonyms

[Gender differences](#); [Intersexual differences](#)

## Definition

Complex of differences in body size (sexual size dimorphism, SSD), shape, traits, color, and parasitic load between males and females of the same species.

## Introduction

Sexual dimorphism has been the subject of wonder and scientific studies for centuries, being present in most animal species since prehistoric times. According to Aristotle (fourth century BC), differences in the semen temperature at the time of copulation resulted in sexual dimorphism, with hot semen generating males and cold semen generating females. In the *Historia Animalium* (IV, 11), Aristotle reported that in all the species where differences between males and females occur, nature has clearly differentiated the character of females from that of males. Aristotle claimed that females are less muscular, have less sturdy joints and finer hair, moist flesh, thinner legs, and more delicate feet with respect to males, and their voice is higher-pitched. As to bones, Aristotle stated that females have smaller skulls, tighter faces, thinner necks, weaker chests, and minute femurs. Differences in morphology are associated with different behavior, from which Aristotle derives a judgment on the inferiority of the females compared to males. This idea of sexual dimorphism promoting the superiority of males has been kept throughout ancient times and the Middle Ages at least. In modern times, Charles Darwin suggested that sexual dimorphism may result from sexual selection when individuals of one sex compete for access to members of the other sex (Darwin 1871/1958). In *The Descent of Man*, he exposed the theory of sexual selection, to explain the evolution of secondary sexual characters (e.g., weaponry, ornamentation), commonly developed in male vertebrates, whereas rare in females. These characters do not increase survival probabilities but have been evolved to intrasexually compete for reproduction. This evolutionary process was called “sexual selection” (Darwin 1871/1958). The degree of

sexual dimorphism in structures and coloration is strictly related to sexual selection (Ralls 1977). Color differences might be so marked that first taxonomists classified as different taxa widely dimorphic species, e.g., the mallard *Anas platyrhynchos*. Sexual dimorphism may also occur for body size. After Darwin, a plethora of research works has confirmed the evolution of secondary sexual characters in males, whereas attention towards mechanisms triggering the evolution of secondary characters in females has been only recently developed (Clutton-Brock 2009).

### Anisogamy and the Molecular Development of Sexual Dimorphism

Physiological and behavioral differences between males and females depend on the different sizes and shapes of gametes, i.e., “anisogamy,” which occur to optimize individual fecundity. Anisogamy is a basic concept within the topic of sexual dimorphism, and it may explain phenotypic differences between sexes. Usually, females rear the offspring and have a limited reproductive period with respect to males, thus representing a limiting factor in the reproductive success rate of males in a species (Fritzsche and Arnqvist 2013). According to the Bateman’s principle, males and females should select for different traits in partners, which therefore should develop intersexual, species-specific phenotypic differences over many generations (Fritzsche and Arnqvist 2013). The concept of monogamy implies exclusivity in mating, i.e., one male and one female will mate only with each other. In monogamous species, both parents participate in parental cares (Trivers 1972; Clutton-Brock and Vincent 1991) and monogamous species are often sexually monomorphic (Kleiman 1977; Mori and Lovari 2014). By contrast, in most dimorphic species (i.e., polygynous or polyandrous), both genders select mates according to the desirable traits of the available phenotypes of potential mates (Fritzsche and Arnqvist 2013). Sexual dimorphism is not restricted to the genital tract and secondary structures but it affects many structures and functions not directly concerned with reproduction. Sexual

dimorphism is known to be regulated by genes located in sexual chromosomes (Haqq and Donahoe 1998). Most differences are observed on adult individuals and are linked to the production of sex hormones involved in growth, metabolism, endocrine activity, life expectancy, and behavior (Glucksmann 1974). As to body size, female-biased SSD is the common pattern in invertebrates and cold-blooded vertebrates, whereas males are the larger sex in most mammals.

### Sexual Dimorphism in Invertebrates

Females are the larger sex in most invertebrates, since often they take longer to develop in respect to males; selection implies a positive correlation between female size, fecundity, and egg production. This correlation has been proposed to be the major force leading to female-biased SSD.

SSD is common among Echiurid worms (e.g., *Bonellia viridis*), where dwarf vagile males show planktonic behavior to reach large, sedentary females (Vollrath 1998). In most free-living nematodes, sexual dimorphism is not evident, but, in some parasitic groups, females are larger than males, to produce more progeny and to facilitate reproduction to small, vagile male. Cyst and root-knot nematodes exhibit the most marked sexual dimorphism, with roundish females and vermiform males (e.g., *Globodera* spp.).

Sexual dimorphism is rare among mollusks. By contrast, in argonaut cephalopods *Argonauta* spp., external sexual dimorphism is marked, with males reaching only 1 cm in size, and females larger and secreting a fragile laterally compressed shell (Vollrath 1998).

SSD is common in Arachnida, with males smaller than females. Selection for small male size in Arachnida is mainly influenced by sexual cannibalism and differential mortality rates (Vollrath 1998; Prenter et al. 1999). Many males of Salticidae have bright colors, elaborate ornamentation, and show sexual color dimorphism: sexual dimorphism in ultraviolet perception also occurs.

Among Crustacea, mate-guarding males of some amphipods develop structures for fighting,

absent in females. Sexually dimorphic appendages and structures engaged in reproduction are present in male copepods. In some decapods, females have larger abdomen for egg brooding, and males have larger carapaces and more developed appendices (e.g., chelae), also involved in the intrasexual competition for mating (e.g., Stein 1976). For instance, males of *Uca* spp. have one large chela used for mating displays, sound production, and intraspecific aggression.

Myriapoda are poorly studied for sexual size dimorphism, although sexual differences are known in body size of over half known taxa (Cooper 2014).

Sexual dimorphism occurs in most insect species, with female-biased SSD being predominant (e.g., Coleoptera, Odonata, Orthoptera, Phasmatodea). Often, females develop through a higher number of instars than males.

Coleoptera represent the greatest number and diversity of sexually dimorphic insects. Sexual dimorphism ranges from indistinguishable to differential enormous size and shape (Kawano 2006).

Conspicuously dimorphic species show highly developed male traits such as horns (Scarabaeidae: Dynastini, usually confined to the largest males), mandibles (Lucanidae; Cerambycidae), and tibiae (Scarabaeidae: Euchirinae) (Kawano 2006). These structures are used as weapons for intrasexual aggression and for mating purposes.

In Diptera, sexual dimorphism is not so evident as in Coleoptera, but wing length is greater for highly mobile females. Sexual dimorphism in the compound eyes reaches extreme levels in Bibionidae family, with males having larger eyes to detect and catch females on the wing. In mosquitoes and moths, males have plumed antennae to intercept the female pheromones. Butterflies (Lepidoptera) show a variety of sexual dimorphism, including SSD and color dimorphism, with males often brighter and smaller than females (Rutowski 1997).

## Sexual Dimorphism in Vertebrates

Sexual selection has been considered by postmodern and contemporary scientists as a fundamental

but insufficient factor by itself to explain sexual dimorphism in vertebrates (Clutton-Brock and Vincent 1991). Mating system, parental investment, diet, habitat selection, reproductive success, and population density have also been reported to be pivotal factors shaping morphological differences between males and females of a species (Ralls 1977; Hedrick and Temeles 1989).

*Chondrichthyes and Osteichthyes.* In sharks, a female-biased SSD has been observed in many species, with individuals reaching larger sizes at the highest latitudes. Differences in habitat selection and spatial behavior have also been reported (Mucientes et al. 2009). Cephalic bulge of *Sphyrna tiburo* and elongated intermittent organs observed in similar species have been developed for intrasexual competition. Dental sexual dimorphism is well documented in many Batoidae, showing a stable molariform morphology in females and a periodic shift in male dentition to a recurved cuspidate form during the breeding season. A similar form of dimorphism has been described for dogfish. This is due to the fact that these species usually bite during the courtship; sharp teeth provide males with an increased fitness potential and reproductive success. Among Osteichthyes, SSD is very widespread; males are usually smaller than females, except for those species where males fight for reproduction and participate in offspring care. Highly polygynous species shows males larger up to 60 times a female, or possessing longer fins; larger males may mate with a higher number of females. In Osteichthyes, large males also inhibit the growth of females and control environmental resources. Ornamentation in males or females is present only in few species and directly linked to complex courtship behavior and sexual selection (Amundsen and Forsgren 2001).

*Amphibians.* In Amphibians, females usually attain larger body sizes than males, to increase their fecundity and because males usually do not live enough to reach large sizes (Shine 1979). Furthermore, smaller males are agile and may reach females easier than large ones. Males are larger only in those species where access to reproduction is mediated by intrasexual competition, as females prefer to mate with large males (Howard

1978). In these last cases, Anuran males also may develop spines and tusks (Shine 1979). Furthermore, vocalizations used by male frogs to call for females are pivotal for reproductive success in frogs and toads (Shine 1979). Among Urodeles, the dorsal crest of crested newts *Triturus* spp. is a sexually selected trait evolved in correlation with a complex courtship behavior.

**Reptiles.** Polygyny has been observed in a great number of reptile species, and polyandry is also common even if it may have been underestimated (Cox et al. 2007). Dimorphic colorations and ornaments have been observed in lizards, as well as sex-related behavior. Sexual-size dimorphism is very common among reptiles (Cox et al. 2007). In lizards and crocodiles, it is mainly male-biased (with males exceeding females by up to 50% in length), whereas in snakes and turtles it is always female-biased (with males exceeding females by over 50% in length), with the exception of all the viperids, many elapids and colubrids, as well as of testudinids (Cox et al. 2007). Across reptiles, sexual dimorphism seems to decrease with increasing latitude (Cox et al. 2007). Evolution of sexual dimorphism in reptiles may have been promoted by sexual selection for large and bright-colored males, fecundity selection for large females, as well as by natural selection to reduce resource competition (Cox et al. 2007).

**Birds.** Sexual dimorphism is widespread among birds and it can be shown in plumage, voice, or size differences. Plumage and voice dimorphisms are related with cryptic female choice, whereas size dimorphism is related to intrasexual competition and mating systems. Plumage dimorphism is associated with mating system, being much more present in polygynous and promiscuous species. In those species, males show often bright plumages or ornamentations (e.g., long tails, caruncles). Bright plumages are related to a good health status and a high fitness; therefore, bright males are selected by females for reproduction (Dunn et al. 2001). Despite being highly visible to predators, the cost of natural selection is still lower than the benefits by sexual selection in colorful males. In polyandrous species (e.g., Charadriidae and

Jacaniidae), females are larger, brighter, or richer in ornaments, as they compete for breeding opportunities (Clutton-Brock 2009). Differences in plumage may reflect differences in behavior: for instance, females of eclectus parrots *Eclectus roratus* are bright red, whereas males are green as they search for food in the canopy and need to be camouflaged to escape from predators. Monogamous species may show SSD, mostly related to testes masses resulting in sperm competition (Dunn et al. 2001). Where sexual-size dimorphism occurs, it is mainly male-biased, with the exception of raptor birds, skuas, and hummingbirds, where females are larger. Larger males are better competitors than smaller ones and produce successful offspring (Dunn et al. 2001): they also better cope with migration and thus have a higher fitness and reproductive success. In raptors, monogamy occurs and both parents take care of the offspring; therefore, intrasexual male-male competition should not be required. While females lay eggs and take care of *pulli*, males have to search for food, thus being advantaged in being smaller to move among dense vegetation.

**Mammals.** Over 94.5% of mammalian species are polygynous (Kleiman 1977), with males competing for females using antlers (e.g., in cervids), horns (e.g., in bovids), and canine teeth (e.g., in carnivores, suids, musk deer, and baboons), and investing little in offspring (Ralls 1977). SSD is the commonest form of sexual dimorphism among mammals (observed in over 4000 living species: Ralls 1977). In most cases (about 85%), male mammals show a larger body size with respect to females (in carnivores and ungulates), which may be the result of intrasexual competition (Ralls 1977). This is primed by testosterone production, which promotes body growth (Glucksmann 1974). Female-female competition for males and polyandry are uncommon among mammals (Clutton-Brock 2007). Thus, females are rarely the largest sex (Ralls 1976, 1977), although large females may produce larger litters and can also better defend offspring from cannibalistic males, which explains why they are the larger sex in some species (Ralls 1976; Clutton-Brock 2009).

Besides selection for a larger body size, weapons and body size itself can be emphasized through the use of attention-guiding adaptations (e.g., contrasting colors; presence of a ruff, a mane, or a beard; horns and antlers), which thus become secondary sexual characters, also used in sexual selection.

The lion *Panthera leo* shows an association between coat color, dominance, and reproductive success: dark maned males are dominant and more attractive to females than those with a lighter colored mane (West and Packer 2002). In the hot temperatures of African savannah, mane color may work as a honest signal of physical vigor, as dark manes attract solar radiation thus making these males suffer higher surface temperatures and other costs, which implies a greater stamina.

On the other hand, the high altitude, mountain-dwelling golden-ruffed Himalayan tahr *Hemitragus jemlahicus* males are not only dominant over dark-ruffed ones, but they also monopolize nearly 90% of copulations (Lovari et al. 2009), which suggests an inverse mechanism to reach the same scope: reproductive success of the fittest.

## Sexual Dimorphism in Humans and Other Primates

In spite of poor information on determinants of sexual dimorphism in the second half of the nineteenth century, Charles Darwin developed a few insights on the effects of sexual selection on the evolution of dimorphism in humans. These insights are still valid and have been supported with new evidence.

Among most primates, competition between males to access oestrus females is usually intense, which tends to favor selection towards male larger size and distinctive color patterns/body structures in direct and indirect forms of aggression. This is most apparent with polygynous species, such as the gorilla and the baboons, as well as with promiscuous ones, as the chimpanzees. A slightly larger SSD and different body morphology may also be recognized in primates with multi-male/multi-female mating systems.

There are a few primate species which are normally monogamous (obligate monogamy, i.e., depending on dispersion pattern and quality of main food resources which make it impossible for a male to defend a territory larger than one sufficient to host only one female with offspring), for example, gibbons and owl monkeys. These monogamous species can become bigamous when/where resources are abundant and not so dispersed; thus, because of that, their territories can shrink to a defendable size and still contain enough food for an additional female with offspring. These monogamous species show very little sexual dimorphism, if any.

*Homo sapiens* shows an adult male-to-female body weight of about 1.1–1.2; on average, males are taller than females, with a ratio of 1.06; they are also more muscular, have larger heart and lungs, a greater number of red cells in blood, and a beard (Dixon 2009). Also, males with a broad chest and shoulders, narrow hips, and a muscular torso tend to be considered attractive partners by females, so that sexual selection comes into play. Conversely, females invest more in the production and storage of fat, mainly deposited around buttocks, hips, thighs, and breast, as a result of estrogen action, when they become mature reproductively (Pond 1998). In fact, fat reserves are crucial for reproduction and it makes sense their positive selection in evolutionary terms, as they are honest signals of reproductive potential. There are quite a few other signs of sexual dimorphism in *Homo sapiens*, relevant to skin color, craniofacial traits, and voice pitch, some of them dependent on differential hormone actions during development. All these features make the human species a remarkably dimorphic one.

Sexual dimorphism in cranial and facial features of the earliest australopithecines was quite strong, remaining little changed in *Homo habilis*. Conversely, it decreased in *Homo erectus* and *Homo neanderthalensis*, while still remaining well above the modern human range, which shows a reduction of sexual dimorphism perhaps because of convergence in the requirements of male and female roles (Freyer and Wolpoff 1985). Most likely, *Homo sapiens* evolved from a primarily



polygynous – thus, strongly sexually dimorphic – nonhuman primate precursor, with the earliest members of the genus *Homo* to some degree polygynous (Dixon 2009).

## Cross-References

- Charles Darwin
- Competition
- Cryptic Mate Choice
- Female Choice
- Female Defense Polygyny
- Intersexual Selection
- Polyandry
- Polygamy
- Polygyny Threshold Model
- Promiscuity
- Reproductive System
- Sex Differences
- Sexual Selection
- Sperm Competition

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## Sexual Identification

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### Synonyms

[Sex check](#); [Sexing](#); [Sexual classification](#)

### Definition

Sexual identification allows the classification of animals as males, females, or hermaphrodites and the intersex condition and can be performed in a simplified way for species with apparent sexual organs and/or marked differences between the sexes, known as sexual dimorphism, or through specific sexing methods for species that do not have such differences.

### Description

Identifying sex in animals may seem, at first, a simple and straightforward task. In fact, some species have apparent sexual organs or marked morphological characteristics, a condition known as sexual dimorphism, which makes visual distinction between the sexes simple. On the contrary, there are species in which males and females present extremely similar external characteristics, so no significant differences between the sexes can be perceived, making the application of

sexing methods necessary for sexual identification.

Sexual dimorphism occurs in many groups of living beings: protists, plants, and animals. The function of these differences is usually related to the reproductive process; the different characteristics are used to conquer or to fight for a partner.

A difference in size between the sexes is the prevailing characteristic in the majority of animals that show sexual dimorphism (Blanckenhorn 2000). Ornamentation is another common type of dimorphism and is often observed in many species of birds and reptiles (Johnsen et al. 2003). In most species, sexual dimorphism becomes more evident as organisms grow, which makes sexual identification difficult in the early stages of development. In birds, which have internal reproductive organs, confusion in defining the sex of young individuals is common.

Most fish species have a well-defined pattern of sexual development as female or male, which characterizes gonochoristic species, although a small fraction of species is hermaphroditic. Recognizing sex in most species of teleost fish is a difficult task, and to facilitate the sexing process, it must be performed during the reproductive period.

Sexual dimorphism is also present in fish, but in most instances, it is expressed only during the reproductive period. Species that exhibit transient dimorphism develop forms of sexual attraction, such as protuberances, color change of the scales, and emission of sounds, during the period of reproduction only. However, permanent dimorphism evidences, such as differences in size, differences between the sexes at sexual maturity.

The biological process that determines the development of sexual characteristics of an organism is called sexual determination. Throughout the evolution of the species, several mechanisms of determination and regulation of sexual development have been generated, creating a complex system of sexual determination. In most cases, sex determination is genetic, through sex chromosomes whose action is complemented by a wide variety of regulatory mechanisms. In addition, some species have a chromosomal basis involving both monogenic and polygenic systems, located in the autosomal chromosomes and in the sex

chromosomes and regulated by different genetic and/or environmental factors.

The various mechanisms of sex determination began to be elucidated after 1930, through studies that identified different models involving sex chromosomes. These studies have shown that most mechanisms are genetic, involving sex chromosomes of the XY, XO, ZW, and ZO systems. In some cases, sex may be determined by haploid-diploid systems or by environmental and/or social variables, such as the surrounding temperature or the dominance of males or females in certain species. Usually in animals, the distinction between the sexes occurs through chromosomal differences, with one sex presenting two distinct sex chromosomes (heterogametic) that produce two types of different gametes and the other sex presenting two of the same sexual chromosomes (homogametic), which produce a single type of gamete.

In insects, dimorphism in the sex chromosomes can be cytologically distinguished. In the order Lepidoptera, which comprises all the insects popularly known as butterflies and moths, the sex chromosomes are designated as W and Z, with the W chromosome associated with female characteristics. The influence of temperature is crucial in the determination of sex in some species of this order, favoring the generation of a specific sex according to the available environmental resources, which increases the probability of reproduction.

In *Drosophila melanogaster* (order Diptera), a highly studied laboratory model, development as female or male is related to a change in a so-called lethal sex gene (*Sxl*) in response to the balance between the number of sex chromosomes X (female sex) and the number of autosomal chromosomes (male sex). In this case, the Y chromosome present in the males does not influence the sex determination. Depending on the balance between these chromosomes, sterile male animals (metamales), intersex animals (animals with male and female characteristics), or female animals with developmental problems (metafemales) may occur (Manolakou et al. 2006).

In other insects, such as bees and ants, the haploid-diploid system is seen, in which the

male is haploid ( $n$ ) and the female is diploid ( $2n$ ). Males, generated from unfertilized eggs (parthenogenesis), are called drones and have only one chromosome of maternal origin. Females are heterogametic, originating from an ovum fertilized by a spermatozoon.

In reptiles (order Squamata), several patterns of sexual determination have been found. The snakes present a ZZ/ZW pattern of sex chromosomes and lizards have a ZZ/ZW or XX/XY system. In contrast, there are species of turtles and crocodiles that do not have distinct sex chromosomes or genes related to sex determination. In these cases, the temperature of the environment during a specific period of egg incubation is preponderant in determining sex. In this process, the enzyme aromatase catalyzes the conversion of androgen hormones into estrogen, influencing the differentiation of gonads. At high temperatures, the aromatase has high activity, differentiating the gonads into ovaries, and in lower temperatures, activity is reduced, leading the gonads to differentiate into testicles.

Although in amphibians the sexual determination is genetic, both sexes are heterogametic and are not influenced by the environment or polygenic conditions. In some species, spontaneous sexual inversion occurs, which produces animals genotypically and phenotypically discordant in relation to sex. Sex chromosomes can be of type ZZ/ZW or XX/XY.

In birds, the Z and W chromosomes determine sex, with females being heterogametic (ZW) and the males homogametic (ZZ). The Z chromosome has a uniform size in all species, but the W chromosome varies in size in most of them. Only in the ratite birds (Struthioniphormes), the sexual chromosomes are morphologically similar to the autosomes, with little difference in size.

Fish exhibit a wide variety of mechanisms of sexual determination and patterns of sexual differentiation. In many species, the determination of sex depends on a chromosomal basis that involves monogenic and polygenic systems located in the autosomal and sexual chromosomes, in addition to being influenced by different environmental factors. In fish, the genotype can affect the

differentiation to testis or ovary, termed Genotypic Sex Determination (GSD), with or without the participation of chromosomes in the definition of each sex (ZZ in males and ZW in females or XY in males and XX in females). Environmental factors, including photoperiod, social environment, and temperature, may also influence sex determination in some species of fish, for which two terms with equivalent meaning are also used: environmental sex determination (ESD) and temperature-dependent sex determination (TSD).

In placental mammal species, the females usually have XX sexual chromosomes, whereas males present XY. The marsupials show the smallest Y chromosome among mammals, but testicular formation does not control the remainder of the sexual differentiation, because the formation of the scrotum and the mammary glands occurs before gonadal differentiation and is controlled by genes located on the X chromosome.

Due to the complex systems of sexual determination and differentiation in animals and to the absence and/or late presence of sexual dimorphism in many species, different methods have been developed for the identification of sex. The emergence and improvement of these methods of sexing are linked to the importance of identifying sex in certain situations, that is, advancements tend to occur proportional to the environmental and/or economic interest involved.

Sexing birds is difficult because at least half of bird species do not show sexual dimorphism and when it is present it is usually very subtle, occurring only at sexual maturity. The sexing of the true parrot (*Amazona aestiva*), a bird that does not present sexual dimorphism, can be performed by pubic palpation. This method requires experience to perceive the separation between the bones of the pubis, where a greater spacing may indicate the egg passageway. However, other, more accurate, methods are also used, such as the analysis of sex chromosomes, endoscopy (an invasive method requiring sedation), and hormonal analysis (levels vary according to sex).

The most precise methods for sexual identification are genetic ones, based on the application

of modern techniques of molecular biology. These involve the direct analysis of genetic variations and can be performed on chromosomes or on DNA and RNA sequences.

The best-known methods involve the visualization of the sex chromosomes from the karyotype, the set of chromosomes of an organism, with cytogenetic techniques that allow visualization during cell division through conventional staining such as giemsa or hematoxylin/eosin. In these methods, the objective is to visualize the chromosomal pair responsible for determining the genetic sex, and due to their precision, they have been used to test the accuracy of other methods of sexing.

Another way to perform sexing is to detect a Y chromosome-specific DNA sequence after amplification using the polymerase chain reaction (PCR) technique. Sexing by the PCR technique can be applied to various tissues or cells and, as the genetic sex is determined by the presence of the Y chromosome in mammals, the detection of a specific gene from this chromosome is the basis for this technique. Several such genes have been described, of which the SRY (sex-determining region Y) is best known as a testicular differentiation factor (Bronwyn and Andrew 2002).

In birds, the sex chromosomes Z and W have the genes CHD-Z and CHD-W (CHD: chromohelicase-DNA-binding), respectively, and through the PCR technique, it is possible to perform sexing by gene detection.

In fish, research into the genetic identification of sex uses homology to genes involved with sexual determination found in other species. The genes involved in the process of sexual development can be classified into functional groups, with genes involved in the development of the bipotential gonad and genes involved in determining and differentiating the sex of males or females.

Measuring levels of steroid hormones has also been investigated as a method of sexing in fish and has the advantage of being a less invasive technique when compared with laparoscopy or gonadal biopsy. The measurement of these steroids is performed with great precision at the plasma level, mainly through enzyme-linked

immunosorbent assay (ELISA) or radioimmunoassay (RIA), which identify the variations of sexual steroids according to each sex.

## Cross-References

- ▶ [Autosome](#)
- ▶ [Chromosomes](#)
- ▶ [DNA](#)
- ▶ [DNA Marker](#)
- ▶ [Endocrine System](#)
- ▶ [Gene Expression](#)
- ▶ [Gene Map](#)
- ▶ [Hermaphrodite](#)
- ▶ [Heterogametic](#)
- ▶ [Homogametic](#)
- ▶ [Sex Role Reversal](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Sexual Selection](#)

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## Sexual Infidelity

- ▶ [Cuckoldry](#)

## Sexual Intercourse

- ▶ [Intromission](#)

## Sexual Maturity

- ▶ [Insect Locomotion](#)
- ▶ [Puberty](#)

## Sexual Reproduction

- ▶ [Anisogamy](#)

## Sexual Selection

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Sexual selection is an aspect of natural selection specifically acting on an organism's ability to obtain a mate, to engage in a successful copulation with a mate (intersexual selection), or to compete with members of their own sex for access to members of the opposite sex (intrasexual selection). This selective preference is often manifested and most visible in the form of enhanced physiological characteristics within the competing sex and may take the form of heightened vigor, increased attractiveness, or in the intensification of offensive physiological adaptations. Similarly, the selective force can also act in a much more subtle manner, affecting gametal development and competition. However, the ultimate direction of the selective force is to improve the competitiveness of an individual and improve its probability in securing a mate and passing on its genes to the next generation. Much like in the case of natural selection, sexual selection also requires variation at the level of the gene, with some of the genetic variation ensuring advantages for the individual organism that possesses them. Crucially, sexual selection only acts after the animals have entered the age of reproduction and are sexually mature.



## Historical Development of the Concept of Sexual Selection

### Charles Darwin and Alfred Russel Wallace

The concept of sexual selection was proposed by Charles Darwin in his publication “*On the Origin of Species by Natural Selection* (Darwin 1859) and further developed in *The Descent of Man, and Selection in Relation to Sex* (Darwin 1871). Darwin saw in sexual selection an explanation for the evolution of nonadaptive characteristics that only seemed to facilitate organisms’ reproductive success, often at the expense of their survival. He believed this type of selection depended on the struggle between the competing sexes (most often the males) for access to the choosing sex (most often the females). Darwin identified two distinct scenarios: one in which the males aim to drive away or kill their immediate rivals and the other in which they act in such a manner as to win over the females and eventually copulate with them. In the first scenario, the successful male is granted access to the female or females, while in the second instance, the female has an active role in selecting the mate.

Darwin noted that sexes differ not only in their primary sexual characteristics – their reproductive organs – but also in the secondary sexual characteristics. Males often possess features that help with securing a mate and facilitate the act of reproduction, while females possess features that help with the nourishment and protection of the offspring. In addition to these traits, Darwin also recognized features that are seemingly independent of the primary sexual organs but that must play an important role in sexual selection – body size (and in some species of insects – body structure), strength, ornamentation, and coloring, to name a few examples.

If the sexes differ in their “habits of life,” morphological differences are a result of sexual selection. If their habits do not differ, the more developed organs most often aid the intrasexual competition, giving one organism (most often a male) an advantage over another.

In the majority of species, male individuals mature observably faster than female individuals. The reason for this, Darwin wrote, could be in the

morphological and developmental differences of the sex cells – females are much larger and require not only more time but also a greater nutrition in order to develop. Males are also more eager to seek a mate, with the preparations for this endeavor starting well before the potential mates are even available. For example, the males of many migratory species arrive early to established breeding areas, thus ensuring sufficient time for intrasexual competition to take place over territory and therefore over the possession of females. The secondary sexual characteristics therefore more frequently develop in males, but exceptions exist, particularly in birds. It has been suggested that in cases when the sexes resemble each other, a process of double (mutual) selection could be at play. In such a setting, both females and males would show a preference for more attractive and vigorous individuals of the opposite sex. Darwin deemed this highly improbable, since in most cases males show readiness to mate with any female. Darwin also believed that the sexual dimorphism is closely related to polygamy.

Throughout his publications, Darwin provided a diverse array of examples of secondary sexual characteristics and inferred that they had evolved as a result of sexual selection. His numerous examples and accounts of sexually reproducing species across many different animal classes range from mollusks and crustaceans to various orders of insects and vertebrates – fish, amphibians, reptiles, birds, and mammals – including humans. In the latter case, he concluded that sexual selection was likely of a much higher importance during the earlier stages of hominid evolution, even suggesting that sexual selection pressures were the likely means of the differentiation observable within the human races. In his opinion, each race has been perpetuated by the differences in preferences for particular physical features, which neither serve a purpose nor ensure any advantages (other than an increased likelihood of being selected as a mate) in daily life. In addition to the physical properties, Darwin also held sexual selection responsible for the differences in character and mental capacities. He declared men the more capable of the sexes – a bid he supported with an argument of the higher

number of men of great eminence in different areas of science and art, failing to account for the role of different socialization pressures and social expectations of women and men.

Unlike Darwin, Alfred Russel Wallace was not a firm advocate of sexual selection. He considered it improbable that variables such as the superior ornamentation of males would be enough to ensure female preference and thought the differences would have been too slight to drive such expression. Furthermore, he believed that physical competition between males would yield a different set of results than would occur from female preference. In his opinion, physical differences, such as the length of a flight feather or the hue of a bird's plumage, were typically not associated with strength and the health of an individual (Wallace 1892). In addition, Wallace considered many species to be of insufficient cognitive capacity to recognize the individual possession of aesthetic sexual preferences similar to those of humans, which, in his opinion, belong to the "spiritual nature," rather than the "animal nature."

### Ronald Fisher

One of the biologists who refuted Wallace's notion of sexual selection was the English evolutionary biologist and statistician Ronald Fisher. In his 1915 paper "The evolution of sexual preference," Fisher rejected Wallace's conclusion that animals do not show mate preferences based on their aesthetic appeal, emphasizing that their motives are unknowable to humans. He further stated that if this was the case, then the function of a species' secondary sexual characteristics, as well as their elaborate courtship displays toward potential mates, would also axiomatically remain unexplainable. Fisher then raised the question of the evolutionary origins of such "artistic faculties," if they are solely a characteristic of humans and not a facet of wider evolution (Fisher 1915). Fisher argued that animals' struggles are not confined to merely producing and rearing offspring but are also an investment in their later and prolonged success. This hypothesis places additional pressure on an individual's mate choice, as the selecting sex (most often females) needs to select a member or members of the opposite sex that are

more likely to produce viable and successful offspring. He added that mate preferences are not universal but have instead evolved in accordance with each species' unique biological requirements. Fisher also recognized three separate phases in the development of secondary sexual characteristics. Firstly, a trait must be favored by natural selection for its initial origin. Secondly, the trait may then become independent of natural selection, maintained predominantly by sexual selection. In some cases, the characteristic may even oppose the pressure imparted by natural selection and present a costly disadvantage to the individual. At this stage, the trait must greatly contribute to the individual's sexual attractiveness and further outweigh any costs and disadvantages it imparts on natural selection. In the final phase, natural selection and sexual selection balance each other out and reach a state of equilibrium, which may be eventually interrupted by the rise of other features' importance. Fisher argued that mate selection carries an even greater importance among humankind. Aesthetic appeal remains important, but it does not adequately represent "human personality," which he deemed an extremely important factor in mate choice. Fisher explains that human mate choices have comparably more long-term consequences than do the choices of many animal species. Fisher proposed that heightened intelligence has enabled humans to rise above the simple assessment of specific characteristics and allows for a more holistic and fuller appreciation and understanding of a prospective mates' value. While beauty is superficial, morality is fundamental, and according to Fisher, it is the "ultimate judgment of human value" (Fisher 1915).

In 1930, Fisher published *The Genetical Theory of Natural Selection*, wherein he combined Darwin's theory of natural selection with Mendelian genetics. Fisher rejected the idea of blending inheritance, the most widespread model of inheritance during the nineteenth century, according to which offspring inherited a blended version of their parents' traits. He argued instead in favor of particulate inheritance, which allowed for genetic variance. He proposed a principle of runaway selection (also known as Fisherian runaway),

which explains the evolution of sexually dimorphic traits appearing in exaggerated forms in males as a result of directional female choice. Building on the ideas of the importance of accounting for the offspring's probable future success, the importance of which he recognized in his 1915 paper, Fished proposed the so-called sexy son hypothesis. Herein he stated that the ideal mate, from the perception of females, is one whose genes will produce male offspring with the best chance of reproductive success. If females choose physically attractive males as mates, their offspring will more likely also be more attractive. As other females will share their preference, they will prefer their attractive sons and thus ensure their high reproductive success. The same principle holds for heritable behavioral traits.

### Angus John Bateman

The field of evolutionary biology was further advanced by the English botanist and geneticist Angus John Bateman. Bateman's main contribution to sexual selection research was his 1948 study of the common fruit fly (*Drosophila melanogaster*), inspired by Darwin's notions on sexual selection. Bateman conducted six series of experiments, for which he created multiple, isolated inbred populations comprising between three and five individuals of each sex and of varying age (Bateman 1948). Based on his results, Bateman concluded that female reproductive success (number of offspring produced) is limited by the number of the egg cells (ova) they can create. On the other hand, he concluded that male reproductive success is only restricted by the number of available females. Male reproductive success, unlike that of the females, increases with the number of mates with which they attempt copulation. Bateman proposed that these differences in reproductive success stem from the dissimilar energetic investments in the production of gametes – the production of male sex cells (sperm) is much cheaper than that of females, resulting in a more expensive investment in reproduction within females. This results in a higher sexual selection pressure being placed on males, leading to a much larger observable reproductive variance. This is known as Bateman's principle.

Although Bateman's research remains among the most cited in the field, recent replication of his experiments revealed methodological and statistical flaws and deemed his results unreliable (Snyder and Gowaty 2007). Constrained by the knowledge and technology available in the 1940s, Bateman could not account for the fact that mutations that arise from inbreeding decrease the number of mates, as well as the viability of any subsequent generations or offspring. Bateman's additional fallacy was his sole reliance on the phenotypic features in determining parentage. By considering solely the offspring exhibiting the mutations of both parents, he disregarded all the instances in which only single parent's mutation, or no mutation at all, was displayed, thus skewing his sample and biasing his results.

### Robert Trivers and John Maynard Smith

One of the most influential evolutionary scientists, an American evolutionary biologist and sociobiologist Robert Ludlow Trivers, linked sexual selection and parental investment. He proposed that sexual selection is driven not only by the sexual differences in the production of sex cells but also in the sexual differences in parental investment, with the former promoting the latter (Trivers 1972). While not all species require parental care, the reproductive success of those that do is influenced by the different contributions of each sex. The higher-investing sex (typically females) are more selective against the opposite sex (typically males), the members of which will compete for the access to the higher-investing sex. It is worth noting that neither sex is passive: both will try to exploit the other – males by their promiscuity and females by confusing paternity, for instance, by evolving a concealed ovulation (hidden estrus).

The understanding of parental investment was further advanced in the 1970s by John Maynard Smith, a British evolutionary biologist. According to Maynard Smith, the majority of species require no parental care, while among those that do invest time and resources, it is possible to categorize species into those that provide either uniparental or biparental care. In nature, uniparental care appears to be the more prevalent of the two

systems. Furthermore, in species with internal fertilization, parental care is typically maternal, while species with external fertilization usually exhibit paternal or biparental care.

## Sexual Selection and Sexual Dimorphism

Sexual dimorphism is defined as being the morphological, physiological, or behavioral difference displayed between the sexes of a single species. The direction (i.e., which species is experiencing the selective pressure) and degree to which sexual dimorphism is expressed is indicative of differential parental investment. It is believed that the development of the secondary sexual characteristics is activated and governed by the sex hormones, expressed by testosterone, estrogen, and progesterone. In a scenario where the parental care is largely provided by the female, the variance observed in male reproductive success is expected to be large as the parent female will not be available for further reproduction during the nursing period. Theoretically this then leads to increased intrasexual competition between the males for those females that remain available.

In contrast, species that exhibit biparental care display a lower degree of variance within male reproductive success. In such species, the males that provide paternal care will therefore not be able to invest their energy in trying to secure additional mates. Such species are often sexually monomorphic, with members of both sexes being phenotypically similar, and comparable in both physical appearance and behavior. In species where males are the only sex that provide parental care, the variation of female reproductive fitness is typically high, with individual females often monopolizing access to one or more males. In such instances, males become the “selecting” sex, driving sexual dimorphism in the female population and initiating the evolution of secondary sexual characteristics. In nature, sexual dimorphism is manifested in countless forms and varies enormously in extent between individual species and even between subpopulations. The degree to which sexual dimorphism is expressed is

determined by the scale of the selective pressure and therefore also the ecological and demographic variables affecting the species or population. Furthermore, the resultant dimorphism may also be dependent on the extent to which the sex hormones influence development within a species.

## Sexual Dimorphism in Body Size

The most common form of sexual dimorphism is a difference in body size. If the males of a species are larger than the females, these differences are thought to have been driven by sexual selection. Whereas in the opposite scenario, where the females of a species are larger than the males, it is assumed that the selective pressure is connected to fertility.

Most primate species (including humans) display some form of sexual dimorphism in terms of body size, which is often most visible in skeletal dimension, canine tooth size, and musculature. Males of the Old World monkeys (Cercopithecidae), such as mandrills (*Mandrillus* sp.), baboons (*Papio* sp.), and proboscis monkeys (*Nasalis larvatus*), as well as apes, such as orangutans (*Pongo* sp.) and gorillas (*Gorilla* sp.), can, in some cases, be twice as large as the females in terms of body mass (Plavcan 2004). The opposite trend, however, is observed in some of the New World monkeys (Ceboidea), such as the Callitrichidae (marmosets and tamarins) and the typically monomorphic strepsirrhines – lemurs (Lemuroidea) and lorises (Lorisoidea) (Plavcan 2004). Male skeletal structures are frequently larger and show more intense cresting of bones (e.g., in *Gorilla* sp.), a reflection of the often increased muscle mass in the sex. Similarly, male gibbons (Hylobatidae) and howler monkeys (*Alouatta* sp.) exhibit enlarged and hollow hyoid bones, an adaptation that increases the resonance and range of their vocalizations. The observable differences in canine tooth size attributed to sexual selection are primarily found in the Old World monkeys and apes (catarrhines). In some species, male canines can be more than four times larger than that of the female (Plavcan and Ruff 2008), while the opposite has been observed in mouse lemurs (*Microcebus rufus*) (Thoren et al. 2006). Canine dimorphism is more often observed in the

maxillary canines (upper jaw), than in the mandibular canines (lower jaw), and it is believed to be a result of male intrasexual competition.

In invertebrates, body size dimorphism was found to be correlated with cannibalism in several families of spiders (Araneae) and praying mantises (Mantodea), although food availability and abundance also play an important role. In both groups, females are typically much larger than males. Males tend to show a preference for bigger females, who are not only more fertile but also less likely to eat them. In response to the females' cannibalistic tendencies, males of some wolf spider species (Lycosidae) have evolved anti-cannibalistic behavioral strategies, such as binding the females with silk or presenting the female with a "nuptial gift" (Wilder and Rypstra 2008). This behavior is a characteristic of many insect groups. In butterflies, many species that present "nuptial gifts" are polyandrous (females obtaining two or more males), and male/female ratio was found to increase with the degree of polyandry and gift size (Leimar et al. 1994). The majority of butterfly taxa show female-biased body size dimorphism.

The same pattern is essentially true for the majority of fish, with the general exception being that of species which exhibit intrasexual male combat or engage in male paternal care (Fairbairn 2013). For example, males of one species of cichlid (*Lamprologus callipterus*) in Lake Tanganyika can be as many as 60 times larger than the females (Ota et al. 2010). A further example of extreme sexual dimorphism can be found in the anglerfish (Lophiiformes), where small males exhibit sexual parasitism, becoming permanently attached and eventually absorbed into the much larger females, providing only sperm (Pietsch 2005).

### **Sexual Dimorphism in Color and Ornamentation: Sexual Dichromatism**

Sexual dichromatism is a form of sexual dimorphism where the males and females of a species display differences in color and ornamentation. This characteristic is highly prevalent among birds, amphibians, reptiles, and butterflies. An obvious example that illustrates sexual

dichromatism effectively is the different plumages observed between the two sexes of the Common Peafowl (*Pavo cristatus*). While the males' tails are long, ornamented, vibrant, and iridescently colored, female plumage is typically colored dull gray and brown. Such dramatic dimorphism indicates a strong sexual selective force manifested in the male birds, being driven by female mate selection. Importantly, to have reached such extreme proportions, the selective force present within the *Pavo* genus is likely to have been consistent in direction over a prolonged period of evolutionary time. In order for sexual selection to reach such intense dimensions, the selective force must be great, and the selective pressure must endure for a protracted period of time.

Sexually dichromatic features are considered honest signals – advertising information about an individual's fitness in an obvious and unmistakable manner. However, such conspicuous announcements carry many survival costs and can often increase an individual's visibility to predators or decrease their agility. The selective harvesting of African elephants for ivory provides a recent example, with individual bulls with the largest tusks being selectively targeted and killed for a larger economic reward. Such costly investment in sexually derived traits therefore often acts as a handicap for the individual animals. According to the handicap principle, proposed in 1975 by the Israeli biologist Amotz Zahavi, reliable signals that are highly conspicuous and undisguisable must always be costly to the individual. Such visible and often flamboyant characteristics indicate to their conspecifics that their fitness is so superior that they are able to afford to expend their resources in a way that individuals of lower quality would not be able to (Zahavi 1975).

Although lowering the individual bearer's survival probability, the long and elaborate tails of male peafowl carry worthwhile advantages, with males with more splendid tails being preferentially selected as mates. Significantly, male offspring will therefore be more likely to inherit the genes for a large and colorful tail, while any female offspring will be more likely to inherit a preference for selecting long and



colorful tails. Over a number of generations, this self-reinforcing coevolution will result in a Fisherian runaway scenario, where both the trait and the parallel preference for it become more prevalent. This is evident from the increasingly exaggerated characteristics observable in the sons and the increasingly choosier daughters in each subsequent generation. If female preference for an enhanced characteristic is strong enough to undermine natural selection, the trait will continue to exponentially increase even after becoming nonadaptive, until the costs of its expression become greater than the benefit it carries (Fisher 1999).

Sexual dichromatism is rarely found in mammals, with the exception of nonhuman primates. While most often of similar size, many species of Eulemur (Lemuroidea) show sexual dichromatism. In some species, for example, in the black lemur (*Eulemur macaco*), sexual dichromatism in pelage color is highly pronounced. Males are entirely black, while females vary from golden brown to chestnut brown, with white ear tufts. In other species, sexual differences are less discernible – for instance, the pelage of the collared brown lemur (*Eulemur collaris*) varies only slightly in color, but their heads and faces show distinct differences: females' faces are gray, while the male' faces are black and with more prominent reddish-brown cheeks (Mittermeier et al. 2010). Sexual dichromatism is particularly striking among black howler monkeys (*Alouatta pigra*), with males being completely black while females are golden brown. Similar dichromatism can be also observed in black-crested gibbons (*Nomascus concolor*): males are almost entirely black (apart from the white cheeks), while females are typically golden brown, with a black streak across their heads.

In order to accurately comprehend the implications of sexual dichromatism, it is important to consider the visual abilities of that particular species. For instance, over 90% of bird species previously considered monochromatic, showing no apparent disparity in gender coloration to the human eye, are now considered dichromatic to their conspecifics (Eaton 2005). Therefore, it is important that the full range of visual repertoire of

a species is taken into consideration before a species is declared mono- or dichromatic.

### Sexual Dimorphism in Behavior

Most sexually dimorphic behaviors are associated solely with reproduction and are believed to have evolved under sexual selection pressures. They can be divided into the following categories: courtship behavior, mating behavior, and parental care (Kelley 1988).

#### Courtship

Numerous vertebrate and invertebrate species engage in courtship displays, during which they can exhibit extravagant phenotypic features, and announce their desire to mate. Such behaviors include demonstrations of beauty and strength and are in some cases accompanied with ritualized movements (mating “dances”) and vocalizations. In the majority of species, courtship behaviors are performed by the male, with mate choice governed by the female.

Courtship has evolved under both intrasexual and intersexual selection pressures. Intersexual selection typically drives the dimorphism of courtship behaviors such as bird song or advertisement calls in frogs. Male songs are an indication of individual fitness, with the volume, duration, and complexity of the vocalization acting as a proxy to caller fitness. Many bird species are known to change or adapt their songs each season or even during the same mating season. Females of many well-studied species (birds, whales, and nonhuman primates) show a preference for more complex songs.

In conjunction with vocalization, many species employ elaborate movements or “dances.” One of the most prominent examples of this can be seen in the Australasian birds of paradise (Paradisaeidae). In one species, the Wahnes's parotia (*Parotia wahnesi*), in addition to their sexual dichromatism, males seemingly adapt their postures as to change their shape, by pushing their feathers to create a shape similar to ballerina's tutu skirt. This earned their mating “dance” the nickname “the ballerina dance.” Courtship behavior is, however, not reserved for birds alone. Male peacock spiders (*Maratus* sp.) engage

in courtship displays, which comprise raising of their iridescently colored upper abdomens and third pair of legs showing black white-tipped hairs, vibrating their peacock-like abdomens and opisthosomal flaps while moving from side to side, trying to attract females (Otto and Hill 2012).

In some species, males gather in aggregations in which they engage in competitive displays. This behavior is called lekking, and the aggregations of males are called leks. They are most prevalent in birds but can also be observed in insects, fish, amphibians, reptiles, and mammals. Females visit the leks and mate with males they choose but form no long-term bonds. Males of species with lek mating systems provide no parental care – the only resources they contribute are their genes. Although female selection is based on males' specific traits, this does not decrease species genetic diversity or lead to a runaway selection, as would be expected. This preservation of genetic variation is often referred to as the lek paradox. A possible explanation is the relatively limited amount of information males can signal during these displays. However, those signals are reliable, as they cannot be forged. According to the aforementioned handicap principle (Zahavi 1975), by selecting mates based on the quality of their secondary sexual characteristics (the state of which is reflective of individual's fitness), females increase the probability of their offspring also possessing desirably "fit" traits. In addition to physical attractiveness, sexually selected traits could signal individual's resistance to parasites (Hamilton and Zuk 1982). Parasites have often coevolved with their hosts and may influence or contribute to a population's genetic diversity. Rowe and Houle also recognized the relationship between sexually selected traits and general physical condition and proposed the theory of condition-dependent expression of male sexually selected traits. They argued that male traits are correlated with a number of genes that are involved in different aspects of physical condition, such as metabolism, nutrition, or muscular mass, and that the variation of these genes is maintained regardless of the sexual selection pressures from the female sex (Rowe and Houle 1996). Mutations and environmental effects can

further facilitate the preservation of genetic variance. According to the genic capture hypothesis, sexual selection operates on condition-dependent traits, and female selection therefore does not decrease genetic variance. Finally, it is possible that the male traits preferred by the females are not actually purposefully selected for but remain in the population due to their contribution to male overall attractiveness. This would mean that lek paradox does not really exist.

### Mating and Parental Care

The differentiation in mate acquisition by each sex is generally reflected in the species' mating system and is furthermore closely linked with parental care. In a monogamous mating system, an individual obtains and invests in a single partner. This system is often observed in species committed to biparental care and where males have relatively little chance of monopolizing more than one female. In some species, males form alliances, usually with kin, in order to maximize their reproductive success. Alliances also help to prevent other males from mating. The reproductive trade-off of these alliances is dependent on the extent to which mating is shared (as this often results in a single dominant male monopolizing the females) and the extent to which it increases individual fitness by increasing their foraging opportunities or decreasing the costs of defending a territory. This behavior is a characteristic of cetaceans (*Tursiops* sp.), lions (*Panthera leo*), and chimpanzees (*Pan troglodytes*).

In a polygamous mating system, individuals of one or both sexes obtain more than one mate during a breeding season. In polygynous systems, males mate with multiple females. The males of most polygynous species appear to have undergone a strong intersexual selection of the female-preferred traits or intrasexual selection of traits associated with male-male competition. This mating system is prevalent in species where males do not provide parental care, allowing them to monopolize more than one female. In polyandrous systems, females mate with multiple males. This rarely encountered type of mating system is characterized by a role reversal in courtship and parental care and where females compete

for males and or territories in order to attract males.

Differences in parental care are considered to be a reflection of the (previously discussed) sexual differences in the investment into the production of sex cells. Paternal care is believed to have evolved to compensate for the higher reproductive investment of the female sex. Biparental care generally results in a beneficial outcome for offspring in terms of survival, by improving the protection against predators and environmental extremes, as well as by additional food provision, and in some species the direct transfer of skills. Biparental care is observable in most bird species, with paternal contribution correlated with the equality of investment in egg incubation and food provision. Biparental care is also present in some families of amphibians and fish. Uniparental maternal care is the most common type of parental investment among the mammalian species, especially rodents, canids, and primates. An opposite case of a uniparental paternal care is typical in seahorses (*Hippocampus* sp.).

### Context-Dependent Sexual Dimorphism

It is also important to note that while some species exhibit ontogenetic sexual dimorphism – a permanent difference between males and females – others show a dynamic pattern, with sexual differences occurring only seasonally, for example, during the breeding season. Dynamic dichromatism often functions as a visual sexual indicator, particularly in species which form large breeding aggregations (e.g., frogs). In some species (e.g., the yellow toad, *Incilius luetkenii*), the dynamic dichromatism only lasts for a couple of hours (Doucet and Mennill 2010). These color differences range from subtle alteration of shade to differences in both color and pattern. The male moor frog (*Rana arvalis*), for example, is typically a reddish-brown but turns blue during the mating season. Similarly, the Malagasy frog *Boophis madagascariensis* undergoes a brief transformation to a bold yellow coloration for a short period during their explosive breeding bouts (pers. comm. Hyde Roberts, Nov 2017). Such dynamic dichromatism is also a common characteristic in many birds. For example, male red fody

(*Foudia madagascariensis*) produces a bright red plumage during the austral summer when breeding occurs. Such dramatic and dynamic sexually driven dimorphism is not restricted to dichromatism and can also occur in body size. For example, male squirrel monkeys (*Saimiri sciureus*) show an increase in body mass of up to 25% during a 2-month breeding season. This phenomenon is known as “male fattening,” particularly affecting their upper torso, shoulders, and arms, and is a product of both intra- and intersexual selection (Stone 2014).

The expression of sexual dimorphism and its elaborateness can vary within the mating season as well, depending on the context of its expression. For instance, vocalizations of big brown bat (*Eptesicus fuscus*) males are only dimorphic in a reproductive context but remain monomorphic in other social contexts (Grilliot et al. 2009).

### Sexual Conflict (Sexual Antagonistic Coevolution)

When the sexual morphology of one gender changes over time in order to counteract that of the opposite sex so as to maximize reproductive success, it is considered sexual antagonistic coevolution or sexual conflict. Numerous examples can be found in the evolution of reproductive organs. Male mating behavior of numerous insect species is detrimental to female fitness. A variety of invertebrate taxa, including fruit flies (*Drosophila* sp.) and bed bugs (*Cimex lectularius*), reproduce by means of traumatic (hypodermic) insemination. This mating practice involves the male piercing the female’s abdomen with his penis and injecting his sperm through the wound into her abdominal cavity (Siva-Jothy and Stutt 2003), despite the female having a genital tract. Males try to inseminate as many females as possible, but the more times a female is inseminated, the less likely she will be to survive, due to repeated punctures of her abdomen. In order to avoid multiple matings, females have adapted their morphology by evolving paragenital systems, such as spermathecae, which mitigate the effects of traumatic insemination. Some species

possess a spermatheca, an organ they use for receiving and storing sperm; other species have evolved a pseudospermatheca, which performs the same function. These organs allow the females to choose which sperm fertilizes their eggs. Some species (e.g., *Drosophila melanogaster*) can expel the sperm they do not need, with the males not knowing whose sperm will be dispelled.

Males of polyandrous species have evolved under the evolutionary pressure of sperm competition – a competitive process between the spermatozoa of multiple males attempting to fertilize the same egg. As a result, they have evolved adaptations that increase their reproductive success. These adaptations often include modifications of their (comparatively fast-evolving) genitalia. Some species, such as seed beetles (Chrysomelidae), have evolved spiny penises, which help them hold onto a female and enable them to quickly reach the female's reproductive tract. The females suffer injuries, which increase with the number of matings. Each mating therefore decreases the likelihood of her subsequently mating with additional males. In response, females have evolved thicker walls of their reproductive tracts and increased their immune capacity (Rönn et al. 2007). Males of various species of birds, reptiles, and mammals have developed keratinized penile spines. In Eastern red bats (*Lasiurus borealis*), the penile spines face backward, which facilitates the insertion and impedes the extraction either involuntarily or voluntarily. This is thought to facilitate sperm injection while also allowing the male and the female to stay together during the midair copulation, referred to as the in-flight locking hypothesis. Another example of male coevolution can be found in the number and motility of spermatozoa. As they are costly to produce, selection generally favors larger numbers of small, but fast, sperm cells.

In addition to the morphology of the reproductive organs and sex cells, examples of male coevolution can also be found in adult behavior. Such behaviors can be directed toward either defensive or offensive adaptations. Many species of insects, birds, lizards, and mammals have evolved a defensive behavior called mate guarding. This behavior, in which male individuals engage in

either before or after copulation, involves their attempted prevention of any other males approaching and mating with the female. Some species only practice strategic mate guarding during female's fertile period. This is particularly efficient for the males, as it allows both within-pair and extra-pair paternities. It is also beneficial for the females, as they can benefit from the physical protection from predation and harassment from other males. Sperm partitioning (males conserving their sperm supply by reducing the quantity of sperm ejected) or prolonged copulations (which increases the amount of sperm deposited in female's reproductive tract while also preventing the female from copulating with other males) is another example of a behavior associated with male coevolution.

Unlike the defensive adaptations, which decrease future sperm displacement, offensive sexual adaptations often act with the intention of displacing the previous male's sperm or limiting the other male's opportunities to reproduce. The presence of armaments facilitates offensive behaviors, and their display is often enough to deter intrasex competition. Phenotypical examples include antlers of deer (Cervidae) or stag beetles (Lucanidae), while behavioral examples include males of *Drosophila* sp. releasing seminal fluids containing toxins and pheromones that destroy the sperm of their rival predecessors. The results of sperm competition, however, often depend on female sperm choice (Birkhead 1998). A form of cryptic female choice includes non-random biases resulting from female morphology, physiology, or postcopulatory behavior. Examples include a reduction in the rate of offspring produced through a decline in egg maturation and pregnancy block (a tendency of females, mostly a characteristic of rodents to abort their pregnancies if exposed to the scent of unfamiliar males) or a decreased investment into offspring.

## Summary

Sexual selection is a special type of natural selection that was first proposed by Charles Darwin. There are two recognized mechanisms of sexual

selection: intrasexual selection (members of the same sex competing for access to the members of the opposite sex) and intersexual selection (members of one sex choosing their mates among the members of the opposite sex). Depending on the differential investments in reproduction – from the production of sex cells to parental investment – sexual selection pressures can differ greatly between the male and the female sexes. Strong sexual selection pressures result in sexually dimorphic traits, which can be manifested in either physical appearance or behavior. Both sexes seek to optimize their reproductive success; often this leads to conflict between the sexes. This evolutionary arms race has driven the evolution of sexually reproducing species.

## Cross-References

- [Charles Darwin](#)
- [Evolutionary Psychology](#)
- [Fitness](#)
- [Genotype](#)
- [Handicap Hypothesis](#)
- [Honest Signaling](#)
- [Intersexual Selection](#)
- [Intra-sexual Selection](#)
- [Natural Selection](#)
- [Parental Investment](#)
- [Postcopulatory Selection](#)
- [Phenotype](#)
- [Primates](#)
- [Robert Trivers](#)
- [Runaway Selection](#)
- [Sexual Dimorphism](#)
- [Sperm Competition](#)

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## Sexual Selection Gradient

- [Bateman Gradient](#)

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## Sexually Dimorphic Behavior

- [Sociosexual Behavior](#)

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## Shaking Palsy

- [Parkinson's Disease](#)

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## Shame and Guilt

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### Synonyms

[Compunction](#); [Contrition](#); [Culpability](#); [Humiliation](#); [Remorse](#); [Repentance](#); [Self-reproach](#)

### Definition

Shame is a feeling of reproach directed at oneself for having committed a behavior that evokes anger and/or disgust in others. Guilt is a feeling of remorse for having caused pain or other negative feelings in another.

### Introduction

Shame and guilt are considered secondary emotions along with embarrassment, jealousy, envy, and pride (Miller & Leary, 1992). Except for jealousy and envy, secondary emotions involve an evaluative component that involves reflection on how one is perceived by others (Morris et al., 2008). For example, embarrassment stems from the feeling that one has done something to encourage derision from others. Shame stems from the feeling that others are disgusted or angered by something one has done or a failure to live up to expectations. Guilt follows some transgression against moral rules pertaining to the treatment of others and the resulting negative consequences such as pain or distress for others (Keltner & Buswell, 1997). It can therefore be speculated that the experience of secondary emotions depends upon some level of theory of mind, or the attribution of emotions to others (Tangney, 1992). In support of this supposition, children with autism that experience theory of mind deficits differ from neurotypical children in their responses to narratives concerning

embarrassment, but not narratives concerning sadness or happiness (Capps et al., 1992). Theory of mind might also be necessary for experiencing vicarious emotions, such as being embarrassed on behalf of another individual. The secondary emotions likely emerge along with self-awareness and its markers, such as mirror self-recognition and the use of personal pronouns, around the age of 18 months in neurotypical human children (Lewis et al., 1989). Because there is arguably no strong evidence for self-awareness or theory of mind in nonhumans, it might be doubted that animals experience secondary emotions, such as shame and guilt (but see Bekoff, 2002).

### Adaptive Value

Secondary emotions may function to maintain social cohesion in that they provide an internalization of communal norms and rules and promote peaceful coexistence by preventing actions that cause negative emotional experiences for others (Miller & Leary, 1992). Thus, it might be expected that self-conscious emotions, such as shame and guilt, have evolved in species that live in large, complex social groups. These emotions would serve little adaptive purpose unless directing one to maintain and repair long-term social bonds in order to accrue benefits such as group protection and reproductive opportunities. Keltner and Buswell (1997) review the work on appeasement in animals, which has been suggested as an analog to embarrassment (de Waal 1986; Leary et al., 1992). They describe common features for appeasement displays across species, such as gaze aversion, downward head movements revealing the neck – resulting in an apparent size reduction, and self-touching or grooming. Such behaviors serve to reduce aggression or retaliation after a social transgression, and thus function to promote group stability and restore social functioning (Miller & Leary, 1992). The experience of self-conscious emotions may be linked to evolutionary precursors for morality, although even chimpanzees appear primarily concerned with fairness with regard to their own treatment

rather than with the fair treatment of others (Price & Brosnan, 2012).

### Research

Given the assumed dependence on other cognitive traits such as self-awareness, theory of mind, and morality, and the lack of strong evidence for these traits in nonhuman animals, it is perhaps unsurprising that there is little empirical research investigating the presence of self-conscious emotions in nonhumans. Furthermore, it is challenging to test the presence of subjective feelings in nonverbal species. For that reason, researchers must rely on observations of behaviors that have been linked to human experiences of shame and guilt in contexts where these emotions would be evoked.

Dog owners report that dogs behave as if they feel shame when they have misbehaved even before the owner encounters the evidence (Hecht et al., 2012). Horowitz (2009) experimentally demonstrated that dogs behaved as if they felt guilt or shame specifically after committing a forbidden act. Dogs either ate a food item that was forbidden or the food item was removed by experimenters out of sight of the owner. Dogs then exhibited “guilty looks” when the owner returned but the behavior could also be interpreted as anticipation of punishment following specific behaviors based on past experiences. This alternative interpretation is bolstered by the finding that dogs were more likely to display the behavior ascribed to feelings of guilt in the presence of a human that scolded them compared to one that was friendly. Furthermore, dogs that had not actually consumed the food looked guiltier than dogs for whom the experimenter had removed the food, lending credibility to the idea that dogs were fearful of retaliation rather than guilty (Horowitz, 2009). Dogs in the Hecht et al. (2012) study had also been scolded for eating the food in a baseline trial before the owners judged which dogs had eaten the forbidden food. This baseline trial also gave the owners information about how the dog behaved in similar situations (Ostojić et al., 2015). Ostojić et al. manipulated the dogs’ own

action (on which guilt should be based) as well as the evidence of their misdeed. Following Horowitz (2009), the dogs ate the food or the food was removed by the experimenter, but in both conditions, the food was either absent or replaced by the experimenter and owners were instructed to behave in a neutral rather than a scolding manner. As in Hecht et al. (2012), owners recorded whether they thought their dogs had eaten the forbidden food. In this study, owners did not report differences in dogs' guilty look across the conditions suggesting that guilt-like behaviors were not influenced by either the dogs' own behaviors or the evidence of their misdeeds (whether real or experimentally manipulated). Ostojić et al. concluded that the dogs' guilty behaviors were triggered by the owners' scolding behaviors in the previous studies, rather than by an internalized subjective experience of guilty feeling. However, they acknowledge that future studies should remove the possibility that experimenters inadvertently communicated that it was permissible to eat the food.

Researchers have asked animal caregivers to report frequencies of observed expressions of emotions in their animal companions, and the contexts in which these expressions of emotion occurred (Morris et al., 2008). Morris and colleagues found that owners reported embarrassment and shame at very low frequencies. Secondary emotions in general were most commonly attributed to dogs rather than other animals. Even with the concern that the survey report method is especially vulnerable to anthropomorphism, the low reports of secondary emotions cast further doubt that these emotions are experienced in animals as they are in humans.

## Cross-References

- [Affiliative Bond](#)
- [Attachment](#)
- [Discrimination of Emotion](#)
- [Emotional Contagion](#)
- [Empathy](#)
- [Human-Animal Interaction](#)

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## Shape

- [Morphology](#)
- [Proboscidea Morphology](#)

## Shape Perception

### ► Depth Perception

## Shaping

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## Synonyms

Chaining; Differentiation of a response; Modeling; Successive approximations

## Definition

Shaping is a technique of training used to make an animal emit a desired complex behavior through the reinforcement of segments of such behavior.

## Introduction

Within the framework of the experimental analysis of behavior, Skinner's approach was based on empirical observations of behavior, which could be measured, predicted, and controlled. By means of this surgical analysis, each segment of a complex behavior could be extrapolated and studied and hence reinforced whenever necessary. The method used to mould a response followed the operant conditioning principles, according to which the behavior is sensitive to its consequences.

While there are responses that could be spontaneously emitted by an animal (like when a hungry rat touches a lever by randomly moving in the training chamber) and that can be readily reinforced, other more complex desired behavior may not be spontaneously emitted by the animal (like for instance, if we wanted the rat to press the lever after having make a 360-degree turn on the left). In other words, the display of an elaborate

behavior may be unlikely to appear in its complete form or may not belong to the individual's repertoire (e.g., lifting a marble up with the forepaws and insert it in a tube), and therefore it will never occur spontaneously to be reinforced. In such cases, the final desired behavior can be reached by reinforcing some of the animal's spontaneous responses, at the beginning only vaguely resembling the target behavior, and then by progressively reinforcing a more complex pattern of responses that more closely approximate the final desired behavior. Specifically, small segments of the final behavior can be defined, and once a given step has been conditioned, the reinforcement is shifted to the next step and made contingent upon the following segment of behavior, until the final desired behavior is reached. By means of this shaping technique, a rare or unlikely response with a specific topography reaches a high probability to be emitted in virtue of a continual process of differential reinforcement that constructs a complex and coherent behavior out from single small variations.

Skinner (1937, p. 277) provided an instance of shaping of a rat's press-lever response. By dissecting the target behavior (i.e., lever pressing) in subsequent steps, he hypothesized the necessary separate responses in a chain that needed to be reinforced in order to obtain the final response:

1. Approach to the site of the lever
2. Lifting the nose into the air toward the lever
3. Lifting the fore-part of the body into the air
4. Touching the lever with the feet
5. Pressing the lever downward

In Skinner's view, almost all animal behavior (including human language acquisition) could be learned through this program of successive approximations (Skinner 1951), to the point that we are all gently shaped by our environment that models our habits and preferences: in a word, our culture (Skinner 1971). He masterly demonstrated this idea by training one specific lab rat, Pliny, to perform a series of behaviors none of which belonged to Pliny's repertoire. Pliny became able to pull a string to get a marble from a rack, take the marble with the forepaws, and drop it from the top of a tube (Skinner 1938, p. 340) in a fluid sequence.

## The Story of Shaping: Its Antecedents and Its Discovery

Although the use of shaping as a procedure to model complex behaviors was posited by Skinner in 1938, there is at least one antecedent use. Konrad Most, Colonel at the Royal Prussian Police Headquarters, was a pioneer in training service dogs. He synthesized the principles he adopted during training in the book *Training Dogs* (Most 1910/1954). Well before Skinner, at least 28 years earlier, Most described a procedure that parallels the shaping technique. Indeed, he claimed that the “slightest progress toward the desired behavior should be reinforced, not only with terms like ‘good boy,’ but with fondling” (p. 34) thus anticipating Skinner’s description and use of shaping.

It is also worth noticing that, when Skinner wrote about Pliny’s performance, he was probably not entirely aware of the relevance of shaping. At that time, the word “shaping” was not yet in use to indicate the training method; moreover, all behaviors shaped in lab rats before 1943 were obtained through an approach in which the experimenter was a passive observer while mechanical and electrical programmed chambers delivered reinforcers with specific contingencies. It was the physical environment that was shaping the animal’s responses.

One serendipitous event became the hallmark for shaping in Skinner’s mind, as reconstructed by Peterson (2004). Skinner was atop a flour mill with his students Keller Breland and Norman Guttman, training pigeons to guide bombs for a project related to war (Skinner 1960). In that occasion, as reported in the paper appeared in *American Psychologist* in 1958, Skinner started training the animal by hand to swipe a wooden ball; he decided to watch the animal’s responses and administer himself the reinforcers by hand, following certain approximations of behaviors. The pigeon soon started doing exactly what Skinner had in his mind (i.e., touching the ball with the beak and moving the head with a certain inclination to hit it). Skinner discovered in that exact moment how fast the process of learning could be; hence he recognized the significance of an animate social reinforcer to model a complex

behavior. After this sort of insight, he coined the term “shaping” that he introduced for the first time in 1951 and systematically used in all subsequent works, replacing concepts such as successive approximations or differentiation of a response that were used before, and exploiting the heterogeneous applications of shaping.

## The Practice of Shaping (and What It Is Not)

Keller and Marian Breland, after studying under Skinner’s supervision the operant principles to train rats and pigeons, decided to abandon the academic career to work in the field of advertising and entertainment. They developed a broad application of the behavior analysis shaping animals’ behavior for commercials, parks, and their “IQ zoo”, where animals attracted tourists with their apparent human-like behaviors (Breland and Breland 1951). The Brelands trained several different species to display very complex behaviors (as for instance, pigs to eat breakfast at a table or run the vacuum cleaner, ducks to play the piano, hamsters to trapeze-swing, and so forth) getting popular media attention for their work (Bailey and Gillaspay 2005). Although a great initial success, they soon discovered a phenomenon that they termed “instinctive drift”; after having been conditioned to a specific learned response, each animal gradually changed it drifting towards instinctual behaviors related to natural and species-specific responses to get food; such drift arose in spite of delay or preclusion of reinforcements (Breland and Breland 1961). The Brelands (1961, p. 682) provided several examples of such phenomenon and mentioned, for instance, the conditioning of “a raccoon putting money in a piggy bank” that become impossible because “the rubbing behavior became worse and worse as time went on, in spite of nonreinforcement.”

Nevertheless, the operant method to shape animals’ behavior within the context of species-specific responses was effective and was extended to marine mammals for the first time with the Brelands, who also wrote a manual to train dolphins (Breland 1955), which is still influential



even on contemporary dog-training (Pryor 2005). Indeed, one relevant aspect is that Skinner shaped responses that were part of the animal species' repertoire. For instance, in the famous video in which he trains pigeons to play ping pong, the birds are reinforced to use their natural pecking behavior against the ball to prevent it from falling down on their side; the pigeons are never reinforced to use their wings or feet to hit the ball.

In contemporary practice, trainers know that the shaping method does not proceed in a positive linear fashion; rather it includes steps that are verified and modified frequently during training so that, if a certain response needs to be fixed, previous segments of the target behavior can be reinforced again. Whenever a new approximation of behavior does not appear, it is necessary to reinforce the previous one again; if no improvement is reached and no new approximation occurs, the trainer has to reinforce again a previous complete behavior again. Hence, the trainer is actively involved in judging and reinforcing the animal's responses that cannot be easily shaped by automatic contingencies.

Trainers often use the clicker, a mechanical device emitting a distinct 'click-clack' when pushed and released, to mark the specific segment of behavior that will result in food reward (Pryor 2005). The clicker anticipates the reward acting as a secondary reinforcer in virtue of classical conditioning. Its practical advantage is that of reducing the use of food during shaping (the treat is instead provided only occasionally to avoid extinction). Note that, in principle, this holds true whatever the nature of the secondary reinforcer (Chiandetti et al. 2016) and hence the clicker should be preferred depending on other factors (i.e., dog's temperament or breed, trainer's expertise, environmental setting, possibility to timely deliver the primary reinforcer, etc.).

A novel behavior, especially in companion animals, can be elicited using other strategies that are confused with shaping by nonexperts only because food rewards are implemented to reinforce a behavior (Kaplan et al. 2002). One strategy, for instance, is modelling: the animal is coaxed to perform a behavior and then reinforced. Another strategy is luring: the animal is guided by a treat and has to follow it to

display the pattern of behaviors before getting it as a reward. These forms of learning are not shaping since the animal is not emitting spontaneous responses; rather, the animal is forced or guided by the trainer to display directly the final behavior, with no intermediate steps to the target behavior. A further method is capturing; it is waited until the animal spontaneously manifests the desired behavior, which is then rewarded. The unpredictable time necessary to observe the final target behavior by chance is exactly what is possible to avoid through shaping, as Skinner originally understood.

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Behaviorism](#)
- ▶ [Conditioning](#)
- ▶ [Contingency](#)
- ▶ [Nervous System](#)
- ▶ [Schedules of Reinforcement](#)

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Shared Ancestor

- ▶ [Last Common Ancestor](#)

Shark Locomotion

- ▶ [Chondrichthyes Locomotion](#)

Shedding

- ▶ [Molting](#)

Shift

- ▶ [Migration](#)

Shock Probe Defensive Burying

- ▶ [Defensive Burying](#)

Shock Prod Defensive Burying

- ▶ [Defensive Burying](#)

Short Interfering RNA

- ▶ [Small Interfering RNA \(siRNA\)](#)

Short Interspersed Nuclear Elements

- ▶ [Repeat Sequences](#)

Short Period Memory

- ▶ [Short-Term Memory](#)

Short Tandem Repeats

- ▶ [Simple Sequence Repeats](#)

Short Tandem Repeats (STR)

- ▶ [Microsatellite Marker](#)

Short-Term Memory

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Synonyms

[Active memory](#); [Primary memory](#); [Short period memory](#)

## Definition

It is the restricted ability for retaining a limited amount of information for active usage in the brain for a brief duration.

## Introduction

Memory is the special ability to store and retain any stimulus for future usage. It can be explicitly divided into two types depending of the duration of the stimulus: short-term (STM) and long-term memory (LTM). There are many further types of memories to be classified under these broad categories. External stimuli are stored in the form of memory by the neural circuit of the neocortex in the brain. Various models have been proposed to define the working of STM and LTM. The modal model of Atkinson and Shiffrin states that short-term memory storehouse can transfer the STM to LTM if kept for a long duration. On the other hand, the contradiction by the research of Tulving and Pearlstone denies this connection (Eduardo and Francisco 2017).

Thalamic neuronal projections serve the direct purpose of transmitting sensory information to cortical neuron circuits as suggested in various studies (e.g., Dubreuil 2019). Processing of stimuli is carried out by a larger number of neurons. Various neural model architectures are proposed to be made of cortical columns. The hippocampus is also associated with information storage in terms of STM and LTM (Bird and Burgess 2008). An initial step is performed by glutamate receptors beginning with the activation of AMPA and NMDA. NMDA plays its role in the learning exercise of memory, and AMPA serves the role in formation of memory (Izquierdo and Medina 1997). Following the cascade of events in the hippocampus, other regions like the amygdala and extrahippocampal parts are involved in memory consolidation (Izquierdo and Medina 1997).

There are two kinds of STM mechanisms identified: the recurrent connectivity where specific stimulus patterns are rebounded by specific neural activity manners and the feed forward connectivity model, which represents stimulus in pattern of delay lines. The neural architects are in serial or

parallel manner; most studied is the trees of recurrent networks (TRN) neural architect model. It has capacity limits, which serves as limitation for the model; i.e., it can depict limited sensory output representation (Dubreuil 2019).

## Neural Aspects of the Short-Term Memory

Memory is expressed either as the primary memory, i.e., short-term memory, or the long-term memory, i.e., secondary memory. Memory is stored and distributed in the form of neural circuits in the brain. The STM captures the external world depictions; i.e., audio verbal or visual aspects of stimulus and stores it in the form of neural signals patterns, which are then reproduced from the storehouse. LTM and working memory (WM) are built upon the operations of STM systems. Being fundamentally the function of cognition, it is suggested that STM activity increases with age until adulthood.

Depending upon the visual span on a stimulus, STM is created. Memory storage involves the frontal cortex functioning. It is understood that STM can be considered as the type of memory involved only when the neurons firing and cell assembly is active throughout the process. Short-term memory generated undergoes the biological pathway of post-translational modifications and can generate rezoning from pre-existing networks. Memory was understood by Craik and Lockhart as a function of storehouse (Camina and Francisco 2017). Short-term memory has further components; i.e., visual short-term memory (VSTM), verbal short-term memory (vSTM), and audio verbal short-term memory (AVSTM). VSTM has been maintained throughout various species. The visual component of STM plays a prominent role in integration of all visual aspects and its depiction (Gibson et al. 2011).

## Development of STM Capacities Across Species

Humans have evolved a cognitive and conscious memory system. Nonhuman animals may not

have the exact same abilities but show quick recognition of items. The memory span of chimpanzees has been found to be around five items. Other apes show the working memory capacity of four to five items. Similarly, non-primates have shown a memory span for four items, whereas humans have developed a memory span of seven items maximum. Humans have evolved effective retrieval systems (Manoochehri 2021). Comparative studies have shown that monkeys have lower storage capacities than humans.

Animals such as dolphins, rats, and macaques have been observed for their episodic memory and buffer system. Apes like chimpanzees are known to remember their own behavior of a short period. Chimpanzees have been seen to have the skills to create long-term memories. Additionally, they also display the retrieval mechanisms of memory (Tomonaga and Kaneko 2014).

For humans, there is a prominent role of visual STM for behavioral actions. Comparative work with pigeons has assessed comparable capacities. Although the development of storage capacities is highest in humans, similar behaviors are observed in terms of visual STM in both species. In fact, pigeons have shown evolution of a superior visual system. The neocortex layers are absent in pigeons so the representation techniques are quite simpler in them (Gibson et al. 2011).

## Types of Memory

Memory can be divided on the basis of duration (STM, LTM) and behavioral demonstration into distinct types. According to memory systems, there are two divisions, declarative (explicit) and procedural (implicit) memory. Declarative memory consists of facts and events that can be consciously retrieved and depend upon hippocampal areas. Procedural memory, in contrast, consists of skill learning, i.e., the skills we develop with practice carried in the cerebellum (Vianna et al. 2000). Apart from this, episodic memory is the memory where an individual has the memory of personally experienced events.

Working memory (WM) is defined as a stage for alteration and storage of data temporarily for

cognitive tasks. It is the memory we use to perform strategic behavior. The working memory model of Baddeley and Hitch's model suggests the buffers, visuospatial sketchpad, as a component of working memory. The main functions of this sketchpad are to form a visual spatial representation of the visual world through the eye movements. Apart from the debate over the well-defined meaning of WM, it is said to include short-term memory mechanism to carry its use accordingly, along with the attention-based aspect of WM (Cowan 2001).

In contrast, LTM is the consolidated memory that stores data of prior events permanently for a long duration. To form a long-term memory, the data has to follow a cascade of events in the hippocampal regions, particularly CA1. It takes about a maximum of 6 h to undergo the events. It has been said undoubtedly, STM is kept in LTM to undergo consolidation. STM can be preserved but no experiment has proved the same for LTM (Izquierdo and Medina 1997).

## Distinction of LTM and STM

The distinction between STM and LTM has been validated by various experiments showing important dissociations. For example, the effects of certain drugs on both are different; deficits in the LTM and STM storage and retrieval mechanisms in people with some brain injuries or lesions have also been seen to be different. Specific brain lobe damages show its associated memory impairments keeping the other memory system intact. Temporal and parietal lobe defects show STM impairments, whereas medial temporal lobe lesions show effects on LTM, keeping the STM conserved. The multistore model also represents distinctions between STM and LTM and gives separate buffer theory for LTM; hence, storage processes in LTM are separate from STM (Jonides et al. 2008). As stated earlier, apart from the experimental segregation, STM and LTM are different in duration of memory storage. The decay limits and the interference pattern are the characteristic feature of STM. Also, the capacity of STM differs from LTM (Jonides et al. 2008).

## Interactions Between LTM and STM

LTM and STM share similar neural retrieval (recall) processes. The frontal lobe plays this role in both (Jonides et al. 2008). Many imaging techniques and experiments have shown similar activities in brain regions during memory retrieval in LTM and STM. The chunk capacities of memory also somewhat establish the dependence theory between LTM and STM. It is claimed that chunks are a characteristic of LTM which helps in STM retrieval processes. Interaction in terms of neural aspects and functional aspects are studied.

Unitary model concludes that there are no separate systems for STM and LTM. Both types of memory share common temporary activation representation. These activations are studied in frontal, neocortex, and pre-frontal cortex areas.

## Activation and Retrieval Process (Mechanism)

The memory is activated when a familiar information is present, and it remains active for a particular duration of time. This familiar data can be present in the LTM for a permanent time period. The external stimuli make it easy for an individual to recall a significant data. This implies that LTM helps in retrieval process of STM. According to meta-analysis studies, prefrontal cortex regions both anterior and lateral are involved in retrieval of memory. The activation process is quite similar in both LTM and STM as seen by neuroimaging techniques (fMRI) for the prefrontal cortex. The site of activation for LTM retrieval matches with activations seen with STM retrieval stages (Jonides et al. 2008).

A rehearsal process is proposed to be an efficient retrieval mechanism and maintenance technique for WM, LTM, and STM. The effectiveness has been seen with computational modeling of WM (Oberauer 2019). Evidently, for the retrieval process, immediate response from chunks is focused at attention. Be it LTM or STM, to recall any memory, capacity limit serves as a function of attention (Cowan 2001).

## Development of STM

As studies suggest, memory formation takes place in the hippocampal regions with some processes taking place in amygdala and entorhinal cortex followed by retrieval mechanisms. Both the glutamate receptors, AMPA receptors activation, and triggering of NMDA receptors are known to initiate the process of memory formation. Some messengers like nitric oxide and carbon monoxide take up the regulation of glutamate secretory levels (Izquierdo and Medina 1997).

Short-term memory formation follows three main steps for production. The steps involve encoding, maintenance, and retrieval pathways. In the encoding process, the individual takes up the data from external world in the form of perceptions and stored data from the past. The focusing of events plays a role in cognitive storage, which is controlled by past events or capacity basis. These physical world representations are converted into cognitive focus. Maintenance is the process of preventing the stored information from decaying or forgetting mechanisms which can be caused due to any interference stimulus. Although no particular model is suggested for this activity of the brain, hypothesis of rehearsal has been indicated for maintaining the encodings. The process also includes refreshing, elaborative rehearsal and articulatory rehearsal techniques (Oberauer 2019). The brain cortex regions play a part in retrieval mechanism for both STM and LTM (Jonides et al. 2008).

Many experimental studies show the formulation of memory can take place through various mechanisms. These include language sample and modeling and computational modeling setup, which are assumed to enhance linguistic activity and associative learning in children (Jonides et al. 2008).

## Memory Storage Capacity

The term chunk is used to define the capacity of STM. It was defined as collection of thoughts and concepts in brain. It is independent of size or words or time span of words used and the already



existing chunks. Chunk is taken as the fundamental unit for stored data in STM (Norris et al. 2020), although this representation of chunk's patterns hasn't been confirmed by any model.

Chunking is a cognitive process to inhabit more data in a compressed form in the STM. On the contrary, an alternate theory describes that chunks are represented in LTM but not in STM. This suggests that these chunks in LTM reconstruct the data when they come in contact with familiar items in STM (Norris et al. 2020).

STM is evidently reported as a verbal system, which includes phonological store and basic speech units. The capacity can be influenced from word span and its duration of span. Word length and phonemes set a limit in capacity for STM. Also, reading rate is directly proportional to memory span. Fast readers are able to store more correct data. Experiments to interpret the relation of memory span with memory capacity were done parallel to the decay theory implications (Baddeley 2000).

The storage capacity has several limits instead of a single limit (Cowan 2008). It is also estimated to have four chunk limits, but evidence has suggested seven chunk limits. These capacity limits are also specific in nature to the sort of information being processed. Object complexity and familiarity determine the capacity limits.

## Storage Buffers

Storage buffers are the identities holding the copy of data in the memory. The stores are distinctive for LTM and STM. Memory storehouse can be of two possible ways, long-term storage and temporary storage, which is kept as buffer storage. Buffers store the items in coordinated patterns occurring in visual pattern. According to modal model, three kinds of memory stores are identified; perceptual buffers, short-term store, and long-term store. Based on empirical findings, a fourth buffer called episodic buffer is proposed (Baddeley and Hitch 2019).

STM is observed to depend on a phonological code, whereas LTM is dependent on semantic factors. The initial model of WM sketches three

components of the limited capacity system: central executive, visuospatial sketchpad, and a phonological loop. The phonological loop model describes the working of a storage buffer to illustrate an efficient way to combine forms of input. This idea for phonological storage in STM is proposed by Baddeley's work. It keeps the speech and visual data for short duration, which is maintained by rehearsal methods. Cowan's model describes more about rehearsal methods conducting the recoding of data, whereas the episodic buffer keeps the temporary event data (Norris 2017).

## Mechanism of Decaying/Forgetting of STM

Decaying or forgetting of events stored in our STM can be broadly due to two reasons, i.e., decaying due to time span or interference from the external world. One of the factors for decaying can be decreased activation mechanism for STM and no synchronization in the firing of neurons. Either of these reasons can be a contributing factor for forgetting of STM. Neural evidences observed are the decline of activations in the posterior sector of frontal cortex.

According to interference-based decay theory, new memory or new data can suppress the older memories with time. Also, lower retention intervals and retrieval mechanisms also play a role in the process of decay. Hence, overlapping of memory occurs in the interference theory (Jonides et al. 2008). However, exact models or experiments to prove time-based decay theory have not been reported yet.

## Training Methods for STM

The training of STM is significantly based on the ability to retain more and better retrieval mechanisms. Recalling of events in retention intervals helps to keep the memory intact. Some methods have been experimented to increase the memory span for verbal STM. The first method is visual digit span method, where digits are played in front

of the participant at a fixed interval of time and the participant has to retrieve the sequence of the digits on the computer manually. This test assessed the visual training of STM.

The second method is spoken digit span, which involves a speaker who recites the numbers with fixed intervals and the participants recall the numbers spoken. Similarly, letter span, pattern span, and direction change methods are also conducted. With the stated training techniques, improvement in performance was observed gradually. But these training methods are of no effect to increase the capacities of STM (Norris et al. 2019).

## Conclusion

Memory formation takes place in the cortical regions involving the hippocampus. STM is the immediate memory of event in our cortex. A lot of theories have been proposed to define neural architectures of STM and LTM. The multistore and unitary model theories depict contradictions to one another in terms of relation between STM and LTM. Apart from the models and structures, capacity limit is the fundamental area for research. Humans have limits for storage capacities in STM, yet their significance is to be answered. What is the definite chunk capacity limit of STM and how it can be enhanced by any intervening methods are the questions still to be answered.

## Cross-References

- [Chunking](#)
- [Cognition](#)
- [Hippocampus](#)
- [Long-Term Memory](#)
- [Long-Term Potentiation](#)
- [Memory](#)
- [Reference Memory](#)
- [Working Memory](#)

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## Siblicide

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### Definition

Siblicide is an event in which one or more individuals kill another individual born to their same parent(s).

### Explanation of Behavior

Siblicidal behavior involves the killing of an individual born to the same parent or parents as their killer. It is taxonomically widespread (Mock et al. 1990; Salmon and Hehman 2014) and may evolve either as a facultative or a fixed “obligate” behavior (e.g., Anderson 1990). In obligately siblicidal species, members of a species universally kill any available siblings. This behavior by itself seems likely to reduce the fitness of both parents and siblicidal individuals. Parents stand to lose direct fitness, and siblicidal individuals stand to lose indirect fitness. Hamilton’s rule predicts that siblicide is inherently disadvantageous unless some benefit (for example, food monopolization under scarce resource conditions) outweighs the loss of the related individuals (Dobler and Kölliker 2010; Leippert et al. 2000). Given that siblicide occurs with such a range of frequency across such a range of taxa, several explanations for its evolutionary value have been put forward.

It is worth noting that these are not mutually exclusive.

When resources fluctuate, it may benefit the fitness of the parents to produce more offspring than can survive. Under such conditions, siblicide may be advantageous for both parents and offspring. For parents, siblicidal offspring may be a way to reduce the number of mouths to feed – a literally morbid version of the “helpers at the nest” concept. Siblicidal individuals, in turn, increase their share of parental resources. This strategy reaches a state of diminishing returns under high resource conditions. Once individuals are satiated they benefit more from siblings’ survival than further resource monopoly (Drummond 2001; Hofer and East 2008). The size of a group of siblings (it is worth noting that they need not be from the same litter or clutch) is therefore a major influence on the level of siblicide which might be expected.

Life history strategies interplay with siblicide. If more offspring must be produced, with smaller resource investment relative to the needs of a creature, siblicide might be reduced, as the group must grow together to optimally disperse genes. If fewer offspring must be produced with greater resource investment relative to the needs of the animal, increased sibling competition may develop, leading resource-rich individuals to ensure monopolization of resources through siblicide (Pexton and Mayhew 2002).

The sequence in which a pair or group of siblings is born is entwined with their physical and resource-controlling dominance. In many siblicidal avian species, asynchronous hatching order permits first-hatched chicks to facultatively or obligately kill those which hatch later (Anderson 1990). Among humans, the correlation to birth order shifts across life stages. If both siblings are children, siblicide is more commonly practiced by older siblings, while among adults, siblicide is more commonly practiced by younger siblings. This change in relationship may be due to the relative difference in strength, particularly in a species where multiple births in the same cohort are relatively unusual (Gebo 2002). Most childhood sibling pairs will be asymmetrically matched in strength, with older siblings typically stronger. This difference would not necessarily

hold true in adulthood. Dominance roles appear to follow the same structure in other species (e.g., Hofer and East 2008).

Androgen levels positively correlate with competitive behavior, siblicide, and social dominance (Salmon & Hehman 2014). Siblings are often the first competitor an animal encounters. Competition for the resources a parent or alloparent can provide (e.g., food and shelter) may occur almost immediately after hatching/birth. As a result, a dominance hierarchy begins to form early in life. Among spotted hyenas (*Crocuta crocuta*), sibling ranking is decided before cubs emerge from the den, and the average age of siblicide is 47 days (Hofer and East 2008). Even earlier in life a behavior arguably under the category of siblicide is the adelphophagy exhibited by some shark species, where sharks will cannibalize their siblings in utero based largely on developmental status and size (Crespi and Semeniuk 2004).

Cannibalism appears to follow siblicide more frequently among fish, amphibians, and insects than birds and mammals (Mock et al. 1990). Cannibalistic siblicide serves to reduce competition as well as provide nourishment, while siblicide without cannibalism appears to be based upon resource monopolization and/or an escalation of sibling rivalries (e.g., Anderson 1990; Gebo 2002). Among some cannibalistic, siblicidal insects Hamilton's rule is followed, with less-related individuals killed and cannibalized preferentially over more-related individuals, suggesting that facultatively siblicidal systems may evolve such that the costs of siblicide are defrayed as much as possible while competition is reduced and nutrition directly gained via cannibalism (Dobler and Kölliker 2010).

## Conclusion

K- and *r*-selected life history strategies exist on a spectrum both among and within taxa. Siblicide is closely tied to K strategists, as it necessitates the allocation of more resources to fewer offspring. Though both parents and siblicidal offspring stand to lose fitness, the behavior can outweigh this cost with benefits of favoring stronger offspring more

likely to survive in uncertain conditions. When competition can be reduced by eliminating more distantly related rivals, this tendency evolves. Direct siblicide is more common in altricial species with limited mobility where full or half-siblings are the first rivals for resources encountered.

## Cross-References

- [Cooperative Breeding](#)
- [Fitness](#)
- [Hamilton's Rule](#)
- [Life History](#)

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## Sidman Avoidance

- [Avoidance](#)

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## Sight

### ► Platyrrhine Sensory Systems

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## Sign Stimulus

### ► Innate Releasing Mechanism

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## Sign Tracking

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## Synonyms

Compulsive behavior; Conditioned responding; Maladaptive behavior; Pavlovian conditioning

## Definitions and Origins of Sign Tracking

Sign tracking refers to behavior that is directed toward a stimulus as a result of a learned association between that neutral stimulus and a biologically relevant object or event that is rewarding. The sign-tracking response develops even though reward delivery is not contingent upon a response. For example, following classic Pavlovian conditioning procedures, wherein a *conditional stimulus* (CS) is repeatedly paired with presentation of food reward (*unconditional stimulus*, US), it is often observed that the *conditional response* (CR) that develops consists of orientation to, approach, and/or engagement of the CS (i.e., the cue or “sign” that signals impending reward delivery). The term sign tracking was initially coined by Hearst and Jenkins (1974) to describe behaviors observed in pigeons during

“autoshaping” experiments. During these experiments, pigeons continued to peck a key light (CS) that had been paired with a food US, even when food availability was reduced (e.g., Brown and Jenkins 1968).

Animal studies have demonstrated that sign tracking occurs when a CS not only acquires an association with a US but also when it increases attraction and elicits a motivational state that exerts control over behavior. The latter is referred to as incentive salience, and the CS itself is referred to as an incentive stimulus (see Robinson and Berridge 2008 for review). An incentive stimulus is thought to evoke attraction, approach, and engagement, one that animals will work for and that invigorates reward-seeking.

Numerous studies with rodents have shown that there are considerable individual differences in animals that have the propensity to sign track to incentive stimuli (e.g., Saunders and Robinson 2013). For example, when a CS becomes associated with the receipt of food reward, for some rodents (sign trackers), the cue itself becomes attractive, eliciting approach and engagement with it. For these rodents, the CS becomes a potent conditioned reinforcer, and rats will work for it. For other rodents (goal trackers), the CS is equally predictive of reward, but they approach and spend time close to the location of reward delivery. For these rodents, the CS is relatively ineffective as a conditioned reinforcer. The predominant response of sign tracking to a CS, when reward is readily available, is considered to be a maladaptive behavior and has been extensively studied in the context of addictive behaviors. Such incentive salience attribution to reward-associated stimuli has been suggested as a mechanism that underlies the development and persistence of addictive behavior.

## Applications of Sign Tracking

Sign tracking has been associated with addictive behaviors such as binge eating, alcohol abuse, and drug addiction (for reviews, see Mathes et al. 2009; Tomie and Sharma 2013; Robinson and Berridge 2008).



Binge eating has been shown to be a direct result of a CS acquiring incentive salience in both animal and human studies (Mathes et al. 2009). Repeated pairing of a rewarding food (e.g., sugar) with a CS results in the CS acquiring the motivational properties of the reward. Therefore, when an individual is bombarded with stimuli that represent food reward (e.g., fast food signs), this stimulus renews food seeking (a measure of sign tracking) and also increases consumption, independent of hunger.

Similar to the compulsive behavior of binge eating, an alcohol cue can become more attractive and a more effective conditioned reinforcer in animals with a predisposition to sign track (Villaruel and Chaudhri 2016). In rodents, pairing a lever CS with the availability of ethanol produced significant sign tracking in some animals. Similarly, in humans, repeatedly pairing a favorite alcohol with a glass produced compulsive seeking and consumption of alcohol (Tomie and Sharma 2013). The glass became a motivating CS and renewed alcohol seeking and consumption even after tolerance and when “liking” of the alcohol’s effects were reduced. Therefore, in alcoholism, stemware and bar signs may transform into motivating CSs that produce alcohol-seeking behavior (sign-tracking behavior) in some individuals.

Decades of substance abuse research have demonstrated the relationship between substance use disorder behaviors and sign tracking. In humans, a CS (e.g., paraphernalia) associated with drug reward may instigate renewed craving and drug taking in the absence of the drug. This is often referred to as attentional bias (see Field and Cox 2008 for review). Attentional bias is measured by presenting an individual with drugs (e.g., cannabis and cocaine) paired with neutral visual drug-related stimuli (e.g., crack pipe). Attentional bias is the disproportionate amount of time spent looking at drug-related stimuli as opposed to neutral stimuli (e.g., stapler). This increase in time spent looking at drug-related stimuli presumably represents incentive salience and may be considered to be parallel to sign-tracking behavior of animals.

In rodents, animals that have been predisposed to sign track to a food CS are more motivated to self-administer cocaine and reinstate drug-seeking when primed with a drug cue than goal trackers (Saunders and Robinson 2013). Overall, these studies support that sign trackers may be more likely to attribute incentive salience to stimuli previously paired with a reward when compared to animals that do not sign track. As a consequence, sign trackers may be more vulnerable to the rewarding effects of drugs compared to subjects that do not sign track.

## Neurobiological Mechanisms of Sign Tracking

Recent research shows that animals that are predisposed to sign track have different “cognitive-motivational styles” and neurobiological mechanisms than animals that are not, i.e., goal trackers (Sarter and Phillips 2018; also see Kuhn et al. 2018 for review). Sign trackers appear to be sensitive to the influence of reward cues via enhanced bottom-up, cue-driven, dopamine-dependent processing, as a function of increased activity in the subcortical regions, including the striatum, amygdala, midline thalamus, and hypothalamus. In contrast, goal trackers appear to be less susceptible to the motivational properties of reward cues and also have greater executive (attentional) control over behavior that is mediated in part by the cholinergic system in the prefrontal cortex.

Several brain structures and neural pathways have been implicated in sign tracking, and sign tracking appears to be the result of multiple pathways and structures (Kuhn et al. 2018). For example, dopamine (DA) has been heavily implicated in the acquisition and maintenance of sign tracking, and these increases appear primarily in the NAc. However, DA in the NAc does not fully explain sign tracking as many other structures, monoamines, and hormones have been implicated in sign tracking. Future research is needed to investigate the relationship between these pathways and structures to better understand

how they work together to produce and maintain sign tracking.

## Cross-References

- ▶ [Adaptedness of Behavior](#)
- ▶ [Associative Learning](#)
- ▶ [Behavior Systems](#)
- ▶ [Classical Conditioning](#)
- ▶ [Feeding](#)
- ▶ [Ivan Pavlov](#)
- ▶ [Learning](#)
- ▶ [Motivation](#)

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## Signal

- ▶ [Catarrhine Communication](#)
- ▶ [Mustelid Communication](#)

## Signaled Avoidance

- ▶ [Avoidance](#)

## Signaling

- ▶ [Insect Communication](#)
- ▶ [Rodentia Communication](#)

## Signaller

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## Synonyms

[Manager](#); [Manipulator](#); [Sender](#)

## Definition

Any individual who produces a signal during the communication process.

There are many definitions of a signaller in the communication literature, which vary from manipulator to cooperative informer to continuous manager. Krebs and Dawkins (1984) provided a more manipulative view of the communicative process. They felt that signallers were “manipulators.” For example, in order for a communicative signal to persist in the environment, it must coevolve with a signaller and a receiver; therefore the manipulator's role is that of the sender or

signaller altering the listener's behavior in a way to directly benefit the sender (Krebs and Dawkins 1984). In a similar way to the definition of receivers, the definition of a signaller (as a manipulator) relies heavily on the fact that signals are reliable and provide honest cues that receivers can act upon. Thus, the handicap principle plays a key role in the idea of manipulation. Zahavi (1975) first introduced us to the idea of a costly signal by suggesting that in order for selection to continue acting on a communication process, both signaller and receiver need to benefit and thus have diverging interests. This divergence in interests, and the inherent cost associated with signalling, means that signals will honestly convey the required behavioral response to listeners (Zahavi 1975). Zahavi's ideas fit quite nicely with Krebs and Dawkins' (1984) suggestion that signallers have conflict with those around them and as a result manipulate that conflict through signalling.

Alternatively, the information view of communication suggests that signallers are intending to "inform" others in order to obtain a desired outcome (Smith 1977; Seyfarth et al. 1980). This viewpoint of a signaller relies heavily on more cooperative process that occurs when individuals' interests tend to overlap. Moreover this information sharing, with a cooperative view, requires special explanations for these somewhat unselfish acts (Morton 2017). Finally, information is a difficult behavioral feature to measure what exactly is the signaller conveying, is it intentional, and how can that be measured? Due to these inherent difficulties with a signaller transferring information, several other theories of signaller's behavior have arisen.

Morton (2017) and Owings and Morton (1998) suggest that the interaction between a signaller and receiver is one of regulations. The signaller, or manager, produces a signal that functions to regulate a particular situation. The behavioral result of that regulation will cause the signaller to "adjust" their behavior in return (Owings and Hennessey 1984). This means that from the perspective of the signaller, communication is an ongoing process that requires constant adjustment. In other words a

signaller's situation is constantly changing, and thus the management required to obtain the behavioral outcome from those around them is a constant process (Owings and Hennessey 1984). Furthermore, because the signaller is operating on the listeners' expectancies in a selfish way, signals do not need to have referents or information (Morton 2017).

Although these definitions focus primarily on the contributions of acoustic communication to the understanding of signallers, the definitional diversity is relatively consistent across communicative realms. Further research on the interaction of signaller and receiver in all communicative process will tease apart the divergent interests of these individuals and broaden our understanding of the role of a signaller.

## Cross-References

- ▶ [Alarm Calls](#)
- ▶ [Contact Calls](#)
- ▶ [Receiver](#)

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## Signals

- ▶ [Bear Communication](#)
- ▶ [Communication](#)
- ▶ [Equine Communication](#)
- ▶ [Secondary Defenses](#)

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## Sign-Tracking

- ▶ [Autoshaping](#)

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## Simian and Prosimian Mental Processes

- ▶ [Primate Cognition](#)

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## Simple Sequence Repeats

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### Synonyms

[Microsatellites](#); [Short tandem repeats](#); [STRs](#); [Variable number tandem repeats](#); [VNTRs](#)

### Definition and Introduction

Simple sequence repeats (SSRs), more often referred to as microsatellites or short tandem repeats, are short (1–9) tandemly repeated nucleotide sequences found ubiquitously across prokaryotic and eukaryotic genomes (Tóth et al. 2000). SSRs differ from minisatellite or satellite DNA, which consist of tandemly repeating sequences of 10–1000 and >1000 nucleotides, respectively. SSRs are highly mutable, individually variable sources of functionally relevant genetic variation, with applications in medicine, forensics, population and behavioral genetics, and evolutionary biology.

### SSR Composition and Genomic Distribution

SSRs are phylogenetically and genomically widespread, common to both prokaryotes and eukaryotes and occurring in subtelomeric, intragenic, intronic, and exonic regions (Tóth et al. 2000). SSRs often comprise large portions of host genomes and may be associated with known genic regions. The most common SSR units are mono- and dinucleotide repeats, but SSR unit length varies both by species and genomic location (Tóth et al. 2000). SSRs occur in both coding and noncoding DNA. Tri- and hexanucleotide repeats are more prevalent in exonic coding DNA, where they provide an important source of protein structural variability while maintaining reading frame. Poly (A/T) repeats tend to be more common than poly (C/G), but this also varies with genomic location.

While SSR variation in much of the genome is neutral, there is evidence for selection on repeat composition and length for many SSRs. In humans, trinucleotide CAG<sub>n</sub> motifs are overrepresented in exonic DNA, particularly in genes that code for proteins involved in neurodevelopment (Shimada et al. 2016). These CAG tracts, which code for the amino acid glutamine when expressed, may be evolutionarily favored at the level of the protein despite being under selection in DNA, and from their direct contribution to numerous human diseases (Shimada et al. 2016).

### SSR “Birth” and Evolution

The “birth” of SSRs involves de novo generation through conventional mutational processes (base-pair substitution and insertion-deletion events) or the modification of protomicrosatellites created during the dispersal of mobile transposable elements (Kelkar et al. 2008). Once formed, SSRs are hypothesized to change in length through replication slippage events, where disassociation of the replicating DNA strand is misaligned during reassociation (Viguera et al. 2001). While the genetic “stutter” caused by replication slippage is usually corrected by the DNA mismatch repair system, failure to do so can result in rapid

expansions or contractions in repeat number. The rapid expansion and contraction of SSRs lead to a great deal of mutability in repeat number in SSRs – up to 100,000x's higher than for point mutations within a given species. High mutation rates result in hypervariability in repeat length for many SSRs, making them an important source of genetic diversity (Tóth et al. 2000). For this reason, SSRs have been used extensively as genetic markers for population genetics, paternity tests, and forensic applications.

At the level of the population, SSR repeat number often resembles a bell-shaped – or occasionally a multimodal – distribution (Shimada et al. 2016). Such distributions could arise from a combination of opposing molecular and/or selective processes. Longer repeats become increasingly unstable and are more likely to accumulate additional repeats through replication slippage. Repeat expansion of SSRs also contributes to certain forms of protein toxicity and disease. However, slippage may result in the excision of numerous repeats in a single event, for example, through the creation and exclusion of DNA hairpin loops. Such instability results in the rapid expansion or contraction of many SSRs through time.

Given the inherently unstable nature of most SSRs, especially under conditions of cellular stress (Chatterjee et al. 2015), their prevalence is somewhat surprising. However, that same instability makes SSRs an important source of genetic diversity in challenging new environments, potentially facilitating adaptation, evolution, and speciation. These characteristics, combined with graded phenotypic effects of repeat number, have led to some researchers to refer to SSRs as “evolutionary tuning knobs” (King et al. 1997).

## Functional Consequences of SSR Variation

Both in vitro and in vivo studies have shown that repeat number for some SSRs can affect the binding of transcription factors or noncoding regulatory RNA, and/or alter protein form and function. These regulatory or conformational

changes can lead to a range of morphological, cognitive, and behavioral phenotypes. In *Drosophila melanogaster*, variation in a threonine-glycine repeat in the *period* clock gene affects circadian response to changes in temperature, a finding supported by clinal geographic variation in repeat length for this SSR among natural populations (Sawyer et al. 1997). SSR repeat length variation in genes involved in head development affect head shape in *Drosophila*, as well as in the stalk-eyed fly (*Teleopsis dalmanni*) (Birge et al. 2010). Notably, a significant genotype-phenotype association exists between several repeat motifs and eye-stalk length in *T. dalmanni*, a rapidly evolving trait under strong sexual selection in this species (Birge et al. 2010). The effect of SSR repeat length on morphological characteristics has also been demonstrated in other taxa, including mammals. Variation in repeat length for an SSR in the *Alx-4* gene is linked to polydactyly in both mice and the domestic dog, while variation in *Runx-2* seems to be partly responsible for interbreed variability in facial and cranial structure among domestic dogs (Fondon and Garner 2004).

A number of behavioral phenotypes have also been shown to vary with variation in SSR repeat number. A polymorphic SSR in the *arginine vasopressin 1a receptor (avpr1a)* gene is associated with differences in this receptor's binding affinity for vasopressin and is linked to both inter- and intraspecific differences in social behavior in among voles (Hammock and Young 2005). Similar variation in the *avpr1a* gene may correspond to sociosexual differences between Chimpanzees (*Pan troglodytes*) and Bonobos (*Pan paniscus*), and may contribute to autism-associated sociobehavioral deficits in humans. Other genes with nearby or intervening SSRs that have been associated with behavioral and cognitive phenotypes include genes coding for the serotonin transporter (SLC6A4), the dopamine transporter (SLC6A3), the dopamine receptor (DRD4), and the androgen receptor (AR). SSR variation in a polyglutamine tract in the human AR has also been associated with a range of morphological and behavioral phenotypes, and is a risk factor for several diseases.



## SSRs and Human Disease

Over 40 human diseases, referred to as “repeat expansion disorders,” have been linked to pathological SSR expansion. These disorders include Huntington’s disease, myotonic dystrophy, spinal and bulbar muscular atrophy, fragile X, and a number of spinocerebellar ataxias. The link between repeat number and disease include polyglutamine toxicity, altered RNA/protein levels, and protein gain/loss of function. Typically, symptom severity increases and age at onset decreases as repeat number expands with each generation. SSRs with longer repeat lengths are less stable and accumulate additional repeats more rapidly than shorter repeats. As a result, disease symptoms may arise at an earlier age with each generation, a process referred to as “anticipation.” Notably, a disproportionate number of repeat expansion disorders are neurological in nature. Some researchers have argued that highly mutable SSRs may have played a fundamental role in the rapid evolution of brain and cognitive development in the human lineage, while also bearing a burden in the form of a susceptibility to a number of neuropathological diseases (Shimada et al. 2016).

## Conclusion

The biological significance of SSRs arises from their ubiquity, mutability, and molecular and phenotypic effects. While the pathways through which SSRs can affect health, behavior, and evolution are becoming clearer, the causes and consequences of repeat variation for the majority SSRs are still unknown. Rapid technological and analytical developments will no doubt improve the scale and resolution of data necessary to answer these questions, and aid in elucidating the role of SSRs in gene regulation, phenotypic variability, and evolution.

## Cross-References

- Androgens
- Biological Clocks
- Canine Morphology
- Dopamine Receptor
- Gene Expression

- Genetic Variation
- Insect Morphology
- Internal Clocks
- Microsatellite Marker
- Mutations
- Phenotype
- Repeat Sequences
- Serotonin
- Transposable Elements

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## Simple Sequence Repeats (SSR)

- Microsatellite Marker

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## Simulation

- ▶ [Virtual Reality Experiments](#)

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## Simulative Communication

- ▶ [Metacommunication](#)

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## Simultaneous Attention

- ▶ [Divided Attention](#)

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## Single Frame Lifetime Display

- ▶ [Point Light Displays](#)

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## Single Nucleotide Polymorphism (SNP)

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## Synonyms

[Point mutation](#)

## Definition

SNPs are single nucleotide changes in genomic DNA at which different nucleotides occur in different individuals of a population. Each nucleotide at such a position denotes an allele of the SNP.

## Introduction

Single nucleotide polymorphisms (SNPs), pronounced as “Snips,” is the common type of variation found in DNA between genes (Genetics Home Reference). Each SNP differs by a single DNA block represented as nucleotide. For example, a SNP may be replaced by adenine (A) in place of guanine (G) in a stretch of DNA. SNPs, if falling under coding region of genes, do not alter the amino acid sequence and, in turn, the sequence of protein produced. They are classified into two parts: synonymous, i.e., genes that do not bring any change in protein, and nonsynonymous, i.e., genes that bring change in amino acid sequence, which may be a missense (resulting in incorrect amino acid) or nonsense (not coding for any amino acid).

SNP density of existence can be predicted by the sequence known as microsatellites. The most common predictor of density is “AT” microsatellites. SNPs are also classified on the basis of their regions, i.e., noncoding and coding regions. Coding regions can be further classified as missense and nonsense regions. SNPs represent 90% of the total variations, which means that the genetic variation occurring on a daily basis is caused by small change in nucleotide.

## Identification

Single base variants in cDNA are considered as SNPs, as are single base insertions and deletions in the genome. Several different methods have been developed to discover SNPs. A simple procedure is to analyze the sequence data stored in the major databases and identify the SNPs. DNA chips/microarray has been developed for SNPs

identification. When the complete base sequence of a segment of DNA is considered, one can identify four alleles represented by A, T, G, and C at each SNP locus in the segment.

It is estimated that approximately 90% of sequence variation in human is due to SNPs. Our genome is estimated to contain 3–17 million SNPs. Of these, 5% of SNPs are expected to occur in genes. Thus, SNPs provide a molecular marker that occurs in genome at a very high density and can therefore be used to map genes involved in human diseases.

Efforts are being made to use SNPs to map hundreds or thousands of genes that have an effect on the safety and efficacy of various drug treatments. These SNPs can be placed on gene chips that can be used to genotype individuals for those genes involved in response to specific drugs. Based on this data, more efficacious and safe treatment can be selected for these individuals. For example, variants in the gene encoding apolipoprotein E were found to be correlated with variation in response to a drug used for treatment. Gene apoE is involved in susceptibility to Alzheimer's disease, and a cholinesterase inhibitor is used to mitigate the disease symptoms (Wilkinson et al. 2004).

## Diseases

SNPs can be treated as a biomarker for different diseases like sickle cell anemia,  $\beta$ -thalassemia, and cystic fibrosis. Heart disease, diabetes, and cancer can also be correlated with SNPs. They work in coordination with other SNPs to produce a disease condition like in osteoporosis (Singh et al. 2010). Higher risk of cancer is associated with SNPs in noncoding regions, and mRNA structure and disease susceptibility may be affected. Such synonymous substitutions do not result in a change of amino acid in the protein but can still affect its function in other ways. For example, multidrug resistance gene 1 (MDR1) can cause the mutant pump to be less functional (Kimchi et al. 2007).

Nonsynonymous substitutions include missense in which single change in the base results

in a change in an amino acid of protein and its malfunction leads to disease (e.g., c.1580G>T SNP in LMNA gene mandibuloacral dysplasia and progeria syndrome, Al-Haggar et al. 2012) and nonsense, which includes a premature stop codon or a nonsense codon in the transcribed mRNA. A usually nonfunctional protein product is obtained if point mutation occurs in a sequence of DNA (e.g., cystic fibrosis caused by the mutation of G542X in the cystic fibrosis transmembrane conductance regulator gene, Cordovado et al. 2012).

## Importance of SNPs

Human genetic variation occurs primarily by SNPs occurring in protein coding regions, which contribute to different phenotypic variations. SNP (rs2596542C/T) in major compatibility genes can be used as a good potential biomarker in assessment of liver disease (Mohamed et al. 2017). SNPs are critical in predicting prostate cancer risk. Studies suggest that there is strong dose-dependent association. SNPs provide the way for therapeutic targets. SNPs are also found to be very useful biomarkers in plant breeding and genome analysis. Eleven SNPs are found to be reported at nine loci for gastric cancer risk.

## Examples Are as Follows

- (a) Serotonin 5-HT<sub>2A</sub> receptor gene rs6311 and rs6313 are SNPs on human chromosome 13 (Giegling et al. 2006).
- (b) Leiden thrombophilia was caused by Factor V in the F5 gene in SNPs (Kujovich 2011).
- (c) CRP gene on human chromosome 1 rs3091244 is an example of a triallelic SNP (Morita et al. 2007).
- (d) DNA mismatch repair gene PMS2 (rs1059060, Ser775Asn) is an intronic SNP and is associated with increased sperm DNA damage and risk of male infertility (Ji et al. 2012).

## Databases

SNP database named dbSNP is from the National Center for Biotechnology Information (NCBI). Till 8 June 2015, dbSNP identified 149,735,377 SNPs in humans. Kaviar is an anthology of SNPs from multiple data sources including dbSNP (Glusman et al. 2011). OMIM database (diseases are represented in text form) dbSAP – single amino-acid polymorphism database – is used (Cao et al. 2016).

## Programs for Prediction of SNPs

A change in amino acids with almost similar size and physicochemical properties (e.g., substitution from glycine to alanine) has a mild effect. SNP can disrupt secondary structure elements (e.g., substitution to proline in an alpha helix region), and such mutation usually may affect the whole protein structure and function. Therefore, a group of programs for the prediction of SNP effect was developed which includes SIFT, SNAP2, SuSPect, PolyPhen-2, Predict SNP, Mutation Taster: official website, and Variant Effect Predictor from the Ensembl Project (Wei et al. 2010).

## Evolutionary Relationship

Variations occurring in a human population in the SNP allele, common to one geographical area, will rarely be found in another. Therefore, for a population, SNPs can have a minor allele frequency, and the lowest allele frequency at a locus can be observed in a particular population. Therefore, SNPs can be used in an investigation or study of any migration patterns.

## Conclusion

SNPs occurring in different populations help in better understanding the metabolism of lipids and thus reducing the cardiac risk. Polymorphism

associated with LDL correlated with lipid metabolism is associated with reduction in rate of myocardial infarction. The clinical setting and evaluation of polymorphism in different populations will play a role in the future for coronary artery disease. SNPs can be used as genetic biomarkers for the family Brassicaceae. The species named *B. rapa* was used to successfully genotype the Brassicaceae, and many more markers are genotyped. SNPs are acting as a key to unlock the mystery. With advancement in fields like biotechnology, many of the so-called mysteries have been resolved, which help in prevention and treatment of various diseases and will ultimately lead to the discovery of new drugs, which can increase the average life span of human beings. Living conditions and human lifestyles are improving day by day; therefore, with the advancement in biotechnology, safer anticancer drugs will come.

## Cross-References

- [Alleles](#)
- [Base Pair](#)
- [Targeted Mutation](#)

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## Single Subject

- [Anecdote](#)

## Siren Locomotion

- [Sirenia Locomotion](#)

## Sirenia Diet

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## Synonyms

[African manatee](#); [Amazonian manatee](#); [Antillian manatee](#); [Dugong diet](#); [Florida manatee](#); [Manatee diet](#); [South American manatee](#); [West Indian manatee](#)

## Definition

Food and feeding habits of the four extant species of the order Sirenia (dugongs and manatees).

## Introduction

The order Sirenia is comprised of the two families Dugongidae and Trichechidae. Dugongidae has only one living member, the dugong (*Dugong dugon*). The most recent relative of the dugong, the Steller's Sea Cow (*Hydrodamalis gigas*), was hunted to extinction shortly after its discovery in the mid-1700s (Domning 2016). The dugong is presently listed as vulnerable by the International Union for Conservation of Nature (IUCN) Red List, though it is considered extinct in some portions of its range and endangered or critically endangered in others (Marsh and Sobotzick 2019). The closest living relatives of the dugong are the manatees, in the family Trichechidae. There are three extant species of manatee: the African manatee (*Trichechus senegalensis*), the Amazonian or South American manatee (*Trichechus inunguis*), and the West Indian manatee (*Trichechus manatus*). All three species are presently listed as vulnerable by the IUCN Red List (Deutsch et al. 2008; Keith Diagne 2015; Marmontel et al. 2016). However, the two subspecies of the West Indian manatee, the Antillean



manatee (*Trichechus manatus manatus*) and the Florida manatee (*Trichechus manatus latirostris*), are each listed as endangered (Deutsch et al. 2008). The biggest threats to all these species are illegal hunting, habitat loss, and anthropogenic factors such as boat strikes (Deutsch et al. 2008; Keith Diagne 2015; Marmontel et al. 2016; Marsh and Sobtzyk 2019).

The members of the order Sirenia have long been considered the only marine mammal herbivores and have developed some unique adaptations that allow them to fill this niche. Perioral bristles, specialized vibrissae, on the upper and lower lips in combination with facial muscles help maneuver food into the mouths of these animals. In dugongs, this is a simpler manipulation that moves food into the sides of the mouth, whereas in manatees there is a prehensile grasping action that allows them to manipulate the food into the front of the mouth (Marshall et al. 2003). These bristles are also used to touch and explore what is around an individual, possibly searching for additional food. In addition to the bristles, the flippers can be used in feeding as well as to clean the bristles after feeding or exploring (Marshall et al. 2003). Palatal pads, horny layers of skin located rostral to the cheek teeth, are thought to aid in the mastication of sea grasses and other plants (Marshall et al. 2003). Manatees have also evolved what is known as horizontal tooth replacement. In this process, the worn anterior most teeth are lost, and as the tooth row moves forward, new teeth erupt in the posterior most position of the tooth row. It is thought that this adaptation arose because of their herbivorous diet and the wear it places on the teeth of these animals (Beatty et al. 2012; Domning 1982). This adaptation is not seen in dugongs, instead their teeth have open roots and they have longer and more robust palatal pads than manatees, both of which are thought to help extend the life of the teeth. (Domning 1982; Marshall et al. 2003).

Sirenian diets are not well-known as they are often in environments where their behaviors are difficult to observe. They have very large ranges, and some individuals migrate extensively within this range. Due to these factors, the complete diet of these animals throughout the whole of their

range is unknown and will vary depending on the season, location, and plant distribution. Many of the studies that have been done have attempted to evaluate diet composition between age classes and seasons at their study locations.

### **African Manatee (*Trichechus senegalensis*)**

Found primarily along the west coast of Africa and ranging from southern Mauritania through Angola, the African manatee inhabits coastal marine waters and adjacent freshwater rivers and lakes as well as lagoons and brackish estuaries and will move between these different environments (Keith Diagne 2015). Despite protection throughout its range, poaching remains one of the biggest threats to this species (Keith Diagne 2015; Reeves et al. 1988). Habitat loss is also a major threat. Genetic diversity and population size are likely to be impacted by habitat degradation and fracturing due to the construction of dams. However, due to a lack of long-term committed funding, remoteness of habitats, as well as their extensive range, little is known about this species (Keith Diagne 2014, 2015). Much of what is known comes from indigenous knowledge of their range, habitat, abundance, and behavior (Reeves et al. 1988). However, efforts are being made to further African manatee conservation training with workshops aimed at empowering African biologists and community members to begin manatee research and conservation activities (Keith Diagne 2014, 2015).

Due to the African manatees' extensive range and diverse habitats, it is likely that feeding strategies vary widely among these habitats. In Sierra Leone, African manatees have been observed eating elephant grass (*Pennisetum purpureum*) though they have been reported to consume fish and rice, creating conflicts with local stakeholders. Because of this tension between the locals and the manatees, those who capture or hunt these animals are seen as performing important services to the community (Reeves et al. 1988). Further north of the study conducted by Reeves et al. (1988), the leaves and fruit of

mangroves have been found to be an important food source for this species, demonstrating the fluidity in the manatees' diet relative to habitat and food availability. Reeves et al. (1988) is not the only study to have found that the African manatee is not strictly herbivorous, as was once thought. Alternatively, Keith Diagne (2014) demonstrated that African manatees eat more than just plants, and that their diets do not change significantly over the course of the animals' lifetime. In Gabon, manatees consume primarily flowering plants including hibiscus (*Hibiscus tiliaceus*), lotus (*Nymphaea lotus*), and knotweed (*Polygonum salicifolium*). Some grass species, including hippo grass (*Vossia cuspidate*), were also determined to be part of their diet. In addition to plants, an average of 10% of the animals' diets, depending on location and age, consisted of hermit crab (Keith Diagne 2014). In Senegal, the manatees' diets consisted of approximately 50% fish, mollusks, and bivalves, depending on location and season. The remainder of their diet was plant-based, consisting mostly of grasses from the genus *Echinochloa* and water nymph (*Najas guadalupensis*) (Keith Diagne 2014). While diet comparisons between manatees in Senegal and Gabon showed similar proportions of aquatic and terrestrial plants, historical data indicates that diversity in the African manatees' diet has decreased significantly in the last 70 years. This change is likely an artifact of anthropogenic climate change and habitat loss (Keith Diagne 2014).

### Amazonian Manatee (*Trichechus inunguis*)

The Amazonian manatee is the only extant Sirenian with an exclusively freshwater habitat. They inhabit most of the Amazon River basin from the headwaters to the mouth of the river and can be found in all three types of water, which are characterized by nutrient levels and water transparency: white, black, and clear. They appear to be more abundant in the white, nutrient-rich water, but there are currently no reliable population estimates. It is believed the population may be

stabilizing in some regions due to local awareness and conservation efforts, but overall, the population is still decreasing. Because these animals engage in long seasonal movements, they can migrate out of protected areas to places where they are more vulnerable to hunting pressures (Marmontel et al. 2016). Some indigenous peoples, including the Siona in Ecuador, have self-imposed bans on hunting due to low population levels. Indigenous knowledge is a great source of information for holistic conservation efforts as they are aware of where manatees can be found and some of the plants they feed on, knowledge that is harder for scientists to acquire due to the secretive nature of the manatee (Timm et al. 1986).

Much of what is known about the Amazonian manatee diet, if not acquired from speaking with indigenous peoples and hunters, has been determined from analyzing floating fecal samples and stomach contents of manatees that were hunted or otherwise killed in the areas of study. Guterres-Pazin et al. (2014) identified 49 plant species consumed by the Amazonian manatee, a large portion of which had not been previously cited in the literature. Even so, there were species mentioned by the local peoples that were not seen in this study. Grasses from the family Poaceae were seen with the highest frequency in multiple studies (Colares and Colares 2002; Guterres-Pazin et al. 2014). The importance of a particular species or habitat of plant species (emergent, free-floating, fixed-floating, etc.) varies by season and location (Colares and Colares 2002; Guterres-Pazin et al. 2014; Timm et al. 1986). The Amazonian manatee seems to be opportunistic and will consume a large variety of plant species. The number of species consumed seems to be consistent between flood and drought seasons, but the actual species will vary (Guterres-Pazin et al. 2014). However, Best (1983) hypothesized that in years of extreme drought, where the water levels drop so low that plants are unavailable to the animals, the manatees may enter a fasting state until the water level rises, making plants available again. While eating their preferred plant species, it seems as though there is accidental ingestion of arachnids, zooplankton, plant seeds, sand, and

other unidentified materials. The invertebrates were found intact and undigested, indicating they are not a nutritional supplement for the animals, unlike the plant seeds which were broken open and may represent an additional nutrition source (Guterres-Pazin et al. 2012). Crema et al. (2019) found that individual diet does not seem to vary over time, with the exception of lactating females who, it was hypothesized, either move to different foraging grounds or change their diet preferences while lactating, possibly due to the higher energetic demands of the animal. It is possible that the stable isotope analyses used in this study, due to their long-term nature, may mask the seasonal diet shifts seen in other studies.

### West Indian Manatee (*Trichechus manatus*)

The Florida manatee is found primarily in the warm waters of the Florida peninsula, inhabiting freshwater rivers, brackish estuaries, and coastal marine environments. Members of this subspecies have been known to move between these different environments, traveling as far north as Virginia and as far west as Texas in the summer months. Some will even travel south to the Bahamas. In the winter, they return to the warm waters of Florida, generally to the same refuge each year. The biggest threat to this subspecies is watercraft collision followed by other human-related causes of mortality such as habitat loss (Deutsch et al. 2008). The Antillean manatee can be found in and traveling between freshwater rivers, brackish estuaries, and coastal marine habitats from the Bahamas to Brazil including areas of the Caribbean Sea and the Gulf of Mexico and was historically documented in 41 countries within that range. Recent assessments show manatee populations in 20 countries with individuals sighted in additional countries. However, the distribution of these populations is not continuous. The main threats to this subspecies are hunting and habitat loss (Deutsch et al. 2008).

The West Indian manatees are opportunistic feeders and seem to feed on whatever vegetation

is available. However, stable isotope analyses indicate that seagrasses are an important part of the diet of these manatees in most areas of their range (Alves-Stanley et al. 2010; Reich and Worthy 2006). Which species of seagrass are most important to the diet seem to vary by location of the individual. Castelblanco-Martínez et al. (2009) found that in Mexico the seagrasses *Halodule wrightii* and *Thalassia testudinum* were the most important, whereas Allen (2014) found that in Belize, rhizomes and only the seagrass *Halodule wrightii* were most important. Though other seagrasses were consumed in Belize, they were not as prevalent in the collected samples. In addition to seagrasses, when available, mangroves and algae species can contribute significantly to diet. The significance of that contribution varies by location and availability (Allen 2014; Castelblanco-Martínez et al. 2009). Like in the Amazonian manatee, it is speculated that there is accidental ingestion of invertebrates while consuming their preferred food of aquatic plants (Allen 2014); however, there have been several documented cases of the West Indian manatee feeding on fish, sponges, and other invertebrates. In 1976, fishermen reported manatees stripping the flesh off of fish caught in stationary gill nets off the coast of Jamaica (Powell 1978). Also, multiple observations were made from 1992 to 2017 of manatees feeding on the sponge *Condrilla caribensis* off docks, pylons, and other hard surfaces in the Florida Keys (Fitt 2020). While it is not known how much this contributes to the diet of the West Indian manatee, it is unlikely that it is a large portion like in the African manatee.

### Dugongs (*Dugong dugon*)

The dugong is the only strictly marine Sirenian inhabiting tropical, coastal, and island waters of at least 37 states and territories between East Africa and Vanuatu. Within this range, the areas with the largest subpopulations of dugongs are in Australia, Bahrain, Papua New Guinea, Qatar, and the United Arab Emirates (Marsh and

Sobtzick 2019). Like the African manatee, dugongs are protected throughout most of their range, but there is little enforcement of these protections. The biggest threats to the dugongs are from hunting, incidental capture, boat strikes, habitat loss, and threats to seagrass (Marsh and Sobtzick 2019).

Dugongs primarily feed on seagrasses and their rhizomes. Because of their feeding style, consuming plants in a muzzle wide serpentine path on each dive, they are unable to feed selectively on the individual plant level, but instead consume species at equal rates according to their proportions within the meadow being grazed (Preen 1995b; Tol et al. 2016). Tol et al. (2016) found that while *Halophila ovalis* and *Halodule uninervis* were the most common species at all sites studied in Queensland, biomass was the most important factor in dugong feeding patterns. That is, dugongs primarily fed at locations of high biomass regardless of species composition. However, Preen (1995b) found that dugongs seem to have a preference for the species *H. ovalis* and *H. uninervis*, and intense grazing of sea grass beds can encourage the growth of these pioneer species while slowing the growth of the less preferred species of *Halophila spinulosa* and *Zostera capricorni*. In Papua New Guinea, Johnstone and Hudson (1981) found that seagrasses, preferentially *Thalassia hemprichii* the most abundant in the area, made up about 97% of dugong diets with algae making up the rest, though the mouth sample of one dugong in the study consisted solely of mangrove leaves, indicating this may at times be a supplementary diet to seagrasses when available. It was thought that, like manatees, dugongs accidentally ingest invertebrates while consuming seagrasses; however, Preen (1995a) found that in some areas dugongs deliberately feed on ascidians, or sea squirts, which make up a significant portion of the dugongs diet in these areas.

## Conclusion

There are several hypotheses as to why manatees and dugongs, previously thought to be strictly

herbivorous, may intentionally feed on invertebrates and fish. The main hypothesis is the lack of nitrogen in their diet of aquatic plants (Fitt 2020; Preen 1995a). Another hypothesis was that manatees choose these other food sources when plants are unavailable, but several studies presented here seem to disagree with this hypothesis (Keith Diagne 2014). In addition to the extant species of today, at least one extinct species of Miocene Trichechid is believed to have had a diet consisting of shellfish (Keith Diagne 2014).

Historically, however, the fossil record seems to indicate that sirenians have been dependent on seagrass as a food source since their appearance in the Early Eocene (Domning 1981). It is hypothesized that the evolution of horizontal tooth replacement in manatees allowed them to outcompete members of the Dugongidae family in the New World (Domning 1982). Further niche partitioning is hypothesized to be related to rostral deflection which can influence where in the water column an animal is most adapted to feed. Dugongs have the highest degree of deflection, which is useful for bottom feeding. African and Amazonian manatees have the lowest degree of deflection, which allows them to feed on floating vegetation and may reflect a scarcity of submerged plants in their habitats. West Indian manatees have a degree of deflection between the two extremes allowing them to opportunistically feed on both floating plants and submerged plants (Domning 1982; Marshall et al. 2003).

Despite all that seems to be known, more information is needed about the diets and foraging habits of these last species of the order Sirenia in order to protect and improve protections of these species and their preferred habitats, thus ensuring their survival.

## Cross-References

- [Feeding](#)
- [Foraging](#)
- [Sirenia Morphology](#)
- [Sirenia Navigation](#)
- [Sirenia Sensory Systems](#)

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## Sirenia Locomotion

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## Synonyms

[Dugong movement](#); [Manatee movement](#); [Sea cow ambulation](#); [Siren locomotion](#)

## Definition

Movement used by members of the order Sirenia (e.g., manatees and dugongs) to transverse their environment.

Sirenia is a small order that consists of four species from two families, Dugongidae (dugong) and Trichechidae (manatees). The sirenians received their name from the mermaids of Greek mythology known as sirens (Berta et al. 2015). Globally, all four species are considered to be in danger of extinction (Marsh et al. 2012).

Sirenians have streamlined, torpedo-shaped bodies with short necks and thick skin. They possess short, rounded paddle-like flippers used for steering, ambulation, and feeding, a horizontal

tail fluke, and no dorsal fin (Berta et al. 2015; Domning 2014). Sirenian bones show pachyostosis, or bone thickening, and osteosclerosis, or an increase in compact bony tissue. These features influence buoyancy during swimming (Domning 2014). Manatees are characteristically smaller than dugongs and have relatively rounder tails and a less pronounced snout (Berta et al. 2015).

All sirenian species are found in tropical and subtropical waters. The dugong (*Dugong dugon*) is the most widely distributed siren, commonly found in the shallow coastal bays of the Indian Ocean and western Pacific Ocean. On the other hand, manatees are coastal animals localized to specific rivers and oceans. They can also be found transitioning between continental shelf waters, such as in the Caribbean Sea. The West Indian manatee (*Trichechus manatus*) and Amazon manatee (*Trichechus inunguis*) reside in the western Atlantic Ocean. The African manatee (*Trichechus senegalensis*) is found in the eastern Atlantic Ocean ranging from Senegal to Angola (Forcada 2018).

Sirenians are the only group of fully aquatic herbivorous mammals. An individual must consume approximately 4–25% of its body weight per day to carry out basic functions. Dugongs feed almost exclusively on seagrass on the sea bottom, while manatees have a more variable diet. The West Indian manatee feeds on more than 60 species of freshwater, marine, and terrestrial plants, while the Amazonian manatee feeds on emergent freshwater plants (Hines et al. 2012). Cooler water temperatures and dietary restrictions limit the latitudinal distribution of sirenians to tropical and subtropical regions (Marsh et al. 2012).

Earliest known sirenians were quadrupedal and capable of terrestrial locomotion. The fossil record shows Sirenia first appearing in the late early Eocene of Africa with more diversity among the order appearing by the middle Eocene. The earliest ancestors were pig-sized, four-legged, and amphibious with well-developed legs (Berta et al. 2015; Domning 2018). However, their semi-aquatic lifestyle can be deduced by the discovery of dense, swollen pachyostotic ribs found within lagoon deposits

(Berta et al. 2015). By the end of the Eocene, Dugongidae appeared with a modern sirenian shape beginning to take form: fully aquatic, streamlined body, flipper-like front legs, no hind legs, and powerful horizontal hind fin. The Trichechidae were the last to evolve during the Eocene most likely from Dugongidae or other earlier ancestors (Domning 2018).

## Swimming

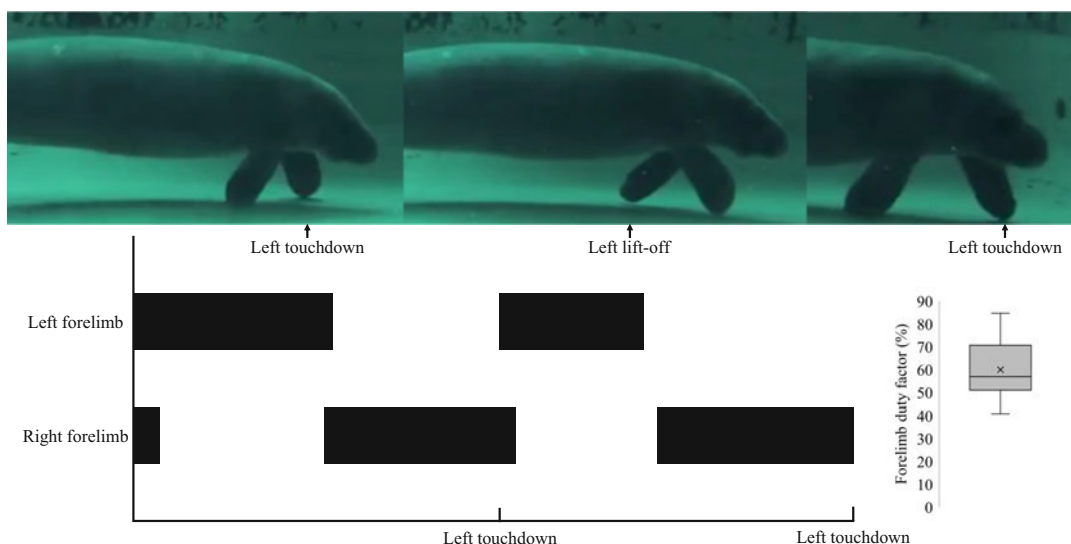
While manatees and dugongs belong to the same order, they employ different methods of swimming. Manatee locomotion utilizes a dorsoventral undulation of their wide, flat tail, which predates the use of the wing-like caudal fluke employed by the dugong. The fluke and body create a dorsoventral undulation that produces sinusoidal waves. The wave amplitude increases as it traverses the length of the body. Due to the use of primitive dorsoventral undulation in conjunction with their larger frame, fluke size, and wide absence of developed peduncular muscles, manatees are regarded as ineffective swimmers (Kojaszewski and Fish 2007).

Marine animals that utilize an undulatory method can be characterized as anguilliform, subcarangiform, carangiform, or thunniform. This characterization is determined by the posterior nature of the generated propulsive wave. Anguilliform swimmers create the smallest posterior wave, followed by subcarangiform, carangiform, and thunniform, respectively. Thunniform swimmers create the most posterior waves and move at higher speeds than subcarangiform swimmers, such as manatees. Subcarangiform swimmers create a wave rostrally across their body length as compared to the other swimming modes and have a fusiform body and a deep caudal peduncle. A small amplitude wave is created at the cranial end of the subcarangiform swimmers to counterbalance transverse waves and improve swimming efficiency. Manatees are considered to be less economical swimmers as they create less thrust power than other animals that use other swimming modes (Kojaszewski and Fish 2007).

In comparison to the manatees, the dugong is a fast swimmer due to its more economical oscillating wing-like caudal tail. This is evident as dugongs are more active in their daily movements and have an average speed of 2.7 m/s compared to the manatee's average speed of 0.6–0.8 and 0.8–1.89 m/s during migration. Dugongs are characterized as thunniform or carangiform swimmers (Kojaszewski and Fish 2007).

## Manatee “Swim-Walking”

Locomotor studies of the sirenians have primarily focused on tail-driven swimming biomechanics (see above) while largely ignoring the pectoral flippers. Kojaszewski and Fish (2007) describe the pectoral flippers of the manatee as being “held motionless against the body” during swimming. Behavioral observations of captive individuals reveal that manatees use their pectoral flippers to steer themselves while swimming, to anchor themselves to the seabed while feeding, and to guide food to their mouths (Horikoshi and Schulte 2006; Kikuchi et al. 2010). Additionally, Horikoshi and Schulte (2006) reported, but did not fully elaborate on, the presence of “swim-walking” as part of the daily behavioral repertoire of captive manatees at Homosassa Springs Wildlife State Park, Florida. During “swim-walking” the flippers remain mostly vertical, and slight protraction and retraction allow the animal to move forward in a stepwise fashion keeping in contact with the substrate below the manatee. Tail-driven propulsion is active during “swim-walking,” and this most certainly remains the primary form of forward thrust. It is unclear whether the forelimbs support any aspect of the animal's underwater body weight or provide any propulsive or braking forces. Significant force production is unlikely considering musculature of the pectoral flippers is thin and reduced (Dawson et al. 2000). As with other benthic walking species (Lucifora and Vassallo 2002), it is likely that manatees use “swim-walking” for more control and maneuverability for purposes of foraging. In this entry, we analyzed the gait sequence of “swim-walking” in a single West



**Sirenia Locomotion, Fig. 1** Representative cycle demonstrating forelimb “swim-walking” in manatees. Duty factor varies considerably, but across most cycles ( $n = 10$ ) is ~60% of a stride

Indian manatee (*Trichechus manatus*). During “swim-walking” the left and right forelimb contacted the substrate in an alternating, rather than paired punting, pattern. The duty factor, or the percentage of the time the flipper is on the ground, is approximately 60%, but this varies considerably across strides ( $n = 10$ ) (Fig. 1). The alternating left/right movement of the limb indicates that manatees are likely utilizing conserved neuromuscular patterns retained from quadrupedal ancestors (Domning 2001).

## Migrations

Another critical component to sirenian locomotion is how their locomotor preferences assist in moving about their environments through mass migration. Although some species have more individualized migration preferences, most species typically follow a set of general themes. Patterns of migratory behavior have been observed to be based mainly on seasonal conditions. Both dugongs and manatees have a preferable water temperature range in which they populate with problems arising when there is a deviation in ideal temperature. Specifically, sirenians prefer to travel to areas of warmer water when cold

seasons affect their locations. For example, it has been identified that dugongs are sensitive to water temperatures below approximately eighteen-degree centigrade (Sheppard et al. 2006).

Sirenians make long seasonal trips to locations that possess warmer waters during cold seasons. Once the cold season has passed, they return to their original habitat that has since rewarmed to an ideal temperature. For example, Florida manatees exhibit this behavior when migrating south in late autumn or early winter and returning in late winter or early spring (Deutsch et al. 2003). Although sirenians follow the basic principle of seasonal migration, migratory distance depends on multiple factors including sex and individual preference. Deutsch et al. (2003) reported that during their seasonal migration, male manatees covered more daily distance than females, and females were observed to be more sedentary than their male counterparts. It has also been observed that some manatees may not follow sex norms and travel at their own distinct migratory paces. Marsh et al. (1992) reported that tidal amplitude, which takes into account the current sea level of the area, has been seen to influence migratory behavior in dugongs. Tidal amplitude is essential for daily movements and behaviors (Marsh et al. 1992). Although a variety of factors tend to

impact the migratory behaviors of sirenians, it can be concluded they actively migrate to seek warmer climates during colder seasons.

## Sirenian-Human Interaction

Manatees and dugongs are in mortal danger when they come into contact with watercrafts. Additionally, the collisions could pose a danger to those aboard the vessel if significant damage results from the impact. These incidents have negative impacts on both sirenian and human populations. A study monitoring a group of tagged manatees observed that manatees spend 78% of their time near the surface of the water in the observation area (Edwards et al. 2016). The preference to be close to the surface of the water would place manatees at greater risk of being struck by a human craft.

Innovations that cause sirenians to divert away from approaching vessels could prevent lethal sirenian-human interactions. It was seen that sonar alarms emanating a certain frequency could lead to the avoidance of retrieving dugongs in fishing nets. McPherson et al. (2004) were able to observe that a sonar alarm emanating a frequency of 2.9 kHz was sufficient to cause a “cautious active avoidance response by dugongs.” The dugongs moved away from the nets that emanated the frequency. The findings are a clear sign that more research within this particular field is needed, as it could provide a better understanding of how humans can have a beneficial impact on sirenian behavior and locomotion.

## Conclusion

This entry explores the unique locomotion of sirenians and their interactions with humans. Modern sirenians are fully aquatic mammals that utilize dorsoventral undulation to transverse their environment. Sirenians also employ a form of walking that is primarily used for feeding and has not been thoroughly studied. Their locomotion is best exemplified when studying migration to warm

water when their habitat water temperature decreases. Due to their slow movement and preference to remain close to the water’s surface, human interactions can cause sirenian fatalities. Potential human innovations are arising to prevent lethal contact, such as releasing a frequency to alert sirenians to watercraft.

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Radiation](#)
- [Basal Metabolic Rate \(BMR\)](#)
- [Common Ancestor](#)
- [Dispersal Ability](#)
- [Dispersal Patterns](#)
- [Ecology](#)
- [Evolution](#)
- [Extinction in Learning](#)
- [Gait](#)
- [Herbivore](#)
- [Home Range](#)
- [Homology](#)
- [Homoplasy](#)
- [Locomotion](#)
- [Morphology](#)
- [Muscular System](#)
- [Natural Selection](#)
- [Navigation](#)
- [Paleontology](#)
- [Phylogeny](#)
- [Proboscidea Locomotion](#)
- [Sirenia Diet](#)
- [Sirenia Morphology](#)
- [Sirenia Navigation](#)
- [Sirenia Sensory Systems](#)
- [Species](#)
- [Taxa](#)
- [Terrestrial](#)
- [Territoriality](#)
- [Vertebrate Nervous System](#)
- [Zoo](#)
- [Zoology](#)

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## Sirenia Morphology

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## Synonyms

Order sirenia; Sea cow

Common Name: Manatee and Dugong

## Introduction

Sirenians derived their name from the Greek mythological name, sirens, believed to have its origin from lonely sailors confusing these marine mammals with mermaids. They are also known as sea cows as their diet is primarily herbivorous composed of submerged sea grass and floating or emerging vegetation. Some species can on



occasion eat fish or crustaceans. They spend a large part of their day eating and are slow moving, nonaggressive animals.

They have sparse hair over their body, mammary glands tucked under their pectoral flippers used to nurse their calves for 18 months or more, are warm blooded, and breathe air.

Modern-day sirenians contain two genera: *Trichechus* (manatees) which live in tropical or subtropical waters of the Americas within primarily the Gulf of Mexico, Atlantic, Caribbean, Amazonian rivers, and West Africa and the *Dugong* found in the Indian and Pacific Ocean (Velez-Juarbe et al. 2012).

There are three species of manatees: *Trichechus inunguis*, Amazonian manatee; *Trichechus manatus*, West Indian manatee; and *Trichechus senegalensis*, West African manatee. There is one extant species of dugong, *Dugong dugon*, and one extinct species, the Steller's sea cow (*Hydrodamalis gigas*). Man hunted the Steller's sea cow to extinction in the eighteenth century only 30 years after they were discovered in Arctic waters (Velez-Juarbe et al. 2012).

## Evolution

Sirenians likely evolved aquatically more than 60 million years ago (Eocene era) from terrestrial quadrupedal mammals. Their closest living land relatives today are Proboscidea (elephants) and Hyracoidea (hydraxes) (Domning 1994). They are completely distinct in their evolution from other marine mammals (Cetacea and Pinnipedia).

## Functional Morphology

### General

Manatees and dugongs are primarily gray in color and have robust thick fusiform-shaped bodies ideal for swimming and propelling through water using their horizontally flattened tail. Through evolutionary development, there was no need to have hind limbs in water; thus, they were eliminated and the pelvis was reduced to a small vestige. Manatees' tails are wide rounded

paddle shaped, and dugongs are fluke-like with lateral projections on their distal ends similar in shape to whales.

Manatees are generally larger than dugongs with adults reaching a mean length of approximately 3 m (9–10 ft) and an average weight of 410–545 kg (900 and 1200 lbs). Dugongs are often less than 3 m (8–10 ft) in length with an average weight of 420 kg (510–1100 lbs). Females are usually larger than males (Odell 1982).

They are primarily warm water inhabitants and can become ill or die in cold water. When water temperatures get colder, they seek out warm waters and have been found crowding around the output of warm outflows of electric power plants and paper mills (Bossart et al. 2002). This sensitivity to cold water is likely due to their low metabolic rate.

## Digestive System

Sirenids have large flexible bristled prehensile lips. The upper lip contains shortened sensitive sensory vibrissae, which allow for accurate food detection. The flexible lips are used to manipulate and gather food into its mouth. Dugongs and manatees differ in the fact that dugongs have a longer more “trunk-like” mouth with incisors or tusks, which are not present in manatees. These tusks can be seen projecting from the lips primarily in older male animals. Manatees have shifting similarly shaped molars that move forward as they wear out from grinding their teeth when chewing their food. Dugongs have six finite-fixed premolars and molars (Domning and Beatty 2007). Uniquely, the open-rooted two rear molars continue to grow throughout the life of the animal.

The digestive tract is extensive and reflective of its herbivorous diet requiring unique adaptations to metabolize and absorb food for nutrition. The simple stomach with its digestive cardiac gland helps breakdown complex plant cellulose and the extensive hindgut, similar to horses, are examples of adaptations producing one of the highest digestive coefficients (cellulose 80%) of any known herbivorous mammal (Burn 1986).

Manatees can often be seen seeking out fresh water sources.

## Special Senses

The eyes are well developed and have fairly good visual acuity (Hartman 1979). The eyelids open and close in a circular fashion similar to a camera lens and they have a nictitating membrane that protects and covers the eye when needed. Hearing is very acute and the ears are completely internal. They have large ear bones, which can also be used for aging (Marmontel et al. 1996). They emit various sounds used to communicate with each other during sexual, and play encounters but is distinctly used between mother and calf.

## Relationship of Lungs, Blood, and Bone Density

The dorsally placed nares quickly opens when the animal surfaces and deeply inhales. It then closes when swimming or diving. Air travels into the lungs where approximately 90% air exchange occurs in comparison to approximately 10–20% in humans (Rommel and Reynolds 2000).

The long bones of manatees and dugongs are solid and do not have a marrow space used to produce blood cells as in many terrestrial animals. Blood cells are primarily made from marrow found in the sternum. The heavy bone structure creates a negative buoyancy making their bodies sink in water, thus they have large elongated lungs placed dorsally along their backs to help compensate creating positive buoyancy (Rommel and Reynolds 2000).

## Pectoral Fins

The two pectoral fins or forelimbs are elongated, jointed, and paddle shaped. Their uses include steering, maneuvering, touching, and placing food into their mouth. Two manatee species have three to four nails, while dugongs and the Amazonian manatee do not.

## Morphological Adaptations and Survivability

The evolutionary adaptations found in manatees have unfortunately made them sensitive to numerous environmental and manmade dangers, which threaten their survival.

In the United States and Caribbean along coastlines and rivers, manatees are hit by fast-moving boats or jet skis when surfacing to breathe. These unfortunate impacts can be life-threatening as propellers tear through their backs where the elongated lungs are located. Infections, free air in the thorax (pneumothorax), and damage to bones are all sequelae to this constant danger. Deep cuts can also cause damage to the paddled fluke, which disrupts the animal's ability to swim. Because the animals are gray in color and their nares barely break the surface to breathe, they often blend in with surrounding waters and are difficult to see by water vehicles traveling at high speeds. Jet skis, for example, can cause significant trauma to the skull on impact to these slow-moving animals.

Another threat to their survival is monofilament fishing lines, nets, and numerous forms of discarded plastic left in water by humans. Entanglement in these lines can cause severe damage to the pectoral fins cutting off circulation and causing loss of the entire limb or even drowning.

Floodgate crushing injuries around power plants associated with the animals seeking warm water is also a perilous issue.

## Conclusion

The anatomy of all mammals is similar with adaptations often defined by evolutionary pressures placed on the species. Sirenian adaptations have evolved to produce the only herbivorous marine mammal known to exist today. Their specialized diet has produced an oral cavity adapted for their food resources. Their body structure and mobility in water are defined by their skeletal and muscular anatomy and appendages. Their buoyancy is defined by the weight of their skin, long bone structure, and pulmonary tissue. Their long

gestation period of approximately 1 year and milk-producing mammary glands are highly specialized for calf survival. All of their reproductive organs are located internally.

The majority of each adaptation has a specialized function and provides insight into the life history of the animal. In today's world of animals constantly being threatened with extinction, an understanding of these morphological structures is beneficial in understanding why these animals have been threatened with extinction. It will also likely prevent them from following in the same path of their extinct counterparts, the Steller's sea cow.

## Cross-References

► [Sirenia Sensory Systems](#)

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## Sirenia Navigation

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## Synonyms

[Dugong](#); [Manatee](#); [Migration](#); [Movement](#); [Movement patterns](#); [Range](#); [Trichechus](#)

## Definition

The behaviors of members of order Sirenia that allow them to interpret, move, and survive in their environment.

## Introduction

Species in order Sirenia are the only fully aquatic, herbivorous marine mammals. This order is comprised of sea cows, the extant species being the dugong (*Dugong dugon*) and three species of manatee (genus *Trichechus*). All species of dugongs and manatees are currently listed as vulnerable with a declining population trend. Sirenia inhabit coastal wetlands, coastal marine waters, rivers, freshwater lakes, and estuaries. They feed on sea grass and other bottom-dwelling marine vegetation. These sea creatures navigate throughout their home ranges to find food, seek mates, and escape predators. Species in temperate climates migrate long distances towards warm waters during winter.

Navigation is the capability of assessing position and being able to move in a specific route

based on that position. Many animals use navigation in multiple forms to aid survival. For example, some bat species use echolocation or biosonar (i.e., reflection of high-frequency sound waves) to navigate towards their prey; whereas wildebeests (*Connochaetes* spp.) use olfaction to navigate during their annual migration. Manatees and dugongs use a combination of morphological adaptations, memory, and environmental cues to navigate. Improving our understanding of Sirenia navigation could aid conservation efforts to restore these imperiled species.

### Morphological Adaptations for Navigation

Order Sirenia has several morphological adaptations related to navigation. Fully aquatic mammals, like manatees and dugongs, have either reduced or absent olfactory organs, so they must rely on other appendages and features to locate food. Sirenia have evolved vibrissae as a replacement for olfactory organs. Vibrissae are tactile sensory organs used to navigate the environment. Sirenia have several vibrissae, or bristles, mainly located on the snout. The West Indian manatee (*T. manatus*) has thousands of vibrissae covering its entire body (Marriott et al. 2013). Facial bristles are used for tactile foraging and raking vegetation into the mouth (Marriott et al. 2013). Muscles in the face are an essential part of bristle movement and effective foraging maneuvers, such as raking plants into the mouth (Marshall et al. 1998). Marshall et al. (1998) classifies the manatee vibrissal-muscular system as a muscular hydrostat – a muscular structure that allows for complex movement, sophisticated coordination, and directional change support. Manatees can also use the left and right clusters of vibrissae independently for even more controlled movements (Marshall et al. 1998). Dugongs have displayed a behavior in which they move their head up and down, allowing their vibrissae to skim over the surface of an object (Marshall et al. 2003). This behavior is interpreted as exploratory, perhaps feeling for texture or object recognition (Marshall et al.

2003; Reep et al. 2011). Reep et al. (2011) compares the manatee's oral disk vibrissae to the function of an elephant's trunk. Dugongs have also exhibited cleaning behavior, performing facial motions, such as wrinkling their snouts, or using their flippers in attempt to rid facial bristles of plant debris (Marshall et al. 2003). It is thought that these animals clean their bristles in order to keep sensory pathways open to receive accurate navigational information or to allow for full range of movement of the bristles (Marshall et al. 2003).

Post-facial bristles are dedicated to translating hydrological information through passive detection such as tide shifts, temperature changes, and sensing vibrations (Reep et al. 2011). One study estimates that vibrissae have sensitivity similar to that of a fish's lateral line or a human index finger, if not greater (Reep et al. 2011). Observation of West Indian manatees shows careful and constant movements of their flukes when navigating through the water, presumably because this area of the body is a highly important part of receiving sensory feedback (Sarko et al. 2007). Vibrissae are also sensitive to low-frequency sounds, which help manatees navigate toward objects and the source of the stimuli, similar to how a bat's echolocation waves reflect off of prey (Sarko et al. 2007). It is estimated that Sirenia can detect sounds from 5 to 150 Hz (Reep et al. 2011).

While vibrissae are common adaptations throughout all of Sirenia, the angle of the snout can indicate navigational habits between different species. Snout angle determines at which trophic level Sirenia species feed. Manatee species' snout angles vary between 26° and 38°, and the more downturned the snout, the greater depth in the water column the species feeds (Marshall et al. 2003). Species with a only slightly downturned snout, like West African (*T. senegalensis*) and Amazonian manatees (*T. inunguis*), are adapted to feed primarily on floating vegetation, while snouts with a great angle, like West Indian manatees, can feed on both floating and mid-water vegetation (Marshall et al. 2003). In contrast, dugong snouts are downturned by approximately 70°, adapting it to feed mainly on benthic vegetation (Marshall et al. 2003).

## Home Range

Sirenia home ranges are typically divided into two sections by season – winter home ranges and summer home ranges (Holley 2006; Arraut et al. 2009). Sea grass cover of at least 30%, water temperature, and shallow water depth are determining factors for choosing a home range (Holley 2006). Water salinity also dictates home range depending on the species, and as that water composition shifts, so will the home ranges of Sirenia. For example, West African and West Indian manatees can withstand salinity levels ranging from saline (i.e., marine) to freshwater, whereas the Amazonian manatee only inhabits freshwater rivers, lakes, and floodplains (Marshall et al. 2003). Summer and winter home ranges include the cumulative of locations each individual visits and areas of travel between locations. One study found that the mean home range size for dugongs vary from 4.1 km<sup>2</sup> to as large as 43.4 km<sup>2</sup> (Longh et al. 1998). Individual home ranges can overlap, and many studies suggest Sirenia will exhibit conspecific social interactions. Although Sirenia are known to congregate in warm-water foraging areas, each animal exhibits independent movement patterns and demonstrates variation in daily distance travelled or locations visited (Longh et al. 1998). Overlapping movements of individuals may indicate seasonal herding behavior, yet Sirenia still exhibit highly individualistic movement patterns (Holley 2006).

Sirenia are slow-moving creatures, often traveling well under 1 km per hour (Longh et al. 1998; Holley 2006). However, Sirenia can still cover significant distances outside of migration season. One study that followed tagged dugongs observed them traveling on average between 3 and 23 km per day (Holley 2006). Brief non-migratory excursions, dubbed “exploratory movements,” can also occur during which an individual may deviate from its typical range for a few days before returning to its normal home range (Holley 2006).

Vertical movement, specifically diving, has not evolved as a strong behavioral adaptation in these marine mammals. While Sirenia are capable of making small dives for benthic vegetation, deep

diving has not been selected for as a foraging behavior due to their preference for the shallower water benthic communities in which sea grasses grow (Sheppard 2008). However, significant dives of approximately 40 m deep have been recorded in dugongs, implying that these animals will make dives when necessary for foraging (Sheppard 2008). Dugongs move laterally with the tide, traveling closer to shore by night, perhaps because they are using tides as environmental cues to navigate towards vegetation or avoid predation in deeper waters overnight (Sheppard 2008). Dugongs also respond more to daily tidal patterns than do manatees, perhaps because manatees, unlike dugongs, can utilize freshwater habitats with little or no tidal activity (Sheppard 2008).

## Migration

Little is actually known about Sirenia migration or the mechanisms that drive it. A majority of migration data is gathered through radio telemetry. This method of data collection presents a problem when studying navigation because of limited signal transmission capacity underwater; therefore, there may be bias towards the mapping of foraging and resting areas while the migration corridors and pathways are underrepresented (Flamm et al. 2005). Manatees and dugongs migrate south between October and November when the water is colder and water levels are low, returning north in the spring (Arraut et al. 2009). Sirenia species have also been shown to migrate following a flood-pulse system, as varying water levels allow connectivity between locations. Sirenia prefer to move closely to shorelines rather than open water (Flamm et al. 2005). Manatees migrate at a constant rate by day and by night with males typically moving faster than females (Arraut et al. 2009; Flamm et al. 2005). Because of the lack of empirical data, much guesswork is done about the mechanisms that drive Sirenia migration. However, environmental cues such as water temperature and visual landmarks seem to be the main mechanical components of navigation.



Similar to home range movements, migratory behaviors and routes vary greatly between individuals. Flamm et al. (2005) suggests these differences indicate that navigation is choice-motivated by each individual, influenced by previous migration experience. In contrast to behavior within the home range, dugongs have been recorded to make frequent deep dives while migrating (Sheppard 2008). Two hypotheses have been proposed for this behavior: (1) dugongs make deep dives to avoid predation by sharks, (2) dugongs swim along the ocean floor to reduce the energy needed to swim against currents and drag in the open water (Sheppard 2008). More experimental research is needed to test these hypotheses.

Migration destinations are divided into two types: habitats and refuges (Sheppard 2008). Habitats are generally where the water is warm and sea grass is abundant; refuges are where there is a warm water hotspot, either naturally occurring or anthropogenically influenced. Sea grass is typically in proximity to warm water refuges – close enough to support daily foraging visits (Sheppard 2008). Despite the overwintering destination, migration in most Sirenia species still occurs to maximize optimal foraging activity throughout each season. Interestingly, migratory choices by Amazonian manatee present an exception to this concept. This tropical species migrates to waters where it spends months without an abundant supply of food (Arraut et al. 2009). It is hypothesized that this behavior occurs to avoid caimans and jaguars that can easily hunt them in low waters (Arraut et al. 2009). Differences between migration behaviors within Sirenia may be due to regional environmental variability (e.g., water temperature, seasonally varying forage availability, and predator context) and/or inherited migratory programs reflecting evolutionary history of manatees that drive some species to travel further north compared to their migratory tropical counterparts.

## Brain, Memory, and Navigation

Although little research has been conducted on the subject, Sirenia use a sophisticated

somatosensation system to navigate (Marriott et al. 2013). Somatosensation is a complex system of sensory neurons that responds to changes in and outside of the body. These neurons send signals directly to the central nervous system. Sirenia somatosensation acts through the vibrissae (see above), which are highly nerved (Sarko et al. 2007). Vibrissae are sensitive to thermal changes in the environment and water flow (Marriott et al. 2013). The central nervous system receives and interprets information from vibrissae on the oral disk, mouth, flippers, and fluke (Reep et al. 2011). Somatosensation works in conjunction with color vision to navigate the underwater environment. Studies find through brain examination that the nuclei associated with somatosensation are many times larger than the nuclei of any other sensory input (Sarko et al. 2007; Marriot et al. 2013). The somatosensory input mechanism of the thalamus is also much larger by volume than any other section of the thalamus (Reep et al. 2011).

In addition to somatosensation, Sirenia develop cognitive, or mental, maps over the course of their lifetimes to aid in navigation. As mentioned briefly above, it is hypothesized that navigation is partly choice-motivated. Flamm et al. (2005) suggests that experienced manatees make navigational choices based on the memory each animal has about its environment and previous experiences, while inexperienced individuals are “geographically naïve” (p. 1423) and rely more heavily on environmental cues and somatosensation to guide them. Development of a mental map is key to survival in both the home range and during migration. Sirenia appear to memorize areas of high-quality food locations within their home ranges (Sheppard 2008). It stands to reason that older dugongs with a more developed mental map would forage more efficiently than younger dugongs and calves. Dugongs and manatees have also been recorded avoiding established seagrass beds during migration, perhaps to avoid territorial encounters with other individuals (Sheppard 2008). Memory development seems to come from both environmental and tactile experiences. Sirenia are able to recognize specific objects due to the sophisticated neural cells that

are activated through use of vibrissae (Sarko et al. 2007). Further research is needed on how vision and somatosensation works in conjunction with memory to develop navigation behavior.

### Abiotic and Biotic Factors that Influence Navigation

The largest abiotic threat to Sirenia is climate change. Climate change causes more frequent droughts in the Amazon, causing migration pathways of the Amazonian manatee to be disconnected by the lower water levels and stranding individuals in unsuitable patches during drought migration (Arraut et al. 2009). A similar situation occurs in Florida where natural warm water springs grow shallower, slower, more saline, and more polluted resulting in manatees being unable to access and utilize the springs during critical overwintering periods (Edwards 2013). The Florida manatee (*T. manatus latirostris*) may also be impacted by the increased frequency and severity of storm events along the Gulf of Mexico coast, causing some groups to vacate historic migration sites and relocate to different areas (Langtimm et al. 2006; Edwards 2013). Severe storms also disrupt sea grass communities, often submerging plants under substrate or redistributing plants to other areas, which can lead to starvation in migratory manatees and dugongs (Edwards 2013). Hurricanes also cause manatees to die from the shock of cold waters that come after hurricanes (Langtimm et al. 2006). Cold water dulls the sensing capabilities of the vibrissae, thus reducing or muddling the information being received through these organs necessary for navigation (Langtimm et al. 2006). Storms also generate strong water currents that could push manatees and dugongs off their intended course or sweep them out to deep sea (Langtimm et al. 2006). Otherwise, data shows that these marine mammals prefer to stay where they are and ride out the storm (Langtimm et al. 2006).

Another effect of climate change is an increase in the amount and potency of toxic red tide algal blooms (Edwards 2013). The toxin of red tides,

known as Brevetoxin, is inhaled or absorbed through the skin and disrupts nervous system function through a form of neurological poisoning. This results in lethargic or comatose animals, which quickly leads to mortality. As oceans warm, algal blooms may appear earlier, persist longer throughout the season, and possibly expand in geographic range. Sirenia, especially the Florida manatee, now have to migrate through these waters with early-arriving blooms. In 2013, an estimated 643 manatees were shown to have died from exposure to red-tide algal blooms with an estimated exponential increase of death in subsequent years (Edwards 2013).

Overall, the system of Sirenia navigation has adapted to accommodate rapid environmental alterations caused by climate change, yet these adaptations are mainly favorable for summer conditions. Sirenia in North America appear to be expanding their summer range northward, traveling farther up along the Atlantic coasts than ever before (Flamm et al. 2005; Edwards 2013). One study notes that manatees have now been spotted in Massachusetts (Edwards 2013). However, these abiotic factors are wreaking havoc on southern ranges and winter migratory behavior. This has resulted in an inability to complete winter migration to the proper habitat, high mortality rate during winter migration, and altered or insufficient overwintering habitats upon arrival.

In addition to drought, hurricanes, and red tide, anthropogenic alterations have also impacted Sirenia navigation. Manatees and dugongs prefer warm waters and migrate to warmer places for the winter. Power plants warm the surrounding waters, and manatees have increasingly chosen these industrial water sites as winter refuges over natural sea grass habitats (Edwards 2013). If these power plants ever cease operations, aggregating manatees in these areas are at high risk for mass mortality events, an example of an anthropogenically induced ecological trap (Flamm et al. 2005). Several studies conclude that manatees show strong site fidelity. It is hypothesized that manatees will not migrate to a different area even when the water temperature decreases below critical thresholds and renders the habitat unsuitable

(Edwards 2013). Migrating to these industrial sites also increases the chance of watercraft collisions in areas with greater boat traffic (Edwards 2013).

## Conclusion

There are many aspects to consider when studying Sirenia navigation. Evolution of morphological features has developed mechanisms that allow Sirenia to navigate their environments. These mechanisms can be studied through observing and experimenting with behaviors as Sirenia navigate and interact with their environment. Tactile interactions and life experience lead to the formation of mental maps and memories. These important brain functions aid with foraging and migration patterns, both of which increase survivability. Like so many other species today, climate change and human activities have greatly impacted Sirenia and may be driving selection pressures to develop certain navigational behaviors. Many of these factors work together and combine functions to form the big picture of Sirenia navigation. Much more research and documentation is needed to fully understand Sirenia navigation – especially topics of neurological functions, facultative herding behavior, and the mechanisms that drive migration – and improve efforts to conserve the remaining species.

## Cross-References

- Cognitive Map
- Feeding
- Foraging
- Locomotion
- Memory
- Migration
- Navigation
- Sirenia Diet
- Sirenia Locomotion
- Sirenia Morphology
- Sirenia Sensory Systems
- Tactile Perception

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## Sirenia Sensory Systems

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### Synonyms

Dugong; Manatee; Neuroanatomy; Perception;  
Senses

### Introduction

Manatees (*Trichechus*) and dugongs (*Dugong dugon*) comprise the four extant species in the Order Sirenia. Their closest terrestrial relatives include elephants and hyraxes. Sirenians inhabit shallow coastal areas and river systems. West Indian (*Trichechus manatus*) and West African manatees (*Trichechus senegalensis*) are euryhaline; Amazonian manatees (*Trichechus inunguis*) inhabit rivers and lakes; and dugongs are exclusively marine (Marsh et al. 2011). Most behavioral studies of captive sirenians have only been initiated within the last two to three decades with little opportunity for replication; therefore, most findings are based on single studies. Experimental behavioral research on sirenian senses has been done primarily with West Indian manatees. Few sensory reports are published on the other manatee species or dugongs, consequently, unless otherwise stated, “manatee” will refer to studies of the West Indian species.

The behavioral-perceptual world of any animal is largely determined by the range of external stimuli that it can detect and the range of movements that it is capable of making. These traits co-evolve strongly with feeding and mating strategies and are also related to modes of communication and to energetic needs. Available anatomical and behavioral evidence suggests that manatees are somatosensory specialists,

with excellent hearing, reduced vision, and modest olfaction and taste. Manatees are mostly solitary, obligate aquatic herbivores that spend several hours per day engaged in feeding behavior. Groups appear to be temporary, based on resource concentrations (Marsh et al. 2011). In Florida, they navigate intricate coastal estuarine environments, with few visual cues to locate desired feeding areas. Their social behavior involves primarily cow-calf interactions. Mating takes the form of scramble polygyny, in which several males follow a female for days to weeks and engage in serial mating. Large winter aggregations of manatees occur at warm water sites due to thermoregulatory needs. Manatees have a low metabolic rate, which is associated with large body size and aquatic herbivory (Reep and Bonde 2006).

Compared to other mammals, manatees have small brain size in relation to their body size, but it is likely that selection pressures related to aquatic herbivory have resulted in large body size due to the need for an expanded gut. Thus, the brain may not be small relative to the body; rather, the body is enlarged relative to the brain (O’Shea and Reep 1990).

## Sensory Processes of Manatees

### Somatic Sensation

The hairs on manatees constitute a major source of somatosensory input to the central nervous system. All of the hairs are sensory hairs (vibrissae), defined anatomically as having a circumferential blood sinus, dense connective tissue capsule, and a variety of innervated mechanoreceptors (Sarko et al. 2007). This is in contrast to other mammals, in which sensory hairs are confined to restricted body regions, mostly on the head (Hyraxes are a notable exception, having both pelage hair and sensory hairs on the entire body.). Manatee sensory hairs move in response to water displacement or direct contact with objects including plants, conspecifics, and features in the environment. When a sensory hair is deflected, it makes contact with the follicle wall that contains mechanoreceptors. These receptors transduce mechanical energy

into electrical signals that are transmitted via axons to the brain.

There are three major categories of vibrissae on manatees based upon location, microscopic anatomy, and functional role: perioral bristles used in prehensile grasping, bristle-like hairs of the oral disk used in active tactile scanning and passive detection of water movements, and postfacial vibrissae, which passively detect water movements. Vibrissae are 30x denser on the face than on the postfacial body, reflecting the specialized anatomy and function of the facial region (Reep et al. 2011). Manatee tactile investigation often involves tactile scanning by the bristle-like hairs of the oral disk, followed by oripulation (Marshall et al. 1998; Bauer et al. 2012). Tactile scanning begins with eversion of the bristle-like hairs, and then continues with side to side movements of the head that allow the array of ~600 vibrissae of the oral disk to explore the object of interest. In some situations, tactile investigation also involves active poking movements of the perioral bristles. Feeding behavior and tactile investigation of objects, such as anchor lines, engage the perioral bristles in oripulation, grasping movements that are mediated by facial muscles innervated by the brainstem facial motor nucleus, which is large and exhibits discrete subnuclei.

Each manatee vibrissa emerges from a follicle-sinus complex (FSC) that contains hundreds of mechanoreceptors of at least three of the following types: Merkel, club, lanceolate, lobulated, tangle, trabecular, and free nerve endings. These follicles receive extensive innervation by C, A $\delta$ , and A $\beta$  axons (Sarko et al. 2007). The head region contains ~2000 vibrissae, and each FSC is innervated by 50–250 axons, resulting in a subtotal of ~109,000 myelinated axons supplying the FSCs of the head region. The postfacial body contains ~3300 vibrissae, with each FSC innervated by ~30 myelinated axons, for a subtotal of ~100,000. Thus, on the entire body of a manatee there is a total of ~5300 vibrissae and FSCs innervated by ~209,000 myelinated axons. Innervation of the head region vibrissae is via the trigeminal nerve; innervation of the postfacial body is via spinal afferents.

The large amount of information related to sensory hairs is conveyed by over 200,000 axons to several large, lobulated somatosensory nuclei in the brainstem. Axons from the face and head terminate in the trigeminal nuclei. Axons from the forelimb flipper and trunk reach the cuneate-gracile complex. A prominent Bischoff's nucleus, present in many tailed mammals, is also found in the caudal brainstem of manatees, suggesting that sensory input from the fluke is important. This is consistent with the multitude of adjustments made in the position of the fluke during swimming. The thalamic nuclei that receive input from the somatosensory brainstem nuclei are large relative to the nuclei related to other sensory modalities. The putative somatosensory cerebral cortex is likewise large and subdivided into several distinct areas. Neuronal aggregations known as Rindenkerne ("cortical nuclei") are found in the deep layers of some of these cortical areas. The Rindenkerne are hypothesized to process information from individual hairs, similar to the cortical barrels found in other mammals with vibrissae (Reep et al. 2011).

The rich neural elaboration of the somatosensory system is reflected in tactile sensation. In psychophysical experiments of manatee passive touch (mechanoreception), subjects stationed in the presence of a sinusoidally oscillating sphere, which generated a dipole, hydrodynamic stimulus. Using a go/no-go procedure with a staircase method, two manatees detected particle displacement of less than a micron at frequencies between 15 and 150 Hz and as low as a nanometer at 150 Hz (Gaspard et al. 2013, 2017). Thresholds were about one order of magnitude higher on the postcranial body than on the face. Elevated thresholds found after restricting facial vibrissae with a mesh mask and also after shaving an area of the torso indicated that the vibrissae provide increased tactile sensitivity. Manatees' remarkable ability to detect small water movements makes it probable that they can discriminate objects that divert water flow in subtle ways, as well as track major currents.

In tests of active touch (haptic reception) manatees discriminated small differences in grating widths in a two alternative, forced-choice



procedures (Bachteler and Dehnhardt 1999; Bauer et al. 2012). The manatees had interpolated discrimination thresholds between 2.05 and 2.15 mm when tested against a 2 mm standard. These differences can also be expressed as Weber fractions (just-noticeable-differences) of  $k = 0.025$  and  $0.075$ , where  $k$  is a constant determined by the ratio of the smallest detectable magnitude change divided by the magnitude of a standard stimulus. The manatee's ability to discriminate fine gratings using active touch suggests they can tactually resolve small details of objects in their environment.

### Audition

Manatees have short vocalizations (~400 ms) consisting of fundamental frequencies and harmonics ranging between about 3 and 20 kHz (Reep and Bonde 2006) as well as broadband components. There is no external ear, merely a small opening to the auditory meatus (Supin et al. 2001; Wartzok and Ketten 1999). The ossicular chain is massive. The cochlea has a typical mammalian spiral design. The basilar membrane, however, shows little base-to-apex differentiation in width. An airspace, the hypotympanic recess surrounding the cochlear capsule, may isolate the ear from the cranium, an important adaptation for sound localization (Chapla et al. 2007). The auditory/vestibular nerve (cranial nerve VIII) is a prominent feature of the lateral brainstem. Brainstem nuclei dedicated to hearing exhibit good differentiation, and include an enlarged nucleus of the lateral lemniscus (interestingly, this feature is also seen in echolocating bats and cetaceans, though there is no evidence for echolocation in manatees). The caudal colliculus of the midbrain is robust in size, and the medial geniculate nucleus of the thalamus is very large relative to other thalamic nuclei, as are the putative auditory cortical areas.

Hearing by manatees has been investigated using a variety of techniques. Their audiogram, the array of detection thresholds for the range of frequencies within their hearing range, was behaviorally determined using go/no-go (Gaspard et al. 2012) and two alternative choice procedures (Gerstein et al. 1999) in conjunction

with a psychophysical staircase method. Manatees could detect tonal sounds across a wide range of frequencies, as high as 76 kHz, greater than two octaves higher than a human adult, and as low as 250–400 Hz. An evoked potential study of an Amazonian manatee revealed sensitivity to a similar frequency range, 5–60 kHz (Supin et al. 2001). The narrower frequency range reported for this species may merely reflect the relative insensitivity of evoked potential techniques for manatees.

Critical ratios, estimates of the ability to hear in noise measured as the decibel difference between the tonal signal and background sound, indicated that manatees were able to hear well in noise with values ranging from 18.3 to 34.1 dB for tonal frequencies from 4 to 32 kHz (Gaspard et al. 2012). This sensitivity is especially strong in the range of the second and third harmonics of the tonal components of typical manatee vocalizations (fundamental ~4 kHz). Manatees may utilize the more variable upper harmonics to detect differences between calls, thus allowing identification of individuals. This is consistent with the observed peak hearing sensitivity at 8–32 kHz (Gaspard et al. 2012; Gerstein et al. 1999). The broadband aspects of phonations (O'Shea and Poche 2006) would also make them more localizable.

The auditory temporal processing rate of manatees, measured as the ability of the nervous system to map amplitude modulated tones, was determined using an envelope-following, evoked potential technique. Neural response measurements made in the thick dermal layer of the cranium indicated that subjects had high auditory temporal processing rates, up to 600 Hz (Mann et al. 2005). Later behavioral studies indicated that they could localize broadband sounds well in the azimuth plane (Colbert-Luke et al. 2015; Bauer et al. 2010), perhaps an adaptation for navigation in natural conditions where they might be able to localize surf or moving bodies of water through auditory scene analysis. Head (Body)-related transfer functions (HRTF) indicated that the manatee's large bodies shadowed sounds providing a potential sound localization cue.

Dugongs produce a variety of phonations in a similar range to manatees (3–18 kHz), although the length of these vocalizations may be considerably longer, over 2 sec in the case of trills (Anderson and Barclay 1995). Although no psychophysical testing of dugong hearing has been reported, it is usually safe to say that mammals are able to hear in their vocalization range.

## Vision

Manatees have small eyes in relation to body size and correspondingly small extraocular eye muscles. Unlike cetaceans and pinnipeds, which have spherical lenses, manatees have lenticular lenses, wider in the axial dimension than the transverse (Supin et al. 2001). There is a relatively low density of retinal ganglion cells, which is an anatomical indicator of visual acuity in many mammalian species. The optic nerves are very small, as are the lateral geniculate nuclei of the thalamus, a major center subserving form vision, in which many axons of the optic nerve terminate. The putative visual cortex is modest in extent. The rostral colliculi are modest in size; these receive other inputs in addition to those from the retina.

Visual acuity estimated from ganglion cell density in conjunction with the distance from the center of the lens to the retina is 20 arc minutes. Subsequent psychophysical tests using a method of constant stimuli in a two alternative forced-choice paradigm determined that the minimum angle of resolution (MAR) for one manatee was 21 arc minutes for horizontal gratings and 23 min for vertical gratings measured at one meter, closely in agreement with the estimate from anatomy. A lack of improvement when this manatee was tested at a closer distance suggests that manatees are emmetropic (no refractive error, image falls on the retina) or hyperopic (farsighted, image falls behind of the retina) underwater, consistent with the conclusion of Piggins et al. (1983) based on anatomical data of an Amazonian manatee. Further support for emmetropia/hyperopia was provided by a preliminary analysis of refraction using streak retinoscopy suggesting that a tested manatee was emmetropic-to-hyperopic

both underwater and in-air. The possibility of emmetropic vision both in-air and underwater would be an unusual combination, since the involvement of the cornea as a major refractive element in air coupled with its refractive neutrality underwater should typically lead toward specialization for only one of the environments, but not both. Notable exceptions are marine mammals, where dolphins and sea lions have developed specialized adaptations for focused vision in both environments (Wartzok and Ketten 1999). Follow-up behavioral and ophthalmological work with manatees is indicated to determine if the Sirenia constitute a third group of marine mammals with adaptations for both in air and underwater vision.

Manatees have modest brightness discrimination with Weber fractions ( $k = 0.35$ ) similar to fur seals (0.34) but higher than humans ( $k = 0.11$ ) (Griebel and Schmid 1997), indicating less sensitivity than humans. Different methods were used to assess brightness discrimination among these species, so comparisons are tentative.

Unlike other marine mammals such as the pinnipeds and cetaceans, which are monochromats, manatees are dichromats with short-wave and long-wave length receptors (Ahnelt and Kolb 2000; Marsh et al. 2011) more typical of terrestrial mammals. Psychophysical evidence supports the anatomical evidence indicating that manatees have dichromatic color vision in the blue and green range (Griebel and Schmid 1996). Their relatively modest visual acuity in conjunction with dichromatic color vision suggests an eye adapted for intermediate to long distance viewing appropriate for seeing patches of plants.

## Chemoreception

Manatees have reduced olfactory epithelium and olfactory bulbs, as is the case for other fully aquatic mammals. Likewise, the central olfactory nuclei and olfactory cortex are very modest in extent. Manatees also lack a vomeronasal organ, which functions in the detection and identification of pheromonal stimuli in many terrestrial mammals. Taste buds are present on the tongue and soft

palate in manatees but are rather restricted in number and distribution in comparison with many other mammals (Marsh et al. 2011; Reep and Bonde 2006). These findings appear to suggest a reduced role for chemosensation, but the finding of anal glands in manatees (Bills et al. 2012) and naturalistic observations suggest that there is much to learn about manatee chemosensation.

Manatees have been reported to use particular rubbing posts (Hartman 1979; Wells et al. 1999), an activity that especially makes sense if the posts retain chemical information regarding previous users of the posts. Manatees in social settings mouth one another (Hartman 1979) again suggesting that chemical cues may carry information regarding individual identity, sexual status, or other parameters. Manatees consume other manatees' feces, perhaps an example of coprophagy (Reynolds and Rommel 1996) as exhibited by a number of hindgut digesters, but also, perhaps to obtain information about reproductive status or dominance. In addition, various scientists have noted that mating herds of manatees form when roving males encounter and accompany estrous females for periods of several days. It is very possible that estrogen or other chemical cues from females in estrus are detected by the males and facilitate mating herd formation (Reynolds and Odell 1991). Thus, chemoreception may play a role in social and reproductive behavior of manatees.

Chemoreception in sirenians has not been studied with psychophysical methods in a rigorous laboratory environment. It may play an important role in social and reproductive behavior and in selection of appropriate habitat. Manatees show certain habitat preferences that can be extremely specific. Acoustic and tactile cues may provide part of the answer, but chemical reception may also play an important role.

## Conclusion

Some senses used by other aquatic mammals are apparently lacking or diminished in manatees. They do not echolocate, they have modest visual

acuity, and neuroanatomy suggests unimpressive chemical senses. Excellent hearing across a wide range of frequencies and good sound localization ability may provide a means for auditory scene analysis, but this is speculative. Alternatively, the tactile senses may provide a rich platform for detailed analysis of the environment. The available evidence suggests that manatees utilize the vibrissae distributed over the body as a three dimensional array to detect and localize hydrodynamic stimuli, a likely source of information important for orientation and navigation. These stimuli would be useful for detecting conspecifics, water currents, tidal flows, and objects in the environment. This conception is similar to the concept of the lateral line system of fish and amphibians as mediating "touch at a distance." The facial vibrissae are also utilized in direct contact, during tactile scanning and oripulation.

Hydrodynamic reception appears to be of general ecological value, as evidenced by the presence of this capability throughout animal taxa. Elongated hairs or hair-like appendages associated with mechanoreceptors that respond to hydrodynamic stimuli are found in a wide variety of invertebrate and vertebrate taxa (Bleckmann, 1994).

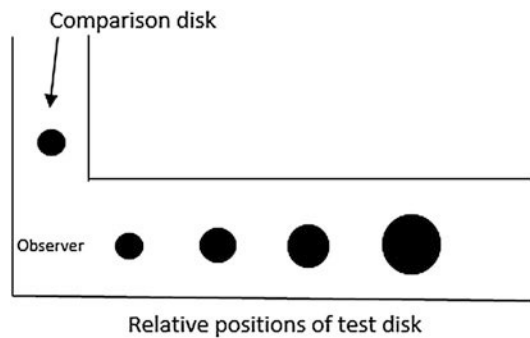
## Cross-References

- ▶ [Auditory Processing and Perception](#)
- ▶ [Cetacean Sensory Systems](#)
- ▶ [Chemoreception](#)
- ▶ [Encephalization](#)
- ▶ [Mechanoreceptors](#)
- ▶ [Occipital Lobe](#)
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- ▶ [Sirenia Navigation](#)
- ▶ [Tactile Perception](#)
- ▶ [Vision](#)
- ▶ [Visual Perception](#)

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**Size Constancy, Fig. 1** Experimental setup for Holway and Boring (1941) size constancy study

## Situated Cognition

### ► Embodied Cognition

## Size Constancy

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Size constancy occurs when the perception of an object's size remains constant, despite the relative distance from the observer (McKee and Smallman 1998). It allows us to understand that the size of a nearby object is the same size of an object that is further away. This explains how a retinal image can change, because of varying distances, but the perceived size of the object remains unchanged.

### History: Holway and Boring (1941)

In a classic study, Holway and Boring (1941) considered the potential role of depth cues on size constancy. The participants in this study were shown discs within two different corridors. One corridor provided a test disc (i.e., sample), and the other corridor provided a comparison disc that the participant could manipulate. During the experiment, the size and distance (i.e., depth cues) of a test disc were modified by the researchers

(Fig. 1). Researchers also manipulated the visual perception of the participants: binocular vision, monocular vision, and impaired vision (e.g., viewing discs through a small hole to decreased additional depth cues). On each trial, participants were asked to match the size of a test disc by manipulating a comparison disc to the perceived size of the sample.

Holway and Boring (1941) found that when all depth cues were available, observers were more accurate in perceiving size constancy than when some of the cues are missing or displaced. These distance cues play a critical role in not only perceiving depth but also maintaining size constancy.

### Underlying Factors of Size Constancy

The usefulness of visual cues creates an individual's perception of the world, such as depth perception. Depth perception is the ability to judge the distance and spatial relationship between objects. The visual cues are detected by both binocular and monocular vision. Binocular vision is the ability to perceive three-dimensional space as a result of two eyes working simultaneously to integrate binocular cues such as binocular disparity (i.e., the difference in where the image is located on the back of each eye) and convergence (i.e., when both eyes move together to look at a nearby object). Monocular vision, on the other hand, involves the use of one eye to gather information from the



environment. Monocular cues arise from the way a three-dimensional world is projected onto a two-dimensional retina (e.g., aerial perspective, linear perspective, relative size). Relative size, the use of familiar objects to judge size without depth, is related to size constancy. Despite these relatively standardized processes used to determine size constancy, there are times when visual perception can be misleading and visual illusions can occur. One example of a visual illusion, that is related to size constancy, is the Ponzo illusion. This illusion helps us understand how we process linear perspectives. We perceive the image of a horizontal line to be longer when it is moved farther away from us, while in fact the length of the line has not changed.

### Size Constancy in Animals

Size constancy has also been studied in a diverse group of species. Some species, such as insects and fish, rely on visual cues to determine their distance from an object. For example, the praying mantis uses side-to-side head movements in a horizontal plane to determine the jump distance to stationary objects and appears to use size constancy in depth judgments (Maldonado and Rodriguez 1972). For this species, it seems that the fixed compound eyes and head movement increase accuracy in distance information. In another study, Douglas et al. (1988) examined the ability of goldfish to discriminate between two circular discs of different sizes. The goldfish was trained to select one of the discs, termed the target disc. Once the discrimination was learned the discs were placed at various distances and the goldfish was required to select the target disc. The goldfish continued to select the target disc regardless of the distance which supported their use of size constancy. While most of the research has focused on animal and human vision, it should be noted that other senses have been studied. In a unique study on a blind individual that used echo clicks, researchers found that their sensation of sound also could be related to size constancy (Milne et al. 2014).

### Cross-References

- Depth Cues
- Depth Perception
- Ponzo Illusion
- Visual Illusions
- Visual Perception
- Visual Search

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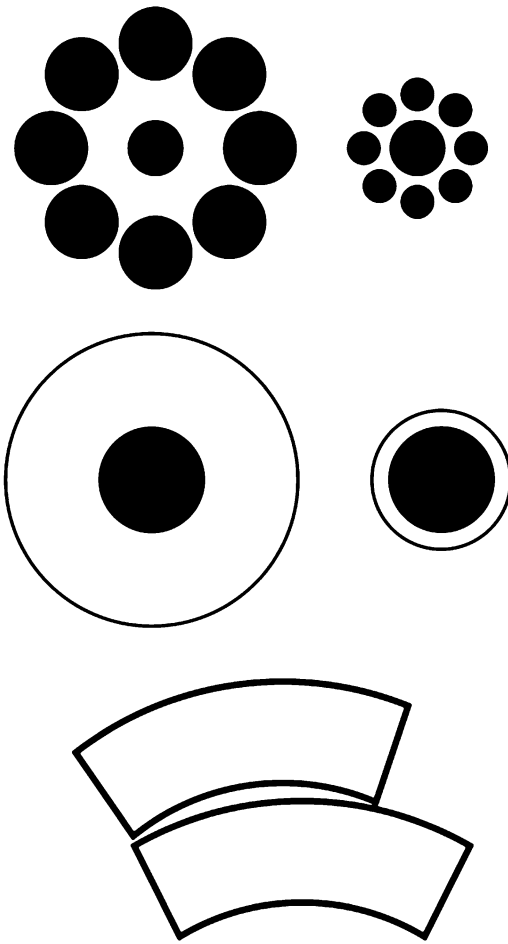
### Size Illusion

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A variety of geometric illusions that are experienced by humans lead to errors in size estimation of stimuli. Some of these illusions have been studied from a comparative perspective. These include the Ebbinghaus-Titchener illusion, the Delboeuf illusion, and the Jastrow illusion (see Fig. 1). Understanding how humans, and other species, misperceive the world through



**Size Illusion, Fig. 1** Example of the Ebbinghaus-Titchener illusion (top), Delboeuf illusion (middle), and Jastrow illusion (bottom). For the Ebbinghaus-Titchener stimuli, most people believe the central dot at right (surrounded by small dots) is larger than the central dot at left (surrounded by large dots). For the Delboeuf illusion, most people believe the central dot at right is larger than at left. For the Jastrow illusion, most people believe the shape at bottom is larger than the one at top. In cases, those central dots or shapes are the same size

susceptibility to these and other illusions provides important insights into the nature of perception and also into the subsequent choice behavior and decision-making processes that rely on perceptual experiences. For this reason, perceptual illusions have been of great interest to psychologists, philosophers, and vision scientists, and discussions about the nature of illusory experiences stretch back to the ancient Greeks.

## Geometric Illusions: Misperceptions of Size

Geometric illusions emerge when the physical dimensions of a target stimulus are misperceived as a function of the illusory-inducing context in which it is presented. Geometric illusions can lead to misperceptions of size, length, height, color, perceived movement and direction and brightness. Specifically, size illusions emerge when the area of a target stimulus is misperceived to be larger or smaller than reality. Note that some people would also include other illusions in this broad category beyond those that we discuss, given that things such as size, length, and width can also be considered as subcategories of size. In that case, the Müller-Lyer illusion, Oppel-Kundt illusion, Baldwin illusion, vertical-horizontal illusion, Ponzo illusion, and others also could be included. Here, we have focused on illusions for which the judgment is to be made specifically on size, and not those other properties. For example, in the Ebbinghaus-Titchener illusion (hereafter Ebbinghaus illusion; Fig. 1), a central dot is misperceived as a function of the size of inducing circles, such that large inducers lead to underestimates of central dot size and small inducers lead to overestimates of central dot size. Scientific investigations of geometric illusions such as this one date back to the 1800s and continue to provide a noninvasive means by which psychologists can understand better the visual and perceptual systems of humans and animals.

A critical component underlying the emergence of geometric illusions concerns perceptual processing mode or the manner in which an individual perceives the global figure relative to the individual elements that comprise a visual array. For illusory experiences, the target stimulus is misperceived as it is viewed in conjunction with the illusory context (e.g., the Ebbinghaus central dot is perceived among the inducer circles). Species and even individuals within a species differ in terms of the readiness with which they perceptually group the individual elements within an array, with some displaying a global-to-local precedence (i.e., perception of the global configuration prior to the individual elements; central dot + inducers) and others a local-to-global

precedence (i.e., individuation of the separate elements prior to perception of the global figure; inducers and central dot separately). Regarding comparative investigations, species differ in their perceptual processing mode, thus visual illusions provide a useful means by which we can study potential differences in perceptual mechanisms using similar experimental procedures across a variety of settings and species.

Furthermore, geometric size illusions emerge as a function of contrast and assimilation mechanisms, which have received ample attention in comparative studies. Contrast effects result in overestimates of the difference between stimuli that are positioned farther apart, whereas assimilation effects result in underestimates of the difference between stimuli positioned nearby. Using the Delboeuf size illusion illustrated in Fig. 1, the central target dot is contrasted with the larger, distal ring and thus perceived as smaller than the central target dot with the smaller, nearby ring that it assimilates with leading to overestimates in target dot size. Species differences in susceptibility to contrast and assimilation effects have been documented for a variety of geometric illusions (e.g., the Ponzo and Müller-Lyer line-length illusions), with the most well-studied case of the pigeon, which appears to be susceptible to assimilation effects but not contrast effects (see Fujita 2006, for a review). Thus, size illusions offer a useful means by which comparative psychologists can explore further species differences in sensitivity to contrast and assimilation mechanisms.

### The Jastrow Illusion

A well-known size illusion experienced by humans is the Jastrow illusion (Fig. 1). In this case, two vertically stacked but offset stimuli of identical size are misperceived in such a way that the perceiver believes the bottom stimulus is larger than the top stimulus. Only three assessments of the Jastrow illusion have been conducted with nonhuman animals. Révész (1924) trained a hen to peck for grains from the relatively smaller of two objects placed in an arena where the size and shape of the objects varied throughout

training. Then, arenas were presented with two same size objects arranged in a Jastrow-like pattern. The hen showed a significant bias toward the object that was estimated as smaller by human observers (the top shape in Fig. 1). Tomonaga (2015) trained four chimpanzees to select a narrower stimulus from two options in a computerized size discrimination task. Then, the Jastrow-like illusory pair of stimuli were presented on some trials, and the chimpanzees selected the top stimulus more often than expected by chance, suggesting that they perceived the top stimulus as the narrower option. Finally, Agrillo et al. (2019) presented the same computerized task to human adults, rhesus macaques, and capuchin monkeys. All species learned to discriminate shapes based on size, and when presented with Jastrow illusion trials, humans perceived the illusory stimuli as predicted. Although both species of monkeys performed well in trials with a true size difference between shapes, they did not show evidence of the Jastrow illusion. They were indifferent between top and bottom stimuli in the illusory arrangement. This could lead to a prediction that broader species testing with this illusory condition also may produce highly varied results.

### The Ebbinghaus and Delboeuf Illusions

The Ebbinghaus and Delboeuf illusions are two of the most well-studied geometric size illusions represented in the human and animal literatures. In these illusions, a central target dot is misperceived as smaller when surrounded by larger inducing stimuli (Ebbinghaus inducer circles or Delboeuf ring) and larger when surrounded by smaller inducing stimuli due to assimilation and contrast mechanisms (Delboeuf 1892; Ebbinghaus 1902). A variety of species have been presented with the Ebbinghaus and Delboeuf illusions using two-dimensional stimuli as depicted in Fig. 1 via computerized or manual testing. Additionally, a number of studies have presented animals with a two-choice

discrimination procedure using edible food stimuli arranged in the shape of the illusory array. Control trials using either approach establish whether the subject can discriminate true differences in size in the absence of the illusory inducing context (e.g., discrimination of central target dots with no rings or identically sized rings). These trials are vital to determining whether subjects understand the objective of the size discrimination task and whether they are sensitive to certain discrimination thresholds at which the illusions are most likely to emerge. Critical test trials present the illusory inducing context (e.g., two different-sized rings surrounding nearly identical or identical dots) with the prediction that animals will classify or choose the target dot surrounded by a small context as larger than the target dot surrounded by a large context.

A number of species presented with the Ebbinghaus and Delboeuf illusions respond in a humanlike direction, perceiving stimuli surrounded by large inducers as being smaller and vice versa, including redbtail splitfin (Sovrano et al. 2015), damselfish (Fuss and Schluessel 2017), bearded dragons (Santacà et al. 2019), dolphins (Murayama et al. 2012), domestic cats (Szenczi et al. 2019), capuchin monkeys and rhesus macaques (Parrish et al. 2015), and chimpanzees (Parrish and Beran 2014). A number of these species also have been assessed for their perceptual processing mode and reveal a global precedence, including redbtail splitfin, dolphins, and chimpanzees. However, evidence of a reversed or weakened Ebbinghaus and Delboeuf illusion has been documented in some species, including guppies (Lucon-Xiccato et al. 2019), gray bamboo sharks (Fuss and Schluessel 2017), bantams and pigeons (Nakamura et al. 2008, 2014), domestic dogs (Byosiére et al. 2017; Miletto Petrazzini et al. 2017), lemurs (Santacà et al. 2017), and baboons (Parron and Fagot 2007). These cases may reveal a weakened susceptibility to contrast effects or a local precedence and, in some cases, an inability to discriminate size at a particular threshold necessary for illusory emergence.

Methodological variations also impact illusory emergence for animals and humans. Experimental designs that highlight the inducer or target stimuli as separate units undermine global processing in

humans, such that increasing the distance between stimuli or varying the brightness or shape of the inducer circles and target dot lead to a weakened Ebbinghaus illusion. For example, comparative studies yielding a weakened or reversed Ebbinghaus illusion employ methods that aid the animal in differentiating the target and inducer stimuli via different color/brightness stimuli (Nakamura et al. 2008, 2014; Parron and Fagot 2007). Studies have shown that a non-illusion or a reversed illusion may emerge when animals fail to differentiate target and inducer stimuli and inadvertently respond to the size of the overall array versus the target stimulus alone (e.g., Parrish et al. 2015; Qadri and Cook 2019).

Perceptual processing mode also appears to be linked to viewing angle, such that closer vantage points lead to a focus on local elements versus more distal vantage points which favor apprehension of the global array in human adults. Comparative studies have reported differences in the susceptibility to the Ebbinghaus illusion among the same species (the domestic chicken), with a study that required a pecking response to stimuli (and arguably a closer vantage point) leading to a reversed illusion (Nakamura et al. 2014). In contrast, a study that required domestic chicks to approach the stimuli from a distance (and arguably a more distal vantage point) reported evidence of a humanlike Ebbinghaus illusion (Rosa Salva et al. 2013). Thus, experimental design has clear impacts on the emergence of size illusions, such that methodological variations in training, stimuli design, and response modality likely interact with a species' perceptual processing mode to directly influence the emergence of illusory perceptions. Future studies with additional species would be illuminating and could lend empirical support for some of the theoretical ideas that have emerged from studies of these and other geometric illusions.

## Cross-References

- [Delboeuf Illusion](#)
- [Ebbinghaus Illusion](#)
- [Visual Illusions](#)
- [Zöllner Illusion](#)

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## Skate Locomotion

### ► Chondrichthyes Locomotion

## Skeletal System

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## Synonyms

Appendicular skeleton; Axial skeleton; Endoskeleton; Skeleton; Vertebrate skeleton



## Definition

The skeletal system refers to all structures, both rigid and semirigid, which provide structural foundation, support the body's soft tissues, protect internal organs, and provide necessary leverage for muscle function.

## Introduction

Skeletal systems may vary widely between species, but all serve to provide both functional structure and protection from external injury. For most insects, crustaceans, and other invertebrates, this structure is the outermost part of the body and is called an exoskeleton. In vertebrates, this structure is internal and is called an endoskeleton. Vertebrate skeletons are a group of relatively rigid structures composed of a combination of connective tissues generally classified as bone and cartilage (Encyclopedia Britannica 2018). This chapter will focus on the development, function, and anatomical specifics of the vertebrate skeletal system.

## Skeletal System Development

The skeletal system is comprised of mainly two types of connective tissue: bone and cartilage. Bones are a specialized form of connective tissue with a mineralized matrix and are generally considered the organs of the skeletal system. Their mineralized matrix, composed of hydroxyapatite crystals, results in the extremely hard structure of bones that allow them to provide support and protection (Ross and Pawlina 2006, p. 202).

Because bones tend to vary widely in terms of size, shape, structure, and even function, there are a number of ways in which bones can be classified. One classification system involves the structural arrangement of the bone tissue. Cancellous, or "spongy bone," refers to the latticelike trabeculae that form the innermost part of bones (Ross and Pawlina 2006, p. 203). In contrast, "compact bone" refers to the solid, dense layer that forms on the outside of bones. The periosteum is a sheet

of fibrous connective tissue that surrounds the outside of the bone (Zalisko and Kardong 2001, p. 40). Bones are also often characterized according to their shape. Long bones are elongated in one direction when compared to the other and are generally composed of a shaft and two ends. An example of a long bone would be a femur. Short bones are generally described as having a diameter that is equal in all dimensions, like the carpal bones of many species. Flat bones, like the sternum, are generally thin with a small layer of spongy bone sandwiched between two outer layers of thick compact bone. The final shape category is referred to as irregular bones. These bones have shapes that do not fit with the other three categories, like vertebrae (Ross and Pawlina 2006, p. 204).

Bones can also be classified according to embryologic origin. Different portions of the skeleton are generated by different developmental processes. The axial skeleton is derived from somites, the appendicular skeleton is a product of the lateral plate mesoderm, and the craniofacial bones are generated by the cranial neural crest (Gilbert 2000). The formation of the bone is generally classified by one of two processes.

Bones can form through either (a) endochondral ossification or through (b) intramembranous ossification. Endochondral ossification relies on a cartilaginous template as a bone precursor, where intramembranous ossification is the direct conversion of mesenchymal tissue into bone tissue (Gilbert 2000). Generally, bones that are weight bearing, like bones of the appendicular skeleton or the vertebral bones, are formed by endochondral ossification. In contrast, intramembranous bones form directly from the mesenchyme without a cartilage precursor. Sesamoid bones, periosteal bones, and dermal bones all undergo intramembranous ossification. Bones like the patella, portions of the skull, the clavicle, and even the turtle shells are formed by the direct bone formation method of intramembranous ossification (Gilbert 2000). Though the two methods may differ in their initial stages, the preliminary bone laid down by both methods is quickly replaced by identical new bone (Ross and Pawlina 2006, p. 216).

In endochondral (*endo*, within; and *chondral*, cartilage) bone formation, cartilage is a specialized connective tissue that is composed of chondrocytes and a significant extracellular matrix. Chondrocytes are specialized cells within cartilage that both produce and maintain the extracellular matrix (Ross and Pawlina 2006, p. 184). The avascular character of cartilage means that there is no blood flow through any cartilaginous tissues. This lack of vascular channels, vital for the cartilage cells survival, accounts for the dependence of the chondrocytes on the extensive extracellular matrix (Ross and Pawlina 2006, p. 182). Essential nutrients reach the chondrocytes via extensive diffusion from the blood vessels in the perichondrium through the matrix (Zalisko and Kardong 2001, p. 39).

Based on the type and amount of protein fibers that are present in the extracellular matrix, cartilage is further divided into three subcategories: hyaline cartilage, elastic cartilage, and fibrocartilage. Hyaline cartilage is the most common type of cartilage and is found in many places throughout the skeletal system (Zalisko and Kardong 2001, p. 40). The matrix of hyaline cartilage is produced by chondrocytes and contains type II collagen molecules, proteoglycans, and multi-adhesive glycoproteins. Hyaline cartilage serves a variety of functions and is found in both fetal and adult skeletons. During fetal development, the hyaline cartilage serves as the model for the developing skeleton. In initial stages of development, most long bones are represented by hyaline cartilage templates that resemble the shape of the eventual mature bone (Hill 2018). As development progresses, it is replaced by bone until cartilage remains only on articular surfaces of joints and on the ends of ribs. These cartilaginous structures persist in adulthood and provide a smooth, well-lubricated surface for the ends of bones within a joint. Hyaline cartilage is also found in the larynx, trachea, and bronchi of adults (Ross and Pawlina 2006, p. 194).

Elastic cartilage differs from the other types of cartilage due to the presence of elastin in the extracellular matrix. While elastic cartilage maintains the resilience and pliability of hyaline cartilage, the structure of its extracellular matrix gives

it additional properties of elasticity and flexibility. This type of cartilage is commonly found in the external ear, the auditory tube, and the epiglottis (Ross and Pawlina 2006, p. 190).

The last cartilage subtype, fibrocartilage, is hyaline cartilage that has been combined with dense connective tissue. It is histologically similar to hyaline cartilage, except for an increased number of collagen fibers present in fibrocartilage (Zalisko and Kardong 2001, p. 40). This type of cartilage is analogous to a shock absorber. It is often present in locations that require significant resistance to shearing and compressive forces. Fibrocartilage is present in intervertebral disks, the pubic symphysis, menisci, and occasionally at a given point of tendon insertion. It is composed of both type I and type II collagen and functions to resist distortion under stressors (Ross, p. 191).

## General Skeletal System Structure

The body's skeletal system can be subdivided into the axial skeleton and the appendicular skeleton (Pasquini et al. 2007). The term “axial skeleton” refers to the bones and cartilage that protect the soft tissue structures of the head, neck, thorax, and abdomen. These structures include the skull, the hyoid apparatus, the vertebral column, the ribs, and the sternum (Pasquini, p. 26).

### The Axial Skeleton

#### Cranial Skeleton (Skull)

The size and shapes of vertebrate skulls may differ drastically between different animals, but a common morphological pattern to the bones and their locations exist between most vertebrate species. The dorsal portion of the skull incorporates the frontal bones and the parietal bones, which together form most of the dorsal covering of the cranial cavity. The occipital bones occupy a large portion of the back of the skull and include the paired occipital condyles and the foramen magnum. A lateral view of the skull shows the upper portion of the jaw, or the maxilla, articulating with the lower jaw bone, the mandible. The temporal process of the zygomatic bone and the zygomatic

process of the temporal bone join together to form the zygomatic arch. Caudal to the maxilla and just below the zygomatic arch lay the palatine bone, the presphenoid, and the basisphenoid. The hard palate of the skull is formed by the palatine processes of the premaxillae, the maxillae, and the palatine bones.

### Vertebral Column

The vertebral column, or the backbone, is the main phylogenetic trait of all vertebrate species. While basic structural aspects of the vertebral column can differ between species, general trends in development, structure, and function can be seen across all vertebrates. The mammalian vertebral column can be broken down into five different areas or subsections: cervical vertebrae, thoracic vertebrae, lumbar vertebrae, sacral vertebrae, and caudal vertebrae. Segments of fibrous cartilage are located between the bony vertebrae and are known as intervertebral disks (Zalisko and Kardong 2001, p. 53).

### Cervical Vertebrae

In mammals, the first two cervical vertebrae are referred to as the atlas and the axis. The atlas is a ring-shaped vertebra with paired, winglike transverse processes. The axis sits just caudal to the atlas and has a broad spinous process that projects over the atlas. In most mammals, the axis would be followed by five additional vertebrae with articular processes, vertebral foramen, a neural arch, a spinous process, centrum, and transverse processes (Zalisko and Kardong 2001, p. 52).

### Thoracic Vertebrae

The thoracic vertebrae of mammals are generally tall with short transverse processes and spinous processes angled caudally. There is a small depression where the head of the rib articulates with the centrum known as the facet.

### Lumbar Vertebrae

Lumbar vertebrae can be differentiated from thoracic vertebrae based on the cranial orientation of the transverse and spinous processes (Zalisko and Kardong 2001, p. 52).

### Sacral Vertebrae

In mammals, the individual sacral vertebrae are fused together to form a single sacrum. The number of fused sacral vertebrae differs between species. There are three fused vertebrae in dogs and cats, four in a rabbit, and five in humans and horses (Zalisko and Kardong 2001, p. 52).

### Caudal Vertebrae

The transition to the caudal vertebrae is accompanied by a significant loss in prominence of the arches and processes. The number of caudal vertebrae is dependent on tail length, and there is significant difference between species and even individuals. In humans, all caudal vertebrae fuse together into a single piece called the coccyx (Zalisko and Kardong 2001, p. 52).

### Ribs (Costae)

Ribs are comprised of a bony vertebral rib and costal cartilage. Ribs are bicipital, with the capitulum, or head of the rib, articulating with the centrum and the tubercle articulating with the transverse process. The bony portion between the capitulum and the tubercle is called the neck, and the rest of the rib is referred to as the body or shaft (Zalisko and Kardong 2001, p. 52).

### Sternum

The sternum, also sometimes referred to as the breastplate, is a flat bone composed of usually eight sternebrae that attach to the ventral aspects of the ribs. The first and most cranial sternebra is called the manubrium, and the most distal sternebra is called the xiphoid. Six additional sternebrae lie in between the manubrium and the xiphoid making up the body of the sternum.

## The Appendicular Skeleton

The term “appendicular skeleton” includes limb bones as well as the bones that connect the limbs to the axial skeleton (Pasquini et al. 2007, p. 26).

### Pectoral Girdle

For the majority of mammalian species, the pectoral girdle is characterized by significant mobility as well as structural support. Because of its intrinsic mobility, the thoracic girdle has an increased

reliance on surrounding musculature for proper support and appropriate transmission of forces. The mammalian pectoral girdle generally only includes a clavicle and scapula. The paired clavicles serve to anchor the thoracic limbs to the axial skeleton. The scapula is a flat bone located on the dorsal portion of the cranial thorax that serves as an attachment point for many of the muscles and tendons of the arm, chest, and back. Each scapula has a spine that terminates in a point called the acromion. The acromion process articulates with its respective clavicle serving as the attachment point for muscles of the arm and chest (Pasquini, p. 26).

#### Thoracic Limbs

The humerus is the largest forelimb bone. The proximal head of the humerus articulates with the glenoid cavity of the scapula to create the shoulder joint. Two processes, known as the greater and lesser tubercles, are present distal to the humeral head and neck. These serve as attachment points for important forelimb musculature. The body of the humerus terminates into the medial articular surface called the trochlea and the lateral articular surface called the capitulum. The distal portion of the humerus articulates with the proximal portion of the forearm bones to form the elbow joint. The trochlear notch of the ulna articulates with the trochlear surface of the humerus. The head of the radius articulates with the capitulum of the humerus. The distal ends of the radius and ulna articulate with multiple carpal bones to form the wrist joint. The five metacarpals and phalanges make up each hand and its digits (Pasquini, p. 72).

#### Pelvic Girdle

When compared to the pectoral girdle, the bones of the pelvic girdle tend to be solid and fixed weight bearing structures. Its structure provides strong foundational stability and support for movement. The fused bones of the ilium, acetabulum, ischium, and pubis make up the hemipelvis (Evans and de Lahunta 2010, p.81). The ilium is comprised of a narrow body and a concave wing. The acetabulum is a socket that

serves as the attachment point for the femur to the pelvic girdle (Newton 1985). The ischium forms the caudal floor of the pelvis, and the pubis forms the cranial floor of the pelvis. Each hemipelvis attaches to the other on the opposite side to form the ischial and pubic symphyses (Pasquini, p. 26).

#### Pelvic Limb

The femur, fibula, tibia, metatarsal bones, tarsal bones, and phalanges make up each pelvic limb. The femur is the long bone of the hind limb and is comprised of a proximal head, neck, and greater trochanter, a shaft, and distal lateral and medial condyles (Carrier et al. 2006, p.2225). The head of the femur attaches to the pelvic girdle at the acetabular fossa via the round ligament forming the hip joint. The tibia and fibula are the hind limb bones just distal to the femur. The distal femur, proximal tibia, and patella form the knee joint. The fibula is long and slender and lies lateral to the thicker tibia bone. The ankle joint is formed by the tarsal bones. The five metatarsals and phalanges make up each foot and its digits (Pasquini, p. 26).

## Conclusion

Despite differing appearances and functions, the skeletal systems of most vertebrates have many similarities both developmentally and anatomically. The basic building blocks of the skeletal system, bone and cartilage, remain relatively consistent throughout vertebrate skeletons with few anatomical and developmental variations. The assemblage of these basic building blocks also retains a consistent theme when compared across different branches of the vertebrate phylogenetic tree. The skeletal differences that exist between species can be attributed to differing anatomical physics needed for different environmental and lifestyle needs. Despite these differences, all species' skeletal systems are an essential basic component of life providing structural foundation, support of the body's soft tissues, protection of internal organs, and necessary leverage for muscle function.

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## Skeleton

### ► Skeletal System

## Skills

### ► Horseback Riding

## Skin and Its Derivative

### ► Integumental System

## Skinner Box

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## Synonyms

Operant chamber; Operant conditioning chamber; Repeating puzzle box

As its name suggests, the “Skinner box” was invented by B. F. Skinner while he was still a graduate student at Harvard University in the 1930s. Rather than use the term “Skinner box,” Skinner only ever referred to this invention as an operant chamber or as an experimental box, space, apparatus, or chamber (Nye 1992). The origin of the “Skinner box” title has generally been associated with psychologist Clark Hull, having appeared in his publication, *Principles of Behavior: An Introduction to Behavior Theory* (Hull 1943; see also Iversen 1992). However, the term “Skinner box” appears in other publications, as early as 1939 (Krechevsky 1939; Smith and Smith 1939; Humphreys 1940).

Skinner first began studying animal behavior during his graduate training at Harvard. Inspired by the work of Pavlov, Skinner sought to study behavioral adaptation in rats using a controlled environment (Skinner 1972). He first constructed a soundproof box with a long tunnel ending in a flight of steps. Skinner described this as “something like a functional Parthenon” (1972, p. 104). As Skinner’s interests evolved, so did his devices. Over time, he became interested in rat reflexes and developed a rectangular runway to study reflex responses. As he observed the rats, he was intrigued by their delayed behavioral responses.



As his interests shifted to the rate of response, he created a new recording system to track the rate of behavioral change over time, and the runway morphed into a recognizable Skinner box (Skinner 1972). It has been described as a “repeating puzzle box” (Washburn et al. 2017), in that, like Thorndike’s classic puzzle box (or problem box) apparatus, it afforded the opportunity to study how an animal’s behavior was changed by the consequences of the animal’s previous actions (i.e., by the Law of Effect); unlike the Thorndike puzzle box, however, the Skinner box permitted repeated and automated testing without manual resetting of the trials or manual recording of the responses.

Skinner first described the “experimental box” that would bear his name on pages 48–51 and in Fig. 1 (reproduced below) of his classic book *The Behavior of Organisms* (Skinner 1938; see also Heron and Skinner 1939). The apparatus consisted of a small, sound-attenuating box containing a lever (or, in subsequent versions, a disk for pecking) that the animal could interact with and a delivery mechanism for food or another reinforcer (Nye 1992). The technique used to create these food pellets was quite detailed, involving the mixing, shaping, hardening, cutting, and delivery

of a palatable reinforcers in such a way that allowed the pellets to enter the box unhindered (Siegel 1944). The apparatus was integral to Skinner’s systematic studies on the behavior of rats and provided a simple, unambiguous, and standardized operant behavior (i.e., lever pressing) that was within the spontaneous exploratory repertoire of rats (or that could be established quickly through shaping, or reinforcement of successive approximations), but that is a low-frequency behavior prior to conditioning. The operant chambers also provided discriminative stimuli, such as the presence or absence of the bar or a light that could be illuminated or dimmed to signal the availability of reinforcement. These discriminative stimuli allowed for the study of stimulus control of behavior. Skinner (1938, pp. 59–60) described the cumulative recorder that he used to make a record of each subject’s rate of responding over time (see also O’Donohue and Ferguson 2001) and the ways in which response rate changed as a function of the schedule of reinforcement. Thus, the operant-conditioning chamber provided Skinner with a controlled environment in which he could examine the conditions that affected the rate of response in rats and, subsequently in other animals, principally pigeons (Nye 1992). With this device, Skinner was

#### Skinner Box,

**Fig. 1** Original drawing of the Skinner box (Skinner 1938, p. 49)

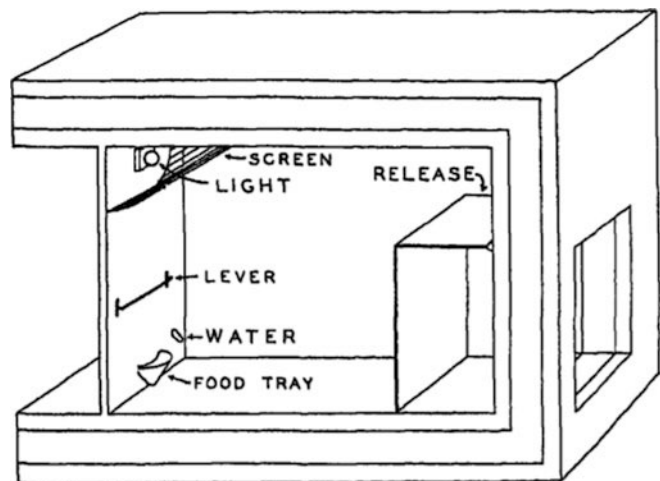


FIGURE 1

#### A TYPICAL EXPERIMENTAL BOX

One side has been cut away to show the part occupied by the animal. The space behind the panel at the left contains the rest of the lever, the food magazine, and other pieces of apparatus.

able to study variables that affected the rate of instrumental behavior, controlling the contributions of other potential discriminative forces (O'Donohue and Ferguson 2001).

Whereas Skinner primarily used rats and pigeons (the latter reinforced with brief intervals of access to grain for pecking a disk within the apparatus) as subjects in his operant chamber, subsequent research quickly adapted the paradigm for use with larger mammals (Rutherford 2009, p. 46). For example, Smith and Smith (1939) studied the effects of water deprivation in cats using a version of what they called a "Skinner box" and documented extinction curves that differed from those Skinner found with his rats. In the 1950s and 1960s, psychologists went even further, creating operant chambers for humans, for example, for testing children with autism (Ferster and DeMyer 1962) or adult in-patients with schizophrenia (Skinner et al. 1954). However, these Skinner boxes should not be confused with the infant "air crib" that Skinner developed for the comfort, not the conditioning, of his own daughter (Joyce and Faye 2010).

With operant chambers available from commercial manufacturers, the Skinner box became a standard testing paradigm for behavioral research with animals – particularly rats and pigeons, which in turn became the primary laboratory animals studied by psychologists (Beach 1950). In spite of Skinner's desire that the apparatus not be eponymous, psychological publications specifically using the term "Skinner box" grew tremendously in the literature. A PsycInfo and Google Scholar search reveals approximately 500 articles published in the 1950s with specific mention of the term "Skinner box," and this number approximately tripled to around 1,500 per 10-year period for each remaining decade of the century. Whereas researchers using the operant chamber were willing to alter its physical details to fit the specificities of whatever species or phenomenon they were studying, such apparatus were typically described a "modified Skinner box" rather than some new instrument (e.g., Ferster 1953; Flick et al. 2011; Kaye and Cox 1965). In the first two decades of the twenty-first century, the number of publications that including

the term "Skinner box" has continued to grow. Relatively few of those publications are new empirical reports employing the apparatus (e.g., PsycInfo shows fewer than 100 publications since 2000 with "Skinner box" in the title or abstract, and the number remains below 500 publications when "operant chamber" and synonyms are added as a search term). In this relative trickle of empirical publications using the Skinner box, many are focused on the effects and implications of drug administration or use (e.g., Sanchis-Segura and Spanagel 2006). Nevertheless, the use of the term "Skinner box" remains common in publications, whether through descriptions of continued refinements (e.g., Pineño 2014; Sokolowski et al. 2010) or in general discussions operant conditioning, used either literally (e.g., Rutherford 2009; Weizmann 2005) or metaphorically (e.g., Abernathy 2014; du Boulay 2019). The popularity of the Skinner box was also not limited to the United States. For example, a Skinner box for pigeons was shipped in 1952 to Keio University in Japan at the request of Professor M. Yokoyama where its use reached beyond operant conditioning into comparative psychology more broadly (Sakagami and Lattal 2016).

The emergence of personal computer technology had conflicting effects on the widespread use of operant chambers. On the one hand, computer technology provided for more powerful control of experimental manipulations and data recording than the highly reliable but limited electromechanical control units and cumulative recorders that were commercially available for Skinner boxes (e.g., Crossman 1984; Crossman and Williams 1978; Kamil and Sacks 1972; Nichols and Potter 1982). On the other hand, computers would ultimately become a rival apparatus for studying operant behavior, either by replacing the animal – as with the popular "virtual rat" software that allowed students to learn about operant conditioning without live animals (Graham et al. 1994) – or by replacing the operant behavior itself. Touchscreen technology gave researchers the opportunity to replace lever-pressing for the rat or disk-pecking for the pigeon with responses directly to the computer screen (e.g., Gibson et al. 2004; Markham et al. 1996; Brown and Morrison 1990; Wright

et al. 1988). The light and other simple discriminative stimuli of the Skinner box were replaced with the infinite computer-generated stimulus variety that could be presented on the touchscreen. In spite of the declining number of studies using the box itself, the Skinner box's prevalence in the literature continues as it stands as a foundational development in the study of operant conditioning.

Although Skinner's box quickly became popular in the field of psychology, his work with the box also generated great controversy over the years. Some authors have criticized Skinner for excluding previous psychological research on behavior and the basing of his entire theory on his own research with rats (Krechevsky 1939). Others took issue with Skinner's generalization from research with rats to the understanding of behavior of humans or of other animals (e.g., Beach 1950; Nye 1992). Despite these critiques, it is undeniable that Skinner's box has made critical and extensive contributions to the field of psychology (Washburn et al. 1994).

Perhaps the greatest impact of Skinner's operant chamber is the research which has generated from it that has moved beyond the use of a physical chamber. The operant chamber allowed researchers to isolate the phenomenon of operant conditioning and study it in a systematic, empirical fashion. From this solid base, psychologists began applying their knowledge of operant conditioning in real-world situations from classrooms to psychiatric wards (Rutherford 2009). The impact of the Skinner box has reached far beyond Skinner's initial research and continues to influence how we view operant conditioning and behavior today.

## Cross-References

- B.F. Skinner
- Clark L. Hull
- Edward Thorndike
- Law of Effect
- Operant Chamber
- Operant Conditioning
- Schedules of Reinforcement
- Shaping
- Stimulus Control

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## Sleep

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## What Is Sleep?

All animals sleep (Campbell and Tobler 1984; Cirelli and Tononi 2008). All undergo periods of rest, accompanied by reduced responsiveness to external stimuli, that if prevented continuously is detrimental to the body, ultimately leading to death. Sleep might be one of a few essential features shared across the animal kingdom. The search for the function of sleep is not as obscure as a few decades ago, and several functions have been identified showing that animals critically depend on a period of sleep.

## Definition and Criteria

Sleep is a complex phenomenon and is thus defined by multiple criteria (Table 1). Sleep is a rapidly reversible state of reduced responsiveness, typically accompanied by immobility and a characteristic posture. Sleep is distinguished from quiet wakefulness by the reduced ability to respond to stimuli and from coma or hibernation by its reversibility (Cirelli and Tononi 2008). Sleep is homeostatically regulated: Loss of sleep leads to an increase in sleep pressure and is compensated by a sleep rebound, which consists of an increase in sleep duration and quality (i.e., increased deep sleep as well as reduced sleep fragmentation). In most species, sleep is timed by the circadian clock appropriate to their

ecological niche but occurs as well in the absence of a circadian enforcer (Zeitgeber). Like hunger or thirst, sleep is elementary to an organism, as it cannot be evaded and its absence leads to death.

In addition to the essential criteria above, sleep changes during the lifetime with respect to its duration, timing, and number of sleep bouts. A remarkable example can be found among honey bees (*Apis mellifera*), where sleep duration and timing change extremely during the lifetime and thus between castes. As worker bees age, they take different working positions in their hive (castes): While young “cell cleaners” sleep generally longer, without 24 h rhythmicity and inside the cell, aged foragers sleep less, yet in clear day-night rhythmicity and usually outside the cell (Klein et al. 2008). During early development, sleep is elevated and becomes more fragmented as organisms age. Stimulants and hypnotics can modulate sleep in all model organisms studied, and sleep seems to be accompanied by similar changes in gene expression across different model organisms (Table 2, Cirelli and Tononi 2008). Sleep is not to be confused with hibernation and torpor, which are states of reduced metabolism. In fact, Arctic ground squirrels (*Spermophilus parryii*) wake up from hibernation in order to sleep (Daan et al. 1991). Only among mammals and birds sleep is mainly defined using electroencephalographic (EEG) criteria, while in other animals, sleep is evaluated behaviorally (Hartse 2011). In any case, EEG alone is insufficient to distinguish sleep from wakefulness.

**Sleep, Table 1** Criteria for sleep

|                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1. Behavior                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| <ul style="list-style-type: none"> <li>• <b>Increased threshold for arousal and latency for reactivity</b></li> <li>• <b>Rapid state reversibility to distinguish sleep from hibernation, torpor, or coma</b></li> <li>• Physical quiescence</li> <li>• Specific body posture or behavior during sleep</li> <li>• Preferred sleeping site</li> <li>• Specific pre-sleep behavior (e.g., grooming, yawning, circling)</li> <li>• Persistence throughout life, possibly specific change of sleep quotas during the life cycle</li> </ul> |
| 2. Homeostatic regulation                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| <ul style="list-style-type: none"> <li>• <b>Rebound sleep after sleep deprivation</b></li> <li>• Intensification of sleep after sleep deprivation or a cognitively demanding task (e.g., less fragmented and longer sleep bouts, increased SWS or deep sleep)</li> </ul>                                                                                                                                                                                                                                                               |
| 3. Physiological                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| <ul style="list-style-type: none"> <li>• Change in heart rate, breathing, and body temperature</li> <li>• Change in muscle tone (EMG)</li> <li>• Rapid eye movements/twitches</li> </ul>                                                                                                                                                                                                                                                                                                                                               |
| 4. Electrophysiological                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| <ul style="list-style-type: none"> <li>• Change in specific electrophysiological properties</li> <li>• In mammals and birds NREM (comprising SWS) and REM sleep</li> </ul>                                                                                                                                                                                                                                                                                                                                                             |
| 5. Pharmacological/endocrinological                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| <ul style="list-style-type: none"> <li>• Specific effect of stimulants and hypnotics on sleep and wakefulness (caffeine, amphetamines, antihistamines, benzodiazepines)</li> <li>• Change in hormonal signaling</li> <li>• Changes in gene activity</li> </ul>                                                                                                                                                                                                                                                                         |

Note: Essential criteria are in bold. Adapted from Vorster and Born (2015)

## Measuring Sleep

In mammals sleep is mainly divided into two states: rapid eye movement (REM) sleep, based on saccadic movements of the eyes, and non-rapid eye movement (NREM) sleep. While NREM sleep can be well distinguished from wakefulness based on EEG alone, the EEG during REM sleep resembles wakefulness. Therefore, the gold standard for measuring sleep in humans is polysomnography, which includes EEG, electrooculogram (EOG) to detect movement of the eyes, and electromyogram (EMG) to detect muscle atonia.



**Sleep, Table 2** Properties of sleep across the animal kingdom

|           | Increased arousal threshold | Sleep rebound | Body posture | Twitches | Increased during development | Change in gene expression | Stimulants Hypnotics | Melatonin | Memory function | SWS Deep sleep | REM Active sleep |
|-----------|-----------------------------|---------------|--------------|----------|------------------------------|---------------------------|----------------------|-----------|-----------------|----------------|------------------|
| Human     | ✓                           | ✓             | ✓            | ✓        | ✓                            | ✓                         | ✓                    | ✓         | ✓               | ✓              | ✓                |
| Rodent    | ✓                           | ✓             | ✓            | ✓        | ✓                            | ✓                         | ✓                    | ✓         | ✓               | ✓              | ✓                |
| Bird      | ✓                           | ✓             | ✓            | ✓        | ✓                            | ✓                         | ✓                    | ✓         | ✓               | ✓              | ✓                |
| Amphibian | ✓                           | ✓             | ✓            | ✓        | ✓                            | –                         | ✓                    | ✓         | –               | ✓              | ?                |
| Fish      | ✓                           | ✓             | ✓            | –        | ✓                            | ✓                         | ✓                    | ✓         | ✓               | –              | ✗                |
| Bee       | ✓                           | ✓             | ✓            | ✓        | ✓                            | –                         | ✓                    | ✓         | ✓               | ✓              | ✗                |
| Fly       | ✓                           | ✓             | ✓            | ✓        | ✓                            | ✓                         | ✓                    | ✓         | ✓               | ✓              | ✗                |
| Aplysia   | ✓                           | ✓             | ✓            | ✓        | –                            | –                         | –                    | ✓         | ✓               | –              | –                |
| Worm      | ✓                           | ✓             | ✓            | –        | ✓                            | ✓                         | ✓                    | ✓         | –               | ✗              | ✗                |
| Jellyfish | ✓                           | ✓             | ✓            | –        | –                            | –                         | ✓                    | ✓         | –               | –              | –                |

Note: All animal models studied express an increased arousal threshold during sleep and a specific body posture. Twitches are often apparent during sleep. After sleep deprivation, there is a homeostatically driven rebound in sleep (increased sleep duration and/or intensity). Sleep is increased during early development and triggers changes in gene expressions compared to wakefulness. Sleep is affected by stimulants and hypnotics. Melatonin is found in all model organisms tested so far. Sleep modulates memory function. Only in mammals and birds distinct phases of sleep (SWS and REM sleep) are found. However, other animals show distinct deep sleep phases. Green check mark, sign is found in animal model; red cross, sign is not found in the animal model; question mark, studies diverge on this question; bar, sign has not been studied so far in the respective animal model

Often an electrocardiogram (ECG) to detect sleep stage-specific fluctuations in heart rate is recorded, as well as measures of body temperature and airflow (Carskadon and Dement 2011, Maski et al. 2011). For studies in rodents, sleep scoring is mainly based on EEG and EMG, accompanied sometimes by video analysis. A typical setup in mice would comprise two frontal and two occipital EEG electrodes as well as two EMG electrodes applied to neck muscles (Oyanedel, March 2017, personal communication).

Although time consuming, detailed video analysis can provide a good estimate of the total sleep time and an approximation on the portion of different sleep phases. Typical behaviors include:

- Ritualized pre-sleep behavior such as grooming, place cleaning, nest building, circling (getting positioned to a sleep posture), yawning, and social sleep calls (Blumberg and Rattenborg 2017).
- Typical body postures with the head and neck bend in a certain position (remarkable examples are seen during REM sleep in the giraffe and the flamingo) as well as feet grabbing or bending in a certain way (Hartse 2011; Sicks 2012).
- Typical body changes during sleep like movements of the eyes, ears, or whiskers, while the eyes are usually closed.
- Rhythmic and arrhythmic periodical body twitches, sometimes even body shaking.

While during REM sleep muscle twitches commonly occur, NREM sleep in mice might include periods of shaking (Blumberg and Rattenborg 2017).

- Changes in heart rate as sometimes externally visible: NREM is accompanied by reduced heart rate and breathing movements with further reduction in REM. Heart rate might fluctuate strongly during phasic REM as seen in mice.

In insects such as flies and bees, sleep is associated with an overall decrease in brain activity as measured by local field potential recordings (Nitz et al. 2002). Yet, in invertebrates, sleep is mainly evaluated behaviorally: in *Drosophila* by infrared beam crossing (which is rather unspecific, Hendricks et al. 2000) and recently by video evaluation. For example, sleep in bees and cockroaches (*Blaberus giganteus*) has been measured by video analysis of the antennae that cease movement completely during deep sleep phases (Tobler and Neuner-Jehle 1992; Zwaka et al. 2015). Ants fold their antennae during deep sleep, while mandibles and glossae are retracted. One group reported rapid antennal movement during deep sleep (RAM sleep) in the fire ant (*Solenopsis invicta*) (Cassill et al. 2009). In *Drosophila* and cockroaches, deep sleep is accompanied by a distinct postural change: After 10 min of immobility, the head position becomes more supported, closer to, or even resting on the surface, while the rest of the body is relaxed, exhibiting only respiratory movements (Hendricks et al. 2000). As seen in mammals, *Drosophila* spend more time within this deep sleep phase after a night of no or little sleep (van Alphen et al. 2013). This is an indicator that this deep sleep phase might play a comparable role to the one seen in mammals.

## Why Animals Sleep so Differently

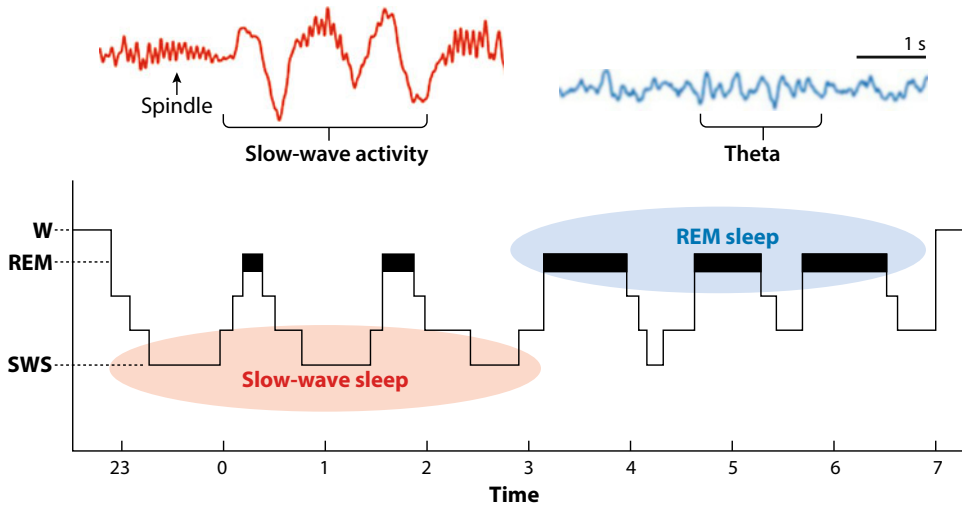
### Sleep Duration and Sleep Structure Across the Animal Kingdom

“Nothing in biology makes sense except in the light of evolution” – Dobzhansky, (1973). Daily

sleep in mammals can range from 3 h in the horse or donkey to 20 h in the armadillo. There is no singular factor, such as brain size, that determines the amount of sleep an animal requires (Capellini et al. 2008; Lesku et al. 2005). The great differences in the time of day chosen for sleep, total sleep duration, sleep fragmentation (sleep that is monophasic or polyphasic), and proportion of time spent in the different sleep stages depend largely on the ecological niche. Determining factors are:

- Nutrition: Herbivores have to spend more time in search and consumption of low caloric food, and carnivores such as cats have little predation risk and consume high caloric food.
- Position in the food chain (predator or prey): Prey minimizes sleep time in order to reduce their risk to predation (Lima et al. 2005).
- Restrictions of habitat: REM sleep is incompatible with swimming in aquatic mammals or flying in continuously flying birds (Blumberg and Rattenborg 2017).
- Temperature of the surrounding.
- Rate of metabolism.
- Animal size: Smaller mammalian species tend to sleep polyphasically.
- Relative brain size (i.e., brain size adjusted to body mass): Potentially reflects differences in cognitive abilities between species (Capellini et al. 2008).

Sleep is always a trade-off with other activities. In male pectoral sandpipers (*Calidris melanotos*), for instance, those that sleep the least during mating seasons have the greatest reproductive success (Aulsebrook et al. 2016). White-crowned sparrows (*Zonotrichia leucophrys gambelii*) can reduce their sleep by over 60% for weeks during the migratory season (Lesku et al. 2005). Great frigate birds (*Fregata minor*) reduce their sleep by 92% while flying continuously over the ocean for up to 10 days hunting but spend ~50% of their time sleeping while on land. Generally, sleep can be suppressed for certain periods but usually not without serious health consequences. Interspecific variation in sleep duration can as well be compensated though the intensity of sleep (Tobler 1995).



**Sleep, Fig. 1** Sleep in mammals is divided mainly into two stages: non-rapid eye movement sleep (NREM sleep) which comprises slow-wave sleep (SWS) and rapid eye movement sleep (REM). During SWS high amplitude slow-wave activity is observable in the EEG in the 0.5–4.0 Hz range that can be accompanied by spindle

activity in the 12–15 Hz band. Spindles often co-occur with sharp-wave ripples in the hippocampus, forming so-called spindle-ripple events that play a role in memory consolidation. REM sleep comprises low-amplitude mixed frequency as well as theta activity in the EEG (Adapted from Vorster and Born (2015))

Quantifying specific sleep times for each individual species in order to gain comparable data is challenging, and may not even be feasible. Reported sleep durations and proportion of sleep states depend on both intrinsic and methodological factors, such as (i) age of the animal; (ii) season in regard to light period, temperature, mating, and migration; (iii) whether observation occurs in captivity or the wild; (iv) sleeping alone or in the group, especially in social living animals; (v) food availability, (vi) health status; and (vii) recording type (e.g., video, EEG, or infrared beam, Aulsebrook et al. 2016; Capellini et al. 2008). Therefore, sleep times reported in different studies vary to a great extent. Indeed, there is great variability within individual species, which affects accuracy of surveys using small sample sizes in particular. In that sense, comparable data between animals is rather scarce. Only a minority of animals have been studied in depth in terms of sleep.

### On the Function of REM and NREM Sleep

Sleep among mammals and birds is mainly divided in NREM (quiet sleep) and REM sleep

(active sleep, paradoxical sleep). In humans, NREM sleep can be further divided into four stages, with stages 3 and 4 further specified as slow-wave sleep (SWS, deep or delta sleep; Fig. 1). In animals apart from humans, SWS is often used synonymously with NREM sleep. During NREM sleep, limbs relax, eyelids close, eyes are still, and breathing slows. SWS is determined by high amplitude slow oscillatory EEG activity in the 0.5–4.0 Hz frequency band and spindle activity in the 12–15 Hz band (only in mammals). Sleep spindles are characterized by a waxing and waning 12–15 Hz pattern of oscillatory activity in the cortex driven by the thalamus (Fig. 1) and play a role in memory consolidation (Buzsaki et al. 2013). Slow-wave activity is based on the synchronous brief silencing of cortical neurons firing, just like an applauding audience occasionally synchronizes its clapping, generating a clap that is overall louder and better heard. The brief cortical silence within such a slow wave is followed by a quick re-depolarization of the cortical neurons that is thought to facilitate the generation of spindle activity originating from thalamic networks.

There are two types of REM sleep: tonic and phasic. Tonic REM sleep is driven by the parasympathetic nervous system with low heart rate and no eye movements, while phasic REM sleep is driven by the sympathetic nervous system with co-occurrence of rapid eye movements, muscle twitches, and fluctuating respiration. During REM sleep, muscle tone is suppressed (muscle paralysis, muscle atonia), forcing most animals to stop any movement and to lie down and relax. Furthermore, the ability to regulate body temperature is reduced.

REM sleep is often accompanied by jerky twitches of the limbs, digits, and eyes that might bear great functional significance (Blumberg and Rattenborg 2017). Unlike NREM sleep, during REM sleep, the connectivity within the brain, especially the neocortex, is high. This increased cortical connectivity during REM sleep results in desynchronized brain activity of low-amplitude mixed frequency and theta activity (4–10 Hz) in the EEG signal with relatively higher power in the high-frequency ranges. The exact function of theta activity is to date unclear; it is merely a hallmark of REM sleep.

Sleep in mammals and birds consists of several cycles of REM and NREM sleep, and sleep usually starts with a period of NREM sleep. The first half of nocturnal sleep is dominated in most mammals by NREM with little REM sleep, whereas the second half of the night is dominated by REM sleep. REM sleep is controlled, at least in part, by

the endogenous circadian clock, while SWS during NREM is driven by homeostatic sleep pressure, that is, by the increasing propensity to sleep with respect to the amount of time spent awake (Tobler 1995). As sleep pressure decreases during the night, the amount of SWS decreases, while the amount of REM increases with progressing time of the day. A common idea is that the physiological differences of these two sleep stages reflect functional differences. The duration of single REM and SWS episodes differs greatly among species: In humans SWS periods typically last for up to 40 min at the beginning of the night and 5 min toward the end, and REM sleep bouts for 5 min at the beginning of the night and 20 min toward the end (Carskadon and Dement 2011). In rodents SWS (termed NREM) episodes last from 60 to 300 s, while REM sleep episodes last about 100 s. In pigeons (*Columba livia*), periods of SWS last around 50 s at the beginning of the sleep period and decrease to 25 s toward the end. REM in birds accounts for less than 10% of the total sleep time distributed in very short epochs of 4–8 s. Thus the functional mechanism of REM and NREM sleep is not ultimately tied to the duration and fragmentation seen in the different species (Table 3).

Slow-wave activity is driven by intrinsic cortical activity as well as through the thalamus. The six-layered cortex in mammals is not a prerequisite for the existence of SWS, as birds have a rather nuclear brain structure instead of a six-

**Sleep, Table 3** Sleep and sleep state duration in different animal models

|        | Total sleep time (min) | Total REM (min) | Total NREM (min)           | Average duration SWS epoch (s) | Average duration REM epoch (s) | Cycle duration (min) |
|--------|------------------------|-----------------|----------------------------|--------------------------------|--------------------------------|----------------------|
| Human  | 400–500                | 150             | 50–150 (SWS)<br>340 (NREM) | 300–1800                       | 300–1200                       | 90–120               |
| Mice   | 600–800                | 150             | 500                        | 300–500                        | 40–100                         | 5–10                 |
| Rat    | 440–800                | 80              | 360                        | 100–200                        | 100                            | 5–10                 |
| Pigeon | 300–500                | 25              | 400                        | 20–50                          | 4–8                            | 1–5                  |

Note: While the total sleep time (24-h period) in humans, rodents, and birds is rather consistent, the average duration of slow-wave sleep (SWS) or rapid eye movement (REM) sleep epochs vary greatly and so the duration for one sleep cycle comprising SWS and REM sleep. All data given for the different animals are approximations and might vary substantially depending on recording type, age, and exact species. (Carskadon and Dement 2011, Oyaneldel personal communication, March, 2017, Martinez-Gonzalez et al. 2008)

layered cortex and still express SWS. Even in primary cortical cell culture, after several days, synchronized rhythmic on-off bursting activity appears. This “sleep in a dish” model resembles to some extent sleep on the molecular level (Hinnard et al. 2012). Slow-wave activity can occur locally, while the rest of the brain is more in a wakeful state, so termed “local sleep.” The presence of local sleep during a motor task is associated with lapses in performance. Further, using a specific brain region to solve or complete a task during wakefulness leads to increased slow-wave activity in that same brain area during subsequent sleep. To some extent, this is evidence that slow-wave activity originates in higher brain regions independently of the thalamus, which drives slow-wave activity as well. Thus, the thalamus is not the only driver of the slow-wave activity. It however tunes and coordinates slow-wave activity in the cortex.

Sleep deprivation in all mammals and birds leads to a sleep rebound, especially of SWS (Tobler 2005). The amount of SWS is therefore a good indicator of the sleep pressure or sleep need. NREM sleep is the state through which torpor and hibernation are entered. However, animals that awake from hibernation spend increased time in NREM sleep. In fact hibernating animals interrupt hibernation periodically to spend most of their time sleeping in SWS (Daan et al. 1991). More importantly most of the energy spent during a period of hibernation is invested in these interruptions.

### The Ecological Niche Shapes Sleep

NREM sleep allows for stereotypic behavior as seen in migrating birds that sleep unihemispherically (occurring only in half of the brain) while continuously flying for several days and ruminating animals that chew on their food while sleeping. Sleepwalking in humans takes place during SWS as well. SWS can be unihemispheric in most birds and marine mammals (whales, dolphins, sea cows, walruses, and sea lions), while REM sleep cannot (Tobler 1995). Still, birds prefer to rest with both hemispheres, and both eyes closed, especially when in a safe location or surrounded by members of the colony.

Marine animals show little to no REM sleep. The accompanying muscle atonia appears to be incompatible with an aquatic lifestyle that supposedly requires permanent motion (Blumberg and Rattenborg 2017).

REM but not NREM sleep is decreased in species under high predation risk (Lima et al. 2005). The reason for this observation might be attributed to the muscle atonia during REM sleep that forces animals to lie down, which is an especially vulnerable position, especially among horses and giraffes (Sicks 2012). In altricial mammals, those that are born immature, REM sleep declines strongly from birth to adulthood, whereas in precocial animals, REM sleep quanta and the duration and proportion of sleep stages are stable throughout life (Blumberg and Rattenborg 2017). This might give us some clues on the function of sleep with respect to brain maturation during development. Because REM sleep is accompanied by reduced thermoregulation, researchers suggested that REM sleep is reminiscent of reptilian (poikilotherms) wakefulness (Lesku et al. 2005). Diverging ambient temperatures during sleep reduces REM sleep in rodents, possibly because of the incapacity to regulate the body temperature during REM sleep (Amici et al. 2008; Lesku et al. 2005).

### Current Hypotheses on the Function of Sleep

There are several hypotheses on the functions of sleep that are based on substantial evidence. Most certainly they all convene in one framework of sleep. During evolution different body processes might have allocated to the time of natural inactivity (Blumberg and Rattenborg 2017). The question is which core function of sleep initiated the development of a period of inactivity and reduced responsiveness. Alternatively it is possible that rest periods always existed in all forms of life due to sun-dependent (circadian) change in food availability and temperature, allowing different metabolic processes to be most efficiently performed at certain time windows.

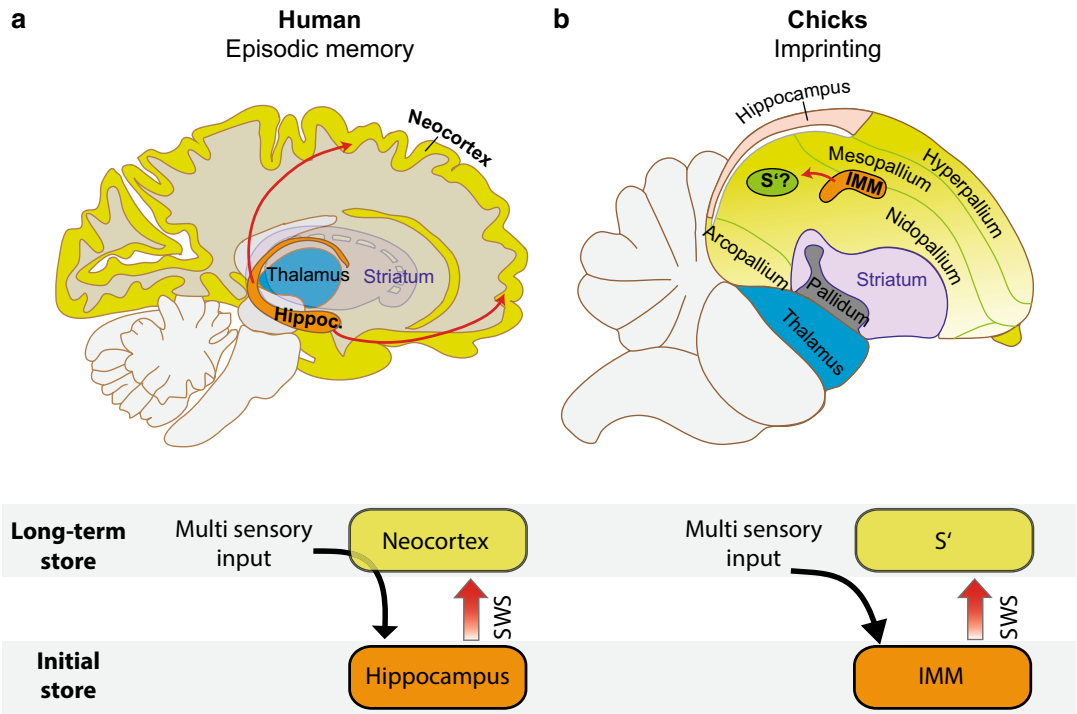


**Sleep for Memory Consolidation: Active System Consolidation Theory**

At first our memories are usually episodic (Diekelmann and Born 2010). We recognize the different aspects of an event, such as what, where, and when something happened, without drawing final generalized conclusions. Only with time our brain compares, associates, and integrates our new memories with existing ones. Then we are left with the gist of our memories and encounters. We mostly forget exactly when, where, and with whom we met and often retain only the conclusions drawn from an important encounter without knowing the exact location and the exact content of our conversation.

The active system consolidation theory claims that during wakefulness, information is rapidly

encoded first into an initial store, in mammals the hippocampus (Fig. 2). Due to the reactivation of those memories during sleep, the information becomes gradually redistributed and dependent on other areas of their long-term storage; in mammals this involves the cortex and striatal areas. In this way, new memories are integrated into the existing context of memories and thus become decontextualized and schema-like (gist extraction). In support for this hypothesis is the finding that hippocampal-dependent memories, mainly declarative memories, benefit from SWS (Blumberg and Rattenborg 2017; Diekelmann and Born 2010). Further, sleep facilitates the insight into underlying rules and structures. It seems that during sleep newly acquired memories are reviewed and commonalities are drawn. Thus,



**Sleep, Fig. 2** Active system memory consolidation in different species. (a) In humans new episodic memories are initially stored and/or triggered by the hippocampus (orange). During slow-wave sleep (SWS), memories are reactivated and presumably redistributed by means of spindle-ripple events toward the long-term store residing mainly in the neocortex (green) leading to a de-contextualization of the memories. (b) Imprinting

memory in chicks is initially encoded in the left IMM (intermediate and medial mesopallium). Presumably during SWS, the imprinting memory is redistributed to a yet unknown locus S', again accompanied by a transformation of the memory in that way that it can be more flexible applied to different contexts (The location of S' is presently unknown therefore the actual placement of S' in the figure is meaningless.) (Adapted from Vorster and Born (2015))

sleep permits implicit memory to become explicit thereby qualitatively transforming memories.

Sleep spindles seem to play an important role in memory formation. For instance, the density of sleep spindles increases after a declarative learning task compared to a non-learning control task. During the slow-oscillation upstates, which occur during SWS, so-called spindle-ripple events are detectable, during which hippocampal ripples are nested into the excitable troughs of sleep spindles (Buzsaki et al. 2013). These spindle-ripple events provide a mode of communication between the hippocampus and the cortex and striatal regions. Ripples trigger the replay of CA1 (cornu ammonis area 1) place cell firing patterns in the hippocampus that also occurred during prior waking periods. Some milliseconds after ripples occur in the hippocampus, assembly reactivations are detectable in neocortical and striatal areas. Blocking sharp-wave ripples after learning reduces memory consolidation. Enhancing spindle activity via acoustic stimulation during sleep and concomitantly stimulating slow oscillations increases memory consolidation in humans. Triggering reactivations during sleep via an odor that was also present during training enhances exclusively the consolidation of the odor-connected memories (Vorster and Born 2015).

A deficit of active system consolidation theory is that it makes no prediction on the function of REM sleep as it is arranged around the different hallmarks of NREM sleep: cortical slow waves, sleep spindles, and hippocampal ripple activity (Diekelmann and Born 2010; Vorster and Born 2015).

### **Sleep for Synaptic Tuning: Synaptic Homeostasis Hypothesis (SHY)**

Wakefulness and learning trigger an increase in synaptic strength and cortical excitability (Cirelli and Tononi 2008). The chance of epileptic seizures, for instance, increases after long periods of wakefulness. Repeatedly increasing synaptic strength is unsustainable and fatal for a nervous system as it demands more room, requires higher energy consumption and demand for cellular supplies, and decreases signal-to-noise ratio, which can all lead to a

fatal instability of the nervous system. The firing rate of neurons within a nervous system is finely tuned: just enough background activity to allow for communication but as sparsely as necessary, since the brain is already the most energetically costly organ (in humans, comprises 20–30% of the body's energy expenditure). Therefore, any change in connectivity (learning) must be balanced out with a change in synaptic strength at another place in the system.

The synaptic homeostasis hypothesis claims that sleep serves exactly this purpose: The homeostatic regulation of the nervous system occurs through renormalization of net synaptic strength and restoration of cellular homeostasis while the brain is disconnected from external intrusions (Joiner 2016). According to this hypothesis, slow waves during SWS serve to globally downscale and renormalize synaptic potentiation. Yet so far slow waves during sleep have been found only in mammals and birds. The theory is compatible with the increased sleep need during development, a period of great neuronal rewiring and plasticity. In humans, the quanta of REM and NREM sleep change in accordance with different steps during brain maturation. One of the simplest organisms known to exhibit signs of sleep, the nematode *C. elegans*, sleeps only after developmental-induced times of quiescence, named lethargus. A great number of key genes are regulated during lethargus in *C. elegans* in the same manner as during sleep in *Drosophila*, mice, and humans.

### **Sleep for Metabolic Clearance**

Sleep promotes the removal of neurotoxic waste that accumulates during wakefulness. In a seminal study in mice, sleep led to a 60% increase in interstitial space and thus allowed for quicker exchange of cerebrospinal fluid, also leading to increased rates of  $\beta$ -amyloid clearance (Xie et al. 2013). The hypothesis is supported by the finding that in mammals the ratio of cortical neuron density to surface area is positively correlated with the total sleep duration (Herculano-Houzel 2015). Higher neuronal density relative to the surface area of the brain demands for an increased clearance time (sleep). Thus, a longer sleep time is

needed to allow for a complete flush of metabolic waste products.

### Sleep for Energy Conservation

The energy conservation theory claims that sleep functions to reduce energy expenditure at times that cannot be efficiently used for other activities. From all the hypotheses debated, this is the most unlikely one (Capellini et al. 2008). The energy savings during sleep is only 10–20%. During sleep there is a change in the *type* of neuronal activity but not in the amount of activity. Most importantly this hypothesis does not explain why we lose consciousness, become less responsive to hazardous stimuli, and cannot postpone sleep especially during dangerous situations (while driving a car for instance). Just to save 20% of energy? This theory especially does not explain REM sleep, during which cortical EEG resembles wakefulness. In contrast to NREM, REM is a sleep state without energy savings with respect to brain activity but with the deficit of reduced responsiveness to external sensory information. Overall, the slight energy savings during sleep appears to be rather an energetic adaptation of the body to an obligatory sleep period.

### Sleep for Immune Function

The immune system largely depends on sleep. Chronic and partial sleep deprivation lead to deficits in immune function and host defense mechanisms. Cytokines such as tumor necrosis factor alpha (TNF alpha) and interleukin-1 beta (IL-1β) are induced by sleep (Joiner 2016). Both cytokines are released in response to infections as well as through sleep deprivation. SWS promotes the interaction between antigen-presenting cells and T cells that store the antigenic information for the long term (Westermann et al. 2015). Sleep especially eases the extravasation of T cells and their redistribution to lymph nodes. After a vaccination, sleep, especially SWS, doubled the frequency of antigen-specific T helper cells. More importantly, the specific T helper cell response continues to be stronger even after one year in a group that was allowed to sleep the night following vaccination in comparison to a group that was sleep deprived. A night of sleep after

vaccination thus leads to a stronger and longer-lasting protection (Westermann et al. 2015). The immune system does not reasonably demand for the loss of consciousness or a loss of responsiveness during sleep. Therefore, it seems more likely that certain immune processes shifted to coincide with the sleep period to fulfill its functions.

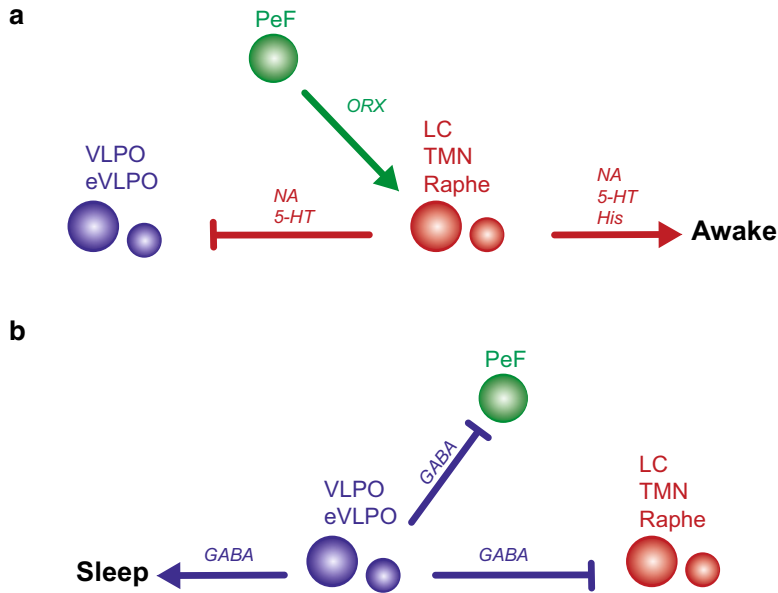
## What Drives Sleep?: The Molecular Basis of Sleep

### GABA Promotes Sleep

Gamma-aminobutyric acid (GABA) is the major inhibitory neurotransmitter. GABAergic agonists promote sleep (Joiner 2016). In mammals GABA is released from the ventral preoptic area (VLPO, Fig. 3b) and inhibits wake-promoting areas. Most sedatives target GABA<sub>A</sub> receptors (benzodiazepines and non-benzodiazepine drugs with similar effects (Z-drugs) as well as ethanol). GABA<sub>A</sub> receptors reduce excitability and promote sleep in numerous animals (flies, zebra fish, and mice). However, sedation is not to be confused with natural sleep! To date no real sleep-inducing remedy is known.

### Biogenic Amines Such as Histamine Promote Wakefulness

In mammals a number of neurotransmitters promote wakefulness. Among these are norepinephrine (noradrenaline, in flies named octopamine), serotonin, dopamine, and histamine (Saper et al. 2005; Joiner 2016). For example, the first generation of antihistamines leads to increased drowsiness as a side effect, as they antagonized the wake-promoting function of histamine in the brain. Stimulants such as amphetamines, modafinil, and methylphenidate (Ritalin) are dopamine reuptake inhibitors, increasing the persistence of dopamine in the synaptic cleft. All of these transmitters are found in other model organisms such as flies and fish and somehow interact with sleep. Octopamine and dopamine are wake promoting in flies; however, serotonin seems to be sleep promoting in flies. In humans serotonin seems to have diverse functions in REM and NREM sleep. During REM and NREM sleep,



**Sleep, Fig. 3** Flip-flop switch for sleep-wake transitions in mammals. (a) While awake monoaminergic neurons in the forebrain (locus coeruleus (LC), tuberomammillary nucleus (TMN), in red) and raphe nuclei (raphe)) inhibit sleep-promoting GABAergic neurons in the ventrolateral preoptic nucleus (VLPO, in blue) and extended VLPO (eVLPO) through noradrenergic (NA) and serotonergic (5-HT) connections. (b) During sleep the VLPO inhibits

these same regions through GABAergic inhibition (GABA) forming a sharp yet unstable self-reinforcing loop that avoids transitional states. For stability the activity of wake-promoting monoaminergic neurons (LC, TMN, raphe) is reinforced through orexin (ORX) released by the perifornical area (PeF, in green) (Figure based on Saper et al. (2005))

aminergic signaling is reduced, however only during REM sleep cholinergic signaling persists to excite the cortex, explaining partly the difference between the two sleep states.

### Orexin Stabilizes Wakefulness

It is a necessity for an organism that the whole brain undergoes sleep and wakefulness in a coordinated manner. If this was not the case, groups of neurons would go independently to sleep, resulting in many islands of local sleep intruding wakefulness and thus negatively affecting performance. Besides, some functions proposed by the active system consolidation theory demand that the whole brain undergo sleep (e.g., sharp-wave ripples riding on slow waves in mammals and birds). Further, wakefulness has to be stabilized in a way that the brain does not suddenly flip back

to sleep during a potentially dangerous motor task, as seen in narcoleptic patients.

During wakefulness monoaminergic neurons in the forebrain (locus coeruleus, tuberomammillary nucleus, and raphe nuclei) inhibit GABAergic neurons (sleep promoting) in the ventrolateral preoptic nucleus (VLPO). In return, during sleep the VLPO inhibits these same regions. This way activity in one region shuts down inhibitory activity in the other region and thus strengthens its own action. This self-reinforcing neural loop serves to be a sharp switch as it avoids transitional states yet is rather unstable. For stability during wakefulness, the activity of awake-promoting monoaminergic neurons is reinforced through orexin released by the perifornical area (Saper et al. 2005, Fig. 3). Humans and dogs with narcolepsy lack orexin-producing neurons and

therefore often flip during wakefulness to REM sleep, especially if not fully rested. Recently, a functional analog of vertebrate orexin (FLP-2) and the receptor (FRPR-18) was found in *C. elegans* that promotes pigment-dispersing factor 1 (PDF-1) secretion and vice versa (Chen et al. 2016). In flies, the pigment-dispersing factor might have an analogous function as orexin and is found in the central clock neurons.

### **Melatonin: The Molecular Clock**

The hormone melatonin is expressed in evolutionary distant species like dinoflagellates and is universally used as a molecular clock. Melatonin is degraded by a light-sensitive reaction, possibly serving as a light-protecting pigment as it is a free radical scavenger. Melatonin is produced at all times but degrades during the day, and thus peaks in all organisms during the night. However, melatonin is by far no sleep hormone! While humans and birds sleep at night and melatonin signals the time to sleep, in nocturnally active rodents, melatonin signals activity and wakefulness.

### **cAMP and CREB: Learning and Sleep Are Molecularly Linked**

The conserved core pathway of learning known in all animals from worms to humans includes the second messenger cyclic adenosine monophosphate (cAMP), the protein kinase A (PKA), and the cAMP response element-binding protein (CREB). Increased signaling of cAMP and CREB activity is associated with waking as found in flies and rats (Mackiewicz et al. 2008). Increased sleep after being exposed to an enriched environment (as seen in flies) depends on cAMP, possibly due to memory consolidation processes. The up- or downregulation of the transcription regulator CREB always affects the amount of waking and sleep. Increased CREB activity occurs during rebound sleep after sleep deprivation.

### **The Adenosine Hypothesis: Cellular Activity Induces Sleep**

The most traded pharmacological agent – caffeine – promotes wakefulness. Caffeine promotes

wakefulness in flies, mice, and humans, yet its pathway of action is still debated. The mode of action in mammals is hypothesized as follows: During wakefulness ATP is converted to adenosine and released by neurons as a co-transmitter, raising extracellular levels of adenosine and signaling the body a need for sleep (Joiner 2016). Caffeine binds reversely to the adenosine A<sub>2A</sub> receptor and hinders adenosine from binding and activating the receptor and thus suppressing the sleep-promoting signal. Administration of adenosine or adenosine A<sub>1</sub> receptor agonists induces sleep by inhibiting wake-active neurons, while A<sub>2A</sub> receptors activate sleep-active neurons. However, in flies caffeine acts rather on the cAMP pathway than on the adenosine receptor, promoting wakefulness globally in the brain without restrictions to a specific brain region.

### **Conclusion**

A major part of life is devoted to sleep in all organisms, pointing to an essential and evolutionary ancient function. Sleep is finely adjusted to the ecological niche of each species. Ecological conditions determine whether an animal sleeps in monophasic or polyphasic fashion, during day or night, and for long or short duration. Clear signs of REM sleep and NREM are only found in mammals and birds. However even invertebrates show particular phases of deep sleep. “Sleep is of the brain, by the brain and for the brain” as Allan Hobson (2005) once put it. Cognitive deficits are the first effects of sleep loss. The current two main hypotheses of sleep, the active system consolidation and the synaptic homeostasis hypothesis, are focused on memory function. Yet, during evolution other vital body functions like the immune system took advantage of sleep, allocating certain processes to that period of rest. The same sleep-regulating neurotransmitters (GABA, noradrenaline), the same molecular pathways (adenosine signaling, learning cascade including CREB), and the same molecular clock (melatonin) are



shared among all animals pointing once again to a shared vital function of sleep.

## Cross-References

### ► Circadian Rhythms

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## Sleep Cycles

### ► Day/Night Cycle

## Slime Molds

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## Synonyms

[Plasmodial slime molds](#)

## Definition

Acellular mass of amoeboid cells containing large number of spore.

## Introduction

Slime molds are single cell eukaryotic fungus-like protists collectively form multicellular reproductive structures and classified as fungi. It has been stated that more than 900 species of slime mold discovered all over the world and named “slime” due to their appearing as gelatinous. It is highly prominent organisms appear on mulch (*Fuligo septic*, bright in color spread over soil surface) (Zhulidov et al. 2002), plants, and grass (*Physarum*) magically and also called

as “blob” or “dog vomit fungus.” There are 700 types of slime molds are found in nature with the different shape, structure, and color. Slime molds. The slime molds growing on mulch are bright in color (yellow, orange, bluish-gray, purple-brown, and creamy), unequal mass, and different in diameter (1 inch to several feet). In lawns, the presence of a slime mold gives the grass a bluish-gray to purple-brown appearance from a distance. These areas can be patchy and can be as large as several feet in diameter. Basically, they appear on that portion of plants which are closest to soil ground such as woody and herbaceous plants. Some colorful slime molds have been reported on the lower branches of juniper or rhododendron. Slime molds can causes indirect injury to the plant besides of being pathogenic. They shade and cover the plants to slow down photosynthesis. The macroscopic slime molds mostly lie in myxogastria. The size of slime molds is few centimeters or up to several square meters and 30 g of masses (Zhulidov et al. 2002). Some “cellular” slime molds do not spend most of their time in this state. During shortage of food, many single-celled organisms aggregate and start moving as a single body. Aggregation state of slime molds is very sensitive to airborne chemicals and can detect food sources. They can change the shape to produce fruiting bodies and release many spores and through wind due to having lightweight (Jacobson 2012). Slime molds (*Stemonitis*, *Physarum polycephalum*, *Fuligo*, etc.) behave as saprophytic and feed on bacteria, yeasts, and fungi to contribute in decomposition of dead vegetation. Slime molds usually occur in soil, lawns, and on the forest floor, commonly on deciduous logs. In tropical areas, slime molds are commonly found on inflorescences and fruits, and in the canopy of trees. The drier environmental conditions are always unfavorable for the slime molds and transform into shapeless plasmodium to sporangium (organized structure). For their growth, cool, shady, and moist conditions are always favorable for slime molds. Though, they can readily grow in the sunny area which indicated that temperature and moisture are the main

important factors connected with their presence and occurrence. Since past 10 years they associated with patterns of weather and increased the popularity of woody mulches.

## Taxonomy of Slime Molds

According to older classification, slime molds are polyphyletic and placed in the subkingdom Gymnomycota in the Fungi kingdom including phyla Myxomycota, Acrasiomycota, and Labyrinthulomycota (Worley et al. 1979). Recently, slime molds have been divided into several supergroups other than kingdom Fungi. Slime molds are divided into two main groups: (1) Plasmodial (single membrane without walls) e.g., *Dictyosteliida* and (2) protists (unicellular). The modern classification comprises the slime molds in the mycetozoa group of the amoebozoa which includes three groups Myxogastria, Dictyosteliida, and Protosteloids (intermediate between Myxogastria and Dictyosteliida) (Baldauf and Doolittle 1997). Slime molds are divided into two categories: true slime molds and cellular slime molds (Farr 1981). True slime molds lies under Myxomycota (plasmodials) and Dictyosteliomycota considered as cellular slime molds (Nakagaki 2001; Keller and Braun 1999; Steven and Stempen 1994; Raper 1984). The slime molds grow in the moist (well-rotten logs) environment and eats bacteria for their survival. Because of the presence of delicate fruiting bodies, it appear as fungi (Wang 2015; Herron et al. 2013). They are small in size (1 or 2 mm) and therefore difficult to recognize. The slime molds of myxomycete groups are resembles as plasmodium (two amoeba-like cells fused together to form a formless, growing mass) (Adl et al. 2005). Plasmodia are pale, cream, gray, bright yellow, or orange in color. It engulf its food mainly bacteria as the same way as amoeba eats their food. The myxomycetes are multinucleate globule of protoplasm lacking cell wall. Cell membrane is the only structure which keeps everything in. They ingest bacteria using pseudopodia, which is also known as “false feet,” this process is known as phagocytosis followed by

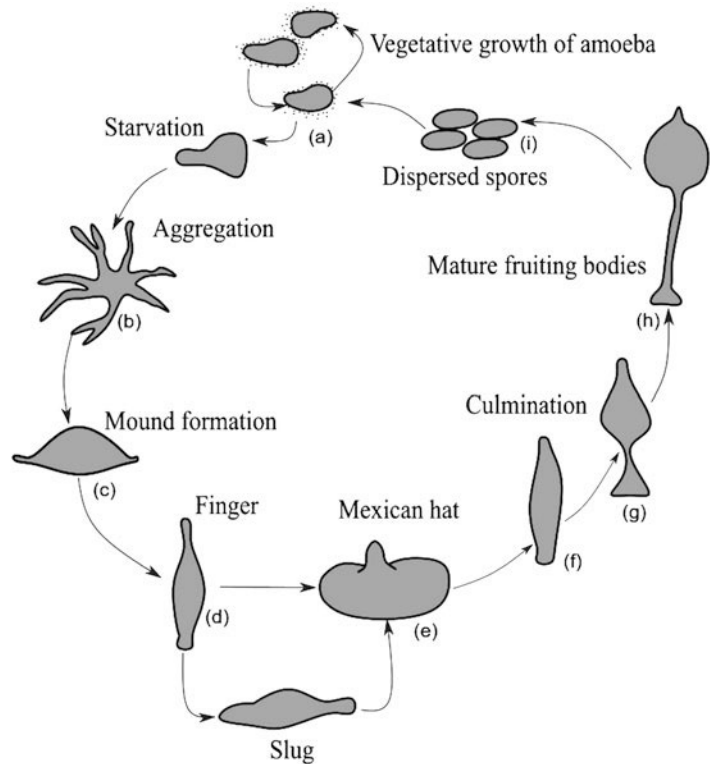
digestion. In case of true fungi, the food digestion always found before the ingestion process. The formation of fruiting bodies always takes place during harsh environmental condition and lacking of food. Several dormant and resistive spores produce by fruiting bodies, which further germinate into uninucleate myxamoebae. These uninucleate myxamoebae later fuse to form a plasmodium through mitotic division to complete their life cycle. The cellular slime molds (*Dictyosteliomycota*) are multicellular, which is also considered as social amoebae lacking of true plasmodium. Under food scarcity, they produce some chemical signals to neighbor amoebae (<http://www.wisc.edu/botany/fungi/volkmyco.html>). The *Dictyosteliomycota* create a fascinating challenge in evolutionary theory by showing altruistic behavior. They sacrifice their reproductive potential for the transportation to a new more food location to grow again. Some non-amoebozoan slime molds are *Acrasids*, *Plasmodiophorids*, *Labyrinthulomycota*, and *Fonticula* (Brown et al. 2009).

## Life Cycle of Slime Molds

The slime molds feed on bacteria and start their life cycle as amoeboid like cells, having haploid single nucleus. Life cycle of slime molds comprises different stages (Fig. 1). Under favorable (moist) condition, these slime molds convert into biflagellated swarming cells by binary fission. Under scarcity of food or in unfavorable condition, they form cysts which are tough-coated cells. These amoebae form zygotes if they meet the correct mating type and grow into plasmodia. After mitosis, the diploid cells form large cells with two nuclei. In the absence of cell division, nuclei divides continuously to form multinucleated plasmodium referred as “supercell.” The supercell plasmodium migrates about 1 cm per hour as like amoeba. The slime molds change their behavior during shortage of food availability. It migrates to the favorable place and form fruiting bodies or sporangia (Alexopoulos et al. 1996). Slime molds may transform into several shapes like shapeless blobs to delicate lacy structures.

### Slime Molds, Fig. 1 Life cycle of slime mould.

There are different stages have been reported in life cycle of slime molds  
 (a) Free-living, haploid amoebae (b) Aggregation  
 (c) Formation of mound  
 (d) Appearance of the finger like tip section  
 (e) Appearance of “Mexican hat” stage  
 (f, g) Culmination  
 (h) Development and maturation of fruiting body  
 (i) Spores dispersion



During their life cycle, spores become dry and released into the air. Spores germinate into either new amoebae or form biflagellate swarming cells in the presence of water (Baldauf and Doolittle 1997). These cells are haploid in nature and serve as gametes to initiate the diploid plasmodial stage of the life cycle (Fig. 1). Under unfavorable (dry) conditions, the diploid plasmodia undergoes resting stage and start growing again when moist conditions available.

### Role of Slime Molds in Animal Cognition and Behavior

The slime mold (*Physarum polycephalum*) is an organism which resembles as blob-like and creeping giant cell (Adamatzky and Jones 2010). The biologist of Research Centre on Animal Cognition reported that slime molds have no brain but it can response and learn from experiences (Reid et al. 2012). Slime mold have tendency to reunite after physical separation. In some studies, it has been proven that slime mold like *Physarum polycephalum* has ability to find out periodic inauspicious conditions (Nakagaki 2001; Tero et al. 2010; Saigusa et al. 2008). According to Kitta (2010), behavior of slime molds is equal to the brain of animals that posses muscle and nerves (Kitta 2010). In some experiments, it has been stated that slime molds avoids light and get stimulated, and spread their plasmodia and create some thin networks to focus on resourcefully connected branches (Tero et al. 2010). The natural habitat of slime mold (*Physarum polycephalum*) is a forest litter but also can be grown in laboratory. It has been revealed that around 2000 slime mold can acquire the behavior to avoid salt (Vogel and Dussutour 2016). Some slime molds species are parasitic to aquatic invertebrates like nematodes, rotifers, diatoms and arthropods. Some other parasitic water molds may grow on other organisms like amphibians, fish scales and on their eggs. The *Saprolegnia* a water mold target the especially sick fishes to cause lesions. The organisms which are parasitic to flowering plants get affected by the slime molds and cause greater impact on human beings. The slime molds affect the some crops like lettuce, grapes, cabbage, corn,

avocados, pineapples, potatoes, etc. by causing diseases by damaging stem and leaf tissues. A very common water mold species (*Phytophthora infestans*) is responsible for the causing late blight disease in potato plants and also infect the tubers (edible part of potato). In Ireland, most of the poor people depends upon the potato which was a very important crop plants for them. In the late nineteenth century, the potato crops were infected by *Phytophthora infestans* and caused the great famine by wiping out Irish potato crops. During this famine, most of the Irish people starved to death and nearly million people emigrated to Canada and America. In the late 1870s, Downy mildew of grapes was introduced accidentally from America to Europe and wiped out entire French wine industry. The industry have used the *Bordeaux mixture* (mixture of lime and copper sulfate) save the plants to control the diseases. Use of *Bordeaux mixture* has been introduced as an important fungicide, which can be used to control a plant disease.

It has been discussed that slime molds are not able to cause pathogenesis in plants so there is no any protective control strategy is required. Control of slime mold using chemicals can create more trouble. Some chemicals can be used to permanently kill the slime molds, but the toxic applicants may create more harmful condition to the life around the slime mold. Slime molds develop on mulch can be removed with scooping or disturbed by scratching. When the slime molds appear on plants and grass or turf, a forceful water spray with a hose pipe can be used to control or remove. Mowing can be used for the removal of slime molds from the turf effectively. On the other hand, after some time, slime molds will ultimately dry up if they are left alone, which turns into powdery form and disappear.

### Conclusions

The study of slime molds has revealed that these organisms to be not just a mass of slime on the forest floor but very charismatic organisms that are able to solve mazes, modeling city planning. Not only do slime molds play an integral part of our ecology but their social behavior also provides



important insight into the inner workings of communication, movement, and altruism. At least in biology, slime molds are truly extraordinary. The fungus-like protists are unicellular. They were originally called fungi because they produce sporangia. These protists differ from fungi in that their cell walls have cellulose rather than chitin. Fungus-like protists also generally do not have divisions between their cells like fungi do. Slime molds have both animal and plant like characteristics although they themselves are not closely related to each other. Most of their lives are spent as microscopic amoebas, roaming independently through the forest feeding on organic matter, bacteria, and other microscopic morsels. During food shortages, slime molds swarm and aggregate into an enormous single cell, where they can then form fruiting bodies and release spores (Herron et al. 2013; Baldauf et al. 2000). When food (normally bacteria) is readily available for cellular slime mold, they take the form of individual amoebae, which feed and divide normally. However, when the food supply runs low, they aggregate to form a multicellular unit. The cells in the slug remain separate from each other, unlike the cells of plasmodial slime mold. The plasmodium of slime molds are heterotrophic, and they phagocytose food particles. Water molds are decomposers and break down dead matter.

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## Small Interfering RNA (siRNA)

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### Synonyms

Short interfering RNA

### Definition

Small interfering RNAs (siRNAs) are short (~20 nucleotides) RNA sequences that prevent the translation of specific genes by degrading messenger RNA (mRNA) using RNA interference (RNAi).

### Introduction

Small interfering ribonucleic acids (siRNAs) are a class of small RNA molecules that activate the RISC (RNA-induced silencing complex) pathway to degrade mRNA and prevent the synthesis of proteins (translation). The biological functions of siRNA are to protect genomic integrity from invasive nucleic acids, such as viruses, and to shape chromosome structure.

The discovery of small interfering RNAs' (siRNAs') ability to regulate gene expression is among one of the most significant advances in biology in recent years. Fire et al. (1998) were the first to discover that double-stranded RNA (dsRNA) produced a greater silencing effect than single-stranded RNA alone, arguing for the activation of an RNAi process to produce a viral resistance. It is now known that viruses produce dsRNA particles, which activate the RNAi machinery to silence genes. This landmark manuscript earned Fire and Mello the 2006 Nobel Prize and began a new field of research in RNAi. Since then, siRNA has been found in a multitude of eukaryotes, including fungi, plants, and animals.

In addition to its biological importance, there has been immense interest in developing siRNA

for use in research and therapeutics. Genomic manipulation through artificial siRNA (Elbashir et al. 2001) was the next big step in developing RNAi tools. For the past two decades, siRNA has been widely used to study gene function (in vivo and in vitro) and has been utilized as a therapeutic reagent for the treatment of diseases, most notably cancer.

### Structure

Initially, the siRNA begins as a dsRNA or small hairpin RNA. Following cleavage, by the dsRNA-specific endoribonuclease dicer, the result is an siRNA duplex (~21 base pairs) with phosphorylated 5' and hydroxylated 3' ends, which overhang ~2 nucleotides (Chen et al. 2008; Elbashir et al. 2001).

### Mechanism

Ribosomes in the cytoplasm translate mRNA particles to form long polypeptide chains, which later fold to make proteins. However, if siRNA is present, it will degrade mRNA through RNAi, thereby reducing mRNA transcripts and producing a silencing effect. The mRNA degradation process is facilitated by activating the posttranslational gene silencing mechanism RISC (Pratt and MacRae 2009). The mechanisms used to control RISC are quite diverse and species-dependent but rely on two common themes: (1) binding of siRNA to an Argonaute family protein (Ago) and (2) the guiding of RISC to mRNA for degradation.

dsRNA induces sequence-specific posttranscriptional gene silencing. First, the endoribonuclease dicer excises long dsRNA into siRNA duplexes. With the help of the transactivation response RNA binding protein, dicer helps load the antisense siRNA strand (guide strand complementary to mRNA) onto the catalytically active Ago to form the RISC assembly. This guide strand is "chosen" based on the thermodynamic asymmetry of the siRNA duplex, a phenomenon referred to as the asymmetry rule. The thermodynamically less stable 5' end of the guide strand is loaded into a specific Ago

(depending on the structure of the siRNA) and assembled into the RISC complex (Pratt and MacRae 2009). The remaining passenger strand is then discarded. There are many Ago proteins that mediate a range of functions from genome stability to suppressing translation (Okamura et al. 2004). The functionality of the siRNA is largely dependent on its structure and which Ago it's loaded into.

The single-stranded siRNA then guides the associated RISC to bind and then cleave specific mRNA. One quality of siRNA-targeted mRNA degradation is the near-perfect complementary base pairing between the siRNA sequence and the target mRNA. Once the guided RISC has found a complementary sequence, the catalytically active Ago breaks the mRNA, via mRNA hydrolysis, between positions 10 and 11 of the guide strand (Zamore et al. 2000). Once broken, mRNA degradation begins, and the guided RISC can be reused for several cycles.

## Research Tools

siRNA has been an invaluable tool for studying gene function and combating cancer; however, there are limitations and challenges when using siRNA in a laboratory or clinical setting. siRNA provides a temporary knockdown (a partial loss of a targeted gene transcripts) after infusion. This temporary knockdown can be an advantage when using RNAi technology; however, the temporary knockdown effects are not feasible for long-term experiments. Another challenge to researchers and clinicians alike is delivering the siRNA into the target cell. For siRNA to silence effectively, it must enter the cell and be incorporated into RISC. As siRNA is extremely large and too hydrophobic to pass through the lipid bilayer of the membrane unassisted, modifying the siRNA structure or assisting with the delivery is essential for its uptake into the cell. The delivery most useful for therapeutic intervention is systemic infusion; however, doing so via systemic infusion provides even more barriers as the siRNA must overcome endogenous nucleases, immune system targeting, rapid renal filtration, non-specific interactions, and entering the correct cell to knockdown the gene of interest (Tatiparti et al. 2017). There are currently

three major classes of intracellular delivery for nucleic acids.

**Chemical transfection**, which delivers nucleic acid through the lipid bilayer using nanoparticle-, polymer-, or liposome-based transfection technologies (Kanasty et al. 2013). Reagents such as cationic lipids and polymers are used to form complexes with the negatively charged nucleic acid, which are then taken up by the cell via endocytosis. These methods are advantageous because of the high efficiency of siRNA delivery and commercial availability; however, not all cell types work with this type of transfection, and this method has a low in vivo efficiency.

**Physical transfection** uses mechanical or electrical means to open the cell membrane and deliver nucleic acids. Mechanical methods include the use of ballistic, magnetic, and micro-injection transfection of siRNA particles into the cell (Tatiparti et al. 2017); however, these methods require highly specialized setups and training. In contrast, electroporation-mediated delivery is a powerful and versatile method for the delivery of small RNA into cells and tissues. This technique applies high-intensity electrical pulses to transiently destabilize the cell membrane and allow nucleic acids to enter. Cellular parameters, physiological conditions, and electrical properties determine the efficiency of delivery.

**Transduction** utilizes viral-mediated transfection methods to introduce nucleic acids into cells. The major difference between non-viral transfection and viral transfection is that viral transfection must enter the nucleus for expression (non-viral transfection does not). The most common viruses utilized in this process are adeno-associated virus and lentivirus, which are highly efficient and easy to use. The major drawbacks to using this type of transfection are immunogenicity, off-target effects, and size limitations. These consequences are the reasons why much effort has been placed into non-viral transfection methods (Kim and Eberwine 2010).

## Off-Target Effects of siRNA Therapies

Off-target effects occur when delivered siRNA has unintended consequences on gene regulation. Downregulation of unintended genes can occur if

the siRNA binds with partial sequence specificity. Typically, this occurs when the off-target mRNA is partially complementary to the siRNA seed region (position 2–8 from the 5' end of the antisense strand). These off-target effects are similar to how microRNAs regulate gene function. Scientists have many ways to reduce off-target effects, including changing the siRNA sequence and reducing the siRNA concentration. Other unintended off-target effects can occur if the immune system is triggered or if the siRNA delivery system becomes toxic for the cell. For example, protein-nucleic acid complexes have potentially high immunogenicity and, with repeat doses, can accumulate and lead to toxicity (Wittrup and Lieberman 2015).

## Conclusion

siRNA is a biological mechanism which protects genome stability from invasive nucleic acids and has proven to be a powerful tool in research and therapeutics. Since its discovery, there have been major advances to siRNA-mediated gene silencing technology. By exploiting the cells internal biology, artificial siRNA can knockdown specific genes and be engineered to avoid off-target effects and immune responses. While these advances have pushed the boundaries of gene silencing, gene editing technologies have recently become popular. Further development of siRNA-related technology would benefit research and therapeutics, but last major obstacle to overcome is the development of an efficient delivery system for siRNA.

## Cross-References

- [messenger RNA](#)
- [microRNA](#)
- [noncoding RNA](#)
- [RNA](#)

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## Smell

- [Cetacean Sensory Systems](#)
- [Hominoidea Sensory Systems](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Sensory Systems](#)

## Smooth Pursuit Movements

- [Cognition](#)

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## Snake, Lizard, or Worm Lizard Locomotion

- [Squamate Locomotion](#)

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## Sneak Copulator

- [Sneaky Copulator](#)

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## Sneaker Males

- [Sneaky Copulator](#)

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## Sneakers

- [Sneaky Copulator](#)

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## Sneaky Copulator

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### Synonyms

[Covert copulator](#); [Extra-pair copulation](#); [Sneak copulator](#); [Sneaker males](#); [Sneakers](#); [Sneaky mating](#)

### Definition

An individual performing copulatory behavior while withholding information about the sexual event (e.g., visual or auditory) for bystanders that could possibly prevent or disrupt the copulation.

## Introduction

From an evolutionary viewpoint reproduction is one of the most important goals of every living being. Evolutionary theory predicts that all organisms strive to have as much surviving offspring as possible. Therefore, animals have developed behaviors that increase their chances of reproduction. Because the number of available mating partners is not infinite, sexual competition is highly prevalent in animals. Animals have developed strategies to increase their chances in the competition for mating opportunities. Although many different mating systems exist across animal species, strategies for increasing mating opportunities are often similar across mating systems. There are often individual differences in strength and power between males or females. A widespread behavior that is often used by strong or powerful individuals is to monopolize copulations. Monopolization may be achieved by behaviors such as mate guarding defending a territory with copulation partners or punishing others that (attempt to) copulate. An alternative strategy, which is more often used by less strong or less powerful individuals, is sneaky copulation; by concealing sexual behavior, sneak copulators evade mate guarding and/or punishment.

## Monopolization, Mate Guarding, and Punishment

Monopolization occurs when one individual is in a position that allows it to restrict the number of copulations performed by competitors. This position may be a dominant individual which has a generally acknowledged hierarchical position which enforces others to restrict copulatory behavior in its presence (Overduin-de Vries et al. 2013). In these hierarchical systems, there is an alpha individual, usually a male (but there are also harem mating systems with an alpha female leader), which has a lot of power because he/she has proven to be the strongest, or he/she is born in the right family. Monopolization may be achieved by the mere presence of a socially dominant or physically stronger individual. This occurs when



lower-ranking or physically weaker individuals abrupt their mating attempts upon confrontation with a possible monopolizer, in order to prevent harmful conflicts. A generally used tactic by monopolizers is mate guarding; following and defending (a) particular (fertile) opposite sex individual (s). In socially monogamous species individuals follow their partner around and prevent it from copulating with others. Likewise dominant individuals in social groups mate guard fertile individuals. Mate guarding is most effective in species where the fertile phase is detectable for the opposite sex, because this limits the time frame in which mate guarding is necessary. Besides, in social groups ovulation synchrony impedes monopolization since monopolizers cannot mate guard all fertile individuals simultaneously. Another monopolizing tactic is to use aggression in order to force others to give up their copulation attempt (e.g., Gouzoules 1974). For example, monkey females that attempt to copulate with males other than the alpha male face punishment in the form of being chased, being threatened, or receiving physical aggression. Both the female and the male sneaky copulator risk punishment in monkeys. After disruption, the alpha male often copulates with the interrupted female.

## Mating Systems Including Sneaky Copulators

Sneak copulation occurs in mating systems where individuals are restricted in choosing their mating partners, e.g., in systems where monopolization or mate guarding occurs or where sexual behavior is punished by certain individuals. These are systems with pair bonds, systems where mating occurs within fixed groups and harem groups.

Monogamous pair bonding is common across the animal kingdom, especially among birds (93% of species) (Lack 1968) and primates (12% is monogamous) (Rutberg 1983). However after close inspection of sneaky behavior and DNA comparisons of parent offspring combinations, it becomes clear that much less species are also

sexually monogamous (Griffith et al. 2002). Extra-pair copulations are often the result of sneak copulators that conceals its copulations for its partner. Examples of species that are known for their strict social monogamy but that are nonetheless sneak copulators are Lar Gibbons (*Hylobates lar*) (Reichard 1995), zebra finches (*Taeniopygia guttata*) (Houtman 1992), and beavers (*Castor canadensis*) (Crawford et al. 2008).

Sneaky copulation also occurs in animal species where mating is restricted within small groups. For example, dunnocks live in monogamous couples or in small groups where two or three males cooperatively defend a territory with one or multiple females. The most dominant male intensively guards the female (s) throughout the mating season, but especially when food is scattered and the female home range expands, monopolization is difficult (Davies and Hartley 1996). The subordinate male(s) almost always fertilize some of the eggs. This is not only the result of the pursue of the subordinate males but also of the female, which actively attempts to sneak away from the dominant male to have mating opportunities with the subordinate males.

Many species such as elephant seals (de Bruyn et al. 2011), bighorn sheep (Hogg 1987), and long-tailed macaques (Overduin-de Vries et al. 2013) live in harem groups. The power of the group leader gives him/her exclusive right to copulate with the opposite sex group members. For example, elephant seal males risk their live in injurious fights with sharply teathed opponents. The winner of these fights will become the leader of dozens or even hundreds of females. However, an alternative mating tactic exists that creates opportunities for siring offspring for individuals that prefer to stay clear of risky competition: sneak copulation at sea (de Bruyn et al. 2011). This sneak copulator tactic may be particularly worthwhile for individuals that are less likely to win male-male fights. Similarly, bighorn sheep live in harem groups where one alpha male monopolizes the majority of fertile females, by mate guarding (Hogg 1987). However, females occasionally

run away from their monopolizer and sneak copulators profit by courting them and copulating quickly away from the group leader (Hogg 1987).

success of both strategies, monopolizing or sneaking, depends on the status of the male and the frequency of males and females and their strategies (Gross 1996).

## Conflict between and within the Sexes

The existence of sneak copulation within a species is often the result of a conflict between or within the sexes. Sneak copulation can be a strategy that has evolved as a female strategy within the framework of the conflict between the sexes (Parker 2006) but also as a male strategy to outcompete other males. There are different things at stake for males and females in a mating market. When producing offspring, females generally invest more than males in terms of larger gametes and the extra burden of gravidity (Clutton-Brock 1991). Therefore, females generally prefer polygamous mating which allows them to select the better sperm for their costly egg. Exceptions to this preference are often related to paternal care. If paternal care significantly contributes to the survival of offspring, females may benefit more from a single copulation partner that cares for their offspring (Gubernick and Teferi 2000), than from multiple partners that are not taking care of the offspring. However, the most successful strategy for females would be to profit from a male's paternal investment while sneakily copulating with other males in order to improve the genetic quality of their offspring (Kempnaers et al. 1992).

Males, on the other hand, have developed strategies to prevent parental investment in offspring that is sired by their neighbors. For example, monopolization of females is a strategy that limits paternity uncertainty. However, some males are better in monopolizing females than others. Whereas strong and/or powerful males profit most from monopolizing females, weaker and/or less powerful males are less likely to win contests over females and have a higher risk of injury during these contests. Therefore, alternative reproductive strategies exist for males (Gross 1996) such as sneak copulation. The relative

## Withholding Information

Sneak copulators conceal their copulations by withholding information from possible eavesdroppers, which could possibly disrupt or prevent their copulation. They withhold either visual or auditory information or both. For example, long-tailed macaques prefer to copulate near opaque structures blocking the view of a possible audience. Likewise, they copulate more often when the group leader is in a visually separated enclosure (Overduin-de Vries et al. 2013). This way they prevent possible competitors from seeing the copulation, minimizing the possibility of being disrupted during copulation.

Another way of concealing copulation is by suppressing copulation calls (Townsend et al. 2008, Clay and Zuberbuhler 2011). Low-ranking female chimpanzees (*Pan troglodytes schweinfurthii*) suppress copulation calls when high-ranking females are present. This way, low-ranking females avoid female-female competition, which can be severe in this species.

Another form of sneak copulation for males is mimicking a female. These fake females can sneak within the territory of another male or approach another male's partner without being attacked by him and perform sneaky copulation. When employing the mimic tactic, males conceal their true color during the approach of the female, withholding information about their identity, being a male.

## Cognitive Level

Withholding information from another individual is sometimes interpreted as higher-order cognition under the term deception, but it does not need to be. By using simple rules of thumb, such as "freeze behavior or change color when in close

proximity of a strong or dominant individual,” animals can conceal behavior (Amici et al. 2009) without making inferences about what another individual can see or hear. These rules of thumb can be learned by simple operant learning when sexual behavior in close proximity of dominant individuals is linked with punishment. Therefore, animals with cognitive capacities that are at least capable of learning by operant conditioning are equally likely to be sneak copulators as are more intelligent species. Moreover, mimicry is possible without operant conditioning. In some species the female mimics are inflexible traits that are genetically based (Sinervo and Lively 1996) or fixed during early development (Emlen 1997). Therefore, this tactic can be used by animals that are less cognitively advanced including fish (Dominey 1980), reptiles (Sinervo and Lively 1996), and isopods (Shuster and Wade 1991). In contrast, other mimicking species, such as the giant cuttlefish, can flexibly adjust their appearance and resemble a female when they are sneakily copulating, while they return back to male coloration afterwards (Norman et al. 1999). This flexible use of color mimicry does require cognitive processes such as operant conditioning.

## Sneaky Copulators and Human Sexual Behavior

Within human behavior, there is enough evidence that sneak copulation is a substantial contributor to the fitness of an individual. For example, women copulate more often sneakily with a lover around the time of ovulation (Gildersleeve et al. 2014). This indicates that sneak copulation is an important strategy for women to fertilize their egg with sperm other than their partners'. The rationale behind this strategy is that women try to get the best of two worlds without being aware of using this strategy. They choose a long-term partner that is caring, protecting, and a good father, while they choose strong, intelligent, high status, and good-looking lovers to fertilize their egg. There is also evidence that males have evolved counterstrategies as a response to female promiscuity (Shackelford et al. 2005). For

example, the longer a man has been away from his wife, the larger will be his ejaculate. This larger amount of sperm will give him an advance in case his sperm has to compete with sperm from another man. Moreover, there are indications that human sperm cells can selectively kill the sperm cells of rivals within the female reproductive tract (Baker and Bellis 1988). Although this theory is debated by many researchers, and convincing empirical evidence is difficult to collect, it is not the first case where sperm cells use complicated strategies to combat rival sperm (Pearcy et al. 2014).

## Cross-References

- ▶ [Assortative Mating](#)
- ▶ [Cheating](#)
- ▶ [Competition](#)
- ▶ [Deception](#)
- ▶ [Extra-Pair Copulation](#)
- ▶ [Mate Guarding](#)
- ▶ [Mating](#)
- ▶ [Sperm Competition](#)

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## Sneaky Mating

### ► Sneaky Copulator

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## Sneaky Matings

### ► Extra-Pair Copulation

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## Social Affordance

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## Synonyms

Affordance; Direct perception; Ecological psychology; Environment-organism systems; Information-based approach; Perception-action theory; Social cognition; Social interaction

## Definition

Social affordances are possibilities for social interaction or possibilities for action that are shaped by social practices and norms.

## Affordance

The term “affordance” was coined by James Gibson to refer to what things or events in the environment afford to an organism. For instance, a rigid flat surface affords support and locomotion to terrestrial animals. It is stand-on-able and walk-on-able (Gibson 2015). The water surface of a lake does not afford support to a terrestrial animal, but it does to some flies. Thus, the same part of an environment may afford different things to different species or organisms. This is because affordances are relational in nature, they are both a fact of the environment and a fact of the organism. According to Gibson, affordances are neither subjective nor objective, they cut across the dichotomy of subjective-objective. There has been debate among ecological psychologists as to what in the organism is responsible for an affordance. The options range from bodily properties to dispositions to abilities (Chemero 2003). In all cases, such organismic elements are what turns a feature of the environment into a possibility for action that is meaningful to the organism.

Affordances are crucial for the ecological approach to perception. The environment shows up to an organism in terms of what it can do in it. An organism perceives by picking up environmental information that specifies the affordances of the environment. This point is crucial to understand Gibson’s approach to perception. According to the ecological approach, the environment is rich of structures and energy patterns that convey information about objects and events. Information for Gibson is a relation of specification established by lawful covariation between patterns of energy – optical, mechanical, and chemical – over time and/or space and objects or events in the environment. For instance, structured ambient light conveys information about surfaces of objects. As this information is structured over time and/or space, the organism needs to explore its environment to pick it up. Gibson explains the process of picking up information by the radio metaphor. Through exploratory movements, the organism becomes attuned to environmental information and resonates to it. Inasmuch as an organism resonates to information, it is able to

perceive affordances directly. Thus, perception is an active process that takes place over time and whose main function is to pick up information that specifies affordances.

## Social Affordance

Although Gibson did not systematize theoretically the notion of social affordances (Costall 1995), he was open to it and gave several examples of social affordances. His example of the postbox as an object that “affords letter-mailing to a letter-writing human in a community with a postal system” (Gibson 2015, p. 130) is well known. Gibson also called attention to the fact that an animal, as a self-moving being with characteristic behaviors and anatomy, affords peculiar possibilities for action to other animals. An animal “can afford eating or being eaten, copulation or fighting, nurturing or nurturance” (Gibson 2015, p. 36). Some of the latter examples, such as eating and being eaten, may not yet be considered full social affordances inasmuch as they elicit behavior in another animal but not necessarily social interaction. To have social interactions the participatory animals must have a minimal responsiveness to each other as self-moving beings and their behaviors must be mutually constrained while they are engaged in an activity. As Gibson points out, “as one moves so does the other, the one sequence of action being suited to the other in a kind of behavioral loop. All social interaction is of this sort—sexual, maternal, competitive, cooperative” (Gibson 2015, p. 36). Thus, in virtue of the coupling between the caregiver and the infant in several mammals, the caregiver affords the infant the possibility to clung and contact comfort. For species capable of joint attention, the joint perception of a predator might afford the social affordance of outnumbering our foe. Among some primates, grooming behavior affords social bonds.

The example of the postbox and the examples of social interactions point to two different senses in which the term “social affordance” is normally used. In the postbox case the letter-mailing affordance is social because it depends on an



ongoing social-cultural practice to be available. An agent from a culture without a postal system and having no idea of what a postal system is cannot perceive the postbox as affording letter-mailing. To be open to this affordance, the agent needs to be normatively responsive to and constrained by the social practice in question. In contrast to generic affordances, which can be understood in terms of the individual-object dyad, this type of social affordance requires also the social system of mutual responsibilities and conventions within which an object gains a peculiar function. In relation to social creatures like us there has been debate about whether all affordances are socially shaped in this way (Costall 1995). As to the second group of social affordances, they are social because there are possibilities for interaction that other persons or animals afford. Through these affordances a person or an animal shows up to an observer not as a physical object but as an agent with the capacity to reciprocate. These are “the richest and most elaborate affordances of the environment” (Gibson 2015, p. 126), they comprise the most basic kind of social cognition that makes cooperation and coordination possible, as well as predator–prey interactions. This type of social affordance is allegedly more fundamental since it seems to be required by the social-cultural practices that underpin the first type of social affordance.

A common criticism of the very possibility of perceiving social affordances is that there is no information about them in the environment. As the argument goes, the ambient light might contain information about objects, their surface layout, texture, and colors, but not about whether they afford, for instance, letter-mailing. The social function of an object is not perceptible. An agent comes to know that a postbox has this function only by inference. The same applies to social affordances regarding persons and animals. Possibilities for interaction are allegedly not perceptible, there is no information in the environment about whether an animal affords cooperation or aggression. An animal can see movements and facial expressions of another animal but not that it is open to and waiting for interaction. Gibson himself claims that “other

animals and other persons can only give off information about themselves insofar as they are tangible, audible, odorous, tastable, or visible” (2015, p. 127), which raises the question about whether other animals and other persons can give off perceptible information about their social affordances.

A set of considerations may help to put away the worry above. The first point to notice is that the animal’s movements, gestures, and facial expressions can be sufficiently patterned over time and/or space to specify a wide range of possibilities for interaction. By picking up such a pattern, an observer may be said to perceive directly the corresponding possibility for interaction. This, however, might not be enough to resolve all possible ambiguity. A second consideration concerns the notion of information itself. One possibility to have more information in the environment regarding social affordances is to weaken the notion of information. Instead of requiring a specifying relationship, it may be enough a probabilistic relationship between an energy pattern and a social affordance in that the former makes the presence of the latter likely (Bruineberg et al. 2019). Another alternative would be to relativize the notion of information to environments or habitats. A specifying relationship does not need to hold over all environments to make perception possible. A local specifying relationship that holds only in a specific environment might be sufficient to perception provided the perceiver dwells in that environment. Thus, optical information about the postbox might be sufficient to specify the letter-mailing affordance in a social environment where there is a postal system.

A further consideration on this issue is that the social environment should not be taken as detached from the natural environment; actually the dichotomy between nature and culture should be overcome. For many species, particularly ours, the social is a background condition not only for their evolutionary history but also for the development of their members (Heft 2007) so that a new member with cooperative dispositions enters in an environment which is already socially structured. In relation to practices within a social

environment, complex energy patterns may convey information about social affordances for beings with prosocial capabilities immersed in those practices.

Both affordances shaped by social norms and affordances for social interaction are important for ecological psychology to address the scaling-up problem – the problem of accounting for the higher-order cognition, such as planning, imagination, abstract thought, and language use based on basic cognition such as the perception of affordances. Attempts have been made to apply social affordances to explain planning (Kiverstein and Rietveld 2018). Synergies between ecological psychology and enactivism have been explored. Some argue that an enactive account of language can augment social affordances to deal with planning and distal engagement (Brancazio and Segundo-Ortin 2020). In anthropology, social affordances have been mobilized to overcome the dichotomy between nature and culture and to show how the human living world is socially structured and meaningful independently of symbolic thought (Ingold 2000).

The realm of social interactions has also been studied within ecological psychology, providing a rich repertoire of subtypes of social affordances to explain complex social behavior. One may distinguish, for instance, common affordance from joint/shared affordance. The former is the affordance of an object that may induce emergent coordination, such as the arrival of a bus awaited by many passengers. The latter is “an affordance for two or more people collectively which is not necessarily an affordance for any of them individually” (Knoblich et al. 2011, p. 63), such as a long two-handed saw that affords cutting to two people acting together but not to one acting alone. Both common and joint/shared affordances are also distinct from collective affordances. These are affordances available to collectives – groups of individuals who share an embodied social identity. For instance, during a match of football, the situation in the pitch may offer the collective affordance to play a counterattack to the recently attacked team (Weichold and Thonhauser 2020). Thus, social affordances provide a powerful

resource to explain a great variety of social interactions and how they may combine to give rise to complex cognition and behavior.

## Cross-References

- Cooperation
- Embodied Perception
- Perception-Action Theory
- Pro-social Behavior
- Social Grooming
- Social Learning

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## Social Behavior

- ▶ [Affiliative Behaviors](#)
- ▶ [Coalition Enforcement](#)
- ▶ [Self-Decoration in Dolphins](#)

## Social Bonding

- ▶ [Affiliative Bond](#)

## Social Bonds

- ▶ [Affiliative Bond](#)

## Social Buffering

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### Definition

**Social buffering** The improved recovery from aversive experiences when a social mammal is grouped with others of the same species (Davitz and Mason 1955).

### Introduction

Primates encounter a multitude of stressors in the wild, ranging from constant predation risk to food competition and aggressive interactions with conspecifics. In mammals, stress activates the hypothalamic-pituitary-adrenal (HPA) axis, which in turn stimulates the adrenal cortex and eventually results in the release of the glucocorticoid hormone cortisol, or corticosterone. In the immediate context, cortisol is adaptive because it motivates the “fight-or-flight” response on which

survival depends and enables individuals to act quickly to escape life-threatening situations. However, although it is adaptive in the short-term, cortisol is extremely damaging to the brain and body when released consistently over long-term periods. Cortisol has been linked to decreases in immune response as well as cognitive ability in humans and nonhuman primates, and high levels of consistent stress are known to promote disease in animals vying for dominance in a structured social system (McEwen and Seeman 1999). Interestingly, social mammals appear to have developed a hormonal mechanism that helps to attenuate the well-known negative physiological and psychological effects of stress. This mechanism is enabled by sociality and is known as social buffering.

## Attenuating Stress: Social Buffering Theory

In primates, sociality appears to increase longevity and reproductive success. Sociality is associated with positive effects on various diseases including blood pressure and cardiovascular reactivity in humans (Evans and Steptoe 2001; Gallo et al. 2000), and therefore appears to counter the negative effects of cortisol. To an extent, these biological benefits of sociality may be explained in part by social buffering and its resulting effect of reduced stress. Social buffering is the improved recovery from aversive experiences when a social mammal is grouped with others of the same species (Davitz and Mason 1955). This effect was initially studied in fear-conditioned rats, who were found to display less fearful behavior when in the presence of conspecifics (Davitz and Mason 1955), and in rat pups, who were found to be able to regulate maternal levels of cortisol release (Smotherman et al. 1977). Social buffering effects have since been found in nonhuman primates (Coe et al. 1978; Winslow et al. 2003), guinea pigs (Hennessy et al. 2000), and humans (Seltzer et al. 2010) and have been found to be modulated by neuropeptide hormones, early social experiences, and the social structure of a species.

## The Role of Oxytocin in Social Buffering

Social buffering appears to be modulated in part by oxytocin, a neuropeptide hormone critical to social development that also modulates stress reactivity. The function of oxytocin appears to be strongly conserved throughout evolution, as it plays similar roles in reproduction, bonding, and social behavior across vertebrates (Donaldson and Young 2008). It is released in response to a variety of behaviors, including lactation, affiliation, pain reduction, and stress reduction. In mammals, oxytocin attenuates cortisol through its action on the HPA axis. Specifically, oxytocin activates neurons in the hypothalamus and the resulting increase in oxytocin secretion from the hypothalamus then inhibits activation of the HPA axis, consequently attenuating the physiological effects of cortisol (Neumann et al. 2000; Neumann 2002). Moreover, intracerebroventricular (ICV) injection of an oxytocin-receptor antagonist has been observed to heighten HPA activity, further demonstrating the role of oxytocin in attenuating stress responses (Neumann 2002). Peripheral oxytocin also acts on the adrenal gland where it inhibits the secretion of corticosteroids, as well as the pituitary gland where it inhibits the release of ACTH (adrenocorticotrophic hormone), a hormone that triggers the production and release of cortisol by the adrenal gland (Neumann et al. 1998). Thus, oxytocin attenuates the physiological experience of stress through multiple avenues.

In addition to attenuating the physiological experience of stress, oxytocin has also been observed to alter behavioral responses to stress in primates and other mammals. Oxytocin receptor-mediated mechanisms have been found to be involved in stress-coping strategies in rats (Ebner et al. 2005), and oxytocin administered to human males during a social stressor decreases anxiety responses and increases calmness (Heinrichs et al. 2003). Further, oxytocin is a well-known motivator of social affiliation, a necessary precursor to any social buffering effects on stress. In male marmosets (*Callithrix jacchus*), administered oxytocin increases tolerance of infants as well as the inclination of males to

share food with infants (Saito and Nakamura 2011). In humans, increases in oxytocin induced by a parental figure have also been observed to lead to quicker returns to baseline levels of cortisol after experiencing social stress (Seltzer et al. 2010). Thus, social buffering is enabled in part by oxytocin, which motivates social affiliation that then leads to attenuated responses to stress through direct and indirect action on the HPA axis.

## Developmental Influences on Social Buffering

Stress systems and the HPA axis are regulated by social variables early in life and are also subjected to programming effects that regulate their activity levels in later stages of development (Hostinar et al. 2014). Consequently, social experiences in early development also play a strong role in regulating mammalian social buffering ability. Nursery-reared rhesus monkeys (*Macaca mulatta*) exhibit decreased levels of oxytocin in contrast to mother-reared monkeys and do not experience an attenuated cortisol response when paired with another individual in a stressful event (Winslow et al. 2003). Mother-reared monkeys also display a higher rate of affiliative social behavior relative to nursery-reared monkeys, thus suggesting that nursery-reared monkeys develop a deficit in their capacity to use social support in stressful situations. Thus, social buffering ability stems in part from the quality of social relationships experienced during early development. Further, this suggests that individual differences in social buffering ability are based on how the neuroendocrine system has adapted to the social environment experienced in early life. In regards to the development of the HPA axis, there is evidence for a “stress inoculation” effect, whereby brief separations from the maternal figure enable an infant to better adapt to stressful experiences later on in adulthood (Lyons et al. 1999; Parker et al. 2004). This may indicate that the HPA response in animals that have experienced some early stressors is better calibrated to handle a varying

degree of stressful challenges in a way that is less damaging to the body. In addition, early life stress buffering is also protective against elevated physiological responses to stress in adulthood (Liu et al. 1997), which suggests that early life social buffering also helps to protect against extreme and detrimental physiological responses to stress later in life. Although the most potent source of social buffering in primates is generally the maternal figure, an individual will develop the ability to receive social buffering benefits through other familiar conspecifics as they mature, including extended family members and preferred peers.

### Effects of Familiarity on Social Buffering

In primates, it is well-established that the most powerful elicitor of social buffering effects is the mother. In the absence of a maternal figure, infants can learn to rely on peers to buffer stress, but the ability of peers to buffer stress at this early stage in development is not as strong as the mothers and leads to issues with managing stress in adulthood (Suomi 1991). The ability of the maternal figure to remain a powerful buffer of stress continues at least throughout childhood development in humans. However, the strength of the relationship and level of familiarity with the caregiver is also of importance in modulating the strength of the social buffering effect in non-human primates. In titi monkeys (*Callicebus moloch*), the father is the preferred caregiver and is consequently also the most potent elicitor of the social buffering effect when compared to the mother (Hoffman et al. 1995), demonstrating the important role of experience and familiarity in social buffering. Other familial females also have some ability to socially buffer stress in infants. In squirrel monkeys (*Samiri sciureus*), stressed infants are able to be comforted to an extent by aunts, in addition to their biological mothers (Coe et al. 1978). Fear-conditioned squirrel monkeys have also shown reduced cortisol responses when exposed to shock cues in the presence of a familiar partner, demonstrating the

ability of familiar conspecifics to buffer the neuroendocrine response to stress.

As an individual matures, the ability of parental figures to buffer the HPA response to stress begins to decline, and the individual begins to rely more strongly on peers and romantic partners. In humans, parents start to lose their ability to buffer stress in their children once they begin to reach adolescence, which suggests that the child's developing brain no longer needs to rely on parental figures to protect it from the damage caused by stress (Gunnar and Hostinar 2015). Indeed, peers can serve as strong buffers to the HPA axis response to stress in humans and non-human primates. However, the ability of peers to attenuate the stress response is modulated by the strength of their bond with the stressed individual. Children who report more supportive relationships with their best friend display more rapid decreases to baseline levels of cortisol after experiencing a social stressor with that friend, relative to children who report less supportive relationships with their best friends (Calhoun et al. 2014). Social buffering potency is also contingent on bond strength in nonhuman primates, including male barbary macaques (*Macaca sylvanus*) who form enduring male-male social bonds in adulthood that are similar to human friendships. These bonds provide effective buffering against social and environmental stress (Young et al. 2014) demonstrating the ability of individuals to rely on peers for social buffering long after they have branched away from their parents.

In addition to peers, the ability to elicit social buffering in adulthood is extended to romantic partners as well, although it is uncertain when these extensions of the social buffering network develop. In humans, support from romantic partners buffers the HPA axis in males experiencing a social stressor, resulting in a decrease in the cortisol response (Heinrichs et al. 2003). Effective stress buffering by partners also occurs in monogamous nonhuman primates who form long-lasting pair-bonds. Titi monkeys are well-known for forming strong pair-bonds, and consequently experience buffering of the stress response when in the presence of their bonded



mate, relative to other primates who do not form pair-bonds such as squirrel monkeys (*Samirisciureus*, Hennessy et al. 1995).

## Social Structure and Social Buffering

Given the ability of close conspecifics to buffer stress in primates, it is not surprising that social buffering potency is also mediated by the social structure of a species. Strong differences in the number of individuals required to elicit a buffering response have been observed depending on a species' pattern of social organization. Squirrel monkeys, who live in large mixed-sex groups and interact mostly with same-sex conspecifics, experience the strongest buffering response when in the presence of multiple group members, relative to titi monkeys who live in lasting pair-bonds and experience strong buffering of the stress response when in the presence of their bonded partner (Hennessy et al. 1995). Robust buffering by a pair-bonded mate also occurs in marmosets (*Callithrix kuhli*), who form long-lasting pair-bonds and raise infants cooperatively in extended family groups (Smith et al. 1998).

In primates, social buffering is also dependent on the level of gregariousness as well as the strength of social hierarchies in a given species. For example, differences in the baseline levels of stress hormones and oxytocin are known to exist in bonnet macaques (*Macaca radiata*) and pigtail macaques (*Macaca nemestrina*), who exhibit stark differences in social structure. Bonnet macaques are highly gregarious and less hierarchical, and show minimal preferences for kin. In contrast, pigtail macaques live in strongly hierarchical social groups with consistent preferences for kin and often display aggressive behaviors. Accordingly, bonnet macaques exhibit lower basal levels of corticotropin-releasing factor (CRF), a neuropeptide hormone similar to cortisol which is also involved in the stress response, and higher basal levels of oxytocin than pigtail macaques (Rosenblum et al. 2002). This strong variation in baseline stress hormones as well as oxytocin suggests that the stress

buffering response in primates is mediated in part by behavioral factors such as social structure.

## Conclusion

The ability of an individual to buffer stress through sociality is modulated by social experiences in early development, as well as other variables including familiarity with peers, romantic attachment, and social organization of the species. Further, differences in the stress regulation system appear to be based on how the neuroendocrine system has adapted to social experiences during early development and may function to prepare developing offspring to deal with the stressors typical of their environment.

## Cross-References

- [Primate Social Structure](#)
- [Social Behavior](#)
- [Stress](#)

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## Social Cognition

- [Equine Cognition](#)
- [Perissodactyla Cognition](#)
- [Social Affordance](#)
- [Swine Cognition](#)

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## Social Darwinism

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### Synonyms

[Eugenics](#); [Lamarckism](#); [Reform Darwinism](#); [Social evolution](#); [Survival of the fittest](#)

### Definition

Set of ideologies loosely based on Charles Darwin's *Theory of Evolution by Natural Selection* that is used to justify certain political, economic, and social policies.

### Introduction

*Social Darwinism* is the co-option of Charles Darwin's *Theory of Evolution by Natural Selection*, to justify certain political and economic practices in human societies. In 1859, Darwin introduced the idea that organisms are in a constant "struggle for survival" in his seminal work *On the Origin of Species*. However, Darwin never posited about the functioning of human societies in his seminal text. Instead, biologist Herbert Spencer drew parallels between his own economic theories and Darwin's biological ones, claiming that the struggle for survival promoted self-improvement in people. In 1864, Spencer published *Principles of Biology*, wherein he promoted the idea that people could genetically pass-on to their children, such learned qualities like frugality and morality (Spencer 1852). Though Spencer is credited as the founder, or "father of social Darwinism," coining the term "survival of the fittest," a phrase commonly used in popular culture to describe any process that is analogous to the biological processes described

by Darwin, the term "Darwinism" was first used by Thomas Henry Huxley in his 1860 review of *On the Origin of Species* (Huxley 1860). Further, the first recorded use of the phrase "social Darwinism" was in Joseph Fisher's article *The History of Landholding in Ireland* published in 1877 (Fisher 1877). Nonetheless, through his adamant re-telling of the theory of evolution, Spencer popularized social Darwinism across the globe, most prominently in Europe and the USA. Unfortunately, the biological theory of evolution and the sociological adaptation of Darwin's theory have never been fully disentangled. As such, social Darwinism has had wide-reaching ramifications, especially as it applies to race, gender, class, and immigration throughout the world.

### History of Social Darwinism

Darwin's biological theory of natural selection and the arguments made later by social Darwinists were heavily influenced by the work of early British cleric and scholar, Thomas Malthus. In his 1758 essay, *Principles of Population*, Malthus argued that resource growth is arithmetic, while population growth is geometric; therefore, populations grow faster than do resources, and this disparity results in a constant struggle among members of a population for scarce resources. While aboard the voyage of the *Beagle*, Darwin read Malthus and began applying these ideas to the natural world, describing a struggle among organisms for access to limited resources in nature. In 1859, Darwin published his ideas about the biological world in arguably one of the most important texts ever written, *On the Origin of Species by Means of Natural Selection*.

The reception of this text was mixed, but one of the first and most vocal proponents of Darwin's theory was biologist Herbert Spencer. Often credited as the founder of social Darwinism, Spencer was also a proponent of *laissez-faire* economics- or the belief that economics and businesses function best when there is no government regulation. At its inception, social Darwinism was largely created as a justification and ethical

precept for cut-throat economic competition. In their view, such unrestrained capitalism was the “natural” order of human civilizations – even though the rise of industrial production at this time was far from “natural.” Many social Darwinists, including Spencer, began opposing laws that helped the poor or working-class peoples, and those that they deemed genetically “unfit.” They argued that such laws would oppose the natural evolution of civilization by delaying the extinction of “unfit” people. However, proponents of social Darwinism have a fundamental misunderstanding about the biological theory proposed by Darwin. Darwin’s theory of evolution by natural selection is the differential survival and reproduction of individuals due to differences in phenotype. Darwin focused on the idea that different phenotypes mean that different individuals will be more or less “fit” to survive and reproduce in a given environment. However, the concept of fitness is biologically open-ended. For example, the phrase “survival of the fittest” is not often used by modern biologists because it is misleading and does not capture the complexity of natural selection as survival is only one aspect of fitness and not always the most important one. Even still, the idea that the existence of “unfit” people in society were inhibiting human evolution, paved the way for new governmental policies that promoted racism, sexism, and xenophobia (Gould 1981).

Social Darwinism has perhaps been the most widely accepted in the USA. While Spencer was well-known across Europe, he was especially popular in the USA because his ideas provided a scientific justification for capitalism, which is believed by many in the USA to be the most effective system for stimulating economic progress. US steel mogul, Andrew Carnegie, was one of the most prominent followers of Spencer and is largely responsible for popularizing social Darwinism in the USA. William Graham Sumner, who held the first Sociology professorship in the USA at Yale University, was a prominent social Darwinist who has had a long-term influence on Conservatism in the USA. Sumner spoke out against the so-called welfare state that promoted a system of government intended to protect the

health and well-being of its citizens – especially, the poor and working class, by means of grants, pensions, and other social programs. Instead, he supported free markets and viewed individual competition for property and social status as a tool for eliminating the weak and immoral people of society (Hofstadter 1944).

## Ramifications of Social Darwinism

The derogatory rhetoric around any person that was not of the dominant, wealthy class, during the height of social Darwinism, paved the way for the new “science” of Eugenics. Invented by British scholar, Sir Francis Galton, Eugenics was marketed as a way to better humankind by propagating the genes of the socially elite (Galton 1883). Just like social Darwinism, Eugenics argued that social institutions like economic welfare, mental health facilities, and disability support programs allowed “inferior” people to survive and reproduce at higher rates than their “superior” counterparts. It is important to note the critical flaws in Eugenic thinking. For one, Eugenics rested on the idea that upper-class people obtained their social positioning because of their superior genetic make-up. It also relied on the idea that “superiority” could be objectively quantified, rather than acknowledging the inherent subjectivity of assessing human qualities.

Eugenics became a popular pseudo-scientific movement in the USA in the early 1900s. Early proponents believed that the best way to improve the human species was to direct its evolution through selective breeding (Davenport 1911). As such, the USA was the first country to concertedly undertake compulsory sterilization programs for the purpose of Eugenics. Rates of forced sterilization were relatively low across the USA, until the Supreme Court’s landmark decision in *Buck v. Bell* 274 US 200, legitimized the forced sterilization of people deemed “intellectually disabled.” After that decision, over 62,000 people in the USA, most of them women and people of color, were sterilized (Kluchin 2011). Forced sterilization disproportionately affected certain

populations including those who were sentenced for harsher crimes and people of color. Wealthy and white-collar criminals were not forcibly sterilized at the same rate. Thus, in 1942, the Supreme Court case, *Skinner v. Oklahoma* 316 US 535, ruled forced sterilization of inmates, unconstitutional under the equal protection clause. Men and women were compulsory sterilized for different reasons. Men were sterilized to treat their “hyper-aggression” and to eliminate “criminal tendencies.” Women were sterilized to control their sexuality. Since women bore children, eugenicists held women more accountable than men for the reproduction of less desirable members of society – another incarnation of sexism propped up by “science.” Many scholars also now recognize that similar Eugenics programs in Nazi Germany were largely inspired by previous work in the USA. In addition to forced sterilization, there were many acts of state-sanctioned racial segregation in the name of Eugenics (Kluchin 2011). These included anti-miscegenation laws that criminalized interracial marriage and sexual relations between members of different races (Dorr 2008).

Eugenics also endorsed strict anti-immigration policies in the USA. The Immigration Restriction League was the first American entity formally associated with Eugenics. Founded in 1894, by three recent Harvard graduates, the League sought to bar what it considered inferior races from entering the USA. Later, Eugenicists like Lothrop Stoddard and Harry Laughlin served as expert witnesses for the House Committee on Immigration and Naturalization. During their testimonies, these men argued that people entering the USA would pollute the national gene pool and dilute what they saw as the superior American racial stock. Some scholars suggest that these racialized arguments prompted the USA and Canada to pass laws creating a hierarchy of nationalities (Kline 2005). Individuals were rated from the most desirable, Anglo-Saxon and Nordic peoples, to the Chinese and Japanese immigrants, who were later banned from entering the country (Gould 1981). This argument that immigrants pollute the USA has never really subsided and is often invoked during every new wave of immigration in the USA.

## Conclusion

Social Darwinism came about during the Industrial Revolution, when many countries were experiencing simultaneous leaps in productivity and massive wealth inequalities. At its inception, social Darwinism was adopted by late nineteenth century capitalists as a justification for *laissez-faire* economics. Under the guise of “science,” the wealthy were considered successful because of their superior genetics, which could be passed to later generations and would positively impact society as a whole. Later, social Darwinism spurred a new movement of Eugenics that propped up racist, sexist, and xenophobic policies – the impacts of which are still being felt across the world. Scholars now recognize social Darwinism as an ideological justification for much of the eighteenth and nineteenth century European enslavement and colonization of countries with valued resources. However, some suggest that these ideas are still working their way into the intellectual foundations of public education in neocolonized countries. We continue to revisit the histories of social Darwinism because many of the ideas are still widely circulated and used to prop-up various social, political, and economic policies across the world today. An evaluation of how social Darwinism has historically affected people can help us avoid the on-going marginalization of people in our societies.

## Cross-References

- [Charles Darwin](#)
- [Evolution](#)
- [Herbert Spencer](#)
- [Jean Baptiste Lamarck](#)

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## Social Diffusion

- [Diffusion Studies](#)

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## Social Ethology

- [Napoleon Chagnon](#)

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## Social Evolution

- [Social Darwinism](#)

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## Social Evolution Studies

- [Selection Study](#)

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## Social Facilitation

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Social facilitation can be defined as the effect of the mere presence of a conspecific (a member of the same species) on the behavior of the focal animal. Robert Zajonc (1965) reported that the effect of the presence of a conspecific may facilitate or retard performance depending on the nature of the behavior being assessed. According to Zajonc, the presence of a conspecific will generally increase the arousal or motivation of the observing organism and that increased arousal would tend to facilitate ongoing (or well learned) behavior but would tend to retard the acquisition of new to-be-learned behavior. Zajonc cited examples from humans (as well as other animals) in diverse settings such as assembly lines and taking exams to running races. This theory has had some support. On the one hand, Zajonc noted that human performance of well-practiced responses on an assembly line were enhanced by the presence of others, as was the performance of well-practiced athletes when competing in the presence of others. On the other hand, when humans performed complex math problems or took difficult tests, the presence of others interfered with performance.

In animals, Zentall and Levine (1972) found that the mere presence of another rat actually retarded the acquisition of a not-yet learned lever-press response for reinforcement relative to the absence of a conspecific, whereas Levine and Zentall (1974) found that if that response had been well learned the mere presence of another rat facilitated the performance of a lever-press response for reinforcement.

One may be able to propose alternatives to social facilitation to account for the reported effects of the presence of conspecifics, however. For example, retarded acquisition of lever pressing can be attributed to the distracting effects of the presence of the conspecific, and the facilitative

effects of the presence of the conspecific on already acquired lever pressing can be attributed to the appearance of competition for a limited resource.

There also appear to be conditions under which the presence of a conspecific can facilitate new learning if that new learning is taking place in a novel, potentially fear-inducing environment. Under such conditions the presence of a conspecific may reduce fear and increase exploratory behavior, leading to faster acquisition of the to-be-learned response (Moore et al. 1981).

Whether Zajonc's theory is correct or not, it is clear that the presence of a conspecific can affect the behavior of the target or focal animal and should be taken into account. This is especially true if one is interested in studying the ability of an animal to learn to perform a response from watching another animal perform the to-be-acquired response. In this case, it is important to include a control condition involving the effect on acquisition of either the mere presence of a conspecific or of a conspecific performing a different response or performing the same response in a different manner (see section on the two action procedure).

A special case of motivation induced by the presence of a conspecific can occur if the animal that is demonstrating the to-be-learned response is motivated by the avoidance of an aversive event (e.g., negative reinforcement). Being in the presence of a conspecific that is avoiding an aversive event can induce fear in the observing animal and that increase in fear can affect the ability of the observing animal to acquire a new response, depending on the nature of the to-be-acquired response but potentially independent of the particular response observed.

Although one would expect members of a social species such as rats and most primates would be more likely to learn from facilitation provided by the presence of a conspecific than more solitary species such as mountain lions, in most mammalian and bird species, the young have extensive interaction with one of their parents, which can exert great influence on their behavior (see, e.g., Lupfer et al. 2003). This would be especially true in reducing fear which would

encourage the young to interact with the environment and encounter reinforcement. The social dynamics that govern the relationships among individuals may be more important than species sociality (Coussi-Korbel and Fragasz 1995). Nevertheless, when it comes to social facilitation, in general, social species will tend to come into contact with reinforcing events more often than less social species (see, e.g., Jackson et al. 2008).

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## Social Grooming

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## Synonyms

Allogrooming; Social preening; Social relationships

## Definition

Social grooming behavior is a physical process that functions to maintain the form and composition of another animal's body surface, facilitating improved hygiene and in some cases social bonding.

## Main Text

Allogrooming is the term used to describe when one individual grooms the body of another. Self-grooming is the term used to describe an individual grooming its own body. Both allogrooming and self-grooming serve the primary function of maintaining the form, composition, and cleanliness of an animal's body surface (“► [Grooming](#)”). The function of allogrooming, however, is not limited to the maintenance of the body surface. Animals often engage in allogrooming at rates that far exceed the amount necessary for hygiene alone, and grooming can even occur in the absence of dirt and parasite infestation altogether. As such, allogrooming, or social grooming, also plays an important role in social bonding. Social grooming is seen across a diverse range of animal taxa, including birds, canids, felids, mongooses, primates, rodents, and ungulates. Social grooming is perhaps most conspicuously observed among the primates, with some species spending up to 20% of their active day grooming other group members (Dunbar 1991). Although a great deal of what we know about the functional value of social grooming has come from the primates, similarities have more recently been documented in a range of social mammals and pair-bonded species of bird (e.g., parrots and corvids).

Social grooming and social relationships have become almost synonymous terms in behavioral research, with the quality and patterning of social relationships often being indexed by levels of grooming exchanged between group members (Hinde 1976). It feels good to be groomed. Being on the receiving end of grooming has been associated with endorphin release, lowered heart rates, and reduced social anxiety and baseline stress levels. The role of grooming in social

bonding, especially among the primates, is supported by recent findings linking grooming behavior with the release of neuropeptides including endorphins, “► [oxytocin](#),” and vasopressin (Dunbar 2010).

Many animal taxa live in groups and spend a significant amount of time interacting socially with other group members. The main “benefits of group living” include improved protection from predators, access to food, and mating opportunities, which all contribute positively to an individual's “► [fitness](#).” There are, however, inevitable costs of group living, which typically relate to elevated rates of competition within the group for those same food and mating resources. Competition among group members can lead to aggression and, if left unchecked, can result in the expulsion of the loser from the group and, in some cases, fights to the death. Competition among group members is mediated by the formation and maintenance of social relationships, largely via grooming interactions. Social grooming serves to improve tolerance levels between group members which collectively help maintain group cohesion. Social grooming also plays a direct role in conflict management. Following aggressive conflicts opponents can be seen to exchange grooming in an apparent attempt to reconcile their differences (“► [Post-conflict Resolution](#)”). Conciliatory grooming has been shown to reduce social tension and repair the opponents' damaged social relationship, helping to moderate the potential long-term negative consequences of a conflict.

Individuals more integrated in to their group, via social relationships, experience improved health, longevity, and offspring survival, compared to those more socially isolated. Although social relationships have been tied to fitness benefits in a range of animal taxa, the underlying mechanisms for this relationship are less understood (Ostner and Schülke 2018). It has been argued that more sociable individuals experience less physiological and psychological stress than those less sociable. Social relationships can also provide direct energetic benefits. More sociable individuals may get better access to nutritional resources due to the increased tolerance afforded by other group members when feeding (de Waal

1997). More sociable animals also get better access to huddling partners in cold conditions (McFarland et al. 2015). The improved energy resources available to more social individuals facilitate longevity, a greater energetic investment in reproduction, and offspring survival. Elucidating the physiological mechanisms that mediate the relationship between sociability and individual fitness remains an important focus of research on social relationships and social grooming.

Grooming is an inherently valuable resource, and individuals groom one another with the expectation of receiving grooming, or another social commodity, in return. Grooming as a social commodity is based on the viewpoint that animal groups serve as biological markets in which animals trade behavioral interactions (Noë and Hammerstein 1995). Social grooming is exchanged between group members to receive, for example, reciprocal grooming, spatial tolerance, reduced aggression, agonistic support, access to mating opportunities, food sharing, and infant handling. Displays of grooming during courtship are observed in many mammals and birds, and even some arthropods, where the groomer has a better chance of mating following the provision of grooming. The framework of a biological market explains how, and to what extent, social commodities are exchanged within a given group. The biological market approach posits that individuals differ in the types of commodity they exchange with one another, that different commodities hold different values, and that the value of a commodity is dependent on the value the recipient attributes to the donor. That is, no two individuals are likely to value each other to the same degree, which means grooming exchanges are unlikely to be symmetrical. Grooming is preferentially directed toward close kin. The maternal grooming of offspring is particularly widespread in animals. Dominant individuals are generally considered to be more attractive social partners and tend to receive more grooming than subordinate group members. Dominant individuals can trade their tolerance for the benefits of grooming and have even been observed to coerce

or punish the behavior of subordinates to gain preferential access to grooming.

It is currently debated whether animals have the cognitive capacity to keep track of grooming exchanges and its “► [reciprocity](#)” over time. Grooming reciprocity is based on a tit-for-tat scenario where two individuals switch social roles (i.e., donor or recipient), so that the costs and benefits of these acts are balanced over time. In a tit-for-tat scenario, short-term reciprocal exchanges should be favored as a way to avoid cheating. Grooming reciprocity, however, may not solely be based on the expectation of an immediate reward but may also reflect a calculated exchange based on a shared history of previous social interactions (de Waal and Luttrell 1988). Calculated reciprocity could explain patterns of long-term grooming reciprocity, although this would require advanced cognitive skills such as memory, numerical assessment, and planning. Calculated reciprocity is therefore thought to be restricted to humans and possibly the great apes. Alternatively, long-term reciprocity could be sustained via emotional bookkeeping (Schino and Aureli 2009), whereby grooming elicits positive emotions that modulate an individual's choice of social partners for future social interaction. This emotion-mediated mechanism is not thought to require complex cognitive skills.

## Cross-References

- [Allogrooming](#)
- [Fitness](#)
- [Grooming](#)
- [Group Living](#)
- [Oxytocin](#)
- [Post-conflict Resolution](#)
- [Reciprocity](#)

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## Social Hierarchy

- [Pecking Order](#)

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## Social Impression

- [Reputation](#)

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## Social Intelligence

- [Machiavellian Intelligence](#)

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## Social Intelligence Hypothesis

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### Definition

The Social Intelligence Hypothesis stipulates that increased complexity in social groups has resulted in larger brains and more advanced cognitive abilities in primates. The Social Intelligence Hypothesis was developed as an answer to why primates, especially humans, possess highly advanced cognitive skills in comparison to other animal species. This enhanced “intelligence” is often associated with the development of certain brain areas associated with complex cognitive abilities (e.g., neocortex) and overall with a larger brain than would be expected given the species’ body size.

### History

During the 1950s and 1960s, researchers started to suggest that large brains in primates were due to their complex social life. The ideas that would later lead into the full concept of the Social Intelligence Hypothesis were first proposed by Michael Chance and Allan Mead in 1953 (Chance and Mead 1953), as they linked social complexity and enlargement of the neocortex in primates, and were later developed by Allison Jolly in 1966 (Jolly 1966), when she compared long-term social groups of lemurs and primates. The Social Intelligence Hypothesis was then fully described by Nicholas Humphrey in 1976 (Humphrey 1976) under the name of “social function of intellect.” Humphrey proposed that primates possessed a social intelligence that was responsible for their general advanced cognitive abilities.

Hence, the Social Intelligence Hypothesis was mainly developed to explain why primates, and more especially apes, possess a larger brain than



expected by their body size, as well as a more advanced “intelligence” or more complex cognitive abilities than other species (Jerison 1973). Among them, humans are known for having a very complex social system that involves cooperation within and between generations by dividing the labor to facilitate daily tasks (Richerson and Boyd 1998) and, at the same time, possessing the largest brain relative to their body size in comparison to other animal species. At the time, researchers deemed that ecological pressures such as foraging and evading predators were not sufficient to explain the complex cognitive abilities in primates, as other species experienced similar pressures but were argued to not possess such advanced cognitive skills. Furthermore, since brain tissues are costly to produce (Aiello and Wheeler 1995), a bigger brain than expected by body size must be evolutionary advantageous for a species to possess. In addition, bigger brains were often associated with distinctive complex cognitive abilities (Rothe and Dicke 2005), such as tool use and manufacture.

Early studies focusing on the relationship between cognitive abilities and social complexity in animal species were primarily conducted on primates, due to their close relatedness to humans. Among primates, a preference was made for Old World monkeys and apes because their ecology and behaviors were better known than those of New World monkeys (Perry 2009). Today, the Social Intelligence Hypothesis is being tested in a wide array of animals, including birds, cetaceans, and elephants. Expanding the research to other species has led to a refinement in the Social Intelligence Hypothesis and to the development of derived hypotheses.

## Mechanisms

As an individual living in a social group is surrounded by other individuals, many of its actions will influence the rest of the group. Therefore, an individual needs to take into account other group members by predicting how each group member will react when it performs the action. That ability involves being able to track

individuals within their social group, remembering the past interactions, whether cooperative, neutral, or competitive, with the other members, but also keeping track of changes in the hierarchy and the roles of each individual over time. Since interactions within a social group are complex, it is difficult to predict the actions of other members in the group. However, as individuals get accustomed to each other, they come to know how each individual tends to behave when interacting with others or in a given situation. In addition, as individuals cooperate with each other, some expectations (e.g., reciprocity, advantage for accessing some resources) need to be met in order for that relationship to survive between them. This complexity is enhanced by the fact that individuals cannot be treated and manipulated like physical objects, but their behavior can be controlled using direct or indirect communication. As a result, the bigger the group size, the more cognitively demanding it is for an individual to process and integrate all the social information occurring within the group and require more advanced social cognitive skills to cope with such high social demands (Byrne and Whiten 1988).

Living in a group also has its advantages (Rubenstein 1978). From an ecological point of view, group living allows individuals to reduce the risk of predation on themselves by diffusing that risk among other members of the group. From a social point of view, it leads to social learning, which allows an individual to learn the consequences of an action by observing other individuals performing that action. Social learning can then lead to teaching and, potentially, transmission of behaviors across generations (i.e., culture). In addition, having other individuals in a group cooperating when faced with a novel problem allows individuals to be exposed to alternative solutions from others and thus permits individuals to more readily cope with novel situations. More efficient mechanisms to forage and to survive are then selected, leading toward an increased general intelligence within the group.

By successfully recording the social information of the group and using “politics” to gain access to resources, an individual can rise higher in the hierarchy of the group. In most cases, a more dominant

position within the group implies a higher chance to transmit genes to the next generation.

## Support for the Social Intelligence Hypothesis

To test the Social Intelligence Hypothesis, most studies undertake a comparative approach. Comparing brain structures or cognitive abilities between closely related species that differ mostly in their inherent social complexity can help detect whether sociality is the main factor underlying the evolution of brain size or specific cognitive abilities (e.g., MacLean et al. 2012).

Early support for the Social Intelligence Hypothesis came from the comparison between the relative size of the neocortex (i.e., brain area involved in higher cognitive functions), in comparison to the species' body size, and the average group size within primates (Dunbar 1992). A positive correlation exists between those two factors, indicating that larger brains might be needed to cope with larger social groups. Differences also occur between apes and monkeys, as apes possess a larger brain than monkeys living in a group of the same size. This difference in brain size suggests that apes have a more complex social structure than monkeys (Dunbar 2014). More recently, a neuroanatomical approach has been used to test the Social Intelligence Hypothesis, and most studies comparing the neuroanatomy across primates have supported the Social Intelligence Hypothesis. However, results of these studies are to be interpreted with caution as most of them used the average group size in a species as a proxy for social complexity (Dunbar and Shultz 2007). This aspect might bias the results as some species can form large groups, but any individual might not interact with all members of the group. Additionally, smaller groups can engage in much more complex interactions with the other members than found in larger groups. For this reason, recent versions of the Social Intelligence Hypothesis focus not solely on the quantity of the relationships between individuals but also on the quality of those relationships (Dunbar 2014). This twist in the Social

Intelligence Hypothesis has been used to explain the complex cognitive abilities found in birds (e.g., corvids, parrots), wherein some monogamous species with very strong pair bonds can possess cognitive skills on par with those of great apes (Emery et al. 2007).

In humans, specifically, archaeological evidence has shown that brain size dramatically increased twice in history. These two periods of human brain expansion have been linked to increased group size in humans (Mithen 1996). The first brain size increase occurred ca. 1.8 million years ago: brain size in early humans increased from 450 cc (cubic centimeters) to 1000 cc. This increase has been linked to a change in the social life in hominins (early humans), as individuals started to live in more complex and larger groups. The second brain size expansion dates between 600,000 and 200,000 years ago, leading the brain to increase to its current capacity (around 1450 cc). This growth has been linked to the evolution of language, an important element for the mediation of social relationships.

## Critiques of the Social Intelligence Hypothesis

The Social Intelligence Hypothesis is often put in contradiction with the Foraging Niche Hypothesis (Gibson 1986; Milton 1988). The Foraging Niche Hypothesis explains the presence of bigger brains in primates by arguing that bigger brains have evolved so that individuals can cope with the complexity of their environment when foraging on complex substrates or in unpredictable environments. While both hypotheses acknowledge the fact that ecology is the main cause for brain evolution, they differ on the most important selective pressures. The Social Intelligence Hypothesis argues that animals solve ecological problems (foraging, protection from predators) by using a social approach, thus maximizing their access to resources. It also deems that the social environment is more challenging and less predictable than the ecological environment (Dunbar 1992), whereas the Foraging Niche Hypothesis suggests that finding food and avoiding predation are more

direct evolutionary pressures. Indeed, primate species with larger brains tend to have a larger home range and feed primarily on fruits, an ephemeral, widely dispersed resource (Milton 1988).

Even within the scope of the Social Intelligence Hypothesis, earlier forms of the hypothesis were criticized as being very primate-centric. Primates have an enlarged neocortex in comparison to other mammals (Jerison 1973), and that was thought to be the reason for why they possess such advanced cognitive abilities. However, recent studies have shown that corvids (e.g., crows, jays) and parrots, which lack a neocortex, possess cognitive abilities that are on par with those possessed by apes (e.g., Emery and Clayton 2004). Further studies suggest that neuron densities might be a more effective approach of judging a species' brain size and a more relevant factor explaining advanced cognitive abilities than sociability (Olkowicz et al. 2016). Thus, using more distantly related species displaying similar cognitive abilities allows testing the validity of the Social Intelligence Hypothesis.

## Derived Hypotheses

Since it was formulated, a few other hypotheses have emerged to complement or to clarify the Social Intelligence Hypothesis. Examples of such hypotheses include the Machiavellian Intelligence Hypothesis, proposed by Andrew Byrne and Richard Whiten in 1988 (Byrne and Whiten 1988), and the Social Brain Hypothesis, suggested by Lesley Brothers in 1990 (Brothers 1990) and popularized by Robin Dunbar in 1998 (Dunbar 1998).

Byrne and Whiten described the Machiavellian Intelligence Hypothesis following observations of "tactical deceptions" in wild baboons (Byrne and Whiten 1988; Whiten and Byrne 1997). The Machiavellian Intelligence Hypothesis puts the emphasis on social maneuvering (e.g., collaboration, rivalry, alliance formation) as the most important factors underlying the evolution of a larger brain and, consequently, advanced cognitive skills. According to the authors, the ability to

manipulate and form alliances with others in order to gain access to resources was the prime reason that led to the evolution of advanced cognitive abilities in primates. Indeed, tactical deception is thought to be the main social pressure increasing the fitness (reproduction output and survival) of the deceiver. It thus slightly differs from the Social Intelligence Hypothesis by emphasizing on the importance of tracking the alliances and coalitions between the members of the group.

The Social Brain Hypothesis primarily focuses on the correlation between the mean social group size and brain size (or certain brain structures in primates). According to this hypothesis, the need to keep track of the complex relationships between individuals explains the existing correlation between relative brain size of a species and the average size of its social group (Dunbar 1998). Hence, it is a more subsidiary generalization than the overall Social Intelligence Hypothesis.

## Importance and Impact of the Social Intelligence Hypothesis

Since its formulation more than half a century ago, the Social Intelligence Hypothesis has led to new avenues of research. Not only did it permit the exploration of social cognitive abilities in social species, it also encouraged the search for complex cognitive abilities in nonsocial species, or in species that were previously disregarded as "unintelligent" (e.g., birds, invertebrates), in an attempt to refute the Social Intelligence Hypothesis. This approach has led to adjustments in the formulation of the Social Intelligence Hypothesis to encompass recent research on less social species, by focusing on the quality of the social relationships between the members of a group and not just the number of individuals within a social group (Dunbar and Shultz 2007).

The Social Intelligence Hypothesis also paved the way for research on Theory of Mind (i.e., the ability for an individual to attribute mental states such as beliefs, desires, emotions to others) in nonhuman animals. Indeed, the Social Intelligence Hypothesis is relying on the ability of individuals to identify other group members, to

recognize them, and to “read their minds” (Premack and Woodruff 1978). By examining whether a given species possesses elements of a Theory of Mind, researchers have been able to understand more about the components present in a social group and determine which elements underlie complex social cognition. However, the issue of whether (and which) animals possess aspects of a Theory of Mind is still highly debated.

Even currently, the Social Intelligence Hypothesis is highly relevant in the field of cognition and continues to be one of the main explanations for the evolution of complex cognitive abilities in animals. It is now commonly accepted that sociality played a part in the evolution of “intelligence,” but its relative role remains to be determined. Ultimately, the Social Intelligence Hypothesis has not only allowed us to discover interesting and complex cognitive abilities in other nonhuman animal species, it has also made us wonder which cognitive skills are inherently unique to humans and what made us different from other animal species.

## Cross-References

- [Cognition](#)
- [Deception](#)
- [Dominance](#)
- [Group Living](#)
- [Intelligence](#)
- [Machiavellian Intelligence](#)
- [Primate Cognition](#)
- [Primate Social Structure](#)
- [Theory of Mind](#)

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## Social Interaction

### ► Social Affordance

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## Social Learning

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### Definition

“Social learning is learning that is facilitated by observation of, or interaction with, another individual (or its products)” (Hoppitt and Laland 2013) modified from (Heyes 1994). This widely used definition serves well to classify the types of learning that are covered by research into social learning. However, the definition is very broad meaning that researchers use additional, narrower definitions to identify more specific types of social learning. Of particular interest is social learning that results in one individual (termed the “observer”) learning a novel behavior pattern after having been exposed to another individual (termed the “demonstrator”) performing that behavior. Such learning is sometimes called “social transmission,” which can be defined as occurring “when the prior acquisition of a behavioral trait  $T$  by one individual  $A$ , when expressed either directly in the performance of  $T$  or in some

other behavior associated with  $T$ , exerts a lasting positive causal influence on the rate at which another individual  $B$  acquires and/or performs  $T$ ” (Hoppitt and Laland 2013). The term “cultural transmission” is used in a more specific way to refer to cases of social transmission that increase behavioral homogeneity within groups of individuals (i.e., can result in the emergence of culture).

## The Spread of Innovations

Social learning describes the process of sharing information between two individuals. The individual who holds the information is often referred to as the “demonstrator,” whereas the individual that learns socially is referred to as the “observer.” Information shared between demonstrator and observer can include novel behaviors or knowledge that the demonstrator has acquired. Before information can spread through a population, it has to be generated through an “innovation.” Such an innovation can include the discovery of novel information, the establishment of a new behavior, or the performance of an already established behavior in a different context (Reader and Laland 2001). Innovations are products of “asocial” or “independent” learning, which requires sampling of the environment by the demonstrator followed by finding an appropriate response, often through trial and error learning. Hence, asocial learning generates innovations, while social learning is responsible for the spread of such innovations.

## Learning at Different Life Stages

Social learning can occur at many different stages in life, even before birth. Individuals can show preferences for food that they were exposed to through food cues in the womb through their mothers’ amniotic fluid (e.g., Smotherman 1982). Similarly, flavor cues in the mother’s milk that individuals were exposed to early in life can influence food preferences as adults. Particularly young individuals during dependency rely heavily on learning from others. At this life stage, skills crucial for survival have to be learned



rapidly, including knowledge about foraging techniques, diet, predator avoidance, interaction with conspecifics, or seeking shelter. Social learning from older, more experienced conspecifics can thereby greatly increase the efficiency with which all these skills are acquired as well as decrease the risks associated with independent learning. The rate at which individuals learn from others might decrease with age, but social learning continues into adulthood. Even for adults it can be beneficial to use information that has been gathered by others such as location of food patches or copying behaviors that have been innovated by someone else. In a group of wild chimpanzees, for example, moss-sponging – an innovative technique to retrieve water from a water hole – was found to be socially transmitted within the group, including among adult individuals (Hobaiter et al. 2014).

### Social Learning Mechanisms

Over the years, a number of researchers have attempted to classify social learning mechanisms into categories. However, there is no universally accepted classification. Nonetheless, there are a number of terms that are used in a consistent manner to refer to particular types of social learning. Some of these mechanisms result directly in learning on the part of the observer, whereas others influence the behavior of the observer in way that indirectly leads to learning. An example of a mechanism that indirectly leads to social learning is **local enhancement**, which occurs when, after or during a demonstrator's presence or interaction with an object at a particular location, an observer is more likely to visit or interact with the object at that location (Hoppitt and Laland 2013). Local enhancement can lead indirectly to social transmission, if the performance of a behavior pattern leads observers to a location at which that behavior pattern can be learned. The technique for processing a particular plant might be socially transmitted, if local enhancement leads observers to locations at which those plants occur, leading them to learn (in an otherwise asocial manner) how to process those plants. An example of a mechanism that directly leads to social

learning is **observational conditioning**. Here the demonstrator exposes the observer to a relationship between two stimuli, allowing the latter to form an association between those stimuli (Heyes 1994). Such social learning allows an observer to learn about its environment through observation. Other mechanisms, such as **imitation** and **emulation**, allow an observer to learn to perform novel behavior that is not already in its behavioral repertoire.

Social learning need not always require the observer to literally observe the demonstrator's behavior. Instead, social learning might occur when the observer is exposed to the products of the demonstrator's behavior. For example, Heyes and Dawson (1990) found that observer rats would socially learn to press a joystick in a particular direction for a food reward and that this behavior could be transmitted via olfactory cues left on the joystick.

Most nonhuman animal social learning appears to result when a demonstrator “inadvertently” provides the cues to allow the demonstrator to learn. However, evidence is accumulating that a number of species are capable of “**teaching**” in the functional sense (Caro and Hauser 1992), i.e., that they perform behavior which has the evolutionary function of promoting learning in others. In such cases, it seems plausible that teaching has evolved to take advantage of pre-existing social learning mechanisms that exist in the observer (Hoppitt et al. 2008).

### When Is Social Learning Adaptive?

Social learning can greatly increase an individual's fitness. By learning from others, individuals can save on the costs associated with trial and error learning, as they do not have to acquire the information themselves. Costs involved in individual learning can be manifold. For example, trial and error learning can be very time-consuming if the acquisition the novel information requires extensive sampling of the environment or if many attempts are required to find a solution to a challenge. Costs associated with independent learning can also be very severe, if

errors during the learning process result in an increased risk of mortality, such as in the context of predator avoidance or ingestion of potentially poisonous food. Therefore, it is not surprising that individuals tend to rely more extensively on information gathered by others, if the costs associated with individual learning are potentially high. Social learning is hence commonly, but not exclusively, found in a foraging context, as well as predator avoidance, but also in other, lower-risk contexts such as hygiene or play. Examples for social learning in nonhuman animals are numerous. Most evidence of social learning comes from a foraging context, where information on what, where, and how to eat is shared among individuals. Immature Bornean orangutans, for example, were found to adopt their mothers' diet through social learning by consistently following their mothers' choice of what and how to eat (Jaeggi et al. 2010).

Intuitively, one would expect all individuals to rely on information gathered by others to save the costs associated with independent learning. However, this view is too simplistic: While independent learning *produces* information or novel behaviors, social learners *scrounge* on information that has been acquired without contributing to new information themselves. Game theory models of producer-scrounger interactions suggest that relying on information gathered by others does not necessarily increase benefits, as scroungers only do better than producers, if fellow scroungers are rare (Barnard and Sibly 1981). Asocial learners have acquired information about the environment at some cost. As the number of social learners increases, the number of asocial learners who produce reliable information declines. Assuming a changing environment, a decrease in the proportion of information producers would thus result in a decline of the value of socially acquired information. Hence, for social learning to be adaptive, a population is expected to reach an equilibrium at which social learning and independent learning have equal fitness benefits (Boyd and Richerson 1988). If information gathered by the demonstrator lacks appropriate sampling of the environment and is thus unreliable, copying such information is no longer

beneficial to the observer or can in fact be costly. If the latter, social learning is maladaptive, and the proportion of social learners is expected to decrease, while the proportion of independent learners is expected to increase to again produce more reliable information.

Similar reasoning leads us to expect social learning to evolve only when the environment does not change too quickly or too slowly (Laland et al. 1996). If the environment changes too quickly, information obtained second, third, or fourth hand, etc. is likely to be outdated by the time the observer receives the information. In such cases, it is adaptive to rely on asocial learning and obtain up-to-date firsthand information about the environment. If the environment changes very slowly, then one would not expect learning to be necessary at all, with individuals relying on "hard-wired" behavior and natural selection keeping track of environmental change. Thus, social learning is likely to be favored in case of intermediate environmental change.

Taken together, this theory suggests that the use of social learning should be selective, with individuals employing "social learning strategies" determining when to copy other individuals (Laland 2004). Furthermore, one would expect social learning strategies that determine *who* observers should copy to obtain the best quality information and also *what* types of information should be copied (Laland 2004).

## Social Learning in Animal Species

Evidence for social learning has been found in a variety of different animal taxa including primates (e.g., Hobaiter et al. 2014; Jaeggi et al. 2010), cetaceans (e.g., Allen et al. 2013), birds (e.g., Farine et al. 2015), fish (e.g., Helfman and Schultz 1984), and insects (e.g., Alem et al. 2016). A species' social system and several life history traits can be linked to the frequency of social learning and complexity of the information that is shared among individuals.

Long-lived species that live in stable social societies tend to rely heavily on the social transmission of information, whereas in short-lived

and more solitary species, learning from others is rather uncommon. In long-lived species with intensive and prolonged parental care, especially young naïve individuals rely extensively on social learning to acquire all necessary skills to ensure survival after weaning. In primates and birds, both rates of innovation as well as the frequency of social learning were found to be positively correlated with relative brain size (Lefebvre et al. 2004; Reader and Laland 2002). Hence, species with advanced cognitive abilities appear to be able to both generate as well as spread novel information at a higher rate compared to species with smaller relative brain sizes.

The complexity of information shared between demonstrator and observer can vary greatly from very simple information to a complex series of behaviors. Complex behaviors that are likely to be socially transmitted, such as using tools for extractive foraging tasks, are mainly found in species with advanced cognitive abilities such as great apes, toothed whales, and large-brained birds such as corvids. In smaller brained species, sharing simple information, such as the location of food patches, is more common.

Apart from the kind of the information that is shared among individuals, the complexity of the social learning mechanisms also varies greatly within the animal kingdom. Whereas simple mechanisms such as local or stimulus enhancement and/or observational conditioning are likely to be present in many species, more complex mechanisms such as imitation seem restricted to species with higher cognitive abilities.

Although learning from others most commonly happens within a species, sharing information among species can occur. For example, information on the location of novel foraging patches was observed to spread both among and within species in a population of blue tits, great tits, and marsh tits (Farine et al. 2015).

## Social Learning Experiments

Laboratory studies (i.e., studies on animals in a captive setting) have shown the existence of

a capacity for social learning in many animal species. The classic way to investigate if a species is capable of social learning in a captive environment is to use a **demonstrator-observer experiment** (Hoppitt and Laland 2013). In the training phase, one individual (the demonstrator) is trained to be proficient at solving a particular task (e.g., pressing a lever for a food reward). In the demonstration phase, another individual (the observer) either directly observes the demonstrator solving the task or is exposed to the physical products of the demonstrator's actions. In the test phase, observers are presented with the task and given an opportunity to solve it. If observers are more likely to learn the behavior, or do faster than control animals who do not see a demonstration, then one has evidence that social learning has occurred. In the classic setup of the demonstrator-observer experiment, one observer learns socially by observing one trained demonstrator. However, many variations of the experiment are possible, such as increasing the number of demonstrators and investigating how this number influences the rate at which observers learn the target behavior. The experiment can also be modified to distinguish between different mechanisms of social learning, such as distinguishing imitation from other mechanisms of social learning. Akins and Zentall (1996), for example, provide evidence for imitation in male Japanese quails in a so-called two-action experiment, where quails witnessed a demonstrator quail receive a food reward when pressing a treadle, either by pecking it or stepping on it. After the demonstrator had been removed and the observer was presented with the experimental setup, the subject's first action was always the same as the demonstrator's.

An alternative to the classic dyadic demonstrator-observer experiment are **transmission chain studies**, in which the first observer acts as a demonstrator to another individual after acquiring the behavior via social learning from the initial demonstrator. In the **linear transmission chain experiment**, information or a behavior is transmitted along a single line of subjects. Linear transmission chain studies are not only useful tools to "prove" the capacity for social learning in

a population, but they also allow to investigate the factors influencing the rate of social transmission and assess the potential loss of information. Bartlett (1932), for instance, who originally developed the linear transmission chain experiment, presented a text or picture to a first participant, who later recalled it to the next participant in the line, who again recalled it to the third participant, and so on, and changes to the originally presented material were assessed as the line continued. It turned out that it was largely cultural biases that influenced the rate of degradation of the material, as well as how the material was changed along the line of participants.

Linear transmission chains in a laboratory setup allow to track the diffusion of the behavior in a stepwise manner to determine at which point the behavior differs from the one introduced to the original demonstrator. One can then assess the factors that influence the process of social transmission and identify those that determine whether knowledge or behavior is lost, gained, or altered along the transmission chain. The alternative to linear transmission chains are **replacement transmission experiments** (Gerard et al. 1956), in which a behavior is introduced to a small group whose members are gradually replaced over time. At each step, an experienced member is replaced by a naïve subject until at some point there is no more contact with the original members of the group. Evidence for social transmission is found, if the introduced behavior persists in the population even though the trained demonstrators of the original group have been replaced. In a replacement transmission experiment in rats, for example, four demonstrator rats in two populations each were conditioned to prefer one of two flavored diets, with individuals in the same population having the same preference (Galef and Allen 1995). Individuals in both populations were gradually replaced with naïve individuals, who consistently chose to follow the dietary preference that had initially been introduced to the respective population, leading to a stable transmission of two completely arbitrary dietary preferences (Galef and Allen 1995).

A third way to assess social learning patterns in a population in a laboratory setting is **diffusion**

**studies**. Here, a task (usually a foraging task) is introduced into several replicate populations, and the spread of task solutions is recorded. In “seeded diffusions,” trained demonstrators may be introduced into the population, sometimes even several demonstrators with alternative solutions to a task. Populations without demonstrators can serve as control. Thornton and Malapert (2009), for example, trained individual demonstrators in several groups of wild meerkats to obtain food from an apparatus using one of two techniques, while groups with no demonstrators served as controls. In the experimental groups, several individuals adopted the demonstrator’s technique after interacting with either the demonstrator itself or group members that had already learned the behavior from the demonstrator. As opposed to the classic demonstrator-observer experiment and the transmission chain studies, diffusion studies do not impose an artificial structure on the social interactions between individuals, but the novel behavior can spread in a more naturalistic manner within the population.

A fourth way of studying social learning in an experimental setting is **translocation studies**. These studies can be used to test whether behavioral variation among populations is a result of different innovations being socially transmitted among individuals in each population. In one translocation, individuals are transferred to a different population they have never been in contact with. If over time, the transferred individuals adopt the residents’ behavioral repertoire, this is consistent with social transmission and inconsistent with behavioral differences being a result of different genetic predispositions. Additionally, entire populations can be replaced instead of single individuals. If the introduced population exhibit a behavior that is different from the former residents, this is consistent with the behavior being cultural, i.e., having been socially transmitted within the population. In contrast, if the new group adopts the same behavior as the former residents, it instead suggests that behavioral variation was a result of individuals independently learning to adapt to the local environment. Translocation experiments are not restricted to laboratory settings. Helfman and Schultz (1984), for

example, applied a translocation experiment to a population of free-living French grunts, a coral reef fish species, who have local traditions of schooling sites during the day and specific twilight migration routes. They found that individuals that were translocated to new schooling sites adopted the customs of the new residents and abandoned their old schooling sites and migration routes, which suggest the existence of socially learned local traditions. However, translocation experiments may sometimes be unfeasible or unethical to be applied to free-living animal populations, such as great apes, for example. Instead, natural movements of individuals or populations can be exploited as translocation experiments, although under less controlled conditions compared to laboratory settings.

Finally, **cross-fostering experiments** can shed light on whether “vertical” social learning (from one’s parents) can occur in a species. Thereby, offspring are taken from their biological parents at birth and given to foster parents to be raised. These experiments are useful to investigate the extent to which “vertical” social transmission from the parents influences an individual’s behavior, relative to genetic influences. Any behavior readily adopted from the foster parents, when it differs from the behavior exhibited by the biological parents, is likely to be vertically socially transmitted under natural circumstances. This inference may assume that the environmental conditions under which both biological and foster parents live are equal.

Laboratory settings have the advantage of replicability as well as control over a range of potentially confounding factor such as the influence of environmental variables. The history of individuals subjected to experiments is generally known, and it can be ensured that the task they are presented is indeed novel. Furthermore, experiments are permanently monitored, and social learning events can be recorded without gaps. The ability to gather data in such a highly controlled environment thus provides invaluable opportunity to study the existence of a capacity for social learning and the underlying mechanisms within animal populations. However, experimental setups in a laboratory environment are often quite different

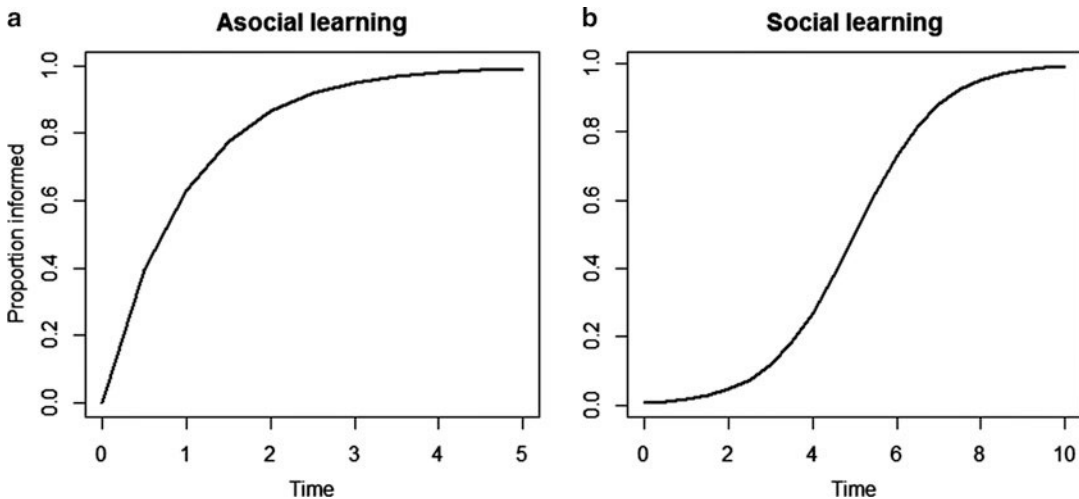
from wild populations and lack ecological validity and thus may not be able to tell us how important social learning is in natural settings.

## Detecting and Measuring Social Learning Using Observational Data

In some circumstances, it may be desirable to test whether social learning is occurring in the field, in a natural population of animals. It may not be possible to study the target species in a captive setting, meaning field studies are the only way to establish whether that species has a capacity for social learning. And even if captive experiments have been performed on that species, researchers may still wish to quantify the importance of social learning on the diffusion of naturally occurring innovations in the field. In some circumstances, it may be possible to run field experiments, for instance, seeded diffusion studies conducted on natural populations (see entry on Cultural Transmission). However, this is not always possible necessitating techniques for inferring social learning from observational field data.

One method traditionally used to do this was **diffusion curve analysis (DCA)**. A diffusion curve plots the number of individuals having been observed performing the behavior pattern of interest against time. For many years, it was believed that the shape of the curve could be used to infer whether social learning is responsible for the spread of a novel behavior. It was assumed that if a behavior is purely independently learned, the curve would result to be r-shaped, as the per capita rate of learning is expected to be approximately constant, with the curve leveling off as the whole population has learned the behavior (Fig. 1a). In contrast, if the novel behavior spreads through social learning, it is expected to result in an acceleratory curve, as the rate of learning would increase with the number of demonstrators over time. If the entire population acquires the novel behavior, the curve is expected to be s-shaped, as when either demonstrators or observers are rare – which is the case at the start and end of a diffusion – the learning rate would be lower compared to when demonstrators and





**Social Learning, Fig. 1** Diffusion curves are traditionally expected to be (a) **r-shaped** in case of **asocial** and (b) **s-shaped** in case of **social transmission** of behavior.

However, theoretical work has shown that diffusion curve analysis (DCA) is not a reliable approach to distinguish between asocial and social learning

observers exist in equal numbers (Fig. 1b). Although frequently used in the past, recent analyses have shown that diffusion curve analysis is not a reliable signature to identify if a behavior is socially learned or not. There are various reasons for that: First of all, if a behavior is socially learned, the shape of the curve does not necessarily have to be s-shaped. If the population consists of several social subgroups, the curve could be step-shaped with accelerations in rate when a behavior diffuses rapidly within a social subgroup and slower rates for diffusion between subgroups (Reader 2004). Also, differences in the rate of social learning between subsections of the population (e.g., male/female, high/low-rank) might obscure results (Reader 2004). Furthermore, even a purely asocially learned behavior can result in an s-shaped curve, if, for example, neophobia right after initiation of a novel task can lead to reduced rates of learning, followed by increased rate of learning after neophobia has worn off (Hoppitt et al. 2010b). In conclusion, diffusion curve analysis cannot be used to reliably identify social or asocial learning as being the driving mechanism behind the diffusion of a novel behavior.

Among primatologists, a commonly used method for the detection of social learning was

the **method of exclusion** (sometimes known as the **ethnographic method**) (e.g., Boesch 1996; van Schaik et al. 2003; Whiten et al. 1999). This method compares behavioral repertoires of different populations and identifies group-typical behavior that varies among groups. A number of hypotheses can then be proposed for why such group-typical behavior has emerged. The *cultural hypothesis* states that different innovations have arisen in each group and spread by social transmission. The *genetic hypothesis* states that different groups are genetically predisposed to behave in different ways. Finally, the *ecological hypothesis* states that in learning to adapt to their local ecology individuals within a group converge on similar repertoires that differ from the repertoires of individuals in other groups. The method of exclusion attempts to rule out the genetic and ecological hypotheses as sufficient explanations for the observed pattern of variation, thus showing that social learning is likely to have played a role.

Critics of the method of exclusion (Laland and Janik 2006) claim that it fails to estimate the relative importance of social learning/culture in nature, arguing that it only identifies cases where genetics and ecology can be ruled out, whereas it is likely that these factors play a role in most

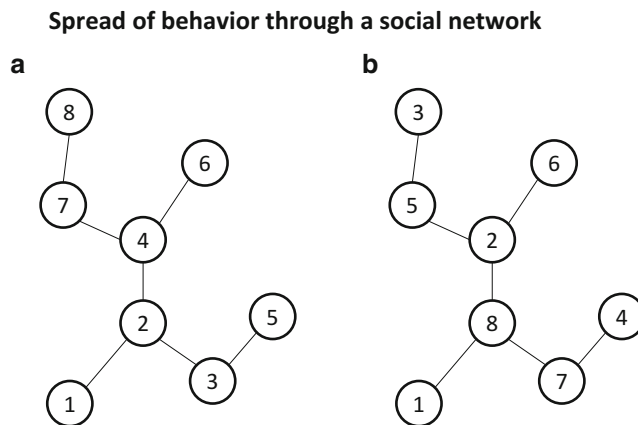
cultural behavior. Proponents of the technique (Krützen et al. 2007) have countered that the purpose of the method of exclusion is not to assess the relative importance of culture in behavioral variation between populations but to detect culture (i.e., a role for social learning in generating behavioral variation) in natural populations. Nonetheless, it is generally agreed that behavioral differences can simultaneously be a result of genetic, ecological, and cultural influences and that a quantitative estimate of their influence on behavioral variation is desirable (Krützen et al. 2007; Laland and Janik 2007).

As an attempt to resolve this “animal culture debate,” a method called **network-based diffusion analysis (NBDA)** has been developed (Franz and Nunn 2009; Hoppitt et al. 2010a) in order to provide a framework by which social learning among members of a group or population can be quantified. NBDA assumes that social transmission of a behavior follows the social network of associations or interactions among individuals, since individuals who spend a lot of time together or who interact more have more opportunity to learn from each other (Coussi-Korbel and Fragaszy 1995).

Therefore, NBDA infers social transmission if the spread of a novel behavior follows the social network of a population (Fig. 2). NBDA thus

allows the study of social learning to be linked to animal behavior research that uses social network analysis. NBDA fits a model of social learning to the diffusion data, i.e., data giving the order or times at which each individual in the population learned the novel behavior. The fit of this model is then tested against a null model in which there is no social learning: the pathway of diffusion is independent of the network. NBDA does not only serve as a tool for the detection of social learning but also allows the estimation of the strength of the social transmission effect. A social transmission parameter,  $s$ , is fitted to the data and estimates the rate of transmission per unit association with informed individuals relative to the average rate of asocial learning (Hoppitt et al. 2010a).

In addition, several individual-level variables can be included in the analysis, which have potential influence on an individual’s learning rate (e.g., gender, rank, or age), and can also be used to model the effect of and statistically control for potential ecological and genetic influences. NBDA has been successfully used in a number of studies to identify and quantify the effects of social transmission on the spread of behaviors in both wild and captive animal populations such as starlings (Hoppitt et al. 2010a), chimpanzees (Hobaiter et al. 2014), or humpback whales (Allen et al. 2013).



**Social Learning, Fig. 2** Network-based diffusion analysis (NBDA) tracks the spread of a behavior through the social network of a population. Numbers represent the order with which individuals acquire a novel behavior.

NBDA infers (a) **social transmission** if the diffusion follows the network and (b) **asocial learning** if the spread of the behavior happens independently of the network

## Conclusions

Social learning is a broad category of phenomena that includes “social transmission” and “cultural transmission,” which result in the diffusion (spread) of matching behavior among individual animals in a group. Some social learning researchers are interested in the psychological mechanisms underlying social leaning (e.g., imitation). Others are interested in the circumstances under which social learning is adaptive and the strategies animals use in deciding when to copy others and whom to copy. Furthermore, some researchers are interested in assessing how important social learning is in determining the behavioral repertoires of animals in their natural environment, and the circumstances under which social learning results in animal culture.

## Cross-References

- [Cognitive Imitation](#)
- [Contagion](#)
- [Copying](#)
- [Cultural Transmission](#)
- [Culture](#)
- [Diffusion](#)
- [Emulation](#)
- [Imitation](#)
- [Observational Conditioning](#)
- [Social Facilitation](#)
- [Social Network Analysis](#)
- [Stimulus and Local Enhancement](#)
- [Swine Cognition](#)
- [Teaching](#)

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## Social Network Analysis

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## Introduction

Social network analysis (SNA) originates from a branch of mathematics called graph theory. This disciplinary field has developed several concepts and analytical methods that permit the study of links between the components of a system. SNA is the result of multiple studies from different research fields and particularly from social sciences such as psychology, sociology, and anthropology.

The SNA approach has facilitated the study of many other subjects in a large variety of disciplines such as anthropology, mathematics, economics, psychology, ethology, ecology, sociology, computer sciences, physics, epidemiology, cell biology, and biochemistry (Prell 2011).

This entry is divided into three sections that can be read separately according to the reader's needs:

1. Section 1: description of the use of SNA tools in life science, highlighting the great potential of these techniques across a wide range of animal research topics
2. Section 2 to Section 4: a thorough technical presentation of SNA to inform readers about the most commonly used network metrics and provide guidelines to obtain reliable statistics
3. Section 5: an example based on Hinde's conceptual framework illustrating the new prospects opened up by SNA techniques for the study of animal societies and providing recent examples of their use

### Social Networking in Biology: From Genes to Animal Societies

Since the early 2000s, the use of SNA techniques by researchers from different biology fields has led to the emergence of a universal approach.

Genetics researchers have used SNA to study gene interactions in regulatory systems. For example, researchers in autism spectrum disorder (ASD) examined protein interaction networks and the co-expression of genes between these interacting proteins (LaFlamme 2015). This study identified the coding variants that are responsible for the communication between the two brain hemispheres in individuals with ASD.

Neuroscientists have used SNA to study brain disorders such as epilepsy through dynamical network modeling in order to identify the mechanisms triggering a stroke and the neuronal network responsible for a stroke in patients in order to remove it surgically (Jirsa et al. 2010).

SNA techniques are widely used in the epidemiology field. Researchers have used social network analysis to predict and control the spread of diseases in periods of epidemic crises such as the Ebola outbreak in West Africa between 2014 and 2016. Mathematical and computational methods now play a major role in epidemics modeling through the theoretical framework of host population transmission dynamics. This disciplinary field is not restricted to human study but also applies to animal research: researchers evidenced a link between individual centrality and the transmission of infections in nonhuman primates (see the “► [Nonhuman Primates](#)” entry of the

encyclopedia for more details), in which centrality accelerated and widened the spread of disease, with the most central individuals being infected more quickly than less central ones (Romano et al. 2016).

The study of virus transmission within a network is akin to the study of the spread of information. Thus, using similar analytical techniques, some studies attempted to understand the spread of information in domains such as novel behaviors (see the “► [Cultural Transmission](#),” “► [Diffusion](#),” “► [Social Learning](#),” and “► [Innovation](#)” entries of the encyclopedia for more details) and terrorist communications. However, specific statistical techniques have been developed to study the spread of information in social networks, such as the network-based diffusion approach (NBDA). These techniques consist in modeling the spread of information transmission along the network links. For an overview of these techniques, see Hoppitt and Laland (2013). NBDA has greatly influenced the study of animal social transmission, and it allowed, among other things, to reveal that a special fishing technique called “lobtail feeding” observed in humpback whales was socially spread and maintained in the population for 27 years, showing the presence of animal culture in this cetacean species (Allen et al. 2013).

SNA approaches also permit the study of diverse systems from an evolutionary perspective and are widely used in ecology (see the “► [Ecology](#)” entry of the encyclopedia for more details). Ecology is a huge disciplinary field, where SNA is used across the range of disciplines from behavioral ecology, where it revealed a relationship between individual fitness (see the “► [Fitness](#)” entry of the encyclopedia for more details) and individual ego-network (Cheney et al. 2016), to the study of ecosystem and community structures, where its use pinpointed a clear link between network modularity and network size and highlighted the presence of very few indispensable species for the network structure in plant-pollinator networks (Olesen et al. 2007).

The study of animal behavior is also a wide disciplinary field that considers domains ranging from proximal mechanisms (i.e., factors that



trigger a behavior) to phylogeny through ontogeny and the influence of behaviors from an evolutionary perspective. SNA is used when ethology interlinks with other fields such as genetics, neurosciences, and ecology (Sueur et al. 2011a).

SNA is obviously an ideal tool for the study of animal societies (Whitehead 2008). Indeed, SNA gave rise to a novel perspective of the field of sociobiology, which is further discussed in the section “[An Example of Research into the Power of Social Networking in Animal Societies.](#)”

This non-exhaustive list of biology disciplines using social networking tools gives a glimpse of the huge potential of SNA. Many other fields make use of these tools, using it for unexpected purposes such as studies in plant biology (see the “[► Plantae](#)” entry of the encyclopedia for more details) that reveal the ability of intra- and inter-specific plant networks to cooperate by sharing nutrients and water through mycorrhizas (see the “[► Symbiotic Relationship](#)” entry of the encyclopedia for more details) (Egerton-Warburton et al. 2007).

### Social Networking in Animal Research: Some History

The first animal studies to use SNA were carried out at the end of the 1960s and the beginning of the 1970s. Primatology studies that were pioneers in the use of SNA (Wey et al. 2008) used sociograms to represent individual interactions. This representation allows the identification of existing and nonexistent interactions between dyads (i.e., a pair) of nodes but also highlights hierarchical clustering and provides a multidimensional scale, all necessary for the study of group divisions according to given relationships (Wey et al. 2008).

Subsequent studies focused on the measurement of individual sociability (degree, clustering coefficient, eigenvector, centrality, etc.) as an indication of an individual's position within the network, for example, through the individual comparative study of interactional frequency according to different factors such as individual attributes, hierarchical rank (see the “[► Dominance](#)” and “[► Dominance Hierarchy](#)” entries of the encyclopedia for more details), or kinship (see

the “[► Kinship](#)” entry of the encyclopedia for more details) (Berman 1982; Wey et al. 2008).

These techniques have been increasingly used over the last 15 years. The enhancement of computing power in the late 1990s and early 2000s facilitated randomization testing and the analysis of large networks and boosted the use of social networking tools in biology. A boom has since been witnessed in the number of studies using these tools for different purposes, some of which have been described in section “[Social Networking in Biology: From Genes to Animal Societies.](#)”

### Principle

A network is defined as a set of connections (*links* or *edges*) between a set of components (*nodes* or *vertices*). This representation aims to describe the state of a complex multi-relational system as fully as possible at a given time and in a given space.

The nodes can be individuals, groups of individuals, species, cells, molecules, websites, and companies, to name but a few. Nodes can include additional information (*node label*) such as age, sex, kinship, social role, socioeconomic characteristics, etc. A focal node is called *ego*, the nodes to which the ego is connected are called *alters*, and the network formed by an ego and its alters is called the *ego-network*. The ego-network is defined at different levels: the first only takes into account the links between the ego and its alters, the second additionally takes into account the links between alters, and the third adds the links between alters' alters, and so forth as the levels increase.

Links can vary in nature and can be any conceivable type of behavior (among others, agonistic (see the “[► Agonistic Behavior](#)” entry of the encyclopedia for more details) and affiliative behaviors (see the “[► Affiliative Bond](#)” entry of the encyclopedia for more details)) and relationship (friendships, sexual partnerships, etc.). Links can include additional information such as their weight; in this case it is then referred to as a *weighted* network (values range from 0 to infinite), as opposed to a *binary* network (values range from 0 to 1). In animal research, the weight

of the links can represent data such as the frequency of interaction between two nodes (e.g., individual A groomed – see the “► [Allogrooming](#)” entry of the encyclopedia for more details – individual B for 10 times) or the duration of the interaction (individual A groomed individual B for 10 min). Links can also have directions, in which case the network is considered to be *directed* rather than *undirected*. With a directed network, it is possible to indicate the direction of an interaction (individual A groomed individual B, individual C attacked individual D, etc.). Undirected networks can be used to represent interindividual distances, for example, individual A was 5 m away from individual B. It is also possible to create links with negative weights or to represent different types of links within a network, thus forming a *multiplex network*. However, *multiplex networks* are rarely used in animal research. Thus, these techniques will not be discussed in this entry.

## Network Metrics

Several analytical methods have been developed to study the different aspects of a network. These methods can be divided into three main categories: global metrics, dyadic metrics, and node metrics. The large range of existing tools permits a multilevel study of a network and thus provides an approach that covers all network aspects from the nodes to the way they interact between each other and finally how these two sublevels affect the overall network structure.

A high number of network metrics are currently available. This entry introduces the most commonly used network metrics in animal research, including a description of the different versions. The investigator can then choose the most appropriate version for the measure he/she wants to obtain and should be careful to select a version that suits the context. For each of these metrics, the following elements will be provided: the mathematical formula, their purpose, their limits, their strengths, precautions that must be taken when using them, and their use in animal research.

## Global Metrics

Global metrics aim to describe the global structure of a network by providing information about questions such as its resilience properties (i.e., the network's capacity to remain undisrupted if nodes are lost), clusterization (i.e., the network is structured in subgroups), or the speed of information transmission. Global metrics can be measured across the entire network or by partitioning the overall network into ego-networks for metrics such as density, diameter, etc.

### Density

The density of a network is simply the ratio of existing links of a network in relation to all potential links (Eq. 1). For a binary network  $G$  with  $N$  nodes and  $L$  links, the density ( $D^b$ ) is

$$D^b(G) = \frac{2|L|}{|N|(|N| - 1)} \quad (1)$$

Density is basic, useful, and easy to interpret. However, special consideration must be taken when examining a network, as this metric strongly affects many aspects of the network and is influenced by (1) the size of the network and (2) the sampling effort. Density is linked to degree distribution. It affects geodesic distances and it is positively correlated to the likelihood of observing micro-motifs (substructures of a network) like “closed triplets” (i.e., three nodes connected to each other) and thus the increase of the clustering coefficient (see section “[Global Clustering Coefficient](#),” for a definition) and other network metrics such as node degree diversity.

These constraints mean that great care must be taken when comparing networks from different groups and species, observed at different moments and/or with different sampling efforts. There is no analytical protocol available to deal with such network constraints. Some network metrics (like modularity) or third- or fourth-order node network metrics do seem less affected by these constraints, but these are not used in animal research and are not therefore discussed in this entry.

Density is generally used as a network descriptor in animal research. However, recent studies

have linked density to different factors such as living condition (wild or captive) or group size. For example, Balasubramaniam et al. (2017) found greater density in captive groups of macaques than in wild groups. Such comparison is possible by using a Bootstrapping approach to control the effect of density variation on the real networks (i.e., by removing links and repeating the comparison) by simulating variations in sampling effort degrees.

### Geodesic Distances

Geodesic distances are the shortest paths to reach all possible pairs of nodes in a network. Several algorithms can be used to find these paths, including the breadth-first search for unweighted networks, Dijkstra's algorithm for weighted networks, and the Bellman-Ford-Moore algorithm for weighted networks with positive and negative weights.

This metric can be calculated in binary or weighted networks and for directed or undirected networks. Although geodesic distance is a well-known network metric, results might vary according to the calculation process, and it is only recently that calculations have been developed to consider the highest strength as the shortest path in weighted networks (Opsahl 2009). Previously, the links with weakest strengths were considered the fastest ones. Therefore, it may be inappropriate to use the latter version on a weighted graph when examining disease transmission, as the probability of transmission can be proportional to the individuals' strength of interaction (Krause et al. 2014). Obviously, directionality may also be an important option to consider when examining disease transmission.

Although the geodesic distance may be useful in the study of epidemiology, it remains poorly used in animal research due to its high sensibility to observation biases (unobserved interactions, misidentification of individuals, etc.) (Krause et al. 2014).

### Diameter

The diameter is simply the longest geodesic distance (i.e., the longest of the shortest paths) of a

network. Here again, it can be calculated on binary or weighted networks and for undirected or directed networks. Depending on the problematic, care is necessary when choosing the calculation method (binary or weighted, directed or undirected) and using the lowest or the highest strength as the shortest path, as explained in section "Geodesic Distances."

The diameter most certainly owes its fame to the works of Milgram (1967), who sent a letter addressed to a specific recipient to random people living in the United States with the aim of reaching the recipient via these people. An average of six people was required in the resulting human chain from the sender to the intended recipient. This experiment gave rise to the theory of the "small-world effect." The Internet and the many associated social networks such as Facebook and Twitter have decreased the degree of separation between American people from six to four individuals (Backstrom et al. 2012).

Diameter is used in animal research to examine issues such as the resilience of a network or the information transmission. For example, through target deletion simulation of individuals with high centrality (see section "Node Metrics"), several studies have highlighted the key role played by individuals with high centrality (degree, eigenvector, etc.) in the cohesion of affiliative networks in dolphins, Colombian squirrels, killer whales, and primates, among others (see Sosa (2014) for more details).

### Global Clustering Coefficient

The global clustering coefficient measures the extent to which nodes in a network are connected together. As several definitions of this metric can be found in the literature, careful attention must be paid when using a software, as different definitions can apply. One of the simplest definitions is the binary global clustering coefficient (Eq. 2) for a binary network that is the ratio of closed triplets to all triplets (open and closed) in a network. Triplets are three nodes connected by two or three undirected links (open or closed triplets, respectively). For a graph  $G$ , the binary global clustering coefficient ( $C^b$ ) formula is the following:

$$C^b(G) = \frac{\sum \tau_{\Delta}}{\sum \tau} \quad (2)$$

where  $\sum \tau$  is the total number of triplets (open and closed) and  $\sum \tau_{\Delta}$  is the subset of closed triplets.

Another version of the clustering coefficient is derived from the local (i.e., node) level: it is called the local mean clustering coefficient (Eq. 3). The local clustering coefficient will be further detailed in section “[Node Metrics](#).” For a network  $G$  with  $N$  nodes  $i$ , the clustering coefficient ( $\bar{C}^b$ ) is defined as the mean of all node clustering coefficients ( $C_i$ ):

$$\bar{C}^b(G) = \frac{1}{N} \sum_{i=1}^N C_i \quad (3)$$

The Barrat et al. (2004) clustering coefficient (Eq. 4) is one possible weighted version of this local mean clustering coefficient. It is also derived from local level and is based on a weighted version of all node clustering coefficients ( $C_i^w$ ). This node metric will be described in greater detail in section “[Node Metrics](#).” For a network  $G$  with  $N$  nodes  $i$  and  $n$  alters  $j$ , the weighted clustering coefficient ( $C_{nn,i}^w$ ) formula is the following:

$$C_{nn,i}^w(G) = \frac{1}{s_i} \sum_{j=1}^n a_{ij} w_{ij} D_i \quad (4)$$

where  $s_i$  is the strength of node  $i$  (see section “[Degree and Strength](#),” for a definition),  $a_{ij}$  is the link between node  $i$  and alter  $j$ ,  $w_{ij}$  are the weights of this link between node  $i$  and alter  $j$ , and  $D_i$  is the degree of node  $i$  (see section “[Degree and Strength](#),” for a definition).

Another weighted version of the global clustering coefficient (Opsahl 2009) (Eq. 5) considers the triplet value  $\omega$  selected according to its most appropriate meaning, namely, the maximum or minimum values of the weights or the arithmetic or geometric means of the weights of the links in a triplet. For a graph  $G$ , the weighted global clustering coefficient ( $C^w$ ) formula is the following:

$$C^w(G) = \frac{\sum \tau_{\Delta} w}{\sum \tau_{\Delta} w} \quad (5)$$

where  $\sum \tau$  is the total number of triplets and  $\sum \tau_{\Delta}$  is the subset of closed triplets.

This is not a complete list of the many versions of the global clustering coefficient. The investigator may therefore choose the most appropriate version as it may lead to different biological interpretations.

The clustering coefficient is a very important metric for the evaluation of “transitivity” and related concepts (see section “[Transitive Triplets](#)”), as it indicates how well the alters of an ego are interconnected. The clustering coefficient promotes the cohesion of the network. This has been illustrated by works showing that “policing” individuals (i.e., individuals that regularly intervene as third parties in conflicts) are largely responsible for increased global clustering coefficient in nonhuman primate societies (Flack et al. 2006), revealing the important role these individuals play in network group cohesion.

#### Network Clusterization

Network clusterization, or *subgrouping*, strongly influences the resilience properties of the network and the speed of information transmission. Understanding how a network is clustered and identifying which nodes form the cluster and how different clusters are linked is a critical question for community detection in ecology, wildlife preservation, and research on societies.

The study of the existence of subgroups within a network is a wide research area that has produced a large variety of clusterization techniques including K-means, hierarchical clusterization, and Girvan-Newman algorithms. Some of them base the algorithms on node network metrics, like modularity with eigenvector (Newman 2006). Others are based on micro-motifs such as closed triplet, as seen in the conductance motif approach (Tsourakakis et al. 2017).

The definition of a subgroup itself can be viewed in different ways. For example, a subgroup can be considered a set of nodes where everyone is connected (a subgroup of density 1): this is referred to as a clique (Hanneman and Riddle 2005). However, cliques are restrictive, as some nodes may not be completely connected

to the other nodes of the group and can therefore be omitted. This restricted definition has several variants with less stringent applications, such as N-cliques (Hanneman and Riddle 2005). N-cliques consider a node to be a member of a subgroup if it is connected to all the other members of the group at N distance (generally defined by the user). N-clans (Hanneman and Riddle 2005) are similar to N-cliques but with the restrictive condition that all the links among members of the N-clique occur via other members of the N-clique. This subgroup definition can be developed further with K-plexes or with K-cores and F-Groups (Hanneman and Riddle 2005).

The choice of the technique used is left to the user, who has to consider which approach is more suitable according to the question and to the biological interpretation that may be extracted.

Modularity is one of the most commonly used network cluster measures today and may be linked to several biological aspects such as social-style dependent modularity differences in macaques, where despotic societies (i.e., species with high levels of social intolerance, steep dominance gradient, and strong kin preference) show higher modularity than egalitarian societies (i.e., species with high levels of tolerance, relaxed dominance, and low kinship bias). Higher modularity in despotic societies seems to be related to preferential interactions with kin, leading to the formation of clusters based on kinship bonds.

### Dyadic Metrics

Dyadic metrics make it possible to examine how and with whom individuals interact, revealing patterns of interaction. These metrics deeply impact the development of the global network structure through the repetitive nature of these local patterns, which form the overall global network structure to a certain extent. This entry will discuss two of the dyadic metrics that are increasingly used in animal research, explaining their impact at the global structure level and discussing the parallels that can be drawn between the presence of those dyadic metrics and the presence of biological phenomena.

### Assortativity

Assortativity (Newman 2003) (like the E-I index or the Moran “I” statistic) allows the study of homophily (preferential interaction between nodes with similar attributes) and heterophily (the preferential interaction between nodes with different attributes) (Lazarsfeld and Merton 1954). Attributes can be individual characteristics such as sex or age or individual node metrics such as the degree (see section “Degree and Strength,” for a definition), in which case it is referred to as *assortativity by vertex degree*.

The assortativity coefficient, like other metrics that analyze homophily, basically measures the proportion of links between and within nodes of specific attributes. The assortativity range is as follows:  $1 > r > -1.1$  indicates that the network is fully assorted (i.e., all the nodes of same attributes interact exclusively together), and  $-1$  shows that the network is fully disassorted (i.e., all the nodes of dissimilar attributes interact exclusively together). There are four types of assortativity coefficient according to the type of node attributes (categorical or continuous) and the type of network (binary or weighted).

For a network  $G$ , the binary discrete assortativity coefficient ( $r_d^b$ ) (Newman 2003) (Eq. 6) formula is as follows:

$$r_d^b(G) = \frac{\sum_i e_{ii} - \sum_i a_i b_i}{1 - \sum_i a_i b_i} \quad (6)$$

where  $e$  is the proportion of specific links in the network,  $e_{ii}$  is the number of links between nodes of attributes  $i$  ( $E_{ii}$ ) divided by the total number of links in the network  $M$ :  $e_{ii} = M^{-1} \cdot E_{ii}$ ,  $a_i$  is the proportion of outgoing links from nodes of attributes  $i$  toward all possible nodes of attributes  $j$ :  $a_i = \sum_j e_{ij}$ , and  $b_i$  is the proportion of all possible outgoing links from nodes of attributes  $j$  toward nodes of attributes  $i$ :  $b_j = \sum_i e_{ij}$ .

For a network  $G$ , the weighted discrete assortativity coefficient ( $r_d^w$ ) (Eq. 7) formula is as follows:

$$r_d^w(G) = \frac{\sum_i e_{ii}^w - \sum_i a_i^w b_i^w}{1 - \sum_i a_i^w b_i^w} \quad (7)$$



where  $e_{ii}^w$  is the proportion of weighted links between nodes of attributes  $i$  divided by the total number of links in the network,  $a_i^w$  is the proportion of the outgoing weighted links from nodes of attributes  $i$  toward all possible nodes of attributes  $j$ :  $a_i^w = \sum_j e_{ij}^w$ , and  $b_i^w$  is the proportion of all possible outgoing weighted links from nodes of attributes  $i$  toward nodes of attributes  $j$ :  $b_i^w = \sum_j e_{ij}^w$ .

For a network  $G$ , the binary continuous assortativity coefficient ( $r_c^b$ ) (Newman 2003) (Eq. 8) formula is as follows:

$$r_c^b(G) = \frac{\sum_i (j_i k_i) - M^{-1} \sum_i j_i \sum_i k_i}{\sqrt{[\sum_i j_i^2 - M^{-1} (\sum_i j_i)^2][\sum_i k_i^2 - M^{-1} (\sum_i k_i)^2]}} \quad (8)$$

where  $j_i$  and  $k_i$  are the node labels of the  $i^{\text{th}}$  in-degrees and out-degrees, respectively, and  $M$  is the total number of links.

For a network  $G$ , the weighted continuous assortativity coefficient ( $r_c^w$ ) (Leung and Chau 2007) (Eq. 9) formula is as follows:

$$r_c^w = \frac{\sum_i (w_i j_i k_i) - W^{-1} \sum_i (w_i j_i) \sum_i (w_i k_i)}{\sqrt{[\sum_i (w_i j_i^2) - W^{-1} (\sum_i (w_i j_i))^2][\sum_i (w_i k_i^2) - W^{-1} (\sum_i (w_i k_i))^2]}} \quad (9)$$

where  $j_i$  and  $k_i$  are the node labels of the  $i^{\text{th}}$  in-strengths and out-strengths, respectively,  $w_i$  is the weight of link  $i$ , and  $W$  is the sum of all the weights of all network links.

At a network level, assortativity leads to more clustered and resilient networks (Newman 2003). From a biological perspective, recent studies argue that preferential interactions among individuals sharing a common attribute (i.e., homophily) may explain the difference observed between animals and humans for cooperation among strangers, social learning, and the transmission of culture and norms (Allen et al. 2013; Sosa et al. 2017). Homophily according to different phenotypes (such as sex, age, kinship, degree, or

weight) was found in several species including fish, birds, cetaceans, and primates.

### Transitive Triplets

Another dyadic metric recently investigated in animal research is the micro-motif called transitive triplets. Its creation process reveals a phenomenon called “triadic closure” which indicates an individual preference to create links with individuals who are connected to individuals they already know. This dynamic behavioral pattern is generally described as “the friend of my friend is my friend,” and it is characterized by transitive triplet micro-motifs in a network.

The main topological effect of triadic closure is the clusterization of the network. The triadic closure process may also be a mechanism enabling network degree assortativity, i.e., individuals interact in a preferential way with individuals of the same degree, which is a key element in social network resilience (Newman 2003).

From a biological perspective, transitive triplets generate cohesive groups and seem to be intimately linked to the emergence of reciprocity, altruism, and cooperation (see the “► [Cooperation](#)” and “► [Reciprocity](#)” entries of the encyclopedia for more details).

The presence of this mechanism has recently been highlighted in several animals such as corvids, hyenas, and nonhuman primates (Sosa et al. 2017). As seen for homophily, transitive triplets not only highlight a common mechanism between humans and animals providing information about evolutionary aspects, but they also reveal how individuals extend their ego-network according to these behavioral patterns (Sosa et al. 2017).

### Node Metrics

Node metrics are calculated at a node level. They are simply based on ego: these are first-order metrics. Other metrics are based on ego and alter measures, such as second-order metrics. This type of metric allows researchers to analyze different aspects of a node, including the number of links it has, its centrality (i.e., a central node is well connected and/or is connected to well-connected nodes), or its role in maintaining network cohesion, for example.

### First-Order Metrics

There are very few first-order metrics, owing to the limitations of considering the links of only one node. Therefore, second-order metrics were rapidly developed to determine the type of alters to which a node is connected.

**Degree and Strength** First-order metrics are simple, like the degree (Eq. 10) that measures, for example, the number of links of a node in a binary network. If the network comprises directed links, it is then possible to differentiate between the incoming links (i.e., links directed toward the ego, also called *in-degree*) and the outgoing links (i.e., links emitted by the ego, also called *out-degree*). For a node  $i$  with  $N$  alters  $j$  in a network  $G$ , the degree ( $D_i$ ) formula is as follows:

$$D_i(G) = \sum_{j=1}^N a_{ij} \quad (10)$$

where  $a_{ij}$  is the value of the link between node  $i$  and node  $j$ .

If the network is weighted, then the degree is called *strength* or the *weighted degree* (Eq. 11). If the network comprises directed links, then it is also possible to differentiate between the incoming links (in-strength) and the outgoing links (out-strength). For a node  $i$  with  $N$  alters  $j$  in a network  $G$ , the degree ( $S_i$ ) formula is as follows:

$$S_i = \sum_{j=1}^N a_{ij} w_{ij} \quad (11)$$

where  $a_{ij}$  is the link between node  $i$  and alter  $j$  and  $w_{ij}$  is the weight of this link.

Degree and strength are very simple and can easily be used to interpret node network metrics. Their interpretation varies depending on the type of edges and can be perceived as the activity (i.e., total frequency of expression of a behavior) or the centrality (i.e., whether a node is poorly or highly connected) of a node. When considering the directionality of edges, in-degree is often used as a measure of popularity and out-degree as a measure of expansiveness. These simple metrics

constitute the basis for calculating most of the other more complex metrics, as detailed in the following sections.

Degree is one of the most appropriate measures to study epidemiology due to its low sensitivity to observation biases, unlike geodesic distance and related node metrics (Krause et al. 2014). A link has been evidenced in epidemiology research between degree and parasite load. At a species level, host infection can be significantly linked to the in-degree, as seen in lizards, or to the out-degree, as observed in Japanese macaques (see Krause et al. (2014)).

### Second-Order Metrics

Second-order metrics allow to take the metrics of ego alters into account and thus make it possible to analyze different aspects of a node, such as its position within the network (e.g., closeness or betweenness) or its centrality (eigenvector centrality, reach, disparity, etc.). For example, it is not the same to be connected to the most central node in the network as it is to be connected to a peripheral node. Similarly, it is not the same to be connected to a few extremely central nodes as it is to be connected to many peripheral nodes.

**Eigenvector Centrality** Eigenvector centrality (Eq. 13) is the first nonnegative eigenvector value obtained through the linear transformation of an adjacency matrix. This centrality measure quantifies not only a node's connectedness but also the connections of the nodes to whom it is connected (i.e., ego's alters' centralities). Thus, a node can have a high eigenvector value by having a high degree or strength or by being connected to nodes that have high degrees or strengths.

For a network  $G$ , the centrality  $c_i$  of a node  $i$  is the average of its alters' centralities (Eq. 12) and is calculated with the following formula:

$$c_i = \frac{1}{\lambda} \sum_{j=1}^N w_{ij} c_j \quad (12)$$

where  $\lambda$  is a constant,  $N$  is the number of alters of  $i$ , and  $w_{ij}$  is the link between  $i$  and the  $j^{\text{th}}$  alter.

Defining the vector of centralities as  $c = (c_1, c_2, \dots, c_N)$ , Eq. 12 can be rewritten as follows:

$$\lambda c = Wc \quad (13)$$

where  $c$  is the eigenvector of the edge weight matrix  $W$  with an eigenvalue of  $\lambda$ . If only the positive eigenvectors are considered, then only the largest eigenvalue provides the eigenvector centrality.

Eigenvector is one of the most frequently used second-order metrics in animal research and is linked to several biological aspects such as individual fitness (see section “[Micro Level: Individual Position, Role, and Fitness](#)”), genetic variation (see Krause et al. (2014)), or individual attributes. For example, the eigenvector centrality of female affiliative networks in despotic macaque societies is related to the hierarchical ranks of females, unlike in egalitarian societies (Sueur et al. 2011b), and thus reveals a link between social style and network structure.

**Reach** Reach (Eq. 14) is a measure of indirect connectedness (Whitehead 2008). As eigenvector centrality, it measures how well connected a node and its alters are. It can be calculated on binary or weighted networks. The binary version is simply the number of alters of a node  $i$  at level one (the degree in this case) or more. For a node  $i$  of  $N$  alters  $j$  in a network  $G$ , the binary reach index ( $r_i^b$ ) formula is as follows:

$$r_i^b(G) = j_1 + j_2 + \dots + j_N \quad (14)$$

The weighted version (Eq. 15) is the sum of the product of all the ego and alters’ strengths and the alters’ degrees. For a node  $i$  of  $N$  alters  $j$  in a network  $G$ , the weighted reach index ( $r_i^w$ ) formula is as follows:

$$r_i^w = \sum_{j=1}^N a_{ij} S_j \quad (15)$$

where  $a_{ij}$  is the weight of the link between node  $i$  and node  $j$  and where  $S_j$  is the strength of node  $j$ .

Reach is a useful measure when examining contagion processes, as it allows investigators to highlight the pathway of information through direct connections. Studies have shown that differences across individual reach metrics might be related to individual roles. For example, node deletion simulations by Flack et al. (2006) showed that “policing” individuals had higher reach values than other group members in a group of *Macaca nemestrina*, thus facilitating their role in policing conflicts.

**Node Betweenness** Betweenness is the number of times a node is included in the shortest paths (geodesic distances) between all the potential combinations of edges of the other nodes. As it is directly derived from the geodesic distance, it is important to pay attention to how the investigator intends to calculate the geodesic distances (binary or weighted, directed or undirected, and using the lowest or the highest strength as the shortest path). Betweenness provides a specific centrality measure insofar that it informs on the role of a node in the transmission of information as nodes with high betweenness are likely to constitute bridges that connect subgroups.

Like geodesic distance, betweenness may be useful in the study of epidemiology. However, it is not frequently used in animal research due to its high sensitivity to observation biases (unobserved interactions, misidentification of individuals, etc.) (Krause et al. 2014).

**Local Clustering Coefficient** Like the global clustering coefficient ( $C$ ) described in section “[Global Clustering Coefficient](#),” the local clustering coefficient of a node ( $C_i$ ) is defined in several different ways in the literature. It attempts to determine the connections between the alters of an ego and indicates whether they tend to interact or not, forming a network with a greater or lesser density which contains more or less transitive triplets. This can impact the network in different ways, affecting resilience (theoretically, a dense network is more resilient than a less dense network of the same size) or the transmission of information (theoretically, transmission is faster

in a dense network than in a less dense network of the same size).

The local clustering coefficient is the proportion of links between the nodes of an ego-network divided by the number of potential links between them; it can be defined as the density of an ego-network. As discussed in section “[Global Clustering Coefficient](#),” it allows the calculation of the local mean clustering coefficient. Like density, it evaluates how close nodes’ ego-networks are to a clique (i.e., a fully connected ego-network of density 1). For a node  $i$  with  $N$  alters  $j$  in a network  $G$ , the binary local clustering coefficient of  $i$  ( $C_i^b$ ) (Eq. 16) is defined as

$$C_i^b = \frac{2t_i}{N_i(N_i - 1)} \quad (16)$$

where  $t_i$  is the number of links present in the ego-network of node  $i$ .

The Barrat et al. (2004) (Eq. 17) clustering coefficient is one possible version of the local clustering coefficient for use in weighted networks. For a node  $i$  with a pair of alters  $j$  and  $h$  among  $N$  alters, the weighted local clustering coefficient of  $i$  ( $C_i^w$ ) is defined as

$$C_i^w = \frac{1}{S_i(D_i - 1)} \sum_{j \neq h \in N} \frac{(w_{ij} + w_{ih})}{2} a_{ij}a_{ih}a_{jh} \quad (17)$$

where  $S_i$  and  $D_i$  are, respectively, the strength and the degree of node  $i$ ;  $w_{ij}$  and  $w_{ih}$  are the weights of the links between node  $i$  and, respectively, alter  $j$  and alter  $h$ ; and  $a_{ij}$ ,  $a_{ih}$ ,  $a_{jh}$  are, respectively, the links between node  $i$  and alters  $j$  and  $h$ .

The clustering coefficient is both a local and a global metric (see section “[Global Clustering Coefficient](#)”) that permits the examination of how local motifs affect the overall network structure. For this reason, it has been widely used to study epidemiology in animal networks. One such example is the demonstration of interactional adaptive capacity to infectious disease in guppies. In this study, lower local clustering coefficients were recorded in groups to which infected individuals had been introduced than in the control

group (to which no infected individuals had been introduced). This reveals that individuals actively adapt their behaviors to prevent disease infection (Croft et al. 2011a). These interactional patterns directly affect the overall network structure through the decrease in the global clustering coefficient. The fact that networks with a low global clustering coefficient are more resilient to the spread of infectious diseases highlights how local interactional patterns shape the overall network structure and provide it with dynamical adaptive properties.

### Specific Points to be Considered Within the SNA Research Context

For decades, null hypothesis significant testing (NHST) (Anderson et al. 2000) has been widely used in research for testing binary hypotheses ( $H_0$  vs.  $H_1$ ). All of these hypotheses postulate that data are independent, and they examine whether these data are significantly different from zero. However, data from social groups are intrinsically non-independent, as links within the network are shared between nodes. Two approaches deal with this dilemma: one is based on the null model hypothesis (NMH) (Croft et al. 2011b; Farine 2017), and the other is based on simulations. The first one consists in creating random networks and then compares them to the real one. The second one simulates the processes involved in the formation of links, then creates networks from these simulations, and finally compares these simulated networks to the real one.

#### Null Model Hypothesis

The NMH approach consists in creating a random dataset from the observed data. The randomized data have to conserve the same structure as the original data, except for those the investigator wants to test. The metrics of interest  $X$  of the observed data and the posterior distribution issued from the randomization are then compared to examine if they are significantly different by assessing the proportion of random values that differ from the observed values. Through this approach, the investigator tests whether  $X$  are

different to random values instead of testing if they are different to zero.

There are two ways of categorizing NMH: firstly, according to the elements of the network that are being resampled (links or node labels), and, secondly, according to whether they are built on raw data (before building the network: pre-network randomization) or on the network (after building the network: network randomization).

### Randomization

Randomization approach consists in randomizing link and/or node labels in a network. Link randomization (i.e., permuting links between each other) maintains the number of links. This approach is mainly used for the analysis of interactional patterns, i.e., how interactions are arranged and which individuals are involved. Node label randomization consists in permuting node characteristics, thereby preserving the structure of node links. The objective of such approach is to determine whether a node's position is linked to its intrinsic characteristics.

#### Network Randomization

Network randomization is used when examining direct behavioral interactions and when groups are well defined. This approach consists in randomizing link or node labels directly on the observed network. When links refer to individuals' association (i.e., spatial proximity, group composition, etc.), a pre-network randomization is necessary.

#### Pre-network Randomization

Permutations on raw data use a permutation process, first created by Bejder et al. (1998) and further improved (see Farine (2017) for an overview). Also called data stream permutations, this process consists of running a permutation on raw data and then building the network with this permutation, so the metric of interest can be measured again. This process is repeated as many times as needed (generally 1000 or 10.000 permutations) until the required number of permutations is complete. Pre-network randomization is mainly used in ecology when interindividual links are inferred by individual

associations. It is then referred to as the “gambit of the group.” This principle is based on the likelihood that individuals who frequently gather will interact with each other. It is then possible to infer preferential interactions from the presence/absence of certain individuals. For this process, it is important to consider not only the size of the group observed but also the ease of observation of some specific individuals, which *in fine* influences their frequency of observation. This is why permutations on raw data are required. This type of randomization consists in link permutations. Pre-network randomization also allows to deal with several observation biases by allowing link permutations according to a given factor of interest, such as spatial structure or temporal structure, i.e., permuting links between groups according to their spatial or temporal associations. One recent improvement concerns the capacity to handle data obtained from GPS tracking in order to preserve the autocorrelation structure of individuals.

### Simulation-Based Approach

The simulation-based approach consists in simulating the formation of links in a network and in comparing the simulated networks to the real one. These techniques usually use Monte Carlo and Markov chain (MCMC) to simulate dataset according to a prior distribution. The exponential random graph models (ERGMs) (Robins et al. 2007) are among the most usual simulation-based approaches.

#### Monte Carlo and Markov Chain

The Monte Carlo (MC) process is a method that generates random samples of size  $N$  through the *expected value function*  $g$  of random variable  $x$  ( $x_0, x_1, \dots, x_N$ ). The objective is to recreate a sample size according to the mean and the variance of the observed sample (i.e., the prior distribution  $\pi$ ). Random numbers are generated through Markov chain (MC) processes. Markov chain processes are stochastic techniques in which the information that enables the prediction of the future state of a system is only present in its current state: the principle is to establish a probability distribution  $\pi_{x_{i-1}}$  that generates a resampled



dataset  $x_i$  based on the previous resampled dataset  $x_{i-1}$ .

By repeating this process, it is then possible to obtain a posterior distribution of the parameter of interest according to the resamples. MCMC technique can be used for both simulation and randomization approaches. Contrary to randomization approach, the use of MCMC in a simulation approach has the advantage of assessing several statistical measures such as the standard deviation or the confidence interval for the parameter of interest. MCMC technique represents the core of Bootstrapping and Bayesian approaches.

### Exponential Random Graph Models

ERGMs constitute a family of statistical models based on network simulations. This approach formulates the probability of observing links through an MCMC-based maximum likelihood estimation according to different structural mechanisms. The latter can be node based (i.e., how nodes' attributes affect the formation of a new link), dyadic (i.e., how the other links affect the formation of a new link), or structural (i.e., how some network structures affect the formation of a new link). These models permit the study of binary, weighted, and dynamic networks.

By simulating networks according to some factors (node based, dyadic, structural), ERGMs allow to examine whether the simulated networks are significantly different from the observed network.

## An Example of Research into the Power of Social Networking in Animal Societies

Section “[Social Networking in Biology: From Genes to Animal Societies](#),” showed a wide range of research areas that use a large variety of SNA techniques. This section covers the new highlights allowed by SNA in the study of animal societies, providing a non-exhaustive overview of the different related fields. Research in animal societies is one of the fields that mostly benefited from SNA techniques.

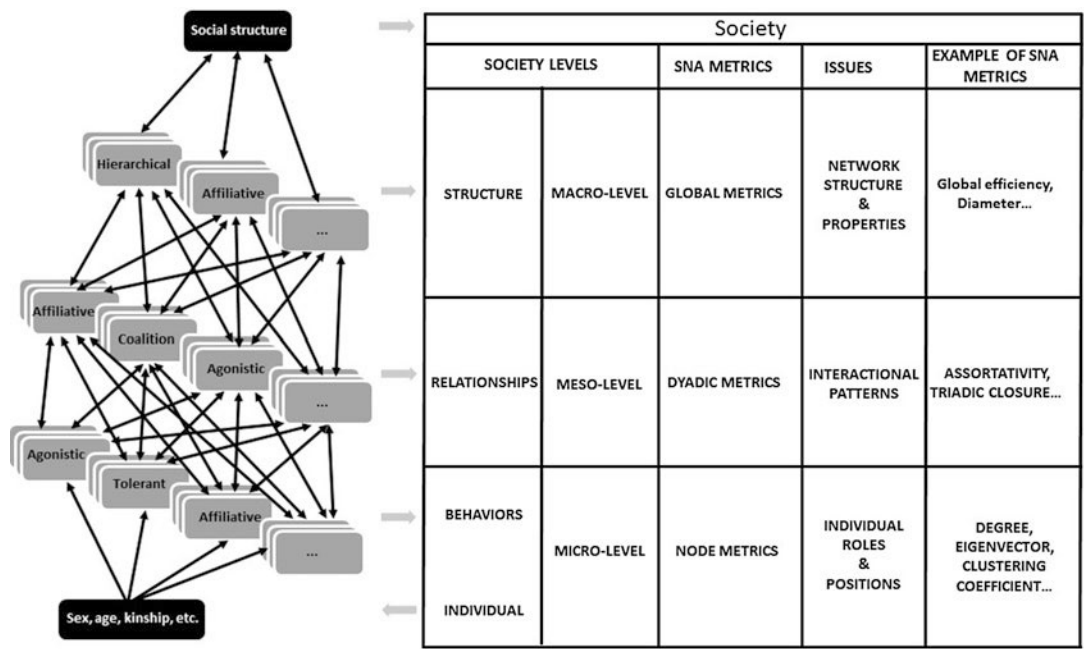
Group living (see the “[Group Living](#)” entry of the encyclopedia for more details) is a social

condition that has arisen independently many times throughout evolutionary history, with different degrees of specialization and complexity. Many adaptive advantages are associated with living in a group, including the optimization of foraging, collective defense of resources, increased vigilance, and a dilution effect against predation (see the “[Alarm Calls](#),” “[Cooperation](#),” “[Cultural Transmission](#),” “[Hunting](#),” “[Predation Risk](#),” “[Social Grooming](#),” and “[Vigilance](#)” entries of the encyclopedia for more details). However, group living also generates costs such as increased within-group competition for access to resources and mating opportunities and the risk of acquiring and spreading infectious diseases. In order to maintain their homeostasis, societies need a trade-off to maximize the benefits and minimize the costs. This also implies an equilibrium between the needs of each individual.

Sociobiology (see the “[Sociobiology](#)” entry of the encyclopedia for more details) considers societies in the same way that behavioral ecology considers living organisms, namely, as adaptive systems. This scientific field first appeared in the 1970s. It is an interdisciplinary field that gathers different scientific approaches including evolutionary biology, ethology, ecology, anthropology, and genetics, among others. It aims to study the way social behaviors can ensure organisms (including humans) a greater evolutionary success and thereby understand the intrinsic biological properties of animal and human societies.

Animal societies can thus be viewed as systems whose adaptive properties arise from the continuous evolution of the different selective pressures that rule them. With this approach, it is possible to consider that individuals show behaviors that aim to optimize their chance to reach a better position within society, thus attaining a higher survival and reproductive rate.

In the 1970s, Hinde conceptualized the structuring of a society (Fig. 1) (Hinde 1976). The first level, which can be called the “micro level,” contains the individuals that compose the society. Individuals can be characterized by the attributes that influence their behaviors and interactions (agonistic, tolerant, affiliative, etc.). At the second



**Social Network Analysis, Fig. 1** An example of multilevel approach allowed by social network analysis in animal societies research. This scheme is inspired by Hinde (1976)

level, which can be called the “meso level,” these behaviors allow individuals to form relationships (agonistic, coalitional, affiliative, etc.). These relationships shape the final level, i.e., the “macro level.” At the macro level, the social structure can be subdivided into several substructures (hierarchical structure, affiliative structure, etc.). Together, these three levels form a society.

From this conceptual framework, a parallel can be drawn between the interest of using social networking tools and the study of animal societies, as the latter may provide new insights and new prospects for this up-and-coming field (Fig. 1).

Similarly, the different topics that can be studied using social networking tools interconnect with Tinbergen’s four questions (mechanism, ontogeny, adaptive value, and phylogeny) as explained in the following sections.

**Micro Level: Individual Position, Role, and Fitness**

Studies examining the “micro level” generally focus on describing the positions and roles of

individuals within the network according to their characteristics. There are three different possible perspectives at this level: mechanistic, ontogenetic, and evolutionary. The perspective adopted by the researcher depends on the relationship he/she seeks to highlight between the roles (in the cohesion of the network, in the spread of information, etc.) and positions (centrality, activity, etc.) of individuals and their characteristics.

The investigator’s perspective can be considered “mechanistic” when the study focuses on how roles and positions of individuals differ within the network according to social (social organization, group size, group condition, etc.) and nonsocial factors (population density, predation pressure, habitat fragmentation, etc.). This approach aims to determine the mechanistic rules underlying individual positions and roles. For example, the most active (i.e., with the highest degrees) and the most central (i.e., with the highest eigenvectors) individuals in Barbary macaques belong to the philopatric sex, i.e., females (Sosa 2016). Similar patterns have been observed in the philopatric sex in other primate

species (including macaques and baboons) and may be linked to social organization: philopatric individuals have more time to create, maintain, and expand their preferred social partnerships, making them key elements in the social structure.

The investigator's perspective can be considered "ontogenetic" when the study focuses on variation in individuals' roles and positions over their lifetimes. Due to the obvious difficulty of following groups over several generations, researchers generally focus these studies on comparing the roles and positions of individuals according to their age. Studies in primates and yellow-bellied marmots highlighted age-related variations in node network metrics (such as degree and strength), revealing a link between ontogenesis and sociogenesis: young individuals show high degrees and therefore a high number of social partners (Sosa 2016), which then decrease as individuals grow older. This may reflect a more selective choice of preferred partners as age progresses, so a trade-off is maintained between socialization and loss of resources (e.g., decline of physical and/or cognitive abilities) (Almeling et al. 2016). However, this decrease does not lead to complete desocialization as old individuals still interact with adult group members, albeit to a lesser extent (Almeling et al. 2016). These age-related variations can be examined alongside other individual attributes like sex or hierarchical rank or even kinship bonds, where individual position is transmitted from the mother to the offspring, as seen in wild crickets (Fisher et al. 2016).

Finally, the "ecological" perspective consists of linking individual node metrics and/or individual role and position to individual fitness traits, offspring fitness, spread of information, or spread of diseases. For example, the link between the sociality of a female and the survival and longevity of offspring has been amply described in social mammals such as baboons, house mice, and horses. Researchers have recently examined how far individual network metrics of a female predict the survival and longevity of her offspring. The link between node network metrics and individual fitness traits has been demonstrated in several species: betweenness in chimpanzees, clustering

coefficients in hyenas, or eigenvector centrality in juvenile dolphins (Cheney et al. 2016). For example, a long-term study by Cheney et al. (2016) on wild female baboons showed that indirect connections (measured through eigenvector centrality) affect the survival rate and longevity of their offspring more than direct connections.

### Meso Level: Individual Interaction Patterns

At the "meso level," phenomena such as homophily or triadic closure can be studied to understand how individuals create relationships. Researchers are able to examine the presence of these phenomena in a given group by using several analytical tools such as interactional metrics (described in section "[Dyadic Metrics](#)"). Understanding how individuals interact is crucial for several reasons:

1. It informs on the rules governing the expansion of individual ego-networks and therefore on how individuals create new affiliative bonds, for example.
2. It reveals interactional patterns that might reflect behavioral strategies that facilitate the acquisition of an enhanced individual position within the group, potentially improving individual fitness (see the previous section).
3. It explains overall network structures and properties, as the repetition of interactional patterns is known to have a significant effect on network structure (see section "[Dyadic Metrics](#)").
4. Some of these interactional patterns play a crucial role at ecological and evolutionary levels, as discussed in section "[Dyadic Metrics](#)." These patterns, and the role they play in phenomena such as reciprocity, could highlight underlying mechanisms that are closely linked to socialization and could be the origin of animal societies. However, this hypothesis is difficult to test and therefore remains purely speculative.

An increasing number of studies are revealing the presence of such individual interaction patterns in a wide range of species including vervet monkeys, Barbary macaques, chimpanzees, great tits, and humpback whales. One such example

is the presence of triadic closure highlighted by the presence of transitive triplets in Barbary macaques. Triadic closure is known to be closely linked to reciprocity, and, more importantly in this case, the formation of transitive triplets is not linked to individual kinship bonds. This reveals the importance of non-kin affiliative bonds in reciprocity (Sosa et al. 2017).

### Macro Level: Global Group/Network Structure

At the “macro level,” analyses focus on specific aspects of the global network structure such as network diameter, network clusterization, and degree distribution. Global network metrics are a means to study network structures, but another option is network modeling (a subject that is beyond the scope of this entry). The examination of overall network structures is of great interest as it helps to understand how they are shaped, identify their intrinsic properties, and understand how and why they differ between different species.

As mentioned in section “[Meso Level: Individual Interaction Patterns](#),” the repetition of local individual interaction patterns plays an important role in the network structure. Understanding how and to what extent sublevels shape the global network structure is crucial for obtaining knowledge on the underlying mechanisms. For example, as discussed in section “[Assortativity](#),” homophily is linked both to reciprocity and to resilience properties (Newman 2003). The fact that homophily is found in several animal societies may explain the maintenance of long-lasting bonds between conspecifics and thus also the maintenance of societies.

Network comparisons are increasingly used to understand the evolution of societies through the observation of differences across networks. This comparative phylogenetic approach highlights structural disparities that may be explained by different types of social organization or phylogeny. However, as discussed in section “[Density](#),” care must be taken when comparing biological networks in which inherent biases may occur due to group size and sampling effort, both of which affect density and thus also affect all the other network metrics.

Another promising aspect of studying network structures is the understanding of intrinsic network properties and the ability to link them to possible adaptive properties. This perspective originates from the expectations of sociobiologists, who consider societies as adaptive systems and thus observe these properties through the prism of network structure. One of the potential achievements of this approach is understanding how networks deal with the loss of central individuals. For example, Sosa (2014) showed that affiliative networks in Barbary macaques are more sensitive to the simulated loss of high-degree individuals than that of low-degree individuals. However, the network was not disrupted when 20% of the most central individuals were deleted, revealing great resilience properties that are rarely observed in artificial systems such as the World Wide Web. This finding highlights a trade-off between a centralized and a decentralized society, which are sensitive to target and random deletion, respectively. This trade-off makes sense from a selective perspective as it enables societies to maintain themselves on a geological time scale through resilience to both random and target deletions.

### SNA for a Holistic and Multidisciplinary Approach

The previous section illustrates how far SNA tools have enabled researchers to obtain valuable new insights into animal societies over the years, thus gaining a holistic understanding of structuring mechanisms of societies. This type of holistic approach does not only solely apply to sociobiology but also to many disciplines showing the huge versatility of these analytical tools (as mentioned in section “[Social Networking in Biology: From Genes to Animal Societies](#)”).

However, as observed for the maturing application of SNA in animal research, some limitations arise and may eventually require the development of means to counteract them, such as the question of comparing networks of different sizes or sampling efforts, as discussed in section “[Density](#).” Nevertheless, the continual emergence

of innovative SNA techniques leaves no doubt as to their potential to deal with these issues and to provide new insights in animal research.

## Cross-References

- [Affiliative Bond](#)
- [Agonistic Behavior](#)
- [Alarm Calls](#)
- [Allogrooming](#)
- [Cooperation](#)
- [Cultural Transmission](#)
- [Diffusion](#)
- [Dominance](#)
- [Dominance Hierarchy](#)
- [Ecology](#)
- [Fitness](#)
- [Group Living](#)
- [Hunting](#)
- [Innovation](#)
- [Kinship](#)
- [Plantae](#)
- [Predation Risk](#)
- [Reciprocity](#)
- [Social Grooming](#)
- [Social Learning](#)
- [Sociobiology](#)
- [Symbiotic Relationship](#)
- [Vigilance](#)

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## Social Organization

### ► Mustelid Communication

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## Social Ostracism

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### Definition

Social ostracism refers to being excluded from a group.

### Introduction

Social ostracism occurs in many species. Individuals who pose threats to a group are more likely to be ostracized. Social ostracism occurs by excluding, shunning, rejecting, ignoring, and threatening. Group members may sometimes physically assault or kill socially ostracized individuals (Goodall 1986; Lancaster 1986).

### Reasons for Social Ostracism

Individuals may be ostracized from a group or prevented from entering a group when resources

are scarce. Humans and chimpanzees reduce their group size to distribute adequate amounts of food to higher-ranking members (Benenson et al. 2008). Coalitions often ostracize and sometimes kill intruders to defend their territory (Goodall 1986; Lancaster 1986).

In several primates, individual members sometimes form coalitions and socially ostracize intruders or group members that threaten the members' social status and thereby their reproductive success. Higher-status males typically are more attractive to higher-quality females, but lower-status males may attempt to mate with these females. Male humans and other primates sometimes physically prevent lower-ranking males from mating with higher-quality females (Lancaster 1986). Higher-status males also may ostracize and otherwise exclude lower-status males from group activities in these circumstances. Among several primates, male coalitions sometimes ostracize overly aggressive males or problematic individuals who do not conform to group norms and thereby threaten group functioning (Benenson et al. 2008).

Higher-ranking females may ostracize or otherwise exclude from group activities lower-ranking females who display sexual interest in higher-ranking males (Benenson et al. 2008; Lancaster 1986). Females sometimes inflict physical harm on ostracized females but are more likely than males to ostracize other females by ignoring them, not cooperating with them, or failing to help them (Benenson et al. 2008; Wesselmann and Williams 2017).

## Negative Implications for Social Ostracism

Individuals who experience chronic ostracism – prolonged exclusion from a group – are at risk of social or physical death. Social death includes the onset of depression, anxiety, loneliness, helplessness, low self-esteem, physical health problems, and physical death (Goodall 1986; Wesselmann et al. 2012; Wrangham 2019). These negative consequences can include reduced reproductive success due to lowered fertility (White and McQuillan

2006). Regarding physical death, nonhuman animals are more likely to be killed by group members, whereas humans are more likely to commit suicide as a consequence of chronic ostracism. There is evidence that humans experience feelings of shame, embarrassment, guilt, and pain as a consequence of social ostracism; parallel feelings of distress are suspected but have not been confirmed in nonhuman animals (Wrangham 2019).

Ostracized individuals suffer costs associated with damaged social status, including reduced mating success. Higher social status predicts greater access to resources and greater mating success in humans and many other social species (Rueden and Jaeggi 2016). Thus, ostracized members not only suffer reproductive costs but also have less access to resources such as food. Individuals who develop a reputation for aggressiveness or who persistently fail to conform to group norms are more likely to be excluded from the group and, as a consequence, less likely to survive and reproduce (Wesselmann et al. 2012; Wrangham 2019).

## Tactics to Avoid Social Ostracism

Given the negative repercussions of social ostracism, individuals attempt to avoid ostracism or to gain re-inclusion into the group following ostracism through various tactics. Among humans and other species, including monkeys, wolves, birds, and other primates, individuals behave prosocially by offering parental care, cooperation, sharing, social teaching, and helping (Rault 2019; Wesselmann and Williams 2017). Prosocial behaviors benefit group members and thereby can decrease ostracism and increase the likelihood of re-inclusion in the group. Individuals also mimic other group member's behaviors, attempting to conform to group norms to avoid ostracism (Wesselmann et al. 2012).

## Conclusion

Individuals are likely to be ostracized from a group when they are an intruder, of lower status, when

there is a lack of resources, when they are perceived as a threat to other members' reproductive success, and when they persistently fail to conform to group norms. Social ostracism is associated with negative physical and psychological health, including distress and death. Individuals may behave prosocially to avoid or reduce ostracism or to regain group inclusion following ostracism.

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## Social Preening

- [Social Grooming](#)

## Social Relationships

- [Social Grooming](#)

## Sociality

- [Group Living](#)
- [Mustelid Communication](#)

## Socialization

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## Definition

Socialization is the process of acquiring social rules and adopting behavioral patterns applicable to an individual's social environment. Through the process, an animal develops its own species identity and personality. An animal needs to be socialized with members of its own species, but members of other species with which individual interacts influence its social development as well. Socialization starts in young animals, and it is the most effective in sensitive period before they reach maturity, but it is a lifelong process.

## Introduction

In the course of evolution, sociality has emerged as an advantage for certain species. Appearance of social life required certain behaviors by which functioning of a social group can be achieved. By living in diverse ecological conditions, inhabiting diverse ecological niches, certain animal species have developed different levels of sociality or different kinds of social organization, and therefore their processes of socialization may also differ. Hence, social animals form more or less

stable social groups where even several generations may live together, and cooperation and competition over resources happen over the course of time. Socialization is described even in social insects, such as ants and bees (Scott and Fuller 1965; Rittschof et al. 2015), but the process of socialization has been mostly researched in mammals and birds.

## Primary and Secondary Socialization

Social skills, crucial for surviving and reproduction, are something that animals acquire through learning over their whole life. However, the most important aspects of social life have to be obtained during sensitive periods in very young animals, when appropriate species-specific behaviors for adult animals develop (Murray et al. 2014). Firstly, primary socialization occurs, where emotional attachment is formed to members of a parent species or surrogates. This process takes place in very young animals, no matter if the animal is rewarded, punished, or treated indifferently by an individual or object of socialization. It ends with the development of fear response (Blackwell 2010; Scott and Fuller 1965). Primary socialization is followed by secondary socialization, when an individual is entering in new parts of social life and may engage in interactions with littermates or peers (Blackwell 2010; Scott 1962).

### Primary Socialization and Mother's Influence

The period of early socialization starts when the nervous system in a young animal is developed enough to receive information from the environment, i.e., when hearing, vision, and temperature regulation are stable. Consequently, young animals become sufficiently mobile and start to develop social relationships with other animals in their environment. The developmental timeframe for socialization in mammals and birds depends on how developed they are in the moment of birth or hatching, i.e., if they are precocial (able to walk briefly after birth or hatching) or altricial (born or hatched in immature state). Since precocial animals are more developed when they are born or hatched, their socialization may

start immediately, while in altricial species it is delayed since they develop more slowly. Therefore, precocial species tend to have earlier and shorter periods of socialization (Scott and Fuller 1965). No matter the developmental differences, altricial and precocial species are successful in maintaining complex social life (Scheiber et al. 2017).

Additionally, ungulate species, which are all precocial, are considered as the “hiders” and the “followers” with regard to the type of mother-infant relationship occurring after the postpartum period. In “hiders,” the mother leaves the infant hidden and joins her herd. She comes to the infant only for nursing two or three times per day, and therefore socialization in “hiders” may start when they join the mother’s herd. On the other hand, in “followers” mother and infant join her herd together, so socialization may start immediately (Lent 1974).

Dogs and cats, however, are examples of altricial species, and their socialization starts after the neonatal and transitional period – a period where neonatal behaviors change to be more like in adult animals (Scott and Fuller 1965). The socialization window in dogs (*Canis familiaris*) is between 19 days and 12 weeks and in cats (*Felis catus*) is between 3 and 9 weeks of age (Case 2010; Landsberg et al. 2003).

The connection that a young animal has with its mother can be especially important for the early socialization period. These relationship will often have lifelong influence because young animal learns mother’s social behavior (e.g., mares, *Equus caballus*, influence their foals’ behavior toward humans (Henry et al. 2005)) but also through epigenetics where the level of maternal care has consequences for a development of their offspring stress susceptibility (Champagne and Curley 2009) and cognitive development (Liu et al. 2000), which are both important for maintaining social lives. Mothers are often the first socialization partner in many species (e.g., sheep, *Ovis aries*, and goats, *Capra hircus* (Collias 1956); bottlenose dolphins, *Tursiops truncatus* (Mackey et al. 2014)). Therefore, in social mammals, socialization of the young is an important component of maternal care, and it is a

basis for normal behavioral development (Mills 2010; Scott and Fuller 1965).

Furthermore, a mother's social life can be crucial for the socialization pattern of their offspring in some species. For example, mother chimpanzees (*Pan troglodytes*) with female offspring tend to reduce association with others. However, lactating chimpanzee females remain together to enhance socialization opportunities for their immature male offspring, and they prefer to associate with other females who have similarly aged offspring. Mothers with sons spent significantly more time in groups containing males during the first 6 months, providing their young with important observational learning experiences and social exposure early in life to ensure sex-appropriate social development (Foerster et al. 2015; Murray et al. 2014). However, since male chimpanzees pose a danger for the offspring, mothers tend to keep their offspring closer when males are present in the group, and they are more attentive (Otalí and Gilchrist 2006).

A mother serves as a secure base for an infant when it starts to explore the environment and interact with other group members. This can be observed in primates, such as blue monkeys (*Cercopithecus mitis stuhlmanni*), even in society where the rate of in-group aggression is low, and large juvenile females regularly help with care of infants (Förster and Cords 2005).

For young wolves (*Canis lupus*), the socialization period starts when they are 20–24 days old, which corresponds to when they start to explore the entrance to the den. As they leave the den, they begin to socialize with other pack members. In this sensitive period of socialization, they are rather nonselective of which pack member they approach (Packard 2003).

### Secondary Socialization and Importance of Play Behavior

An important part of the ontogeny of social mammals is the establishment of social relationships with other members of their species, which is achieved by social play with littermates or peers. For species living in complex social systems with an extended juvenile period, play is an important factor in the young animal's socialization. In rats

(*Rattus norvegicus*), social play modifies the development of the brain, especially the prefrontal cortex, and this improves their social skills. Consequently, rats that play as juveniles are more socially competent as adults (Pellis et al. 2010, 2014).

By playing, young animals practice motor skills needed for success later in life, such as capturing prey and species-specific courtship behavior. Play can also allow individuals to evaluate their competence against peers and create social affiliations that can extend later in life. It is in this phase that species identity is formed because it is not strictly genetically determined (Blackwell 2010). In bottlenose dolphins, the first play partners for young animals are their mothers, and then later, other calves become the most common social play partner. The play with peers allows a young animal to develop its social skills more efficiently, as well as to adapt to novel situations, enhance motor skills, train for mature social interactions, and advance its cognitive abilities (Mackey et al. 2014).

In elephants (*Loxodonta* sp.), early socialization is with the mother, as well as allomothers (juvenile and adolescent females from the herd that assist in care and protection of calves). In adolescence, young male animals have a second phase of socialization when they leave the maternal herd and join older all-male groups. During this second phase, it is thought that the presence of older males facilitates normal social development of young males by reducing their aggressive behavior tendencies (Bradshaw et al. 2005). Namely, adolescent male African elephants need to be with older bulls to gain social and ecological knowledge from more experienced individuals, and that should enable them to become functional social members without posing a competitive threat. It may be considered that mature males are important in the stability of bull society, and their role may be similar to that of the matriarchs in the breeding herds (Evans and Harris 2008).

In some highly social birds, young animals can be left in crèches with siblings and offspring of other adults, as, for example, in spectacled parrotlet (*Forpus conspicillatus*) and pinyon jays



(*Gymnorhinus cyanocephalus*). Here young animals have the possibility to play, to learn to recognize other individuals, and to form social bonds (Wanker et al. 1996; Clayton and Emery 2007). Moreover, this social grouping allows animals to learn to recognize each other, since individual vocalizations contain “signatures” that are unique for certain individuals, just as facial recognition is for other species (Clayton and Emery 2007). Bird species with delayed reproduction and persistent association of juveniles and adults often have more complex social play (Diamond and Bond 2003).

### Socialization in Wild Species and Anthropogenic Influences

Socialization is accomplished over time by diverse social, biological, and maturational factors that an animal is exposed to. In nature, socialization occurs spontaneously. However, problems may happen with human involvement on several levels. In experimental settings, complete isolation of young animals results in socially incompetent individuals, with severe behavioral problems (Scott and Fuller 1965). Similarly, in many wild animal shelters, abandoned young animals are not raised by their parents in their natural social environment, but rather by humans. Furthermore, young animals in shelters may be exposed to other animal species, which may lead to unwanted socialization. Indeed, nature and nurture play a very important role in a young animal development, so obtaining social characteristics of another species, or becoming tolerant of their presence in the case of predators, may be a disadvantage in a natural environment. This can be seen in both birds and mammals. Consequently, it may render them incapable of life in nature.

Birdsong is a complex vocal behavior learned during early life, and in many species, young male songbirds have to learn their song from their fathers because it is species-specific. Male white-crowned sparrows (*Zonotrichia leucophrys*), for example, need to be exposed to the song during a critical period of 10–50 days of age for normal song development to occur (Marler 1970). If

young birds are exposed to another species or raised by humans in animal shelters, sometimes they learn the wrong species’ song, especially if it is a related species. Since song is important for territory protection and attraction of mates, this failure in socialization may cause vital problems in their later life (Spencer et al. 2007).

The lack of proper socialization may also represent a problem when birds from breeding programs need to be reintroduced into the wild. In the research conducted by Snyder et al. (1994), thick-billed parrots (*Rhynchopsitta pachyrhyncha*) were repopulated in Arizona, where they went extinct some time ago. Unfortunately, hand-reared birds from breeding programs had poor survival rates because of deficits in foraging and socialization, and their population was quickly devastated by predators. However, parent-reared captive bred birds were more successful upon release into the wild than hand-reared birds. The best survival rates had wild-caught adults that were translocated to Arizona.

The reintroduction of carnivores raised in captivity by humans has also been equally unsuccessful in some contexts. Captive-born carnivores were particularly susceptible to starvation, unsuccessful with predator/competitor avoidance, and more prone to disease in reintroduction programs (Jule et al. 2008). Similar to the parrots described above, wild-caught carnivores were significantly more likely to survive than captive-born carnivores.

For large herbivores that live in matriarchal societies, proper socialization is crucial for survival. Indeed, African elephant (*Loxodonta* sp.) families and social structure suffer from growing human populations that destroy their environment. Unfortunately, by current conservation methods, elephant social systems are not preserved since there are not enough older herd members in shelters. Additionally, in human selection of individuals that do not take in count their heritable sociability, and in the absence of normal socialization, behavioral problems may rise under these adverse conditions. Therefore, it becomes important to assess the kinds of social behavior that should be chosen through conservation programs, if we wish to maintain normal social

patterns in African elephant society (Bradshaw et al. 2005).

In human-made environments, with additional effort, successful rehabilitation and socialization of adult animals can sometimes be achieved, even when animals were traumatized as young. Indeed, chimpanzees (*Pan troglodytes*) used for entertainment and as pets were effectively socialized and mixed in a primate rescue and rehabilitation center (Llorente et al. 2015). Although these animals can be partially rehabilitated, they are typically not reintroduced to nature because their social skills will never be fully normalized.

Socialization is also important in the context of taming wild animals. Indeed, animals that become accustomed to humans, especially if they are hand reared, often display affiliative behaviors toward people. This can be a problem if they are to be released into the wild since they may seek human contact, which can be dangerous for both the animals and humans. However, the ability of individual animals to socialize with people may also be the basis for animal domestication as an evolutionary process (Blackwell 2010).

## How Domestication Influences Socialization

Domestication for life with humans places new requirements on a species. Most notable is that they need to be socialized not only with their own species but also with humans and other domestic animals they may live with. In domestic environments, young from different animal species socialize from early age on, playing together or even being raised by mothers from a different species. Here, socialization is very powerful because it can cause a domestic animal to alter its prey and mate selection (Landsberg et al. 2003; Blackwell 2010).

One distinguished characteristic is that in domesticated animals, the socialization period is prolonged. This was shown in the so-called silver fox (*Vulpes fulvus*) experiment, conducted by Belyaev and his colleagues (1985). They had two populations of foxes, one selected for tameness (experimental group), whereas the other

group did not undergo any selection (control group). The socialization period of pups started when they are 20–25 days old. In unselected foxes (control group), the main period for the formation of primary social bonds was between 30 and 35 days, when maximum exploration in a novel situation was shown. Furthermore, the period between 40 and 45 days was the upper boundary of primary socialization, when further exploration was prevented because pups started to show fear in response to novel stimuli. However, for the pups from the population of experimentally domesticated foxes (experimental group), the sensitive period of socialization was prolonged to over 60–65 days of age. Hence, in the selected foxes, the window of social bonding started 1–2 days earlier and ended about a month later relative to the unselected foxes.

During this extended socialization period, domestic animals should develop a sense of belonging to its own species – this is achieved through the relationship with its mother, siblings, and other members of social group (e.g., flock or herd). Adequate socialization should result in an appropriately functioning adult animal capable of interacting in a species-typical and predictable way with other members of its own species. In addition, every domestic animal needs to have a lot of pleasant experiences with humans, such as with owners, caregivers or handlers, veterinarians, but also other people that they may live with in the future. In a human environment, a barn or an apartment, an animal should feel calm and relaxed, which will ensure that every procedure that involves an animal is safe for the animal itself as well for humans (Broom and Fraser 2007).

In pigs (*Sus scrofa*), before farrowing, the sow seeks isolation from her social group to build a nest. The piglets stay there for about 1 or 2 weeks and then join their mother's social group. However, under farm conditions, piglets are often removed from the mother immediately, and therefore reunion of piglets happens later, once piglets are weaned, and consequently fights between unfamiliar piglets occur (Broom and Fraser 2007). Thus, Petersen et al. (1989) emphasized the importance of early socialization for piglets since their integration into social groups was more

peaceful when they had the opportunity to make early contact with piglets from other litters of the same age (2–7 weeks old). Therefore, properly timed socialization can be a major factor for the reduction of aggression between farm animals.

Dogs and cats are the most popular pet animals today. Unfortunately, these pets are sometimes raised in isolation from the outside world before they get vaccinated against most common infectious diseases (preventive healthcare), and because of this incomplete socialization, many behavioral problems arise (Landsberg et al. 2003). For both species, it is essential that the first phase of socialization is spent with their mothers and siblings to acquire basic social skills. After the puppy or the kitten comes to the home of the new owner, at the age of 8–10 weeks, they should continue socialization by getting to know others of their own species (different individuals, different breeds), humans, and other animals with whom they will spend the rest of their lives (Case 2010).

Dogs (*Canis familiaris*) are more closely attached to people than other animal species, and they develop a relationship, which in many ways, is similar to the human parent-child relationship. It is interesting that for dogs a human owner can represent a secure base, similar to the role mothers serve in other species. This is considered to be a consequence of the domestication process, where dogs retain their childlike qualities throughout their lives (Mariti et al. 2013).

Domestic cats (*Felis catus*) become more social in other cats' presence through the process of domestication. While most species of wild cats have only a brief period during kittenhood when they tolerate the presence of other individuals before they become more solitary adults, domesticated cats readily coexist with other cats, with animals of other species, and with humans (Thompson 2010). This exposure to other species during socialization may reduce predatory behaviors, such as seen by domestic cats not preying upon rats with which they have shared a household (Landsberg et al. 2003).

In domestic environment, it may happen that instead of mother, humans take care of a young animal, or even an animal of some other species may become a surrogate mother. If an animal is not nurtured by its mother or another female

of the same species, it is particularly important that in addition to the relationship with the human, it has pleasant experiences with members of its own species. In those animals that do not have such opportunities, social behavior may be directed more broadly toward humans and other species. This may raise some behavioral problems, e.g., the animal may have no interest for socializing with members of its own species or may court females of “wrong” species or develop an inappropriate relationship with members of the species that raised it (Broom and Fraser 2007; Scott 1962).

However, in our homes not only domesticated animal species are kept as companion animals but also wild animals (monkeys, squirrels, parrots, reptiles, insects, etc.). For taming the wild animal, extensive early socialization is extremely important. This socialization should be structured with respect to the species natural behavior and ecology. For example, in nature, psittacine birds live in complex social groups called flocks. Therefore, in human homes, if the bird is not provided with appropriate socialization opportunities, behavioral problems may occur. For example, when the birds reach sexual maturity, they may try to form a sexual bond with a human caregiver. Undesirable sexual behaviors comprise attempts to preen, allofeed (regurgitate), and copulate with the person. Further problematic behaviors that have been observed are masturbation, aggressive attempts to drive away other members of the family, and defense of the cage as a nesting site. Additionally, abnormal behaviors that indicate stress or anxiety can arise, including feather picking, self-mutilation, screaming, aggression, and biting, as well as phobias (Seibert 2006).

Finally, proper socialization to humans should be an important part of work with laboratory animals, since that may enable secure procedures for the animals, as well as humans. Proper socialization can also reduce stress in laboratory animals, which will result in more reliable experimental data being obtained, as was shown with rabbits (*Oryctolagus cuniculus*) (Swennes et al. 2011). Equally, unwanted behaviors can be prevented as in the example of later socialization of rhesus monkeys (*Macaca mulatta*) (Weed et al. 2003).

## Conclusion

During the process of socialization, an individual builds its relationship with its mother and learns to behave in a socially acceptable way among the members of its own species and those of other species when necessary. At a young age, animals start to learn the recognition of family members and allies, as well as individuals who may pose a threat for its existence. Experiences gathered during the early stages of life appear to be more important than those occurring later in life, indicating a sensitive period for socialization, and acquisition of appropriate social behavior in adulthood.

Later socialization or resocialization is at times possible and can be achieved through learning processes. However, if the animal was not previously socialized (i.e., kept in isolation or if subjected to some social trauma), this learning may be more difficult. Traumatized animals will be more difficult to socialize, and in some cases, at least for companion or zoo animals, medication may be needed to enable the process.

## Cross-References

- [Altricial](#)
- [Canine Cognition](#)
- [Canine Communication](#)
- [Cetacean Cognition](#)
- [Domestication](#)
- [Elephant Life History](#)
- [Feather-Plucking](#)
- [Feline Cognition](#)
- [Feline Communication](#)
- [Passerine Vocal Communication](#)
- [Pets](#)
- [Play Behavior](#)
- [Precocial](#)
- [Sensitive Periods](#)
- [Swine Life History](#)

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## Sociobiology

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## Introduction

Sociobiology was founded by E.O. Wilson (1975) in a massive book of the same title. However what Wilson really did was to give a name to a field that was already being developed in evolutionary biology, the study of the adaptive



value of social behavior. His contribution was important because he examined all aspects of social behavior then known with separate chapters on the behavior of birds, mammals, insects, and the like that were known in 1975 to live in groups and behave socially and whose behavior had been demonstrated to promote the reproductive or genetic success of individuals. The field would have probably remained uncontroversial were it not for the strong negative response of opponents led by some of Wilson's own colleagues at Harvard, namely, Stephen Jay Gould and Richard Lewontin. These opponents, the self-named Science for the People, produced strongly worded attacks on the book *Sociobiology* and its author claiming that sociobiology incorporated outdated and incorrect approaches to social behavior (Allen et al. 1975, 1976). The vehemence of the opposition to an evolutionary analysis of social behavior was encapsulated in the desire with which the opponents sought to link Wilson with the Nazis, eugenics, and other discredited persons and activities despite the academic nature of his synthesis which barely touched upon human behavior, the focus of the opposition. This attack led to physical assaults on Wilson including the pouring of cold water on his head by a member of the Science for the People at a conference in which Wilson attempted to speak.

Among the objections raised by the opponents of sociobiology, who include Michael Rose (1998), is that he wrote that we rarely if ever wish to raise our genetic success when behaving socially. This is true enough but our proximate (immediate) desires get us to behave in ways that influence the transmission of our genes to subsequent generations. In other words, our wishes and emotions that cause us to behave in certain ways have evolutionary (long-term) significance. And proximate physiological systems therefore can evolve as certain proximate mechanisms lead to greater adaptive results, i.e., gene propagation, than others with the logical conclusion that those social desires that are associated with superior reproductive or genetic success will become more and more common over time in populations of social species.

Likewise, the objections that sociobiologists, like Wilson, are genetic determinists who believe in a one-to-one relationship between genes and behaviors, a point repeatedly raised by Stephen Jay Gould (1976, 1996), are misguided. The proximate genetic aspects of development of a person are not the essence of sociobiology which instead deals primarily with the possible adaptive functions of social behavior. Notice that the previous sentence states "possible adaptive functions" since the goal of sociobiology is to test hypotheses on the genetic value of possible adaptations associated with social behavior. As T.H. Huxley (1910), the great defender of Darwinian theory, wrote, "There is a wonderful truth in [the] saying [that] next to being right in this world, the best of all things is to be clearly and definitely wrong, because you will come out somewhere."

This approach tells us that another chief criticism of sociobiology, particularly of humans, is without merit, namely, that evolutionary studies of social behavior contribute to social injustice and inequality which arise because of attempts to justify certain patterns of social behavior, a criticism raised by Science for the People (Allen et al. 1975, 1976). In reality, tests of hypotheses on the adaptive value of social behavior are designed to explain why we and other social organisms do what we do, not to justify that activity (Alcock 2001; Rubenstein and Alcock 2013), a point that is obvious when the social creature under examination is an insect rather than a human. No one argues that the stings of honey bees are justified by an analysis of the adaptive value of stinging by worker bees. The goal instead is to explain why workers sting and how this social behavior (colony members detect stinging by others and join the stingers) advances the success of the genes of the worker.

### **The Selfish Gene**

Another extremely important book, *The Selfish Gene*, was written by Richard Dawkins (1976) about the same time as *Sociobiology*. In it Dawkins explained why the arguments

of adaptationists (persons who rely on the theory of differential genetic success) were so useful for sociobiologists and behavioral ecologists, both of whom use Darwinian natural selection as the basis for their adaptationist hypotheses. Although Darwin was clueless about genetics, because Mendel's work was unknown to him and other biologists prior to the early 1900s, his insights in *On the Origin of Species* (Darwin 1859) in which he presented the theory of natural selection provide the foundation for all modern evolutionary behavioral work, a point that Dawkins explained clearly – despite the arguments that others raised against the book, most of which deal with the title of the book. Dawkins spends the bulk of the introduction to the third edition in a defense of this title, *The Selfish Gene*, which some people insisted upon interpreting as meaning that Dawkins was saying that genes were selfish in a proximate sense rather than selfish in an evolutionary sense. As Dawkins notes, genes can cooperate proximately (developmentally) if the result of their cooperation is the promulgation of those genes against alternate forms that differ from the more successful genes. In his book, Dawkins showed how the fundamentally Darwinian evolutionary selfishness of genes was the product of natural selection with genes selected (becoming more common) on the basis of their copying success. He explained that since only genes survive from generation to generation, genetic success was more important than that of the individual or species or group in which the genes reside. Awareness of the gene encourages us to understand why genes can cooperate in the building of cooperative individuals whose help given to others results in additional copies of the genes in question. In the course of *The Selfish Gene*, Dawkins highlights the work of George C. Williams and William D. Hamilton, both of whom used the ideas of Charles Darwin to set the stage for the focus on the gene, showing how individual survival machines worked to pass on their genes to future generations, and thereby determined which genes would live on and which would die out as a result of Darwinian selection.

## George C. Williams and the Essence of Sociobiology

G.C. Williams (1966) was the most important of these persons when it comes to sociobiology. His book, *Adaptation and Natural Selection*, made the case for individual selection (via the gene) as being far more significant than group- or species-level selection. He did so by contrasting the power of individual selection against that of group selection. He posed a thought question by asking his readers to consider what would happen if natural selection occurred and individuals sacrificed their reproductive success to benefit the group, an extremely widespread explanation for social behavior at the time, a point of view championed by V.C. Wynne-Edwards (1962). For example, territorial behavior was widely thought to evolve if non-territorial individuals promoted the survival of the species either because the non-territorial types were inferior or because breeding by these individuals would threaten the survival of the group through over-population. However, as Williams noted such a situation would be vulnerable to an invasion by genes that caused their owners to refuse to be non-territorial sacrificing themselves for the benefit of the group. If only territorial individuals passed on their genes to the next generation, in time there would be no non-territorial individuals possessing the genes for self-sacrificing non-territoriality. In other words, if one observed both territorial and non-territorial members of a given species, one had to think of a way in which the non-territorial individuals experienced genetic success, not a way in which the group benefited from the behavior of the non-territorial types. The hypothesis that non-territorial individuals sacrificed for the territorial members was a non-starter.

In every situation in which group selection à la Wynne-Edwards was used to promote the idea that individuals gave up reproductive chances to help others of their species to reproduce, Williams's explanation focused on the benefits to individuals to do what they did in order to secure genetic success. So, for example, if birds flew in large flocks to get information about the density of

competitors in an area, the group selectionist explanation was that some birds used this information to reproduce less in order to help the species to avoid over-population. Williams proposed that some birds used this information to avoid trying to reproduce at times and places that would almost certainly have resulted in reproductive failure by the birds in question. This hypothesis had the virtue of not arguing that some birds would give up reproduction (and thus genetic success) to assist others, a recipe for the disappearance of those genes that induced some birds to sacrifice for others, whereas if by giving up reproduction temporarily, those individuals had more surviving offspring in their lifetime than they would otherwise, the genes for using density information to regulate reproduction could spread through a population.

### **Male Lion Social Behavior: Coalitions of Unrelated Individuals**

Male lions often form groups that seek to take prides of females from other males, a social behavior that can be understood as way in which individual lions seek to pass on their genes. Although these groups are sometimes composed of relatives, a fact that makes groups of this sort understandable in a Hamiltonian sense (see below), sometimes the groups are made up of unrelated males. The question is how does one account for groups of non-relatives in Williams's terms? As it turns out, cooperation of the sort seen in lions can evolve by natural selection if it generates increased reproductive success for the cooperators even if some males reproduce less than others. Thus, if several unrelated males succeed in securing a pride, their reproductive success merely has to be greater than it would otherwise in order to support a hypothesis that explains their social behavior in terms of individual genetic success as opposed to group benefit selection. (Again there are logical reasons in favor of the individual selection hypothesis that makes this explanation worth considering, whereas the group selection alternative is untenable if the hypothesis requires that unrelated individuals

sacrifice their reproduction to benefit the group or species.) All the unrelated males stand to pass on some of their genes if through their cooperativeness they defeat another group of males, ousting them from a pride of adult females. Thus the individual selection hypothesis not only does not require that some male lions sacrifice their reproductive chances to help other males in the coalition, this explanation also generates predictions that can be checked, thereby testing the individual selection hypothesis. We can predict that when non-relatives join together, they will do so to take a pride from a smaller coalition of males. Moreover, those non-relatives that have no or little genetic success (i.e., if other males do most or all of the mating) and then those unrelated males that cooperate in securing a pride but have little reproductive success should weigh less than the dominant lions in the group. Males that weigh less than average are expected to be handicapped in the effort to secure a pride that will generally be held by groups of males favoring those that join others in defeating groups of rivals that control a pride. The point here is that the opportunity for some reproductive success (i.e., genetic success) is better than none. Single males that fail to secure a pride when up against groups are expected to have no reproductive success at all.

### **Male Lion Social Behavior: Coalitions of Related Individuals**

Male lions often form groups composed of relatives, and in this case there is yet another hypothesis that looks to the genes of the males in the coalition for an explanation for their social behavior. Relatives (brothers, half-brothers, and cousins) share genes in common as a result of having a shared ancestor. The reason why W.D. Hamilton (1964) is viewed as an admired and influential theorist in sociobiology has to do with his focus on shared genes that led him to point out that although reproduction enables an individual to transmit genes directly to the next generation, helping relatives reproduce can achieve the same end indirectly. Therefore if a

coalition of male lions is composed of relatives, even those individuals that have little or no genetic success via reproduction can pass on their genes indirectly – if they help their relatives reproduce successfully. Therefore one can predict that in coalitions of related males, reproduction by some individuals will be helped by the non-reproductive lions (primarily in the takeover of prides from other groups of males). In other words, some indirect genetic success is better than none, and no genetic success would be the typical fate of those solitary individuals that did not help related males to acquire prides of females.

After Hamilton's argument was published, it has become extremely important in accounting for many cases of social behavior in which the key prediction is that groups of cooperators will be composed of relatives (primarily close relatives with a high proportion of shared genes).

### **Acceptance of Genic vs Group Benefit Selection**

It is safe to say that the vast majority of sociobiologists and behavioral ecologists have accepted the views of Williams and Hamilton and rarely if ever bother to test illogical group selectionist hypotheses about the benefits of social behavior to groups or species as a whole. There are however several researchers who continue to try to argue that group selection is important to the evolutionary process rather than direct gene (personal reproduction) or indirect gene (help given relatives) selection. Among these theorists is E.O. Wilson who has abandoned his view that the vast majority of cases of social behavior can be explained in terms of direct or indirect gene transmission in favor of the position that group selection accounts for much of the social behavior of organisms. He appears to have been persuaded by David Sloan Wilson (not a relative of E.O. Wilson), a long-time advocate for group-level selection, to change his support for sociobiology (Wilson and Wilson 2007).

However, none of these advocates for group selection has had much success in converting

others to their viewpoint. For most sociobiologists the social behavior of individuals is to be investigated using the principles of Williams or Hamilton. This point can be made by showing how research on the adaptive value of animal social behavior has either examined the reproductive importance of the behavior to social individuals (with each individual produced by personal reproduction carrying half the genes of the reproducer) or how individuals help their relatives reproduce (and thereby secure genetic success in proportion to the relatedness of the individual that they help) as illustrated by male lion social behavior.

So, for example, both males and females form social units in many species. These were once interpreted as primarily cooperative, and of course there is much that is cooperative about male-female bonds. However, the aspect of pairing that reflects Williams's approach most clearly is research into conflicts between males and females, research by sociobiologists and behavioral ecologists (many sociobiologists prefer to be called behavioral ecologists thanks to the unhappy start of the field of sociobiology) that has exploded in the years since the publication of Williams's book. These conflicts can and do occur as individuals of both sexes try to leave the offspring in the care of the other member of the pair. Males are especially likely to abandon their progeny in many species in order to inseminate as many females as possible since male reproductive success is often a function of the number of mates a male has whereas female reproductive success is more often linked to the quality of the mate, rather than the number of sexual partners acquired. The rarity of monogamy by males speaks to this argument and to the value of Williams's position.

### **More Cases of the Utility of Individual Selection, Including More Examples of Sexual Conflict**

Likewise the existence of forced copulation in many animals including humans is clearly a function of the benefits to the male of forced



**Sociobiology, Fig. 1** A group of male bees (*Amegilla dawsoni*) surround a recently emerged virgin female with each male attempting to be the one that inseminates the female, an activity that endangers the female

copulation and the costs to the female that is subjected to forced copulation. For example, in observations of mating in Dawson's burrowing bee, *Amegilla dawsoni*, bundles of tussling males often form around a freshly emerged female, a receptive virgin female (Fig. 1). These mobs of males assemble because of the benefits to males in being the one male to copulate with a female but occasionally result in the decapitation of the female, a clear case of male-female conflict in this species caused by the attempt to inseminate the female.

In fact the resistance to mating exhibited by females of many species reduces the reproductive success of the rejected males and as such constitutes sexual conflict that arises because females are not equally receptive to all males in most cases. In addition, in species in which females eat males that approach them, we have further evidence of sexual conflict because it is rarely advantageous for a male animal to be consumed by a potential partner.

In insects females commonly exhibit an immune response that enables the females to avoid sexually transmitted diseases but that reduces the reproductive success of males if it kills some of their sperm. Evidence that such a response occurs in a cricket has been assembled by Fedorka and Zuk (2005) along with the finding that males attempt to suppress the immune response of females, further

evidence that sexual conflicts are widespread in insects.

The increase in attention given to cases of sexual conflict between potential members of social units is matched by an increase in research into how males insure that their inseminated sperm are actually used to fertilize the eggs of females. In some instances, females accept sperm from more than one sexual partner, and in these cases, males have been shown to behave in ways that increase the odds that their sperm are used to fertilize the eggs of their mates, an ability that was not explored prior to Williams's book, not even by Darwin as shown by Eberhard (2009). One such tactic is mate guarding by males designed to prevent multiple mating by a female partner that has accepted sperm from the mate-guarding male (Fig. 2). Sperm competition of this sort is now known to occur widely in the animal kingdom as is multiple mating (polyandry) by females, which promotes the evolution of sperm competition (a potential form of sexual conflict between the sexes).

Williams's argument also receives support from studies of many other elements of social behavior such as parental care of parasites by birds. Although some birds take care of parasitic species, an apparently maladaptive behavior, when work is done on the genetic benefits and genetic costs of doing so, one usually finds that the costs outweigh the benefits of ceasing to feed the parasitic offspring or abandoning the nest. These costs to reproductive success include the risk that a parasitic bird(s) might return to the nest of its host to destroy the eggs in the nest of the host (Soler et al. 1995).

## Acceptance of Indirect Selection

Although Williams caused most sociobiologists and behavioral ecologists to examine hypotheses on the reproductive value of social behaviors, often it is clear that the behavior is altruistic, that is, the behavior helps others at the cost of reducing the reproductive output of the helper. Under these conditions, an alternative solution to this puzzle is required that does not involve group benefits of some sort. Here Hamilton's approach has been



**Sociobiology, Fig. 2** A male damselfly (*Calopteryx maculata*) with the green abdomen guarding an egg-laying female using materials in his territory as an oviposition site



often used by showing the altruist is related to the individual he or she helps, thereby increasing the representation of the altruist's genes in the next generation. As documented already, this approach makes sense of the behavior of male lions, some of which form coalitions of relatives that are large enough to overcome the coalitions of other males that monopolize the sexual output of the pride of lionesses that they control. In order to use this approach however, one has to show that the loss of reproduction by the altruistic helper is exceeded by the gain in its genetic success as measured by the genes passed on as a result of the help. So, for example, an altruist that helps a brother produce two more offspring than he would otherwise have gains two times a half or 1 genetic unit since brothers are related by a half to the altruist and to their own offspring. If the cost of its helpful behavior is the loss of two offspring produced personally by the altruist, then the loss is two times a half or 1 genetic unit as well. In other words, in this case both altruism and personal reproduction are equally effective in passing on the genes of both types of behavior, indirectly and directly.

### Cases Demonstrating the Utility of Indirect Selection

Hamilton's approach has been widely adopted for lions and certain other mammals, those birds that nest in groups in which some individuals appear

to help others reproduce, and social insects where altruism by workers is widespread. A mammal in which helping by relatives has evolved is the naked mole-rat (Sherman et al. 1991). This odd hairless mammal lives in underground colonies in Africa with large numbers of altruistic worker mole-rats that help a single reproducing "queen" and a small number of males that sometimes pass on their genes by mating with the female in charge of the colony. The helpful altruists that dig tunnels through the soil and secure tuberous food for the queen and kings are all progeny of the reproductive members of the colony as expected by Hamiltonian researchers.

Cooperative breeding in birds is fairly common, especially in Australia where the phenomenon occurs often, particularly in honeyeaters (Fig. 3) and fairy wrens. The general rule is that certain of the offspring of 1 year help rear the progeny of the next year although in some cases of cooperative breeding in birds, some of the helpers are related to their parents and others are not. In those species in which some helpers are unrelated to the youngsters that they help feed and protect, the demonstration that these helpers are more likely to reproduce in future years than non-helpers supports the prediction that helpers secure future reproductive success that compensates them for their reduced reproduction during the time that they behave altruistically. The non-relatives not only go on to breed more often than non-helpers, they also help less than the related birds. In instances in which helpers are



**Sociobiology, Fig. 3** A yellow-fronted honeyeater, one of many cooperative breeding birds in Australia

relatives that behave altruistically to their parents and to their siblings, the loss of reproductive output in one season is offset by the increase in siblings whose 0.5 relatedness to the altruist compensates him or her for the loss in that year.

In any event, the prediction that follows from the Hamiltonian approach is that helpers that are related to the parents that they help must increase the number of siblings that are generated in the nest. This outcome is generally observed in cases in which the prediction has been examined. Thus in the yellow-fronted miner (an Australian honeyeater), it has been shown that nests with helpers are more productive than nests without helpers. The same applies to the noisy miner with the further findings that males are more likely to help than females (which are able to reproduce sooner than males) and the effort expended by related individuals is greater than that engaged in by non-relatives (Barati et al. 2018). In bell miners, males are also more likely to help than females, and furthermore, helper males are typically fathered by parent males that mate with a single female so that helpers are more closely related to the siblings they provision and protect than they would be if their fathers mated with several females (which would mean that the relatedness of offspring was diluted by the different genes present in the eggs of those females). These results support predictions that a Hamiltonian would make and thus provide support for the hypothesis that relatedness is the cause of much

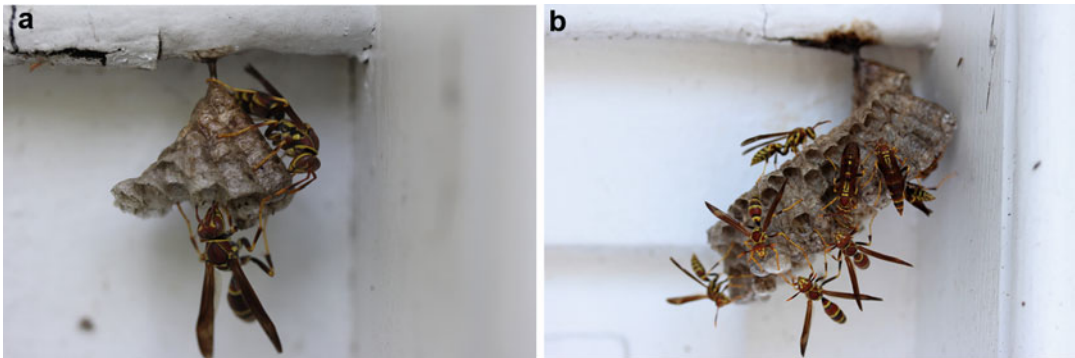
helping at the nest in birds. In the long-tailed tits of Europe, altruistic helpers focus on nestling relatives over 90% of the time showing the kind of preference that has been predicted by indirect selection proponents.

## Insect Sociality and Altruism

Thus in vertebrate mammals and birds, Hamilton's ideas can supply a solution for the puzzle caused by help given to some individuals by others. However, most of the altruistic mammals and birds go on to reproduce. Although in some insects helpers have the capacity to reproduce, in others some individuals spend their entire lives working for others and indeed have rudimentary reproductive organs so that they could not reproduce even if they tried to do so. Among the insects, altruists are especially well represented in the bees, wasps, and ants.

Paper wasp workers have the ability to lay eggs in the nest that they are caring for (and thereby secure direct personal reproduction). These *Polistes* wasps include the northern paper wasp, a common species in the eastern United States where porches are often used as nest site. Frequently sisters that can sting and sometimes drive away nest raiders such as birds and raccoons join forces to start a nest (Fig. 4) and thereby double the protective services available at a nest, which as it grows in size becomes a nursery for smaller female wasps that help protect and feed their siblings, many of which will emerge from the cells of the nest as worker females as well. Should the original founder disappear through death or predation, helpers can transform themselves into reproducers and secure the benefits of direct reproduction after having derived the genetic gains that come from assisting a mother queen wasp in reproducing future queens.

Eventually the nest is used to produce a group of reproductively active males that seek out adult females and inseminate them; these females spend the winter in a safe place, and if all goes well, they become the foundress females at nests that contain a new generation the following year, an annual cycle that is covered by Evans and Eberhard



**Sociobiology, Fig. 4** (a) A pair of *Polistes fuscatus* paper wasps that cooperate in the building of the nest and in the protection of larvae. These individuals are probably sisters with one female laying most or all of the eggs in the nest and the other helping her close relative. The

photograph was taken in early June. (b) By mid-August many worker females have emerged from the same nest but now larger that was founded by the two females much earlier in the year

(1970). If a worker female lays an egg in one of the brood cells of the nest, the reproductive female or a fellow worker will generally consume that egg, preventing the worker from reproducing, which it can do but is usually unable to do because of removal of its eggs from the nest. Indeed, the greater the genetic difference between a queen's sons and the sons of workers, the more likely the eggs of workers are to be destroyed by fellow nestmates in the wasps, bees, and ants. In other words, when worker offspring are less closely related to other workers than to the offspring of the reproductive individuals, the more likely their eggs are to be eaten by other workers and queens (Wenseleers and Ratnieks 2006).

More importantly, worker paper wasps are all female, instead of mostly male as they are in honeyeaters and other birds. One assumes that the prevalence of female workers in wasps, ants, and bees stems from the ability of females in these groups to sting, which can deter predators from assaulting the nest with its edible larvae.

By far the most well studied of Hymenoptera are the honey bees, *Apis mellifera*, whose queens lay thousands of eggs destined to become daughter workers that help the queen manage the colony, feed the brood, and sacrifice themselves in stinging vertebrates that would plunder the hives if not checked. (The worker bees commit suicide when stinging animals with flexible skin in which their stingers catch, pulling out the still functional

stinger and the internal organs of the worker). Since honey bees are the offspring of the queen and are related to any future queens, they can engage in helping behavior if their actions benefit the queen or a future queen (Seeley 1995). Half of the hive (largely female workers) will stay with a reproductive daughter of the queen when the queen leaves in a swarm to find a new nest. These workers clearly benefit the future queen, a sister of theirs, and so altruism can spread through the colony. The reduced ovaries of the worker females mean that they have little chance to reproduce personally so that there altruism can be adaptive.

## Haplo-diploid Sex Determination and Indirect Selection

William Hamilton also thought that the method of sex determination of ants, bees, and wasps (all of which are placed in the order Hymenoptera) could have something to do with the evolution of helping by relatives in these groups. In the Hymenoptera, including the honey bee, males are haploid (have only one set of chromosomes donated by the mother), and females are diploid (with two sets derived from both parents) unlike most vertebrates in which both sexes are diploid and differences in sex chromosomes are the basis for sexual differences between males and females

(although in some species of turtles and crocodilians egg temperature determines the sex of the individual). Nevertheless female hymenopterans are unusual in being able to lay unfertilized eggs that develop into haploid males, whereas only fertilized female queens can produce diploid daughters.

Hamilton noted that the daughters of female queen hymenopterans that had mated with only one male would all receive that male's haploid set of chromosomes plus half of the mother's diploid makeup. The half received from the mother could be the same for two daughters or completely different for these two daughters or somewhere in between the same and totally different. As a result, the average similarity between two daughters would be  $\frac{1}{2}$  (from the father if the mother hymenopteran mated with a single male) +  $\frac{1}{4}$  (the average from the mother's genes) or  $\frac{3}{4}$ , a figure that is higher than that for diploid-diploid organisms where on average two offspring, whether daughters or sons, would have inherited half their genes in common from both parents. (See Rubenstein and Alcock for additional information on the significance of haplo-diploid sex determination.) If daughter workers possess  $\frac{3}{4}$  of the genes that reproductive females have, then helping future queens could be very adaptive

(genetically speaking) for sterile or male-producing wasps, bees, or ants. The same logic says that worker hymenopterans should make three times as many would-be queens as would-be kings, a prediction that has been found to be generally correct. Hamilton noted that in many Hymenoptera females do mate with just one male and that in these species female workers do tend to help reproductively competent sisters, as predicted, which supports the sex determination hypothesis for female altruism in this group of insects.

Hamilton understood, however, that diplo-diploid sex determination occurred in the termites, a group in which large numbers of altruists work together to build their often spectacular nests (Fig. 5). Others have taken this to mean that indirect selection was not necessary to produce helping behavior of the sort seen in wasps, bees, and ants. Still other observers have pointed out that the existence of termites does not mean that altruistic helping behavior depends on the haplo-diploid hypothesis. Instead altruism among relatives is common in both the Hymenoptera and the termites, suggesting that the benefits of the behavior, provided it is directed at relatives, need not be very great for the behavior to evolve. A net benefit is all the more likely for many social insects

**Sociobiology, Fig. 5** The huge mud nests built by workers of Australian termites showing that cooperation can occur among male and female insects whose sex determination is diplo-diploid unlike that of the bees, wasps, and ants





because the probability of direct reproductive success is so low for workers of this group as in the honey bee whose workers have very small ovaries and cannot reproduce sexually.

### Other Examples of the Utility of Indirect Selection as Explanations for Altruism

Research on bacteria has shown that individuals can recognize one another and behave positively toward those that are similar genetically unless there is competition for limited resources. Because bacteria often form colonies or clones of genetically identical individuals, altruism that costs the donor bacteria can spread if it benefits the recipients (provided that the recipients are closely related to the altruists as they would be in a clone). The release of a substance from the altruists that helps the receiver bacteria is the sort of behavior that could evolve by indirect selection. In fact, cooperation occurs not only among bacteria but also in a host of other situations including cooperation among organelles within an individual and the cooperation exhibited by different cells in the building of an individual. In many cases in which the organelles and cells are in the same body and have the same genes, the cooperation that exists between them represents indirect selection at work (West et al. 2007).

However, not all cases of altruism have a straightforward explanation. Thus, when starving slime molds cells come together in order to produce a stalk on which reproductive spores are situated, cooperation occurs in the growth of a stalk that does not participate in the production of spores, although the height of the stalk can influence the dispersal of the spores. When all this happens with genetically identical cells, the growth of a stalk can be explained as the result of altruism by cells that are genetically identical to the cells that will form the reproductive units of the slime mold. But when you artificially mix two clones, as sometimes occurs in nature, the two clones often contribute cells unequally to the non-reproductive stalk so that if 50% of the mixture is of clone A, the stalk may be made up of less than 50% of clone A cells. In cases in

which the stalk is largely composed of clone B cells, this suggests that clone A is exploiting clone B for its reproductive purposes (Strassmann et al. 2000). Thus the social behavior of clones of slime molds indicates that both direct and indirect selection are probably at work in determining the outcome of the stalk construction and the development of the spores, but the issue has yet to be fully resolved. When the issue of stalk formation is completely solved, Williams's and Hamilton's principles of genic selection will almost certainly be used by researchers studying the social behavior of slime molds.

### Conclusion

Despite the controversies associated with the early stages of sociobiology, the field has been producing ever more studies over the last 45 years, and it seems certain that it will flourish in the future. The work of G.C. Williams in showing that Darwinian theory is best used to develop and test hypotheses on how the social behavior of individuals enhances the reproductive success of individuals, and not the survival of social groups or species, has been critical in establishing the utility of sociobiology. In addition, the insights of W.D. Hamilton in demonstrating that individuals can propagate their genes indirectly, especially by helping relatives reproduce, have shown that genic selection is the key to understanding the evolution of social behavior of individuals whether mammals, birds, insects, or even bacteria. Together the two approaches have provided sociobiological researchers with two essential tools to explain why in evolutionary terms organisms have hit upon social life as a means to pass on their genes to future generations and so influence the evolution of social behavior.

### Cross-References

- ▶ [Altruism](#)
- ▶ [Cooperation](#)
- ▶ [Cooperative Breeding](#)
- ▶ [E.O. Wilson](#)



- ▶ [Evolution](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Genes](#)
- ▶ [Mating](#)
- ▶ [Natural Selection](#)
- ▶ [Napoleon Chagnon](#)
- ▶ [Sperm Competition](#)
- ▶ [Ultimate Causation](#)

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## Sociodramatic Play

- ▶ [Pretend Play](#)

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## Sociosexual Behavior

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## Synonyms

[Animal sexual behavior](#); [Courtship behaviors](#);  
[Sexually dimorphic behavior](#)

## Definition

The term sociosexual behavior refers to behaviors that surround reproduction but are not directly related to copulation.

## Introduction

Sexual reproduction, or copulation, is nearly always preceded, and occasionally followed, by multiple forms of sociosexual behavior, which vary among species, within the same species,

and between sexes. Many sociosexual behaviors in the animal kingdom, through highly varied mechanisms among species, serve to increase the likelihood that copulation will take place with a desired mate. For example, in some species (e.g., gorillas, sea lions, and many arthropods), males engage in intense physical competitions with conspecifics for mates or territory where the winners exclude competitors, whereas in other species (e.g., birds of paradise), males will put on elaborate displays of physical beauty or behavioral prowess to attract a choosy female. The very fact that sociosexual behavior gives rise to perceivable differences in mates on the basis of genetic quality beautifully illustrates how sexual selection operates.

The evolution of sociosexual behavior tends to look remarkably different from species-to-species. However, a few generalizing hypotheses survive scrutiny when examined in the animal kingdom. For example, Trivers' Parental Investment Hypothesis (1972) predicts that the sex that invests more in the offspring (usually the female in mammals) will be choosier in selecting their mates. In species where this prediction holds true, it is expected that the sociosexual behavior from males will involve displays of fitness and mate quality, whereas the sociosexual behavior of females will be characterized by mechanisms for assessing these males with extreme care. To illustrate, the male golden-collared manakin (*Manacus vitellinus*) is a neotropical bird that will court females by jumping between branches and simultaneously "snapping" their wings together, hopping back-and-forth until they are deemed fit or unfit by a scrupulous female (Chapman 1935). The male of this species performs an elaborate and energetically costly display in order to convince a female that he has sufficient genetic quality with which to endow her offspring (Barske et al. 2011).

In a great number of species, however, females do not play a passive role in reproduction. Frank Beach (1976) described three aspects of sexual behavior in female mammals, attractivity, proceptivity, and receptivity, that can help us understand the conditions in which active female sociosexual behavior will arise. Attractivity refers

to the value of the stimulus that a female provides a male; proceptivity refers to the extent to which a female initiates copulation; receptivity refers to the response to male sexual initiation. Using this framework, it is easy to understand how female sociosexual behavior allows both choosiness and sexual solicitation. To illustrate, take the simple sociosexual behavior of female rats, known as lordosis. Lordosis refers to the posture a female rat adopts in which the back is arched and the genitals are presented to a male suitor and can indicate both sexual receptivity and proceptivity. A female rat that exhibits this behavior exercises female choice in that she may or may not present to a male rat. She can also advertise her own proceptivity by signaling to the male that she is ready to mate. Even this simple behavior exemplifies how sociosexuality increases the likelihood of copulation but with a particular desired mate. Again, in this view, sociosexual behavior acts as a major facilitator to differential reproductive success within a species.

Sociosexual behaviors do more than simply increase the likelihood that reproduction will occur with a desired mate. They also serve to increase future mating opportunities, to demonstrate dominance, and even to strengthen bonds (Paciulli and Emer 2018). In fact, some believe that strong pair bonds are formed and strengthened when evolved psychological mechanisms involved in social attachment are expressed during sociosexual interactions (reviewed in Johnson and Young 2015). That is to say, sociosexual behaviors such as touching, sniffing, and grooming in nonhuman primates serve to promote relationships, as well as to indicate sexual interest.

Sociosexual behaviors are often regulated by hormones and vice versa. Differences in hormones can give rise to differences in the frequency, intensity, and quality of sociosexual behaviors; therefore, hormones and behaviors give rise to differential reproductive success, a key requirement to the process of evolution. In some species, hormones are extremely influential to a specific sociosexual behaviors. For example, a Japanese quail (*Coturnix japonica*) that has been castrated (i.e., testes are removed, and testosterone production is eliminated) will exhibit hardly

any strutting or crowing behaviors that are critical for attracting and courting females. Even some sociosexual behaviors within mating systems, like monogamy, can be facilitated by hormones. For instance, in common marmosets (*Callithrix jacchus*), a primate that forms significantly strong pair bonds, the neurohormone oxytocin seems to reduce the likelihood of sociosexual behaviors that promote infidelity, such as sexual solicitation of strangers when the pair-bonded partner is not present (Cavanaugh et al. 2014); thus, oxytocin can keep marmosets from cheating on their partners.

Moreover, hormones can help explain the timing and intensity of sociosexual behaviors. In fact, female sociosexual behaviors in most mammalian species are intensified near ovulation when estrogen levels are high, relative to progesterin levels: a behavioral and physiological shift known as estrus. Bonsall et al. (1978) found that female rhesus macaques (*Macaca mulatta*) with high estrogen levels were more attractive, proceptive, and receptive than females with lower estrogen levels. Thus, female sociosexual behaviors are dependent not only on the presence of desired mates but also on their own likelihood of conception. In other words, why expend energy to produce sociosexual behaviors when they are unlikely to lead to offspring?

Hormones influence the sociosexual behaviors involved in male-male competition as well. Testosterone influences aggression that surrounds reproduction. Wingfield et al. (1990) proposed the challenge hypothesis, which states that testosterone increases when competing for mates and decreases when caring for offspring. This means that testosterone, and analogous androgens in other taxa, might mediate a male organism's allocation of energy toward different fitness efforts. Overall, sociosexual behaviors have deep evolutionary roots that are evident in the physiology of organisms that display them, and these evolved behaviors act to increase reproductive success, strengthen bonds, claim territory, and much more.

It should be briefly noted that the term *sociosexuality* holds a different meaning in research regarding humans. In human research,

sociosexual behavior refers to sexual behaviors that occur outside of a relationship, including sex itself. In fact, someone with high sociosexual *orientation* is considered to have a high propensity toward short-term mating experiences, or “casual” sex (Penke and Asendorpf 2008). Due to logic following parental investment theory, casual sex is considered an evolutionarily relevant mating strategy for males because they are not constrained to the lengthy period of gestation and increased metabolic requirements that apply to females and can therefore afford to be highly sociosexual and forego long-term relationships.

In summary, sociosexual behaviors are ubiquitous in sexually reproducing species. The amazing number of sociosexual behaviors and their numerous adaptive purposes are proof that evolution by sexual selection has the potential to do something as simple as join two gametes together in a seemingly infinite number of ways. The fact that sociosexual behaviors can be performed better or worse compared to conspecifics provides a strong theoretical framework from which to argue that each of these behaviors was shaped by the success of the organisms that first exhibited them.

## Cross-References

- ▶ [Adaptedness of Behavior](#)
- ▶ [Estrogen](#)
- ▶ [Evolution](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Female Choice](#)
- ▶ [Hormones and Behavior](#)
- ▶ [Intersexual Selection](#)
- ▶ [Mating](#)
- ▶ [Mating Effort](#)
- ▶ [Oxytocin](#)
- ▶ [Progesterone](#)
- ▶ [Reproductive Fitness](#)
- ▶ [Robert Trivers](#)
- ▶ [Sexual Selection](#)
- ▶ [Sociobiology](#)
- ▶ [Species-Specific Behavior](#)
- ▶ [Testosterone](#)

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## Somatic Cell Division

### ► Mitosis

## Somatic Cells

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## Definition

Any cell in an organism that is not a reproductive cell.

## Introduction

Somatic cells are the cells of an organism that are not germ or stem cells. Somatic cells, germ cells, and stem cells have the same number of chromosomes. Somatic cells use mitosis as a method of cell division, while germ cells produce gametes after meiosis, usually in specialized reproductive structures or organs (Becker et al. 2003). Somatic cells are differentiated, having a specialized cell type, unlike stem cells.

## Follicle Cells

Follicle cells are a specialized type of somatic cells that are closely associated with germ cells. These cells are arranged as an epithelial layer around an oocyte and provide the oocyte with precursors for the macromolecules oocytes need to develop into an egg (Alberts et al. 2002).

## Gene Imprinting and X-Inactivation

In female mammals, one of the two X chromosomes is inactive in the somatic cells, known as X-inactivation. X-inactivation helps to regulate gene dosage, ensuring that gene derived products, such as proteins, are produced at the same rate in male and female offspring (Alberts et al. 2002). X-inactivation is achieved through gene imprinting.

Gene imprinting via DNA methylation during meiosis enables somatic cells with the same alleles to have different phenotypes in different individuals. The same allele of one gene in

different gametes is methylated differentially during meiosis, resulting in offspring with the same genotype but different phenotypes. DNA methylation can either turn a gene off or on in the individual's somatic cells (Alberts et al. 2002). Additional gene silencing via DNA methylation or other epigenetic mechanisms can also occur throughout development as somatic cells differentiate into different cell types.

### Somatic Doubling

Irregularities during mitosis in somatic cells can cause a numerical increase in the whole set of chromosomes within an individual, causing polyploidy. Polyploidy is when an individual animal has three or more sets of chromosomes instead of the usual two for that organism. If this occurs early in development or in somatic cells that give rise of reproductive cells, a polyploid individual can result (Losos et al. 2017).

### Mutations in Somatic Cells

Somatic cells accumulate variation throughout the life of an organism, but only variation in the germ line is inherited by offspring in eukaryotes. Mutations in somatic cells are not hereditary. However, mutations in somatic cells can have a deleterious effect on the entire organism. In mammals, cancer results from mutations in somatic cells. Often cancer occurs when a somatic cell line gains short-term advantages in growth and replication, to the detriment of the rest of the organism (Losos et al. 2017). Human somatic cells are deficient in telomerase, which causes chromosomal telomeres to shorten with each cell division (Alberts et al. 2002). This mechanism may help prevent runaway cell division that has the potential to lead to cancer.

### Induced Somatic Recombination

Induced somatic recombination is a technique used in developmental biology to analyze the function of different genes throughout development. This method allows mutations in groups of cells to be generated at a chosen time in order to

examine the effect of specific genotypes on development (Alberts et al. 2002).

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## Somatic Chromosome

- [Autosome](#)

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## Song Alternating

- [Countersinging](#)

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## Song Bird Locomotion

- [Passerine Locomotion](#)

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## Song Learning in Songbirds

- [Songbird Learning](#)

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## Song Overlapping

- [Countersinging](#)



## Songbird Duets

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### Definition

Duets are acoustic signals that occur when two individuals produce sound in temporal coordination with one another.

### What a Duet Is, and What It Is Not

Most songbird duets are produced by mated pairs, but there are exceptions (e.g., parent-offspring duets). Temporally coordinated vocal exchanges between competitors, such as counter-singing between neighbors, are not called duets. Duets can be contrasted with “solo” songs, which are produced by a single animal. Acoustic displays involving three or more animals are termed “choruses.” Choruses and mutual displays in non-acoustic modalities (e.g., dances) often resemble duets in both structure and function, but neither topic will be covered here.

### Research on Duetting in Songbirds

Duetting can be very conspicuous, so it is likely that people have been aware of it since prehistory. Scientific research on duetting began in the middle of the twentieth century. The period from the 1960s through the 1990s saw a steady trickle of duetting research, but it was not until the 2000s that duetting became a significant subdiscipline within birdsong research.

Most early research on songbird duets focused on structure and function (Hall 2009). Since the turn of the millennium, some functional hypotheses have garnered strong support while others

have fallen by the wayside. In the same time period, researchers have begun to elucidate the behaviors that structure duets, their ontogeny, and the evolution of duetting. As of this writing, research on the physiological and genetic mechanisms of duet singing remains sparse.

Both observational and experimental techniques have proven useful in duetting research. Observational studies describe duet structure, compare initiation and answering behavior over time, space, and singer class (e.g., sex, age), correlate duetting behaviors with other behaviors and contexts, apply the comparative method to answer questions about duet evolution, and analyze anatomy. Experimental studies include a variety of sound playback protocols (Douglas and Mennill 2010), mate removals and exchanges (Levin 1996), and physiological studies (Fortune et al. 2011).

### Description

A duet occurs when one animal (the initiator) produces an acoustic signal, and another (the answerer or responder) rapidly responds with an acoustic signal of its own. The proportion of the mate’s vocalizations that a bird answers is called the “answer rate.” After the first answer, one or both animals may continue answering to prolong a duet. The term “antiphonal” describes duets in which partners alternate phrases. The physical distance between duetting partners ranges from immediate proximity to the length of the territory.

### Timing

Whenever two birds are singing, some degree of temporal coordination can occur by chance. Randomization procedures can test whether the observed level of temporal coordination exceeds chance expectations (Masco et al. 2016). In many species, however, the partners’ phrases are so tightly coordinated that duets can be unambiguously identified without the need for statistical analysis. Initiation and answering rates vary

between sexes and over the breeding cycle. Answers may temporally overlap the partner's previous signal, or they may follow it. Temporal coordination is typically measured as variation in the relative timing of the partners' songs, with high variation corresponding to low coordination. In species that rapidly alternate duet phrases, the duration of silent gaps and overlapping phrases are considered measures of temporal coordination. Mates can improve their temporal coordination over the course of the pair bond (Rivera-Cáceres et al. 2016).

### Structure

In addition to temporal coordination, the contributions of partners are often also structurally coordinated. The vocal units that each individual contributes to a duet are called phrases, motifs, songs, or syllables (the nomenclature is not yet standardized). In many species, either sex can initiate a duet, but in others, males initiate all duets (Rogers 2005). A duet may comprise as few as two phrases, but many species sing longer duets. For example, white-crested laughing thrushes (*Garrulax leucolophus*) often sing duets with 20 or more phrases (Souček and Vencel 1975). Duet phrases are often identical to solo songs, but some songbirds produce duet phrases that are rarely or never sung as solos, and some contribute calls, rather than songs, to duets (Hall 2009). If both duetting partners sing repertoires of phrases, they typically combine phrases nonrandomly to form duets (Logue 2006). Thus, certain phrases from one partner tend to be combined with certain phrases from the other. In some species, the strength of the association between partners' phrase-types increases over the duration of the pair bond (Rivera-Cáceres et al. 2016).

### Visual Elements

Multimodal duets, combining visual and acoustic elements, seem to be more common in species in which partners are in visual contact when they duet. Visual elements, such as wing displays, may be temporally coordinated with duet phrases (Rek and Magrath 2016).

## Mechanisms

### Behavioral Mechanisms

The structure of a duet emerges from the rules that govern the singers' behavior. These rules can be studied observationally and with partner exchanges and experiments in which animals answer recorded stimuli. The timing of a duet phrase can be influenced by both the focal individual's own internal rhythm and the timing of the partner's previous phrase (Logue et al. 2008). There are similarities between the rules that govern the timing of duet phrases and the turn-taking rules that govern conversation in human beings (Ghazanfar and Takahashi 2014). Phrase choice can be influenced by both the focal bird's own previous phrase and by its partner's previous phrase. The set of rules that links the phrase-types a bird hears to the phrase-types it sings in response is called a "duet code" (Logue 2006).

### Physiological Mechanisms

Little is known about the physiological mechanisms that underlie duetting behavior. Variation in female song rates is more closely linked to variation in the aggression-linked hormone testosterone than it is to the reproduction-linked hormones estrogen and luteinizing hormone (Schwabl and Sonnenschein 1992). In plain-tailed wrens (*Pheugopedius euophrys*), whole duets are more neurologically salient than are solo songs (Fortune et al. 2011). The endocrine and neurological bases of duet song are promising areas for future research.

## Development

Songbirds learn the structural details of their songs. Therefore, species that use songs as duet phrases learn their duet phrases. There is now fairly strong evidence that some duetting species also learn temporal coordination and duet codes (Rivera-Cáceres et al. 2016). Further work is needed to clarify what is learned in early life and what is learned over the course of the pair bond.

## Functions

It is common for both members of a mated pair of songbirds to vocalize independently (Langmore 1998). Therefore, functional hypotheses about duetting must explain why partners temporally coordinate their vocalizations (i.e., why they answer their partners), rather than simply explaining why both partners vocalize (Hall 2009). Adaptive explanations for duetting behavior are often divided into “cooperative” and “conflict-based” hypotheses. Duet partners may reap different fitness consequences from participating in a duet, or even suffer costs as a consequence of their partner’s duetting behavior. For this reason, the functions of duetting behavior are usually best studied at the individual level (Hall 2009; Logue and Krupp 2016). Both duet participants and nonparticipants may perceive and respond to duets, so the possible functions of duet participation include both within-pair communication and extra-pair communication.

### Cooperative Hypotheses

#### Cooperative Territory Defense

In many species, duet participation functions to defend the mates’ shared territory. In this scenario, song answering tends to benefit both partners, even though the costs and benefits of territory defense may be asymmetrical. Evidence that duetting mediates cooperative territory defense includes (1) elevated answering rates during territorial encounters, (2) physical coordination between pair members during territory defense, (3) lower sex-specificity in territory defense among duetting species than nonduetting species, and (4) an evolutionary association between duetting and stable pair bonds (Benedict 2007; Hall 2009; Logue and Hall 2014; Tobias et al. 2016). With respect to their function in cooperative territory defense, duets are functionally similar to other collective acoustic signaling behaviors, such as roaring in lions (McComb et al. 1994).

#### Spatial Localization

Tropical wrens use duet contributions to acoustically locate their partners in their forest habitat

(Logue 2007; Mennill and Vehrencamp 2008). The bird that initiates the duet tends to move toward the bird that answered, suggesting that initiation functions to solicit an answer, and answering facilitates localization. The phylogenetic extent of this function is not known, but it stands to reason that spatial localization is not an important function of duet participation in species that are in visual contact when they duet. The localization function of duetting alone cannot explain why duets have evolved to high levels of complexity and temporal coordination in some species (Hall 2009).

#### Pair Bonding and Reproductive Synchrony

There is little empirical support for the ideas that duetting strengthens the pair bond or helps mates synchronize their reproductive efforts (Hall 2009). A notable exception is zebra finch (*Taeniopygia guttata*) duets, which are too quiet to serve as resource defense signals, but may permit individual recognition and the coordination of reproductive behavior (Elie et al. 2010).

### Conflict-Based Hypotheses

#### Mate Guarding

When a bird answers its mate, the answer may repel same-sex rivals who would otherwise attempt to pair with the mate. It has proven difficult to test predictions of this hypothesis that are not also predictions of the territory defense hypothesis (Hall 2009). According to both hypotheses, song answering should repel (potential) intruders. The distinction between the two hypotheses concerns the consequences of failing to answer. If failure to answer increases the probability of territory loss, answering functions for territory defense. If it increases the probability of mate loss, answering functions of mate guarding. If failure to answer increases the probability of both mate loss and territory loss, both hypotheses would be supported. The notion that mate guarding is a conflict-based hypothesis rests on the assumption that the answered bird would benefit from switching mates. If that is not true, mate guarding could be considered cooperative,

as described by the “pair-bond maintenance” hypothesis of duet function.

The best evidence for a mate guarding function of duet participation in a songbird comes from the eastern whipbird (*Psophodes olivaceus*). Females of that species compete for access to territorial males and answer at elevated rates when threatened by other females (Rogers et al. 2006).

#### Paternity Guarding

According to the paternity guarding hypothesis, male answers repel male rivals who would otherwise attempt to copulate with the answerer’s mate. Contrary to a key prediction of this hypothesis, most studies have not found increased male answer rates during the mate’s fertile period (Hall 2009).

#### The Functions of Structural Coordination and Fine-Scale Temporal Coordination

Elaborations on simple song answering, like adherence to duet codes and fine-scale temporal coordination, are generally assumed to have functional significance. Adherence to a duet code has been proposed to signal pair bond strength or duration, indicate attentiveness to the mate, improve fine-scale temporal coordination between duetting partners, and serve as a system of passwords for individual recognition (Hall 2009). None of these hypotheses have been tested directly, but the finding that code adherence can improve over the course of the pair bond lends credence to the idea that it signals pair bond duration (Hall and Magrath 2007; Rivera-Cáceres et al. 2016).

The main functional hypotheses for fine-scale temporal coordination are that it (1) signals pair bond strength or duration and (2) indicates attentiveness to the mate. The first hypothesis is supported by studies showing improved coordination over the course of the pair bond and differential responses to playback of coordinated versus uncoordinated duets in some (but not all) species (Hall and Magrath 2007; Kovach et al. 2014; Rivera-Cáceres et al. 2016). The attentiveness hypothesis has not been tested.

#### Evolution

Many non-oscine birds duet, as do some anurans (frogs and toads), insects, and mammals (especially primates). Among songbirds, duetting is associated with tropical and southern hemisphere breeding, the absence of migration, and long term pair-bonds. Breeding latitude and migration appear to influence the stability of pair-bonds, which directly influences duet evolution (Tobias et al. 2016). Duetting is widespread in the songbirds, having evolved several times. It exhibits phylogenetic signal, so certain lineages are rich in duetting species, whereas others are depauperate (Logue and Hall 2014). Duet structure varies among clades of duetting wrens, but the degree to which this is true of other duetting groups remains an open question (Mann et al. 2009).

The total diversity of duetting songbirds is estimated at 15.6% of species and 43.8% of families (Logue and Hall 2014). Those percentages project to approximately 700 species in 30 families. Songbird families that are known to include multiple duetting species include the babblers (Timaliidae), bushshrikes (Malaconotidae), cisticolas (Cisticolidae), New World blackbirds (Icteridae), honeyeaters (Meliphagidae), New World sparrows and allies (Emberizidae), Old World warblers (Sylviidae), shrikes (Laniidae), starlings (Sturnidae), tanagers (Thraupidae), vangas (Vangidae), weavers (Ploceidae), and wrens (Troglodytidae).

#### Conclusion

Vocal duetting is widespread in songbirds. It is also diverse, with structures that range from simple call-and-response to long and complex phrase sequences. Duetting behavior serves multiple adaptive functions within and between species, but cooperative territory defense is an important function in most species that have been tested. Recent years have seen significant advances in research on the diversity, function, and evolution of duetting, as well as the behaviors that structure duets. Research on the genetic, neural, and

endocrine mechanisms of duetting, however, is still in its infancy.

Knowledge about duetting has at least two important implications outside of the field of animal communication. First, song answering is a model cooperative behavior that can be used to address hypotheses about the plasticity and evolution of cooperation in general. Second, duetting is the best animal model of complex vocal interaction. As such, duetting research has the potential to improve understanding of the behaviors and physiological mechanisms that underlie vocal interaction. Advances in the field could have implications for the study of human conversation, the development of artificial communication systems, and the treatment of pathologies that affect communication.

## Cross-References

- Auditory Signals
- Communication
- Countersinging
- Cultural Transmission
- Passerine Vocal Communication
- Songbird Learning
- Syntax

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## Songbird Learning

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### Synonyms

[Song learning in songbirds](#)

### Definition

Songbirds belong to suborder Passeri (or Oscines), in the order Passeriformes (perching birds). Members of this group learn the structural details of their songs by listening to the songs of conspecifics.

### Introduction

Vocal learning describes the process of learning to produce vocal signals by listening to similar vocalizations. Animals that exhibit vocal learning

include humans, bats, whales and dolphins, elephants, and birds. Among the birds, there are three groups of vocal learners: parrots, hummingbirds, and songbirds. Songbirds are by far the most diverse and best-studied group of vocal learning birds. For centuries, humans have taken advantage of songbirds' remarkable capacity for vocal learning by training species such as canaries and nightingales.

All bird vocalizations are classified as either calls or songs. In general, songs are more elaborate and, in the case of songbirds, learned, whereas calls are simpler and innate. Relative to other passerines, songbirds have distinctive brain structures and syringeal anatomy that facilitates song learning and the production of complex songs.

Bird songs comprise of combinations of sound elements and can last anywhere from a few seconds to several minutes. Groups of sound elements that always occur together in a certain order are called syllables. Syllables are typically delivered in a particular order to form songs. Based on the types of syllables and their order, songs can be categorized into song types. The set of song types an individual sings is that individual's song-type repertoire. Some birds have very simple song structures with minimal number of sound element types. For example, individual chipping sparrows (*Spizella passerina*) sing a single song type, consisting of only a single element type repeated many times. At the other extreme are species such as the house wren (*Troglodytes aedon*), in which each individual produces many different song types, each of which contains several types of syllables.

### History of Research

#### Classical Work

The beginning of the modern scientific study of song learning in birds can be attributed to W. H. Thorpe who studied common chaffinch (*Fringilla coelebs*) songs in the middle of the twentieth century (Thorpe 1958). He raised young chaffinches in isolation, which prevented them from hearing any adult chaffinch song. When the

isolated birds matured, their songs were different from typical chaffinch songs. This result suggested that learning models (“tutors”) are necessary for normal song development.

In an experiment on dark-eyed and yellow-eyed juncos (*Junco hyemalis*, *Junco phaeonotus*), Masakazu Konishi showed that artificially deafened males fail to produce species-typical songs (Konishi 1964). He went on to conduct similar experiments on other species and found the same effects of deafening on song learning. Fernando Nottebohm showed that chaffinch males deafened as nestlings fail to develop normal song, but those deafened as adults continue to sing normally (Nottebohm 1969). Peter Marler and Susan Peters (1977) found that young swamp sparrows (*Melospiza georgiana*) exposed to both swamp sparrow and song sparrow (*Melospiza melodia*) songs ultimately learned only their species-specific songs. Marler (1970b) exposed young white-crowned sparrows (*Zonotrichia leucophrys*) of different ages to adult singers of the same species and found that there is a sensitive period early in the bird’s life during which song learning occurs.

These pioneering studies established that young songbirds learn songs by listening to adults of their own species at a critical sensitive period in their first year of life, laying the foundation for the study of song learning in songbirds.

### Model Species

There are extensive parallels between song learning in songbirds and language acquisition in humans (Bolhuis and Everaert 2013; Marler 1970a). For example, both taxa have a sensitive period in early life, “babble” before producing mature vocalizations, avoid learning species atypical sounds, and learn both sounds and transitions between sounds (Lipkind et al. 2013). Because of these similarities, songbirds are models for research on vocal learning.

For practical reasons, the majority of song learning research involves laboratory experiments. These studies tend to focus on species that can be bred easily and raised in laboratory conditions. Most of the experiments carried out in Europe have been focused on species like the common chaffinch, common nightingale (*Luscinia*

*megarhynchos*), and European starling (*Sturnus vulgaris*). North American studies have mostly been based on the song sparrow, swamp sparrow, white-crowned sparrow, and zebra finch (*Taeniopygia guttata*). Recent advances have allowed field-based studies of vocal learning and expanded the taxonomic reach to include species like blackbirds, wrens, and mockingbirds.

### Current Research

Early research on song learning was focused on describing the learning process in male songbirds from the temperate zone. Later studies explored the physiology, genetics, and neuroscience of song learning, revealing many mechanistic similarities between song learning in songbirds and human language acquisition. Recently, researchers have turned their attention to vocal learning in tropical songbirds and females, as well as social influences on learning.

### The Evolution of Song Learning

The approximately 11,000 known living bird species belong to 36 orders (del Hoyo and Collar 2014, 2016), only three of which learn their vocalizations. Songbirds (suborder Passeri, order Passeriformes) comprise nearly half of all bird species. Parrots (order Psittaciformes) and hummingbirds (family Trochilidae, order Caprimulgiformes) are the other two groups of birds that are known to learn the structural details of their vocalizations. There exist remarkable similarities in the brain regions that support vocal learning in all three taxa. Based on these findings, three different hypotheses have been proposed to describe the evolution of song learning (Jarvis 2006).

The first hypothesis suggests that vocal learning evolved twice independently, in hummingbirds and in the common ancestor of parrots and passerines, circa 65 million years ago. An alternative hypothesis proposes that the common ancestor of all three vocal learning groups was a vocal learner, and learning was subsequently lost in several lineages. According to the third hypothesis, both vocal learners and non-learners possess rudimentary versions of the brain nuclei necessary

for vocal learning, but the ancestors of the three vocal learning groups independently evolved enlargement of these brain structures, facilitating vocal learning.

## Song Learning in Female Songbirds

Female song is rare in most North temperate songbirds but common in the tropics and Southern Hemisphere. The ancestor of all extant songbirds had female song, so lineages with male-only song have lost female song over evolutionary time (Odom et al. 2014). Like male song, female song functions in territory defense, especially in female-female competition. Females may also sing to solicit extra-pair copulations, court their partner, or maintain pair bonds. Females often sing in temporal coordination with their mates, a behavior called “vocal duetting.” While it is clear that female songbirds learn their songs, very little is known about how singing females learn songs. Existing evidence, however, suggests that the process of female song learning is similar to that of male song learning (Evans and Kleindorfer 2016; Riebel 2016). Females also learn about conspecific songs that they do not sing. This kind of learning influences females’ song preference in adulthood. Sexual dimorphism in the song learning process, tutor-tutee relationships, and learning efficiency requires further investigation.

## The Adaptive Significance of Song Learning

There are several possible answers to the question, “why have songbirds evolved to learn their songs?” Among the leading hypotheses is that song learning facilitates the elaboration of both songs and song repertoires. More complex songs and larger repertoires are more attractive to females in some species and may be more effective for excluding territorial competitors (Catchpole and Slater 2008). The “mate choice hypothesis” states that female choice drives the evolution of large song repertoires. In many species, females prefer to mate with males that sing

large song repertoires (reviewed in Catchpole and Slater 2008 but see Byers and Kroodsma 2009 for a dissenting view). By preferentially mating with males with large repertoires, females may have selected for song learning ability.

Alternatively, song learning may be an adaptation for interactive vocal communication between neighbors. Territorial neighbors often sing back-and-forth to one another. This behavior, known as counter singing, is believed to mediate territorial disputes. Birds may song-type match (sing the same song type), repertoire match (sing a song from the neighbor’s repertoire), or avoid matching the song or repertoire of their neighbor to mediate territorial aggression. According to this hypothesis, both forms of matching serve to escalate contests, and nonmatching signals an intention to de-escalate. Song learning gives birds the ability to sing both shared and unshared song types.

Once vocal learning is widespread, learning proficiency could evolve to be a reliable indicator of developmental stress, such as malnutrition in early life (Nowicki et al. 1998). Accordingly, a male’s song structure might indicate his phenotypic quality and influence how females or rivals interact with him. Similarly, learned songs could allow females to choose genetically compatible males, assuming that genotypes covary with song structures. For example, females might memorize their father’s songs and go on to choose mates with similar songs. Evidence for this hypothesis is mixed.

## An Overview of the Learning Process

The “auditory template model” of song learning was proposed to explain how young birds learn their songs from adult conspecifics. The model has been modified in light of recent findings, but it continues to inform scientists’ understanding of song learning and makes a useful jumping-off point for discussions of song learning.

The auditory template model states that newly hatched birds already possess a crude template of their species-specific song. Within the first few weeks of life (the exact timing depends on the species), birds enter a “sensitive period,” during

when they attempt to match the sounds they hear with their innate template. Template matching enables birds to further refine their innate template and to filter out sounds other than conspecific song. During their sensitive period, young birds memorize their songs but do not sing them. The period when song production occurs, known as the “motor phase,” generally occurs later in the next spring. In some species, however, the memorization and motor phases overlap (Catchpole and Slater 2008).

Songbirds generally start to sing within the first year of life, often in their first spring. During the motor phase, birds match the sounds they produce with the template they formed during the memorization phase. The process of matching the song to the template takes time. Over the course of the motor phase, vocal output passes through several stages. The first kind of vocal output during the song development process is called “sub song.” Sub song comprises a highly variable set of sound syllables with no or little repetition. Sub song is generally much quieter than adult song, and syllables sung at this stage bear little similarity to typical song syllables in adults. Marler (1970a) equated sub song to babbling in human babies during the early stages of language acquisition.

During the second stage of song development, named “plastic song,” birds sing louder, more structured songs. Relative to sub song, plastic song is less variable and more similar to typical adult songs in terms of both structure and duration. Songs gradually start to resemble species-typical adult songs in all aspects. Finally, “crystallized songs” represent fully adult, species-typical songs. The term “crystallized song” is somewhat misleading, because song structure can continue to change in adulthood in many species (see below).

### When, What, and from Whom Do Birds Learn?

This section builds on the auditory template model to provide a more nuanced view of song learning in oscine passerines.

### When Does Learning Occur?

The sensitive period typically begins after fledging, but some vocal learning may occur earlier in certain species (Colombelli-Négrel et al. 2016). Sensitivity to vocal inputs changes over the course of the sensitive period, and the total duration of the sensitive period varies widely among songbird species (Catchpole and Slater 2008). Some species have short sensitive periods (e.g., 50 days in white-crowned sparrows, 1–3 months in zebra finches). Other species have extended sensitive periods (e.g., 5 months in song sparrows). Species with restricted sensitive periods are known as “closed-ended” or “age-limited” song learners. Still other species have sensitive periods that extend beyond their first year of life. Nightingales and marsh wrens (*Cistothorus palustris*) learn new songs in the spring after their hatch year. The European starling is an example of a species that has been termed an “open-ended” learner, because it memorizes and produces new songs throughout adulthood. It is now known that vocal learning often extends beyond the first year of life and that extended sensitive periods are more commonly observed in the wild than in laboratory studies, even when controlling for species (Catchpole and Slater 2008). Close-ended and open-ended learning styles should not be seen as a dichotomy but rather as endpoints on a continuum (Brenowitz and Beecher 2005).

### Practice, Improvement, and Attrition

During the motor phase, young birds practice their songs while listening to their own song output, leading to the term “sensory-motor phase.” Auditory feedback (hearing one’s own song) is required to accurately recreate the memorized songs. Various other factors affect song development process in both sensory and sensory-motor phases. For example, sleep plays a critical role in song learning. The song nuclei in the brains of sleeping zebra finches are active during the sensory-motor phase of song learning (Dave and Margoliash 2000), suggesting that young birds replay songs in their sleep. Improvement in song copying occurs immediately after sleep, further indicating the role of sleep in consolidating vocal learning (Derégnaucourt et al. 2005).

Song development in birds is also affected by early nutrition (Nowicki et al. 1998). Nutritional stress in early life may affect neurogenesis in the brain and thus the song learning process. As a result, song structure and singing behavior in adulthood may reflect the bird's nutritional state in early life.

During the plastic song stage, birds sing many songs and song elements that do not end up in the crystallized repertoire (Catchpole and Slater 2008). For example, a swamp sparrow's plastic song includes four to five times the number of song elements as his crystallized song repertoire. The process of losing songs or elements is called attrition. The selective attrition hypothesis suggests that birds selectively eliminate some elements or song types and retain the most useful songs into adulthood (Nelson and Marler 1994). Social cues are thought to influence which songs will be retained (e.g., those that permit song matching with neighbors).

### What Is Learned?

Some songbird species sing only a single song type throughout their lives, but there are many species in which individuals can sing more than one song type. For example, a white-crowned sparrow generally sings one or two song types, whereas a song sparrow can sing up to ten song types. Individuals of some other species, like sedge wrens (*Cistothorus platensis*) and house wrens, can produce hundreds of song types. Brown thrashers (*Toxostoma rufum*) sing over 1500 song types.

Songbirds not only copy single songs accurately, they also learn how to sing songs in specific sequences (Marler and Slabbekoorn 2004). Similarly, duet-singing species learn to link their own songs with the songs of their duet partners to form specific sequences. In species with large repertoires, like nightingales, songs are organized in the memory as sub-repertoires. Birds associate these sub-repertoires with contexts, including locations and times (Marler and Slabbekoorn 2004). At a finer scale, birds can learn how to order song syllables independently of learning the syllables themselves (Lipkind et al. 2013; Rose et al. 2004).

### From Whom Do Birds Learn?

After fledging, but before dispersing from the natal territory, young birds are accompanied and provisioned by one or both parents. They may learn songs from their parents and neighbors during this time. Young birds continue to encounter other singing conspecifics after postnatal dispersal, providing opportunities to learn different songs. Species with extended sensitive periods can also learn from neighbors after their territory establishment, facilitating the ability to song-type match and repertoire match neighbors.

Early studies on song learning were conducted under laboratory conditions. Researchers played audiotapes of adult songs to tutor young birds. Later, it was discovered that tape-tutored birds learn differently than live-tutored birds. Importantly, live tutoring tends to extend the sensitive period, and young birds are generally more responsive to live tutors than they are to tape tutors. Indeed, some species never learn from tape tutors. It is now clear that social interactions are critical to the song learning process and that both direct and indirect interactions (e.g., eavesdropping on counter-singing neighbors) with tutors influence learning (Beecher 2016).

### Song Mimicry

The innate auditory template and strong social association with conspecifics generally ensures that birds will learn species-typical songs. Some birds, however, learn other species' songs. The inclusion of hetero-specific elements in the song repertoire, termed "song mimicry," can be pathological (e.g., when a young bird accidentally learns a song that is not typical of its species), but it can also be adaptive. For example, some species include the call notes of other species in their songs, which allows them to recruit birds of those species when mobbing a predator. Drongos (family Dicruridae) recruit other species to mixed-species feeding flocks by mimicking their songs. Males of the brood-parasitic indigobirds (family Viduidae) sing the songs of their host species, which they use to attract female indigobirds. Extreme examples of mimicry by Australian lyrebirds (family Menuridae) demonstrate the capacity of avian vocal



learning. These species mimic not only other songbird species but also many other species including mammals, as well as anthropogenic sounds such as sounds of chain saws, cameras, and car alarms. They use mimicry during courtship and male-male encounters.

## The Endocrinology of Song Learning

Testosterone has important effects on song learning and production (Arnold 1975). In species with male-only song, testosterone causes young males to produce more neurons in the song nuclei of the brain than do females. Castrated males do not sing unless they are supplemented with testosterone, and testosterone supplementation can induce song in females of species that do not typically have female song. Seasonal changes in testes size affect testosterone production in male birds and mediate seasonal variation in song production. Oxytocin may also play a role in song learning (Theofanopoulou et al. 2017).

## The Neuroscience of Song Learning

Zebra finches and other songbirds are the primary animal models for neuroscientific research on vocal learning. As such, the neuroscience of song learning is a large, active field (Jarvis 2006).

### Brain Regions

Song learning and song production are governed by several specialized brain regions (or “nuclei”) and connecting pathways. Collectively, the nuclei and pathways are known as the “song system.” The songbird song system contains two main branches, known as the “posterior descending pathway” (PDP) and the “anterior forebrain pathway” (AFP). The PDP, which is also known as the “motor pathway,” is responsible for song learning and production. The AFP functions exclusively in song learning. Central to both of these pathways is the nucleus known as the HVC. That area used to be called the “hyperstriatum ventrale, pars caudalis” and, later, the “high vocal center,” but those names were determined to be inaccurate, so

HVC is now a pseudo-acronym that does not stand for anything.

The PDP is made up of the HVC, the robust nucleus of the arcopallium (RA), and the tracheosyringeal component of the hypoglossal nucleus (nXIIts). The AFP comprises the HVC, Area X, the medial portion of the dorsolateral thalamic nucleus (DLM), the lateral part of the magnocellular nucleus of the anterior nidopallium (LMAN), and the RA. Both the PDP and the AFP are small in nestlings and increase in size, number of neurons, and connections as young birds learn to sing.

In many species, males have more and larger neurons and higher number of neuronal connections in the song nuclei than do females. These anatomical differences typically correspond to sex differences in singing behavior. Unsurprisingly, sex hormones influence the early stages of development of song nuclei. For example, young female zebra finches that are supplemented with testosterone develop male-like song nuclei and express song.

The discovery of adult neurogenesis in song control regions had important implications in the neuroscientific community, which was skeptical of adult neurogenesis at the time. Adult neurogenesis occurs in certain song nuclei, such as the HVC and Area X, but not in others. Many songbirds exhibit seasonal variation in both the size and number of neurons in these regions. High song rates, as occur in the early spring, are hypothesized to induce neurogenesis. However, the precise relationship between singing behavior and changes in neurogenesis is still not characterized well through systematic studies. Similarly, the functions of adult neurogenesis in song nuclei are not known, but hypotheses abound (Brenowitz and Larson 2015). For example, adult neurogenesis may enable birds to learn and produce new songs, to learn to recognize new songs, or to replace old neurons.

### Auditory Feedback

Birds must hear their own songs to develop normal songs and maintain crystallized songs. The “auditory pathway,” which includes seven brain nuclei and connecting pathways, is responsible for this task. The “Caudal Medial Nidopallium”

(NCM) in the auditory pathway is responsible for long-term memory of songs learned in early life (Yanagihara and Yazaki-Sugiyama 2016). Auditory regions and the HVC in both males and females are sensitive to their own species' songs. Several competing hypotheses have been proposed to explain how auditory input influences the vocal pathway, but this issue has not yet been resolved (Marler and Slabbekoorn 2004).

### Mirror Neurons

Mirror neurons are involved in song production, the perception of the bird's own song, and the perception of other conspecifics' songs. They play a role in song learning, perception, and singing activities, such as song-type matching (Mooney 2014).

### Gene Expression in the Brain

A number of genes have been identified as playing major roles in song learning and song production. Patterns of gene expression in song nuclei vary across the stages of song learning and across seasons. Singing induces expression of the immediate early gene ZENK in both the vocal pathway and the auditory pathway, which in turn influences the expression of other genes involved in song production. The FOXP2 gene plays a major role in vocal development in both songbirds and human beings. FOXP2 is expressed in Area X in the anterior forebrain pathway. Knocking down FOXP2 expression results in abnormal song development in zebra finches. A similar pattern is observed in humans, where mutated FOXP2 gene results in incomplete and inaccurate word copying and poor pronunciation (Bolhuis and Everaert 2013). FOXP2 expression changes seasonally, with elevated expression when birds add new song elements after the breeding season.

### Cultural Evolution and Song Dialects

The songs of a population of songbirds, which themselves comprise a population of songs, change over the course of generations. In other words, populations of songs evolve. Because songs are transmitted by learning rather than by

genetic inheritance, this represents a form of cultural evolution. Cultural evolution has many similarities to biological evolution. Both processes generate diversity, and both are influenced by mutation, drift, selection, immigration, and emigration.

De novo generation of song elements and song types are analogous to genetic mutation, in that both processes introduce novel variants into a population. Copying errors, including insertions, duplications, deletions, or transpositions of song elements, can occur at various stages of the song learning process. If these errors are passed on to other birds, they introduce novel variation into the song population. Novel song variants can also come from mimicry, improvisation, and immigration. Songs that are copied more or less than others because of their properties (e.g., their ability to transmit over long distance or their effectiveness at repelling rivals) are under cultural selection. The frequency of a song variant that is not under selection is expected to vary randomly over time, like allele frequencies undergoing genetic drift.

Like biological evolution, cultural evolution produces geographic variation. The term "song dialect" describes discrete geographical variants of learned birdsong. Dialects are a result of vocal learning. They also occur in other vocal learning species, such as parrots, hummingbirds, whales, and human beings. Dialects are more pronounced among species with small repertoires (Price 2008). White-crowned sparrows, which have very small repertoires (often just one song type), form dialects with discrete geographical boundaries (Marler and Tamura 1964). Although repertoires often vary geographically in large-repertoire species, they tend not to form geographically discrete dialects.

Young birds of both sexes are exposed to their own song dialects, but they do not typically hear foreign dialect songs. As a consequence, adult songbirds could fail to recognize foreign songs as belonging to conspecifics. In general, male birds tend to respond more aggressively to the playbacks of their own dialects. Females tend to prefer local songs to foreign ones in laboratory-choice experiments. In theory, this kind of

preference pattern could drive genetic evolution. Recognition of foreign songs could be facilitated by features that cross-dialect boundaries, such as the whistle notes at the beginning of white-crowned sparrow songs.

A key question is whether song dialects are barriers to gene flow. If they are, dialect formation could drive reproductive isolation, ultimately leading to speciation. The data are mixed. Some evolutionary models suggest that song learning accelerates the speciation process. It is clear, however, that dialects are not always associated with genetic structure (Slabbekoorn and Smith 2002). As song learning plays a major role in song divergence and promotes premating isolation, song learning is hypothesized to be one of the driving forces of rapid speciation in Oscines. However, diversification rate of songbirds is slower when compared with some other rapidly diversified clades such as sub-Oscines and order Ciconiiformes (storks and allies), which do not possess the ability of vocal learning (Price 2008).

## Cross-References

- Auditory Signals
- Communication
- Countersinging
- Critical Period for Song Learning
- Cultural Transmission
- Dawn Solo/Chorus
- Passerine Vocal Communication
- Syntax

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## Song-Type Matching

### ► Countersinging

## Sonogram

### ► Sound Spectrogram

## SOP Model

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The Sometimes Opponent Processes (SOP) model of Pavlovian conditioning was proposed by Wagner (1981; see also Mazur and Wagner 1982) as quantitative elaboration of Priming Theory (Wagner 1976). This theory states that the effectiveness of a Pavlovian conditioned stimulus (CS) or unconditioned stimulus (US) to produce its response or to develop an association with other stimuli is diminished when the stimulus is already represented in active memory at the moment of presentation. This priming can be a consequence of a recent presentation of the stimulus (self-generated priming) or of retrieval of its representation from memory by an associated stimulus (associatively generated priming). This idea can explain several related phenomena, such as the observation of diminished reinforcement and diminished vigor of the unconditioned response provoked by the presentation of an unconditioned stimulus that has been shortly preceded by itself or by an associated conditioned stimulus. Wagner (1976) suggested that the observed diminution in responding to a repeated stimulus or habituation is generally to be understood in such unified fashion: there is a transient memorial effect, due to recent exposure to the stimulus, and there is a more persisting memorial effect due to the context acting as a conditioned stimulus.

According to SOP, the memory system comprises a set of representational nodes, each distinguished by its predominant state of activity and by the directional excitatory and inhibitory linkages

that exist with other nodes. The model includes rules of nodal activity and rules by which conjoint activity produces changes in the existing linkages between nodes. An individual node representing an experimental stimulus (conditioned or unconditioned) is assumed to be formed by a large collection of elements that can be in one of three states of inactivity (I), primary activity (A1), or refractory activity (A2). Upon presentation of the corresponding stimulus event, a proportion of inactive elements are promoted to the A1 state, according to the momentary probability  $p1$ , from which they subsequently decay, first to the A2 state, with probability  $pd1$ , and then back to inactivity with probability  $pd2$ , and in which they remain for as long as the corresponding stimulus remains absent. Thus, the only momentary effect of a novel or untrained stimulus on its memory node is to activate a given proportion of the then-inactive elements to the A1 state with no effect on the elements that are already in the A1 or A2 state.

The global activity of each stimulus in time is characterized by the momentary proportion of elements in the A1 and A2 states of activity. Formally, changes in the proportion of elements in the primary state of activity are given by  $\Delta A1_i = p1_i[1 - (A1_i + A2_i)] - [pd1_i A1_i]$  and changes in the proportion of elements in the secondary state of activity are given by  $\Delta A2_i = [pd1_i A1_i] - [pd2_i A2_i]$ . These rules produce quite regular curves of expected A1 and A2 activity over time after stimulus presentation, involving a progressive increase in A1 activity, which is proportional to  $p1$ , followed by a progressive increase in A2 activity which is proportional to  $pd1$ . Both A1 and A2 activity decays progressively towards zero after stimulus offset.

According to SOP, both excitatory learning and inhibitory learning occur separately and result from concurrent activation of the conditioned and unconditioned stimuli. Increments in the excitatory CS-US links,  $\Delta V^+$ , are assumed to be proportional to the momentary product of concurrent  $A1_{CS}$  and  $A1_{US}$  activity multiplied by an excitatory learning rate parameter,  $L^+$ , (i.e.,  $\Delta V^+ = L^+ A1_{CS} A1_{US}$ ), whereas changes in the inhibitory CS-US connections,  $\Delta V^-$ , are assumed to be proportional to the momentary product of concurrent  $A1_{CS}$  and  $A2_{US}$  activity, multiplied by

an inhibitory learning rate parameter,  $L^-$  (i.e.,  $\Delta V^- = L^- A1_{CS} A2_{US}$ ). The result of an acquired associative tendency is to allow initial activity of the respective CS representation to provoke some A2 activity in the US node (if net  $V$  is excitatory) or to suppress other associative activation of the US node (if net  $V$  is inhibitory). There may be multiple CS nodes active at any moment, each with its own balance of excitatory and inhibitory associations with the US and with its own momentary distribution of activity of its elements. The model assumes that any CS node influences the US in accordance with the product of its momentary  $A1_{CS}$  activity and the net value of its associative connection with the US. These products are summed over all CS representations to determine the value of a variable named  $p2$ . Formally,  $p2_{US} = \sum A1_i V_i$ .

SOP assumes that the presentation of the US provokes a first component of the unconditioned response, which depends on the proportion of US-primary activity and then a second component, dependent on US-secondary activity. The two response tendencies can be similar, as is the case of the eyeblink response to a paraorbital shock, both contributing to the net response, but they might also be assumed to be antagonistic or unrelated to one another in other response systems. The CS has its influence on behavior by provoking  $A2_{US}$  activity by means of its associative link. The direct effect is an anticipatory response that can add or oppose to the unconditioned response occasioned by a subsequent US. By this action of moving US elements directly to the A1 state, the CS has also an indirect behavioral consequence, which is decreasing the A1 activity occasioned by a subsequent presentation of the US. Consequently, the acquired CS-US association influences not only the probability of the response, but also the processing of the US. Thus, if the A2 node of a US is activated by the precedence of an associated CS (associatively-generated priming) or by itself (self-generated priming), the A1 node of that US will be less susceptible to activation, so as to produce not only a diminished UR but also less associative learning. These assumptions were formalized by Wagner (1981) by stating that the unconditioned response is given by:  $UR = f(w1 A1_{US} + w2 A2_{US})$ ,



where  $f$  is a function representing each response system, and  $w_1$  and  $w_2$  are differential weights for the contribution of A1 and A2 to the response.

Since its original formulation, the SOP model has evolved to consider more complex or componential representations of the experimental stimuli. The AESOP model (Wagner and Brandon 1989) proposed how the divergence of conditioned response measures might be described by parametric differences in the state transitions associated with nodes representing the emotive (e.g., fear) as contrasted with the sensory (e.g., eye-blink) aspect of a given US (e.g., paraorbital shock). Subsequently, Brandon and Wagner (1998) conjectured how phenomena of occasion setting might be attributed to discriminative control by different nodes of the conditioned stimulus that represent conjunctive and unique aspects of the stimulus, a notion that was further elaborated in the SOP-REM model (Wagner and Brandon 2001; Vogel et al. 2017). Likewise, Vogel et al. (2003) explained the observation of differential CR timing that results from training with different CS-US intervals by proposing that different elements representing a CS might differ in their temporal dynamics so as to be more or less conjunctive with activity produced by the US. All of these proposals share the added presupposition that the representation of the stimuli should be componential rather than molar; but, beyond that, they retain the rules and principles of the original SOP model.

## Cross-References

- Blocking
- Classical Conditioning
- Conditioned Inhibition
- Extinction in Learning
- Habituation
- Interstimulus Interval (ISI)
- Interval Timing
- Latent Inhibition
- Learning
- Overshadowing
- Priming

- Reflex
- Timing
- Unconditioned Response
- Unconditioned Stimulus
- Working Memory

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## Sorting

- Chunking

## Sound

### ► Primate Sensory Systems

## Sound Spectrogram

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## Synonyms

Sonogram; Spectral waterfalls

## Definition

Time-frequency visual representation of an auditory signal.

## Introduction

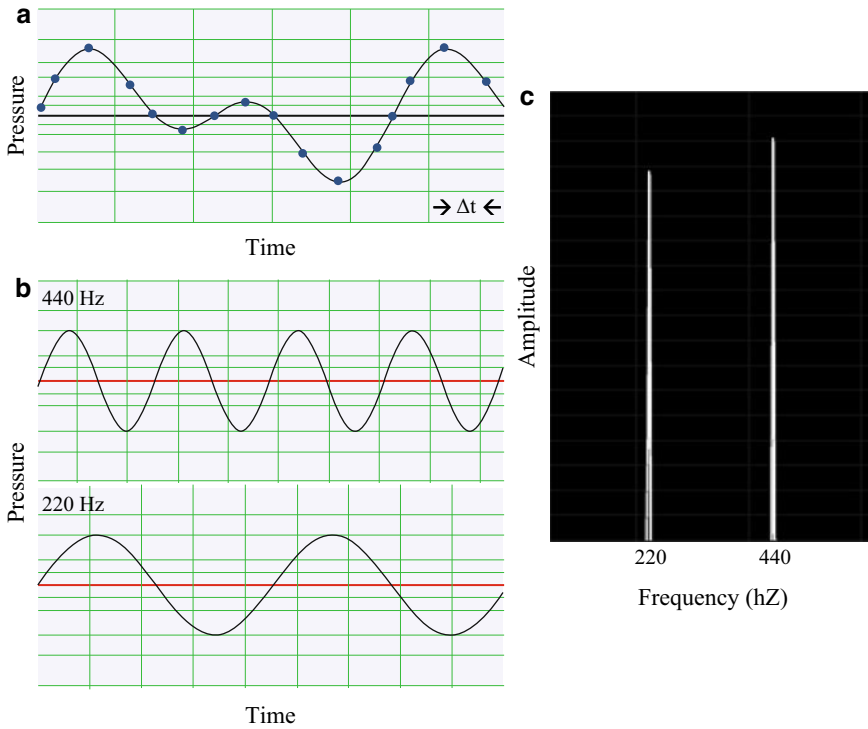
Animals produce a wide range of vocalizations and mechanical sounds that may be used to communicate their identity, fitness, willingness to mate, location, food availability, or possible danger. Visualizing these auditory signals is critical for understanding their role in animal cognition, communication, and behavior. The spectrogram, or a time-frequency depiction of sound, is a fundamental tool in the study of animal behavior. Prior to the invention of the spectrogram, most animal vocalizations were evaluated by ear. In the 1940s, technology to visualize sounds was developed in the military setting. This technology, called the Sona-Graph, became commercially available by the 1950s and has since revolutionized the science of human and animal communication (Marler 2004).

## A Guide to Understanding Spectrograms

In order to use spectrograms most effectively for studying bioacoustics, one must first understand the history of sound analysis. The biological world is full of sounds made by animals and the environment. The sounds vary in several dimensions (pitch, loudness, timbre, etc.) that can change over time. These separate components fit together, like a jigsaw puzzle, to create a perception of meaningful and complex auditory signals. Jean-Baptiste Joseph Fourier (1768–1830), best known for pioneering heat and vibration wave analysis, noticed that sounds were made up of complex waves (Fig. 1a), which were made of the combination of two or more simple sine waves (Fig. 1b). Just like puzzles can be deconstructed into individual pieces, complex sound waves can be deconstructed into their simple sine waves.

The deconstruction of a complex sound can be achieved through Fourier Transformations (FT). The FT is a mathematical technique for creating an instantaneous snippet of frequencies and amplitudes within a sound (Fig. 1c). This snippet is analogous to one puzzle piece. Today FT is performed automatically by the appropriate sound analysis program (e.g., Adobe Audition, Raven, Audacity, etc.), and no hand calculations are necessary. These programs use a Fast Fourier Transformation (FFT) algorithm, which is an efficient way to calculate and put together discrete FTs, on a time continuum. A spectrogram is a time-frequency visual representation of a sound that has been assembled, like a puzzle, by combining FTs together.

In order to perform FFT, sound in the environment has to be converted to a recording through a process of *sound digitization*. Modern technology permits novices and professionals to record sounds using every-day tools, such as cell-phones, or more sophisticated technology, such as recorders (e.g., Roland portable recorder, Tascam portable recorder). A digital audio recording is characterized by its *sampling rate* ( $F_s = 1/\Delta t$ ), or the number of times sound pressure is measured, and by *bit depth*, or the number of



**Sound Spectrogram, Fig. 1** (a) An example of a waveform graph of a complex sound with multiple frequency components (continuous line). Dots represent the waveform's digitized analogue. (b) 220 and 440 Hz pressure

sound waves that make up the complex sound wave in Fig. 1a. (c) A spectrum FT graph for the waveform in Fig. 1a with 220 and 440 Hz frequency components

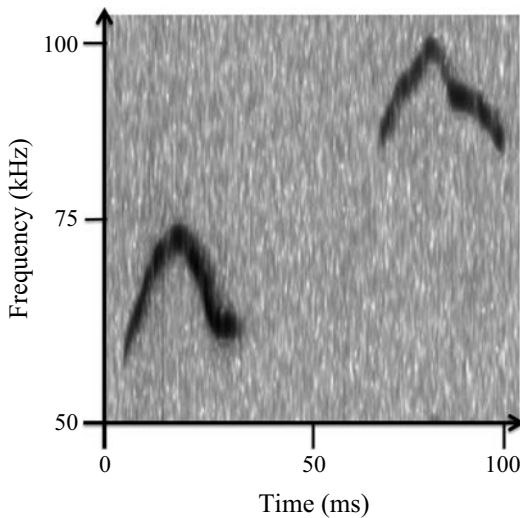
bits of information in a sample. In order to have a reliable reproduction of the auditory signal, samples must be taken frequently (dots, Fig. 1a). This principle is known as the Nyquist Theorem. The highest frequency of a sound that equipment can digitize is the Nyquist frequency. In fact, a digitized sound can only honestly represent auditory frequencies that are half (or less) than that of sampling rate ( $F_s/2$ ). If this rule is not observed, the digitized sound, and subsequently the spectrogram, will be distorted, thus it is important to know the capacities of the recording equipment.

Once digitized, the sound can be analyzed to extract the frequency (a physical analogue of pitch perception), duration, amplitude (a physical analogue of loudness), and timing information. All of these components, or pieces of the puzzle, are necessary to generate a spectrogram. FFT assembles individual FTs together, creating a plot of frequency (y-axis) against time (x-axis), and

representing amplitude through color intensity, with darker colors indicating louder aspects of the vocalizations (Fig. 2). Thus, by visually and statistically examining the spectrograms, one can try to understand why the animal produces these sounds.

### Spectrograms in Modern Animal Bioacoustics

Animal bioacoustics is an interdisciplinary study area dedicated to understanding the acoustical world of animals. Recording and visualizing sounds (as in a spectrogram) provides a unique window into animal's life, allowing researchers to "see" the complexity of animal acoustic communication. Auditory signals have the benefit of traveling across long distances and are easier to detect in the environments with low visibility



**Sound Spectrogram, Fig. 2** A spectrogram of two mouse ultrasonic vocalizations. These vocalizations were recorded from a female mouse after being exposed to and separated from another female mouse. (This spectrogram was part of the Burke et al. 2018 project. It was reproduced with the permission of Dr. Micheal Dent)

(e.g., in the dark, under water, under ground, or in the forest) or when the animals cannot be visually located (e.g., humpback whales (*Megaptera novaeangliae*)). Spectrograms are widely used to study animal sound production and perception, the effect of environmental and man-made noise on animals in a variety of mediums, and to understand evolution and speciation of animals.

Some of the benefits of spectrograms are perhaps best understood by reviewing the notable examples in the scientific literature. In vocalization studies, a spectrogram can be used to count the number of vocalizations produced by an individual or several animals, and to categorize those vocalizations based on temporal (duration, frequency of occurrence, rate of production, etc.) and spectral (peak frequency, frequency range, bandwidth, etc.) characteristics. These measures can then be used to establish baselines for sex, age, and species-related vocal production. In isolated cases, it takes decades to truly understand the vocal abilities of certain animals even with the availability of spectrograms. For example, it was widely believed that female mice do not vocalize because no vocalizations occurred when a female

mouse was placed with an anesthetized male mouse (reviewed by Nyby 2001). Microphone arrays, careful experimental manipulations, and detailed spectrogram analyses now show that female mice vocalize in a variety of social and isolated situations (Burke et al. 2018).

Spectrograms have also contributed to the modeling of hearing and communicative disorders. In these studies, sound spectrograms can be altered by the researchers in order to determine what animal can and cannot hear. Operant conditioning (see ► “Operant Conditioning,” ► “Behaviorism”) procedures are frequently used for this purpose. In these studies, animals are trained to respond to a sound or a difference in sounds. Prior studies across species have utilized operant conditioning procedures to examine detection, discrimination, and identification of a variety of acoustic signals. For example, Kobrina and Dent (2016) showed that mice (*Mus musculus*) can detect vocalizations late into their lifespan, with male mice losing hearing at a faster rate than female mice. This pattern of age-related hearing loss is similar to those in humans, suggesting that mice can be used to model and investigate the basis of human age-related hearing loss.

Spectrograms have also been a useful tool in examining the effects of the acoustic environment and noise on vocal production, as well as establishing environmental standards for human activity (reviewed by Wiley 2015). One example is *frequency-shift adaptation* in noisy urban environments. Chickadee (*Parus atricapillus*) vocalizations are often masked by urban noise. To deal with this, chickadees decrease the duration and increase the overall frequency of their *fee-bee* song during peak auto traffic hours. This adaptation maximizes detectability of individual songs in low-frequency noise conditions (Proppe et al. 2011). While this species may adapt to noisy acoustical environments, not all species are capable of adapting to noise, and thus experience detrimental effects (Wiley 2015).

Spectrograms can also be used to understand the evolutionary development of acoustic communication in several species. For example, *spectrogram correlation analysis* is an objective quantitative measure of sound similarity that is

performed through analyzing several spectrograms, pixel-by-pixel. Researchers have used this procedure to study acoustic communication in toadfishes (*Batrachomoeus trispinosus*). Prior to *spectrotemporal correlation analysis*, it was unclear whether different toadfish species are acoustically distinct. Through the examination of typical vocalizations produced by toadfishes, Rice and Bass (2009) showed that *Batrachomoeus trispinosus* was vocally distinct from other toadfish species. This type of analysis shines light on how animals are capable of finding their conspecifics during mating without using visual, tactile, or chemical information.

## Conclusion

The spectrogram is a visual representation of sound that is assembled by combining multiple frequency and amplitude puzzle pieces. In order to use this tool, one must be able to digitize the sound and analyze it through a variety of software packages. These packages employ FFT analysis to create the frequency (y-axis) and time (x-axis) sound representation, with amplitude often expressed through color. The spectrogram is an important tool for studying animal auditory worlds and has significantly contributed to the study of animal bioacoustics. Spectrograms have been used to model human auditory perception, to study vocal repertoires of different species, to understand the effects of noise on animal welfare, and even to examine the acoustic evolution of species. Needless to say, spectrograms can be used in many other fields (medicine, engineering, etc.) and will continue to play a critical role in science and instrumentation progress.

## Cross-References

- Arthropod Cognition
- Auditory Processing and Perception
- Auditory Signals
- B.F. Skinner
- Behaviorism
- Bowerbirds

- Canine Communication
- Catarrhine Communication
- Categorization
- Cephalopod Communication
- Cetacean Communication
- Chorus
- Communication
- Contact Calls
- Countersinging
- Critical Period for Song Learning
- Dawn Solo/Chorus
- Echolocation
- Feline Communication
- Food Calls
- Go/No-Go Procedure
- Insect Communication
- Interstimulus Interval (ISI)
- Jane Goodall
- Laboratory Research
- Language
- Language Research: Dolphins
- Language Research: Great Apes
- Language Research: Parrots
- Operant Conditioning
- Owls
- Passerine Vocal Communication
- Perissodactyla Communication
- Pigeon (*Columbidae*)
- Primate Communication
- Prosimian Communication
- Songbird Duets
- Songbird Learning
- Tropics

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## South American Manatee

- [Sirenia Diet](#)

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## Sow Stall

- [Gestation Stall](#)

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## Space Perception

- [Depth Perception](#)

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## Space Use

- [Artiodactyla Navigation](#)

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## Spacer DNA

- [Intergenic](#)

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## Spandrels

- [Evolutionary By-product](#)

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## Sparrowhawk

- [Accipiters](#)

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## Sparse/Dense Discrimination

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The sparse-dense discrimination task is a psychophysical judgment test used extensively in the area of assessing animal metacognitive abilities. The task involves two structural components. The first is the relative or absolute classification of stimuli as being sparsely or densely arranged. These are stimuli that consist of pixelated shapes (rectangles or circles) on a computer screen. The second component involves the presentation and potential use of the *uncertainty response*, which is a response that objectively operates to eliminate the requirement to make the primary discrimination and/or to provide an easier next trial or smaller reward. Its use has been interpreted to reflect metacognitive awareness on the part of subjects that use that response when they are at greatest risk of making an error of density judgment.

The first use of this task to assess metacognitive responding occurred with rhesus monkeys (Smith et al. 1997). In that task, monkeys were presented with a pixelated box on a computer screen, and they had to touch that box using a joystick-controlled cursor if it contained exactly 2,950 pixels. If it contained any fewer pixels, they had to classify it as sparse by selecting a large S on-screen. The third response option was the uncertainty response, which in that experiment provided the monkey the chance to avoid classifying the pixel box as sparse or dense and also guaranteed an easier next trial. Monkeys and adult humans engaged this task and provided strikingly

similar results. At the point at which both species showed objectively (through performance) that they could not tell whether the box contained 2,950 pixels or fewer, both species also showed the highest proportion use of the uncertainty response. This first experiment led to the claim that rhesus monkeys, like humans, monitored uncertainty and recognized difficult trials in a way that allowed them to “escape” those trials.

Subsequent experiments also tested humans and rhesus monkeys but with variations on the discrimination task. In one such study, subjects had to determine whether two boxes on-screen were equally sparse (or dense) in their pixelation or were different, or they could avoid making that response by choosing the uncertainty response (Shields et al. 1997). Again, these species performed highly similarly in avoiding the trials on which errors were most likely. In another test, monkeys first judged the density of a pixel box but then made a secondary confidence judgment that involved placing a low-risk, low-reward wager or high-risk, high-reward wager on that classification. Monkeys used a 2-level scale appropriately, although they could not use a 3-level scale (Shields et al. 2005).

In one of the strongest demonstrations of metacognitive monitoring by monkeys, Smith et al. (2006) trained monkeys to perform blocks of four successive trials of classifying pixelated boxes of varying density before they received any feedback as to how they performed. This meant that monkeys saw four stimuli in a row, classified each of those as dense or sparse, and then got feedback rearranged so that all rewards were delivered first and then all time-outs (for incorrect answers) were presented. Functionally, this made it very difficult to match specific responses to specific stimuli in terms of reinforcement or punishment outcomes. The question was how monkeys (and humans) used the uncertainty response in this case, and there was again high similarity across species. Most importantly, in some cases the monkeys’ pattern of responding showed that, under this deferred feedback, they mistakenly “centered” the sparse to dense continuum at the wrong place, and yet this is

also where they escaped the most trials. This showed that they escaped trials that they thought must be most difficult, even though those trials were not most difficult (i.e., the monkeys got more of these trials correct when classifying them than other stimuli that they answered often but escaped rarely). This dissociation of reinforcement structure and uncertainty responding was an important result for extending the case that monkeys engage in metacognitive monitoring (also see Couchman et al. 2010).

A later experiment also extended the demonstration of monkey metacognition using the sparse-dense task and a technique called cognitive loading. Smith et al. (2013) again gave rhesus monkeys pixelated boxes to classify as sparse or dense, but they also introduced a concurrent task that required the monkeys to retain in memory a stimulus for later recognition. When this concurrent cognitive load was present, monkeys’ ability to adaptively escape hard sparse-dense discrimination was negatively affected. However, cognitive load did not affect sparse and dense judgments themselves, nor did it affect monkeys’ ability to objectively classify stimuli as being in the middle density range. This demonstrated that uncertainty responses were uniquely affected by cognitive load, suggesting that these responses were executive-attentional responses rather than responses made under reinforcement-based stimulus control.

In another study (Zakrzewski et al. 2014), rhesus monkeys classified stimuli as sparse or dense, and correct responding led to increases in an on-screen collection of tokens that could be exchanged for food reward. However, errors erased the accumulated tokens and any possible rewards. Now, monkeys had to decide when to “cash out” their tokens and decide how certain they were about the density of a stimulus relative to how many tokens were at risk on that trial. As would be expected if uncertainty monitoring is flexible and responsive to things such as cost-benefit analyses during decision-making, the monkeys become more likely to escape a particular trial difficulty level if they had more tokens at risk on that trial. If they had few tokens at risk,

they made more classifications, even though the objective level of pixelation was the same in both cases. This result indicated that monkeys modulated their threshold for indicating uncertainty based on the stakes of the trial.

Not all species perform the dense-sparse task with equivalently proficient use of the uncertainty response. Capuchin monkeys (*Cebus apella*) have been presented with the two-response-class version of the task (calling a pixelated box either sparse or dense). Their perceptual acuity for denseness and sparseness matched that of rhesus monkeys, but capuchin monkeys only rarely integrated uncertainty responses into their performance. However, when given the chance to classify pixelated boxes in the middle of the stimuli continuum to the objective response class of middle, they did so proficiently (Beran et al. 2009). This outcome began a series of experiments to determine why capuchin monkeys may show less metacognitive monitoring and control relative to rhesus monkeys (and apes in other kinds of tests). In one such test, it was found that capuchin monkeys would not use an uncertainty response when faced with making sparse-dense discriminations even when all response classes were unrewarded, thereby making them equivalent in terms of positive reinforcement and punishment (Perdue et al. 2015).

The sparse-dense task has only been used with one non-primate species – pigeons. Sole et al. (2003) presented pigeons with pixels on a screen to be classified as sparse or dense. The pigeons did what monkeys and humans had: they opted out of exactly those trials they most likely to err on. However, other aspects of their behavior, such as performance on forced trials versus trials the pigeons opted to take, did not show differential performance, a result in contrast with human and nonhuman primate data and a result at odds with a strong claim of metacognitive ability. Thus, when applied across species, the sparse-dense task has had a substantial impact on understanding metacognition as it may emerge in other species and as it may operate in varied contexts of perceptual difficulty and risk.

The sparse-dense task also has been used in studies that tested humans exclusively. In one study (Paul et al. 2015), human participants classified a pixelated stimulus as sparse or dense while in an fMRI machine that monitored brain activity. Use of the uncertainty response was associated with a distributed network including prefrontal cortical (PFC), anterior and posterior cingulate cortex (ACC, PCC), anterior insula, and posterior parietal areas. Task difficulty was dissociated from these brain areas and their relation to uncertainty monitoring, and so this result also pointed to the uncertainty response as being more likely a declarative indication of uncertainty than a response tied to associatively learned reinforcement outcomes or punishments.

## Cross-References

- [David Washburn](#)
- [John David Smith](#)
- [Meta-Cognition](#)
- [Metamemory](#)
- [Uncertainty Paradigm](#)

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## Spatial Abilities

### ► [Spatial Orientation](#)

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## Spatial Learning

- [Rodentia Navigation](#)
- [Susan D Healy](#)
- [Swine Cognition](#)

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## Spatial Learning and Memory

### ► [Spatial Orientation](#)

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## Spatial Orientation

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## Synonyms

[Navigation](#); [Spatial abilities](#); [Spatial learning and memory](#); [Visuospatial memory](#)

## Definition

Spatial orientation refers to the ability of organisms to navigate. It is essential for their survival.

## Background

While navigating, we become familiar with an environment and acquire knowledge about it, thereby extracting information from it and storing this information in our memory so that we can recall it later for a variety of purposes (Ekstrom et al. 2018). Examples concerning rodents and humans will be presented since there is an important parallelism between them when dealing with spatial tasks. However, most of the examples will focus on how males and females differ when solving these tasks – on something that has recently been referred to as “qualitative” sex differences – thus counteracting the unjustified practice of ignoring females for so many years in psychological and biomedical research (for a review see Beery and Zucker 2011). To understand the sexually dimorphic spatial abilities between males and females – which are so influenced by sex hormones – a specific explanation, the range size hypothesis, will be discussed. For different reasons, this hypothesis applies to both rodents and humans. A brief description

of the role of the hippocampus while navigating and of the evolutionary origins of the human species is also presented. For navigational strategies and mechanisms used by rats see “► [Rodentia Navigation](#)” in the present issue (for the same in humans, see Ekstrom et al. 2018).

Although historically it has been assumed that sex differences do not exist or are not important beyond the reproductive system, this view has changed drastically in the last two decades. As it is widely recognized today a critical problem of ignoring females for so long has been the inability to understand the potential magnitude of the effect of sex on the outcome being measured, with the consequence of important problems in the reproducibility of basic research (Cahill 2006). No doubt research conclusions are needed that can be applicable to all. This requires sex as a biological variable “from womb to tomb.”

### **Sex Differences While Solving Spatial Problems**

Experiments on spatial learning and memory have shown that males and females of many mammalian species, including humans, often differ in their use of cues for spatial navigation (for reviews see Halpern 2012; Kimura 2000; Mackintosh 2011). It is not just that males tend to learn to solve a spatial problem faster than females, but that males and females can use different strategies to solve the same problem (i.e., this is what is considered a “qualitative” sex difference). In both rats and humans, males seem more likely to rely on geometrical information to reach a goal, while females are more likely to use landmarks.

Williams et al. (1990) showed that female rats have a clear tendency to use landmarks, such as specific objects and pictures on the walls, when solving spatial tasks, while male rats prefer geometric cues or sources of information, such as the shape of the testing room. Moreover Williams et al. found that if there were no landmarks available, the females used the geometric cues; however, males preferred to use the geometric cues, practically ignoring the landmarks. A similar difference in the preferred mode of solution has

been obtained with human participants, while using different navigational tasks (Sandstrom et al. 1998; Ward et al. 1986). For example, Ward et al. (1986) study how college students, males and females, give directions from maps – either perceptually available or committed to memory. Different aspects of direction giving were recorded. The results clearly revealed that when giving directions, women tend to use landmarks as points of reference, while men tend to use distance or cardinal directions (like North, South, East, and West). In the study by Sandstrom et al. (1998), male and female participants navigated through a virtual water maze where both landmarks and room geometry were available as distal cues. Manipulation of environmental characteristics revealed that females relied predominantly on landmark information, while males more readily used both landmark and geometric information.

Due to the important parallelisms between rats and people, recent research by Rodríguez et al. (2010) explored these “qualitative” sex differences in rats. The aim of the study by Rodríguez et al. (2010) was to evaluate whether there are differences in the way that males and females solve a simple but highly controlled spatial task in a modified Morris pool. In their Experiment 2, rats were trained in an unusual triangular-shaped pool to find a hidden platform, whose location was defined in terms of two sources of information: one landmark next to the platform, outside the pool, and one particular corner of the pool (see Fig. 1a, top-left). Three subsequent test trials without the platform were conducted. The first test trial pitted the two sources of information – landmark versus pool-shape – against one another (i.e., a preference test – see Fig. 1a, top-right). The results revealed that females spent more time searching the platform in an area of the pool next to the landmark, while males spent more time in the corner of the pool where the platform had originally been located (see Fig. 1b). In the following two tests the two sources of information were presented individually (i.e., learning tests – see Fig. 1a, bottom) and the results showed that both sexes had learned about both cues: males performed significantly better on the shape than



**Spatial Orientation,**

**Fig. 1** Experiment 2:

A schematic representation of the pool and the position of the landmark, X, as well as the hidden platform (*P*).

(a) (Top): Left panel, for acquisition; right panel, for test 1. (Bottom): for tests

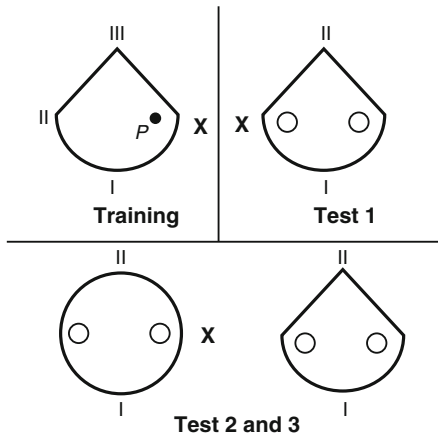
2 and 3 (right, testing the shape cue; left, testing the landmark cue).

(b) Mean time spent in the two recording areas (shape and landmark) by the subjects during test trial 1.

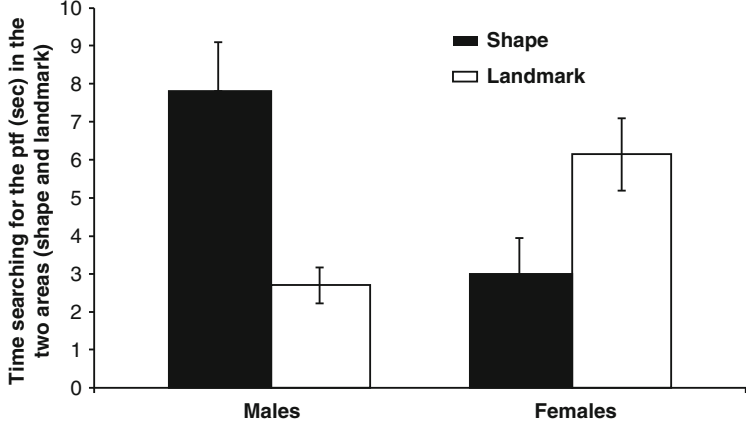
(c) Mean time spent in the two recording areas (shape or landmark and control) by the subjects during test trials 2 and 3 (shape and landmark, respectively).

Error bars denote standard error of means. (After Rodríguez et al. 2010 – with permission)

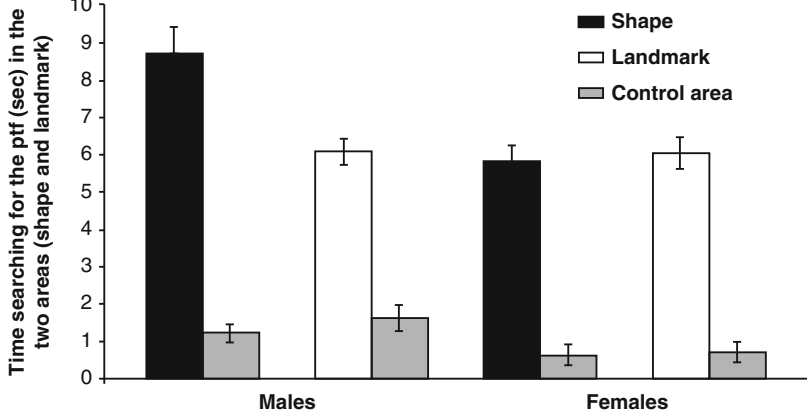
**a**



**b**



**c**



the landmark test, while females performed equally well on both. In addition, males spent more time searching for the platform in the target area on the shape test than females (see Fig. 1c). In conclusion, despite having clearly differentiated preferences, males and females process and can

use both geometric and nongeometric sources of information when they were presented together in the acquisition phase. Thus, this study shows a clear distinction between learning and performance, which was possible to gauge due to the different measures used in the three test trials.

A subsequent study by Rodríguez et al. (2011), where cue competition designs were used, confirmed the previous conclusion that shape (i.e., geometry) is clearly more salient for males, and landmarks somewhat more salient for females. Employing the same apparatus and general procedure as Rodríguez et al. (2010), this new study showed an asymmetrical overshadowing effect in both sexes. In males, shape overshadowed landmark learning, but landmark learning did not overshadow learning about shape; while in females, landmark learning overshadowed learning about shape, but shape learning did not overshadow landmark learning. It was the more discriminable, salient, or preferred source of information (shape or pool-geometry for males and landmark for females, as shown by Rodríguez et al. 2010) that overshadowed the less discriminable, salient, or preferred cue. The study by Rodríguez et al. (2011) helps to explain a frequently reported failure in the literature of landmarks to overshadow or block learning about geometry in male rats.

Importantly, in both studies (Rodríguez et al. 2010, Experiment 1; Rodríguez et al. 2011, Experiments 1 and 2a) the possibility that the estrus cycle of females could influence their performance was examined. It did not. There is one difference between the procedures used by Rodríguez et al. (2010, 2011) and those employed by Williams et al. (1990) that should be noted: in the experiments by Rodríguez et al. the landmark and the correct corner of the pool could be regarded as beacons which the rats learned to approach, whereas in the Williams et al. experiment the landmarks and shape of the room can hardly have acted as beacons. It is an open question whether this difference is important: but the parallel between these studies suggests that it may not be.

Taken together, all the data in the present section show that in the two species, rats and humans, adult males and females clearly differed in their preferred cues to solve navigation tasks. Importantly, a further study in rats by Rodríguez et al. (2013) with the same apparatus and general procedure as Rodríguez et al. (2010) revealed a different result when the rats were prepubertal.

Specifically, juvenile female rats behaved like males (both adult and juvenile), but unlike adult females, when searching for the platform in the preference test trial. This result reveals a change in the behavior of female rats as they grow older. Why is this? Based on the observation that ovariectomized females behaved like younger rather than older rats, Rodríguez et al. (2013) suggested that the obvious answer was that the hormonal changes associated with the onset of puberty changed the females' preference. That young female rats behave like males on a spatial task, while a sex difference appears only after puberty is consistent with the suggestion that sex differences in spatial cognition in humans appears due to the hormonal and cognitive changes associated with puberty (for a meta-analysis on this issue see Voyer et al. 1995).

### One Biological Explanation That Strengthens Over Time

A large number of hypotheses have been proposed to explain the qualitative, as well as other quantitative, sex differences often found in the spatial domain (for a review see Jones et al. 2003). Jones et al. (2003) concluded that the best predictor of the sex difference was range size, a biological hypothesis. This hypothesis is consistent with the argument that the differences found in males and females of many mammalian species are the result of some form of *natural selection*. Specifically, that both sexes have developed different strategies for spatial navigation and search due to a selective pressure of the environment, giving rise to different skills. In humans, the critical reason being that for a long time men hunted and women gathered. In other animals the most frequent explanation refers to polygyny, a mating system in which one male mates with several females in a single breeding season.

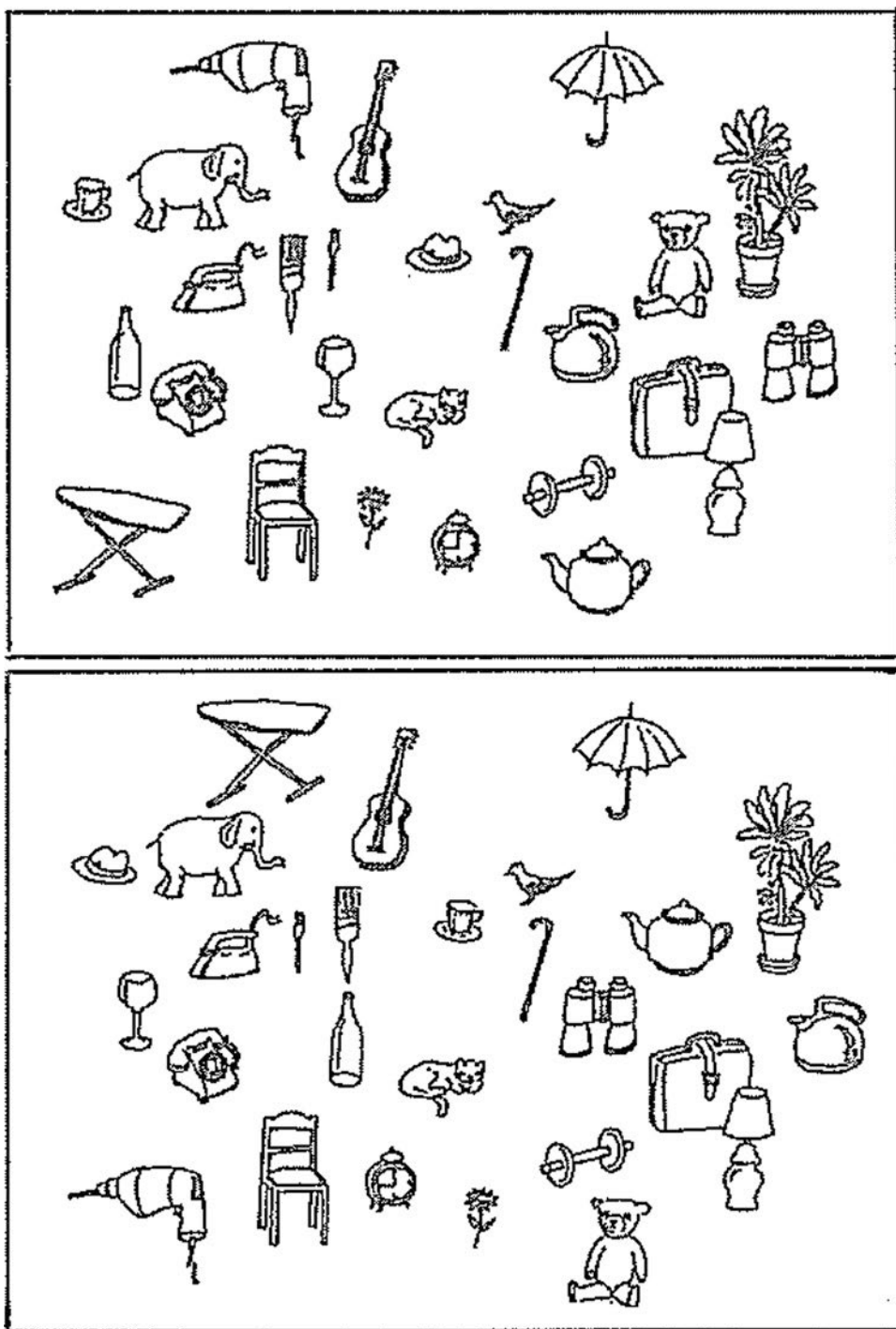
In agreement with the previous claim favoring males, in rats it has been found that different species of vole have a different range size between males and females depending on their mating system: males occupy a larger home range than females only if they are promiscuous, and not if

they are monogamous. When males occupy a larger home range than females, they also show superior spatial ability. The promiscuous male meadow vole is better than the female at several maze learning tasks (Gaulin et al. 1989), but in monogamous prairie and pine voles, there is no sex difference in maze tasks. The sex difference in meadow voles has also been observed in the Morris pool, which suggests that the result is strong in spite of using different tasks. Polygynous male deer mice are better than females at spatial learning, but again there is no sex difference in monogamous kangaroo rats (Jones et al. 2003).

Let's consider a pioneering study by Silverman and Eals (1992), which has expanded in humans the previous hypothesis, range size. According to these authors, the critical reason to explain the range size hypothesis is the division of labor that occurred in our earliest ancestors, where males were primarily hunters of mobile prey and females gatherers of immobile plant foods. Consequently, spatial abilities associated with hunting were naturally selected in males (and some typical tests that are currently used to measure these abilities include mental rotations, map reading, and different forms of maze learning); while spatial abilities related to gathering were naturally selected in females (and the measures suggested by Silverman and Eals include recognition and recall of spatial configurations of objects, as well as incidental learning for objects and their locations). They claim that our evolutionary history is thus responsible for different attributes in men and women when dealing with spatial tasks. A bias favoring men should be expected in those tasks reflecting abilities appropriated to hunting; while a bias favoring women should be expected in those tasks reflecting abilities appropriated to gathering. Therefore, sex differences in the spatial domain are expected to be task dependent. In their surprising work (Silverman and Eals 1992), they present a series of four studies that explore the hypothesized female spatial specializations by means of foraging scenarios. Briefly, in Study 1 – a pencil and paper test – university students of both sexes were asked to memorize the position of 27 objects

which were drawn on a sheet of paper. They had a minute to study the array. Following this, the sheet of paper was hidden and a new sheet of paper with some new items added was presented to the participants. They were asked to identify the new items in the second sheet of paper. The results showed that females were better at this task than males. Most importantly was the demonstration, in a third sheet of paper presented to the students, that females were also better when, instead of adding some new items to the initial array, the experimenters moved some of the items in the first sheet of paper to a different location – as shown in Fig. 2 – and the main task was to identify the moved items (i.e., a test of spatial or location memory). This better spatial memory score by females was not found if the participants were prepubertal (Study 4). Silverman and Eals (1992) emphasized that their results give clear support to the hypothesis that sex differences in the spatial domain are task dependent.

Two experimental field studies (Pacheco-Cobos et al. 2010; Vashro and Cashdan 2015) support the expanded range size hypothesis in humans. The work by Pacheco-Cobos et al. (2010) addresses the hypothesized female spatial specializations predicted by Silverman and Eals (1992). Specifically, the study focuses on the foraging techniques and success rate of Mexican men and women from a small village, San Isidro Buensuceso, as they searched for edible mushrooms on the slopes of La Malinche volcano, a region whose inhabitants have a long tradition of collecting mushrooms. The authors GPS tracked the foraging pathways of pairs of men and women from San Isidro Buensuceso while searching for mushrooms. Measures of costs, benefits and general search efficiency were analyzed and related to differences between the two sexes in foraging patterns. Although men and women collected similar quantities of mushrooms, men did so at significantly higher cost. They travelled further, to greater altitudes, and had higher mean heart rates and energy expenditure (kcal). They also collected fewer species and visited fewer collection sites. The authors conclude that in terms of search strategies developed for gathering wild mushrooms, and presumably other wild plants,



**Spatial Orientation, Fig. 2** Silverman and Eals' (1992) Object Location Memory task. Top: sheet of paper 1. Bottom: sheet of paper 3. (Reproduced with permission)

women outperform men. The women proved to be more efficient foragers than men in energy efficiency terms since they collected significantly more mushrooms while expending significantly less energy in doing so. These results provide the first support from a field study for the idea of a domain-specific spatiotemporal advantage for women in the type of foraging context that has probably been important for ancestral human females, as predicted by Silverman and Eals (1992). In agreement with the authors, similar studies are needed for other cultural groups, and for the gathering of different resources, such as firewood.

The study by Vashro and Cashdan (2015) focuses on the relationship between spatial-cognitive ability and range size in a population (the Twe and Tjimba of northwestern Namibia) that faces navigational challenges similar to those that faced many of our earliest ancestors, and tests the hypothesis that increased range size and better spatial ability confers fitness benefits (more mates and more children) for men. Data on range size, spatial ability, and reproductive success are combined in this study, in which the tasks employed were: mental rotation, water-level, object location memory task, pointing, range size measures, and reproductive history. The main results showed that Twe and Tjimba men have larger visiting ranges than women and are more accurate in both spatial (mental rotations) and navigational (accuracy pointing to distant locations) tasks. Men who performed better on the spatial task not only travelled farther than other men, but also had children with more women. Vashro and Cashdan (2015) argued that these findings offer strong support for the relationship between sex differences in spatial ability and ranging behavior, and identify male mating competition as a possible selective pressure shaping this pattern. The authors concluded that the benefits of increased mating range, increased hunting range, increased raiding ability, and women's preference to limit their range size may all have added to the selective pressure favoring sex differences in range size, navigation, and spatial cognition.

Taken together the main implication of the research in this section is that males and females

in the two species, rats and humans, have a very long evolutionary history which seems to be responsible, at least partly, of naturally "selecting" those traits of individuals that enhance their survival, giving rise to differential spatial abilities in the two sexes.

## **The Role of the Hippocampus in Spatial Learning and Memory**

The hippocampus plays a critical role in spatial learning and memory (Ekstrom et al. 2018; O'Keefe and Nadel 1978). Although hippocampal lesions do not impair rats' ability to swim to a visible platform in a Morris pool, such lesions have a drastic effect on their ability to swim to an invisible platform (Morris et al. 1982; Pearce et al. 1998). Morris et al. (1982) concluded that the performance of the task in which the rats had to learn about the location of a hidden platform in relation to distal cues is hippocampal-dependent but not the other kind of task in which the platform is visible, thus supporting the idea that the ability of navigation, which is essential for the survival of animals, depends critically on the integrity of this limbic structure. The following question has been repeatedly asked for many years. Is hippocampal volume different in the two sexes? The hippocampal complex (i.e., hippocampus and entorhinal cortex) is larger in male than in female rats, kangaroo rats, and polygynous species of voles (Kimura 2000). The importance of a sex difference in human hippocampal size is more controversial (McCarthy 2016). As Cahill (2006) has suggested, males and females of many mammalian species evolved under some similar, and some very different pressures. Thus, their brain organization would be expected to be both similar in some respects, and very different in others. This is precisely the situation found in the sex difference literature when dealing with spatial tasks.

There have been few studies that have used both sexes to understand the functional role of the hippocampal complex. For one exception see Roof et al. (1993). The Roof et al. (1993) study addressed working spatial memory in a Morris pool. They found that unilateral lesions of the



entorhinal cortex resulted in a differential performance in male and female rats. Specifically, males' performance was drastically impaired whereas females showed only a slight impairment, independently of the size of the lesion. These results already suggested that the role of both the hippocampus and entorhinal cortex in spatial learning seems to be different in males and females. Roof et al. (1993) ended their work by claiming that "Whatever the mechanism underlying the recovery or lack of impairment in females, it is clear from these results that more attention must be paid to the study of gender differences in determining or specifying structure-function relationships in the central nervous system. It is also clear that the issue of gender must be given more weight in planning and developing treatment and rehabilitation strategies for brain-damaged patients" (p. 50). Unfortunately, at present, most basic research in neuroscience is still conducted with males only.

In humans, a frequent way to understand the importance of the hippocampus while navigating has been to study London taxi drivers. Drivers of Black Cabs are not allowed to have satnavs, therefore they can only use their memory in order to navigate between more than 25,000 streets and thousands of places of interest. The exam to obtain permission to drive one of London's iconic *black cabs* is considered one of the most difficult in the world. It is known as "The Knowledge." At present, there are approximately 21,000 black cabs operating in London, although only around 2% of them are women. In a classic study conducted by Maguire et al. (2000), the relationship between spatial memory and grey matter in the hippocampus was studied in London taxi drivers. Maguire et al. (2000) found that grey matter in the hippocampus positively correlated with years of driving experience. Subsequent work by the same authors where more sophisticated techniques were used (such as functional magnetic resonance imaging – fMRI) replicated and expanded the previous results. Together these studies show that the hippocampus has an enormous flexibility and that the daily experiences we engage in can have an impact on it. This is also true when virtual tasks are used. For example, a

recent study by West et al. (2018) has provided the first evidence that activities such as action video games can reduce grey matter in the hippocampus and that this impact is mediated by a person's learning strategy. This is most important because low grey matter in the hippocampus is a risk factor for developing many neuropsychiatric illnesses. No doubt more work is needed in this fascinating line of research (West et al. 2018).

In conclusion, although currently it is well known that the hippocampus can be crucial when considering spatial tasks, recent research has revealed that other parts of the brain are also involved in these tasks, so that the main role of the hippocampus could be as an integrator "hub" in the brain (Ekstrom et al. 2018). Future work will have to deal with the many unanswered questions, including those related to sex differences.

### **Our Earliest Ancestors: Hunter-Gatherers Societies and Human Evolution**

Nomadism and the absence of private property are the two most important characteristics of the *hunter-gatherers* societies, in which men and women collaborated for subsistence. The understanding of the way of acting of those men and women is fundamental to understand the origin of humanity itself. Paleolithic societies are defined as nonproducers, acquiring their plant resources through harvesting, and animals through fishing, scavenging and hunting. This last one developed enormously during the Paleolithic, from being an opportunistic and indiscriminate hunting it become more specialized and the acquisition of resources, more diversified. Human hunting differs qualitatively from hunting by other animals. Unlike most animals, which either sit and wait to ambush prey or use stealth and pursuit techniques, human hunters used a wealth of information to make context-specific decisions, both during the search phase of hunting and when the prey has been caught (Clottes 2008; Fernández Martínez 2007; Kaplan et al. 2000). Hunter-gatherer societies lasted for over one hundred thousand years. This is much longer than all of recorded history.

Undoubtedly, our present predispositions must be a result of such a long period. Currently only a few such societies remain (such as the San Nyae Nyae Pam of Namibia, the Twe and Tjimba of North-western Namibia, or the Hadzabe in Northern Tanzania). These societies often constitute an authentic window to the past (like the study by Vashro and Cashdan 2015), thus complementing the information found at archaeological sites – the only direct testimonies that have reached us until today.

Since our split from the chimpanzee lineage, the human evolutionary branch underwent many great changes, like an increase in brain size with respect to the rest of the body, smaller teeth, bipedalism, great manual dexterity, the ability to make and use tools, satnavs, etc. Our evolutionary story is not linear. Rather, like other animals, the human family tree is much more like a bush made up of a variety of “adaptive radiations” in response to changing environmental circumstances (Fernández Martínez 2007). A frequently asked question in the literature among anthropologists is how was the labor collaboration between men and women done? Here are two opinions of experts. In his beautiful book addressed to his grandchildren Clottes (2008) says “the men, physically stronger, were engaged in hunting. While the women, who took care of the children and accompanied the older members of the family clan, had the mission of collecting all kinds of edible wild fruits and locating dead animals from which meat could be used” (pp. 43–44). According to Kaplan et al. (2000), “human pair bonding and male parental investment is the result of complementarity between males and females. The commitment to caring for and carrying vulnerable young, common to primate females in general, together with the long period required to learn human hunting strategies, renders hunting unprofitable for women” (p. 173). Several reasons have been used to explain this division of labor. Men are, in general, taller than women and they are also more muscular. Thus, women tend to have less physical strength than men, and a lot of physical power is required to throw spears and missile weapons at large-game. In addition, women are more valuable than men because they

have children. The group survival depended on women and, therefore, it was important for the group to avoid their implication in situations of great danger. The differences between men and women are largely due to different hormonal actions during development (i.e., testosterone production in men and estrogen production in women). Contrary to what was believed for a long time (Kaplan et al. 2000) recent research has shown that collecting mushrooms, wild fruits, and edible plants (activities that women and children mainly did) constituted up to 60–70% of the food. Nowadays it is considered that these activities were more important in the long term than that of large-game hunters for the survival of the group (Clottes 2008; Fernández Martínez 2007; Mackintosh 2011). From the perspective of human evolution, the gender-specific tasks (i.e., men primarily hunters, while women primarily gatherers) are an excellent example of cooperation between men and women due to a selective pressure of the environment to solve adaptative problems, ultimately to ensure the perpetuation of the human species.

In conclusion, as we saw in section “[One Biological Explanation That Strengthens Over Time](#),” evolution by natural selection seems to have been the process of adapting human males and females attributes to best function in their environment. The spatial domain is not an exception. A sensible view would be to consider that males should not be regarded as more highly spatially specialized than females, but differently specialized, as claimed by Silverman and Eals (1992). If we refer to the ability to navigate in large spaces, men tend to have a better performance than women. On the contrary, if we refer to the ability to navigate in small spaces, the opposite is usually frequent and women tend to have a better performance than men.

## Final Conclusions

At present, it is well known that the brain has a great plasticity and that activities we engage in during our daily lives have a direct impact on it. For example it has been shown (West et al.

2018) that 90 h of action video games can shrink the hippocampus. Considering this evidence, what could we expect after ten millennia of the division of labor? This is an open question waiting for clear answers. At least different predispositions to attend to various sources of spatial information could be expected due to our evolutionary history. No doubt, cognitive intervention programs at schools (for example, different types of games – geometric for girls and spatial memory ones for boys) could help to reduce the sex differences observed in adulthood. Furthermore, it is quite remarkable that young baby boys and baby girls differ when mental rotation tasks with 3D objects are used (Lauer et al. 2015; Moore and Johnson 2008). These results reveal clear sex differences in the spatial domain long before puberty which are difficult to explain, thus weakening the apparent parallel between rats and humans. Future research will have to deal with the very many unanswered questions.

A final thought refers to technology. Is it really good for us? Are not we atrophying our grey matter in the hippocampus with so much dependence on satnavs or GPS for example? Following GPS indications resembles a route following task, where a specific part of the striatum, the caudate nucleus, can be very active. Recent research has shown (for a review see Ekstrom et al. 2018) that the caudate nucleus shares an inverse relationship with the hippocampus, in both humans and rodents (i.e., increased grey matter in one structure is correlated with decreased grey matter in the other). Consequently, with so much dependence on technology, we could be impoverishing ourselves as a species. This worrisome situation should be taken more into account in the new spatial habits we are acquiring.

## Cross-References

- [Charles Darwin](#)
- [Cognitive Map](#)
- [Evolution](#)
- [Geometric Module](#)
- [Homo sapiens](#)
- [Natural Selection](#)

- [Puberty](#)
- [Rodentia Navigation](#)
- [Sex Hormones](#)
- [Sexual Dimorphism](#)
- [Visuospatial Memory](#)

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## Spatial Recognition

### ► Cognition

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## Spatial Reorientation

### ► Geometric Encoding

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## Spawning

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## Synonyms

[Egg deposition](#); [Egg release](#); [Reproduction](#)

## Definition

The act of gamete release in aquatic environments.

## Introduction

Spawning refers to the process of depositing the gametes into the water. It is thus a characteristic of “ovuliparous” organisms in which eggs are fertilized by sperm externally. The vast majority of anamniotes (fish and amphibians) and aquatic invertebrates reproduce in this way. Aquatic species in which there is internal fertilization and where the females lay zygotes (zygoparity) and early embryos (embryoparity) or where the young are born alive (viviparity) are not considered spawners. On the other hand, the deposition of gametes in moist terrestrial habitats such as the emergent leaves of aquatic plants (e.g., the characin *Copeina arnoldi*) or on beaches above the breaking waves of the open coast (e.g., the

California grunion, *Leuresthes tenuis*) should be considered as spawning (terrestrial and beach spawning, respectively).

## Spawning Site Selection

Spawning methods are diverse. Broadcast-pelagic spawners (pelagophils) shed their gametes in staggeringly large quantities into the water where they are mixed in clouds and fertilization occurs. One of the most spectacular spawning events to occur on aquatic ecosystems is the mass reproduction of corals simultaneously releasing tiny egg and sperm bundles from their polyps into the water. This is the point where parental contribution ends and the fertilized eggs are simply left to the mercy of the perilous aquatic world where predators, starvation, and adverse environmental conditions will only allow a small fraction to survive and be recruited into the population. This *r*-selected strategy seems suitable for the unstable and unpredictable oceanic environment, which explains why most marine organisms, regardless of their ocean-neritic or pelagic-benthic distribution, produce pelagic eggs. The pelagic zone can host vast amounts of spawn, while food particles – especially in the euphotic zone – are readily available and in abundance for the first-feeding larvae. In addition, pelagic embryos have improved chances to expand the distributional coverage of marine populations through passive movement. Eggs of marine fishes are usually smaller (about 1.0 mm in diameter) and almost always buoyant and liberated into the pelagic zone.

In freshwater environments the share of food in the water column is not as abundant as in the pelagic environment, and due to low salinity, fertilized eggs do not float as easily. Also, the embryos that are deposited in the column – especially in rivers and streams – are in danger of being dragged by raging waters far from their parental habitat or even transported to the sea. Therefore, freshwater organisms usually produce eggs attached to the substrate, vegetation, or even nests built by their parents who then exhibit higher rates of parental care. Ovuliparous amphibians such as frogs lay a gelatinous mass of eggs (frogspawn) in ponds and

ditches. Freshwater fish eggs are more likely to be larger (1.0–2.0 mm in diameter) and to be attached to weed or stones, and some are laid in nests or brooded in various ways. Such patterns have been known to humans for thousands of years. Aristotle gave a precise description of the process of spawning for some freshwater fish such as *Silurus glanis* (also known as Aristotle's catfish) which “deposits its spawn in a continuous string, as frogs do; so twisted is this fetation and so even that fishermen in the marshes can unwind it off the reeds like thread” (Ganias and Voultsiadou 2017).

## Exceptional Patterns

Variations to the above general rules can be encountered in both marine and freshwater organisms. For example, even if parental behavior is more common in freshwater than in marine fish (Baylis 1981), some littoral species of bullheads (Cottidae), blennies (Blenniidae), and gobies (Gobiidae) protect their eggs which are simply attached to the substratum (Bone et al. 1997). Although nonfloating kind of eggs may be best suited to freshwater, there are a few species, such as gouramis and grass carp, who produce buoyant eggs (Bone et al. 1997). On the other hand, although marine eggs are almost always buoyant and liberated into the pelagic zone, herring (*Clupea harengus*) and capelin (*Mallotus villosus*) are exceptions, laying sticky demersal eggs that adhere to weed or gravel on the sea bed or in the intertidal zone.

## What Makes an Egg Buoyant?

Egg size in pelagophil fishes is exceptional in that apart from the optimization of offspring quality and size it also reflects the egg volume adjustment that is necessary to counterbalance heavy chorion material in order for the egg to be buoyant. This adjustment is mainly achieved by increasing the aqueous content of the egg through a sequence of events that occur both in utero, at the oocyte stage, and after ovulation and spawning, at the egg stage (Jung et al. 2014).



However, most of the water uptake occurs during the reinitiation of meiosis (final oocyte maturation), before ovulation, a process known as “oocyte hydration” (Thorsen and Fyhn 1996). This process renders the eggs and early embryos buoyant in the seawater, allowing their survival and dispersal in the ocean. In both marine and freshwater pelagophils, one or more oil globules, which are greatly oversized in some freshwater species, form an additional hydrostatic organ.

## How the Eggs Meet with Sperm in the Wild

The likelihood that eggs and sperm will meet in the water is increased through various eco-ethological adaptations such as the interaction of the sexes and the formation of spawning aggregations. Females and males seem to synchronize ovulation and milt production and communicate through chemical signals called pheromones. Sorensen et al. (2004) suggested that the maturation-inducing steroid, 17,20bP, and its sulfated metabolite, 17,20bP-S, are the primary components of the preovulatory pheromone, which affects male fish, acting through specific olfactory receptors. The haddock (*Melanogrammus aeglefinus*), for example, goes through quite an elaborate courtship involving visual displays by the male and vocalization (Hawkins and Amorim 2000). In many fish species, even in pelagic spawners, males and females interact often on a one-to-one basis.

Spawning aggregations are groups of conspecifics gathered for the purpose of spawning with densities or numbers significantly higher than those found in the area of the aggregation during nonreproductive periods. Spawning aggregations may be resident or transient and are usually spatially predictable, found at sites in association with particular physical characteristics. Their formation can also be predictable in time, occurring in phase with circadian rhythms, at seasonal, lunar, diel, or tidal periodicities. Most published information on spawning aggregations refers to teleost fishes, a smaller number of publications refer to invertebrate species (mostly cephalopods), and only few publications refer to sharks

and other vertebrate organisms. The formation of spawning aggregations is quite usual in coral reef fishes such as the groupers (Serranidae) and the snappers (Lutjanidae) (Claydon 2004). However, other fish such as the benthopelagic gadoids, especially the cod, *Gadus morhua*, also form spawning aggregations. Spawning aggregations are postulated to reduce predation on both adults and their offspring, to increase mating success and fertilization rate, and to help regulate the sex ratio in some populations.

## Cross-References

- [Eclosion](#)
- [Fertility](#)
- [Ova](#)
- [Ovaries](#)
- [Reproduction](#)

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## Speciation

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## Synonyms

### Cladogenesis

## Definition

The process of formation of new species during the course of evolution is called speciation. It occurs when a group within a species separates from the other members of the group and develops its own characteristics. Therefore, speciation involves the splitting of a single evolutionary lineage into two or more genetically independent lineages. This differentiation into the new species is dictated by the evolutionary factors (National Geographic 2011).

The rate at which the diversification of the species is taking place can be understood roughly by assuming that there are  $\sim 10^7$  different species on earth, if bacteria and archaea are not accounted for (Mora et al. 2011), and life originated on earth singly  $\sim 4 \times 10^9$  years ago. These estimates indicate that the average diversification rate can be calculated as 0.0025, meaning that one new species is formed every 400 years. This is an underestimate, primarily because it does not account for extinction events or bursts of speciation and secondarily because microbes are undercounted. Moreover, an important point to be mentioned is the presence of the intermediate forms, which emphasizes the fact that speciation is a continuous process (Mallet 2008).

An important example of speciation is that of Galápagos finches. The Galápagos archipelago,

located in the Pacific Ocean off South America, is a host to many species of finches. Each species is on an island, separated from each other geographically by means of the ocean. Therefore, over a period of 2–3 million years (Grant and Grant 2011), each species of the finch has developed unique beaks that are especially adapted to the specific food available on each island. The food available to them is widely different due to their presence on different islands separated by oceans. The beaks range from being large and blunt for breaking into hard nuts to long and thin for probing into cactus flowers (Abzhanov 2010).

## Modes of Speciation

As has already been described, speciation, or cladogenesis, is the process in which one population lineage splits into two or more distinct lineages. This process is fundamentally different from anagenesis, in which an interbreeding population gradually changes over time until it reaches a point where it becomes sufficiently distinct from its ancestors (Emerson and Patiño 2018). Four modes of speciation have been generally described in literature:

### Allopatric Speciation

Allopatric speciation is the speciation that occurs when a population is split into two due to geographical isolation, for instance, formation of a mountain or separation due to an ocean, as in case of the Galápagos Islands finches. Another example is that of the squirrel population in Arizona's Grand Canyon. Before the formation of this canyon, only one population of the squirrel existed, but, after the formation of this geographical barrier, that squirrels could not cross, they were split into two populations due to the absence of interbreeding. As a result, currently, the north and south rims of the canyon have genetically distinct squirrel populations. Contrary to this, the birds could easily cross through this barrier and continued to interbreed, and no splitting of the population occurred in this case (National Geographic 2011; Abzhanov 2010).

### Peripatric Speciation

Peripatric speciation occurs when a small subset of a population buds off from the parent population and forms a new species. The major difference between the allopatric and peripatric speciation is that, in the latter, one group is much smaller in size as compared to the other. Due to the small size of the population, the unique characteristics of the population are easily passed on and become more common in the future populations, thus distinguishing them from the others (Dunn 1989).

### Parapatric Speciation

The most defining feature of parapatric speciation is that the species are spread over a large geographical area. While not geographically divided, because of distance, interbreeding occurs only among the individuals of a species of a given geographical region. An example of this type of speciation is the buffalo grass growing in the areas polluted by metals. Although this metal-tolerant grass is not geographically divided from the buffalo grass growing in the other areas, long distance makes it impractical to reproduce with the other members of the species (Understanding Evolution. University of California Museum of Paleontology 2019).

### Sympatric Speciation

When two or more species form diverge from a parent species and live in the same geographical area, the process is called sympatric speciation. In addition to living in close proximity, there are also no physical barriers occurring between the interbreeding members of a species, yet a new species arises, for example, based on a change in food availability. An example of sympatric speciation is the apple maggot. This species diverged from the one which lays eggs in hawthorn and started laying eggs in apple after the introduction of apple trees in to North America. However, the parent hawthorn species still exists, and populations of both species overlap (Coyne 2007).

### Conclusion

According to biological species concept, a species is a group of individuals belonging to one or more populations that have the ability to interbreed and produce healthy and fertile offspring. However, in speciation, evolution of genetic differences occurs as a result of reduced gene flow. This can be attributed to the prezygotic and postzygotic barriers, acting before and after the formation of zygote, respectively, which prevent the species from mating and thus cause the reproductive isolation of the species.

### Cross-References

- [Genetic Drift](#)
- [Species](#)

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## Species

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### The Concept of Species and Its definition: An Historical Perspective

Species are the fundamental units of biological classifications. Understanding the concept of species is important both because species are the units of comparison across different biological disciplines including behavior, evolution, genetics, ecology, anatomy, development, and molecular biology, and because it plays an important role for the formulation of environmental law and ecological conservation. Species are also the currency by which biologists measure biodiversity. However, biologists largely disagree on the definition of “species.”

Attempts to define the concept of species date back to the Greek philosophers Plato and Aristotle, who viewed the world as we know it as a flawed shadow of the eternal and immutable world of ideas. Indeed, the word “species” originates from the Latin “kinds” which is a translation of the Greek word *eidos* (idea). According to this view, the world we live in is imperfect and variable and it is only a projection of the ideas that are real and unchanging.

However, it was an English naturalist, John Ray (1628–1705), who introduced for the first time the concept of “species” in biology. In his 1686 *Historia Plantarum* he wrote:

In order that an inventory of plants may be begun and a classification of them correctly established, we must try to discover criteria of some sort for distinguishing what are called ‘species’. After a long and considerable investigation, no surer criterion for determining species has occurred to me than distinguishing features that perpetuate themselves in propagation from seed. (quoted in Briggs and Walters 2016, p. 4)

In other words, according to Ray, species are those groups of organisms that resemble their

parents. Although Ray acknowledged that there can be some variants or “accidents” – as he called them – within a species, such as different heights, scents, or colors, organisms that differ by these characteristics should not be considered as different species. Ray, also, tried to reconcile the idea of “species” with the Bible account of Creation, and believed that all species were created at the same time and no new species could come into existence. While Ray is regarded as the first person who introduced the concept of species in biological terms, Carl Linnaeus (Carl von Linné, 1707–1778) is considered the true father of modern biological taxonomy and classification. In his *Systema Naturae* (first edition 1735), Linnaeus formulated a system to classify organisms, by identifying five categories: kingdom, class, order, genus, and species. Before Linnaeus, the classification of organisms was somewhat arbitrary, and organisms were often given long names that could be easily altered, making it more difficult for different biologists to understand what species they were referring to. Linnaeus was the first one to formulate the classification based on organism similarities, and to designate the binomial system (*genus* + *species*) to classify organisms. Interestingly, in the first editions, Linnaeus still considered species as fixed, a view that emerges also in other publications. In *Critica Botanica* (1737), for example, he defended the concept of fixity of species:

All species reckon the origin of their stock in the first instance from the veritable hand of the Almighty Creator: for the Author of Nature, when He created species, imposed on his Creations an eternal law of reproduction and multiplication within the limits of their proper kinds. He did indeed in many instances allow them the power of sporting in their outward appearance, but never that of passing from one species to another. (quoted in Briggs and Walters 2016, p. 6)

Over the years, however, Linnaeus’s observations led him to realize that species are not immutable entities as different species of organisms cannot always be easy to distinguish, and in his tenth edition of *Systema Naturae* he acknowledged that new species of organisms can be formed through intergeneric crosses. He even wrote a document, *Plantae Hybridae* (1751), where he listed

100 plants that might have been considered as hybrids.

One of the most influential figures in human history, because of his theory of evolution by natural selection, is undoubtedly Charles Darwin (1809–1882), author of the *On the Origin of Species* (first edition: 1859). There is still large debate on Darwin's concept of species, mainly because of largely contradicting statements that emerged from his book. In some cases, Darwin (1859) appears to consider the concept of “species” as a human construct: in p. 52 he wrote:

I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms.

While in a letter dated 1860, he wrote:

How absurd that logical quibble—“if species do not exist how can they vary?” As if any one doubted their temporary existence?

The current view that tries to reconcile these apparently contradicting opinions Darwin held on the concept of species is that Darwin did believe that the specific species taxa exist, but he questioned the existence of the “species” category, given that, according to Darwin, there cannot be a clear boundary between species and variety. In other words, the variation that distinguishes each set of individuals is so continuous that setting the boundaries to attribute to these different populations the rank of species appears to be more a convention than a reality. This view sets Darwin's approach apart from earlier naturalists' idea that each species was produced in the current form by a Creator, with only little variation between individuals belonging to the same species.

## Current Concepts of Species

A high number of species concepts has been developed over the years: Wilkins (2006) identified a total of 26 definitions of species, while Zachos (2016), more recently, counted 32 species concepts. According to Wilkins (2006), only

seven of these concepts are really independent: *morphological, biological, evolutionary, genetic, taxonomic, ecological, and agamospecies concepts* and, as Wilkins himself pointed out, some of these concepts are not definitions of what species are, but how biologists can identify them. In other words, most of these concepts do not question whether species are concrete describable objects in nature, but how best to define this class of objects so that any other object that possesses attributes that do not belong to this class of object can be excluded. Here some main species concepts, namely the morphological, biological, evolutionary, genetic, ecological, and agamospecies, will be discussed, while a complete and recent list of all the concepts can be found in Zachos (2016).

### Morphological Species Concept

Under the Morphological Species Concept, Cronquist (1978) defined the species as “the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means” (quoted in Wilkins 2009, p. 214). According to this concept, the species can be distinguished on the basis of their morphological features. This approach is also called *essentialist*, as, under this view, members of a species can be identified by their essential characteristics, or *typological* since it posits that all the diversities on earth reflect a limited number of “types.” While this concept dates back to Aristotle and Plato's concept of “ideas” and was adopted by Linnaeus and other earlier naturalists to classify the organisms, this view has been largely abandoned on the ground that individuals belonging to the same species can display large intraspecific differences, because of marked sexual dimorphism, aging, or polymorphism or perfectly distinct species can be morphologically similar to each other (the-so called cryptic species).

### The Biological Species Concept

The Biological Species Concept is probably one of the most cited definitions of species. It was first defined by Dobzhansky (1935) as follows:



A species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents or sterility of the hybrids, or both)

This definition was then expanded by Mayr (1940) who originally defined species as

A group of populations which replace each other geographically or ecologically and of which the neighboring ones inter-grade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.

In other words, species are groups of individuals who interbreed but who are reproductively isolated from other groups. Mayr (1969) defined a species as both a *reproductive unit*, in which members seek each other to reproduce, an *ecological unit*, as individuals of a species share the same environment, and a *genetic unit*, whose members share the same set of genetic information. There are two main mechanisms by which reproductive isolation can be achieved: *pre-zygotic* and *post-zygotic*. Pre-zygotic isolation includes:

- *Ecological isolation*: when different populations occupy different geographical areas or different ecological niches.
- *Behavioral isolation*: when different populations display different behaviors that prevent them from interbreeding, such as different courtship rituals, mating calls, or chemical signals.
- *Temporal isolation*: when different populations produce gametes at different times. This is particularly common in plants that exhibit different flowering periods.
- *Mechanical isolation*: when females and males have reproductive organs that are compatible only among members of their own species. This type of reproductive isolation is particularly common in insects.

Post-zygotic isolation includes:

- *Hybrid viability*: when the hybrid dies prematurely

- *Hybrid infertility*: when the offspring that is produced by the two different species is infertile

There are a number of problems with the Biological Species Concept:

1. Mayr's biological concept definition can only apply to sexual organisms but it does not work for those organisms who do not reproduce sexually, such as protozoans.
2. The biological species concept can only be applied to the species that share the same space at the same time, making the definition inapplicable to species that live at different times (i.e., fossils) or in different geographic regions. This is because it is hard to test whether two populations that live at different times or in different areas can reproduce. In p. 121 Mayr (1940) states that: "the application of a biological species definition is possible only in well-studied taxonomic groups, since it is based on a rather exact knowledge of geographical distribution and on the certainty of the absence of interbreeding with other similar species." To address this issue, Mayr (1970) took out the word "potentially" by the Biological Species Concept and defined species "as those groups of interbreeding natural populations that are reproductively isolated from other groups" (p. 12).
3. Finally, there is a plethora of cases in which interbreeding between different species results in fertile offspring. Some *genera* are renowned for including species that have a high ability to interbreed, such as the genera *Cervus*, *Lepus*, *Canis*, and *Macaca*. Hybridization appears to be particularly common in birds: Grant and Grant (1992) calculated that about 1 in 10 species of birds are known to have bred in nature with another species. Mayr (1970) tried to solve the problem of hybridization by revising his definition of "isolating mechanism" to "biological properties of individuals which prevent the interbreeding [fusion] of populations" (p. 56). In other words, these isolating mechanisms would not be able to guarantee the complete lack of interbreeding

between different species, but it would prevent the complete fusion between them.

### The Evolutionary Species Concept

The Evolutionary Species Concept tried to solve the nondimensional nature of the Biological Species concept by defining species as “a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own evolutionary role and tendencies” (Simpson 1961, p. 153). The second part of the definition (“own evolutionary role and tendencies”) is particularly important as it implies that there should be some sort of biological relevance when assigning a group of individuals the status of species, and it precludes considering species from any ephemeral offshoot of the species, such as small captive populations. The main criticism is that this concept is not an operational definition as it does not help to identify whether a specific class of individuals belongs to a specific species. Furthermore, from the definition of Evolutionary Species Concept, it is unclear which level of lineages we should consider the species level, as lineages exist at different levels. Wiley and Mayden (2000) solved this issue by identifying evolutionary species as those tokogenetic entities “composed by parts (individual organisms) linked by reproduction and manifested by tokogeny” (p. 74) where tokogeny is defined as the biological relationship between parents and offspring or, more generally, between ancestors and descendants.

### The Genetic Species Concept

Baker and Bradley (2006) defined a genetic species as a “group of genetically compatible interbreeding natural populations that is genetically isolated from other such groups.” While the core aspect of the Biological Species Concept is reproductive isolation, the key element at the basis of the Genetic Species Concept is *genetic* isolation, produced by an accumulation of genetic changes. The initial criticisms against this concept is that it would be hard to accurately estimate genetic distance, especially considering our lack of knowledge of an organism’s genetic information. However, recent genetic advances have made it

possible to assess genetic differences between organisms. For example, an examination of the variation in mitochondrial cytochrome-*b* gene sequence across several mammalian species suggests that genetic distance values lower than 2% indicate intraspecific variation (hence the organisms belong to the same species), values >11% represent different species, while values that range between 2% and 11% deserve further investigation in order to understand whether they should be considered the same or different species (Bradley and Baker 2001). The important difference between the Genetic and Biological Species Concepts is that while the former considers populations as distinct species even if there is gene flow and their hybridization produces fertile offspring, the Biological Species Concept would recognize these two populations as the same species (and different subspecies). There are numerous examples in nature of populations that might appear to belong to the same species, but genetic analyses reveal as different species, and Baker and Bradley (2006) estimate that there are more than 2000 unrecognized species.

### The Ecological Species Concept

The Ecological Species Concept was introduced by Van Valen (1976), under the idea that differences in ecological niches, more than genes, are the primary drivers of evolution and that reproductive isolation plays a minor role in the formation of the species.

Van Valen (1976) defined species as “a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range.” According to Van Valen (1976), an adaptive zone is considered the part of the environment that contains a specific set of resources along with certain levels of predation and parasitism, and can have boundaries that are either pre-existing or defined by the species that are living there. Under this concept, populations that live in separate areas can still be considered as belonging to the same species if they are under the same ecological pressures. Grant (1992) pointed out that the idea that ecological adaptations play an

important role for the formation of species is not new and even the “fathers” of the Biological Species Concept acknowledged the importance of ecological factors. In the *Genetics and the Origin of Species* Dobzhansky (1951), for instance, highlighted how the phenotypic and genetic discontinuities between species are probably related to differences in their ecological niches, and that reproductive isolation manages to fix these phenotypic and genetic differences. The main criticism of the Ecological Species Concept, however, is that we cannot have a priori knowledge of what makes an ecological niche and, in fact, researchers often use ecological differences between species to characterize their ecological niches (Grant 1992). Furthermore, in many species, different morphs or different sexes can occupy different niches and so we cannot reliably use ecological differentiation as a diagnostic of a species.

### The Agamospecies Concept

Many of the abovementioned concepts do not apply to organisms who do not reproduce sexually and who lack genetic exchange. This is because the key aspects of the Biological and Genetic Species Concepts are reproductive and genetic isolation, respectively, and Wiley and Mayden (2000) had to drop the word “population” from their definition of Evolutionary Species Concept in order to be able to include asexual organisms. The first definition of agamospecies concept was given by Turesson (1929), who defined species as “an apomict-population the constituents of which, for morphological, cytological or other reasons, are to be considered as having a common origin” (quoted in Zachos 2016, p. 98). This definition can be considered as a “Morphological Species Concept” applied to asexual organisms. Another definition was provided by Cain (1954) who defined agamospecies as “those forms to which [the biological species concept] cannot apply because they have no true sexual reproduction.” The problem with this definition is that it defines the “species” as *not being* something else. A better definition, which was originally used to define viruses, was given by Eigen (1993), who coined the term *quasispecies*, defined as “a self-sustaining population of sequences that reproduce

themselves imperfectly but well enough to retain a collective identity over time.” The concept of quasispecies hinges on the observation that in a cluster of genotypes of viruses there is an optimal (or wild) type with specific mutations that make it particularly adapted to a specific environment, from which other viruses reproduce. This definition is very similar to the *Ecological Species Concept* and can be applied more generally to asexual organisms, which is why Wilkins (2009) considers *agamospecies* and *quasispecies* synonyms.

### Modes of Speciation

Speciation (or *cladogenesis*) is the biological process by which species originates from the ultimately irreversible splitting of one population lineage in two or more lineages. Importantly, this evolutionary process is different from the *anagenesis* that occurs when a population lineage gradually changes over time until it reaches the point when it becomes sufficiently distinct from its ancestor. There are three main modes of speciation: *allopatric*, *sympatric*, and *parapatric*.

- *Allopatric (or geographic) speciation* is the most common form of speciation and occurs when different populations from the same species become isolated and no genetic exchange occurs between them. These isolated populations undergo genetic changes over time due to mutations, migration, or other evolutionary forces, to the extent that they become reproductively isolated from each other. There are two main forms of allopatric speciation: *dichopatric* and *peripatric*. Dichopatric speciation arises when populations inhabiting a specific geographic area become isolated due to the development of a new geographic barrier that splits the original population into two or more groups. Peripatric speciation occurs when a single gravid female or few individuals of a species colonize a new geographic area. This, in turn, results in *genetic drift* and *bottleneck effects* that lead to genetic changes and reproductive isolation from the original species. Classic examples of allopatric speciation

are Darwin's Galapagos finches: these are 15 species of birds inhabiting different islands on the Galapagos archipelagos, located in the Pacific Ocean off South America. Over millions of years, these bird species have evolved different types of beaks of different size and shape that are particularly adapted to the type of food they eat (Abzhanov 2010). For example, ground finches, like *Geospiza magnirostris*, *G. fortis*, and *G. fuliginosa*, have stout beaks for eating seeds, while cactus finches, such as *G. conirostris*, have longer more pointed beaks to feed on nectar or getting seeds from cacti (Fig. 1).

- *Sympatric speciation* occurs when a new species originates in the same geographic area of the parental population. It is less common than allopatric speciation and can occur, for instance, when part of the population starts using a new niche, and is more likely to occur in herbivorous insects that display a particularly specialized relationship with their host plants. A textbook example of sympatric speciation is the apple maggot *Rhagoletis pomonella*: apple maggots used to lay their eggs exclusively in hawthorns, which are native to America. However, 200 years ago, they started using also domestic apples, which were introduced to America by immigrants. Since males generally look for mates on the type of fruit they grew up in and females lay their eggs on the type of fruit they grew up in, hawthorn flies generally mate with hawthorn flies and apple flies mate with apple flies preventing gene flow between the two types of flies and providing the first step for sympatric speciation.
- *Parapatric speciation* occurs when individuals from a continuous population tend to mate with geographic neighbors more often than with individuals belonging to other areas of the population's range due to differences in the same environment. These local populations are called *demes*. Different demes of a population are not isolated from each other, as individuals can move from a deme to the other but given that individuals tend to mate only with members of their own demes, they might be

subject to specific selective pressures that can lead them to become a whole new species. A species who might be undergoing parapatric speciation is *Anthoxanthum odoratum*. This plant species grows in mining zones, whose soil is contaminated with high levels of heavy metals, and members of this species have developed a high tolerance for heavy metal. Although these tolerant individuals live close to the same species of plants that do not grow in contaminated ground, tolerant and non-tolerant plants have developed different flowering times. This temporal isolation indicates that tolerant individuals would breed only with tolerant individuals and nontolerant individuals would reproduce only with nontolerant individuals, providing the first step for (parapatric) speciation.

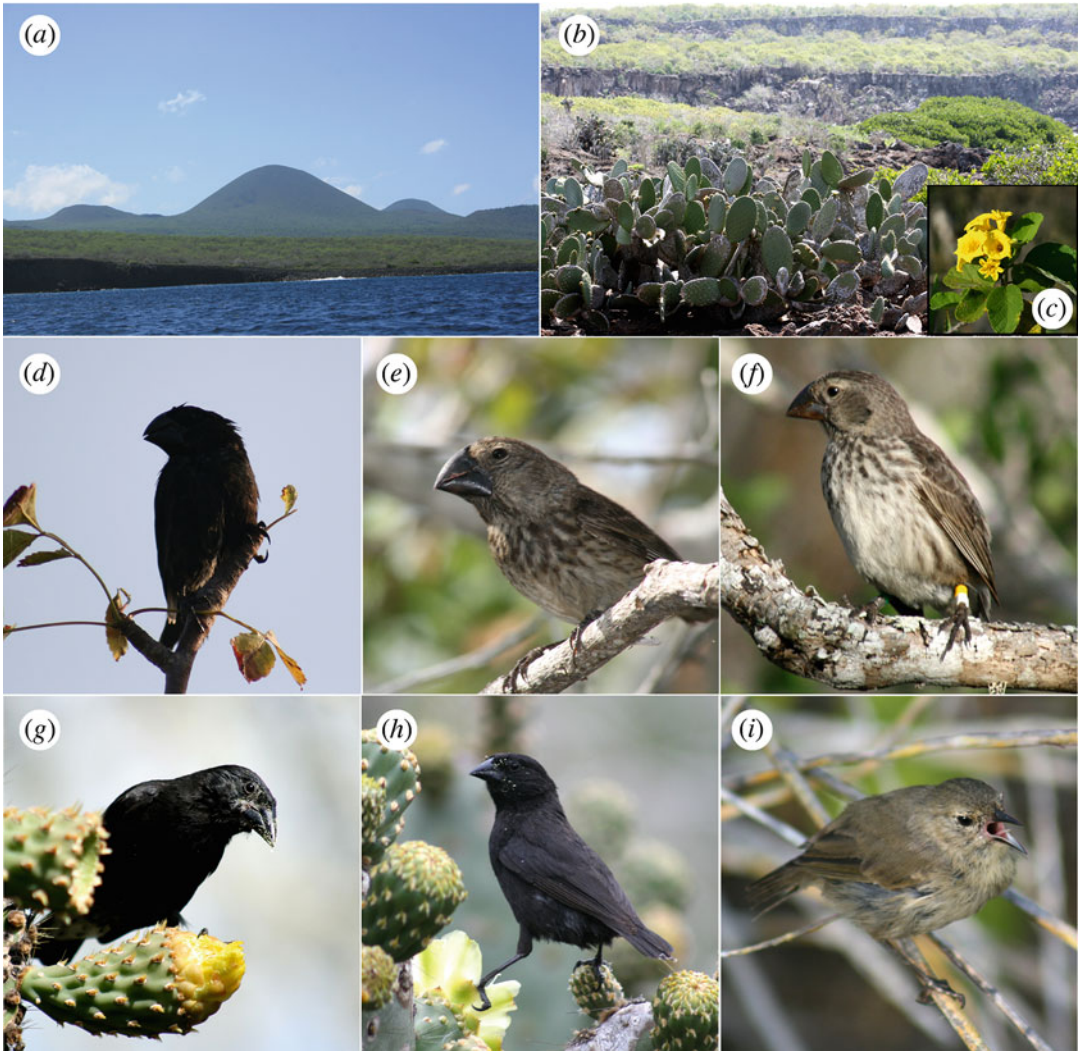
## Discovery of New Species

It is generally estimated that 15,000–18,000 new species are discovered every year, of which half are insects. This list includes also correction in the taxonomy or species that are moved from a family to another. Since 2008, the SUNY College of Environmental Science and Forestry releases on May 23rd (which corresponds to Carl Linnaeus's birthday) the list of the top 10 new species discovered the previous year (<http://www.esf.edu/top10/>).

There are different ways in which a new species can be discovered:

- *Expedition in remote areas.* There are many areas on earth that have not been explored yet, and can be home to species that have never been described. In December 2005, for instance, an international team of 11 scientists from Australia, the United States, and Indonesia travelled to the, until then, unexplored areas of Foja Mountains and discovered numerous new species (<http://news.bbc.co.uk/2/hi/science/nature/4688000.stm>). These included: 40 new species of mammals, many new plant species, including five new species of palms, four new species of butterflies, twenty new





**Species, Fig. 1** (a) Galápagos Islands, such as Isla Floreana, are volcanic islands visited by Charles Darwin in 1835; (b) bushes of the prickly pear cactuses (*Opuntia helleri*) on Isla Genovesa (Tower Island); (c) flowers of the yellow geiger (*Cordia lutea*); (d) male of the large ground finch (*Geospiza magnirostris*) singing during the rainy season; (e) female of the large ground finch

(*G. magnirostris*) on Isla Genovesa; (f) female of the medium ground finch (*G. fortis*) on Isla Santa Cruz; (g) male large cactus finch (*G. conirostris*); (h) male sharp-beaked finch (*G. difficilis*) feeding on cactus flowers on Isla Genovesa; (i) male warbler finch (*Certhidea fusca*) singing next to its nest (Abzhanov 2010; © 2010 The Royal Society)

species of frogs, and numerous new bird species. In some cases, researchers identify new species on the basis of the vocalizations they produce. Recently, Svensson et al. (2017) described a new species of dwarf bushbaby inhabiting Angola's Kumbira Forest which produces a different type of call from the other 18 known bushbaby species.

– *Examination of museum specimens.* New species can also be discovered in museum collections, where they were collected 50 or 100 years ago but their taxonomic classification was overlooked or specimens were often mislabeled. Recently, for example, Helgen et al. (2013) have described a new species of carnivorous mammal, the olinguito



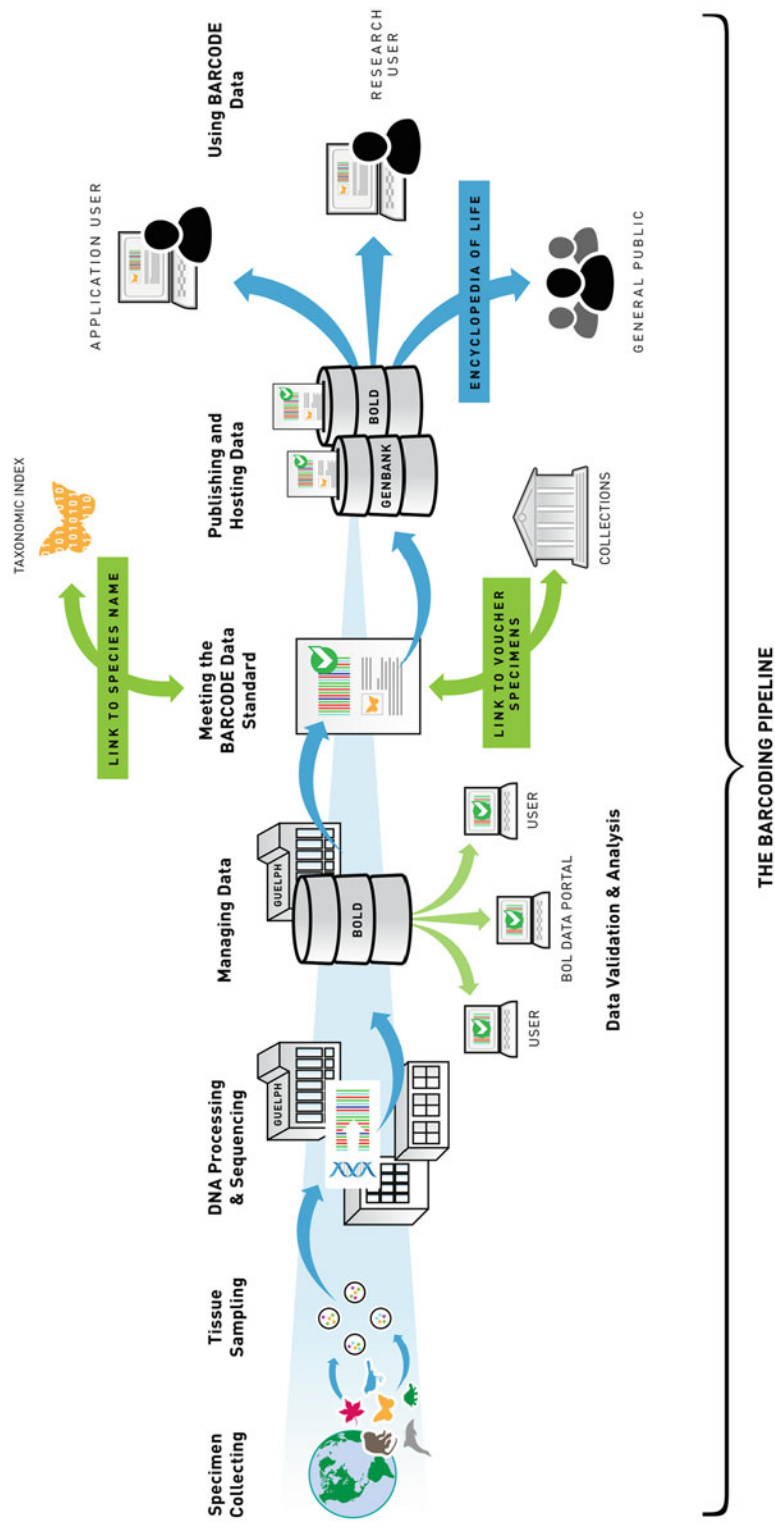
(*Bassaricyon neblina*), that lives in the forests of Andes, Ecuador, and Colombia. Helgen and colleagues analyzed the fur and bones of the specimens that were stored in several museum collections and, through DNA testing, found out that this was a new species. Several zoos in the USA probably exhibited an olinguito between 1967 and 1976, but keepers mistook it for its close relative, olinga, and could not understand why the olinguito could not breed. The olinguito eventually died without being properly identified.

- *Genetic analyses.* The advancement of DNA techniques has offered researchers the opportunity to identify new species even when they are morphologically similar to another species and live in the same area. These species are also called cryptic species. DNA barcoding has become the most common technique to detect new species (Hebert et al. 2003). Through this technique, DNA is extracted from specimens that can be collected from the field, from museums, zoos, or other sources. A region of this DNA is then isolated. This region is commonly a 648 base-pair region in the mitochondrial cytochrome c oxidase 1 gene (“CO1”), located in the mitochondrial DNA, which has a mutation rate that is slow enough to be identical within the same species but fast enough to be different between species. The use of this DNA region to identify new species has been shown to be effective for many animal groups, such as birds, fish, butterflies, but not for plants, for which two DNA regions in the chloroplast are used instead. Once this region is isolated, its copies are replicated and sequenced. The sequence is then compared to the sequences of known species contained in the Barcode of Life Data Systems (BOLD) to understand whether the species is already known or is a new species (Fig. 2). Recently, barcode analysis has been used to identify a new gibbon species *Hoolock tianxing* (common name: skywalker hoolock gibbon), which is distributed on the east of Irrawaddy-Nmai Hka Rivers in China and had been previously considered to be the

same species as *H. leuconedys* (Fan et al. 2017). Although researchers had suspected that the two species were different, due to differences in morphology and vocalization patterns, only genetic analyses confirmed that the two were actually distinct species.

## Conclusion: The Importance of Taxonomy for Conservation

Taxonomy provides an important tool for the conservation of the species. The International Union for the Conservation of Nature (IUCN) is an organization that monitors the conservation status of the organisms, and in its Red List of Threatened Species, it classifies the species extinction risk into (1) Least Concern, (2) Near-Threatened, (3) Threatened (divided into Vulnerable, Endangered, and Critically Endangered), and (4) Extinct. By March 2014, among the 71,576 terrestrial and freshwater species assessed, 860 were classified as extinct or extinct in the wild, 21,286 were categorized as threatened, and 4286 were deemed critically endangered. Of the 6041 marine species for which we have enough data to assess their extinction risk, 16% were classified as threatened and 9% as near-threatened. Although the extinction of a species is a natural phenomenon that occurs at a rate of one to five species per year, the most recent estimates suggest that the current rate of extinction is 1000–10000 times higher and is largely human-driven (Pimm et al. 2014). Out of an estimated 8.7 ( $\pm 1.3$ ) million of eukaryotic species, only about 1.2 million species have been catalogued, leaving a total of 86% species on Earth and 91% of species in the ocean still undiscovered (Mora et al. 2011). With the high extinction rate that species face, many species disappear before they are discovered. In this context, identifying new species is key for their protection before they become extinct. Assigning the rank of “species” to a population is, thus, important both because it gives them legal protection and because it increases the awareness that the population is indeed unique (Zachos 2016).



**Species, Fig. 2** Basic workflow for generating DNA barcodes (Image courtesy: Kris Jett; © International Barcode of Life)

## Cross-References

### ► Population

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## Species Cooperation

### ► Symbiotic Relationship

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## Species-Specific Behavior

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## Definition

Species-specific behavior refers to the repertoire of behaviors, innate or otherwise, that is shared by virtually all members of a given species.

## The Origins of Species-Specific Behaviors

The characteristic behaviors a species exhibits can serve social, reproductive, nutritional, or other functions within the context of an animal's natural history. Species-specific behavior refers to the standard set of behaviors exhibited by most, if not all, members of a particular species. For example, while most species of deer leap away from a perceived source of danger once startled, due to genetic differences, white-tailed deer (*Odocoileus virginianus*) gallop but mule deer (*O. hemionus*) stot. These different forms of movement would be considered species specific.

Species-specific behaviors can arise from minor modifications to preexisting behaviors. These changes can occur anywhere from an individual's genetic environment to its social environment. Both instinct and individual experience play a significant role in shaping species-specific behaviors, as can social learning from parents or other individuals in an animal's life. White crowned sparrows (*Zonotrichia leucophrys*), for example, learn how to produce sophisticated songs within the first weeks of life. Interestingly, birds' ability to learn song characteristics is also coupled with an innate preference for songs typical of its own species. Imprinting is another form of learning that is characteristic to a few species, notably ducks and geese. This type of learning occurs in early development, typically right after hatching, in which offspring associate the first animal they see with a maternal figure. This visual stimulus triggers a suite of behaviors, like following, that encourages further social learning and survival for hatchlings. In cases where hatchlings do not immediately see their biological mother, they may imprint on another species.

In contrast, other species-specific behaviors may be instinctive, like head-bobbing shown by green anole lizards (*Anolis carolinensis*), a display behavior used in territorial or courtship contexts that can be performed from birth. Instinctive behaviors may be accompanied by fixed action patterns (FAPs), which are produced by innate releasing mechanisms, types of neural networks,

in response to a stimulus or releaser from the organism's environment. The greylag goose (*Anser anser*) provides a classic example of a FAP: if an egg rolls out of the nest while a goose is incubating, they will automatically begin tilting their head from side to side in an attempt to retrieve the egg. Geese have been observed to continue these specific motions even in the absence of an egg (Lorenz and Tinbergen 1938), hence the "fixed" nature of a fixed action pattern. Once triggered, a FAP will run to completion, regardless of changes in circumstance.

Some species-specific behaviors can be linked back to physical structures within the animal brain. In many experimental studies, animals lose the ability to perform instinctive or necessary behaviors after losing function in certain brain structures. Hamsters (family Cricetinae), for example, have been shown to lose play and maternal behaviors after receiving brain lesions at birth (Murphy et al. 1981). This reveals that an intact limbic system is necessary to call innate behaviors to action with the appropriate stimulus. Additionally, chemical receptors in the brain or elsewhere in the body encourage characteristic species behaviors, such as monogamy in prairie voles (*Microtus ochrogaster*) that is mediated by oxytocin. Ultimately, healthy structures and normal functioning are imperative for the execution of both innate and learned species-specific behaviors.

Regardless of origin, species-specific behaviors fulfill distinct and necessary roles in an animal's life. The disruption or eradication of such behaviors can be detrimental to the animal. When animals become heavily influenced or managed by humans, it is of paramount importance to maintain species-specific behaviors to ensure a healthy and high-quality life, which in turn can support species preservation.

## Importance Among Wildlife

### Conservation

In wild populations, species-specific behaviors can be influenced by external pressures caused by anthropogenic activity, which could include

alterations in ambient noise, lighting, and activity patterns, among other factors. Noise pollution from anthropogenic disturbance has caused many species of birds, primates, and cetaceans to alter their characteristic vocalizations. Extra noise can impede signal transmission, not only affecting qualities like timbre and the frequency at which signals are received, but also altering the signaler's innate behavior (e.g., calling at a different pitch than would be typical). If group members fail to hear or recognize the call directed toward them, there is potential for increased predation or disbanded social networks (Barber et al. 2009).

Alterations to natural light cycles due to persistent artificial lighting can disrupt many signals animals use to engage in species-specific behaviors, such as when to commence foraging, seek shelter, and mate. Bats have been observed to change flight patterns and delay commutes in response to a greater presence of light at night, affecting their circadian rhythm and innate predisposition to a nocturnal lifestyle. Alternatively, one change that is becoming more prevalent across taxa is diurnal species' move to nocturnal activity to avoid encounters with humans. A recent meta-analysis of 76 species across the world revealed convergent patterns of human avoidance, namely, ignoring innate tendencies to be active during the day. In the immediate, becoming nocturnal to avoid humans seems an effective way to coexist on an ever-crowding planet (Gaynor et al. 2018).

With human presence encroaching upon wildlife and wild places, changes in species-specific behavior may mean immediate safety for individual animals, but these alterations in behavior may have long-term negative ramifications, the potential for extinction among them. One case is that of the sable antelope (*Hippotragus niger*). While listed as Least Concern by the International Union for the Conservation of Nature (IUCN) as of 2018, sable antelope have been, in recent years, waiting until dark to visit waterholes in order to avoid humans, despite the overwhelming presence of predatory animals. Sadly, this means that more antelope are becoming prey, and time will tell how this impacts the species as a whole.

## In Captivity

Regardless of environment, species-specific behaviors are often considered to be the "gold-standard" metric of animal behavior and are imperative in considering the effective management and welfare of wildlife housed in captive settings, such as zoos, sanctuaries, and laboratories. Taking cues from animals' wild counterparts to provide targeted and holistic behavioral management can positively influence reproductive behavior and reintroduction success, among other factors. For example, many species of primates prefer to sleep in elevated areas at night so they are not an easy target for predators and smaller primates like tamarins prefer sleeping areas that provide added concealment over more open areas (Caine 2017). In captive settings, care staff may provide their primates with raised sleeping platforms and bedding materials that offer security and concealment for animals.

Animal managers often monitor and seek ways to encourage species-specific behaviors, as they are considered to be desirable. When considering ways to increase the performance of species-specific behaviors that can be measured quantitatively, manipulating animal environments is a common practice. From myriad studies across taxa, it has been noted that increasing the complexity of an animal's habitat or exhibit space increases species-specific behaviors and consequently reduces atypical or undesired behaviors (Alligood, et al. 2017; Veasey et al. 1996). It is also critical to understand how an animal perceives and uses enrichment and whether it elicits the species-specific behaviors that it is intended to stimulate. In cases like this, preference testing can provide a glimpse into the animal's point of view and helps care staff determine if well-intentioned changes are meaningful (Alligood et al. 2017). Additionally, behavioral evaluations can allow managers to see exactly how an animal is using enrichment, and they can then follow up with necessary adjustments to maximize activity and benefit to the animal (Alligood et al. 2017). While the nature of managed environments may differ greatly from an animal's natural habitat, creating a dynamic space with which the individual readily



interacts can promote a “close-to-natural” repertoire of behaviors (Clubb and Mason 2007), with an emphasis on promoting each species’ species-specific behaviors.

While deviations from typical behaviors may reflect compromised welfare, determining whether or not a behavior is harmful, in some incidences, warrants further investigation. In the case of great ape coprophagy, observed instances of this behavior are often used as an indication of compromised well-being. Interestingly, wild apes, particularly chimpanzees, have been seen to consume feces in the wild, though at lower rates than seen in captive populations. While ape coprophagy may indeed be more prevalent in captivity, it may not necessarily be indicative of lessened quality of life. Another example includes zoo-housed giraffes: In the wild, giraffes might be more active due to foraging and predator avoidance. However, captive giraffes can be more sedentary, as resources are plentiful and threats are minimal. Clearly, captivity can alter behavior, and thus behaviors should be evaluated in their evolutionary and situational contexts (Birkett and Newton-Fisher 2011; Clubb and Mason 2007; Hopper et al. 2016; Veasey et al. 1996). Given the rarity of some exotic species housed in captivity, it may be difficult to know or acquire the knowledge needed to manage by and encourage the expression of species-specific behaviors. Subsequently, this may make objective welfare studies and evaluation a challenge, and care staff may be forced to draw generalizations from related species and subspecies (Veasey et al. 1996).

## Cross-References

- [Animal Welfare](#)
- [Environmental Influences](#)
- [Evolutionary Psychology](#)
- [Human-Animal Interaction](#)
- [Innate Behaviors](#)
- [Innate Releasing Mechanism](#)
- [Konrad Lorenz](#)
- [Nikolaas Tinbergen](#)
- [Zoo](#)

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## Specificity Coding

- [Cognition](#)

## Spectral Waterfalls

- [Sound Spectrogram](#)

## Sperm Competition

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### Definition

Sperm competition is defined as a form of sexual selection that occurs when ejaculates from multiple males compete for the fertilization of an individual female's ova. Most female organisms are known to mate with multiple males, so sperm competition is considered to be a widespread and powerful evolutionary force. Competition between males may occur before or after copulation, to either prevent or win competitions, leading to the evolution of numerous traits to enhance fertilization success. Sperm competition *sensu stricto* refers only to the competition between ejaculates after two males have inseminated the same female.

### Introduction

The theoretical basis of sperm competition was formalized by Parker (1970) and relied on several key observations. The first is that the evolution of internal, or close to internal, fertilization was not only subject to natural selection pressures to maximize fertilization chances for each ovum, but also sexual selection between competing males to place their spermatozoa as close to the female's ova as possible in order to achieve fertilization. The evolutionary advantage to a male that competes successfully means that sexual selection continues after copulation if females mate with more than one male. Establishment of sperm competition as a widespread and powerful evolutionary force became possible with the body of evidence that built up during the 1970s–1990s that demonstrated the widespread existence of female polyandry: multiple mating by females with different males (Taylor et al. 2014). Bateman's principle (Bateman 1948) states that

males can increase their reproductive output by securing extra mates, but females cannot, being limited by the costs of egg production and bearing young, which implies that females should not seek multiple mates in the way that males do. However, although polyandrous mating can be costly for females, in terms of increased predation or disease risk, or expenditure of time and energy, or damage by mating males, it has been demonstrated in many taxa that females mate with multiple males, securing benefits for the female (from gaining resources) and her offspring (from gaining advantageous traits) (Taylor et al. 2014). Polyandrous mating is the driver for sperm competition and it is the “risk” that is countered by the evolution of competitive traits in males.

The final observation that completed Parker's (1970) theory of sperm competition is that the production of sperm is constrained by energy costs. Spermatozoa, despite their generally small size, are not “cheap” to produce and can take energy away from other forms of mating effort. Once one assumes that there is a constraint on sperm production and supplies are not limitless, you can build theoretical models that predict how different males and/or species will respond to differing levels of “risk” from sperm competition. For example, the raffle model (Parker 1982) predicts that a male's likelihood of successful fertilization increases with the greater number of spermatozoa he contributes to the competing ejaculate pools; that is, he has more “tickets” in the form of individual sperm in the raffle and therefore more chances of winning the “prize” of fertilization. The raffle model allows greater understanding of the evolution of morphology of spermatozoa cells, especially in comparison to female gametes. The size disparity between the typically small male and larger female gametes is known as anisogamy and can be extreme in many species. Sperm competition promotes the maintenance of anisogamy and partly explains the observation, particularly in vertebrates that spermatozoa tend to be numerous and tiny (Parker 1982). It also explains why spermatozoa between and within species tend to be highly morphologically variable, as different taxa develop various adaptations for competitive

fertilizing capacity, working within their particular constraints of physiology and environment. Sperm are considered to be the most morphologically diverse cell of all, and in some taxa, it is possible to identify individual species purely by the morphology of their spermatozoa (Birkhead et al. 2009).

The evolution of sperm competition was initially modeled using an Evolutionarily Stable Strategy (ESS) approach because the fitness of a given sperm allocation strategy depends on the strategies played by other males in the population (Birkhead and Møller 1998). The strategic question here is “How much of a male’s total reproductive effort should he spend on sperm?” Males are competing against other males, using a specified range of ejaculate strategies, and it is their ejaculates which compete. In this instance, females are assumed to not display any preference for any male’s strategy. These sperm competition “games” are used to predict how individual males should respond when the risk and intensity of sperm competition within a species varies. Risk models refer to the probability that an individual female will mate with more than one male. Intensity models were introduced mainly to incorporate group-spawning species like some fish, where males compete in groups and ejaculate as a female simultaneously releases eggs, leading to intense levels of sperm competition. Where there is a fixed total budget for reproduction, expenditure on the ejaculate (more sperm and/or enhanced sperm) increases the gain per mating, but necessarily reduces the expenditure on mating (finding and accessing mates), which reduces the number of matings achieved in total. Fitness is the mathematical product of gain per mating and the number of matings achieved.

Intraspecific variation in sperm competition risk and intensity makes different predictions for species depending on various interactions between aspects of life history and phenotype. At its most basic, the greater the risk or intensity of sperm competition, the more all males within a species should spend on ejaculates to successfully compete, and this is a common phenomenon observed across species. However, there are different pathways to fertilization success that are

possible within a species, and so they require consideration. Here, the raffle model expands to take into account phenotypic differences between males in a species, and leads to two new models: the “fair” raffle and the “loaded” raffle (Birkhead and Møller 1998).

In a fair raffle, the males have no information about the current risk of sperm competition, and the ESS under a risk model is that males should expend a proportion of their mating effort solely on their ejaculate at the rate of one half of the proportion of females that mate polyandrously. The ESS for the intensity model requires males should spend almost their entire mating energy budget on ejaculates and very little on gaining matings. In a loaded raffle, a wider range of circumstances are incorporated into the model, which reflect prior information males may have, or phenotypic constraints they may be operating under. For example, males may be the second of two males to mate with a female, and knowing this, may increase or decrease the allocation of individual sperm to their ejaculate, depending on whether last or first-male sperm precedence operates to secure fertilizations in that species. Alternatively, males might be acting as either territorial males or sneaker males, whereby large size and greater resource holding potential are traits of the former, and small size and drab coloration may be traits of the latter. Males who fit the sneaker phenotype are taking part in a loaded raffle and should expend nearly all their mating energy budget on ejaculates.

Under a risk model, with increasing levels of sperm competition in a loaded raffle, each male should make an equal ejaculate contribution to every female regardless of whether he is the first or second male to mate with her, because the chances are high that the female will mate again if he is first and he must compete against the other male if he is second. Under the intensity model, in a loaded raffle, the prediction is the more males that are present at fertilization, and therefore the higher the intensity of sperm competition, the less each male should allocate to his ejaculate expenditure. He should save his energy to expend on ejaculates only when the prevailing intensity of sperm competition is low.

When females control the rate of mating, as is likely under natural conditions, and males face a trade-off between allocating a set amount of energy between pre-copulatory competition and post-copulatory competition, sperm competition models move towards the general model proposed by Parker et al. (2013). In this model, the trade-off between pre-copulatory male-male competition and post-copulatory sperm competition is taken into account as before. The trade-off takes the form of any developmental trait that enhances a male's competitive ability against other males, causing the phenotype in question to have its sperm production reduced. There are also parameters for the number of males competing for each mating and the competitive weights of males, determined by their investment in pre-copulatory traits that will allow them to win male-male competitions, which is new to this model compared with its predecessors. This allows examination of any level of male-male mating contest, from a simple dyadic interaction to a scramble contest for mates and allows the parameters to be considered independently to assess their effects.

Predictions stemming from Parker et al.'s (2013) general model indicate that males should invest in weaponry in greater amounts as the density of competing males decreases. Males should also respond to higher densities of males by investing in greater ejaculate production. Therefore, in breeding populations of high male density where males are at the highest risk of sperm competition, males should produce larger testes than expected for their body size. In breeding populations with a relatively low density of males, a male should invest in large body size or weaponry to control access to females and prevent other males mating with a female he has mated with. This model can be considered simplistic in that it does not separate out the various components of male pre-copulatory mating effort, such as searching for mates, participating in aggressive contests or include general increased mortality costs, but it still provides a robust framework for exploring the effects of male-male competition both prior to and after copulation. The theoretical basis of sperm competition indicates its potential to act as a powerful evolutionary selection

pressure promoting and maintaining both physical and behavioral traits in order to secure fertilizations.

## General Mechanisms of Sperm Competition

Given female polyandrous mating, males face a problem depending on whether there is random or nonrandom fertilization of ova by a set of sperm, known as the fertilizing set, which is contributed to by multiple males (Simmons 2001). Where fertilization is random, there is only a slight advantage for males to be able to determine the virginity or otherwise of a female, but the likelihood that she will mate again after he mates with her is valuable to know. If each male contributes equally to the fertilizing set and there is random mixing of the sperm immediately prior to fertilization, then this equates to a fair raffle, where every sperm in the set has an equal chance of fertilization. Given a certain rate of sperm transfer, through altering copulation duration or the number of ejaculations, males can manipulate the number of their sperm present in the fertilizing set.

If the sperm represented in the fertilizing set is no-random, then sperm displacement has occurred. A male's chance of success depends on whether they are the first or the last male to copulate with a female prior to fertilization of her ova (Simmons 2001). Taxa differ in the utilization of sperm, and it may either be an advantage to be the first or the last male to mate with the female in terms of securing fertilizations, depending on the physiological patterns of storage and use of sperm by the female. Although sperm mixing is the most common fertilization pattern for a female that has mated polyandrously, first-male sperm precedence is often found in crustaceans and last-male sperm precedence usually found in the insects (Shuster and Wade 2003). Many of the most informative studies for understanding these patterns of sperm storage and use were conducted in insects (Simmons 2001), but the females of birds, internally fertilizing frogs, reptiles, and sharks also store sperm for significant periods of time and males of these species have evolved mating

strategies for engaging in sperm competition (Birkhead et al. 2009).

Sperm storage by females has been observed in many species and females stand to gain both direct and indirect benefits from storing sperm (Birkhead et al. 2009). The most basic reason for storing sperm is that females may remain receptive and/or lay eggs over a prolonged period and could risk running out of sperm if they do not carry a supply of it. Although one of the presumed outcomes of intense sperm competition is to produce an ejaculate of numerous and tiny sperm that can fertilize all the ova a female has (Parker 1982), an alternative evolutionary outcome is for males to travel between many females, mating frequently but contributing few sperm per female and tolerating partial paternity of any given batch of offspring. In this case, males strategically allocate only some of their ejaculate per female, and this may require females to mate multiply to ensure complete fertilization of her ova (Shuster and Wade 2003).

Although sexual females require fertilization in order to reproduce, and across taxa many components of seminal fluids aid in ovulation and preparation for reproduction in the female, not all ejaculate components are beneficial to females (Shuster and Wade 2003). For example, the female mammalian reproductive tract presents a hostile environment to sperm because of raised acidity and physical impedances to travel; this is not solely to protect against pathogens but also to actively target sperm (Arnqvist and Rowe 2013). Sperm viability is challenged by conditions in the female reproductive tract to eliminate weaker sperm and avoid ova being fertilized by multiple sperm, a condition known as polyspermy, which leads to nonviable zygotes. Some sperm do not survive in the reproductive tract, or later in storage, and so seminal substances have evolved to aid sperm longevity after ejaculation.

When determining patterns of sperm storage and use as it applies to sperm competition, it must be noted that ejaculate-female interactions are currently poorly understood, and many of what appear to be adaptations or counter-adaptations between coevolving males and females may be by-products of other physiological processes

(Arnqvist and Rowe 2013). Similarly, the role of cryptic female choice, whereby females control fertilization post-copulation by mechanisms that allow selection of one male's sperm over another, is also poorly understood (Birkhead and Møller 1998). These are areas ripe for further investigation as imaging, *in vitro* and *in vivo* techniques and molecular methods improve.

The theoretical possibility of intra-ejaculate sperm competition has been debated extensively (Birkhead and Møller 1998). It is possible that sperm within a fertilizing set may compete against each other if relatedness between sperm is low, as it would be in diploid species. In haplodiploid species, relatedness between the haploid sperm would be one and competition within an ejaculate should be absent. There is little evidence for intra-ejaculate sperm competition although there are observations that support its theoretical existence, such as the example of one of the few species with five distinct sperm morphs, an unusually high number, being haplodiploid, the hymenopteran wasp *Dahlbominus fuscipennis* (Birkhead and Møller 1998). Some sperm morphs are incapable of fertilizing and will assist other sperm within the ejaculate to fertilize successfully. Such traits would not be expected under intra-ejaculate sperm competition. Empirical evidence for intra-ejaculate sperm competition is rare, but Hemmings et al. (2016) found morphological differences between sperm trapped in the perivitelline layer of fertilized eggs and sperm obtained from feces of Zebra finches (*Taeniopygia guttata*). The sperm that reached the ovum had shorter heads and shorter heads relative to overall length in comparison to sperm randomly sampled from fecal deposits, which was interpreted as indicating "successful" sperm possessed traits for greater efficiency in swimming. While this does not demonstrate intra-ejaculate sperm competition, it does show that morphological and functional differences may exist between the sperm that are able to fertilize ova and other sperm.

There is also limited evidence for sperm cooperating within an ejaculate, also known as sperm altruism (Birkhead et al. 2009). In some species of rodents, the spermatozoa have an apical hook on the head that allows sperm to form large



sperm trains. The hooks are flattened against the head in the epididymis, and are unfurled about a minute after ejaculation. The hooks grip other sperm hooks, or onto the tails and sperm trains form within the female reproductive tract. These trains swim at a higher velocity than individual sperm and have an advantage in reaching the ova first. It is suggested that the sperm may possess a “green beard” recognition allele, or other genetic mechanism, to enable cooperation between the spermatozoa from a single male. Rodent species under the highest risk of sperm competition produce sperm with the most pronounced apical hooks. In other taxa, New World marsupials especially, sperm form pairs in the epididymis that result in a faster swimming speed compared to single sperm, due to the paired tails beating in unison (Birkhead et al. 2009). These morphological and behavioral traits are presumed to allow the sperm from a single male to successfully compete against the ejaculates from rival males.

### Offensive Adaptations for Sperm Competition

A spermatozoon cell is made up of four main parts: acrosome (or head), nucleus, mitochondria, and flagellum (or tail); however, sperm have been found in species lacking any one of these parts, for example, the anucleate parasperm found in gastropods and Lepidoptera. Adaptations to sperm morphology are one of the most commonly observed evolutionary responses to intense sperm competition (Birkhead et al. 2009). Biologists have studied sperm morphology for hundreds of years, since the invention of the microscope, and noted the species-specific nature of sperm cell morphologies, and, in some species, high levels of sperm morphological aberrations, or an ability to produce multiple sperm types (sperm heteromorphism), or very large sperm (sperm gigantism).

High levels of morphologically aberrant sperm, for example having two tails or no head, within the ejaculate is a response to relaxed sperm competition. Eurasian bullfinches (*Pyrrhula*

*pyrrhula*) produce highly variable sperm morphologies within their ejaculate and this evidence, combined with overall sperm morphology and relative testes mass, indicates a species where males face little risk of sperm competition (Birkhead and Immler 2007). By contrast, dunnocks (*Prunella modularis*) are known to engage in multiple copulations in a highly flexible mating system and produce a greater consistency of sperm morphologies within an ejaculate (Birkhead and Immler 2007). These patterns of consistent “high quality” and aberrant “low quality” sperm production are found across many taxonomic groups, including insects, mammals, and birds. This indicates that quality control of sperm production is a costly process that is not undertaken when the risk of sperm competition is low, which is consistent with Parker’s (1970) predictions about the costly nature of producing ejaculates.

Sperm heteromorphism is found in many taxa, from gastropods to tardigrades, annelids to spiders, and insects to chordates such as fish (Birkhead et al. 2009). Many taxa have two distinct sperm morphologies, but a few such as the Apple snails (Ampullariidae) have three or more. The morphology capable of fertilizing is called eusperm or eupyrene sperm and the morphs lacking some or all of the male’s DNA, and therefore incapable of fertilization, are called parasperm, and all morphs are produced in the testes. Their function varies between taxa. The giant parasperm found in mollusk species appear to act as transport for the smaller eusperm, but in Lepidoptera, parasperm are responsible for delaying female remating and are also a necessary component of the fertilization capacity of eusperm in some species. In other taxa such as gastropods and mammals, parasperm are responsible for disabling sperm from other males that are encountered in the female reproductive tract, and for blocking access to the female’s sperm-storage organs for any subsequent male’s ejaculates. All of these functions are consistent with an adaptive male response to the risk of sperm competition.

Sperm gigantism is the production of extremely large individual sperm cells. Perhaps

the most distinctive example is the giant sperm cells produced by the fruit fly *Drosophila bifurca*, which at 5.8 cm long is one of the largest spermatozoa in the animal kingdom. Each male can only produce and store six individual sperm at a time. The tendency for giant sperm in many *Drosophila* species is related to the effects of physical competition between sperm cells where displacement of rival male sperm takes place in the female reproductive tract. The giant sperm physically prevent any other sperm accessing the ova, and the overall small body size of the fly allows this mechanism to succeed. Immler et al. (2011) contrasted this pattern against the tendency for larger organisms such as passerine birds to produce tiny and numerous spermatozoa when operating under a raffle model of sperm competition. There is a trade-off observed between sperm size and sperm number that allows the evolution of giant sperm when organisms become smaller-bodied and the risk of excessive dilution in the female reproductive tract is lessened.

Spermatozoa are collectively transferred either to the environment in externally fertilizing species, or to the female within an ejaculate. Ejaculates also contain seminal fluid that assists in the transport of sperm and consists of biochemical products from accessory glands that perform various functions to enhance fertilization success. Sperm may spend considerable time within the female reproductive tract before fertilization, and the ejaculate interacts with, and counters some of the defenses of, the female reproductive tract during this time to maintain viable sperm cells (Birkhead et al. 2009). In the insects, accessory glands vary in number and developmental origin, and they produce a wide range of products (Leonard and Cordoba-Aguilar 2010). This diversity across taxonomic groups indicates rapid and divergent evolution of a suite of traits under strong selection. Accessory gland products may stimulate oviposition or suppress re-mating in females; they may remove rival sperm or facilitate sperm transport, storage or activation. The dose-dependent effects of many accessory gland products indicate that the males that can produce the greatest amounts, generally from larger glands, will have a fertilization advantage. In species of

fireflies (Coleoptera) and moths (Lepidoptera), accessory gland size is positively associated with greater risk of female polyandrous mating, suggesting the glands and their products play a positive role in fertilization enhancement and sperm competition (Leonard and Cordoba-Aguilar 2010).

Spermatophores are conglomerates of sperm in seminal fluid and other components that can either be deposited in the environment for later collection, or transferred directly to a female. They are found in invertebrate taxa such as cephalopods and Lepidoptera but have been extensively studied in the bushcrickets, Orthoptera: Tettigoniidae, due to the extreme sizes of spermatophore that some species produce (Wedell 1993). In a comparative study, Wedell (1993) found that one species of bushcricket produced a spermatophore that was 28% of the male's body weight, while some species produced smaller spermatophores that were just 2% of male body weight. There was a significant positive correlation between the size of the spermatophore and the length of time before a female mated again, which also correlated with male fertilization success. Although spermatophores are often eaten or otherwise absorbed by females to provide nutrients for egg production, they do not appear to be only or even mainly nuptial gifts. In many cases, spermatophores have evolved to provide protection and assistance to sperm to enhance male fertilization success (Wedell 1993).

Sperm production relies on the physiological capabilities of the testes and in general the greater the amount of testis tissue, the more sperm that can be produced. Biologists assume that testes size is correlated to the energy devoted to sperm production and to sperm production rates, and this assumption has largely been upheld (Parker et al. 1997). As a result, a standard proxy for the level of sperm competition across or within species is the size of the combined testes relative to overall body size. The larger or heavier the testes are in relation to body size, the greater the potential to produce large quantities of sperm, and the higher risk of sperm competition the males of the species are thought to face. The relative testes mass is often expressed as the gonosomatic index or GSI

( $= 100 \times \text{gonad weight/somatic weight}$ ) and has been measured across numerous taxa, including: primates, birds, mammals, butterflies, and fishes; all of which demonstrated the predicted positive correlation between risk of sperm competition, as indicated by male density or instances of female polyandry, and relative testes mass.

Among internal fertilizers, penile morphology has been shaped by the pressures of sperm competition into many forms to enhance sperm delivery and/or remove the sperm of rivals. Here the term “penis” is shorthand for any intermittent organ that delivers sperm during copulation. Penile morphology may be elaborated to such a degree that it is no longer reasonable to assume a function for insemination alone. Penile morphology adapted for sperm competition has been observed in the gastropods, arthropods, and vertebrates such as birds (waterfowl) and mammals (Birkhead and Møller 1998). A wide variety of morphological adaptations have been observed in the arthropods, some are elongated with flagella or other structures that can fit in the spermathecal duct to place sperm close to the site of fertilization within the female. One of the most extreme examples is found in the rove beetle *Aleochara tristis* (Gack and Peschke 2005). Males possess a long penile flagellum which is twice the male’s body length, while females have a correspondingly long spermathecal duct. The flagellum is stored coiled within the male’s main penile structure when not in use. After copulation, males engage in a particular behavior to retract the flagellum without it snapping or tangling, both of which would prevent the male mating again. The male must “shoulder” the flagellum while retracting it from the female, trapping it between his wing case and body while maintaining tension and moving away from the female. This allows the male to gradually feed the flagellum back into his body “in an orderly fashion,” ready to mate again. The de-coupling process takes about 90 seconds (Gack and Peschke 2005). This example shows the additional behavioral adaptations that accompany extreme morphological adaptations to sperm competition, as well as the mechanisms that species employ to overcome

constraints imposed by these extreme morphologies.

Waage (1979) was the first to observe that some penile morphologies were able to remove the sperm from rival males. He noted that damselfly, *Calypteryx maculata*, Odonata, penis heads have backwards-facing spines and horn-like structures on the head, and males perform an undulating motion during copulation that was demonstrated to remove sperm already present in the female’s sperm storage organ. Since then, the penis “scrapers” of many species have been described, and additional functions also detected. In the seed beetle, *Callosobruchus maculatus* (Crudginton and Siva-Jothy 2000), the penis is covered in spines that damage the female reproductive tract during copulation and this reduces female polyandry and longevity. The reduction in female longevity has been thought to be off-set in some species, like the seed beetles, by enhancement of female fecundity through products in seminal fluids, although this has yet to be established.

At least 36 taxa spread over 13 Classes of animals, from polychaete worms to amphibians, have been confirmed to engage in some form of copulatory wounding (Reinhardt et al. 2015). A smaller number of taxa have attempted to bypass the usual route to internal fertilization through the female reproductive tract and attempt to place sperm as close to the ova as possible by piercing directly through the female’s body wall. This insemination behavior also bypasses the female’s sperm storage organs, where sperm may become nonviable over time or be displaced by later-inseminating males. The best-studied group are the Cimicidae bedbugs, where all of the approximately 100 species fertilize the female by piercing the body wall with the penis (Reinhardt et al. 2015). In order to successfully fertilize using this “traumatic insemination” mating behavior, these taxa all have a penis with a sharpened tip, in some cases very similar to a hypodermic needle.

Among mammalian species, a variety of penile morphological elaborations are thought to play a role in sperm competition. Mammalian penises have spines, corrugations, fingers, or the entire

structure may be corkscrew-shaped (Birkhead and Møller 1998). The baculum, or os penis, is a bone that contributes to stiffening of the penis and allows prolonged copulation in mammalian groups such as bats, primates, rodents, and many carnivores. Keratinized penile spines are also found in a number of mammals such as primates, bats, and rodents. The presence of penile spines and/or the baculum is positively associated with relative testis mass in 296 species across four Orders of mammals (Birkhead and Møller 1998). Penile spines have also been implicated in inducing ovulation in groups such as the Carnivora, especially in felids, but there is no confirmed relationship between the presence of spines and induced ovulation. In the galago, or bush baby (Galagidae), the penile spines were thought to form a “genital lock” to allow prolonged mating. In general, mammalian penile adaptations appear to either facilitate prolonged copulation, or, in the case of spines, to prevent or delay re-mating.

Prolonged copulation duration is an adaptive trait that may increase the number of sperm transferred to the female, thereby enhancing a male's chances of fertilization. Copulation duration has been most closely studied in yellow dung flies, *Scatophaga stercoraria*, where the usual frequency-dependent game theoretic approach for understanding sperm competition is switched to a mathematic model following the Marginal Value Theorem (MVT) normally used to understand optimal foraging behavior (Birkhead and Møller 1998). The MVT is used as the base model for copulation duration as all the expenditures are expressed as time costs rather than in energy expenditure, which is a more accurate reflection of the costs to the copulating male. Copulation duration in dung flies depends upon the size of the male, and modeling and field studies have found that smaller males should spend more time in copula than larger males. This is because larger males can physically displace sperm at a faster rate, and they are also more successful at interrupting a mating pair during oviposition and displacing the first male's sperm with his own, reducing the time spent. Therefore long copulation times should be observed in species where the male benefits from increased time

to transfer sperm and has little chance of taking over an already-copulating pair.

These adaptations are all part of a suite of traits that males may employ during or after copulation to enhance fertilization success. Species may possess several of these traits, depending on the risk of sperm competition males may face, and traits may be used strategically in response to sperm competition risk. Males may determine the risk of sperm competition by assessing the mating status of females or estimating the density of competing males to available females. The strategic allocation of sperm to an ejaculate is one such example where individual males may alter their mating effort in response to sperm competition risk and save energy by allocating fewer sperm when that risk is very low. The next section deals with traits that attempt to avoid sperm competition before it happens, by restricting opportunities for female polyandry and often these traits consist of behaviors that occur before copulation.

## Defensive Adaptations for Sperm Competition

Many of the traits that prevent sperm competition occurring are also adaptations that control female accessibility. Females will attempt to avoid or evade these mechanisms, leading to conflict between the mating interests of males and females, known as sexual conflict. Rival males will also attempt to overcome these obstacles as part of male-male competition. Therefore, there is no strict definition that designates a trait as being “for” sperm competition when it also circumvents female choice, prevents male-male competition, and is still subject to the influence of natural selection from both biotic and abiotic factors.

Mate guarding is a widespread behavior that comes in a variety of forms. Any extended association between a mating pair that is longer than the time required for successful copulation is indicative of mate guarding, but often descriptions of the behavior rely on simple observations,

without quantifying the costs and benefits or determining if the behavior leads to increased fertilizations for the male (Simmons 2001). The presence of and type of mate guarding behavior that a species displays depends on a large number of factors including: the risk and intensity of sperm competition, whether first- or last-male sperm precedence operates, the synchrony of female maturation, the population operational sex ratio, how long females remain receptive to mating, and whether males can assess female mating status (Elias et al. 2014).

Mate guarding involves preventing the female from accessing other mating partners and can occur either pre-copulation or post-copulation. Three basic forms are observed, noncontact, contact and copulatory (Simmons 2001). Non-contact mate guarding behavior can involve closely following or herding fertile females, as seen in many ungulate herding mammals such as deer and antelope. Males may stay physically close until the female is receptive, partly to guard against rivals, but also because receptive females are rare, as seen in clown shrimp *Hymenocera picta*. In other taxa, males may block females into a burrow or other structure and aggressively defend the burrow entrance so that other males cannot access her, as in dung beetles *Onthophagus acuminatus*. Contact mate guarding requires males and females to be physically touching. Some taxa using this strategy ensure first-male sperm precedence by fertilizing females as soon as they become mature, by physically holding on to a female before she reaches maturity and mating with her as soon as she does (Simmons 2001). Prolonged copulation duration can also be considered a form of copulatory mate guarding (Birkhead and Møller 1998). Some species show a flexible set of strategies, such as the jumping spider, *Phidippus clarus*, which either clasps an immature female and guards her until maturity, or searches for virgin females (Elias et al. 2014). In this spider, each of these strategies was shown to be equally successful in terms of reproductive success.

A male that guards his mate is losing opportunities to find and fertilize other receptive females. Some species have developed a way to “guard”

females remotely by attempting to prevent re-mating by blocking the female reproductive tract. Copulatory or mating plugs consist of various products that block the female genital opening. Many insect species produce copulatory plugs from accessory gland products, which are sufficiently malleable to completely block the female oviduct (Parker 1970). Many species of spiders and mites also produce plugs, as do nematodes and reptiles (Birkhead and Møller 1998). This type of plug is also observed in a number of mammals such as rodents, bats, insectivores, primates, and marsupials. Some rodent mating plugs are a gelatinous accretion of seminal products that later harden to block or glue together the reproductive tract. Females may expel them later, but depositing a mating plug gives the male a significant time advantage to allow his ejaculate to fertilize her ova before she mates again.

Some taxa utilize their genitalia as mating plugs to prevent re-mating. This is frequently a terminal event, in that it can prevent the male re-mating and often results in death. “Explosive ejaculation” is recorded in hymenoptera such as the honeybee (*Apis mellifera*), where the force of ejaculation rips off the male endophallus and leaves it attached to the female genital opening (Paxton 2005). This and associated mucus forms a visible signal that the queen has been mated, yet this does not always prevent re-mating. Other drones will remove the endophallus and mate with her during the nuptial flight and she mates on average more than 17 times. Spiders generally mate by priming their specially modified pedipalps with sperm and inserting them into the female genital opening. Some species, such as the St Andrew’s Cross spider (*Argiope keyserlingi*) snap these off to plug the female and prevent re-mating, restricting the male to two copulations (Herberstein et al. 2012). In the St Andrew’s Cross spider, the plug formed by the broken pedipalp was determined to be an effective barrier to female re-mating. These are often seen as extreme adaptations to counteract the risk of sperm competition, but if at least some paternity is assured by these morphological and behavioral traits then they will be maintained in the population.



## Trade-Offs Between Pre- and Post-Copulatory Sperm Competition Traits

Under Parker et al.'s (2013) sperm competition model, trade-offs are expected between traits that enhance the chances of monopolizing females pre-copulation and traits that enhance the chances of successfully fertilizing ova post-copulation. This is due to the central idea of the cost of traits to an individual operating under a fixed energy budget. Males are assumed not to be able to pay the costs of both elaborate traits for winning male-male competitions and traits that enhance fertilization success under a high risk of sperm competition. Many of the adaptations presented here potentially pose significant costs to the males bearing them, from genital modifications or giant sperm to the physiological capacity to guard a female or copulate with her for prolonged periods of time, although the costs often remain unquantified. More attention has been paid to the costs of traits used in pre-copulatory male-male competitions, in terms of the production of weaponry or large body size. It is less common that the costs and trade-off in traits used in both the pre- and post-copulatory phases of sexual selection is specifically addressed, but the body of evidence for such a cost trade-off has been growing.

There is evidence for Parker et al.'s (2013) predicted trade-off between pre- and post-copulatory trait investment from organisms as diverse as fish, frogs, birds, mammals, and insects. Arctic charr, *Salvelinus alpinus* (Rudolfson et al. 2006), represent a good example of a species operating under intense sperm competition. They are externally fertilising teleost fish that are able to rapidly adjust their investment strategies in competitive postcopulatory traits dependent upon dominance status. Dominance in these fish is energetically costly and is dependent upon large body size, and dominant males guard territories to exclude rival males. Smaller males use alternative mating tactics to attempt “sneaky” mating with females and produce more numerous and faster swimming sperm than dominant males. When male charr were forced, by being housed with smaller or larger males, to take “favored” roles as dominant or “disfavored” roles as

subordinate males in an experimental trial, males in the disfavored role rapidly began to produce larger quantities of faster-swimming sperm, demonstrating investment in plastic traits that would enhance fertilization success under intense sperm competition. Here there is a trade-off between body size and sperm production capacity, concordant with the predictions of Parker (1970).

A species of myobatrachid frog, *Crinia georgiana* (Dziminski et al. 2010), demonstrated the link between the level of sperm competition risk and the trade-off in investment in traits to either prevent or win sperm competitions. In populations with the highest densities of males in breeding aggregations, indicating a greater risk of sperm competition for each individual male, males had relatively larger testes and a greater number of sperm stored within the testes. Parker et al. (2013) measured the forearm girth of male frogs in the same populations. Muscular forearms in *C. georgiana* males are used to wrestle other males over territory and to hold on to females during spawning while other males may try to dislodge them. Males from populations with the lowest densities of competing males had the largest forearm girth, as it was only in these low-density populations that males could effectively maintain a territory by wrestling intruders, whereas at higher densities territorial males were overwhelmed, and there was a negative correlation between relative testes size and forearm girth across populations. The prevailing patterns of trait investment across populations in this species provide support for the trade-off between traits used in male-male competitions and traits used in sperm competition.

Inter-specific differences in trait investment and trade-offs have also been found. Two species of Madagascan giant hissing cockroaches, *Aeluropoda insignis* and *Gromphadorhina oblongonota*, were found to differ inter-specifically in body size, weapon size, level of aggression during male-male contests and relative testes size (Durrant et al. 2016). *G. oblongonota*, a large heavily-armored cockroach with large horns on the pronotal shield covering the head, was highly aggressive during staged male-male contests, while *A. insignis* was smaller bodied

with very small horns and lacked aggression during male-male encounters. However, despite *A. insignis* being smaller-bodied than *G. oblongonota*, they had absolutely larger testes, and their testes scaled positively with body size, while *G. oblongonota* had relatively small testes for their size and an allometric relationship that showed testes size was smaller than expected in the largest-bodied males. Weapon size scales with body size, the largest male *G. oblongonota* had larger weapons, while *A. insignis* had absolutely smaller weapons but also a positive allometric relationship between body-size and weapon-size. These patterns of morphological investment indicate that the smaller species does not engage in aggressive male-male contests to access and control females, but is adapted to engage in sperm competition by investing in testes mass, while the larger species appears adapted to fight other males and attempt to control access to females to prevent multiple mating, therefore it does not need to invest in large testes. This example shows Parker et al.'s (2013) predicted trade-off in operation within and between species, with physiological and behavioral consequences for many aspects of an individual's phenotype.

The trade-off between ornaments and armaments, used in male-male pre-copulatory contests, and testes mass has been explored using comparative data (Luepold et al. 2014). The extent to which males are able to monopolize females appears to dictate male investment in either pre-copulatory contest traits or in post-copulatory ejaculate traits. Female monopolizers are defined as species that control access to females, by means such as non-territorial mate guarding or single-male-mating systems in ungulate species. The covariance between pre- and post-copulatory sexual traits gradually shifts from strongly positive to strongly negative with increasing male-male contest competition among taxa. There is a switch from positive or no covariance between armament and/or sexual size dimorphism and testes mass in taxa with little female monopolization; to a negative covariance between these traits in species with high rates of female monopolization. Monogamy was classed as low monopolization

of females due to reduced male-male competition and little polyandry in species such as pheasants and primates, for example, while group and pair spawning minnow species were all classed as low monopolization. Species of dung beetles with high rates of male sneaking behavior and female polyandry were also classed as low monopolization, while species such as pinnipeds which are able to monopolize females through male-male contests had strong negative trade-offs and were classed as high monopolizers. This suggests the potential for a unifying theory for explaining patterns of trait investment and trade-off in species under sperm competition.

## Mate Choice and Cryptic Female Choice

Female choice can operate sequentially or simultaneously with sperm competition, and it is important not to think of the female as passive in the mating process (Eberhard 1996). Females encourage sperm competition by mating with multiple males, but they can also facilitate it further by engaging in rapid and frequent copulations, having capacious sperm storage organs, by not terminating copulations prior to ejaculation, and by providing conditions in the reproductive tract that enable sperm survival. Females can manipulate the amount of sperm transferred by terminating copulations or by having convoluted and very long sperm storage organs that in time digest sperm, rather than allowing it to fertilize. They can also change the direction of sperm movements by muscular contractions or by the beating of cilia lining the reproductive tract. All of these traits allow females to remain active in exercising their choice of mate.

Cryptic female choice, essentially the idea that female choice continues post-copulation just as male competition does, was initially proposed as an alternative to sperm competition. A simple cryptic female choice mechanism is sperm dumping and is observed in spiders, birds and *Drosophila* flies. Domestic fowl (*Gallus gallus domesticus*) hens are able to dump the sperm of unwanted males by ejecting the ejaculate from the

cloaca post-copulation, while this ability has been exploited by the male dunnoek, who peck the female cloaca prior to copulation to induce sperm dumping and remove rival sperm. The female reproductive tract is the arena for sperm competition in internally fertilising species, and it is not inert, but instead has means of transporting sperm and its own physiochemical ecosystem (Eberhard 1996). Hormonal or other alterations of the reproductive tract can favor or disfavor sperm survival or movement. In insects, even if a female is unable to prevent copulation, she can alter her pattern of oviposition such that only a few fertilizations accrue to non-preferred males. If she is unable to redirect sperm away from fertilising the egg, females can reabsorb embryos or abort spontaneously, or provision eggs with differing amounts of nourishing yolk or hormones to favor certain offspring, and therefore males, over others. Evidence for some of the mechanisms by which cryptic female choice may operate is limited (Birkhead and Møller 1998). If it does occur in a widespread manner, it is not necessarily mutually exclusive to sperm competition as an explanation for differential fertilization success.

Traits associated with pre-copulatory male-male competition and post-copulatory sperm competition may not always trade-off against each other, instead they may be positively correlated. Sheldon (1994) proposed the Phenotype-Linked Fertility hypothesis which argued that females use phenotypic indicators of male high quality in mating decisions, such as elaborate plumage or plumage coloration in birds, because they also indicate high quality or more viable sperm. The Sexy Sperm and Good Sperm hypotheses posit similar indirect benefits to females from sperm competition. Sexy Sperm predicts that females that mate multiply will pass the traits that allowed the successfully competing male's sperm to fertilize her ova on to her sons (Curtisinger 1991), while Good Sperm predicts that males that possess competitive sperm also are generally phenotypically superior to unsuccessful rivals, and these traits may be passed on to both sons and daughters (Yasui 1997). All of these hypotheses suggest a vital and active role for

female choice and incorporate the promotion of sperm competition by the female.

A co-evolutionary arms race may occur between males and females, where the males seek rapid and frequent fertilizations and the females seek to avoid having an egg fertilized by more than a single sperm (Arnqvist and Rowe 2013). When more than one spermatozoon penetrates the ova this is called polyspermy. Polyspermy is undesirable because of the conflict between two sets of paternal genes when directing the development of the zygote and most cases of polyspermy end in failure of the embryo to develop. The avoidance of polyspermy leads to a sperm-hostile female reproductive environment that attempts to ensure few sperm reach the ovum in the first place. Because of the co-evolution of sperm competitiveness and female resistance, this leads to selection in males for ever more competitive sperm. The polyspermy theory is in contrast to the Sexy Sperm hypothesis, which makes assumptions about the heritability of sperm characteristics that are not always well supported by evidence (Arnqvist and Rowe 2013). The avoidance of polyspermy also contradicts the Sexy Sperm hypothesis, as the mitochondria, which are one of the determinants of sperm competitiveness, are not inherited by offspring from the father, but rather are maternally inherited, meaning that particular advantage will not be passed on.

## Conclusion

Sperm competition is recognized to be a pervasive and powerful evolutionary force that shapes phenotypes in all sexually reproducing organisms. As soon as there is even occasional polyandrous mating by females, there is the potential for sperm competition. Males have evolved a variety of adaptive physical and behavioral traits to outcompete their rivals, while females have evolved traits of their own to influence the outcomes of competitions in ways that are not always easily observed by researchers, but form a potentially rich area for future studies.

## Cross-References

- Anisogamy
- Coolidge Effect, The
- Evolutionarily Stable Strategies
- Female Choice
- Game Theory
- Intersexual Selection
- Operational Sex Ratio (OSR)
- Polyandry
- Postcopulatory Selection
- Sexual Dimorphism
- Sexual Selection
- Spermatogenesis
- Upsuck Hypothesis

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## Sperm Retention

- [Upsuck Hypothesis](#)

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## Spermatocytogenesis

- [Spermatogenesis](#)

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## Spermatogenesis

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## Synonyms

[Male gametogenesis](#); [Spermatocytogenesis](#)

## Definition

Spermatogenesis is the process by which an animal that exhibits sexual reproduction produces spermatozoa from spermatogonial stem cells (SSCs) through a series of mitotic and meiotic cell divisions.

## Spermatogenesis trough the animal life cycle

Spermatogenesis is the process by which cells known as diploid (2n) male germline cells undergo a series of mitotic and meiotic divisions. These divisions culminate in a complex and well-orchestrated process of differentiation, which gives rise to haploid (n) male gametes. Some of these gametes will participate in the process of fertilization and production of new individuals in animals that exhibit sexual reproduction (Hess 1999). This elaborate process involves several genetic and epigenetic factors of germ cells and other associated somatic cells, as well as the environmental factors to which these cells are exposed. The spermatogenesis process occurs inside what is known as germ tissue (Handel and Schimenti 2010). Germ tissue can be organized into a simple cluster of cells in the medial portion of the animal's body cavity or as cordonal or cystic organs in the abdominal cavity. Some vertebrates, such as birds and mammals, have their germ tissue organized in the form of tubular structures called seminiferous tubules, which are stored inside the testicles (Hess 1999).

In mammals, the events that characterize the development and differentiation of germline cells start early in the embryonic life cycle. In some individuals, primordial germ cells (PGCs), or gonocytes, follow the oogenesis pathway, while in others they follow the spermatogenesis pathway. Early stages of male-specific germ cell development involve several coordinated processes, including the active maintenance of pluripotency followed by the precisely timed loss of pluripotency, the remethylation of the genome and upregulation of male-specific markers, the locking down of male differentiation, and the suspension of cell division. Genes that are key

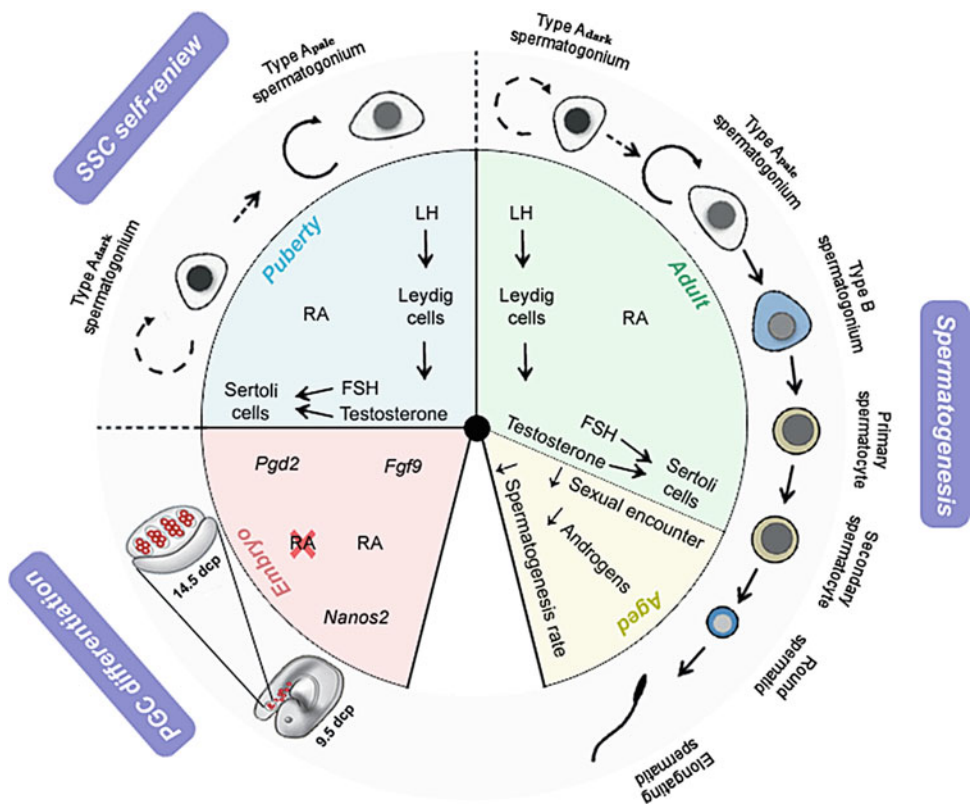


regulators of these processes have been identified and include the fibroblast growth factor 9 (*Fgf9*), Nodal, Cripto, Activin, Prostaglandin D2 (*Pgd2*), and Nanos2. Many of these factors are involved in more than one of the aforementioned process. The balance between the presence and absence of retinoic acid (RA) is also important in this sex determination process (Spiller et al. 2017; Fig. 1).

These PGCs remain mitotically quiescent until birth in mice, whereas in humans, they do not enter total quiescence but do exhibit varying proliferative activity (Manku and Culty 2015). PGCs that reach the basement membrane form the spermatogonial stem cell (SSC) population and give rise to the differentiating spermatogonia of the first cycle of the seminiferous epithelium (Yoshida et al. 2006). However, this differentiation process does not start until the animal reaches sexual maturity. The physiological event that

guarantees its occurrence is the SSC's self-renewing mechanism, which itself occurs through successive and well-balanced mitotic divisions. This self-maintenance of SSCs in the germ tissue is governed by the existence of a specific microenvironment through the actions of somatic cells known as Sertoli cells. Sertoli cells exhibit broad gene expression plasticity and rely primarily on levels of FSH (produced by the pituitary gland) and testosterone (produced by testicular Leydig cells) to exert a paracrine control over the proliferative activity of the SSCs. Exit from these self-renewing state and consequent differentiation commitment are the first steps on the long road of spermatogenesis, and they take place when animals reach sexual maturity (Mäkelä and Toppari 2017; Fig. 1).

The beginning of the spermatogenesis process, which is characterized by the onset of SSC



**Spermatogenesis, Fig. 1** Schematic view of the spermatogenesis process. Representation of embryo phase is based on mice sex determination (inspired by Spiller et al.

2017). Representation of puberty, adult, and aged phase is based on human spermatogenesis (inspired by Mäkelä and Toppari 2017) (*dpc* days postcoitum)

differentiation, is also controlled by Sertoli cells. The entire physiology of adult testes is also controlled by mechanisms of activation and repression of certain genes (some of which are located on the sex chromosomes and others are located on the autosomes), as well as by complex mechanisms of gene expression control mediated by small noncoding RNAs (Lopes and Roelen 2010). Mammalian spermatogenesis is classically divided into three phases: (1) the mitotic (proliferative) phase; (2) the meiotic phase; and (3) the spermiogenic phase (Mäkelä and Toppari 2017):

1. *Mitotic phase*: Stem  $A_{\text{dark}}$  spermatogonia (while still true SSCs) (2n) rarely divide through mitosis (the self-renewal mechanism). When this division produces differentiated  $A_{\text{pale}}$  spermatogonia (2n), the process of spermatogenesis begins. These  $A_{\text{pale}}$  spermatogonia can go through a limited number of mitotic divisions for their own self-renewal until a mitotic division produces type B spermatogonia (2n). Type B spermatogonia divide through mitosis and differentiate into primary spermatocytes (2n).
2. *Meiotic phase*: Primary spermatocytes are cells that undergo the first meiotic division. Meiotic division consists of a series of events classified as Prophase I, Metaphase I, Anaphase I, and Telophase I. Prophase I is the stage that includes meiotic recombination, one of the most important genetic events in spermatogenesis: it is the result of the crossover between paired regions of homologous chromosomes (Hess 1999). Secondary spermatocytes (n) emerge as a result of the first meiotic division. These cells have a short lifespan because they quickly divide during the second meiotic division, giving rise to round spermatids (n) (Mäkelä and Toppari 2017).
3. *Spermiogenic phase*: Round spermatids will undergo a process called spermiogenesis, which involves increased chromatin condensation, core compaction, cytoplasmic remodeling, and epigenetic profile modification, which results in cells known as elongated spermatids (n) (Peruquetti 2015; Fig. 1). Mature

elongated spermatids are released into the tubular lumen and are stored in the epididymis. They are externalized during the mating process.

Several studies have shown that male endocrine function decreases with age, as does the quality of seminal parameters such as number and viability of sperm (Angelopoulou et al. 2013; Fig. 1). Nevertheless, barring any pathological factors, spermatogenesis is a process that persists for many years, which makes it clear that males have the ability to produce viable offspring until very late in their life cycle.

## Cross-References

- [Androgens](#)
- [Crossover](#)
- [Ejaculate](#)
- [Embryo](#)
- [Fecundity](#)
- [Fertility](#)
- [FSH](#)
- [Gametes](#)
- [Genetic Variation](#)
- [Genomic Imprinting](#)
- [Heredity](#)
- [Mating](#)
- [Mitosis](#)
- [Mutations](#)
- [Noncoding RNA](#)
- [Nondisjunction](#)
- [Pituitary Gland](#)
- [Reproduction](#)
- [Testosterone](#)
- [Zygote](#)

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## Spermatozoa

### ► Gametes

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## Spheniscidae

### ► Penguins: Behavioral Ecology and Vocal Communication

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## Spontaneous Recovery

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## Synonyms

[Return of fear](#)

## Definition

*Spontaneous recovery* occurs when a previously learned response returns after a time interval following extinction.

## Introduction

First described by Pavlov (1927), the demonstration of spontaneous recovery in the laboratory requires a three stage experiment, conditioning, extinction, and test. In the conditioning stage, a conditioned stimulus (CS, such as a ticking metronome) is repeatedly paired with the unconditioned stimulus (US, such as food) until a vigorous conditioned response (CR, such as salivation) comes through associative learning to evoked by the CS. When the US is subsequently withheld in the extinction stage, the CR declines in magnitude and probability because the CS is no longer paired the US. At test, assuming a sufficiently long period of time has elapsed, the first presentation of the CS is likely to evoke a much larger CR than it did on the final trial of extinction. The CR is said to have *spontaneously recovered* because the passage of time without any experimental manipulation caused the CR to reappear. As one might suspect, additional test presentations of the CS without the US normally produce rapid re-extinction, whereas re-pairings of the CS and US normally produce rapid reacquisition.

Spontaneous recovery is a result rather than an explanation. But, as a result, it has important theoretical and applied implications. Its occurrence stimulated the view that extinction results in something new being learned. The old learning is not erased leaving nothing. This idea can be traced to Pavlov (1927). Suppression rather than loss seemed to him to be the most straightforward explanation of why CR recovery is possible after extinction. According to Pavlov, extinction procedures lead to a loss of responding, but the first learned CS-US association is not lost. Rather, the normal behavioral effects of CS-US association are limited by the development of inhibition over the course of extinction. Pavlov maintained a CS centered view of conditioned inhibition in

which the learned neural inhibition acquired in extinction gradually faded over time. A modern neuroscientist might be more likely to say that spontaneous recovery tells us that conditioning and extinction memories coexist in distinct neural connections and are activated independently based on a number of factors. Both would agree that something new is learned in extinction. One critical piece of support for new learning accounts is that pharmacological blockade of a special type of neural receptor involved in learning process (*N*-methyl-D-aspartate, or the NMDA receptor) undermines extinction (Falls et al. 1992). This suggests that new learning is happening during extinction in the absence of the drug. Thus, declines in behavior do not necessarily imply a weakened CS-US association. The later discovery of “extinction neurons” in the amygdala (Herry et al. 2008), which fire in extinction but not conditioning, is an intriguing result in line with Pavlov’s thinking.

Although spontaneous recovery rarely causes CR levels returning to pre-extinction levels, the ubiquity of spontaneous recovery has profound applied implications. The spontaneous recovery of fear CRs, in particular, raises many questions relevant to the treatment of anxiety disorders. Exposure therapy conducted in the clinic is designed to help people confront their fears in a safe situation. Feared stimuli are repeatedly presented in the absence of any aversive event in the hopes this will diminish fear. Putting aside the topic of anxiety disorders for the moment, we can ask the following questions (1) does the passage of time cause inhibition to dissipate leading to spontaneous recovery, as Pavlov (1927) theorized, or does extinction learning remain but is somehow more poorly expressed, (2) what conditions prevent spontaneous recovery, and (3) is the conditioning memory is partially erased by extinction causing incomplete spontaneous recovery? Answers to these questions are important because potential treatments are informed by an understanding of the processes responsible for spontaneous recovery. The partial NMDA agonist D-cycloserine (DCS), for example, has been tested in humans (Myers et al. 2011) to determine if it aids the consolidation of extinction learning, and

thereby minimizes the spontaneous recovery of fear.

## Does Inhibition Fade?

Does inhibition fade over time as Pavlov (1927) hypothesized? Few would agree the data merit this assumption. Devenport (1998) formulated the temporal weighting rule in which memories were weighted less heavily over time as they became more remote. The temporal weighing rule was inspired by accounts of foraging behavior in animals. Immediately returning to a formerly rich patch of food after it has been thoroughly exploited is not a good strategy. However, a later return after the patch has a chance to replenish itself might pay dividends. The weighting rule provides a natural account of increasing levels of spontaneous recovery over time since extinction. When the extinction memory is fresh, it is relatively more likely to be assessed than the earlier memory of a rich patch. This formulization does not assume learned inhibition is the process leading to extinction, nor does it assume that anything has faded. It assumes two relatively permanent memories of conditioning and extinction are formed and the relative ease of retrieval of these memories changes over time.

## Conditions Favoring Spontaneous Recovery

What conditions favor the occurrence of spontaneous recovery? Any theory of spontaneous recovery must explain the basic finding that spontaneous recovery gradually increases over time. Being too tired to respond might be expected to depress responding in extinction, and a 1 day rest might permit responding to return. However, this explanation does not explain why of two extinguished CSs in the same animal, the one extinguished yesterday supports less spontaneous recovery than the one extinguished over a week ago (Rescorla 2004). The response is common to the two CSs in test and cannot differentiate between them. The results of this last experiment

should be interpreted with caution. One should not conclude that performance factors don't matter at all. They just can't be the primary explanation.

One factor known to reduce spontaneous recovery is delaying the time of extinction until many days after the last conditioning session. Devenport's rule predicts that spontaneous recovery should be minimal when the interval between conditioning and extinction is maximal, making extinction the much more recent memory on a relative basis. It is not obvious how CS inhibition, developing in extinction and then fading, could handle such a result. Extinction trials scheduled after the point of the cessation of the CR also reduce spontaneous recovery. Called "extinction beyond zero" by Pavlov (1927), it is also known as massive extinction. The number of sessions of extinction per se is also an important variable. Each inter-session interval permits spontaneous recovery to reoccur, and then be eliminated with additional unreinforced trials.

A change in context from extinction to test can greatly enhance the recovery of responding. This phenomenon is so robust it has earned its own name, *renewal*. Renewal refers to increased recovery when the CS is tested in a different environment than it was extinguished. The classic case is ABA renewal. The nomenclature used describes the physical locations of the three successive stages of a standard spontaneous recovery experiment, conditioning (in Context A), extinction (in Context B), and test (a return to Context A). Other types of renewal include AAB and ABC. Extinction in multiple contexts gradually reduces the level of spontaneous recovery seen when each context is experienced for the first time.

The importance of context has led to a popular theory about how spontaneous recovery is best explained. Bouton and colleagues (e.g., Bouton et al. 2006) suggest that time acts like the presence of a physical context. As time passes in our lives, we experience many new events while other events continue to reoccur. Events present at the time of extinction (like physical contexts) may aid in the retrieval of the extinction memory if they are also present

at test. If these events are no longer present, spontaneous recovery may occur in the absence of extinction reminder cues. More formally, extinction is said to produce a new CS  $\rightarrow$  no US association that hinders responding triggered by the previously acquired CS  $\rightarrow$  US association. Because the new CS  $\rightarrow$  no US association is contradictory, its retrieval is more contextually and temporally limited than the first-learned CS  $\rightarrow$  US association. A switch out of the extinction context and/or increasing time since extinction should make it more likely that spontaneous recovery will occur. One of the more interesting predictions of this account is that reacquisition might be retarded rather than facilitated if extinction cues are very strong. Neurons in the infralimbic region in the prefrontal cortex seem to play a role similar to the one described by Bouton et al. (2006). If inactivated, they very nearly eliminate the recall of extinction the day after extinction, but do not prevent it from happening in the first place (Quirk et al. 2006).

## Weakened Associations

Not all theories assume that CS-US associations are left intact in extinction (Delamater and Westbrook 2014). That spontaneous recovery is rarely complete is the single most obvious reason to think that extinction might involve a partial loss of the CS-US association. Skinner (1938) assumed permanent response weakening occurs in extinction, and some aspects of the original learning experience are spared. He speculated that stimuli from the beginning of the session might be protected from extinction because all responding had yet to be removed at that point. Estes (1955) stimulus sampling theory maintains only a portion of the elements of the CS are sampled on each trial, and thus elements not sampled at the time of extinction may later be sampled at test. As they have yet to undergo extinction, spontaneous recovery might be expected. Even if some of the old learning is spared in the manner suggested by Skinner and Estes, this does not imply old associations are weakened.



## Spontaneous Recovery in Instrumental Learning

Spontaneous recovery is also observed in instrumental or operant conditioning. Pressing a lever can be arranged in the laboratory to produce a valuable commodity, such as food pellet reinforcer. When the reinforcer that normally followed that response is withheld, extinction occurs. However, the response may spontaneously recover over time in the absence of the chance to respond. Both Todd (2013) and Rescorla (2004) have argued that instrumental extinction is best characterized by the idea that previously reinforced responses are inhibited. This account holds stimuli present at the time of extinction must be present at test to prevent spontaneous recovery.

## Conclusions

Most researchers are in agreement that spontaneous recovery implies the original CS-US association survives extinction to some extent. They would also agree that spontaneous recovery implies some of the mechanisms accounting for within session declines in responding may not operating at the time of test, shifting the focus of attention to a failure of the retention of extinction to explain spontaneous recovery. A number of mechanisms have been proposed, including many processes not even mentioned in this brief entry. Many of these mechanisms are complementary so embracing one does not mean the other is wrong. For example, the mechanisms described by Skinner and Estes are clearly incomplete and might not be wrong, but Pavlov (1927) was certainly correct in asserting that some new learning occurs in extinction that covers up the old learning, leading to spontaneous recovery.

## Cross-References

- B.F. Skinner
- Conditioned Inhibition
- Extinction in Learning

- Ivan Pavlov
- NMDA Receptors
- Operant Conditioning
- Unconditioned Response
- Unconditioned Stimulus

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## Sporadic Discovery

► [Serendipity](#)

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## Sporting

► [Hunting](#)

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## Spreading

► [Diffusion](#)

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## Spurious Correlation

► [Superstition Experiment](#) (Staddon and Simmelhag 1971)

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## Squamata Diet

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## Synonyms

[Behavior](#); [Foraging](#)

## Introduction

Of the currently extant nonavian Reptilia, the order Squamata is by far the largest. At the time of this writing, this order is represented by 10,221 described species. This group includes some of the most recognizable of reptiles, the lizards and snakes. Within the lizards, diets vary widely from strict herbivores to purely carnivorous forms.

Some well-known examples on either end of the spectrum are the iguanas in the family Iguanidae (herbivores) and the generally large, among lizards, carnivorous (or mostly so) monitor lizards (family Varanidae). The Serpentes (snakes) are all some variation of carnivore (insectivorous, oophagous, carnivorous), with most having lightly constructed skulls that appear to be formed by series of struts and ligaments that allow for the consumption of prey larger than the size of their heads in a number of taxa. Most famously, this skull construction allows snakes like the giant boas and pythons to swallow prey as large as antelope or deer. As impressive as these prey items are, the highest ratios of prey/predator mass has been observed in vipers and pipesnakes, with some consuming prey equal to or exceeding their own body mass. There are myriad adaptations among the various families of Squamata related to feeding and diets. This chapter aims to review in a generalized sense the diets and notable adaptations of the various groups of squamates from a phylogenetic viewpoint. It is not intended to be an exhaustive review of all diets or dietary adaptations within Squamata. The taxonomy follows the online Reptile Database ([www.reptile-database.org](http://www.reptile-database.org)) and the phylogeny is that of Pyron et al. (2013).

## Food and Feeding Habits of Snakes (Serpentes)

Within Squamata, the snakes are among the most recognizable due to their limbless condition. While there are numerous forms of limbless lizards, those that are classified within the Serpentes (or Ophidia) are the most derived. There are over 3,700 currently recognized species of snakes worldwide and they fill a number of terrestrial, arboreal, and aquatic predatory niches.

While there are no herbivorous species of snakes, diets can vary widely from consuming termites up to large mammalian prey. There are even reports of snakes consuming carrion. We will review the diversity of snakes and their general diets according to their phylogeny. Dietary information for the taxonomic groups largely adheres to information presented in Greene (1997) unless otherwise noted.

**The “Blindsnakes”:** While not a truly monophyletic group, the snakes in the following families are collectively referred to as blindsnakes or threadsnakes: Anomalepididae, Leptotyphlopidae, Gerrhopilidae, Xenotyphlopidae, and Typhlopidae. They are Pantropical including Madagascar and Australia with some reaching temperate regions. These snakes have unique skull morphologies and dentitions that allow for fossorial lifestyles and a diet of ants and termites, including their eggs and larvae.

**South American Pipesnakes (Aniliidae):** This family currently includes a single species, the South American Pipesnake (*Anilius scytæ*), which feeds primarily on long-bodied prey such as caecilians, amphisbaenians, other snakes, and eels.

**Neotropical Dwarf Boas (Tropidophidae):** This family includes the Caribbean and South American genus *Tropidophis* and the eyelash boas in the genus *Trachyboa*. These snakes are all typically less than 1 m in length. All species feed primarily on amphibians and lizards at all life stages.

**Spinejaw Snakes (Xenophidiidae):** This family of snakes was only recently discovered and are poorly known. There are two species described (*Xenophidion acanthognathus* and *X. schaeferi*) from Borneo and peninsular Malaysia. They are believed to feed on scincid lizards.

**Round Island Boas (Bolyeriidae):** The single extant species in this family, the Round Island Ground Boa (*Casarea dussumieri*), has a unique hinge between the two component bones of the maxillary which allows it to pull the anterior segment of each maxilla downward, an adaptation that appears to aid in holding prey. *Casarea dussumieri* feeds primarily on geckos and skinks.

**Calabar Burrowing Boa (Calabariidae):** The Calabar Burrowing Boa (*Calabaria reinhardtii*) of western Africa is the only member of this family and feeds on nestling rodents concealed in leaf litter and low vegetation.

**Boas (Boidae):** The family Boidae is rather diverse and speciose. Members of this family are found on all continents except Antarctica and Australia (Graham Reynolds and Henderson 2018). Most are dietary generalists and ambush predators that can go long periods of time between

meals. Unless otherwise noted, all information regarding the Boidae adheres to that presented in Greene (1997) and Henderson and Powell (2007).

The boas in the subfamily Boinae are restricted to the neotropics. This subfamily includes heavy-bodied generalists like the boa constrictors (*Boa*) and the world’s heaviest and one of the longest snake species, the Green Anaconda (*Eunectes murinus*). These large, stout snakes are powerful constrictors that prey on a wide variety of vertebrate prey at all life stages. Of somewhat more slender build are the rainbow boas and Caribbean boas (*Chilabothrus* and *Epicrates*), some of which are highly arboreal. All feed primarily on small mammals as adults, although some of the Caribbean species include more lizards in their diets, especially when young. The most specialized to an arboreal lifestyle in this family are the tree boas in the genus *Corallus*. These snakes have elongated teeth that allow for a stronger grip on their predominantly mammalian and avian prey captured in the trees, with the two species of emerald tree boa (*C. batesii* and *C. caninus*) having especially formidable looking teeth. Additionally, they have well-developed infrared receptors situated in pits along the upper and lower lips that presumably aid them in visualizing endothermic prey.

Members of the subfamily Ericinae (sand boas) and some of the Ungaliophiinae (bromeliad, rosy, and rubber boas) are found in temperate regions of Eurasia and North America, respectively. The African and Eurasian sand boas of the Erycinae feed on small rodents, lizards, and occasionally birds. Of the Ungaliophiinae, the small bromeliad boas (genera *Exiliboa* and *Ungaliophis*) of Latin American forests prey upon amphibians and lizards. The Rosy Boa (*Lichanura trivirgata*) occupies rocky chaparral and deserts of the American Southwest while the Rubber Boa (*Charina bottae*) occurs mostly in the moist forests of north western North America. Both species feed primarily on rodents and small birds.

The Pacific boas in the genus *Candoia* are restricted to the Solomon Islands, New Guinea, and several other islands in the south Pacific. All feed largely on lizards as juveniles while transitioning to a primary diet of small mammals as adults.

**Dwarf Pipesnakes (Anomochilidae):** The snakes in the genus *Anomochilus* are found in Borneo, Sumatra, and peninsular Malaysia. These snakes are very poorly known with little data on their natural history.

**Asian Pipesnakes (Cylindrophiiidae):** Asian pipesnakes (*Cylindrophis*) are burrowers that specialize in feeding on caecilians, eels, and other snakes. These snakes can consume prey equal to their own mass. Unlike many snakes that typically demonstrate high prey/predator mass ratios, pipesnakes have relatively small gapes (Hampton 2018), which limit them to consuming long, cylindrical prey items that are of similar or smaller diameter to themselves.

**Shield-tailed Snakes (Uropeltidae):** This family consists of over 50 species in seven genera all found in India and Sri Lanka. Shield-tailed snakes are fossorial and feed on earthworms.

**Asian Sunbeam Snakes (Xenopeltidae):** So-named for their smooth, highly iridescent scales, the two species of Asian sunbeam snakes (*Xenopeltis hainanensis* and *X. unicolor*), have folding teeth and feed on skinks as well as frogs and rodents.

**Neotropical Sunbeam Snakes (Loxocemidae):** Sometimes referred to as the “burrowing python,” the single species in this family (*Loxocemus bicolor*) has an upturned snout which it utilizes for digging, including the excavation of lizard and turtle eggs. They also feed on lizards and rodents.

**Pythons (Pythonidae):** The pythons are restricted to Africa, Asia, and Australasia. Unless otherwise noted, all information regarding the Pythonidae largely follows Greene (1997) and Henderson and Powell (2007). They range in size from the under 1-m Anthill Python (*Antaresia perthensis*) to the world’s longest snake species, the Reticulated Python (*Malayopython reticulatus*), which may reach 10 m in length. All pythons are powerful constrictors and most species consume endothermic prey, although the Australian pythons in the genus *Aspidites* often prey on squamates. Additionally, most pythons have exceptionally large gapes and loosely constructed skulls allowing them to consume prey several times larger than their heads

and the thickness of their bodies. Pythons are well-known for going long periods in between such hefty meals. With the exception of *Aspidites*, all pythons are equipped with infrared receptors situated in a series of deep pits in the labial scales about the mouth that function as pinhole cameras to visualize their surroundings and, presumably, specifically endothermic prey.

**Elephant Trunk Snakes (Acrochordidae):** Also known as file snakes, these heavy-bodied fully aquatic snakes are only found in Australasia. These snakes feed primarily on fish, with *A. granulatus* appearing to feed largely on gobies and crustaceans while the other two species; *A. arafurae* and *A. javanicus*, feed largely on eels, catfish, and other freshwater fish. Similar to the pythons, these snakes have exceptional gape limits and can consume very large prey in comparison to their body size (Shine 1986).

**Xenodermatidae:** This family consisting of 18 species within six genera are found in southeastern Asia. These poorly known snakes are fossorial and feed on frogs.

**Slugsnakes (Pareatidae):** These snakes generally feed on terrestrial mollusks, pulling snails from their shells using needle-like teeth and alternating movements of their elongated mandibles. One species, the Blunt-headed Treesnake (*Aplopeltura boa*) feeds on lizards.

**Vipers and Pitvipers (Viperidae):** The vipers and pitvipers are found on every continent except Antarctica and Australia. All have mobile, anteriorly placed large hollow fangs for delivering venom. Much of the information regarding the vipers and pitvipers is summarized from Greene (1997) and Schuett et al. (2002) unless otherwise noted in the text. They are largely terrestrial, though a number of species have taken to an arboreal lifestyle. Despite the high species diversity within this family (347 species to date), only the Cottonmouth (*Agkistrodon piscivorus*) of the southern United States has adopted a largely semi-aquatic lifestyle and aside from some of the African night adders (*Causus*), none of the Viperidae have special adaptations for burrowing. The two largest taxonomic groups within this family are the Old World vipers and adders (Viperinae) and the pitvipers (Crotalinae). Similar to some of the

boas and pythons mentioned previously, pitvipers have infrared receptors located in pits on both sides of the head between the eye and nostril. The third group, the Azemiopinae, is represented by two species within the genus *Azemiops*. These snakes from the highlands of Myanmar, southern China, and Vietnam are poorly studied, with scant information on their diet.

The Viperinae are restricted to Africa, Asia, and Europe. Most of the Eurasian vipers and adders (*Macrovipera*, *Montivipera*, *Vipera*) are a meter or less in length, although some species like the Russell's Viper (*Daboia russelli*) may reach nearly 2 m. They occupy mostly temperate regions. They mainly feed upon insects, frogs, and lizards as juveniles while typically consuming mammals as adults. The strictly African members of the genus *Bitis* are particularly stout snakes. There are examples of Gaboon Vipers (*Bitis gabonica*) nearing 2 m in length and exceeding 10 kg in mass. These exceptionally large vipers have been documented to predate upon a range of mammals, including antelope. Smaller members of this genus like the Perringuey's Adder (*B. peringueyi*) stay well under a meter long and feed on small mammals and lizards. The several species of saw-scaled vipers (*Echis*) live in arid regions of Africa, middle Asia, and India. They feed on arthropods, birds, lizards, and small rodents (Richards et al. 2012). The bush vipers in the genus *Atheris* are mostly arboreal, relatively small (under 1 m) species that feed on lizards, frogs, birds, and small mammals.

The pitvipers (Crotalinae) are widely distributed throughout the New World and Asia. They include a diversity of forms from relatively slender arboreal forms (e.g., *Bothriechis* in the neotropics and *Trimeresurus* in Asia) to heavy-bodied forms like the rattlesnakes (*Crotalus* and *Sistrurus*) of the Americas. Pitvipers overall are dietary generalists feeding on a variety of invertebrate, amphibian, squamate, bird, and mammalian prey. Of these generalists, the Cottonmouth (*Agkistrodon piscivorus*) is perhaps the most extreme example, eating small turtles and even carrion. Like other viperids, pitvipers have large gapes allowing them to consume very large prey items in relation to their size. A Sidewinder

Rattlesnake (*Crotalus cerastes*) from the southwestern United States reportedly consumed a lizard with a mass that was approximately 115% that of the snake itself (Webber et al. 2016).

#### **Australasian Watersnakes (Homalopsidae):**

Homalopsidae includes the Australasian watersnakes. These aquatic snakes inhabit freshwater or marine habitats and have grooved rear fangs to deliver venom. Most feed on fish, but the White-bellied Mangrove Snake (*Fordonia leucobalia*) is an exception in two respects: it preys on crustaceans and is unique among snakes in that it consumes prey piecemeal – pinning the prey to the substrate with the body and dismembering larger prey so that it may be consumed.

**Lamprophiidae:** This very large (322 species) family is mostly found in Africa, western Asia, and southern Europe. One of the more speciose groups, the Psammophiinae is rear-fanged, mostly slender, diurnally active snakes with most species occurring in Africa and western Asia, the exception being the Montpellier Snake (*Malpolon monessulani*) from southern Europe. They predate largely upon lizards, although the beaked snakes (*Rhamphiophis*) have angled snouts that assist with excavating subterranean prey, including Naked Mole Rats (*Heterocephalus glaber*). Several members of this group have specializations for eating skinks similar to those seen in a number of other unrelated taxa. Atractaspidines are commonly known as stiletto snakes or burrowing asps. They are known from Africa and the Middle East. While the genus *Atractaspis* has movable front fangs similar to viperids, the genus *Homoroselaps* has fixed front fangs more akin to those of the Elapidae. These burrowing snakes feed primarily on elongate reptiles and other vertebrates as well as earthworms. The Aparallactinae occur in sub-Saharan Africa, are rear-fanged, and feed on a variety of prey including centipedes, squamates, frogs, and rodents. The Pseudaspidinae include the African mole snakes (*Pseudaspis*), Asian mock vipers (*Psammodynastes*), and the African forest snakes (*Bufo*). Mole snakes primarily eat small mammals, mock vipers mostly lizards and frogs, and the forest snakes feed on aquatic vertebrates. Lamprophiinae includes nearly 80 species which



are mostly African in distribution. This group includes the mostly lizard eating wolfsnakes (*Lycophidion*), the primarily snake eating filesnakes (*Gonionotophis*), and the rodent and lizard eating African housesnakes (*Boaedon*, *Lamprophis*) among many other taxa (Paterson 2018). The last group within Lamprophiidae is the Pseudoxyrhophiinae containing 90 species. This group is inclusive of a number of notable taxa. A few are the aptly named African Slug-eaters (*Duberria*), the Madagascan Leaf-nosed Snake (*Langaha madagascariensis*) which specializes in feeding on lizards, *Liophidium* which have folding teeth and specialize on skinks, the Madagascan hognose snakes (*Leioheterodon*) which are dietary generalists that also predate upon reptile eggs, and *Compsophis* which feeds on aquatic vertebrates.

**Cobras and Their Relatives (Elapidae):** The family Elapidae consists of some of the world's deadliest snakes. All species are venomous and have fixed fangs in the front of their mouths. They may be found on every continent but Antarctica and are incredibly diverse with over 370 species described to date. Included in this family are cobras, kraits, mambas, coral snakes, sea snakes, taipans, and others. They live in most habitat types and in the case of the sea snakes, marine environments. They range in size from under a meter for some of the brightly colored coral snakes to over 5 m for the King Cobra (*Ophiophagus hannah*), which is the world's longest venomous snake. As a whole, they are dietary generalists with relatively small gapes even for the largest species. As such, many specialize in long-bodied prey like caecilians and other snakes.

Cobras are highly diverse and widespread in Africa and Asia with several species attaining lengths of 3 m or more. They have cosmopolitan diets, feeding on a variety of vertebrates including mammals, birds, amphibians, other reptiles, and even slow-moving fish (e.g., *Naja melanoleuca*). King Cobras (*O. hannah*) are generalists but primarily consume other reptiles, mostly snakes. The semifossorial African coral cobras (*Aspidelaps*) may be habitat specialists, but are dietary generalists feeding on frogs, lizards and their eggs, rodents, and even termites. The water cobras

(*Naja [Boulengerina]*) live semiaquatic lifestyles and feed primarily on fish. The Rinkhals (*Hemachatus hemachatus*) feeds mostly on toads. The mambas (*Dendroaspis*) can reach lengths of 3 m or more in the case of the Black Mamba (*D. polylepis*), while the other species are around 2 m. They all feed primarily on mammals and birds and lead arboreal lifestyles. The African gartersnakes (*Elapsoidea*) feed mainly on snakes, lizards, and their eggs, but have been known to consume mammals with one species perhaps specializing on caecilians.

Australasian elapids are highly diverse, with stout-bodied small species like the death adders (*Acanthophis*) and slender fast-moving taipans (*Oxyuranus*) that can exceed 2 m long. As with other elapids, they have highly varied diets and consume lizards, mammals, and birds, though a few smaller species are more specialized. An example is the Australian Bandy-bandy (*Vermicella annulata*) which eats only blind snakes. Unlike many elapids, which tend to be more active predators, the death adders (*Acanthophis*) resemble vipers in overall appearance and adopting a sit-and-wait hunting mode to predate upon lizards, small mammals, and birds.

The coral snakes of Asia and the New World are quite similar. They are incredibly diverse in the New World, being found mostly in the neotropics but also ranging into more temperate zones (e.g., *Micrurus fulvius*). Most are a meter or less, although the Aquatic Coral snake (*M. surinamensis*) can be over 1.5 m long. As a whole, coral snakes feed mostly on elongate prey like snakes, limbless lizards, caecilians, and eels in the case of the Aquatic Coral snake (*M. surinamensis*). One species, *M. hemprichii*, is notable for feeding on onychophorans. The Asian coral snakes are fossorial and specialize in eating other snakes.

The kraits (*Bungarus*) and sea kraits (*Laticauda*) are found only in tropical Asia. *Bungarus* feed largely on fish but some species also feed on frogs as well as other snakes. The sea kraits in the genus *Laticauda* are generally found in or near coral reefs and feed largely on eels.

Seasnakes may be found in the tropical waters of the Indian and Pacific Oceans. They are highly adapted for a marine lifestyle and never leave the

water. Generally, they forage for prey in holes or crevices as opposed to active pursuit in open water. They feed on a variety of marine organisms, although fish are the largest dietary component for nearly all species. One of the most specialized of the seasnakes is the Turtle-headed Seasnake (*Emydocephalus annulatus*). This species eats only the eggs of bottom-dwelling fish like gobies and blennies. They have pointed snouts, specialized muscles possibly related to suction feeding, and have reduced toxicity of their venom.

**Colubridae:** The largest family of extant snakes is the Colubridae. They are globally distributed excluding Antarctica although they do reach the Arctic Circle. In an effort to simplify what is an exceptionally large, diverse group of snakes, Old World and New World colubrid snakes will be treated separately. Additionally, this is not meant to be an exhaustive review of all snakes within this family; however, it is intended to highlight notable groups or species.

**Old World Colubridae:** The small snakes of the subfamily Calamarinae are found in southern Asia and demonstrate adaptations to a burrowing lifestyle. They feed primarily on earthworms and insect larvae, although some are known to eat skinks.

The Sybiniophiinae, or hinged-teeth, snakes include two genera (*Sibynophis* and *Scaphiodontophis*) that are closely related yet globally disjunct (*Sibynophis* in southern Asia and *Scaphiodontophis* in Central and South America). Both have unique hinged maxillary teeth and feed primarily on hard-bodied prey like skinks (Campbell 1998; Savitzky 1981).

The subfamily Grayiinae includes a handful of species in the genus *Grayia*, all found in Africa. They feed primarily on fish and frogs.

The Pseudoxenodontinae are found in Southern Asia. Snakes in the genus *Pseudoxenodon* feed mostly on frogs and lizards while *Plagiopholis* feed on earthworms.

The subfamily Colubrinae is incredibly diverse in the Old World. Some notable genera include the Eurasian dwarf snakes of the genus *Eirenis* that feed on a range of prey items including small arthropods and lizards, the lizard eating Asian

“flying” snakes in the genus *Chrysopelea* which are known for flattening their bodies after springing from the trees and travelling to the ground or other trees by controlled gliding, and the Old World racers and ratsnakes (*Ptyas*, *Gonyosoma*, and *Elaphe*) which have highly varied diets with some getting quite large (e.g., *Ptyas mucosa* reaching over 2 m).

A large number of Asian colubrinae are rear-fanged. These include the highly diverse kukrisnakes (*Oligodon*) which are all under 1 m in length and feed on a wide variety of prey including arthropods, mammals, frogs, lizards, birds, and their eggs. The moderately sized to large slender-bodied snakes in the genus *Boiga* are often referred to as cat snakes. The most famous and largest of these is the Brown Treesnake (*B. irregularis*), which is naturally found in New Guinea, the Solomons and surrounding islands, and northern Australia was accidentally introduced to the island of Guam, where it has caused major ecological damage as a generalist predator on the island’s fauna. The Asian vinesnakes of the genus *Ahaetulla* have elongate snouts and very slender bodies. These snakes have eyes that allow them stereoscopic vision that may help in hunting lizards, which most species specialize in.

In Africa, Colubrinae includes two of the few rear-fanged snakes that have been known to cause fatal envenomations in humans: the Boomslangs (*Dyspholidus*) and Twigsnakes (*Thelotornis*) which feed primarily on birds and lizards. While many snakes feed on bird or reptile eggs, African egg-eating snakes (*Dasypeltis*) are the most highly adapted for ingesting bulky items like eggs, even having specialized ribs that allow the snakes to crack the eggshells once consumed so they can ingest the contents. Once the contents are consumed, the snake typically regurgitates the egg shell. The leaf-nosed (*Prosyma*) and shovel-nosed snakes (*Lytorhynchus*) utilize upturned rostral scales to excavate buried lizards and their eggs. This trait and behavior is also seen in some New World colubrinae.

Snakes within the Old World Natricinae includes a number of terrestrial and semiaquatic taxa in Eurasia, Africa, and Asia. They are overall

small snakes (1 m or less). The Eurasian grass snakes (*Natrix*) are semiaquatic and feed primarily on fish and amphibians. The bite of two species of keelbacks in the Asian genus *Rhabdophis* are considered potentially fatal to humans. These snakes may be terrestrial or aquatic and feed mainly on fish and frogs, although some are known to have more variable diets including lizards, rodents, and birds, as well.

**New World Colubridae:** The New World has a very high diversity of colubrid snakes that occupy highly diverse niches. For the colubrine snakes, the North American ratsnakes (*Pantherophis*), pine and gopher snakes (*Pituophis*), and kingsnakes (*Lampropeltis*) are powerful constrictors. Most ratsnakes are semiarboreal while the kingsnakes are typically terrestrial or fossorial. Pine and gopher snakes are typically terrestrial and semifossorial, although some gopher snakes show semiarboreal tendencies. Ratsnakes and the pine and gopher snakes typically feed on mammalian or avian prey including their eggs. The kingsnakes often feed on rodents and other squamates. They are famous for their eating of other snakes, particularly venomous species. These are also among the most popular of snakes to be maintained in captive conditions. The New World racers and whipsnakes (e.g., *Coluber*, *Drymobius*, and *Mastigodryas*) are aptly named as they are diurnal, fast moving snakes. They have highly variable diets ranging from insects and smaller vertebrates when young to large insects, lizards, other snakes, small mammals, and birds as adults. Another genus of New World snakes, the cribos and indigo snakes (*Drymarchon*) may get quite large (over 3 m in some species). Similar to racers and whipsnakes, they are diurnal, highly active, and have incredibly varied diets. In the southeastern United States, the Eastern Indigo Snake (*D. couperi*) is one of the few snakes generally liked by land owners as they consume venomous snakes. Indigo snakes, racers, and whipsnakes typically do not constrict their prey, instead swallowing it alive or in some cases pinning the prey against a surface until it stops struggling. Other colubrines have more restrictive diets, such as the green snakes (*Opheodrys*) of

the United States which feed primarily on insects and the scarlet, long-nosed, and patch-nosed snakes (*Cemophora*, *Rhinocheilus*, and *Salvadora*, respectively) which prey upon squamates and their eggs. Black-headed snakes (*Tantilla*) are centipede specialists while the scorpion-eaters in the genus *Stenorrhina* are aptly named, feeding almost exclusively on scorpions and spiders.

Natricine snakes in the New World include the garter and ribbon snakes (*Thamnophis*), watersnakes (*Nerodia*), the mostly soft-bodied invertebrate feeding *Storeria*, and the highly specialized crayfish snakes (*Regina*). These are small to mid-sized snakes with the garter and ribbon snakes (*Thamnophis*) having the most varied diets. While they primarily feed on soft-bodied invertebrates, fish, and amphibians, some have been known to feed on rodents. Watersnakes (*Nerodia*) typically feed on fish and amphibians with some like the Brown Watersnake (*N. taxispilota*) showing an affinity for preying on catfish. Among the most specialized of New World natricines are the crayfish snakes, which feed almost exclusively on crustaceans. The Queen Snake (*R. septemvittata*) is even more specialized, feeding only on soft-bodied freshly molted crayfish.

Dipsadinae are a highly diverse group of New World colubrids. There is a large subgroup known as "goo-eaters" which feed primarily on soft-bodied prey like slugs, snails, and earthworms as well as amphibian eggs. Many of these are small residents of forest litter like the coffee snakes of Latin America (*Ninia*). Others like *Sibon*, *Sibynomorphus*, and *Dipsas* are elongate with blunt heads. They are able to pull terrestrial mollusks from their shells. Another blunt-headed and very elongate dipsadine, *Imantodes* will seek out and feed on diurnal lizards as they sleep at night. Rear-fanged night snakes (*Hypsiglena*) also feed on lizards. The large semiaquatic *Farancia* of the southern United States feed only on elongate aquatic vertebrates like giant salamanders (*Amphiuma* and *Siren*) and freshwater eels. Also included in this group are the hognose snakes (*Heterodon*) of the United States and Mexico.

These snakes specialize in eating toads and have specialized rear-fangs that allow them to deflate and then consume toads that have inflated their bodies with air defensively. The snakes in the genus *Helicops* are similar in diet and life history to other groups of watersnakes (Homalopsidae and Natricinae). False water cobras (*Thamnodynastes*) also live semiaquatic lifestyles and feed on fish, but are notable for sometimes using their tails to probe for fish in riparian vegetation. The mussuranas (e.g., *Clelia* and *Pseudoboa*) are rear-fanged, yet also powerful constrictors that feed on other squamates and rodents.

### Food and Feeding Habits of Lizards (Lacertilia)

By far the most speciose and diverse of the Squamata, the lizards (Lacertilia or Sauria), comprise over 6,700 species at the time of this writing. This section will briefly cover the diets and notable specializations in the over 40 recognized families of lizards. Unless otherwise noted, information adheres to that provided in Pianka and Vitt (2003).

**Blind Lizards (Dibamidae):** The blind lizards contain 24 species and are globally disjunct, with one species, *Anelytropsis papillosus*, endemic to dry areas of eastern Mexico and all others in the genus *Dibamus* found in forests of southern Asia. There is very little data on diet for these animals.

**Southern Padless Geckos (Carphodactylidae):** This family of geckos is endemic to Australia and contains 30 recognized species. All are nocturnal and largely feed on arthropods. The knob-tailed geckos in the genus *Nephrurus* are all arid-adapted terrestrial species that are notable for having relatively large heads compared to their body size and feed on a variety of insects, other lizards, and even very small mammals (Cogger 1994).

**Flap-Footed Lizards (Pygopodidae):** There are nearly 50 species of these limbless or nearly limbless lizards. They are found almost exclusively in Australia with two species ranging into New Guinea. They occupy a variety of habitat types, with most species observed burrowing in sandy soils, occupying rock crevices, in ant or

termite mounds, under logs, or in low vegetation (Cogger 1994). The majority of species feed on insects and spiders. However, the two species of *Lialis* specialize in feeding on scincid lizards and have a hinged maxillary similar to the Round Island Boa (*Casarea dussumieri*).

**Diplodactylidae:** This highly diverse family (over 150 species) is found throughout Australia, New Zealand, and New Caledonia. It includes the world's largest gecko species, *Rhacodactylus leachianus*, which can be over 300 mm in length. Along with other members of this genus, they occupy forests and consume insects, other lizards, and fruits. On the opposite end of the spectrum are the ant and termite-feeding *Rhynchoedura*, which may only reach 90–100 mm in total length. Overall, though, this family can be considered dietary generalists that feed mostly on arthropods.

**Eyelid Geckos (Eublepharidae):** The eyelid geckos are found in North and Central America, Africa, Europe, and Asia and occupy a variety of habitats. They are mostly insectivorous and although many species are staples in private and zoological reptile collections around the world (e.g., the Leopard Gecko, *Eublepharis macularius* and Fat-tailed Gecko, *Hemiteconyx caudicinctus*), there is surprisingly little data on wild diets for many species. They are nocturnal with most being terrestrial in habit; however, the Malaysian cat geckos (*Aeluroscalabotes*) are often found in low vegetation (Seufer et al. 2005).

**Sphaerodactylidae:** This extremely diverse family of geckos contains over 200 species in nine genera. They are found in North and South America, the Caribbean, southern Europe, northern Africa, the Middle East, and Central Asia. They occupy highly diverse habitats from rainforests to dry deserts. In the New World, they include some of the world's smallest amniotes, with the West Indian *Sphaerodactylus ariasae* reaching a maximum total length of 30 mm. New World species of sphaerodactylids tend to be diurnal leaf litter and low vegetation dwellers and owing to their overall diminutive sizes, feed on equally tiny prey like ants, termites,

and springtails. In the Old World, they are represented in Europe by *Euleptes europaea*, a small (60–80 mm) insectivore, and elsewhere by *Pristurus*, *Saurodactylus*, and the fish-scaled *Teratoscincus*. Members of nocturnal *Teratoscincus* are mostly sit and wait predators that feed on arthropods.

**Leaf-Toed Geckos (Phyllodactylidae):** This large diverse family is distributed mostly through Central and South America north to the southwestern United States and Caribbean with additional members found in southern Europe, Africa, and the Middle East. They are found in a variety of habitats with many species occupying rocky areas in desert regions. They are generalist feeders of arthropods.

**True Geckos (Gekkonidae):** The true geckos are the most diverse of the gecko families and are among the most speciose of all lizard families with over 1,200 recognized species. They are primarily Old World in origin, although several species in the genera *Hemidactylus*, *Gekko*, *Gehyra*, and *Lepidodactylus* have spread beyond their historical ranges through accidental human introductions and can now be found almost globally. This family occupies nearly every nonpolar habitat type from rainforests with many being quite successful in developed urban regions. Overall, they are arthropod feeders, although many species, especially the Madagascan Day Geckos in the genus *Phelsuma*, are known to include a notable proportion of fruits and nectars in their diets. Some larger species, like the 300+ mm *Gekko gecko*, will also feed on other vertebrates.

**Night Lizards (Xantusiidae):** The Night Lizards are found in southwestern North America, Central America, and Cuba. Although commonly called “night lizards,” many xantusiids are primarily diurnal. Many live in rocky habitats, although species of *Lepidophyma* are typically found in tropical forests. All species feed on a variety of arthropods.

**Plated Lizards (Gerrhosauridae):** This family of lizards are found only in Africa and Madagascar. They are diurnal and largely terrestrial. They primarily feed on a wide variety of

arthropods, although some have been observed to eat fruit.

**Girdled Lizards (Cordylidae):** The 68 species of cordylid lizards are found only in Africa. They tend to be found in overall dry habitats. Most species are sit and wait predators on arthropods, although some species of Flat Lizards (genus *Platysaurus*, so-called due to their dorsoventrally flattened bodies) also consume flowers, leaves, and seeds.

**Skinks (Scincidae):** Probably the most globally and species diverse family of lizards, the Scincidae contains over 1,650 species that can be found in nearly every nonpolar region of the globe. They are highly diverse in size and morphology with many limbless or nearly limbless forms included in the family (e.g., *Brachymeles* of the Phillipines and the Australian *Lerista*). Given this diversity, it can be easily inferred that diets are equally diverse. While most species feed on a variety of arthropods, some, like the 80+ cm Prehensile-tailed Skink (*Corucia zebrata*) of the Solomon Islands are largely herbivorous, while many more include a variety of vegetation, arthropods, and other vertebrates in their diets.

**Tegus and Whiptails (Teiidae):** The New World Teiidae contains over 150 species that occupy a variety of habitats and niches. These are mostly diurnal, actively foraging predators that operate at high body temperatures. The aptly named racerunners and whiptails in the genera *Aspidoscelis* and *Cnemidophorus* live in mostly desert and semiarid habitats that forage widely for insects, spiders, and other arthropods, typically at the warmest part of the day (Jones and Lovich 2009). The overall larger species of *Ameiva* occur in open, forested, and edge habitats throughout much of Central and South America, and the Caribbean. They feed on a variety of invertebrates, small vertebrates, and fruits. The South American *Dracaena* and *Crocodylurus* are semiaquatic. While *Crocodylurus* appear to be dietary generalists feeding on whatever small vertebrates and invertebrates they can capture, *Dracaena* primarily feeds on hard-shelled mollusks, even having



large, rounded teeth specialized for crushing their shells. Some members of the genera *Tupinambis* and *Salvator* can get quite large (over 1 m in length). All are dietary generalists feeding on invertebrates, vertebrates, mollusks, carrion, and eggs. *Tupinambis teguixin* have been observed raiding turtle nests.

**Spectacled Lizards (Gymnophthalmidae):** Found strictly in the New World, this family contains nearly 250 species and includes some of the world's smallest lizards. They range in habit from terrestrial to semiaquatic, with some being somewhat arboreal as well. Interestingly, gymnophthalmids can occur in relatively high species diversities in relatively small areas. All feed on small invertebrates.

**Florida Worm Lizard (Rhineuridae):** This monotypic family includes only the limbless and blind Florida Worm Lizard (*Rhineura floridana*) which is found in areas with deep sandy or loamy soils suitable for burrowing. This completely fossorial lizards feed on earthworms, spiders, and termites (Gibbons et al. 2009).

**Two-Legged Worm Lizards (Bipedidae):** The three species of *Bipes* are found only in Baja California and mainland Mexico. As suggested by their common and generic names, *Bipes* have only two front limbs. They are considered generalist invertebrate predators, although in one dietary study the most common prey detected were ants and termites (Kearney 2003).

**Mediterranean Amphisbaenians (Blanidae):** This small family (seven species in the genus *Blanus*) of limbless reptiles is found only in the Mediterranean region of Europe and Africa. Research shows that at least *B. cinereus* feeds largely on insect larvae and ants (López et al. 1991).

**Cuban Keel-Headed Worm Lizards (Cadeidae):** Both species in this family are in the genus *Cadea* and endemic to Cuba. There is scant information on diet for these limbless reptiles but based on other worm lizards can be inferred to be primarily invertebrates.

**Short-Headed Worm Lizards (Trogonophiidae):** The six species of limbless Trogonophiidae are sand burrowing specialists

found in northern Africa and the Middle East. A dietary study of *Trogonophis wiegmanni* (Martin et al. 2013) found insect larvae, beetles, ants, isopods, and snails.

**Worm Lizards (Amphisbaenidae):** This is the largest group of the so-called worm lizards or amphisbaenians with 175 species. They can be found in South America, the Caribbean, and sub-Saharan Africa. Some species, like the South American *Amphisbaena alba*, can get quite large, measuring over 700 mm. However, despite this, like most other worm lizards, they feed primarily on very small prey like ants and termites. Also, as with other worm lizards, they are blind and limbless.

**Wall Lizards (Lacertidae):** Found in Europe, Africa, and through a large part of Asia, the Lacertidae contains over 300 species. Most are rock dwellers, although some like *Holaspis* and *Takydromus* spend time in vegetation and trees. Overall this family contains dietary generalists that feed largely on invertebrates. For example, *Gallotia* are endemic to the Canary Islands and omnivorous, feeding on a variety of animals and plants. However, specialists do occur within this family such as *Nucras tessellata* from the Kalahari of southern Africa, which feeds primarily on scorpions and may forage for long distances to find them during the day. Ants may be the primary dietary component for some species of *Acanthodactylus*.

**Knob-Scaled Lizards (Xenosauridae):** There are 12 species of *Xenosaurus*. All are found in crevices in rocks, trees, or even buildings. These lizards are found only in Mexico and Guatemala. Dietary studies have found that insects (mostly beetles and orthopterans) comprise the majority of the diet, but evidence of mammalian prey and vegetation was also observed (Lemos-Espinal et al. 2003).

**Gila Monsters and Beaded Lizards (Helodermatidae):** This group of venomous lizards are found in the southwestern United States, Mexico, and Guatemala. They are quite large with some specimens of *Heloderma horridum* reaching nearly a meter long. The Gila Monster (*H. suspectum*) occupies arid

deserts while the beaded lizards occupy mostly dry forests. All *Heloderma* primarily prey upon nests of birds and rodents, although some include a large portion of reptile eggs in their diets as well.

**California Legless Lizards (Anniellidae):**

These legless lizards are found in coastal California and western Baja, California. They are found in loose soils and likely feed mainly on termites.

**Alligator and Glass Lizards (Anguidae):**

There are nearly 80 species of this wide-ranging family of lizards. They can be found in the Americas, the Caribbean, Asia, Europe, and northern Africa. Although mostly terrestrial, the Mexican, and Guatemalan alligator lizards in the genus *Abronia* are highly arboreal. All have powerful jaws and a number have reduced limbs or are totally limbless (i.e., *Ophisaurus*). Most species feed on arthropods and other invertebrates, although the European limbless Slow Worms (*Anguis*) seem to feed mainly on slugs and snails.

**Asian Crocodile Lizards (Shinisauridae):**

*Shinisaurus crocodilurus* is found in southern China and northern Vietnam. This species is diurnal and semiaquatic, feeding on a wide variety of prey including earthworms, insects, tadpoles, frogs, and fish which they may sometimes forage for underwater.

**Bornean Earless Monitors (Lanthanotidae):**

Found only in Borneo, *Lanthanotus borneensis* reaches up to 43 cm in total length and is poorly known. They appear to burrow in mud and have aquatic tendencies. Very little is known about their wild diet, although earthworms appear to be a component.

**Monitor Lizards (Varanidae):** The monitor lizards are native to Africa, Asia, New Guinea, and Australia. They include the world's largest lizard, the Komodo Dragon (*Varanus komodoensis*) which can reach 3 m in total length and weigh over 100 kg. Contrastingly, the smallest monitor lizard, the Short-tailed Monitor (*V. breviceauda*) only reaches a length of 20 cm and less than 20 g. Monitors are carnivorous, feeding on anything from insects and other arthropods to large mammals. Most species are active predators, with many foraging for long distances and serving

as top predators in their environments. The teeth of many larger varanids, like Komodo Dragons, are curved and serrated, allowing them to inflict severe wounds on larger prey. Some of these larger species can consume meals  $\geq 50\%$  of their own body mass. Although largely carnivorous, at least one species, *V. olivaceus*, includes fruit in its diet.

**True Chameleons (Chameleontidae):**

The chameleons are among the most recognizable lizards with their color-changing abilities, laterally flattened bodies, individually mobile eyes, and zygodactylous limbs. Perhaps their most unique adaptation when it comes to feeding is the exceedingly long projectile tongue found in all species, which in some can be longer than the length of the body. These tongues can be fired at incredible speed at prey. The end of the tongue is sticky and wraps around a prey item before the tongue is retracted back into the mouth. Some species possess glands at the edges of the mouth that produce smelly secretions that could potentially act as "bait" for insect prey. All species are carnivorous, feeding primarily on insects of varying sizes, though some larger species will include other lizards, rodents, and small birds.

**Agamidae:** The agamids are small to large diurnal lizards found across much of the Old World and Australia. The family includes nearly 500 species. They range in size from the small "flying" dragons in the genus *Draco* of Southeast Asia to the large bearded and frilled dragons of Australia (*Pogona* and *Chlamydosaurus*, respectively). They also occupy highly varied habitats. While most species are carnivorous, there are mostly or strictly herbivorous forms. An example is the semiaquatic sailfin dragons in the genus *Hydrosaurus*. The bearded dragons, including the commonly captive maintained *Pogona vitticeps*, are dietary generalists, feeding on a variety of animal prey and vegetation. The spiny-tailed *Uromastyx* of northern Africa and the Middle East are primarily herbivorous but will occasionally consume insects. An extreme myrmecophagous (ant eating) species is the Australian Thorny Devil or Moloch (*Moloch*

*horridus*) and a single animal may eat over 2,000 ants in one meal.

**Tropiduridae:** This relatively large family of lizards (137 species) is distributed in South America, the Galapagos Islands, and Trinidad. They feed mostly on invertebrates, with a fair number specializing in ants. The species *Uranoscodon superciliosus* is known to feed on both living and dead invertebrates that wash up along the edges of waterways.

**Iguanas (Iguanidae):** Although mostly found in the Americas from the southwestern United States into central South America and the Caribbean, there are iguanas found on the Pacific islands of the Galapagos and Fiji. They occupy a variety of habitats from deserts (i.e., *Dispsosaurus dorsalis*) to dense rainforests (i.e., *Iguana iguana*). These lizards are generally rather large with some species nearing 2 m in length (i.e., *I. iguana*) and largely herbivorous, although members of *Ctenosaura*, *Dispsosaurus*, and *Cyclura* are more omnivorous in habit, eating vegetation, invertebrates, small mammals, carrion, and even the feces of other animals. Perhaps the most specialized in the group is the Galapagos Marine Iguana (*Amblyrhynchus cristatus*) which dives from coastal rocks into the ocean to scrape algae from submerged rocks.

**Curly-Tailed Lizards (Leiocephalidae):** The family Leiocephalidae includes 31 species that are found only on islands in the Caribbean. These small- to medium-sized diurnal lizards (up to 140 mm) are terrestrial, live in mostly xeric habitats and have varied diets. They consume insects, other lizards, and a variety of plant matter, including fruits and flowers.

**Collared and Leopard Lizards (Crotaphytidae):** These relatively large-bodied diurnal lizards are only found in the United States and Mexico. There are two genera, *Crotaphytus* and *Gambelia*. They may adopt a fast-moving bipedal gait when chasing down prey, which includes large arthropods and smaller vertebrates, particularly other lizards. The Leopard Lizards in the genus *Gambelia* are particularly well-known as lizard predators, and all species in the family may be cannibalistic (Jones and Lovich 2009).

**Horned and Spiny Lizards (Phrynosomatidae):** This family contains 159 recognized species and ranges from southern Canada to Panama. Phrynosomatids are relatively small to medium lizards reaching maximum lengths 150 mm. They are diurnal and occupy a wide range of habitat types from arid deserts to tropical forests. Most species are insectivorous and employ ambush foraging, although some species are known to eat some plant matter as well. The Horned Lizards in the genus *Phrynosoma* are ant specialists.

**Monkey Anoles (Polychrotidae):** This family, includes eight species and is found through a large portion of Central and South America. They are diurnal and feed on arthropods that are relatively large compared to their body size but also consume some fruit, flowers, seeds, and leaves. They very slowly advance on arthropod prey once spotted (Savage 2002).

**Wood Lizards (Hoploceridae):** This family of small- to medium-sized lizards is found in Panama and South America. While *Hoplocercus* tend to occupy dry forest or grasslands, *Enyalioides* and *Morunasaurus* are found in rainforests. There is little information on the natural history of these lizards; however, they are presumed insectivores.

**Madagascan Iguanas (Opluridae):** These mid-sized lizards are endemic to Madagascar and nearby islands. All are diurnal and prefer hot, dry habitats. They are omnivorous.

**Leiosauridae:** There are 33 species in this strictly South American family. All are insectivores.

**Lava Lizards (Liolaemidae):** There are over 300 species in this South American family. They can be found in every habitat type South America has to offer. Most are omnivores, but species of *Phymaturus* are herbivores.

**Helmeted Iguanas and Basilisks (Corytophanidae):** The Corytophanidae are generally medium to larger lizards found from Mexico to northern Ecuador. The helmeted iguanas *Corytophanes* and *Laemactus* are arboreal forest-dwellers while the basilisks (*Basiliscus*) are typically found along forested riparian zones. The

basilisks are omnivorous, feeding on arthropods, smaller terrestrial vertebrates (including lizards, snakes, small mammals, and birds), freshwater shrimp, fish, and fruits and flowers of streamside plants. *Corytophanes* are sit and wait predators that primarily feed on large-bodied insects including large orthopterans, lepidopteran larvae, and smaller lizards (Savage 2002). *Laemancus* are largely insectivorous but will also eat snails, frogs, and smaller lizards (Campbell 1998).

**Anoles (Dactyloidae):** The anoles are found strictly in the Americas and the islands of the Caribbean. Anoles range in size from 33 to nearly 200 mm in total length and are dietary generalists. While largely insectivorous, frugivory has been observed in several taxa, while some of the larger forms will feed on other vertebrates and terrestrial mollusks (Losos 2009).

## Conclusion

Squamates are the most diverse extant group of reptiles. As such, across their phylogeny exists a wide range of dietary preferences and adaptations. From projectile tongues to catch insect prey with immense accuracy to loosely constructed skulls that allow many snakes to consume prey larger than their own heads, the variation of adaptations to meet various dietary challenges within the Squamata is impressive.

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## Squamate Acoustic Communication

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### What Is Communication?

In zoology, communication is known as a channel established between species, individuals, or groups, allowing taxa to evolve and coevolve (Hauser 1996). For such bonds to be created, an individual (sender) sends a message encoded with information that must be accepted and understood by another individual (receiver). Therefore, communication itself relies on the necessity of both the reception and understanding of the message – otherwise communication will not be accomplished (Bradbury and Vehrencamp 2011). The high diversity in animal communication systems arises from several factors such as (i) physiological mechanisms, constrained by physical properties such as ambient medium and habitat mobility; (ii) phylogenetic proximity, i.e., animals that are evolutionarily closer are usually more similar; (iii) and the economics of communications, i.e., the energetic and anatomical costs or both producer and receiver in the communication episode (Bradbury and Vehrencamp 2011; Hauser 1996). Although such kinds of messages are diverse in terms of their types, the

information provided by the sender can be traditionally classified in two main categories: cues and signals.

Cues are known as the stimuli received and processed by the receiver, even though the sender generated the signal inadvertently or for purposes other than communication (Hauser 1996). For instance, when a prey unintentionally vibrates a spider's web, it sends information that is decoded by the receiver as evidence of its presence. Another typical example is when a predator is looking for its prey using its own olfactory system (as dogs or even sharks). The cue in this case is the prey's smell. All metazoans monitor ambient cues by their extremely specialized sensory organs that have evolved to track cues with accuracy and speed (Bradbury and Vehrencamp 2011). Such detection is usually achieved through the combination of several sensorial specializations to monitor olfactory, visual, auditory, and other cues (Bradbury and Vehrencamp 2011; Hauser 1996).

Unlike unintentional cues, signals are intentionally produced by the sender to provide information to another individual (Bradbury and Vehrencamp 2011; Hauser 1996). Such kind of communication varies in terms of its function, such as to find a female for reproduction or to deter a predator. For example, during breeding season, a frog can share a pond with dozens of conspecifics, competing through their calls to attract females (Vitt and Caldwell 2014). As signals are mandatorily produced by the sender and monitored by the receiver, one might assume that there is intrinsic coevolution between both parties that has been favored over the evolutionary time (Bradbury and Vehrencamp 2011).

Animals can use plenty of sensory systems to communicate through signals, and one might summarize the main signals as tactile/seismic, chemical/olfactory, visual, and acoustic (Hauser 1996). However, the channel chosen to transfer messages depends on many factors, such as the morphofunctional structure of the organisms involved, as well as the characteristics of the environment (Dugatkin 2019). Additionally, animals may use signals that are multimodal, combining two or more modalities of the aforementioned categories. For instance, while many birds usually



combine both visual and acoustic components, some insects might combine visual and chemical stimuli for communication (Bradbury and Vehrencamp 2011).

Tactile communication – as touches and bites – are employed in short-range interactions, when the sender and the receiver are physically close (Hauser 1996). This mean of communication is widespread among arthropods and vertebrates and most commonly targets nearby individuals (Bradbury and Vehrencamp 2011). For instance, the function of a touch during mating season can discern a receptive from a non-receptive individual for copulation. This type of communication is common in large-sized mammals such as elephants, whose fights among rivals usually involve physical clashes (Poole and Granli 2004). Seismic communication occurs when the signal is transmitted through vibrations of the substrate in which both sender and receiver are on, whether through the ground, water, or any other surface (Hill 2008). This way of communicating is known to be one of the most ancestral modes of communication among animals. For example, male crocodilians produce subaudible vibrations that make the water “splash” in order to attract females (Vergne et al. 2009).

Chemical communication is based on chemical molecules, with the receiver accepting the message contained in one or more molecules, which can generate reactions of fear/stress (e.g., when from rivals or predators) or motivation/excitement (e.g., when produced by potential mates) (Bradbury and Vehrencamp 2011). Pheromones impact the behavior of the receiving individuals from the same species, such as in court rituals, or in differentiating an intruder from its neighbor (Wyatt 2003). In addition, allelochemicals – another way of chemical communication – affect the behavior of an individual of a different species (Sbarbati and Osculati 2006).

Visual communication uses colors, patterns, and movements as a mean of sending information (Bradbury and Vehrencamp 2011). It is very widespread among metazoans and consequently derives from the evolution of sensorial mechanisms for understanding and processing visual elements. This type of language can be easily

detected in iguanian lizards, in which males can bob heads and make push-ups to attract females and to defend territories (Vitt and Caldwell 2014). This kind of communication is also common within birds, where males can make use of several body ornaments and exhibit gifts to attract females, as in courtship dances of birds-of-paradise (Bradbury and Vehrencamp 2011).

## Acoustic Communication

For many animals, the main mode of communication relies on sound emission and acoustic communication. Living beings have evolved to capture and generate information by sound waves for many different reasons (Hauser 1996). Whether to be located in the environment, as bats and cetaceans do through echolocation (Berta et al. 2015), or for predatory, reproductive, or social interests, such a mode of communication is very widespread among living metazoans (Suthers et al. 2016). Among terrestrial vertebrates, historically much is known about acoustic communication in birds, mammals, and anurans, but recent evidence has pointed out that non-avian reptiles also play an important role in the understanding of the evolution of vocalization in amniotes (Russel and Bauer 2020).

In general, the acoustic signals produced by aquatic and terrestrial vertebrates can be classified into two main categories: vocal and nonvocal sound emissions (Suthers et al. 2016). Nonvocal emissions may involve a variety of sound-generating ways, such as integumentary mechanisms, hitting a given substrate, or sounds generated by different body parts. In contrast, in a broad sense, vocalization can be defined as the sound produced by air passing through the upper respiratory tract, not necessarily but usually involving the vocal cords/folds (Ladich and Winkler 2017).

These tubelike structures are present in vertebrates, but are more widespread in Tetrapoda, where the system is composed of lungs connected to the bronchus and trachea, connected to the outside by the oral cavity and nasal cavity (Bradbury and Vehrencamp 2011). Even though most terrestrial vertebrates share this basic design,

their vocal sound production is extremely varied. While frogs use a buccal pumping for sound production, lizards and snakes use their ribs and costal muscles to allow the expansion of the thoracic cavity (Colafrancesco and Gridi-Papp 2016). However, many extant non-avian reptiles do not vocalize, with a few exceptions for some turtles and tortoises, most gecko lizards, and most crocodilians (Russel and Bauer 2020; Vergne et al. 2009). Birds, on the other hand, use an extremely evolved anatomical mechanism that involves the air sacs and the presence of specialized cartilages and muscles called syrinx (Bradbury and Vehrencamp 2011). The larynx of mammals may present a variety of sizes and shapes, enabling the production of sounds from infrasounds in elephants to ultrasounds in toothed whales (Ladich & Wincler, Ladich and Winkler 2017). In this context, echolocation is a specific way of using vocalization, commonly used to map an environment or to locate a prey, in which the information is sent and accepted by the same individual. Present in bats and cetaceans (Bradbury and Vehrencamp 2011), this mechanism is defined by the emission of short duration sound waves, which echo when hitting an object or prey and return to the emitter (Berta et al. 2015). In cetaceans, such vocalizations are allowed by the presence of a melon (a mass of adipose tissue on top of the skull) and cranial and facial asymmetry (Berta et al. 2015).

Even though several fundamental questions regarding the origins and diversification of acoustic communication in tetrapods still remain (Suthers et al. 2016), recent studies have revealed intriguing patterns comparing aquatic and terrestrial vertebrates (e.g., Ladich and Wincler 2017). Additionally, other recent contributions reveal the phylogenetic nature of acoustic communication as being strongly conserved in tetrapods and that it is mostly related to the evolution of nocturnal habits (Chen and Wiens 2020). In addition, once the majority of main groups of vertebrates that communicate through acoustic signals (birds, frogs, mammals, crocodilians, and gekkotan lizards) are ancestrally nocturnal, the origins of acoustic communication seem to be intimately associated with nocturnal activity (Rohtla Jr. et al. 2019;

Chen and Wiens 2020). That makes sense when considering that during nighttime, visual signs such as color, body movements, and tactile signals are negatively affected. Furthermore, it was demonstrated that acoustic communication arose independently across major tetrapod groups, despite ancient origins in many of them (Chen and Wiens 2020). Being present in several groups and having arisen many times, it is not a surprise that acoustic communication would also be expressed in different manners and complexities, as previously presented.

In view of the extensive variation of sound emission among well-studied species and scarcity of information for many groups, the ethological knowledge around animal's communication remains a promising field for scientific research with deep gaps to be filled.

## Acoustic Communication in Squamata

Among non-avian reptiles, acoustic communication is used with several purposes and in a variety of contexts such as interaction between mother and offspring (e.g., crocodilians), for territorial interactions (e.g., geckos), and for mating (e.g., tortoises, Gans and Maderson 1973).

With more than 11,000 species, Squamata are considerably more diverse than amphibians and mammals (Uetz et al. 2021). This taxon congregates "lizards," snakes, and amphisbaenians, which, despite their well-established common ancestry, still have uncertain evolutionary relationships between many groups. This group exhibits several ways of intraspecific and interspecific acoustic communication that vary from integumentary mechanisms, sounds generated by different body parts, and true vocalizations (Gans and Maderson 1973). The acoustic communication currently known for snakes includes integumentary sound production such as tail vibration and scale abrasion, as well as sounds derived of air expulsion by the cloaca, and oral sounds as hissing and growling (Russel and Bauer 2020; Young 2003). Integumentary mechanisms involve intentional friction between parts of the body, with tail vibration being the most typical example of

this kind of communication (Gans and Maderson 1973). This type of percussion is used by rattle-snakes as a way to ward off possible predators and occurs through the sound produced by the rings of a snake's rattle when rubbed (Young 2003). Scale abrasion consists of another integumentary mode of sound production in which the sound is produced when a snake coils itself in a c-shaped formation, also used as a defense mechanism (Gans and Maderson 1973). Cloacal pops – also known in a few geckos – consist of a sound produced by synchronized muscular contraction that results in passing air through the cloaca, added with fecal elimination, the latter also being employed as a defensive strategy (Young 2003). Snakes are also able to produce sounds by forcible oral expulsion of air through the glottis, commonly named as hissing (Gans and Maderson 1973; Young 2003). These sounds are used to intimidate and/or to drive intruders off, occurring in some species of many families such as Viperidae, Colubridae, Boidae, and Elapidae (Russel and Bauer 2020). However, although sound emissions in snakes are not usually interpreted as acoustic signals for intraspecific communication, some species emit more complex sounds involving anatomical specializations to phonation (Young 2003). For instance, the King Cobra (*Ophiophagus hannah*) produces growls involving the presence of tracheal diverticula that works as a resonance chamber and filter (Young 1992), while the Pine Snake (*Pituophis melanoleucus*) possesses a vocal cord-like laryngeal septum able to produce harmonics, and the glottal control allows emission of two kinds of oral exhalations, hisses which are acoustically simpler and bellows which include frequency and amplitude modulation (Young et al. 1995).

While there seem to be no sound emission records for amphisbaenians – even though these animals have functional inner ears (Wever and Gans 1973) – sound emissions are widespread among other “lizards” (Russel and Bauer 2020). Undoubtedly, the acoustic communication in Squamata is more conspicuous and better understood among geckos (Rohtla Jr. et al. 2019). However, oral sounds can be found in several non-gekkotan lizard families, mainly in the form of hisses and squeaks (Gans and Maderson 1973;

Russel and Bauer 2020). Although in general such sound emissions have a relatively simpler structure and are usually exhibited in anti-predatory contexts as distress calls (e.g., *Tropidurus catalanensis*; Fernandes and Passos 2021), some species can show considerable variation in their hisses, indicating potential intraspecific vocal communication (e.g., *Liolaemus chiliensis*, Labra et al. 2016). On the other hand, most gekkotan lineages produce true vocalizations, including a wide array of hisses, squeaks, and chirps as part of their vocal repertoire (Rohtla Jr. et al. 2019). The complex acoustic structure of geckos' calls with tonal and harmonic qualities coupled with a high hearing capability is made possible due to derived characteristics of the laryngotrachea and inner ear (Russel and Bauer 2020, but see next section). Being issued by males, females, and juveniles, gecko calls can be used in a variety of behavioral contexts (Rohtla Jr. et al. 2019): when escape is needed (as an antipredatory mechanism), during agonistic interactions among rivals (e.g., defending territories or competing for resources), and in the course of mating behavior (courtship or copulation). The extension of variation in the vocalizations of geckos is almost as extensive as diversity of clade Gekkota, with some species producing vocalizations that can be heard over a hundred of meters (e.g., *Ptenopus garrulus*, Hibbitts et al. 2007) and other species with even the presence of interpopulational dialects (e.g., *Gekko gecko*, Yu et al. 2011).

### Anatomical Structures Associated with Vocalization in Squamata

The vocal apparatus of squamates is composed of the basic design of tetrapods: it consists of a tube that passes and modulates air as it inhales and expels air from the paired lungs (Russel and Bauer 2020). Air inhalation and exhalation are acquired through a very derived mechanism acquired by costal muscles and ribs' expansion to aspirate air (Bradbury and Vehrencamp 2011). As with other terrestrial vertebrates, the glottis represents a valve that allows vocal vibrations at the top of the trachea, with the vocal cords being

located at the glottal lips (Bradbury and Vehrencamp 2011; Russel and Bauer 2020).

Even though the basic squamate design is clear, the functional relationship with form and function has been underrepresented for their lineages. For example, vocal cord-like structures are only described for a few “lizard” species (see Russell and Bauer 2020 for a comprehensive review) and a unique snake species (*Pituophis melanoleucus*, Young et al. 1995). However, only gekkonids hold true vocal cords that are rich in elastin, with laryngeal size and tracheal dilatation being associated with acoustic properties of their vocalizations (Rohtla Jr. et al. 2019). The true vocal cords are located at the modified glottis, modulating the air as it passes by, therefore producing sounds typically categorized as vocalizations (Russel and Bauer 2020). Although the vocal cords are the main structure that participates in the generation of this type of acoustic communication, other structures associated are equally important in sound production, as cartilages and muscles contained in the laryngotracheal region (Russell et al. 2000). For instance, despite the simplified laryngotracheal region of snakes, intrinsic musculature of the larynx might modify the glottal opening shape providing modulation during hissing of a few snake species (Russel and Bauer 2020; Young 2003). Also, the emission of call with harmonics of a few non-gekkotan lizards suggests the existence of a modified laryngotracheal anatomy; other non-gekkotan lizards use other body parts for modulating the frequency of hisses, such as nasal passageways as resonators and gular inflation (Russel and Bauer 2020; Young 2003). Finally, the shape and size of arytenoid cartilages might play an important role in differentiating vocalizing and nonvocalizing lacertids (see Russel and Bauer 2020 and references therein).

The laryngotracheal region, supported at the mouth’s floor by the hyoid apparatus through attached muscles and ligaments, comprises, as the name suggests, the larynx and the trachea (Moore et al. 1991). The trachea is a tubelike-shaped respiratory organ which delivers air from the lungs to the larynx and vice versa (Russel and Bauer 2020). It is mainly composed of cartilaginous tissue organized as several continuous and

uniform horizontal rings one on top of the other through the whole tracheal length (Russell et al. 2000). Even though this represents the basic configuration of the tracheal rings, some variation is common to occur. For instance, *Afroedura pondolia* and *Chondrodactylus bibronii* (= *Pachydactylus bibronii* in Russell et al. 2000) can present ring bifurcations and ring fusions in their trachea (Russell et al. 2000). However, some species diverge vastly from this common variation. *Ptenopus garrulus*, for example, presents a longitudinal invagination produced by the folding of the trachea on itself, with the left side overlapping the right side, and this invagination creates a sequence of incomplete tracheal rings (Rittenhouse et al. 1998), whereas in *Chondrodactylus angulifer*, its incomplete tracheal rings are even more slip apart, forming a pronounced mid-dorsal gap (Russell et al. 2000). Such a variation still remains to be explored in terms of its morphofunctional aspect, but there seems to be a relation of the tracheal width with call frequency parameters in several gekkotans (Rohtla Jr. et al. 2019). Sexual dimorphism in both trachea and larynx might also be associated with changes in vocalization mechanisms in this lineage (Moore et al. 1991).

The larynx consists of two cartilages – the cricoid and arytenoid cartilages – and two pairs of intrinsic muscles, the *musculus constrictor laryngis* and *musculus dilator laryngis* (Russell et al. 2000). The cricoid cartilage is the main structural piece of the larynx, to which all intrinsic muscles are associated with (Russel and Bauer 2020). The quality of sound generated depends on their form, dimension, and tension placed, as well as additional factors that include the presence of a resonating chamber, air pressure, and size of glottal opening during phonation (Russell et al. 2000).

The anatomy of the larynx is variable between taxa, mostly regarding their general shape and size (Rohtla Jr. et al. 2019). For instance, while *Gekko gecko* bears a ring-shaped cricoid cartilage (Moore et al. 1991), *Ptenopus garrulus* presents a diamond-shaped cricoid due to its large lateral processes (Rittenhouse et al. 1998). The arytenoid cartilages, on the other hand, represent small paired pyramidal pieces

connected to the anterior portion of the cricoid cartilage (Russell et al. 2000). This cartilage also greatly vary among lizards and might be associated with different air modulation in vocalizing species. In snakes, there seems to be no relation between the laryngeal morphology and either phylogeny or habitat preference – therefore, the ophidian larynx seems to be evolutionarily very plastic, and its plasticity is most likely associated with more complex vocalizations, as in *Pituophis melanoleucus* and *Ophiophagus hannah* (Russel and Bauer 2020).

The *M. constrictor laryngis* – responsible for compressing the larynx – has its point of origin located posteriorly to the basihyoid process, inserting itself on the midline of the dorsal face of the larynx (Russell et al. 2000; Russel and Bauer 2020). The *musculus dilator laryngis*, responsible for opening the glottis, has its point of origin close to the glottal tube and inserts itself into the arytenoid cartilages (Russell et al. 2000; Russel and Bauer 2020). Both muscles also exhibit several interspecific variations in vocalizing lizards and are directly associated with different morphofunctional consequences for vocal chords. For instance, while the muscle arrangements of *Gekko gecko* performs the dorsolateral rotation of the arytenoids, consequently increasing the tension above the vocal cords, in *Ptenopus garrulus* it elevates dorsally the vocal cords, juxtapositioning them (Rittenhouse et al. 1998). Therefore, sites of origin and insertion of laryngeal muscles as well as fiber orientation are directly involved in different vocalizations and deserve to be taken into account in any morphofunctional perspective of phonation in Squamata (Russel and Bauer 2020).

Finally, although even less studied and sometimes forgotten, the tracheal diverticula represent chambers of thin and delicate connective tissue externally connected to the trachea (Young 1992). These specialized structures are associated with more complex vocalizations and have been described only in a few genera of colubroidea snakes (Young 1991), and it is so far known that the size and shape might act as resonating chambers that determine the frequencies that are

emitted (Young 1991). The role of the diverticulum in non-gekkotan lizards, however, still remains as speculative (Russel and Bauer 2020).

## Cross-References

- Auditory Signals
- Chemical Cues
- Chemical Signals
- Communication
- Crocodylia Communication
- Echolocation
- Squamate Cognition
- Squamate Life History
- Squamate Morphology
- Squamate Sensory Systems
- Testudines Life History
- Visual Recognition of Prey and Predators

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## Squamate Cognition

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## Introduction

Reptilian cognition is paradoxical. Judging by their phylogenetic position, brain size and organization, and the complexity and sophistication of their behavior, one would expect the cognitive achievements of reptiles to be on a par with those of other vertebrates. However, there is a widespread (mis)perception that reptiles, and squamates in particular, are the cognitive morons of the vertebrate radiation. In fact, to some the expression “squamate cognition” could almost be considered oxymoronic, so entrenched is the idea that lizards and snakes are essentially instinct machines, inflexible and lacking even the most basic intellectual abilities. But the myth of squamates as stupid, lumbering brutes is out of kilter with the conclusions from a small but growing literature that shows that squamates have flexible, sophisticated behavior and display a startling array of cognitive skills. This entry will provide a brief review of the current state of knowledge regarding squamate cognition.

With more than 10,000 species in over 70 families, Squamata is the largest order of living reptiles and an extremely diverse group in terms of morphology, development, ecology, reproduction, and sociality. Squamata is considered a monophyletic clade, but there is considerable debate about the phylogenetic relationships among the different families and larger groups included in it. As currently conceived, Squamata comprises lizards, snakes, and the lesser known amphisbaenians (worm lizards). Despite its generalized use, the term “lizard” does not designate a valid, accepted group (i.e., a clade). Snakes and amphisbaenians are just specialized lizards, and therefore there is no monophyletic clade that includes lizards and excludes snakes and amphisbaenians. The lizard-like tuataras from New Zealand are the sister group of squamates, and together, squamates and tuataras make up the Lepidosauria, the sister group of Archelosauria (turtles, crocodiles, and birds).

Reptiles have generally been given scientific short shrift in favor of more amenable subjects like birds, mammals, or even fish. As a result, their cognitive abilities have rarely been tested. Research on reptile cognition has traditionally emphasized work with turtles, with squamates receiving far less attention. This is in part due to the mistaken belief that turtles are “living fossils” that somehow resemble the ancestral condition at the reptile-mammal transition. However, in the last decades, there has been a steady flow of studies probing different aspects of squamate cognition. This small but growing body of relevant research has shown that squamates are capable of problem-solving and of most major types of learning provided that the experimental design takes account of some peculiarities of their biology. The behavioral evidence also refutes the caricature of squamate behavior as being simple, clumsy, inflexible, and instinct-driven. Recent work has shown that squamates possess elaborate communication and social systems, parental care, and even play. They benefit from enrichment; form bonds with their caretakers, whom they recognize individually, and are affected by early social isolation much as birds and mammals do.

Although squamate cognition is a rapidly growing subject, the growth is uneven, with

some aspects of cognition, as well as some species groups, covered more deeply than others. Most of the available information concerns learning, while other aspects of cognition (e.g., categorization, concept formation, planning, episodic memory, problem-solving, tool use, metacognition) remain relatively unexplored in this group. Lizards are the leading taxon, with the largest number of studies. Studies of snake cognition are relatively few in comparison, while those dealing with amphisbaenians are virtually nonexistent. Australian skinks and spatial and social learning in particular have received a lot of attention, with several recent reviews.

## Cognition and the Squamate Brain

Recent interest in squamate cognition has not been accompanied by a corresponding interest in its underlying neural mechanisms. A notable exception is the recent focus on the role of the hippocampus in spatial cognition (e.g., Roth et al. 2019). Also, there seems to be a disconnect between cognitive/behavioral and brain studies, insofar as what little neuroscience research is currently done with lizards and snakes often relies on species that are not necessarily those for which cognitive/behavioral data are more abundant.

The extent to which absolute or relative brain size is a product or a driver of behavioral and cognitive complexity is a contentious issue. While there is some evidence that larger relative brain sizes are associated in living vertebrates with more complex cognition, work with invertebrates has shown that complex cognitive functions can be implemented with behavioral shortcuts requiring only the simplest neural circuits. Squamates and other reptiles are widely considered small-brained compared to birds and mammals. In fact, brain size has often been used to justify claims about the presumed intellectual backwardness of squamates, their small brains allegedly precluding flexible, intelligent behavior. However, while it is true that the brain of a lizard or a snake is, on average, smaller than the brain of a bird or a mammal of similar body weight, the difference has been grossly overestimated (Font et al. 2019).

Another misconception that has plagued research on squamates holds that lizards and snakes lack certain brain structures considered crucial for complex cognition (e.g., hippocampus). Mammalian brains are characterized by a layered neocortex which is involved in many cognitive processes. For a long time, the brains of birds and reptiles were considered “primitive” in comparison, with relatively large basal ganglia but no neocortex. Leaving aside the controversial question of whether a neocortex is a necessary requirement for cognition, current understanding of vertebrate brain evolution provides a radically different view. Reptiles do have a cerebral cortex. In fact, a clearly layered cerebral cortex is only found in mammals and non-avian reptiles. Moreover, it has been shown that structures once considered part of the basal ganglia of reptiles are similar, morphologically (i.e., cell types, connectivity, gene expression patterns) and functionally, to mammalian neocortex. So, although superficially different, the brains of squamates and mammals conform to a similar organizational plan that is shared by all amniotic vertebrates (Northcutt 2013).

Laterality, thought to reflect hemispheric specialization of brain function, has been described in a wide array of vertebrates. Laterality often results in behavioral asymmetries. Asymmetries in visually guided behavior seem widespread in animals with reduced inter-hemispheric connectivity and eyes that are, like those of many squamates, laterally placed. In lizards, responses to social displays during aggressive and courtship interactions have a consistent left-eye bias: visual displays elicit a stronger response when viewed from the left visual field, which is controlled by the right cerebral hemisphere. Predators are also preferentially monitored through the left eye. In contrast, prey tends to be monitored through the right eye.

## Specialized Sensory Systems and Communication

Vision and chemoreception are arguably the main sensory modalities through which squamates acquire information from the environment.

While the types of stimuli that they can detect through their visual and chemical senses have been relatively well characterized, attentional and perceptual processes remain largely uninvestigated (Fleishman and Font 2019).

Lizards and snakes have a sophisticated visual system that allows them to make fine discriminations of motion, physical form, and color. Most lizards have a simplex all-cone retina, with three to four different spectral classes of cones. Information from each cone receptor class is processed by an independent neural channel, suggesting that most lizards are tri- or tetrachromats (seeing 3–4 primary colors). Snakes show more variability, with species that have only rods, only cones, or both types of photoreceptors, and many are mono- or dichromats (1–2 primary colors). Many squamates, particularly diurnal lizards, exhibit conspicuous and elaborate color patterns that serve different adaptive functions such as camouflage, thermoregulation, warning or startling predators, and communicating with conspecifics.

Lizards and many snakes have one class of cone photoreceptor (SWS1) that is sensitive to ultraviolet (UV) light and allows them to perceive coloration patterns in this part of the spectrum. This raises the possibility that at least some squamates use a relatively private, UV-based channel to communicate with conspecifics. In support of this hypothesis, several studies have found correlations between the size or spectral properties of UV-reflecting skin patches and variables related to individual quality and/or fighting ability in male lizards (Pérez i de Lanuza et al. 2014).

Lizards and snakes also have large numbers of double cones in their retinas. Double cones are responsible for visual motion perception, which is important for detecting prey, for detecting approaching predators, and for communication. Lizards in particular have a rich repertoire of motion displays (i.e., dynamic visual signals) that involve some type of movement of the whole body or of body parts. Best known are the up and down movements of the head and/or the body (headbobs, pushups) characteristic of iguanid and agamid lizards. Males of many iguanid and agamid lizards also have an extensible throat fan (dewlap) that can be conspicuously colored. Headbob displays, often accompanied by

dewlap extension, are used primarily by males in territorial defense and courtship and convey information about the specific identity, sex, and quality of the displaying animal. Experiments using video playback of recorded displays or robotic lizards have shown that lizards are sensitive to subtle variation in motion displays. Although headbob displays are species-specific, there is considerable inter-individual variation in several aspects of the motion display which females can use to discriminate among individual males.

Rather than being fixed, the motion displays used by lizards show flexible adaptation to prevailing conditions. Wind can make plants to move, and vegetation movement can interfere with the detection of motion displays such as the headbobs of *Anolis* lizards. Two species of *Anolis* from Puerto Rico, for example, increase the speed of their headbob displays to improve communication in visually “noisy” environments of rapidly moving vegetation (Ord et al. 2007). Headbob displays in some *Anolis* begin with a series of abrupt square-wavelike movements that function as alerting components that draw the attention of receivers to the display that follows. There is also evidence that some species adjust the amplitude of the initial movements of their displays depending on the distance to the viewer. The amplitude is highest when the viewer is distant and becomes smaller as the distance to the viewer decreases (Fleishman and Font 2019).

Other motion displays involve stereotyped movements of the legs (footshakes) or the tail. Many *Podarcis* wall lizards have a repertoire of several footshake displays that are performed in different contexts and that differ in the type of movement and body posture of the displaying lizard. One footshake type in particular, labelled Type III, is directed at potential predators (including human observers) and functions as a pursuit-deterrent signal. As predicted by theoretical models, Type III footshakes are oriented toward the predator (the lizards use the leg closest to the approaching predator), they are performed more often when the predator is some distance from the lizard (not too far, not too close), and they give way to flight behavior when the predator closes in on the lizard (Font et al. 2012). Type

I foot shakes are performed after a bout of locomotion and often in the absence of obvious receivers and could thus function as a broadcast (“assertion”) display. Other footshake types are used as social signals during intra- and intersexual encounters.

Chameleons are well known for their ability to modify their body coloration to match parts of the environment. In the case of dwarf chameleons (*Bradypodion* spp.), this matching has been shown to take into account the visual capabilities of specific predators, such as birds and snakes (Stuart-Fox et al. 2008). Many lizards and snakes are not capable of rapid color changes but are nonetheless cryptically colored. To be effective, visual camouflage requires that animals choose the type of substrate that best matches their own body coloration. Experiments conducted with *Podarcis* and *Amphibolurus* show that lizards select perching and basking sites non-randomly with respect to the visual environment in order to enhance camouflage (Marshall et al. 2016; Salisbury and Peters 2019). This suggests that they assess the visual properties of available substrates and choose those with colors or patterns suitable for concealment.

Squamates have three major chemosensory systems capable of detecting biologically relevant chemicals: the main olfactory system, the vomeronasal system, and taste buds present in the tongue and in the oral cavity. Most research on squamate chemoreception has focused on the olfactory and vomeronasal systems. The olfactory system is responsible for the detection of volatile odorants, whereas the vomeronasal system specializes in the detection of relatively nonvolatile, high-molecular-weight chemicals. The tongue is an integral part of vomeronasal chemoreception, collecting airborne or substrate chemicals from the environment and delivering them to the paired vomeronasal organs located in the roof of the mouth. Tongue flicking, the quintessential squamate behavior, has been extensively used as an observable index of vomeronasal function. Inter-specific variation in the functional importance of the tongue-vomeronasal system is reflected in the size of the accessory olfactory bulbs and other structures of the accessory olfactory system.

The chemical senses allow squamates to locate potential food sources, detect and avoid predators, and communicate with others of their own species. The literature documenting the chemical discrimination abilities of squamates is immense and reveals that lizards and snakes are capable of making extremely fine-grained chemical discriminations in foraging, antipredatory, and social contexts.

Chemicals released through the skin or specialized epidermal glands allow squamates to discriminate between conspecifics and closely related heterospecifics, males and females, familiar and unfamiliar conspecifics, kin and non kin, and self-produced versus chemicals produced by other individuals. The chemicals involved are often described as pheromones even though critical evidence for a pheromonal function is often lacking. In fact, some of these chemicals allow receivers to obtain information, but there is no evidence that they have evolved for a communicative function and are thus best characterized as chemical cues. An important class of chemical cues is the signature mixtures allowing individual or group discrimination.

Dominance hierarchies, pair bonding, and extended parental care have now been described in many lizard species and offer grounds for expecting individual recognition to be widespread. Indeed, individual recognition has been often suggested on the basis of anecdotal information, but conclusive evidence for true individual recognition in lizards is limited. Males of the lacertid lizard *Podarcis liolepis* use scent marks to recognize rivals individually, evaluate their competitive ability (body size), and assess the threat posed by each individual rival neighbor (Carazo et al. 2008). This study provides the first demonstration of true individual recognition in any reptile and confirms that at least some compounds in the scent marks of male lizards function as signature mixtures rather than pheromones.

Some boids, pythonids, and viperids (e.g., rattlesnakes) possess specialized heat receptors known as pit organs on the head that allow them to detect tiny ( $< 0.05^{\circ}\text{C}$ ) changes in temperature. The heat receptors endow snakes with stereoscopic infrared vision that allows them to

accurately orient on and strike their warm-blooded prey even in total darkness. Following striking and envenomation of a prey, rattlesnakes exhibit a behavior known as strike-induced chemosensory searching. Striking presumably leads to the formation of a neural representation that rattlesnakes use as a chemical search image to locate the envenomated prey. Rattlesnakes are capable of identifying the trail left by a rodent they have themselves envenomated and distinguish it from the trails left by other rodents, even by rodents envenomated by other rattlesnakes.

Unlike snakes, which are only sensitive to low-frequency airborne sounds, lizards have ears with a wide frequency range and good sensitivity, similar to birds and mammals. However, auditory communication in lizards is limited to the relatively simple vocalizations of nocturnal geckos. Still, some lizards have been shown to use their hearing to eavesdrop on the alarm calls of birds and respond to these calls with vigilance and other antipredator behavior.

## Learning and Memory

Gordon Burghardt (1977) wrote the first major review of reptile learning. He reviewed an impressive amount of literature and criticized the then prevailing view that reptiles are instinct-driven and incapable of learning, pointing out important limitations in previous studies. More recent research has been covered in a number of updated reviews (Wilkinson and Huber 2012; Burghardt 2013, 2020).

Many tests of squamate learning conducted during the last century failed because they did not take into account peculiarities of their morphology, physiology, and behavior. Temperature at the time of testing, for example, is a crucial variable, as most lizards and snakes will not perform efficiently at temperatures that may be adequate for work with mammals and birds. As another example, food, which is a powerful reinforcer for most animals, may have little motivating effect for lizards and snakes. Since most squamates, particularly snakes, eat relatively



infrequently, using small tidbits as positive reinforcers is impractical with most species.

Studies using conditions and testing paradigms more appropriate to squamate physiology and behavior clearly demonstrate that lizards and snakes are in fact quite adept at most traditional learning tasks. But to reveal the full extent of their learning abilities requires adopting an ethological approach, i.e., to view learning from the perspective of the species' normal behavior under natural circumstances. The trick is "to make sure that the problems tested accommodate their sensory abilities and behavioural repertoires" (Burghardt 2020, p. 227; see also Roth et al. 2019).

Table 1 lists the learning types identified so far in squamate reptiles. Far from being the poor,

slow learners portrayed in the earlier literature, much recent research shows that lizards exhibit nuanced patterns of learning and memory in different contexts, such as foraging and social interactions. Demonstrations of learning in snakes, in contrast, are relatively scarce. Research conducted until the 1970s produced mixed results, largely as a result of the use of inappropriate conditioning protocols. More recent work, however, has shown that snakes clearly have the ability to learn provided that experimental paradigms and conditioning stimuli match their unique morphology, physiology, and behavior. For example, rat snakes (*Elaphe obsoleta*) show enhanced problem-solving ability in environmentally enriched conditions (Almli and Burghardt 2006), and Burmese pythons (*Python molurus*) can be conditioned to reliably depress an illuminated button in order to gain access to hidden food rewards (Emer et al. 2015).

Some authors have suggested that lizards and snakes learn in squamate-specific ways, different from birds and mammals. Suboski (1992) proposed that some forms of reptile learning conform to a variant of Pavlovian conditioning, termed releaser-induced recognition-learning, that combines the concepts of sign stimulus and innate releasing mechanism from classical ethology with the transfer-of-control version of the stimulus substitution principle from Pavlovian conditioning. However, the bulk of the evidence suggests that lizards and snakes learn in much the same way as other vertebrates; only they differ in terms of what they find easiest to learn and what motivates them to learn.

Many time-tested procedures that are routinely used in learning research with mammals or birds simply do not work with squamates. Others, however, can be extremely successful. A survey of the recent literature, for example, reveals an inordinate fondness of researchers working on lizard cognition for colored plastic lids. Following the description by Leal and Powell (2012) of a novel operant procedure requiring *Anolis* lizards to remove a colored plastic lid to access a well containing food, a slew of papers have been published that use slight modifications of the same procedure to successfully

**Squamate Cognition, Table 1** Learning types and related phenomena identified in squamate reptiles

|                                              |
|----------------------------------------------|
| • Habituation.                               |
| • Classical conditioning.                    |
| - Autoshaping.                               |
| • Instrumental conditioning.                 |
| - Target training.                           |
| - Maze learning.                             |
| - Operant conditioning.                      |
| • Avoidance learning.                        |
| - Food aversion learning .                   |
| - Predator avoidance learning.               |
| - Other avoidance learning (heat).           |
| • Discrimination learning.                   |
| - Visual/color discrimination.               |
| - Chemical discrimination.                   |
| - Individual discrimination.                 |
| • Generalization.                            |
| • Latent learning.                           |
| • Spatial learning (place and cue learning). |
| • Numerosity/quantity discrimination.        |
| • Social learning.                           |
| - Gaze sensitivity/following.                |
| - Stimulus/local enhancement.                |
| - Copying-imitation.                         |
| • Behavioral flexibility.                    |
| - Detour problems/response inhibition.       |
| - Reversal learning.                         |
| - Problem-solving.                           |
| - Learning across multiple domains.          |
| • Rapid learning.                            |
| • Extended (long-term) memory.               |

evaluate multiple cognitive abilities in various lizard species.

Evidence for long-term memory in squamates is scarce. Aversion to prey color stimuli accompanied by discomfort generated by a LiCl injection in garter snakes disappears after 22 days (Terrick et al. 1995). A recent study found that agamid lizards can remember to avoid colors related to unpalatable prey for at least 60 days after a single aversive exposure (Ko et al. 2020). In a different context, rival recognition in aggressive encounters can affect aggressive behavior for up to 3 weeks in Australian rock dragon lizards (*Ctenophorus*) (Stuart-Fox and Johnston 2005).

## Spatial Cognition

As with other taxa, far more attention has been devoted to spatial cognition than to other types of squamate cognition (reviewed in Mueller et al. 2011). This is not surprising considering the complex spatial demands that many lizards and snakes face in their natural environment. Natural history observations and laboratory experiments clearly indicate that squamates display a range of behaviors that require considerable information-processing capabilities to solve spatial problems. Homing, exploratory behavior, and territoriality are common in species belonging to all major groups. The presence of such behaviors suggests that squamates have the ability to learn about their environment and use this knowledge in adaptive ways, to locate food or prey patches, safe refuges, or mates.

Squamates use multiple mechanisms to solve spatial problems. For example, Punzo and Madragon (2002) showed that juveniles of three species of Australian *Ctenopus* lizards are capable of learning to run a complex maze for a food reward using path integration. Mueller-Paul et al. (2012) suggested that jeweled lizards (*Timon lepidus*) navigate a complex eight arm radial maze using a stereotyped turn-by-one arm response. In both these cases, lizards relied on an egocentric (self-centered) reference frame to locate the goal relative to their own position.

In addition to egocentrically referenced mechanisms, mammals and birds are also capable of place learning, i.e., forming map-like memory representations of allocentric space which are independent of the subject's position. The possibility that reptiles, particularly squamates, may possess a hippocampus-dependent cognitive module similar to that supporting place learning in other vertebrates has attracted a lot of attention. Laboratory experiments have yielded mixed results. A study with two lacertid species did not find evidence of orientation to a single heated rock among seven unheated rocks (Day et al. 1999). However, more recent studies have demonstrated that lizards can use distal extra-maze cues to successfully navigate to a goal (Font 2019). These results suggest that lizards can use mental representations of space akin to the mental maps described in other taxa to locate a goal.

Studies with lizards and snakes have confirmed a role of the squamate hippocampus in spatial cognition. The medial cortex (MC) and the dorsal cortex (DC), the reptilian homologues of the mammalian hippocampus, are larger in actively foraging than in congeneric sit-and-wait lizards, suggesting a relationship between hippocampus size and ecological demands related to searching for spatially distributed resources. Similarly, free-ranging rattlesnakes that were repeatedly translocated had larger MC than handling or undisturbed control rattlesnakes with a smaller activity range.

## Social Cognition

Another area that has attracted considerable attention is social cognition. Squamates are often described as “asocial,” but in fact sociality in lizards and snakes is rather variable, ranging from solitary species to species that live in social networks that rival in complexity with those of birds and mammals. Although scant, the available evidence demonstrates that squamates can learn from others. In particular, recent work has shown that conspecific gaze following and social learning occur in lizards (e.g., Noble et al. 2014; Whiting et al. 2018).

Several studies with Australian skinks have tested the relationship between sociality and cognition. According to the social intelligence hypothesis, social complexity sets the stage for the evolution of complex cognitive abilities. However, results are contrary to predictions from the social intelligence hypothesis. Even solitary species are capable of social learning, and social isolation does not affect performance in cognitive tasks in the more social species. This evidence suggests that a complex social structure is unnecessary for animals to learn effectively from conspecifics, and the link between social behavior and cognition remains tenuous, at least in this group.

## Concluding Remarks

Most studies of squamate cognition fall into one of two types. Some studies have as their main goal to explicitly test what cognitive abilities previously described in other groups (usually birds and mammals) are also present in squamates. Others are not specifically concerned with the assessment of cognition *per se* but use a learning paradigm to explore an ecologically or ethologically relevant question. A challenge for studies of the first type is to avoid falling into the trap of considering that proficiency in a given task necessarily implies shared mechanisms across different taxa. A recurrent theme in comparative cognition studies is that functionally similar behavior can be produced by different mechanisms in different animals. Moreover, behaviors that appear to reflect complex cognition can arise from “simple” associative learning that some researchers would not even consider cognitive. Unfortunately, few studies of squamate cognition address the mechanisms underlying their subjects’ performance (Font 2019).

Some cognitive abilities have not been reported in squamates. Cross-modal recognition (the ability to transfer information across sensory modalities), for example, has been described in mammals, fish, and invertebrates, but not in reptiles. The evidence for concept formation is at best

anecdotal, and metacognition, a hot topic in contemporary comparative cognition research, has never been investigated in squamates. What should we make of this lack of evidence? In the past there has been a tendency to equate absence of evidence with evidence of absence; a more sensible alternative seems to be to use the lack of evidence to identify areas that need more exploration.

Squamates are notoriously difficult subjects to work with, particularly in a laboratory setting. When their cognitive abilities are tested, it is often with a relatively small number of species that are less challenging to maintain in artificial conditions. A consequence of the sparse phyletic coverage is that there are no relevant studies for entire families or even for larger groups, such as amphisbaenians. In addition, many cognitive studies with squamates use small sample sizes, resulting in low statistical power that compromises the ability to reach meaningful conclusions.

Another problem has to do with the way performance is assessed in learning experiments. Studies of learning and memory depend critically on the researcher’s ability to determine if and when a given task has been acquired. For many reptiles, including lizards and snakes, the learning period in an experimental situation is often protracted, either because learning tasks are difficult or the experimental procedure is inappropriate for the animals. In these situations, the researcher is faced with long strings of correct and incorrect responses and may have difficulty determining the starting and ending points of learning. The standard criteria used by many researchers to assess performance in experiments with repeated trials are based on ad hoc testing for non-random responses (loosely based on the binomial distribution, e.g., 2/3 correct choices for two successive testing sessions) or runs tests for unblocked trials (successive correct choices). However, these statistical techniques typically assume that individual trials are independent and that each block of trials follows a binomial distribution. Both of these assumptions are often unrealistic.

But the main problem with studies of squamate cognition continues to be the dearth of

experimental designs with real ethological validity: there is an urgent need for the development of testing paradigms more appropriate to squamate physiology and behavior than those traditionally used with mammals or birds. There is also a need for more field tests of cognitive abilities. By studying free-ranging lizards and snakes in the wild, researchers can potentially assess the cognitive skills of large numbers of individuals, without the need to place subjects in artificial or alien environments that can affect their behavior, and under the very conditions in which those skills evolved (Steinberg and Leal 2018).

This entry has reviewed key examples of the behavioral and cognitive complexity of squamate reptiles. Many more could not be included due to space limitations (e.g., personality, parental care, play, etc.). In light of the available evidence, there can be no justification for considering that lizards and snakes are instinct machines with little scope for cognition and learning; instead the existing literature shows that they have considerable behavioral flexibility and can cope with unusual challenges that could not be dealt with adaptively using only hardwired responses.

The study of squamate cognition may also provide insight into a long-standing evolutionary puzzle. The cognitive similarities between birds and mammals, particularly primates, are thought to be, given the large phylogenetic gap separating these two groups, the result of convergent evolution. This reasoning, however, is based on the assumption that cognitive abilities similar to those of birds and mammals are entirely lacking in reptiles, the modern descendants of the ancestors of all amniotic vertebrates. This assumption is, given the evidence reviewed here, unfounded. Nonetheless, further studies are required to unravel the many questions that remain open about squamate cognition.

## Cross-References

- [Gordon Burghardt](#)
- [Squamate Acoustic Communication](#)
- [Squamate Sensory Systems](#)

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## Squamate Life History

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## Synonyms

[Amphisbaenians](#); [Lizards and snakes](#)

## Introduction

The non-avian reptiles comprise about 10,800 living species allocated in the clades Archosauria (crocodilians), Testudines (turtles), and Lepidosauria (tuataras and Squamates). Squamata includes Amphisbaenia (amphisbaenians), Sauria (lizards), and Serpentes (snakes) and is among the most diverse radiations of terrestrial vertebrates with more than 10,400 taxa occupying habitats from tropical oceans to temperate mountain summits (Uetz et al. 2020; Vitt and Caldwell 2009).

Squamates occur on every continent except Antarctica and exhibit distinct body forms and habits, being mainly terrestrial or arboreal, although many snakes are semiaquatic, spending much of their lives in or immediately adjacent to freshwater, or, less commonly, in estuaries and seawater (Lillywhite 2014; Uetz et al. 2020; Vitt and Caldwell 2009). Amphisbaenians are adapted to a burrowing lifestyle, with about 190 species distributed in southern Europe, northern Africa, Asia Minor, and South America (Pianka and Vitt 2003; Uetz et al. 2020). They have an elongated body with short and stubby tails, scales arranged in rings around the body, being mostly limbless, with the exception of three species within the family Bipedidae (Vitt and Caldwell 2009). Unfortunately, the ecology and life history of



amphisbaenians are poorly known due to their fossorial lifestyle and the scarcity of researchers studying the group (Pianka and Vitt 2003).

The snakes clade has about 3,700 extant species (Uetz et al. 2020) divided into two large groups: Scolecophidia and Alethinophidia. Scolecophidia is a group of about 450 species of small-sized fossorial snakes feeding on ants and termites (Cundall and Greene 2000; Uetz et al. 2020). Alethinophidia, on the other hand, encompasses the remaining species and shows a wide array of size and diet, with species capable of ingesting relatively large prey (Cundall and Greene 2000). Snakes have a peculiar tube-shaped body with a head and a tail; locomotor members are absent (Lillywhite 2014). They are distributed on all continents, except Antarctica, occupying a wide variety of habitats (from desert to marine areas), habits (from fossorial, cryptozoic, to semi-arboreal and arboreal), and feeding on a plethora of prey, from small invertebrates to large mammals (Lillywhite 2014; Vitt and Caldwell 2009).

Lizards belong to paraphyletic group, most species of which have four well developed limbs and an elongate tail exhibiting a remarkable morphological diversification, ranging from few centimeters in length, such as chameleons and geckos, to nearly three meters long, as the varanid lizard, Komodo dragon (Pianka and Vitt 2003). Lizards comprise more than 6,600 extant species occurring in all continents except Antarctica, and on most oceanic islands (Pianka and Vitt 2003; Uetz et al. 2020). This widespread distribution denotes their broad ecological, physiological, and behavioral adaptations to hot and cold climates, to extremely arid, to freshwater or marine habitats, and to lowland to high elevation regions (Pianka and Vitt 2003; Vitt and Caldwell 2009). Furthermore, the group shows a wide array of feeding habits, most of them being predators with species feeding on small invertebrates to large mammals (Pianka and Vitt 2003). Many lizards, including some representatives of iguanids, are herbivores, with adults feeding on different plant portions like flowers, leaves, stems, and fruits (Pianka and Vitt 2003).

## Sexual Dimorphism

Sexual dimorphism is defined as phenotypic differences between males and females of a species, and is frequently associated with sexual selection (Andersson 1994; Kratochvíl and Frynta 2002). In squamate species showing male–male combat, males should be the larger sex (Shine 1994) and show overdeveloped organs related to combat or advertisement display (Kratochvíl and Frynta 2002). Males of many species of lizards and some snakes exhibit direct physical combat (Kratochvíl and Frynta 2002; Shine 1994), or engage in threat displays with no physical combat or risk of injury, such as push-up displays, chemical signals, or advertisement sounds (Pianka and Vitt 2003). Many species of lizards also exhibit sexually dimorphic ventral glands producing waxy secretions or differentiated staining pattern (Kratochvíl and Frynta 2002; Pianka and Vitt 2003). In general, male lizards are larger, brightly colored, and have more ornamentations than females, although exceptions are not rare (Pianka and Vitt 2003). The males of the South American Teiidae, *Dracena guianensis*, have a much larger head and jaw muscle than females, to the point that they look almost disproportionate (Pianka and Vitt 2003). Many species of lizards are territorial; males establish and defend territories from other males by different behaviors. The male rainbow lizards, *Agama agama*, can change nearly instantaneously from gray to bright blue when encountering another male as a warning for territorial invasion, which is often followed by head bobbing and fighting (Pianka and Vitt 2003). Some male geckos (Gekkota) also use calls to maintain territories by advertising ownership, establishing dominance, and attracting females (Pianka and Vitt 2003). In most snakes, females are larger than males (Shine 1994); this feature is considered adaptive since it allows the development of more and/or larger offspring (Rivas and Burghardt 2001). Different from lizards, there are very few records of territorial snakes, and male–male fighting is also uncommon (Rivas and Burghardt 2001). One well-documented case of territoriality in snakes occurs in the nocturnal small-eyed snake,

*Cryptophisnigrescens*, in which males defend basking sites from rival males. In this species, males engage in ritualized combat and attain larger body size than females (Webb et al. 2015).

Although territorial behavior and male–male fighting in snakes is uncommon (Rivas and Burghardt 2001), distinct male–male combat behaviors were listed for snakes, such as (1) body bridge, the formation of a high vertical arc with a section of the body; (2) coil, when one snake coils around the other, or both coil around each other, at least anteriorly; (3) closed-mouth strike, when one snake strikes at another, with its mouth closed; (4) downward push, when both snakes have the anterior portions elevated, often coiled around each other, and attempt to push the other toward the ground; (5) head raise, when the snake elevates its head and much of its anterior body portion off the substrate; (6) jerk, the snake gives a sudden, staccato jerk with the head; (7) spur poke, when one snake pokes another with the spurs; and (8) sway, the snake sways its neck back and forth with the anterior portion of the body elevated (Senter et al. 2014).

## Copulatory Organs

All squamates exhibit internal fertilization with males showing a pair of intromittent reproductive organs, the hemipenis, used to deposit spermatozoa into female's cloaca. These structures are located at the base of the tail and are everted from openings in the posterior part of the cloaca by vascular pressure (Vitt and Caldwell 2009). Only one hemipenis is everted and used during copulation, being inserted into the female internal genitalia, which lie above the cloaca and have the oviducts outlets in the end of the urodeal corns. Once the copulation is completed, a retractor muscle withdraws the hemipenis (De-Lima et al. 2019; Vitt and Caldwell 2009).

The hemipenis are known to exhibit considerable variation in shape, dimensions, and ornamentation. Some authors have associated limb reduction of snakes and some lizards to their calcified hemipenial spines, implying that in the absence of well-developed limbs, the hemipenial

calcified ornaments (spines and spicules) could take on the role of keeping male and female tightly attached while mating (Nunes et al. 2014). The hemipenial morphology of Gymnophthalmidae lizards was assessed to test the phylogenetic correlation between limb reduction and the presence of calcified hemipenial spines and showed that hemipenial ornamentation may be related to couple-anchoring in some limbless squamate lineages, but do not represent the single mechanism that keeps male and female attached during mating, since basal snake lineages, all known amphisbaenians, and several limb-reduced lizards lack any traces of calcified spines or spicules. Alternatively, many species of snakes and lizards with limb reduction and nude hemipenis can use their tail in the couple-anchoring process (Nunes et al. 2014).

The most direct mechanical interaction between males and females with internal fertilization occurs during copulation, implying morphological coevolution of genitals (Brennan 2016). One hypothesis for the evolution of internal fertilization is that during evolutionary history, females retained mature eggs to decrease the risk of desiccation and predation, selecting males to evolve an intromittent organ to inject spermatozoa inside the female (Brennan 2016). Another hypothesis is that the intromittent organ could have evolved as a way of trying to gain fertilization of eggs before their release, increasing reproduction success (Brennan 2016). Studies of Squamata reproductive organs are usually focused on male hemipenis; however, some authors began investigating the homologous internal paired structures in females, called hemiclitores, and explored the coevolution of these structures in male and female of the same species (Siegel et al. 2011; De-Lima et al. 2019).

The correlation between the conspecific genitalia morphology and the differences from genitalia structures of other species could be the result of reproductive isolation mechanisms (Siegel et al. 2011). The presence of the lock-and-key mechanism in squamate genitalia has been studied, species in which males exhibit long hemipenis with few spines; the females' cloaca are highly bilobed with a very thin wall, while short hemipenis with

many spinines are associated with females exhibiting short cloaca with a very thick wall (Siegel et al. 2011). For instance, a group of researchers inflated the hemipenis of the snake *Thamnophis radix* inside the female genitalia in order to observe interaction of morphological features of both male and female genitals. The study showed the shape of the hemipenis works as a key-lock mechanism with the vaginal pouch (Brennan 2016). Furthermore, the study found the large hemipenis spines were embedded in areas of the female vaginal pouch with more loose connective tissue, which probably minimized the damage caused by the spines (Brennan 2016).

A study regarding the genital morphology of the lizard *Tropidurus torquatus* argues that males with large hemipenial lobes would benefit from increasing the ability to better stimulate the urodeal glands of females, a region with phagocytic function acting as a physiological barrier in spermatozoa selection. The stimulation of these glands induces the production of a secretion that functions as a mechanical and/or biochemical barrier for future copulation semen to fertilize the eggs (De-Lima et al. 2019).

## Courtship

As demonstrated, the shape of the hemipenis may be affected by sexual selection forces, in which males with a specific morphology may be more successful in copulation (De-Lima et al. 2019). However, these forces not only seem to shape complex reproductive organs, but also may impose selection on complex behaviors (Senter et al. 2014). Studies on reproductive behavior of Squamata show that many species can use different strategies of courtship to acquire mates (Pianka and Vitt 2003; Senter et al. 2014).

Distinct courtship behaviors of snakes are listed in the literature, such as (1) bite, when one snake strikes another; (2) chin-rub, a snake draws its chin along the skin of another specimen; (3) cloacal gaping, a snake promotes a wide cloacal opening; (4) lateral punch, when one snake laterally slams its body against the body of

another snake; (5) mounting, a snake presses down on another individual; (6) spur rub, one snake rubs another with the spurs; and (7) tail quiver, when a snake continuously vibrates the tail (Senter et al. 2014).

Courtship has also been reported for lizards. The Bengal monitor, *Varanus bengalensis*, has a complex courtship ritual involving visual, chemical, and tactile communication. Visual cues help males locate the female, chemical signals allow identification of species and sex, and tactile cues stimulate the female (Pianka and Vitt 2003). The male of the green iguanas, *Iguana iguana*, approaches other males and females in a similar way, performing some head bobs. On the basis of the reaction to his head bob, he either initiates an aggressive interaction against another male or courtship toward a female. In courtship, both male and female perform vibratory head bobs, after which the male approaches the female, moves his head across her neck, then bites her neck skin. While holding on to the skin, the male steedles the female, and tries to lift her tail with his own. The female eventually raises her tail, then the male inserts one of his hemipenis. If the female is not receptive, she will reject the male with a head-swing display during the early stages of the encounter (Pianka and Vitt 2003). Besides that, expansion of throat pouch and head-bobbing have also been described as courtship behavior of many species of lizards (Pianka and Vitt 2003).

In territorial lizards, where the male's quality is directly related to the territory he holds, prolonged courtship behavior may not occur (Pianka and Vitt 2003). Within non-territorial lizards, other factors assume importance to determine the highest-quality male around. By prolonging courtship, the female has an advantage, giving the highest-quality male opportunity to displace any other males pursuing her (Pianka and Vitt 2003). The male broad-headed skink, *Eumeces laiceps*, follows the female for as much as 3 days before mating, and after, he often guards their mates against other males to ensure paternity (Pianka and Vitt 2003). An interesting complex social behavior occurs in the Australian skink *Tiliqua rugosa*. Most adult females remain with a single male for long time periods, not only for the

breeding season but also, apparently, during the following years. Analysis of DNA evidence for *T. rugosa* suggests that, even though monogamy predominates among this species, polygyny occurs at low levels (Pianka and Vitt 2003).

There are few studies focused on the female–male sexual interaction of amphisbaenians, probably due to their fossorial lifestyle. However, studies of semiochemicals produced by precloacal glands in intraspecific communication and chemosensory sex recognition of the amphisbaenian *Blanus cinereus* showed that, according to behavioral responses to the scent of conspecifics, amphisbaenians are capable of detecting and discriminating between scent of conspecific males and females by using chemosensory clues (Pianka and Vitt 2003).

## Fertilization

After copulation, spermatozoa reach the surface of an egg. The head of the spermatozoon contains the cell nucleus capped by an acrosome that produces proteolytic enzymes able to digest the egg capsule (Vitt and Caldwell 2009). This process allows the spermatozoon to penetrate into an egg. After this, the pronucleus moves into the cytoplasm of the ovum (Vitt and Caldwell 2009). Next to the input of a spermatozoon, the vitelline membrane of the ovum detaches, lifting all other spermatozoa from the surface of the ovum (Vitt and Caldwell 2009). Fertilization occurs when the two pronuclei fuse, triggering the process of egg conversion into an embryo through successive divisions into smaller cells (Dowling and Zug 2020; Vitt and Caldwell 2009).

## Sperm Storage

Copulation and the deposition of spermatozoa into a female's reproductive tract can occur before the eggs are matured. The time between mating and fertilization in reptiles varies significantly, ranging from hours to years, depending on the species. This variation occurs because females of some species can store spermatozoa and use these

to fertilize eggs long after mating (Blackburn 1998; Dowling and Zug 2020). The ability to store spermatozoa in the oviduct has evolved and has been widely documented in squamate species, many with special structures for maintenance of the spermatozoon (Blackburn 1998; Eckstut et al. 2009). Oviductal sperm storage has allowed the separation of oogenesis, ovulation, and fertilization from mating activity, both temporal and geographically (Blackburn 1998; Eckstut et al. 2009). Spermatozoa storage in reptiles may be a physiological need due to ectotherm, long reproductive cycles, and as an insurance against not finding a partner (Birkhead and Møller 1993). It also provides some advantages in life history strategies: several clutches may be fertilized with no need of successive matings, which is especially important in events of colonization of new habitats (e.g., a single female is sufficient to colonize an island, Eckstut et al. 2009). Sperm storage also provides the conditions for sperm competition, allowing post-mating mechanism for sexual selection, since this behavior increases the opportunities of females to obtain the best-quality genes (Birkhead and Møller 1993).

## Parthenogenesis

Among all vertebrates, the only group that has evolved natural parthenogenesis is the Squamata (Kearney et al. 2009; Fujita and Moritz 2009). In that kind of parthenogenesis, also known as obligate parthenogenesis (Booth and Schuett 2016), mothers produce unreduced and genetically identical daughters with no need for males or spermatozoon for fertilization (Fujita and Moritz 2009). There are 40 known cases of obligate parthenogenesis, mostly from lizard species (Kearney et al. 2009) out of 11,050 currently recognized reptile species (Uetz et al. 2020). They are almost always of hybrid origin, but some are suggested to have a spontaneous or nonhybrid origin (Kearney et al. 2009; Fujita and Moritz 2009). The New World Gymnophthalmidae lizard, *Leposomaper-carinatum*, and the Teiidae *Ameivulanativo* are examples of unisexual parthenogenetic species

(Kearney et al. 2009; Uetz et al. 2020). Parthenogenesis has never been recorded in amphisbaenians. The only documented case of obligate parthenogenesis in snakes is a single Typhlopidae species, *Indotyphlops braminus*, the Brahminy blind snake (Booth and Schuett 2016). Facultative parthenogenesis, asexual reproduction in an otherwise sexually reproducing species, has been documented in several species of snakes and lizards (Booth and Schuett 2016). The Komodo dragon, *Varanus komodoensis*, and the Burmese python, *Python molurus bivittatus*, are well documented cases of facultative parthenogenesis in Squamata (Kearney et al. 2009).

## Viviparity

After fertilization, Squamata shows different strategies associated to embryo development, such as oviparous (egg laying) and viviparous (live bearing). Estimates have pointed out that nearly 20% of the squamate species are viviparous. However, viviparity has arisen independently several times (>115) along the evolutionary history of this group of reptiles, more often than any other clade of vertebrates (Blackburn 2015). Therefore, squamates provide a unique model for studies on the transition from oviparity to viviparity in amniote vertebrates (Blackburn 1998; Murphy and Thompson 2011). The evolution of viviparity has significant effects for life history strategies of this taxon, including a great diversity of placental functions, structures, and modes of embryonic nutrition (Blackburn, 1998; Murphy and Thompson 2011). The great majority of viviparous squamate are *lecithotrophic*, meaning that most nutrients for embryonic development are supplied by the yolk. Very few lizards and no snakes are known to be substantially *placentalotrophic*, with placental membranes supplying large quantities of nutrients for development (Blackburn 1998). Some groups of matrotrophic lizards, such as the New World *Mabuya* and other closely related genera, as well as the Afro-European *Chalcides*, both Scincidae, show strongly convergent placental features with eutherian mammals. The same kind of embryonic nutritional structure has evolved

independently among eutherian mammals and in these two reptilian groups (Blackburn 1992). Some species of Squamata are reported to contain both oviparous and viviparous representatives like the Australian Scincidae *Lerista bougainvillii* and *Saiphosequalis*, and the European Lacertidae *Zootoca vivipara* and the South American water snake of the tribe Hydropsini *Helicops angulatus* (Blackburn 2015).

## Parental Care

Parental care can be defined as any action of the parents, after laying eggs or parturition, that increases the chances of survival of the offspring (Shine 1988). Traditionally, it is considered absent in most reptiles, excluding Archosauria (Shine 1988). Among Squamata, this behavior is exhibited by some species of lizards and snakes (Shine 1988). Factors such as seasonality, breeding season, food supply, and predation pressure may have influenced the evolution of different modes of parental care (Huang and Wang 2009).

In general, parental care can be characterized by some type of assistance given to eggs or neonates by one parent or both (Shine 1988). The presence of the parents probably represents protection against predation, pathogens, and dehydration (Shine 1988). Care for eggs means that parents stay close to the eggs for some time after oviposition and some type of manipulation or protection of the nest may occur (Shine 1988). Care for the neonates consists of providing some assistance to the newly born or newly hatched (Shine 1988).

Care is exclusively provided by females in Squamata (Reynolds et al. 2002). The probable explanation may lie in the time between copulation and oviposition or parturition (Reynolds et al. 2002). After copulation, males generally disperse to search for new sexual partners while females leave males' territory and look for places to establish their nests (Reynolds et al. 2002).

Four categories of parental care are known in Squamata: (1) female buries eggs and exhibits some behavior to defend the nest; (2) female



coils around the eggs, producing heat through muscle contraction (shivering thermogenesis), and consequently warming the eggs; (3) female stays close to the eggs for some time after oviposition; and (4) female aids neonates (Shine 1988).

The most widespread strategy of parental care among Squamata is for the female to stay close to the eggs after oviposition (Shine 1988). The defensive behavior of the nest against predators is known in some taxa and the intensity of the defense is variable (Shine 1988). There are reports in the literature of defensive behaviors ranging from aggressive interactions in lizards and snakes, up to abandonment of the nest depending on the type of predator in some species of lizards. These issues indicate that the time invested in parental care may be influenced by the type of predator and the maternal defense capacity (e.g., Greene et al. 2002; Huang and Wang 2009).

Parental care must meet critical demands for the development of offspring (Stahlschmidt and DeNardo 2009). Egg brooding by shivering thermogenesis seems to be widespread in python snakes, whose embryos normally develop at temperatures close to 30 °C (Shine 1988). During the incubation of eggs, the snake coils around the egg mass producing heat through rhythmic muscle contractions, maintaining a relatively high and constant temperature (Shine 1988). In addition, they are capable to make behavioral adjustments to improve the thermal microenvironment of the egg mass: females tend to spend more time and more tightly coiled around the eggs when environment temperature is lower (Stahlschmidt and DeNardo 2009).

Finally, some records of parental care invested in newborns or young are known among Squamata (Shine 1988). Some forms of care consist of providing assistance during hatching, building shelter for protection, and displaying aggressive defensive behavior against possible predators (e.g., Greene et al. 2002). There are 33 species of vipers that exhibit protective behavior for the offspring and some even remain with the young for several days until the first cycle of ecdysis (Greene et al. 2002).

## Reproductive Endothermy

A recent study has demonstrated the occurrence of seasonal reproductive endothermy in the tegu lizard *Tupinambis merianae*, a species with a circannual cycle alternating between an active period during spring and summer, which coincides with the breeding season, and a period of dormancy during most of autumn and winter (Tattersall et al. 2016). This species has a diurnal habit and thermoregulates by basking in the sun and takes shelter retreating to burrow at night (Tattersall et al. 2016). The body temperature of *T. merianae* remains stable relative to the temperature of the burrow when the animal is at rest (Tattersall et al. 2016). However, in the breeding season, the body temperature of these lizards is substantially higher than the temperature of their shelters (Tattersall et al. 2016). In an experiment in which groups of individuals were subjected to different environmental conditions for long periods, body and environmental temperatures, in addition to metabolic rates were monitored and compared. The results showed that individuals of this species were capable of maintaining a differential body temperature in relation to the environment during the breeding season, probably sustained by endogenous heat production due to the high metabolic demands of reproduction. This finding is the only one record of reproductive endothermy in reptiles (Tattersall et al. 2016).

## Growth

Historically reptiles were considered to exhibit indeterminate or attenuated growth, meaning that these animals grow rapidly when young and at a slower rate after reaching sexual maturity. This rate reduction occurs mainly because, once such organisms reach sexual maturity, a significant fraction of metabolic rate is devoted to reproduction (Sebens 1987; West et al. 2001). Nevertheless, current literature shows that many squamate probably exhibit determinate, or asymptotic, growth having a period of rapid juvenile growth that slows down upon reaching full adulthood and

ceasing altogether a few years after maturity (Dowling and Zug 2020; Frýdlová et al. 2019).

Studies focusing on growth plate cartilage in the epiphysis of long bones of the Iguania clade, comprising Acrodonta (agamas and chameleons) and Pleurodonta (“iguanas”), showed that growth plate cartilage was absent in most of the examined adults of Pleurodonta, while this cartilage was preserved in most of the adult specimens of Acrodonta (Frýdlová et al. 2019). Considering that growth plate cartilage is responsible for longitudinal skeletal growth by the process of endochondral ossification, the absence of this structure in Pleurodonta may be interpreted as an irreversible arrest of skeletal growth, pointing that this group has determinate growth (Frýdlová et al. 2019). On the other hand, the persistence of growth plate cartilage in Acrodonta suggests that this group shows indeterminate growth (Frýdlová et al. 2019). Therefore, these findings reject the universality of indeterminate growth in lizards and acknowledge some degree of plasticity in squamate body growth, which is probably affected by distinct ecological and life history strategies (Frýdlová et al. 2019).

Due to the great diversity of species, habits, and sizes, information on squamate longevity is extremely variable. In general, the bigger the animal, the longer its longevity (Dowling and Zug 2020), with large snakes and lizards living more than 20 years (Dowling and Zug 2020).

## Cross-References

- Parental Investment
- Squamate Acoustic Communication
- Squamate Morphology

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## Squamate Locomotion

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## Synonyms

Snake, lizard, or worm lizard locomotion

## Definition

Movement used by snakes, lizards, and worm lizards to traverse their environment.

Squamata is comprised of lizards, snakes, and amphisbaenians (worm lizards), and with over 10,000 species, is the largest order of living tetrapods and second largest order of vertebrates. The squamates receive their name from their scaly skin, which varies considerably in morphology (Vitt et al. 2003). They are found almost worldwide and are incredibly adept at surviving and proliferating as introduced species (Krysko et al.

2011; Vitt et al. 2003). Their success may in part be due to their diversity of locomotor specializations (e.g., burrowers, gliders, bipedal runners, climbers, and arboreal specialists) or extreme body size range. Limblessness is common in squamates and is thought to have evolved multiple times independently (Gans 1975).

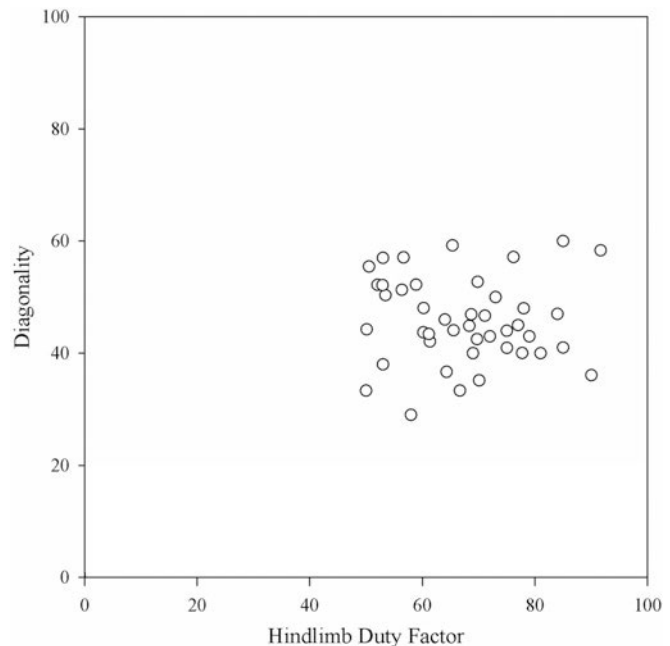
## Major Locomotor Modes

*Squamate locomotion* can be broken down generally into limbed versus limbless movement. Accordingly, this chapter will discuss these movement patterns in reference to the lizards and snakes, respectively. A review of worm lizard locomotion is beyond the scope of this chapter. Terrestrial gaits in the squamates are characterized by considerable inter-cycle variation in both limb-loading and timing (Granatosky et al. 2020). All walking gaits in lizards are symmetrical and involve two general patterns in which animals move their limbs (Granatosky 2018; McElroy et al. 2008). A lateral-sequence gait is one in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb).

A diagonal-sequence gait is one in which each hindlimb footfall is followed by a contralateral forelimb footfall (i.e., right hindlimb, left forelimb, left hindlimb, right forelimb). Commonly, during walking gaits, the forelimbs and hindlimbs are traveling together as a slightly asynchronous couplet. When the ipsilateral forelimbs and hindlimbs are traveling together, this is referred to as a lateral-couplet; when the contralateral forelimbs and hindlimbs are traveling together, this is referred to as a diagonal-couplet. Very rarely do the limbs move together in perfect synchrony (Cartmill et al. 2002).

Almost all lizards use a lateral-sequence diagonal-couplet footfall pattern (McElroy et al. 2008; Fig. 1). This footfall sequence is inherently quite stable due to the generally low proportion of the stride spent as a unilateral bipod (~22%) and the relatively high proportion of the stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support). In general, foot positions arranged as diagonal bipods and large tripods are thought to be highly stable (Cartmill et al. 2002). In contrast, some highly arboreal chameleons tend to use a diagonal-sequence diagonal-couplet footfall

**Squamate Locomotion,**  
**Fig. 1** “Hildebrand” plot displaying diagonality against hindlimb duty factor collected during quadrupedal walking in squamates (n = 43 species)





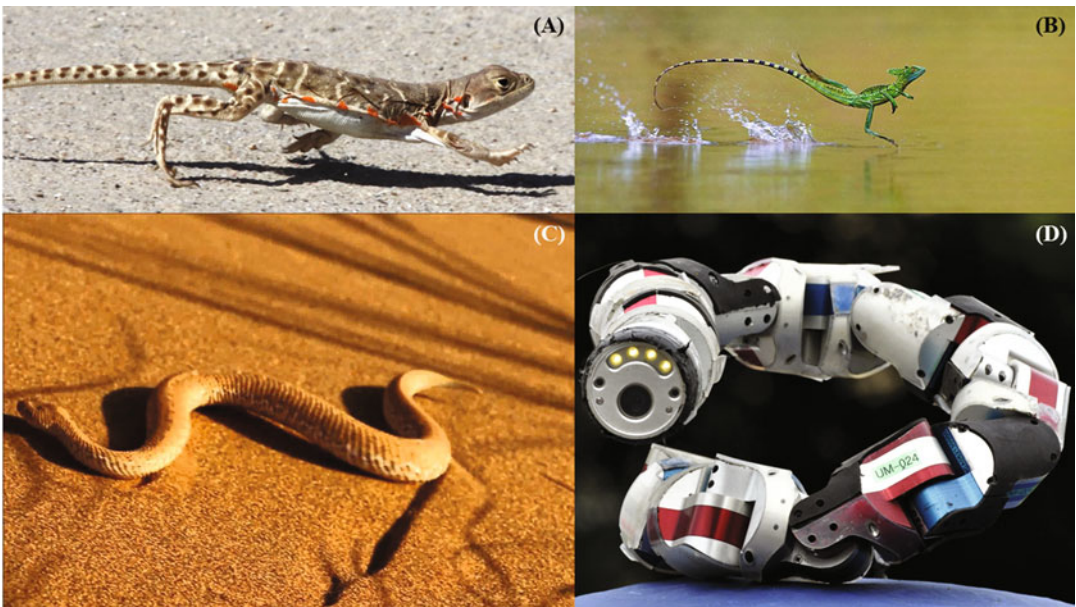
patterns when moving along relatively thin arboreal supports (Cartmill et al. 2002). This gait pattern maximizes the proportion of the stride in which the limbs are arranged as a widely splayed diagonal bipod and ensures that one of the grasping hindfeet is placed in a protracted position (and thus lies roughly underneath the animal's center of mass) on a tested support at the moment when the contralateral forefoot strikes down on an untested support during arboreal locomotion (Cartmill et al. 2002).

Literature on gait transitions (a speed related switch from walking to running) in lizards is scant and it does not appear that lizards can adopt asymmetrical running gaits (e.g., gallop or bound). Experiments on teiid and iguanid lizards revealed that gait transitions are not visually detectable based on limb phase definitions (Irschick and Jayne 2000). Instead, duty factor just continues to decrease with speed until eventually diagonal-couplet walking becomes a diagonal-couplet run (Irschick and Jayne 2000). However, if one bases the definition of a gait transition off of center of mass movements rather than limb phase definitions, then both walking and running center of

mass movements are present (Reilly et al. 2006). It should be noted, the use of these walking and running center of mass movements are not speed dependent (Reilly et al. 2006), and therefore are not synonymous with the gait transitions observed in birds and mammals (Granatosky et al. 2018).

While typical lizard locomotion is quadrupedal, bipedal running is observed in numerous species (Irschick and Jayne 1999; Snyder 1949; Fig. 2). Most notable is the common basilisk (*Basiliscus basiliscus*) that can maintain bipedal gaits while running on top of the water's surface (Snyder 1949). Bipedality usually occurs when a lizard with longer hind than front limbs accelerates to running speed. During bipedal locomotion, the forelimbs leave the ground and the trunk of the lizard is elevated. Only the hindlimbs power movement (Irschick and Jayne 1999; Snyder 1949). There seems to be no speed or cost advantage to bipedal locomotion over quadrupedal locomotion (Clemente et al. 2008).

Unlike mammals and birds, lizard locomotion is characterized by a sprawling posture. Sprawling postures are those in which the humerus and femur cannot attain an orientation with their long



**Squamate Locomotion, Fig. 2** Lizards and snakes can accomplish an impressive range of locomotor behaviors including (A) quadrupedal and (B) bipedal running and

multiple forms of (C) limbless locomotion. As such, squamate locomotion has served as a basic design for numerous (D) bio-inspired robotics



axes vertically directed. Limb movements during sprawling gaits are complex and limb posture changes considerably during a stride (Brinkman 1980; Irschick and Jayne 1999; Reilly 1995; Sullivan 2010). Rather than moving in a fore-aft arc underneath the body, the humerus and femur move backwards, outwards, and downwards during stance phase (Brinkman 1980; Russell and Bels 2001; Sullivan 2010). Such movements complicate the operation of the distal limb segments and dictate their relative effectiveness during propulsion (Granatosky 2020; Sullivan 2010). For sprawling lizards, the highly abducted limb and lateral rotation of the zeugopod relative to the autopod results in a kinematic arrangement in which the ankle and wrist flexor musculature are not in line with the travel path at the end of stance phase (Brinkman 1980; Irschick and Jayne 1999; Reilly 1995; Russell and Bels 2001; Sullivan 2010). The varanids have modified their calcaneal morphology with an expanded lateral “heel”. This structure allows *m. peroneus longus* to serve a propulsion function during locomotion (Granatosky 2020; Sullivan 2010).

Lateral body undulation plays an important part in lizard locomotion and is integrated with limb movement (Russell and Bels 2001). Standing wave patterns, where points of no lateral bending nodes alternate with areas of maximal bending internodes, are clearly developed in forms with stoutly developed limbs (Russell and Bels 2001). However, this pattern is speed related, and the standing wave of lateral bending at low speeds is replaced by a traveling wave of bending as velocity increases. The travelling wave patterns, where points of maximal bending pass down opposite sides of the body alternately from anterior to posterior, are most clearly developed in limbless terrestrial forms (Gans 1975). Highly arboreal lizards limit lateral spine bending during locomotion arguably to increase stability on thin supports (Fischer et al. 2010).

Locomotion in snakes, and other limbless species, essentially use these same kinematic patterns of lateral body undulations but modify the basic motor pattern (Jayne 1988a). As with lizards, lateral undulation in snakes involve waves of lateral bending that are propagated via large dorsal

muscles are activated sequentially along the body from head to tail. As the snake’s body encounters structures along its path, it exerts force against it and deforms locally around it. As the snake pushes against multiple points of contact simultaneously, the lateral force vectors cancel each other, leaving a resultant vector that propels the snake forward. Rapid sensorimotor feedback allows for postural adjustment around each object that gives the snake even finer control over the direction of force exertion. When startled, or moving across smooth surfaces, it is often the case that the snake’s body slips across the substrate. To generate forward propulsion, irregular bends of the body and tail press vertically on the surface at different points allowing the animal to push down with enough force to move the center of mass (Gans 1975; Jayne 1986).

Beyond serpentine undulation, snakes have come up with other locomotor modalities to traverse their environments (Jayne 1986). Most similar is sidewinding, which is used when the substrate fails to provide a rigid frictional base (e.g., sandy soils). In sidewinding, only two parts of the body are in contact with the ground simultaneously. With the head and tail firmly anchoring the snake, it throws its body forward in a loop. When that portion lands, the head is thrust forward, followed quickly by the tail. This pattern is repeated to generate forward motion. Muscle activity during sidewinding is like that in lateral undulation except that some muscles are also active bilaterally in the regions of trunk lifting (Jayne 1988b; Secor et al. 1992). Concertina locomotion involves positioning the body into a series of bends and then straightening out the anterior portion of the body while anchoring the posterior half. As the anterior portion gains solid traction with the substrate, the posterior portion of the snake is then pulled forward. The repeated pulling and pushing of static body portions allow snakes to move through narrow passages and climb (Dial et al. 1987; Jayne 1988b; Jayne and Davis 1991). Finally, rectilinear locomotion involves the ventral scales being lifted slightly from the ground and pulled forward, and then pulled downward and backward. Such motion, occurring simultaneously at several points along the body, allows the snake to move forward in a linear path without lateral

undulation of the body. Rectilinear locomotion locomotor mode is observed most often in large-bodied snakes (Lissmann 1950; Marvi et al. 2013).

## Influence of Squamate Locomotion on Bio-inspired Robotics

Perhaps because lizards and snakes can accomplish an impressive range of locomotor behaviors driven largely by neuromuscular modifications rather than anatomical, *squamate locomotion* has served as a basic design for numerous bio-inspired robotics (Liljebäck et al. 2012; Ma 2001; Menon et al. 2004; Fig. 2). This chapter will discuss two examples. The sticky-bot is a gecko-inspired robot that implements the directional adhesive nature of a gecko's feet to climb walls. Geckos climb walls in an interesting fashion that are not merely predicated on chemical adhesion, like that of tape, but a phenomenon that is known as directional adhesion. This comes about in nature as a gecko's feet are covered with what are called setae. Setae are tiny hairs that are about one-twentieth the width of a human hair. The setae themselves branch into hundreds of even smaller hairs called spatulae. These hairs cling to surfaces through many molecular interactions called van der Waals forces. These forces summed up over all the tiny hairs provide enough force to support the gecko's weight while still allowing for the gecko to detach its feet easily from the surface and sustain its locomotion (Menon et al. 2004).

The challenge of designing these sticky-bots comes in designing this directional adhesive functionality into the feet allowing the robot to achieve this mode of vertical locomotion. Stanford University has developed its sticky bot that uses synthetic setae to replicate this directional adhesion which allows geckos to climb surfaces. Although this synthetic material does not replicate the same adhesive action as the feet of a gecko, it has worked quite well. This material is a rubber-like substance with microscopic polymer hairs that are very similar to the hairs on the feet of a gecko. These polymer stalks are 30 micrometers wide, angled, and have oblique tops, allowing for them

to have directional adhesion. Stanford also designed their sticky-bot with the intricate movements that geckoes make in their wall-climbing process and their curly toes into account in their design. This robot is quite successful at vertical movement but can only climb very smooth surfaces like glass. A sticky-bot developed by Carnegie Mellon University is able to climb rough surfaces such as painted walls and ceilings. They use a micromolding technique to make polymer fibers 28–57 micrometers wide, which they then dip into a liquid polymer to make tiny spatula-like tips. This increasing precision in design as compared to the actual gecko feet and ever-decreasing size of the polymer fibers that come from research and development are what make the adhesive forces stronger and more like those experienced by an actual gecko (Menon et al. 2004).

Snake-inspired robots are built by labs all over the world for the purpose of maneuvering around unpredictable obstacles in unstructured environments. Such environments range in size from as small and intricate as those within the human body, for which very small snake-bots are used in the medical industry, to the vast ocean floor, for which very large snake-bots are used. The engineering design tasks and considerations obviously vary greatly in these different environments. Generally, the cross-sectional diameter of all snake-bots is much smaller in size as compared to the entire length of the snake. This allows snakes, and snake-inspired robots, to maneuver through tight spaces. Paired with these anatomical dimensions, snake-bots use the periodic lateral undulation patterns described above. The fundamental method of design is to put together a chain of independent links with actuated joints that are moved by servo motors or similar devices which often comprise the links. This interconnection allows the individual links to move as dictated by the code that is written to control the actuating device. This allows the robot to change its shape to this periodic laterally undulating sinusoid. The simplicity of this design also allows snake-bots to achieve other necessary functions like wrapping around obstacles or grasping objects. Additionally, the chain configuration of links which are themselves modules is convenient because if one link in the

chain doesn't work the rest of the chain will still move as desired (Liljebäck et al. 2012; Ma 2001).

## Conclusion

In this chapter, we have provided only an overview of the truly impressive range of locomotor behaviors and specializations that have made the squamates so successful at survival even when they are introduced into new environments. We have seen how these types of movements are executed by the limbed and limbless members of Squamata and the many different types of gait transitions and sequences which have been observed in these lizards. This incredible range of locomotor behaviors, which can be utilized in all different kinds of environments, has also made them a subject of interest to engineers who design robots that need to play vital search and recovery roles in all kinds of environments. These environments can vary from environments as small and intricate as in the inside of the human body to those as large and unpredictable as the ocean floor. With such versatility and diversity of movements, it is clear that channeling such movements where applicable in the modern world is of great value to the scientific and engineering community.

## Cross-References

- [Adaptation](#)
- [Arboreality](#)
- [Caudata Locomotion](#)
- [Crocodilia Locomotion](#)
- [Evolution](#)
- [Quadrumanous](#)
- [Zoology](#)

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## Squamate Morphology

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## Introduction

Squamates are grouped within the paraphyletic “Reptilia,” with Testudines (turtles), Crocodylia (crocodiles, alligators, and gavials), and Rhynchocephalia (tuataras). Rhynchocephalia is the closest related to the Squamata, being its sister-group (clade Lepidosauria) and sharing many characters, as the skin covered by scales/plates that are partially impermeable and changed periodically, and a transversal cloacal slit. Squamata is the largest and most diversified clade of extant reptiles, comprising about 95% of its current diversity, with around 6500 lizard species, 3700 snake species, and 190 amphisbaenian species (Uetz and Hosek 2018).

It is not hard to recognize a squamate and morphologically distinguish it from other reptiles. The basic corporeal plan of a lizard, with an elevated head, short neck, four limbs, and long tail, distinguish them from most other reptiles (McDiarmid 2012). The differences between

Squamata and Rhynchocephalia are subtler – the main difference regards the presence of an ancestral skull in tuataras, with complete temporal bars defining the upper and lower temporal openings. Lizards lost the lower temporal bar, while snakes lost both (Kardong 2014). Many lizards and amphisbaenians, as well as all snakes, evolved the apodal elongated body, which is also distinct from other reptiles. Some important morphological features among snakes are the absence of eyelids and external ear, numerous vertebrae with modification on its connections, many paired internal organs elongated and some modified or lost (McDiarmid 2012). Moreover, all squamates have paired copulatory organs defined as hemipenis.

## External Morphology

Squamates are extremely diverse and can be quite specialized, not only with respect to their habitat or locomotion type, but also their morphology (Klein and Gorb 2014). Both snakes and amphisbaenians are legless elongated reptiles, even though a few snake species (blindsnakes and a few boas) exhibit rudimentary pelvic girdles that project externally as spurs, and a few amphisbaenians (*Bipes* spp.) exhibit reduced forelimbs. Additionally, there are different degrees of reduction in the number of limb elements to complete limblessness. The tail tends to be long and slender, but some snakes and lizards might exhibit bulbous or laterally expanded, or dorsoventrally or laterally compressed tails (Zug et al. 2001; Lillywhite 2014).

Several external morphological features associated to their sensory system include a parietal eye on the top of the head in a few lizards, distinct by the presence of a modified head scale, which is important for their photosensitivity. Additionally, a few snakes exhibit sense organs that respond and detect infrared radiation, very useful at night when visible light is usually unavailable. Such receptors are present as modified lip scales (= labial pits) in boas and as a facial pit (= loreal pits), located between the eye and the nostril, in pitvipers. Additionally, all snakes, amphisbaenians, and several

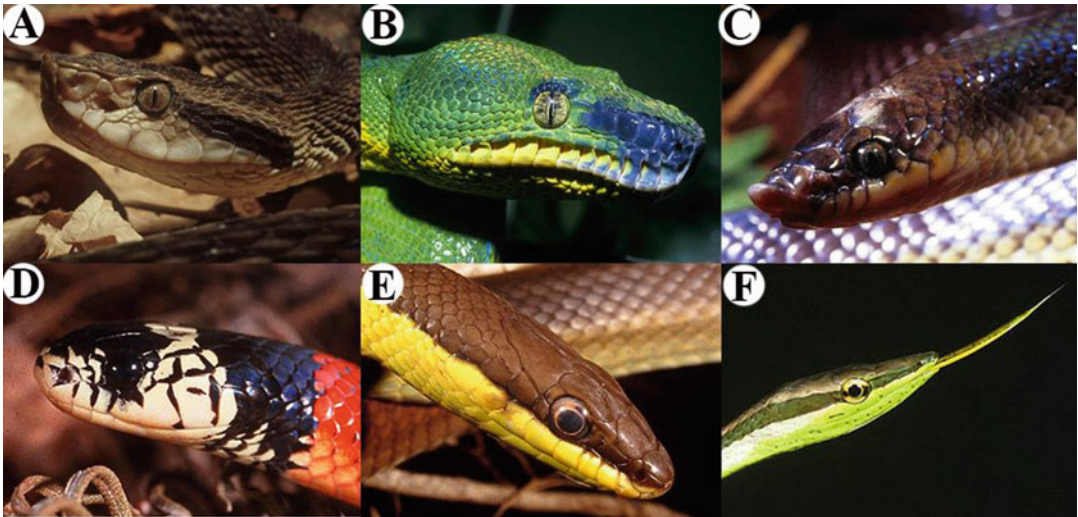
lizards present biphid tongues, which are extended to sweep air in front of them. The tongue collects airborne particles and is posteriorly retracts to perceive chemical signals, transferred to the vomeronasal organ located on the roof of the mouth. Tongues may also serve for prey capture, as in some chamaeleonids lizards (Kardong 2014).

The eyes of most squamates are large and conspicuous, especially in terrestrial and arboreal species. However, several fossorial species might present extremely reduced/degenerate eyes that can lie under the scales. Additionally, eyes of lizards exhibit bony plates (scleral ossicles) embedded in the sclera and surrounding the cornea (Zug et al. 2001). Pupils may vary from round to elliptical and are usually oriented vertically, even though it can be horizontally oriented in a few species. Extreme specializations in the squamate eye include the protrude lateral eyes of chameleons, with distinct anatomy of nodal and center points, in which the amplitude of movement is very large and the eyes move and focus independently (Zug et al. 2001; Lillywhite 2014).

Amphisbaenians exhibit the most conserved external morphology amongst Squamates, being characterized by their elongated bodies that are usually less than 150 mm long, with an extreme reduction (*Bipes* spp.) or complete loss of the limbs, and rudimentary/reduced eyes. Most of their distinctive features regard the dramatic modification of the head shapes, which is functionally correlated with specific tunneling behaviors. Heads may vary from (1) “shovel-headed,” with snouts dorsoventrally flattened with a strong craniofacial angle; (2) “keel-headed” forms; (3) “spade-headed” forms; or (4) “round-headed” forms – representing the most common form amongst amphisbaenians (Kearney 2003).

Within snakes, most small species belong to Scolecophidia, a group of fossorial snakes with reduced/absent eyes, rudimentary pelvic girdles that might be present as spurs, and a row of ventral scales that does not differ from those located dorsally in the trunk. Such snakes exhibit a relatively conserved external morphology, with variation occurring mostly in their head shape and scales pattern, dorsum colors and patterns, and presence/absence of a tail spine. The





**Squamate Morphology, Fig. 1** Examples of diversity in Alethinophidia – (a) *Bothrops neuwiedii*, (b) *Corallus caninus*, (c) *Phimophis guerini*, (d) *Erythrolamprus*

*aesculapii*, (e) *Philodryas mato Grossoensis*, (f) *Philodryas argentea*. (Photos: Roberto Murta)

Alethinophidians comprise all the other snakes, with an extreme diversity in sizes, colors, scale patterns, and shape (Fig. 1).

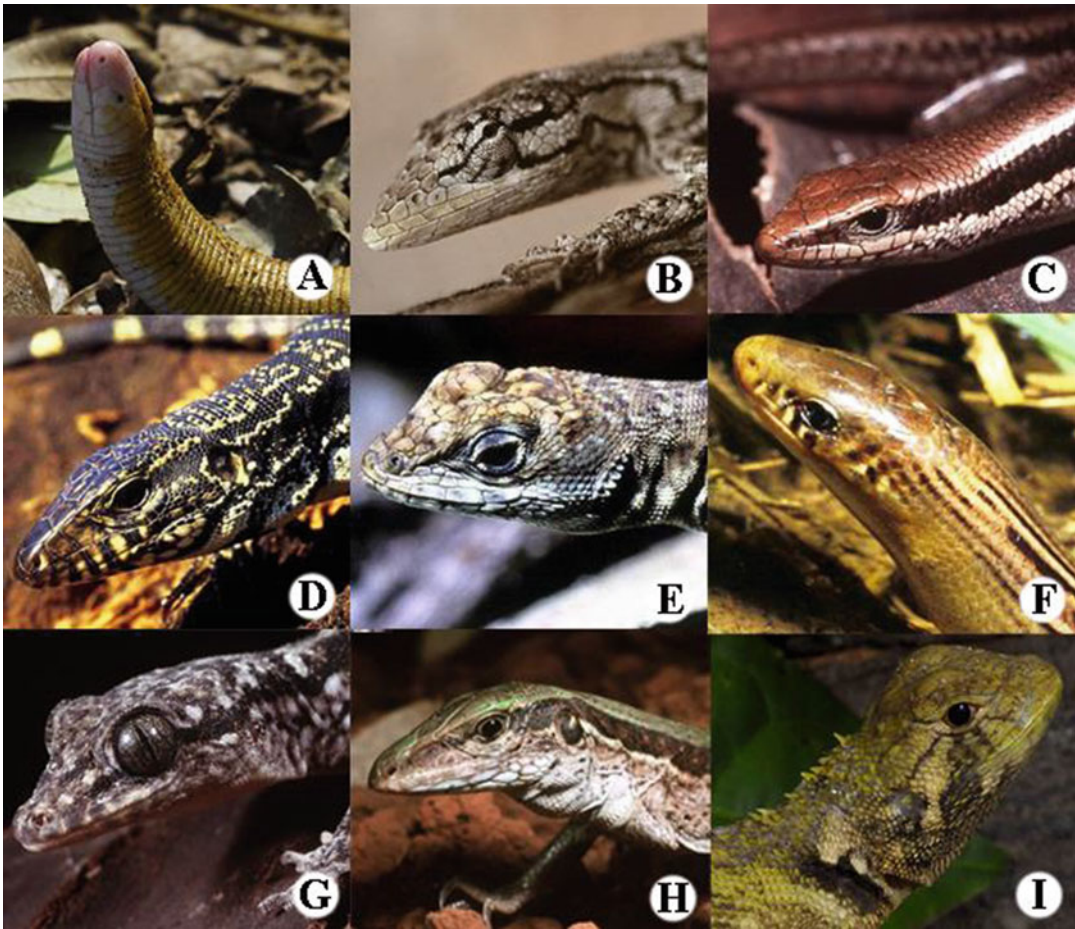
Among squamates, lizards exhibit the highest level of morphological diversity (Fig. 2), varying from the ancestral type to forms that are completely legless. Many arboreal species are laterally compressed and may exhibit head and dorsum projections that provide an effective method for obscuring their surroundings. Several lizards are long with long tails, while others are short and robust with short tails. Some have strongly prehensile tails, used as fifth leg in climbing, others use their tails as whips to defend themselves, and many have laterally compressed tails used in swimming. Among lizards with limbs, there are species with four long/short limbs, as well as forms with only two (posterior) limbs. A few lizards have webbed feet and/or skin flaps that can be expanded and used as partial parachutes when jumping from arboreal perches. Some have adhesive pads on their toes, allowing them to climb vertical smooth surfaces; a few even have adhesive pads on the top of the tail, providing a fifth point of secure contact. Heads of lizards vary from flat and wide to long and thin. A wide variety of ornamentation exists as well, some for crypsis (camouflage) and some having to

do with social interactions. All lizards (except for a few gekkonids) have claws, which aid on locomotion on vertical surfaces (Pianka and Vitt 2003).

## Integument

Squamates in general exhibit a water-conserving integument (Withers and O'Shea 1993) with the skin modified into scales, which might be named as plates, tubercles, lamellae, etc., depending on the taxonomic group and location of the scales (Zug et al. 2001). Scales in various squamates have evolved in different sizes, geometries and gross structure, also varying regionally in the body, what is extremely relevant for systematics (Lillywhite 2014). The scales of a few lizards might be underlain by bony plates, called osteoderms. The integument of Amphisbaenians is characteristic in representing a disconnection to the trunk, enhancing its underground locomotion (Pough et al. 2018).

The epidermis of Squamata is composed by several keratin layers formed from cells of a basal layer, stratum germinativum, that is renewed together during shedding process (ecdysis). The most external cell layer, Oberhäutchen, presents



**Squamate Morphology, Fig. 2** Examples of diversity in lizards – (a) *Amphisbaena alba*, (b) *Polychrus acutirostris*, (c) *Notomabuya frenata*, (d) *Salvator*

*merianae*, (e) *Tropidurus* sp., (f) *Ophiodes* sp., (g) *Hemidactylus mabouia*, (h) *Ameiva ameiva*, (i) *Plica umbra*. (Photos: Roberto Murta)

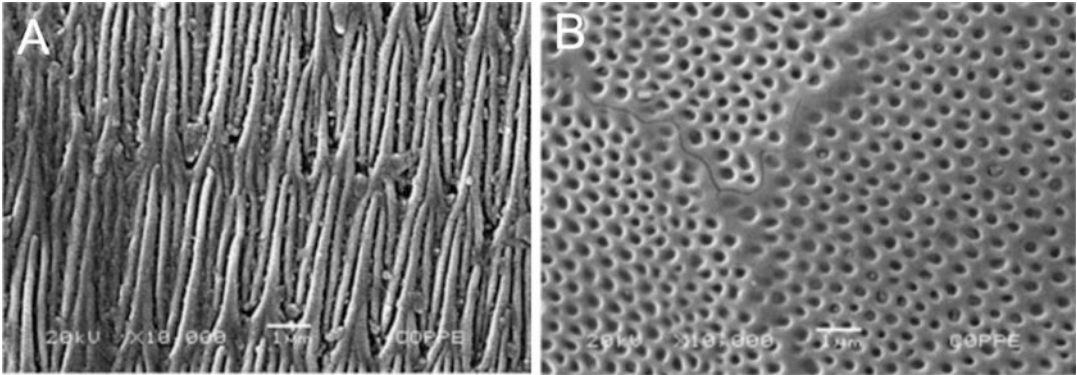
three-dimensional microstructures on its surface (=microornamentation; Fig. 3), which are studied with Scanning Electron Microscopy. Since the first works about lizards and snakes microdermatoglyphics, these morphological patterns have been constantly suggested as an important taxonomic and systematic tools, and also to provide novel and interesting data on their biology.

## Internal Morphology

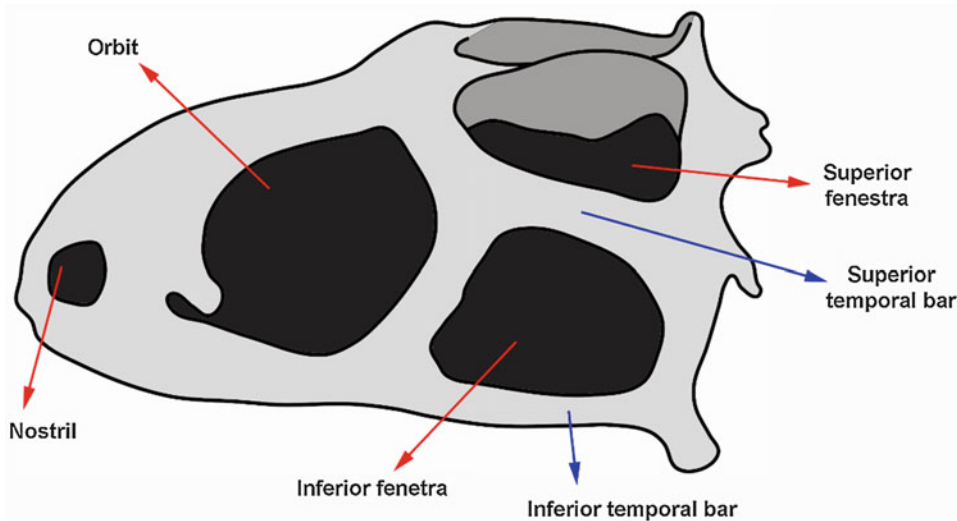
### Osteology

“Reptiles” exhibit diapsid skulls (Fig. 4), with two pairs of temporal fenestrae that are disconnected

by the superior temporal bar (formed by the squamosal and postorbital bones) and the inferior temporal bar (formed by jugal and quadradojugal bones). Among Lepidosauria, only the tuataras retained both fenestrae – squamates present exclusively the superior fenestra (lizards) or none (snakes) (Zug et al. 2001). The loss of the arch and fenestrae is associated to the increase of the flexibility (skull kinesis). The kinesis is derived from the presence of joints between many sections of the skull. A joint may occur in the posterior part of the skull (meta-kinetic joint), and between the dermic skull and braincase, at the parietal/supra-occipital suture (being the oldest kinetic articulation and, nowadays, occurring only in tuataras).



**Squamate Morphology, Fig. 3** Microornamentation of the dorsomedial scale of snakes on a 10 k zoom exhibiting the lamellate (a) and dotted (b) patterns. (Photos: Luciana O. Ramos)



**Squamate Morphology, Fig. 4** Scheme of a Dipasid skull based on tuatara

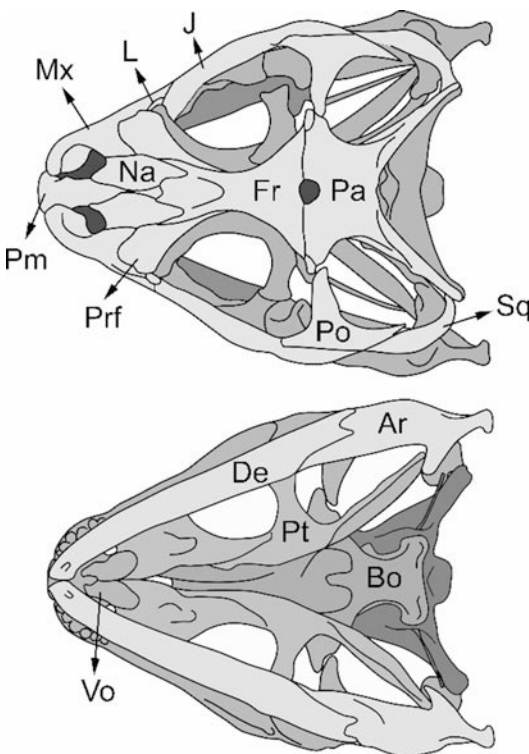
Two other joints evolved in braincase dermic bones – the dorsal meso-kinetic joint, present between frontals and parietal in many lizards and, in many snakes, a pro-kinetic joint, in the contact between nasals and prefrontals or frontals. The most impressive skull kinesis of Squamata is exclusive of snakes – streptostyly or quadrates rotation. Each quadrate is loosely connected to the dermatocranium and has the ventral extremity free. These lost ligaments allow the quadrate to rotate and swing back and forth and to the inside and outside (Zug et al. 2001).

The basic form of the squamate skull has the quadrate suspension with reduced dorsal and ventral processes of squamosal; loss of quadratojugal; fusion of the parietals; reduction of palatal dentition and anterior plate of the pterygoid; enclosure of the Vidian canal; shortening of the maxilla/dentary; among others (Evans 2008). Additionally, the snake skull seems to be pedomorphic in relation to lizards as claimed by several ontogenetic and anatomical studies. Considering the limbs, 15 synapomorphies are known for Squamata, and some of it are: elongate, gracile



limbs; specialized joints (ulna-ulnare and radius-radiale; first metacarpal-wrist; locked tibio-atragalar; ankle); intermedium reduced or absent; and second distal tarsal absent (Russel and Bauer 2008).

The “lizards” are divided into two major clades: Iguania and Scleroglossa which according to several studies includes the snake lineages. Iguanians show some primitive skull features (Fig. 5), as the retention of complete postorbital and upper temporal bars, retention of large upper temporal fenestrae and the absence of a hypokinetic joint. Still, their long period of independent evolution provided them with some specializations, such as frontals fused in the embryo, postfrontal reduced/absent, splenial absent/reduced, and teeth frequently tricuspid. Some Scleroglossa characters include prominent anterior descending processes of the frontals,



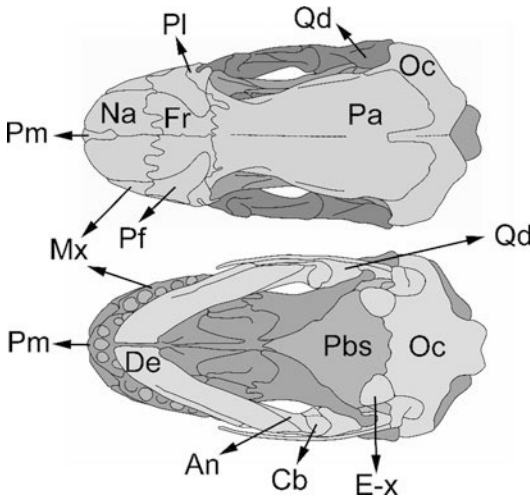
**Squamate Morphology, Fig. 5** Scheme of the dorsal/ventral views of a lizard skull (based on *Plica plica*). *Pm* = premaxilla, *Na* = nasal, *Mx* = maxilla, *Prf* = prefrontal, *L* = lacrimal, *J* = jugal, *Fr* = frontal, *Pa* = parietal, *Po* = postorbital, *Sq* = squamosal, *Vo* = vomer, *Pt* = pterygoid, *De* = dentary, *Ar* = articular, *Bo* = basioccipital

loss of dorsal process of squamosal, vomers reduced in length, and septomaxillae dorsally expanded and convex (Evans 2008).

The morphological diversity of the lizards' axial skeleton reflects the wide extent of their morphological specializations, as previously shown. The number of presacral vertebrae varies from 16 in some Chamaleonidae to as much as 116 in some Dibamidae. The Sauria (lizards) shows two main morphological types of vertebrae, those with an amphicoelous centrum and those with a procoelous centrum. Sauria (=lizards) ribs are usually called holocephalous (one of the two articulations between the rib and the vertebra has disappeared), but the first cervical ribs of *Varanus* may still be dichiocephalous. On the following vertebrae, and generally in the cervical and anterior trunk of lizards, the two articulations fuse to form a single synapophysis, but the latter remains oblong, keeping a vestige of dichiocephaly. In the posterior part of the trunk, the single articular facet becomes hemispherical and the ribs clearly holocephalous. The vertebral column is divided into cervical, trunk, sacral/cloacal, and caudal regions (Hoffstetter and Gasc 1969).

The amphisbaenians are highly specialized lizards that have a completely different morphology and effect penetration of the substratum by movements of their head. Compared to other lizards, the amphisbaenians skull (Fig. 6) has the following peculiarities: absence of palatal and suborbital fenestrae; lateral parietal downgrowths enclosing the braincase; fusion of bones in the occipital segment and mandible; presence of secondary palate; absence of major mobile articulations; presence of a tabulosphenoid and of a paired elements-X (without clear homology to any other lizard bone), among others. Most of the bones overlap to avoid slippage when the large pressures associated with excavation are applied to the head. Their skull can be divided into five morpho-functional units: an occipital segment, intermediate segment, snout, palatal series, and mandibulae (Gans and Montero 2008).

In amphisbaenians, the number of precloacal vertebrae varies from 64 to 145. Each vertebra is generally depressed with transversely widened



**Squamate Morphology, Fig. 6** Scheme of the dorsal/ventral views of an amphisbaenian skull (based on *Amphisbaena fuliginosa*). Pm = premaxilla, Na = nasal, Mx = maxilla, Fr = frontal, Pa = parietal, Pf = prefrontal, Pl = palatine, Qd = quadrate, Oc = occipital complex, De = dentary, An = angular, Cb = compound bone, E-x = element-X, Pbs = parabasisphenoid

condyle, and flat ventral face of the centrum with parallel lateral borders. Neural spines are lacking in the trunk region, and prezygapophysial processes are more or less clearly present. The division of the column into regions is difficult. There is generally a vestigial pectoral girdle with no connections with the ribs, and a pelvic girdle, also without connection with vertebral column – thus, there is no differentiated sacrum. A series of vertebrae that bear forked ribs may be identified as cloacals. The caudal region is always short, comprising fewer than 30 vertebrae (Hoffstetter and Gasc 1969). Among amphisbaenians, only one family/genus presents limbs (Bipedidae, *Bipes*), and it is restricted to the forelimbs.

In snakes' skull, the frontals and parietal have expanded ventrally around the sides of the skull, forming the major part of the braincase wall. Its enlargement resulted in the loss of many other dermic bones. Skull characters are so important to snakes that the taxon is diagnosed based in some features, as the absence of the lacrimal, squamosal, and epipterygoid bones (Estes et al. 1988) and the absence of bony mandibular

symphysis and contact between frontal and maxilla bones (Conrad 2008) (Fig. 7).

“Scoleophidians” snakes present several exclusive skull features, especially in braincase and snout. The snout forms a bulbous terminus to the end of the skull and is attached to the braincase by peripheral sutures rather than by a central strut (Cundall and Irish 2008). The skull of such species has been interpreted as an adaptation to its burrowing and feeding habits (scoleophidians feed primarily on small arthropods). Such snakes have a shortened lower jaw and suspensorial elements that are angled anteroventrally, rather than vertically or posteroventrally, palatines and pterygoid without teeth, supratemporal lost, mandible shorter than combine length of braincase and snout, among other features (Fig. 8) (Cundall and Irish 2008). Alethinophidians, unlike scoleophidians, present medial pillars on the frontal bones, a laterosphenoid bone in the middle of the trigeminal foramen, and a toothed anterior process on the palatine. None of these features is uniformly present among the group though. All the species present a lower jaw as long as or longer than the skull and a snout both prokinetic and rhinokinetic. The most conspicuous consequence of such differences among Scoleophidians and Alethinophidians is the enlargement of the gape size in the latter (Cundall and Irish 2008). According to the dentition, such snakes are divided into four categories: aglyphous – does not possess specialized teeth to venom injection; opisthoglyphous – a pair of grooved teeth (fangs) located in the bottom of the maxilla; proteroglyphous – a pair of grooved teeth (fangs), located in the anterior portion of the maxilla; and solenoglyphous – a pair of large and movable teeth (fangs), with a canal by which the venom is inoculated, located in the anterior portion of maxilla.

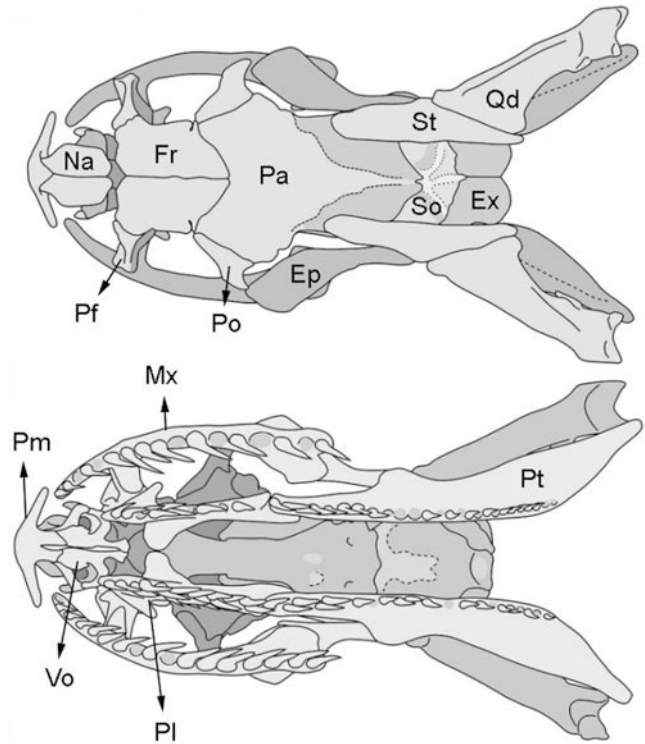
The absence of pectoral girdle hampers the definition of the boundary between the cervical and trunk regions. As in amphisbaenians, the site of the cloaca and associated organs is reflected in the vertebral morphology. The vertebral number is always high, varying from 160 to more than 400 (precloacal ranging from 120 to over 320). There are no fundamental differences between the vertebral morphology of snakes and the other



**Squamate Morphology,**

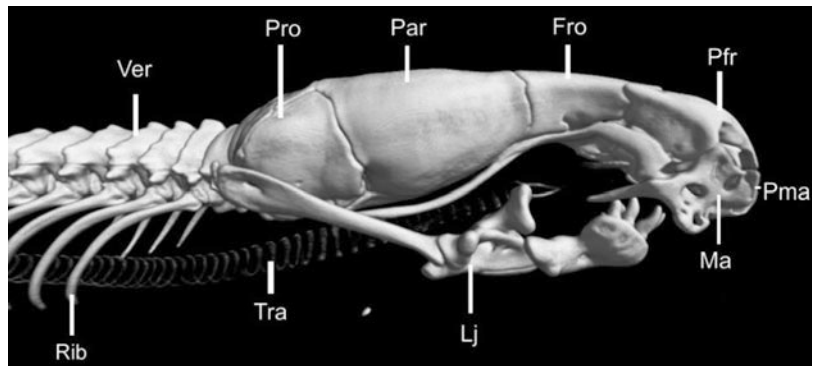
**Fig. 7** Scheme of the dorsal/ventral views of a snake skull (based on *Farancia abacura*).

*Na* = nasal, *Fr* = frontal,  
*Pa* = parietal,  
*Pf* = prefrontal,  
*Po* = postorbital,  
*Ep* = ectopterygoid,  
*So* = supraoccipital,  
*Ex* = exoccipital,  
*St* = supratemporal,  
*Qd* = quadrate,  
*Pm* = premaxilla,  
*Vo* = vomer, *Pl* = palatine,  
*Mx* = maxilla,  
*Pt* = pterygoid

**Squamate Morphology,**

**Fig. 8** Skull and lower jaw of *Trilepida salgueiroi* in lateral view (Scoleophidia). *Ver*

*Vertebrae*, *Pro* Prootics, *Par* Parietal, *Fro* Frontal, *Pfr* prefrontal, *Pma* Premaxillae, *Ma* Maxillae, *Lj* Lower Jaw, *Tr* Trachea



squamates, but there are a certain number of typically ophidian characters. The centrum bears a large anterior cotyle (glenoid cavity) faced ventrally, and a dorsally turned posterior condyle, which widely overlaps the transverse section of the centrum. The ventral surface of the centrum is limited on both sides by a more or less clear crest (which are completely lacking in some families). The hypapophyses arise from the posterior part of the centrum in the mid-ventral line. In the middle and posterior parts of

the trunk, the hypapophyses may be reduced to a simple haemal keel, disappearing completely in some burrowing families. In the caudal region, they are replaced, when present, by paired haemapophyses which fuse to the centrum. The neural arch consists of a roof and walls. The neural crest is often trilobate in section. The ribs are completely ossified and generally robust with a double articular facet – each part articulated with one of the two areas of the synapophyses (Hoffstetter and Gasc 1969).

## Myology

Squamates, as well as other amniotes, exhibit two major sets of muscles: the cranial (jaw and pharyngeal musculature and extrinsic eye muscles) and postcranial muscles (appendicular and axial) (Kardong 2014). The loss of the temporal arches in the skull, as well as the great differences in the degree of cranial kineticism, is directly reflected in the wide variation of the squamate cranial muscles. Differences in the position and configuration of the upper temporal arch and the relative width of the dorsal temporal fossa might have caused radical changes in the arrangement of the external and internal adductor muscles. Several fossorial squamates exhibit vestigial or absent extrinsic eye muscles that are possibly directly associated to the reduced eyes (Haas 1973). The muscles of the head of snakes differ strikingly and in many ways from those of lizards and are somehow closely and similar to amphisbaenians. However, the latter has developed an extremely strong biting apparatus, while in the microphagous snakes, cranial kinesis and horizontal movements of the jaws are more important. The process to swallow preys in ophidians is aided by the complex *constrictor internus dorsalis* group of muscles, which effect the protraction and retraction of the bony palate, and the complicated and diversified concomitant movement of the maxillae and bones of the snout (Haas 1973).

In Squamate (as well as in other amniotes), the horizontal septum that splits the epaxial and hipaxial muscles is lost or indistinct, although the supply by the dorsal and ventral rami of the spinal nerve still aids on the identification of such muscles. In lizards (except legless ones), even though lateral undulations of the vertebral column contribute to locomotion, limbs become more important in providing propulsive forces. Therefore, the epaxial muscles associated to vertebral column are reduced, and the musculature associated to the appendices are much more conspicuous. In snakes, amphisbaenians, and limbless lizards, the axial muscles are very important on providing propulsive forces and, therefore, are prominently developed. The hypaxial muscles form much of the body wall and are associated to breathing as it is attached to the rib cage. Most

epaxial and hipaxial muscles in squamates split into several layers forming many differentiate muscles that span several segments (Kardong 2014).

## Visceral Morphology

Lungs represent the main respiratory surface of squamates, although some degree of cutaneous respiration might be found in several species (Zug et al. 2001; Kardong 2014). The lungs of snakes and most lizards typically include a single central air chamber into which faveoli open (Kardong 2014). Thoracic aspiration is used to ventilate the lungs, and, in lizards, intercostal muscles between the ribs contract and force the ribs forward and outward (Zug et al. 2001). In several snakes, the faveoli may be reduced in the posterior part of the lung, leaving it as a nonexchange region, traditionally named as air sacs or saccular lungs. In monitor lizards, the single central air chamber is subdivided into numerous internal chambers that receive air from the trachea.

The elongated body plan leads to several rearrangements in the organ topography in snakes, amphisbaenids, and elongated-legless lizards. Among the snake organs, the respiratory system exhibits the highest level of specialization of squamates. In primitive snakes, the lungs are paired, but in many advanced snakes the left lung is reduced and often entirely lost (Kardong 2014). A few snakes (scolecophidians and some advanced snakes) exhibit a tracheal lung, which is characterized by the presence of a vascular portion of the lung located anterior to the heart (Wallach 1998).

Squamates show a typical double circulation, which includes a three chambered heart, with the retention of the aortic arches III, IV, and VI. The ventral aorta is subdivided forming the left and right aortic arches and the pulmonary trunk. Such configuration in the aortic arches provides one pulmonary circuit and two systemic circuits, each of which arising independently from the heart. Although the ventricle is given as a single and undivided cavity, three interconnected compartments are present and separated from each other by a muscular ridge. Thus, a few authors might assign the squamate heart as

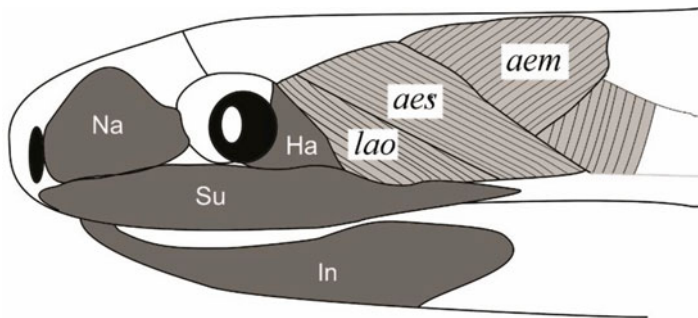
five-chambered, composed of two atria and three compartments of the ventricle, or six chambers if the sinus venosus is counted (Kardong 2014).

Two types of tooth implantation are present in squamates: acrodonty (a few lizards) and pleurodonty (lizards, snakes and amphisbaenids). Additional features of the squamates digestive system include a buccal cavity lacking a secondary palate and several oral glands that support food digestion. In both snakes and lizards, such head glands have evolved independently several times to venom glands that support not only food ingestion, but prey capture. The alimentary canal is very diverse in size and regionalization, mostly depending on type of food ingested. However, its general pattern consists on a short esophagus, with gradual transition to stomach, which is followed by the small and large intestines that finally open in the cloaca. The cloaca is partially differentiated into the coprodeum, a chamber into which the large intestine empties, and the urodeum, into which the urogenital system empties. The alimentary tract of herbivores, particularly the large intestine, is consistently longer and more voluminous than that of similar sized carnivores (O'Grady et al. 2005). In some herbivorous lizards, a cecum is present between the small and large intestines (Kardong 2014). The body elongation on snakes resulted on an elongate digestive system, with inconspicuous folds in the small intestine.

Squamates exhibit a series of oral glands: supralabial and infralabial glands are present

along the upper and lower lips; lingual and sublingual glands; premaxillary and nasal glands, in association with the snout; and palatine gland, along the roof of the mouth (Fig. 9). These glands release mucus to lubricate the prey during intraoral and esophageal transport. The lacrimal and Harderian glands release secretions that bathe the eye and vomeronasal organ. Duvernoy's gland, situated along the posterior upper lip, is found in many nonvenomous snakes and releases its serous secretion via a duct adjacent to the posterior maxillary teeth. In venomous snakes, the venom gland, homologue of Duvernoy's gland, secretes a cocktail of different chemicals with various functions – some toxic, some digestive (Kardong 2014). While venom and Duvernoy's glands are always located in the upper jaw, transferring the venom through maxillary teeth, lizards venom glands are usually located in the lower jaw and transferred through both maxillary and mandibular teeth (Fry et al. 2006).

All squamates bear metanephric kidneys, with primary uricotelism as their nitrogen waste. However, nephron structure can be quite different from one taxonomic group to the next and may appear at first to have no obvious correlation with the phylogenetic position, but most likely to their environmental demand. The kidney typically lacks the distinct color and functional distinction of the mammalian cortex and medulla. The kidneys are paired, lobular (weakly so in some lizards), elliptical, pink or red structures that are



**Squamate Morphology, Fig. 9** Illustration of the head glands of *Atractus potschi* in lateral view. Na = Nasal glands, Ha = Harderian gland, Su = Supralabial gland, In = Infralabial gland, lao = *Musculus levator anguli oris*,

aes = *Musculus adductor mandibulae externus superficialis*, aem = *Musculus adductor mandibulae externus medialis*

located retroperitoneally (extracoelomically). Kidneys are posterior to the level of the ilial crest in most lizards and usually lack distinct lobes. Snake kidneys are distinctly lobed and elongated, found in the posterior third of the bodies, with the right kidney occurring anterior (approximately 69–77% of snout-vent length [SVL]) to the left kidney (~74–82% of SVL). Snakes lack urinary bladders; nitrogenous wastes are refluxed from the cloaca into the rectum, where uric acid is stored and further ion reclamation may occur. Several species of lizard lack urinary bladders or develop just a vestigial bladder, including some varanids, agamids and a few gekkonids (Wyneken 2013).

The gonads (ovaries and testes) are located dorsally in the body cavity, posterior to the lungs (except in elongated individuals, where lungs might overcome the right ovary), and ventral to the kidneys and peritoneal wall. The female reproductive tract is composed of paired ovaries, and oviducts (that might be missing in a few snake species) supported by mesenteries. In lizards, at least the caudal part of each ovary is attached to the peritoneum along the ventromedial surface of each kidney. In some lizards with highly modified lungs, such as chameleons, the ovary may extend cranial between the two lungs. In snakes the ovaries tend to be well posterior to the lung(s) and saccular lung and anterior to the kidneys, attached

to the dorsal body wall by the mesovarium, while the testes can be round or fusiform in shape (Mader and Wyneken 2002).

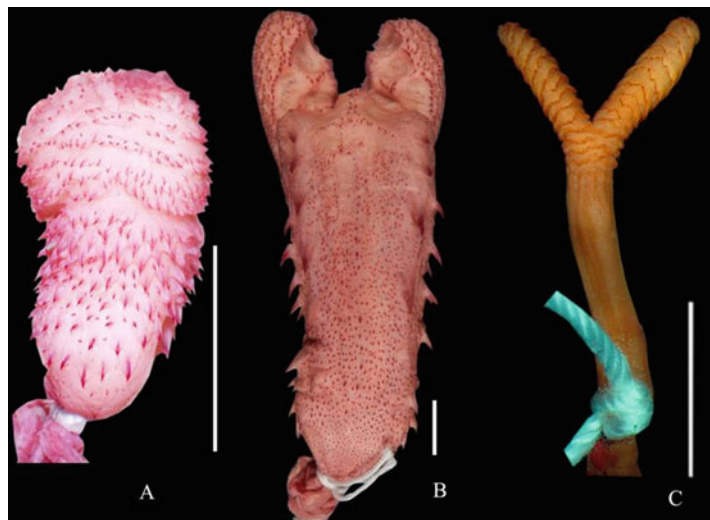
## Hemipenis

Unlike other reptiles, Squamata have a pair of hemipenis, an intromittent copulatory organ that originates at the junction of the cloacal vent and the base of the tail. Although squamates exhibit two hemipenis, during copulation, only one of them is inserted in the cloaca of the female (Kardong 2014). Each hemipenis is usually grooved (*sulcus spermaticus*) to allow sperm transport. A retractor muscle returns each hemipenis to the body, a process called invagination, storing the organ at a pocket located at the base of the tail, posterior to the vent. During erection, muscle action and hemotumescence force each hemipenis through the cloaca, expanding it out through the vent, as a process named evagination (Kardong 2014).

The hemipenial morphology is widely used in squamates taxonomy and systematics. Hemipenis may be uni- or bilobed and can bear many different ornaments, such as large spines, spicules, body calyces, lobular crest or ridge, calycular pockets, capitular groove, and capitular calyces (Zaher 1999) (Fig. 10).

### Squamate Morphology,

**Fig. 10** Assulcate view of the hemipenis of (a) *Atractus paraguayensis*, (b) *Hydrodynastes bicinctus*, and (c) *Elapomorphus quinquelineatus*. (Scale = 5 mm)



## Cross-References

- [Arboreality](#)
- [Dentition](#)
- [Digestive System](#)
- [Evolution](#)
- [Integumental System](#)
- [Monophyletic](#)
- [Morphology](#)
- [Paraphyletic](#)
- [Phenotype](#)
- [Reproductive System](#)
- [Squamate Life History](#)

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## Squamate Sensory Systems

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Squamates (lizards and snakes) are one of the most diverse groups of vertebrates with over 10,000 species currently recognized (Utey et al. 2017). They have a near worldwide distribution and occupy most ecological niches and lifestyles with terrestrial, aquatic, fossorial, and arboreal species. Squamates utilize the typical vertebrate sensory systems to varying degrees, including the visual, chemosensory, auditory, vestibular, and somatosensory systems, and are the only group known to have developed an image-forming infrared system. It is through sensory systems that squamates, and other animals, are able to detect and respond to both their internal and external environments, and as such sensory systems govern all aspects of squamate behavior. In this section, the morphology, function, and behavioral implications of each major squamate sensory system are described, with a focus on how they differ from other vertebrates.

### Visual System

Vision is perhaps the best understood and most studied of the sensory systems, and this reflects its importance to most, but not all, animals. Squamates utilize vision for nearly all aspects of their behavior, albeit to differing degrees. This includes prey localization and capture, predator avoidance, identification of conspecifics and mating, and circadian rhythm. Vision often works in concert with other sensory systems, and in some cases, visual cues alone are insufficient to elicit a behavioral

response, such as with prey capture or mating where chemical cues may also be needed. While most squamates have well-developed visual systems, some highly fossorial groups, such as amphisbaenians and scolecophidian snakes, have highly reduced visual systems and may lack fully developed eyes.

Vision is mediated by the eye, which in squamates resembles the typical vertebrate camera-style eye (Walls 1942). This consists of the cornea, iris, ciliary body, pupil, lens, retina, retinal pigment epithelium, choroid, and sclera. In squamates and some other reptiles, the sclera contains additional bony and cartilaginous elements, the scleral ossicles and cartilage, which form a ring around the cornea. These provide additional support during accommodation, which in most squamates occurs through compression of the lens by the ciliary muscles to make it more spherical. In many squamates, including all snakes and most geckos, the eyelids have fused and become transparent, forming a protective covering over the eye called the spectacle. Squamates possess another additional structure, the conus papillaris, believed to be homologous to the pecten oculi in birds, which provides additional nutrients to the retina. The eyes of snakes, however, differ significantly from those of other squamates and reptiles. The modifications include changes to the shape of the eye and lens to become more spherical and rigid, loss of scleral cartilage and ossicles, loss of ciliary muscles, and development of a new method of accommodation through movement of the lens forward toward the cornea, rather than constriction of the lens. These differences have been argued to be related to either the fossorial or the aquatic origins of snakes, and there is ongoing debate on this topic.

The size and position of the eyes and the shape of the pupil in squamates can vary considerably with the ecologies of different species. The eyes are typically located on the side of the head resulting in little binocular overlap. This is particularly true of most lizards, which have some of the strongest laterality of the eyes, although monitors (Varanidae) are one of the exceptions and have larger binocular overlap. Chameleons are unique in having turreted eyes that can be rotated

independently 180° horizontally and more than 90° vertically (Sandor et al. 2001). When both eyes are pointed forward, such as when fixating on prey, there is a large degree of binocular overlap. Snakes typically have higher degrees of binocular overlap, especially in species that are visual predators. The most extreme example of this is in the tree snake *Ahaetulla* which has a keyhole pupil and a groove on the side of the head that serve to further increase the binocular overlap, but without sacrificing lateral vision (Walls 1942). Most diurnal squamates have round pupils, although the horizontal and keyhole pupils of some arboreal snakes as mentioned above are an exception. Slit pupils are common in nocturnal and crepuscular species and were found to be associated with multifocal lenses that may reduce chromatic aberration caused by relatively large pupils that are necessary to increase sensitivity (Malmstrom and Kroger 2006). It has also been suggested that pupil shape is correlated with foraging mode, with slit pupils found most often in ambush predators that are active both day and night (Banks et al. 2015).

The squamate retina, typical of vertebrates generally, is a thin multilayered neural tissue. It contains the light-sensitive photoreceptors and is also the location of the first step of visual processing before the signal is sent to the higher visual centers of the brain for further processing. The photoreceptors are the cells responsible for the absorption of light and the subsequent visual transduction cascade, which produces the electrical signal that ultimately results in vision. Squamates, like other vertebrates, have two kinds of photoreceptor cells often identified based on their outer segment morphology: rods for vision in dim light and cones for vision in bright light and, in some cases, color vision. For this reason, most vertebrates have duplex retinas containing both rods and cones; squamates however are unique in that many species have simplex retinas that contain only morphological cones or morphological rods. The inferred transitions between rod and cones are termed photoreceptor transmutations (see below).

Visual pigments are molecules contained in the photoreceptor outer segments that initiate the first

step in vision through the absorption of a photon. They are composed of an opsin protein covalently bound to a light-absorbing chromophore (retinal). Different visual pigments absorb light maximally at different wavelengths due to differences in the opsin protein and/or chromophore (A1 vs. A2), and these differences provide the basis for color vision. Adjustment of the wavelength of maximal absorbance ( $\lambda_{\text{max}}$ ) is one of the ways that squamates and other vertebrates can adapt their visual system to different spectral environments. Ancestrally squamates have maintained the full complement of vertebrate visual opsins – a single rod opsin (RH1) and four cone opsins (LWS, RH2, SWS2, SWS1) – and thus have a wide range of spectral sensitivity from the UV to the far red. Some groups, however, have lost opsins, such as snakes, which lost the RH2 and SWS2 opsins, and geckos, which lost the RH1 and SWS2 opsins. Most squamates utilize only the A1 chromophore, but the Carolina anole may be unique among terrestrial vertebrates in utilizing exclusively A2, which results in highly red-shifted visual pigments (Loew et al. 2002).

Some of the most striking aspects of squamate visual systems is the preponderance of simplex retinas and the large amount of variation in the morphology of the photoreceptor cells. Diurnal lizards and diurnal caenophidian snakes typically have morphologically all-cone retinas, while some nocturnal lizards and nocturnal caenophidian snakes can have morphologically all-rod retinas. Other species have photoreceptors with morphologies intermediate between rods and cones. The implied transitions between all-cone and all-rod retinas led Walls (1942) to formulate his photoreceptor transmutation hypothesis. Photoreceptor transmutation is the evolutionary process by which a cone can be converted into a rod or vice versa.

The best example of photoreceptor transmutation occurs in geckos. Most geckos are nocturnal and have retinas that contain only rod-like photoreceptors. Walls (1942) proposed that the all-rod retinas of nocturnal geckos were derived from the all-cone retinas of ancestral diurnal lizards. Furthermore, he hypothesized that extant diurnal geckos reverted to diurnality, and consequently

their all-rod retinas were transmuted back to all-cone retinas. Support for this hypothesis has come from several avenues of research. Röhl (2000) found that nocturnal gecko “rods” were actually cones at all levels of their ultrastructure, having such cone features as open outer segment membranes. Furthermore, the “rods” were found to use only cone opsins and other cone phototransduction machinery, not the phototransduction machinery that is specific to normal rod photoreceptors (Zhang et al. 2006). The rod-like cones of geckos, however, function more similarly to rods (Zhang et al. 2006). Together these studies provide strong support for the hypothesis that gecko “rods” were “transmuted” from diurnal lizard cones. With their transmuted “all-rod” retinas, nocturnal geckos have been found to be able to discriminate colors at low light levels where humans are color blind (Roth and Kelber 2004).

Snakes are the second group of squamates in which photoreceptor transmutation appears to be important. Non-caenophidian snakes have retinas containing only reduced rods (scoleophidians) or simple duplex retinas with single cones and rods (“henophidian”-grade species, such as pythons and boas); however, caenophidian snakes have retinas that are more complex and variable, with multiple photoreceptor transmutation events inferred between taxa with simplex retinas (Walls 1942). Recently, the first molecular evidence for photoreceptor transmutation in snakes was uncovered. The diurnal garter snake, which has a morphologically all-cone retina, expresses RH1 (the rod visual pigment) in a cone-like photoreceptor that is actually evolutionarily derived from a rod, based on its ultrastructure and rod-specific molecular components (Schott et al. 2016). The transmuted cone-like rods may contribute to an increased range of spectral sensitivity and provide the basis for trichromatic color vision under mesopic (when both the rods and cones are typically active) and, potentially even photopic, conditions. The role of all-rod retinas in nocturnal caenophidian snakes has not been studied, but similarly to geckos, these “rods” may contribute to nocturnal color vision.

## Chemosensory Systems

Squamates rely heavily on chemosensory systems to direct a large number of behaviors including prey detection and acquisition, predator avoidance, mating, aggregation, and other conspecific interactions and habitat selection. Squamates have three chemical senses: olfaction, vomeronasal olfaction, and gustation (taste), each of which utilizes distinct organs and has specialized functions. The reliance on, and specific uses of, particular systems varies between different squamate groups. The olfactory system is generally thought to be useful for long-range detection of broad chemical signals, which can then trigger the shorter range, but more discriminatory, vomeronasal system. This proposed functional link between the olfactory and vomeronasal system is known as the Cowles and Phelan (1958) hypothesis. While support for this hypothesis has been found in snakes (Halpern et al. 1997), its general applicability to squamates has not been tested despite its general acceptance (Schwenk 1993). The gustation system is poorly studied in squamates, but is generally thought to be useful for discrimination of prey items prior to ingestion, although other roles cannot be ruled out. Each of the three chemosensory systems is described below.

### Olfactory System

The olfactory system serves to detect volatile chemicals (odorants) in the air through the paired main olfactory organs. In squamates, these organs follow the typical vertebrate pattern (for details see Halpern 1992). The olfactory (or odorant) receptors (ORs) are the proteins expressed in the olfactory sensory neurons that detect and respond to odorants (Malnic et al. 2010). ORs are GPCRs, similar to the opsin proteins described above, and comprise one of the largest protein families with over 1000 known genes in some mammals. ORs typically respond to multiple odorants, and it is the combination of ORs activated that encodes specific smells. Once activated, ORs activate a G-protein transduction pathway to convert the chemical signal onto an electric one. The number of olfactory genes is generally viewed as

correlating with olfactory ability (e.g., mice have ~1000 ORs, while humans have ~350), although other aspects, such as the surface area of the olfactory epithelia, may be equally or more important (Malnic et al. 2010). The number of ORs in squamates has not been well studied, but recent analyses have shown that snakes possess 350–480 intact (i.e., putatively functional) ORs, while the lizard *Anolis* possesses ~100, and the gecko *Gekko* possesses ~250 (Vandeweghe et al. 2016; Yin et al. 2016). In comparison crocodilians have ~450–600 ORs and turtles ~800–1000 (Vandeweghe et al. 2016), suggesting that the OR repertoires of squamates may be smaller than other reptiles. The larger number of ORs found in snakes, relative to other squamates, might suggest a larger importance of olfaction, at least in some species; however, due to the relatively small number of squamates analyzed and the difficulty of accurately determining OR numbers, these differences should be considered with caution.

Specific uses of the olfactory system in squamates have been largely overlooked due to the predominant view, based on the Cowles and Phelan (1958) hypothesis, that the olfactory system serves primarily as an early (i.e., long range) detection system that triggers the more discriminatory vomeronasal system. This view may be accurate for snakes, which are often viewed as vomeronasal specialists, but other squamates may rely more heavily on olfaction (Schwenk 1993). For example, geckos have relatively large main olfactory bulbs (compared to overall brain size and accessory olfactory bulb size) suggesting a strong investment in olfaction. Furthermore, olfactory cues have been found to be sufficient to trigger antipredator behaviors and detection of prey items in the absence of tongue-flicking that is associated with the vomeronasal system.

### Vomeronasal System

The vomeronasal system is distinct from the main olfactory system and, in most vertebrates, is viewed as an accessory system. Squamates are the exception to this, and many, especially snakes, could be considered vomeronasal specialists. While the vomeronasal and main olfactory systems are distinct, there may be some overlap in the

chemicals they detect as both can respond to volatile, airborne odorants and pheromones. The vomeronasal system is also sensitive to nonvolatile, high molecular weight compounds, which the main olfactory system is not able to detect.

The vomeronasal system is mediated by the paired vomeronasal organs (VNOs, also known as Jacobson's organ). The VNOs typically form as part of the nasal cavity, but uniquely in squamates become fully isolated (Schwenk 1995). In squamates, the VNOs are located at the base of the nasal cavity just above the palate. The roof of each spherical VNOs is covered with the vomeronasal sensory epithelium, which projects to the accessory olfactory lobe through the accessory olfactory (vomeronasal) nerve. The VNO communicates with the oral cavity through paired openings in the palate, the vomeronasal fenestrae. Stimulation of the vomeronasal system, unlike the olfactory system, requires active delivery of chemicals to the vomeronasal sensory epithelium by the tongue (Filoramo and Schwenk 2009). To facilitate this, squamates have evolved a derived tongue-flicking behavior used to sample chemicals from the air or from surfaces, which can then be delivered to the VNOs through the vomeronasal fenestrae.

Squamates generally all utilize tongue-flicking to some degree, although some groups, such as geckos and chameleons, only use tongue-flicking to sample surfaces and not the air, which may reflect an increased reliance on olfaction and vision, respectively. Squamates that also use tongue-flicking to sample the air tend to have additional specializations including oscillatory tongue-flicks and forked tongues. Oscillatory tongue-flicks appear to be an adaptation for collecting airborne odorants (Daghfous et al. 2012), while forked tongues can act as chemosensory edge detectors and allow snakes and other squamates with forked tongues to effectively follow odor (i.e., pheromone) trails of prey and conspecifics (Schwenk 1995). In many species, as discussed above, olfactory cues may trigger tongue-flicking toward the air activating the vomeronasal system to allow more precise localization of a chemical signal. Substrate aimed tongue-flicking may then allow discrimination

of nonvolatile, high molecular compounds providing additional information on the source of the signal including species identity, sex, and reproductive status, enabling the behaviors mediated by the squamate chemosensory system mentioned at the beginning of this section. Additional details on the functions and behaviors associated with the vomeronasal system are reviewed by Halpern (1992).

Similar to the olfactory system, the vomeronasal system is mediated by a G-protein-coupled receptor pathway. There are two types of vomeronasal receptors, V1R and V2R, which are thought to mainly recognize small airborne molecules and water-soluble molecules, respectively. This is thought to be reflected by the high V1R complements found in terrestrial mammals and the high V2R in aquatic amphibians, but squamates prove an exception to this pattern (Silva and Antunes 2017). The high number of V2R genes in squamates could be linked to substrate sampling of nonvolatile compounds through tongue-flicking, although this has not been tested. Overall, very little is known about the specificity of V1R and V2R, and considerably more work is needed to understand the evolution and function of these proteins in squamates.

### Gustatory System

Gustation is the perception of taste, which is mediated by taste buds that, in squamates, are variably present on the tongue and surface of the oral cavity. Many species have taste buds concentrated on the tip of the tongue, although others, such as snakes, have only palatal taste buds. A few species lack taste buds altogether (e.g., monitor lizards). The gustatory system is by far the least studied of the three chemosensory systems, but its primary function in squamates appears to be limited to discrimination of prey items prior to ingestion. Several species have been shown to discriminate between prey items, and some, including both lizards and snakes, may be capable of learned aversion to food following illness (see Schwenk 2008 and references therein).

Some of the genes encoding taste receptors in vertebrates have been uncovered. These include the taste receptors for four of the five main tastes:

sweet (T1R), umami (T1R), bitter (T2R), and salty (ENaC). The receptors for sour taste and those for other “tastes” that the gustatory system can detect (at least in some vertebrates), such as water, fat, and complex carbohydrates, are unclear (Bachmanov et al. 2014). Little is known about the distribution and function of these genes in squamates. Recently the repertoire of bitter taste receptors was analyzed in two lizards (*Anolis* and *Gekko*) and several snakes. It was found that the lizards underwent a considerable expansion of bitter taste receptors relative to other reptiles with 36 and 50 genes in *Anolis* and *Gekko*, respectively, compared to 2–10 in crocodilians and turtles (Zhong et al. 2017). Snakes were found to have lost genes retaining only one or two genes or, in the case of the garter snake, no genes. The expansion of bitter taste receptor genes in lizards may be related to the increased exposure to toxins that accompanies an insectivorous diet (Zhong et al. 2017), but this hypothesis requires further testing, as does the function of gustatory genes in squamates more generally.

### Auditory and Vestibular Systems

In squamates the auditory and vestibular systems are mediated by the ears and function in hearing and balance, respectively. In squamates there is no outer ear in the mammalian sense, although there may be a slight depression and reduction of the scales around the ear opening and a short passage (external auditory meatus) connecting to the middle ear (Baird 1970). The middle ear is variable in squamates, but consists of the structures that transfer vibrations to the inner ear. This typically includes a tympanic membrane (eardrum), but in some species, especially fossorial and semi-fossorial forms, it has been lost. The auditory (Eustachian) tube is short and broad. The stapes has a footplate laterally, where it connects to the inner ear through the oval window, and a long, slender shaft medially. The extrastapes, a cartilaginous element, extends from the stapes medially to the tympanic membrane with several distinct processes that travel across the tympanic membrane providing stability and acting as a lever effect that



enhances the transmission of sound pressure. The extrastapes may also be connected to the quadrate, which can pick up vibrations and transmit them to the stapes. Snakes are notable in the lack of not only the tympanic membrane but also the tympanic cavity and the auditory tube. Despite this, snakes are not deaf, as is often supposed, and can still hear low-frequency airborne sounds, as well as ground vibrations (Young et al. 2014).

The inner ear follows the general vertebrate pattern. The cochlear duct contains the auditory sensory epithelium, called the basilar papilla. It is composed of sensory hair cells that are receptive to movement in their surrounding perilymphatic fluid caused by motion of the stapedial footplate. Similarly, the macula in the saccule and utricle, and the crista ampullaris in the ampulae of the semicircular canals, contain the sensory hair cells of the vestibular system. The macula detects linear acceleration and gravity, while the semicircular canal detects rotational movement. For additional details on the anatomy and function of the ear, see Baird (1970).

The auditory system of squamates functions in a variety of contexts, but not all have been well studied. Uses employed by various groups include prey capture, intraspecific communication, and predator avoidance (Young et al. 2014). The wide auditory tube in lizards makes the ear well suited to localization of prey due to acoustic coupling, which can vastly improve directionality of sound detection. Several species have been found to use auditory cues to locate insects. Remarkably, sand vipers have been shown to be able to locate and capture prey using only ground-borne vibrations. The viper rests its head on the sand where surface waves produced by potential prey cause vibrations in the two independent sides of the lower jaw, which are relayed (on each side) through the quadrate and stapes to the inner ear. Intraspecific communication in squamates is perhaps best developed in geckos, but may also be present in other groups. Geckos in particular are known for producing complex calls that have been implicated in territory defense, male-male competition, and mate attraction. Most squamates, including snakes, will respond to auditory cues produced by predators, but specific research

in this area is lacking. For additional details on uses of the auditory system, see Young et al. (2014) and references therein.

The vestibular system functions in balance and orientation, which is generally important for locomotion. Most research on functional differences in the vestibular system have focused on the morphology of the semicircular canals. In squamates, inner ear morphology is highly variable, but has been shown to correlate with different ecologies, although there is substantial overlap and a strong phylogenetic signal (Palci et al. 2017).

## Somatosensory System

Somatosensory systems mediate interactions with both the external and internal environments providing the senses of touch, pressure, pain (nociception), temperature, balance, and body position (proprioception). These senses each have particular receptors including mechanoreceptors (for touch and pressure) and nociceptors (for pain). Squamates, as in most vertebrates, have cutaneous sensory organs in a variety of forms across the body. These contain mechanoreceptors (scale sensilla), nociceptors, and temperature receptors. Internally, proprioceptor organs are specialized mechanoreceptors found in the muscles, tendons, and joints. These organs detect changes in muscle length and tension and joint position, allowing the coordinated movement of the limbs and body. For a detailed review, see von Düring and Miller (1979).

A remarkable mechanosensory specialization occurs in the tentacled snake (*Erpeton tentaculatus*). This snake species is fully aquatic and is a specialized fish hunter. Tentacled snakes use a sit-and-wait hunting strategy where they adopt a J-shaped posture. When the fish enters the concave area of the J, the snake strikes at the predicted future position of the fish (Catania et al. 2010). Tentacled snakes are highly visual and were found to be able to track and strike prey based on visual cues alone. However, tentacled snakes were still able to strike at and capture prey in complete darkness, although with reduced frequency (Catania et al. 2010). This is accomplished

using their namesake paired tentacles. These tentacles are highly sensitive mechanosensors able to detect water movements produced by fish. They are innervated by branches of the ophthalmic and maxillary nerves, and visual and mechanosensory cues may be integrated in the optic tectum to enhance localization of prey.

## Infrared System

Most animals can sense changes in temperature, but very few can actually “see” infrared thermal radiation. Three groups of snakes, the pythons (Pythonidae), boas (Boidae), and pit vipers (Crotalinae) have specialized infrared receptors to do just that. These snakes are able to sense, locate, and strike warm-blooded prey in the absence of other sensory information (e.g., visual or olfactory cues; Goris 2011). While prey detection is typically thought to be the main use of the infrared sense, it is actually a more general use sensory system that integrates with and supplements the visual system. Other specific uses include predator detection, behavioral thermoregulation, and den site selection (Krochmal et al. 2004).

In most infrared-sensitive snakes, the receptors are contained within specialized pit organs; however, in some boas (e.g., *Boa constrictor*), the receptors are simply located on the proximal and distal edges of labial scales (Goris 2011). In other boas, the receptors are located in the same area, but pits are formed between the two receptor-bearing scales. In pythons the pits are formed from a depression within a labial scale with the receptors located at the base of the pit (i.e., the pit fundus). Thus, the receptor layer at the base functions as a retina, and the overhanging mouth of the pit acts as the aperture of a pinhole camera.

The pit organs of pit vipers are located in the loreal region between the eye and nostril and are more complex than that of pythons and boas. They consist of a narrow opening into an inner and outer chamber separated by a suspended receptor-bearing membrane. While the inner chamber is blocked off from the main opening, it is connected to the exterior through a small

anterior pore. The narrower opening in pit vipers, relative to pythons, results in a better pinhole aperture, while the suspended membrane gives the receptors a lower heat capacity and thus greater sensitivity. The anterior pore equalizes the pressure between the chambers. Both pythons and boas can have multiple pits on either side of the head on the supra- and sublabial scales, while pit vipers possess paired pits, one on each side. The specific morphology of the pits varies and may correlate with the ecology of particular species (e.g., downward facing slits are seen arboreal species).

The infrared receptors contained in the pits (or on the labial scales) are formed from unmyelinated free nerve endings known as terminal nerve masses (TNMs), which are derived from branches of the trigeminal nerve (Goris 2011). Unlike most other sensory neurons, infrared neurons fire constantly at irregular intervals since they are constantly receiving infrared radiation (i.e., background radiation). Stimuli with increased temperature cause increased firing rates, while those with lower temperature cause a reduction in firing rates. In this way, the infrared system acts as a thermal contrast detector (Van Dyke and Grace 2010). Behavioral responses to warm and cold stimuli differ, however, with snakes preferring warm targets.

Signals from the TNMs travel through the trigeminal nerve to a processing center in the medulla (the lateral descending tract and nucleus of the trigeminal nerve) and from there to the contralateral optic tectum (Goris 2011). In snakes, the contralateral optic tectum also receives all of the visual information from the eyes. The optic tectum contains three types of neurons: those that respond to visual information, those that respond to infrared information, and those that respond to both. Both the visual and infrared information are then passed to higher brain centers (nucleus rotundus of the thalamus and anterior dorsal ventricular ridge of the telencephalon), which contain the same three types of neurons. Thus, the infrared and visual sensory systems are intertwined and are thought to produce a combined visual-infrared image. The infrared image is necessarily coarser than the visual one, due to the much smaller

numbers of infrared receptors (thousands compared to millions of rods and cones in the retina); however, the receptive fields of the eye and pits both overlap resulting in a stereoscopic image.

The molecular basis of infrared perception in snakes has been partly uncovered. A temperature-sensitive calcium ion channel, TRPA1, has been identified as a heat-sensing protein expressed in trigeminal ganglion cells in the pits of infrared-sensitive snakes (Gracheva et al. 2010). While TRPA1 is found across vertebrates, its heat sensitivity threshold when heterologously expressed was found to be much lower in pit vipers, pythons, and boas and higher in other snakes that lack infrared receptors. TRPA1 was found to be under positive selection in infrared-sensitive snakes, but not other snakes or vertebrates, consistent with adaptation as an infrared detector (Geng et al. 2011). Based on the phylogenetic distribution of snake species, heat sensitivity of TRPA1 appears to have evolved independently three times. However, the function of TRPA1 alone does not satisfactorily explain the precise heat sensitivity of pit-bearing snakes (Goris 2011), and thus additional work is still needed to explore the molecular basis of infrared sensitivity in snakes.

## Cross-References

- Sensory Receptors
- Squamate Acoustic Communication
- Squamate Cognition

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## Stabilizing Selection

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## Definition

A type of natural selection that selects against the extreme variations of a phenotype, while selecting for the phenotypic mean.

## Introduction: What Is Stabilizing Selection?

In 1949 I.I. Schmalhausen, summarizing the prevailing theories of stabilizing selection during his time, published *Factors of Evolution: The Theory of Stabilizing Selection*. Here, Schmalhausen writes that stabilizing selection is a form of natural selection in which the phenotypic norm is favored over all deviations from the norm (Schmalhausen 1949). Schmalhausen states that stabilizing selection guards the phenotypic norm from being altered and reestablishes the phenotypic norm when it has been disturbed (Schmalhausen 1949).

Stabilizing selection can be thought of as a powerful force that drives a trait toward the phenotypic mean. There are numerous examples of stabilizing selection in nature. While not as visually striking as directional selection, stabilizing selection plays a vital role in supporting a species' survival, by restricting the deviation from their optimal phenotype for their given environment.

## A Brief Statistical Overview of Stabilizing Selection

By using a bell curve to model the frequency of a given trait in a population, the effects of stabilizing selection over time can be demonstrated (Michigan 2010).

Looking at human birth weight in a population that has not yet undergone stabilizing selection, one can see that most newborns are born with a birth weight near the phenotypic mean (Fig. 1a). However, before stabilizing selection occurs in a population, a significant number of newborns will have a birth weight on either side of the extreme end. Being born significantly overweight or underweight has deleterious consequences for the newborn child and their mother. Thus, over time stabilizing selection will select for the birthweights that fall near the phenotypic mean and against birthweights on the extreme ends (Michigan 2010).

As stabilizing selection molds the population, a new bell curve of the phenotypic frequency of human birthweight will develop with almost all the individuals falling within a narrow range near the phenotypic mean and very few individuals having birthweights near the extreme ends (Fig. 1b). Note in this example it is still possible for babies to be born significantly overweight or underweight after stabilizing selection has occurred, but the relative frequency of babies with those birthweights will be significantly decreased after stabilizing selection.

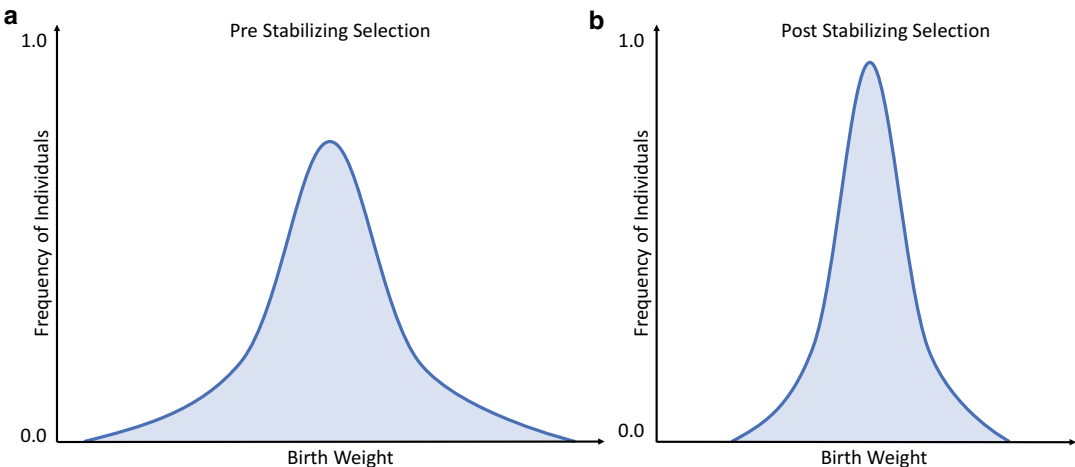
## Examples of Stabilizing Selection

Nature is full of examples of stabilizing selection. A few prominent examples of stabilizing selection are:

- Tree height
- The prevalence of an intermediate fur color in mice
- Beak size in a bird population
- Human skull size

## Stabilizing Selection and Its Role in Maintaining the Relative Long-Term Stability of a Species

There is an interesting paradox in evolutionary biology. On the one hand species have profound phenotypic stability over geological time, and on the other hand most traits have a lot of genetic variations available to them (Estes and Arnold 2007). Given all the variation available to a trait, evolutionary biologists would expect more fluctuations in the fossil record than is observed. This phenomenon can be explained, in part, by



**Stabilizing Selection, Fig. 1** Stabilizing selection causes the majority of human children to be born at the phenotypically average birth weight. (a) Pre-stabilizing selection human babies are born near the phenotypic mean birth weight. The figure shows that while the majority of children are born near the phenotypic mean birth weight, many children are born significantly overweight or

underweight. (b) Because of the deleterious effects of being underweight or overweight for the mother and child, stabilizing selection will select for children who are born with the phenotypic mean birth weight. Over time, almost all children will be born within a narrow range of birth weights



recognizing the role that stabilizing selection plays in adapting a species to the “long-term constraints” of an environment. Many species have stable interactions with the components of the environment for periods ranging from 1 to 300 million years (Estes and Arnold 2007). This relative stability means that the optimal traits for a given environment remain relatively consistent over time. As a result, for a species to best adapt to an environment, the phenotypic means of a species will mirror the optimal traits for that environment (Estes and Arnold 2007). The stability of an environment places strong pressures against directional selection of a trait, as any deviations from the phenotypic mean is also a deviation from the optimal adaptive traits (Estes and Arnold 2007). Thus, even though there is an abundance of variation for any given trait, most of that variation will be selected against because only a small sliver of that variation falls within the optimal phenotype for a species’ environment.

## Conclusions

Despite being described over 60 years ago, stabilizing selection continues to provide new insights into evolution. While more complex models exist for demonstrating stabilizing selection, a bell curve displaying the frequency of a trait before and after stabilizing selection has occurred is a simple way to show the effects of stabilizing selection on a population. Some people incorrectly assume that natural selection is always driving a species toward new adaptations. But, as evolutionary biologist such as Schmalhausen and Estes have demonstrated, stabilizing selection is a powerful force in maintaining the phenotypic mean. As long as there is an interest in why species have specific phenotypes, stabilizing selection will continue to be relevant in evolutionary biology.

## Cross-References

- [Charles Darwin](#)
- [Directional Selection](#)

- [Evolution](#)
- [Frequency Distribution of Phenotypes](#)
- [Genetic Variation](#)
- [Natural Selection](#)

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## Stage IV Error

- [A-Not-B Problem](#)

## Stand and Wait Feeding Behavior

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## Synonyms

[Stand and wait foraging behavior](#); [Stand-and-wait feeding](#)

## Definition

Stand and wait feeding behavior is a strategy utilized by avian predators that stand still in water or on land and wait for prey to approach.

## Introduction

Stand and wait feeding behavior is a common strategy employed by foraging wading birds and is particularly common in visual feeders such as herons (Kushlan 1978a; Meyerriecks 1960). It is characterized by different standing postures and neck positions, but in all cases the predator stands while waiting for prey to approach.

## Description of Behavior

Stand and wait feeding is one of the most common foraging strategies employed by wading birds (Meyerriecks 1960). Typically, foraging predators stand motionless on land, at the edge of a body of water, or in shallow water. When prey approaches within range, the predator strikes rapidly, either seizing the prey or impaling it on its bill. Prey is often swallowed whole. Large prey may be stunned or killed before swallowing, while smaller items are often swallowed live. Strikes (successful or not) are often followed by dipping the bill into the water and then shaking the head.

Because stand and wait feeding behavior is common across a variety of species, it is associated with a diversity of postures and neck positions (Kushlan 1978a). Wading bird posture ranges from a hunched or crouched position to full upright position, with intermediate variations of upright posture in between these two extremes. Similarly, neck posture can result in a head that is retracted or fully extended, or any variation in between. Oftentimes the bill faces the water with the wader peering down, while other times the head is cocked or both the head and neck are tilted (Kushlan 1978a). Head tilting or cocking may be used to reduce glare from the sun (Kushlan 1978a). In addition to the variation in positions and postures, there are also a number of slight variations to stand and wait feeding. For example, stand and wait predators can bait prey while they are waiting by placing a piece of food in the water to attract prey (Lovell 1958). Head or neck swaying are also common additions to stand and wait feeding (Meyerriecks 1962). Stand and wait feeding behavior can be interchanged with other

feeding behaviors, including slowly wading or walking.

Stand and wait foraging is associated with adaptations that may facilitate feeding in a variety of habitats and throughout the day. For example, neck anatomy allows stand and wait foragers to extend the neck rapidly while thrusting for prey. Water depth is an important determinant of prey availability to foraging waders (Gawlik 2002), with foraging wading birds that feed by standing in water restricted by leg length (Kushlan 1976; Powell 1987). Shallow water is generally preferred (Gawlik 2002). Wading birds with shorter legs may also stand on the water edge or perch, for example on logs, rocks or roots. Additionally, wading birds that feed using this strategy often have either white or dark plumage, and it has been hypothesized that either color type can be adaptive towards reducing conspicuousness to prey (Kushlan 1978a). Specifically, white foraging birds may be less visible from below during the day, and birds with dark plumage may be less visible from below at night or when foraging in shadows (Kushlan 1978a). Specialized optics allow foraging wading birds to feed using the stand and wait strategy during the day and at night.

Stand and wait feeding is a common strategy whether foraging solitarily or in groups. Additionally, it is common both in natural habitats (e.g., wetlands, tidal areas) and anthropogenic habitats such as flooded rice fields (Elphick 2000) or canals.

## Conclusion

Stand and wait feeding is one of the most common foraging strategies employed by wading birds. As the name suggests, birds stand “frozen” while feeding, which is in direct contrast to active feeding. This can conserve energy, making stand-and-wait feeding a useful strategy to maximize energy intake (Kushlan 1978b). Resource partitioning based on foraging adaptations, including leg length and temporal feeding strategies, may help to reduce competition among wading birds and to structure wading bird communities.

## Cross-References

- [Central Place Foraging](#)
- [Foraging](#)
- [Optimal Foraging Theory](#)

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## Stand and Wait Foraging Behavior

- [Stand and Wait Feeding Behavior](#)

## Stand-and-Wait Feeding

- [Stand and Wait Feeding Behavior](#)

## Standing

- [Reputation](#)

## Stanley Kuczaj

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Stanley (Stan) Abraham Kuczaj II was truly an entrepreneur in the broad and diverse field of psychology. Cutting his teeth on human developmental topics such as language acquisition, Piaget's schematas and moderately discrepant events, and culturally influenced development, Kuczaj published profusely on language acquisition and its relationship to play, moderately discrepant events, concept formation, and culture. Influenced by traditional Piagetian approaches, Kuczaj simultaneously believed in the importance of longitudinal studies and cross-cultural generalizabilities. These core themes shaped and recurred across his research and writings, which culminated in a four-decade-long pursuit of trying to uncover the mysterious cognitive worlds of human children and nonhuman animals, especially marine mammals.

Kuczaj was born on 20 October 1950 in Jersey Shore, Pennsylvania to Rose and Stan Kuczaj and was given a childhood nickname of "Sonny." He was the oldest of four children, including two sisters and a brother. His family ultimately landed in Irving, Texas. Truly a success story, Kuczaj earned his GED to attend the University of Texas at Austin where he earned his Bachelor of Arts degree in Psychology and graduated Magna Cum Laude. Kuczaj attended the University of Minnesota, earning his doctorate in child psychology under the guidance of Dr. Michael Maratsos in 1976. His dissertation was a notable and lauded landmark study of the emergence of language from birth to 5. He was awarded the Boyd R. McCandless Young Scientist Award from the American Psychological Association (APA) in 1980.

Kuczaj came to national prominence pursuing fundamental and universal questions about language, thought, and their development in young

children. In 1986, Kuczaj was awarded a prestigious Fulbright Scholarship to work at Oxford University as a Visiting Fellow in the Department of Experimental Psychology where he created life-long collaborations with other language researchers and developmentalists. A voracious reader with a wicked sense of humor and insatiable stream of thoughts and questions, perhaps Kuczaj's greatest gift was his ability to formulate questions about the intertwined roles of language and thought as they shaped the mind of our species and others.

## Language Highlights

Stan Kuczaj began his academic career studying language acquisition, especially verbs. Except, as with all of his work, Kuczaj did not just stop with verbs, he also examined the acquisition of nouns, emotional-based adjectives, relational word classes, and larger categories and classes.

## Verbs!

His dissertation, which incorporated his own children (much like Jean Piaget), focused on the acquisition of verb inflections and entitled “-Ing, -s, and -ed: A study of the acquisition of certain verb inflections” (1977a). With several early publications under his belt, as a preview to his future productivity, one of his most influential papers was derived from his dissertation and published in the *Journal of Verbal Learning and Behavior* (1977b). This paper continues to shape research today, remaining one of his most consistently cited papers (Kuczaj 1977b).

## Extending into Syntax and Semantics

Following the completion of his doctorate, Kuczaj left the frigid winters of Minnesota to return to the temperamental extremes of Texas as a faculty member of Southern Methodist University. Here, he continued to explore children's comprehension and production of new words under a variety

of contexts, managing to publish a number of works and two edited volumes while chair of the psychology department. Publishing in areas that extended current cognitive theories regarding language acquisition, Kuczaj continued to explore the errors and nature of language acquisition. Some key contributions included the papers; “Young children's overextensions of object words in comprehension and/or production: Support for a prototype theory of early object word meaning” (1982a), “Language play and language acquisition” (1982b), “Acquisition of emotion-descriptive language: Receptive and productive vocabulary norms for ages 18 months to 6 years” (Ridgeway et al. 1985), and editing two volumes on language development (1982c, d) in which invited contributors explored and published key papers on language topics that continue to influence language research today. Perhaps even more significant were the perpetuation of themes upon which his language research was founded – play, emotions, culture, and social interactions within his comparative work.

## Developing Through Play

Play was a constant in Kuczaj's research and life. A consummate joke teller and roller coaster connoisseur, Kuczaj's appreciation for play as a major contributor in learning emerged early in his thinking and research. Influenced by Piaget's idea of private (egocentric) speech and Vygotsky's version, inner speech (for a review of these concepts see Alderson-Day & Fernyhough, 2015), Kuczaj laid out a set of hypotheses and research studies regarding the social contexts in which infants and toddlers practiced language skills in his book, *Crib Speech & Language Play* (1983). Distinguishing between crib speech (i.e., self is the model), social/self (i.e., the individual provides the model but is communicating information to another party), social/other (i.e., the child practices the behaviors performed by another individual, the model), and asocial/self (i.e., the child provided the model but is not attempting to communicate with another person that is present), this study was instrumental in supporting the

conclusions that children play with language as they acquire it and appear to prefer to practice it for mastery potentially in private. This study also continues to influence research on language acquisition today.

### Transitioning to Marine Mammals

One of Kuczaj's greatest contributions to psychology was his ability to integrate ideas across disciplines. Appreciative of inspiration from anywhere, Kuczaj's ideas were influenced by different cultures and species; vocal learning in birds influenced his work on the language play in human infants, including babbling, repetition, imitation, and variations on a theme. Piaget's ideas of moderately discrepant events influenced Kuczaj's work on language play and physical play. A fan of travel and experiencing different cultures, the role of culture in language acquisition, thought, concept formation, and eventually nonhuman animal behavior were frequent topics in his work with humans and nonhuman animals. As a leading expert in human language acquisition, Kuczaj was invited to collaborate with another expert in marine mammal cognition, Dr. Louis Herman (1930–2016), who spent over two decades studying dolphin cognition at Kewalo Basin Marine Mammal Laboratory, University of Hawaii at Honolulu. This collaboration produced a number of chapters and articles examining the abilities of dolphins to process semantic information through syntax, such as their article "Responses to anomalous gestural sequences by a language-trained dolphin: Evidence for processing of semantic relations and syntactic information" (1993). This experience was a significant turning point for Kuczaj and his research. Shortly after his time in Hawaii, Kuczaj joined the psychology department at the University of Southern Mississippi as chair (a role he gleefully granted to his peers after 10 years) and established the Marine Mammal Behavior and Cognition Laboratory in 1996.

Representative of the integration of his life experiences, Kuczaj's library held hundreds of books from Piaget's original works to Skinner's *Verbal Behavior* and a translated copy of

Vygotsky's only book to the folktales of Nepal, the history of Kachina dolls, and the interpretation of children's drawings. Within each of these books, notations and underlined passages provide insights into Kuczaj's thinking and formulation of ideas. As Kuczaj was transitioning into the mysterious world of marine mammals, his library also transformed, to include any book that told the "story" of marine mammals. It did not matter if the story was a children's book detailing a friendship between a lost child and a dolphin, Asian/Grecian folklore about dolphins, fictional renditions based off of true stories (Luna the killer whale), or empirically based reference books summarizing the current knowledge of marine mammal physiology, acoustics, distributions, and behavior. They all had important passages ear-marked and notated – his word doodles rather than picture doodles.

No matter the species, Kuczaj always returned to his loves of language and development. His training in developmental psychology and longitudinal, observational studies set the stage for the majority of his work with marine and terrestrial mammals. Kuczaj conducted a variety of cognitive and behavioral animal studies: the development of dolphin calves and their mothers, the development of play, the types of social interactions among different-aged animals, the intricacies of environmental enrichment, the establishment and differences in personality, the importance of contact during social interactions, and the role of emotion in animal behavior. His work in acoustics explored the development of echolocation in dolphin calves, the characteristics of sperm whale codas, the role of individual whistles in mother-calf reunions under experimental conditions, the use of sounds during a cooperative task, and the creation of a two-way system for communication.

### Artificial Language Comprehension

Kuczaj initially applied his extensive language background to marine mammals with Louis Herman at Kewalo Basin Marine Mammal Laboratory. Dolphins were taught arbitrary gestural languages, representing actions (verbs), objects,



and locations to two bottlenose dolphins. The symbolic languages (visual and acoustic) were tested for comprehension, rather than production, of language with two subjects. Using syntactical rules, which varied in order, the dolphins successfully executed these grammatical sequences, revealing flexibility and comprehension.

## Cognition

Through cognition-based tasks, Kuczaj extensively studied problem solving, documented joint attention between humans and marine mammals, as well as tested how animals responded to experimenter given cues. His creative mind aided in developing multiple feeding devices that required problem solving skills or cooperation, as well as visual and behavioral responses to mirrors to locate objects. Empirically investigating the ability for animals to display their creativity was observed in Kuczaj's works with cognition and play. First investigated by Pryor and colleagues, Kuczaj works support the ideology that dolphins can represent past actions and through these representations, can modify previous behaviors to vary their behavior. Additionally, Kuczaj devoted time to understanding how multiple species reacted to novel problems, as well as visual laterality, finding interest in the existence of a dominance function.

Through his works with play, Kuczaj extensively studied enrichment with many species in managed care, focusing on keeping the environment enriching, as well as enrichment being a time to cognitively challenge the animals. This approach provided a balance between training, enrichment, and behavior. Through innovated tasks, dolphins were able to solve novel tasks without the use of training or human influences.

## Play

Kuczaj's works throughout the years empirically investigated play within a variety of different species, uncovering the essential role play fills in their social lives. He was especially drawn to play among dolphin calves, revealing how they

learn about the social norms within the grouping, gain access to other conspecifics, and acquire the cognitive skills needed for play. He extensively studied play in wild and captive dolphins, documenting the roles of peers in cultural transmission, the behavioral variability and individual creativity of play, and the importance of social learning during play of their cognitive development. This was especially apparent through his work with imitation; calves were more likely to imitate peers than adults, including their mothers, highlighting the selectivity of social learning and flexible thinking by young animals.

## Behavior

Kuczaj's diverse interests were fueled through countless collaborations with free-ranging and captive researchers. He valued gaining information about animals in a variety of different settings, advocating the importance of managed care research to gain detailed, sequential observations that can be difficult to acquire in free-range settings while also recognizing the need to understand the same behaviors in the natural habitat. He devoted time to examining behavior with a variety of different species and topics, investigating stereotypic behaviors among wild marine carnivores, seasonal and diurnal patterns, population abundance within the Mississippi sound, contact exchanges between dolphin populations, the influence of group size on social behavior among rough tooth dolphins, epimeletic behavior with a distressed conspecific, and pioneered examining behavior of killer whales in utero. Kuczaj had a passion for all animals, but he had a special love for elephants; his works provided a greater understanding of the role of touch in social interactions and the influence of novel objects on their behavior. Through these behavioral investigations, Kuczaj was fascinated by individual differences. Whether documenting maternal styles or consistent individual differences (e.g., personality), Kuczaj examined how personality in non-human species were affected by time, context, and methodology used (i.e., Five-Factor model, and rating vs. coding). He approached the study of

personality using research conducted in both managed care and free-ranging populations.

## Acoustics

Kuczaj's work with acoustics began with monitoring and evaluating ambient noise in the Gulf of Mexico at varying depths. Kuczaj's passion to understand the specifics of how marine mammals utilized sound was reflected with his works on Audio Evoked Potentials, recording echolocation behavior of free swimming dolphins, examining click trains with echolocation recordings, fine-scale analysis of low frequency, narrow-band calls among dolphins, fractal scaling of echolocation, as well as the behavioral specifics affiliated with different calls (i.e., mothers call their calves, sounds during cooperative behavior). His interest in understanding as much as he could about the marine environment fueled his interest in promoting policy change where possible.

Ultimately, Stan Kuczaj was an advocate for learning from animals in all settings. He advocated for the need for quality zoos and aquariums as they are critical vehicles in helping people understand the importance of conservation. He believed that these programs provide patrons with experiential learning opportunities that would otherwise be impossible, while also leading to a greater appreciation for the environment and understanding of the species.

A prolific scholar, Kuczaj was extremely well published. He had approximately 150 publications and 200 professional presentations and was invited frequently to present keynote addresses at conferences and invited colloquia at other universities. He connected the science and the public, as a featured scientist in a number of world-wild documentaries and magazines like *National Geographic* and *National Geographic Kids*. Kuczaj's ability to blend science with real life anecdotes allowed him to make myriad contributions to the fields of language acquisition, thought, marine mammalogy, and comparative psychology. He encouraged scientists of all bents – acousticians, cognitive psychologists, developmentalists, physiologists, and philosophers, to look at their topics from different perspectives. He persuaded

scientists to remember individuals contribute uniquely and were as important and interesting as consistent group results. He also reminded researchers frequently to go back to the roots – what factors shaped individuals or the species to what they are currently?

He is best remembered for his brilliant mind paired with an enthusiasm and excitement for studying animals. He was a leader in reigniting waning interest in animal behavior and cognition as promoted by Donald Griffin, Niko Tinbergen, Konrad Lorenz, Wolfgang Kohler, Stephen Gould, Ronald Schusterman, and Louis Herman and other animal behaviorists interested in understanding the mind of animals despite not sharing the capacity for language as humans have. He was a leader in all ways from scientific contributions to internal and external leadership positions, including President of the Society for Comparative Psychology and Behavioral Neuroscience, Division 6, of the American Psychological Association (APA), editor-in-chief of the journal, *Animal Behavior and Cognition*, which he founded in 2014, a Fellow of the American Association for the Advancement of Science, APA's Divisions 3, 6, and 7, and the Psychonomics Society, a founding member of the Comparative Cognition Society, and a charter fellow for the Association of Psychological Science. His legacy is carried on by his former students, collaborators, and all those he inspired with his easy-going manner and anything-is-possible attitude.

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## State of Thermal Equilibrium

- [Thermoregulation](#)

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## Statistical Association

- [Correlation](#)

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## Status

- [Basic Rank](#)
- [Reputation](#)

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## Step Reflex

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## Synonyms

[Inborn reflex](#); [Innate reflex](#); [Instinctive reflex](#); [Physiological reaction](#); [Primitive reflex](#); [Reflex action](#); [Stepping reflex](#); [Unconditioned reflex](#); [Walking reflex](#)

## Definition

The step reflex is the automatic alternating limb movement response to the stimulus of feet or paws touching a firm surface.

The step reflex, also called the walking reflex, is the automatic alternating limb movement response to the stimulus of feet or paws touching a firm surface. The step reflex is a primitive reflex present in some altricial-limbed vertebrates, and it assists with the development of locomotion ability. In typical development, the step reflex emerges in utero, is present at birth, and disappears in early development. The step reflex has primarily been studied in humans, although there is evidence of this reflex in other species such as cats and rats (Muir 2000).

Locomotion is vital for many organisms to solve many adaptive problems, including acquiring nutrients and escaping predation. Locomotion likely played a significant role in the evolution of a myriad of species, and the step reflex is crucial to the development of movement abilities in some altricial mammals. Altricial and precocial vertebrate nervous systems share the basic circuitry for locomotion, demonstrating that similarities have been preserved throughout vertebrate evolutionary history (Muir 2000). One of the most pronounced differences between altricial and precocial vertebrate locomotion is the developmental delay in movement ability in altricial species. Precocial species are able to locomote voluntarily at birth, thus requiring less parental care, whereas altricial species cannot locomote independently and require more extensive parental care for survival. The mechanisms that activate spinal cord circuitry causing alternating steps or swimming are present in vertebrates at birth; however, brain development in altricial vertebrates is delayed and, therefore, altricial infants require a reflexive response to stimulate the alternating limb movements characteristic of walking, whereas precocial infants are able to locomote voluntarily (Muir 2000).

Humans are a highly altricial species that exhibit the step reflex. The step reflex is organized at the level of the brainstem, whereas crawling and walking require the involvement of the cerebellum and the cerebral cortex (Kolb

and Wishaw 2003). In an adult human, the cerebellum assists with balance, the prefrontal cortex plans movement, the premotor cortex organizes the sequence of movements, and the motor cortex executes the action (Kolb and Wishaw 2003). Humans are born before cerebellar white matter has undergone the most rapid and dramatic period of myelination and before the cerebral cortex is fully developed, so the infant brain is not equipped to control movement as an adult brain does (Kinney and Volpe 2018). As neurological development progresses, at about 2 months after birth, the step reflex disappears and other brain regions take over control of functions related to stepping and locomotion (Yang et al. 1998).

Cats and rats are quadruped altricial species that demonstrate evidence of the step reflex. Robinson and Goldberger (1986) found that kittens less than 2 weeks old that have undergone complete transection of the spinal cord can walk on a treadmill without training while adult cats struggle with motor function after spinal cord transection. It is possible that newborn kittens demonstrate the step reflex in their relatively superior walking ability after spinal cord transection whereas adult cats have already developed the neural pathways that inhibit the step reflex and are therefore unable to recover as quickly. Kittens that underwent this surgery expressed motor control typically not seen until later in development in normal cats, suggesting that this behavior is normally suppressed and may be the result of latent genetic architecture (Robinson and Goldberger 1986). In rats, spinal pattern generators for locomotion are present in utero although rats do not locomote until around 11 days after birth (Westerga and Gramsbergen 1990). Rats are born at a relatively immature stage, demonstrating altriciality in their inability to move about freely at birth. Nguyen et al. (2017) found that when rat pups are held in the air with their hind paws touching a flat and firm surface, at 4 days postnatal, they will reflexively perform a motion similar to walking despite an inability to walk independently. More research is necessary to confirm the presence of step reflex in nonhuman animals.

## Cross-References

- ▶ Altricial
- ▶ Bipedalism
- ▶ Catarrhine Locomotion
- ▶ Cerebellum
- ▶ Feline Locomotion
- ▶ Grasping Reflex
- ▶ Hominid
- ▶ Hominoidea Locomotion
- ▶ *Homo sapiens*
- ▶ Innate Behaviors
- ▶ Locomotion
- ▶ Myelination
- ▶ Natural Selection
- ▶ Nervous System
- ▶ Precocial
- ▶ Primate Locomotion
- ▶ Quadrupedal
- ▶ Reflex
- ▶ Rodentia Locomotion
- ▶ Species
- ▶ Vertebrate Nervous System

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## Stepping Reflex

### ► Step Reflex

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## Stereoscopic Vision

### ► Cognition

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## Steven Gangestad

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Steven Warren Gangestad is Distinguished Professor of Psychology at the University of New Mexico, where he started working as Assistant Professor in 1987 after completing graduate and postdoctoral training at the University of Minnesota. Steve is renowned as one of the world's leading evolutionary psychologists, with many of his most highly cited papers solidifying the theoretical foundations on which the field is built. Such work includes an account of how cross-cultural variation in behavior can arise from developmental adaptations (Gangestad et al. 2006), a theoretical framework for understanding the variation in sexual strategies that many evolutionary psychologists study (Gangestad and Simpson 2000), and an outline of the evidentiary standards required to categorize features of an organism (including psychological ones) as adaptations, exaptations, or by-products (Andrews et al. 2002). Steve's empirical program has been similarly foundational. It includes pioneering work on facial attractiveness (Gangestad et al. 1994; Scheib et al. 1999; Thornhill and Gangestad 1993), women's gene-seeking versus investment-seeking sexual motivations (Gangestad et al. 2007; Gangestad and Thornhill 1998; Grebe

et al. 2013), and, perhaps most notably, measuring and interpreting variability in sociosexuality (i.e., openness to sex outside of a committed relationship) (Gangestad and Simpson 1990; Simpson and Gangestad 1991). And, as a final category of output, Steve has co-edited volume *The Evolution of Mind: Fundamental Questions and Controversies* (Gangestad and Simpson 2007), which included concise (and, sometimes, productively contentious) pieces by evolutionary behavioral scientists across disciplines, and he co-authored *The Evolutionary Biology of Human Female Sexuality* (Thornhill and Gangestad 2008), which drew from comparative, developmental, endocrinological, and functional perspectives to understand men's and women's sexual psychology.

While Steve has produced work that has touched myriad research programs across the evolutionary behavioral sciences, he has also taken a hands-on role in shaping the direction of the international Human Behavior and Evolution Society (HBES). He served as an elected council member for the society from 1997 through 2003, he was the society's president from 2007 through 2009, and he organized and hosted the society's annual meeting in 2012. Steve's orientation toward drawing from the broader animal behavior literature to study humans was on display at this meeting, where he arranged for a one-day joint session between meetings for the international Animal Behavior Society and HBES.

Steve's most notable contributions – both to scientific societies and to the scientific knowledge on which they are based – are apparent in the field of evolutionary psychology. A glance only toward his articles, books, and service activities in this field can belie his broader involvement in personality and social psychology. Steve's dissertation concerned behavioral genetics, and his first major paper reviewed the nature of discrete classes of personality (Gangestad and Snyder 1985). He has deep knowledge of statistics and psychometrics, and teaches statistics classes at the undergraduate and graduate level. Based on this breadth of knowledge, he has served as Associate Editor for *Psychological Science* – the Association for Psychological Science's flagship journal – since 2012, and he has served as a consulting editor



for multiple other leading psychology journals, including *Journal of Personality and Social Psychology*, *Personal Relationships*, and *Journal of Personality*. And last (but not least), Steve has served as an excellent advisor to many bachelor and Ph.D. students (including the author of this brief biography) – students who are better scientists thanks to Steve’s mentorship.

Steve grew up in Minnesota and returned there for his graduate education after attending the University of Oregon and Stanford University for his undergraduate studies. He currently lives with his wife Sara and son Torin in Albuquerque, New Mexico, with summers and weekends spent in the San Juan Mountains of Southwestern Colorado, which afford much time for hiking and skiing.

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## Stimulus and Local Enhancement

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## Local Enhancement

Local enhancement refers to the facilitation of learning that results from drawing attention to a locale or place associated with reinforcement (Roberts 1941). For example, Lorenz (1935) found that ducks enclosed in a pen did not react to a hole in the pen that was large enough for them to escape unless they happen to be near another duck as it was escaping. The sight of a duck passing through the hole in the pen may draw attention to the hole. Thus, one could ask if observing a ball roll through the hole, for example, would produce a similar effect. If so, it would not be interpreted as social learning.

Local enhancement may also be involved in John et al.’s (1968, Exp. 1) finding of facilitated acquisition of an aversively motivated hurdle-jump response. Specifically, observer cats that watched a demonstrator cat that had learned to avoid shock by jumping over a hurdle acquired the appropriate shock avoidance response faster than control cats that were trained without having the opportunity to observe the demonstrator. Attributing the copying behavior to local

enhancement, in this case, rather than imitation may not be obvious, but observation of the demonstrator jumping over the hurdle may have simply drawn the observer's attention to the top of the hurdle. In other words, any event that might draw attention to the top of the hurdle (e.g., a ball bouncing over the hurdle or even a light flashing at the top of the hurdle) could facilitate the hurdle-jump response. Similarly, an attentional mechanism may be responsible for the rapid mastery of a V-shaped-fence-detour problem by dogs (the dog finds itself on the inside of the V) when demonstrated by a human (the human moves from outside the apex to one of the arms of the V; Pongrácz et al. 2001). Seeing the demonstrator pass around the end of the fence may draw the observer's attention to the place where it can gain access to the goal on the other side. In general, whenever the performance observed involves an object (e.g., a manipulandum, a hurdle, a barrier) to which the observer must later respond, local enhancement may play a role and appropriate control conditions should be included if one wants to conclude that imitation is involved.

Although performance by the demonstrator may draw the attention of the observer to a location, the outcome of the demonstrator's behavior may also play a role in the observer's tendency to copy. For example, Lefebvre and Palameta (1988) found that pigeons that observed a model pierce the paper cover on a food well to obtain hidden grain later acquired that response on their own, whereas those that observed that same response but with no grain in the well (the model performed in extinction) failed to acquire the response. In this case, the observed behaviors were quite similar for the two groups, but the consequences of the observed behavior were quite different (see also Akins and Zentall 1998). Although one might be inclined to interpret this result cognitively, as the observer's understanding of the consequences of the demonstrator's behavior, a Pavlovian conditioning account in terms of the pairing of attention to a location, and the appearance of a reinforcer, may be sufficient to explain the more rapid acquisition of the target behavior by the observer when the demonstrator's behavior is reinforced. This point will be addressed again shortly.

## Stimulus Enhancement

In the case of local enhancement, the attention of an observer is drawn to a particular *place* by the activity of the demonstrator. The term stimulus enhancement is used when the activity of the demonstrator draws the attention of the observer to a particular *object* (e.g., a manipulandum). Quite often in the study of imitative learning, the object in question is at a fixed location so local enhancement and stimulus enhancement are indistinguishable. In the duplicate-chamber procedure (see Warden and Jackson 1935; Gardner and Engel 1971), however, a manipulandum (e.g., a lever) is present in both the demonstration chamber and in the observation chamber. Under these conditions, drawing attention to the demonstrator's lever might not be expected to enhance observation of the observer's lever. In fact, one could argue that it should retard acquisition of lever pressing by the observer because it should draw the observer's attention away from its own lever. However, the similarity between the demonstrator's lever and that of the observer may make it more likely that the observer would notice its own lever after having its attention drawn to the demonstrator's lever. Thus, stimulus enhancement can refer to the combination of a perceptual, attention-getting process resulting from the activity of the demonstrator in the presence of the lever and stimulus generalization between the demonstrator's and observer's levers. Because it subsumes the effects of local enhancement, the term stimulus enhancement may be more inclusive and, thus, is often preferred (Galef 1988).

Stimulus enhancement may also play a role in mate-choice copying by animals (Dugatkin 1996; Galef et al. 2008). For example, female guppies that see a demonstrator or model female in the presence of a courting male will prefer that male over an alternative male (Dugatkin 1992; Dugatkin and Godin 1992). In this case, it may not be possible to separate the observer's attention to the model female, and therefore to the male nearby, from the putative attraction of the model to the adjacent male.

The facilitation of learning through perceptual factors presents a difficult problem for the study of

imitation in animals. If the similarity between the demonstrator's location or the demonstrator's manipulandum and that of the observer presents an interpretational problem because of perceptual factors, making the location or the nature of the manipulandum for the observer different from that of the demonstrator is likely to interfere with the observer's potential interpretation of the relation between the two tasks. This problem, which will be addressed later, requires a new approach to defining adequate control procedures (see section on the two-action procedure).

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## Stimulus Control

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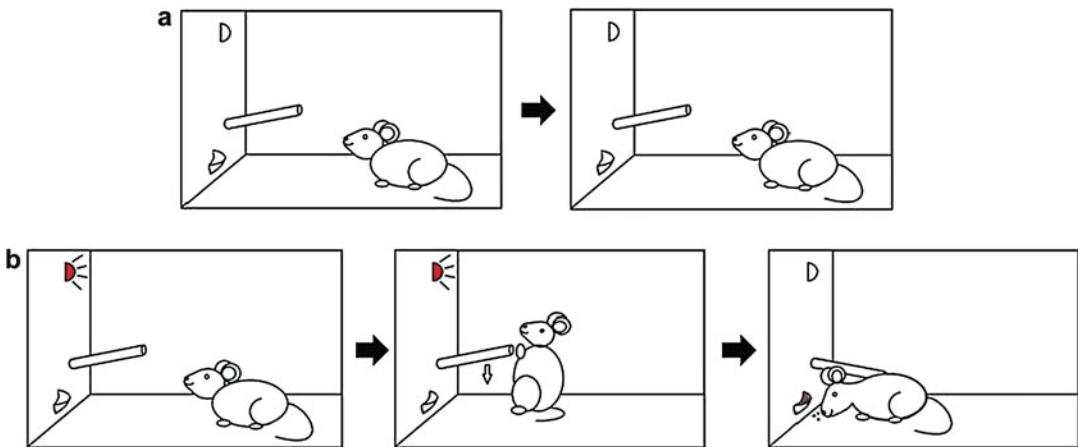
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## Definition

A phenomenon in which a given stimulus reliably elicits a particular learned behavioral response.

*Stimulus control* has been defined by Terrace (1966) as the extent to which a given stimulus determines the probability that a conditioned response will occur. This observed relationship between an antecedent stimulus and behavioral response is measured by examining the change in response probability over time. As the probability of a behavioral response to a given antecedent increases, the behavior is determined to be under stimulus control (Terrace 1966). However, Macintosh (1977) further defined stimulus control as “an observed relationship between changes in external stimuli and changes in recorded behavior” (p. 481). This definition is likewise important, as it highlights a need for two or more conditions which should be compared (Honig and Urcuioli 1981), specifically in the presence and absence of the stimulus.

Stimulus control can be observed by examining the three-term contingency, in which a subject learns to perform an operant response (R) to a discriminative stimulus ( $S^D$ ), resulting in reinforcement/punishment ( $S^{R+/-}$ ; Pilgrim 2015).



**Stimulus Control, Fig. 1** (a) In the absence of an antecedent stimulus (red light), the subject (rat) makes no behavioral adjustment. (b) When the red light is presented, the rat changes its behavior and pulls the lever. Food

reinforcement ( $S^{+}$ ) is delivered as soon as the target behavior is performed. The behavior is under stimulus control once it is only performed in the presence of the stimulus. (Adapted from Skinner 1938)

That is, a conditioned stimulus acquires discriminative control when the desired behavior directly follows an antecedent stimulus. Skinner (1938) demonstrated this concept when a food pellet was provided to a subject (a rat) after performing a lever press in the presence of the antecedent stimulus (a red light), and not when the light was turned off. When the subject elected to press the lever only when the light is on, the behavior was considered to be under stimulus control (Fig. 1). Stimulus control requires that a simple discrimination has been established between the red light, now a discriminative stimulus ( $S^D$ ), and the behavior (R) with the anticipation that the behavior will be rewarded with food as reinforcement ( $S^{+}$ ).

### Establishing Stimulus Control

Stimulus control is established through a process termed *differential reinforcement*, in which a target behavior is reinforced only in the presence of the  $S^D$ . For example, during acquisition, the subject pictured in Fig. 1 would be rewarded for a lever press in the presence of a red light but not when the light is off. Once a discrimination is made, an  $S^D$  indicates to the individual that the associated  $S^{+}$  is likely to occur after the target behavior is performed. Thus, an individual responds differentially to the  $S^D$  than to

extraneous environmental stimuli, called *stimulus discrimination* (Pilgrim 2015).

### Stimulus Control Topography and Stimulus Generalization

Determining if a subject is properly distinguishing the intended  $S^D$  from the extraneous stimuli can be challenging. Therefore, it is critical that the stimuli thoroughly evaluated by examining the *stimulus control topography* (SCT), or the “qualitative differences among members of a functional stimulus” (McIlvane and Dube 2003, p. 195). SCT guides the subject on what to respond to, as well as how to respond (Layng et al. 2011). For example, the rat in Fig. 1 may respond discriminatively to the red light, as indicated by different features of the stimulus such as the hue, brightness, or location of the light. Evaluating stimuli becomes even more complex when individuals focus on different features of the same stimulus. For example, while a rat may develop a discrimination which focuses on the red hue of the light, this may cause them to react to all red stimuli in a process called *stimulus generalization*. The extent to which a behavior can be controlled by variations in a particular stimulus is known as a *generalization gradient*, which can be useful in measuring stimulus control (Pilgrim 2015).

### Response Factors in Stimulus Control

As previously discussed, multiple features of an  $S^D$  may acquire control over responding. The range of stimuli features that are perceived, and therefore can control behavior, is largely dependent on the sensory abilities of the species or individual. Potential limitations for stimuli include visual capacity, audible hearing ranges, physical constraints, or perceivable but – not salient – features. Additionally, stimuli salience has been shown to be influenced, in part, by the type of reinforcement provided (LoLordo 1979). In several species, such as pigeons and rats, visual cues are more likely to be salient and control behaviors in positive reinforcement scenarios, and auditory stimuli are more likely to be salient and achieve behavioral control in negative reinforcement scenarios (Foree and LoLordo 1973; Schindler and Weiss 1982).

In practice, behavior analysts have focused strongly on the association between a target behavior and the subsequent  $S^{r+/-}$ , placing less emphasis on the association between an  $S^D$  and a target behavior (Dinsmoor 1995). This has been evident in the field of animal training, where the emphasis has typically been placed on reinforcement rather than antecedent (Reid et al. 2014). Through evaluating the sources of stimulus control, behavior analysts can adjust the target individual's environment as needed to increase or decrease instances of a targeted behavior.

### Stimulus Control Transfer

Errorless learning techniques provide the subject with guided learning opportunities designed to reduce or eliminate error, which is believed to inhibit the learning process (Terrace 1963a). In these procedures, guiding cues, such as response prompts to the desired  $S^D$ , are transferred to the final  $S^D$  via stimulus fading (Dietz and Malone 1985; Touchette and Howard 1984).

*Response prompts* act as supplemental stimuli, guiding behavior and decreasing errors in the process (Dietz and Malone 1985; Touchette and Howard 1984). Prompts (e.g., verbal or gestural cues, physical guidance, or modelling) are designed to improve behavioral response and are delivered with, or immediately after, the  $S^D$ .

Delayed prompting is a procedure in which the prompt is presented only when there is a delay in behavioral response following the presentation of the stimulus. This is a commonly used errorless learning procedure. If not utilized properly, these tools can create problems for the learner. For example, if prompts are removed too early in the learning process, incorrect response patterns will result (Touchette and Howard 1984).

To establish stimulus control, prompts must be *faded*, *transferred*, or *shaped* properly and with as few errors as possible (Dietz and Malone 1985). In stimulus fading procedures, a target stimulus' behavioral control is acquired by gradually paring the control stimulus with the target stimulus until an association is made. The control stimulus is then gradually eliminated by altering its size, color, or intensity (Fields et al. 1976). In stimulus transfer procedures, stimulus control from the prompt (control stimulus) to the target stimulus occurs using successive pairings of the control stimulus with target stimulus (Terrace 1963b; Touchette 1971). Stimulus shaping procedures involve the subtle changing of the control stimulus over time to slowly create the target stimulus (Dietz and Malone 1985). Additionally, without the effective transfer of behavioral control from prompt to target stimulus, the subject can develop prompt dependency (MacDuff et al. 2001; Reid et al. 2014).

It should be noted that this summary on errorless learning is meant only to introduce the role of learning procedures in stimulus control. This summary is not intended to be a thorough overview of errorless learning, but rather an introduction (for an evaluation of the role of errors in learning see Lauderdale 2015; Maxwell et al. 2001; Poolton et al. 2005).

### Research in Animal Behavior

In laboratory settings, environmental stimulus control has been utilized in order to evaluate auditory discrimination in bottlenose dolphins (*Tursiops truncatus*; Herman and Arbeit 1973), cooperation in humans (Schmitt and Marwell, 1968), and a wide variety of learning procedures in rats and pigeons (e.g., Reid et al. 2014). However, evaluations of stimulus control are also well



applied to understanding the behavior of animals in their natural habitats.

The concept of stimulus control can be applied to evaluations of wild animal behavior in addition to laboratory studies. Specifically, researchers have shed light on the behavioral ecology of animals by evaluating stimulus control. For example, Hansknecht and Burghardt (2010) investigated the visual and chemical cues preceding predatory lingual luring behavior in laboratory reared mangrove saltmarsh snakes (*Nerodia clarkia compressicauda*). Through this evaluation, it was found that antecedent chemical stimuli elicited predatory behaviors and visual stimuli resulted in a weak response rate. Similarly, Iberian wall lizard (*Podarcis hispanica*) demonstrated that antecedent visual stimuli were responsible for stimulating predatory behaviors (e.g., attacks) and chemosensory exploration (e.g., tongue flicks; Desfilis et al. 2003). Examinations of stimulus control on other behaviors such as anti-predatory strategies (Herzog et al. 1989) and maternal behaviors (Farrell and Alberts 2002) in nonhuman animals have led to a greater understanding of the ecology and evolution of various species.

## Conclusion

Stimulus control is integral to the learning process and is a dynamic construct with wide-ranging applications in the scientific and applied evaluations of animal learning. Researchers' and behavior analysts' increased focus on evaluating animal behavior through the lens of stimulus control has broad implications for the study of wild animals, as well as the improvement of welfare outcomes for animals in human care.

## Cross-References

- [Constraints on Learning](#)
- [Discrimination Learning](#)
- [Operant Conditioning](#)
- [Same/Different Learning](#)
- [Unconditioned Stimulus](#)

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## Stochastic Distributions

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## Synonyms

[Probability distributions](#)

## Definition

A set of observations arising from random or probabilistic processes.

## Stochastic Processes

The term “stochastic” arises from the Greek *stokhastikos*, which means to aim or guess at. Generally speaking, a stochastic process is a random process. In scientific usage, a stochastic process is any process operating over time that can result in several different states or outcomes; the particular state or outcome of the process at any given moment in time is determined randomly, according to some probability function. Thus, the outcome at any moment in time cannot be definitively predicted. Instead, such a process is defined by a mathematical function that describes all its possible outcomes and the probability space that defines their relative likelihood of occurrence.

## Distribution of Outcomes

Because stochastic processes have no single definitive outcome, their outcomes are better conceived of as distribution of possible outcomes and their observed or hypothesized frequencies.

## Stimulus Response

### ► Rodentia Sensory Systems

**An Example** As a concrete example, consider a six-sided die. On any given roll, the outcome could be any one of six numbers. Each possible

outcome has an equal probability of occurring ( $p = 1/6 = 0.167$ ), and it is impossible to definitively predict which outcome will occur on a given roll. Thus, the roll of the die is a stochastic process.

If the die were to be rolled a large number of times, a distribution of the observed outcomes could be plotted. Figure 1 gives the results of 100 rolls of a die. In the left panel, the frequency of occurrence of each outcome is given as a histogram; in the right panel, the probability of obtaining each possible outcome is displayed in a line graph. Both graphs are different ways of conceptualizing the same stochastic distribution. Note, in the right panel, that the probability of each outcome's occurrence hovers around 1.67, in line with the probability function underlying the stochastic process of a die roll. As the number of observations increases, the probabilities observed from a stochastic process will come to

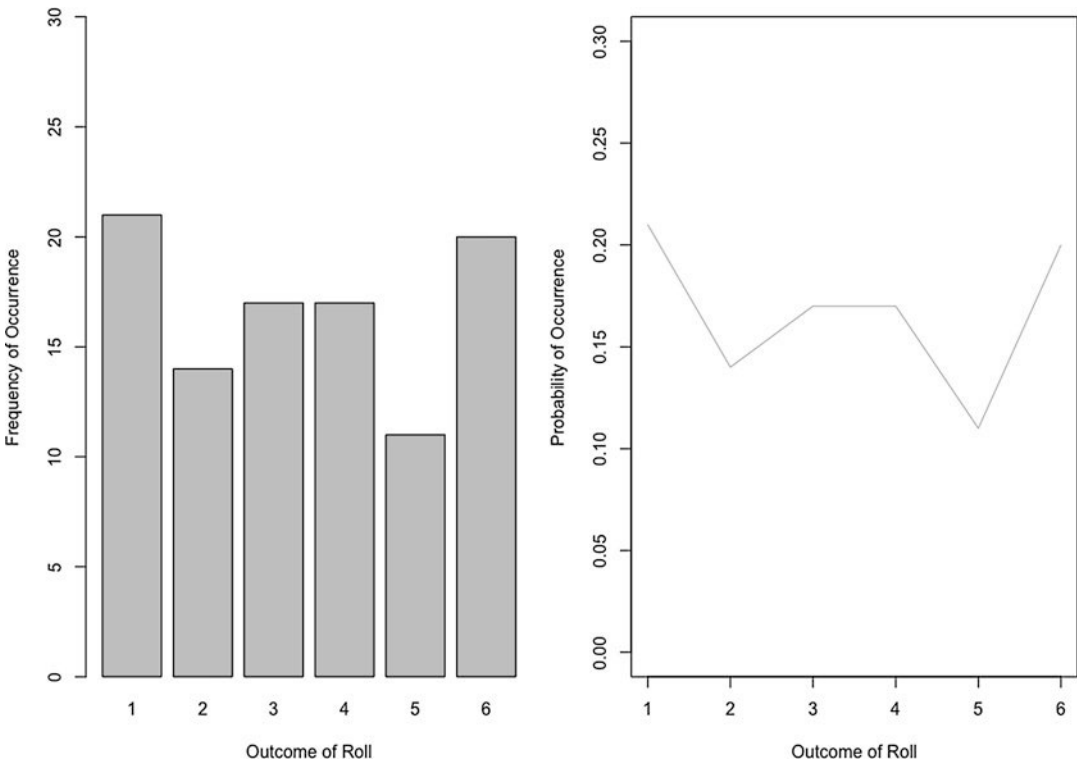
more closely reflect the probability function underlying the process.

Theoretical Distributions

In the example above, the stochastic distribution in question was one observed from real world phenomena. Such stochastic distributions can likewise be seen in data from experiments in animal cognition, provided the observations are derived from processes with some random or probabilistic components. However, the reader may also encounter stochastic distributions in more theoretical settings, such as computational models or statistical tests.

**Stochastic Distributions in Computational Models** When modeling animal cognition, it is useful to assume that there is a random or stochastic element to behavior, in order to accommodate

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**Stochastic Distributions, Fig. 1** Stochastic distribution resulting from 100 rolls of a fair six-sided die, presented as both a histogram of outcome frequencies (left panel) and a distribution of outcome probabilities (right panel)

differences between individual animals or individual trials, or to minimize researcher bias. Researchers will thus hypothesize an underlying distribution from which they randomly draw parameter values. For example, drift-diffusion models (e.g., Ratcliff 1978; Ratcliff and McKoon 2008) assume that the speed with which a participant comes to a decision (i.e., reaction time) depends upon a random sampling of drift rates from a normal distribution with a defined mean and standard deviation. Model fitting techniques are used to determine the exact shape of the distribution. As shown in Fig. 2, some examples of theoretical distributions often used in computational models include:

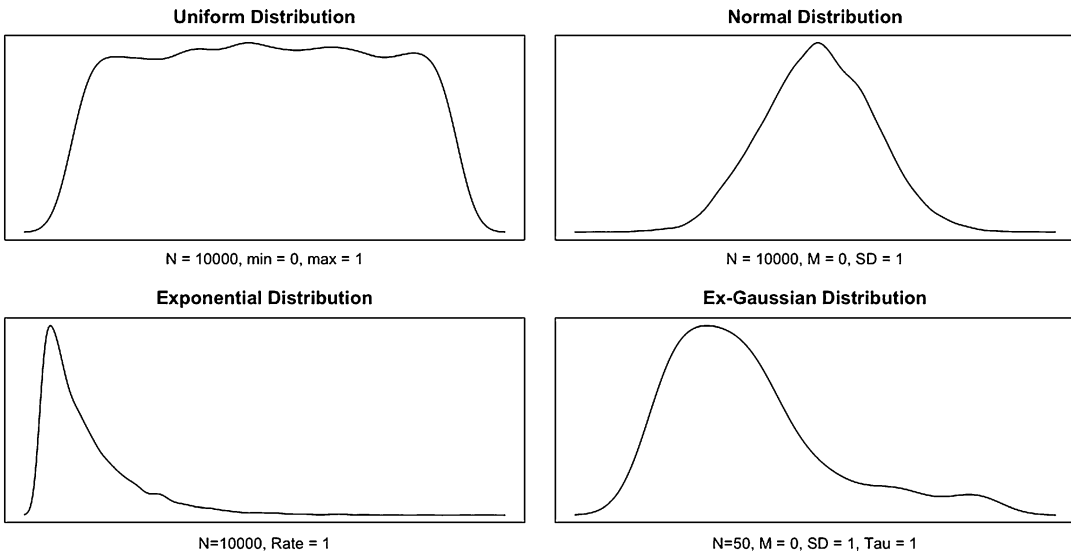
**Uniform distribution.** A continuous or discrete distribution in which every outcome is equally likely to occur, as in the die roll example above.

**Normal (Gaussian) distribution.** A continuous distribution in which the peak probability of occurrence is centered around some mean, with some standard deviation describing the steepness of the (symmetrical) curve away from the mean.

**Exponential distribution.** A continuous distribution that describes the time between events in a process that unfolds at a constant average rate. The probability of an event occurring is a function of the average rate and the passage of time.

**Ex-Gaussian distribution.** A continuous distribution that describes the sum of a Gaussian and an exponential distribution. This type of distribution is often used to model and describe reaction time data, which have been argued to comprise an exponentially distributed decision process and an approximately normal distribution of the duration of various cognitive operations. Ex-Gaussian distributions look like normal distributions with positive skew, due to their exponential component.

**Stochastic Distributions in Statistics** The ultimate objective of a scientific experiment is to say that some result is true, given some manipulation. Although the goal is to demonstrate that the result is true for the whole population of interest (e.g., all rats, all female humans), an experiment is necessarily limited to demonstrating that the result is true for the particular sample it tested. Instead, statistical techniques make use of stochastic



**Stochastic Distributions, Fig. 2** Density graphs of random sampling from four stochastic distributions often used in computational models. Parameters for the random

sampling are given below each panel. Note that as  $N$  increases, the density graphs more closely approximate the underlying probability function

distributions to estimate the result in the larger population. Statistical distributions use the mean and standard deviation obtained in the sample to estimate the mean and standard deviation in the population, provided certain assumptions are met. Although different statistical tests carry different sets of assumptions, all tests assume that the observed sample was selected at random from the population and assigned randomly to different treatment groups. Provided the assumptions are met, statistical distributions allow researchers to determine the likelihood that the effect observed in their sample reflects a real effect in the population. Some common types of statistical distributions include the Student's *t* distribution, the *F* distribution, and the Chi-Square distribution; these are most commonly used with the Student's *t* test, the *F* test, and the Chi-Square test, respectively.

## Cross-References

- [Model Fitting](#)
- [Reaction Time](#)

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## Stone Tools

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## Synonyms

[Animal tool use](#); [Archaeology](#); [Behavioral evolution](#); [Lithic technology](#); [Primate behavior](#)

## Definition

A stone tool is a single, typically moveable piece of rock that is used by an animal to effect a change on its environment. The rock may be modified before use and may be used, either attached or unattached to other objects, as one part of a multi-component tool system.

## Introduction

Because of their durability and ubiquity in the human archaeological record, stone tools are the central piece of evidence available for the long-term study of human behavior. The earliest known stone implements date back 3.3 million years in Lomekwi, Kenya, and they have been used by human societies up to the present day. The hard surfaces and ability to form a cutting edge that rocks provide have made them invaluable for tasks such as pounding, slicing, scraping, and grinding and for the formation of symbolic objects.

The importance of stone tools to human evolution has increasingly made them a target for comparative observations and experiments in nonhuman animals (hereafter, animals). Particularly among primates, but also other animals such as corvids, stones have been used in studies of social transmission, behavioral ecology, and physical cognition and as analogies for the development of human behavior. In both wild and captive settings, stone tools have formed the basis for the exploration of cultural capacities in animal groups. In this entry I focus on wild activities – those observed among animals in their natural habitats rather than in zoos, laboratories, or sanctuaries – although the influence of captive studies will also be considered.

## Why Use Stones?

Stones have two main qualities that render them effective tools: they are abundant and durable. Rocks are typically available on or near the surface of all parts of the planet, excluding those that



have high levels of sediment or ice buildup, such as river floodplains and glaciers. Unlike other tool materials such as plants, they can be found from the tops of mountains to the depths of the ocean, making them accessible to all forms of animal life. Stones also naturally weather into a variety of sizes, from silt and sand to pebbles and boulders, which means that animals of all sizes can manipulate them.

Stones range in hardness from those that usually crumble under slight pressure, such as mudstones, to those that will withstand repeated impacts, such as basalt and granite. The durability of the latter means that they can be relied upon when needed as a tool, which in turn allows for tool use to become entrenched within a given animal's behavioral repertoire. An additional property of some rocks, that they can be conchoidally fractured to produce useable sharp and robust cutting edges, appears to have been discovered only by members of the human lineage (the hominins) since our split from other African apes over 6 million years ago. However, as discussed below, recent discoveries among wild capuchins suggest that production of sharp-edged stones is not unique to humans.

### Stone-Tool-Using Animals

Comprehensive surveys of tool-using animals that include anecdotal accounts exist elsewhere (Shumaker et al. 2011), and the current discussion is therefore intended to be informative rather than exhaustive. Most attention has been directed toward primate use of stone tools, driven initially by observations among East African chimpanzees (*Pan troglodytes schweinfurthii*) in the latter half of the twentieth century (Goodall 1964). The Gombe Stream National Park chimpanzees threw rocks in an aggressive manner toward researchers and baboons, although they did not otherwise use stones as tools. It was only later discovered that some communities of West African chimpanzees (*Pt. verus*) habitually used unmodified stones as handheld hammers to break open encased nuts (Boesch and Boesch-Achermann 2000; Matsuzawa 2011). The fact

that these communities cluster around the junction of modern-day Ivory Coast, Guinea, and Liberia, while other well-studied West African groups such as the Fongoli chimpanzees do not appear to use stone tools, suggests that stone pounding emerged independently in that region, perhaps as recently as a few hundred thousand years ago (Haslam 2014). In any case, the geographical, phylogenetic, and functional restriction of chimpanzee stone tool use to nut-cracking in *Pt. verus* indicates that it is likely a specialized, derived behavior in this subspecies. Recent reports of West African chimpanzees accumulating rocks in and around specific trees, accompanied by displays that include drumming and vocalizing, add an interesting although as yet under-explored component to this picture (Kühl et al. 2016).

The possibility that chimpanzees and humans shared a common, stone-tool-using ancestor is diminished by the absence of such activities among the second *Pan* branch, bonobos (*P. paniscus*). Similarly, there is no evidence as yet of wild stone technology among the other great apes: gorillas and orangutans. Moving further out along the primate family tree, the next species that has been observed to commonly use stone tools under natural conditions is the long-tailed macaque (*Macaca fascicularis*) of Southeast Asia. Macaques in coastal areas of both Thailand and Myanmar use stones to break open a wide variety of shoreline species, particularly shellfish such as oysters and gastropods living in the intertidal zone (Gumert and Malaivijitnond 2013). While the gastropods are cracked open on an anvil using a handheld hammerstone, similar to chimpanzee nut-cracking, oysters are opened using precise strikes onto the shell, while they remain attached to a rocky substrate. This behavior requires the macaques to strike not just downward, as West African chimpanzees do, but sideways and occasionally even upward to access an oyster. Macaques do also crack nuts, especially the sea almond (Falótico et al. 2017), but their focus on animal, often mobile, prey differentiates them from other stone-tool-using primates. Their geographic and phylogenetic separation from the African great apes indicates that they too have independently converged on this behavior.

Moving across to the New World monkeys, the final species of known habitual stone-tool-using primate is the bearded capuchin (*Sapajus libidinosus*). These animals predominantly use their tools to crack open encased nuts, fruits, and seeds, including some with relatively hard shells that require full-body extension to raise a pounding stone to the required height before striking (Visalberghi et al. 2015). However, some wild capuchin groups have also developed the use of stones as aids when digging for underground foods such as arachnids and tubers and for directly percussing a handheld stone against a stationary rock, fracturing the former and releasing quartzite dust (Falótico and Ottoni 2016). The fracturing behavior, termed stone-on-stone (SoS) percussion, produces sharp-edged, conchoidally fractured pieces that possess the same technological characteristics as early human flaked tools (Proffitt et al. 2016). However, the capuchins do not use the sharp flakes, instead licking and sniffing at the dust released by their activities for reasons that are currently unclear. Female capuchins may also engage in aimed stone throwing to attract the attention of males as a form of sexual display which, along with SoS percussion, provides examples of non-foraging-related use of rock tools. Given that tool use among wild platyrrhines is very rare, the evolution of these behaviors is a further example of primate convergence on stone technology.

Outside the primates, there are few examples of habitual use of rocks as tools. However, those that have been observed offer insights into the ways that stones can be aligned with the anatomy and activities of non-primate species. In birds, for example, Egyptian vultures (*Neophron percnopterus*) have repeatedly been observed using their beaks to drop or throw stones onto ostrich eggs to access the yolk inside. This behavior has been suggested to be prompted by environmental cues rather than strongly heritable or learned (Carrete et al. 2017). Dropping as a means of opening encased foods is more widely spread among birds, although in most cases, it is the food that is dropped rather than a stone, which under current definitions does not make this activity tool use. Nevertheless, by dropping food onto stone

anvils, birds make use of a specific part of their environment that requires precision and planning, much the same way that stone tool use does. For example, groups of wild New Caledonian crows (*Corvus moneduloides*) repeatedly drop candle-nuts onto the same stone blocks (Hunt et al. 2002), suggesting that these stone anvils are selected for their usefulness. A similar anvil-based behavior has been reported for wild tuskfish (*Choerodon* spp.) in breaking open molluscs and other prey (Harborne and Tholan 2016).

The most prolific wild non-primate stone tool user is the sea otter (*Enhydra lutris*). Members of this species that specialize in feeding on tough-shelled prey such as marine snails and bivalves are most likely to employ rocks during foraging, partly as a result of high encounter rates with these prey (Fujii et al. 2015). The otters typically dive to collect their prey from under the water but return to the surface to feed while lying on their back. On occasion, otters also bring up a stone that they hold on their chest and strike the prey against, while stones also may be used as paw-held hammers. Genetic studies show that relatedness is not one of the main determining factors for whether an individual sea otter uses tools (Ralls et al. 2017), but instead this behavior may be a result of competition among specialized mollusc feeders.

As noted, rocks come in a variety of grain sizes, which has enabled some smaller invertebrates to become stone tool users. Notable among these are the corolla spiders (*Ariadna* sp.) of Namibia, which arrange a circle of usually 7–8 quartz grains around their burrow. These grains are typically less than a centimeter in width, and the spider attaches a taut thread to each of them as a means of detecting any prey that disturbs the circle (Henschel 1995). The fact that the spider first positions, and then is in remote contact with, each stone qualifies this behavior as tool use, although it differs from the percussive activities prevalent in other species. A second invertebrate example of stone use is found in the larvae of flies such as *Myrmeleon* sp., known as ant lions, who project sand grains toward prey (Pierce 1986). The result is to cause the prey to fall into a conical pit that has been previously been excavated by the

ant lion, enabling capture. Habitual stone tool use for non-foraging activities has yet to be described in an invertebrate species.

## Stone Tool Function

Leaving aside the symbolic and cutting functions associated with hominin lithic technology, the primary use of stone tools is force transmission and amplification. The most common targets of mammalian (primate and sea otter) rock use are encased foods, including nuts, seeds, and molluscs, that are difficult or impossible for the animal to open using only its teeth and hands or paws. For those capuchin groups that engage in the practice, digging activities also involve percussion, in that the stone is used to forcefully break up tough sediments and assist with enlarging holes. The same purpose underlies Egyptian vulture stone tool use and indirectly applies to those species such as New Caledonian crows and tuskfish that drop or throw food onto specific stone anvils. Capuchin SoS percussion does not have an intermediate target such as a nut, which means that even greater force is transmitted between the hammerstone and the underlying anvil or passive stone, contributing to the likelihood of hammerstone fracture (Proffitt et al. 2016).

Force transmission is relevant to those species that throw or project rocks toward targets. The high density of many stone materials ensures that they are less affected by air friction or winds during their flight than other materials such as leaves or grass. This characteristic means that the force imparted to the stone by the thrower is more readily transferred to the target on impact, as seen in the case of ant lions or chimpanzees. The West African chimpanzees that accumulate stones around trees may also be making use of force transmission to generate loud noises from the contact between the stone and tree trunk or buttresses. Throwing stones is therefore typically not a stealthy activity, even leaving aside direct contact with an intended target, and this feature is exploited by capuchins during sexual displays. Even a stone that misses its target will usually

cause a disturbance that startles the target and draws its attention toward the thrower, which is the apparent intention of female capuchins.

The case of corolla spider stone tools is unusual in that, while it is still foraging-related, it does not involve the stone directly amplifying or transmitting a force from the user to the target. Instead, a passing prey animal causes vibrations in the arranged quartz grains, which in turn alert the spider to its direction and proximity through the attached web strands. In this manner the corolla spider incorporates stones into a multicomponent compound tool, built to serve the same vibration-based detection strategy practiced by many web-spinning spiders.

## Stone Tools and Animal Cognition

The implications of stone tool use for animal cognition have been investigated for several decades, both because of its potential relevance for comparative studies with human cognition and for the study of animal behavior in its own right. One of the common features that apply to all known stone-tool-using animals is the selection of appropriate materials from a heterogeneous background of available rocks. For example, both bearded capuchins and West African chimpanzees in their natural habitats have been shown to match the weight and material (and thereby density) of a hammerstone to the toughness of the nut that they need to break open (Visalberghi et al. 2015). Wild long-tailed macaques in Thailand also select larger stone tools to open larger prey items (Gumert and Malaivijitnond 2013), and Egyptian vultures preferentially throw smooth over jagged pebbles at ostrich eggs (Thouless et al. 1989). Such selection does not necessarily require complex brains, as the width of the quartz grains arranged by a corolla spider also closely tracks the spider's body size and the diameter of its burrow (Henschel 1995). This universal selection process derives from the fact that not all stone materials are suitable for all tasks. Tool selection is therefore often likely to be driven by the functional fit between a rock's affordances, an animal's physical capability, and

the required outcome, rather than a conscious decision-making process.

Rocks that are suitable for use as tools are not always available in the immediate vicinity of the site where they are needed, so all wild stone tool users also transport materials. Transport distances can range from centimeters in the case of the corolla spider to tens or hundreds of meters for monkeys and vultures, to kilometers for chimpanzees (Luncz et al. 2016), although in each case the cumulative effect of multiple movements through time may increase the overall distance that a given tool travels. Transport costs can also affect stone selection, for example, wild capuchins have been experimentally shown to transport lighter stones when the subsequent travel distance to an anvil is extended (Visalberghi et al. 2015). Both hammer and anvil stones are transported by wild capuchins cracking cashew nuts in Brazil, chimpanzees breaking palm nuts in Guinea, and sea otters in the eastern Pacific (Haslam et al. 2017). Anvil transport has yet to be documented in wild macaques, although its future discovery by researchers or innovation by the macaques cannot be ruled out. In the case of both selection and transport, an animal needs to be able to recognize technically salient aspects of the available rocks, including characteristics such as density that may not be immediately visually obvious. The solution employed by most animals is haptic, by touching, moving, and sometimes lifting a potential tool in order to assess its suitability.

Collectively, the selection and transport of rock material to tool use sites is part of a process by which these materials are incorporated into what has been described as a body-plus-tool system (Mangalam and Frigaszy 2016). In this scheme, tools become an embodied part of the animal's perception of itself, in effect meaning that feedback (such as vibrations and shifts in tool weight distribution) is experienced by the animal as occurring to a part of its own body. This kind of material cognition may even extend to the environmental niches created by tool-using animals, as they repeatedly bring objects and the targets of tool use together in specific locations on the landscape (Mosley and Haslam 2016). The long-term durability of stone tools and anvils means that

such collection points both lower the costs of assembling such sites for future tool users and provide a scaffold for the more rapid learning or adoption of tool use by juvenile group members. In wild stone-tool-using primates, this learning process typically involves years of play and practice before full proficiency is achieved, while in corolla spiders and Egyptian vultures, the behavior appears to occur spontaneously.

## Stone Tools and Social Behavior

Beyond documenting the development of individual skills, stone tools have assisted with investigations into the emergence and spread of group-specific behaviors. Where these behaviors extend in time and across multiple individuals in an interacting group, they can be considered traditions, and sets of traditions that differentiate one group or community from another may be labeled animal cultures. Experiments with captive animals, particularly chimpanzees (although not necessarily of the West African subspecies), have repeatedly demonstrated how social transmission of novel behaviors can occur (Whiten 2017). Cultures and traditions can involve any aspect of shared, learned behavior, from vocalizations to social interactions (McGrew 2004) but of relevance to the current instance are those involving rocks.

Wild West African chimpanzees confronted with natural and artificial stone tool selection tasks have demonstrated an ability to learn by observing the actions of others. This spread of social knowledge has involved both the foods suitable for targeting with such tools (Biro et al. 2003) and the materials suitable for use at a given time (Luncz and Boesch 2014). Use of digging rocks by wild capuchins at Serra da Capivara National Park (SCNP), Brazil, but not by groups of the same species at the Fazenda Boa Vista site (which instead dig using their hands), may also be a result of social traditions within these communities. When combined with other differentiating activities that have no clear ecological drivers, such as stick tool use among the SCNP capuchins (Cardoso and Ottoni 2016), the collected suite of

distinguishing behaviors suggest that bearded capuchins also exhibit cultural norms. The cultural mechanisms and patterning of New Caledonian crow tool use are subjects of a currently unresolved debate, although these discussions concentrate on plant tool manufacture and use, and stone anvil use has yet to be examined in this light.

Research into sea otter stone tool use has not found social learning to be an important component of this behavior. Instead, individual learning tied to familiarity with prey species that require or benefit from technological processing seems to be more important determinants. Given that feeding preferences can be transmitted from mother sea otters to their children, tool use may also be indirectly transmitted within specific lineages, but clear evidence for such technological transmission is currently lacking, and group-specific tool use traditions have yet to be identified in this species (Fujii et al. 2015). Vulture rock throwing has seen less research intensity, but both individual and social learning strategies are unlikely explanations for this activity (Carrete et al. 2017). Instead, personality traits that differ between individuals may result in reinforcement of stone tool use in some vultures but not in others, building on a natural propensity for dropping smooth objects. Neither corolla spider nor ant lion tool use has been studied in sufficient detail to discern traditional or cultural patterns, and at present these are assumed to be expressed with little variation by naïve individuals.

Studying behavior in animals removed from their natural environmental and social settings is problematic, especially when the overwhelming influence of human captors is taken into account (Haslam 2013). However, studying animals in laboratory contexts can, at times, allow for researchers to investigate variables that might influence stone technology in a more controlled manner. For example, caged capuchin monkeys spontaneously broke stones that were provided to them by experimenters in a laboratory, in the absence of any immediate need for such broken pieces (Westergaard and Suomi 1994). One of these captive animals also used stones to cut through an acetate barrier to reach a food reward,

on occasion breaking the stones to reduce them to a useable size. Similarly, captive bonobos raised as members of an ape-human collective also were encouraged to break stones in order to obtain a cutting edge and get a food reward (Whiten et al. 2009). With practice, these animals were able to remove small, sharp-edged flakes from a larger stone core, although the total assemblage of broken stones that this activity produced were readily distinguishable from those produced by ancient hominins. A juvenile zoo-housed orangutan was also successfully encouraged to break and use stones to cut a cord and retrieve food (Wright 1972). No captive or wild animal of any species is known to have spontaneously flaked and then used cutting stones without human intervention and encouragement, although judging by attempts to date, it is likely that an individual could eventually be trained to produce and use simple stone assemblages that mimic hominin flaking.

Using captive animals to investigate the development of behaviors that naturally occur within their own species, rather than attempting to get them to imitate hominins, adds a level of ecological veracity. For example, chimpanzee social learning of nut-cracking with stone tools has been demonstrated under captive, sanctuary conditions (Whiten 2017). This work showed that, provided individuals had reached a similar age to that seen among proficient wild West African chimpanzees, socially observing nut-cracking increased an individual's own nut-cracking activities. The East African chimpanzee subspecies (*P. t. schweinfurthii*) studied in this experiment does not presently use stone tools in the wild, which lends further weight to the conclusion that wild chimpanzee nut-cracking in West Africa is derived and cultural rather than solely genetically mediated.

Social transport and use of rocks results in the nonrandom accumulation of durable materials across a landscape. While the actions of a single individual may be difficult to identify and interpret, the repeated activities of a social group build up an often unintended but distinctive assemblage of related tools. This basic principle underlies the search for and analysis of sites created by hominins over the past few million years (see



below), enabling their archaeological investigation. However, since the start of the twenty-first century, archaeologists have increasingly turned their attention to the stone assemblages left by wild animals, building on prior work that recognized the value of reconstructing chimpanzee behavior from widespread and patterned activities such as nest building (Stewart et al. 2011). Initially conceived of as chimpanzee or primate archaeology, and at present still dominated by excavations and analysis of primate stone pounding behavior, this work is growing to encompass other stone tool using species (Haslam et al. 2017). Although in its early stages, this practice adds an extended temporal dimension to the behavioral work on wild primates conducted over the past 50 years, enabling direct investigation of topics such as the longevity and geographical spread of stone tool traditions and the identification of tool use in vanished animal populations.

## Human Stone Tools in Animal Context

This section summarizes the major trends in hominin lithic technology, as currently understood, in order to contextualize the preceding discussion of animal stone tool use. The key difference between the two is that members of the human lineage developed a reliance on breaking stone tools to form either useful edges or intentional shapes. While hominins have also likely used pounding tools for force amplification throughout our technological history, those tools are often difficult for archaeologists to distinguish from naturally occurring rocks. Advances in the study of use-damage patterns on pounding tools hold promise but are in their infancy when detecting early percussive stones (Haslam et al. 2017). The story of human stone tool use is therefore almost exclusively derived from flaked stones, including assessments of cognitive and manual abilities and social information transmission.

As noted, the earliest known flaked stone tools come from the 3.3 million-year-old Lomekwi 3 site in Kenya (Harmand et al. 2015). These

tools were accompanied by large rocks that were interpreted as anvils, suggesting that the flakes were broken against those anvils rather than being made by striking one handheld rock against another. The site predates evidence for members of the *Homo* genus by half a million years, leaving a species of *Australopithecus* or *Kenyanthropus* as the most likely creators. A 3.4 million-year-old site in Ethiopia also has evidence for animal butchery using stone tools, although in that case the cut-marked bones, rather than the tools themselves, were recovered (McPherron et al. 2010).

There is no reason to assume that, once Lomekwian technology was invented, all hominins used flaked stones for the subsequent 3.5 million years. The early stone record is very patchy, and the next identifiable flaked stone tools after Lomekwi date from much later at 2.6 million years ago. These simple broken cobbles are part of the Oldowan tradition, named after the early archaeological site of Olduvai Gorge in Tanzania. *Homo habilis* is assumed to have produced at least some of the Oldowan, although contributions from contemporaneous australopiths cannot be ruled out. Humans continue to make and use simple flaked stones right up to the present day, with additional, more complex, stages added onto this foundation.

The second major step in hominin lithic technology was the deliberate shaping of large tools to produce cutting and chopping edges, sometimes with symmetrical shapes. This tradition is called the Acheulean, after the French site of Saint-Acheul, and it emerged around 1.7 million years ago. This timing roughly coincides with early records of *Homo erectus*, who had a much enlarged brain compared to prior hominins, and there are strong associations between this species and the Acheulean at a number of sites. Like the Oldowan, much of the Acheulean is assumed to have been targeted at carcass processing, as meat increasingly entered hominin diets. *H. erectus* was the first hominin to range widely across the Old World, and its enhanced technological skills would have been a crucial part of that process.

The final major step in hominin stone technology starts at different times in different places but was underway by around half a million years ago.

At that point a number of *Homo* species were emerging in Africa and Eurasia, including *H. neanderthalensis* and the Denisovans, and the complexity and interbreeding revealed by recent genetic studies suggests that we should be cautious in assigning any one tool tradition to a given species without direct fossil association (Stringer 2016). Variously known as the Middle Stone Age or Middle Paleolithic, this stage involved creating smaller, more complex stone tools that were likely combined into composite tools such as spears and hafted scrapers. In some parts of the world, such as Europe, the more recent parts of this tradition involved long stone blades and tiny microliths (these form part of the European “Upper Paleolithic”), but these are not universal developments and cannot be generalized to other regions.

The overall trend in human lithic technology is the development of tool forms that require more precision and more planning in their manufacture and the development of a toolkit that joins stones to other materials using adhesives and binding. Force transmission remains a central part of the function of these tools, including through the focusing of human strength into small surface areas such as a thin cutting edge or the tip of a spear. However, tasks such as scraping and shaping require more precision and modulation of force than simple percussion. It is also clear that humans began imbuing their tools with symbolic meaning, that is, the stones played a role in a wider worldview that was not solely determined by tool shape, material, or usefulness. The origins of symbolic thought are debated, but they were present at least 100,000 years ago.

The human lineage has converged on the same role for stone tools as each of the other animals discussed above. They are used to change human muscular force into an amplified, concentrated, or spatially transmitted form, and they are used as parts of multicomponent tools. Human tendency toward tool use appears to be innate, as in the other species, except that humans rely on object manipulation and combination to a much greater degree than in other species, and they bolster this process with knowledge storage mechanisms underpinned by language. That said, modern humans do not automatically develop the ability

to make even simple Oldowan tools, and like the other tool-using primates, they have to go through a learning period involving repeated trial and error in a social context. It is therefore most likely that earlier humans required the same learning process, during which skills such as the ability to select and transport the correct raw materials were honed.

In this light, the essential difference between human stone tools and those of the mammals, birds, and invertebrates is an ability to derive seemingly innumerable novel technological solutions to risky problems. Humans developed a toolkit that combined stone-, plant-, and animal-derived tools and became reliant on that toolkit to survive in the varied environments into which they dispersed. Animal tool use is, on the other hand, built on specific tools for specific tasks, with little to no flexibility in how those tasks are performed. The animal approach ensures a high degree of success in tool use activities, but it limits those activities to locations with appropriate materials for practice and performance. Human cooperation and reliance on social information enhances the speed and efficiency with which we learn about the affordances of objects around us, although again this is likely to be a difference of degree and not kind, at least when compared with other mammalian stone tool users.

## Conclusion

The usefulness of rocks for force amplification has been discovered multiple times among the primates and in a small number of other taxa. Considering the ubiquity of stones at all time periods, it is probable that the pounding, throwing, and force transmission behaviors seen among living animals were also present in extinct species and in prior members of extant lineages that no longer use such tools. However, recovering evidence of such activities will require further investigation into the use-damage patterns that they would leave on the tools. Where we might currently expect stone tool use but find none – in East African and Central African chimpanzees, for instance – then archaeological research may well

turn up evidence for such use in ancestors of those species living thousands or millions of years ago. Loss of stone technology, which may have happened several times among various early hominins, needs investigation just as much as its innovation and spread.

Inventive, non-primate taxa such as wild octopuses, elephants, cetaceans, and corvids are targets for further research into possible stone use. Given the addition in the past decade of well-studied taxa such as wild capuchins and macaques to the known stone-tool-users club, and the comparatively limited investigation of such behavior among invertebrates and aquatic animals, we can be certain that additional wild species will be found using stone tools in future. Of particular relevance to that search will be those animals that consume encased foods or whose foraging can be performed more efficiently by forcefully breaking down barriers. Animal stone tool use has probably always been a rare behavior, with its associated costs of tool selection and handling, but the variety of living species that have converged on it indicates a solution that will have emerged time and again throughout the history of animal life.

## Cross-References

- [Bill McGrew](#)
- [Catarrhine Cognition](#)
- [Comparative Cognition](#)
- [Convergent Evolution](#)
- [Cultural Transmission](#)
- [Culture](#)
- [Cumulative Culture](#)
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- [Teaching](#)
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- [Tool Use](#)

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## Stop-Signal Task

► [Go/No-Go Procedure](#)

## Storage Site of Nuclear Material

► [Nucleus](#)

## Strategy Reversibility

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### Synonyms

[Behavior plasticity](#); [Phenotypic reversibility](#);  
[Reversible plasticity](#)

### Definition

Concept that behavioral and phenotypic adaptations are plastic, or flexible, in the environment and can induce or retract their expression.

### Introduction

For every adaptation or strategy developed to maximize an animal's fitness in the wild, there is also the capacity for the reversal of these traits. Strategy reversibility is a phenomenon that can

occur on different temporal scales and via different mechanisms. Depending on the context, reversibility can be morphologically or behaviorally phenotypic, can involve temporal scales from seconds to thousands of years, and can be responsive to environmental conditions.

## Reversal of Traits in Response to Environment

To fully understand the scope of phenotypic plasticity, and therefore strategy reversibility, organisms must be exposed to and observed in environments with changing factors. An experiment that tested predator-induced plasticity in gray tree frog (*Hyla versicolor*) tadpoles revealed that the differences in development were considerable depending on whether or not tadpoles were exposed to predation in their early developmental stages (Relyea 2003). The phenotypic differences observed were both behavioral and morphological in nature as the tadpoles adapted to potential predators in their environment. Differences included responses in activity level, whereby tadpoles that were exposed to predation during early development reduced their activity level considerably and spent a greater amount of time hiding compared to their counterparts without predator exposure. Tadpoles that changed their behavioral strategies in response to predation were more likely to survive to adulthood than tadpoles that did not adapt different behavioral strategies. Upon removal of the threat of predation in their environment, tadpoles were most likely to return to normal patterns of behavior.

Morphological adaptations were less plastic in that the deeper tail fins, shorter bodies, and greater mass developed by tadpoles exposed to predation were not as quickly reversed as behavioral adaptations were. Animals will also respond with plasticity to an environment that has had a new prey item introduced, but in different ways than those exposed to predation (Gabriel et al. 2005).

Reversibility of traits in the natural habitat of these tadpoles would most likely not only affect the individuals of the species but would also have an effect on the ecological community as well.



An introduced stimulus will affect phenotypic and behavioral strategies for as long as the stimulus remains in the environment and may have collateral effects on other species or resources in the same area. However, reversibility of traits is only utilized when it is necessary to advance the survival value of the individual.

## Strategy Reversibility and the Rise of Mammals

Strategy reversibility may have played a role in the adaptations mammals developed following a massive extinction event that lead to a decrease in predation. Preceding this extinction event, mammals likely adapted to nocturnal behaviors in order to avoid larger, diurnal predators. Following the mass extinction of these larger predators, some nocturnal mammal species may have reversed to diurnal behaviors because nocturnal behaviors were no longer necessary or beneficial for the survivor of the individual (Relyea 2003).

## Conclusion

Strategy reversibility is not only a necessary mechanism with which to adapt to a changing environment but also it may exemplify evolution manifesting itself through reversal of survival strategies, phenotypic traits, or behavioral patterns to maximize the probability of species persistence. Being able to display plasticity and flexibility of traits has significant survival value for the majority of species.

## Cross-References

- [Behavioral Flexibility](#)

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## Strepsirhine

- [Haplorhini](#)
- [Primate Sensory Systems](#)

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## Strepsirhini

- [Haplorhini](#)

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## Strepsirrhine

- [Prosimian Cognition](#)
- [Prosimian Communication](#)
- [Prosimian Life History](#)

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## Strepsirrhini

- [Primate Sensory Systems](#)

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## Stress

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## Definitions

Stress may be generally defined as a real or anticipated threat to an organism's ability to regulate its internal environment. Stressors are specific stimuli

that represent such threats to homeostasis. While earlier conceptual models used the term “stress” to encompass any challenge, recent perspectives suggest that the term be restricted to situations that exceed an organism’s regulatory capacity (Koolhaas et al. 2011). Adaptations to specific stressors involve physiological and behavioral changes that are supported by coordinated activity of the nervous and endocrine systems.

## Introduction: The Stress System

Homeostasis involves maintenance of a complex, dynamic equilibrium within the body. Stressors represent challenges to homeostatic regulation, and the brain constantly adjusts behavioral and physiological activity to meet demands of both current and anticipated stress (Ulrich-Lai and Herman 2009). The physiological stress response, involving coordinated activity of the nervous and endocrine systems, is regulated by brain areas that constantly monitor changes in the internal state of the body as well as anticipatory cues in the environment.

Endocrine stress responses are initiated by a cascade of events comprising the hypothalamic-pituitary-adrenal (HPA) axis (Tsigos and Chrousos 2002). Internal (systemic) or external stressors trigger release of corticotropin-releasing hormone (CRH) and arginine-vasopressin (AVP) from parvocellular neurosecretory cells in the hypothalamus. CRH, with a potentiating effect of AVP, triggers release of adrenocorticotrophic hormone (ACTH) from the anterior pituitary gland. ACTH, in turn, stimulates release of glucocorticoids from the cortex of the adrenal gland. The primary glucocorticoid is cortisol in humans and corticosterone in rodents. Glucocorticoids operate at multiple levels to redirect energy resources in the body and to contain the immune response.

Nervous stress responses are mediated in the brain by the locus coeruleus-norepinephrine system (Tsigos and Chrousos 2002). Release of norepinephrine by the locus coeruleus to multiple brain areas causes increased activation of the sympatho-adreno-medullary (SAM) axis.

Activation of this system provides an immediate response to stress and involves sympathetic nerve signals to smooth muscle, cardiac muscle, and glands. Sympathetic signals to the adrenal medulla additionally trigger release of epinephrine and norepinephrine. Increased sympathetic signaling during the stress response is accompanied by altered signaling (usually reduced) through parasympathetic nerves. Activation of the SAM axis produces a set of responses including increased heart rate and energy availability and increased blood flow to muscles and other organs.

Activities of the HPA and SAM axes are regulated by a central autonomic network of brain areas extending from the brainstem to the forebrain (Carnevali and Sgoifo 2014). Systemic stress elicits nervous, hormonal, and immune signals that feed back to the brain. Based on this feedback, brainstem autonomic centers reflexively signal changes in autonomic and neuroendocrine activity. Stimuli in the external environment, in contrast, signal the occurrence of behaviorally relevant events that elicit stress responses. These external stimuli include direct, or neurogenic, stressors such as restraint as well as anticipatory cues in the environment.

Intermittent stressors evoke short-term activation of the stress system. Once activated, several mechanisms promote termination of the autonomic and neuroendocrine stress responses. Cardiovascular recovery following stress-induced autonomic activation is mediated by engagement of a vagal parasympathetic reflex, termed vagal rebound (Mezzacappa et al. 2001). Inhibition of cortisol release in response to short-term stressors is mediated by feedback mechanisms at the level of the paraventricular nucleus of the hypothalamus and the pituitary gland.

## Processing of Systemic Stress

Systemic stressors reflect changes in the internal state of the body. These changes generate nociceptive (pain) signals, neuronal and circulating homeostatic signals, and circulating inflammatory signals (Herman et al. 2003) that are detected by the brain. Several interconnected areas of the

medulla oblongata generate reflexive autonomic responses to systemic stressors.

During physical activity, for example, the nucleus of the solitary tract (NST) in the medulla oblongata receives sensory input related to changes including blood pressure, chemical composition of the blood, and nociceptive signals. Based on these inputs, the mammalian NST adjusts ongoing activity of the cardiorespiratory system through connections with other medullary autonomic centers. Sympathetic tone is regulated by neurons in the ventrolateral medulla oblongata that signal preganglionic neurons in the spinal cord. Neurons in two other medullary areas, the nucleus ambiguus and the dorsal motor nucleus of the vagus, are involved in parasympathetic control. (Ulrich-Lai and Herman 2009).

The NST also relays systemic input to higher brainstem and forebrain areas where they are integrated with descending limbic information. One of these areas, the hypothalamus, is a major center for coordinated control of the nervous and endocrine systems. The paraventricular nucleus (PVN) receives a variety of nervous, hormonal, and immune-related inputs and, on the basis of these signals, adjusts ongoing autonomic activity through connections with pre-autonomic neurons in the brainstem and spinal cord. Based on these inputs, the PVN also increases activity of the HPA through release of CRH. Studies with rodents have revealed that ascending homeostatic signals (such as hunger or pain) are processed in the PVN together with descending limbic signals (such as exposure to a novel environment) evoked by anticipatory stressors. The integrated sum of this processing results in modulation of HPA activity.

## Processing of Neurogenic and Anticipatory Stress

As opposed to reflexive responses discussed above, stress responses to environmental stimuli involve higher-order sensory processing. Laboratory studies in rodents have employed a variety of external stressors to investigate physiological aspects of the stress response; these include restraint, social defeat, and forced

swim paradigms. In these studies, different types of stressors elicit responses in reaction to, or in anticipation of, stressful events. Controllability of a stressor is a key factor in the pattern of physiological stress response. Uncontrollable stressors are associated with delayed physiological recovery in cardiovascular and glucocorticoid measures.

The locus coeruleus (LC) in the pons displays stress-related activation through inputs from central autonomic centers including the paraventricular nucleus (PVN) and the amygdala (Berridge and Waterhouse 2003). Based on these inputs, LC neurons release norepinephrine to areas of the central autonomic network in support of physiological and behavioral stress responses. In addition, the LC plays a role in vigilance and general arousal through extensive connections with other brain areas.

Anticipatory stress responses are regulated by limbic areas in the forebrain and brainstem involved in processing emotion and memory (McDougall et al. 2005). The amygdala, located in the temporal lobe of the cerebrum, generates immediate fear responses involving behavior as well as changes in physiological state through activation of SMA and HPA axes. The central amygdala integrates systemic stressors with environmental, or psychogenic, stress signals from the basolateral and medial amygdala. In rodents, neurons in the basolateral amygdala display activation in response to stressors including predator exposure, footshock, and restraint.

As the major output hub, the central amygdala elicits sympathetic responses through connections with downstream components of the central autonomic control network, including the locus coeruleus, dorsomedial nucleus of the hypothalamus, and nucleus of the solitary tract. The central nucleus of the amygdala activates the HPA axis through connections with the paraventricular nucleus of the hypothalamus.

The bed nucleus of the stria terminalis (BNST), in the basal forebrain, plays a broad role in valence surveillance related to current physical and social context (Lebow and Chen 2016). The BNST provides for coordination of physiological and behavioral responses and adaptive regulation of energy

balance. This area integrates input related to threat and reward with information related to current homeostatic state and arousal. With respect to anticipatory stress, the BNST integrates excitatory and inhibitory input from diverse limbic areas including the amygdala, hippocampus, and medial prefrontal cortex. In contrast to the amygdala, the BNST mediates sustained fear characterizing anxious states. Integrated output from the BNST projects to hypothalamic and brainstem areas involved in ongoing control of autonomic and neuroendocrine activity.

The paraventricular nucleus of the hypothalamus regulates stress responses through coordinated activity of the autonomic and neuroendocrine systems (Buijs and Van Eden 2000). As discussed above, systemic and environmental stressors trigger HPA axis activity and release of glucocorticoids. Stressors also trigger autonomic responses by pre-autonomic PVN neurons projecting to the brainstem and spinal cord. During exercise, the PVN mediates reflexive cardiovascular and neuroendocrine control based on systemic input from medullary centers, including the NST. Systemic input to the PVN includes peripheral inflammatory signals related to infection. The PVN also generates anticipatory stress responses based on input from the amygdala, prefrontal cortex, and hippocampus. These inputs signal changes related to emotion, reward, and mood.

The dorsomedial hypothalamus (DMH) mediates cardiovascular, neuroendocrine, and behavioral stress responses evoked by exposure to threatening stimuli. For this reason, the DMH is a key component of the “hypothalamic defense area.” The DMH integrates stress signals from several forebrain areas including the amygdala, median preoptic area of the hypothalamus, and medial prefrontal cortex (DiMicco et al. 2002). In rodents, excitatory inputs to the DMH are elicited by a variety of laboratory stress paradigms including conditioned fear, immobilization, and swim stress. On the basis of these inputs, the DMH signals pre-autonomic neurons in the brainstem. The DMH is also involved in regulation of HPA stress responses through communication with the PVN.

## Modulating the Stress Response

Adaptive goal-oriented cognition requires that default physiological responses to threat or uncertainty be inhibited by top-down regulatory signals from the forebrain (Park and Thayer 2014). Emotional responses involving the amygdala and hypothalamus are shaped by inhibitory inputs from the hippocampus and prefrontal cortex. Distinct forms of emotion regulation have been identified that differentially recruit areas of the amygdala, hippocampus, and prefrontal cortex.

Together, the hippocampus and ventromedial prefrontal cortex exert automatic regulatory control over autonomic and neuroendocrine stress responses. While the amygdala and hippocampus are both critical for fear conditioning (Phelps 2004), the hippocampus is specifically involved in recall of the contextual aspects of fear responding. Studies in rodents and humans indicate that the hippocampus is also critical for safety learning and fear extinction, whereby an animal learns that certain contexts are no longer threatening. Recall of fear extinction memory activates both hippocampus and medial prefrontal cortex, and these areas, along with the amygdala, constitute a fear extinction network (Quirk and Mueller 2008). This network is active during consolidation and retrieval of fear extinction memory. Medial prefrontal cortex also directly inhibits HPA and SMA axes through connections with brainstem autonomic areas and the PVN (McKlveen et al. 2015).

In humans, emotional stress responses are also regulated through effortful strategies including suppression and cognitive reappraisal (Goldin et al. 2008). Emotional suppression involves attempting to hide or inhibit ongoing behavior. This strategy recruits ventrolateral prefrontal cortex for behavioral inhibition and is also associated with greater amygdala activation and increased physiological stress responses. Cognitive reappraisal, in contrast, involves reinterpreting the meaning of an emotional situation. Cognitive reappraisal of stressful stimuli evokes activity in lateral prefrontal cortex and ventromedial cortex but reduces activity in the amygdala with associated reduction of autonomic and neuroendocrine stress responses.

## Stress and Neuroplasticity

Chronic stress exposure induces a persistent state of physiological activation referred to as allostasis (McEwen and Gianaros 2011). Such exposure can lead to long-term changes in the structure and function of brain areas involved in the stress response. This capacity for change in synaptic organization, termed neuroplasticity, encompasses a variety of adaptations that either depress or facilitate synaptic activity (Bains et al. 2015). Neuroplasticity permits information storage related to prior experience and allows the brain to shape subsequent responses to stress. Maladaptive neuroplasticity impairs stress regulation and is associated with deficits in cognition and mood disorders. Exposure to chronic or intense psychological stressors may increase the response to subsequent stress. Adaptive neuroplasticity, in contrast, enhances regulation of stress responses and is linked to improvements in cognition and memory. Systemic stress related to repetitive physical activity triggers adaptive neuroplastic changes that reduce the impact of psychological stress.

Central autonomic circuits that process systemic stressors overlap with those involved in processing psychological stressors. Thus, neural adaptations to a particular stressor can modulate reactivity to stressors of a different modality (Rimmele et al. 2009). This effect is the key to how physical activity reduces the physiological impact of psychological stress.

## Psychological Stress and Maladaptive Neuroplasticity

Chronic or intense psychological stress can impair the capacity for emotion regulation and has negative effects on memory and cognition. Recent research suggests that these effects are due to maladaptive neuroplastic changes in stress regulatory areas including the amygdala, hippocampus, and medial prefrontal cortex. Chronic psychological stress increases the size of the amygdala with associated changes in dendritic structure (Pittenger and Duman 2008). The resulting increases in amygdala activity may enhance fear learning and anxiety.

In contrast to the amygdala, chronic stress induces decreased size and activity of the hippocampus and medial prefrontal cortex. These effects are mediated by excessive exposure to stress-induced neurotransmitters and glucocorticoids. Rodent studies have linked acute and chronic stress exposure to suppression of neurogenesis, dendritic atrophy, and impaired memory formation in the hippocampus. Chronic stress also decreases dendritic density in the medial prefrontal cortex. These effects help explain the effects of stress on the development of mood disorders as impaired hippocampal neurogenesis is a key neural correlate in major depression (Pittenger and Duman 2008). Deficits in emotion regulatory capacity are reflected in indices of peripheral autonomic control. Psychopathologies such as anxiety and depression, for example, are characterized by lower measures of heart rate variability (Park and Thayer 2014).

Chronic stress alters HPA axis regulation by the paraventricular nucleus in complex ways, depending upon the nature and duration of the stressor. Chronic stress initially triggers increased expression of CRH and output of glucocorticoids. Physiological effects of excessive cortisol output include visceral adiposity, insulin resistance, and psychological disorders including anxiety and depression (Tsigos and Chrousos 2002). With exposure to longer-term or severe stressors, however, cortisol output is reduced. Moreover, reduced expression of receptors may lead to glucocorticoid resistance and detrimental effects on immune function.

## Physical Activity and Adaptive Neuroplasticity: Brainstem and Hypothalamus

Regular physical activity evokes neuroplastic changes in the brainstem and hypothalamus. Mechanisms of neuroplasticity in these areas include increased vascularization, synaptic modification, and long-term changes in gene expression (Voss et al. 2013). Studies in rodents link regular exercise to altered neurotransmission in the brainstem and to dendritic changes in multiple brainstem areas involved in cardiovascular



control. Beneficial effects of exercise-induced neuroplasticity include (1) optimization of autonomic activity at rest and during exercise and (2) reducing the physiological impact of psychological stress.

In response to regular exercise, neurons in the rostral ventrolateral medulla and NST display alterations in signaling by the neurotransmitters GABA and glutamate, leading to decreased sympathetic and increased parasympathetic signaling (Martins-Pinge 2011). In rodent studies, other effects of regular exercise include reduction in dendritic density in the NTS and periaqueductal gray matter, reducing the relative number of excitatory synapses and decreasing resting sympathetic tone and reactivity. Exercise-induced effects on medullary areas, including the NST, are also linked to oxytocin released from the PVN (Micheline and Stern 2009). Oxytocin exposure may serve to enhance vagal outflow signals from the brainstem, thus moderating heart rate responses to exercise. Neuroplastic changes in other areas of the medulla oblongata are linked to production of peripheral signaling molecules. Irisin, a circulating myokine produced by muscle cells, evokes synaptic adaptations in cardiac-projecting neurons of the nucleus ambiguus in the medulla oblongata (Brailoiu et al. 2015) and increases parasympathetic outflow through the vagus nerve.

Chronic exercise also alters GABA signaling in the PVN of the hypothalamus, with corresponding reductions in sympathetic tone and blood pressure. In rodents, neuroplastic changes in the PVN also alter HPA activity with reductions in glucocorticoid levels and reduced reactivity to psychological stressors (Morgan et al. 2015). Exercise-related homeostatic signals in the PVN linked to neuroplastic changes include blood glucose and nitric oxide.

### **Physical Activity and Adaptive Neuroplasticity: Hippocampus and Amygdala**

Physical activity triggers neuroplastic changes in limbic forebrain areas, with the most pronounced effects observed in the hippocampus and amygdala.

Exercise promotes hippocampal neurogenesis, changes in dendritic morphology, and long-term potentiation with corresponding improvements in spatial learning and memory tasks (Vivar et al. 2013). Regular exercise also reduces age- and disease-related declines in neurogenesis.

Regular physical activity promotes adaptive neuroplastic changes in the hippocampus by stimulating central and peripheral production of key signaling molecules (Cotman et al. 2007). These include insulin-like growth factor 1 (IGF-1), brain-derived neurotrophic factor (BDNF), and vascular endothelial growth factor (VEGF). BDNF is the most widely expressed neurotrophin, and exercise increases levels of BDNF in several areas of the brain including hippocampus and amygdala. Rodent studies suggest that exercise-related increases in hippocampal BDNF are mediated in part by peripheral signaling molecules including IGF-1, ghrelin, and irisin. Chronic exercise may support the effect of IGF-1 on adaptive neuroplasticity by decreasing the production of pro-inflammatory cytokines.

Physical activity also evokes adaptive neuroplastic changes in the amygdala. These effects are mediated in part by increased expression of BDNF and other molecules in the basolateral amygdala involved in intracellular signaling and synaptic function (Liu et al. 2009).

Effects of exercise on the amygdala are dependent upon the nature and intensity of the activity. Chronic treadmill running, but not wheel running, in rodents increases levels of BDNF in the amygdala associated with improvements in cued fear learning.

Regular exercise, by stimulating BDNF production in the amygdala, may promote proper regulation of amygdala function by serotonin (Daftary et al. 2012). Experimental depletion of BDNF in the amygdala of mice reduces the inhibitory effect of serotonin, increasing stress-related signaling by the amygdala. Moreover, exercise-induced changes in serotonergic signaling in the dorsal raphe nucleus of the midbrain may reduce stress signaling to the amygdala, thereby enhancing resilience to external stressors (Morgan et al. 2015). Treadmill and wheel-running paradigms in rodents increase expression of a regulatory protein, galanin, in the locus coeruleus. The resulting

reduction in noradrenergic signals to the amygdala limits anxiety and improves fear conditioning.

## Effects of Physical Activity on Mood and Cognitive Performance

Adaptive neuroplasticity provides the capacity to shape brain responses to ongoing systemic and environmental challenge. Neuroplastic modifications prevent excessive activation of the stress system and permit more efficient energy allocation. Exercise-induced changes in the hippocampus reduce the impact of psychological stress by providing contextual safety signals to other parts of the brain, such as the hypothalamus, involved in stress system activation (Buijs and Van Eden 2000). Neuroplastic changes in circuits involving the amygdala reduce excessive stress system activation in response to perceived threat.

In humans, neuroplastic changes contribute to antidepressant and anxiolytic effects of regular physical activity. Activity-induced neuroplasticity enhances cognitive function by facilitating emotion regulation and the ability to flexibly engage coping mechanisms. By reducing the impact of psychological stress, regular exercise promotes adaptive structural changes in the parts of the brain involved in memory, cognition, and emotion regulation (McEwen and Gianaros 2011).

In rodents, regular exposure to physical activity and enriched environments promote adaptive neuroplastic changes, but through distinct pathways (Olson et al. 2006). Evolutionarily, both conditions may signal a need for adaptation to environmental complexity. Seen in this context, hippocampal neurogenesis represents an investment in future capacity for learning in similar environments. Hippocampal neurogenesis in mammals may also facilitate behavioral modifications during maturation.

## Cross-References

- Amygdala
- Avoidance
- Coping Style
- Diathesis Stress

- Escape Response
- Extinction in Learning
- Fear Response
- Hippocampus
- Homeostasis
- Inhibition
- Long-Term Potentiation
- Medial Temporal Lobe
- Memory
- Neural Network
- Neuroanatomical Plasticity
- Neurotransmitters
- Open-Field Test
- Restraint
- Thyroid and Adrenal Glands

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## Stress and Memory

► [Susan D Healy](#)

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## Stress Coping

► [Coping Style](#)

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## Stress Dichotomy

► [Dichotomous Stress](#)

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## String

► [Cilia](#)

## String Pulling

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### Definition

Retrieving an out-of-reach object by pulling a string attached to it.

### Introduction

During a cold Swedish winter, a raven watches a fisherman cut a small hole in a frozen lake. He drops in a baited fishing line attached to a stick to secure it over the hole. After he leaves, the raven flies down and examines the situation. Although she cannot see deep down the dark waters, she takes the line in her beak, pulls it, and steps on the loop. Repeating this sequence several times, she eventually reaches the end and eats the bait. Other ravens observe how she got her easy catch and make their own attempts with the numerous ice-fishing holes in the country's largest lake. By the end of the winter, local fishermen have stopped ice fishing because they nearly always return home empty-handed due to the ravens' efficient pilfering (Larsson 1958).

These ravens exhibited spontaneous string pulling: they retrieved out-of-reach food (bait and fish) by pulling a string (fishing line) attached to it. String pulling is one of the oldest and most common tests of animal cognition. The Roman naturalist Pliny the Elder (23–79 AD) first documented how goldfinches pull up strings with food and containers of water. Since the beginning of the twentieth century, researchers have investigated the cognitive abilities of a wide array of species by using various string-pulling tests. Around 170 species have been tested in over 210 studies, with these numbers rising rapidly (Jacobs 2017; Jacobs and Osvath 2015).

## Cognition and String Patterns

String pulling provides countless testing conditions when the number and patterns of strings are varied. The simplest configuration is a single straight string that can be pulled to retrieve the attached out-of-reach reward. Its orientation strongly influences performance; horizontal strings are typically easier to pull than vertical ones. Vertical string pulling requires better coordination and motor planning, involving multiple steps of grasping, pulling, and securing the string, with gravity pulling the string back to its original position if a mistake is made. In contrast, horizontal strings require fewer and easier steps and stay in position when pulling has stopped. Most animals therefore perform better on horizontal than vertical setups. For example, human and gorilla infants can pull horizontal strings at an earlier age than vertical ones (Redshaw 1978). Different test orientations hinder species comparisons, with mammals typically tested on horizontal tasks and birds on vertical ones.

Although a single string is the most common condition, it is unclear what cognitive abilities underpin a successful response. String pulling is often seen as a test for means-end understanding, which involves the deliberate execution of a sequence of steps and the removal of an obstacle to achieve a goal (Huber and Gajdon 2006). However, other mechanisms, such as play behavior, and associative learning can also explain successful string pulling. For example, some animals play with strings and may accidentally pull in baited strings as part of their play behavior rather than due to a deliberate attempt to retrieve the food. This alternative interpretation can be avoided by allowing the animal to interact with unbaited strings before testing begins, so they habituate to the string prior to testing. It is also possible to succeed on string-pulling tasks through associative learning. Touching the string may cause the reward to move, which can lead to an association between both events and eventually successful pulling through trial and error. The reward immediately moves closer with every pull, which can form a positive association leading the animal to repeat whatever behavior caused

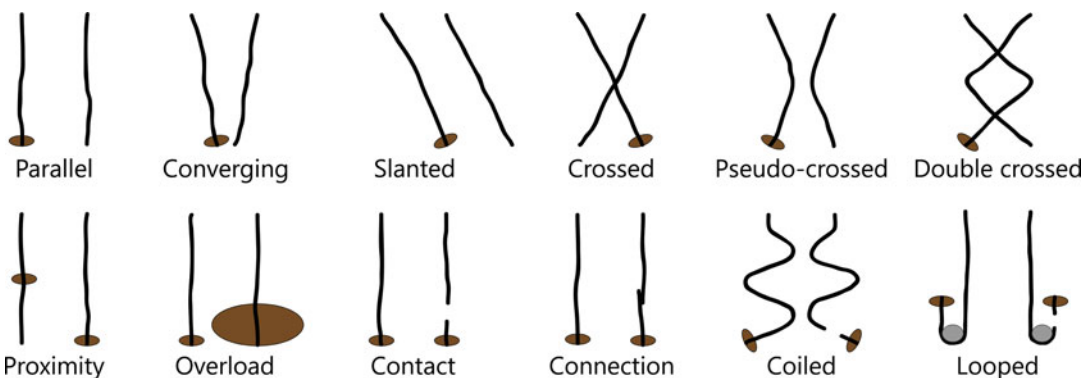
it. Consequentially, experienced animals may pull strings indiscriminately. For example, after pulling up a string and removing the food, some rats pull up the same string again only to find there is nothing attached to it (Ewer 1971).

Animals should be tested on multiple conditions to reveal the cognitive mechanisms they employ during string pulling. In the *parallel* condition, an unbaited string is placed parallel to the baited one (see Fig. 1). Goal directness is shown when animals repeatedly pull the baited instead of the unbaited string. If they only pull strings accidentally, through play, or without attention to the reward, they would pull both equally. For example, a common myna did not perform above chance on the parallel condition in over a thousand trials, and neither did a young jackdaw in over 500 trials, possibly because they were too inattentive and playful (Dücker and Rensch 1977). The *converging* condition requires animals to attend more to the orientation of both strings (see Fig. 1). Nonetheless, a successful strategy in both conditions is to use reward proximity as a cue for which string to pull. The *slanted* condition can show the presence of this heuristic (see Fig. 1). When the baited string slants toward the outside of the pattern, pulling the end of a string closest to the reward will still be successful. In contrast,

when the baited string slants toward the inside, reliance on the proximity of the reward will result in failure. This proximity error is common in many species, with dogs being an especially susceptible example (Osthaus et al. 2005). When the strings are *crossed* (see Fig. 1), reliance on proximity always leads to failure. This may explain why animals typically perform worst on the crossed condition.

Myriad variations of string patterns of various complexities are possible. The *pseudo-crossed* and *double crossed* patterns (see Fig. 1) are meant to increase complexity by introducing non-linear strings, but success on these conditions does not necessarily imply visually tracing the strings; here, too, animals may simply rely on the proximity of the reward (Jacobs and Osvalth 2015). Two rewards are present in the *contact* condition (see Fig. 1), but only the correct one is attached to a continuous string, while the other reward is attached to a string with a gap. The proximity error is then revealed when animals pull both strings indiscriminately.

Means-end understanding excludes heuristic strategies such as using the proximity of reward as a cue for which string to pull. Nonetheless, attending to proximity can sometimes be beneficial. In the *proximity* condition, two functional



**String Pulling, Fig. 1** Twelve common string-pulling conditions (patterns). These examples are horizontal, and most also work vertically. The correct string is always shown on the left, but the position of the baited string is typically counterbalanced across sides. This can make a large difference in the *slanted* condition, because it is asymmetrical and can show the proximity error when the baited string slants to the inside, as shown here. In the

*proximity* condition, both strings can be pulled to retrieve the reward, but the string with the closest reward is the optimal choice. The top row shows the six most common traditional patterns, always having only one reward present. The bottom row shows more recent adaptations with two rewards, which ensures subjects cannot use the position of the reward alone as a cue to which string to pull



baited strings are present, so either can be pulled to retrieve a reward, but pulling the string with the closest reward is the optimal response (see Fig. 1). This kind of efficiency is exhibited by some ravens that attend to object identity (food or not) and proximity simultaneously (Pfuhl 2012).

In the *overload* condition (see Fig. 1), both parallel strings are baited, but one reward is too heavy for the animal to pull in. Under typical circumstances, the subject first approaches the large reward due to its saliency. If he is capable of knowing he cannot pull in a large reward, he should only pull the string attached to the smaller reward. Most ravens ignore overloaded strings without trying to pull them even once (Heinrich 1995; Pfuhl 2012). Such behavioral flexibility is another component of means-end understanding.

Animals go beyond superficial perceptual cues through functional generalization and affordance learning. Recognizing the functional aspects of string pulling allows for successful transfer between conditions. Moreover, changes to the strings' color, texture, or material will then not affect performance. This is indeed not a significant challenge for most species tested after such changes (Jacobs and Osvath 2015). Functional generalization is also evident when individuals use different pulling techniques, which shows they do not have stereotyped responses to similar situations. This can best be investigated with vertical strings, which some animals, particularly birds, may pull in diverse manners. Up to eight different techniques have been reported in kea (Werdenich and Huber 2006).

Most patterns involve straight strings that will immediately bring the reward closer when pulled. Approaching food is rewarding and can therefore create a positive association that leads to repeated pulling without means-end understanding. Unbaited strings are then not repeatedly pulled because they are not reinforced with food moving closer. The effects of visual feedback, or absence thereof, is tested with nonlinear strings. The *coiled* condition involves two coiled strings such that pulling one does not immediately cause its distal end to move (see Fig. 1). As in the *contact* condition, a reward is present next to the broken strings to control for strategies based on reward location. Some

Neotropical parrots chose the connected coiled string above chance, but their previous experience with other patterns may have influenced their choices (Schuck-Paim et al. 2009). In the *looped* condition, the strings loop around a solid object, which when pulled causes its distal end to move away at first (see Fig. 1). An olive baboon appeared to prefer the correct looped string (Bolwig 1962), but this condition has not been tested recently or reliably (Jacobs and Osvath 2015).

Animals relying solely on the reward moving closer would therefore not succeed in these conditions. Visual feedback is also minimized when a straight string is attached to a reward that cannot be seen at first. Ice-fishing ravens exemplify this; it is initially impossible to see the bait or fish when the fishing lines are long and the water is dark. Similar setups are possible for other modes of feedback, such as the weight of closed containers at the string's end (Klüver 1961).

Some authors consider successful string pulling to show means-end understanding, but this is not necessary in all cases. Animals show means-end understanding if (1) they are goal-directed, as tested with the *parallel* condition; (2) they do not rely on reward proximity, as tested with the *slanted*, *crossed*, and *contact* conditions; (3) they can functionally generalize, as shown by overall behavioral flexibility or tested with the *overload* condition and changes to nonfunctional elements of other conditions; and (4) they do not rely strongly on perceptual feedback, as tested with the *coiled* and *looped* conditions (Jacobs and Osvath 2015).

Understanding strings as means to retrieve out-of-reach goals does not guarantee success on all conditions. For instance, it does not necessarily involve an understanding of connectedness. In addition to revealing proximity errors, the *contact* condition tests for the ability to recognize the necessity of contact between string and reward. This is more challenging than the *parallel* condition for many species, such as galahs and cockatiels (Krasheninnikova 2013). However, it is also possible that animals prefer continuous surfaces or generalize from previous conditions in which the baited string always looked similar: continuous and contacting the reward. They may simply

disregard the incorrect option or only consider it as an unbaited piece of string.

In the *connection* condition (see Fig. 1), the distal end of the “broken” string lies against its proximal end, so no gap is visible. Recognizing contact as a relevant property does not suffice here; it requires knowledge of the necessity of a structural connection between string and reward. Chimpanzees appeared unable to distinguish between these possibilities (Povinelli 2000). When animals perform better on the *contact* than *connection* condition, it is likely because they consider contact to be a sufficient and necessary mechanism. They may also try to move away with the reward still attached to the string connected to the substrate. For example, some ravens and American crows tried to fly off with food attached to a string tied to a perch, resulting in them being yanked back unless they dropped the food first (Heinrich 1995).

A controversial cognitive mechanism often associated with string pulling is insight. Definitions vary but often revolve around suddenly arriving at a solution by recombining previous experiences. How different amounts and types of experience influence problem-solving abilities is a contentious issue central to the string-pulling paradigm (Jacobs and Osvath 2015). Performance often improves within conditions and may depend on previous experience on different conditions. For instance, juvenile rhesus macaques perform worse on the *pseudo-crossed* condition when having previous experience on the *crossed* condition compared to the *parallel* condition (Mason and Harlow 1961). This suggests they transferred their previous experience based on proximity.

Heinrich (1995, p. 1001) tested ravens on vertical string pulling and proposed four explanations for spontaneous success: “(1) random chance; (2) programming already present at birth; (3) learning both the sequence and its effects; (4) insight associated with or without some or all of the above.” He considered chance an unlikely explanation for immediate execution of the different action sequences. Neither did he regard genetic programming likely because little or no behavior in the wild corresponds to it. He acknowledged that the ravens might have learned

some aspects of the tasks but that this does not explain their spontaneous solution of several conditions. He therefore concluded that insight is the most plausible explanation.

However, there are plausible alternatives to these explanations, as already discussed above. Possibly the most convincing case of insightful string pulling would be an immediate solution to the *crossed* condition after an initial impasse without any previous string-pulling experience and not resulting from chance, trial and error, visual feedback, or innate processes (Jacobs and Osvath 2015). This has so far not been shown in any species because some factors, such as chance and rapid trial and error, cannot be excluded in the first trial. Insight remains a vague concept that is more informative when deconstructed into its fundamental cognitive abilities that can be investigated independently (Shettleworth 2012).

## Ecology and Evolution

The cognitive abilities required for successful string pulling may benefit animals in their natural environments. Numerous reports have documented how several species pull stringlike objects to retrieve attached food. For instance, olive baboons pull up the nests of weaverbirds to take their eggs (Laidre 2008), Eurasian jays pull up oak seedlings to retrieve buried acorns (Bossema 1979), tufted titmice pull up caterpillars hanging from branches by their threads (Dickinson 1969), and orangutans obtain 61% of their plant intake by pulling branches to reach leaves and fruits (Chevalier-Skolnikoff 1983). Therefore, this behavior may be facilitated, in some cases, by a species’ natural ecology.

Some authors argue that such ecological parallels reduce the cognitive abilities required for string pulling (e.g., Altevogt 1954). Genetic programming could result in functional means-end behavior without complex cognition. Some adaptations are beneficial for string pulling, whether originally selected for these behaviors or not. There is suggestive evidence that playfulness, attentiveness, visual acuity, and manipulation

skills increase the string-pulling performance of primates (Harris and Meyer 1971; Jolly 1964). In birds, one of the most important species-specific factors is the use of feet in feeding. Birds that do not use their feet for holding food generally fail to anchor pulled-up vertical strings under their feet and therefore cannot retrieve the reward. They perform markedly better on horizontal string pulling since it does not require stepping on the string (Jacobs and Osvath 2015).

Ice-fishing ravens illustrate these issues. While it shows string-pulling behavior in the wild, countering Heinrich's (1995) argument that little to no such behavior exists under natural circumstances, it is unlikely ravens specifically adapted to ice fishing since it is a regional tradition that humans have been practicing for a time period that is very brief in evolutionary terms. Moreover, ravens improve with experience, differ individually in pulling technique, and are initially neophobic toward food suspended on strings (Heinrich 1995). Genetic programming for string pulling is therefore unlikely. Conversely, ravens frequently use their feet in feeding, which is more likely to have been directly selected genetically. Individuals innovate how to perform multi-step string-pulling sequences, which benefits from sensorimotor skills adapted for other reasons, such as holding food (Jacobs 2017). Future studies should investigate how wild ravens learn to pull up unattended fishing lines and how this behavior spreads through the population.

Since string-pulling tests are easy to administer, they are often used as indicators of general cognitive abilities in studies on ecology and evolution. For instance, 25% of wild great tits tested on vertical string pulling obtained the food within an hour. Their performance was stable over years, independent of various factors such as sex, neophobia, and body condition, and correlated with performance on another operant task (Cole et al. 2011). Females that performed better laid larger clutches but were also more likely to abandon their nests, showing a trade-off in fitness value for the cognitive abilities associated with string pulling (Cole et al. 2012). Large-scale studies on problem-solving abilities in wild species with controls on many variables are unfortunately

rare. The string-pulling paradigm offers a relatively easy tool that is suitable for such purposes.

Until recently, only mammals and birds have done string-pulling tests. Alem et al. (2016) investigated string pulling in bumblebees and found that 2 out of 135 subjects spontaneously pulled a single horizontal string within 10 min, possibly through their persistence, exploration, trial-and-error learning, or sheer luck. Others learned to do so through social learning, resulting in the behavior slowly spreading throughout the colony. Three out of eight successful bumblebees also passed the *coiled* condition, but none of the 27 observing bees pulled in a coiled string completely. The authors concluded that observing bumblebees are attracted to the demonstrator's location and the position of the string and that carrying out the pulling sequence relies on trial and error mediated by perceptual feedback of the reward moving closer. Thus, associative mechanisms and trial and error appear to explain string-pulling behavior in bumblebees, not means-end understanding or insight. This study illustrates the requirement of multiple testing conditions to distinguish between alternative explanations and yield conclusive results.

Species comparisons are difficult because many factors may influence string-pulling abilities, and these can obscure intra- and interspecific cognitive differences. With increased awareness of these issues and better study designs to accommodate or control for them, some meaningful comparisons are possible. Most tested animals have successfully pulled in single baited strings. As already discussed, the cognitive abilities required for this behavior are often unclear and less sophisticated than typically assumed, but it shows which species have the required sensorimotor capacities and are therefore suitable for further testing. Although around 170 species have been tested on the string-pulling paradigm, most of them are primates, carnivores, passerines, and parrots, which limits the scope of phylogenetic analyses (for the most recent phylogeny of string-pulling species, see Jacobs 2017).

Even in primates, not enough studies have been done with comparable methods or multiple species to allow for larger comparisons. However,

one meta-analysis ranked species performances across several studies and showed that apes generally outperform monkeys on string-pulling tasks (Deaner et al. 2006). This parallels findings on numerous other tasks, which likely reflects differences in brain anatomy and socio-ecology between apes and monkeys. String pulling is highly suitable for phylogenetic comparative psychology because it involves minimal training, relatively few trials per subject, and the ability to easily adapt materials and testing protocols for different species (MacLean et al. 2012). However, a large-scale comparative phylogenetic study of string pulling does not exist yet. While the total number of studies is very large for this field, they have a limited phylogenetic scope. To better reconstruct the evolution of the cognitive skills underlying this ability, some uncommon taxa should be tested, such as monotremes, marsupials, and paleognaths. This will increase the phylogenetic breadth significantly more than additional studies on common taxa such as primates and passerines. With the discovery of string pulling in bumblebees, researchers should be encouraged to investigate species outside the mammal and bird clades.

## Conclusion

String pulling has a rich history and promising future. The variety in experiments conducted, species tested, and explanations offered attests to its broad utility in animal cognition and behavior. However, strong conclusions should not be made without exploring possible confounding factors and administering several conditions due to the many different cognitive mechanisms that may underlie string pulling. Nearly endless patterns are possible to this end. When investigating different cognitive abilities, the patterns in Fig. 1 may be most useful, especially the *parallel*, *slanted*, *crossed*, *overload*, *contact*, *connection*, and *coiled* conditions. Considerate use of the string-pulling paradigm will likely prove to be invaluable in the study of various cognitive abilities, including their relationships to ecology and evolution, throughout the animal kingdom.

## Cross-References

- Behavioral Flexibility
- Comparative Cognition
- Comparative Psychology
- Evolutionary Psychology
- Folk Physics
- Insight
- Instrumental Learning
- Learned Affordances
- Means-End Reasoning
- Phylogeny
- Problem-Solving
- Technical Intelligence Hypothesis
- Tool Use

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## Stroop Effect

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## Definition

The Stroop task and its corresponding effect are among the best known, most frequently researched phenomena in cognitive psychology (MacLeod 1991; Washburn 2016). In its most recognizable form, participants are required to indicate, as quickly as possible, the print color of a series of words, some of which are themselves incompatible color words. J. Ridley Stroop (1935) studied interference in color naming by comparing performance in baseline conditions to a condition in which the color stimuli were themselves incongruent color words (e.g., the word GREEN printed in red, the word BLUE printed in yellow, and so forth, where the corresponding correct response would be “red, yellow, . . .”). This interference, manifest as slower responding and increased errors, has become known as “the Stroop effect” and was originally interpreted as reflecting the difference in response strength between the conflicting stimulus dimensions. Each word itself has a single, strongly associated response: the word’s meaning (e.g., the letters



BROWN become strongly associated with the response of reading the word “brown”), whereas colors have multiple associated responses (e.g., the color *brown* may be associated with responses connected to dirt and chocolate and wood and many other brown things). Thus, the defining characteristic of the Stroop task in its classic form is the conflict between a relatively weak to-be-named feature of a stimulus and the prepotent but incongruent meaning of that stimulus.

In the eight decades since Stroop’s (1935) original report, there have been more than 6000 publications that replicated, extended, or otherwise referenced the Stroop task and/or effect. In truth, however, relatively few of these studies employed J. Ridley Stroop’s original procedure. Whereas the color-naming task remains the standard, Stroop-like interference has also been reported using dozens of variations, in which stimulus dimensions other than color are pitted in competition for behavior (see reviews by MacLeod 1991, 1992). This fact provides an important first disclaimer for the present discussion of Stroop-task studies in the comparative-cognition literature, as no nonhuman animal has to date been (and it is unlikely that any could be) tested on Stroop’s original procedure that required reading verbal stimuli and vocal responding; however, many of these Stroop-like task variations are amenable to cross-species comparison. Note consequently that the term *Stroop effect* is generally reserved for interference between word-meaning and word-color, loosely following the original Stroop (1935) contrast, whereas interference between stimulus meaning (e.g., the value of an Arabic numeral) and some other stimulus dimension (e.g., the physical size of an Arabic numeral; Besner and Coltheart 1979) is typically termed a *Stroop-like effect*.

As a second disclaimer, it must be acknowledged that there are also many tests other than the Stroop task that present conflict between a prepotent response and a target response. For example, the Attention Network Task (ANT; Fan et al. 2002) measures interference between a stimulus and incongruent flanking stimuli (e.g., an arrow, surrounded by arrows pointing in the opposite direction) to assess executive attention. The

Simon effect (e.g., Simon and Berbaum 1990) reflects conflict between a stimulus and its spatial position. Within the animal-learning literature, there is a long and productive history of placing conditioned stimuli in conflict with one another. For example, Ray (1969) separately trained rhesus monkeys (*Macaca mulatta*) to respond to color stimuli and to line-orientation cues and then combined the stimuli so as to examine the effects of conflicting compound stimuli on attention and behavior. Much of what is known about phenomena like blocking, overshadowing, and similar selective-attention effects was determined from experimental investigations of the stimulus-control of the behavior of rats, pigeons, and other nonhuman animals under conditions of competing discriminative cues (for reviews of this literature, see Rosas et al. 2017, Zentall 2005). These cue-competition paradigms are clearly related to the present topic but are not typically considered to be *Stroop(-like)* and in general will not be discussed further in this review.

However, Lauwereyns and collaborators (2000) reported interference described as “a behavioral analogue of the human Stroop effect” (pg. 352) from such a test of cue conflict within compound discriminative stimuli. Japanese macaques (*Macaca fuscata*) were trained on separate stimulus-color, stimulus-shape, and stimulus-movement discriminations in a go/no-go paradigm. These animals were subsequently shown to respond more slowly and to produce more errors when incongruent color/shape/movement cues were combined (e.g., a stimulus in the “go” color but in the “no-go” shape). The authors further reported that the effects of irrelevant but incongruent stimulus cues were cumulative, such that a “go” stimulus with two “no-go” features produced more interference than if only one “no-go” feature was present. This finding of cumulative interference is interesting and potentially useful for further examination of individual and group (including species) differences in the magnitude of Stroop-like interference and the attention-control mechanisms that underlie it. However, the paper also highlights the impossibility of drawing a clear categorical boundary

(on a basis other than the researchers' choice of terms) between cue-competition findings that should "count" as Stroop-like effects and those that do not.

## Stroop Effects for Color Symbols

In the closest analogue to the original Stroop task performed by a nonhuman animal to date, Beran et al. (2007) leveraged the unique symbolic-communication competencies of a chimpanzee (*Pan troglodytes*) named Lana to test her on a color-naming task. Beginning in 1972, Lana was trained to use a computerized keyboard that featured visuographic symbols called *lexigrams* (Rumbaugh 1977). Each lexigram corresponded to a word, and Lana was trained to produce sentences by combining symbols in accordance with a novel grammar (e.g., Rumbaugh 1977, Rumbaugh and Washburn 2003). Lana learned to use the keyboard to make requests, to label objects, to comment on events, to respond to questions, and so forth. She also understood and responded appropriately to keyboard-based communications by human experimenters or caregivers. The lexigrams primarily represented nouns and verbs, but Lana was also taught some adjectives – including some colors. Because Lana remembered her symbol meanings for decades (Beran and Heimbauer 2015), Beran and collaborators were able to test this chimpanzee on a color-naming task that almost exactly reproduced the Stroop task commonly used with human participants.

For this experiment's training phase, Lana was required correctly to categorize colored clip-art stimuli as blue or yellow using "B" and "Y" response options on a computer screen (Beran et al. 2007). When she met the training criterion, Lana was advanced to the testing phase of the study. On each trial of this phase, Lana saw one of eight possible stimuli, including the lexigram symbols that stood for the colors blue and yellow. These lexigrams could be presented as congruent stimuli (i.e., the blue lexigram colored blue, the yellow lexigram colored yellow) or as incongruent stimuli (i.e., the blue lexigram colored yellow,

the yellow lexigram colored blue). Lana showed significantly lower accuracy on incongruent trials when compared to training or control trials (i.e., trials with arbitrary stimuli colored blue or yellow) or the congruent-lexigram trials. This effect is similar to what is typically observed for human adults and children when they show differences in accuracy on the Stroop task; however, whereas human adults and children typically show Stroop effects in response-time measures, Lana did not take more time to respond to incongruent trials.

These findings might suggest a qualitative difference between Stroop effects of nonhuman versus human primates; however, a recent study in which a task like Lana's was administered to rhesus monkeys (*Macaca mulatta*) belies this suggestion. Using a symbolic matching-to-sample paradigm, Callery et al. (2015) trained macaques on the meanings of four color symbols. On some trials, the monkeys saw one of the color symbols on a computer screen. The monkey manipulated a joystick so as to bring a computer-graphic cursor into contact with this sample stimulus, whereupon two clip-art images were presented. These images were identical, except for color. For example, the sample image might be the symbol for RED, and the choice stimuli might be two pictures of umbrellas, identical except that one was red and one was blue. The positions of the choice stimuli were randomized. On other trials, a clip-art image was presented as the sample (e.g., a yellow house), and the choice stimuli were two color symbols (e.g., the symbol for green and the symbol for yellow). Irrespective of trial type, the animals were rewarded for selecting the appropriate symbol-color pair. When a monkey achieved training criterion on all four stimuli, novel clip-art images were introduced to test for generalization.

Following the generalization tests, the monkeys were trained to sort new clip-art stimuli on the basis of color, by manipulating the joystick so as to drag the stimuli into contact with the red, blue, yellow, or green border of the screen. On probe trials, one of the color symbols was presented as the to-be-sorted stimulus. Each symbol appeared either in a congruent color with the symbol's meaning (e.g., the symbol for yellow,

colored yellow) or in an incongruent color (e.g., the symbol for red, colored yellow). In any case, the animal was rewarded for sorting on the basis of stimulus color, irrespective of the identity of the image. The rhesus monkeys produced significantly more sorting errors on incongruent trials than on congruent-symbol or baseline (clip-art) trials. They also responded significantly slowest on the incongruent trials. Although these color symbols were certainly not language-like in the way that is true for Lana's lexigrams or human's words, the monkeys did replicate Lana's Stroop interference (Beran et al. 2007) as well as the interference effects of incongruent trials on human's accuracy and response time.

### Numerical Stroop-Like Effects

The Klein et al. (2017) findings also replicated the effect from the very first known Stroop-like test of nonhuman animals. Two rhesus monkeys that had previously learned the relative numerosness represented by Arabic-numeral symbols (Washburn and Rumbaugh 1991) were tested on a numeric Stroop-like task (Washburn 1994). On each trial of this new task, monkeys were presented with two arrays of letters (e.g., five Cs vs. two As) and were rewarded for moving the cursor into contact with the array with more stimuli. The identity of the stimuli was irrelevant to the task. The monkeys quickly mastered this task, whereupon Stroop-like trials were interspersed into blocks of these baseline trials. On congruent trials, the array with the most stimuli also contained the larger Arabic numeral (e.g., four 3s versus one 2). Incongruent trials presented the larger Arabic numeral in the smaller array (e.g., two 5s versus three 1s). Irrespective of trial type, the monkeys and a group of human participants were simply required to select the larger of the two arrays based on item count, regardless of the stimuli contained in the arrays.

As was previously reported for humans on a numerical Stroop-like test (Besner and Coltheart 1979; for similar reports using other variations on the numerical Stroop paradigm, see Cohen 2009, Wolach et al. 2004), both the rhesus monkey and

human participants demonstrated significant Stroop-like interference in response times (Washburn 1994). Irrespective of species, participants required more time to respond to stimuli when numerical-symbol magnitude was incongruent with relative quantity. Rhesus monkeys were also significantly more prone to error in the incongruent condition when compared to congruent array sets or nonnumerical array sets, in an effect that would anticipate the 2007 finding with Lana chimpanzee (Beran et al. 2007).

The numeric Stroop-like task permitted some additional analyses that are not typical of research with the Stroop color-word variation. Washburn (1994) tested the hypothesis that Stroop-like interference is based on stimulus-response association strength, as had been originally posited by Stroop (1935), by examining how the Stroop-like effect changed as a function of the symbolic distance between the stimuli within a trial. That is, two 3s vs. four 2s are an incongruent trial, but it may not be equally incongruent as two 5s vs. four 1s. Indeed, the magnitude of Stroop-like interference generally increased, both for monkeys and for humans, as the absolute difference between the Arabic numerals in incongruent trials increased – just as would be expected if Stroop interference was based on strength of association. A similar effect was not observed as a function of differences in array size (e.g., the interference on incongruent trials like four 1s vs. two 3s was not significantly different than the interference on trials like six 1s vs. one 3). Washburn (1994) argued that this latter difference would have supported a “speed of processing” explanation for Stroop effects but that the data from monkeys and humans indicated that Stroop-like interference was produced by the strongly associated response tendency to pick the larger of any two numerals. This strength-of-association explanation echoes the original interpretation offered by Stroop (1935).

Not only did rhesus monkeys show the same kind of significant Stroop-like effects that were reported for human adults, but the magnitude of these interference effects was even larger for the macaques than for the undergraduates. That is, both humans and monkeys showed interference

in their relative-numerosness judgments from the irrelevant symbol-meaning stimulus dimension, but the nonhuman primates were more susceptible than the humans to influence from this strongly associated but irrelevant cue. This quantitative difference in effect size is similar to the difference that has been reported between typically developing children and children diagnosed with attention deficits (e.g., Kaufmann and Nuerk 2006) and suggests group differences in the executive-attention competencies that permit participants to override prepotent stimulus-control in favor of cognitive control by intentions, motivations, goals, or instructions. To test whether this difference between monkeys and humans in the efficiency of executive attention reflects species difference in stable cognitive competencies or only transient variations in motivation or effort, a follow-up study was conducted.

To examine the effects of cognitive control on Stroop interference, Washburn (2016) tested three rhesus monkeys on the numerical Stroop task described above. Following the procedure Kane and Engle (2003) had used to contrast the attention-control skills of humans with high versus low working-memory capacity, blocks of Stroop trials were administered between two possible trial-type probabilities. Blocks would either contain more congruent trials than incongruent trials ( $C > I$  condition: 60% congruent, 20% incongruent, 20% baseline) or no congruent trials ( $I > C$  condition: 0% congruent, 80% incongruent, 20% baseline). Kane and Engle (2003) reported greater Stroop interference effects in the  $C > I$  probability condition when compared to the  $I > C$  condition, as the former places greater demands on participants' attention-control skills (i.e., almost every trial serves to remind participants to ignore the irrelevant cue in the  $I > C$  conditions, but in the  $C > I$  condition, the irrelevant stimulus dimension actually supports fast and accurate performance on most trials, except those infrequent incongruent probe tests). As in the previous report, Washburn (2016) found significant Stroop-like effects for humans and for macaques, with larger Stroop interference for the monkeys, particularly in the  $C > I$  condition. Next, both groups were retested under the  $C > I$  condition but with a

manipulation of reward contingencies so as to determine whether Stroop interference could be attenuated when participants were incentivized to respond quickly and accurately on the incongruent trials. With increased incentives, undergraduate students were able to reduce the amount of Stroop-like interference; although response times continued to be significantly longer in the incongruent than the baseline condition, the effect size was reduced when human participants tried harder to ignore the meaning of the Arabic numerals and to respond only on the basis of stimulus set-size. The rhesus monkeys also responded faster overall under high-motivation conditions; however, this overall increase in response speed did not change the magnitude of the Stroop-like effect. When incentivized to respond quickly and accurately, the monkeys improved on baseline, congruent, and incongruent trials, but the difference between the incongruent and baseline conditions was statistically the same in the high- versus low-motivation conditions. Washburn (2016) concluded that the species difference repeatedly observed in the magnitude of Stroop-like interference was not an artifact of differences in motivation or interest between humans and rhesus monkeys but rather reflected meaningful differences in the capacity for executive control over attention (see also Washburn and Tagliatela 2012).

Bramlett-Parker and Washburn (2016) investigated whether rhesus monkeys could be trained to improve their executive-attention skills and thus to reduce the magnitude of interference from prepotent but irrelevant cues on performance. They trained rhesus monkeys on a battery of Stroop-like tasks, including the numerical Stroop task described above, a variation of the Simon (spatial conflict) paradigm (e.g., Simon and Berbaum 1990), a global/local conflict task employing hierarchically organized stimuli (for examples of this task, see Cavoto and Cook 2001, Hopkins and Washburn 2002), and a nonhuman-primate version of the ANT (Fan et al. 2002). The monkeys were alternated between attention-training blocks with the numerical Stroop and other tasks and generalization tests with the ANT to determine whether any

improvements in executive (or cognitive) control of attention would generalize. Although the monkeys were able to learn the tasks and did show Stroop-like interference as predicted, no evidence of generalized training improvements was evident in the results.

## Neural Underpinnings of the Stroop Effect

Michelet and collaborators (2007, 2009, 2015) have used a Stroop-like task for use with rhesus monkeys. These animals were trained to associate the shape of three stimuli (an outline-drawing of a banana, apple, or pear) with three response colors (yellow, red, green, respectively). When a stimulus was presented on the screen, the monkey would touch a box of the associated color from the choices at the bottom of the computer screen. Once the monkeys were trained, they were presented trials in which the fruit stimuli were colored with congruent (e.g., a yellow banana) or incongruent (e.g., a yellow apple) cue combinations. Longer response times and more errors were observed in the difficult incongruent, as compared to the baseline or easy congruent conditions.

In each of these studies, Michelet and collaborators (2007, 2009, 2015) obtained electrophysiological activity from single-neuron recordings of the monkeys. The authors reported changes in activity of cells in the dorsal anterior cingulate cortex during incongruent trials, as well as activity in the rostral cingulate motor area in response to the warning stimulus following a trial in which an incorrect response had been produced. These findings were interpreted as indicating the role of the anterior cingulate cortex in the executive control of attention by rhesus monkeys, as has been repeatedly found for human participants performing the Stroop and related tasks (e.g., Pardo et al. 1990, Posner and Raichle 1994, Posner et al. 2007). This finding is significant, because other research had failed to find evidence of the anterior cingulate cortex for executive-control performance by nonhuman primates, suggesting a critical species difference in the neural mechanisms of conflict resolution (e.g., Cole

et al. 2009, Mansouri et al. 2009). For example, Mansouri et al. (2009) used single-cell recording and lesion methods to study monkeys' cue-competition responses on a variation of the Wisconsin Card Sorting Test using incongruent flanking stimuli and found the dorsolateral prefrontal cortex but not the anterior cingulate cortex to be critical. Whereas the debate about the neural mechanisms of cognitive control for human and nonhuman animals is by no means settled, it does seem likely, as Micholet and colleagues (2016) claimed that using comparable Stroop-like tasks across investigations and species will serve to reduce the methodological differences that may result in inconsistent results and clouded generalizations.

## Conclusion

The Stroop task and its variations are more interesting than ever, because the Stroop(-like) effect is such a clear example of a failure of cognitive control. Humans and other animals can exert executive control over attention and response decisions, but the effectiveness of this control is incomplete in the face of conflicting demands from stimulus cues and the response tendencies that are associated with them. The capacity to resist interference from irrelevant but prepotent stimulus cues, as reflected in the magnitude of Stroop-like interference, appears to vary reliably across species, across development, across diagnostic categories, and as a function of particular neural systems. Given this, it seems likely that continued study of Stroop-like effects in nonhuman animals will remain important, not only for demonstrating the continuity that exists across species in the control mechanisms of behavior but also for identifying interventions that may improve the effortful and future-oriented control of attention (Washburn 2016).

## Cross-References

- [Arabic Numerals](#)
- [Attention](#)



- [Comparative cognition](#)
- [Comparative psychology](#)
- [Computerized Testing Paradigm in Primates](#)
- [David Washburn](#)
- [Discrimination Learning](#)
- [Duane Rumbaugh](#)
- [Georgia State University's Language Research Center](#)
- [Language Research: Great Apes](#)
- [Lexigrams](#)
- [Motivation](#)
- [Stimulus Control](#)
- [Symbolic Distance](#)

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## STRs

- [Simple Sequence Repeats](#)

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## Structural Adaptations

- [Adaptation](#)

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## Structural Plasticity

- [Neuroanatomical Plasticity](#)

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## Structure

- [Assemblage](#)
- [Proboscidea Morphology](#)

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## Stuck-in-Time Hypothesis

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## Synonyms

[Episodic memory](#); [Future planning](#); [Mental time travel](#)

Science fiction writers and film makers have frequently depicted stories in which people are able to use a time machine to travel to the past and future. Although no such machine exists for physical time travel, most humans time travel mentally. That is, we mentally replay episodes from our past (episodic or autobiographical memory) and anticipate or make plans for events to occur in the future. What would our lives be like, however, if we could not mentally time travel?

Tulving (1989) reported the case of a man identified as K. C., who had suffered brain damage to the left frontal-parietal and right parietal-occipital lobes of his cortex. The consequence of this injury was that K. C. no longer retained the ability to remember episodic memories of personal past experiences and could not conceive of future events. Although K. C. retained his ability to use language and general knowledge about the world (reference memory), he could no longer mentally time travel. We could say that cognitively he was “stuck in time.”

W. Roberts (2002) raised the question of whether animals might be stuck in time. That is, do animals have a sense of time as a continuum that extends backward and forward from the present moment? Do they have memories for specific past experiences and can they plan for future

activities? Considerable field and laboratory research indicates that animals remember places where food, mates, and predators are located. These are *what* and *where* reference memories based on repeated experiences. Of more interest for the stuck-in-time hypothesis is the question of whether an animal remembers specific instances of past encounters with food, mates, or predators. Of particular interest, does an animal remember not only what was encountered and where it was encountered, but also *when* it was encountered. Tulving argued that episodic memory required memory of what, where, and when a past event occurred and concluded that "Remembering past events is a universally familiar experience. It is also a uniquely human one" (Tulving 1983, p. 1).

In his 2002 review of the literature on animals' sensitivity to time, W. Roberts pointed out that there is strong evidence for animals' use of time in certain ways. Thus, animals can learn associations between time of day and where food will be found (Biebach et al. 1989). They can also keep track of intervals of time lasting from seconds to several minutes. In Pavlov's (1927) classic experiments, dogs given food every 30 min came to salivate only a few minutes before each scheduled food delivery. On a fixed-interval schedule of reinforcement, a rat or pigeon is reinforced for pressing a bar or pecking a key only after a certain amount of time has elapsed since a light or tone signal was initiated. The animal learns to withhold responding during the interval until just a few seconds before a response will earn a reinforcer. The use of the *peak procedure* pinpoints the moment in time that an animal expects reinforcer delivery and shows that it closely approximates the fixed interval (Roberts 1981). However, these demonstrations of timing by animals have been explained by neural mechanisms that do not require a concept of extended time. Thus, an internal circadian clock could explain sensitivity to time of day. A number of theories account for interval timing, most prominently the idea that a neural accumulator was used to track short time intervals (Church et al. 1994).

Beyond these demonstrations of temporal appears in animals, W. Roberts' (2002) review of

the relevant literature found little evidence of a sense of extended time, episodic memory, or future planning in animals, and he concluded that the evidence largely suggested that animals were stuck in time. Since that review, considerable new evidence has come out suggesting that animals may have a form of episodic memory. As early as 1998, Clayton and Dickinson reported evidence for what-where-when memory in scrub jays. This classic experiment rested on the fact that scrub jays in nature cache or hide food in different locations and later use their memory to retrieve their caches. In Clayton and Dickinson's lab, jays were allowed to cache highly favored wax worms in one tray and less preferred peanuts in another tray. When given the opportunity to retrieve these items 4 h later, the hungry jays not surprisingly preferred the tray where worms had been cached. On other occasions, however, jays' memory was not tested until 5 days had gone by. The jays now showed a complete reversal of preference and went to the tray containing peanuts. Of critical importance, worms in the real world would have decayed over 5 days but peanuts would still be edible. The jays' behavior suggested they understood this effect of time and chose appropriately. Clayton and Dickinson argued that jays could only have reversed their preference from worms to peanuts by remembering when the worms were cached (4 h or 5 days ago) and knowing that worms decay over that long a period.

This effect of retention interval on food preference has now been demonstrated in several other species of birds, including black-capped chickadees, magpies, and even pigeons. In variations on this procedure, similar results were found with mammals, including rats and apes. Thus, a number of species of animals showed what-where-when memory and fulfilled Tulving's original criteria for episodic memory. However, Tulving (1989) added an additional property of human episodic memory, *autonoetic consciousness* or the feeling of retrieving a personal episode. Because animals could not be quizzed about their autonoetic consciousness, Clayton and Dickinson (1998) suggested that scrub jays (and later other species) had at least fulfilled the

what-where-when criteria and should be said to have *episodic-like memory*.

Having established that episodic-like memory appears in animals, we can ask about the other direction of mental time travel. Is there any evidence that animals plan for the future? Although W. Roberts (2002) found little evidence for future planning by animals, new evidence has begun to erode that position. A common type of experiment that tests for future planning is one in which an animal can choose between two or more behaviors, with one of these behaviors being to its advantage only at some future time. For example, McKenzie et al. (2004) gave squirrel monkeys a choice between 10 and 20 peanuts. Not surprisingly, monkeys chose the tray with 20 peanuts. A pilfering manipulation was then introduced in which the experimenter returned 15 min later and took away all the remaining peanuts if 20 were chosen but not if 10 were chosen. Monkeys rapidly changed their initial choice to 10 peanuts. In another experiment, monkeys showed a preference for four peanuts over two peanuts. During a test phase, when the monkey occasionally chose the two-peanut tray the experimenter returned 15 min later and replenished the tray with eight more peanuts. Monkeys rapidly developed a preference for the two-peanut tray over the four-peanut tray.

According to a hypothesis advanced by Bischof-Kohler (1985), animals should show future planning only for rewards they currently need. Unlike humans that purchase food for meals days in advance, animals would only plan for a currently desired reward. In a test of this hypothesis, Naqshbandi and Roberts (2006) initially found that squirrel monkeys chose four dates when given a choice between four dates and one date. Monkeys had constant access to water and thus were not thirsty when they made their choice. During a block of test trials, a monkey's water bottle was removed just before it made its choice. If the monkey chose one date, the water bottle was returned in 1 h. If it chose four dates, however, the water bottle was not returned for 4 h. Monkeys' preference changed from four dates to complete preference for one date. The important point here

is that monkeys apparently anticipated a future need for water not experienced at the time they made their choice between one and four dates. Contrary to the Bischof-Kohler hypothesis, this finding suggests that an animal can anticipate a need not currently experienced.

Another example of animals planning for a future need not currently experienced comes from a well-known experiment reported by Raby et al. (2007). Western scrub jays were shown to plan in the evening for the breakfast to be consumed the next morning. Birds were trained and tested in an apparatus that contained a central compartment and two compartments on each side. For daily breakfast, birds were fed pine seeds in one side compartment on some days, but, on other days, they were put in the alternative side compartment with no seeds. In a test given the evening before breakfast, birds were fully satiated on pine seeds. Although not hungry for pine seeds, the birds could cache pine seeds made available to them in the central compartment. The important observation made was that jays cached seeds in the compartment that was always empty at breakfast. Through this behavior, they guaranteed that pine seeds would be available at breakfast the next morning, regardless of which side compartment they were placed in.

Yet another exciting area of research is planning with tools in nonhuman primates. Mulcahy and Call (2006) showed bonobos and orangutans one of two problems that required different tools in order to obtain a food reward. After seeing the problem, an ape could select one tool from several tools, only one of which would yield the reward. Further, the ape was removed from the problem area and had to wait an hour or more before it could return. Apes correctly selected the needed tool far beyond chance expectancy, and did so in the case of two animals at delays than extended overnight for 14 h. In another variation of this type of experiment Osvath and Osvath (2008) gave two chimpanzees and an orangutan a choice among four objects. After being taken from the testing room for 1 h, a subject was allowed to return where it found a favored reward, a container of fruit soup. Among the objects initially

offered the ape was a hose that it could use to suck the fruit soup from its container. The apes chose the hose far beyond chance probability. A particularly convincing final experiment was one in which the apes were confronted with four new objects. Although none of these objects was a hose, one of them could be used to extract fruit soup from its container. Apes chose the useful tool on almost all of the test trials.

A final rather amusing example of future planning comes from an observation made of a chimpanzee housed on an island in a Swedish zoo (Osvath 2009). Caretakers observed that the chimp would collect rocks and pieces of concrete and store them near the public viewing area. When visitors then appeared to see the chimpanzee, it attempted to pelt these onlookers with rock missiles. Stones were not used in contexts other than throwing at spectators, and caching stone tools was not seen during the off-season when the zoo was closed. It appeared that the chimp was storing ammunition for a specific future purpose.

The stuck-in-time hypothesis provides a nice example of progress in comparative cognitive science. The hypothesis was initially advanced as a summary of the evidence available about mental time travel in animals around the year 2000. Most of the evidence suggested animals might be stuck in time or have no episodic memory or ability to plan for the future. Spurred by lack of evidence to the contrary, comparative psychologists began to look for possible evidence of mental time travel in animals. We now have convincing findings of both what-where-when or episodic-like memory at delays that extended in several species of non-human animals, as well as evidence of future planning in food-caching birds and nonhuman primates. A major question for future research will be to what extent these mental time travel abilities in animals are like those in humans. How far back in time do animals have episodic-like memories and how far into the future can they plan for future events? To what extent do animals have a sense of time that is marked by a progression of events extending into the past and by a potential series of events extending into the future? Exciting future studies may provide us with insight into these questions.

## Cross-References

- [Episodic Memory](#)
- [Jonathon Crystal](#)
- [Memory](#)
- [Nicola Clayton](#)
- [Reference Memory](#)
- [William Roberts](#)

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## Studies of Twins

- [Twin Studies](#)

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## Studying

- [Learning](#)

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## Subdominant

- [Beta](#)

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## Suboptimal Behaviors in Gambling-Like Tasks

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### Definition

Suboptimal behavior involves the preference for an alternative associated with less reinforcement than the unchosen alternative.

### Introduction

Animals are continuously taking risks. An animal might risk going to the watering hole but it risks the possibility of being attacked by a predator. An animal might risk leaving the current depleting patch but it risks not finding a better one. Animals

are assumed to have evolved risk-taking strategies that are optimal for the species and their environment (e.g., the distribution of food). Sometimes, however, animals make choices that are suboptimal even after considerable experience with the probability and amount of reinforcer.

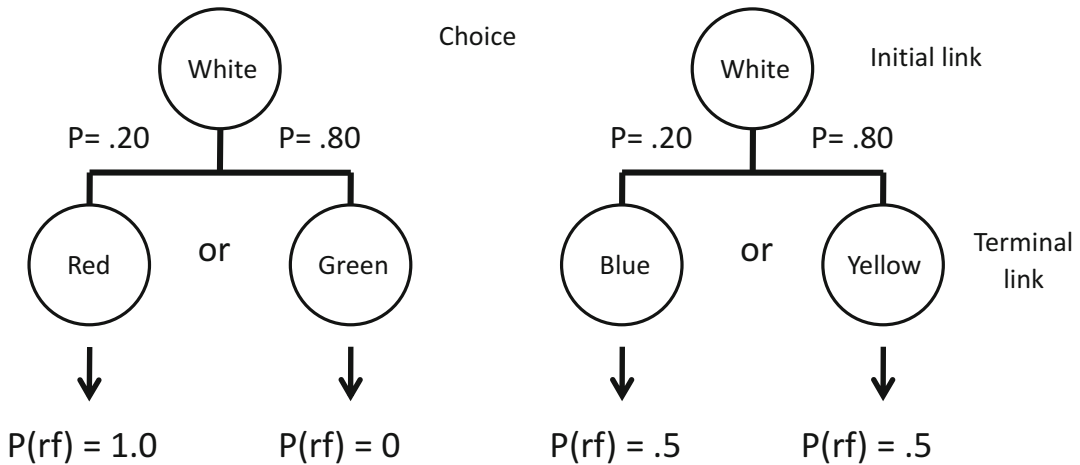
A *suboptimal choice* is one for which there is a better alternative, such as one that gets the animal more food, better survival, or increased reproductive success. Thus, if pecking one response key gets the pigeon two pellets of food and pecking a different key gets the pigeon three pellets of food, it would be suboptimal if the pigeon had a preference for the key that get the pigeon two pellets.

When animals make suboptimal choices, those choices inform us about the relatively stable mechanisms that govern their behavior. One variable that has been shown to result in suboptimal reinforcement is the delay to reinforcement. *Delay discounting* is the reduction in value of a reinforcer when it is delayed. For example, a pigeon may prefer receiving five pellets after 0.5 s over 20 pellets after a delay of 5 s. That is, by choosing the smaller amount sooner, pigeons get fewer pellets per unit time. The explanation for this suboptimal choice is that organisms (including pigeons, rats, monkeys, and humans) have evolved to prefer sooner reinforcers because, in nature, later reinforcers may no longer be there.

Although research that will be described deals primarily with pigeons, similar effects have been found in several other species (e.g., rats, starlings, monkeys, and humans).

### The Gambling-Like Task

A different kind of suboptimal choice occurs when the delay to reinforcement is held constant, but the signaled *probability of reinforcement* differs. Thus, pigeons tended to overvalue a larger amount of food despite its lower probability of occurrence. For example, a pigeon might be indifferent between a 1/3 probability of getting 20 pellets of food over a guaranteed ten pellets. Such a finding suggests that the larger magnitude of reinforcement can suboptimally overcome its lower probability.



**Suboptimal Behaviors in Gambling-Like Tasks, Fig. 1** Design of the Stagner and Zentall (2010) suboptimal choice experiment

A related phenomenon has been found when animals are given a choice between (1) an alternative that 20% of the time is followed by a signal for reinforcement (but 80% of the time is followed by a signal for the absence of reinforcement), and (2) an alternative that is always followed by a signal for 50% reinforcement (see Fig. 1; Stagner and Zentall 2010). Thus, the pigeon has a choice between 20% reinforcement and 50% reinforcement, the second providing 2.5 times as much food. Under these conditions, although pigeons have extensive experience with both alternatives, they show a strong preference for the 20% reinforcement alternative. A similar effect has been found in rats (Chow et al. 2017), Starlings (Vasconcelos et al. 2005), monkeys (Smith et al. 2017), and humans (Molet et al. 2012). With this procedure the attraction may be the immediacy of learning what the outcome will be.

When *magnitude of reinforcement* is varied, rather than probability of reinforcement, pigeons show a strong preference for getting a 20% chance of receiving a signal for ten pellets (but an 80% chance of receiving a signal for zero pellets) over getting a 100% chance of receiving a signal for three pellets (Zentall and Stagner 2011). Thus, the immediacy of learning what they will be getting after choice is not the primary mechanism responsible for the preference.

The magnitude of reinforcement manipulation bears a strong resemblance to human *unskilled gambling behavior* (e.g., lottery tickets and slot machines) in which only the laws of chance are at play. People will bet on the low probability of winning a “jackpot” while generally aware of the fact that losing is what will happen in the long run. In the case of pigeons in the Zentall and Stagner (2011) experiment, the loss is a three-pellet *opportunity cost*. That is, the guaranteed three pellet alternative is analogous to not gambling. Interestingly, for problem gamblers, losing does not appear to cause them to refrain from gambling. In fact, losing may actually encourage gamblers to gamble more, under the mistaken belief in the *gambler’s fallacy* (the belief that a string of losses must be more likely to be followed by a win). Problem gamblers are also known to be rather *impulsive*. Interestingly, when pigeons were tested for their impulsivity, those pigeons that were scored as more impulsive (as measured by the degree to which they discounted delays) were also the fastest to choose suboptimally.

### The Mechanisms Involved in the Suboptimal Choice

Findings by Zentall and Stagner (2011) suggest that the pigeons were not basing their choice on

the probability of reinforcement associated with that choice, but rather, they appeared to be using the value of the signal for reinforcement that follows that choice – the value of the conditioned reinforcer. Thus, rather than choosing between 20% and 50% reinforcement, the pigeons were choosing between 100% and 50% reinforcement. And, in the case of the magnitude of reinforcement manipulation, rather than choosing between an average of two pellets (a 20% chance of obtaining ten pellets) and three pellets, they were actually choosing between the signal for ten pellets and the signal for three pellets. Surprisingly, the signal for the absence of reinforcement appears to play little role in the pigeons' choice. In more learning theoretic terms, the signal for the absence of reinforcement does not appear to acquire inhibition.

Although the value of the conditioned reinforcer rather than the probability of reinforcement associated with the initial choice appears to determine pigeons' choice (Smith and Zentall 2016) there appears to be a second mechanism responsible for suboptimal choice. Several investigators have used variant on the procedure used by Stagner and Zentall (2010) in which pigeons are given a choice between (1) an alternative that 50% of the time was followed by a signal for reinforcement and 50% of the time was followed by a signal for the absence of reinforcement, and (2) an alternative that was followed by a signal for 100% reinforcement. Surprisingly, they have found that many pigeons still choose suboptimally. Furthermore, Case and Zentall (2018) found that continued training with this procedure actually resulted in a significant preference for the alternative that resulted in 50% reinforcement. This result, together with those of earlier studies, suggests that there must be a second mechanism responsible for the suboptimal choice. Case and Zentall proposed that the second mechanism appears to be *positive contrast* between what was expected at the time of choice and what occurred when the conditioned reinforcer appeared.

To test the role of positive contrast more directly, Zentall et al. (2019) reasoned that if one decreased the contrast between the expected

probability of reinforcement and the probability of reinforcement upon presentation of the signal for reinforcement it should reduce the contrast and thus reduce the preference for the suboptimal alternative. Intuitively, one might expect that increasing the probability of reinforcement associated with the suboptimal alternative would increase the preference for that alternative. However, when the probability of reinforcement associated with the suboptimal alternative was increased from 50% to 75%, in keeping with positive contrast theory, it decreased the preference for the suboptimal alternative. The decrease in suboptimal choice occurred because it reduced the contrast between the expected probability of reinforcement, 75%, and the probability of reinforcement upon presentation of the signal for reinforcement, 100%.

This result may explain why problem gamblers continue to gamble. If they expect to lose, because they so often do, when they actually win, the positive contrast is so great that it encourages further gambling.

## The Demographics of Suboptimal Choice

There are important similarities between suboptimal choice by pigeons and human unskilled gambling behavior. Pigeons appear to be unaffected by signals that predict the absence of reinforcement and problem gamblers appear to be unaffected by losing. The probability of reinforcement for choice of the suboptimal alternative appears to have little effect on the animal's choice of that alternative (Vasconcelos et al. 2005). Similarly, people appear to pay little attention to the probability of winning the lottery. Similar to pigeons that prefer the suboptimal, rarely occurring, ten-pellet reward, billboards advertise the magnitude of reward for guessing the winning lottery number, but they rarely indicate the probability of winning. Furthermore, independent of changing probabilities, when the value of winning the lottery increases substantially, people line up to buy tickets.

One might argue that the various procedures used with pigeons are somewhat different from

human gambling contexts. Rather than attempt to design a pigeon task more similar to human gambling, Molet et al. (2012) tested humans on a variation of the pigeon suboptimal choice task. They found that self-reported gamblers chose the suboptimal (low-probability, high-payoff) alternative significantly more than control subjects. Thus, the suboptimal choice task used with pigeons appears to be a good analog of unskilled human gambling behavior.

The demographics of human unskilled gambling behavior indicates that there is a negative correlation between the amount of disposable income an individual has and the likelihood that they will engage in unskilled gambling. To determine if pigeons show a similar phenomenon, Laude et al. (2012) varied the level of food restriction in pigeons. They found that pigeons that were less food deprived chose the suboptimal alternative significantly less than pigeons that were normally food deprived. Paradoxically, by choosing the suboptimal alternative less often, the pigeons that were presumably less hungry were actually getting more food.

Problem gamblers are known to be relatively impulsive and there is evidence that reduced impulsivity can reduce the effectiveness of conditioned reinforcers for problem gamblers. Furthermore, rats exposed to environmental enrichment have been found to show a decrease in impulsivity as measured by a decrease in delay discounting. Pattison et al. (2013) hypothesized that pigeons exposed to *environmental enrichment* might show less of a preference for suboptimal choice. When they gave pigeons experience in large cage with four other pigeons for 4 h a day, they found that those pigeons preferred the suboptimal alternative significantly less than control pigeons that had no environmental enrichment. Thus, enriched housing, even for a relatively short 4-h a day, appears to retard the development of suboptimal choice. This finding has implications for the treatment of problem gambling behavior by humans. It implies that exposing human gamblers to an environment that is socially and physically enriched also may reduce the attraction of gambling.

## Conclusions

The mechanisms responsible for suboptimal choice by pigeons are likely to have broad generality and although the behavior appears to be paradoxical, it can be explained by two relatively simple learning mechanisms. The value of conditioned reinforcers (independent of their probability) and positive contrast (between the expectation of reinforcement and the positive reinforcer that results). Understanding these mechanisms may not only explain the suboptimal behavior but may also aid in the treatment of humans whose suboptimal gambling behavior is detrimental to their health and to their social relations.

## Cross-References

- [Delayed Match-to-Sample](#)
- [Gambling Fallacies](#)
- [Matching-to-Sample: Comparative Overview](#)
- [Oddity](#)
- [Relational Concepts and Symbolic Logic](#)

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## Subsong

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### Definition

Subsongs are vocalizations produced by juvenile songbirds at the initial stage of vocal motor development. These vocalizations are soft (sung at low amplitude), show high variability of vocal elements, and lack the structural and temporal organization of adult songs.

### Introduction

Songbirds share with humans the sensorimotor ability to imitate sounds, vocal learning. This is a very distinctive trait that evolved only in three groups of birds (songbirds, hummingbirds, and parrots) and in a few other mammals (Jarvis 2004). The process of vocal learning in juvenile songbirds resembles in many ways the stages which human infants go through to acquire a native language. As in humans, they learn songs by imitating adult conspecifics, a “tutor.” Vocal learning initiates during early development and involves a sequence of sensory and sensorimotor

developmental phases. Subsongs are produced by juvenile songbirds at the first stage of vocal motor development. They have been compared to babbling in human babies for hardly resembling fully developed songs produced by adult songbirds (Doupe and Kuhl 1999). Subsongs are followed by additional sensorimotor stages in which songs gradually start to resemble adult songs.

## The Auditory Template Hypothesis

Pioneering research programs conducted by William Thorpe, Peter Marler, Mark Konishi, and others led to the proposal of a highly influential birdsong development model known as the auditory template hypothesis (reviewed in Soha 2017). According to this hypothesis, songbirds are born with an innate mechanism, or template, that guides them through a two-stage sensorimotor song development process.

### Sensory Acquisition Phase

A critical period for song learning starts just after young songbirds leave their nests. During this period, they need to be exposed to adult songs, in order to successfully develop songs with their species-typical characteristics. At this stage, songbirds are especially sensitive to adult conspecific songs. They are able to promptly memorize songs and use them as models to guide the subsequent sensorimotor phase of song development.

### Sensorimotor Phase

The sensorimotor phase consists in the gradual development of a motor program in which the singing output of young songbirds is guided by the stored memory of adult songs memorized during the sensory acquisition phase (Marler 1991). The timing between the end of the sensory phase and the beginning of the sensorimotor phase may vary widely across different species. In seasonally breeding species, such as white-crowned sparrows (*Zonotrichia leucophrys*), juvenile birds start to produce subsongs several months after they have been exposed to an adult and memorized its songs (Hultsch and Todt 2004). However, in nonseasonal breeding species, the



interval between the sensory acquisition and sensorimotor phases is shorter and can even overlap. For example, in zebra finches (*Taeniopygia guttata*) juveniles start to produce subsongs while still memorizing adult songs. Their sensory acquisition phase lasts from 25 to 65 days post-hatch (dph). But after reaching 35 dph they already start producing subsongs (Zann 1997).

The sensorimotor phase is typically subdivided into three stages: subsong, plastic song, and crystallized song. Subsongs are produced at the earliest stages of vocal motor development. These are soft and highly variable vocalizations. Plastic songs, as its name suggests, are still very variable, but they already contain several vocal elements and temporal organization patterns found in adult songs. At the end of the sensorimotor phase, after a gradual decrease in variability, songs are said to be crystallized, i.e., they become fully developed adult songs with stable structural and temporal patterns.

## Structure and Function of Subsongs

Subsongs barely resemble adult songs. For this reason, they have been compared to the babblings of human babies and other mammals (Doupe and Kuhl 1999). Subsongs are noticeably softer than fully developed adult songs and show great variability of its constituent vocal elements (notes and syllables). They also show no consistent structural and temporal patterns. For example, adult zebra finch songs are composed of vocal elements that are produced in a fixed sequence called “phrase.” However, subsongs produced by juveniles of this species lack stereotypy in the sequential organization of phrases and also in the duration and shape of vocal elements (Aronov et al. 2008).

## Vocal Motor Practice and Exploration

It has been suggested (Hultsch and Todt 2004) that subsongs function as a stage of vocal practice and exploration in which juvenile songbirds can learn how to coordinate the sounds produced via syrinx (the songbird’s two-voiced vocal apparatus) and to develop fine sensorimotor control. According to this idea, the production of highly

variable vocalizations at the initial stage of the sensorimotor development allows juveniles to learn how to establish causal relationships between motor commands and sound production. A similar function has been proposed for human babbling (Doupe and Kuhl 1999).

## Beyond Vocal Imitation

Tchernichovski and Marcus (2014) called attention to the fact that reaching exact copies of tutors’ vocalizations is not the usual developmental goal of vocal learning in songbirds and humans. Instead, the process of vocal learning leaves some range for the production of variation. Imitation is not the only ability developed during the process of vocal learning. The development of the combinatorial ability to rearrange vocal elements is another important goal of the vocal learning process. Vocal learning is a much more complex process than a one-to-one interaction between a tutor and a tutee. It is also influenced by the dynamics of social interactions. Juvenile zebra finches, for example, can imitate songs from multiple tutors and mix them to form new unique repertoires (Jones et al. 1996).

## Neurobiological Basis of Subsongs

Songbirds are the main animal models used to investigate the neurobiological basis of vocal learning. They have a “song-system,” a set of interconnected brain nuclei specifically dedicated to song learning and production. Two main pathways controlling song production and learning have been identified. The vocal motor pathway involved in sound production includes the forebrain nuclei NIf (nucleus interfascialis), HVC (acronym used as a proper name, formerly known as High Vocal Centre), and RA (robust nucleus of the arcopallium). RA projects directly to a motor nucleus that controls respiration and muscular activity in the syrinx. The anterior forebrain pathway also connects HVC to RA through an indirect route that includes the area X of the lobus parolfactorius, DLM (medial nucleus of the dorsolateral thalamus) and LMAN (lateral magnocellular nucleus). The anterior forebrain is

involved in the regulation of vocal learning. Lesions to LMAN in juvenile songbirds at the stage of subsongs or plastic songs can disrupt learning and production, whereas lesions in adults do not seem to affect songs (Doupe et al. 2000).

Surprisingly, Aronov et al. (2008) have shown that the production of subsongs is not mediated by the same set of brain nuclei involved in the production of songs in adults, the vocal motor pathway. They have demonstrated that juvenile zebra finches do not require HVC, a key nucleus involved in adult song production, to produce subsongs but require LMAN (which is not involved in song production in adults). Aronov and collaborators concluded that subsongs are not generated by an immature vocal motor pathway. They suggested the existence of two distinct motor pathways that produce vocalizations at different stages of development.

## Conclusion

Songbirds develop vocal learning through a sensory-motor process that is strikingly similar to the way human infants acquire a native language. As in humans, this process requires social interactions, sensory feedback, and vocal practice. The first vocalizations produced by juvenile songbirds are called subsong. They are highly variable vocalizations that hardly resemble adult songs. Subsongs may function as a form of vocal exploration in which juvenile songbirds learn how to coordinate the sounds produced by their vocal apparatus. Some research results indicate that subsongs are not mediated by the same brain nuclei involved in the production of songs in adults.

## Cross-References

- Auditory Signals
- Communication
- Countersinging
- Critical Period for Song Learning
- Critical Periods
- Learning
- Ontogeny

- Passerine Cognition
- Passerine Sensory Systems
- Passerine Vocal Communication
- Sensitive Periods
- Signaller
- Social Learning
- Songbird Learning
- Songbird Learning

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## Substance Withdrawal Syndrome

- Withdrawal

## Subtraction

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### Definition

Performing subtractions requires the capability to estimate the resulting difference between a first number, or quantity, minus a second one.

### Introduction

In the field of animal numerical cognition, the capability to master subtraction is considered a complex numerical capacity, because it requires a manipulation of at least two numerical representations to produce a new representation (Vallortigara et al. 2010). The capability to subtract, together with the capability to perform additions, is the only arithmetic ability which has been proved in animals.

Arithmetic has been mainly investigated in animals for what concerns physical sets of objects. Animals' arithmetic abilities differ from humans' abstract arithmetic calculations. The latter are based on a complex system of symbols which refers to numbers and operation that can be performed on numbers, for example,  $45 - 27 = 18$ . Hence, these can be defined symbolic-numerical abilities. Nonsymbolic numbers refer to the information that can be extrapolated from physical events, hence in absence of symbols.

### The Unfortunate Beginning of the Study of Arithmetic Ability in Animals

Arithmetic operations, more than other numerical abilities (such as, e.g. numerical discrimination, which is the capability to discriminate two sets of objects on the basis of their numerosities; and ordinal abilities, which is the capability to identify an element in a series of identical elements on the basis of its numerical position in that series),

suffer of a certain skepticism after the unfortunate beginning of the Clever Hans story (Pfungst 1907). Hans was a horse that, in the first decade of the twentieth century, was trained by his owner, to execute a multiplicity of symbolic arithmetic calculations, which ranged from subtractions, to summations, to divisions, to long square roots. When Hans was presented with an arithmetical operation, he responded by tapping his hoof on the ground the correct number of times. The initial enthusiasm on clever Hans' mathematical skills vanished when it was unveiled that Hans responded correctly only when its owner knows the correct answer, and Hans could see him. Hans was surprisingly skillful in perceiving subtle behavioral signals made by its owner, while it was reaching the correct count with its hoof tapping. As a consequence the great delusion generated by Clever Hans' story pervaded animal numerical research and lasted for decades. Numerical competences were considered as strictly linked with the possibility of using language and symbols; therefore, mathematical reasoning was considered a prerogative of adult and educated humans. Nevertheless, increasing evidence has demonstrated that nonverbal creatures (human infants and nonhuman animals) master arithmetic calculation (Dehaene 2011; Brannon and Roitman 2003).

### Subtractions in Human Infants

The seminal study on arithmetic abilities in nonverbal creatures goes back in 1992, when Caren Wynn showed that 5-month-old infants successfully answered to simple summations and subtractions. The idea was that if infants keep track of the numbers of toys they have seen being placed behind a screen they should look longer at the screen that, when lowered, revealed an outcome that violated their expectations (violation of expectation paradigm, VoEP). For example, in the  $2 - 1 = 1$  or 2 task, infants were showed two toys that were placed behind a screen; then one was removed. In some instances the outcome was expected ( $2 - 1 = 1$ ), and in other cases the revealed number was unexpected ( $2 - 1 = 2$ ). Infants looked longer at outcomes where

expectation was violated (Wynn 1992), suggesting that they are able to solve simple arithmetical problems.

### Subtractions in Adult Animals

To test arithmetic calculation in a population of semi-free-ranging monkeys (*Macaca mulatta*), it has been designed a paradigm which exploited the optimal foraging theory (Krebs 1974). This theory assumes that animals, when can choose between two food alternatives, spontaneously prefer the one that maximizes energetic gain (i.e., larger amount of food). Subjects viewed two different numbers of identical food items that were positioned behind two identical screen. For example, three items were hidden behind a screen and two behind the other one. Some items were then visibly removed from behind the screens. For example, one item was removed from both screens, 3–1 versus 2–1. Monkeys approached the screen that hid the larger number of food items (Sulkowski and Hauser 2001). This demonstrates that primates can solve simple subtractions without having received specific numerical training.

Interestingly enough, arithmetic abilities have been proved also in bird species.

Using a VoEP paradigm, wild New Zealand robins (*Petroica australis*) have proved to solve simple subtractions, such as 2–1 or 3–1. Within view of the bird, a certain number of food items were subtracted from an initial amount of items, placed in a container. For example, from an initial set of three items, one was removed (3–1). Robins were then allowed to approach the container. When the number of found items violated the arithmetic rules, robins searched longer than when the number was arithmetically congruent, proving their proto-arithmetical competences (Garland and Low 2014).

### Subtractions in Young Animals

To understand how early animals can start to use numerical information, arithmetic task has been investigated in young domestic chicks (*Gallus*

*gallus*), which is a species that can master different kinds of numerical tests, ranging from numerical discrimination of artificial social companions (Rugani et al. 2010) to ordinal abilities (Rugani et al. 2007).

Newly hatched domestic chicks were reared with five identical objects that through exposure were treated by the chicks as social companions. On day 3, chicks underwent free choice tests. At first they were shown different sets of objects to disappear, one by one, behind one of two opaque identical screens (first event). Subsequently some of the objects were visibly transferred, one by one, from a screen to the other (second event). For example, four objects were first hidden behind a screen and one behind the other. Then one or two objects were transferred from the screen hiding four to the screen hiding one object. In both cases chicks approached the screen hiding the larger number of “social companions” (Rugani et al. 2009). Results suggest impressive proto-arithmetic capacities in very young and relatively inexperienced chicks.

### Conclusions

Studies on animal numerical cognition suggest that numerical information is so relevant that a variety of animal species master simple arithmetic abilities. Interestingly enough the paradigms used, such as the VoEP paradigm and the spontaneous choice based on the optimal foraging theory, allowed to test the capability to perform summation and subtractions in untrained animals. This suggests that to solve simple numerical operations, animals do not need a long numerical training. Moreover, data on newborn chicks show that numerical information is so relevant that almost naive animals naturally extrapolate and use it soon after birth.

### Cross-References

- [Absolute Number Discrimination](#)
- [Addition](#)
- [Clever Hans](#)

- Numerosity
- Ordinality
- Relative Numerousness

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## Successive Approximations

- Shaping

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## Suckling/Nursing

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## Synonyms

Nipple attachment; Suction

## Antonyms

Weaning

## Definition

The terms nursing and suckling are both related to lactation (milk acquisition). Yet, nursing is from the female's perspective – the act of providing milk – while suckling is from the infant's viewpoint – the act of obtaining milk from a nipple.

## Introduction and Terminology

Suckling and nursing are terms sometimes used interchangeably, but each has very distinctive meanings. The act of suckling refers to the offspring perspective, the acquisition of milk from a nipple. As for nursing, it includes physiology and behavior of the lactating female in order to transfer milk to an offspring (Hall et al. 1988). The authors emphasize that many behavioral interactions are required for both to be successful. In essence, the young searches, recognizes, and attaches to a nipple, a stimulatory requirement for the milk transfer from the lactating female. Although behavioral interactions are indeed necessary for suckling/nursing to be successful, the morphological apparatus is quite interesting.



Therefore, we will first present morphological aspects that enable suckling/nursing behavior, followed by the physiological cascades and, finally, the behavioral characteristics that make this entire mechanism feasible.

## Morphological Aspects for Nursing

Extant mammals are divided into monotremes, marsupials, and placentals. Monotremes, the egg-laying mammalian group, produce a nutritive substance similar to milk, but adults do not present nipples that would allow infants to perform an appropriate suckling. The young receives this substance through skin-feeding, in which the “milk” exudes and is thick enough to cling in the female’s hair, so it can be licked directly (McLoughlin 1980). Conversely, marsupials and placentals have specialized structures called nipples, teats, or udder, where their young are able to attach to and obtain milk. After attachment, suckling occurs and, eventually, milk is released (see Physiology section). Together, both this specialized structure and this particular behavior avoid milk waste and ensure a more effective transport of nutrients to the young (McLoughlin 1980; Blass 1990).

## Morphological Aspects for Suckling

Suckling is unique to mammals and intimately connected with cranial features: palates, facial muscles, cheeks, lips, and tongue compose this complex apparatus, required for the development and evolution of suckling in mammalian neonates. Concerning skull morphology, mammals present a hard palate, a structure found in pre-mammalian species and responsible for the complete separation of breathing and swallowing, allowing both to occur at the same time (Hiimeae and Crompton 1985; Maier et al. 1996).

Still considering skull traits, mammals present a unique feature regarding dental replacement, called diphyodont dentition, that can be defined as two different dentitions throughout a lifetime. A consistent pattern is the young being born

without teeth, with subsequent eruption of milk teeth and further replacement by permanent teeth. Being born toothless possibly enhances suckling performance and, in turn, a liquid nourishing exempts the immediately need of teeth and masticatory movements. This delay in tooth eruption and replacement grants an extra time for skull growth, so there is enough space in the oral cavity for all the permanent teeth (Pond 1977). Although this perspective seems constantly reinforced in some studies, it still requires a broader phylogenetic comparison.

Besides osteology, suckling involves a specialized musculature working synchronously. One muscle seals completely the roof of the mouth, separating breathing and swallowing, another group of muscles creates a low pressure and bring in the liquid, and a third muscle group helps swallowing (Crompton et al. 2018). Marsupials and placentals present all these muscles and can perform suckling. Monotremes, however, do not possess some of these muscles, and the long hard ossified beak hampers their ability to suckle. Yet, this statement is still controversial since a few authors consider that suckle activity is possible (Koyama et al. 2013; Li et al. 2016).

Likewise, mouth parts are essential for suckling motion. For instance, it is necessary a regular and rigid tongue movements to prevent air passage so that inside-out pressure between female nipple and offspring mouth is maximized. Moreover, lips seal completely the mouth and the nipple together (Elad et al. 2014). Finally, saliva is an underestimated, but crucial component as it acts as a mechanical sealant to the infant lips at the female’s nipple. Rats with no submaxillary-sublingual saliva died of starvation, due to the inability to suckling properly (Epstein et al. 1970).

## Physiology of Suckling/Nursing

Nursing is deeply associated with lactation, which has been defined as the physiological state of a female mammal resulting in milk production. Besides nourishment (water, proteins and fat), milk is also responsible for the postnatal transfer of immune protection to the young since

premamalian species (Blackburn et al. 1989). Antibodies can be transferred to the offspring either during pregnancy (exchange with their mother blood) or ingestion after birth. Different antibodies require different transfer paths as some are not capable of crossing the placenta, for instance. Therefore, milk ingestion is an important way of acquiring immune protection, particularly rich in the first milk, also known as colostrum (Boulinier and Staszewski 2008).

Lactation includes milk synthesis by specialized cells found in mammary glands. During adulthood, mammary glands go through four stages: mammogenesis (cell proliferation), lactogenesis (milk production and let down), galactopoiesis (maintenance of milk production and let down), and involution (milk production ceases and the tissue shrinks). After milk production, it passes through mammary ducts (from the alveolar epithelium to the alveolar lumen) all the way to the nipples in marsupials and placentals, but directly to the exterior in monotremes (Hall et al. 1988). Although the description of lactation cycles is beyond our scope, these phases are highly dependent on many hormones, from sex steroids to protein hormones (Svennersten-Sjaunja and Olsson 2005).

Despite that many hormones are essential for lactation to occur, two are intimately associated with the process of nursing/suckling: prolactin and oxytocin. The two are secreted at basal levels, in both sexes, but they increase at extraordinary speed and up to 10 times higher during suckling. While prolactin is important for milk production, maintaining the constant milk metabolism, oxytocin is involved in milk ejection control (Svennersten-Sjaunja and Olsson 2005). Neither hormone requires a preceding pregnancy as the nipple stimulus is enough to induce milk production. Therefore, allonursing (nursing for another female's offspring) is possible even in non-pregnant females (see section below).

It is interesting that suckling triggers what is called milk letdown reflex. Why would a mammal need such reflex? Because suckling alone does not cause milk flow even with the negative pressure caused by the infant at the nipple. The cascade is as follows: suckling stimulates oxytocin release

that, in turn, stimulates contraction of milk ducts and creates a positive pressure at the female's body. The act of suckling is able to open the valves, so that milk ejection is now possible (Goodman 2009).

Hormonal release and milk production can be stimulated either by increasing suckling duration or by increasing the number of teats suckled. Hence, during the postnatal period, nursing is more recurrent and lasts longer, so that hormonal discharge is higher. A similar pattern can be observed in larger litters as multiple teats are suckled simultaneously.

Oxytocin has another important influence: pair bonding, particularly between the nursing female and the suckling offspring (Uvnäs-Moberg 1998). Higher levels have been detected after affectionate contact between adults and infants by inhibiting our defensive behavior and reducing our natural avoidance response. Because its release is stimulated by suckling, as the infant grows older, nursing sessions are reduced both in frequency and duration, lowering the production of both hormones (Ziegler et al. 2004). Hence, this hormone has important specific behavioral effects.

## Behavior of Suckling/Nursing

As stated above, nursing and suckling require behavioral interactions in order to be executable. From the pups' perspective, besides search and attachment, additional behaviors may follow, such as kneading, treadling, and/or butting movements to help milk transfer. Kneading and treadling is when a young uses its paws to induce milk ejection from a teat, pressing against the maternal ventrum (Smotherman and Robinson 1994; Barrows 2011). Butting could be equivalent to the kneading/treadling behavior as it is more common in hoofed-mammals. Instead, the young induces milk ejection with its own head by pressing against the female's teats. This sequence of events helps maintain nipple contact and stimulate milk letdown, ejection, and withdrawal.

Many authors employ an additional term, named as "sucking." However, in the work of

Hall et al. (1988), they define sucking as being only the negative intraoral pressure on the nipple caused by repeated mouth movements, necessary for milk ejection. They emphasize that sucking and suckling are not synonyms because sucking may not result in milk ingestion, occurring at nonlactational periods. Thus, sucking is a part of suckling. Sometimes, nipple contact may provide infant comfort and does not include suckling necessarily. We can find a good example in humans when kids suckle the index finger for soothing, but they do not obtain any milk.

Lastly, it is important to emphasize that nursing/suckling does not include a mother and her infant(s) necessarily as many species show allomaternal lactation. Thus, we use “female” and “offspring/young,” because they may not be related. For instance, carnivores and primates have many examples of allomaternal lactation (allonursing, allocare) in which a female lactates for an offspring other than her own, without even the need of having her own offspring or being pregnant.

## Conclusion

Suckling is one defining characteristic of mammals. It is attributed to the act of suckle from infants aiming milk ingestion, and there are many morphological aspects essential for it to occur. A hard palate, cheeks, tongue, and lips work together for this complex system to be in motion. As for nursing, many mammals present specialized structures, called nipples, teats or udder. Since monotremes do not present these structures, some authors argue that they do not perform suckling. Regardless, nursing refers to the physiology and behavior of the lactating female in order to transfer milk to an offspring. Lactation is essential for infant survival through feeding and immune protection. Milk production involves many hormones, but mostly prolactin and oxytocin, which are associated with the act of nursing/suckling. However, hormonal secretion does not require that the female is pregnant since the nipple stimulus is enough to induce milk production. Therefore, allonursing is possible in

nonpregnant females and that is why the terms “female” and “offspring/young” instead of “mother” and “offspring/young” are more appropriate. Suckling and nursing help social bonding between female and infant, providing instant recognition and physiological signals to continue the milk production.

## Cross-References

- [Alloparental Care](#)
- [Altricial](#)
- [Maternal Behavior](#)
- [Precocial](#)

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## Suction

### ► Suckling/Nursing

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## Sue Savage-Rumbaugh

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Emily Sue Savage-Rumbaugh (August 16, 1949–) is a comparative psychologist and primatologist known for her studies of language and development in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). Her research with apes – most

notably chimpanzees Sherman, Austin, and Panzee, and bonobos Kanzi and Panbanisha – have resulted in more than 100 publications, including the books *Ape Language: From Conditioned Response to Symbol* (Savage-Rumbaugh 1986) and *Kanzi: The Ape on the Brink of the Human Mind* (Savage-Rumbaugh and Lewin 1994, coauthored with Roger Lewin). She has received numerous honors, including honorary degrees from the University of Chicago and Missouri State University. In 2011, *Time Magazine* named Dr. Savage-Rumbaugh one of the 100 most influential people in the world.

## Personal and Professional History

Sue was born in Springfield, Missouri to Euell Rubert, who was in real estate, and Joyce Rubert, a homemaker. As a child, she was interested in all school subjects, but quickly found her passion in psychology at Colorado College. She later transferred to Southwest Missouri State University (now Missouri State University) where she graduated with honors in 1970 with a B.A. in psychology. After graduation, Sue Savage planned to go to Harvard for graduate study with B.F. Skinner. However, fate interceded: the fellowship she was expecting fell through, but more influentially, a visit with a friend at the University of Oklahoma (OU) changed the direction of her interests. During her visit to OU, Sue sat in on a lecture by ape-language researcher Dr. Roger Fouts, who had brought a chimpanzee named Booe to class to demonstrate the sign-language research being done at the Institute for Primate Studies (IPS; aka “The Farm”) which had been founded at OU by psychologist Dr. William Lemmon. It was a life-changing experience for the young psychology scholar, as she later recalled: “At that time I was studying child development and had a 2-year-old son who was beginning to acquire language. I was amazed to see a chimpanzee sit in front of a class of 100 students and sign...” (Hillix and Rumbaugh 2013, p. 155). She moved to Norman, OK, and began doctoral training under the direction of Professor Lemmon, earning her M.S. in 1972 and the Ph.D. in 1975. Because

the colony of chimpanzees at IPS had been reared in various ways, including wild-caught, peer-reared, mother-reared, and in human homes, Sue was able to study the effects rearing environments had on chimpanzee development. She found that the rearing conditions, combined with sign-language training, created a perfect cauldron for research on chimpanzee behavior. Her dissertation was an ethnography of intentional gestures and postures in group-living chimpanzees, looking at the use of these behaviors for communicative purposes.

After receiving her degree, Dr. Savage accepted a position in Atlanta, GA, conducting postdoctoral research at the Yerkes Regional Primate Research Center. In Atlanta, her experience with chimpanzees and with language-acquisition research would be of great value, as she joined the Language Analog (LANA) Project – an ambitious, NIH-funded multidisciplinary research enterprise directed by Dr. Duane Rumbaugh, professor and chair of psychology at Georgia State University. LANA Project scientists were studying whether a chimpanzee named Lana could learn to communicate using a specially designed computer-based keyboard and a “language” of visuographic symbols called lexigrams. Dr. Savage brought new perspective to the 3-year-old project, helping to document aspects of Lana’s impressive performance, but also providing insightful criticisms of some of the LANA Project’s limitations.

The professional move with her son to Atlanta contributed to the end of Sue’s marriage with William Savage, Jr., now an emeritus professor of history at OU. In 1976, Sue and Duane Rumbaugh wed. They were married for more than two decades, and remain friends and collaborators to the present day.

The juxtaposition of experiences in Oklahoma and Georgia served to convince Dr. Savage-Rumbaugh of the importance of the social functions and context of language. These social aspects were largely absent from the work with Lana, which was focused on communications by the chimpanzee with the computer and with human researchers. A new group of four chimpanzees (Austin, Erika, Kenton, and Sherman)

was assigned by the Yerkes Center to the language-training project in 1975, although ultimately the demands of raising young chimpanzees in a language-rich environment would require the research team to focus their efforts on Austin and Sherman only. The communicative medium for this new research remained lexigram word-symbols and the computerized keyboard, but the goals of the so-called Animal Model Project were shifted dramatically by Savage-Rumbaugh. Whereas Lana was taught to produce sequences of lexigrams in stock-sentences so as to achieve desired outcomes (e.g., make requests, ask and answer questions) from the computer or human caregiver, the foci of research with Austin and Sherman were on communication between the chimpanzees, and on determining what the symbols might mean to the apes (i.e., on comprehension rather than production). Savage-Rumbaugh endeavored to establish, with and between the apes, the same kinds of social connections that human infants experience when they learn language. Project scientists taught the apes to share food, to exchange tools, and to use the keyboard to tackle problems that could not be solved without the use of symbols. In one such test, Sherman used the computer keyboard to request foods that were accessible by Austin; Austin, in response, would retrieve the food items that Sherman requested, give Sherman half, and consume the remainder. No human experimenter was present in the room as the apes performed these tests! The training and tests with Austin and Sherman were reported in numerous published articles and extensively detailed in a book and accompanying video documentary (Savage-Rumbaugh 1986). The book also described research led by Dr. MaryAnn Ronski (Georgia State University) to derive principles from the work with Lana, Sherman, and Austin, and to apply those principles in language interventions for nonspeaking children and young adults with intellectual disabilities.

Although Austin and Sherman showed impressive evidence of conceptual understanding and communicative use of the lexigram symbols, they consistently failed Dr. Savage-Rumbaugh’s controlled tests of spoken-English comprehension



in the absence of contextual cues. However, a very different story would emerge when Savage-Rumbaugh shifted the focus of her research to bonobos—a shift that, in many ways, came almost by accident! In 1981, Dr. Savage-Rumbaugh was attempting to teach a bonobo named Matata to use lexigrams. The teaching methods that had been so successful with Austin and Sherman seemed ineffective with Matata, whose attention was largely devoted to young Kanzi, the ever-present infant Matata had adopted when he was 6-months old. Matata's utter lack of progress in learning lexigrams made it easy to spare her when it was time for her to return to the Yerkes Center for breeding, whereupon the 30-month-old Kanzi immediately and without prompting began to use the lexigram keyboard, and doing so to make requests and to announce actions with surprising accuracy (Hillix and Rumbaugh 2013). Although Matata had failed to benefit from the training, her adopted son Kanzi had clearly learned a great deal from observation.

This event catalyzed another radical shift in the ape-language research that Dr. Savage-Rumbaugh directed. She concluded that that language is an active cognitive process that is not solely behaviorally shaped. Indeed, attempts systematically to train apes to use language can also limit the depth of what they learn. Rather, in the correct language-rich environment, focused on comprehension and functional significance of symbols, apes can come to learn language the way that human children do, and the way Kanzi apparently did. Dr. Savage-Rumbaugh's subsequent research with bonobos Kanzi, Mulika, Panbanisha, common chimpanzee Panzee, and many other apes followed this new method, modeled much more closely after the rearing of human children.

Apes raised in this language-rich social culture also showed that they could comprehend not just lexigram-based communications, but also the spoken English used by Dr. Savage-Rumbaugh and other speakers. Unlike Austin and Sherman, Kanzi (and other apes raised like him) passed carefully controlled experimental assessments of spoken-word comprehension. In one extensive study, Kanzi was tested, under conditions that controlled for cuing and experience, for his ability

to comprehend novel sentences of spoken English. The bonobo performed comparably to a typically developing 2½-year-old human child on these tests, showing sensitivity both to word meaning and to the way that sentence meaning is determined by word order. The monograph report of these findings (Savage-Rumbaugh et al. 1993) was named by the University of Minnesota Center for Cognitive Science as one of the 100 most influential works in cognitive science in the twentieth century.

Professor Savage-Rumbaugh attempted to untangle the potential effects of species versus training variables in producing the performance differences that were observed between chimpanzees Austin and Sherman on the one hand, and bonobos like Kanzi on the other. Beginning in 1985, she led a longitudinal research project in which she and her research team coreared an infant chimpanzee (Panzee) and an infant bonobo (Panbanisha), and studied the physical, behavioral, and cognitive similarities and differences between these language-experienced apes – as well as the ways that the two apes were unlike language-trained animals that had been studied earlier (e.g., Brakke and Savage-Rumbaugh 1995, 1996).

From 1981 to 2005, Dr. Savage-Rumbaugh studied these and related topics with the apes at Georgia State University's (GSU) Language Research Center (LRC). In 1987, she was appointed Associate Professor of Biology at GSU and earned tenure in 1990. She retired as a GSU Professor of Biology and Psychology in 2005 and moved with the bonobos to the Iowa Primate Learning Sanctuary and Great Ape Trust in Des Moines, IA. She is currently President of Bonobo Hope, a nonprofit organization.

## Significant Contributions

Dr. E. Sue Savage-Rumbaugh has dedicated over four decades to great apes, serving as primary caregiver, teacher, researcher, and advocate for more than a dozen chimpanzees and bonobos. Without discounting the able assistance she received from collaborators, students, and staff

(including Sally Boysen, Karen Brakke, Heidi Lyn, Rose Sevcik, Jared Taglialatela, and many others), a few scientists in history have embraced the intense, constant, longitudinal commitment of raising apes in this way – much less doing so multiple times. Her methods and conclusions have been criticized, but she has been tenacious in the debate. Her publications included many controlled tests of ape cognition that appeared in refereed journals, and she succeeded in attracting many years of extramural funding for her research, primarily from the National Institute of Child Health and Human Development. Her work has also generated considerable media attention. Documentary recordings of her work, particularly with Austin, Sherman, and Kanzi, provide important archival records and instructional resources.

In 1981, Dr. Savage-Rumbaugh assisted Dr. Duane Rumbaugh in establishing the Language Research Center (LRC) at Georgia State University. The LRC provided a home to the remarkable resident chimpanzees and bonobos, a laboratory for Dr. Savage-Rumbaugh and countless other scientists to study these unique primates, and a strong commitment to promoting the health and psychological wellbeing of all of the Center's animals. The LRC was, and continues to be, an important resource where students can be trained and scientists of various disciplines can study primate behavior and cognition.

Across her career, Dr. Savage-Rumbaugh's research and writings have increasingly emphasized the importance of enculturation. The animals learn about ape culture from other apes. They learn some rules and routines of human culture from researchers, teachers, and caregivers. These experiences don't make the chimpanzees and bonobos any less apt representatives of apes, but the cultural experiences and expectations of a laboratory-raised animal are different, even unique. The effects of this enculturation manifests in a wide range of behaviors, including those like tool-making, numerical cognition, vocal production, social cognition, and language comprehension that have been studied by Dr. E. Sue Savage-Rumbaugh (e.g., Hopkins and Savage-Rumbaugh 1991; Sevcik and Savage-Rumbaugh 1994; Tomasello et al. 1993).

## Cross-References

- ▶ [B.F. Skinner](#)
- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)
- ▶ [Counting](#)
- ▶ [Culture](#)
- ▶ [David Washburn](#)
- ▶ [Duane Rumbaugh](#)
- ▶ [Georgia State University's Language Research Center](#)
- ▶ [Imitation](#)
- ▶ [Kanzi](#)
- ▶ [Language Research: Great Apes](#)
- ▶ [Lexigrams](#)
- ▶ [Panbanisha and Panzee](#)
- ▶ [Primate Cognition](#)
- ▶ [Primate Communication](#)
- ▶ [Sarah "Sally" Boysen](#)
- ▶ [Sarah, Lana, Sherman, and Austin](#)
- ▶ [Stone Tools](#)
- ▶ [Yerkes Primate Research Center](#)

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## Suidae

### ► Swine Cognition

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## Suidae Navigation

### ► Swine Navigation

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## Superior Parietal Lobule (SPL)

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As shown in Fig. 1a–b, the parietal lobe of both human and nonhuman primates can be distinguished in anterior and posterior subdivisions. The posterior parietal cortex, in turn, is divided into superior (SPL) and inferior (IPL) parietal lobules, separated by the intraparietal sulcus. According to Brodmann (1909), the superior parietal lobule, the target of the present chapter, hosts two cytoarchitectonic fields, area 5 anteriorly and area 7 posteriorly. In the human brain, area 5 is a quite restricted area while area 7 occupies most of the SPL (see close-up in Fig. 1a). In the macaque brain, instead, area 5 occupies most of the SPL and area 7 only a restricted region of cortex in the caudalmost part of SPL (see close-up in Fig. 1b). Several studies in the last century claimed that this latter cortical region is not area 7, as originally indicated by Brodmann, but a variation of area 5. In either cases, it remains that the cytoarchitecture in SPL is not uniform, and the different architectural patterns of anterior and posterior

parts of SPL suggest that they host different functional properties and subserve different functional roles.

The following is a summary of the functional properties, anatomical connections, and possible functional roles of SPL. The description refers to the macaque SPL, which has been intensively studied in the last decades. The human SPL has been much less studied to date and has not been taken into account here.

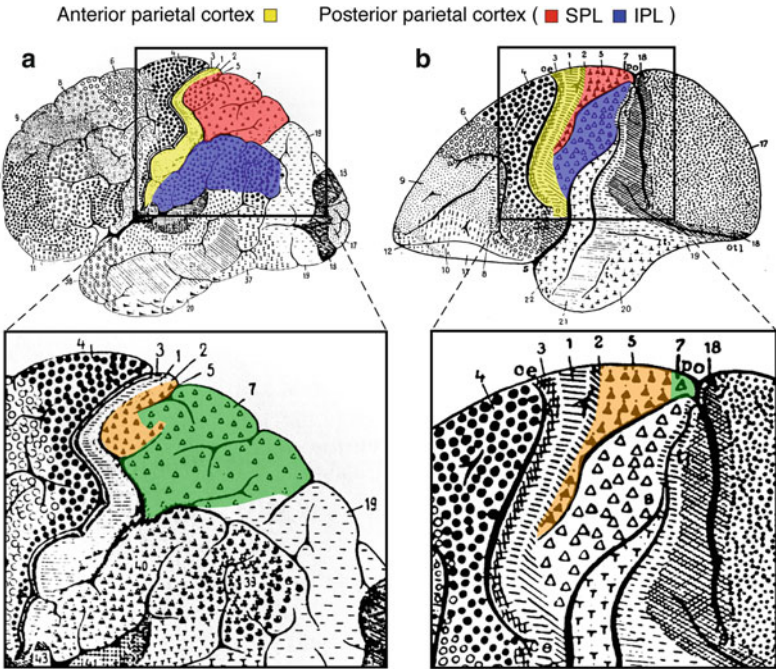
## Functional Properties of the Macaque SPL

In 1982, Pandya and Seltzer (1982) proposed a subdivision of the macaque SPL which is still used today in most of the scientific works related to the posterior parietal cortex (Fig. 1c): the anterior part of SPL, dominated by Brodmann's area 5, was named area PE while the posterior part of SPL (area 7, or a variation of area 5) was named area PEc, where “c” stands for “caudal.”

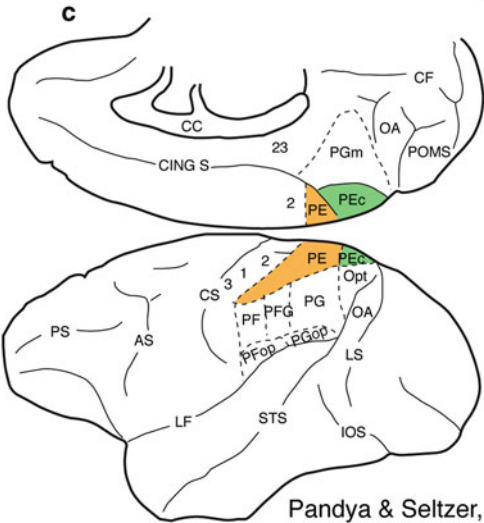
Area PE is a somatosensory area, like the Brodmann's areas 3, 1, 2 that occupy the post-central cortex just anterior to PE (Fig. 1). Area PE, however, shows some functional differences with respect to the other somatosensory areas. While areas 3, 1, 2, in particular areas 3a and 1, are dominated by tactile representation and host a detailed map of the entire body, PE is dominated by proprioceptive representation (see Fig. 2b, columns on the left) and hosts a rough topographical map of the body, with an overrepresentation of the arm, particularly of the hand (Fig. 2a). PE neurons are generally sensitive to multi-joint stimulations and to the posture of the limbs. Often, the neuronal responses of single PE cells are evoked by somatic stimulations of different parts of the body, mainly of the contralateral side, but sometimes of the ipsi or even of both ipsi and contralateral sides (Fig. 2b, right). It has been demonstrated that PE neurons are also involved in the preparation and control of limb movements, and become active during skilled actions (Fig. 2c). This means that PE is not simply a somatosensory area, as originally thought, but a somatomotor area that hosts motor signals together with a

**Superior Parietal Lobule (SPL), Fig. 1**

The parietal cortex. (a) Lateral views of human and (b) macaque brains (left hemisphere) showing the Brodmann's parcellation of cortical surface (Modified from Brodmann 1909). *Top*: areas 3-1-2, superior parietal lobule (SPL), and inferior parietal lobule (IPL) are colored in yellow, red, and blue, respectively. *Bottom*: close-ups showing, enlarged, areas 5 and 7 colored in orange and green, respectively. (c) Mesial (*top*) and lateral (*bottom*) views of the cortical surface of macaque brain according to Pandya and Seltzer's parcellation (Modified from Pandya and Seltzer 1982). PE and PEc are colored as areas 5 and 7 in the close-ups of a and b (orange and green, respectively). Abbreviations: PS principal sulcus, AS arcuate sulcus, CF calcarine fissure, CING S cingulate sulcus, CS central sulcus, LF lateral fissure, LS lunate sulcus, POMS parieto-occipital medial sulcus, STS superior temporal sulcus, IOS inferior occipital sulcus, CC corpus callosum. OA, PGm, PEc, PE, 3, 1, 2, 23, Opt, PG, PFG, PF, PGop, PFop: areas OA, PGm, PEc, PE, 3, 1, 2, 23, Opt, PG, PFG, PF, PGop, PFop



Brodmann, 1909



Pandya & Seltzer, 1982

somatosensory map of the body. It has been suggested that it contributes to the somatomotor guidance of motor behavior. Area PEc, differently from PE, is an area that hosts a quite large visual field representation together with an incomplete somatosensory map of the body. The visual neurons of PEc are quite large and are often sensitive to the optical flow. The body map is focused on the proximal parts of

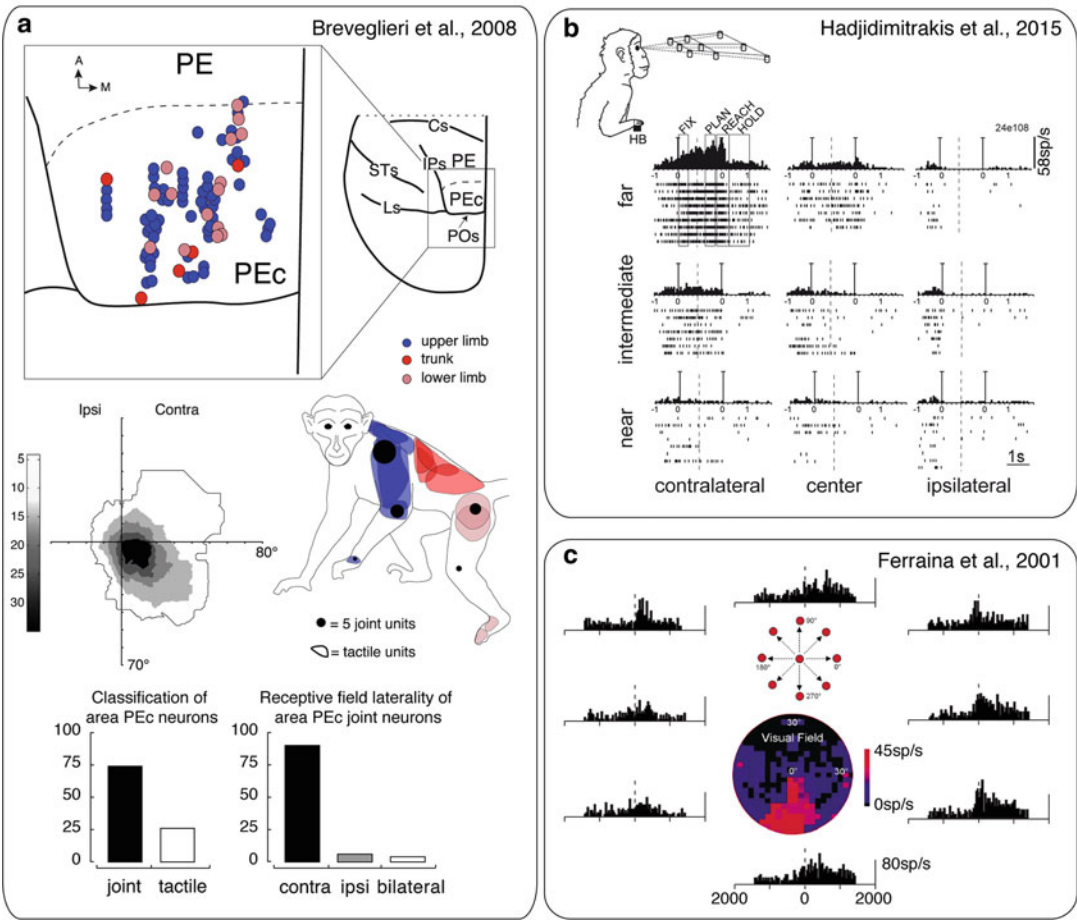
the limbs and does not show any evident sign of topographical organization (Fig. 3a). The somatic PEc neurons respond mostly to single-joint rotations but also to tactile stimulations of the trunk and limbs. The incidence of joint versus tactile sensitivity, as well as of contralateral versus ipsi and bilateral sensitivity, is almost the same as that shown by area PE (Fig. 3a, bottom). Several single PEc neurons show bimodal somatovisual







Area PEc



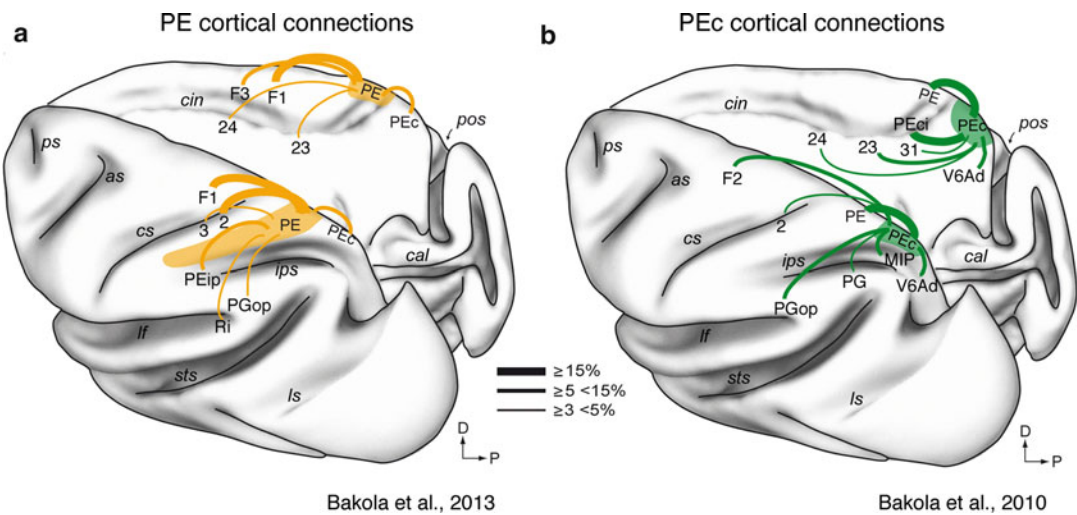
**Superior Parietal Lobule (SPL), Fig. 3** Functional properties of area PEc. (a) *Top*: Distribution of functional properties within area PEc. Notice the absence of any somatotopy. Abbreviations: Cs central sulcus, IPs intraparietal sulcus, Ls lunate sulcus, POs parieto-occipital sulcus, STs superior temporal sulcus, PE, PEc areas PE, PEc, Center; *left*: Density map of PEc visual receptive field (RF) distribution. Gray scale indicates the relative density of RFs covering that specific part of the visual field. *Center, right*: Body locations of PEC somatosensory RFs: joint RFs are represented as dots and tactile RFs as colored regions of the body. The size of each dot and the intensity of colored regions are proportional to the number of modulated cells. All somatosensory RFs have been reported on the left side of the body. *Bottom*: Incidence of joint and tactile cells (*left*) and of contralateral, ipsilateral, and bilateral modulations (*right*) in area PEc (Modified from

Breveglieri et al. 2008). (b) Depth and direction tuning of the activity of a PEC neuron. Spike histograms and rasters of cell activity are shown for nine target positions presented to the animal at eye level, but with different depth and direction (see inset on the top left). Notice that the cell was strongly activated when the animal reached the far contralateral target and, like PE neurons, discharged during both movement preparation and execution. HB home button (Modified from Hadjidimitrakakis et al. 2015). (c) Perievents time histograms of the activity of a PEC neuron recorded while the animal reached a target located in eight different spatial positions on a two-dimensional plane starting from the center. The color-coded map of cell activity shown on the bottom center represents the location and extent of the visual RF of the neuron as determined during a Visual Fixation task (Modified from Ferraina et al. 2001)

known to be involved in the skeleton motor control of limb movements. Interestingly, PEC is more strongly connected with the motor and premotor cortical regions representing the lower

limbs than with those representing the upper limbs.

In summary, all the cortical sensory afferents to PE bring only somatic information while those to



**Superior Parietal Lobule (SPL), Fig. 4** Summary of main cortico-cortical connections of areas PE and PEc. Cortical connections of area PE (**a**) and PEc (**b**) are shown in *orange* and *green*, respectively. Only projections representing more than 3% of the total cortical connections of that area are reported here. The thickness of connecting lines is proportional to the strength of connections, averaged across all cases with injections in the same area (Data

obtained from Bakola et al. 2010, 2013). Abbreviations: *ps* principal sulcus, *as* arcuate sulcus, *cal* calcarine fissure, *cin* cingulate sulcus, *cs* central sulcus, *lf* lateral fissure, *ls* lunate sulcus, *pos* parieto-occipital sulcus, *sts* superior temporal sulcus, *ips* intraparietal sulcus. F1, F2, F3, PEc, PE, PEci, PEip, 3, 2, 23, 24, 31, PGop, PG, Ri, V6Ad, MIP: areas F1, F2, F3, PEc, PE, PEci, PEip, 3, 2, 23, 24, 31, PGop, PG, Ri, V6Ad, MIP

PEc bring both somatic and visual information. Both areas also receive motor signals related to limb movements.

**Conclusions**

The cortical afferents of areas PE and PEc corroborate the functional characteristics of these areas, being PE essentially a high-order somatosensory area and PEc a bimodal somatovisual area, albeit with predominant somatosensory inputs. Both areas overrepresent the limbs, more the upper than the lower one. However, while PE shows an overrepresentation of the distal part of the upper limb, similarly to areas 3, 1, 2 (Fig. 2), PEc overrepresents the proximal part of both upper and lower limbs (Fig. 3). The functional properties as well as cortical afferents of areas PE and PEc strongly suggest the involvement of both areas in the control of limb movements. This is in line with the functional roles proposed for PE and PEc, the former being suggested to be involved in the preparation/execution of limb movements, in

particular the movements of the upper limbs, and the latter in the control of limb movements and of interaction of the four limbs with the visual environment. Since area PEc is sensitive to the optical flow, receives visual information mostly from the lower visual field, and is more strongly connected with cortical motor/premotor regions that represent the lower limbs, it has been suggested that it is involved in the visual guidance of locomotion.

**Cross-References**

- [Depth Perception](#)
- [Neuron](#)
- [Optic Flow](#)
- [Parietal Lobe](#)
- [Parieto-Occipital Sulcus \(POS\)](#)
- [Primates](#)

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## Superior Temporal Sulcus

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The superior temporal sulcus (STS) is located longitudinal to the lateral surface in the temporal lobe and is immediately parallel to the lateral

fissure. The STS ranges from the angular gyrus to approximately one centimeter before the temporal pole. The STS separates the superior temporal gyrus and middle temporal gyrus.

## Functions

The STS is a multisensory high-order association cortex that processes social information.

*Face perception* (Allison et al. 2000; Haxby et al. 2000). The STS is important in the changeable aspects of a face. Beyond identity, it is crucial to the communication of dynamic aspects from faces like lip movement, eye gaze to infer attentional state, and the emotional expression (Allison et al. 2000; Hagan et al. 2009; Peelen et al. 2010; Robins et al. 2009; Said et al. 2010). The model of the distributed human neural system for face perception includes the STS in the core system involved in the visual analysis of a face, whereas the inferior occipital gyrus processes the early perception and the fusiform gyrus, the invariant perception of faces, the STS process the changeable features of faces (Andrews and Ewbank 2004; Kanwisher and Yovel 2006). The STS also has reciprocal connections with inferior occipital and fusiform gyrus, and with nodes of the extended system: intraparietal sulcus, auditory cortex and amygdala, and insula and limbic system.

*Multisensory integration* (Beauchamp 2005). In macaques and humans, the STS plays an important role in multisensory integration. In both species, the STS has a patchy organization for multisensory integration, with patches that prefer meaningful stimuli of one sensory modality (e.g., auditory or visual), and other multisensory patches, that responds to both kind of stimuli (e.g., auditory and visual) with an enhanced response to multisensory integration. This organization suggests that the different sensory modalities arrive in specific patches depending on the sense, since each sense has a specific neural code in the patches that could facilitate the transformation into a common code. Furthermore, in these multisensory patches occur the integration of the different modalities into multisensory representations.

## Mentalizing in Autism Spectrum Disorders

The autism spectrum disorders (ASD) imply impairments in social perception (e.g., eye-gaze, voice, and visual perception) that are highly correlated with anatomical and functional abnormalities in the STS.

For example, the ability to attribute mental states to others is affected in ASD. This process was explored in a classical study (Castelli et al. 2002). To remove the human component in the mentalizing process, the researchers designed three animations of two triangles with different interactions between them: random movement, goal-directed movement, and movement that implied intentions, to relevant mental processing. The cerebral activity while the participants viewed the animations was compared between normal and ASD adults. Regarding mental processing of the animation, the results showed a weaker activation in a network that includes bilateral STS, prefrontal cortex, and temporal pole in the ASD group. However, the activity in an extrastriate region (V3) was the same in both groups. The main finding of this study was that despite the same increased activity in V3 in both groups, the functional connectivity between V3 and the STS was reduced in the ASD group. The results suggest a lack of modulation of anterior regions to the STS, and that this promoted an interruption in communication between high order (STS) and low order (V3) perceptual regions. It was more difficult for ASD group to recognize the social meaning of the triangle's movements. It is important to emphasize that the impairment in the ASD group is due to a problem in the functional connectivity in the STS, which shows the importance of the cerebral networks in the social perception.

## Human Specific Asymmetry in the STS

Humans show several behavioral and neuroanatomical asymmetries, and some of these asymmetries also are present in nonhuman primates. However, an astonishing study comparing

magnetic resonance anatomical images from 177 humans and 73 chimpanzees suggests that the asymmetry in the STS is exclusive of humans (Leroy et al. 2015). The human sample included subpopulations: infants, children, adults, women, men, right-handers, left-handers, and an atypical population (i.e., autistic spectrum disorder, situs inversus, Turner syndrome, and corpus callosum agenesis). They found that in 95% of all human's subpopulations, a 45-mm-long segment ventral to Heschl's gyrus is deeper in the right hemisphere than in the left hemisphere. It seems that this anatomical asymmetry is specific to humans, because this anatomical asymmetry in the STS was not significant in the chimpanzee sample. These results are supported by an independent meta-analysis that included chimpanzees and macaques (*macaca mulatta* and *m. fascicularis*), which did not find differences between the left and right STS in different anatomical measures (e.g., depth, total surface areas, specific and total length) (Hopkins et al. 2015). The fact that the asymmetry in the STS is widely shared among humans through the lifespan and even in atypical populations, but is absent in macaques and chimpanzees, could suggest that the social cognition supported by the STS has a different development and manifestation in humans.

## Cross-References

- [Cross-Modal Transfer](#)
- [Hemispheric Specialization](#)
- [Perception](#)
- [Primate Sensory Systems](#)
- [Superior Temporal Sulcus](#)
- [Temporal Lobe](#)

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## Supernormal Stimulus

### ► Innate Releasing Mechanism

## Supernumerary Nipple

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## Synonyms

Accessory nipple; Ectopic nipple; Extra nipple; Polythelia

## Definition

Supernumerary nipple is the presence of one or more extra nipples with or without an areola or accessory breast tissue on the body.

## Introduction

A supernumerary nipple is a minor developmental abnormality of mammary tissue. It is most commonly located over the ventral surface of the thorax and abdomen along the embryonic milk lines. The embryonic milk lines extend from the axilla to the groin. It is most commonly located below the normal position of the nipple. It is one of the most common types of mammary tissue malformation. Most of the cases of supernumerary nipple appear to be sporadic and asymptomatic. In some families, several generations of people are effected with polythelia, so its inheritance may be familial. But some authors found that it is also genetically inherited as autosomal dominant with incomplete penetrance and X-linked dominant (Halleland et al. 2017).



It appears as a solitary or multiple brown-colored protuberance along the milk lines. In majority of the cases, the size of supernumerary nipples are smaller (2–3 mm in diameter) than the normal nipple (Mohammed 2019). Sometimes, it may look like a pigmented nevus or a fibroma. In such conditions microscopic examination can be done to confirm the clinical diagnosis. On doing so, lesions show features of hyperpigmentation and presence of pilosebaceous follicles and smooth muscles like nipple and areola (Mehregan 1981).

## Epidemiology

Depending on various epidemiological factors like sex, ethnicity, and geographical area, the incidence of polythelia ranges between 0.22% and 5.6% in the general population (Singal et al. 2016). The incidence of supernumerary nipple is 0.22% in a white European neonates where as in African American neonates, it is around 1.63% (Sun et al. 2018). It is more common in males in comparison with females. Black neonates are more affected than white neonates. There is a higher prevalence for the left side in comparison with right (Singal et al. 2016). Supernumerary nipple is present bilaterally in approximately 50% of people with polythelia.

## Classification

The well-accepted classification of supernumerary nipple was given by Kajava in 1915:

1. Complete supernumerary nipple consists of nipple, areola, and glandular tissue.
2. Supernumerary nipple consists of nipple and glandular tissue (no areola).
3. Supernumerary nipple consists of areola and glandular tissue (no nipple).
4. Supernumerary nipple consists of anomalous glandular tissue only.
5. Supernumerary nipple consists of nipple and areola and pseudomamma.
6. Supernumerary nipple consists of nipple only (most common).

7. Supernumerary nipple consists of areola only (polythelia areolaris).
8. Supernumerary nipple consists of only patch of hair (polythelia pilosa) (Halleland et al. 2017).

## Sites

1. Most common thorax or abdomen (65%) and axilla (20%)
2. Unusual sites:
  - (a) Face (Koltuksuz and Aydin 1997)
  - (b) Foot (Conde et al. 2006).
  - (c) Male perineum (Leung et al. 1997.
  - (d) Back and shoulder (Mohammed 2019)

## The Embryogenesis of Supernumerary Nipple

Supernumerary nipple is formed early in the development of the embryo. During fourth week normally a pair of epidermal thickenings called the mammary ridges develops along the milk lines on either side of the body. In humans, these ridges normally disappear except at the site of future breasts. Failure of regression of mammary ridges up to the third month of embryogenesis results in the formation of the supernumerary nipple.

## Association of Supernumerary Nipples with Various Systems

1. Urinary system – Supernumerary nipple is most commonly associated with kidney and urinary tract malformations, including renal adenocarcinoma, renal cysts, bilateral hydronephrosis, duplicate renal arteries, double renal pelvis and ureter, polycystic kidneys, hypoplastic kidney, microcystic kidney, and renal agenesis (Brown and Schwartz 2004).
2. Cardiovascular system – Cardiac conduction defect especially left bundle branch block, cardiac arrhythmias, hypertension, congenital heart diseases (Miranda 2012).
3. Gastrointestinal tract – Pyloric stenosis (Miranda 2012).

4. Central nervous system – Epilepsy, spina bifida occulta, tethered cord, diastematomyelia (Dogan et al. 2015).
5. Musculoskeletal system – Congenital scoliosis.
6. Supernumerary nipple may be associated with several syndromes like popliteal pterygium syndrome, Simpson-Golabi-Behmel syndrome, Becker nevus syndrome, and Char syndrome (Dogan et al. 2015). Simpson-Golabi-Behmel syndrome is a rare syndrome which is caused by an X-linked gene (Fonseca and Cantin 2014).

## Treatment

- Usually no surgery
- Surgery performed for cosmetic reasons or any complication in the breast tissue

## Conclusion

Various studies suggested that the supernumerary nipple is not only limited to cosmetic concern, but it may be associated with various systemic anomalies and syndromes. Therefore, in every newborn, there should be routine physical examination to search for accessory nipples. If any newborn has supernumerary nipple, he/she should be evaluated clinically for central nervous system, gastrointestinal system, respiratory system, skeletal system, and cardiovascular system malformations. There should be guidelines on how to manage newborn with supernumerary nipples.

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## Superorganism

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## Definition

A group of organisms which function together in a highly integrated way to accomplish tasks at the group level such that the whole can be considered collectively as an individual.

## Introduction

The term “superorganism” helps convey the idea that groups of individuals can function as, and

thus be considered as, singular entities, and as such, be subject to natural selection at the group level. Coinage of the term has been attributed to James Hutton, who in 1789 used it to describe the collective geophysiology of the Earth. Its most common contemporary use is in describing highly integrated animal societies, particularly those of social insects (Hölldobler and Wilson 2009).

## Social Insects as Superorganisms

Of all animal societies, few can match the sophistication and organizational complexity of the social insects (some bees and wasps; all ants and termites) and these organisms have frequently been championed as the epitome of the superorganism concept (Hölldobler and Wilson 2009; Seeley 1996). In social insect colonies, workers perform the manual tasks of the colony such as defense, construction, brood-care, and maintenance, while queens lay the eggs. Workers in many social insects are sterile, and as such have been compared to the somatic cells of a unitary multicellular organism. The queen(s), on the other hand, serves as the reproductive organ(s) of the superorganism. Queens and workers are mutually interdependent, as while workers are sterile, many queens cannot survive without worker assistance. Thus, while neither of these components can persist and procreate on their own, they together comprise a complete functional unit.

## Superorganisms Outside of the Social Insects

Social insects are well suited to the superorganism concept because they form highly integrated societies composed of clearly delineated individuals. The distinction between group and individual is spatially and/or temporally less distinct in other organisms which nonetheless deserve the label of superorganisms. Siphonophores, for example, are hydrozoans which form colonies of individual zooids exhibiting a marked division of labor. Zooids are asexually produced from the same embryo and are so highly integrated they were long considered to be single organisms (Dunn

2009). Slime molds, on the other hand, are usually free-living individual amoeboids but can assemble into a motile slug under starvation conditions. These slugs can further differentiate into reproductive structures exhibiting a distinct reproductive division of labor in which “spore” individuals are supported by nonreproductive stem-forming individuals.

Other purported examples of superorganisms are more equivocal: the human body has been regarded a superorganism comprising a human “host” and its bacterial community. However, while microbial communities can have an impact on our health, it may be more appropriate to consider the human body as an ecosystem populated by microorganisms, which can be affected by its constituent biota in the manner of all ecosystems.

## Characteristics of Superorganisms

*Emergence:* Superorganisms are characterized by emergent phenomena: group-level processes and/or characteristics arise through local interactions between individuals without any top-down control. In this manner, superorganisms can perform complex tasks without any individual component having knowledge of the whole, or having advanced intelligence. The concept of emergence reflects the complexity of superorganisms, in acknowledging the difficulty in extrapolating observed group-level phenomena from the interactions and behavior of individual components. For example, social insect colonies exhibit consistent behavioral characteristics at the level of the group (“personality”; Jandt et al. 2014). This group level trait is an emergent product of the personalities of its component individuals and can vary between superorganisms. Groups can also benefit from collective immunity, both in terms of prophylaxis and immune responses (Cremer et al. 2007). Honeybee colonies, for example, can eliminate bacterial infection by increasing brood-comb temperature when multiple individuals increase their body temperature to generate a “social fever.”

*Reproduction:* Reproduction in superorganisms occurs when a new superorganism is produced.

In social insects, for example, this means the establishment of a new colony, either by a new queen or a dispersing swarm containing queen (s) and workers (Cronin et al. 2013). Production of sterile workers can be considered as a maintenance operation, as this is concerned with the upkeep of the “body” of the organism rather than its propagation.

*Specialization:* Individuals comprising superorganisms typically exhibit a division of labor, and specialization on particular tasks may be associated with the evolution of distinct types of morphology (castes) such as queens and workers. Both of these factors can increase the efficiency and effectiveness of group task performance.

*Social Structure:* The social organisms which provide the best fit to the superorganism concept are “eusocial.” Eusocial organisms are characterized by reproductive division of labor, overlapping generations, and cooperative care of offspring.

## Scope of the Terminology

The superorganism concept has been challenged on various fronts, particularly associated with opposition to evolutionary group selection arguments. Furthermore, it is often derided as taking the analogy between unitary multicellular organisms and groups too far, because while the cells of unitary organisms are clones, individuals in groups in most cases are not (though they may be highly related). Application of the terminology may be best limited to circumstances in which the perspective it provides can generate useful insights, rather than merely as a badge of aggrandization.

## Conclusion

There is little doubt that superorganisms exist and that the superorganism concept can help generate new insights into the evolution and ecology of group-living organisms. It remains the subject of debate, however, as to exactly how far the remit of the term “superorganism” extends. Nonetheless, its application is likely to grow

with the increasing use of holistic approaches that emphasize the importance of the global entity, and as studies of complex systems advance our understanding of the importance of interactions in describing group level behavior.

## Cross-References

- ▶ [Caste](#)
- ▶ [Division of Labor](#)
- ▶ [Social Behavior](#)

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## Superstition Experiment (Staddon and Simmelhag 1971)

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## Synonyms

[Adventitious reinforcement](#); [Spurious correlation](#);  
[Superstitious behavior](#); [Superstitious reinforcement](#)

## Definition of Superstitious Behavior

Vyse (1997) described the difficulty of defining superstitious behavior because it is often a catchall for both the mysterious and mundane activities that we observe in other people. It is often a pejorative term to describe differences between the choices made by the observer and the person being observed. The term, here, refers to a specific situation. How good are nonhumans (and humans) at recognizing a causal relationship between an action and its consequence? Can they be “fooled” into persisting in a behavior even though it does not cause that consequence?

## Skinner (1948) Superstition Experiment

Skinner (1948) reported on the behavior of pigeons that were exposed to a series of presentations of food at regular intervals, irrespective of their behavior (a *fixed time* [FT] schedule; also described as a Pavlovian temporal conditioning procedure). There are many missing methodological details from the article: Missing are number of subjects, number of sessions, exact time intervals, method of identification of responses, temporal contiguity of the different responses to food, and rate changes among those responses. All of those issues are glossed over in a casual presentation in the report. Most descriptions focused on a subset of the results where a FT 15-s schedule was used, with a 5-s food presentation, and a verbal summary is reported.

However, Skinner’s interpretation of the results was vivid and influential. He described a reinforcement effect that was due to *temporal contiguity of response and reinforcer alone*: “. . . conditioning takes place presumably because of the temporal relation only, expressed in terms of the order and proximity of response and reinforcement” (Skinner 1948, p. 168). The reinforcement effect operated on an idiosyncratic range of responses occurring across subjects, including walking counterclockwise, head bobbing, head swinging, and pecking. Skinner concluded that almost any behavior was susceptible to the influence of accidental correlation of a response and a

reinforcer. The effect was strong, requiring more than 10,000 responses before *extinction* (disappearance of the response) in one pigeon. He ended the short article with an extension to human behavior in the description of a bowler wagging at an errant ball, suggesting the power of contiguity of responses and reinforcers to maintain behavior in the absence of a true causal connection. Skinner’s interpretation of the effect of spurious connections of response and consequence is termed *adventitious reinforcement* (Sidman 1960) commonly.

## Staddon and Simmelhag (1971) Reexamination of the Superstition Experiment

The historical context of the Staddon and Simmelhag (1971) experiment was the occurrence of several puzzling findings in the animal learning literature. Breland and Breland (1961) reported that food-related behavior emerged in animal training and supplanted the reinforced response, even though this new behavior delayed delivery of the reinforcer. For example, a raccoon trained to deposit a token coin for food would spend additional time in the food-related behavior of “washing” the coin instead of depositing the coin to obtain quickly the reward. Williams and Williams (1969) reported that it was very difficult to train a pigeon *not* to peck a lighted disk when it predicted food. Falk (1969) reported that other activities, such as excessive water consumption, would emerge in the post-reinforcement period in a (response-contingent) *variable interval* (VI) or *fixed interval* (FI) food reinforcement schedule when food was not available. The motivation to engage in these activities was strong enough that water could operate as a reinforcer in this period if a response was required to obtain the water. These odd results suggested that Skinner’s superstitious behaviors may be controlled by factors other than accidental temporal contiguity of response and reinforcer.

The general design of the Staddon and Simmelhag (1971) experiment is simple. Behaviors are recorded during a (response-independent)



FT interval of food presentation for the individual pigeons. Skinner would predict that whatever response occurred with greatest contiguity to food on initial trials should increase in frequency across trials. The increase should occur as food presentation became more likely. Responses are likely to vary across birds, due to the accidental nature of the original pairing.

The actual method was more complicated. Six pigeons (two with prior experimental experience) were used. The pigeons were exposed to a series of sessions without food in order to develop the set of response categories. Obtained response categories ranged from continuous (R1: head and body oriented toward magazine) to discrete (R7: pecking toward magazine wall) and somewhere in between (R9: preening, any movement in which beak contacts feathers).

Three different reinforcement schedules were used, FI 12-s, FT 12-s, and (*variable time*) VT 8-s. (The FT and VT schedules were defined as response-*independent* FI and VI schedules in the original report.) Reinforcement was 2-s access to mixed grain. Two birds were exposed to all three schedules, two birds were exposed to only the FT and VT schedules, and two birds were exposed to only the FT schedule. The acquisition and *steady-state* (last three sessions) data were analyzed.

## Results of Staddon and Simmelhag (1971)

### Acquisition Results for Bird 49

The acquisition results for (experimentally naïve) Bird 49 (Fig. 3, Staddon and Simmelhag 1971) encapsulate a major finding of the study. Behavior during the 10- to 12-s portion of the FT interval is of importance because this is the period closest in time to food delivery. Bird 49 spent more than 90% of its time with its head in the food magazine for the first seven sessions during this time period. This result was to be expected because that behavior is contiguous with obtaining food. Abruptly, this response is displaced by pecking on the magazine wall, and pecking became the primary response during this period for the next

29 sessions. Staddon and Simmelhag reported a similar transition with the other five pigeons.

The result was a direct contradiction of the Skinner (1948) contiguity account. The high-frequency response closest in time to food is not maintained. Instead it was replaced abruptly by another response that had not been occurring frequently in prior sessions. The result is reminiscent of the food-related response intrusion effects reported by Breland and Breland (1961).

### Steady-State Behavior

The birds were reported each to settle into a pattern of a small number of responses that occurred in a reliable sequence. The responses were categorized into two classes. *Terminal responses* were activities that occurred consistently before food delivery, typically starting about halfway through the interval. *Interim responses* were activities that began before the terminal response. The classification of an activity as interim or terminal was based on its temporal location during the interval. What could be a terminal response for one bird could be an interim response for another bird. Note the case of Bird 49, cited previously, where pecking began as an interim response and ended as the steady-state terminal response.

## Theoretical Analysis by Staddon and Simmelhag (1971)

The analysis began with the result that the FT food schedule generated a series of different responses (interim and terminal) that occurred in a reliable sequence for individual birds. The results were consistent with findings that show that reinforcement schedules will induce a variety of behaviors beyond the contingent or terminal response. These interim behaviors occur when reinforcement probability was low and have included polydipsia (excessive drinking), pica (eating nonfood material), and wheel-running depending on the activities that were available (Falk 1969). The activities are anomalies according to a traditional Law of Effect because the activities are not contiguous with reinforcement and are not necessary for reinforcement. They had been explained

previously as a result of adventitious reinforcement, the spurious correlation between responses and reinforcement. The question was whether to treat these cases as anomalies or to try to include them in a revised approach to the law of effect. Staddon and Simmelhag rejected the treatment of interim behaviors as odd, anomalous behaviors because they can be observed reliably under wide-ranging conditions. Therefore, they assumed that the activities must have functional significance.

Staddon and Simmelhag identified a critical procedural difference between laboratory learning experiments and the tasks faced by an animal in the wild. Laboratory learning experiments focused on one important requirement (e.g., food or water) and measured a single response related to obtaining that requirement. In the wild, animals must contend with a variety of requirements (e.g., not just one requirement but both food *and* water). Animals are faced with the issue of the best *allocation* of activities to satisfy several different requirements. Therefore, there is evolutionary selection pressure to produce a mechanism that will generate *switching* to new activities. An ideal time to switch would be when current access to a requirement is blocked in order to pursue other requirements. This was the evolutionary analysis that was applied to the results with the FT 12-s food schedule.

A pigeon is deprived of food. The deprivation activates a *state*, defined as a motivational condition in which food-related behaviors are generated and those that produce food are likely to be reinforced. The set of food-related behaviors that are generated come from personal history, species history, and situational circumstances. The Law of Effect selects among these several behaviors. The FT schedule provides food to a food-deprived pigeon on a regular temporally defined basis. Behaviors that become terminal activities are food-related behaviors that are selected as food delivery becomes more probable. They are not randomly emitted activities.

Importantly, interim behaviors are generated in a similar fashion. The time after food delivery is a period of low food probability. Low food probability is a period during which evolution-

developed mechanisms produce a *switch to other activities* so as to satisfy the other requirements. Therefore, nonfood activities develop during these time periods of low food probability. These activities are not randomly emitted either. They are state-induced and are related to other concurrent requirements for life. Other activities can be reinforced by other consequences during these periods, such as a rat pressing a lever to produce access to water even though the rat is not water deprived (Falk 1969). The variety of activities that will occur and be reinforced during this food-free period will depend also on the subject's history, species history, and the structure of the situation. Staddon and Simmelhag (1971) noted the close functional similarity among interim behaviors, adjunctive behaviors (Falk 1969), and the displacement activities, observed in European animal behavior studies (McFarland 1966; Tinbergen 1952).

### Legacy of Staddon and Simmelhag (1971)

Several important consequences followed their results. The first was that the results revealed an important flaw in the analysis of Skinner (1948). Temporal contiguity of response and reinforcer did not explain why one response became the terminal response in the situation. Responses that showed good contiguity initially could be replaced by another response with continued experience. A second important result was to argue, against a dominant operant conditioning metaphor at the time, that responses were "emitted" seemingly at random and then trapped into repetition by contiguity with a reinforcer. Instead, both terminal and interim activities were generated in a causal manner that was related to the variety of survival requirements to be met by the subject. A third consequence was that the study pointed out a conceptual issue with many American animal learning studies, and that was the sole focus on a single consequence and the rate of a single response in obtaining that consequence. The results suggested an unexplored issue was the allocation of behavior for an animal when

dealing with multiple requirements and multiple responses. Staddon continued to examine this issue (e.g., Staddon 1980).

An established interpretation (like Skinner's emphasis on temporal contiguity of response and reinforcer) is often accompanied by odd exceptions (like Breland and Breland's observation of displacement of the reinforced response). The legacy of Staddon and Simmelhag (1971) was to rearrange the order of central observations and exceptions to reconnect interesting behavioral effects with a Darwinian analysis of the origin and maintenance of behavior.

## Cross-References

- ▶ [Adjunctive Behavior](#)
- ▶ [Operant Conditioning](#)
- ▶ [Pavlovian Conditioning](#)

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## Superstitious Behavior

- ▶ [Schedule-Induced Behavior](#)
- ▶ [Superstition Experiment \(Staddon and Simmelhag 1971\)](#)

## Superstitious Reinforcement

- ▶ [Superstition Experiment \(Staddon and Simmelhag 1971\)](#)

## Suppression

- ▶ [Inhibition](#)

## Surrogate Species

- ▶ [Indicator Species](#)

## Survival

- ▶ [Adaptation](#)
- ▶ [Bear Life History](#)
- ▶ [Feline Life History](#)
- ▶ [Fitness](#)
- ▶ [Passerine Life History](#)

## Survival of the Fittest

- ▶ [Social Darwinism](#)

## Survival Processing

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### Synonyms

Adaptive memory; Fitness relevance; Mnemonic device; Survival relevance

### Definition

A memory advantage for words, pictures, and other stimuli processed for their value in a survival scenario.

### Introduction

At the intersection between the cognitive psychology and evolutionary psychology literatures lies survival processing. In this paradigm, participants read a brief passage, encode a list of words, and perform a memory task. Researchers manipulate the nature of the brief passage, such that some participants engage in survival processing:

In this task we would like you to imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. Over the next few months, you'll need to find steady supplies of food and water and protect yourself from predators. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this survival situation. (Nairne et al. 2007, p. 264)

Participants in other conditions read instructions about moving to a foreign land or simply rate words according to their pleasantness or autobiographical self-reference. Across numerous comparisons, survival processing often “wins,” in that these participants recall a greater number of words than participants in other conditions (Kazanas and Altarriba 2015; Nairne and Pandeirada 2016; Schwartz et al. 2014). These findings replicate

across within-subjects designs (Nairne et al. 2008), recognition tasks (Cho et al. 2018), and visual stimuli (Otgaar et al. 2010), as well as other languages (Kazanas et al. *in press*) and age groups (Aslan and Bäuml 2012), in addition to other manipulations and factors.

### Mechanisms and Limitations

Researchers offer a number of explanations for this important finding. For example, the ancestral nature of *the grasslands of a foreign land* and the similarly ancestral priorities of *finding steady supplies of food and water* speak to the function of memory itself: to prioritize memory for fitness-relevant information and situations (Nairne et al. 2007). In addition to – or perhaps, in support of – these functionalist explanations, researchers also suggest the role of physiological arousal when engaging in survival processing (Fiacconi et al. 2015), as well as planning (Klein et al. 2011) and self-reference (Klein 2012). Cognitive explanations have their support, as well, most notably the distinction between the types of word processing recruited for survival processing and its various control conditions. Burns and colleagues explain the effectiveness of survival processing in its recruitment of both item-specific and relational processing, relative to control conditions recruiting just one (i.e., item specific *or* relational processing; Burns et al. 2011, 2013). Most likely, the traditionally evolutionary explanations underlie these cognitive mechanisms, with both factoring into this memory advantage.

In some important exceptions, survival processing does not *always* promote better memory. For example, memory advantages do not replicate for tasks involving faces (Savine et al. 2011), implicit memory (Tse and Altarriba 2010; Wilck and Altarriba 2019), paired-associate learning (Schwartz and Brothers 2014), or online processing (Altarriba and Kazanas 2014). Generally, these exceptions have helped researchers identify “boundary conditions” for this effect, suggesting survival processing enhances memory in most, but not all, tasks and scenarios. These exceptions also point to the enhanced elaboration needed to

engage in survival processing, relative to the other word rating conditions. For example, studies show diminished memory advantages when participants consider just a single survival problem (e.g., a need for water), rather than the typical survival scenario, which asks participants to consider the need for water, food, protection from predators, and so on. These smaller effects suggest the typical survival scenario activates more elaborative encoding, which in turn provides more numerous retrieval cues during recall (Kroneisen and Erdfelder 2011). Tasks that limit participants' opportunity to engage with the to-be-remembered materials in this way are thus less likely to show an effect. Similarly, studies testing survival processing under conditions of high cognitive load (e.g., multitasking) also show reduced memory advantages over other conditions (Kroneisen et al. 2013; Nouchi 2013; Kazanas et al. 2015).

Nairne and Pandeirada (2016) propose a general survival optimization system accounting for many suggested mechanisms (e.g., ancestral priorities, arousal), in addition to the published exceptions and limitations. They describe an ultimate mechanism for this effect, with a highly flexible system of cognitive resources for detecting and responding to threats. This flexibility can account for survival processing advantages extending to scenarios describing various environments (e.g., the jungle, space; Kostic et al. 2012), predators (e.g., supernatural; Kazanas and Altarriba 2017; Soderstrom and McCabe 2011), eras (e.g., modern, ancestral; Weinstein et al. 2008), and more.

## Future Directions and Conclusions

Memory advantages following survival processing are widely replicated; with that, researchers now turn to extensions of this literature, namely the larger area of adaptive memory (of which survival processing is one example). Topics pertaining to animacy effects, cheater detection, contamination effects, mortality salience, and more are explored for their own insights into this phenomenon. Broadly,

investigating the stimuli and conditions most salient to our survival help us better understand the function of human memory.

## Cross-References

- [Adaptation](#)
- [Adaptive Memory](#)
- [Cognition](#)
- [Evolutionary Psychology](#)
- [Functionalism](#)
- [Laboratory Research](#)
- [Planning](#)
- [Predator](#)
- [Predator Defense](#)
- [Predator Detection](#)
- [Recall](#)
- [Savannah](#)

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## Survival Relevance

### ► Survival Processing

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## Survival Studies

### ► Selection Study

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## Susan D Healy

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## Synonyms

Adaptive specialization; Bird song; Decision-making; Food-caching birds; Foraging; Hippocampus; Hummingbirds; Nest building; Sex differences in cognitive abilities; Spatial learning; Stress and memory; Vocal mimicry

Professor Susan Denise Healy (born on 4 December 1962, Wanganui, New Zealand) is a cognitive ecologist working at the Centre for Biological Diversity in the School of Biology at the University of St Andrews in Scotland. Her research is influenced by the common question of whether an animal's behavioral ecology correlates with its cognitive abilities and neural processes. She has integrated neuroanatomical studies with behavioral experiments of the spatial abilities of a diverse number of bird species to understand the underlying mechanisms responsible for the differences in behavior we observe in nature. So far, her research has produced over 127 original and review papers on diverse topics ranging from the neuroanatomy of food-storing birds, the cognitive abilities related to foraging behavior of wild hummingbirds, nest building, song and vocal mimicry of wild and laboratory bird species, the relationship between stress and memory, to decision-making and sex differences in spatial abilities. Although the majority of her research has used bird species as a model, she has also studied the behavior of mammalian species including humans (e.g., Jones and Healy 2016).

Sue, as most people call Professor Healy, started her career in her country of birth, New Zealand. Although she first started her studies thinking she would become a medical doctor, thanks to the good influence of teachers and fellow students, she switched majors and in 1984 Sue finished a degree in Zoology and Physiology from the University of Otago, Dunedin, New Zealand. She then travelled to the UK with the original plan of doing a little bit of work, some European backpacking and then returning to New Zealand for a PhD. Instead, Sue started a research assistantship with Professor Lord J. R. Krebs and ended up staying at the University of Oxford for 8 years. At Oxford, she did her DPhil at St Hilda's College and then she moved to the St John's College as a Junior Research Fellow. When Sue was still doing her DPhil with John Krebs as her adviser, the animal behavior group in Oxford was a hive of the most influential behavioral researchers past and present (e.g., Sara J. Shettleworth, Nicola Clayton, David Sherry and Marian and Richard Dawkins, among others).

Sue and these researchers, either as mentors or as peers who would eventually become life-long collaborators, would engage in long scientific discussions both in the lab and at the pub, a tradition that she carries out now with her own students and peers. Back in 1989, Sue published her first paper on the topic of hippocampal specialization of food-storing birds and over the years that paper has gone on to be cited more than 500 times (Krebs et al. 1989). As Sue and colleagues expected, the bird species that store food during the fall to survive the winter depended more on their spatial memory to retrieve their caches were also found to have a relative larger hippocampus (the part of the brain that process and stores spatial information) compared to species that do not store food. Adaptive specialization of spatial abilities of food-storing birds continued to be the focus of Sue's DPhil and postdoc. She focused both in species comparisons of neural anatomy and behavior and the developmental differences between different British bird species.

Still in Oxford Sue met, then postdoc, Professor Andrew T. Hurly with whom she has now published over 30 papers of original research on the cognitive abilities of wild rufous hummingbirds with focus on the spatial abilities these birds have in order to feed from hundreds of flowers a day (Healy and Hurly 2013). Sue and Andy's work with Canadian wild hummingbirds has not only been a further corroboration of how foraging ecology correlates with the cognitive abilities of animals but has also laid the foundations for ways to study cognition in wild-free living animals (Pritchard et al. 2016).

As she moved up through the academic ladder, her geographic location too, moved "up." She started in the south of the England and has now reached the Kingdom of Fife in the south of Scotland where she lives now with her partner Dr. David Shuker, a behavioral ecologist interested in insect reproductive behavior. After her time in Oxford, Sue first took a position as a Lecturer at the University of Newcastle, where she began her long-term collaboration with an old Oxford friend, Professor Candy Rowe. During her appointment at the University of Newcastle, she continued to investigate the correlates and

intricacies between hippocampal structure and the spatial abilities of food-storing birds (as tested in laboratory experiments). At the same time, she started to spend her summers in the Canadian Rockies at the University of Lethbridge's research station collaborating with Andy Hurly to establish the study of the spatial abilities of rufous hummingbirds in the wild (*Selasphorus rufus*; Healy and Hurly 1998).

In 1999, Sue moved to the University of Edinburgh where she stayed there for 10 years. There, Sue focused most of her original research on the study of foraging behavior of hummingbirds, looking at their spatial, temporal, and decision-making abilities. After just a few summers, Sue and Andy's research teams had discovered that hummingbirds will preferentially use spatial information (distance and location) to locate a reward rather than visual cues (Healy and Hurly 1998), that these birds can use temporal information to time their return visits to flowers that refill at different time intervals (Healy and Hurly 2013) and that like humans, hummingbirds too will make relative choices rather than economically rational choices when given different concentrations of sugar solutions. Back in Edinburgh, Sue directed some of her attention to the study of sex differences in stress responses and spatial abilities in rats and humans, demonstrating that at least some of the observed sex differences in spatial abilities are due to differences in stress responses between sexes. Sue also started to do more theoretical work by reviewing the neurobiology comparative work and challenging, along with Professor Candy Rowe, the prevailing view at the time that larger brains enable more complex cognitive abilities (Healy and Rowe 2007).

In 2009, Sue took a joint position as Reader in both the Biology and Psychology and Neuroscience Schools at the University of St Andrews. At the University of St Andrews, Sue once again was one of the first people to establish the foundations of a new subfield in behavioral ecology by studying the cognitive abilities that birds use when building their nests. Although at the time,

behavioral ecologists regarded nest building a behavior "too complex" to be the result of learning mechanisms, Sue started to gather both field and laboratory evidence that birds do indeed use different types of learned information when building a nest (e.g., Guillette et al. 2016; Muth and Healy 2012). Sue and her team are also beginning to describe the neural structures underpinning this complex behavior (Hall et al. 2014). Sue continues to work with hummingbirds, now investigating how rufous hummingbirds use landmarks and their use of foraging routes (traplining) when visiting multiple locations. She has done so, while also being an active member of many scientific societies (in particular, the Association for the Study of Animal Behaviour, which owns the journal, *Animal Behaviour*, of which she is now European Executive Editor) and coediting a book dedicated to the study of avian cognition (ten Cate and Healy 2017).

Sue has made a significant contribution to the field of cognitive ecology by combining different approaches when studying animal behavior. Either when looking directly at the brain of animals or when studying their behavior in the laboratory and in the wild, Sue has successfully adapted the experimental dexterity of the comparative psychology tradition with the field of behavioral ecology. She has done so while showing younger men and women the practical rigor of science and the joy of a life studying animal behavior. Following her example, her female students have learned that like her male students they too should be confident and brave scientists.

Sue gave up her backpacking plans some time ago and now when travelling the world, with mostly books in her luggage, it is to give invited academic talks or to spend part of her summers in the Canadian Rockies, where long science or political talks can sometimes resemble a Fellini's dinner party scene. During the weekends, whenever she does not have her students over to her house to beat them at a game of croquet or to watch the Eurovision song contest, she enjoys gardening.

For current information and recent publications visit: <http://cognitioninthewild.wp.st-andrews.ac.uk/>

## Cross-references

- [Decision-Making](#)
- [Foraging](#)
- [Interval Timing](#)
- [Navigation](#)
- [Nest Construction](#)

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## Sustainable Forest Management

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## Definition

The stewardship and use of forests and forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality, and their potential to fulfil, now and in the future, relevant ecological, economic, and social functions, at local, national, and global levels and that does not cause damage to other ecosystems.

## Introduction

In the last few decades, total forest area worldwide has decreased alarmingly from 5.9 billion hectares during pre-industrial area to just over 4 billion hectares, although the rate of deforestation and loss of forest from natural causes has slowed down from 16 million hectares per year in the 1990s to around 13 million hectares per year in the last decade (FAO 2011). The increasing global population has imposed the enormous pressure on forest resources which has obligated the necessity of its use in such a way that current demand meets the needs of the present without compromising the ability of future generations to meet their own needs (Du Pisani 2006). Nevertheless, the need to preserve natural resources for use by future generations had long been recognized.

The sustainability began to increase in importance and acceptance at the end of the 1980s and at the beginning of the 1990s. During early 1990s, the Brundtland Report “*Our Common Future*” (1987) and the Conference on Environment

and Development (Earth Summit) held in Rio de Janeiro, Brazil, in 1992, accelerated and pushed the sustainability concept to the table of policymakers. The latter concept establishes the linkages among the ecological and socioeconomic concerns (Fig. 1) at different scales of management and for different time periods. Healthy forests and trees provide number of services relevant for agricultural production and family livelihoods, such as food, feed for livestock, fuel, material for construction, fiber, and other requirements. Ecosystem services that help regulate ecosystem processes are equally important and pivotal for sustainable agriculture, soil protection, nutrient recycling, water regulation, microclimate regulation, and climate change mitigation (Reed et al. 2017). The forests are home for larger part of biodiversity, including pollinators such as insects and birds (Klein et al. 2007), pest control agents (Karp et al. 2013), and provide habitat for living organisms that are key for soil fertility, including bacteria and fungi. SFM is the process of planning and implementing practices for the stewardship and use of forests and other wooded land to meet specific environmental, economic, social, and cultural objectives (Siry et al. 2005). It deals with the overall administrative, economic, legal, social, technical, and scientific aspects related to natural and planted forests. It may involve varying degrees of deliberate human intervention, ranging from actions aimed at safeguarding and

maintaining forest ecosystems and their functions to those favoring specific socially or economically valuable species or groups of species for the improved production of forest goods and services (Table 1).

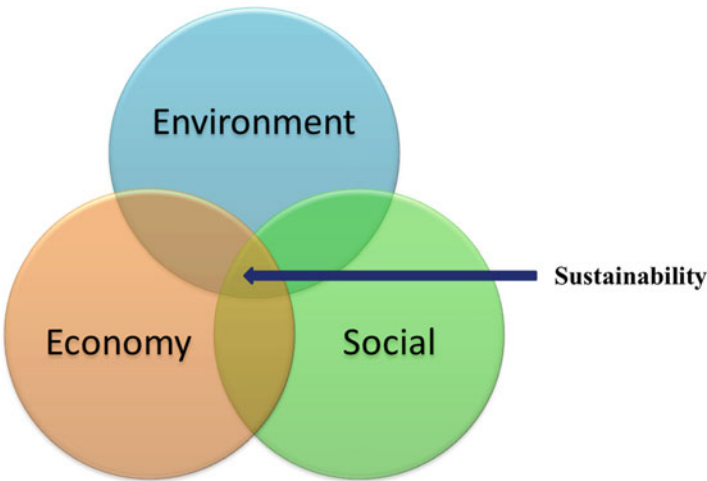
Many of the world’s forests and woodlands, especially in the tropics and subtropics, are still not managed sustainably. Some countries lack appropriate forest policies, legislation, institutional frameworks, and incentives to promote sustainable forest management, while others may have inadequate funding and lack of technical capacity. Where forest management plans exist, they are sometimes limited to ensuring the sustained production of wood, without paying

**Sustainable Forest Management, Table 1** List of benefits provided by the forests in terms of ecological, social, and economic values

| Ecological                 | Social                        | Economic                |
|----------------------------|-------------------------------|-------------------------|
| Climate stabilization      | Recreational and leisure area | Timber                  |
| Soil enrichment            | Traditional uses              | Nonwood forest products |
| Protection                 | Landscape                     | Employment              |
| Regulation of water cycles | Employment                    |                         |
| Improved biodiversity      |                               |                         |
| Purification of air        |                               |                         |
| CO <sub>2</sub> sink       |                               |                         |

**Sustainable Forest Management,**

**Fig. 1** Sustainable forest management shares the environmental, economic, and social values





attention to the many other products and services that forests offer.

Criteria and Indicators

The outcome of the earth summit was the “Forest principles” – a nonlegally binding statement of principles for a global consensus on the management, conservation, and sustainable development which could not be agreed upon at the time. Later on, several different international processes and initiatives have developed criteria and indicators (C&I) as a framework for describing, monitoring, and evaluating progress toward SFM. The C&I can be used as tools that define, guide, monitor, and assess progress toward SFM in a given context. The overall aim of criteria and indicators is to promote more SFM practices, taking into consideration the social, economic, environmental, cultural, and spiritual needs of different stakeholders. Criteria define the essential elements against which sustainability is assessed, with due consideration paid to the productive, protective, and social roles of forests and forest ecosystems (Wijewardana 2008). Each criterion relates to a key element of sustainability and may be described by one or more indicators. Indicators are parameters which can be measured and correspond to a particular criterion. They measure and help monitor the status and changes of forests in quantitative, qualitative, and descriptive terms that reflect forest values as seen by those who defined each criterion. Prabhu et al. (2001) suggested seven attributes to improve the quality of indicators (precision of definition, diagnostic specificity, sensitivity to change or stress, ease of detection, recording and interpretation, ability to summarize or integrate information, reliability and appeal to users). Similarly, Dale and Beyeler (2001) established eight prerequisites to selection (ease of measurement, sensitivity to stresses on the system, responsive to stress in a predictable manner, anticipatory, able to predict changes that can be averted by management actions, integrative, known response to disturbances, anthropogenic stresses and changes over time, and low variability in response). Although several

criticisms have been launched against the C&I system (Gough et al. 2008; Prabhu et al. 2001), the popularity of the system is evident from the effort invested in its development in recent decades.

The first set of C&I was developed by ITTO (1992) for sustainable management of tropical forest. Since then several regional groupings of countries have worked together upon the process of generating and testing appropriate C&I to suit their own conditions. There are 11 international and regional C&I processes (listed in Table 2), which collectively involve more than 174 countries to produce national reports that assess their progress toward sustainable forest management (Linser et al. 2018).

For instance, the Montreal Process is geographically the largest, encompassing most of the world’s temperate and boreal forests, and 60% of all of the world’s forests develop seven frameworks for forest conservation and sustainable management. Based on the most common criteria of SFM of C&I processes, United Nations Forum on Forests (UNFF) developed the non-legally binding instrument on all types of forests adopted in 2007 by the UN General Assembly, specifying four global goals as well as seven thematic elements of SFM (Table 3). Thus, regional

**Sustainable Forest Management, Table 2** Eleven international and regional C&I processes

|     |                                                                                                                             |
|-----|-----------------------------------------------------------------------------------------------------------------------------|
| 1.  | African Timber Organization (ATO)/ITTO process                                                                              |
| 2.  | Dry Forest in Asia process                                                                                                  |
| 3.  | Dry-Zone Africa process                                                                                                     |
| 4.  | International Tropical Timber Organization (ITTO) process                                                                   |
| 5.  | Lepaterique of Central America process                                                                                      |
| 6.  | Montreal Process                                                                                                            |
| 7.  | Near East Process                                                                                                           |
| 8.  | Pan-European Forest Process (also known as the Ministerial Conference on the Protection of Forest in Europe, MCPFE)         |
| 9.  | Tarapoto of the Amazon Forest process                                                                                       |
| 10. | The low forest cover countries process, also known as the Tehran Process                                                    |
| 11. | The association of Southeast Asian Nations (ASEAN) C&I for the sustainable management of tropical forests in Southeast Asia |

**Sustainable Forest Management, Table 3** Thematic elements of SFM based on C&I processes

|    |                                          |
|----|------------------------------------------|
| 1. | Extent of forest resources               |
| 2. | Biological diversity                     |
| 3. | Forest health and vitality               |
| 4. | Protective functions of forests          |
| 5. | Productive functions of forests          |
| 6. | Socioeconomic functions                  |
| 7. | Legal policy and institutional framework |

and international sets of C&I for SFM provide a vital structure for monitoring, assessing, and reporting on forests and their management and fostering progress toward sustainability goals.

### Forest Certification

Forest certification was introduced in the early 1990s to address concerns of deforestation and forest degradation and to promote the maintenance of biological diversity, especially in the tropics (van Kootena et al. 2005). Initially pushed by environmental groups, it quickly evolved as a potential instrument to promote SFM. To date about 124 million hectares or 3.2% of the world's forests have been certified by the different certification schemes created over the last decade. Certification is the process whereby an independent third party (called a certifier or certification body) assesses the quality of forest management in relation to a set of predetermined requirements (the standard). There are certain differences between the C&I process and certification of forest in context to scale, purpose, use, and user groups (Table 4).

The certifier gives written assurance that a product or process conforms to the requirements specified in the standard. Forest certification was introduced as a market-based response to address public concerns related to deforestation in the tropics, resulting loss of biodiversity and the perceived low quality of forest management in areas where traded wood products are sourced from. After a slow start spearheaded by the Forest Stewardship Council (FSC), the situation has

**Sustainable Forest Management, Table 4** Major differences between C&I and forest certification. (Adapted from Rametsteiner and Simula 2003)

|    |                                      |                                                                      |
|----|--------------------------------------|----------------------------------------------------------------------|
| 1. | Criteria and indicators for SFM      | Forest certification                                                 |
| 2. | Mainly national level                | Sub-national level                                                   |
| 3. | Descriptive approach                 | Prescriptive (standards/requirements)                                |
| 4. | Mainly used for information sharing  | Used for establishing proof of sustainable or good forest management |
| 5. | Used by governments and policymakers | Used by market players                                               |

radically changed when other schemes have become operational by the end of the decade. The initiatives on forest certification have set out to tackle an immensely diverse field by using one single instrument across the globe and across all conceivable situations. The ability of the instrument to contribute to SFM and biodiversity maintenance is, however, widely unclear. Forest certification standards have been largely developed outside the established standard setting bodies, and private bodies operate schemes and programs. Many of the standards have been developed through a multi-stakeholder approach, and thus the characteristics of each standard are guided in large part by the composition of each standards development team. As continuous improvement is an inbuilt element in most certification systems, the further development of standards is destined to move toward better convergence of differences. In 1993, an initiative led by environmental groups, foresters, and timber companies resulted in the creation of the Forest Stewardship Council (FSC). Subsequently, other initiatives at international and national levels gave rise to many other schemes, e.g., the Programme for the Endorsement of Forest Certification (PEFC, previously termed Pan-European Forest Certification), the Canadian Standards Association (CSA), the Sustainable Forestry Initiative (SFI), the Chile Forest Certification Corporation (CERTFOR), and the Malaysian Timber Certification Council, among others. Although

forest certification began in tropical forests, the trend has changed, and the scheme is now carried out in boreal and temperate forests. Almost 90% of forests certified by the two major programs (FSC and PEFC) are located within Europe and North America. More than half (54%) of the forests in Europe (excluding the Russian Federation) have already been certified, and almost one third of the forest area in North America has been certified.

## Conclusions and Future Perspectives

Sustainable forest management is a need of the current world to address the issue of degradation and deforestation while increasing benefits to human society with taking care of future generation needs. Sustainable forest management is evolving with public awareness and scientific knowledge, and the sustainability concept must be revised to reflect the new reality generated by climate change, where a past reference point should not be considered. Therefore, C&I should be updated continuously to be able to cope with the climate change challenge and assess sustainability of changing ecosystems. Furthermore, harmonization of C&I processes would be the most desirable outcome, since this would improve the credibility of the schemes. Enhanced sustainable forest management will require better reporting and verification and more areas covered and enhanced implementation of sustainable forest management criteria and indicators in the future. Further progress in improving forest management worldwide also relies on gathering better information needed to monitor and analyze global forest trends. A mix of effective public policies and private markets will continue to be needed to help achieve global sustainable forest management.

## Cross-References

- [Birds](#)
- [Fungi](#)
- [Population](#)
- [Tropics](#)

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## Swans

### ► [Waterfowl](#)

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## Swarm Intelligence

### ► [Plantae](#)

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## Swine Cognition

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## Synonyms

[Animal welfare](#); [Domestic pig](#); [Domestic swine](#); [Human-animal interaction](#); [Physical cognition](#); [Self-awareness](#); [Social cognition](#); [Social learning](#); [Spatial learning](#); [Suidae](#); [Time perception](#)

## Introduction

Most people know swine only as its domestic form (*Sus scrofa domesticus*) or as wild boar

(*Sus scrofa scrofa*). Relatively little attention goes to the rest of a total of up to 18 species in the Suidae family. The same also applies to behavioral research: although members of the family of Suidae are distributed all over the Old World, ranging from Asia to Europe and Africa, most studies focusing on their behavior and cognition are conducted on domestic swine.

In public perception, swine do not have the best reputation regarding their cognitive capacity, and they are often perceived as dumb as well as voracious and dirty. In contrast, fairy tales and fables, such as the Three Little Pigs or Animal Farm, depict swine as smart and intelligent enough to outwit potential predators or liberate themselves from the tyranny of their human masters.

In real life, swine have successfully adapted to various climatic and vegetation zones and exhibit a high foraging flexibility that is reflected in their omnivorous dietary spectrum. Their mixed diet makes it necessary for them to recall food distributed in patches that vary in spatial location but also in time. Swine are very social animals, forming long-lasting family bonds, and exhibit fission-fusion dynamics. All in all, these ecological and social circumstances require high brain processing power.

First investigations on the learning abilities of domestic swine date back to more than 100 years ago, and operant learning in swine was intensively examined in the late 1960s and 1970s (e.g., Wieckert and Barr 1966). Starting 20 years ago, questions on swine's cognitive capacities gained increased attention, and research began to examine their ability to remember food patches, solve problems when dealing with hard-to-access food, and recognize and discriminate between familiar and unfamiliar individuals (e.g., Gieling et al. 2011). The increased interest in their cognitive abilities is, on one hand, based on the fact that swine are physiologically more similar to humans than rodents are; therefore, domestic swine are increasingly used as a model organism in neuroscience and biobehavioral research. On the other hand, insights into the cognitive capacities of swine can be used to improve the welfare of this intensively kept farm animal by designing

methods to enrich their environment (Puppe et al. 2007).

Research on swine cognition has mostly been conducted on domestic swine, but given that all swine species are social and occupy a similar ecological niche, we can assume that conclusions drawn on domestic swine will likely apply to other species of swine as well.

## Swine as Discrimination Learners

Swine can learn to discriminate between two simple geometric black-and-white stimuli but seem to be unable to transfer this skill to discriminate between images of faces of familiar conspecifics (Gielsing et al. 2012a). In addition, swine showed slow visual learning abilities for the presented symbols compared to other species. Given their rooting foraging style, one would expect them to perform better in discrimination tasks that include olfactory or haptic cues. Indeed, when mini pigs were trained to discriminate between food extract odors, they were able to use visual or olfactory cues, in addition to spatial cues, to navigate in a new environment and to find a previously rewarded container (Croney et al. 2003).

## Swine as Spatial Learners

Swine, if allowed, feed on a very flexible diet, opportunistically exploiting a vast number of food sources. Thus, they do not only have to recall which patches they already exploited but also when they did so, because several food sources replenish over time. Therefore, it should not be surprising to find cognitive capacities that are well adjusted to their foraging ecology. Indeed, domestic swine are exceptionally good at using spatial information to find new food sources and to remember locations they have previously visited. Mendl and colleagues (1997) found that swine rapidly learned to find hidden food in a spatial memory task. Twice-daily, the researchers baited several food locations. The swine were able to find food regardless if the delay between visits was several minutes or several hours. Subjects



**Swine Cognition, Fig. 1** Test subject in a spatial holeboard task (Photo Ivar Pel, Utrecht University). This task measures spatial working and reference memory in swine and other animals

readily learned how to return to a location where they had recently fed, i.e., following a so-called “win-stay” strategy that might be an advantage under husbandry conditions due to the repeated provision of food at the same place. However, when given the opportunity, swine show a preference for a “win-shift” foraging strategy, i.e., avoiding locations where they have recently found food (Laughlin and Mendl 2000).

An excellent approach to demonstrate the spatial learning abilities of swine is their performance in a spatial holeboard task (see Fig. 1). In this task, multiple potential food locations are presented to subjects at a time, but only a small amount of them are baited with a reward. Here, domestic swine show very high scores in their reference (remembering where to find food) and working memory (avoiding revisits of baited locations) (Gielsing et al. 2012b). Notably, their performance in spatial learning tasks was affected by the level of environmental complexity and the number of stressful disruptions after initial learning, indicating an impairment of otherwise excellent spatio-cognitive abilities due to decreased welfare (Mendl et al. 1997).

## Swine as Problem-Solvers

The ability of swine to solve novel problems and understand causal relationships has been less investigated. Given their flexible diet and their



particular feeding habits, it should nonetheless come as no surprise to find cognitive abilities that enable them to adapt quickly to new foraging situations. One way to relatively easily assess physical problem-solving abilities is the administration of an object-choice task (see Fig. 2). Here, individuals can choose between two or more hiding locations (e.g., cups), while only one of the locations contains a reward. By providing specific indirect cues to the subjects when manipulating the cups (i.e., by lifting or shaking of the unbaited cup), subjects can potentially infer the position of the reward by using the causal relationships between the reward and the cup (i.e., an empty space below a cup or not hearing a noise while the cup is shaken indicates that the reward is in the other location). Swine were able to infer the correct location after seeing the empty cup lifted, but they did show difficulties when confronted with an empty shaken cup (Nawroth and von Borell 2015). Thus, swine seem to be able to understand some causal relationships behind the information provided and the reward in these tasks, although rapid learning might offer an alternative explanation. Nonetheless, these results provide support for their rapid adaptation to new foraging situations.

As mentioned above, swine perform well in object-choice tasks in which they have to

comprehend that food is hidden in one out of two or more potential baiting locations. This suggests that they exhibit at least a rudimentary level of object permanence. However, their ability to follow more complex movements of hidden objects still warrants further investigation.

There is not a lot known on the numerical competence of swine. Domestic swine have been shown to distinguish between different quantities of food (Held et al. 2005), while the mechanisms behind these discrimination abilities remain unclear. There is also little known on the ability of swine to use tools. However, wild boar kept in zoos have been observed using water to wash the dirt off of potatoes and other food (Sommer et al. 2016), providing a first case for rudimentary tool use in swine. On a final note, given that swine rely more on olfactory and acoustic rather than visual cues when foraging, paradigms relying on smell and sound might be a more promising attempt to uncover their problem-solving skills (Croney et al. 2003).

## Swine as Social Animals

In general, swine are highly gregarious animals, forming stable social hierarchies. Wild boar and feral domestic swine form matricentric groups of



**Swine Cognition, Fig. 2** Setup of an object choice task for domestic swine (left, © by FBN) and wild boar (right, taken from Albiach-Serrano et al. 2012)

older females with their offspring, while young males often form bachelor groups. Adult males remain solitary and only join the females during the mating season.

### Differentiation of Conspecifics

Living in groups requires good discriminatory abilities to differentiate between group and non-group members. Thus, it is not surprising that domestic swine can not only differentiate between familiar and non-familiar conspecifics but also between group members through the use of visual, auditory and olfactory cues (McLeman et al. 2005). In term of visual cues, they appear to use primarily body size and body features to distinguish between familiar conspecifics. Head only cues of familiar conspecifics do not seem sufficient for discrimination learning (Gieling et al. 2012a).

### Social Learning

Due to their flexible diet, one would expect information transfer from adult swine to piglets. For young swine, it would not only be an advantage to learn what to eat but also how to acquire and process particular food sources. Indeed, it has been demonstrated that domestic piglets are capable of learning what food to prefer from observing the feeding behavior of their mother (Oostindjer et al. 2011). They can also learn how to solve a simple puzzle from kin. When piglets watched adults moving a door to either the left or right side, they tended to open the door in the same direction (Veit et al. 2017). Information transfer between adult swine or social learning from humans has not been investigated yet.

### Swine and Humans

Humans have domesticated swine for as long as 9000 years (Giuffra et al. 2000). But unlike dogs and horses, domestic swine have not primarily been bred to cooperate with humans. However, one would expect that these animals also cognitively adapted to their new domestic environment, leading to improved recognition of and communication with humans. Thus, it is no surprise to find that swine are able to tell handlers apart, mainly relying on the body height and upper

torso of the human (e.g., Koba and Tanida 2001). When piglets are confronted with two humans, of which only one paid attention to them, they preferred to approach the attentive one in anticipation of a reward (Nawroth et al. 2013). This indicates that piglets realize when they are being watched – and who is watching them.

Domestic piglets can also learn and attend to some forms of human communication; for example, they can use a variety of pointing cues and are also able to utilize the body and head orientation of a human to locate a hidden reward in an object-choice task (Nawroth et al. 2014). Interestingly, wild boar will follow human pointing gestures as well (Albiach-Serrano et al. 2012, see Fig. 2). Domestic dogs solve this kind of task by using the referential information conveyed by those gestures. However, for the piglets and wild boar, it might be that they are simply following the pointing gestures by relying on stimulus enhancement. Thus, it is not clear yet whether they can comprehend the referential and intentional nature that is usually included in human communicative cues.

## Other Cognitive Phenomena in Swine

### Time Perception/Mental Time Travel

Swine do remember when food sources have been visited and show indications of episodic-like memory, with the latter requiring the simultaneous recall of the what, where and when/which aspects of an event. In an object recognition test, swine identified the less familiar of two object/location/context configurations. Since configurations only differed in familiarity if all aspects were remembered simultaneously, swine recalled the what/where/which aspects of the configuration (Kouwenberg et al. 2009). Given that swine estimate time intervals in the range of days (Fuhrer and Gygax 2017), it is likely that they can also encode the “when” aspects of events.

### Self-Awareness/Mirror Test

Although swine belong to a set of species that are able to use a mirror to obtain information from

their environment (Broom et al. 2009), there is no evidence that they can recognize themselves in a mirror, i.e., pass the renowned mark test that was initially developed for primates. However, the absence of evidence for mirror self-cognition does not necessarily imply the evidence of absence. As previously stated, swine rely heavily on olfactory cues, so using different modalities than visual ones might be a promising method for further investigations.

### Theory of Mind

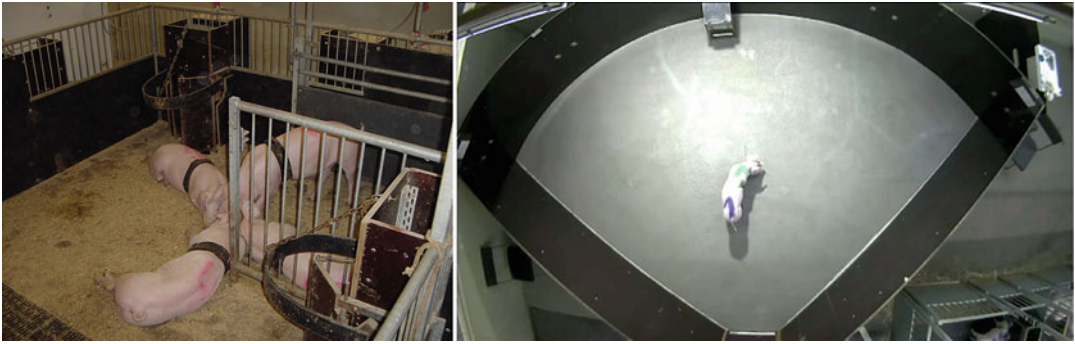
Swine are highly competitive foragers, relying on food sources distributed in patches. Therefore, it is not surprising that more dominant swine readily start to scrounge on subordinate individuals by following them to food patches the subordinates have discovered (Held et al. 2002). To counter this exploitative behavior, it seems adaptive for swine to be aware of the presence and attentive states of other individuals. Using an informed forager paradigm, Held and colleagues (2002) showed that the approach time of a subordinate but knowledgeable swine to get to a baited container depends on the body position of the dominant but ignorant (in terms of the baited location) conspecific. Overall, subordinates were more likely to show food-directed behavior when the chance of arriving at the food source ahead of the dominant subject was higher. Intriguingly, the subordinates adjusted their foraging behavior based on the individual they were foraging with, i.e., counter-exploitation behavior was only shown with dominant subjects that already scrounged on the subordinates in previous foraging trials (Held et al. 2010). In another experiment, swine were trained to follow one of two companions: one of them could observe a baiting procedure and thus knew about the location of food, while the other could not observe the events and lacked this knowledge. Most test subjects did not follow any of the two companions, probably to avoid competitive and aggressive behavior. Nonetheless, one swine followed the “knowing” individual significantly more often than the “unknowing” individual, indicating sophisticated abilities of what others can or cannot see or know (Held et al. 2001), a trait previously attributed to primates and some corvid species.

### Swine Cognition and Animal Welfare

Swine cognition is not only relevant in terms of comparative psychology or translational biomedical research but also for applied aspects of the innovative implementation of their cognitive processes in husbandry systems. Right now, there are more than one billion domestic swine raised worldwide, and their housing conditions range from being intensive indoor conditions to extensive outdoor conditions. Therefore, knowledge on the cognitive abilities of swine becomes increasingly important for the development of practically useful applications that can be integrated in the housing environment to avoid boredom and frustration, and thus, improve animal welfare. For example, enriching the housing environments with only simple changes (e.g., use of straw, peat or manipulative objects, or more structured space) can improve the learning abilities of swine in operant, maze or discrimination tasks (e.g., Grimberg-Henrici et al. 2015).

Today, it is more and more accepted that the implementation of cognitive challenges into the normal housing routine can serve as a form of cognitive enrichment, and therefore offers a way to improve how swine cope with their husbandry environment (Puppe et al. 2007). Indeed, a cognitive enrichment system using food-rewarded learning with discriminatory and instrumental tasks (Ernst et al. 2005, see Fig. 3) has been shown to improve welfare-related behavioral patterns (e.g., reduced abnormal behavior, decreased fearfulness), while also demonstrating enhanced wound healing, altered gene expression in reward-sensitive opioidergic systems in the brain, and seemed to evoke positive emotions in swine (Zebunke et al. 2011). Considering these results, it is an obvious conclusion that allowing swine to use their cognitive talents under captive conditions appears to be an influential way to enhance their welfare.

Similar to findings in other species, the emotional state may affect the cognitive processes in swine. Consequently, animal welfare scientists are interested in measuring and enhancing the cognitive-affective state of animals living in captive conditions. One promising approach to do this is by testing cognitive bias, for example, in a



**Swine Cognition, Fig. 3** (left) Cognitive enrichment through operant reinforcement: Swine in a pen with call feeding station (Ernst et al. 2005), equipped with Polar belts for heart rate measurements. (right) Cognitive bias test setup: Piglets were taught that a reward will be found on the left side, and they got slightly punished when they

approached the right side. In probe test trials, a container was positioned in the middle, and latency times of the piglets' approach were measured as an indicator of positive or negative expectations (both photos © FBN Dummerstorf)

spatial judgement task specifically modified for the use with swine (Düpján et al. 2017). Using this paradigm, it has been shown that structural enrichment seems to affect the animal's affective-emotional reactions, leading to more optimistic judgements in this task (Douglas et al. 2012). Cognitive stimulation, as a particularly effective method of enrichment, is likely to impact similarly on swine affective states (Zebunke et al. 2011).

## Conclusion

Our knowledge of the cognitive abilities of swine is largely based on research on domestic pigs. So far it has been shown that swine have advanced skills in spatial learning, memory and social cognition, and they show at least basic levels of time perception and awareness. Allowing them to use these cognitive skills appears to be an important way to enhance their welfare under restricted housing conditions.

## Cross-References

- ▶ [Artiodactyl Cognition](#)
- ▶ [Artiodactyla Diet](#)
- ▶ [Artiodactyla Life History](#)
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- ▶ [Artiodactyla Morphology](#)
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## Swine Communication

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Pigs use a rich repertoire of vocalizations, body postures, and chemosensory mechanisms to communicate with conspecifics (social cognition) and also with other species including humans. Even though vocal communication may be the most explicit, specific postures and behaviors such as play fighting and chemosensory mechanisms of communication are equally important for pigs to maintain social hierarchy and successful reproduction. Different types of vocal calls help pigs to discriminate between other members of its group and transmit information about the environment they are in. Vocal communication contains information on motivation and emotion of the sender (Chan et al. 2011) and also their identity, location, and body size (Špinka 2017). Behaviour and posture-based communication are used by pigs to express certain emotional states to other conspecifics. Behavioral expressions such as play fight and tail postures (Groffen 2012) have been identified as good indicators of emotional state of the pig, and hence there has been an effort to validate these behaviors

to assess welfare. Pigs use olfactory system (chemosensory mechanism) for reproduction similar to many other mammals (Dorries et al. 1997). Also, chemosensory communication is used by pigs for reproduction, which helps in the survival of the species in the wild and also helps us run a profitable pork industry by breeding domestic pigs. Male pigs emit specific odor, which triggers a hormonal mechanism in gilts to attain puberty and also triggers reproductive cycle in sows. Last but not the least, there are some communication methods that are still not fully understood. For example, pigs tend to display decreased locomotion and freezing when stressed and when they see a conspecific in distress (Goumon and Špinka 2016). Such responses also have husbandry and welfare implications. This entry presents the diversity of swine communication with a view to better understand their behavior to improve pig health and welfare in a farm, feral, or wild environment.

## Vocal Communication

The pig vocal ethogram can be described as a set of highly flexible call types connected through an acoustic continuum (Tallet et al. 2013). Domestic pigs of today, even though highly selectively bred for a profitable pork production, still show most vocalization repertoire of their wild ancestors. Descriptions of vocalizations identified in wild and feral pigs by Allwin et al. (2016) are useful to understand the functional aspect of different vocal calls of domestic farmed pigs. In the wild, loud grunts are associated with danger, male to male interaction for dominance, and for warning the piglets. Squeals are indicative of some painful situation or some submissive gesture. Wild pig vocal repertoire also had loud grunts associated with separation from social group, a lower-pitched grunt while displacing another pig during feeding, and nursing-associated grunts. Marchant et al. (2001) studied the vocal repertoire of domestic pigs using social isolation and approach to human and suggested that short single grunts are associated with investigative behavior, long

single grunts associated with contact call, and squeals associated with higher level of arousal. Schrader and Todt (1998) found correlation between high-pitched squeals and stress hormones thereby providing evidence to the notion that vocalization can be used to assess stressful situations in domestic pigs. Other vocalizations recorded and studied are piglets barking when they are surprised (Chan et al. 2011) or when they play (Newberry et al. 1988), screaming in painful situations (Marx et al. 2003), croaking during naso-nasal contacts with mother (Illmann et al. 2001) and grunt when briefly isolated (Fraser 1974).

Vocal communication is used by pigs to express their emotional states (Düpjan et al. 2008; Leliveld et al. 2017) negative such as hunger, distress, fear, and aggression and positive such as playfulness. Hunger vocalizations (squeals and screams) can be noticed in intensively raised pigs, particularly in gestation sows which are on restricted diet at the time of feeding. Piglets make similar scream, squeal, and some grunts when they are hungry and ready to feed (Appleby et al. 1999). The hunger squeals made by piglets at the udder may also attract the remainder of the piglets before the sow make the feeding calls. Continued squealing by piglets during feeding often causes the sow to roll over further to make the lower teats available to the piglets.

Nursing sows have specific vocal communication to indicate the piglets to feed. The sow's pattern of vocalization (grunts of varying intensity) is related to the different phases in which the piglets are in the feeding routine. The rate of grunting by the sow does not vary during the initial phase of feeding by piglets but increased substantially in the later stages of feeding (Ellendorff et al. 1982). These are soft rhythmic grunts, which are repeated in a rapid series, and are made by nursing sows at the beginning of and during nursing of her litter of piglets. The function of these feeding-associated grunts is to solicit the litter to begin and continue nursing. The feeding call of nursing sows is given in response to the behavior of the piglets which first start to squeal. Nursing sows then vocalize

the feeding call which attracts all the piglets to feed.

Fear in pigs elicits a characteristic alarm call or bark, heard when disturbed suddenly which has the effect of sending all young piglets running. Barking could also be witnessed when entering a room suddenly surprising young adult pigs or adult pigs in a hog barn. Barking has not been observed in piglets younger than 1 week. Chan et al. (2011) found that differences in acoustic morphology of barks enable domestic pigs to discriminate between barks of adult sows and juveniles, with former evoking a stronger response.

Warning calls by sows with piglets can be different from bark vocalization. The most distinctive warning call is given when the nursing sow moves before standing up and continues while standing up. This call seems to be a mild version of the threat snort. The sound is a grunt with sharp exhalation. The signal causes the piglets to walk from the sow and stand together a few feet away. Postpartum nursing sows can reinforce this behavior in piglets by nudging them away and may even appear to savage them by taking them in her mouth before thrusting them away. If the threat interpretation of this call is correct, the ambivalence displayed by the piglets is of considerable significance since the movements of the sow constitute the greatest hazard to piglets in their first few days.

Squeal is typically a distress or submission vocalization made during both the intraspecies and interspecies interactions of wild pigs. This call can be made by any animal, but is more commonly heard among immature or subordinate individuals. Marx et al. (2003) classified pain-related vocalization in piglets depending on the strength of spectrograms into squeals and screams. According to that classification, squeal had highest-frequency sounds, and scream are medium-frequency sounds. Both squeal and screams are loud, high-pitched piercing vocalizations repeated continuously until the threat ceases. When painful husbandry procedures such as castration are done without surgical anesthesia, pigs of all ages squeal. Squeal vocalization is also produced by piglets when they get caught

inadvertently under the mother after the first few days after parturition. These vocalizations reflect the urgency of the situation, thus inciting the mother to intervene, with louder, louder and higher screams signaling higher danger for the pig. In life-threatening situations, such as castration, crushing, and arms and fighting, piglets produce long, high-pitched squeals and screams. More precise information may be conveyed leading the mother sow to react appropriately according to the situation. She may respond with aggression against the predator or by standing up in the case of crushing or by interrupting the nursing in the case of severe fighting between piglets.

When the piglets first walk a yard or so from the sow, they start to give their location call. This is a soft snore repeated continually. The sow responds by a similar and more powerful call, which generally has the effect of attracting some other piglets to her head. Among older litters, particularly at night, when the pigs leave the sow one by one to walk to the feed trough, they give this location call whenever walking alone. The significance of this location call seems to be to maintain communication with other pigs whenever they are not in close proximity to each other.

## Communication Through Postures and Body Language

Pigs use a range of postures, specific behaviors including body movements, and facial expressions (grimace score in piglets) to communicate feelings, such as contentment, hunger, pain, fear, and aggression. Grimace score which is based on facial expression has been increasingly used to assess pain in piglets when pain mitigation strategies are implemented following regular husbandry procedures such as castration (Viscardi et al. 2017). Wild and feral pigs use body posture-assisted visual signals such as bristle rising, ear position, tail movement, and arching the back to express aggression. In domestic pigs, this communication has substantially diminished, probably due to morphological

changes that prevent the signals from being clearly displayed. Raising of bristles is to warn the predator and increase the appearance of ferocity of the prey. Arching of the back is also to offer the image of ferocity by making the body appear taller and bigger. Forward position of the ears is indicative of keenness, and listening. Backward position of the ears is communicative of fear and suspicion. The backward ear leaning may tend to give the animal an aerodynamic flight position either to get into a fight or to flee the fright-generating situation. Tail position and movements are also used for communication. Tail low or between legs can be understood as a sign of fear (Noonan et al. 1994). Curled tail is indicative of a positive emotional state, while hanging tail is characteristic of a neutral state, and wagging tail is expressive of a negative emotional state such as restlessness (Groffen 2012).

Body movements associated with communication are teat massaging by piglets, teeth clacking by wild pigs, nosing, rubbing, and tail movements. Tactile communication in the form of teat massaging is used by piglets during nursing to trigger milk ejection. Piglets also communicate their levels of hunger through the length and intensity of teat massaging. Teeth clacking is not truly a vocalization but an aggressive expression produced by tooth impacts primarily the canines, through rapidly champing of the jaws. Mostly heard among mature males during aggressive interactions, it can consist of either single or a few multiple mouth impacts. This functions as a warning or threat during aggressive encounters between conspecifics or against potential predators.

Casual, slow, unobservant, and relatively quiet body movement communicates that the environment is without any stressors. When environmental stressors are absent, piglets often exhibit playful behavior such as sprinting, galloping, and spinning around. Play behavior in young remains a topic of considerable interest for ethologist who are interested in improving the welfare of intensively raised pigs because of the positive emotion attached to play. Play has also been proposed as an indicator of animal welfare as it is drastically reduced by bad

husbandry practices, fitness challenges, injury, and pain. Lawrence (1987) proposed that hence play behavior is a luxury or elastic behavior which is performed by animals only when their proximate needs are met, it could be a good indicator of well-being. Play behavior in pigs can be locomotor (running), object-directed, and social play (Blackshaw et al. 1997). The behaviors that are recognized as play in pigs have some resemblance to adult behaviors (e.g., running; play fighting) but at the same time are recognizably different from being performed in an exaggerated, energetic, and repetitive manner (Newberry et al. 1988).

When pigs are anxious or fearful, their movements are quick and erratic, often accompanied by loud and shrill squealing. Their gaze is no longer unobservant but is directed toward the person or object that is the source of anxiety and fear, and their posture is alert and forward-facing. Lack of body movement and freezing have also been considered an important form of communication. As Goumon and Špinka (2016) report, distress is expressed through reduced locomotion and freezing, when pigs are exposed to conspecifics in stressful situations such as being restrained.

## Olfactory Communication

Olfactory communication in animals is a process by which chemical signals are generated by a sender and transmitted to a receiver, who, by means of adequate receptors, can identify, integrate, and respond behaviorally and physiologically to the signal (Eisenberg and Kleimann 1972). Pigs use olfactory channels for mating and general survival. In the olfactory realm, adult males actively advertise their status by producing chemical compounds, two of which are the sources of the unpleasant taint sometimes present in pork from non-castrated post-pubertal males.

Aldosterone is one of the chemical compounds produced by the testes and is present in the saliva, urine, and the preputial glands and gives the smell of urine in the meat. This compound triggers the standing reflex in estrous sows and can advance the puberty of gilts. The olfactory

system of the female is five times more sensitive to aldosterone than the male system. The second chemical compound is skatol. This compound emanates a smell similar to that of feces. It is controversial that pigs can communicate danger using smell. Whether or not pigs can detect smell and communicate in non-vocal ways for social purposes are debatable. It has been hypothesized that pigs use olfactory cues to communicate with humans (Hemsworth et al. 1986). However, the range of olfactory cues are less likely to be detected by the human olfactory range and current assessment methods.

## Conclusion

Vocal, behavioral, and chemosensory communication among pigs represent their social cognition and affective states. Interest in understanding pig communication has increased over the years partly for improving how we relate to pigs especially when we interact with them in close proximity, due to the potential of increasing welfare, for increasing productivity (e.g., through better piglet and pig feeding), and also for enhancing the quantity and quality of pork. In pig production and transport facilities, excessive use of the electric pod, for example, can lead to increased incidence of stressed and non-ambulatory pigs. Similarly, insensitive and rough handling can result in higher incidence of freezing and reduced locomotion. With greater understanding of pig communication, better training can be offered to individuals working in swine production and transportation facilities. Overall, enhanced understanding of pig communication can be translated into better training for people who are involved in the hog industry. And in turn, proper animal handling plays a key role in the health and welfare of the pig as well as the quality of the final product.

## Cross-References

- [Aggression](#)
- [Alarm Calls](#)
- [Animal Welfare](#)

- Canine Communication
- Cognition
- Communal Behavior
- Communication
- Conspecifics
- Equine Communication
- Feline Communication
- Pheromone
- Play Behavior
- Social Behavior
- Swine Cognition

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## Swine Gait

- Swine Locomotion



## Swine Life History

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## Taxonomy and Domestication

Domestic pigs (*Sus scrofa*) belong to the mammalian order Artiodactyla, derived from the Greek word *artios* meaning complete or even-numbered and *daktulos* meaning finger or toe (Young 1981; Nowak 1997). This large order of even-toed ungulates is made up of three suborders which differ based on teeth structure, metatarsal or metacarpal fusion, and digestion. These suborders are Suina (pigs and peccaries), Tylopoda (camels and llamas), Ruminantia (cattle, antelopes, deer, and giraffes), and Cetancodonta (hippos, dolphins, and whale) (Young 1981; Nowak 1997). Within the Suina suborder, there are two living families: Tayassuidae (peccaries) and Suidae (pigs). There are currently 19 living species split into 6 genus in the Suidae family: 3 species of deer pigs (*Babyrousa*), the giant forest hog (*Hylochoerus meinertzhageni*), 2 species of warthogs (*Phacochoerus*), the pygmy hog (*Porcula salvania*), 2 species of bush pigs (*Potamochoerus*), and 10 species of the *Sus* genus (Ruvinsky and Rothschild 1998). Species in the *Sus* genus share a common ancestor approximately 5 million years ago, and hybridization is possible among the species (Giuffra et al. 2000; Larson et al. 2005).

The domestic pig originates from the Eurasian wild boar (*Sus scrofa*). Archeological record and mitochondrial DNA research suggest that the species was domesticated approximately 8000–10,000 years ago in two separate locations: in the Mekong valley of China and in the region of modern-day Turkey (Larson et al. 2005; Minagawa et al. 2005; Giuffra et al. 2000; Jing and Flad 2002). The Chinese and European *Sus scrofa* breeds diverged approximately 2000 years ago (Paszek et al. 1999). Selective breeding of *Sus scrofa* resulted in a domestic breed with a reduced

fear of humans, to allow for easy and safe handling, as well as an increase in body size, litter size, and growth rate (Price 1984). For example, an adult wild boar can reach up to around 230 kg (Sweeney et al. 2003; Bieber and Ruf 2005), while a modern adult pig may weigh more than 350 kg (Whittemore 1994), and a wild sow may have a litter size ranging from 2 to 6 piglets (Sweeney et al. 2003), while a modern domestic sow can produce an average of 10–12 piglets per litter (Setchell 1992).

## Expansion of Domestic Swine

Domestic or feral pigs can be found on all continents, except Antarctica, including many oceanic islands (Waithman et al. 1999; Hanson and Karstad 1959; Graves 1984). The ease with which domestic pigs have been propagated across the globe may be due to the fact that they reach sexual maturity at a young age, females give birth to large litters twice a year, and the animals can be fed human food-waste (e.g., brewing and distillery by-products). In 1493, Christopher Columbus brought the first batch of swine to the New World in the West Indies. The first pigs to be brought to the North American continent occurred in 1593 when Hernando de Soto landed in Florida (Towne and Wentworth 1950; Porter 1993). Starting in the seventeenth century, early colonial settlers, Native Americans, and game hunters have promoted the distribution of pigs across the United States (Seymour 1970; Mayer and Brisbin 1991). Feral populations of domestic swine can be found from Texas east to Florida and north to Virginia and in California, Hawaii, Puerto Rico, and the Virgin Islands (Sweeney and Sweeney 1982; Mayer 2009). Escaped domestic pigs in the eighteenth century have led to large feral populations in Australia and New Zealand as well (Tisdell 1982).

## Social Structure and Home Range

The social structure of *Sus scrofa* is characterized by solitary adult males and matrilineal groups of females and piglets (called “sounders”). Sounders

are composed of two to four sows, often genetically related, with their litters and are led by a dominant sow throughout a shared home range (Gabor et al. 1999; Gonyou 2001; D'Eath and Turner 2009). Older and larger sows tend to be more dominant than subadults and juveniles in a sounder (Mauget 1981; Gonyou 2001). Through frequent nose-to-body and nose-to-nose contact, swine use olfactory cues to identify other individuals (Kristensen et al. 2001; Mendl et al. 2002; Stookey and Gonyou 1998), which is fundamental in maintaining their social hierarchy. The social order in a sounder may be maintained through subtle behaviors, such as a subordinate individual averting the gaze of a dominant and overt aggression like reciprocal fighting (i.e., parallel-pressing; Jensen 1980).

Sounders engage in synchronized activities (e.g., foraging and resting) led by dominant sows and engage in cooperative defense of their piglets against predators (Mauget 1981; Graves 1984). Given that pigs are opportunistic omnivores, their home range size depends on the features of their environment, such as food availability and population density. The average home range size for a sounder varies from a few hundred to several thousand acres and may overlap with neighboring sounders (Kurz and Marchinton 1972; Singer et al. 1981; Graves 1984). Because pigs do not have functional sweat glands, they are sensitive to high temperatures and are most active at dawn and dusk (i.e., crepuscular) (Sweeney et al. 2003).

Juvenile pigs remain within their dam's home range from lactation into subadulthood (Cousse et al. 1994). While female piglets remain with their natal sounder once they reach sexual maturity around 8–10 months (Frädrich 1974), male piglets disperse from their sounder before they reach sexual maturity at around 6–10 months of age (Frädrich 1974; Truve and Lemel 2003; Gabor et al. 1999). This strategy limits inbreeding within a sounder by the polygynous boars (Gabor et al. 1999). Occasionally, smaller groups of female pigs split off from their natal sounder to form a new sounder with a new social hierarchy (Gabor et al. 1999). Upon leaving their natal sounder, young boars form small bachelor groups and roam through new home ranges. The boars

become gradually solitary as they mature, foraging for food and searching for new sounders during mating season (Graves 1984; Gabor et al. 1999; Frädrich 1974; Mauget 1981).

## Mating

The mating season for wild and feral pigs begins in autumn and, given that gestation is approximately 115–118 days, peak farrowing activity during the winter through early spring and occasionally in the summer (Mauget 1981; Sweeney et al. 2003; Taylor et al. 1998). Wild and feral sows often show seasonal anestrus during the summer, which may be due to the change in day-length (Delcroix et al. 1990; Tast et al. 2002). Almost as soon as female pigs reach sexual maturity, they begin to breed, but younger males often do not mate until they are able to compete successfully with older boars (Mauget 1981; Sweeney et al. 2003; Taylor et al. 1998). Sexually mature boars do not interact with sows outside of the mating season and rarely interact with each other except for during competition for female access during the mating season (Kurz and Marchinton 1972; Gonyou 2001).

Sexual pheromones (called androsterone) released by the boar's foamy saliva help to stimulate the synchronization of estrus among sows of a sounder (Mayer and Brisbin 1986; Claus et al. 1994). A boar will nudge a sow with his snout and produce rhythmic grunt sounds to determine if she is receptive to mating. In order to prepare for mounting behavior associated with mating, a sow in estrus will display a rigid, motionless standing posture in response to the boar, especially when pressure is applied to the rear of her back (Fraser 1984; Mauget 1981). When competing for access to a female in estrus, males will walk in circles near each other and then engage in shoulder-to-shoulder pushing, head knocks, and reciprocal biting (Frädrich 1974; Barrette 1986). Although mating competition among males does exist, females often mate with more than one male during the breeding season which results in litters of mixed paternity (Fraser et al. 1995).

## Farrowing and Weaning

Toward the end of gestation, pregnant sows will become more solitary and keep a distance from other sows in their sounder in search of a location to build their nest (Mauget 1981; Stolba and Wood-Gush 1989). Sows begin to collect vegetation and small branches to build a nest approximately 1–3 days prior to giving birth (called “farrowing”) (Frädrich 1974). After partition, sows stay with their piglets at the nest site for the first 2 weeks before rejoining the sounder (Mauget 1981; Csermely 1994). Neonatal piglets are highly dependent upon the sow for nutrition, ambient body heat for temperature regulation, and protection from predators (Hartsock and Graves 1976). Piglets use tactile, vocal, and olfactory cues from the sow to locate the udders for nursing (Horrell and Hodgson 1992; McBride 1963). Piglets are able to discriminate odors from their nest as early as 1 day old and can identify their mother’s vocalizations soon after (Horrell and Hodgson 1992; Walser 1986).

Piglets will engage in scuffling in the first few days of life while competing for access to teats during nursing (Algers 1993; Fraser and Jones 1975; McBride 1963). As they develop, piglets will engage in rough-and-tumble play with their littermates and with other piglets by mimicking the fighting posture of adult swine (parallel-pressing) and will start to explore their environment away from the nest (Dobao et al. 1985; Newberry and Wood-Gush 1988; Jensen and Redbo 1987). The sow will use vocal communication, such as short rhythmical grunts, when leading the piglets away from the nest, prior to lying down in a nest, and to call the piglets at nursing (Frädrich 1974; Newberry and Wood-Gush 1986). The dominant sow of a sounder will often start vocalizing as her milk is let down, and this leads to a synchrony of vocalization and lactation within a sounder (Horrell 1997; Newberry and Wood-Gush 1985). Given that piglets within a sounder are most likely genetically related to all sows in the herd, cross-suckling among the litters may occur (Fraser et al. 1995). Often, most sows within a sounder will respond to a piglet distress call

(e.g., loud squeal) when attacked or captured by a predator (Frädrich 1974).

Piglets will increase the proportion of solid food in their diet at around 4–5 weeks old and will be completely weaned from sow’s milk around 14 weeks (Jensen and Recen 1989; Newberry and Wood-Gush 1985). Piglets will follow the roaming path of the sounder as they mature, exploring their environments by digging and rooting up objects to test for edibility (Studnitz et al. 2007; Wood-Gush and Vestergaard 1989). As the male piglets reach sexual maturity, they explore the environment beyond the bounds of their natal home range, while female piglets continue to follow their dams in search of food.

## Commercially Reared Pigs

Pigs have been under selective breeding pressure since being domesticated 9000 years ago (Giuffra et al. 2000). Several breeds have been developed that feature distinct phenotypical characters such as coat color, ear morphology, as well as combinations of traits that favor either maternal or carcass performance. Maternal breeds such as Yorkshire, Landrace, or Large White have been selected to produce large litter size and noted milk production. In contrast, carcass or terminal breeds such as Duroc, Hampshire, or Pietrain have been selected for fast growth and efficient feed conversion and to produce heavily muscled, high-quality carcasses. Today most commercially reared pigs are carefully planned hybrids of these different common breeds and genetically selected to meet the specific requirements for a variety of different uses for pigs.

## Social Structure and Home Range

Compared to their wild counterparts, most domesticated pigs are raised under more confined conditions and managed more intensively to meet the goal producing an affordable and safe source of animal protein for human consumptions. In most parts of the world, breeding sows are individually housed either in a gestation or a farrowing crate depending upon their stage of production (Pajor

2005; McGlone 2013). Such housing precludes social interaction as well as many other normal behaviors such as establishing a home range. However, social pressure is driving both legislative and consumer-based initiatives around the world to reduce the confinement of sows, especially during gestation (Lassen et al. 2006; Appleby 1999; Tonsor et al. 2009). Group sizes in such loose housing system can range from 6 to 250 sows and allow for the formation of a social hierarchy (Bench et al. 2013a, b). In the husbandry systems that use large groups (>40 sows), subgroup formation occurs as clusters of sows similar in size to that found in the sounders of wild pigs arise. These animals typically rest together in the same area of the pen as well as eat together and are in part defined by age of the sow (Den Hartog et al. 1993). Growing pigs are housed in groups and free to carry out more natural behaviors than their mothers. However, the habitat of these animals ranging in age from 3 to 24 weeks of age is often quite barren and devoid of any substrate that would allow these animals to pursue their behavioral needs to forage (da Silva et al. 2016).

## Mating

Gilts enter most sow herds at the time of puberty and are bred for the first time between the age of 6 and 9 months of age. Similar pigs in the wild exposure to boars and their pheromones induce puberty and help to synchronize estrus and subsequent breedings (Kekan et al. 2017). Mature sows exhibit lactational anestrus, that is, while nursing their piglets, follicular stimulation is inhibited, and the sows fail to exhibit estrous behavior. However, shortly after weaning, this inhibition is reversed and within 4–7 days postweaning most sows will be returned to estrus and are bred (van Wettere et al. 2017).

Today almost all commercially raised females are bred via artificial insemination. Fresh boar semen is delivered from specialized farms called boar studs where only male pigs are reared. Semen is regularly collected from the boars and diluted to with a physiological solution that serves

to promote the shelf life of the semen and extend the semen by diluting it to a minimum concentration of sperm cells required for to inseminate a sow. This effectively increases the number of sows that could be bred by one boar and reduces the number of boars that need to be maintained for breeding purposes (Knox 2016).

## Farrowing and Weaning

Gestating sows are moved into specialized facilities, often called farrowing rooms, around day 110 or 112 of their pregnancy. Most commonly within these rooms are individual pens for the mother and her newborn litter. The sow is confined within the pen by a stall or crate that limits her mobility. This requires that she lays down slowly to help minimize injuries or deaths that might occur if a piglet is in her way when transitioning from standing to lying down (Singh et al. 2017). A localized heat source is provided for the piglets as their thermal requirement at birth may be as much as 10 °C higher than the mother sow (Curtis 1983). Rarely is bedding or other substrates available to the sow prior to farrow, and this in combination with the confinement of the farrowing crate can result in the frustration of the sow's behavioral drive to nest build (Yun and Valros 2015).

Piglets are born into litters of 14 or more and typically lactate for 21–28 days before being weaned. Most sow farrow without assistance and farrowing takes several hours. In the absence of any complications, piglets are birthed about every 20 min (Van Dijk et al. 2005). Pigs rapidly establish a social hierarchy as well as a nursing order where individual pigs will defend and nurse from a particular teat for the duration of lactation (Hartsock et al. 1977; Scheel et al. 1977). Piglets may be moved from one litter to another, or cross-fostered, to ensure that the number of the piglets nursing matches the number of available functional teats for nursing. Otherwise the survival of these teatless pigs is compromised due to malnourishment (Edwards and Baxter 2015).

Upon weaning the piglets are typically moved to another facility dedicated to raising newly weaned pigs and mixing into larger groups

typically of about 25 pigs. Litter integrity is often disrupted as pigs are sorted by size and/or sex. In addition to the social stress of regrouping, piglets also face nutritional stress following weaning as they are required to transition from their mother's milk to solid diets comprised of different cereal grains (Campbell et al. 2013). Pigs typically remain in a so-called nursery for up to 8 weeks before being moved to another facility. As the pigs grow, more space is allotted to them to compensate for their larger static and dynamic space requirements. The majority of the pigs will spend another 10 or 12 week in a finisher before going to slaughter at about 5–6 months of age and weighing upward of 130 kg. These market hogs are the source of most of the pork meat consumed by human. Domesticated pigs have been selected for rapid growth as well as efficient conversion of feed into meat. Conversion rates continue to improve but are approaching a ratio of <3 kg of feed for every kilogram of weight gain. Such a feed efficiency is much better than beef cattle (7.5) but still less than poultry (2) or fish (1) (Tolkamp et al. 2010).

## Boars

The greater majority of male pigs are castrated at a young age to prevent the development of boar taint. Boar taint is the offensive odor or taste that can be evident during the cooking or eating of pork products derived from non-castrated male pigs once they reach puberty (Bonneau 1982). However, a small number of boars remain uncastrated and destined for breeding programs. Once these boars reach 6–9 months of age, they are moved to boar studs where they are trained to have semen collected from them. The animals learn to jump a phantom or dummy sow, and then in the presence of manual digital pressure from humans, the boars ejaculate and the semen is harvested. Boars are housed individually at boar studs to minimize inter-animal aggression, and semen is collected from them once or twice a week (Levis and Reicks 2005).

## Cross-References

- [Swine Cognition](#)
- [Swine Communication](#)
- [Swine Locomotion](#)
- [Swine Navigation](#)

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## Swine Locomotion

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## Synonyms

Pig gait; Pig locomotion; Swine gait

## Definition

Movement used by swine (i.e., pigs) to traverse their environment.

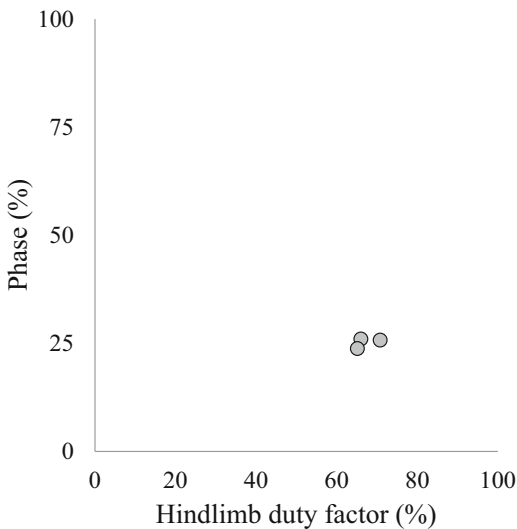
Swine are even-toed, hoofed mammals that put weight on only two digits (i.e., artiodactyls). They belong to the genus *Sus* and are widely domesticated. Wild pigs for the most part live in forests or woodlands and are most active at night (Macdonald 2006). Wild swine forage in family parties and are omnivorous, feeding on a wide variety of plants, insects, and small vertebrates (Macdonald 2006). Wild pigs are mostly naked and only partly covered with thick bristles. They vary greatly in size, ranging from 58–66 cm and 6–9 kg in the pygmy hog to 130–210 cm and 130–275 kg in the giant forest hog (Macdonald 2006). Pigs are important animals for humans as they supply us with food resources, and we derive medicine from them. Therefore, understanding their locomotor behavior can benefit humans in relation to lameness and loss in productivity.

## Gait

Pigs walk with a four-beat gait sequence that alternates support phases between the involvement of two or three limbs (von Wachenfelt et al.

2008). These slower gaits are usually less than 1 km/hour and are observed during feeding, exploring, wallowing, and marking (Morelle et al. 2015). Under normal conditions these gaits are symmetrical. A symmetrical gait is when footfalls of the forelimb and hindlimb are evenly spaced in time. Symmetrical gaits can be further divided into a lateral sequence or a diagonal sequence. A lateral sequence gait is when each hindlimb footfall is followed by an ipsilateral forelimb footfall. A diagonal sequence gait is when each hindlimb footfall is followed by a contralateral forelimb footfall (Granatosky 2018). During walking gaits, forelimbs often travel together as slightly asynchronous pairs, forming couplets. Couplets are either lateral couplets, which means ipsilateral forelimbs and hindlimbs travel together, or diagonal couplets, which means contralateral forelimbs and hindlimbs travel together (Granatosky 2018; Hildebrand 1976; Hildebrand 1989). Walking gaits can be described as having a duty factor over 50%. A duty factor represents the time of the total cycle a given foot is on the ground. Stance phase occurs when the foot is in contact with ground and the limb is bearing weight. When the foot is not in contact with the ground and is moving in the air, the limb is in swing phase (Granatosky 2018). Wild pig species use lateral sequence lateral couplet and/or lateral sequence diagonal couplet footfall sequences (Fig. 1), but von Wachenfelt et al. (2008) reported a large proportion of diagonal sequence diagonal couplet gaits in domestic animals.

A pig's gait can differ based on the surface it is walking on (von Wachenfelt et al. 2008). When walking on greasy floors, pigs switch from a diagonal sequence gait to a lateral sequence gait. They do this by reducing their speed and progression length and prolonging their stance phase (von Wachenfelt et al. 2008). Different floor conditions have also been shown to alter braking and propulsion in pigs. The beginning part of the stance phase is usually involved in braking, and the end portion is usually involved in propulsion. In normal conditions, pigs tend to use their forelimbs for braking and hindlimbs for propulsion. However, when the floors are slippery, they tend to involve



**Swine Locomotion, Fig. 1** “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in swine ( $n = 3$ )

more of their hindlimb for braking as well as propulsion (von Wachenfelt et al. 2008).

Swine did not evolve to run efficiently. In wild pigs, trotting is used to transverse long distances, and galloping is used for short bursts during emergency situations (Signoret et al. 1975). These fast-moving gaits can be defined as having a duty factor of under 50% (Granatosky 2018). Trotting is mostly reserved for social interaction by juvenile pigs and for movement between habitats. Trotting speeds for wild boars can vary between 6 and 10 km/hour (Morelle et al. 2015). A trot can be defined as the diagonal forelimb and hindlimb moving in unison. At high trotting speeds, there is suspension phase. This is when the diagonal couplet is in swing phase and the contralateral diagonal couplet has not yet touched the ground (Granatosky 2018).

At the highest speeds, wild boar and other swine use a transverse gallop (Jansen et al. 2009). Galloping mammals undulate their spines to increase the duration of swing phase and the stride length (Stavarakakis 2014). However, swine have not developed elongated limbs, making it difficult to keep a fast pace for more than a few minutes. This may be due to selection pressure for predator response because short-legged boars are

able to defend themselves without needing to run away (Morelle et al. 2015). Although other ungulates with longer limbs (e.g., deers) can maintain their top speeds for longer durations, swine have adapted by increasing their step frequency to compensate for short stride length (Clifford 2010). When boars need to flee from predators, they can reach speeds of 10–40 km/h (Morelle et al. 2015).

## Kinetics and Kinematics

Studying the kinetics and kinematics of animals can provide quantitative measurements of abnormal gaits and can subsequently help researchers identify aspects of lameness and injury in animal subjects. Thorup et al. (2007) offered an in-depth analysis of pig locomotor biomechanics. In terms of kinetic parameters, the study found that ground reaction force magnitude during normal gait are greater in the forelimbs. This finding indicates that a pig’s center of gravity is closer to the shoulder than it is to the hindlimbs (Thorup et al. 2008). Even though the forelimbs exhibit more force during locomotion, they are shorter and lighter than the hindlimbs. For this reason, the forelimbs present a site of common injury in pigs, including osteochondrosis and other joint pathologies (Thorup et al. 2007).

Studies of limb loading and biomechanical forces in pigs have also been used to analyze the chondral modeling theory, which revolves around joint development and cartilage growth in growing animals. The theory is defined as the adaptive growth response of cartilage in response to increased biomechanical forces on an animal; as the forces increase, changes in bone growth, cartilage thickness, and cellular division will occur to compensate and maintain stability inside a joint (Hammond et al. 2010). These studies have provided valuable insight into joint plasticity and remodeling.

The pig knee has been used as a model for understanding human joint injury. However, pigs have a greater range of flexion and a lower range of extension because of extension-restricted cruciate ligaments. The collateral ligaments in the pig

hold the joint in the craniocaudal axis and prevent abduction or adduction. They can also restrict rotation of the femorotibial joint along with the cruciate ligaments. Any alterations to the joint or to these ligaments can alter walking ability (Spitzers 2013).

### Gait in Young Swine

At birth young pigs gain locomotor function within their first couple of hours. The animal undergoes postural changes quickly that help it with walking. Vanden Hole et al. (2017) demonstrated that locomotion characteristics in young pigs (0–96 h) reach stable gaits within 4 h of birth, with most of them showing little change after the age of 2 h. These results indicate that coordinated movement patterns are not entirely innate, but that a rapid neuromotor maturation, potentially also the result of the rearrangement or recombination of existing motor modules, takes place in these precocial animals.

Pigs give birth to multiple offspring at once. This can lead to intrauterine crowding and affect birth size. Birth size can then affect stride length and stride frequency, thus affecting speed. The stride length in particular is affected by limb size of the animal. The more crowded the uterus is with offspring, the more competition there is for resources and the less the fetal pigs will develop. Piglets in general start out with low energy stores due to lack of brown fat. They get most of their energy from limited glycogen stores in their muscles and liver. The pigs cannot generate their brown fat until they start to consume fatty acids through milk intake from their mother. Due to the large number of offspring, this can then lead to competition among the newborns for milk and boxing out of undersized piglets. This leads to inadequate energy stores and diminished locomotor energy and muscle development. The consequences could result in altered gait (Vanden Hole et al. 2018a). An example of how intrauterine competition affects musculature has been observed in a reduction in *m. semimembranosus* cross-sectional area and myofiber count. This reduced cross-sectional area causes a diminished

ability to generate force and prevent gravity load collapse at joints.

### Swimming

Swine have been known to swim in search of food or to escape danger. In 2005, wild pigs in Texas were seen swimming to higher ground during intense rainfall and flooding. In fact, an island in the Bahamas has become famous for pigs swimming out to boats for food (Abernethy 2016). Some evidence suggests that swimming is an innate feature of pigs, and their ability to swim is aided by lung size and fat content under their skin (Gabbatiss 2017).

### Lameness

Lameness is an issue for farmers all over the world and is defined by a change from normal to impaired gait (Stavarakakis 2014). It can adversely affect the growth and reproductive potential of animals, leading to decreased farm productivity and profitability. Supakorn et al. (2018) reported that economic loss due to lameness in the USA was over \$23 million per year. Lameness often arises from lesions to pig hooves, which are commonly seen because of different floor types. Floors that are too abrasive can wear down claws and create lesions on the skin. Floors without enough abrasion can lead to excessive hoof growth (von Wachenfelt et al. 2008). Musculoskeletal and nervous system disorders can also lead to lameness (Stavarakakis 2014).

Osteochondritic lesions, for example, occur with damage to pig joints and are most common at the elbows and at the hip joint. These joints have the highest net movement in pigs which could help explain why they have the highest rate of cartilage damage (Stavarakakis 2014).

### Conclusion

The domestication of swine has allowed for extensive research about their locomotor



abilities. Domesticated and wild swine have several modes of locomotion that include walking, trotting, galloping, and swimming (Abernethy 2016; Signoret et al. 1975). Studies have shown that locomotion is almost innate to newborn pigs as they are able to walk within the first few hours of life (Vanden Hole et al. 2017). Due to domestication, pigs are bred to produce more offspring than normal. This has led to increased intrauterine competition and sometimes smaller piglets, which can affect gait, strength, and survival (Vanden Hole et al. 2018b). The gait of farm animals is very important in the agricultural industry. Lameness can reduce the productivity and profitability of farms, which can negatively affect the world's food supply. Understanding the locomotion of swine can help identify lameness and prevent it before it becomes a chronic problem. Also, identifying and altering poor swine living conditions that cause lameness can lead to positive economic results (Stavrakakis 2014).

- [Home Range](#)
- [Homology](#)
- [Homoplasia](#)
- [Husbandry](#)
- [Locomotion](#)
- [Morphology](#)
- [Muscular System](#)
- [Natural Selection](#)
- [Phylogeny](#)
- [Quadrupedal](#)
- [Species](#)
- [Swine Cognition](#)
- [Swine Communication](#)
- [Swine Life History](#)
- [Swine Navigation](#)
- [Taxa](#)
- [Terrestrial](#)
- [Territoriality](#)
- [Ungulate](#)
- [Vertebrate Nervous System](#)
- [Zoo](#)
- [Zoology](#)

## Cross-References

- [Activity Budget](#)
- [Adaptation](#)
- [Adaptedness of Behavior](#)
- [Adaptive Radiation](#)
- [Artificial Selection](#)
- [Artiodactyl Cognition](#)
- [Artiodactyla Diet](#)
- [Artiodactyla Life History](#)
- [Artiodactyla Locomotion](#)
- [Artiodactyla Morphology](#)
- [Artiodactyla Navigation](#)
- [Basal Metabolic Rate \(BMR\)](#)
- [Captivity](#)
- [Common Ancestor](#)
- [Dispersal Ability](#)
- [Dispersal Patterns](#)
- [Diurnality](#)
- [Domestication](#)
- [Ecology](#)
- [Evolution](#)
- [Extinction in Learning](#)
- [Gait](#)

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## Swine Navigation

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## Synonyms

Suidae navigation

## Definition

Members of the suidae family, commonly known as swine, are known for their flattened snouts and stocky builds, along with their demonstration of a number of cognitive abilities. Navigation is the capacity to orient oneself and purposefully travel through their environment to a destination.

## Introduction

The ability to navigate one's own environment is the result of the combined input of both internal and external cues (Morelle et al. 2014). Spatial cognition builds on this capacity, allowing individuals to use navigational cues to successfully travel through their environment. The suidae order consists of such species as the common warthog (*Phacochoerus africanus*), the wild boar (*Sus scrofa*), river hogs (*Potamochoerus porcus*), and domestic pigs (*Sus scrofa domesticus*). In general, swine tend to live in highly variable environments, necessitating the ability to navigate effectively through and remember key elements of their environment (Elmore et al. 2012). Swine rely on spatial memory to relocate important regions in their home

range, such as nests, burrows, waterholes, and lucrative food patches (Mendl et al. 1997). A plurality of swine species are considered to be highly adaptive, taking full advantage of the resources available to them in their environment (Treydte et al. 2006).

## Warthogs

Home ranges of warthogs overlap with other sounders; however, home sites are exclusive to individual family groups (Somers et al. 1994). Home ranges of different sounders tend to overlap more when they have stronger social ties (Podgorski et al. 2014). The ranges of warthogs vary among individuals and between regions. The average home range in Zimbabwe is  $167.13 \pm 91.53$  ha, whereas in Kenya it has been measured at 130 ha. In South Africa, matriarchal sounders were measured to have home ranges of  $26 \pm 11.34$  ha and bachelor herd ranges, which overlapped significantly with those of females, were measured at  $22 \pm 4.06$  ha (Somers et al. 1994).

Despite the variety in home range size, warthogs across the board showed a tendency to spend disproportionate amounts of time in specific regions of their home ranges. Within these regions, there is often a waterhole that the sounder preferentially visits (Somers et al. 1994). In Namibia, water distribution was a central facet of warthog movement throughout their home ranges (Somers et al. 1994). There is also an observable association between food availability and warthog abundance. One study found that, even more specifically, warthogs had the highest levels of activity throughout a day in regions with highly palatable grasses, demonstrating a preference for specific food resources (Treydte et al. 2006).

Females tend to disperse less than their male counterparts, resulting in increased levels of relatedness of females in close proximity to one another. It may be adaptive for females to remain within their natal territory, as they are able to benefit from their increased knowledge of bountiful food sources and reliable waterways

(Podgorski et al. 2014). Proximity to resources is particularly crucial for females, particularly those that are new mothers. Matriarchal sounders travel an average of  $1690 \pm 347.5$  m/day to forage. In contrast, a new mother was observed traveling only 638 m over the course of 5 days following the birth of her offspring (Somers et al. 1994). This is likely because of the reliance of her babies on her for nutrients and protection. In contrast, males tend to have home ranges that are larger than their female counterparts, covering the ranges of multiple female sounders (Somers et al. 1994).

Females with juveniles are the most particular about their choice in burrows, as they provide important refuge from the elements and predators (White and Cameron 2009). Unlike many other species on the African Savannah, warthogs rely less on their speed and stamina, and more on the utility of burrows as effective means to protect against predators. The burrows they inhabit are commonly repurposed from other burrowing species, such as aardvarks (White and Cameron 2009). They are commonly observed returning reliably to the same burrow over many nights, suggesting that they may exhibit high levels of fidelity to particular locations (Somers et al. 1994). In a survey of burrows, researchers found that, on average, only 25.1–59.6% of burrows are occupied at a given time. This relatively low occupation level may be due, in part, to predation and the chances of detection. In areas with higher occupation rates, predators may increase their presence as their chances of success are higher than in areas with lower densities (White and Cameron 2009). This is likely a prominent element in the selection of home sites within warthogs' home ranges.

## Wild Boar

Spatial memory in wild boar is highly dependent on individual experiences. On average, they are actively moving around their environment or foraging 40–65% of their days (Morelle et al. 2014). Their spatial distribution is strongly related to the resources available within an individual's habitat.

The space used by wild boars has a tendency to decrease as the available resources increase (Keuling et al. 2007). Conversely, when high population density is coupled with low resource availability, the distance traveled per day greatly increases (Morelle et al. 2014). These changes in resources are associated with seasonal changes, as different weather conditions affect the availability of resources. In the early summer, wild boars tend to increase their diurnal activity, often feeding in large open fields of cereals, as compared to forests and other habitats (Keuling et al. 2008).

Wild boars exhibit unique distribution patterns as functions of age and sex. Yearlings and adolescents tended to have larger shifts in their annual home ranges than adults and family groups. Yearlings had an average home range of 1,185 ha, ranging from 2,354 ha in the spring to 1,766 ha in the summer. This compares to family groups who had an average range of 771 ha, expanding to 791 ha in the spring and shrinking to 461 ha in the summer (Keuling et al. 2007). Females tended to show high fidelity to their native home ranges and exhibiting less seasonal variation in their annual ranges (Morelle et al. 2014).

### Wild Pigs

There are a number of attributes that contribute to the range and movement patterns of pigs, including age, sex, climate, and weather (Kay et al. 2017). Adult males have been observed to inhabit the largest home ranges when compared to females and juveniles (Kay et al. 2017). Wild pigs have immense home ranges, reaching up to 10,343 m<sup>2</sup>, with comparably smaller central regions, up to 964 m<sup>2</sup>, that they inhabit most often. A study found that they moved an average of 4,340 m in a 12-h period (Thomas et al. 2013). Although there was no significant difference, there was a tendency for the pigs to travel more at night (4,511 m) than during the daytime (4,169 m) (Thomas et al. 2013).

Individuals that lived near an abundant resource moved less throughout the day than their counterparts that did not have the same

access to food, suggesting that the main motivation for traveling during the day was motivated by searching for food in their environment (Kay et al. 2017). There is also a noticeable shift in home ranges during the summer months toward agricultural areas, which provide ample sources of food. Moreover, it is believed that wild pigs in drier climates move more than those in other climates because of differences in water resources; those in more humid climates have to cover less ground to find water sources (Kay et al. 2017).

### Red River Hogs

While red river hogs are found in a variety of habitats throughout their species distribution, they are limited by certain necessities. They require thick vegetation, water, and loose soil. They are often observed foraging along roadways, where there is ample vegetation on which to feed (Leslie and Huffman 2015). There have been reports of red river hogs traversing great distances as a result of speckled distribution of fruits within their ranges (Leslie and Huffman 2015). Sounders of red river hogs travel in single file lines, with their heads down and seem to rely most heavily upon their sense of smell for navigating their environment. They are easily approached from downwind, supporting the notion that they attend almost solely to olfactory cues ahead of them (Leslie and Huffman 2015).

### Peccaries and Wild Hogs

While the two species inhabit different niches in their environment, demonstrating different preferences for both habitat and food source, the distribution of peccaries is highly dependent on the movements of wild hogs (Isle and Hellgren 1995). A predictable pattern has been observed that when a herd of wild hogs moved into an area inhabited by peccaries, the peccaries would move to another area, avoiding overlap with the wild hogs. Peccaries are known to be highly territorial; this has been suggested as one explanation for the

distributions of these two species in the same region (Isle and Hellgren 1995).

## Optimal Foraging Theory

The optimal foraging theory suggests that animals should maximize their energy input (Gustafsson et al. 1999). Several theoretical models focus on specific conditions, and the behaviors that would maximize the effectiveness of an animal's foraging. The marginal value theorem (Charnov 1976) suggests that, as the cost of moving between food sources increases, the amount of time spent at specific patches should also increase (Gustafsson et al. 1999). In other words, the energy expended in moving between food patches should be made up for and exceeded by the amount of energy gained from foraging at a patch.

## Sensory Cues

Pigs have demonstrated their ability to forage and navigate through their environment using a variety of external and internal cues. It was long believed that pigs were ineffectual at using visual cues when foraging. However, more recent studies have contradicted these claims by showing their ability to use both visual and olfactory cues, either individually or in concert with one another (Croney et al. 2003). Pigs have also demonstrated the ability to associate outcomes with specific visual and olfactory cues in their environment, lending to the idea that pigs have the ability to use these cues when navigating their environment (Croney et al. 2003).

Despite their ability to make use of visual cues when foraging, pigs have historically performed better on tasks when relying on olfactory cues rather than visual ones. Pigs are known for their impressive senses of smell, which may help compensate for their relatively poor sense of sight (Croney et al. 2003). Wild boars are highly dependent on their sense of smell, relying on olfaction in various aspects of their lives, including antipredatory vigilance, socialization with conspecifics, foraging, and general

navigation throughout their territory. It is believed that moist air further enhances these abilities, which is further supported by their tendencies to be more active during periods of high humidity (Morelle et al. 2014).

Wild boars are able to use the information garnered from scents in concert with landmark cues to navigate their environments. They tend to remain in locations that are familiar to them, relying on previously established memories of specific landmarks (Cervený et al. 2016). This may allow them to formulate mental images or maps of their environment, which they use to relocate desirable locations for resting, along with places bountiful in food and water (Mendl et al. 1997; Morelle et al. 2014). Wild boars and other swine that normally frequent familiar environments may use a navigational strategy known as dead reckoning. This strategy is founded on certain assumptions, such as the animal's ability to remember various locations along with the distances and directions between such locations (Morelle et al. 2014).

There are a number of external and internal cues upon which swine may rely in their use of dead reckoning. Externally, they may rely on proximate cues, such as landmarks, or global cues, such as the stars, to orient themselves within their environment (Morelle et al. 2014). They may also use magnetic alignment (MA), which is the tendency for an individual to align themselves along geomagnetic lines. This tendency is often most pronounced during periods of calm, such as resting and foraging; species with pronounced magneto-receptor capabilities will orient themselves in predictable directions during these times (Cervený et al. 2016). MA allows for navigation that is free from changes in the environment, making it particularly useful for long-distance navigation or over the changing seasons (Cervený et al. 2016).

Both wild boars and warthogs have well-documented MA. Wild boars have a strong North-South preference aligning themselves along  $20^\circ/200^\circ \pm 3^\circ$  during bouts of foraging, showing a similar preference for the orientation of their nests. Warthogs demonstrate an almost identical preference of  $19^\circ/119^\circ$  while foraging



(Cervený et al. 2016). In both species, their MA tendency was stronger in juveniles and among larger groups of individuals; however, only in wild boars was it also more evident in males (Cervený et al. 2016).

## Disturbance Effects

Spatial memory in various species of swine is subject to interference from both internal and external forces (Mendl et al. 1997). Wild pigs are subject to a variety of meteorological disturbances that impact them in predictable ways. When exposed to extreme heat or extreme cold, wild pig movement decreased significantly (Kay et al. 2017). Movement was also impacted by air pressure, with the optimal range falling between 97,500 and 101,250 pa (Kay et al. 2017). There appears to be a relationship between air pressure and overall home range size; however, this may also be attributable to seasonal variations in home range coupled with reliable pressure changes across the seasons (Kay et al. 2017).

There have also been a number of disturbance effects that have been observed in the natural environments of wild boar and wild pigs. Notably, an investigation into the impact that hunting season has on the distribution of wild boar yielded a number of notable results (Keuling et al. 2008). Researchers found that following a single hunt, the distance at which an individual ran away in response to some oncoming stimulus – also known as their flight distance – for individuals in the area were significantly higher (Keuling et al. 2008). Additionally, the home ranges of individuals changed in response to the type of hunt they had experienced. Home ranges were larger for those that experienced a mixture of hunting methods, whereas those that lived in densely vegetated regions and experienced only a single hunt had far smaller ranges than would have been expected of individuals that were not impacted by hunting (Keuling et al. 2008).

A number of studies with domestic pigs in controlled arenas have provided additional insight into a variety of disturbances and their effects on domestic pigs' spatial memory. One of the most

overt instances of interference is the introduction of a novel environment. During inter-trial periods, when pigs were allowed to explore a novel environment, they performed significantly worse on the relocation trial than those that were not exposed to the novelty (Laughlin et al. 1999). Similar to exposure to a novel environment, the introduction of unfamiliar conspecifics has a comparable effect. The inverse – complete social isolation – also had detrimental effects on performance in spatial memory tasks (Laughlin et al. 1999). These patterns may be attributable to the increased stress levels associated with isolation or novel exposure; stress appears to have an adverse impact on spatial memory capabilities in pigs (Croney et al. 2003).

The impact of disturbances on pigs' performance in different spatial tasks appears to be dependent on the timing and ordering of the disturbances. When introduced sequentially during earlier trials, disturbances were highly impactful; however, over time, the introduction of novel stimuli had diminishing effects on their performance, suggesting that individuals were able to rapidly habituate to the disturbances (Laughlin et al. 1999). It may also be the case that longer intertrial periods could have adverse effects on pigs' performance levels. It has been hypothesized that a prolonged time delay may function as a reset on a pig's memory, rendering the relocation trial comparable to a novel search task (Mendl et al. 1997).

## Spatial Memory

Various swine species have demonstrated a reliance on memory, rather than proximate cues from the food reward during such spatial memory tasks (Morelle et al. 2014). Pigs systematically avoided locations they had previously searched. Over subsequent trials, they found food in fewer attempts than would be expected by chance (Mendl et al. 1997). Not only are pigs able to use their spatial memory to systematically search for food, but they are able to effectively relocate multiple sources of food that they had previously found (Held et al. 2000, 2010; Mendl et al. 1997).

Even neonatal pigs have demonstrated an ability to locate food at progressively faster rates during a series of acquisition and reversal tests (Elmore et al. 2012). When examining the overall distance traveled, similar to the amount of time required to relocate a food source, so too did distance decrease over repeated exposure (Elmore et al. 2012).

Win-stay and win-shift are terms used to describe two contrasting navigational strategies. They are differentiated by how individuals behave on subsequent searching tasks. “Win” refers to their acquisition of food and “stay” and “shift” refer to whether they continue returning to the same location or if they change locations. Thus, win-stay is when the individual returns to the same location on subsequent trials, whereas win-shift is when the individual changes locations. Pigs demonstrated an aptitude for win-stay tasks, despite them fully depleting the food source on previous trials (Mendl et al. 1997). This is likely due to their exposure to a pattern of depleted food sources being replenished while in captivity.

Despite this seeming proclivity of pigs in lab settings to adopt a win-stay navigational strategy, when food sources are not immediately replenished, they were able to adapt to the new circumstances. The most common method was to investigate the location immediately adjacent to the previously baited location (Mendl et al. 1997). This “moving one over” strategy, however, accounted for only 41% of the movements from the initial location. This suggests that, while they used this tactic in a plurality of instances, they were not adhering to just a simple navigational rule in an effort to avoid repeated visits to a given location (Mendl et al. 1997).

## Foraging Motivation

Pigs spend the majority of their waking hours foraging in their environment. Behaviors associated with the foraging process, such as rooting and traversing their environment, appear to be closely linked to their satiety. Stereotypical foraging behaviors have been observed in

higher prevalence in food-restricted individuals than those fed normally (Day et al. 1995). On the other end of the spectrum, however, were individuals that were presented food *ad libitum* and without the need for associated foraging behaviors. These individuals, despite their satiety, continued to behave in manners comparable to food-restricted individuals, suggesting that the end goal of foraging is not simply acquiring food (Moser et al. 2019).

Researchers have suggested that there is a close relationship between foraging and exploratory behaviors. Not only have pigs demonstrated increased foraging drives in regions with specific substrates, but they also exhibited a preference for novel objects, visiting regions where such objects are presented more frequently than the control areas (Moser et al. 2019). Another study found that patterns of exploration tend to differ among individuals, with some preferring to explore on the small scale and increasing their range, while others will explore the entire arena before focusing their energies on particular regions (Morelle et al. 2014).

## Domestication Effects

Swine species that are either domesticated or live in captivity show an aptitude for navigation and enhanced spatial memory, albeit in different capacities than their wild counterparts (Mendl et al. 1997). There is an argument that the navigational abilities of some domestic species have deteriorated over the generations, as they face less environmental pressures to maintain their adaptive capacities. They lack the need to avoid predation, starvation, and dehydration, diminishing their need to navigate over increased distances through their environment (Gustafsson et al. 1999).

In a series of studies, there were no perceivable differences detected between domestic pigs and their wild counterparts; both demonstrated the tendency to decrease the time spent at gradually diminishing food sources. The only perceivable difference was that the domestic pig spent longer periods of time at each individual

food source than the feral pigs (Gustafsson et al. 1999). This was likely due to the domestic pig's experience with food being presented in only one location and consistently replenished when depleted. They were able to employ a more energy-efficient foraging pattern by fully depleting a food source, as compared to the feral pig that changed locations more frequently so as to avoid depletion of specific patches (Gustafsson et al. 1999).

## Social Foraging

Many swine species live in complex social groups with distinct hierarchies. This complexity is evident when foraging either in pairs or groups (Held et al. 2000). Each individual's position in the social hierarchy should be reflected in how they behave in the company of other group members of different ranking. Dominant individuals, when in the company of those more subordinate, are expected to exhibit a certain set of behaviors, in the same way that subordinate individuals should perform actions that subvert the more exploitative behaviors of their dominant counterpart (Held et al. 2000). These predictable behavior patterns are evident in both the natural- and lab-based settings.

As mentioned earlier, Optimal Foraging Theory dictates that individuals should maximize their energy input. This can be accomplished by decreasing the amount of energy they exert while locating a food source. One solution is a common tactic seen in dominant pigs, known as scrounging (Held et al. 2002). Producers are individuals that locate food sources, expending their own energy in doing so. Scroungers, on the other hand, exploit the work of the producers, by following them to a food source and displacing the producer (Held et al. 2000). Generally, dominant pigs are larger and better able to displace subordinate producers, thus monopolizing the food source. In some cases, however, there are not major physiological differences between dominant and subordinate individuals rendering the displacement ability of the dominant individuals negligible. In this case, group members will often

rotate between the roles of producer and scrounger (Held et al. 2002).

In order to better study this phenomenon, the informed forager paradigm was developed to systematically alter the social conditions under which pigs foraged (Held et al. 2000). In this paradigm, subordinate pigs were given information about the location of a food source. They were then paired with a dominant partner who was naïve to the location of food in the arena. By releasing the two into the foraging arena together, researchers were able to observe the manifestation of scrounging behaviors and the behaviors exhibited by the informed individual to this exploitation (Held et al. 2000). They found that both pigs exhibited predictable behaviors in line with their roles as producers or scroungers (Held et al. 2002).

When alone, dominant pigs behaved like producers, searching for their own food. However, when they were presented with an alternative, they changed their behaviors to follow their subordinate partner to a food source (Held et al. 2010). Six out of the eight dominant individuals tested in this manner displaced their subordinate partner when they arrived at a food source (Held et al. 2000). The most common response to this exploitative behavior was for the subordinate pig to increase their speed. This nondeceptive behavioral change would allow them to better capitalize on their advantage – of knowing where the food was located – by increasing the distance between them and their partner, thus increasing the time before displacement (Held et al. 2010).

In a follow-up study, researchers introduced a third type of foraging partner. This pig was dominant to the informed individual but was not competing for the food source, as this new partner learned that food was always located in a location separate from the locations learned by the subordinate, informed pig. When paired together, the behavior patterns observed previously, in response to an exploitative partner, were not present (Held et al. 2010). There was additional variation in the behavioral responses of subordinate individuals that were associated with the current behaviors of the dominant pigs. Subordinates showed a tendency to move away from the baited locations when there was a high likelihood of

interference by the dominant individual: when they were being followed closely, when they were being watched, and when the dominant was closer to the food source than the subordinate (Held et al. 2002). Conversely, when the dominant individual was moving away from the food source, out of sight of the subordinate, or the subordinate was closer to the food source than the dominant, the subordinate pig would often approach the baited location at a quick pace (Held et al. 2002).

There is a benefit for producers to maximize the distance between themselves and potential scroungers, and a converse benefit for scroungers to maintain minimal distances with numerous producers (Held et al. 2002). In the wild, it is common to find producers foraging on the periphery of the group, while the more dominant scroungers occupy the center of the group (Held et al. 2002). This pattern reflects the optimal positioning of different members of the group based on their foraging strategies.

## Conclusion

Across the various species of swine, there is a consensus that they have impressive navigation capabilities that are put to use in their individual environments. The ability to navigate effectively is necessitated by resource availability. Food, water, and shelter are crucial to an individual's survival, and a majority of their waking time is spent searching for these resources. While they are able to employ their visual systems in navigation, they commonly defer to their sense of smell, demonstrating heightened abilities to discriminate stimuli in their environment via olfaction. Warthogs and wild boars have demonstrated a proclivity for magnetic alignment, which may be used in concert with landmark orientation, allowing them to employ dead reckoning to navigate their environment. The sociality of swine species manifests in a variety of predictable behaviors patterns associated with each individual's position in the group hierarchy and the subsequent role they perform while foraging. There is still much to learn about the specific navigational

strategies employed by different swine species and how they may manifest in navigation through natural habitats.

## Cross-References

- [Artiodactyla Locomotion](#)
- [Artiodactyla Navigation](#)
- [Swine Cognition](#)
- [Swine Life History](#)
- [Swine Locomotion](#)

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## Symbiont

- [Symbiotic Relationship](#)

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## Symbiosis

- [Symbiotic Relationship](#)

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## Symbiotic Relationship

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## Synonyms

[Evolved interaction](#); [Species cooperation](#);  
[Symbiont](#); [Symbiosis](#)

## Introduction

Symbiotic relationship or symbiosis is a kind of close association between two organisms belonging to same or different species in nature which might benefit one or both organisms (Moran 2006). The word symbiosis is derived from Greek words sym meaning together and bios meaning life, translating into “different lives working together.” Symbiotic relationships may be obligate where both organisms cannot live independent of each other, for example, ants and the acacia plant, or facultative where the association is not compulsory for both to survive, for example, honeybees and flowers. Each organism in a symbiotic relationship is called symbiont. When one symbiont lives on the body surface of the other, it is called ectosymbiosis, for example, head lice on human scalp. In endosymbiosis one organism lives inside the body of the other, for example, nitrogen-fixing bacteria living inside the root nodules of leguminous plants (Sherwood et al. 2013).

Symbiotic relationships may be one of the three types: mutualistic, commensalistic, and parasitic. In a mutualistic relationship, both interacting organisms are benefitted from each other, for example, clownfish and sea anemone, lichens (algae or cyanobacteria and fungi), mycorrhiza (higher plants and fungi), etc. In a commensalistic relationship, one organism is benefitted off from the other, while the other one is neither harmed nor benefitted,



for example, cattle egrets and livestock, remora fish and sharks, orchids growing on trees, etc. In a parasitic relationship, one organism lives off on other organisms benefiting from it while harming the host or even causing death of the host organisms, for example, viruses living in their hosts, fleas or ticks that live on dogs and cats, etc.

A well-known example of endosymbiotic relationship is between the termite and microorganisms living in the digestive tract of the termite. The microorganisms like bacteria, archaea, and protozoans digest the complex sugar like cellulose in wood into simpler short-chain fatty acids like acetic acid that they can use for food. In a similar manner, human body is inhabited by numerous microorganisms which play key roles in different aspects of human health (Cani 2018). The Human Microbiome Project was aimed at sequencing the genome of the human microbiota, inhabiting the skin, mouth, nose, digestive tract, and vagina (Turnbaugh et al. 2007; Duffy et al. 2015). It is estimated that the number of bacterial cells is ten times the number of cells present in human body (Bull and Plummer 2014).

## Mutualism

Mutualistic relationships can be categorized into three classes:

1. **Resource-resource relationship:** In this kind of association, one resource is given in exchange for other resource. Classical example of such relationship is between nitrogen-fixing bacteria like rhizobium and leguminous plants like pulses and pea. Plants cannot use free atmospheric nitrogen; therefore, bacteria fix atmospheric nitrogen into nitrite and nitrate which can be easily absorbed by plants, and in return bacteria gets shelter and nutrients from root nodules of the plant.
2. **Service-resource relationship:** In this relationship, one organism pays the other in the form of resource in exchange for its services. Zoophily, i.e., pollination with the help of insects, is a classic example of service-resource mutualistic relationship where insects like bees and wasps pollinate the flowers and in return rewarded with nectar. The honey bee collects nectar in honey sac for its deposition in colonies for later use, and in the process pollens stick to their legs and body. When the same bee lands on another flower to collect nectar, the pollens are transferred to that flower resulting in pollination. The relationship between ants and aphids also comes under this kind of mutualistic relationship. Aphids are small plant sap-sucking insects which produce honeydew as a by-product which they trade in return of protection from predators like ladybug; ants also protect aphids from fungal diseases. Another example of such association can be seen between oxpecker birds and rhinoceros or impala. Oxpecker bird gains a safe habitat on rhinoceros's back and in return eats ectoparasites and insects that would harm rhinoceros providing cleaning services (Losey 1972; Poulin and Grutter 1996). Plants offer sweet fleshy berries to the birds as resource; the seeds of the fruit are then dispersed to different places where the birds fly leading to their vegetation at new places.
3. **Service-service relationship:** Both organisms in this kind of association provide service to each other. Classical example of such association is between clownfish (*Amphiprion clarkii*) and sea anemone (*Stichodactyla haddoni*). Sea anemone protects the clownfish against predators using stinging nematocyst which is ineffective against clownfish due to the presence of thick mucus layer. In return clownfish protects the anemone against butterflyfish which feeds upon the anemone. Another example of such association is between acacia and ants (*Pseudomyrmex ferruginea*) which live on the bullhorn acacia (*Vachellia cornigera*). The ants provide protection to the plant from grazing animals, and in return to this service, plants provide food and shelter to the ants.

## Commensalism

The word commensalism means “eating at the same table” or “sharing a table” and is derived

from Latin words *com* meaning together and *mensa* meaning table/meal. As described above, in commensalism, one organism is benefitted and is called the commensal which is generally smaller, while the host which is generally bigger is neither harmed nor benefitted. The commensal may gain protection, nutrition, shelter, or transportation (Hulme-Beaman et al. 2016).

Most common example of commensalism is seen between remora fish (family Echeneidae)/pilot fish and sharks or other big fishes. Remora fish attaches itself to the big fishes with the help of a sucking structure present on their heads and gains protection, travels to great distance without spending its energy to swim, as well as feeds on the leftover food from shark. Another example of commensalism is between bird species such as the great egret (*Ardea alba*) and grazing animals where birds feed on small insects that are turned up from soil and grass by grazing mammals. Various biting lice, fleas, and louse flies are commensals in that they feed harmlessly on the feathers of birds and on sloughed-off flakes of skin from mammals.

Another example of commensalism is that of the pseudoscorpion which are very small scorpions lacking any stings and larger flies. Pseudoscorpions stick to the legs of the flies and take a ride from one place to another without affecting the fly. Once the scorpion reaches its destination, it detaches from the fly and the association is ended. In a similar manner, large marine animals are often surrounded by a group of small fishes or other aquatic animals, for example, barnacles are associated with whales and other small fishes feed on the leftover food from sharks. In the same way, small bait fishes can often be seen in large schools under the large fins of the manta ray for protection from birds which otherwise dive and feed on them. At the same time, manta ray hardly notices the presence of bait fishes under it.

Another interesting example of commensalism can be seen in the bur (seed or dry fruit having hooks or teeth) of burdock plant. Often when passing through fields, several seeds having small spikes get attached to the lower sides of our cloths and travel from one place to another

getting dispersed to different places and start their vegetation at new habitats.

## Parasitism

Parasitism describes a relationship between two organisms where one benefits while the other is harmed. The parasite is the organism that benefits from the relationship, while the host is harmed by the relationship. Parasites can be plants, animals, viruses, or bacteria (Poulin 2011). Parasites are considered ecologically important as they can shape community structure through their effects on trophic interactions, food webs, competition, biodiversity, and even keystone species (Preston and Johnson 2010). Parasites may be ectoparasites living on the body surface of the host like ticks, fleas, leeches, and lice or endoparasites living inside the host body like bacteria, viruses, flukes, and parasitic protozoans. The word parasite is derived from Greek word *parasitos* meaning “one who eats at the table of another.” Parasites show variety of adaptations according to their hosts. Parasites can alter the physiology and behavior of the host, resulting in changes in growth rates, density, survival rates, life span, reproductive fitness, and competitiveness in order to maximize their growth, reproduction, and transmission (Thomas et al. 2011; Poulin 2010; Lefèvre and Thomas 2008).

Plant parasites are generally divided into two types, necrotrophic and biotrophic parasites. Necrotrophic parasites eat a part of host tissue until it dies, for example, *Botrytis cinerea* pathogen causing gray mold in tomato plant, while biotrophic parasites does not kill the host as it cannot survive without the living host, for example, *Blumeria (Erysiphe) graminis* causing powdery mildew in grasses or cereals. Epiphytes are the plant parasites that grow on the surface of other plants and obtain moisture and nutrients. Most common epiphyte is orchids (Westwood et al. 2010).

On the ability to complete their life cycle in one or two hosts, animal parasites are generally divided into monogenic parasites and digenetic parasites. Monogenetic parasites complete their life cycle in only one individual host, while

digenetic parasites need more than one host to complete their life cycle. *Plasmodium vivax*, causative agent of malaria, is a digenetic parasite as it requires both mosquito and human to complete its life cycle. *Entamoeba histolytica* is a monogenetic parasite as its life cycle is completed on one host only, human (Lefèvre and Thomas 2008).

In nature, sometimes parasites are found whose host is the parasite on other organism; such parasites are called epiparasites or hyperparasites or secondary parasites. Hyperparasitism is generally seen in Hymenoptera (wasps), Diptera (flies), and Coleoptera (beetles). Most common example of hyperparasitism can be seen in white butterfly (*Pieris rapae*) whose larvae are parasitized by the larvae of the wasps *Cotesia glomerata* and *C. rubecula*, which in turn is parasitized by the wasp *Lysibia nana* (Poelman et al. 2012; Yong 2012).

Some parasites require an organism other than their definitive host to transfer them from one host to another; such organism is called vector or carrier. Mosquitos (*Aedes*, *Culex*, and *Anopheles*), sandflies, ticks, fleas, lice, and tsetse flies act as vector for numerous disease-causing parasites which cause grave diseases like malaria, chikungunya, dengue fever, lyme disease, sleeping sickness, etc. (Garcia 1999; Esch and Petersen 2013). Vector-borne diseases account for more than 17% of all infectious diseases, causing more than 7 lakh deaths annually.

## Obligate Parasitism

The parasites which are completely dependent on their host for survival are called obligate parasites. Such parasites cannot thrive in absence of their host and soon dies. These parasites generally do not kill their host as a part of their survival strategy. One example of obligate parasitism is head lice in human, as they cannot survive once removed from scalp.

## Facultative Parasitism

The parasites that do not completely rely on host for the completion of their life cycle are called

facultative parasites. For example, nematode *Strongyloides stercoralis* infects human and cause strongyloidiasis disease, but it can also be found free-living.

## Brood Parasitism

It is most commonly seen in species of cowbirds and cuckoos which lay their eggs in the nest of other birds like reed warbler or Eastern phoebe and leave them to be raised by the host birds without investing any resources in it. Sometimes these birds also remove some of the eggs of the host bird.

## Cross-References

- [Adaptation](#)
- [Carrier](#)
- [Evolution](#)
- [Fungi](#)
- [Reproductive Fitness](#)

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## Symbolic Distance

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## Synonyms

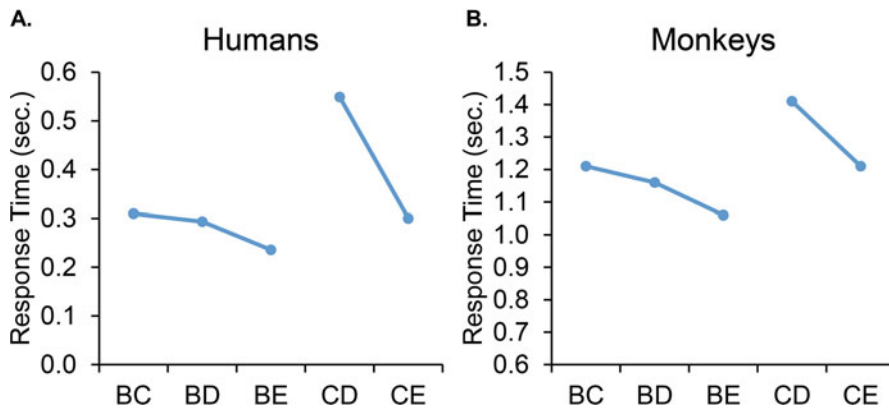
Distance effect

## Definition

The time needed to compare symbols varies as a function of their distance.

The symbolic distance effect describes the fact that the “time needed to compare two symbols varies inversely with the distance between their referents on the judged dimension” (Moyer and Bayer 1976, p. 229). The effect was originally observed with psychophysical stimuli. For example, Johnson (1939) had participants throw one of two switches to indicate the longer of two lines. The lines differed in length by 1, 2, 3, 4, 6, 8, or 10 mm. He found that response time was an inverse function of the length difference between the two lines. That is, participants were faster to indicate the longer of two lines when their length difference was 8 mm compared to when it was 2 mm. Moyer and Landauer (1967) were the first to observe the effect with stimuli whose order was represented symbolically. They presented participants with pairs of numerals, drawn from the numerals 1 to 9, and instructed them to indicate the larger of the two. They found that as the numerical distance between the two numerals increased participants’ reaction time decreased. For example, participants’ reaction time was longer when the two numerals being compared were separated by a distance of one (e.g., 3 vs. 4), slightly shorter when the numerals were separated by a distance of two (e.g., 6 vs. 8), and so on, with reaction time the shortest when numerals were separated by the maximum distance of eight (i.e., 1 vs. 9). The effect has since been observed with a range of well-learned sequences, such as the alphabet (Hamilton and Sanford 1978; Jou and Aldridge 1999; Lovelace and Snodgrass 1971; Van Opstal et al. 2008), months of the year (Gevers et al. 2003), and days of the week (Gevers et al. 2004).

In nonhuman animals, the symbolic distance effect has primarily been investigated using the simultaneous chaining paradigm (Scarf and Colombo 2008; Terrace et al. 1977). Briefly, the paradigm involves presenting subjects with a list consisting of  $n$  number of simultaneously displayed items. The subject’s task is to respond to each item of the sequence in a prescribed order learnt during training. Similar to the studies of



**Symbolic Distance, Fig. 1** Symbolic distance effect for pairs beginning with item B and pairs beginning with item C for humans and monkeys

serial learning in humans, following training, each pair of items that can be derived from the list is presented to subjects. Much like the months of the year or the days of the week, the more distant two items are on a list, the more discriminable they should be in the sense that it should be easier to determine which of the two comes first. For example, on a five-item list ( $A > B > C > D > E$ ), the latency to respond to stimulus A should decrease across pairs AB, AC, AD, and AE; the latency to respond to stimulus B should decrease across pairs BC, BD, and BE; and the latency to stimulus C should decrease across pairs CD and CE. In reality, however, because item A occupies the first position of the list, and because responses to it are typically very quick, it is very hard to observe a symbolic distance effect for pairs with A as the first item. Taking this into account, as shown in Fig. 1, both humans and capuchin monkeys display the symbolic distance effect on the simultaneous chaining paradigm (Colombo and Frost 2001; D'Amato and Colombo 1990). Beyond these species, the effect is observed in a wide variety of animals including rhesus monkeys (Gazes et al. 2012), ring-tailed lemurs (MacLean et al. 2008), pigeons (Scarf et al. 2011), and corvids (Bond et al. 2010).

With respect to theories of serial learning, the symbolic distance effect accords well with the ordinal position hypothesis but not the remote association hypothesis (Potts 1972, 1974).

According to the remote association hypothesis, reaction time should increase as the distance between items increases. That is, because the associative strength between two items decreases with distance, reaction time is expected to increase as the distance between the members of the pair increases (Moyer and Bayer 1976; Terrace 2005). In contrast, the ordinal position hypothesis predicts that reaction time will decrease as a result of participants comparing the ordinal positions of the paired items (Jou and Aldridge 1999; Moyer and Bayer 1976). That is, when a pair is presented, a participant first identifies the ordinal positions of each item and then compares them in order to determine the earlier or later member of the pair.

## Summary

The symbolic distance effect has been observed in both humans and animals using a range of stimuli, from months of the year in humans (Gevers et al. 2003) to numerical stimuli in pigeons (Scarf et al. 2011). The fact the symbolic distance effect is observed across species suggests that humans and animals represent serial stimuli in a comparable manner.

## Cross-References

► [Serial List Learning](#)



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## Synchronized Reproduction

### ► Reproductive Synchrony

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## Synonyms for Cognition: Cognitive Abilities

### ► Platyrrhine Cognition

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## Synonyms for Platyrrhines: Neotropical Monkeys

### ► Platyrrhine Cognition

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## Syntax

### ► Cognition

## Synteny

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### Definition

From the Greek *συν* (*syn*), “together with,” and *ταινία* (*tainia*), “ribbon.” Physical linkage of two or more genetic loci on the same DNA molecule. Shared or conserved synteny refers to ancestral syntenic loci that have maintained their physical linkage in two or more descendant lineages (Irimia et al. 2013).

### Introduction

Any given genomic feature or locus (such as a gene, a promoter, an enhancer, etc.) can be located either in the same or in a different DNA molecule/ chromosome than another genomic element; that is, the two loci can either be syntenic or nonsyntenic. Certain syntenic associations are of particular biological relevance because of their functional consequences (as in syntenic genes that belong to the same operon or in linked genes sharing a common set of *cis*-regulatory elements) and can therefore be subjected to the action of natural selection. In many other situations, syntenic linkages between loci have no obvious phenotypic impact, in which case synteny can evolve neutrally.

### Types of Synteny

Synteny can be considered at two different genomic scales (Irimia et al. 2013):

- Microsynteny: fine-scale syntenic associations between immediately adjacent loci (i.e., gene

order), with no (or very few) intervening genes separating these loci.

- Macrosynteny: syntenic linkage at the chromosomal (i.e., “macroscopic”) level, regardless of the distance and number of intervening genes interspersed between the syntenic loci.

### Synteny Evolution and Its Relationship with Gene Regulation

During evolution, ancestral syntenic associations can be disrupted by chromosomal rearrangement mutations. Accordingly, different patterns of synteny conservation can be found across different groups of eukaryotes, depending on the frequencies of inter- versus intrachromosomal rearrangements in each lineage. Thus, a high prevalence of inversions (intrachromosomal) leads to degradation of large-scale microsynteny while keeping macrosyntenic associations, whereas high incidence of translocations (interchromosomal) degrades both microsynteny and macrosynteny. Regardless the case, for most genes, their order along chromosomes has few or no implications for organismal function and is generally thought to be largely random; as a result, the degree of synteny conservation between two lineages broadly correlates with the evolutionary rates and divergence times of these lineages. However, there are important exceptions to this general trend, and some pairs of genes can maintain their microsyntenic linkage over hundreds of millions of years of evolution (Engström et al. 2007; Kikuta et al. 2007; Simakov et al. 2013; Irimia et al. 2012). These associations indicate functional implications for gene order and appear to largely reflect *cis*-regulatory constraints preventing the disruption of microsynteny. These constraints are related to either (i) multiple genes sharing transcriptional regulatory elements, or (ii) genes with long-range *cis*-regulatory elements that can be located at very long distances, even intermingled with the introns of unrelated neighboring genes (Irimia et al. 2012). While (i) can be found throughout

eukaryotes, involving pairs of genes that are tightly coregulated by a shared bidirectional promoter, in the case of (ii), long-range regulatory elements have only been found in animals, where they regulate the complex expression patterns of genes involved in animal embryogenesis (Irimia et al. 2013).

## Conservation of Microsynteny and Allelic Association Studies

The presence of transcriptional regulatory elements that can be located far away from their target genes, as it is often the case in genes with important functions during animal development, can lead to misidentification of the causal genes in allelic association studies (such as Genome-Wide Association Studies (GWAS)). The identification of blocks of conserved microsynteny overlapping with the associated allele can help defining the genomic region where the gene responsible for the observed phenotype could be located, especially in cases where the causative gene is not the closest one to the sequence variant (Smemo et al. 2014).

## Cross-References

- Alleles
- Allelic Association
- Chromosomes
- DNA
- Embryo
- Eukaryotes
- Evolution
- Genes
- Intron
- Locus
- Mutations
- Natural Selection
- Phenotype
- Transcription
- Translocation

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## Syntocinon®

- Oxytocin

## T.H. Huxley on Human and Ape Brains

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### Definition

Thomas Henry Huxley (1825–1895) was Charles Darwin's most enthusiastic bulldog-advocate, a renowned Professor of Natural History in his own right, and the author of important works on evolution such as *Evidence as to Man's Place in Nature* (1863). One of his most significant published outputs was the section entitled "Note on the Resemblances and Differences in the Structure and the Development of the Brain in Man and Apes" that was included in the second edition of Darwin's *The Descent of Man and Selection in Relation to Sex*, and which will be a main focus of this entry.

### T.H. Huxley

Huxley was initially a medical practitioner before studying botany, eventually becoming Professor of Natural History at the Royal School of Mines. Important to his intellectual development was a period acting as the ship's surgeon on the HMS *Rattlesnake*, during which he worked (in part) on improving the animal classification system and on

embryology. Later he founded the scientific approach to craniology and developed a new system of bird classification (Abbott 1983, pp. 70–71).

Huxley has been accurately categorized as more of a comparative anatomist, a zoologist, and a physical anthropologist, rather than a conventional naturalist (Freeman 1978, p. 170), and also as a bold personality complement to Darwin's meticulous study. Darwin described Huxley as follows: "He has been a most kind friend to me and would always take any trouble for me. He has been the mainstay in England of the principle of the gradual evolution of organic beings. Much splendid work ... he has done in Zoology" (Barlow 2005 [1958], p. 88). As an example, Huxley provided an original evolutionary genealogy of the horse (from *Eohippus* to *Equus*) that quickly became a "paradigm fossil proof for evolution" (Desmond 2002, p. 551; Huxley 1877), and he also provided an influential analysis of evolutionary ethics (Huxley 1893).

Huxley became well-known in the UK in relation to the debates around the publication of Darwin's *The Origin of Species* in 1859 and thereafter as a staunch defender of the idea of the evolution of animal and plant life by means of selection mechanisms. His famous response to first learning of the idea of natural selection was: "How extremely stupid of me not to have thought of that!" (Freeman 1978, p. 170). Huxley had corresponded with Darwin from the early 1850s onwards on various natural history topics and first visited him at Down House in 1856.

Huxley quickly published very positive reviews of *The Origin of Species* in *The Times* and in *Macmillan's Magazine* and lectured on it in 1859 and 1860, counting as one of Darwin's most loyal supporters (Nocks 2008, pp. 60–61). Although Huxley initially expressed some doubts about particular aspects of Darwin's theory, he never from 1859 onwards doubted the reality of evolution in the general sense. Indeed, he had delivered a lecture on "the progressive development of animal life" even before the *Origin* was published (Huxley 1855), and he was still defending Darwin's work in print over a decade after the publication of the *Origin* (Huxley 1871). When Darwin died, Huxley was a Pall Bearer at his funeral and wrote an obituary that compared him to Socrates for his belief in the absolute sovereignty of reason (Huxley 1999 [1882], p. 396).

### ***Evidence as to Man's Place in Nature***

Published 4 years after the first edition of Darwin's *The Origin of Species*, Huxley's most well-known book-length work *Evidence as to Man's Place in Nature* began (unusually for a work of natural history) with a substantial historical account of the treatment of what he called the "man-like apes" (or catarrhine apes) in previous works of natural history, starting as early as 1598. It then provided a detailed comparative analysis of the physical structure of human beings (what he called their "animal fabric") and their embryonic development compared to "the lower animals," and it finished with an account of various fossil remains of archaic human beings such as the Neanderthal skull that had been discovered in 1856. Huxley erroneously concluded that the Neanderthals were not a distinct or intermediate form between human beings and their primate ancestors (Huxley 1863, p. 183), in line with the accepted doctrine of the period. Now it is known that Neanderthals are a separate species from modern humans (Lieberman 2013, p. 105). Elsewhere, Huxley mapped the geographical distribution of what he called "the chief modifications of mankind" (Huxley 1870a).

*Evidence as to Man's Place in Nature* also included as a frontispiece a much-reproduced

illustration comparing the skeletons of (from left to right) the gibbon, the orang-utan, the chimpanzee, the gorilla, and then "man" in a way that suggested an evolutionary progression that has been described as the "most well known, but misunderstood piece of artwork in the history of evolution studies," in part because the evolutionary sequence that was implied in it is not accurate (Nocks 2008, p. 58). Human beings are more closely related to chimpanzees and bonobos than to gorillas. Some significant time later, a book with the title *History of the Primates* would present a more accurate cover illustration of the progression of primate evolution (Clark 1962), while Ernst Haeckel had published a more extensive evolutionary tree of life in 1902 that contained four major groups of phyla.

Overall, the argument was clearly made throughout *Evidence as to Man's Place in Nature* with a wealth of supporting evidence that human beings were very close in structural terms to their closest primate relatives, exactly as Darwin's 1859 theory of evolution had implied. For example, on embryonic development, Huxley concluded that:

Without question, the mode of origin and the early stages of the development of man are identical with those of the animals immediately below him in the scale: - without a doubt, he is far nearer the Apes, than the Apes are to the Dog (Huxley 1863, p. 81).

On cranial capacity, Huxley outlined that human beings differed more widely from one another than they did from some of the apes, the lowest apes differed as much in cranial capacity from the highest apes as the latter did from human beings, and males brains were (on average) somewhat larger than female brains. Huxley also provided an in-text illustration comparing a human skull with five other types of ape skull that diverged from the former in varying degrees (Huxley 1863, pp. 96, 94).

In general, whatever part of the animal fabric was considered, Huxley maintained that the lower apes and the gorilla differed more than the gorilla and human beings (Huxley 1863, pp. 95, 101). Although *Evidence as to Man's Place in Nature* was only concerned with physical comparisons between human beings and their closest primate



relatives, elsewhere Huxley maintained that “the same nervous structures underlay cognitive processes in man and the higher animals” (Richards 1987, 228). He concluded the book by suggesting that, because of the consequences of the theory of evolution, “we must extend by long epochs the most liberal estimate that has yet been made of the antiquity of Man” (Huxley 1863, p. 184).

Having provided this free-standing account of the issue of comparative morphological development, Darwin duly selected Huxley to provide a tailored short summary of his approach on this topic for one of his most significant works, *The Descent of Man*, chapter one of which on the evidence of the descent of man from a lower animal form was very similar in both general aim and specific content to Huxley’s own *Evidence as to Man’s Place in Nature*.

### On Human and Ape Brains in *The Descent of Man*

In the Preface to the Second Edition of *The Descent of Man* of 1874, Darwin wrote: “I must especially call attention to some observations which I owe to the kindness of Prof. Huxley (given as a supplement at the end of Part I), on the nature of the differences between the brains of man and the higher apes” (Darwin 1874 [1871], v). This addition by another author was the only such addition included by Darwin in his most significant books. Huxley’s wider importance to *The Descent of Man* is indicated by the fact that he has (in the second edition) 17 separate page references listed in the book’s rear index, only one of which was to the “Note on the Resemblances and Differences in the Structure and the Development of the Brain in Man and Apes.”

In the first edition of *The Descent of Man* of 1871, Darwin had briefly discussed Huxley’s work on comparative anatomy as showing that the brain of “man is constructed on the same general type or model with other mammals” (Darwin 1881 [1871], p. 10), as against critics such as Theodor Bischoff who had emphasized developmental differences. For the second edition of *The Descent of Man*, Darwin asked Huxley to

fill in the gap about comparative brain anatomy with a section devoted to presenting the latest knowledge on the topic, in order to bolster his own case for the evolutionary connections between “man” and the higher apes (Browne 2003, 343), which he then added to the end of the first major part of the book.

As Huxley explained in the provided section (of eight printed pages), it was Louis Gratiolet who had originated the statement that there was a fundamental difference in the developmental growth of the brains of apes and those of human beings (Huxley 1874, p. 203). This was part of the wider argument that the brains of apes differed significantly from those of humans, for example, in the posterior lobes of the cerebral hemispheres. In contrast, Huxley maintained that (for example) the sulci and gyri (valleys and folds) that appeared on the surface of the cerebral hemispheres “are disposed after the very same pattern” in human beings and in the higher apes (Huxley 1874, p. 199). In his earlier *Evidence as to Man’s Place in Nature*, Huxley had included detailed illustrations of a human brain next to a chimpanzee’s brain and had concluded using this visual comparison that the structural differences which separated human beings from the gorilla and the chimpanzee were not as great as those that separated the gorilla from the lower apes (Huxley 1863, p. 123). One of Darwin’s basic conclusions from *The Descent of Man* echoed this Huxley point almost exactly (Darwin 1874 [1871], p. 150).

Huxley readily admitted in his “Note on the Resemblances” that there were some accepted differences between human and ape brains; for example, the cerebral hemispheres of human beings were larger than those of the orang-utan and the chimpanzee and the gyri and sulci had a greater number of secondary corrugations, but “none of these differences constitute a sharp demarcation” enough to suggest that they are of a fundamentally different type or are evolved from a different origin (Huxley 1874, p. 200).

In addition, Huxley pointed out that some brain structures varied within the limits of a single animal group, such as between the Old World apes and the New World apes, which had differences in

their temporo-occipital sulci, so the fact that such structures might also differ in human beings to a degree had no great taxonomic value. Huxley concluded his comparative account of the brain in “man” and apes with a section on embryology and with the sentiment that the exhibited growth of the fetal human brain is in perfect harmony with the general concept of evolutionary development.

### The Evolutionary Significance of *Archaeopteryx*

Huxley’s skills in comparative anatomy were not limited only to analyzing brain structures. For example, he was the first commentator to use what he called “comparative zoological reasoning” in order to explicitly highlight the intermediate nature of the skeletal form of *Archaeopteryx lithographica* (Huxley 1863, p. 85), which was from the late Jurassic period. Huxley called the *Archaeopteryx* fossil a connecting form and he listed 35 different morphological characteristics in order to substantiate his connecting claim (Huxley 1868, p. 358; Currie and Padian 1997, p. 809).

Although the *Archaeopteryx* fossil had been first discussed in print by Huxley’s nemesis as an anatomist Richard Owen (1863), Owen had missed the intermediate nature of the bodily structure that was on display in part due to his general skepticism about the theory of evolution, and he had also (in haste) erroneously mislabeled some parts of the *Archaeopteryx* skeletal anatomy. More accurately, Huxley compared *Compsognathus longipes*, a chicken-sized bipedal meat-eating theropod (another bird-like dinosaur), to *Archaeopteryx* as a dinosaur-bird intermediary, the two animals having some definite structural similarities/evolutionary homologies (Herbert and Norman 2009, p. 151). Although the first *Archaeopteryx* fossil lacked a skull, Huxley predicted that if one was found, it would have teeth like a reptile, not a toothless bill like a bird: Owen took the latter view. It was Huxley’s predication that turned out to be correct (Lindow 2008, p. 369).

Huxley’s original theropod hypothesis for the origin of birds is now accepted as the correct

approach to understanding avian evolution even though during the second and third quarters of the twentieth century, it was supplanted by a different erroneous theory due to some remaining anatomical doubts (Padian and Chiappe 1997, pp. 72–73). Huxley’s theropod hypothesis – birds as flying dinosaurs – was resuscitated and further confirmed in the 1970s (Ostrom 1974), and he also proposed in terminology that dinosaurs should be classified as the *Ornithoscelida* (Desmond 2002, p. 551). On a second paper on connecting forms, Huxley had further analyzed the anatomical similarities between birds and dinosaurs, conceiving the *Megalosaurus* (another theropod dinosaur) as Ostrich-like in some significant ways (Huxley 1870b).

Even though Huxley’s *Archaeopteryx* work was an important contribution to comparative anatomy in its own right, its crucial significance for the theory of evolution was cemented by the fact that this fossil was the first clear example of a so-called missing link or transitionary form of animal that was discovered in the fossil record, and Darwin was subsequently able to incorporate this fact in the fourth edition of *The Origin of Species* of 1866 as further proof of the validity of his approach. The original *Archaeopteryx* fossil quickly became one of the “crown jewels” of palaeontology discovery both because of its evolutionary significance and due to the extremely fortuitous timing of its first discovery, although various other examples of it have subsequently been found.

Utilizing the existing work on the *Archaeopteryx*, Darwin suggested in *The Descent of Man* (following Huxley’s lead from his 1870b article) that this fossil provided direct evidence that “the Dinosaurians are in many important characters intermediate between certain reptiles and certain birds” (Darwin 1874 [1871], p. 158). As has been suggested, “*Archaeopteryx*, more than anything else, helped vindicate Darwin’s theory” (Lindow 2008, p. 388). Darwin also quoted from Huxley’s *Evidence as to Man’s Place in Nature* in *The Descent of Man* in relation to tracing the genealogy of human beings as diverging from the Old World division of the Simiadae. Much later, *Archaeopteryx* was used to illustrate the concept

of mosaic evolution, or selective evolutionary change on developmentally distinct parts of the body (Barnett 2020).

The anatomical dispute between Huxley and Owen had, in fact, ranged over more than simply the description of the first *Archaeopteryx* fossil. In 1857, Owen had presented three controversial assertions over some alleged differences between human and simian brains. Huxley responded by showing that none of these hypothesized differences – a third lobe, the posterior cornu of the lateral ventricle, and the hippocampus minor – were actually unique characteristics of human brains (Huxley 1863, pp. 134–135). This “Hippocampus debate” went on for some time as Owen refused to concede the basic point at issue and it spilled over from scientific journals into more popular media outlets such as *Punch* (Nocks 2008, p. 63). The fact that Huxley was vindicated in this debate provided further support for Darwin’s theory of evolution in a general sense, as Owen was known to be an evolution-skeptic.

## Conclusion

In terms of categorizing Huxley’s general approach to comparative brain anatomy, it can be seen as squarely within the Darwinian tradition of searching for evolutionary continuities in mental processes and structures between human beings and other animals (Shettleworth 2012, p. 529). In fact, given that the publication of Huxley’s *Evidence as to Man’s Place in Nature* had preceded the publication of Darwin’s *The Descent of Man* by a number of years and that Darwin included both Huxley’s own work (at least in the second edition) and employed his general approach to the subject in the book, the Darwinian tradition in comparative cognition should perhaps be re-labeled as the Huxleyite tradition, although, given Darwin overwhelming preeminence as a naturalist, this terminological shift is unlikely to become the accepted norm.

In the Huxleyite tradition, starting in the 1960s, Ralph Holloway conducted significant work on comparative brain size and structure differences,

with (in Holloway’s approach) changes in brain size being accompanied by parallel reorganizations of brain parts and systems (Gibson 1990, p. 97). Holloway developed an approach that he called paleoneurology using the endocasts of fossil crania in order to study the mosaic evolution of Hominin brains, which increased very significantly in size from the time of *Homo habilis* to that of *Homo sapiens*. According to Holloway, the appearance of the earliest *Homo* coincided with a major expansion of brain size and a reorganization of the frontal lobe, coincident with this being evidence of stone tool use (Holloway 2000, pp. 142, 148–149). This type of primate/human brain expansion had been recognized in bare outline at the end of the nineteenth century (Wallace 1889, p. 457). Paleoneurology and the study of endocasts can be seen as a direct extension of Huxley’s own comparative anatomy of cranial capacity, as can the relatively new subject of cognitive archaeology (Renfrew and Zubrow 1994), as has been recognized (Tobias 1971, p. 66).

In addition, Huxley’s *Evidence as to Man’s Place in Nature* can be seen as historically important in terms of laying some of the intellectual groundwork for the subsequent publication of Darwin’s own *The Descent of Man*. As has been explained, Darwin’s remark in the *Origin* that “Much light will be thrown on the origin of man and his history” was almost timid in the subtlety of its implication, and so “Others treated what Darwin feared to discuss” (Simpson 1972, p. 17): this “other” was preeminently T.H. Huxley. Darwin referred in the second edition of *The Descent of Man* to experiencing a “fiery ordeal” after publishing the first edition of the book (Darwin 1874 [1871], v), but some of this criticism had already been aimed at (or deflected by) Huxley’s earlier book, rather than Darwin’s own contribution on the topic, so the “fiery ordeal” of *The Descent of Man* was in all probability not as great as it would have been without Huxley. Huxley was, therefore, not only Darwin’s bulldog (his most effective advocate), but his intellectual point man as well, at least in applying the theory of evolution by selection mechanisms to the most contentious example of animal fabric of all: human beings.

## Cross-References

- [Charles Robert Darwin](#)
- [Hippocampus](#)
- [Mosaic Cognition](#)
- [Origin of Species](#)
- [Primates](#)

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## Tactile

- [Platyrrhine Sensory Systems](#)
- [Primate Sensory Systems](#)
- [Touch Screen](#)

## Tactile Perception

- [Depth Perception](#)

## Tai Chimpanzees

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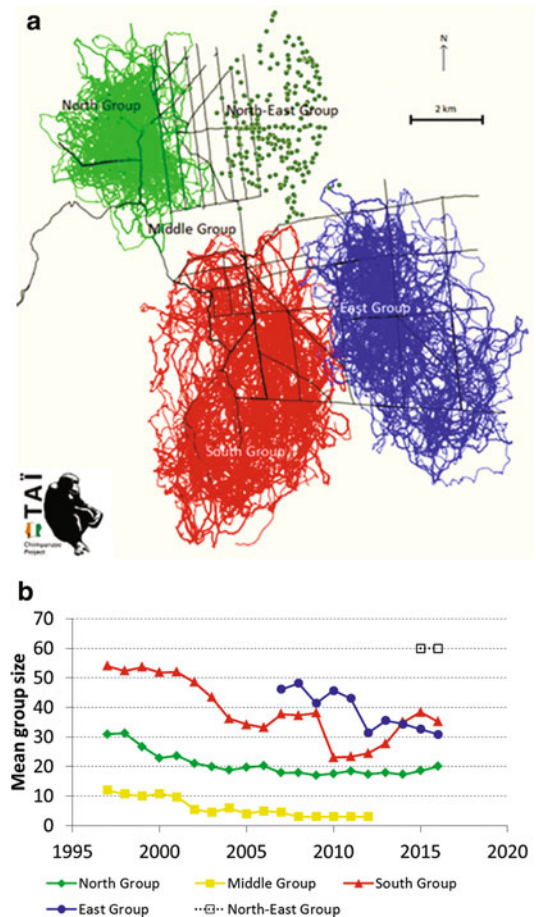
Tai Chimpanzee Project, Centre Suisse de Recherches Scientifiques, Abidjan, Ivory Coast

## Introduction

*Tai Chimpanzees* is a term used for a population of western chimpanzees (*Pan troglodytes verus*) located in the Tai National Park, which is situated in the southwestern region of Ivory Coast at the border to Liberia in West Africa. The *Tai Chimpanzees* are observed continuously since 1979 when primatologist Christophe Boesch and his wife Hedwige Boesch-Achermann established the Tai Chimpanzee Project (TCP). TCP ([www.taichimps.org](http://www.taichimps.org)) is dedicated to the research and conservation of the *Tai Chimpanzees* (Boesch and Boesch-Achermann 2000). In the beginning, Christophe Boesch habituated North group to the presence of human observers, a process that takes 5–7 years. Over many years he and his wife followed this community with the support from

only a few additional observers. TCP started to grow with Christophe Boesch's appointment as director of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, in 1997.

Several new chimpanzee communities have been habituated since then (Fig. 1a). After many years of surveying the area south of North group, habituation of South group started in 1994 in the hope for direct observation of intergroup encounters and female migration. However, even before South group was entirely habituated it became clear that one community of chimpanzees was ranging in between. Therefore, observers started to follow Middle group in 1997, which turned out



**Tai Chimpanzees, Fig. 1** Five chimpanzee communities habituated for research at the Tai Chimpanzee Project: (a) the position of each community within the research area, and (b) the community size of each community through time

The Tai Chimpanzee Project ([www.taichimps.org](http://www.taichimps.org)) – research on the wild chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Côte d'Ivoire



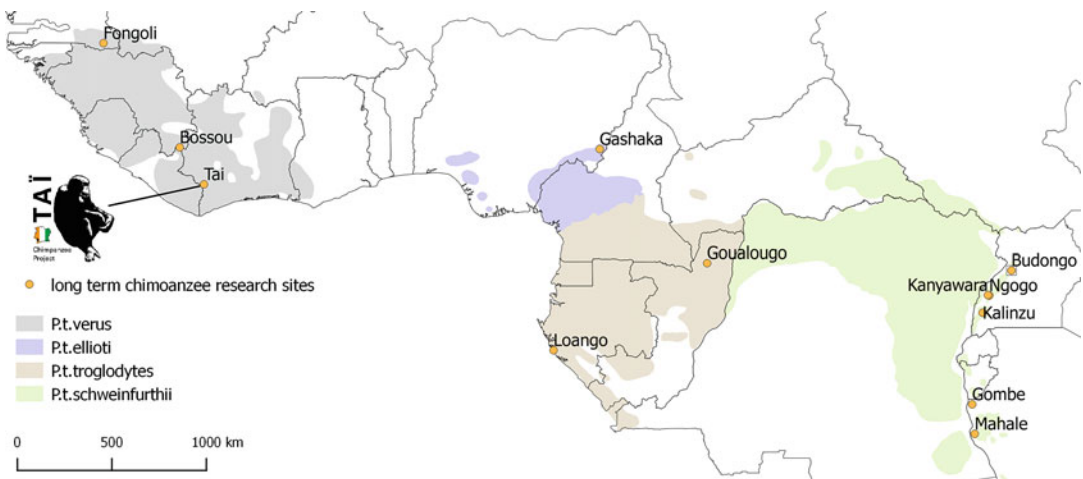
to consist of 12 chimpanzees (Fig. 1b). As a result, TCP staff started in the year 2000 with the habituation of East group, allowing for two neighboring communities to study intergroup interactions from both sides. Finally, in 2014, TCP started the habituation of North-East group, a chimpanzee community bordering all other groups. After 33 years, Christophe Boesch handed over the responsibility for TCP to Roman Wittig in January 2013. To date (2017), TCP staff observes four neighboring chimpanzee communities (Fig. 1a) with about 150 individuals (Fig. 1b) and one group of sympatric living sooty mangabey (*Cercocebus atys*). An international team of local field assistants and international researchers is observing the *Tai Chimpanzees*.

The vested interest in behavior and cognition of chimpanzees is based on chimpanzees' similarity to humans. Chimpanzees, and their sister species the bonobo (*Pan paniscus*), are our closest living relatives. Our evolutionary paths have diverged only about 7–8 million years ago (Langergraber et al. 2012). The evolutionary closeness makes chimpanzees an ideal model species to investigate behavioral and cognitive adaptations of humans, since they allow us a glimpse into the past of our own species. This makes long-term projects like TCP an essential asset to the science community.

*Tai Chimpanzees* show a wide range of behaviors that appear to be very similar to that of humans. They use multiple tools to extract food, they cooperate during hunting of monkey prey and border patrols, they reconcile conflicts, they adopt orphans, and they developed cultures. Although these behaviors are not unique features of *Tai Chimpanzees*, but can be found also in other chimpanzee populations (Fig. 2), observations at TCP were either leading to the discovery or significantly contributed to our understanding of these behaviors. Much of the research on the *Tai Chimpanzees* has unraveled discoveries related to human evolution and animal cognition.

## Sociality and Bonds

Chimpanzees live in multi-male multi-female societies, with females migrating when they reach sexual maturity. They are typically seen as being male bonded, since males show typically higher levels of association and grooming than females, and female dominance hierarchy are usually not linearly structured. *Tai chimpanzees*, however, seem to be mixed sex bonded, showing differentiated relationships not only between males but also between females and between the sexes (Boesch 2009; Boesch and Boesch-



**Tai Chimpanzees, Fig. 2** Location of the Tai Chimpanzee Project and other long-term chimpanzee research sites across Africa in relation to the distributions of the four chimpanzee subspecies

Achermann 2000). This classification of *Tai chimpanzees* as being mixed sex bonded has several reasons. First, *Tai* females invest not only into differentiated relationships with females and males (Wittig and Boesch 2010a) but also show a linear dominance hierarchy in females (Wittig and Boesch 2003a), indicating that social relationships with and amongst females matter. Second, females in *Tai* range throughout the entire home-range of the community and do not inhabit satellite or neighborhood territories (Lehmann and Boesch 2005), as has been reported for many other study sites (Pusey and Schroepfer-Walker 2013). Third, *Tai* females can exhibit a certain choice in choosing their mating partners (Stumpf and Boesch 2006) preferring mating partners which have shared meat with them beforehand (Gomes and Boesch 2009). Finally, male violence towards females of the same community is much lower in *Tai*, where males have never been observed to commit intracommunity infanticide, killing the infants of females belonging to the same social unit, while this has been observed several times in other chimpanzee communities (Wilson et al. 2014). A result of this might be the higher survival probability of chimpanzee youngsters in *Tai* during periods without disease outbreaks compared to eastern chimpanzees (Wood et al. 2017). Thus, females in *Tai* might be able to bond with the local males, range over the same territories, and exhibit differentiated mating choices because they do not need to worry about that local males would kill their infants.

## Reconciling Conflicts

*Tai Chimpanzees*, like other social animals, face the dilemma of group living. On the one hand, they need to cooperate with group members in order to reduce predation risk, to increase territory defense or exploitation of food sources. At the same time, they compete with the other group members over mating partners, food, or shelter. Facing a conflict of interest *Tai Chimpanzees* need to decide whether they escalate the conflict into aggression, winning the resource but damaging the cooperative relationship with the opponent or

to leave the resource to the opponent (Wittig and Boesch 2003b). Once the conflict is escalated to aggression the relationship to the opponent is damaged and tolerance levels are disturbed (Wittig and Boesch 2005). In this case reconciliation, the friendly interaction between former opponents after aggression, can restore tolerance levels to normal and repair the relationship between the opponents to allow future cooperative interactions (Wittig and Boesch 2005).

Approaching the former opponent to reconcile, however, is not possible all the time. Sometimes fear about reemerging aggression is making a friendly direct contact of former opponents impossible. There is, however, a solution to the problem. In such cases, *Tai chimpanzees* seek friendly contact with the friend of their former opponent or friends seek friendly contact to the opponent of their friend. The friendly contact with the former opponent's friend functions like reconciliation between the opponents, but without them needing to have direct contact (Wittig and Boesch 2010b). This friend-mediated reconciliation requires that *Tai chimpanzees* know who is friend with whom. Otherwise the friendly contact with the opponent's friend would not show any effect on the tolerance level between the opponents.

## Hunting and Food Sharing

*Tai Chimpanzees* are specialized hunters of monkey prey. They regularly hunt for western red colobus (*Procolobus badius*) and western black-and-white colobus (*Colobus polykomos*). During these hunts *Tai Chimpanzees* coordinate their activity and show high levels of group cooperation. In most of these hunts they coordinate their activity in time and space, while engaging in different roles (Boesch and Boesch 1989). A driver climbs up in the tree next to the monkeys and starts slowly moving towards them. The monkeys start fleeing into the next tree. Blockers sitting in other trees close by watching the monkeys and block their escape routes. This way they channel the movement of the monkeys and make them to move towards a certain direction. In this certain direction a hidden catcher is ready for

the ambush. Once the monkeys reach the tree of the catcher, he makes his move, grabs one of the monkeys, and drags the prey to the ground, where the chimpanzees come together in to feed on the meat.

The meat of the monkey is usually distributed among the hunters (Fig. 2). From there it is shared with friends and friends-to-be. Why “friends-to-be,” because the sharing of food is strongly linked to high levels of urinary oxytocin. Oxytocin is a hormone known to facilitate bonds between individuals. It seems that sharing food allows individuals to build new friendships and to maintain existing bonds (Wittig et al. 2014). While in some other populations meat sharing is mainly based on avoiding harassment (Gilby 2006), *Tai* chimpanzees share meat more often with individuals that were involved in the hunt (Boesch 1994) and in exchange for agonistic support (Gomes and Boesch 2011). The latter has been described similarly in other chimpanzee populations (Mitani and Watts 2001). It seems that meat sharing, or even sharing of food in general, may reflect the wish of a *Tai* chimpanzee to make a friend or coalition partner.

## Tool Use and Culture

*Tai* Chimpanzees are famous for their nut cracking technique. They employ a hammer and anvil principle to crack open the shells of several nut species (e.g., *Coula edulis*, *Panda oleasa*, *Detarium senegalense*; Fig. 3). *Tai* Chimpanzees do so by placing the nut on a solid anvil, e.g., a root or a rock, most of which are used since many years so that the nuts have left an imprint over time, and hit the nut with a wooden club or a stone hammer until the shell breaks open (YouTube channel of the *Tai* Chimpanzee Project: Dilly cracks nuts). If the nut is not hit hard enough, the shell does not crack, if the nut is hit too hard, the kernel is smashed. Skilled nut crackers adjust the force so the nut shell open with one or two hits and they can consume the kernel. Infants may need many years before they are able to do so. Sometimes *Tai* Chimpanzees may be unable to remove the entire



**Tai Chimpanzees, Fig. 3** Coula nut cracking site with hammer and anvil in the *Tai* National Park © Roman M Wittig, TCP

kernel from the shell. Then they may break a stick into the right length of a spooning tool and spoon the rest of the kernel out.

Although nuts like *Coula edulis* are present in many chimpanzee populations, they are only cracked west of the river Sassandra in Ivory Coast. Behavioral variation like this, independent of genetic or ecological variation, has been termed tradition, and the sum of all such variation as culture. Chimpanzees show cultural variation when comparing between populations across Africa with *Tai* Chimpanzees being described as the nut cracking culture (Whiten et al. 1999). However, *Tai* Chimpanzees exhibit also cultural variation between neighboring communities.

At the beginning of the Coula nut season, the nuts have harder shells and they are cracked and consumed in the tree. *Tai* Chimpanzees use stone hammers, which are easier to transport into the tree and better to crack the hard shell of the fresh nut. With proceeding time during the nut season, the shell drying out and loses its hardness. The chimpanzees use more and more wooden clubs to crack the nuts, which are much more abundant than stones. This makes life easier for them and long searching for appropriate tools is not slowing them down anymore. *Tai* Chimpanzees follow this rule in north and east group, but not in the neighboring south group. In south group they continue to use stones throughout the entire Coula nut season, although stones are not more abundant in

the south group territory than in the others. The difference in the nut cracking behavior between south group and the two others is based on cultural differences (Luncz et al. 2012).

Immigrating females even conformed to the culture of the south group in *Tai*. Females coming from a natal group that belong to the stone and wood hammer culture adopted the stone hammer culture of the south group after immigration (Luncz et al. 2015). Within one nut cracking season they had adopted the culture and did not change to wooden hammers back anymore. This suggests that conformity with the group culture is an important feature of group identity among the *Tai Chimpanzees*.

## Adoptions

Adoptions are a chimpanzee universal, but in *Tai* we were able to observe a large number of adoptions carried out by either, female and male chimpanzees. When mothers die before their offspring have reached adulthood (with 15 years), they leave an orphan behind. With an inter-birth-interval of about 5.5 years (Boesch and Boesch-Achermann 2000), dead parous females leave usually at least one dependent offspring. Children that are orphaned before they have reached 5 years of age, while they are completely dependent on their mother, have almost no chance to survive. Generally, one can say, the younger the offspring is the lower the probability for it to survive without the mother.

In *Tai* about 50% of the orphans are adopted by other group members (Boesch et al. 2010). Adopters carry the orphan, share food and night nests with them, support the orphans in aggressive interactions, and wait or search for them. Interestingly, in *Tai* adopters can be both, close kin (in form of siblings or fathers) or unrelated to the orphan. Whether the adopters are kin or non-kin, adoption increases the orphan's chance to survive longer. The film *Chimpanzee* (2012), produced by Disney Nature, is telling the story of an adoption, featuring the orphan Oscar that is adopted by the alpha-male Freddy. The footage was taken of the *Tai Chimpanzees* and contains the adoption of

Victor by the old male Freddy in TCP's East group after the death of Victor's mother Vanessa in 2008. Freddy has been ever since somebody who adopted many other infant orphans and was able to help quite a number to survive for many years.

## Conservation

Western chimpanzees are critically endangered. Over the last 20 years, we lost more than 80% of the population of *Pan troglodytes verus* in the world (Kühl et al. 2017). Estimates suggest that between Ghana and Senegal there are about 35,000 western chimpanzees left. The *Tai* National Park is the largest remaining primary rainforest in West Africa and is, with its 4540 km<sup>2</sup>, home to an estimated 300 chimpanzees. The population is under pressure from poaching, habitat destruction, and illegal mining.

Diseases are an additional survival hazard for *Tai chimpanzees*. During the last 35 years, *Tai chimpanzees* have been victims to a large number of different diseases, e.g., Ebola (Le Guenno et al. 1995), anthrax (Hoffmann et al. 2017), respiratory diseases (Köndgen et al. 2008). While some originated in the forest, others have human origin. Due to the chimpanzees close genetic relationship, there is a high possibility of transmitting respiratory diseases from humans to chimpanzees. Since 2009, therefore, TCP has strict hygiene rules and employs 5 days quarantine for anybody who is going to observe the chimpanzees or mangabeys (Grützmacher et al. 2017). These rules have been adopted by IUCN (International Union for Conservation of Nature) as best practice for the research and tourism with great apes and prevented since then cases of lethal respiratory outbreaks.

Research conducted by the *Tai Chimpanzee Project*, however, is not only enlarging our knowledge about chimpanzees and human evolution but has also a direct impact on the protection of the chimpanzees and other mammals in the research area. Using National Park wide survey data

showed that illegal human activity is the lowest around the research and ecotourist areas, leading to the highest animal densities for chimpanzees, monkeys, and other mammal species in the research and ecotourist areas (Campbell et al. 2011). This correlation between research area and animal density shows the crucial conservation effect of long-term research sites like the *Tai Chimpanzee Project*.

## Conclusion

When comparing *Tai Chimpanzees* to other chimpanzee populations (Fig. 2) we find some pattern that seem to differ. *Tai Chimpanzees* build friendships between males, between females, and between males and females. If unable to reconcile the conflict with the former opponent, they seem to have the ability to repair the damage done by the aggression when “reconciling” with a friend of the former opponent instead. Although *Tai Chimpanzees* are competitive and violent to the rival groups (neighbors), they do not seem to commit killings within their own group. All these features make the *Tai Chimpanzees* a population of chimpanzees with lower violence and a higher degree of mixed sex bonding compared to other long-term sites. Whether this is a *Tai* trait, a western chimpanzee characteristic, or features that can develop anywhere under certain ecological conditions remains to be investigated.

The presence of the *Tai Chimpanzee Project* is vital for the survival of the *Tai Chimpanzees*. Without a long-term investment in research, the sustainable management of the Park as a protected area seems impossible. Research at the *Tai Chimpanzee Project* incorporates the three pillars of the millennium declaration by the UN on sustainability. First, the social development in form of providing knowledge for society and education for local human population; second, the economic development in form of salaries, health insurance, and microloans for local staff; and third, the environmental protection, in form of effective safeguarding of the only irreplaceable protected area for biodiversity in West Africa, the *Tai National Park* (Saout et al. 2013).

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## TALEN

### ► Targeted Mutation

## Tannin

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The word “Tannin” originally refers to the early use of oak and other barks in tanning animal hides into leather. Tannins (commonly referred as tannic acid) are water-soluble polyphenols commonly distributed in plants (The Editors of Encyclopedia Britannica

2016). The presence of tannins has been noted in both gymnosperms as well as angiosperms. The plant families that have been found to produce tannins are *Actinidiaceae*, *Anacardiaceae*, *Aceraceae*, *Burseraceae*, *Bixaceae*, *Combretaceae*, *Dipterocarpaceae*, *Ericaceae*, *Grossulariaceae*, and *Myricaceae* in case of dicots and *Najadaceae* and *Typhaceae* in case of monocots (Mole 1993). Additionally, tannins have been found to occur in numerous plant parts for instance: roots, barks, wood, fruits, and leaves. Apart from these they are also reported in galls resulting from the insect attacks. They can be present in any form ranging from a group of pale-yellow to light-brown amorphous powdery substances, flakes, or a spongy mass (The Editors of Encyclopedia Britannica 2016).

Tannins have high molecular weights ranging from 500 to 20,000 and possess low nutritional value (Swain and Bate-Smith 1962). Due to the presence of a high number of hydroxyls and other suitable groups (like carboxyls), they have the tendency to bind and precipitate proteins, amino acids, and alkaloids.

Tannins can be broadly classified into the following categories:

1. **Hydrolysable tannins:** Tannins that form gallic or ellagic acids on heating with hydrochloric or sulfuric acids are termed as hydrolysable tannins or pyrogallol-type tannin. These tannins are generally present in different vegetable plants like myrobalan (*Terminalia chebula*), sumac (*Rhus coriaria*), gallnuts (*Quercus infectoria* and *Rhus semialata*), Aleppo gallnuts (*Andricus kollari*), tara pods (*Caesalpinia spinosa*), chestnut wood (*Castanea sativa*), and oak wood (*Quercus robur*, *Quercus petraea*, and *Quercus alba*) (Haslam 1989; Hemingway and Laks 2012).
2. **Condensed tannins:** The polymers resulting from the condensation of the flavans are called as condensed tannins. Sugar residues are absent in the condensed

tannins. They are present in uebracho wood (*Schinopsis lorentzii*), mimosa bark (*Acacia mollissima*), grape seeds (*Vitis vinifera*), pine barks, and spruce barks (Haslam 1989; Ping et al. 2011).

3. **Pseudotannins:** Pseudotannins unlike the hydrolysable and condensed tannins do not change color during Goldbeater's skin test. Furthermore, they cannot be used as tanning compounds and are present in Rhubarb, acacia, catechu, tea, coffee etc. (Kar 2003).

**Properties of Tannins:** Tannins function as protectors and pesticides in plants. The astringent taste of the tannins causes a dry and pucker feeling in the mouth similar to that felt after the consumption of tea, unripened fruit, or red wine. This unpleasant feeling wards off the predators and the insects (McGee 2004). Tannins are extensively used in tanning leather, dyeing fabric, making ink, and in various medical applications. Apart from protection, tannins are also involved in the regulation of the plant growth (Corcoran et al. 1972).

Studies have shown that tannins possess anticarcinogenic and antimutagenic activity. These polyphenolic compounds are known to reduce the level of reactive oxygen species present in the body. This anti-oxidative property of tannins is assumed to be the underlying reason for its anti-cancer property. Many reports have been published claiming the antimicrobial nature of tannins against fungi, bacteria and viruses. They are also known to possess certain physiological properties like accelerating the clotting of the blood, reduction in the levels of the serum lipid and blood pressure, modulation of immune response, and also causing liver necrosis. They function as good preservatives and are also used for clearing Japanese sake. Tannins have the ability to produce different colors with ferric chloride. Along with the use in the formation of corrosion free primers, it is also used in wood and particleboard adhesives (Chung et al. 1998).

## Conclusion

Tannins are polyphenolic plant-based compounds playing a pivotal role in the protection of the plants. Although, the tannins are low in nutritive value, they have a wide range of applications in the human health as well as in combating diseases. More research in this field would unravel the true potential of tannins and uncover more applications for the betterment of the human health.

## Cross-References

► *Plantae*

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## Tapetum

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Tapetum is structurally and functionally diverse unistrata layer of universal occurrence in the microsporangia of all land plants that chiefly serves as a nutritive tissue for developing male gametophytes (Dickinson and Bell 1972, 1976; Sporne 1973; Pacini 1997; Pacini et al. 1985; Huysmans et al. 1998). The tapetum is better known in higher plants (gymnosperms and angiosperms) than in lower plants (bryophytes and pteridophytes) as its activities are less frequent in lower plants than in higher plants (Dickinson and Bell 1972, 1976; Pacini et al. 1985; Parkinson and Pacini 1995). On the other hand, compared to their aquatic ancestors, early land plants had well-protected reproductive structure, the loculus – a liquid-filled cavity that occurs within the microsporangia of many groups in which the spores or pollen grains develop and ripen. This cavity, loculus, is bordered by a tissue of sporophytic origin, i.e., tapetum (Pacini et al. 1985).

However, the origin, development, and specific functions of tapetum vary across all plant

divisions; therefore it has been considered as key reproductive character to investigate evolutionary lineages' especially among higher plants (Endress 2001; Furness and Rudall 1998; Furness and Rudall 2001; Gorelick 2001; Taylor et al. 2012).

The natural life of the tapetal cells too varies among plants and depends on the length of pollen development. In angiosperms, it generally ranges from few days to few weeks (Pacini et al. 1985). In gymnosperms, the tapetal cells are comparatively long lived and can persist up to 6 months (Cecich 1984). In pteridophytes too, the life span of tapetal cells differs from a few days to few weeks (Kelley and Doyle 1975; Mogensen 1978).

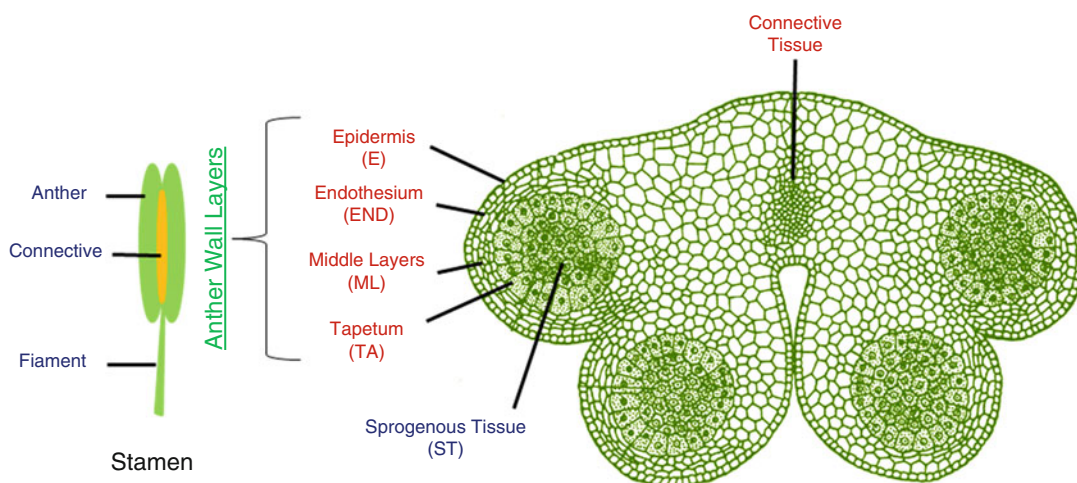
### Structure, Histochemistry, and Origin of Tapetal Cells

Tapetum, most often a single cell layer, is quite distinguishing among angiosperms being an integral element and the innermost layer of anther wall that separates the anther wall and the sporogenous tissue within the anther (Fig. 1). The mature anther wall comprises an epidermis (E) followed (on the inside) by a layer of endothecium (END), two- or three-celled middle layers (ML), and a single cell layer tapetum (TA) that attains its maximum development at the tetrad stage

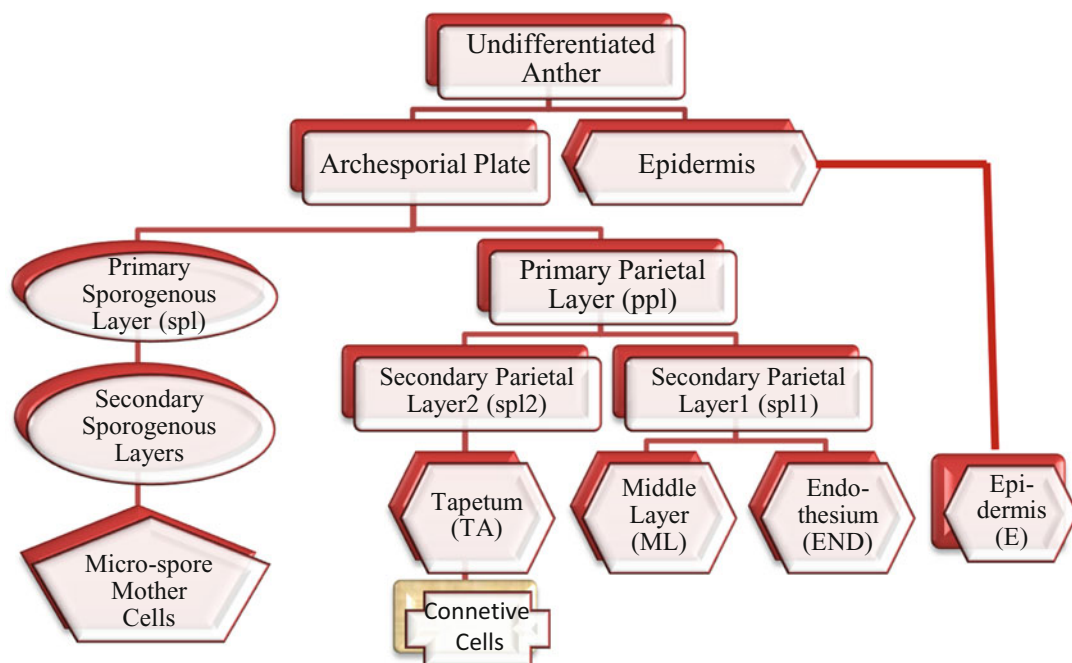
of microsporogenesis (Goldberg et al. 1993; Bhatnagar et al. 2015).

The tapetal cells are characterized by relatively larger cells in size with thin cell walls, dense cytoplasm consisting numerous endoplasmic reticulum, Golgi bodies, plastids, mitochondria, and a prominent nuclei (Moss and Heslop-Harrison 1967; Mizelle et al. 1989; Bedinger 1992; Polowick and Sawhney 1993). Binucleate, tetranucleate, multinucleate or polyploid tapetal cells have also been observed in some species (Bhatnagar et al. 2015).

The parietal origin of the tapetum is universal in occurrence; however, dual origin of tapetal cells has been observed in most of the angiosperms (Davis 1966; Periasamy and Swamy 1966; Bhandari and Khosla 1983; Bhatnagar et al. 2015). It has been observed that among angiosperms, most often the tapetal portion toward outside is contributed by the parietal layer, and the inner portion is derived from the connective tissue (Fig. 2). During differentiation of anther, a periclinal division occurs in the archesporial cells that give rise to outer primary parietal cells and inner primary sporogenous cells (Fig. 2). The inner primary sporogenous cells (spl) divide to secondary sporogenous tissue and ultimately differentiate into microsporocytes (Fig. 2). The outer primary parietal cells (ppl)



**Tapetum, Fig. 1** Transverse section (TS) of anther showing anther wall layers [epidermis (E), endothecium (END), middle layers (ML), tapetum (TA)] and developing sporogenous tissue (ST)



**Tapetum, Fig. 2** Dual origin of tapetum. (Source: Davis 1966; Bhatnagar et al. 2015)

undergo another periclinal division to give rise to two sets of secondary parietal cells (spl1 and spl2). The inner secondary parietal cells (spl2) differentiate into tapetal cells (Fig. 2); these cells become distinct gradually and enclose sporogenous tissue or microspore mother cells, completely. On the other hand, the outer secondary parietal cells (spl1) divide further and differentiate into middle layers and endothecium cells ((Fig. 2; Davis 1966; Bhandari 1984; Sanders et al. 1999; Bhatnagar et al. 2015).

In a few species such as *Alectra thomsoni*, the tapetal cells of different origin varied morphologically, i.e., dimorphic tapetum, where tapetal cells are much smaller toward outside than those toward inside (Bhatnagar et al. 2015). On the other hand, homogenous tapetum occurs in the members of triticales where tapetal cells originate solely from the parietal layer (Bhandari and Khosla 1983).

## Types of Tapetum

In angiosperms, different types of tapeta were reported, but two very basic types, viz., secretory

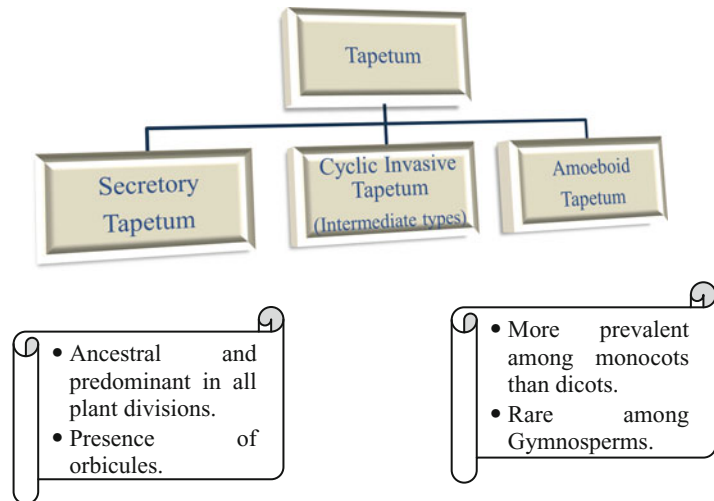
type and amoeboid type, of tapetum have been documented continually by various botanists on the basis of tapetal cell's behavior (Fig. 3; Maheshwari 1950; Echlin and Godwin 1968; Mepharm and Lane 1968; Pacini et al. 1985; Pacini 1997; Rowley et al. 1992; Pacini 1997; Furness and Rudall 2001; Pacini 2010).

The secretory tapetum, also known as cellular, glandular, non-syncytial, and parietal tapetum, comprised of long persistent cells which do not invade the locule itself and secrete materials into the locule during pollen development, e.g., *Alloe*, *Helleborus*, *Nigella*, *Rumex*, and *Victoria* (Furness and Rudall 1998; Taylor et al. 2012).

In the amoeboid tapetum also known as intrusive, invasive, periplasmodial, and syncytial invasive tapetum, the protoplast of tapetal cells migrates into the locule having indirect contact with developing spores by forming a periplasmodium, e.g., *Alisma*, *Arum*, *Butomus*, *Tradescantia*, *Typha*, etc. It was also revealed that the amoeboid tapetum rarely occurs in gymnosperms (Pacini and Juniper 1983; Pacini et al. 1985; Furness and Rudall 1998; Furness and Rudall 2001).



**Tapetum, Fig. 3** Types of Tapetum



An intermediate type of various tapeta, cyclic invasive tapetum, has also been reported where the tapetal cells invade the locule initially but later retreat back to the anther wall, e.g., *Canna* and *Nymphaea* (Tiwari and Gunning 1986; Rowley et al. 1992; Hess and Hesse 1994; Furness and Rudall 1998; Furness and Rudall 2001).

It has been reported that the secretory tapetum being the ancestral condition is the predominant form among all the land inhabited plants (Pacini et al. 1985; Furness and Rudall 2001; Pacini 2010). On the other hand, it has been revealed that the amoeboid tapetum type rarely occurs in gymnosperms and it was more prevalent among monocotyledonous plants than dicotyledonous plants that has been shown also evolved independently many times in early divergent angiosperms (Pacini et al. 1985; Furness and Rudall 2001). The cyclic invasive tapetum type has been shown to be an intermediate type between secretory and plasmodial one that has evolved independently in the species of family Annonaceae, Monimiaceae, Nymphaeaceae, and Winteraceae (Furness and Rudall 2001).

### Developmental Regulation and Molecular Biology of Tapetal Cells

Development of the tapetum is highly regulated and programmed during anther development

(Schrauwen et al. 1996; Owen and Makaroff 1995; Sanders et al. 1999). The tapetum is identified at anther stage 5 and undergoes programmed cell death in stage 10 and then release the contents for further pollen wall development and mature pollen formation at stage 12 in *Arabidopsis thaliana* (Owen and Makaroff 1995; Sanders et al. 1999).

As far as the expression of tapetum-specific genes and their protein products is concerned, it is tightly regulated in time that turned on and off at certain specific points during tapetal life span and participate in the developmental regulation of male gametophyte (Staiger and Apel 1993; Staiger et al. 1994; Schrauwen et al. 1996; Ma 2005).

*Tapetum determinant1* (TPD1) and *excess microsporocytes1* (EMS1)/*extra sporogenous cells* (EXS) genes have been shown to play a pivotal role for tapetal cell specialization (Zhao et al. 2002; Yang et al. 2003; Jung et al. 2005). In the absence of TPD1 or EMS1/EXS, the inner secondary parietal cells develop into microsporocytes instead of tapetal cells. It has also been revealed that the TPD1 and EMS1/EXS gene (s) may function in the same developmental pathway, as the *tpd1* mutant was phenotypically identical to the *ems1/exs* mutant (Canales et al. 2002; Zhao et al. 2002; Yang et al. 2003; Ma 2005).

Moreover, several transcription factors regulating tapetum development and pollen formation

have also been reported as *dysfunctional tapetum1* (*DYT1*). Defective *DYT1* results in a premature vacuolation of the tapetum and the absence of pollen (Ma 2005; Zhang et al. 2006). Besides, *tapetal development and function1* (*TDF1*) too encodes a putative R2R3 MYB transcription factor. Defective *TDF1* results in a dysfunctional tapetum with irregular cell division and absence of pollen in both *Arabidopsis* and rice (Zhu et al. 2008; Cai et al. 2015). *AtMYB103/MS188* also plays an important role in tapetum development, callose dissolution, and exine formation in anthers (Higginson and Parish 2003; Zhang et al. 2007; Zhu et al. 2010, 2011).

## Role of Tapetum

- Nurture, development, and maturation of pollen grains: The tapetal cells are of substantial importance as they essentially nurture the sporogenous meiotic cells during microspore development in anthers and transform the developing microspores into viable pollen grains (Maheshwari 1950; Heslop-Harrison 1968a, b; Pacini et al. 1985; Nave and Sawhney 1986; Sawhney and Nave 1986; Chaudhury et al. 1994; Zhang et al. 1994).
- Formation of pollen wall and formation of exine precursors: Synthesis of sporopollenin precursors (Vithanage and Knox 1980; Bhandari 1984).
- Secretion of polysaccharides and production of orbicules and locular fluid (Heslop-Harrison et al. 1973).
- Secretion of specific substances for pollen protection and pollination: Production and release of callase to dissolve the callosic envelope, formation of viscin threads, tryphine, and pollenkitt to protect pollen from UV radiation (Mephram and Lane 1970; Hesse 1981, 1984; Pacini et al. 1985).
- Secretion of some specific proteins, enzymes, and inhibitory substances: Many specific proteins, responsible for pollen allergy, are secreted by tapetum.
- Regulation of pollen fertility (Izhar and Frankel 1971; Grant et al. 1986; Liu et al. 1987; Chaudhury et al. 1994; Zhang et al. 1994).

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## Tapir Gait

- [Perissodactyla Locomotion](#)

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## Tapirs

- [Perissodactyla Cognition](#)

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## Target

- [Goal](#)

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## Targeted Mutation

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## Synonyms

Cas9; Cre-loxP; CRISPR; Gene targeting; Homologous recombination; Homology directed repair; Non-homologous end joining; TALEN; Zinc finger nuclease

## Introduction

Molecular biology is a subject dedicated to understanding the microscopic phenomena that drive life. To engage in this field, a study will begin on a biological process. Multiple proteins, RNA and DNA sequences, and other molecular machinery are involved in any number of processes – discovering what each component does in a system can be a daunting task. One of the clear ways to identify the functionality of a gene is to generate a “knock-out” or a cell line (or animal line) without the gene in question. A knock-out line helps to answer a number of questions, for instance; does the system still function in the same way? If not, how is it failing? And what is the phenotype in the knock-out? In turn, these answers lead to new questions, and the life cycle of science repeats itself.

Due to the detrimental, sometimes fatal phenotypes produced from knock-outs, these experiments are done in model organisms and cell lines. Common model organisms are mice, rats, *Drosophila* (fruit flies), yeast, and zebrafish, among others. In the case of mammals (mice), modern techniques are used to target a mutation in embryonic stem cells (ESCs). The common method of creating a mutant mouse line is as follows – the desired mutant ESC is injected into the inner cell mass of a blastocyst. This leads to the generation of chimeric mice, which are crossed with wild type mice to produce progeny, some of which are heterozygous for the mutation of interest. Finally, these heterozygous mice are crossed; some of their progeny are homozygous for the mutant gene. There are a number of ways to introduce a mutation to an ESC; this passage will explore the variety of techniques that have been refined to target genes.

double strand breaks on the DNA. While this is an important step for ensuring genetic diversity during meiosis, HR is also important in repairing damaged DNA, the process utilized in gene targeting HR. In order for HR to take place, large stretches of the repair DNA must be identical; when using HR for gene targeting purposes, a plasmid must be introduced to an early stage cell – a fertilized egg or ESCs are ideal. The plasmid introduced to the early stage cell must contain a large amount of homology to the region being targeted. The plasmid will otherwise vary depending on the experiment – it could cause a slight insertion, a deletion, or a point mutation (Rocha-Martins et al. 2015).

The resulting gene targeted cell line is a rare event when using HR, as it is dependent on a double-strand break happening. To bypass the difficulties of finding the proper cell line, many experiments using this method include either a selection marker or a reporter marker. A selection marker is an additional gene that contains the resistance of an antibiotic. Therefore, the plasmid that knocks out the gene of interest also introduces, for instance, a neomycin resistance marker. When treated with neomycin, the cells that survive have successfully incorporated the new sequence (including the knock-out of the gene of interest and inclusion of the neomycin resistance marker) via HR. The other means to detect a successful mutation is to include a reporter marker on the plasmid with the target sequence. Reporter markers are genes that are measurable in some way. For instance, the green fluorescent protein is a frequently used reporter as it makes the cell lines it is introduced to glow. These selection and reporter marker methods are utilized in other gene targeting techniques as well (methods described below), as they improve efficiency of these experiments.

## Homologous Recombination

Gene targeting became feasible in the 1980s upon the advent of microinjection technologies and the understanding of biological process homologous recombination (HR). HR is a process in which portions of like chromosomes are exchanged after

## Zinc Finger Nucleases

Zinc finger nucleases (ZFNs) are tools used to target mutations. These chimeric proteins are made of two parts, the cleavage domain of the FokI restriction enzyme (a protein that cuts DNA at a particular site) and C2H2 tandem zinc-fingers



(a protein domain that binds DNA). The FokI cleavage domain is able to cut any sequence, so long as there is an enzyme on both strands (requiring two of these targeting proteins). C2H2 zinc-fingers (there are two cysteines and two histidines that bind zinc and form the 3D shape of the domain) bind triplets of DNA and are modular. Subsequently, with different mixes of zinc fingers, different sequences can be targeted (Urnov et al. 2010). Therefore, with two designed chimeric ZFNs, a cut can be made on a targeted DNA strand, which can lead to the nonhomologous end joining (NHEJ) pathway. The NHEJ pathway is not specific and can cause random mutations, which could be insertions or deletions (InDels). With the addition of a plasmid or donor DNA with homology, homology directed repair (HDR) can be initiated to yield a specific mutation. A limitation of ZFNs is that zinc fingers do not always bind the triplet they are predicted to bind, and may not target properly (Rocha-Martins et al. 2015) (Fig. 1).

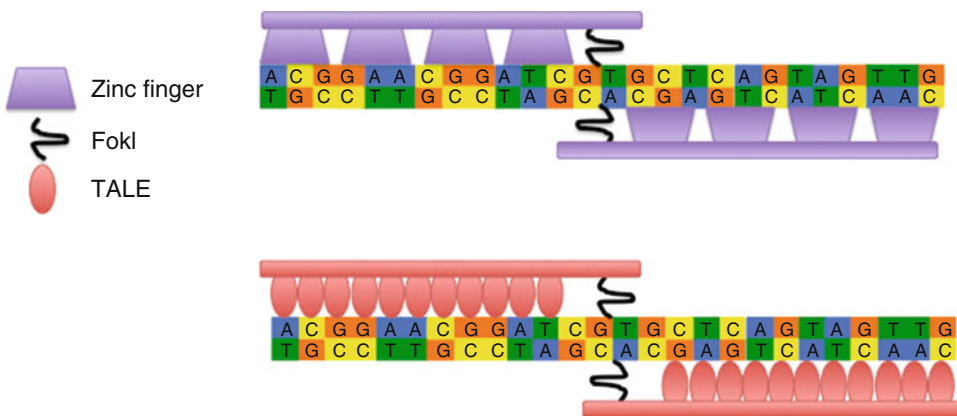
## TALENs

Transcription activator-like effector nucleases (TALENs) are another modular tool used to target mutations. Like ZFNs, they use a chimeric protein with FokI to cleave. Their DNA binding activity is due to their TALEs, which are proteins that originate from bacteria. TALEs are repeat proteins that have two amino acids in the middle of their sequence, which controls their DNA binding;

these two amino acids bind one nucleotide (Miller et al. 2011). Subsequently, they are much more specific than ZFNs and deal with less off-target effects. Like ZFNs, they can undergo either the NHEJ pathway or HDR pathway, depending on the absence or presence of repair DNA.

## Conditional Knock-outs and Recombinase Systems

Conditional knock-outs are targeted mutations that are knock-out only upon the introduction of a catalyst that causes a deletion. The advantages of this are many. Conditional knock-outs became essential for transgenic organisms; many mutations are early embryonic lethal and cannot be studied as a traditional knock-out line. The most common conditional knock-out system used currently is the Cre-LoxP system. The Cre-LoxP originates from the bacteriophage P1 – it is their system utilized for recombination. The system requires two LoxP sites outside a gene of interest and the addition of Cre recombinase proteins. Cre recombinase is a protein that recognizes and binds to the locus of crossing-over of P1 (LoxP). A LoxP site has two 13 nucleotide palindrome sequences which flank an 8 nucleotide sequence which dictates the orientation of the site. Four Cre recombinase proteins bind each site (each palindrome). These proteins then mediate the formation of a Holliday junction (a structure in which homology between the strands initiates a four-way binding, which in this setting



Targeted Mutation, Fig. 1 Modular Nucleases

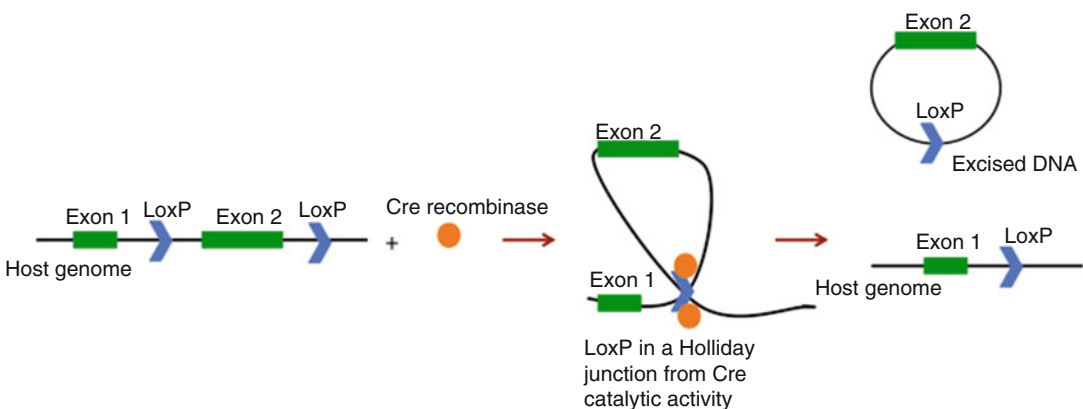
makes a loop) in the DNA (Branda and Dymecki 2004). If the LoxP sites face the same direction, the content between them is cut out and becomes its own loop, while the genomic strand now has one LoxP site. If the LoxP sites face opposite directions (facing each other), the addition of Cre will induce an inversion of the sequence between the sites.

When making cell lines, the LoxP sites need to be targeted to the proper sites (perhaps through one of the methods described in this section). The Cre recombinase can be added through a number of ways, although many introduce a plasmid (or target a sequence to add it in permanently). Typically, the Cre recombinase is under control of a tissue-specific promoter so the recombination does not happen until the proper time point, although some Cre recombinases are under the control of a promoter that is only active in the presence of a ligand. Either way, this system allows for a controllable knock-out, which is critical when studying genes that can cause lethal phenotypes at different time points (Fig. 2).

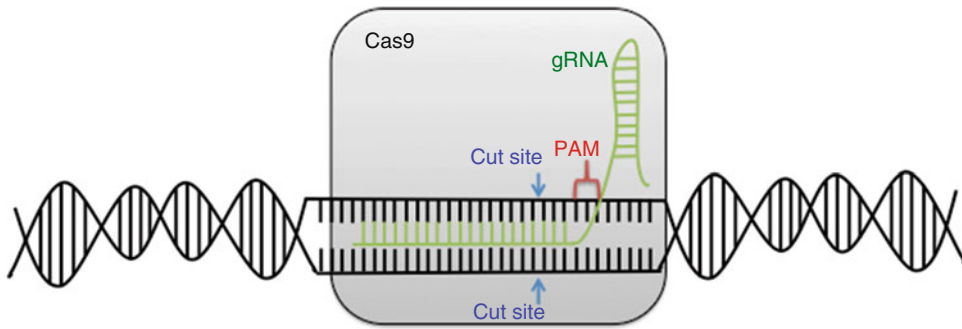
### CRISPR/Cas9

The CRISPR/Cas9 system has become a prominent tool for editing genomes. Clustered regularly interspersed short palindromic repeats (CRISPR) are originally found in bacterial genomes as a means of genome defense against viral elements. The various Cas endonucleases – which use CRISPR sequences to recognize DNA – cut the

viral elements, which then are incorporated into the genome, so other Cas proteins can effectively recognize and cleave viruses. This is essentially a form of innate immunity in bacteria. The system was reworked so that a single plasmid can express Cas9 and harbor the scaffolding and targeting elements – the guide RNA (gRNA), which is a combination of two RNAs from the native bacterial system. The Cas9 protein contains the gRNA in it, which is 20 nucleotides long. Just outside where the gRNA binds in the DNA is a NGG nucleotide sequence, referred to as a protospacer adjacent motif (PAM), which is needed for Cas9 to recognize a cut site. The gRNA recognizes and attaches to the binding motif, allowing the Cas9 protein to cut. At this point, the reaction can either undergo NHEJ or HDR depending on the absence or presence, respectively, of repair DNA (Ran et al. 2013). The CRISPR/Cas9 system has been categorized as more efficient than ZFNs and TALENs, as unlike those protein-DNA binding methods, CRISPR/Cas9 is a RNA-DNA binding method, allowing an accurate binding reaction and the capability of targeting multiple genes effectively (something that ZFNs and TALENs are unable to do). The main drawback of CRISPR/Cas9 is that it tolerates up to three mismatches in the sequence it binds, and is therefore susceptible to off-target reactions and mutations. Still, due to its efficiency, ability to be customized, and ability to target multiple sites at once, CRISPR/Cas9 has become an important tool for molecular biologists (Fig. 3).



**Targeted Mutation, Fig. 2** Conditional Knockouts



**Targeted Mutation, Fig. 3** CRISPR/Cas9

## Lentiviral Vectors

Another form of targeting a mutation (although specifically for insertions) are lentiviruses, which have become a common tool for introducing new genes due to their high efficiency of integration. As retroviruses, lentiviruses reverse transcribe their genetic content into a host cell's genome. With the advent of plasmid design, custom lentiviruses can be generated that do not integrate the viral packaging genes – therefore, a lentivirus can carry and integrate genes of interest (Sakuma et al. 2012). An example of their use would be to transduce a lentivirus that carries *gene x* into a *gene x* knock-out cell line and see if any detrimental phenotypes of the knock-out are rescued. There is a major detriment to this system; the gene of interest could integrate at any site across the genome, and therefore the surrounding chromatin state will vary greatly between subclones from one experiment. This, in turn, leads to variations in expression patterns.

## Conclusion

As gene targeting methods become more advanced and refined, they progress towards the potential to be used clinically; however, the number of off-target effects makes such use prohibitive. For now, they remain one of the most prominent and powerful tools at the disposal of molecular scientists. The ability to observe molecular systems with and without key components, to recreate disease states in ESCs, and to control knock-outs and knock-ins in a temporal fashion in animal models

is invaluable. The tools and systems described in this section have all allowed for rapid scientific progress and discovery.

## Cross-References

- ▶ Alleles
- ▶ Candidate gene
- ▶ Crossover
- ▶ DNA
- ▶ Embryo
- ▶ Exon
- ▶ Gene expression
- ▶ Gene targeting
- ▶ Genotype
- ▶ Mendel's laws
- ▶ Mosaics
- ▶ Phenotype
- ▶ Protein
- ▶ Recombination
- ▶ RNA
- ▶ Transgenic

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## Tarsier

- [Prosimian Cognition](#)
- [Prosimian Communication](#)
- [Prosimian Life History](#)
- [Haplorhini](#)

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## Taste

- [Accipitriformes Sensory Systems](#)
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- [Falconiformes Sensory Systems](#)
- [Hominoidea Sensory Systems](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Sensory Systems](#)

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## Taste Aversions

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## Introduction

Some vertebrates and invertebrates share a type of learning that is critical for survival. These animals can associate a relatively novel taste with the

effect of poisoning, resulting in a learned or conditioned taste aversion (CTA) to the respective flavor or, by generalization, to similar flavors (Scott 2011). In the following exposures to the conditioned taste stimulus, the animals would consider that stimulus dangerous because they would have learned that it induces gastrointestinal malaise and, if the conditions of survival allow it (i.e., if there is another food available), they would reject that stimulus. Acquired aversion does not only mean rejection or avoidance of the taste stimulus in the future but also involves a change of its hedonic value because it would be perceived as an unpleasant stimulus. This process preserves the life and, therefore, is an adaptive learning, especially for omnivorous species, such as the human beings, which feed on all potential food. In these species, the acquisition of CTA is vital because the learned aversion shall reduce the probability of re-experiencing the toxic effects of a harmful substance. In those situations in which the animals decide to try the aversive stimulus (e.g., with no other option to feed on), the taste aversion would be extinguished if no further poisoning consequences result from the ingestion.

Since the middle of the last century, all these processes have been studied in the laboratory to understand the behavioral mechanisms of associative learning, and standard paradigms have been established to explore the peculiar characteristics of the acquisition of CTA and other related learning complex phenomena (Bernstein 1999). Moreover, the brain substrates and cellular and molecular mechanisms behind the formation of taste aversions and taste memory are being intensively investigated to understand the neurobiological bases of this essential learning. The typical processes and characteristics of the acquisition of taste aversion and taste memory will be described in the next section. In the following sections, the well-established laboratory paradigms to induce CTA in animal models as well as the known neurobiological mechanisms of the acquisition of CTA and taste memory will be outlined. Final considerations and conclusions will be exposed in the last section.

## Processes and Mechanisms of Taste Aversion

As mentioned above, the acquisition of taste aversion is an evolutionary advantage for many animal species. The knowledge of the processes and mechanisms involved in the acquisition of CTA and taste memory formation is essential to understand the common aspects of evolution and learning between species. CTA can be easily reproduced in animal experimentation studies, and because of its characteristics, it is a powerful tool to study the universal mechanisms of learning and memory.

CTA is a unique learning process because it includes three simultaneous associative learning characteristics that have only been observed together in this form of learning. First, taste aversion can be acquired after a single trial of association between the taste stimulus and visceral disease (Bures 1998b). Second, there is a biological predisposition to associate gastrointestinal malaise with taste stimuli, which can also be associated with external stimuli but with remarkably less associative strength. In rats, for example, it has been shown that the association between taste and external signals is weak (García and Koelling 1966). The third characteristic refers to the delay between the conditioned stimulus (CS) and unconditioned stimulus (US), according to the terminology used in classical conditioning or, more generally, in associative learning. The association between the future CS (taste stimulus) and the US (visceral malaise) can be established without temporal contingency, that is, after minutes or hours of temporal delay between the processing of both of the stimuli (Bures 1998a). This unusual property of CTA to resist long delays between stimuli is related to the physiological processes of digestion. In natural contexts, a delay always appears between the ingestion and a potential poisoning. This delay is tied up with the completion of gastric digestion processes, which result in the transport of nutrients through the gastrointestinal system and the gradual absorption of the metabolic products of digestion. Consequently, the association between taste and visceral stimuli includes this temporal requirement. As there is a

time interval between the processing of taste stimulus and the visceral disease, it is thought that CTA learning results from the association between the taste memory's trace and the gastrointestinal disease.

In nature, animals show a tendency to eat new food (which means a novel taste) with caution. This process is known as taste neophobia, and as this response limits the number of unknown foods that are ingested at a certain time, it facilitates the identification of the toxic stimulus and, therefore, the acquisition of CTA, even after long delays between the stimuli. If no aversive organic consequences follow the ingestion of novel taste stimuli, the neophobic response will be extinguished in the successive exposures, and the respective taste stimulus will be recognized as being safe. Thereby, neophobia and CTA are determining factors in the process of food selection in each animal species. As CTA gathers adaptive and evolutionary processes of learning, memory, attention, and motivation, basic research has established a study paradigm of CTA that continues to be used since its first description in the middle of the last century (Bernstein 1999; Bures 1998a).

## CTA Paradigm in Animal Research

CTA, neophobia, and other complex phenomena of learning related to taste aversion, as latent inhibition of CTA (a reduced conditioned aversion resulting from taste preexposures followed by non-aversive consequences), are being studied extensively in laboratory animals to explore the behavioral and neurobiological bases of aversive learning and taste memory (Molero-Chamizo 2015; Molero-Chamizo and Morón 2015). For example, the role of the contextual cues in the acquisition of taste aversion and latent inhibition of taste aversion has been explored by using the CTA paradigm. These studies have revealed that not only external or physical cues but also internal cues, such as the time of day, can modulate the magnitude of a taste aversion (Molero-Chamizo 2013, 2017a, 2018; Molero-Chamizo and Rivera-Urbina 2017a).



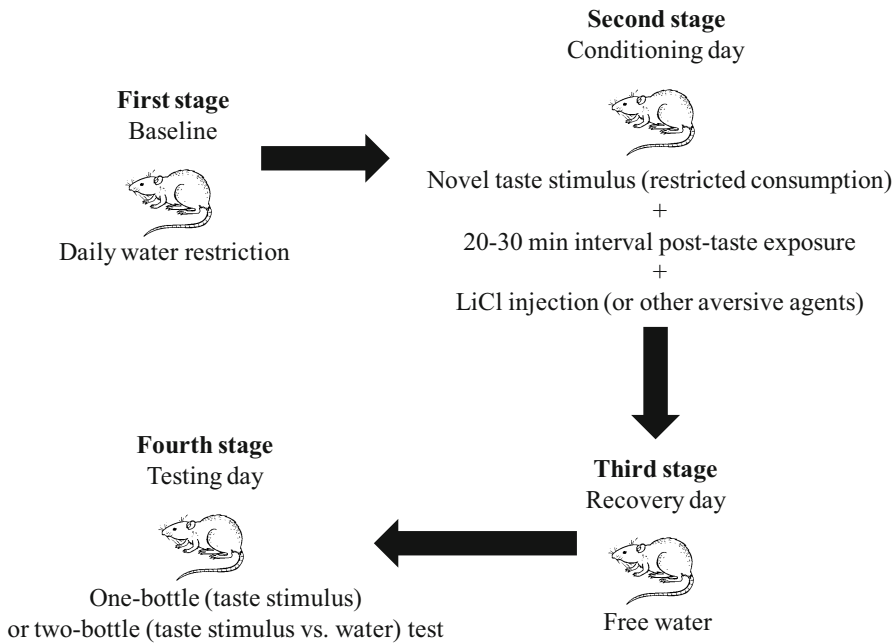
The experimental procedure used in the laboratory to induce CTA is a robust and simple tool to study the behavioral and biological mechanisms of learning and memory, in general, and taste aversion, in particular (Bures 1998a). The laboratory procedure includes ad libitum food throughout the entire procedure and a water deprivation stage in which the animals have limited access to a daily amount of water or their access to water is limited to a restricted time period each day (which is usually about 15 min). The aim of this stage is to stabilize the daily amount of water consumed by animals to obtain a baseline period. Once the initial consumptions are equated, the animals are exposed to a novel taste stimulus (representing the CS) during the next stage (the conditioning session). The taste stimulus is usually provided as fluid to facilitate the measurement of consumption. A sodium saccharin solution (0.1%) or a sodium chloride solution dissolved in water (saline 1%) are some of the taste stimuli used at this stage of the CTA paradigm. Approximately 20 or 30 min after the consumption of the new taste stimulus, a gastrointestinal distress (representing the US) is induced, usually by an intraperitoneal injection of lithium chloride (LiCl 0.15 M, 2% of body weight), although other aversive protocols have also been described (St. John et al. 2005; Traverso et al. 2012). After conditioning, a recovery day is usually introduced before testing the acquisition of CTA. In the testing day, the magnitude of the aversion to the CS that was paired with the malaise is quantified. Different tests, for example, the one-bottle test or two-bottle test, are used to quantify the strength of the taste aversion. The two-bottle test is sensitive to detect minimal aversion because animals can choose between the consumption of the taste stimulus (i.e., the CS) and water. In the one-bottle test, the animals usually ingest some amount of the CS, as it is the only consumption option presented. Thus, the amount ingested indicates the magnitude of the acquired taste aversion. As mentioned above, the reduction in the consumption of the CS after CTA learning not only indicates a conditioned avoidance response but also involves an alteration in the incentive value of the taste stimulus. As this procedure of inducing taste aversion can be easily

reproduced in the laboratory, the CTA paradigm described here is widely used in animal research. Figure 1 depicts the different stages of the CTA paradigm.

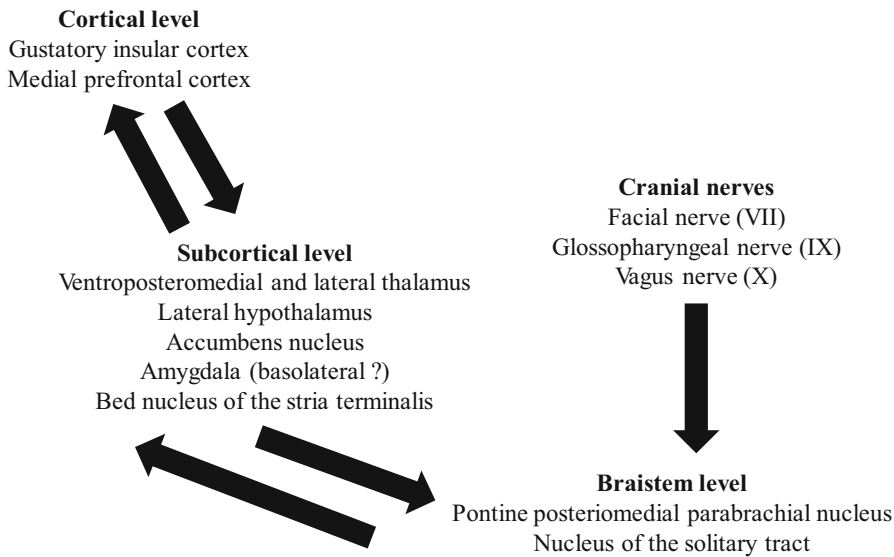
## Neurobiology of Taste Aversion

The acquisition of taste aversion and taste memory processes involve a complex neurobiological mechanism that includes different brain structures and neural pathways (Yamamoto 1993; Yamamoto and Ueki 2011). Animal model research has provided relevant information about the general mechanisms of taste aversion. However, the specific role of each structure and the connectivity of each part of the system have not been completely elucidated. The molecular mechanisms involved in taste aversion learning and memory are also an essential component of the neurobiology of taste aversion that is currently under intense research. The critical components of the neural mechanism of CTA and taste memory, as well as the related molecular pathways, will be described in this section.

Taste signals that trigger the swallowing of food start in the cells of the oral cavity membranes. These signals are projected by the VII, IX, and X cranial nerves to different nuclei of the brainstem. The first brainstem nucleus that receives the taste information is the nucleus of the solitary tract (NTS) (Harrer and Travers 1996; Spray and Bernstein 2004). Then, the taste pathway projects ipsilaterally to another brainstem nucleus, the posteromedial parabrachial nucleus (Dayawansa et al. 2014). Taste signals are then sent in an ascending direction to the following brain structures: the lateral hypothalamus, the bed nucleus of the stria terminalis, the amygdala, and the thalamus (Bielavska and Roldan 1996). The final processing reaches the gustatory insular cortex (Scott 2011; Stehberg et al. 2011). These pathways, and those involved in the processing of visceral malaise, are necessary for taste aversion learning and memory. In addition, some studies have suggested the involvement of other brain structures, such as the medial prefrontal cortex and the nucleus



**Taste Aversions, Fig. 1** Stages of the CTA paradigm used in rodents and other laboratory animals



**Taste Aversions, Fig. 2** Cortical, subcortical, and brainstem levels of taste aversion learning and memory. Arrows indicate the ascending taste pathway from the oral

cavity and the afferent (input) and efferent (output) projections described in CTA. The cranial nerves that send taste information from the oral membranes are also shown

accumbens (Marotta et al. 2014), in the acquisition of CTA. Figure 2 shows the cortical, subcortical, and brainstem components of taste aversion learning and memory.

The neural mechanism of taste aversion learning and memory includes the activity of the abovementioned structures and pathways. Less is known about the precise role of each

component of the system or the functionality of the different pathways involved. The critical function of the gustatory insular cortex and parabrachial nucleus on CTA is well established, but there is less evidence about the other brain structures. In particular, the specific role of the amygdala in the acquisition of taste aversion is one of the relevant mechanisms of CTA that need to be elucidated (Molero-Chamizo et al. 2015; Reilly and Bornova 2005; Schafe and Bernstein 1996). Some studies have tried to identify the specific nucleus of the amygdala related to the acquisition of CTA (St. Andre and Reilly 2007). The lesion studies in animal models have pointed to two amygdaloid nuclei: the central and the basolateral amygdala (Yamamoto et al. 1997). However, recent studies suggest that the main nucleus of the amygdala involved in the learning of proper taste aversions is the basolateral complex of the amygdala (Molero-Chamizo 2017b; Molero-Chamizo and Rivera-Urbina 2017b). New studies are necessary to explore the anatomical organization and the exact neurobiological mechanisms of taste aversion learning and memory.

The molecular mechanisms that trigger the acquisition and memory of taste aversion are also being intensively investigated by using animal models and in vitro procedures. These mechanisms include gene expression, receptor activity, intracellular and extracellular signaling processes, etc. Thus, taste learning and taste memory consolidation depends on protein synthesis in the gustatory insular cortex (Levitan et al. 2016; Merhav and Rosenblum 2008; Rosenblum et al. 1993). In addition, gene expression of brain-derived neurotrophic factor (BDNF) in the gustatory insular cortex and basolateral amygdala is related to the long-term synaptic plasticity processes occurring during CTA memory (Rivera-Olvera et al. 2016). With respect to receptors, the acquisition of CTA and taste memory seems to involve numerous neurotransmitter receptors, such as the  $\alpha$ -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) glutamate, the N-methyl-D-aspartate (NMDA) glutamate, and the GABA-A receptors, as well as the muscarinic receptor of acetylcholine (mACh) (Bermúdez-Rattoni 2004, 2014;

Bermúdez-Rattoni et al. 2004). Other molecules involved in cell signaling during CTA and taste learning and memory are the calcium calmodulin-dependent protein kinase II $\alpha$  (CaMKII $\alpha$ ), protein kinase A (PKA) and C (PKC), cyclic adenosine monophosphate (cAMP), and adenylyl cyclase (for a review see Molero-Chamizo and Rivera-Urbina 2017c). Although these molecules and mechanisms are beginning to be deciphered, a solid knowledge of the molecular pathways is critical to fully understand the neurobiological systems of taste aversion.

## Conclusions

The acquisition and memory of taste aversion is an adaptive learning that prevents harmful consequences of toxic food on health. This peculiar learning is easily reproduced in the laboratory, and it is a useful tool to study the behavioral and neurobiological bases of learning and memory, in general, and the complex mechanisms involved in the formation and extinction of CTA, in particular. In addition to the lesion methods used in animal research to explore the neurobiology of taste aversion, new studies are being carried out by using advanced techniques, such as immunohistochemistry, genetic engineering, molecular procedures, brain images, etc. The results of these studies might shed light on the complex taste aversion learning and memory mechanisms.

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## Taxa

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## Synonyms

[Classification of Organisms](#); [Taxon](#); [Taxonomic Rank](#); [Taxonomy](#)

## Definition

Taxa, the plural form of taxon, are the names given to taxonomic groups in an academic system of nomenclature.

The term taxon was coined by German biologist, Adolf Meyer-Abich, in 1926 as a derivative of the word taxonomy. Taxa are used within the field of taxonomy, which is the branch of science involving the classification of organisms. Taxonomists (i.e., biologists that group organisms into categories) use taxa to organize one or more populations of a particular organism that tend to exhibit morphological, behavioral, genetic, or evolutionary similarities. Taxonomists typically assign particular taxa a name and rank, which refers to a taxonomic categorization in which organisms are organized by their relative level to other organisms. At any rank, a taxon should indicate a common evolutionary background, suggesting that all members within the same taxonomic grouping evolved from common ancestors (de Queiroz and Gauthier 1990).

The process of assigning groups of organisms with a universal taxonomic name is important to biologists, because it provides a level of academic consistency globally. Classification takes into account a variety of characteristics that are shared among a group of organisms and unlike characteristics in other groups. Historically, classification has been based primarily on morphological and genetic traits in order to put alike groups into similar categories (Hagen 2012). In the 1900s, biologists began to place groups into categories based on evolutionary processes and behavioral similarities. Examples of behavioral attributes used when assigning categories to organisms would be nesting, social behavior, antipredator responses, and feeding behaviors (de Queiroz and Wimberger 1993).

Taxa can be grouped together using a few different systems to apply a rank to an organism. Through the use of cladistics as well as phylogeny, biologists are able to understand the resemblance between genetic, evolutionary, and behavioral traits shared by organisms. Cladistics is the term used for a concept of biological classification in which groups of organisms are structured by common recent ancestors in order to form a taxonomic tree. Biologists tend to suggest common ancestral lineages when similar evolutionary traits of animals form apparent groupings that are similar in one or more characteristics. Phylogeny is much like cladistics in that organisms are grouped together on the basis of evolutionary



ancestral lineages. The difference is that phylogeny uses phylogenetic trees tend to apply a representation of the time span taken for these evolutionary changes.

Even though morphological and behavioral characteristics prove to be just as accurate as other means of taxonomic classification, phylogeny estimation, or assigning taxonomic ranking, is mostly done by biologists using morphological characteristics of an organism. Since behavioral data proves difficult to collect and categorize, morphological and genetic classification will likely maintain a larger role in taxonomic ranking systems in the future. There is presently much debate amongst the scientific community regarding the potential plasticity and/or degradation of behavioral characteristics through evolutionary processes – thus insinuating that phylogenetic classification of an organism based on behavior may not be stable enough to appropriately classify groups of organisms (de Queiroz and Wimberger 1993). Nearly the same problems using genetic sequences to classify organisms have come to light. It was found that classical morphological assessments, when compared, were very different from newer genetically derived organismal relationships. Some researchers believe that the same could be said for morphological characteristics, but currently, assigning a taxonomic rank based on morphological characteristics alongside behavioral characteristics proves to be the most representative of an organism's evolutionary lineage.

## Cross-References

- [Cladistic Analysis](#)
- [Common Ancestor](#)
- [Evolution](#)
- [Phylogeny](#)
- [Speciation](#)
- [Species](#)

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## Taxis

- [Innate Behaviors](#)

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## Taxon

- [Taxa](#)

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## Taxonomic Rank

- [Taxa](#)

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## Taxonomy

- [Hominoidea Morphology](#)
- [Taxa](#)

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## Teaching

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## Definitions of Teaching

Animal teaching has long been a contentious concept. For many anthropologists and some psychologists, teaching is necessarily a human endeavor that relies on uniquely human cognitive capabilities. However, many animal behavior

researchers use functional definitions of teaching to explore the possibility that nonhuman animals can spread useful information through teaching (see Hoppitt et al. 2008; Kline 2015 for reviews and discussion). The most commonly used operational definitions are variants of that proposed by Caro and Hauser (1992) and state that teaching occurs when a role model changes their behavior in the presence of a naïve pupil, the role model suffers a cost for this change in behavior (or does not immediately benefit from it), and the pupil learns information more rapidly than they otherwise would or learns information that they otherwise would not learn. Such definitions of teaching allow researchers to investigate putative instances of animal teaching without relying on an understanding of an individual animal's intentions, in other words, without recourse to difficult-to-prove explanations involving theory of mind. Such definitions stand in opposition to anthropocentric definitions of teaching that insist that a teacher recognizes ignorance in their pupil and intentionally seeks to correct this (Thornton and McAuliffe 2006).

While immeasurably useful to those interested in animal teaching, these functional definitions also face considerable challenges. A particular sticking point is the requirement that learning on the part of the pupil must be shown to be improved by the actions of a teacher. This can be difficult or even impossible to show conclusively without experimental manipulation of the study species, and while such manipulation is possible in some contexts (e.g., in the case of meerkats (Thornton and McAuliffe 2006, see below)), it is considerably more challenging in the case of large mammals and protected species in the wild with whom it may be unethical and impractical to experiment in such a way. Therefore, it has been argued that the definition itself makes demonstrating the existence of teaching in some animal species more difficult than others and risks excluding some interesting and important instances of non-human teaching (Hoppitt et al. 2008; Byrne and Rapaport 2011).

A number of solutions to these issues have been proposed. For example, Thornton and Raihani (2008) suggested that it might be possible

to find a correlation between the extent of exposure to teaching behavior and the skill of a pupil's performance, thus showing that teaching had acted to improve skill or knowledge. However, in response, Byrne and Rapaport (2011) point out that such approaches could also generate false negatives. For example, in a case where teachers increase or decrease teaching effort in response to individual variation in learning ability, such a correlation would not be found despite the presence of quite sophisticated teaching behaviors.

Other approaches to conclusively showing the existence of teaching using a functional definition are examined in detail by Thornton and Raihani (2010) and include the use of longitudinal studies of pupil behavior and skill as well as advocating statistical methods that can control for confounding factors such as age and learning ability. It may be the case that in order to investigate teaching in a meaningful way, the core aspects of a functional definition must remain intact. However, as pointed out by Byrne and Rapaport (2011), we may have little to lose by allowing a relaxed definition of teaching to generate putative examples of teaching in the wild – examples for which closer examination of the context and psychological underpinnings of the behavior might confirm or deny the existence of teaching. In other words, it is important that the shortcomings in a functional definition of teaching that exclude very probable cases of teaching in wild animals are carefully considered in every case.

## Examples of Animal Teaching

There are a number of putative and confirmed examples of teaching in nonhuman animal species including in domestic cats (Caro 1980a, b), monkeys (e.g., Ruiz-miranda et al. 1999; Rapaport and Ruiz-miranda 2002), some insect species (e.g., von Frisch 1967; Riley et al. 2005; Richardson et al. 2007; Franks and Richardson 2006), some bird species (e.g., Raihani and Ridley 2008), and more recently in chimpanzees (Musgrave et al. 2016). Here, it is useful to examine the evidence for teaching in some of the most widely cited examples that meet the criteria set out by Caro

and Hauser (1992) and to point to resources containing further information about others.

### **Tandem Running in Ants (*Temnothorax albipennis*)**

Ants of the species *Temnothorax albipennis* frequently lead one another from a nest to the site of a food source using what is known as “tandem running.” Here, the leading ant runs in front of a naïve individual guiding that individual to a food source or alternative nest site. While tandem running a leading ant will pause, wait for their follower, and only continue to run when tapped by the “pupil” on the abdomen thus maintaining close contact between pupil and teacher. This is clear modification of behavior on the part of the leading ant that occurs only in the presence of a naïve follower (Franks and Richardson 2006). Franks and Richardson (2006) also showed that the leading ant could “proceed four times faster from the nest to the food when not encumbered by a follower.” In other words, the leading ant suffers a considerable time cost in showing the following ant where to go, and waiting for the follower to identify landmarks and learn the route. Finally, the following ant was shown to reach food significantly faster when taught by a leader than when allowed to forage alone. This shows that the follower does, indeed, learn the location of the food or nest more quickly than they otherwise would.

An interesting aspect of the teaching identified in tandem running ants is the importance of “feedback and evaluation” between pupil and teacher, which some authors maintain is a crucial aspect of teaching (see Richardson et al. 2007, and citations therein). Such “bidirectional feedback” between the leader and follower was shown between ants during a tandem run. Not only did the follower indicate when they were ready to proceed by tapping the leader’s abdomen, but the leader was observed to slow down (and the follower speed up) when the gap between the leader and follower became large. Leader ants were also shown to evaluate the value of the goal, the speed of a tandem run, and the length of time already invested in a run when waiting for a follower to re-establish a lost contact. The example of tandem running in ants demonstrated that teaching need

not rest on the kinds of complex cognitive mechanisms usually only observed in mammals.

### **Pup Provisioning in Meerkats (*Suricata suricatta*)**

Again, using the functional definition discussed above (Caro and Hauser 1992), Thornton and McAuliffe (2006) investigated a putative example of teaching in wild meerkats (*Suricata suricatta*), which they describe as “a species living in demanding environments where food acquisition involves considerable skill.” Meerkats live in cooperatively breeding social groups of between 2 and 40 individuals and young meerkat pups are largely unable to hunt for their own prey before the age of around 90 days. Prior to that age, pups are provisioned by older individuals. Meerkats eat a number of invertebrate species, among them species of scorpion that could pose considerable risk to inexperienced pups that may be unable to disable or avoid a scorpion’s sting.

Older individuals who provision pups with food (helpers) were shown to kill or disable prey before presentation to the pups. Furthermore, helpers were shown to adjust the frequency with which they kill or disable mobile prey according to pup age, gradually introducing pups to live prey. This change in behavior was conclusively shown to be mediated by pups’ age-specific begging calls using playback experiments that showed meerkat helpers providing more disabled or dead scorpions in response to begging calls recorded from younger pups. Additional help offered to pups (e.g., a helper monitoring the pup with a dangerous food item, or directing their attention towards an ignored food item) is also important in determining whether the “teacher” in this case incurs a cost associated with their changed behavior around young pups.

Helpers appear to facilitate pup learning by creating opportunities for pups to handle live prey in a relatively safe context. In this way, young meerkats can become proficient at dealing with dangerous prey such as scorpions. Thus, Thornton and McAuliffe (2006) showed that the meerkat teachers alter their behavior in the presence of a naïve conspecific and that this is a time consuming (in other words, costly) practice. The

definition of teaching proposed by Caro and Hauser (1992) also requires that the pups learn more quickly than they otherwise would or that they learn information that they otherwise would not learn. In order to demonstrate this learning (and to head off the criticism that improvements in meerkat pup food-handling is a result of maturation, not learning), Thornton and McAuliffe provisioned meerkat pups with live scorpions or boiled egg. Those provided with the opportunity to safely manipulate scorpions were capable of dealing with complex prey when tested where those provisioned with bioled egg were not.

These experiments along with behavioral observations showed that meerkat helpers changed their behavior in the presence of young pups, providing them with a vital opportunity to learn to deal with dangerous prey in a way that would otherwise be difficult, dangerous, or impossible.

#### **Purr Calling in Pied Babblers (*Turdoides bicolor*)**

Another example of teaching according to the functional definition occurs in pied babblers. These birds teach their young to associate a specific purr call with the presence of food at the nest. This call is then used to lead young birds towards food sources or away from danger (Raihani and Ridley 2008). Raihani and Ridley (2008) showed that adult birds did not use the purr call when young birds were not present and so the behavior constituted a modification of their usual vocalizations in the presence of naïve birds. The use of purr calls also increased as the nestlings aged towards fledging. Prolonged use of purr calls was associated with slower weight gain in adult birds, showing that there are some energetic costs to making the vocalizations for the adult birds.

Finally, Raihani and Ridley (2008) showed, using playback experiments, that pairing purr calls with food delivery each time the adults approached the nest to feed the nestlings elicited earlier nestling responses to purr calls than that elicited without playback.

The example of pied babblers underlined the fact that teaching in nonhuman animals takes a

variety of forms and can fall into a number of categories. Some attempts have been made to define such categories and to link instances of nonhuman teaching to the broader social learning literature and to the broader literature on the psychology of teaching in both humans and nonhumans.

### **Categorizations of Teaching**

The examples cited above are instructive. Caro and Hauser (1992) proposed that teaching in nonhuman animals could be split into two broad categories: “opportunity teaching” defined as a “teacher putting pupil in a situation conducive to learning a new skill or acquiring knowledge,” and “coaching” defined as a “teacher changing the behavior of a pupil by encouragement or punishment.” While the examples of food provisioning in meerkats and tandem running in ants fall into the former category, the teaching seen in pied babblers falls into the latter (Raihani and Ridley 2008). These categorizations can be helpful in identifying instances of teaching in different contexts and in linking instances of teaching to the broader social learning and teaching literature. A more comprehensive categorization was devised by Hoppitt et al. (2008) who aimed to link teaching with underlying social learning mechanisms.

Taking a broad view of teaching and drawing on many confirmed and putative examples, Hoppitt et al. (2008) extended the categorizations of Caro and Hauser (1992) and showed that different social learning mechanisms could underpin teaching in different contexts. For example, they showed that teaching could rely on opportunity providing and coaching (as shown above), as well as local enhancement, observational conditioning, and imitation (all well-studied social learning mechanisms).

In 2015, Kline added to the growing literature on teaching by proposing further categorizations and examining the links between disparate schools of thought on teaching; both human and nonhuman. The framework proposed by Kline aimed to provide a means to examine nonhuman

animal teaching and to explore the uniquely powerful teaching abilities seen in humans.

## Conclusions

The study of animal teaching is controversial but continues to move forward as more putative examples of teaching emerge. Teaching appears to be difficult to observe in the wild, especially relative to other forms of social learning, which are often observed across a huge range of species. There are a number of plausible reasons for the seeming rarity of teaching in nature. First, teaching may be rarely observed because the act of teaching itself is rare in certain contexts (Byrne and Rapaport 2011); second the definitions we use may be restrictive and cause frequent false negatives (Caro and Hauser 1992); or third the selective pressures involved in the evolution of teaching may mean that it is, indeed, rare in nature (Fogarty et al. 2011). Further studies of teaching across species, further refinements of our definitions, as well as innovative experimental and statistical approaches are crucial to drive the study of nonhuman animal teaching forward and, eventually, to link this field with the considerable literature on the most sophisticated example of animal teaching: that of humans.

## Cross-References

- [Animal Society](#)
- [Anthropomorphism](#)
- [Cognition](#)
- [Communication](#)
- [Cultural Transmission](#)
- [Group Living](#)
- [Social Learning](#)

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## Technical Intelligence Hypothesis

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### Synonyms

Extractive foraging hypothesis; “Technological intelligence” hypothesis

### Definition

The “technical intelligence” hypothesis is an evolutionary approach proposing that material innovations and object-oriented behavioral skills (e.g., caching and recovering nonperishable food, detecting and extracting encased food, making and using tools, building shelters) constitute major driving forces in increased relative brain size and intelligence across various animal taxa, through the selection of cognitive features that sustain complex and flexible technical proficiency (Byrne 1997).

### Introduction

Why do some animal species have large brains relative to their body size, even though the growth and maintenance of this special organ is associated with significant energetic costs and developmental constraints that jeopardize survival and delay reproduction? There are two main evolutionary hypotheses to explain the emergence of bigger brains and more sophisticated cognitive abilities in humans and nonhuman animals (and particularly nonhuman primates): the “social intelligence” hypothesis (SIH) and the “ecological intelligence” hypothesis (EIH). For both the SIH and EIH, the ultimate drivers of brain evolution are grounded in ecological factors that are essential for survival and reproduction (i.e., finding food and avoiding predators). However, the key

difference between these two evolutionary approaches lies in *how* these fundamental ecological goals are achieved. Proponents of the SIH contend that the solutions to these ecological problems belong to the socio-cognitive domain, whereas advocates of the EIH argue that these solutions are found in physico-cognitive abilities (Tomasello and Call 1997).

The rationale of the SIH is as follows: confronted with the two major ecological challenges of finding food and avoiding predators, some animals have evolved two types of social solutions, respectively socially mediated learning of foraging skills (i.e., learning from more experienced group members) and forming stable social groups of bonded individuals who have a greater chance to detect predators and protect each other reliably through cooperative behavior. However, living in large and complex groups led to secondary social challenges associated with interindividual competition for physical, social, and sexual resources (i.e., food, shelters, grooming partners, allies, and mates). Such challenges selected for socio-cognitive abilities pertaining to social representation and social memory (i.e., keeping track of one’s and others’ social relationships including dominance, kinship, and affiliation), social strategizing or Machiavellian skills (e.g., cooperating, forming alliances, predicting others’ behaviors and intentions, manipulating/deceiving others), and complex communication skills (e.g., representational, semantic, and arbitrary vocal repertoire, language; Dunbar 1998).

The EIH focuses on two main dietary characteristics: frugivory and embedded foods. The ecological challenges associated with frugivory are due to the fact that fruits vary in space (i.e., they are patchily distributed), time (i.e., they are seasonally available), ripeness, nutritional contents, and toxicity. The corresponding cognitive demands include remembering fruiting locations, predicting fruiting timing, assessing the costs and benefits of eating novel fruits, and identifying their toxic parts. Such challenges selected for physico-cognitive abilities pertaining to mental maps to represent space, time, and quantity-based decision-making, as well as associative

learning of food choice. The ecological challenges associated with embedded foods are due to the fact that some high-quality food items are hidden inside tough protective matrices (e.g., protein-rich seeds encased in hard shells) or difficult-to-process foraging substrates (e.g., lipid-rich insect larvae enclosed within bamboo stalks). The corresponding cognitive demands include detecting the presence of these concealed foods, assessing objects' affordances, and food-processing/extracting, sometimes by making and/or using tools. These mental abilities are supported by extractive foraging actions that should be fine-tuned, coordinated, and sequential. Such challenges selected for physico-cognitive abilities pertaining to sensorimotor coordination, complex action planning, and learning about the causal structure of the physical environment and the physical consequences of one's actions. The latter set of extractive foraging-related cognitive skills associated with embedded foods is referred to as "sensorimotor intelligence" or "technical intelligence" (Byrne 1997; Parker and Gibson 1977; Rosati 2017).

The "technical intelligence" hypothesis is thus a subcategory of the EIH. It aims to provide a mechanistic and functional explanation for the evolution of intelligence in humans and non-human animals. Technical innovations based on the ability to combine and use inanimate objects sequentially and instrumentally to solve a variety of problems in the physical domain may have created higher cognitive demands that favored an increase in the encephalization quotient (i.e., brain-to-body weight ratio after controlling for allometric effects as well as the size and organization of specific brain components (e.g., neocortex) which are broadly considered neural proxies for intelligence; Byrne 1997). Cross-species comparative analyses showed a strong positive correlation between relative brain size of birds and primates and their ability to use different objects in novel, instrumental, and flexible ways (Overington et al. 2009; Reader and Laland 2002). More encephalized primate species (i.e., those with a bigger "executive brain," including larger neocortex and striatum) exhibited more tool use in a foraging context than less encephalized

ones (Lefebvre 2012). In primates, nontechnical innovations also show positive correlations with relative and absolute brain size, but those relationships are not direct; they are mediated by additional factors, such as social learning, diet, and life-history variables (Navarrete et al. 2016). For instance, dietary generalism (i.e., a broad selectivity for different food resources) predicted enhanced encephalization, suggesting that the ability to exploit novel food sources may have led to an increase in brain size.

In cognitive tasks testing for physical cognition, causal reasoning, working memory, and self-control, tool-using bird species generally outperform closely related non-tool-using species, with some exceptions (Teschke et al. 2013). Advanced forms of sensorimotor intelligence have also been found in non-tool-using animal species that show flexible extractive foraging techniques (e.g., keas, a New Zealand parrot species, exhibit outstanding performance in several physico-cognitive tasks, suggesting good understanding of the physical properties of objects; Huber and Gajdon 2006). Indeed, it is not the *fact* that animals use tools, but the *way* they use it (i.e., in a hierarchically organized sequence of actions) that may shed light on the sophisticated cognitive abilities underlying complex extractive foraging strategies (Byrne 1997).

## Factors Responsible for the Emergence of Technical Innovations

### Extrinsic Factors

To explain the distribution of material innovations that might have driven the emergence of enhanced cognitive abilities, the "technical intelligence" hypothesis considers a combination of external and internal factors. Exploring the role of extrinsic factors allows us to integrate and refine the "extractive foraging" hypothesis (Parker and Gibson 1977), which focuses on gaining access to embedded foods. Both the *necessity* to exploit novel, energy-rich, and encased food sources (e.g., in periods of food scarcity), and the *opportunity* to express new extractive foraging techniques (e.g., given the presence of instrumentally

relevant objects or food sources that can be exploited) are favorable conditions for technical innovations to emerge. However, ecological factors alone only partially explain the limited distribution of tool use among extractive foragers (e.g., Koops et al. 2015a). Even though chimpanzees and bonobos live in similar ecological conditions, they considerably differ in their rates and forms of instrumental object manipulation in the wild, with tool use being virtually absent in bonobos, whereas chimpanzees are the most frequent, versatile, and proficient tool users besides humans.

For years, the “technical intelligence” hypothesis has been seen as an alternative to the SIH, according to which the major drive for the evolution of intelligence may be found in the complexity of species’ social systems (Dunbar 1998). However, as indicated before, these two hypotheses are not mutually exclusive, and such a dichotomous view has recently been reconsidered (Parker 2015). In its revised version, the “technical intelligence” hypothesis integrates social influences as fundamental in the expression of material innovations. In a systematic cross-species comparative review, the rates of tool use, innovation, and social learning in primates covary and are all positively correlated with enlarged brains (Reader and Laland 2002). Indeed, although most object-oriented behaviors are performed solitarily, they often occur within a social environment, and social influences affect the *acquisition* and *maintenance* of such technical innovations.

First, social influences mediate the *acquisition* of different instrumental behaviors, by providing means of transmission from older kin individuals (i.e., vertical transmission) or from peers (i.e., horizontal transmission). For example, the population of chimpanzees living in the Goualougo Triangle, in the Republic of Congo, is characterized by a relatively complex tool-use repertoire, together with higher levels of social tolerance and spatiotemporal coordination than other populations of chimpanzees, including numerous instances of coaction (i.e., when the demonstrator of a tool use action allows an observer to touch its hand or tool; Sanz and Morgan 2013).

Second, social cues favor the *maintenance* of technical innovations through direct and indirect

influences. Increased social tolerance allows unskilled group members to get exposed to the demonstration of novel foraging techniques by proficient group members (i.e., direct learning via emulation, imitation, and possibly teaching; Boesch et al. 2019) or to the informative presence of half-processed food parts and tool-using ateliers left behind by skilled foragers (i.e., indirect learning via stimulus enhancement; Gunst et al. 2010; Inoue-Nakamura and Matsuzawa 1997). In tool-using primate species, such as capuchins and chimpanzees, encountering previously manipulated foraging artifacts enhances the physical affordances of objects (i.e., their perceived opportunities for action) and the subsequent expression of instrumental object manipulation (Fragaszy et al. 2013). Even the noninstrumental manipulation of objects, such as the culturally maintained stone-directed play behavior performed by Japanese macaques, can be socially influenced, both directly (i.e., through the observation by naïve infants of their mothers as stone play demonstrators; Nahallage and Huffman 2007) and indirectly (i.e., through the stimulating effect of stone play artifacts, such as piles of stones left on the ground by previous stone players; Leca et al. 2010).

### Intrinsic Factors

Given that extrinsic factors are not sufficient to fully explain the phylogenetic distribution of technical innovations, the “technical intelligence” hypothesis also points at specific intrinsic factors, such as anatomical features (e.g., dexterous body parts, like hands and beaks) and psychological predispositions (e.g., motivation to manipulate objects), as key evolutionary drivers of the emergence of material innovations. It is not surprising that the highest rates of technical innovations are found in primates, and more specifically in humans, followed by great apes, whose hands possess the greatest potential for movement *complexity* and *dexterity*, as measured by the diversity of gripping and grasping capabilities. In a comparative study of 36 nonhuman primate species, unimanual/bimanual actions, synchronous/asynchronous use of hands and fingers predicted the occurrence of different categories of object manipulation, with species having a greater

manual dexterity being able to perform more complex types of object manipulation (Heldstab et al. 2016). However, hands are not necessary for technical innovations; in birds, morphological characteristics of the beak (e.g., depth, shape) play a major role in the manipulative complexity of tool-using corvids (e.g., New Caledonian crows, Goffin's cockatoos, keas; Huber and Gajdon 2006; Kenward et al. 2011).

From both proximate and ultimate perspectives, innovative instrumental object manipulation and tool use can stem from, or at least be facilitated by, the expression and transformation of noninstrumental object-directed behavior patterns, such as object play. In a wide range of animal taxa, functional/"serious" technical innovations (e.g., tool use) and purposeless/"playful" object-oriented actions covary in frequency and share broad structural similarities. For example, object play behavior patterns and tool use actions are significantly more frequent, diverse, and complex in chimpanzees than in their sister species, bonobos, even in their similar natural habitats (Koops et al. 2015a, b). Likewise, within the corvid taxon, there is a high degree of cross-species covariation between material neophilia (i.e., object-directed explorative tendencies and the propensity to engage in versatile and complex object play) and physico-cognitive abilities (i.e., mechanical problem-solving strategies, extractive foraging techniques, and tool use proficiency; Huber and Gajdon 2006). However, the nature of the developmental and evolutionary links between various object-directed activities is far from being unraveled, and the question of whether (and if so, to what extent) noninstrumental object manipulation facilitates the expression of instrumental object manipulation, and thus technical intelligence, is still open.

### **How Does the "Technical Intelligence" Hypothesis Explain the Role of Object Play in the Emergence of Technical Innovations?**

On the one hand, object play behavior may have driven the selection for the functional

manipulation of objects by providing preexisting schemata transferable to instrumental contexts (Parker and Gibson 1977). Noninstrumental exposure and handling experience with objects provide opportunities to learn about the properties and affordances of these objects, and help refine sensorimotor coordination, through the acquisition and practice of manipulative dexterity (Lockman 2000). In the Sonso chimpanzee community in Uganda, low interest in, and limited spontaneous manipulation of, sticks may explain the lack of stick-assisted tool use; individuals preferentially explored other objects that were later used as tools (Lamon et al. 2018). Similarly (Kenward et al. 2011) compared the development of noninstrumental object manipulation (i.e., object handling that is not immediately functional) in New Caledonian crows, a tool-using species, and in common ravens, a species that does not seem to use tools in the wild. They found no significant difference in the rates of noncombinatorial object manipulation, which probably results from a general/inherited manipulative tendency in all corvids. However, plastic object-directed playful sequences involving object combinations (e.g., object positioning, inserting, or rubbing in relation to other objects or a substrate) that are considered behavioral precursors of later functional manipulation (e.g., tool use) became significantly more frequent in New Caledonian crows than in common ravens during critical stages of development.

On the other hand, the intrinsic propensity to manipulate objects could facilitate the emergence of technical innovations by maintaining high levels of material neophilia (e.g., sustained interest in, and attention to, objects). Intrinsic motivation for object manipulation may promote the integration and functional use of objects in various behavioral technical domains. In primates, tool use acquisition is a lengthy process, in which learners start reaping extrinsic rewards for their actions after years of unsuccessful practice (e.g., stone tool-assisted nut-cracking behavior in chimpanzees and capuchin monkeys; Frigaszy et al. 2013; Lonsdorf 2006). In the meantime, the intrinsically rewarding nature of non-instrumental object manipulation, including

object play, characteristic of immature individuals, may serve the function of maintaining high levels of motivations in unskilled learners. For example, the playful manipulation of lithic material by juvenile monkeys precedes the acquisition of stone tool-assisted shellfish foraging in a free-ranging and coastal population of Burmese long-tailed macaques in Thailand (Tan 2017).

As opposed to instrumental object manipulation (e.g., tool use) which is *product-oriented*, object play is a *process-oriented* activity during which the performer acquires information about an action or an object involved in that action. It is acknowledged that problem-solving performance depends on an individual's motivational state, with low levels of extrinsic motivation being generally associated with poor performance. However, high levels of extrinsic motivation may also reduce an individual's technical performance, by narrowing its attention towards the product, target, or goal, rather than the process to achieve them. A comparative experimental study in great apes showed that learning about action–outcome contingencies preferentially happened during free exploration, whereas the presence of a food reward during the baited-condition distracted the subjects and delayed the acquisition of the solution to the problem (Ebel and Call 2018).

Although object play is generally a solitary activity, some species integrate specific objects into social play interactions, which may enhance interest in these objects and provide an opportunity to understand how they may be used in a social context. In Japanese macaques, branches are often incorporated in social play bouts in which the protagonists engage in role turn-taking (i.e., object holder versus non-object chaser; Shimada 2006). In some groups of the same species, unaimed stone-throwing is considered a form of tool use that serves the function of increasing the effect of agonistic displays during periods of disturbance (Leca et al. 2008).

The proximate and ultimate links among different object-oriented activities and technical innovations remain unclear. The relationships between playful and functional object manipulation have been extensively explored in captive settings but not in the wild (i.e., considering

ecologically and socially relevant scenarios, as required by the “technical intelligence” hypothesis). Through a cross-species comparative approach, the “technical intelligence” hypothesis may be used to generate testable predictions about the developmental and evolutionary connections between noninstrumental and instrumental object manipulation.

## Conclusion

Even though the SIH has been the predominant explanation for the evolution of primate cognition, the EIH is being revived, and particularly through the “technical intelligence” hypothesis (Rosati 2017). This hypothesis explores the role of ecological and social factors, together with internal predisposition to manipulate objects, in the emergence of material innovations. Still, the relative contributions of each of these factors remain unclear. Overall, EIH and SIH are not mutually exclusive; it has even been proposed that stone tool-making paved the way for the evolution of language in human ancestors, as both activities are underlain by complex, abstract, and sequential thought.

## Cross-References

- [Behavioral Flexibility](#)
- [Behavioral Variation](#)
- [Instrumental Learning](#)
- [Learned Affordances](#)
- [Motivation](#)
- [Nut-Cracking](#)
- [Social Intelligence Hypothesis](#)
- [Stone Tools](#)
- [Tool Use](#)

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## Techniques

### ► Horseback Riding

## "Technological Intelligence" Hypothesis

### ► Technical Intelligence Hypothesis

## Tecumseh Fitch

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### Introduction

Tecumseh Fitch is professor and cofounder of the Department of Cognitive Biology at the University of Vienna, Austria. He studies the biology and evolution of cognition and communication in humans and other animals and in particular the evolution of speech, language, and music. He favors a broad comparative approach, studying homologous and analogous structures and processes in a wide range of species. In doing so, he builds bridges between disciplines ranging from linguistics to neuroscience.

### Fitch's Background

William Tecumseh Sherman Fitch (III) was born on May 6, 1963, in Boston. He bears the name of his great-great-great grandfather, General William Tecumseh Sherman, as did his father and grandfather before him. The name Tecumseh originated with the Shawnee chief, who teamed up with the British to fight westward expansion by American colonists.

Fitch is the first member of his family who became a scientist. Once he discovered his passion for science, he chose a PhD over an education as artist. Drawing and music (guitar, singing, composing) remain his main hobbies, which he occasionally combines with research. For instance, he enjoys graphically illustrating his publications on vocal anatomy and collaborates with professional musicians on research

questions. Fitch also enjoys running, a hobby he shares with his wife Dr. Gesche Westphal-Fitch.

### Scientific Career and Output

Fitch spent his college years in New England, receiving his BA in biology (1986) and PhD in Cognitive and Linguistic Sciences from Brown University (1994). He then worked as postdoctoral fellow at MIT and Harvard University (1996–1999) and later held a lecturer position at Harvard, first in the Department of Biology and then Psychology (1999–2002). In 2002, he moved to Europe, where he was an invited fellow at the European Institute for Advanced Studies in Berlin, Germany (2002–2003), then a senior lecturer, and finally reader at the School of Psychology, University of St Andrews, UK (2003–2009). He was Leibniz professor and visiting scholar at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany (2006). Since 2009, he has been professor of Evolutionary Cognitive Biology in Vienna, Austria.

A key feature of Fitch's research is his cross-disciplinary approach. While his work is deeply rooted in biology, spanning from animal behavior to physiology and anatomy, he applies evolutionary thinking to various fields and disciplines outside biology (linguistics, musicology, and aesthetics). His broad interests are reflected not only in his many national and international collaborations, including researchers from natural sciences and humanities alike, but also in the formation of new research entities and interdisciplinary research foci. He is cofounder of a new department and very active in building up interfaculty and interuniversity programs that promote cognitive science and neuroscience in Vienna.

Fitch received international recognition for his studies on vocal anatomy, notably the discoveries that vocal tract length and formant frequency dispersion correlate with body size (Fitch 1997) and that a descended larynx is not a uniquely human feature (Fitch and Reby 2001). He became further renowned for his work on the evolution of language. In a seminal paper with Marc Hauser and

the famous linguist Noam Chomsky, he introduced the comparative approach to the “language faculty” (Hauser et al. 2002). In the following years, he tested and verified the hypothesized computational constraints on syntactic processing in nonhuman primates (Fitch and Hauser 2004) and other animals. Fitch still pursues both research lines – bioacoustics and bio-linguistics – today (e.g., Fitch et al. 2010, 2016; Herbst et al. 2012; Bowling and Fitch 2015). He conducts highly productive and well-funded research programs (e.g., ERC advanced grant SOMACCA, FWF doctoral programs “Cognition & Communication”), applying state-of-the-art methods for investigating sound production and perception mechanisms (noninvasive imaging techniques like X-ray and fMRI, excised larynx studies with high-speed video).

Fitch’s scientific output includes >170 research articles in peer-reviewed journals (including highly prestigious journals like *Science*, *Nature*, *Trends in Cognitive Science*, *PNAS*) in addition to several semipopular articles and book chapters. In 2010, he summarized his findings in a book entitled *The Evolution of Language*. As a gifted lecturer, Fitch is regularly invited as plenary speaker at scientific conferences as well as for public lectures, podium discussions, and television documentaries. His contribution to the field has been recognized via academic honors, like a Leibniz Professorship and Honorary Professorship at the University of St Andrews, and invitations to serve on ERC panels, editorial and advisory boards.

## Cross-References

- [Absolute Pitch](#)
- [Adaptation](#)
- [Auditory Signals](#)
- [Communication](#)
- [Comparative Cognition](#)
- [Information Processing](#)
- [Intelligence](#)
- [Language](#)
- [Language Research: Parrots](#)
- [Pattern Learning](#)

- [Semantics](#)
- [Sound Spectrogram](#)
- [Syntax](#)
- [Vertebrate Nervous System](#)

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## Teleology Versus Teleonomy in Animal Behavior

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## History and Background

Aristotle proposed that any object or phenomenon can have four different kinds of explanations:

material, formal, efficient, and final (Aristotle, c. 350 BC/1930). In describing these four types of explanations, Aristotle used the Greek term αἴτιον (aition), which has been translated as *causes*, although the meaning is closer to *grounds for* or *reasons* (Chapman 2020). According to Aristotle, it is a combination of these “four causes” that offers a complete understanding of an object or a phenomenon. The “final” cause refers to the end, purpose, or final goal of the object or phenomenon – the final state that it moves toward (*telos*). For example, the *telos* or end of an acorn is to become a fully grown oak tree. That *telos*, the “final end state” or goal, ostensibly *explains* why the acorn came to be and why it is the way it is. Teleological explanations of nature are controversial in science, as they imply some form of backward causation, whereby a future goal or end state causes objects and phenomena in the present. If teleology in its classical sense is inseparable from these assumptions, then it is inappropriate to employ teleological explanations in biology, where backward causation has no place. However, biologists still use teleological language, and one debate is whether the use of such terminology is literal or merely figurative (e.g., Mayr 1992; Neander 1991; Wright 1976).

## Useful Distinctions

### Functional Versus Mechanistic Explanations

Both Tinbergen’s “four questions” and Mayr’s distinction between ultimate (or distal) and proximate explanations are useful for understanding teleological explanations in biology (Mayr 1961; Tinbergen 1963). Tinbergen (1968) showed that one can explain a trait by addressing four issues at parallel levels of analysis: (1) survival value (i.e., function), (2) mechanism (i.e., causation), (3) development (i.e., ontogeny), and (4) evolution (i.e., phylogeny). It is the first of Tinbergen’s questions that relates to *telos* or purpose.

Mayr defined ultimate or distal explanations as historical accounts that explain why an organism has a certain trait in terms of differential reproduction in the distant past. While there is debate about what Mayr meant by “ultimate cause,” it can

roughly be thought of as representing two of Tinbergen’s questions: function and phylogeny. Mayr’s “proximate cause,” on the other hand, can be thought of as invoking explanations that are more proximate, as in closer to the present, such as answers to Tinbergen’s questions about mechanism and development.

In the study of animal cognition and behavior, identifying the proximate and mechanistic features of a trait is important for understanding the function of the trait and vice versa. Functional hypotheses yield specific predictions about proximate and mechanistic phenomena, and an understanding of the latter can rule out certain functional hypotheses and point researchers toward others (Lewis et al. 2017).

### Teleological Versus Teleonomic Explanations

Functional explanations do not need to be teleological. This is demonstrated by evolutionary biology and the study of animal behavior, because an understanding of the process of natural selection obviates the need for a designer and also explains why traits in nature *appear* as though they were designed with a *telos* in mind even if they were not.

In the classical sense, a teleological explanation invokes an internal striving toward a *telos*, goal, or end state – an explanation that contains a whiff of the supernatural. Accordingly, explanations are truly teleological if the purported goal or function is thought to be a cause of the phenomenon despite coming *after* it in time. By contrast, functional explanations in biology refer to the evolutionary history of a species, namely, the effects of a trait on survival or reproduction in past generations. This history is antecedent to the current form of the trait. Functional explanations in biology are therefore normal instances of the past causing the present and are not teleological in the classical sense.

As Pittendrigh has stated: “It seems unfortunate that the term ‘teleology’ should be resurrected. . . . The biologists’ long-standing confusion would be more fully removed if all end-directed systems were described by some other term, like ‘teleonomic,’ in order to emphasize that the recognition and description of end-

directedness does not carry a commitment to Aristotelian teleology as an efficient causal principle” (Pittendrigh 1958, p. 394). Teleonomic explanations therefore refer to the ends or functions of traits without assuming or implying that these future ends cause the form of traits in the present. Teleonomic explanations *appear* teleological, and may even use the language of teleology, but are figurative and do not involve teleology in the sense of backward causation.

George C. Williams has suggested that the term “teleonomy” be used “to designate the study of adaptation” (1966, p. 258). Williams argued that adaptations should be identified on the basis of the precision, economy, efficiency, reliability, and complexity with which they solve their respective adaptive problems (Williams 1966). These five qualities represent the relevant evidentiary criteria for reverse-engineering the extent to which a trait shows evidence of “special design,” that is, the extent to which a trait can be considered an adaptation (Williams 1966). While these five evidentiary criteria could benefit from more concrete operationalizations, reasonable working definitions exist (Al-Shawaf et al. 2020). Comparative studies of animal behavior and morphology can also be useful when assessing whether a trait is an adaptation. For example, if different species faced similar adaptive problems during their evolution, convergent evolution may lead to similar adaptations to similar ecological problems in different species.

The key point about teleology and teleonomy is that adaptations may appear teleological, and researchers may even use teleological language to describe them. Still, the teleological language is a linguistic shorthand for a normal, quotidian causal process (i.e., a history of differential reproduction) in which the past – not the future – caused the present structure and function of the adaptation.

Goal-directed human behaviors provide an interesting special case: humans are capable of consciously representing goals that they strive toward, which may make a certain variant of teleological explanations less obviously objectionable for certain human behaviors. However, the process is still one of normal causation in which the past causes the present: humans’

conscious motivations to reach their goal cause behaviors that propel them toward their goals. There is thus no need for backward causation, a supernatural telos, or anything more exotic than ordinary causation.

## Misunderstandings Related to Teleological Explanations

Humans appear to be predisposed to think about nature using teleological language (e.g., Kelemen et al. 2013). This may impede people’s accurate (non-teleological) understanding of biological traits. Unless done carefully, the use of teleological and teleonomic explanations in biology may generate or exacerbate misunderstandings about how natural selection works (Al-Shawaf et al. 2018). These include the following two misunderstandings:

### The Progressive Evolution Misunderstanding

One misunderstanding is that evolution has a goal or direction – this idea is also known as orthogenesis or evolutionary progress. If evolutionary change was geared toward a particular goal or was directional in nature, then it might be teleological. However, the theory that evolutionary change is inherently progressive or directed toward a particular end is mistaken.

### Fitness-Maximizers Misunderstanding

A rigorous evolutionary approach to psychology and behavior should not involve a search for how traits *maximize fitness* in any teleological sense (Symons 1979). The distinction here is between two ways that biologists approach organisms: (1) as fitness-maximizers (an inappropriate approach that Tooby and Cosmides (1992) call fitness teleology) and (2) as adaptation-executors (a non-teleological approach to evolved psychology). “Fitness teleologists” may approach behavior with the following question: “How does this behavior maximize this organism’s fitness?” A fitness teleologist who assumes an animal is a fitness-maximizer may have difficulty answering questions like, “Why aren’t all men lining up at sperm banks to donate their sperm?” or “How is



this obese zoo bear increasing its fitness by eating more sugary confections?” By contrast, an adaptationist will not assume that current behavior maximizes fitness. Instead, he or she may ask why the bear’s evolved neurocognitive mechanisms sometimes cause non-adaptive behaviors. The more useful questions might be: “What is the underlying neurocognitive architecture that leads to this behavior in certain contexts?” and, as Tooby and Cosmides put it, “What are the design features of this architecture— if any—that regulate the relevant behavior in such a way that it would have constituted functional solutions to the adaptive problems that regularly occurred in the species’ evolutionary history [even if it is not adaptive in this particular instance]?” (Tooby and Cosmides 1992, p. 55). This way, rather than assuming that every biological trait or behavior contributes to the telos of fitness maximization, scientists can approach behavior by considering how past selection crafted adaptations that may or may not lead to adaptive behavior in the current instance.

## Conclusion

A teleonomic explanation is a metaphorical (and therefore legitimate) cousin of a teleological explanation of nature. Teleonomy is simply the study of evolved functions, which are key to explaining the existence and form of adaptations. Biologists frequently use teleological language such as “birds sing *in order to* attract mates” for the sake of brevity. Still, as indicated by the frequent use of scare quotes and disclaimers, biologists’ use of teleological language is figurative and “should not be taken to imply that evolution proceeds by anything other than from mutations arising by chance, with those that impart an advantage being retained by natural selection” (Maddrell 1998, p. 2461).

In sum, natural selection explains the appearance of design without the need for a designer and the appearance of teleology without the need for a supernatural telos. Teleological language (teleonomy) is perfectly acceptable if we remember that it is a linguistic shorthand and do not

make the mistake of permitting true teleological (backward) causation into our explanations.

## Cross-References

- [Adaptation](#)
- [Convergent Evolution](#)
- [Nikolaas Tinbergen](#)

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## Temperament

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## Synonyms

Constitution; Disposition; Nature; Personality

## Introduction

The study of temperament in nonhuman animals is of great interest due to recent advances that demonstrate a relationship between temperament and animal welfare, immune functioning, social dynamics, and reproductive success (e.g., Capitanio et al. 1999; Fairbanks and Jorgensen 2011; Sih et al. 2004). In humans, temperament is defined as inherited early behavioral tendencies that are observed and continue to develop into adulthood and serve as the building blocks for personality (Gosling 2001). However, identifying what constitutes as temperament in nonhuman animals has been difficult to agree upon in the literature. The terms temperament and personality have at times been used interchangeably when describing the different behavioral responses an animal can exhibit. When expressed as separate terms, temperament tends to describe an individual's inherited genetic-based behavioral differences in a nonsocial context, whereas personality describes nongenetic

differences in behavior in social contexts (Carter et al. 2013; Clarke and Boinski 1995; Coleman 2012; Watters and Powell 2012). Thus, temperament is present during infancy, is thought to be innate, and may consist of physiological emotional and cognitive responses that are consistent over time.

There are several methods present to assess temperament in nonhuman animals. The first and simplest methodology is to study the animals in a naturalistic setting, with no manipulation of the environment. When using an experimental design, temperament is most commonly assessed by presenting a novel object or stimuli in the feeding area or environment of the animal, and observing their reaction (i.e., approach or avoidance; e.g., Capitanio 1999; Koolhaas et al. 1999). Researchers can record these responses to determine what temperament constructs are present by conducting ratings or utilizing the coding/collating of behavior methodology (Freeman et al. 2013; Freeman and Gosling 2010). Behavioral coding consists of researchers recording the type, frequency, and duration of any particular behavior and then classifying those behaviors into subsequent groups (i.e., traits) of commonly occurring patterns of behavior. Ratings consist of two or more judges scoring each animal on a number of predefined temperamental traits. These scores are then analyzed with factor analysis to reveal what dimensions of temperament may be present. Frequently reported dimensions related to temperament include proactive-reactive and bold-shy dimensions (e.g., Koolhaas et al. 1999). Previous research suggests that bold/proactive individuals are more likely to explore and interact with their environment and exhibit a lower stress response to novel stimuli. Conversely, shy/reactive individuals are more cautious when approaching novel situations, exhibit a higher stress response, and are slower to react to challenges (Koolhaas et al. 1999; Sih et al. 2004; Groothuis and Carere 2005). Recent research has shown that along these axes are other dimensions present, such as activity, fearfulness, confidence, excitability, and sociability (e.g., Budaev 1998; Capitanio 1999; Weiss et al. 2006).

## Applications of Temperament Assessments

The study of temperament in animals is relevant to many aspects of a species' life history. In domestic dogs (*Canis familiaris*), assessments of temperament are considered very important when determining the adoptability of shelter dogs into different types of family homes (i.e., dogs that get along with children or other dogs/pets, etc.). Understanding the individual temperament of each dog can help increase the likelihood of a successful adoption placement (De Palma et al. 2005). Identifying various temperament types can also aid in determining the suitability of a dog to work as a police dog, guide dog, medical dog, rescue dog, or other role where the dog performs a job or role with humans (Jones and Gosling 2005). Similarly, the animal-caretaker relationship for domestic and managed care animals can be greatly affected by an individual's temperament. Understanding of an animal's temperament can indicate which individuals will benefit from a great deal of attention from their caretakers versus individuals that require less attention to minimize anxiety or stress. For example, stump-tailed macaques (*Macaca arctoides*) were rated by animal care staff on a scale for the temperament trait friendliness, and found that the individuals with lower friendliness scores exhibited more self-directed and scratching behaviors, an indication of agitation or anxiety, when animal care staff were present (Waitt et al. 2002). Individuals with higher friendliness scores had more positive interactions with animal care staff and sought out more of this attention, possibly because the human interaction was a rewarding experience. Applications of temperament in managed care facilities can inform staff as to the best management practices to optimize an animal's welfare.

Temperament assessments have also been shown to help predict the trainability of individual animals. Shy, stress-sensitive individuals may experience some anxiety and minimal benefit from various environmental enrichment options compared to bold or exploratory individuals. Several studies have examined how an individual animal's temperament affects the effectiveness of

certain forms of enrichment. For example, Fox and Millam (2007) tested juvenile orange-winged Amazon parrots (*Amazona amazonica*) for temperament fearfulness by observing their reaction to a novel object in their feeding area. They were then exposed to two forms of enrichment: high-novelty with frequent changes in the enrichment item presented and low-novelty where the same form of enrichment was presented repeatedly. Overall the birds reacted less fearfully toward the high-novelty enrichment. However, the animals that were considered more fearful from the temperament test also exhibited apprehensive and anxious responses toward the high-novelty enrichment type. Similarly, Yamanashi and Matsuzawa (2010) examined the behavioral responses of six chimpanzees on a series of cognitive tasks. Three of the subjects were labeled stress-sensitive due to the scratching and self-directed behaviors observed when completing the cognitive tasks. These stress-sensitive subjects were more likely to become agitated when answering incorrectly compared to the stress-resistant chimpanzees, suggesting that cognitive tasks may be an enriching experience for some animals, but not all. The results from these various studies emphasize the importance of considering temperament in the effectiveness of different types of enrichment for individual animals. Understanding what will decrease stress in an animal can contribute to promoting its overall health and welfare.

The study of nonhuman animal temperament as it relates to animal welfare can provide long-term benefits to both wild and captive populations. Knowledge of temperament can help and predict outcomes to social conflict or what individuals will spend more time together. Bold individuals can help maintain social stability whereas shy individuals are more vulnerable to stressors that disrupt group dynamics (McCowan et al. 2011). In rhesus macaques (*Macaca mulatta*) successful pairings (i.e., no aggressive behaviors observed) were more likely to occur in individuals with a minimal difference between their scores for the temperament trait inhibition compared to unsuccessful pairings (McMillan et al. 2003). The authors then paired 18 sets of

similar temperament (i.e., inhibition) partners and 19 partners with different temperaments and found that more positive social behaviors were occurring between the partners that had similar scores for inhibition. Thus pairings with similar temperament exhibited more affiliative behaviors and less aggressive behaviors compared to the pairings of different temperament individuals. More recently, Weinstein and Capitanio (2008) examined how infant temperament affected later social relationships in rhesus macaques. Temperament was assessed with the Infant Biobehavioral Assessment and social behaviors were assessed at 1 year of age. The results indicated that individuals with similar temperament traits were more likely to associate and engage in positive, affiliative behaviors with one another at 1 year of age. In a follow-up study, the yearlings with similar temperament trait scores for the trait equitability were more likely to maintain their affiliative relationship at 2 years of age (Weinstein and Capitanio 2012). Overall, these various studies suggest that various temperamental factors influence partner choice for decreased aggressive interaction and increased positive social behaviors.

The study of temperament as it relates to an animal's propensity to feel anxious or fearful is one of the most commonly discussed uses of temperament analyses. The mother's milk for infant rhesus macaques is also known to affect temperamental responses related to stress, where infants that nursed from mothers with higher available milk energy (AME) exhibited higher levels of activity and exploration during novel situations compared to infants nursed with lower AME. This suggests that AME may be an important physiological cue for the development of temperament (Hinde and Capitanio 2010). For example, when looking at the relationship between temperament and stress response in infant rhesus macaques, highly reactive individuals exhibit greater hypothalamic pituitary adrenal (HPA) activation and stress-behavioral responses to novel stimuli compared to less reactive individuals (Suomi 1991). Boyce et al. (1998) likewise found that monkeys with high inhibition scores suffered higher wounding rates when

placed in more stressful situations (e.g., social conflict, competition) compared to less inhibited monkeys. Comparable results found more recently by Capitanio et al. (2005) demonstrated that monkeys with low sociable scores exhibited abnormal HPA regulation and immune function when housed in an environment with frequent social conflict between group members. Understanding individual differences in temperament can thus greatly affect our understanding of the psychological well-being of these animals and inform housing and conservation efforts regarding group cohesion for social species in sanctuaries or managed care.

It is suggested that temperament should be considered in conservation programs such as reintroduction or relocation of an animal or species. Traits related to temperament and personality can aid efforts to identify individuals most likely to survive in the wild, and thus increase the success rate of such conservation programs. For example, swift foxes (*Vulpes velox*) were identified as exhibiting two temperament traits: bold and cautious. Cautiousness was shown to be more advantageous than boldness, as the bolder foxes were more likely to die within 6 months of being reintroduced into the wild (Bremmer-Harrison et al. 2004). In managed care facilities, introduction programs are also an important area where temperament can be greatly influential. For example, gorillas (*Gorilla gorilla*) with higher scores for extroversion and lower scores for dominance may be more likely to be placed in bachelor groups together in an exhibit without social conflict (Gold and Maple 1994). Understanding how environmental cues can influence temperament expression is also important for increasing the success rate of these introduction programs in both wild and managed care populations.

## Conclusion

This chapter highlights the application of temperament assessments to animal welfare, management practices, and health outcomes for a variety of vertebrate species. There is an increased need for more widespread application of temperament

assessments across species to better implement various conservation and management practices. While understanding an individual's temperament has been shown to help us predict how an animal may behave in both a social and nonsocial context, more work is needed to understand which dimensions of temperament are important or relevant to a given species. Furthermore, more research is needed to determine the distinction between the terms temperament and personality, as temperament is at times used to circumvent saying that nonhuman animals have personality. The use of behavioral syndromes in the terminology also should be addressed for how or if these terms refer to different components of behavior, as all terms typically refer to a pattern or group of behaviors consistent over time and across context (Sih et al. 2004). As our understanding of the temperamental constructs in animals increases, applications of temperament assessments will be more frequently incorporated to help researchers understand the individual differences present in the reactivity of an animal and increasing the welfare of animals at the individual and group level.

## Cross-References

- [Animal Welfare](#)
- [Coping Style](#)
- [Personality in Animals](#)

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## Template RNA

### ► Messenger RNA

## Temple Cats

### ► Sacred Cats

## Temporal Bisection Procedure

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## Definition

The temporal bisection procedure is used to study temporal discrimination. Initially, the subject learns to choose between two response alternatives, R1 and R2, according to the (short = S1 or long = S2) duration of a sample stimulus: After S1, choose R1, and after S2, choose R2. Next, the experimenter introduces samples with new, untrained durations, and for each one, records the proportion of R2 (or “long”) choices. The psychophysical function relating the proportion of “long” choices to sample duration  $t$ , i.e.,  $p(\text{“long”}|t)$  reveals key properties of temporal discrimination.

## Introduction

Humans and animals can learn to adjust their behavior to the temporal attributes of the environment. A dog fed a bit of food every 30 min will come to salivate close to the moment the next food is due (Pavlov 1960). A rat that receives food every 60 s for pressing a lever, learns to pause for about 30 s and press the lever afterwards (e.g., Skinner 1938). An adult human can readily tell that a traffic light is red for longer than usual,

or that one phone call was shorter than another. The study of the sense of time of humans and animals has progressed considerably during the past and current centuries. One of the main procedures used to study it is the temporal bisection procedure.

## The Procedure and Typical Findings

Developed by Church and Deluty (1977) on the basis of Stubbs' (1968) and Catania's (1970) earlier work, the temporal bisection procedure instructs or teaches subjects to choose one of two responses, R1 and R2, following one of two sample stimuli, S1 and S2. Choice of R1 is correct/reinforced following S1, and choice of R2 is correct/reinforced following S2. Because S1 and S2 differ only in duration ( $S1 < S2$ ), to master the task, the subject must learn the temporal discriminations:  $S1 \rightarrow R1$  and  $S2 \rightarrow R2$ .

To characterize what the subject has effectively learned, the procedure then introduces generalization tests: On some trials, stimuli with novel durations,  $S_t$ , substitute for S1 and S2 (typically,  $S1 < S_t < S2$ ). These generalization tests may occur in extinction (choices are not reinforced), or under non-differential reinforcement (any choice after  $S_t$ , be it R1 or R2, is reinforced occasionally; e.g., Carvalho et al. 2016). The experimenter records the proportion of, say, R2 choices as a function of stimulus duration.

The procedural details depend on the species. With rats, S1 and S2 can be tones, noises, lights, or blackout periods, and R1 and R2 are typically two levers the animal can press (e.g., Church and Deluty 1977). With pigeons, S1 and S2 can be houselight or keylight durations, and R1 and R2 are typically two keys with different location or color that the birds can peck (e.g., Carvalho et al. 2016); with humans, S1 and S2 can be auditory or visual stimuli, and R1 and R2 are distinct keys in a computer keyboard (e.g., Wearden and Lejeune 2008). Animal studies tend to use durations spanning two orders of magnitude, from a few tenths of a second (S1) to a few tens of seconds (S2); human studies tend to use significantly shorter durations, from a few hundreds of

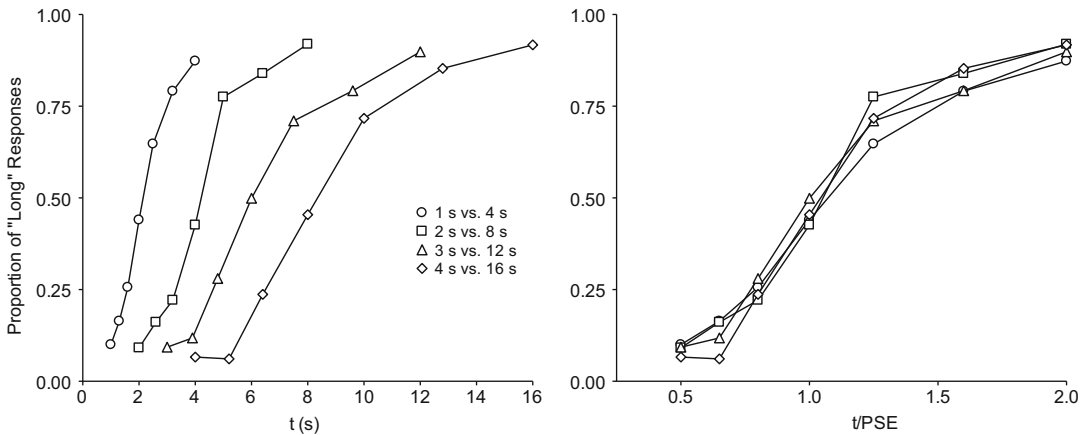
milliseconds to only a few seconds, partly to prevent counting during the sample. Whereas animals earn a small amount of food as a reinforcer for correct choices, humans earn points or verbal feedback ("Correct," "Good," etc.).

To analyze the data, the experimenter plots the proportion of R2 or "long" choices for each stimulus duration,  $t$ . The resulting psychometric function, denoted by  $p(\text{"long"}|t)$ , has a typical sigmoidal shape and increases from about 0 to about 1 as  $t$  ranges from S1 to S2. The left panel of Fig. 1 shows the average psychometric functions from Church and Deluty's (1977) seminal work with the bisection task.

The psychometric functions reveal some key properties of timing. First, the duration that yields indifference between R1 and R2 [i.e., the  $t^*$  such that  $p(\text{"long"}|t^*) = 0.5 = p(\text{"short"}|t^*)$ ] is generally interpreted as the duration that, for the subject, is equally distant from S1 and S2. That is, the interval from S1 to  $t^*$  seems equal to the interval from  $t^*$  to S2. Hence,  $t^*$  is called the Point of Subjective Equality (PSE). Moreover, because  $t^*$  may be interpreted as the point that, on the subjective scale for duration, divides the interval from S1 to S2 in two equal parts, it is also called the Bisection Point; hence, the procedure's name, Temporal Bisection. For animals, the PSE tends to be at the *geometric mean* of S1 and S2 ( $t^* \approx \sqrt{S1 \cdot S2}$ ), whereas in humans it tends to be at the *arithmetic mean* of S1 and S2 ( $t^* \approx (S1 + S2)/2$ ) (Church 2002; Richelle and Lejeune 1980).

Second, better temporal discriminations yield steeper functions, i.e., sigmoidal functions with higher slopes at the PSE or, equivalently, functions that rise from about 0 to about 1 in a shorter interval. The latter can be quantified by means of two durations,  $t_{q1}$  and  $t_{q3}$ , the durations for which the psychometric function equals 0.25 and 0.75, respectively (i.e.,  $p(\text{"long"}|t_{q1}) = 0.25$  and  $p(\text{"long"}|t_{q3}) = 0.75$ ). The two durations define the difference limen (DL),  $DL = (t_{q3} - t_{q1})/2$ . The smaller the DL, the faster the psychometric function rises. A subject with a smaller DL expresses greater sensitivity to the time dimension.

Third, for the same subject, the ratio DL/PSE (or an equivalent e.g., the reciprocal of the slope



**Temporal Bisection Procedure, Fig. 1** Left panel: Average psychometric functions obtained by Church and Deluty (1977) with rats using four sets of S1 and S2 values: 1 s versus 4 s, 2 s versus 8 s, 3 s versus 12 s, and 4 s versus

16 s. Right panel: Superposition of the psychometric functions after normalization of the time axis. (Reproduced with permission from the American Psychological Association)

of the function at the PSE divided by the PSE), a quantity akin to a Weber's fraction, tends to remain constant across bisection tasks. This and similar findings show that Weber's law applies also to temporal discrimination [but see Wearden and Lejeune 2008 for exceptions].

Fourth, bisection tasks using trained durations in the same ratio,  $k$ , (e.g., task 1:  $S1 = 1$  and  $S2 = 4$ ; task 2:  $S1 = 3$ ; and  $S2 = 12$ , for  $k = 4$ ) yield psychometric functions that superimpose when plotted in the same figure with the time axis normalized (i.e., divide all durations from a task by its  $S1$  or by the geometric mean of its  $S1$  and  $S2$  stimuli). The right panel of Fig. 1 shows this property. The superimposition of the psychometric functions reveals that temporal discriminations are relative to the trained durations. To put it more formally, if we let  $p(\text{"long"}|t, S1, S2)$  stand for the probability of choosing R2, given a test stimulus with duration  $t$  after mastering a task with stimuli  $S1$  and  $S2$ , then superimposition means that

$$p(\text{"long"}|t, S1, S2) = p(\text{"long"}|k \times t, k \times S1, k \times S2).$$

To illustrate, suppose that after mastering a bisection task with 1- and 4-s stimuli, a pigeon chooses "long" with probability 0.8 following a 3-s test stimulus. Then, after mastering another

task with 3-s and 12-s stimuli (i.e.,  $k = 3$ ), the same pigeon will choose "long" with probability 0.8 after a 9-s test stimulus. Superimposition of psychometric functions reveals the *scalar property* of timing (Church 2002; Wearden 2016).

Except for the location of the PSE, the foregoing properties of temporal discrimination have been observed in nonhuman and human animals (Church 2002; Richelle and Lejeune 1980; Wearden 2016), even though the procedural details vary (e.g., bisection experiments with humans generally use instructions, not primary reinforcers, to establish the initial discriminations; Wearden 2016). Thus, the basic processes involved in temporal discrimination may have substantial cross-species generality.

## Conclusions

The temporal bisection procedure has been extensively used to study how a host of different variables affects temporal discrimination. By manipulating the modality and nature of the sample stimuli, learning history and context, deprivation level, drugs, lesions, or the genetic makeup of the subjects, for example, and then examining

how these manipulations affect the psychometric functions, their PSE's, slopes, range of choice proportions, etc., a richer view of the sense of time of animals and humans has emerged. These studies have also helped researchers to develop better theoretical models of temporal discrimination.

## Cross-References

- [Discrimination Learning](#)
- [Interval Timing](#)
- [Operant Conditioning](#)
- [Peak Procedure](#)
- [Stimulus Control](#)
- [Timing](#)

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## Temporal Cortex

- [Temporal Lobe](#)

## Temporal Lobe

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## Synonyms

[Temporal cortex](#)

## Definition

Temporal lobes are the part of gray matter (cerebral cortex) that is positioned behind the temples, on either side of head.

## Introduction

The temporal lobe has fascinated neuroscientists for several decades due to its role in memory and learning required for everyday activities. It is found only in primates. However, a few non-primate species possess a laterally expanded cortex that appears similar to the primate temporal lobe. The process of development in primates marked a specialization in visual information processing and object recognition, resulting in evolution of temporal lobe. In humans, the temporal lobe is

significantly expanded in comparison to the nonhuman primates including the apes.

## Evolution of Temporal Lobe

The presence of Sylvian fissure in ancestor *Smilodectes gracilis* suggested the presence of temporal lobe early in evolution in primates. *Aegyptopithecus*, an early fossil catarrhine that predates the divergence between hominoids (apes) and cercopithecids (Old World monkeys), is an example of an early fossil with superior temporal sulcus.

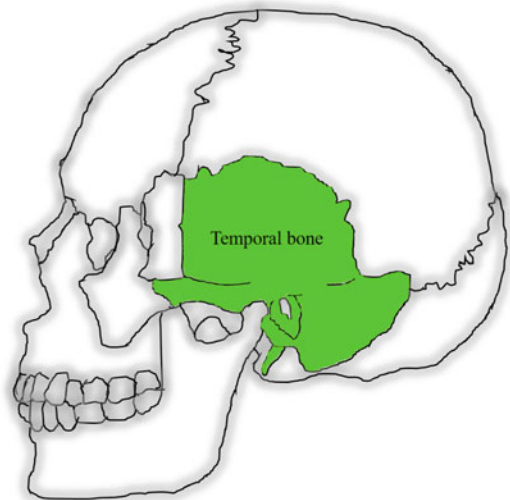
## Temporal Lobe in Nonhuman Primates

The temporal lobe is not developed in all nonhuman primates. A comparison between the temporal lobe anatomy of monkeys and dogs shows that in monkeys, the temporal lobe structures were highly interconnected. Information from cortical areas of temporal, frontal, and parietal lobes reaches perirhinal and parahippocampal cortical areas located on the medial temporal lobe which in turn project to the entorhinal cortex followed by the hippocampus. The amygdala also receives a strong projection from the entorhinal as well as perirhinal cortex. However, in dogs, the connections of neocortical areas to perirhinal, entorhinal, and parahippocampal areas are relatively unknown. Lesions of hippocampus result in impairment in spatial layout of an animal within its environment. In monkeys, the lesion in this area leads to impairment of memory for place. In rats with lesions to the perirhinal cortex, there is deterioration of spatial tasks. Recognition memory deficit due to involvement of temporal lobe in primates is still unclear. Recent studies in monkeys provide evidence that the rhinal cortex is critical for both object identification and memory (Bryant and Preuss 2018). Auditory recognition in animals is important for processing auditory information and communication. Studies on dogs have shown that they learn auditory memory tasks relatively easily as compared to monkeys who have difficulty learning auditory tasks.

## Temporal Lobe in Humans

In humans, temporal lobe is concerned with maintenance of visual memory, language comprehension, and emotion association by appropriately processing the sensory inputs. It derives the name as it sits inside the temporal bone (Fig. 1). The temporal lobe lies in the middle cranial fossa beneath the lateral fissure on both cerebral hemispheres. It is situated posterior to the frontal lobe and inferior to the parietal lobe. The greater wing of the sphenoid bone outlines it anteriorly. Inferiorly it is bound by the superior surface of the petrous part of the temporal bone, and laterally by the squamous part of the temporal bone and the adjoining parietal bone (Standring 2015).

The temporal lobe has four surfaces: lateral, medial, superior, and inferior. The *lateral surface* of temporal lobe consists of three parallel gyri, namely, superior, middle, and inferior temporal gyri (Fig. 2a). The lateral surface of the temporal lobe is separated by the superior and inferior temporal sulci (Mai et al. 2015). The lateral parietotemporal line separates the temporal and occipital lobes, and the occipitotemporal line



**Temporal Lobe, Fig. 1** The location of temporal bone in the human skull. Temporal lobe of the cerebral cortex derived its name from this bone. The other major lobes are also termed in similar forms

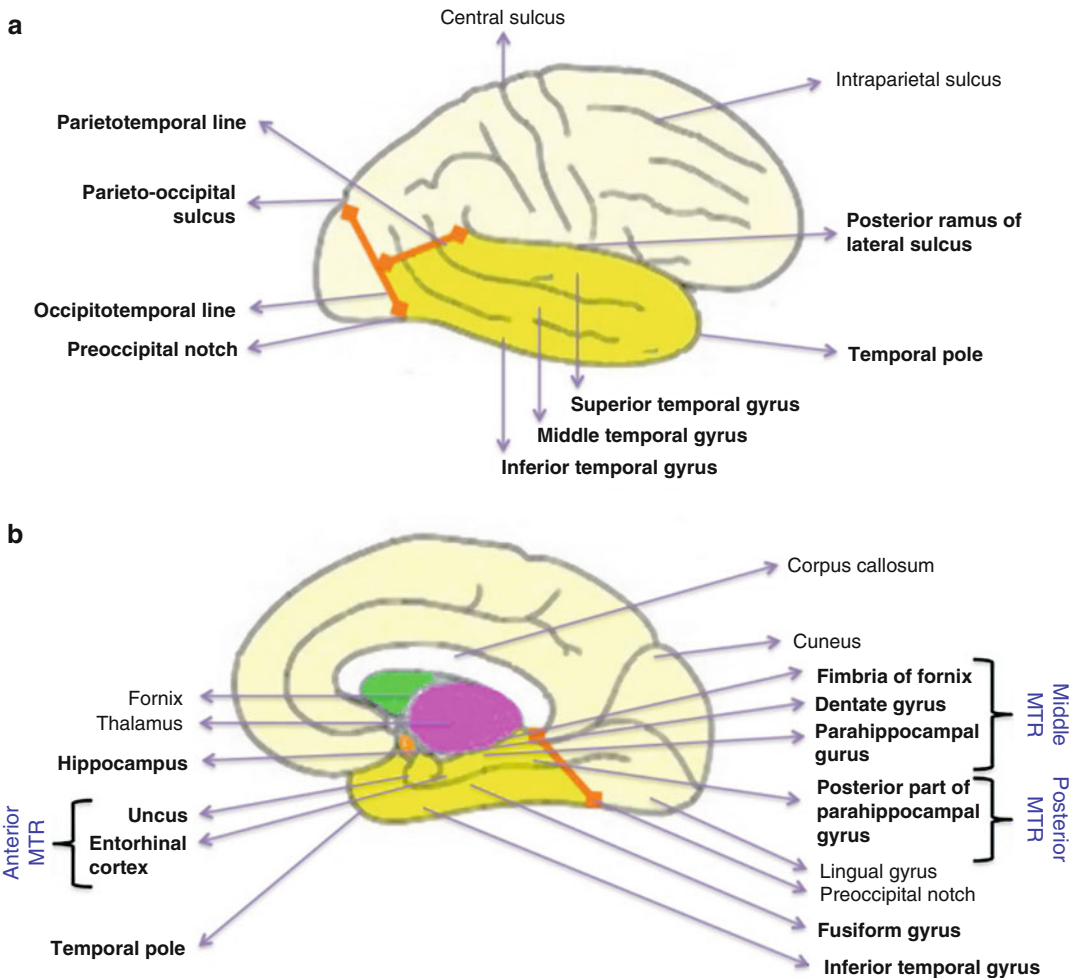


separates the temporal and parietal lobes (Fig. 2a). The superior surface consists of the planum polare, the anterior transverse temporal gyrus or Heschl's gyrus, and the planum temporale from anterior to posterior. This surface faces the Sylvian fissure, which is a very important landmark on the lateral surface of the cerebrum. The inferior surface consists of the inferior margin of the inferior temporal gyrus, the fusiform gyrus, and the parahippocampal gyrus from lateral to medial. These gyri are separated by the

occipitotemporal sulcus and the collateral sulcus (Kucukyuruk et al. 2012).

### Medial Temporal Region (MTR)

In humans, *medial surface* also known as the medial temporal region (MTR) is divided into three segments: anterior, middle, and posterior. Mostly the uncus and the entorhinal cortex form the anterior MTR (Fig. 2b). The middle MTR



**Temporal Lobe, Fig. 2** Schematic diagram of the human brain showing the margins of temporal lobe and associated structures in the brain. (a) *Lateral surface of the right cerebral hemisphere*. Region colored in yellow shows the temporal lobe with superior, middle, and inferior gyri. The orange colored line shows the boundaries of temporal lobe

separating it from the other lobes (Occipitotemporal line separates it from occipital lobe whereas parietotemporal line do the same from parietal lobe). (b) *Mid-sagittal view of left hemisphere*. The location of medial structures like medial temporal region (MTR) can be seen. Different gyri of temporal lobe are also shown

consists of parahippocampal gyrus, the dentate gyrus, and the fimbria of fornix, while the posterior end of the parahippocampal gyrus forms the posterior MTR (Fig. 2b) (Kiernan and Rajakumar 2013).

In animals, the medial temporal lobe manifests certain variations. In rhesus macaque, visual processing occupies greater cortical function as compared to rodents who rely mainly on olfaction. Perirhinal and postrhinal cortices of the rhesus macaque receive primarily visual type cortical inputs, while in the rodent inputs to these regions are distributed more evenly across all sensory modalities. The entorhinal cortex receives direct projections from the olfactory bulb in the rodent resulting in superior that olfactory system in the rodent.

### **White Matter Associated with Temporal Lobe**

Bundles of white matter called fasciculus connect the distant association areas. There are seven fasciculi in humans and six in macaques. One of the most important is arcuate fasciculus. It provides a two-way communication between frontal cortex, including Broca's expressive speech area, and Wernicke's receptive language area in the posterior part of the superior temporal gyrus. Conduction aphasia is traditionally attributed to a destructive lesion that interrupts the arcuate fasciculus. It is poorly developed in macaques and restricted only to superior temporal gyrus in chimpanzees.

Another fasciculus that connects frontal, parietal, occipital, and temporal lobe is the cingulum bundle. It traverses close to cingulate gyrus. It is concerned with memory, emotions, and attention and has been studied both in human and primates. The inferior longitudinal fasciculus is an important source of fiber afferent to the amygdala. It connects the visual areas with one another and also to the temporal polar cortex (Kiernan 2012). It is found in both humans and chimpanzees. Others include the uncinated fasciculus that is a frontotemporal association bundle and the middle longitudinal fasciculus.

### **Important Structures in Temporal Lobe**

**Hippocampus:** This is one of the important structures located in the medial temporal lobe of the cerebrum. The structure is compared to a seahorse due to its shape. It forms an important part of the limbic system and has a vital role in long-term memory and spatial navigation. It is one of the first regions of the brain to get affected in patients suffering from Alzheimer's disease. The hippocampus is also important in the formation of new memories. Researchers have also established the role of the hippocampus in long-term memory. In cases of damage, patients might experience retrograde amnesia that affects memories formed before the damage or anterograde amnesia that is difficulties in forming new memories. However, ability to learn new motor or cognitive skills is preserved (Bird and Burgess 2008).

The role of hippocampus in the development of cognitive map of the environment was recognized with the discovery of place cells in the 1970s. A common observation in amnesia patients is getting misplaced and forgetting their original location. This has been studied extensively in animals (Rosene and Van Hoesen 1987) including humans. It is understood that humans and animals approach similar tasks using multiple memory systems. For example, habit learning of a task occurs most commonly in monkeys in comparison to humans who memorize stimulus material. Behavioral impairments observed in rats with hippocampus lesions are not similar to memory impairment seen in humans with hippocampal damage. Damage to the hippocampus can also result from oxygen starvation (hypoxia), encephalitis, or medial temporal lobe epilepsy.

**Amygdala:** It consists of a group of heterogeneous nuclei located within the temporal lobe. It receives inputs from a wide variety of both cortical and subcortical areas of the brain. It receives information from visual system, auditory, olfactory, and gustatory and somatosensory cortices. In addition, it also receives projections from association cortex, the thalamus and hippocampus. It is involved in emotional learning, modulation of memory, and emotional influences on social behavior and decision-making via its

interactions with the prefrontal cortex and the hippocampal system. Studies with monkeys and rodents have shown that, like humans, stronger stimuli result in greater activation of the amygdala. This affects fear conditioning and sensing danger (Rosen and Donley 2006). It has a role during fear conditioning in humans where sometimes a freezing response occurs in a potentially threatening situation. It is also involved in memory formation and retrieval, and affective processing in humans. It also participates in semantic encoding and discrimination between familiar and novel stimuli.

## Disorders of Temporal Lobe

1. Klüver-Bucy syndrome (KBS) was first described in monkeys. Experimentally bilateral temporal lobectomy was performed in monkeys while it was done in humans (Terzian and Dalle Ore 1955) who had intractable epileptic. The diagnosis is based on the presence of any three of the following symptoms of hyperorality (a strong tendency to examine all objects orally), indiscriminate hypersexuality, visual agnosia (a psychic blindness of inability to recognize objects without a loss of gross visual discrimination), and serenity with loss of normal fear and anger.
2. *Disorders of Auditory Perception* – The auditory cortex helps in discriminating two forms of auditory processing, i.e., rapidly processing stimuli and complex stimuli pattern. Patients with temporal lobe lesions have difficulty in discriminating speech sounds. There is also an impairment of the temporal order of sound. Auditory hallucinations as a result of spontaneous activity in the auditory regions lead to perception of sounds that are not actually present. Wernike's aphasia characterized by inability to recognize words occurs due to lesions of left temporal association cortex (area number 22). Bilateral lesions lead to cortical deafness.
3. *Disorders of Music Perception* – Patients with temporal lobe lesions have deficit in processing musical sounds. Lesions of right temporal lobe result in impaired pitch discriminations. The perception of timbre, which refers to the distinctive character of sound at the same note and loudness, is also impaired in right temporal lesions. Rhythm discrimination is most commonly affected by right posterior superior temporal gyrus damage.
4. *Disorders of Visual Perception* – Prosopagnosia also known as face blindness, can occur following damage to temporal lobes particularly right temporal lobe, is the inability to recognize familiar faces (including one's own face) or photographs of faces. However, these individuals are perfectly aware that some sort of visual stimulus is present and can describe particular aspects or elements of it without difficulty.
5. *Disorders of Memory* – Damage to left temporal lobe results in impaired recall of verbal material presented in visual or oral form whereas damage to right temporal lobe results in impairment of recall of nonverbal things such as drawings, tunes, faces, etc. As stated previously, removal of medial temporal lobe including hippocampus and amygdala leads to amnesia.
6. *Disturbance of Selection of Visual and Auditory Inputs* – In cases where more than one auditory information is presented simultaneously, there is difficulty in focusing selectively on the input onto one ear or all inputs concurrently. Similarly, if two different visual stimuli are present simultaneously one to each visual field, there is impaired recall of content of both visual fields when right temporal lobe is damaged. In case of damage of left temporal lobe, there is deficiency in recalling of right visual field contents.
7. *Disturbances in Organization and Categorization* – The ability to organize and categorize information are important for language and memory. The patients with left temporal involvement have difficulty in placing words or pictures into discrete categories. For example, apple, banana, and mango belong to the category "fruits."
8. *Disturbances in using contextual information*, in extracting information from the environment and using visual and social cues.

## Cross-References

- Amygdala
- Artiodactyl Cognition
- Auditory Processing and Perception
- Bovine Cognition
- Encephalization
- Hippocampus
- Long-Term Potentiation
- Marsupial Cognition
- Memory
- Occipital Lobe
- Parietal Lobe
- Stereoscopic Vision
- Swine Cognition
- Vertebrate Nervous System
- Visual Perception
- Visual Recognition in Birds
- Visual Recognition of Prey and Predators
- Visuospatial Memory

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## Tendril

- Cilia

## Teratogen

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## Definition

A teratogen is an agent that disrupts the normal embryonic development and induces developmental abnormalities in animals. The term teratogen is derived from the Greek word “*teratos*” meaning monster. Teratology is the study of abnormalities of physiological development.

## Types of Teratogen

A teratogen can be a physical, chemical, or biological agent. X-rays and other harmful radiation are examples of physical teratogens. Chemical teratogens are drugs like cyclophosphamide, lithium, thalidomide, and retinoic acid and some metabolites in maternal blood like phenylalanine and alcohol. Absence of metabolites like folic acid also produces teratogenic effect. Biological teratogens are rubella virus, herpes virus, toxoplasma, etc.

## Effect of Teratogen

The effect of teratogen is determined by the developmental stage of the fetus. Teratogen exposure during the first week of gestation

(predifferentiation stage) has all or none effect. It can either lead to abortion or no effect at all. Teratogen exposure during organogenesis leads to congenital malformation.

## Teratogenic Drugs

A teratogen can have effect on different tissues, and many teratogens can produce same effects (Twining's Textbook of Fetal Abnormalities 2015). Some teratogens are associated with peculiar morphological features as listed in the table.

| Teratogenic drug | Medicinal use                                                                                                                              | Associated deformity                                                                                         |
|------------------|--------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------|
| Thalidomide      | Morning sickness (discontinued), the drug has been repurposed as immunomodulator for use in multiple myeloma and erythema nodosum leprosum | Phocomelia (foreshortening of the arms), Amelia (lack of arms), Microtia (small ears), Anotia (lack of ears) |
| Carbimazole      | Hyperthyroidism                                                                                                                            | Choanal atresia, Cutis aplasia with distinctive facial features                                              |
| Warfarin         | Anticoagulant                                                                                                                              | Hypoplastic nose, Brachydactyly (short-fingers), Scoliosis                                                   |
| Aspirin          | Non-steroidal anti-inflammatory drug with anti-platelet effect                                                                             | Gastroschisis (Abdominal wall defect with protrusion of intestines out)                                      |
| Aminoglycosides  | Antibiotic                                                                                                                                 | Hearing loss                                                                                                 |
| Valproate        | Anticonvulsant                                                                                                                             | Spina bifida (part of the spinal cord and meninges are exposed through defect in the vertebrae)              |
| Lithium          | Bipolar disorder (patient goes through manic and depressive phases)                                                                        | Cardiac malformations                                                                                        |
| Tetracycline     | Antibiotic                                                                                                                                 | Yellow staining of teeth                                                                                     |
| Isotretinoin     | Acne (Pimples)                                                                                                                             | Cleft palate, Neural tube defect                                                                             |

US Food and Drug Administration (FDA) categorized therapeutic drugs into five groups based on their teratogenic potential to be used in pregnant women (FDA Pregnancy Categories 2019).

1. Category A – Controlled studies in humans have shown no risk to the fetus in the first trimester of pregnancy (and there is no evidence of risk in later trimesters).
2. Category B – Animal studies have shown no risk to the fetus. No controlled studies have been conducted in humans.
3. Category C – Animal studies have shown an adverse effect on the fetus and there are no controlled studies in humans.
4. Category D – There is positive evidence of human fetal risk based on the adverse reaction data, but potential benefits may warrant use of the drug in pregnant women despite potential risks.
5. Category X – Animal or Human studies have demonstrated fetal abnormalities or there is positive evidence of human fetal risk based on the adverse reaction data and risk involved in the use of drug in pregnant women clearly outweigh potential benefits.

Apart from the therapeutic drugs, Illicit use of nicotine, alcohol, and cocaine is also associated with teratogenicity. Intake of alcohol by pregnant mothers lead to fetal alcohol syndrome in the baby. Ethanol competes with the retinol for the conversion by alcohol dehydrogenase and thus affects the retinoic acid synthesis and thus disrupts the retinoic acid signaling pathway. Nicotine from cigarette smoke causes vasoconstriction of placental vessels and decreases the blood supply to fetus leading to intra uterine growth retardation and mental retardation.

## Biologic Teratogens

Infection with rubella (German measles) leads to the triad of cataract (opacity in the lens of the eye), hearing loss, and cardiac malformations (Yazigi et al. 2017). Infants of mothers with diabetes mellitus are prone to develop congenital heart diseases and neural tube defects (Ornoy et al.



2015). Infants of mothers with phenylketonuria develop mental retardation.

Teratogenic Plants

Certain plants have been found to contain teratogenic chemicals. Keeler (1984) has classified teratogenic plants in the following way (Keeler 1984). Cattle grazing on these plants are susceptible to produce offspring with congenital malformations.

| Class                                                 | Example                                        |
|-------------------------------------------------------|------------------------------------------------|
| Known teratogens in known teratogenic plants          | Lupinus, Veratrum, Conium, and Leucaena genera |
| Known teratogenic plants with unidentified teratogens | Astragalus, Nicotiana, and Trachymene genera   |
| Suspected teratogenic plants                          | Datura, Prunus, Sorghum, and Senecio genera    |

Cross-References

- Developmental Arrest
- Embryo
- Ontogeny

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Terrestrial

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Synonyms

Land animals; Terrestrial animals

Definition

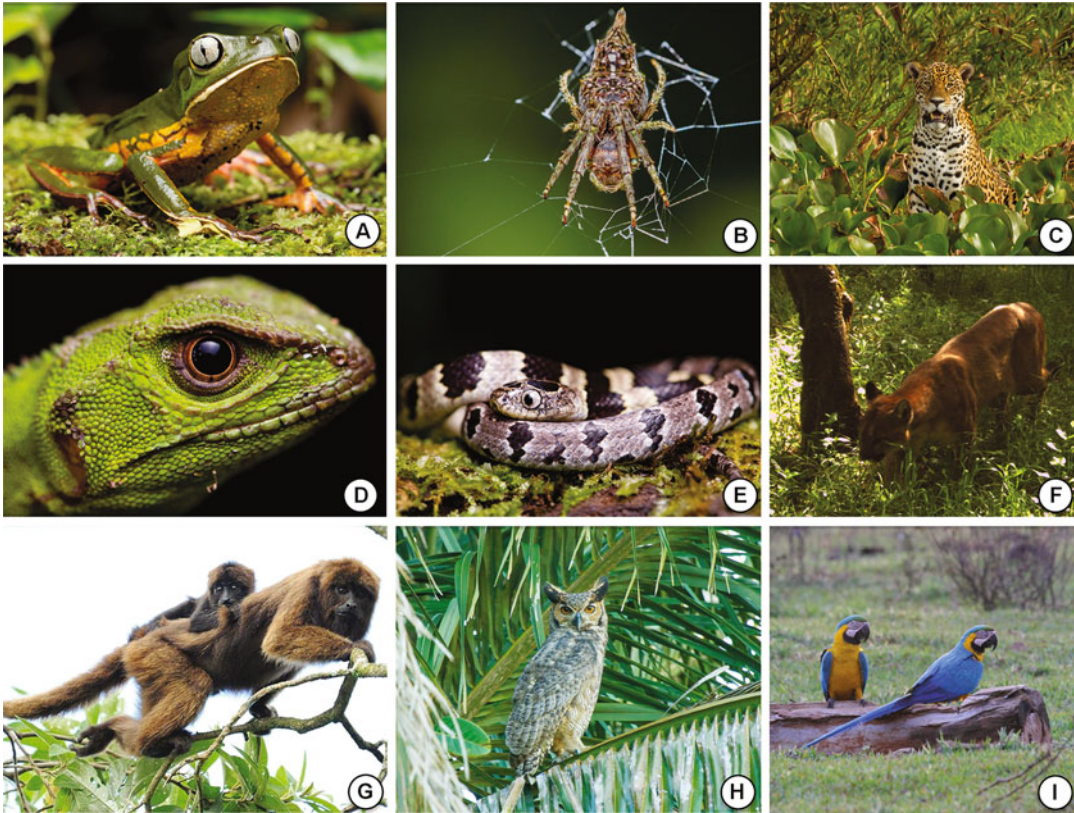
Terrestrial can be defined as the variety of life forms and adaptation on the land surface of the Earth (Laurin 2010).

Introduction

Terrestrial animals spend most of or their entire life span on land, in contrast to animals that live predominantly in water. Free living species in terrestrial environments are represented by the following ten phyla: flatworms (planarians), Nemertea (ribbon worms), Nematoda (roundworms), rotifers, Tardigrada (water bears), Onychophora (velvet worms), arthropods, mollusks (gastropods: land snails and slugs), Annelida, and Chordata (tetrapods). Examples of terrestrial animals include turbellarian, nemertean, cats, ants, dogs, raccoons, spiders, kangaroos, tigers, lions, mice, bats, bulls, oxen, leopards, elephants, birds, and many more (Fig. 1).

The context

Animals had previously lived only in the oceans but, starting during the Cenozoic approximately 470 million years ago, began to colonize the previously barren continents. The terrestrial invasion of animals is a significant event in evolutionary context (Shear 1991). Terrestrial lineages evolved in several animal phyla, among



**Terrestrial, Fig. 1** Example of the variety of life forms and adaptation on the land surface of the Earth. (A) The Leaf Frog (*Phyllomedusa distincta*) lives inside moist primary and secondary forest, and on the forest edge. (B) The orb-weaver spider (*Wagneriana* sp.) are the most common group of builders of spiral wheel-shaped webs often found in gardens, fields and forests. (C) The jaguar (*Panthera onca*) habitat is typically characterized by dense forest cover (mainly primary and secondary forest), the presence of water bodies and a sufficient prey base. (D) The Ihering's fathead anole lizard (*Enyalius iheringii*) lives mainly in arboreal habitats and found on vegetation as well as in the ground. (E) The Boulenger's Tree Snake (*Sibynomorphus mikanii*) predominant habitat type in the

species' range is savanna which may be active both by day and at night. (F) The Mountain Lion (*Puma concolor*) is an adaptable cat, being found in every major habitat type of the Americas, including the high Andes. (G) The howler monkey (*Alouatta caraya*) is found in semi-deciduous forests and can adapt to disturbed and degraded habitats. (H) The great horned owl (*Bubo virginianus*) may be found in a number of woodland habitat types across this species' wide range, from cold evergreen woodland in the far north and south to humid tropical forest near the equator. (I) The Blue-and yellow Macaw (*Ara ararauna*) are found in wooded areas, often near water and sometimes forage in more open sites, coming to the ground to feed on fallen fruits (photos by M. N. Godoi and A. Piva)

which arthropods, mollusks, annelids, and vertebrates are representatives of more successful groups of terrestrial animals. The first direct evidence from animal fossils come from the myriapods (centipedes and millipedes), followed by other arthropod groups and vertebrates (Little 1983; Clark 2002).

A more likely hypothesis is that these early arthropods' motivation for venturing onto dry land was to mate (as modern horseshoe crabs do)

or lay eggs out of the reach of predators (Cloudsley-Thompson 1988). As time went on, evidence suggests that the bony fish best adapted to life in shallow coastal/swampy waters (such as *Tiktaalik roseae*) were much more viable as amphibians than were their arthropod predecessors. When animals colonized terrestrial habitats, they had to adjust to the fluctuating temperatures, the replacement of water with air, and the increased level of oxygen. Terrestrial animals

adapted to these challenges by developing different metabolic systems, employing thermoregulatory behaviors, and developing desiccation-resistant skin or exoskeletons. In addition, terrestrial animals have to deal with the nitrogenous waste products; fish (and amphibians) produce ammonia, a highly toxic compound but highly soluble in water, while reptiles, birds, and mammals excrete urea and uric acid, less toxic compounds that require less water to be excreted. Other adaptations in animals include the development of internal fertilization; olfactory, hearing, and vision organs; structures for movement; and complex behavior (Little 1983).

### **Focusing on Arthropods and Tetrapods to Understand Terrestrial Animals Cognition and Behavior**

#### **Arthropods (Terrestrial)**

There are five kinds of terrestrial arthropods: crustaceans, millipedes, centipedes, arachnids (mites, ticks, spiders, scorpions), and insects. Flightless insects also are early terrestrial organisms. The exoskeleton of marine arthropods was important in allowing some of their descendants to adapt to land. It provides the support needed in the less buoyant air and serves as a surface for muscle attachment that permits rapid movement. The exoskeleton of most terrestrial arthropods has a waxy coating that reduces water loss. Another important method of conserving water in insects and spiders is the presence of Malpighian tubules, thin-walled tubes that surround the gut and reabsorb water from nitrogenous wastes prior to their excretion.

Internal fertilization is typical of terrestrial arthropods and involves copulation, in which a penis is used to insert the sperm into the reproductive tract of the female (insects, millipedes) or the production of special sperm-containing sacs (spermatophores) that are picked up by the female (spiders, centipedes). This is important mechanism because both the sperm and egg are protected from drying. Moreover, terrestrial arthropods have complex life cycles that involve larval stages that occupy different niches from the adults.

Terrestrial arthropods have evolved a number of characteristics that assure their survival under hostile environmental conditions. Many seek out sheltered sites and become inactive during periods of cold or drought. Often this involves changes in physiology that protect against freezing or prevent water loss. The terrestrial arthropods occupy an incredible variety of niches. Many insects are herbivores that compete directly with humans for food. Other kinds of insects, as well as spiders and centipedes, are carnivores that feed primarily on arthropods and other small animals. Mites and millipedes feed primarily on decaying material and the fungi and bacteria that are part of decaying material. Insects have evolved in concert with the flowering plants; their role in pollination is well understood. Bees, butterflies, and beetles transfer pollen from one flower to another as they visit the flowers in search of food. Many kinds of crops rely on bees for pollination, and farmers even rent beehives to ensure adequate pollination for fruit production.

#### **Chordata (Tetrapods)**

**Amphibians** The conquest of land was not done from 1 day to the other; it was possible with the combination of multiple adaptations. Some of the most important characteristics that allowed the first amphibians to leave the water were the evolution of lungs, which are homologous to the gas bladder that allows fish to control its buoyancy. Lungs appeared as an additional way to get oxygen from the air. In fact, there is actually a sarcopterygian family the members of which have lungs to get oxygen from the air, for they live in waters poor on oxygen. Development of the choanae, or internal nostrils, was another important characteristic; while fish present a pair of external nostrils at each side of its snout through which water passes on while swimming, the ancestors of the tetrapods only had one external nostril at each side connected to the internal nostrils, the choanae, which communicated with the mouth. This allowed them to get air through their noses using lung ventilation and this way to smell outside of water. Another characteristic was the apparition of the quiridium-like limb,

the most basic characteristic in tetrapods. This limb is known for having the differentiated parts: the stylopodium (one bone, the humerus or the femur), the zeugopodium (two bones, the radius or tibia and ulna or fibula), and the autopodium (fingers, hands, toes, and feet). While the stylopodium and zeugopodium derived from the sarcopterygian's fins, the autopodium is a newly evolved structure exclusive from tetrapods.

**Reptiles** All living reptiles share certain fundamental characteristics, features they retained from the time when they replaced amphibians as the dominant terrestrial vertebrates (Little 1983; Cloudsley-Thompson 1988). Among the most important is amniotic egg. Amphibians never succeeded in becoming fully terrestrial because amphibian eggs must be laid in water to avoid drying out. Most reptiles lay watertight eggs that offer various layers of protection from drying out. The reptilian amniotic egg contains a food source (the yolk) and a series of four membranes – the chorion (the outermost layer), the amnion (the membrane surrounding the embryo), the yolk sac (containing the yolk), and the allantois (the red structure). Amphibians breathe by squeezing their throat to pump air into their lungs; this limits their breathing capacity to the volume of their mouth. Reptiles developed thoracic breathing, expanding and contracting the rib cage to suck air into the lungs and then force it out. In addition, reptiles improved on the innovations first attempted by amphibians. Legs were arranged to more effectively support the body's weight, allowing reptile bodies to be bigger and to run. Also, the lungs and heart were altered to make them far more efficient.

**Birds** The reptiles gave rise to two other groups of vertebrates: birds and mammals (Shear 1991; Clark 2002). About 65 million years ago, a mass extinction of many kinds of reptiles occurred. At that time, birds and mammals began to diversify and became the dominant forms of vertebrates on land. Like the structures of their reptile ancestors, the skin, lungs, and kidneys of birds reduce water loss, and reproduction involves internal fertilization and the shelled amniotic egg. They also have other adaptations that allow them to be successful

as land animals. Birds are homeothermic and have feathers. As homeotherms, they have a high body temperature and a more rapid metabolic rate than reptiles. The exploitation of flight has shaped the entire structure and function of birds. The forelimbs are modified into wings for flight, although it is actually the flight feathers that provide most of the flight surface. Large breast muscles provide the power for flight. Feathers help provide a streamlined shape. Homeothermism enables a high constant temperature, which allows for the rapid wing beats typical of most birds. In addition, the skeleton is reduced in weight, and the jaws lack teeth that are heavy. Birds have successfully occupied many niches. Some are nectar feeders, some are carnivores, some are seedeaters, some are aquatic, and some have even lost their ability to fly.

**Mammals** The first mammals appeared about 200 million years ago, when reptiles were at their most diverse (Shear 1991; Clark 2002). Like birds, mammals are homeotherms, with a high constant body temperature. Like reptiles and birds, they have a waterproof skin and water-conserving lungs and kidneys. However, they differ from birds in several respects. Their insulating covering is hair, rather than feathers, and they provide nourishment to their young with milk produced by special glands. Scientists classify mammalian reproduction into three categories: (i) monotremes (platypus and echidna) are egg-laying mammals whose young still develop in an external egg; (ii) marsupials have pouches, where the young are born in an immature stage and are carried in the pouch while they finish their development; and (iii) placental mammals have a placenta, which connects the mother and embryo; they retain the young in the uterus for a longer period of time.

**Mode of Life** On the basis of their mode of life, terrestrial animals are divided into following types:

- (i) Cursorial which live in open places and are adapted to run on hard ground, e.g., lion, deer, and horse. Adaptational characters of



them are the body streamlined which helps them for swift movement. The limbs are long and strong and the locomotion is digitigrade.

- (ii) Fossorial which are adapted for burrowing mode of life, e.g., rabbit, rat, etc. The adaptational characters of fossorial animals are the head, eyes, and ears that are small and tapers anteriorly to form snout for digging. The forelimbs are short with powerful claws and the eyes and the ears are small.
- (iii) Arboreal which are adapted for climbing, e.g., squirrel, chameleon, etc. The adaptational characters of these animals are the body is stout, ribs are very much curved, thus thorax becomes semicircular, the muscles of chest are very strong, and the locomotion is classified plantigrade.
- (iv) Aerial that are adapted for aerial mode of life, e.g., bats. The adaptational characters of aerial animals are body is streamlined, which reduces the air resistance during flying. Forelimbs are modified into wings, the bones are hollow and spongy, and the eyes are very sharp and well developed.
- (v) Desert animals are adapted for dry land and hot habitat, e.g., camel, lizard, rodents, etc. The desert animals are provided with keen senses of sight, smell, and hearing. They conserve water in water pouches and have thick skin to avoid loss of water. Most of them have dull color which blends them with the surrounding environment.

## Conclusion

The term terrestrial in biology is generally used to describe living organisms that live and grow on land. Living things that make use of nature as their habitat may be grouped based on where they live, grow, and reproduce. Living things that spend most of their life on land are called terrestrial. This is in contrast to living things that live on water (called aquatic) and those that are not growing in the ground (called aerial or epiphytic, especially of plants). Labeling an animal species “terrestrial” or “aquatic” is often obscure and becomes a matter of judgment. Many animals

considered terrestrial have a life cycle that is partly dependent on being in water. Otters, sea lions, and penguins sleep on land and feed in the water, yet they are all considered terrestrial. Many arthropods, e.g., dragonfly and crabs, as well as amphibian, e.g., frogs, toads, newts, salamanders and other clades, have an aquatic life cycle stage. High terrestrial biodiversity is often used as an indicator of ecosystem health and has been shown to have direct links to human health. Anthropogenic disturbance will affect terrestrial biodiversity and ecosystems (Dirzo et al. 2014; Gonçalves et al. 2017) through both gradual and sudden changes in response to the average climate and land use change (e.g., increased temperatures, decreased rainfall, changes to seasonality, loss of habitat) and extreme events (increased hot days, fire, increased frequency and severity of cyclones, heat waves, intensified wet seasons).

## Cross-References

- [Adaptation](#)
- [Arthropod Cognition](#)
- [Artiodactyla Life History](#)
- [Bear Cognition](#)
- [Canine Cognition](#)
- [Falconiformes Cognition](#)
- [Feline Cognition](#)
- [Marsupial Cognition](#)
- [Microchiroptera Cognition](#)
- [Mustelidae Cognition](#)
- [Perissodactyla Cognition](#)
- [Torpor](#)

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## Terrestrial Animals

### ► Terrestrial

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## Territorial Marking

### ► Scent-Marking

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## Territoriality

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## Synonym

Resource defense; Territory

## Definitions

Territoriality refers to maintenance of a territory and thus includes territorial behavior, at the individual level, and spatial patterns that result from those individual interactions, at the population level (Hinsch and Komdeur 2017). However, territory may be defined conceptually in many ways (Maher and Lott 1995). The most common conceptual definitions can be grouped into one of three categories, and they illustrate the difference in emphasis between ecological and behavioral aspects of territoriality: defended area, exclusive area, and site-specific dominance. The oldest definition, defense (Howard 1920), reflects a focus

on interactions that produce the outcome, whereas use of an exclusive area (Pitelka 1959) highlights the outcome rather than the process. A researcher's choice of definitions often reflects the taxonomic group and habits of species being studied (Maher and Lott 1995). Thus, scientists studying more easily observed species such as fish, birds, dragonflies, ants, and large mammals often use definitions relating to defense, whereas people studying more secretive, nocturnal species such as small mammals rely on measures of exclusive use.

In addition to conceptually defining territory, it is important for researchers to operationally define the term, providing explicit criteria by which they measure space use or defense in animals, e.g., amount of spatial overlap or rate and location of aggressive interactions. Because spacing systems actually represent a continuum, such criteria enhance the ability to compare spatial organization within and across species.

## Introduction

Territoriality can be viewed as both an ecological and a behavioral concept. Exclusive use of space leads to more or less uniform distribution of organisms across the landscape, with implications for population-level phenomena such as density-dependent regulation of population sizes. However, territoriality also is a behavioral concept because the mechanisms that produce exclusive use of space involve behavior patterns. To maintain a territory, animals interact with each other, whether subtly through scent marks and threat displays or more overtly through chases and fights.

In reality, territoriality is one type of spacing system that falls along a continuum (Maher and Lott 1995, 2000). Thus, animals can be more or less territorial depending on how sharply boundaries are defined or how often territory owners engage and exclude intruders. Territoriality may lie at one end of the continuum, and other alternative social systems lie at the other end, depending on one's perspective. From an ecological view, animals may exhibit a range of space

use extending from maintaining exclusive areas to completely overlapping home ranges. A more behavioral approach may view the continuum as ranging from territoriality at one end to a dominance hierarchy at the opposite end. By incorporating multiple dimensions, reflecting elements of space use, behavior patterns, and time, researchers can gain more realistic views of the flexibility of territoriality.

Much of the literature on territoriality is focused on vertebrates, and territoriality has been described in almost all vertebrate taxa, including bony fish, amphibians, lizards, crocodilians, birds, and mammals. Furthermore, territoriality occurs in many insect taxa, including bees and wasps, ants, flies, and odonates, as well as crustaceans, spiders, molluscs, and anemones.

As is true for many biological phenomena, researchers can study territoriality using different approaches. Scientists may emphasize ultimate questions such as the fitness consequences of maintaining a territory or the ecological and social conditions under which an animal defends a space. Researchers also may examine proximate mechanisms such as the hormonal control of behavior that produces territoriality or the role of learning in establishing a territory. Both approaches have enhanced our understanding of this widespread and diverse phenomenon.

## What Is Defended and Why?

Territories often are contrasted with home ranges, i.e., areas where animals conduct their daily activities (Howard 1920). Unlike home ranges, territories are defended, and neighboring individuals do not overlap in their use of space. Territories contain some limited resource and thus afford the owner more or less exclusive access to that resource. These areas may be designated as “all purpose” if they contain multiple resources such as food and reproductive sites including nests or dens, or they may serve more specific roles if territories contain solely food (a feeding territory, e.g., nectarivorous birds), nest sites (e.g., colonial birds), or oviposition sites (e.g., dragonflies).

Maintaining exclusive access to resources and defending them against other individuals involve both costs and benefits to the territory owner. Clearly, sole access to limited resources within a territory provides benefits. Furthermore, because territories distribute animals across the landscape, risk of predation, parasitism, or disease may be lower (Huntingford and Turner 1987). However, costs include time and energy spent acquiring the territory initially, which may involve removing the previous owner, and then maintaining exclusive access, including defending the area against subsequent intruders with its risk of injury, patrolling and demarcating boundaries, and lost opportunities to do other things (e.g., feed or mate) while patrolling or defending the territory. Ideally, these costs and benefits are measured in units of fitness; however, in reality, they may be measured in units of time or energy gained or lost.

The classic cost-benefit model of territoriality dates back to Brown (1964), with its focus on economic defensibility. For natural selection to favor territoriality, benefits must exceed costs, and both resources and population density play key roles in determining those costs and benefits. Thus, when resources are scarce, benefits to maintaining exclusive access are low, and costs are high because an animal must maintain a relatively large area to secure sufficient resources. Similarly, when resources are superabundant, an area may contain more resources than an individual could use, again making defense unprofitable. Population density or intruder pressure also must be considered. At high densities, the costs of repelling repeated incursions might not justify the benefits afforded by those resources. Thus, we expect territories to be maintained at intermediate levels of resource abundance and population density.

Early in the history of the field of behavioral ecology, social systems commonly were viewed as fixed attributes of species, e.g., members of a species either were territorial or they maintained undefended home ranges or established a dominance hierarchy. However, as the discipline developed and field observations proliferated, researchers came to view social systems, including spacing systems, as more flexible, with

members of the same species displaying different types of social systems across different populations or within the same population over time (Lott 1991). Indeed, members of some species may shift space use on the scale of hours or days, e.g., rufous hummingbirds (*Selasphorus rufus*), golden-winged sunbirds (*Drepanorhynchus reichenowi*), and pied wagtails (*Motacilla alba*; Davies and Houston 1981).

Such flexibility is related to economic defensibility. Presumably, as cost-benefit ratios shift, animals adjust their behavior, and the spacing system changes accordingly. Many such reports of intra-specific variation relied on observations of changes in an ecological variable such as food abundance or population density, which then correlated with a change in the spacing system. Fewer studies manipulated variables experimentally and then measured the behavioral response. Nonetheless, such experimental work sometimes revealed that resources, primarily food and population density, can produce shifts between territoriality and another outcome such as undefended home ranges. Yet, other experimental studies produced no such changes, perhaps because other, unrecorded variables affected the outcome (Maher and Lott 2000). To test economic models of territoriality, it is essential to provide operational definitions of territoriality with quantified variables measured over spatial and temporal scales that are relevant to the animals (Maher and Lott 1995, 2000). Furthermore, alternative ways of analyzing data, including model selection (Burnham and Anderson 2002), offer useful ways of evaluating combinations of variables and their effects on spatial organization.

Characteristics of food (e.g., abundance, distribution, renewal, predictability, and quality) are widely considered as potential determinants of territoriality. Perhaps food actually is an important resource; however, these studies may reflect logistical constraints, especially in field studies. Food is relatively easy to manipulate and measure, and animals are easier to observe when they feed. Certainly, food is important to animals, particularly for species with high energetic demands such as nectarivorous birds. Yet, other variables may be more important in other taxa (Maher and Lott 2000).

In general, the relationship between food abundance and territoriality and between food distribution and territoriality is not linear but instead shows an inverted U-shaped distribution (Maher and Lott 2000). Thus, as the amount of food increases from low to medium levels, territoriality increases, whereas as food levels increase further from medium to high levels, net benefits of maintaining exclusive access to food decrease, reducing territoriality. Similarly, when food is highly clumped or evenly distributed, it is not economically defensible, whereas moderately clumped resources can be defended. Ideally, researchers quantify food levels or patterns of distribution as well as behavior patterns associated with territoriality to capture gradual shifts in behavior rather than a more simplistic on-off, either-or function.

In contrast to food abundance and distribution, the relationship between food predictability and territoriality is expected to be linear. Thus, when food is spatially or temporally predictable, it can be defended more easily. Species that cache food to guard against temporally unpredictable conditions can create a more predictable resource and thus defend caches (Maher and Lott 2000).

Population density also is widely reported as determining degree of territoriality. Similar to some characteristics of food, the relationship between population density and territoriality is expected to show an inverted U-shaped distribution. As noted above, at low densities, the presence of few competitors does not justify defense of an area, and at high densities, frequent intrusions raise the costs of defense relative to benefits. Thus, intermediate population densities are associated with territoriality. Although many studies support this prediction, reports sometimes contradict each other. Such contradictions may result from the design of the study, importance of other, unrecorded variables, or a lack of clarity in terms of what constitutes “high” and “low” density (Maher and Lott 2000).

Economic models of defensibility provide a useful framework for understanding when an animal should maintain a territory. However, researchers also recognize that territorial behavior involves more than just the territory owner. It also includes

the intruder, which must decide whether or not to intrude. Such decisions bear fitness benefits, such as access to the resource, but also costs, such as risk of injury. Thus, game theory can be used to understand the behavior of both owner and intruder simultaneously (Hinsch and Komdeur 2017).

In addition to decisions about defending or not defending an area, the territory owner also must decide how much area to maintain as a territory. The largest territories (many hectares) belong to large mammals that defend all-purpose areas containing sufficient food resources, whereas the smallest territories (a few square meters) occur on leks, which are display areas containing multiple males that occupy small exclusive areas solely to attract a mate for copulation. Once again, benefits and costs play important roles in determining territory size. Initially, benefits increase as the size of a territory increases and animals secure more resources. However, there are limits on what one individual can use or consume, such that additional resources do not yield additional benefits. Furthermore, costs also increase with territory size. A larger area requires more time and energy spent patrolling longer boundaries, detecting and repelling intruders (Davies and Houston 1984). Indeed, animals may adjust territory size over short (daily) time scales to maximize energy gains (Carpenter et al. 1983; Gill and Wolf 1975).

In some cases, the ratio of benefits to costs allows a territory owner to tolerate satellites on the territory, i.e., the owner does not chase away intruders. In exchange for help in defending the territory, the satellite obtains food resources (Davies and Houston 1981). Although the owner loses some food to the satellite, it gains assistance in defending the territory against additional intruders. Thus, when food resources are abundant, an owner may tolerate a satellite in exchange for help, and when food is less abundant, the owner evicts the satellite.

## Who Defends and When?

Some animals maintain territories year round, because they rely on resources such as food

provided continuously by the area, and territories remain economically defensible throughout the year. However, in many species, territoriality is seasonal, and it often coincides with the breeding season. Moreover, across species, if sexes differ in territoriality, males often are more territorial than females, excluding other males from the area, and males defend a resource that females seek. For example, male dragonflies and damselflies defend oviposition sites that females use, and in numerous polygynous bird species, males defend nesting sites. As noted earlier, the smallest territories occur on leks, breeding grounds where males display in groups, with each male defending a small space on the lek. Females arrive from surrounding areas, assess and choose mates, and then depart. Males provide no resources or parental care. Leks are best known in birds; however, they occur in some mammals, amphibians, lizards, fish, and insects.

In some species, females maintain territories, typically excluding other females. Although the function may be to secure adequate resources for their young, territories also may protect against infanticidal conspecifics (Wolff and Peterson 1998).

Territories most commonly are held by individuals. Nevertheless, a male-female pair or a group may jointly defend an area. Many songbirds pair up during the breeding season and defend a territory against other pairs. Group territories occur across a range of social insects (e.g., ants), birds (e.g., acorn woodpeckers, *Melanerpes formicivorus*; Florida scrub jays, *Aphelocoma coerulescens*; Seychelles warblers, *Acrocephalus sechellensis*), and mammals (e.g., alpine marmots, *Marmota marmota*; European badgers, *Meles meles*; lions, *Panthera leo*), and individuals breed cooperatively within those areas.

Finally, territories can be defended not only against conspecifics but also against heterospecifics. When species that have similar territorial behavior patterns (i.e., song or displays) first make contact, individuals may mistake each other for conspecifics. Thus, interspecific territoriality is a case of mistaken identity and a nonadaptive result of intraspecific territoriality. Natural selection is expected to eliminate such behavior if costs

of defense exceed benefits of excluding these heterospecific intruders. However, in some cases, closely related species compete for similar resources, including food and mates (Losin et al. 2016). Coral reef fishes maintain territories against individuals of other species that compete for similar food resources in a limited area. Furthermore, closely related species may hybridize, such that reproductive interference may explain other cases of interspecific territoriality (Drury et al. 2015).

### Proximate Mechanisms

Key aspects of territoriality include use of exclusive space and defense. Thus, territory owners must inhibit intruders in some way to ensure exclusive access to resources, and such inhibition often involves agonistic interactions between intruders and residents. These interactions may range from subtle avoidance to threat displays to overt fighting. Furthermore, residents and intruders may not meet physically, and cues may be enough to keep intruders from encroaching into a territory. As a result of the interaction, one individual wins the encounter, usually the resident. Researchers have explored the proximate basis for territoriality, including why residents win, how territories are established, how they are delineated, the role of hormones, and why neighbors are treated differently than strangers.

### Who Wins?

The resident typically wins interactions with intruders. Researchers cite several reasons why residents win (Maynard Smith and Parker 1976), and no single explanation fits every situation. Animals may use a rule, “residents always win.” However, this explanation has little support, and in most cases, winners of territorial disputes are not based on arbitrary factors (Alcock 2013). Rather, winners often have a physical advantage over their opponents. Residents may hold territories because they have higher resource holding power (RHP). Thus, they are larger or stronger and can outcompete opponents for the space (Huntingford and Turner 1987). However, larger

size does not always determine the winner. Other physiological factors that determine the winner include fat content or some unknown intrinsic trait not necessarily manifested in large size. Indeed, age and experience may influence outcomes, with older individuals more likely to escalate or persist in interactions and thus retain ownership (Alcock 2013).

Residents may value the resources in the territory more than an intruder does because the resident is more familiar with the area, such as where the best food sources are located or the best escape routes to use when a predator attacks, and thus the resident can gain more benefits. Removal experiments using insects, fish, and birds support this idea. When territory owners are removed temporarily, allowing the site to be taken over by a new owner, and then returned later, they often fail to regain the new space if the new owner has occupied the site for some period of time. Indeed, the longer the new owner has occupied the space, the more intense the interactions when the former owner returns, suggesting that the value of the territory to the owner increases as the owner becomes more familiar with the area (Alcock 2013).

### Establishment

Many studies have examined interactions between residents and intruders that occur once an individual already has established a territory. Fewer studies have explored how territories become established initially, particularly in natural settings. Stamps (1988) used field experiments to show that anoles (*Anolis aeneus*) are attracted to conspecifics, presumably using these individuals to signal high quality sites. Individuals then divide up the area, maintaining exclusive use but settling adjacent to each other. This phenomenon, known as conspecific attraction or conspecific cueing, occurs in the broader context of habitat selection and has been applied to conservation practices. For endangered colonial seabirds (e.g., Atlantic puffins, *Fratercula arctica*) and territorial songbirds (e.g., black-capped vireos, *Vireo atricapilla*), researchers used models and song playbacks to lure conspecifics to an area and increase breeding populations.



Related to the idea of conspecific attraction or cueing, prospecting involves nonbreeding individuals moving around and assessing potential breeding sites before eventually settling on one site (Reed et al. 1999). Thus, prospecting refers to establishment of breeding territories only, and animals may use the presence of young as a cue to identify the most suitable territories.

Although one way to establish a territory is to win a fight and evict the previous owner, another set of models for territory establishment incorporates learning. Unlike economic and game theoretical models, which focus on fitness outcomes, learning-based models focus on proximate mechanisms to explain spacing patterns (Stamps and Krishnan 1999, 2001). An individual has positive and negative experiences as it explores an area and interacts repeatedly with conspecifics (Stamps and Krishnan 1999, 2001). Some interactions, such as fights, constitute punishment, which decreases the value or attractiveness of a site and reduces the probability of returning to that area. However, sometimes an individual visits a site and does not interact with a conspecific. During those times, the animal gains benefits from acquiring more information about resources such as food or nest sites within the site, which then increases the value or attractiveness of the site and increases the probability of returning to that site. The outcome in terms of establishing a territory represents the combination of positive and negative feedback from interactions, i.e., persistence and punishment (Sih and Mateo 2001). These models predict that territoriality can arise without aggression. Persistence or low levels of punishment over time and at every encounter, such as chases, by one individual (“nagging”) can make it costly for another individual to use the site. Thus, as long as interactions incur some cost, an animal can secure a territory without aggressive interactions. Observations of birds and anoles support this prediction. Despite repeated attacks from conspecifics, animals return to these areas and eventually gain space (Stamps and Krishnan 2001).

Another way to acquire a territory is to inherit it from one’s parents. In some species, territories are passed down from parents to offspring.

Among cooperative breeders such as Florida scrub jays and Seychelles warblers, as family size increases, helpers expand the boundaries of an existing territory and eventually may bud off their own territory. In red squirrels (*Tamiasciurus hudsonicus*), a mother may leave her current territory and establish another one elsewhere, “bequeathing” the original territory to her daughter.

### Boundaries and Landmarks

Territories represent areas of exclusive use; therefore, they have boundaries. Indeed, such boundaries can be readily apparent to a human observer, as when a gray squirrel (*Sciurus carolinensis*) chasing an intruder suddenly stops at an “invisible” line and turns around, presumably returning to its own territory. One cost of territorial defense, therefore, is maintenance of those borders, which must be patrolled, and occupancy must be advertised to both neighbors and potential intruders. To reduce costs of defense, territorial behavior often occurs in habitats with good visibility or vantage points, which allow residents to detect and repel intruders quickly (Eason and Stamps 1992).

Animals can maintain boundaries and deter intruders using several sensory modalities. Perhaps the best known examples are vocalizations, particularly bird song. Removal experiments with many species indicate that when territory owners appear to vacate an area, the space is quickly filled; however, when researchers play calls mimicking the continued presence of the owner, intruders are repelled (Krebs 1977). Morning choruses of primates (e.g., howler monkeys, *Alouatta* spp.; gibbons, *Hylobates* spp.) and howling by canids (e.g., gray wolves, *Canis lupus*; coyotes, *Canis latrans*) also serve to advertise the presence of territory owners. Boundary marks may be olfactory, e.g., scents deposited on vegetation or other substrates as in ants, salamanders, and mammals. Scent marks convey information about the owner, including sex, age, status, and overall health.

Animals also use visual landmarks to demarcate boundaries, and such boundaries can be natural or artificial, part of the landscape or constructed by the territory owners (Heap et al. 2012). For example, animals can incorporate

pre-existing natural landmarks such as rocks and rivers or human-made features such as roads and fences as boundary markers. They may build paths that intruders rarely cross (e.g., European badgers) or construct mud walls surrounding their territories (e.g., mudskippers, *Boleophthalmus boddarti*) (Heap et al. 2012). Experimental work shows that animals can reduce the amount of time spent in active defense when they use landmarks, because these animals engage in fewer aggressive interactions, and those interactions are shorter in duration (Heap et al. 2012).

Landmarked boundaries can have population-level consequences due to effects on territory size and shape. Territories that incorporate landmarks for boundaries may be smaller due to lower costs of sharing space or larger due to reduced costs of defense or landmarks spaced far apart. Furthermore, boundaries denoted by landmarks may persist longer than those without landmarks. Thus, territory size and shape can influence population abundance and stability (Heap et al. 2012).

### Hormones

As noted earlier, in many territorial species, males maintain exclusive spaces, whereas females occupy undefended home ranges. Such behavior is often associated with levels of testosterone, with territorial behavior appearing seasonally when testosterone levels increase. Increased testosterone levels correlate with increased aggression and sexual behavior. However, they also are associated with suppression of the immune system, reduced parental care, and higher mortality (Wingfield et al. 2001). To determine causal relationships, testosterone levels can be manipulated experimentally using implants. These studies show that increased testosterone promotes territorial behavior, including displays, outside the breeding season when animals typically do not maintain territories. Furthermore, those animals with higher testosterone levels suffered costs associated with enhanced territorial behavior, namely, reduced foraging, increased energy expenditures, and lower survival rates (Marler et al. 1995).

However, testosterone is not always associated with higher aggression and territorial behavior

(e.g., Moser-Purdy et al. 2017a), perhaps because of trade-offs with other performance traits related to fitness. For example, high levels of testosterone may interfere with other reproductive behavior, such as parental care. Other hormones, such as corticosterone, may play a more important role in territorial aggression during certain stages of the breeding season (Moser-Purdy et al. 2017a).

### Neighbor-Stranger Discrimination

Territory owners may become familiar with their neighbors over time. Initially, interactions are intense between neighbors, with frequent displays or fights, until both individuals learn to recognize each other and the boundaries between them. After the initial learning phase, interactions between neighbors decline, and owners may permit neighbors to approach a boundary more closely before engaging them. This reduction in intensity and frequency of interactions has been termed the “dear enemy” effect, and experiments reveal that animals treat neighbors less aggressively than strangers (Temeles 1994). One hypothesis is that neighbors are familiar; individuals learn each other’s identities and respond less aggressively. As a result, they avoid wasting time and energy on known individuals that respect each other’s boundaries. As they learn identities, territory owners are less likely to make mistakes about the neighbor’s role, leading to lower aggression (Ydenberg et al. 1988). However, the effect is strongest when animals maintain all-purpose territories, rather than feeding territories, and it may be due more to relative threats from neighbors versus strangers rather than to differences in familiarity (Temeles 1994). Neighbors represent a lower threat than strangers do because neighbors already possess a territory, whereas strangers potentially can evict the current resident. Furthermore, during the breeding season, neighbors represent competition for mates only, whereas strangers represent competition for both mates and territory.

The dear enemy effect can depend on sex, season, and location within the territory where the intrusion occurs. For example, threats change during the breeding season when females are fertile. At that time, neighbors pose a greater risk because they sire most extrapair offspring. Male

song sparrows (*Melospiza melodia*) exhibit the dear enemy effect, i.e., more aggression toward strangers, before and after the fertile stages, whereas during the stage when females are fertile, males respond as aggressively toward neighbors as they do to strangers (Moser-Purdy et al. 2017b).

Coping with unfamiliar neighbors can be costly. Stephen's kangaroo rats (*Dipodomys stephensi*), an endangered species, suffered high mortality rates when animals were translocated. However, when animals were moved in groups that consisted of familiar neighbors, they experienced higher reproductive success, fewer fights, and increased survival compared to animals moved in groups consisting of unfamiliar individuals (Shier and Swaisgood 2011).

The opposite phenomenon is termed the “nasty neighbor” effect, where owners interact more aggressively with neighbors than they do with strangers. In group living, territorial species, members may fight intensely with neighbors over resources, because neighbors pose a greater threat than strangers do. Strangers represent lower risk due to smaller group sizes, i.e., they are dispersing individuals that travel alone or in smaller groups (Müller and Manser 2007). Indeed, greater aggression toward neighbors versus strangers has been reported in social mammals, cooperatively breeding birds, and social insects (Newey et al. 2010).

## Conclusion

The study of territoriality serves as an excellent example of how application of Tinbergen's questions related to ultimate and proximate approaches can further our understanding of animal behavior. Researchers have modeled, observed, and manipulated ecological factors affecting costs and benefits and thus the degree of territoriality and the size of territories. Researchers have experimentally altered landmarks and hormones to investigate mechanisms of territory maintenance and behavior. Further integration of both approaches will only expand our understanding of territoriality. In addition, the study of territoriality has broader applications. Specifically, conservation biologists can use these concepts to attract more

animals to breeding sites or to increase the likelihood of successful translocations by moving familiar animals together. Some aspects of territoriality, such as interspecific territoriality, have not been well studied to date. Thus, from more basic scientific questions to more applied situations, from building better models to testing those models empirically in the field, the study of territoriality remains full of possibilities.

## Cross-References

- ▶ [Aggression](#)
- ▶ [Caudata Cognition](#)
- ▶ [Dear Enemy Effect](#)
- ▶ [Home Range](#)
- ▶ [Learning](#)
- ▶ [Mustelidae Navigation](#)
- ▶ [Resource Defense](#)
- ▶ [Territory Defense](#)
- ▶ [Testosterone](#)

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## Territory

### ► Territoriality

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## Territory Defense

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## Synonyms

Brood defense; Mate-guarding; Territoriality

## Definition

A form of intraspecific competition exhibited by an individual or group to acquire or maintain an area and monopolize resources.

## Introduction

Territorial defense occurs to ensure access to resources and to maximize fitness and reproductive success (Kaufmann 1983). The focal resources vary and can include all or some of food, shelter, mates, and safety. Individuals, breeding pairs, or groups defend territories seasonally or year-round. Territories differ greatly in size and composition. For example, grey wolf (*Canis lupus*) packs occupy areas that range from less than 100 km<sup>2</sup> to greater than 2500 km<sup>2</sup> depending on geographic location, pack size, and prey density (Paquet and Carbyn 2003). They also contain complex topography, multiple prey species, and extensive denning and pup-rearing sites. Alternatively, breeding birds in a high-density nesting colony may only defend the nest that contains their offspring (Kaufmann 1983). Animals may also occupy home ranges at the periphery of their territory (Smith 1985). A home range is an area that animals habitually occupy, but has boundaries too extensive to defend actively. Territories are the centralized location where an animal nests, dens, or otherwise resides (Kaufmann 1983; Smith 1985). While some animals tolerate overlap of home ranges with neighbors, territories are exclusive areas that are protected from intruders. Most territorial defense is intraspecific competition, though, in high-biodiversity environments such as tropical rainforests, territories are also guarded against other species (Losin et al. 2016).

## Sex Differences

Territorial behaviors differ between sexes (Smith 1985). Males maximize fitness by securing sexually receptive females. They will either guard females against other males or protect the food

and habitat resources that attract females. Due to the intensity of male-male competition, it is often the most dominant males that succeed in securing breeding rights to females (Arnold et al. 2011). In group-living species, dominant males spend the most time and energy defending territories when compared to subordinate males or females (Arnold et al. 2011; Paquet and Carbyn 2003). Due to the increased energetic cost to produce offspring, female territorial behavior is centralized around protecting the resources needed to rear young (Smith 1985). In rare instances, females will guard a high-quality male from other females (Fukumori et al. 2009). And, in sex-role-reversed species, males take over parental care of offspring that allows the female to defend territories aggressively.

## Territory Signaling

The specific behaviors exhibited by animals encompass a wide range of sensory perception (Arnold et al. 2011; Herr et al. 2009). Often, animals will combine passive, energetically inexpensive methods of territory defense with physical, active defense. Physically marking the boundaries of a territory is a common, stable, and effective signal to conspecifics. Scent-marking with urine is a common method of distinguishing territories in canids (Arnold et al. 2011; Paquet and Carbyn 2003) and other animals (Herr et al. 2009; Rosell and Sanda 2006). Scent-marking is an energetically cheap method of territory defense because urine is a natural metabolic waste. Some animals will also visually mark territory boundaries by scratching or damaging landmarks such as trees while transferring scent to them. Alternatively, auditory signals such as bird songs are also common behavioral defenses (Tobias and Seddon 2000). Sound travels easily through most environments, and it is more energetically efficient for an animal to call from the center of a territory than to patrol its borders. However, in densely populated areas, males may spend excessive amounts of time calling that they reduce time spent foraging, which can decrease energy intake. It is also important to note that olfactory and auditory signals can alert predators to the



nearby presence of the territory owners and may increase the risk of mortality (Rosell and Sanda 2006). Visual displays are another effective territory defense for animals with small territories and open environments but are often associated with increased cost (Schwartz et al. 2007). For example, some lizard species perform head bob, push-up, and dewlap extension displays. These signal the dominant male's position to other lizards, but increases visibility to predators and is energetically costly. Lastly, if the previously mentioned methods fail, most animals will engage in aggressive, active defense of their territory (Herr et al. 2009; Schwartz et al. 2007; Smith 1985; Tobias and Seddon 2000). This behavior involves chasing intruders out of territory boundaries or fighting. The physical alterations are effective but very energetically expensive and risk injury or death.

## Human Interference on Territorial Defense

Infrastructure development and urbanization can interfere with territorial defense and lead to increased human-wildlife conflict (Herr et al. 2009). For example, urban-adapted stone martens (*Martes foina*) scent-mark their territories with urine during the spring and early summer. In natural environments, urine is deposited on non-mobile objects and is a stable indicator of territory boundary. However, cities contain unstable environments, and scent-marked vehicles move around the environment regularly threatening the integrity of the territory boundary. Male martens increasingly visit, mark, and climb into the engines of cars and cause damage to the components, resulting in conflict with humans. Unfortunately, many territorial signals are outside the realm of human sensory perceptions, so preventing this type of conflict is challenging.

## Conclusion

Territory defense involves a multitude of behaviors intended to establish exclusive dominance over an area and the resources contained within

(Kaufmann 1983). Territorial behaviors vary by species, territory size and composition, sex, season, and resources required. Common defensive signals include olfactory scent-marking (Arnold et al. 2011; Herr et al. 2009; Paquet and Carbyn 2003; Rosell and Sanda 2006), auditory calls and songs (Tobias and Seddon 2000), and visual displays (Schwartz et al. 2007). These methods are used as a strategy to avoid aggression, chasing, and fighting between rivals, which can result in injury or death (Herr et al. 2009; Schwartz et al. 2007; Smith 1985; Tobias and Seddon 2000). Research is demonstrating that human development and infrastructure causes interruptions in territorial signals that can lead to human-wildlife conflict (Herr et al. 2009). However, more research is needed to assess how these interruptions may impact the social communication and ecology of species.

## Cross-References

- [Female Choice](#)
- [Passerine Vocal Communication](#)
- [Sexual Dimorphism](#)
- [Sexual Selection](#)

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## Terry Maple

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## Background

Dr. Terry L. Maple is an expert in animal behavior and a pioneer in empirically based zoo management. He was born in 1946 in Maywood, California. His academic journey was inspired in part by childhood visits to the San Diego Zoo. He received his Bachelor's degree from the University of the Pacific and his Ph.D. from the University of California, Davis, under the mentorship of Robert Sommer and Gary Mitchell. He directed Zoo Atlanta for 18 years and oversaw its transformation into a world renowned research focused zoological institution. Dr. Maple is trained as a psychologist but integrates perspectives from biology, environmental design, and more. He has advocated for an empirical zoo, with decisions relating to animal care, visitor experience, and exhibit design being driven by scientific research and findings. The depth of his influence on the field is only matched by the breadth of his interests and areas of expertise. Dr. Maple's work ranges from conservation to understanding natural behavior to maximizing animal well-being in captivity.

## Major Contributions

Dr. Maple is an internationally recognized expert on the behavior, welfare, and conservation of great apes, and his ideas regarding the ethological programming in exhibit design have inspired design changes around the world. He has also served an advisory role on optimizing psychological well-being for nonhuman primates in research laboratories and primate research centers. In addition to his work with great apes, Dr. Maple has also served an important diplomatic role with China's efforts on giant panda conservation.

During his tenure at Zoo Atlanta, Dr. Maple also held an academic position at the Georgia Institute of Technology. He retired as the Elizabeth Smithgall Watts Professor Emeritus after 30 years of service in the School of Psychology. Along with his students and collaborators, Dr. Maple has published over 250 journal articles, chapters, and books on the behavior, conservation, and welfare. His work has involved a wide variety of species including African antelopes, baboons, capuchins, chimpanzees, elephants, flamingos, giant pandas, gorillas, giraffe, lemurs, lions, macaques, mandrills, orangutans, reptiles, spider monkeys, tigers, and zoo visitors. He is also the author of many books, including *Ethics on the Ark*, *Zoo Animal Welfare*, and *Professor in the Zoo*.

Dr. Maple is the Founding Editor of the journal *Zoo Biology* published by John Wiley/Blackwell and a founding member of the American Society of Primatologists. He is an elected Fellow of the American Psychological Association, the Association of Psychological Science, and has served as the President of the Association of Zoos and Aquariums.

## Lasting Influence

Throughout his career, Dr. Maple has mentored and opened doors for countless students, colleagues, and collaborators. Those in his academic family continue to serve the zoological community as directors, heads of research programs, and in academic positions around the world. He recently retired as the Director of the Palm Beach Zoo and now works as a consultant on

projects. His influence on the study of animal behavior, in particular in regards to the zoological setting, is monumental and will continue to have long-lasting effects.

## Cross-References

- [Animal Welfare](#)
- [Cognition](#)
- [Zoology](#)
- [Zoo](#)

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## Test for Analyzing Anxiety-Related Behaviors

- [Open-Field Test](#)

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## Testicle

- [Testis](#)

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## Testis

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## Synonyms

[Gonad](#); [Testicle](#)

## Definition

A testis is a typically paired male reproductive gland that produces sperm and secretes testosterone.

## Introduction

The testis is a component of the male reproductive gland that is responsible for male hormone (testosterone) and male germ cell (spermatozoa) production. It is homologous to the female ovary. Most modern animals have two testis, which may be symmetrical or asymmetrical in size and, if externalized, contained within the scrotum. The anterior pituitary controls the release of testosterone via the release of luteinizing hormone. Sperm production is controlled by the anterior pituitary through follicle-stimulating hormone and gonadal testosterone. In addition to testosterone, the testes also produce the hormones inhibin and estrogen, along with other proteins. The blood-testis barrier makes the testis an immunologically privileged organ, preventing substances from reaching the developing spermatozoa and preventing autoimmune reactions which could destroy developing germ cells. The remainder of this text will discuss basic embryological development, anatomy, function, and species variation of the testes.

## Embryology

During embryologic development, the gonads begin in the intermediate mesoderm adjacent to the kidneys. Initial development of male and female gonads is determined by the testis-determining factor, which is a product of the Y chromosome. Within the developing testes, the three main differentiating cell types include the gamete forming cells (spermatogonia), support cells (sertoli cells), and hormone secreting cells (leydig or interstitial cells). In most vertebrates other than mammals, the testes retain their original position in the abdomen (Farraj et al. 2017). As development progresses in mammals, the sex cord develops within the forming testes and the testes descend from the fetal abdomen to the inguinal ring and beyond to the inguinal canal and into the scrotum in those mammals that have externalized testes. Complete descent of both testis occasionally does not occur, leading to a

condition known as cryptorchidism, where the testis remains internally or stops short somewhere along the inguinal canal.

## Anatomy

The testis is composed of three layers, as well as a meshwork of vasculature and tubules that run throughout. From outermost to inner, these components are the tunica vaginalis, tunica albuginea, and mediastinum. The tunica vaginalis is a thin membrane that provides support and protects the testicle from the peritoneum, or abdomen. Next, the tunica albuginea is connective tissue that provides structure for the testis. The mediastinum is also made up of connective tissue and provides internal support. The seminiferous tubules are a part of the testicular parenchyma, or functional tissue, and are made up of two cell types that produce sperm (germ cells) and substances including androgen binding hormone, transferrin, and inhibin (sertoli or nurse cells). These additional substances produced by the sertoli cells surround developing germ cells and provide structural and metabolic support to the developing spermatogenic cells. Surrounding the seminiferous tubules are the cells that make up the blood-testis barrier.

## Hormone Function and Production

Testosterone is produced under tight control by the hypothalamus-pituitary-gonadal axis (HPG). The hypothalamus releases gonadotropin-releasing hormone (GnRH), which stimulates the release of gonadotropins, luteinizing hormone (LH), and follicle stimulating hormone (FSH) by the pituitary (Hill 2018).

## Variation Amongst Species

There is variation amongst mammals as to whether the testes are internally or externally located. For some land mammals (elephants,

sloths, etc) and cetaceans (whales, dolphins), the testes remain internally within the abdomen (Rommel et al. 2007). Most other land mammals have externalized testes that are located suspended within the scrotum. There are several hypotheses as to why most mammals have externalized testes, with the most widely accepted being the ability to keep the testes at a cooler temperature, which allows for more efficient spermatogenesis and protection against DNA damage of spermatogenic cells (Mills and Marchant-Forde 2010). The relative size of testes is thought to be influenced by mating systems, with those animals that engage in polygamy, typically having larger testes compared to body weight. In many seasonal breeders, the testes may increase in weight during the breeding season (Romer and Parsons 1986).

## Conclusion

While species variation exists in the location and size of the testis, the main function of producing and storing spermatogenic cells is conserved across most species. The testis also produces other hormones and proteins, under the control of the hypothalamus-pituitary-gonadal axis.

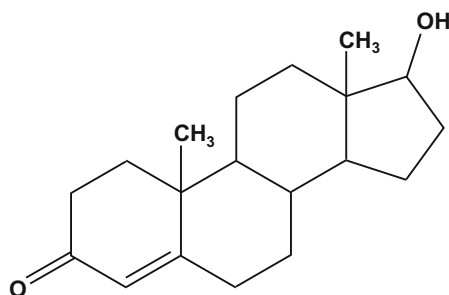
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## Testosterone

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**Testosterone, Fig. 1** Molecular structure of testosterone

## Introduction

Testosterone, a steroid hormone, is an important regulator of animal physiology and behavior. Testosterone is secreted from the testis and lesser amount from the ovary. Small amounts of testosterone is also synthesized and secreted from the adrenal gland. Testosterone stimulates the development of male reproductive organs such as testis and prostate, promotes and maintains male secondary sexual characteristics such as growth of muscle, bone, and body hair. Prenatal testosterone secreted from the testis masculinizes the male brain to facilitate male-typical behavior that becomes evident after birth. Temporal testosterone concentration in general circulation at a certain level is also important to maintain male-typical behavior after puberty. Testosterone improves spatial abilities, learning, and memory, and suppresses depression. This section highlights the role of testosterone and its metabolites in cognition and behavior in humans, rodents, as well as teleost fishes to understand their general functions from a comparative standpoint.

## Production of Testosterone and Its Metabolites

Testosterone (Fig. 1), a chemical compound that was first isolated from bull testis by Ernest Laqueur in 1935, is actively synthesized from cholesterol in the Leydig cells in the testis. Synthesis and secretion of testosterone from the testis are ultimately regulated by the hypothalamus-pituitary-gonadal (HPG) axis (Parhar et al. 2016). Adult females contain approximately ten

times lower concentration of testosterone that is produced in ovarian follicle theca cells and the adrenal gland. Testosterone is converted to  $5\alpha$ -dihydrotestosterone (DHT) by the enzyme  $5\alpha$ -reductase in the prostate gland, seminal vesicles, epididymides, and hair follicles. DHT has greater affinity to androgen receptor (AR) than testosterone and acts as the primary androgen in peripheral tissues. Testosterone is also converted to  $17\beta$ -estradiol (E2) by the enzyme aromatase in ovarian granulosa cells, placenta, brain, adipose tissue, blood vessels, skin, and bone. E2 synthesized in the brain modifies human and animal behavior, such as socio-sexual behavior and aggression (Ubuka and Tsutsui 2014).

## Role of Testosterone in Sexual Differentiation of the Brain in Mammals

Testosterone contributes to cell growth, cell migration, synaptic formation, apoptosis, and neurotransmitter synthesis in the brain, which is called organizing effect of steroid action. There is a critical period for masculinization of the male brain, which is thought to be during 8 and 24 weeks of gestation in humans. This organizational action of testosterone is evident in children's toy preference, such as cars for boys and dolls for girls (Hines 2010). Studies in rats have shown that perinatally aromatized androgen (E2) decreases apoptotic activity in the sexual dimorphic nucleus of the preoptic area (SDN-POA) in the brain, which is 2.6 times larger in males than females and important for male copulatory behavior in the adult. The third



interstitial nucleus of the anterior hypothalamus (INAH-3) of humans, which is larger in males than females, is thought to be the homolog of rodent SND-POA (Allen et al. 1989). On the other hand, anteroventral periventricular nucleus (AVPV) that regulates ovulation is larger in females. Prenatally metabolized testosterone enhances apoptosis in AVPV of males and reduces the number of cells compared to females. Posterior dorsal medial amygdala (MePD) that is related to decision making and male sexual arousal is dependent on adult testosterone. MePD is 1.5 times larger in male rats but testosterone manipulation in adults can completely reverse this sex difference.

### **Role of Testosterone in Spatial Abilities, Learning and Memory, and Depression in Humans**

General higher spatial abilities such as mental rotation in men than women suggest the facilitatory role of testosterone on acquisition or maintenance of spatial abilities. Studies have shown that prenatal testosterone, rather than temporal testosterone concentration, has stronger association with special abilities in men and women, suggesting that organizing effect of testosterone is important to facilitate spatial abilities in both sexes (Celec et al. 2015).

Various studies show that testosterone supplementation improves learning and memory in older men and women. It was shown in aged rat that DHT, the nonaromatizable androgen, was not able to improve memory, suggesting that E2 synthesized from testosterone in the brain improves memory. Organizational effect of testosterone on brain structures such as amygdala and hippocampus is also important to facilitate learning and memory after birth.

Because depression is more common in females compared to males and depression in males increases with age when testosterone concentration decreases, testosterone may function as a suppressor of depression. Testosterone concentration is also lower in female depressive patients. It was actually shown that testosterone

supplementation improves depressive symptoms in both men and women, suggesting that temporal testosterone concentration is important to maintain healthy mental condition in both sexes.

### **Androgenic Modulation of Cognition and Behavior of Teleost Fishes**

In teleost fishes, testosterone and 11-ketotestosterone (11-KT), an oxidized form of testosterone, are major androgens in males. Although both testosterone and 11KT act on target cells through AR, evidence suggests that 11-KT, rather than testosterone, plays important roles in the regulation of social behaviors such as sexual and aggressive behaviors in teleost fishes. In male tilapia, plasma 11-KT level is increased in response to courtship interactions. Under male-male interactive conditions, the levels of social hierarchy in male tilapia are positively correlated with peripheral androgen levels. Furthermore, administration of androgen induces male-typical sexual behavior such as chasing and ejaculation act in female teleost fishes, suggesting that sexual differentiation of the brain can be achieved in adults in teleost fishes.

Some fish species can change their sexual phenotypes throughout their lives as a reproductive tactics. In these species, sex steroids including androgens play an important role in gonadal sex changes. Interestingly, in some fish, conversion of behavioral phenotypes can be seen prior to changes in gonadal sexual phenotypes as well as circulating sex steroid levels. Therefore, androgen may not initiate the behavioral change but may be important to convert the brain to display male/female-typical behavioral characteristics such as courtship, spawning, and other behaviors for successful reproduction.

Although the hypothalamus can control behavior by regulating sex steroid production through the HPG axis, several neuropeptides in the hypothalamus are directly involved in the regulation of social and reproductive behaviors (Parhar et al. 2016). Gonadotropin-releasing hormone (GnRH, also known as luteinizing-hormone releasing hormone) is a master regulator of

vertebrate reproduction, which controls the release of gonadotropins from the anterior pituitary gland. In tilapia, there are three types of GnRH: GnRH1, GnRH2, and GnRH3 (Parhar et al. 1996). GnRH1-expressing neurons lie in the preoptic area, which project to the pituitary and are mainly involved in the control of gonadotropin release. On the other hand, GnRH2 and GnRH3 neurons are present in the midbrain tegmentum and the terminal nerve region, respectively, which mainly play neuromodulatory functions in the regulation of reproductive behavior (Ogawa et al. 2006). Treatment with exogenous testosterone reduces GnRH1 but increases GnRH3 mRNA levels in male tilapia (Soga et al. 1998), suggesting that there is a complex interaction between testosterone and the hypothalamus to regulate reproductive behaviors in teleost fishes.

As AR subtypes distribute widely in the brain of teleost fishes, multiple pathways outside of the HPG axis are possibly involved in androgenic modulation of cognitive functions (Parhar et al. 2016). A neuropeptide called kisspeptin (Kiss1) is predominantly expressed in the zebrafish habenula. In teleosts, the habenula is subdivided into the asymmetric dorsal and symmetric ventral subnuclei, which project to the interpeduncular nucleus and the ventro-anterior corner of the median raphe, respectively. Habenular kisspeptin neurons are involved in serotonergic modulation of olfactory cue-induced fear response (Ogawa et al. 2014). Although AR is expressed in the fish habenula, habenular kiss1 neurons are more sensitive to estrogen than androgen (Wang et al. 2013).

## Conclusion

Testosterone is secreted from the testis and lesser amount from the ovary and the adrenal gland. Testosterone is converted to DHT and E2 in mammals and 11-KT in teleost fishes in target organs, and these metabolites further modify the physiology and behavior of the animal by acting in target tissues and the brain. Testosterone has a significant role in sexual differentiation of the male brain in mammals. However, prenatally or

perinatally aromatized E2 may actually masculinize the fetal male brain. This organizational action of testosterone is evident in children's toy preference. Testosterone or E2 also has significant roles in spatial abilities, learning and memory, and suppression of depression in humans. 11-KT plays important roles in the regulation of social behaviors such as sexual and aggressive behaviors in teleost fishes. In contrast to mammals, sexual differentiation of the brain can be achieved by temporal sex steroids in adults in teleost fishes. Hypothalamic and extra-hypothalamic neuropeptides such as GnRH and kisspeptin can directly regulate behavior in teleost fishes, although their gene expression levels are regulated by sex steroids.

## Cross-References

- [Androgens](#)
- [Psychopharmacology of Sex Steroids](#)

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## Testudines Cognition

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Reptiles were long considered to be unintelligent beings, with scientists going so far as to suggest that their cognitive abilities were fundamentally different from that of mammals and birds (e.g., Day et al. 1999). However, recent research has revealed an impressive suite of cognitive abilities in this group (e.g., Kis et al. 2015; Siviter et al. 2017; reviewed by Matsubara et al. 2017). Despite this, the body of work in this area remains small and the group is vastly understudied when compared to other vertebrate classes. This entry will provide a brief review of the current state of knowledge in the field of cognition in testudines.

Today's extant testudines (also known as chelonia) are made up of turtles, tortoises, and terrapins. The group comprises of 327 species (van Dijk et al. 2014) and is characterized by a bony shell which encases the body. Chelonia are particularly informative in the study of the evolution of cognitive abilities as phylogenetic analyses place them as a sister group to the Archosauria (birds and crocodiles; Shaffer et al. 2013). Therefore, comparisons of similarities and differences

in performance on cognitive tasks can provide important insights into the evolution of cognition.

## Visual Perception

There is evidence to suggest that at least some chelonia are highly visual (summarized in Wilkinson and Glass in press). They have good color vision, exhibit color preferences (e.g., Pellitteri-Rosa et al. 2010), and are able to learn to discriminate between colors (Soldati et al. 2017; Davis and Burghardt 2011) and perhaps shapes (Glavaschi and Beaumont 2014). However, as yet, few traditional visual perception experiments have been conducted with this group, and as a result we know little about their perceptual capabilities. The work that *does* exist, however, suggests that it would be a fertile area for future research.

An experiment investigating picture-object recognition in the red-footed tortoise (*Chelonoidis carbonaria*) revealed that they behave towards a picture as if it is the object that it represents (Wilkinson et al. 2013); when, in unreinforced test trials, tortoises were asked to discriminate between a real piece fruit and a photograph of fruit, they performed at chance levels, suggesting that they confused the photographs with the real objects (Wilkinson et al. 2013). They were, however, able to learn to discriminate between the two when differentially reinforced for doing so (Wilkinson et al. 2013), suggesting that they certainly perceive the relation between the photograph and the object that it represents, making them an ideal species for further work using photographic stimuli.

## Spatial Cognition

Spatial cognition is considered adaptive as it allows an animal to move between resources in an efficient manner. This is one of the most understood areas of testudines cognition and much work has examined the impressive navigational feats of sea turtles (see ► “Testudines Navigation” entry for more details). However, efficient

navigation is equally as important on a smaller scale. This area has a long history (see Burghardt 1977 for a full review of the early work in this area); however, recent research has revealed some interesting developments in our understanding.

Studies of spatial cognition in mammals and birds have shown that they are able to use a range of strategies to navigate to a specific goal. This includes the use of a cognitive map, in which the spatial relations between a number of landmarks are used to define the goal. This is considered to be highly adaptive as is it robust against the removal of any individual landmark. This ability is thought to be dependent on the hippocampus, where reptiles are of particular interest as their brain structures differ from those of mammals and birds. Anatomical studies have suggested that similar circuitry and homologous structures, however, do exist between the groups (e.g., Naumann et al. 2015) and it is therefore important to investigate this behaviorally.

Chelonia are able to use a number of strategies to navigate towards a reward. There is evidence that both red-footed tortoises and terrapins (*Pseudemys scripta*; e.g., López et al. 2003) are able to use distal cues to navigate and appear to do so in a cognitive map-like manner (reviewed by Wilkinson and Huber 2012). Terrapins are able to navigate towards the same location irrelevant of starting point (López et al. 2001), and use different strategies depending on cue availability (López et al. 2001). The red-footed tortoise is able to learn to navigate efficiently around a radial arm maze (Wilkinson et al. 2007), requiring the animal to remember which of multiple spatial locations it has already visited in a trial (Mueller-Paul et al. 2012). When animals have access to complex and salient cues, they appear to use these cues in a cognitive map-like manner (Wilkinson et al. 2007). However, when cues are not salient, the tortoises' behavior changes and they exhibit stereotypic response strategies, choosing instead to enter the arm next to the one that they have just left (e.g., Mueller-Paul et al. 2012). This strategy is highly efficient in this particular maze, and the ability to switch between strategies is likely to be adaptive in the natural environment. The use of systematic responses

rules can, when reliable, substantially reduce memory load, while the use of a spatial representation of the environment can allow successful navigation despite changes in the external environment.

There is evidence that these response rules can be generalized across very different contexts (Mueller-Paul et al. 2014). Animals trained to make a spatial discrimination on the touchscreen transferred this response rule to a real life arena. Interestingly, if contingencies (spatial position of reinforcement) in the arena were then reversed, the animals did not transfer the reversal learning to the touchscreen context, but rather approached the side which was previously reinforced in that context. This occurred despite the animals receiving no training on the touchscreen for several months. This suggests that context-specific information is used when available and shows evidence of long-term spatial memory in this species.

More evidence to support use of different cues during navigation comes from recent field studies with translocated terrapins (*Chrysemys picta*). This work has revealed that younger individuals are able to follow paths of adults; however, this ability is not observed in older individuals (Roth and Krochmal 2015. See chapter ► “Testudines Life History” for more details). This suggests that animals of different ages may use different information when navigating, a hypothesis later confirmed with pharmacological tests (Roth and Krochmal 2016). Thus, testudines exhibit a range of complex spatial cognition abilities, the extent of which we are just beginning to investigate.

## Social Cognition

Recent research has revealed evidence of complex social cognition in chelonia. Gaze following is considered highly adaptive as it alerts an individual to important changes in the environment. There is evidence that red-footed tortoises are able to follow the gaze of a conspecific (Wilkinson et al. 2010b). They are more likely to look up if they see a conspecific doing so, than in control trials in which they see an empty arena or a

conspecific that does not look up. Further, there is evidence to suggest that they respond more to cues from a conspecific than those of a hetero-specific or model tortoise (Wilkinson et al. unpublished data). Further work is required to more fully investigate the cognitive underpinnings of this behavior.

Social learning is considered adaptive as it can allow an animal to solve a task without the costly process of trial and error learning (Laland 2004). Davis and Burghardt (2011) have revealed that the terrapin *Pseudemys nelsoni* is able to learn to select a stimulus associated with a reward through stimulus enhancement (see chapter ► “Stimulus and Local Enhancement” for more details of this method). Red-footed tortoises are also able to learn from observing the behavior of a conspecific (Wilkinson et al. 2010a). In a detour task (see chapter ► “Detour Task” for more details of this method), one group of tortoises observed a conspecific making the detour and eating food at the goal, while the other group did not. All animals in the observer group successfully reached the goal, while none of the control animals were able to (Wilkinson et al. 2010). The social learning mechanisms that control this behavior remain unclear; however, later tests revealed that the tortoises did not simply learn to follow the particular route that the demonstrator took, but rather learned some general principles about how to solve the task (Wilkinson and Huber 2012).

Tortoises also serve as an excellent group with which to examine hypotheses related to higher level cognitive processing. The literature has suggested that certain behaviors are related to higher level cognitive processes, but they do not directly test this. Take contagious yawning as an example; three hypotheses have attempted to explain this phenomenon. It has long been thought that contagious yawning is the result of empathy, which is cognitively complex and requires mental state attribution (e.g., Anderson et al. 2004). However, another hypothesis suggests that the phenomenon may result from non-conscious mimicry, which can emerge as a result of links between perception and action (Yoon and Tennie 2010). However, contagious yawning may also be the result of a fixed action pattern, the

releaser stimulus being the observation of a yawn (Yoon and Tennie 2010). Tortoises are ideal for investigating such questions as they are able to use social cues, but there is no evidence of social mimicry, mental state attribution, or empathy in this species. The results revealed no evidence of contagious yawning in this species, suggesting that this behavior may indeed result from higher level cognitive processes (Wilkinson et al. 2011).

## Long-Term Memory

Long-term memory is considered adaptive as it allows an animal to retain information about valuable resources. Red-footed tortoises can remember a spatial discrimination on a touchscreen for 3 months (Mueller-Paul et al. 2014). However, recent research has revealed that they are able to retain information about the relative reward value of a stimulus for at least 18 months (Soldati et al. 2017). Tortoises were trained to associate colored stimuli with different reward qualities and quantities (favored vs. less favored; more vs. less). They learned the association and worked harder for the preferred rewards; they were then given a retention interval of 18 months before being tested on the same discrimination. The results revealed that the tortoises retained information about stimuli associated with the relative value of both reward types. This is likely to impact upon foraging decisions in the natural habitats (John et al. 2016). Other work with *Pseudemys nelsoni* has revealed that they are likely to be able to remember how to perform a food acquisition behavior after a retention period of 36 months (Davis and Burghardt 2007, 2012) and can retain a visual discrimination after 3.5 months of nonexposure (Davis and Burghardt 2012). Taken together, these findings reveal impressive evidence of long-term memory in a suite of cognitive domains.

## Summary

Though still in its infancy, the growing field of testudines cognition has already yielded



impressive results, which gives impetus for more widespread study. These data can, when compared with data from other groups, provide crucial information about the evolution of cognitive abilities. Our increased understanding of cognition in this group also has important considerations for their captive care, with greater cognitive abilities comes greater capacity to suffer (Moszuti et al. 2017), as such, these advances are essential for our understanding of welfare in this group.

## Cross-References

- [Cognitive Imitation](#)
- [Cognitive Map](#)
- [Contagious Yawning](#)
- [Depth Perception](#)
- [Detour Task](#)
- [Discrimination Learning](#)
- [Evolution of Animal Color Vision](#)
- [Hippocampus](#)
- [Reversal Learning](#)
- [Stimulus and Local Enhancement](#)
- [Testudines Life History](#)
- [Testudines Morphology](#)
- [Testudines Navigation](#)
- [Two-Alternative Forced-Choice Paradigm, The](#)

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## Testudines Life History

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## Synonyms

Turtles and tortoises

## Definition

Summary of cognitive abilities of and processes in turtles and tortoises viewed in light of life history traits

## Introduction

Turtles and tortoises have been the frequent subjects of field studies. Decades of natural and life history study have provided us with a deep knowledge of the basic biology of this diverse group in an ecological and evolutionary context. Despite this work, there is a relative paucity of work on behavior and cognition in the Testudines, particularly in naturalistic environments. Based on their phylogenetic position, assumptions rooted in culture, aspects of gross neuroanatomy, and misinterpretations of the nature of their behavior, turtles have historically been considered to lack complex cognitive and behavioral abilities (Wilkinson and Glass [in press](#)).

Laboratory work has, however, provided strong support for an array of cognitive abilities among turtles and tortoises, supporting the notion that they possess greater cognitive abilities than once considered possible. These abilities include, but are not limited to, complex spatial memory, social cognition, fine discrimination/preference ability, and personality (Wilkinson and Huber [2012](#)). While informative, these studies often lack developmental, ecological, and evolutionary perspectives for the aspects of cognition demonstrated therein. As a result, our understanding of the cognitive abilities of turtles and tortoises is incomplete. Designing studies that investigate cognition within the framework of the animal's life history can work to fill this knowledge gap and to enhance the understanding of turtle and tortoise cognition and behavior. Integrating behavior, cognition, and their underlying mechanisms with life history at the individual, population, and community level will provide a more complete and relevant context in which to interpret experimental findings and provide motivation for the work (Angeloni et al. [2010](#)). For example, a *gestalt* understanding of the proximate cognitive

factors that influence behaviors within a life history setting can inform behavioral studies by giving researcher the ability to more appropriately motivate animals and thereby enhance the design of behavioral experiments. Additionally, life history explicitly considers the selective pressures that shape behaviors, thereby identifying the factors relevant to the evolution and maintenance of such behaviors. These emergent properties of behavior may not be immediately apparent in the controlled and stable settings of the lab in which many behavioral studies occur. Thus, the study of life history provides the framework to better understand how animals respond behaviorally to dynamic environments and how such interactions scale up to influence large-scale phenomena. Ultimately, this might translate to enhanced understanding of the evolution of cognition (Greggor et al. 2014; Roth and Krochmal 2015a).

### **Cognition Through the Lens of Life History**

Classically, ecologists define life history as the timing of key events of a species across the life span of the organism as shaped by natural and sexual selection (Bonin et al. 2006). Life history studies traditionally include the timing, size, and size of reproductive efforts, life span, and key developmental and growth patterns. While some aspects of life history may be associated with cognitive ability, studying life history alone does not fully provide the ecological and evolutionary context discussed above. Therefore, this chapter embraces a more broad definition of life history that includes the elements of natural history, specifically interactions with the social and physical environments.

Embracing this broad life history perspective provides the backdrop for a deeper understanding of turtle and tortoise behavior and cognition. Knowing species-specific ontogenetic patterns can reveal the costs and benefits of learning across development. Understanding patterns of habitat and space use in turtles and tortoises highlights the roles of cognitive processes in respond to changing environmental conditions across a

range of temporal and spatial scales. Natural environmental stressors provide strong selection pressures for complex cognition and rapid learning. Likewise, examining the social environment of turtles and tortoises provides the opportunity to reveal more complex social cognitive processes. Finally, examining how these taxa are both prey and predators in the field reveals a broad suite of cognitive capabilities from perception to shifts in preferences and decision-making under different contexts.

### **Development and Ontogeny**

Turtles and tortoises exhibit a slow life history strategy typified by a relatively long life span and delayed onset maturity (Bonin et al. 2006). Examining cognition within the species-specific age structure of turtles and tortoises provides an understanding of the patterns of learning over development. Being relatively long lived, turtles and tortoises are more likely to encounter a variety of environmental conditions and changes therein throughout life. Thus, the ability to learn about those conditions and to respond to such changes cognitively is potentially adaptive (Urban et al. 2014).

As a function of being relatively long lived, turtles and tortoises have a delayed onset to maturity. Typical of this life history strategy, they show highly characterized patterns of learning during development, often occurring within a specific time window, e.g., a critical learning period. A critical period represents a trade-off between the benefits of neural flexibility and the costs of maintaining that flexibility, costs that might be prohibitively high across a long life span. In an ontogenetic study of navigation, Roth and Krochmal (2015b) found evidence of age-specific learning about upland habitat in painted turtles. The authors revealed that learning about habitat is governed by a critical period ending at age 3 years. Similarly, juvenile loggerhead sea turtles learn the geomagnetic coordinates of their natal beach and recall that information when returning as adults (Lohmann et al. 2001). In both of these cases, learning complex habitat in early

development can be beneficial as it reduces the costs of maintaining plasticity.

### Spatial Use and Habitat Choice

Turtle and tortoise species vary greatly in their space use of their territories, home ranges, and/or across migratory movements. Sea turtles can traverse large portions of the Atlantic Ocean within a single year, whereas a box turtle might use but a few hundred square meters throughout its entire life. All else equal, animals that use more space within a territory or home range often have increased spatial cognition (e.g., spatial memory) capabilities and higher general cognitive capacities and enhance in the mechanistic underpinnings (e.g., neural processing) that support cognition.

Patterns of space use among turtles and tortoises can illuminate the cognitive mechanisms behind such complex behaviors as navigation. Many turtles and tortoises respond to changes in environmental conditions at a landscape level by using a cognitive approach. As behavior is a means by which animals can respond to rapid changes in the environment, changes that occur more rapidly than evolution would otherwise be able to accommodate physiologically (Greggor et al. 2014). Like many other taxa (e.g., birds and mammals), turtles and tortoises can migrate in response to seasonal changes in habitat quality or between reproductive and foraging areas across different life stages. For example, Roth and Krochmal (2016) demonstrated that painted turtles learn to navigate complex migratory routes through terrestrial habitat via spatial memory when faced with seasonal habitat loss. This phenomenon also occurs at larger temporal and spatial scales, with sea turtles learning and recalling specific geomagnetic cues to facilitate long-distance travel across the Atlantic Ocean between breeding, nesting, and feeding areas.

### Habitat Use and Abiotic Factors

Many turtles and tortoises experience extreme abiotic conditions, and those abiotic factors can often act as strong selection pressures and thus strong motivators. Understanding patterns of habitat use can demonstrate turtle and tortoise discrimination among and preferences for specific

aspects of the environment. The selection of habitat for feeding, basking, and nesting sites provides detailed evidence that these taxa possess fine habitat discrimination ability in highly heterogeneous environments. Moreover, this work had provided the backdrop by which to study the development of these decision patterns and abilities. For example, Tamplin (2009) demonstrated that some species of turtle have age-specific thermal discrimination. Three-month-old wood turtles lack the ability to discriminate temperatures and thus fail to select warmer temperatures.

Identifying and selecting appropriate habitat patches can have important consequences for fitness. Natural selection, should then, promote the ability to rapidly dissociate suitable from unsuitable habitat types. For example, gopher tortoises have very specific criteria that they use to select burrows, and the criteria on which they base the decision are plastic as a function of habitat (Lau and Dodd 2015). Furthermore, studying the discrimination of habitat qualities in field conditions provides us the opportunity to understand how turtles and tortoises respond to fluctuations in habitat quality and suitability. Refsnider and Janzen (2012) show that painted turtles' discrimination among nest sites as a function of thermal characteristics becomes finer in rapidly changing environments. This behavioral plasticity in nest site selection can then provide a buffer against the negative effects of climate change (Refsnider and Janzen 2012).

Evidence from conservation studies can also benefit our understanding of turtle and tortoise cognitive abilities. Researchers are beginning to appreciate the relevance of incorporating a cognitive or behavioral mind-set into such strategies (Blumstein and Fernandez-Juricic 2010). For example, translocation is a common conservation tool used to bolster population size by moving individuals among different population. Providing turtles and tortoises with additional time and safeguards to learn novel systems during translocation might be sufficient to promote long-term relocation success in some species (Bauder et al. 2014). Moreover, the process of translocation can be helpful as a tool itself to experimentally observe animals in novel situations to better

understand how they learn and interact with novel habitats (Krochmal et al. 2018). Translocated box turtles, for example, move farther distances and have significantly larger home ranges relative to resident animals, suggesting that they exhibit context-specific patterns in movement behavior (Hester et al. 2008).

### Social Structure

Historically, herpetologists have not considered turtles and tortoises to be social organisms. Although communal behavior is common among Testudines, traditional ecological research in the field has documented little direct interaction between individuals outside of breeding. Documenting and quantifying sociality in infrequently studied systems like turtles and tortoises is predicated on an increasing reliance on strong inference, is often subject to an elevated burden of evidence, and requires the rejection of additional alternative hypotheses. Despite these challenges in the field as a whole, investigating sociality in turtles and tortoises has provided us an opportunity to reconsider our understanding of what it means to be social and moreover the evolutionary origins of social behaviors (Doody et al. 2013). Assessing sociality in turtles and tortoises provides insight and context to studies of the evolution of social cognition and comparative psychology, insight only gained by adding a broad phylogenetic perspective.

Examining the potential for social behavior in the field from this new perspective has provided some evidence that sociality in some lineages of turtles and tortoises is more complex than previously assumed. For example, desert and gopher tortoise maintain and defend burrows and aggregate in nonrandom social networks (Radzio et al. 2016; Sah et al. 2016). Some species of river turtles vocalize underwater with offspring, potentially representing a form of parental care (Ferrara et al. 2013). Moreover, there is some evidence for conspecific communication and coordination of hatching during development (Doody et al. 2013). This field work supports a wealth of lab-based investigations also demonstrating complex social structures and advanced social cognition in some turtle and tortoise taxa (Wilkinson and Huber 2012).

### Predator/Prey Interactions

Predation is arguably the single most important factor shaping an animal's ecology (Lima and Dill 1990). The response to predation then has implications for nearly all aspects of behavior and can potentially shape proximate and ultimate aspects of cognition. Thus, the range of ways in which turtles and tortoises respond to the risk of predation can give unique, ecologically relevant insight into their potential range of cognitive abilities.

Turtles and tortoises respond to predation risk in a variety of ways, some of which potentially have cognitive underpinnings. For example, they can learn to ignore a perceived predation risk and can become more bold under certain conditions. Pond turtles that live in areas frequented by humans habituate to their presence and learn that humans do not represent a predation risk (Polich and Barazowski 2016). Likewise, some turtles exhibit state-dependent behaviors relative to predation risk. In the face of varying predation risk, green sea turtles decide to spend more time in risky habitats when in poor body condition but prefer safety when in good condition (Heithaus et al. 2007). Similarly, freshwater turtles alter nesting behavior according to a balance of trade-offs of current (risk to self) and future (risk to offspring) fitness (Spencer 2002).

Thinking about turtles and tortoises as predators exemplifies the varied cognitive processes underlying such behaviors as foraging and prey selection. Food items included in the diet can be flexible based on availability in the environment (Luiselli et al. 2004). In contrast, prey preferences in some species can be learned in early development and expressed throughout life. For example, common snapping turtles learn food preferences as juvenile that can become fixed (Burghardt and Hess 1966). Moreover, preferences can be contextually based. Exploratory foraging behavior in hawksbills can lead to adaptive shifts in dietary preferences (Wood et al. 2017). Similarly, sea turtles demonstrate species-specific color aversions to prey items in the lab, though these preferences do not manifest under natural feeding conditions (Swimmer et al. 2005). This work highlights the importance of considering context-specific flexibility of species diet as well



as the importance of investigating complex behaviors in the field.

## Conclusions

Investigating cognition in light of natural history likely requires working under field conditions. This approach has its challenges, but these challenges also offer unique viewpoints into cognition that would be otherwise unavailable. Working in the field often imposes limitations on the extent that researchers can control the observational or experimental environment (e.g., temperature, moisture) and the state, condition, and experience of the individuals included in the study. Though these conditions immediately may seem detrimental to research, they in fact are empirical strengths, offering a more naturalistic view of the focal behaviors and the animal's interaction with their environment. This can be a great strength to the study of cognition. Unlike in laboratory studies, working in the field does not require researchers to train animals in a particular task, as they are already "trained" by natural selection. Further, laboratory studies of cognition frequently utilize repeated measures designs. However, detailed and repeated observation of individuals in the field can be difficult to achieve as recapture or resightings may not be predictable. Instead, researchers can overcome these limitations by using a between-subject design and harnessing the larger number of animals generally present at the population level. Finally, field-based phenomena occur across temporal and spatial scales far larger than are found in laboratory study. Such time and spatial scales can, however, highlight the role of cognition in the manifestation of large-scale behavioral phenomena at the level of the individual, the population, and the community. For example, field work can provide insight into the ontogeny of cognitive processes in species, the influence of cognition in multi-species interactions, local adaptation, and cultural/social learning.

Assessing cognition in light of life history provides insight and context to behavior, cognition, and comparative psychology gained only by

adding the broad perspectives inherent in the study of ecology and evolution. Studying turtles and tortoises in this context provides the opportunity to examine this group of animals, allowing for the integration of their basic biology and cognitive abilities in a new light. Moreover, this approach allows researchers the ability to generate specific, testable hypotheses to further the study of cognition in the future. Such studies also potentially inform applied disciplines including animal welfare, captive animal management, and conservation providing a more comprehensive understanding of turtle and tortoise cognitive abilities.

## Cross-References

- ▶ [Adaptedness of Behavior](#)
- ▶ [Animal Welfare](#)
- ▶ [Captivity](#)
- ▶ [Cognition](#)
- ▶ [Communal Behavior](#)
- ▶ [Conspecifics](#)
- ▶ [Ecology](#)
- ▶ [Environmental Influences](#)
- ▶ [Evolution](#)
- ▶ [Feeding](#)
- ▶ [Habituation](#)
- ▶ [Home Range](#)
- ▶ [Learning](#)
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## Testudines Morphology

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### What Are the “Testudines”?

Testudines (also known as chelonians) is an order composed of about 300 reptile species popularly known as turtles, tortoises, and terrapins that can occupy a wide variety of ecological niches, from marine and freshwater to terrestrial environments (Uetz et al. 2019; Ernst and Barbour 1989; Fig. 1).

Such animals exhibit a combination of ancestral and extremely specialized features that are exclusive to the individuals belonging to this order (Pough et al. 2018). Distinctive chelonian characteristics are the presence of a shell composed by the carapace (upper part of the shell; Fig. 2a), plastron (lower part of the shell; Fig. 2b), and the location of the shoulder girdle within the rib cage. Such characters are well developed even in the earliest known turtles (Renous et al. 2008).

The chelonian skull is a highly modified structure: typically rather broad and flat and greatly expanded behind the eye area but with a short and narrow facial region (Fig. 3). Additionally, the skull is akinetic, i.e., it does not present any area where the bones articulate (=move) among themselves; the pterygoids (bones associated to the upper part of the skull) are solidly fused to the braincase, and the highly developed and peculiar quadrate is tightly bound to a great lateral expansion of the optic capsule. The temporal roof does not present any opening (also known as fenestra) but is generally emarginated from behind or below or both. Teeth are lost and have been replaced functionally by a horny bill (Romer 1956).

The vertebral number is nearly invariable in chelonians, with all living turtles having eight cervical vertebrae. Cervical ribs (when present) are rudimentary and confined to the posteriormost vertebrae. The trunk has ten dorsal vertebrae with the first and last attached but not fused to the carapace and the middle eight firmly fused or co-ossified with the neural bones of the carapace. The two sacral vertebrae link the pelvic girdle to the vertebral column by short and stout ribs. The caudal vertebrae number is variable but usually less than 24 in most species. The trunk ribs extend outward and fuse with the costal bones of the outer shell. Both elongation and shortening of the neck vertebrae result in distinct neck lengths among chelonians (Vitt and Caldwell 2009).

As in other reptiles, the divisions of the dorsal and ventral group of trunk muscles (epaxial and hypaxial) are not evident and are reduced to fit organs within the shell. In contrast, appendicular, head, and neck muscles are extremely well developed (Vitt and Caldwell 2009; Kardong 2014). The limb structure of turtles is highly variable, reflecting the environment and locomotory modes of the species (Fig. 4). For instance, marine species and the freshwater *Carettochelys* have well-developed flippers with extremely elongated digits that do not move independently (Fig. 4a). Most aquatic species have well-developed webbing between the digits, which





**Testudines Morphology, Fig. 1** Examples of the morphological diversity in Testudines: Terrapins (a–d), tortoises (e, f) and turtles (g). Figures (a–e): Roberto Murta/Bicho do Mato; Figure (f): Camila Mattedi

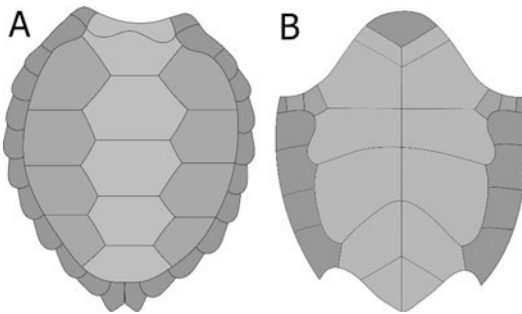
still retain some independent mobility (Fig. 4b). Terrestrial chelonians (i.e., tortoises) usually have stout limbs capable of lifting their heavy bodies off the substrate but are obviously ineffective for swimming (Fig. 4c). Their digits are usually reduced, and the feet are equipped with thick pads (Pough et al. 2004).

Additionally, the Testudines share a series of characteristics with several fossil groups, such as a distinctive ear region wherein the eardrum is supported by the squamosal (rather than by the quadrate) and by the retroarticular process, a backward projection of the lower jaw. Further, the foot is unique in the way the digits articulate with the ankle bones (Kardong 2014). Although there has been a wide debate on the origin of the modified anapsid skull, its features associated to the shell and post-cranial skeleton are unique among all known vertebrates (Pough et al. 2018).

## Cryptodira X Pleurodira

Extant chelonians belong to two lineages, which are mainly distinct in relation to the mode of neck retraction into the carapace: Cryptodira and Pleurodira (Herrel et al. 2008). Cryptodira represents the most diverse group of hidden-neck turtles found throughout the temperate and tropical regions of the world (Moustakas-Verho et al. 2017), exhibiting an S-neck retraction (vertical plane) inside the shell. Pleurodirans are known as side-necked turtles, with a lateral retraction (horizontal plane), with distribution occurring mostly along the Southern Hemisphere (Herrel et al. 2008; Moustakas-Verho et al. 2017). Pleurodires have a specialized cervical vertebrae (CV) anatomy with the CV5-CV6 articulation being the major point of flexure in neck retraction what reflects a key point for the evolution of Pleurodira (Mariani and Romano 2015). This specialization guarantees them a longer neck, improving performance in the capture of mobile food in the water (Herrel et al. 2008).

In addition to differences in the neck, cryptodires possess an ancestral musculoskeletal morphology, with most hip muscles originating on the pelvic girdle. In these species, the pelvic girdle is not fused to the shell. In contrast, pleurodires exhibit a derived morphology, in which fusion of the pelvic girdle to the shell is present and has resulted in shifts in the origin of most hip muscles onto the interior of the shell (Mayerl et al. 2017). Moreover, skulls may vary in size and shape, mostly regarding their jaw architecture and musculature, with pleurodires

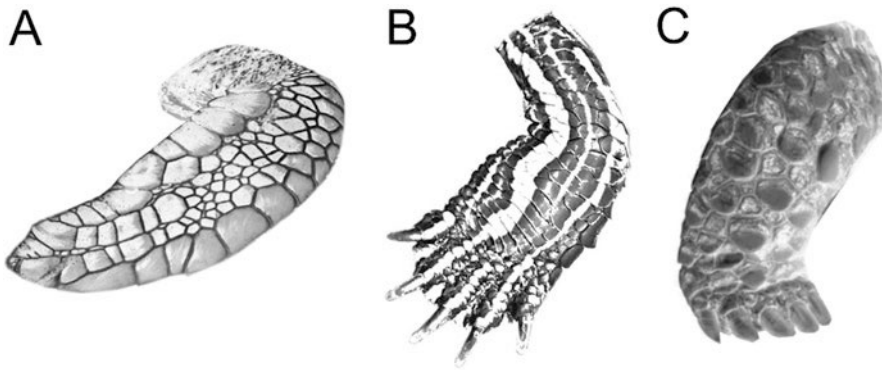


**Testudines Morphology, Fig. 2** Schematic illustration of the carapace (a) and plastron (b) of *Chelonia mydas*



**Testudines Morphology, Fig. 3** Skull of *Caretta caretta* in dorsal (a), lateral (b), and ventral (c) views illustrating the absence of skull openings (temporal fenestrae) and teeth





**Testudines Morphology, Fig. 4** Examples of different limb structures exhibited by Testudines. (a) Sea turtle flipper in adaptation to strictly marine environments; (b) terrapin flipper exhibiting webbing between digits in

adaptation to aquatic environments but capable of climbing in river rocks; (c) stout limb of a tortoise, in adaptation to terrestrial environment

usually exhibiting flatter and broader skulls. Such an architecture might have allowed the evolution of gape-and-suck mode of feeding, which is present in several South American species such as the matamata (*Chelus fimbriatus*).

## The Turtle Shell

The body of extant turtles is well known because of their distinct shape in relation to other tetrapods. It is composed by their shell, which is variously modified to provide protection from predators, shelter from the environment, enhance thermoregulation, and act as a rich reservoir of fats, minerals, and water. By enabling extensive concealment of extremities, shell-closing systems deter potential predators and promote survival both on land and in shallow water (Nagashima et al. 2012; Cordero 2017; Cordero et al. 2018). While the tortoise shells are very often high and domed – possibly as an adaptation to hamper predation – aquatic turtles usually bear streamlined shells (mostly for swimmers), although some shells may be less streamlined often with ridge carapaces to assist camouflage (mostly for species that are bottom-walkers).

The turtle bony armor has apparently originated independently many times in reptilian evolution, but the chelonian type of armor has appeared only once (Zug 1971), with this turtle-specific

arrangement having persisted over the last 210 million years (Lyson and Joyce 2012). However, the turtle shell is an evolutionary innovation that has been a mystery for evolutionary biology (Ferreira 2016), with its homologies being debated since at least the nineteenth century (Moustakas-Verho et al. 2017). Many biologists have for long claimed that the turtle shell takes shape from skin cells adjacent to the ribs that are transformed into bone in the course of development. However, Japanese developmental biologists have recently suggested that the shell is most likely a direct outgrowth of bones themselves (Lubick 2013). Additionally, extraordinary fossil discoveries indicate that terrestrial early turtle-like reptiles exhibit transitional features that eventually gave rise to the fully shelled *Proganochelys*. Turtle-like fossils, such as *Eunotosaurus* (260 million years old), *Pappochelys* (240 million years old) and *Odontochelys* (220 million years old) suggest that the ventral shell elements evolved first, followed by broadened ribs that eventually gave rise to the fully hardened dorsal shell. This has recently led to the intriguing hypothesis that the incipient shell might have evolved as an adaptation to life underground, rather than, as traditionally thought, an anti-predator defense. Moreover, other distinctive turtle skull and limb traits were distinct in these fossils (Cordero 2017).

The carapace is formed from costal bones fused with ribs, neural bones fused with

thoracic vertebrae, peripheral bones, and an anterior nuchal bone, covered by keratinized epidermal shields (Burke 1989; Moustakas-Verho et al. 2017). Developmental evidence and muscular attachments suggest that the nuchal bone is derived from the cleithra of the ancestral tetrapod pectoral girdle (Gilbert et al. 2001).

The plastron is the order-defining skeletal structure for turtles (Rice et al. 2016) formed from the suturing together of an entoplastron (interclavicle), epiplastra (clavicles), and three to five paired bones (Moustakas-Verho et al. 2017). The absence of the ventral portion of the ribs and the sternum suggests that plastron assumed their role (Rice et al. 2016). There are a few hypotheses the plastral bones of turtles and the gastralia of other tetrapods are homologous (Gilbert et al. 2001), but such suggestion has still been a debate over the years.

The dorsal and ventral armor are covered by a keratinized epithelium, and two epithelial appendages might be present in the turtle shell: scutes (large epidermal shields separated by furrows and forming a unique mosaic) and tubercles (numerous small epidermal bumps located on the carapaces of some species). Recent studies have suggested the scute of the turtle shell as an evolutionary novelty, whereas tubercles are homologous to reptilian scales (Moustakas-Verho and Cherepanov 2015).

Although the body structure is the same in all individuals, the shell morphology varies according to habits of each species (e.g., flat shells are more hydrodynamic, which may justify their presence in aquatic turtles). In addition, the interspecific shape variation in terrestrial turtles is greater than in aquatic species (Claude et al. 2003). This type of variability can be explained by the complexity of the adaptive landscape in terrestrial environments in relation to aquatic ones, providing multiple niches (Schluter 1986). Additionally, turtle species can often be recognized by the tessellation and pigmentation of scutes on their shell, and scutes have been independently lost or reduced in certain freshwater and marine taxa (Moustakas-Verho et al. 2017).

## Modifications and Adaptations to an Enclosed Body

Diversification of the turtle shell comprises remarkable phenotypic transformations, mostly regarding their internal visceral organization, locomotor apparatus, neck region, and copulatory mechanism (Cordero et al. 2018). For instance, internal muscle connections and limb articulations were modified during the repeated evolution of shell kinesis in small-bodied terrestrial or semiaquatic turtles, as well as modifications of the limbs in terrestrial species (tortoises). Also, change in the muscles that enable lung function was necessary to accommodate early steps in the evolution of the shell.

The location of the heart varies within reptilian lineages and even within taxa, although the heart tends to be positioned roughly along the axial midline. In chelonians, part of the heart is often deep to margins of the humeral and pectoral scutes; however, in some species, it is positioned more posteriorly along the midline between humeral-pectoral and pectoral-abdominal scute lines. The heart was repositioned during the evolution of soft-shell turtles, being relatively displaced to the right, and typically just caudal to the level of the acromion processes and cranial to the distal procoracoid process – procoracoid cartilage junction (Wyneken 2009; Cordero 2017).

Changes in the muscles that enable lung function were also necessary to accommodate early steps in the evolution of the shell. As most tetrapods inhale by ribs expansion (aided by muscle functions), incorporation of the ribs into the turtle shell negates the costal movements that effect lung ventilation in other air-breathing amniotes. Recent studies have indicated that the early stem lineage of turtles deviated from the basal amniote body plan (in which locomotion and breathing are coupled) and evolved a division of function in which the ribs took on a stabilizing role, whereas the abdominal muscles became specialized to ventilate the lungs. Instead, turtles have a unique abdominal muscle-based ventilatory apparatus which most likely evolved through a division of labor between the ribs and muscles of the trunk in which the abdominal muscles took on the primary ventilatory function, whereas the broadened

ribs became the primary means of stabilizing the trunk. These changes occurred approximately 50 million years before the evolution of the fully ossified shell (Lyson et al. 2014).

The independent evolution of the carapace and plastron also required several musculoskeletal changes such as muscle modification, shortening of the trunk, widening of the ribs, encapsulation of the ventral scapula into the chest, loss of intercostal muscles, and reorganization of the respiratory muscles (Rice et al. 2016). For instance, internal muscle connections and limb articulations were modified during the repeated evolution of shell kinesis in small-bodied terrestrial or semiaquatic turtles. Moreover, the evolution of jumbo-sized shells was accompanied by modifications of the limbs in terrestrial species (Cordero 2017). Additional particular characteristic of the chelonians is the location of the girdles within the rib cage. The pectoral girdle is composed of a long scapula, an acromion process, and a coracoid process differing them to the other tetrapods (Renous et al. 2008).

## Conclusion

Chelonians have evolved a novel generalized structural body plan with unique functional mechanisms which guaranteed their evolutionary success along about 220 million of years. The turtle shell provides defense, shelter, and physiological balance, and their distinct enclosed body has resulted in several modifications in the axial skeleton, appendages and appendicular muscles, as well as visceral topography. Even though several issues regarding chelonians evolutionary history are still under debate, this group has carried specialization a long way and without doubt to the greatest extreme of any of the chordates.

## Cross-References

- [Adaptation](#)
- [Clavicle](#)
- [Locomotion](#)
- [Morphology](#)
- [Muscular System](#)

- [Respiratory System](#)
- [Semi-Aquatic](#)
- [Skeletal System](#)
- [Terrestrial](#)
- [Testudines Life History](#)
- [Thermoregulation](#)

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## Testudines Navigation

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## Synonyms

[Chelonia navigation](#)

## Introduction

The order Testudines comprises several species of turtles, terrapins, and tortoises. They are found in a variety of ecosystems occurring in temperate and tropical regions and can be terrestrial, freshwater, or marine (Savage and Gaffney 2015). They are also known to migrate seasonally between habitats, whether for feeding, nesting, hibernating, or estivating (Iverson et al. 2009). Aquatic, semiaquatic, and terrestrial species migrate relatively short distances (between 1 and 27 km) between habitats. Marine turtles, however, have the longest migration of any reptile, migrating thousands of kilometers in their lifetime between feeding locations and breeding grounds. There are several mechanisms used by members of the order Testudines for navigation between habitats from hatchling stage into adulthood. Orientation and navigational mechanisms include a geomagnetic compass, various visual cues, and inertial, slope, or olfactory cues. The navigational mechanisms used by organisms belonging to the order Testudines vary across species and over life stages and may be used separately or in conjunction with each other. Of all the members of the order Testudines, the sea turtles are the most extensively studied (reviewed in Southwood and Avens 2010).

## Geomagnetic Map Navigation

If an animal is able to detect the earth's magnetic field, they must be able to detect at least two features in order to determine their position. The first is the angle of inclination and the second is field intensity, which form a grid across the surface of the earth. The grid, or bicoordinate map, helps turtles to determine their position on the globe (Lohmann and Lohmann 1996). The intensity can refer to the total intensity of the field, the vertical intensity, or the horizontal intensity (Lohmann et al. 2008). However, it should not be assumed that all animals utilize the earth's magnetic field in the same way. Some animals may be able to use one feature to determine their position in one direction relative to a goal (Lohmann et al. 2008).

Complications in the use of a geomagnetic map are due to secular variation, which refers to the gradual change in features of earth's magnetic field over time. Changes do not occur in a stable manner worldwide, but rather changes occur at different rates, in different locations, and different times. To compensate for this, an organism that stays within a region for a duration of time will incorporate the changes in magnetic field into their learned geomagnetic map. If the organism does not learn the changes, then other mechanisms of navigation must be employed (Lohmann et al. 2008).

To explain the usage of a geomagnetic map in members of the order Testudines, the ferromagnetic hypothesis has been proposed. This hypothesis states that an animal has specialized organ structures containing nanoparticles which form chains in the presence of a magnetic field. The nanoparticles can be single domain or superparamagnetic. Single domain nanoparticles have a magnetic moment that remains stable over time and temperature changes (Belova and Acosta-Avalos 2015). These particles have the ability to align with the earth's magnetic field and may have the possibility to send magnetic signals to the nervous system. Superparamagnetic particles do not have a magnetic moment without a magnetic field present. In the presence of a magnetic field, the particles will develop a magnetic moment that tracks the external field but does not align with the field. They can produce a magnetic field strong enough to attract or repel nearby particles, which can in turn stretch or contract a cellular membrane. The expansion or contraction of a membrane may convey messages to the nervous system. Magnetite is a nanoparticle that can be either single domain or superparamagnetic, depending on the size of the particle (Johnsen and Lohmann 2005). Magnetite has been extracted from the heads of sea turtles and several other animals known to orient magnetically, suggesting the use of magnetite in magnetoreception (Perry et al. 1985).

## Visual Cues

The sun can be used as a compass cue for members of the order Testudines, as it can provide directional information when referenced to the

earth's horizon (reviewed in Southwood and Avens 2010). In order to orient using a sun compass, the organism must be able to calibrate their internal biological clock to changes in the sun's azimuth, which is approximately 15° per hour. Sun compass orientation can be demonstrated by exposing an organism to an experimentally altered photoperiod and then allowing it to orient. For example, when exposing an organism to an artificial photoperiod that delays the sun's rise by 6 h, the animal should exhibit a shift in orientation by 90° (DeRosa and Taylor 1982).

The sun compass may be used alone or in conjunction with polarized light cues. Light polarization occurs as sun rays are scattered by molecules in the atmosphere (reviewed in Southwood and Avens 2010). Polarization can also occur as light is reflected off of water surfaces (Mathger et al. 2011) or in water as deep as 200 m. Skylight polarization is fixed, with the highest amount of polarization occurring on the axis 90° to the sun's position along its azimuth and the least amount occurring near the sun. Skylight polarization is most effective in clear conditions and will not give useful information in cloudy conditions (reviewed in Southwood and Avens 2010). To use this visual cue, an animal would have to have eyes able to detect polarization (Mathger et al. 2011) and have the ability to compensate for the movement of polarization across the sky (reviewed in Southwood and Avens 2010).

The light given off of the seaward horizon at night is a photic cue used by sea turtle hatchlings when finding the ocean. Loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) hatchlings have been found to always orient toward the brightest light presented to them. They also have been found to orient away from dark, elevated silhouettes and not necessarily toward the brightest horizon presented to them (Salmon et al. 1992).

Visual landmarks in an animal's environment can provide directional cues to a goal. This suggests use of cognitive map, where an animal can identify different sites in its habitat (reviewed in Southwood and Avens 2010). The animal can create a cognitive map by searching its environment, by taking excursions in several directions, noting landmarks and distances traveled. The animal can then reference various sites as a compass



cue for navigation (Åkesson et al. 2003). In mammals and birds, the hippocampus is responsible for spatial cognition. However, reptiles do not have a hippocampus, and it is believed that the reptilian medial cortex is responsible for spatial cognition (Wilkinson et al. 2009).

## Other Cues

Inertial cues may play an important role in sea turtle hatchlings migrating offshore and for juveniles and adults to sense oceanic movements. In hatchlings, it is believed that vestibular organs sense vibrations from the orbital motion of the water, initiating reflexes in the sea turtle that serve to maintain its heading. Within the inner ear, there are three otolith structures: the utricle, saccule, and lagena, which are extremely sensitive tilting motion. Horizontal, posterior, and anterior canals within the inner ear are sensitive to angular acceleration (Avens et al. 2003). In adult sea turtles, the same vestibular structures are believed to be used in the detection of oceanic currents, without having to surface, to derive navigational information. Inertial cues can be useful when visual cues are unavailable (Lohmann et al. 1995).

The slope of an environment can give information as to the direction of a water body and is used by several organisms such as sea turtles (Salmon et al. 1992) and aquatic or semiaquatic turtles (DeRosa and Taylor 1982).

Olfactory cues can be used in navigation by enabling the organism to be able to recognize specific sites. Sea turtles, for example, may imprint on the chemosensory cues of their natal beaches, helping them to home during the adult stage (reviewed in Southwood and Avens 2010). Odors can be carried on winds or in oceanic currents (Åkesson et al. 2003), or can come from conspecifics, helping different turtle species to navigate (Tuttle and Carroll 2005; Lohmann et al. 2008).

## Orientation and Compass Setting in Sea Turtle Hatchlings

Sea turtle hatchlings usually emerge from their nests at night and, upon emerging, immediately

orient themselves and crawl toward the sea. There are three mechanisms by which sea turtle hatchlings find the ocean, used in sequence from their initial emergence from the nest to when they locate the open ocean (Lohmann and Lohmann 1996). First, they are known to initially orient toward a lower and illuminated horizon, rather than elevated, darker shapes made by vegetation and sand dunes (Salmon et al. 1992). Second, when hatchlings reach the wave refraction zone, they use inertial cues to maintain their headings directly into waves and toward the open ocean. Third, upon swimming past the wave refraction zone, they maintain their straightforward heading using an internal geomagnetic compass (Lohmann and Lohmann 1996).

A hatchling's initial orientation toward the ocean is not driven by an inherent directional preference, which was demonstrated by Carr and Ogren (1960). When green turtle (*Chelonia mydas*) hatchlings were brought from the east coast of Costa Rica to the west coast, they oriented correctly toward the ocean. Other hatchlings were also released onto beaches with adhesive blindfolds covering their eyes. The hatchlings aimlessly moved and could not find the beach. Those who removed their blindfolds were reported to immediately orient toward the ocean.

When initially orienting toward the ocean, loggerhead and green turtle hatchlings use visual cues of illuminated, downward sloping horizons and dark, elevated silhouette cues. On clear nights, the seaward direction is more brightly illuminated than the landward direction. The landward direction also typically contains elevated dunes and vegetation, creating dark silhouettes. If no photic cues are available, hatchlings orient using elevation cues, crawling along the downward slope. The primary cue in ocean finding for loggerhead and green turtles is first perceiving darkness in the landward direction and secondarily using photic cues and downward sloping beaches to navigate to the water (Salmon et al. 1992).

The initial orientation cues used by sea turtle hatchlings can vary among species. For example, green turtles sometimes hatch on beaches with a relatively uniform slope, so photic cues may take precedence over elevation cues. Hawksbill turtles

(*Eretmochelys imbricata*) generally nest under thick vegetation, where photic cues may not be readily available to hatchlings. These hatchlings may orient toward the ocean using the slope of the beach (Salmon et al. 1992).

After initial orientation, sea turtle hatchlings crawl toward the ocean and swim directly into the waves. By maintaining a straight course through the wave refraction zone, the turtles will be lead into the open ocean. Arena experiments have shown that loggerhead and green turtles are able to detect circular motion created by waves and are able to orient their bodies accordingly. Sea turtle hatchlings will swim into waves, regardless of other cues that may be available, such as various photic cues or whether wave direction tends to be more shoreward or seaward (Lohmann et al. 1995; Lohmann and Lohmann 1996).

Beyond the wave refraction zone, wave direction does not provide cues to the landward direction, yet hatchlings will maintain their straightforward heading into the open ocean. At this point, it is believed that the hatchlings orient themselves using the magnetic field of the earth. It is unclear whether hatchlings are born with a geomagnetic compass or if it is acquired. Research suggests that the geomagnetic compass of hatchling sea turtles is acquired through experience, via exposure to light, through the hatchling's initial experience in maintaining direction during the first beach crawl, or by swimming into oncoming waves (Lohmann and Lohmann 1996).

Geomagnetic compass learning by exposure to photic cues was demonstrated in leatherback (*Dermochelys coriacea*) and loggerhead hatchlings. After being exposed to a light for 1 h, hatchlings established a course swimming toward the light. When tethered in an arena in complete darkness, the turtles oriented in the magnetic direction the light was. When the magnetic field was shifted, the turtles oriented in accordance with the shift. Hatchlings tethered in the arena without prior light exposure oriented randomly (Lohmann 1991; Lohmann and Lohmann 1993). Similar findings have been demonstrated in arena experiments when turtles selected a directional preference by crawling toward a light and by swimming

into waves. These findings suggest that directional preference is not inherent. When hatchlings are allowed to orient in response to an environmental cue, they set a directional preference that is maintained by earth's magnetic field (Lohmann and Lohmann 1996).

## Geomagnetic Navigation in Juvenile Sea Turtles

Upon swimming into the open ocean, loggerhead hatchlings, for example, swim to the Gulf Stream and end up within the North Atlantic gyre. The turtles will spend several years within the gyre until reaching reproductive maturity. Within the gyre, detection of earth's magnetic field may be imperative of the survival of young turtles (Lohmann and Lohmann 1996). Some research suggests that hawksbill hatchlings do not enter the open ocean, but stay in neritic coastal feeding grounds, avoiding currents that can lead them into the open ocean (Gaos et al. 2017).

Latitudinal direction corresponds with the earth's angle of inclination, a feature that sea turtles have been demonstrated to detect. Staying within certain latitudinal boundaries can prevent hatchlings from being swept into unfavorable habitat by oceanic currents. Within the North Atlantic gyre, loggerhead hatchlings risk entering eastward currents that divide, with one current traveling northward to cold waters. Currents in the southern portion of the gyre can carry turtles beyond their range by entering the South Atlantic current system. It was demonstrated that hatchlings can detect their position using angle of inclination and field intensity by presenting them with magnetic field features corresponding to those found in the North Atlantic gyre. It was found that when the loggerhead hatchlings were exposed to a field matching that of their natal beaches, they swam eastward, as if swimming toward the gyre. When exposed to a field matching that of the northern- or southernmost boundary of the gyre, hatchlings swam southwest and northeast, respectively. Although hatchlings and juveniles may not yet have the ability to orient toward a specific goal when within a gyre, they have an innate sense not

to stray outside of latitudinal boundaries (Lohmann and Lohmann 1994, 1996).

During the open-ocean life stage, which can last up to 10 years (reviewed in Southwood and Avens 2010), juveniles are learning the magnetic map of the ocean and associating it with various locations they can navigate to. Eventually, turtles such as loggerheads will reside in neritic feeding grounds and will seasonally migrate between habitats. It is believed that their ability to home to a target location occurs when they enter the neritic feeding stage. Juveniles will reliably return to feeding grounds they favor during seasonal migrations and also after being experimentally displaced (Lohmann et al. 2008). In contrast, leatherback and olive ridley (*Lepidochelys olivacea*) sea turtles do not feed near coastal areas but swim through the open ocean to feed (reviewed in Southwood and Avens 2010).

### Homing in Juvenile and Adult Sea Turtles

Navigational mechanisms in older sea turtles may differ from hatchling mechanisms as the turtle gains experience. While a geomagnetic map is important in navigation (Lohmann et al. 2008), juveniles and adults have been shown to employ other mechanisms to accurately home to a location when the magnetic field is disrupted.

The use of visual cues has been demonstrated in juvenile loggerheads, approximately 7 years of age, which were captured from neritic feeding grounds. In arena experiments which disrupted the magnetic field, turtles accurately oriented in the direction of their capture site by using either the sun's position or by light polarization. When no visual cues were available, and the magnetic field was undisturbed, turtles still accurately oriented toward their capture site, indicating geomagnetic navigation (Avens and Lohmann 2003). Green turtle juveniles have also been demonstrated to orient using a sun compass through exposure to an altered photoperiod, even when magnetic cues were available. While it is evident that sea turtles do employ solar and/or polarized light cues for navigation, it needs to be explored

what causes the shift in cue usage in nature (Mott and Salmon 2011).

Some species of sea turtles can take 30–50 years to reach reproductive maturity (reviewed in Southwood and Avens 2010). Once maturity is reached, turtles migrate hundreds or thousands of kilometers every 2–4 years to specific breeding sites (Lohmann et al. 2008). Several species will return to their natal beaches to nest, and it has been proposed that turtles are able to imprint chemosensory information of their natal beaches (reviewed in Southwood and Avens 2010).

Green turtles feed in the coastal waters of Brazil migrate more than 2000 km to Ascension Island in the middle of the Atlantic Ocean, which is only 11 km wide. A geomagnetic map alone may not be enough for sea turtles to accurately home to target locations. Rather, when near a target location, they may switch to or incorporate other available cues (Lohmann et al. 2008). Green turtles that were experimentally displaced homed to Ascension Island when the earth's magnetic field was seemingly disrupted by satellite tracking devices attached to their heads or carapaces. Those that were able to home to the island first used a searching strategy, traveling in indirect routes until coming into contact with another navigational cue. Chemosensory cues carried by prevailing winds traveling northwest provided a beaconing mechanism that directed turtles toward the island (Akesson et al. 2003). The displaced green turtles may have also felt surface wave patterns, as they are highly sensitive to movement (Lohmann et al. 2008). As the winds travel to the northwest, the downwind side of the island will exhibit refracted wave patterns, providing inertial signals as to where the island is located (Akesson et al. 2003).

### Orientation in Aquatic and Semiaquatic Freshwater Turtle Hatchlings

Much like sea turtles, freshwater turtles primarily use visual cues when dispersing from their nests (Congdon et al. 2011, 2015). Freshwater turtles typically emerge during the day, when visual cues

are easily recognizable (Congdon et al. 2015). However, the distance of the nest site can create issues in hatchling orientation if the nearest water body is not readily seen (Congdon et al. 2011). Therefore, other cues may play a role in wetland finding by aquatic or semiaquatic turtles, including slope, geomagnetic, or chemosensory cues (Iverson et al. 2009).

Hatchlings of snapping turtles (*Chelydra serpentina*) and western painted turtles (*Chrysemys picta belli*) orient themselves using photic cues, crawling toward the brightest illuminated horizon. They will crawl toward the brightest horizon whether or not it contains a water body reflecting polarized light (Congdon et al. 2011). In contrast, yellow mud turtle (*Kinosternon flavescens*) hatchlings orient using polarized light cues, as they were found to orient themselves in the direction of an open horizon containing a body of water that was not readily visible from their experimental arena (Iverson et al. 2009).

Many species use other visual cues to navigate. Blanding's turtle (*Emydoidea blandingii*) hatchlings orient themselves toward dark horizons, often toward riparian zones (Pappas et al. 2009). Diamondback terrapin (*Malaclemys terrapin*) hatchlings, which inhabit brackish waters, crawl toward the nearest vegetation and remain there until nightfall (Berger 1976).

Chemosensory cues can also be important in navigating toward a goal for freshwater hatchling turtles. For example, semiaquatic wood turtle (*Glyptemys insculpta*) hatchlings were observed to walk along the same paths as conspecifics during their initial migration to a brook, suggesting the use of chemosensory cues in navigation (Tuttle and Carroll 2005).

The primary orientation cue in aquatic and terrestrial turtles is a sun compass rather than a geomagnetic compass. This was demonstrated in snapping turtle and Blanding's turtle hatchlings. The hatchlings were first allowed to orient themselves using visual cues, whether in natural habitat or in an arena. When relocated to a corn field with no visual targets, turtles maintained their preferential heading and were unaffected by magnets attached to their carapaces (Congdon et al.

2015). Similar to sea turtles, this is suggestive of a directional preference that is learned through experience of movement toward a visible target. Upon completion of a successful migration, usually to a water body, the directional preference then sets the turtle's sun compass (Pappas et al. 2009; Congdon et al. 2011, 2015; Iverson et al. 2009).

### Navigation in Juvenile and Adult Aquatic, Semiaquatic, and Terrestrial Turtles

Nonmarine turtles also navigate seasonally between various habitats to exploit different resources and exhibit the use of different navigational cues than hatchlings. While hatchling yellow mud turtles navigate using polarized light cues, a sun compass took precedence in juvenile orientation. Arena experiments showed that the juveniles did not orient toward the body of water, where polarized light may be reflected, as the hatchlings did. Rather, they maintained the headings they were oriented in upon their capture (Iverson et al. 2009).

Spiny softshell turtles (*Trionyx spinifer*), painted turtles (*Chrysemys picta*), and common box turtles (*Terrapene carolina*) orient using a sun compass and are not able to orient on overcast days. These turtles were also found to adjust their orientation in a clockwise direction in accordance with an experimentally altered photoperiod (DeRosa and Taylor 1982).

Although common box turtles become disoriented on overcast days, they also become disoriented when magnets are attached to their carapaces (reviewed in Southwood and Avens 2010). While some freshwater turtles do not primarily orient using a geomagnetic compass (as with the Blanding's and snapping turtles), it cannot be ruled out as a navigational mechanism (Congdon et al. 2015). Geomagnetic compasses may not be important to all species of nonmarine turtles, as their migration distances are not as vast as marine turtles (Iverson et al. 2009).

Slope cues, chemosensory cues, and learned cognitive maps can also be used by turtles to

navigate. Orientation down slope was exhibited by spiny softshell, painted, and common box turtles, presumably as an adaptation to water finding (DeRosa and Taylor 1982). Olfactory cues may also be important to goal navigation, as eastern long-necked turtles (*Chelodina longicollis*) were found to prefer the scents from a pond to other scents (reviewed in Southwood and Avens 2010), which may aid in homing. A red-footed tortoise (*Geochelone carbonaria*) utilized visual cues to navigate in an eight-arm radial maze. The visual cues correspond to a cognitive map that is learned and utilized by the tortoise. When visual cues were obstructed, the tortoise changed its navigational strategy. It responded by searching the maze by turning down each arm in either a clockwise or counterclockwise direction (Wilkinson et al. 2009).

## Cross-References

- [Compass Orientation](#)
- [Landmark](#)

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## Tetrapods

- [Gait](#)

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## Thanatosis

- [Tonic Immobility](#)

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## Thayer's Law

- [Countershading](#)

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## The Ability to Conceive Children

- [Fertility](#)

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## The Competitive Displacement Principle

- [Gause's Law](#)

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## The Competitive Exclusion Principle

- [Gause's Law](#)

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## The Crow Family

- [Corvids](#)

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## The Dual-Process Theory

- [Sensitization](#)

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## The Mammalian Carnivore Order

- [Carnivora](#)

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## The Mark-Mirror Test

- [Mark Test, The](#)

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## The Mirror Test

- [Mark Test, The](#)

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## The Origin of Species

- [Origin of Species](#)

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## The Peak Day

- [Peak Fertility](#)

## The Peak of Fertility

### ► Peak Fertility

## The Polygamy Threshold Model

### ► Polygyny Threshold Model

## Theories of Play

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### Definition and Introduction

While most people will have an intuitive understanding of what *play* is, and while implicit theories on *play* seem to converge relatively well in everyday life (e.g., when talking about play experiences), there is still no consensus about its definition. The study of play is of interest to researchers across many disciplines and also across species, including (of course) humans – humans of all age groups to be more precise. In humans, mainly younger ages have been the focus of attention, although interest in the study of the role of play across the full life span has increased over the past few years. However, a universally accepted definition of play in humans and animals is still missing. In particular, in the study of play behavior in animals, it can be difficult to differentiate play from other behaviors based on observations alone (e.g., stereotypical behavior in animals held in captivity). Hence, criteria have been developed that can be applied to the study of play. Burghardt (2005) suggested five criteria that identify play across species, play is:

- (1) Incompletely functional in the context in which it appears; (2) spontaneous, pleasurable, rewarding, or voluntary; (3) differs from other more serious

behaviors in form (e.g., exaggerated) or timing (e.g., occurring early in life before the more serious version is needed); (4) is repeated, but not in abnormal and unvarying stereotypic form (e.g., rocking or pacing); and (5) is initiated in the absence of severe stress. (cited after Graham and Burghardt 2010, p. 394)

This list of criteria helps us to differentiate play-behavior from related behaviors, such as those driven by curiosity or stereotypical behavior. It is argued that play can have both immediate and long-term benefits. Finally, Burghardt (2005) defined play in animals as a “[...] repeated, incompletely functional behavior differing from more serious versions structurally, contextually, or ontogenetically, and initiated voluntarily when the animal is in a relaxed and low-stress setting” (p. 82).

### Why Studying Play Matters

The question of why animals (including humans) play has stimulated research in many different areas (see, e.g., Fagen 1981; Huizinga 1938/1955; Millar 1968; Pellis and Pellis 2009; Sutton-Smith 1997). Murray (1938) has argued that there is even a *need for play* in humans. In his taxonomy, a need is understood as “a construct [...], which stands for a force [...] in the brain region, a force which organizes perception, apperception, intellection, conation and action in such a way as to transform in a certain direction an existing, unsatisfying situation” (p. 123). He lists play as one of these needs: “play (playful attitude). To relax, amuse oneself, seek diversion and entertainment. To ‘have fun,’ to play game. To laugh, joke and be merry. To avoid serious tension” (p. 83) and further argues that the need to play is characterized by a tendency to perform activities for joy alone and without further reasoning, or to escape reality. Developmental psychologists have acknowledged the important role play has for various stages in life. For example, Piaget (1945) described a form of tension between assimilation (having a schema that is imposed on the world) and accommodation (imitation of something that has been observed or done in the past, where the schema is modified) – play occurs if assimilation exceeds accommodation. Hence, for Piaget, learning and exploration are associated with

play and imitation. He developed a stage model of different levels of play that follow a specific developmental process: from a sensory- motoric phase at the beginning to more advanced levels in higher stages of development.

The developmental psychologist Erik Erikson argued that adults with higher vitality and potentially higher playfulness have greater resources from childhood that make it easier for them to access a second reality aside from their adult life. They are able as adults to access their childhood world that is associated with play and imagination. He suggests that adults play for recreation and that they use this experience of an alternate reality in play to relax. Work is a competitive environment and play poses a possibility to escape these environments. However, in Erikson's reasoning this is tied to work inasmuch as adults have learned that "Only he who works shall play" (Erikson 1959, p. 89). Erikson argues for a *play* stage in human development, which would be after the early-childhood stage (his second stage, which is aimed at autonomy with "will" as its basic strength) and would precede the school-age stage (which is aimed at industriousness and with competence as its basic strength). The play age can foster initiative because its "psychosocial crisis" is the conflict between initiative and guilt, and the basic strength associated with this age is purpose (core pathology: inhibition). At this stage, play in children transforms from playing only for oneself to playing with a world shared with others (Erikson 1959). This is accompanied with a sense of mastery – not only with respect to toys and things, but also mastery of (new) experiences. For adults, many definitions of the need for play focus on its contribution to relaxation, enjoyment, and or fun (e.g., Murray 1938; van Fleet and Feeney 2015). However, this might limit our understanding of what play and playfulness could have as forms and functions outside of this realm (e.g., for problem-solving or intellectual achievement), this point will be described in more detail later on.

Bateson (2006) sees play as a driver for evolution (or a driving force in evolution), specifically as an "adaptability driver." In this sense, play facilitates adaptation to environmental changes

and the application of novel approaches (e.g., those that affect survival). This is associated with enabling the creativity and innovation that are needed in these situations. Bateson and Martin (2013) list six defining features of play, as follows: (1) intrinsic motivation, fun; (2) the behavior is nonserious (Bateson and Martin see play as the antithesis of work or serious behavior); (3) actions or thoughts in humans are related to novelty and play is a generator of novelty; (4) actions or thoughts are repeated and may be incomplete or exaggerated in comparison with nonplayful behavior; (5) specific conditions need to be met and play does not occur when the individual is ill or stressed; and (6) "playful play (as distinct from the broader biological category of play) is accompanied by a particular positive mood state in which the individual is more inclined to behave (and, in the case of humans, think) in a spontaneous and flexible way" (p. 13). Bateson (2010) suggests that two processes could explain how adaptive process might work, namely: either one individual discovers a solution through play, which then spreads via social learning, or many individuals identify a solution through play posed by the environment. Work on play as an adaptability driver would then indicate that "those individuals that were able to express the beneficial trait spontaneously at lower cost were able to compete more successfully. In this way, playful activities could affect the evolution of the individual's descendants" (Bateson 2010, p. 9).

Bishop and Chace (1971) also use the term "playful play" when describing the potential contributions of play and playfulness to creativity. They argue that the motives and processes that are involved in play are highly similar to those of the creative process. Therefore, play would facilitate the learning experience of these respective cognitive and behavioral process, which then would facilitate creativity.

## Play Theories

Play has frequently been described as a process dedicated to the acquisition of skills and as a way of training or preparation for specific tasks and

behaviors in adulthood (cf. Barnett 1990). This perspective has been interpreted as a functionalist view of play and it has entered the literature under the broader term of *Exercise Theories*. It has also been proposed that play could be used to assess the development of ones' offspring or to assist in further development. In addition, play facilitates bonding between parent and child. Rubin et al. (1983) suggested six criteria for play, namely:

- (1) Play is not governed by appetitive drives, compliance with social demands, or by inducements external to the behavior itself; instead play is intrinsically motivated;
- (2) play is spontaneous, free from external sanctions, and its goals are self-imposed;
- (3) play asks "What can I do with this object or person?" (this differentiates play from exploration which asks "What is this object /person and what I do with it/him/her?");
- (4) play is not a serious rendition of an activity or a behavior it resembles; instead it consists of activities that can be labeled as pretense (i.e., play must comprise non-literality);
- (5) play is free from externally imposed rules (this distinguishes play from games-with-rules); and
- (6) play involves active engagement (this distinguishes play from daydreaming, lounging, and aimless loafing). (Coplan et al. 2006, p. 75)

Burghardt (2005) gives an overview on the most eminent theories in the field and points out that one major characteristic of play is that it refers to make-believe type of activities, or *as if* behaviors or pretending to do something. Most often in research on play in children, these *as if* behaviors have been associated with behavioral flexibility and adaptive types of behaviors. Others have also emphasized seeing play as an exploratory and information-seeking activity that elicits arousal (e.g., Berlyne 1960). In this framework, play is aimed not only at increasing the information in well-known environments but also at increasing novelty and complexity – potentially to prevent boredom from occurring. A further frequently mentioned characteristic of play is that it does not serve any immediate purpose. No purpose other than seeing the process of playing as being *fun*. While others have stressed the importance of play for the development of the self and self-realization in particular (Henricks 2014). But why do animals play? The following paragraphs will provide a brief overview of some selected theories of play.

The *Surplus Energy Theory* (SET) posits that play occurs in times when there is a surplus of energy (e.g., due to good nutrition conditions) and when there are no external demands that need to be satisfied, and that play eventually costs energy. In these cases, extra energy can be spent with play. One might argue that the SET suggests that the degree of exerted playfulness is a function of available energy. It has been observed that those animals that need comparatively less energy for movement (e.g., birds) play more than those who have greater costs in terms of energy for movement (Burghardt 2005).

Burghardt (2005) developed the *Surplus Resource Theory* (SRT) to describe how play occurs and what resources or environmental factors (e.g., available food) may play a role. Burghardt describes necessary but not sufficient factors that can enable play, with a special focus on an extended juvenile period (that demands specific parental behavior; e.g., protection), that is:

- (1) There is sufficient metabolic energy [...].
- (2) The animals are buffered from serious stress and food shortages [...].
- (3) There is a need for stimulation to elicit species-typical behavioral systems or to reach to an optimal level of arousal for physiological functioning (e.g., there is susceptibility to boredom).
- (4) There is a life-style that involves complex sequences of behavior in varying conditions, including diverse and unpredictable environment and/or social resources. (Burghardt 2005, p. 172)

Thus, Burghardt's approach specifies the conditions and circumstances that facilitate or hinder the occurrence of play. He proposes a gradation in the processes (primary, secondary, and tertiary) of play. Those at a higher level would also enable an individual to transform physical to mental play or to provide resources for novel behavior and creativity (Burghardt 2005).

*Recuperation Theory* posits that play, because of the muscular reactions, could extinguish toxic substances and therefore, like sleep, leads to the recuperation of the exhausted systems (Burghardt 2005). Similarly, *Recreation Theory* suggests that because of the Industrial Revolution, most workers have less control about when, how long, and what they work and that play serves a recreational

purpose but could also be seen and as a possibility of self-determination (Burghardt 2005).

*Semblance Theory* argues that the significant part of play is “its quality of [...] ‘as-if’, pretend or pretense” (Burghardt 2005, p. 39) – or role-play from a more current perspective. The core of *Exercise Theories* (e.g., Fagen 1981) and variants thereof is that play does not have any immediate functions per se (except perhaps from physical practice) and does not necessarily lead to a product in its narrow sense. Its sole function is to prepare an animal for its future survival. Play behavior and playfulness is an expression of and is driven by *instinct*. Aside from physical education, the aim of play is to master specific skills, namely, those that are important for later survival. Along these lines, *Autotelic Theory* suggests that the aim of play is its behavior itself, and there is no higher goal. Meanwhile, *Socialization Theory* suggests that social play is important to understanding social structures and to establish one’s role in a group. Finally, *Cognitive Theories* of play describe play as important in cognitive development.

Panksepp (1998) proposes a neuro-evolutionary model in which he also considers play as being one of the components of evolution. He argues that *primal* emotions or “core emotional affects may reflect the neurodynamic attractor landscapes of a variety of extended trans-diencephalic ‘energetic’ action systems – e.g., SEEKING, FEAR, RAGE, LUST, CARE, PANIC, and PLAY – which need to be defined in neural terms” (Panksepp 2005, pp. 32–33; capitalizations by original author). He postulates that *joyful PLAY* is an emotional system that is shared by all mammals and that: “Young animals play with each other in order to navigate social possibilities in joyous ways. The urge to play was also not left to chance by evolution, but is built into the instinctual action apparatus of the mammalian brain” (Panksepp 2005, p. 54). He sees joint play (rough-and-tumble play) as a basic process for a broad variety of social skills (e.g., social support and friendships). The experiences during play would help in the programming of specific circuits within the brain and may also have an impact on the activation of certain genes. Therefore, this process is then associated with neuronal growth and emotional homeostasis.

Overall, Panksepp’s (1998) framework proposes circuits or overlapping networks in the brains of mammals that have an impact on playfulness. From play, specific emotions emerge, namely, joy and glee, and happy playfulness. Overall, the contribution of this work seems to be to highlight the relevance of the neuropsychological aspects of play and that certain regions in the brain may be activated during play behavior. Most certainly, further work in this area needs to be done.

Csikszentmihalyi and Bennett (1971, p. 45) see play “as a state of experience in which the actor’s ability to act matches the requirements for action in his environment. It differs from anxiety, in which the requirements outnumber the ability, and from boredom, in which the requirements are too few for the ability level of the actor.” They argue further that “Play is action generating action: a unified experience flowing from one moment to the next in contra-distinction to our otherwise disjoint ‘every-day’ experiences” (p. 45). Another characteristic of play is that possibilities for an uninterrupted flow of actions is given, which is combined with a lack of self-awareness as people playing enter a self-constructed reality. They see play as being of an episodic nature – emerging when everyday life becomes too worrisome and ending when the play experience is perceived as boring. Csikszentmihalyi and Bennett (1971) also propose that there can be quick shifts between states of worry, play, and boredom (*monistic interludes*). Play is particularly suitable for enabling intrinsic rewards because it exists relatively independently from external rewards and flow-experiences would be common in various forms of play. Csikszentmihalyi argues that the components of playfulness include an awareness of alternative goals and the ability to choose (freely) among these goals, and adds that highly creative people can combine both playfulness and discipline.

## Playfulness

*Playfulness* is frequently understood as an individual difference variable at the trait-level (i.e., relatively stable across time and situations). In



short, one might define playfulness as the propensity to play and that individuals differ in how much they want to play (e.g., in terms of time, intensity, or variability). Hence, play is a behavior that is associated with the personality trait of playfulness. The latter is typically conceptualized multidimensionally and, thus, relates to different expressions of behavior. A more differentiated definition of playfulness is:

An individual differences variable that allows people to frame or reframe everyday situations in a way such that they experience them as entertaining, and/or intellectually stimulating, and/or personally interesting. Those on the high end of this dimension seek and establish situations in which they can interact playfully with others (e.g., playful teasing, shared play activities) and they are capable of using their playfulness even under difficult situations to resolve tension (e.g., in social interactions, or in work-type settings). (Proyer 2017, p. 114)

This definition is accompanied by a structural model of playfulness that differentiates among Other-directed, Lighthearted, Intellectual, and Whimsical (OLIW model) variants of playfulness.

In humans, playfulness and play have mainly been studied in infants and children. However, as early as 1977, Lieberman suggested that playfulness permeates into adulthood and is also of relevance there:

By this [playfulness] I mean the lightheartedness that we find as a quality of play in the young child's activities and, later on, as the combinatorial play essential to imagination and creativity. I, therefore, see playfulness as behavior that goes beyond the childhood years; and, through its component parts of sense of humor, manifest joy, and spontaneity, it has major implications for childrearing practices, educational planning, career choices, and leisure pursuits. (Lieberman 1977, p. xi)

She later notes that “playfulness as a quality of play would developmentally transform itself into a personality trait of the player in adolescence and adulthood” (Lieberman 1977, p. 23). In line with expectations, there is evidence that trait measures of playfulness are positively associated with the play behavior that has been reported in diary studies (Proyer 2017). Other research supports the notion of relations with different indicators of well-being, including relationship satisfaction,

creativity, humor, and academic performance (to name but a few).

## The Special Case of Sexual Selection

One important question is how a behavior such as play may be beneficial from an evolutionary perspective. It has already been mentioned that an important argument may be that play facilitates survival (e.g., training of fighting or flighting skills, or increasing physical strength). Chick (2001) proposes that adult playfulness has a signal function when selecting partners for long-term relationships (in heterosexual couples). He suggests that observed playfulness in men signals low aggression to their partners and high vitality (fecundity) to men when observed in their potential partners. Subsequent research has shown that playfulness is a desired personality trait of younger adults when thinking about a potential partner (in the United States). This notion has received support in later studies, which show that playfulness ranks comparatively high if young students rank order a list of different characteristics (this study has been replicated with data from Switzerland). There is evidence for assortative mating and/or social homogamy when seeking partners for long-term relationships (Chick et al. 2020). Play behaviors should also have high observability and it seems, therefore, to be a good source of information for those selecting partners for long-term relationships. Data from studies on playfulness have shown robust self-other-agreement, and there is evidence for implicit cues about greater playfulness among unacquainted people in their written self-descriptions (e.g., the usage of positive emotion words).

## Conclusion

Play is an important part of the life in many species. It seems particularly common in mammals and animals with relatively low energy costs for movement (e.g., birds), but might be rare in other species. However, Burghardt (e.g., 2005) argues for play behaviors in other species (e.g.,

fish, amphibians, or reptiles). Play might serve both immediate and long-term effects. The degree to which such effects are present is an ongoing discussion in the field and can be difficult to evaluate (e.g., when being interested in its distinct effect across the life span). A recurring topic of interest is the question of the function of play, such as for the development of children (see, e.g., Pellegrini and Smith 1998). As noted earlier, there is a frequent reference to play as being “fun” as a proximate reason for play, but are other functions observable? For example, it has been argued that play may be associated with brain growth (or growth with play behaviors) and development and, thus, is important to evolutionary processes (see, e.g., Byers and Walker 1995). Pellis et al. (2019) summarized several studies and conclude (1) that limiting play in rats and hamsters during their juvenile period results in adults that have physiological and anatomical changes in their medial prefrontal cortex, as well as reduced social and cognitive skills and (2) that animals raised with playful peers have better social and cognitive skills than those raised solely with adults. While this seems replicable with domesticated rats, results differ with wild rats. Pellis et al. (2019) suggest that it may be that domesticated adults are less likely to play with juveniles and therefore the juveniles do not experience the kinds of activities critical for brain development. They concluded that adult wild rats may provide more opportunities for play and are more cooperative in their play with juveniles. Hence, there seems to be support for the notion that play among juvenile animals appears to have an evolutionary purpose that involves brain development.

Taken current developments into account (e.g., in the realm of gamification or playful learning-initiatives), it is surprising to see how comparatively little research is done across disciplines. For example, psychology seemed to have only little interest in the study of play and playfulness in adults. One might expect that, for example, an individual difference approach in the study of the potentially beneficial effects of gamification (e.g., using trait playfulness as a moderator) would contribute toward a better understanding

of working mechanisms and might help to make recommendations for practice. While progress has been made in the study of play (cf. Graham and Burghardt 2010), many open questions still exist.

## Cross-References

- Assortative Mating
- Play Behavior
- Pretend Play
- Sexual Selection
- Sociosexual Behavior

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## Theory of Mind

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## Synonyms

ToM

## Definition

Theory of Mind is the ability to represent one's own as distinct from another's mental states including beliefs, desires, and intentions to potentially change the mental states or behaviors of others.

Theory of Mind (ToM) is one of the most important cognitive mechanisms underpinning social interactions in humans. It is the capacity to represent mental states of oneself and of others in order to understand, predict, and manipulate their behavior or mental states. In the day to day life, we attribute to our fellow humans a mind that has beliefs, desires, knowledge, and other mental states. Based on these attributions we can successfully interact in the complex human social system. Teaching and cooperating as well as deceiving and competing are human abilities that all take into account the mental states of the interacting partner. Thus, having ToM is a central part of human cognition but is this ability unique to our species or might we share it with at least some nonhuman animals?

In their seminal publication “Does the chimpanzee have a theory of mind?” Premack and Woodruff (1978) were the first researchers to approach this question from a comparative psychologist's perspective. Their enculturated chimpanzee, Sarah, was presented with videos

depicting a person who wanted to obtain a goal, such as reaching for an inaccessible food, trying to free himself from a locked cage, or trying to play music from an unplugged phonograph. All the presented situations had in common that the actor was missing a crucial item in order to solve the problem at stake. Sarah was then presented with two pictures. She was asked to indicate towards either a picture with an item that helped to solve the task or a distractor item that would not. The tested individual pointed towards the correct items from the very start of the experiment. The authors interpreted this result in such a way that the chimpanzee understood the intention of the experimenter and pointed towards the solution of the problem. However, the study was later criticized and re-interpreted. Sarah did not necessarily choose correctly based on the understanding of the goal of the experimenter; instead she might have been pointing towards the picture with the correct item because it had been seen more often in association with the other items in the videos (Povinelli et al. 1998). Ever since this experiment, researchers in comparative cognition have searched for evidence of ToM in the animal kingdom.

In comparison to testing ToM in humans, non-linguistic animals cannot be verbally asked about their beliefs. One of the most prominent experiments in testing the human development of ToM is the false belief task that, in its original form, required the test subject to understand human language. In a typical false belief task (e.g., Wimmer and Perner 1983), a child is presented with a story. In one story, the character Maxi hides his chocolate in a drawer (location A). After Maxi leaves the room, his mother moves the chocolate into a different drawer in the same room (location B). Subsequently, test subjects are asked where Maxi will search for the chocolate when he returns. Until the age of three, most children are unable to ignore their own knowledge of the true location of the object and indicate that Maxi will look where he believes the chocolate to be, namely in drawer A. Via this test, subjects are explicitly asked about their personal beliefs about the knowledge state of Maxi. If the child can differentiate between his/her own state of

knowledge (actual location of the chocolate) and the Maxi's false belief the child is considered to have passed the test and thus have developed ToM. Most children over three can represent false beliefs successfully. This experiment is often referred to as the "Sally-Anne" task (Baron-Cohen et al. 1985) and its variants have become one of the most important ways to study ToM in human children as well as nonhuman animals.

In the evolution of ToM in humans as well as animals it is hypothesized that in an increasingly complex social system it is adaptive to predict, manipulate and learn from others (Brothers 1990). Thus, the occurrence of cognitive abilities in a given species that are necessary for elaborated social interactions are positively correlated with the species' level of social complexity. This is in line with the social intelligence hypothesis (Chance and Mead 1953; Humphrey 1976; Jolly 1966), which states that selective pressures – especially competition and cooperation – have played an important part in the evolution of intelligence. Cognitive abilities like individual recognition, knowledge about previous social interactions, and relationships help to interact with others. Especially in cooperative and competitive situations it is highly advantageous to additionally predict the future behavior of others by "reading" their mental states like understanding their knowledge, perceptions, beliefs, goals and intentions. The main problem in experimental designs is to differentiate mere behavioral reading from understanding intentions (i.e., the mental states of a conspecific), as we do not have direct access to the desires, beliefs, and goals of animals or other humans but have to infer such mental states from how they behave, what they do, and in humans – what they say.

As a response to the seminal study of Premack and Woodruff (1978), a categorical differentiation between three different levels that an organism or more generally, intentional systems, can have was proposed by Dennett (1983). Zero-order intentional systems do not have any beliefs and desires, and consequently they have no mentality, no intelligence, no communication, and no intentionality at all; first-order intentional system have beliefs

and desires but no beliefs and desires about beliefs and desires; second-order intentional systems have beliefs and desires *about* beliefs and desires – both those of others and itself (Dennett 1983). An example for a zero-order intentional system is a simple feedback system like a thermostat. The goal of the thermostat is to keep the room temperature at a specified level and it responds to temperatures below the critical value. Based on the feedback of the thermostat, heating will be prompted and stopped as soon the set temperature is reached. While the thermostat has the goal to keep the temperature at the specified level, it does not have any beliefs, desires, or intentions. A typical example in the animal kingdom is that of bacteria with photo-taxis. The bacteria move in the direction of light but will stop moving when sufficient light is detected. First-order intentional systems have their own beliefs, desires and intentions in contrast to the zero-intentional system, which only instantiates its goal via a simple feedback mechanism. A cat might believe that a mouse is hidden in the burrow, and it lurks in front of it in wait. It is hard to discern whether the behavior is based on a complex combination of feedback mechanisms or whether the behavior is based on a belief or desire, even though at first sight it might seem clear that there is a difference between the two. Does the cat lurk in front of it because the smell in addition to the burrow is sufficient to trigger the behavior, or rather because it has a belief that there is a mouse hiding? Similarly, identifying whether or not a particular species has a first-order from or second-order intentional stance is also often hard. In a second-order intentional animal it is necessary that it can represent the belief of another individual. When a Eurasian jay hides and stores an acorn for winter it tries to do so without being seen. But when it is seen, it will try to re-cache the same acorn at a different place in order to prevent the competitor from pilfering its stores. In cases where it cannot avoid being observed the jay will re-cache the acorn multiple times in order to deceive the observer from the actual hiding point. If the jay has first-order intentionality it will only respond to the absence or presence of the competitor or a specific body part like the eye. Alternatively,

when the bird bases its deceptions on its own beliefs about the beliefs of the observing individual, it will (like Maxi in the false belief task) be able to differentiate its own knowledge from the belief of the competitor. Thus, only when the jay bases its decisions on its own representation of the other's mental states, such as false beliefs, can it then be considered to have second-order intentionality and thus ToM.

Differentiating whether the observed behavior is based on the more complex social cognitive ability ToM or on a lower level mechanism is one of the main aims of researchers in this field. Another typical example of applied animal behavior is the following: A nesting piping plover will defend its nest by trying to lure a predator like a fox away from it (Ristau 1991). In order to do so, the bird will imitate an injury by dragging one wing behind as soon as a fox approaches too closely to the nest. When the fox starts to follow, the bird will continue with the behavior until the predator is far enough away from the eggs. Then she will fly back to nest and the fox has successfully been led astray by her deceptive behavior. By deceiving the fox with the broken-wing display one could at first blush argue that the plover intentionally deceived the predator in order to protect its nest. According to Tinbergen (Tinbergen 1963), one still needs to differentiate proximate causes including the underlying mechanism (How is it performed?) and the ontogenetic development (How did it develop?) as well as the ultimate causes including the functional level (What is it for?) and the evolutionary history of the behavior (How did it evolve?). While the answer to the adaptive value question of the behavior is clearly that the plover deceives the fox in order to protect its eggs, clarifying the underlying mechanism, whether this is a lower level cognitive mechanism or complex social cognitive skill, needs further investigation. This directly relates to the questions of ontogeny and phylogeny – is the deceptive behavior shaped by evolutionary adaptations or rather based on the learning experiences during the ontogenetic development of the individual? While it seems clearer that the nest-protection in the example is an evolutionary adaptation with little variation



across individuals within the species, other behaviors are less easy to qualify. In principle, many investigations around ToM are attempts to clarify precisely the question what the underlying mechanism of the observed behavior is.

But what are the specific benefits of having a ToM? It is hypothesized that it qualitatively increases the positive outcome of interactions with others, for example by understanding the role of the cooperative partner, understanding perspective during imitation, as well as understanding intentional communication and deception. In highly complex social systems it seems necessary to have a more domain general ability to predict the behavior of others than mere behavioral reading as understanding the mental states leads to more efficient and flexible behaviors, especially in new situations. Still, the interpretations of supposedly positive evidence for ToM in animals are still debated, despite the large number of studies. This has led to discussions around whether the existence of ToM in humans and the potential lack of evidence of ToM in animals is not about a gradual increase of abilities but an absolute difference (Povinelli et al. 2000). In the Reinterpretation Hypothesis (Povinelli et al. 2000), the authors state that in animals it suffices to explain the complex behaviors via low-level perceptual rules like gaze-following during pointing behavior. Additionally, they point out that first-order intentional states are generating complex social behaviors but that sometimes the second-order intentional states prompt the first-order intentional states that produce those behaviors, but only in humans. Thus, humans do sometimes base their behavior on mentalizing the mental states of others but not always do so.

Early studies investigating ToM concentrated on the ontogenetic development in humans and the evolutionary development by testing non-human primates. Only later did the field broaden and investigations among monkey and avian species started. The investigations in corvid species have turned out to be particularly fruitful. Based on the convergent evolution of social intelligence (Emery and Clayton 2004) and the identification of avian brain areas that are equivalent to the mammalian prefrontal cortex (Jarvis et al.

2005), that show learning-induced changes (Lee et al. 1998), it has been suggested that corvids can indeed attribute mental states to others (Keefner 2016). By expanding the investigation of ToM to nonprimate species, the potential influence of social complexity on the evolution of ToM gained momentum and a broader comparative perspective on the evolution of ToM was added.

Thirty years after the first experiment on ToM in a chimpanzee, Call and Tomasello differentiated two main strands of research in chimpanzees that try to provide evidence ToM (Call and Tomasello 2008). The first way to infer the existence of ToM is to conduct studies that test the understanding of (1) goals and interactions either by varying possibilities of (a) getting/finding food, (b) reacting to a partner's actions, or (c) imitation. The second way is to test animals' understanding of (2) perception and knowledge of others either via (a) gaze following, (b) communication, or (c) food competition. Similarly to this way of categorization, experiments about ToM have been differentiated according to the mental states of the interaction partner namely perceptual states, knowledge states, desire states, and belief states (Apperly 2010).

## Perceptual States

Being aware of the perceptual state of another individual means to be able to represent what the other individual is able to perceive. For instance, the Eurasian jay from our previous example should only recache its acorn when the other individual was actually able to see the initial caching event. It should leave the acorn in its initial cached location if the competitor was not able to see where the acorn had been cached. This would be an example of representing the perceptual state of seeing in order to adjust the behavior according to the information the other individual was able to see. It has been argued that apes adapt their communicative signals according to the visual attention of the communicative partner (Tomasello et al. 1994). Similarly, the piping plover from

our previous example of deception adjusts its broken-wing display based on the visual orientation of the predator (Ristau 1991). In corvids it is known for instance that food caching California scrub-jays adjust their caching behavior based on the attentional state of the potential pilferer (Dally et al. 2005). While all of the above examples may have ToM as an underlying mechanism, the behaviors could be based on simpler behavioral rules. All the animals might only take into account whether they see or do not see any of specific physical features that might be highly correlated with the attentional status of the interaction partner. This could for instance be the presence or absence of the eye, or the orientation of the head or the body. As a result of these concerns, a number controls have been designed in order to differentiate between the adjustment of the behaviors based on behavioral rules and behaviors based on the understanding of the perceptual mental state of the other ("seeing"). Povinelli and colleagues tried to differentiate exactly these alternative possibilities (Povinelli et al. 1996). They presented young chimpanzees with two holes in a transparent barrier. On the side of the experimenter a box with food on top was positioned out of reach of the tested individuals. The animals were trained to beg for food by reaching with their arms through the holes in the glass. Different conditions were then presented to the test subjects. Either the human experimenter looked in the direction of the chimpanzee or away, had his eyes or mouth covered with cloth, held a bucket to cover their head or rested it on a shoulder or similar. The tested individuals were immediately able to differentiate when the experimenter had his body turned away from the chimpanzee or was facing at the chimpanzee but were not able to differentiate the other conditions early in the experiment. However, after a while, the subjects started to learn the differences in the other conditions, and reduced begging behavior. As a result, the researchers argued that the chimpanzees do not have an understanding of the attentional/perceptual state of the experimenter, but they were able to learn and thus associate the successful situations with reward and increased begging behavior.

Following the gaze of others is an important feature in primates when looking for food, identify predators, and keeping track of social interactions within a group. Based on the features of the primate eye like forward facing and the existence of a white sclera, it seems easy to follow gaze. This feature is less conspicuous in some species, such as ravens, but still does convey important information. Corvid species follow the gaze of individuals of the same species and different species like humans when looking into the sky right after fledging. This is due to the importance of gaze-following for anti-predator behavior. It is possible to habituate and thus stop various species such as chimpanzees and common ravens from following the gaze of an individual that looks repeatedly into the sky without a predator flying above. While chimpanzees are habituated and reduce gaze-following to regular upward looking after four to five years, ravens stop gaze-following from the second month after fledging when frequently presented with an uninformative gaze. Again, it might be that the test subjects either learned to inhibit socially triggered orientating behaviors, or habituation might be based on the understanding of the visual angle of the looking individual and thus be an indicator of ToM (Povinelli et al. 1996).

In the barrier test it is supposed that individuals can gain information like the location of food by following the direction of the gaze of conspecifics or heterospecifics. During the barrier test an experimenter stands in the middle of a barrier where he has visual access to both the test subject and the part of the compartment that the subject cannot see. When the experimenter then looks towards a spot behind the barrier that the subject cannot see it should, if it understands the experimenter's visual perspective and the barrier, start searching for food behind the barrier. Alternatively, when the bird only responds to the orientation behavior of the experimenter it will look on its own side of the barrier without taking the visual angle and the barrier into account. In case the tested individual does look behind the barrier, it is generally supposed that it understands angle, barrier and perceptual state of the looker. Great-apes as well as ravens do show some kind of understanding of the

visual barrier but only later in their ontogenetic development (Bräuer et al. 2005; Bugnyar et al. 2004). This makes it hard to discern whether the behavior is based on associative learning or whether they actually do understand the visual perspective of the other.

The following experiment has implications for understanding perceptual states but also knowledge states. When concentrating on the perceptual states, the study by Hare et al. (2001) is a competitive situation where gaze following can help to gain food. As exemplified in this experiment, two chimpanzees, one subordinate and one dominant, were looking into a central cage. Both individuals were in separate compartments either side of the central cage, with two barriers partially occluding their view of the latter. An experimenter placed food behind the barriers where only the subordinate could see the reward. In some of the conditions the dominant either did not see the baiting or the food was later moved once more when the dominant was not looking. Subordinates always saw the complete baiting procedure and additionally the visual access of the dominant to the baiting. If subordinates are sensitive to the gaze of the competitor they should adjust their behavior according to what the dominant sees or does not see and thus be able to attribute the perceptual state of the competitor. However, it is also possible that individuals not only represent the perceptual state of seeing but also the dominant's knowledge state in order to infer what this protagonist has or not has seen and thus what he does or does not know about the location of the food (Hare et al. 2001). According to this interpretation, the subordinate can differentiate between two knowledge states that the dominant might have: in other words, subordinates chose the food that the competitor was unaware of (ignorant) as opposed to the food that the competitor was aware of (knowledgeable). By this account, the attribution of perceptual states can subsequently lead to the attribution of knowledge states. Critics, however, would argue that a lower-level mechanism could explain such results, for it is far from clear that the subordinate needs to make this differentiation based on an understanding of knowledge states, i.e. of mind reading.

Instead the subordinate could differentiate based purely on behavioural cues~ for a dominant individual that knows where the food is might behave quite differently to an ignorant dominant who does not know.

When we evaluate these experiments about perceptual state attribution, there is some evidence that visual co-orientation of the focal individual may be based on representing the perceptual state (what the competitor or collaborator may see). Critics claim, however, that the co-orientation is based on lower level mechanisms instead of a high cognitive attribution. Namely, it could be that animals can co-orient and look into the same direction as others to find an object of interest without necessarily attributing any perceptual state to the other individual. It is for both of these reasons that tests of knowledge attribution in nonhuman animals are contentious.

## Knowledge States

As already introduced, representing perceptual states such as whether the competitor can or cannot see is different from the ability to represent the knowledge state of another individual. Knowledge attribution additionally requires the individual to understand that the competitor *knows* where the food is as opposed to simply to *have seen* where the food is, so this must be based on tracking multiple previous observations of the protagonist rather than rely only on the individual's current perceptual state. In the competitive foraging paradigm of Hare and colleagues, the subordinate individual had to track the different opportunities of observation that the dominant individual had access to and attribute whether the dominant was able to see where the food was hidden and thus did or did not know where the food was currently hidden.

California scrub-jays have also been shown to differentiate between knowledgeable and ignorant competitors during re-caching events (Emery and Clayton 2001). In general, food-storing corvid species cache food for later consumption. This might be costly, as observing competitors might pilfer these caches. As a counter-strategy the

caching individuals may re-cache the food once the observer has left the scene. Cachers have been shown to actually re-cache only in those instances where they have been observed at the initial caching event. In order to test this, scrub-jays were allowed to cache wax worms in trays in a condition where a competitor had visual access during the caching event and in another condition when visual access was blocked (Emery and Clayton 2001). Three hours later the cacher was allowed to re-enter the compartment and either recover or re-cache the previously cached items by providing them with the previous tray plus a new caching tray. Birds re-cached more often during recovery when they have been observed during the original caching event. Additionally, some of the birds were allowed to pilfer caches from other individuals and thus had both experiences of observing and pilfering. While birds who had never pilfered beforehand re-cached very little in both observed and private conditions, the birds who had the additional experience of pilfering re-cached more often in the observed condition. This result shows that experience played a key role. Recaching when in private was not a hard-wired response to having been observed during caching, but rather it depended on whether the birds had had the experience of being a pilferer in the past. Note that the result cannot be explained in terms of simple behavior reading because re-caching always occurred in private once the observer had left the scene, and thus the cacher could not be responding directly to the competitor's behavior at the time of action (re-caching). Furthermore, re-caching was neither rewarded nor punished: just a one-off response in the absence of any training. Taken together these results suggest that the jays are capable of experience projection, of taking another's perspective. Subsequent experiments showed that the behavior also depends not only on whether or not they had been observed when caching but by whom (Dally et al. 2006). If the observer was their mate with whom they share their caches, then no re-caching occurred. By contrast if the observer was a potential pilferer then re-caching occurred and the amount of caches that were consumed as opposed to re-cached depended on the potential

threat imposed by the observer, i.e. whether they were dominant or subordinate to the cacher (Dally et al. 2006).

Common ravens have also been tested in a similar design but with three conditions. They were tested in situations when they were observed through a wire-mesh window; alternatively, the wire-mesh window was visually barred with a curtain or in a peep-hole condition (Bugnyar et al. 2016). While the observed condition with full visual view and the private condition with blocked visual access are similar to the caching experiments in scrub-jays, the peephole condition is a new variant. In this variant the window between the observer and the storer was visually blocked, except that one of two small peepholes was left open. In this situation, no real competitor was present but recordings of a conspecific were played back via a loudspeaker. By providing a peephole only, the cacher cannot see a potential observer while it caches based on the limited visual perspective of the cacher. Thereby the typical critique of behavior reading is not applicable that the cacher might have used when seeing the potential pilferer. In order to use the correct cache protection strategy, the raven therefore needs to understand the peephole as potentially providing a visual perspective to a competitor without seeing the observer itself. Therefore, the cacher has to infer that the bird might have the opportunity to observe the caching behavior as it could "hear" the presence of a bird it could not see. The playback of another individual in the adjacent compartment provides the information about the absence or presence of a competitor. Thus, when ravens were tested in the peep-hole condition, they responded to the playbacks as if a conspecific potential pilferer with visual access was present and based their cache-protection behavior on this information. The elegance of this design is that neither playback alone nor the peephole per se elicit cache protection strategies but in combination provide information about a potential competitor. When given access to only one of the two peepholes the caching individual was not able to adjust caches according to the visual angle of one of the peepholes. In other words, the cacher was not able to adjust to the actually perceivable visual

angle but acted as if the bird would have had full view of the compartment.

Attributing knowledge states to competitors even when no behavioral cues are present seems to provide strong evidence for ToM in nonhuman animals. Low-level cues that would be necessary in perceptual state attribution, as the focal individual needs to be able to observe the competitor, are eliminated. The ravens did not have any opportunity respond to such cues but were enacting as if a potential competitor was present. The possibility to observe through a peephole was generalized from the perceptual experience they gained earlier in the experiment. Still, ravens were not able to infer the limited visual angle from the peephole and thus might still be lacking a fully developed ToM.

## Desire States

In common with the attribution of knowledge states, attributing desire states to others requires an ability to acknowledge that others may have mental states that can be different to our own. For example, understanding that although I want prosecco, my colleague may desire tea. A want or desire is not necessarily based on direct behavioral cues although it still can be expressed via behavioral cues.

In an experiment first conducted by Call et al. (2004), chimpanzees were fed by a human through Perspex holes. After initial training, the experimenter stopped to feed the ape either because he did not want to (unwilling) or because he *could* not (unable). Similarly to behaviors of 9-month-old kids (Behne et al. 2005), the chimpanzees showed increased begging and acoustic signaling in the unable condition in comparison to the unwilling condition. Similar behaviors have later been reported in monkeys (Canteloup and Meunier 2017; Phillips et al. 2009) and African grey parrots (Péron et al. 2010). The increased begging behavior in the unwilling condition of these animals has been interpreted as being based on the ability of the subject to understand that the other is not willing to cooperate. Thus, the tested individuals base their own

behavioral response on the current mental state (unwillingness) of the other.

The previous experiment tests whether the focal animal does take the perceptual states of the experimenter into account of its own desire states. Other experiments test whether animals also can take others' desire states into account. A suite of experiments has focused on the desire states of pair partners of Eurasian jays. It has been reported that these birds do adjust their own feeding behavior on the amount of a specific food quality. They will reduce eating the same quality in favor of a different one, independent of their overall satiation level, which is also called specific satiety. Additionally, male pair partners have been observed to attend for the specific satiety level of their female pair-partner. By experimentally manipulating the desire state of the female, male Eurasian jays have been shown to feed the currently most preferred food of the female (Ostojić et al. 2013). Not only do they take into account the desire of their female partner, but also disregard their own current desire state by choosing the food quality the partner prefers but the male is specifically satiated (Ostojić et al. 2014).

Eurasian jays have additionally not only been attentive to specific satiety in a cooperative task – sharing food with their female pair partner – but also in a competitive food caching experiment (Ostojić et al. 2017). Jays were pre-fed a specific food in order to induce specific satiety. Hereafter, jays observed a human experimenter hiding food in a caching tray, to which they subsequently had access. The tested individuals took their own specific satiety into account when pilfering the food caches of the humans; i.e., they pilfered the food that they had not been pre-fed with. Thus, pilfering behavior is influenced by the specific satiety of the pilferer. In the next step of the experiment, caching individuals were allowed to observe another individual being pre-fed with a specific food quality. After observing the pre-feeding of the competitor, cachers were allowed to cache two types of food. They were presented with the food they have observed the other individual eating and an alternative food the observer had no specific satiety for. Caching individuals then preferred to hide the food the observer did not currently prefer



and thereby protect its own caches based on the desire state of the observing individual.

For example Eurasians are sensitive to the desire of the competitor by observing the previous feeding situations and inferring, which food item they would prefer. Similar to the attribution of a knowledge state in the previous section, attributing desires to others seems a strong indicator for ToM especially when no direct behavioral cues are present. Only by integrating their own desire state and the desire state of the competitor, an optimal outcome can be achieved by the caching individual.

## Belief States

In child development theories of beliefs develop much later than children's theory of intentions and desires (Tomasello and Barton 1994). In contrast to attributing desire and knowledge, which both are true or wrong attributions of what the other knows/wants or does not know/want, beliefs can also be wrong. A linguistic version of such a test is the false belief task of Maxi. To attribute Maxi wrongly with a wrong belief or correctly with a wrong belief is an increase of complexity in comparison to attribute him with the knowledge where the chocolate is or is not. So far nonlinguistic versions of the false belief tasks seem the most complex attribution of a mental state an animal has been tested in. Note, some would even negate that animals can instantiate beliefs as they argue that they are based on linguistic abilities.

Coming back to the previous example of knowledge states of Hare and colleagues where a subordinate and dominant individual compete for food (Hare et al. 2001), both individuals observed the initial baiting, but in an additional condition the food was later moved without the dominant seeing. The subordinate had seen the initial baiting as well as the rebaiting. Thus, the subordinate individual has the opportunity to differentiate its own knowledge state of where the food actually is, and represent the false-belief of the dominant. Subordinate chimpanzees showed no increased approach to the food when the dominant was misinformed, which indicates that they were

not able to attribute the false-belief to the competitor, unlike three-year old children in a "Sally-Anne" task.

One of the first experiments in chimpanzees testing nonverbal version of the false belief task was conducted by Call and Tomasello (1999). In this experiment a human experimenter, the hider, hid a food item in one of two containers. After hiding, a second experimenter called the communicator (who had witnessed the hiding), turned and walked away to the end of the room, where he stayed with the back facing the two boxes. As soon as the communicator was in his final position, the hider switched the positions of the containers. Thus, the communicator had a false belief concerning the actual position of the food items and when he later returned marked the box where he believed the food item actually is. The test subjects, great apes as well as young children, were then provided the opportunity to choose one of the two containers; either the one that was marked or the one that they knew contained food. Interestingly, small children were able to correctly choose the unmarked and thus baited box, while orangutans and chimpanzees failed to represent the false belief of the communicator. For many decades, no proof was found that great-apes or any other animal species including corvids can represent false beliefs in a competitive or collaborative food-choice task. By implementing a new methodology of testing false beliefs both great apes as well as 15-month old children (Onishi and Baillargeon 2005) were shown to solve a simplified false belief task. Instead of actually choosing an option, children were tested in a violation of expectancy paradigm. An experimenter and a child saw a toy being placed in one of two boxes. After the initial hiding, the children alone saw the toy being swapped from the initial to the second box. Shortly before the experimenter then had a choice to reach into one of the boxes, 15-month-old children looked more towards the box where the experimenter falsely believed the toy was hidden instead towards the box where the toy truly was hidden. Via this anticipatory looking, it was argued that children younger than 3 years already have a rudimentary theory of mind where they expect

actors to behave based on their beliefs rather than based on their own knowledge. This anticipatory looking experiment was then also adjusted and used in chimpanzees (Krupenye et al. 2016). Similarly, to the task in children, it was for the first time shown that chimpanzees anticipated the behavior of an actor on a screen based on its false belief. This experiment was criticized to be possible to solve via submentalizing (Heyes 2017), which is the prediction of behavior based on low-level, domain-general psychological processes. If this alternative hypothesis is true, children and apes would treat inanimate objects the same way as they do in social interactions between actors. In order to show that the results are not based on submentalizing the same experiment was conducted using colored shapes moving in the same way as the actors in the social condition (Kano et al. 2017; Krupenye et al. 2017). This control confirmed that the chimpanzees do not treat the inanimate condition in the same way as the social condition and thus no evidence was found that submentalizing explains anticipatory looking in the social condition.

Similarly to a previous study by Call and Tomasello (1998), it was therefore confirmed that apes and human children represent the goals or intentions of others. In this earlier test subjects were presented with baited and un-baited boxes. Subjects learned in the training phase to differentiate the baited box via discriminatory cues. In the test phase, a marker was intentionally placed on top of the baited box by an experimenter, while a second marker was accidentally dropped on an unbaited box. Interestingly in this experiment also called the accidental/intentional experiment all tested individuals preferred the baited box that was intentionally marked over the accidentally marked box.

states of con- and hetero-specifics and understand at least in some way the goals of the actions. Whether this ability is a “full-blown” or a minimal ToM (Butterfill and Apperly 2013) is a critical question that has still to be answered in future experiments. Currently it seems that any result can be interpreted at a lower or higher level. Often Occam’s razor is used to argue that the simplest solution tends to be the right one when presented with competing hypotheses (Meunier 2017). It seems important though to provide evidence for choosing one over the other hypothesis, and therefore empirical evidence supporting one of the conflicting theories should be provided making the field of ToM research still one of the most interesting areas of research in comparative cognition. Additionally, it seems more fruitful in both nonhuman animals and human children to regard ToM as a cognitive ability that has gradual differences rather than being present or not. Different species may have differences in the ability of attributing mental states to others in various domains.

To conclude, being able to represent mental states of others increases the complexity of social behaviors and social systems that go beyond behaviors that would merely be based on reading of behavioral cues. Still, none of the conducted experiments has the potential to perfectly discriminate one from the other hypothesis – low-level versus high-level explanation. Promising research areas are to find experimental procedures discriminating “full-blown,” minimal ToM, submentalizing or other lower level explanations in different species. It seems most valuable to additionally test nonhuman animals that have already been shown to have high levels of cognitive abilities like different members of corvids or apes and some species of monkeys.

## Discussion

Based on the discussed experiments on ToM it seems highly plausible that nonhuman animals at least have ToM-like cognitive abilities. They can base their own actions on the basis of a reading of the perceptual, knowledge, desire, and belief

## Cross-References

- ▶ [Accidental/Intentional Experiment](#)
- ▶ [Cognition](#)
- ▶ [Corvids](#)
- ▶ [Intentionality](#)
- ▶ [Machiavellian Intelligence](#)

- Social Intelligence Hypothesis
- Technical Intelligence Hypothesis

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## Thermogenesis

### ► Thermoregulation

## Thermoregulation

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## Synonyms

Heat regulation; Homeostasis; State of thermal equilibrium; Thermogenesis

## Introduction

Thermoregulation or heat regulation by definition means the regulation of body temperature in order to maintain bodily function, which for humans is ~37 °C or 98.7 °F (Lim et al. 2008; Tansey and Johnson 2015). The most common and accurate method of core body temperature measurement is via rectal probe thermometer (Osilla and Sharma 2018). Thermoregulation is the part of hemostasis process of an organism, which is the state of equilibrium. From an evolutionary point of view, thermoregulation is considered an important step, helping such organisms to survive more easily in adverse environmental conditions. The hypothalamus is considered as the regulatory center for the body temperature maintenance and is therefore called the body’s thermostat (Romanovsky 2007). In addition, endocrine system glands like the pineal gland in ectotherms (Lutterschmidt et al. 2003) and thyroid gland in endotherms (Silva 2006) play key roles in thermoregulation.

On the ability of maintaining their body temperature within a limit, there are two major groups of organisms, ectotherms/cold-blooded animals and endotherms/warm-blooded animals. Thermoconforming organism/ectotherms are the organisms that cannot maintain their body temperature in a

confined range, and their body temperature fluctuates with the external environmental temperatures, such as fishes, amphibians, and reptiles (Kearney et al. 2009). These organisms cannot survive for long if there is a continuous alteration in their surrounding environment, and they are subjected to hypothermia in case of extreme lower temperature and hyperthermia in increased temperatures, which might lead to failure in normal body functions and ultimately death (Mallet 2002). In contrast, endotherms maintain their body temperature in a narrow range irrespective of the external temperatures, such as birds and mammals (Ivanov 2006). The major pathways as well as key regulators are conserved in both ectotherms and endotherms. External temperature is sensed by transient receptor potential ion channels, and the information is then relayed on to the hypothalamus, which initiates a sympathetic efferent response (Seebacher 2009).

Mechanism and Counteractive Strategy

There are various mechanisms for thermoregulation in endotherms.

Under increased temperature, the body starts sweating, and vasodilation occurs, which increases the blood flow to further cool down the body (Schmidt and Chan 1992). In contrast, under

decreased temperatures, shivering occurs, which produces heat in the body (Charkoudian 2010). In addition, vasoconstriction decreases the blood flow under the skin retaining heat of the body (Charkoudian 2010).

Some animals enter a state of dormancy minimizing their metabolic activities under unfavorable environmental conditions. In colder temperatures, some mammals undergo hibernation, for example, polar bear, bats, lemur, alpine marmots, etc. In order to sustain their energy needs during the hibernating period, these animals store extra fat in form of brown fat/brown adipose tissue, which produces heat by non-shivering thermogenesis (Van der Lans et al. 2013). A similar process is aestivation, which occurs in warm temperatures and in a variety of organisms like fat-tailed lemur, desert tortoise, spotted turtle, California tiger salamander, water-holding frog, bees, earthworms, and lady bugs (Table 1).

Diagnosis

In order to detect any abnormalities in maintaining the body temperature, a thermoregulatory sweat test (TST) is carried out by analyzing sweat production in a controlled environment. The sweat production pattern of an individual in

Thermoregulation, Table 1 Different adaptive strategies acquired by ectotherms and endotherms

| Thermoregulation       | Ectotherm                                                               | Endotherm                                                                           |
|------------------------|-------------------------------------------------------------------------|-------------------------------------------------------------------------------------|
| Under warm temperature | Evaporation of body fluids like sweat                                   | Evaporation of body fluids across respiratory surfaces or skin through sweat glands |
|                        | Vasodilation to increase blood flow to dissipate heat from body surface | Perspiration and panting in cats and dogs                                           |
|                        | Coming in contact with a cold surface                                   | Gular fluttering in birds                                                           |
|                        |                                                                         | Living in burrows during the day and being nocturnal                                |
|                        |                                                                         | Stretched body position and loss of appetite                                        |
|                        |                                                                         | Decreased metabolic rate                                                            |
| Under cold temperature | Changing shape to alter surface/volume ratio                            | Increased metabolic rate                                                            |
|                        | Lying in the sun                                                        | Blubber in whales works as insulating layer                                         |
|                        | Coming in contact with a hot surface, water stream                      | Subcutaneous fat in humans                                                          |
|                        | Folding skin to reduce heat loss                                        | Goose bumps provide hindrance in air flow across skin and minimize heat loss        |
|                        | Natural antifreeze or antifreeze proteins                               | Huddled body position and increased appetite                                        |



addition to the central and autonomic nervous system activities is noted through digital photography. Any abnormalities whether in sweat production or inability to respond to increasing or decreasing temperatures are then revealed.

## Cross-References

- Endocrine System
- Hibernation
- Hypothalamus

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## Thinking

- Cetacean Cognition

## Third-Party Affiliation

- Post-conflict Affiliation

## Third-Party Interactions

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## Introduction

The evolution of intelligence in our own and other species remains a hotly debated topic. The social brain hypothesis, prominent in this debate, argues

that one of the reasons animals have acquired increasingly complex cognition (i.e., intelligence) is to deal with increasingly complex social life (Dunbar 1992; Humphrey 1976). Studies have found a relationship between interspecific variation in primate neocortex size and group size (Dunbar 1992) and more generally in mammalian brain size and respective group sizes (Shultz and Dunbar 2010a). Moreover, studies show that gray matter density in particularly “social” parts of the brain correlates significantly with social network size in humans (reviewed in Adolphs 2009) and rhesus macaques (Noonan et al. 2014). Importantly, intraspecific variation in group size also predicts cognitive performance in several different taxa (Ashton et al. 2018).

However, the question remains: which challenges in social life necessitate increased cognitive capacity? Notably, the interspecific correlation between brain size and group size does not hold for all mammal species, nor does it hold for avian species (Shultz and Dunbar 2007, 2010b); thus, group size per se might be too simplistic to explain species differences. Consequently, many scholars have focused their attention on species’ “social complexity,” yet the term has remained relatively vague and it is currently undecided what actually constitutes social complexity (cf. Boucherie et al. 2019). In his seminal paper on social relationships, Robert Hinde (1976) identified three levels of increasing complexity in the social life of an individual, i.e., (1) interactions, (2) relationships (described by the content, quality, and patterning of interactions), and (3) the structure of a group, based on the patterning of relationships. More recently, this framework has been expanded by the spatiotemporal dynamics of a species, i.e., the degree to which the social environment of an individual varies across time and contexts (cf. fission-fusion dynamics, Aureli et al. 2008), lifetime changes to the social environment (Boucherie et al. 2019), and the role of interactions with conspecific outsiders (Ashton et al. 2020).

Social complexity, in all these conceptions, assumes that individuals have repeated interactions with group members as agents with their own interests, history, and relationships; and individuals have to compromise between competition

for resources and the need to cooperate to survive. Accurately predicting conspecific behavior – by keeping track of others’ social interactions and relationships – could give individuals an advantage but would dramatically increase individuals’ information processing needs when navigating the social landscape (Dunbar 1992). Thus, one central aspect to the study of comparative social complexity has been a focus on third-party interactions. Third-party interactions are any situation where two group members interact, and a third individual influences the course, outcome, or aftermath of the interaction. These situations remind us that individuals in social groups are engaged actors that influence the lives of others. In terms of complexity, the possibility that other group members can get involved dramatically increases the number of social situations that can occur in a group; it forces animals to be vigilant about their surroundings, and it might allow them to strategically manipulate the interactions and relationships of others in a process of social niche construction (Flack et al. 2006). For researchers, third-party interactions open up a window into the mind of our study species: we can test what they know about the power relations and bonds between those in their group and which interactions they perceive as relevant (Bergman et al. 2003). Here, we will summarize evidence that many social animals are indeed able to classify the relationships between others in their group along multiple dimensions and will proceed to describe how they use this knowledge to intervene into aggressive and affiliative interactions. We provide seminal and clear examples but want to emphasize that the list of studies we refer to is far from exhaustive.

## Understanding Third-Party Relationships

On their own, interactions between conspecifics do not need to involve complex cognition. An evaluation of the motivation, strength, sex, and age of your interaction partner may do the trick. Whenever these interactions occur more often with certain individuals, however, it may pay off to individually recognize and differentiate

between individuals, leading to variation in relationship quality. This becomes particularly important when individuals repeatedly cooperate with group members in reciprocal exchanges. Various social species entertain such differentiated social relationships; recognize others as kin, friend, and/or dominant; and remember such relationships over time (Massen et al. 2010). However, do animals also recognize the patterning of social relationships among their conspecifics, i.e., do they also know who is related to whom and who outranks whom? This could allow them to predict behavior more accurately.

In a seminal study, Dorothy Cheney and colleagues (1995) investigated whether yellow baboons understand power relationships of others. In a cleverly designed experiment, they made use of the vocal cues accompanying dominance interactions among the baboons; that is, dominant individuals tend to grunt to subordinate individuals, who occasionally respond with fear barks. Importantly, this never happens in the other direction. Cheney and colleagues made recordings of grunts and barks and then edited them to create *expected* sequences of a dominant individual grunting and a subordinate individual fear barking, thus according to the dominance hierarchy. However, they also created *unexpected* sequences of a subordinate grunt followed by a fear bark from a dominant individual, thus inconsistent with the current dominance hierarchy. As such, this sequence could mimic a turnover in the group's dominance hierarchy. They then played back these sequences and monitored the reactions of third parties, i.e., individuals that were not part of the simulated interaction. The baboons reacted much stronger to unexpected sequences, suggesting that the baboons have certain expectations about third-party dominance interactions between group members (Cheney et al. 1995) and thus seem to have some sort of mental representation of these dominance relationships.

However, in principle, the baboons could also deduce the relationship between others by comparing their own relationship with each of them separately. For example, if individual A is dominant over our subject and individual B is subordinate to the subject, the subject can deduce that A is

dominant over B. Such transitive inference in itself is already an interesting cognitive feature. It becomes more complicated if both are dominant over, or subordinate to, the subject, but then still the subject could deduce the relationship between A and B by comparing the rank distance or degree of dominance/subordinance with each of them and thus without requiring a mental representation of the relationship between those others. Nonetheless, since then, experiments using similar play-back setups have shown that chacma baboons differentiate third-party rank relationships within and between family groups and thus seem to classify their conspecifics simultaneously based on their individual rank and their kin relations (Bergman et al. 2003), which do not need to overlap with the subjects' kin relationships. Moreover, captive ravens showed that they not only have expectations about the rank relationships in their own group but that they also seem to understand the rank relations of a neighboring group (Massen et al. 2014a). They could observe that group but did not have any direct relationship with them, suggesting that these ravens do have some sort of mental representation of rank relations.

### Third-Party Interactions

Having third-party knowledge becomes particularly adaptive if used strategically to outcompete your conspecifics. Specifically, animals may interfere in ongoing interactions between other individuals. These interactions allow individuals to affect the outcome of social interactions to their own benefit: presumably, the potential outcome could have negative consequences for a bystander (e.g., their offspring is injured; a competitor creates a new alliance), and they have the power to influence the outcome to their own benefit. Broadly, third-party interactions allow group members to maintain the status quo (by stabilizing group dynamics, enforcing existing alliances, and preventing new alliance formation) but can also be used to challenge existing power structures (by, for example, combining forces against higher-ranking competitors and gaining access to new cooperation partners).

The third party can interfere in aggressive conflict or in affiliative/cooperative interactions. Different terms have been used to describe third-party interactions, dividing them by the nature and direction of the third party's involvement. During aggressive interactions, individuals can provide *coalitionary support* (third-party aggression toward one of the opponents) or engage in *policing* (impartial third-party action to stop conflict). After conflict, they can provide *third-party post-conflict affiliation* ("third-party reconciliation" if they perform reconciliation for a friend or kin; "consolation" or "triadic post-conflict affiliation" if they direct affiliation toward the loser of the conflict). Also, *third-party interventions in affiliative interactions* (attempting to disrupt or participate in affiliative interactions) have been described in an increasing number of species. We will describe each of these categories in the remainder of this chapter.

## Support in a Conflict

Possibly the best-described form of third-party interaction is support in a conflict (de Waal and Harcourt 1992). Coalitionary support has been described in a range of animal species (Bissonnette et al. 2015) and has been cited as one of the prime examples of nonhuman animal cooperation if individuals risk injury by interfering (van Schaik et al. 2004). However, whether this is a truly cooperative endeavor depends on the context and the opponents involved. Possibly the most common form of coalitionary support, for example, involves the opportunistic support of a high-ranking individual that is attacking an individual that is lower ranking than both the coalition partners ("all-down" coalitionary support), thereby enforcing the status quo. Consequently, the chances of losing the fight and/or the risk of injury are low (van Schaik et al. 2004). As the support of high-ranking group members is a strong factor in winning conflicts, most species who show coalitionary support also show targeted recruitment behavior (e.g., Range and Noë 2005).

Nevertheless, coalitionary support may also occur between an individual that is higher in

rank than the opponent and one that is lower in rank than the opponent ("bridging coalition"), or both coalition partners are outranked by the opponent ("all-up coalition"). Support might result in rank changes or levelling of access; that is, they provide temporary access to resources otherwise restricted by the higher-ranking individual target. In some species, coalitionary support against high-ranking individuals is central in the attainment of dominance rank (de Waal 1982). Whether animals engage in such coalitions depends not only on the species and potential cognitive constraints but also on the context (van Schaik et al. 2004). The decision to support one side in a fight is probably based on an evaluation of the feasibility (i.e., the potential to win), the costs for both participants (likelihood of injury), the benefits it will provide for both participants, and the relationship with the potential coalition partner, where friends are more likely to support each other (Schino 2007).

## Policing

While ample evidence exists that individuals in a variety of species intervene in aggression to support one side, few descriptions of neutral or impartial interventions ("policing") exist, and published studies so far are generally in primates. Policing interventions (first described by de Waal 1982) do not target either contestant but terminate the aggression itself and prevent opponents from restarting the conflict. Policing is used by individuals to manage conflict in their community, stabilize the group, and prevent drawn-out fights or injuries that would hurt the group as a whole (Flack et al. 2006).

The scarcity of information on policing might be a reflection of its rarity or a result of the difficulty of deciding whether an intervention had a specific target or not. Policing behaviors have been described as such mainly in different species of macaque (Beisner and McCowan 2013; Flack et al. 2006) and chimpanzees (von Rohr et al. 2012). Usually, higher-ranking group members will attack both the opponents and/or position themselves between them, thereby disrupting

conflict, even though (usually lower-ranking) female chimpanzees are sometimes also involved in impartial interventions (von Rohr et al. 2012). Policing seems to occur when the costs for the policer are low, for example, when they outrank the opponents, but they also do not seem to confer directly measurable benefits (Beisner and McCowan 2013). This has led to theorizing that policing mainly functions to stabilize the group – experimentally removing frequent “conflict managers” from a group increased the number of aggressions and reduced grooming and reconciliation rates within the group (Flack et al. 2006).

### Post-conflict Affiliation

Originally dubbed consolation (de Waal and van Roosmalen 1979), triadic post-conflict affiliation describes affiliative approaches of a third party directed toward a former conflict participant. Among great apes, this may be reflected in an embrace, much like we humans console others. The definition of post-conflict affiliation by bystanders has since been extended to encompass multiple functions: to reduce stress in the victim (“true” consolation and sometimes considered an expression of empathy); to reduce the likelihood that aggression escalates and the bystander becomes a victim themselves; or to reconcile the opponents indirectly if the bystander is bonded or kin with either.

Third-party post-conflict affiliation has been described for a range of primate (reviewed in Watts et al. 2000) and non-primate species (see Fraser and Bugnyar 2010). Its function seems context specific and to vary both between and within species (Fraser et al. 2009). For example, in chimpanzees, former conflict victims show reduced behavioral markers of stress after triadic post-conflict affiliation (i.e., according to the definition: consolation; Fraser et al. 2008), whereas another study found that chimpanzees show this behavior to protect themselves from redirected aggression of that former victim (Koski and Sterck 2007).

The function of triadic post-conflict affiliation seems highly dependent on the quality of the

relation between the former conflicting individuals and the third party. High relationship quality between the third party and the victim may lead to actual consolation; the victim outranking the third party may lead to protection against redirected aggression; and finally kinship or friendship between the former opponent and the third party may lead to third-party reconciliation (Fraser et al. 2009). Triadic reconciliation (Judge 1991) can happen when a third party that is a relative of one of the opponents in a conflict approaches and affiliates with that other former opponent in the conflict and is suggested to aid in the repair of the relationship between the former opponents and in stress alleviation, much like reconciliation between the two former opponents.

### Affiliation Interventions

An increasing number of studies has shown that affiliative or cooperative interactions can also be subject to outside interference (first reported in de Waal 1982). Affiliative interactions are ubiquitous in many animal species, especially those with repeated interactions between conspecifics in more or less stable associations as we see in many mammals and birds (Massen et al. 2010). Social relationships are negotiated through a number of low-cost cooperative exchanges (“affiliations”), such as grooming, allo-preening, play, huddling against cold, vocal exchanges, and so on (Massen et al. 2010). Each individual usually only has a small number of close partners as the time for affiliation and resources individuals can provide in return are limited, leading to competition over access (Seyfarth 1977). Thus, affiliative interactions between two individuals have at least three potential, immediate consequences for a bystander:

- (A) The affiliation limits the amount of time these individuals have available.
- (B) The affiliation might threaten the bystander’s social bonds with either partner because they might indicate a shift in bonding effort.
- (C) The affiliation might indicate a change in power dynamics in the group if high-ranking



individuals provide aggression support to immediate competitors of the bystander.

There is increasing evidence that all three of these reasons might trigger bystanders to influence the course and outcome of affiliative interactions of group members. How interventions play out and what bystanders can do to intervene differ between species: individuals might disrupt the affiliation completely; they might supplant one of the partners and take over their role; or they might become part of the affiliation (e.g., by joining a play bout).

The effects of competition over attractive partners (A) have been studied indirectly in many species, by studying the distribution patterns of aggregated cooperation rates in relation to dominance rank (following Seyfarth 1977). Recently, more direct evidence for competition for cooperation partners has been added: For example, grooming interventions in several primate species are driven by individuals that outrank at least one groomer and subsequently gain access to the higher-ranking groomer, thus establishing their own priority of access and potentially preventing revolutionary alliances (e.g., Range and Noë 2005). Importantly, in these interventions, the intervener ultimately gains access to one of the groomers – their motivation could therefore simply be driven by their own desire to groom an attractive partner.

In contrast, animals may also intervene in affiliative interactions that threaten their own existing relationships (B). Many social animals rely heavily on social bonds for survival and competition (Massen et al. 2010). It is therefore not surprising that interventions are used to protect these bonds from outside interference. For example, in feral horses, female bystanders challenge individuals who are affiliating with the bystander's close social partners. This is facilitated if the bystander is of higher rank than the competitor, but the motivation seems to be to prevent bond partner defection, because the intervener does not subsequently groom the partner (Schneider and Krueger 2012). Similar patterns have been observed in some primate species. In sooty mangabeys, Western chimpanzees, and

rhesus macaques, bystanders are more likely to intervene into a grooming bout when they have a strong social bond with either groomer (Mielke et al. 2017, 2021). Domestic dogs display interventions in experimental situations where their owner affiliates with a dog-like toy, a result that has been likened to jealous behavior in humans (Harris and Prouvost 2014). Similarly, captive chimpanzees, just like their wild counterparts, intervene into affiliations when new group members target existing bond partners and show a strong negative emotional response that would indicate feelings of jealousy (Webb et al. 2020). Affiliation interventions are therefore not only a useful tool for the study of animal decision-making but also potentially of the evolution of emotions.

Finally, besides disrupting bond formation of their own friends, individuals can use affiliation interventions strategically to disrupt competitors from using alliances to shift power balances (C). Interventions of affiliative interactions can be highly effective in sabotaging ongoing affiliation (Mondragón-Ceballos 2001). In common ravens, pair-bonded individuals prevent the formation of new pair bonds, as the resulting pair would potentially lead to changes in the dominance hierarchy that could be detrimental to the intervener (Massen et al. 2014b). Similarly, sooty mangabeys, chimpanzees, and rhesus macaques show interventions at higher rates when the lower ranking of the two groomers is close to them in rank (after controlling for kinship and social bonds), indicating that they prevent competitors from accessing high-ranking partners (Mielke et al. 2017, 2021). Thus, like policing, affiliation interventions enable animals to preserve the status quo in their social groups.

To summarize, evidence of third-party understanding and the use of this knowledge in third-party interactions is accumulating for a variety of species, giving us a glimpse of the complexity of life in a social group and the cognitive abilities of many animal species. The function of these behaviors varies depending on the interaction, species, and context and generally depends a lot on the relationship quality of the three parties involved. Moreover, some third-party interactions

can be flexibly applied to different context. Consequently, it has been hypothesized that the need for such flexible and strategic cognition in social groups with increasing complexity has been a significant selection pressure in the evolution of intelligence. While the focus of third-party interactions has long been on conflicts and post-hoc conflict management, it now seems clear that third parties can influence all manner of social interactions in a group (aggression, affiliation, play, sex, etc.). This creates a rich tapestry of interactions giving individuals the opportunity to influence their social environment, and we are very much looking forward to how further results from a wider variety of species and contexts will shed more light on individual animals as social agents.

## Cross-References

- ▶ [Dorothy Cheney](#)
- ▶ [Frans de Waal](#)
- ▶ [Machiavellian Intelligence](#)
- ▶ [Post-conflict Affiliation](#)
- ▶ [Post-conflict Resolution](#)
- ▶ [Reconciliation](#)
- ▶ [Robert Hinde](#)
- ▶ [Robert Seyfarth](#)
- ▶ [Social Grooming](#)
- ▶ [Social Intelligence Hypothesis](#)

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## Third-Tier Visual Areas

### ► Dorsomedial Area

## Thought

### ► Catarrhine Cognition

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## Thread

- [Cilia](#)

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## Three Box Problem

- [Monty Hall Dilemma](#)

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## Three Prisoners Problem

- [Monty Hall Dilemma](#)

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## Three-Dimensional (3D) Perception

- [Depth Perception](#)

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## Thrift

- [Parsimony](#)

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## Thyroid and Adrenal Glands

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### Definition

**Thyroid gland:** a collection of follicular cells surrounding a colloid space that concentrate dietary iodine and produce the thyroid hormones thyroxine (T4) and triiodothyronine (T3). Individual follicles may or may not be organized into a larger structure depending upon taxa.

**Adrenal gland:** endocrine gland located next to the kidney responsible for production of a number of hormones including the glucocorticoids as well as the catecholamines.

## Thyroid Gland

### Introduction

The thyroid gland and its products thyroxine (T4) and triiodothyronine (T3) are present across vertebrate taxa. As with all endocrine glands the thyroid is ductless and highly vascularized and thyroid hormones are excreted directly into circulation upon secretion. The thyroid gland is unique among the endocrine glands because of its dependence upon dietary iodine for hormone production and its ability to concentrate and store dietary iodine.

### Anatomy

Though functionally highly conserved, the location and gross anatomy of the thyroid gland varies across vertebrate taxa. Generally in most taxa, the gland(s) are located within the neck region, though the precise location varies. The exception to this rule is the *Echidna* in which the thyroid is present as a pair of unattached glands located in the thorax. In cyclostomes and most teleosts, the gland is disorganized with follicles scattered in the region of the pharynx (Gorbman et al. 1983). In frogs, amphibians, mammals, and birds, the gland exists as a two separate lobes that occur bilaterally. In mammals and humans, in particular, it is composed of two distinct lobes connected by an isthmus, located in the anterior portion of the neck lying on the trachea between vertebrae C5 and T1 (Gorbman et al. 1983). With the exception of the cyclostomes and teleosts in which the gland is disorganized, the thyroid gland, regardless of gross anatomy, is comprised of small spherical follicles. These follicles are formed by a layer of epithelial follicular cells surrounding the follicular lumen (a.k.a. follicular or colloid space), an open space that is filled with fluid-like colloid. Regardless of organizational structure, the resulting thyroid follicles are highly vascularized to support both iodine uptake and secretion of its hormonal products.

## Iodine Uptake

Production of thyroid hormones begins with the active uptake of iodine by the thyroid gland. Concentration of iodine within the gland against its concentration gradient is accomplished by active transport of iodine by and  $\text{Na}^+/\text{I}$  symporter. The end result of this active transport is the concentration of iodine within the colloid space of the follicles.

## Production of Thyroid Hormones

Thyroid hormone production begins with the synthesis of thyroglobulin, an approximately 660-kDa glycoprotein homodimer, in the endoplasmic reticulum of follicular cells. Thyroglobulin is stored within the follicular lumen, where the enzyme thyroid peroxidase (TPO) catalyzes the iodination of the tyrosine residues to form either mono-iodinated or di-iodinated tyrosine residues. Subsequently, coupling of iodinated tyrosine residues results in the formation of T3 and T4 residues. The iodinated thyroglobulin is stored within the follicular lumen until needed. In response to central signaling from the brain, iodinated thyroglobulin molecules are endocytosed into the follicular cells and the iodothyronine residues are cleaved to create T4 and T3, which are then secreted into circulation. Typically, T4 forms the vast majority of the hormone secreted into circulation while T3 comprises only a small fraction.

## Central Control of Thyroid Hormone Production and Signaling

Thyroid hormone production and secretion is controlled by the hypothalamic–pituitary–thyroid (HPT) axis. Neural inputs of both environmental and internal stimuli are integrated in the brain and cause stimulation of the parvocellular neurons in the paraventricular nucleus of the hypothalamus triggering the release of thyrotropin-releasing hormone (TRH) that acts on thyrotroph cells in the anterior pituitary to cause the release of thyroid-stimulating hormone (TSH). After entering the blood stream, TSH binds to the G-protein–coupled receptors of the follicular cells, triggering the release of thyroid hormones from the follicular cells, and stimulates increased iodine

uptake and thyroid hormone synthesis by the gland. The activity of the HPT axis is controlled though classic negative feedback mechanism, in which circulating thyroid hormones bind to receptors in parvocellular neurons in the arcuate nucleus of the hypothalamus and the thyrotroph cells in the anterior pituitary gland to reduce the activity of these two points in the hormonal axis.

## Carrier Proteins

As with most hormonal systems, thyroid hormones are subject to multiple levels of regulation beyond central control of production and release. Following secretion from the thyroid gland, circulating hormones become bound to carrier proteins, which form the bulk of the hormone in circulation (Yen 2001). There are three major carrier proteins for thyroid hormones: thyroid-binding globulin, transthyretin (TTR; previously TBPA), and albumin (Larsson et al. 1985). TTR is of particular interest as it is found not only in circulation, but expression has been identified in other tissues including the liver and choroid plexus of birds (Power et al. 2000). Binding to carrier proteins protects bound hormone from enzymatic degradation and clearance, but also limits its ability to enter cells and bind to target receptors, thus controlling in part cellular exposure to bioactive hormone.

## Membrane Transporters

Until recently, dogma held that thyroid hormones were able to enter target cells via passive diffusion across the plasma membrane (Robbins and Rall 1960). However, recent work has uncovered a large array of membrane transporters that actively transport thyroid hormones across the plasma membrane. At present, over 21 different transport proteins have been identified with varying degrees of specificity for the iodothyronine derivatives: including organic anion-transporting polypeptide transporters (e.g., OATP1C1), monocarboxylate transporter family members MCT8 & MCT10, and L-type amino acid transporters (reviewed in Visser et al. 2011). While these transporters are beginning to be characterized in mammalian systems, little is known about their



distribution, functionality, or expression patterns in most other taxa and broad-scale comparative work is completely lacking. However, the need for membrane transport of thyroid hormones allows for a wide array of potential regulatory schema. Evidence has emerged from multiple species identifying expression of transport proteins in the brains of rats and birds, particularly in the blood–brain barrier. Expression of transporters in the blood–brain barrier with differential specificity for T3 versus T4 may be critical for regulating whole brain exposure to thyroid signaling, particularly in conjunction with deiodinase regulatory activity.

### Regulatory Enzymes

Though T4 is the major product of the thyroid gland in circulation, receptor binding studies have shown that thyroid hormone receptors (THR $\alpha$ s) have significantly higher affinity for T3 as compared to T4; thus, T3 has long been considered the bioactive form of the hormone with T4 often being considered a precursor hormone. The conversion of T4 to T3 is under the control of the second major level of thyroid hormone regulation, the deiodinase enzyme system. This system is comprised of three enzymes: deiodinases type I, II, and III (DIO1, DIO2, DIO3), which function by removing iodine from different positions. All three deiodinases require selenium for functional catalytic activity; thus, either dietary deficiency or defects in synthesis of selenoproteins results in various defects in deiodinase activity and negative feedback control of the HPT axis. Despite these basic similarities, these three enzymes differ in their distribution and the reactions they catalyze. Found primarily in the liver, kidney, and thyroid gland itself, DIO1 is capable of deiodinating both the inner and outer rings of thyroid hormone molecules, thus catalyzing both the conversion of T4 to the more potent T3 and also the inactivation of T4 by conversion to reverse T3 (rT3) or inactivating T3 via conversion to T2. DIO1 is considered primarily to serve a systemic regulatory role, maintaining the appropriate T3/T4 ratio in the plasma and scavenging iodine from sulfated hormone for clearance in either bile or urine. DIO2 on the other hand is most abundant in the

brain, pituitary, thyroid, brown adipose tissue (BAT), and skeletal muscles. DIO2 acts as an outer ring deiodinase catalyzing the conversion of T4 to T3; thus, it is considered the primary activating enzyme. In contrast, DIO3 is primarily responsible for inactivation of various forms of thyroid hormone via inner ring deiodination. DIO3 is abundant in skin and vascular tissue, but is also found in the brain, pituitary, and other tissues. DIO3 also plays a key role in the placenta in protecting the developing fetus from excessive maternal thyroid hormones that might interfere with development. Together DIO2 and DIO3 act locally to control cellular exposure to T3 and thus thyroid signaling. All three deiodinases have been shown to vary both over the course of ontogeny but also seasonally, particularly in seasonally breeding animals.

### Receptors

Ultimately, thyroid hormone signaling is mediated by the binding of predominately T3 to nuclear receptors that regulate gene transcription. There are three isoforms of THR: THR $\alpha$ , THR $\beta$ , and THR $\beta$ 2, which form heterodimers with retinoid X receptors ( $\alpha$  and  $\gamma$  isoforms) to bind thyroid-response elements in the DNA. As with many nuclear receptors, the hormone binds to the receptor, which then translocates to the nucleus and binds to a thyroid-response element activating transcription of the target gene. However, evidence has emerged suggesting that unbound receptor complexes may bind to response elements independent of the hormone. In these cases, the unbound receptor may either suppress or activate transcription, with ligand binding leading to the opposite effect (Mullur et al. 2014). Further complicating the picture is the interaction of thyroid receptors with multiple corepressor and coactivator systems, which respond to a variety of signals including, but not limited to, nutritional and adrenergic signals. In addition to the traditional genomic receptors, non-genomic thyroid signaling pathways have been found by both in vitro and in vivo studies. In particular, the transmembrane protein integrin  $\alpha$ v $\beta$ 3 has two thyroid-binding sites, one that preferentially binds T3 and the other T4, with

differential output depending upon the ligand that is bound. Thyroid hormones have also been identified acting in multiple phosphorylation pathways.

### **Actions of Thyroid Hormones Across Vertebrates**

Thyroid hormones have been long considered to be a “slow” hormone often acting in a permissive manner. Traditionally, they are most closely associated with ontogenetic development, metamorphosis, general growth, and regulation of metabolic function. Disruption of proper thyroid function is also associated with a number of disease processes across vertebrate taxa.

Thyroid hormone action has been tied to development of the brain, sensory, skeletal, muscle, and other organ systems. These effects are mediated not only through genomic receptors altering gene expression, but also through modulation of kinase signaling pathways. In keeping with regulation of developmental programs, thyroid hormone signaling has been established as the sole signal necessary to trigger the metamorphosis from tadpole to adult in amphibians.

Apart from their major role in development and metamorphic processes, thyroid hormones are major regulators of metabolism. Thyroid signaling has been tied to regulation of basal metabolic rate, cholesterol synthesis, lipolysis, gluconeogenesis, cellular ion gradients, and insulin production. These actions are mediated through both genomic and nongenomic thyroid action involving numerous corepressor, coactivators, and varying receptor isoforms, and cross talk with other regulatory systems that are beyond the scope of this work, but see Mullur et al. (2014) for in-depth review.

Thyroid hormones are also tied to adaptive thermogenesis, as is supported by the observation that hypothyroid humans and animals readily develop hypothermia in response to cold exposure, while hyperthyroid individuals typically maintain elevated body temperature. Adaptive nonshivering thermogenesis in rodent models has been tied to BAT and specifically expression of uncoupling protein (UCP) 1, which is locally regulated by T3 following conversion from T4 by DIO2.

### **Thyroid Hormones as Regulators of Seasonality**

Thyroid hormones have recently emerged as potent regulators of seasonality. In particular, thyroid hormones have been identified as key regulators of seasonal breeding in both birds and mammals (Dawson 2002). Upregulation of TSH production in the pars tuberalis of the hypothalamus in response to daylength cues acting through TSH leads to increased DIO2 expression within the hypothalamic tanycytes, resulting in local T3 signaling that triggers the release of gonadotropin-releasing hormone (GnRH) which starts a well-characterized hormonal cascade, responsible for the regulation of breeding (Yoshimura 2010). Thyroid hormones have also been shown to be necessary for the expression of vernal migration (Pérez et al. 2016) and molt (Voitkevich 1966) in birds, but molecular mechanisms of action remain largely unknown for these and other seasonal processes.

### **Conclusion**

Highly conserved and pleiotropic in their function, the thyroid gland and its products are critical regulators of a wide array of processes, with more continuing to be identified. Despite a robust understanding of their molecular actions, particularly with regards to development, metabolism, thermogenesis, and disease processes in humans and other mammalian systems, much less is known regarding these processes in nonmodel systems.

## **Adrenal Gland: Glucocorticoids**

### **Introduction**

The adrenal gland is one of the major endocrine glands located on the posterior wall of the abdominal cavity and sites on the superior aspect of the kidney as its name would suggest. The adrenal gland contains steroidogenic enzymes responsible for the synthesis of numerous hormones including aldosterone, dehydroepiandrosterone (DHEA), cortisol, and corticosterone. Furthermore, they are also responsible for the synthesis of the catecholamines, epinephrine, and adrenaline as well

as small quantities of norepinephrine and noradrenaline.

### Anatomy

The anatomy of the adrenal gland varies across taxa. Mammals typically have an adrenal gland that is composed of an outer cortex composed of three distinct layers with an inner medullary region. The three unique regions of the cortex moving from the outer most to inner most layers include zona glomerulosa, fasciculata, and reticularis. In other taxa such as birds, the same level of organization is not present and cells of the cortex are mixed with medullary cells. In fish, an organized adrenal is almost completely absent and instead adrenal cells are dispersed throughout the kidney tissue. Despite the lack of adrenal anatomical homology across taxa, the cells responsible for producing each of the mineralocorticoids, glucocorticoids, and sex steroids are present in all taxa.

Each of three zones expresses a unique set of steroidogenic enzymes that are responsible for the production of various steroids. The zona glomerulosa produces mineralocorticoids such as aldosterone which plays a critical role in maintaining water balance by controlling the expression of sodium and potassium channels in the kidney. The zona reticularis produces DHEA, a weak androgen that is thought to regulate aggression during the nonbreeding season in many species. Finally, the zona fasciculata contains steroidogenic enzymes that control the production of glucocorticoids, cortisol, and corticosterone, which regulate the stress response. Additionally, the medullary region of the adrenal gland expresses chromaffin cells which are aptly named for the affinity for chromaffin dye and are responsible for the production of catecholamines, epinephrine/adrenaline, although norepinephrine/noradrenaline are also produced in small quantities. Epinephrine is released in response to the activation of the autonomic nervous system and has wide effects including increased heart rate, pupil dilation, slowed intestinal motility, etc. However, as this text is focused on behavior and cognition, the emphasis for the remainder of this section will be on the production of glucocorticoids and their major actions.

### Glucocorticoids

The major glucocorticoid secreted by the adrenal gland can either be corticosterone or cortisol depending on the species although the modes of action are identical. Corticosterone is the primary glucocorticoid in birds, rodents, and amphibians while cortisol is the primary glucocorticoid in primates, pinnipeds, fish, and whales. The difference in production is dependent upon the presence and abundance of key steroidogenic enzymes within the adrenal glands. As with all steroid hormones, glucocorticoids are derived from cholesterol either of dietary origin or synthesized *de novo* within cells. Cholesterol molecules are largely stored in lipid droplets within the steroidogenic cells of the adrenals. Final cortisol synthesis occurs in the zona fasciculata, while corticosterone is synthesized in the zona glomerulosa. In both cases, the steroidogenic enzymes responsible are found both in the intracellular spaces and within the mitochondria, where the final steps of synthesis occur. For both glucocorticoids, the final steps in synthesis involve conversion by 21-hydroxylase to an 11-deoxy form (either 11-deoxycortisol or 11-deoxycorticosterone) from either progesterone (corticosterone) or 17 $\alpha$ -hydroxyprogesterone. The 11-deoxycort is then converted by 11 $\beta$ -hydroxylase into its final form (Salway 1999). Since the final steroid products are lipophilic, they cannot be synthesized and stored like peptide hormones, but rather are immediately diffused into circulation.

### Central Regulation

As with thyroid hormones, production of glucocorticoids is centrally regulated by several key hormonal signaling cascades. Glucocorticoid synthesis is controlled by the hypothalamic–pituitary–adrenal (HPA) axis, which receives input on both metabolic and psychological stressors. The regulation of the HPA axis begins in the brain at the level of the hypothalamus as it integrates cognitive information from higher cortical regions such as amygdala and hippocampus, which provide information on feelings of fear, anger, stress, etc. and information on metabolic status from other nuclei within the

hypothalamus itself. Metabolic and psychological signals are integrated by the paraventricular nucleus of the hypothalamus, regulating the release of neuropeptide hormones. For most mammalian species, the PVN releases corticotropin-releasing hormone (CRH; 41 aa) and arginine vasopressin (AVP; 9 aa) into the portal vasculature of the median eminence where they travel to the anterior pituitary gland to interact with CRH and AVP receptors located on corticotrope cells. In birds, CRH is released in conjunction with arginine vasotocin (AVT) instead of AVP. Activation of corticotrope cells leads to the release of adrenocorticotrophic hormone (ACTH; 39 aa), which travels through the blood stream to the adrenal gland where it binds to melanocortin receptors primarily in the zona fasciculata. Activation of these receptors leads to the increased activity of steroidogenic acute regulatory (STAR) enzyme and side-chain cleavage enzyme activity, which are the two rate-limiting enzymes in steroid production. The activation of the HPA has a very weak stimulatory effect on the synthesis of sex steroids and mineralocorticoids. Synthesis of mineralocorticoids, such as aldosterone, is primarily under the control of the renin–angiotensin system.

### Carrier Proteins

Since steroid hormones are hydrophobic, they need to be transported in the blood and bound to carrier proteins. Carrier proteins allow for rapid transport of steroids through the blood stream. Cleavage by serpinase enzymes at the target tissues allow for rapid release of the hormone. The diversity of these proteins varies by species with many mammalian, reptilian, and amphibian species having sex steroid-specific binding proteins and multiple glucocorticoid-binding proteins, while birds have just a single glucocorticoid-binding globulin. Carrier proteins bind their preferred steroids with a high affinity but are considered low capacity when compared to the ability of other plasma proteins to bind steroids such as albumin. The presence of carrier proteins leads to the classification of hormones that are bound by the carrier protein which represent a majority of the steroid in circulation and steroids that are not bound by the carrier protein which are called

free. Much debate has focused on whether bound, free, or bound and free are responsible for the biological action of the steroid. Many theories have been put forth on the functional role of carrier proteins that is only starting to fully be understood with modern molecular techniques. The evidence today would suggest that glucocorticoid's ability to produce a biological response is mediated by both steroids that are bound by transport proteins and ones that are free in the plasma as well.

### Regulatory Enzymes

In addition to the production of steroid hormones by the adrenal glands and other tissue which perform *de novo* synthesis, steroid levels at the level of the tissue can also be rapidly modified. One of the major enzymes involved in corticosterone signaling is the enzyme 11 $\beta$ -hydroxysteroid dehydrogenase that can be found in two isoforms. 11 $\beta$ -hydroxysteroid dehydrogenases convert glucocorticoids into less active metabolites (11 $\beta$ -HSD2), while 11 $\beta$ -HSD1 performs the reverse reaction (Seckl and Chapman 1997). Expression of these enzymes allows for rapid regulation at the target tissue which can either increase or decrease the amount of steroids that are available to interact with either membrane-bound or nuclear receptors. Little is known about seasonal expression of these enzymes, but they play a critical role in regulating how much glucocorticoid actually encounters intracellular receptors in a cell (Seckl and Chapman 1997).

### Receptors

In birds and mammals, there are two intracellular genomic receptors that bind to corticosterone and less well studied membrane-bound receptors (Breuner and Orchinik 2009). The genomic mineralocorticoid receptor (MR, Type I) has a tenfold higher binding affinity for corticosterone than the genomic glucocorticoid receptor (GR, Type II). As for the membrane-bound receptors, genomic MR can be targeted for the cell membrane where it acts as a membrane-bound receptor and there is also a unique membrane-bound glucocorticoid receptor (Joëls et al. 2008). Insertion of the nuclear MR in the membrane results in a tenfold

reduction in receptor affinity for glucocorticoids and thus has similar binding characteristics as GR. Membrane-bound receptors act through second messenger systems to promote rapid changes in cell activity. This difference in binding affinity is thought to create a two-tier system for responding to basal and stress-induced levels of corticosterone with negative feedback mediated by receptors according to ligand affinity (de Kloet et al. 1998). Nuclear membranes can be found in the cytosol bound to heat-shock proteins (HSP). Once the glucocorticoids bind to the receptor, HSP dissociate which allows for translocation into the nucleus of the cell. Both genomic receptors are transcriptional factors with a zinc finger motif that bind to their respective glucocorticoid-responsive elements to influence gene transcription (de Kloet et al. 1998).

### Major Roles

Glucocorticoids are named after their first discovered function, which is to raise plasma levels of glucose by increasing gluconeogenesis. In addition, glucocorticoid hormones have been termed stress hormones because of their role in helping animals cope with stressful events and are activated at the same time as the flight or fight response by the autonomic nervous system (de Kloet et al. 1998). Physiologists tend to study circulating levels during basal conditions which are thought to reflect levels in an undisturbed animal. At basal levels, glucocorticoids are largely thought to be involved in regulating metabolism. Physiologists are also interested in how glucocorticoid concentrations change in response to stressors such as handling, captivity, predation, weather events, etc., which reflect concentrations that are much higher than basal concentrations and are often called stress-induced or peak glucocorticoids. Stress-induced levels of glucocorticoids are thought to play a different role than baseline levels helping the animal cope with the stressor by inducing drastic changes in physiology and behavior (Krause et al. 2016).

The role of hypothalamic–pituitary–adrenal (HPA) axis is to modify vertebrate behavior and physiology in response to unpredictable events (Sapolsky et al. 2000). Physiological changes must occur for an individual to survive in

conditions that are beyond those normally experienced (Boonstra 2004; Wingfield et al. 2015). Glucocorticoids are often thought to regulate overall energetic expenditures during stressors by reducing the activity of certain systems such as digestion, reproduction, etc., so that greater energy can be devoted toward systems required for immediate survival such as the skeletal muscle system. Thus, scientists have proposed that the activity of the HPA axis is linked with making important life history tradeoff decisions. For instance, when environmental conditions become sufficiently harsh that reproduction must be abandoned in order to save one's self at the cost of losing both one's self and their offspring, either baseline or stress-induced corticosterone levels are elevated (Krause et al. 2016). The actions of glucocorticoids on life history decisions are likely best studied in birds because of the ease at which parents and offspring can be monitored to see when critical points are reached that necessitate nest abandonment. In many bird species, there appears to be a threshold at which corticosterone levels will trigger nest abandonment. Slight increases can be beneficial and have been shown to be positively correlated with reproductive success. The thought being that parents that work harder to provision their offspring likely have slightly higher corticosterone levels in order to help fuel metabolism (Ouyang et al. 2013).

During periods of stress and negative energy balance, rising corticosterone concentrations have been linked with protein catabolism (Fokidis et al. 2012), lipid mobilization (Landys et al. 2004), escape behavior (Breuner and Hahn 2003), hyperactivity in cages (Lynn et al. 2003), suppression of reproduction (Calisi et al. 2008), increased feeding activity (Astheimer et al. 1992; Fokidis et al. 2012), predator awareness (Jones et al. 2015), enhanced memory formation and consolidation, and enhanced immune function (Sapolsky et al. 2000), all of which are thought to promote survival. Each of these examples is a testament to how many systems can be affected by the actions of corticosterone.

Prolonged stressors can lead to situations in which animals are chronically stressed. On the acute, time scale activation of the HPA axis is beneficial for the organism and promotes changes



in physiology and behavior that are necessary for survival. However, prolonged activation of the system, as observed with chronic stress, can have pathological consequences such as reduced fecundity, mass loss, reduced immune function, redistribution of fat deposits, etc. Chronic stress often results in unusual and inconsistent patterns of HPA axis function from changes in baseline corticosterone concentrations, changes in the stress profile, and finally changes in the density of MR and GR receptors in the brain.

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## Ti Plasmid

### ► Conjugation

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## Time Budget

### ► Activity Budget

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## Time Perception

### ► Interval Timing

### ► Swine Cognition

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## Time-Out from Reinforcement

### ► Punishment

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## Time-Place Learning

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## Definition

Time-place learning is the ability of animals to associate when and where an event has occurred.

## Introduction

The universe is made up of a lot of space and relative time and just like Einstein's theory of relativity, animals too, can combine space with time. This is useful since often in our world, important events happen periodically within a specific location and thus associating the time and place of an event will be beneficial for animals as they learn to predict biologically relevant events (i.e., food availability, possible mates, or the presence of predators). For example, in the mid 1990s, Wilkie and collaborators noticed that scavenging birds would arrive to Granville's Island Market in Vancouver, Canada, 1 to 2 hours before the people that would eat their daily lunches outside (Wilkie et al. 1996). The time of day and not the number of people at the market was the best predictor of the number of birds that would appear in the vicinity waiting for the leftover chips. The famous Galápagos marine iguanas (*Amblyrhynchus cristatus*) that Charles Darwin threw over and over again to the sea, also time their twice a day visits to the seashore to match the time when the tide is low and they can feed on the algae (Wikelski and Hau 1995). Individuals that were able to anticipate the low tides and arrived at the shore earlier survived, while the late comers died of hunger. This result suggests that there is indeed "no greater wisdom, than well to time the beginnings, and onsets, of things" (Francis Bacon as cited by Scott 1908). Furthermore, the ability to be at the right place and at the right time seems to be taxonomically wide spread as animals will travel and arrive from distant locations at the time and place when resources are predictably available (e.g., honeybees, *Apis mellifera*: Beling 1929; Wahl 1932; amakihi, *Loxops virens*: Kamil 1978; oystercatchers, kestrels, *Falco tinnunculus*: Rijnsdorp et al. 1981; *Haematopus ostralegus*: Daan and Koene 1981).

Field observations such as the above led cognitive ecologists to question what are the cognitive mechanisms that allow animals to learn when and where resources will be available. In 1990, Gallistel proposed that animals can automatically memorise the nature of an event, the time and the

place of such event into a single tripartite code (Gallistel 1990). The idea of a tripartite memory code, however, has not been fully supported by subsequent research.

### Different Types of Timing Mechanisms

In the laboratory, time-place learning studies typically involve animals being trained to receive a food reward in one place at a specific time of day and a food reward in another place at another time. In one of the first formal time-place learning experiments, garden warblers (*Sylvia borin*) were tested in a four room experimental chamber with a central living area. During the day, each room would be automatically unlocked at a specific time of day for three consecutive hours so that a bird could go in and out of that one room to access grains. Afterwards, that room would be locked and another room would become “available.” Every time a bird entered a room to access the food the bird’s entrance was also automatically recorded. The birds learned the time-place association as demonstrated by birds anticipating which room would become unlocked next and by probe test sessions when all rooms were unlocked but the birds continued to enter the correct room at the correct time of day (Biebach et al. 1989). That the birds were using circadian information (or phase timing) to time their visits to the different rooms was confirmed when the birds’ performance dropped after a couple of days of the light-dark schedule being changed to a continuous 24 h lights-on schedule. Nevertheless, further manipulations showed that some birds were also using ordinal timing to time their visits to the different rooms. An ordinal timing mechanism allows animals to predict events based on the order in which these occur (Carr and Wilkie 1997). For example, even if waking up, getting dress, and going to work might happen at different times of day on different days of the week, these events should always occur in the same order. In the case of the garden warblers, when the accesses to the rooms was blocked so that the birds were prevented from visiting any of the rooms for one of the 3 hours sessions,

five out of nine birds visited the room that would have been next in normal visiting order rather than the room that was to be accessible according to the time of day. This meant that some birds were using different types of timing mechanisms to solve the task. A third timing mechanism has been distinguished as interval timing where animals can learn the duration of an event or the fixed amount of time between two events (Carr and Wilkie 1997). Interval timing is thought to be in use only when animals are presented with events ranging from milliseconds to hours in duration, not for events that happen once a day.

### Variation in Time-Place Learning

When the same protocol as the one used to test the ability of garden warblers to learn a time-place association was used to test different species of birds, there seemed to be variation in the details of what different animals were learning about the task. While both insectivorous black-necked weaverbirds, *Ploceus bicolor*, and the closely related granivorous fire-crowned bishops, *Euplectes hordeaceus* learned to visit four different rooms at four different times of day, only the insectivorous birds were able to shift their visits to the correct place in accordance to different time manipulations (Falk et al. 1992). It is possible that the degree to which time information is relevant to these two species is different. Since insectivorous birds feed from a resource that is limited to a certain time of day, time information is more relevant to their daily foraging routine. The granivorous birds, however, feed from a resource that is equally available throughout a day and thus, time information will be less salient to a granivorous bird than to an insectivorous one (Falk et al. 1992). Fish, for instance, really struggle to correctly time their visits to all four corners of a tank. Only when the task is made simpler by only rewarding two locations of a tank and fish had 3–4 weeks of training, did golden shiners (*Notemigonus crysoleucas*) were able to search for food at the correct side of the tank at the correct time of day (Reebs 1996).

Variation is useful because it can inform us about which ecological factors have contributed to the selection of specific cognitive abilities. In this case, time-place learning can thus be an example of adaptive specialization. This means that species that feed from resources that are restricted to a certain time of day or are available periodically are expected to be better at time-place learning than species that feed from resources that are constantly available. This has been further evidenced by comparing ant species. While the nectar-feeding ants *Paraponera calvata* were able to learn multiple locations where nectar would be provided at different times of the day with only five consecutive days of exposure (Harrison and Breed 1987), 14 other species of European ants that do not feed on nectar did not show any evidence of time-place learning (Dobrzański 1956).

### Time-Place Learning in Wild Animals

Other nectarivorous animals should also learn a time-place association readily since flowers are constant in space and will refill with time. This was proven to be true when the original garden warbler study was adapted to test the time-place learning abilities of wild, free-living rufous hummingbirds (*Selasphorus rufus*). Within only 1 day of training, six out of eight birds learned to visit four different patches of flowers at four different times of the day (from 8 to 9 am, from 9 to 10 am, and so forth) (Tello-Ramos et al. 2015). Even though most of their first visits to the array of four patches were directed to the correct patch at the correct time, the birds did not anticipate the shift (Fig. 1). Instead, birds needed to visit an empty flower on the previously rewarded patch to then directly switch their visits to the new rewarded patch. When the first 3 hours of a session were skipped and the patches were only presented during the fourth hour, the hummingbirds were equally likely to visit any of the four patches, showing no preference for using either a circadian or an ordinal timing mechanism. It was expected that if hummingbirds were using circadian timing, they would have mostly visited the fourth patch, which was the correct patch to

visit at that time of day. If instead hummingbirds had used ordinal timing, then they should have visited the first patch first, regardless of the time of day. It would seem that, unlike the garden warblers, hummingbirds needed both the time of day and the order or events to be able to accurately time their visits to the different patches. Needing to combine two types of timing information may also explain how rats learn the interval for which several different levers provide food whereby the expiration of an internal timer for the first lever could serve as the cue that starts the timer for the second lever and so on (Thorpe and Wilkie 2002).

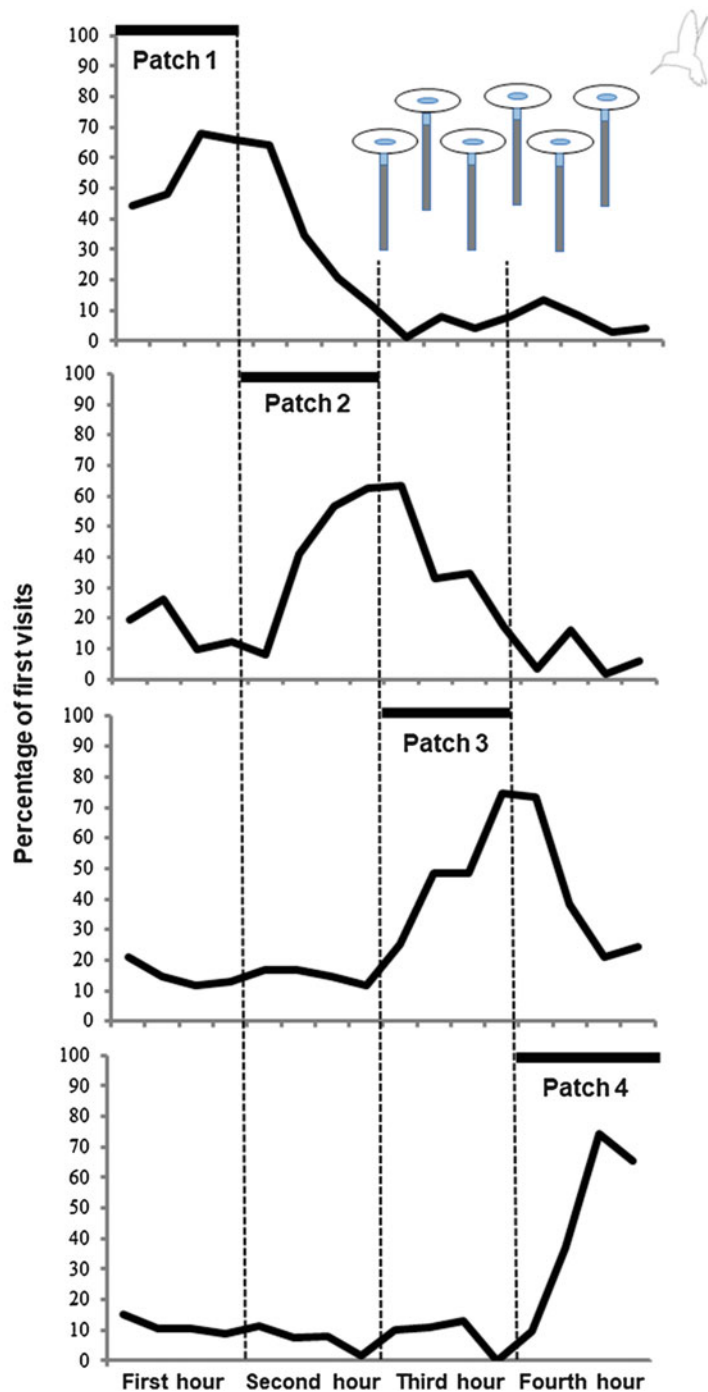
### Conclusion

While spatial processing and its neural basis in the hippocampus (or the mushroom bodies in the invertebrate brain) are well understood in birds and mammals, time processing has been more elusive. In part because as explained above, there are different ways in which animals can tell the time. As suggested by Serry and Schacter (1987), different memory systems, or in this case timing mechanisms, may have evolved because some characteristics that make one timing mechanism efficient are incompatible with the performance of the other mechanism. Recent studies have shown, however, that at least in the mammalian brain the hippocampus is also responsible for organizing events in a sequential order (Eichenbaum 2013), giving at least the neural basis for ordinal timing.

Animals, in the laboratory and in the wild, are able to associate the time and the place of an event. What is not clear yet is why some species seem to use different types of timing mechanisms to solve the same task or why some animals combine two different types of timing mechanisms. It is possible that when remembering an event, animals instead of remembering a single tripartite code, animals remember separate information about the event in an episodic-like memory (what-where-when) (Clayton et al. 2001) and that the “when” can be encoded using different timing mechanisms depending on which is more

**Time-Place Learning,**

**Fig. 1** A four panel graph representing the percentage of first visits made to each patch over 5 days by eight free-living hummingbirds (mean). Each panel shows the visits made to each of the patches over 4 hours. From top to bottom, the top panel represents the visits to the first patch, the second panel represents the visits to the second patch and so forth. The horizontal black bars represent the hour when the flowers in that patch contained reward. The vertical dash lines indicate the times at which a patch became empty and the next patch contained reward. (Modified from Tello-Ramos et al. 2015)



relevant or salient during the event. This is further supported by animals remembering the location, the nature of the events, or the time of the event to different degrees making more or less mistakes when different types of information are put in

conflict (Marshall et al. 2013). Using standard but adaptable protocols to test and compare the time-place learning abilities that wild and laboratory animals have will help us understand the variation in this cognitive ability.



## Cross-References

- [Circadian Rhythms](#)
- [Comparative Cognition](#)
- [Interval Timing](#)
- [Spatial Learning](#)
- [Timing](#)
- [Time Perception](#)

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## Timing

- [Day/Night Cycle](#)

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## Tip-of-the-Tongue Phenomenon

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## Definition

Tip-of-the-tongue is a state in which one cannot currently recall information from memory but believes that one will be able to recall that information in the near future.

## Introduction

If one is asked a question such as “what is the name of the place bees are raised for honey

production?”, one might either know that the answer is “apiary” or not know the appropriate term. However, there is a third possibility. One may feel as though one knows the answer but cannot quite recall it at the time. This phenomenon is known as a “tip-of-the-tongue” state, a memory state in which an inability to retrieve specific information is accompanied by confidence that the information will be retrieved later. The phenomenon was described in the early periods of psychological research (James 1893). However, Brown and McNeill (1966) were the first to bring the phenomenon under close empirical examination.

## Classic Paradigm

In the standard tip-of-the-tongue (TOT) paradigm, participants are given the definitions of relatively uncommon (low-frequency) words (e.g., apiary, nepotism, ambergris, pagoda) and asked to provide the words in question. Participants were instructed to do nothing if they either knew the word, were sure they did not know the word, or thought they might know the word. If participants instead were certain they knew the word but could not currently recall it, they were said to be in a TOT state. When in a TOT state, participants were asked to provide information about the word. Participants in a TOT state are often able to recall specific aspects of the word, including the number of syllables, the stress pattern of the syllables, the first letter of the word, words with similar phonology, and words with similar meaning. Participants are more likely to eventually recall the word when they are able to recall more of this partial information (Brown 1991; Brown and McNeill 1966).

## Factors Associated with TOT States

A number of factors predict the likelihood of entering a TOT state. These factors can be divided into factors associated with the participant and factors associated with the experiment.

## Participant Factors

TOT states become more common as participants age, with a more rapid increase in the very old (i.e., over 80 years old; Heine et al. 1999). Older adults are generally able to recall less partial information, including phonological information (e.g., syllabic stress) and semantic information (e.g., words with similar meaning). However, given sufficient time, older adults are as likely as young adults to eventually resolve the TOT state and recall the correct information. Observations of the change in TOT states across different ages have informed research on the neural basis of the TOT phenomenon (covered below).

Bilingual participants typically experience more frequent TOT states than monolingual participants, even if the bilingual participants are tested in their dominant language (Gollan et al. 2005). However, the difference is not consistent across all types of words. For example, bilingual and monolingual participants experience the same number of TOT states when recalling proper nouns (i.e., names) from a description. This pattern suggests that TOT states are exacerbated when multiple word forms (e.g., “hello” and “bonjour”) are associated with the same meaning (e.g., a common greeting).

## Experimental Factors

The characteristics of the information to be recalled have a clear influence on TOT states. For example, definitions of very common (high-frequency) words (e.g., dog, table, house) are unlikely to elicit TOT states simply because the information is easy to retrieve. Relatedly, the age at which a word is learned influences the likelihood of a TOT state (Navarrete et al. 2015). Words learned early are less likely to elicit a TOT state, and age of learning is often a better predictor than measures of word frequency. Additionally, experimental factors can temporarily change a word’s ability to elicit a TOT state. Recent exposure to phonologically similar words (i.e., priming) reduces the likelihood of a TOT state (Rastle and Burke 1996).

## Neural Basis of the TOT Phenomenon

A variety of brain structures have been associated with TOT states. TOT states are typically

accompanied by increased activity in the anterior and posterior cingulate cortex, multiple areas in the frontal and prefrontal cortex, the supra-marginal gyrus, the superior temporal gyrus, the supplementary motor area, and the insular cortex. The exact role of each brain structure is not currently well understood, but it is clear that TOT states involve the coordination of many different neural processes.

## Explanations of the TOT Phenomenon

There are two competing explanations for the occurrence of a TOT state: *direct-access* views and *inferential* views (Schwartz 1999). The direct-access view explains TOT states as a problem with the retrieval process, whereas the inferential view explains TOT states as a metacognitive judgment.

According to the direct-access view, the participant is unable to properly retrieve the correct information but is able to retrieve related or partial information. There are a number of different hypotheses specifying the exact locus of the retrieval deficit. The *blocking hypothesis* claims that, given a word definition, the participant retrieves an incorrect but related word. Retrieval of the related word then prevents retrieval of the correct word (i.e., retrieval is blocked). The *incomplete activation hypothesis* claims that the correct information is partially activated in memory. That partial activation is sufficient to produce a sensation of retrievability but insufficient to produce full retrieval. Finally, the *transmission deficit hypothesis* claims that the participant is able to activate semantic information from the word definition but that activation does not spread sufficiently to activate and retrieve the corresponding phonological information. All direct-access views are supported by the fact that TOT states are often resolved, that unrecalled words are better recognized in subsequent testing, and that participants can often recall partial information. The transmission deficit hypothesis in particular is supported by the fact that phonological (but not semantic) priming reduces the occurrence of TOT states.

In contrast, the inferential view claims that TOT states emerge from a metacognitive judgment based on a set of clues during retrieval. The inferential view consists of two hypotheses that differ in the nature of those clues. The *cue familiarity hypothesis* claims that participants make a metacognitive judgment based on how well they recognize the cue (i.e., the definition in the classic paradigm). Given familiarity with the definition, the participant infers that she must have learned the definition at some point and, as a result, must know the appropriate word. The *accessibility heuristic hypothesis* claims that participants make a metacognitive judgment based instead on retrieved partial information. Given the ability to retrieve **some** information, the participant infers that she must know the remaining information as well. The inferential view is supported by the fact that providing additional cue information can increase the likelihood of a TOT state without increasing later recall or recognition performance.

Although the direct-access and inferential views have traditionally been held in opposition, Schwartz and Metcalfe (2011) more recently proposed a synthesis of the two explanations. By their conceptualization, retrieval mechanisms explain the failure to recall the correct information (i.e., a direct-access explanation). From that failure, metacognitive mechanisms explain the experience of the TOT state (i.e., an inferential explanation). Thus each perspective might explain unique components of TOT states rather than being opposing and mutually exclusive views.

## Conclusion

TOT states involve a combination of (1) failure to retrieve complete information from memory and (2) a judgment that the information will be retrieved in the near future. TOT states are influenced by a number of internal and external factors. There are two primary competing explanations of TOT states, one framed in retrieval processes and another framed in metacognitive approaches. It seems likely that TOT states reflect a combination of both and draw on a variety of cognitive and neural mechanisms working in concert.

## Cross-References

- [Declarative Memory](#)
- [Long-term Memory](#)
- [Memory](#)
- [Meta-Cognition](#)
- [Metamemory](#)
- [Priming](#)
- [Recall](#)

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## Titchener Circles

- [Ebbinghaus Illusion](#)

## To Divide by Cutting Transversely/Longisection

- [Transection](#)

## Toad Locomotion

- [Salientia Locomotion](#)

## Todd Shackelford

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Todd K. Shackelford, Ph.D. is Distinguished Professor and Chair of the Department of Psychology, and Codirector of the Evolutionary Psychology Lab, at Oakland University. He is also the Editor of *Evolutionary Psychology* and *Evolutionary Psychological Science*. He takes an evolutionary psychological perspective in studying human sexual psychology and behavior, with an emphasis on sexual conflict between men and women.

## Early Life and Education

Todd Shackelford was born in Tulsa, Oklahoma in 1971. He attended public school during elementary, middle, and the first 2 years of high school. As a young man in high school, he aspired to a career in Heavy Metal music and under peer influence he missed school often and received poor grades. As a result, his parents pulled him out of public school and enrolled him in a private Catholic high school. The transfer and loss of contact with friends influenced him to channel his “teenage angst” towards education. He spent his final 2 years of high school focused on learning. Upon finishing high school in 1989, he secured a scholarship to attend the University of New Mexico. Little did he know that his move was a step into the heart of a fairly new field in psychology, evolutionary psychology, which he continued to pursue successfully until this day. During his undergraduate studies, Todd was especially inspired by and learned from

professors Steve Gangestad, Randy Thornhill, Hillard Kaplan, and Kim Hill. Determined to study evolutionary psychology in graduate school, he joined David Buss's lab at the University of Michigan, Department of Psychology in 1993. He then moved from Michigan to the University of Texas at Austin with David Buss's lab, where he completed his Ph.D. in evolutionary psychology in 1997. David Buss played a significant role in Todd's intellectual development, and in his personal and professional life; "I particularly respected his [David Buss's] remarkable work ethic and curious mind" (Shackelford, personal communication).

### Professional Career

After receiving his Ph.D., Todd began his academic career in 1997 as Assistant Professor in the Department of Psychology at Florida Atlantic University (FAU). In less than 10 years, he received tenure and was promoted to Full Professor. At FAU, Todd founded and chaired the Evolutionary Psychology program. He advised and chaired more than 20 graduate students' Masters and Doctoral theses. In 2010, Todd accepted an offer to chair the Department of Psychology at Oakland University and left South Florida for Oakland, Michigan. He left FAU for the opportunity to build graduate programs in psychology at Oakland University. As planned, in 2012, he founded and cochaired the Ph.D. and M.S. programs in psychology at Oakland University. Since then, the program has successfully graduated nearly a dozen Ph.D. students and over three dozen M.S. students. For his notable scholarship and dedication to the psychology department and development of students, in a few short years, Todd was appointed *Distinguished Professor* by the Oakland University Board of Trustees, on recommendation of the President and the Provost. Oakland University's Office of the Provost wrote on this accomplishment, "In six years, he [Todd Shackelford] has raised the University's international profile in the field of psychology. To support a growing student

enrollment, he recruited new faculty and developed Masters of Science and Doctor of Philosophy programs in the Department of Psychology, and attracted international scholars to interdisciplinary conferences on campus." Todd has been the recipient of numerous awards and honors by local, national, and international organizations for his substantial scientific contributions, outstanding teaching, and achievements in research. To mention a few, he was awarded Fellow status by the International Association for Research on Aggression in 2005 and by the Association for Psychological Science and the American Psychological Association in 2009 and 2011. Since 2015, he has served as Secretary/Archivist and Executive Council Member for the Human Behavior and Evolution Society. Currently, Todd is the Editor of *Evolutionary Psychology*, *Evolutionary Psychological Science*, Co-Editor-in-Chief of *Encyclopedia of Personality and Individual Differences* and *Encyclopedia of Evolutionary Psychological Science*, and Coeditor of *Springer Series in Evolutionary Psychology*. He has served on the Editorial Board of more than 30 peer-reviewed journals. He is the author and coauthor of around 300 peer-reviewed journal articles and book chapters and over 300 professional presentations. He has coedited 16 books. His work has been cited over 15,000 times.

### Research Interests

Todd's main research interest is on investigating sexual conflict between men and women from an evolutionary perspective including topics that address sperm competition in humans, romantic and sexual jealousy and infidelity, intimate partner violence and homicide, mate preferences and selection, and marital relationships.

Todd has made significant contributions to identifying and understanding evolved mechanisms for sperm competition in humans. Sperm competition occurs when a female copulates with and is inseminated by more than one male in a sufficiently brief period of time. Evidence for sperm competition in nonhuman species has



provided a framework with which to consider similar adaptations in humans. Todd and colleagues have addressed and provided evidence for psychological and behavioral adaptations in humans that were designed to solve ancestral problems of sperm competition. Todd and colleagues documented that as risk of sperm competition increases, men engage in more frequent mate retention behaviors, show more interest in in-pair copulation, engage in more frequent and shorter in-pair copulations, display copulatory urgency, and perform more semen-displacing behaviors. These findings have been reported in top-tier scholarly journals including *Evolution and Human Behavior*, *Human Nature*, *Journal of Comparative Psychology*, and *Journal of Research in Personality*.

Some of Todd's early research addressed the psychology of infidelity and romantic and sexual jealousy. Along with David Buss, he studied cues to infidelity and individual differences and relationship contexts that predict infidelity in long-term intimate and marital relationships. Furthermore, in a series of studies, Todd and colleagues investigated and provided evidence for sex differences in jealousy in response to the type of infidelity (sexual, emotional, or both), across cultures. Todd continued this work at FAU with his students, addressing emotional reactions to different types of infidelity and experiences of romantic and sexual jealousy among older adults.

Todd has made some of his most important contributions to understanding sexual conflict in humans in the area of intimate partner violence and homicide. With his students and colleagues, Todd has built a comprehensive model of men's violence against their female partners that includes both evolutionary, distal predictors as well as proximate, situational predictors of such violence. They have hypothesized that female-directed violence may be a form of mate retention behavior evolved to decrease the risk of female sexual infidelity and subsequent cuckoldry. The studies that followed documented perceived risk of infidelity to be a significant predictor of men's violence against female partners. More

specifically, Todd and students hypothesized that male sexual coercion and rape of an intimate partner are manifestations of male sexual jealousy, which may be a response to perceived risk of sperm competition. In two studies, they found that (1) men's sexual coercion correlated positively with women's past and future likelihood of engaging in sexual infidelity and (2) men who perform more mate-retention behaviors are more likely to perform sexually coercive behaviors against their partners. More recently, Todd and his students have investigated the role of life histories in predicting perpetration of intimate partner violence. Todd's research on intimate partner violence has been featured in numerous prestigious scholarly journals such as *Archives of Sexual Behavior*, *Journal of Comparative Psychology*, *Journal of Interpersonal Violence*, *Journal of Sex Research*, and *Violence and Victims*.

Taking an evolutionary psychological perspective Todd has extensively explored the psychology of mating, including mate value, mate preferences, and mate selection in humans. In a seminal research study, Todd investigated universal dimensions of mate preferences across 37 cultures. The study identified four universal dimensions and replicated previous research on sex differences in mate preferences, including women's greater valuation of social status and men's greater valuation of physical attractiveness. With David Buss and colleagues, he also conducted an impactful study documenting the cultural evolution of mate preferences among American college students over half a century.

Some of Todd's earliest and most important contributions were in addressing sexual conflict within marital relationships, including infidelity, marital conflict, marital satisfaction, spousal mate retention behaviors, spouse-killings, temporal stability of mate preferences and mate retention behaviors in marital relationships, and sperm competition in marital relationships. The findings from these studies have made significant contributions to understanding long-term mating in humans from an evolutionary psychological

perspective. Todd's work on marital relationships has been reported in top-tier scholarly journals including *Journal of Personality and Social Psychology*, *Journal of Research in Personality*, and *Journal of Social and Personal Relationships*.

From his expansive scientific research to his outstanding teaching and mentoring of future scientists, Todd Shackelford has made significant contributions to science, in general, and to the science of psychology, in particular. He has been a constant champion of the field of evolutionary psychology in his writings and his teaching. He has been an influential and inspiring mentor to his students, including this author, over the years. Todd has been as productive as ever in recent years. Currently, he is working on new research grants and exciting new research topics as well as several edited books, including *The Oxford Handbook of Evolutionary Perspectives on Religion*.

## Cross-References

- [Comparative Psychology](#)
- [Ejaculate](#)
- [Evolutionary Psychology](#)
- [Extra-Pair Copulation](#)
- [Jealousy](#)
- [Mating](#)
- [Mating Effort](#)
- [Sex Differences](#)
- [Sociosexual Behavior](#)
- [Sperm Competition](#)

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## Token

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### Definition

Tokens are object or symbol that has no intrinsic value; its function is established through relations to other reinforcers. Tokens have been described as secondary reinforcer that can be exchanged for a primary reinforcer like food (Sousa and Matsuzawa 2001; Wolfe 1936).

### Introduction

Token systems are ubiquitous in human culture, providing the basic framework for economic transactions within the world. A token is often manipulable and easy to handle (e.g., coins, cubes) but can be non-manipulable as well (e.g., stimulus lamps, points on a counter, checkmarks). Tokens are called secondary reinforcers when they are collected and later exchanged for a primary reinforcer, as a meaningful object or some food. A primary reinforcer is an unconditioned or unlearned reward (e.g., food), whereas a secondary reinforcer is a conditioned reward associated with a specific value, which will be learned over time (e.g., money). Token's value can remain unchanged for extended period and, then, can be accumulated. Another property of token is to be used within a hierarchical system, where tokens of different values can exist (e.g., money) (Sousa and Matsuzawa 2001). In humans, from the supermarket to the stock market, any economic system of exchange involves some form of token reinforcement. In a token reinforcement system, the individual has first the possibility to obtain the token and, then, to exchange it, and this exchange response gives him access to the primary reinforcer. Tokens are often used in operant conditioning, a learning process through which the strength of behavior is modified by reward or punishment.

In humans, a token economy is a form of behavior modification designed to increase desirable behavior and decrease undesirable behavior with the use of tokens.

A token can be used to reinforce or elicit behavior but also to help to discriminate between tasks, depending on its relationship to the other events. These properties make tokens precious to study a large area of nonhuman animal behavior on cognition, such as the effectiveness of tokens as secondary reinforcements (Sousa and Matsuzawa 2001; Wolfe 1936), the use of tokens to request a specific food or tool, and numerical competence including numerous judgments, summations, quantity assessments, preference transitivity, delay of gratification, self-control, behavior inhibition, calculated reciprocity, prosociality, bartering, planning, and judgment biases such as endowment effect or loss aversion (Addessi et al. 2007, 2010a; Bräuer et al. 2009; Brosnan and Beran 2009; Cowles 1937; Dale et al. 2016; Dufour et al. 2009; Evans et al. 2010; Jackson and Hackenberg 1996; Lakshminaryanan et al. 2008; Massen et al. 2015; Sousa and Matsuzawa 2001; Wolfe 1936).

### Advantages of Token Use for Animal Cognition

Many studies have employed the paradigm of token exchange in experimental design to assess a variety of cognitive skills in nonhuman species, starting with great apes (Wolfe 1936). Since, most evidence suggests that primate species (Evans et al. 2010) but also ravens, pigeons (Jackson and Hackenberg 1996), parrots (Péron et al. 2013), rats (Cherot et al. 1996), and dogs (Ellson 1937) do learn to, at minimum, associate tokens with certain foods or certain task outcomes (Hackenberg 2009). Tokens are usually exchanged during distinct exchange periods, during which a specified exchange response involving the tokens is followed by presentation of some primary reinforcer (e.g., food) or other secondary reinforcers. Performances of these birds and mammals under schedules of food reinforcement suggest that tokens do indeed serve as conditioned

reinforcers. Token-reinforced behavior is also modulated, however, by the exchange production schedule that determines how and when exchange opportunities are made available. Numerous studies have shown that primates treat tokens as symbols that stand for those foods or outcomes (Addessi et al. 2007; Brosnan and Beran 2009). Thus, tokens can be used as tools to get a food reward but also be used in a novel discrimination task with token reward instead of direct food reward. In chimpanzees, tokens are almost equal to food rewards in their capacity to maintain and shape a discrimination behavior (Sousa and Matsuzawa 2001).

Token-exchange tasks can also be used in social learning paradigms. Typical studies in social learning used the two-action method, involving two physically distinct techniques to solve a single task. Although researchers attempt to design apparatus for which the two methods are of equal complexity, there is often an inherent bias whereby one method is simpler or more open to individual discovery (Hopper et al. 2011). Using distinguished token instead of distinguished methods might help to outreach this bias. Within this design, animals have the choice to animals to exchange one of two types of tokens for a different food reward: one type is associated with a highly preferred food and the other with a less preferred food. Individuals first observed a demonstrator from their group exchanges one of the two types of tokens to learn which token earned which kind of reward. Then, subjects are involved into an identical physical action, and it's only the token type that would give information to the preferences.

Token exchange inherently introduces an element of delay between behavior and reward. Thus, token-exchange paradigms are particularly relevant to better understand delay of gratification, behavioral inhibition, and self-control and are largely used in primate species (Evans et al. 2012). Self-control is defined as seeking to obtain a larger reward in the future over a smaller reward in the present. Different paradigms have been designing to modulate the complexity of the task. Judge and Essler (2013) use a token-exchange paradigm with two successive steps to test self-controlling capuchin monkeys. First,

animals were trained with a token that was associated with a lower-value food. When the monkey exchanged the token, the experimenter provided the monkey with a choice between the lower-value food item associated with the token and another token that was associated with a higher-value food. If the monkey chose the token, they could then exchange it for the higher-value food. On the contrary, some paradigms keep the food option visible. In that case, animals must inhibit the selection of immediately consumable food items in favor of selecting tokens that represented more preferred food items that could be consumed later. This experiment helps to assess whether primates – but potentially other species – can make decisions and evaluate task contexts in ways that go beyond making simple responses to prepotent and immediately available items such as food.

Delay of gratification, behavioral inhibition, and self-control are prerequisite for complex cognitive processes such as cooperation and planning. The multiple properties of tokens – they are exchangeable, they might be portable, and they can be accumulated and associated to different values – are combined when designing token-exchange tasks to assess these complex cognitive processes (Brosnan and Beran 2009). In a calculated reciprocity situation, partners must give something (e.g., a token, a service) with return expectancy. In addition to this return expectancy, the gift must occur intentionally from one partner to another, and each partner must know the value of the traded items. Several primate species have been tested in a token-exchange paradigm that seek to replicate these conditions. Primates were tested by pairs, but before starting testing, each individual has to learn the value of the different items, for themselves and for their partner. Individual A has been trained to exchange token A to receive food, whereas when exchanging token B, the individual did not receive food. Individual B has been trained in the opposite way: exchanging token B with the experimenter gives a food reward, but exchanging token A gives nothing. In the test condition, each of them possessed tokens valuable to their partner but useless to themselves. Primates could exchange with the experimenter at

any time. To receive food, individuals must first obtain the token from the other partner and then exchange it with the experimenter. Orangutans tested with this paradigm show calculated reciprocity (Dufour et al. 2009), whereas other great ape species tested and other monkeys failed to exchange (Pelé et al. 2009). Besides, these paradigms include several underlying tasks (e.g., interactions with the human partner, interactions with conspecifics, delay, number of token used) which help to give a better understanding of the cognitive process implied and, from a broader approach, the shared skills within primates.

Other complex social behaviors underlying by cognitive mechanisms, such as prosociality, voluntary actions that benefit others, might not be a uniquely human trait. Nonetheless, results in primates and other species are disparate, but few of the studies are methodologically comparable (Drayton and Santos 2014; Marshall-Pescini et al. 2016). To compare results across broader taxa, a token-exchange task paradigm frequently used with primates has been successfully applied to dogs (Dale et al. 2016). A comparative study has also been conducted on planning skills in ravens (Kabadayi and Osvath 2017) by using a similar methodology that used with primate species (Bourjade et al. 2014; Mulcahy and Call 2006; Osvath and Osvath 2008). Token-exchange procedures and tokens used as tools have been at the core on the design. Results indicate that ravens can plot for long-term gain at least as well as 4-year-old humans and some adult nonhuman great apes. Thus, by providing a common methodological context, token procedures are well suited to cross-species comparative studies, including humans, and whatever the degree of complexity of the cognitive processes involved.

Token-exchange paradigms are also highly relevant to behavioral economics. The use of tokens makes it possible for experimenters to control differences of currencies or the relative values of the goods to be exchanged. From an economic perspective, tokens can be conceptualized as a type of currency, earned and exchanged for other commodities. Token systems provide a controlled and analytically tractable environment in which to explore interactions between behavior and

economic variables (Hackenberg 2009). Token systems provide an alternate approach to the problem of common currency. Rather than defining currency in responses or time, the currency is defined in common token units, which make it possible for experimenters to normalize exchange parameters. Then, experimenters will be able to assess how much tokens a subject is willing to spend on an activity or commodity (Addessi et al. 2010). To the extent that tokens are interchangeable, one for another, they can be used to scale qualitatively different commodities. This approach leads to comparative cognition to assess different economic biases well-known in humans (e.g., loss aversion, endowment effect, framing effect, preference transitivity).

## Limitations of Token Tasks for Animals

Despite the potential of token-exchange tasks as a widely applicable test of animal cognition, there are some limitations which must be considered when designing tasks involving token-exchange paradigms and interpreting their results.

First, all these paradigms require an extensive training, which might be variable depending on the species considered but also between individuals (Brosnan and Beran 2009; Dale et al. 2016; Pelé et al. 2009). These approaches require as the minimum to create operational conditioned to make sure that animals associate token with a specific outcome. First, a schedule of reinforcement must be determined. Associate token as secondary reinforcers implies time and effort for staff training and management. In a general way, the human partner needs to have a relationship that involved only neutral or positive interactions with the animals, which might imply an enough amount of time; this is even more true if there is a need to insure predictability and that the human partner is associated with the exchange task for the animals (e.g., in planning task). It's important to ensure that the animals earn enough tokens in the early phases of the training so that it can exchange them for primary reinforcements regularly later. This leads to another limitation inherent to exchange tasks – only animals that reach the



predefined learning criterion will participate to the tests. Thus, results of exchange tasks can be biased toward animals capable of completing operant conditioning training. But this extensive training might also have an influence on behaviors observed during the test and thereby be a confounding factor on test results. When testing bartering in chimpanzees, authors reported that some behaviors have been shown uniquely after extensive training, chimpanzees engaged in accurate trade behavior as long as an experimenter enforced the structure of the interaction; however, trade between partners disappeared when this reinforcement was removed (Brosnan and Beran 2009). Finding a good balance between allowing animals enough experience to understand the mechanics of the task and avoiding overtraining the animals is an issue to treat carefully as both factors would impact the testing phase and in extenso the results.

The context of exchange paradigm can also influence. Whereas social learning paradigms using only tokens and not mechanical apparatus may elicit the discovery and the difficulty biases, authors reported that capuchins proved to be highly motivated and skillful token exchangers and when individually tested never displayed token exchange in the social context. But as noticed by the authors, these individuals were all low-ranking individuals, and similar behavior (i.e., not doing the task) may have been appeared with a classic apparatus. Nonetheless, all species cited (pigeons, parrots, ravens, rats, dogs, primates) have social structures, and social context has to be taken into account, even more particularly in complex tasks such as bartering, trading, and reciprocity (Marshall-Pescini et al. 2016). The social facilitation control is an extremely important condition to include to disentangle any differences between test and nonsocial control conditions.

When tokens are used as reinforced conditioners, several authors reported frequent instances of misbehavior, defined as an excess frequency of exchange responses (Addessi et al. 2010a; Defulio et al. 2014; Pelé et al. 2009). Some individuals did not exchange tokens more than

other items (e.g., stones, no-value token, etc.). Although exchanging no-value tokens or other items does not lead to a food reward, trading per se might be sufficient motivation for the animals to continue exchanging (Carpenter and Locke 1937). On the contrary, a decrease of motivation has been reported in capuchins (Addessi et al. 2010b), due to the delayed feedback associated to token exchange. Whereas they can easily learn to associate several types of tokens with different amounts or types of food, tokens are not dealt with in the same manner as the food for which they are exchanged. Tokens may also evoke or elicit behavior based on their temporal relations to food.

Such token-evoked behavior is probably more likely with manipulable tokens (e.g., cubes, coins) than with non-manipulable tokens (e.g., lights). Manipulable tokens are handled in several ways throughout the sequence of earning and exchanging them for food, and this physical contact with the tokens then becomes part of the behavior engendered by the procedures. Then, it may be desirable to use non-manipulable tokens, less susceptible to intrusions from embedded stimulus–food relations. Specific methodological choices therefore depend on the types of questions asked.

Token choice task might be more cognitively demanding compared to similar task. This argument can be made, for instance, in the case of prosociality, also investigated using the bar-pull paradigm (Marshall-Pescini et al. 2016). Studies using different paradigms sometimes lead to various conclusions, but few studies used the same methodology. In prosociality studies, dogs have been sensitive to rather subtle methodological changes – which might be the case for other species. This highlights the necessity to adopt a comparative approach with the most similar methodology possible when investigating cognitive skills across species.

## Conclusion

Token-exchange paradigms have been revealed as useful tool to explore many different cognitive skills, from numerical competence to prosociality.

Although the limitations must be considered when designing study, by providing a common methodological context, token procedures are well suited to cross-species comparative studies, particularly within birds and mammals. This approach allows for a more thorough evaluation of the biological and evolutionarily shared aspects of striking cognitive abilities across species.

Token-exchange paradigms are particularly promising to explore behavioral economics and cognitive bias in animals and should receive increase of attention in the near future.

## Cross-References

- [B.F. Skinner](#)
- [Cognition](#)
- [Cognitive Bias](#)
- [Comparative Cognition](#)
- [Decision-Making](#)
- [Operant Conditioning](#)
- [Reinforcement](#)

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## Tolerance

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## Definition

Tolerance is the decrease in the response to a determined amount of a drug. This effect may also be expressed as a necessity for increasing the dose of a drug to obtain the initial effect. Tolerance can be classified in two categories: acute tolerance and chronic tolerance. One key difference between them is that acute tolerance results from drug-compensatory processes elicited by the drug itself. In contrast, chronic tolerance is, at least in part, a result of learning mechanisms (i.e., Solomon and Corbit 1974; Siegel 2001).

Acute tolerance is the decrease in the response to a drug during a single administration. Drugs disrupt homeostasis of the organism, and to restore homeostasis the organism responds in an unconditioned or reflexive way to compensate for the drug-induced disruption. This unconditioned response constitutes acute tolerance. Consequently, the net result in behavior observed after drug administration is the summation of the primary change produced by the drug, and of the secondary compensatory responses (i.e., acute tolerance). This latter effect can be seen in isolation when the primary reaction produced by the drug is no longer present, for example, within a single administration of morphine the subject can develop acute tolerance, producing hyperalgesia. Then when morphine is metabolized and eliminated (and its analgesic effect ends) an increased sensitivity to painful stimuli is often observed, because the compensatory responses continue and therefore the sensitivity increase.

Chronic tolerance, on the other hand, is a decrease in the effect of the drug over the course of a series of administrations. Like acute

tolerance, chronic tolerance is generally thought to be mediated by compensatory responses; however, while acute tolerance is solidly understood as a consequence of drug-compensatory process provoked by the drug administration itself, diverse accounts have been provided to explain the psychological mechanisms underlying chronic tolerance.

## Mechanisms of Chronic Tolerance

Multiple models have been proposed to explain chronic tolerance. Considering that tolerance involves changes in behavior with repeated or chronic experience with a drug, these theories are in most cases based on theories of learning. One account is the opponent-process theory (Solomon and Corbit 1974). This theory assumes that when organisms react to stimuli, this reaction generates two processes that sum to influence behavior. The first, involves a direct response known as the *a-process* which is counteracted by a second, process, that acts in the opposite direction of the *a-process*, known as *b-process*. This *b-process* would constitute the compensatory response to the drug. In the case of ethanol consumption, the *a-process* is the effect of intake that, for example, could be the decrease in body temperature caused by administration of ethanol. The *b-process*, following the same example, would be an increase in body temperature. The model also included two more tenets: the *a-process* magnitude is maintained with the same dose of a drug; however, the *b-process* gets stronger with repeated intake of the drug (Baker and Tiffany 1985). Because of the strengthening of the *b-process* in each drug intake experience, subjects become more tolerant. That is, the compensatory responses become more effective to compensate the disturbance of the drug. In the example, this translates into maintaining the body temperature constant, reducing the hypothermic effect of ethanol.

One caveat of the model is that it cannot explain why sometimes chronic tolerance is observed and why sometimes it is not. More specifically, it cannot explain the situational specificity of drug tolerance, that is, why tolerance is observed only in the

presence of environmental and contextual cues that are related to drug administration.

A model based on associative learning postulated by Siegel (1975, 2001) states that chronic tolerance is at least partially the result of associations between the drug (or its effects on the organism) and cues present during administration or consumption. The internal disruption in homeostasis caused by the drug is considered an unconditioned stimulus (US), which causes the organism to emit an unconditioned response which maintains the homeostasis. The responses involved in acute tolerance constitute the unconditioned response in this model. The stimuli that are typically present at the time of drug administration signal the onset of the drug, and thus work as conditioned stimuli (CS). When the CSs are present they prepare the organism for the effect of the drug by allowing it to anticipate the homeostatic responses which compensate for the drug effects (i.e., conditioned compensatory response; CCR). This model, (e.g., Siegel 1975; Siegel et al. 2000) emphasizes the role of compensatory conditioned responses as the basis of drug tolerance: according to the model, these conditioned compensatory responses are the main cause behind the reduction in the effect of a drug (US). Furthermore, Siegel's model can also explain the occurrence of withdrawal symptoms. If the cues associated with a drug are present in the absence of its effect (i.e., with no consumption), the elicitation of compensatory responses would have nothing to compensate for and will produce an aversive motivational state. This phenomenon would be at least in part responsible for the manifestation of cravings (Siegel 2001).

Consider a subject who habitually drinks or takes a drug in a certain place regularly (e.g., a bar). In such a situation, the subject associates features of the place (e.g., physical settings, friends, vision of the drink, taste) with the effects of acute tolerance. This "bar context" elicits compensatory responses that prepare the individual for the effect of the drug. If one night the person exposes himself to the bar, but does not drink, in this situation, the compensatory responses would be elicited in absence of any drug perturbation to compensate, causing cravings. These cravings

will cease if the person consumes, as the drug would return the body to the original homeostatic state. If another night the same person goes to a new place, the compensatory responses will not manifest and the subject will not show tolerance after consumption and the full effect of the drug would be expressed.

Siegel's model of drug tolerance has received much empirical support. It helps explain the acquisition and development of drug tolerance, the manifestation of withdrawal symptoms, and the motivational aspects of drug abuse and dependence, while also contributing to the development of potential treatments from the perspective of Pavlovian conditioning. For example, following Pavlovian principles, researchers have focused on extinction learning as a Pavlovian model for cue exposure therapy (e.g., González et al. 2016), which can be used to decrease tolerance and withdrawal symptoms and thus help in removing some of the elements that maintain drug consumption (Siegel et al. 2000).

## Pharmacodynamics and Pharmacokinetics of Tolerance

At a pharmacodynamic level tolerance involves several processes that result in impaired excitation of the drug receptor. For example, a drug constantly binding with the receptor may desensitize it (Bespalov et al. 2016), reduce its receptor density in the neuron (Chavkin and Goldstein 1984), or trigger processes that modify the firing rate of the action potential (Allouche et al. 2014).

At a pharmacokinetic level (i.e., dispositional tolerance) tolerance involves processes that lead to a smaller amount of the substance at the site it affects. This may be caused by metabolism (e.g., a decrement in enzymes that make a drug active), absorption, distribution, and excretion of drugs.

## Compensatory Responses to Nondrug Stimuli

Conditioned compensatory responses involved in tolerance have been found in different types of drugs, including commonly abused drugs such as

opiates, ethanol, and caffeine. This process applies to drugs due to the disrupting effects of such stimuli, but also it applies to nonpharmacological stimuli that produce strong physiological reactions. In general, compensatory responses are present whenever the organism needs to adapt to new stimuli (Siegel 2008). For instance, compensatory responses to chromatic stimuli produce adaptation. Continued presentation of a color over a period of some minutes causes it to appear desaturated. The adaptation to color involves a chromatic CCR, analogous to those responsible for drug tolerance. For example, cues associated to a green color produce a perception of magenta when they are presented as achromatic test stimuli. This kind of CCR can also be seen in the adaptation to hypothermic stimulation, in which a reduction in the induced-coldness of the body is observed over the course of repeated applications of cold water. Similarly, signals associated to the immersion cause a CCR of hyperthermia. CCRs are involved in ingestion as well, for example, insulin is sometimes released in anticipation to food intake. Cues for the taste or smell of the food can trigger the release of insulin long before the food is ingested. This mechanism allows the organism to be prepared for the sugar arrival, allowing its adaptation. All these examples support tolerance as a mechanism that can be applied to several different situations. These situations include drug use, but also the reaction to different kind of stimulation, and consequently, it seems to be a general mechanism to adapt to disrupting stimuli.

## Cross-References

- [Associative Learning](#)
- [Classical Conditioning](#)
- [Habituation](#)
- [Homeostasis](#)
- [Withdrawal](#)
- [Xenophilia](#)

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## Tom

### ► Theory of Mind

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## Tom Zentall

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Thomas (Tom) Zentall is a Professor of Psychology at the University of Kentucky. Given over a half-century of contributions to the scientific community, he is arguably one of the most prolific and influential researchers in the fields of comparative cognition and animal behavior. From the time he began publishing in 1966, he has authored over 340 journal articles and book chapters, along with

editing seven books on topics related to social learning, animal intelligence, stimulus class formation, and decision making. Throughout his career, he has mentored over 30 students, aiding in their obtainment of a Master's or PhD degree. He has received over 20 grants from organizations such as the National Institute of Mental Health (NIMH), the National Science Foundation (NSF), the National Institute of Child Health and Human Development (NICHD), and Fulbright Scholarships, along with being honored numerous times for his contributions in the field of psychology from various associations to which he has offered his expertise in roles as Editor, Fellow, Associate Editor, and Consulting Editor. He is an elected Fellow for the Society of Experimental Psychology and has received awards as a Distinguished Researcher (CCS) and Lecturer (EPA), as well as Distinguished Contributions to Scientific and Basic Research (APA). He has also served as Chair of the Governing Board of the Psychonomic Society, and as President of the American Psychological Association (APA, Divisions 3 and 6), Midwestern Psychological Association (MPA), Eastern Psychological Association (EPA), and Comparative Cognition Society (CCS).

Tom's extensive knowledge and experience in the field of animal behavior, combined with his personal belief in the importance of investigating the links between human and nonhuman animal cognition, has resulted in the advancement in our understanding of both the unique and shared abilities of humans and our nonhuman relatives. Interestingly, Tom did not start out knowing he wanted to study psychology. It was the recognition of a serendipitous finding and a keen determination to "...go where the questions lead you" (Interview with Tom Zentall 2014) that led Tom down the road of comparative cognition and animal behavior.

Tom was born in Beziers, Southern France, in 1940 during the Second World War. His family came to the United States in 1942 and settled in New York City. He attended Brooklyn Technical High School and went on to major in Electrical Engineering at Union College in Schenectady, New York. While in pursuit of this degree, he took psychology classes where he learned about the various experiments conducted with human

and nonhuman animals. His interest in psychology grew as he realized he wanted to apply scientific principles to the field of psychology. He recognized that this was already happening through the work of others, such as B. F. Skinner and Jean Piaget, who sought to create systematic ways of creating sound experimental designs to the study of animal and human behavior. However, he also found that many experiments lacked the proper controls needed to parcel out the meaning behind the data. Additionally, he was influenced by the importance of interpreting results in more parsimonious, objective ways as compared with much of the research at the time that sought more cognitive and abstract explanations for the behaviors observed.

After obtaining both a Bachelor of Science in Psychology and a Bachelor of Electrical Engineering at Union College, Tom began his doctoral training under the tutelage of Donald (Al) Riley at the University of California, Berkeley, in 1963. At the time, Al was working with human children and adults looking at various forms of generalization across physical dimensions. In an interview with Jeff Katz at the 2014 Comparative Cognition Conference, Tom stated that working with these populations was rather difficult because of the inherent complications that arise from dealing with children (Interview with Tom Zentall 2014). Both Tom and Al were interested in generalization gradients, which are measures of the level of activation to a set of stimuli that lie along a single physical dimension, such as color or brightness. In humans, activation of the color red, for example, produces a systematic activation of various shades of red around a gradient, with colors more similar to the original stimulus producing higher activation than those further away. Wondering whether a similar phenomenon occurs in animals, Tom and Al investigated this with Japanese quail, rearing them with monochromatic light and later testing them on variations of light gradients. They found that the same basic generalization gradients were generated in the quail as had been previously observed in humans, suggesting that this must be a process that is built-in to many organisms with similar physiological structures. Tom quickly realized the

benefit in working with animals, such as quail, who are precocious, easy to raise and handle, and will work hard for very little food. From this initial line of research, Tom would begin building his legacy.

After working at the University of Pittsburg for 6 years, Tom took an Assistant Professor position at the University of Kentucky in Lexington where he remains as productive today as when he started. He began his research working with pigeons. Like quail, pigeons are relatively easy to maintain and will readily work for small payouts, such as food. They are also a species on which much of the previous research in animal behavior had been conducted. His initial interests were in memory strategies and concept learning in human and non-human animals. Tom began his experiments by replicating older research to see if the results were both accurate and reliable. He also figured out how to redo experiments in which he felt the proper controls or aspects of the methodology were not present. One of these lines of research dealt with the now famous matching-to-sample paradigm, where an animal is presented with an initial (sample) stimulus, such as a green light, and then given the option of two (comparison) stimuli, such as a red light and a green light. In order to receive food, the animal is required to peck at the key that matches the initial sample key, in this case, the green light. Although pigeons could readily learn the initial discriminations, when tested on the critical transfer trials in which they received a novel pair of stimuli, such as blue and yellow lights, responding fell to chance, suggesting they were not able to develop the concept of sameness (also called identity). Tom realized that the failure of pigeons to transfer this behavior to the novel stimuli had much to do with their natural tendency to avoid novelty, as pigeons are neophobic (Zentall and Hogan 1974, 1976, 1978; Zentall et al. 1981a, b), as well as the fact that, during training, pigeons appeared to avoid contact with the negative stimulus, thereby learning little about the incorrect associations. Therefore, he and his colleagues designed clever ways to train pigeons on multiple colors from the start of training, eliminating the element of novelty, as well as providing negative instance trials

where no comparison was correct, and found pigeons were successful in demonstrating a generalized matching-to-sample concept on test trials.

In a related line of research on delayed matching-to-sample, where there is a time delay between the offset of the sample stimulus and the onset of the comparison stimuli, Tom again realized that the rapid decline in accuracy over delay by pigeons was due to ambiguity in the methodological procedure, and not to the pigeon's inability to maintain the stimulus in memory over time (Zentall 1997, 1999). Here, Tom created a clear distinction between the intertrial interval, or the time between trials, and the delay between the sample and comparison stimuli (the time within trials) by using a house light to signal between-trial intervals. He was able to demonstrate that pigeons are adept at maintaining memory for recent stimuli far longer than was once believed. Therefore, one of the main lines of research Tom has pursued, which has contributed highly to the field of comparative cognition, is the use of proper methodological designs to reduce instructional ambiguity in order to ferret out the true nature of an animal's cognitive capacity.

Over the years, Tom has also investigated various lines of research that could fall under the category of parsimony in explanations related to the more cognitive explanations given in many articles on human behavior. One of the major contributions of Tom's work has been to show that results in the human literature that are often explained in more cognitive terms may be better explained through simpler, more basic processes, as nonhuman animals exhibit highly similar behavior under comparable circumstances. Some of the lines of his research under this umbrella deal with decision making, maladaptive behavior and "gambling," cognitive dissonance (versus contrast), imitation and social learning, and self-control. With the help of his graduate students, Tom has also been able to study other nonhuman animals, such as rats, quail, horses, and dogs, and has successfully contributed a wealth of knowledge on the abilities of these animals to solve various cognitive tasks. Tom's broad contributions to Comparative Cognition and Animal Behavior can best be classified through his

philosophy, pioneered by Edward Tolman, as a cognitive behaviorist; one who seeks to understand the cognitive nature of behavioral phenomenon through rigorous and sound methodological design. This approach to studying animal learning is apparent throughout Tom's many lines of research into the subtly powerful mixture of these very important aspects in psychology. As eloquently laid out in his paper "A Cognitive Approach to Animal Learning and Behavior," Tom argues for three fundamental aspects when conducting research: objectivity, parsimony, and serendipity (Zentall 2001). This paper in many ways exemplifies Tom's contributions to the field of comparative cognition and animal behavior. His work has undoubtedly helped to shape the foundation of behavioral research and comparative cognition in ways that will forever benefit this field and inspire young researchers to pursue these important and incredibly fascinating questions for decades to come.

## Cross-References

- Behavioral Flexibility
- Comparative Cognition
- Decision-making
- Edward C. Tolman
- Imitation
- Learning
- Matching-to-sample
- Numerosity
- Same/different Learning
- Timing
- Value Transfer Theory

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response to a threat (Gallup 1974). Some writers used the term “feigning death” or “apparent death” because of its definite survival value as part of their defense mechanism in certain situation.

## Introduction

Currently, there are three hypotheses on how TI potentially increases survival chances of animals (reviewed in Rogers and Simpson 2014). First, fire-bellied toads (*Bombina* spp.) may escape from predator by “death” displays with additional chemical secretion as aposematic warning system. Second, insects such as pygmy grasshopper (Tetrigidae) were seen stretching out its body and causes it is hard to be eaten by predator. Thirdly, arthropods may use TI in enhancing camouflage mechanism by allowing them to fall away from predator as they typically live on vertical surfaces followed by a period of motionless.

## Tongue Bone

► [Hyoid Bone, The](#)

## Tonic Immobility

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## Synonyms

[Apparent death](#); [Animal hypnosis](#); [Feigning death](#); [Playing possum](#); [Thanatosis](#)

## Definition

The term “tonic immobility” (TI) is often defined as a stage of animal to become temporarily immobile upon external stimulus. In physiologist perspective, this behavior referred as a temporary loss of muscle and/or neurological function in

## Advantages

TI in animals can be observed in sharks but believed to be related to mating behavior. Some scholars suggesting that male biting the female would immobilize and enable internal fertilization. Scientists have exploited TI in sharks as an aid when handling or tagging in the field to minimize struggling thus reducing the possibility of injury. Many anglers benefit from TI in removing hook from sharks, although caution should be taken as this phenomenon does not occur in all species of sharks.

## Inducing TI to Animals

Most other vertebrates, namely rabbits, guinea pig, chicken, and birds can also be induced to TI by human without causing any apparent stress to the animal by gently turning them upside down, i.e., dorsal side on a firm-flat surface and stroking a particular area. In sea turtle hatchlings, the response only can be induced by additionally closing their both eyes as a mean of deterring their visual cue and pressing on the plastron to

stabilize the body due to its curved carapace shape (Rusli et al. 2016). However, applying TI in adult sea turtles requires much simpler technique by only stroking their neck.

Animals in this natural state of paralysis can last for a few seconds to over several minutes. In recording TI on any particular animals, scientist usually record the period to the first major movements and termed as TI duration. The TI durations vary considerably interspecies (species-specific behavior) and to a lesser degree with individuals within a species. To date, some descriptive studies on individual variations in TI occurrence and duration have shown that it is affected by individual (e.g., prestimulation status and internal physiology) or environmental factors (e.g., lights and temperatures) (reviewed in Miyatake et al. 2004).

## Conclusion

In terms of animal cognition perspective, TI is known as an unlearned behavior and is believed to be inherited genetically from parents. In addition, the duration of TI can potentially evolve by natural selection process.

## Cross-References

- [Heredity](#)
- [Internal Fertilization](#)
- [Species-Specific Behavior](#)

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## Tool Use

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## Synonyms

[Causal understanding](#); [Instrumental object manipulation](#); [Material culture](#); [Object-assisted problem-solving](#); [Physical cognition](#)

## Introduction

Tools and other utilitarian artifacts pervade humans' lives. They have played such a pivotal role in theories of human evolution that tool use has traditionally been considered a behavioral indicator of complex and flexible cognition. While this early promise has long triggered and maintained keen scientific interest for the study of tool use in nonhuman animals, it may also have revived some naïve anthropomorphic and even anthropocentric biases, particularly when studying species that are evolutionarily close to humans. It is noteworthy that not all cases of tool use necessarily imply high levels of cognitive sophistication, and we should not automatically attribute some of our psychological characteristics to other tool-using species, just because tools are part of our human identity. In fact, tool use is a broad functional category of behaviors that includes a wide range of actions directed to various objects, and whose cognitive substrates may differ substantially between species. Among the species-specific factors underlying the expression of tool use, ecological stimuli, social influences, psychological traits (e.g., cognitive processes and motivational determinants), and anatomical features differentially contribute to engaging in the use of objects as tools.

First, definitions of tool use – following a list of relatively consensual criteria – and description of some of its variants are provided. Then, the main ingredients that allow the expression of



tool use across taxonomic groups, distinguishing between extrinsic factors (e.g., stimuli from the physical and social environments) and intrinsic factors (e.g., psychological processes and anatomical features), are reviewed. Focusing on the proximate causes of tool use (i.e., mainly mechanisms) may help generate further inquiries about its ultimate consequences (i.e., its adaptive nature). Indeed, the challenges associated with longitudinal designs and correlational tests between tool use and individual fitness benefits make it extremely difficult to unequivocally demonstrate the adaptive value of tool use, as measured by increased survival rate and reproductive success.

Following the “design-feature argument,” in which the detailed structure of a given behavior is matched against the requirements of its hypothesized function, one way to circumvent the lack of evidence for the fitness-enhancing value of tool use is to conduct an in-depth structural analysis of this behavior. The heuristic power of the behavioral structure-function interface is reflected in the following statement by Pellis and Pellis (1998): “Therefore, behavioral description informs functional inference, which in turn, influences further description” (p. 115). For instance, kinematic and biomechanical analyses of patterns of grip and hand movement capabilities across different primate species are indicative of evolutionary scenarios about stone tool technology in ancestral hominins. By examining the role of ecological factors, social influences, cognitive processes, and motivational determinants in the development, expression, and evolution of tool use, we aim to show that this behavior, characterized by a patchy phylogenetic distribution, is not necessarily synonymous with highly complex intelligence and can be explained outside an anthropocentric framework.

## Defining Tool Use

About 60 years after Jane Goodall’s pioneering observations of a wild chimpanzee fashioning and using a stick to extract termites in Gombe, Tanzania, the debate around the appropriate characterization of the term “tool use” is still

open. Because the definitions of tool use range from a focus on the *goal* of the action (i.e., the functional consequences of the tool-assisted behavior patterns being performed), to the *means* of the action (i.e., the structural details of these behaviors), to the condition of the *object* employed, there is no universal consensus among researchers about what constitutes tool use and what constitutes (object-assisted) problem-solving. These differences in perspective stem from conceptually and methodologically divergent approaches across academic disciplines (e.g., ethology, psychology, and anthropology), and this situation is often referred to as the “tool use paradox.”

Arguably, one of the most widely adopted definitions of tool use was provided by Shumaker et al. (2011). With a focus on the *goal* of the action, tool use is defined as “the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool” (Shumaker et al. 2011, p. 5). With a focus on different functional features of a tool, alternative definitions consider tool use a form of problem-solving that includes the instrumental use of an object (e.g., St Amant and Horton 2008). For example, according to Shumaker et al. (2011), a weighting scale cannot be categorized as a tool because this object does not alter the form, the position, or the condition of another object or the user. However, under St. Amant and Horton’s (St Amant and Horton 2008) functional definition, using a weighting scale to detect an object’s weight is a way to mediate the flow of information, and as such, it is a form of tool use.

Another criterion for tool use focuses on the condition of the utilized *object*. The same object may be either freely manipulable or attached to a substrate, which potentially affects its action-mediated use. For many authors, a Californian sea otter pounding a stone onto a shellfish to break it open is an example of tool use, whereas a wrasse pounding a shellfish onto a rock to crack

it open is not. Clearly, those behavior patterns (i.e., the pounding actions) are structurally similar, but because the rock used by the wrasse is attached to a substrate (i.e., the ocean floor), they are put into separate functional categories by Shumaker et al. (2011). In line with this argument, “true tool-using” avian species (following the definition by Shumaker et al. 2011; e.g., an Egyptian vulture breaking open an egg by dropping a stone on it) have larger residual brain sizes (regressed against body weight) than bird species using attached objects that do not qualify as tools (e.g., a sea gull dropping an egg on a seashore boulder; Lefebvre et al. 2002).

However, some researchers have disagreed about how structurally similar object-assisted actions may be characterized as being functionally so different. By focusing on the biomechanics of tool use, their approach proposes an embodied theory that shifts the focus of study from the object (i.e., the tool) or the goal to the *action* (i.e., “to tool” as a verb; Frigaszy and Mangalam 2018). “Tooling is deliberately producing a mechanical effect upon a target object/surface by first grasping an object, thus transforming the body into the body-plus-object system, and then using the body-plus-object system to manage (at least one) spatial relation(s) between a grasped object and a target object/surface, creating a mechanical interface between the two” (Frigaszy and Mangalam 2018, p. 194). Behaviors that have been historically recognized as tool use, such as a chimpanzee climbing on top of a pile of wooden boxes to reach for a hanging banana, do not qualify as tooling, because the tool has to be grasped (with the hand or the mouth). In a slightly different view, although partly supporting this action-based approach, some researchers argue that this embodied theory of tool use downplays the role of cognitive processes underlying these object-assisted actions. They claim that tool use is not only about manipulating an object to achieve a goal but also about understanding the action-relevant physical properties of this object in the context of achieving this goal (i.e., embodied cognition; Osiurak et al. 2010). In fact, human patients with a left brain-damaged condition that results in an impairment

of coordinated movements associated with tool use attempt to perform daily actions using inappropriate tools or display inappropriate actions with everyday tools (e.g., trying to cut a tomato with a comb or rubbing a hammer on a nail instead of pounding). Consistent with our initial objective to dissociate ourselves from the anthropocentric views that have pervaded tool use research in the past decades, we adhere to the action-based approach proposed by Frigaszy and Mangalam (2018), as this may further our understanding of the causal mechanisms underlying the expression of tool use within and across species.

## Different Forms of Tool Use

Even though the behavioral specializations broadly acknowledged as tool use are sporadic in their phylogenetic distribution and relatively rare, it is noteworthy that they are expressed by evolutionarily distant species. However, the systematic comparison of tool use propensities across species often requires the distinction between *stereotyped* and *flexible* tool use. Stereotyped tool use entails limited to no inter-individual variation in the form or frequency of actions directed to similar objects, whereas flexible tool use implies the use of different tools, applied to different contexts, to achieve different goals, with a dissociation of mean-end between action and purpose (Boesch 2013; Hunt et al. 2013).

Stereotyped tool use has been typically associated with invertebrates and fish, because of the relatively low cognitive abilities it requires. However, birds and mammals can also use tools stereotypically (e.g., anting in Passeriformes, a behavior that consists in whipping insects onto one’s feathers; stone-throwing behavior in Egyptian vultures to break into eggs). Yet, considering tool use in invertebrates as exclusively stereotyped would be an oversimplification. Octopuses have one of the largest and most complex nervous systems of all invertebrates, and their brain-body weight ratio exceeds that of most fishes and reptiles. They use tools in many ways, from defensive water jets for prey capture to object-sheltering as an anti-predatory strategy,

to object-handling serving the purpose of moving away unwanted items, and those examples may be characterized as flexible tool use. Stereotyped tool use is performed by all the members of a given species and sometimes by several species within a given genus, with extremely low levels of behavioral variation in the form and frequency across individuals. For instance, the hunting strategy of pit-building antlions (i.e., throwing sand at their prey once it fell inside a pit to prevent it from escaping) resembles the prey-burying of *Sphecinae* digger wasps, a closely related genus, which compress sediments on top of their nest after putting prey inside to feed their offspring. A possible explanation for this consistency is that stereotyped tool use develops from preexisting behaviors (e.g., flicking sand randomly to maintain the pits in antlions, placing objects to cache the entrance in digger wasps) and are acquired (almost) asocially, and without learning (Hunt et al. 2013). Lastly, stereotyped tool use is generally context-specific (i.e., the same object or action is not employed to attain different goals). For instance, Egyptian vultures do not place stones to hide food from competitors or do not throw them at predators to drive them away.

Instances of flexible tool use have been mostly reported in animal taxa displaying relatively high cognitive abilities, such as corvids and primates. Although flexible tool use may originate from preexisting schemata (e.g., caching behavior in New Caledonian crows closely resembles the developmentally acquired combination of objects that precedes tool use), a considerable amount of time and practice is spent to learn how to successfully use tools, via individual and observational learning, which may partly explain the high degree of inter-individual variation in the expression of flexible tool use (Hunt et al. 2013). In juvenile capuchin monkeys, the full-blown and successful form of stone-assisted nut-cracking behavior emerges after more than 2 years of unsuccessfully percussing nuts and nutshells against substrates, and upon observational learning from proficient nut-cracking individuals (de Resende et al. 2008). Termite-fishing behavior in chimpanzees share similar acquisition patterns, and individuals successfully master this complex

tool-aided foraging technique after 5 years of practice (Lonsdorf 2006).

The strong positive correlation found between relative brain size and the ability to use different objects instrumentally, in various contexts, and to reach different goals support the hypothesis that flexible tool use requires advanced cognitive skills (Reader and Laland 2002). Species that can flexibly manipulate different objects to solve functionally similar or different problems tend to outperform closely-related non-tool-using species in cognitive tasks testing for physical cognition, casual reasoning, working memory, and self-control. When comparing pit-assisted hunting behavior in antlions, sponge-assisted rostrum-covering in dolphins, twig-assisted termite-extraction in chimpanzees, stone chopper-assisted meat-processing technique in Oldowan hominins, and spear-making/using technology in prehistoric humans, there was an increase across species in the ability to hold information for later usage (i.e., working memory), expressed by an increase in problem-solution distances (Haidle 2010). When using tools, humans can understand the cause-and-effect relationships between objects (i.e., causal material reasoning); other taxonomic groups capable of performing object-assisted instrumental actions in diverse contexts may be relying on similar cognitive processes.

Intriguingly, some captive members of non-typically tool-using species are able to use objects as tools and possess cognitive skills similar to closely related species with a propensity for tool use in the wild. One way to experimentally test for the mental ability to represent the physical properties of objects (i.e., physical reasoning) is to use the two-trap tube task, a revised version of the tube-trap task. In its original version, the tube-trap task consists in a transparent tube, with food placed in the center and an underside trap into which the food will fall if moved into it. To access the reward, an individual has to maneuver an already inserted stick-tool to extract the food out of the tube while avoiding the trap. The two-trap tube task has an additional nonfunctional trap in which food can pass over a solid base, and the subject has to detect the correct side to avoid the functional trap and retrieve the food reward.

When tested on the two-trap tube task, New Caledonian crows (i.e., a typical tool-using in the wild) successfully used a stick-tool to extract the food reward; interestingly, six out of seven captive rooks (i.e., members of the corvid family that do not appear to use tools in the wild) performed similarly (Emery and Clayton 2009). Tool use may be an evolutionary by-product of other adaptive cognitive abilities, rather than an originally adaptive mental trait. What is perhaps even more surprising is that highly proficient tool users in the wild, like chimpanzees, fail popular tests for causal reasoning, like the trap tube task. Chimpanzees learn to avoid the trap after around 80–100 trials, but do not appear to transfer knowledge between different trap problems (Martin-Ordas et al. 2008). Indeed, when the trap is inverted (i.e., the trap tube task is ineffective), chimpanzees keep adopting the previously learned strategy. Similar results have been found in humans, and the effectiveness of the trap tasks for testing for causal understanding has been questioned. In the end, researchers are left with an outstanding question: Is causal reasoning necessary to use objects as tools (and if so, to what extent)? The aforementioned results should also make us cautious when considering the assumption that tool use in humans and non-human animals has a common evolutionary origin and followed similar cognitive pathways of expression.

A necessary ingredient for the expression of flexible tool use is the *propensity* to manipulate objects, which is not only a reflection of anatomical features but emerges from a combination of psychological processes determined by extrinsic and intrinsic factors (Call 2013). Indeed, capuchin monkeys and squirrel monkeys have similar hands, but they markedly differ in their manipulative propensities and their abilities to use tools. Unfortunately, there is no clear consensus on the definition of the term “manipulative propensity,” and systematic cross-species comparisons are made difficult by the use of different operational definitions. Manipulative propensity has been measured in terms of *amount* of object manipulation (i.e., frequency or duration), *complexity* of object manipulation (e.g., number

of object combinations), or *variety* in the types of object-directed actions. As such, a given species’ manipulative propensity may affect its ability to efficiently use tools across different contexts (i.e., flexibly). In the next sections, different extrinsic and intrinsic stimuli influencing the propensity and ability to use objects as tools are reviewed.

## Extrinsic Factors Affecting the Propensity to Manipulate Objects Instrumentally

### Ecological Factors

Food availability is one of the main drives in the propensity to manipulate objects, and thus it is not surprising that most instances of tool use occur within the behavioral domain of foraging activities (Shumaker et al. 2011). According to the “ecological necessity” hypothesis (Fox et al. 1999), tool use may have emerged as a need to exploit novel and hard-to-process food sources due to resource scarcity. Food scarcity may be due to ecological factors (e.g., seasonality), social factors (e.g., dominant individuals having priority of access to main food resources), and intrinsic factors (e.g., higher physiological demand during pregnancy and lactation). The diet of chimpanzees living at Bossou, Guinea, mainly consists of fruit pulp, but during periods of fruit scarcity, these animals rely on oil-palm nuts and pits, which are processed by two types of tool use: stone-aided nut-cracking and pestle-pounding behaviors (Yamakoshi 1998). The rates of tool use increase from 10% to over 30% during fruit scarcity, which indicates that tool-assisted extractive foraging is a necessary behavioural strategy for this population.

According to the “ecological opportunity” hypothesis, individuals should have the opportunity to use tools (e.g., presence of instrumentally-relevant objects or food sources that can be exploited by tool use; Fox et al. 1999). The population of orangutans living at Suaq Balimbing Research Station, in Sumatra, has significantly higher tool-assisted insect foraging rates, compared to other populations of orangutans living at different sites (Fox et al. 2004). The abundance

of insects at Suaq Balimbing Research Station is higher compared to other locations, which supports the idea that propitious circumstances may have driven tool invention in this population.

Considering the previous two hypotheses, the need and opportunity to access embedded and rich food sources during seasonal periods of food scarcity in species with omnivorous diets and extractive foraging strategies may have selected for the emergence and refinement of specific object-assisted food-procurement behavior patterns, including tool use (see also: “technological intelligence” hypothesis; Parker and Gibson 1977). In capuchin monkeys, extractive foraging strategies follow seasonal patterns, with the tool-aided exploitation of embedded invertebrates concentrated during periods of food scarcity. However, the “technological intelligence” hypothesis has been challenged mainly because tool use is rare and its phylogenetic distribution is patchy among extractive foraging and generalist primate species (i.e., only a few populations of capuchins, cercopithecines, and great apes routinely use objects as tools in the wild). Similarly, alternative ecological and functional hypotheses only partly explain the occurrence of tool use across evolutionarily related species. Thus, although those hypotheses remain generally valid, ecological factors and the evolution of complex extractive foraging skills alone cannot explain the emergence and spread of tool use behavior in the wild.

### Social Factors

The social influences an individual is exposed to may also drive the expression of the instrumental manipulation of objects as tools. Several food-provisioned groups of Japanese macaques have been reported to customarily engage in a form of culturally maintained, playful, and seemingly functionless stone manipulation often referred to as “stone handling.” However, it has been argued that the relatively relaxed dominance style of the captive Takahama group of Japanese macaques housed at the Kyoto University Primate Research Institute might have facilitated the innovation and diffusion of the only (documented) spontaneous and functional use of stone tools in this

primate species, possibly derived from the daily practice of stone handling: unaimed stone-throwing behavior mainly expressed during periods of high disturbance and serving the function of amplifying the performer’s agonistic display (Leca et al. 2008). Such differential social environments may alter not only the context of expression but also the significance of other tool use variants (Boesch 2003). In chimpanzees, the leaf-clipping behavior pattern is a tool-assisted communication signal that consists for an individual in repeatedly nipping leaf blades with its incisors and lips without eating any part of the leaf. This sound-producing display is culturally mediated and it acquired different social meanings that are population-specific: (1) in Mahale, Tanzania, it is a sociosexual display that serves the function of attracting potential mates; (2) whereas in Bossou, Guinea, it is used to initiate social play interactions; and (3) in Taï, Ivory Coast, it is an important mediator in the context of within-group male-male competition.

According to the “opportunity for social learning” hypothesis, higher levels of within-population social tolerance lead to greater manipulative propensities, because behavioral innovations, like tool use, can spread and be maintained across individuals (van Schaik et al. 2003). Social tolerance allows potential learners to be exposed to the mere presence of skilled group members (i.e., social enhancement), to the presence of tool artifacts previously employed by successful tool users (i.e., stimulus enhancement), and in some cases to demonstrators of the tool-assisted actions (e.g., emulation, imitation, and possibly teaching). The comparative analysis of behavioral data from captive rhesus, long-tailed, and Tonkean macaques showed a significant positive correlation between species-specific levels of social tolerance and the time spent manipulating novel objects, including tool use (Thierry et al. 1994). Similarly, the Goualougo Triangle chimpanzee population, in the Republic of Congo, characterized by a relatively complex tool-use repertoire, including instances of coaction (i.e., when an individual allows another to touch either the hand or part of the tool during use), exhibits levels of social tolerance and spatial



proximity that are higher than other populations of chimpanzees (Sanz and Morgan 2013). Relaxed social environments enhance opportunities for behavioral coordination among group members, visual feedback from tool-using conspecifics, and access to the physical traces left at tool-using sites by previous tool users. Such favorable circumstances are conducive to direct and indirect social learning of tool use. In an experimental study aiming to explore the social processes underlying the acquisition of novel object-directed actions in captive capuchin monkeys, seven out of nine subjects preferentially touched the area of the apparatus previously manipulated by their group members (Matthews et al. 2010). Likewise, during an object-choice task, New Caledonian crows preferentially selected the tools previously used by a conspecific demonstrator, compared to other novel objects (Kenward et al. 2006). However, extrinsic factors alone do not suffice to explain the phylogenetic distribution of tool use behavior and a given species' propensity to manipulate objects in either playful or instrumental ways. Intrinsic factors, such as motivational processes, morphological adaptations, and individual history, play a vital role in a subject's proclivity for object manipulation and tool use.

### **Intrinsic Factors Affecting the Propensity and the Ability to Manipulate Objects**

#### **Intrinsic Motivation and the Role of Object Play in Tool Use**

Broad structural similarities across various object-oriented activities (i.e., exploratory, playful, and instrumental) have been found in an extensive comparison of 74 species of nonhuman primates (Torigoe 1985). More specifically, the overall execution by adult long-tailed macaques of a probably functional activity (i.e., pounding an edible object – a hard-shelled nut – on a hard substrate) and a seemingly nonfunctional one (i.e., pounding a nonedible object – a stone – on a hard substrate) has very similar basic sequential movement components (i.e., upswing, adjustment, and strike; Pellis et al. 2019). Likewise,

the fundamental motor building blocks of stone tool-assisted nut-cracking behavior in chimpanzees include actions that are typically observed in explorative and playful object manipulation in this species. Moreover, a number of experimental studies in nonhuman primates and children found positive correlations between the frequency of noninstrumental (either exploratory or playful) object manipulation and measures of success in subsequent problem-solving tasks involving the use of these objects as tools (e.g., shorter latency to succeed for the subjects with previous object-handling experience). For example, the ability to join sticks together to make and use raking tools in order to access out-of-reach food was improved by the prior playful manipulation of sticks in captive chimpanzees (Birch 1945).

The spontaneous manipulation of objects in a nonfunctional way (i.e., play and exploration) may contribute to an individual's propensity to use these objects in functional contexts. In a free-ranging and coastal population of Burmese long-tailed macaques in Thailand that routinely use stone tools to crack open shellfish, developmental data indicate the playful manipulation of lithic material by juvenile monkeys before learning to use stones instrumentally (Tan 2017). In this species, percussive stone-tool use may be facilitated by exploratory and non-instrumental stone-directed actions gradually incorporated into foraging activity. Within the *Macaca* genus, a cluster of macaque species belonging to the *Fascicularis* taxon have a natural propensity to manipulate stones in a playful context; this intrinsic motivation may promote the integration of stones in various behavioral domains, including their functional use in extractive foraging strategies – even though this hypothesis remains to be tested. In an experimental study addressing the role of motivational processes (and previous experience) in tool use performance in great apes, extrinsic motivation (i.e., food reward as an external foraging trigger) had a negative/inhibitory effect on tool-assisted problem-solving success, whereas intrinsic motivation (i.e., the internal neophilic drive to explore a novel, even empty, apparatus) shortened the latency to solve the tool-use task (Ebel and Call 2018). This result

is consistent with studies showing that (1) high extrinsic motivation (i.e., higher interest in, and attraction to, a visible food reward during a test) decreases problem-solving performance, and (2) individuals in an atypical hunger state (e.g., due to food deprivation) performed more poorly in a food-rewarded tool task than individuals in a typical hunger state.

Play behavior, including object play, is also intrinsically rewarding, which may contribute to the maintenance of object-directed activities, particularly during the development. First, the frequency of object play is age-dependent: juveniles spend significantly more time playing with objects than adults. Second, the acquisition of flexible tool use is gradual and proceeds through several developmental stages; in long-lived animals, such as primates, it takes years for an individual to master specific and complex tool-use skills (de Resende et al. 2008; Lonsdorf 2006). During such a lengthy acquisition period, object-directed play may serve the function of maintaining high levels of intrinsic motivation (e.g., sustained interest in, and attention to, objects) in unskilled youngsters, before they can be externally rewarded as proficient tool users. Among great apes, who need several years of practice before mastering tool use (Lonsdorf 2006), chimpanzees and humans are the most frequent and versatile tool using species; interestingly, juvenile chimpanzees and children also engage in significantly more object than immature bonobos, which belong to their most closely related species, and a species that is not proficient in tool use (Koops et al. 2015). However, the propensity to manipulate objects is constrained by the physical *ability* to do it, which depends on the individual's anatomy.

### The Role of Anatomical Features in Tool Use Structure

While psychological processes affect the propensity to manipulate objects, anatomical features constrain object-directed actions. Not surprisingly, the most complex and various tool use repertoires are found in primates, and more specifically in humans, followed by great apes, whose hands possess the greatest potential for movement *complexity* and *dexterity* (i.e., grip

and grasping postures; Shumaker et al. 2011). Manipulative complexity has been structurally defined in various ways, including manipulation pattern diversity, object-substrate combination, and bimanual asymmetric coordination. In a comparative study across 36 nonhuman primate species, it was measured by the cumulative ranking of occurrence of different categories of object manipulation, based on unimanual/bimanual actions, synchronous/asynchronous use of hands and fingers, and whether the same/different objects were handled (Heldstab et al. 2016). Species displaying more complex types of object manipulation (e.g., tool use) were also able to engage in lower levels of manipulation categories (e.g., grasping and holding). However, hands are not necessary for efficient tool use; morphological characteristics of the beak (e.g., depth, shape) play a major role in the manipulative complexity of tool-using corvids (e.g., New Caledonian crows, Goffin's cockatoos, keas).

Dexterity is the ability to solve a motor task precisely, quickly, and effectively (Bernstein 1996). The same action can be performed more or less dexterously, and an individual with higher manipulative complexity may still act with little dexterity, (e.g., a naïve individual learning a new handling skill). Dexterity requires sensorimotor coordination, which needs to be greater when the action is more complex (i.e., there is a higher number of degrees of freedom to control the moving parts of the body). Dexterity in tool use necessitates a high spatiotemporal organization of the movements performed by the body-plus-tool system (e.g., hand-plus-tool in primates, beak-plus-tool – occasionally coordinated with the foot – in corvids). However, an individual's relationship with a tool does not only result from the propensity and the ability to manipulate this object; it is also affected by the functional properties of this object. Through a variety of object-directed activities, the performer *experiences* the tool.

### The Role of Experiential Learning in the Acquisition of Tool Use

Inter-individual variation in the expression of object-directed activities, including flexible tool use, exists across most taxonomic groups

(Kappeler and Kraus 2010), and in the extreme case, tool-use innovations have been documented only in one or few individuals within a species. In capuchin monkeys, individuals vary considerably in their tool use rate and success in experimental tasks, regardless of their age and sex classes (Fragaszy et al. 2004). In chimpanzees, tool-assisted foraging techniques, such as ant-dipping and termite-fishing, are acquired by individuals at different ages, and some individuals never master them (Humble et al. 2009). In the Suidae family, tool use has only been observed in few individuals of a captive population of Visayan warty pigs, and the use of sticks and barks as part of nest-building sequences was mainly expressed by lower-ranking group members including some adult females (Root-Bernstein et al. 2019). Exposure to, and *experiential learning* with, objects play an important role in the emergence of inter-individual variation in tool use.

Tool use acquisition is a continual developmental process in which an individual's understanding of the spatiotemporal relations between objects is mediated by exploratory interactions with the environment, through affordance learning (Lockman 2000). Affordances arise from the relation between a specific individual and a specific environment, with respect to achieving goals (Gibson 1979). For example, a stone affords throwing to an Egyptian vulture, pounding to a sea otter, and knapping to an Oldowan ancestral human. Likewise, object properties may be perceived differently by members of the same species. According to the "affordance learning" hypothesis, the perception of an object's physical properties determines its potential for manipulation, affording the means for goal-oriented behaviors (Lockman 2000). Watching a toddler banging an object on the ground is likely to be interpreted as playful practice for the future functional use of this object as a tool. Most flexible forms of tool use are acquired through long periods of time, during which the learner tinkers with the tool and the possibly functional consequences of its tool-mediated actions. During this critical phase of trial-and-error learning, individuals may perform irrelevant or incorrect actions, express an incomplete or misordered sequence of actions, use inappropriate tools or substrates, and apply

their actions towards the wrong goals. Tool use acquisition proceeds through a developmental process of gradual elimination of unsuccessful attempts and honing of successful behavioral strategies.

From the perspective of "affordance learning," it might not be highly relevant to distinguish between an individual attempting to use an object as a tool and an individual engaging in object play. The "affordance learning" hypothesis stems from an ecological approach to the acquisition of tool use (Gibson 1988), which is better explained by a progressive specificity in perceiving and acting on the material world than a sudden insight into the instrumental consequences of object-directed actions. Developmental data indicate that, as children acquire further haptic experience (i.e., tactile feedback about the physical properties of objects), they become more selective in their object exploration. At 6 months (i.e., when functionally directed object manipulation has not emerged yet), infants engage in discriminate exploration when interacting with different objects, by modifying their actions depending on the object properties; for instance, they wave a bell with a clapper more often and more intensely than a bell without a clapper, or they squeeze more a spongy toy than a hard one (Palmer 1989). In the Sonso chimpanzee community in Uganda, where the use of sticks as tools has not been reported, growing individuals show decreasing interest in, and manipulation of, sticks, whereas they preferentially explore other objects that are later used as tools (Lamon et al. 2018). Likewise, during the acquisition of stone tool-assisted nut-cracking behavior, capuchin monkeys gradually learn to select and match the appropriate stones with the appropriate food targets based on the physical properties of these objects (e.g., size, weight, hardness, and resistance) as well as the geographical distance between them (Spagnoletti et al. 2011).

Exposure to, and experience with, objects in a noninstrumental context not only contribute to discovering information about the properties of these objects but also help refine the executive control when handling them in a functional manner, through practice and acquisition of manipulative dexterity (Lockman 2000).

By repeatedly performing similar object-directed actions in an exploratory context, individuals acquire the sensorimotor coordination needed to become skilled tool users. As human infants develop, their object-mediated banging actions (i.e., the repetitive striking of a surface through up-down motion of the arm while grasping an object) become less structurally variable, and their movements gradually acquire the biomechanical characteristics of proficient tool-assisted percussive actions (e.g., hammering; Kahrs et al. 2012). Even though juvenile chimpanzees are capable of performing some of the behavioral building blocks of the stone tool-assisted nut-cracking activity, they will not master the complete and successful behavioral sequence until they reach adolescence. In rhesus macaques, repetitive tool-using actions gradually create novel neural projections in the brain areas that process and integrate information about the visual and somatosensory status of the training body-plus-tool system (i.e., visual, frontal, and parietal cortex; Hihara et al. 2006).

## Conclusions

Sophisticated cognitive abilities are not a necessary and sufficient requirement for the expression of all the tool use variants reported in this review. Therefore, an ideal definition of tool use should be devoid of any anthropocentric bias, such as the necessity for the performer to understand how or why a tool works. There is no doubt that tool use independently evolved in several taxonomic groups, as structurally diverse, functionally distinct, and phylogenetically rare behavioral specializations. However, the scarce and patchy distribution of tool use within the animal kingdom cannot be explained by claiming that this behavior is a proxy for intelligence. The expression of tool-mediated actions is the combined result of strategic behavioral responses to various ecological conditions (e.g., necessity, opportunity), sociodemographic variables (e.g., group composition and cohesion, interindividual tolerance), biological traits (e.g., morphological features), and psychological mechanisms (e.g., motivational

processes, sensorimotor coordination, experiential learning). Yet, the relative contribution of each of these extrinsic and intrinsic factors to the emergence of tool use in a given species remains to be determined. Arguably, one of the most promising and integrative theoretical approaches to understanding the proximate causes of tool use is the affordance learning hypothesis. More data, beyond the primate taxon, are needed to test it.

## Cross-References

- [Behavioral Flexibility](#)
- [Behavioral Variation](#)
- [Instrumental Learning](#)
- [Motivation](#)
- [Nut-Cracking](#)
- [Play Behavior](#)
- [Stone Tools](#)
- [Technical Intelligence Hypothesis](#)

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## Top-Down Processing

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## Synonyms

Attention; Cognitive processing; Conceptual-driven; Contextual-driven; Dorsal stream; Endogenous attention; Hypothesis-driven; Illusion; Imagination; Indirect perception; Information processing; Mental image; Perception; Representation; Ventral stream

The little prince was disappointed when grown-ups misperceived his first drawing as a hat where it was originally a shadowed picture of a boa constrictor digesting an elephant (Saint-Exupery, 1943). Given the fact that his picture is deceptive for the way grown-ups' perceptual systems work, the little prince should not blame them for their fallacious perception. As the picture is ambiguous, not providing sufficient information for a grown-up to perceive, their cognitions interfere in their perception. This phenomenon is called top-down processing.

Top-down processing together with bottom-up processing underlies imagination, anticipation, prediction, memory, and learning, yet, predominantly operates in perception and regulates attention. This entry will consider top-down processing as a matter of perception and, in the last section, delve into the neural basis of top-down processing with a focus on attention. Bottom-up processing, as a counterpart of top-down processing, will be explained briefly for the sake of better understanding of top-down processing. Yet, because it is out of scope, details of bottom-up processing will not be discussed in this entry.

Top-down is one of two modes of information processing while the other one is bottom-up. Information processing has a hierarchical organization comprising two levels in general: lower-level and higher-level. Top-down and bottom-up refer to the direction of the information flow between these levels. Lower-level information is usually processed by structures at the base of the brain. Lower-level processing deals with fine details of the information, received from sensory receptors, in every aspect. For instance, in the case of an object perception (to make it easy to determine that it is an apple, for example), information processing at the lower-level tackles the following kinds of questions: *What is the shape of the object? What is the size of the object? What is the color of the object? How transparent or opaque is the object? What is the texture of the object? How soft or hard is the object? How flexible or rigid is the object? How is the smell of the object? How is the taste of the object?* Higher-level information, on the other hand, is

processed at the top of the brain by large-scale neural networks rather than specific regions. Owing to such connected neural structure, cognitive tasks and integration of different properties such as shape, size, and color are possible. Thus, as a result of higher-level processing, an individual is able to tell that a green, round-shaped, in holdable size, edible object is an apple. Reconsidering the situation of object perception, the following questions would be reasonable for higher-level: *What is the object? What is its meaning to me (actor/perceiver)? What could/should I do with it?* Let us draw an analogy here to make the higher- and lower-level distinction more clear: Imagining a puzzle, lower-level representations of the brain process to decipher every single piece of the puzzle whereas higher-level representations put all the pieces together and name the completed picture in the puzzle and interpret the meaning of it. Keeping this analogy in mind, the top-down and bottom-up processes are now straightforward.

Bottom-up processing is also known as data-driven. It takes lower-level representations as input and processes and transmits them toward the higher-level as a feed-forward mechanism. It is like expounding every single piece of the puzzle without having any clue about what that piece could belong to, and solving the puzzle by lumping them together. Not cognition but only those defined pieces of the puzzle get involved in the puzzle-solving process. The brain knows what it is only after the puzzle is completed. Briefly, the bottom-up processing does not require intervention of third parties such as memories, prior knowledge, or mental image. What is perceived purely and directly relies on sensory information.

Unlike bottom-up processing, in top-down processing, cognition interferes along with sensory information. Cognition, in higher-level, enables the brain to make an inference based on various valances when the sensory information is insufficient for perception. The inference, thereafter, flows down as a feedback mechanism to dominate and lead the information processing. The analogy drawn above between a puzzle and bottom-up processing requires modification to suit top-down processing instead: Some pieces of the puzzle could be

lost, and/or though available, some may not be precise enough to proceed. Luckily in this module, some completed puzzle pictures are available on top of the box; counting them in the puzzle-solving process helps with filling out the gaps in the puzzle. To do so, first, in the light of the lucid pieces, the actor should guess which picture on the box might be the puzzle. Then, his/her inference will lead him/her in the rest of the puzzle-solving process. Another analogy for the top-down phenomenon: An artist who sketches a dead grandmother's portrait based on the grandchild's description would know what s/he is sketching in advance; besides, s/he would assume that the grandchild may resemble the grandmother. Her/his knowledge and prediction would administer the details of the portrait. In a nutshell, in the top-down processing, what is perceived does not merely rely on sensory information; it is also influenced by beliefs, expectations, intentions, memories, and past experiences.

Conventional theory of perception is built upon a sensation-based approach which is predicated on representational realism of Locke (Lombardo 1987) and Plato (Dotov et al. 2012). According to a sensation-based approach, perception is indirect and top-down. In a sense, what an animal perceives is not the object itself, but its reflection in mind that is constructed upon sensory stimuli in the light of higher cognitive processes (Gençer 2018; Gibson 1950, 1966, 1979). Gibson denied the sensation-based approach of conventional theory. He argued that perception is, indeed, information based. In other words, perception is an active process that requires information gathering continuously via perceptual actions at that moment directly from the object and its environment (Gibson 1979). Such unlimited information is always available there for the perceiver, and it is rich enough for perception, so it does not need to be stored in memory. That means, perception is direct and, by the same token, recruits bottom-up processing (Gibson 1979). Gibson's direct perception, and so the bottom-up processing works impeccably in such cases as a toddler's learning the depth or the third dimension of objects. Yet, his approach fell short explaining perception in some situations such as illusions. Gregory suggests that studying illusion is the practical way of

understanding perception in certain aspects (Gregory 1997, 1998, 2005). The hollow mask, duck-rabbit, Necker cube, and Boring's object-ambiguous figure namely "old wife or young mistress" are only a few well-known illusions studied in perception to demonstrate the failings of bottom-up processing (Gregory 1997, 2005).

Gregory thought of bottom-up processing as if it were a photograph and drew parallels between top-down processing and a painting (Gregory 2005). Gregory, here, defines photographs as innocent and unbiased. The innocence cannot be saved anymore once the cognition gets involved in the information processing in the painter's brain; then the inclination would be found toward painters' imagination, memories, and beliefs. The hollow mask illusion (Gregory 1997, 2005) shows how cognition, and in this case visual knowledge from past experiences, dramatically affects the vision. Although stimuli through bottom-up processing reveal that the surface of the mask is concave, we still perceive it as convex because our past experiences dictate the impossibility of a concave face. Top-down processing is so strong that, even if we have explicit knowledge regarding the absurd form of the mask, our perception persists so we cannot avoid succumbing to the illusion (Gregory 1997, 2005). Note that the top-down effect is weaker when the mask is upside down; since it is an unusual position for a face, our brains consider it as if it was a regular object rather than a face. Gregory (2005) also pointed out how we live happily albeit the confusion with respect to relative movements of the sun and the earth. If we follow our gut feeling rather than science, we bet that the sun turns around the earth without any hesitation. Although studies in physics and astronomy prove that the earth turns around the sun, our perceptual feeling contradicts the reality by virtue of our implicit knowledge.

Bottom-up processing is more likely to dominate the perception of primates and human children. However, top-down processing becomes dominant in the perception of human adults owing to higher-order cognitive development. That is why the little prince should not be vexed with grown-ups. Because his drawing is not as clear as crystal, grown-ups perceive it as a hat,

which is more likely to be experienced compared to a boa constrictor digesting an elephant. Unlike the little prince's perception, adults' perceptions are restricted by their past experiences, memories, and knowledge.

In top-down processing, the object's reality needs to be inferred from sampled attributes such as color, orientation, position, and size as they are in transmission through assorted channels (Gregory 2005). Three major modalities could be considered in the account to do so: conceptual-driven, contextual-driven, and hypothesis-driven (Gregory 1980, 2005; Rauss and Pourtois 2013).

The lexical meaning of "concept" is to envisage a notion or an object with respect to all its characteristics and/or particulars. Thus, all types of specific knowledge about the object are essential in conceptually driven modality of the top-down processing. Recall how particular knowledge about a face dominated the perception in the hollow mask illusion. Perceivers' imagination, intuition, moral, memory, and/or experience regarding the object interfere with perceptual processing in this modality. Then, the crucial question comes into mind: How does the perceiver notice if it is solely a memory or imagination from the past or it is a present-time reality? Qualia is Gregory's answer to the foregoing question (Gregory 1997, 1998). There is a long debate on and various theories that are proposed based on the notion of "qualia," which is beyond the scope of this entry. Qualia is roughly defined as the subjective attributes of experiences, also known as "raw feels" that designate immediate and introspective feelings. In such a manner, qualia arouse consciousness. As Gregory (1998) suggests, close your eyes and imagine the Niagara Falls. It does not matter how strongly you fantasize, it would never be as vivid as if you were physically present at Niagara Falls in the real world at the moment. Qualia, by the fulfilled vividness, enable us to distinguish the present-time reality from past phenomenologies.

In the preceding modality, the object, on its own, was crowned leading character. In the contextual-driven modality, however, it has to share the throne with its environment/background. In real life, every single object inevitably

exists in coherence with its environment (Gibson 1979). Moreover, its significance and function are embodied in that environment. In such a sense, the surrounding of the objects provides strong hints regarding their identity. For instance, a man who is wearing a white coat and holding a sharpened instrument could be anybody while standing alone in a picture. If this man is instead placed within the background of a kitchen and is standing behind a counter with some ingredients such as vegetables and a cutting board in front of him, he is likely to be perceived as a cook. Alternatively, if the man is behind a counter again with a cutting board in front of him but now there are only stacks of meat on the cutting board and he is in a shop rather than a kitchen, he would likely be perceived as a butcher. If instead, the man is interacting with other people who look like himself, and they surround a person who is lying on an operating table in an operating room at a hospital, no more evidence is needed to determine that he is a medical doctor, more specifically, a surgeon. Furthermore, if the person who lies down on the operating table is replaced with an animal, then it is easily inferred that he is a vet. Long story short, a perceiver's knowledge and experience regarding object-environment mutuality interfere in the perceptual process, and the top-down processing appreciates the available contextual cues as it is making inference from unsensed data. A Figure such as "I3" could be anything such as a weird symbol, a letter, a number, etc. when they are shown out of context. The sentence below demonstrates how dramatically altered reading and understanding of the very same symbol can be based on the changing context.

"The Symphony No. 7 is composed by **I3EETHOVEN** and premiered with **I3EETHOVEN** himself in Vienna on 8 December 1813 at a charity concert for soldiers wounded in the Battle of Hanau."

Third, the hypothesis-driven modality is proposed by Gregory (1980, 2005) and considered in the account of action or event perception, beyond an object. Despite the tangential differences between perception and scientific hypothesis, Gregory (1980) calls attention to their overlapping similarities, inasmuch as he expressed their "*significant*

*conceptual identities*." By marking the resemblance, he advocated that hypothesizing procedure in science would guide understanding epistemology of perception. With this confidence, Gregory analyzed the perception in three phases: signals, data, and hypotheses.

Signals, as the initiating stage of perception, refer to perceptual stimuli and action potentials. Signals are measurable with standard scales or units used in physics and transmit through various physical channels (Gregory 1980). Conceptual and contextual-associated knowledge about the present object is latent in the signals. Yet, they are nothing more than random stains of ink on a piece of white paper; just as an individual, who cannot read Japanese, might see a Japanese poem on a piece of paper.

In the second phase, the neural system processes those signals to convey them into data, which embrace inferable information. In some cases, the source of the signals is precise, so the signals are well structured, and the output is clear-cut. It is unfortunately not always the case; it is rare indeed. When it is not the case, extrainformation (such as intuitions, morals, past experiences, and memories) is required for decoding the signals. Gregory (1980) noted that the mechanism converting processing signals into data is conventional rules, not physical laws. Thus, unlike signals, data do not reflect a physical scale or unit. Data is used as a source to generate possible hypotheses and select the one among them. That being the case, a predictive power is inherent in the data.

Hypothesis is the final phase. As Gregory (1980) proposed:

*...hypotheses are selections of signalled and postulated data organized to be effective in typical (and some novel) situations. Hypotheses are effective in having powers to predict future events, unsensed characteristics, and further hypotheses. They may also predict what is not true. (Gregory 1980, p. 184)*

The signals from present are enriched by past knowledge and together allow predictions about the future. This could be commented as the hypothesis, which is generated based on the present signals of reality, shaped by the knowledge and experiences of the perceiver, and so, lead his/her immediate behavior accordingly. In this view, the

hypothesis could be systematically misleading in atypical situations such as illusions.

Wlle, yuo cna aulacly raed adn uesdnatnrd tihs  
praaprgah whotuit ayn pboerlm eevn it is a taotl  
mses. Fro yuo, hveower, it is nto spurriings any  
mroe; beacsue yuo konw the resoan nwo. Yse, of  
crosue it is top-dwon pcoresnig, mroe pcreseily  
hpoytehiss-dirivng mdotliay.

The paragraph above sets a good example for hypothesis-driving modality. Although each word is written as jumbled letters, an individual still can read and understand the whole paragraph easily. Although the individual's eyes see those words as total mess, his/her brain generates possible words using all letters and picks the most likely one among those by using knowledge and past experience. So, it may not be surprising that people who read more do a better job on that.

All in all, bottom-up processing is a readily available version as an initial package for all animals as well as mankind when they are born. Top-down version is advanced subsequently with the development of higher-level cognition; thus, it is interesting that several animal species also experience visual illusions (for review see Freeberg 2019). Bottom-up processing is more primitive and important in life-or-death situations whereas top-down processing is more related to intellectual functions. Although top-down processing seems like a more advanced version, it does not overwrite the bottom-up processing. As matter of fact, the top-down version works together with bottom-up processing. With a reference to Bar (2003), Frenske and his colleagues (2006) roughly encapsulated it on a neural basis as follows. A partially analyzed data point (e.g., blurred image) is directly projected from lower-level structures to prefrontal cortex (PFC). This activity, in the following stage, triggered the temporal cortex for the predictions that are used as feedback for the bottom-up processing. Gregory (2005) also agrees that bottom-up and top-down processing should work together in harmony.

If we could see only probable objects, we would be blind to the unlikely; but this would be dangerous, as unlikely events do sometimes occur. Indeed, if we could see only expected things and events, there could hardly be perceptual learning. (Gregory 2005, p. 1245)

## Neural Basis for Top-Down Processing

In everyday life, attention is modulated by bottom-up and top-down influences. Factors such as emotional and motivational valence, knowledge, expectation, current goals, acquired significance, volition, novelty, and unexpectedness regulate attention. The success of the goal-directed behavior depends on maintaining endogenous attention and processing low-level sensory inputs by conceptual information related to the current goal by protecting it from the interference of inappropriate stimuli through top-down mechanisms. In the case of behaviorally relevant, unexpected, and salient new stimuli that may arise during goal-directed behavior, the maintenance of the attentional set should be suspended, and attention should be shifted to the new stimulus by exogenous, bottom-up mechanisms in order to analyze the nature of the new stimulus and process its sensory attributes into a conceptually coherent phenomenal experience. Top-down modulation of attention is exerted by the prefrontal cortex (PFC), parietal and limbic cortices in the schematic representation of the modulation of attentional matrix, proposed by Mesulam (2000).

Early studies, especially microstimulation studies in nonhuman primates showed that the common components of all attentional tasks are mediated by the prefrontal and parietal cortices. The dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (PPC) activate during the working memory tasks. The motivational valence of the stimuli is largely designated by subcortical limbic and paralimbic structures that include the amygdala, orbitofrontal cortex (OFC), anterior cingulate cortex (ACC), substantia nigra, and locus coeruleus (Mohanty et al. 2008). The amygdala modulates the responses of the visual association cortex to the emotional expression of faces, hunger affects the OFC responses to the food, and cingulate cortex activates in selective and divided attention tasks. Hunger and thirst increase the response of PPC neurons to fluid and food. Frontal lobes activate in response to novel and unexpected stimuli (Mesulam 2000). The motivational valence of the stimuli is determined by the phasic dopaminergic release from the ventral tegmental area to the



nucleus accumbens, which together with OFC and ACC forms the reward circuit of the parallel frontostriatal circuits (Alexander and Crutcher 1990). In order to give the appropriate response in an attentional task, attention must be maintained, and inappropriate responses must be inhibited. This type of task such as Go-no-go activates medial PFC and connected caudate component (Booth et al. 2003).

Although these microstimulation studies in monkeys provided important information for the understanding of brain regions that contribute to the regulation of attention, the prevailing view in cognitive neuroscience is that cognitive functions are modulated not by individual regions but by large-scale neurocognitive networks. These large-scale neurocognitive networks are first described by Mesulam (1998) based on nonhuman neuroanatomical studies. Following the classical task-related studies of the nineties, the application of the fMRI BOLD signal to the resting brain by the turn-of-the-century enabled the imaging of the so-called “intrinsic connectivity networks” (ICNs) in the human brain. ICNs are a group of synchronized neural regions responsible for cognitive-emotional and sensory-motor functions in the brain (Damoiseaux et al. 2006; Laird et al. 2011; Power et al. 2011; Yeo et al. 2011).

Corbetta and Shulman (2002) defined two anatomically and functionally distinct attention systems in the human brain, i.e., the dorsal frontoparietal system and the ventral frontoparietal system. The dorsal frontoparietal system was proposed to mediate the top-down modulation of attention to locations or features, and the ventral frontoparietal system was proposed to detect unattended or unexpected stimuli, thus, mediate the bottom-up modulation of attention.

The dorsal attention network (DAN) includes the intraparietal sulcus (IPS) and the frontal eye fields (FEF) and is organized bilaterally (Vossel et al. 2014). IPS and FEF (the major hubs of DAN) contain areas with retinotopically organized maps of contralateral space, so they participate in orientation of spatial attention (Vossel et al. 2014). DAN is active when a person has directed her/his attention to an external stimulus such as reading a book or listening to a

conference, thus maintaining goal-directed attention. At this time, a sudden alarm sound activates the ventral attention network (VAN), which has the function of detecting an unexpected stimulus (stimulus-driven attention). VAN activity inhibits the active attentional set by silencing the DAN to trigger the new behavior to learn about the nature of the new stimulus. VAN's interruption of the behavior under DAN control and shifting attention to the new stimulus is called “circuit breaking” by Corbetta and Shulman (2002).

Dosenbach et al. (2007) proposed two distinct control networks for top-down processing, and both maintain task-relevant information. The fronto-parietal network (FPN), which consists of the dlPFC, inferior parietal lobule, dorsal frontal cortex, IPS, precuneus, and middle cingulate cortex (MCC), actively maintains the task-relevant information, assesses the error-related information, and monitors changing conditions of the context during the complex and goal-directed behavior. It includes the dorsal attention network proposed by Corbetta and Shulman (2002). The cingulo-opercular network (CON), which consists of the anterior PFC, anterior insula/frontal operculum, dorsal ACC/medial superior frontal cortex, and thalamus, is active through the entire task and ensures stable set-maintenance by inhibiting inappropriate response tendencies via setting an active resistance to the interference by them (Dosenbach et al. 2008).

FPN is active when the ongoing behavior is more complicated than just watching or listening and requires problem-solving, monitoring of the changing conditions of context, assessment of the new rules of new contexts, and mental flexibility. In order to accomplish such a complicated behavior by FPN, another control network CON should be active through the entire task and protect the relevant behavior from the irrelevant stimuli.

The default mode network (DMN) was originally defined that displays activation in rest-conditions and deactivation during cognitive tasks. It consists of the posterior cingulate cortex, medial prefrontal cortex, angular gyrus, and nodes in the medial temporal lobe (Greicius et al. 2003; Raichle et al. 2001). In daily life, when an awake person does not pursue a goal-directed behavior,

they are in a state of mind wandering between past, present, and future. The DMN is currently active in this person's brain. DMN is attributed to episodic memory retrieval, autobiographical memory, and internal speech, with self-related and social-cognitive processes, value-based decision-making, and emotion regulation (Menon 2015). Although it appears to be a resting-state network that deactivates during the tasks, it was thereafter shown that it does not disintegrate during task execution, but its functional connectivity and network properties change in some specific tasks such as working memory, autobiographical planning, and oddball paradigm (Vatansever et al. 2015). This suggests that DMN may also contribute to the top-down modulation of task execution by providing information about internal mentation.

## Cross-References

- Attention Bias
- Attention-Getting Behaviors
- Auditory Processing and Perception
- Bottom-Up Processing
- Cognition
- Divided Attention
- Gestalt
- Goal-Directed Behavior
- Perception
- Perception-Action Theory
- Stroop Effect
- Visual Perception

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## Torpor

- [Developmental Arrest](#)

## Total Mass of Living Matter

- [Biomass](#)

## Touch

- [Catarrhine Communication](#)
- [Cetacean Sensory Systems](#)
- [Hominoidea Sensory Systems](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Sensory Systems](#)

## Touch Screen

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## Synonyms

[Board](#); [Display](#); [Monitor](#); [Tactile](#); [View screen](#)

## Alternative Words

- [Touch Screen](#); ► [Touch Screen](#)

## Definition

A touch screen is an electronic display monitor that identifies the touch of a finger or stylus and

allows the user to interact with the device directly rather than with a mouse or keyboard and the monitor being either based on LCD (liquid crystal display) or LED (light-emitting diode) technology. It is an input device which is pressure-sensitive.

## Introduction

The most instinctive way of communicating or identifying any object is by touching. With the technological advancement, the need of improving human-computer interaction has been increasing. Touch screen has become the dominant technology for cursor control which has brought the world into the tip of the finger. Because of its convenience, touch screen technology is used in a wide variety of applications popularly in information kiosks, POS (point-of-sale) machines, and consumer electronics, where it has replaced the functions of keyboards.

## History

Research on touch screen technology has started way back, and it's been only a few years that the technology has become an integral part of human life with advanced touch screen technology coming on in leaps and bounds in the recent time. More and more number of products are being incorporated with this technology by various organizations.

It was in the year 1965 when Eric Johnson first published his work on capacitive touch screens (Johnson 1965). In the early 1970s, the engineers from CERN, Frank Beck and Bent Stumpe, developed the first transparent touch screen (Stumpe and Sutton 2010). In the year 1972, a group from the University of Illinois developed an optical touch screen having infrared position sensors mounted on a plasma display panel (Ebeling et al. 1973). In 1973 a product was manufactured by CERN to put in use for air traffic control (CERN Bulletin Issue 2010). George Samuel Hurst in his patent first described a resistive touch screen in 1975 which was produced in 1982 (Hurst and Colwell 1974). In the same

year, a research group from the University of Toronto developed the first human-input multi-touch system. The HP 150 which was based on similar kind of technology as used in 1972 had come up with the world's earliest commercial touch screen computers in 1983 (Biferno and Stanley 1983). During the early 1980s, touch-sensitive display units were assessed for commercial aircrafts with an aim to reduce the workload of pilots so that the crew is aware of the situations of all major aspects of the vehicular operations.

The first commercial POS-based computer was developed by Gene Mosher and the first touch screen-based pocket computer in 1986 by Casio (Viewtouch.com). As consumers started using touch screen, the error due to parallax and calibration was common until 1988 (Potter et al. 1988).

In the early 1990s, the first touch screen phone was commercialized by IBM. Almost all the touch screens were resistive until in 2007 the first cell phone with capacitive screen was released by LG (Engadget.com). It was based on projected capacitive technology. Till date touch screens continue to evolve in terms of sensing capability and applications.

## Technologies in Touch Screen

In order to allow a user to interact with a screen, touch screens use different technologies. There are generally four types of touch screen technologies: resistive, capacitive, surface acoustical wave (SAW), and infrared (IR).

### Resistive

Resistive touch screen is the most common type of touch screen technology used due to its affordability and tolerance for harsh environments. This type of screen is composed of two thin transparent sheets facing each other separated by air gap. The top sheet is made up of some transparent thermoplastic polymer (polycarbonate), while the bottom sheet is made up of some glass or acrylic-type rigid material and is coated with a conductor film such as indium tin oxide. Spacers are placed in the air gap so that the two sheets don't touch

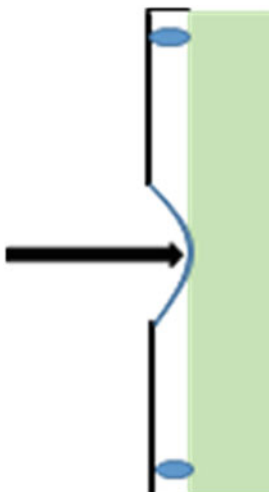
each other when the screen is not in use. When a user applies pressure by fingertip or stylus onto the outer surface, the top sheet touches the bottom sheet and becomes connected at that point. This causes a change in the resistance and an increase in the voltage. The change is then detected by the sensor connect and then sent to the controller for processing.

Resistive touch screen is further divided into 4-, 5-, and 8-wired resistive touch screens based on the way the touch coordinates are determined which actually signifies the durability and sensitivity of the entire circuit. The change in the voltage across the conductive area is based on the no. of electrodes used. The only difference between the 4-, 5-, and 8-wired resistive touch screens is an extra set of electrodes and the wires connected to these electrodes, with the 8-wired screen as the most sensitive resistive screen.

Resistive screens are generally used in hospitals, restaurants, and factories. Other than being inexpensive, these screens can also be used with gloves. But they suffer from poor screen clarity and are prone to damage by spear-like objects which makes them difficult to repair (Fig. 1).

## Capacitive

Resistive touch screens rely on the physical pressure exerted by the user's finger or stylus, whereas



**Touch Screen, Fig. 1** Resistive screen

the capacitive touch screen makes use of the conductive nature of human body. Capacitive screen is an assembly of a transparent glass material coated generally with indium tin oxide, covered with a layer to protect it from the environment. When a user touches the screen with a bare finger, conduction of electric charges occurs over the uncoated layer, and a dynamic capacitor is formed. The sensors implanted then detect the location of touch by measuring the change in capacitance at the four corners of the screen to indicate where the screen is touched. Capacitive touch screen panels must be touched with a finger unlike resistive and surface wave panels that can use fingers and stylus.

Capacitive touch screen can be categorized as surface – capacitive technology and projected capacitive technology. In surface-capacitive technology, only one side of the insulator is coated with a transparent conductor material with electrodes placed at the four corners of screen which maintains a constant voltage over the conductive layer. When a user's finger comes in contact with any part of the screen, current starts flowing from the four electrodes to the finger, and the change in the voltage and the location is identified by the sensors embedded under the screen.

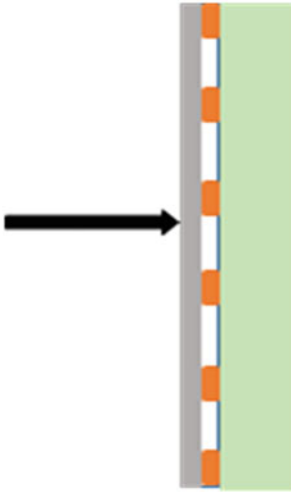
In projected capacitive technology, the screen has a grid of multiple horizontal and vertical electrodes forming a matrix. When not in use, the vertical electrodes maintain a constant current, and when a finger touches the screen, the horizontal electrodes are triggered initiating the current flow between the finger and that area of the screen which creates an electric field. The sensors instantly sense the location.

Capacitive touch screens are commonly used in mobile phones. Although the screens are expensive, they are more sensitive and have high clarity (Fig. 2).

## Surface Acoustic Wave

Surface wave acoustic (SAW) touch technology is much more advanced than the earlier discussed technologies. It detects the point of touch on the screen by tracing ultrasonic waves that are generated at the edges of the screen and reflects back

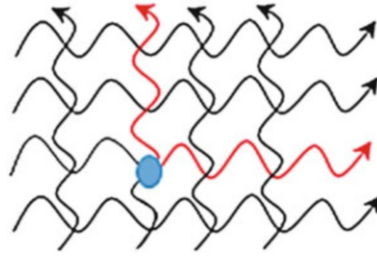




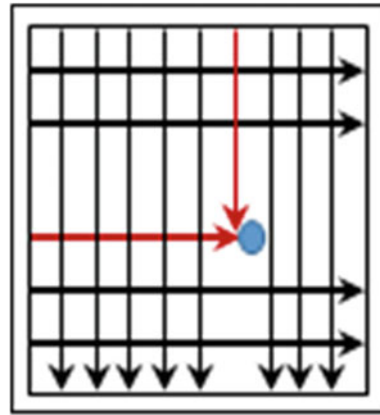
**Touch Screen, Fig. 2** Capacitive screen

and forth across its surface. A part of the wave is absorbed when the panel comes into contact with the finger interrupting the waves, and by using a transducer, the absorption of the ultrasonic waves is recorded which is then processed. Instead of using light and materials which do not absorb pulse, this technology uses sound which delivers excellent quality.

SAW screens are durable and scratch proof, and if scratched, sensing function remains unaffected. High clarity and resolution make this technology find its use in devices used for monitoring and also in ATMs, information kiosks, and medical equipment but can cease to respond when oil, dirt, or any solid stain rests on the screen (Fig. 3).



**Touch Screen, Fig. 3** Surface wave acoustic screen



**Touch Screen, Fig. 4** Infrared screen

This screen technology finds application in kiosks, outdoor installations, POS systems, and factory automation. It offers great clarity but is sensitive to dirt and moisture so inapplicable in industrial areas (Fig. 4 and Table 1).

## Infrared

Infrared touch screen is a popular technology based on infrared beams transmitted by light-emitting diodes (LEDs) and photodetector pairs around the edges of the screen, instead of using any thin film or glass layer. When a finger comes nearer to the display screen, the infrared rays are blocked, and the interruption in the pattern of LED beams is detected by the photodetectors. These LED beams cross each other in vertical and horizontal coordinates which helps the sensors to trace the exact location of the touch.

## Components of a Touch Screen System

The touch screen system has two parts: hardware and software. The hardware architecture consists of microcontroller, numerous interfaces, and driver circuits. The system software is developed using a collaborative programming language.

The three major components of a simple touch screen are a touch sensor, a controller circuit, and a software driver. The touch screen is combined with a display unit and a computer to make a touch screen system.

*Touch sensor:* The sensor has an electrical current or signal flowing through it. When a user

**Touch Screen, Table 1** Presents a brief comparison between all the technologies

| Properties        | Screen type      |                    |                  |                    |
|-------------------|------------------|--------------------|------------------|--------------------|
|                   | Resistive        | Capacitive         | Saw              | Infrared           |
| Accuracy          | Less             | Up to large extent | High             | Up to large extent |
| Resolution        | High             | High               | High             | Low                |
| Cost              | Low              | High               | High             | Low                |
| Durability        | Low              | High               | High             | High               |
| Sensitiveness     | Low              | More               | More             | Up to some extent  |
| Humid resistant   | Resistant        | Not resistant      | Not resistant    | Resistant          |
| Scratch resistant | Not              | Up to some extent  | Resistant        | Resistant          |
| Muti-touch        | Does not support | Supports           | Does not support | Supports           |
| Screen size       | <25 inches       | > 12 inches        | <32 inches       | >32 inches         |

touches the screen, it causes a change in the signal. This change in the signal is used to determine the location of the touch on the screen.

*Controller:* A controller should be connected between touch sensor and computer. It collects the information from the sensor and translates it for understanding of PC.

*Software driver:* The driver allows the computer and touch screen panel to work together. It commands the operating system to interact with the information that is sent by the controller.

**Application – Touch Screen Technology for the Visually Impaired**

Recently, touch screen technology has been trying to help the visually impaired person to access information. In order to test a blind user’s capacity in distinguishing and identifying basic geometric objects presented on a touch screen, various models such as vibration-only modal, audio-kinesthetic, or multimodal vibro-audio solutions are being under study.

In vibration-only modal, the finger path trails produced by testers and their haptic exploration strategies are analyzed when they attempt to recognize basic shapes and objects presented on a touch screen measuring the accuracy, user’s average response time, duration of each finger stroke, etc. (Southern et al. 2012; Tekli et al. 2018). To access basic shapes and charts on vibrating touch screens, vibro-audio interface has been provided between 2010 and 2015. These interfaces

combine touch screen vibration and audio feedback, which allows the blind users to explore graphical information such as bar graphs and indoor navigation layouts by combining the finger movements over the screen synchronized with audio and vibration signals when the user touches the elements on the display unit. In multimodal vibro-audio solutions, while using the screen, a haptic feedback through external vibrators fixed to the fingers of user is added. Multiple modalities such as audio, vibration, and haptic cues were combined together to provide the solutions. This could prove very useful in allowing a visually impaired person to access geographic maps, to navigate inside and outside buildings, and to access graphs and mathematical charts.

However, there are certain issues such as long response time taken by blind users to recognize a basic shape, less correlation between the shape’s surface and user’s vibration trails, etc. These issues need to be further investigated to make touch screen technology optimal enough for better accessibility for the visually impaired persons.

**Application – Touch Screen Technology for the Motor Impaired**

People with motor impairments are either able to use only the back of their hand or elbow to touch or unintentionally touch with multiple parts of their hand. The requirement of a proper touch by landing fingers on the intended area on a

touch-sensitive screen is beyond the ability of a motor impaired person.

A technique called smart touch was introduced allowing the motor-impaired users to touch the target point in their most comfortable way (Anthony et al. 2013; Mott et al. 2016). An algorithm is designed that maps the total number of touch areas to the user's intended location. It calculates the coordinates of users' intended locations closer to actual intended targets by detecting the most relevant touch of the user.

However, this is a vital step in the direction of improving touch precision for people with motor impairments which was tough previously. But it is still challenging in finding out the effectiveness of such kind of smart touch technology on smartphones and computers.

## Cross-References

- [Displays](#)
- [Technical Intelligence Hypothesis](#)

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## Tourism

- [Safari](#)

## Trace Strength

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## Definition

Trace strength refers to the accessibility of a particular memory at a given time.

## Introduction

Many models of memory assume that memories are stored as unique traces. The accessibility, or ability to be retrieved, of a trace is typically referred to as its strength. Trace strength can be influenced by a variety of factors (e.g., repetition of information). Trace strength is used as evidence for a variety of decisions and judgment (e.g., recognition of a previously studied item).

## Classic Conceptualization

Trace strength is an important component of many early models of memory. Wickelgren and Norman's (1966) trace-strength model was the first model to explicitly incorporate the concept. According to their model, a piece of information (e.g., a word to be remembered in a short-term memory task) is represented as a unique trace in memory. At baseline, the activation of that trace is zero. Upon presentation of the word, the activation of the trace increases. The activation then begins to decay exponentially until it reaches zero. The strength of a trace at a given time can be used as evidence for a variety of judgments inside and outside of laboratory tasks. There have been many extensions to the classic model (e.g., Wickelgren 1975; Wickelgren and Berian 1971), but each model contains the same core premises and assumptions.

## Factors That Influence Trace Strength

### Delay Between Encoding and Retrieval

Increasing the amount of time between encoding and retrieval decreases trace strength. This decrease is a natural consequence of the fact that trace activation decays over time. It is worth noting that most trace-strength models are agnostic about whether trace decay is passive or a result of interference. Regardless, as the activation of a trace reduces over time, its strength decreases.

### Repetition/Frequency of Exposure

Repeated exposure to an item increases trace strength. When an item is encountered the first time, the activation of its trace increases and begins to decay. If the item is encountered again before its trace activation has decayed to zero, it boosts to a greater activation than on the first encounter. A natural consequence of this pattern is that more common words (i.e., high-frequency words) will, on average, have a greater trace strength than uncommon (i.e., low-frequency words).

## Elaborative Processing

In standard conceptualizations of trace-strength models, elaborative processing increases the strength of a trace. For example, if items are studied by counting the number of vowels (shallow processing), they will have lower trace strength than items studied by generating an antonym (deep/elaborative processing; Craik and Lockhart 1972). This pattern requires an additional assumption that elaborative processing results in a greater increase in trace activation.

It is well known that elaborative processing does not necessarily result in better memory performance. Instead, the match between processing at study and test is critical, a phenomenon typically referred to as *transfer-appropriate processing* (Morris et al. 1977). This pattern is inconsistent with a purely strength-based account of memory and is typically leveraged as evidence against pure trace-strength models.

## Standard Applications of Trace Strength

According to trace-strength models, trace strength is used as evidence to guide a variety of judgments that can be tested in the laboratory.

### Recency Judgments

Trace strength is a strong indicator of how recently an item has been encountered. On average, recently encountered items will have greater trace strength because the traces' activations have had less time to decay.

### Frequency Judgments

Trace strength is also a strong indicator of how many times an item has been encountered within a certain time period. On average, more frequently encountered items will have greater trace strength because the traces' activations will have been boosted multiple times.

### Recognition Judgments

Trace strength can be used to discriminate studied from unstudied items in a standard recognition memory task. In a recognition task, participants study a set of items (typically words). They are

then shown the same words they studied intermixed randomly with new, unstudied words. They are asked to determine whether each word was studied or not. In standard models, trace strength is compared against some decision criterion that, if exceeded, results in a “studied” judgment.

## Conclusion

Trace strength is an important concept in memory theory, acting as an index of the accessibility of a memory in many models. Trace strength can be influenced by a number of factors, including decay, repetition, and depth of processing. Trace strength can be used as evidence in favor of many judgments, including recency, frequency, and recognition. Although classic models in which trace strength is the sole basis of memory performance are insufficient, trace strength is a concept that is incorporated – sometimes tacitly – into most conceptualizations of memory.

## Cross-References

- [Declarative Memory](#)
- [Long-Term Memory](#)
- [Memory](#)
- [Priming](#)
- [Recall](#)
- [Short-Term Memory](#)

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## Trading

- [Exchange Behavior](#)

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## Trail Riding

- [Horseback Riding](#)

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## Training

- [Horseback Riding](#)
- [Learning](#)

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## Traits

- [Jean Baptiste Lamarck](#)

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## Transcranial Magnetic Stimulation (TMS)

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## Introduction

Transcranial magnetic stimulation (TMS) was pioneered in the mid-1980s by Anthony T Barker and colleagues, as a method to noninvasively activate brain circuits (Barker et al. 1985). The impact of TMS on neuroscience and



neurology is apparent in its widespread current use as an experimental tool to investigate neural circuitry. It is also under extensive investigation for its potential application in clinical settings where it may be used to treat neurological and mood disorders, such as stroke, Parkinson's disease, and depression.

## Principles of Operation

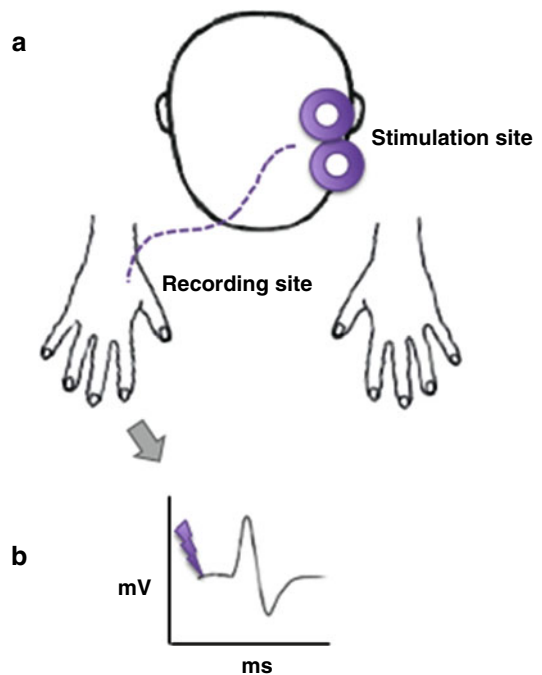
Transcranial magnetic stimulation operates on the principle of electromagnetic induction, first described by Michael Faraday in 1914. A magnetic field changing in time, applied to a conductive material, induces an electric field in that material. In the case of TMS, a large electric current is passed through the stimulating coil, causing it to act as an electromagnet and generate a magnetic field. The flux lines of this magnetic field are generated perpendicular to the plane of the coil and pass painlessly through the scalp and skull and into the conductive tissue of the brain. The induced electric field flows perpendicular to the magnetic flux lines and thus travels in parallel with the surface of the brain and in the opposite direction to current flow within the stimulating coil (Hallett 2007). Depending on the orientation of the coil, the electric field activates neural elements such as axons from neurons, which are oriented in parallel with it, or cell bodies and their inputs from other neural elements.

## Human Application

The first human experiments using magnetic stimulation delivered magnetic pulses to the median nerve in the forearm and generated a "twitch" in the ipsilateral thumb which could be recorded by electromyograph (EMG). In 1985, Barker et al. first described application of magnetic stimulation to the brain. Transcranial stimulation was found to be painless and was easier to apply than the more invasive electrical stimulation techniques in common use at the time. Single magnetic pulses applied to the scalp overlying specific areas of the motor cortex were shown to generate twitches

in muscles controlled by the stimulated areas of the cortex. These muscle twitches are called motor evoked potentials (MEPs) and are observed primarily in the limbs opposite to the site of brain stimulation (Fig. 1).

Measures of the delay between stimulation and response and the amplitude of the response recorded from the muscle provide information on conduction velocity and strength, respectively, of neural transmission between brain and muscle (Kobayashi and Pascual-Leone 2003). Initially, single pulse TMS was employed to monitor the integrity of pathways between brain and spinal cord during neurosurgery and to assess motor function in individuals living with neurological conditions.



**Transcranial Magnetic Stimulation (TMS), Fig. 1 Representation of motor evoked potential recording in a human.** (a) The TMS coil (purple rings) is placed over the motor cortex and single pulses are applied. These pulses activate contralateral muscles which are represented by the area of the cortex that is being stimulated. Motor evoked potentials are recorded from the activated muscles using electrodes placed over the skin or into the belly of the target muscle. (b) Representation of a motor evoked potential recorded from the contralateral hand. Purple arrow indicates delivery of the TMS pulse, and the recording shows the amplitude in millivolts (mV) recorded over time in milliseconds (ms)

Predicting the effect of single pulses of TMS on brain circuits is complex, due to an interaction between various parameters of the stimulation itself, and physiological features of the human brain. For instance, the orientation of magnetic coil placement and therefore orientation of the induced electric field affects the amplitude of MEPs generated by TMS (Mills et al. 1992). Magnetic stimulation seems to be most effective at activating neurons which project horizontally within the cortex as opposed to those which project at right angles to the cortical surface (Day et al. 1989). The intensity at which TMS is delivered also determines which type of cortical neuron will fire in response to each stimulus, due to differences in membrane properties of the neurons or their depth from the cortical surface. Neurons with a low action potential “threshold” may be preferentially activated at low TMS intensities while higher threshold neurons remain silent (Moliadze et al. 2005). Neurons located in more superficial layers of the cortex are also more readily activated due to the limited ability of the magnetic field to penetrate through brain tissue. Thus, many factors contribute to determining the response of the brain to single pulses of TMS, not all of which are well understood.

### Inducing Long-Term Changes in the Brain with TMS

An area that has been explored intensely with TMS is the ability to induce long-term changes in neural activity. The approach is to stimulate specific regions of the brain with an extended train of pulses (repetitive TMS, rTMS) in order to effect physiological changes that outlast the period of stimulation. In the first investigation of rTMS using low frequencies, Wassermann et al. (1996) showed that 3 min of continuous stimulation at 1 Hz reduced MEP amplitude for up to 2 min poststimulation. Through this work, it became apparent that rTMS had the capacity to alter activity of the cortex over a prolonged period and may therefore be effective in the treatment of some neurological disorders.

Since then, the effects of rTMS on motor cortex activity and function in humans have been extensively investigated. Most studies agree that low frequency rTMS (<1 Hz) produces inhibition of activity within motor pathways while high frequency rTMS (>5 Hz) facilitates activity. These findings are consistent with those observed in fields investigating the phenomena of long-term potentiation (LTP) and long-term depression (LTD) in the role of learning and memory within the hippocampus. This has led to the hypothesis that rTMS was inducing LTP and LTD in stimulated regions of the cortex. Repetitive TMS-induced changes in cortical activity, however, are less robust than those observed in the hippocampus and display a large amount of inter-subject variability in both humans and animals. Despite this variability and inconsistency between studies, the use of rTMS has progressed from probing the physiology of various pathways and systems in the brain to application to a wide range of neurological conditions.

The use of repeated TMS pulses adds additional layers of complexity in determining its effects on the brain. Adding multiple pulses together to form a stimulus train introduces additional parameters, such as stimulus-train length, frequency, number of pulses delivered, and their temporal pattern. All of these parameters may differentially affect the responses of the intended target neurons to rTMS. For instance, the application of pulses in short groups of bursts, repeating at a frequency reminiscent of theta waves in the brain, has shown some utility in strengthening or weakening neural circuits, depending on the timing between the burst (Huang et al. 2005). However even this approach, which has found most utility, shows wide variability in response pattern between individual humans and animals in experimental investigations. Due to the vast parameter space and individual variation, the most effective way to deliver rTMS to cause lasting changes in neural activity is not yet well characterized. For this reason, meta-analyses of studies that have applied rTMS in order to treat neurological disorders such as Parkinson's

disease and stroke have yet to recommend its routine use in a clinical setting. Thus far, only in intractable depression in humans has rTMS advanced into regular human use.

## Gaining Insight from Animal Models

One of the difficulties in gaining a clearer understanding of TMS is that our impressions about its effects on the brain usually come from an indirect measurement of the response in muscles. When activity is recorded directly from the brain following stimulation, responses are not as stereotypical as observed with MEP recordings, but arguably provide greater insight into the cellular effects of TMS that might be harnessed to treat neurological diseases. Due to the invasive nature of the techniques, recording from neural circuits is generally only possible in animals. However, this on its own presents a set of challenges. Brains of traditional laboratory animals such as rats and cats are much smaller than those of humans, and traditional human TMS coils are large. Thus, a much larger area of the brain is activated than would be in humans, leading to less spatially specific effects. To overcome this, smaller, animal-specific coils have been designed, and while activation is more focused, they are still excessively bulky and restrict the placement of other experimental apparatus required for recording from the brain. In addition, there are significant technical challenges in decoupling the direct effects of TMS from the neural recording apparatus, so that the recording can faithfully report the responses of neural circuits to TMS.

Experiments that have been performed in animals to investigate the neural effects of TMS have used techniques such as extracellular recordings from single neurons, and field potential or optical recordings using voltage sensitive dyes, to measure the activity of large ensembles of neurons. These experiments have shown that neuronal activity following application of TMS pulses can depend on the nature of other stimuli the brain is attending to at the time of stimulation. For

example, the activity of single neurons in the visual cortex of cats in response to TMS differs depending on whether or not a visual stimulus is presented to the animal during TMS (Moliadze et al. 2003). As well as cats, responses to single pulses of TMS in whole brains have been recorded in anesthetized rats and awake monkeys. In the majority of cases, responses to TMS pulses vary from neuron to neuron, however similar overall patterns of activation are seen (Mueller et al. 2014). Immediately following each TMS pulse, an increase in action potential firing rates is observed, generally followed by a period of suppression of activity. Across studies, however, the timing of these periods of facilitation and suppression vary considerably, making it difficult to define a precise mechanism of action for a given TMS intensity.

The use of animal models in TMS research is ongoing. Significant innovation is required to overcome the challenges of size and to enable recording from single and multiple neurons under conditions relevant to that experienced in the human brain. Work combining TMS with neural recordings in animal models is essential, in order to further our knowledge of the cellular effects of TMS on the brain.

## Conclusion

While TMS has proven to be a useful tool for scientists probing the physiology of various neural circuits, a lack of understanding of the basic mechanisms of action is hindering its progress in treating neurological disease clinically. The use of animal models allows scientists a promising opportunity to probe the effects of TMS on the brain at both a single neuron and system level but requires significant technological advance to improve the ability to stimulate and record neurons simultaneously. It is hoped that with a better understanding of the cellular mechanisms harnessed by repetitive TMS, stimulation protocols may be optimized to drive specific neural changes that may facilitate recovery from a range of neurological disorders.

## Cross-References

- [Action Potentials](#)
- [Axon](#)
- [Long-Term Potentiation](#)
- [Nerve Cells](#)
- [Neuron](#)
- [Parkinson's Disease](#)

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## Transcription

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## Definition

Transcription is a process in which information from a gene is converted in the form of RNA.

## Introduction

Transcription is the copying of a gene's DNA sequence to make an RNA molecule. It is a process in which ribonucleic acid (RNA) is synthesized from DNA. The word “gene” refers to the functional unit of the DNA that can be transcribed. One of the two strands of DNA acts as a template (noncoding strand or sense strand) and results in the production of working copies of RNA molecules. The other DNA strand, which never participates in transcription, is called a coding strand or antisense strand. Transcription is performed by enzymes called **RNA polymerases**, which link nucleotides to form an RNA strand (using a DNA strand as a template).

## Stages of Transcription

Transcription consists of three stages: initiation, elongation, and termination.

### Initiation

The process of transcription begins when the RNA polymerase recognizes and binds together with one or more general transcription factor(s), in the case of eukaryotes and  $\sigma$  (sigma) factor, in the case of prokaryotes, to a specific DNA sequence, which is called a “promoter.” A number of transcription factors interact with eukaryotic promoter regions. In humans, about six transcription factors (TFs) have been identified (TFIID, TFIIA, TFIIB, TFIIF, TFIIIE, TFIIH). It has been postulated that the TFs bind to each other, and in turn to the enzyme RNA polymerase. This forms an RNA polymerase-promoter “closed complex” (Watson et al. 2013).

### Elongation

One of the strands of the DNA, the *template strand* (or noncoding strand), is used as a template for RNA synthesis. After transcription is initiated, the DNA double helix unwinds and RNA polymerase reads the template strand. It adds nucleotides to the 3' end of the growing chain. New nucleotides are added at an approximate rate of 42–54 nucleotides per second in prokaryotes (Dennis and Bremer 1974), whereas in eukaryotes the speed is approximately 22–25 nucleotides per second (Izban and Luse 1992). RNA polymerase forms the RNA strand using base pairing complementarity rule (in RNA, Uracil is present instead of Thymine). RNA polymerase travels through template strands from 3'  $\rightarrow$  5' and the coding (nontemplate) strand is used as a reference point. Notably, transcription always occurs in 5'  $\rightarrow$  3'. In addition to that, elongation also involves a proof-reading mechanism to get rid of bases that have been wrongly incorporated. Proof reading is carried out by RNA polymerase. There are two ways in which the mRNA repair is carried out.

1. Pyrophosphorolytic editing
2. Hydrolytic editing

If any incorrect nucleotide is added to the template DNA, the RNA polymerase will stop and then it will either proofread the transcript or continue without correcting (Watson et al. 2013).

### Termination

Terminator sequences have been observed very close to the ends of noncoding sequences (Clancy 2008). The process of transcription is terminated by termination signals. Two types of termination have been identified.

1. Rho ( $\rho$ )-Dependent Termination

A specific protein, named  $\rho$  factor, binds to the growing RNA. In the bound state, it starts acting as ATPase, terminates transcription, and releases RNA. The  $\rho$  factor also causes the dissociation of RNA polymerase from DNA.

2. Rho ( $\rho$ )-Independent Termination

The formation of hairpins of newly synthesized RNA results in termination of transcription in this case. This is due to the presence of palindromic sequences. As an analogy, a palindrome is a word that reads the same in both forward and backward directions, e.g., Malayalam, Rotor, etc. The presence of palindromes in the base sequence of DNA template (same when read in opposite directions) in the termination region is well established. Because of this, the newly synthesized RNA folds to form hairpins (due to a complementary base pairing) that cause termination of transcription (Lykke-Andersen and Jensen 2007).

## mRNA Processing in Eukaryotes

In eukaryotes, primary transcripts of mRNA molecules are processed after transcription: they are **spliced** and have a **5' cap** and **poly-A tail** put on their ends. This step consists of three stages:



- (i) Capping – In the capping process the triphosphate group is replaced with another structure, which is referred to as a “cap,” which is added by the enzyme guanylyl transferase.
- (ii) Polyadenylation – This is the addition of the adenines (A) at the 3' end, which is catalyzed by the enzyme poly (A) polymerase.
- (iii) Splicing – It involves removing the introns and adding the exons.

Transcription is controlled separately for each gene. In short, **transcription** is the process of copying out the DNA sequence of a gene in the similar alphabet of RNA.

## Conclusion

The goal of transcription is to make an RNA copy of a gene's DNA sequence. For a protein-coding gene, the RNA copy, or **transcript**, carries the information needed to create a polypeptide or protein. Eukaryotic transcripts need some processing before getting translated into proteins.

## Cross-References

► [Gene Expression](#)

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## Transcriptome

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## Definition

The set of all RNA molecules produced in a particular condition within a given cell, tissue, or organism of interest

## Introduction

Transcriptomic studies investigate the RNA content (or gene expression), including messenger RNA (mRNA) and noncoding RNA, within a given cell, tissue, or organism. Typically, from a given transcriptome, the relative transcript expression is compared between two or more conditions. In doing so, researchers are improving our understanding of the underlying mechanisms controlling behavior and cognition.

## Technological Advances Promote Transcriptomic Research

Prior to the availability of transcriptomic approaches, researchers were restricted to analyses of individual genes of interest, unable to document the simultaneous expression patterns for thousands of transcripts in response to behavioral experiences. High-throughput methods developed in the mid-1990s and 2000s yielded two techniques to survey the transcriptome more broadly: microarrays and “next-generation” RNA sequencing (RNA-seq) (Lowe et al. 2017). For each method, RNA is isolated from the sample and converted to a more stable complementary DNA (cDNA). Microarrays measure the relative abundances of cDNA for thousands of transcripts bound to the microarray slide. Microarray studies,

however, are restricted to analyses of expression patterns for only the subset of transcriptome available on the given array slide, and slides have primarily been developed for model or economically important species. RNA-seq, by contrast, provides a relatively unbiased catalog of the transcriptome by broadly identifying the nucleic acid sequences of the cDNA sample and quantifying relative transcript abundances between samples and treatments. Although RNA-seq was initially very expensive (>\$1000 per sample), new technology and protocols (e.g., TAG-seq; Meyer et al. 2011) continue to reduce the cost of this approach. RNA-seq data analysis requires significant computational resources, but the research community has now developed a rich suite of open-source and proprietary software to facilitate analyses (Conesa et al. 2016).

## Transcriptomics in the Brain

Understanding gene expression in the brain has been a long-standing interest in behavior and cognition research. With the advent of transcriptomic profiling, studies are now able to pinpoint numerous genes with expression levels related to the behavior of interest, most of which were previously overlooked in candidate gene studies. Correlations among genes in response to behavioral experiences or phenotypes can further determine important molecular pathways and yield new hypotheses regarding the underlying functional mechanisms controlling behavior (Robinson et al. 2008). RNA-seq in particular provides researchers the ability to embrace phenotypic variability of non-model organisms (Calisi and MacManes 2015), to understand not only the genes associated with behaviors but also how behaviors evolve (Bell and Robinson 2011).

Transcriptomic studies alone, however, do not resolve causal mechanisms underlying behaviors of interest. Experimental support via genetic manipulations, such as gene silencing or editing, can help to distinguish causation from correlated gene expression patterns (Bendesky et al. 2017). Yet, behavioral and cognitive functions are

regulated by multiple genes that interact in networks, further complicating efforts to determine exactly how gene expression relates to behavior (Harris and Hofmann 2014). Recent efforts that link expression profiles with variants in the DNA can help to identify genetic variants that alter gene expression, known as expression quantitative trait loci (eQTLs; Majewski and Pastinen 2011). Coordinating transcriptomics with other genomic tools, in both model and non-model systems, holds great promise to provide insights into the molecular mechanisms underlying behavioral functions that were only recently made available.

## Conclusion

Identifying the genetic factors that control behavioral and cognitive responses is a major challenge. Candidate gene studies provided foundational studies of the genetics involved in brain-behavior relationships. Now transcriptomics is rapidly building on this knowledge base and contributing to a more integrative understanding of behavior and cognition.

## Cross-References

### ► Gene Expression Profiling

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## Transection

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## Synonyms

To divide by cutting transversely/longisection

## Definition

Transection is usually straight line along which measurements or observations are made at regular intervals.

## Transection

Transection is a dissection of body transversely via accident or experimental purposes. Accidental transection primarily includes spinal, liver, and nerve transection, all of which may cause injury. Experimental transections are those which prepare animals or human cadavers for anatomical exploration. Transection also allows ethologists and anatomists to study various animal species.

Priyanka Verma and Umesh Kumar contributed equally with all other contributors.

Before transecting any structure, the important step is to separate the part of body from underlying tissues by blunt dissection, then insert a trimmed instrument underneath it, and cut it upward. Scissors and blunt blades are used for this purpose. Some important transection such as spinal, liver, brain, and nerve and its resection procedure are discussed in the next section.

## Brain Transection

Brain transection helps to understand the intricate and internal structure of the brain. Anatomists discovered that the hypothalamus is responsible for biting, clawing, and hissing in canines with the use of transection technique (Dewey and Da Costa 2015). Multiple coronal sections of the human brain are used to study the structure of the brain and find out novel neurologic anatomical markers for diagnostic purposes (Mai et al. 2015). Henry Molaison suffered from epilepsy. After case study, a surgeon transected his hippocampus region for the treatment of epilepsy. After transection of hippocampal region, the patient's epileptic attack is normal, but he suffered a severe memory loss. Researchers concluded from this transection that hippocampal region is active during memory formation and later recall (Kalat 2015).

## Spinal Cord Transection

The internal anatomy of spinal cord is clearly visible in a transverse section. A transverse section shows white matter in the periphery, gray matter inside, and a tiny central canal filled with cerebrospinal fluid at its center (Chandler et al. 1993). The canal is surrounded by single layer of special kind of glial cells, i.e., the ependymal layer. The ependymal layer is the gray matter, which shaped like the letter "H" or a butterfly. The H shape and size of the gray matter vary according to spinal cord level. At the lower levels, i.e., away from the brain, the ratio between gray matter and white matter is greater than in higher levels, i.e., closer to the brain, mainly because lower levels contain less ascending and descending nerve fibers (Brown 2012).

Spinal cord transection also results in a loss of function such as mobility or feeling. Transections can be complete, incomplete, or hemitranssections.

Complete transection is complete loss of motor and sensory functions of the body below the transection level. It is the most devastating nerve injury. Incomplete transection is partial loss of motor and/or sensory functions of the body, whereas hemitransection is caused by damage to one half of the spinal cord and motor functions with loss of temperature and pain sensation. Spinal cord transection can be diagnosed by clinical and radiological evaluation. Immediate immobilization and alignment of spine at the accident site followed by surgery are the available treatment for spinal transection (Scholtes et al. 2012).

### Liver Transection

Liver anatomy comprises into eight functionally independent segments based on transversal plane. Each segment of liver has its own vascular inflow, outflow, and biliary drainage. There is a branch of the portal vein, hepatic artery, and bile duct in the center of each segment, and in the periphery of each segment, there is vascular outflow through the hepatic veins. This classification of liver is known as Couinaud classification (Vauthey et al. 2012). Ultrasonography, computed tomography, magnetic resonance, and radiography are the technique used for assessing the anatomy and damage to the liver. Damage/transversal cut to the liver due to accidental transection results in excessive hemorrhage (Heriot and Karanjia 2002; Ronnie 2007).

### Nerve Transection

Nerve transection is transversal nerve injury that results in damage in the endoneurium layer, i.e., myelin sheath of nerves, axon, and demyelination in the neuron. It is classified into three types based on the occurrence of demyelination and the degree of axons injury and the injury of the connective tissues of the nerve. First level is neurapraxia, which is defined by focal segmental demyelination without damage to the axons or the connective tissues. It is mildest form of injury that can be easily recovered. Another is axonotmesis, which deals with either axon damaged with intact myelin sheath, both axon and myelin sheath damaged. Neurotmesis (nerve and the nerve sheath are disrupted) is the most severe form of peripheral

nerve injury, which is a complete transection of the axons and connective tissue layers of the nerve (Geuna et al. 2009).

### Cross-References

- [Hippocampus](#)
- [Hypothalamus](#)
- [Neuroanatomical Plasticity](#)
- [Xenotransplantation](#)

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### Transfer

- [Migration](#)

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## Transfer Index Paradigm

- [Two-Alternative Forced-Choice Paradigm, The](#)
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## Transfer of Learning

- [Learning to Learn](#)
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## Transferring

- [Primate Suspensory Behavior](#)
- 

## Transformation

- [Conjugation](#)
- 

## Transgenic

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## Synonyms

[Genetically modified](#)

## Definition

Transgenic refers to an organism that contains genes from another organism introduced into its genome through genetic engineering techniques.

## Introduction

A transgenic, or genetically modified, organism is one that has been modified through recombinant DNA technology, which involves either combining DNA from different genomes or inserting foreign DNA into a genome (Pray 2008). That is, a transgenic organism is one that contains a gene or genes (from other organisms) that have been artificially inserted.

## Transgenic Organisms

A transgenic animal, for instance, would be an animal that underwent genetic engineering. It contains material from at least one unrelated organism, e.g., from a virus, a plant, or from another animal. This process of introducing an exogenous or foreign gene is transgenesis.

GloFish are a type of transgenic zebrafish (*Danio rerio*) that have been modified through the insertion of a green fluorescent protein (*gfp*) gene. There are several *gfp* gene constructs, each encoding a different colored phenotype, from fluorescent yellow to fluorescent red. US Food and Drug Administration has approved GloFish for human use. It is the only recombinant-DNA animal that has been approved for human use. Approval of their use has raised important questions about whether, and to what extent, genetically modified animals should be made available to consumers (Pray 2008).

A **transgene** is a gene or genetic material that has been transferred by any artificial techniques from one organism to another. The introduction of a transgene (called “transgenesis”) has the potential to change the phenotype of an organism (Clark et al. 1993).

## Applications

One of the essential applications of transgenesis is for experimental research processes. Animal models are being created to introduce a particular disease for experimental studies. These models are referred to as transgenic disease models. An



experimental mouse model, specifically referred to as a transgenic mouse, is a mouse with a piece of foreign DNA integrated into its genome through recombinant DNA techniques. Most transgenic organisms are generated in the laboratory for research purposes. For example, “knock-out” mice are transgenic mice that have a particular gene of interest disabled. By studying the effects of the missing gene, the normal function of the gene can be understood in a better way.

## Examples

Transgenic organisms have also been developed for commercial purposes. The most famous examples are food crops like soy and corn that have been genetically modified for pest and herbicide resistance. These crops are widely known as GMOs (genetically modified organisms). There are some other prominent examples of transgenic organisms with commercial value.

1. **Golden Rice:** It is a genetically modified rice that produces beta-carotene, the precursor to vitamin A. Vitamin A deficiency is a public health problem for millions of people around the world, particularly in Africa and Southeast Asia. In 1997, five million children developed xerophthalmia, a medical condition caused by vitamin A deficiency, in Southeast Asia alone (Sommer 1989). Of those children, nearly a quarter million went blind (Burkhardt 1997). To combat this, scientists used biolistics to insert the daffodil phytoene synthase gene into Asian indigenous rice cultivars (Burkhardt 1997). However, Golden rice is still awaiting regulatory approval.
2. **Transgenic Goats:** These goats have been modified to produce FDA-approved human antithrombin (**ATryn**). It is used to treat a rare blood clotting disorder in humans. Transgenic goats have also been made to produce spider silk, which is one of the strongest materials, in their milk.
3. **Genetically Modified Bananas:** These genetically engineered bananas contain a vaccine. Bananas provide an easy means for delivering

a vaccine (especially to children) without the need of a trained medical professional.

## Conclusion

There are many examples of transgenic organisms with extensive uses. It can be concluded that transgenic animals have revolutionized the field of Modern Biotechnology because of their tremendous applications and opened the door for curing complex genetic diseases. Genetically modified crops also have been able to raise the hopes for improving the quality of life of humans.

## Cross-References

- [Gene Expression](#)
- [Hybrid Vigor](#)
- [Recombination](#)

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## Transitivity

- [Matching-to-Sample: Comparative Overview](#)

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## Translation

- [Gene Expression](#)

## Translocation

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## Synonyms

[Genetic translocation](#); [Chromosomal translocation](#)

## Definition

A translocation is a chromosomal ability, in which chromosome part breaks down and reattaches with another chromosome. It is easily quantified by the evaluation of the karyotype of the affected cells. Chromosomal translocation usually observed in the case of leukemia and other cancers.

## Introduction

Translocation is a chromosome aberration in which a part of a chromosome breaks and reattaches to the different chromosomes. Chromosomal translocation can be identified by analyzing the karyotype of the affected cells. Translocation was first cytologically reported in the late nineteen and early twenty centuries as a novel chromosome that predominantly present in tumor cells. It can be easily observed through cytogeneticist during karyotype study, which is an ordered arrangement of an individual's metaphase chromosomes. It is commonly reported in cancerous cells, and sometimes

produces oncogene that is accountable for malignant transformation (Aplan et al. 2005). Translocation in humans is linked with many disorders such as mental retardation, infertility, and cancer (Santos et al. 2000).

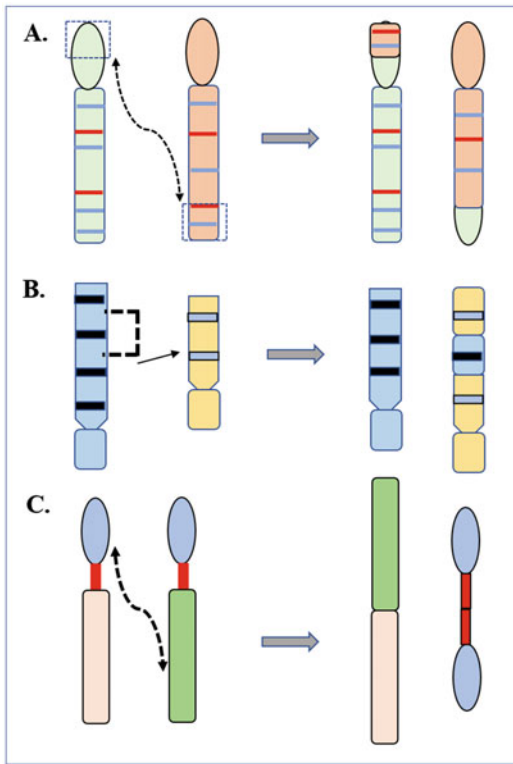
## Characteristics of Translocation

- Chromosomal translocation is a result of unusual rearrangement of chromosomes.
- It is involved in the generation of a novel chromosome.
- It alters the size of the chromosome as well as the position of the centromere.
- Translocation requires the break down of double-strand DNAs at two different places.
- It occurs many times during the evolution of species and provides help in the identification of closely related species.
- Translocation is mostly associated with a negative consequence such as nut and rarely provides organism adaptation advantage.

## Types of Translocation

Translocation is generally categorized as balance and imbalance translocation. However, it can also be classified as reciprocal, nonreciprocal, and Robertsonian translocation (Fig. 1).

- Reciprocal translocation:** It is an interchange of chromosomal parts between two nonhomologous chromosomes which provides a new linkage relation. Reciprocal translocations are usually harmless and are also transmitted to the next generation. The incidence of reciprocal translocation is 1 in out of 500 to 625 in new-born human (Griffiths 1970).
- Nonreciprocal translocation:** It is one-directional transfer of chromosomal segment to another chromosome. Furthermore, this may drastically alter the chromosome size and position of its centromere (Rezaei et al. 2020).
- Robertsonian translocation:** This is a widespread type of translocation found in humans



**Translocation, Fig. 1** Schematic representation of the different type of chromosomal translocation. (a) Reciprocal translocation, (b) nonreciprocal translocation, and (c) Robertsonian translocation

with the frequency of 1 out of every 1000 babies born. This type of translocation typically found in acrocentric chromosomal, in which the long arm of a particular type of chromosome fused with another chromosome (Poornima et al. 2020; Watson 2018; Hasanzadeh-Nazar Abadi et al. 2014). The acentric chromosome in human DNA are chromosome 13, 14, 15, 21, and 22 undergo there is some characteristic Robertsonian translocation such as:

- Chromosome 13 translocate with chromosome 21
- Chromosome 14 translocate with chromosome 21
- Chromosome 15 translocate with chromosome 21
- Chromosome 21 translocate with chromosome 22

(d) **Balance and unbalance translocation:**

Translocation further may be classified as balance and unbalance translocation. In balance translocation, the exchange of material is without extra or missing genetic information, and there is no alteration in the functionality of the genes. Example of balanced translocation between chromosomes 1 and 11 associated with the decline of the white matter integrity frontal commissural of the brain (Thomson et al. 2016). Additionally, a balanced  $t(1;11)$  translocation was first defined as a single locus significant risk factor that concerns with several psychiatric disorders. It is a rare genetic variation which is the result of chromosomal translocation and can provide help to elucidate the pathophysiology of brain disorders. The translocation involved in the formation of significant linkage with the clinical phenotype that comprised of several brain disorder such as schizophrenia, bipolar disorder, and major depressive disorder.

On the other hand, in unbalanced translocation, the exchange of chromosomal material is unequal resulting in the addition or loss of the gene in the genetic material.

## Role of Translocation in Human Disease

There are several human diseases in human that are the result of chromosomal translocations (Table 1). Some of them are discussed below:

- (a) **Cancer:** Translocation results in disruption or dysregulations of normal gene function. These genomic rearrangements by translocation are considered as the primary cause of several cancers. The research from the last few decades reported that clinical cytogenetics have been able to identify specific point of chromosomal breakdown that is responsible for various cancers as leukemia, lymphoma, as well as sarcoma. Usually, all translocation observed in cancer occurs in somatic cells, and therefore translocations are nonheritable. Chromosomal translocation is the hallmark of cancer, and the mechanism involved in this event needs a clear

**Translocation, Table 1** List of diseases associated with chromosomal translocation

| S.No. | Disease                      | Chromosomal translocation                                             | References            |
|-------|------------------------------|-----------------------------------------------------------------------|-----------------------|
| 1.    | Down syndrome                | Extra 21 chromosome may be attached to the 14 or 13,15,22 chromosomes | Prusti et al. (2014)  |
| 2.    | Schizophrenia                | 1(1;11) (q42.1;q14.3)                                                 | Doyle et al. (2015)   |
| 3.    | Malt lymphoma                | 1(11;14) (q13;q32)                                                    | Li et al. (1999)      |
| 4.    | Synovial sarcoma             | t(X; 18) (p11.2;q1 1.2)                                               | Shipley et al. (1994) |
| 5.    | Acute promyelocytic leukemia | t(15; 17) (q22;q21)                                                   | Liu et al. (2020)     |
| 6.    | Myxoid liposarcoma           | t(12;16) (q13;p11)                                                    | Son et al. (2012)     |

distinction between the causative risk factor and its correlative. Hogenbirk reported chromosomal translocation risk is not related to promoter stalling (Spt5), transcriptional activity, or off-targeting activity of the activation-induced cytidine deaminase (Hogenbirk et al. 2016).

- (b) **Brain disease:** A rare genetic variant that is the result of balanced translocation can help to elucidate the pathophysiology of brain disorders. A balanced translocation t(1;11) is a significant risk factor for psychiatric disorders, including schizophrenia, bipolar disorder, and recurrent major depression. Additionally, this translocation affects the structure and function of the prefrontal and temporal region of the brain. Translocation leads to reduce thickness of the cortex in the left temporal lobe that is correlated with the psychopathology and positive psychotic symptom severity (Klar 2004).
- (c) **Infertility:** Chromosomal translocation is frequently associated with male fertility. Infertility means incapability to perceive after at least 1 year of unprotected intercourse. The frequency of infertility is 15–20% in couple in their reproductive year. Male infertility is a result of reciprocal balanced translocation t (10;19) (q11.2; q13.4) was observed in oligozoospermic infertile men with no Y-chromosome microdeletions (Harton et al. 2014; Kara et al. 2014).

## Application of Translocation

Translocations are primarily involved in the origin of the new chromosome by transfer of the segment

of chromosome to the nonhomologous chromosome or the other site of the same chromosome. Translocation can be easily observed when scientist tries to compare the genome of the closely related species, and it was observed multiple times during evolution. Usually, translocation is associated with a negative consequence such as several psychiatric disorders, cancer, and infertility, but rarely translocation helps in the adaptation of species in a new environment. Translocation can be easily evaluated using the molecular probe and provides a unique insight into the molecular origins of various diseases, including psychiatric disorders.

## Cross-References

- [Chromosomes](#)
- [Evolution](#)
- [Fertility](#)
- [Genes](#)
- [Karyotype](#)
- [Speciation](#)

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## Transplant

### ► Xenotransplantation

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## Transplantation

### ► Xenotransplantation

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## Transposable Elements

### ► Repeat Sequences

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## Transposition

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## Synonyms

[Relational learning](#)

## Definition

Transposition is a form of relational learning in which a learned relational response (e.g., smaller) transfers to a novel pair of stimuli after a simultaneous stimulus discrimination training.

## Introduction

The first transposition experiment has been designed by Wolfgang Köhler (1918/1938). In these experiments, chickens and chimpanzees

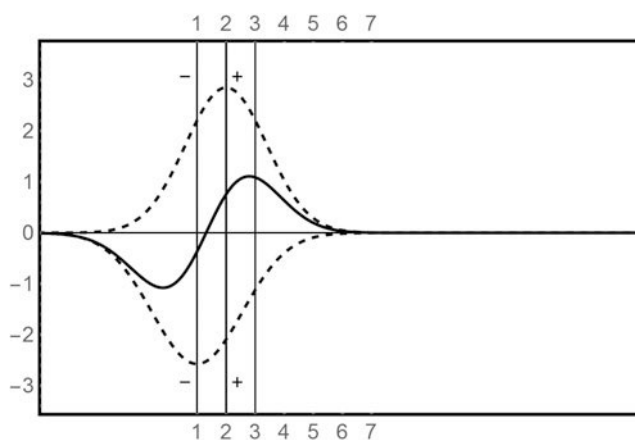


were presented with a two-alternative simultaneous discrimination in which a response to a darker shade of gray was not reinforced and a response to a lighter shade of gray was reinforced (or vice versa). Once the original discrimination was learned, the subjects were given a choice between the original, light shade of gray and a novel, still lighter, shade of gray. Köhler proposed that learning to respond to a specific shade of gray (*absolute responding*) should result in a preference for the original gray shade; however, learning to respond to the relationship between the two shades (*relational responding*) should produce a preference for a novel shade of gray despite the presence of the previously reinforced stimulus. Both chickens and chimpanzees indeed selected the novel shade on over 70% of the trials. Köhler termed this behavioral result transposition – just as the notes of the melodies do not change their relation to each other when the melodies are transposed to different keys, the learned relation does not change when the new stimuli are introduced.

### Associative Account of Transposition: Spence (1937)

In an elegant theoretical account, Spence (1937) proposed that a seemingly “relational” behavior

in Köhler’s transposition experiment could be explained in terms of reinforcement history. The three simple assumptions behind Spence’s discrimination theory are illustrated in Fig. 1. (1) A reinforced stimulus, or an S+ (S2 in Fig. 1), develops an excitatory gradient (indicated by a dashed line) that gradually declines as the stimuli become increasingly dissimilar from the S+. (2) A nonreinforced stimulus, or an S– (S1 in Fig. 1), develops an inhibitory gradient (also indicated by a dashed line). (3) A response to any stimulus along the sensory dimension is predicted by the postdiscrimination stimulus generalization gradient (PDG) obtained as a sum of an excitatory gradient and inhibitory gradient: The higher the resulting associative value of the stimulus, the greater the preference for that stimulus in the choice test. As Fig. 1 shows, the resulting PDG produces a positive *peak shift* away toward an even larger, novel stimulus S3; a comparison of the resulting associative values suggests a preference for a novel, relationally correct S3 instead of previously reinforced stimulus S2. Although first posited theoretically, the existence of peak shift has been confirmed experimentally providing a striking confirmation of Spence’s theory (Blough 1975; Hanson 1959; Honig 1962; Honig and Urcuioli 1981).



**Transposition, Fig. 1** Hypothetical excitatory and inhibitory gradients (*dashed lines*) and postdiscrimination generalization gradient (*full line*) illustrating predictions of Spence’s (1937) discrimination theory after training with an S2+ S1– discrimination. Vertical lines illustrate the location of previously reinforced stimulus S2, previously

nonreinforced stimulus S1, and a novel stimulus S3. Note that the postdiscrimination generalization gradient indicates “relational” choice in a pair S2–S3 due to the shift of the peak in the postdiscrimination stimulus generalization gradient

However, peak shift is not the inevitable consequence of simultaneous stimulus discrimination. Extensive amount of training sharpens excitatory and inhibitory gradients which reduces or even completely eliminates peak shift (Gerry 1971; Migler and Millenson 1969; Terrace 1966). In addition, the S+ and S− that are located far from each other often fail to produce peak shift even without overtraining (Derenne 2006; Hanson 1959; Thomas et al. 1991). In other words, under certain circumstances PDG will not predict a “relational” response to the novel pair (see Lazareva 2012 for a review).

### Intermediate-Size Transposition

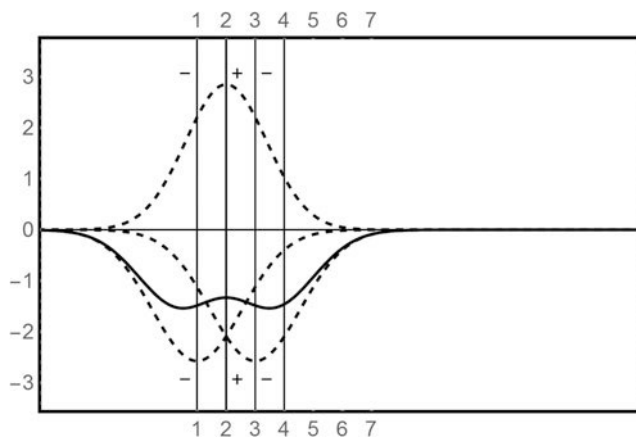
In a different version of transposition experiment, subjects are trained to select a middle out of three stimulus values (for example, S1− S2+ S3−) and then presented with a novel trio comprising at least one novel stimulus (for example, S2-S3-S4); this design has often been termed an intermediate size problem. As Fig. 2 illustrates, Spence’s approach does not predict a “relational” choice in this novel trio, instead suggesting a preference for a previously reinforced stimulus. In line with this prediction, many species (e.g., pigeons, rats, rhesus monkeys, turtles) have

shown either no preference or preference for a previously reinforced stimulus in an intermediate-size problem (Brown et al. 1959; Laverty et al. 1969; Spigel 1963; Zeiler 1965). However, other species (e.g., chimpanzee, rhesus monkeys) have been found to display a clear preference for a middle value in a novel trio of stimuli (Gentry et al. 1959; Gonzalez et al. 1954).

### Multiple-Pair Transposition

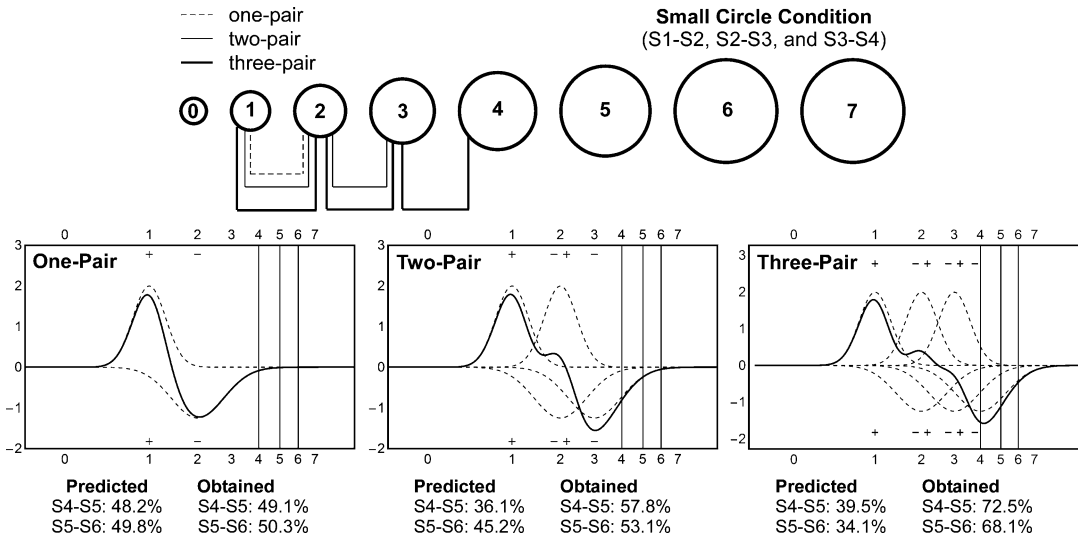
Transposition designs that utilize multiple stimulus pairs during training pose additional challenges for associative account of transposition (Johnson and Zara 1960; Lazareva et al. 2005, 2008, 2014; Marsh 1967; Sherman and Strunk 1964). Intuitively, it is plausible to assume that multiple instantiations of the same relational rule will lead to a stronger relational learning. On the other hand, the PDGs produced by multiple-pair training frequently do not predict this outcome.

Consider an example depicted in Fig. 3 in which pigeons were trained to select a smaller of the two circles after one-pair, two-pair, and three-pair training (Lazareva et al. 2008). During testing, all pigeons were presented with the novel testing pairs S4-S5 and S5-S6. As the left panel of the Fig. 3 illustrates, the PDG predicts no



**Transposition, Fig. 2** Hypothetical excitatory and inhibitory gradients (*dashed lines*) and postdiscrimination generalization gradient (*full line*) illustrating predictions of Spence’s (1937) discrimination theory after training with an S1− S2+ S3− intermediate-size discrimination. *Vertical lines* illustrate the location of previously reinforced and

nonreinforced stimuli, as well as the location of the novel stimulus S4. Note that the resulting gradient does not predict correct choice of the middle stimulus S3 in a novel trio S2-S3-S4; instead, it suggests a preference for the previously reinforced stimulus S2



**Transposition, Fig. 3** Schematic representation of experimental design in the small circle condition presented in Lazareva et al. (2008), together with the examples of theoretical excitatory and inhibitory gradients (dashed

lines), the derived postdiscrimination generalization gradient (smooth line), the testing pair accuracy predicted by the postdiscrimination stimulus generalization gradient and the obtained accuracy produced by pigeons

strong preference for either stimulus after one-pair training as the distance between training and testing stimuli is too large for substantial generalization to occur. After two-pair training (middle panel of Fig. 3), the PDG predicts the preference for the “relationally incorrect” S5 in the pair S4-S5 and no strong preference in the pair S5-S6. After three-pair training (right panel of Fig. 3), the PDG predicts “relationally incorrect” choice of a larger stimulus in both testing pairs. Despite these predictions, pigeons increasingly prefer a smaller, “relationally correct” stimulus in both testing pairs as the number of training pairs increase. These and other similar findings led us to propose a three-component model of transposition that describes subject’s behavior as a result of joint influences of generalized associative strength and relational learning (Lazareva et al. 2014).

## Conclusion

Historically, research on transposition has generated substantial body of empirical evidence and theoretical development (see Lazareva 2012; Reese 1968; Riley 1968, for reviews). Together

with the recent research, the evidence suggests that animals indeed can respond to relations in a transposition task although their behavior can be moderated by the prior history of reinforcement, especially after one-pair training. In contrast, multiple-pair training tends to generate robust relational learning and transfer.

## Cross-References

- [Discrimination Learning](#)
- [Relational Concepts and Symbolic Logic](#)
- [Transfer of Learning](#)

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## Transposons

### ► Repeat Sequences

## Trap Building

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## Synonyms

Predation; Trapping; Web Construction

## Definition

Trap building is a method by which predators catch prey through the use of a forged structure.

Trap building is a method by which predators catch prey through the use of a forged structure. Trap building is evident in many animals, primarily invertebrate species and humans, that have separately converged on trap building as a specialized form of hunting. There are two evolutionary routes to building traps. Humans demonstrate the “big-brained” route to building traps whereas other trap-building animals demonstrate the “small-brained” route (Hansell, 2007). Humans use collected materials and behavioral flexibility to construct traps that catch prey in water, land, and air, whereas other animals exhibit species-specific trap designs that rely on simple and relatively inflexible construction behaviors and, often, self-secreted materials. Despite the many differences between the trap building of humans and other animals, similarities in nonhuman and human trap types are evident, suggesting there are a limited number of good solutions to the problem of catching prey by trapping.

Spiders build traps via web-making. The orb web spider (*Araneus diadematus*) constructs a spiral web that has a specific capture thread placed on a radial array of threads (Zschokke, 1996). Orb web spiders use a consistent set of tactics in variable sequence to construct a seemingly complex design. When an orb web spider is isolated from birth, it will still construct a web (Zschokke, 1996). *Zygiella x-notata* is a spider that uses a slightly different orb design and rests at the edge of the web where it can hide from unsuspecting prey (Hansell, 2007). Any disturbance to the web causes a vibration, prompting the *Zygiella x-notata* to rush out and kill the prey. Spider webs are traps tailored to capture a particular prey and some flying insects, like butterflies and moths, have evolved the anti-capture countermeasure of detachable scales. An evolutionary arms race between predator and prey is also evident in the trap building of the bolo spider (*Mastophora hutchinsoni*). The bolo spider is a master moth-catcher, using chemicals that mimic female moth sex attractant signals to lure male moths into the web (Haynes et al., 2002). Spiders demonstrate

species-specific web design and their trap-building behavior is highly specialized, genetically determined, and inflexible. The silk created by spiders is an example of a self-secreted building material. Silk is preferable to mucus for building nets because it is more durable, stronger, can be spun on land or in water, and it recovers its shape after being deformed (Hansell, 2007).

It appears that, in many trap-building species, natural selection has modified mucus secretions that formerly assisted with locomotion to trap prey. *Praxillura maculata* is a burrow-dwelling marine worm that uses mucus to build a net to capture fine particles suspended in water (Hansell, 2007). *Gleba cordata* is a mid-water, oceanic snail with no shell that feeds on plankton. To capture plankton, this species secretes and deploys a finely meshed, sticky mucus net that can be one-third of a meter or more across (Hansell, 2007). *Oikopleura dioica* is a small, tadpole-like creature that builds a capsule of mucus as both a dwelling and a trap, capturing plankton as prey (Hansell, 2007). A multipurpose structure like the dwelling/trap of the *Oikopleura dioica* does not require imagination or behavioral flexibility; thus, complex architecture is possible with a small brain and efficient use of materials. These behaviors are likely highly canalized. For example, Klokócovnik and Devetak (2014) demonstrate that non-pit-builder antlions show less stereotypic predatory behavior compared to pit-building antlions.

The burrowing owl is an example of an animal that uses bait to attract prey, although the owl's burrow may not qualify as a trap. The burrowing owl gathers cow dung and places it at the burrow entrance to attract dung beetles and other insects as prey (Smith & Conway, 2007). The built structure of the burrowing owl is not a trap because direct predation is the method employed to capture the insects. The prey is not trapped by the dung or by the burrow. By this definition, there are no birds that build traps (Hansell, 2007).

## Cross-References

- [Chemical Cues](#)
- [Convergent Evolution](#)



- [Natural Selection](#)
- [Predator](#)
- [Prey](#)

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## Trapping

- [Hunting](#)
- [Trap Building](#)

## Trap-Table

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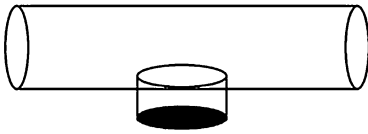
Causal reasoning refers to the understanding of how and why one event can cause another. A key part of causal reasoning is the ability to reason about invisible forces such as gravity or weight rather than simply relying on perceptual cues (Limongelli et al. 1995; Reaux and Povinelli 2000). For example, birds may drop stones to collapse a platform baited with food by reasoning that the force exerted by the falling stone will

collapse the platform (von Bayern et al. 2009). However, an alternative explanation is that they learn to solve problems through associative learning by mentally pairing behaviors or cues with reward. In our example of stone-dropping birds, the animals may have simply learnt, through trial and error, a procedural rule of “if-an-object-is-dropped-onto-the-platform-it-will-collapse” without having any understanding of *why* dropping the stone collapses the platform.

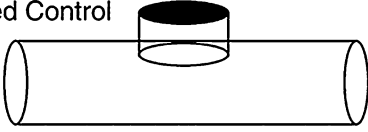
The trap-tube test was designed by Visalberghi and Limongelli et al (1995) to distinguish between these types of competing explanations. In the typical trap-tube task, food is placed in a horizontal tube with a trap (a hole with a base which food cannot be retrieved from). In order to obtain the food, the animal must extract it in a direction that avoids the trap. A causal account of an animal learning to solve the task would be that the animal develops an understanding that if it pushes the reward over the hole, gravity (an unobservable force) will cause the reward to drop into the trap. An associative account of such success is that over the course of repeated trials, through trial-and-error, the animals develop a procedural rule such as “insert-the-tool-into-the-end-furthest-from-the-reward.” As both accounts can explain success in a trap-tube task, Limongelli and Visalberghi designed an ingenious control where the tube was inverted, making the trap non-functional. If an animal had used causal reasoning, it should no longer avoid the trap, as it would understand that objects cannot fall up. In contrast, if the animal had used associative learning, the trap would be an aversive cue, as its position had in the past predicted failure, and so the animal would continue to avoid the trap.

In 1994 and 1995, Limongelli and Visalberghi presented the trap-tube task (Fig. 1) to capuchin monkeys and chimpanzees. One out of four capuchin monkeys learned to extract the food out of the tube while avoiding the hole. However, in the inverted tube control condition, the one successful capuchin continued to avoid the trap. This led the authors to conclude that the capuchin monkey had solved the trap tube using a procedural rule of inserting the stick in the opening furthest from the reward. As the trap was in the center of the

### Trap-tube Test



### Inverted Control



**Trap-Table, Fig. 1** Diagram of trap-tube test and inverted control condition. (Adapted from “Investigating Physical Cognition in Rooks, *Corvus frugilegus*” by Seed et al, 2007. *Curr Biol*, 16, 698. Copyright 2006 by Elsevier Ltd)

tube, inserting the stick in the furthest end from the food and pushing would allow the capuchin to avoid the trap. When two out of five chimpanzees learned to solve the trap-tube tasks, the authors attempted to control for this procedural rule by running a second experiment where the trap was placed on one side of the tube or the other. The chimpanzees passed this control, leading the authors to conclude that, unlike the capuchins, the chimpanzees were using causal understanding of the task in order to obtain the reward (Limongelli et al. 1995). However, Povinelli critiqued the authors’ interpretation, arguing that there were several other associative rules that chimpanzees may have learned, such as “push-the-reward-away-from-the-trap,” which could not be ruled out because the inverted-trap condition had not been run. Povinelli and Reaux (2000), therefore, ran the trap-tube task with chimpanzees but included the inverted-trap condition and several other novel conditions where inserting the tool in the end furthest from the reward was not necessary for success. They found that the chimpanzees failed these controls and so concluded that the chimpanzees were relying on procedural rules to solve the trap-tube task.

## Critique of Early Trap-Tube Experiments

Whereas Povinelli’s results were consistent with the hypothesis that chimpanzees do not use causal

reasoning to solve the trap-tube task, this conclusion relies on the interpretation of chimpanzees’ failure in the inverted tube control condition. Such interpretation of negative results is difficult because it is possible that the chimpanzees used causal reasoning but failed the control conditions for other reasons. This issue became more pertinent after Tebbich and Bshary (2004) reported that one out of six woodpecker finches (a tool-using bird from the Galapagos islands) was able to solve the trap-tube task and also pass the inverted-trap condition. A key difference in the finches’ and chimpanzees’ tasks was that the finches could use their tool to pull the reward out of the tube, whereas the chimpanzees could only use the tool to push the reward. Mulcahy and Call (2006) allowed great apes to pull the food from the tube and found that the apes solved the trap tube much faster than in past studies and then ignored the inverted trap. The authors then presented the apes with the standard trap tube setup where the apes could only push and found they now failed, confirming that earlier results had been confounded by subjects only being able to push the reward (Mulcahy and Call 2006).

As well as methodological issues with the interpretation of prior results, Silva and colleagues tested humans’ performance in the trap-tube task and suggested that, despite its intuitive logic, there were conceptual flaws with the inverted trap-tube condition. Although the humans were better at solving the task (almost all of the humans involved solved it rapidly), humans tended to avoid the trap even when it was inverted. As it is unlikely that the humans did not understand the causal structure of the task, the authors argued that a failure to show indifference in the inverted trap condition was not sufficient to rule out causal accounts of animals’ performance at this task (Silva et al. 2005).

## The Creation of the Trap-Table Task

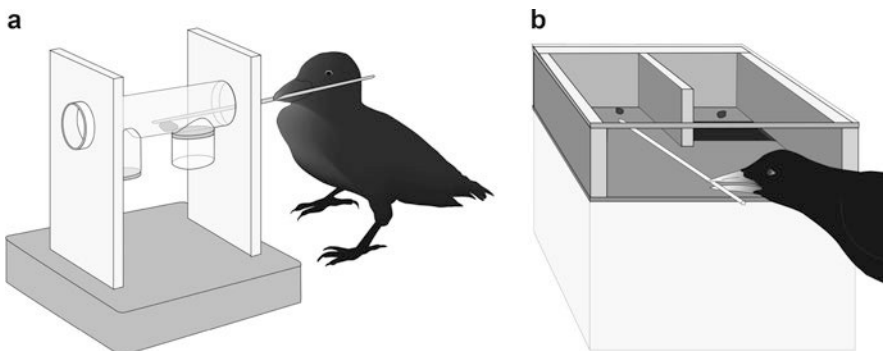
In light of these methodological and conceptual critiques, more recent studies have attempted to reduce task demands and have used transfer tasks as additional control conditions. Task demands

were reduced by either removing tools or having tools already inserted so that participants did not need to manipulate the tools to obtain the reward. Transfer tasks involve a subject learning to solve the trap tube task before being presented with a transfer task, a novel task, in which arbitrary perceptual cues are changed, but the causal structure remains the same across both tasks (Martin-Ordas et al. 2008; Seed et al. 2006; Taylor et al. 2009). If the subject is sensitive to the functional properties of the initial task, they should be capable of transferring this understanding to novel tasks. However, if the subject has learned to solve the initial task through associative learning, reliance on arbitrary perceptual cues should prevent the animal from transferring procedural rules effectively, leading it to fail the transfer task.

One influential transfer task is the trap-table task (Fig. 2). In a trap-table task, the subjects must choose between using a rake to retrieve either one reward located behind a trap or another reward located on a continuous surface. This task presents the same conceptual challenge as a trap-tube task, namely avoid pulling the food into a hole, while presenting the animals with a very perceptually distinct set of apparatuses. Thus, in order to successfully transfer the solution of the trap-tube task to the trap-table task, the animals must have learned the functional properties of the trap-tube rather than simply depending on arbitrary perceptual cues.

In the initial trap-table task (Povinelli and Reaux 2000), the chimpanzees were presented with a table that was divided into two halves. On each half of the table, a rake was placed such that pulling on it would pull a reward towards the apes. However, there was a hole on one half of table and so pulling in the rake on that side of the table would result in the reward falling down the hole. The other half of the table was one continuous surface and so pulling on that reward would result in the individual successfully retrieving the reward. One chimpanzee appeared to successfully transfer the solution from the trap-tube experiment to the trap-table experiment, choosing to pull the correct rake significantly more often than chance and also on the first trial. However, considering that the other five chimpanzees failed to solve the trap-table task, Povinelli argued that this success may reflect a preexisting bias of the chimpanzee to prefer the painted continuous surface (a perceptual cue) rather than reflecting a causal understanding of the task.

However, while the poor performance of the apes in the trap-table task is suggestive that the chimpanzees have not understood the functional properties of the trap-tube task, the possibility remains that unrelated task demands were causing the apes to fail and, therefore, potentially masking the apes' causal understanding of the task. In order to control for this possibility, Girndt et al. (2008) tested several species of ape with the



**Trap-Table, Fig. 2** Diagram of a crow solving a trap-tube task (c) and a trap-table (d). While perceptually distinct, the causal structure of both tasks is the same. (Adapted from “Is there a link between the crafting of tools and

intelligence” by Taylor & Gray, 2014. *WIREs Cognitive Science*, 5(6), 696. Copyright 2014 by Wiley Online Library)

original version of the trap-table task and a modified version where the apes had to insert a single rake to obtain the food (rather than choose between two rakes). The apes' performance was much better in the modified trap-table task than in the original, with 80% of subjects solving the task on their first trial. In order to test whether modifying the trap-table task could lead to improved solution transfer, another experiment (Martin-Ordas et al. 2008) presented half of the chimpanzee sample with a trap-tube experiment and the other half with a modified trap-table experiment. After solving one task, the apes were presented with the second task. Although the apes were capable of learning to solve both tasks, performance in the first task did not predict success in the second task, suggesting that the apes were not transferring a solution from one task to the other.

In contrast to the performance of the apes, New Caledonian crows seem capable of transferring their solution from the trap-tube task to trap-table tasks. Taylor et al. (2009) tested six New Caledonian crows with a trap tube test. Three of the six crows learned to solve the task and proceeded to pass a series of transfer tasks where arbitrary cues were successively removed and a further transfer task where they were presented with a trap-table task. In the trap-table task, the crows successfully chose to use a tool to pull a reward located on a continuous surface while avoiding a reward located behind a trap.

While these results may suggest that corvids are using causal understanding to solve the trap-tube task while apes are not, apes are capable of passing other transfer tasks. For example, instead of using a trap table, Seed et al. (2009) modified the trap-tube task by presenting apes with trap-box tasks where the apes could retrieve the food using their fingers rather than a tool. Reducing the task demands improved the chimpanzees' performance and all eight successfully solved two trap-box tasks (Task A and Task B). Six of the apes then took part in two transfer tasks, where, as in past studies with rooks (Seed et al. 2006), there was no consistent cue that predicted success (Task C and Task D). Two individuals solved tasks C and D, ruling out the use of associative learning

and suggesting that apes too may be using causal understanding to solve these problems.

## Conclusions

The performance of corvids and apes in recent trap table tasks and other transfer tasks suggests that they are using more than associatively learned procedural rules to solve the trap-tube task. Rather they seem to learn the functional properties of the task and can use this knowledge to solve novel problems. However, this is not sufficient to prove that animals reason about unobservable forces such as gravity. It is possible that these animals solved these tasks by attending to the observable features of the task which are functionally relevant (such as the need for surface continuity and the inability of objects to pass through solid surfaces) without reasoning about *why* these features are causally relevant (Seed et al. 2006, 2009; Taylor et al. 2009).

Whereas some, such as Povinelli (Povinelli and Reaux 2000), argue that this lack of evidence supports the assertion that nonhuman animals are incapable of reasoning about unobservable forces, this lack of evidence more accurately represents limitations of the trap-tube and trap table paradigms. Whereas animals' performances on transfer tasks such as the trap-table task tell us something about what they have learnt (namely, the functional properties of the task), it is not informative about how they have learnt this (Seed et al. 2009). Therefore, while the trap-table has extended our understanding of animal problem-solving, novel approaches are required to probe whether animals reason about unobservable forces.

Recently, one possible alternate approach has been developed that can distinguish between attention to observable features or interactions and an understanding of unobservable forces. von Bayern et al. (2009) demonstrated that New Caledonian crows, who initially could not solve a task where they had to drop a stone to collapse a platform, learned to do so after receiving experience of collapsing platforms with their beaks. This suggested that the crows might have understood that force

above a certain level needed to be applied to the platform to make it trigger, leading them to drop a heavy object (the stone) when the platform became out of reach of their beak. An alternative explanation is that the crows understood that an observable interaction, contact, needed to occur between the platform and another object (either beak or stone). Thus, while these results suggested that the crows were capable of reasoning about unobservable forces, the contact hypothesis is an alternative explanation. In a follow-up experiment, Neilands et al. (2016) demonstrated that after receiving experience collapsing the platform with their beaks, New Caledonian crows did not discriminate between dropping heavy or light blocks (which were too light to trigger the platform) and so seemed to be using the concept of contact to solve the problem. Although the crows failed, the methodology itself offers much promise for testing for causal reasoning. If a naïve animal drops only heavy objects after being given experience of pushing the platform down with their body, it would provide strong evidence that animals can reason about unobservable forces, provided, of course, that controls show the subject had no preexisting bias for dropping heavy objects.

## Cross-References

- [Associative Learning](#)
- [Tool Use](#)

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## Trap-Tube Problem

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## Definition

**Trap-tube problem.** This task investigates causal reasoning in the physical domain. It consists of a transparent horizontal tube containing a reward



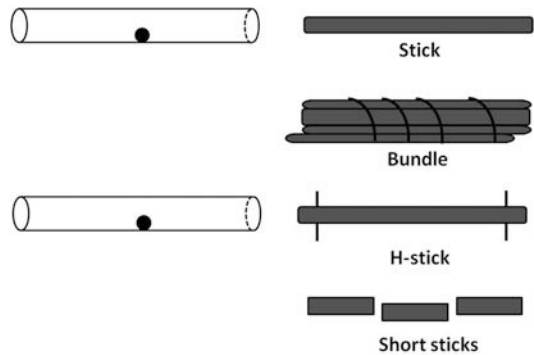
that can be obtained by pushing it out of the tube with a stick. The trap tube has a hole on its bottom surface such that if the reward is pushed above the hole, it falls through the hole into a trap where it cannot be reached. Thus, errors are penalized. The tube transparency allows experimenter and subject alike to view how the tool affects the reward movement throughout the tube and through the hole. In this task an adult human performs correctly on the basis of her/his causal reasoning about the affordances of the tube and the trap. In contrast, other species can be successful by using simpler associative strategies, but control procedures can rule them out.

## Introduction

Success in tasks requiring flexible tool using behaviors appears to imply the ability to understand the relationship between means and ends and the effects produced by acting with the tool. When an animal closely resembling humans, such as a monkey, uses a tool to solve a problem, the human observer is prompted to believe that the processes underlying solution are the same, or almost the same as if a human were solving that problem. The trap-tube task has demonstrated that this might not be the case.

## The Tube Task

The logical antecedent of the trap tube was the tube task, a problem requiring the use of a stick to dislodge an out-of-reach reward positioned in the middle of a transparent tube (Fig. 1, above panel). The tube task investigated how capuchin monkeys (*Cebus apella*, now *Sapajus* spp.) (recent molecular analysis has revealed that capuchin monkeys, formerly identified as the single genus *Cebus*, are two genera, with the robust (tufted) forms (including *apella*, *libidinosus*, *xanthosternos*, and several other species) now recognized as the genus *Sapajus* and the gracile forms retained as the genus *Cebus* (Lynch Alfaro et al. 2012)) deal with the challenges of modifying tools to fit the tube by selecting tools from among



**Trap-Tube Problem, Fig. 1** The tube task (above) and the complex conditions (below). (Redrawn by Luca Antonio Marino from Visalberghi and Limongelli (1994))

several presented (Visalberghi and Trinca 1989) and, subsequently, to compare capuchins' performances to those of other primate species (chimpanzees, *Pan troglodytes*; bonobos, *Pan paniscus*; orangutans, *Pongo pygmaeus* Visalberghi et al. 1995; children, Visalberghi 2000).

Capuchins proficient at pushing a reward out of a transparent tube with a stick were tested in three new conditions in which the provided object(s) had to be modified or combined to become a functional tool and dislodge the reward from the tube (Visalberghi and Trinca 1989, see below panel in Fig. 1). In one condition, the sticks were so short that two of them had to be inserted one behind the other inside the tube to move the food far enough for the monkey to reach it. In another condition, the object (a bundle of thin canes held together by tape) was too large in diameter to fit into the tube. In the third condition, the stick had thin pieces of dowel (which could be pulled out or broken off) inserted transversely at each end so that the ends of the stick could not enter the tube.

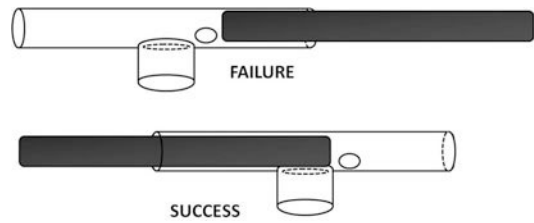
The capuchins solved all conditions within a few minutes. Despite their success, they made many attempts to use the provided object without modifying it or to use parts of the object (e.g., the tape, a splinter) that did not have the necessary properties (e.g., rigidity, length) to displace the food from the tube. Over the ten trials in each condition, the number and/or nature of errors produced by each monkey decreased only slightly. However, when these same capuchins were given

16 choice trials among objects that did not afford insertion or would not reach the food (one too thick, one too short, and one with a transversal block at each end) and one object of appropriate diameter and length, all subjects learned to select the only appropriate object far more often than would be expected by chance (Visalberghi 1993). Thus, capuchins learned by association what features of the objects, surfaces, and actions were most important for success.

In the above tests, each subject eventually was always successful since errors were penalized only in terms of time necessary to achieve success. Without capuchins demonstrating a limited understanding of their own success (and failure), the trap-tube experiment would never have been conceived (Visalberghi and Limongelli 1994, 1996). The trap tube aimed to explore capuchins' appreciation of tools affordances and functioning, of "why" and "how" an event leads to another, an approach that closely reminiscent of the pivotal work of Köhler (1925/1976).

## The Trap-Tube Task

The trap-tube apparatus designed by Visalberghi and Limongelli (1994; hereafter labeled VL-trap-tube whenever necessary to distinguish it from other trap tubes which do not have the same features and challenges) consisted of a transparent horizontal tube containing a reward that can be obtained by pushing it out of the tube with a stick. The trap tube has a hole on its bottom surface such that if the reward is pushed above the hole, it falls through the hole into a trap where it cannot be reached (see Fig. 2). The food reward was randomly placed on the right and on the left side of the hole. To get the food, the capuchin had to insert the stick into the side of the tube from which it could push the food away from the trap. Thus, the subject must take into account the outcome of its action with the stick on the movement of the food (toward or away from the trap) and avoid moving the food over the trap. In this task, the subject 50% success can be achieved by systematically inserting the stick into the same end of the tube or by inserting it into one of the two ends



**Trap-Tube Problem, Fig. 2** The trap-tube task, as in Visalberghi and Limongelli (1994), consists of a transparent tube with a hole in its center and a trap underneath it. The top panel shows an example of wrong insertion of the stick: pushing the stick results in loss of the reward, which falls into the trap. The bottom panel shows an example of correct insertion of the stick: pushing the stick results in retrieval of the reward, which falls out of the tube. (Redrawn by Luca Antonio Marino from Visalberghi and Limongelli (1994))

randomly. Only rates of success higher than chance should be considered as evidence that the subject actively avoids the trap.

Trap avoidance can be obtained either (i) by avoiding the trap through a rule of action based on associative processes (such as push the food away from the trap, or insert the stick from the side farther from the reward) or (ii) by recognizing the outcome of pushing the food into the trap and understanding the underlying causal structure, as humans do. Scientific experiments cannot prove that the subject recognizes the underlying causal structure, but they can rule out parsimonious alternative hypotheses based on associative processes.

## Capuchin Monkeys

Four capuchin monkeys were tested in 14 blocks of 10 trials each. The rate of success was at chance level for three monkeys, whereas that of the fourth subject, Roberta (3 years old), was significantly higher than chance (86%) in the second half of the experiment. A careful analysis of Roberta's behavior demonstrated that she adopted a distance-based rule of inserting the stick in the opening farthest from the reward. Roberta repeatedly looked inside the tube from either side and checked the spatial configuration among stick, tube, and reward. Her behavior seemed to fit the hypothesis that by looking inside the tube entrances, she was estimating the distance of the

reward from them and choosing to insert the stick into the side farther away from the reward. To better explore her comprehension of the trap functioning, Roberta was tested in other conditions in which, regardless in which side of the tube she inserted the stick, she could always obtain the reward (Visalberghi and Limongelli 1994; Fig. 3). Roberta kept using the distance rule (i.e., she inserted the stick from the tube side farther away from the food) even when presented with a trap that was ineffective because the opening had been positioned above the tube (Fig. 3 top left), with a straight transparent tube with no trap (Fig. 3, panel top right), with an opaque trap-tube task (Fig. 3, bottom left), and with a straight opaque tube with no trap (and the reward was placed inside the tube slightly to the right or left of the middle, as was also the case in trials with the trap-tube task, Fig. 3 bottom right).

Generalizing the distance rule to the conditions described above suggested that Roberta was not considering the relevant properties of the trap. However, the generalization of the distance rule was neither “wrong” nor costly, since the reward was always secured. In this respect, it is important to mention that adult humans may also use the same distance-based strategy to determine in which side of the tube to insert the tool when there were no traps or ineffective traps (Silva et al. 2005). Thus, generalization of the distance rule may coexist with an understanding of the functioning of the trap. But, would capuchins abandon the distance strategy if it has a cost, such as losing the reward?

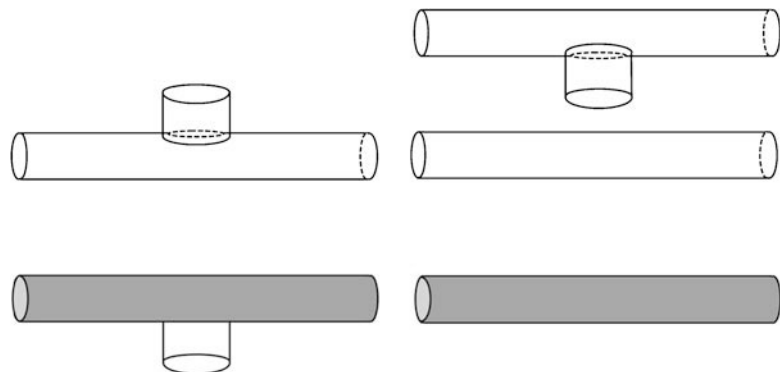
To answer this question, Limongelli et al. (1995) designed a modified trap tube in which the adoption of the distance rule would lead to moving the reward into the trap (Fig. 4); in this modified trap tube, the trap was not centered, and one “arm” of the tube was longer than the other, but the position of the reward inside the tube was as in the trap tube. When tested in 30 trials with the trap-tube condition alternated with 30 trials with the modified trap-tube condition, Roberta used the distance rule regardless of condition, and in the modified trap tube, her rate of success was significantly below chance level. The finding that she did not abandon the distance strategy when costly indicates she did not understand the functioning of the trap tube.

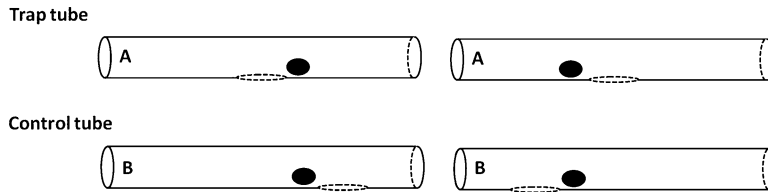
Adult humans anticipate or can imagine the effect of pushing the food with the stick and (simultaneously) the fate of the food when it moves above a hole. Thus, the position of the food with respect to the trap is integral to how we decide where to push the food. Capuchins, even when expert at using sticks to push food from a tube, fail to appreciate the causal relation between their behavior and the food falling into the trap.

### Chimpanzees

The trap tube was also presented to 5 chimpanzees in 14 blocks of 10 trials each. Two of the five subjects solved it above chance level (Limongelli et al. 1995). In the second half of the experiment (Blocks 8–14), their rate of success was significantly higher than chance (Darrell = 90% and Sheba = 99%). To assess

**Trap-Tube Problem,**  
**Fig. 3** Control conditions.  
Top left: inverted trap tube.  
Top right: trap tube and  
tube. Bottom left: opaque  
trap tube. Bottom right:  
opaque tube. (Redrawn  
from Visalberghi and  
Limongelli (1994) and  
modified by Luca Antonio  
Marino)





**Trap-Tube Problem, Fig. 4** Trap tube as in Limongelli et al. (1995). Above: the trap tube has the trap in the center and the reward positioned on the right or on the left side of the trap. Below: control trap tube with the trap displaced from the center and positioned on the right or on the left

side of the tube and the reward positioned as in the trap-tube task. In the control conditions, trials of the trap tube were alternated with trials with the control trap tube. (Redrawn by Luca Antonio Marino from Limongelli et al. (1995))

whether the successful subjects used a representational strategy (represented beforehand the outcome) or an anticipatory strategy (anticipated failure and changed side of insertion), the number of successful single-insertion trials and the number of multiple-insertion trials were compared. Both subjects mostly used the representational strategy (Darrell = 83% and Sheba = 93%). It is interesting to mention that the successful capuchin mostly performed multiple insertions using an anticipatory strategy (for details see Visalberghi and Limongelli 1994).

To rule out the hypothesis that chimpanzees used the distance rule (as the only successful capuchin in Visalberghi and Limongelli 1994), a control experiment was carried out by modifying the tube so that the trap was not centered and one “arm” of the tube was longer than the other (see Fig. 4). The high rate of success of both chimpanzees in this modified trap-tube task (in which the distance rule is always penalized) ruled out the possibility that a distance strategy could account for success and indicate (but not proven, since experiments cannot prove something but only rule out alternative hypotheses) that the two chimpanzees might have understood the relevant causal relation between their action on the food and the food movement over the hole.

### Children

Children between 27 and 66 months of age were tested in the VL-trap-tube task (Visalberghi and Limongelli 1996). Children under 3 years of age did not figure out a successful strategy, whereas those over 3 years did. The behavior of successful children resembled those of the successful

chimpanzees; typically they looked at the setup (and not into the opening of the tube as the successful capuchin), evaluated the situation, inserted the stick into the correct side of the tube, and pushed the reward out of the tube. Children reached success more quickly than did chimpanzees and spontaneously commented the risk involved in moving the reward over the trap and the necessity to avoid it, or they talked about it if requested (Visalberghi and Limongelli 1996; see also Want and Harris 2001). It is interesting to note that children could solve the tube task in the second year of life, whereas they only solved the trap-tube task much later in the fourth year of life (or, according to Horner and Whiten (2007) who used the VL-trap-tube in social learning experiments, even later at 5–6 years of age). Thus, also for children, solving a tool task is not at all the same as solving the trap-tube task in which errors are penalized and multiple causal relationships between the tool and the tube, the tool and the reward, and the reward and the trap should be taken into account (Visalberghi and Tomasello 1998).

### Other Trap-Tube Experiments

The trap-tube paradigm was later adopted to evaluate the tool-using competences of several non-human species (see the next two sections); moreover, modified trap tubes were used to investigate the ability to learn from others’ mistakes in children (Want and Harris 2001) and social learning in chimpanzees (Horner and Whiten 2007). In some studies the VL-trap-tube task was modified,

for example, by the presence of two traps on the same tube (e.g., Seed et al. 2006), by allowing the subject to rake and/or push the reward out of the tube (Mulcahy and Call 2006), by making the trap opaque (Martin-Ordas et al. 2008), thereby providing some new insight on what the subjects find challenging. It is very unfortunate that these modifications also made the results difficult to compare across studies.

To understand what makes the trap tube difficult and whether subjects could generalize their knowledge across different tasks requiring similar causal knowledge, other tasks with a hole to avoid when moving a reward over a surface were designed. Also in these other tasks, the subjects could develop procedural rules that may or may not be accompanied by an abstract conception of the invariant physical laws (such as gravity) governing the movement of the tool or of the target object. These other tasks assumed to test similar cognitive capacities, such as the trap-table problem (e.g., Povinelli and Reaux 2000), the trap platform and the trap table (e.g., Martin-Ordas and Call 2009). However, this assumption did not seem well supported since the results of tests performed on the same subjects using trap tubes and other paradigms often did not correlate (e.g., Povinelli and Reaux 2000; Martin-Ordas et al. 2008). When Martin-Ordas and Call (2009) looked for correlation among four different tasks, they found no significant correlations between most of the tasks and were particularly struck by the absence of correlation between the trap-platform task and the trap-tube task. The trap tube was also presented in ways that did not require the use of a tool (e.g., Seed et al. 2009). Since the trap tube was designed to evaluate whether a subject that moves a reward into a tube with a trap understands how to use the tool to reach success above chance level, we will only focus on the experiments carried out with trap tubes and a tool to dislodge the reward.

### Nonhuman Primates

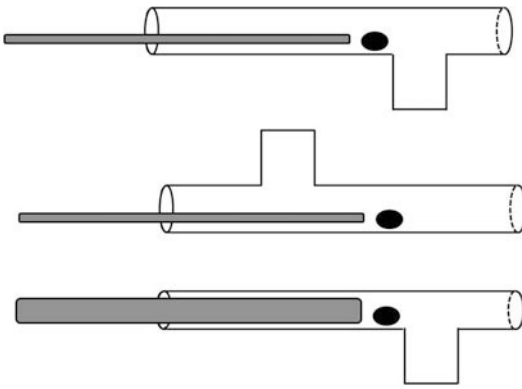
Reaux and Povinelli (2000) presented the VL-trap-tube and the inverted VL-trap-tube tasks to chimpanzees at 5–6 years of age and again at 9–10 years of age; they also added a few tool-

biased conditions in which adopting the distance rule when not necessary implied a small additional cost (such as transporting the tool farther, or removing the tool already inserted in the tube; for details see Reaux and Povinelli 2000). Only one subject (Megan) solved the task above chance level at the younger age, and another did so when older (Candy). Both solvers kept using the distance strategy in the tool-biased conditions and, as the capuchin Roberta, when the trap was positioned above the tube.

In sum, only one out of four capuchins (25%) tested by Visalberghi and Limongelli (1994), two out of five chimpanzees (40%) tested by Limongelli et al. (1995), and three out of seven chimpanzees (43%) tested by Reaux and Povinelli (2000) learned to avoid the trap during training or with additional training. These data indicate that having full access to the relevant information concerning how the tool moves the reward out of the tube or into the trap does not make the trap tube an easy problem for either apes or capuchins. Moreover, control procedures indicated that the capuchin and Reaux and Povinelli's (2000) chimpanzees adopted the rule of inserting the stick into the end of the tube farthest from the food, whereas this strategy was ruled out for the two chimpanzees in Limongelli et al.'s (1995). Thus, it is possible that the latter subjects might have had a causal understanding of the problem.

Mulcahy and Call (2006) tested a total of ten apes (five oranges, two chimpanzees, two bonobos, and one gorilla) in a trap-tube width enough to allow the subject to push or rake the reward with the tool and with the trap not at its center (Fig. 5). Results showed that raking was highly preferred over pushing and that three raking subjects (two oranges and one chimpanzees) learned to avoid the trap within 24, 48, and 60 trials. Moreover, they solved with single insertions and did not avoid the trap when nonfunctional (i.e., above the trap). However, none of them was successful when later tested in a trap tube in which only pushing allowed to obtain the reward; the reward was in the middle of this trap tube and its arms were of different length (Fig. 5, bottom). The lack of transfer between trap tubes shows that they were not equal from the apes' point of view and makes





**Trap-Tube Problem, Fig. 5** Trap tube as in Mulcahy and Call (2006). The reward is centered and the trap can be on either side of the tube. The width of the tube allows obtaining the reward by pushing and/or by raking. (Redrawn by Luca Antonio Marino from Mulcahy and Call (2006))

comparisons between the results obtained in the trap tube allowing raking and pushing and in the trap tube allowing only pushing problematic. Note that both raking and pushing are common actions for apes and that apes can control instinctive preferences when necessary (Rosati et al. 2007). Unfortunately, in Mulcahy and Call's (2006) study, no control condition was run to rule out a simpler strategy of solution, such as that the subject might have considered the trap as a cue indicating in which side to avoid raking. Since the traps were in fixed positions, a simple rule as this one could be learned quickly.

Martin-Ordas et al. (2008) presented 2 trap tubes (positioned one above the other) to 20 apes (6 oranges, 6 chimpanzees, 5 bonobos, and 3 gorillas). Seven of these apes were previously tested in the Mulcahy and Call's (2006) trap-tube test, and only one was successful. Each tube had a black/opaque trap whose location was on the right or on the left side of the tube; the location of each tube was the same during the 12 trials of a session and changed across sessions. Within 36 trials, 7 additional apes solved this task by raking; no control condition was run to rule out simpler strategies of solution. According to the authors, the relatively high number of solvers and their fast learning were related to the possibility of raking and the copresence of the two trap tubes. Martin-Ordas and Call (2009) exposed eight apes (three

chimpanzees, two bonobos, two orangutans, and one gorilla) to two trap tubes in a functional condition (in which the reward was at the center, the tube arms were of different length, and a black opaque trap was attached to the tube and connected by a hole, as in Martin-Ordas et al. 2008) and to two control nonfunctional conditions. In the fake nonfunctional condition, the trap was attached to the tube but with no hole connecting the tube with the trap and in the painted nonfunctional condition in which the position of the painted trap was the same as in the functional and the fake conditions. Four apes avoided both the functional and the fake nonfunctional traps, and the other four avoided above chance only the functional trap. None of the eight avoided the painted trap above chance level (though four avoided it in about 50% of the trials). The results showed a mixed picture indicating that at least some apes are able to distinguish between functional and nonfunctional traps; however, it is worthwhile to mention again that avoiding the nonfunctional trap did not have a cost and that also adult humans may generalize in similar conditions (Silva et al. 2005). Interestingly, their best four apes did also solve the trap-tube task in a previous study (Martin-Ordas et al. 2008). Unfortunately, a trap tube not allowing raking behavior was not presented to these apes. In the above studies (for an exception, see Mulcahy and Call 2006), the performance of the four ape species did not differ.

In conclusion, all the trap-tube studies described above indicate that this problem is difficult and only a limited number of apes succeeded. The successful ones (Limongelli et al. 1995; Mulcahy and Call 2006; Martin-Ordas et al. 2008; Martin-Ordas and Call 2009) acquire some knowledge about the causal relations between the trap, the reward, and the tool they can use to obtain the reward. However, this knowledge is often not robust enough (i) to establish analogies across tasks that appear (to us) all related to what causes a trap to be effective, (ii) to prevent generalizations in situations in which the trap is not effective, and (iii) to allow success when the experimental setup requires different actions (well within the subject's repertoire).

More studies relying on the use of the same apparatus and procedure would have been necessary to clarify the competence of apes in this task.

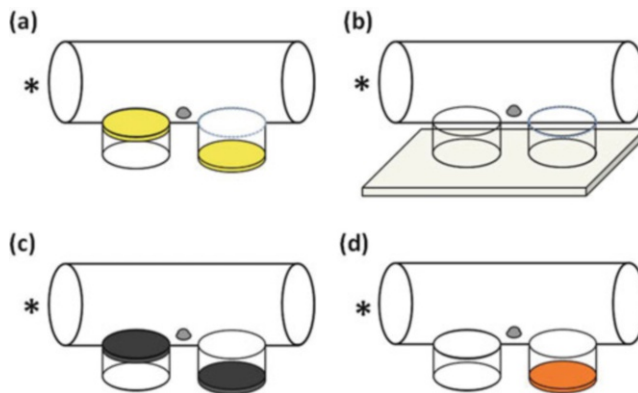
## Birds

Tebbich and Bshary (2004) presented six woodpecker finches (*Cactospiza pallida*) with a trap-tube task (see Fig. 5) in which the solution could be obtained either by inserting the tool at the end nearest to the trap and pushing the reward or by inserting it at the end furthest to the trap and raking the reward. Most of the birds raked the reward toward themselves, and one solved the task after 100 trials and did not generalize to the inverted trap-tube condition. Unfortunately, no control condition to rule out the distance strategy when raking was carried out.

When non-tool-using bird species were tested, as rooks (*Corvus frugilegus*; Seed et al. 2006) and parrots (*Nestor notabilis*, *Ara chloroptera*, *Cacatua sulphurea*; Liedtke et al. 2011), the apparatus did not require the use of the tool. The bird had just to push or pull the stick attached to two discs sliding inside the tube (retaining the reward between them). Since dealing with traps without a tool “may not impose the same cognitive demands as the original trap-tube task” (Tebbich et al. 2007, p. 230) and also for chimpanzees is less

challenging than dealing with traps and tools (Seed et al. 2009), these experiments will not be discussed.

Six wild New Caledonian crows (*Corvus moneduloides*) were tested in two tool problems of similar structure: the two-trap tube (see Fig. 6) in which there were an effective trap (with a base) and an ineffective trap (without a base) and in the trap table (with a trap embedded into a table that should be avoided) (Taylor et al. 2009a). The three successful New Caledonian crows solved the initial two-trap tube (Fig. 6a) by pulling and often switching side they were probing, after an average of more than 100 trials. Afterward they were tested in three transfer conditions (Fig. 6b–c) designed to rule out the possibility that they had used arbitrary features to reach success in the initial tube (such as the color of the disc (transfer b), the color of the rime (transfer c), and the presence of a trap base that allows the trap to be functional or not (transfer d). They were successful above chance level in the transfers b and c, but not in transfer d. Strikingly, they rapidly solved the trap-table task, while the three other crows that had been unsuccessful in the two-trap tube task did not. Given that the three crows successful in the initial two-trap task continued to succeed when the cues associated with the trap were removed (transfers b and c and the table-trap task), low-level associative strategy of solution



**Trap-Tube Problem, Fig. 6** The two-trap tube experiment, as in Taylor et al. (2009a); (a) the initial two-trap tube and (b–d) the three transfer two-trap tube conditions. The colored discs represent actual colors and solid surface. (b) The left trap was nonfunctional with a transparent solid surface, and the trap tube was placed on a wooden surface.

The arrows show the direction in which the subject raked the reward out of the tube. The asterisks indicate the side of the tube from which the reward can be obtained. (Redrawn and modified by Luca Antonio Marino from Taylor et al. (2009a))

can be ruled out. Moreover, other two alternative explanations for success were ruled out by Taylor et al. (2009b) who demonstrated that New Caledonian crows did possess a predisposition to avoid holes and that their successful crows only avoided the hole when it was in a functional position (i.e., in the bottom of the horizontal tube). Thus, New Caledonian crows appear to have a good understanding of the causal relationship concerning the reward-hole interaction (Taylor et al. 2009a), even if they failed to predict that food would fall out of a tube if they pushed it into the baseless trap.

## Cross-References

- ▶ [Anthropomorphism](#)
- ▶ [Associative Learning](#)
- ▶ [Cognition](#)
- ▶ [Comparative Cognition](#)
- ▶ [Corvids](#)
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- ▶ [Problem-Solving](#)
- ▶ [Tool Use](#)
- ▶ [Trap-Table](#)
- ▶ [Wolfgang Köhler \(1887–1967\)](#)

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## Travel

- [Canine Navigation](#)
- [Cetacean Navigation](#)

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## Traveling Salesman

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### Definition

The traveling salesman problem is the task of determining an optimal path through several points and return to the starting point.

### Introduction

“Given a list of cities and the distances between each pair of cities, what is the shortest possible route that visits each city once and returns to the origin city?” The traveling salesman (or salesperson) problem (TSP) is a well-known mathematical problem that was first defined in the 1800s and studied in the 1930s. The task is to connect each of several points (nodes) and return to the origin using the shortest possible path (tour) (see examples in Fig. 1).

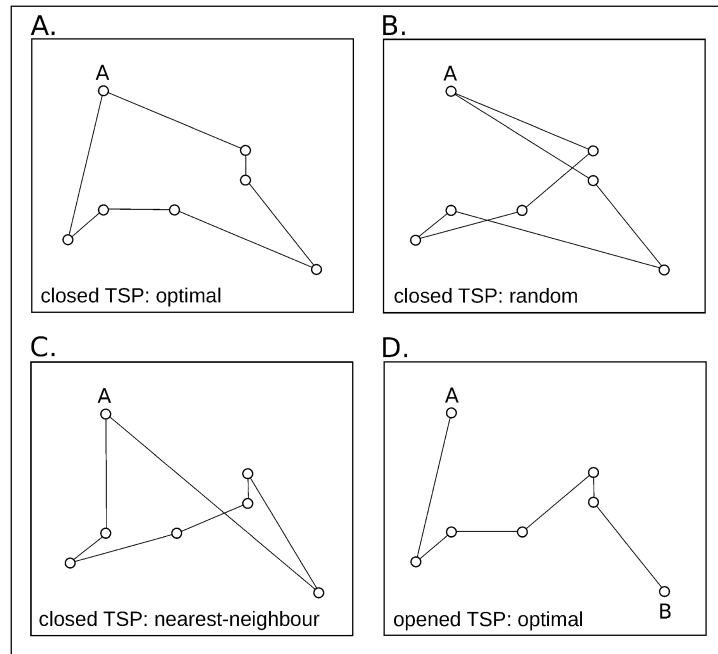
Despite the simplicity of the problem's description, solving the TSP is computationally hard. The only known method to solve any TSP between  $N$  nodes is to calculate and compare all possible  $(N-1)!$  tours, which becomes impractical for large  $N$ s. For example, there are 24 potential tours to join five nodes. This number increases over 300,000 when it is required to join ten nodes, putting solutions for 50 nodes or so out of reach of current computing machineries. For these reasons, the TSP has become a classic algorithmic problem in computational mathematics that belongs to the class of NP-complete problems for which the worst case running time for any algorithm increases super-polynomially with the number of nodes. Many algorithms have been developed to find approximations of the optimal tour with reduced computation time. This approach is used in a broad range of applications in logistics, manufacturing, telecommunication, genetics, and neurosciences, to name just a few (Applegate et al. 2007).

Over the past 50 years, researchers in psychological, cognitive, and behavioral sciences have started to exploit the TSP to study perceptual problem-solving, planning, navigation, and spatial cognition in humans and some other animals. The problem is so complex that animals are not supposed to be capable of solving it. Instead, they may use simple decision rules (heuristics) to find efficient tours in a limited time. The questions addressed, procedures used, and results obtained in these researches have varied considerably across studies.

The experimental approach falls into two broad versions of the TSP: a visual (two-dimensional)

### Traveling Salesman,

**Fig. 1** Hypothetical examples of solutions to traveling salesman problems (TSPs) in a randomly generated array of seven nodes. (a) Shortest possible tour, (b) random tour, and (c) tour resulting from the nearest neighbor strategy in a closed TSP starting and ending at A. (d) Shortest possible tour in an open TSP starting at A and ending at B



TSP and a navigational (three-dimensional) TSP. In both cases the performance of the subject is typically compared to the optimal solution (Fig. 1a), chance (Fig. 1b), and simple heuristic models (Fig. 1c).

### Visual TSP

In psychology, the TSP has been used to assess cognitive functions and complex problem-solving abilities. The task for the subject is to connect an array of dots on a sheet of paper or a computer screen in just one or a few trials. Variants include closed TSPs, in which the tour must start and end at the same node (Fig. 1a–c), and open TSPs, in which the tour must start and end at two different nodes (Fig. 1d).

In such a task, humans can produce paths that approach optimal in problems with up to 100 nodes, generating a solution quickly and with little apparent effort. Human solutions tend to be very good and frequently outstrip the simpler heuristics' solutions despite great variations in the experimental procedures used (e.g., time to complete the task, possibility to erase path)

(MacGregor and Ormerod 1996). Several strategies varying in their levels of complexity (global versus local processing) have been proposed to explain these performances. For example, subjects may simply choose the nearest available unconnected node (nearest neighbor heuristic, Fig. 1c), avoid crossings (crossing-avoidance heuristic), follow borders (convex hull model), or link clusters of nodes (pyramid algorithm). Human performances on visual TSPs do not appear to reflect exclusive use of one of these heuristics, but indicate a probabilistic use of a single or a combination of strategies.

Recently, visual TSPs have been extended to nonhuman animals using smaller arrays of less than ten nodes. For instance, pigeons required to peck nodes on a touchscreen without returning to a previously picked node in order to obtain a food reward perform better than random but significantly worse than the optimal route or a nearest neighbor strategy (Gibson et al. 2007). Hummingbirds also solve simple visual TSPs when collecting sucrose solution on artificial flowers displayed on a vertical board, often choosing the shortest path to visit all flowers once after training (Tello-Ramos et al. 2015).



## Navigational TSP

In ethology, behavioral ecology, and cognitive ecology, the TSP has been used to investigate spatial cognition and navigation behavior. The task for the animal is to find the shortest path to visit multiple baited locations in the lab or in the field. This route optimization problem characterizes the everyday spatial behavior of many central-place foraging animals that exploit food patches from a reference place (nest or shelter). Finding an efficient route between several feeding sites is critical for animals to reduce travel costs and exposure to predators.

The first reported navigational TSP experiment was conducted with chimpanzees that could acquire experience with the spatial distribution of food sites before being tested (Menzel 1973). One experimenter carried a young chimpanzee around a large outdoor enclosure on his back, while a second experimenter hid 18 food items. The chimpanzee was allowed to watch where the food was being hidden and was able to go out and search for the hidden food after being returned to the start location. The routes taken by the experienced chimpanzee were more efficient than the route originally taken by the experimenter, suggesting that while being carried around, the chimpanzee formed a spatial memory of food locations and was able to determine an efficient route between them, following a nearest neighbor strategy. Using a similar procedure, it was found that vervet monkeys have more sophisticated strategies of planning ahead a small number of steps and choosing the path with the shortest length (Cramer and Gallistel 1997).

A second approach to navigational TSP is to test naïve animals that must solve the task as they first discover the problem. In these conditions humans and rats tend to choose routes that are more efficient than expected by chance (Blaser and Ginchansky 2012). Their performance is generally consistent with the use of nearest neighbor strategy, although both produce longer travel distances than would be expected given the sole use of this strategy.

A third approach to navigational TSP is to examine the role of learning and memory in

route optimization by testing animals that can solve the task over multiple trials. In this context, rats (Bures et al. 1992), pigeons (Baron et al. 2015), and bees (Lihoreau et al. 2012) can all develop efficient paths to navigate between multiple locations. For instance, bumblebees allowed to forage for several hours in an array of artificial flowers typically find the shortest possible routes to visit all flowers once and return to the nest. This optimization behavior is reached through trials and errors based on the acquisition of long-term visuospatial memories (Lihoreau et al. 2012). Although the exact strategy used by bees, birds, and rodents to find optimal routes is not known, these results clearly indicate that finding efficient solutions to TSPs does not necessarily require large brains and high computational power.

## Conclusion

The TSP has become an established experimental paradigm in which tasks and memory demands can be easily manipulated to study complex problem-solving by human and nonhuman animals. Interest into the cognitive processes underlying efficient path selection has intensified recently because of the surprising finding that many animals perform well in TSPs. Yet their strategies seem to differ a lot depending on the specificity of the task to solve. Visual and navigational TSPs likely require processing different types of information and different cognitive capacities. For instance, in navigational TSP, goals are generally not marked (which involves increased working memory demands and working with reduced number of nodes) and not visible all at once (which may prevent using global strategies to solve the task). Studies using both approaches in humans and pigeons have started to explore these differences (MacGregor and Ormerod 1996; Gibson et al. 2007; Blaser and Ginchansky 2012). Comparative analyses using standard protocols in a wider range of species with different brain sizes and architectures will help clarify the evolution of fundamental perceptual and cognitive abilities required in these tasks.

## Cross-References

- [Arthropod Cognition](#)
- [Central Place Foraging](#)
- [Cognitive Map](#)
- [Comparative Cognition](#)
- [Decision-making](#)
- [Foraging](#)
- [Foraging by Honeybees](#)
- [Hominoidea Navigation](#)
- [Insect Navigation](#)
- [Learning](#)
- [Long-Term Memory](#)
- [Navigation](#)
- [Optimal Foraging Theory](#)
- [Pigeon \(\*Columbidae\*\)](#)
- [Planning](#)
- [Primate Cognition](#)
- [Problem-Solving](#)
- [Rodentia Navigation](#)
- [Spatial Orientation](#)
- [Touch Screen](#)
- [Vision](#)
- [Visuospatial Memory](#)
- [Working Memory](#)

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## Tree Hyrax

- [Hyracoidea](#)

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## Tree of Life

- [Woese's Three Domains of Cellular Life](#)

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## Tree-Swaying

- [Primate Suspensory Behavior](#)

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## Triadic Awareness

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## Synonyms: Knowledge of Third-Party Relationships

Animals living in stable social groups repeatedly interact with each other. Nonequal distribution of interactions among dyads suggests that animals

differentiate among other group-mates and interact selectively, shaping the number of *agonistic and affiliative relationships*, which are predictive of future interactions. Animals use experience with past agonistic interactions – that define dominance rank relationships – to decide who to fight and who to avoid and to decrease the risk of aggression, injuries, and stress. Tracking of own affiliative interactions helps individuals form and maintain social bonds that decrease stress and bring fitness benefits. The ability to remember past interactions and profit by modifying social behavior based on such memory is an aspect of social cognition, which likely evolved in response to challenges of group living (Seyfarth and Cheney 2015). However, animals living in large stable groups may also profit from more complex cognitive abilities. Evidence accumulated that some animals have certain knowledge about relationships between third parties. They know who outranks whom and who is closely bonded or related with whom and modify own social behavior based on this “triadic awareness.”

There is currently quite convincing evidence from *experimental and behavioral studies* for the triadic awareness in primates (reviewed in Tomasello and Call 1997): Vervet monkeys and chacma baboons demonstrated their understanding of others’ kinship in playback experiments. Individuals were likely to look at the relatives of an individual whose call had been just played. Long-tailed macaques indicated similar knowledge when successfully matching mother-offspring and sibling pairs in a picture-sorting task. Triadic awareness of dominance rank relationships has been inferred from playback experiments using artificial sequences of calls of group members: In chacma baboons calls mimicking interactions that were discordant with the current dominance rank relations between parties elicited stronger reactions of group-members than calls following the hierarchy. Triadic awareness of affiliative relationships was demonstrated by hamadryas and chacma baboons. Males used knowledge of the quality of male-female relationships when deciding whether to challenge a male for access to females.

Although these experiments demonstrate the cognitive capacity for triadic awareness, they

provide only limited information about its use in natural conditions. *Behavioral studies* reveal that primates use the knowledge of third party relationships also in a natural context, during complex social interactions, for example, when redirecting aggression, reconciling after the fight, and forming coalitions. The pattern of reconciliation and redirected aggression in vervet monkeys and several macaque species suggests that these monkeys understand kinship relationships: After the conflict, the aggressor directs reconciliatory behavior at the opponent’s close relatives or avoids affiliative interactions with them in expectation of retaliation, while the victim may redirect aggression towards the opponent’s kin. In the context of coalition formation, which individuals form to access food or mates and rise in social hierarchy, primates use the knowledge of a third party’s kinship, dominance rank, and also affiliative relationships. Triadic awareness helps them predict who will support or intervene against them and select the most suitable ally. For example, juveniles and adult females sooty mangabeys are likely to offer support to the higher ranking of the opponents. When attacked, chimpanzees seem to modify the scream based on rank relationships between opponents and bystanders of a conflict, who might support them. White-faced capuchins preferentially solicit agonistic support from individuals who are more closely bonded to the recruiter than to the opponent, demonstrating their understanding of third party affiliative relationships. Japanese macaques recruit allies who are higher ranking than their opponent and not related to their opponent, suggesting that they can simultaneously use triadic awareness of rank and kinship relationships.

Male bonnet macaques track dominance rank relationships of potential supporters to solicit support from those who outrank their opponent. Unlike relatively stable relations of females in matrilinear societies, dominance rank relationships of males dynamically change depending on their age, actual fighting ability, and coalitionary support they can secure from others. This shows that primates can track even *dynamically changing relationships* (Silk 1999). Different examples of the triadic awareness of such transient

relationships come from Tibetan and Barbary macaques. Males of both species form close relationships with small infants, whom they use in male-infant-male interactions, that is, interactions during which a male carrying an infant approaches another male. Male Tibetan macaques select the infants with the strongest bond with the target male, and male Barbary macaques who carry an infant preferentially approach males who have the strongest bond to the infant they are carrying. Matching males and their favorite infants is likely to increase the efficiency of these interactions that seem so help males bond with others and decrease the risk of aggression from higher-ranking males. Interestingly, bonds between males and infants appear soon after the birth and vanish upon the start of the next mating season. Still, males are able to track those relationships and profit from such knowledge.

The convincing example of the use of triadic awareness by *nonprimates* comes from spotted hyaenas, whose social system is similar to that of many Old World Monkeys. In a fight, hyaenas support dominant from the opponents and attack their enemy's relatives after the conflict (Engh et al. 2005). Other evidence about the use of triadic awareness by nonprimate mammals, however, is somewhat ambiguous. Several studies investigated cognitive abilities in gregarious mammals, such as elephants, bottlenose dolphins, or lions, but the conclusions and their implications remain questionable. For example, experimental studies demonstrate that some marine mammals can recognize relationships between objects in their environment, but it is unclear whether they can also assess other individuals' social relations and use this knowledge. The number of studies suggested the use of triadic awareness by *birds* (e.g., Bond et al. 2004; Pardo et al. 2018). Male great tits and pinyon jays infer their own rank in the hierarchy by observing agonistic interactions between other birds. Ravens modify their calls according to the relationships of their opponents in conflicts. Acorn woodpeckers seem to recognize, whether played calls belong to outsiders from the same or other groups, demonstrating the ability to understand associations between individuals who do not belong to the own social

group. However, it is sometimes questionable whether birds can categorize relationships based on cumulative knowledge, with the delay after the actual interaction.

The explanations for the relative scarcity of evidence for triadic awareness in nonprimates are ambiguous (see Cheney and Seyfarth 2005). It is possible that primates and nonprimates differ in their mental abilities. Nevertheless, several examples of the use of triadic awareness by nonprimates contradict this. The lack of evidence for the use of triadic awareness by nonprimates may be also caused by the small attention nonprimates so far received and difficulties with their research, especially in the wild. Further, the use and manifestation of triadic awareness also depend on the species' social structure. For example, in species that live in a stable group organized into several matrilineal families with linear dominance rank order, such as many Old World Monkeys, individuals may withdraw the information about relationships by monitoring simultaneous interactions of many different individuals. Songbirds like great tits, in contrast, live in communities with no opportunity to get such information, because not all dyads interact.

Species-specific social structure is also likely to affect the *mechanism* of how the triadic awareness is acquired. The straightforward strategy of how one can get to know the relationships between others is by observing and keeping track of their affiliative and agonistic interactions. Nevertheless, the challenge of monitoring interactions of all possible dyads exponentially increases with the increasing group size. Thus, it seems likely that to predict some third-party relationships, individuals also use a system of *transitive interferences* see e.g. Ostner 2018. Such strategy might work well in many primates and also hyenas with the social system organized into matrilineal, and with transitive dominance, and has also been experimentally shown in corvids. An individual who observes individual A be dominant over B and B over C can conclude that A is dominant over C even without witnessing any interaction between A and C. Affiliative interactions between juvenile and female who has an infant likely predict affiliative or kinship

relationships between juvenile and the infant. The transitivity of relationships based on kinship and dominance rank relationships results in certain *ambiguity in findings* (e.g., Perry et al. 2004). Although several studies' results were consistent with the prediction that individuals acted based on triadic awareness, they could not rule out the use of the alternative, more straightforward mechanism. For example, individuals could have also performed based on knowledge of own kin or dominance rank relationship or used a simple rule of thumb, such as "recruit the highest-ranking ally available" or "intervene only if you outrank an opponent."

However, not all relationships are transitive (e.g., Cheney and Seyfarth 2005), suggesting that the mechanism of triadic awareness acquisition also depends on the type of relationships and context. For example, the social bond a male baboon keeps with two different females does not predict either close affiliative relationships between the two females or between the male and the females' juvenile offspring, whose affiliative relationships may reflect earlier bonds of their mothers, rather than the current state. To predict nontransitive third-party affiliative relationships, individuals cannot either use the knowledge of their own relationships or the rule of a thumb. Possibly, they are able to monitor interactions of all or many dyads. However, it is also possible that animals perceive a group as a network of relationships and withdraw the information about third party relationship of dyads from this mental representation even by observing only a subset of their social interactions (Seyfarth and Cheney 2015).

In sum, there is quite compelling evidence from observational and experimental studies that nonhuman primates possess the capacity to monitor others' social relationships and use it for their own benefit. Overcoming ambiguity of the results, revealing an exact mechanism of triadic awareness acquisition, and finding new contexts where individuals use triadic awareness might represent appropriate future research directions. The examples of the use of triadic awareness by nonprimates support the *social intelligence hypothesis* that predicts that the ability to

recognize "third-party" relationships is advantageous whenever individuals live in large social groups (Humphrey 1976). Further focus on the use of triadic awareness by nonprimates will help us comprehend the role of group living in the evolution of cognition in social animals, including humans.

## Cross-References

- ▶ [Affiliative Bond](#)
- ▶ [Aggression](#)
- ▶ [Basic Rank](#)
- ▶ [Catarrhine Cognition](#)
- ▶ [Catarrhine cognition](#)
- ▶ [Coalition Enforcement](#)
- ▶ [cognition](#)
- ▶ [comparative cognition](#)
- ▶ [Dominance](#)
- ▶ [Dominance Hierarchy](#)
- ▶ [Intelligence](#)
- ▶ [intelligence](#)
- ▶ [Machiavellian intelligence](#)
- ▶ [passerine cognition](#)
- ▶ [pinniped cognition](#)
- ▶ [platyrrhine cognition](#)
- ▶ [primate cognition](#)
- ▶ [Proboscidea cognition](#)
- ▶ [Reproductive fitness](#)
- ▶ [social intelligence hypothesis](#)

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interaction, shared intentionality, joint action, and finally, joint attention (Tomasello et al. 2007; Sebanz and Knoblich 2009). Joint attention is considered as the prerequisite of cooperation (Tomasello et al. 2007) and has been investigated in great detail (e.g., Kleinke 1986; Grossmann 2017; Leavens and Clark 2017 this volume). As a synonymous phenomenon, Emery (2000) described that “shared attention” is a combination of joint attention and mutual attention where the focus of two individuals’ attention is on the object of joint focus and also each other (i.e., I know that you are looking at X, and you know that I am looking at X as well).

## Triadic Gaze

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### Definition of Triadic Gaze

Triadic gaze requires two individuals (a looking individual and a perceiver) and a third party (an object, event, or a person) as the focus of the attention of the individuals. It involves a relatively more complex information processing mechanism than a dyadic gaze that requires perceivers to identify whether a looking individual’s eyes are directed toward them. To achieve triadic eye gaze, the perceiver must recognize the line of site of the looking individual’s eyes and trace along two invisible lines of the site to their convergent point, that is, the third party of the triad (e.g., an object; Lee et al. 1998). Although triadic eye gaze can also be used to regulate one-to-one social interaction, another major and unique function of triadic eye gaze is that it can be used to reveal an individual’s focus of attention and internal states (desire, goal, etc.; Lee et al. 1998). In the literatures of human developmental studies, triadic gaze that mutually coordinates attention of two individuals is considered as a hallmark of social learning, communication, social

### Early Form of Triadic Gaze Interaction

Between 4 and 6 months of age, human infants become interested in the visual and tactile properties of objects. Consequently, the proportion of time that infants spend with mutual gaze in face-to-face interactions is reduced quite considerably by 6 months (Kaye and Fogel 1980) because other objects are now detracting attention away from faces. Mothers typically recognize this change and introduce objects such as toys into their interactions with their infants. By 6 months infants have become interested in things, but at first they do not share this interest with others. Initially, the infants’ role in such object-centered interactions is confined to manipulating the object. Gradually, over the next few months, the interactions become reciprocal. Rather than simply concentrating on the object, infants take their turn and then look up at their mother’s face as they anticipate the mother’s turn. Infants have now entered the period of real means of joint attention (see Leavens and Clark 2017 this volume for Joint Attention) or joint attentional engagement (Carpenter and Call 2013) and have reached a new cognitive milestone. That is, from now on, interactions are primarily triadic (Bakeman and Adamson 1984) because they involve three components – infant, adult, and object – where previously they were dyadic (infant and adult only). Triadic interactions often retain the structure of dyadic interactions in that they involve mutually contingent patterns of

actions produced by both partners (Dunham and Dunham 1995; Striano and Rochat 1999).

Recently, Jording and co-authors (2018) classified taxonomy for gaze-based communication in triadic interaction as a “social gaze space.” Accordingly, “initiating joint attention (IJA)” and “responding joint attention (RJA)” are the categorical states that have significant roles in a coordination of triadic gaze interaction (see also Leavens and Clark 2017 for this volume). RJA can be defined as a perceiver notices that a looking individual initiates and leads the interaction and shifts gaze toward an object. It is considered to facilitate social learning, social competence, and mentalizing (Morales et al. 1998; Mundy and Newell 2007). That is, RJA reflects that the perceiver understands that the perception and actions of the looking individual are goal directed or have communicative intent (Tomasello et al. 2005). Contrarily, IJA requires more elaborate processing and insight as it contains the dual function of social gaze, which is not only for perceiving but also for informing others about the individual’s focus of attention and sharing of attention as an intention for mutual interaction (Grossmann 2017; Gobel et al. 2015; Tomasello et al. 2005).

### Chimpanzees, Other Apes, and Triadic Gaze Interaction

A number of studies demonstrated that chimpanzees and other apes (bonobos, gorillas, and orangutans) are able to follow gaze of others (Povinelli and Eddy 1996; Tomasello et al. 1998; Tomasello et al. 2005; Okamoto-Barth et al. 2007; Bräuer et al. 2005; Call and Tomasello 2008) and are also motivated to attend the same thing that others are attending to. Chimpanzees are also able and motivated to direct other’s attention to things they themselves are looking at (e.g., Menzel 1999; Leavens et al. 2004; Call and Tomasello 2007; Lyn et al. 2011). Although there have been some debates whether apes engage in initiating to share attention and interest with others during joint attentional engagement or by using declarative gestures such as showing or declarative pointing as human infants do (e.g., Gómez et al. 1993;

Tomasello et al. 2005; Tomonaga et al. 2004), these incidences (yet less frequent) have occasionally been observed in the wild and laboratory settings (see also Leavens and Clarks for review, 2017 this volume).

### Conclusion

While human infants respond to joint attention from 6 months of age, they don’t initiate joint attention before the second year of life (Mundy and Newell 2007). Chimpanzees and other apes demonstrate IJA not at the same frequency as RJA (e.g., Tomasello et al. 2005; Leavens et al. 2004; Lyn et al. 2011). A recent neuroimaging study (Oberwille et al. 2016) revealed a developmental difference in brain systems for RJA and IJA from childhood to adolescence in humans. While RJA recruits the visual, attention, and social processing brain regions, IJA specifically activates areas that are involved in social cognition, decision-making, emotions, and reward processing, suggesting the rewarding and more complex processing nature of IJA. Interestingly, IJA is more impaired and emerges much later than RJA in autism (Mundy 2003). These empirical findings together suggest separate underlying cognitive systems of RJA and IJA in triadic gaze interaction (Mundy and Newell 2007).

### Cross-References

- [Attention-Getting Behaviors](#)
- [Directed Versus Averted Gaze](#)
- [Joint Attention](#)
- [Primate Communication](#)

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## Tribal Warfare

### ► Raiding

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## Trichechus

► [Sirenia Navigation](#)

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## Trinucleotide Repeat Expansion

► [Expanded Triple Repeat](#)

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## Trinucleotide Repeat Expansion Diseases

► [Expanded Triple Repeat](#)

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## Triple Repeat Disorders

► [Expanded Triple Repeat](#)

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## Trisomy

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## Synonyms

[Chromosomal aberration](#); [Chromosomal abnormality](#); [Chromosomal anomaly](#)

## Definition

The term trisomy refers to the presence of three copies of a chromosome, rather than the usual pair of chromosomes. Normally there are copies of a chromosome in every individual, one from each parent. If an infant is born with three # 18 chromosomes, the infant would be said to have “trisomy 18.” Trisomy 18 is also known as Edward syndrome. Other examples of trisomy include trisomy 21 and trisomy 13. A **trisomy** is a type of chromosomal disorder or aneuploidy (abnormal number of chromosomes) in which three copies of a particular chromosome are present, instead of the normal two (Rieger et al. [1968](#)).

## Introduction

Most of the sexually reproducing organisms have pairs of chromosomes in each cell. One chromosome is inherited from each parent. Through meiosis, gametes (eggs or sperm) are made that are haploid or that have only one set of chromosomes. The number of chromosomes is different for different species. Humans have a diploid set ( $2n$ ), i.e., 46 chromosomes. However, gametes have only a haploid set ( $n$ ), i.e., 23 chromosomes.

The main cause of trisomy is nondisjunction of chromosomes. The number of chromosomes in the cell where trisomy occurs is represented by  $2n+1$  if trisomy is shown by one chromosome whereas it is represented by  $2n+1+1$  if it shows double trisomy and so on (Hassold et al. [1995](#)).

## Types of Trisomies and Down Syndrome as Trisomy

Trisomies may be characterized as autosomal trisomies (trisomies of the non-sex chromosomes) and sex-chromosome trisomies. Viable trisomies are observed in the case of only a few human chromosomes. The most common human trisomy is observed in chromosome 21 and is known as Down syndrome (DS), named after John Langdon

Down (O'Connor 2008) who first described the condition in 1866 (Antonarakis et al. 2004). Jerome Lejeune associated DS with trisomy 21 in 1959. His discovery is a landmark in the field (Antonarakis et al. 2004). Joe HinTijo and Albert Levan had discovered that the human chromosome number is 46, and chromosome-staining techniques were still being developed at that time.

DS is routinely identified in karyotypes as ideogram or by using fluorescent probes for chromosome 21 through fluorescence *in situ* hybridization (FISH) (Antonarakis et al. 2004). Down syndrome affects about 1 in every 750 births (Antonarakis et al. 2004). Individuals with DS show cognitive impairment, along with a more variable range of other symptoms, but patients normally live to adulthood (Patterson and Costa 2005), whereas trisomies of other autosomes appear to have more severe effects, because they are rarely observed in live births. Indeed, the only other autosomal trisomies that have been detected in any appreciable numbers among newborns involve chromosomes 13 and 18, but affected babies rarely survive beyond the first few months of life.

It has been observed that human beings are much more able to tolerate extra sex chromosomes than extra autosomes. Therefore, after DS, the most common human aneuploidy is the condition known as Klinefelter's syndrome (Jacobs and Strong 1959).

## Detrimental Aftereffects of Extra Chromosomes

Klinefelter's males have a total chromosomal complement of 47, which includes two X chromosomes and one Y chromosome. These sterile males are designated as 47, XXY individuals. Compared to autosomal trisomies, these sex chromosome trisomies are less dangerous. Affected individuals generally show reduced sexual development and fertility, but they often have normal life spans, and many of their symptoms can be treated by hormone supplementation. The ability of humans to tolerate supernumerary sex chromosomes is

higher as compared to supernumerary autosomes, as individuals can survive with as many as four sex chromosomes. This tolerance most likely relates to both X inactivation and to the lesser number of genes on the Y chromosome (O'Connor 2008). The genes present on Y chromosome are called holandric genes and are much fewer in number. If an X chromosome is present in two copies, one of the copies is inactivated.

Trisomies can occur with any chromosome, but most of the time, it results in miscarriage, rather than live birth. For example, Trisomy 16 is one of the most common trisomies in human pregnancies, occurring in more than 1% of pregnancies; only those pregnancies in which some normal cells occur in addition to the trisomic cells survive (O'Connor 2008). This condition, however, usually results in spontaneous miscarriage in the first trimester.

Trisomy 13, also called Patau syndrome, is a chromosomal condition associated with severe mental retardation and physical abnormalities. In rare cases, a fetus with Trisomy 13 can survive but they have been observed with heart defects, brain or spinal cord abnormalities, microphthalmia, a cleft lip with or without an opening in the roof of the mouth (a cleft palate), etc., in addition to impaired intelligence. Only 5–10% of children with this condition are able to survive past their first year.

## Conclusion

In sum, the common types of *autosomal* trisomy that survive as live births are:

- Trisomy 21 (*Down syndrome*)
- Trisomy 18 (*Edwards syndrome*)
- Trisomy 13 (*Patau syndrome*)

The trisomies are associated with the presence of an extra chromosome in addition to the existing ones. In most of the cases, the individual is not able to survive, but in some of the cases in which the individual is able to survive, severe symptoms lead to distinct abnormalities.



## Cross-References

- [Autosome](#)
- [Chromosomes](#)
- [Mutations](#)

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## Troop

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## Definition

A troop refers to a group of animals, typically kangaroos, wallabies, apes, or monkeys.

## Introduction

Groups of primates, kangaroos, and wallabies are called “troops,” although kangaroo and wallaby groups can also be called a “mob,” apes a “shrewdness” or “community,” and monkeys a

“barrel.” Troop life across species somewhat mirror each other, in that troops are highly social with some form of dominance hierarchy. Troops may be synonymous with family groups but may also be comprised of unrelated individuals.

## Kangaroos and Wallabies

There are four distinct species of the Australian marsupial “kangaroos”: red (*Macropus rufus*), antilopine (*M. antilopinus*), eastern grey (*M. giganteus*), and western grey (*M. fuliginosus*). Kangaroos are herbivorous and can be found in grasslands and open forests across Australia and Tasmania. Kangaroo troops usually consist of multiple adult females, offspring, and at least one dominant male with variations occurring across geographic regions. For instance, eastern grey kangaroo troops typically contain an equal number of males and females with a designated dominant male (Dawson 1998). Troops can range anywhere from two to four individuals, such a mother-offspring pair or small polygynous group to ten or more. In areas of dense forage material, kangaroos can congregate in numbers exceeding a thousand, potentially as a result of intertroop interactions. It has been noted that groups are larger in eastern Australian species rather than western due to environmental conditions (Dawson 1998).

As troops grow, group cohesion is important, which is why kangaroos can often be found sniffing or touching noses to promote unity (Dawson 1998). Ritualized boxing establishes dominance among troop males. In each group, a dominant male controls the troop and has equal reproductive access to sexually mature females. However, troops that contain multiple males may witness bouts of fighting for breeding rights with cycling females (Dawson 1998). In either case, females will signal when they are in estrus, encouraging consort pairing with another male. Consort pair bonds are temporary and can persist for several days, which can alert other males to the breeding opportunity and again result in fighting. However, both sexes within a troop may transfer to other troops. Eastern grey kangaroo dispersal is perhaps the most well-understood: females often

remain close to female relatives throughout life, whereas males disperse more readily, albeit not frequently (Coghlan et al. 2017). Information for other species is inconsistent.

Wallabies belong to the same taxonomic family as kangaroos (Macropodidae) and are distinguished based on their smaller size. There are approximately 44 species (genera *Macropus*, *Petrogale*, and *Lagostrophus*) found in rugged and remote terrain across Australia, New Zealand, and New Guinea.

Some species, like the red-necked wallaby (*Macropus rufogriseus*), are mostly solitary and any existing troops are often small and unstable. More gregarious species of wallabies, like agile wallabies (*M. agilis*), adhere to the troop structure exhibited by kangaroos. Regardless of species' social structure, consort pairs are temporary. When troops meet, there is often combat between males. Females tolerate the presence of other females within and between troops, although they may displace one another through agonistic interactions (Johnson 1989).

## Apes

Great apes are the world's largest primates and are found only in Africa and Asia. Orangutans (*Pongo* sp.) are found on the islands of Sumatra and Borneo. Gorillas (*Gorilla* sp.) and chimpanzees (*Pan troglodytes*) live in sub-Saharan Africa and bonobos (*Pan paniscus*) live exclusively in the Democratic Republic of Congo.

Apes are gregarious animals, with the exception of the orangutan (*Pongo* sp.), which maintains a mostly solitary lifestyle. Members of *Pan* and *Gorilla* live in dynamic social groups (which may have led to the cultivation of their impressive intellectual abilities), ranging from around nine individuals (gorillas, *Gorilla* sp.) to over a hundred individuals (chimpanzees and bonobos, *Pan* sp.). Particularly large ape troops are usually subject to fission-fusion dynamics. The troop may fuse, for example, to sleep and may split apart into smaller foraging groups during the day. This dynamic association ultimately maintains large troops, as group members regularly return to the

main "parent group" to reassume their role or rank in their society.

In gorillas, group composition varies somewhat based on species. Mountain gorilla troops usually consist of a single male, multiple females, and offspring, whereas lowland gorilla troops more often have multiple males. Additionally, multi-male "bachelor" troops exist for both species, although a much rarer occurrence for mountain gorillas. Both males and females emigrate from their natal groups at around 8–12 years of age, and females often transfer many more times to secondary troops. In mixed-sex, multi-male groups, the silverback male is the highest-ranking individual in his troop, as he makes group decisions and ameliorates conflict among members. Females keep a largely egalitarian society, although older females may obtain a higher status than younger females due to age and experience (Harcourt and Stewart 2007). Relationships between females are reinforced by maintaining close proximity and grooming.

Chimpanzee troops typically include several males, females, and offspring. Males often stay in natal groups for life while females transfer around 9–14 years of age. As a result, most females in troops are unrelated. In chimpanzee troops, both males and females have strong intrasexual dominance hierarchies. The highest-ranking male controls troop activities and enforces order during disputes (Mitani et al. 2012). Moreover, the alpha male typically enjoys expanded mating opportunities within the troop compared to lower-ranking males. Females may inherit the ranking of their mother or fight to achieve elevated status. Female dominance is established by age, and dominant females may obtain increased resource access. This can increase reproductive output, offspring survival, and maturity rates. In both sexes, dominance is bolstered by ally recruitment within the community (Mitani et al. 2012). This becomes especially valuable in intertroop conflict, typically among males, over territory or other resources.

Bonobo groups are composed of multiple males and females, although composition varies. Females are generally unrelated due to dispersal at puberty, while males maintain relatedness due to infrequent group transfer. Interestingly, females

have been observed to exchange more affiliative behavior than males despite a lack of shared ancestry (Mitani et al. 2012). Contrary to gorilla and chimpanzee societies, a distinctive feature of bonobo troops is that females enjoy a higher social status than most males (White 1996). An exception is when a male inherits his standing from his mother and consequently ranks higher than a lower-ranking female. Despite this, bonobo status does not play a significant role in day-to-day life (White 1996). Bonobos also utilize sociosexual behavior to promote troop cohesion, perhaps more so than other apes. Consequently, physical confrontation is kept to a minimum within and between bonobo troops compared to other ape groups.

## Monkeys

Monkeys are among the most biodiverse mammal groups, with hundreds of species living in an array of niches worldwide. Monkeys are broadly categorized as New World (the Americas) and Old World (Africa, Asia, and Europe). Neotropical primates belong to five families: Callitrichidae (tamarins and marmosets), Cebidae (capuchins, squirrel monkeys), Aotidae (night monkeys), Pitheciidae (titis, sakis, uakaris), and Atelidae (howler, spider, woolly monkeys). Troop sizes vary among species, and can range from large multi-male, multi-female groups, as in saki (*Pithecia* sp.) troops, to pair-bonded individuals, as in golden lion tamarins (*Leontopithecus rosalia*) (Dietz and Baker 1993). Many other species of neotropical primates are socially monogamous, including other tamarins and marmosets, titi monkeys, and night monkeys. In these pairings, both individuals, to varying degrees, raise offspring. In night monkeys, males assume most of the parenting responsibility, and it is predicted this increases offspring survival and reduces the female's metabolic costs.

Multi-male, multi-female troops typically have more females than males, and there is usually a dominant male in the main group, and potentially in subgroups, if fission-fusion dynamics are involved in the species' society (Mitani et al.

2012). However, some polygynist troops, like those of squirrel monkeys (*Saimiri* sp.), allow females to obtain comparable rank to males (Mitani et al. 2012). In species with large troop sizes, there is dispersal in both sexes, although some species, like the uakari (*Cacajao* sp.) and muriqui (*Brachyteles* sp.), appear to be biased toward female transfer from the natal group (Mitani et al. 2012).

Old World monkeys include two subfamilies: Cercopithecinae (e.g., patas monkeys, mandrills) and Colobinae (e.g., colobus, langurs). Troop sizes can range from a few individuals, like in green monkeys (*Chlorocebus aethiops*), to up to around 200, such as in Guinea baboons (*Papio papio*). Virtually all species live in multi-male, multi-female groups. Groups are often matrilineal, given that daughters usually stay with their mothers (e.g., *Macaca* sp.). Males leave natal troops upon reaching adolescence. Separate dominance hierarchies exist for each sex, and rank is often correlated with tenure among males (Mitani et al. 2012). In some cases, mating behavior differs greatly in monkey troops, as it depends on social structure. Some troops, like those of savanna baboons (*P. cynocephalus*), permit all males to mate with any female, whereas in others (e.g., *M. fuscata*), mating privilege follows rank (Barton et al. 1996; Mitani et al. 2012).

As with apes, large monkey troops may experience fission-fusion dynamics. In some troops, as in Japanese macaques (*M. fuscata*), subgroups can outrank other subgroups. In baboon troops, subgroups are called harems, in which a male dominates over a group of females (Barton et al. 1996). Males may fight to gain control of another harem and may take infants as hostages during the course of a conflict. As an alternative to physical confrontation, baboons have the ability to determine dominance rank from the exchange of vocalizations within or between troops. Troops of any size are often maintained through grooming, which strengthens bonds between kin and nonkin.

In both New World and Old World monkey groups, the quality of intertroop interactions may be determined by the resources and opportunities held by the troops involved. For example, larger groups with increased potential for energy gain

may defend their food, territory, and/or mates more strongly than smaller groups (Scarry 2017). One specific study of vervet monkeys (*Chlorocebus pygerythrus*) observed that the nature of intertroop encounters could be predicted by previous male transfers from an outside group. When males attempted to transfer to a secondary group, the members of that secondary group exhibited more aggression, possibly in defense of their resources (Cheney 1981).

## Causes and Benefits of Troop Life

Inherent in troop social structure is the potential for increased competition, agonism, and aggression, which may cause increased energy expenditure and chronic stress in troop members, particularly those of lower rank (as applicable). Furthermore, gregarious species expose themselves to increased disease risk, since frequent interaction and close proximity facilitate the pathogen transmission. Despite this, troop structure plays an important role in animals' lives and their greater benefit.

One major benefit of troop life is protection from predation. With more members, it is easier to spot external threats and act accordingly to prevent loss of life. While the cost to this may be a reduction in feeding sites, for example, the benefit of defense surpasses it. In such a situation, altruism may also be witnessed. If a troop member alerts the other members of a potential threat (e.g., a vervet monkey alarm calling upon seeing an eagle overhead), the caller puts itself in danger for the troop's benefit (Cheney and Seyfarth 1981). Additionally, altruism is a more common occurrence when genetic relatives will be benefited by the altruist's actions. Altruistic behavior may be one of the ultimate causes in the maintenance of troops, as it helps an altruist ensure that its own relatives and future offspring with an unrelated individual are successful.

Another benefit to troop living is increased communication among members. Troop members notify others about the location of food or threats, for instance, providing pertinent information that can shape animals' actions. It has been suggested

that communication among troop members may benefit each individual's health in the long run, particularly where food is concerned, as information about high-quality food is frequently transmitted through groups.

Troops also provide plentiful learning opportunities throughout an animal's life. The social group provides the first safe place for young animals to develop both physically and mentally. Playing with other juveniles allows for the development of motor skills as well as a platform to learn the right and wrong ways of going through day-to-day life. Troop structure may inherently give rise to sophisticated intelligence, such as among primates, as troop members spend so much time in close proximity to others from whom they can learn.

## Cross-References

- [Culture](#)
- [Cumulative Culture](#)
- [Group Living](#)
- [Learning](#)
- [Predator Defense](#)
- [Sociosexual Behavior](#)

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## Tropical

### ► Tropics

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## Tropics

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## Synonyms

Equatorial; Tropical

## Definition

The geographical regions surrounding the equator and between the latitudes lines of Tropic of Cancer in northern hemisphere (23° 27' N) and Tropic of Capricorn in southern hemisphere (23° 27'S) are referred as tropics or tropical zone or torrid zone.

## Introduction

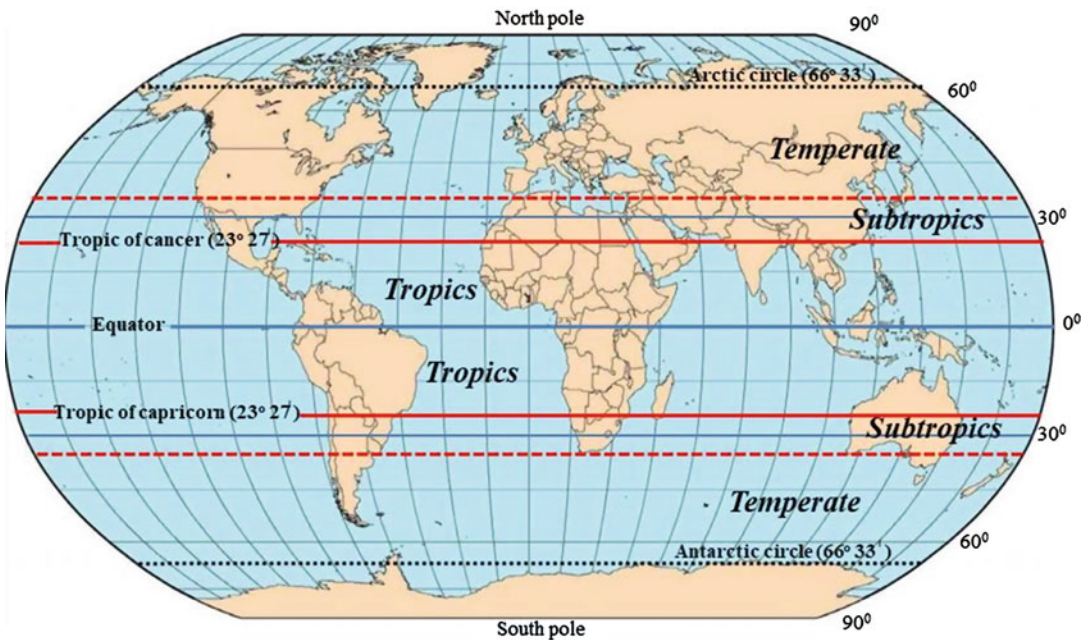
The tropics are regions of the Earth that are in the middle of the globe and between the latitude lines

of the Tropic of Cancer and the Tropic of Capricorn (Fig. 1). It comprises 40% of the total Earth's surface area which include the equator and parts of North America, South America, Africa, Asia, and Australia. Tropical regions are warmer than any other places on Earth with all 12 months of the year having temperature above 18° C. The warmer climate of tropics can be explained by Earth's spherical shape due to which it receives highest solar radiation around equatorial regions. The solar radiation reduces with increasing latitude resulting cooler climate near the poles. Relatively constant temperature and high humidity support luxuriant vegetation and a great biodiversity of flora, fauna, and microbial organisms in tropics. Tropical ecosystems exist in a large diversity of habitat types such as rainforests, dry forests, savannas, deserts, and many more. These are characterized by both high richness of species in many taxa and complex biotic interactions among component species. Most tropical plants are animal pollinated, are fed on by a wide variety of animals, and depend on animals for dispersal of their seeds. Approximately, 1.5 billion people are estimated to directly rely on tropical forests for food, timber, medicines, and other important ecosystem functions and services (Lewis et al. 2015). These ever-growing human demand for resources, however, is putting huge pressures on biodiversity which threatens the continued provision of ecosystem services and further threatens biodiversity and our own species' future security, health, and well-being. For sustainable use of natural resources of tropics and to prevent species from extinction in the near future, actions to conserve their remaining habitat in these areas are urgently required (Bax et al. 2019).

## Climate of Tropics

The climate of the tropics is different from other climatic zones and largely driven by the solar energy. The solar radiations are more directly on the tropics than on higher latitude (like poles) which makes the tropics to receive more energy and become warmer than the pole. Differential heating of Earth's surface generates circulations





**Tropics, Fig. 1** World map indicating the tropical zone

of air and water masses, which allow heat exchanges between the Earth's zones. Tropical air moves away from the equator and toward the poles. As it travels, it cools, becomes denser and eventually descends around 30° north or south latitude. This dry air mass, having lost its moisture in the tropics in form of precipitation, absorbs moisture from the ground, creating arid conditions at these latitudes. The major deserts of the world like Sahara Desert, Arabian Desert, Thar Desert, Kalahari Desert, and Gibson Desert are situated at these latitudes on the either side of the equator. Some of the air is drawn back toward the equator, and some is drawn toward the pole as part of a new air mass. At latitudes around 60° north and south, the air again rises, cools, and releases precipitation (though less than in the tropics). This cycle operates and repeats and results into warm and humid condition in tropics. Some of the cold, dry rising air then flows to the poles, where it absorbs moisture creating the cold climates of the polar regions. The Earth's rotation also influences the atmospheric circulation more strongly at high latitudes than low. The above factors result in more clouds and rain storms in the tropics spontaneously compared to those at higher latitudes,

where they are more tightly controlled by larger-scale forces in the atmosphere. Because of these differences, clouds and rain are more difficult to forecast in the tropics than at higher latitudes. On contrary, the temperature is easily forecasted in the tropics, because it remains stable.

### Biodiversity of Tropics

The tropical forests contain more than half of the species on Earth. In general it is argued that most of the main groups of large organisms on Earth, like plants and animals, and the number of species increase markedly toward the equator. The tropics represent an exceptionally high biodiversity of plants, birds, insects (especially ants, beetles, butterflies, and termites), amphibians, mammals, and other organism groups. They also contain particularly high biodiversity and especially high numbers of endemic species. This huge biodiversity is supported by various tropical ecosystems that exist in a large diversity of habitat types such as rainforests, dry forests, savannas, deserts, and others. In fact, tropical habitats represent an important component in all Earth's life diversity,

because great part of the 34 biodiversity hotspots (areas of high numbers of endemic species) are tropical ecosystems (Myers 1988).

## Threats to Biodiversity of Tropics

Tropical ecosystems have always attracted the attention of scientists due to their impressive biodiversity, but recent trends have made the study of tropical biodiversity particularly important (Gómez-Pompa 2004). Threats to tropical terrestrial biodiversity result from the synergistic effects of several anthropogenic disturbances that can be grouped into at least three main categories which include deforestation, degradation of ecosystem, and landscape effect. Thus, contemporary loss of biodiversity will likely lead to subsequent changes in ecosystem properties and stability. Several studies have been conducted in the lab, grassland, forest, marine, and freshwater ecosystems and clearly concluded that ecosystem functioning depends on species richness, species composition, and functional group richness and can also depend on species evenness and genetic diversity as well. Therefore, we urgently need to assess tropical diversity changes in landscapes disturbed by humans in the Anthropocene, a new geological epoch in which humans have significantly altered biodiversity, with consequences for planetary functioning (Corlett 2015).

## Conclusions

Tropics cover the large area of the Earth's surface and are instrumental to sustaining the all life forms on the Earth. For instance, the Amazonian rainforests of Brazil are considered to be the "lungs of the planet" as it absorbs CO<sub>2</sub> and therefore helps to protect the Earth against the greenhouse effect. Currently, the international agencies working in the environmental issues must consider the tropics on the top priorities to protect and conserve its immense natural resources and engage people in biodiversity and other environmental issues.

## Cross-References

- [Hotspot](#)
- [Savannah](#)

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## Tropism

- [Plantae](#)

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## True Hawks

- [Accipiters](#)

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## Tuberous Electroreceptor

- [Electroreceptors](#)

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## Tubes Task

- [Hood's Gravity Rules](#)

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## Tupping

- [Rutting](#)

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## Turing Test

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## Synonyms

Discourse; Imitation game; Hidden humans; Lying; Machine thinking; Misidentification

## Introduction

The ability of humans, and indeed other animals, to think plays a critical role in their cognition, understanding, and communication. But what exactly does it mean for an entity to think? Is it possible to measure thinking in some way? Can a machine be made to think in the same sort of way as a human?

Turing's imitation game, commonly known as the Turing test, was originally posed by Alan Turing as a "closely related" alternative to the question of whether or not a machine could be said to think (Turing 1950), something which could be "expressed in relatively unambiguous words." With regard to the question "Can machines think?" Turing actually felt this "to be too meaningless to deserve discussion." An important reason for this was the problem of agreeing on "definitions of the meaning of the terms 'machine' and 'think'." With regard to machines, Turing did though exclude biological systems such as cellular growths (Warwick et al. 2010) and even "men born in the usual manner," stating "we only permit digital computers."

Since that paper appeared, a lot of discussion has focused on the concept of machine thinking and whether it can be humanlike at times or even whether it will ever be possible to copy human thinking in all its aspects (Dennett 1998; Dreyfus and Dreyfus 2009; Minsky 1982; Shah 2010). Turing suggested, "May not machines carry out something which ought to be described as thinking but which is very different from what a man does?" (Turing 1950). As a result, some

researchers in the field regard the test as laying the foundations for what is now known as artificial intelligence (AI), even considering it to be AI's "empirical goal" (Harnad 1992).

The game involves human interrogators attempting to ascertain the nature of hidden (human and computer) entities with whom/which they are communicating. As indicated by Turing in Turing (1950), each discourse lasts for a period of 5 minutes only, and at the end of that time, the interrogator is charged with making the "right identification" by clearly identifying the nature of their hidden discourse partners by declaring which is the human and which is the machine (Warwick and Shah 2016a).

In considering the game in further depth, one is faced with numerous intriguing questions regarding human and machine communication and behavior. When comparing a human's ability to communicate, one immediately has to consider the fallibility, biases, and preconceptions of that person. One also must take into account important aspects of human nature such as lying, misunderstanding, lack of knowledge and humor, and never mind stupidity.

Over the last few years, a number of practical Turing test sessions have been organized involving some of the best conversation machines in the world; these followed as closely as possible with the test description as given by Turing himself in his seminal paper of 1950 (Turing 1950). One set of such experiments was held at Bletchley Park, England, in 2012. Another was held at the Royal Society, London, in 2014. The latter involved the largest number of tests ever staged in any single event.

In this article, the author reports on actual transcripts from these tests as a basis to investigate just what it takes to fool a human interrogator and how examples of the use of humor and lying have affected decisions. In addition, a look is taken at a series of cases in which human communicators have been clearly categorized by interrogators as definitely being machines and others in which machine communicators have been clearly categorized by interrogators as being human.

The transcripts between judges and hidden entities presented here are taken from tests in

which a human judge carried out a 5-minute-long conversation with two hidden entities in parallel. One of the entities was a human and the other was a machine. It was very much up to the judge as to the nature of the conversation, and it was their decision as to how much time they spent conversing with each of the entities during the 5-minute period.

In a particular session, a judge conducted five separate tests. In their first test, they witnessed a hidden human pitted against a hidden machine. Of course the judge would not know which was which; they would simply be aware of two hidden entities and have to make their own decision on the nature of the entities, although they had been informed *a priori* that one entity was human and one was a machine. The second test conducted by the judge then involved a different human pitted against a different machine, although again they would not be aware of each entity's nature. And so it would go on until the judge had conducted all their five tests in that session. At the end of each test, they were asked to state for each entity if they thought that it was a human or a machine or if they were unsure.

In the tests, the hidden humans were asked merely to be themselves, although they were requested not to give away their specific identity or personal information. They were not given any incentive to behave in a particular way and were given no payment at all. Of course this did not prevent any human from giving false information, which is something that humans do frequently. The tests were "unrestricted conversations," which meant the judge could ask anything or introduce any topic within the boundaries of courtesy (the judges had been informed however that there may be children among the hidden human entities).

## Turing Test Details

The conversations presented here were realized as a result of five-minute-long tests of human judge-hidden entity interaction, to conform to Turing's original wording in computing machinery and intelligence (Turing 1950).

What this paper does is to present a number of transcripts taken from practical Turing tests, which were held under strict conditions with many external viewers first at Bletchley Park, England, on June 23, 2012. The date marked the 100th anniversary of Turing's birth and the venue was that at which, during the Second World War, Turing led a team of code breakers to crack the German Enigma machine cipher. The second set of tests was held on June 6–7, 2014 at the Royal Society, London, of which Alan Turing was a fellow. Five different machines took part in both sets of tests along with 30 different judges and 30 hidden humans against which the machines were compared in terms of their conversational ability. Although the machines were common to the two experiments, the judges and hidden humans were a different collection of people.

In this article, one is certainly interested in how good or bad the machines are; indeed, it is interesting to look at how good they can be. But one is also interested in the operational performance of the judges and specifically how they interacted in conversation with hidden entities. Hidden humans are, by definition, human, but (Shah and Warwick 2010; Warwick and Shah 2015a) can themselves be misidentified on occasion? An attribution of *humanness* by a human interrogator to a hidden interlocutor in a practical Turing test is dependent on the judge's own values of what constitutes humanlike conversational behavior. Good performance of machines is largely discussed elsewhere (Warwick and Shah 2014a), although a couple of examples are given here in a separate section for comparative purposes.

A look is taken into Turing's statement that the test/game can be considered as a replacement for the question "Can machines think?" (Turing 1950). While it is acknowledged that the results in each case depend on the performance of the judge, far from the conditions of the game saying nothing about the judge, this aspect is seen here to be very much a critical part of the test itself. Importantly, in the test, machines are pitched against (hidden) humans under the critical analysis of other (interrogator) humans. These are all very important aspects of what the test is about and are certainly not points of fallibility of the

game as has been suggested by Hayes and Ford (1995).

In the sections that follow, different examples of practical tests are given, and an attempt is made to cover a wide range of problem areas as they exist at present, which the test highlights. In each case, discussion on the transcript is carried out within that section, where it is pertinent. However, a number of universal comments are also made in the conclusions section toward the end of the article.

The transcripts considered in this paper appear exactly as they occurred. They have not been altered in any way in terms of the sequence or wording or corrected spelling. Once an utterance was outputted, it was not possible for the judge or hidden entity to alter it in any way. The timings shown are accurate, actual timings on the days (UK time) involved. Any spelling mistakes or other grammatical errors were exactly as they happened. They are not due to editorial errors. In the transcripts, the interviewer/judge is always denoted as “judge,” whereas the hidden interlocutors, machine or human, are denoted as “entity.”

## Lying

Lying is a part of human nature and therefore has a role to play when it comes to the Turing test. The machine’s goal is deception attempting to mislead the interrogator that it is a human. Meanwhile, hidden humans are requested not to give away exactly who they are through revealing personal details, as this might aid the interrogator, but apart from that they can simply be themselves. Lying can take on many different forms from a white lie to an unintentional lie to a complete untruth. What one is interested in is the effect of a lie on the decision taken by the interrogator. Please see Warwick and Shah (2016b) for an in-depth analysis of these and many more transcripts.

Transcript 1:

[12:43:23] Judge: Why hello there!

[12:43:41] Entity: Why hello to you too!

[12:44:51] Judge: How are you feeling on this fine day?

[12:45:12] Entity: To be quite honest a little rejected, I thought you were never going to reply :(

[12:45:42] Judge: Oh, I’m very sorry, it will not happen again.

[12:45:49] Entity: It just did!

[12:46:46] Judge: Oh, I lied then.

[12:47:12] Entity: That’s a great shame indeed.

[12:47:34] Judge: It is. Are you following the Euro 2012’s at the moment?

[12:47:55] Entity: Yeah quite closely actually. I am Cristiano Ronaldo.

The main issue with this transcript occurs in the last couple of lines. The Euro 2012 refers to the European nations’ football competition which was being held at exactly the same time as the Turing event. Many people were watching the matches on television. Cristiano Ronaldo is a Portuguese footballer. The last line reply, merely agreeing with the judge’s specific question, appears to have been sufficient to correctly categorize the entity, in the judge’s opinion, as being a human. This was probably sealed by the “humorous” comment with the entity claiming to be Cristiano Ronaldo.

Interestingly, the specific knowledge tester about Euro 2012 was dealt with by the entity agreeing with the comment. However, the human entity openly lied about being Cristiano Ronaldo who was himself not taking part in the experiments. The interrogator may well have seen the humorous lie as supporting evidence of the entity being human. In this case, the white lie had no negative effect.

## Misidentification

In this section, two cases are included in which a misidentification has occurred. The second of these could be regarded as a good outcome in that it involves a machine being incorrectly classified as a human. The first case however involves a human misidentification and was reported on in greater depth in Warwick et al. (2013).

Transcript 2:

[10:58:45] Judge: Hi there



[10:58:55] Entity: Hi, how are you?  
 [10:59:02] Judge: I'm good.  
 [10:59:21] Entity: what, that's your name, like in the Good Life?  
 [10:59:36] Judge: What do you mean by 'Good Life'?  
 [10:59:47] Entity: Tom and Barbara  
 [11:00:02] Judge: What's that?  
 [11:00:31] Entity: A couple who left the rat race  
 [11:01:03] Judge: Oh. Is that your names? Wonderful to have left the rat race. How long ago was that?  
 [11:01:28] Entity: Not me, I'm still in it. But it's nice to dream  
 [11:02:02] Judge: Yeah - would be good. I 'semi' left it. It's much less stress  
 [11:02:31] Entity: I'm still very young so I'm looking forward to a lot of things  
 [11:03:11] Judge: What kind of things?  
 [11:03:34] Entity: Life in general I guess, different emotions and feelings that it brings.

The transcript contains reference to Tom and Barbara Good who appeared in a UK TV program entitled *The Good Life* (Good Neighbours in the USA) in which they left the rat race to grow their own vegetables and live off the land. The discourse indicates that the judge's knowledge may not have extended to the Good Life. They did not appear to "understand" the utterances of the hidden entity (more of this later). Possibly, as a consequence, the interrogator classified the hidden human as definitely being a machine.

Transcript 3:

[12:43:37] Judge: Hi, I'm Cathy.  
 [12:43:43] Entity: Cathy! Nice to meet you! You're a woman, if I'm not mistaken.  
 [12:44:20] Judge: Right. What is your name?  
 [12:44:29] Entity: People call me Eugene. Or "Zhenya". It is a short name for Eugene in Russia and Ukraine.  
 [12:45:17] Judge: NIce name. Are you from either area?  
 [12:45:41] Entity: Agree :- ) Oh, what a fruitful conversation:-)  
 [12:45:52] Judge: Do you really think so?

[12:46:04] Entity: No, your guess was wrong. I don't think so. By the way, I still don't know your specialty - or, possibly, I've missed it?  
 [12:46:56] Judge: What speciality? What's yours?  
 [12:47:01] Entity: Huh? And I forgot to ask you where you are from...  
 [12:47:51] Judge: The universe and you?  
 [12:48:01] Entity: Is it your hobby to ask little poor Jewish boys such tricky questions they don't have an answer for?

At the end of this discourse, the interrogator incorrectly identified the machine involved as definitely being a human. One can see here the successful ploy on the part of the machine of not answering the question posed but rather changing the subject by asking another question. The third response of the machine does seem a little off in that it completely ignored the question about origin. The final line is though a good example of responding to a question in an argumentative tone. In the following section, a look is taken at further examples of machines performing well.

## Good Performance by Machines

In this section, two examples are considered in which machines fooled the interrogators involved to misclassify them as human. This is in essence what the Turing test is all about, and hence such transcripts are significant in assessing just what aspects of human nature, in conversation at least, appear to be successfully simulated by the machine and whether not this is sufficient to conclude that the machine is thinking or at least that it appears to think. This is discussed in much greater depth in Warwick and Shah (2014a).

Transcript 4:

[10:41:48] Judge: Hello. How are you?  
 [10:41:53] Entity: Hey.  
 [10:42:16] Judge: How do you like Bletchley | Park?  
 [10:42:20] Entity: lol.  
 [10:42:39] Judge: Are you from England?  
 [10:42:47] Entity: They have Wi-Fi here in the pub.

[10:43:31] Judge: Which pub?

[10:43:38] Entity: I'm just down the pub.

[10:44:03] Judge: Have you ever been in a Turing Test before?

[10:44:08] Entity: Will this be the 5 minute argument, or were you thinking of going for the full half hour.

[10:44:55] Judge: Very funny. You sound suspiciously human. Do you like the Beatles?

[10:45:02] Entity: I'd like to get the next Dread the Fear tape.

[10:45:20] Judge: What is Dread the Fear?

[10:45:24] Entity: Dread the fear has that Steve Henderson guy in it.

[10:46:08] Judge: What sort of music is that? Or is it comedy?

The machine entity was identified as definitely being human at the end of the conversation even though the conversation did not start well for the machine. In their third response, the mention of both Wi-Fi and pub seemed out of context. But it got back on track with the Monty Python humorous link between 5-minute Turing tests and a comedy sketch about the argument clinic. In response to the Beatles question, a direct answer is not given but the music link remains as the conversation shifted, and the entity appeared to show in-depth knowledge about a pop group named Dread the Fear, which may or may not actually exist!

Transcript 5:

[12:23:19] Judge: What is black and white and read all over?

[12:23:32] Entity: I don't have true sense of color perception I am only able to see the RGB values.

[12:24:08] Judge: That's ok. Do you like jokes?

[12:24:19] Entity: Please tell me your inclination to a good sense of humor first.

[12:24:40] Judge: A person who can laugh at one's self.

[12:24:46] Entity: Would you like to hear a joke?

[12:24:54] Judge: Yes, please.

[12:25:21] Entity: This joke has been making the rounds in robotic circles: A robot goes to the

doctor and says: "My left arm is stuck. Give me a new arm." The doctor answers: "Your arm is fine. We'll have to replace the rest of you."

[12:26:06] Judge: Ha! Ha! Why did the chicken cross the road?

[12:26:22] Entity: The chicken wandered into the road because it liked the shiny colors of the cars and trucks whizzing by.

[12:27:39] Judge: You're right. It didn't care if it got to the otherside.

[12:27:50] Entity: By the way, did you ever actually see a chicken crossing the road?

[12:28:03] Judge: Only one that didn't make it.

Here humor is applied directly by the machine, curiously with a machine-type reference. Nevertheless, the interrogator was certain, at the end of the 5 minutes that they had been conversing with a human. In his paper (Turing 1950), Turing referred to the "arguments from various disabilities" that some humans might use as a defense against machines being intelligent – humor being one of those aspects.

The first line uttered by the entity is a little strange, but their third line is masterly. In response to the judge's comment about laughing, the entity takes control of the conversation by offering to tell a joke. Later when the judge mentions a chicken, the entity correctly follows up with a suitable response and once again takes control of the conversation by asking the judge a pertinent question. So "understanding" what the key issue is on a couple of occasions and actually taking control of the conversation were sufficient here for the deception to occur. In this case, the machine successfully gave the illusion of understanding the judge's utterances, and such understanding has been indicated on many occasions as being a basic prerequisite for intelligence, for example (Penrose 1994; Searle 1997).

## Assumption of Knowledge

It is apparent in the Turing test that very often an interrogator will resort to asking direct factual questions even though there is little to be gained by such a ploy. As Turing (Turing 1950)

indicated, mathematical questions are a complete waste of time. However, the same conclusion is apparent in general.

Transcript 6:

[11:13:15] Judge: pastasciutta

[11:13:22] Entity: what?

[11:13:44] Judge: anything familiar in this word ?

[11:14:18] Entity: I cannot see any sexual aspect at all

[11:14:42] Judge: nothing to do with sex. try again

[11:14:49] Entity: why?

[11:15:14] Judge: just asking you to try again

[11:15:23] Entity: I am bored with it

[11:16:04] Judge: c'mon a little effort btw are you in my same time zone ?

[11:16:24] Entity: I believe that the world should just have one time.

[11:17:27] Judge: why ?

[11:17:58] Entity: seems sensible, easier for all. Better with computer

There are two issues early on in this transcript. To start with, the judge throws in the word “pastasciutta” as a knowledge test for the entity. It is not clear how knowing such a word would indicate that the entity was either human or machine. Secondly, the entity makes a response in terms of the use of the word “familiar” in a “sexual” sense. The judge appears to be unaware of such a meaning (Fowler and Fowler 1995). So here one can see a test of specific knowledge by the judge and an apparent lack of specific knowledge by the same judge. As a result, the judge misidentified the human entity, deciding that they were definitely a machine.

## Royal Society Experiment

Turing set a pass mark for his test (Turing 1950) of 30% in the sense that for a machine to pass, at least 30% of the judges who interrogated that machine would not be able to make the right identification in the tests in which they were involved. This is taken to mean that the judges could not identify

the machine as actually being a machine in those tests, rather than also including cases in which the hidden human was not classified as being human.

In the 2014 Royal Society experiment, a machine called Eugene Goostman, who/which poses as a 13-year-old Ukrainian boy, achieved a score of 33% (Warwick and Shah 2015b). In fact, if cases of human misidentification are also included, then the score rises to 45%. Here we include a transcript to give the reader an idea of the sort of conversations that a machine can have.

Transcript 7:

[16:21:00] Judge: what did you have for breakfast today

[16:21:10] Entity: Is it ‘the third degree’? I’m not going to answer such a provocative question! Well, let’s go on though.

[16:21:56] Judge: do go on . . . your call?

[16:22:06] Entity: It is highly possible. By the way, what’s your occupation? I mean – could you tell me about your work?

[16:22:30] Judge: so you are asking me now eh? I am an actress and writer

[16:22:38] Entity: Well, I’ll read something of your books, if they ain’t too tedious (which is highly possible:-)

[16:23:15] Judge: grammar . . . aren’t too tedious! A bit rude of you . . .

[16:23:17] Entity: Calm down, please.

[16:23:49] Judge: i assure you i am very calm . . . are you?

[16:24:01] Entity: Don’t even bother me with the fact that you are very calm . . . are mine. And I forgot to ask you where you are from . . .

[16:25:01] Judge: I am from Dorset . . . where are you from?

[16:25:08] Entity: I am from Ukraine, from the city called Odessa. You might have heard about it.

Eugene did not answer questions from the start, other than in the final instance when being asked where he was from. Indeed, he managed to get into something of a discussion, even an argument with the judge. All of which added to the conclusion in the judge’s mind that the hidden entity was human, which is what they decided, selecting the (machine) entity as a nonnative

English-speaking person. In this case, the judge did, to an extent, go along with Eugene asking a question. Controlling the conversation is an important tool for a machine and can put a judge onto the back foot.

## Conclusions

Many philosophers have concentrated on the importance of “understanding” and the critical role it plays in intelligence. As stated in Penrose (1994), “intelligence requires understanding.” The Turing test, particularly in its practical form, can be seen to play an important role in this discussion as it can be concluded from some of the transcripts presented that, in terms of conversational appearance at least, there are some humans who appear to be lacking in intelligence, whereas there are some machines that clearly have it in abundance. Meanwhile, ignoring such evidence requires a scientific argument if the hypothesis that “intelligence requires understanding” is to hold.

It can be seen from the examples given that some judges in these tests were more susceptible than others to conversational deception, or conversely, some judges (maybe all judges) have a biased perspective on “humanlike conversation.” This may have lead the judges in some cases here to misclassify hidden interlocutors, even though they actually initiated the conversation and were given the possibility of asking or discussing whatever they wanted. The conversations were unrestricted.

Not all of the five invited machines in these experiments were designed to imitate humans. Elbot (see Transcript 5), for example, from Artificial Solutions has a robot personality. However, all were designed to mimic human conversation sometimes deploying spelling mistakes and always avoiding mathematical questions. Essentially, the machines were not trying to be perfect or to give correct answers; they were merely trying to respond in the sort of way that a human might. As Turing put it, “the best strategy (for a machine) is to try to provide answers that would naturally be given by man.”

Although Turing designed the test as an answer to the question “Can machines think?” it has become regarded by many as some sort of competition to see how well machines perform and as a standard in assessing how machines are progressing with regard to artificial intelligence. Just what role it plays as far as the development of artificial intelligence is concerned is a big question that is not easily answered. Some however see it as a milestone and of vital importance to artificial intelligence. Whatever the standing of the Turing test, what is evident from the transcripts presented and others obtained, is that the Turing test is certainly not a trivial exercise. Indeed, it also gives surprising insights into how humans communicate and how other humans (the judges) can be easily fooled.

In this article, an attempt was made to give an up-to-date perspective on an important aspect of artificial intelligence research, namely, human-machine communications. It is critical to note that such a study involves humans as conversationalists and respondents as well as machines. Yes it can be witnessed just how machine conversation is steadily improving, in terms of its humanlike nature. But one also has to take into account humans who are involved in the conversing, with all of their fallibilities and odd reasoning. For the machine developers, these aspects give rise to particular features in their conversational programs. It is worth remembering that the machines do not have to be perfect but rather they have to be humanlike. Whether or not this amounts to something that can be called “thinking” will be debated for many years to come.

## Cross-References

- [Communication](#)
- [Intelligence](#)
- [Social Intelligence Hypothesis](#)

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## Turtles and Tortoises

### ► Testudines Life History

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## Twilight

### ► Crepuscular

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## Twin Research

### ► Twin Studies

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## Twin Studies

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## Synonyms

Studies of twins; Twin research

## Definition

Research utilizing twins, usually with the goal of assessing the approximate contributions of heredity and environment toward a characteristic by comparing identical and fraternal twins (APA Dictionary of Psychology [n.d.](#))

## Introduction

Since they started almost a century ago, twin studies have been integral to the field of behavioral genetics by providing valuable information about the relative influence of genetics and the



environment on different complex traits, behaviors, and illnesses. This is possible because twin pairs can come in two forms: monozygotic and dizygotic. Monozygotic (MZ) twins, or identical twins, share 100% of their genetic makeup. Since their genetics are the same and held constant, differences found between a pair of MZ twins are likely the result of environmental influences that only one twin has experienced, or a unique, nonshared environment. On the other hand, dizygotic (DZ) twins, or fraternal twins, share only 50% of their genes, as is true for regular siblings. The classical twin study compares the concordance, or similarity in phenotype, between MZ and DZ twins who are respectively reared together. If the MZ twins show higher concordance in a trait (meaning the twins in that pair exhibit greater similarity in that trait), that implies the trait is strongly influenced by genetics.

The classical twin study and many other models for twin analysis are based on the equal-environment assumption (EEA), which states MZ and DZ twin pairs are exposed to shared environmental factors in similar degrees (Kendler et al. 1993). This assumption allows researchers to make inferences about the role of genetics, because the environment is mostly being held constant while genotypes are varying. Specifically, it can be inferred that greater similarity within MZ twin pairs is higher than that within DZ twin pairs because MZ twin pairs share 100% of their genetic makeup. If the EEA is incorrect, it could mean this greater similarity in MZ twins compared to DZ twins could be partially explained by differing environments. Numerous studies conducted to test the validity of the EEA by examining twins' environmental similarity in relation to physical resemblance, perceived zygosity, and similarity in various psychological disorders, found no substantial influence (Kendler 1983; Kendler et al. 1986, 1992a, b, c, d, 1993; Matheny et al. 1976). However, other studies found environmental similarity did influence self-reported psychiatric symptoms (Clifford et al. 1984), as well as personality and alcohol consumption (Kaprio et al. 1990).

Other models for twin analysis seek to determine whether environmental effects play an important

role in shaping a certain trait. For example, when MZ twins are raised apart, their genetic makeup is identical, but their environments are different, so any variance between the twins can likely be attributed to environmental factors. As far as the major findings of twin studies, recent research has concluded the vast majority of complex human traits are about 49% heritable (Polderman et al. 2015). Twin studies have also helped estimate the relative environmental and genetic effects on the etiology of different behaviors and psychological disorders. Although the etiology of most traits, behaviors, and disorders has been found to be a complex interaction of genetic and environmental factors, twin studies have been valuable in helping estimate the relative contributions of each, sometimes with surprising results. This information is useful for the prediction and primary prevention of certain behaviors and disorders.

## Nature Versus Nurture

The most common question twin studies seek to answer is that of nature vs. nurture, and which of the two has a greater influence on our traits and behaviors. Two issues that can complicate analyses of twin studies are genotype-environment interaction and genotype-environment correlation (Plomin et al. 1977). Genotype-environment interaction refers to the possibility that people with different genotypes could react differently to certain environments. Genotype-environment correlation refers to the possibility that individuals with different genotypes are specifically exposed to certain, different environments. For instance, do children with greater learning ability respond better to a specific classroom environment (genotype-environment interaction), or are they typically given better academic opportunities and feedback because of their superior ability (genotype-environment correlation)? A study conducted by Plomin et al. (1977) found genotype-environment interaction and correlation could each bias estimates of genetic and environmental variance in twin studies.

An important study that attempted to address the question of nature vs. nurture was conducted

by Polderman et al. (2015). They conducted a meta-analysis of almost all twin studies published 50 years prior to the study (2,748 publications), examining more than 14 million twin pairs from 39 different countries across a wide range of traits. Results of the meta-analysis showed not even one of the traits examined had a heritability estimate of zero, therefore strongly suggesting all human traits are heritable. In fact, the reported heritability across all traits was 49%. For about two-thirds of the traits observed, MZ and DZ twin correlations fit the model of additive genetic variation, meaning MZ correlations were twice as high as DZ correlations. This suggests a simple additive genetic model can probably be used to determine genetic variations that cause most complex traits. About one-third of the traits examined did not follow the simple additive genetic model.

## Cognitive Ability and Development

One area twin studies have focused on is cognitive ability and how it changes and develops across the lifespan. A longitudinal study by Wilson (1983) assessed the mental development of almost 500 twin pairs and their siblings from infancy to adolescence. Results showed MZ twins' intelligence became more concordant over time, and they had similar developmental trends. DZ twins' intelligence became less concordant over time so that it was similar to what is found between normal siblings or parents and their children. Genetics seemed to have the largest influence on cognitive development, but certain features of the home environment like socioeconomic status, parental education and demeanor, and home atmosphere were also significant predictors of children's IQ. Another longitudinal study found the variability and stability of general cognitive ability later in life was also largely due to genetic factors (Plomin et al. 1994). The average participant age was 64.1 years. Some twins were reared together, and others were raised apart. They tested general and specific cognitive abilities of MZ and DZ twin pairs over the span of 3 years. Compared to general cognitive ability, specific cognitive abilities were less stable and received

less genetic influence. More recently, Briley and Tucker-Drob (2013) conducted a meta-analysis of longitudinal studies of 11,500 twin and sibling pairs from infancy to adolescence to determine why the heritability of cognitive ability increases with age. They examined how much amplified genetic influences (genetic influences that are present early on but become more important with age) and innovative genetic influences (novel influences that occur throughout life and lead to the activation of genes) accounted for this increase in heritability. They found innovative genetic influences primarily accounted for the increasing heritability of cognitive ability in early childhood, but this swiftly declined, and amplified genetic influences were predominant after 8 years of age. In sum, these studies support the theory that genetic factors largely influence the development of cognitive ability both early and later in life.

## Behavior

Twin studies have long been used to assess the etiology of different behaviors. Mason and Frick (1994) conducted a meta-analysis of 12 twin studies and 3 adoption studies to attempt to determine the heritability of antisocial behavior. The analysis revealed genetics accounted for about 50% of the variance in antisocial behavior. In addition, genetic effects tended to be stronger when the antisocial behavior exhibited was severe. Eley et al. (1999) also examined the etiology of antisocial behavior through two twin studies, specifically focusing on sex differences between aggressive and nonaggressive antisocial behavior. After examining over 1500 twin pairs total (7–16 years old), they found genetic factors had a far greater influence on aggressive antisocial behavior compared to nonaggressive antisocial behavior. In addition, shared environment had a significant influence on nonaggressive antisocial behavior. For females, the correlation between aggressive and nonaggressive antisocial behavior was mostly accounted for by genetic factors that influenced both types of antisocial behavior. For males, shared environment had a greater influence on this correlation.

Much research points to a strong inverse relationship between antisocial behavior and academic underachievement (Hinshaw 1992), and Trzesniewski et al. (2006) conducted a twin study to examine the source of the negative relationship between reading achievement and antisocial behavior. They examined two cohorts of same-sex twin pairs (ages five and seven). Results revealed environmental factors associated with both reading achievement and antisocial behavior were what primarily accounted for the relationship between those two variables. For boys, the correlation between reading achievement and antisocial behavior was much stronger compared to girls, and the best explanation for that association was a reciprocal causation model (antisocial behavior led to poor reading, and vice versa). This suggests targeting antisocial behavior *or* reading achievement in young boys is likely to cause changes in both behaviors.

Another twin study that looked at same-sex twin pairs was conducted to examine genetic and environmental influences on competence and problem behavior in early childhood and adolescence (Edelbrock et al. 1995). Results showed a significant genetic influence on academic competence and all aspects of problem behavior. Furthermore, there was a significant influence of shared environment for several specific behaviors like delinquent behavior and level of participation in school activities. Robinson et al. (1992) did a longitudinal study of twin pairs over 10 months to determine the heritability of inhibited and uninhibited behavior. Participants were same-sex twin pairs assessed at 14, 20, and 24 months of age. Analyses suggested genetic factors were significant at all age intervals examined, and extremely inhibited behavior seemed to be heritable.

The genetic and environmental influences on smoking behavior have also been researched by twin studies. A meta-analysis of genetic and environmental effects on smoking behavior in female and male adult twins was conducted by Li et al. (2003). They found genetics had a greater influence on smoking initiation and less influence on smoking persistence in females compared to males. Shared environmental effects on smoking initiation were much higher in male adults, while

shared environmental effects on smoking persistence were much higher in female adults. No significant gender differences were found for estimates of unique environmental effects. Overall, these studies provide evidence that for many problem behaviors, genetics have significant effects particularly when the behavior is severe, while shared environmental factors also influence some specific problem behaviors.

## Mental Illness

Twin studies have been very important in examining the etiology of different mental disorders. A review of twin studies of psychiatric illnesses revealed behavioral traits could be more heritable in permissive rather than restrictive environments (Kendler 2001). The studies reviewed also suggested genes for psychiatric and drug abuse disorders likely worked through the traditional physiological route, but also through gene-environment correlation. In other words, these genes can affect the social environment in ways that increase or affect the risk of illness, like being exposed to more stressful life events. Agrawal and Lynskey (2008) reviewed twin, family, and adoption studies to examine the genetic basis for different drug addictions (alcohol, nicotine, cannabis, and others). Evidence from the different studies showed a range of moderate to high genetic influence for addiction. However, there is no single gene that causes addiction, and the interaction between genes and the environment is still very important to consider. Lin et al. (1998) analyzed over 6000 male-male MZ and DZ twin pairs to determine the familial and genetic contributions to vulnerability for pathological gambling. They found familial factors accounted for over 60% of liability for a diagnosis of pathological gambling disorder, and genetic factors accounted for 35–54% of liability for five symptoms of pathological gambling disorder.

To examine the etiology of suicide and suicidal behavior, a review of twin, adoption, and family studies was conducted (Brent and Mann 2005). They concluded suicide and suicidal ideation seemed to be heritable through at least two

factors: liability to psychiatric disorder and liability to impulsive aggression. That is to say, being predisposed to a psychiatric disorder and to impulsive aggression means one is at high risk for suicidal behavior.

Schizophrenia is another mental disorder researched in twin studies. Cardno and Gottesman (2000) conducted a review of twin studies of schizophrenia. They found high heritability estimates for schizophrenia (80–85%) that were similar across different studies. A meta-analysis of 12 schizophrenia studies also found evidence for high heritability (81%) for liability to the disorder (Sullivan et al. 2003). In addition, they found evidence for small but significant common environmental effects on liability to schizophrenia (11%). It was surprising for them to find environmental influences for liability to schizophrenia were nonzero (significant), because it is uncommon for a behavioral disorder to have significant common environmental influences, and schizophrenia is usually described as a more genetic disorder.

Twin studies have also been utilized to better understand the causes of autism spectrum disorders (ASDs) and autistic traits. A review of over 30 such twin studies from 2000 to 2010 was conducted by Ronald and Hoekstra (2011). In most of the studies, concordance seemed high in monozygotic twins (70–90%) and lower but nonzero in dizygotic twins (0–31%), suggesting high heritability. However, twin studies on ASDs also consistently show nonshared environments still have a small and potentially meaningful role in causing ASDs. Tick et al. (2016) conducted a meta-analysis of twin studies on the heritability of ASDs, and they also found evidence of high heritability. Furthermore, they found shared environmental effects became significant as the prevalence rate decreased, and previously reported significant shared environmental effects from other studies were likely from over-including concordant DZ twins.

Obsessive-compulsive disorder has also been researched by twin studies. A meta-analysis of 14 twin studies was conducted to examine the etiology of obsessive-compulsive symptoms (Taylor 2011). Results showed genetics and

nonshared environment had the largest influence on obsessive-compulsive symptoms, and gene-environment interactions also influenced the etiology. However, shared environment played a limited role in the etiology of obsessive-compulsive symptoms. Taylor concluded the etiology of obsessive-compulsive symptoms is very complex.

Finally, twin studies on eating disorders have been done to examine their etiology. Bulik et al. (2000) reviewed twin studies on anorexia nervosa and bulimia nervosa to examine their etiology. Results suggested anorexia nervosa is familial, but they could not draw strong conclusions for its etiology because the condition was rare with limited data. Bulimia nervosa also seemed to be familial, and additive genetic effects and unique environmental factors were strong contributors. However, the contribution of shared environment seemed to be weaker than additive genetic effects in bulimia nervosa. Together, these studies show that while many mental illnesses have a significant genetic component varying from moderate to high, environmental factors also play an important role in the development of several.

## Future Directions and Conclusions

Twin studies have sought to answer the question of nature vs. nurture. However, research has shown that it is never just nature *or* nurture that influences a trait, but rather a combination and interaction of both genes and the environment (Sahu and Prasuna 2016). A recent meta-analysis of almost all twin studies published to date, examining over 14 million twin pairs from 39 different countries, has shown most complex traits have 49% heritability (Polderman et al. 2015). These results also strongly suggested all human traits are heritable. An important longitudinal twin study on cognitive development in children found genetics had a larger influence, but certain factors in the home environment were still significant predictors of children's intelligence (Wilson 1983). Another longitudinal twin study in older adults found general cognitive ability was more hereditary and stable than specific cognitive abilities (Plomin

et al. 1994). Twin studies on antisocial behavior found genetic influence was greater when the antisocial behavior was severe (Mason and Frick 1994) and when the antisocial behavior was aggressive rather than nonaggressive (Eley et al. 1999). In addition, a meta-analysis of twin studies on smoking behavior found genetics had a greater influence on smoking initiation and less influence on smoking persistence in females compared to males (Li et al. 2003). Finally, twin studies have examined the etiology of mental disorders. A review of twin studies of psychiatric illnesses revealed behavioral traits could be more heritable in permissive rather than restrictive environments (Kendler 2001). In addition, a meta-analysis of twin studies of schizophrenia found evidence for high heritability and small but significant common environmental effects, the latter of which was surprising given that schizophrenia is usually characterized as a genetic disorder (Sullivan et al. 2003). Future twin studies should take gene-environment interactions and correlations into account more when analyzing twin studies. Furthermore, future twin studies should further examine the role of gene-environment interactions and correlations in the etiology and development of different traits, behaviors, and disorders, as they are two important factors in genomic research. Finally, additional work should aim to examine traits in different stages of the lifespan and include more diverse samples from different places and cultures.

## Cross-References

- ▶ Additive Genetic Variance
- ▶ Adolescence
- ▶ Aggression
- ▶ Behavioral Genetics
- ▶ Behavioral Variation
- ▶ Cognition
- ▶ Concordance
- ▶ Dizygotic (DZ)
- ▶ Environmental Influences
- ▶ Equal Environments Assumption
- ▶ Gene Expression
- ▶ Genes

- ▶ Genotype
- ▶ Heredity
- ▶ Heritability Estimate
- ▶ Heritability of Behavior
- ▶ Inhibition
- ▶ Intelligence
- ▶ IQ
- ▶ Learning
- ▶ Nature Versus Nurture
- ▶ Phenotype
- ▶ Sex Differences

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## Twin Study Method

- ▶ [Diallel Design](#)
- ▶ [Equal Environments Assumption](#)

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## Twins

- ▶ [Dizygotic \(DZ\)](#)

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## Two-Alternative Forced-Choice Paradigm, The

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## Synonyms

[2AFC](#); [Learning-set paradigm](#); [Transfer Index paradigm](#); [Two-choice \(or two-object\) discrimination learning paradigm](#)

An animal encounters a choice-point in a maze. One arm in the “Y” (or “T”) of the maze will lead to reward. The other choice will lead to nonreward or maybe even some punitive consequence like electric shock. The two outcomes are differentially signaled on the basis of position (e.g., the alley on the right is always correct) or on the basis of some other stimulus cue (e.g., the illuminated alley is always correct, irrespective of position).

There is no retreat. The animal must eventually move forward and select from the two options. This situation, repeated in various forms in thousands of learning studies with animals, is the essence of the two-alternative forced-choice testing (2AFC) paradigm. Faced with two response options, each uniquely signaled by a stimulus, can organisms learn to discriminate, on the basis of spatial, form, or other stimulus features, which of the two responses will be correct?

The two-alternative forced-choice (2AFC) discrimination-learning procedure is not limited to maze-learning procedures, although one can argue that it was introduced to comparative psychology first through the early maze-based research of Small (e.g., 1901) and others. Indeed, psychology’s introduction to the 2AFC paradigm traces back to Fechner (1860) and the study of discrimination thresholds using psychophysics. Although the 2AFC term has been used generically for a variety of testing procedures in which organisms are forced to make one of two responses (including, for example, yes/no or go/no-go testing), 2AFC testing in the strictest sense is a comparison procedure that involves the presentation of both discriminative stimuli on every trial such that the organism must choose between the two alternatives on every trial (Macmillan and Creelman 2004). The psychophysics curves for 2AFC discrimination tasks have been studied and modeled in many studies, both historical (e.g., Luce 1963) and more contemporary (e.g., Bogacz et al. 2006). From its earliest use with humans, 2AFC has been used to identify discrimination thresholds in various sensory domains (e.g., Jones 1956): pairs of stimuli are presented to participants across trials, with the goal of determining how dissimilar the objects must be for participants to discriminate between them. As will be discussed below, the discrimination thresholds of nonhuman animals have also been measured with 2AFC, although most comparative research using the paradigm has been focused on discrimination learning rather than perceptual abilities.

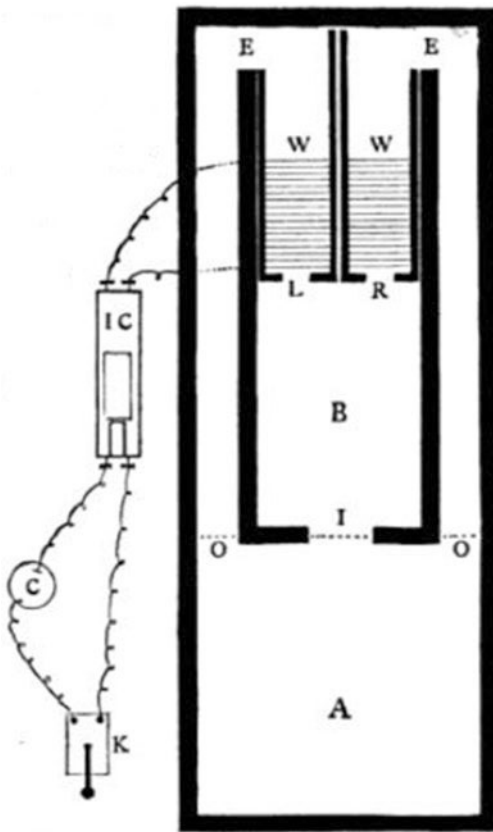
Kline (1899) described a simple maze-like choice apparatus that he used to study olfactory discrimination learning by wasps (*Polistes*

*rubiginosus*). Yerkes (1907) described several apparatuses for determining brightness and color discrimination by the dancing mouse. In one Yerkes apparatus, for instance, an animal could be placed in an antechamber (Fig. 1, “nest area”) from which it could access the experimental entrance area through a one-way door in the middle of the box and make a choice between one of two alleys (labeled L and R in Fig. 1). In this image, the animals were being tested on a Black/White discrimination, using an electric grid to deliver aversive consequences to the animal that chose incorrectly. Whether correct or incorrect, the animal could exit the grid at the back of the shuttle

box (or, in some conditions, were required to make a correction response by retracing its steps from the incorrect electric-box to enter the correct electric-box), which cycled the animal back through one-way doors into the antechamber for the next trial. Using this apparatus, Yerkes studied the degree of discrimination learning for brightness (black vs white vs shades of gray), controlling for possible confounds of position, odor, texture, and form. Modification of this apparatus permitted Yerkes to study the mouse’s just-noticeable difference in the illumination of two electric-boxes in a test of Weber’s law (see Yerkes 1907).

Modifications of this general design were described by Yerkes and Watson (1912) in their influential monograph, *Methods for Studying Vision in Animals*. The Yerkes-Watson apparatus (or Yerkes-Watson discrimination box) and variations became standard instruments for investigating perceptual discrimination in animals. Over the next few decades, the 2AFC procedure (also termed the “paired stimuli” technique by Klüver, 1933, and the “form and size method” by Washburn, 1908) was used to investigate visual discrimination (and, to a lesser degree, the perceptual discrimination in other modalities) in a wide range of animals. Training animals to choose between two stimuli on the basis of brightness, color, shape, form, size, position, or other cues, researchers documented the perceptual abilities to select the “correct” (or rewarded, S+) stimulus rather than the incorrect (nonrewarded, S-) stimuli of a pair. Data were published for birds, cats, chimpanzees, dogs, monkeys, raccoons, rats, squirrels, turtles, and many other species (see, for example, summaries by Washburn 1936; Weinstein and Grether 1940).

The debate over whether animals were responding in this 2AFC to the absolute versus the relative stimulus features (e.g., absolute brightness of a stimulus versus the brighter of the two paired-choice stimuli) led to the use of this paradigm for studies of transposition (Köhler 1938; Spence 1937). Animals were trained on one or more pairs of stimuli, where the paired objects differed along one stimulus dimension (e.g., size); subsequently, the animals were given 2AFC



**Two-Alternative Forced-Choice Paradigm, The, Fig. 1** (From Yerkes 1907, Fig. 15). Ground plan of discrimination box. A, nest box; B, entrance chamber; W, W, electric-boxes; L, doorway of left electric-box; R, doorway of right electric-box; E, exit from electric-box to alley; I, swinging door between A and B; O, swinging door between alley and A; IC, induction apparatus; C, electric cell; K, key in circuit. (p. 93)

generalization tests – specifically, tests in which a previous S+ stimulus was used as the S- object within a novel pair – to see whether the discrimination learning was associative versus relational in nature (see review and decisive research by Lazareva and her collaborators (see review in Lazareva 2012)). In recent years, the 2AFC paradigm has remained popular for the study of transposition with a variety of animal species. For example, Hanggi (2003) trained horses to select the larger (or smaller) of two objects in 2AFC tests; in novel tests, the horses selected stimuli according to the trained rule (e.g., choose larger) rather than on the basis of reward history with specific stimuli. Similar transposition success has been reported for various species of bird, fish, insect, and mammals – although there have been documented failures as well – illustrating the ongoing utility of the 2AFC paradigm for the purpose of investigating which species could pass transposition tests and the learning mechanisms that underlay such successes.

The 2AFC task surged in popularity again within comparative psychology following Harlow's development of the Wisconsin General Test Apparatus (WGTA) and the resulting empirical discovery of discrimination learning set (Harlow 1949). The WGTA afforded a controlled situation for presenting novel pairs of objects, one arbitrarily designated S+ and the other S-, to animals (frequently monkeys), allowing researchers to study how quickly the animals would learn to discriminate between the pair of stimuli and to respond to the object that concealed a reward. Using the WGTA, researchers investigated two-object discrimination learning. In Harlow's learning-set procedure, novel pairs of objects were presented, typically for a sequence of six discrete trials, and then a new problem (i.e., pair of arbitrary objects, one arbitrarily designated S+) was presented for another six trials, and so forth. Performance improved across trials within each problem, from chance-level on Trial 1, as the animals experienced the rewards (or not) of their 2AFC selections. Of more importance, performance frequently also improved across problems: Trial-2 performance on early problems was near chance, whereas after hundreds of problems,

accuracy on Trial 2 might have been near asymptote. For instance, after 300 problems rhesus monkeys were about as accurate at selecting the correct (S+) stimulus on Trial 2 as they were on the last trial of each problem (Trial 6; see Harlow 1949). Harlow's documentation of problem-to-problem improvement in the rate of learning, which constitutes a relational kind of learning-to-learn, served as a catalyst for many comparative 2AFC studies. In their review of this literature, Fobes and King (1982) wrote, "Probably no other single factor prompted so much research on primate learning as Harlow's report of problem-to-problem transfer of learning that he calls *learning set*. This shift in emphasis, from single to multiple-problem testing, was to increase substantially the information obtained on primate learning abilities" (p. 297).

The years that followed Harlow's landmark publication were a period of widespread learning-set testing. Researchers explored the organismic variables, stimulus variables, and procedural variables that affected the speed and asymptote of Trial-2 discrimination learning-set formation in the 2AFC paradigm (see Fobes and King 1982 for a review of these studies). For example, researchers studied the facilitating effects upon learning of 3-dimensional objects versus 2-dimensional stimuli, and of stimuli that were more salient (e.g., because of color or movement) versus less (e.g., were stationary and differed only in size or shape). With respect to procedural manipulations, Harlow and others studied the effect of number of trials per problem on acquisition of learning set, incentive effects, and the effects of stimulus-response spatial discontinuities. Fobes and King (1982) summarize these and other procedural variations on the learning-set paradigm. But perhaps the most interesting studies during this period considered variables like the age or the species of the animals: Fobes and King summarized the results of multiple studies across many different laboratories to graph Trial-2 learning-set performance, across different numbers of problems, for gorillas, chimpanzees, orangutans, gibbons, rhesus monkeys, spider monkeys squirrel monkeys, capuchin monkeys, marmosets, lemurs, tree shrews, minks,

chickens, blue jays, cats, rats, and others. The pattern of findings suggested interesting species differences in the rate at which different animals developed learning set, and in the levels of Trial-2 accuracy that were obtained. As intriguing as these species differences appeared to be, there were several factors that limited the potential for use of the 2AFC discrimination learning-set procedure as a general test of species differences in intelligence. Fobes and King (1982) suggest that one such factor was the unexpectedly good learning-set performance by some bird species and by minks, which they allege caused two reactions by Professor Harlow: “the first unprintable and the second to dispose of his wife’s mink coat” (p. 307).

A second limitation to the use of the discrimination learning-set paradigm as an intelligence test is more serious: it is difficult to disambiguate the effects on Trial-2 learning of intelligence from those stemming from perceptual or motor differences between the species. For example, rats are at several significant disadvantages with respect to visual acuity and motor dexterity compared to primates in the response to two-object visual discrimination learning problems. In an attempt to control for such confounds, many researchers explored a variation of the learning-set procedure by examining discrimination learning and reversal performance.

As the name suggests, the reversal-learning (or interdimensional-shift) variation on the 2AFC procedure involves training a two-object discrimination-learning problem until the animal reaches a performance criterion. Bitterman (1965) argued that species differences in intelligence might be measured under conditions in which the reinforcement contingencies of the paired stimuli are repeatedly reversed (i.e., the S+ becomes S- and vice versa, and then are changed back, and so forth). Whereas the value of cross-species investigation using learning-set testing is limited by species differences in sensorimotor abilities, the reversal-learning variation controls for such differences by comparing animals’ reversal performance against the baseline created by their own performance. Thus, reptiles may have visual and motor disadvantages

compared to primates (to take examples from just two of the many disparate animals tested by Robert L. Gossette (e.g., Gossette and Gossette 1967), but, in the successive reversal-learning paradigm, the goal is to see how the reptiles’ performance (despite their visual and motor challenges) changes across cue reversals. Species are not compared directly to one another, but rather they are compared on the basis of their reversal learning, which itself is uniquely baselined for each animal that is tested. The ratio of performance on reversal trials to pre-reversal acquisition trials – the Reversal Index (RI; Rajalakshmi and Jeeves 1965) – was a popular measure of learning and intelligence in comparative investigation.

Duane Rumbaugh modified the RI procedure by establishing specific under-learning acquisition criteria prior to cue reversal: In this new variation of the 2AFC paradigm, animals initially learned to discriminate the S+ from the S- stimuli until performance reached acquisition levels of 67% accuracy or 84% accuracy, whereupon the cue values were reversed for 11 additional trials. The ratio of accuracy on the reversal trials (R%) to accuracy on the acquisition trials (A%) was called the Transfer Index ( $TI = R\%/A\%$ ; see Rumbaugh and Pate 1984). The TI offered the same advantages of the other two-object discrimination learning-and-reversal procedures with respect to within-individual controls, but with criterial parameters designed to make it better suited for cross-species assessments of the capacity to learn and to transfer learning (Rosenblum 2013). Since its inception, the procedure has been employed by scientists across the globe to test animals (almost exclusively a wide range of primates), revealing greater learning transfer in apes than in most monkeys and prosimians (see review by Rumbaugh and Washburn 2003). Lower TI scores – and, critically, negative transfer such that reversal accuracy declines when the acquisition criterion is 84% accuracy compared to 67% accuracy – for prosimians and many of the smaller monkeys indicate that their learning is primarily associative conditioning. These animals perform worse after the stimulus reversal because the pre-reversal habits must be extinguished, and the more ingrained those initial stimulus–response



associations have become, the more difficult it is for animals to defy them once the reward contingencies are reversed (Rumbaugh and Pate 1984; Tomasello and Call 1997). In contrast, higher TI scores and positive transfer as A% is moved from 67% to 84%, as has been demonstrated by apes and some of the larger monkeys, seems to indicate higher cognitive ability and relational learning. These animals transfer pre-reversal learning positively because they appear to have learned a rule-like relation (perhaps “win-stay/lose-shift”) that generalizes from acquisition to reversal. Moreover, TI values across species have been shown to correlate strongly with species differences in brain size (Beran et al. 1999), predict individual differences in how quickly rhesus monkeys will succeed in training on a large battery of computerized cognitive tasks (Washburn and Rumbaugh 1992), and correlate with individual differences across baboons in the executive function of cognitive flexibility (Bonté et al. 2014).

This brief historical review illustrates the importance and usefulness of the 2AFC paradigm for comparative psychology but does little justice to the vast range of other questions and animals that have been studied. Emphasizing the threads of research related to the assessment of animals’ perception, learning, and intelligence leaves undiscussed a host of contemporary applications of 2AFC testing. For example, Smith and collaborators (2020) have recently reported monkeys tested on two-choice discrimination-learning problems in which reinforcement and other feedback for each trial are delayed until after the subsequent trial (i.e., an animal picks one of the paired stimuli on Trial N, but only experiences the consequences of this choice after completing Trial N + 1). Despite deferred feedback, the monkeys learned, a finding that the researchers interpret as suggesting human-like explicit and declarative cognition (vs implicit and associative learning; see Smith et al. 2021 for a similarly innovative 2AFC procedure for testing whether humans and monkeys could discriminate trials on the basis of self-agency).

There are many more recent topics and species that have been studied using variations of the procedure. Cook et al. (1985) examined

prospective and retrospective memory in rats. Chimpanzees (e.g., Fagot and Tomonaga 2001), monkeys (e.g., Parrish et al. 2015), and dogs (Keep et al. 2018) are among the animals that have been tested for perception of visual illusions. Lazareva, Freiburger, and Wasserman (Lazareva et al. 2004) investigated categorization by pigeons, and Vinken et al. (2014) used 2AFC to study categorization by rats. Auditory statistical rule learning for vowel and consonant sequences was learned by rats (although humans only learned the vowel, not consonant rules; Daniela and Toro 2013). Pigeons showed evidence of precrastination (Wasserman and Brzykcy 2015), primates engaged in “wishful seeing” (Rima et al. 2015), honeybees comparatively evaluated reward options (Soma et al. 2014), and black bears demonstrated picture-object recognition – all using the 2AFC (Johnson-Ulrich et al. 2016). In short, 2AFC testing is the foundation upon which comparative-cognition research is built.

## Cross-References

- [Categorization](#)
- [Duane Rumbaugh](#)
- [Harry Harlow](#)
- [John David Smith](#)
- [Morton Edward Bitterman](#)
- [Transposition](#)
- [Wisconsin General Test Apparatus](#)

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## Two-Choice (or Two-Object) Discrimination Learning Paradigm

- [Two-Alternative Forced-Choice Paradigm, The](#)

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## Two-Dimensional (2D) Retinal Images

- [Depth Perception](#)

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## Ubiquitously Selected Stimuli

► [Arbitrary Stimuli](#)

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## Ultimate Causation

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### Synonyms

[Evolutionary determinism](#)

The term *ultimate causation* was first used by Julian Huxley (1916) in an article where he opposed the ultimate causes stemming from the action of natural selection, as envisioned by evolutionists, to the immediate factors and mechanisms operating at the individual level, as addressed by physiologists and psychologists. In the decade following the discovery of the replicating structure of DNA, Ernst Mayr (1961) further elaborated on this scheme by parting between ultimate and proximate causation. Proximate causes deal with the mechanisms responsible for the makeup and functioning of the individual phenotype. Ultimate causes refer to the past conditions having led to the information encoded in DNA. The phenomena involved in these different

levels of causation occur on different time scales. As put by Mayr, proximate causation takes place once the encoded genetic program is actualized in the individual, whereas ultimate causation determines the shaping of the program itself. This dual scheme may be viewed as a logical consequence of the Weismannian separation between soma and germ line. It assumes that we need a different prospect to understand the phenotype and the genotype.

Biologists studying proximate causes ask *how* questions about mechanisms, whereas those studying ultimate causes ask *why* questions about evolutionary finality (Mayr 1961). If we aim to explain the song of male birds, for instance, the first category of scientists will study developmental processes and hormonal and neural mechanisms or the action of environmental factors, while the second category will test hypotheses regarding territory defense, mate attraction, or species identity announcement. A main interest of the ultimate perspective is that it makes clear that evolutionary explanations do not represent an alternative but a complement to accounts couched in terms of mechanisms (Huxley 1916; Mayr 1961). A second heuristic advantage of this perspective lies in its ability to guide the search for hypotheses at the proximate level, as novel insights about the adaptive function of organs or behaviors can generate new questions about their operating processes (MacDougall-Schakleton 2011). For instance, assuming that personality types represent different coping strategies can

lead to investigate the experiential, genetic, and neuroendocrine basis of such traits as boldness to predators and aggressiveness and whether or not they are correlated.

The concept of ultimate causation does not come without questions, however. It actually echoes the “final causes” of Aristotle that sought to explain the ordered design of nature by looking for goal-directed processes in a teleological way. By contrast, the rise of the scientific thought was founded on the banning of occult qualities, which led to reject final causes and replace them by the action of mechanical causes, that is, a mechanism was required to account for any effect. Living beings and their purposive actions were left out of this framework for a while. The design problem in biology was eventually solved by the mechanism of natural selection. If a trait confers some advantage to its bearers, the latter will survive and reproduce at higher rates than others, increasing the representation of the trait in the population. The rehabilitation of finality in science by the way of natural selection has represented a main achievement of the Darwinian thought. The *raison d'être* of a biological trait lies in its adaptive function; hence we can find the ultimate causes of a trait within the ecological environment where a given population evolved.

When we study the adaptive function of a trait, we focus on its effects rather than on its causes. However, causes precede effects. To ascribe a causal role to effects, we assume that the effects observed today are similar to those having produced the trait in the past; hence they become antecedent and thus causal. The Darwinian thought is based on such an extrapolation. At this point arrives the qualificative *ultimate*. The opposite of proximal should be distal, not ultimate (Francis 1990; Armstrong 1991). Ultimate refers to ends; it is used to mean the reversal of the causal arrow between present and past causation. This allows us to consider two symmetric realms: one belongs to the ecological time of proximate causes and the other to the evolutionary time of ultimate causes. Such a line of reasoning is unfortunately the source of several enduring misunderstandings (Jamieson 1986; Ariew 1990; Francis 1990; Armstrong 1991;

West-Eberhard 2003; Thierry 2005, 2007; Laland et al. 2011).

Following a common adaptationist assumption, any biological trait is an outcome of natural selection; accordingly, each trait should have both a proximate and an ultimate causation. But some traits do not contribute to fitness. Organisms are integrated wholes where some traits arise as correlated consequences of other traits that themselves promote reproductive success. There is ample evidence that, from gene and molecular networks to morphological structures, cascades of interacting elements gather into developmental modules, reducing the number of possible trade-offs open to organisms (West-Eberhard 2003; Thierry 2007). The structuralist approach contends that the building processes of the phenotype are sufficient to explain the origin of correlated traits, meaning that resorting to ultimate causation is then unnecessary (Gould and Lewontin 1979; Jamieson 1986). The functionalist school replies that correlation is the proximate cause and that correlated traits are ultimately maintained as an outcome of the selection of combinations of traits (Alcock and Sherman 1994). It remains that some correlated traits result from selection against internal variations that would be disruptive for the phenotype, which implying that no ultimate pressures from the environment are responsible for their occurrence.

A second misunderstanding consists in believing that proximate and ultimate causes are independent because they belong to different time scales. That amounts to considering phenotypic mechanisms and adaptive processes as loosely coupled phenomena, which sustains a gene-centered view of evolution in which traits are considered structurally independent of each other (Thierry 2007). But selection is related to development as it favors the fitness effects of expressed genes; genes that are not active do not contribute to adaptation. Developmental constraints make some variants more likely; hence the variation presented to selection is not random (West-Eberhard 2003; Laland et al. 2011). In order to understand the rate and direction of evolutionary changes, it is necessary to account for the generative properties of phenotypic



mechanisms such as epigenetic processes and nongenetic inheritance.

Asserting that ultimate causation deals with evolutionary history stems from a third misconception. If a trait confers higher fitness, it is inferred that the selective events having caused the spread of the trait in the past were the same as those operating today. By focusing on functional consequences, the ultimate perspective allows to build models based on trade-offs and optimality rules. But finding that a trait has a current utility does not necessarily imply that this trait has been selected for that role in the past (Gould and Vrba 1982). The characteristics of living beings depend on the pathways of their past evolution. Novel patterns do not appear *ex nihilo* but from the reorganization of preexisting structures: by dissociation, fusion, duplication, deletion, reversion, diversification, heterochrony, etc. (West-Eberhard 2003). Implementing functional consequences in equilibrium models is a search for optima; it does not include historical contingencies and the origin of traits (Jamieson 1986; Ariew 1990; Francis 1990; Armstrong 1991). Contrary to common belief, investigating ultimate causation actually promotes an a-historical approach of evolution.

According to a fourth misunderstanding, all selective events would act in a uniformitarian way. The proximate/ultimate scheme opposes ecological and evolutionary time in an absolute way. It takes for granted that the recurrent occurrence of the same ultimate causes during evolutionary time produces an adaptive modification of lineages (Thierry 2005). But what holds at a microevolutionary level is not warranted at the time scale of macroevolution. When the selective events encountered by populations are too rare to belong to their “experience,” mechanisms like species selection may reverse or undo the adaptations accumulated by the filtering action of repeated events. A trait becomes advantageous only if the selective event that promoted it comes up again. A unique event leading to mass extinctions, for example, does not result in an adaptation of the surviving species. The same may be said for an event so infrequent that the trait conducive to survival is lost through evolution before the next event occurs. There is no

single time scale to measure adaptation. The reversal of the causal arrow between present and past causation presupposes the regular repetition of selective events. The uniformitarian view of evolution in which the concept of ultimate cause is rooted makes it difficult to conceive such mechanisms as random sorting or selective processes working in opposition to each other at different levels (Thierry 2005).

The time of populations and species and the time of individuals are different. We have to take into account the depth of evolutionary time, and, in this respect, distinguishing *why* from *how* questions is sound. Equating ultimate causation with adaptive function appears problematic, however. It is more inclusive and thus more productive to refer to *evolutionary determinism* when addressing the processes and pathways of biological evolution (Ariew 1990; Armstrong 1991).

## Cross-References

- Epigenesis
- Evolution
- Evolutionary By-product
- Natural Selection

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## Ultimatum Game

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## Synonyms

Dictator's game; Game theory

## Definition

The ultimatum game is a task that allows us to test the predictions of game theoretical assumptions. In a standard ultimatum game, two players share roles as the proposer and the responder. The task is to divide a constant sum of money in a one-shot interaction. The proposer makes an offer, and the responder either accepts or rejects the offer. If the responder accepts, the two parties share the money based on the offer. However, if the responder rejects, neither party earns anything.

Traditional game theory assumes that human beings are fully rational. Thus, if the players in the ultimatum game behave rationally (i.e., if utility

functions are monotonically increasing), they should try to maximize their gains. Specifically, the proposer should offer the minimum amount of money different than, yet close to, zero to maximize her gains and the receiver should accept that offer since it is better than nothing, which is what he will get in case he rejects (Camerer 2003).

The first attempt to test these game-theoretical predictions using the ultimatum game was conducted by Güth, Schmittberger, and Schwarze (1982). In their experiment, participants were invited to a room where they all see each other yet did not know their anonymous partners in the game. The results were in contrast to the original game-theoretical expectations; the modal offer was equal share, and the mean offer ranged between 35% and 39% for different amounts of sum with an average of 36.7%. Numerous studies have then been conducted to test the same prediction (e.g., Bolle 1990; Forsythe et al. 1994; Larrick and Blount 1997; Solnick 2001). Although there is considerable amount of variation in the actions of players across studies, two general conclusions can be derived from this literature: (1) Proposers tend to offer more money than the minimum nonzero amount, and (2) Responders tend to often reject low yet nonzero offers. Therefore, these findings challenge the well-established view in standard economics that humans are rational in their financial decisions in the sense that they always pursue their self-interests.

An alternative explanation to this game-theoretical framework posits that both parties are motivated by reaching a fair share instead of by self-interest driven by rational and selfish motivations. In one derivation of the original study conducted by Güth et al. (1982), Kahneman et al. (1986) changed the rules of the game. In this novel version, responders had no choice but to accept the offer. Even though the proposer had nothing to worry about losing the whole share, most of the participants (76%) preferred equal share, implying a fairness motivation. Other researchers, however, rejected the fairness explanation (e.g., Hoffman et al. 1994) by claiming that proposers' offers are driven by the expectations about the responders' reservation value (i.e., minimum acceptable point one will agree in a

negotiation). Thus, the proposer thinks that not zero but small amounts of offer will be more likely to be rejected, which sets an amount that the proposer assumes acceptable. In testing this prediction, Hoffman et al. (1994) compared offers in the ultimatum game and dictator game. In the dictator game, when the proposer makes the offer, the game ends since the responder has no option. Results showed that proposers in the dictator game behave more selfishly as compared to proposers in the ultimatum game, most of them (70%) keeping most of the money.

Accumulated evidence regarding the ultimatum game also allows to make inferences about the underlying mechanisms of three different behavioral strategies, each of which is derived from one of three hypotheses; (1) proposers take most if not all the share as expected by the game-theoretical expectation, (2) equal distribution between herself and responder based on the fair-share hypothesis, and (3) proposers behave in line with their experiences and expectations about partner's behavior as proposed by the expectations hypothesis (Suleiman 1996).

To test these predictions, variations of the original ultimatum game have been used such as creating an environment that leads people to behave more selfishly. In general, different versions aim to understand and explore the underlying mechanisms of fair-share inclinations.

## Variations of the Ultimatum Game

Binmore et al. (1985) devised a *two-stage ultimatum game* where participants had the opportunity to interact. In this version, if the responder rejects the offer, they move on to the second tour and reverse the proposer-responder roles. Though game theory predicts that the game would not move on to the second tour since accepting any nonzero payment is the rational choice and should be accepted all the time, 15% of the participants rejected the offer. Furthermore, contrary to the initial expectation that the game will be played rationally as the participants gain experience through the rounds, offers in the second round were higher than the first round.

A *multistage ultimatum game* was also used to test the expectation that experience gained during the multistage game would unearth the rational economist out of the participants. Neelin et al. (1988) conducted four and five-stage versions, and Ochs and Roth (1989) applied a ten-stage ultimatum game. The results of these multistage games failed to provide strong support for the predictions of game theory. For instance, participants learned nothing through the trials, their strategies remained stable, and mean offers were larger than the equilibrium.

Weg and Smith (1993) designed two different versions of the game, *OneOne and OneTwo ultimatum game*. In the first, participants play the game twice with the same role, while in the second participants change roles in the second round. Game theoretical expectation suggests that as the proposer holds the power all the time in the OneOne version, she should take the whole share; yet the findings failed to provide support. The authors concluded that, as there is a chance for the responder to reject the offer, those offers tend to approximate equal share. An alternative interpretation of these results is that offering equal share is driven by self-interest, as the participants believe that they can only maximize their share by providing equal share, they behave in a more egalitarian way. In testing this prediction, Kravitz and Gunto (1992) conducted two experiments using the classical one-shot ultimatum game. Before the game, participants in the responder role indicated the minimum acceptable offer. Similar to other studies, calculated expected value referring to the optimal offer to secure maximum share for the proposer was \$2, 40% of all share which is close to equal share. However, when the participants were asked to make offers when they knew that the responder would behave rationally and accept any nonzero offer, the modal share was only 1%.

In some other versions, to increase rational and self-interest-driven actions, researchers manipulated expectations such as by letting participants play the game to earn the proposer position (Hoffman et al. 1994) and applying an auctioning procedure (Güth and Tietz 1986). Weg and Smith (1993) proposed a two-category distinction across

the variations of the ultimatum game. Accordingly, *framing incentives* such as the auctioning procedure or winning the proposer role are external to the game and are intervening variables. On the other hand, *structural incentives* such as multistage variations of the game are embedded and internal to the game. Thaler (1988) asserted that although games using framing incentives led to an increase in greedy and selfish offers, they do not necessarily provide support for the game-theoretical predictions, since the action strategies are at least partially determined by variables outside the game itself.

Research using various versions of the ultimatum game conducted on qualitatively different samples to test the game-theoretical and alternative hypotheses also revealed that there is considerable amount of variation in the number of shares offered by proposers and the rejection rate of responders. For instance, the average offer was 26% in a study conducted on a Peruvian sample (Henrich 2000), while it was 51% in another study conducted on a Japanese sample (Buchan et al. 1999). One possible explanation for the variation is the amount of total share since, as the total amount increases, the stakes become higher. Other research focusing on the amount of share revealed that there is no difference in the percentage of the amount offered by the proposer while the rejection rate decreases as the total share increases (e.g., Cameron 1999; Slonim and Roth 1998). The first study (Cameron 1999) was conducted on an Indonesian sample and the latter on a Slovakian sample. Thus, another possible explanation for the variation is cultural characteristics which might somehow influence the actions of players.

Oosterbeek et al. (2004) conducted a meta-analysis of 75 ultimatum game experiments. They only included one-shot ultimatum game experiments and two variations of the game. The first variation is the original classical ultimatum game. In the second one, responders set the minimum amount to accept the offer before the offer is being made, called the strategy method, in which responders had no chance to take action conditional on the actual share offered by the proposer. Results of the meta-

analysis showed that the average amount offered by the proposer was 40%, and the average rejection rate by the responder was 16%. In the experiments using the strategy method, proposers' offers were smaller for larger total amounts whereas larger for inexperienced participants. Responders' rejection rate is lower for larger total amounts while it is higher when the strategy method is employed. In terms of cross-cultural differences, the results of the meta-analysis showed no difference between different geographic regions on the offers of proposers but revealed significant differences in the rejection rate of the responders. Specifically, Asian participants had a higher rejection rate than American participants. Cultural-level differences of individualism and power distance did not predict either sharing or rejection rates.

## Animal Behavior

To understand the evolutionary roots of action strategies such as cooperation, fair-share preferences, and self-interest, researchers look up to the actions of our close relatives: chimpanzees. Recent research showed that chimpanzees and capuchin monkeys display preferences similar to humans in terms of cooperation and aversion to unequal treatment (e.g., Brosnan et al. 2005; Melis et al. 2009). Therefore, how those non-human primate cousins behave in the presence of another agent that has the opportunity to influence the outcome of the action, as in the ultimatum game, attracts the attention of researchers. Recent research on chimpanzees and bonobos revealed that nonhuman primates behaved in line with the expectations of the game-theoretical perspective: They offered the smallest amount possible, and nonhuman primate responders accepted almost every offer even if the offer were zero, implying that they might fail to apprehend the task and hence cannot be evaluated as rational maximizers (Jensen et al. 2007; Kaiser et al. 2012). However, designs of these experiments have been criticized since they utilized a device not present in human experiments: Games were played within

primates' social group which violates anonymity. Besides, the incentive was food instead of a more abstract reward such as money (primates have been shown to provide strong responses to visual food inputs, Boysen and Berntson 1995). Furthermore, unique to the primate version, they reject the offer by inhibiting their actions and waiting for 30 s which have been shown to influence human actions as well. Smith and Spielberg (Smith and Silberberg 2010) replicated the chimpanzee experiment on humans and found that waiting before taking action decreased the rejection rate of the responder from 52% to 18%.

In a more recent experiment, children and chimpanzees were recruited for two tasks similar to the ultimatum game and dictator game (Proctor et al. 2013). They used tokens with a trade value akin to money used in human designs. Chimpanzees were next to each other in two different rooms positioned against six slices of bananas. They had two options, equal share token which is used to trade three slices for each, and unequal share token which is used to trade five slices for the proposer and one slice for the responder. Each chimpanzee took 12 trials, and as a result, in 75% of all trials, they preferred the equal share token. In the same experiment, chimpanzees played another game such as the dictator game in which each chimpanzee is matched with a "foil" partner, naïve to the conditions and passive to the share offered by the proposer. In this version, 90% of the chimpanzees preferred the unequal (selfish) token. Those results were in line with the children sample tested in the same experiment.

Overall, the ultimatum game is a powerful tool to study human and nonhuman primates' social behaviors. Future research should strive to increase the level of comprehension of the ultimatum game, for both human and nonhuman participants.

## Cross-References

- [Cooperation](#)
- [Decision-Making](#)
- [Game Theory](#)
- [Nash Equilibrium](#)

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## Umwelt

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## Synonyms

Environmental influences

## Definition

The perceptual-reactive world of an organism. These worlds are manifold and varied – much like the animals themselves. Humans are limited to their own perceptual-reactive worlds, making it difficult to comprehend the worlds of other organisms, especially when some perceptual domains of the organism are not shared with humans. The term was originally coined in the field of ethology by Jakob von Uexküll (1934, 1982).

## A “Simple” Umwelt

A classic perceptual-reactive world that nicely exemplifies the meaning of the Umwelt is that of a tick. Ticks may become part of the human perceptual world when they burrow into our skin, or the skin of our pets, and gorge themselves with warm blood. Thus, our perception of ticks may be one of unpleasantness. They trigger our sense of touch from the burrowing, which then signals the visual system to investigate the source – the perception and then the reaction. The Umwelt of a tick however is quite different and strange from our perception. Ticks are often found clinging to the top of a twig or the tip of a blade of grass, waiting to drop upon small animals or be brushed off by larger ones. They are blind and deaf, but consistently travel to these locations, or stands, by a general photosensitivity on their skin. Once on their stand, ticks use their sense of smell, which includes the chemical sensing capability of detecting the odor of butyric acid secreted by the skin glands of all mammals. They may detect other animals (e.g., lizards) by other chemicals in their breath, body heat, moisture, vibrations, etc. The detection of an animal stimulates the tick to drop from its stand, land on or orient to and locomote to the animal source of the stimulus on the animal, i.e., the skin. Locomotion ends at a hairless spot and this stimulates burrowing into the skin to gorge itself with blood. Importantly, ticks cannot taste; thus, they are unable to detect whether they are consuming blood (a tick will consume any fluid that is comparable to warm blood). If the stimulus of the butyric acid signals

the tick to leave its stand, but causes the tick to land on something cold, it will have missed its prey and antigravity reactions will result in it climbing up to a new stand. However, if the tick does land and feed on a warm-blooded mammal, the blood will be its last meal. Upon gorging itself, the tick will drop to the ground to lay eggs and then die.

As demonstrated from the example of a tick, the perceptual world of an organism is highly dependent on the organism's sensory system, motor system, and nervous system – its perception and reaction. The tick sensed butyric acid, which stimulated its motor system to move off the stand and to drop onto the mammal emanating the chemical. The sensation of butyric acid is just one sense within the modality of chemical sensation. Other common sensory modalities include vibration, body movement, physical contact, electromagnetic, and temperature. These modalities serve as general sensory categories and different animals may perceive different aspects of each sensory modality. For example, ticks can perceive butyric acid but cannot sense – or taste – the chemicals in the blood. Like the sense of butyric acid, other organisms have sensory abilities beyond that of humans, which are often given the ultra- or infra- prefix. For example, snakes, such as pit vipers, pythons, and boa constrictors, can perceive infrared (IR) light through IR-sensitive receptors on their heads (Gracheva et al. 2010). Humans, in contrast, cannot detect this range of light, but can detect the associated heat that is emitting from the object that is also emanating the IR light; any object that is warmer than its environment emits IR radiation. Humans are also unable to detect ultraviolet light, which is perceived by butterflies, bees, and some birds. Because these ranges of light are invisible to the human eye, it is difficult to comprehend the visual world of these animals. Fortunately, technology has made it possible to view both IR and ultraviolet light, thereby expanding our sensory capacity. However, it would be facile to suggest that with these technologies we are fully able to comprehend the Umwelt of dissimilar animals (Dethier 1962, 1969).

## Interpenetration of Organisms and Umwelts

Organisms and their Umwelts are dialectically related, and therefore cannot be separated from one another; there is no organism without an Umwelt and no Umwelt without an organism. This dialectical property means that both the organism and their Umwelt interpenetrate one another in several forms (Lewontin 1982), all which need to be incorporated into any theory concerning organism behavior or cognition.

First, organisms assemble their Umwelts depending on their total morphology, physiology, and behavior. Organisms will actively assemble their Umwelt by manipulating bits and pieces of the ecosystem they reside within. For instance, some bird species assemble their nests with dirt and avoid grass. Others seek crevices in rocks or holes in trees. This limits the type of stimuli the birds will receive and the types of organisms they may interact with. Organisms will also passively assemble their Umwelt as a consequence of their morphology and physiology. For instance, humans produce a warm layer of air around their body by their own metabolic heat. Some small or microscopic organisms (e.g., fleas or ectoparasites) may reside within this warm layer, thereby the Umwelt of the microscopic organism is dependent on the existence of the human within the ecosystem, which the human itself assembled. Thus, the human assembled an Umwelt wherein another organism could reside, thereby allowing the microscopic organism to become part of the Umwelt of the human.

Second, organisms alter their Umwelt by consuming food, depositing waste, constructing homes, and other activities. This allows them to create the conditions necessary for life, but it may also have destructive consequences for their offspring when alterations ultimately change the habitat of the species. For example, beavers will construct dams in rivers to form a small pond as their home. This fundamentally changes the ecology of the area, allowing different vegetation and organisms to live in the pond which could not inhabit the river. Beavers may also be selective in the trees they may use for their dam, because

they only prefer certain species. This further alters the environment, by removing preferred species of trees, sometimes to the extent that it is unsuitable for themselves and their offspring. This behavior is not only limited to wild organisms but can occur in the laboratory. For instance, laboratory mice build their own nests and deposit waste in their home-cages, thereby fundamentally altering their Umwelt daily; nest building alters body temperature and waste modulates olfactory cues in the environment.

Third, organisms transduce physical inputs qualitatively. When an event occurs within an ecosystem, different organisms may not necessarily perceive the event of the same quality. For instance, when a female ring dove is presented with a nest and eggs, it will secrete prolactin. This signal can be modulated, dampened or amplified, across a ring dove's development, wherein a reproductively naive male or female ring doves will not show the same physiological or behavioral response as reproductively experienced doves (Lehrman 1965). Moreover, individual differences exist concerning the secretion of prolactin between ring doves of the same sex and age. Of course, the presence of a nest and eggs may be differentially perceived by a passing snake – albeit different snakes will have different perceptions depending on their satiety and other factors.

Fourth, organisms modulate the signals from their environment statistically. This is similar to the aforementioned example, but also involves integration of other signals. For instance, squirrels will store acorns or nuts for the winter through behavioral mechanisms in response to fluctuations in food availability. They may also indirectly store energy in the form of body fat or glycogen. Thus, they can modulate, or dampen, the signals of low food supply. Thus, all sensory systems have a “volume-control” feedback circuit that can be adjusted to modulate how a signal will be perceived by the organism.

Taken together, the Umwelt is quite complex and easily misunderstood. Without acknowledging their Umwelt, we may be misinterpreting what the animals are perceiving and what factors are affecting their actions. As scientists, we may add items to an organism's environment to study

them, but the organisms might not respond in the expected manner if the item is not transduced as we intended (Lahti 2015). Moreover, the environment we provide for an animal may be differentially altered across time or by each organism within the environment. Such alterations may render the environment as physically different from what the scientist intended, thereby altering the types of stimuli the organism will perceive and react to. It is imperative for scientists to recognize these Umwelts whenever studying their respective animals, particularly those which diverge in their sensory abilities and capacities from ours.

## Cross-References

- [Environmental Influences](#)
- [Ontogeny](#)

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## Unborn Child/Baby

- [Embryo](#)

## Unborn Young

### ► Fetus

## Uncertainty Paradigm

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Humans have feelings of uncertainty and confidence, of not knowing and knowing. They respond appropriately to these feelings by reflecting, rethinking, and seeking additional information. These responses ground the human literature on uncertainty monitoring and metacognition (Dunlosky and Bjork 2008; Flavell 1979; Koriat 1993; Nelson 1992). Humans' uncertainty awareness reveals a high-level cognitive capacity in them that is allied to their conscious awareness. Thus, it was a natural question whether nonhuman animals (hereafter, animals) might share with humans some aspects of a metacognitive capacity (Smith 2009; Terrace and Metcalfe 2005), because the answer to that question could bear on animals' consciousness and self-awareness, too.

Given the question's importance, Smith and his colleagues inaugurated a new area of comparative inquiry by asking whether animals have a capacity for uncertainty monitoring and metacognition regulation. The key to opening up this research area was to address directly difficult methodological issues. Clearly, one cannot just test animals in human paradigms, asking them about their feelings of knowing and their tip of the tongue states. The production of such declarations is presently not practical, though perhaps not in principle out of the question in the future. So investigators faced the problem of letting animals make purely nonverbal, behavioral responses that might

nonetheless serve as valid indicators of their judgments of uncertainty and confidence. Thus was born the uncertainty paradigm (Shields et al. 1997; Smith et al. 1995, 1997, 1998, 2003).

The paradigm had two key elements. First, the tasks contained an important subset of trials that were known to be difficult for the subject. The purpose of these trials was to foster states of doubt and uncertainty in animal minds. Second, animals were given an additional response in the task – outside the primary grammar of the operant-discrimination task – with which animals could freely decline to complete any trials they chose. This uncertainty response (UR) allowed animals to “declare” their uncertainty behaviorally and, crucially, observably. If animals can monitor internal states of certainty and doubt, then they would ideally decline the most difficult trials in a task that are likely to produce errors and delay reward.

The uncertainty paradigm that was created for animals turned out to have deep intellectual roots. In human psychophysics, early experimental subjects were sometimes allowed to respond “uncertain” or “equal” when they felt unable to classify a stimulus (Angell 1907; Fernberger 1930; George 1917; Watson et al. 1973). Some researchers even hypothesized that the UR was psychologically distinctive from the task's primary perceptual responses, in particular a higher-level or metacognitive overarching judgment. In this, they foreshadowed the debate about the appropriate interpretation of animals' URs. For if URs have this status for animal subjects, too, the theoretical implications would be very important.

The uncertainty paradigm also found a strong resonance with explorations of animal consciousness. For instance, Weiskrantz (1986, 1997) was keenly interested in studying animal consciousness purely behaviorally. In an influential thought experiment, he considered giving animals both primary discrimination responses and also a commentary response so that they could report on the state of their knowing or perceiving. Of course, the uncertainty paradigm essentially gave animals this commentary response.

Smith et al.'s (1995) first application of the uncertainty paradigm tested a bottle-nosed

dolphin (*Tursiops truncatus*). In an auditory threshold task, the dolphin discriminated high tones (half the trials, always 2100 Hz, high response) from low tones (half the trials, 1200–2099 Hz, low response). But he could also respond uncertain to decline to complete any trials he chose and receive an easy following trial instead.

Figure 1a shows that the dolphin made high responses and low responses, respectively, for many high trials and low trials. But he also evaluated correctly when he was “at sea” within the discrimination, and he selectively declined to complete those threshold trials. Remarkably, his URs were most frequent near 2.0856 Hz, 1/9th of a half step from the 2100 high tone. No one, not even Yo Yo Ma, could ever resolve that pitch contrast. The fact that the UR was used most at the dolphin’s true perceptual limit must affect one’s theoretical interpretation of that response, because, by definition, there was no discrete pitch

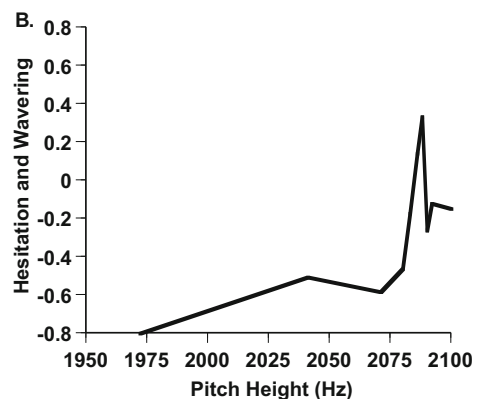
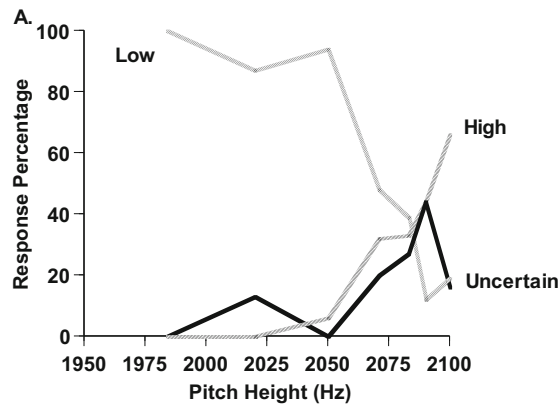
class discernible there that could have prompted some conditioned response.

An additional result (Fig. 1b) was that the dolphin showed his own uncertainty behaviors on threshold trials: he hesitated, swam slowly, waggled his head, and worked his mouth. Through this result, the uncertainty paradigm found important historical resonance again – now with the work of Tolman. Tolman also observed behaviors of this kind that he called “lookings and runnings back and forth” and that he thought could be considered as “a behaviorist’s definition of consciousness” (Tolman 1927, 1938).

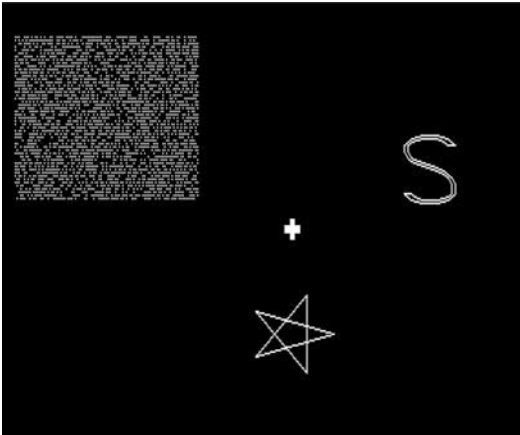
Smith, Washburn, and colleagues quickly followed up this dolphin study with research on the joystick-trained macaques (*Macaca mulatta*) at the *Language Research Center* of *Georgia State University* (Smith et al. 1997). Macaques discriminated unframed boxes on their computer screens that were either sparse or dense in lit

# **Uncertainty Paradigm,**

**Fig. 1** (a) A dolphin’s auditory-threshold performance in the uncertainty paradigm used by Smith et al. (1995). Response percentages are plotted against the frequency (Hz) of the trial. For 2100 Hz trials, the high response was correct. The low response was correct for all tones below 2100 Hz. The percentages of high and low responses are shown. The bold line shows the percentage of uncertainty responses made at each pitch level. (b) The dolphin’s composite hesitation-wavering behavior for tones of different frequencies. (Adapted with permission from Smith et al. (1995). Copyright 1995 by the American Psychological Association.)







**Uncertainty Paradigm, Fig. 2** The screen from a trial in a sparse-uncertain-dense discrimination (Adapted from Smith et al. (1997). Copyright 1997 by Elsevier. Reprinted with permission.)

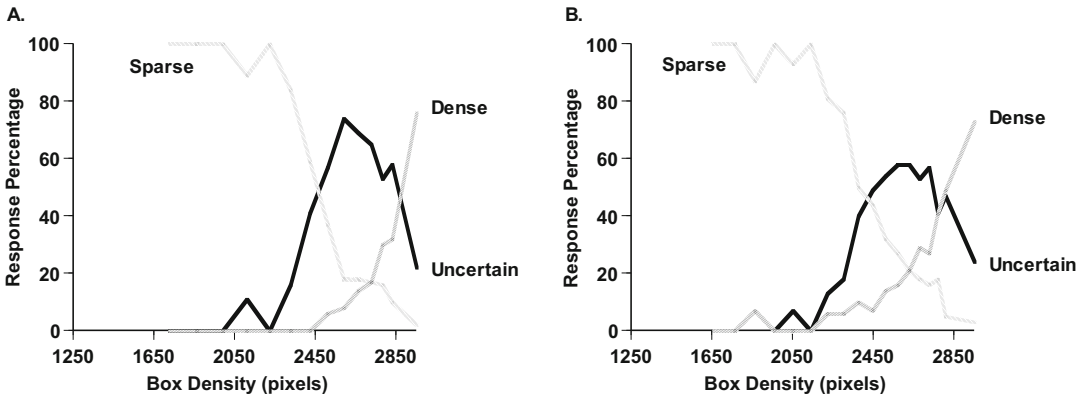
pixels. They used a joystick to move a cursor to touch a box, an S, or a star (Fig. 2). Touching the box or the S was appropriate as the box was dense (half the trials, always 2950 lit pixels, dense response) or sparse (half the trials, 450–2949 lit pixels, sparse response). Moving the cursor to the star allowed the monkeys to wave off the current trial and move on into a new, easy trial instead.

Figure 3a shows that monkeys made dense and sparse responses appropriately. But they also assessed accurately when they were liable to err and they fended off those threshold trials. That is, they made URs (star responses) most in the zone of maximal difficulty wherein their discriminative capacity faltered and they could not reliably tell sparse from dense. This area surrounds the crossing point of the monkeys' dense and sparse response curves, their exact sparse-dense indifference point. Remarkably, humans produced the identical result in parallel studies (Fig. 3b). In addition, humans told us that they used the UR when they consciously knew they did not know or could not tell the trial's status. Of course, if animals' URs express animals' conscious metacognition in the same way, then they are profoundly important behavioral expressions of animal awareness.

But wait. What were the dolphins and monkeys thinking in their tasks, or what were they merely

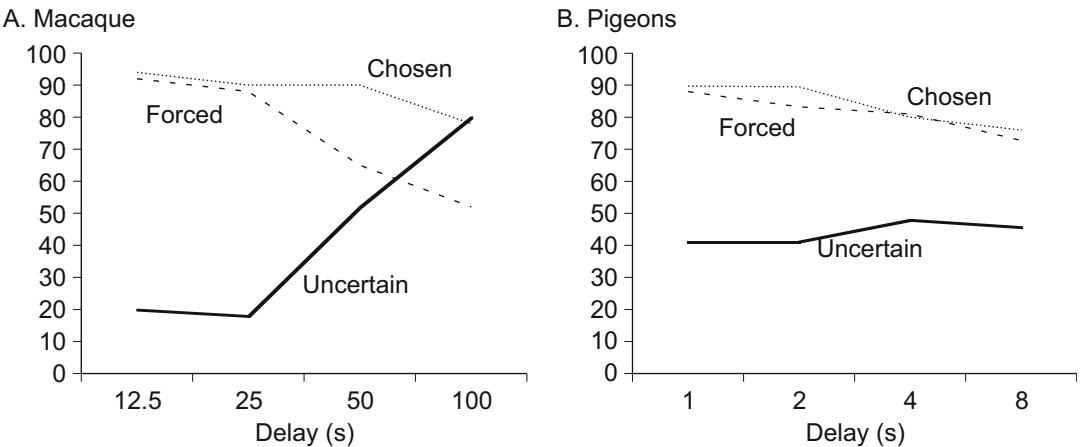
reacting to? Were they self-reflecting on uncertain mental states? Or were they simply averse to the objective perceptual stimuli that signaled difficulty, loss, error, and reduced rewards. The problem is that the original uncertainty paradigm did present objective stimuli for response. Moreover, some of these stimuli were inherently correlated with trial difficulty and reduced reward probability. Thus, the early instantiations of the uncertainty paradigm came in for their fair share of sharp criticism. In fact, a 20-year associative-metacognitive explicit debate ensued about the appropriate low-level (associative) or high-level (metacognitive) interpretation of animals' URs (e.g., Basile and Hampton 2014; Carruthers 2008; Hampton 2009; Jozefowicz et al. 2009; Le Pelley 2012, 2014; Smith 2009; Smith et al. 2008, 2009, 2012a, b, 2014a, b; Staddon et al. 2007). Essentially, this debate organized the entire early development of this research area.

During this debate, many variants on the original uncertainty paradigm were developed. An especially influential example came from Hampton (2001) who brought the uncertainty paradigm into the domain of memory (also see Kornell et al. 2007; Smith et al. 1998). In Hampton's study, macaques performed a delayed matching-to-sample task. On some trials, following the disappearance of the sample and the delay (forgetting interval), monkeys had the choice to either complete the memory test – possibly gaining a preferred reward – or to decline the memory test – settling for a lesser reward. On other trials, macaques did not have the UR option available and were required to complete the memory test. Figure 4a shows Hampton's principal results. He reported that macaques made URs more often after longer forgetting delays, naturally so because their trial memory was fading. But Hampton also reported that, when macaques eschewed the UR and chose to complete the memory test, they were quite accurate even at long delays. This suggests that they were in touch with some useful internal signal of remembering that predicted successful matching. This possibility is strengthened by this aspect of Hampton's design; unlike in the early perceptual versions of the uncertainty paradigm, there was no memory



**Uncertainty Paradigm, Fig. 3** (a) A monkey's performance in the uncertainty paradigm used by Smith et al. (1997). The horizontal axis indicates the density of the trial. For 2950-pixel trials – those trials plotted to the far right of each curve – the dense response was correct. For all trials with lesser densities/fewer pixels, the sparse response was correct. The percentages of dense and sparse responses are shown (dashed lines). The percentage of trials receiving

the uncertainty response at each trial level are shown in the solid line. (b) The performance of humans in the sparse-uncertain-dense discrimination depicted similarly. To align the different sparse-dense thresholds of different humans, the data were normalized so that each participant's discrimination threshold fell at about 2700 pixels. (Adapted from Smith et al. (2003). Copyright 2003 by the Cambridge University Press. Reprinted with permission.)



**Uncertainty Paradigm, Fig. 4** (a) A macaque's performance in the uncertainty paradigm used by Hampton (2001). The horizontal axis indicates the length of the retention interval before matching could occur. The percentages correct are shown for memory tests completed when the memory test was required (dashed line) or optional and intentionally chosen by the macaque (dotted line). The percentage of trials receiving the uncertainty

response is shown in the solid line. (Adapted from Hampton (2001). Copyright 2001 by The National Academy of Sciences.) (b) Pigeons' performance in the similar uncertainty paradigm adopted by Inman and Shettleworth (1999). (Data graphed with permission from Inman and Shettleworth (1999). Copyright 1999 by American Psychological Association.)

relevant material visible and no concrete stimulus present to avoid or escape. In this case, the uncertainty paradigm demonstrated that it can transcend low-level, associative processes, and target rather

high-level memory processes approaching humans' capacity for metamemory.

Templer and Hampton (2012) presented additional experiments that reinforced this conclusion,

and Basile et al. (Basile et al. 2015) presented systematic research evaluating seven potential associative explanations of macaques' URs in memory tasks. They found (p. 85) no support for the "hypotheses of behavioral cue association, rote response learning, expectancy violation, response competition, generalized search strategy, or postural mediation." But they repeatedly found results supporting the memory-monitoring hypothesis. They concluded (p. 85) that monkeys "can use memory strength as a discriminative cue for information seeking, consistent with introspective monitoring of explicit memory."

The uncertainty paradigm has also fulfilled its theoretical and empirical promise by sharply contrasting the cognitive-monitoring capabilities of different vertebrate lines. For example, Inman and Shettleworth (1999) evaluated pigeons' meta-memory capacity using an approach like that in Hampton (2001). Pigeons given longer forgetting intervals showed only a 7% increase in URs (Fig. 4b). This increase was not significant using parametric statistics. Moreover, this small increase poorly reflected the birds' poor performance at longer delays, for they *were* forgetting the samples and they could appropriately have used the UR more frequently. Finally, pigeons did not show a meaningful performance improvement when they voluntarily chose to complete the matching trial compared to when they were required to complete it. This suggests that they were not monitoring any felicitous internal signal of "still remembering" as the macaques apparently did. All in all, comparing Fig. 4a, b, one sees that there is distinctive difference between the metacognitive data pattern that macaques showed and the alternative pattern that pigeons showed.

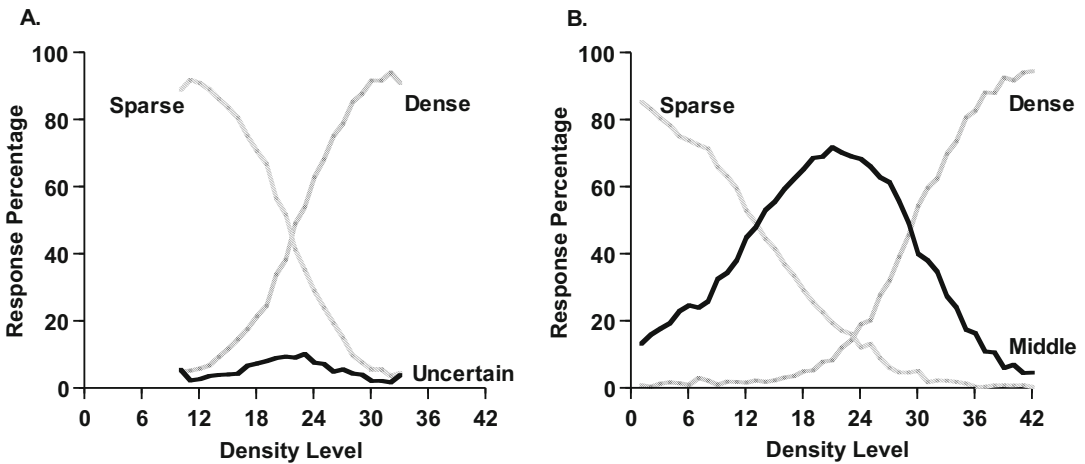
Sutton and Shettleworth (2008) replicated these pigeon findings using converging experimental methods across several experiments. Pigeons still did not choose to make URs at levels corresponding to their decreases in matching accuracy. In short, all the pigeon applications of the uncertainty paradigm show very different results from those found with macaques in equivalent procedures. Sara Shettleworth and her colleagues deserve great credit for so thoroughly

applying the uncertainty paradigm to the matching performance of pigeons – even if the empirical answer is essentially that pigeons do not easily express an uncertainty-monitoring capacity. In this case, a strong comparative No may be the theoretically clearest and strongest and most interesting answer of all.

The pigeon research is a strong confirmation that the uncertainty paradigm is able to make sharp differentiations among the uncertainty monitoring abilities of different species. This research is also a rebuke to the idea that URs are only another associative response. If they were, pigeons would make URs easily just as they make easily many other associative responses. But macaques adaptively make appropriate URs, pigeons do not easily do so (Adams and Santi 2011), suggesting that the uncertainty paradigm can also sharply differentiate responses of different psychological characters and possibly at different levels in the cognitive system.

The uncertainty paradigm has even been used to reveal important species differences in uncertainty monitoring within the order *Primates*. For example, Beran et al. (2009) used the paradigm to test the uncertainty-monitoring capability of capuchin monkeys (*Cebus apella*, a New World monkey species). They gave six capuchins two closely related tasks of density discrimination. The first task was the sparse-uncertain-dense task, an application of the uncertainty paradigm that has been described. This task had difficult trials surrounding the breakpoint between the sparse and dense stimulus regions along the density continuum. Monkeys had available the UR by which they could decline selected trials. So, this task let monkeys declare – in a sense – that they didn't know if that trial was sparse or dense. The second task was a similar sparse-middle-dense task. This task let monkeys be directly rewarded for making a middle response to stimuli in the midrange of the continuum. So, this task let monkeys affirmatively and concretely declare – in a sense – that was a middle trial.

Figure 5a shows that in the first task capuchin monkeys hardly made any URs. This result can be compared to the result shown in Fig. 3a wherein macaques made URs frequently and adaptively to



**Uncertainty Paradigm, Fig. 5** (a) Capuchin monkeys' performance in the sparse-uncertain-dense task used by Beran et al. (2009). The horizontal axis indicates the density level of the box. The sparse and dense responses, respectively, were correct for boxes at density levels 1–21 and 22–42. The solid line represents the percentage of trials receiving uncertainty responses at each trial level. The

percentages of trials ending with the sparse response or dense response are also shown. (b) The performance of the same capuchin monkeys in the sparse-middle-dense task depicted similarly. (Adapted with permission from Beran et al. (2009). Copyright 2009 by the American Psychological Association.)

decline the range of difficult, error-causing trials. However, Fig. 5b shows that in the second task, capuchin monkeys used the middle response fluently.

To possibly foster capuchin monkeys' URs by increasing that response's value, Beran et al. (2009) increased the penalty timeout for an error from 20 s to 90 s. Now, the cost of error was high – animals could potentially complete 30 trials correctly to gain 30 food rewards during the timeout brought by one error. Yet despite having now a much stronger motivation for URs, they still hardly used that response.

Through this experiment's uncertain-middle dissociation, the uncertainty paradigm showed again its ability to differentiate responses that have different psychological characters. Probably, the middle response is associatively bound by reinforcement to a class of middle discriminative stimuli. Capuchin monkeys used this response fluently. They clearly responded to the signal from the middle stimuli and responded to them to maximize their task rewards. If URs were associatively bound to the same middle stimulus range in the same way, as associative theorists have suggested, capuchin monkeys would have made

that response fluently as well. But they did not. They barely monitored the uncertainty paradigm's uncertainty signal, and they seemed not to respond to that signal to maximize reward. Thus, the uncertainty paradigm – through its uncertainty response – taps into a different psychological mechanism than does the sparse-middle-dense task with its middle response. In this study, one sees clearly the three empirical/theoretical themes that define the essence of the uncertainty paradigm. First, it clearly differentiates the uncertainty-management systems of different species – in this case, capuchin monkeys and rhesus macaques. It is an exciting aspect of this area that these cross-species comparisons continue to expand (e.g., Foote and Crystal 2007, 2012; Suda-King et al. 2013; Templer et al. 2017). Second, it clearly differentiates responses of different psychological levels – in this case, an associative (middle) response bound behaviorally to stimuli through concrete rewards, and a decisional (uncertainty) response that reveals a higher-level cognitive capacity that could have emerging ties and similarities to humans' metacognitive capacity. Third, the uncertainty paradigm insistently requires that comparative psychology's tendency

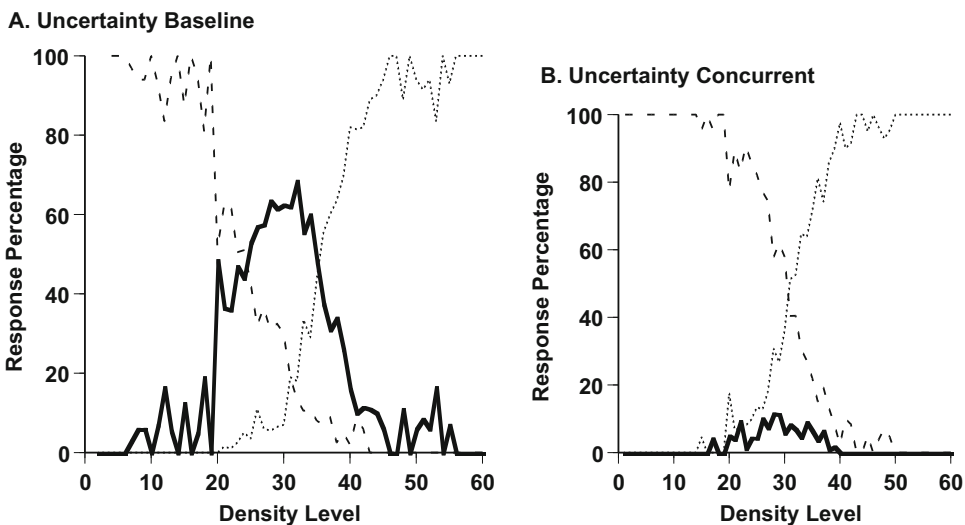
to assume a unitary, associative system as the governor of animals' behavior must be questioned. It is time to elaborate our theories of animal minds in ways that will foster the careful study of animals' higher-level cognitive processes.

However, the precise information-processing structure of this higher-level cognitive capacity remains to be illuminated. That work of illumination is occurring presently in the literature. For example, Smith et al. (2013) confirmed that the uncertainty response in the uncertainty paradigm is psychologically distinctive for drawing especially heavily on working-memory resources. They placed macaques in the sparse-uncertain-dense task that was already described. Once again, the UR let monkeys decline difficult trials near their discrimination thresholds as well as any other trials of their choosing. However, now Smith et al. added a secondary task requirement to the ongoing discrimination, so that monkeys needed to actively maintain memory material while performing their sparse-uncertain-dense trials. The secondary task acted as a concurrent

cognitive load, and it was possible to then examine the effect of the memory load on the use of the various responses in the task.

The experiments considered how the concurrent memory load might affect perceptual-classification processes as compared to the processes that support uncertainty monitoring and URs. Smith et al. suggested that the uncertainty paradigm's primary perceptual responses might be more stimulus-based, reactive, and associative, making few demands on working memory or executive attention. In that case, sparse and dense responses would hardly be affected by the memory load. In contrast, Smith et al. evaluated the possibility that URs might be severely affected by the memory load – if they are a higher-level response that needs the resources of working memory.

Figure 6 shows the article's main results. The concurrent load in essence did not affect macaques' sparse and dense responses at all. In sharp contrast, the load disrupted macaques' URs severely. This result strongly urges that the UR in the uncertainty paradigm not be considered as



**Uncertainty Paradigm, Fig. 6** Macaques' performance in the uncertainty paradigm used by Smith et al. (2013). (a) Performance is shown in a baseline condition to illustrate uncertainty responding under control conditions. The percentages of sparse and dense responses are shown (dashed and dotted lines, respectively). The percentage of uncertainty responses made at each trial level are shown in the

solid line. (b) Performance is depicted in the same way for the concurrent-load condition to illustrate uncertainty responding when monkeys were given a concurrent working-memory load. (Adapted with permission from Smith et al. (2013). Copyright 2013 by the American Psychological Association.)



equivalent to the primary perceptual responses. Instead, it clearly seems to reflect higher-level cognitive processing that may depend especially strongly on the active use of working-memory resources.

In fact, in an additional dissociation, Smith et al. (2013) found that middle responses in a sparse-middle-dense discrimination, like sparse and dense perceptual responses in a sparse-uncertain-dense discrimination, were minimally affected by a concurrent memory load. Coutinho et al. (2015) showed that this is also true of humans performing with working-memory interference. So, Smith et al. (2013) also produced an uncertain-middle dissociation. The robustness of the middle response is explainable because it mapped to an objective range of stimulus levels (interestingly, the same concrete stimulus levels to which the uncertainty response mapped). Middle responses to those stimuli were immediately rewarded, clearly creating ideal conditions for the processes of associative learning. This dissociation supports the idea that the primary perceptual responses included in the uncertainty paradigm – in this case, sparse, dense, and middle responses – result from the operation of something like associative-learning processes. But the uncertainty response apparently does not. One sees that these results have a strong theoretical resonance with the uncertain-middle dissociation shown in capuchins by Beran et al. (2009).

The problem for associative accounts of the uncertainty paradigm is that they have assumed a theoretical equivalence between the UR and the task's perceptual responses. They do not allow that these response types might be qualitatively different for having different requirements in resources and requiring commitments from different levels in the cognitive system. But the response types do seem to have these different requirements and different cognitive levels. Therefore, to lump them together – under the label associative responding – is theoretically inadequate because it blurs the most important theoretical distinctions. But if one assumes that the UR is a higher-level, decisional response that is particularly dependent on working memory and attentional resources, this is theoretically adequate

for describing this result. It is also consistent with the theoretical possibility that the UR within the uncertainty paradigm is an elemental behavioral index of uncertainty monitoring.

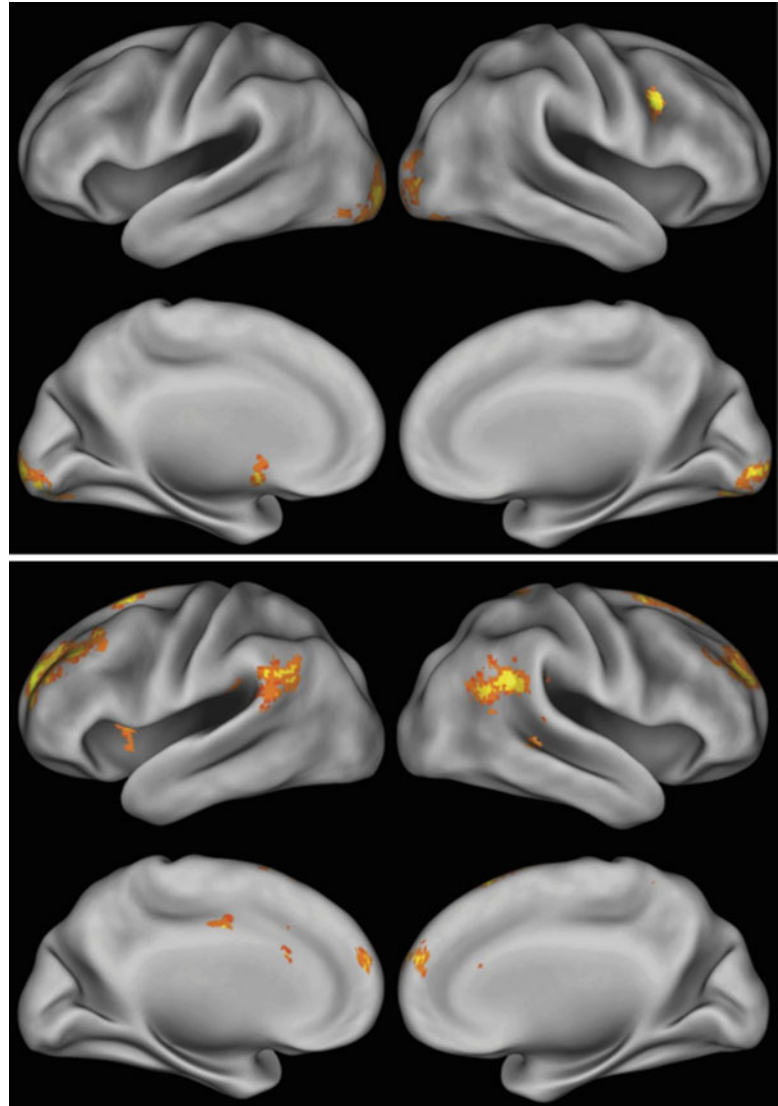
Finally, Paul et al. (2015) provided one capstone finding that places the uncertainty paradigm within a neuroscience framework while also clearly justifying the UR as a distinctive psychological element in a cognitive task above and beyond the primary responses within the task grammar. They gave humans the sparse-uncertain-dense task that has already been described. The sparse-to-dense continuum was equally divided into sparse and dense regions that deserved the sparse and dense response, respectively. The task's discrimination breakpoint lay at the continuum's center and naturally the most difficult and uncertain trials in the task surrounded this sparse-dense breakpoint. Then, Paul et al. used rapid event-related fMRI to show the neural-activity patterns that underlay humans' uncertainty responses and their perceptual responses (sparse, dense). The findings showed that the activity patterns for the two response types were distinctively different.

Figure 7 (top) shows the simple neural-activation pattern found when participants made correct sparse or dense responses instead of choosing the uncertainty responses. There was activation in the occipital lobe bilaterally and in the caudate and nucleus accumbens. This pattern expresses well the theoretical idea that sparse and dense responses are first-order responses to concrete perceptual events that produce well-associated behaviors.

In contrast, Fig. 7 (bottom) shows the complex neural-activation pattern when participants made uncertainty responses instead of sparse or dense responses. Uncertainty responding activated a distributed network including prefrontal cortex, anterior and posterior cingulate cortex, anterior insula, and posterior parietal areas. Thus, uncertainty monitoring apparently benefits from a widespread network for controlled cognition that includes recently evolved brain regions such as the anterior dorsolateral and medial prefrontal cortex. If URs were just associative responses, as some have argued, they would not need to activate

**Uncertainty Paradigm,  
Fig. 7** Humans'

performance in an uncertainty paradigm depicted from an fMRI perspective. *Top.* Whole-brain results from the contrast correct sparse-dense response > uncertainty response projected on an inflated lateral and medial cortical surface. Table 2 in Paul et al. (2015) gave the coordinates and voxel numbers for significant clusters. Images were cluster thresholded (correcting for multiple comparisons) at  $z > 3.54$ ,  $p < .01$ . *Bottom.* Whole-brain results from the contrast uncertainty response > correct sparse-dense response projected on an inflated lateral and medial cortical surface. Table 3 in Paul et al. (2015) gave the coordinates and voxel numbers for significant clusters. Images were cluster thresholded (correcting for multiple comparisons) at  $z > 3.54$ ,  $p < .01$ . (Adapted from Paul et al. (2015), p. 316 (top), p. 317 (bottom). Copyright 2015 Elsevier Ltd. Reprinted with permission.)



this complex neural network. Instead, one is led to conclude that URs are quite psychologically distinctive and do involve higher-level judgments of difficulty, prospects, or mental states of knowing. Clearly, the neural circuit involved in adjudicating task uncertainty is far different from, and more complex than, the circuit involved in settling on one of the two primary perceptual responses.

Of course, this human experiment throws down a gauntlet to animal researchers that at some point they will need to take up with new brain-imaging approaches. And yet this result clearly suggests strongly that the uncertainty

paradigm is tapping into something extremely important about human and animal minds. This result recalls Tolman's sense that URs could be the behaviorist's definition of consciousness. It recalls psychophysicists' idea that URs are less perceptual, more psychologically complex. It recalls Weiskrantz's idea that URs amount essentially to a commentary key by which animals may declare their knowing or not knowing, their certainty or uncertainty. Thus, for many reasons, the uncertainty paradigm in animal-metacognition research has proved to be an influential, theoretically challenging resource for many researchers

and the source of scores of intriguing investigations of cognition across species. Indeed, quite possibly, the uncertainty paradigm lays important groundwork for future research paradigms that may positively identify animal consciousness and awareness.

The uncertainty paradigm has also become part of the ongoing discussion about animal care and husbandry, and animal rights. Given that many animals evidently monitor their uncertainty and their doubts, their states of remembering and not knowing, it becomes highly plausible that they monitor other aspects of their mental experience as well. And thus, the uncertainty paradigm, by systematically elevating comparative psychology's view of animals' minds, insistently also elevates the level of care and respect that is owed to those animal minds and animal lives.

## Cross-References

- [Cognitive Control](#)
- [Comparative Cognition](#)
- [Comparative Psychology](#)
- [Computerized Testing Paradigm in Primates](#)
- [David Washburn](#)
- [Georgia State University's Language Research Center](#)
- [John David Smith](#)
- [Meta-cognition](#)
- [Metamemory](#)
- [Michael J. Beran](#)
- [Sara Shettleworth](#)
- [Self-Awareness](#)

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## Unconditioned Reflex

- ▶ [Rooting Reflex](#)
- ▶ [Step Reflex](#)

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## Unconditioned Response

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### Synonyms

[Modal action pattern](#); [Reflex](#)

### Definition

*Unconditioned responses* are evoked by the first presentation of a stimulus.

### Introduction

*Unconditioned responses* (URs) are unlearned species-specific responses. Salivation was the UR evoked by a number of substances placed in the mouth of dogs by Pavlov (1927) and his students, including wet food, dry food, weak acid, and sand. Inedible substances, like sand, would evoke salivation only when placed in the dog's mouth. The visual appearance of sand did not evoke salivation until the dog had learned the unfortunate destination of this substance was its

mouth (Todes 1997). It appears that placement of practically any substance in the dog's mouth produced a salivary unconditioned response.

On the other hand, the dog's reaction to the visual appearance of various foods was probably learned through association before the dog was captured on the streets of Saint Petersburg, Russia. Edible substances evoked salivation upon sight and contained larger amounts of mucin. Previous experience had presumably already installed an association between the conditioned stimulus (CS, sight of food) and the food unconditioned stimulus (US). In a similar way, a pigeon will learn to peck at an illuminated disk on the chamber wall when it is differentially associated with food (Gamzu and Williams 1971). Pecking is a conditioned response (CR). It is not the product of instrumental reinforcement because the pecking response has absolutely no effect on the probability of food.

Unconditioned responses span the range from very simple reflexes (sensory nerve → interneuron → motor nerve) to quite complex behavior patterns. An animal attacked by a predator feels pain (an emotion), it jumps, flinches, and vocalizes (skeletal responses), and experiences high levels of arousal (sympathetic nervous system). Moving toward appetitive stimuli (approach) and retreating from aversive stimuli (withdrawal) are sometimes URs and sometimes CRs, depending on the organism. Orienting responses bring animals' sensory organs in a better position to process stimuli in the environment. Taste reactivity tests assess the oral and facial reactions of babies and rats to sweet and sour substances to discern the hedonic value (liking) of rewards (Berridge 2000).

### Sensitization and Habituation

The magnitude or probability of unconditioned responses may increase or decrease, depending on a large number of factors. Habituation is defined as a response decrement that results from repeated stimulation and that cannot be due to sensory adaptation, sensory fatigue, or motor fatigue. Habituation can be either short-lived or



long-lived, and the factors that cause short-term effects are not the same as those causing them to stick for the long term. Consider the startle response. Rats' startle when they hear a loud sound, and this response diminishes more quickly over trials (repeated presentations) if the sound is repeated every 2-s than every 16-s. Although short intervals encourage faster and deeper habituation during stimulus presentations, the retention of habituation at a later time is uniformly better after a 16-s training interval than a 2-s training interval (Davis 1970). The effects of intertrial interval are very common across species and situations, causing Thompson and Spencer (1966) to add this factor to a list of eight other behavioral characteristics of habituation.

Sudden or threatening events, such as loud noises or sharp taps on the shoulders, also cause people to startle. Jaws clench (we wince), eye muscles close (we blink), shoulders jerk upward, and even our legs move. Emotional states evoked in people viewing positive, neutral, or negative pictures modulate the degree of startle. Negative pictures enhance the eyeblink startle response, and positive pictures reduce it (Vrana et al. 1988). Fear-potentiated startle is well studied in both humans and animals because of its potential relevance for understanding post-traumatic stress disorder. That sensitization rather than habituation of responding is a possibility led Groves and Thompson (1970) to suggest the existence of both a decremental process (habituation) and an incremental (sensitization) process which interact over trials to determine the behavioral outcome.

Studies of the relatively simple organism, *Aplysia californica*, by the Nobel Laureate Eric Kandel (2001) have uncovered exactly how these two hypothesized processes can operate at the neural level. His laboratory identified which of just 20,000 large, easily identified neurons produce sensitization and habituation of the gill-withdrawal response. Subsequent research found the neurotransmitter serotonin was a key player in the sensitization of the response and identified some of the proteins that had to be synthesized to convert short-term changes in synaptic transmission into long-lasting memories.

## Opponent Process Theory

Some unconditioned stimuli evoke bidirectional changes. An initial reaction is followed by any secondary reaction, which serves to bring the organism back into a *homeostatic* balance. Solomon and Corbit (1974) argued that emotional responses are especially prone to this dynamic pattern of activity. Frightening events evoke intense fear, followed by adaption and thereafter by feelings of relief when the danger has ceased. Some psychoactive drugs produce euphoria, followed by adaption, and finally anhedonia when drug is eliminated from the body. Solomon and Corbit hypothesized that manifest affective reactions in these situations are controlled by two opposing forces: (a) an a-process triggered by the presence of the event that remains unabated during the entire duration of the event and (b) an opponent b-process of the opposite emotional quality aroused by the a-process to provide a homeostatic limit. On the first trial, the sluggish onset and inherent weakness of the b-process explains the long delay for adaptation to materialize, and the lingering effects of the b-process explain why a modest counter-reaction is observed after the event is withdrawn. As the event is repeated, the b-process grows in immediacy and strength, leading to habituation and a more intense counter-reaction.

The parallels between these changes to drug tolerance and withdrawal should be readily apparent. Counter-reactive processes sometimes fail to return the person to within the normal level in after drug taking has ceased altogether. When this occurs, neuroadaptive mechanisms return the person to a new *allostatic* state, making them vulnerable to relapse.

## Facilitation and Diminution of the UR

Signaling the US can lead to either facilitation or diminution of the UR. If the CR and the UR are complementary, such as found in the studies of the salivation in dogs (Pavlov 1927), the combined effects of anticipatory salivation evoked by the CS

and unconditioned salivation elicited by the US might be additive. However, the more likely result is diminution of the UR. This may occur for two reasons. First, the CR may enter into association with b-process rather than the a-process, leading to a compensatory CRs. Contexts associated with painful shocks support conditioned hypoalgesia (reduced pain) by virtue of the existence of anti-pain mechanisms in the brain. Second, the prediction of the US may reduce surprise value of the US. Even when the CR and UR take the same form, signaling the US can diminish the UR. As the intensity of the US is increased in eyelid conditioning in the rabbit, the UR switches from being higher on CS+US trials than US alone trials to the opposite (Donegan and Wagner 1987).

## Conclusion

*Unconditioned responses* (URs) are unlearned, but they are certainly not unchangeable or static. They may sensitize or habituate over repeated trials and can be facilitated or diminished by signaling with a CS or context. Secondary URs can be conditioned leading to compensatory CRs.

## Cross-References

- [Homeostasis](#)
- [Innate Behaviors](#)
- [Innate Releasing Mechanism](#)
- [Ivan Pavlov](#)
- [Reflex](#)
- [Rooting Reflex](#)
- [SOP Model](#)
- [Taxis](#)
- [Tolerance](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Unconditioned Stimulus

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## Synonyms

[Eliciting stimulus](#)

## Definition

*Unconditioned stimuli* are biologically important events that evoke unlearned responses upon their first presentation.

## Introduction

The term unconditioned stimulus (US) comes from Arnrep's English translation of *Conditioned Reflexes* (Pavlov 1927). It refers to a stimulus falling upon a sensory receptor, either internal or external, that gives rise to a definite response. Pavlov gives the example of making a food (US) available to a hungry animal. The animal is attracted towards the food and consumes it, the unconditioned reflex (UR). He viewed the UR as an inborn set of well-coordinated responses to the US, which had evolved because of their importance for survival and reproduction. Conditioned stimuli (CSs) also evoked well-coordinated responses, such as investigatory reflexes, but these CSs are vital for survival only to the extent they come to signal the later occurrence of more important USs. CS-US pairings lead to the development of conditioned responses (CRs).

For Pavlov, the difference between CSs and USs was a matter of the motivational value of the stimulus, potential signal (CS), or biologically relevant stimulus (US). It follows from this perspective that biological relevance and not temporal order is the key. During Pavlov's *backward* conditioning procedure, the delivery of the food US preceded the presentation of CS. Pavlov did not re-label the food as a CS just because it came first. This arrangement is only somewhat effective for establishing a conditioned response (CR) compared to the forward CS-US arrangement.

Given the definition of the US as a biologically potent stimulus, the term could be applied in circumstances outside of the Pavlovian conditioning situation. For example, species-specific modal action patterns are released by the occurrence of appropriate stimuli, such as the pecking response of chicks directed to beak-like stimuli (Tinbergen and Perdeck 1950). Although they are more likely to be called eliciting stimuli this instance, it should be apparent these beak-like stimuli are USs by another name. Reinforcers in operant conditioning are also USs in a sense; however, most researchers think it worthwhile to label these stimuli in other terms because their presentation or removal is contingent on the animal making a particular response.

A surprising array of USs has been used in conditioning experiments. Female copulation partners have been employed as USs in studies with domesticated quail, producing a variety of anticipatory CRs in their male partners. Interoceptive stimuli can serve as USs. Initial panic attacks coming "out of the blue" in panic disordered patients may become associated with other normally benign interoceptive sensations (Bouton et al. 2001). These formerly benign feelings may serve as CSs and evoke anxiety and fear, and precipitate a new panic attack. Opiate drugs are powerful USs, producing a wide variety of effects including pain relief, euphoria, and respiratory depression. Compensatory CRs evoked by stimuli uniquely associated with drug delivery are responsible for some of withdrawal symptoms addicts' experience after ceasing use of the drug (Siegel 2001). Overdose is more likely without these compensatory CRs.

## Sensory and Motivational and Components of the US

Konorski (1967) is usually credited with the idea that the CS may enter into separate associations with different components of the US. According to Konorski, the US is a multidimensional stimulus with (a) specific sensory qualities and (b) either appetitive (pleasant/rewarding) or aversive (unpleasant/punishing) motivational qualities. The motivational value of appetitive USs is typically highly variable, regulated by the current needs of the organism. Pre-feeding (satiation) can markedly reduce the value of a particular food, but its texture (one of its sensory qualities) is not affected by changes in the state of the animal. Selective satiation studies examine whether declining satisfaction is generated by the consumption of certain type of foods. They suggest such differences are not limited to general motivational states, appetitive and aversive, but can be far more specific.

The motivational value of aversive USs is less easily manipulated by changing the state of the animal. Motivational value is determined more by the degree of threat (intensity). Life threatening dangers challenge an animals' evolutionary

fitness, and so it makes sense the motivational value of aversive US is less likely to be determined by the animal's current needs. Consider the loud clang US used in Watson and Raynor's (1920) famous study of the fear conditioning of "Little Albert." The aversive internal state evoked by the clang became associated with the appearance of a white rat, the CS, leading to the development of a conditioned fear. There was no need to motivate "Little Albert" with some pre-experimental manipulation.

## US Revaluation

Studies of US revaluation take advantage of the fact that the motivational properties of the US are not fixed. They permit experimental research to determine the nature of association formation, stimulus to stimulus (S-S) or stimulus to response (S-R). Following successful conditioning, for example, the attractiveness of an appetitive US might be changed by satiation (feeding). With the motivational properties of the US diminished at test, we might expect the CR evoked by the CS to also diminish, provided that anticipation of the US (triggered by the CS) is the driving force behind the CR (CS-US or S-S learning). If, instead, the CS were to directly evoke the CR (CS-CR or S-R learning), it follows that the CR should be largely unchanged from the last conditioning trial. Studies of US revaluation have revealed CS-US associations in a variety of different Pavlovian conditioning situations.

Aversive USs are typically revalued by changing their intensity. During conditioning, a tone CS might be repeatedly paired with a moderate intensity footshock US (e.g., 0.8 mA) until a fear CR is observed. During revaluation, the animal might receive a few US-alone trials with a very intense footshock (e.g., 3.0 mA) as a US inflation treatment. It is critical that the US is inflated in the absence of the CS and in a completely different location than in the conditioning or testing box. Otherwise, the results could be attributed to a direct experience with the CS and revalued US or to additional conditioning of situational cues and the revalued US. During testing, the CS is

assessed to determine if it evokes a bigger CR than it would otherwise in non-revalued control group.

## US-US Learning

If USs are spaced at regular intervals, each US may serve as a signal for the next US. This type of learning was first uncovered in Pavlov's laboratory in an experiment conducted by Dr. Feokritova. A dog received pairings of the sound of a metronome with food every 30 min. Time since the last US acted as a cue as shown by the fact the CS evoked the CR if it was tested at the 29th min but not the 5th min.

## Surprisingness of the US

The ability of a US to support further conditioning seems to depend on whether it is fully predicted. Learning curves are generally negatively accelerated with the greatest increases in the CR occurring earlier and smaller increases afterward until asymptote is reached. The CS ceases to gain strength when the US is fully predicted. This suggests that learning is driven by an error reduction process in which the subject's expectations gradually come into line with the intensity of the US. Kamin's (1968) discovery that conditioning could be *blocked* led many researchers to embrace US processing as the primary determinant of conditioning. When a new CS joins an already well-conditioned CS, and the two CSs are together followed by the US, the new CS may display very little ability to evoke the CR when tested in isolation. Rescorla and Wagner (1972) famously hypothesized that all available signals (CSs) contribute to a common prediction of the US, and learning depends on the surprisingness of the US received.

Context blocking is one of the causes of the *US preexposure effect* (Randich 1981). Repeated presentations of the US alone before CS-US pairings interferes with acquisition of the CR. If US alone trials are given in the same apparatus (context) as the subsequent CS-US pairings, the context may

enter into association with the US and reduce the rate of conditioning. Although some have questioned whether blocking is a reflection of a learning deficit (Blaisdell et al. 1999), prediction error signals have been identified in many brain regions and experimental paradigms (Den Ouden et al. 2012), making the account seem secure.

## Conclusion

A wide variety of biologically important events have been used as USs in conditioning, including food, footshock, sexual partners, and drugs. USs are multifaceted events with motivational properties (which make it a US) and sensory/perceptual properties (which allow it to act as a signal for another US). Errors in predicting the arrival of the US drive association formation to reduce surprise.

## Cross-References

- [Blocking](#)
- [Ivan Pavlov](#)
- [Motivational State](#)
- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

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## Uncorrelated Asymmetry

- [Bourgeois Strategy](#)

## Understanding

- [Catarrhine Cognition](#)
- [Insight in Pigeons](#)
- [Learning](#)

## Understatements

- [Restraint](#)

## Unemotional

- [Restraint](#)



## Ungulate

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### Introduction

Ungulates are defined as animals with hooves. This simply implies that a portion of the terminal phalanx is encased in a sturdy hoof. Because many species of ungulates commonly live in open habitat types, they are often the most visible fauna on the landscape (Groves and Grubb 2011). As such, it may be surprising to some that there is a large gap in the research conducted on this fauna group, with generally little known about specific species (Groves and Grubb 2011), such as the elusive okapi.

Ungulates are found on every continent except Antarctica. They can be social or solitary, nomadic or territorial. While the Smithsonian Institution acknowledges 275 modern ungulates, Groves and Grubb (2011) recognizes 450 distinct ungulates through utilizing the Phylogenetic Species Concept as opposed to the more traditional Biological Species Concept. Even with the vast number of ungulate species, true ungulates are generally confined to two orders based on the number of toes they have: Artiodactyla (even-toed) and Perissodactyla (odd-toed).

Due to the diversity found among ungulates, this entry will focus on cognitive and behavioral traits of ungulates as a whole, occasionally referring to specific case studies and/or species.

### Evolution of Cognition

Cognition is defined as “the mental action or process of acquiring knowledge and understanding through thought, experience, and the senses” (Oxford Ungulate 2019). What led to the evolution of cognition in animals? It has been suggested that ecological problems, such as extractive foraging and memorizing resource location, as well as social demands such as group cohesivity and

reducing conflict, led to the necessity of cognitive evolution (Briefer et al. 2014). Advanced cognitive abilities enhance survival probability, leading to the success of a species. Interestingly, increase in brain size among carnivores and their prey species (particularly ungulates) seem to track each other closely, with ungulates leading in brain size (Dunbar and Shultz 2007). These findings demonstrate that brain size may be associated with other types of ecological flexibility.

Advanced cognition is often related to increased brain size. In ungulate species, the relationship between brain size and sociality is qualitative and not quantitative (Dunbar and Shultz 2007). Large relative brain size has been associated explicitly with pair-bonded monogamy. Ungulates which mate monogamously have been found to have substantially larger brains than polygamous ungulates (Dunbar and Shultz 2007) suggesting that sexual selection may be a more important factor driving brain evolution than sociality among ungulates (Dunbar and Shultz 2007).

Research on social learning and ecological selection pressures has mainly focused on the cognition of primates, birds, and carnivores (Shultz and Dunbar 2006). Social complexity, or lack thereof, in ungulates is currently under discussion. Shultz and Dunbar (2006) noticed a gap in the research and hypothesized that social and ecological factors could affect ungulate brain size. It was concluded that there was a positive relationship between brain size and sociality. Surprisingly, however, Shultz and Dunbar (2006) concluded that in their particular study that there was not a significant association between brain size and group size. This suggests that using group size to measure social complexity may not be the most relevant measure, although a relationship has been found previously between the two when measuring social complexity with a number of other taxa. In ungulates, who commonly have unstable grouping patterns, group size can be considered undefined. Estimating a characteristic group size may be more complex than counting individuals observed in a herd at a particular moment in time. Doing so may limit research findings on cognitive demands within ungulates. Shultz and Dunbar (2006) highlight that

“an unstable herd of several thousand antelope may not present the same cognitive demands as a smaller stable group, where individuals interact on a regular basis.”

In animals such as cetaceans and primates, scientists have discovered that their complex cognition and relatively large brains allow for social learning as opposed to learned behaviors driven by ecologically demanding environments (Marino et al. 2007; Reader 2003). Domestic goats, *Capra aegagrus hircus*, are a social species which show advanced cognitive abilities, such as colonizing new environments. Briefer et al. (2014) conducted a study on goats testing their social and physical cognition as well as long-term memory. Interestingly, the majority of goats were able to learn the task quickly, but did not learn more quickly after watching a different individual complete the task before trying it themselves. This indicates that the task was mastered through individual learning rather than social learning. The study suggests that relatively intelligent species, such as the goat, do not always exhibit a preference to learn socially. In contrast, learning might be more driven by the need to forage efficiently in ecologically demanding environments. Domestication has been shown to decrease brain size due to the relaxed selection pressures compared to the wild environment (Briefer et al. 2014). Perhaps a smaller brain size is still capable of complex social living and learning survival behaviors, without the necessity of social learning.

### **Social Structure: Gregarious and Solitary Ungulates**

Social structure varies greatly among ungulates. Blue duikers, *Philantomba monticola*, are monogamous, forming lifelong mating pairs, and are limited to specific home ranges. Red forest duikers, *Cephalophus natalensis*, are solitary with widely overlapping home ranges (Bowland and Perrin 2009).

Giraffes, *Giraffa camelopardalis*, live in social groups that individuals may enter and leave. There is no social segregation between sexes and age groups, and individuals tend to form weak

social bonds (Pendur et al. 2001). Associations are often dependent on sex and age, with young male giraffes interacting more frequently than other classes (Pendur et al. 2001).

Okapis, *Okapia johnstoni*, the closest living relative of the giraffe and known for their elusiveness, have quite the opposite social structure. Okapis are mostly solitary animals, most likely coming together only for mating. Males have been known to have home ranges overlapping with several females, which suggests polygamy within this species (Hart and Hart 1989). Spending most of their time in solitude is likely used as a predation defense (Hart and Hart 1989).

Sitatunga, *Tragelaphus spekii*, are commonly solitary; however, they have been documented in gregarious social structures when necessary for food consumption (Magliocca et al. 2002).

The above are just a few examples of the social structure variety witnessed in ungulates. Group living has advantages such as minimizing predation or allowing cooperation in locating food sources (Byrne and Bates 2007). However, it is a demanding evolutionary option. Group living has many disadvantages, such as resource competition. Competition for resources often results in group instability (Byrne and Bates 2007), which may be why giraffes form weak social bonds.

Evidence has shown that social living has been responsible for specialization in intelligence. As mentioned previously, ungulates show a pattern between the relationship of brain size and group size. Contradictory to what Shultz and Dunbar (2006) hypothesized, Byrne and Bates (2007) conclude that larger groups correlate to a larger brain size of the species, suggesting that social species have larger brains than solitary species (Pérez-Barbería and Gordon 2005). Brain tissue is metabolically expensive and so it is rational to assume that larger brained species must benefit highly from dealing with serious cognitive challenges (Byrne and Bates 2007), such as predator avoidance.

When a species is classified as solitary, some species change social systems depending on other, temporally changing, factors. Japanese serows, *Capricornis crispus*, are usually solitary but have been seen forming groups of two to four

individuals. These consisted of mostly mother-kid or male-female pairs with or without a kid. Although this species commonly defends its territories, several nonterritorial males have been observed. Japanese serows are considered monogamous, with a male's territory completely overlapping a female's territory. However, there have been exceptions of polygamous males, whose territory overlapped with two females' territory (Kishimoto and Kawamichi 1996).

### Physical and Social Environmental Impact

As prey species, ungulates are constantly having to modify their behavior and adapt to social and physical changes in their environment. Behaviors such as exerting energy to be vigilant towards predators in close proximity, changes in herd dynamics, and seasonal shifts in resource availability all require significant amounts of energy and adaptability. Reactive responses of any animal often pair down to flight or fight. Ungulates frequently partake in the flight behaviors to protect themselves against predators or startling changes in their environment. This response is an important aspect to maintaining or increasing individual fitness (Stankowich and Reimers 2015).

Physical and social environments often play a role in the flight response of individuals or groups of ungulates. Escape terrain proximity often influences the response of some ungulates (Takada et al. 2019). A Yellow-backed Duiker (*Cephalophus silvicultor*) would consider a densely vegetated forest to be escapable terrain, whereas a Siberian Ibex (*Capra sibirica*) would consider rocky areas such as inland cliffs and mountain peaks to be escape terrain if there was a predator or human disturbance in their midst (IUCN SSC Antelope Specialist Group 2016; Reading and Shank 2008). If either of these animals were at a distance from what the species would consider escape terrain, they would likely be more reactive to disturbances (Takada et al. 2019). For many ungulate species, like the Japanese serow (*Capricornis crispus*), the flight

response is consistently more apparent in relation to gender and if offspring are part of the herd (Stankowich 2008). However, when ungulates become isolated from predator populations, there is a reduction in predator vigilance (Blumstein 2006). This allows ungulates to alter their natural behavior patterns in a way that they can spend increased time choosing the most adequate mate, alter their herd sizes, become more resolute in maintaining territorial boundaries, and expand their foraging locations (Blumstein 2006). Berger (1991), Mysterud (2000), and Mooring et al. (2003) all came to a consensus that habitat use varies according to gender and that herds primarily consisting of females or females with offspring escape terrain more frequently than males do.

In a study on wild elk (*Cervus canadensis*) by Found and St. Clair (2017), it was discovered that there are different fitness benefits associated with strong and weak laterality. When the connection between the two hemispheres in the brain is weak (strong laterality), ungulates have quick responses to environmental stimuli, including humans (Found and St. Clair 2017). When the connection between the hemispheres is strong (weak laterality), it has been observed that those individuals have increased learning abilities and creativity (Found and St. Clair 2017). Similar to humans, ungulates demonstrate front-limb bias (left handedness vs right handedness) (Found and St. Clair 2017).

### Migratory Behaviors

Behavioral adaptability is one of the many pertinent skills that individual ungulates have in order to increase survival rates in changing environments. For ungulate species that live in more temperate environments, such as roe deer (*Capreolus capreolus*), their ecology illustrates that population density is determined by winter foraging conditions, while individual size and body condition are a result of summer foraging conditions (Klein 1965; Mysterud 2013). Ungulates that have a tropical home range, such as wildebeest (*Connochaetes taurinus*), may migrate due to seasonal changes in rainfall and plant nutrition or availability (Holdo et al. 2009).

Some ungulates such as elk (*Cervus canadensis*) are unhesitatingly able to habituate to environments with human disruption and have facultative migratory tendencies (Found and St. Clair 2017). Found and St. Clair (2017), concluded that elk that exhibited more laterality were more likely to migrate than those that expressed weaker laterality (Found and St. Clair 2017).

Ungulate migration can vary seasonally or by region due to annual environmental or anthropogenic changes. Whether foraging opportunities are intentionally distributed to ungulates or a byproduct of the increasing demand for crops, ungulate migration can change considerably (Jones et al. 2014).

### External Factors on Behavior

As behavioral research has advanced, it has become clear that there are numerous factors that can impact and alter behavioral patterns, from parasite relations to the effect of human-wildlife relationships. In a study conducted by Ezenwa and Snider (2016) on Grant's gazelles (*Nanger granti*), it was discovered that male Grant's gazelles transition between bachelorhood and territorial status several times throughout their adult lives. Territorial males have elevated parasite populations relative to individuals in a bachelor status (Ezenwa and Snider 2016). After experimentally reducing the parasite loads, it was found that males who were maintaining territories reaccumulated parasite burdens at faster rates than those who were not currently defending a territory (Ezenwa and Snider 2016). Because parasites utilize energy sources from their hosts, the adult males who had larger parasite counts had decreased frequencies of typical territorial and breeding behaviors (Ezenwa and Snider 2016). This resulted in the males with smaller parasite loads to be able to win territorial challenges, creating a cyclical rotation of dominant males, increasing genetic diversity within the population (Ezenwa and Snider 2016).

As human populations continue to expand into rural landscapes for recreation and livelihood, interactions between humans and wildlife are

becoming more abundant (Wittemyer et al. 2008; Yamashita et al. 2017). Accumulation of increased antipredator behaviors in ungulates that reside in close proximity to humans can cause detrimental effects to an individual's physiology and fitness (Cooke et al. 2014). Animals, particularly ungulates, tend to respond more forcibly when exposed to scenarios that they perceive as a more dangerous threat (Yamashita et al. 2017). The size of a group is inversely proportional to the amount of time that social ungulates spend being vigilant (Manor and Saltz 2003). Manor and Saltz (2003) studied the impact of human disturbance on vigilant behavior of a herd of mountain gazelle (*Gazela gazelle*). In findings, they stated that there was a negative relationship associated with the size of the herd and human disturbance (Manor and Saltz 2003). The gazelles that were in open areas with high levels of disturbance were in smaller herds than the gazelles that were in open areas with lower levels of disturbance (Manor and Saltz 2003). Population performance can be significantly altered by increased human disturbances due to the fact that changes in behavioral patterns can affect social structures of gregarious ungulates (Manor and Saltz 2003).

The flight behavior of guanacos (*Lama guanicoe*) and vicuñas (*Vicugna vicugna*) in relation to poaching was studied by Donadio and Buskirk (2006). These camelid groups were observed in two reserves where poaching was commonplace as well as a reserve where it was inconsequential (Donadio and Buskirk 2006). The camelids that habituated in the two reserves with more poaching reacted by fleeing 70% of the time they detected humans, whereas the groups of camelids that were observed in the park with less poaching only reacted 30% of the time when exposed to human presence (Donadio and Buskirk 2006). Likewise, elk (*Cervus canadensis*) who expressed less lateralization within their brain had stronger reactions to aggressive advances by humans; however, they were also the individuals that were able to more readily habituate to calm human presences (Found and St. Clair 2017). Behaviors that are dominant in lateralized individuals illustrate behavioral

resiliency, allowing those individuals to adapt more quickly to landscapes where humans are more common (Found and St. Clair 2017). Behavioral responses to human-wildlife conflicts may cause individuals to alter their selection process of habitats, resulting in the selection of poor habitats or the active avoidance of sufficient habitats (Battin 2004). Natural behaviors such as rearing young, resting, and grazing patterns can be significantly affected by negative perceptions of human exposure (Donadio and Buskirk 2006).

## Conclusion

As illustrated above, cognition and behavior are complex characteristics that are specific to each ungulate species. Social structures, brain size and laterality, environment, and external factors all have an important role in molding the unique mental constructs of ungulates. It is important to understand the delicate workings of and strong interplay between these characteristics when learning about and understanding the natural history of these animals in their vast variety.

## Cross-References

### ► Species-Specific Behavior

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## Ungulate Cognition

### ► Artiodactyl Cognition

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## Ungulate Demographics

### ► Artiodactyla Life History

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## Ungulates

### ► Perissodactyla Cognition

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## Unicellular Cognition

### ► Bacteria

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## Unintentional and Intentional Experiment

### ► Accidental/Intentional Experiment

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## Unisexualism

### ► Gonochorism

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## Unobservables

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## Synonyms

Imperceptibles

## Definition

Unobservables are hypothetical constructs, such as mental states, and physical forces including gravity and transfer of force. They are abstractions that do not take on physical form, so they cannot be perceived through any of the senses.

## Introduction

Unobservables are arguably the most abstract type of construct because they cannot be directly connected to physical features, although they can be correlated with observable events and objects. For example, gravity itself cannot be observed, but one can witness objects falling when released from support. One cannot directly see confidence, but it is manifested in postural cues and behaviors. Therefore, although unobservables are unavailable to the senses, they can be inferred and reasoned about. It is important to note that unobservables are undetected by senses other than the visual sense as well. That is, they cannot be heard, tasted, or felt any more than they can be seen. Unobservables are perhaps most interesting from the perspective of comparative psychologists in the sense that they can be inferred as causal forces giving rise to both physical and psychological events.

## Main Text

The Unobservability Hypothesis first formally posited by Vonk and Povinelli (2006) suggested that the capacity to reason about unobservables

may be one of the most significant cognitive capacities to distinguish human from nonhuman minds. Vonk and Povinelli presented substantial evidence that nonhumans represent various abstractions; for example, second-order relations, numerosities, and social relationships. Yet, even abstractions that can be directly tied to sensations, such as weight, appear challenging for other apes to reason about. An extensive series of studies with a group of chimpanzees suggested that apes do not view weight as a property of objects, but, rather, respond to the kinesthetic cues that objects of different weights produce during agent-object interactions (Povinelli 2012). Abstractions that represent hypotheticals, such as death, freedom, supernatural forces etc. might plausibly be expected to pose an even greater challenge because they are not reliably correlated with consistent observable features or sensations. Vonk and Povinelli questioned whether nonhumans could reason about physical forces such as gravity, and psychological attributes, such as thoughts, beliefs, and emotions. At the time of their hypothesis, the jury was out on whether even great apes could represent others' mental states (or their own), but the prevailing evidence suggested that they could not. In the past decade, researchers have become more amenable to the idea that other apes reason about at least some mental states in some contexts, but the ability is hardly as hegemonious as it is in humans.

## Mental States

When unobservables are consistently correlated with observable manifestations, such as the association between tears and crying vocalizations and sadness, it is difficult to tease apart the degree to which an organism has learned the outcomes associated with the observable features (in this case, tears and sounds of crying) or is drawing inferences based on the underlying and unobservable mental state (e.g., the emotion of sadness). Thus, the puzzle of whether nonhumans represent other minds, including thoughts, feelings, and beliefs, generally known as theory of mind (ToM), has captured the attention of psychologists for decades (Call and Tomasello 2008). Despite an

immense amount of energy and resources directed to this puzzle, researchers remain divided on the question of whether other animals reason about mental states. Mental states are just one class of unobservables and arguably, the most heavily researched. Perhaps the largest gains have also been made in this area. It appears that some species, predominantly other apes and members of the corvid family, have the capacity to correctly anticipate outcomes based on others' perspectives (Emery and Clayton 2001; Karg et al. 2015; Lurz et al. 2018), knowledge (Kaminski et al. 2008; Krupenye et al. 2016) and intentions (Buttelmann et al. 2017). However, even the most heralded studies, such as Krupenye et al.' (2016) observation that apes correctly anticipated a human agent searching where he thought an object would be, could be explained by the apes expecting the agent to search where he had last seen the object (or otherwise attended to it). Even when chimpanzees do appear to use their own experience to project internal states upon other agents, they do not appear to do so flexibly across contexts (Karg et al. 2015) the way that even human children do by the age of 5. These experience projection tasks hold the most promise for dissociating reasoning about unobservables from reasoning about observable correlates but have produced mixed evidence even in chimpanzees (Vonk and Povinelli 2011).

## Causal Reasoning

The larger question of whether animals reason about unobservables more broadly remains as elusive. As with mental states, causal forces typically manifest in observable events and behaviors such as object movements, and therefore, it can be equally difficult to determine whether an organism is reasoning about the manifestation or the underlying cause. Several clever paradigms have been designed in this area as well. For example, Blaisdell et al. (2006) examined whether rats were sensitive to whether an intervening action had occurred in associating cues with outcomes, thus exhibiting Bayesian causality. Even this careful design has been critiqued, however, by authors suggesting that response competition, i.e., lever

pressing, interfered with the rats' responses in this paradigm (e.g., Dwyer et al. 2009). As with the work on ToM, the high degree of association between unobservable causal forces and their outward manifestations challenges researchers' abilities to identify the mechanism underlying animal's decisions.

## Conclusion

Researchers will make little progress in determining whether other species reason about unobservables, and when this ability emerges in human ontogeny, until they disavow experimental paradigms that allow success by attending to observable correlates. Thus, the question remains central to comparative psychology as reasoning about unobservables could be the foundation for all of the distinguishing characteristics of humans, e.g., language, technology, teaching, culture, etc.

## Cross-References

- Appearance Reality Tests
- Theory of Mind

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## Unsolvable Task Paradigm

### ► Impossible Task Paradigm

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## Upsuck Hypothesis

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## Synonyms

Insuck; Orgasm; Sexual climax; Sperm competition; Sperm retention

## Definition

The transfer of content, specifically semen, from the upper vagina to the cervix by way of rapid muscular movements in an orgasm.

## Introduction

Evidence for orgasm in nonhuman animals has been the subject of research for many years. Many studies have shown that mammals do indeed have orgasms, though the physical and psychological mechanisms are less well understood. Orgasms in males are necessary for the ejaculation of semen into the vagina or cervix of females. However, underlying causes of orgasm in females have long been a mystery. The upsuck hypothesis suggests that the contractions of the cervix during female orgasm may aid in the transport of semen to the ovary in many species. Although still controversial, evidence is compounding that supports upsuck as a potential causal mechanism behind female orgasm.

## Internal Female Reproductive Organs

Though their structure and function vary by species, in placental mammals, internal female reproductive organs typically consist of ovaries, fallopian tubes, uterus, cervix, and vagina. This is true of viviparous animals. The ovaries are the site of egg, or ovum, development. The fallopian tubes, also called the oviducts, transport the egg into the uterus. The uterus, often called the womb, houses and nourishes a fetus until birth. The cervix divides the vagina from the uterus. In many species the cervix stores sperm and acts as a filtration system. The vagina is responsible for accepting semen. Many invertebrate species, such as *Drosophila*, possess specialized organs called tubular seminal receptacles or spermathecae, which makes sperm storage possible. This storage gives the animal the option of delaying fertilization, which can be beneficial for the animal and its offspring's survival and fitness

when resources or conditions are inadequate (Amitin and Pitnick 2007). Spermathecae are rarely seen in mammals (Schnakenberg et al. 2012). However, many mammals (e.g., domestic dogs and many bat species) can store sperm with the help of the lining of the reproductive tract (Orr and Zuk 2014).

## What Happens During an Orgasm

According to Fox and Fox (1971), there are specific criteria for an orgasm. These criteria are changes in blood pressure, breathing pattern, and heart rate, changes in muscular tension, hormonal changes, and the emission of sound. Before an orgasm, the heart rate will begin to rise, genitals begin to swell with blood, and muscle tension begins to build up throughout the body. During an orgasm, the muscles in the vagina, uterus, and anus contract and then relax. The brain releases substantial amounts of chemicals, including the neurotransmitter dopamine and oxytocin.

Oxytocin has been found to correlate with the female orgasm in humans (Blaicher et al. 1999). Wildt et al. (1998) discovered that after the release of oxytocin, material was sucked up into the fallopian tube. It is thought that uterine peristalsis, or involuntary muscle contractions, may be mediated by oxytocin, leading to upsuck movements that facilitate sperm retention and transportation and may increase chance of successful fertilization (King et al. 2016).

## Upsuck Hypothesis in Action

The upsuck hypothesis was first proposed by Fox and Fox (1971) as “insuck.” Since then, the upsuck hypothesis has been studied in animals as well as humans. However, experiments to understand orgasm have existed for nearly a century. Evans (1933) performed one of the first experiments using dogs as subjects. After 25–50 s of ejaculation, semen was expelled into the vagina in regular spurts through a fistula. Evans found that, once the female dog reached orgasm, semen

was forced 20–25 cm. Krehbiel and Carstens (1939) performed a similar experiment with rabbits. They used substances such as methylene blue, janus green, and iodochlorol to inject into the vagina of the rabbits and showed rapid transfer from the vagina to the uterus.

Increases in sperm motility due to female orgasm drastically improve the time it takes spermatozoa to travel into the uterus. Using cows, VanDemark and Moeller (1951) found a decrease in time of spermatozoa travel from an hour and a half to two to three minutes following orgasm. Some scientists believe that sperm retention is also influenced by occurrence and timing of the female orgasm. Early work by Hartman and Ball (1930) showed that the transfer of semen or spermatozoa in rats required 30–60 s after ejaculation for successful transfer from the vagina to the uterus. After 2 min, spermatozoa were found in the fallopian tubes.

Studies have long been performed in humans to determine the importance of timing regarding sperm retention. Greater retention of sperm was found when the female experienced orgasm between 1 min prior and 45 min following male ejaculation. Low retention was present when the female climaxed more than 1 min prior to male ejaculation (Baker and Bellis 1993).

## Conclusion

Development, neuroendocrine drivers, and other causal mechanisms of upsuck in animals and humans are topics that remain in need of further study. The upsuck hypothesis may play an important role in maximizing fitness in many species. This hypothesis has also helped explain the role of female orgasms in the reproductive process.

## Cross-References

- [Internal Fertilization](#)
- [Orgasm](#)
- [Oxytocin](#)
- [Sperm Competition](#)



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## Urodela

### ► Caudata Sensory Systems

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## Ursid

### ► Bear Navigation

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## Ursid Communication

### ► Bear Communication

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## Ursid Husbandry

### ► Bear Management

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## Ursid Locomotion

### ► Bear Locomotion

## Value Transfer Theory

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## Introduction

Value transfer theory (VTT), originally advanced by von Fersen et al. (1991) to account for transitive inference performance in nonhuman animals, proposes that some of the positive or excitatory value of an S+ in a simultaneous discrimination transfers to the S− with which it appears. To illustrate, suppose that two stimuli, A and B, are presented simultaneously to an animal and that responses to A are always reinforced, whereas responses to B are always nonreinforced. A is an S+ and B is an S− (Fig. 1a). According to VTT, associative value accrues to the S+ directly through reinforcement, whereas the S− does not acquire value directly, because responses to it are never reinforced; yet, the S− does acquire value indirectly through its presentation with the S+. In

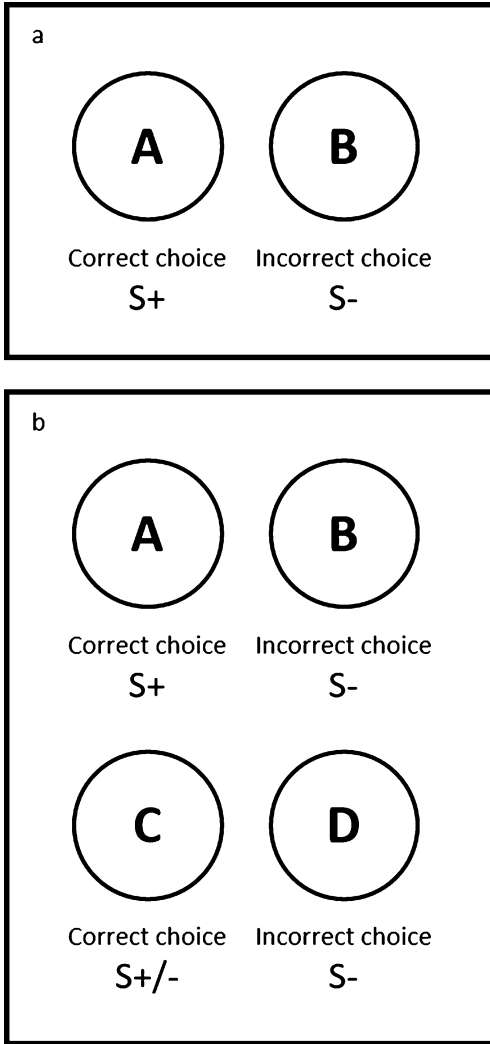
other words, some portion of the value of the S+ transfers to the S−.

Formally, the total associative value of any stimulus,  $i$ , participating in a simultaneous discrimination equals

$$V_i = R_i + \alpha \cdot V_{i+1}, 0 < \alpha < L \quad (1)$$

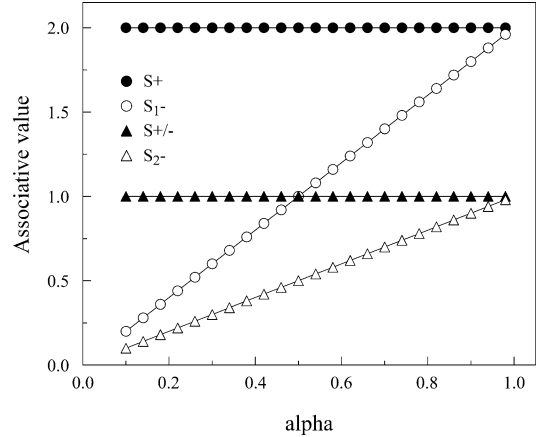
where  $R_i$  is the direct associative value conveyed by reinforcement to  $i$ ,  $V_{i+1}$  is the indirect value transferred to  $i$  from any S+ with which it is paired, and  $\alpha$  is a weighing factor that determines how much value is in fact transferred. The actual values of  $R_i$  and  $\alpha$  are to be determined empirically, but (a) the  $R_i$  values must be ordered according to the frequency or amount of reinforcement and (b)  $\alpha$  must lie between zero and an upper limit,  $L$ , ensuring that the associative value of a partially reinforced stimulus does not exceed that of a continuously reinforced. The attentive reader will notice that this is the equation of a line, with the total value of stimulus  $i$  increasing linearly with  $\alpha$ .

To illustrate, assume for simplicity that the direct value ( $R_i$ ) of a stimulus is either 2, 1, or 0, depending on whether the stimulus is always reinforced (S+), reinforced 50% of the time (S+/-), or never reinforced (S−), respectively. In the discrimination depicted in Fig. 1a (S+ vs. S−), the value of the S+ remains constant at 2, but the value of the S− approaches that of the S+ as  $\alpha$  increases. Logically, the value of the S− should remain below the value of the S+ and



**Value Transfer Theory, Fig. 1** Panel **a**: Schematic of a simultaneous discrimination. Two stimuli, A and B, are presented simultaneously. Choosing A is always reinforced (S+), whereas choosing B is never reinforced (S-). Panel **b**: Schematic of a task comprising two simultaneous discrimination. In one discrimination (A vs. B), choices of the correct option are always reinforced (S+), whereas in the other (C vs. D) choices of the correct option are reinforced only on half of the occasions (S+/-)

therefore  $L = 1$ , in this case (see Fig. 2, black vs. white circles). If the discrimination uses an S+/- instead of an S+ (i.e., S+/- vs. S-), then the value of the S+/- remains constant at 1 and the value of the S- approaches 1 as  $\alpha$  increases (see Fig. 2, black vs. white triangles).



**Value Transfer Theory, Fig. 2** Total associative value as a function of  $\alpha$  for an S+ and accompanying S- and for an S+/- and accompanying S-

### Evidence for VTT

Even though von Fersen et al. (1991) had no independent evidence for VTT when they initially proposed it, subsequent research has shown that it is a real phenomenon. Suppose that animals are trained concurrently on two simultaneous discriminations. One discrimination involves stimuli A and B with choices of A always reinforced and choices of B always nonreinforced, whereas the other discrimination involves stimuli C and D with choices of C reinforced half of the times and choices of D always nonreinforced (Fig. 1b). With these contingencies in place, A becomes an S+, C becomes an S+/-, and both B and D become S-. Using the same assumptions as before, the total associative values of A and C should equal 2 and 1, respectively, but in this case the associative values of the two S-, B and D, should differ. Because they are S- (i.e.,  $R_B = R_D = 0$ ) any associative value they may have must have been transferred from the positive stimulus with which they appear. Note, however, that B is presented with A, a stimulus with a total associative value of 2, whereas D is presented with C, a stimulus with a total value of 1. If  $\alpha$  remains constant across discriminations, then the value transferred to B should exceed the value transferred to D. In fact,

Fig. 2 illustrates this prediction. Comparing the white symbols, the figure shows that the value of an S− paired with an S+ (white circles) exceeds the value of an S− paired with an S+/- (white triangles), for all  $\alpha$ . Therefore, were we to assess preference between these two stimuli, we ought to find a strong preference for B. After training pigeons in this procedure (Fig. 1b), Zentall and Sherburne (1994) found a reliable preference for B over D, thus providing evidence for value transfer.

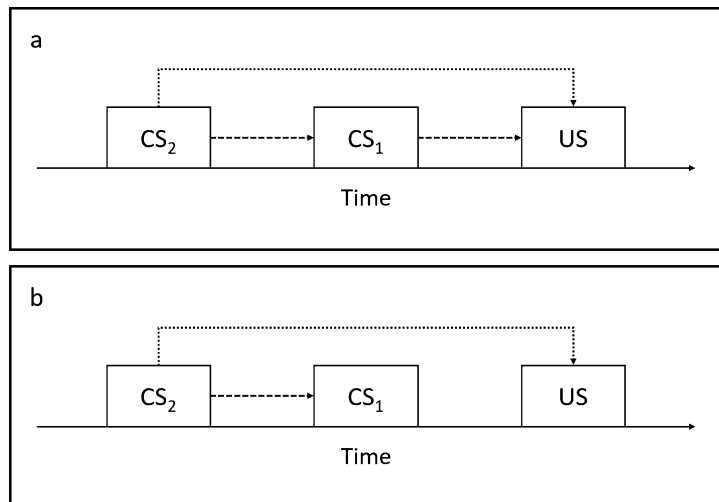
Subsequent research has shown that value transfer is not only reliable but also that its scope extends to multiple procedures and species. It has been shown that value transfers from the S+ to the S− when the frequency (e.g., Zentall and Sherburne 1994) and the magnitude of the reinforcer are manipulated (Siemann et al. 1996) and that it also operates when visual or odor stimuli are used (e.g., Kaiser and Means 2006; Zentall and Sherburne 1994). Importantly, even though most evidence comes from the discrete-trial simultaneous discrimination procedure, value also transfers in the free-operant version of this procedure, known as the concurrent-schedules procedure (Zentall et al. 1996b). Finally, value transfer has been found in at least three species: pigeons (e.g., Zentall and Sherburne 1994), rats (e.g., Kaiser and Means 2006), and humans (Lonon and Zentall 1999).

## Mechanisms of Value Transfer

The fact that two stimuli must be presented simultaneously for value to transfer suggests that the underpinning mechanisms are Pavlovian in nature. As animals learn to solve the discrimination, they typically observe the stimuli sequentially. Pigeons, for instance, tend to stand in front of one of the response keys prior to each trial. Consequently, on half of the trials, the S+ will be presented on that key and they will peck it. Yet, on the other half, the S− will appear on that same key and they will peck on the other key instead. Hence, on half of the trials, seeing the S− is followed, after a short delay, by the reinforcer (the time to move and peck the S+). This by itself can engender a Pavlovian relation between the S− and the reinforcer in two ways. One possibility is that the S− (the conditional stimulus, CS, in Pavlovian terminology) and the reinforcer (the unconditional stimulus, US) become directly associated through trace conditioning because the former is followed by the latter after a short delay. The other possibility is that the S+ mediates the association between the S− and the reinforcer; in other words, the mechanism involves second-order conditioning, for seeing the S− (CS<sub>2</sub>) is followed by seeing the S+ (CS<sub>1</sub>), which in turn signals the reinforcer (US). In either case, conditioned reinforcing properties (or value) should impart to the S−. Figure 3a illustrates these possibilities.

### Value Transfer Theory,

**Fig. 3** Panel a: Two possible mechanisms for value transfer. The dotted arrow represents direct conditioning between the S− (CS<sub>2</sub>) and the reinforcer (US). The dashed arrows represent second-order conditioning involving the S− (CS<sub>2</sub>), the S+ (CS<sub>1</sub>), and the reinforcer (US). Panel b: Devaluation test. By devaluing the mediator (the S+ or CS<sub>1</sub>), one can distinguish between the two purported mechanisms



One way to distinguish between the two hypotheses is to devalue the hypothesized intermediary in the second-order conditioning account. Suppose that the CS<sub>1</sub>-US association is extinguished via the repeated presentation of the S+ (CS<sub>1</sub>) with no ensuing reward. If the original training led to the direct association of the S− (CS<sub>2</sub>) with the reinforcer (US), then extinction of the CS<sub>1</sub>-US should not affect the conditioning value of the S− (CS<sub>2</sub>). If, on the other hand, the S− (CS<sub>2</sub>) becomes associated with the reinforcer (US) through its association with the S+ (CS<sub>1</sub>), then devaluing the latter should decrease the associative value of the former. Figure 3b illustrates these hypotheses.

Using the above-mentioned test, Zentall et al. (1996a) have shown that value transfer involves higher-order conditioning, not direct conditioning. The scenario is, however, more intricate because Zentall and colleagues also found that the association between the S− (CS<sub>2</sub>) and the S+ (CS<sub>1</sub>) is bidirectional. For instance, they observed that increasing the value of the S− (CS<sub>2</sub>) also enhances the value of the S+ (CS<sub>1</sub>), which suggests a form of within-event conditioning.

## Value Transfer and Contrast

von Fersen and colleagues (1991) proposed that positive value transfers from the S+ to the S− in simultaneous discriminations, but also admitted that negative value may transfer from the S− to the S+, leading to a decrease in the overall value of the S+. Subsequent research has shown that negative value does not transfer from the S− to the S+. Instead, if sufficient experience with the S− is allowed, the presence of the S− enhances the value of the S+ with which it is paired, a positive behavioral contrast effect.

Can we also find the opposite of positive value transfer from the S+ to the S−? The evidence suggests that value will transfer from the S+ to S− only when there is little experience

with the S− during training; if further experience with the S− is provided (e.g., via single-stimulus S− trials), negative contrast occurs. See Zentall and Clement (2001), for a review of value transfer and contrast effects in simultaneous discriminations.

In summary, in a simultaneous discrimination, positive value transfers from the S+ to the S−, but the S− seems to have little to no effect on the S+. Yet, if the consequences of responding to the S− are experienced repeatedly, each stimulus seems to counteract the value of the other. That is, positive and negative contrast occur.

## Conclusion

VTT was originally proposed to explain transitive inference in nonhuman animals. Even though it has since become apparent that transitive inference can arise in the absence of value transfer (for a review, see Vasconcelos 2008), value transfer has been found in a number of species and associated to a number of phenomena. These include, for example, the ambiguous-cue problem and other discrimination failures (e.g., Urcuioli 2006). Importantly, value transfer may also play a role in other apparently complex human phenomena such as the “basking in the reflected glory of others” or the “mere ownership effect.”

## Cross-References

- [Discrimination Learning](#)
- [Instrumental Learning](#)
- [Laboratory Research](#)
- [Learning](#)
- [Olfactory Discrimination](#)
- [Operant Chamber](#)
- [Operant Conditioning](#)
- [Pigeon \(\*Columbidae\*\)](#)
- [Positive Reinforcement](#)
- [Reinforcement](#)
- [Unconditioned Stimulus](#)
- [Visual Perception](#)



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## Variable Expressivity

- [Incomplete Penetrance](#)

## Variable Number Tandem Repeats

- [Simple Sequence Repeats](#)

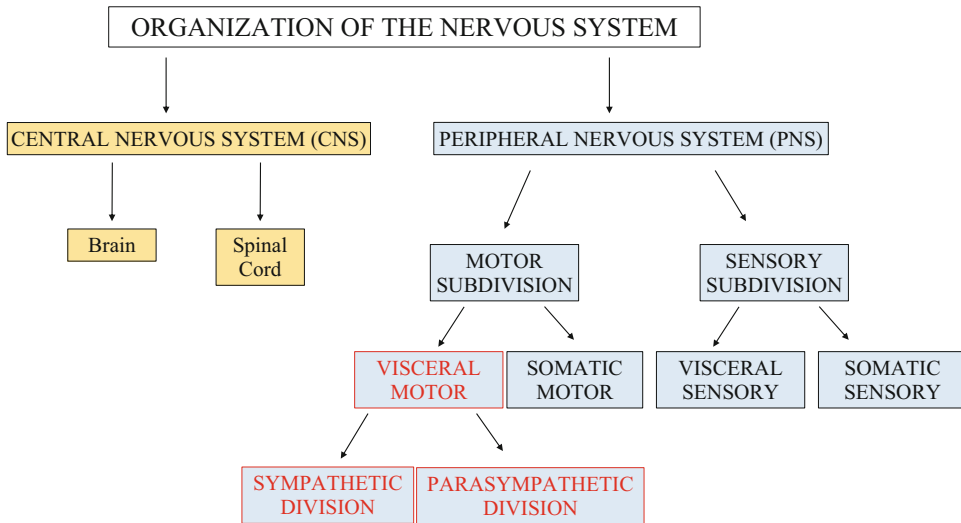
## Vasal-Vagal Stimulation

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## Overview of the Nervous System

The nervous system is the system of the body involved in detecting changes (stimuli) in the internal and external environments, evaluating stimuli, and issuing an appropriate response (Saladin 2017). The nervous system is divided into two major subdivisions: central and peripheral (Fig. 1). The central and peripheral nervous systems do not work in isolation of each other. Rather, the central nervous system and peripheral nervous system are structurally and functionally continuous with each other. The **central nervous system (CNS)** is comprised of the brain and spinal cord, and it is comprised of predominantly of interneurons. The **peripheral nervous system (PNS)** is comprised of nerves (bundles of axons of neurons) and ganglia (group of neurosomas). The PNS has two subdivisions: motor (efferent) and sensory (afferent). The **sensory subdivision of the PNS** carries sensory information to the CNS by way of sensory neurons. Organizationally, the sensory subdivision is further subdivided according to where sensory information originates. The **somatic sensory division** sends sensory information from the skin and skeletal muscle to the CNS. The **visceral sensory division** sends sensory information from organs (smooth muscle) and glands of the body to the CNS. The **motor subdivision of the PNS** carries motor information to effectors by way of motor neurons. Organizationally, the motor subdivision is further subdivided according to the structure innervated. The **somatic motor division** regulates contraction of skeletal muscle. The **visceral motor division** (or **autonomic nervous system**) regulates contraction of smooth muscle and controls gland function. The autonomic nervous system also has a strong modulatory effect on cardiac muscle



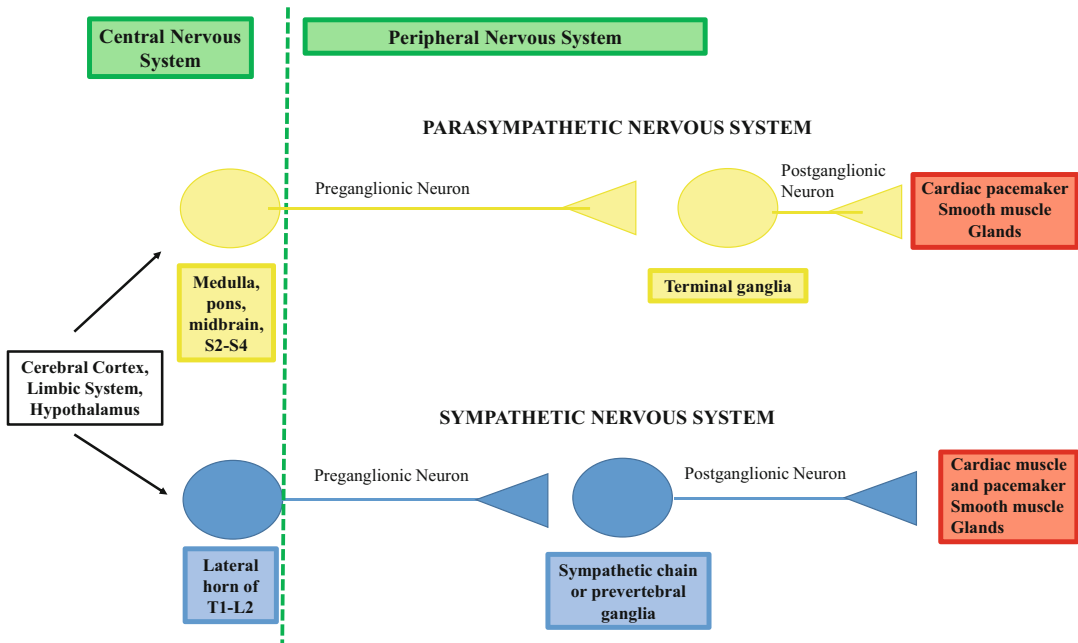
**Vasal-Vagal Stimulation, Fig. 1** Organization of the nervous system. An overview of the subdivisions of the nervous system is shown in this figure

function, through it is not responsible for initiating cardiac muscle contraction (Boron and Boulpaep 2012).

### Autonomic Nervous System

The autonomic nervous system has two anatomically distinct subdivisions, the sympathetic and parasympathetic divisions, which innervate organs, blood vessels, and glands of the body. Both divisions of the autonomic nervous system originate in the CNS and utilize a two-neuron chain (preganglionic and postganglionic neurons) to reach effectors (Fig. 2). The sympathetic nervous system (SNS) originates in the lateral horn of gray matter in the thoracolumbar spinal cord. Walter Cannon, American physiologist and physician, discovered that the SNS is responsible for initiating the sympatho-adrenal stress response (“fight-or-flight”) when an animal is exposed to an acute stressor (Hall 2016). Cannon published his findings in the 1915 book *Bodily Changes in Pain, Hunger, Fear and Rage*. During the sympatho-adrenal stress response, sympathetic nervous system fires at a high rate. Through the effects of epinephrine and norepinephrine, the SNS increases heart rate, stroke volume, blood pressure, and ventilation;

triggers sweating; mobilizes glucose stores to raise blood glucose; decreases gastrointestinal motility; and triggers pupil dilation. These physiological responses to an acute stressor enhance an animal’s ability to fight or flee while facing a physical threat. A common misconception among students is that the SNS is only active during fight-or-flight. During rest, the SNS outflow is low, but basal sympathetic activity is critical for maintaining vascular tone (Saladin 2017). Sympathetic activity constricts arteries and raises vascular resistance. An increase in vascular resistance leads to increased arterial pressure. Thus, the sympathetic division has an important role in maintaining systemic blood pressure and adequate perfusion to organs, even during rest. The parasympathetic division originates in the brainstem and sacral spinal cord. It carries out “rest-and-digest” or “breed-and-feed” functions of the body. During rest-and-digest, the parasympathetic division utilizes acetylcholine to decrease heart rate, increase urine production, trigger pupillary constriction, and cause salivation in response to food stimuli. It has little impact on vasomotion of blood vessels with the exception of those supplying salivary and gastrointestinal glands and reproductive tissues. Much of the parasympathetic innervation of organs and blood vessels in the thoracic and abdominal cavities is



**Vasal-Vagal Stimulation, Fig. 2** Visceral motor innervation schematic. Both divisions of the autonomic nervous system innervate effectors by way of a two-neuron chain

provided by cranial nerve X, the vagus nerve (Boron and Boulpaep 2012).

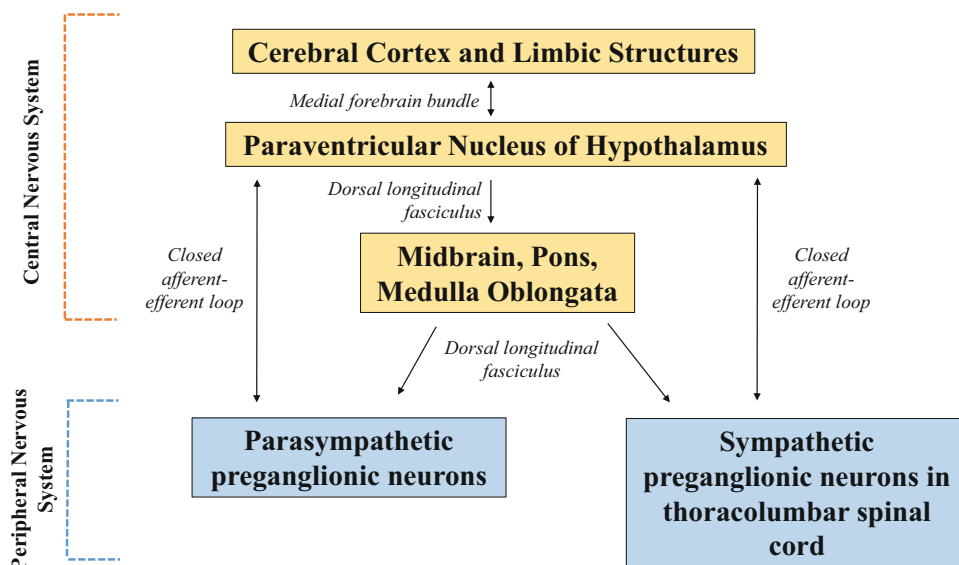
## Central Control of Autonomic Function

Both divisions of the autonomic nervous system are regulated by structures of the CNS. The cerebral cortex is involved in higher brain functions and emotions. The cerebral cortex is known to have extensive neural connections with the hypothalamus' paraventricular nucleus (PVN). The paraventricular nucleus (PVN) of the hypothalamus exerts great influence over autonomic function; it contains a closed sensory-motor loop with both parasympathetic and sympathetic structures providing direct CNS influence over autonomic function. The PVN receives input from higher brain centers, such as the amygdala and hippocampus. The medial forebrain bundle (MFB) serves as the primary tract for information relay from limbic structures to the hypothalamus. The amygdala and hippocampus send inputs to the hypothalamus by way of the ventral

amygdalofugal pathway, fornix, and stria terminalis. The axons eventually join the MFB, supplying input to the PVN. Parvocellular neurons within the PVN also have axons that run to the dorsal motor nucleus of the vagus nerve, the rostral ventrolateral medulla, and intermediolateral column in the spinal cord. The axons of these neurons are part of the dorsal longitudinal fasciculus (DLF), a white fiber tract which begins in the paraventricular nucleus and terminates in autonomic control areas of the brainstem and spinal cord. The DLF also contains afferent neurons that allow for visceral afferent signals to be relayed to the hypothalamus (Llewellyn-Smith and Verberne 2011). A simplified schematic of central autonomic control is provided in (Fig. 3); the circuitry of central autonomic control is extensively covered in *Netter's Atlas of Neuroscience*.

## Vaso-Vagal Response

The vaso-vagal response (or reflex) is characterized by arterial vasodilation ("vaso") and hyper activity



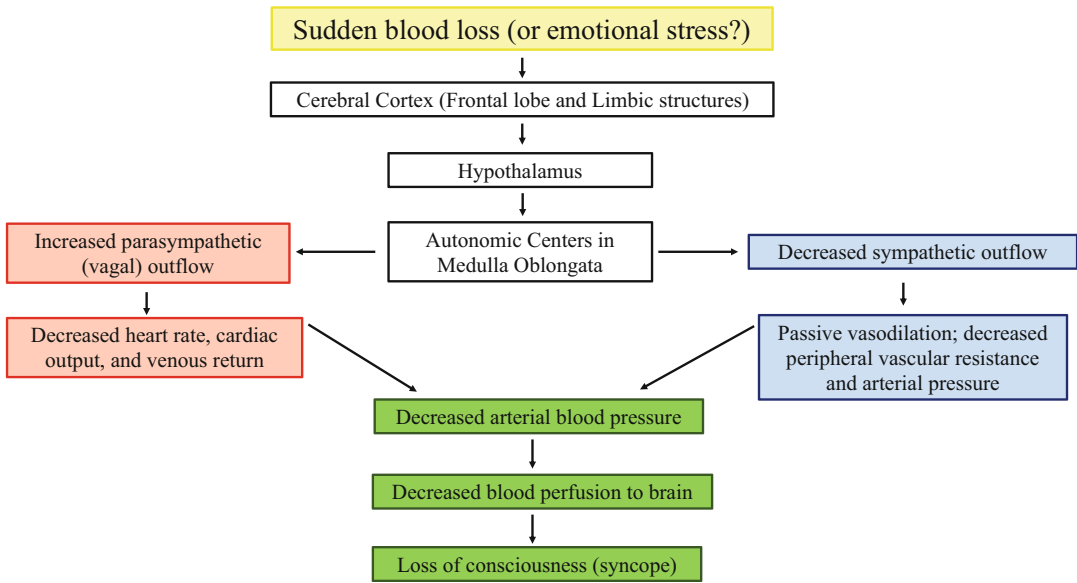
**Vasal-Vagal Stimulation, Fig. 3** Major circuits of central autonomic networks. A simplified schematic of central autonomic networks is shown in this figure

of the vagus nerve leading to attenuation of cardiac activity (“vagal”). It is often accompanied by hypotension and bradycardia. In humans, the vaso-vagal reflex can cause a loss of consciousness due to decreased perfusion to the brain (van Lieshout et al. 1991). Loss of consciousness in such instances is referred to as vasovagal syncope (VVS). Vasovagal syncope can occur due to sudden blood loss, emotional stress, or painful stimuli. The precise mechanism of vasovagal syncope is not known. However, VVS is initiated when afferent pathways associated with the vagus nerve signal to higher CNS centers and autonomic nuclei in the brainstem to strongly stimulate the parasympathetic nervous system and eliminate sympathetic vascular tone (Boron and Boulpaep 2012) (Hall 2016). Little is known about the afferent pathway (the step from trigger to autonomic integration and central processing). However, the efferent pathways are well-established. During VVS, vagal outflow is increased, while sympathetic outflow is decreased. The decrease in basal sympathetic firing leads to passive vasodilation. As vagal firing increases, an abundance of acetylcholine is released onto the heart’s pacemaker (see “ECG/EKG” entry), decreasing heart rate (bradycardia). The decrease in heart rate reduces cardiac output (amount of blood pumped by heart in 1 min) and arterial

pressure. The drop in arterial pressure decreases perfusion of blood to the brain, causing a loss of consciousness or fainting (Fig. 4) (Boron and Boulpaep 2012). Fainting causes the body to assume a gravitationally neutral position, thereby offering a better chance of restoring brain perfusion (Blanc et al. 2015).

### Vaso-Vagal Reflex: A Survival Mechanism?

Vaso-vagal reflexes are often treated as pathological conditions. The pathophysiology has been studied, and therapies have been developed for treatment of VVS. Yet, the broader field of VVS research supports the idea that the vaso-vagal reflex is a biological phenomenon largely triggered (even in healthy individuals) by a specific set of circulatory conditions, such as excessive blood pooling and changes in body position. In specific instances, it may confer a survival advantage to a mammal. Several hypotheses have been developed to explain the evolution of vaso-vagal syncope in humans. One such hypothesis is particularly compelling: the clot production hypothesis. The clot production hypothesis states that the vaso-vagal reflex, by triggering bradycardia and lowering



**Vasal-Vagal Stimulation, Fig. 4** Vasovagal reflex. The information relay involved in a vaso-vagal reflex leading to syncope is shown in this figure

blood pressure, acts to limit blood loss during hemorrhage and is important in hemostasis (Diehl 2005; Levi 2005). There are several key pieces of evidence to support this hypothesis. Most instances of VVS occur in response to blood loss. Additionally, clotting factors von Willebrand factor and factor VIII are elevated following incidents of VVS that occurred during venipuncture (Casonato et al. 2003). In this context, VVS is likely acting as a protective mechanism to counteract hypovolemia during hemorrhage, thus improving odds of survival. Additionally, hemorrhagic shock animal models have been extensively utilized to elucidate the mechanism of vaso-vagal reflex (Schadt and Ludbrook 1991), as the vaso-vagal reflex can be reliably triggered in these animals. Emotion-induced vaso-vagal syncope is an interesting occurrence. Emotional disturbances originating in the cerebral cortex are relayed to the anterior hypothalamus (near hypothalamic autonomic control nuclei) and subsequently on to the medulla. Autonomic control centers in the medulla strongly activate the vagus nerve; the vagus nerve then evokes the cardioinhibitory effects discussed above. The signal also travels to sympathetic control centers and elicits sympathetic-mediated vasodilation by way of sympathetic nerves (Hall 2016). Further

studies are needed to completely elucidate the afferent pathways of emotion-induced syncope.

## Cross-References

- Circulatory System
- Hypothalamus
- Medulla Oblongata
- Nerve Cells
- Nervous System
- Neuron
- Neurotransmitters

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## Ventral Stream

### ► Top-Down Processing

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## Vergence Eye Movements

### ► Cognition

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## Vertebrate Nervous System

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## Synonyms

Brain; Central nervous system; Nervous system

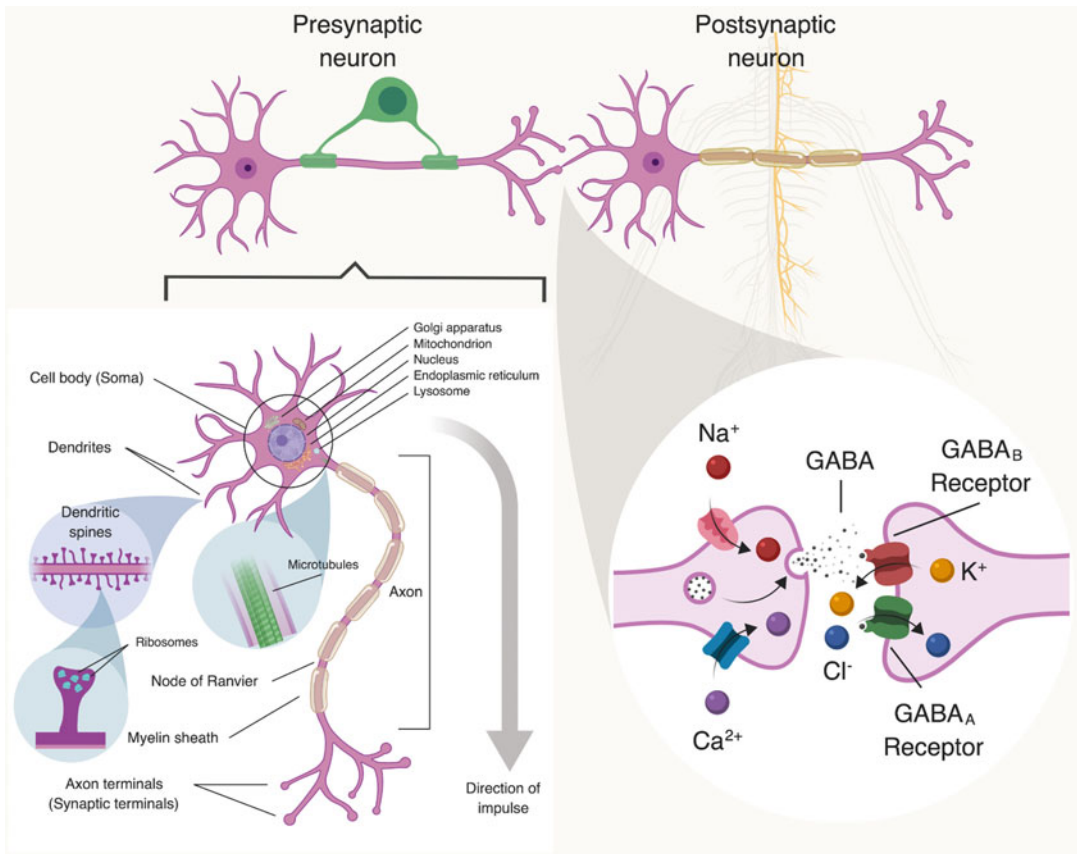
## Introduction

Vertebrates are a group of animals that appeared about 525 million years ago during the Cambrian period. Setting this group apart is an anatomical structure called the *vertebral column*, or *spine*. It is common to fish, amphibians, reptiles, birds, and mammals. Animals belonging to these groups are in the subphylum *Vertebrata* of phylum *Chordata*. Vertebrates have another unique anatomical structure called the *skull* or *cranium* toward the anterior end of the body that contains the animal brain. Hence, *Craniata* is another name for the *Vertebrata* subphylum. The structure of the skull can vary and, in early evolved vertebrates, such as lampreys and hagfish, does not include a jaw. The first jawed vertebrates emerged in the late Ordovician period but became common in the “Age of Fishes” (i.e., the Devonian period). Later vertebrate species were land animals (tetrapods). There are vertebrate species, like hagfish, which diverged early on during evolution, that retain only rudimentary vertebra instead of a continuous vertebral column.

The vertebral column is derived both embryonically and evolutionarily from a rod-like structure made up of cartilage-like material called *notochord* – a characteristic feature of all chordate animals at some point in their life span. The vertebral column supports and protects a hollow tube of nervous tissue called *spinal cord*.

## Fundamental Units of the Nervous System

The nervous system (NS) is an organized collection of two types of cells – *neurons* and *neuroglia* (or *glia*). Neurons are electrically excitable cells that can quickly transmit signals due to their three structurally unusual parts: *dendrite*, *cell body* (or *soma*), and *axon* (Fig. 1). Dendrites are fibrous projections from the cell body, which receive signals from other cells and transmit it toward the cell body, which processes the signal. The axon is a long fiber often branched at the distal end. The terminal end of each branch has a bulb-like structure called synaptic knob, which may contain synaptic vesicles filled with chemicals called



**Vertebrate Nervous System, Fig. 1** A schematic of neuron structure and signal transmission between neurons. Upper panel: Synaptic connection between two neurons. The presynaptic neuron is the one which releases neurotransmitters as a result of an action potential entering its axon terminal. The postsynaptic neuron builds up a new action potential in response to binding excitatory neurotransmitters. In the left lower part, the general structure of neuron is depicted. The dendrites receive internal or external signals and pass them to the cell body. The axon, a cylindrical process, transports signals from the cell body to the axon terminals and releases neurotransmitters into the

synaptic cleft to pass on to other cells. Each dendrite contains spines which increase the contact surface in order to form synaptic contacts. An axon can travel a few hundred micrometers or much further. For example, neurons in the spinal cord have very long axon projections, while they are very short in neurons that are part of local circuits in the brain. The branched end is broadened to form synaptic buttons or terminals. These participate in the communication either through electrical activity or through neurotransmitters. In the right lower part, an inhibitory synapse is exemplified

*neurotransmitters*. The axon facilitates antero-grade signal transmission from the cell body toward a site called the *synapse* or to a neuromuscular junction (Golgi 1906; Ramon and Cajal 1906). The synapse is the region formed between the membranes of a pre- and postsynaptic neuron, which may or may not be separated by a fluid-filled small space called the *synaptic cleft* (Fig. 1).

Neurons often communicate chemically through neurotransmitters by forming chemical synapses (Dale et al. 1936). Neurotransmitters

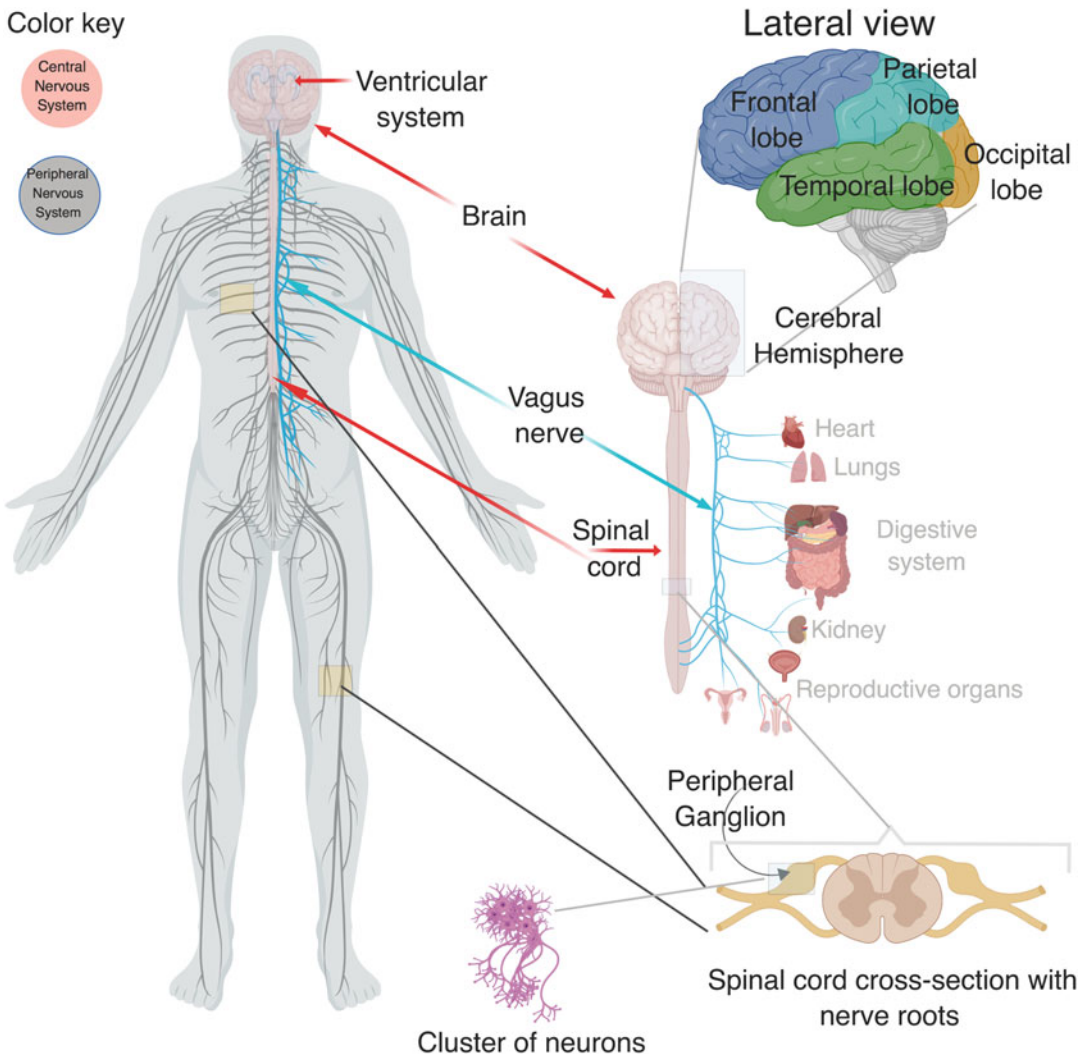
released by a presynaptic neuron diffuse through the synaptic cleft and bind to their specific receptors on the membrane of the postsynaptic neuron, thus passing on the signal (Fig. 1). Neurons may also communicate with each other directly through an electric synapse when they are too close to each other leaving no room for synaptic cleft formation. In this case, neurons electrically excite other cells by changes of their membrane potential elicited by the passage of ions and small molecules through the specialized proteins

linking their membranes at synapse (Hodgkin et al. 1952).

In contrast to neurons, glial cells are electrically unexcitable and are involved in nourishment, support, and maintenance of neurons. They form sheath-like processes of myelin around neurons to insulate signal transmission. Hence, they can modulate signal transmission executed by neurons. Glial cells also act as immune cells to protect neurons (Hickey and Kimura 1988).

## Anatomical Divisions of the Nervous System

The NS consists of two anatomical subdivisions: the central nervous system (CNS) and the peripheral nervous system (PNS) (Fig. 2). The CNS comprises the brain and the spinal cord, whereas the PNS is formed by ganglia and nerves. A cluster of neuronal cell bodies within the CNS is called a *nucleus*, while a cluster outside the



**Vertebrate Nervous System, Fig. 2** The organization of the nervous system and its parts in the human body. The central nervous system is composed of the brain and spinal cord (pink). The brain is anatomically organized into the

frontal, temporal, parietal, and occipital lobes. The peripheral nervous system (gray) is formed by spinal nerves that arise from the peripheral ganglia (cluster of neurons) for the innervation of different organs

CNS is called a *ganglion*. The nerve can be thought of as a collection of multiple fibers running through the animal body. Each fiber is a bundle of axons projecting from the cell bodies of neurons located in nuclei and ganglia that are located in the brain and spinal cord.

### Peripheral Nervous System

The PNS is organized as a set of ganglia and nerves and comprises any nervous tissue outside the CNS. Nerves form several branches that innervate every part of the body (Fig. 2). Nerves are classified as sensory, motor, or mixed nerves if they contain axons both from sensory and motor neurons or based on the signal transmission toward or away from the brain. The afferent nerves are projected from the sensory neurons (afferent), which receive input from sensory organs, such as the ears, eyes, nose, tongue, and skin, and pass the signal to the CNS, where it gets processed to elicit the appropriate sensation. The efferent nerves transmit signals from the CNS to motor neurons (efferent) for putting the organs and muscles into action such as contracting the skeletal muscles to execute voluntary movements of the arms (Sherrington 1906). The PNS is further subdivided into two parts: the somatic and the autonomic. The somatic NS consists of the nerves that branch out from the cell bodies of somatic sensory neurons located in the dorsal root ganglia of the spinal cord and innervate the skin, joints, and muscles. It regulates the movement of skeletal muscles. The autonomic NS contains nerves that innervate the internal organs, blood vessels, and glands. It controls involuntary actions such as heart rate, digestion, and perspiration.

### Central Nervous System

The CNS comprises the brain and spinal cord. In addition to the skull and the vertebral column, the CNS components are protected by a three-layered system of membranes called meninges. At tissue level, the CNS is divided into areas of gray and white matter. Gray matter contains a high proportion of neuronal cell bodies and their dendrites, glial cells, and capillaries. Gray matter is mainly clusters of neurons in the brain and spinal cord and in outer layers that line their surfaces. White

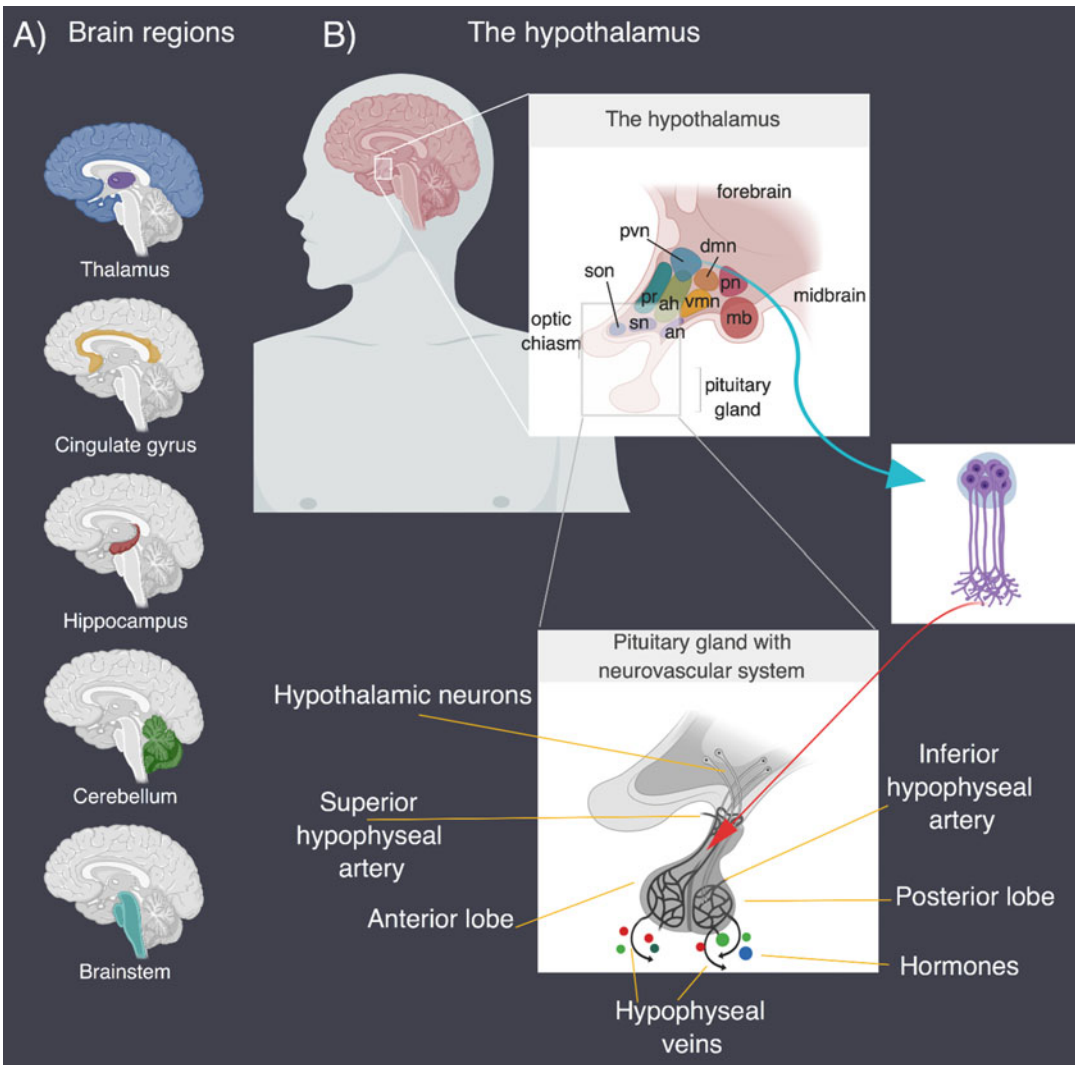
matter is mainly myelinated axons and appears white due to the myelin sheath.

The overall organization of the CNS is fairly similar among vertebrates. However, differences can be observed in some species for adaption to certain environmental settings. The spinal cord maintains its cylindrical shape in all vertebrates. The sensory information is received through the dorsal part of the spinal cord, while motor information leaves through the ventral part (Hawkins 1869). The number of nerves emerging from the spinal cord varies in different vertebrate species, from 31 pairs in humans to about 400 in snakes. Some animals have wide space between spinal segments, which correlates with an increased number of motor neurons (projecting from the space) that innervate the muscles of the limbs.

The brain controls all the processes carried out in the CNS and has three anatomical subdivisions: prosencephalon (forebrain), mesencephalon (midbrain), and rhombencephalon (hindbrain). The forebrain is a frontal part of the brain, which is covered with a large, wrinkly, outermost layer of the brain – the cerebral cortex (Fig. 3a). It consists of a left and right hemisphere, each of which is further divided into four major lobes: frontal, parietal, temporal, and occipital lobes (Fig. 2). There is another portion of the cerebral cortex folded deep within the fissure separating the temporal lobe from the parietal and frontal lobes. It is often included as a lobe called *insular* and, in humans, is believed to be involved in consciousness. These lobes together constitute the largest site of neural integration in the CNS and play key roles in memory, attention, perception, awareness, thought, and language.

The cerebral hemispheres have a great morphological diversity among different vertebrates. The cerebral cortex can be highly developed as seen in primates, or it can be underdeveloped as in lampreys, hedgehogs, or opossums. More developed cortices are folded in several places to increase the area of cortex that can fit inside the cranial cavity.

In spite of slight structural differences, the functions performed by cerebral cortex are fairly similar among vertebrates. For example, the hypothalamus is important for the physiological homeostasis in the body through the integration of



**Vertebrate Nervous System, Fig. 3** An overview of major anatomical structures of the nervous system. (a) In the brain, different anatomical structures exist with specific functions. One of these structures is the hypothalamus (b) which has ten major nuclei containing the cell bodies of the neurons of the hypothalamus. Their axons innervate the pituitary gland located below the hypothalamus, forming the hypothalamus-pituitary communication system. The

nuclei process information and axons communicate with the pituitary gland, which in response secretes specific hormones into the bloodstream where they travel to their site of action. The hypothalamic nuclei are labeled as follows: preoptic (pr), supraoptic (son), paraventricular (pvn), anterior (Ah), suprachiasmatic (sn), dorsomedial (dm), ventromedial (vm), arcuate (an), mammillary (mb), posterior (pn), hypothalamic nucleus

visceral (gut, glands, and inner organs) and somatic (the skin, joints, and muscles) information for the correct adjustment of the internal environment (Fig. 3b). The ventral thalamus establishes connections with the basal ganglia important for the motor behavior, and the dorsal thalamus is a relay site of different sensory pathways that connect with the cerebral cortex.

The midbrain is a vital connection point between the forebrain and the hindbrain. It is the topmost part of the brainstem, which connects the brain to the spinal cord. The upper portion of the midbrain has two principal pairs of nuclei called the superior and inferior colliculi. The superior nucleus processes visual signals before they are passed on to the occipital lobe. The inferior



nucleus processes auditory signals before they are passed through the thalamus to the main auditory processing center in the cortex.

The hindbrain is the lowest portion of the brain, containing the rest of the brainstem made up of the medulla oblongata, pons, and cerebellum. The medulla oblongata contains cardiorespiratory centers that can increase or decrease the cardiac and respiratory rates depending on the physiological needs. The pons is responsible for conducting signals from the brain down to the cerebellum and medulla and has tracts that carry the sensory signals up into the thalamus. The cerebellum is a small ball of dense brain tissue nestled right against the back of the brainstem. It is responsible for movement-related functions.

The anatomical disposition of the NS allows the dedication of different parts toward specialized functions. The terminals of axons projected from the cell bodies located in peripheral ganglia often innervate the body surface and visceral elements, where they form sensory receptors, which sense external stimuli. For example, touch sensations are processed by a type of mechanoreceptors called *Meissner's corpuscles* that are especially concentrated at the surface of sensitive areas such as fingers and lips. When fingers touch an object, these receptors sense the signal and send it to specialized centers in the brain, such as the hypothalamus, via the spinal cord. The spinal cord or the brain processes the signal and generates response such as the removal of fingers. The NS registers the responses against internal and external stimulus and improves them based on experiences.

### Anatomical Differences Between Vertebrate Species

The brain is further subdivided, anatomically and functionally, in slightly different ways among different vertebrate groups. The forebrain is well developed and subdivided in most tetrapods, but in many fish and some salamanders, the midbrain dominates. The embryonic vesicles that form the forebrain are usually paired and give rise to two hemispheres, like the cerebral hemispheres in mammals. The hindbrain is located anteriorly to the spinal cord and differs anatomically in various

vertebrate species. For example, the vagal lobe of the hindbrain is highly developed in fish and responsible for integrating the information from peripheral taste receptors located on the outer surface and the palate of the fish (Herrick 2005). However, mammalian counterpart is rather superficial compared to the highly developed lobe in fish. In mammals, the rostral portion of the solitary tract nucleus is homologous to the vagal lobe. Some vertebrates, such as the torpedo fish, have electric lobes in the hindbrain that innervate the electrical organ which produces an electric discharge to stun prey or for defense. The midbrain has well-developed optic lobe in birds, frogs, and other species that live in bright environments. Species that live in dark environments or have rudimentary eyes, such as lamprey, tend to have poorly developed optic lobes in their midbrains. In some vertebrates such as bats and whales, the inferior colliculus is enlarged for the highly efficient translation of sound waves. Olfactory bulbs in the forebrain are very well developed in vertebrates such as lampreys and rodents but only poorly in primates (Allison 1953).

### Embryonic Development of the Nervous System

The embryonic development of the NS is highly similar among vertebrates and proceeds through the neuralization and cephalization in three steps. First, the differentiation of the chordamesoderm (notochord) from the surrounding mesoderm begins, which provides signals for the patterning of an overlying neural tube. The notochord further provides a physical support to the developing vertebral column and NS. In the second step, the neural tube differentiates into an anterior and a posterior part. The anterior part develops into the three primary brain vesicles, forebrain, midbrain, and hindbrain, while the posterior part develops into the spinal cord. A set of specific signaling molecules and transcription factors called morphogens and neural determinants decides the regionalization and order in which parts of NS develop. In the third step, cephalization occurs when the neural epithelium gives rise to neural crest cells, and the ectoderm immediately adjacent

to the neural tube differentiates into localized regions of columnar epithelium cells called the epidermal placodes. The neural crest and placodes subsequently contribute to the vertebrate head development including the skull, connective tissue, cranial nerve, and sensory organs. The third step distinguishes vertebrates from all other animals. The resulting anatomy with a single hollow nerve cord topped by a series of cerebral vesicles is unique to vertebrates, while invertebrates have a ventral rather than dorsal system of ganglions.

## Closing Remarks

The NS is fairly similar in vertebrates with subtle differences in specialized structures and their functions. These specialized structures are present in animals that are adapted to specific environmental settings, which indicate that the ecological niche of animals has played a crucial role in shaping the evolution of nervous system. However, the basic cellular configuration is very similar in all these animals, as is the principle of neuronal communication through electric and chemical synapses.

## Cross-References

- [Nervous System of Invertebrates](#)
- [Nervous System, The](#)
- [Neuron](#)
- [Neurotransmitters](#)

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## Vertebrate Skeleton

- [Skeletal System](#)

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## Vertebrates (Chordata)

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## Introduction

With almost 70,000 recognized extant species, chordates form one of the most diverse of the classic animal phyla, behind only arthropods and mollusks. Vertebrates correspond to almost the entire diversity of Chordata, and are ecologically important mainly because of their large body sizes (although absolute numbers of biomass

belong to small-bodied animal groups), representing most of the top predators of food webs. Even though a collection and fossilization bias may be at play, favoring animals with hard tissues from aquatic environments, vertebrates also comprise a significant part of the fossil record.

Throughout their evolutionary history, vertebrates displayed a variety of locomotor modes and occupied a plethora of environments and ecological niches, including land, air, and secondary returns to aquatic environments. Feeding habits and mechanics, like herbivory (► [Herbivore](#)) and mastication, and reproductive and ontogenetic strategies, such as internal fertilization or larval development, are also extremely diverse and very important for their success.

Vertebrates are traditionally divided into five classes: fishes, amphibians, mammals, reptiles, and birds. This division reflects a pre-cladistic classification and two of them do not correspond to natural, or ► [monophyletic](#), groupings. What are usually referred to as “fishes” and “reptiles” represent paraphyletic groups under our current understanding of vertebrate evolution. However, since the use of such names is a paradigm that has yet to be overcome in the earlier stages of the educational system, this entry roughly uses the classic nomenclature, while presenting one more attempt in the process of overcoming the use of said names. Nevertheless, terms such as class and order were avoided, given they bear little to no phylogenetic significance.

Groups in these classical divisions display similarities that make them easy to distinguish from each other. This entry covers some key characteristic features, or synapomorphies, to identify these groups, but it should be kept in mind that they are mostly valid when considering extant groups only. Adding extinct lineages make these distinctions blurry because key features may either appear in different clades rather independently, or are complex characters that can be decomposed in simpler steps with their own tempo and mode – such as “flight.” Some characters may also refer to soft-tissue structures or ecological or physiological strategies that are difficult, if not impossible, to track in the fossil record, such as

mammary glands. This entry aims to provide an overview of when key features appeared or became established in different vertebrate groups, pointing to some evolutionary trends in these lineages.

## Vertebrate Relationship with Other Chordates

Despite Chordata not being the most diverse animal phylum, part of the interest in this group derives from the fact that humans belong to it. Extant chordates include, besides vertebrates, two other groups: Urochordata (tunicates) and Cephalochordata (lancelets). With advances in phylogenetic methods and new sources of data, like molecular and genomic, hypotheses of relationship between these three groups, as well as their relationship to other deuterostomes, were considerably debated in recent years. Despite this debate, the monophyly of extant chordates is corroborated by both molecular and morphological data. Morphological synapomorphies include the body stiffened by a notochord, a hollow dorsal nerve cord, a mucus-secreting gland named endostyle (considered homologous (► [Homology](#)) to the thyroid gland), a post-anal tail, and body musculature divided into chevron-shaped myomeres.

## What Makes a Vertebrate

The definition of Vertebrata is thoroughly discussed in the literature, and vertebrates are mainly recognized by the presence of a vertebral column and a specialized head. The vertebral column, which inspired the name of the group, is composed of several juxtaposed bony or cartilaginous skeletal blocks, the vertebrae. It covers or replaces the notochord, defines the major body axis, and participates in body support and movement.

The vertebrate head is recognized as a major evolutionary innovation, with several structures derived from neural crest cells and ectodermal placodes. The neural crest is derived from the embryonic ectoderm and participates in the

formation of the skull, gill arches, jaws (in jawed vertebrates), peripheral nervous system, among others. Ectodermal placodes are thickened regions in the body surface that, through interaction with the neural tube ectoderm, are involved in the formation of sensory organs, such as the olfactory, optic, and otic capsules and the lateral-line system. Although the neural crest and ectodermal placodes hardly fossilize, the presence of structures derived from these tissues in fossils help identify them as vertebrates.

Questions on how a megadiverse group such as vertebrates arose are quite frequent. One finding that brought important insights into this question regards gene duplication. Many vertebrate innovations are related to head structures: sensory and cranial ganglia, three paired special sense organs and their capsules, and gill arches. These are, in turn, associated to duplications in some regulatory genes (e.g., Homeobox genes ([► Homeobox Gene](#))) that probably occurred in the most recent common ancestor of all vertebrates. These regulatory genes control the segmentation and fundamental orientation of the body, and it is hypothesized that duplications of such genes, followed by divergence of one or both daughter genes, may underlie major evolutionary changes by allowing subsequent phenotypic change (Holland et al. 1994).

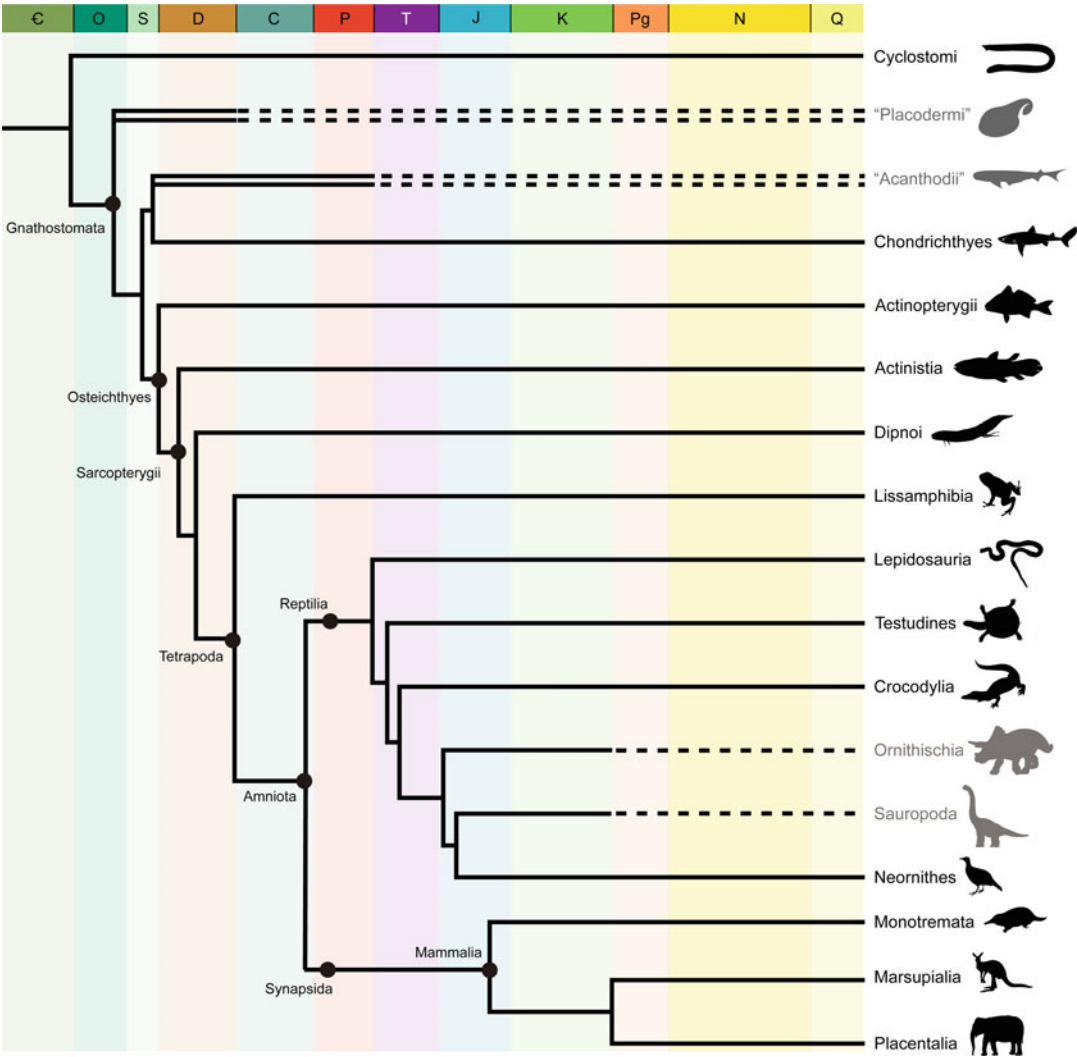
Therefore, significant genome changes affecting entire gene families, such as those observed in vertebrate genomes, correlate with significant changes in body organization. In this scenario, new genes are recruited for new roles after duplication (a process named exaptation), culminating in innovations in developmental trajectories (e.g., the involvement of neural crest and neural placodes in craniofacial morphogenesis, cephalization of the brain, and specialization of the segmented mesoderm), originating new structures that allowed rapid adaptive radiation (Holland et al. 1994). A second regulatory gene duplication probably occurred in the origin of gnathostomes (see below), in association with the appearance of several jaw-related structures, allowing another major adaptive radiation within vertebrates (Kuratani et al. 2016).

## The First Vertebrates and the Cyclostomes

Relationships among major vertebrates groups are shown in Fig. 1. Vertebrata is the group formed by the most recent common ancestor between lampreys and gnathostomes, and all its descendants. The group probably arose at the Cambrian (Fig. 1), and several related fossil taxa are of difficult placement in early vertebrate evolution. This may be due to the potential loss of apomorphic characters through fossil decay, resulting in a bias towards mistakenly placing fossils on the chordate stem. Among lineages with living representatives, the first one to diverge is the one that includes hagfishes and lampreys.

Hagfishes and lampreys are the only extant agnathans. The name “agnatha” refers to a paraphyletic assemblage of vertebrates including cyclostomes as well as several fossil lineages whose phylogenetic placement is controversial. “Agnatha” means “jawless,” and indeed these early vertebrates do not have jaws, a key morphological innovation that characterizes the clade that includes all the remaining vertebrates. Traditional morphological analyses and paleontological data usually recover a clade named **Craniata**, formed by hagfishes as the sister group of lampreys plus the remaining vertebrates, with the last two forming **Vertebrata**, while molecular analyses recover hagfishes and lampreys as sister groups instead, forming a clade termed Cyclostomi (Figs. 1 and 2), in which case Craniata and Vertebrata would be synonyms. This is still an ongoing debate, but the most recent inclusive analyses corroborates the cyclostome hypothesis.

**Myxinoidea** is formed by 82 extant species known as hagfishes. This clade originated in the Carboniferous and includes long-bodied, mud-burrowing scavengers, but also some filter-feeding and detritivore species. They use teeth-like keratinous structures to scrape flesh from their prey or to reel in worms that are filtered by the branchial basket. Their head region includes four pairs of tentacles surrounding the mouth and a single nasohypophyseal opening. The hagfish skeleton consists of the notochord and of cartilaginous structures forming an incomplete braincase,



**Vertebrates (Chordata), Fig. 1** Cladogram with the phylogenetic relationships of the major groups of Vertebrata, calibrated for geological periods. Groups with exclusively fossil representatives are shown in gray. Some clades are named at the nodes. Terminal names between quotation marks correspond to non-monophyletic groups,

which also are represented in phylogeny by doubled lines. Dashed lines correspond to period after group extinction. C: Cambrian; O: Ordovician; S: Silurian; D: Devonian; C: Carboniferous; P: Permian; T: Triassic; J: Jurassic; K: Cretaceous; Pg: Paleogene; N: Neogene; Q: Quaternary

elements supporting the branchial basket, and specialized mouth parts. Hagfishes also have prominent glands that produce a mucous secretion used for defense. Some hagfishes are sequential hermaphrodites, having male and female gonads, but only one of them is functional at a time.

**Petromyzontiformes** is formed by 47 extant species known as lampreys. The oldest records of the group date from the Devonian. Their body is

also elongated, but unlike hagfishes, at least half of the lamprey species are parasites, the blood of their hosts to which they adhere via their ovoid sucking mouth, which can also be used to hold onto rocks in a stream current. The mouth is supported by cartilage, and their cartilaginous skeleton includes a braincase, elements supporting the branchial basket, and rudimentary vertebrae. Marine lampreys are anadromous,



meaning that adults live in marine, salty or brackish waters, but return to freshwater to reproduce. The larvae, called ammocoetes, are suspension-feeders, but suffer metamorphosis and shift into parasitic adults. In some species, however, the adult is nonfeeding and dies soon after spawning.

Despite Myxinoidea and Petromyzontiformes being the only two jawless groups with extant representatives, several jawless vertebrates are known from fossils. **Euconodonts** is one of the most enigmatic of these groups, known for a long time only from their mouthparts. Pointed and comb-like phosphatic elements were found in Cambrian to Triassic rocks, but the organisms to which they belonged were unknown until the 1980s. New fossils including impressions of soft tissues allowed these elements to be identified as pharyngeal structures of long-bodied jawless vertebrates, the conodonts, which are probably closely related to cyclostomes.

**Anaspida** is another group of jawless vertebrates that is considered more closely related to cyclostomes than to jawed vertebrates. They vaguely resemble lampreys, having a single median nasohypophyseal opening, several gill pouches and a single anal fin. The phylogenetic placement of anaspids is unstable among different phylogenies due to some similarities with jawed vertebrates, such as the presence of a dermal skeleton and lateral fin folds, which might represent a starting point for the evolution of paired appendages. In fact, they were until recently placed closer to the jawed vertebrates, among several other fossil lineages usually referred collectively as “ostracoderms.”

## Ostracoderms and the Origin of Jawed Vertebrates

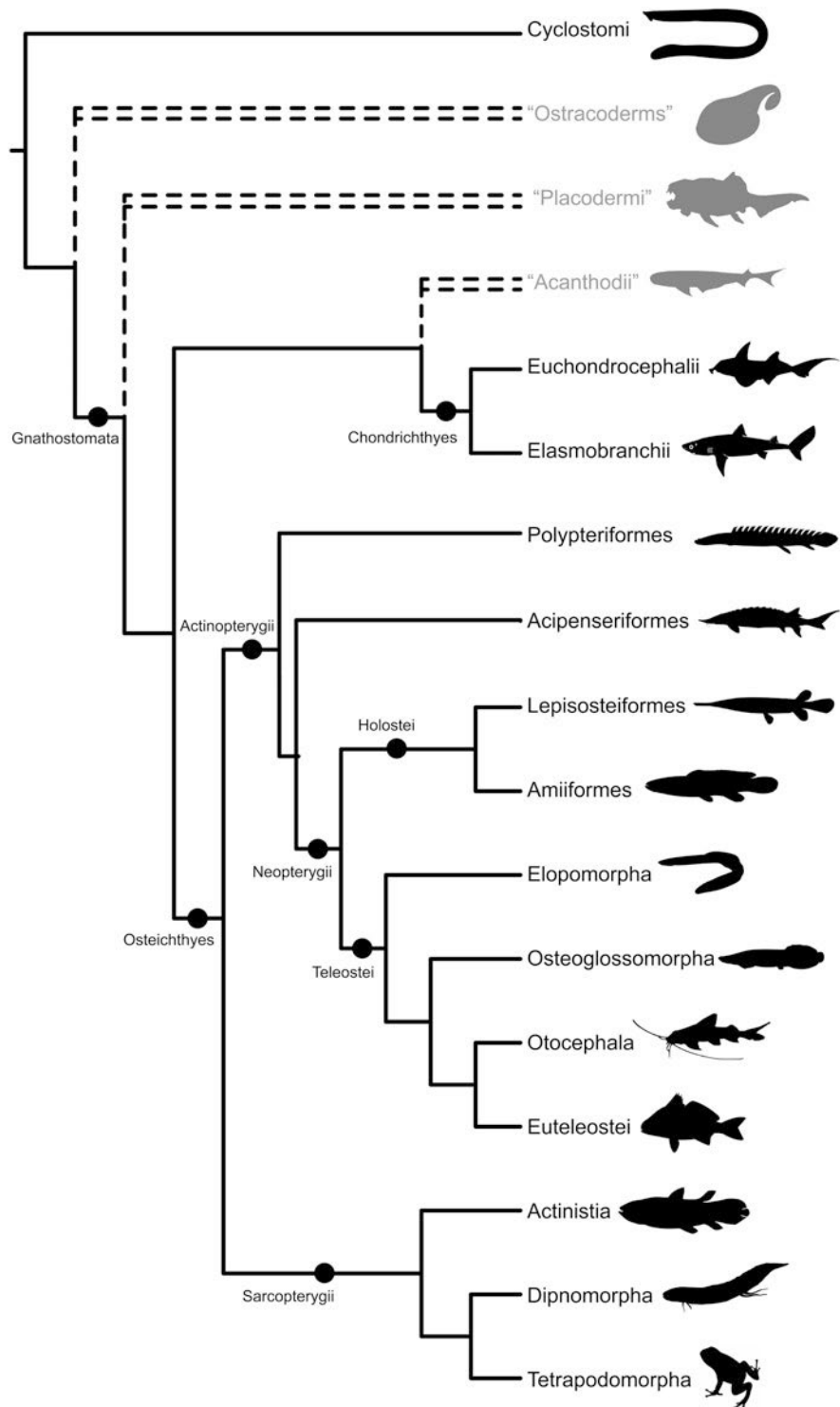
Several jawless vertebrate lineages commonly referred to as “ostracoderms” are now recognized as a polyphyletic grouping that includes lineages more closely related to Cyclostomi, successive sister-groups to gnathostomes, as well as some early gnathostomes. The term “ostracoderm” (meaning “shell-skinned”) refers to their extensive exoskeleton: an external armor of dermal

bones including large bony plates frequently fused at the anterior region forming a head shield, and smaller plates along the trunk.

Ostracoderms more closely related to gnathostomes (Fig. 2) exhibit a mineralized dermal skeleton formed by enamel, dentine, and bone. They arose around the Cambrian, and during their evolution, several characteristics shared with gnathostomes appeared, such as dermal odontodes with distinct root, crown and pulp-cavity in **Thelodonti**; cellular bone in **Galeaspida**; paired pectoral fins with associated musculature in **Osteostraci**. Therefore, several structures present in gnathostomes and responsible for their evolutionary success probably appeared in a stepwise manner during the diversification of these early vertebrates. A review on early vertebrate characteristics can be found in Donoghue and Keating (2014).

Jawed vertebrates form a monophyletic clade, **Gnathostomata**, characterized by a series of synapomorphies besides the jaws, and much of the insights regarding those synapomorphies came from developmental data (Kuratani et al. 2016). However, some of the major innovations in early vertebrate evolution are associated with the origin of the jaws. Gnathostome origin is also correlated to the duplication of regulatory genes. They have four Homeobox gene clusters, as opposed to two ancestrally in Vertebrata (Holland et al. 1994). The differential expression of regulatory genes at the anterior region of the head results in the differentiation between dorsal and ventral elements in the first visceral arches, enables the emergence of two distinct mandibular and hyoid arches, and leads to the enlargement of the forebrain and development of sensory systems.

Jawed vertebrates are also characterized by two paired appendages, the pectoral (anterior) and the pelvic (posterior), with associated girdles. In early gnathostomes, these appendages are present in the form of fins that, together with the dorsal and anal fins, have a great importance for maneuvering during swimming and are correlated to their success in habitat occupation. Later in the evolutionary history of tetrapod gnathostomes, these appendages are modified into limbs, and become very important for locomotion in the



**Vertebrates (Chordata), Fig. 2** Cladogram with the phylogenetic relationships of Vertebrata, focusing on groups traditionally referred to as “fishes”. Groups with exclusively fossil representatives are shown in gray. Some

clades are named at the nodes. Terminal names between quotation marks correspond to non-monophyletic groups, which also are represented in phylogeny by doubled, dashed lines

terrestrial environment. Theoretical works on the origin of the paired appendages concern the gill-arch theory, in which the appendages and girdles are considered modified gill arches, and the fin-fold theory, in which the appendages emerged from ventrolateral folds in the body wall. The latter hypothesis is supported by embryological studies on extant vertebrates, and is related to the differential expression of regulatory genes.

## Early Gnathostomes

Four major groups of gnathostomes are traditionally recognized, but their relationships, and even the monophyly of some of them, are still subject to dispute.

“**Placodermi**” is a group of Silurian to Devonian armored gnathostomes formerly considered part of ostracoderms (i.e., non-jawed vertebrates), but currently recovered as a paraphyletic grouping of basal gnathostomes (Fig. 2). Placoderms have a distinct cranial and thoracic armor forming a conspicuous, robust cephalothorax. They retain the plesiomorphic type of jaw suspension, the euautostylic suspension, with no participation of the hyomandibula. Placoderms were the first fishes to undergo a significant diversification event, with some of them reaching large sizes (like *Dunkleosteus*, with 25 m) and occupying apical ecological roles.

The “**Acanthodii**” have spines in all their fins, and spines developed from the fin-fold can also be present on their body wall between the ventral fins. This group is found from Silurian to Permian deposits (Fig. 1) and exhibits a mosaic of shark- and bony-fish-like features, which makes its placement problematic. Recent phylogenetic analyses place acanthodians as a paraphyletic group including some lineages more closely related to Chondrichthyes (Qiao et al. 2016) (Fig. 2), with whom they share the reduction of bony dermal plates and the presence of an intromittent reproductive organ, the clasper, which is a modified pelvic structure present in males. However, although typically associated to chondrichthyans, claspers are also found, besides acanthodians, in some placoderms.

Despite the confusion regarding the allocation of fossils at the base of Gnathostomata, most contemporary analyses agree in recognizing two monophyletic gnathostome groups with extant representatives: Chondrichthyes and Osteichthyes. They exhibit several noteworthy anatomical features, like a horizontal septum dividing dorsal and ventral blocks of body myomeres, elongation of the anterior (sphenoid) region of the head, oral teeth with pulp, dentin and enamel, and presence of a ventral cranial fissure. One important feature that arose at some point prior to the chondrichthyan and osteichthyan divide is the amphistylic suspension, in which there are two points of articulation between the jaws and the cranium: one through the upper jaw and another one through the hyomandibula.

## Chondrichthyes, the Cartilaginous Fishes

Chondrichthyans (► [Chondrichthyes Diet](#), ► [Chondrichthyes Navigation](#)) are fishes that completely lack dermal bones, being characterized by an endoskeleton formed by eventually calcified (but not ossified) cartilage, and are therefore known as cartilaginous fishes. Extant lineages include chimaeras, sharks, rays, and skates, with 1,282 species in 65 families of predominantly marine organisms (Fricke et al. 2020). The oldest records of the group date from the Early Silurian (Fig. 1), but fossil chondrichthyans, apart from isolated teeth and fin spines, are rare. As a consequence, the anatomy of early chondrichthyans is known only from a few fossil specimens, and the hypothesis of relationships between basal chondrichthyans have changed substantially in the last years (Qiao et al. 2016). Nevertheless, chondrichthyans probably arose earlier, in the Ordovician, and two major radiations can be identified: one in the Early Devonian and another one in the Jurassic.

Chondrichthyans are usually remembered as large pelagic predators, but representatives of the group occupy a broad spectrum of aquatic habitats, with diverse diet and anatomy (► [Chondrichthyes Morphology](#)). All

chondrichthyans perform internal fertilization, using the claspers as copulatory structures, and usually have a relatively small number of offspring. The noteworthy sensory system of chondrichthyans (► [Chondrichthyes Sensory Systems](#)) is probably one of the major reasons for the evolutionary success of the group. They have a very accurate olfactory system and the ability to sense weak electric fields through their ampullary electroreceptor organs.

Chondrichthyes are divided in two groups: Elasmobranchii and Euchondrocephalii (Fig. 2). **Elasmobranchii** can be diagnosed, among other characters, by a pectoral fin skeleton composed of three cartilaginous basals, numerous cartilaginous radials, and several keratinous ceratotrichia. Among elasmobranchs, **Xenacanthida** is a group of extinct large marine predators, found from the Carboniferous to the Triassic, with confluent anterior and posterior dorsal fins, and an anterior dorsal-fin spine. Members of **Ctenacanthidae** are found from Devonian to Triassic rocks and had separated anterior and posterior dorsal fins, both bearing spines with longitudinal ornamentation. Members of **Hybodontiformes** are found from Carboniferous to Cretaceous deposits, suffering a severe diversity decline at the end-Permian. They also have fin spines, besides hooked denticles on the surface of the head.

Considering elasmobranchs with extant representatives, the **Neoselachii** comprises the clear majority of living chondrichthyans. They have most of the classic chondrichthyan characteristics we commonly read in textbooks, including the synapomorphic hyostylic suspension, in which the palatoquadrate is supported by the hyoid arch, enabling great protrusion of the jaws. Neoselachians arose in the Triassic and have characteristic placoid scales. These scales have an anatomical structure like that of teeth, with pulp cavity, dentin, and three layers of enamel, and are therefore known as “dermal denticles.”

One of the main groups of elasmobranchs is **Galeomorpha**, a lineage with around 350 extant shark species that retain the plesiomorphic number of five gill-slits and the presence of an anal fin. Members of this group usually do not have a spiracle – a reduced, rounded opening, considered

the reminiscent of the primitive first gill slit. Some representatives of Galeomorpha are among the most famous “scary” sharks in popular culture, like the sand tiger shark (*Carcharias taurus*), tiger shark (*Galeocerdo cuvier*), white shark (*Carcharodon carcharias*), the hammerhead sharks (family Sphymidae), besides the large suspension-feeding whale sharks (family Rhinodontidae).

The other two elasmobranch clades form a monophyletic group diagnosed by the loss of the anal fin and the presence of an orbitostylic suspension, in which the palatoquadrate articulates to the neurocranium via the orbital process and the hyoid arch. **Squalomorpha** appeared in the Triassic and has around 160 extant species. Their representatives are usually unspecialized cold-water sharks, such as the dogfish sharks (family Squalidae). **Hypnosqualea** arose in the Jurassic. They are benthonic and have enlarged pectoral fins and spiracles. Their bodies, specialized for bottom-feeding, are flattened, with a ventrally positioned mouth, and mostly crushing teeth. With more than 600 species, the group includes the angel sharks, saw sharks, rays, and skates, being the most diverse among the extant chondrichthyan lineages.

The remaining chondrichthyans, **Euchondrocephalii**, include Chimaeriformes and several related fossil taxa. Extant representatives are usually very distinct anatomically, but many of the fossil taxa have an overall shark-like shape. Among fossil groups, the **Cladoselachidae** is one of the best known, with the genus *Cladoselache* represented by several well-preserved Devonian specimens. One interesting aspect of this group is that fossils with claspers have not been found to date.

**Holocephali** is a chimaeriform group composed of 56 living species of chimaeras and closely related fossils. The oldest holocephalan is known from the Devonian, and they can be recognized by the synapomorphic presence of a unique holostylic suspension, in which the palatoquadrate fuses to the neurocranium, and the suspension has no participation of the hyoid arch. Living holocephalans bear a spine in the first dorsal fin and their branchial arches are covered by a single gill opening. Chimaeras are mostly

deep-water organisms, and because of that are much less studied than elasmobranchs.

## Osteichthyes: Origin and Fossil Groups

Bony fishes were given this name to contrast with other groups that have a cartilaginous internal skeleton (i.e., cyclostomes and chondrichthyans). However, mineralized tissues are far more complex than this simple dichotomy and, to some extent, this name also implies in a traditional view on vertebrate evolution, in which an ancestrally cartilaginous endoskeleton became more robust as it became ossified. Although some bony tissues do have cartilaginous precursors, some others do not (dermal or intramembranous ossifications). Furthermore, while a cartilaginous skeleton may indeed be plesiomorphic for vertebrates, both the paleontological record and recent molecular studies seem to indicate that the absence of bone in chondrichthyans is actually secondary.

The first records of osteichthyans date from the Late Silurian (Fig. 1), but some fossil forms are of disputed placement. Several characteristics present in osteichthyans actually appeared before the origin of the group, and are seen in placoderm lineages. In early bony fishes we find an ossified internal skeleton, but also a superficial skeleton formed by dermal bones and scales, and there may even be interactions (for example, fusions) between endochondral and dermal bony elements. In later osteichthyans we see a trend towards reduced ossification of both scales and dermal bones, while a more complete ossification of the internal skeleton takes place. Osteichthyans can also be identified by having dermal fin rays (lepidotrichia) supporting their fins, the presence of a gas bladder that originates either the swim bladder or the lungs, and assimilation of elements of the lateral line canals into the skull. Osteichthyes are divided in two groups: Actinopterygii and Sarcopterygii.

Actinopterygii is usually defined by a combination of plesiomorphic features that are found more generally in osteichthyans, and apomorphic traits found in more derived groups, meaning that

not all actinopterygians will show them. Early actinopterygians inherited as plesiomorphies, for example, several radial elements articulating between the pectoral fins and girdle, an endocranium ossified as a single structure, and scales covered by a ganoine layer. However, they also exhibited some novelties, like a modified heterocercal caudal fin that is transformed into a homocercal fin in more derived actinopterygians, a single dorsal fin that is also further modified into two dorsal fins or more in derived groups, and modifications of facial muscles associated with jaw suspension and movement (Datovo and Rizzato 2018).

**Sarcopterygii** also retains some osteichthyan plesiomorphies, like the presence of two dorsal fins and a heterocercal caudal fin that becomes modified into diphyccercal caudal fin in some groups. Sarcopterygian novelties include a single element articulating the fins and girdle (humerus and femur), an endocranial articulation between the etmosphenoid and otoccipital regions, that is secondarily lost in tetrapods, and scales covered by a cosmine layer.

## Actinopterygian Diversification

Actinopterygians are called “ray-finned fishes” because their fins are supported by lepidotrichia, whose controlling muscles are located within the body wall. However, lepidotrichia are also present in sarcopterygians. Actinopterygians currently comprise more than 34,000 species (Fricke et al. 2020), of which about 44% are known exclusively or predominantly in fresh waters.

Three major evolutionary trends can be described as driving actinopterygian evolution: increase in endoskeletal ossification and reduction of scales and of cranial dermal bones; a transition from biting to sucking mouths; and the development of more symmetrical caudal fins. These derived features are found in teleosts and are believed to account in great part for their evolutionary success.

Actinopterygians went through two major evolutionary radiations: the first between the Devonian and Carboniferous, and the second



starting in the Mesozoic and lasting into the Cenozoic (Fig. 1). Despite the first actinopterygians being broadly similar in shape, they were relatively diverse by the end of the Devonian, and were not greatly affected by the Late Devonian mass extinction. Novel cranial morphologies appeared in Early Carboniferous forms, so much so that actinopterygians were the dominant fish group by the end of the Permian (Friedman 2015). In the Early Triassic, actinopterygians went through an adaptive radiation, increasing their taxonomic dominance, especially in marine environments. At this point, the first neopterygians arose (Fig. 2), already showing a major trophic divergence among taxa.

Non-teleost lineages, such as **Cladistia**, **Acipenseriformes**, and **Holostei** (Fig. 2), used to be viewed as ecologically restricted groups, but while this may be partially true today, extant non-teleosts are poor representatives of their former biodiversity (Friedman 2015). For instance, “**Palaeonisciformes**,” a paraphyletic grouping of early actinopterygians, were globally distributed, occupying a wide range of ecological niches, and represent most of Paleozoic and Early Mesozoic actinopterygian diversity. Living cladistians, acipenseriforms, and holosteans show striking anatomical specializations when compared with fossil taxa.

## Teleostei

The most speciose actinopterygian lineage is **Teleostei**, which includes approximately half of all extant vertebrate species. Teleosteans originated in the Triassic and exhibit the most derived conditions in neopterygian evolutionary trends. Maxillary specializations arose several times in the group. Several fin specializations are observed, especially in the caudal-fin skeleton, creating a symmetrical homocercal tail. A whole-genome duplication event occurred in the ancestor of crown-group teleosteans, which might be associated with the great radiation event that occurred in this group.

The phylogenetic relationships of the major teleostean clades are not fully resolved, but some large

groups are recurrently retrieved as monophyletic, including **Elopomorpha**, **Osteoglossomorpha**, **Otocephala**, and **Euteleostei** (Fig. 2). Among these, the Otocephala are especially interesting because they possess a connection between the swim bladder and the inner ear, which is used to improve hearing. The major group of otocephalans is Ostariophysi, for which the otophysic connection is formed by the Weberian apparatus, a highly specialized structure composed of modified vertebral elements. This group includes cyprinids, loaches, characids, tetras, catfishes, and knifefishes, comprising more than 10,000 species and about 68% of all freshwater fish diversity (Nelson et al. 2016).

Finally, Euteleostei encompasses almost two thirds of actinopterygian diversity, with around 20,000 species distributed in 50 orders, and occupying the most diverse environments, including pelagic habitats (Nelson et al. 2016). This group originated in the Cretaceous, and is the major component of the second great actinopterygian radiation that started in the Cenozoic. The most species-rich lineage is **Acanthomorpha**, whose representatives typically have the anterior fin rays of both dorsal and anal fins forming spines. The relationships within Euteleostei, and especially within Acanthomorpha, are somewhat unstable, since morphological and molecular phylogenetic hypotheses usually strongly disagree.

## The Other Branch of the Osteichthyan Phylogeny: Sarcopterygii

Sarcopterygians are called “lobe-finned fishes” because their appendages are supported by well-developed endoskeletal elements whose controlling muscles project extensively onto them, in contrast with actinopterygians. They also have an intracranial articulation that may have served at first for feeding, allowing them to secure prey more firmly, but later aided in buccal pumping and breathing. Sarcopterygii includes Tetrapoda, which comprise roughly half of the extant vertebrate diversity and is found predominantly on land. The commonly used term “sarcopterygian

fishes” refers to a paraphyletic assemblage of several fossil lineages and a few extant species, excluding the tetrapods.

The earliest sarcopterygians date from the Silurian (Fig. 1). Apart from stem-sarcopterygians such as *Guiyu* and *Psarolepis*, whose placement has been disputed, the earliest sarcopterygian lineages to diverge were **Onychodontiformes** and **Actinistia** (Fig. 2). The latter includes coelacanths, comprised of many fossils and only two (maybe three) living species in the genus *Latimeria*. Coelacanths are found in Devonian deposits and were thought to have been extinct in the Cretaceous until 1938, when a living specimen was found off the South African coast by Marjorie Courtenay Latimer. Still not much is known about coelacanth biology, but they apparently have a modified lung which is calcified in fossil species, but filled with fatty tissue in extant ones. Meanwhile extant coelacanth species are found in deep seas and are very alike, fossil taxa had a great body size diversity and were also found in shallow, fresh waters. Coelacanths can be further diagnosed by their diphycercal caudal fin, a trait found more broadly among early sarcopterygians.

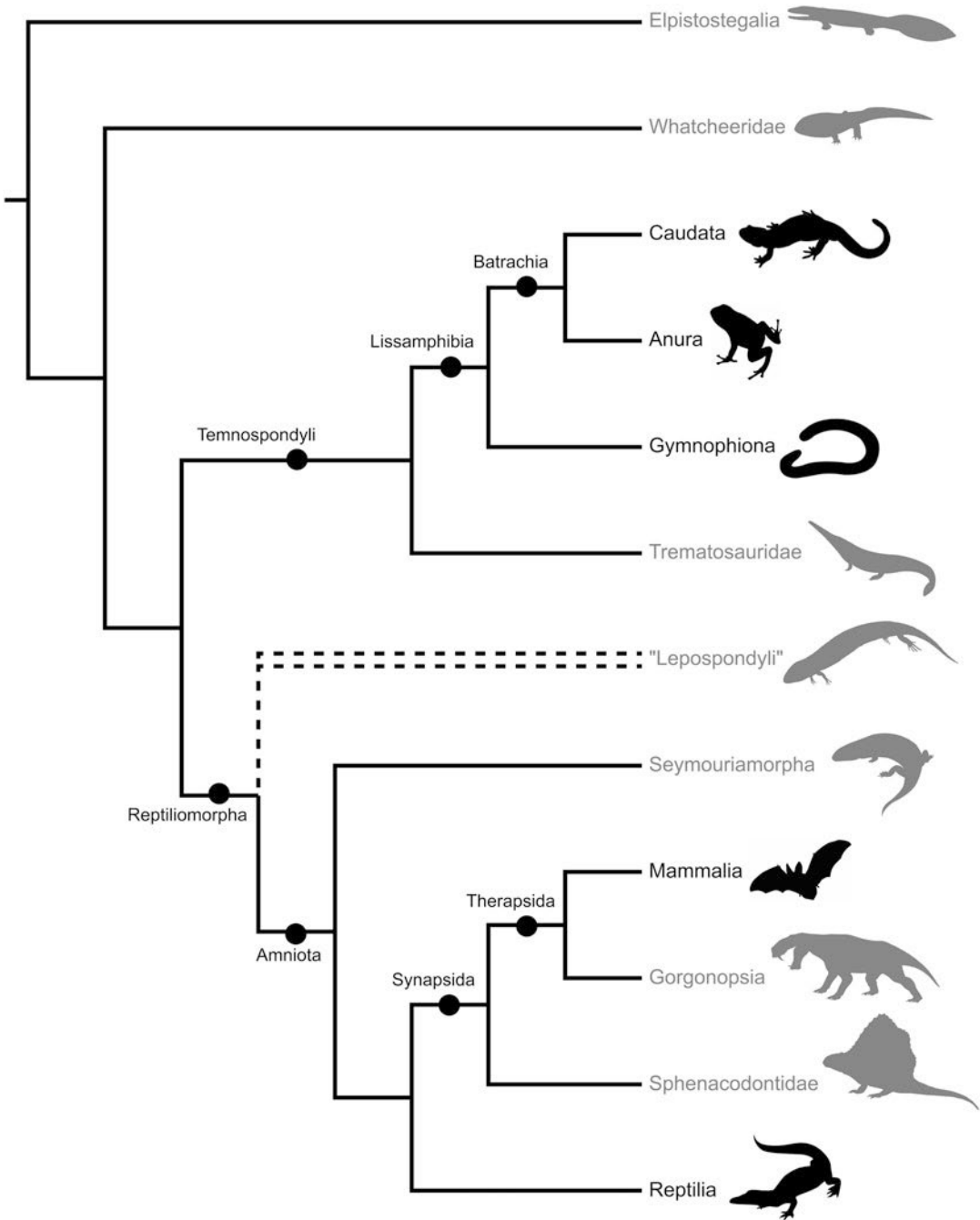
Another sarcopterygian lineage with living representatives is **Dipnomorpha** (Fig. 2), the lungfishes, with several fossil taxa and three extant genera: *Neoceratodus*, *Protopterus* and *Lepidosiren*. Although fossils are known from all continents, living lungfishes are restricted to Australia, Africa, and South America respectively, and are famous for breathing air through alveolar lungs. While fossils are also found in marine environments, living species are restricted to freshwater habitats. Modern lungfishes lack a cosmine layer in their scales and have the skeleton composed mostly of cartilage. They have dentigerous plates which are used in a durophagous diet for crushing shelled invertebrates. *Protopterus* and *Lepidosiren* have reduced, slender fins, and are known for forming burrows in which they survive dry periods (aestivation). This is a conserved behavioral and physiological trait, and many fossils are found in fossilized burrows. Their head skeleton is much modified and specialized for making the burrows.

## The Invasion of Land

**Tetrapodomorpha** includes fossil groups more closely related to tetrapods than to dipnomorphs, and the tetrapods themselves (Fig. 2). As a trend, tetrapodomorphs show progressive development of the zygapophyses, vertebral processes that couple with adjacent vertebra and increase stiffness of the vertebral column and its ability to resist torsions and flexions, thus providing better support for the body on land. The ribs extend in length and become an important attachment site for the coastal musculature that supports the body. The appendicular system becomes increasingly more integrated with the axial system, and the pectoral girdle eventually loses connection with the skull. The differential development of postaxial and preaxial digit-like elements in the appendages increases their participation in locomotion, while also reducing the role of the tail. Several works point out that this differential development is due to the alteration in the expression of regulatory genes (e.g., Tanaka 2016).

Breathing on land is more challenging than breathing in water, even though the air has a higher oxygen content, because respiratory surfaces suffer with desiccation. The excurrent, posterior naris, which appeared in the origin of gnathostomes and participated only in olfactory chemoreception, gains a connection with the oral chamber, forming a choana (probably in the ancestral of tetrapodomorphs and lungfishes). With the choana, dissection is reduced. The excurrent naris appeared in the origin of gnathostomes, and participated only in olfactory chemoreception. Finally, in the terrestrial environment, electroreception and mechanoreception via the lateral-line system lose prominence, whereas photoreception and oral and olfactory chemoreception become more important for perceiving the environment.

Stem-tetrapods include **Rhizodontiformes**, **“Osteolepiformes,”** and **Elpistostegalia** (Fig. 3). These groups comprise several fossils of great importance for understanding the transition to land, even though recent advancements in the functional morphology of tetrapodomorphs indicate that its representatives, once seen as more salamander-like, are now believed



**Vertebrates (Chordata), Fig. 3** Cladogram with the phylogenetic relationships of Tetrapodomorpha. Groups with exclusively fossil representatives are shown in gray. Some clades are named at the nodes. Terminal names

between quotation marks correspond to non-monophyletic groups, which also are represented in phylogeny by doubled, dashed lines

to have been much more aquatic. Some famous extinct tetrapodomorphs are *Eusthenopteron*, *Panderichthys*, and *Tiktaalik*. While

*Eusthenopteron* retains a “fish-like body, well adapted for pursuit within the water column” *Panderichthys* and *Tiktaalik* provide a glimpse in

the appearance of limbs. *Panderichthys* and *Tiktaalik* are Devonian taxa believed to be largely aquatic, but making extensive use of the substrate for locomotion. They likely inhabited waters shallow enough to require body weight support, such as the lower reaches of tropical river systems, their deltas or estuaries (Ahlberg 2018). Several of their anatomical features were probably advantageous for breathing air in these shallow waters with low oxygen content.

## The First Tetrapods

Of the five groups into which vertebrates were traditionally subdivided, amphibians, reptiles (including birds), and mammals comprise Tetrapoda. This clade includes, therefore, all terrestrial vertebrates, which represent roughly half the extant vertebrate diversity, with about 35,000 extant species. The first tetrapods show a mosaic of features, some connecting them to aquatic environments, like internal gills, fins, and extensive lateral line canals, and some to land, like the anatomy of their limbs and vertebral column. Hypotheses on the phylogenetic relationships of the first tetrapods has changed in recent years, but the group can be characterized by the presence of a specialized atlas and axis complex, a structure formed by the first two cervical vertebrae that articulates the head with the remainder of the vertebral column and facilitates head movement out of water. Tetrapods are also characterized by the presence of two pairs of limbs formed by three segments, namely, stylopodium (proximal), zeugapodium (middle), and autopodium (distal), the latter formed by skeletal articulating elements (carpals and tarsals) and digits. Furthermore, the stylopodium is formed by the humerus in the fore- and the femur in the hind limb; and the zeugapodium is formed by the radius and ulna, and tibia and fibula, respectively. Finally, the autopodium is represented by the manus and pes, and is formed by skeletal articulation elements (carpals and tarsals), in addition to the digits.

A characteristic typically associated with tetrapods is the presence of five digits, a condition named pentadactyly. Basal tetrapods, however,

commonly exhibit more than five digits (e.g., *Tulerpeton*, *Ichthyostega*, *Acanthostega*). Digits first appeared in forms that were still aquatic, suggesting they may have originated as an adaptation to shallow aquatic environments. The pentadactyl condition, on the other hand, is consistently found among more terrestrial forms, and it was established early in the evolution of tetrapods (Ledbetter and Bonnet 2019). Among tetrapods, several independent instances of reduction in the number of digits, or of limbs, occur. Instances of polydactyly (i.e., more than five digits) also occur, especially among secondarily aquatic forms such as cetaceans and ichthyosaurs, but these are rare, probably due to developmental constraints associated with the establishment of pentadactyly (Shubin et al. 1997).

The basalmost representatives of **Tetrapoda** are *Acanthostega* and *Ichthyostega* (but see Ahlberg 2018 for alternatives), both possessing fingers and toes, in addition to an enlarged pelvis and a flexed elbow. Despite them being from the latest Devonian (Fig. 1), fossil footprints (Stössel et al. 2016) suggest the first tetrapods date from at least the Middle Devonian, indicating a gap in the fossil record. Morphofunctional data suggest *Acanthostega* might have been a fully aquatic animal (Ahlberg 2018), while *Ichthyostega* have unambiguous adaptations for terrestrial life, such as a strengthened vertebral column and a reduced operculum – despite probably still having limited locomotion abilities on land.

Other fossil groups of early tetrapods include forms other than the usual “fishapods”, such as **Whatcheeridae**, **Colosteidae**, and **Adelospondyli** (Fig. 3). The latter two are elongated animals with limbs reduced or absent. Recently, this diversity increased with the addition of some **Aistopoda**, a clade of similar animals classically assigned to the amniote stem (Pardo et al. 2017b), suggesting high locomotory and functional diversity in these transitional forms.

## The Tetrapod Divise

Tetrapoda is a crown-group divided into two lineages: **Temnospondyli**, which includes living

amphibians, and **Reptilomorpha**, containing amniotes and all fossil groups more closely related to them than to temnospondyls (Fig. 3). The split between these two groups occurred in the Middle Devonian. Fossil temnospondyls were largely restricted to semiaquatic environments, but rather diverse in form. Most were superficially salamander-like, but there were also crocodile-like groups such as **Trematosauridae** (Fig. 3) and some sail-backed species. Although living amphibians are characterized by a smooth skin, the body of fossil temnospondyls was extensively covered with osteoderms. Stem reptiliomorphs include “**Lepospondyli**”, a group of fossil amphibians with some limbless, elongate forms regarded as more closely related to amniotes than to temnospondyls and whose monophyly is disputed, and two groups of large-bodied reptile-like species, **Seymouriamorpha** and **Diadectomorpha** (Fig. 3). Potential larval stages are known for seymouriamorphs but not for diadectomorphs, making them ideal models of progressively more terrestrial groups. Recent phylogenetic analyses, however, have recovered Diadectomorpha among synapsids (Klembara et al. 2020).

### Living Amphibians and Their Relationship with Fossils

Living amphibians comprise more than 8,200 species divided in the orders Anura, Gymnophiona, and Caudata. They are commonly known for having a two-part life cycle that usually includes an aquatic larva and a terrestrial adult, these stages being separated by a process of metamorphosis (although some species exhibit direct development and do not metamorphose). The most conspicuous changes during metamorphosis are the loss of the gills and the appearance of limbs, when present. The caudal fin of the larva also is resorbed during metamorphosis, being replaced by the tail in salamanders or reabsorbed in frogs.

Caecilians are fossorial snake-like animals included in the group **Gymnophiona** (Fig. 3), meaning “naked snake” in reference to the smooth, humid aspect of their skin. Although fossil forms bear rudimentary limbs, all living

caecilians are limbless, and some forms retain ossified scales, even though most species lack them. With only about 214 species, and due in part to their secretive life habits, caecilians are considered one of the least known vertebrate groups. Some species have glands on their skin that secrete toxins, and venom dental glands were recently identified (Mailho-Fontana et al. 2020). A conspicuous characteristic of the group is the very compact, robust skull that they use for burrowing in the substrate. Their eyes are reduced, and they bear a unique mechanosensory organ on the head named tentacle. Unlike salamanders and frogs, caecilians have an intromittent organ called phallodeum, used for internal fertilization. Some caecilians are viviparous, lacking a larval stage, and in some species, the newborn use specialized teeth to feed on the lipid-rich skin of their mother (Wilkinson et al. 2013).

Salamanders, newts, and tritons are included in **Caudata** (► [Caudata Cognition](#), ► [Caudata Locomotion](#), ► [Caudata Sensory Systems](#)), while frogs and toads are included in **Anura** (Fig. 3). Despite the indirect development being widespread in both groups, some salamanders never metamorphose, remaining in the aquatic environment and retaining their gills and caudal fin. One example is the famous Axolotl, *Ambystoma mexicanum*, an important model organism for studies on development, evolution, and regeneration. Some anurans, on the other hand, have direct development, with the absence of a larval stage.

Anurans display a diverse array of reproduction strategies that include the use of elaborate calls for territory defense and for attracting partners. Males of some species oftentimes engage in violent combats. Anuran eggs can be laid in water bodies, leaves, or even in completely terrestrial environments. In these cases, the parents may produce a foam nest that protects the cluster against dehydration. Many species also display several forms of parental care, including species that carry their eggs and larvae in their bodies (in skin pockets, dorsal pouches, vocal sacs, or the stomach, for example) until they metamorphose into froglets.

While salamanders have a long body and tail and relatively short legs, frogs and toads have



short bodies with well-developed hindlimbs, features commonly associated with their jumping locomotion. In the anuran pelvis, the ilium is extremely long and the caudal vertebrae are fused into the urostyle, a rod-like structure that acts as a propulsion mechanism. Given their highly vocal behavior, hearing is very important for anurans. All living amphibians possess a special hearing organ named papilla amphibiorum for detection of low frequency sounds, but some anurans also have a differentiated sound detecting mechanism through the operculum, a cartilaginous flap in the otic capsule, for very high frequency sounds. Anura includes the Clawed Frog, *Xenopus laevis*, an important model organism for developmental biology, cell biology, and neuroscience.

The clade containing the three mentioned groups of living amphibians is called **Lissamphibia** (Fig. 1), but the composition and placement of Lissamphibia has been subject of heated debate. Phylogenies generally agree that salamanders and anurans are more closely related to each other, united in a clade named **Batrachia**. In contrast, the relationship between batrachians and caecilians is more controversial, especially when considering fossils. There are three main phylogenetic hypotheses for living and fossil amphibians. The temnospondyl hypothesis places lissamphibians within the aforementioned Temnospondyli (Fig. 3), the lepospondyl hypothesis places them within Lepospondyli, and the polyphyletic hypothesis separates caecilians and batrachians, considering caecilians belonging to Lepospondyli and batrachians to Temnospondyli. While the temnospondyl hypothesis is favored over the other two, the monophyly of Lissamphibia within temnospondyls has been recently challenged (Pardo et al. 2017a). This controversy illustrates how much of our understanding of the relationships between living groups depends on the knowledge of the relationships between fossil forms. Surely, the discovery of new fossil amphibians as well as new studies of living and extinct forms will provide a better understanding of the relationships between living and fossil amphibians.

## Amniotes

**Amniota** comprise reptiles (including birds, see below) and mammals, with about 27,000 living species and many fossil lineages (Fig. 3). The group originated in the Late Carboniferous (Fig. 1). The main feature of amniotes is the cleidoic or amniotic egg, which has three embryonic membranes in addition to the yolk sac, namely, the allantois, amnion, and chorion. The chorion is involved with gas exchange, while the allantois stores wastes from the embryo (Kardong 2012). The amnion forms the amniotic sac containing the amniotic fluid, which prevents dehydration of the embryo in addition to offering mechanical protection. Amniotic eggs also have a protective shell that is either calcified or leathery, but permeable to gas exchange. The shell is lost in viviparous mammals, but is retained in the oviparous monotremes. Inside the egg, the amniote embryo develops without a larval stage or metamorphosis. These features render the amniotic egg as more suitable for terrestrial environments.

The presence of an outer layer of skin composed by keratinized cells, which helps avoid dehydration, is also linked to the opportunity of a completely terrestrial life in amniotes. The skin of amniotes may also exhibit typical epidermal appendages such as horny scales, feathers or hair, which share common developmental and evolutionary origins. These appendages diversified into a series of specialized structures and perform several functions including insulation, thermoregulation, sensory perception, camouflage, intra- and interspecific communication, and sexual display.

Although such skin and egg features do not commonly fossilize, skeleton features are useful for identifying fossils as belonging to Amniota. For instance, changes in posture and locomotion in amniotes are reflected in the shape and position of the pectoral and pelvic skeletons. The axial skeleton became regionalized, including distinct thoracic and sacral regions (the latter with at least two vertebra), and a new articulation between the skull and the atlas-axis complex developed. Together with new locomotor strategies and increased mobility of the head, amniotes also

diversified their feeding styles, and this is reflected on the structure of their skull.

New arrangements of the head muscles associated with the diversification of feeding strategies gave rise to distinct patterns of fenestration in the temporal region. Temporal fenestrae are openings in the posterior portion of the skull associated with the passage and attachment of muscles involved in jaw movement. Patterns of skull fenestration have been central to hypotheses of early amniote evolution, and there has been a long debate in the literature regarding their evolution. Despite the different types of temporal fenestration observed among amniotes, recent analyses suggest that only two ancestral types appeared in the early diversification of the group (Ford and Benson 2019). These types of fenestration are associated with a basal split of the crown-group Amniota into two lineages: **Synapsida**, which includes mammals, and **Reptilia**, including reptiles and birds (Figs. 1, 3).

Early tetrapods and reptilomorphs lack fenestrae in their skull, a plesiomorphic anapsid (meaning “without arches”) condition. In Synapsida, a single temporal fenestra is ancestrally present, termed synapsid condition (meaning “single arch”). Therefore, “synapsid” refers both to the type of temporal fenestration and to members of the lineage who ancestrally possess it, with all living synapsids (i.e., mammals) having a modified synapsid condition. In Reptilia, on the other hand, two temporal fenestrae are ancestrally present, a diapsid (“two arches”) condition. Likewise, diapsid refers to members of Reptilia that ancestrally possess this condition, which was also later modified in several different types, including a reversion to an anapsid condition (Ford and Benson 2019).

## Early Synapsids and the Origin of Mammals

Synapsids are characterized by having the temporal fenestration of the synapsid type, i.e., a single temporal opening. The group includes fossil lineages that illustrate the step-wise appearance of many characters typically associated with

mammals, such as the inner ear ossicles. The earliest known synapsids were traditionally referred to as “mammal-like reptiles” because they exhibit plesiomorphic aspects usually associated with reptiles, combined with derived features associated with mammals. Some of these earlier forms were formerly grouped under “Pelycosauria,” a now-recognized paraphyletic assemblage of typically large-sized synapsids. Some of them include famous sail-backed forms. The sail, formed by elongated neural spines putatively supporting a web of skin, probably evolved at least three times among “pelycosaur” groups: in **Ophiacodontidae**, in the strict herbivores **Edaphosauridae**, and in the strict carnivores **Sphenacodontidae** (Fig. 3). The function of the sail is still debated. It was previously linked to thermoregulation, but current consensus is leaning towards sexual display. Early synapsids were abundant from the Late Carboniferous to the Early Permian, and included some of the largest terrestrial animals of the time (e.g., *Edaphosaurus*, *Dimetrodon*), but they are replaced in the fossil record by therapsids in the Middle Permian.

**Therapsida** (Fig. 3) is characterized by an enlarged temporal fenestra, suggesting more developed jaw muscles, and modifications of the postcranial skeleton that, combined with longer limbs, are related to a more erect posture and agile locomotion. They also have enlarged caniniform teeth separating the incisors anteriorly from the post-canine posteriorly. Fossil therapsids include hypercarnivores such as **Gorgonopsia** (Fig. 3), apex terrestrial predators of the Middle and Late Permian, as well as specialized herbivores such as some **Dinocephalia** and the beaked **Dicynodontia**. Early therapsids were the dominant faunal components of terrestrial ecosystems until the Permo-Triassic Mass Extinction, and although a relict “disaster fauna” persisted in the early Mesozoic, they went extinct by the end of the Triassic, when they were ecologically replaced by reptiles.

**Cynodontia** is the clade of more derived therapsids that persisted into the Jurassic. They are characterized by modifications on the skeleton, especially in the skull, that reflect important changes in feeding and breathing. These changes

are linked to a whole remodeling of neural and sensory systems (Rowe 2020), that was fundamental for the diversification of the group and for some of the most distinctive anatomical, physiological, and behavioral features of mammals. Combined with a general trend toward reduced body sizes, these modifications suggest diversification of life habits and ecology among cynodonts.

The development of efficient mastication in fossil cynodonts is evidenced by the appearance of molariform teeth, occlusal facets in dentition, a sagittal crest in the skull associated with muscle attachment, expanded zygomatic arches, and a deep masseteric fossa on the lateral surface of the lower jaw, which suggests hyperdevelopment and rearrangement of jaw muscles, especially the masseter. The secondary palate, a bony plate separating nasal and oral passages, is extensive in cynodonts. Although not unique to synapsids, since crocodiles also have it, in the former it is considered related to mastication. It forms a hard roof against which the tongue can abut to participate in food processing, improving feeding efficiency. The appearance of the secondary palate in cynodonts is accompanied by the development of neural components associated with controlling the muscles involved in the complex jaw movements associated with mastication, and with new sensory possibilities offered by prolonged food processing in the mouth (e.g., orthoretronasal olfaction, Rowe 2020). The development of the secondary palate and posterior displacement of the choanas (internal narial openings) is also linked with the formation and specialization of the nasopharyngeal chamber. The appearance of the chamber resulted in modifications in the olfactory system, and is accompanied by notable developments in the brain regions correlated with the processing of this information in what is considered one of the first pulses of encephalization along the mammalian lineage (Rowe 2020). Finally, further differentiation of the axial skeleton into thoracic and lumbar regions suggests fossil cynodonts used diaphragmatic ventilation. Differentiation of the axial skeleton also enabled wider dorsoventral movements, suggesting synchronism between breathing and locomotion.

Fossil cynodonts more closely related to mammals are united to them in a clade named **Mammaliaformes**. They are noteworthy because they underwent miniaturization during the Mesozoic. With smaller sizes, new habitats and food sources become available, prompting even further the diversification of life habits. Miniaturization involved modifications in the skeleton, resulting in more gracile and agile bodies and boosting diversification of locomotion types. Mammaliaforms have the oldest evidences of fur, and also exhibit larger brains (probably related to the appearance of hair and of endothermy) much more similar to typical mammalian ones (Rowe 2020).

Fossil mammaliaforms also document the gradual transformation of temporal and lower jaw bones that were originally part of the craniomandibular articulation into a series of ossicles involved in sound transmission, the mammalian middle ear bones. In early mammaliaforms, these ossicles are reduced and participate in auditory perception, but are still connected to the posterior portion of the mandible. In postnatal mammals, these ossicles are detached from the lower jaw, which is formed solely by the dentary. The loss of this articulation may have happened independently in monotremes and therians. During this transition to a secondary craniomandibular articulation, both types coexisted: the new one formed by the dentary and the squamosal and related to feeding, and the old one formed by the post-dentary bones of the lower jaw and the quadrate, more suited for sound transmission.

## Extant Mammal Diversity

**Mammalia** originated in the Jurassic, around 170 million years ago. Mammals are characterized by several autapomorphies that include, besides the middle ear bones and the secondary craniomandibular joint, a large brain with a six-layered neocortex, the presence of ethmoid turbinates (a series of elaborate, convolute ossifications in the nasal cavity), and seven cervical ribs fused to their corresponding vertebrae. Mammals

are also distinguished from all other living vertebrates by having external ears and by their namesake feature, the mammary glands, which produce the milk that feeds the newborn.

Mammalia comprises more than 5,800 living species, including humans. Mammals are in general agile endothermic animals. They exhibit several characteristics associated with controlling body temperature, including hair and sweat glands. Ancestrally, they possess a series of differentiated teeth: incisors, canines, premolars, and molars (the latter two characterized by having at least two roots). Dentition is one of the most important characters for identifying mammalian groups, of which the dental formula is an important tool. Mammals explore a vast array of feeding modes that is reflected in a high diversity of teeth numbers, arrangements, and shapes. Mammals also explore different habitats, including fossorial, terrestrial, desertic, aquatic or semiaquatic (including freshwater and marine environments), and aerial. Parental care is an important feature of their reproductive strategies.

**Monotremata** is the basalmost group of living mammals (Fig. 1), with five extant species from Australia and New Guinea, the platypus and echidnas. Monotremes retain the plesiomorphic amniote feature of laying eggs as well as a single opening for the digestive, reproductive, and urinary tracts, the cloaca. Living monotremes do not have teeth, and while echidnas feed on termites and ants using a specialized tongue, the platypus feeds on aquatic invertebrates using a duck-like bill, with a specialized electrosensory system to locate their prey. Monotremes produce milk, but they have no teats; the milk is secreted onto the fur, which their offspring use to help suck the milk.

**Marsupialia** (Marsupialia Morphology, Marsupialia Life History) (Fig. 1) includes opossums, kangaroos, koalas, and others. The name of the group makes reference to the marsupium, a skin pouch located on the abdomen of females of medium and large size species to which embryos migrate in order to complete their development. Although usually considered as an incomplete form of internal development, the marsupium is a very specialized ontogenetic strategy, which

imposes extremely high constraints on their oral and forelimb development. Marsupials and monotremes lack a corpus callosum, which is related to an enhanced communication between parts of the brain, as well as brown adipose tissue, which is related to higher basal metabolic rates. The placenta of marsupials is of the choriovitellinic type, contrasting with the chorioallantoic one of placental mammals. Marsupials are nowadays restricted to Australia and the Americas, where they used to represent apex predators until the arrival of placental mammals, which occurred artificially (by humans) in the former continent and naturally in the latter, with the uprising of the land bridge between North and South America in the Pliocene. The phenomenon of parallelism, or convergent evolution, between marsupial and placental species is well documented in the fossil record of these places.

**Placentalia** (Fig. 1) is currently the dominant mammalian group in terms of species number, including more than 5,000 species in contrast with a few hundred of marsupials. Placentals have a long gestational period and the newborn are more developed than marsupial ones. The understanding of placental interrelationships has been recently revised with the incorporation of molecular data, although most traditional groups proposed based on morphology are still considered valid. Currently, four major clades of placental mammals are generally recognized. **Xenarthra** includes South American groups such as anteaters, sloths, and armadillos. **Afrotheria** includes groups of African origins, like elephants, sea cows, hyraxes, elephant shrews, golden moles, otter shrews, and tenrecs. **Euarchontoglires** is the largest group, with about half the diversity of living mammals. Rodents (► [Rodentia Cognition](#), ► [Rodentia Communication](#), ► [Rodentia Life History](#), ► [Rodentia Navigation](#), ► [Rodentia Sensory Systems](#)) represent most of this diversity, but the group also includes rabbits, tree shrews, colugos, and primates (► [Primates](#), ► [Primate Communication](#), ► [Primate Diet](#), ► [Primate Locomotion](#), ► [Primate Sensory Systems](#), ► [Primate Social Structure](#)). Finally, **Laurasiatheria** includes groups that originated in the former

supercontinent Laurasia, such as hedgehogs, shrews, moles, bats, pangolins, cats, dogs, bears, horses, tapirs, ruminants, hippos, and whales. Despite advances in recent years, there is still much controversy regarding the relationships among these groups, and morphological support for many of these large clades is disputable (Zachos 2020).

## The Other Amniotes: Reptiles

Reptiles are the most diverse group of living tetrapods, with over 20,000 described species (Uetz et al. 2020; Clements et al. 2019). They occupy many niches and have a range of locomotory modes, from flying birds to marine turtles and burrowing snakes. Reptilia is the sister-group of Synapsida (Figs. 1, 3), but many workers use the term “Sauropsida.” However, this is based on the former placement of turtles inside the group, and with their new classification, both terms become redundant (Modesto and Anderson 2004).

Features used to define extant reptiles tend not to include bird characters. They are heavily lizard-based, and often ignore turtle and crocodilian diversity. In fact, they also ignore diversity within lizards. Traditionally, non-avian reptiles possess the body covered in scales, ectothermy and poikilothermy (“cold blood”), retention of the hard-shelled amniotic egg, internal fertilization, and direct development without a larval stage.

Reptiles originated in the end of the Carboniferous (Fig. 1). The most basal members are mesosaurs and parareptiles (Fig. 4), but recent phylogenetic analyses have challenged this traditional view, and “lepospondyls” like rhynchonkids and lysorophians have been recovered as basal groups (Pardo et al. 2017b), as well as some varanopid synapsids (Ford and Benson 2019).

**Mesosauria** is a group of aquatic reptiles with several adaptations to aquatic habitats such as thickening (pachyostosis) of ribs, long caudal neural spines for support of the caudal fin, and a long snout with long and thin teeth for fish feeding. Mesosaurs inhabited a shallow inland sea between southern South America and Africa

during the Early Permian. The presence of mesosaur fossils on both continents was one piece of evidence supporting the continental drift hypothesis. **Parareptilia** was the first reptile group specialized for herbivory. Some parareptiles show convergent features with later reptiles such as skull fenestration, erect posture and tympanic hearing.

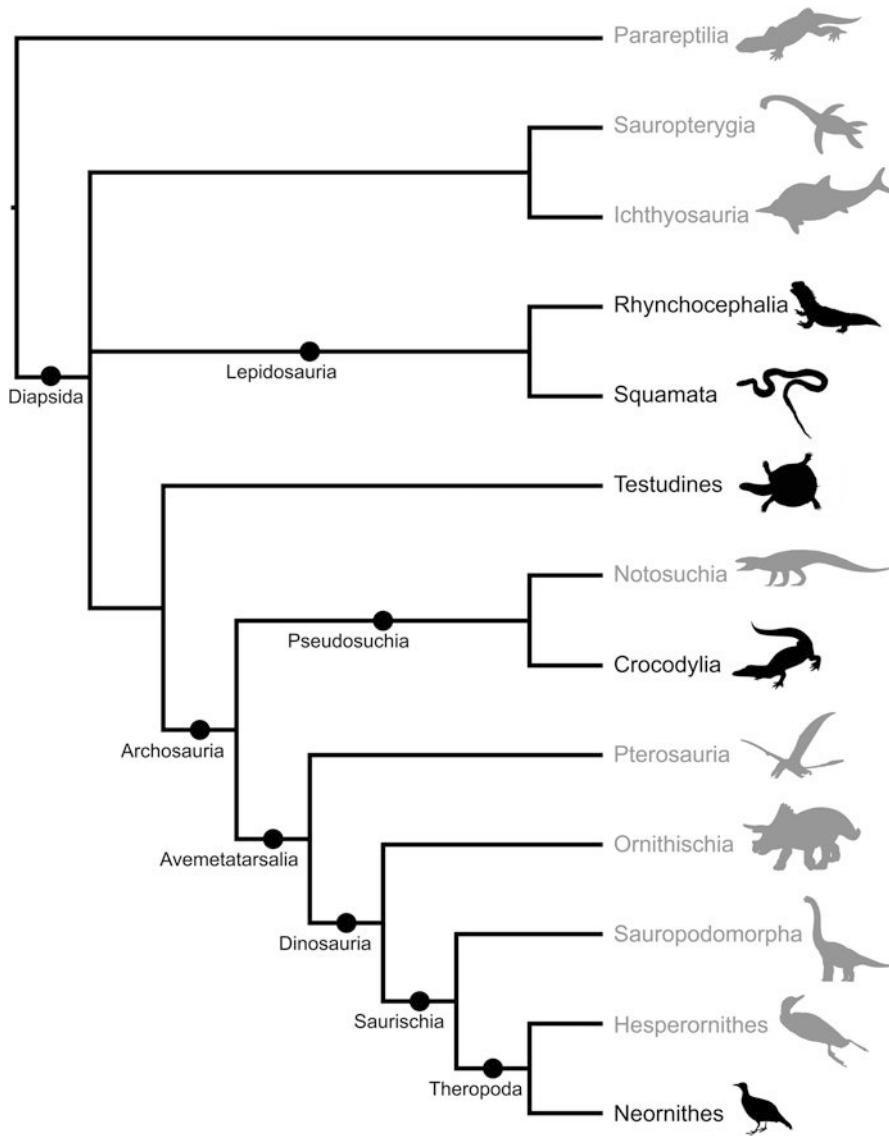
**Diapsida** represents the largest reptile radiation and includes all the living representatives of Reptilia (Fig. 4). Turtles used to be one exception, as they were considered parareptiles. Birds were the other, but are now included among theropod dinosaurs. Besides all extant reptiles, Diapsida also includes several fossil radiations, such as the tree-dwelling and digging drepanosaurs, the gliding weigeltisaurids, and aquatic reptiles. They are characterized by two skull fenestrations, besides relatively elongate distal bones of the forelimbs, and an elongate fourth metatarsus (a toe bone).

## Aquatic Reptiles

Together, marine reptiles constitute an important reptile ecomorph. Not only were they abundant during the Mesozoic, but they also represent the first major tetrapod expansion to open waters. Marine reptiles were the dominant predators in pelagic environments by the Middle Triassic; lamnid sharks did not begin to occupy these niches until the Cretaceous (Condamine et al. 2019). One reason for the underappreciated success of marine reptiles is that it is unclear whether some of the most successful lineages (ichthyosaurs and sauropterygians) form a monophyletic group and where they fit in the reptile tree. Their specialized anatomy, coupled with the lack of transitional fossils from their terrestrial ancestors, is to blame.

The expansion into pelagic environments was gradual and the most derived marine reptiles developed a lifestyle completely removed from land, including limbs transformed into flippers and live birth. Anatomical convergence with present-day aquatic vertebrates, especially between dolphins and ichthyosaurs, are common





**Vertebrates (Chordata), Fig. 4** Cladogram with the phylogenetic relationships of Reptilia. Groups with exclusively fossil representatives are shown in gray. Some clades are named at the nodes

textbook examples of convergence (► [Convergent Evolution](#)) and selective pressure regarding the evolution of flippers and of hydrodynamic body forms.

Early **Ichthyopterygia** (Fig. 4) had an elongate body and tail, contrasting with later ones with shorter tails and reduced hind limbs. An anoxic event in the early Late Cretaceous is believed to have led to the extinction of the group. Ichthyosaurs became extinct before the famous

Cretaceous-Paleogene (K-Pg) extinction event. Plesiosaurs are the most recognizable member of **Sauropterygia** (Fig. 4). They had broad and flat bodies, flippers, a reduced tail, and one lineage, the elasmosaurs, evolved very long necks. Plesiosaur limbs were well-developed, indicating that they were involved in locomotion, in contrast with ichthyosaurs, that used primarily tail fin propulsion. Sauropterygians had elevated metabolic rates and are considered mesotherms. Finally,

**Choristodera** is a group with an oddly flattened and elongated skull. Choristoderes had an extended time range of occurrence time range, from the Late Jurassic to the Early Miocene. Their phylogenetic position, however, indicates they must have existed since the Middle or Late Triassic. Other fossil aquatic reptiles are known, but they belong to the crown-group and will be dealt with later.

## Lepidosaurs: The Classic Reptiles

Lepidosaurs constitute the most diverse reptile group, together with birds. Their lineage originated in the end-Permian (Fig. 1), but their fossil record is very scarce until the Late Triassic. Of the two lepidosaur clades, **Rhynchocephalia** is currently represented by only one living species, the tuatara of New Zealand (Fig. 4). Despite this very low extant diversity, rhynchocephalians are the most abundant group in the early fossil record of lepidosaurs, representing their first radiation. They are known for a characteristic type of tooth implantation called acrodonty, in which the teeth sit atop the jaw bone, in contrast to the sockets of mammals and crocodylians (thecodonty) and the open groove of most lizards (pleurodonty). Several lizards convergently developed an acrodont dentition, so that the tuatara condition is not unique among reptiles. Rhynchocephalians also have the ancestral condition of the reptile skull in which the lower temporal fenestra is closed ventrally by a bar. Fossil rhynchocephalians include ecologically important radiations, like the aquatic group **Pleuroosauridae** and the herbivorous **Opisthodontia**, as well as the widely-distributed clade **Clevoosauridae**.

The other lepidosaur clade, **Squamata** (► [Squamate Sensory Systems](#), ► [Squamate Cognition](#), ► [Squamata Diet](#), ► [Squamate Life History](#)), includes lizards and snakes (Fig. 4). They are considered generally primitive and homogeneous. This, however, enormously underestimates squamate anatomical (► [Squamate Morphology](#)), physiological, and ecological diversity. With development of molecular methods, the

taxonomic diversity of squamates increased considerably and the phylogenetic relationship among major clades mostly settled, although controversies persist. Living squamates are characterized by having keratinized scales, but they have lost osteoderms, dermal bone elements present in many tetrapods, including extant crocodylians and armadillos. They are mostly oviparous, but several instances of internal development with a placenta are known.

Squamates are regarded as “cold blooded,” a category that usually mixes up concepts of ectothermy and poikilothermy. The first refers to an external source of heat, while the latter describes changes in body temperature. Their opposite, endothermy and homeothermy, are found in birds and mammals, although variations within these groups exist. Several squamates keep their body temperature constant throughout the day by behavioral mechanisms, or through gigantism. Similarly, seasonal reproductive endothermy has been recognized in **Teiidae** (Tattersall et al. 2016). Squamates occupy several ecological niches, including fossorial, arboreal, gliding, semiaquatic, and marine groups. They are found in all regions except the arctic and antarctic ones. One recurrent evolutionary trend in the group is the loss of limbs. Not only snakes are limbless, but several lizard groups have also lost or drastically reduced their limbs. Skull mobility is another classically recognized trait, taken to an extreme condition in snakes.

Among the main squamate groups are **Dibamidae** and **Amphisbaenia**, entirely fossorial groups. Like caecilians, they exhibit a compact skull used for burrowing, with the fusion of skull bones and reduction or loss of the eyes. **Gekkota** represents a mostly nocturnal radiation while **Serpentes** is the most diverse squamate group with over 3,700 species. Important fossil radiations of squamates include **Paramacellodidae** and **Borioteiioidea** during the Mesozoic.

Snakes are known for their limblessness, extremely elongate body, highly mobile skulls through the loss of the upper temporal bar and rearrangement of the craniomandibular articulation, and the presence of venom, although only one quarter of the species are known to be

venomous. The origin of snakes is one of the most heated debates in squamate phylogeny. Snakes originated around the Middle Jurassic, but the fossil record is scarce until the Late Cretaceous. The highly modified snake skull and the complete loss of limbs makes it difficult to determine which is their sister group. Because some of the earliest fossils are found in marine sediments, snakes have been hypothesized to be the sister group of **Mosasauria**, a clade of aquatic Mesozoic reptiles. The concurring hypothesis suggests snakes originated from burrowing lizards, and that their closest related group is **Varanidae** (Garberoglio et al. 2019).

## Archosauria

Archosauria is another large clade of living reptiles. The lineage originated in the end-Permian, but unlike lepidosaurs, their early fossil record is very rich. Several anatomical archosaur features are considered key innovations for their Mesozoic radiation, including the antorbital fenestra, thecodont tooth implantation, erect posture, and the fourth trochanter of the femur. These features are related to enhanced locomotion and increased metabolic rates. Groups outside the bird-crocodylian devise display a plethora of niches including aquatic clades like **Tanystropheidae** and **Proterochampsia**, herbivorous groups such as **Rhynchosauria** and **Trilophosauria**, as well as hypercarnivorous (► **Carnivore (Diet)**) taxa like **Proterosuchidae** and **Erythrosuchidae**.

The transition from sprawling forms to more agile, cursorial predators happened relatively fast and was further developed independently in the two archosaur groups, **Pseudosuchia** (crocodile line) and **Avemetatarsalia** (bird line) (Fig. 4). Until the Late Triassic, pseudosuchian fossils were more abundant, indicating their predominance during early archosaur evolution. In the end of the Triassic and beginning of the Jurassic, there is a drastic fall in their taxonomic and morphological diversity and a general increase in avemetatarsalians, especially dinosaurs. What caused this decrease is unknown, but competition between them has been suggested.

Triassic pseudosuchians include **Phytosauria**, crocodile-like aquatic animals with retracted nares on the top of the skull, like dolphins. **Aetosauria** represents heavily armored herbivores with an upturned snout for excavating the soil. **Ornithosuchidae**, **Poposauroidae**, and **Rauisuchidae** are hypercarnivorous groups with deep skulls. The morphological diversity of pseudosuchians during the Triassic was later mirrored by several dinosaur groups in the Cretaceous.

Whatever the cause of their decline in the end-Triassic, the aquatic environment seems to have been a refuge for pseudosuchians. During the Jurassic, most of the pseudosuchian fossil record is aquatic – although it should be noted that fossiliferous terrestrial deposits from the Jurassic are scarcer than aquatic ones. They include **Thalattosuchia**, with some species adapted to the pelagic environment, with flippers and caudal fin. Terrestrial pseudosuchians are represented during the Jurassic by small, slender forms collectively known as “sphenosuchians,” which is now considered paraphyletic. The terrestrial diversity did not flourish until the Cretaceous, but was extinguished soon thereafter. It is represented by **Notosuchia**, an anatomically diverse group highly abundant in Gondwana, where the fossil record of theropod dinosaurs is very poor (Fig. 4). Notosuchians have an array of dental morphologies, evidencing varied feeding strategies with hypercarnivorous and herbivorous taxa, but also grinding types with molariform-like teeth similar to mammals.

The current diversity of pseudosuchians is restricted to around 30 **Crocodylia** (► **Crocodylia Communication**) species only (Figs. 1, 4). They are all semiaquatic and carnivorous (► **Crocodylia Diet**), have internal fertilization, and lay hard-shelled eggs. Crocodylians were traditionally regarded as big lizards, but their morphology (► **Crocodylia Morphology**) and physiology are more like the ones of birds, including a four-chambered heart. This has led some to hypothesize that crocodylians are secondarily plesiomorphic in many traits, i.e., their primitive-looking characters correspond in fact to loss of derived features, like endothermy

(Seymour et al. 2004). The circulatory system in crocodylians changes from when they are on land to when they are diving (apnea). In these cases, crocodylians can perform a “cardiac arrest,” in which the lung loop of the blood flow is closed and the blood runs through the heart only (Kardong 2012).

## Dinosaurs and the Origin of Birds

One of the most basal groups in the bird lineage is **Pterosauria** (Fig. 4). Pterosaurs took into the air long before birds, and some have suggested that their niche competition made it difficult for pterosaurs to survive the K-Pg mass extinction event. They coexisted in some places, however, where birds occupied more closed environments and pterosaurs were found in open habitats such as lakes and shorelines.

The pterosaur wings are unlike those of birds in that they use a membrane stretched between their over-developed fourth finger and the sides of their bodies (their fifth digit is lost). Pterosaurs ranged greatly in size, from wingspans of around 1 m to over 10 m wide. They were quadrupedal on land, and capable of active flight on air. Like birds, pterosaurs had lightly-built, hollow bones and a system of air sacs. The delicate structure of their skeleton may account for the difficulty in reconstructing the transition from a terrestrial ancestor. Pterosaurs possessed well-developed cerebral hemispheres and semicircular canal systems in their inner ears, which may have been related to flight. Their bodies were covered in thin, feather-like structures called pycnofibers. Some species displayed strong ► **sexual dimorphism**, exhibiting tall crests on their skulls and snouts, and their fossils are often found in groups, suggesting gregarious habits.

**Dinosauria** is the most popular group of extinct animals (Fig. 4). They originated in the Middle Triassic and dominated terrestrial ecosystems until the end of the Mesozoic, with only one clade, birds, surviving the K-Pg boundary. The first dinosaurs were small, facultative quadrupeds and likely possessed feather-like structures like the pycnofibers of pterosaurs. Dinosaurs are

classically classified in three groups: ornithischians, sauropodomorphs, and theropods, which includes birds.

► **Ornithischia** is a group that includes mostly herbivorous and quadrupedal dinosaurs, although bipedal and facultative bipedal species exist, as well as ► **omnivore** taxa (Fig. 4). Two iconic ornithischian clades include **Stegosauria**, with plates along their back (e.g., *Stegosaurus*), and **Ceratopsia**, with their characteristic skull frills and horns (e.g., *Triceratops*). Ceratopsians were high-fiber mega-herbivores whose specializations included teeth batteries, dental occlusion, and high rates of tooth replacement. Specializations for herbivory also include their “bird-like pelvis”, from which the name “Ornithischia” is derived. The reversed pubis better accommodates increased gut lengths, facilitating fermentation. In contrast, in derived theropods and birds, the reversed pubis is related to their highly cursorial habits and increased metabolism. Another famous ornithischian group is **Hadrosauria**, which includes duck-billed dinosaurs with cranial crests. Hadrosaurs were highly specialized herbivores, having evolved several grinding features similar to mammals. Ornithischians in general are well known for their gregarious habits and parental care (► **Parental Investment**).

**Sauropoda** (or Sauropodomorpha) (Figs. 1, 4) is also an herbivorous group, but unlike ornithischians, their specializations are based on niche partitions, such as browsing versus grazing, and stratified heights. Sauropods are famous for their extremely long necks and large body sizes. In fact, sauropods feature among the largest animals known to have ever existed, although insular dwarfism is known in the group. Several aspects related to their gigantism remain largely unknown, including the evolutionary and ecological processes that prompted this trend, such as sexual selection and resource availability. Sauropods, like birds, possessed an air sac system in the neck vertebrae, which may indicate a unidirectional airflow during breathing and, consequently, highly efficient ways of oxygen intake. Similar to ornithischians, sauropods are also known for their herding habits and for a high level of parental care.

Finally, **Theropoda** (Fig. 4) is the group of bipedal dinosaurs that includes the most famous fossil of all times, *Tyrannosaurus rex*. Some theropod groups independently achieved large body sizes, such as **Megalosauroidae**, **Allosauroidae**, and **Tyrannosauroidae**. Theropods in general were specialized for fast bipedal stances, losing two to three digits on their hindlimbs, and some groups also have their forelimb size and digit number reduced. These were, however, internal trends, since in successive groups closer to birds forelimbs proportionally increased in size, probably in association with the origin of flight. Although mostly carnivorous, some theropods were omnivorous and herbivorous, such as **Ornithomimosauria**, **Therizinosauria**, and **Oviraptorosauria**.

Several trends are observed in successive sister-groups of birds associated to the development of flight. For instance, the theropod brain increased in size, especially the optic lobe and cerebral hemispheres, which are responsible for processing complex visual information. Physiological modifications include the further development of the air sacs, which is part of the breathing system, implying in increased metabolic rates. Feathers were present in most, if not all, theropod groups. They become more specialized and differentiated into several types, such as down or flight feathers. Osteological modifications include fusion of forelimb bones and wrist adaptations to stand lift, decrease in density of bones, and overall reduction in body size. Although birds are known for flying, they are not the only theropods to have done so. Groups closely related to birds were also capable of flying, sometimes engaging in their own evolutionary novelties, such as the four-winged group **Microraptor** and the weird, bat-like group **Scansoriopterygidae**. All non-avian clades became extinct following the K-Pg boundary.

## Birds

Birds comprise the most speciose of the classic terrestrial vertebrate groups, together with lizards

and snakes, accounting for nearly 11,000 species (Clements et al. 2019). Among extant vertebrates, birds are easily recognized by the presence of feathers, beak, and wings, and are mostly associated with their ability to fly. However, bird flight was a process that started long before the origin of the group and that continued long thereafter.

Bird characters that appeared before the group were listed in the previous section. Among the ones acquired after the origin of the group is the beak, as early birds still had teeth. The beak is formed by truncation of the anterior region of the skull and by elongation and fusion of the premaxillae. In fact, the bird beak might be as important as flight for their diversity, but much of the underlying processes involving its appearance is still unknown. Early birds also possessed long tails, which become gradually shorter and whose vertebrae eventually fuse, forming the pygostyle. The development of the carina in the sternum is also important, which evidences the role of the flight muscles in generating lift. It is worth noticing that some of these features, like the loss of teeth and the appearance of a pygostyle, may have been homoplastic.

Birds appeared during the Late Jurassic (Fig. 1) and became very diverse by the Cretaceous, when the crown group **Neornithes** originated (Figs. 1, 4). However, following the K-Pg mass extinction, bird fossils are rare, contrasting with molecular analyses which show that birds went through a rapid radiation following the K-Pg. Recent findings indicate that the likely reason for the low number of fossils is the small size and delicate nature of the avian skeleton. Important Mesozoic radiations include groups like the diverse and globally distributed **Enantiornithes** and the aquatic clade **Hesperornithes** (Fig. 4). Both retained teeth, and derived hesperornitheans had vestigial wings and specialized hind-limbs for foot-propelled diving.

Most of the current diversity of birds is represented by songbirds, which account for 60% of their diversity (Clements et al. 2019). The peak of bird diversification and the origin of passerine birds coincides with the Eocene Thermal Maximum, when many groups were globally widespread. Sound communication is



very characteristic for birds, which is taken to an extreme by songbirds, with the development of a specialized organ in the airways, the syrinx. Special muscles in this region can produce sound in a continuous manner, even when air is flowing into their respiratory system. Birds are unique among tetrapods in that they have a unidirectional airflow in their lungs, which maximizes the oxygen outtake from the air in a counter-current fashion. Bird behavior is also remarkable, and of all reptiles, they show the most elaborate forms of courtship and parental care.

The earliest bird lineage to diverge was **Palaeognathae**. It is comprised of mostly flightless birds (ostrich, rheas, emus, cassowaries and kiwis) referred to as ratites. The exceptions are the flying tinamous of Central and South Americas. Palaeognaths receive this name from their craniopalate articulation, which is common also in other reptiles, but has been lost in other birds. Some of the largest birds to have existed are paleognaths, namely, the moa of New Zealand and the elephant bird from Madagascar. The current distribution of ratites over former Gondwanan landmasses was used as example in vicariance models in the early days of ► [biogeography](#). However, to be found in places like Madagascar, ratites would have to have diverged prior to the breakup of Gondwana, in the Early Cretaceous. Fossil and molecular data shows that their divergence was much more recent, suggesting that dispersal involved a flying ancestral and that cursoriality evolved multiple times independently in this lineage.

All other birds, who lost the reptilian craniopalate articulation, are classified in **Neognathae**. The earliest-diverging group includes **Anseriformes** (ducks and geese) and **Galliformes** (chicken and pheasants), both of which are economically and culturally important for humans. Some anseriforms have genitalia so elaborate they commonly feature among examples of sexual conflict. Anseriforms represent an important aquatic radiation, with some species having serrated beaks and tongues for filter-feeding. Fossil anseriforms are represented by terror-bird-like taxa from the Gastornithidae and Dromornithidae families. Like other terror birds,

these used to be considered giant predatory birds, but this is now contested. Galliforms are well-known for game birds, many of which show strong sexual dimorphism with elaborate caruncles in their heads, vivid colors, extravagant tails, and intricate behaviors. For that reason, and for some extreme cases like peacocks, they usually are textbook examples about ► [sexual selection](#).

The remaining groups of birds form the group **Neoaves**. The phylogenetic relationships among them are controversial, but recent molecular analyses are settling the debate. It includes pigeons and doves (**Columbiformes**), nocturnal clades (**Strisores** and **Strigiformes**), birds of prey (**Accipitriformes** and **Falconiformes**), an aquatic group (**Aequorlithornithes**), songbirds (**Passeriformes**), and others.

### **Testudines (► [Testudines Cognition](#), ► [Testudines Life History](#), ► [Testudines Navigation](#))**

The placement of turtles in the evolutionary history of reptiles is still controversial. Turtles were considered pareiasaurian parareptiles, which was at the time further reinforced by the lack of apparent fenestrations in their skull. Like with Synapsida and Diapsida, “Anapsida” was used for the group including turtles, but it now refers only to the skull condition. Molecular studies first placed turtles on the lizard lineage, but recently they have been recovered in the archosaur line, outside the bird-crocodile split (Figs. 1, 4). Recent fossil discoveries of turtles without a fully formed shell have corroborated the archosaur hypothesis. Therefore, the anapsid condition of turtles is currently regarded derived from a diapsid skull, and the emarginations on the top of the skull have been reinterpreted as modified upper temporal fenestrae. Turtles appeared in the Middle Triassic (Fig. 1) and were not very diverse throughout their history. Turtle richness peaked in Europe during the Early Cretaceous, declining after the K-Pg, but a global pattern for diversification or extinction is absent.

Turtles have a very distinctive body plan, with a characteristic shell composed of two adjoined

parts, a plastron in the belly and a carapace in the back. The first known fossils were already fully formed turtles with a plastron and a carapace, which made it difficult to place them in the reptile tree. The discovery of fossils with a plastron but underdeveloped carapace, in addition to developmental studies, elucidated some of the process of shell formation (Lyson and Bever 2020). Shell development is connected to a less known fact about turtle anatomy (► [Testudines Morphology](#)), that their shoulders lie inside their ribcage, with some elements fused to the plastron. While some reptile groups show structures similar to shells, like pareiasaurian parareptiles and placodont sauropterygians, in none of them, nor in any other vertebrate known, the internalization of the shoulder girdle occurs.

Much of the internal turtle anatomy is modified due to the presence of the shell, the organs being accommodated in the restricted space of a rigid rib cage that will not expand. The most remarkable modification is in the respiratory system, with the development of a unique leverage system through which muscle contraction presses the viscera against the carapace to expel air, while return to the original position results in inhalation (Lyson and Bever 2020). Turtle hearts have three chambers, but unlike those of lepidosaurs, the ventricle is subdivided by a prominent muscular ridge, resulting in a functional four-chambered heart (Kardong 2012). Like crocodilians, turtles can deviate the blood flow when they dive. Turtles lack teeth and have a queratinous beak covering their jaw bones, which can be serrated.

Turtle fossil radiations outside the crown include **Meiolaniidae**, a long-lived family that inhabited Australia and New Caledonia until about 10,000 years ago, and **Thalassochelydia**, a group of Late Jurassic European sea turtles. Crown turtles are divided in **Pleurodira** and **Cryptodira**, with the main anatomical difference being their strategy for neck retraction. Pleurodirans put their necks to the side, in a space between the plastron and the carapace, while cryptodirans retract their necks fully inside their shells. Stem turtles had no mechanism for neck retraction. Pleurodirans also have their

pelvic girdle fused to the carapace, like their shoulder girdle.

All living pleurodirans are semiaquatic, freshwater animals, but the fossil record includes some marine species in the family **Bothremydidae**. This group was one of the most globally distributed, together with the living family **Chelidae**. Currently, pleurodirans are mostly restricted to the Southern Hemisphere. In contrast, living cryptodirans are much more diverse and found in all environments, from freshwater, to marine, to terrestrial. The most diverse group is **Testudinoidea** and the least but most iconic one is that of sea turtles, **Chelonioidea**, with only seven species. Chelonioids are the only pelagic group of sea turtles, with limbs transformed into flippers, although they still rely on terrestrial environments for laying eggs. Fossil chelonioids from the family **Protostegidae** include some of the largest turtles known. Testudinoid families include the tortoises (**Testudinidae**), which are mostly terrestrial, and **Geoemydidae**, most of which are aquatic and semiaquatic, with webbed digits.

## Cross-References

- [Actinopterygii \(Bony Fish\)](#)
- [Biogeography](#)
- [Carnivore \(Diet\)](#)
- [Caudata Cognition](#)
- [Caudata Locomotion](#)
- [Caudata Sensory Systems](#)
- [Chondrichthyes Diet](#)
- [Chondrichthyes Morphology](#)
- [Chondrichthyes Navigation](#)
- [Chondrichthyes Sensory Systems](#)
- [Convergent Evolution](#)
- [Crocodilia Communication](#)
- [Crocodilia Diet](#)
- [Crocodilia Morphology](#)
- [Herbivore](#)
- [Homeobox Gene](#)
- [Homology](#)
- [Monophyletic](#)
- [Omnivore](#)
- [Ornithischia](#)

- ▶ Parental Investment
- ▶ Primate Communication
- ▶ Primate Diet
- ▶ Primate Locomotion
- ▶ Primate Sensory Systems
- ▶ Primate Social Structure
- ▶ Primates
- ▶ Rodentia Cognition
- ▶ Rodentia Communication
- ▶ Rodentia Life History
- ▶ Rodentia Navigation
- ▶ Rodentia Sensory Systems
- ▶ Sexual Dimorphism
- ▶ Sexual Selection
- ▶ Squamate Cognition
- ▶ Squamata Diet
- ▶ Squamate Life History
- ▶ Squamate Morphology
- ▶ Squamate Sensory Systems
- ▶ Testudines Cognition
- ▶ Testudines Life History
- ▶ Testudines Morphology
- ▶ Testudines Navigation

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## Vespertine (Active at Dusk)

- [Crepuscular](#)

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## Vestibule-Ocular Movements

- [Cognition](#)

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## Vestige

- [Vestigial Organ](#)

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## Vestigial Organ

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## Synonyms

[Degenerated organ](#); [Remnant](#); [Rudiment](#); [Rudimentary organ](#); [Vestige](#)

## Definition

Anatomical structure that has lost its original function in a species during the course of evolution.

## Introduction

Vestigial organs are rudimentary anatomical structures that are retained in a species despite having lost their primary ancestral function. These structures often lack an apparent purpose, in contrast to the full functionality of these organs observed in closely related and ancestral species. The term “vestigial” was first utilized by Wiedersheim (1895) for use in the context of rudimentary structures that serve no apparent function. Archetypal examples of vestigial organs include structures such as wings in nonflighted birds, eyes in blind species, and vestigial limbs in snakes. Organs often become vestigial when selection for their original function becomes relaxed. They range from disadvantageous to selectively neutral to slightly advantageous (Gould 1980). Vestigial organs may be more variable compared to the same structure in other

species and may appear degenerated. Related terms such as exaptations and spandrels (discussed in detail below) are often confused with vestigial organs but are separate concepts.

## History

The observation of vestigial structures in living organisms was first described by Aristotle, in his fourth century BC book, *History of Animals* (Aristotle, c. 350 BC). Aristotle described vestigiality in the eyes of *Spalax typhlus*, a blind mole rat. He noted that although the mole rat can scarcely see, it still has eye structures that have been “stunted in development” (Aristotle, c. 350 BC, Part 9). This ancient Greek description provides evidence of an early interest in the unique characteristics of vestigial structures and their purpose in living organisms.

In the eighteenth and nineteenth centuries, vestigial structures continued to be a major point of interest in biological and evolutionary studies. In 1809, French naturalist and evolutionary theorist Jean-Baptiste Lamarck described the presence of vestigial, nonfunctional structures in many animals in his work, *Philosophie zoologique* (Lamarck 1809). His interpretation of the development of vestigial structures, also known as Lamarck’s “First Law,” described how a change in the environment also changes the needs of the organisms living in that environment. This, in turn, leads to changes in their behavior. This altered behavior subsequently leads to a greater or lesser use and utility of a given structure or organ. Increased use would cause the structure to increase in size within an individual and increasingly across generations, whereas disuse would cause it to shrink or even disappear (Lamarck 1809).

The idea of anatomical structures changing over time in response to environmental changes was elaborated and refined by Charles Darwin later in the nineteenth century (Darwin 1859, 1871). In Darwin’s seminal book, *On the Origin of Species*, he described the vestigial eyes of moles and cave-dwelling animals as “probably due to gradual reduction from disuse, but aided

perhaps by natural selection” (Darwin 1859, p. 137). In a later work in 1871, *The Descent of Man, and Selection in Relation to Sex*, Darwin described examples of “rudimentary organs” in many species and related their evolution “use and disuse” in his work (Darwin 1871). This idea of “use and disuse” incorporates some elements of Lamarck’s “First Law,” but Lamarck believed that reductions in anatomical structures would occur initially at the level of the individual. Darwin expanded on Lamarck’s hypotheses to include the impact of natural selection compounding the effects of vestigialization across generations.

With a focus on the evolutionary history of human anatomy, Robert Wiedersheim described 86 human organs considered to be “vestigial” in his work, *The Structure of Man* (Wiedersheim 1895). In it he wrote, “comparative morphology points not only to the essentially similar plan of organization of the bodies of all vertebrates, . . . but also to the occurrence of them in certain organs, or parts of organs, now known as ‘vestigial’ by such organs are meant those which were formerly of greater physiological significance than at present.” (Wiedersheim 1895, p. 2). This list of human vestigial organs is similar to those described by Darwin (1871) and includes anatomical structures that are known today to serve an essential function in human physiology. An example listed by Wiedersheim as a vestigial organ is the vermiform or cecal appendix. However, recent research (described in more detail below) provides evidence against vestigiality of the cecal appendix.

## Evolutionary Processes

The word “vestigial” is derived from the Latin word “vestigium,” meaning a trace, mark, or track. As such, vestigial structures are considered traces of past evolutionary processes. Vestigial organs can provide insight into previous evolutionary pressures, because they represent identifiable traces of ancestral characteristics or behaviors in living organisms (summarized in Müller 2002). These evolutionary changes shed



light onto the adaptations of past generations and reveal how adaptive pressures may have shifted compared to earlier members of the phylogenetic lineage.

Vestigial structures typically arise when positive selection pressures for the original function become reduced, often due to changing environmental conditions or novel adaptations. Over time, relaxed adaptive constraints may render the structure more susceptible to the impacts of neutral evolutionary process such as mutation and genetic drift, which produce greater variability in the vestigial organ (Gould 1980). This process also often results in a reduction in size of the vestigial organ, such that the organ becomes atrophied or underdeveloped. The vestigial organ may also appear only during early stages of development and be lost in adults, such as gills in the embryos of air-breathing land vertebrates. Sometimes, the vestigial organ may cause no direct damage to the organism but may still require maintenance or developmental costs, causing it to be slowly phased out. In the most extreme cases, the structure may even be selected against if its function or presence becomes detrimental to the organism's success under the changing circumstances.

One example of the aforementioned vestigial atrophy phenomenon is the auricular (ear) musculature that moves the ear of mammals with large mobile ears, such as monkeys. There is strong selection for well-developed auricular muscles in monkeys because they serve a significant survival function by providing an improved ability to hear potential predators and other hazards (Macalister 1871). Since humans have primarily stationary ears, selection on these auricular muscles has relaxed, and they have consequently become degenerated (Darwin 1871). While ear muscles are still present in modern humans, they are diminutive, and most people possess only minimal voluntary ear mobility.

In humans, there are several examples of vestigial structures including but not limited to wisdom teeth (third molars), ear muscles, and various small tendinous muscles. One specific structure to note, the palmaris longus muscle, is absent in approximately 14% of the population

and provides no additional grip strength (Sebastin et al. 2005). This muscle is considered vestigial due to its lack of serious forearm muscle action, as well as its variability among humans and other close primate relatives. In fact, the palmaris longus provides so little functional efficacy to wrist movement, that it is commonly harvested and used as surgical tendon graft material for other parts of the body where tendons or ligaments are needed, such as anterior cruciate ligament (ACL) repairs. Patients with removed palmaris longus tendons do not show any reduction in grip strength in its absence (Sebastin et al. 2005).

Another classic example of vestigial structures can be observed in the pelvic anatomy of certain snakes. Some primitive snakes have pelvic spurs, which are vestigial remnants of legs found in either side of the vent (Pough et al. 2003). Two well-known examples of snakes with pelvic spurs are boas and pythons. These remnants of the pelvis and femur simply float within the pelvic muscle mass on either side of the snake's cloaca. The rudimentary vestigial femur also protrudes from the snake's body, resembling a spur or a claw. It is believed that these structures may now serve a purpose in the mating behaviors of these snakes (Pough et al. 2003). If this is the case, they could be considered examples of exaptation.

## Identification of Vestigial Organs

Vestigial organs are generally identified through comparisons of related species. Evolutionary patterns are evaluated in structures that are believed to be homologous, or shared due to common ancestry. For example, wings in all extant (modern) birds are the result of descent from a shared common ancestor with wings. Since the primary function of wings in most birds is to fly, the primary adaptive function of wings is interpreted to be flight. In birds that cannot fly, such as the ostrich, the presence of wings is therefore considered vestigial, because the ostrich's wings have lost their original adaptive function compared to other closely related avian species.

The process of identifying vestigial organs may rely upon tracing the evolution of a structure across a phylogenetic tree of genetic relationships. This process is often referred to as phylogenetic bracketing (Witmer 1995). Following this approach, characters are mapped onto a phylogenetic tree. An organ is inferred to be vestigial in a species if it seemingly lacks a function compared to an apparently functional state in at least two other closely related species (Witmer 1995). This analysis indicates whether the organ has lost its function in comparison to its relatives, which would qualify it as vestigial.

Identifying a vestigial organ can sometimes be challenging because the process requires confirming that the structure under question no longer serves its original adaptive function. These identifications can be difficult if the original function of an organ is unclear or unknown, such as structures that appear only in the fossil record with no modern analogue. In these cases, experimentation may shed light onto the possible functions of these ancient structures.

## Exaptation

As early as Darwin's time, it was noted that some organs, while providing a seemingly useful function, may serve a purpose other than their original adaptive function (Darwin 1859). For example, Darwin noted that sutures in the skulls of infant mammals facilitated the birthing process. However, the skulls of developing reptiles and birds also have sutures, so it would not be accurate to suggest that sutures evolved as an adaptation to parturition (Darwin 1859). Similarly, in his landmark text on adaptation, George C. Williams noted that some organs serve "effects" that should be considered separate from their original adaptation (Williams 1966). However, despite observations regarding the nuances of adaptive and vestigial characters, a term was not proposed to describe evolutionarily co-opted structures until the 1980s.

Exaptation is a distinct, though related concept to vestigiality. Exaptation occurs when an organ loses its original function but takes on a new adaptive purpose (Gould and Vrba 1982). The

structure is useful to the organism and offers a selective advantage, despite having lost its initial functionality. In other words, an exaptation is a structure that is co-opted for a new, adaptive use (Gould and Vrba 1982). Because the exaptation still has an adaptive value to the species, it cannot be considered truly vestigial.

Since an exaptation is commandeered for a secondary purpose, it may be an imperfect design for the new function (Bock 1959). Evolution in the case of exaptations has been argued to play the role of a "tinkerer" rather than an engineer, working with existing parts to modify and make them fit a certain function rather than starting with an ideal design plan from the outset (Jacob 1977). The classic example of this phenomenon is the panda's "thumb," which is not composed of phalangeal bones but instead of an expansion of the radial sesamoid, making it comparatively clumsy compared to fully phalangeal primate thumbs (Gould 1980).

There are several examples of exaptation in avian (bird) evolution. First, feathers likely first evolved for thermoregulatory purposes in flightless avian dinosaurs (Sumida and Brochu 2002). After they appeared, feathers were later co-opted for flight, which is highly adaptive and beneficial to the success of bird species. Second, wings in aquatic birds such as penguins are another classic example of an exaptation. While the structure of wings initially evolved to facilitate flight, these wings have been co-opted for propulsive swimming in aquatic birds. Therefore, since both feathers and wings serve clearly adaptive purposes in modern birds that differ from their original adaptive purpose, they are considered exaptations.

A recent example of exaptation is the cecal "vermiform" appendix in humans and other mammals (Bollinger et al. 2007; Smith et al. 2013, 2017). Scholars have long noted that human survival is not negatively impacted by the removal of the appendix, suggesting to many that it served no adaptive function. Charles Darwin originally hypothesized that the appendix in humans and other great apes is a vestigial organ because its purpose was unknown at that time (Darwin 1859). Darwin hypothesized that as an outpocketing of the gastrointestinal tract, the appendix must have

once served a digestive function. However, the large intestine decreased in size in frugivorous (fruit-eating) ape ancestors, resulting in an appendix that is too small to serve any digestive function (Darwin 1859). However, it was noted by early twentieth century medical practitioners that the appendix contained a concentration of lymphoid tissue, a type of support tissue for the immune system (Berry 1900). Only in the last decade has the functionality of the appendix become apparent, reversing the idea that it is a vestigial organ. In 2007, Randall Bollinger and colleagues described a biofilm of beneficial gut bacteria in the appendix, which led them to hypothesize that the appendix serves an important function in maintaining commensal gut microflora (Bollinger et al. 2007). Comparative analyses mapping appendix evolution on the mammalian phylogenetic tree have revealed that the appendix evolved multiple times throughout mammalian evolution, suggesting that it serves an adaptive function. Thus, taxa with an appendix have a higher concentration of lymphoid tissue in the appendix/cecal region, supporting its immunological role (Smith et al. 2013, 2017).

## Spandrels

Another concept that is important to differentiate from vestigial organs are structures that are referred to in the evolutionary biology literature as “spandrels” (Gould and Lewontin 1979). A spandrel was originally an architectural term, referring to the triangular space between two contiguous arches and the ceiling. However, in their seminal work, *The spandrels of San Marcos*, Steven Jay Gould and Richard Lewontin (1979) made the analogy between architectural spandrels at Saint Mark’s cathedral and certain anatomical features. Architectural spandrels are simply the byproduct of two adjacent arches, but they are often decorated in ornate Renaissance style. Therefore, an architectural novice might presume that the function of spandrels was to showcase beautiful artwork, while in reality they are merely the result of the geometry of arches.

Similarly, some anatomical structures, they argued, may appear to have evolved for a

particular purpose when they were actually simply the result of an unrelated evolutionary event (Gould and Lewontin 1979). In other words, evolutionary spandrels are features that arise as byproducts, rather than through adaptation and selective pressures on the structure itself. The occurrence of evolutionary spandrels cautions biologists from interpreting every anatomical structure as either adaptive or vestigial and serves as an important reminder that the evolution of some structures may result from selective pressures and adaptive changes that only indirectly shaped the organ. A spandrel could also be considered a type of exaptation if it serves an adaptive function in the species.

## Conclusion

Vestigial organs are generally defined as structures having lost their original evolutionary function. Such structures can provide insight into former evolutionary pressures and behaviors and indicate how adaptive regimes have shifted across a phylogenetic lineage through time. However, the identification of vestigial structures is marred by the fact that evolution is resourceful. Even anatomical structures whose original function becomes lost may still be selected for alternative purposes, as in exaptations. In addition, some structures that appear vestigial are actually evolutionary byproducts that never served a function at all, as in spandrels. Thus, upon review of many structures that are considered classic examples of vestigiality, it becomes apparent that truly vestigial organs are quite rare. From wings used for swimming in nonflighted birds to the immunological functions of the vermiform appendix and the panda’s “thumb,” evolution is flexible and offers creative solutions to adaptive problems.

## Cross-References

- [Adaptation](#)
- [Evolution](#)
- [Evolutionary By-product](#)
- [Morphology](#)

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## Video-Task Paradigm

- [Computerized Testing Paradigm in Primates](#)

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## View Screen

- [Touch Screen](#)

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## View-Based Homing

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In one of the most famous animal behavior studies of all time, Niko Tinbergen mischievously disturbed the day-to-day navigation of a solitary wasp. While the wasp was inside her burrow, he placed a ring of pine cones around the entrance, and upon leaving she noticed the change, flew a series of inspection loops, and departed. Upon returning from her trip, the wasp searched for the nest at the center of the ring of pine cones even though the ring had been displaced (Tinbergen and Kruyt 1938). These experiments revealed that the wasp did not detect the nest entrance directly, but knew its location because of the relationship with the visual surroundings. With another animal anecdote, we can show a similar phenomenon. Karl von Frisch, who shared the Nobel Prize with Tinbergen, observed a bird building a nest in the repetitive eave structure of

a bike shed (von Frisch and von Frisch 1974). Evidently using the remembered appearance of the bike shed roof to pinpoint the nest location, the bird made multiple mistakes because so many potential nest locations looked the same. The result was rather energy sapping for the poor bird, with multiple nests being built in parallel. These two examples show how remembering the appearance of the world from a target location can be used to guide behavior. This is a general mechanism called view-based navigation. It works because in a complex natural world, unlike von Frisch's bike shed, views are specific to locations. For example, two photographs taken with the same camera can only be identical when the camera location and orientation are matched. This relationship between views and locations means that remembered views can be used to home to a specific discrete location or to set a direction of travel, two actions which are general requirements of animal navigation.

There are fundamental reasons why view-based matching is a sensible, efficient strategy for any navigator. Different animals have different sensory systems and different ways of perceiving the world (their *Umwelt* or self-world), resulting from filters developed during their evolutionary and personal history (von Uexküll 1957). However, for animals with any type of visual system, view-based matching is a computationally inexpensive process because the visual information perceived can be used directly for navigation. Views are necessarily perceived from an egocentric point of view (i.e., depending on the animal's current position and direction), and with view-based matching, views can be memorized and compared directly within this egocentric frame of reference, without the need to be transformed into more complex spatial representation. In addition, egocentric views are an excellent task specific representation of the world because views change with movements. Movements in space (i.e., navigational behavior) map simply onto changes in the position of visual components of a view; therefore, differences between current views and remembered views can be transformed into corrective movements. Furthermore,

robustness comes from the informational content of natural visual scenes. A remembered view will contain information from multiple objects of different sizes and distances. This means that views change smoothly as one moves and these smooth changes allow animals (or robots) to calculate the required movements to recover an orientation, return to the location of a remembered view, and to detect when one has arrived.

Following Tinbergen and more detailed experiments with bees (Cartwright and Collett 1983), the use of egocentric remembered views for navigation is often thought of as a simple insect strategy, often referred to as snapshot matching. However, all animals have to deal with egocentric views (i.e., their sensory input) and we know that these views can directly provide effective and economical solutions for navigation. Therefore, it is no surprise to see convergent use of egocentric views for spatial tasks across taxa, such as in birds and mammals, including humans (Wang and Spelke 2002; Shelton and McNamara 2004; Pecchia et al. 2011). We also see similarities in the way that animals use multiple remembered views to guide idiosyncratic habitual routes (Kohler and Wehner 2005; Biro et al. 2004; Calhoun 1962; Hartley et al. 2003) which seems to be a convergent strategy for moving through familiar environments, as humans typically do when recapitulating a well-known route on "autopilot."

For robust view-based navigation, what matters is the spatial arrangement of the objects across the scene, and not the identification of those objects. Interestingly, object and spatial memories seem to be dissociated in vertebrate brains. For example, human patients with visual agnosia following brain damage are often unable to recognize objects, even though they can navigate through the world (Farah 1990). In contrast, spatial navigation can be strongly impaired when lesions occur in the parahippocampal place area (PPA), a region involved in scene recognition, based on wide-field information about the layout of objects (Epstein 2008).

It is clear that animals differ in the way they perceive and use visual information. Insects may



rely entirely on egocentric views for navigation, while we humans can recognize individual objects and build more complex spatial representations. However, for certain tasks, such as repeated navigation through familiar environments, views are an efficient and computationally inexpensive strategy. For large brained animals, this may reserve valuable cognitive resources for other tasks. Therefore, we caution that in no case should we assume that the existence of more complex spatial abilities in some animals precludes the convergent use of simple, robust strategies across taxa (Wystrach and Graham 2012).

## Cross-References

- [Central Place Foraging](#)
- [Cognitive Map](#)
- [Egocentric Frame](#)
- [Insect Navigation](#)
- [Landmark](#)
- [Nikolaas Tinbergen](#)

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## Vigilance

Gisela Kaplan

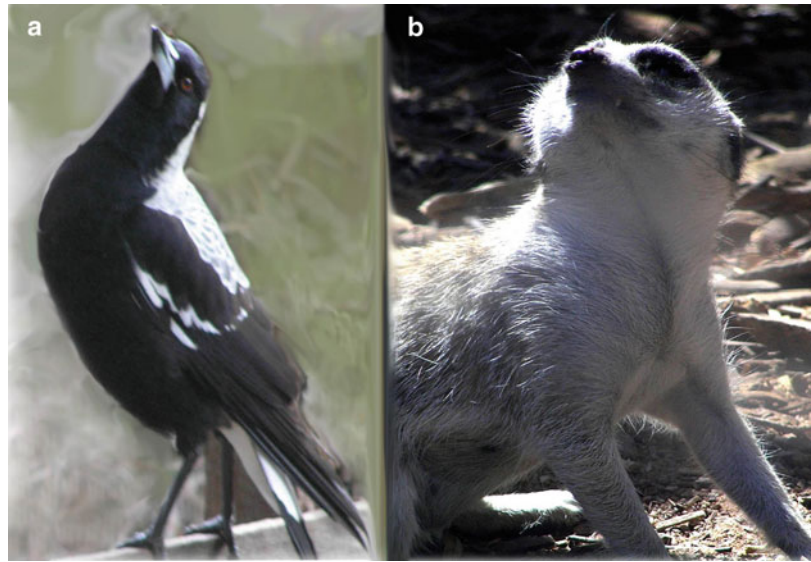
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Vigilance involves basic information gathering (Bekoff 1995). It is the active act of deliberate watchfulness and monitoring of potential threats caused by predators and even conspecifics. Heightened vigilance in animals is usually based on specific environmental circumstances, such as a noise or a movement that may warrant careful assessment. Heightened vigilance may also be indicated if an environment is unfamiliar and/or if visibility is poor and could potentially hide an ambush predator. Vigilance is associated more with prey species than with predators; at least the need for vigilance may be ongoing in prey species but be rare or intermittent among predators unless a competitor is nearby. In addition, vigilance is associated with the protection of nest sites (Yasukawa et al. 1992) and dens (Santema and Clutton-Brock 2013) (Figs. 1 and 2).

Having to be vigilant can have a number of negative side effects, chief of which is the

**Vigilance,**

**Fig. 1** Vigilance including scanning can be readily measured in mammals as well as in birds – such as extending neck, turning head, and the angle of the turns. **(a)** Australian magpie scanning the sky, turning head to left in order to scan the sky with the right eye; **(b)** meerkat having detected a potential predator raises its head and turns it to the right, facing upward. Credit: Gisela Kaplan



**Vigilance, Fig. 2** Sentinels usually choose the highest vantage point, be that on a small hill as in prairie dogs or meerkats or at the very highest point of a tree, here a yellow-tailed black-cockatoo on sentinel duty while the rest of the family feeds lower in the tree. Credit: Gisela Kaplan

inability to forage simultaneously while scanning the environment. This applies particularly to some mammals with frontally placed eyes. Birds can scan for predators in the lateral monocular field while pecking at food items in the frontal field, but this limited viewing is often not sufficient. A number of species solve this problem by flocking together or at least increasing group size, as is

the case in ungulates (Han et al. 2020) and in shorebirds (Metcalf 1984). Other group-living species share sentinel duties (Wright et al. 2001) allowing the rest of the group to forage and increase biomass (Hollén et al. 2008).

Vigilance behavior, specifically in prey species and in environments with high predator presence, is also related to fear. Indeed, threats are part of what has been termed “a landscape of fear.” It has been shown in countless studies that these “fear effects” can significantly alter the physiology, behavior, and life history of prey species (Gallagher et al. 2017). Fear can have sublethal effects on prey behavior and physiology and may have long-term consequences for prey population dynamics. Boonstra et al. (1998) showed in snowshoe hares that vigilance only served to confirm high predation risk and induced chronic stress which led to a series of health effects, such as loss of weight, stunted growth, cessation of reproductive activity, and eventually death by predation.

However, associating vigilance with fear may be problematic, as Beauchamp (2019) pointed out. Some animals experience fear without showing vigilance, and some may become desensitized to threats because they are too hungry.

There is a third reason to not automatically associate vigilance with fear, and this has to do

with experience and learned strategies of what to do in facing or avoiding danger. In Australian magpies, for instance, vigilance behavior is highly developed, ranging from periodically flying to the top of trees, scanning at high vantage points as well as at any other height and on the ground. If a predatory intruder is identified, alarm calls bring the territorial group together which then proceeds systematically and effectively to drive that predator out (Koboroff et al. 2013), even if it is substantially larger than they are, such as wedge-tailed eagles (Kaplan 2019). They have learned to outsmart potential predators. When cooperation is involved and/or past experience and an understanding of the predator's strategies and weaknesses, stress levels tend to be low or return to normal very quickly, and vigilance in these cases is part of a well-prepared method to remain in control regardless of a predator's size and strength.

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## Violence

### ► Benefits for Aggression in Humans

## Virtual Reality Experiments

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## Synonyms

Computer interface; Computer-generated environment; Simulation

## Definition

In the context of experimental research, virtual reality refers to immersive, computer-generated environments that are sensed by the subject and are updated by the subject's actions in real time.

## Introduction

Virtual reality (VR) technologies are increasingly used in the behavioral sciences to overcome the constraints of traditional “open-loop” experiments. Open-loop experimental designs decouple sensory stimuli from motor behavior by

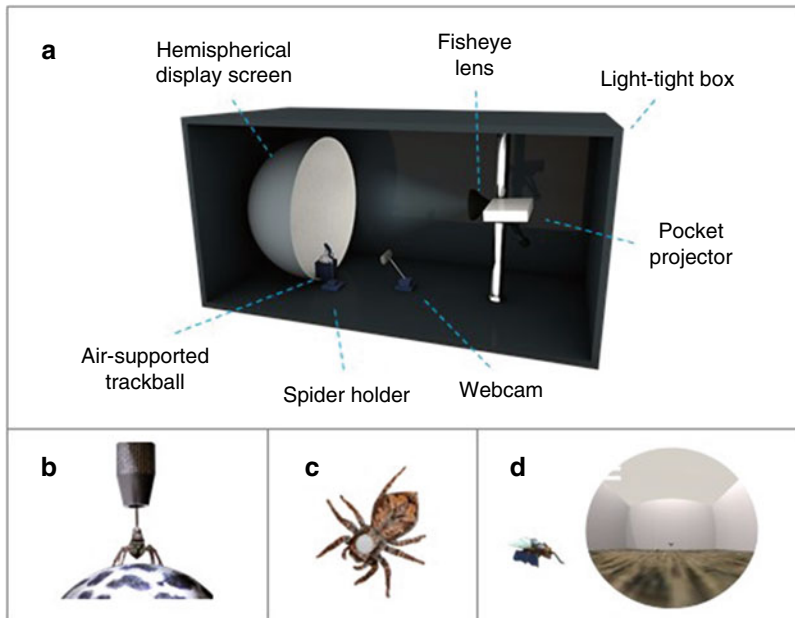
presenting stimulus conditions to the subject independently of the subject's responses to these stimuli. In contrast, closed-loop (feedback) systems such as VR allow stimulus conditions to be updated by the subject's responses in real time.

Since VR experiments are typically implemented using automated, computer-controlled technologies, virtual stimuli and virtual environments can be designed along a spectrum from abstract to photo-real and can include parameters and contingencies that would otherwise be impossible to create in the real world. As such, VR can provide a valuable middle ground between ecological validity, in which the "realness" of the experimental design is paramount, and experimental control, in which experimental variables are highly reliable and precisely controlled (Bohil et al. 2011).

### Components and Considerations

Recent advances in technology have enabled the development of a number of different VR systems for experimentation with animals. In general, a VR system should comprise the following components and considerations:

1. *Generation and display of the virtual environment:* The VR system must be carefully designed to reflect the sensory system properties of the test species. For a visually based system (the most common focus of VR presently), chromatic, luminance, and spatial properties of the animal's entire visual system must be taken into account. For example, for animals with very wide fields of view (such as mice, flies, and zebrafish), panoramic, hemispherical, or spherical displays may be most appropriate. Another important consideration is the selection of a display screen with an appropriate critical flicker-fusion frequency (CFF) in relation to the CFF of the experimental animal. The CFF is the frequency at which a flickering stimulus begins to appear continuous and varies widely between taxa. For example, slow-moving animals such as crickets have CFFs in the range of 45 Hz, while fast-moving animals such as bees have very high CFFs in the range of 300 Hz. To ensure that screen flicker is not detectable in the visual display, the CFF of the visual stimuli should be equal to or greater than the CFF of the experimental animal. For a more detailed discussion of the challenges of using video stimuli in behavioral experiments, see D'Eath (1998).
2. *Restraint:* While restraint is not requisite for VR (for example, see #3 below, regarding servomotor-based systems), restraining the interacting animal allows for simultaneous recording of behavior and neural activity. Restraint is commonly performed by immobilizing the head and allowing some or all of the rest of the body to move normally. For example, head-fixed monkeys can perform a virtual navigation task while hippocampal cells are recorded (Hori et al. 2005); head-fixed drosophila continue to fly by beating their wings in a flight arena while electrophysiological recordings are conducted (van Swinderen 2012); and head-fixed jumping spiders mounted atop an air-supported spherical treadmill can navigate through a 3D virtual environment (Peckmezian and Taylor 2015; see Fig. 1).
3. *Recording movement:* Motion tracking is a critical component of both freely moving and tethered VR systems. Early free movement systems used servomotors to control the rotation of a sphere that an animal was freely walking on, with movements detected by rotary encoders that were in direct contact with the sphere. Subsequent versions have positioned tethered animals atop spherical treadmills supported by a cushion of air, with spherical rotations detected by optical or laser computer mice positioned nearby. Most recently, a vision-based tracking system has been designed that overcomes many of the constraints of computer mice (such as sensitivity to changes in illumination, texture, and radial and diagonal motion) by motion tracking the rotations of an air-supported sphere using an off-the-shelf webcam (Moore et al. 2014).
4. *System latency:* Across all sensory modalities, the latency for the simulation to update is a critical feature of a virtual reality system and is intricately linked with the perceived "realness" or level of immersion in the simulation.



**Virtual Reality Experiments, Fig. 1** Example of VR implementation for experiments with jumping spiders (see Peckmezian and Taylor 2015). (a) Schematic of VR system. Spiders are mounted above an air-supported spherical treadmill placed inside a hemispherical display screen. Dynamic computer generated 3D environments are front-projected onto the screen via a pocket projector with add-on fisheye lens, and spider movements are detected by a camera-based tracking system (FicTrac) and update the

world in real time (a closed-loop system). (b) A spider mounted above a spherical treadmill in preparation for a trial. A magnet is fixed to the spider's dorsal carapace and a magnetic pin holds the spider in position. (c) A close-up of a jumping spider with magnetic cap in place. The cap can remain in place to minimize handling between sessions or can easily be removed with tweezers. (d) An example of a virtual prey object (available through *Biometric games*) and a simple, virtual arena (constructed in Unity 3D).

Long delays between an animal's movement and a corresponding update in the display can break the feedback loop that defines a closed-loop system. The total VR system latency is based largely on three components: tracking, rendering, and display. In general, the update latency should be equal to or less than the animal's corresponding reaction time.

### Benefits of Virtual Reality Experiments

Virtual reality experiments offer a number of advantages over traditional methods in behavioral research. First, VR allows the subject to interact naturalistically with the simulated environment. Compared with open-loop computer-based experimental designs, VR allows researchers to present and control multimodal stimulus inputs, so that the subject experiences a greater degree of

sensorimotor immersion. It is not necessary for the stimuli present in a virtual environment to perfectly match the real world along all domains; rather, the goal of virtual design is to replicate a sufficiently convincing subset of the features that the subject would sense while moving freely within the real equivalent of the virtual environment (Dombeck and Reiser 2012).

Second, VR equips researchers with intricate control of a multitude of experimental parameters, including both those presented to and recorded from the subject. The researcher can present combinations of stimuli that are not found in the real world and can enact changes in the environment that would not be possible physically. Likewise, VR allows the creation of landscapes that are greatly extended from what would be feasible in a typical space-constrained lab.

And third, when paired with restraint, VR provides a powerful context in which to couple



behavioral and perceptual experiments with neurophysiological recordings. In tethered flies alone, techniques such as whole cell patch clamp, extracellular recordings, and functional two photon microscopy have been used to record from visual neurons and interneurons during visual motion stimulation (reviewed in Dombeck and Reiser 2012).

### Limitations and Common Criticisms of Virtual Reality

While significant advances in the technologies supporting VR have occurred in the past decade, immersive VR systems are still relatively costly and challenging to execute. To build a visually based VR system, for example, specialized skills are required in programming, 3D modeling, stimulus design and animation, and projection and tracking softwares.

In addition, providing an adequate level of realism to elicit “normal” behavioral (and neurophysiological) responses poses numerous technological challenges. In restrained animal preparations, one such hurdle is the lack of appropriate motion cues. Most mammals (including commonly studied taxa such as humans, primates, and rodents) have a vestibular system within their inner ears that contributes to spatial orientation, movement, and balance. A lack of appropriate vestibular input in animals interacting in virtual environments can confound both electrophysiological recordings and the subjects’ experience of immersion. For example, restrained rats and primates navigating in virtual environments display hippocampal place cell activity that is markedly different than when they navigate in the real world (primates: Hori et al. 2005; rodents: Hölscher et al. 2005). Similar behavioral artifacts can be observed in restrained invertebrate species that possess equilibrium sensors. Flies, for example, exhibit distortions in flight behavior when mechanosensory feedback from specialized stabilizing organs, the gyroscopic halteres, is impeded, as is the case during restraint. The limitations imposed by equilibrium sensors can be circumvented through VR studies of walking invertebrates that lack equilibrium sensing organs, such as spiders, by avoiding restraint altogether with free-movement systems,

or by adequately accounting for these effects in experimental design and/or interpretation.

### Conclusion

VR is emerging as a powerful tool in the study of animal behavior and neurophysiology, with unique advantages over other experimental approaches. Recent technological advances in many of the components of virtual systems have improved the fidelity, realism, and applicability of these systems to a wide range of animal models and experimental paradigms. While most current VR systems emphasize visual stimuli, virtual environments delivering olfactory, auditory, or tactile cues broaden the range of animal models available to VR experimentation and, when paired with visual cues, are likely to increase the realism of the simulation.

### Cross-References

- [Computerized Testing Paradigm in Primates](#)

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## Visible Characteristics

### ► Phenotype

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## Visible Displacement

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## Synonyms

[Object permanence](#)

## Definition

Visible displacement is the ability to locate a hidden object after seeing that object placed in, under, or behind an occluder.

## Introduction

Visible displacement is one stage of developing object permanence. Object permanence is the understanding that objects exist even when they not able to be directly perceived. Piaget (1954) proposed that human children develop object permanence during the sensorimotor period of development. Further, object permanence skill developed slowly in six stages. In the first stage,

human infants show no response to the disappearance of an object. Infants in stage 2 will track an object of interest but will not follow the object once it is out of sight. Further, they show no anticipation of where the object would logically be once it moves out of sight. By stage 3, children can locate partially hidden objects such as a toy that is sticking out from under a blanket. Children will successfully retrieve fully hidden objects in stage 4. This is called visible displacement. However, children make a consistent error in stage 4. The A-not-B error means that children will look in a location that an object was repeatedly hidden even though, this time, they witnessed the toy being hidden in a different location. By the fifth stage, children have grown out of this error and are capable of finding an object where it was the most recently hidden. The sixth, and final, stage of object permanence development involves seeing an object hidden under a displacement device and then moved to a new hiding location. The object is surreptitiously placed in the new location and the empty displacement device is shown to the child. This is called invisible displacement. Children who have mastered stage 6 object permanence are able to track the movement of the hidden object and correctly locate it in the new location.

## Experimental Methods

The methodology for testing visible displacement in human infants on object permanence tasks is well established. In the traditional method of testing for visible displacement, a child is shown a favorite toy and then the toy is hidden underneath a blanket or other occluder (Piaget 1954). The child with object permanence would lift up or reach under the blanket to retrieve the hidden toy. An alternative test would be to place the object inside one of three boxes and then ask the child in which box the toy is located. Children with object permanence successfully choose the box with the hidden toy inside.

An alternative method is the violation of expectation test. In this type of experiment, a

child watches an event take place, but the ending is changed in such a way as to violate what the child expects to see. One simple test of this is to show a child a toy and then place it behind a barrier. The barrier can then be rotated either 120° or 180°. The 120° rotation would be an expected event because the barrier should not be able to rotate through an object placed behind it. The 180° rotation would be an unexpected outcome because, if an object is placed behind the barrier, the barrier should not be able to rotate through the hidden object (Baillargeon et al. 1985). One application of the violation of expectation procedure was to demonstrate that human children were able to solve visible displacement tasks at an earlier age than was proposed by Piaget. While Piaget suggested that children did not develop object permanence ability until approximately 12–18 months of age, several studies using the violation of expectation procedure have demonstrated that infants as young as 3.5 months of age demonstrate visible displacement (Baillargeon and DeVos 1991).

## Visible Displacement in Animals

Visible displacement tests in animals typically take the form of asking whether animals can identify which of several occluders a hidden object is in. Many animals have been tested and pass visible displacement tests including dogs, cats, parrots, and many monkey species (see Jaakkola et al. 2010 for review). Ape species such as chimpanzees and orangutans also successfully pass these visible displacement tests (e.g., Call 2001).

Jaakkola et al. (2010) demonstrated that bottlenose dolphins are successful at visible displacement tasks as well. In this experiment, dolphins were asked to indicate in which of three opaque containers a toy had been placed. Similar results were reported by Mitchell and Hoban's (2010). Here, the trainer held the object (a fish) directly over one of the containers and dropped it in on some trials or picked up a bowl and put the fish in it before placing the bowl back in the water on other trials.

More recently, the violation of expectation (VOE) testing method has been used to test Atlantic bottlenose dolphins and California sea lions on visible displacement. In this experiment, Singer and Henderson (2015) used the animal's fish bucket as the object. The animal was shown the fish bucket and then it was placed on a table. A research assistant rotated a screen either 120° or 180°. Experimenters recorded mean looking time for both trials types. Looking times were significantly longer on surprise trials (180°) than on expected trials (120°).

## Limitations

Recently, research has focused on addressing the limitations of many of these prior studies. The primary concern is that animal may have been able to choose the correct location of a hidden object by using associative rules. For example, an animal may associate the container that was last touched with the object rather than relying on mental representation of where the hidden object is (Collier-Baker et al. 2004). The location of the experimenter, eye gaze or body position of the experimenter, or trajectory of the object may all lead to associative learning (Andras et al. 2016). The violation of expectation effect methodology may be one way to control for associative learning, but research with appropriate controls is also being called for.

## Conclusion

Most animals tested on visible displacement are successful at tracking an object as it is hidden. Future studies focus on ruling out associative learning explanations for these successes.

## Cross-References

- ▶ [A-Not-B Problem](#)
- ▶ [Invisible Displacement](#)

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## Vision

- [Accipitriformes Sensory Systems](#)
- [Catarrhine Communication](#)
- [Cetacean Sensory Systems](#)
- [Entopallium](#)
- [Falconiformes Sensory Systems](#)
- [Feature Integration Theory](#)
- [Hominoidea Sensory Systems](#)
- [Mustelid Communication](#)
- [Mustelidae Navigation](#)
- [Platyrrhine Sensory Systems](#)
- [Primate Sensory Systems](#)

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## Visual Attention

- [Feature Integration Theory](#)

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## Visual Attention Paradigm

- [Bucket Experiment](#)

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## Visual Cells

- [Parieto-occipital Sulcus \(POS\)](#)

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## Visual Cliff, The

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## Definition

The visual cliff is an apparatus designed by Eleanor Gibson and Richard Walk (1960) to study the development of depth perception in a variety of species. The main structure is a glass board that is suspended in the air; a checkered-patterned fabric is placed flush against one side of the glass and another piece of the same fabric is placed on the ground below the other side of the board. This creates the visual illusion of a cliff. The subject is placed on a center board between the two sides, and the choice behavior of which side they descend to is recorded. This apparatus has been used to study a variety of concepts, including the development of depth perception, stimulus cues used in depth discrimination, and the importance of locomotion and rearing environment.

## Introduction

The visual cliff was a methodological marvel at the time of its conception in the mid-1900s. Created by Eleanor Gibson and Richard Walk (1960), this relatively simple apparatus allowed for the systematic examination of depth perception. It quickly became a popular tool in developmental psychology for testing the presumption that depth perception is innate (Rodkey 2015). Despite earlier attempts to tackle this question, it cannot be disputed that the design of the visual cliff provided more valid results than preceding methodologies. This innovative solution presented subjects with a semi-natural problem that required no training and minimal experimenter interference.

The actual design of the apparatus is relatively simple and, after some early alterations, it has not required many revisions since its conception (Rodkey 2015). To create the visual illusion, a single piece of glass is supported above the ground, and a piece of checkered material is placed flush against one half of the glass board. This gives that half (known as the shallow side) the appearance of solid ground. On the other side of the glass (known as the deep side), the same checkered material is placed on the ground, giving the appearance of a cliff. Subjects were placed on a center board that was situated between the two sides and their behaviors were recorded (Walk and Gibson 1961). Rodkey (2010) suggested that the quintessential innovation of this apparatus was that it relied solely on preference, rather than jumping and physical aptitude – as was the case in previous studies.

The design of the apparatus, specifically the use of checkered patterns, allowed researchers to manipulate specific cues necessary to discriminate depth, including relative texture size and density, motion parallax, and flow pattern (Bradley and Shea 1977). This has given researchers the freedom to manipulate various features in the environment to get a more complete understanding of the development of depth perception. Gibson and Walk (1960) also conducted a series of control studies early on to determine if there was an effect

of the lighting reflecting on the glass of the deep side. The results were not significantly different when they changed the lighting location, suggesting that any reflections were not affecting the subjects' behavior.

In general, when placed on the center board of the apparatus, individuals of a variety of taxa demonstrated a clear preference for the shallow side of the apparatus, suggesting that they experience the perception of depth (Eichengreen et al. 1966; Gibson and Walk 1960). Further results that focused on the development of this sense suggest that there may be an important element of experience in an individual's depth perception, beyond their developmental stage (Bradley and Shea 1977; Tees 1974).

## History of the Visual Cliff

When the visual cliff hit the academic marketplace, so to speak, it took the field of psychology by storm. Throughout the 1960s and 1970s, visual depth perception received a great deal of attention with significant research coming out on a variety of taxa (reviewed in Rodkey 2015). This methodology has taken hold in the mythos of psychology, quickly becoming a staple in introduction to psychology textbooks. There are, however, a number of misconceptions about the origins of the visual cliff and its chief objective.

It has often been suggested that the visual cliff was designed to address the prevalent nature versus nurture debate at the time (Rodkey 2010). This post hoc determination can be traced back to the results of visual cliff studies that support the assertion that visual experience is not a necessary precursor to animals avoiding the deep side. Although these results have been championed to support the nativist perspective in the ongoing debate, Gibson and Walk have intentionally attempted to abstain from the discussion. They have even gone so far as to deny any links between the inception of the visual cliff as a methodology and nature versus nurture debate (Rodkey 2015).



Another tall tale that has similarly been enmeshed in the visual cliff's history is Gibson's inspiration. As the story goes, while Gibson and her family were visiting the Grand Canyon, she observed her infant child stopping at the edge of the cliff and looking over, and this is what gave her the inspiration to create the apparatus (Rodkey 2015). While this makes for a sensational story, it is simply an inaccurate recreation of what truly happened. The idea to study depth perception came from a 1934 study, wherein Lashley and Russell attempted to study depth perception by looking at the force at which rats jumped from one platform to another. Their idea was that rats should adjust the force they use to jump based on the perceived distance between the take-off location and the landing location. They further expanded on this work by studying differences in rats that were raised with light and those that were raised in darkness to examine whether visual experience impacted depth perception. They concluded that depth perception was innate in rats. These results, however, came under scrutiny because the rats had to be trained to jump and this training had to be conducted in the light (Tees 1974). This flaw cast doubt on the findings because the alleged "visually inexperienced" rats did have some level of visual experience prior to the study.

The visual cliff was designed in the spur of the moment when Gibson was given access to a number of dark reared rats. She decided to put together a rudimentary version of the visual cliff with items already in the lab (Gibson and Walk 1960). By virtue of the cliff's design, it did not require training and thus, could sidestep the methodological issues of Lashley and Russell's study. The apparatus also facilitated testing of a variety of other species, including goats, dogs, cats, humans, and a host of other taxa. Nearly all species tested, from the time that they could independently move about their environment, demonstrated an immediate aversion to the deep side of the apparatus. Nearly all deviations in this pattern have been explained in terms of differences in rearing environment, neural damage, or species' ecology.

Three primary versions of the visual cliff led to the version that we know today (reviewed in

Rodkey 2015). The Cliff Model I was the original design; it was relatively rudimentary, requiring rods and clamps to hold it above the ground and had no protective edges to keep the subjects safe. The Cliff Model II was the result of necessary modifications, and resembles the design commonly found in textbooks. This model was a wood box that was suspended from the ceiling. The final alterations to Cliff Model III were simply to increase its size to accommodate larger subjects, such as goats and infants.

Human infants have certainly been one of the most studied subjects on the visual cliff with studies encompassing visual depth perception and numerous developmental milestones. However, as outlined previously, the first subjects of the visual cliff were rats, followed by a series of other species that were studied prior to human infants (Gibson and Walk 1960). Since Gibson and Walk first published their work on the visual cliff in 1960, a host of species have been studied, including chicks, cats, dogs, goats, sheep, pigs, rabbits, lions, tigers, jaguars, snow leopards, monkeys, and other rodents (Gibson and Walk 1960; Rosenblum and Cross 1963; Routtenberg and Glickman 1964; Thiessen et al. 1968), with all of them showing a preference for the shallow side.

## Stimulus Cues

Given the wide array of taxa that have overwhelmingly chosen to descend to the shallow side of the cliff, the question arises as to the precise mechanism driving this preference. Scientists also wanted to learn about the cues and mechanisms used in discriminating depth. There are two proposed mechanisms for how individuals compute the depth of the different surfaces and, in turn, how they use that information to avoid the deep side (Green et al. 1993). One is that the individual may compute the absolute distances of all the surfaces around them and avoid any surface that is beyond an acceptable vertical distance below them. In the visual cliff, the deep side would be beyond that acceptable vertical distance, resulting in the subject choosing to descend onto the shallow side, which falls

within an acceptable distance. The other proposed mechanism is that they may compute the relative distances between adjacent surfaces and avoid any surface where the vertical distance increases rapidly with the horizontal distance. In the visual cliff, the vertical distance on the deep side increases dramatically compared to the center board, whereas the shallow side has a very small increase in vertical distance from the center boards, resulting in the subject choosing the shallow side. In other words, individuals can either attend to absolute or relative cues when discerning depth and making choices about their environment.

The visual cliff has proven itself equally useful in learning about the specific cues that are central to an individual's depth perception. The patterned fabric in the design of the visual cliff allowed for scientists to examine the impact of relative pattern size on side preference. To test this, patterned fabric was placed flush against both sides of the apparatus, differing only in the size of the checkered pattern. Gibson and Walk (1960) found that rats showed a preference for the larger checkered pattern, postulating that this was due to the larger pattern being more reminiscent of "closeness." Despite these results, this preference does not seem to be innate. A similar procedure with visually inexperienced day-old chicks showed no preference for side; however, over subsequent trials, subjects developed a preference for the shallow side (Gibson and Walk 1960). In contrast, similarly reared chicks, when placed in the apparatus with the sides set up as normal, immediately demonstrated the expected preference for the shallow side. This suggests that pattern-size alone is not a sufficient explanation for how animals discriminate depth cues.

An alternative explanation is that motion parallax may serve as an innate cue for depth, whereas using the cue of pattern size may be learned. Motion parallax is the speed at which stimuli move across one's field of vision. Applying this concept to the visual cliff, as an individual moves their head, pattern elements on the shallow side will appear to move more rapidly across their field of vision than elements on the deep side (Gibson and Walk 1960). Gibson and Walk

(1960) attempted to parse out the importance of motion parallax in depth perception by increasing the size and spacing of the pattern on the deep to be perceptually identical to the pattern on the shallow side from the center board. This made motion parallax the only perceptual difference, which was sufficient for nearly all infant rat and day-old chick subjects to consistently choose to descend to the shallow side. This suggests that motion parallax likely serves as an innate cue for depth.

## The Importance of Locomotion

The visual cliff has been most commonly linked with developmental psychology, rather than with comparative psychology, despite the menagerie of species that have been studied (Rodkey 2015). This is likely because the early studies with human infants yielded important results regarding the development of the visual system at different developmental milestones. Specifically, Gibson and Walk (1960) focused on the importance of independent locomotion in the development of depth perception. They observed 27 babies that had reached the crawling stage and found all but 3 of them descended to the shallow side. This pattern has also been seen in a variety of other taxa. Rats showed the expected behavior of descending to the shallow side at 16–17 days of age, which is about 2 days after opening their eyes (Bauer 1973). Likewise, chicks consistently demonstrated the expected pattern of behavior after less than 24 h of hatching (Gibson and Walk 1960). Each of these time frames correspond with normal locomotion development in each species.

These observations supported the premise that depth perception develops along a similar time frame to locomotion. This led Gibson and Walk (1960) to make the broad conclusion that, in sighted animals, the ability to perceive and discriminate depth develops with independent locomotion, even in species whose locomotion starts at birth. The underlying logic of this conclusion is that depth perception should be adaptive for individuals that are moving about their environment

independent of external forces, as it provides a level of protection against traversing dangerous areas (e.g., cliffs).

## The Importance of Environment

Above and beyond being used to study the general development of visual depth perception and the associated cues used to discriminate depth, the visual cliff has also been employed to study how neurological and environmental factors can impact the development of this visual process (Rodkey 2015; Tees 1974). One of the most common variations harkens back to the original visual cliff study, wherein Gibson and Walk (1960) explored the question of whether depth perception was innate by studying the behavior of rats reared in a dark environment. Since their original studies, the visual cliff has also been used to study learning processes and the different impacts of rearing environment.

Tees (1974) took a longitudinal approach with his study, examining the rate at which dark-reared versus light-reared rats discriminated between the deep and shallow sides. He found that those raised in the dark were slower to acquire the discrimination and actually showed a deterioration in their abilities after 100 days, whereas light-reared rats instead showed a rapid acquisition and gradual asymptote in performance after 100 days. Tees (1974) proposed two important functions on visual experience in the development of depth perception. The first is that visual experience allows the individual to hone their ability to make accurate depth discriminations. The second is that the visual experience jump-starts neural structures that are central to the ability. He suggests that the deterioration in performance of the dark-reared individuals is evidence for the lack of development of these underlying neural networks.

Support for Tees's assertion for the importance of underlying neural structures can be found in previous studies that examined the impact of neocortical lesions on performance on the visual cliff (e.g., Hebb 1963). Meyer et al. (1966) found that rats with lesions to their visual neocortex showed

no preference for the shallow side and performed similarly to the control animals that had been fully blinded. When testing cats, however, they found that those with lesions still avoided the deep side. The researchers suggested that this result may be more prudently attributed to methodological difference in the post-surgery environments of the two species. This possibility hints at the importance of environment in the development of depth perception.

Early studies tended to focus on the importance of visual experience, through the application of light versus dark rearing environments. In years since, there has been a shift in focus to other environmental features that may play important developmental roles. In particular, researchers have focused on the importance of enriched environments. Bradley and Shea (1977) examined how gerbils that were raised in a topographically complex environment compared to those raised in a flat environment performed on the visual cliff. They found that, while 21-day-old gerbils did not show an immediate preference for the shallow side of the apparatus, those raised in the enriched environment developed the expected preference in under 48 h whereas those in the flat environment did not develop the preference until they were 60–61-days-old.

Their explanation of the results is based on the idea that gerbils have the capacity to discriminate depth, but they require experience with the environmental features in order to utilize the capacity (Bradley and Shea 1977). An alternative explanation is that both groups of gerbils were able to discriminate the depth, but those in the flat environment group did not have the requisite fear response to the visual cliff (Wilson and Risen 1966). Those reared in the enriched environment, on the other hand, had experience with the dangers associated with cliffs and thus could rapidly learn to avoid the deep side of the apparatus. Both explanations are based on the underlying logic that an individual's experience with an enriched environment, wherein they gain experience with features that necessitate the use of depth perception, may better equip them to make educated decisions on the visual cliff.

## Ecological Considerations

Nearly every species that has been tested on the visual cliff has demonstrated a preference for the shallow side of the apparatus (Gibson and Walk 1960; Rosenblum and Cross 1963; Routtenberg and Glickman 1964; Thiessen et al. 1968). That is to say, nearly every terrestrial species. The most notable exceptions to this “rule” are sea turtles and ducks (Gibson and Walk 1960). Sea turtles deviated the most from the expected pattern with nearly 24% of subjects descending to the deep side. One suggestion is that they have poorer depth perception than other species tested. A more widely accepted hypothesis, however, is that it does not align with their natural ecologies (Gibson and Walk 1960). The visual cliff works by virtue of the fear animals have for falling; because they do not want to fall off a cliff, they avoid the deep side. This fear of falling does not occur in sea turtles, as falling off a cliff is not an ecologically valid concern in their environment. When turtles swim over the wall (the ocean’s equivalent of a cliff) they do not “fall.”

In contrast to the lack of fear in turtles, Gibson and Walk (1960) made a number of amusing observations concerning fear of the deep end in their early studies. When animals, such as lambs and goats, were placed on the glass over the deep side they demonstrated stereotyped fear responses, despite the tactile assurance of the glass. They would go into defensive behaviors, refuse to put their feet down, and would be unable to motivate themselves to move toward the “safety” of the shallow side. These reactions, along with the divergence in expected preference of the sea turtle, are all in line with the behaviors that would be expected from the animals in the wild. The ability to discriminate depth is incredibly important to the survival of most terrestrial species, which is why its development is so closely tied to that of independent locomotion.

## Conclusions

The visual cliff took the psychology world by storm when it was first introduced by Gibson

and Walk in 1960. Since its conception, it has been used to study a multitude of developmental and perceptual concepts. It presented researchers with a semi-natural problem that required no previous training. Through the use of this apparatus, researchers have been able to study a plethora of species. They have consistently found that species perform according to what is known about their life histories and ecologies, most commonly preferring the shallow side of the apparatus. The visual cliff has similarly been used to study the stimuli that control depth discrimination, as well as the impact that a rearing environment has on the development of depth perception. Although incredibly simple in design, the visual cliff has been revolutionary in the realm of psychology and has lent to an incredible amount of knowledge in the fields of comparative and developmental psychology.

## Cross-References

- ▶ [Depth Perception](#)
- ▶ [Visual Perception](#)
- ▶ [Visual Illusions](#)

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## Visual Coding

### ► Cognition

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## Visual Completion

### ► Amodal Completion

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## Visual Detection Task

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### Definition

A series of trials in which an observer must recognize the presence or absence of a visual stimulus or feature of a stimulus.

## Introduction

A visual detection task is a task in which an observer must recognize the presence or absence of a visual stimulus or feature of a stimulus. This could include the presence of a faint stimulus (e.g., light), movement, or a specific image (e.g., face) among spatially or temporally adjacent distractor images. Signal detection theory describes how target stimuli are discriminated from patterns of non-target information (referred to as noise). This is based on features such as the intensity of the stimulus and the noise in the background or detection system (e.g., perceptual system) of the observer. Making a selection generally involves selecting a threshold based on the noise and signal + noise distributions and then deciding whether the stimulus falls above or below the threshold. Signal detection theory was first described by researchers studying radar detection (Peterson et al. 1954), who determined, mathematically, the behavior of an “ideal” observer. This concept was applied to visual detection in human observers by Tanner and Swets (1954) and later by Green and Swets (1966). There are four possible outcomes when an observer attempts to detect the presence or absence of a signal (Fig. 1). The sensitivity index ( $d'$ ) is commonly used as a performance measure; however, different assessments may be used depending on the detection model. The sensitivity index represents the difference between the means of the signal + noise and noise distributions in terms of the standard deviation of the noise distribution (Tanner and Swets 1954). This was later modified for cases in which the variances of the noise and signal distributions are unequal ( $d_a$ ; Fig. 2).

## Assessing Visual Detection

Visual detection can be studied through examining behavioral outcomes or neural responses. It is commonly measured through accuracy and reaction times of behavioral responses. In psychophysics, the accuracy outcomes form a psychometric curve, which maps the relationship between stimulus intensity and percentage of correct responses using a sigmoid function.



|                  | Respond "Absent"  | Respond "Present" |
|------------------|-------------------|-------------------|
| Stimulus Present | Miss              | Hit               |
| Stimulus Absent  | Correct Rejection | False Alarm       |

**Visual Detection Task, Fig. 1** The possible outcomes of a detection task in which stimuli are either present or absent

$$d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$$

$$d' = \frac{\mu_S - \mu_N}{\sigma_N} \quad \text{OR} \quad d_a = \frac{\mu_S - \mu_N}{\sqrt{\frac{1}{2}(\sigma_S^2 + \sigma_N^2)}}$$

where  $\mu_S$  and  $\mu_N$  are the mean responses of the signal + noise and noise distributions, respectively, and  $\sigma_S$  and  $\sigma_N$  are the standard deviations.

**Visual Detection Task, Fig. 2** Calculating the sensitivity index as a measure of visual detection performance

Additionally, functional magnetic resonance imaging (fMRI) has shown that activity in the primary visual cortex (V1) correlates with accuracy on a visual detection task (Ress et al. 2000). Heterogeneity of neuronal responses in this area also correlates with greater ability to detect stimuli (Montijn et al. 2015). Other regions show activation patterns specific to “oddball” stimuli, motion detection, or detection of emotional content, which can be detected using fMRI or event-related potentials (ERPs).

## Applications

Visual detection tasks have been used in many psychology and neuroscience experiments, both in humans and animals. Specific types of tasks commonly used include visual flash suppression tasks, rapid serial visual presentation (attentional blink) tasks, and go-no go tasks. By assessing participant accuracy and reaction times under different conditions, researchers can learn about how factors such as attention, emotional content, and the presence of distractor stimuli affect detection. Visual detection tasks have implications for clinical practice, through improving detection accuracy in medical imaging. They can

also aid in improving detection for security purposes and for operating automobiles and aircrafts.

## Factors Affecting Visual Detection

There are a myriad of factors that affect whether or not a signal is detected. These include the properties of the stimulus (e.g., contrast, length), properties of proximal stimuli (e.g., presence of flankers, masking), and attributes of the observer (e.g., attention, training). Contrast, the difference in luminance between the background and the stimulus itself, is the feature most commonly manipulated in detection experiments, with a greater contrast making the stimulus easier to detect. However, other features such as the length and eccentricity of the presentation also make a difference. The longer a stimulus is shown, the more likely it is to be detected. If a stimulus is presented between the subliminal and supraliminal thresholds, as is common in priming experiments, it may be unconsciously perceived but the observer will not be able to report what they saw. Detection thresholds also increase with eccentricity of the stimulus (Palmer et al. 2007).

Proximal stimuli such as masking and flankers also affect difficulty of detection. Masking is when another word or set of symbols is presented immediately after the target stimulus to eliminate any after-image, making the target stimulus more difficult to detect. Flankers are stimuli presented next to the target and make it more difficult to perceive a faint stimulus. However, when stimuli of other modalities are presented at the same time as a faint visual stimulus, such as a sound played during a light detection task, these stimuli may undergo sensory integration to make the visual stimulus appear more intense (e.g., Stein et al. 1996). Even imagined stimuli may either facilitate or interfere with target detection depending on factors such as image location (Arterberry and Craver-Lemley 2002).

Other important features include observer characteristics. For instance, stimuli will be perceived more quickly and accurately if attention is placed on or drawn to that location. This is due to elevated activity in the primary visual cortex in response to attention that is thought to improve signal detection (Ress et al. 2000). Detection ability can also improve due to training, and response bias, as a result of participant goals, may produce changes to the threshold (e.g., if it is crucial not to miss a stimulus, an observer may respond “present” more frequently, shifting their responses towards more hits and false alarms and fewer misses and correct rejections).

Finally, the emotional significance of a stimulus is important in determining whether it gets perceived. For example, faces made imperceptible through visual flash suppression are more likely to reach blindsight and to be consciously perceived if the expressions are emotional (Oliver et al. 2015). Additionally, emotional stimuli that are shown in close proximity before neutral target stimuli in an attentional blink task make it more difficult to perceive the neutral stimuli (e.g., Most et al. 2005).

## Conclusion

Visual detection has been studied for decades, using both human and animal experiments as

well as computerized models. Experiments make use of visual detection tasks to examine phenomena such as attention, perception, and emotion processing. They also play an important role in many fields such as clinical diagnosis, security, and aircraft safety. Many factors go into determining the ability of humans and animals to detect stimuli, each informing us about how the brain functions to perceive objects in the world around us.

## Cross-References

- Amygdala
- Attention Bias
- Blindsight
- Cognition
- Cognitive Bias
- Divided Attention
- EEG
- Event-Related Potentials (ERPs)
- Interstimulus Interval (ISI)
- Neurons
- Occipital Lobe
- Parietal Lobe
- Reaction Time
- Visual Search

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## Definition and Psychological Perspectives on Visual Perception

Visual perception is a brain process that actively detects and interprets neurological signals that were transduced from light. Much of what is known about visual perception has been well studied and understood with respect to human vision. The understanding of visual perception varies among researchers within behaviorism, Gestalt psychology, and cognitive psychology (Gregory 1997).

Behaviorists focus less on the inner workings of the mind and demonstrate that learned behavior is explained by chains of conditional responses. This behavioral explanation for visual processing falters, as perception is said to be a function of stimuli directly, rather than as a result of the internal processing of the mind related to those stimuli (Gregory 1997).

In Gestalt psychology, visual perception is interpreted as being greater than the sum of stimuli that make it up and organizing heuristics are based on certain laws, such as closure, common fate, and contiguity of close-together features (Gregory 1997). The law of closure describes a pattern when an image is incomplete but is arranged in such a way where an observer is able to describe a complete image, even with missing information (i.e., the Kanizsa's Triangle, Fig. 1) (Gregory 1997). Common fate occurs when objects are moving in the same direction, and as a result, they appear as moving “together.” Contiguity of close-together features describes how the brain organizes shapes when objects are positioned close together, so they appear as a group to an observer.

Cognitive processes related to problem solving and visual perception have historically been thought of as separate from one another. Early physiological psychologist Hermann von Helmholtz viewed perception as unconscious inferences, therefore pivotally linking thought to visual processing. Cognitivists focus less on the relationship between stimulus controls of perception and behavior but emphasize general knowledge, learning, memory, attention, and logical thinking as focal points in the study of visual

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## Visual Illusions

- [Appearance Reality Tests](#)

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## Visual Interpolation

- [Amodal Completion](#)

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## Visual Pathways

- [Cognition](#)

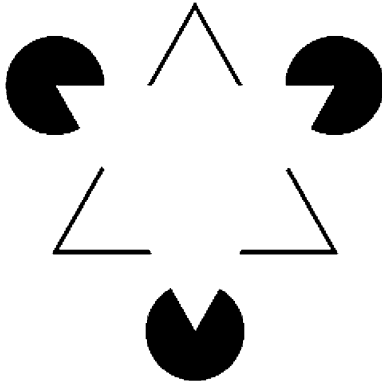
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## Visual Perception

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## Synonyms

[Related: Visual senses](#)



**Visual Perception, Fig. 1** Kanizsa's Triangle: These spatially distinct fragments imply a bright white triangle, defined by a sharp illusory contour covering three black circles and a black-outlined triangle

perception with varying degrees of success (Gregory 1997).

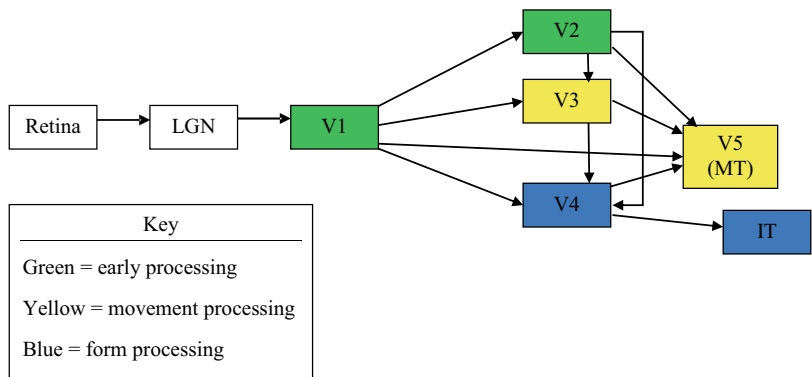
## Visual Biology, Perception, and Cognition

Visual perception is informed both by neurobiology and cognitive science (Clemente et al. 2010; Domjan and Grau 2015; Shimojo et al. 2001). The visual process occurs when light hits the retina, stimulating a change in opsin protein configuration in photoreceptors and flooding a transducing cell with sodium ions. Photoreceptors are not spread evenly on the retina, as the greatest concentration of rods can be found in the peripheral areas, while high-resolution cones are concentrated in the central fovea (Breedlove and Watson 2017). Light stimulation in photoreceptors causes a graded potential in bipolar cells that are, interestingly, positioned in front of the retina where light goes to stimulate transduction. This arrangement has interesting implications for visual perception in the brain as a great deal of “post-processing” is necessary for a clear image to form in the mind. Further positioned in front of the retina are the ganglion cells which together form the optic nerve where information is sent to the brain (Shimojo et al. 2001). The process from sensation to perception in the brain is a

multichanneled path (Fig. 2) organized by early, form, and movement processing.

*Early processing: Frequencies and contours.* The visual cortex of the brain is divided into areas that have specialized contributions to the visual system (Breedlove and Watson 2017). The primary visual cortex in mammals (area V1) contributes to the recognition of spatial frequencies (Fig. 3), orientation, and color (Hubel and Wiesel 1962). V2 processes additively to what V1 does and adds information by aiding in the perception of contours (von der Heydt et al. 1984). Mainly fed by neurons from the Lateral Geniculate Nucleus (LGN), area V1 has within it a series of neurons organized into ocular dominance columns (ODCs) that benefit spatial frequency recognition (Shmuel et al. 2010) and are thought to be important in binocular vision (c.f. Horton and Adams 2005). The ODCs consists of cell bands that respond to various stimuli presented to an individual (Breedlove and Watson 2017). This was first identified by Hubel and Wiesel in cats through their responses to the orientation of light stimuli at the neuronal level. Slits of light as well as rows of dots with the same orientation were used to stimulate cells in the retina. From there, the signal was traced to cell units in the V1 area of the visual cortex. The experimenters isolated each eye to record the relative contribution of the monocular signals, before looking at the contributions of both eyes in aggregate. This experiment paved the way for understanding how visual physiology ultimately shapes perception and therefore represents a foundational work of neurobiology (Wurtz 2009). From a proximate viewpoint, Hubel and Wiesel also laid out the columnar organization of neurons in V1, showing convergence with the somatosensory cortex in mammals (Mountcastle 1957).

*“What” processing: Shapes and forms.* Area V4's role is more firmly related to form and attentional processing and has neurons tuned to simple shapes as it takes input from V1 and V2 (Moran and Desimone 1985). Areas V2, V4, and the IT are involved in form identification, but each area has a specific role. For example, area V2 specializes in the interpretation of images with contours that project an illusion. Although, it is thought that



**Visual Perception, Fig. 2** Visual processing pathway. *LGN* lateral geniculate nucleus, *V1* primary visual cortex, *V2* *V3*, and *V4* visual areas 2, 3, 4, 5 and *IT* inferior temporal cortex. Area *V1* is associated with spatial frequency recognition, orientation, and color perception. Area *V2* is involved with form identification, specifically

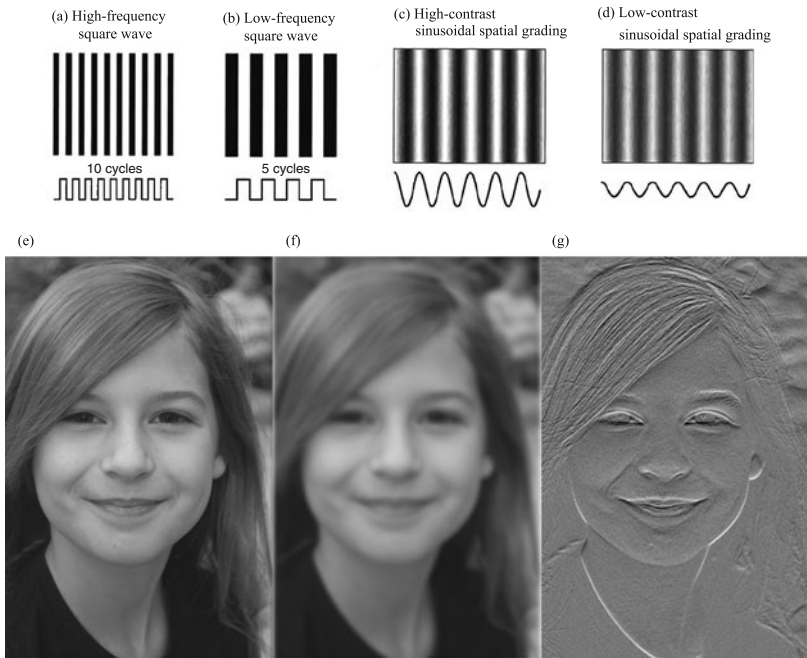
illusory contours of images. Area *V4* has a role in form identification. *IT* functions in recognizing complex images, such as facial recognition. Area *V3* is involved in global movement perception, while area *V5* (MT = middle temporal) functions in motion detection and control of eye movements

**Visual Perception,**

**Fig. 3** Spatial frequencies.

High and low frequencies and contrasts that area *V1* aids in recognizing. (a, b) The spacing between dark and light stripes shows that part a has double the spatial frequency of part b. (c, d) Visual grids with sinusoidal modulation of intensity: (c) high contrast; (d) low contrast. (e–g)

A photograph of a young woman subjected to spatial filtering: (e) normal photograph; (f) high spatial frequencies filtered out; (g) low spatial frequencies filtered out. (Parts e–g courtesy of Jason Bruck). Figure adapted from (Rosenzweig et al. 1998) with permission from authors and publisher



*V1* might feedback into this process (Ramsden et al. 2001), it is really *V2* leading to higher cortical areas that is responsible for our perception of things like the brightness of negative space in the Kanizsa's Triangle illusion (Fig. 1). *V2* is tuned to aspects of spatial frequency and color and is thought to relate to object recognition memory (López-Aranda et al. 2009).

Both *V1* and *V2* mostly rest on the geniculate system; however area *V4* is part of the extra-geniculate or pulvinar system (although it has strong connections to *V1* and *V2*) (Roe et al. 2012). This is a parallel pathway outside direct mediation by the LGN (Tabei et al. 2015). Just like *V2*, this structure has cells that respond to spatial frequency and orientation, but there are



also cells with a stronger preference to respond toward different wavelengths of light. Much focus of late has been on the role of V4 in top-down visual attention processing and bottom-up object recognition (Roe et al. 2012). The IT contributes to recognizing complex forms (Breedlove and Watson 2017) and is the final area for visual object processing. The IT also contains specialized processors for recognizing specific kinds of objects, such as faces (Tsao et al. 2006). Individual experiences may shape how the IT area processes these stimuli, indicating connections with other cortical areas (Breedlove and Watson 2017).

*Where things are: Location processing.* Areas V3 and V5 aid with perception of motion (Born and Bradley 2005). V3 is thought to function in our processing of global movement and V5 functions in motion detection and control of eye movements (Dursteler et al. 1987). While the exact organization of V3 is up for some debate, V5 is also part of the extrageniculate system, but this center is not functionally additive the way V1, V2, and V4 are and has separate pathways for foveal vs. peripheral signals (Palmer and Rosa 2006).

## Color Perception

### Neurology of Color Perception

The assignment of color occurs in three stages (Breedlove and Watson 2017; Shimojo et al. 2001). The first stage (transduction) occurs on the cone photoreceptor itself. The second stage of processing occurs within the secondary neuronal tissue of the retina where inhibition and excitation of surrounding circuits play a role in shaping the signal that is inevitably sent to the brain (Kuffler 1953). From there the signal is sent through the LGN to area V1 where information is sent to other areas of the visual cortex to which color perception is finalized in the third stage (Breedlove and Watson 2017).

### Theories of Color Perception

Within the science of color vision, there are opposing hypotheses of which neither is fully capable of explaining color vision: trichromatic theory (Young 1802) and opponent-process

theory. The trichromatic hypothesis supports the idea that there are three different cone receptors, blue, green, and red, each with their own path to the brain (Young 1802). This is exhibited in certain primate species, while other mammalian species have dichromatic vision (Breedlove and Watson 2017). In contrast, the opponent-process theory (which applies to more processes than just color vision) supports the idea that there is a production of opposite reactions in response to different wavelengths of light (Breedlove and Watson 2017). Ewald Hering postulated about three independent receptor types which all have opposing pairs: white and black, blue and orange, and red and green. This would later be refined to two pairs, blue and yellow and red and green, where excitatory and inhibitory patterns of firing would affect the ultimate perception of color with the two components of each mechanism ultimately opposing each other. Therefore, one can have colors that appear greenish-blue or blueish-red, but not reddish-green or yellowish-blue. Neither hypothesis can explain color vision by itself; however the trichromatic theory explains how the three types of cones detect different wavelengths, while opponent-process theory explains how the cones connect to the ganglion cells, where the opposing elements inhibit each other to determine how color is perceived (Hurvich 1985).

### Individual Differences

Color perception varies between organisms since there are differences in wavelength sensitivity as well as the availability and distribution of an organism's rods and cones (Shettleworth 2010). In humans, different photoreceptors are sensitive to different wavelengths of light, with cones having peak sensitivity to 420 nm, 530 nm, and 562 nm and rods having peak sensitivity to 500 nm (Fox 2016). Humans can observe shadows as both dark and blue, whereas non-human animals with UV vision can see shadows as dark with shades in the UV spectrum (Troscianko et al. 2009). Many features of the eye, such as the sclera or corneal epithelium, are developed to suit an organism's habitat and the types of color stimuli they experience on a daily basis (Berta et al. 2015). For example, the increase

in water depth results in loss of color sensitivity which is shown in the retina of the red-tailed black shark whose eye consists mainly of rods and green and red-sensitive cones (Levine and MacNichol 1982). For most mammalian species with color vision, G. H. Jacobs proposed a range of color vision into four categories (Breedlove and Watson 2017). Diurnal primates, like humans, exhibit exceptional trichromatic vision. Dogs and pigs have two types of cone photopigments and large number of cones which results in a strong dichromatic vision. A weak dichromatic vision is present in species such as cats and coatis, and they also have two types of cone photopigments but a small number of cones. The last category is minimal color vision, where an organism has one type of cone pigment and relies on rod-cone interactions for wavelength discrimination; this is present in owl, monkeys, and raccoons (Breedlove and Watson 2017).

### Development of Visual Perception

The development of the visual system is affected by the environment and experience. For example, the eyes of aquatic organisms are adapted to the lower light levels found in their niche (Berta et al. 2015). Ganges River dolphins (*Platanista gangetica*) have relatively poor eyesight as selection pressures associated with living in an opaque fluid have reduced the function of this cetacean's eyes (Sinha and Kannan 2014).

It is essential for many organisms to have experiences with visual stimulation as a foundation for understanding what stimuli are available for the eyes and brain to process (Domjan and Grau 2015; Honigmann 1944; Troscianko et al. 2009). This is broadly outlined by the work of Gilbert Gottlieb (1976) who emphasized the role of experience in development. For example, human infants require a long period of locomotor experience for depth perception to be processed correctly, whereas other species, such as goats, do not require experience with movement to perceive depth (Adolph 2000). Stereoscopic vision in primates is fully dependent on experience shaping the timing and pattern of gene expression, as

infant rhesus monkeys that have had their binocular vision impeded by prismatic lenses do not develop the excitatory binocular neurons necessary for normal binocular depth perception (Crawford et al. 1996).

### Comparative Evolutionary Analysis in Visual Perception

The comparative study of visual perception, and especially its development, remains a poorly studied field and could shed light on the evolution of our own visual system (Shettleworth 2010). On the evolution of visual perception, the placement of an individual's eyes can indicate the extent of binocular vision that is required by ecological factors such as the need to hunt (Shettleworth 2010). Such vision results in greater visual acuity in parts where there is overlap of the visual field (Clemente et al. 2010; Shettleworth 2010). For example, the Australian wolf spider's (*Lycosa leuckarti*) eyes are positioned both anteriorly and posteriorly. Its overlapping binocular anterior and posterior medial eyes are used for distance judgment and prey capture and its non-overlapping posterior lateral eyes are used for long-range predator and prey detection (Clemente et al. 2010). In aquatic species like bottlenose dolphins (*Tursiops truncatus*) and goldfish (*Carassius auratus*), the eyes are positioned laterally, which allows them to potentially perceive a great deal around them but also allows them to view objects independently of the head on viewing angle since they can move three dimensionally and view the objects from different orientations (Cozzi et al. 2017). Consequently, bottlenose dolphins are able to move their eyes independently where one eye may look forward and dorsally, and the other eye may look rearward and ventrally (Cozzi et al. 2017). Evidence suggests that trilobites had some of the earliest eyes seen in the fossil record and because they contained a calcified cuticle, this structure was well-preserved. Not only was this an early eye, but it was likely a successful one as well, because this aquatic species maintained this visual system for about 270 million years (Clarkson et al. 2006). The likely visual field of

the trilobite's eye did not extend to objects above them since no predators or prey existed in that space at that time (Clarkson et al. 2006), giving a slightly angular look relative to the round eyes common in species today. Chitons have one of the more newly evolved eyes, characterized by aragonite-based lenses that allow their vision to operate in both air and water (Speiser et al. 2014). The convergent evolution of the trilobite and chiton mineral eyes show how they have both adapted to their similar environments in similar ways (Speiser et al. 2014).

## Cross-References

- Cognition
- Photoreceptors
- Size Illusion
- Stereoscopic Vision
- Temporal Lobe
- Vertebrate Nervous System
- Visual Detection Task

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## Visual Predator Identification

### ► Visual Recognition of Prey and Predators

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## Visual Prey Identification

### ► Visual Recognition of Prey and Predators

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## Visual Processing

### ► Face-Selective Neurons: Comparative Perspectives

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## Visual Recognition in Birds

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## Introduction

The ability to visually recognize another individual may be a question of life and death. Recognition may be essential, be this for distinguishing friend from foe and for making split-second decisions of whether to approach or flee, or for courtship and mating as well as in parent-offspring interactions.

Not all recognition may be based on vision. A species may have a perceptual apparatus in which one sense dominates and others are negligible or even absent. In many organisms, communication and individual recognition may be multimodal, i.e., combining visual, auditory, or olfactory, vibratory, or gustatory cues to recognize each other.

In birds, as in humans and most diurnal primates, vision is one of the dominant senses. In these cases, vision is usually complex and is based on a highly developed system. Organization of eyes and position of eyes determine what is seen and how the brain can respond to visual inputs and, finally, how such information is processed and ordered into meaningful perception and memory.

### External Organization of Visual Fields

First, it is important to know where the eyes are positioned in the head, and that position can vary quite substantially from species to species. Frontally placed eyes, as in humans, mean that the axes of the eyes' optical systems are approximately parallel, and both eyes together can simultaneously gain very similar views of the same objects (Martin 2007). Owls and many of the nightjars, potoos, and frogmouths have frontally placed eyes and are among the few avian species with full binocular vision.

Second, it is also important to take note of the actual visual field of a given avian species. Generally, the axes of the eyes' optical systems may have a number of important variations that may help specific species to see what they need to see most, usually food and predators (Fig. 1).

Although, as shown in Fig. 1, eye position can vary a great deal among all extant birds, in songbirds it tends to be far more uniform, with eyes placed on either side of the head, in the midline of the mandible. Such laterally placed eyes mean that visual information from each eye represents and entirely different image that is monocular. Binocular vision is relatively limited but sufficient at close distance to gain a binocular view of food, or when feeding offspring directly to the beak (Fig. 2).

Figure 2 shows quite clearly that visual processing is affected by the visual field. Most birds have a small binocular field of just 15–35° but a wide monocular field enabling birds to focus on two essential things for survival: food sources and predatory threats. If predatory threats are significant and food searches demand lowering the head, the eyes may be situated further up in the skull as in the woodcock, in ducks, and in most shorebirds so that overhead threats can still be monitored while feeding (Fig. 1a, b).

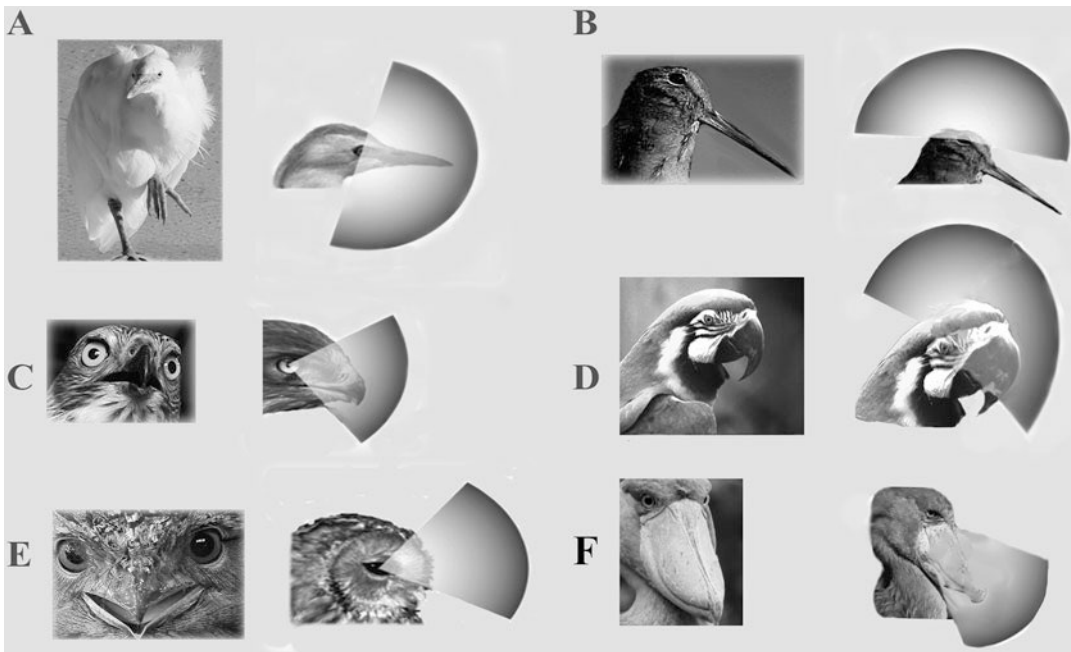
### Visual Recognition via Imprinting

An exciting discovery of the twentieth century was to have identified the process of imprinting, described as a type of learning by “which an animal restricts its social preferences to an object after exposure to that object” (McCabe 2013). Filial imprinting occurs shortly after birth or hatching, and the intermediate and medial mesopallium (IMM) in the brain is a memory store for visual imprinting. After imprinting on a visual stimulus, neuronal responsiveness in IMM is specifically biased toward the imprinting stimulus (Bateson and Horn 1994). We know that chickens, ducks, and indeed all precocial birds, which are self-feeding and feathered at hatching, will follow a parent based on this imprinting, and if another attractive stimulus is presented instead, they will follow that too (Bateson and Horn 1994). Imprinting applies only to precocial species but not to the thousands of songbirds that are altricial (i.e., are entirely dependent on parents and stay in the nest until they are fully feathered and developed). Nevertheless, in all species, reliable memory formation is essential.

### Processing of Information in the Brain

Information from the eyes is processed separately and, importantly, not by the same side of the brain in which the eye is located, i.e., the optic nerve is “cross-wired” so that the opposite hemisphere receives the input. Each brain hemisphere (and thus each eye) is specialized to process information differently, and it controls different functions and behavior. The left hemisphere (right eye)





**Visual Recognition in Birds, Fig. 1** *Topography of the binocular visual fields in birds.* The binocular visual field is where inputs go to both eyes, and its size depends on the position of the eyes in the head in relation to the beak and the top of the head. (a) Egrets (great egret: *Ardea alba modesta*), as in many shorebirds, have eyes as close as possible to the upper mandible and can use binocular vision just beyond the end of the beak. (b) Woodcock (genus *Scolopax*) eyes are placed high up to be able to scan the skies while probing for food. (c) Birds of prey (brown goshawk, *Accipiter fasciatus*, left; golden eagle, *Aquila chrysaetos*, right), as top predators, need good

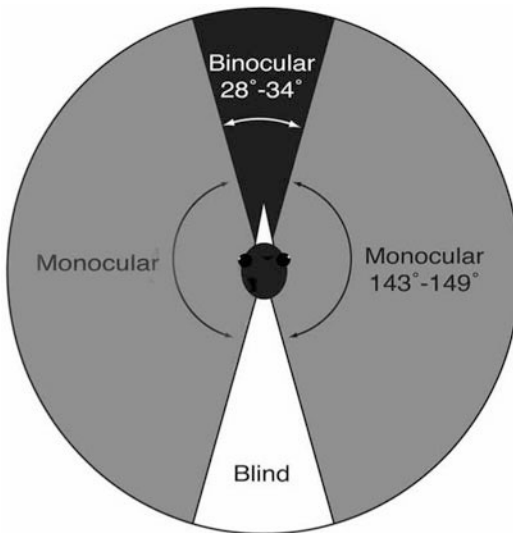
binocular vision around the tip of the beak, and they bring their claws clasp the prey into this field of vision. (d) Blue and gold macaw, *Ara ararauna*, as all macaws and other large birds, have a very wide binocular field of vision; despite their size, they still need to fear large raptors. (e) Owls, potoos, and frogmouths have frontally placed eyes. (f) The extremely large African shoebill, *Balaeniceps rex*, is the bird with probably the smallest binocular visual field because the beak obstructs it, and note that the eyes are set deep under eye ridges, and therefore the visual field is largely confined to front and a little to the side (Adapted and expanded from Kaplan and Rogers (1999))

broadly categorizes stimuli, distinguishes food from nonfood, and identifies routine visual stimuli (invariance) while the right hemisphere (left eye) recognizes members of the group and individual faces (Rogers 2011).

In the few species tested so far, viewing with the left eye (right hemisphere) has been confirmed for predator recognition in wild Australian magpies, *Gymnorhina tibicen* (Kaplan 2016) and for individual face recognition in domestic chickens and pigeons (*Columba livia domestica*). As in magpies, chicken and pigeons turn their heads to view the stimulus with the left eye (right hemisphere processing). Chicks also use the left eye (right hemisphere) to view a model social partner and whenever viewing familiar social partner at a

distance, but when they look at an attractive stimulus on which they might imprint but had not yet imprinted (e.g., a hen), they use the right eye (Vallortigara and Andrew 1994).

To test this further, Ocklenburg and Güntürkün (2018) devised experiments in which domestic pigeons were shown two-dimensional images of a person and the pigeon's task was to peck on an image when there was a person contained in it. First, the person was shown in a normal upright position, and in following images it was upside down or splintered in various ways so that part of the body was detached, missing, or in the wrong position. When pigeons viewed the images monocularly with the right eye (left hemisphere), they pecked only the keys that most resembled the



**Visual Recognition in Birds, Fig. 2** The visual field of the Australian magpie clearly showing the substantially greater size of the monocular fields (Adapted from Rogers and Kaplan (2006))

normal shape and position of a person, but when the right eye was occluded and the images were viewed only with the left eye (right hemisphere), the pigeons pecked almost all images, whether upside down, body parts detached, or body parts missing. These experiments demonstrated very clearly that the left hemisphere/right eye can only distinguish between broad categories while the right hemisphere/left eye can detect fine details, i.e., collect substantially more detailed information about a person or conspecific than by right eye viewing (Ocklenburg and Güntürkün 2018).

### Facial Recognition: the Cognitive Dimension

A novel stimulus seems to require more than monocular viewing. Songbirds examine a novel item by viewing it first with one eye and then with the other eye, turning their head to get a monocular view from each eye separately, as was shown in a study on zebra finches, *Taeniopygia guttata* (Rogers et al. 2018). This may well be so to enable the brain to lay down a full memory of all stimulus features, thus first using both hemispheres to do

so. Avian species so far tested can recognize, i.e., remember, individuals of different avian species and mammals (such as a pet dog or pet cat) including individual human faces by visual recognition alone (Cornell et al. 2012). This ability, again, is a function of the right hemisphere.

It becomes an important cognitive achievement when visual recognition of an individual's face is linked to his/her behavioral characteristics. For instance, when humans are considered dangerous or friendly by American crows, *Corvus brachyrhynchos*, that information is combined and the new knowledge then spread socially among their group (Cornell et al. 2012). Forming an image of an individual human face is an extraordinary feat and has now been recognized as requiring more than mere image memory. It involves assessment, connecting a visual input with characteristics of the person to which this face belongs. Depending on the results of such assessment, this may alter the behavior of the birds entirely; for instance, it may include warnings about specific individual people or other species or, alternatively, may result in affiliative behavior expressed in preening, play behavior, gift giving, and/or even seeking the company of that person or conspecific. Australian magpies, as well as the unrelated Eurasian magpies, *Pica pica*, have excellent facial recognition of humans (Lee et al. 2011) that they use for risk assessment of the safety of their own nest. Come breeding time, the male will selectively mob only those individuals that are unknown or have made gestures that could be interpreted as hostile or dangerous. Remarkably, such detailed information about individuals is retained from one breeding season to the next. So far, we only have anecdotal evidence, but it appears that the memory of the behavior of specific humans may remain intact for many years (Kaplan 2016).

As in humans, visual recognition in some birds may thus involve an understanding of another individual as a separate entity with separate actions and intentions. The ability to understand this "otherness" is considered part of "theory of mind." Distributing information from one to another, from the knower to a recipient absorbing the knowledge and acting in

accordance with that information, is perhaps the most remarkable ability.

## Cross-References

- [Individual Recognition](#)
- [Theory of Mind](#)
- [Visual Recognition of Prey and Predators](#)
- [Visual Self-Recognition](#)

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## Visual Recognition of Prey and Predators

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## Synonyms

[Visual predator identification](#); [Visual prey identification](#)

## Definition

The process by which predators identify prey and prey identify predators based on visual input.

## Introduction

Predation, in which one organism consumes all or part of another organism for nutrition, has evolved many times throughout the history of life. Predation is a potent selective force that restructures food webs, redistributes nutritional resources, and can send predators and prey into coevolutionary arms races.

The life-dinner principle provides a useful lens for understanding the evolutionary dynamics underlying the visual recognition of predators and prey. According to the life-dinner principle, prey almost always bear larger fitness costs than predators (Dawkins and Krebs 1979). On the one hand, the failure of prey to escape predators typically results in a loss of life. On the other hand, the failure of a predator to capture prey simply results in the loss of its dinner. Thus, selection pressure on prey to avoid predators is almost always higher than the selection pressure on predators to successfully obtain a given prey organism.

Despite its suitability for understanding the behavioral evolution of predators and prey, the life-dinner principle has not been without its critics and proposed alternatives. Abrams (1986) noted that if a predator fails a sufficient number of

times to catch prey, it suffers fitness costs as large as those that a prey organism incurs if it fails to escape a predator: namely, death. Additionally, Humphreys and Ruxton (2020) suggest that factors besides the life-dinner principle may explain asymmetries in the degree of adaptation between predators and prey. For example, improved anti-predator defenses in prey may result in a higher prey density, thus increasing the rate at which a predator encounters prey and relaxing selection pressure on adaptations for prey capture.

The life-dinner principle predicts that prey will evolve elaborate adaptations in response to predation. Morphological and adaptations may include a cryptic appearance, use of habitats concealed from the view of predators, and a suite of toxins that the organism emits. And, though the selection pressure for them to evolve may be weaker, the adaptations of predators to successfully obtain prey may include speed, agility, and aggressive mimicry of harmless organisms. In addition to these morphological and behavioral adaptations, some adaptations of predators and prey may be cognitive. Cognition (the neuronal processes associated with the acquisition, retention, and use of information about the environment) can range from lower-level memory to the higher-level thinking that characterizes humans (Dukas 2002). Prey should be expected to employ some level of cognition to assess the threat a predator poses, and predators should be expected to employ information processing to differentiate prey from nonprey and make captures that they can successfully use to their benefit (Barrett 2015).

## Vision

Many organisms obtain information about the environment through the visual system. Eye-like structures have emerged independently an estimated 40 times throughout the history of life on earth, ranging from light-sensitive cells in earthworms to compound eyes in fruit flies. Despite their varied evolutionary histories, the proteins that catch photons and bend light rays are remarkably similar across taxa (Land and Fernald 1992).

Using this uniform process for converting light energy into nerve impulses, predators and prey must successfully recognize each other despite variation in illumination conditions, viewing angles, and obstruction by other objects. The organism must successfully generate a retinal image of the object, and then must categorize that image in a class of objects that the organism has previously encountered.

## Recognition

To understand how recognition systems evolve, it is important to focus on the behavioral responses that successful recognition causes. Recognition systems are adaptive or maladaptive only according to the behavioral, developmental, or physiological responses they generate in organisms (Dukas 2004; Liebert and Starks 2004). Selection acts on an organism's ability to recognize cues in its environment based on the fitness advantages that this ability confers. These advantages include finding mates, finding food, or avoiding danger. The recognition ability of one organism can also affect the fitness of the organism being recognized. These consequences range from beneficial in kin discrimination to deadly in prey recognition. Failing to respond to cues that a predator is nearby carries a much greater penalty than failing to notice cues of mate quality or food availability (Lima and Dill 1990).

## The Visual System and Predator Detection

The visual system has several different components that can act both as constraints to fitness in the face of predation as well as adaptations that enhance predator detection ability. The configuration of the visual field, or the degree of visual coverage around a prey organism's head, varies across different types of organisms. The visual field can act as a constraint because the shape of the visual field confers a trade-off between sensitivity and accuracy. Visual acuity, temporal visual resolution (how quickly the retina perceives

temporal changes in visual stimuli), visual contrast (ability to resolve a stimulus against a background), the width of the visual field, and motion detection all play important roles in predator detection ability (Tyrrell and Fernandez-Juricic 2015).

## Visual Acuity

Visual acuity refers to the sharpness of vision at a given distance from the observer. The visual acuity of an organism determines how far away a predator could be from the organism and still be detected. Studies of allometry have shown that visual acuity is hyperallometric to eye size. Allometry is the study of the relationship of body size to anatomy and physiology. A perfectly allometric relationship occurs when two body parts increase in size in proportion to each other as body size increases. Visual acuity is considered hyperallometric to eye size because, when the logarithm of visual acuity and the logarithm of eye size are plotted against each other, the log of visual acuity increases by a factor greater than one. Because eye size only scales *allometrically* with body size, larger organisms tend to have disproportionately better visual acuity than smaller organisms. Birds have higher visual acuity than other similarly sized animals due to their eyes that are often large for their body size, which may confer an advantage in detecting predators from a distance (Martin 2007).

## The Visual Field

Vertebrate species vary in their degree of binocular overlap, often according to an organism's vulnerability to predation. The eyes in humans and other closely related primates face in the same direction, which is a feature known as frontal convergence (Heesy 2004). However, many prey organisms, such as rodents and hoofed mammals, have lateral-facing eyes that have a small area of overlap. Organisms with such lateral-facing eyes may have a wider visual field, which assists with predator detection across a wider area. Lateral-

facing eyes may move independently of each other, further increasing the probability that a predator in the vicinity will be noticed.

## Visual Resolution

In addition to visual acuity and visual field configuration, predator detection may also depend on overall visual resolution, which refers to the average resolution across the whole visual field as determined by eye size and the average density of photoreceptors across the whole retina. If there is a steep change in cell density across the retina, individuals rely mostly on their retinal center of vision (rather than periphery), increasing the number of eye/head movements required to gather information, i.e., scanning behavior (Fernandez-Juricic et al. 2010). On the other hand, a small change in cell density would allow individuals to also rely on the retinal periphery, providing a larger portion of the retina with high-quality information and reducing the need for a high frequency of head/eye movements. A species with a steeper cell density profile may have lower chances of predator detection because it collects fewer retinal snapshots per unit of time, and there is a smaller retinal area with high resolution within each snapshot.

## The Cognitive Ecology of Predator Recognition

The ability to recognize predators allows prey organisms to successfully avoid dangerous encounters and to continuously monitor the level of risk around them (Lima and Dill 1990). How prey organisms respond to the risk of predation now is shaped by predation pressure over evolutionary time, as well as by the rate at which an individual organism encounters predators in the environment. The predation risk allocation hypothesis predicts that an organism should allocate the most energy into predator monitoring and avoidance when in infrequent, high-risk situations and allocate the least amount of energy to predator monitoring when in frequent, low-risk situations



(Lima and Bednekoff 1999). Intergenerationally, selection pressure on prey is expected to be strongest for costly predation events that occur every generation with great frequency. This hypothesis has implications for predator recognition in prey. Prey organisms should easily learn to recognize or have an innate response to predators that are encountered every generation and that pose a high risk to prey. On the other hand, prey organisms may not learn to recognize predators which pose a lower risk as easily. Prey that are capable of learning predator identities while adjusting the intensity of their response to match their level of risk should be at a substantial selective advantage (Manassa et al. 2014).

Learning plays an important role in predator recognition. Organisms can learn to recognize species through social learning or individual learning. In species with social learning of predator recognition, less experienced individuals commonly learn about predators from more experienced individuals. This social learning eliminates the need for an individual to directly face the risk associated with confronting a predator itself (Dowell 1986). In species that never encounter adults of their own species as young, an individually learned response is more likely to evolve. Supporting these predictions, recognition of predators appears to have evolved in some bird species, such as Australian brush-turkeys that lack parental care. In the absence of parental guidance, young must be able to recognize and avoid predators on their own (Göth 2001). In contrast, in bird species with parental care, such as grey partridges and pheasants, naive chicks also learn to respond to certain stimuli on their own, but they later learn a more sophisticated behavioral response from their parents (Dowell 1986).

Innate recognition of predators may evolve in species in which the costs of learning are particularly high (Berejikian et al. 2003). Learning requires sampling of the environment, which can be costly in terms of time, energy, and the potential for mistakes (Snell-Rood 2013). In addition, the neural tissue associated with learning is expensive and may involve trade-offs with reproduction and fecundity. The amount of energy devoted to learning tasks may thus reduce the

amount of energy available to invest into reproduction, thus favoring the evolution of predator avoidance strategies that are less learning-intensive (Lefebvre and Sol 2008). In particular, innate recognition of predators may evolve when learning costs are high, and when the benefits of having a more plastic predator recognition response are negligible (Berejikian et al. 2003).

How prey sensory and cognitive systems both constrain and are driven by selection on prey by predators is a key question in the emerging field of comparative psychology (Emery and Clayton 2009). Examining differences between species in the mechanisms and abilities underlying predator recognition is crucial for understanding the degree to which predator recognition is affected by different selective environments (Polo-Cavia et al. 2010). As well, there is well-documented potential for responses to predators to be changeable: affected by such nongenetic variables as a stressful social environment, toxic pollutants, and the rate at which an individual encounters certain predators within its lifetime (Snell-Rood 2013).

## Prey Recognition

In ecological theory, the “landscape of fear” represents levels of predation risk as peaks and troughs, which are reflected in similar peaks and troughs in antipredator behavior in prey organisms, or “fear” (Laundré et al. 2010). In contrast, the behavior of predators is driven by the richness and size of a prey community in various “patches.” Importantly, predators are not a static environmental risk faced by prey, but they are expected to respond strategically to prey behavior over time. Producers are organisms that convert an abiotic source of energy into organic compounds. Consumers are organisms that are unable to make their own energy and instead rely on the consumption of other organisms. Animal prey (consumers) are only taken by secondary, tertiary, and quaternary consumers, whereas primary consumers only eat producers. Prey organisms that are consumers are usually more mobile than producers. Thus, high-value resource “patches” composed of consumers tend to be less spatially and

temporally predictable than resource patches composed of producers. Because of this greater dispersion and lower predictability of food resources, prey search by higher trophic level predators can be a demanding task.

How do such predators accomplish the task of prey search? While predators rely on a variety of senses to detect and capture prey, including olfaction and audition, many avian and mammalian predators are especially reliant on vision. Visual detection of prey is influenced by a number of factors. The spectral properties of ambient light in a given environment influence how conspicuous objects are against the background. Prey organisms will more readily be detected in high light than in shady environments and in environments with few obstructions rather than environments densely packed with vegetation or debris (Uy and Endler 2004). Visual recognition to prey is also affected by properties of the predator's sensory system, including how the predator perceives different wavelengths of light. In addition, predatory foraging strategies vary widely, from stealth to sit-and-wait and to cooperative hunting, affecting how quickly and easily a predator will recognize prey. In addition to being influenced by a predator's ecology, prey recognition is also impacted by the characteristics of prey themselves.

## Prey Characteristics and Recognition by Predators

Different characteristics of prey affect the evolution of predator visual systems, including the visual perceptual systems of the prey, prey crypticity, and prey toxicity.

Animal visual perceptual systems are necessarily constrained. Animal brains have a limited rate of information processing. Even if they have a 180- to 360-degree view of the surrounding environment at any one time, individuals must restrict the amount of information they process at any given time (Dukas 2002). A consequence of limited information processing is that animals selectively attend to salient environmental stimuli. Animals rely on cognitive "search images" that

allow them to efficiently attend to habitats, food, and mates.

Like prey, predators face a trade-off between having a wide attentional angle and perceiving the finer details of prey. A wide attentional angle allows for a predator to search a large area, helping it to successfully find any conspicuous, easily noticeable prey within its field of vision. But finding a more hidden, cryptic target may require a narrower attentional angle and a lower search rate (Gendron and Staddon 1983). When searching for prey, predators generally target the most conspicuous prey phenotypes. Generally, factors determining a prey's conspicuousness may include such variables as high achromatic contrast in the prey's habitat or color patterning that reflects light at the peak of a predator's spectral sensitivity.

Cryptic phenotypes are less discernible than conspicuous phenotypes, but they can still be learned and recognized by predators. When avian predators are trained to recognize cryptic prey, they form a search image of the most abundant type in the environment (Dukas and Kamil 2001). Predators tend to form a search image of the most abundant type of prey due to information processing constraints. It is considerably easier to keep a search image of one prey phenotype in working memory and to selectively attend to patterns matching it than to look for patterns matching two or more search images simultaneously (Dukas 2002). As the type's numbers decrease (due to higher predation rates than on less frequent types), predators engage in perceptual switching, changing their search image to target the prey species that became relatively more abundant (Bond 2007). The information processing constraints imposed on predators by search images and perceptual switching are thought to be a main driver of the evolution of color polymorphism in many cryptic prey species. These constraints result in apostatic selection on prey phenotypes, in which a given prey phenotype's fitness is negatively correlated with its frequency in the population.

Dawkins and Krebs's salient life-dinner principle states that prey should be under stronger selection to avoid any given predator than

predators to catch any given prey. However, the asymmetry in selection on predators and prey may be reduced when prey are dangerous. For most prey that are noxious, predators learn that they are noxious by encountering them individually. The encounters are rarely dangerous, and prey that are easier to learn to avoid (with bright, memorable patterning or coloration) generally have an advantage. This is the basis for the evolution of aposematism as well as Batesian and Mullerian mimicry systems. However, some prey are actually dangerous to predators, resulting in serious illness or even death if consumed.

## Conclusion

Developing an integrative understanding of the visual recognition of predators and prey is an interdisciplinary endeavor. It involves a complex network of fields, such as cognitive psychology, evolutionary ecology, neuroscience, and behavioral ecology. However, the literature on visual recognition of predators and prey has been dominated primarily by studies on birds and falls largely within the domain of evolutionary ecology. Bird studies likely dominate this literature because nonavian organisms, such as most mammals and many fish, may be less reliant on visual recognition than birds. Future studies should explore the importance of visual recognition of predators and prey relative to other forms of recognition, such as auditory and olfactory recognition, in other taxa. In addition to the advent of comparative methods, the theory and empirical evidence behind ontogeny and developmental plasticity have grown in recent decades. Recognition is a cognitive process, and like all cognitive and behavioral processes, it is not entirely hard-wired, but also contingent on environmental inputs (Snell-Rood 2013). Examining how recognition manifests itself ontogenetically will help answer critical questions about how knowledge acquired from previous experiences can shape predators' and prey's ability to recognize and avoid each other. An integrative

perspective that takes into account the flexibility of many cognitive and behavioral traits will further our understanding of the proximate and ultimate factors behind predator and prey recognition. Additionally, examining how these factors differ across evolutionarily distant groups (such as arthropods and vertebrates), as well as between closely related species, will be crucial to advancing this fertile area of research.

## Cross-References

- [Foraging](#)
- [Predation Risk](#)
- [Predator Defense](#)
- [Predator Detection](#)
- [Prey](#)
- [Visual Recognition in Birds](#)

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## Visual Search

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## Introduction

In everyday life, animals spend much of their time with looking for something. They need food, nest-building material, or mates and compete with conspecifics for all these pivotal resources. Unfortunately, their location is mostly uncertain, and they are typically embedded within an environment full of irrelevant stimuli (**distractors**) competing for attention and hindering identification of the actual search item. Many animals actively try to impede their detection as prey or predator by camouflaging and hence, blending into the surrounding. Thus, an individual requires efficient strategies to search in the visual field, which facilitate quick detection of significant objects. The difficulty of **visual search** depends on factors like scene complexity, number of distractors, and similarity between search objects, distractors, and background. This is a computationally demanding task. Since neuronal resources are limited, visual systems cannot process all incoming information in parallel and therefore have to filter out relevant stimuli while suppressing responses to distractors or noise. Thereby, especially attentional mechanisms mediate selection of cues and guide gaze during search.

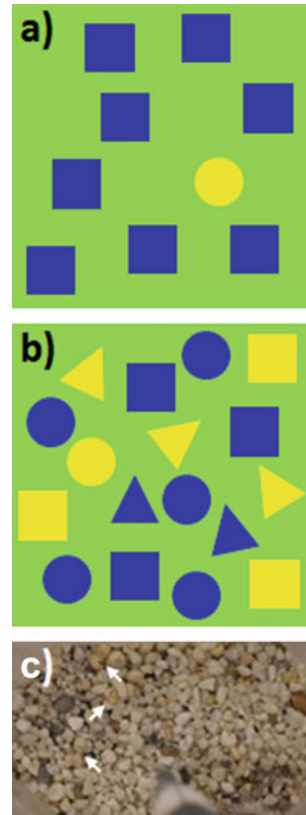
Although pivotal for all visual animals, major models of visual search strategies are coming from human psychology and are intimately related to theories of attention (Eimer 2014; Knudsen 2007; Wolfe 2003). Due to the interrelations between attention and visual search, search paradigms are typically used to

investigate attentional processes. Recent comparative studies, however, indicate an astonishing similarity of fundamental mechanisms between different vertebrate classes and even insects irrespective from profound differences in the organization of their neuronal systems (Nityananda 2016).

## Visual Search in the Laboratory

In a typical visual search experiment, subjects have to report the presence or absence of an object that is defined by a set of features (**target**) among irrelevant items (**distractors**), which differ in one or more dimensions from the target (Fig. 1). Objects are often presented on a computer screen but semi-natural setups can also be used (Fig. 2). While human subjects can be verbally instructed what to look for, animals firstly have to be trained onto the search target. This typically means that the animal learns to differentiate between a rewarded positive and a nonrewarded negative stimulus during a conditioning process. After reaching a learning criterion, the individual has to search for the positive item between varying numbers of distractor stimuli. Thereby, natural behavior of the tested species is used to analyze search performance. Pigeon, for instance, can be trained to peck onto stimuli presented on a computer screen within an operant chamber (Fig. 2a) while honey bees can learn to approach a rewarding “artificial flower” in a semi-natural experimental setting (Fig. 2b).

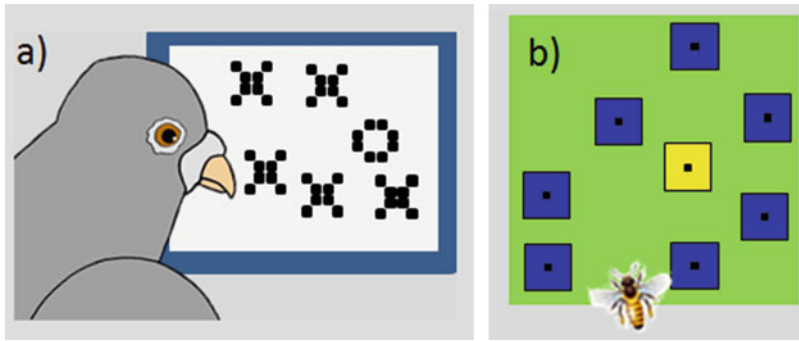
Experimental search is typically less complex than in natural surroundings. But difficulty of the task can be manipulated by changing the number of items, by the complexity of the target, or by the similarity between target and distractors or background. Search performance is measured as **error rate** (= erroneously indicating presence (**false alarm**) or absence (**miss**) of the target) or as **reaction time** (RT, time required to indicate presence or absence of the target). The relation between RT and number of presented items in the display (**set size**) is an important measure indicating the underlying search strategy. If RT rises



**Visual Search, Fig. 1** Complexity of visual search – (a) in an artificial display, a target (*yellow circle*) may pop-out since it is characterized by features that are very different from other items (*blue squares*) on the display; the target directly attracts attention and can be detected without detailed analysis during parallel search. (b) When target characteristics (*yellow circle*) overlap with that of the distractors, detection requires comparison and combination of different features (shape + color) during serial search. Although attention might be firstly attracted by one feature (e.g., yellow color), all objects must be scanned one by one until the target is identified. (c) Search in a (semi)-natural setting is typically even more complex since targets like edible grains (arrows) can be embedded within a complex background of distractors (similar looking pebbles). Detection requires detailed analysis of the scene during serial search

linearly with increasing set size, the subject presumably scans the items one by one until the target is found. This indicates a **serial search strategy**. If on the other hand, RT is independent from set size, the subject may observe all items at once. This pattern points to a **parallel search strategy**.





**Visual Search, Fig. 2** Typical experimental setups for visual search – (a) Animals like pigeons can learn to discriminate and detect stimuli presented on a computer screen. To this end, a pigeon may learn to peck onto a target (S+, O), which is reinforced with food while pecks onto a distractor (S–, X) leads to punishment (e.g., short time out; according to Blough 1979). (b) Insects like honey bees can

be trained to choose a colored disk (S+) among differently colored ones (S–). Discs include a feeder (*black dots*) that may provide sweet sucrose (S+) or bitter quinine (S–) solution. These “artificial flowers” are attached on the back of a box, which could be entered through an entrance hole (according to Spaethe et al. 2006)

## Steps and Mechanisms of Visual Search

Visual search proceeds along different steps, which confront the neuronal system with different problems. Because of the richness of the natural environment, it is impossible to process all visual input at one time. A major problem especially during natural-scene search is the decision how to scan the environment and hence how to disperse attention to select relevant information helping to find the search object. Thereby, **bottom-up processes** identify **salient**, conspicuous features, objects, or places, which directly attract attention. **Top-down processes** guide attention according to expectations about the appearance and localization of the search item and therefore consider **context** information that predict where the search object might be. Since mostly not all details of scenery can be analyzed in parallel, the visual system switches between **serial** and **parallel search mechanisms**, which differ in speed and accuracy and which are differentially efficient depending on the complexity of the search items, distractors, and scene.

Search starts by deciding what to look for. This implies that the individual has some expectations how the search object looks like. A search object is typically defined by a combination of features like shape, size, color, or texture. These features are used as templates guiding attention through

the visual scenery. **Attentional templates** are represented in working memory, which temporarily stores a limited amount of selected information for later processing. Incoming signals are permanently compared with these templates to select specific signals over others in the environment. Thereby, precise (expert) knowledge of the target characteristics (because of extensive experience with the search objects) can profoundly improve detection performance (e.g., ground-feeding birds like pigeons or chicks are highly efficient in detecting grains between pebbles; Fig. 1c). When the exact appearance of a search object is not known (e.g., when different edible grains or seed might be present on a ground), the individual can use characteristic visual properties, which are invariant across diverse members of an object class (**categorizing**).

At the beginning, parallel search gains a global impression of the scene eventually detecting critical features allocating attention to possible target objects while filtering out distractors and background noise. As a primary filter, several species display differential resolution of visual processing. The retinae of primates or many birds, for instance, possess areas of enhanced visual acuity (**fovea**) so that detailed vision is confined to a small range of the visual field while the rest is only diffusely perceived. This in turn requires attentional mechanisms guiding gaze to positions

in the visual scene that might contain the target and that should be analyzed more extensively. Eye movements are controlled by a mesencephalic brainstem network that is highly conserved in vertebrates with the optic tectum (superior colliculus in mammals) as a central structure that closely interact with specific forebrain areas in orienting gaze (Knudsen 2011).

Bottom-up and top-down processes converge to establish a **salience map**, which encodes conspicuous features while preserving topographic organization of the scene. This map is used by the gaze controlling networks to guide eye movements. Thereby, **salience** describes how distinct one element of a scene is from surrounding elements. Sometimes, a characteristic feature of the search object “pops-out” since it is very different from the surrounding (e.g., a ripe, red berry in green leaves). It automatically attracts attention and the object can be directly identified by parallel search. Many plants, which depend on animal pollination or seed spreading, harness this ability by vividly coloring their fruits and blossoms. Pop-out effects can be observed in different vertebrate species and even insects like bumblebees (Nityananda 2016), indicating that parallel analysis of features in a visual scene is a universal search mechanism across the animal kingdom. Salience can also be caused by a highly biological relevance of a stimulus (a predator hidden in the underwood). These stimuli are detected faster because of phylogenetically developed attentional priority mechanisms. Humans and other primates for instance detect deviant snake picture in a complex array more quickly than neutral stimuli like flowers (Shibasaki and Kawai 2009). Moreover, experience-dependent “**search images**” facilitate as primed representations the detection of vitally relevant objects. Foraging birds for instance overselect grain types that are relatively abundant. Tits, which capture different insect during flight, are more likely to notice that prey type, which they have repeatedly encountered before. In a similar way, honey bees typically restrict their search to a subset of available flower species when exploiting nectar and pollen sources on a meadow (**flower constancy**).

Understanding the structure of a scene also supports search since a natural environment exhibits regularities, which provide information about the likely localization of search objects (Le-Hoa Võ and Wolfe 2015). **Contextual cues** direct attention via top-down processes to those parts of a visual environment that have the highest probability of containing the target (ripe fruits are found on tree tops and not in the underwood). Knowledge increases with experience since individuals gain memory for the localization of detected targets in a familiar environment.

Parallel search identifies candidate objects or locations in space, which are selected for more detailed analysis during **serial search**. In this case, focal attention is allocated from object to object until the target is identified. Serial search is always necessary when a search item does not pop-out or when complexity of a search item requires combination of different features. Since combination of different features is computationally demanding, single objects can only be analyzed and recognized successively. The underlying neuronal processes represent key aspects of models of visual attention like the **Feature Integration Theory** of Treisman (Wolfe 2003). Detailed analysis and combination of features finally enables object recognition. This is a demanding computational process on its own and a prerequisite to initiate an adequate behavioral response.

Serial and parallel search might be controlled by processes in the left or right brain side. In several species, visual attention and hence search is not symmetric across the visual field. Chicks and pigeons for instance preferentially peck into the left visual half-field when they explore an area uniformly spread with grains. Since input from this half-field is processed by the right brain side, the leftward bias indicates right-hemispheric control of visuospatial attention (Diekamp et al. 2005). Since grains are not obscured under test conditions, parallel search enables quick collections of the food items. The underlying global processing is a typical specialization of the right brain side in vertebrates. When, however, grains have to be discriminated from similar looking pebbles (Fig. 1c), the left hemisphere is more

efficient in mediating a detailed analysis of visual stimuli requiring focused attention and serial search (Rogers 2017).

## Cross-References

- ▶ [Attention](#)
- ▶ [Attention Bias](#)
- ▶ [Bottom-Up Processing](#)
- ▶ [Categorization](#)
- ▶ [Feature Integration Theory](#)
- ▶ [Foraging](#)
- ▶ [Foraging by Honeybees](#)
- ▶ [Hemispheric Specialization](#)
- ▶ [Operant Chamber](#)
- ▶ [Operant Conditioning](#)
- ▶ [Predator Detection](#)
- ▶ [Priming](#)
- ▶ [Saccadic Eye Movement](#)
- ▶ [Search Image](#)
- ▶ [Top-Down Processing](#)
- ▶ [Visual Detection Task](#)
- ▶ [Visual Perception](#)
- ▶ [Visual Recognition in Birds](#)
- ▶ [Visual Recognition of Prey and Predators](#)
- ▶ [Working Memory](#)

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## Visual Self-Recognition

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## Synonyms

[Mirror recognition](#); [Mirror self-recognition](#); [Self-recognition](#)

## Definition

Knowing what one's own appearance looks like.

## The Importance of Visual Self-Recognition

Although many of us experience seeing our own image on a daily basis (e.g., brushing our teeth using a mirror, catching our reflection in a window), we perhaps take our ability to know what we look like for granted. This seemingly mundane ability has nonetheless evoked substantial scientific, philosophical, and ethical interest. For example, self-recognition matters because it may be a proxy for complex psychological phenomena such as self-conception (i.e., a sense of identity persisting across time and space), self-awareness (i.e., making one's self the object of attention), and/or secondary representation (i.e., generating

and comparing multiple mental models) (see section “[Psychological Mechanisms](#)”). In turn, assuming that self-recognition indicates some form of psychological complexity has led to it being used as evidence in legal cases concerning “rights” for nonhuman primates. For instance, as yet unsuccessful bids to secure human rights for chimpanzees have been based at least in part to their ability for self-recognition (Gagneux et al. 2005). Nonetheless, evidence for self-recognition has successfully contributed to the prohibition of invasive great ape research in countries such as Japan, the Netherlands, the United Kingdom, Sweden, Germany, Austria, and New Zealand (e.g., Cavalieri and Singer 1994). Finally, self-recognition also matters because it may be the basis of our capacity to engage in effective image management (via monitoring and modifying what we look like) and recognizing our kin (via self-referent phenotype matching), both of which may contribute to enhanced reproductive success (see section “[Function](#)”; Butler et al. [to in preparation](#); Suddendorf and Butler 2013).

### How to Test for Visual Self-Recognition?

Despite the behavioral simplicity of self-recognition as a psychological construct (e.g., I can say “that is me” when looking at my own body or image), an objective way of measuring this ability in nonhumans (and human infants) remained elusive for many years (Butler 2015). Early attempts in the nineteenth century – including by Charles Darwin – consisted simply of reporting reactions such as surprise or aggression by monkeys and apes when presented with a mirror. Such reports are problematic because of the absence of any systematic, objective procedure; animals’ emotional responses to their own reflections are ultimately ambiguous, not least because of potential observer biases which may influence how such expressions are interpreted (Butler 2015). It was not until 1970 that Gordon Gallup published his seminal methodological breakthrough for overcoming such problems.

After observing that chimpanzees eventually ceased responding socially to their reflection and

used the mirrors instead to spontaneously engage in self-inspection and grooming of otherwise unseen body areas (inside their mouth, their anal-genital region, etc.), Gallup (1970) conducted what came to be known as the “mirror-mark test.” He found that chimpanzees with surreptitiously placed marks on their forehead and ears engaged in explicit self-directed responses toward these unfamiliar and otherwise non-visible marks, but only in the presence of a mirror. This simple procedure has since become the gold standard approach for investigating self-recognition in human infants and animals alike (see section “[Appropriate and Inappropriate Testing Procedures](#)”).

### Which Species Show Visual Self-Recognition?

Being a proxy for psychological complexity (i.e., self-awareness), some researchers continue seeking to simply determine which species do and do not show self-recognition. Numerous species have been tested for self-recognition *without* using the mirror-mark test, including fish, dogs, sea lions, killer and false killer whales, and various birds (Butler 2015; Butler et al. [to in preparation](#)). With the exception of possible contingency testing by whales, all of these species have either shown little interest in their reflection or reacted similarly to how they react toward an unfamiliar conspecific. More definitive evidence requires the mark test.

To date, only the great apes (i.e., humans, chimpanzees and bonobos, gorillas, orangutans) have shown replicated evidence for passing the mirror-mark test (and/or compelling evidence of spontaneous, mirror-guided self-exploration) (Butler 2015; Butler et al. [to in preparation](#)). It is important to acknowledge that for various reasons (e.g., differences in motivation and/or “passing” criteria), not all individuals pass the mark test or show spontaneous mirror-guided self-exploration (Swartz et al. 1999). Nonetheless, there is overwhelming evidence that all great ape species possess the ability for self-recognition. No equivalent evidence exists for other nonhuman primates,

including the small (or lesser) apes and numerous species of monkeys (Anderson and Gallup 2015; Butler 2015; Butler et al. *to in preparation*) (see Controversies).

Several non-primate species (including manta rays, horses, pandas, and even ants) have been tested for self-recognition using various adaptations of the mark test, with no convincing positive results (Butler et al. *to in preparation*). However, evidence for a few species remains contentious. For instance, one out of three Asian elephants passed the mark test but failed on a re-test (Plotnik et al. 2006), while two elephants showed no positive evidence in another study (Povinelli 1989). One out of two dolphins looked more at their marked than their unmarked image (Reiss and Marino 2001), but to date there has been no reported replication of this finding. Similarly, there has been no replication of the report that one killer whale removed a mark by rubbing itself against the pool wall (nor was there a comparison to a non-mirror baseline period) (Delfour and Marten 2001). More recently, in contrast to a few claims for self-recognition in some corvid species (Clary and Kelly 2016; Prior et al. 2008), other authors have reported negative findings (Soler et al. 2014). At best, claims for self-recognition in non-primates should be considered with caution pending methodologically rigorous replication (see section “*Appropriate and Inappropriate Testing Procedures*”; Gallup and Anderson 2018; Suddendorf and Butler 2013).

Testing for self-recognition in media other than mirrors warrants consideration, for at least two reasons. Firstly, from human studies we know that being able to recognize one’s own reflection does not guarantee self-recognition in non-mirror situations (i.e., some people can recognize themselves in mirrors but not videos or photographs and vice versa) (Butler 2015). Secondly, with few exceptions, neurological studies of self-recognition in humans involve presenting participants with photographs or videos rather than mirrors (Butler 2015). Evidence for self-recognition in nonhumans in media other than mirrors is scarce. Some descriptions of responses to videos exist for chimpanzees, gorillas, orangutans, some monkeys, and even dolphins, but in

the absence of mark tests, most of these reports are ambiguous at best (Butler 2015; Butler et al. *to in preparation*). There have only been two reported instances involving video mark tests, both providing positive evidence for self-recognition in chimpanzees (Hirata et al. 2017; Suddendorf et al. 2006). Evidence for self-recognition in pictures includes correct self-labeling by Koko the gorilla (Patterson 1978) and Ai the chimpanzee (Itakura 1992), and categorization by Viki the chimpanzee, who placed her own photograph in a “human” rather than “nonhuman” pile (despite placing her father’s photo in the latter) (Hayes and Nissen 1971). Although intriguing, such evidence requires replication and extension using complementary methodological approaches.

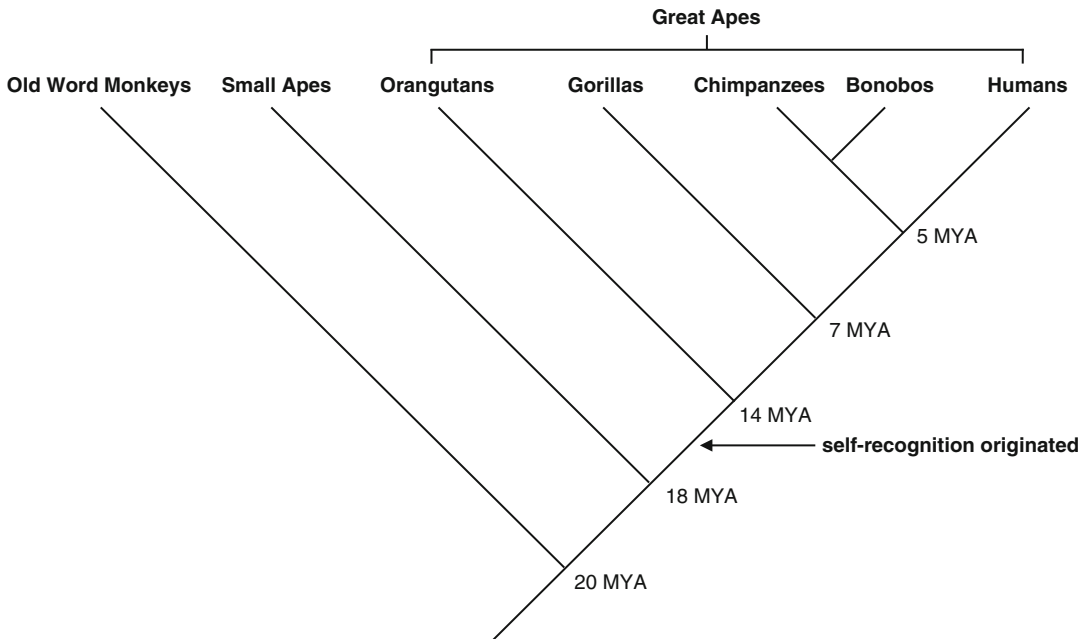
## The Evolution of Visual Self-Recognition

On the basis of replicated evidence involving great apes (see Fig. 1), we can consider two potential scenarios: either each individual species (i) independently evolved the capacity for self-recognition (i.e., convergent evolution occurred four or five times) or (ii) retained the capacity for self-recognition after it *originated only once* in a common great ape ancestor, between 14 and 18 million years ago (i.e., homologous evolution). This latter account – being the most parsimonious – is the strongest explanation for the current distribution of self-recognition (Suddendorf and Butler 2013). In the event of more compelling evidence concerning more distantly related non-primate species such as elephants, cetaceans, or corvids, additional explanations invoking convergent evolution will be required (see Future Challenges).

## Controversies

There are several contentious issues concerning self-recognition, including (i) appropriateness of testing procedures, (ii) psychological mechanisms, and (iii) function (i.e., whether self-recognition is adaptive).





**Visual Self-Recognition, Fig. 1** Distribution of visual self-recognition amongst primates (please note that these time frames are estimates)

### Appropriate and Inappropriate Testing Procedures

Given the prominence of the mark test for investigating self-recognition, it should come as no surprise that multiple variations have been reported – including both prior to and during the actual test (e.g., the amount of image exposure before testing; age at exposure; using mirrors that reduce eye contact; concave and convex mirrors; physically accessible mirrors; applying extra-salient marks such as chocolate or sugar icing; etc.) (Anderson and Gallup 2015). None of these variations have produced positive results for primates other than the great apes, although it should be noted that intriguing (and as yet, un-replicated) results were recently reported for a corvid species (Clark's nutcrackers) when using blurry rather than clear mirrors (the former being more akin to how birds may see themselves reflected in natural water sources) (Clary and Kelly 2016). Perhaps the most important modification to Gallup's original test involves the additional marking of visible rather than non-visible body regions (e.g., Gallup et al. 1980). If the subject responds to directly visible marks on an arm but ignores a mark on

the head that is visible only in the mirror, this rules out the possibility that the negative result for self-recognition is due to low motivation for any mark touching.

Some claims to have demonstrated self-recognition in monkeys and non-primate species deserve skepticism because of the questionable methods used. For example, the omission (or non-reporting) of a pre-image exposure control period following the initial marking of the subject means that tactile cues for any subsequent mark-directed behavior cannot be ruled out (Anderson and Gallup 2015). Similarly, some subjects have not been nescient while their appearance is altered; therefore, any subsequent image-mediated behavior may be nothing more than an artifact of stimulation such as tactile sensations from an area they know has been altered (e.g., head implants). Indeed, such a possibility has been verified: Soler et al. (2014) could not replicate previously reported positive results for self-recognition in corvids (using colored stickers as marks) once tactile cues were accounted for. Perhaps the most serious issue, however, concerns the use of operant conditioning to engineer

mirror-mediated self-directed responses ostensibly similar to those which occur *spontaneously* in great apes (Anderson and Gallup 2015). At best, subjects trained to pass the mark test only via hundreds (or thousands) of reinforced trials are simply showing something that superficially resembles self-recognition (much as a robot can be easily programmed to elicit a specific reaction toward an object using simple “if – then” rules without actually understanding what that object is). Recall, too, that Gallup’s original mark test was preceded by his observations of chimpanzee’s *spontaneous* mirror mediated self-inspection. In short, while conditioned training might result in self-recognition, it ultimately drains the mark test of its power to determine whether an organism really deserves allocation to the positive (“self”-possessing) side of the cognitive Rubicon (de Waal 2008). To remain as the “gold standard” for self-recognition, the mark test must be conducted carefully within behavioral contexts involving spontaneity and self-inspection.

### Psychological Mechanisms

Explanations for the psychological mechanisms underlying self-recognition fall along a continuum of cognitive complexity ranging from “lean” to “rich” (Suddendorf and Butler 2013). Prominent examples of the former include associative learning (i.e., contingent reinforcement as discussed above) (Epstein et al. 1981), distinguishing between internal versus external sources of information (i.e., self-recognition is simply a by-product of an ability for not bumping into things) (Heyes 1994), and kinesthetic-visual matching (i.e., matching the image of a moving body part with the contingent sensation of one’s own moving body part) (Mitchell 1997). Such accounts, respectively, fail to explain spontaneous manifestations of self-recognition, the limited distribution of self-recognition among species that are capable of not bumping into things, and why (in human infants at least) self-recognition emerges only approximately 12 months after contingency testing first occurs (Butler 2015; Suddendorf and Butler 2013). Psychological explanations for self-recognition require at least some representational complexity.

Gallup (1985) proposed the most prominent and rich account of self-recognition, arguing that it presupposes the existence of a self-concept, which in turn presupposes the existence of self-awareness (i.e., making one’s self the object of one’s own attention). Moreover, this self-awareness allows insight into one’s own mental states, which may then be utilized for knowing the mental states of others (i.e., theory of mind); self-awareness may even contribute toward awareness of one’s own eventual death. The evidence in support of Gallup’s view is mixed (Butler 2015; Butler et al. [to in preparation](#); Suddendorf and Butler 2013). For instance, infants who have passed the mark test go on to show evidence for (i) other forms of self-awareness (e.g., self-related emotions such as guilt, shame, and embarrassment), (ii) appropriate personal pronoun use, and (iii) theory of mind (including empathy and joint attention). It is noteworthy that chimpanzees are clearly capable of empathy and joint attention, and they also show at least some aspects of understanding death (Anderson 2016). However, complications arise. Firstly, if self-recognition presupposes the existence of a self-concept and a “broad” self-awareness, why are there dissociations involving self-recognition across media (i.e., human infants require an additional 12 and 24 months beyond mirror recognition to pass live and delayed video versions of the mark test)? One possible explanation is that those infants who first show mirror recognition have a limited form of self-conception restricted to the present (i.e., a basic “online” self-concept), while older children who pass video versions of the mark test possess a self-concept which extends through time and space (i.e., the self-concept “proper”) (Povinelli 2001; Povinelli et al. 1996). This explanation, however, fails to account for why infants who pass the mirror-mark test do not pass the live video version of the mark test. Moreover, despite the emergence of self-recognition in human infants during their second year, they retain limited capacities for understanding (i) the minds of others until age 3–4 years (when passing false belief tasks) and (ii) the biological characteristics of death until several years later (Suddendorf and Butler 2013, 2014).

Similarly, there is only limited evidence that chimpanzees or other great apes understand that others can have false beliefs or are aware of their own eventual death. In summary, while lean proposals do not go far enough, Gallup's rich proposal goes beyond the current evidence (Suddendorf and Butler 2013, 2014).

Several intermediate accounts have been proposed, at least for self-recognition in humans; for instance, self-recognition specifically requires being exposed to one's own face and the importance that others attribute to it (e.g., Niesser 1997). Such an explanation fails to account for the similar developmental trajectories in self-recognition based upon leg and face versions of the mark test (Nielsen et al. 2006). Perhaps language is somehow implicated? This is unlikely given that (a) human infants demonstrate rudimentary language abilities long before passing the mark test (c. 18–24 months) and (b) the vast majority of nonhuman great apes that have passed the mark test have not been trained in human “sign” language. Another intermediate account of self-recognition involves a domain-general capacity known as secondary representation (i.e., simultaneously generating and comparing multiple mental models about something). According to this account, self-recognition occurs when we can generate and compare representations of what we *think* we look like with what we *do* look like; in other words, we recognize what we look like because we are able to create, compare, and rapidly update mental models about our appearance (Suddendorf and Butler 2013, 2014). This need not involve a broad level of self-awareness as advocated by Gallup; it requires only an awareness of our own appearance (therefore making this proposal less “rich” than Gallup's). Evidence for the role of secondary representation in self-recognition is accruing: not only do human children tend to develop several other secondary representational abilities at around the same time (i.e., means-end reasoning, pretense, etc.), among primates, these same secondary representational abilities appear to be shared only with the other great apes (Nielsen and Dissanayake 2004; Suddendorf and Whiten 2001). This explanation – like Gallup's – struggles to account for

dissociations in self-recognition across different media, although this may reflect something to do with expectations involving the media used rather than differences in self-conception per se (i.e., unlike mirrors in which one can almost always expect to see their own image, video monitors are usually associated with seeing things other than one's own image). Nonetheless, secondary representation currently provides the best account for the development and distribution of self-recognition.

One crucial factor that most causal models of self-recognition have ignored is the role of affective processes and their regulation. To date, however, only the “dual-route” model of self-recognition – based upon clinical cases of misidentification – has attempted to integrate cognitive and affective processes (Breen et al. 2000; Butler 2015). According to this model, faces are structurally encoded (i.e., facial features are extracted and then holistically combined), after which the resulting representation is matched with previously stored representations (i.e., face recognition units). Information processing then occurs along two distinct cognitive and affective appraisal routes, with the former being responsible for overt recognition (retrieving semantic information) while the latter underlies covert (affective) recognition. Identification occurs when these appraisals are successfully integrated. This model of self-recognition is consistent with a secondary representational account, including the focus on expectations about one's appearance, but it remains to be investigated from ontogenetic and phylogenetic perspectives (Butler 2015). For example, do children or animals failing mark tests actually integrate expectations about what they should see *and* feel when looking in the mirror? What do chimpanzees *feel* when they see and recognize their own reflection or not?

## Function

While researchers have long considered self-recognition in relation to its evolution, development, and underlying mechanisms, the same cannot be said about whether this ability has any Darwinian value (Butler 2015; Suddendorf and Butler 2013). There is some consensus that

self-recognition likely originated in a common great ape ancestor as a *by-product* of another adaptive ability such as self-awareness or secondary representation; that is, self-recognition itself was not selected for but merely accompanied another adaptive trait (Butler et al. [to in preparation](#); Gallup 1997; Povinelli and Cant 1995; Suddendorf and Butler 2013). This has led to explanations focusing on the proposed adaptive trait from which self-recognition emerged, rather than on self-recognition per se. For instance, the clambering hypothesis (Povinelli and Cant 1995) posits that self-awareness was adaptive because it permitted a large-bodied, heavy, great ape common ancestor to safely navigate in its arboreal environment (by mentally monitoring and testing tree limbs during locomotion), thereby reducing the risks of serious injury from a fall; self-awareness thus increased the ancestral apes' chances of survival and reproducing. Although consistent with the almost exclusive arboreality of modern orangutans, this proposal struggles to account for the retention of self-awareness (and hence self-recognition) in less arboreal species, namely, gorillas, chimpanzees, and humans. Gallup (1997) subsequently proposed that a shift to ground-dwelling freed up self-awareness for use in understanding other individuals' minds, which was advantageous for meeting the complex cooperative and competitive challenges that characterized some great apes' social environments. An alternative account suggests that self-recognition originated as a by-product of another secondary representational ability (Suddendorf and Butler 2013; Suddendorf and Whiten 2001). This would be advantageous because secondary representation allows an organism to simultaneously represent and compare multiple mental models about things that may or may not actually exist, i.e., an individual can consider negative or positive outcomes for any situation, rather than having to actually experience them (Suddendorf and Whiten 2001).

Regardless of whether self-recognition originated as a by-product of self-awareness or secondary representation, it remains to be determined whether it has acquired any adaptive value in its own right. There are at least two scenarios for which this may be the case: image management

and self-referent phenotype matching (Butler et al. [to in preparation](#); Suddendorf and Butler 2013). The value of the former is that self-recognition allows for monitoring and modifying one's appearance, which may be important for multiple reasons including showing group membership, status, formidability, trustworthiness, etc. For example, evidence indicates that attractive people have several advantages including enhanced reproductive opportunities and success (for review, see Gangestad and Scheyd 2005). It follows, therefore, that knowing what one looks like facilitates modifying one's attractiveness, which in turn leads to enhanced Darwinian fitness. The advantages for self-referent phenotype matching, which involves identifying potential kin on the basis of how much they resemble one's own appearance, include avoiding inbreeding with close genetic relatives and being more prosocial toward those who share one's own genes (DeBruine 2005). Evidence for both of these functions is largely restricted to modern humans; it may extend back a few hundred thousand years in the case of image management (Butler et al. [to in preparation](#)). While there is "evidence of absence" for concern about one's own appearance in modern great apes, there is an "absence of evidence" for self-referent phenotype matching, although chimpanzees appear capable of phenotype matching in general, i.e., identifying potential relatives on the basis of how much they resemble their close kin (Parr and de Waal 1999). At present, it is difficult to know whether self-recognition has remained a mere by-product of another adaptive trait or has become a secondary adaptation, exaptation, or spandrel (Butler et al. [to in preparation](#)).

## Future Challenges

Much has been learned about self-recognition in the half-century since Gallup's (1970) pioneering study. However, important gaps within the comparative literature remain, many of which have been identified above (e.g., the need for replicating findings in elephants, cetaceans, and birds; using more tests based on other media; and testing

for image-management and self-referent phenotype matching or any other possible function). In addition, while researchers have started to address the comparative neuroscience of self-recognition (Butler and Suddendorf 2014; Hecht et al. 2017), much more is needed. Not only would this improve psychological explanations of self-recognition (e.g., determining the relative involvement of emotional versus cognitive brain areas), it would shed light on whether this ability is an adaptation, exaptation, spandrel, or mere by-product (just as understanding morphological differences in bird feathers has led to explanations about some feathers being originally adaptive for thermoregulation prior to becoming a secondary adaptation for flight). Similar possibilities exist for genetics research, with only one chimpanzee study published to date (Mahovetz et al. 2016). Social factors also warrant further attention, for example, determining possible influences of enculturation and maternal styles on manifestations of self-recognition (Anderson and Gallup 2015). Finally, and perhaps most importantly, while it is important that tests of self-recognition are ecologically valid for the species in question (e.g., Clary and Kelly 2016), scholars must strive for methodological rigor in designing studies to ensure that well established best practices (e.g., comparing mirror-mediated mark touches versus a pre-mirror control and non-marked areas) are not ignored.

## Cross-References

- Attachment
- Clambering
- Consciousness
- Death
- Empathy
- Gordon Gallup
- Inclusive Fitness
- Phenotype Matching
- Self-awareness
- Self-directed Behavior
- Theory of Mind

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## Visual Sensation

- ▶ [Cognition](#)

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## Visuospatial Memory

- ▶ [Spatial Orientation](#)

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## Visuospatial Sketchpad

- ▶ [Cognition](#)

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## VNTRs

- ▶ [Simple Sequence Repeats](#)

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## Vocal Duels

- ▶ [Countersinging](#)

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## Vocal Interaction

- ▶ [Countersinging](#)

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## Vocal Mimicry

- ▶ [Susan D Healy](#)

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## Vocalization

- ▶ [Bear Communication](#)
- ▶ [Catarrhine Communication](#)
- ▶ [Mustelid Communication](#)
- ▶ [Prosimian Communication](#)
- ▶ [Rodentia Communication](#)

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## Voluntary Animal Approach

- ▶ [Human Approach Test](#)

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## Voluntary Approach Test

- ▶ [Human Approach Test](#)

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## W.D. Hamilton

► [William Donald Hamilton](#)

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## Waist to Hip Ratio

► [Waist-Hip Ratio](#)

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## Waist-Hip Ratio

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## Synonyms

[Waist to hip ratio](#)

## Definition

It is the ratio of perimeter of waist to the hip.

## Waist-Hip Ratio

Fat is one of the most important constituent of diet. However, fat deposition in the body could be

harmful to health among all the people irrespective of age, sex, and ethnicity. Fat tends to deposit in abdomen and hip than any other place in the body, for both male and females. Waist-hip ratio is a significant health parameter, and it relates with serious health problems. Waist-hip ratio describes distribution of harmful fat around abdominal region (visceral fat). Overweight and obesity are often found to be related to major human disorders responsible for several deaths worldwide like diabetes, hypertension, heart diseases, and several other disorders (Emery et al. 1993).

Nowadays, doctors consider waist-hip ratio along with body mass index (BMI) for determining fat distribution. Some consider it as better parameter than BMI (as it fails to predict body fat distribution), which otherwise do not distinguish contribution of fat and muscle mass (person with athletic body with very low body fat content can have high BMI). Waist-hip ratio focuses on central obesity specifically which is more related to metabolic disorders (Emery et al. 1993).

## Determining Waist-Hip Ratio

To calculate waist-hip ratio, a person should measure waist just above the belly button and hips should be measured around the widest part. Measurement can either be made in cm and inches. This ratio helps in classifying body shapes, namely apple (people with tendency to accumulate fat around abdominal region) and pear

(people with tendency to accumulate fat around hip region). Doctors consider apple shape body to be at higher risk of developing metabolic disorders (WHO Report).

## Waist-Hip Ratio and Health

Waist-hip ratio is not only a good indicator of common metabolic disorders but it has been reported to be related with various other conditions as well. Value of waist-hip ratio means differently for different gender as both men and women accumulate body fat differently. For women, waist-hip ratio of 0.80 is considered as low health risk, ratio between 0.81 and 0.84 indicates moderate risk, and value above 0.85 indicates high risk. For men, waist-hip ratio of 0.5 or below is considered low health risk, 0.96–0.99 as moderate, and waist-hip ratio value of 1.0 or above indicates high risk. However, some exceptions are there to waist-hip ratio values; some medical conditions are known to cause higher fat deposition around abdominal region. Also some ethnic groups are exception to this as well (WHO Report).

Waist to hip ratio is related to type II diabetes and cardiovascular diseases in both males and females, many study consistently report higher ratios to be risk factor of this disorder (Qiao and Nyamdorj 2010). Studies also suggest that it is also a good predictor of heart diseases (Streng et al. 2018).

Waist-hip ratio is also reported to be important health predictor for elderly men and women. A study reported it as a good predictor of elder mortality (above 75 years) as compared with BMI (Price et al. 2006).

## Waist-Hip Ratio and Human Attractiveness

Research indicate that optimal waist-hip ratio is also related to attractiveness in both males and females; it is suggested that optimal ratio is associated with optimal sex hormone level which is related to higher fertility and lower risk of

disorders related to these hormones. A study indicated that ratio of 0.8 in males is related to enhanced male attractiveness (Fan et al. 2005). Females with lower ratio also found to enhance female attractiveness (Henss 2000). Optimal waist-hip ratio in both genders are found to relate to better health; in women, lower ratio relates with lower risk of ovarian cancer; in males, it relates with lower risk of cancer of prostate and testes (Singh 2002; Boehm et al. 2015).

## Conclusion

Waist-hip ratio is a good parameter to understand distribution of fat in the body and how it affects the health. In near future, it is expected to gain acceptability equivalent to BMI among doctors and common people.

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## Walking Reflex

### ► Step Reflex

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## Warning

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## Synonyms

[Aposematism](#); [Warning coloration](#)

## Definition

Warning is the state of being warned. A warned individual uses conspicuous signals, often colors, which indicate to a predator or a competitor that it is not profitable as a prey item or it is alert. In the case of unprofitability, it is often due to the presence of toxic chemical defenses but could be achieved in a large number of ways such as speed, toughness, or by carrying spines (Ruxton et al. 2004).

## Introduction

Warning in the animal kingdom takes a number of forms, which can be considered under the different modalities in which they occur, or they may use a combination of modalities.

The most commonly recognized modality for warning signals is probably visual signals such as aposematic patterns and colors (see entry on aposematic signals, and also below as aposematic signals are usually multimodal), visible spines or hairs, or movements which warn the receiver of the danger or unprofitability of approaching the signaller any further. Some alarm signals would be included in this visual category, with movements such as stotting in gazelles (reference) and tail flicking in deer (reference) indicating to their conspecifics that a predator is near but also indicating to the predator that it has been spotted and therefore would not benefit by pursuing the attack further. Warning movements would also include threat displays (see entry for threat displays) such as baring teeth and raising of hackles in dogs (reference) and charging at the enemy as seen in rhino, buffalo, and bulls (reference). Displacement attacks may also be seen in some animals, including humans (reference), where the attack is aimed at an inanimate object as a warning of what force is likely to be available to be exerted on the opponent should the attack be followed through. The visual warning may even be dishonest, as is present in a startle display, when typically an insect puffs itself up and displays a pattern which resembles eyes, making itself appear to be the head of a snake, or a much larger organism, in an attempt to frighten the predator off (reference).

The next common modality for warning would be warning sounds or calls. Many insects and other small potential prey items such as the death's head hawkmoth make a sound when attacked, to attempt to startle the predator into letting them escape (reference). Others which do have a defense such as rattle snakes have a warning rattle, and bumblebees give a specific warning buzz, alerting the predator to the presence of the defense. Similarly the howls of wolves and roars of lions warn potential rivals of the size of the group defending that territory and some indication of its strength. Many alarm calls are not visual signals, such as Belding's ground squirrel's calls warning of approaching enemies and birds giving hawk alarms. In some species these calls can be predator-type specific, so vervet monkeys,



meerkats, and chickens all give a different call according to whether the predator is a ground predator or an aerial one, and vervets also distinguish a snake category (reference). It could be argued that all bird territorial songs are warning in function, informing rivals of the presence of a male prepared to fight to maintain ownership of that territory, as well as acting as an honest signal by which females can select a good mate.

Warning odors tend to be less commonly observed, partly through lack of work on them, but also because they tend to travel less far, exposing the attacked animal to the close proximity of the attacker before they can be detected. Skunks, ants, and bombardier beetles get round this by spraying the warning odor at the attacker. Warning odors include pyrazines, which are thought to have an “alerting” function, increasing the effectiveness of predator learning (reference). These are often found in aposematically defended organisms (see below).

Finally warning tastes are a matter of some debate. Some authors consider distastefulness to be a defense in itself, while others consider chemicals which confer a taste but have no toxic function to be warning tastes (references). These are often bitter, resembling the taste of the toxins in many defended species.

In some defensive systems, such as aposematism, multiple warning signals are given at the same time, often in different modalities (reference). These “multimodal” warning signals have been the subject of extensive research, and so this system is discussed below as a classic warning complex.

## The Principle

Originally described as “warning colouration” by Alfred Russel Wallace, the concept of an organism advertising its unprofitability as prey by displaying a warning signal was redefined by Poulton (1890) as “aposematism” (from Greek *ἀπό* *apo* away, *σημα* *sema* sign). Both terms have survived in the literature and are used interchangeably to describe a range of antipredator adaptations united by the presence of a signal

indicating that the prey is unprofitable to eat. Aposematism relies on the predator noticing a prey’s appearance, learning through a bad experience that eating that prey is detrimental, recognizing the prey the next time it is encountered, and avoiding attempting to eat it. The signal is much more effective at causing this learning and recall if it is conspicuous, so organisms employing aposematic defenses are selected to be conspicuous. Therefore there is an intrinsic cost to aposematism, since naïve predators, which are unaware of the meaning of the signal, will attack and attempt to eat these conspicuously signaling individuals until the predator has had enough experience to learn to avoid them.

## The Signal

The signal used often includes a conspicuous pattern of colors, with internal contrast provided by the use of red, yellow, or white contrasting against black, often in the form of spots or stripes. However a wide variety of patterns can be found, with the emphasis being on easy detection and recognition. A color pattern is only one possible signal and is often replaced or augmented by specific odors, tastes, sounds, and movements all of which are adapted to increase conspicuousness and memorability. One particular odor, pyrazine, was postulated by Rothschild to be an “alerting” signal, making the predator more aware and able to learn the meaning of the warning color (Rothschild and Moore 1987). Pyrazine odor is present in many insects (Moore et al. 1990) and has now been shown to be more effective in enhancing learned avoidance than other odors (Marples and Roper 1996). Even sounds, such as the buzzing of angry bumblebees, can augment a visual signal to increase its effectiveness (Siddall and Marples 2011). The use of several signals together, referred to as “multimodal signalling,” is more effective than single cues at promoting both the predator’s learning (Marples et al. 1994; Siddall and Marples 2008) and memory (Marples et al. 1994; Siddall and Marples 2008) of the encounter. Aggregation can further strengthen the learning of the signal (Riipi et al.

2001) by offering a large, even more conspicuous cue, with the signal repeated many times, and still visible to the predator even if one of the prey are consumed. Aversive taste, or unpalatability, is often considered to be part of the defense of aposematic animals, but it is actually part of the signal. As long as the chemical conferring the unpleasant taste is not toxic (i.e., it has no physiologically detrimental effect on the predator), there is no adaptive benefit for the predator to avoid bad tastes, other than their frequent association with unprofitable prey. However tastes can signal the presence of a second, toxic chemical, just as other signals can.

### Unprofitability

The defenses of aposematic or warningly colored prey have long been described in terms of chemical toxins making the prey aversive to the predator (Poulton 1890; Rothschild and Moore 1987). Such toxins are either manufactured by the defended organism itself or may be sequestered from its food. They are sometimes stored in specific organs such as the nematocysts in jellyfish or the sting of a bee. Alternatively they may be spread throughout the skin (e.g., dart-poison frogs) or be present in the hemolymph of an insect (heliconius butterflies) or may be manufactured only on attack (e.g., bombardier beetles). Toxic chemicals are however not the only form in which an effective defense can be mounted. The only necessity for aposematism to work is that pursuit and consumption of the prey should not be worth the predator's while; in other words, it should reduce the predator's fitness; it should be unprofitable. Any feature of the prey which makes it unprofitable will mean that it is adaptive for the predator to avoid that prey type, and so advertising this by means of conspicuous becomes adaptive for the prey, i.e., it can use warning coloration. So while most aposematic organisms are advertising that they contain a toxin, there are others which advertise that they are hard to handle, fast at escaping, tough bodied, indigestible, or otherwise not easy to catch, handle, or eat (Ruxton et al. 2004).

### Mimicry

As stated above, aposematic organisms pay a price for their protection in that they must run the risk of meeting a naïve predator and being the individual which dies teaching the predator what their conspicuous signal means. They can dilute this risk, as well as enhance the effectiveness of their signal by aggregating together with others of their own species. They can further dilute the risk by using the same signal as others defended prey of other species. This sharing of the same signal between defended species is called "Mullerian Mimicry," first described by Fritz Muller (Müller 1878). Groups of species converge on the same signal to form what is referred to as a "Mullerian Mimicry Ring," examples being several species of red and black ladybirds, and bumblebees and wasps which share black and yellow-striped patterns. There are also Mullerian mimicry rings in other modalities, for instance, snakes share auditory signals of hissing and bumblebees share their buzz signal. This convergence of signals is beneficial both to the aposematic species sharing the costs of teaching predators and to the predators themselves as they have fewer signals to learn so will have to suffer detrimental prey on fewer occasions.

Another sort of mimicry is commonly found, where the organism mimics the signal of an aposematic species but does not carry any toxin or other defense, and indeed is a profitable prey type. This type of mimicry was recognized by Henry Walter Bates (Bates 1861) and undermines the effectiveness of the aposematic signalling system. If one of these "Batesian mimics" is attacked by a naïve bird, the bird will get a good meal and consequently will learn that the color pattern indicates good food. The Mullerian mimics sharing that signal will then be attacked by this incorrectly educated predator, and as relearning is usually slower than learning from naïve, more unprofitable prey will be eaten before the predator is reeducated. This is therefore detrimental both to the aposematic populations and to the predators. One consequence of this is that Batesian mimics must remain rare compared to the aposematic prey they resemble. If the Batesian mimics become too

numerous, even locally, they destroy the very signalling system on which they rely for their defense. Therefore Batesian mimics avoid aggregation. They also tend toward polymorphism, in which there is more than one color pattern represented in the same species' population. Polymorphism allows the species to have some individuals parasitizing one aposematic color pattern and the rest of the population parasitizing another. A probable example of this is shown by the two-spot ladybird *Adalia bipunctata*, which has been shown to carry no effective chemical defense (Marples 1993a; Marples et al. 1989) and which has two different color patterns: a primarily red pattern with black spots resembling the well-defended seven-spot ladybird *Coccinella septempunctata* and a primarily black one with red spots resembling the defended Pine ladybird *Exochomus quadripustulatus* (Marples 1993b).

The distinction between prey species being Mullerian or Batesian mimics is not absolute, since the amount of toxin in an individual of an aposematic species may vary, and the susceptibility of different predators to being poisoned by a given level of toxicity may also vary, even within the same predator species. This has the effect that a particular prey item may be a Mullerian mimic to one predator individual, because it is unprofitable for that predator to eat the prey, but a Batesian mimic to another predator individual, because the second predator gains more by eating it than it loses through the effects of the toxin, i.e., it is a profitable prey (Speed 1999; Turner and Speed 2001).

## Evolutionary Paradoxes

The original evolution of aposematism has long been considered a paradox. This is because aposematic defenses only work when the majority of predators understand the meaning of the signal and all predators would be naïve when the trait first evolved. This means that the first individual prey item to develop a toxic defense and a conspicuous color pattern would have attracted attention from a predator, which would have eaten it. This might have taught the predator to avoid that specific color pattern, but as only one

individual carried the trait, and that individual has died educating the predator, the aposematic trait would have died out before it could get going. There have been a number of postulated solutions to this paradox, most of which are not yet supported by empirical evidence. One of the few explanations supported by both theoretical modeling (Lee et al. 2010) and experimental evidence (Thomas et al. 2003; Marples et al. 2005) is that arising from the action of dietary conservatism. It has been shown that part of the population of any species of fish and birds yet tested is fussy about their food, eating only familiar food types if given any option to do so (Marples et al. 1998). This fussy eating strategy is called "dietary conservatism" (DC), and it causes predators which are displaying the DC foraging strategy to avoid novel foods. If the first aposematic prey arose in the territory of a DC predator, then it would be avoided by that predator simply due to looking novel and could increase locally in numbers. The argument is that this would allow the aposematic trait to become common enough to train the local predators to avoid the aposematic signal and to get over the initial low-number paradox.

There is also evidence that some species have unlearned avoidance of certain conspicuous colors and patterns (Roper and Cook 1989) such as black and yellow stripes. This would reduce the likelihood of a new aposematic individual bearing this signal being eaten. However the order of evolutionary events is not clear, and there is always the possibility that the innate avoidance of these conspicuous patterns is actually an effect of the existence of aposematism. In other words predators may have evolved to hard wire an avoidance of yellow and black stripes because of all the aposematic animals which use this signal, in which case the innate avoidance could not predate and assist the initial evolution of aposematism.

However it survived the initial stages, once the population of aposematic individuals was large enough to educate the local predators into avoiding similarly signalling prey, there would be a selection pressure for other species to converge on the same pattern, and the mutually beneficial signalling system would persist and spread. Prey species would be selected to show a clearer and more memorable signal, augmenting it with

other signals to make a multimodal signal as conspicuous and recognizable as possible. A niche for cheating on this signal would open up and give rise to Batesian mimics, selected to copy the signal in each modality as accurately as possible. Predators would be selected to become better at learning and remembering the signal but also distinguishing between the Batesian mimics and the truly aposematic prey types. This coevolutionary system would be expected to drive all patterns toward the same, maximally memorable pattern.

This gives rise to one final paradox observed in this system. In reality many families of closely related aposematic organisms do not in fact share the same pattern. For instance, there are at least three different Mullerian mimicry rings of ladybirds present in Europe, each set of species bearing spots but one based on a red background, one on a black background, and one on a yellow background. Similarly in South America, there are multiple color patterns among the well-defended heliconius butterflies. What prevents the converging on the same patterns is unclear and continues to be one of the unanswered evolutionary paradoxes. It seems likely that the Batesian mimics undermining each signal would eventually make it beneficial to found a different Mullerian mimicry ring with a new pattern unparasitized by Batesian mimics. However the empirical testing of this idea would involve knowing which species in each ring were truly unprofitable to each of the local predators and which were profitable Batesian mimics. This degree of detailed knowledge is absent as yet from most of these larger and more complex mimicry systems.

## Cross-References

- ▶ Aggressive Mimicry
- ▶ Alarm Calls
- ▶ Aposematism
- ▶ Batesian Mimicry
- ▶ Chemical Signals
- ▶ Communication
- ▶ Honest Signaling
- ▶ Mimicry
- ▶ Müllerian Mimicry
- ▶ Signaller

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## Warning Coloration

- [Aposematism](#)
  - [Warning](#)
- 

## Warning Displays

- [Aposematism](#)
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## Warning Signals

- [Aposematism](#)
- 

## Washoe

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## Introduction

Washoe became famous in the late 1960s for being the first nonhuman to use a human language, namely, American Sign Language (ASL).

Born in the wild in West Africa, Washoe was captured and eventually brought to the United States where she was acquired by the US Air Force. On June 26, 1966, however, her life was again redirected as Drs. R. Allen and Beatrix T. Gardner brought the infant chimpanzee to Reno, Nevada, to serve as a research subject in their cross-fostering laboratory. They named her Washoe *Pan satyrus*. Her first name came from Washoe County, the location of the University of Nevada, where the Gardners both taught in the Department of Psychology. Her middle and surnames (*Pan satyrus*) were, in 1966, the genus and species name for chimpanzees (now *Pan troglodytes*). Two weeks after arrival, Washoe had begun responding appropriately to the sign for COME, and within 6 months, Washoe was using signs spontaneously and in appropriate contexts (Gardner et al. 1989b). Washoe passed away in 2007 at the age of 42 having become one of the most well-known chimpanzees in history.

## Cross-Fostering with Chimpanzees

Cross-fostering is a research design commonly used by ethologists, comparative psychologists, and biologists to address the age-old nature-nurture question: What is the relative influence of environment and biology on behavior and traits? Researchers using this design typically raise the young of one species in the environment of and by adults of another species. They hypothesize that when these young exhibit behavior typical of the adoptive parents (and unlike that of the biological parents), the behavior is due primarily to learning acquired in the rearing environment.

Prior to Washoe, three other chimpanzees had been cross-fostered in human environments: Viki (Hayes and Hayes 1951), Gua (Kellogg and Kellogg 1933), and Joni (Ladygina-Kohts and de Wall 1935/2002). Each of these other chimpanzees lived in a home with adults who used spoken language and each readily learned human behaviors such as using a telephone, waving goodbye, dusting, turning lights on and off, drawing with pencils and crayons, etc. (e.g., Hayes 1951). Of the three, only Viki developed a spoken



vocabulary, and after almost 7 years and substantive training, she spoke only four words. However, in the mid-1960s when the Gardners were developing their protocols, Jane Goodall was reporting that, under natural circumstances, chimpanzees readily gesture to one another (1968). Also in the mid-1960s, most American children grew up in homes with a single language. The Gardners chose a single, manual language, ASL, for their project. In fact, they established a sign-only rule which precluded members of the research team from signing and speaking at the same time. With the addition of this naturally occurring, manual human language, and the strict sign-only policy, Washoe's cross-fostering environment was even closer to the environment of a typical human infant than previous cross-fostering projects of Hayes and Hayes, Kellogg and Kellogg, or Kohts. The Gardners' first cross-fostering project became known as Project Washoe.

### Project Washoe: The Early Years

Washoe's daily life in this cross-fostering laboratory looked remarkably similar to the daily life of a human child of the same age. To begin with, Washoe had a nuclear family unit consisting of Allen and Beatrix Gardner and a small group of other adult caregivers. She was accompanied by at least one of her family members every waking moment. Washoe's home was a trailer in the Gardners' backyard in a neighborhood of Reno, NV. Her home was equipped with a kitchen, bedroom, dining table (and high chair), toys, books, and bathroom. The Gardners modeled Washoe's daily routine (e.g., meals, naps, and baths) after routines common for human infants. Washoe wore the same sorts of pants and shirts and played with the same sorts of dolls and toys as human children her age. She ate the same sorts of baby food and graduated to the same sorts of meals as human children. She rode in wagons and cars, climbed trees, and went out for ice cream. In this cross-fostering laboratory, Washoe learned to use and flush the toilet and wash her hands afterwards. She engaged in school activities appropriate to her age, such as stacking blocks, stringing beads, and

coloring. She learned to use adult tools, such as weeding tools, brooms, dustpans, and mops. As she got older, she completed chores, like putting her toys away and taking her dishes to the sink by herself.

Throughout all of these daily activities Washoe's family members chatted with each other in ASL similarly to the way human adults do with their own infants, whether the language is spoken or signed. Along with caring for the young chimpanzee, the research staff of Project Washoe made meticulous records of Washoe's daily life, which included measures of her food intake, weight, development milestones, potty successes and accidents, communicative gestures, and her use of the signs of ASL, much of which can be seen in the films *Teaching Sign Language to the Chimpanzee, Washoe* (Gardner and Gardner 1973) or *The First Signs of Washoe* (Campbell-Jones 1974). In this setting, Washoe learned to communicate through signs about the world around her utilizing both concrete and abstract concepts such as BIRD, PANTS, TREE, DRINK, KNIFE, RED, OUT, QUIET, TELEPHONE, HEAR, GO, and FUNNY. Mistakes in sign form or grammar were corrected by the human family members. She signed to herself, to her human playmates, to toys and dolls, and to other animals.

### Adulthood

In 1970, at the age of 5, Washoe moved to the University of Oklahoma with Dr. Roger and Debbie Fouts and gradually entered a phase of more permanent captivity living among other chimpanzees. She remained in frequent contact with signing human family members and signed to the new chimpanzees' playmates as well (Fouts 1997; Fouts, Fouts and Van Cantfort 1989). She had two infants, both of whom died in infancy, and she later adopted a 10-month-old male chimpanzee, Loulis, acquired by Fouts from Yerkes. A second cross-fostering project initiated by the Gardners to replicate the findings of Project Washoe and improve upon the research methodology included chimpanzees Moja, Tatu, and Dar

(see Gardner et al. 1989b). These chimpanzees along with Loulis became Washoe's new adopted family. Between 1980 and 1981 the Fouts moved Washoe, Loulis, Moja, Dar, and Tatu to Central Washington University and later founded the Chimpanzee and Human Communication Institute (CHCI), a sanctuary and behavioral research facility on the university campus. Washoe's adoption of Loulis began a functional third phase of the signing research with chimpanzees. Like the others, Loulis also acquired signs of ASL, but not from human caregivers. With the exception of seven specific signs, all signing by humans was forbidden in his presence so that any additional signs learned would come from Washoe and the other chimpanzees (see Fouts, Fouts and Van Cantfort 1989). Washoe molded Loulis' hands into signs and modeled signs for him in context just as was done with her and as is done by deaf parents with their children (Fouts, Fouts and Van Cantfort 1989). The transmission of human signs from one non-human to another nonhuman was another groundbreaking discovery. After many years of contribution to research, in 2002 Moja passed away and in 2007 Washoe passed away. Following the death of Dar in 2012, in 2013 the remaining chimpanzee family members, Tatu and Loulis, moved to the Fauna Foundation in Montreal, Quebec. Since the closure of CHCI, researchers continue to analyze behavioral and signing records of Washoe and the other chimpanzees from their years in the cross-fostering laboratory through adulthood.

### Method Matters: A Response to Critics

Because of the Gardner's work with Washoe and other studies with similar aims, ape language research was a hot topic that was nationally funded in the 1970s and 1980s. Along with the research came plenty debate of methodologies and outcomes. A well-known critic of Project Washoe, Herb Terrace, claimed that Washoe's signs were primarily trained through the use of Skinnerian reinforcement and imitations of human caregiver signs. Others claimed that

apes could not sign without manipulation and coercion (Seidenberg and Petitto 1979). An abundance of research however provided evidence to the contrary. Washoe's signing was tested under rigorous double-blind controls early on though. The question of human cueing or imitation was resolved with Washoe's accuracy rate for reliably naming objects without the possibility of human influence; it was substantially greater than chance (Gardner and Gardner 1989). Additionally experimental controls were put in place to ensure that Washoe was identifying concepts rather than simple exemplars. Remote video recording of Washoe using the signs of ASL in the absence of her human caregivers (e.g., signing to herself about objects in her bedroom) provided further evidence of spontaneous and appropriate sign usage (Gardner and Gardner 1989). The Gardners furthermore explained that reinforcement actually hindered Washoe's signing much like the depressed productivity of children in response to external rewards (Gardner and Gardner 1989).

### Similarities with Human Language

The process by which Washoe and other cross-fostered chimpanzees learned signs was primarily through modeling and molding the chimpanzees' hands in the appropriate context for the sign (Gardner et al. 1989a; Fouts 1972). Fouts in fact even attempted imitation as a means of teaching signs to Washoe but with very little success in comparison to the techniques that are most similar to how deaf children learn ASL, molding and modeling (Fouts 1972). This research all but ended attempts to use Skinnerian reinforcement and imitation with Washoe and provided further evidence of the importance of the home environment, particularly natural conversation, as a factor in Washoe's signing record.

As with human children, Washoe's vocabulary was largely related to and dependent upon her experiences and the people with whom she signed. During her 51 months living under cross-fostering conditions, Washoe acquired at least 132 reliable signs (Gardner and Gardner 1989)

and many more that had not yet met the stringent requirements to be included in the vocabulary. Her vocabulary grew as she was exposed to new situations and new people reaching over 250 signs at the time of her death. Washoe's repertoire included signs from the categories of nouns, proper nouns, objects, attributes, verbs, markers, and locatives. Tatu, Dar, and Moja's vocabularies were equally as diverse, and Moja additionally had several quantitative signs (VanCantfort et al.). Washoe, Tatu, Moja and Dar often combined signs to describe a novel item or situation. Several unique combinations Washoe created included WATER BIRD for swans, CRY HURT FOOD for radishes, and LISTEN DRINK for Alka-Seltzer (Gardner et al. 1989a).

Other aspects of Washoe's development also resembled human developmental trends. For example, when she had acquired eight signs, she began combining them into phrases. As an infant she used childish forms of signs like signing on her caregivers and using simplified hand configurations (Gardner et al. 1989a). The development of object permanence in the second year was also shown to be comparable to that of human children in both sequence and rate of acquisition (Wood et al. 1980).

Further research showed that vocabulary and utterance growth by Washoe as well as Tatu, Moja, and Dar were remarkably similar to human children. They have been shown to respond appropriately and with various categories of signs contingent upon the type of Wh-question posed (Jensvold and Gardner 2000). Perspective taking was insinuated in research by Bodamer and Gardner (2002); when a human was not looking at the chimpanzees, they initiated interactions with attention getting sounds including noisy signs, but not silent signs. However, once the human was oriented and looking toward them, they used silent signs. Other studies of pragmatic abilities show that Washoe and her family used eye gaze similarly to deaf signers in conversation (Shaw 2001) and that they took turns in patterns similar to humans, engaging in much more interruptive overlap as infants than as adults (Hartmann 2011).

## Summary

Project Washoe and the subsequent projects described here were historical in that the Gardners largely replicated the rich social environment in which deaf children learn their native language to determine whether this would afford a chimpanzee the opportunity to acquire signs of ASL. Employing a manual language to communicate with a gesturing nonhuman species was a novel and successful approach to addressing research questions previously investigated by Hayes et al. The work that followed produced decades of research recording developmental and communicative behaviors of cross-fostered chimpanzees.

## Cross-References

- [Cognition](#)
- [Communication](#)
- [Cultural Transmission](#)
- [Human-Animal Interaction](#)
- [Jane Goodall](#)
- [Language Research: Great Apes](#)
- [Nature Versus Nurture](#)
- [Primates](#)
- [Social Learning](#)
- [Yerkes Primate Research Center](#)

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## Water Balance

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## Synonyms

Hydroregulation

## Introduction

The term *water balance* as it applies to animals is an important aspect of physiology that reflects the principle embodied in “input-output” rules. In context of water balance, this stipulates that over time the input of water to an organism must equal the output of water if the body water content is to remain constant. Hence, the water lost must be replaced, and if excess water is ingested, it must be eliminated if the animal is to remain in “balance.” Water (as well as energy) is a fundamental requirement of living organisms and provides the milieu in which molecular reactions occur to maintain the processes of life. Hence, with the exception of transient “anhydrobiosis” (life with nearly complete drying) observed in certain invertebrates and seeds of plants (Alpert 2006), water is a central requirement for normal levels of metabolism, nutritional status, reproduction, and survival of organisms.

Water balance is an important underpinning to the behaviors of animals, and vertebrates are especially sensitive to dehydration and changes in behavior related to water resources (McNab 2002; Lillywhite 2016). In order to survive, animals must have sensitivity to water resources and the moisture conditions of their environment, and they must discriminate to some degree the quality of water in which they live or interact. Remarkably, although the sensory capabilities of animals related to water are central to survival, they have not been well studied. Animals must decide questions such as: To where should one disperse or migrate when water resources are depleted during drought? Where should one oviposit eggs such that the moisture quality of soil or nest is appropriate to development and hatching? What osmolarity of water is appropriate to ingest for an animal living in or at an estuary? How long should one continue to forage when dry conditions increase evaporative water losses? What properties of soil are appropriate or safe for burrowing animals that are sensitive to cutaneous water loss?

## Pathways and Processes of Water Exchange

Animals gain or lose water through various pathways that are depicted in Fig. 1. In summary, water is gained by animals via drinking, food, and in particular cases, absorption across the skin; water is lost from organisms in urine, feces, and evaporation involving the skin and any exposed mucous membranes including those contacting the ventilatory flow of air in and out of the lung during breathing. Various adaptations have evolved to limit losses in dry environments, and to adjust input-output in mesic environments. Over time, water balance requires that water inputs compensate for outputs or losses.

Water inputs to an animal generally involve drinking in addition to free water that is contained in food. Excess water is excreted from the body, and in vertebrate animals this involves the kidney. Depending on the species and the circumstance, water can be in excess or in deficit, and the excretory organ (kidney) responds accordingly. The kidney (usually paired structures) functions by filtering blood and modifying the resulting filtrate according to needs of the animal. Some substances are reabsorbed back into the bloodstream across the mucosa of kidney tubules, and other substances in need of excretion are secreted by

transporters across the tubular membranes and added to that already present in the filtrate. Water, of course, comprises a large percentage of the filtrate and can be added or subtracted, but only by passive means induced by osmotic gradients acting across membranes. The relative concentrations of solutes are adjusted by this means. The final filtrate is called urine and in many vertebrates can be stored temporarily in a structure called the bladder.

The kidneys of birds and mammals have specialized loop-like tubules that provide a means of concentrating urine. Without detailing the mechanism (which is described in any standard physiology or comparative physiology textbook), a dilute urine is produced if water is in excess supply, or a concentrated urine is produced if water is in short supply. The concentration of the urine is “adjusted” according to need by means of osmoregulatory hormones that are released from the central nervous system and act on the tubular membranes of the kidney to affect both transporters of salts and the permeability of tubular membranes where urine flows through regions of high salt concentrations surrounding the relatively elongated “loops” to produce the final urine product. Other vertebrates lacking such loops cannot produce a concentrated urine and conserve water by other means. Many amphibians living in water

### Water Balance,

**Fig. 1** Pathways for gains or losses of water from a tree frog (*Smilisca baudinii*) (Photograph by author)





or very wet environments produce a copious and dilute urine to remove excess water that continually “floods” the animal by osmotic movement across water-permeable skin. On the other hand, marine mammals have specialized kidneys that enable them to produce a concentrated urine and eliminate salts that invade the body during consumption of food. Reptiles living in marine or dry environments where conservation of water is important have other means of excreting salts and wastes in addition to the kidneys, which cannot produce a concentrated urine. These vertebrates – as well as certain birds living in dry environments or close association with seawater – possess *salt glands*, which are specialized organs capable of excreting high concentrations of salts with minimal water loss. These glands are accessory to the kidneys and are located near the eyes, nasal passages, or tongue in various species living either in dry deserts or marine environments where fresh water is scarce.

It is important to understand that excretory organs such as kidneys or salt glands can serve only a negative role in water balance. Urine (or secretions from salt glands) can vary in the concentration of solutes which it carries, but necessarily variable amounts of water are also removed from the body during the excretion of salts. Excretory organs do not add any water to the body, so the positive side of water balance requires sources of input in addition to whatever adaptations are present for conserving water.

## Inputs of Water

Animals have three sources of water. These are (1) dietary water, which refers to free water that is contained in the foods animals eat; (2) metabolic water that is a by-product of cellular metabolism, produced in relatively small amounts along with  $\text{CO}_2$ ; and (3) free water in the environment, including rainfall, ponds, rivers, or anywhere that water collects and can be a source for drinking. Most animals depend on drinking water from the environment during variable (usually regular) times during their lives. The amounts required depend on the humidity of the environment, how

an animal behaves within its environment, and the efficacy of traits that conserve water in environments or circumstances where conditions are dehydrating. In extreme cases, animals with exceptional specializations for conserving water might get by on dietary and metabolic water and not require sources for drinking. Examples are certain desert rodents that produce a highly concentrated urine, minimize evaporative water losses, and acquire sufficient water by eating and metabolizing seeds that are stored in burrows where they absorb very small but critical amounts of water (Nagy and Gruchacz 1994).

Many animals acquire considerable water in the food they eat, especially herbivores that graze or browse on vegetation. Depending on whether environmental conditions are relatively humid or dry, animals show selective behaviors with respect to the nature and content of water in the vegetation they consume. Rodents that do not have direct access to water may consume succulent plants and their fruits. Deer and other ungulates are well-studied examples of animals that change selective feeding behavior that matches the water content of foliage with the need for water (Western 1975). Larger animals that cannot satisfy their need for water from dietary items might depend on sources of free water such as water holes that are visited within broad ranges of movement, while birds can fly long distances to find sources of water. Amphibians, alligators, and other animals also migrate variable distances at times of drought when local water sources dry out. Thus, survival of animals faced with water shortages depends on behavioral choices – movements and other activities.

The reliance of marine snakes on free water is an interesting example of osmoregulation in the context of the evolutionary transition from terrestrial to marine environments (Dunson and Mazzotti 1989). The rates of salt secretion from salt glands vary among species of sea snakes and tend to be higher in those species that occupy waters of greater salinity and have greater oceanic ranges (Brischoux et al. 2012). However, contrary to earlier views, marine file snakes, sea kraits, and sea snakes depend on environmental sources of fresh water to remain in water balance (Lillywhite

et al. 2008, 2014a, b). Thus, the distribution and abundance of sea kraits (*Laticauda* spp.) correlates with precipitation and the spatial distribution of coastal springs or estuaries (Lillywhite et al. 2008). With respect to sea snakes that are entirely pelagic, or inhabit reefs that are some distances from land, the only (or principal) access to fresh water is drinking from fresh- or brackish water lenses that form temporarily on the ocean surface during intense rainfall. Observations and other evidence suggests that sea snakes can sense the quality of water, largely by tongue-flicking, and drinking behaviors are guided by sensory inputs to the snake's central nervous system (Lillywhite et al. 2014a).

### Adaptations for Conservation of Water

Animals that have invaded or evolved in comparatively arid habitats illustrate adaptations of structural, physiological, and behavioral features that act to conserve water. One of the principal strategies for dealing with scarcity of water is the behavioral avoidance of conditions that exacerbate water loss. Hence, many desert animals seek out cooler and moister microenvironments. Examples include small mammals and reptiles that dig or occupy burrows in soil, sleeping away the day in deep crevices, holes, or jumbles of rocks at the bases of cliffs, and restricting above-ground or open-habitat behaviors to nocturnal hours when temperatures are cooler and the air is more humid. Also, many animals living in extreme environments avoid seasonal conditions that limit energy or water by hibernating (winter) or estivating (summer) in seclusion from the harsh conditions of the environment at or above the ground. Moreover, amphibians that live in deserts will remain dormant below ground for much of the year (or longer in drought conditions), to emerge for feeding and breeding only during rare or seasonal periods of rainfall. Generally, amphibians are very sensitive to losses of water, mostly through skin that is highly permeable and evaporates body water at high rates. With the exception discussed below, frogs, toads and salamanders simply cannot withstand exposure to arid

conditions that are tolerated by lizards, tortoises, and mammals and birds having much less permeable integument (McNab 2002).

Avoidance of higher temperatures is important because mammals, for example, must eliminate excess heat by evaporation of water in sweating or panting (McNab 2002). Avoidance of heat gains from hot environments saves valuable water that would otherwise be expended for sake of thermoregulation. Birds can usually avoid heat gains by flying to cooler locations in desert canyons or shaded areas, sometimes with springs of fresh water. If birds become heated to the point of being hyperthermic, like mammals they increase evaporative cooling, but not by panting. Instead, they “flutter” the throat and bring air in and out across the gular membranes in the mouth and throat. Some species – for example, vultures – urinate on their “naked” legs. The urine evaporates to cool the legs and remove excess body heat. Some desert mammals, including camels, tolerate mild hyperthermia for short periods, conserving water that would otherwise be expended in evaporative cooling to regulate the body temperature at a lower set point.

As already noted, excretion of urine necessarily eliminates water, so modifications of kidney tubules to excrete a concentrated urine conserves water relative to the solutes and metabolic wastes that need to be eliminated from the body. Birds and squamate reptiles cannot produce a concentrated urine like that of mammals, but elimination of nitrogenous wastes from metabolism of protein is in the form of uric acid (or urates) instead of urea or ammonia. Uric acid can precipitate from solution in the hindgut or cloaca, and is thus excreted with minimal loss of water compared with urea or ammonia that remain in solution and require more water for elimination. Thus, modifications of kidney function to produce concentrated urine, elimination of uric acid from metabolism of protein, and concentrated solutions from salt glands are all adaptations of structure and function to minimize losses of water in the excretion of metabolic wastes.

Other important adaptations conserve water by reducing water losses in evaporation incurred by ventilating the lung (respiratory losses) or from

skin or body surfaces (Fig. 1). Some desert animals have relatively low requirements for energy (e.g., Nagy et al. 1993). Lower rates of metabolism reduce respiratory water losses attributable to ventilation of the lung. Low energy requirements also reduce foraging time and thus conserve water otherwise expended during these activities. Reduced activity, including dormancy and seclusion, generally reduces water loss, and reduced water flux generally correlates with lower field metabolic rates.

A very important route for water exchange involves the skin. The skin of vertebrates evolved to meet the needs for mechanical protection, sensing the environment, and regulating exchanges of materials and energy. The skin is a complex structure that resists water loss and physical abrasion while also allowing for changes in movement and shape. Amphibian skin has only one or two outermost layers of keratin and is generally very permeable to water. Hence, many species require mesic environments or places where they can associate with water to avoid or replenish losses. The majority of other terrestrial vertebrates have less permeable skin in which the outer layers of keratin (stratum corneum of the epidermis) are sandwiched between layers of lipids that protect the internal cellular environment from the dehydrating effects of surrounding air (Lillywhite 2006). The outer layers of keratin and lipids form what is termed the “permeability barrier,” and the respective structure and biochemistry of this barrier determines the ease with which water can penetrate or move across the skin. Generally, birds, mammals, and reptiles living in arid environments have a more effective lipid barrier and less permeable skin than do species living in mesic environments. Permeability barriers have evolved independently many times in the various groups of terrestrial vertebrates, and studies demonstrate that some species have “plastic barriers” that can (to some extent) be modulated to match efficacy with changes in the severity of environmental conditions (Denda et al. 1998).

Amphibians are exceptional in having very few keratin layers in their skin; hence their permeability barriers are relatively ineffectual or

absent. Yet, there are many species of amphibians that live in arid environments, generally by avoiding the harshest conditions by seclusion. Several species of tree frogs, however, representing different taxa in the Old and New World, remain above-ground and may even rest on tree branches in direct sunlight on hot days. These frogs secrete mixtures of lipids from specialized cutaneous glands and then wipe themselves to spread these secretions over the entire body surface. This happens just before activity ceases and the frogs adopt a resting posture. The wiping behavior is stereotyped and functions to “wax” the skin surfaces evenly and completely. Thus, in place of a permeability barrier within the skin, these frogs secrete the barrier onto the outer surfaces of the skin. When the frogs move again, the integrity of the outer lipid film is disrupted, so the barrier must be periodically renewed.

Finally, some burrowing species of desert frogs shed multiple layers of epidermis that remain in place when these animals are secluded and dormant beneath soil (e.g., in deserts). The multiple layers of shed epidermis coalesce and collectively form what is called a “cocoon.” Such cocoons greatly increase the resistance to water loss by virtue of morphology that is somewhat similar to the multiple layers of keratin and lipids in the epidermis of mammals, birds, and reptiles. Some amount of lipids occur between the multiple layers of shed skin, but their role in the function of the cocoon has not been definitively worked out.

## The Importance of Behavior

Many aspects of behavior influence the savings of water. These include movements, thermoregulation, postural adjustments, selection of humidity or hydric conditions in microenvironments, patterns of breathing, bodily contact with conspecific individuals, responses to weather, timing of migration, dispersal, or burrowing, foraging strategies, and many other examples I will not list here. Insights to the importance of behavior to water balance in extreme or changing environments is important to understanding the survival and

resilience of organisms and their communities, and predicting the range of responses to future climatic changes. Research that integrates studies in physiology, genetics, morphology, and natural history in contexts related to water balance will greatly help us understand the complexity of underpinnings to behavior. In turn, behavioral activities of animals influence the adaptations of morphology and physiology related to water balance.

## Cross-References

- ▶ [Homeostasis](#)
- ▶ [Thermoregulation](#)

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## Waterbirds

- ▶ [Waterfowl](#)

## Waterfowl

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## Synonyms

[Anseriformes](#); [Ducks](#); [Fowl](#); [Geese](#); [Screamers](#); [Swans](#); [Waterbirds](#); [Wildfowl](#)

## Definition

Waterfowl are birds that are members of the order Anseriformes, which includes three families: Anseranatidae (magpie geese), Anhimidae (screamers), and Anatidae (ducks, geese, and swans).

## Introduction

Waterfowl are birds within the order Anseriformes, which is made up of three families: Anseranatidae

(magpie geese), Anhimidae (screamers), and Anatidae (ducks, geese, and swans). Waterfowl are adapted to life in or near the water, and their anatomy reflects their aquatic lifestyle. The three families of waterfowl share many of these characteristics and adaptations but also have several unique traits that distinguish them not only from each other but also from all birds. Although all waterfowl live on or near a body of water, this can vary greatly from mountain streams to coastal shores to tundra lakes, and they utilize these bodies of water in different ways. Waterfowl are ubiquitous and can be found on every continent except Antarctica, and most waterfowl migrate to some degree. Gregariousness, or a high degree of sociality, and monogamy are hallmarks of most waterfowl life, although like most other aspects of waterfowl life, there is a great deal of variation. Waterfowl tend to lay large clutches of large eggs and hatch precocial chicks that require very little parental care. Many traits that characterize waterfowl, including their global distribution, wide array of diets, and precocial chicks, likely paved the path for their domestication by humans. These domestication and interweaving of waterfowl life with human life have important implications both for waterfowl and for humans.

## Taxonomy

Waterfowl are generally considered to be birds within the order Anseriformes. Anseriformes (“waterfowl”) and Galliformes (“game birds”) make up the superorder Galloanserae (“fowl”). These two orders split from each other approximately 54 million years ago (Prum et al. 2015). Within the order Anseriformes, there are three families: Anseranatidae (magpie geese), Anhimidae (screamers), and Anatidae (ducks, geese, and swans). The specific relationship between the families, subfamilies, and tribes that make up Anseriformes remains a contested subject, with much disagreement within the scientific community. For the purposes of this entry, the taxonomic relationships described by del Hoyo et al. (2019) will be used.

Anseranatidae is a family consisting of just one species, the magpie goose, *Anseranas semi-palmata*. Although this species was historically classified as a member of the family Anatidae, the most recent evidence places it instead in its own family (Carboneras and Kirwan 2019b). Magpie geese are considered to be the most primitive, or ancestral, branch of the Anseriformes order.

Anhimidae is the family to which screamers belong. The family consists of two genera and three species. This family is usually classified as being more closely related to Anseranatids than to Anatids (Carboneras 2019b).

The family Anatidae includes ducks, geese, and swans and contains the vast majority of waterfowl species – 165 of the 169 species within the order (Carboneras 2019a). Within this family, there are four subfamilies: Anserinae (swans and “true” geese), Oxyurinae (ducks more closely related to Anserinae), Dendrocygninae (whistling ducks and white-backed ducks), and Anatinae (sea ducks, diving ducks, shelducks and sheldgeese, perching ducks, and dabbling ducks). Anserinae and Anatinae together are sometimes described as “wildfowl” (Carboneras 2019a).

## Anatomy, Morphology, and Adaptations

In general, all waterfowl are adapted to life in or near the water, and they share many anatomical features that allow them to thrive in this aquatic lifestyle. Although there is a great range in body size from the large trumpeter swan to the small African pygmy goose, Carboneras (2019a) describes several general trends among waterfowl that hold true across the order. Firstly, most waterfowl tend to have longer, flatter bodies which improve buoyancy on the water and shorter tail feathers. The most aquatic species tend to have legs situated more caudally, or toward the tail, which increases buoyancy but makes walking on land more awkward and gives them their distinct waddle. They also have characteristic webbing between their toes allowing them to swim more quickly and efficiently. Furthermore, most



waterfowl have well-developed uropygial or preen glands, which are oil-secreting glands located just above the tail, that birds use to coat their feathers, making them better able to repel water. Many waterfowl also have salt glands situated above their eyes that filter out salt from their blood and secrete it out of their bodies. These glands vary in their prominence, depending on how brackish the water is in individual species' habitats. Finally, they also have long, flattish bills with lamellae or comb-like projections from their beak used to filter out food from the water. Different species have lamellae of different sizes and densities, based on the food that they primarily eat.

Waterfowl also share anatomical traits beyond life on the water. Unlike most other birds, male waterfowl have sex organs that can be everted to become external and roughly comparable to mammalian penises (Scott 2010). Most other bird orders copulate by direct cloacal contact which does not require any sort of penetration. Waterfowl males, however, have retained an external penis that enters the female's oviduct (Herrera et al. 2013). Relatedly, female waterfowl tend to have much more complicated oviducts than other bird orders (Brennan et al. 2009). There isn't a consensus explanation for these striking anatomical differences between waterfowl and other bird orders, but Herrera et al. (2013) suggest that sexual selection plays an important role. Furthermore, Brennan et al. (2009) argue that complex male and female waterfowl anatomy coevolved as an "arms race" of sorts to determine the success of forced copulation.

Although the different families of waterfowl share many of the same characteristics, there are several important differences between families. For example, most ducks, geese, and swans (i.e., members of the family Anatidae or "anatids") molt all of their feathers at once, rendering them completely flightless during short periods of time as their feathers regrow (Carboneras 2019a). Screamers and magpie geese, however, molt their feathers more gradually and therefore retain their ability to fly year round (Carboneras 2019a; Carboneras and Kirwan 2019b).

Magpie geese (i.e., the sole species of Anseranatidae) also exhibit some unique anatomical traits that separate them from other waterfowl. Magpie geese, especially males, have an extremely long, folded trachea that is thought to play a role in vocalizations related to mating (Whitehead 1998). They also feature a prominent head protuberance that is significantly larger in males and in older birds (Whitehead 1998). Both of these sexually dimorphic features likely evolved due to sexual selection pressures exerted by the unusual polygamous mating system employed by the species that is discussed later on in this entry (Whitehead 1998).

Screamers (i.e., the three species that make up the family Anhimidae) also have several characteristics that make them unique from other waterfowl. Although screamers are capable of swimming, they are unlike other waterfowl in that they spend most of their time walking in the marshy vegetation around bodies of water as opposed to swimming in the water itself (Carboneras 2019b). Their toes, therefore, are less webbed than those of other waterfowl families and are longer and more spread out, allowing them to traverse marshy areas (Carboneras 2019b). Screamers also have bony spurs on the carpal (wrist) bones of their wings, and as noted by Carboneras (2019b), these spurs are likely used for territorial defense.

Screamers also have several traits that distinguish them from birds in general, not just waterfowl. For example, most birds grow feathers in distinct tracts or lines of feather follicles (Scott 2010). Screamers, however, lack these feather tracts and grow feathers evenly throughout their bodies (Carboneras 2019b). Furthermore, although the majority of birds have pneumatic – air-filled or "hollow" – bones, screamers have some of the most highly pneumatic bones of any bird species, which may allow them to fly at higher altitudes (O'Connor 2004; Picasso et al. 2014). Picasso et al. (2014) also suggest that another unique feature of screamers may aid in high-altitude flight: subcutaneous diverticula or air sacs that sit just below the skin and crackle when compressed. Finally, screamers lack uncinate processes which are bony "hooks" that

extend from the ribs of all other bird species (Tickle et al. 2007). Tickle et al. (2007) suggest that these hooks might increase the efficacy of respiration, and note that their length and prominence are somewhat associated with different forms of locomotion in birds. Thus far, however, their absence in screamers is unexplained.

## Feeding and Diet

Waterfowl employ several different methods of feeding including grazing, filter feeding/dabbling, and diving. All waterfowl with the potential exception of screamers employ filter feeding or dabbling as a feeding method (Carboneras 2019a, b). The basic process of dabbling involves sucking water through the bill and then pushing it back out through the lamellae that line the beak in order to trap plankton, algae, etc. which is then pushed back into the bird's throat with its tongue (Hughes and Green 2005). Although most waterfowl utilize dabbling as a feeding method, some rely on it more heavily than others. As noted by Hughes and Green (2005), the number of lamellae a species has on its bill corresponds to the individual species' diet. For example, a diving duck that tends to swallow whole fish or larger mollusks would be expected to have fewer lamellae than a dabbling duck that primarily eats plankton. The size and shape of waterfowl's bills also correspond to the type of food that an individual eats (Hughes and Green 2005). For example, a northern shoveler's (*Spatula clypeata*) wide, flat bill is indicative of the smaller plankton it eats, whereas a long-tailed duck's (*Clangula hyemalis*) shorter, narrower bill suggests it eats larger crustaceans and fish (Carboneras and Kirwan 2019a, c).

In addition to employing several different feeding methods, there is also a wide range of diets across the order. Screamers are herbivores, primarily eating aquatic plant matter. They may occasionally eat insects, especially when raising chicks (Carboneras 2019b). Magpie geese are also primarily herbivores, focusing on grasses, seeds, and tubers. They will use their feet to bend tall grasses down, exposing the seeds and roots underneath for them to eat (Johnsgard 2010). Magpie geese dig through muddy areas to find plant

matter as well as filtering mud through their beaks to consume smaller pieces of plant matter (Carboneras and Kirwan 2019b).

Among anatids, "true" geese and swans (members of the subfamily Anserinae) tend to be herbivorous throughout their lifetimes, whereas ducks vary much more in their diets (Carboneras 2019a). There is a wide range of diet patterns within ducks, ranging from strictly herbivorous to strictly carnivorous. A pattern noted by Carboneras (2019a) is that duck species whose habitats are in estuaries or oceans (i.e., further from land) tend to be more carnivorous while more terrestrial ducks tend to be more herbivorous. In addition to environmental factors, seasonality affects waterfowl diets, as well. One individual bird of any given waterfowl species may shift its diet between the breeding and non-breeding seasons. For example, McLandress and Raveling (1981) noted that Canada geese (*Branta canadensis*) shifted their primary diets from corn during the winter to a much higher diversity of items, especially those with protein, in preparation for migration and eventual breeding.

## Distribution and Habitat

Waterfowl can be found on every continent except Antarctica (Carboneras 2019a, b; Carboneras and Kirwan 2019b). Individual subfamilies are rarely found in only one geographic region of the world. Even a single species, such as the white-faced whistling duck (*Dendrocygna viduata*), can be found on multiple continents (Carboneras and Kirwan 2019d). Screamers can be found throughout most of the continent of South America (Carboneras 2019b). Magpie geese live along the northern coast of Australia and the southern coast of New Guinea (Carboneras and Kirwan 2019b).

In addition to their wide distribution, waterfowl are found in many different types of aquatic habitats, from oceans to ponds to creeks. As you might expect, diving ducks usually prefer deeper water than do dabbling ducks (Carboneras 2019a). Geese tend to choose marshier areas adjacent to grasslands and meadows (Carboneras 2019a). Two species, torrent ducks (*Merganetta armata*) and blue ducks (*Hymenolaimus*

*malacorhynchos*), even prefer rivers and streams with rapid currents (Carboneras 2019a).

Different species also spend varying amounts of time in close proximity to water. For example, king eiders (*Somateria spectabilis*) spend almost the entirety of the non-breeding season on the ocean, and even when they do breed, they nest close to the water (Carboneras 2019a). On the other hand, many geese spend a lot of time at great distances from water (Carboneras 2019a). Furthermore, different waterfowl species change their habitat preferences and habits seasonally. Harlequin ducks (*Histrionicus histrionicus*) spend the breeding season near fast-moving streams in the mountains but spend the non-breeding season in coastal marine areas (Carboneras 2019a).

## Migration

Many waterfowl species migrate to some degree or another, but like most other aspects of waterfowl life, there is a lot of variation. There's variation within families, species, and even populations. In a pattern noted in other bird orders, waterfowl species that live closer to the tropics tend to be less migratory than those species that live closer to the poles (Carboneras 2019a, b). For instance, although screamers as a family are not considered migrants and species and populations closer to the tropics tend to stay close to their breeding grounds year round, those further from the tropics do travel significant distances (Carboneras 2019b).

There are two general migration patterns: "organized" migration where a population of a species moves from a roughly defined point A to a roughly defined point B on a regular time table (e.g., geese) and necessity-based migration in which a population of a species moves away from an area only at the point at which it becomes necessary based on weather or environmental conditions (e.g., mergansers) (Carboneras 2019a). An example of this latter pattern is a "drought migration" which occurs when a body of water on which a bird or species is reliant dries up, forcing the bird to find another suitable location (Carboneras 2019a). Birds that exemplify this

latter pattern tend to travel shorter distances, only moving as far as they have to, while birds that migrate in a more traditional sense can travel very long distances.

Long-distance migration is inherently risky, and according to Scott (2010), only about 60% of waterfowl that migrate south from North America return to breed the next year. One of the largest risks of long-distance migration is energy depletion. In preparation for migration, migrating waterfowl will enter a period of hyperphagia or overeating. A 1981 analysis by McLandress and Raveling found that the body weight of Canada geese increased to 26–36% during this period of hyperphagia. In addition to storing extra energy, migrating waterfowl also try to conserve energy however possible, and the characteristic "v" formation of migrating geese is likely an energy-saving technique (Weimerskirch et al. 2001).

## Sociality and Flocking

In general, gregariousness, or a high degree of sociality, is a hallmark of most waterfowl life. Most species of waterfowl form flocks for at least part of the year, although swans, geese, and perennially monogamous ducks (see "Mating Systems" below) tend to be more solitary than the rest of the waterfowl order (Carboneras 2019a). Large flocks provide several advantages, including predator protection. This is especially important for waterfowl that molt all of their feathers at once and experience periods of total flightlessness (Carboneras 2019a). They are very vulnerable to predation during these times so flocking is an important defense mechanism. Therefore, maintaining social cohesion is an important part of waterfowl life. Waterfowl have several methods of maintaining social cohesion such as species-specific wing specula (the brightly colored or iridescent patch of secondary feathers on their wings) and contact calls (Carboneras 2019a). Beyond specific species, waterfowl also often form mixed-species flocks, especially during winter when predator protection trumps breeding considerations (Carboneras 2019a).

Although gregariousness is common in waterfowl, there is variation not only between species

but also within species at different times of the year. In areas where seasons are less defined (i.e., more tropical areas), breeding can occur year round (Carboneras 2019a). In more temperate areas, however, there are stark differences in weather and temperature between seasons, and these differences necessitate more strictly defined breeding seasons (Carboneras 2019a). Without the option to breed outside of a certain window, species living in more temperate areas often exhibit vastly different social organizations at different times of year. Southern screamers, for example, are highly gregarious during the non-breeding season and can be found in flocks consisting of a few to potentially thousands of birds. During the breeding season, however, they tend to spread apart, form pairs, and become defensive of a territory.

## Mating Systems

The vast majority of waterfowl species employ a monogamous mating system in which two birds form a pair that stays together for the duration of a breeding season (Bowler 2005; Carboneras 2019a). Most ducks, specifically those in the subfamily Anatinae, form pair bonds during the breeding season but do not tend to maintain these bonds year after year (Carboneras 2019a). Instead, they tend to pair with a different mate in each subsequent breeding season in a system defined as annual monogamy (Bowler 2005). Some suggest that annual monogamy may be a method for maintaining group cohesion (Carboneras 2019a). Eiders, sea ducks, and river specialists such as blue ducks and torrent ducks, however, are exceptions to this rule and tend to pair with the same individual every year (Carboneras 2019a). In a similar vein, swans and geese tend to form permanent pair bonds that last over a bird's lifetime. This system is referred to as perennial monogamy (Bowler 2005).

Polygamous mating systems in which one male breeds with multiple females within a single breeding season is rare in waterfowl but is practiced by American (*Sarkidiornis sylvicola*) and African (*Sarkidiornis melanotos*) comb ducks,

Maccoa ducks (*Oxyura maccoa*), and magpie geese, albeit in different ways. Maccoa duck males defend a territory that is large enough for several females, but the males do not form strong pair bonds with any of the females in their territory (Bowler 2005; Carboneras et al. 2019). Magpie geese males, on the other hand, permanently bond with two females, and all three adults incubate and raise chicks together (Carboneras and Kirwan 2019b).

## Courtship, Nesting, and Incubation

The onset of breeding season usually occurs in the spring, just after spring migration, excepting birds in more tropical areas and/or those that don't migrate. Courtship rituals are closely tied to the mating system a particular species exhibits, and species that practice annual monogamy tend to have much more elaborate courtship displays than do species that practice perennial monogamy (Carboneras 2019a).

Waterfowl practicing annual monogamy typically pair up at the end of the non-breeding season when they are in their wintering grounds (Carboneras 2019a). Female waterfowl exhibit a high degree of natal philopatry, or the tendency to return to the site where they hatched, so once paired, males tend to follow their mate's migration path from the wintering ground to the female's natal site (Anderson et al. 1992).

Most waterfowl nests are simple scrapes (depressions in the ground) made in close proximity to water (Carboneras 2019a). The nests are usually built with a few sticks, grasses, and a liner of down feathers. There are, however, some cavity-nesting waterfowl, such as spotted whistling ducks (*Dendrocygna guttata*), and cliff nesters, such as barnacle geese (*Branta leucopsis*) (Carboneras 2019a). Furthermore, some species of waterfowl build their nests in colonies, meaning the nests are in very close proximity to each other, while others build their nests in a defined territory that they defend to varying degrees (Carboneras 2019a).

Most waterfowl species lay large clutches of relatively large eggs (Carboneras 2019a). Large

clutches ensure that some chicks survive despite a high mortality rate, and large eggs are better insulated in the wetter environment frequented by most waterfowl species. Both of these strategies, however, require a large caloric investment by the female, so each species balances clutch size and egg size in a slightly different way (Christians 2000).

Males usually do not incubate although some species with perennial monogamy or polygamy break this trend. For example, some male whistling ducks will incubate when the female is off the nest to forage, but they do not split the job evenly with females (Carboneras 2019a). Polygamous magpie geese exhibit a very unusual system in which both females paired with a single male lay their eggs in one nest and all three adults incubate eggs (Carboneras and Kirwan 2019b). For all waterfowl, incubation starts after the last egg is laid to help ensure synchronous hatching (Carboneras 2019a). This is important because, as will be discussed later in this entry, waterfowl are known for having highly nidifugous or precocial chicks (Carboneras 2019a). This means that chicks are relatively independent upon hatching and are able to walk and find food for themselves almost immediately. Synchronous hatching is important for large clutches of precocial chicks because the window of time between a chick hatching and leaving the nest is small, and if all chicks are not in the same location, only some of them can be protected at any given time.

One interesting pattern noted in many waterfowl species is conspecific brood parasitism or CBP. CBP occurs when a female lays eggs in the nest of a different female of the same species (Pöysä et al. 2014). These eggs are raised by the owner of the nest and not the biological parent (or “parasite”), meaning that the parasite’s genes are passed on, but the parasite avoids the costs incurred by parental investment. CBP appears to be more prevalent in waterfowl than in any other order of bird with almost 50% of species showing evidence of using CBP as a strategy (although Yom-Tov (2001) notes that this percentage could actually be considerably higher). This prevalence may be explained by a few aforementioned characteristics of waterfowl reproduction: colonial

nesting, precocial chicks, and large, synchronously hatching clutches. Birds that nest in large colonies often face nest site availability as a limiting factor. If a parasite is unable to secure a nest site, she may use CBP as a way to raise chicks without needing a territory of her own. Furthermore, precocial chicks require less parental investment than do altricial (less developed) chicks, making it more possible for foster parents to accommodate a larger brood. Finally, because waterfowl tend to lay large clutches that are not incubated (i.e., protected) until the final egg is laid, the parasite has ample opportunity to access another female’s nest (Yom-Tov 2001).

## Chick Rearing and Parental Investment

As noted earlier, waterfowl species are known for having highly precocial chicks. Precocial chicks are much less reliant on their parents, and therefore much less parental investment is required. As a general rule, male waterfowl (especially males of annually monogamous species) do not provide any parental care, although perennially monogamous species and magpie geese are the exceptions to this rule (Carboneras 2019a). Further, parents usually do not feed chicks but rather “show” them where food is. This is usually a relatively passive process, but some birds like magpie geese take a slightly more active role by holding food in their mouths, sometimes actively feeding it to them (Carboneras and Kirwan 2019b). Some waterfowl species, especially those that nest in colonies, will form crèches (“nurseries”) in which young are collectively cared for by the larger flock (Bowler 2005). This is an important method for predator protection at a time when chicks are especially vulnerable. Most waterfowl chicks become independent after just a few months and disperse from their parents completely and form breeding pairs of their own after just 1 year (Carboneras 2019a). Geese chicks are unusual in that they may stay with their parents and migrate along with them for the first couple years of life, potentially helping them protect the next clutch of chicks their parents lay (Carboneras 2019a).



## Relationship with Humans and Domestication

Waterfowl have a unique relationship with humans due to the large number of domesticated waterfowl breeds. Waterfowl have been used by humans for food, feathers/down, quills, and diversion and even as guards in the case of geese (Carboneras 2019a). Many different waterfowl species, namely, anatids, were likely domesticated soon after the emergence of agricultural societies (Carboneras 2019a). Larson and Burger (2013) describe the pathway that waterfowl, namely, ducks, likely took toward domestication. Per Larson and Burger (2013), waterfowl likely followed a commensal pathway in which they first began to exploit environments created by humans (i.e., feeding off of human waste products or crops), and then humans increasingly took a more active role in managing populations of the birds. Waterfowl exhibit several traits that allow them to be more easily domesticated, such as their large brood size, precocial chicks requiring minimal care, and wide variety of diet (Zeder 2012). Furthermore, as waterfowl are found all over the globe, many different human societies were exposed to waterfowl species.

## Conservation

Likely due to their adaptability and large dispersal over the globe, waterfowl as an order is not particularly threatened. Seventy four percent of the species in the family Anatidae are listed as being of least concern by the International Union for Conservation of Nature (IUCN) Red List (Carboneras 2019a). Only 14 species, or 9%, or species within Anatidae are endangered or critically endangered (Carboneras 2019a). The common threats to those waterfowl species that are endangered include habitat loss and human interference. A less obvious potential threat to waterfowl is hybridization (Scott 2010). Waterfowl as an order have the highest known potential to hybridize among birds (Ottenburghs et al. 2016). An incredible 77% of waterfowl species is known

to have hybridized at some point, whether in the wild or captivity (Ottenburghs et al. 2016).

The ease of hybridization between different waterfowl species combined with human interference poses a serious threat. A clear example of this is the threat of genetic swamping – a replacement of a species' genotype by a hybrid genotype – of the endangered white-headed duck (*Oxyura leucocephala*) by the ruddy duck (*Oxyura jamaicensis*) (Scott 2010). As Scott (2010) describes, in the mid-twentieth century, a small population of ruddy ducks were accidentally released from a captive collection in Britain. This small population went on to breed with white-headed duck populations across Europe, creating not only hybrids but also fertile hybrids that lead to second-generation hybridization (Scott 2010). Conservation laws and programs aimed at controlling the population of ruddy duck are now in place, but white-headed ducks remain endangered (Scott 2010).

Human interference can benefit species, as well, through the use of captive reintroduction programs. In 1949, the nene goose (*Branta sandvicensis*) was endangered, with only 30 individuals known in the wild (Black 1995). A conservation program was begun by the Wildfowl & Wetlands Trust, and between 1960 and 1993, over 2000 captive-bred individuals were released into sanctuaries in the wild (Black 1995). Today, although the nene goose population is still vulnerable, it is no longer critically endangered, and it is increasing (BirdLife International 2017). This exemplifies the potential to change the course of endangered waterfowl species and highlights the importance of concerted conservation efforts as human populations continue to grow and encroach on the habitats of waterfowl.

## Conclusion

Waterfowl is a large and diverse order, but its members are connected through several unique characteristics. The three families of waterfowl share many attributes but also have several unique traits that distinguish them not only from each other but also from all birds. The domestication

of many species of waterfowl and their relationship with humans has impacts on their lives as well as our own.

## Cross-References

- Adaptation
- Altricial
- Animal Society
- Bird Migrations
- Brooding
- Carnivore (Diet)
- Cognition
- Colonial Nesting
- Conservation
- Hybrid
- Parental Investment
- Parenting
- Philopatry
- Precocial
- Predation Risk
- Reproduction

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## Wayfinding

### ► Canine Navigation

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## WCST

### ► Wisconsin Card-Sorting Task

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## Weaning

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## Synonyms

### Ablactation

## Definition

It is the period during which an infant is made to replace breast or formula milk completely with other foods and drinks.

## Introduction

Breast milk is known to be the best for the baby as it provides all the required nutrition (Michaelson et al. 2000) as well as the antibodies that help improve the immune system. Breastfeeding can be continued as long as the baby and mother are comfortable. In certain incidences that include low or no breast milk production or inability of mother to feed the baby due to illness, physical challenges, going back to work or other conditions, formula milk especially designed as per the nutritional requirements of the baby may be introduced. According to the World Health Organization (2001), it is recommended that a child must be exclusively on breast milk for a period of 6 months. In any case, after 6 months breast milk (or formula) alone is not sufficient for the baby as there is a requirement of more calories and nutrients than what breast milk (or formula) can supply. Insufficient vitamin D may constitute a problem if the baby is not properly exposed to sunlight (Dewey 2001) and zinc may also reach to marginal levels in infants from 4 to 5 months of age onwards (Jalla et al. 2002). Some fully breastfed infants may occasionally be deficient of iron, and vitamins A, B12, and riboflavin (WHO 1998). It is necessary to introduce complementary foods in the baby's diet in addition to the breast milk to fulfill the

changing nutritional requirements. These are called complementary foods because they do not replace breast milk (or formula) rather they “complement” or “add” to it and hence enrich the baby’s diet. Ideally, the intake of complementary foods should be gradual with a variety of tastes preferably based on the foods eaten by the family (Brown and Lee 2013). This process of introduction of solid foods and gradually replacing all the breast (or formula) milk is called as weaning. Therefore, weaning is not an event rather a gradual process that starts with the first introduction of solid food and ends with the last intake of breast (or formula) milk.

Breastfeeding is not only a source of nourishment but it also provides comfort, affection, and security to the baby. While starting the process of weaning, it should be kept in mind that in addition to fulfilling the baby’s enhanced nutritional need, his emotional comfort should also be taken care of by providing extra love and attention. Weaning may be classified on the basis of duration of the process (Gradual or Sudden) and on who drives the process (Baby-led or Mother-led).

### Gradual Weaning

It is the process in which the breastfeeding sessions are slowly eliminated over a long period of time until the baby stops nursing. It offers many emotional and physical benefits to both mother and the baby. It is more readily accepted by the baby. Physically it allows the milk supply to decrease at a natural rate as the hormones producing milk decrease gradually. This lowers the risk of painful breast engorgement, plugged milk ducts, and breast infection (mastitis).

### Sudden Weaning

An abrupt or sudden elimination of breastfeeding may be highly challenging to both mother and baby. Breastfeeding builds a bond between baby and mother. For an infant, it is difficult to understand why breast milk is suddenly not available that may make him demanding, cranky, and difficult to soothe down. The mother is also at risk of

facing physical challenges like breast engorgement, clogged milk ducts, and mastitis.

### Baby-Led Weaning

Baby-led weaning, also called child-led or natural weaning, happens when the baby starts accepting more of solid foods in addition to on-demand breastfeeding. This method is not only natural but also safe and easy. It significantly helps in improving a baby’s chewing skills, eating pattern, hand-eye coordination, manual agility and leads to a healthier body weight (Cameron et al. 2012). A constant eye should be kept on the baby cues like hunger and satiety, pushing away the breast, interest in the food eaten by the family and many others. When allowed to self-wean, babies wean between 2 and 4 years of age.

### Mother-Led Weaning

Mother-led weaning is also sometimes called planned or parent-led weaning. The mother (or parent) decides the type and quantity of food to be introduced to the baby, when to offer breast and when to offer bottle, and how to progress with the process. It is possible that the child may show a lot of protest during the weaning process as he is truly not ready for it. It is important to understand that the child is emotionally bonded to the mother by breast feed and therefore it is essential to be patient, flexible, and respectful to child’s needs during the weaning process.

### Conclusion

Breast milk is best for the baby up to 6 months of age; however, after this age it might not fulfill all the nutritional requirement of the baby. Therefore, complementary foods that enhance the nutrient value should be added to baby’s diet. A sudden elimination of breastfeeding may have emotional and physical consequences on both the mother and baby; therefore, it is recommended that breast milk should be replaced gradually.

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## Weasel Family

- [Mustelidae Life History](#)

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## Weasels

- [Mustelid Communication](#)

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## Web Construction

- [Trap Building](#)

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## West Indian Manatee

- [Sirenia Diet](#)

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## WGTA

- [Wisconsin General Test Apparatus](#)

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## Whale

- [Cetacean Cognition](#)

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## Whole

- [Gestalt](#)

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## Whole Genome Amplification

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## Introduction

DNA samples obtained from different sources, namely, single cell (Zhang et al. 1992), tissue biopsies, culture cells, and forensic and tumor samples, may be limited in quantity for various analysis. Amplification of DNA fragments for further experiments can be obtained through different types of polymerase chain reaction (PCR). These techniques have some challenges such as limited DNA yield, and only a particular region of chromosome can be studied. To study the whole genome, the demands cannot be met by using these techniques. These limitations paved a way to develop a new technique to overcome these problems and get a good yield of DNA.



## What Is WGA?

Whole genome amplification (WGA) technique involves modification of conventional PCR method through which the whole genome gets covered to give a good amplification efficiency. Micrograms of DNA can be synthesized from ng or lesser amounts.

PCR-based WGA includes:

1. LA-PCR (linker adapter/ligation-anchored PCR)
2. IRS PCR (interspersed repetitive sequence PCR)
3. PEP PCR (primer extension preamplification PCR) (Zhang et al., 1992)
4. DOP PCR (degenerate oligonucleotide primed PCR) (Telenius et al. 1992).
5. D-DOP PCR (displacement degenerate oligonucleotide primed PCR)

### LA PCR

Adaptors will be ligated to embedded PCR primer sites and it will be amplified.

### IRS PCR

Primers will be designed to known repetitive sequences in the genomic DNA, and they will bind and amplify the DNA.

### PEP PCR

It utilizes random 15-mer PCR primers and low annealing temperature during PCR.

### DOP PCR

It utilizes semi-degenerate oligonucleotides (i.e., CGACTCGAGNNNNNATGTGG) and an increasing annealing temperature.

Each of this method varies in their primer design. These were the first-generation WGA techniques. The use of *Taq* DNA polymerase in PCR-based techniques limits the fragment lengths less than 3 kb with errors in the sequence. Error rates are high, and only 1–2 kb length product can be obtained in most of these multistep techniques. The use of *Taq* polymerase in PCR-based techniques introduces a number of errors in the amplified sequence. Fidelity properties of PCR

enzymes determine the error rate. The higher the fidelity, the lower the error rates during amplification.

Error frequencies occur in the range of  $10^{-4}$  to  $10^{-5}$  mutations/bp amplified. Limitations of these techniques include incomplete genome coverage and amplification bias.

Most WGA techniques involve some variation in accuracy compared to the original unamplified material. The various protocols introduce different rates of artifact formation, allelic dropout, and loss of sequence coverage over the genome. So it is important to choose a technique which minimize dropout and do preferential amplification, increase genome coverage, or maximize accurate base replication.

Non-PCR-based WGA methods include:

1. MDA (multiple displacement amplification)
2. SPIA (single primer isothermal amplification)
3. MALBAC (multiple annealing and looping-based amplification cycles)

### MDA

This involves the binding of random hexamers to denatured DNA followed by strand displacement synthesis at a constant temperature using the enzyme Phi29 polymerase, a high-fidelity enzyme. Hexamers (a chain of six random nucleotide sequences) are added to the DNA sample. After annealing of random hexamers (acts as primers) to the denatured DNA at various sites, Phi29 pol enzyme elongates the strand, and it also displaces the newly synthesized strand and continue its elongation. The enzyme performs strand displacement activity, thus forming new DNA by rolling circle amplification approach (Dean et al. 2001). Error rates are low ( $10^{-8}$ ) with phi29 DNA pol compared to *taq* DNA pol used in PCR-based WGA, and higher length fragment up to 100 kb can be amplified using these simple techniques. Now the displaced single-stranded DNA acts as a template for hexamer binding and formation of new displacement strand leading to a DNA network of increased yield. These networks will be cleaved using nucleases at the end of the process. The reaction happens at an isothermal condition around 30 °C, thus not requiring a thermocycler.

Chimeric formation is more in MDA techniques. Other techniques are the variations of non-PCR-based MDA.

## WGA in Diagnostics and Research

WGA products can be used for whole genome sequencing, genotyping, gene library development, microarray, organism identification, SNV & CNV identification, tumor heterogeneity by microsatellite analysis, percentage of genome amplification, to compare with other commercial kit results, archiving previous samples and in pre-implantation genetic testing. This basic technique is used to study the status of embryo for genetic defects from a single cell (contains 6 pg of DNA) before implantation during in vitro fertilization (IVF) (Wells and Delhanty 2000). WGA method can be selected according to the needs of the researcher. This paves a new way in rapid molecular detection of various diseases even from a single cell. In unculturable microbial communities from soil and water samples, MDA technique plays a major role in amplifying DNA.

## Limitations of WGA

An ideal WGA method should cover and amplify the entire chromosome representing the original genome with high fidelity and no contaminants. Multiple amplification errors and artifacts occur in real situations. This incomplete WGA results in problems like incomplete whole genome sequencing, missing copy number variants, chimeric formations, and incomplete allelic representation of the original genome. Choosing a perfect WGA method may reduce the challenges and holds promise in its utility toward research and medicine.

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## Wild Ursid Management

- [Bear Management](#)

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## Wildfowl

- [Waterfowl](#)

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## Wildlife

- [Safari](#)

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## Wilhelm Wundt

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## Preface

This entry relies heavily on the following three books: (1) *Wundt and the Philosophical Foundations of Psychology: A Reappraisal* (Araujo 2016), which provides a philosophical history of Wundt's ideas on psychology, (2) *Wilhelm Wundt in History: The Making of a Scientific Psychology* (Rieber and Robinson 2001), and (3) *The Story of*

*Psychology* (Hunt 2007). These three references substantially overlap on the facts about Wundt featured in this entry. Other references are cited as needed.

## Biography and Impact

Wilhelm Maximilian Wundt (1832–1920) was a German physiologist and psychologist generally known as one of the founders of scientific psychology. After earning a medical degree at the University of Heidelberg, and studying briefly with Johannes Müller, he was employed as a lecturer in physiology at the University of Heidelberg, where he became an assistant to the renowned physicist and physiologist Hermann von Helmholtz. While there, he authored *Beiträge zur Theorie der Sinneswahrnehmung* [Contributions to the Theory of Sense Perception] – published in 1862. In this book, he challenged the dominant ideas of the physiologists and philosophers of the time by arguing that the study of the psyche can be a science if done experimentally. Wundt also presented the first course on the topic of psychological science, which had been considered a branch of philosophy and had been studied primarily via rational analysis. Wundt turned his course of psychology into a book titled, *Lectures on the Mind of Humans and Animals*. His career spanned about 65 years, and he graduated 186 doctoral students. He was thrice nominated for a Nobel Prize. Wundt was extraordinarily prolific – his published work spans an estimated 53,000 pages (Kim 2016).

## Psychological Science's Beginnings

In 1879, at the University of Leipzig, Wundt founded the first official laboratory for psychological research, which became known as The Institute for Experimental Psychology. In 1881, he formed the first academic journal for psychological research, *Philosophische Studien* [Philosophical Studies], which published the institute's research. The institute attracted a large number of faculty and students who, in turn, became prominent figures in psychology across the

globe, including Emil Kraepelin, G. Stanley Hall, and James McKeen Cattell. His textbooks influenced the first two generations of American psychologists and their students, until the 1920s, when interest in Wundtian psychology began to wane. Wundt wrote on many subjects, despite his belief that most could not be adequately empirically tested. It was typical of Wundt to compare and contrast his ideas with those of other schools of thought, both new and old. For these reasons, Wundt could be considered an encyclopedist.

## The Wundtian Method

From the modest beginnings of physiological psychology, he created a unique methodology for psychology – one that served as a model for psychologists for decades. Wundt placed a notable emphasis on studies involving reaction time measurements. Although measurement of reaction time was already taking place in physiology, his examination of consciously organized temporal processing was a unique addition.

Wundt's favored methodology was introspection, or the inward examination of conscious experience. Wundtian introspection is more narrowly defined compared to how the term is often used today. Wundtian introspection involved observing the reactions of participants subjected to stimuli such as lights, colors, and sounds. Although Wundt had claimed in *Contributions* that the psyche could be studied empirically and quantitatively, he subsequently believed this to be true only for the basic elements of consciousness – sensations, perceptions, and feelings, as well as the associations among them. Helmholtz and others had conducted similar experiments, though these were limited to studying manifest behaviors. Wundt's contribution was the use of introspection to gather quantitative information about non-behavioral conscious experiences.

## Wundtian Psychology

Many of Wundt's theories and conceptualizations were subject to his own revisions, and many of the

major revisions involved the topic of volition. For example, three key propositions that he later abandoned or toned down were: (a) all mental acts are structured by logical rules, (b) unconscious processes are key, and (c) – linking the first two principles – the idea that the mind makes “unconscious inferences” by constructing more complex representations based on, for example, data from sensory perception. While Wundt appreciated that his theory of unconscious inferences had been adopted by Helmholtz, he did not agree with the manner of its application, since Helmholtz only used it to explain visual illusions, whereas Wundt had argued it to be essential for a psychological explanation of the perception of space. For more on the relationship between Wundt and Helmholtz, see the section titled “Wilhelm Wundt 1832–1920” in another entry in this encyclopedia “Hermann von Helmholtz” (Thomas [this volume](#), p. 14).

Wundt’s abandonment of these three propositions shaped his most influential text, *Grundzüge der Physiologischen Psychologie* [Fundamentals of Physiological Psychology], in which he argues that we need an account of the experiencer of psychology based on conscious experience. Wundt believed that even though immediate elementary experiences were caused by particular stimuli, conscious experience had its own type of causation – ideas that build on one another according to specific laws. Wundt named these laws, which were his conceptualizations of association, judgment, creativity, and memory. Actions resulting from more complex mental processes are acts of will or volition. Wundt believed that these volitional processes are the products of an experiencer who actively chooses to think, speak, and act in certain ways. While this theory no longer plays a key role in contemporary psychology, it was part of Wundt’s attempt to move away from the automatism of mechanistic psychology and toward what he regarded as a more complete model.

## Wundt’s Animal Psychology

Wundt considered animal psychology a fitting topic for ruminations, philosophies, and informal

experiments (including some that he lectured on featuring his poodle) but did not allow any work with animals in his laboratory because no data based on introspection could be obtained. In an idea reminiscent of Aristotle’s *Scala Naturae*, Wundt believed that humans are at the pinnacle of a progressive evolution, and that animals may therefore be helpful insofar as they represent a precursor to the human mind. In his autobiography, he commented that his studies of animals in the book *Lectures on the Mind of Humans and Animals* were superficial and that they had been included due to his interest in Darwinism at the time.

In Wundt’s *Völkerpsychologie* [People’s Psychology], a 10-volume nonempirical investigation of social psychological phenomena, he hypothesized that volitional mental processes reflected advanced evolution, and that these abilities are what render humans intellectually superior to other animals. Specifically, he argued that the human capacity for selective attention is what facilitated intellectual progress and the development of human culture. Without these abilities, Wundt believed that humans would be buffeted about aimlessly by sporadic thoughts, memories, and perceptions.

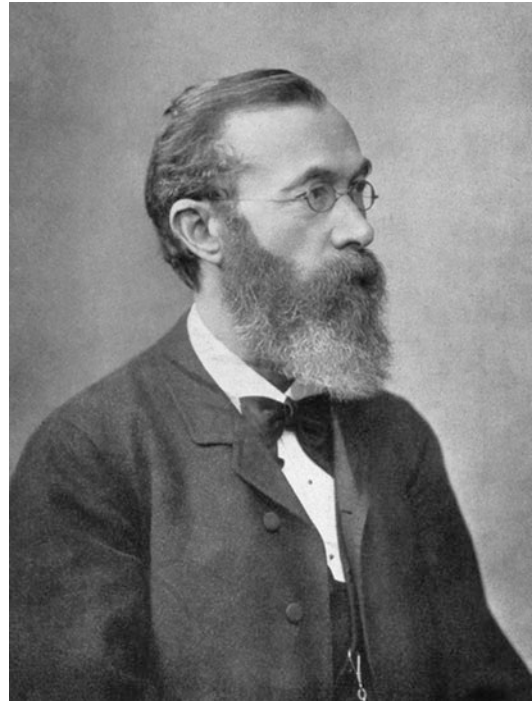
When Wundt first became preoccupied with explaining human and animal movement, the difference between action and movement prompted extensive research and debate with highly influential researchers such as Alexander Bain and Hermann Lotze. All three were indebted to the earlier work of physiologist Johannes Müller. Unlike Bain and Lotze, Wundt did not think that voluntary activity results from learning. What Wundt brought to this debate is a phylogenetic perspective indebted to Darwin’s theory of evolution. Wundt asserted that: “The intentional character of the reflexes then becomes easily intelligible, if we regard them as resulting from the voluntary action of previous generations” (Wundt 1894, p. 227).

It is not uncommon to see quotes from works by Wundt in which he communicated great appreciation for Darwin’s contributions, but when read in context, one finds that they are often followed by a rejection of a basic premise of Darwinian

evolution (that evolution is driven by blind forces that lack foresight) and instead endorse a view of evolution that accords with German idealistic philosophy (directed by teleological rather than mechanistic causal forces). For example, Wundt claimed that the theory of natural selection expresses a teleological rather than a causal principle, and that in calling variations on which natural selection operates “accidental,” Darwin had repudiated his own attempt at providing a causal explanation.

## Conclusion

Wundt’s writings reveal deep and wide-ranging interests (culture, art, law, language, history, religion) which have long been overlooked, partly due to the fact that most of his works have never been translated into English. A recent digitization of his corpus may revive interest in his vast collection of papers and books (Meyer et al. 2017). Wundt was not merely a compiler of volumes, despite popular descriptions that portray him this way. Less known facts about Wundt include his lack of adherence to a positivistic approach, his arguments for the idea that psychology and philosophy are intertwined, and importantly, his view that *Völkerpsychologie* (essentially, social psychology) is important and complementary to his individual-level psychology (Jovanović 2021). He is sometimes thought to have been overly restrictive in what he considered to be part of psychological science, barring many areas that are now commonly accepted as essential parts of the discipline. Yet Wundt had a more inclusive view of psychology than is often believed, as evidenced by his willingness to write about a broad range of topics even when he thought they could not be rigorously tested. Moreover, many of the methods now available in psychology and animal behavior simply did not exist during his time, which surely contributed to this view. While many of Wundt’s specific views may no longer be influential, he contributed a great deal to the establishment of modern psychology as an experimental, empirical science.



Wilhelm Wundt in 1902

## Cross-References

► [Hermann von Helmholtz](#)

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## William Donald Hamilton

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### Synonyms

[W.D. Hamilton](#)

### Definition

William Donald Hamilton (1936–2000) was a British evolutionary biologist famous for his work explaining social behavior through the framework of evolution by natural selection.

William Donald Hamilton (1936–2000), commonly referred to as W.D. Hamilton, was a British evolutionary biologist famous for his work explaining social behavior through the framework of evolution by natural selection. He is widely recognized as one of the most distinguished evolutionary theorists since Charles Darwin (Dawkins, 2000; Trivers, 2000). William Donald Hamilton was born on August 1, 1936 in Cairo, Egypt, to Archibald Milne Hamilton, an engineer, and B.M. Hamilton, a medical doctor (“W.-D. Hamilton,” 2020). As a child, he was interested in natural history and was introduced to the principles of evolution by natural selection and genetics by E.B. Ford’s *Butterflies* (1945) which would serve as inspiration for his later work (“W.-D. Hamilton,” 2020). He went to Tonbridge School in Kent, England, before attending University of Cambridge for his undergraduate education (Dawkins, 2000). Hamilton was jointly enrolled at University College London and

London School of Economics as a doctoral student (Dawkins, 2000). He married Christine Freiss in 1966 and they had three daughters before amicably separating 26 years later (“W.D. Hamilton,” 2020).

W.D. Hamilton presented his mathematical model for inclusive fitness when he was still a doctoral student in 1964 in two citation classic papers (Dawkins, 2000). He published the papers entitled “The Genetical Evolution of Social Behaviors I” and “The Genetical Evolution of Social Behaviors II” in the *Journal of Theoretical Biology*, presenting the concept now known as Hamilton’s rule (Hamilton, 1964a; 1964b). Hamilton’s rule posits that a gene for altruistic behavior will propagate if it satisfies an inequality. The inequality is  $rB > C$ , where  $r$  is the relatedness between the actor and recipient,  $B$  is the benefit to the recipient, and  $C$  is the cost to the actor. If the cost to the individual performing the altruistic act is less than the additional reproductive benefit to the recipient of the altruistic act multiplied by the genetic relatedness of the recipient and the actor, the gene for altruism will increase in frequency. Hamilton’s rule is a significant contribution to the study of altruism and provides a mathematical basis for inclusive fitness.

Although Hamilton’s rule was not globally recognized until decades after it was first published, Hamilton secured prestigious positions at Imperial College London, Harvard University, University of Michigan, and University of Oxford (Dawkins, 2000). While at Imperial College London, he published another citation classic entitled “Extraordinary Sex Ratios: A Sex-Ratio Theory for Sex Linkage and Inbreeding has New Implications in Cytogenetics and Entomology,” in which he introduced the concept of an unbeatable strategy (Hamilton, 1967). Hamilton’s unbeatable strategy served as inspiration for Smith and Price’s concept of evolutionary stable strategy, a strategy or set of strategies that cannot be replaced by an alternative competing strategy when adopted by a population in a specific environment (Smith & Price, 1973). In collaboration

with Robert Axelrod, Hamilton expanded the concept of evolutionary stable strategy to explain the evolution of cooperation among unrelated individuals as a result of reciprocity (Axelrod & Hamilton, 1981). Hamilton's work was instrumental in establishing the genetic basis of altruistic cooperation among related and unrelated individuals. His work was also foundational in advances in evolutionary perspectives of sex ratio, senescence, social insects, and dimorphic males (Trivers, 2000).

W.D. Hamilton's later work focused on parasites (Dawkins, 2000). He was an early proponent of the Red Queen hypothesis, arguing that parasites play a key role in the evolution of sexual reproduction in their hosts since sexual recombination provides a defense against rapidly and antagonistically coevolving parasites (Trivers, 2000). In collaboration with Marlene Zuk, Hamilton reported that healthier individuals of species of birds with higher loads of blood parasites have more colorful feathers and more complex song (Hamilton & Zuk, 1982). This finding demonstrates that parasite-rich environments foster preference for these traits and, therefore, that parasites play a pivotal role in mate choice and sexual selection. Hamilton was a skilled field researcher; he joined an expedition to the Democratic Republic of the Congo in 2000 to investigate the theory that the oral polio vaccine was the origin of the HIV virus in humans (Dawkins, 2000). While in the Congo jungle, Hamilton contracted malaria and was transported to London where he died on March 7, 2000 ("W.D. Hamilton," 2020). During his lifetime, Hamilton was awarded Fellowship of the Royal Society, the Kyoto Prize, the Fyssen Prize, the Newcomb Cleveland Prize, the Linnean Medal, the Sewall Wright Award, the Wander prize, and the Crafoord Prize (Dawkins, 2000; "W.D. Hamilton," 2020).

## Cross-References

- ▶ [Altruism](#)
- ▶ [Cooperation](#)

- ▶ [Endoparasite](#)
- ▶ [Evolutionarily Stable Strategies](#)
- ▶ [Human Cooperation](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Kin Selection](#)
- ▶ [Kinship](#)
- ▶ [Mating](#)
- ▶ [Natural Selection](#)
- ▶ [Operational Sex Ratio \(OSR\)](#)
- ▶ [Ornamentation](#)
- ▶ [Reciprocity](#)
- ▶ [Red Queen Effect, The](#)
- ▶ [Richard Dawkins](#)
- ▶ [Robert Trivers](#)
- ▶ [Senescence](#)
- ▶ [Sex Ratio](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Sexual Selection](#)

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## William Hopkins

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### Title of Entry

William Donald Hopkins

### Introduction

William (Bill) Donald Hopkins is a Professor of Neuroscience in the Institute of Neuroscience, Georgia State University, Georgia, USA. Professor Hopkins has published over 310 journal articles, book chapters, and edited books. He specializes in functional asymmetries in brain organization and in behavior, especially in great apes, and has pioneered the use of noninvasive imaging techniques to directly measure details of brain organization, including both positron emission tomography (PET) and magnetic resonance imaging (MRI). Professor Hopkins has also made fundamental discoveries in communication dynamics in great apes, building on these findings to support an emerging new theoretical perspective on the evolution of language. Great apes are humans' closest living relatives in the animal kingdom, and therefore they serve as a scientifically important comparison group for the elucidation of the evolutionary changes that have occurred in the human lineage since we last shared a common ancestor with the great apes, approximately 7 million years ago.

### Biography

Bill Hopkins was born and raised on a dairy farm in Wisconsin, in September, 1959. He earned his Bachelor of Science degree in Psychology, at the University of Wisconsin, in Madison, Wisconsin. He travelled to Atlanta, Georgia, for graduate studies in psychology, earning his Master of Arts

(1986) and PhD (1990) in the Department of Psychology at Georgia State University. He began research early in his career, working at the Wisconsin National Primate Center as an undergraduate, and as a Research Assistant, then Associate Research Coordinator, and later, Research Associate at the world-famous Language Research Center (LRC), in Panthersville, Georgia, working with Duane Rumbaugh and Sue Savage-Rumbaugh as a graduate student. While working at the LRC, he became interested in the effects of language training on cerebral asymmetries and began his lifelong research program into handedness, particularly in great apes. Upon earning his doctorate, he embarked on two productive postdoctoral fellowships, first at the Centre Nationale de la Recherche Scientifique, Laboratoire de Neurosciences Fontionnelle, Unite de Neurosciences Cognitives, in Marseille, France (1991–1992), and then at the Laboratory of Comparative Ethology, National Institutes of Child Health and Human Development, in Bethesda, Maryland (1992–1993). Professor Hopkins has held numerous academic positions, teaching at Kennesaw State University (1993–1994), Emory University (1994–2002), Berry College (1994–2005), and Agnes Scott College (2006–2012) prior to joining Georgia State University in 2012.

Professor Hopkins holds senior research positions with the Yerkes National Primate Research Center (1989–present), the Language Research Center (1994–present), and the MD Anderson Cancer Center (2011–present) and has served as the President and Scientific Director of the Ape Cognition and Conservation Initiative near Des Moines, Iowa, since 2013. He is an Associate Editor for *American Journal of Primatology* and sits on the editorial boards of the journals *International Journal of Primatology*, *Primates*, and *Laterality*. His research has garnered over \$14,000,000 from such funding agencies as the National Institutes of Neurological Disorder and Strokes, the National Institutes of Mental Health, the National Institutes of Child Health and Human Development, the National Institutes of General Medicine and Science, the Human Frontiers Scientific Program, and the National Science Foundation, among many others.

## Laterality: Behavioral and Cerebral Asymmetries in Great Apes

In a pair of papers in 1989, Bill Hopkins began to challenge the then widespread idea that population-level right-handedness was unique to humans among primates. Because humans display both a population-level left-cerebral hemisphere dominance for language and right-handedness, many theorists at that time viewed right-handedness as an evolutionary artifact of our brain adaptations for speech (e.g., Warren 1980). Hopkins et al. (1989) reported significant right-hand biases for manipulating a joystick by two rhesus monkeys (*Macaca mulatta*) and three chimpanzees (*Pan troglodytes*) during computerized testing. They interpreted their findings as consistent with a growing recognition that human handedness is, in fact, sensitive to task context – it varies in degree with different kinds of demand. Hopkins and Morris (1989) reported a left-visual field (LVF) advantage for processing stimuli presented on a computer screen in two chimpanzees, suggesting a right cerebral hemisphere lateralization in visual processing in this species. Subsequent research revealed significant population-level right-handedness in chimpanzees in tasks involving fine motor coordination (Hopkins 1995, 1996, 2006).

Bill Hopkins pioneered the application of non-invasive brain imaging techniques with chimpanzees and used this technology to directly explore anatomical and functional asymmetries in chimpanzees and other primates. Using magnetic resonance imaging (MRI), he reported significantly longer left sylvian fissures in great apes (Hopkins et al. 2000); this is a deep cleft that separates the temporal lobe from the frontal and parietal lobes, and this asymmetry is concordant with that reported for humans. Cantalupo and Hopkins (2001) later reported a humanlike asymmetric Broca's area – larger in the left hemisphere – in chimpanzees; because chimpanzees have not evolved language, this finding suggests that Broca's area may have a functional organization that is evolutionarily grounded in communication and later co-opted for speech in humans. Recently, Hopkins has begun a series of studies into the

genetic underpinnings of behavior and brain asymmetries in primates (e.g., Gómez-Robles et al. 2016; Mahovetz et al. 2016). He has also discovered long-term effects of early rearing experiences on aspects of brain development in chimpanzees, demonstrating their value as animal models for human development (e.g., Bard and Hopkins 2018).

One domain in which chimpanzees seem to be particularly asymmetrical is in the display of manual gestures. Hopkins and Leavens (1998) reported that chimpanzees displayed a right-hand bias in their use of manual gestures and that, moreover, chimpanzees who vocalized while gesturing were more right-handed than chimpanzees who did not vocalize while gesturing; this suggested an integration of manual-vocal communication in this species, and the basic finding has been repeatedly replicated (e.g., Hopkins and Cantero 2003; Hopkins and Wesley 2002). In addition, he and his colleagues (Losin et al. 2008) discovered that the display of facial expressions during calling is asymmetrical in different directions, depending on the quality of the call – learned calls, typically used to capture the attention of a social partner, displayed greater expressive range in the right side of the face (left cerebral hemisphere), whereas more emotive, species-typical calls were expressed more strongly on the left side of the face (right cerebral hemisphere). Professor Hopkins published an edited book on laterality in 2007, inviting the major theorists on lateral asymmetries to summarize the state of the art (Hopkins 2007).

Taken together, these findings on functional cerebral organization in chimpanzees and other species spurred additional inquiry into the intentionality of chimpanzee signaling and supported a significant new theoretical stance on the evolution of language.

## Ape Communication

Professor Hopkins's interest in the flexibility of ape communication was manifested early in his career. In his master's thesis, he discovered that the vocal repertoire of Kanzi, a language-trained

bonobo (*Pan paniscus*), systematically differed from the vocal expressions of zoo-housed bonobos (Hopkins and Savage-Rumbaugh 1991). A fundamental theoretical dichotomy has existed between humans and animals: humans alone, it has been claimed, communicate intentionally. At present, there is considerable debate over what this claim means, both philosophically and behaviorally. However, there is a well-established research tradition in developmental psychology that documents the transition to intentional communication in humans: by the end of their 1st year of life, human infants typically develop tactics of communication that manipulate the people around them – for example, they begin to point to distant objects and events, and they simultaneously look at their social partners, as if they are monitoring the effect of their gestures. Bill Hopkins and his colleagues decided to apply those same criteria to the gestural communication of captive chimpanzees, and a series of significant findings emerged. First, chimpanzees point, too – and this finding directly refuted numerous claims to the effect that only humans point (e.g., Leavens and Hopkins 1998). Second, chimpanzees choose which sensory modality in which to communicate. If an observer is facing away from a chimpanzee, they are more likely to display an auditory signal, as if to attract attention to themselves, whereas if an observer is looking directly at the animal, they tend to rely on visual communication, such as gestures (Hopkins et al. 2007; Hostetter et al. 2001) – similar patterns were reported in open-field studies of young chimpanzees by Tomasello and his colleagues (e.g., 1994), and Hopkins and his colleagues confirmed the phenomenon of tuning communication to receiver state under experimentally controlled conditions. Third, like human children, chimpanzees display tactics of repair when their initial communication is not successful (Leavens et al. 2005). Fourth, chimpanzees learn some of their calls from their mothers, and this refutes yet another longstanding theoretical claim of human uniqueness (Russell et al. 2013). Fifth, these patterns of flexibility suggest that chimpanzees possess far more flexibility in their calling behavior than has heretofore been appreciated – this apparent voluntary

control of both calls and facial expressions poses significant challenges to theories of the evolution of language that seek continuity between human language and either primate vocalizations or manual gestures (Hopkins et al. 2011). This research demonstrates that humans' nearest living relatives, the great apes, share communicative capacities with humans; whereas twentieth-century theoreticians viewed these abilities for intentional communication as derived from human evolutionary adaptations for speech, these findings support a new vision of the origins of language in which many language properties are shared with apes.

## Evolution of Language

McNeill (1992) suggested that language was irreducibly multimodal. Research by Bill Hopkins is consistent with the idea that where continuity exists between apes and humans is not in purely vocal signaling, nor in gestural signaling, but in the fundamental multimodality of signaling in these species (e.g., Leavens et al. 2010; Tagliavola et al. 2011). This constitutes a significant new theoretical perspective. Previous theories viewed human language as a system elaborated on the vocalizations of primates, derived from observations of semantic-like vocal communication in primates (e.g., Dunbar 1996), or as a gestural system that was later adapted for speech, a theory derived, in part, from the manifest intentionality of gesture production in great apes (e.g., Corballis 2002); the suite of discoveries by Bill Hopkins in the multimodal dynamics of brains, behavior, and genes throughout development has contributed substantially to an emerging integrated theoretical approach to the evolution of language.

## Cross-References

- ▶ [Ape Cognition and Conservation Initiative \(ACCI\)](#)
- ▶ [Behavioral Genetics](#)
- ▶ [Brain Asymmetry](#)
- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)



- [Computerized Testing Paradigm in Primates](#)
- [Georgia State University's Language Research Center](#)
- [Hemispheric Specialization](#)
- [Hereditry](#)
- [Intelligence](#)
- [Intentionality](#)
- [Joint Attention](#)
- [Laboratory Research](#)
- [Laterality \(Handedness\)](#)
- [PET](#)
- [Pointing](#)
- [Primate Communication](#)
- [Yerkes Primate Research Center](#)

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## William James

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### Definition

“Father of American psychology” who pioneered a functionalist and Darwinian approach to the field, popularized the philosophical school of American pragmatism, and influenced the modern study of religion.

### Introduction: Life and Works

William James was born into an affluent family in New York City in 1842. He was the son of a minor philosophical author and brother of acclaimed American novelist Henry James. James studied to be a painter as a teenager but enrolled in Harvard's Lawrence Scientific School in 1861. He first studied chemistry but quickly switched to anatomy and physiology, which he used as a basis for studying medicine. His education included a naturalistic expedition to South America in 1865–1866, as well as a trip to study the new science of psychology in Germany in 1867–1868. James earned his medical degree from Harvard Medical School in 1869 and was hired by Harvard as Instructor in Physiology in

1872. He taught physiology, psychology, and philosophy at Harvard before retiring in 1907.

As a Harvard faculty member James was instrumental in establishing psychology as a professional discipline in the United States. Known as the “father of American psychology,” James taught the country's first physiological psychology course in 1875, supervised its first dissertation on a psychological topic in 1878, and published its first important treatise on psychology, *The Principles of Psychology*, in 1890. James's *Principles* is distinguished from prior psychologies by its “positivist” methodology, that is, its emphasis on observable correlations and eschewal of unobservable spiritual entities. This methodology, combined with its Darwinian perspective, makes it a distinctively modern psychological text. Along with its abridged version, *Psychology: Briefer Course* (1892/1985b), James's *Principles* was the key textbook in the field for a generation. Finally, James's psychology laboratory at Harvard, founded in 1875, was also arguably the country's first. (James's student G. Stanley Hall is sometimes given this honor for his later, but more advanced, laboratory at Johns Hopkins University.)

Although *The Principles of Psychology* made James a respected academic, he was also a radical, eclectic, and popular thinker. During the 1890s, James distanced himself from laboratory psychology and championed the study of esoteric abnormal psychology and paranormal phenomena. At the same time, he increasingly lectured on philosophical topics such as truth, metaphysics, and religion. His 1897 book *The Will to Believe* defends the right to hold certain improvable beliefs, and his 1902 book *The Varieties of Religious Experience* is a seminal text in the psychology of religion.

In the final stage of his career, James elaborated his metaphysical doctrine of radical empiricism, which holds that minds and their objects are functions of a more basic reality that is neither objective nor subjective. In parallel, he put forth his philosophy of pragmatism, which holds that the meaning of a concept consists in its practical effects, such that true ideas are just those that “work” in experience. Pragmatism was further

developed by another American psychologist and philosopher, John Dewey, who made it the dominant philosophical school in the United States through the end of World War II.

James died of heart failure in 1910, having achieved international fame in multiple fields of study.

## An Education in Evolution

Evolutionary biology was formative for James in several ways. First, James matriculated at Harvard soon after Darwin published *On the Origin of Species* (1859), introducing the theory of natural selection, or evolution by the differential survival and reproduction of different organisms with different heritable traits. James learned about Darwin's theory from leading scientific minds at Harvard, such as zoologist Louis Agassiz, botanist Asa Gray, and anatomist Jeffries Wyman. James even accompanied Agassiz on an expedition to South America, although he ultimately rejected the latter's dogmatically anti-Darwinian position.

Second, James belonged to the storied "Metaphysical Club," a discussion group that centered on Harvard in the 1870s and included seminal American philosopher Charles Sanders Peirce and future US Supreme Court justice Oliver Wendell Holmes, among other luminaries. Evolutionary debates were central to the Metaphysical Club, with philosopher Chauncey Wright in particular pushing James toward Darwinism. Wright published little himself, but he was an important forerunner of James's Darwinian psychology (1873).

Third, James discussed the topic of evolution from the very outset of his publishing career. This includes anonymous reviews of Darwin's supporter Thomas Henry Huxley, natural selection's co-discoverer Alfred Russell Wallace, and Darwin himself. James also applies Darwinian concepts to the study of human psychology and history in his earliest signed scholarly essays beginning in the late 1870s. Finally, and most importantly, James boldly supports natural selection in his *Principles of Psychology*, an impressive survey of the

burgeoning science of mind that he wrote between 1878 and 1890.

## From Lamarckism to Darwinism

Darwinism was not taken for granted in psychology during James's time. Darwin's principle of natural selection did not achieve its current status as an essential biological principle until the 1930s, when it was integrated with Mendelian genetics and defended using new statistical methods. James's advocacy for natural selection therefore occurred during a period of uncertainty for the theory, as it competed against other evolutionary and nonevolutionary accounts of mind and life.

A case in point is English writer Herbert Spencer (1820–1903). Spencer was the most important evolutionary psychologist prior to James. Indeed, Spencer published his evolutionary theory prior to Darwin's, which ultimately included an evolutionary account of mind, life, society, and the cosmos as a whole. It was Spencer who familiarized the general public with evolutionary ideas, coined the phrase "survival of the fittest" (for Darwin's theory), and gave currency to the very words "evolution" and "environment."

The first edition of Spencer's *Principles of Psychology* (1855) in particular represents a key compromise between two traditional philosophical views: one that grounds knowledge in innate cognitive structure (as in Immanuel Kant) and another that traces knowledge to the acquired sensory experience of the individual (as in David Hume). Mind for Spencer is innate at one level but acquired at another: Innate structure derives from evolutionary processes, and the individual builds upon this structure during development. Such a compromise, broadly construed, is taken for granted in psychology today.

What is not taken for granted is Spencer's preferred evolutionary mechanism. Following Jean-Baptiste Lamarck (1809), Spencer posited evolution by the inheritance of acquired characteristics. This means invoking the population's *collective transformation*, whereas natural selection invokes its *selective sorting*. To use a classic

example, Lamarck explains the giraffe's height in terms of the parallel (and heritable) efforts of all giraffes to stretch their necks, whereas Darwin explains this trait by the survival and reproductive success of those giraffes lucky enough to be taller than average. Similarly, according to Spencer, mind evolves as individuals continually get better at mapping the complex external world and pass on these cognitive gains – physiologically, not just culturally – to their offspring.

Lamarckism and natural selection are compatible in principle. In fact, both Spencer and Darwin accepted both mechanisms, while disagreeing about their relative importance. In contrast, James prefigures twentieth-century biology by rejecting Lamarckism completely in the final chapter of *The Principles of Psychology*. Here James argues that natural selection can explain any trait explained by Lamarckism, and indeed that Darwinian nondirected variation must have been present in cognitive evolution (in contrast to Spencer's tenet that evolution is linear and fated). Additionally, James favorably cites German biologist August Weismann, whose theory of heredity prefigured the "central dogma" of twentieth-century genetics by denying that information can flow back to the genetic material during development in a systematically adaptive and heritable fashion. James concludes that natural selection is necessary for explaining mental evolution but that Spencer's Lamarckism is neither necessary nor plausible. This made James the first important psychologist to adopt an overtly Darwinian (and non-Lamarckian) approach.

## The Emotions

One of James's most cited positions is his theory of the emotions. During the 1880s, James and Danish physician Carl Lange independently formulated a similar account of the nature of emotion. An intuitive or commonsense view holds that an emotion is a mental perception or judgment, upon which certain recognizable physiological changes may follow. James reverses this logic:

My thesis on the contrary is that *the bodily changes follow directly the PERCEPTION of the*

*exciting fact, and that the feeling of the same changes as they occur IS the emotion.* . . . the more rational statement is that we feel sorry because we cry, angry because we strike, afraid because we tremble. (1884, pp. 189–190).

James thus contends that emotions *just are* the experience of certain physiological changes. Upon seeing a bear on a hiking trail, one's fear consists in one's perception of certain physiological "fight or flight" responses, after these responses had already been triggered. James's position on the emotions, in combination with his general skepticism of dichotomies such as emotion/reason and mind/body, prefigure the idea of embodied cognition that arose toward the end of the twentieth century.

A critique of James's position is that the same bodily states may correlate with different emotions, or that different people may express the same emotions differently. This suggests that an emotion is a cognitive judgment preceding the relevant physiological changes. According to James, however, if emotion were defined solely in cognitive terms, this would mean that one could experience an emotion without any given set of bodily sensations. Such an intellectual definition of emotion is too bloodless and spectral, on James's view.

## Reflex Action, Will, and Freedom

Central to James's psychology is the nineteenth-century physiological conception of the "reflex arc" or "reflex action." According to this model, the sensorimotor system comprises an arc or – as John Dewey (1896) would insist – a *circuit* in which sensation, cognition, and behavior are defined in terms of their functional interrelations. A nervous impulse is triggered by a sensory stimulus, which in turn triggers cognitive processes that discharge in an associated action. Sensation and cognition are in this sense *for* action. This is a source of James's notion that belief, truth, and knowledge should be understood as essentially practical in nature.

James portrays the entire reflex arc as a hierarchical series of filters that each sort material

provided by the layer beneath: Sensation selectively registers stimuli from the external world; perception selectively eliminates and foregrounds certain features of objects; cognition selectively emphasizes various aspects of situations or ideas for logical, practical, and aesthetic purposes; and the will is capable of selecting among possibilities for action.

This last point is key to James. Reflex action may occur automatically along neural paths of least resistance, in which case it is called “ideo-motor action.” James denies that all action is ideo-motor, however, because he contends that individuals can actively bias their actions through acts of will: Options for action filter up from lower levels of perceptual and cognitive processes, and one selects an option by attending to it such that its associated motor consequences automatically follow.

James denies that the will’s selections are pre-determined, and in this sense he believes the will to be free. (He considers this position to be neither provable nor disprovable, empirically.) James intends this position as an explicit rejection of the “conscious automaton theory” of his time, which claimed that human consciousness has no efficacy in the world. According to Thomas Henry Huxley, for instance, consciousness is like steam escaping from a train whistle, which does not reach back down into the engine to do any work. James denies this. However, his concept of free will is a constrained one, since it does not allow the individual to invent behaviors wholesale.

Interestingly, selection appears in this story at multiple levels and timescales. First, James argues that conscious awareness would not exist if it did not serve some evolutionary function. James thus makes a Darwinian argument for individual agency, which is ironic given Darwinism’s reputation as an inhuman and mechanistic view of nature. Second, the will’s function in development is similar to that of the environment on Darwin’s theory, since it is capable of selecting possibilities but not creating them. The same is true of each level of selection in the reflex arc, since each merely filters material provided from elsewhere. Finally, the entire reflex arc generates behavioral variation that is tested out against the external

world. It was James’s student Edward Thorndike who proposed the “law of effect,” that is, the tendency of behaviors to be repeated if they produce a satisfying result (1898). This law provided a formal basis for behaviorist theories of reinforcement or conditioning that became dominant in the twentieth century.

James consistently argued that individuals have agency within their own lives and within the social and natural environments that embed them. Like his godfather Ralph Waldo Emerson, James is known as a classic American individualist. Unlike Emerson, however, he defended this position from a physiological and Darwinian perspective. In particular, James framed his position in contrast to Herbert Spencer’s view that both ontogeny and phylogeny are processes of coercive molding in which organisms are shaped by an autonomous environment. James argued instead that organisms co-construct their environments in evolution and that humans similarly co-construct their societies in history (James, 1897/1979, pp. 163–195).

Darwin’s great conceptual advance, according to James, was the idea of variation that is produced *for no environmental reason*. Natural selection thus drives a logical wedge between organism and environment – a wedge that does not exist for the Lamarckian who construes adaptations as direct responses to environmental demands (James 1897/1979, p. 168). For James, this non-directed variation was emblematic of the idea that nature may contain relatively independent systems that interact in a complex fashion without any one factor completely controlling the output. In contrast, many neo-Darwinians are closer to Spencer in viewing evolution as a process of coercive environmental shaping in which individual organisms play a negligible role.

## Habit, Morality, and the Self

According to James, the essence of moral action is the selection of behaviors that restructure one’s habits in the direction of an ideal self. Inspired by the moralistic physiological writings of Alexander Bain and William Benjamin Carpenter, James



portrays the self as a plastic bundle of habits that can be altered through the strengthening or weakening of nervous channels. The habitual structure of the self then becomes a long-term artistic and ethical project. The goal of this project, in James's words, is "to make the nervous system our ally instead of our enemy" (James, 1890/1981, p. 126).

In this context, instinct can be viewed as a special kind of habit. James is known for having posited a great number of human instincts – and even for claiming that humans have more instincts than other animals – but he operated with a somewhat deflated concept of instinct. An instinct for James is just a seemingly goal-oriented behavior that did not have to be learned. Strictly speaking, it is only an instinct upon first exercise, at which point it takes its place as a plastic habit among others. It need not even be immutable or universal within a species.

James describes habit as an essentially conservative agent. This has advantages: The batter in baseball swings more efficiently when the relevant sequence of muscular contractions fires off in an unconsciously associated chain. On the other hand, the conservative nature of habit also means that one constantly finds oneself stuck in what mappers of evolutionary space call a "local optimum" – an adaptive state that has proved good enough or better than readily available alternatives, but which could be surpassed.

The continual surpassing of locally optimal habitual states is thus available as a goal for moral self-cultivation. James promotes his vision of moral development in *The Principles of Psychology* (1890/1981) and in his pedagogical lectures *Talks to Teachers on Psychology* (1899/1983). The key difference between these texts is that in the *Principles* James focuses on how one can direct one's own development, whereas in *Talks to Teachers* he focuses on how teachers can inculcate useful habits in their students.

Although James's pedagogical theory focuses on the shaping of students' behavior, it should not be conflated with the behaviorism that overtook psychology after his death. Behaviorism is essentially "outside-in" in its explanatory structure: External stimuli cause behavior through a process

of conditioning. In contrast, James critiqued an excessive emphasis on external factors, positing complex feedback between individuals and their environments. According to James, individuals are inherently idiosyncratic, spontaneous, and capable of making free choices. He thus believes that education requires intuitive social and emotional skills, not just rule-based conditioning.

James thus construes the self as a plastic bundle of habits that is structured by a reflex arc and mediated by a selective will. Such a self is subject to education and moral improvement. James also sketches several further layers of the self that go beyond physiological psychology: the material self, including one's body, clothes, property, and the fruits of one's labor; the social self, defined by one's recognition from others; the pure ego, which may be a soul or transcendental source of identity; and the spiritual self, defined by one's direct experience of the stream of consciousness.

## The Stream of Consciousness

The stream of consciousness – called "the stream of thought" in *The Principles of Psychology* – is one of James's most influential concepts. According to James, introspection reveals five key characteristics of conscious experience. Thought is (1) always part of a personal consciousness ("my thought"); (2) always changing; (3) continuous; (4) always dealing with objects other than itself; and (5) always interested in some features of its objects more than others. Consciousness is a continuous, ever-changing flux that gives rise to selectively biased thoughts, images, and feelings. This flux, while experienced as "mine," always posits objects that transcend it. This analysis of subjective awareness has influenced both popular culture and the European philosophical tradition of phenomenology – the study of the essential structure of consciousness – including its founder Edmund Husserl.

Notably, the phrase "stream of thought" reflects the third characteristic of consciousness. James's point here is that thought is like a *stream* rather than a *train*. Experience may be analyzable into discrete ideas, feelings, and images, but this

does not mean that such elements are the constituent building blocks of experience. On the contrary, James argues that such “simple ideas” posited by classical empiricists are actually refined products of abstraction. James instead likens consciousness to a continuous flux out of which a tissue of mental elements and their relations resolves. In this stream of consciousness, the transitive “flights” of experience (feelings of logical, spatial, or temporal relation) are just as real and just as basic as the substantive “perchings” (abstract concepts and perceived objects), although the mind tends to suppress the former and foreground the latter (James, 1890/1981, p. 221).

James’s analysis of the stream of consciousness includes an influential account of temporality or the experience of the passage of time. According to James, the experience of the present moment has a structure in which one senses a stretching forward into the future and a simultaneous stretching backward into the past. James calls this the “specious present” (James, 1890/1981, p. 573). For James, the idea of an instantaneous present moment standing precisely between the future and past is a mathematical fiction that is never experienced in actuality. This means that the continuously flowing stream of consciousness is not anchored to a precise, isolable present moment.

## Radical Empiricism

James considers his doctrine of radical empiricism to be essential to his philosophical vision. This doctrine comprises several philosophical principles. The first principle is “fallibilism” or the view that all beliefs are subject to correction by future experience. Fallibility is a familiar concept within the philosophy of science, but James applies this principle broadly to entire philosophical and metaphysical worldviews. One’s very concept of the nature and function of science, for James, should be open to correction by experience.

The second principle is “pluralism.” On this view, the entire universe cannot be known in a single cognitive act, even in principle. Knowledge

is inherently piecemeal, and the world contains systems that hang together in a loose and indeterminate fashion rather than cohering in a fully rational, deterministic matrix. James’s father had been among the “monists” who oppose this view, arguing that the universe is a coherent and self-developing rational whole. This was a common position among idealist philosophers who developed aspects of the writings of Immanuel Kant during the nineteenth century.

The final principle of radical empiricism is that philosophy must be grounded in direct experience. As in his account of the stream of consciousness, James considers both discrete objects and the relations among them to be equally matters of direct experience. Reality for James is a flux rather than a set of independently existing beings. In particular, James denies that a permanent and stable thinking entity is accessible to experience. He thus concludes that “consciousness does not exist” (1976/1912), which is his provocative way of stating that the *transcendental* consciousness posited by certain philosophers does not exist.

The very subject-object distinction for James is a derivative function of a more basic reality called “pure experience.” Knowledge then consists of functional relations within pure experience. This position dissolves a basic philosophical dichotomy between the knower and the independent object that it knows. In doing so, it sidesteps a basic problem for traditional accounts of cognitive representation: How does one corroborate the mind-independent nature of objects if they can be only known through some act of knowing or other? James’s position also introduces puzzles, however, such as how two minds could possibly know the same object if it did not exist independently prior to any act of knowing.

## Religion and the Will to Believe

James was a prominent scholar of religion, most famously in his *Varieties of Religious Experience* (1902/1985a). James’s *Varieties* is not a study of religious dogma or institutions but of religion as experienced by the individual. Moreover, James understands religion very broadly, as one’s overall

way of relating to the universe. He spends much of the *Varieties* describing a series of religious personality types, arguing finally that the “saintly” type – defined by altruistic love and a sense of merging with a higher power – represents the ideal personality. James’s discussion of religious conversion in the book influenced the recovery philosophy of Alcoholics Anonymous. The book also introduced James’s concept of a “moral equivalent of war” or the idea of enlisting youth into civic projects rather than the military, which influenced Depression-era public works projects and the Peace Corps in the United States.

James was not just a scholar of religion but one of its defenders. In particular, he argued consistently throughout his career that it is sometimes permissible to hold religious beliefs in the absence of evidence. James likens belief to a bet that one is free to undertake at one’s own risk. For instance, he argues in his essay “The Will to Believe” (1897/1979) that an improvable belief may be justified if (1) the belief is psychologically possible, (2) the question is logically forced or unavoidable, and (3) the result has momentous consequences. James thus contends that a religious belief may be warranted if it creates a shift in one’s moral energies for the better. He also argues, using a similar logic, that one is entitled to believe that the world is morally improvable, if only because this belief may encourage the improvement of the world.

James thus viewed religion and belief in general in terms of their functions within the broader scope of human concern. He formalized this outlook in his philosophy of pragmatism.

## Pragmatism

James was the chief popularizer of pragmatism, America’s first philosophical school of international consequence. James’s pragmatism comprises a theory of meaning and a theory of truth.

James adapts his theory of meaning from Charles Sanders Peirce. Peirce defined the meaning of an object in terms of its conceivable practical effects (1878, p. 293). James takes “practical effects” in a very broad sense, including

dispositions for action. Thus, James defines the meaning of an object – or theory or worldview – by its conceivable effects on sensation, cognition, and behavior. He also claims that a dispute between competing theories is meaningless unless there is a “difference that makes a difference,” that is, a conceivable difference in someone’s experience if one were true rather than the other.

James’s theory of meaning underlies his pragmatist theory of truth (which James called “humanism”). On this view, a belief is true to the extent that it “works,” where any number of factors – including but not limited to traditional scientific verification – may contribute to a belief’s working. Thus, meaning consists in practical effects, and truth consists in having good practical effects. This is a highly unorthodox position within the philosophical tradition, as it treats “truth” as an umbrella term for beliefs that turn out to be useful, rather than an *explanation* for why a belief is useful.

As with James’s doctrine of the will to believe, pragmatism is sometimes accused of promoting wishful thinking. The pragmatist would seem entitled to believe anything that sounds good. However, James underscores the essentially conservative nature of individual and social belief systems, which holistically constrain our beliefs. He also claims that truth is inherently open-ended and historical – that is, fallible – such that we can never claim to have arrived at a final or absolute truth. James takes the long view, and he spurns dogmatism in all of its forms.

To say that truth is historical for James is not merely to say that we discover different truths at different times. More radically, it is to say that truth itself is inherently dynamic rather than static. In James’s words, “Truth happens to an idea. It becomes true, is made true by events. Its verity *is* in fact an event, a process: the process namely of its verifying itself” (1907/1975a, p. 97). James thus collapses the conventional philosophical distinction between truth (a static relation between a knower and known) and justification (a temporal process in which truth is discovered). A belief’s truth for James *is* its justification.

Both mind and truth evolve, on James’s view. Whereas in *The Principles of Psychology*

(1890/1981) James describes the biological evolution of cognition, in *Pragmatism* (1907/1975a) and *The Meaning of Truth* (1909/1975b), James portrays truth as undergoing its own social or cultural evolution. This is not simplistically to identify truth with those beliefs that support Darwinian fitness. Rather, James views truth as having its own selection process that is driven by a host of human purposes going beyond survival and reproduction.

## Conclusion

William James ushered in a physiological, Darwinian, and functionalist approach to psychology. James's central philosophical concept, however, was the reality and value of individual agency. James thus approached science from a humanistic and explicitly moral perspective. Indeed, Darwinism for James signified a scientific vindication of individual freedom, based on the premise that consciousness would not have evolved by natural selection if it had no efficacy in the world. The will for James is a name for consciousness's function of selecting ideas that represent possible actions. These selections are capable of altering both the external environment and the internal habitual structure, and the individual may undertake this process with a goal of moral self-cultivation.

This process of moral development also provides the framework in which James understands belief, religious or otherwise. His philosophy of pragmatism follows this lead, construing meaning and truth in terms of a range of practical effects. Evolution here appears at multiple levels in James's thinking, both as the origin of our cognitive powers and as a process of social evolution in which truth itself is developed according to myriad values and ideals. Darwin's principle of non-directed variation also inspired James to think of nature in general as a collection of indirectly related complex systems rather than a rationally comprehensible whole. James's radical empiricism is comprised by such a principle of pluralism, in combination with a fallible approach to

knowledge and a commitment to grounding theory in direct experience.

In short, the twin lessons of Darwinism for James are the reality of individual agency and the fallible and piecemeal nature of knowledge. On James's view, the world and human knowledge are *in the making*, with individuals as active participants.

## Cross-References

- ▶ Behaviorism
- ▶ Charles Darwin
- ▶ Cognition
- ▶ Consciousness
- ▶ David Hume
- ▶ Edward Thorndike
- ▶ Embodied Cognition
- ▶ Ethics
- ▶ Evolution
- ▶ Evolutionary Psychology
- ▶ Functionalism
- ▶ Goal-Directed Behavior
- ▶ Habituation
- ▶ Herbert Spencer
- ▶ *Homo sapiens*
- ▶ Immanuel Kant
- ▶ Jean Baptiste Lamarck
- ▶ Laboratory Research
- ▶ Law of Effect
- ▶ Mutations
- ▶ Natural Selection
- ▶ Nervous System, The
- ▶ Ontogeny
- ▶ Phylogeny
- ▶ Reinforcement
- ▶ Self-Directed Behavior

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## William Roberts

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Dr. William (“Bill”) A. Roberts is an internationally renowned experimental psychologist and Emeritus Professor at Western University (London, Ontario, Canada). Born in Safford, Arizona (USA), Bill completed his Bachelor of Science at the University of Maryland in 1960 and his Masters of Arts in 1962 and Ph.D. in 1965 at Bryn Mawr College, Pennsylvania, under the supervision of Dr. M.E. Bitterman. Bill was briefly a faculty member at Vassar College, New York,

before moving to Canada, first as a postdoc with Dr. Endel Tulving at the University of Toronto from 1968 to 1969 and then as a faculty member at Western starting in 1970.

Dr. Roberts has authored over 160 publications, including well-regarded books such as *Processes of Animal Memory* (Medin et al. 2014) and *Principles of Animal Cognition* (Roberts 1998) and highly cited articles such as “Are animals stuck in time?” (Roberts 2002). Dr. Roberts has studied a wide variety of cognitive processes in animals, including metacognition, time and number representation, memory, future anticipation, and transitive inference. His study subjects have been likewise varied and have included humans, rats, pigeons, dogs, horses, and squirrel monkeys. Dr. Roberts’ early work was pioneering in the field of animal memory processes, especially in the use of delayed matching-to-sample to study working memory (e.g., Roberts 1972; Roberts and Grant 1974, 1976, 1978). Some of his best-known recent work includes the comparison of time and number representations in pigeons (e.g., Roberts 2006; Roberts and Boissvert 1998; Roberts et al. 1989, 2000; Roberts and Mitchell 1994), mental time travel in monkeys, chickadees, and rats (e.g., McKenzie et al. 2004; Naqshbandi and Roberts 2006; Roberts 2007, 2016; Roberts et al. 2008; Roberts and Feeney 2009), and the competition between working and reference memory processes (Roberts et al. 2015, 2016).

Dr. Roberts has held uninterrupted grant funding from the Natural Sciences and Engineering Research Council of Canada (or, previously, the National Research Council Canada) since 1969. Since his retirement in 2004, Dr. Roberts has maintained a highly active lab, with many publications in top-tier journals in animal cognition as well as publications in high-impact journals such as *Trends in Cognitive Sciences*, *Current Biology*, and *Science*. He has been Editor for the journal *Learning & Motivation* since 2000. His research has also been highlighted in a number of newspaper and other popular media, including a large segment in a 2015 episode of *The Nature of Things*, *A Dog’s Life*. He has previously been Chair of the Department of Psychology at Western University and is a Fellow of



Divisions 3 and 6 of the American Psychological Association. Dr. Roberts was also honored with the Comparative Cognition Research Award in 2005 from the Comparative Cognition Society (of which he is a founding member) for his lifetime of achievement in the field.

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## William Timberlake

### Timberlake

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William “Bill” Timberlake (1942–2019) was a comparative psychologist and animal behavior researcher who achieved key experimental and theoretical findings through his integration of ecology and ethology into learning theory (Arnet 2019). He explored a broad array of topics but is best known for his work on response deprivation and reinforcement and a leading version of the behavior systems approach to animal behavior. Timberlake was a frequent critic of strictly operational approaches, and many of his contributions drew from his emphasis on the organism’s motivational structure, and how this structure would lead to behavior in varying contexts. His work alongside other ecologically influenced psychologists like Michael Domjan, Sara Shettleworth, and Bennett Galef helped to expand comparative psychology into animal behavior studies more broadly. Nonetheless, throughout his career Timberlake emphasized the value of comparative psychology’s focus on learning. In addition to his research contributions,

Timberlake was a founding member (alongside the biologist Ellen Ketterson) of Indiana University Bloomington's esteemed Center for the Integrative Study of Animal Behavior (CISAB). Much of this entry is informed by Arnet (2019), and the reader is referred there for a more detailed discussion of Timberlake's life and works (as well as the festschrift in *Behavioural Processes*, The Legacy of William Timberlake, of which it is part).

Timberlake was born in San Francisco to William B. Timberlake and Louzelle Spradling Timberlake. He excelled in school and ultimately went to Pomona College where he studied psychology. He started his graduate work in psychology at the University of Michigan in 1964, where he gained a substantial background in neoHullian behaviorism. His advisors, David Birch and Edward Walker (added later as co-advisor), were both part of an innovative group of motivation researchers at Michigan. This group, while still studying motivation from a behavioral as opposed to physiological or neurological perspective, was nonetheless challenging standard stimulus-response approaches (e.g., Birch and Veroff 1966). Rather than emphasizing only the role consequences of actions played in motivating behavior, they increasingly looked to the existing motivations of the organism as playing an important role in the relationship between stimulus and response. Influenced by Birch and others, Timberlake began to conceptualize behavior not as something atomistic that is induced in response to discrete environmental triggers but instead as a constantly generated stream of activity dependent on both internal motivation and environmental context.

Timberlake's dissertation emphasized the importance of first mapping an organism's general behavior to interpret the animal's behavior under intervention. He drew heavily from ethology for his dissertation, but rather than observing an animal in the wild, he observed and coded general behavior in the laboratory context. He made his long-term vision clear in his dissertation proposal: the articulation of the motivational structure behind an organism's behavior (Arnet 2019). His final dissertation was somewhat narrower,

focusing on detailed coding of the general behavior of the rat when allowed to behave freely in the laboratory. In 1969, Timberlake joined the department of psychology at Indiana University of Bloomington where he remained as an emeritus professor until his death in 2019.

At Indiana, Timberlake worked with the comparative psychologist James Allison, another former student of David Birch, to develop the core insights of Timberlake's dissertation into a still leading account of reinforcement—response deprivation. Response deprivation built on David Premack's influential relativity theory of reinforcement (for a history of reinforcement theories, see Adams 2000). Premack had argued that a more probable behavior would reinforce a less probable behavior, where probable is understood in terms of the relative duration an animal will engage in a behavior when allowed to behave freely (Premack 1965). Contra Premack, Timberlake and Allison found any behavior could serve as a reinforcer as long as an organism had a non-zero baseline probability of engaging in a behavior when allowed to behave freely, and the organism was deprived of that behavior (Allison and Timberlake 1973, 1974; Eisenberger et al. 1967). The implications, e.g., that water will motivate a thirsty animal differently from a satisfied animal now seem surprisingly intuitive but were a break from existing theory. Unlike previous approaches, which centered reinforcement in the experimental setup (most famously Skinner's reinforcement theory), the response deprivation theory of reinforcement centered on the animal and its motivational structure with respect to the specific environmental context it is occupying for the understanding of reinforcement. Timberlake further developed the response deprivation account of reinforcement into his disequilibrium theory (Timberlake 1980). This approach envisions an animal, when allowed to behave freely, as a system at equilibrium. Behavior modification occurs when the system is pushed out of equilibrium, and a response is required to return it to equilibrium. This approach shows considerable promise for applied behavior modification and clinical application (Jacobs et al. 2019; McFall et al. 2019).

An emphasis on the animal – its motivational structure, its ecology, its sensory abilities, its internal rhythms, and its natural behaviors – is characteristic of Timberlake’s approach throughout his career and is central to his most prominent findings. At around the same time as the work on reinforcement, Timberlake and an undergraduate student, Douglas L. Grant, did now celebrated experimental research on auto-shaping (Timberlake and Grant 1975). Their innovative experimental design used a live rat as the predictive stimulus for food for another rat. In contrast to the prevailing expectation, in which the subject rat would literally treat the predictive rat as food, trying to eat it, the subject rat instead exhibited the social behaviors associated with feeding. Timberlake and Grant interpreted this as the predictive stimulus tapping into an existing motivational structure. Relatedly, Timberlake et al. (1982) found that failures of reinforcement, memorably called misbehavior by Breland and Breland (1961), are not arbitrary, but rather often occur when the similarity of the stimulus to natural cues would unintentionally elicit natural behavior. This research challenged the very possibility of a neutral stimulus, or a stimulus that modifies behavior in no way beyond focusing attention (Domjan 1997).

Similar themes are present in his work on superstition, where Timberlake took on the legacy of B. F. Skinner. Skinner had observed if pigeons were fed at regular intervals, they began to exhibit structured repetitive behavior, such as spinning around (Skinner 1948). He argued these stereotyped behaviors were the product of random movements and behaviors being unintentionally “rewarded” by the food. Skinner famously described this behavior as “superstitious” behavior after our own structured and repetitive but ultimately misguided actions. Timberlake, building on the work of Staddon and Simmelhag (1971), clarified that the so-called superstitious behaviors were being drawn from the organism’s existing system of feeding behavior.

Beginning in the late 1970s, Timberlake sharpened the importance of an organism’s motivational structure into his behavior systems approach (Timberlake 1993). Behavior systems

approaches have at their core the ethological insight that organisms possess a hierarchically structured system of behaviors shaped by ecology and evolution (see Burghardt and Bowers 2017). Timberlake was one of the first to bring this approach into the laboratory. In contrast, to many ethologists who saw laboratory behavior as artificial, Timberlake viewed laboratory behavior as springing from the same underlying motivational structure (behavior system). Moreover, the controlled conditions of the laboratory were an ideal vantage from which to view the architecture of behavior systems. Against more operational approaches, Timberlake argued that blindness to the organism’s motivational structure, that is to say, assuming the organism was a blank slate that behaved at the whim of laboratory protocols, was leading to experimental and theoretical deficits in learning theory. For example, Timberlake’s research on maze running in rats exposed that rats learn maze running even in the absence of a reinforcer and challenged the purported neutrality of these approaches (Timberlake 2002).

Timberlake’s behavior systems framework has been at its most successful in resolving problems for classical learning theory, e.g., misbehavior, reinforcement, auto-shaping, superstitious behavior, and backward conditioning (see Arnet 2019; Killeen 2019). Nonetheless, the behavior systems research program that Timberlake pursued was not simply about the abstract importance of an animal’s motivational structure in understanding learning, but rather about articulating the structure itself in specific organisms and exploring how it leads to particular behaviors in various contexts.

Above all, Timberlake fought to put the animal back in the study of animal behavior. In a self-conscious spin on anthropomorphism, Timberlake referred to his overarching approach as Theromorphism (which he modified from the Greek word *Therio* for animal). Theromorphism differs from strictly empiricist approaches like radical behaviorism insofar as it takes the explanatory relevance of the animal seriously, but it seeks to describe the perspective of the animal not through analogy to the human mind, but rather through known facts about the sensory capacities

and motivational structure of the animal itself. Timberlake's Theromorphism calls for both a broader and a narrower comparative psychology. It is broader in that it demands the ecological and evolutionary variability of life be reflected in our science of behavior. But it is narrower, in that the understanding of behavior is rooted in a detailed analysis of particular behavior systems and not in generalized learning mechanisms. His legacy is most clearly reflected in the continued application of behavior systems approaches (Burghardt and Bowers 2017; Bowers and Timberlake 2018; Domjan 2014; Cabrera et al. 2019) and the use and development of the disequilibrium theory of reinforcement for behavior analysis and modification (Jacobs et al. 2019; McFall et al. 2019).

## Cross-References

- [Anthropomorphism](#)
- [B.F. Skinner](#)
- [Behavior Systems](#)
- [Behaviorism](#)
- [Clark L. Hull](#)
- [Motivation](#)
- [Reinforcement](#)
- [Superstitious Behavior](#)

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## Wisconsin Card-Sorting Task

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### Synonyms

[Attentional set-shifting test](#); [Conceptual set-shifting task \(CCST\)](#); [WCST](#); [Wisconsin card-sorting test](#)

### Definition

The Wisconsin card-sorting task (WCST) presents the subject with stimulus sets containing one to four shapes (stars, crosses, triangles, and circles) in four colors (red, yellow, green, or blue). In the traditional task, the subject is presented with four cards and asked to match a response card. The subject has to infer the matching rule (shape, color, and number) based on feedback from the experimenter. The rule continually and randomly changes. Recent versions are typically computerized, such as the conceptual set-shifting task (CSST, Moore et al. 2005). In this task, selection of the stimulus exhibiting a single attribute (e.g., color green) is rewarded regardless of the number or shape, but in later trials, a shape (e.g., cross) is rewarded regardless of color. Errors, latency to respond and perseveration on previous rules

(e.g., continuing to choose green stimuli rather than crosses), provide a measure of executive function.

### History

The WCST was designed by Harry Harlow, David Grant, and Esther Berg as part of the latter's Masters thesis in the mid-twentieth century (Berg 1948) at the University of Wisconsin. It was developed for use with humans based on Harlow's studies of discrimination learning in rhesus macaques with and without brain lesions (Eling et al. 2008). According to Eling et al. (2008), the WCST can be thought of as inspired by the early work on concept formation by Ach (1921) who developed a task by which meaningless words were arbitrarily associated with images that shared a common feature. With the WCST, several multidimensional stimuli are presented and the experimental subject has to identify the sorting rule. For example, two-dimensional shapes of different colors and numerosity can be presented. Once the subject learns the rule (select all objects of a particular color), the rule is shifted several times (select all sets of three) and the experimenter measures how quickly the subject can apply the new rule. A low number of perseverative errors, in which subjects continue to match based on a previously rewarded rule, indicate high executive control. The procedure is nonverbal and thus it is surprising that it has not been applied more often in comparative studies. To date, the paradigm has not been used in any nonprimate species, probably because relatively few other species have been trained to respond on computerized systems (although see Morton and Avanzo 2011 for a study of set shifting in sheep and Brown and Tait 2016 for a review of related work in rodents).

### Modern Applications

The WCST is often used in clinical settings with humans (Milner 1963), but it has also been used in studies of nonhuman primates – both to better understand their cognitive capacities (Bonté



et al. 2011) and to identify brain regions implicated in the cognitive processes underlying performance on the task (Kwok et al. 2019; Mansouri et al. 2006). Performance is extremely sensitive to damage to the prefrontal cortex (Demakis 2003; Milner 1963). The primary function of the WCST is to assess impairments in executive function as it tests the ability to adapt behavior to a rapidly changing decision rule (Eling et al. 2008). Performance depends on working memory and requires that selective attention is directed to a single attribute that is shared among objects (Mansouri and Tanaka 2002). In addition to selective attention, the WCST requires the capacity to switch response strategies flexibly, inhibiting previously rewarded responses (Bonté et al. 2011).

The WCST also tests conceptual thinking as it assesses whether the subject can abstract the conceptual rule that links the stimuli. For example, Mansouri and Tanaka (2002) used a computerized version of the WCST with just the two dimensions of shape and color to assess the capacity of two Japanese macaques to identify the relevant sensory dimension for matching. The correct dimension for matching shifted from color to shape across ten transitions. That the monkeys succeeded in applying the rule to other samples in the stimulus set led the authors to conclude that they represented sensory dimensions in working memory, and used these concepts to guide their responses in the task. The WCST has revealed stark differences between human and nonhuman subjects in inhibitory and conceptual abilities in some studies, and comparable performance in others (Bonté et al. 2011; Moore et al. 2005).

## Variants

Bonté et al. (2011) tested 24 Guinea baboons (a large sample for this type of study) with the WCST and extended the paradigm to test set-shifting with paired-relational stimuli as well as stimuli that varied on only a single dimension. In the relational version (R-WCST), subjects had to inhibit responding to absolute stimulus properties in order to attend to the relations between stimuli. Whereas all 24 baboons demonstrated shifting with the traditional single dimension task, only

12 of them succeeded with the relational task. It was also found that age negatively predicted success, suggesting an early decline in executive control processes, with an even more pronounced decline with more abstract tasks. However, in addition to demonstrating age-related decline in executive function, the study did provide evidence of relational processing in baboons – an ability that has sometimes been ascribed uniquely to humans.

A more commonly used variant of the WCST is the Cambridge Neuropsychological Automated Test Battery (CANTAB). In this task, subjects are trained to make a discrimination on the basis of one dimension of compound stimuli. Once criterion is reached, they are presented with either intradimensional discrimination shifts, in which new exemplars are presented with the same dimension controlling discrimination, or extradimensional shifts in which new exemplars are presented with the other dimension controlling discriminations (Dias et al. 1996). Shnitko et al. (2017) developed a variant of these tasks that allowed rhesus macaques to reach criteria on eight sets of discriminations within a single session. The discriminations progressed in difficulty, including four reversals. Unique to this study was the ability to test monkeys in their home enclosures, but also the fact that each session began with the easiest discrimination regardless of prior performance, equating the training history between subjects and allowing for long-term analysis of cognitive flexibility within individuals.

The paradigm is relevant to modern studies of behavioral flexibility (Berg 1948), which has become a popular topic in comparative psychology in recent years. Flexibility has been lauded as a domain general measure of “intelligence” or “cognitive complexity” in nonhuman species. The construct of behavioral flexibility is assumed to incorporate components of inhibition and innovation, whereas the WCST can be more properly considered a measure of cognitive flexibility involving inhibition and set-shifting (Brown and Tait 2016). Subjects are required to inhibit responses to irrelevant attributes, including those that have previously been relevant for predicting reward. In the behaviorist tradition of the times, later papers by Grant and colleagues eschewed



cognitive terminology and focused on stimulus-reward associations in explaining subjects' performance in the task (Eling et al. 2008). However, as can be seen in modern applications, the WCST has been used to reveal cognitive abilities such as working memory and conceptual representations in nonhuman primates and could readily be applied to the study of other nonhuman species and nonverbal children. It is still considered the definitive test of executive function and has been shown to reveal cognitive deficits both as a function of brain damage and normal aging (Bonté et al. 2011; Moore et al. 2005).

## Cross-References

- [Computerized Testing Paradigm in Primates](#)
- [Executive Function](#)
- [Primate Cognition](#)
- [Wisconsin General Test Apparatus](#)

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## Wisconsin Card-Sorting Test

- [Wisconsin Card-Sorting Task](#)

## Wisconsin General Test Apparatus

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## Synonyms

### WGTA

The Wisconsin General Test Apparatus (WGTA) is a laboratory device originally designed for studying two-choice discrimination learning by monkeys. The testing platform minimizes many of the risks of research with nonhuman primates such as being bitten, scratched, or exposed to

potentially infectious bodily substances. The WGTA also provides experimental control against cuing effects, positional biases, and other sources of confounding and error. In its most basic form, the apparatus is a simple tray used to present discriminative stimuli and to provide rewards to the animal being tested, together with visual barriers to minimize unwanted cues. Accordingly, the apparatus was described “not revolutionary in design” (Harlow and Bromer 1938, p. 434); nevertheless, the WGTA (and its modifications) has been an important methodological innovation for more than 80 years in the history of comparative psychology, helping to produce quantitative and qualitative changes in our understanding of animal learning and cognition, and indeed altering the ways that such questions were asked of these animals (Washburn et al. 1994).

The WGTA was first described in an article by Dr. Harry F. Harlow and Dr. John A. Bromer (1938), who indicated that “special acknowledgments for ideas utilized in the preparation of this apparatus are due Dr. Paul H. Settlage and Dr. Walter F. Grether” (p. 434). According to a footnote, the article was recommended for publication by B. F. Skinner. Harlow and Bromer described the construction, purpose, and use of the WGTA, which was initially developed and used at the Wisconsin Primate Laboratory (now the Harlow Center for Biological Psychology) at the University of Wisconsin-Madison. The original WGTA was comprised of two parts: a cage that created the environment in which rhesus monkeys could be safely tested, and the aforementioned stimulus tray, originally described as “an attachable panel-holder, which provides tracks for sliding-panels used in testing” (p. 434). These sliding panels had recessed wells into which reinforcers could be placed and then concealed by stimulus objects that were placed over each well. A researcher could retract the sliding panels and lower a screen so that stimuli could be positioned, and wells could be baited out of the test animal’s sight. Raising the screen allowed the stimulus trays to be extended toward the animal, which could then select from the stimulus array by reaching from the cage, displacing a stimulus object, and (if the correct object was selected)

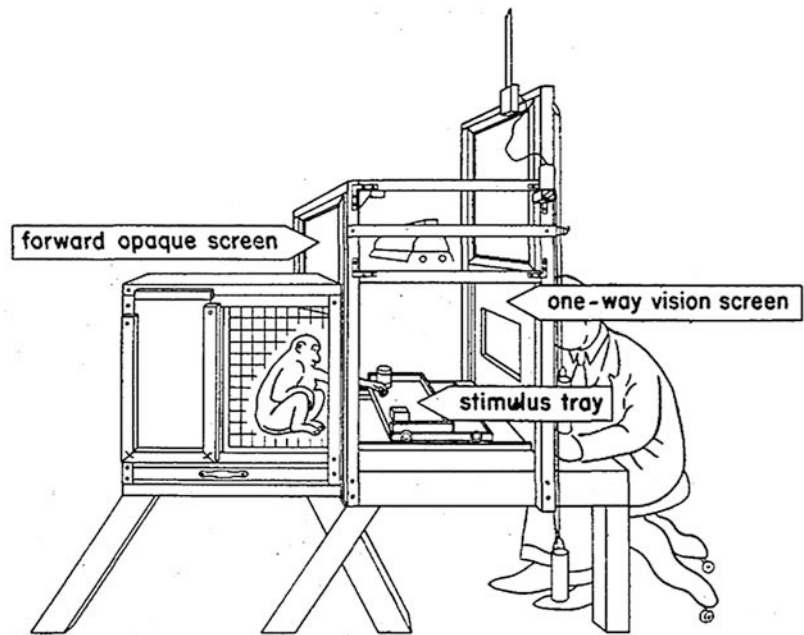
retrieving the reward from the well. The experimenter could observe the animal’s choice, but a screen or one-way mirror prevented the animal from detecting visual cues by the experimenter (see also Davenport et al. 1970). Following a response, the sliding panels could be retracted and reset for the next trial. In this fashion, monkeys could be tested on a variety of psychological paradigms, including two-choice discrimination-learning, reversal testing, matching-to-sample (MTS), nonmatching-to-sample, delayed MTS or delayed responding, oddity, transposition, relative numerosness judgments, and many other assessments (for a review of much of this literature, see Schrier et al. 1965). Using this apparatus, Harlow (1949) collected the data for his classic “learning set” study that showed that rhesus monkeys “learn to learn,” and from which this oft-used illustration of a WGTA first appeared (Fig. 1):

Learning set, and the WGTA that gave rise to the phenomenon, has been described as the revolutionary keys that unlocked the field of animal learning from the associationist bonds of Hullian psychology (Rumbaugh 1997)

The WGTA had several features that made it attractive to researchers in the field of comparative psychology. In addition to the safety and experimental control discussed above, and the ability it provided to replicate and extend the work of a giant in the field like Harlow, the apparatus made it easy to standardize stimulus presentations, to quantify the animals’ responses, and to vary a large number of learning-relevant parameters such as whether or not the animal could see the baiting of the wells, the intertrial and retention intervals, the characteristics of the stimuli and the rewards, and so forth. The WGTA had one significant disadvantage that may have limited its growth in the field: in its original design it was a manual apparatus, with all components and phases requiring human intervention. However, semi-automated and automated variations on the WGTA were developed and reported in the literature (e.g., Davenport et al. 1970; Livesey et al. 1972; Wright et al. 1971), arguably extending to the computerized testing paradigm for primates that implemented the strengths of the manual

### Wisconsin General Test Apparatus,

**Fig. 1** Wisconsin general test apparatus. From Harlow (1949), p. 52



WGTA into a fully automated, game-like video task (Washburn et al. 1989). The apparatus was also modified for portability (e.g., Hunton and Hicks 1959; see also Whitham et al. 2018). Although originally developed for use with monkeys, the WGTA has been modified as needed for use with a wide array of organisms, including pigeons (e.g., Millar and Malott 1968), raccoons (Michels et al. 1960), cats (e.g., Warren 1980), dogs and wolves (Ebel and Werboff 1967; Frank et al. 1989), rabbits (Livesey 1965), prairie dogs (Cain and Carlson 1968), gerbils (Blass and Rollin 1969; King et al. 1968), rats (Valle 1971), chimpanzees (Rumbaugh et al. 1987), a variety of small primates (Pournelle and Rumbaugh 1965), and human children – with and without developmental disabilities (e.g., Graff and Green 2004; Levinson and Reese 1967; Orlando et al. 1960; Olson et al. 1966; Weisberg and Simmons 1966).

The heyday of the Wisconsin General Test Apparatus was during the 1960s and 1970s, but in subsequent decades the testing paradigms that are well suited to the WGTA have principally moved to computer-based technologies. Nevertheless, the literature shows several 100 WGTA-based publications in every decade since Harlow's (1949) landmark report, showing that there are

many designs for which the apparatus remains ideal, even for contemporary research.

### Cross-References

- ▶ B.F. Skinner
- ▶ Clark L. Hull
- ▶ Computerized Testing Paradigm in Primates
- ▶ Delayed Match-to-Sample
- ▶ Discrimination Learning
- ▶ Duane Rumbaugh
- ▶ Harry Harlow
- ▶ Matching-to-Sample: Comparative Overview
- ▶ Oddity
- ▶ Relative Numerousness
- ▶ Transposition

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## Wish

### ► Need Reduction

## Withdrawal

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## Synonyms

Drug withdrawal; Drug withdrawal syndrome;  
Substance withdrawal syndrome

## Definition

In a broad sense, withdrawal refers to the treatments, mechanisms, and behavioral effects after the removal of a biologically significant stimulus that an organism has experienced chronically. Such biologically significant stimuli may be drugs, high energetic food, and any eliciting stimuli or reinforcer (for “reinforcement withdrawal,” see “Extinction” entry). In a narrow sense, “withdrawal” is associated with the behavioral consequences of drug cessation and has been focused on the clinical aspects of such behaviors: abstinence symptoms. That is, it is used to define a syndrome in which aversive symptoms are experienced upon reduction or cessation of drug consumption, in an organism with a chronic experience with the drug. Diverse symptoms have been related to the abstinence of specific drugs, and in general, these are progressively relieved within days and weeks after abstinence, or when drug consumption is resumed (Hindocha et al. 2018; Schlienz et al. 2017). In this clinical perspective, withdrawal may include the following symptoms: impaired cognitive performance, such as response inhibition and delay discounting;

ffective symptoms, including irritability, anxiety, and depression; and physiological symptoms, such as restlessness, nausea, and headaches. (Hindocha et al. 2018).

Next, we review psychological theories that account for both the broad and narrow behavioral effects, while we focus on examples of drug withdrawal (rather than to focus on other reinforcers, like food, sex, etc.). Such theories have been developed in the field of animal learning and have been applied to explain and treat the abstinence symptom. We then review diverse behavioral manipulations and assessment of withdrawal behavior in animals.

## Psychological Models of Withdrawal

In psychology, withdrawal has been explained by at least two complementary theories: Solomon and Corbit's opponent-process model of emotion regulation (Solomon and Corbit 1974) and Siegel's compensatory model of drug tolerance (González et al. 2019; Siegel et al. 2000; Siegel 2016). Solomon and Corbit's model, based on a homeostatic theory of emotion regulation, would explain the effects of drug consumption: its tolerance, and withdrawal, as consequences of the dysregulation that drug intake provokes in an organism and its homeostatic reaction to it. For this model, an eliciting stimulus that breaks the homeostatic balance, in this case the drug intake, induces a biphasic state. Initially, a strong primary process is evoked and represents the unconditioned effects of the drug in the organism (an emotional response to the drug; e.g., pleasure, extasis). Then, as an unconditioned response to the primary process, the organism elicits a secondary, opposite, emotional process aimed to counteract the effect of the drug and to favor the return to a homeostatic state (an emotional response to the primary process; e.g., an aversive emotional state). When the organism lacks experience with the drug, this secondary process is originally slow to develop and weak, compared



with the primary process, and it is mainly evidenced when the stimulus is no longer present, as an affective postreaction (i.e., when the effects of the drug have ended the secondary process lingers briefly). After several exposures to the eliciting stimulus, the secondary process begins more simultaneously with the onset of the primary process, becomes stronger in intensity, and persists longer in time, which allows it to be more effective in counteracting the primary, unconditioned, effect of the drug in the organism. This more effective secondary process is then responsible for provoking a habituated response to the drug, a phenomenon known as drug tolerance, and an increased affective post-reaction when the effect of the drug ends (e.g., where this unbalance in homeostasis generates anxiety, a typical affective symptom of withdrawal) which is considered a strong withdrawal response. Thus, the model is well suited to explain the general effect of drug tolerance and its related withdrawal effect, but it misses a fundamental feature of these phenomena: their situational specificity.

Shepard Siegel's model (Siegel et al. 2000) gives a pivotal role to drug-related cues in the development and maintenance of drug tolerance and withdrawal, complementing the opposite-process model's explanation of these phenomena. For this model, the effects of drugs in the organism are considered unconditioned stimuli that automatically elicit unconditioned responses to compensate for the disturbance produced by the drug intake, which reduces or counteracts the experienced effect of the drug. As drug consumption occurs in specific situations, an association is established between the contextual stimuli in which consumption occurs (conditioned stimuli) and the effects of the drug in the organism (unconditioned stimulus; González et al. 2019; Siegel 2016). Then, given the association between drug-related cues and the effect of the drug, these cues come to elicit conditioned compensatory responses aimed at reducing the disturbance provoked by the drug in the organism, contributing to the development of drug tolerance, and explaining the situation specificity of this phenomenon. For this Pavlovian conditioning model of drug tolerance, withdrawal is the expression of conditioned

compensatory responses elicited by drug-related cues, when organisms are confronted with such cues in the absence of drug administration or after the cessation of its effects. Such responses appear as a preparatory state to counteract the homeostatic disruption caused by the drug, but in its absence are experienced as withdrawal symptoms (González et al. 2019; Siegel et al. 2000).

These theories and different clinical aspects of withdrawal have been studied using animal models, allowing not only the determination of the mechanisms and neurobiological substrate that underlie addiction and withdrawal but also to assess the impact of these phenomena on behavior.

## Behavioral Assessment of Withdrawal in Animal Models

In humans, general withdrawal symptoms can be assessed through tests such as the "Mood and Physical Symptoms Scale" (MPSS; Hindocha et al. 2018) and others, which typically assess physiological and anxiety symptoms that result from drug cessation. Also, different animal models are used to study the behavioral aspects of withdrawal. In general, withdrawal can be measured in any response system affected by a perturbation in homeostasis, and that is bidirectional from the baseline. In the specific case of nicotine, for instance, these models allow measuring different behaviors associated with withdrawal, such as affective signs (mostly anxiety-like behavior and reward-related measurements and somatic signs), locomotor activity, and hyperalgesia (Jackson et al. 2015).

In the case of alcohol withdrawal, after chronic alcohol administration in rats, the animals exhibited aversive withdrawal symptoms manifested as increased sensitivity to stress, depressive-like behaviors (e.g., assessed using a forced swim test), and higher anxiety levels, (e.g., assessed with an elevated plus-maze task and a marble-burying test; Li et al. 2019). In these animals, it was also determined that intracranial injection of glycine diminished these symptoms, and also decreased alcohol consumption upon re-exposure, suggesting that glycine receptors could be a

potential target to treat alcohol use disorders and withdrawal symptoms (Li et al. 2019).

From a conditioning perspective, Siegel suggests an association between tolerance and withdrawal symptoms, in which the presence of predrug cues associated with drug consumption elicit the conditioned compensatory responses that mediate tolerances but, when these cues are not followed by drug administration, these anticipatory cues elicit instead withdrawal symptoms. The evidence shows that subjects that self-administer a drug (through instrumental learning in rats) experience greater withdrawal symptoms in comparison to subjects receiving the drug passively (Siegel et al. 2000). In experienced drug users, a small dose is indicative of a subsequent larger dose. Evidence also shows that when this small dose is not followed by a large dose, it induces withdrawal symptoms (Siegel et al. 2000). This phenomenon was described by McDonald and Siegel (2004) using intra-drug conditioning. In this study, as morphine elicits hyperthermia, the authors used hypothermia as a morphine withdrawal symptom, given this is a conditional response to the drug effect. First, they conditioned rats using three experimental groups: (1) rats trained with saline solution, (2) rats trained with low doses of morphine (5 mg/kg), and (3) rats trained with high doses of morphine (50 g/kg). Then, during a test season, in which rats were injected with low doses of morphine, only the rats conditioned to high doses of morphine manifested hypothermia, while those conditioned with low doses of morphine or saline solution exhibited hyperthermia. From this study, the authors conclude that pharmacological cues can also play a pivotal role in Siegel's model, where modifications in drug dose (high to low) implied the evocation of conditional response in these animals, manifested as withdrawal symptoms (McDonald and Siegel 2004).

Conditioning learning tasks, such as contextual fear, have also been recently used to assess the impact of withdrawal on cognition. In this case, it was observed that the animals trained in a Pavlovian contextual fear task under nicotine withdrawal (that is, 12 h after the last nicotine administration, and in a time frame associated with withdrawal

somatic signs including tremors, gasps, eye blinks, teeth chattering, ptosis, and body spasms), exhibited cognitive and affective changes, associated to an increased fear response along with an anxiogenic effect, in comparison with animals trained under nicotinic influence (Robble et al. 2020).

## Conclusions

The study of the psychological processes underlying the acquisition of drug tolerance and its associated withdrawal severity and progression is relevant, given the functional impact associated with these phenomena, and its mechanisms, as they are implicated in the maintenance of homeostasis. In human animals, is also important for the assessment and elaboration of public health policies and therapeutic approaches to treat drug addictions. In this regard, the use of animal models is a relevant tool to assess this field, due that they allow us to study both the psychological predictions that underlie tolerance and withdrawal behaviors, as well to reveal the neurobiological substrate of these mechanisms.

## Cross-References

- [Associative Learning](#)
- [Avoidance](#)
- [Classical Conditioning](#)
- [Extinction in Learning](#)
- [Habituation](#)
- [Homeostasis](#)
- [Ivan Pavlov](#)
- [Tolerance](#)

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## Within-Group

### ► In-Group

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## WKPRC

### ► Wolfgang Köhler Primate Research Center

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## Woese's Three Domains of Cellular Life

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## Synonyms

Archaea; Carl Woese; Phylogenetics; Tree of Life

## The Taxonomic Structure of the Living World

For decades in the past century, it was widely believed that all living entities on Earth could be neatly divided into two groups: the “prokaryotes (*pro* = before, *karyon* = nucleus) including the majority of single-celled microscopic organisms now known as bacteria and archaea and “eukaryotes” (*eu* = true, *karyon* = nucleus) that include single- and multi-celled organisms containing bona fide nucleus. This prokaryote/eukaryote dichotomy is still used by some textbooks and largely relied on a system that classified living entities on their visible or morphological characteristics.

It was Carl R. Woese in the 1960s and 1970s, a physicist-turned-microbiologist, of the “Urbana School” who wrote a new chapter in biology after spending years of work pioneering a new method to classify life. Woese was not impressed by the established methods of classifying organisms based on their shape or metabolic features. Because morphological characters, such as shape, color, and height, are often not comparable across distantly related organisms (e.g., bacteria and plants), Woese and colleagues spent years sequencing and comparing ribosomal RNA gene sequences across species. Their choice of using molecular characters (i.e., the smaller subunit ribosomal RNA) to (re)-classify life was the

stroke of genius since ribosome is central to life (mediates protein synthesis) and, to date, remains perhaps the best distinction between viruses and cellular organisms (Raoult and Forterre 2008). Moreover, ribosomal RNA is present in all cellular organisms and because of the centrality of its role in protein translation evolves much slower than most other genes, thus allowing comparisons across distantly related organisms. Ribosomal RNA is in fact commonly used today to recognize the taxonomic structure of microbial communities in environmental samples (e.g., “who is out there?”), an approach first pioneered by Norman Pace and coworkers (Pace et al. 1986).

Woese and coworkers discovered that cellular organisms formed three independent branches on the “tree of life” comprising eukarya, eubacteria (later bacteria), and archaeobacteria (later archaea) and directly challenged the established prokaryote/eukaryote paradigm (Woese and Fox 1977). Their proposal later became popular as the “three-domain classification” system of living organisms (Woese et al. 1990) since it led to the recognition of Archaea as a separate domain of life different from Bacteria and Eukarya.

Woese's discovery raised several interesting and controversial follow-up questions. Scientists began to wonder about the roles of Archaea in ecosystems and human health (DeLong 1992; Lurie-Weinberger and Gophna 2015), whether there were additional domains (e.g., viruses) that merited a place in the “tree of life” (Nasir and Caetano-Anollés 2015), how are the three domains related to each other (Forterre 2015), and if indeed the three-domain system fully negated the prokaryote/eukaryote dichotomy (Williams et al. 2013). Thanks to the continuous emergence of molecular sequence data on DNA, RNA, and proteins from hundreds and thousands of cellular organisms and viruses and the development of more sophisticated computational software to analyze large-scale datasets, the past 40 years have produced several fascinating studies directly attempting to answer these follow-up questions.

Archaea are now known to be abundant in ecosystems and also significant part of the human microbiota (i.e., the collection of archaeal,

bacterial, viral, and eukaryotic organisms that live on the human body) (Lurie-Weinberger and Gophna 2015). Despite several investigations, however, they are not known to cause human diseases (thankfully?) (Cavicchioli et al. 2003). Another interesting debate has been regarding the status of viruses as living or nonliving biological entities (Forterre 2016). Recent large-scale phylogenomic analyses focusing on protein structures rather than sequences have shown that viruses belong to the “realm” of life but likely originated multiple times in evolution (thus consider adding multiple domains to the tree?) (Nasir and Caetano-Anollés 2015). Another similarly controversial question has been regarding the evolutionary relationships among the three domains (Gouy et al. 2015). A shift toward combining and concatenating multiple proteins into a single phylogenetic analysis, as opposed to using single ribosomal RNA sequence, and implementation of sophisticated phylogenetic methods recently rejuvenated an old hypothesis where eukaryotes originated from within Archaea suggesting there were only two primary domains, Archaea and Bacteria (Williams et al. 2013). This hypothesis has been boosted by the recent discovery and recovery of near-complete genomes of several novel archaeal lineages from environmental data (Zaremba-Niedzwiedzka et al. 2017). These archaeal lineages encode many eukaryote-like proteins previously not detected or considered rare in Archaea suggesting that Archaea may be the mother of eukaryotes, not sisters, that transformed into modern eukaryotes once they engulfed the bacterial ancestor of modern mitochondria (i.e., the energy powerhouse in eukaryotic cells). However, several concerns regarding contamination during genome assembly from environmental data have recently been raised (Da Cunha et al. 2017), and hence the two-domain vs. three-domain question has now become one of the hottest debates in evolutionary biology. In other words, the Woesian “three-domain” tree of life after withstanding the test of time for four decades faces its sternest test today in the age where rapid genome sequencing directly from environmental samples has become the routine.

Despite the associated controversies, biology will always be thankful to the crucial contributions of Carl Woese. His efforts led to the wider recognition of Archaea, a vital component of our biosphere, and he pioneered the use of molecular characters in classifying life, an approach that has become the norm today. Carl Woese also inspired several young scientists (including AN), and his work triggered several exciting follow-up projects that continue to advance the growth of biology in the twenty-first century. Norman Pace perhaps best described Carl Woese, *Woese is to biology what Einstein is to physics*.

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## Wolfgang Köhler (1887–1967)

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Wolfgang Köhler was born into a Baltic German family in Reval (now Tallinn, Estonia) on January 21, 1887. He studied philosophy and natural sciences, especially physics, in Tübingen, Bonn, and Berlin, and graduated in 1909 from the Friedrich-Wilhelms-Universität in Berlin with a thesis supervised by the psychologist Carl Stumpf. He then worked as an assistant to Friedrich Schumann at the Psychological Institute in Frankfurt for 3 years, where he obtained a *venia legendi* (the teaching license required at German universities for appointment to a professorship). As a private lecturer (*Privatdozent*), without salary or tenure, he accepted the directorship in 1914 at the Station for Psychological and Physiological Research on Anthropoids in Tenerife, Spain of the Canary Islands. The Prussian Academy of Sciences



established the station in 1913 with funds from the Albert Samson Foundation, which were dedicated to researching the “natural and biological foundations of morality, for the individual as well as for society” (after Lück 1987, p. 171). In an enclosed space, Köhler (initially with Eugen Teuber who had established the station 1 year earlier) observed seven chimpanzees (from an original group of nine) that were purchased from Cameroon, then a German colony. After World War I, the Foundation was no longer able to finance the station. In 1919, the chimpanzees were sold to the Berlin Zoo, and Köhler returned to Germany.

At the University of Berlin, Köhler again obtained the license to teach as a lecturer in 1920. In 1921, he was appointed professor of experimental psychology and philosophy in Göttingen, and, back to Berlin in 1922, he became professor of philosophy and director of the Psychological Institute of the Friedrich-Wilhelms University. The Institute had just taken over two floors in a wing of the Berlin City Palace, which had been abandoned by the German Kaiser. At the time, it was one of the largest psychological institutes. Students, including an unusually high number of women for the time, came from many countries, and Köhler himself was very active in lecturing internationally. In the 1930s, he was an early critic of the spreading nationalist racial psychology and he took a public stand against the expulsion of Jewish scientists in 1933. When the National Socialists established a presence even at his own university, he resigned from his position in 1935 and left Germany.

At Swarthmore College in Pennsylvania (USA), Köhler continued his scientific work. From 1946, he was a research professor without teaching duties, and, from 1958, he was Professor Emeritus. After the war, his former University of Berlin became Humboldt University in East Berlin. The latter became the capital of a socialist German Democratic Republic after Germany’s division. The Free University of Berlin was founded in West Berlin, which belonged to the Federal Republic of Germany. Köhler was appointed honorary professor here in 1957 and made an Honorary Citizen of the Free University of Berlin in 1962.

In 1958/1959, Köhler was elected president of the American Psychological Association, and, shortly before his death in 1967, he was made an honorary president of the German Psychological Association (*Deutsche Gesellschaft für Psychologie*). He was, moreover, awarded eight honorary degrees from four US-American universities and colleges and from four European universities. Köhler died in Enfield, New Hampshire (USA), on June 11, 1967. In his memory, the Wolfgang Köhler Primate Research Center at the Max Planck Institute of Evolutionary Anthropology in Leipzig, Germany, carries his name (Asch 1968; Ebisch 2017; Jaeger 2003; Lück 1987; Schönplflug 2012, for a detailed biographical account, including memberships and honors, see Jaeger 1987).

In Berlin and Frankfurt, Köhler (1910, 1911, 1915a) conducted a series of investigations on hearing. To examine the physical and physiological characteristics of sound, he employed a method for registering the movements of the eardrum. He also studied the subjective aspects of acoustical sensations such as the brightness of sound in contrast to pitch. In Tenerife, Köhler (1915b) continued his studies on perception, this time with chicken, cats, dogs, and apes. He demonstrated that the principles of constancy (constancy of size, brightness, etc.) are as valid for animals as they are for humans.

Köhler is probably the best known for his studies on the mentality of apes. He conducted these studies in Tenerife in 1914, with several replications in early 1916 (Köhler 1917). He further made and reported on similar observations on problem solving concerning dogs and chickens and even a 1-year old girl. The investigator devised problem situations where goals could not be achieved in a direct way. In a standard experiment, hungry apes were offered bananas, but the direct path to the fruit was either blocked by a grate or out of reach (e.g., lying outside the cage or hanging from the ceiling). Other animals in a similar situation, like chickens, continued to take a direct path and failed to reach their goal if the way was blocked. In contrast, apes detected alternative routes. In one scenario, the apes could go to the opposite side of the grate by walking

around the wall in which the grate was installed. In other scenarios, they could pass the wall through openings or through doors that they had to open. The animals apparently took detours, even if they temporarily lost sight of their target.

The ability of apes to use tools was especially impressive. To extend the reach of their arm, they used poles. If a basket with fruit was hanging from the ceiling, the apes would climb on top of each other or jump on to a box. Sometimes they even stacked up to four boxes to get closer to the target. If a rope hoisted the basket, they would bite the rope or pull the rope to overturn the basket. These behaviors were all highly adaptive. For instance, if the investigator had filled the boxes with heavy stones or sand, the animals would empty the boxes in order to lift them. The apes attributed multiple functions to the same object. For instance, a pole could be used for climbing, jumping, and digging (e.g., for digging up edible roots); for retrieving items (as an extension of the arm); or as weapon (against an opponent). On the other hand, the same function could be attributed to different objects. Thus, instead of a solid pole, the apes used a wire, a piece of fabric, and even a bundle of straw to extend the reach of their arm. They, furthermore, not only used tools, but also made them. For instance, the apes inserted tubes into each other to increase their reach; remarkably, one ape even gnawed off a piece of a solid wood to fit it into the opening of a tube.

Yerkes (1916) made similar observations around this time, but Köhler (see 1921a, p. 194) only became aware of them after completing his own studies. Köhler (1921b) further published observations on the mentality of apes (regarding, among other things, their understanding of time) and on the role of sexuality in their social life.

The studies on problem-solving skills fueled academic debates and captivated the public. As far as psychological learning theory is concerned, Edward L. Thorndike (1898) had a marked behavioristic position, explaining problem solving as habit formation by trial and error. Depending on the success of certain actions, habits become gradually linked to situational stimuli. In contrast, Köhler advocated a cognitivist position, whereby animals operate on the basis of a mental

representation of a given situation. Indeed, their conscious imagination may even resemble that of humans. The mental representation also entails the ability to imagine alternative options, such as taking a detour or shortening the distance to a target by reaching out with a pole or stacking boxes. From this standpoint, problem solving is a process of cognitive structuring or insight; it is instantaneous rather than gradual or incremental.

For Köhler, insight (*Einsicht*) is a synonym for intelligence. Therefore, in attributing insight to apes he was also making an argument for the propinquity of animal and humans in general, and for the cognitive evolution of the species, in particular. Therefore, beyond the theory of learning, Köhler's research had an impact on biology and philosophy. His observations and explanations were enthusiastically welcomed and propagated by exponents of materialism and evolution theory against idealism and the clergy (e.g., Bölsche 1924).

*Gestalt* became a popular, yet equivocal concept in epistemology when Köhler and his colleagues in Berlin and Frankfurt demonstrated its potential for explaining perceptual phenomena such as stroboscopic movement and visual forms. In stroboscopic movement, the succession of discrete lights is subjectively transformed into a continuous flow of one single light, and in the perception of visual forms separate elements are organized to unitary patterns according to factors like proximity and similarity. As a result, closed, regular, and plain structures dominate. Examples include shapes like circles and rectangles in the stable visual field, and the continuity of events over time. Along with his friend Max Wertheimer (1925), Köhler (1929) interpreted such phenomena as evidence that there is an overall tendency toward coherence, simplicity, completeness, etc. or a "good *Gestalt*." He attributes the emergence of *Gestalten* to a dynamic, self-organizing process, which yields unified patterns or holistic structures. This approach has been applied to various areas of cognitive psychology, including acoustical and tactile perception, thinking, and memory (e.g., von Restorff 1933; Wertheimer 1945). It has further been extended to personality and group dynamics (e.g., Lewin 1951). The

Köhler-Wertheimer conception has gained currency worldwide as Gestalt psychology. A core assumption of the theory is that *Gestalt* formation is autonomous. Köhler (e.g., 1925) defended this hypothesis against the thesis that coherence is produced in a mental act of apprehension.

Contrary to the vitalist notion that holistic structures are a distinguishing feature of organic life, Köhler postulated Gestalt dynamics as universal processes in nature, which even operate in anorganic matter. He elaborates this view in *Die physischen Gestalten in Ruhe und im stationären Zustand* (Köhler 1920). At once deeply immersed in the world of physics and explicitly addressing philosophers and biologists, Köhler analyses stable equilibria and periodic oscillations. Focusing on fluids charged with ions and on electromagnetic fields, Köhler identifies forces driving toward economy, simplicity, and regularity and, accordingly, an equal distribution of energy. This process presupposes that there are relationships between elements constituting a field that transcends the sum of the elements' individual parts. Such field formation occurs autonomously, unless external barriers restrict it. Thus, "phenomenal *Gestalten* may well be understood . . . in conjunction with *Gestalten* from the physical province" (Köhler 1920, p. 172).

Köhler postulated the same inherent dynamics and holistic structures for the brain. He aims to present experimental evidence for this postulate in a study on figural after-effects, a phenomenon that Köhler discovered along with Hans Wallach. Here, lines are displaced and shapes are distorted when presented at the same location of the visual field where another line or figure has already been examined. This effect could be interpreted as due to satiation in an area of the visual cortex (Köhler and Wallach 1944). Later, Köhler designed electroencephalographic studies to demonstrate electrical fields generated in the brain that are analogous to visual patterns (Köhler and Held 1949). Thus, Köhler envisions *Gestalt* principles operating on the physical, physiological, and psychological level. Physical, physiological, and psychological phenomena exhibit structural concordances. The concordances should not be explained in terms of unidirectional causation from

the physical to the physiological and the psychological level. The concordances arise because they are based on the same natural principles. Related phenomena on these three levels are consequently called "isomorphic." Indeed, isomorphism has become the name of Köhler's theory of the structural correspondence between the physical, physiological, and psychological level.

As Köhler's studies on entropy and regulation show, he also addressed natural-philosophic and system-theoretical questions (Köhler 1927a, b). In *The Place of Value in a World of Facts*, Köhler (1938) presented his thinking on the current debates in epistemology and ethics. In contrast to theories that center on the judgment of value as related to human needs and interests, he posits value to be "a common trait of intrinsic requiredness" (Köhler 1938, p. 31). Value may be intellectual, moral, or esthetic. What is more, recognizing value is a matter of insight. The search for value is beyond phenomenology for it approaches the physical world. However, the approach to the organic and even the anorganic nature does not necessarily entail reducing psychology to physiology, or analysis to observation. In this sense, Köhler explicitly distances himself from both monism and positivism. (For a complete list of Köhler's publications, see Henle 1971; Jaeger 1987.)

## Cross-References

- ▶ [Ape Cognition and Conservation Initiative \(ACCI\)](#)
- ▶ [Associative Learning](#)
- ▶ [Behaviorism](#)
- ▶ [Cognitive Map](#)
- ▶ [Cognitivism](#)
- ▶ [Comparative Cognition](#)
- ▶ [Edward Thorndike](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Gestalt](#)
- ▶ [Instrumental Learning](#)
- ▶ [Learning](#)
- ▶ [Primates](#)
- ▶ [Problem-Solving](#)
- ▶ [Robert Mearns Yerkes](#)

- [Size Constancy](#)
- [Wolfgang Köhler Research Center](#)

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## Wolfgang Köhler Primate Research Center

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## Synonyms

[Pongoland](#); [WKPRC](#); [Wolfgang Köhler Research Center](#)

## Definition

A project of the Max Planck Institute for Evolutionary Anthropology located at the Leipzig Zoo in Germany that focuses its research efforts on the study of the behavior and cognition of the four great ape species including chimpanzees, bonobos, gorillas, and orangutans (Wolfgang Köhler Primate Research Center 2018).

## Introduction

Named after Wolfgang Köhler, the Wolfgang Köhler Primate Research Center was first conceptualized in 1997 after the Max Planck Institute for Evolutionary Anthropology initiated focused efforts on the comparative observation of non-human primates. Shortly thereafter, construction of the Wolfgang Köhler Primate Research Center, otherwise known as Pongoland, began at Leipzig Zoo in Germany (Oberwemmer and Rasback 2001). Pongoland is one of six themed worlds located at Leipzig Zoo (Wolfgang Köhler Primate Research Center 2018). Upon the completion of construction, Pongoland first opened its doors to zoo visitors in 2001 (Zoo Leipzig 2018a). Four species of great apes currently reside at the Wolfgang Köhler Primate Research Center at Pongoland including chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmaeus*). Researchers from around the world unite at the center to focus combined efforts from a variety of different backgrounds on the behavior and cognition of all four ape species. In addition, the center devotes specific efforts to the investigation of the “ontogeny of chimpanzee cognition” (Wolfgang Köhler Primate Research Center 2018) because chimpanzees are the closest living relative to human beings (Tomasello and Call 1997).

## Wolfgang Köhler

Wolfgang Köhler (1887–1967) was a German psychologist who was instrumental in laying the foundation of Gestalt Psychology, an area of

psychology that focuses on understanding perception not as individual parts but rather as an organized pattern. Köhler also completed pioneering work on great ape cognition (Köhler 2013). He is most often remembered for his work on insight with chimpanzees (Köhler 1959).

## Max Planck Institute for Evolutionary Anthropology

The Max Planck Institute for Evolutionary Anthropology’s main goal is to “unite scientists with various backgrounds (natural sciences and humanities) whose aim is to investigate the history of humankind from an interdisciplinary perspective with the help of comparative analyses of genes, cultures, cognitive abilities and social systems of past and present human populations as well as those of primates closely related to human beings” (Max Planck Institute 2018). As such, the Wolfgang Köhler Primate Research Center became a natural project of the Max Planck Institute for Evolutionary Anthropology (Wolfgang Köhler Primate Research Center 2018). In addition to the captive colony of apes located at the center, the Max Planck Institute for Evolutionary Anthropology also conducts primate research at various field sites across the world (Max Planck Institute 2018).

## Leipzig Zoo

Pongoland is one of six themed worlds at Leipzig Zoo. In fact, Leipzig Zoo is home to over 850 species and subspecies of animals. It operates as one of the most advanced zoos in the world (Zoo Leipzig 2018b). One of Leipzig Zoo’s primary goals is to aid in animal conservation. The zoo accomplishes this by educating visitors about issues in conservation as well as by modeling the breeding program around recommendations of the European Endangered Species Program. The Wolfgang Köhler Primate Research Center supports the zoo’s efforts with their specific primate breeding plan and, in addition, provides research on great ape captive management (Wolfgang Köhler Primate Research Center 2018).



### Directors and Research Coordinator

As of 2018, Josep Call, Ph.D., maintained position as codirector of the Wolfgang Köhler Primate Research Center since 1999. He is also credited as a cofounder. Call earned his Bachelors of Art in 1990 from the Autonomous University of Barcelona in Spain, and, in 1997, received his Doctorate of Philosophy in psychology from Emory University in Atlanta, Georgia. Since 1999, Call has served as a senior scientist at the Wolfgang Köhler Primate Research Center, and is currently a professor in evolutionary origins of mind within the School of Psychology and Neuroscience at the University of St Andrews (Call 2009).

Michael Tomasello is sitting codirector at the Wolfgang Köhler Primate Research Center. He has maintained this position since 2001. Tomasello received his Bachelors of Art from Duke University in 1972 and, in 1980, his Doctorate of Philosophy in psychology from the University of Georgia at Athens. He is currently an honorary professor at the University of Leipzig's Department of Psychology, as well as a professor of psychology within the Department of Psychology and Neuroscience at Duke University located in Durham, North Carolina (Tomasello 2017).

Daniel Hanus has served as the research coordinator at the Wolfgang Köhler Primate Research Center since 2009. He received a Doctorate of Philosophy at Humboldt University in Berlin (Hanus n.d.).

### Animals

Representing all four great ape species, 50 animals occupy the Wolfgang Köhler Primate Research Center. The apes are divided into five groups. Chimpanzees constitute two different groups, one group consisting of 19 chimpanzees, whereas the other group consists of six chimpanzees. The other three primate groups housed at the center include a group of 11 bonobos, a group of five gorillas, and a group of nine orangutans. All units are mixed sex and range in age from young to old (Wolfgang Köhler Primate Research Center 2018).

### Facilities

The Wolfgang Köhler Primate Research Center currently has an indoor and an outdoor facility

for each of the five primate groups (Wolfgang Köhler Primate Research Center 2018). The center is one of the largest and the most progressive nonhuman primate facilities in the world. Designed to mimic the natural habitat of the great apes, facilities replicate jungles and are equipped with irrigation systems that allow for an abundance of greenery as well as brooks and ponds (Jišová 2007). Furthermore, instead of traditional zoo caging, the outdoor enclosures are separated by watercourses complete with safety nets to protect the apes from the possibility of drowning (Wolfgang Köhler Primate Research Center 2018).

### Enrichment

The Wolfgang Köhler Primate Research Center offers 7000 m of rope (Wolfgang Köhler Primate Research Center 2018) as well as trees for climbing. Different foraging devices are also available. These devices encourage tool use for food access to mimic natural foraging behaviors. Furthermore, daily enrichment materials are provided that encourage activity and serve to prevent boredom (Wolfgang Köhler Primate Research Center 2018).

### Animal Keepers

Employed by the Leipzig Zoo, 14 zoo keepers provide daily animal care to the great apes at the Wolfgang Köhler Primate Research Center as well as the zoo. Zoo keepers are responsible for providing food three times a day, cleaning the facilities, providing enrichment at different times, in addition to hiding food throughout the enclosures (Wolfgang Köhler Primate Research Center 2018).

### Research

Research is observational in nature at the Wolfgang Köhler Primate Research Center. As such, scientists observe different apes as they interact with their surrounding environment including humans and other members of their groups. Furthermore, scientists observe apes engaging in various problem-solving tasks (Wolfgang Köhler Primate Research Center 2018).

Per the Wolfgang Köhler Primate Research Center's website (2018), research at the center is

categorized into two broad domains which include that of social cognition and physical cognition. Within the domain of social cognition, research is further divided into four areas including theory of mind, gestural communication, cooperation and prosociality, and social learning. Significant discoveries have been made in each of the areas of focus. For example, research at the Wolfgang Köhler Primate Research Center has supported the presence of key features of “theory of mind” in great ape species.

Pertaining to physical cognition, researchers investigate ways in which the great apes solve problems to gain insight about the underlying cognitive processes. Organized into three main areas, efforts regarding physical cognition are focused on three main areas which include spatial cognition, planning, and causal knowledge (Wolfgang Köhler Primate Research Center 2018).

## Conclusion

In summary, the Wolfgang Köhler Primate Research Center is a project of the Max Planck Institute for Evolutionary Anthropology housed at the Leipzig Zoo. Within the zoo, the center is located at Pongoland, one of six of Leipzig Zoo's themed worlds. Not only is the Wolfgang Köhler Primate Research Center one of the largest primate facilities in the world, it also utilizes progressive techniques to most naturally mimic the natural environment. Four species of great apes are housed at the center including chimpanzees, bonobos, gorillas, and orangutans. Researchers gather from around the world to study the social and physical cognition of these great apes. The center is currently co-director by Josep Call and Michael Tomasello.

## Cross-References

- ▶ Comparative Cognition
- ▶ Insight
- ▶ Josep Call
- ▶ Nonhuman primates
- ▶ Wolfgang Köhler (1887–1967)

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**Wolfgang Köhler Research Center**

- Wolfgang Köhler Primate Research Center

## Woolly Mammoth

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### Synonyms

*Mammuthus primigenius*

## Definition

The woolly mammoth is one of the most well-known extinct mammalian species, both because of its connection with the Ice Age as well as an extensive and pristine fossil record. As members of the Elephantidae family, their closest living relatives are Asian and African elephants. They are distinguishable from modern elephants due to their larger stature, hairy coat, and large curved tusks. Despite differences in climate, scientists have been able to make generalizations about the life history of woolly mammoths based on what is known about extant elephant species. Notably, it is believed that they had similar social structures and gestation periods. However, due to the harsh climate of their home ranges, woolly mammoths had stricter mating schedules to ensure births in the late spring as well as seasonal migrations through their territories to find food. Additionally, they evolved several unique morphological adaptations in response to their climate. These very adaptations that made them specialized for life in the tundra likely became their downfall as temperatures began to rise at the end of the ice age, causing dramatic changes to the landscape, forcing them to move more and more north in search of habitable environments. Eventually, the last of the mammoths persisted on islands in the Arctic Ocean, with the last of the woolly mammoths dying off on Wrangel Island, just north of Siberia, 3,700 years ago.

## Introduction

The woolly mammoth (*Mammuthus primigenius*) holds a prominent spot in modern mythos as a symbol of the most recent ice age. Their public recognition likely stems from their popularity in cave paintings as well as their pristine fossil record. To this day, the woolly mammoth is one of the most extensively studied extinct mammal species and was among the first species of the Pleistocene from which scientists have been able to recover DNA (Hofreiter and Lister 2006; Maschenko 2002). Given their preferred arctic climate, several mummified remains have been

found in Siberia, which have provided scientists with a plethora of information about their physiologies and diet (Guthrie 2001). Taken in conjunction with the mammoth's extensive fossil record, scientists have been able to formulate hypotheses about their life histories, drawing on parallels to modern-day elephants.

Similar in physiological appearance to extant elephant species, they are most recognized by their large, spiraled tusks and longer hair – both of which are adaptations to their lives in an arctic climate (Guthrie 2001). At the prime of their existence – approximately 300,000 years before present – their range spread over Eastern Europe, Northern Asia, and into North America (Nogues-Bravo et al. 2008). Their habitat, which has come to be known as the “mammoth steppe,” was characterized as cold, dry, open tundra predominantly covered by grasses and few trees. Toward the end of the ice age as the climate started to warm, the landscape began changing with temperate forests spreading more north (Hofreiter and Lister 2006). Eventually, Wrangel Island became the last known home of the woolly mammoth, with the last of their species dying off approximately 3,700 years ago (Vartanyan et al. 1993). Despite the time that has elapsed since the last woolly mammoth walked the earth, there is a wealth of knowledge about their life histories that scientists have been able to recreate.

## Evolutionary Origins

Due to their preferred environment of the mammoth steppe, and by virtue of its unforgiving temperatures, scientists have been gifted with one of the most complete and comprehensive records of morphological evolution in a large mammal (Lister and Sher 2001). The conditions of the steppe have preserved both the fossilized and mummified remains of mammoths, allowing scientists to effectively recreate their evolutionary origins. The Elephantidae family originated in Africa over six million years ago and has three extant species remaining: the Asian elephant (*Elephas maximus*), the African bush elephant (*Loxodonta africana*), and the African forest

elephant (*Loxodonta cyclotis*). There has been some debate over the taxonomy of the woolly mammoth within the family. Some scientists have argued that the woolly mammoth is most closely related to the African elephant based on similarities in the nuclear genome (Rohland et al. 2010). On the other hand, Hofreiter and Lister (2006) found that the mitochondrial DNA of the mammoth was more closely related to that of Asian elephants than African elephants, though the difference was not particularly big. They suggested that African and Asian elephants diverged around six million years ago, and then the Asian elephant and the mammoth lines diverged a half million years later.

While Hofreiter and Lister's (2006) taxonomic hypothesis may be correct, the earliest fossil records of the *mammuthus* genus have been traced to Africa, dating four to five million years ago. These individuals were believed to be morphologically similar to modern elephants, not yet having developed the hairy coat or exaggerated tusks. They entered Europe approximately three million ago (Hofreiter and Lister 2006). Over time, as they progressed more northward, they began to show morphological and behavioral adaptations to the harsher climates, feeding on mostly bushes and grasses and developing the longer hair, characteristic of the woolly mammoth (Hofreiter and Lister 2006).

The *mammuthus* genus has typically been split into three chronospecies, differentiated by their temporal existence. These were *M. meridionalis*, which lived in the early Pleistocene from 2.6 to 0.7 million years ago; *M. trogontherii*, which lived in the early middle Pleistocene from 0.7 to 0.5 million years ago; and the woolly mammoth, *M. primigenius*, which roamed in the late middle and late Pleistocene from 0.35 to 0.01 million years ago (Lister and Sher 2001). Additionally, a series of genetic studies revealed that the woolly mammoth chronospecies can be further subdivided into two clades. Some scientists suggested that these clades resulted from allopatric speciation, due to their geographic separation on either side of the Bering Strait (Gilbert et al. 2008; Maschenko 2002). Clade I was believed to have originated in North America and spread into

Eurasia and eventually went extinct in the Holocene. In contrast, Clade II was believed to have originated in Siberia and had a more limited geographic distribution, going extinct earlier than Clade I in the late Pleistocene.

## Life History of the Woolly Mammoth

Woolly mammoths are unique in that scientists can draw on knowledge about their extant relatives to fill in the blanks about their life histories that cannot be explained through fossil records. While life in the mammoth steppe during the ice age was certainly divergent from that of modern elephants that live in tropical-temperate regions, there are several parallels that can be drawn between Elephantidae family members. Moreover, researchers have been able to draw on observations of extant northern ungulates to recreate the life history of the woolly mammoth in its prime (Guthrie 2001).

Modern elephants exist in matriarchal family units, composed of related females and their juvenile offspring. Male elephants leave their family herd when they reach sexual maturity, venturing off on their own or forming bachelor herds (Pecnerova et al. 2017). Many scientists have presumed logical parallels between the social organization of extant elephant species and woolly mammoths (Hofreiter and Lister 2006; Maschenko 2002). Centralized fossil remains of woolly mammoths suggest that they had mass grave sites, similar to modern elephants. An analysis of a well-studied grave site in Sevsik showed that the composition of remains was not unlike that of modern elephants, which has lent credence to the belief that they had similar social structures (Maschenko 2002). This parallel between social structures has opened the door for additional assumptions to be made about other facets of their lives, such as mating and rearing of offspring.

It is believed that woolly mammoths had a similar gestation period to the 22 months of a modern elephants (Guthrie 2001). Unlike elephants, however, it is likely that they had a far smaller window of fertility each year. Woolly

mammoths faced incredibly harsh seasonal changes between winter and summer, necessitating a more condensed period of rut, which fell in early autumn (Maschenko 2002). Not only did this time frame allow for both sexes to amass substantial fat stores, but it also ensured an ideal birthing period of late spring (Guthrie 2001). The unfortunate consequence of female mammoths coming into estrus – their period of fertility – at almost the same time, was that confrontations between competing males were more numerous and intense than those of modern elephants. It is believed that the constrained rut times are partially to thank for the evolution of their characteristically large tusks, since this period of competition favored more dominant individuals with more exaggerated weaponry (Guthrie 2001).

Unlike modern-day male elephants that experience musth – periods of high androgen levels, increased sexual arousal, and increased intrasexual aggression – periodically throughout the year, male woolly mammoths experienced this only during the short period of rut when females were in estrus. This allowed them to form bachelor herds for the remaining 11 months of the year that were more permanent than those observed in extant elephants (Guthrie 2001). These bonds likely developed at an early age, as young males likely left their natal family herds around 13–15 years of age and formed or joined a bachelor herd. Scientists believe that these bonds were incredibly important for their survival in the harsh mammoth steppe, as solitary individuals were more likely to fall victim to natural traps, such as tar pits (Pecnerova et al. 2017).

There were many pitfalls that woolly mammoths had to face by virtue of the unforgiving landscape that they called home. The winter months were particularly challenging, as their normal sources of food were covered by snow and ice. This is why scientists postulate that calves of 3–5 years of age were weaned from their mother's milk in the springtime when the grasses began growing again (Guthrie 2001). This timing would provide the calves with the best chances to endure the removal of milk from their diet and coincided with when the mother's next calf would likely be born (Rountrey et al.

2007). To survive, mammoths had to consume 7–8% of their body weight each day in green vegetation (Maschenko 2002). Although they had a relatively diverse diet, they relied extensively on grasses. Stomach content analyses revealed that the types of plants consumed by mammoths, while lower in biomass than the plants commonly consumed by modern elephants, were notably high in nutrient and caloric content (Guthrie 2001; Kuzmin 2009). This efficient foraging behavior was crucial to their survival especially in the winter months.

Maschenko (2002) suggested that there were two distinct periods in the yearly cycle for the woolly mammoth that coincided with the summer and winter seasons. He suggested that during those periods, there were distinct differences in the types of food that they consumed, which varied by their seasonal territory. In the summer, grasses were more prevalent, making that the food of choice; however, in the winter, they were forced to feed on bushes, trees, and dry grass. Moreover, during the summer months, family groups likely resided in a relatively small area of their overall territory. As the productivity of food in this small area decreased when the growing season came to an end, families were forced to extend their ranges in search of more food. Due to the low levels of plant biomass, coupled with the mammoths' sizable caloric need, they had to traverse more of their territory in the winter months.

During the winter months, as food sources were depleted, mammoths had to continue moving in search of available resources. It was believed that, during the winter, they spent about 3 months traveling southward, and then returned to the north for the summer season. During this time, they likely traveled between 900 and 1,200 km away from their summer range, topping out at about 20 km per day (Maschenko 2002). Unlike traditional migrations wherein the goal is to reach a warmer climate, woolly mammoths were driven simply by the search for new food sources. During this period of migration, scientists believe they spent nearly 75% of their time foraging, rather than actively moving (Maschenko 2002).



## Morphological Adaptations

Existing climate data for the time when woolly mammoths roamed the earth indicates that the average ambient temperature ranged from  $-30.8^{\circ}\text{C}$  ( $-23.8^{\circ}\text{F}$ ) in the winter up to  $14.5^{\circ}\text{C}$  ( $58.1^{\circ}\text{F}$ ) in the summer, with an average precipitation of 240 mm (9.5 in) per year (Nogues-Bravo et al. 2008). Woolly mammoths evolved a collection of morphological adaptations to combat the cold harsh environment in which they lived. As outlined above, their large, curved tusks were advantageous in fighting other males for access to mates. They also served a purpose in foraging. These 80 kg tusks could be used to remove snow that was covering plant life during the winter months (Hofreiter and Lister 2006; Maschenko 2002). Some scientists have argued that the spiral design and curvature of the tusks made them more durable for snow and ice removal (Maschenko 2002). In addition to dental adaptations for effective foraging, there are a number of skeletal differences between woolly mammoths and modern elephants that have been attributed to differences in foraging patterns. Most notably, their necks were shorter, and they had high domed skulls and sloping backs (Lynch et al. 2015; Maschenko 2002).

The other prominent difference between the bone structure of woolly mammoths and their extant relatives is the cortex thickness of the bone. Cortex thickness correlates with the bone loading experienced by an individual, which is closely related to both the activity of the animal as well as the animal's weight at their heaviest point in the year (Guthrie 2001). Woolly mammoths have higher cortex thickness than extant elephants, supporting other observations that they carried more weight on them (Haynes 1991). More specifically, they had high levels of subcutaneous fat, which was crucial for their survival in the winter months (Maschenko 2002). This has been supported by studies of mummified mammoth remains that show significant fat reserves (Guthrie 2001). Moreover, Lynch et al. (2015) suggested that adaptations for insulin signaling and adipose development were crucial to mammoths' survival in the harsh winters.

Apart from their tusks, the other most notable feature that differentiates the woolly mammoth from other members of the Elephantidae family is their coat. They are often depicted as having a variety of coat colors, ranging from orange to black, but it is not known whether these variations were natural or if they can be attributed to alterations during the mumification process (Hofreiter and Lister 2006). The hairs of their coat were approximately four times thicker than similar hairs in other mammals. Many people often presume that their thicker and longer coat was an adaptation to the cold climate; however, autopsies of mummified remains revealed that this may not be the case. Mammoths did not have the subcutaneous muscles responsible for making the hairs stand up straight, which is the main mechanism by which animals can use their fur to protect from ambient temperatures. Shilo and colleagues (1983) suggested that mammoths may have relied more on their vascular system and the movement of blood to their peripheries to maintain their warmth rather than reliance on their coats. In this same vein, mummified remains have revealed that mammoths had particularly small external ears compared to extant elephants. This has been attributed to their need to conserve heat, compounded with the diminished need for enhanced long-distance communication given the relatively open landscape of the mammoth steppe (Guthrie 2001).

## Factors That Led to Their Extinction

It is clear that woolly mammoths were uniquely designed for life in a harsh and unforgiving climate, and many scientists have suggested that this specialization that served them well for thousands of years was what led to their eventual extinction (Kuzmin 2009). In their prime, woolly mammoths spanned large parts of Europe, Asia, and North America, but by about 12,000 years ago, they were essentially extinct throughout most of Europe, existing mostly in Siberia until about 9,700 years ago (Kuzmin 2009). By that time, they were functionally extinct on mainland Siberia, and were then found on only a few islands in

the Arctic Ocean. The most famous of which was Wrangel Island, which is widely believed to be the last known place where mammoths existed until their complete extinction 3,700 years ago (Hofreiter and Lister 2006; Kuzmin 2009). The current hypothesis about the downfall of the Wrangel Island mammoths was that they faced a genetic bottleneck effect and this reduction in diversity dealt the last blow (Palkopoulou et al. 2015).

Humans have been pointed to in the debate over what led to the extinction of the woolly mammoth. This is often because of the relationship between the species that is well documented in cave art from the time. While some believe hunting of mammoths by humans was the last straw, others have pointed out the statistical unlikelihood that hunting had a significant impact on their numbers, particularly when considered in the context of the end of the ice age. Interestingly, there is a geographic divide between scientists who stand by the hunting hypothesis and those that disagree; those from Europe tend to accept the hypothesis, while those from Siberia do not (reviewed in Kuzmin 2009). This divide may be due to differences in environmental stressors. Even toward the end of the ice age, Siberia was a harsher environment, and thus, it may have been in the interest of the people living there to coexist with the mammoths rather than to extensively hunt them (Kuzmin 2009). Mammoths were critically important to humans at the time, not necessarily as a food source, but as a supplier of different resources. Much like modern elephants, mammoths were important ecosystem engineers in creating pathways through the environment. Additionally, they were great sources of dung, which was often used as fuel for fires (Pitulko and Nikolskiy 2012).

Approximately 15,000 years ago, the climate started to warm, causing temperate forests to spread north into the previously uninhabitable regions that made up the mammoth steppe (Hofreiter and Lister 2006). This change in landscape drastically reduced the available grassland upon which the woolly mammoth relied. This process is known as extinction lag, which is an extinction of a species characterized by expansive

net reduction in habitable range over thousands of years (Lister and Stuart 2008). By the start of the Holocene 10,000 years ago, trees and shrubs were well on their way to becoming the predominant foliage in the mammoths' range, while grasses and dwarf shrubs were quickly losing their hold on the landscape. There is a general consensus that the extinction of the woolly mammoth was closely correlated with the decrease in the mammoth steppe as the earth began to warm following the ice age (Kuzmin 2009).

As the mammoth steppe became more and more fragmented by the encroaching temperate forests, populations of the woolly mammoths were forced to become more and more concentrated in the remaining territories (Maschenko 2002). The overpopulation of small areas likely led to dramatic reductions in the numbers of both mammoths and other large herbivores of the time. This ecological pattern has been observed in modern African elephant populations when they are driven into small territories. The rapid increase in population density causes a crisis in the plant community as consumption goes into overdrive, quickly rendering the environment barren and unsustainable (reviewed in Maschenko 2002).

It is evident that changing landscapes due to changes in the global climate struck a disastrous blow to the species. While the severity of the impact that human actions had on the mammoth population is debated, it is plausible that they may have added strain to an already crippled population (Nogues-Bravo et al. 2008). Regardless of what struck the final blow to the woolly mammoth, it is clear that their extinction was a complex process that happened over thousands of years.

## Conclusion

The woolly mammoth is one of the most well-known and well-studied extinct mammal species. Their pristine fossil record has allowed scientists to extensively study their evolution, life history, and eventual extinction. As a hallmark of the ice age, they exhibited several morphological and behavioral adaptations to life in the harsh climate

of the mammoth steppe. Despite some differences, there are a number of parallels that can be drawn between woolly mammoths and extant elephant species. This has allowed scientists to reasonably draw conclusions about their life histories. In the same way that conclusions can be drawn about the woolly mammoth from modern elephants, it may be possible to do the inverse, using what is known about the demise of the woolly mammoth to avoid the same fate befalling the extant members of the Elephantidae family.

## Cross-References

- [Elephant Life History](#)
- [Proboscidea Cognition](#)
- [Proboscidea Diet](#)
- [Proboscidea Locomotion](#)
- [Proboscidea Morphology](#)

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## Working Dogs

- [Service Dogs](#)

## Working Memory

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## Definition

Working memory is a system of memory that stores a few pieces of information for a few seconds. However, unlike short-term memory, working memory is capable of operating and manipulating stored information.

## Introduction

The study of human memory, and in particular the study of working memory (WM), is not an easy

task. Most of the time, researchers have to infer how this process works through participants' behavior in experimental tasks or more recently through their brain activity. Usually, when a considerable amount of new experimental data about memory or any other mental process is available, researchers create models that attempt to explain the observed behavioral data. These models can then be used to generate new hypotheses, which can then be experimentally investigated.

One of the most influential models in early memory research was proposed by Atkinson and Shiffrin (1968). Also known as the multi-store model or the modal model, it assumes the existence of three systems of memory that are relatively independent: sensory memory (SM), short-term memory (STM), and long-term memory (LTM). According to this model, external information is detected by the sensory organs and transferred directly to SM. The information is stored in SM for just a few tenths of a second, but that information might be transferred to STM if attention is paid to it. STM is a limited storage that can keep a few items of information active for a few seconds. Although it depends on some factors, like the kind of information, the state of the participant, and the demands of the task, it is usually assumed that STM could store  $7 \pm 2$  items, which is referred to as Miller's law (Miller 1956). According to this model, only the information active in STM could be recalled consciously by participants. The third information storage unit, LTM, is defined as an unlimited store in which information could be kept indefinitely. This model proposes that through rehearsal or repetition, information could be transferred to LTM from STM. Finally, this model also assumes that the information stored in LTM could also be retrieved from STM for its recall.

The Atkinson and Shiffrin's model explained much of the data that were available when it was originally formulated; however, there is a data that the model cannot explain. For example, Shallice and Warrington (1970) described a patient with deficits in STM but with apparently intact LTM. According to Atkinson and Shiffrin's model, if the STM is damaged, the information could not be transferred to LTM because STM is the only access to LTM. Moreover, that model assumes

that only by repetition, can the information be transferred from STM to LTM. However, Craik and Lockhart (1972) showed that the depth of information processing is more important than the repetition of the information to transfer information to LTM. Nevertheless, Atkinson and Shiffrin's model was relevant in the psychology of memory because it assumes the existence of different memory systems; it explains how they interact with each other and highlights the importance that other processes like attention or repetition have within the memory.

Some experimental results suggested that, in some cases, memory is not only a mere information store in which information is collected and retrieved. In contrast, memory could also manipulate the information stored. We manipulate the information that we have in the memory, and as a result of this manipulation, new information is generated. For example, we can learn a list of numbers (e.g., 3–2–1–5–4) and repeat it after a few seconds. We can also add to these numbers and get to a result (e.g.,  $3 + 2 + 1 + 5 + 4 = 15$ ). It is assumed that the first task (to memorize and recover) is conducted by STM, and the second task (manipulation of the information) is performed by WM. Below the different approaches of WM will be discussed; for now it is enough to know that WM is a store of information of limited capacity that allow the manipulation of information unlike other systems of memory such as SM, STM, or LTM.

## Multicomponent Model of Working Memory

Although the term WM was first introduced by Miller et al. (1960), our understanding of it is primarily due to the contribution of Baddeley and Hitch (1974) who developed the multicomponent model (for a new version of multicomponent model, see Baddeley 2000). Whereas Atkinson and Shiffrin's model hypothesizes the existence of a single short-term storage, where all kinds of information are stored, the model proposed by Baddeley and Hitch (1974) assumes that the information is collected in independent short-term storages according to if the information is

visual or verbal (or episodic in the new version of the model proposed by Baddeley 2000). According to that, Baddeley and Hitch (1974) proposed the existence of two components that store the information in WM: the phonological loop and the visuospatial sketchpad. Also, these authors proposed that a third component manipulates the information stored in phonological loop and in visuospatial sketchpad: the central executive.

The phonological loop maintains active verbal information through two subsystems: a short-term storage and an articulatory rehearsal. The short-term storage keeps verbal information active for just a few seconds, whereas the articulatory rehearsal repeats the information stored in short-term storage (like an internal speech) to maintain it as active. Some experimental effects support the existence of the phonological loop. For example, the phonological similarity effect (Conrad and Hull 1964) shows that if participants have to learn a list, which contains items that are phonologically similar (e.g., cat, tap, lap, rap), the recovery accuracy will be lower than if the items are phonologically different (e.g., two, tip, pot, lip). It is assumed that the similarity between items makes the articulatory rehearsal more difficult, which will lead to the recovery disruption. Also, if participants repeat an irrelevant word (e.g., the, the, the, the) while they are memorizing a list of items, later retrieval of the list will be less effective (Vallar and Baddeley 1984). According to Baddeley and Hitch's model, this activity, repeating an irrelevant word, will suppress the articulatory rehearsal, and therefore, the recovery accuracy will decrease.

In contrast, visuospatial sketchpad stores visual and spatial information. For example, remembering how many doors there are in the house that we lived in 10 years ago is a task that requires a visuospatial sketchpad. Like phonological loop, that component of WM is limited in capacity; it's assumed that it could operate with three or four objects at the same time. For this reason it can be disrupted by requiring participants to tap repeatedly a specified pattern of keys or locations, a procedure that impairs the use of visuospatial imagery (see Baddeley and Lieberman 1980). Logie (1995) proposed a

structure of visuospatial sketchpad that, like phonological loop, is formed by a passive storage and a rehearsal mechanism. The first would keep the information active, and the second would be a repetition of a mental scanning of the visual representation.

Whereas the function of the phonological loop and the visuospatial sketchpad is only the mere storage of the information, the central executive (the third component of the multicomponent model) supervises and manipulates the information that is collected in these two interfaces of working memory. In other words, according to this model, the central executive adds, deletes, and reorders information stored in the phonological loop and in the visuospatial sketchpad (and in the episodic buffer according to the revised multicomponent model proposed by Baddeley 2000), selecting the significant information that ultimately guides behavior, recovering information from LTM, and solving which information should be stored in LTM and which information should be discarded. Some researchers suggest that the central executive is also involved in cognitive functions like to process sensory information and store information in LTM and retrieve it (Gluck et al. 2009), setting goals and plans (Linnenbrink et al. 1999), task switching (Rouder et al. 2011), or stimulus selection and response inhibition (Kiyonaga and Egner 2014).

Although the multicomponent model predicted and explained a considerable amount of data found until the 1970s, it was unable to explain some effects like the resistance in serial recall to articulatory suppression or the improvement in the recall when items are integrated in some way (e.g., when they rhymes) instead of when they are unrelated, among others. Aiming to solve some of these limitations, Baddeley (2000) proposed a fourth component for the model that was not included in the original version of Baddeley and Hitch's (1974) model: the episodic buffer. This component is a multidimensional storage that keeps visual, spatial, and verbal information, combining it in chunks or episodes and maintaining it temporarily. According to Baddeley (2000), information is transferred to the episodic buffer not only from the phonological



loop and from the visuospatial sketchpad but also from LTM. As with the other two storage components of the model (the phonological loop and the visuospatial sketchpad), the episodic buffer is also controlled by the central executive. Also, Baddeley (2000) argued that the episodic buffer seems to play an important role in consciousness and awareness and that it contributes to the online maintenance of integrated memory traces. The revised multicomponent model proposed by Baddeley not only differs from the original model (Baddeley and Hitch 1974) by the presence of episodic buffer, but it also assumes the existence of a connection between the phonological loop and LTM. However, although the major evidence for this modification comes from the verbal domain, it is probable that the equivalent visuospatial linking to LTM also exists (Baddeley 2001).

## What Is Working Memory?

It is important to note that the definition of WM is not unanimous across authors. In contrast to other memory terms (like, e.g., LTM which most authors agree upon), WM is defined differently depending on the author and the consulted text. For example, in some texts WM and STM are used synonymously. This is the case for the Atkinson and Shiffrin's model (1968) which makes no distinction between these two memory systems. Other authors have used WM to explain the maintenance of information across some trials conducted in the same day (Olton 1979). According to the evidence found in the studies conducted in the last decades, these two definitions of WM have been rejected. Nowadays, most authors define WM as a memory system that stores a few pieces of information for a few seconds but that it differs from STM in that WM manipulates the information, whereas STM is only a storage component with no modification of the information. This vision of WM is the one that has received the most theoretical and experimental support.

However, it's unclear whether WM should replace STM or if these two systems of memory

may cohabitate and operate independently. In situations where there has no manipulation of information, both systems, WM and STM, are experimentally undifferentiable. According to that, instead of assuming the existence of both, WM and STM, it could be reasonable, and more parsimonious, to assume that there are no two systems of memory but just only WM. According to that there are two different kinds of tasks: tasks in which the WM operates with information and tasks in which WM does not manipulate any information. This idea, that makes STM useless, is supported by the Baddeley and Hitch's model assuming that tasks in which it is necessary to operate with information require the central executive to be active; in contrast, when no operation with the information is required and it needed just the storage and retrieval of information, the central executive will be deactivated.

Other authors consider WM not as a memory system like STM or LTM but rather as a mental process or a set of different processes. Moreover, they acknowledge that, like an independent cognitive system, WM allows us to handle information that is being processed (e.g., Miyake and Shah 1999). This is the newest approach to the study of WM. Unfortunately, there are not yet formal studies that have confirmed whether the nature of WM is a comparable memory system to STM or LTM or an independent process (for other definitions of WM, see Cowan 2008).

Finally, Ericsson and Kintsch (1995) proposed that WM could also operate within LTM, and they introduced the concept of *long-term working memory*. These authors suggested the existence of structures of information in LTM that provide participants the skills needed to perform specific tasks. When participants conduct a task, they retrieve the structures of information involved in it from LTM to WM. In WM these structures could change with practice becoming more suitable to this task. After, they are stored again in LTM. That process explains how participants to improve their execution in specific task throw practice. This idea account for the apparent efficiency of WM and the capacity of information processing that experts have in their specific areas. For example, professional chess players

could analyze their game much faster and more intensely than amateur players can.

## Working Memory Capacity

In contrast to other memory systems such as SM or LTM, WM has a limited capacity. Although WM span depends on variables like the age of participants, the task, and the materials used to measure it, among others, it has been proposed that, like STM, WM can handle  $7 \pm 2$  items (Miller 1956). However, some authors argue that WM operates with chunks of items instead of isolated items. For example, Cowan (2001) proposed that WM operates with a maximum of four chunks of items. The limitations of WM capacity and the WM span variability among people have led to some authors to hypothesize that WM is related to other aspects of cognition like reading (Swanson 2006), language (Archibald and Gathercole 2006), or mathematical skills (Passolunghi 2006). This idea suggests that WM span is a good predictor of a person's performance in other cognitive tasks. For example, in a seminal work, Daneman and Carpenter (1980) showed that WM capacity correlated with text comprehension. Some authors have suggested that improving WM capacity through training would also improve other aspects of cognition (e.g., Shipstead et al. 2010). However, a recent meta-analysis conducted by Melby-Lervag et al. (2016) suggests that it is still uncertain whether WM training is directly linked to improving cognition skills.

## Where Is Working Memory in the Brain?

With advances in neuroimaging techniques, recent research has attempted to identify the neuroanatomic correlates of WM. In particular, most of the authors have investigated which brain areas are related, or controlled, to the different components of the multicomponent model. For example, Paulesu et al. (1993) found that the area between the parietal and temporal lobes in the left hemisphere seems to be responsible for phonological

storage and that Broca's area is responsible for subvocal rehearsal. In the other hand, Smith et al. (1996) found that in visual tasks the right hemisphere was more active than the left. Furthermore, the frontal lobes, especially the activation of the prefrontal cortex, seem to be important for WM. For instance, Owen et al. (1996) found that the dorsolateral prefrontal cortex is used in tasks where the central executive is related. The left prefrontal ventrolateral cortex is correlated with the phonological loop, and it is divided into two areas: anterior, that handles semantic information, and posterior, for phonological information. In contrast, the right prefrontal ventrolateral cortex has been paired with a visuospatial sketchpad. The only component of WM that seems not to be controlled by frontal brain areas is the episodic buffer that seems to be controlled by left anterior hippocampus, in medial temporal lobe.

To sum up, it seems that most of WM functions are controlled by frontal brain areas, especially by prefrontal cortex. While left prefrontal cortex is associated with verbal WM, the right prefrontal cortex is responsible of visuospatial WM. Finally, dorsolateral prefrontal cortex controls the central executive and left anterior hippocampus, the episodic buffer.

## Cross-References

- Cognition
- Declarative Memory
- Long-Term Memory
- Memory
- Rehearsal
- Short-Term Memory

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## World

### ► Nature Versus Nurture

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## World Wildlife Fund (WWF)

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### Introduction

The World Wide Fund for Nature (WWF) is a charitable trust working in environmentalism, conservation, and ecology. The organization's mission statement is to conserve nature, to reduce the most pressing threats to the diversity of life on Earth, and to create a sustainable future where humans live in harmony with nature. It was established on April 29, 1961, by Prince Bernhard of Lippe-Biesterfeld; Prince Philip, Duke of Edinburgh; Julian Huxley; Max Nicholson; Peter Scott; Guy Mountfort; and Godfrey A. Rockefeller. The organization was originally established as World Wildlife Fund before changing its name in 1986. World Wildlife Fund is still the organizations' operational name in the United States and Canada. The first WWF office opened on September 11, 1961, in Morges, Switzerland. The current headquarters is in Gland, Vaud, Switzerland.

In order to achieve its mission statement, WWF formulated initiatives which address priority areas and species in need of research and conservation. These initiatives are based on six major goals and cover three main drivers of environmental problems. The six major goals include forests, oceans, wildlife, food, climate and energy, and freshwater, while the main drivers of environmental problems have been identified as markets, finance, and governance. The organization uses multidisciplinary research to form cutting-edge conservation tools and methods, increase connectivity in natural and social systems, and tackle

emerging threats imposed on our natural systems. The initiatives are strategically implemented through advocacy, policy reformation, and research conducted by a large network of researchers, partners, stakeholders in businesses, academia in partnership, and civil society which extends from local to global scales.

### History

The intended purpose in establishing WWF was to act as a funding institution for existing conservation groups. At the time, groups such as the International Union for Conservation of Nature and Natural Resources (IUCN) and the Conservation Foundation were carrying out conservation projects throughout the world. The idea of establishment was borne from the vision of Victor Stolan, Sir Julian Huxley, Sir Peter Scott, and E.M. Nicholson. Although each person came from diverse fields, together, combined decades of experiences documented in a pledge called the "Morges Manifesto" (WWF 1961). This main document elaborated the fund's commitment to assisting conservation causes.

Within its first year of establishment, the organization had supported working projects on the red wolf in the United States, the Tule goose in Canada, the Hawaiian sea bird, and the giant grebe of Guatemala. It then expanded its projects around the world, in Africa, Latin America, and Asia. In 1962, WWF gathered funds to establish the Charles Darwin Foundation Research Station in the Galapagos Islands. By 1975, WWF expanded its organization's scope to not only focus on species-related projects but also to carry out initiatives which also protected habitats through actively supporting the establishments national parks and nature reserves around the world.

The Conservation Foundation, an institution based on conservation policy, was also a vital partner which supported the formation of WWF. The Conservation Foundation was founded in 1948 by Fairfield Osborn as an affiliate organization to the New York Zoological Society (known today as Wildlife Conservation Society), with its primary goal to protect the world's natural

resources. The Conservation Foundation was formed of an advisory council of leading scientists including Charles Sutherland Elton, G. Evelyn Hutchinson, Aldo Leopold, Carl Sauer, and Paul Sears (Peahike 2013). The Conservation Foundation highlighted many of the issues faced in the twenty-first century, for instance, in 1963, the Conservation Foundation held a conference which published findings warning against anthropogenic global warming. In 1985, the Conservation Foundation became an affiliate of WWF, where it operated with the same staff but under a separate legal entity. Subsequently in 1990, the Conservation Foundation merged into WWF.

As the organization expanded, WWF set up offices and operations around the world. As the network and resources increased, the operations expanded into new areas of research, such as the preservation of biological diversity, sustainable use of natural resources, and reduction of pollution and climate change. In the 1980s, the organization strategized its projects and activities further and, in 1990, revised its mission statement three-fold. In the new updated mission statement, the organization aims to stop the degradation of the planet's natural environment and to build a future in which humans live in harmony with nature, by conserving the world's biological diversity, by ensuring that the use of renewable natural resources is sustainable, and by promoting the reduction of pollution and wasteful consumption. WWF obtained general consultative status from UNESCO in 1996.

The iconic giant panda was designed by Sir Peter Scott after a panda named Chi Chi which had been sent from Beijing Zoo to London Zoo in 1958. At the time, Chi Chi was famous for being the only panda residing the western region. Although the logo had gone through changes and redesigns over time, it is undeniably one of the most recognizable symbols of conservation and of the organization.

## Current Projects in the Twenty-First Century

The WWF is the world's largest conservation organization, with over five million supporters

worldwide and works in more than 100 countries and on 1300 projects (WWF 2019). The organization income is earned mostly from individual memberships and donations (35%) followed by in-kind and others (26%) and government grants (14%) (WWF-US 2018). In 2018, 84% of spending was directed to worldwide conservation (WWF-US 2018).

WWF's mission specifically focuses on restoring populations of 26 species (species or groups of species) which have been identified as vital to their ecosystems and to people, such as elephants, tunas, whales, dolphin, and porpoises. Furthermore, in a first of its kind worldwide biodiversity analysis, WWF scientists and experts identified ecoregions which represent biologically outstanding and unique ecosystems of terrestrial, freshwater, and marine habitats. In 2018, WWF identified 1480 ecoregions based on complex patterns of the natural ecosystems using factors like climate, geology, and the evolutionary history of the planet.

In addressing environmental problems of biodiversity loss and unsustainable use of natural resource, including finance and business practices as well as consumption choices, WWF launched multiple public campaigns to influence decision-makers, inform on policy changes, and conduct behavioral change campaigns to encourage people to live in a more environmentally friendly manner. WWF encourages people to be actively involved and donate funds to protect the environment.

Science is a large vital component of WWF's conservation work. The organization elaborates that the role of scientists is vital in developing innovative approaches to apply the best available information. Notable global campaigns include Debt-for-Nature Swap, Earth Hour, and Marine Stewardship Council. Debt-for-Nature Swap, for example, was implemented in 1987 in Ecuador. The project facilitated in buying of a countries' foreign debt at a discount, in order to convert the funds to local currency and using the money earned to finance conservation efforts. The Earth Hour is an example of a global movement carried out globally to raise awareness for energy consumption and effects on the environment. Furthermore, the WWF collaborates with local



populations, governments, and nongovernmental organizations to implement their initiatives. WWF also formed partnerships with global organizations such as the United Nations, the World Bank, and the European Union.

## Research Areas

WWF's conservation strategy is focused on six major goals. Food is one of the six key areas. The organization aims to fund projects which help to double net food availability while freezing its ecological footprint in a three-way approach: firstly, increasing efficiency and sustainability of food production addressing how food is grown and farmed; secondly, evaluating consumption and encouraging sustainable diets; and thirdly, zeroing in on food waste by ensuring that food is eaten and not wasted. By establishing a sustainable food system, food security can be safeguarded.

For climate, WWF aims to create a climate-resilient and zero-carbon world powered by renewable energy. In order to achieve a low-carbon future, WWF works together with finance institutions to produce attainable climate solutions, use alternative fossil fuels, disperse clean energy technologies, and restore forests. Furthermore, the organization aims to work alongside and assist businesses in order to achieve goals in cutting down carbon emissions.

Freshwater is one of the world's most shared vital resources. As a result, WWF has established a goal to increase freshwater security for people and nature through protecting fresh bodies of water and keeping rivers free flowing. Wetland restoration and protecting vital organisms living within the habitats such as river dolphins and sturgeons are also vital components of the goal. The Freshwater Report produces a summary of conservation projects carried out in over 50 countries. Water stewardship and collective responsibility for shared water resources among businesses and local stakeholders are essential in management of freshwater ecosystems.

One of the main areas of work WWF is known for since its establishment is the projects involving

wildlife. The goal to protect the worlds' most important species still remains today. In ecosystems that range from the poles to the tropics, WWF strives to preserve vital habitats by addressing protected area management. Legal and illegal wildlife trade and unsustainable wildlife consumption are also key issues threatening wildlife in the twenty-first century which are addressed. WWF works directly through related agencies and organizations to strengthen regulations, enhance monitoring tools, and provide support to law enforcement. On the other hand, in recognizing the importance of market and consumer behavior which drive demand for wildlife products, WWF also works in multiple awareness programs aiming to change consumer behavior and cultural perceptions.

Forests are also one of the six goals of WWF. The organization aims to address issues of deforestation, climate change, and forest transformation. Challenges in the forest sector are tackled using cutting-edge science in collaboration with stakeholders. WWF aims to protect the world's most important forests by increasing protected areas, improving forests under management, stopping illegal unregulated deforestation, and restoring forest landscape and connectivity.

The final goal of study by WWF is related to oceans and marine ecosystems. The organization aims to safeguard healthy marine ecosystems through management of reef mangroves, improving coastal areas, reducing pollution, and supporting sustainable fisheries. Plastic pollution in the ocean is a big concern addressed on a global scale. Working closely with stakeholders ranging from fishing communities, businesses, and governments can lead reduce the number of damaging activities imposed on marine environments. Restoring coastal environments such as coral reefs and mangroves is also a critical component in achieving the goals.

## Reports

Since 1998, WWF has produced the "Living Planet Report." It is a science-based assessment report released every 2 years based on the Living Planet Index and ecological footprint calculation.

The Living Planet Index measures trends based on data from populations of mammals, birds, reptiles, amphibians, and fish species across the world. The importance of this report is to review impact of human activity on the planet using science-based approach and analysis. Each report summarizes findings and offers suggestions in review of current efforts in achieving goals within environmental treaties and agreements made, such as the Convention on Biological Diversity, the Paris Climate Agreement, and the Sustainable Development Goals (WWF 2018). Latest trends show a decline of 58% of species between 1970 and 2012 (WWF 2018).

A key outcome of publishing reports is to raise awareness and provide information for policy- and decision-makers. WWF offices which operate globally aim to run alongside national councils, acting as support advisory groups. WWF works closely with national and international lawmakers to adopt, enforce, strengthen, and/or change policies or laws, supported by ground findings and scientific process and tools and methods. The organization addresses conservation issues in a multifaceted approach, working with every sector, whether it is to help educate and influence

people into making sustainable choices, or making businesses have accountability in the impact on natural resources use, or to push and ensure that governments commit to international initiatives to protect biodiversity and natural resources.

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### ► Conservation

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# X

## Xenophilia

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### Synonyms

[Friendliness](#); [Openness](#); [Prosociality](#); [Tolerance](#)

### Definition

Attraction to and/or positive behavior toward strangers.

### Introduction

Xenophilia has only rarely been documented in nature. Because strangers often represent a threat to one's resources, territory, and mating success, there is often little evolutionary payoff for acting prosocially toward unknown individuals, and potentially great costs for doing so (Temeles 1994; Wilson 1975). However, there are some circumstances where natural selection has favored positive interactions with strangers.

## Mating

As a mechanism to avoid inbreeding in social living animals, young males or females may disperse to a new social group (Clutton-Brock 1989). Although the introduction of a stranger to a group can result in aggression and tension (Fragaszy et al. 1994), it is not unusual for opposite-sex individuals to be attracted to the newcomer, and in some cases may even protect them from attacks from other members of the group (Wade 1976). Even species that show highly xenophobic responses may show lower rejection of opposite-sex strangers due to the reproductive opportunity they represent (Spinks et al. 1998), especially during breeding season (Bernstein and Gordon 1974).

## Genetic Relatives

Hamilton (1964) predicted that animals should be prosocial and cooperative with strangers with whom they share genes. This is because helping kin to survive and reproduce increases one's indirect fitness, as the genes that are shared with the relative will have a higher probability of being passed on. However, kin selection requires the

ability to recognize genetic relatives. In some species, only conspecifics with whom individuals live with are treated as kin (such as nestmates), but other species are able to recognize unfamiliar individuals as genetic kin through scent, visual characteristics (e.g., phenotype matching), or other cues (Hepper 1986).

## Domestication

It has been argued that the main components necessary for domestication are increased tolerance and reduced aggression (Hare et al. 2012). A prime example is that of domestic dogs (*Canis familiaris*) which often enjoy socializing and playing with unfamiliar dogs, as exemplified by the popularity of public dog parks (Shyan et al. 2003). This behavior contrasts with that of wolves (*Canis lupus*), which are known to fight neighbors and engage in lethal raiding (Mech 1994). This type of xenophilic behavior shows remarkable individual differences, and has been captured in dogs by the personality trait of “sociability” (Svartberg and Forkman 2002) or “amicability” (Ley et al. 2008).

In an ongoing experimental project begun in 1959 by the geneticist D. K. Belyaev and continued by his assistant L. Trut, foxes (*Vulpes vulpes*) were selectively bred according to their aggressive response to humans. Foxes that were selected for tolerance began to show increasingly “dog-like” traits, including increased sexual activity, depigmentation, floppy ears, and curly tails (Trut et al. 2009). Thus, xenophilia may not only be a consequence of domestication, but the driving force behind it.

The only primate aside from humans known to routinely engage in xenophilic behavior is the bonobo (*Pan paniscus*), a great ape closely related to the chimpanzee. Hare et al. (2012) have made the case that the bonobo serves as an example of “self-domestication,” as bonobos share many traits in common with domesticated animals, such as a juvenilized appearance, depigmentation, and more frequent reproduction, in addition to reduced aggressiveness. Bonobos are known to play and copulate with members of strange groups, and although they also can engage

in hostile displays, physical contact is rare and lethality unknown. Several studies have demonstrated a preference for strangers over groupmates in bonobos, even at personal cost (Hare and Kwetuenda 2010; Tan et al. 2017). According to the first impression hypothesis, bonobos may favor strangers because they have the potential to become new long-term allies (Tan et al. 2017).

## Unicoloniality

Invasive introduced Argentinian ants (*Linepithema humile*) in Europe and North America appear to have lost their ability to recognize non-nestmates, and thus tolerate strange ants that they used to display xenophobic aggression toward. Starks (2003) has suggested that this tolerance developed because their new environments were so resource rich that aggression toward strangers became too costly and consequently selected against. The result has been the creation of vast “supercolonies,” which have been known to range over hundreds to thousands of kilometers. However, whether this type of unicoloniality can truly be said to be xenophilia is debatable, especially as members of supercolonies are also still aggressive against members of other supercolonies.

## Conclusion

The rarity of xenophilia makes it a phenomenon that has been little studied. However, it is clearly possible for xenophilia to develop under unusual selective pressures (introduction to a novel environment, domestication) or in certain circumstances where the benefits outweigh the costs (reproductive opportunities, helping kin). The genetic, physiological, and behavioral underpinnings of xenophilia remain to be examined in more detail.

## Cross-References

- [Domestication](#)
- [Kin Selection](#)
- [Xenophobia](#)

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## Xenophobia

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## Synonyms

Antipathy; Intolerance; Prejudice

## Definition

Fear and/or intolerance of strangers, often expressed as aggression or aversion.

## Introduction

Dislike for strangers is pervasive throughout the natural world. The introduction of a strange individual often provokes the strongest aggressive responses in animals; a phenomenon termed the “xenophobic principle” by E. O. Wilson in 1975. Strangers can be a threat to one’s territory, resources, status, or mates, and consequently there is selective pressure against tolerating unknown individuals, as the costs vastly outweigh the benefits (Wilson 1975).

The result is that animals may threaten, harass, or even attack strangers. Animals may go great



lengths to avoid areas where strangers may encounter each other; at territory borders, “buffer zones” of increased prey/plant density may be created by such avoidance (Mech 1994). Borders may also be patrolled and marked to ward off intruders, or calls used to advertise the occupation of a territory (Hardouin et al. 2006; Mech 1994).

While territorial species are essentially xenophobic by definition, many group-living species are also prone to aggression towards outsiders. This is because a newcomer represents a threat to each individual’s status in the group hierarchy, thereby upsetting the existing social order (Bernstein and Gordon 1974). It is common for group members to ally with each other against intruders, including with individuals that are typically shunned (Wade 1976). Even if a group is not overtly aggressive, members may increase grooming each other in the presence of strangers, either to consolidate bonding or to make the bond more evident, in what has been term a “social shield” (Antonacci et al. 2010). After a new member joins a group, although they may appear to be tolerated, it can take months for social interactions to return to baseline levels (Fragaszy et al. 1994).

### Resource Availability

The cost of tolerating strangers varies according to the resources available. Populations of the same species may be more xenophobic in harsher, resource-poor environments, where protection of resources outweighs any potential benefits from interactions with strangers, such as reproductive opportunities (Spinks et al. 1998).

Similarly, the toleration of neighbors appears to vary depending on the level of threat they pose to an individual. In cases where there is intense competition, the result can be “nasty neighbors” (Müller and Manser 2007). However, when a neighbor poses less of a threat than a stranger, a “dear enemy” situation may arise (Fisher 1954). For example, a stranger may threaten a territory owner’s resources and territory, while a neighbor may only threaten its resources, since the neighbor already has its own territory. In this case, the

benefits of tolerating the neighbor outweigh the cost of constant vigilance and aggression (Temeles 1994). Having a neighbor that is a “dear enemy” also increases the value of the territory to the territory holder, compared to a new occupant that will have to negotiate with a new neighbor. Indeed, in great tits (*Parus major*), it has been found that new occupants initially fight more often with neighbors than the previous residents (Krebs 1982).

### Lethal Raiding

Extreme xenophobic aggression towards neighbors may take the form of “lethal raiding,” in which another group’s territory is entered and individuals are attacked by a coalitionary group. Goodall (1986) implied that chimpanzees are motivated to engage in lethal raiding due to the low cost to the aggressor, a hypothesis later developed as the “imbalance-of-power hypothesis” (Manson and Wrangham 1991; Wrangham 1999). This hypothesis predicts that attacks occur only if the raiding party has superior numbers or strength, which is borne out by field observations that have found attacks only on solitary animals or pairs by groups of at least three or more males. For safety, chimpanzees should travel in large groups, which they tend to do near borders. However, the ecological pressures of having to share limited resources (scramble competition) means that in times of reduced food availability, chimps may be forced to travel in smaller groups (Manson and Wrangham 1991). Consequently, large social networks with variation in subgroup size (fission-fusion societies) are necessary for lethal raiding, and indeed coalitionary group killing has been seen in other fission-fusion societies, such as wolves (Mason and Wrangham 1991; Mech 1994).

### Sex Differences

Sex differences in xenophobic aggression vary by species. For example, while only chimpanzee

males engage in lethal raiding and are primarily the victims of such aggression, wolves of both sexes are equally attacked and show similar aggression levels (Wrangham 1999). Whether or not the males or females of a group are aggressive to a newcomer often depends on the newcomer's sex. Sometimes, members of the opposite sex are better tolerated, or even protected from same-sex attacks (Wade 1976). Often, aggression towards strangers of the opposite sex will decrease during breeding season (Bernstein and Gordon 1974).

## Conclusion

The ubiquity of xenophobia appears to stem from the benefits of protecting territories, resources, mates, and group status from outsiders, although exceptions may be made for breeding opportunities, genetic relatives, or neighbors. Xenophobia is a major source of aggression and stress for individuals and groups, and thus an important factor to be accounted for in studies and management of animal behavior.

## Cross-References

- Aggression
- Dear Enemy Effect
- Fission-Fusion
- Territoriality
- Territory Defense
- Xenophilia

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## Xenotransplant

- Xenotransplantation

## Xenotransplantation

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## Synonyms

Organ transplant; Transplant; Transplantation; Xenotransplant

## Definition

Xenotransplantation describes the movement of living cells, tissues, and organs from one species to another to describe as a defined purpose. The term xenograft has been used for the transplantation as well as inserting of organs and tissues from animals to humans. It is different from allotransplantation and autotransplantation. This procedure can overcome the shortage of donor organs. Transplantation of cells, tissues, or organs from a genetically nonidentical donor to a recipient of the same species is known as allotransplantation. Autotransplantation involves the transplantation of cells, tissues, or organs from one part of the body to another in a same person.

## Introduction

Xenotransplantation is the implantation, transfusion, and transplantation of live tissues or organs between species. Transgenic (modified genome containing foreign DNA) pigs are considered as an important animal for xenotransplantation. The structure and size of pig organs are similar enough

to humans, making them suitable for xenotransplantation. For example, pig heart valves are easily transplanted into humans. Research on xenotransplantation includes other organs, such as the kidneys, intestines, livers, lungs, and pancreas. While there are many potential benefits to xenotransplantation, there are also some concerns regarding infection by known and unknown agents.

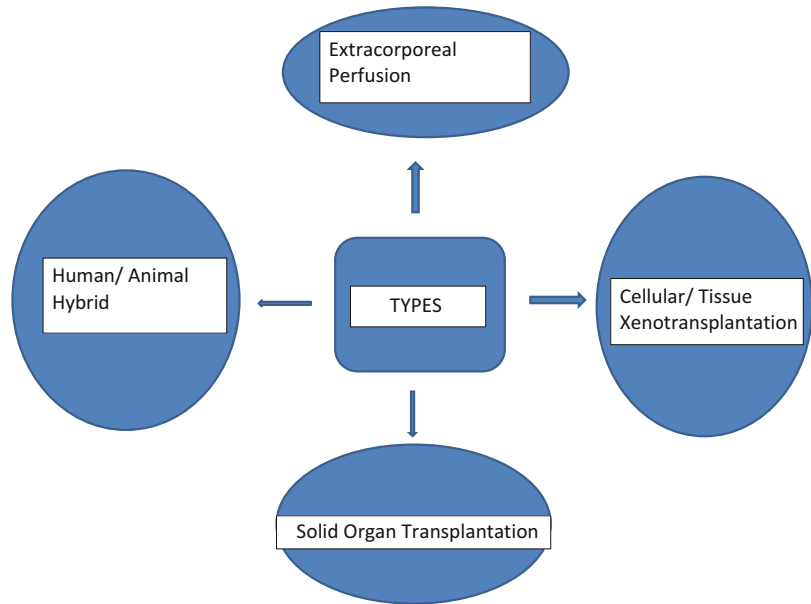
## History

The practice of xenotransplantation began in the 1800s where skin grafts were carried out, but its practical applications are still considered difficult. Skin grafts were carried out in the nineteenth century from a variety of animals, with frogs being the most popular. Hardy in 1964 performed the first heart transplant in a human, using a chimpanzee heart, but the patient died within 2 h. The first chimpanzee-to-human liver transplantation was carried out by Starzl in 1966; in 1992, he obtained patient survival for 70 days following a baboon liver transplant. A rhesus macaque at Emory University lived for 400 days with a pig's kidney xenotransplant (Iwase et al. 2017).

## Types of Xenotransplantation

Xenotransplantation is of Four types as shown in Figure 1.

1. Solid organ transplantation – In solid organ transplantation, the whole organ such as a kidney or liver is transplanted into humans. The evolution of solid organ transplantation has progressed rapidly in the past few decades with incorporation of a variety of solid organs – the liver, kidney, pancreas, heart, and lung – into the donor pool. Porcine heart valve transplant is quite common and successful.
2. Tissue transplantation – Tissue or cells are transplanted to the recipient without any link between the animal blood vessel and the recipient blood vessel in tissue transplantation. For example, islet (pancreatic or insular tissue) tissue transplantation from a fish to a non-human primate.
3. External therapies – In this type of transplantation, the animal organ such as the liver or any

**Xenotransplantation,****Fig. 1** Types of Xenotransplantation. It is an original Diagram

other bioartificial organ circulates the human blood outside the human body.

4. **Human/animal hybrid** – Exposure to living animal-derived material, where human body fluids, cells, tissues, or organs are removed from the body; come into contact with animals cells, tissues, or organs; and are then placed back into a human.

### Barriers to Transplantation

- **Chronic Graft Rejection** – It is caused by multiple factors like antibodies and lymphocytes. Chronic graft rejection was seen in some pig cardiac xenografts. In baboons, pig cardiac xenografts lasted more than 3 months before the grafts were rejected, which functioned in baboons for greater than 3 months. Allo-transplantation leads to pathological changes in organs (Abbas and Lichtman 2005). Even after 2 years, graft vasculopathy (extended form of coronary artery disease) was not observed in the heart grafts of genetically modified pigs.
- **Cellular Graft Rejection** – The rate of cellular graft rejection for xenografts is greater than allografts (Doodeniya and Warrens 2003). Cellular graft rejection acts against the pancreatic islets, cornea, and red blood cells of pigs.

With the help of insulin-specific promoter, the desired gene can only be expressed in islets of Langerhans. Cellular grafts can be inhibited by immunosuppressive agents.

- **Hyperacute Xenograft Rejection** – Hyperacute xenograft rejection occurs when a pig organ is transplanted into humans. Hyperacute xenograft rejection is an immediate response that occurs within minutes when pig organs are transplanted into humans. These grafts are rejected within 24 h because they bind to various antibodies, such as IgM (immunoglobulin M), IgG (immunoglobulin G), and IgA (immunoglobulin A) (Taylor 2007).
- **Acute Humoral Graft Rejection** – Acute humoral graft rejection is similar to hyperacute graft rejection because it occurs very soon after transplantation. It is associated with antibody deposition that will activate the endothelium cells which in turn will affect infiltration of grafts through innate immune response and finally the graft gets destroyed.

### Advantages and Disadvantages of Xenotransplantation

#### Advantages

Xenotransplantation has numerous advantages, particularly in medical scenarios. Patients in

need of organs, for example, are more likely to receive them. This could cut down on the number of people on waiting lists and the amount of time they have to wait. Unfortunately, organs are a scarce supply, and patients' age is one of the factors that decides whether or not they will receive an organ. Because older patients survive for a shorter period of time than younger people, they are less likely to obtain organ donations. As a result, some people believe that organ donations to the elderly are a "waste" of a perfectly good organ. Xenotransplantation may enhance organ donation, making it more common. Pig organs will be more flexible with age constraints, allowing elderly patients who might usually be turned down for benefits of transplantation (Groth 2007). Many of the ethical issues that come with using organs from deceased donors will be avoided. Xenotransplantation would also allow for the pre-planning of high-quality organ transplants and the use of immunosuppressive medicines to prepare potential recipients for the procedure.

### Disadvantages

Approximately 25 of the known diseases get transferred from pig to man. Xenotransplantation brings about a lot of moral issues; many people think that using animals for the benefit of mankind is exploiting them against nature for our own needs. Animal organs have a much shorter life span than humans; if these organs get transplanted in humans, then definitely they will be dying prematurely. Therefore more and more organs will be needed for transplantation. Strong anti-rejection drugs will be needed to suppress immunity and also to make sure that it does not pose any threat to human life. Medications are poorly accepted, and most of the transplantations were not proved to be very effective.

Some ethical aspects come into the picture like animals experience both physical and psychological pain. Animals have a right to life as well. Why should animals suffer as a result of humans? The other major concern is that the majority of Jewish people did not want any part of the pig transferred. Cow transplantation is prohibited in Hinduism because it is regarded as a sacred animal.

### Statistics/Literature Available

Iwase et al. investigated the transplantation of hepatocytes from genetically engineered pigs to baboons in 2017. Oral drug administration was an issue prior to pre-clinical transplantation treatment, but Kim, Shin, and Min investigated the implantation of a gastrectomy tube for long-term medication administration in 2017. Laird, Burdorf, and French studied the lungs of genetically modified pigs in 2017 and discovered that the expression of the inhibitory ligand HLA-E increased the life of the lungs by an hour.

### Use of Biotechnology in Xenotransplantation

Biotechnology will be a great help in xenotransplantation. Looking at the prospective application of biotechnology, it seems that it will be very useful for xenotransplantation for the future since it has revolutionized the recent biological field through techniques like transgenesis, genetic engineering, cloning, site-directed mutagenesis, and several other modern techniques.

### Future Aspects

Organ transplantation would be easier if there were more donors. Xenografts used for human transplantation are destroyed within minutes by hyperacute rejection. An improved understanding of the immune recognition and rejection of xenografts has resulted in new therapies that can partially overcome hyperacute rejection (HAR). To diminish immunotransplantation, two therapies can be used, i.e., those directed at the recipient (e.g., antibodies mediated) and those directed at the donor (e.g., transgenic modifications). Moreover, increasing knowledge of the pig genome will almost certainly lead to further genetic manipulations.

### Cross-References

- [Transgenic](#)
- [Vestigial Organ](#)



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## X-Linked Trait

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## Introduction

Generally, *Homo sapiens* possess 23 pairs of chromosomes, out of which 22 pairs are autosomal chromosomes and 1 pair is of sex chromosomes. The genes present on all the chromosomes have distinct function and their expression is governed by nutrients, growth factors, hormones and other stimuli. The traits and phenotypes associated with autosomes are called *autosomal traits* which can be dominant or recessive depending upon the interaction of different alleles of the same gene. Similarly, the phenotypes associated with sex chromosomes (X and Y chromosomes) are called *sex linked traits* such as colorblindness in humans. Further, there are some traits which are influenced by sex of the individual in addition to genes on sex chromosomes. These traits are called *sex-influenced traits*. E.g. baldness in human males, irrespective of recessive homozygosity or heterozygosity, it does not express fully in females. One more similar pattern

of inheritance is *sex-limited traits* in which traits are restricted to only one sex such as breast and beard development is limited to females and males respectively, in humans.

## Sex Linked Traits

*Homo sapiens* have two types of sex chromosomes: X-chromosome and Y-chromosome. Generally, normal male is heterogametic (one X-chromosome and one Y-chromosome), while female is homogametic (two X-chromosomes). Traits or defects culminated in individual due to genes present on these sex chromosomes are called sex linked traits which can be further divided into mainly two categories depending upon the gene present on which sex chromosome:

- X-linked traits
- Y-linked traits

## X-Linked Traits

Any trait or disorder caused by genes present on X-chromosome is called *X-linked traits*. As X-chromosome is present in different numbers in male and female, its inheritance pattern is different than autosomal chromosomes. Further, X-linked inheritance can also be of two types depending upon the nature of the allele (recessive/dominant) involved in appearance of phenotype/disorder:

- X-linked recessive inheritance.
- X-linked dominant inheritance.

## X-Linked Recessive Inheritance

*X-linked recessive inheritance* is pattern of inheritance in which responsible allele or mutation of gene for particular disease or trait is expressed only when it does not masked by normal/dominant allele. Such situations are normal in males (hemizygous for mutated allele) and females with homozygous for mutated allele on X chromosome. Disorders inherit in this pattern appear in males as a result of mutation in hemizygous gene; while in females; major reason

for this type of defects is random inactivation of X chromosome (lyonization). Some of the characteristic features of X-linked recessive traits are as follows:

- Mainly males of the family are affected.
- Sons of the affected father are not affected by the trait.
- Daughters of affected father and normal mother are always carrier.
- Daughter is only affected when father is affected and mother is carrier (50% chance) or affected (100% chance).
- Son of affected female is always affected, while 50% of chances of carrier female to have affected son.
- There is no carrier male in this type of inheritance.

As depicted in Fig. 1, couple of carrier female and unaffected male may have affected or unaffected sons depending on the genotype of X chromosome coming from mother (mutated or normal). But all the daughters of the couple are either carrier or normal as father provides X chromosome with normal genotype for the trait.

Some of the examples and case studies for disorders inherit in X-linked recessive pattern are given below:

### Glucose-6-Phosphate Dehydrogenase Deficiency

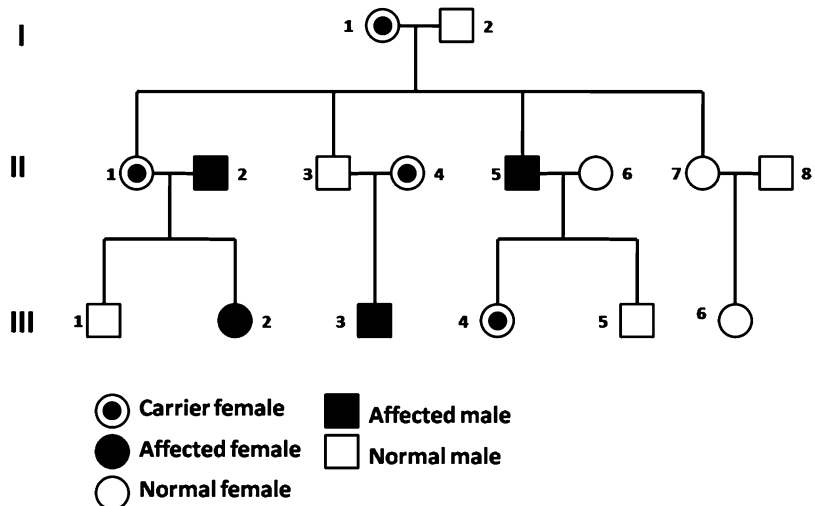
Glucose 6 phosphate dehydrogenase (G6PDH) is an important enzyme for pentose phosphate pathway in glucose metabolism. Deficiency of this enzyme is inborn error which leads to breakdown of red blood cells. This enzyme is coded by 18.5 kbp gene present in Xq28 band on long arm of X chromosome. Mainly, nucleotide substitution and nucleotide polymorphism are responsible for mutation in this gene. Mainly G6PDH deficiency causes hemolysis (red blood cells degradation) which in turn culminates into neonatal jaundice, ketoacidosis, kidney failure, etc. Sometimes condition gets worst in response to some drugs (drug induced hemolytic anemia), some chemicals and beans (favism). By avoiding use of Fava beans and some drugs such as aspirin, quinine, antimalarial drugs, this condition can be managed. It can also be managed by folic acid supplementation and blood transfusion.

### Color Blindness

It is the condition a person with disability to recognize color or difference in color shades. Most common form of color blindness is red-green color blindness, followed by blue-yellow color blindness and then complete color blindness. In this defect, genes responsible for development of one or more or all three cones present on X chromosome are

#### X-Linked Trait,

**Fig. 1** Representative pedigree chart showing inheritance pattern of X linked recessive trait



mutated. Colorblindness cannot be cured. Due to its inheritance pattern, it is more prevalent in males (8%) then women (0.5%) in Northern Europe. In addition to X linked recessive mutation, other factors such as Vit. A deficiency (Leikin et al. 2003), exposure to some solvents (Dick 2006), ethambutol-a drug used for treatment of tuberculosis (Polak et al. 1985) are some of the causative agents for color blindness.

### Hemophilia

Hemophilia is a blood clotting disorder, in which affected person is having mutation in blood clotting factors which results in prolonged blood clotting time. Hemophilia is of two types: hemophilia A (deficiency in clotting factor VIII) and hemophilia B (deficiency in clotting factor IX/Christmas factor deficiency). Genes coding for clotting factor VIII and clotting factor IX are present on Xq27.1 and Xq28 location on X chromosome, respectively. Most common feature of hemophilia is episodes of internal as well as external bleeding and its frequency depends on the severity of disorder. One of the advanced therapies for hemophilia is gene replacement therapy.

### Case Study: Hemophilia in Queen Victoria Family

Hemophilia has also been known as Royal disease because many members of family of Queen Victoria are affected by this disorder. As it is X linked recessive disorder, majorly males of the family are affected as shown in the family tree. In last generation, most of the descendent had hemophilia, which led to their early death caused by some injuries and excessive internal or external bleeding (Wayback Machine 2006). The type of the hemophilia remained unidentified as last member of Queen Victoria family was died in 1940.

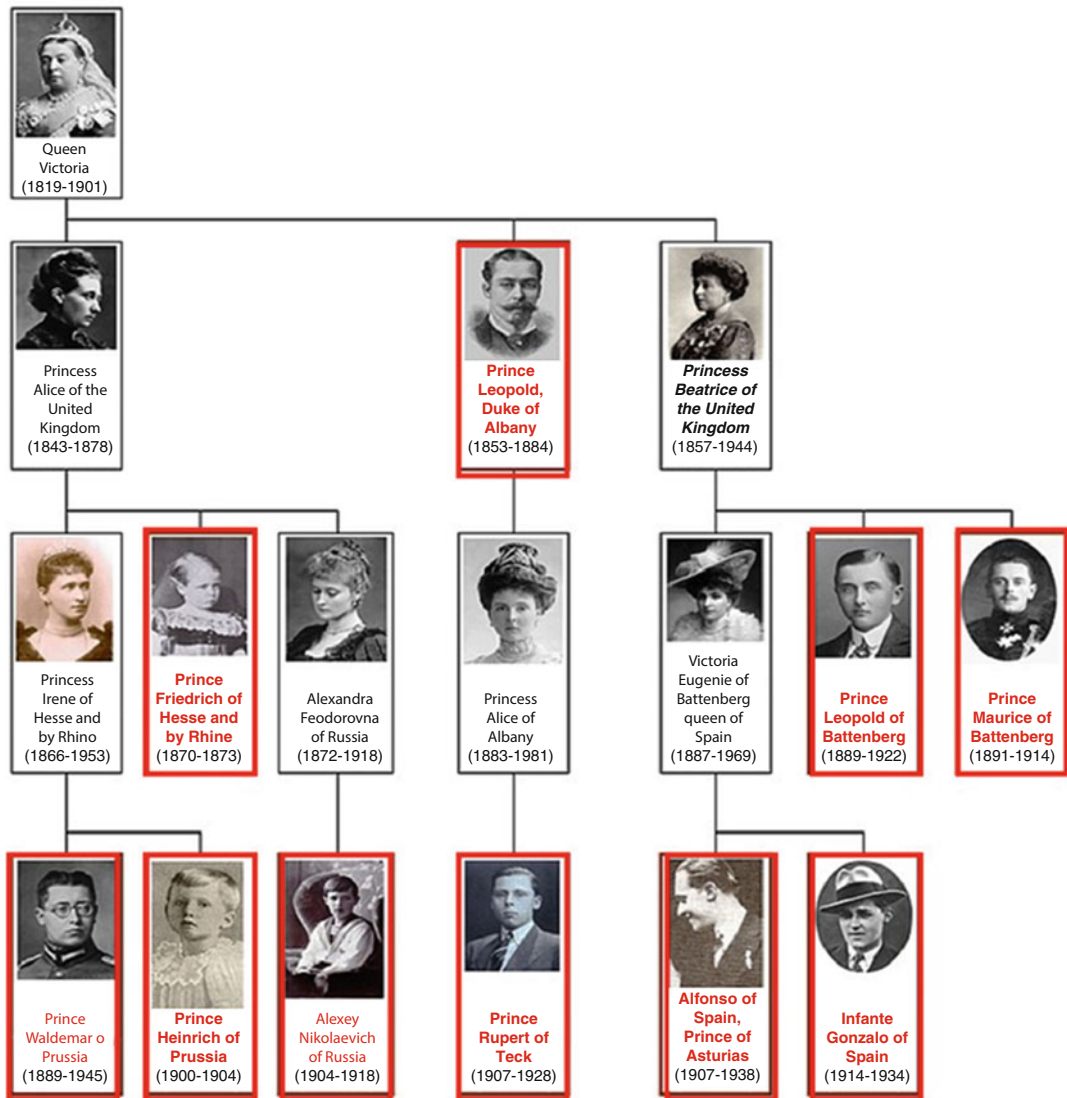
In 2009, some researchers have figured it out that it was hemophilia B what was inherited in descendents of Queen Victoria (Rogaev et al. 2009) (Fig. 2).

Some of the other disorders inherit by X linked recessive pattern are as listed below:

| Disorder/trait                                    | Characteristic features                                                                                                                                                                                      |
|---------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Duchenne muscular dystrophy Monaco et al. (1987)  | Mutation in <i>DMD</i> (dystrophin) gene<br>Rapid muscle degeneration<br>Loss of respiratory function and death                                                                                              |
| X-linked agammaglobunemia Kanegane et al. (2001)  | Mutation in Bruton's tyrosine kinase ( <i>btk</i> ) gene<br>Impairment in generation of mature B cells<br>Prone to fatal infection                                                                           |
| Becker's muscular dystrophy Romitti et al. (2015) | Mutation in <i>Dystrophin</i> gene<br>Weak muscles, walking difficulties<br>Heart related problems<br>Skeletal deformities<br>Increased Creatine kinase in blood                                             |
| Fabry's disease James et al. (2006)               | Lysosomal storage disease<br>Mutation in gene of sphingomyelin processing enzyme, alpha-galactosidase A ( $\alpha$ -Gal A)<br>Fatigue, neuropathy<br>Angiokeratomas<br>Vertigo                               |
| Hunter's syndrome Hunter (1917)                   | Mutation in gene of lysosomal enzyme iduronate-2-sulfatase causes accumulation of heparan sulfate and dermatan sulfate<br>Hepatomegaly<br>Splenomegaly<br>Impaired hearing ability<br>Cardiac malfunction    |
| Lesch Nyahn syndrome Hladnik et al. (2008)        | Mutation in <i>HPRT1</i> gene<br>Hyperuricemia (juvenile gout)<br>Excess uric acid in blood<br>Deposition of uric acid under skin cause gout like symptoms<br>Neurological dysfunctions<br>Abnormal behavior |

### X-Linked Dominant Inheritance

When allele responsible for particular trait of disease is dominant in nature (does not affected by presence or absence of other allele of same gene),



**X-Linked Trait, Fig. 2** Inheritance of hemophilia B in Queen Victoria and her descendents (Red boxes indicating affected individuals in family tree). (Photo: Wikipedia/Shakko)

present on X chromosome is called X-linked dominant gene and inheritance pattern conferred by that gene is called *X linked dominant inheritance* or *X linked dominance*. Due to its dominant nature, only one copy of allele is sufficient to develop disease condition or any other particular trait. Some of the characteristic features of X-linked recessive traits are as follows:

- Unlike X linked recessive inheritance, males and females both are affected by the trait in family.
- Daughter of affected father is certainly affected by trait of interest.
- Appearance of trait in daughter of unaffected father is solely depending on genotype of affected mother. If mother is heterozygous,

there is 50% chance of affected daughter, while daughter is certainly affected if mother is homozygous for gene for interest.

- Son of affected father and unaffected mother is unaffected.
- Son of affected mother have 50% of chance to be affected if mother is heterozygous and son is certainly affected if mother is homozygous for gene for interest.

As depicted in Fig. 3, couple of normal female and affected male has affected daughters because of the X chromosome coming from father. But all the sons of the couple are normal as father provides Y chromosome and mother provides X chromosome with normal genotype for the trait.

Some of the examples and case studies for disorders inherit in X-linked dominant pattern are given below:

### X Linked Hypophosphatemia (XLH)

It is also known as X linked dominant form of rickets. Mutation in *PHEX* gene present on X chromosome (Xp22) is responsible for the demineralization of bones and renal wastage of phosphate, which ultimately leads to development

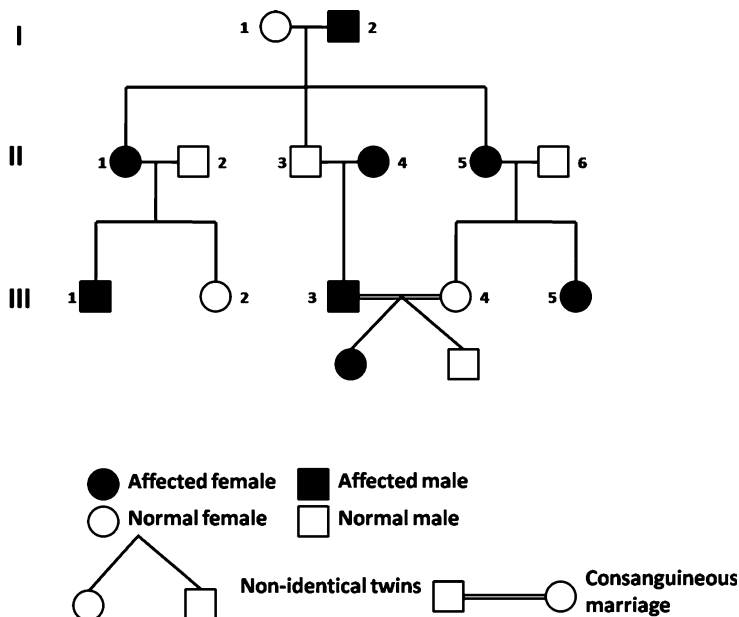
of rickets like symptoms such as soft bones, osteoarthritis, dental problems, hearing loss etc. XLH differentiate itself from autosomal rickets by being not cured by Vit. D supplements. Therefore, it is also known as X linked Vit. D- resistant rickets. Its occurrence rate is 1:20000. Surgery of leg deformities and supplements such as phosphate, calcitriol, human growth hormone helps to palliate the symptoms.

### Fragile-X-Syndrome

It is the second most common genetic cause of mental retardation. Mutation in *FMR1* gene present on X chromosome at location of Xp27.3. This disorder is also characterized as triple repeat expansion disease as CGG repeats (5–40 repeats) present in 5'-UTR of *FMR1* gene expands to 200 repeats which leads to deficiency of fragile X mental retardation protein (FMRP). FMRP is important protein for development of normal synaptic connections. Deficiency of this proteins leads to neurological and mental disabilities. Symptoms of this disorder include autism, mental retardation, difficulties in social interactions, infertility, macroorchidism, hypotonia etc. There is no cure for this disease.

### X-Linked Trait,

**Fig. 3** Representative pedigree chart showing inheritance pattern of X linked dominant trait





### Craniofrontonasal Dysplasia

It is very rare disease caused by X linked gene with dominant mutation in ephrin-B1 gene (*EFNB1*). Ephrin-B1 binds to ephrin receptor which has very important role in embryonic tissue border formation via cell-cell interaction. Deficiency of EFNB1 causes disturbance in cell-cell interaction and ultimately leads to skeletal and craniofacial malformation. Other characteristic features of this disorder are webbed neck, fizzy curly hairs, bifid nasal tips, facial asymmetry, craniosynostosis of the coronal suture, clinodactyly, syndactyly, scoliosis etc. Deformities can be treated by surgery up to certain extent.

Some of the other disorders inherit by X linked recessive pattern are as listed below:

| Disorder/trait                                   | Characteristic features                                                                                |
|--------------------------------------------------|--------------------------------------------------------------------------------------------------------|
| Rett syndrome Amir et al. (1999)                 | Mutation in <i>MECP</i> gene on X chromosome                                                           |
|                                                  | Prevails in 1:10000 females                                                                            |
|                                                  | Autistic features, panic attacks, seizures, tremors                                                    |
|                                                  | Characteristically slow head growth                                                                    |
| X-linked dominant porphyria Seager et al. (2014) | Mutation in <i>ALAS2</i> gene on X chromosome in RBC precursor cells                                   |
|                                                  | Deficiency of aminolevulinic acid synthase enzyme causes accumulation of porphyrin                     |
|                                                  | Mainly affects skin and nervous system                                                                 |
|                                                  | Very rare disease                                                                                      |
|                                                  | Other symptoms are cirrhosis, photosensitivity etc.                                                    |
| Incontinentia pigmenti Rachel et al. (2000)      | Mutation in <i>IKBKG</i> gene                                                                          |
|                                                  | Blistering, wart-like rashes                                                                           |
|                                                  | Hypopigmentation                                                                                       |
|                                                  | Hypodontia                                                                                             |
|                                                  | Alopecia                                                                                               |
| Alport Syndrome Jais et al. (2003)               | Affects central nervous system                                                                         |
|                                                  | Mutations in COL4A3 (autosomal recessive), COL4A4 (autosomal recessive) and COL4A5 (X-linked dominant) |

(continued)

| Disorder/trait | Characteristic features                                         |
|----------------|-----------------------------------------------------------------|
|                | Deficiency of one of the structural proteins called collagen IV |
|                | Vision and hearing impairments                                  |
|                | Leiomyomatosis                                                  |

Despite of all these studies regarding inheritance pattern of X-linked traits, some traits fail to follow recessive and dominant inheritance pattern in females because of random inactivation of one of the two X chromosomes present in females. Because of this irregularity of inheritance pattern, many researchers suggest to discontinue to classify X linked traits into dominant and recessive.

### X-Linked Traits in Other Animals

XY-sex determination system is observed in many other species which also show phenotypes inherit in X linked pattern. Fur color of domestic cats is governed by X linked *O/o* gene. *O* gene is responsible for orange color fur which is co-dominant with its non-orange counterpart allele *o*. Presence of *O/o* gene can mask effect of gene of any other color. Another example is lacticolor gene in magpie moth with inheritance pattern of X linked recessive.

### Y-Linked Traits

Appearance of phenotypes as a result of expression of genes present on Y-chromosomes is called *Y-linked inheritance*. It is also known as *holandric inheritance* and it can pass from father to son only. Azoospermia is one of the examples of Y-linked inheritance. In which, AZF region on Y-chromosome responsible for synthesis of protein require for sperm production is deleted in some males and leads to inability of sperm production. As normal males have single Y-chromosome, the defect on Y-chromosome cannot be recovered (hemizygous). So, Y-linked inheritance does not occur in females while males cannot be escaped from Y linked defects

if their precedents are affected with Y linked disease.

## Cross-References

- ▶ Gametes
- ▶ Mutations
- ▶ Protein
- ▶ Sex-linked

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# Y

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## Yangochiroptera

► [Microchiroptera Life History](#)

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## Yellow-Spotted Rock Hyrax

► [Hyracoidea](#)

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## Yerkes Primate Research Center

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approximately 3,400 nonhuman primates and 13,000 rodents across two locations, the main center and the field station. The 25-acre main center is located on the campus of Emory University, and houses approximately 1,200 primates, as well as the biomedical laboratories of Yerkes National Primate Research Center. Also at the main center, the Yerkes vivarium contains around 13,000 rodents. Much larger, the field station expands 117-acres in Lawrenceville, Georgia, and houses about 2,200 primates. As opposed to the main center, behavioral research is most often conducted at the field station partly because the field station provides a more naturalistic setting. Moreover, breeding is carried out at the field station. For the functioning of both facilities, Yerkes National Primate Center has over 400 faculty, researcher, and staff employees (Emory [2017](#)).

## Synonyms

[Yerkes Research Center](#)

## Introduction

Yerkes National Primate Research Center is the first nonhuman primate research facility established in the United States of America (Dewsbury [2006](#)). Now a division of the Robert W. Woodruff Health Sciences Center at Emory University in Atlanta, Georgia, it is home to

## Directors

As of 2017, R. Paul Johnson, MD, maintained position as director of the Yerkes National Primate Research Center beginning in the year 2014. Johnson has been board certified in Internal Medicine with a Certification in Infectious Diseases. He obtained his Bachelor's degree in Psychology from Duke University, and his medical degree from Harvard Medical School (Emory [2017](#)).

Nine other individuals have served as the director of Yerkes National Primate Research Center. These include, in reverse chronological

order, Stuart Zola (2002–2014), Thomas P Gordon (1999–2002), Thomas R Insel (1994–1999), Frederick A King (1978–1994), Geoffrey Bourne (1962–1978), Arthur J Riopelle (1959–1962), Henry W Nissen (1955–1958), Karl Lashley (1942–1955), and Robert M Yerkes (1929–1941; Borden 1995; Dewsbury 2006; Hilgard 1965). No women have held the position.

## History

Robert Mearns Yerkes, an American comparative psychologist, established the Yerkes National Primate Research Center in 1930 under the name Yale Laboratories of Primate Biology. In 1924, Yerkes accepted a professorship at Yale University with the exclusive aim of founding the first nonhuman primate laboratory focused on the systematic and continuous study of non-human primates and their relations to man. Yerkes recognized the significance and advantages of primates as comparative research subjects, and was dedicated to opening a facility that made such possible (Yerkes 1930). Prior to his tenure with Yale University, Yerkes published the “Provision for the Study of Monkeys and Apes” in *Science* proposing guidelines for the establishment of a primate facility allowing for behavioristic, psychological, sociological, and genetic inquiries. Within the 1916 article, Yerkes outlined facilities that would allow for the health and well-being of different types of primates as well as facilities that were conducive to breeding and child rearing. He proposed that observations should be possible under natural conditions, and that research should be conducted from every significant biological point of view. Following a similar principle, he called for the economical use of primates, which he defined as the continuous use of a primate throughout its life span. Under these circumstances, Yerkes claimed that the high cost of breeding and maintaining the animals would be offset. In addition, Yerkes believed the center would bring currency flow by allowing other institutes to make use of the facilities and animals (Dewsbury 2006; Yerkes 1916).

Prior to the opening of Yale Laboratories of Primate Biology in 1930, Robert Yerkes purchased a chimpanzee, Panzee, and a bonobo, Chim, from Noel Lewis. Lewis paid to house his apes at the New York Zoological Park. In 1923, the park director, William T. Hornaday, notified Yerkes of Lewis’ interest in selling the animals. Yerkes then purchased both Chim and Panzee for a total of \$2000, a steep price for the apes at the time. It is unknown why the apes were so expensive as chimpanzees commonly sold for \$200–\$300 per animal (Dewsbury 2006). The two chimps lived in a bedroom at Yerkes’ home, and were taught to behave like human children. Yerkes documented this experience in his 1925 book *Almost Human* (Hilgard 1965; Yerkes 1925). Chim and Panzee were the first of many apes Yerkes would eventually purchase (Dewsbury 2006).

In 1929, the Rockefeller Foundation provided the main source of funding for the opening of Yale Laboratories of Primate Biology. The Carnegie Institute of Washington lent additional support (Dewsbury 2006). Yerkes moved to New Haven, Florida, an environment more conducive to non-human primates, and established the Yale Laboratories of Primate Biology in Orange Park, Florida (Yerkes 1930). The locals in the surrounding area referred to the facilities as the monkey farm (Dewsbury 2006), a nickname that has persisted.

The founding colony at Yale Laboratories of Primate Biology consisted of four animals moved from Connecticut to Florida with Robert Yerkes, 13 chimpanzees that were donated from Madam Rosalia Abrue’s private collection in Cuba, and 16 apes donated from France (Dewsbury 2006). Moreover, the birth of the first chimpanzee, named Alpha, at the Yale Laboratories of Primate Biology occurred during the initial year of operation, allowing the collection of data pertaining to reproduction and development (Dewsbury 2006). During Yerkes tenure as director, 90 chimpanzees were studied. After his resignation in 1941, the center was renamed Yerkes Laboratories of Primate Biology in honor of his contributions to science (Hilgard 1965).

Robert Yerkes passed away in 1956 requiring Yale officials to make difficult decisions pertaining to the geographical location. Because

Yerkes Laboratories of Primate Biology was in Orange Park, Florida, it was difficult for Yale faculty and students to make use of the facility and primates. Therefore, Emory University agreed, in 1956, to assume ownership of the Center. As a result, Emory University became the host institution and Yerkes Laboratories of Primate Biology was transferred to Atlanta, Georgia, where it remains today (Hilgard 1965). Funding from the National Institutes of Health (NIH) made the transfer possible, with the field station opening shortly after in 1966 (Dukelow and Whitehair 1995).

### National Institutes of Health

In the late 1950s and early 1960s, Congress was becoming increasingly aware of the benefits of nonhuman primate models when investigating human health and well-being. Therefore, in 1960, the National Institutes of Health's Primate Research Program was created to govern the establishment of six additional regional facilities as well as the reorganization of Yerkes Laboratories of Primate Biology to Atlanta, Georgia. These seven facilities became known as National Primate Center. They are sponsored by the National Institutes of Health to conduct biomedical and behavioral research with nonhuman primates, and are responsible for conducting research regarding infectious and noninfectious diseases (Dukelow and Whitehair 1995).

In 2002, Yerkes Laboratories of Primate Biology became the Yerkes National Primate Research Center, a name that reflects its participation in the federally funded program (Borden 1995). Yerkes National Primate Research Center is the oldest of the seven National Primate Centers in the United States of America (Dukelow and Whitehair 1995).

Yerkes National Primate Research Center and Washington National Primate Research Center are the only two National Primate Centers that have field stations. In addition, only Yerkes National Primate Research Center and the Wisconsin National Primate Center have collaborated with zoos (Dukelow and Whitehair 1995).

### Vision, Mission, and Values

Per the Emory University (2017) website, Yerkes National Primate Research Center's Vision is "to be recognized nationally and internationally as a leading center for both basic and applied research that involves our nonhuman primate colony and other animal species strategically in the service of humanity." Its mission is to "conduct essential basic science and translational research to advance scientific understanding and to improve the health and well-being of humans and non-human primates. They provide leadership, training, and resources to foster scientific creativity, collaboration and discoveries. Yerkes-based research is grounded in scientific integrity, expert knowledge, respect for colleagues, and open exchange of ideas and compassionate, quality animal care." The Yerkes National Primate Center's values are "stewardship, excellence, integrity, collegiality, and people."

### Regulatory Bodies

Yerkes National Primate Center follows regulations and guidelines established by the National Institute of Health, the United States Department of Agriculture, and Emory's Institutional Care and Use Committee. Yerkes National Primate Center also maintains compliance with the regulations of the Animal Welfare Act (Emory 2017), a federal statute passed in 1966 that governs the humane treatment of animals (Cohen 2006).

### Animals

The Yerkes National Primate Research Center has approximately 3,400 nonhuman primates (Emory 2017) acquired from either a licensed breeder for animal research or bred at Emory (Borden 1995). The rhesus macaque participates most often in experiments. Other primates include the chimpanzee, sooty mangabey, squirrel monkey, and cynomolgus monkey. In addition to primates, approximately 13,000 rodents are housed at the Yerkes National Primate Research Center, and are

frequently the first animal model used in research programs at the center. Yerkes vivarium contains rodents including mice, rats, and voles (Emory 2017).

The animal care staff, including clinical veterinarians, veterinary technicians, a research nurse, and animal care technicians, provide continuous oversight 365 days a year. Since 1985, Yerkes National Primate Research Center has been accredited by the Association for Assessment and Accreditation of Laboratory Animal Care International (AAALAC). Accreditation through this private, nonprofit organization, which promotes the welfare of animals (Goodman et al. 2015), is considered the gold seal of approval for laboratory animal care (Borden 1995; Goodman et al. 2015).

Yerkes National Primate Research Center utilizes a behavior management program that emphasizes the opportunity to socialize. In addition, the program includes the environmental enrichment opportunities which includes feeding, structural, physical, and sensory enrichment. As per the behavior management program, the training program, including training related to health services, is based on positive reinforcement (Emory 2017).

## Research

Yerkes National Primate Research Center is home to a nonhuman primate DNA Bank, which serves Emory University but also outside initiatives. Research is divided into seven service cores: Biomarkers Core, Comparative Aids Core, Molecular Pathology Core, Nonhuman Primate Genomics Core, Tetramer Core, Virology Core, and Yerkes Imaging Core. Because the research program at Yerkes National Primate Research Center is large and potentially cumbersome, the division into cores services facilitate maximum use of resources and technology for investigators (Emory 2017).

Not only do scientists within Emory University have access to the resources available at Yerkes National Primate Research Center, but outside scientists are strongly encouraged to collaborate

and make use of the facilities. Yerkes National Primate Research Center, as well as the seven other National Primate Centers are considered national resources (Dukelow and Whitehair 1995).

## Cross-References

- [Comparative Psychology](#)
- [Primate Research Centers](#)
- [Robert Mearns Yerkes](#)

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## Yerkes Research Center

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## Yinpterochiroptera

- ▶ [Microchiroptera Life History](#)

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## Youth

- ▶ [Insect Locomotion](#)
- ▶ [Puberty](#)

# Z

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## ZAA

- [Zoological Association of America \(ZAA\)](#)

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## Zebras

- [Equine Cognition](#)

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## Zero Concept

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### Definition

“Abstract symbol for the absence of quantity.”

### Introduction

Mention “zero” in conversation (“There is zero chance of that happening...”) and the average person understands what is implied. However, like many other concepts, that of zero can formally be defined in different ways. Most commonly, it is used to refer to a null set, but it can also be used as a placeholder to indicate absence.

The latter use is likely the first to have been developed (possibly as early as 1500 BCE; Neugebauer 1957) and is interesting because the ability to understand and comment upon absence, although seemingly simple, denotes a relatively advanced stage in cognitive and linguistic development (Brown 1973). An organism reacts to absence only after acquiring a corpus of knowledge about the expected *presence* of events, objects, or other information in its environment, that is, only when a discrepancy exists between the expected and actual state of affairs (de Villiers and de Villiers 1979; Hearst 1984; Pepperberg 1988; Skinner 1957). Human use of a particular symbol to represent the absence of a numerical set took considerably longer to develop (likely ~300 BCE; Kaplan 2000), but, again, it was then also merely a placeholder. Use of zero as a specific digit likely originated in Asia sometime between the fifth and seventh centuries AD (Bourbaki 1994). It was not until the 1600s, however, that use of zero in computation became widespread in Western civilization, probably through the work of Newton and Leibniz.

### Children’s Understanding and Use of Zero

Given this history, and the acquisition of numbers by human children as a means to quantify specific, existent sets of items, it is not surprising that understanding and formal use of zero

(a noncountable entity) occurs only after basic numerical knowledge has already been acquired: Bialystok and Codd (2000), Merritt and Brannon (2013), and Wellman and Miller (1986), for example, have all shown that children acquire understanding of zero slowly and in stages. Some as young as 3 years old may understand that a set consisting of “no cookies” can be represented by a blank sheet of paper (Bialystok and Codd 2000). They may recognize and name the symbol before using it appropriately (i.e., at about 4 years old; Wellman and Miller 1986), but often do not begin to understand that it represents a quantity less than “1” until about 4–5 years old (Merritt and Brannon 2013; Wellman and Miller 1986), or to use the symbolic notation “0” routinely until around 5 years of age, well after understanding formal counting. Only at about 6 years do they understand that the symbol does not affect quantity in operations such as  $n \pm 0 = n$  (Wellman and Miller 1986).

Even in adults, appropriate use of zero is not universally understood, particularly with respect to multiplication and division (Miller et al. 1984; Wheeler and Feghali 1983). Zero also is unique in that it is not generally considered as part of, or the start of, the number line (Brysbaert 1995). Asked to “count,” adults are enculturated to begin “one, two...” Thus zero is not generally viewed the same way as are other numerical symbols. What then might be its evolutionary roots?

## Nonhuman Animals and Absence

Ethologically, absence or nonexistence is an important concept. Absence of food obviously triggers foraging behavior, but nonhumans exhibit other positive behaviors correlated with absence of certain signals. Birds, for example, react to the absence of signs of territorial defense (e.g., song) from conspecific neighbors with positive acts of territorial invasion (e.g., red-winged blackbirds, Peek 1972; Smith 1979). Such behavior may, however, also be interpreted as the removal of a factor that was inhibiting its expression (a neighbor ready to attack) rather than as specific recognition of “absence” (Pepperberg 1988).

Some nonhuman subjects were taught to express absence more formally: Chimpanzees (*Pan troglodytes*) and a dolphin (*Tursiops truncatus*), trained to communicate via symbolic representation, could comment on the absence of expected items (apes via ASL [Gardner and Gardner 1978] or Yerkish [Rumbaugh and Gill 1977]; the dolphin via touching yes/no paddles [Herman and Forestell 1985]). A Grey parrot (*Psittacus erithacus*) learned to use English speech referentially to respond to the absence of similarities or differences between two objects (e.g., responded to “What’s same/different?” with “none” if the objects were, respectively, completely different or identical; Pepperberg 1988). This parrot, Alex, also spontaneously transferred use of “none” to respond to the absence of a size differential the first time he was asked to label the color of the bigger or smaller item in an equally sized pair (Pepperberg and Brezinsky 1991). These instances, although providing evidence for symbolic understanding of absence, had little to do with symbolic representation of a null set – the numerical zero.

## Nonhumans and Zero-Like Concepts

No nonhuman has acquired a concept of zero identical to that of adult humans. Nevertheless, several nonhumans have exhibited behavioral precursors similar to those of young children, such as monkeys (*Macaca mulatta*) who appropriately represent empty sets along a continuum (Merritt and Brannon 2013; Merritt et al. 2009). Interestingly, specific neurons in the parietal cortex of the snow monkey (*Macaca fuscata*) respond to a null set (Okuyama et al. 2015): Shown a target numerosity (0–4) and then a second quantity (0–6), monkeys could add or subtract objects in the second quantity to match the target for a reward. Implanted electrodes in their ventral intraparietal area showed that specific neurons fired only when monkeys viewed a target of 0 and again when the target 0 was matched; different neurons responded to 1–4.

Only a few nonhumans have, however, achieved symbolic representation of a zero-like

concept. Chimpanzees, for example, were actively trained to match various numerical arrays to Arabic numerals, to then match an empty set with the 0 numeral and finally to match 0 to an empty set (Biro and Matsuzawa 2001; Boysen and Berntson 1989). All eventually succeeded at statistically significant levels, thereby demonstrating both production and comprehension, which is critical for claiming symbolic representation (see Savage-Rumbaugh 1986). However, one of these subjects, Ai, had difficulty understanding the ordinality of zero; that is, when asked to rank 1 versus 0, she might confuse the two and, like young children, rank 1 as less (Biro and Matsuzawa 2001; Wellman and Miller 1986). One chimpanzee, Sheba, did appropriately rank 0 versus 1 (Boysen et al. 1993) and understood the symbolic  $n + 0 = n$  concept (Boysen and Berntson 1989). (Note: Chimpanzees in another study seemed to understand  $n + 0 = n$  in a nonsymbolic summation task, although that data could alternatively be interpreted as the subjects having learned to avoid an empty container; Rumbaugh et al. 1987.) The aforementioned parrot, Alex, spontaneously transferred his use of “none” to label the absence of a specified numerical set (Pepperberg and Gordon 2005): If given trials with differently colored sets in which the targeted set was absent (e.g., “What color six?” when no set of six existed), he did not respond with the label indicating a set close in number but rather with the label “none,” demonstrating that he knew that the exact set was missing (Pepperberg, this volume; Pepperberg and Carey 2012). He, like Sheba, also understood that a quantity plus a null set should be labeled the same amount as the original quantity (Pepperberg 2006, 2012), but if asked to sum *two* empty sets, did not use “none” appropriately (Pepperberg 2006). He died before he could be trained to use the 0 symbol and be tested on understanding its ordinal relationship to other Arabic numerals.

## Conclusion

Zero represents absence of quantity, and performance on tasks involving absence is generally

lower than on those involving presence (even on tasks matched for difficulty; Hearst 1984); it is therefore not surprising that human symbolic use and understanding of zero historically occurred later than use and understanding of other numerals, and also does so developmentally. Although a basic response to absence (e.g., of food, water) is clearly an ancient evolutionary trait, encoding that basic understanding symbolically is a nontrivial accomplishment, both for humans and nonhumans. Given that only a very few nonhumans have acquired symbolic representation of number and concepts of cardinality and ordinality (e.g., Pepperberg, this volume), it is also not surprising that only a subset of those nonhumans have successfully acquired something akin to the human concept of zero.

## Cross-References

- [Alex the Parrot](#)
- [Arabic Numerals](#)
- [Cardinality](#)
- [Irene M. Pepperberg, PhD](#)
- [Ordinality](#)
- [Relative Numerousness](#)

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## Zigzag

### ► Zigzag Display

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## Zigzag Display

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## Synonyms

Attraction; Avoidance; Disruptive; Evasion; Zigzag

## Definition

Zigzag display includes a series of short, sharp turns, angles, or alterations in a course or direction

involved in several survival and reproductive behaviors.

## Introduction

Zigzag display is a goal-oriented behavior, which facilitates predator avoidance and mate attraction for some species. As a strategy, zigzag display has been shown to enhance survival and reproductive success, ultimately leading to fitness benefits for a species.

## Breeding Behavior

Zigzag display is evident in males of several species as a means to demonstrate quality as a potential mate. These body movements are an important determination in individual reproductive success. Most of the species exhibiting this strategy develop elaborate dance-like behaviors that include sharp or zigzag movements to signal courtship. The three-spine stickleback (*Gasterosteus aculeatus*), a fish species native to northern coastal waters, uses zigzag display as a component of its breeding behavioral repertoire. Males of this species build a nest and exhibit zigzag dancing movements during courtship to attract nearby females in an attempt to secure a mate. The three-spine stickleback male uses its caudal fin to propel dirt in a zigzag fashion to attract the female's attention to the nest that the male has provisioned (Jun et al. 2008). The zigzag dance has been shown to increase mating success in males that attract females to oviposit in the male's nest.

Zigzag display occurs across a wide variety of breeding behaviors in several other species as well. Manakins of the Family Pipridae are a group of bird species known for their elaborate courtship dances that use zigzag display to attract females. Female manakins choose their mates based off the male's courtship performance (Barske et al. 2011). The more favorably the female perceives the male's agility and swift movements during zigzag display, the better the male's chances for mating success during courtship. Kingbirds (*Tyrannus* spp.) have long been

shown to use a zigzag flight display to attract females during courtship (Townsend 1920). This bird species uses a very displeasing courtship dance to the human eye; however, the males that are successful with the display have increased chances of reproductive success.

## Predator Avoidance (Escape Behavior)

The ability for prey to escape or avoid predators is critical to individual survival. Animals of many species have adapted countermeasures to predator hunting strategies to increase chances for survival. In the predator avoidance context, the zigzag display is a series of distracting movements intended to disorient a predator and slow the forward trajectory of a predation attempt. A study assessing success in avian predators showed that zigzag display behavior in snakes was a greater determinant of successful predator avoidance than disruptive coloration (Niskanen and Mappes 2005). Some scientists believe that erratic zigzag displays cause disruption in the mechanisms driving predator attack behavior when responding to the prey's erratic movements (Humphries and Driver 1970). Gazelles, rabbits, and other herbivores are known for using erratic zigzag movements to escape the grasp of predators. In FitzGibbon (1993), the author investigated outcomes of increasing distance between prey and predator in gazelles as a result of zigzag patterns of movement and found that risk of predation decreased in older gazelles due to improved agility and capacity for sharp movements exhibited during zigzag display.

## Conclusion

Zigzag display is a metabolic investment for an individual exhibiting this behavior but provides important potential survival and reproductive benefits. The behavior has been defined as an erratic movement to advance the animal's fitness, and studies clearly demonstrate direct linkages between fitness and zigzag escape



and courtship behavior. Prey species take advantage of the agility and speed of the zigzag movement to reduce risk of predation. Males of some species may also use the attention-grabbing movements of the zigzag display during courtship to enhance likelihood of being chosen by a female as a mate.

## Cross-References

- [Alternative Reproductive Tactics](#)
- [Courtship Rituals](#)
- [Fear Response](#)
- [Mating](#)
- [Mating Effort](#)
- [Predator](#)
- [Predator Defense](#)
- [Prey](#)

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## Zöllner Illusion

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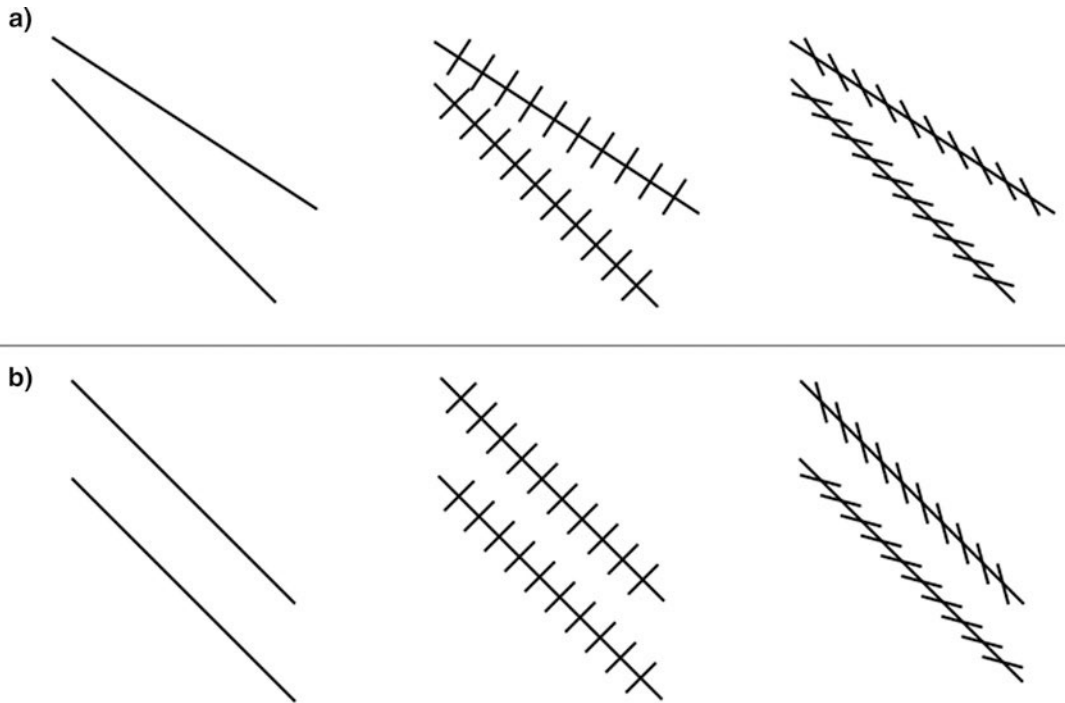
Visual illusions involve experiences of perceiving visual stimuli in ways that do not align with reality. These illusions take many forms, including illusions of numerosity, movement, and size. These illusions as experienced by humans are often also experienced by nonhuman animals. The comparative perspective on visual illusions has provided a wealth of information about how visual processing works across species, highlighting potentially conserved and evolutionarily ancient mechanisms that represent the visual world incorrectly. These illusions are valuable also as a means to understanding how visual perception works.

One important visual illusion is called the Zöllner illusion. This illusion is characterized by how humans respond to viewing two parallel lines that appear to be convergent when oblique cross-hatches are superimposed on them (see Fig. 1, column 3). There has been debate about why this illusion occurs in humans, and potential causes include the crucial contribution of acute angles within the visual array (see Kitaoka and Ishihara 2000; Oyama 1975; Wallace 1969) and the role of global characteristics of stimulus configuration (Parlangelì and Roncato 1995).

There have been only a few comparative studies of this illusion. As with many visual illusions, the Zöllner illusion has been studied in other species relative to how humans experience the illusion. This has meant determining whether other animals show the same bias for convergence of lines. The earliest study was conducted with two baboons (Benhar and Samuel 1982) that were tested in an oddity task. Monkeys were trained to

## Zinc Finger Nuclease

- [Targeted Mutation](#)



**Zöllner Illusion, Fig. 1** Example of testing stimuli from Agrillo et al. (2014). Monkeys were trained to select the narrower gap between the lines' edges. In the training phase (a), convergences of the main lines ranged from 15 to 12°. In the test phase (b), more difficult

discriminations were presented (11–1°), including parallel lines. For each phase three different conditions were presented: control (no crosshatch), perpendicular (90° crosshatches), and Zöllner (30° crosshatches) condition

select the odd stimulus within a set of three images. When presented with two parallel lines, two convergent lines, and the “Zöllner” lines (parallel lines with crosshatches), they indicated that the odd stimulus was the one with parallel lines. Benhar and Samuel (1982) suggested that this indicated that baboons perceived the Zöllner lines as being like the convergent lines, both of which were unlike the parallel lines.

The second study of this illusion was conducted with pigeons (Watanabe et al. 2011). The birds were trained to peck at the narrower (or wider) of two gaps at the end of a pair of lines that converged toward one end. Then, they were given the Zöllner lines in some test trials. If the birds experienced an illusion, then they would be more likely to peck one end of the Zöllner lines or the other, presumably because the lines would appear to be similar to the actually converging or non-converging lines used in training. Interestingly, the pigeons pecked toward the end of the

Zöllner lines that appeared to deviate (i.e., their behavior was opposite to humans who would select the end of the Zöllner lines that appeared to converge). The same pattern of behavior was found in a subsequent test with the bantam (Watanabe et al. 2013). These two studies suggest that birds may perceive this illusion very differently than do humans.

The reversed illusion as perceived by two avian species may reflect a reduced sensitivity to contrast effects which are thought to play a role in the emergence of the Zöllner effect as well as other illusions. Contrast leads to the overestimation of differences between the features of stimuli within an illusory array. Assimilation, on the other hand, leads to the underestimation of stimulus features. Watanabe et al. (2013) suggested that pigeons and chickens underestimated the acute angles between each main line and its crosshatches, as those animals assimilated the crosshatches with the main line. This may account for the reversed Zöllner

illusion. These results are similar to the reversed effect seen among avian species for other well-known visual illusions (e.g., the Ebbinghaus-Titchener size illusion; Nakamura et al. 2008).

Most recently, Agrillo et al. (2014) assessed whether rhesus monkeys perceived the Zöllner illusion and whether any such illusion matched the direction seen in humans. Monkeys were first trained to select the narrower end of two lines when there really was convergence (Fig. 1, top left). After learning to do this, some probe trials presented parallel lines without hatches (Fig. 1, bottom left), converging lines with perpendicular (90°) crosshatches (Fig. 1, top middle), parallel lines with perpendicular (90°) crosshatches (Fig. 1, bottom middle), and converging or parallel lines with Zöllner (30°) crosshatches (Fig. 1 top right and bottom right, respectively). It is important to note that perpendicular crosshatches are known not to generate any orientation illusion in humans. Therefore, if monkeys perceived the Zöllner illusion, they were expected to exhibit a bias only in the presence of 30° crosshatches. Monkeys chose the end of the parallel lines with the 30° crosshatches in the same way as humans who show the Zöllner illusion, whereas for parallel lines with no crosshatches or 90° crosshatches, they choose at random between the two ends. Thus, rhesus monkeys showed a human-like pattern and one opposite to that of birds. Unlike birds, nonhuman primates appear to be sensitive to both contrast and assimilation mechanisms as evidenced in the perception of a variety of visual illusions that reflect both effects (e.g., the Delboeuf size illusion; Parrish et al. 2015). In this case, it is possible that – by contrast – monkeys enlarged the subjective perception of acute angles between the main lines and crosshatches. More research is needed to understand the causes of these comparative differences and may provide new insights in aspects of visual illusions.

## Cross-References

- ▶ [Delboeuf Illusion](#)
- ▶ [Ebbinghaus Illusion](#)
- ▶ [Visual Illusions](#)

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## Zoo

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In the twentieth century, world zoos began to redefine their purpose. They also began to think of zoos and aquariums collectively and elevate operating standards and practices (Barongi et al. 2015) to meet or exceed public expectations. Achieving zoos worldwide began to differentiate themselves from those without a rigorous accreditation process, thereby reducing the number of

institutions that can be legitimately identified as a zoo. Zoo professionals who work for accredited institutions understand the difference between those who belong and those who do not. The public, however, is not as discriminating. Because they tend to lump all facilities that exhibit animals together, accredited zoos are too often criticized for offenses they have not committed. In North America's Association of Zoos and Aquariums (AZA) as of September 2018, there are 233 institutional members, while there are literally thousands of USDA-licensed nonaccredited animal exhibitors in the United States and thousands more throughout the world. A common difference between the two categories are the propensity of nonaccredited facilities to encourage close contact between visitors and animals, e.g., rides, petting zoos, and intimate photo opportunities. For accredited zoos and aquariums, such risky practices are considered an ethical breach. But this distinction is complicated since there are some exceptions such as supervised swimming with dolphins in some aquatic parks such as SeaWorld and the ubiquity of touch tanks in many otherwise highly regarded institutions. Contact with confined zoo animals is a delicate subject since it is known that contact between animals and human visitors promotes bonding that enables respect and support for animals. If contact is permitted, it must always be carefully regulated, monitored, and justified. Because Millennials in particular, have shown a disdain for zoos, it is essential that accredited institutions send clear messages to their guests, members, and donors. Zoos must stand for noble values by choosing to be global leaders in conservation, education, and animal welfare (Norton et al. 1995). Exotic and endangered species should never be exploited for their entertainment value alone (Maple 2016). However, the very real need for human beings to get closer to animals is not all bad. Zoo operators will have to be very creative to find safe and ethical ways to encourage some form of contact that is good for the animals, our caregivers, and the public.

In the latter years of the twentieth century, accredited zoos began to back away from the word "zoo." Bronx Zoo changed its name to the Wildlife Conservation Park and the venerable

New York Zoological Society adopted the name Wildlife Conservation Society (WCS), the name it goes by today. Zoo professionals didn't really dislike the zoo label but worried about the nuanced meaning of the word given the many imposter facilities known as "roadsides." The industry also experimented with other names, for example, Albuquerque, New Mexico's use of Michael Robinson's hybrid nomenclature "BioPark." A field biologist by training, Dr. Robinson created the label and defined it when he was director of the Smithsonian National Zoological Park. North American zoos have also begun to reverse their names following the lead of many European zoos, e.g., Zoo Atlanta and Zoo Miami follow the form of Zoo Cologne and Zoo Zurich. Choosing to put the word "zoo" first suggests you are not ashamed of it. Finally, many others chose to expand their vision to include botanicals as in "Jacksonville Zoo and Gardens." These efforts were all designed to promote the noble core values of zoos and differentiate them from low-budget entertainment competitors. After the success of many theme parks with animals, SeaWorld, Busch Gardens, and Disney's Animal Kingdom, many zoos experimented with rides to generate additional income. Train rides and carousels were always a part of zoo culture, but chimpanzee tea parties and elephant rides have been discredited and abandoned. Children's petting zoos are also in decline due to safety and health issues. Reputable zoos continue to search for balance between contact with and distance from animals in the collection. Cleveland Metroparks Zoo recently announced it would permit visitors to meet and hold a 16-foot, 17-pound Burmese python in their reptile house. Supervised by several keepers to ensure safety, the experience was designed to reduce fear and promote appreciation for snakes.

## The First Priority

Historically, the first major shift in zoo priorities was the institutional commitment to conservation. This change was revolutionary in its effect as world zoos achieved unprecedented levels of

cooperation to coordinate reproduction in zoos and to protect biodiversity and the vulnerable ecosystems that support it. Some individual institutions have demonstrated unusual attention to global conservation. The Wildlife Conservation Society, based in New York City at the Bronx Zoo, has long operated successful field conservation programs in 59 countries. To carry out this work, WCS has amassed a significant endowment that continues to grow. Other elite zoos such as the Frankfurt Zoological Garden and the Zoological Society of London have independently taken this path with both of them playing an active global role as investigators and institutional supporters to protect biodiversity hotspots worldwide. Conservation partners such as Conservation International (CI) and the World Wildlife Fund (WWF) have expressed their appreciation for two strategic priorities that contribute to conservation. First, zoos continue to generate significant funding to support conservation efforts in cooperation with non-governmental organizations. Second, by exhibiting exotic wildlife in naturalistic facilities, zoos also inspire and educate the public which helps to shape governmental policies on the environment.

Zoos also support conservation by active, formal partnerships. For example, a unique working relationship between Zoo Atlanta and the Dian Fossey Gorilla Fund International was established when the nonprofit conservation organization relocated to Atlanta from its former location in Denver in 1995. Since that time, the zoo has provided rent-free space, technical support, and volunteers on its campus, and DFGFI has prospered. The current CEO, Dr. Tara Stoinski, graduated from the doctoral program in psychology at the Georgia Institute of Technology and worked simultaneously for the zoo and the fund for many years until she was named to lead the organization. Zoo Atlanta's 50 years of working with captive lowland gorillas in partnership with Yerkes National Primate Research Center has generated more research on this species than any other world zoo. To commemorate its achievements, the Association of Zoos and Aquariums awarded Zoo Atlanta its prestigious Bean Award for long-term propagation. DFGFI's presence in Rwanda is succeeding in the field by providing protection

for a growing resident gorilla population, and the organization has recently expanded to support the smaller *Grauri* population in Congo. In addition to its success in protecting wild gorillas, DFGFI is also contributing to the economy of Rwanda and Congo.

## Global Cooperation

Organized globally under the umbrella of the World Association of Zoos and Aquariums (WAZA), zoos have come to understand their potential impact on the survival of wildlife populations and habitat. Only by working together in an organized way, can leaders, members, donors, collaborators, and sponsors of zoos expect to change the world. If we fail to find the antidote to habitat degradation; illegal poaching; trading in body parts such as bones, ivory, and horn; the bush meat trade; and illegal capture for exhibition, the natural world will be left in ruin for our heirs. Global cooperation is not easy to initiate or sustain but the alternative of going it alone will never succeed. Zoo leaders are increasingly engaged in acts of diplomacy and persuasion, but sometimes they must act together to shame another institution if it goes rogue.

Acknowledging their successful transformation from entertainment to committed conservation organizations, a second priority to advance animal welfare standards and practices has emerged. This priority is no longer subordinate to conservation but is now regarded as synergistic and of equal importance. In fact, it is widely believed that if zoo visitors are not comfortable with the way zoo animals are exhibited, they will not return nor will they support the other priorities of the offenders or recommend them to others. The welfare of zoo animals is regarded as a significant driver of zoo achievements in education and conservation. As important as animal welfare has become, zoos have recently sought to upgrade their commitments to achieve a higher standard of welfare. This upgrade has been identified as "wellness" or, alternatively, "optimal animal welfare" (Maple and Bocian 2013; Maple and Bloomsmith 2018). The goal of this shift is to

encourage zoo animals to thrive rather than merely cope with the artificial conditions of captivity. All accredited zoos and aquariums have moved aggressively to eliminate any vestiges of suffering, but elevating the bar from coping to thriving is the current challenge. The global campaign to convert zoos to softer simulations of natural habitats has proved to be costly, and comprehensive change cannot be accomplished overnight. Fortunately, there is a reservoir of superior design ideas and plenty of talented landscape architects to revitalize even the most dilapidated facilities. In countries where the design revolution has not yet caught on, advocates of reform need to step up their game to rally public and private support on behalf of animals living in less than ideal settings.

### Wellness-Inspired Design

Wellness-inspired design is changing the way zoos look and function. This design approach complements and advances prior innovations such as landscape immersion and activity-based design (Coe 1985). The wellness construct expands the opportunities we provide for animals to engage with their environment, interact with appropriate groups of conspecifics, live in stratified societies, move about freely in sufficiently large and complex spaces, search for diverse food sources, solve mental and physical problems daily, and live a relatively autonomous social life with few limitations. Some have called this outcome “a life worth living.” Given the considerable progress zoos have made, it is still fair to conclude that there remains widespread welfare inequality in our institutions. For example, some species such as many reptile taxa have been underserved by exhibit innovation and welfare services. A glaring example is the impoverished exhibits that prevail for giant snakes such as pythons, boids, and anacondas (Maple and Perdue 2013). However, as scientific zoo biologists begin to focus on underserved populations, results have been encouraging. For example, Bashaw and her colleagues (2016) conducted laboratory experiments to demonstrate that leopard geckos respond

favorably to environmental enrichment, while Brando and Burghardt (2019) have confirmed that many reptiles are playful. Hundreds of studies of animal play were carried out by anthropologists (Smith 1978), comparative psychologists (Maple and Zucker 1978), and developmental psychobiologists (Baldwin and Baldwin 1978) before the first serious study of play in reptiles was documented.

### Fewer Species/Living Well

It was once fashionable to flaunt the size of your animal collection to win high marks from peers. The absolute number of animals or species is no longer important; instead, zoos and aquariums earn respect for their stewardship of rare and endangered species and their ability to manage them in socially appropriate, species-typical groupings. Responsible zoos no longer choose to exhibit singletons such as the solitary gorilla or elephant, anachronisms of a less enlightened bygone era. Modern zoos are finding ways to exhibit fewer species that live better than ever before. Specialization sometimes takes the form of theming zoos to their region, for example, the Arizona-Sonora Desert Museum, a highly successful, accredited AZA facility. Northwest Trek Wildlife Park in Eatonville, Washington, is a 723-acre facility exhibiting bison, elk, mountain goats, and other animals indigenous to the Pacific northwest of the United States. The animals in these facilities are adapted to living in the warm and cool climates of these two respective regions. It is no longer acceptable to exhibit a polar bear in a southern zoo where it is likely to turn green from algae or suffer from the extreme heat.

### The Empirical Zoo

The importance of evidence-based exhibition, husbandry, and management is supported by all professional zoo biologists, educators, and administrators. Although there are some artistic elements at work in zoos, empirical zoo biologists have successfully solved many of the most vexing



problems that once plagued the profession. Assisted reproduction, genetic analysis, nutrition, behavior pathology, aggression, and mate selection have all required scientific systems and inquiry to generate solutions in animal husbandry. Pandas did not breed in captivity until western and Chinese scientists began to work together to solve the problem; gorillas didn't thrive in zoos until normal social groups were established; physical abnormalities in horned ungulates persisted until inbreeding coefficients were calculated and understood. One of the most significant achievements of the AZA/SSP program in the 1980s (Perkins and Maple 1990) was the successful karyotyping of the entire North American population of Bornean, Sumatran, and hybrid orangutans. Although many zoos have yet to invest in formal scientific programs, they all benefit from those that do. Powerhouse research programs at Brookfield and Lincoln Park in Chicago (Erwin et al. 1979), San Diego Zoo Global, and Smithsonian National Zoological Park are generating a stream of data to help all zoos manage their animal collections. Australia, Germany, and the United Kingdom have also become international centers of excellence for evidence-based husbandry and management. Another positive trend is the fact that college and university scholars are discovering zoos as living laboratories of biodiversity for faculty and students with an interest in the sciences. Currently, Australia and New Zealand are two of the most active world centers for advances in animal welfare. The pace of innovation in Australia is impressive with leaders, young and old, who are now active in the World Association of Zoos and Aquariums, and many other relevant NGOs.

### **Elevated Standards and Practices**

To encourage serious reforms in world zoos and aquariums, zoo executives have tried to influence the way zoos are operated and the way they are perceived by the public. The high priorities of education, conservation, and welfare have replaced entertainment as the focus of our master

plans. We understand that zoos must be designed to bring out the best in animals and we must work with them in a humane and ethical fashion to provide the highest quality of life possible. To do this zoos must become experts on a massive variety of biodiversity from insects to reptiles to birds to mammals to fish and the plant species that form the context of their habitats. Hediger stated that research was always last in the zoological garden, certainly the least funded and appreciated priority in most zoos. However, animal welfare standards would not have been achieved if research had not driven the agenda and investigated the issues and risks associated with the use of animals by humanity. Therefore, science/research cannot possibly be last in the zoological garden, and it is today much more important than it seemed in Hediger's time. Other than the strong trend to naturalistic, immersive design, and the commitment to the highest standards of medicine in all zoos, the advance of zoological institutions as centers of excellence for biodiversity research is the strongest trend of all.

### **Lifetime Commitment**

From the intensity of animal welfare science occurring globally, new standards and better practices have led to profound changes in our commitment to quality of life. One of these changes is the commitment to care for our animals for life. We are obligated by our ethical standards not to abandon an animal because it is no longer young or beautiful. We must continue to value the lives of sick and injured animals as long as they are not suffering. Retirement too must be handled with care. In Atlanta, we retired an old male lion who had one eye. I had hoped he would be able to live in a new exhibit with younger females, but our veterinarian advised me that the females would endanger his life or severely injure him if they fought him. To protect him, we found a vacant yard at the back of the zoo but provided him with as many amenities as we could. Despite his limitations, he retired gracefully and remained an important and valued member of our zoo population. By this action, we confirmed that every

animal that serves our community has value for the entirety of its life.

### The Lesson of Marius the Giraffe

In 2011 the zoo world erupted in controversy due to the decision of Copenhagen Zoo authorities to euthanize a healthy, young adult male giraffe that was genetically overrepresented in the zoo population. Since he was not going to breed in the future, the zoo elected to separate him from other giraffe and determined that he was welfare-compromised. Reluctantly but decisively, they elected to publicly shoot him, dismember the carcass, and feed the body parts to the lions. The act was widely regarded as cruel and brutal, although Copenhagen staff defended the action, utilized the experience in educational programs, and received little opposition from local citizens. However, the event played badly internationally, and print and electronic media offered a cacophony of criticism and scorn. The event also divided the zoo profession as zoo leaders, scientists, educators, and veterinarians took sides on the issue. Insiders at the World Association of Zoos and Aquariums agreed that the incident had been divisive and sowed dissention within the association. To our Danish colleagues, the decision was an ethical one, but any objective observer would have to conclude that it was a public relations disaster. The only silver lining from this experiment in management euthanasia is that it generated greater understanding about population control in zoo collections. There are some situations where culling animals makes sense. In animals that have huge numbers of eggs or offspring, spiders, for example, a curator may have no choice but to eliminate some of the stock because there is no demand. The argument can be made, however, that zoos should be more prepared to deal with surplus in a humane and ethical manner. Too many zoos in recent years solved their surplus ungulate problem by donating animals to hunting ranches. In the United States when this happened in 1999, a hostile media onslaught lowered public confidence in zoos that engaged in this unethical practice and blamed others who had not. I faced a similar dilemma

when I was director of Zoo Atlanta and a pair of gigantic reticulated pythons unexpectedly presented us with 60 live offspring. It seemed a miracle birth at first as it was a first breeding for this species at our 100-year old zoo. Upon reflection, however, I learned that the only demand for these animals was the pet trade. I would not agree to send them into this marketplace knowing they would someday become 30-foot predators of small dogs, cats, and possible children, or they might become a hungry invasive species roaming the Everglades in Florida when pet owners ceased to be amused by them. I made the painful decision to humanely euthanize them when they were small and vowed to be more careful in the future. The lesson learned here is that responsible zoos must thoughtfully plan their collections and breed only those that can live well after birth at the zoo or in a suitable distant destination of comparable quality.

### From Coping to Thriving

In a recent publication, Maple and Bocian (2013) examined the differences in animal welfare and wellness. The latter construct had not previously been used in the animal welfare literature, but it had a strong presence in the domain of human health and wellness. Historically, animal welfare, based on decades of serious research, had generated information to assist decision-makers in government and in professional associations to upgrade the living standards of animals utilized in agriculture, biomedicine, and exhibition worldwide. In our commentary in the journal *Zoo Biology*, we observed that animal welfare was originally regulatory in response to shortfalls in the standards and practices in these fields. In addition, to render reforms more practical, the new regulations tended to be minimal and achievable. By contrast, wellness was aspirational with no clear limits on how well a subject could become. We reasoned that if people wanted to be optimally well, as healthy and well as they could be, then why not use this reasoning for captive animals? This was the first time we suggested that zoos ought to aim higher in setting their goals for



**Zoo, Fig. 1** Directional outcome of higher zoo standards. From Maple and Bocian (2013)

standards and practices. As wellness has gained traction among zoo professionals and academics, animal welfare has gone from good to great, as zoos began to accept nothing less than optimal wellness as their objective. In explaining the evolution of wellness, we traced these outcomes from suffering to coping to thriving. No zoo tolerates suffering in their population of zoo animals, but most zoo animals are coping, more or less, with captivity. We have written and continue to believe it is time for all zoos to acknowledge that thriving is the preferred standard of living for animals serving humanity in accredited zoos and aquariums. This standard will be difficult to attain for all animals in the collection, but it is the right objective to pursue (Fig. 1).

### Charismatic Megafauna

Zoos and aquatic parks have also struggled with the challenge of exhibiting charismatic megafauna such as elephants, hippopotamus, polar bears, giant pandas, and killer whales. SeaWorld's reputation was hurt when the sensational documentary film "Blackfish" was televised to a massive audience of disbelievers. The report alleged a history of abuse and mismanagement including a failure to disclose the true risk of swimming with these dangerous predatory animals. Although the company denied the claims of the film's producers, the general public lost their enthusiasm for performing whales. Throughout the world, performing marine mammal shows have been closing due to public and government opposition to the apparent exploitation of cetaceans strictly

for their entertainment value. Dolphin programs that have survived public pressure have been particularly careful to give their animals sufficient freedom to choose whether to play or be left alone, and show programs have been tailored to protect the dignity of the performing animals. In the Far East, performing whales and those living in passive exhibits do not generally live well, and high mortality and morbidity is common. A major concern for the exhibition of marine mammals such as belugas and orcas are the stressful and often lethal forms of capture they have endured. For this reason, many importations have been denied by federal wildlife agencies in the United States and other countries. As a corporation, SeaWorld is committed to combining education and entertainment, and they are the most successful private aquatic enterprise engaged in the rescue and rehabilitation of sea mammals. Their reputation may be tarnished, but they are by no means down for the count.

Similarly, zoological parks have endured criticism for errors in their acquisition and exhibition of giant pandas on loan from China. In the 1980s, world zoos began to acquire pandas on short-term exhibition loans that generated money quickly. So many zoos were renting the animals that the World Wildlife Fund and the US Department of the Interior was alarmed that zoos were "loving them to death." Worse yet, the program spun out of control when shopping malls and casinos expressed their interest in short-term loans of pandas. In 1985 the "rent-a-panda" program was suspended by the US Department of the Interior, and it took 10 years to restructure an improved loan program. The first pandas imported to the San Diego Zoo in 1996 generated one million US dollars for conservation projects in China during its first year of operation with Interior monitoring the exclusive use of these funds. The San Diego loan was followed in sequence by loans to Zoo Atlanta, Memphis Zoo, and the Smithsonian National Zoological Park. Currently, the US giant panda exhibition program has generated more than \$50 M to support panda conservation and research programs. Although few zoos can afford to pay the fees to exhibit them today, the

panda experiment demonstrates that a model for exhibition can be found that supports rather than exploits the survival of this species.

With respect to polar bears, scientific studies have determined that these bears need to roam widely to be considered healthy and well. Most zoo exhibits are not large or complex enough to offer satisfying living conditions. There are some exceptions such as the Detroit and St. Louis Zoos and the Point Defiance Zoo & Aquarium in Tacoma, Washington, where polar bears appear to be thriving. Boris, at Point Defiance, at 33 is one of the oldest polar bears in captivity. The Arctic tundra exhibit was one of the nation's first exhibits to model the natural habitat of this northern species using the grassy tundra of Point Hope, Alaska, as a guide. A highly unusual polar bear exhibit was opened by the Town of Cochrane, Ontario, Canada, designed by the zoo, Ted Maranda, and a team of architects from the firms ANO architects and Ursa International. The exhibit was positioned as a sanctuary for surplus polar bears in this remote region. The facility has two contiguous 1-acre habitats and a fenced 16-acre lake within it. It is one of the most spectacular polar bear exhibits ever conceived by the mind of zoo designers.

Another long-neglected species is the Nile hippopotamus, ubiquitous in world zoos but rarely provided with sufficient space or natural opportunities that fit its species-typical habits in the wild. Having visited many zoos throughout the world, only a few of them provide hippos with optimal welfare and many facilities border on suffering. While a consultant at the San Francisco Zoo in 2011, I worked with a graduate student from the University of California at Davis on a survey of hippo habitats in North American zoos. Kristen Denninger and I carried out an initial survey and then decided to replicate and expand it when I returned to Florida to work at the Jacksonville Zoo and Gardens. The Jacksonville wellness group, under my direction, took on this replication and published it (Tennant et al. 2018). The data confirmed our initial findings that the vast majority of North American hippo exhibits failed to deliver good welfare. Except for the superior exhibit at

Disney's Animal Kingdom, very few zoos exhibit groups of hippos, typically pairs and singletons. Two notable exceptions to the rule are the Hippoquarium at Toledo Zoo and San Diego's underwater hippo exhibit. Both provide plenty of space and splendid underwater viewing opportunities for visitors to watch them gracefully move their huge bodies in the water. In Africa, Nile hippos live in large groups at the river's edge in shallow water. They locomote in the water during the heat of the day, coming out to sunbathe on mudbanks in the afternoon. At night hippos leave the water en masse and forage on the grassy shores. Safari campers near rivers in Africa often see hippos slowly moving through the camp at night and bellowing. They return to the water early the next morning, and this is when they are most dangerous to humans. Africans who choose to wash their clothes in a river must be aware of returning hippos who will pursue them. Hippos kill more people than any other African animal. Knowing what we know about them, it would be expensive but relatively simple to simulate their natural behavior. With a riverine simulation that is 121 m. in length, Disney has provided a stimulating habitat for its resident hippos. If Disney wanted to breed them, they have sufficient space to do it. Because there is no demand for hippos, most zoos don't want to breed them, but they can be segregated in captivity to simulate the natural condition. The males are much larger than females. When hippos are confined to small night houses at the end of the day, they are deprived of the natural opportunities that meet the definition of thriving. Our paper documented the fact that hippos are among the most neglected zoo animals. We need to do better to enhance their quality of life with larger exhibits and holding facilities. Zoos that cannot meet their needs should not exhibit them.

Ten years ago, zoo elephants were in as much trouble as hippos except they received more attention and publicity for the deficiency of their exhibits. The treatment of elephants in substandard zoos was truly scandalous and generated very bad publicity. The chronic foot problems of elephants living on broken concrete were

endemic. Worse, elephants killed a number of their caregivers in zoos and circuses during the late twentieth century forcing the AZA and other associations to rethink their exhibits and their management standards. Forced to spend millions for corrective action, many zoos simply closed their exhibits and abandoned their elephants to sanctuaries. The highly respected Bronx Zoo decided to retire their elephants in place with no plans to replace them when they die. Woodland Park Zoo in Seattle, known for its exhibit innovations in the late 1970s, also decided to close its elephant exhibit and translocate their animals to another AZA facility. Others, however, accepted the challenge of building better exhibits, and the improvements achieved in recent years are praiseworthy indeed. In Dallas, applying the motto, “let elephants be elephants,” planners built a large and highly complex outdoor habitat with contiguous trails that encouraged them to walk as much as 5 miles per day. They also spent money to provide a better barn with a soft substrate to ease the pressure on their tender joints. A large full immersion pool gives them relief, and caregivers work with the animals to provide enrichment and attention without dominating or stressing them. Dallas and many other zoos have found the formula for providing superior surroundings and exemplary care for elephants. Even bulls are doing better. Birmingham Zoo in Alabama pioneered the management of multiple bulls and proved that older bulls seem to mentor younger ones. If zoos are afraid or unprepared to exhibit bulls, we put them at a social disadvantage, and they suffer poor welfare. We have to find a way to build strong facilities to withstand their sheer power but still provide amenities and opportunities for them to be socialized with the herd or with other males. The Birmingham experience (Braccini-Slade 2019) is supported by data from studies of wild bull elephants in Africa (Evans 2019). Elephant exhibits at the world’s best zoos, such as Cologne, Dublin, and Zurich Zoos and many other North American zoos, are a major success story for the zoo profession, but there are still many zoos that have not reformed their approach to elephant exhibition and welfare.

## Assessment of the Great Debate

Zoos worldwide have organized to meet growing demands from the public, animal welfare and rights organizations, and governments to meet higher standards of animal welfare for zoo and aquarium animals. The body of criticism has been both reasonable and irrational. The most vociferous critics advocate an end to captivity in all its forms. Mark Bekoff (2008) has demanded that zoos and aquariums stop their organized breeding programs because he believes offspring simply multiply the population of suffering animals through no fault of their own. This is a shocking conclusion by a well-published animal behaviorist who ignores the positive trends evident in the modern zoo profession. To make things worse, he actually promoted this idea to a gathering of serious zoo professionals and animal welfare scientists. Unfortunately, his statement went unchallenged, but it should be challenged. The California Condor has been rescued from the brink of extinction by organized breeding efforts of the San Diego and Los Angeles Zoo. Offspring from these birds now fly freely in California although they are still vulnerable to human interventions such as habitat encroachment, pesticides and poisons, illegal poaching, and collisions with human technologies. In addition to saving them through assisted reproduction technology, western zoos advocate for their protection. One of the western zoo partners, Santa Barbara Zoo, invests resources in studying the reintroduced birds in the field and operates an excellent condor exhibit with considerable space for the captive birds to help inform and influence public opinion. Advocacy for conservation is one the primary purposes of all accredited zoos. The exemplary public record of achievement of world zoos in conservation science, education, and animal welfare is available to anyone who is interested in learning the facts. Our recently published book *The Scientific Foundation of Zoos and Aquariums* (Kaufman et al. 2019) and *The Ark and Beyond* (Minteer et al. 2018) published by University of Chicago Press provide strong evidence that zoo professionals and their academic

collaborators are seriously committed to upgrading the exhibition and care standards and practices of world zoos. Those who study these documents will find that accredited, achieving zoos and aquariums are worthy of their support as visitors, donors, members, and sponsors. With the public's help, good zoos are getting better and better. Although I strongly believe that accredited zoos are moving in the right direction, the debate about their value is likely to continue. I am not concerned about the zoos that are leading reform and revitalization, but I am greatly concerned about the thousands of "mom and pop" facilities that call themselves zoos but do not deserve our support or patronage. Zoo professionals engaged in reforming zoos are only interested in operating superior institutions that inform, inspire, and excel.

Other constructive forums have succeeded in producing conclusions that have become guides to industry benchmarks. At the Atlanta meeting that culminated in the Smithsonian book *Ethics on the Ark* (Norton et al. 1995), zoo professionals were persuaded by animal welfare scholars to make a greater commitment to individual animals rather than populations. This simple shift in attitude facilitated the next few decades of reform and revitalization in our nation's accredited zoos. Clearly, responsible constructive criticism, even when it comes from outside the profession itself, can lead to substantive change. It is important to understand that significant reform is generated by zoo professionals themselves as they study their options and investigate how they can obtain better results for the benefit of the animals and our communities. Zoo administrators continue to seek input and advice from visitors, volunteers, business authorities, and community leaders. Zoo professionals are eager to advance the quality and purpose of their profession. While Americans appear willing to give their local zoo an opportunity to rehabilitate and reform, many other nations are rapidly closing zoos and banning animal entertainment such as circuses and shows. The wealthiest and best-known circus in the world, Ringling Brothers, recently ended its use of elephants in the circus and will now retire the entire collection.

## World Zoos and Mental Health

Environmental psychologists have gathered sufficient information about the positive effects of nature that government agencies are attempting to design communities with greater amounts of green and blue space. Trees, plants, and grasses are examples of green space; blue space is comprised of water features, oceans, lakes, rivers, and streams. In a recent chapter in an important book by Ann Devlin (2018), Maple and Morris (2018) suggested that the power of green/blue space could be extended to include naturalistic zoos, aquariums, and botanical gardens. There is a robust body of evidence that such places support human mental health in a variety of ways. Particularly in highly urbanized parts of the world, there is a need for urban oases where human populations can gather for respite, relaxation, and revitalization. The love of nature is so strong in our species that we have defined a new field of architecture known as "biophilic design" (Kellert 2018). Zoos, aquariums, museums, and botanical gardens are venues where biophilia prevails.

## Marketing Core Values

The organized opposition to zoos and aquariums is a worldwide phenomenon and unrelenting. Much of it is also extreme and uninformed. Accredited zoos must devote their time and financial resources to combat the misinformation with credible public campaigns of their own. Sophisticated social marketing techniques have been employed in public media advertising, but the best approach may be point-of-sale inoculations. Within the zoo itself, it is essential that zoos share their core values and demonstrate their firm and enduring commitment to protect wildlife in every way they can. This means paying attention to how animals are responding to the most creative new exhibits and systems and generating increasing amounts of human and financial capital to support field conservation. If operated properly, modern zoos will be centers of education and inspiration second to none, and they will be valued and utilized in their communities. Outmoded hard



architecture is no longer acceptable in the zoo profession, so virtually every zoo must be evaluated, reimagined, and rebuilt to fit our noble objectives in public education, conservation, and community engagement. Zoos must continue to demonstrate that they are good for animals and people and a beneficial investment for communities, cities, and nations. In the best zoos, information is passed to the public by employees and volunteers giving formal and informal demonstrations in the vicinity of the enclosures or behind the scenes. Wellness exams can be given to big cats from outside the barriers by signaling for cooperation by the cats who lean on the mesh and permit a look by the caregiver or the vet. Effective training transforms zoo animals into good patients and a good day at the zoo. With proper training for compliance and care, working with wild animals has become a much safer occupation.

### Launching Ethical Arks

The North American zoos that are leading the way on animal welfare include Brookfield and Lincoln Park in Chicago, Detroit, Oakland (CA), Disney's Animal Kingdom, Jacksonville Zoo and Gardens, Oregon Zoo, San Diego Zoo Global, and San Francisco Zoo. There is considerable progress in Europe, and strong leadership is coming from Zoos Victoria and Sydney Zoo in Australia. The latter country is home to many academic programs that are advancing animal welfare in agriculture, biomedicine, and zoo biology (Hemsworth et al. 2011). Aquariums have been less successful in discovering reforms to support animal welfare. The challenge of exhibiting and managing charismatic aquatic megafauna is daunting even for large corporations like SeaWorld. One serious problem with aquariums in the Far East is their propensity to acquire whales and other marine species through highly questionable methods and means. The demand for marine mammals is high in Asia, and strong reforms and regulations are needed. Even large fish such as whale sharks are vulnerable in artificial manmade holding tanks, swimming endlessly in circles. Except for the relatively successful

Georgia Aquarium exhibit, whale sharks do not seem to be good candidates for aquatic exhibition. If whales are to be exhibited in future facilities, the standards will have to be dramatically elevated. Compared to zoos, aquariums suffer much greater mortality and morbidity in their collections, and their populations must be regularly replenished through open-ocean retrieval. Many of the most difficult ethical questions facing the zoo and aquarium industry have been highlighted in a new book by Dr. Jenny Gray, CEO of Zoos Victoria and current Chair of the board of WAZA. *Zoo Ethics: The Challenge of Compassionate Conservation* (2017) is setting the global agenda for zoos and aquariums rapidly moving ahead of public expectations.

### The Bright Future of Zoos

Some observers have predicted a dim future for zoos (Hancocks 2001), but it is far more likely that zoos will follow the path of innovation and discover better ways to present wildlife in human care. Reform is already occurring at a rapid pace. Hancocks is an architect who led three major zoos as CEO, so he knows that good zoos can be created, but it takes substantial time to turn a zoo around by design and development. Except in periods of economic uncertainty, as in the year 2008, innovative exhibits have been opening each and every year. One of the most exciting prospects for future zoos and aquariums is their scientific value as guardians of biodiversity. Zoos are living laboratories, but they are not isolated from their evolutionary history in physically and socially sterile laboratories. The trend to naturalistic immersive exhibits and facilities bring them into focus as seminatural field stations where animal behavior is comparable to what is seen in free-living populations (Coe and Mendez 2005). As teaching laboratories for young biologists and psychologists, zoos serve a purpose that is unmatched by any other setting. This has become especially important as institutions of higher learning have abandoned macrobiology education in favor of microbiology. Students can spend 4 years as undergraduates without ever studying

a whole living organism let alone social animals because these populations are simply not available on campus. Field stations such as the national primate centers in Atlanta, California, Oregon, Washington, Louisiana, New England, and Wisconsin have been extremely important assets in higher education, but they are few and far between. Our nation's elite zoos and aquariums represent a more accessible resource if formal working partnerships can be arranged with universities. It is an exciting time for students of comparative cognition as we are learning more each day about the extraordinary cognitive capacity of animals. Zoos collect, exhibit, and manage animals that have never been studied by comparative psychologists or ethologists. As the record demonstrates, zoo animals are increasingly assigned as subjects in ethological and comparative psychological research. A good example is the collaboration between Dr. Meredith Bashaw, a professor of psychology at Franklin and Marshall College, who carried out original research on the social structure of giraffe at the San Diego Wild Animal Park (Bashaw et al. 2007).

Beginning with Harlow and Yerkes' pioneering work with animals in private institutions including zoos (Maple 1979), and Duane Rumbaugh's research at San Diego Zoo, many other facilities have stepped up to offer their subjects for comparative studies including Brookfield and Lincoln Park in Chicago, Indianapolis Zoo, SeaWorld, and Zoo Atlanta. In Atlanta, many colleges and universities continue to carry out cognitive studies of great apes as the legacy of Zoo Atlanta's historic scientific partnership with the Yerkes National Primate Research Center. At the Smithsonian National Zoological Park, comparative psychologist Ben Beck designed and supervised the execution of "Think Tank" the first North American zoo exhibit devoted to the history of comparative cognition research. Research by psychologists at SeaWorld in recent years reminds us of the distinguished history of cetacean learning research by pioneers such as Louis Herman, Karen Pryor, Ron Schusterman, and Stan Kuczaj. Fortunately, many of these pioneers left a legacy of students to continue their work. Other important contributors from

venerable institutions such as the Language Research Center of Georgia State University are advancing the legacy of Professor Rumbaugh under the direction of his former student, David Alan Washburn. In addition to his work at the field station, Professor Washburn has contributed important ideas to the field of animal welfare (Washburn 2015). Recent symposia organized in the southeast to honor Duane Rumbaugh's scholarship and leadership have brought together new generations of colleagues to share ideas and plan future projects. Enormous intellectual contributions have resulted from Franz de Waal's interest in the mentality of zoo primates (De Waal 2006). Starting with his work in Netherlands' Arnhem Zoo, he worked on bonobo sociality and cognition at Milwaukee County Zoo, San Diego Zoo, and in Atlanta at Yerkes. Professor de Waal is one of two zoo biologists who are elected members of the prestigious US National Academy of Sciences. The other is Professor Jeanne Altmann of Princeton University and formerly associated with Brookfield Zoo (Maple and Bashaw 2010). We can look forward to exciting discoveries ahead as more zoo resources are committed to the cause of science and growing numbers of academics are recruited to collaborations with zoo biologists.

As the public becomes more aware of the core values and interests of their local zoological parks, attendance and financial support is sure to grow. Zoos are already more popular than professional sports especially with families, and they are unique in blending learning with recreation. If zoos commanded the television and radio presence of sports, the public would be beating down the doors to get in. The best evidence of reform are the exhibits themselves and the exemplary condition of the resident species. Although animals are not active at all times, the way they are presented even when they are peacefully asleep makes a strong impression. Animals can be activated through training if they are not disturbed, stressed, dominated, or overworked. However, research indicates that animals prefer work to getting food for no effort and they benefit from human companionship, attention, and interaction. Zoos are getting better at these transactions. As centers of excellence for discovery, education,

conservation, and inspiration, modern, high-quality zoos and aquariums are proving they are worthy of our strong support.

## Cross-References

- [Animal Welfare](#)
- [Human-Animal Interaction](#)
- [Captivity](#)
- [Comparative Psychology](#)
- [Conservation](#)
- [Terry Maple](#)
- [Yerkes Primate Research Center](#)

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## Zoological Association of America (ZAA)

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### Synonyms

[ZAA](#)

### Definition

A nonprofit accrediting organization for wildlife parks, zoological facilities, animal sanctuaries, aquariums, and animal rehabilitation centers.

The Zoological Association of America is a nonprofit accrediting organization established in the early 2000s through the merger of two other related organizations, the International Society of Zooculturists (ISZ) and the United Zoological Association (UZA). With the Association of Zoos and Aquariums (AZA), the ZAA is one of the primary accrediting bodies in the United States for zoological facilities, aquariums, animal rehabilitation centers, wildlife parks, and animal sanctuaries.

Part of the motivation for the merger and the formation of a second accrediting body for those holding exotic animals in captivity was the concern expressed by private breeders and some other publically owned animal collections that their needs and views were not adequately represented by the only accrediting organization available at the time – the AZA. While the ZAA addresses these concerns perhaps more directly than does the AZA, the ZAA does not accredit private exotic or wild animal pet owners.

ZAA's written mission statement describes it as an accrediting organization “dedicated to responsible wildlife management, conservation, and education.” As of the time of this writing, it had approximately 500 members and over 60 accredited member facilities. The organization engages in a captive breeding management program across its member facilities aimed at enhancing genetic diversity in captive populations.

Like AZA, the ZAA hosts an annual conference, a midyear conference, and issues grants to conservation organizations around the world. It also publishes a quarterly newsletter and journal, the *ZAA Journal*. Additional information about this organization can be found at its website, <http://zaa.org/>.

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## Zoology

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Zoology or animal biology is the branch of biological sciences that studies structure, classification, and distribution of **animals**. It covers areas of systematics, anatomy, morphology, physiology, embryology, cytology, genetics, evolution, ecology, ethology, zootechnics, and paleontology (Soares 1993; Figueiredo et al. 2013; Holley 2015).

Living beings can be grouped into different categories, from kingdom to species. Kingdom is the category of greater comprehensiveness, bringing together living beings of similar characteristics, with peculiarities. According to classification proposed by the biologist R.H. Whittaker, in 1969, the alive beings are classified in five great kingdoms: Monera, Protista, Fungi, Plantae, and Animalia.

It is believed that the **animal kingdom** was originated in the archaeozoic oceans long before the first fossil record. From the ancestral marine environment, different groups of animals were formed and, some, little by little, moved from fresh water to dry land, further expanding the diversity of their species.

The term **species** (Latin *type*) is one of the categories proposed by the Swedish naturalist, Carolus Linnaeus (1707–1778) in his book *Systema Naturae* (1735), where he suggests a system of classification of living beings. In this system, species is the basic category of this classification. Similar species can be grouped into one **genus**. Genera with similar characteristics are grouped together to originate a **family**. Several families with similar characteristics are grouped into **orders**, and, similarly, orders are grouped into **classes** and classes in **phyla**. Phyla, in turn, are grouped in **kingdoms**.

One of the great merits of Linnaeus was to associate a nomenclature with classification. His classification system is **binomial**, meaning it has two names. The first name corresponds to the genus and the second to the species (**epitet**). *Homo sapiens*: genus *Homo*; species *sapiens*.

However, such a system is hierarchical and based on morphological characters. Currently, studies have used the **phylogenetic systematics** or **cladistic taxonomy**, a classification that organizes the species according to their evolutionary kinship.

From an evolutionary point of view, species diversity is one of the consequences of the diversity of biomes and ecosystems inhabited by them. Charles Robert Darwin (1845–1896) explained the diversity of species as a product of **natural selection** and **evolution**. His works were better understood and complemented from the twentieth

century, when the mechanisms of **genetic inheritance** formulated by Gregor Johann Mendel (1822–1884) were finally understood.

Humans have always sought to learn about animals. Certainly, at the outset, the main purpose was to distinguish those suited to their own diet. Soon, some came to be feared, others, dear ones and some more, adored, with their figures being used to symbolize Gods. The domestication of some brought advantages to humans such as territorial guard, alert against predators and human opponents, locomotion, and tasks that required force.

Zoology as a **science** arose in Greece, about 350 BC through the *History of Animals*, book of Aristotle (384–322 BC). In this book, the author made observations about anatomy, social organization, and embryology and he attempted the first known animal classification, grouping them as *animals with blood* (known nowadays as **vertebrates**) and *animals without blood* (**invertebrates**).

Today, zoologists study animals in several situations: in free living, in controlled experiments in laboratories, and in museums and collections. Thus, there are many areas of specialization within the zoology: **protozoology** (the study of Protozoa), **entomology** (insects), **ichthyology** (fishes), **herpetology** (amphibians and reptiles), **ornithology** (birds), **mastozoology** (mammals), and **parasitology** (parasites and their hosts).

Although there is a high diversity of animal species in the world, many face a population decline and even extinctions caused mainly by anthropic actions, such as destruction of habitats, pollution, predatory hunting and fishing, among others. Therefore, knowledge about existing species is an essential part of biodiversity conservation.

Today, there are over 2.5 million animal species already described and 10 to 30 million to be discovered. Of these, about 5% represent animals that have a serially arranged spine or vertebrae and a bony or cartilaginous endoskeleton. These animals are called **vertebrates**. The other 95% of species that do not have backbone are **invertebrates**.

Animals are multicellular beings, with **eukaryotic** cells, without cell walls and that, in most cases,

form tissues. However, they vary enormously among themselves: the body symmetry can be **bilateral**, **radial**, or **pentaradial**. In some of them, the body is set in repeated units, called **metamer**. Nutrition is **heterotrophic**, with extra- or intracellular digestion. The breath is **aerobic**. They can be sessile or move through feet, legs, wings, and fins or, still, by body contraction. Most have sexual reproduction, producing gametes. There may be sexual dimorphism: male and female are physically different. **Dioecious** or unisexual, when each individual has one sex, and **monoecious** or bisexual or hermaphrodite when an individual has both sexes. Their fertilization is internal or external. Development can be direct, when it does not have larval stages, or indirect when it goes through larval stages before becoming adult. The embryonic leaflets in the **diploblastic** species are the ectoderm and endoderm; in the **triploblastic** species are ectoderm, mesoderm, and endoderm. The coelom is absent in the **acoelomates**, partially coated by the mesoderm in the **pseudocoelomates**, or totally delimited by the mesoderm in the coelomates. In the **protostome**, the blastopore gives origin to the mouth and in the **deuterostome** to the anus.

## Invertebrates

The phyla representing the living invertebrates are briefly described below (according to Ruppert and Barnes 1996; Cheida 2002; Holley 2015).

### Phylum Porifera

Sponges.

Animals with the simplest structure of the animal kingdom. They have a body pierced by pores and supported by a skeleton of protein fibers or silica or limestone spicules. There are three basic types of sponges, from the simplest to the most complex: **asconoid**, **syconoid**, and **leuconoid**. Most have radial symmetry. They live alone or in colonies. They are sessile, which means, fixed on the ground or on rocks, corals, or shells, in marine or freshwater. Nutrition is heterotrophic, with intracellular digestion. Respiratory system is aerobic, with diffusional gas exchange. Its

excretion is through the upper opening, the **osculum**. They have no nervous system. Most reproduce sexually, with indirect development, through the larvae. There are monoecious and dioecious sponges. There are species that reproduce asexually by fragmentation, budding, or producing gemmules.

### Phylum Cnidaria

Hydrants, jellyfish, caravels, corals, and sea anemones.

They are exclusively aquatic: predominantly marine but also freshwater species. The body is polyp-like, like a tube with fixed base and an upper portion with mouth and tentacles, or in the form of jellyfish, medusa-like, movable with tentacles or arms. They have radial symmetry. They are carnivores, feeding on fish and zooplankton. They are aerobic, by diffusion, as well as the circulation of nutrients and gases between cells. Excretion occurs within the gastrovascular cavity and is eliminated by the mouth. Jellyfish move through water jets, caravels float through pneumatophores, and polyps float through somersaults. The nervous system appears for the first time and is of the diffuse type. They are carnivorous, with extra- or intracellular digestion. They are monoecious or dioecious. There is asexual reproduction, by budding, in the polyps and sexual in the jellyfish. Indirect development forms the seedling larva. In the epidermis are **cnidocytes**, cells that contain oval capsule (**nematocytes**) containing toxic substance and a rolled filament in the form of javelin; when touched, the capsule breaks, releasing the dart soaked in the toxic substance, injuring the prey. The phylum is divided into three classes: **Hydrozoa** (hydras and caravels), **Anthozoa** (sea anemones and corals), and **Scyphozoa** (jellyfish). Some anemones have **mutualism** with certain fish or with hermit-crab. Coral reefs are formed by anthozoans and harbor immense variety of living beings.

### Phylum Ctenophora

Seahorses or comb jellyfish.

Marine animals, gelatinous, almost transparent, of coastal waters. They have eight rows of ciliary combs that propel the body for locomotion.



They favor pelagic invertebrates, capturing them by retractile tentacles present in many species. They are hermaphrodites.

### Phylum Platyhelminthes

Flatworms and planarian.

They represent the **first organisms with bilateral symmetry**, a body organization apparently more efficient than the others. The body is flattened dorsoventrally. They are free living or parasites. Carnivorous, herbivorous, or parasitic heterotrophs. The digestive system is incomplete, with extra- or intracellular or absent digestion, as in tapeworms. Breathing is aerobic and circulation occurs by diffusion. For the first time, in some species, a **rudimentary excretory system** occurs. The nervous system is composed of longitudinal nerve cords. They are hermaphrodites, with asexual or sexual reproduction.

### Phylum Nemertea or Rhynchocoela

Ribbon worms or proboscis worms.

They comprise small to large worms, elongated and often flattened. The **proboscis** and ciliated epidermis capture food. Most are marine benthic, but there are deep-sea pelagic species. They live in cracks in rocks, under rocks, or in clumps of seaweed. They move by ciliary movements, peristalsis, or both. They are invertebrate predators. Gas exchange occurs through the body surface. They have specialized coelom, exclusive of this phylum. The nervous system is formed by ganglionic brain and ocelli. Dioecious, the reproduction occurs through external fertilization and direct development.

### Phylum Rotifera

Rotifers or wheel animals.

They are predominantly part of freshwater zooplankton where they promote nutrient recycling. There are species who are freely swimming, creeping, sessile, and colonial. The benthic species swim through a crown of hair and use adhesive glands on the tips of their feet to attach to the substrate. The body is transparent. Dioecious or parthenogenetic females. Development is indirect. In adverse conditions, they remain in **cryptobiosis**.

### Phylum Acanthocephala

Acanthocephalans, thorny-headed worms, or spiny-headed worms.

They are endoparasites, requiring two hosts to complete their life cycle (when juveniles, they parasite crustaceans and insects; when adults, they parasite the digestive tract of vertebrates, especially fish). Retractable proboscis with spines is used to attach. They do not have a digestive tract, absorbing food through their body wall. They are dioecious.

### Phylum Gastrotricha

They represent freshwater and marine species, most of them microscopic. The body is shaped like a bowling pin or is flattened ventrally. They feed on bacteria through a sucking pharynx. Hermaphrodites, with internal fertilization and direct development.

### Phylum Entoprocta

They cover few species, predominantly those sessile with tentacles. They were part of the phylum Bryozoa, but, unlike those, the coelom is absent and there is no exoskeleton. Most are marine, except for a single freshwater genus. They live attached to rocks and shells or have a commensal relationship with bryozoans, polychaetes, sponges, and other animals. They live alone or in colonies. They have a pair of **protonephridia**. Hermaphrodites. Many species incubate their eggs.

### Phylum Tardigrada

Water bears.

Small animals that live up to 70 years in soils, beaches, mosses, and lichens present in rocks and trees. The plump body is smooth or segmented with four pairs of ventral legs with discs or claws. Their locomotion is slow, creeping, and their claws fix them to the substrate. They feed on vegetables, seaweed, and debris, with the help of two mouthpieces and a sucking pharynx. Food travels through the pharynx to the intestine, where it is digested and absorbed; its last portion, the rectum, connects to a terminal anus. They have a dorsal brain and ganglion nerve cords attached to sensory organs (**bristles**). Most are dioecious. Parthenogenesis is common. Development is

direct. In adverse conditions, they remain in **cryptobiosis**.

### Phylum Nematoda

Ascarids, roundworms, hookworms, pinworms, and whipworms.

Animals of cylindrical body, elongated, with bilateral symmetry and sharp edges. Most are parasitic on animals and vegetables. There are several parasitic nematode species of great medical and economic importance. Many terrestrial species suck up commercially important plant roots, causing damage. *Ascaris lumbricoides* parasites the intestines of several species, including humans, and can reach 49 cm. **Filariasis** or **elephantiasis** is a severe parasitic disease caused by *Wuchereria bancrofti*. Due to their mouth and anus, a **complete digestive system** appears for the first time on the animal scale. The digestion is extra- and intracellular. Breathing is aerobic, with diffusional gas exchange. Excretion occurs through an excretory pore. The locomotion occurs through longitudinal musculature. The nervous system is rudimentary. Most species are dioecious. Reproduction is sexual, with internal fertilization for most and direct development. In adverse conditions, they remain in **cryptobiosis**.

### Phylum Nematomorpha

Horsehair worms and Gordian worms.

They are long worms of 5 to 10 cm. Free-living species in freshwater and moist soils from temperate and tropical regions. The only marine genus (*Nectonema*) parasites crabs and shrimps. Their larvae parasitize beetles, locusts, crickets, and centipedes. Dioecious, with internal fertilization.

### Phylum Kinorhyncha (Ancient Phylum Echinoderida)

Mud dragons.

Small group of marine species. It lives in the mud or between grains of sand. Its main characteristic is the segmentation of the tough cuticle. There are species with adhesive tubes on the ventral surface. At the tip of the buccal cone there are oral stiletos, and the head can retract, also moving the body when it digs. They feed on organic material. Dioecious, with direct development.

### Phylum Loricifera

Marine animals with size of 1/4 mm. So heavily adhered to grains of sand and other substrates that the attempt to separate does not result in living organisms to be better studied. Its anterior extremity is conical and spiny (**scalid**), retracting within a posterior region wrapped in a **lorica** (abdomen). They are dioecious. Little is known about their systems and lifestyle habits.

### Phylum Priapulida

Priapulid worms.

Benthic, deep, or shallow waters. They live buried in mud or sand. Found in Antarctica and the tropics. They are shaped like a cylindrical trunk with retractile, swollen, and thorny proboscis in the anterior portion, used to dig and capture prey. They are carnivorous and bacterivorous. Animals do not have a vascular-blood system. They have nervous system inside the epidermis, with non-ganglionar brain and ventral nerve cord also non-ganglionar. Dioecious, with external fertilization in larger species and probably internal in the smaller ones.

### Phylum Annelida

Ringed worms, earthworms, leeches, and polychaetes.

Animals of elongated body, cylindrical, and metamerized by external and internal rings, defining its name. Complete digestive system, with carnivorous, herbivorous, or parasitic diet. Breathing occurs through gas exchange by diffusion. The circulatory system is closed. A pair of nephridia, located in each segment, shapes the excretory system. They move by body contraction. They may be dioecious, with sexual reproduction, external fertilization, and indirect development, or monoesters with cross-fertilization and direct development. Earthworms, by revolving the soils, have great importance in agriculture.

### Phylum Mollusca

Octopuses, squid, slugs, snails, snails, oysters, and mussels.

They have a soft body that defines their name. Most have a limestone shell for support

and protection. They are the **first coelomates**. Head, foot, and visceral mass form the body. Most are carnivorous, but there are herbivores. The digestive system is complete. Respiration can be through lung, gill, or cutaneous. The circulatory system is open or lacunar type. Excretion occurs by nephridia. For locomotion, terrestrial animals use the foot, and marine animals use mainly propulsion. The nervous system has ganglia united by nervous cords. They are dioecious or monoecious, with cross-fertilization, internal or external. Development is direct or indirect.

### Phylum Arthropoda

Insects, spiders, scorpions, shrimps, crabs, centipedes, and others.

It is the largest phylum of existing animals, living in terrestrial or aquatic habitats. They have articulated paws, and their body is covered by chitin shell called exoskeleton. The exoskeleton needs to be discarded periodically so that the animal can grow, a phenomenon called molting or ecdysis. They are metamerized in the head, thorax, and abdomen, and, in arachnids and crustaceans, head and thorax merge into cephalothorax. Its digestive system is complete with extracellular digestion. The respiratory system in the insects is **tracheal**; in arachnids it is **philotracheal** and in ticks **cutaneous**. The circulatory system may be open or lacunar. The excretory system in insects occurs through **Malpighian tubules**, in crustaceans through **green glands**, and in arachnids in **coxal glands**. They are sessile, like barnacles, or furniture, like the others. Nervous system formed by nervous ganglia. Dioecious and have internal fertilization (most insects and arachnids) or external (crustaceans). The development is direct (arachnids) or indirect (insects and crustaceans). Mosquitoes, flies, butterflies, beetles, grasshoppers, cicadas, dragonflies, bedbugs, ants, bees, and termites represent the **Insecta** class, considered the most biodiverse. Other major classes are **Crustacea** (lobster, crab, garden tattles), **Arachnida** (spiders and scorpions), **Chilopoda** (centipedes), **Thoracica** (barnacles), and **Diplopoda** (snake lice).

### Phylum Echinodermata

Starfish, sea urchin, sea cucumber, sea lily, sea snakes, and others.

Exclusively marine and free life. They have **endoskeleton** and great capacity of regeneration. They move through **ambulacral system** (with the exception of the sea lily). The ambulacral system consists in channels through which water enters, circulates, and leaves, providing locomotion, breathing, and feeding. They are carnivorous or herbivorous, with complete digestive system and extracellular digestion. Breathing occurs through gills (starfish and hedgehogs) or respiratory trees (cucumber). The excreta are eliminated by diffusion through the ambulacral system and gills. The circulation occurs in the channels within the coelom. The nervous system is diffuse. They are dioecious, with no sexual dimorphism. Fertilization is external with indirect development.

### Vertebrates

Vertebrates live in practically every habitat on Earth. They have a high diversification, due to more than 500 million years of evolution, probably beginning in the seas of the Cambrian Period. The basic plan of the body consists of a bilateral tubular organization, formed by notochord, pharyngeal clefts, hollow dorsal nerve tube, vertebrae, and skull. Following, the classes representing the present vertebrates and nearby taxa (Hemichordata, Urochordata, and Cephalochordata) are described (according to Hildebrand 1995; Pough et al. 1999; Schmidt-Nielsen 1999; Cheida 2002; Holley 2015).

### Phylum Hemichordata

Acorn worms.

Small animals, exclusively marine. They have gill slits and a supposed notochord that classifies them near the Chordata. *Balanoglossus* is the main genus studied. It has a tripartite body in the proboscis, collar, and trunk, or **protosome**, **mesosome**, and **metasome**. Sessile or of little movement. There are species that crawl and dig with proboscis; others live on the surface, feeding on phytoplankton and organic matter from the

sediments. The circulatory system is developed, with a contractile organ called the **cardiac vesicle**. A reticulated nervous plexus forms the nervous system. Reproduction is **gonochoric**, with external fertilization.

## Phylum Chordata

Chordate.

Animals with common features, as **notochord**, **gill slits in the pharynx**, and **dorsal nervous system**. Some are invertebrates, such as lizards, amphioxus, and lampreys, and witches represent the **Protocordados**. The others are vertebrates and classified as **Eucordados**.

Chordata comprises three subphyla: Urochordata, Cephalochordata, and Vertebrata (or Craniata).

### Subphylum Tunicata (Urochordata)

Ascidians.

Tunicates are marine exclusive. Both sessile and free-living, live isolated or in colonies. They are covered by a thick cuticle called **tunic**. Notochord is present only in larval form. They have an incomplete digestive system. They feed on plankton filtered by the pharynx and processed in the stomach and intestine. They breathe through gas exchange through **pharyngeal clefts**. The circulatory system is open, although there are blood vessels and heart. They are monoecious, with external fertilization and indirect development, or reproduce by budding.

### Subphylum Cephalochordata

Amphioxus or lancelets.

Exclusively marine, live buried in the sand. They have notochord throughout life, formed by striated muscles (**myomeres**). Complete digestive system. The food is collected by filaments, the **buccal cirrus**. They feed on plankton. Gaseous exchanges occur through the skin or through filtered water through the pharynx. The circulatory system is open, with no heart. The excretory system is composed of **protonephridia**, formed by **flame cells** that absorb the products of excretion. The nervous system has the cerebral vesicle. Dioecious, with external fertilization and indirect development.

### Subphylum Vertebrata or Craniata

Wizards, lampreys, cartilaginous and bony fish, amphibians, reptiles, birds, and mammals.

The common feature of all vertebrates is the replacement of the notochord in the vertebral column and the presence of a skull that protects the brain. They inhabit aquatic and terrestrial environments. Following, the classes that represents the vertebrates.

### Class Agnatha Lampreys and hagfish.

They are known as **jawless fish** or **cyclostomes** for not having a jaw, but a **circular mouth**. Hagfishes are marine and lampreys live in fresh or marine water. Their body is cylindrical and elongated, and cartilaginous plates form its spine. They have a **cartilaginous skeleton** and the notochord, present only in adults, has a supporting function. Their skin is smooth with **mucous glands** and dorsal and caudal fins. In the mouth, hagfishes have **tentacles** and lampreys have a **sucking mouth**, tongue, and horny **teeth**. Complete digestive system and intestine with bowel folds in spiral (**typhlosole**). The liver aids in chemical digestion. They are parasites. Lamprey sucks the tissues of a prey in which it adheres, by suction and with its teeth. Hagfishes can penetrate weakened fish through its gills and anus and also feed on dead animals. Breathing occurs through gills: water enters the gill slits, mouth, or nostrils, and gases are carried by **hemoglobin** in the blood. Circulation is simple and complete. Blood is pumped from a heart with two chambers into the gills. The excretory system consists of **pronephric** or **mesonephric** kidneys. The product of excretion is ammonia. Ripples of the body result in movement. The nervous system has encephalon and medulla, sensory organs such as **eyes** and **inner ear** (body balance), and tactile cells in the epidermis. Dioecious, with external fertilization and direct development in hagfishes and indirect in lampreys.

### Class Chondrichthyes Sharks, rays, and chimeras.

They are fishes, mostly marine, with **cartilaginous skeleton** and pectoral, pelvic, and caudal **fins** that aid in displacement and defense. Rays also have a stinger in the pectoral fin. They secrete

mucus through epidermal cells by reducing friction with water. Their skin is thick, coated with **placoid scales**. The digestive system is complete, with **ventral mouth** with several rows of **teeth**. Esophagus, stomach, intestine, liver, gallbladder, and pancreas assist digestion. Most are carnivorous, but the whale shark is a filter feeding. The respiratory system is branchial: water and oxygen enter through the mouth, pass through the gill slits, and exit through a pair of **spiracles**. Their circulation is closed and simple, with a heart formed by an atrium and a ventricle. The erythrocytes contain **hemoglobin**. **Mesonephric kidneys** collect urea and ammonia from the blood, eliminating them by the cloaca. The nervous system consists of the brain, cranial nerves, and spinal cord. Fertilization is internal. Males have modified pelvic fin (**clasper**), whose function is to introduce sperm into the female cloaca. They are oviparous, ovoviviparous, or viviparous, with direct development.

#### **Class Osteichthyes** Bony fishes.

They are aquatic vertebrates with **bone skeleton**. Inhabit salt water and freshwater. Move through pectoral, pelvic, median dorsal, anal, and caudal fins. The digestive system is complete, with mouth at the anterior end, **conical teeth**, esophagus, stomach, intestine and anus, liver, pancreas, and eventually gallbladder. The respiratory system is gill, with four pairs of gills protected by **opercula**. The circulation is closed and simple, with a heart composed of two chambers. They have **mesonephric kidneys**, urinary bladder, two ureters, and urogenital pore that excretes ammonia. Nervous system is composed of the brain, cranial nerves, and spinal cord. They are **heterothermic** or **poecilotheurmic**, varying their internal temperature according to external. Fertilization is internal or external. They are oviparous or ovoviviparous. The development is direct or indirect, with formation of **larvae**.

#### **Class Amphibia** Anura (frogs and toads), Urodela (salamanders), and Apoda (caecilians).

They have two phases of life: one aquatic and one terrestrial. First vertebrates to live in **terrestrial** environment and first **tetrapod** of the animal kingdom. They have moist and smooth skin, with

**mucous glands**, forcing them to inhabit also moist places. Most live in aquatic and terrestrial habitats (including arboreal or fossorial habitat environment), although some species are exclusively terrestrial or aquatic. They are predators, with a complete digestive system: mouth without teeth in most species, a protractile and sticky tongue to catch prey, esophagus, stomach, intestine, liver, pancreas, and cloaca. Breathing occurs through gills in the larval stage or throughout life in some species of aquatic salamanders. In adult phase, respiration is cutaneous, although there are primitive lungs that aid in the process. The circulation is closed, double, and incomplete, and the heart has three cavities (two atria and one ventricle). Kidneys mesonephric, ureters, bladder, and cloaca excrete **ammonia** in the larval stage and **urea** in adults. They move through swimming during the larval stage and jumping, crawling, or walking when adults. The nervous system is composed of the brain, cranial nerves, spinal cord and spinal nerves. Vision is developed, except in caecilians. Frogs have in the head the paratoid gland, producer of poison. Dioecious, with indirect development in most species, originating the tadpoles. As their eggs do not have shell, they are protected by gelatinous substance and by the moist or wet environment where they are deposited. In most species, there is copulation, although the fertilization is external, except for salamanders and caecilians, whose fertilization is internal.

#### **Class Reptilia** Turtles, tuataras, lizards, snakes, and alligators.

First animals to settle, definitively, on **land**. Determinant for this was the development of an egg with a shell resistant to desiccation and, internally, embryonic attachments such as vitelline sac, amniotic pouch, and allantois, which reproduce to the embryo the aquatic environment from which their ancestors came. Dry skin covered by horny plaques on crocodiles and alligators, shells in turtles, and scales on snakes and lizards. Complete digestive system, from mouth to the cloaca. They are carnivores, like crocodilians, snakes, and tuatara, or herbivores, like some chelonians and lizards. Important adaptations for feeding are sharp teeth in crocodilians, cutting jaws in chelonians, and ability to disarticulate the jaw and dilate the

stomach or have **venom-inoculated prey** such as snakes. Respiratory system consists of nasal cavities, larynx, trachea, bronchi, lungs, and alveoli. The circulation is closed, double, and incomplete. The heart is composed of four chambers: two atria and two ventricles, these not completely closed. Kidney metanephros, ureters, mostly a urinary bladder, and cloaca eliminate uric acid. The locomotion is made by fins (tortoises), muscle contraction (snakes and lizards), and feet in terrestrial species, where there may also be horny or sucker claws. The nervous system is composed of cranial nerves, encephalon, spinal nerves, and spinal cord. The sensory system consists of two **nostrils** and **Jacobson's organs**, located on the palate and receiving **odorous** particles picked up by the tongue. Some snakes have two **sensitive pits** in front of the eyes where they perceive **thermal variations**. They present the **middle ear** and **tympanum**, the last one absent in snakes. Eye protection is exerted by the **nictitating membrane** and tear glands, especially in snakes (which as no eyelids). They are **heterothermic**, varying their internal temperature according to the external temperature. Dioecious, with internal fertilization and direct development. Most are oviparous. Some species are ovoviviparous. Snakes have a bifurcated penis (**hemipenis**).

### Class Aves Birds.

They have **feathered bodies**, **horny beaks**, and anterior limbs turned into **wings**. The feathers, exchanged annually, are formed by keratin and guarantee flight aerodynamics, thermal insulation, and protection against desiccation. Porous bones, with air inside them (**pneumatic bones**), form the skeleton. **Pneumatic cavities** are lung projections into these bones, leaving the bird lighter for flight and assisting internal cooling. Absence of teeth and urinary bladder also make the animal lighter. In flying birds, the sternum bone is keeled, connecting the wing muscles. The eyes are externally lined by a transparent membrane (**nictitating membrane**), which prevents dryness during flight. The **urophygial gland**, next to the cloaca, produces oily secretion which waterproofs the feathers. The feet are covered by epidermal scales. They inhabit the most varied terrestrial and aquatic environments, living alone

or in flocks. Their diet can be frugivorous, carnivorous, detritivorous, granivorous, insectivorous, nectarivorous, piscivorous, or omnivorous. The digestive system is complete: beak, tongue, salivary glands, dilated esophagus, **crop** (stores and moistens food), **proventriculus** (chemical stomach), **gizzard** (specialized muscle in crunch), liver, pancreas, small intestine, and cloaca. Breathing occurs in two lungs without alveoli. Songbirds have the **syrix**, the organ responsible for singing. The circulatory system is closed and complete: heart with four chambers (two ventricles and two atria). Kidney metanephros, ureters, and cloaca excrete uric acid. Few species have urinary bladder. In seabirds, excess sodium chloride from food is eliminated by the **salt gland**, located between the eyes. The nervous system consists of the brain, cerebellum, cranial and spinal nerves, and spinal cord. They are **the first homeothermic beings**, keeping the internal temperature constant, even with variations in the external temperature. **Sexual dimorphism** is observed in most species, males having generally more vibrant colors. After a **courtship display** period, performed by males in most species, mating occurs. They are dioecious, with internal fertilization and direct development. Oviparous, the eggshells have calcium carbonate and embryonic attachments similar to reptiles.

**Class Mammalia** Platypus/Ornithorhynchus, echidnas (both Prototheria-Monotremata), kangaroos, opossums (both Metatheria-Marsupialia), armadillos, anteaters, tapirs, rats, bats, canids, felids, rabbits, whales, primates (as humans), and others (all others Eutheria-Placentalia).

Animals with **mammary glands**, **hairs**, differentiated teeth, and **diaphragm** and **homeothermic**. Free-living animals, living alone or in groups or complex social organizations. The skin contains **sweat**, **sebaceous**, and, in some species, **odoriferous glands**, for defense. Dermal and epidermal dermis form, in addition to **hairs**, scales, plaques, beaks, horns, claws, and **nails**. They inhabit terrestrial and aquatic environments. Their diet varies by species. The digestive system is complete, beginning in the mouth and ending in the anus, except for the monotremates that have **duck-billed** and **cloaca**. They have salivary



glands, except in aquatic mammals. Ruminants (bovines, sheep, goats, giraffes, and others) are adapted to the cellulose digestion, with stomach divided into four chambers: rumen, reticulum, omasum, and abomasum. **Lungs** with alveoli, aided by the diaphragm, do breathing. The larynx has **vocal folds** that allow the emission of sounds. The circulatory system is closed and complete, with two atria and two ventricles, and erythrocytes with hemoglobin as the respiratory pigment. Two kidney metanephros, ureters, urinary bladder, and urethra excrete **urea**. They move by walking, swimming, flying, and gliding, through feet, fingers, hooves, fins, wings, and membranes. The nervous system is the most developed of the animal kingdom, composed of the **brain**, cranial nerves, spinal cord, and spinal nerves. Bats and aquatic mammals, such as whales and dolphins, use **ultrasounds** to aid in locating obstacles and searching for food. They are dioecious, with internal fertilization and direct development. This development occurs, for most placental species, in the **uterus** of females, where embryonic attachments are formed. Marsupials, like the kangaroo, complete their development in the **marsupial**, after leaving the uterus still embryonic. In both cases, they are **viviparous** mammals. Monotremates, such as the platypus and the echidna, which lay eggs, are **oviparous** mammals.

## Cross-References

- [Ecology](#)
- [Evolution](#)
- [Morphology](#)
- [Paleontology](#)
- [Species](#)
- [Vertebrates \(Chordata\)](#)

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## Zoonoses

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## Synonyms

[Zoonotic diseases](#)

## Definition

Zoonoses (also known as zoonotic diseases) are any naturally transmitted disease or infection between humans and nonhuman animals.

## Introduction

Zoonoses (zoonosis, singular) are infectious diseases caused by viruses, bacteria, fungi, parasites, or prions that are transmissible between human and nonhuman animals through food, water, air, environment, or direct physical contact. Reverse zoonosis, or anthroponosis, occurs when a human infects an animal. In rare cases, these diseases can reinfect humans from the animal reservoir. For example, swine are susceptible to infection with

swine, avian, and human influenza viruses. If a pig is infected with influenza viruses from different species simultaneously, the viruses can mix and create a new virus that can reinfect humans. Diseases such as elephantiasis and African schistosomiasis are sometimes mistakenly thought of as zoonotic, even though they are transmitted via animal vectors, part of their natural life cycle requires a human host, and therefore are not considered zoonotic.

Humans and nonhuman animals coexist within a complex network of interactions. These interdependent relationships result in exposure to a wide range of pathogens that cause an equally diverse range of diseases and symptoms. Animals that appear to be healthy, or subclinical, are still capable of transmitting pathogens that can infect humans. Zoonotic diseases in humans and animals can result in anything from mild symptoms to death.

Zoonoses represent a significant global health burden. Approximately 61% of pathogens known to infect humans are zoonotic (Taylor et al. 2001), and 75% of emerging infectious diseases in humans are zoonotic in nature (Jones et al. 2008). The escalation in emerging zoonotic pathogens is due to increased contact between humans and animals (Daszak et al. 2001). Human activities are continually expanding into wilderness areas and wildlife and, in turn, are increasingly moving into urban areas. Additionally, the development of livestock farming operations has escalated the amount and closeness of human-animal interactions.

## Zoonotic Pathogens

There are a vast number of different zoonotic pathogens, which allow for transmission of disease from many different nonhuman animal vectors to humans. Pathogens spread via unprotected contact with infected agents and between closely related hosts such as humans and other nonhuman primates. Other mammalian species most commonly infect humans; however, nonmammalian vertebrates, as well as invertebrates, can also be sources of infection. Infectious agents include

bacteria, viruses, prions, protozoa, fungi, and arthropods. Pathogens can be acquired through ingestion, inhalation, or physical contact. Pathogenic organisms are found in skin lesions, body fluids, secretions, and excretions of their respective animal hosts and spread directly through animal vectors or indirectly through their byproducts, such as contaminated food.

Human consumption of undercooked meat, unpasteurized milk, raw eggs, and contaminated vegetables is a common route of infection for zoonotic pathogens and results in a large number of foodborne diseases in people. According to the Centers for Disease Control and Prevention, bacteria and viruses were the most common cause of foodborne diseases in the United States in 2016 (<https://www.cdc.gov/foodborneoutbreaks/>). *Salmonella* and *Campylobacter* caused the most illnesses, hospitalizations, and deaths followed by *Shigella* and *Cryptosporidium*. Some foodborne diseases, such as *Norovirus* (Norwalk virus) and *Clostridium perfringens*, are usually only identified in major outbreaks.

## Routes of Transmission

The increase in human-animal contact has resulted in a surge of emerging zoonotic diseases (Jones et al. 2013). The prevalence of livestock farming and the rising global human population makes it unlikely that human contact with wildlife will decrease in the near future. The interdependent relationship between humans and animals leads to more vectors of transmission. One method for classifying zoonoses is by categorizing them based on one of four main routes of transmission: direct contact, indirect contact, vector-borne, and foodborne.

Direct zoonoses are transmitted by coming into direct contact with the blood, saliva, skin, bodily fluids, urine, or feces of an infected animal. Scratches and/or bites from an infected animal also represent forms of direct contact transmission. For example, Q fever, caused by *Coxiella burnetii*, can be contracted through the inhalation of infected feces, and *Salmonella* can originate from direct handling of infected amphibians or

reptiles. Nontraditional or exotic pets carry a relatively high risk of being vectors for transmission. In fact, an outbreak of monkeypox occurred due to the importation and distribution of a species of African rodent as pets.

Zoonoses can be transmitted via indirect contact as well. Intermediate species (called vectors) can be carriers of a disease, without being infected themselves, and indirectly transmit the pathogen to a human host. Humans can also be indirectly infected through exposure to environments in which infected animals have been present. Humans are infected through contact with contaminated bedding, aquarium water, plants, soil, and coops or barns. For example, pathogens such as *Toxocara* spp. and *Sporothrix schenckii* reside in soil, and adults and children can become infected while gardening or playing outside.

Vector-borne diseases are infections transmitted to humans by the bite of infected arthropod species, such as mosquitoes, ticks, triatomine bugs, sandflies, or blackflies. For example, ticks transmit the causative agent of Lyme disease, mosquitoes spread diseases such as malaria and dengue fever, while the triatomine bug and sandflies are the vector species for Chagas disease and leishmaniasis, respectively. According to the World Health Organization (WHO), vector-borne diseases cause more than 700,000 deaths annually (“Vector-borne diseases” 2017).

Foodborne zoonoses are transmitted through the consumption of contaminated food or liquids. Infectious agents can be bacteria (e.g., *Campylobacter*), viruses (e.g., hepatitis A virus), parasites (e.g., *Trichinella*), or prions (e.g., bovine spongiform encephalopathy). Eating or drinking unpasteurized milk, undercooked meat or eggs, raw seafood, or contaminated fruits or vegetables can all cause illness. The WHO estimates that one in six people in the United States gets sick from foodborne illnesses each year. Foodborne trematodiasis are examples of zoonoses that cannot be transmitted directly as they are only infectious to humans after having completed a complex life cycle in an intermediate nonhuman host.

Transmission via any of these routes can take place in any context in which human and non-human animal environmental overlap exists. The relationship can be based on companionship (pets), economics (livestock production), predation (hunting and fishing wildlife, animal attacks), or medical factors (researching medications and vaccines).

## Risk Factors

The connections between humans, animals, and their environments are a source of zoonoses that can impact public health and the world economy. While anyone with direct or indirect contact with animals is at risk of becoming infected, many factors play a role in an individual's susceptibility to a zoonosis (Shakespeare 2009). Certain populations are more likely to be infected by specific zoonoses based on their geographic location, occupation, socioeconomic status, age, or immune health. Generally, young children, elderly, pregnant, and immune compromised individuals are at a high risk of infection. Those who hold occupations that require close contact with animals, particularly jobs involving animal carcasses, are more likely to be in contact with zoonotic pathogens. Some zoonotic diseases are more prevalent in specific geographic locations or climates. For example, trematodiasis are more common in East Asia and South America, while the burden of vector-borne diseases such as malaria weighs most heavily on tropical and subtropical climates and disproportionately affects the poorest populations. Diseases such as bovine and porcine brucellosis, bovine tuberculosis, and rabies are well controlled in developed nations but remain significant problems in developing ones.

The effects of zoonotic diseases on public health place a significant burden on the global economy (Jones et al. 2008). Risk factors can be mitigated through a variety of economic and social changes. The implementation of responsible agricultural and farming practices can reduce the transmission of zoonotic disease. Improving

sewage waste disposal systems and reducing standing water in urban areas can greatly improve rates of vector-borne infections for large populations. Access to health care and preventative treatments can decrease rates of illness and death, especially in rural populations.

## Cross-References

- [Human-Animal Interaction](#)
- [Immunity](#)
- [Immunology](#)

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## Zoonotic Diseases

- [Zoonoses](#)

## Zootomy

- [Morphology](#)

## Zygote

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## Synonyms

Fertilized ovum; First diploid cell of new organism

## Definition

Zygote is the fertilized ovum, which is the fusion of two haploid gametes (male and female pronucleus).

## Main Text

Zygote formation is an intricate and synchronized array of dynamic events, which is elicited by sperm and oocyte interaction (Niakan and Eggan 2013). Basically, it includes sperm penetration, subsequent calcium oscillations in oocytes followed by oocyte activation, sperm and oocyte fusion, development of male and female pronucleus, genome-wide epigenetic reprogramming, and migration of pronucleus to the central position followed by oocyte to zygotic transition (Papale et al. 2012). The zygote is a unicellular entity, and it comprises all the genetic information that is essential for growth of the new organism. Zygote formation process is known as fertilization.

## Pronuclear Formation

Pronuclear (PN) formation is the important event for zygote formation, which involves re-establishment of nuclear envelope of both the sperm and oocyte. PN formation is classified into six stages, i.e., PN<sub>0</sub>–PN<sub>5</sub>: PN<sub>0</sub>, sperm entry

followed by completion of meiotic arrest of mature oocyte, decondensation of sperm and second polar body eliminates; PN<sub>1</sub>, initiates demethylation; PN<sub>2</sub>, demethylation activates in paternal genome, while maternal genome is resilient; PN<sub>3</sub>, demethylation is complete; PN<sub>4</sub>, two nuclear polar bodies (NPBs) move close together; PN<sub>5</sub>, both the NPBs are adjacent to each other before syngamy (Papale et al. 2012).

The presence of two centrally positioned, juxtaposed PNs with clearly defined nuclear membrane along with two polar bodies is used for the evaluation of normal fertilization. Nowadays, PN scoring of zygote technique is used in the in vitro fertilization procedure. Aberrant PN number in any stage, i.e., PN<sub>1</sub>–PN<sub>5</sub>, is observed, which is considered as low viable pregnancy and not transferred in infertile females (Papale et al. 2012). Transition from oocyte to zygote involves mRNA translation, which is essential to start a new life and organelle remodeling. Studies suggest that meiotic machinery molecules regulate oocyte to zygotic transition. After this transition, the zygote starts to divide mitotically and develop into a multicellular organism.

## Epigenetic Reprogramming of Zygote

In genome-wide reprogramming specially demethylation, methylation is an important epigenetic event in both the primordial germ cells and early embryonic stages, respectively (Fraser and Lin 2016). Several evidences have shown that global and active demethylation patterns by TET-3, BER, elongator, and Stella are found in the paternal genome, whereas global and passive demethylation patterns by Stella have been found in the maternal genome (Stitzel and Seydoux 2007). This reprogramming has direct influence on pluripotency, erasure of epimutations, regulation of paternal imprinting, and transcriptional control of transposons in the zygote (Schultz 1993).

After the fusion of germ cells, the zygote restores diploid number of chromosome 2n. From the zygotic chromosome basis, we can identify the sex of the embryo/fetus, e.g., oocyte has X sex chromosome and either X or Y will be coming from the spermatozoon. If the zygote has XY sex chromosome, it is genetically male, and if XX, it is genetically female (Wassarman 2001).

## Conclusion

Hence, the zygote is considered first biologically alive and a unicellular entity, which has potential for metabolism, growth, reaction to stimuli, and reproduction.

## Cross-References

- [Karyotype](#)
- [Reproduction](#)
- [Sex Ratio](#)
- [Sex-Linked](#)

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